An anatomico-physiological study of the posterior longitudinal bundle in its relation to forced movements / by L.J.J. Muskens.

Contributors

Muskens, Louis Jacob Josef, 1872-1937.
Royal College of Surgeons of England

Publication/Creation

London : John Bale, Sons & Danielsson, 1914.

Persistent URL

https://wellcomecollection.org/works/jwshkdcu

Provider

Royal College of Surgeons

License and attribution

An Anatomico-Physiological Study of the Posterior Longitudinal Bundle in its Relation to Forced Movements.

6.

BY

L. J. J. MUSKENS.

CONTENTS.

AN ANATOMICO-PHYSIOLOGICAL STUDY OF THE POSTERIOR LONGITUDINAL BUNDLE IN ITS RELATION TO FORCED MOVEMENTS.

BY L. J. J. MUSKENS, M.D.

Amsterdam.

INTRODUCTION.

IN previous investigations respecting the circus and rolling movements occurring in different species of vertebrates, I had observed the important part played by the posterior longitudinal bundle, when injured, in producing these phenomena [107,113] ; I resolved therefore to make special experiments in this subject, and by means of the Probst " concealed needle " I made lesions in all directions, chiefly in cats, in the area between the nucleus of the abducens nerve and the posterior commissure. In each case the forced movements were noted, whether in the horizontal plane (circus movements) or in the plane vertical to the longitudinal axis of the animal (rolling movements). Forced movements were considered to be present, first, so long as the head and eyes remained deviated or so long as there was an inclination to go to one side, circus movements in a slight degree ; and secondly, as long as there was an inclination to lie down or to fall to one side, which I look upon as a slight manifestation of rolling movement. The character of the movements and the direction of the locomotion which is the consequence of them are determined in accordance with the normal anatomical position of the animal, the normal posture being always reduced to that of the primary vertebrate exhibiting the simplest forced movements, for instance the fish.

A rolling movement exhibited by a patient, therefore, which commences with the turning of the chin to the left shoulder is, according to my nomenclature, a rolling towards the right, for, after reducing the posture and the movement to that of the primary vertebrate, this movement produces locomotion to the right from the original position of the animal.

The significance of the exact direction of the forced movement becomes at once apparent as soon as we begin to study the different pathological conditions of the ocular movements, conjugate deviation of head and eyes, and other neurological syndromes.

During my experiments, it was found necessary to draw a sharp distinction between forced movements in the horizontal plane, or circus movements, and those in the plane vertical to the longitudinal axis of the animal, or rolling movements. Various combinations of movements, however, were by no means infrequent, so that different animals appear in the table more than once ; the character of the forced movements present being employed as a means of dividing them into groups.
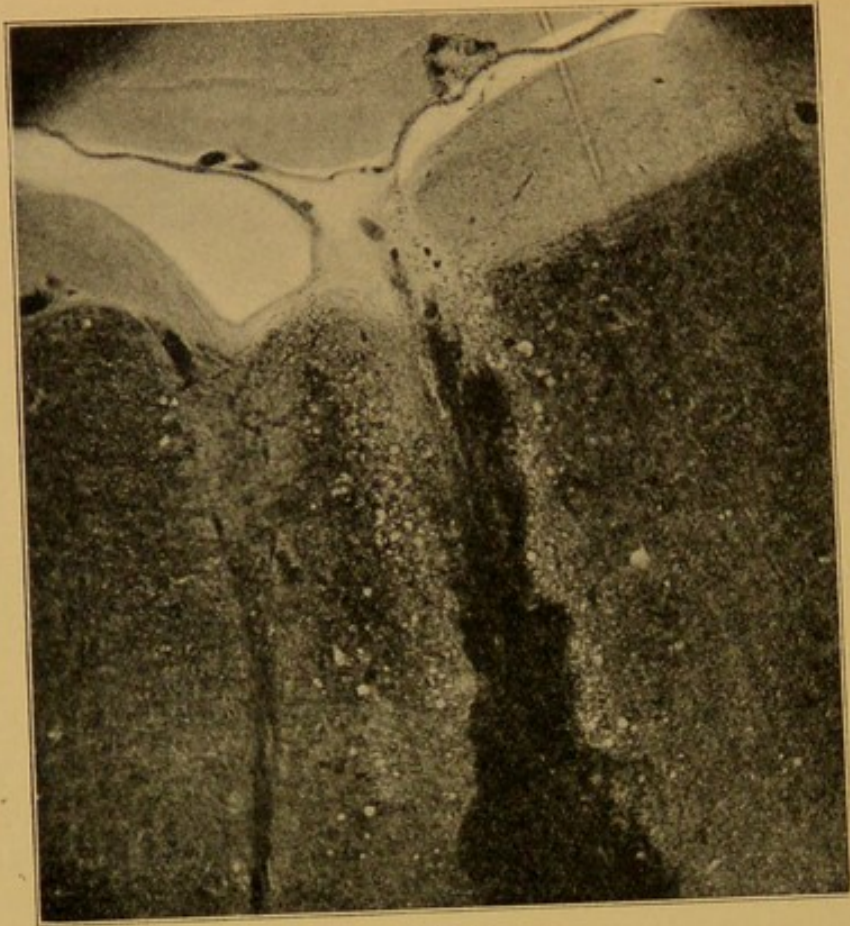
Fig. 1a.

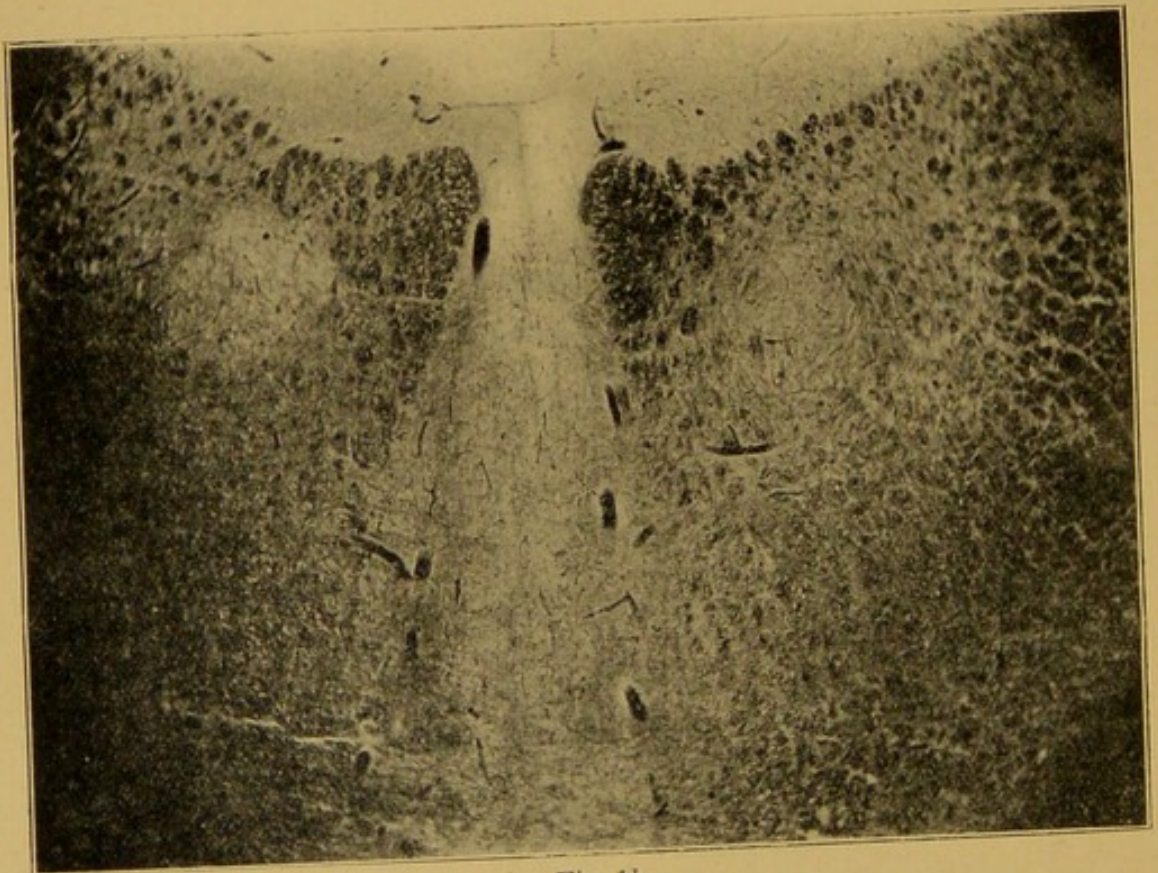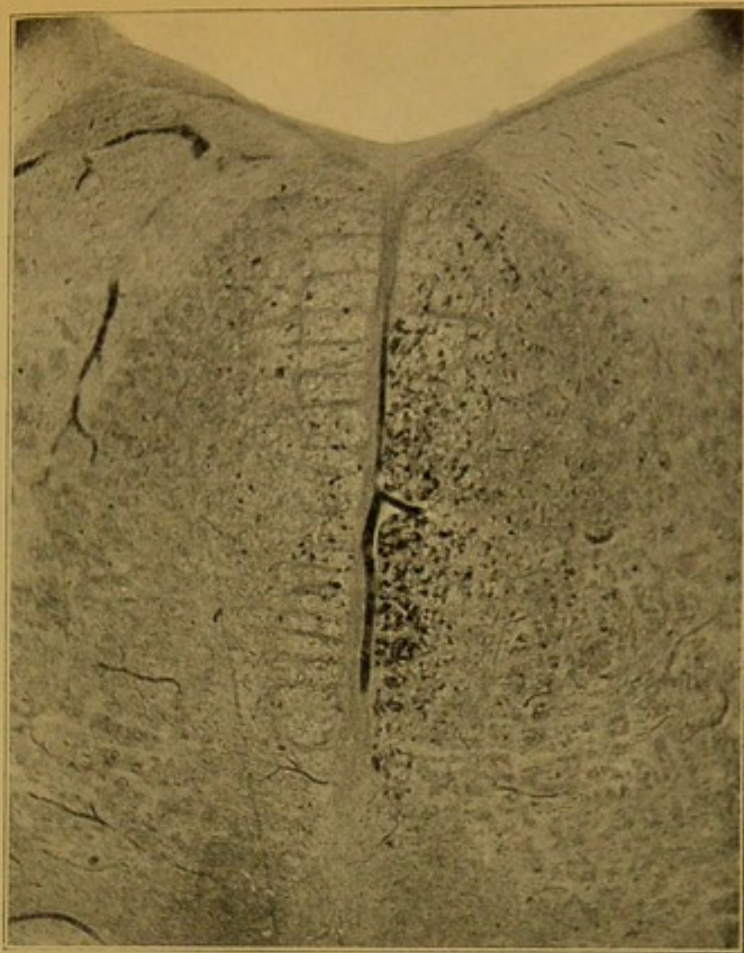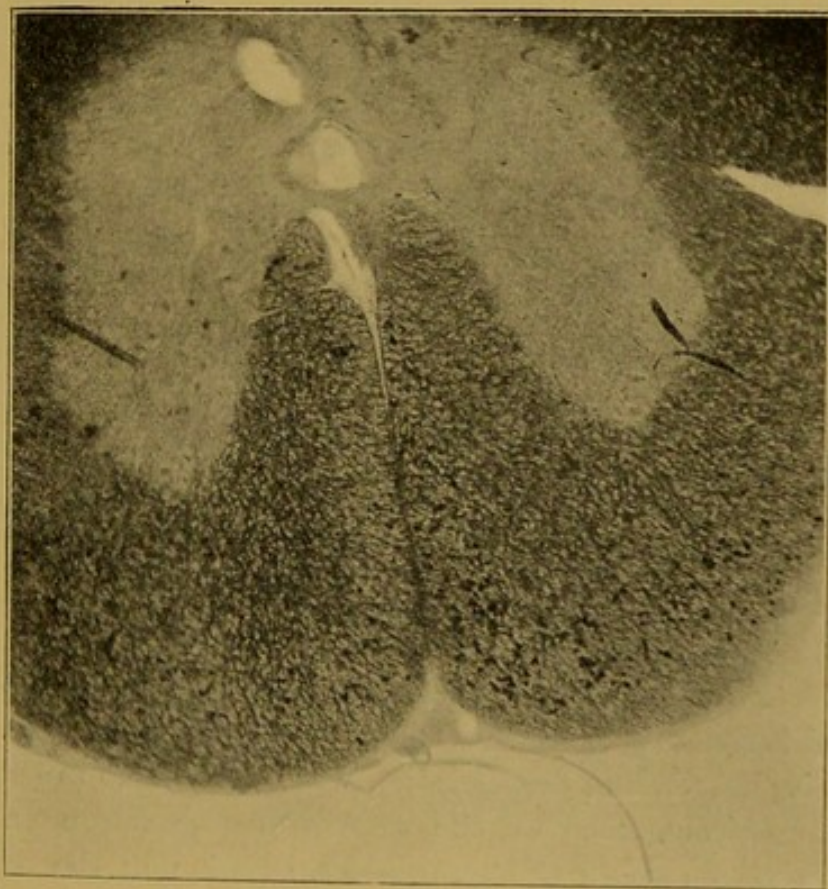Fig. 1b.

Fig. 1c.

Fig. 1d.

FIGS. 1a, 1b, 1c, 1d.—Cross sections of cat No. 139.

Fig. 1a.—Stab through the posterior longitudinal fasciculus in the pontine region.
Fig. 1b.—Ascending degeneration in the region of nuc. tegmenti profundus.
Fig. 1c.—Descending degeneration in the medulla oblongata.
Fig. 1d.—Descending degeneration in the medulla spinalis dorsalis.

Chapter I.—Secondary Vestibular Connexions and Forced Movements in the Horizontal Plane (Circus Movements).

§ 1.—*Lesion of the Mesial Part of the Posterior Longitudinal Bundle on one Side (Table I, Group 1, p. 26).*

In order to analyse the physiological functions of the different parts of the posterior longitudinal bundle, I endeavoured first to divide its mesial part on one side proximal to the sixth nucleus. In this I was successful in three animals (Nos. 91, 119 and 139); in one of these (No. 91) the lateral horn of the bundle was injured as well. Fig. 1 illustrates the lesion in the pons in one of these experiments and the resulting ascending and descending degenerations (cat No. 139).

In these animals circus movements towards the side opposite the lesion were observed for longer or shorter periods. This agrees with the results obtained by other investigators (*see* Table, Group 1) and is in harmony with the observations of Schiff and Probst that a hemisection of the pons causes circus movements to the intact side, but it would seem to show further that a total hemisection is not necessary in order to produce these movements, a lesion of the mesial part of the posterior longitudinal bundle being sufficient.

In all these cases there was a definite cerebro-petal degeneration in the posterior longitudinal bundle on the side of the lesion. This degeneration involved thick fibres which occupy a fixed position in the bundle, namely, in its mesial part and which correspond very closely in situation to the ascending bundle that, according to Thomas, Russell, Probst, Fraser, Lewandowsky, and van Gehuchten, is found degenerated after a lesion of Deiters' nucleus. Not infrequently some of the fibres of this latter bundle are found outside the actual area of the posterior longitudinal bundle and especially to its ventral side (Table I, No. 139 and No. 158). It ends close to the nucleus of the posterior commissure and appears to give off a number of fibres to the third nucleus. As far as I can judge from my own observations and those of others, these anatomical and physiological relationships are constant, and they suggest that we have to do here with an ascending vestibulo-mesencephalic bundle which controls circus movements to the opposite side.

A definite descending degeneration was present also in these animals. It was more pronounced on the side of the operation and could be followed on that side to the lumbo-sacral region in the antero-lateral column of the cord. On the other side, however, a few fibres were degenerated; these were situated more ventrally and laterally (Probst and van Gehuchten's reticulo-spinal bundle).

In the medulla, both these descending tracts leave their dorsal position in the posterior longitudinal bundle, and, according to Hösel, Probst, Winkler, Economo, and Karplus, take up a more ventral position. According to Wallenberg, the same change of position occurs in pigeons. Fraser observed it also in his experiments, but it must be borne in mind that he injured the posterior longitudinal bundle at the spot where the fibres enter it from Deiters' nucleus.

We shall have to consider presently the anatomical connexions of these descending fibres of the posterior longitudinal bundle. In order to simplify the narration of my results, however, I shall merely specify here what fibres were found degenerated. They were :—

(1) The descending fibres which, according to Held, Boyce, Redlich, van Gehuchten, Probst, Economo, and Karplus, degenerate on the side of the operation after lesion in the vicinity of the posterior commissure.

(2) Homolateral ponto-spinal or reticulo-spinal fibres which degenerate downwards after lesion of the substantia reticularis of the pons, as discovered by Probst, and confirmed by Lewandowsky and van Gehuchten.

(3) Heterolateral fibres constituting the crossed reticulo-spinal bundle which is found degenerated after lesion of the substantia reticularis of the pons (Kohnstamm, van Gehuchten).

§ 2.—*Lesion of the Posterior Longitudinal Bundle on both Sides*
(*Table I, Group* 2, *p.* 26).

In a number of cats, I endeavoured to divide the mesial parts of both posterior longitudinal bundles and succeeded in doing so in four animals (Nos. 90, 92, 97, 114) ; in one of these (No. 114) they were divided in the neighbourhood of the posterior corpora quadrigemina, together with both lateral parts of the bundle (fig. 2) ; in another animal (No. 92) the mesial part of the posterior longitudinal bundle was cut on both sides, on the left somewhat frontally as compared with the right, and at the same time the lateral part also was divided on the left side (fig. 12). Three of these animals were incapable of locomotion ; they could neither stand nor run, and their condition in many ways resembled that of rabbits during the first period after extirpation of both labyrinths (Winkler). There was conspicuous absence of lateral conjugate eye movements.[1]

[1] Observations on pathological cases with comparable symptoms and probably a similar lesion of the posterior longitudinal bundle have been recorded also by Parinaud, Priestley-Smith, Sauvineau Nieden, Long, Schöler, and Spiller.

In animal No. 90 both posterior longitudinal bundles were cut right across at the level of the exit of the trigeminal nerve except for the lateral part of the left bundle (figs. 11a and 11b, p. 37). In this case hæmorrhage took place exactly at the section of the left bundle, and this probably irritated the fibres without completely destroying them. At any rate, both the ascending and the descending degeneration was less pronounced on the left side, where the hæmorrhage occurred, than on the right side, where the bundle was cut across without hæmorrhage. This was the only animal in this group that was able to perform circus movements (to the right) ; it had also conjugate deviation of the head and eyes to the right for six days.

FIG. 2.—Lesion in the region of the corpora quadrigemina posteriores of cat 114.

After the operation, in all these cases of lesion of the middle parts of both posterior longitudinal bundles, there was present on both sides an ascending and descending degeneration in the areas described in the first group, where the lesion was unilateral. A lesion of both longitudinal bundles in the region of the posterior corpora quadrigemina produces forced movements in a vertical plane coinciding with the longitudinal axis of the animal, such as staggering and tumbling, which are not discussed in this paper.

§ 3.—*Lesion of Different Parts of Deiters' Nucleus (Ventral or Tri-angular Part, and Dorsal or Larger-celled Part) (Table I, Group 3, p. 26).*

We must consider whether the supposition that we have to deal with a vestibulo-mesencephalic tract in the mesial part of the posterior longitudinal bundle is correct; in other words, whether this mesial part is actually identical with the crossed vestibulo-mesencephalic bundle of Fraser, Hösel and van Gehuchten.

For this purpose we have at our disposal two experiments with lesions of different parts of Deiters' nucleus (No. 113, figs. 3a and 3b, and No. 118), and one with an extensive sagittal lesion lateral to the left posterior longitudinal bundle, and cutting Deiters' complex from the raphe (No. 158, fig. 10). In all three cases we find a degeneration undoubtedly of the same ascending bundle which we described in §§ 1 and 2. The area of the degeneration is exactly the same; it is here found on the side opposite the lesion. The crossing over of the fibres is visible between the level of the distal end of the triangular part of Deiters' nucleus (Fuse) and the decussation of the fourth nerve. This ascending degeneration is more extensive in No. 113 (fig. 3b), where the entire triangular part of Deiters' nucleus is cut through, than in No. 118, where it is principally the dorsal large-celled part of the nucleus which is injured. From this we may infer that the crossed vestibulo-mesencephalic bundle originates more especially in the tri-angular ventral part of the nucleus of Deiters.

Besides this compact bundle on the opposite side, there is a less compact bundle degenerated on the side of the lesion. This ascends in the extreme lateral part of the posterior longitudinal bundle formation (Winkler's fasciculus Deiters ascendens). In No. 158, however, the homolateral ascending degeneration is differently situated. The significance of this ascending degeneration will be considered in Chapter III, §§ 4 and 5.

A comparison of No. 113 with No. 118 affords us a special opportunity of determining more exactly the origin of the direct vestibulo-spinal bundle. In No. 118 (lesion of Deiters' nucleus in the narrower sense) this bundle is completely degenerated, although the lesion is limited; in No. 113 (lesion of the triangular part) there is far less degeneration. From this we may conclude that the direct vestibulo-spinal bundle originates more particularly in Deiters' nucleus in the narrower sense, and this agrees with v. Monakow's original
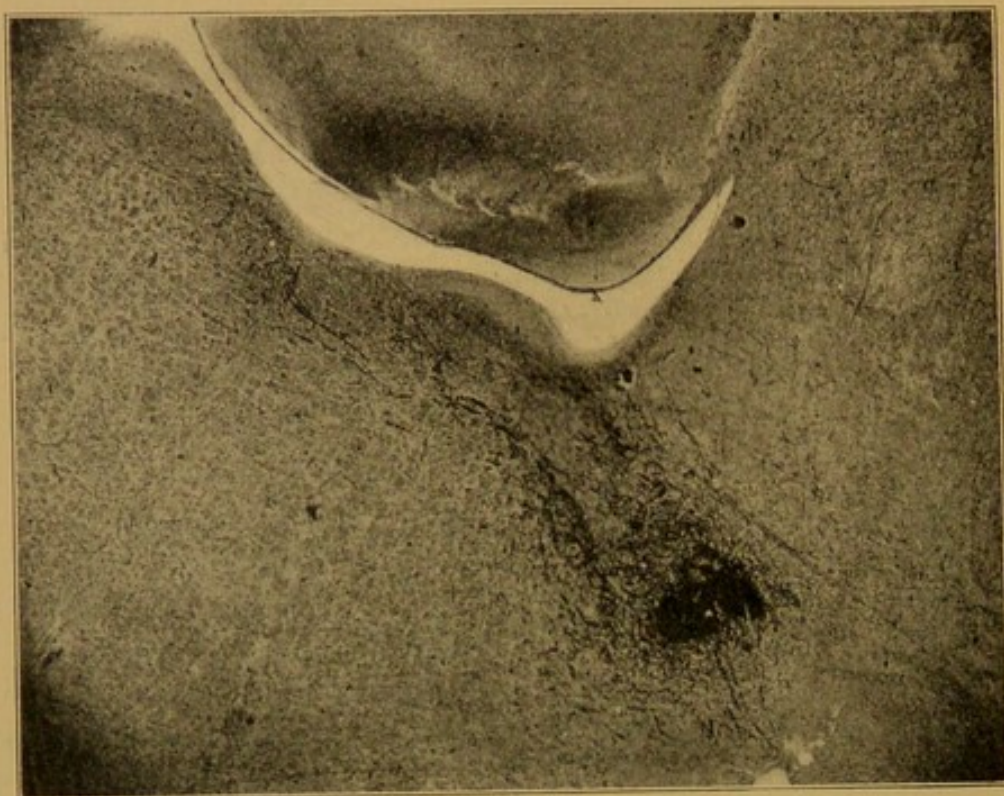
Fig. 3a.

Fig. 3b.

FIGS. 3a, 3b.—Cross sections of cat 113.

Fig. 3a.—Stab through Deiters' nucleus.
Fig. 3b.—Ascending degenerations in the upper pontine region.

description, and with the findings of Ferrier and Turner, Risien Russell, Thomas, and others.

A descending degeneration in the fibres of the posterior longitudinal bundle also is found on the side of the lesion in any case (particularly after lesion of Deiters' nucleus in the narrower sense). The situation of this homolateral, vestibulo-spinal bundle in the spinal cord is more dorsal and lateral than that of the corresponding crossed bundle. In the region of the cord its fibres intermingle with those of the direct dorsal vestibulo-spinal bundle just described, and which in these cases is also degenerated. This intermingling of the two homolateral descending bundles, their mutual origin from Deiters' nucleus in the narrower sense, and the fact that everywhere in the medulla oblongata degenerated fibres are found, which occupy the intervening space between their two areas, lead us to suppose that these two bundles are identical, both genetically and functionally.

As regards these *homolateral vestibulo-posterior longitudinal bundle-fibres* of Probst, van Gehuchten, and others, I would agree with Thomas and van Gehuchten, that in lesions in the region of Deiters' nucleus one is constantly struck by the great and apparently fundamental differences in the descending degenerations found.[1]

This may be due to the peculiar shape the lesion takes, but it may also be due to the circumstance that Deiters' nucleus, as Kohnstamm has mentioned, is composed of cells of various sizes, which possibly do not all suffer in the like degree from a lesion in this region. Something similar is found in regard to the different bundles of the posterior longitudinal bundle formation, which do not suffer equally when the posterior longitudinal bundle passes through a softened area, for some of the fasciculæ degenerate, and others remain intact [108]. In the same way differences appear to occur in different species in the relative position of the descending bundles, which has led even van Gehuchten to suppose that in the rabbit the homolateral descending vestibular fibres in the posterior longitudinal bundle are missing.

The situation of the homolateral descending Deiters' fibres in the spinal region of the longitudinal bundle is about the same as that of the descending homolateral degeneration, after incision of one posterior

---

[1] To give a typical example, I would refer to cat No. 7, of Lewandowsky. From the character and situation of the ascending degenerations (both exclusively on the same side as the lesion, cf. § 5 of this Chapter) in the posterior longitudinal bundle formation, there seems to be no doubt that Bechterew's nucleus is affected. Nevertheless one still finds in this case of limited lesion of the *oral* part of the vestibular region the direct vestibulo-spinal bundle considerably degenerated.

longitudinal bundle in the pons region (Chapter I, § 1). In some cases, however, we find the Deiters' fibres more dorsally situated. This fact, coupled with our observations to be referred to presently in regard to the heterolateral descending bundle, makes us question whether it is possible to determine which part of the descending fibres originates in the reticular cells in the region of Deiters' nucleus, and which part in Deiters' nucleus proper. This may be determined possibly by the application of Clarke and Horsley's method of localized lesion. Lewandowsky declared that it was impossible to define Deiters' nucleus sharply from the cells of the reticular formation. The observations of Kohnstamm and Lloyd, however valuable in other respects, did not bring conclusive evidence to bear upon this subject.

Generally speaking, we may say that the course of the crossed ascending vestibulo-mesencephalic bundle, of the direct vestibulo-spinal bundle, and of the homolateral descending bundle in the posterior longitudinal bundle formation, after lesion of Deiters' nucleus, as described by the first authors upon this subject (Held, Ferrier, Turner, Russell, and Thomas), corresponds with the results of the later investigators just mentioned and also with my own, save for the data in regard to the reticulo- or ponto-spinal fibres.

Heterolateral descending bundles from Deiters' nucleus. — This matter we shall have to discuss at some length, since opinions differ regarding it.

The cause of these differences of opinion, as far as I can see, is due to the variety of methods adopted in operating, and to the fact that it is not generally recognized that there exist marked anatomical and physiological differences amongst secondary connexions of the different parts of Deiters' nucleus, a circumstance which complicates their analysis very much.

Although we are much indebted to the investigations of Probst, Winkler, and Lewandowsky for our present knowledge of this region, the extensive lesions made by these experimenters cause such widespread degeneration that one is scarcely warranted in drawing definite conclusions in regard to these bundles. Fraser [59] avoids this difficulty by first severing the occipito-atlantal ligament and then incising the most distal parts of Deiters' region with a pointed galvano-cautery. Van Gehuchten experimented with rabbits, and injured, to judge from his figures, the caudal part of the vestibular region, by extracting the facial nerve. Probst's and my own lesions were made by means of a concealed needle piercing the cerebellum; as Horsley and Clarke have

definitely shown that neither from the cortex cerebelli, nor from the intrinsic nuclei do any fibres degenerate directly in the spinal cord, this method seems the most suitable for our purpose.

Wallenberg experimented on pigeons. Although his observations are models of clearness, yet the great disadvantage of experiments upon these birds is the minute extent of the relative parts, so that any advance in the differentiation of the various parts of the vestibular nuclei is not likely from them.

We owe our knowledge to von Monakow and Kohnstamm, and above all to Probst and van Gehuchten that, in addition to a homolateral bundle, there exists also a crossed ponto-spinal or reticulo-spinal bundle, which descends in the area of the posterior longitudinal bundle.

It appears to me that the degeneration of this bundle has interfered to an extraordinary degree with the analysis of numerous experiments, because of the peculiar and capricious shape of its field of origin (Kohnstamm). Thus, for example, I find it degenerated in No. 139 (fig. 1c), where there was a sharply defined lesion of the mesial part of the posterior longitudinal bundle (fig. 1a), and from this and other experiments I have come to the conclusion that the ganglion-cells for this tract must be present undoubtedly in the immediate vicinity of the posterior longitudinal bundle from below the exit of the sixth nerve (cf. Fraser's monkey, A 2) up to the posterior corpora quadrigemina.

I have shown (No. 93, fig. 5c, and No. 95, § 5) that subsequent to a lesion limited to Bechterew's nucleus, there is no crossed descending degeneration of posterior longitudinal bundle fibres, and although in lesions such as those of van Gehuchten's experiments, where the distal part of Deiters' nucleus was involved, there was such degeneration, I do not consider, as I have said, that such experiments can be regarded as conclusive and do not feel justified therefore in assuming with Fraser, Winkler and van Gehuchten, that Deiters' nucleus regularly possesses a crossed descending connexion with the posterior longitudinal bundle. In many cases of lesion of Deiters' nucleus the direct vestibulo-spinal bundle, and also the homolateral Deiters' posterior longitudinal bundle fibres are degenerated, but crossed fibres are lacking, and until some further advance has taken place in our knowledge of the anatomical and physiological relations of this region it is impossible to decide whether any part of Deiters' nucleus, much less what part, gives rise to heterolateral descending fibres.

§ 4.—*Lesion of the Mesial part of the Lateral Horn of the Posterior Longitudinal Bundle (Homolateral Vestibulo-mesencephalic Bundle) (Table I, Group 4, p. 26).*

In one cat with a lesion low down in the pons region, the larger fibres of the crossed vestibulo-mesencephalic bundle remained intact, but an area lateral to this bundle was degenerated on the side of the lesion (No. 68).

This case appears especially interesting from the fact that hæmorrhage took place exactly in the area of the posterior longitudinal bundle (fig. 4) ; in this animal there was noted a circus movement, or rather a maximal conjugate deviation of head, neck and eyes to the non-operated side, for thirteen days.
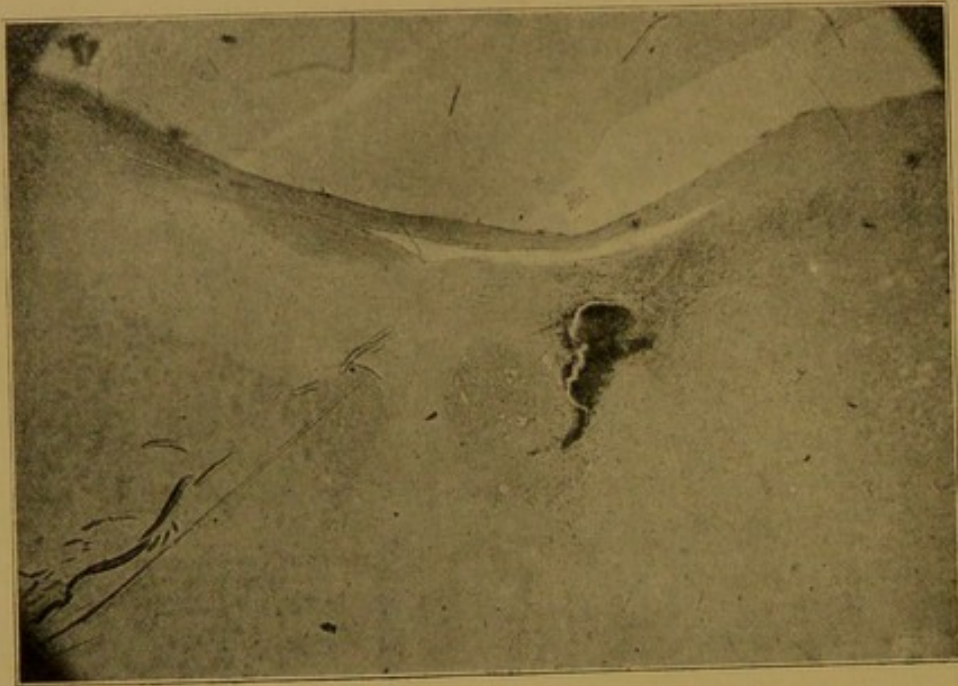
FIG. 4.—Lesion (hæmorrhage) in lateral horn of posterior longitudinal bundle of cat 68.

These degenerated fibres may belong to the area of the crossed vestibulo-mesencephalic bundle ; however, Deiters' nucleus of the other side is intact ; no descending degenerated fibres in the posterior longitudinal bundle were present except on the side of the lesion and these were situated dorsally and laterally and the direct vestibulo-spinal bundle was not degenerated ; moreover, the fibres were of more delicate structure than those of the crossed vestibulo-mesencephalic bundle and were situated more laterally in the posterior longitudinal bundle formation. It seemed, therefore, likely that these degenerated fibres might

have a different origin from that of the crossed vestibulo-mesencephalic bundle.

§ 5.—*Lesion of Bechterew's Nucleus* (*Table I, Group 5, p. 26*).

This supposition was strengthened as soon as we examined two animals that had sustained a lesion limited to the situation of Bechterew's nucleus (No. 93, figs. 5a, 5b, 5c, 5d, and No. 95, figs. 6a, 6b). In these we found this ascending bundle, and also a bundle of fibres descending in the spinal part of the posterior longitudinal bundle degenerated, but only on the side of the lesion. The origin of this ascending bundle could hardly be other than Bechterew's nucleus. It is then a homolateral vestibulo-mesencephalic bundle (as described by Wallenberg, Winkler and van Gehuchten) which ascends in the direction of the posterior commissure.

The physiological significance of this homolateral ascending bundle which pursues its course lateral to the crossed vestibulo-mesencephalic bundle, appeared closely connected with that of the crossed bundle. This is probable from the fact that animals in which one of these bundles (crossed or uncrossed) was degenerated performed circus movements to the healthy side (*cf.* §§ 1 and 3 of this chapter), or else conjugate deviation of head and eyes (fig. 5d) was present.

The homolateral descending fibres of Bechterew's nucleus (less in number in cat 95, where Deiters' nucleus was entirely intact) occupy a more dorsal and lateral position in the spinal part of the posterior longitudinal bundle formation than do the descending homolateral fibres from Deiters' nucleus.

CHAPTER II.—A CENTRIFUGAL BUNDLE IN THE POSTERIOR LONGITUDINAL BUNDLE-FORMATION WHICH CONTROLS CIRCUS MOVEMENT TO THE SIDE OF THE LESION.

Up till now we have become acquainted with two vestibulomesencephalic bundles, the mesial one of which is crossed and ascends from the ventral triangular part of Deiters' nucleus, while the lateral one ascends uncrossed from Bechterew's nucleus. The ascending degeneration of either of these tracts and the associated descending degenerations in the spinal part of the posterior longitudinal bundle are apparently always accompanied by circus movements or with conjugate deviation of head and eyes to the non-degenerated side. We
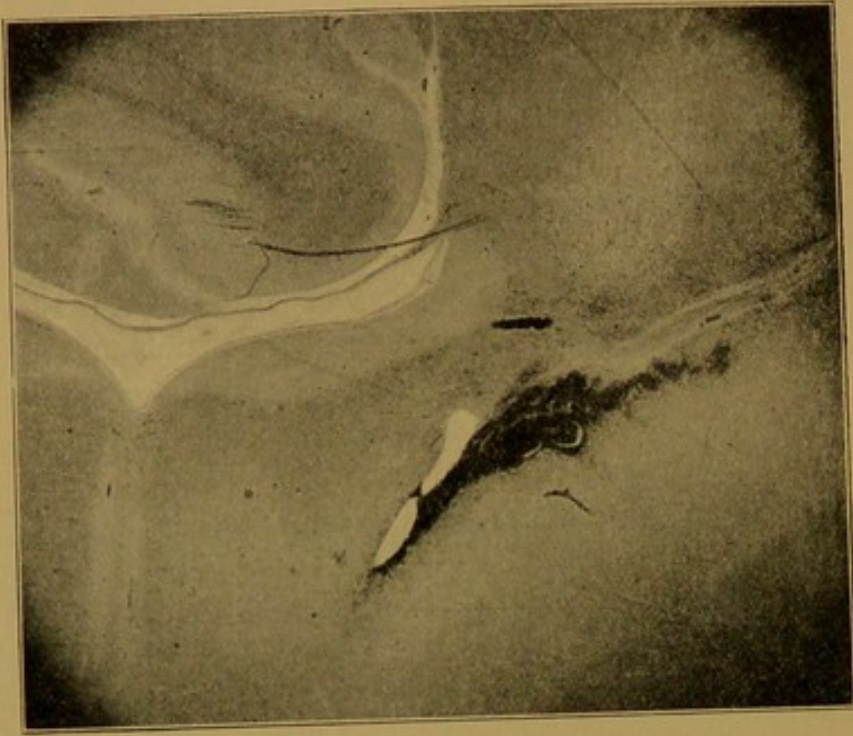
Fig. 5a.

Fig. 5b.
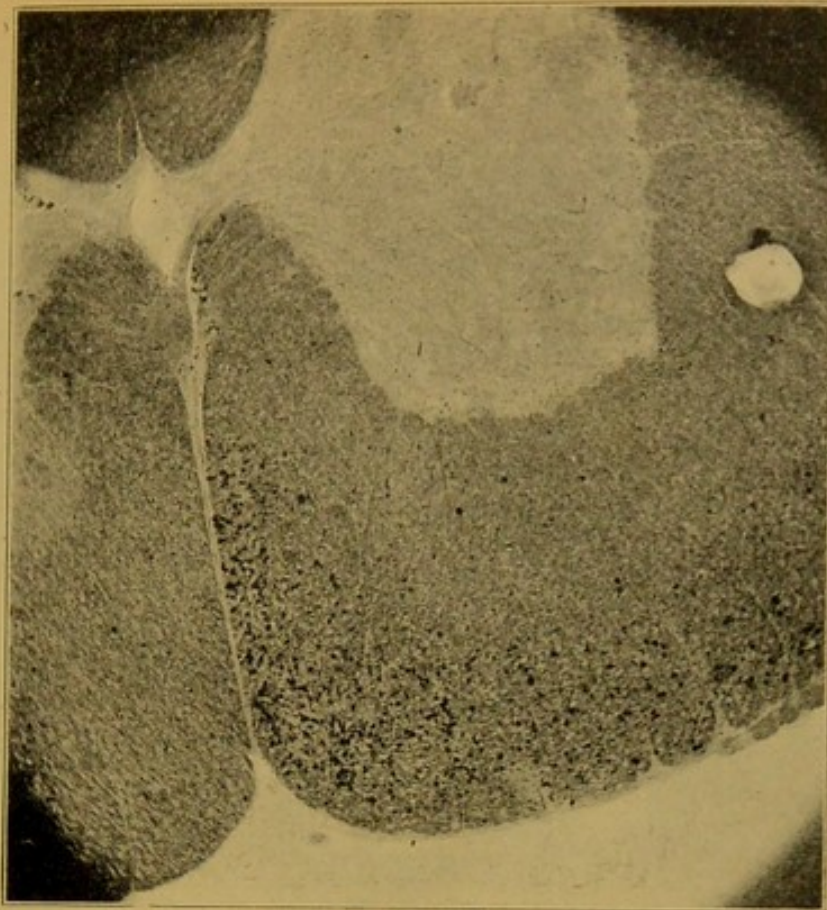
Fig. 5c.

Fig. 5d.

FIGS. 5a, 5b, 5c, 5d.—Taken from cat 93.

Fig. 5a.—Lesion in the region of Bechterew's nucleus.

Fig. 5b.—Ascending degeneration in the mesial part of the lateral horn of the posterior longitudinal bundle in the upper pontine region.

Fig. 5c.—Descending degeneration in the upper dorsal region of spinal cord.

Fig. 5d.—Photograph of cat 93, taken thirteen days after operation. Note conjugate deviation of head and eyes towards the left side.
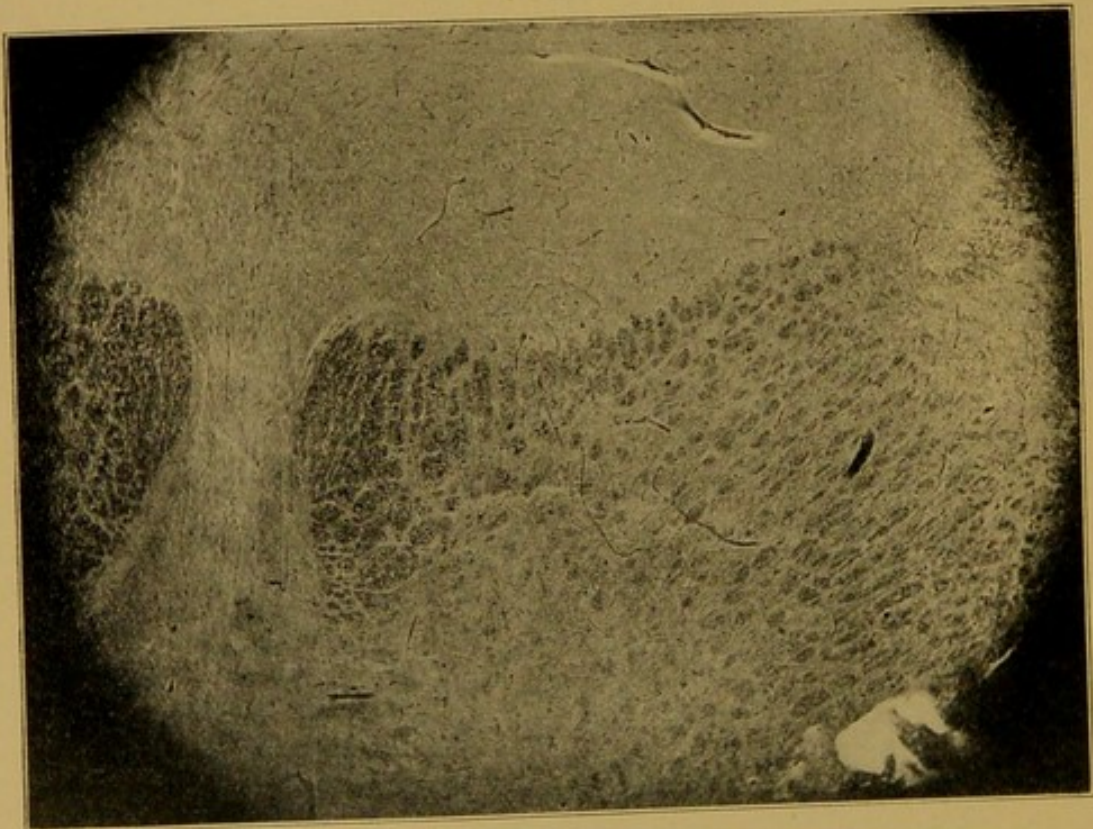
Fig. 6a.

Fig. 6b.

FIGS. 6a, 6b.—Cross sections of cat 95.

Fig. 6a.—Lesion in the region of Bechterew's nucleus.
Fig. 6b.—Ascending degeneration in the upper pontine region.

have now to determine, therefore, whether our experiments afford any support for the theory, so constantly advanced by recognized authorities, that the posterior longitudinal bundle and its connexions should be looked upon as the pathway of the reflex mechanism for the maintenance of equilibrium. This supposition has been discussed by Edinger, Bleuler, R. Russell, v. Bechterew and Wallenberg, and has been definitely accepted as correct by Spitzer and Kohnstamm. From a clinical point of view, arguments in support of it have been advanced by Prévost, v. Monakow, Spitzka, Gowers, Gee, Tooth, Kaplan, Finklenburg, and others, and these have been accepted on anatomical grounds by Bielschowsky, Bertelse and Rönne, and Lewandowsky. We would consider it our duty, therefore, to examine specially our present material, in order to determine whether it justifies us in dismissing the idea as purely hypothetical, or whether it contributes any definite experimental proof in support of this theory which has been arrived at by such a variety of physiological, pathological and clinical means. It would be a strong argument for the conception of the posterior longitudinal bundle as a pathway for the mechanism of the equilibrium of motion in the horizontal plane, if we were to find that the bundle also contains fibres, the descending degeneration of which is associated almost constantly with circus movements.

With this object in view, we naturally turn our attention to the region where our ascending bundles terminate, and which is obviously closely connected with forced movements, namely, the region of the posterior commissure. We must first determine, therefore, what are the physiological and anatomical consequences of a lesion in this region, and then particularly look for the descending degenerations in the posterior longitudinal bundle, consequent to those lesions, that were associated with circus movements.[1]

For this purpose we have at our disposal seven of my own experiments (Nos. 107, 108, 106, 109, 98, 61, Table II, Group 10, p. 28).

---

[1] The origin and termination of two descending bundles had already been recognized by myself for some time, and they had been termed fasciculus commissuro-medullaris and fasciculus interstitio-spinalis, not only in my article in the *Nederl. Koninklijke Academie* of October and November, 1912, but also in the manuscript which I sent in December, 1912, to the editor of *Neuraxe*, together with a table and rough outlines of the results of twenty-five experiments; these latter only were published in that journal. My communication concerning circus movements was published in the *Neuraxe* of January, 1914. Since then v. d. Schueren has confirmed the existence of the commissuro-medullary and interstitio-spinal bundle (*Neuraxe*, May, 1913).
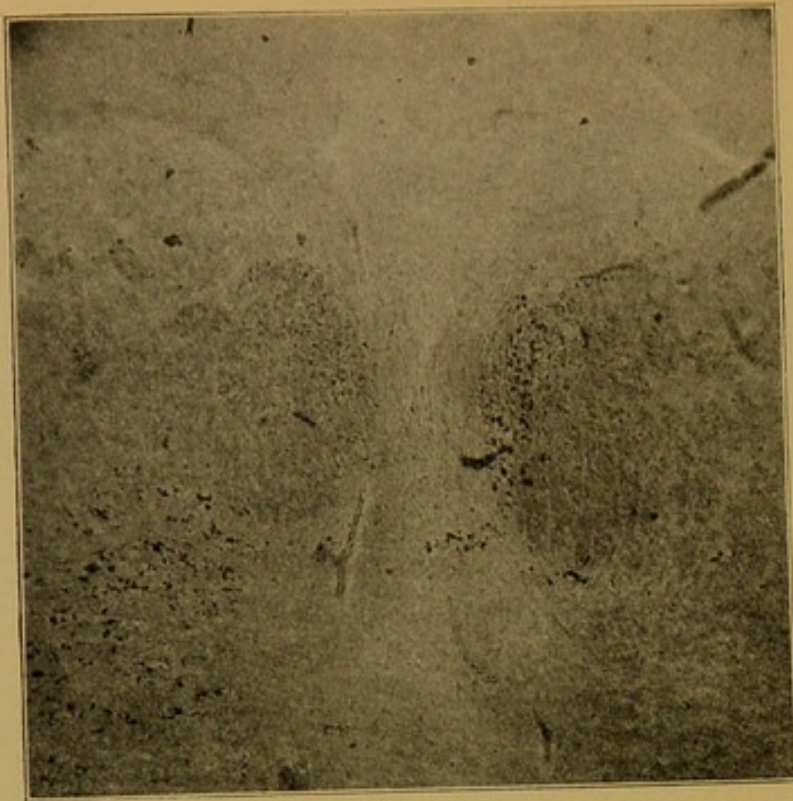
Fig. 7a.
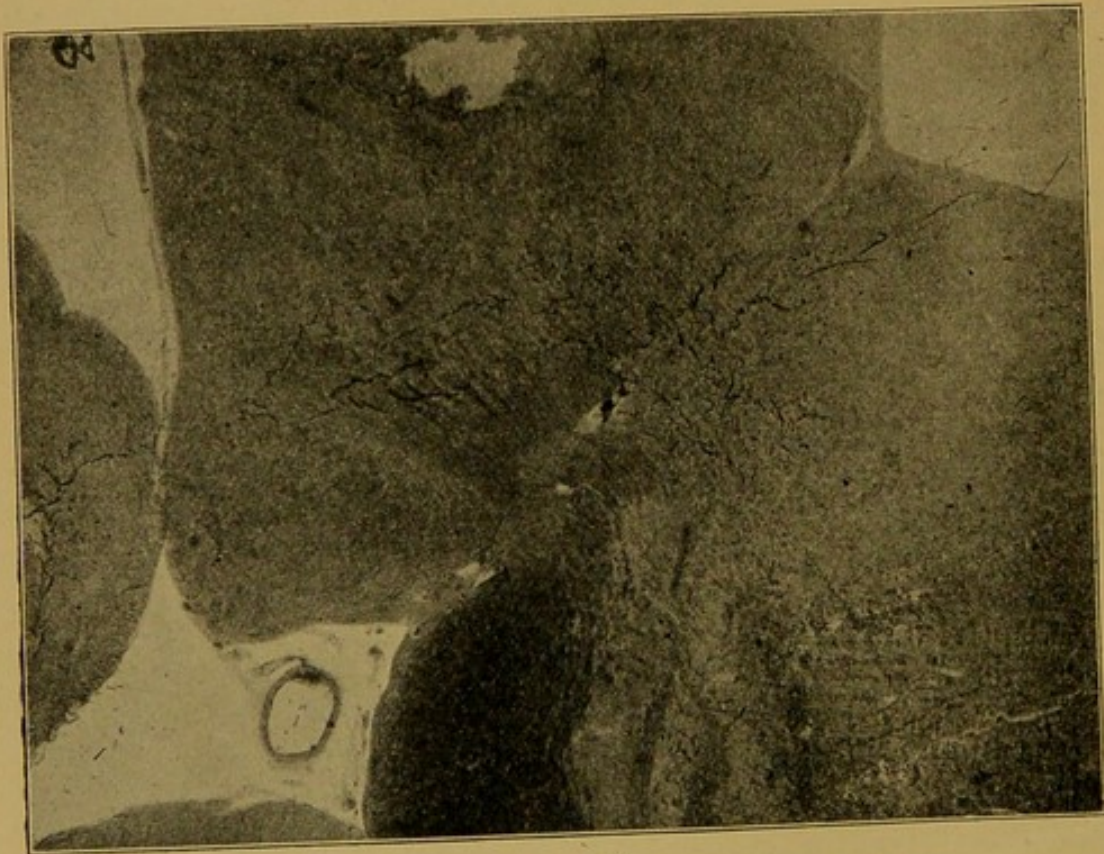
Fig. 7b.

Figs. 7a, 7b.—Cross sections of cat 108.

Fig. 7a.—Descending degenerations in the posterior longitudinal bundles in the region of the trochlear nucleus. Note on the right side the coarse-fibred tractus interstitio-spinalis, on the left the fine-fibred tractus commissuro-medullaris.

Fig. 7b.—Descending degenerations in the medulla oblongata. Note on the right side presence of coarse-fibred fibres; no degeneration on the left.

By reference to Table II we notice that, again in accordance with the law of Schiff and Probst ("a hemisection in the caudal parts of the optic thalamus causes circus movements to the side of the operation"), five of these animals executed circus movements to the side of operation for longer or shorter periods. Cat No. 108 was an exception, as it performed rolling movements to the left side or side of operation for a very unusual length of time and circus movement to the left side for one day only. This case exhibited an extraordinary localization of the lesion, which caused degeneration of the commissuro-medullary bundle on the left, and of the interstitio-spinal bundle on the right side (figs. 7a, 7b).

In this connexion we would recall that in the year 1881 v. Bechterew had already noted circus and rolling movements after lesion of this region; these he afterwards described in detail [11]. Lewandowsky [89] (p. 137), obtained similar results. Both these writers remark, and rightly, that these movements are never characterized by the vehemence which so regularly occurs after lesion of the vestibular region.

A delicately granuled tract was found more or less degenerated in all these five animals, on the side of the lesion, in the mesial part of the posterior longitudinal bundle. In No. 61 it was on both sides of the middle line as the results of the bilateral character of the lesion.

Before proceeding to correlate the anatomical data and the physiological consequences observed, we must exclude any accidental injury of the vestibular nerve, as even limited lesions in its area are so peculiarly liable to bring about forced movements (cf. Chapter III, §§ 1, 2, & 3).

In No. 106, for example, we find the nervus vestibularis on the left side slightly speckled with black dots, a condition similar to what was observed in No. 61. If, however, we remember that a lesion of this nerve invariably produces rolling movements to the side of the lesion, we can safely set aside the objection that the circus movements to the right and the left in this group of animals which we are considering, were due to an indirect lesion of the nerve root. It is also unlikely that the slight speckling of the two vestibular nerves (equally) in No. 108, could cause the prolonged tendency to fall to the left side. In No. 109 numerous delicate black granules were found in the two Deiters' nuclei, and as regards this animal we cannot say positively that the circus movement to the right for one whole day was not owing to this unintentional indirect lesion of Deiters' nuclei.

In regard to five animals then, we have notes of the duration and the nature of the forced movements, and also of the different

Left.
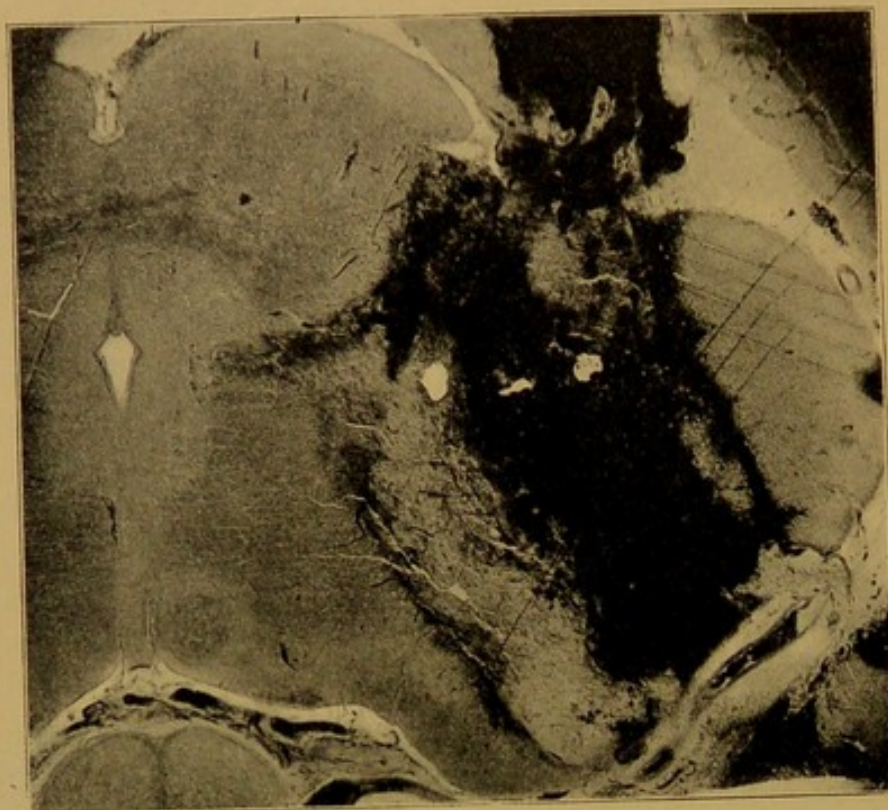
Right.

Fig. 8a.

Left.
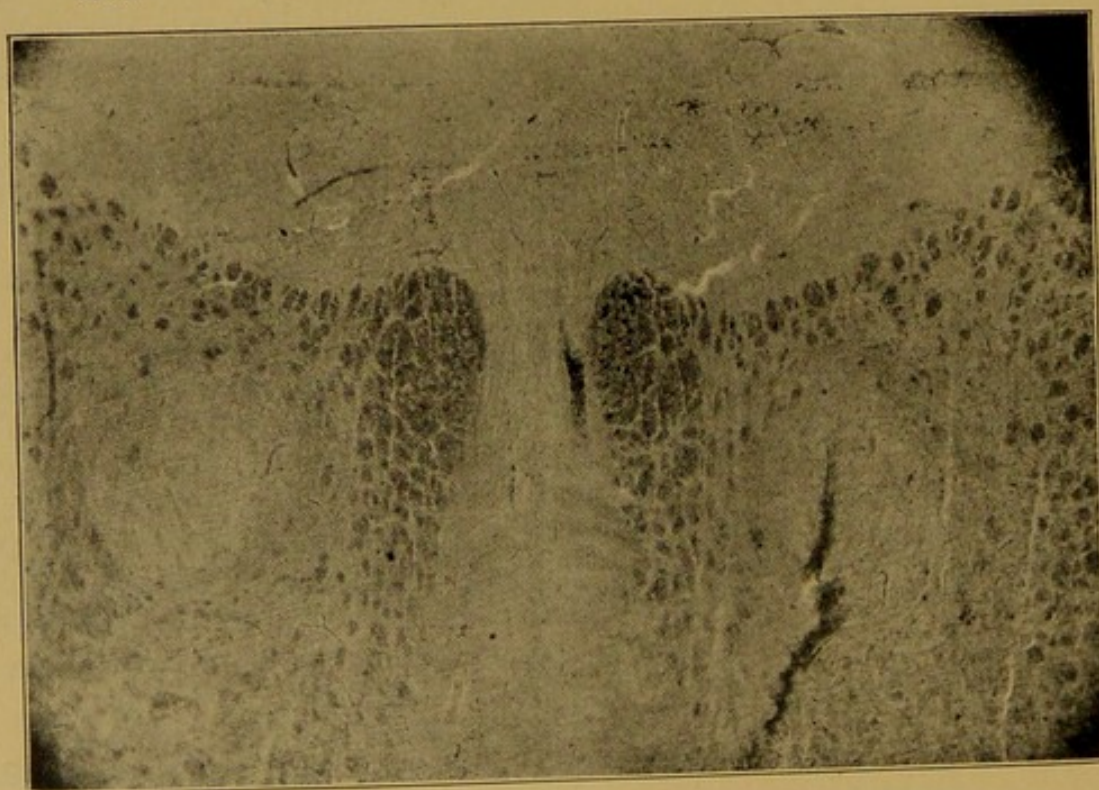
Right.

Fig. 8b.
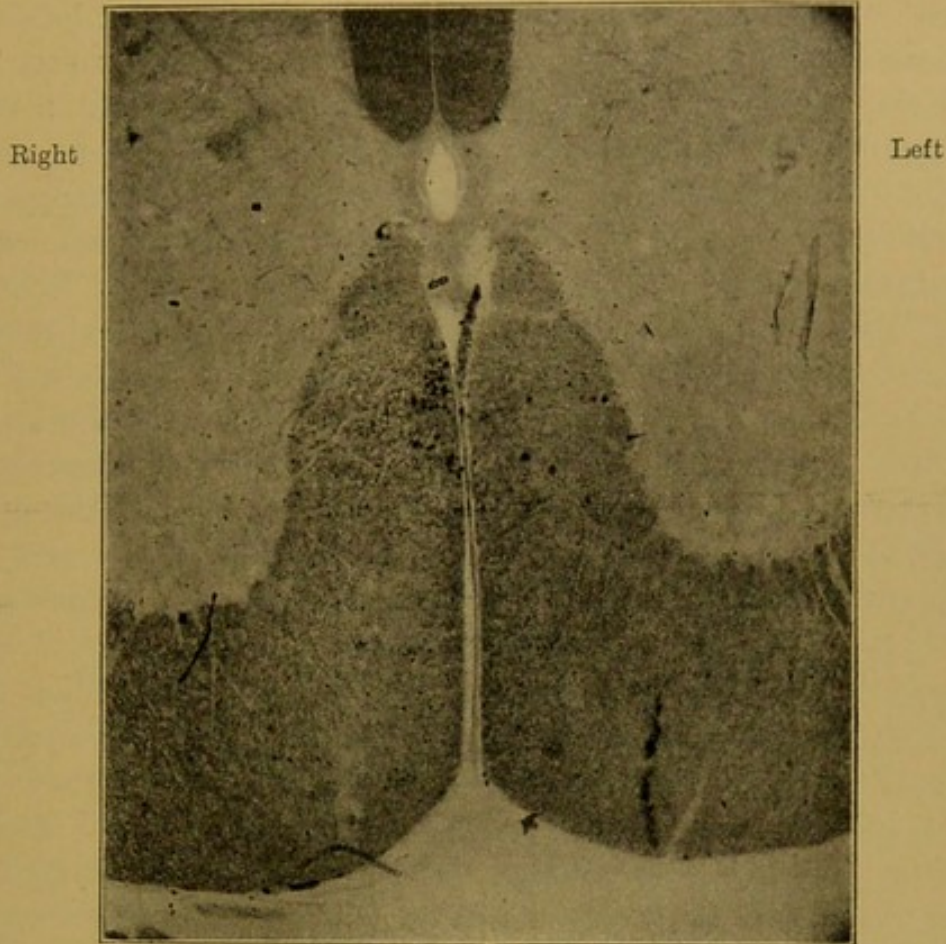
Fig. 8c.

FIG. 8a, 8b, 8c.—Cross sections of cat 107.

Fig. 8a.—Extent of the lesion at the level of the anterior quadrigeminate body.

Fig. 8b.—Level of the nucleus tegmenti profundus. Note the coarse-fibred tractus inter-stitio-spinalis on the side of the lesion.

Fig. 8c.—This same tract in the dorsal region of the spinal cord, on the side of the lesion (by mistake sides reversed).

descending degenerations in the area of the posterior longitudinal bundle, which may possibly be responsible for these movements. The bundle lateral to the posterior longitudinal bundle, as described by Probst, Economo and Karplus, was found degenerated only in Nos. 106 and 108, and was perfectly intact in Nos. 107 and 61, which animals executed distinct circus and rolling movements. From the hypothesis we have mentioned, and which regards the posterior longitudinal bundle as the pathway of a reflex mechanism, we may suppose that there exists a centrifugal component controlling the circus movement. We must investigate, therefore, the condition of the descending tracts within the posterior longitudinal bundle, the lateral bundle having probably nothing to do with these movements.

These descending mesencephalic fibres in the posterior longitudinal bundle, already noted by Held, have been examined after the Marchi method and described by Boyce, Redlich, and Probst in mammals. In them, however, we have to deal with a double bundle, the component parts of which begin and end differently. Their different course was first described in the year 1912 [108], and the bundles were termed the commissuro-medullary and interstitio-spinal bundle. Cajal, Wallenberg, and van Gehuchten discovered the descending mesencephalic fibres of this region in birds and fishes. De Lange studied them in different species of animals, and considered them homologous with the uncrossed tecto-bulbar bundle of the fish. In a rabbit he followed them right into the sacral region. As regards man, centrifugal fibres in the posterior longitudinal bundle have been described by Gee, Tooth and Roussy as being situated in its mesial segment, and, according to Roussy, also in its dorsal part.

Where we can follow this part of the posterior longitudinal bundle in its downward course as in Nos. 107 and 108, we can readily determine that we have before us here two separate anatomical entities; in No. 107 we can follow the interstitio-spinal bundle as a separate strand of coarse fibres well into the lumbar region of the spinal cord (fig. 8c). It is situated in the anterior column and runs close to the anterior fissure, about two-thirds of the way from the ventral to the dorsal end of the fissure. On the other hand, in No. 108 we see that the delicately fibred tract on the left side (fig. 7a), most mesially situated in the posterior longitudinal bundle, disappears caudally in the abducens nucleus in the oblongata (fig. 7b), and only a few solitary fibres from it can be followed into the cervical spinal cord, or lower.

When we now consider (Table II) that in unilateral lesions of the region of the posterior commissure, which are followed by circus movements to the side of the lesion, with conjugate deviation of the head and eyes, we constantly find degenerated fibres in the innermost part of the posterior longitudinal bundle, descending towards the medulla, it thus seems likely that we have here the centrifugal limb of the reflex arc which controls circus movements to the side of the mesencephalic lesion.

We must conclude therefore that in the posterior longitudinal bundle there are found not only two tracts on each side of ascending fibres, the degeneration of which occurs simultaneously with circus movements to the healthy side, but also on each side a centrifugal "final common path" [Sherrington 147], the descending degeneration

of which is associated with circus movements to the side of the lesion. In agreement with this theory of Sherrington's is the circumstance that the ascending fibres of this reflex arc are much more abundant than the descending. The condition resembles that of the single giant Mauthner-fibre of fishes, which, according to Kohnstamm, controls the motion of the tail fin.

None of my experiments is in direct opposition to this supposition; one of Economo and Karplus's experiments also (referred to in Table II) may be regarded as supporting it, and Roussy's [135] results and Kohnstamm's may be interpreted also as in agreement with it.

It is true that I find in some of my thalamic lesions in certain animals the same phenomena as were present in cat No. 1 of Roussy's series. This animal, although the nucleus of the posterior commissure and the commissuro-medullary bundle were intact, performed circus movements towards the operated side for some time. But in Chapter VI this class of experiments will be dealt with especially, i.e., lesions of a tract of fibres that connects the cerebral hemisphere (striate body) with the region of the posterior commissure. To declare, as Roussy does, the degree of circus movement to be in proportion to the injury of the pedunculi, would be neither in accordance with my own results, nor with those of other authors, Roussy's included.

Direct electric stimulation of this region may contribute towards the ultimate solution of this anatomo-physiological problem. This question also will be taken up further in Chapter VI.

CHAPTER III.—THE PRIMARY AND SECONDARY VESTIBULAR CONNEXIONS, AND FORCED MOVEMENTS IN THE PLANE VERTICAL TO THE LONGITUDINAL AXIS OF THE ANIMAL (ROLLING MOVEMENTS).

§ 1.—*Lesion of the Vestibular Root (Table I, Group 6, p. 26).*

In Group 6 of Table I we have included those cases in which the vestibular root itself was injured by the instrument, or was found degenerated to such an extent that some indirect injury to it must have taken place by stretching, or hæmorrhage, or in some such way.

The forced movements after direct lesion of the vestibular root, that is to say in the cases with definitely confirmed total degeneration in the nerve-root, are of far longer duration than those after indirect lesions or

TABLE I.—CENTRIPETAL TRACTS IN

Experiment	Lesion	Duration of life	Circus movement
	Group I.—Section of the median part of the bundle on one side. (Compare		
139	In middle pontine region, on right side	15 days	To the left ..
119	Region of posterior corpus quadrigeminum, on left side	7 ,,	To the right ..
91	Lower pontine region, on left side	16 ,,	,, ,, ..
	Group II.—Section of median part of bundle on both sides.		
114	Oral to 4th nucleus	21 days	—
97	,, ,, ...	6 ,,	—
92	Both bundles and left lateral horn, in lower pontine region	14 ,,	Head deviated to right side
90	Both bundles and right lateral horn, in lower pontine region	21 ,,	To right side, with conjugate deviation of head and eyes
	Group III.—Lesions of different		
113	Nucleus Deiters (triangular part), on right side ..	20 days	To the right ..
118	Nucleus Deiters proper on right side..	28 ,,	,, .. (?) ..
158	Sagittal lesion, cutting off vestibular region from raphe, on left side	15 ,,	To the left ..
	Group IV.—Lesion of the homolateral		
68	Softening of lateral part of pons ; hæmorrhage in lateral horn, on right side	14 days	Maximal conjugate deviation to left
	Group V.—Lesions of		
93	Bechterew's nucleus and dorsal part of crus cerebelli ant., on right side	28 days	Tendency to walk to left
95	Bechterew's nucleus and nucleus brachii pontis sup., on right side	24 ,,	To the left ..
	Group VI.—Lesion		
23.5.00	Acustico-vestibular region, on right side	28 days	Head turned to right
Rabbit V	Extirpation of so-called flocculus, on right side ..	11 ,,	—
42	Acustico-vestibular exit, on right side	33 ,,	—
67	Destruction of nucleus vestibularis and ganglion ventrale, on right side	20 ,,	—
	Group VII.—Lesion of Ramus		
VIII	Cyst in caudal part of ram. desc. viii, on right side	34 days	—
18	Flocculus cerebelli, corpus restiforme, and ram. desc., on right side	11 ,,	To the right ..
35	Corpus restiforme, nucleus desc. v and viii, softened, on left side	34 ,,	—
146	Sagittal lesion through caudal part of corpus trapezoides, on right side	13 ,,	Tendency to walk to left
158	Compare Group III.		
	Group VIII.—Lesion of Deiters' nucleus.		
	Group IX.—Lesion of lateral horn of posterior longitudinal bundle. (Compare Group		
62	Incision in crus cerebelli ant., and lateral horn, on right side	14 days	—
150	Lesion of lateral part of lateral horn, on right side	15 ,,	—
221	Two punctures through lateral horn, on left side ..	14 ,,	Head bent to left(?)
	Group X.—Lesion of median part of lateral horn of posterior longitudinal		
	No. 158, and Cat 5		

Duration	Rolling movement	Duration of movement	Area of P.L.B. to 4th nucleus
Probst's Case IX [123, p. 72] and Economo's Case V [78, p. 411].)			
10 days	.. ..	—	
2 ,,	.. ..	—	
8 ,,	Falls on right ; lies down on right side ..	14 days	
(Compare Fraser's Monkey No. 2 [59, p. 383].)			
—	Staggers	—	
—	"Tumbling"; falls to left and right.. ..	5 days	
4 days	Falls to left ; eyes rotated to left	4 days ; 12 days	
9 ,,	Head rotated to right	2 days	
parts of Deiters' nucleus.			
8 days	Head rotated to right	8 days	
1 day	Falls to right	7 ,,	
9 days	,, ,, ...	11 ,,	
vestibulo-mesencephalic bundle.			
10 days	Lies on left side..	Few days	
Bechterew's nucleus.			
6 days	Rolls to right ; falls to right	8 days ; 22 days	
5 ,,	.. ..	—	
of vestibular root.			
25 days	Rolls and falls to right ; lies on right side	28 days	
—	Head rotated and bent to left	11 ,,	
—	Vehement rolling to right ; rotation of eyes	33 ,,	
—	,, ,, ,, ,, ,,	20 ,,	
descendens nuclei vestibularis.			
—	Rolls to left ; head and eyes rotated to left	2 days ; 4 days	
3 days	Rolls to left	3 days	
—	Tendency to roll to right	12 ,,	
Some days	Slight tendency to roll to left	Some days	
(Compare Group III, Nos. 113 and 118.)			
II, Nos. 90 and 92 ; Group V, No. 93, and Kohnstamm's Rabbit IV [81].)			
—	Rolls to right	6 days	
—	,, ...	5 ,,	
1 day	Lies down exclusively on left side	3 ,,	
bundle. (Compare Group I, No. 91 ; Group IV, No. 68 ; Group VII, of Karplus [78].)			

TABLE II.—CENTRIFUGAL TRACTS IN

Experiment	Lesion	Duration of life	Fasc. commissuro-medullaris	Circus movement
107	Lesion of lateral part of posterior commissure (middle division), on right side	11 days	Degenerated on right side	To the right
108	Region antero-lateral to red nucleus, on right side	18 ,,	Degenerated on left side	To the left
106	Extreme antero-lateral part of posterior commissure, on right side	21 ,,	Few fibres, right > left	—
109	Extreme oral part of posterior commissure, on right side	17 ,,	,, ,,	Tendency to walk to right
98	Lesion of latero-posterior part of posterior commissure, on right side	19 ,,	Degenerated on right side	To the right
61	Region of posterior commissure, on right and left sides	26 ,,	Left > right..	Tendency to walk to left

Compare also Probst's Case [123, p. 527], Besta's Cat [17, p. 417],

than the forced movements described in the first two chapters of this paper. Also the character of the rolling associated as a rule with the Hertwig-Magendie squint (the eyeball of the side of the lesion being deviated downward, that of the other side being directed upward) is far more vehement in the case of a direct root lesion. In cats it is only after direct injury of the vestibular nerve that rolling movements continue for weeks; after secondary or indirect lesions of the vestibular nerve, and *a fortiori* after lesion of the ascending systems only, minor phases only of forced movements were noticed, such as a tendency to lie on one side, to fall to one side, or a rotation of the head to one side, when the chin was moved away from the direction of the rolling.

As soon as the anæsthesia passes off in lesions of the vestibular root, there occurs usually a rotation of the eyeballs on their antero-posterior axis towards the side of the lesion, a rotation which is easily demonstrated in cats because of the slit-like shape of the pupil, and in rabbits can be made apparent by the performance of a preliminary iridectomy [107]. The upper half of both eyeballs is seen to be rotated towards the side of the lesion, the lower half from the side of the lesion. Further nystagmoid movements of the eyeballs can be observed, slow in character in the direction of the rotation, but rapid in character in the opposite direction. This rotatory nystagmus usually lasts for a few days only, and is increased by turning the head in the direction *opposite* to that of the rotation.

After compensation of the rolling movements has taken place, they may be renewed by blindfolding the animal. For a long time

POSTERIOR LONGITUDINAL BUNDLE.

Duration	Fasc. interstitio-spinalis	Rolling movements	Duration of movements	Area of P.L.B.
8 days	Degenerated on right side	Head rotated to left side	8 days	
1 day	Degenerated on right side	Tendency to fall on left side	9 ,,	
—	—	.. ..	—	
Few hours	Few fibres (?)..	.. ..	—	
1 day	Few fibres on left > right	Slow rotatory jerks to right side	Few hours	
3 days	—	Slight tendency to roll to right side	3 days	

and Karplus's Cat 3 and Macacus 3 [78, pp. 298 and 342].

the animal can also be pressed down more easily to the side to which he tended to roll than to the other side. By Marey's falling experiment (the normal cat on being taken up by its legs, and dropped, invariably lands upon its paws) the rolling can be brought about again, and in epileptic fits it may also recur. It is remarkable, however, that in ether narcosis a rotation in the opposite direction [137, cf. also 133] is observed.

In studying this group of animals (Group 6) we notice that, with the exception of rabbit V, the rolling movements invariably occurred in such a manner that the locomotion was always to the side of the injured vestibular nerve. This accords with the earlier experiments of Flourens, Schiff and Cyon, and with those of Ewald, Breuer, Winkler, Camis, Bartels, and others of later date, dealing with lesions of the semicircular canals and section of the nervus acustico-vestibularis.

It is outside the province of this paper to discuss the hydrokinetic theory of these organs, simultaneously brought forward by Crum Brown, Breuer and Mach, or to recall the extensive literature concerned with stimulation experiments performed upon the semicircular canals and the acoustic maculæ. I will merely remark that a lesion of one canal tends to produce deviation or movement in the plane of that canal as well as corresponding alterations in the compensatory changes in position of the eyeballs that take place during movements of the body [31, 70, 84, 87] (pathological observations of Stein, Stenger, Bourgois, Bezold, van Uffenorde). It is well known

that not only in vertebrates, but also in invertebrates, for example in octopods (v. Uexkull, Muskens [110] Prentiss), removal of the whole otolitic organ invariably causes rolling movements to the side of the lesion, together with corresponding disturbance of independently moving parts of the body (eyeballs, fins, tail, &c. [18, 93]).

As regards the more recent researches concerning the vestibular nerve itself, I would quote those of Biehl [21], relating to direct electrical stimulation of this nerve in horses and sheep. During the stimulation, for instance, of the right nerve, a deviation was observed of both eyes to the right side, with small rapid nystagmus in the same direction; at the same time there was a squint present, the left eye being below, the right above, a deviation which is found in animals that roll to the left side. Immediately after severance of the vestibular nerve, on the other hand, the deviation of the eyeballs and the squinting were in exactly the opposite direction ; thus, after section of the right root, the horizontal deviation of the eyes was to the left, the left eye was turned upwards, and the right downwards. To conclude, as Biehl does, from these observations (which are partially at variance with those of some experienced physiologists) that the stimulation experiment indicates the character of the normal working of the vestibular nerve appears hardly justifiable. We should rather assume that the vestibular root comprises so many different physiological entities, all in connexion with the preservation of static and dynamic equilibrium, that it will depend upon the details of the experiment as to what results will ensue from stimulation or injury of the root. Thus from my own experiments it would appear that a lesion of the proximal parts of the vestibular nuclei causes forced movements, the direction of which may be the reverse of that of movements caused by lesion of the caudal parts of the nuclei. It would, therefore, hardly be surprising if direct stimulation of the proximal and caudal fibres of the root produced oppositely directed conjugate deviations. Stimulation and section of the whole of the vestibular root gives evidence, I consider, of the function of the preponderant semicircular canal in that particular animal.

As regards the anatomical results in this group of animals we are considering, I must make particular mention of rabbit V, where the pars petrosa cerebelli, according to Bolk [26], or the so-called flocculus was extirpated, and a part of the vestibular nerve was injured, an associated lesion which occurs very rarely with this operation. Amongst a large number of experiments I consider this case the only one which can be utilized for the study of the intracerebral degeneration that occurs after a lesion of the vestibular root alone, since all other experiments in rabbits and cats showed, on careful microscopic examination, complications caused by associated lesions in adjoining regions. In this animal we could follow the degenerated vestibular nerve-sheaths

into three cell groups, to the descending ramus of the vestibular nucleus, to Deiters' nucleus (both to its ventral distal division—nucleus triangularis—and to its dorsal large-celled division—Deiters' nucleus in the narrower sense), and to the region of Bechterew's nucleus and the nucleus tecti [112]. Meynert, Sala and Thomas also traced vestibular fibres directly into the roof nuclei.

In none of my numerous experiments with lesions of the vestibular nerve could I succeed in following the course of the root-fibres towards the area of the posterior longitudinal bundle and its lateral horns, or towards the pons or mid-brain, or descending directly into the spinal cord. In vain did I endeavour to convince myself, by means of the osmic acid method, of the existence of direct vestibular fibres which cross the raphe (Cajal and Wallenberg in birds, Deganello [46] in frogs, Lewandowsky in mammals). I should almost doubt that such fibres exist, although the silver method of Cajal strongly suggests them ; what may happen, with the osmic acid method, I think, is that in extensive injury of the elements of the vestibular nerve, a few fibres originating from Deiters' nucleus degenerate upwards, and thus simulate direct root-fibres. Further, I cannot agree with Lewy [91] that the structures in the posterior longitudinal bundle are more likely than those in other regions to contain fibres coloured by osmic acid. On the contrary, by carefully avoiding all compression of the brain, I have obtained ample proof that even extensive lesions of the cerebellum (including the nucleus dentatus) never cause the slightest degeneration in the posterior longitudinal bundle; in these cases I never observed the slightest sign of forced movements in the two planes (circus movement in the horizontal plane, and rolling movement in the vertical plane, vertical to the long axis of the animal) which are discussed in this paper.

As regards the striking difference in the physiological effects produced by the lesion in rabbit V, and those produced by all the other lesions of the vestibular root, I must observe again that the rolling movements in this case were never of a vehement character, and, as already stated, were directed to the side opposite to the lesion. Seeing that this sort of rolling movement never resulted in numerous other rabbits in which the flocculus alone was removed, together with the part of the nucleus dentatus enclosed in it [114], it must probably depend in this case upon the unusual lesion of the vestibular root that was present. In this case (rabbit V) it was especially the caudal part of the vestibular root and the ramus descendens that were degenerated,

and the limited extent of the lesion is proved by the absence of degeneration in the tuberculum acusticum and the corpus trapezoides.

§ 2.—*Lesion of the Descending Ramus of the Vestibular Nucleus*
(Table I, Group 7, p. 26).

The next group to be considered contains the animals with lesion of the descending ramus of the vestibular nucleus; either a total destruction of the cell area as in cat No. 8 (fig. 9) or a partial lesion as in Nos. 18 and 35. The chief point in connexion with this lesion is that
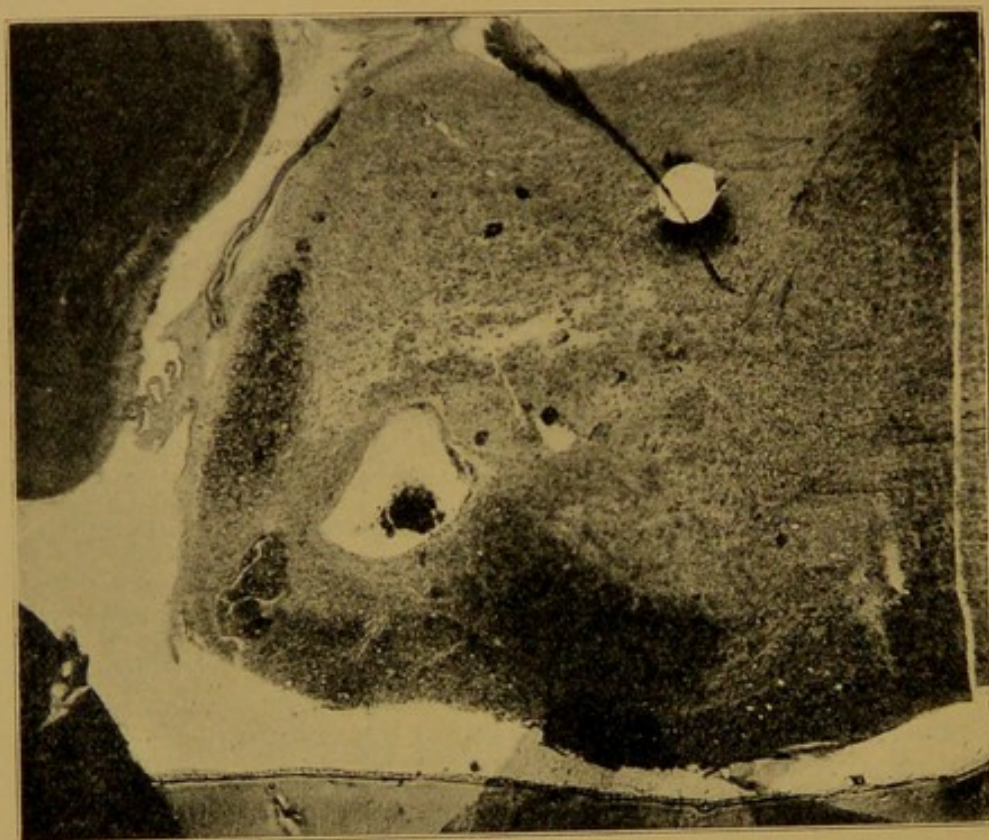
Fig. 9.—Lesion of the medulla oblongata of cat 8, softening with cystic degeneration, including the ramus descendens nuclei vestibularis.

in these cases rolling movements to the healthy side, or at any rate an inclination thereto, were observed during the life of the animal. The intensity and the duration of these rolling movements and of the corresponding deviation and rotation of the eyeballs around their axes that accompanied them [107, 113] appear to be in direct proportion to the intensity of the lesion in this part of the vestibular complex, or to the completeness with which, as in some other experiments, this part

of the complex is cut off from the raphe, and from the more proximally situated parts of the cerebrum.

In cat No. 8 we have to deal with a complete cystic degeneration of the entire region (fig. 9). In cats Nos. 18 and 35, the lesion is partial only and caused apparently by indirect temporary pressure; in the latter of these two animals rolling movement never actually ensued. In cat No. 146 it was the distal part of the ramus descendens only that was cut off from the raphe and the proximal parts of the brain; in cat No. 158 the sagittal lesion was immediately lateral to the left posterior longitudinal bundle and severed the entire vestibular region from the raphe (figs. 10a and 10b). This last animal fell for several days towards the side opposite the lesion.

I must admit that my material is inadequate to allow the conclusion to be drawn absolutely that this part of the vestibular system specially controls this function of rolling movements towards the non-severed side, or rather this negative function, because, according to Munk [106] rolling movements are to be considered as the result only of an inability to maintain the normal posture. However, I consider this conclusion is in accordance with the facts so far obtained by a physiological analysis of the Deiters' complex, and it is such a relatively rare occurrence that, after a lesion of the descending ramus, an animal remains alive long enough to admit of observations being made, that I consider these preliminary results worth noticing. I have to confess that all the lesions in this group involved accidentally the ramus descendens. Only once did I succeed in my attempts to produce a lesion of the descending branch and in this way to observe rolling movements towards the healthy side.

As regards the secondary degenerations which are due to a lesion of the ramus descendens, it is only in No. 158 that I have been able to obtain positive (?) data. In this animal an ascending degeneration is present in the mesial part of the lateral horn of the posterior longitudinal bundle (fig. 10b), but the situation and the extent of the sagittal lesion in this case are not such as to justify us in concluding that this ascending bundle actually originates in the ramus descendens of the vestibular nucleus; probably it is the one which was affected in the case discussed in § 5 of this chapter. This much is certain, however, that in cat No. 8, with a complete destruction, and in cat No. 18, with a slight lesion of the ramus descendens, there is strangely enough only the merest trace of ascending degeneration in the heterolateral posterior longitudinal bundle, and at the same time only exceedingly
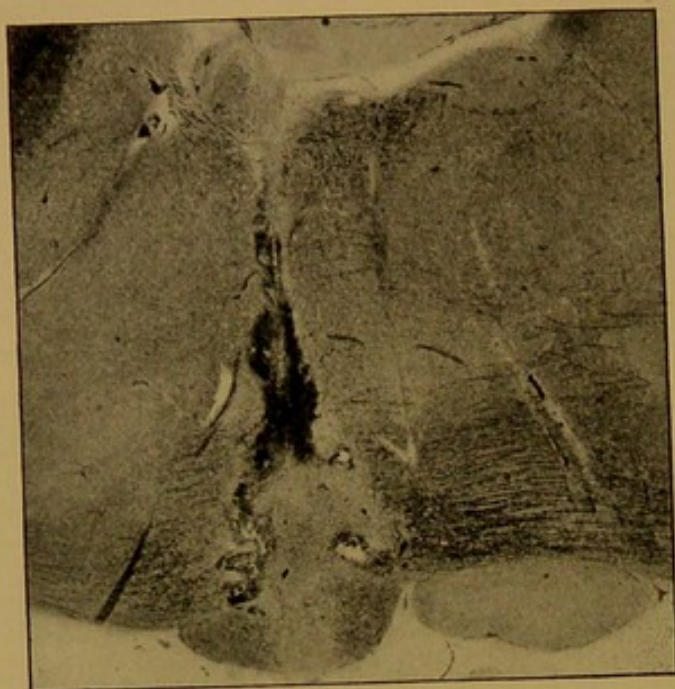
3

34

Fig. 10a.

Fig. 10b.

Figs. 10a, 10b.—Taken from cat 158.

Fig. 10a.—Sagittal lesion on the left side of the posterior longitudinal bundle, cutting off the vestibular region from the raphe.

Fig. 10b.—Ascending degeneration in the region of the nucleus tegmenti profundus. Note also degeneration of the tractus vestibulo-mesencephalicus cruciatus.

slight descending degeneration either on the side of the lesion or on the opposite side. As to No. 158 the degenerated fibres may be merely crossed ones.

In the literature I find certain facts which are in support of my views. This is the case in the discussion by Longet [94] on the rolling movements which occur after a lesion behind the fifth nerve. Luciani and Sergi [96] confess that they cannot explain why, after lesion of the lower posterior part of the cerebellum, rolling movements should appear which take an opposite direction to those seen after ablation of a hemisphere. Russell [138] observed the same movements after lesions of the restiform body.

As it is impossible for a lesion to be confined absolutely to the ramus descendens, the restiform body being usually involved, it might be suggested that the ascending olivo-cerebellar fibres took part in this phenomenon. If, however, it be considered certain that all the olivo-cerebellar fibres terminate in the cerebellar cortex, the fact that no lesion of the cerebellar cortex alone is associated with the demonstration of this phenomenon renders the supposition improbable.

§ 3.—*Lesion of Deiters' Nucleus (Table I, Group 8, p. 26)*.

In two animals (Nos. 113 and 118) the lesion was limited to Deiters' nucleus on the right side (Group 8 of Table I). In both these animals, circus movement to the side of operation was observed. In Chapter I, §§ 1 and 3, I have discussed the crossed ascending degeneration of fibres, passing from this nucleus into the posterior longitudinal bundle, and in these two animals there was also a falling movement to the side of the lesion as well as a circus movement. In both animals ascending degeneration was found in the most lateral part of the lateral horn of the posterior longitudinal bundle, and could be followed in an upward direction as far as the region of the tegmentum. A few fibres, however, could be followed into the posterior commissure at its extreme caudal level (lateral fibres seen in fig. 3b, on right side).

In § 4 of this chapter, it is shown that a direct lesion of the lateral part of the posterior longitudinal bundle is followed by an ascending degeneration of the fasciculus vestibulo-tegmentalis lateralis, which is in all cases accompanied by rolling movements towards the side of the lesion.

After a careful examination of the cases and their anatomical lesions, one feels bound to admit that different parts of Deiters' nucleus control

the circus movements to the operated side, and the rolling movements towards the side of the lesion. This is illustrated in cases Nos. 113 and 118. In the first case the circus movements lasted a whole week, while in the second they were present for one day only; in the first case the entire caudal triangular part of Deiters' nucleus was injured, and the ascending crossed vestibulo-mesencephalic bundle was far more extensively degenerated than in the second case. From the physiological analysis one may further deduce that the magno-cellular part of Deiters' nucleus, or what is termed Deiters' nucleus in the narrow sense, which controls the rolling to the side of the lesion, sends out more descending fibres towards the spinal cord on the side of the lesion, than the ventral part which controls the circus movements to the side of the lesion.
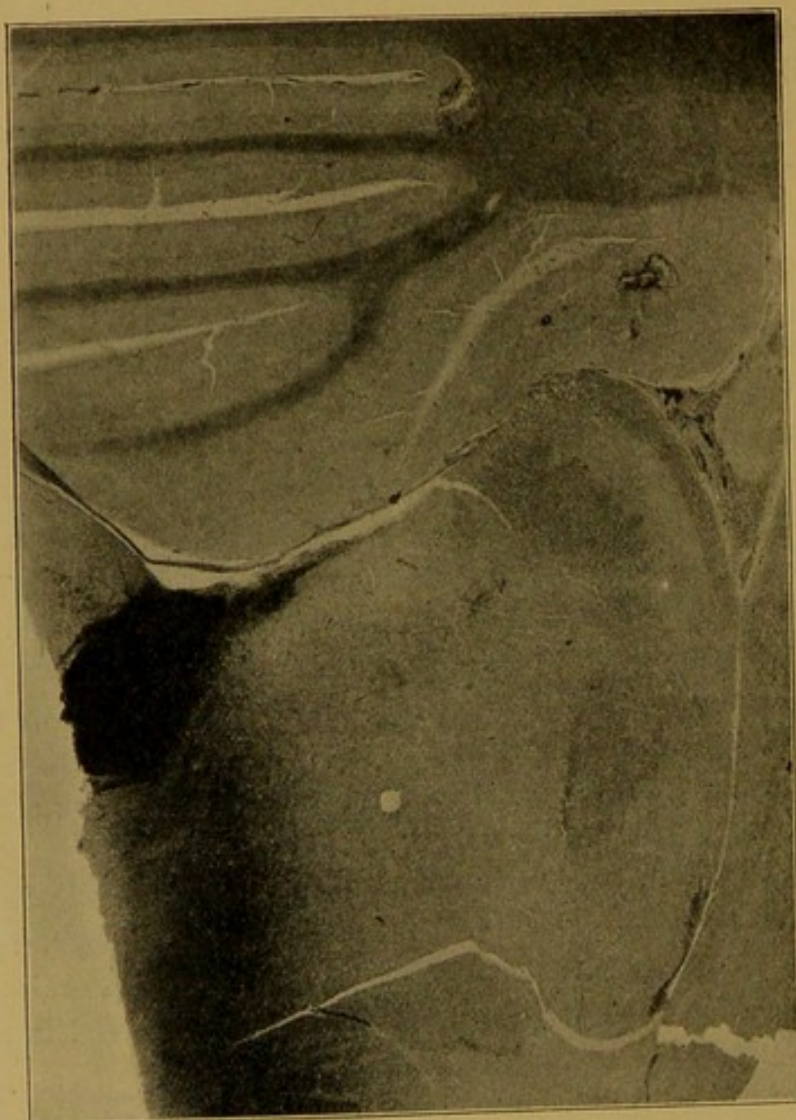
Fig. 11a.
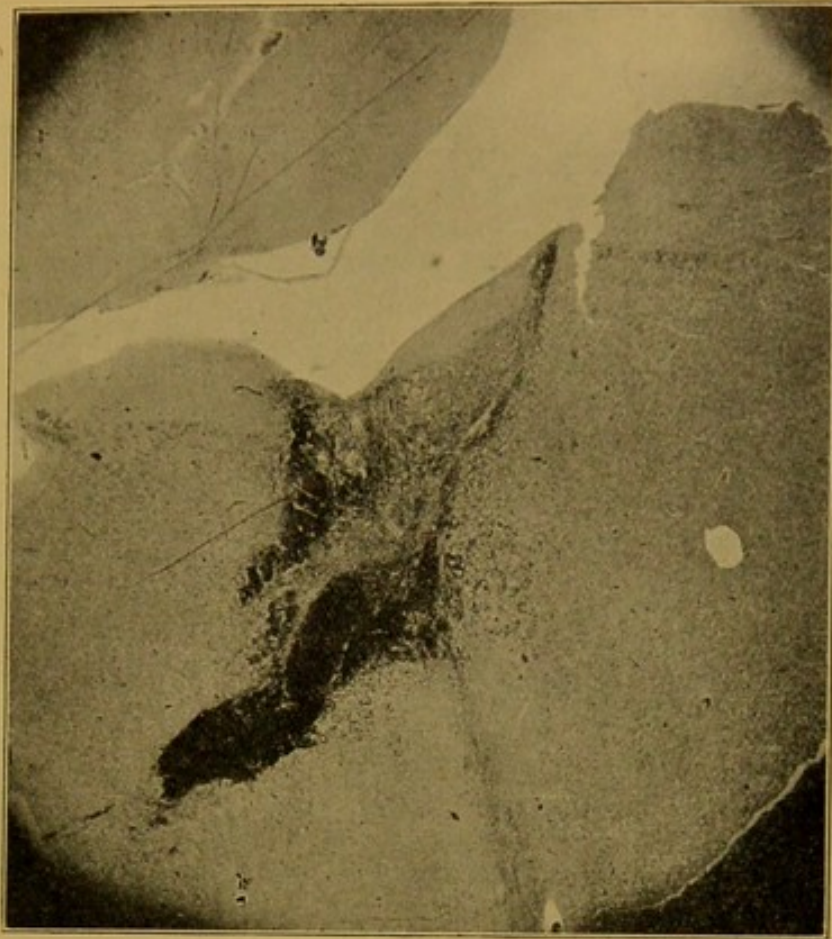
Fig. 11b.
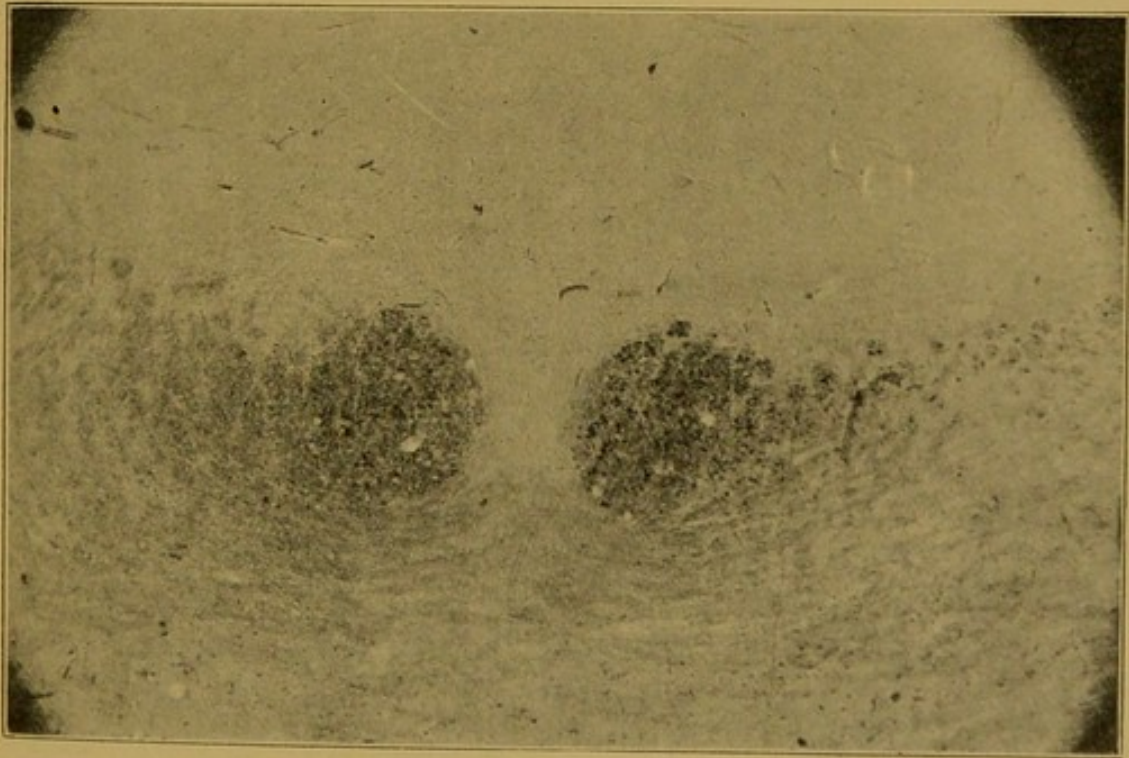
Fig. 11c.

FIGS. 11a, 11b, 11c.—Cross-sections of cat 90.

Figs. 11a and 11b.—Lesion of the posterior longitudinal bundles in the pontine region. Note destruction of the lateral horn on the right side.

Fig. 11c.—Ascending degeneration of the lateral horn on right side.
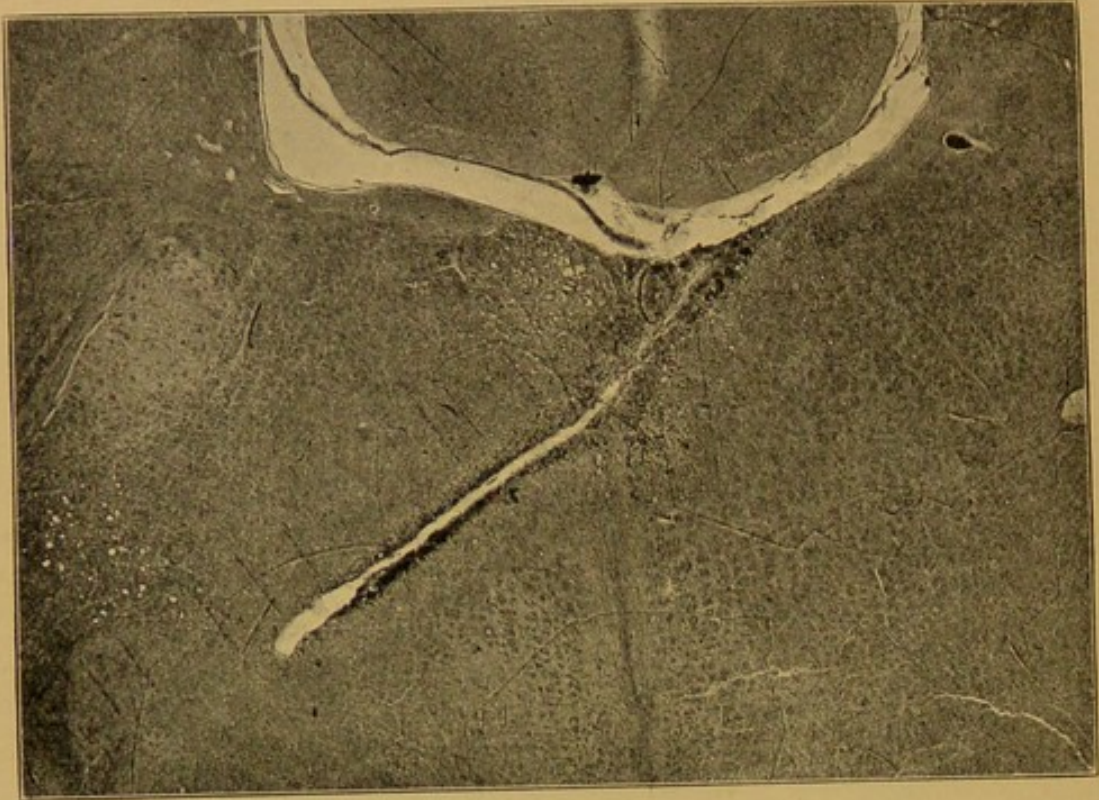
FIG. 12*a*.
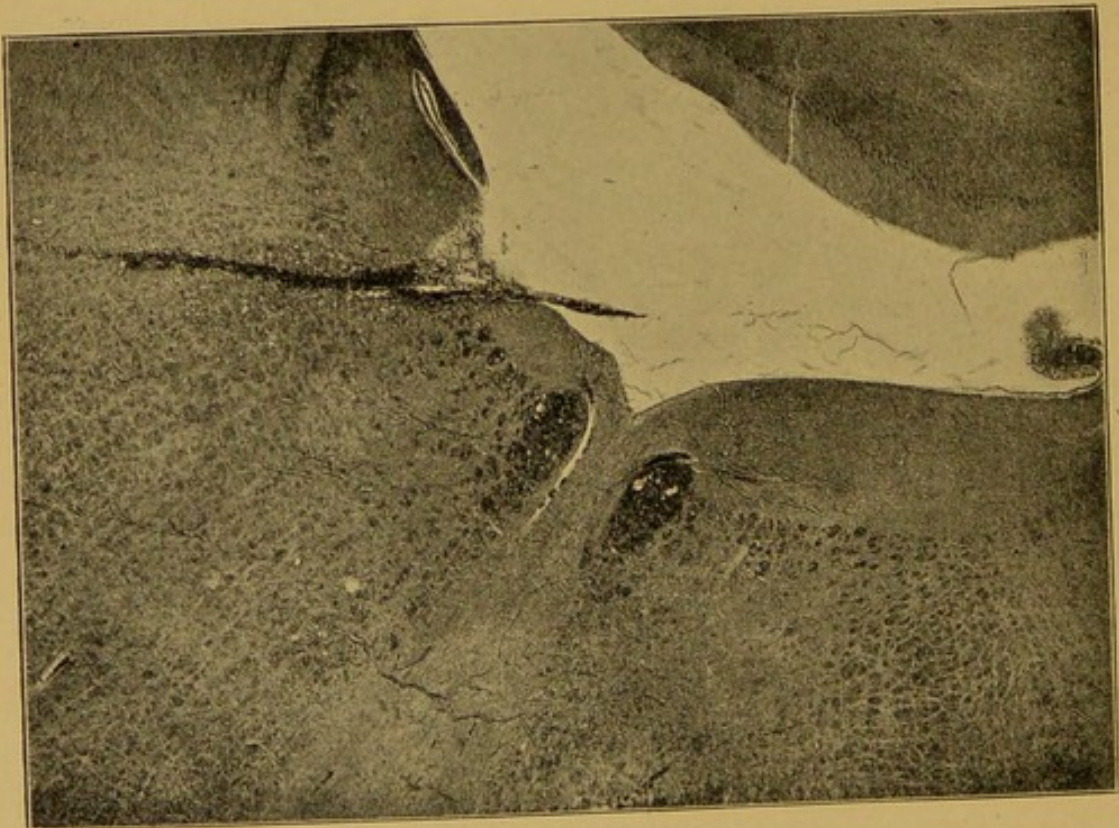
FIG. 12*b*.
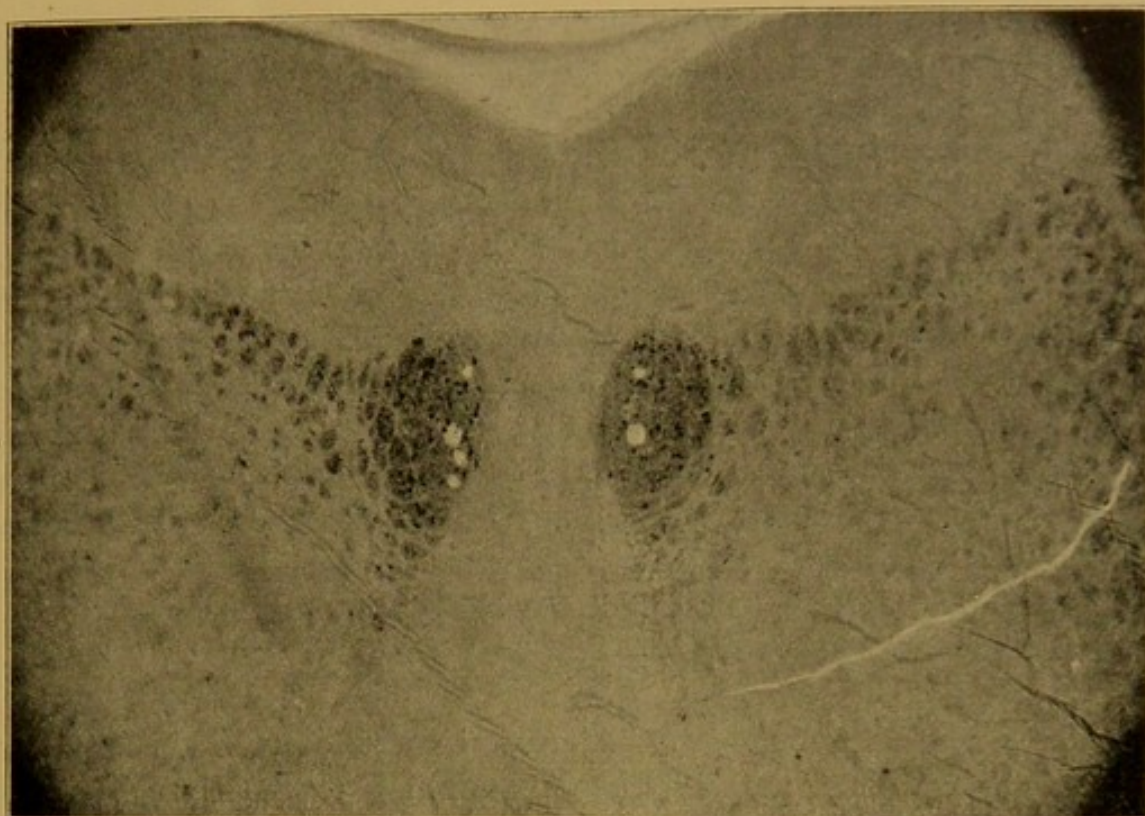
FIG. 12c.

FIGS. 12a, 12b, 12c.—Cross-sections of Cat 92.

Figs. 12a and 12b.—Lesion of the posterior longitudinal bundles in the pontine region. Note destruction of the lateral horn on the left side.

Fig. 12c.—Ascending degeneration of lateral horn on left side.

As has already been pointed out in Chapter I, § 3, it has not yet been possible to determine which part of the homolateral, and particularly of the heterolateral descending posterior longitudinal bundle fibres originate in the reticular cells (fasciculus reticulo-spinalis), and which from Deiters' nucleus.

§ 4.—*Lesion of the Lateral Horn of the Posterior Longitudinal Bundle (P.L.B.) or Fasciculus Deiters' Ascendens (F.D.A. of Lewandowsky and Winkler) (Table I, Group 9, p. 26).*

The following groups of experiments (Groups 9 and 10) concern the direct lesions of the lateral part of the posterior longitudinal bundle), which is acknowledged by Winkler [169], Lewandowsky [89], and van Gehuchten [63], to be an anatomical entity, and named by them the fasciculus Deiters' ascendens (F.D.A.), or faisceau triangulaire.

Special attention should be paid to experiments Nos. 90 and 92 (cf. the diagrams of the table, Group 2, and the figures 11c and 12c),

because in those animals both the posterior longitudinal bundles were cut between the sixth and fourth nuclei. In No. 90 the *right* fasciculus Deiters' ascendens was also cut (figs. 11a, 11b), while in No. 92 the *left* fasciculus Deiters' ascendens was cut (figs. 12a and 12c).[1]

We here observe a remarkable parallelism between the physiological and anatomical data given in the table. In Case 90, where the right fasciculus Deiters' ascendens was severed, it showed degeneration upwards to the right, while the animal displayed a rolling movement to the right side. In Case 92 the left fasciculus Deiters' ascendens showed degeneration upwards to the left, while the animal also displayed a rolling movement to the left side.

In not a single case was there any trace of a lesion in either the vestibular root, Deiters' nucleus, or the ramus descendens of the eighth nucleus, which might be the cause of this phenomenon.

In Case 114 both the posterior longitudinal bundles were severed orally to the fourth nucleus, while the right fasciculus Deiters' ascendens was also cut. In this case it was only in epileptic fits induced by camphor monobromate that falling to the right side was observed.

In the next five experiments the extreme lateral part of the fasciculus Deiters' ascendens was either injured directly, or it was found degenerated in consequence of a lesion of Deiters' nucleus associated with extirpation of a cerebellar hemisphere.

In some cases, such as No. 150 (cf. also Quensel's case No. 1 [128]), only the extreme lateral fibres of the fasciculus Deiters' ascendens were affected on one side, yet the animal showed a decided tendency to fall to the same side. In such cases the ascending degeneration can only be followed for a short way, which evidently shows that these lateral fibres lose their sheaths immediately they enter the region of the posterior commissure.

It is not necessary to go further into detail concerning these experiments, seeing that the diagrams of the table (Group 9) furnish all the necessary data.

From a consideration of the data it seems probable that there is a vestibular ascending bundle (or one of several such bundles) in the lateral part of the fasciculus Deiters' ascendens, which controls the

---

[1] As regards the circus movements to the right shown by Case 90, it should be remembered that in this animal hæmorrhage ensued into the posterior longitudinal bundle, which presumably caused an unequal lesion of the mesial parts of the posterior longitudinal bundles, causing circus movement.

rolling movements to that side. This bundle may be termed the fasciculus vestibulo-tegmentalis lateralis.

From the results obtained after lesion of the principal division of Deiters' nucleus (Chapter III, § 3), it may be deduced that the medium or small cells of the dorsal division of Deiters' nucleus (that is Deiters' nucleus in the narrow sense) constitute the origin of this bundle. This conclusion is come to in consequence of the total degeneration of the giant cells seen after hemisection of the cervical cord (v. Monakow [104]).

In numerous other lesions made in the pontine region I have never observed any rolling movement when the vestibular nuclei and their ascending systems remained intact. I can further confirm for one experiment the observation of Spitzer and Karplus [150], that a longitudinal incision in the middle cerebellar peduncle is not associated with circus movements.

§ 5.—*Lesion of the Mesial Part of the Fasciculus Deiters' Ascendens (F.D.A.). (Table I, Group 10, p. 26).*

Among the numerous experiments in which lesions were made in the region oral to the Deiters' nucleus, there are certain cases which are in apparent conflict with the results discussed in the foregoing paragraph as regards the physiological phenomena, and also, I believe, as regards the anatomical data.

In none of these cases did the rolling movements actually appear. At most there was a tendency for the animal to roll or fall on to the non-operated side. In Case 91 there was found only a slight degeneration of the left vestibular root and of the right Deiters' nucleus which might possibly account for this phenomenon.[1]

In the other cases I can assign no cause for this tendency to fall towards the normal side.

In these three cases under consideration there is an ascending degeneration predominating in the mesial part of the fasciculus Deiters' ascendens which appears to me to afford good ground for supposing that

[1] Although I have considered it necessary for the physiological analysis of the posterior longitudinal bundle to exclude all the cases in which collateral injury of the vestibular roots and Deiters' nucleus occurred, it yet appears highly improbable in Case 91 that the slight lesion of these parts was the cause of the protracted inclination to fall to the non-operated side. If we accept this, the case would bear out what is maintained in this paragraph. In Case 68 the objection is justified that the same injury which caused degeneration of the descending fifth root and of the restiform body on the right side, may have involved the descending eighth root on the same side.

there is an ascending vestibular connexion with this part of the fasciculus Deiters' ascendens, which controls the rolling movement to the healthy side (fig. 13).

In these cases there is a moderate descending degeneration in the spinal posterior longitudinal bundle of the same side, down to the dorsal region.

There are, however, too few cases to allow of any positive conclusions being formed as to the existence of such a bundle.

Should further investigation, however, confirm this supposition, the bundle might appropriately be named the fasciculus vestibulo-tegmentalis medialis. (Cf. the ascending degeneration in the posterior longitudinal bundle on the left side in Case 91, fig. 13, and Case 158, fig. 10*b*, respectively.)
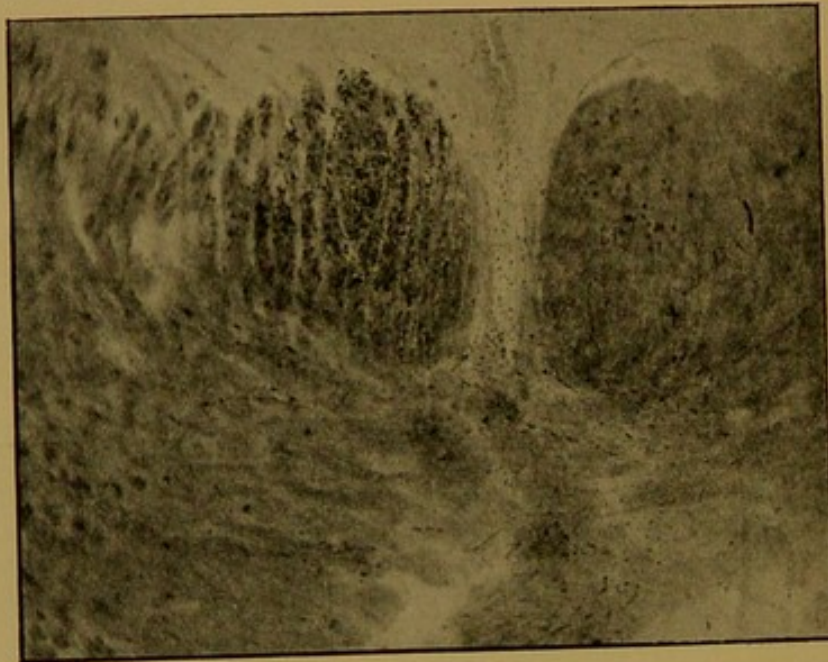
FIG. 13.—Taken from cat 91 (Table I, Group 1, p. 26). Ascending degeneration after section of the posterior longitudinal bundle on left side. Note degeneration of fibres on the left side of the area in fig. 3*b*.

If the experiments and anatomical data contained in Chapter III, § 2, be considered, it would seem possible that the cases dealt with in this section demonstrate a secondary ascending connexion of the descending ramus of the vestibular nucleus. As evidence in support of this view are the three cases (VIII, Nos. 18 and 35) where, after lesion of this part of Deiters' nucleus rolling movements to the non-operated side followed. As, however, it was impossible in these three cases to determine positively that there was an ascending degeneration in the posterior longi-

tudinal bundle after lesion of the ramus descendens, with the Marchi method, one is not justified in drawing any further conclusions. Unless we can assume that the axons which ascend from that part of the vestibular nucleus form a synapse with an adjoining group of cells— e.g., in the nucleus triangularis or nucleus raphe—we are unable to explain the exceptional behaviour of the ramus descendens as compared with all other primary centres of the vestibular nerve. In the light of the physiological facts brought forward in §§ 4 and 5 of this chapter, it is interesting that according to Cajal (vol. ii, p. 267) the collaterals from the posterior longitudinal bundle to the fourth nucleus take their origin, without exception, from the *lateral* parts of the posterior longitudinal bundle.

Chapter IV.—A Centrifugal Bundle which controls the Rolling Movements to the Non-operated Side.

In Chapter II the material of this investigation was considered with reference to its bearing on the supposition of several authors, anatomists, physiologists, and clinicians, that not only the centripetal bundles which control the equilibrium of motion in the horizontal plane form an important part in the posterior longitudinal bundle, but that the tracts which control that function in a centrifugal sense also find a place in this structure. Table II, p. 28, certainly contributes fresh evidence in favour of this supposition. In those animals where a lesion of the ventral part of the mid-brain is associated with circus movements towards the side of the lesion the probability is certainly furnished of the existence of a descending bundle which originates in the region of the posterior commissure. The experiments not only confirm the law of Schiff and Probst (" after hemisection of the posterior part of the optic thalamus circus-movements follow to the side of the lesion "), but they furnish experimental data which tend to prove that in such cases the lesion of a certain group of cells and the consequent degeneration in the extreme mesial part of the posterior longitudinal bundle are responsible for this form of forced movements. The conclusion is therefore arrived at that the maintenance of the equilibrium in the *horizontal* plane is assured by a double system of ascending connexions situated on either side of the mesial line, and also by a descending tract between the posterior commissure and the region of the vestibular nuclei. This system of tracts shows distinct connexions with the nuclei of the ocular nerves, which are quite sufficient to

explain the conjugate deviation of the eyes in the horizontal plane which regularly accompanies the circus movements.[1]

Owing to the descending connexions with the medulla oblongata, the concomitant action of the neck, trunk, and extremities may be regarded as assured. By means of this double system the compensatory movements of the head and eyes are accomplished after unilateral lesion of the tracts, either ascending or descending, which are associated with circus movement and conjugate deviation in the *horizontal* plane of the eyes.

In conclusion, the experiments made in connexion with this investigation are examined as to their bearing on the question of the arrangements for rotatory movement, or locomotion in a plane vertical to the long axis of the animal. Is there an arrangement of tracts similar to that involved in the forced movements already discussed?

Physiologists, anatomists, and clinicians have shown less interest in this problem than in that dealing with the circus movement and conjugate deviation in the horizontal plane. This is partly due to the fact that this particular form of conjugated deviation (Hertwig-Magendie squint) is only rarely met with in pathological conditions, and also because the rolling and allied phenomena seen in physiological experiments are but very imperfectly understood.

Vulpian [159], Schwahn [145], Russell [138], and recently Biehl [21], have proved that as a forced movement or as a forced position it

---

[1] The conjugate deviation of the eyes and neck is directed, as a rule, towards the same side as the circus movement, but Grasset [66] maintains there are exceptions to this rule. This author observed a case where there was conjugate deviation of the eyes to one side and lateral deviation of head to the other side. He ascribed this occurrence to an uncommon combination of lesion in different tracts. A case which illustrates this better is that reported by Kooyker [83] where a hæmorrhage had occurred in the upper part of the internal capsule on the right side. As a result, there was conjugate deviation of eyes to the right and deviation of the head to the left side so long as the symptoms of irritation were present. It must be admitted that besides the destruction of some tracts others were probably subjected to irritative lesions. (Cf. Chapter VII.)

Another very common combination in all classes of vertebrates (cf. 211 and 217, p. 107) is circus movement to one side and rolling movement to the other. This is, of course, easily explained by the peculiar arrangement of the ascending vestibulo-mesencephalic and the descending mesencephalic tracts (fig. 14). This rule also has its exceptions which can be accounted for by an unusual combination of lesion. Thus in No. 108 (cf. Group 11 of the table) the interstitio-spinal tract on one side and the commissuro-medullary tract on the other side are degenerated, while the animal shows a rolling movement to the left side, combined with a circus movement to the same side. In sharks and frogs I found this association of circus movements to one and rolling movements to the other side a very common combination; also in octopods after extirpation of one otolith [110]. It is of interest to note that equally in crustaceans unilateral lesions of the central plexus is associated with circus movement to the intact side and rolling movement to the other side [47].

appears especially after lesion of the restiform bodies.[1] Hogyes [70], and Kubo [84] have noted this form of squint as a reflex phenomenon brought on by certain passive rotations of the head. Hunnius [75], MacGregor [97], and Stewart and Holmes [71], have found it in cases of cerebellar and pontine tumours. Friedberg [60] and Meynert also observed true rolling movements. In diseases of sheep it appears to have distinct diagnostic value [152]. An extensive literature such as there is on the subject of conjugate deviation in the horizontal plane is quite lacking.

The rare occurrence of the skew deviation in the higher organized animals with a combined visual field is explained by Clarke, working in Horsley's laboratory, as a vestigial trace of a former phylogenetic condition where this form of squint was a useful reflex mechanism associated with monocular vision ! Where so little is known about the phenomenon and the centripetal tracts controlling it in experiment or in disease, it is not surprising that, so far as I am aware at least, the problem as to whether there exists a tract or centre, the descending degeneration or lesion of which is associated with a rolling movement round the axis of the body and other minor allied symptoms, has not arisen. This problem is embodied in the question as to whether in the present investigation there is any experimental evidence of a descending tract originating from a centre in the region of the posterior commissure which when degenerated is associated with rolling movements and allied phenomena.

The Table II and Chapter II afford information about the tracts which were found to be degenerated in or about the posterior longitudinal bundle after lesion in the region of the posterior commissure. They are : (1) the fine fibred commissuro-medullary bundle ; (2) the thick fibred interstitio-spinal tract ;[2] (3) the bundle lateral to the posterior longitudinal bundle described by Probst, Economo and Karplus, and van Valkenburg [158]. From the physiological analysis

---

[1] The author disposes of several extensive degenerations of this body in animals that performed no forced movements.

[2] The interstitial nucleus was recognized to be an anatomical entity in fishes by Fritsch and Mayser before Cajal (1896) described it ; the nucleus commissuræ posterioris, lying caudally to the radiation of the posterior commissure, by Darkschewitsch. The commissuro-medullary tract was not, so far as I am aware, described until my paper appeared in 1912 [108]. In this paper I described the origin and termination of this tract, and of the interstitio-spinal tract of Boyce and Cajal (1895). The same subject was dealt with in a second paper which was published in 1913 [109]. The existence of the commissuro-medullary tract was, however, strongly indicated by the interesting data collected by Kohnstamm and Quensel [80] on axonal reactions in the commissural region after a lesion of more caudal parts.

of the cases where circus movement was found, it seemed highly probable that the commissuro-medullary bundle is the centrifugal tract controlling this movement.

In this connexion (rolling movements) we have to consider the second and third of the descending bundles especially. If the cases where the rolling movements or some of the allied minor phenomena were maintained for a longer period be picked out, then the Cases 107 and 108, the case of Probst and that of cat No. 3, recorded by Economo and Karplus, stand apart. From the consideration of these cases it was concluded that the interstitio-spinal tract was degenerated on the side of the lesion in the post-thalamic region. Further, in these animals the rolling movements or allied phenomena were always towards the normal side. The question now arises : Is this a simple coincidence or is the rotation dependent on the degeneration of the centrifugal limb of a reflex mechanism for the equilibrium in the plane vertical to the long axis of the animal?

As yet I do not consider that sufficient evidence has been collected to allow of a definite decision being come to on this point, but the question is one well worthy of further investigation.

Only in very localized lesions in the region of the posterior commissure was it possible to localize the probable origin of the interstitio-spinal tract, as the Marchi method in most cases is worthless for recognizing definite cell groups.

Case 108 (fig. 7) afforded evidence for determining the lateral boundary of the origin of this tract, while Case 23 afforded evidence for the dorsal boundary. From such evidence the identity of this nucleus and tract with that described by Cajal is established, while they are definitely differentiated from the nucleus of the posterior commissure and its commissuro-medullary bundle.

The tract lateral to the posterior longitudinal bundle was first described by Probst [124, vol. xxiii, p. 54], and later by Economo and Karplus [78], and Besta [17]. It consists of a bundle of widespread delicate fibres which originate in the præubral region, and, as shown in Case 108 (not in the figure), appear lateral to the nucleus interstitialis. It does not enter into relation with the third nucleus but descends on the same side latero-ventrally to the posterior longitudinal bundle, terminating in the ganglion tegmenti profundum (Gudden) immediately caudal to the fourth nucleus.

As already stated, I am not prepared either to deny or affirm that this tract has anything to do with the functions discussed in this paper.

I would, however, point out that it is exceedingly improbable that this tract corresponds with the descending tract of Collier and Buzzard [42], since in my preparations none of its fibres descend lower than the pontine region.

A study of the various lesions of the posterior commissure described by the above-mentioned authors and myself, leads to the conclusion that these fibres do not cross the commissure or the raphe. From the direction of the fibres it would seem that they originated in the nucleus intra-commissuralis of the same side, which lies in the middle of the commissure, antero-posteriorly. This nucleus, according to Kohnstamm [80], does not degenerate after hemisection of the cord, but after lesion of the brain-stem. Economo and Karplus [78], however, advance the theory that this tract originates in the corpus mammillare (p. 395, cat No. 3), while also the observations of Probst, Lewandowsky, Flatschek and van Valkenburg [158] seem to lend confirmation to the view that it is part of the tractus mammillo-tegmentalis.

On the whole the results of the present investigation tend to show that a lesion of the nucleus interstitialis (Cajal) is followed by a rolling movement towards the opposite side from the lesion. This direction of the movement is in agreement with the results obtained by v. Bechterew [10] in his experiments on the infundibular region in dogs.

In these cases the fasciculus interstitio-spinalis was found degenerated with such regularity that it seems highly probable that it contains the centrifugal limb of the superimposed vestibular reflex arc dealing with this function. Knoll [79] and Topolanski [155] by electrical stimulation of the region of the posterior commissure caused rolling movements towards the side of the irritation, i.e., opposite to the direction observed in my cases of direct lesion[1].

In this connexion it may be recalled that hemisection of the base of the mid-brain of the frog and fishes causes, according to Steiner, circus movements towards the non-sectioned side; this again is in accordance with our results with section of the posterior longitudinal bundle caudal to the nuclei of the posterior commissure. According to my own experiments on frogs and sharks the accordance between the experiments in lower and higher animals in this structure goes still further, in that also the lower animals, in performing this circus

---

[1] Pathological observations regarding this matter seem to be wanting. The only case, so far as I know, which was examined with the Marchi method was Case 4, recorded by Roussy [135], where the left eye is described as turned downwards, while the fasciculus interstitio-spinalis was degenerated.

movement, show a tendency to roll to the side of the lesion (cf. Flourens and Baudelot). A fundamental difference in these groups of animals lies however in the fact that in the lower ones no lesion oral to the commissura posterior brings about forced movements, whereas in the higher animals they do, the direction of these movements being inverse to that caused by a lesion of the posterior longitudinal bundle. Physiologically speaking, we have probably to deal here with a very old phylogenetic arrangement. At least it is interesting to note that Wallenberg [164, p. 393] came to the conclusion, on purely anatomical grounds, that the ventro-median part of the thalamencephalon of vertebrates subserves octavo-lateral functions, and is phylogenetically of far older date than the dorso-lateral part, which represents a recent acquisition and is associated with somatic sensory impulses.

The literature on the effects of the prosencephalon on conjugate deviation in the lower animals is very scanty and unsatisfactory. Boyce and Warrington [29] observed that in birds stimulation of the lateral ventral part of the fore-brain, or the origin of the strio-mesencephalic tract, is associated with conjugate deviation of the head and eyes to the other side. In fish, amphibians, and reptiles, both the free movement of the head and neck in the horizontal plane and the cerebral centre for this movement are probably too poorly developed to allow of the demonstration of conjugate deviation by electrical stimulation of the striate connexion of the posterior commissural nucleus. It has been shown above that in these animals, as in birds, the removal of one cerebral hemisphere does not produce the circus movements or conjugate deviation towards the side of the lesion seen in all the higher vertebrates (cf. Chapter VI).

CHAPTER V.—CONCLUSIONS AND DISCUSSION OF RESULTS.

§ 1.—*Plan adopted.*

The main object of this paper is to attempt to analyse the complicated vestibular system with its ascending and descending connexions by physiological and anatomical methods. Since it was demonstrated in a former investigation that a lesion of the posterior longitudinal bundle is primarily associated with two forced movements, it seemed possible that a study of these movements might help to elucidate a number of fundamental points, about the structure and function of Deiters' region and the posterior longitudinal bundle formation, where

a purely anatomical analysis fails.[1] Thus Flechsig, v. Bechterew, Ziehen, and particularly Hösel [72] have drawn attention to the fact that some strands in the medulla and the posterior longitudinal bundle are the first to become myelinated. The presence of the posterior longitudinal bundle as a separate tract even in the lowest vertebrates, including the eyeless mammals, is but imperfectly understood. Further, it has long been known [116] that in embryonic rays, as soon as locomotion is possible, a fine puncture involving the posterior longitudinal bundle region causes vehement rolling movements so long as the umbilical cord permits.

These facts led us to adopt the phenomena observed after a localized lesion of the posterior longitudinal bundle formation as a starting point for such an analysis.

§ 2.—*Forced Movements and Semicircular Canals.*

In this analysis the vestibular nuclei must be considered as a system of cell masses, each one of which controls the condition of equilibrium in one of two different planes,[2] and is provided with separate ascending and descending connexions.

Flourens [57], Spamer and particularly Breuer [31] and Kubo [84] have proved that irritation of any semicircular canal elicits movements in the plane coinciding with the canal experimented upon. Breuer and Kubo lay stress upon the fact that movement of the labyrinthine fluid towards the ampulla causes reflexly a conjugated movement of the eyeballs, in the direction opposite to that caused by movement of the fluid from the ampulla. Ewald [52] equally insists that each labyrinth rotates the head and eyes to either side. Each canal therefore should have a double representation in Deiters' complex. Hence in the schematic representation of the results of this investigation (fig. 14),

---

[1] Although I personally prefer the Marchi method (Busch's modification) to any other, even to the combination of the Marchi and Nissl methods, which is increasing in popularity, yet I consider it inadequate to decide such questions as to whether the vestibular fibres terminate in Deiters' nucleus proper or not. In this region one is particularly liable to fall a victim to false conclusions, since any lesion of the posterior brain cavity, even the removal of the bone, may bring about slight degenerations in the cell masses. Here therefore is an opening for anatomo-physiological research, based upon a large number of experiments.

[2] In this communication the cell masses and ascending connexions which control forced movements in the third plane, that is the plane coinciding with the long axis of the body vertical to the horizontal plane and in which tumbling and staggering occur, are not discussed.

4

a close functional relation is anticipated between the horizontal canal and Deiters' nucleus (triangular part), together with Bechterew's nucleus, and also between the anterior vertical canal and the descending branch of the nucleus vestibularis, together with the dorsal part of Deiters' nucleus. Should this relationship prove to be anatomically correct it does not of course indicate that the two forced movements, conjugated deviation and reflex nystagmus, coincide with the planes of the canals. It is almost certain that the anatomical arrangement of the skull and the customary mode of progression of the animal will also play a part. The latter factor will undoubtedly influence all reflex phenomena dependent on the vestibular system [32]. It may also be responsible for the prevalence of rolling movements after labyrinthine lesions in most vertebrates [1] for, according to Breuer [31], the mobility of those animals is most dependent on equilibration, in the plane vertical to their long axis. Biach and Bauer [19] came to a similar conclusion, a result of their own experiments and those of Marburg and Bing on the ascending spino-cerebellar tract. In my schematic diagram (fig. 14) no reference is made to the otoliths which are probably, as Breuer [31], Kreidl and Kubo [84] believe, connected with the perception of linear movement, while the semicircular canals are associated with the perception of angular movement. Both organs are evidently closely associated in their action, and there is no doubt that hardly any movement of the head is associated with the stimulation of one semicircular canal only (Ewald [51]).

§ 3.—*Character and Mechanism of the Forced Movements, in Lower and Higher Animals.*

Although in the anatomical and physiological analysis of the posterior longitudinal bundle formation dealt with in this paper, parallels have more than once been drawn between the two forms of forced movements, it must be borne in mind that, from a physiological standpoint, the character of these movements, circus and rolling, is very different. The rolling movements when present and well developed are mostly characterized by their vehement nature, while the circus movements are

[1] An exception to this rule is found in turtles, where the shape of the carapace prevents any falling to the side. In these animals even lesions in the region of Deiters' nucleus do not apparently cause true rolling movements (Fano, Bickel [20]).

quieter and more deliberate. Where both are present in a medullary lesion the rolling movements are nearly always the more conspicuous, in fact it is only after the rolling movements have been partly compensated for that the tendency to go to one side manifests itself ; if both are present in thalamic and quadrigeminal lesions, the circus movements are far more pronounced.

Usually, owing to the peculiar arrangement of the ascending and descending tracts in the posterior longitudinal bundle formation, subserving these functions, circus movement to one side is accompanied by rolling movements to the other side. This rule has in a large number of experiments its exceptions, owing to peculiar situation of the lesion. On this ground, as on many others, Brown-Séquard's and Prévost's doctrine on the identity of the two types of forced movements can no longer be maintained. This theory has until very recently found supporters amongst physiologists.

In a physiological sense, there are even more points of difference between the two forms of forced movement. Goltz has shown that after bilateral section of the cerebrospinal stem in the frog, the hind part of the brain which is still in connexion with the vestibular apparatus is sufficient to maintain equilibrium in the vertical plane, vertical to the long axis. If the animal be laid on its side it returns to the normal position, executing a rolling movement. From this the conclusion seems inevitable that for the maintenance of the equilibrium in the plane vertical to the long axis of the animal the peripheral reflex arc in the frog (anterior vertical canal—Deiters' complex —descending tracts into the spinal cord) is endowed with a certain amount of autonomy. It has not yet been proved that the lower vertebrates have like the higher a mesencephalic reflex arc in the posterior longitudinal bundle formation, which, with the medullary reflex arc, dominates the compensatory movements in the vertical and horizontal planes, but it is possible that such an arc does exist. It is noteworthy that in the lower vertebrates the direction of the forced movements does not change when the lesion extends to the region of the posterior commissure.

As to the higher animals, attention may be here drawn to the fact that both the peripheral reflex centres (for both types of forced movements) are provided with spinal axons, but far more important in one case than in the other. It may be recalled that the axons from Deiters' nucleus, as well as those from the nucleus interstitialis, descend into the sacral region, while from the Bechterew nucleus and from the nucleus commissuræ posterioris, they rarely reach beyond the cervical

region.[1] If these physiological and anatomical differences be kept in view, and also the opinion urged by Breuer that the equilibrium in the plane vertical to the long axis of the animal is extremely delicate, more especially in quadruped vertebrates, and therefore in need of constant adjustment, it is evident that the different characteristics of the forced movements after cerebral lesion appear in a new light. The fact that distinct rolling movements are never observed after cortical lesions of the cerebral hemisphere supports the view taken by Hughlings Jackson, that the cerebellum acts as a reinforcing organ for the function of gait and station represented in the mesencephalon, independently from the pyramidal tracts. Prus [127], in his experiments, demonstrated that the co-ordinated running about movements induced by stimulation of the lenticular nucleus are not interfered with by section of the pyramidal tracts.

Further the experiments of Mingazzini [101], Probst [123], Karplus and myself, all furnish evidence in favour of the view that the pyramidal tracts have little influence on locomotion in the quadruped.

The readjustment of the normal position in a plane vertical to the long axis of the animal requires an instantaneous activity of its reflex arcs. I hold that the tonic influence of the cerebellum [Luciani 95] by virtue of its relationship with the vestibular and kinæsthetic impulses (Jelgersma, Lewandowsky, and Lusanna's doctrine) is an indispensable factor. Its absence in cerebellar disease has lately been clearly demonstrated by Babinski's adiadokokinesis. Thomas [154] and Cajal rightly insist that the reflex arrangement, which brings about instantaneously the compensatory movements that ensure the maintenance of the equilibrium during any voluntary movement, largely depends on vestibulo-cerebellar connexions and the cerebellum. Whether, as Bolk [26] and van Rynberk [139] think, this function has a definite localization in the cerebellar lobes is uncertain, but it seems rather probable, since the afferent tracts are not spread diffusely over the entire organ. Magnus and de Kleyn's labyrinthine reflexes depend probably exclusively on our peripheral reflex arcs, which, by virtue of the transverse section in the mid-brain, have acquired a certain amount of autonomy.

[1] It is also very interesting to note the fact recorded in the paper of Magnus and de Kleyn [98] that rotation of the head influences reflexly the innervation of the extremities and consequently their position. Lateral deviation in the same mammals has, on the other hand, no apparent influence.

§ 4.—*Forced Movements after Lesion of Deiters' Complex and Ascending Connexions.*

As the result of experiments on different parts of Deiters' complex, the following conclusions have been come to. As regards locomotion in the horizontal plane :—

(1) Circus movement *towards the affected side* is seen after lesion of the triangular part of Deiters' nucleus and after destruction of its *crossed* vestibulo-mesencephalic tract, originating in this nucleus.

(2) The circus movement, or rather conjugate deviation, is *towards the non-affected* side after lesion of Bechterew's nucleus and the *homolateral* vestibulo-mesencephalic bundle which originates in this nucleus.

It is therefore physiologically demonstrated that there is a functional difference between these nuclei and also between their ascending and descending connexions.

As regards the locomotion in the vertical plane, vertical to the long axis of the body, experiments on the ramus descendens of the vestibular nucleus and on the magno-cellular dorsal portion of Deiters' nucleus, or Deiters' nucleus proper, lead to forced movements in this plane.

(3) Rolling movements *towards the affected side* are seen after lesions of Deiters' nucleus proper, and the lateral horn of the posterior longitudinal bundle *of the same side* or tractus vestibulo-tegmentalis lateralis, that originates in that nucleus.

(4) Rolling movements *towards the non-affected side* appear to occur after lesion of the descending branch of the vestibular nucleus, and also, it appears, in some cases after a local lesion in the mesial portion of the lateral horn of the posterior longitudinal bundle on the same side. This bundle, if proven to exist, may probably be termed the tractus vestibulo-tegmentalis medialis.

From these anatomical and physiological facts we are inclined to infer that the horizontal and anterior vertical canals of each side are doubly represented in the vestibular complex of that side.

§ 5.—*Localization of Tracts in the Posterior Longitudinal Bundle Formation.*

In fig. 14 the relative positions of the six tracts which lie in the posterior longitudinal bundle formation and control the forced

Comm. post.

Striatal connections (glob. pall.?)

Nuc. commiss. poster.

Nuc. interstitialis

Fasc. commissuro-medullaris

Fasc. interstitio-spinalis

Fasc. vestibulo-mesenceph. cruciatus

Fasc. vestibulo-mesencephal. homolat.

Fasc. vestibulo-tegmentalis lat.

Fasc. vestibulo-tegm. medial. (?)

Nuc. Bechterew

Nuc. triang.

Nuc. Deiters

Canal horizont.

Canal vertic. ant.
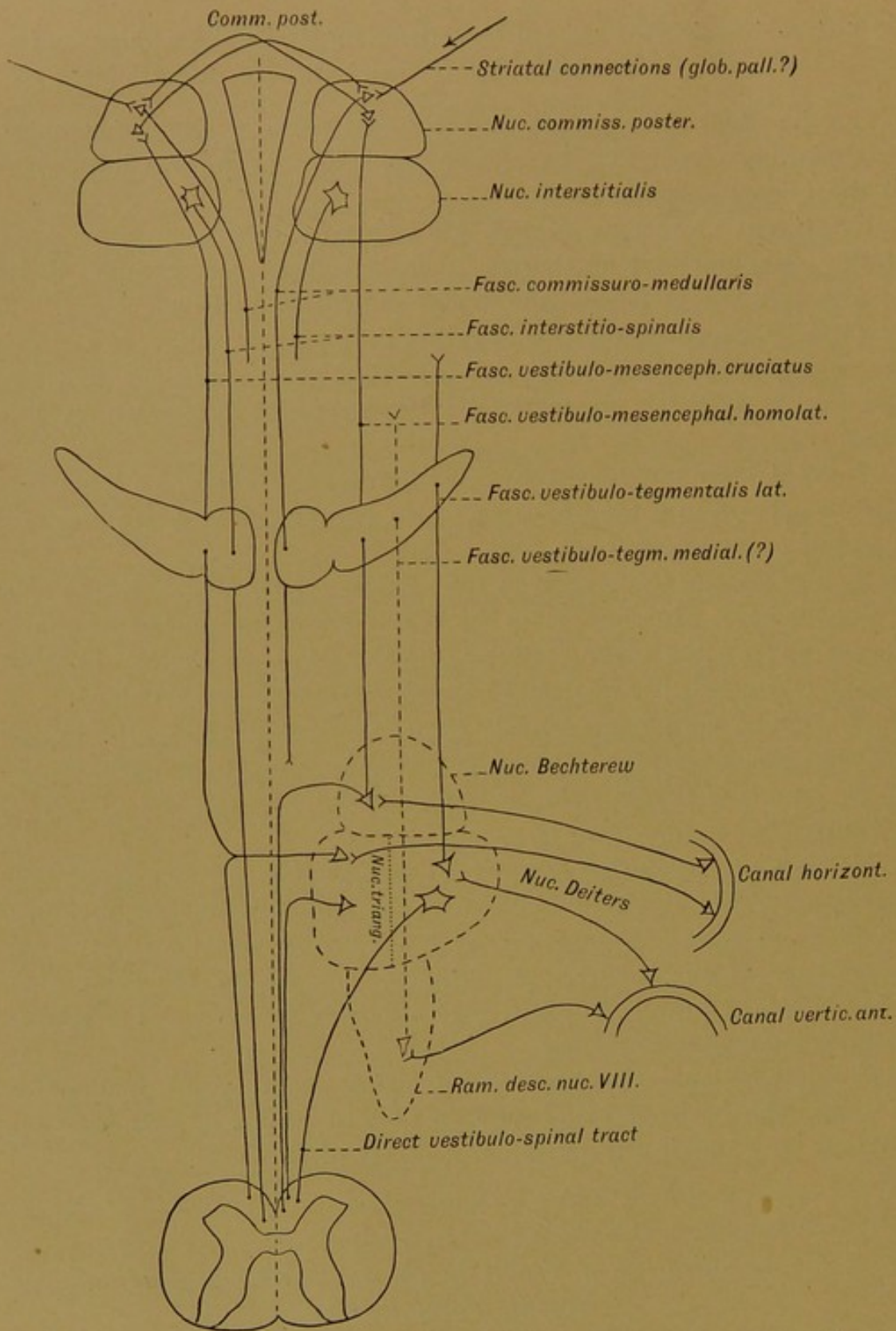
Ram. desc. nuc. VIII.

Direct vestibulo-spinal tract

FIG. 14.—Schematic representation of tracts and centres, discussed in this paper. According to Bernheimer, the hemispheral connections with the nucleus commissuræ posterioris should be exclusively crossed ones.

movements in the two planes[1] are demonstrated. In the innermost segment lies the finely granular tractus commissuro-medullaris and the coarsely granular tractus interstitio-spinalis. The rest of the posterior longitudinal bundle formation consists exclusively of centripetal tracts which ascend from Deiters' complex. The ascending fibres lying in the posterior longitudinal bundle are arranged in the following manner from within out: First is the crossed tract which ascends from the nucleus triangularis; next is the homolateral vestibulo-mesencephalic tract which ascends from Bechterew's nucleus. The tractus vestibulo-tegmentalis lateralis, which is an ascending tract from Deiters' nucleus proper, lies in the most lateral part of the posterior longitudinal bundle, while a tractus vestibulo-tegmentalis medialis, possibly originating from the ramus descendens, is supposed to lie mesial to it.

Generally speaking, therefore, the centrifugal fibres lie in the cat at the inner margin of the posterior longitudinal bundle. Next in order are the crossed fibres, and then the homolateral fibres (this agrees with Wallenberg's findings in birds). The bulk of the fibres of the posterior longitudinal bundle formation, oral to the vestibular complex, is therefore composed of tracts carrying centripetal impulses associated with the equilibrium of motion in the two principal planes. Since the centrifugal tracts which participate in the posterior longitudinal bundle formation appear to be equally associated with locomotion in these planes, the supposition advanced by Cajal, Spitzer [149], Kohnstamm [81], Hogyes, Marina [100], and others, that the posterior longitudinal bundle formation in the brain-stem and medulla is primarily associated with reflex locomotion in these planes, together with allied compensatory movements necessary for equilibration, seems justifiable.

The only nerves which besides the vestibular have an important reflex action on this system are the optic and acoustic (less so the olfactory) nerves; all three are situated orally to the vestibular complex. It is not surprising, therefore, that, as the researches of Wallenberg, Fraser [59], Probst, and Kohnstamm have shown, there are probably no centripetal fibres below the vestibular complex at all.

When the results of a series of lesions made in the posterior longitudinal bundle formation from the vestibular complex to the posterior commissure are considered from the physiological standpoint, two facts

[1] It will be shown, in a subsequent paper, that the forced movements in a plane vertical to the longitudinal axis of the animal, such as staggering and tumbling, are also controlled by similar nuclei and tracts. Wallenberg's basal olfactory bundle and its fibres joining the posterior longitudinal bundle and Tschermak's (from the central median nucleus?) ascending fibres in the same fascicle are not taken into consideration in this study.

become evident. First, the forced movements caused by ascending degeneration of the vestibulo-mesencephalic and vestibulo-tegmental tracts are of correspondingly shorter duration the nearer the lesion is to the posterior commissure. As a matter of fact, it has also been noted by v. Bechterew [12] and Lewandowsky [89] that forced movements after mesencephalic lesions are of a less pronounced character than those seen after lesion of the posterior longitudinal bundle formation, and of a far less pronounced character than those occurring after lesion of the vestibular complex.

This I formerly held to be due to the fact that the degeneration of the nerve-sheaths progresses at a certain rate, and the stimulation necessary for the production of those forced movements, being dependent on this degeneration, is naturally more transient the nearer the lesion is to the end station. It is interesting to note that, according to the statement by Kohnstamm and Quensel [80], the tigrolytic action is better marked the nearer the lesion of the axis-cylinder is to the end station. Since, however, I got convincing proof, from experiments in the thalamic region, that the forced movements of a longer duration are probably always due to a deficiency of the nerve influences on the one side and the unantagonized action of the analogous structures on the other side, a simpler explanation offers itself. It is this, the functional arrangement of the ascending vestibular system is such that the further the lesion is from the vestibular region the more easily and completely does the compensatory mechanism step in. This holds good particularly for rolling movements. We are not, however, prepared to give anatomical data in support of this generalization.

Secondly, it appears evident that in the higher mammals in a series of lesions, from below upwards, the direction of both forced movements changes abruptly as soon as the region of the posterior commissure is reached. In the lower animals (fishes and reptiles), on the other hand, forced movements are absent after lesions lying higher in the cerebrospinal axis than that commissure.

I held formerly that this change of direction of forced movements in higher mammals was due to the fact that the major irritation which is dependent on the ascending degeneration of the above mentioned tracts, and which acts by means of the posterior commissure on the heterolateral reflex centre, is put out of action, while the weaker stimulus of the descending degeneration of the commissuro-medullary and the interstitio-spinal tract comes into force. Later observations in lower animals led to the belief that in these simpler creatures the ascending vestibular system stops short in the mesencephalon ; where, as in the higher ones, the superimposed reflex centres are linked to newly acquired neurons in the striate body, thalamus and pallium (Ariens Kappers [3]). Hence in reptiles ablation of a cerebral hemisphere causes no circus movement

to the side of lesion, nor does faradic stimulation of the striate body cause conjugate deviation of head and eyes to the other side, as it does in all higher vertebrates, including birds.

CHAPTER VI.—FORCED MOVEMENTS AFTER A LESION IN THE MESEN-CEPHALIC AND THALAMIC REGIONS; THE SUPERIMPOSED REFLEX ARC AND ITS AFFERENT SYSTEMS.

As regards the constituents of the posterior longitudinal bundle formation, fresh evidence is afforded by the former chapters in support of the view taken by other workers that this bundle contains centrifugal as well as centripetal bundles, and further arguments are brought forward that these centrifugal tracts control the equilibrium of movement in two planes.

It appeared probable that the commissuro-medullary bundle is the carrier of the centrifugal limb of the superimposed reflex mechanism concerned with the circus movements, while the interstitio-spinal tract is considered the centrifugal one for the rolling movements.

In the controversy on the anatomical side of this subject, between Cajal [40] and de Lange, as to the mesencephalic descending fibres passing into the posterior longitudinal bundle formation certain statements made by both authors may be taken as correct. For example, Cajal describes a strand of fibres passing downwards from the interstitial nucleus in the innermost portion of the posterior longitudinal bundle, while de Lange [86] describes a similar strand of descending fibres in the same part of the posterior longitudinal bundle, but shows that it originates in the nucleus of the posterior commissure. As we have seen in Chapters II and IV, we deal here with two different tracts, each having its own origin and termination, the fibres from the interstitial nucleus passing far down into the cord, while those from the nucleus of the posterior commissure do not extend beyond the medullary region. Arguments are also brought forward to prove that the two tracts subserve different functions. From a study of the results following different lesions in the hypothalamic region and mid-brain, it would appear that forced movements which persist, mostly occur when the region of the nucleus interstitialis and the nucleus of the posterior commissure is injured. In such cases the tracts just described are more or less degenerated.

With these facts to go on one is led to a different conclusion from that arrived at by Boyce [28], who, in discussing the forced movements

and positions, observed after similar lesions, remarked, "It would of course be difficult, with the slight knowledge before us, to attempt an explanation of these phenomena"; Probst's similar opinion was expressed in 1900 [124].

Sufficient advance has been made in recent years in our knowledge of the minute anatomy of the brain, thanks to the London, Vienna, Paris, Frankfort, Madrid and Amsterdam[1] schools of anatomy, to ascertain some details of the anatomical structure of both the peripheral and superimposed vestibular reflex arcs. Two peripheral arcs on either side may deal with the compensatory movements in both the horizontal plane and the plane vertical to the long axis. Ascending fibres pass from those double systems to the mesencephalic or hypothalamic nuclei. The arrangement of the fibres, moreover, which pass to those nuclei from the posterior commissure and the cerebral hemisphere is such that a lesion of the nuclei, or of the region immediately oral and lateral to them, is followed by a change in the direction of the forced movements.

The question now arises, have we sufficient anatomical knowledge to trace out accurately the course of these secondary ascending vestibular fibres into the mesencephalic nuclei? It must be frankly admitted that the present methods for staining medullated nerve-fibres are inadequate.

In the case of rolling movements it is even more difficult to demonstrate a complete reflex arc than for circus movements. In the schematic drawing appended the vestibulo-mesencephalic tracts, which control the circus movements centripetally, terminate near the posterior commissural nucleus. So far, my efforts to trace the vestibulo-tegmental tract up to its nodular point have failed, although the nucleus interstitialis has been demonstrated, as far as this physiologically seems possible, as controlling the rolling movements centrifugally. It must, however, be remembered that the Marchi method, which was used, is only effective with myelinated nerve-fibres.

In order to judge by means of a method that brings the non-medullated nerve-fibres to evidence, about the anatomical connexions of the commissural nuclei (nuc. commissur. post. and nuc. interstitialis), I have, with Dr. Bok, carefully examined frontal and sagittal series of sections through chicks' brains, stained after Cajal's silver method. It was easy to confirm Cajal's statement

[1] Personally I feel particularly indebted to Dr. Ariens Kappers for his permission to use his private anatomical library and that of the Dutch Central Brain Institute, and to Prof. C. Winkler, and also Dr. van Valkenburg, for having more than once looked into my series of specimens, and to all of them for having given useful suggestions.

that the majority of neurites descend into the posterior longitudinal bundle, but besides that we found not rarely the axons take a direction towards and into the posterior commissure (ventral division). We saw no axons take an oral direction, but convinced ourselves that the dendrites of a good number of cells of the nuc. commissuræ posterioris are directed towards the oral and ventral parts. This suggests accepting the theory, defended by Tretjakoff and other anatomists, that the dendrites grow out towards the side from which the impulses arrive—that a good number of centrifugal striatal connexions exist in the chick at least that innervate the nuclei in question.

For the anatomical details of the mesencephalic nuclei themselves I must refer to the masterly description given by Ramon y Cajal [40] and to the work of Dejerine [44], who considers that they belong to the ganglia of the central grey matter. In my own investigations I have found, even in selachians, the characteristic large cells of the interstitial nucleus which spread over a large area, and the more definitely localized small-cell nucleus of the posterior commissure.

Passing next to the consideration of the physiological significance of the parts oral to those nuclei, we find that we must confine ourselves to the higher vertebrates, since only in this class does a lesion of the mesencephalic nuclei and the tracts cephalic to them cause forced movements at all, the direction of the movement being opposite to those associated with unilateral lesion of the posterior longitudinal bundle. In this connexion it is interesting to find that all authors are in agreement; in fish and amphibians (Steiner [153, p. 83]), reptiles (Fano [53] and Bickel [20]), and birds, ablation of one cerebral hemisphere is not associated with the development of forced movements. My own experiments, which deal particularly with cats, are in complete agreement with those of Schiff [144], who stated that no local cortical lesion is followed by circus movements which continue for any length of time. A lesion of the deeper parts, such as the striate body or the lateral parts of the thalamus, is, however, followed by circus movements, and conjugate deviation of the eyeballs towards the side of the lesion. This condition may persist for a longer period. It is interesting to note that the circus movement towards the side of the lesion is usually accompanied by a slight rotation round the bodily axis towards the non-operated side. This fact was also noted by Prévost [122]. From an examination of my own material I find in these cases a strand of degenerated nerve fibres, which runs in a latero-median and slightly antero-posterior direction through the external medullary lamina, spreads out in the field of Forel, and disappears near the frontal part of the red nucleus (figs. 15a and 15b).
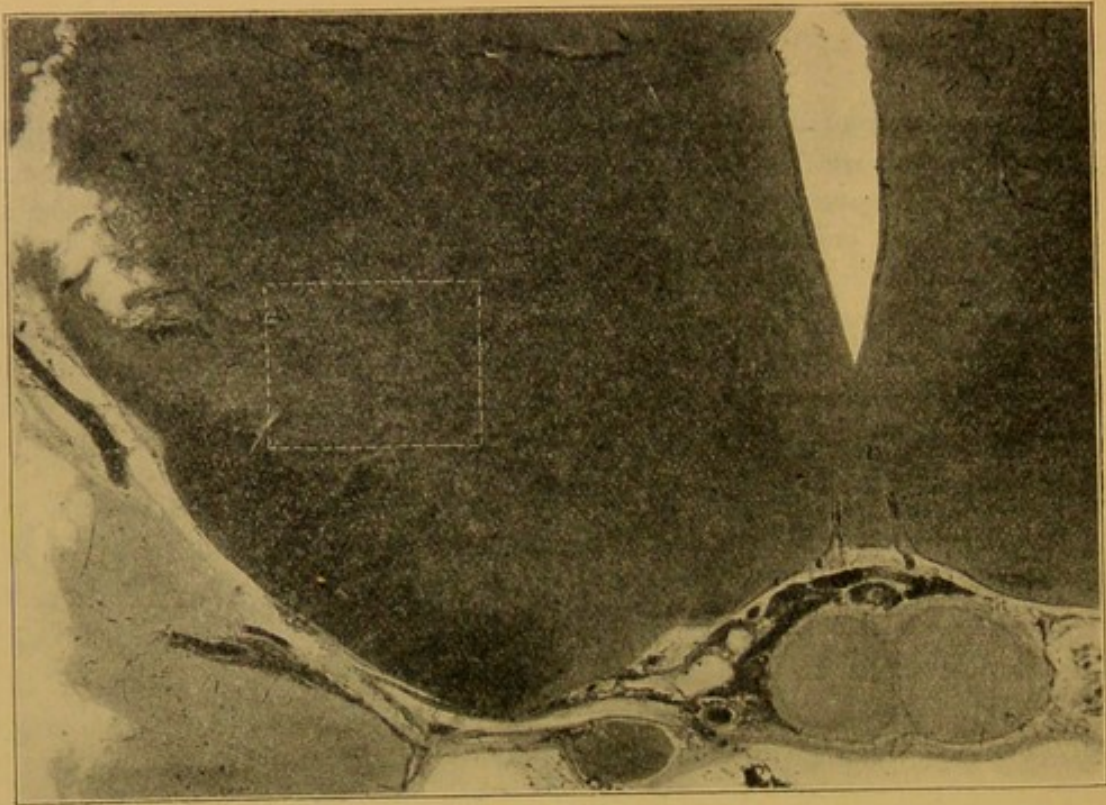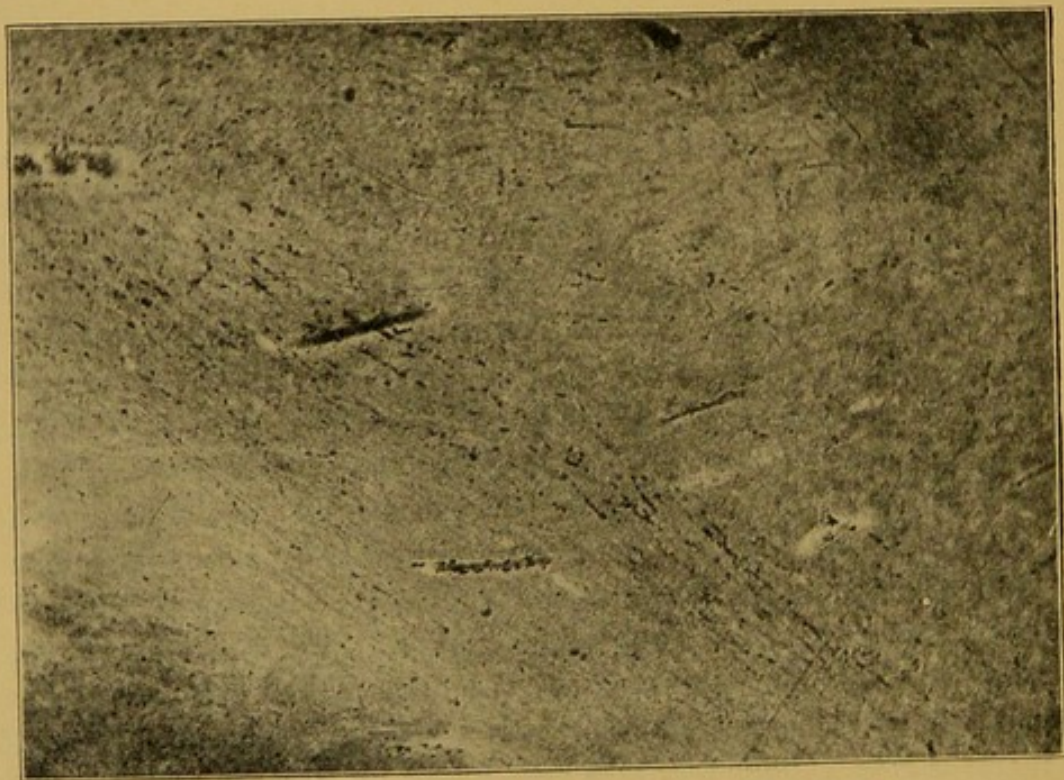
Fig. 15a.

Fig. 15b.

FIGS. 15a, 15b.—Cross sections from cat 186.

Fig. 15a.—Region of the lesion. Destruction on the left side of the ventral part of the striate body.

Fig. 15b.—Magnified portion of fig. 15a. Note degenerated strand of fibres in the lamina medullaris externa.

This strand of fibres lies therefore in the same region in which Dejerine [45], Probst [125], and Roussy [135] find that a large number of fibres disappear after lesion of the lateral parts of the optic thalamus.

The first question now is where do those fibres go to?

It is interesting to note that Sachs [140], working in Sir Victor Horsley's laboratory, reported the case of a rhesus, where the lesion lay in the external medullary lamina, and which showed a similar strand of degenerated nerve-fibres. This author believes that those fibres terminate in the red nucleus. From the evidence already discussed, it seems to me more probable that they terminate in the nucleus of the posterior commissure, and, from Bernheimer's experiments, possibly in the interstitial nucleus of the opposite side. This view is further supported by another case reported by Sachs in which the lesion was in the field of Forel; the same bundle of fibres was degenerated, while some fibres in the posterior longitudinal bundle of the same side also showed degeneration, proving that the interstitial nucleus (at least cells, from which the posterior longitudinal bundle fibres originate) was involved in the lesion.

Where does this bundle of fibres described by Sachs [140] and myself originate?

Up to the present time no conclusive evidence on this point has been furnished by our experiments. At the same time I make the suggestion that their origin lies either in the globus pallidus or in the putamen. This theory is suggested by the fact that in none of my cases of lesion involving the cortex alone were these fibres found degenerated, but only when the deeper parts such as the striate body or the lateral parts of the thalamus were involved. It is further supported by the work of Sachs [140], who succeeded in tracing a thalamo-fugal tract, lying in the same situation and following the same course, from the external medullary lamina to the globus pallidus. The data afforded by the pathological cases discussed in Chapter VII, together with the anatomical data supplied by v. Bechterew [11], Ariens Kappers [3] and de Vries seem also to support this theory.

As regards the physiological significance of this bundle the experiments of Horsley, Sachs and Clarke [41] appear to speak in the same sense. They tend to prove that faradic stimulation of the posterior third of the lateral nucleus thalami, that is the region in the immediate neighbourhood of the external medullary lamina, causes deviation of head and eyes to the opposite side. My observation quite fits in here. Section of the bundle causes circus movements and conjugate deviation

to the side of the lesion. Turning to the records given by other workers I find no arguments against my view in the cases given by Probst [125] and Roussy [135]. The older work of v. Monakow [104] and Mingazzini [101] is not suitable for application of this problem, since the brains were not examined by the Marchi method. In some of the older work by Ferrier and Yeo [56] dealing with suboccipital lesions, and in one of Schäfer and Horsley's experiments [142, Case 6], observations of forced movements occurring after lesion of the region under discussion are recorded. These movements consisted of conjugate deviation to the side of the lesion, falling to one side, or rotation of the head towards the uninjured side.

It is now interesting to see whether any of the old ablation or stimulation experiments, carried out when the present anatomical knowledge had not been arrived at, serve to confirm or deny the views put forward in this paper. The experiments by Adamuk [2] and Topolanski [155] are extremely interesting since the gross resections of the brain-substance indicate fairly accurately that our commissuro-medullary and interstitio-spinal tracts, and also the ascending fibres of the posterior longitudinal bundle, are the elements the destruction of which destroys the co-ordinated ocular movements induced by electrical stimulation of the brain-stem.

So easily were those movements elicited even with slight currents that Knoll [79] suggested that a good many of the results of the stimulation experiments of the cerebral cortex really depended upon current loops [cf. Mott, Schuster and Sherrington, 105]. It will be recalled that Ferrier [54], Schäfer [142], Horsley [14], Beevor and Vogt successfully elicited conjugate deviation of the head and eyes by stimulation over a large frontal area, while Bernheimer [15] and Levinsohn got the same results by stimulating other areas.

From the clinical point of view Landouzy [85] and Grasset long ago pointed out that in disease of the hemisphere conjugate deviation of the head and eyes towards the lesion is due to the paralysis of those structures which on faradic stimulation cause conjugate deviation towards the opposite side. Whether the voluntary impulses from the cerebral cortex, which are associated with forced movements or conjugated lateral movements of the eyeballs, are at all times transmitted through the centrifugal limb of the superimposed reflex arc, as described in Chapter III and in this chapter, must in the meantime remain an open question. It may be, however, admitted that the results of Munk [106] and Levinsohn [88] support this suggestion. Further, in the

light of our results, it seems highly probable that Bernheimer [15] is right in believing that these impulses must travel along paths situated on the ventral side of the sylvian aqueduct.

My experiments, taken in conjunction with those of Horsley and Sachs, lead to the supposition that the inner portion of the lenticular nucleus and its connexions with the nuclei of the posterior commissure are associated particularly with the conjugate deviation of the head and eyes towards the side of the lesion in the case of destruction, and towards the other side with electrical stimulation. Also Ferrier [54] found in the genu of the striate body a centre, electrical stimulation of which caused conjugate deviation from the side of stimulation.

Clinical and anatomical observations also tend to corroborate this view. Uhthoff [157], in his interesting article dealing with a series of anatomical lesions in the cerebral hemisphere in man which had caused conjugate deviation during life, describes the lentiform nucleus, claustrum, internal capsule, optic thalamus, and caudate nucleus as being most frequently involved. Prévost and Broadbent had made similar remarks before. Hösel [72] also found that one of the first tracts to become medullated is that which connects the region anterior to the red nucleus with the globus pallidus.

All this independent evidence seems to urge the necessity for a further investigation on the relationship between strial and cortical influx and the conjugate deviation of the head and eyes, from the newly acquired points of view.

CHAPTER VII.—CONJUGATE DEVIATION OF HEAD AND EYES, AND DIFFERENT FORMS OF NYSTAGMUS IN CLINICAL NEUROLOGY. THEIR LOCALIZATION VALUE.

The physiological analysis of the posterior longitudinal bundle formation has undoubtedly an important bearing on the clinical problem, afforded by the conjugate deviation of both eyes in cerebral disease generally, and particularly in pontine disease involving the sixth nucleus. Unless the physiological analysis of this formation be taken into consideration it is impossible to explain the additional conjugate deviation of the heterolateral rectus internus, with the rectus externus of the diseased side in an organic affection of the sixth nucleus. Foville [58], Hughlings Jackson [74], Duval, Wernicke [166], Bleuler [25], Bruce [37], Bischoff, Spitzer [149] and others, accept the view that

the nervous influx for the lateral movement of both eyes descends to the sixth nucleus and ascends to the third nucleus; they also consider that there is a recrossing of the pyramidal fibres dealing with this movement.

Many authors have felt the difficulty of accepting this somewhat improbable supposition, for which there is further no anatomical basis. If, however, the forced movements in the horizonal plane and the closely associated conjugate deviation in the same plane be carefully considered in the light of the above data, it is evident that there is no need to fall back on this theory.

A full discussion on this subject will be reserved for a later communication, but it may be said here that, after a careful scrutiny of the writings, hardly a case is found where there is not a lesion in the posterior longitudinal bundle formation as well as in the sixth nucleus.

If we consider the conjugated deviation [107, p. 216] as a minor degree of circus movement as well as a part of it, it is seen that this conjugate deviation of head and eyes in pontine diseases to the non-affected side is closely related to the circus movement towards the normal side, seen after one-sided lesion of the posterior longitudinal bundle formation between Deiters' nucleus and the posterior commissure in our experiments.

It is quite natural that in primates this forced movement, with conjugate deviation of the head and eyes, associated with pontine lesion, is to a greater extent under the power of the will than in the case of the lower vertebrates, a more or less continuous effort being made to counteract it. In fact, in the monkey it is rare to find a regular circus movement associated with a conjugate deviation to one side. In any case it never amounts to more than a slight circus movement, such as is seen in cats just before the symptom disappears, which passes, leaving a tendency to conjugate deviation of the head and eyes. Even conjugate deviation is overcome in primates with a certain ease. So it is that Munk [106], Ferrier and Yeo, as also Hunnius and Bernheimer, rightly insist that an unwillingness to look to one side must be looked for in the proper cases. Indeed, circus movement and conjugate deviation of the eyeballs in the horizontal plane, e.g., to the right side, and unwillingness to look to the left side, are all different degrees of the same fundamental phenomenon. It is therefore not surprising to find the heterolateral eyeball in pontine disease of man deviated inward, since a lesion of the eminentia teres and the

sixth nucleus by virtue of its vicinity to the posterior longitudinal bundle involves this bundle also. In this connexion the cases recorded by Rickards [131], Wiersma [167], Bristowe [33], Byrom Bramwell [30], Bruce [37], and Hunt should be examined.

It is only in cases of pontine tumour with no involvement of the posterior longitudinal bundle, but affection of the sixth nerve, that the internal rectus muscle of the other side may be expected to act normally. Reference may here be made to the work of Graux [67], Bennet and Savill [141] and others.

Regarding conjugated deviation in disease of the hemisphere, Wernicke's case [166] has long been regarded, in the German literature, as decisive proof that in man the angular gyrus is a special centre for this deviation. Destruction of this centre has long been supposed to cause conjugate deviation towards the side of the lesion, while irritation of the centre is associated with deviation towards the other side. This theory found support in the fact that in monkeys stimulation of the angular gyrus with the faradic current causes conjugate deviation to the opposite side. A careful scrutiny, however, of the anatomical findings of this case and of Prévost's [123] classical work, and Broadbent's cases [34], taken in the light of our observations on the superimposed vestibular reflex arcs, leads to the conclusion that there is considerable doubt on this point (Klaas). In Wernicke's case the third zone of the lenticular nucleus was involved as well as the cortex of the angular gyrus. This part of the striate body can therefore not be discarded as a centre in connexion with which the symptom of conjugate deviation arises.

Stimulation of the human cortex by minimal faradic currents has never, in my experience, been associated with conjugate deviation, nor, so far as I am aware, have Horsley, Krause or Cushing recorded this result. Unipolar stimulation is for several reasons, already pointed out in this paper, unsuitable for this purpose. For the present, therefore, it seems to me that the localizing value of the hemispheral conjugate deviation must remain *sub judice*. At the same time, I think that the ocular symptoms which occur in cases like No. 11 of Oppenheim's series [119] where the lenticular nucleus is involved, are worthy of considerable attention. If, in addition to paralysis of the nucleus abducens of the one side, there are indications of some paresis of the internal rectus muscle of the opposite side, when both are brought into action simultaneously, the condition may be diagnosed as conjugate deviation to one side or as defective movement

to the opposite side. It must not be regarded as a secondary pressure symptom.

It is interesting to note how clinical observations, quite apart from physiological research, have led to the appreciation of the fact that a destructive lesion of the cerebral hemisphere and optic thalamus is associated with conjugate deviation to the side of the lesion, and that a similar unilateral lesion in the pontine region causes the same deviation from the side of the lesion.

Long ago Grasset and Landouzy stated, "Dans les lésions de l'hémisphère le malade regarde ses membres convulsés, s'il y a excitation, et regarde sa lésion, s'il y a paralysie. A partir d'un certain point mal défini, à la limite des parties supérieures et moyennes de la protubérance, la formule doit être renversée." D'Astros [4] writing in 1894, considers it impossible to localize this "reversal point."

As a result of the observations now recorded there seems to me to be little doubt but that this point is situated in the posterior commissure, probably in the nucleus, both in man and in the lower type of mammal exemplified in the cat.

The question of the exact topographical distribution of conjugate deviation in the frontal and occipital regions dealt with by Ferrier, Schäfer, Horsley, Marina [100], and that which is discussed in the controversy between Luciani [96] and other workers, seems to me to be, after what has been said above, only of secondary interest. Regarding cerebellar disease, I may recall the fact, dealt with in Chapter II, that forced movements were never associated with my experiments involving lesions of the cerebellar cortex, or of the dentate nucleus [8].

The question which Bonnier [27], Launois, Chèze and others have attempted to answer as to whether a special Deiters' syndrome can be recognized in pontine disease, also lies outside this paper.

It is quite evident from what has been said regarding forced movements in quadrupeds that very careful distinction must be made in man between deviation in the horizontal plane and falling to a side. As regards the latter phenomenon it seems certain, from the work of Marburg [99], that besides the falling movements towards the medullary lesion the same movement towards the normal side is not infrequently observed. This latter condition is in agreement with the results got in my experiments on the ramus descendens of the vestibular nucleus. For the most recent observations on this subject I must refer to the second case recorded by Wallenberg [161], to the work of Schwarz [146]

and to the case of thrombosis of the posterior inferior cerebellar artery recorded by Goldstein and Baum [64]. It seems, however, to be the general rule in man, as in the cat, that a lesion of the vestibular nerve-roots and of the more oral parts of Deiters' complex are associated with falling to the side of the lesion. This phenomenon of falling to the side must be specially examined in man since the erect posture makes it impossible to bring it quite into line with the condition as it occurs in quadrupeds, where it really is a minor degree of the rolling movements.

From my observations [107, 113] on the direction of the different forms of nystagmus found associated with lesion of the hind-brain which have been confirmed and extended by Bárány [6], there can be little doubt but that the mechanism in such cases is as complicated as that described for the forced movements, and that the two mechanisms are closely related. I will merely recall that some authors (Marburg and Bartels) believe that the rapid and slow jerk seen in vestibular nystagmus have different localization.

In my experiments the slow jerk of the nystagmus accompanying the forced movements and forced position of the eyeballs always took the same direction as that in which the eyeballs were deviated. In lesions of Bechterew's nucleus and the homolateral vestibulo-mesencephalic tract in the posterior longitudinal bundle, the slow jerk of the horizontal nystagmus is directed towards the uninjured side. If the lesion be situated in the right vestibular root and the right Deiters' nucleus proper then the slow jerk of the nystagmus, associated with this condition, accentuated the already existing divergent squint, the right eye being directed downwards, the left eye upwards. Do these facts justify us in deducing diagnostic points for use in localizing the lesion in cases where one-sided nystagmus is present, but where, as is not infrequently the case in subtentorial lesions, forced movements or conjugate deviation are both absent? It seems to me that this is a point worthy of further consideration, but my own experience furnishes no conclusive evidence on the question.

Generally speaking, this anatomical and physiological research tends to show the importance of accurate clinical observation of even slight defects in the co-ordinated ocular movements in brain disease. Some of these lesions and their accompanying symptoms are as follows: A lesion anywhere from the descending ramus of the eighth nerve up to the striate body is liable to cause certain disturbances. In man these disturbances are more commonly in the horizontal plane, and are at

present so little understood that only a rough outline can be given of the pathological conditions which possibly induce the symptoms.

A *destructive* lesion of the posterior longitudinal bundle on the right side of the brain between the vestibular region and the posterior commissure is liable to cause conjugate deviation of the head and eyes to the left side, or else incomplete lateral deviation to the right side. If this symptom occur when the lesion is oral to the posterior commissure it is indicative of an organic destructive lesion on the left side. If there is conjugate deviation of head and eyes to the left side, and an *irritative* lesion, cephalad to the posterior commissure is probable (eventually convulsions of muscles on the left side), the irritative lesion may be localized in the thalamus and striate body on the right side.

If the symptom of Magendie-Hertwig squint (right eye directed downwards, left eye upwards) occur either alone or concurrently with conjugate deviation of the head and eyes, or if there is a tendency to fall or lie down on the right side, then the lesion (if situated in the medulla or truncus cerebri) probably has involved the vestibulary region or the lateral part of the posterior longitudinal bundle on the right side. If this symptom is present where the disease is localized cephalad to the posterior commissure, then, from experimental findings, the lesion is to be localized in the optic thalamus or striate body on the left side. If a destructive lesion is situated in the vestibular or cerebellar regions, and there appears deviation of the head and eyes to one side, for instance the left, we deal either with a conjugate deviation in the horizontal plane to the *left*, or with a condition allied to the rolling movement to the *right*. A careful searching for the Magendie-Hertwig squint (left eye down, right eye up) or a tendency to lie down on one side (the left) or a divergent nystagmus, slow in the sense of the deviation, will enable us to diagnose a condition allied to rolling movements to the right. Since unilateral cerebellar disease is very liable to affect the vestibular nerve and Deiters' nucleus, it is clear why in this type of case there is frequently a tendency to lie down on the diseased side. It is only in cases where the ramus descendens of the eighth nerve is involved that one is likely to get exceptions to this rule.

After what has been said, it need hardly be pointed out that Bruns' symptom of disequilibration in frontal tumour [38] cannot be discussed, unless the above observations be taken into consideration.

In examining for ocular deviation the voluntary and automatic deviation of the eyeballs must be tested separately. Wernicke [166] states that Tiling long ago pointed out that reflex deviation, such

as is seen when a moving object is followed by the eyes, may be demonstrated while voluntary lateral deviation is lacking. Bielschowsky [22] further emphasized the importance of this fact in routine examination. The symptom of " Vorbeizeigen " in cerebellar disease observed by Bárány may, I think, be due entirely to involvement of the vestibular structures. The fact that horizontal nystagmus is never accompanied by a tendency to fall to one side is quite readily understood when the mechanism of the two types of forced movements is taken into consideration.

The observation that a large percentage of deaf people do not suffer from dizziness, as noted by James and Kreidl, and further, that in very young infants sea-sickness does not occur, seems to indicate that there is some connexion between those conditions and imperfect functioning of the vestibular complex, either peripherally or centrally. The experiments of Nagel [118], Bishop Harman [24], Quix [129], Bartels and Rothfeld [132] render it extremely probable that the compensatory movements of the eyeballs in different movements of the head, and also the reflex adjustment of the eyes in vertical and other directions during rotation, are dependent on the labyrinthine reflexes. Where there is, e.g., circus movement or conjugate deviation to the right side, the compensatory deviation to the contralateral side during and after rotation are found absent. Reddingius, Marina [100], F. B. Hoffmann, and Bielschowsky have investigated the question of the reflex adjustment of the eyes in vertical and other directions during ocular movements ; these reflexes will probably be proved to be equally dependent on a normal activity of these reflex mechanisms and their conduction by the posterior longitudinal fascicle [cf. Cajal, 40, i, p. 728].

In the case of octopods [110], it has been shown that the reflex adjustment of the eyeball by the otolithic organ is in this animal predominantly homolateral ; by this reflex the pupillary slit is maintained in the horizontal position in practically all the positions assumed by the body. A similar condition seems to exist in the python, as here also the pupillary slit is held constantly vertical.

The very delicate muscular adjustment of the eyeballs in the higher vertebrates which is necessary, according to Mulder, Nagel [118], Hering and Bielschowsky, for the localizing of the visual field to the same part in the two retinæ in all changing positions of the head, is probably also a vestibular reflex system ; the innate tendency to fuse the two visual fields, even when anatomical or nervous defects exist, also plays an important part. The work of Marina on this subject is worthy of attention.

SUMMARY.

In reviewing this physiological analysis of the vestibulary system and the posterior longitudinal bundle formation, certain facts, both physiological and anatomical, stand out clearly, while other points can only be considered as suggestions or probabilities.

(1) The study of the physiological phenomena observed after lesions of different parts of this system demonstrates that there is a far-reaching differentiation of function in the primary end-stations of the vestibulary nerve. Further, it also shows that the different strands of fibres which connect the vestibular nuclei with the various nuclei in the mid-brain and with the region of the posterior commissure in a cerebro-petal direction may be more accurately analysed.

(2) The principal vestibular nuclei are the following: (a) The descending branch of the vestibular nucleus; (b) Deiters' nucleus composed of a ventral caudal division, named the nucleus triangularis, and a dorsal magnocellular division or Deiters' nucleus proper; (c) Bechterew's nucleus with the nucleus tecti.

(3) Physiological analysis affords a practical method of establishing the existence of important differences in the ascending and descending connexions of the above-mentioned nuclei, and of establishing equally important differences in the functions of the nuclei.

(4) The starting point of this analysis is the fact that an ascending degeneration of the crossed vestibulo-mesencephalic bundle, which forms the bulk of the mesial part of the posterior longitudinal bundle till near the nucleus of the posterior commissure, is always found associated with circus movements to the side of the intact posterior longitudinal bundle. This rule holds good so long as the lesion leaves the other parts of the vestibular systems intact. It is immaterial whether the degeneration of this vestibulo-mesencephalic tract is the result of a cross section of the median part of the posterior longitudinal bundle, or of a lesion of the heterolateral Deiters' nucleus. Experimental evidence tends to show that in the Deiters' complex the nucleus triangularis is the principal origin of this tract (fasciculus vestibulo-mesencephalicus cruciatus).

(5) The degeneration of an ascending tract lying immediately lateral to the crossed vestibulo-mesencephalic tract in the posterior longitudinal bundle formation appears to be equally associated with a circus movement (or rather conjugate deviation) to the side of the normal posterior longitudinal bundle. This tract is further shown to be a homolateral tract originating exclusively in the nucleus of Bechterew,

at least in the oral parts of the vestibular region, and terminating in the region of the posterior commissural nucleus. This bundle may be styled the homolateral vestibulo-mesencephalic fasciculus.

This tract is only partially identical with that described anatomically by Probst [124]. Van Gehuchten [63] in 1904 suggested that the whole of the lateral part of the posterior longitudinal bundle (fasciculus Deiters' ascendens, Lewandowsky, Winkler [169]) consisted of fibres, ascending from Bechterew's nucleus. This origin, for this limited portion at least of the posterior longitudinal bundle, may now be held as proved [cf. 108], as may also the association of its upward degeneration with circus movements or conjugate deviation to the normal side.

Both the circus movements observed after lesion of the homolateral or crossed vestibulo-mesencephalic tracts are associated with conjugate deviation of the head and eyes to the side of the movement, or with loss of lateral deviation of the eyeballs to the opposite side.

(6) According to the notions advanced by Duval, Bleuler, Edinger, Bischoff, Spitzer, Kohnstamm, Bernheimer, Fraser, Wallenberg, Wiersma, and others, the posterior longitudinal bundle represents a combination of ascending and descending tracts, which control the co-ordinated movements of the eyes, head, and trunk, and control or direct the maintenance of the equilibrium of motion. Now, from experimental data furnished by the present investigation, it is seen that after a direct lesion in the region of the posterior commissure of the cat on one side, where the resulting circus movements were directed to the side of the lesion, a descending tract degenerates which lies at the innermost part of the posterior longitudinal bundle of the same side. This tract probably originates in the posterior commissural nucleus. As it stops short in the medulla it is suggested that it may be termed the fasciculus commissuro-medullaris [cf. 108].

(7) Although it is probable that this mesencephalo-medullary tract exists in all the higher organized vertebrates such as selachians, teleosteans, amphibians, reptiles, birds and mammals, it is only in the mammal that a destructive lesion of the nucleus and of its efferent tracts from the striate body is associated with circus movements towards the side of the lesion. In the lower animals a lesion oral to the posterior commissure is not followed by any circus movements.

The anatomical explanation of this fact seems to be that only in mammals are the hypothalamic and commissural nuclei sufficiently connected with the prosencephalon that section of the connexions should be followed by asymmetrical locomotion, as evidenced in circus

movements and conjugate deviation towards the side of the lesion. Further, it is only in mammals that stimulation of certain definite areas of the cortex is followed by conjugate deviation of the head and eyes towards the opposite side. Birds seem to form in this respect a group between the reptiles and mammals. In the prosencephalon of the bird is an area, faradization of which is associated with conjugate deviation towards the opposite side (Boyce and Warrington). The section of the connexions of this area is not, however, associated with any alteration in the mode of locomotion. As regards those cases (cats), where, after lesion of the thalamus and cerebral hemisphere, circus movements towards the side of the (destructive) lesion were observed over a longer period, it was found that there was a tract of degenerated fibres in the lamina medullaris externa. These fibres, which probably emanate from the striate body, pass to the hypothalamic region, where they lose their medullary sheaths. The termination of these fibres, probably in the nucleus of the posterior commissure, can, therefore, not be demonstrated. The circus movement in such cases is always accompanied by conjugate deviation towards the side of a destructive lesion, or in less pronounced cases by loss of lateral deviation to the other side.

(8) Like the circus movements the rolling movements may serve as a guide in working out the anatomo-physiological analysis of the vestibular complex and the posterior longitudinal bundle formation.

(9) After a direct lesion of the complicated nerve-fibres, which help to form the vestibular root, a rolling movement towards the injured side is constantly observed, mostly associated with a skew deviation and conjugate rotation of the eyeballs around their antero-posterior axis. In only one case (rabbit, direct lesion in the caudal part of the vestibular root) were rolling movements towards the non-injured side observed.

(10) In three cases of lesion of the descending branch of the nucleus vestibularis rolling movements towards the normal side were seen lasting over several days. Although this experiment was repeated several times, I failed to localize any distinct ascending or descending connexions from this part of Deiters' complex.

(11) Lesion of Deiters' nucleus proper is found in two cases associated with rolling movements, moderate in character, towards the side of the lesion. From this nucleus the degeneration spreads upwards along a tract which lies in the outermost part of the lateral horn of the posterior longitudinal bundle. A direct lesion of this ascending tract or connexion is also associated with a tendency to roll towards the side of the lesion. This was demonstrated in five cases.

The fibres of this tract appear to end mostly in the tegmentum, although some may be traced to the caudal part of the posterior commissure, where the fibres appear to lose their medullary sheath ; it is therefore suggested that it should be styled the tractus vestibulo-tegmentalis lateralis. Its origin is apparently in the medium-sized cells of Deiters' nucleus proper, its termination probably in the interstitial nucleus.

(12) A comparison of the cases where the lesion is situated in the region of the posterior commissure leads us to postulate in that region a centre, probably the nucleus interstitialis, injury of which (or of its afferent tracts from other parts) in the cat is constantly followed by rolling movements to the normal side. The existence of a descending interstitio-spinal tract in the innermost section of the posterior longitudinal bundle in these cases in which rolling movements or, in less pronounced cases, a tendency to fall to the normal side are observed seems to justify this supposition to a certain extent.

(13) The physiological combined with the degenerative method does not afford such ample information as regards the tracts from Deiters' complex to the posterior longitudinal bundle formation of the spinal cord. This is partly due to the irregular form of the collection of reticular cells which give rise to the ponto- or reticulo-spinal tracts. It seems certain that heterolateral descending fibres of the posterior longitudinal bundle do not come from Bechterew's nucleus, although descending homolateral fibres are given off from both Deiters' and Bechterew's nuclei. After experimental lesion of Deiters' nucleus it was not in all cases possible to decide from what cells the heterolateral fibres originate. If the descending connexions of the vestibular structures which control the circus and rolling movements and those of the superimposed mesencephalic structures be compared, the conclusion seems warranted that the descending connexions are far more important in the case of the rolling movements. Relatively few descending fibres which originate in the structures associated with circus movements pass beyond the sixth nucleus.

BIBLIOGRAPHY.

[1] D' ABUNDO. *Arch. Ital. de Biol.*, 1910, t. liii, p. 321.
[2] ADAMUK, E. *Centralbl. f. d. med. Wissensch.*, 1870, S. 65.
[3] ARIENS, KAPPERS. *Anat. Anzeig.*, 1908, Bd. xxxiii, S. 321.
[4] D'ASTROS. *Rev. de Méd.*, 1894, t. xiv, p. 152.
[5] BABINSKI, J. *Rev. neurol.*, 1902, t. x, p. 1012.
[6] BÁRÁNY. "Vestibular-apparat," Berlin, 1906, S. 14.
[7] *Idem. Wien. klin. Wochenschr.*, 1912, Bd. xxv, S. 2023.
[8] BATTEN. *Brain*, 1906, vol. xxix, p. 494.
[9] BECHTEREW, W. v. *Deutsche Zeitschr. f. Nervenheilk.*, 1900, Bd. xvii, S. 221.
[10] *Idem. St. Petersburger med. Wochenschr.*, 1882, Bd. vii, S. 97.

[11] BECHTEREW, W. v. "Physiologie d. Nervensystems," Jena, 1908, Heft ii, S. 1119.

[12] *Idem. Pflüger's Archiv*, 1883, Bd. xxxi, S. 479.

[13] *Idem.* "Leitungsbahnen," Leipzig, 1899, p. 295.

[14] BEEVOR, C., and HORSLEY, V. *Phil. Trans. Roy. Soc.*, 1887, vol. clxxviii, p. 153.

[15] BERNHEIMER. *Arch. f. Ophth.*, 1903, Bd. lvii, S. 363.

[16] BERTELSEN und RÖNNE. *Monatsschr. f. Psychiat. u. Neurol.*, 1909, Bd. xxv, S. 148.

[17] BESTA, C. *Arch. f. Psychiat.*, 1913, Bd. l, S. 323.

[18] BETHE. *Pflüger's Archiv*, 1899, Bd. lxxvi, S. 470.

[19] BIACH und BAUER. *Obersteiner's Arbeiten a. d. Neurol. Inst. Wien*, 1911, Bd. xix, S. 56.

[20] BICKEL, A. *Arch. f. Anat. u. Physiol.*, 1901, S. 56.

[21] BIEHL. *Obersteiner's Arbeiten a. d. Neurol. Inst. Wien*, 1907, Bd. xv, S. 71.

[22] BIELSCHOWSKY. *Monatsschr. f. Psychiat. u. Neurol.*, 1909, Bd. xxv, S. 267.

[23] *Idem. Deutsche Zeitschr. f. Nervenheilk.*, 1902, Bd. xxii, S. 54.

[24] BISHOP-HARMAN. *Journ. of Anat. and Physiol.*, 1900, vol. xxxiv, p. 27.

[25] BLEULER. *Deutsche Arch. f. klin. Med.*, 1885, Bd. xxxvii, S. 27 ; *ibid.*, 1885, Bd. xxxviii, S. 28.

[26] BOLK, L. "Petrus Camper," Bd. iii, Aufl. 1, Blz. 28.

[27] BONNIER, P. *Presse Méd.*, 1903, t. xi, p. 861.

[28] BOYCE, R. *Phil. Trans. Roy. Soc.*, 1895, B., vol. clxxxvi, pp. 335 and 361.

[29] BOYCE and WARRINGTON. *Ibid.*, 1899, vol. cxci, p. 308.

[30] BRAMWELL, BYROM. *Edin. Med. Journ.*, 1909, n. s., vol. ii, p. 129.

[31] BREUER. *Pflüger's Archiv*, 1891, Bd. xlviii, S. 195.

[32] *Idem. Sitzungsb. der Kais. Akad. der Wissensch.*, 1903, Bd. cxii, Abth. 3, S. 315.

[33] BRISTOWE. *Brain*, 1891, vol. xiv, p. 289.

[34] BROADBENT, W. *Lancet*, 1897, vol. ii, p. 862.

[35] BROWN, CRUM. *Nature*, 1895, vol. lii, p. 185.

[36] BROWN-SÉQUARD. "Experimental Researches," New York, 1853, p. 18.

[37] BRUCE, A. *Rev. of Neurol.*, 1903, vol. i, p. 329.

[38] BRUNS, L. *Deutsche med. Wochenschr.*, 1892, S. 138.

[39] CAJAL, S. R. "Travaux du Laboratoire de Recherches biologiques de l'université de Madrid," 1908, t. vi, p. 145.

[40] *Idem.* "Histologie du système nerveux," 1911, t. ii, p. 267.

[41] CLARKE, R. H., and HORSLEY, V. *Brain*, 1905, vol. xxviii, p. 13.

[42] COLLIER and BUZZARD. *Brain*, 1901, vol. xxiv, p. 198, Pl. XV, Tract Y.

[43] CURSCHMANN. *Deutsche Arch. f. klin. med.*, 1874, Bd. xii, S. 356.

[44] DEJERINE. "Anatomie des centres nerveux," Paris, 1901, ii, p. 405.

[45] DEJERINE et ROUSSY, G. *Rev. neurol.*, 1905, t. xiii, p. 161.

[46] DEGANELLO. *Riv. sper. di freniatr.*, 1899, vol. xxv, p. 1.

[47] DEMOOR. *Arch. de Zool. Exper.*, 1891, 2me sér., t. ix, p. 196.

[48] ECONOMO, C. v. *Jahrb. f. Psychiat. u. Neurol.*, 1911, Bd. xxxii, S. 107.

[49] EDINGER, E. "Vorlesungen über die Nervösen Centralorgane," Leipzig, 1904, S. 249.

[50] *Idem. Neurol. Centralbl.*, 1899, Bd. xviii, S. 95.

[51] EWALD, W. F. *Pflüger's Archiv*, 1907, Bd. cxvi, S. 188.

[52] *Idem. Arch. f. Psychiat.*, 1910, Bd. xlvii, S. 954.

[53] FANO, G. *Riv. sper. di freniatr.*, 1885, vol. xi, p. 480.

[54] FERRIER, D. *Proc. Roy. Soc.*, 1890, No. 286.

[55] FERRIER, D., and TURNER, A. *Phil. Trans. Roy. Soc.*, 1894, B., vol. clxxxv, p. 719.

[56] FERRIER, D., and YEO. *Phil. Trans. Roy. Soc.*, 1884, B., vol. clxxv, p. 561.

[57] FLOURENS, P. "Recherches expérimentales sur le système nerveux," 2me ed., Paris, 1842, p. 15.

[58] FOVILLE. *Gaz. hebdom.*, 1859, t. vi, p. 146.

[59] FRASER, E. N. *Journ. of Physiol.*, 1901-02, vol. xxvii, p. 372.

[60] FRIEDBERG. *Arch. d. Heilk.*, 1861, Bd. ii, S. 385.

[61] FUSE, G. *Arbeiten a. d. hirn. Anat. Inst. des Univer. Zürich.* 1912, Heft vi, S. 29.

[62] GEE and TOOTH. *Brain*, 1898, vol. xxi, p. 15.

[63] GEHUCHTEN, V. VAN. *Névraxe*, 1904, t. vi, p. 63.

[64] GOLDSTEIN, K., und BAUMM, H. *Arch. f. Psychiat.*, 1913, Bd. lii, S. 373.

[65] GOWERS, W. R. "Manual of Nervous Disease," London, 1893, vol. ii, p, 185.

[66] GRASSET. *Sem. méd.*, 1904, t. xxiv, p. 153.

[67] GRAUX. "Paralysie de l'oculomotion externe," *Thèse de Paris*, 1878, Obs. x.

[68] HELD. *Arch. f. Anat. u. Physiol.*, 1893 (Anat. Abth.), S. 229.

[69] HÖGYES. *Pflüger's Archiv*, 1881, Bd. xxvi, S. 558.

[70] *Idem. Ungar. Akad. d. Wissensch.*, Mat. phys. Klasse, 1885, Bd. xi, No. 1.

[71] HOLMES, G., and STEWART. *Brain*, 1905, vol. xxviii, p. 522.

[72] HÖSEL. *Monatsschr. f. Psychiat. u. Neurol.* 1899, Bd. vi, S. 168.

[73] *Idem. Arch. f. Psychiat.*, 1905, Bd. xxxix, S. 195.

[74] HUGHLINGS JACKSON. *Med. Times and Gaz.*, 1874, vol. i, p. 6.

[75] HUNNIUS. "Zur Symptomatologie der Brückenerkrankungen," Bonn, 1851, S. 15.

[76] JELGERSMA, G. "Physiologie van het Cerebellum," 1904, Amsterdam Scheltema, Bl. xxiv.

[77] KAPLAN und FINKELNBURG. *Monatsschr. f. Psychiat.*, 1900, Bd. viii, S. 210.

[78] KARPLUS und ECONOMO. *Arch. f. Psychiat.*, 1910, Bd. xlvi, S. 275.

[79] KNOLL, PH. *Sitzungsb. der Kais. Akad. der Wissensch.*, 1886, Bd. xciv, Abth. 3, S. 220.

[80] KOHNSTAMM, O., und QUENSEL, F. *Neurol. Centralbl.*, 1908, Bd. xxvii, S. 242.

[81] *Idem. Monatsschr. f. Psychiat. u. Neurol.*, 1900, Bd. viii, S. 261.

[82] *Idem. Journ. f. Psychol. u. Neurol.*, 1910, vol. xvi, p. 93.

[83] KOOYKER, H. A. *Zeitschr. f. klin. Med.*, 1894, Bd. xxiv, S. 605.

[84] KUBO. *Pflüger's Archiv*, 1906, Bd. cxiv, S. 143; *ibid.*, 1906, Bd. cxv, S. 457.

[85] LANDOUZY, L. "Etude des Convulsions," *Thèse de Paris*, 1876, p. 20.

[86] LANGE, J. DE. *Fol. Neurobiol.*, 1909, vol. iii, p. 649.

[87] LEE, F. S. *Journ. of Physiol.*, 1894, vol. xvii, p. 192.

[88] LEVINSOHN. *Arch. f. Ophthal.*, 1909, Bd. lxxi, S. 313.

[89] LEWANDOWSKY. "Leitungsbahnen des Truncus Cerebri," &c., Jena, 1904, p. 80.

[90] *Idem. Lehrb. f. Nervenkrankh.*, 1910, Bd. ii, S. 733.

[91] LEWY. *Fol. Neurobiol.*, 1909, vol. ii, p. 479.

[92] LLOYD. *Journ. of Physiol.*, 1899-1900, vol. xxv, p. 191.

[93] LOEB, J. *Pflüger's Archiv*, 1891, Bd. l, S. 66.

[94] LONGET. "Anatomie und Physiologie des Zentralnervensystem," 1847, Bd. i, S. 355.

[95] LUCIANI, L. "Cerveletto," 1892,

[96] *Idem.* "Physiologie des Menschen," 1907, vol. iii, p. 454.

[97] MACGREGOR, A. *Lancet*, 1886, vol. ii, p. 1127.

[98] MAGNUS und DE KLEIJN. *Pflüger's Archiv*, 1912, Bd. cxlv, S. 467.

[99] MARBURG. *Deutsche Zeitschr. f. Nervenheilk.*, 1911, Bd. xli, S. 41.

[100] MARINA, A. *Deutsche Zeitschr. f. Nervenheilk.*, 1912, Bd. xliv, S. 138.

[101] MINGAZZINI. *Deutsche Zeitschr. f. Nervenheilk.*, 1901, Bd. xix, p. 1.

[102] MINGAZZINI und POLIMENTI. *Monatsschr. f. Psychiat. u. Neurol.*, 1906, Bd. xx, S. 403.

[103] MONAKOW, C. VON. "Gehirnpathologie," "Nothnagel's Handbuch,' Wien, Bd. ix, T. i, S. 581.

[104] *Idem. Arch. f. Psychiat.*, 1895, Bd. xxvii (Beobachtung ii), S. 101.

[105] MOTT, SCHUSTER and SHERRINGTON. *Proc. Roy. Soc.*, 1911, B, vol. lxxxiv, p. 67.

[106] MUNK, H. *Sitzungsb. der Kais. Preusz. Akad. der Wissensch.*, 1906, S. 443.

[107] MUSKENS, L. J. J. *Journ. of Physiol.*, 1904, vol. xxxi, p. 204.

[108] *Idem. Trans. Roy. Acad. Amsterdam*, Communication, October 25, 1912, Bl. 656; *Nederl. Dierk. Vereen.*, Juli, 1913.

[109] *Idem. Trans. Roy. Acad. Amsterdam*, Communication, April 19, 1913, Bl. 1474.

[110] *Idem. Arch. f. Anat. u. Physiol.*, 1904 (Physiol. Abth.), S. 49.

[111] *Idem. Epilepsia*, 1912-13, Bd. iv, Fasc. 4, S. 429.

[112] *Idem. Psychiat. en Neurol. Bl.*, 1906, Bd. x, S. 68.

[113] *Idem. Verhandl. der Kon. Acad. Amsterdam*, 1902, Bd. viii, No. 5.

[114] *Idem. Trans. Roy. Acad. Amsterdam*, Communication, January 25, 1906.

[115] *Idem. Neuraxe*, 1913, vol. xiv, p. 299.

[116] *Idem.* "Report Zoological Station den Helder Staatscourant," 1894.

[117] *Idem. Psychiat. en Neurol. Bl.*, 1897, S. 328.

[118] NAGEL, W. *Zeitschr. f. Psychol.*, 1896, vol. xii, S. 331.

[119] OPPENHEIM, H. *Arch. f. Psychiat.*, 1891, Bd. xxii, S. 27.

[120] POLIMANTI. *Zool. Jahrb.*, 1911, Bd. xxx (Zool. Abth.), S. 512.

[121] PRÉVOST. "Cinquantenaire de la Societé de Biologie," 1899, p. 99.

[122] *Idem.* "Déviation conjugée," *Thèse de Paris*, 1868, p. 123.

[123] PROBST, M. *Jahrb. f. Psychiat.*, 1901, Bd. xx, S. 41; *ibid.*, 1903, Bd. xxiii, S. 63.

[124] *Idem.* *Arch. f. Psychiat.*, 1900, Bd. xxxiii, S. 783; 1902, Bd. xxxv, S. 22.

[125] *Idem.* *Sitzungsb. der Kais. Akad. der Wissensch.*, 1905, Bd. cxiv, Abth. 3, S. 173.

[126] *Idem.* *Deutsche Zeitschr. f. Nervenheilk.*, 1898, Bd. xiii, S. 384.

[127] PRUS, J. *Wien. klin. Wochenschr.*, 1898, Bd. xi, S. 857.

[128] QUENSEL, F. *Pflüger's Archiv*, 1911, Bd. cxxxix, S. 47.

[129] QUIX. *Tijdschr. der Nederland. Dierk. Vereeniging*, 1903, p. 1.

[130] REDLICH, E. *Monatsschr. f. Psychiat.*, 1899, Bd. v, S. 119.

[131] RICKARDS. *Brit. Med. Journ.*, 1886, vol. i, p. 774.

[132] ROTHFELD, J. VON. *Verhandl. deut. Naturforsch. und Aerzt.*, 1913, 85 Versamml., T. i, S. 269.

[133] *Idem.* *Pflüger's Archiv*, 1912, Bd. xlix, S. 440.

[134] ROTHMANN. *Neurolog. Centralbl.*, 1900, vol. xix, p. 44.

[135] ROUSSY, G. "Couche Optique," *Thèse de Paris*, 1907, pp. 175-177.

[136] RUSSELL, R. *Phil. Trans. Roy. Soc.*, 1894, B., vol. clxxxv, p. 837.

[137] *Idem.* *Journ. of Physiol.*, 1894-95, vol. xvii, pp. 1 and 385.

[138] *Idem.* *Brit. Med. Journ.*, 1896, vol. ii, p. 914.

[139] RYNBERK, VAN. "Cerebellum. Bataafsch Genootschap," 1906, Blz. ii, 35.

[140] SACHS, E. *Brain*, 1909, vol. xxxii, p. 180.

[141] SAVILL and BENNETT. *Brain*, 1890, vol. xii, p. 102.

[142] SCHÄFER and HORSLEY. *Phil. Trans. Roy. Soc.*, 1888, vol. clxxix, pp. 29 and 32.

[143] SCHIFF, M. *Arch. de sci. phys. et natur.*, Geneva, 1891, 3me sér., t. xxv, p. 194.

[144] *Idem.* *Arch. f. physiol. Heilk.*, 1846, Bd. v, S. 667.

[145] SCHWAHN. "Beiträge zur Anatomie und Physiologie, v. Eckhard," Bd. viii, Heft iii, und Bd. ix, S. 193.

[146] SCHWARZ, E. *Monatsschr. f. Psychiat. u. Neurol.*, 1912, Bd. xxxii, S. 149 und S. 153.

[147] SHERRINGTON, C. S. "The Integrative Nervous System," London, 1910, p. 55.

[148] SPILLER, G. *Journ. of Nerv. and Ment. Dis.*, 1905, p. 569.

[149] SPITZER, A. *Obersteiner's Arbeiten a. d. Neurol. Inst.*, *Wien*, 1899, Heft vi, S. 38.

[150] SPITZER und KARPLUS, J. P. *Hidirn, ibid.*, 1907, Bd. xvi (T. ii), S. 348.

[151] SPITZKA, G. *Neurolog. Centralbl.*, 1885, p. 246.

[152] STEEL, J. J. "Diseases of Sheep," London, 1890, p. 338.

[153] STEINER. "Functionen des Centralnervensystem," Brunswick, 1886, p. 56.

[154] THOMAS. *Rev. Neurol.*, 1903, vol. xi, p. 95.

[155] TOPOLANSKI, A. *Arch. f. Ophthal.*, 1898, Bd. xlvi, S. 452.

[156] UEXKULL. *Zeitschr. f. Biol.*, 1895, Bd. xxxi, S. 593.

[157] UHTHOFF. Graefe-Saemisch, "Handbuch der Augenheilkunde," 1911, Bd. xi, Abth. 2A, S. 1180.

[158] VALKENBURG, C. V. *Proc. Roy. Acad. Amsterdam*, March 30, 1912.

[159] VULPIAN. "Leçons sur la Physiologie du Système nerveux," Paris, 1866.

[160] *Idem.* *Gaz. méd. de Paris*, 1862, t. xxxii, p. 312.

[161] WALLENBERG, W. *Deutsche Zeitschr. f. Nervenheilk.*, 1911, Bd. xli, S. 8.

[162] *Idem.* *Anat. Anzeig.*, 1900, Bd. xvii, S. 107.

[163] *Idem.* *Ibid.*, 1904, Bd. xxiv, S. 142.

[164] *Idem.* *Ibid.*, 1907, Bd. xxxi, S. 369.

[165] *Idem.* *Deutsche med. Wochenschr.*, 1910, Bd. xxxvi, S. 2229.

[166] WERNICKE. *Arch. f. Psychiat.*, 1889, Bd. xx, S. 243.

[167] WIERSMA, E. *Psychiat. en Neurol. Bladen*, 1899, Blz. 603.

[168] WINKLER, C. *Trans. of Third Internat. Neurol. Psychiat. Congress of Amsterdam*, 1908, p. 132.

[169] *Idem.* "Nervus Octavus," *Verhandl. der Kon. Acad. Amsterdam*, 1907, second section, vol. xiv, p. 26.