THE FIBER CONNECTIONS OF THE

POSTERIOR PARTS OF THE CEREBELLUM

by

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INTRODUCTION

Johnston ('02) and Herrick ('14) have laid the foundations for an understanding of the morphology of the cerebellum by their studies of the organ in Petromyzon and urodeles respectively. Elliot Smith ('02, '03) in his comparative study of the mammalian cerebellum broke away, largely, from the older description of surface anatomy and provided a departure for all subsequent studies. Bolk ('06) also studying the mammalian cerebellum, made important contributions to an understanding of its morphology. DeLange ('15) described the cerebellar connections in several reptiles on the basis of Weigert series, but it remained for Ingvar ('18) to illuminate the whole subject of cerebellar morphology and functional anatomy. Ingvar studying reptiles, birds and mammals, combined the methods of embryology, comparative anatomy and experimentation. He did not, however, recognize the fundamental distinction between corpus cerebelli and flocculonodular lobe. He includes flocculus, paraflocculus, nodulus, uvula and pyramis in his posterior cerebellar lobe, which differs from the posterior lobe of Elliot Smith ('02) in being bounded anteriorly by the prepyramidal fissure instead of the fissura secunda. The flocular lobe of Elliot Smith, corresponding to the formatio vermicularis of Bolk ('06), and including flocculus and paraflocculus, is retained by Ingvar.

Although Stroud (1895) pointed out the fact that the flocculus and the paraflocculus are distinct structures in mammals they have nearly always been considered together, both anatomically and experimentally, no doubt because of their close topographical relationships in the adult human cerebellum and in the common laboratory animals used for experimentation. The studies of Larsell ('20, '23, '25, '26, '31, '32) on amphibians and reptiles more recently supplemented by an analysis of the primitive mammalian cerebellum ('34, '35, '36) and by an embryological study of the cerebellum in a small and primitive mammal, the bat, (Larsell and Dow '35), show clearly that the fundamental division into corpus cerebelli and auricular lobe holds good also in mammals. The corpus cerebelli on morphological grounds should be concerned chiefly with muscle sense stimuli, while the flocculonodular lobe should be chiefly or entirely vestibular. The studies cited also indicate that the paraflocculus is quite unrelated, in development, both phylogenetic and ontogenetic, to the flocculus. The present study was, therefore, undertaken at the suggestion of Doctor Larsell in order to check by experimental methods the conclusions reached by the methods of embryology and comparative anatomy.

Attention has been paid chiefly to the region caudal to the prepyramidal fissure, the flocculus, the paraflocculus, and the cerebellar base. The vestibular connections of the cerebellum have received especial attention.

MATERIAL AND METHODS

The present study has been based on surgical lesions on the cat and white rat. The lesions were confined, as nearly as possible to the parts of the cerebellum selected for special study. The cats were anaesthetized with dial (Ciba) given intraperitonealy in a dosage of 0.5 c.c. of a 10% solution per kilo. The rats were anaesthetized by nembutal (Abbott) given intraperitoneally in a dosage of 1 c.c. of a special dilution (the standard veterinary solution one part and water six parts) per 200 grams.

The animals were kept alive for two weeks after operation and the brains were then treated by the Marchi technique for degenerating fiber tracts as described by Allen ('19, p.178) or by the Nissl method for chromatolysis of nerve cells as described by Allen ('23, p.295). Serial sections were made of the whole cerebellum and medulla of the animals which survived for two weeks. The cat material, which was all stained by the Marchi technique was imbedded in celloidin and cut sagittally at 52 micra. The

The rat material was embedded in paraffin. The Marchi material was cut sagittally at 25 micra and the Nissl material was cut transversely at 18 micra. 13 cats and 55 rats survived the operations and the experiments on 4 cats and 28 rats were sufficiently successful to be used in this study.

Those who have worked with the Marchi method are aware of the frequency with which granules resembling degenerated myelin are found in regions which are entirely unaffected by the operative procedure. In the following text degeneration is described as present only where black granules were found in excess of those present in normal controls of the same region. Conversely, where drawings or description indicate a particular area to be free of degeneration, it is to be understood that the number of granules present was no greater than those in the normal controls. All degenerated tracts described were traced without interruption from the lesion.

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REVIEW OF EXPERIMENTAL LITERATURE

The fiber tract connections of the cerebellum have been studied by various workers using gross dissection, observation of myelinzation, and various neurohistological staining methods. By these procedures, however, it is well nigh impossible to determine the origin and destination of any tract which may be identified. The Marchi technique has made the greatest contribution in this direction. By its use Marchi ('91), Russell ('94-'97), Biedl ('95), Munzer and Wiener ('95), Andre-Thomas ('97), Klimoff ('99), Probst ('02), and others carried out the early work on the connections of the cerebellum with the rest of the central nervous system.

Thomas and Klimoff both attempted to find out the fiber connections of specific parts of the cerebellum, but little was definitely known in this field until the work of Clark and Horsley in 1905. Van Gehuchten ('00 to '06) described carefully the origin, course and termination of most of the afferent and efferent cerebellar tracts. These earliest workers, as well as many who have followed, have failed to take sufficiently into consideration the facts which have been gleaned from the field of comparative morphology. This is especially true of the work done on the fiber connections of the flocculus and paraflocculus. Most experimenters have used the terminology of Elliot

Smith ('03) or of Bolk ('06), neither of whom recognized any essential difference between the flocculus and the paraflocculus but grouped them together into "floccular lobe" and "formatio vermicularis" respectively.

Many workers in this field have failed to describe their lesions specifically enough to enable one to judge whether they were dealing with the flocculus, paraflocculus or both. Frequently, the paraflocculus has been miscalled flocculus. Barany's ('14) often quoted work on the function of the flocculus appears to have been done entirely on the paraflocculus. The difficulties of interpreting much previous work is at once apparent.

Ferrier and Turner ('97, p.627) observed that, in monkeys, following lesions of the "pedunculus flocculi" degenerations were traced to Deiter's nucleus, the vermis cerebelli and the tegmentum pontis.

Klimoff ('99, p.11) destroyed a part of the cerebellum of the rabbit which he called "flocculus" but which was probably flocculus and paraflocculus. He found degeneration to the lateral part of the dentate nucleus and possibly to Deiter's nucleus. He observed arcuate fibers connecting the folia of the flocculus to each other and to the nearest folia of the hemisphere and vermis.

Van Gehuchten ('00, p.52) stated that the complete extirpation of the "flocculus" of the rabbit's cerebellum always causes a lesion of greater or lesser depth in the "cerebellar olive" which in turn produces a degeneration in the homolateral superior cerebellar peduncle. His promised complete report of this work to have been published with Pavlow, with whom the work was done, has not as yet been located.

Muskens ('04), according to Lowy ('16, p.358), observed after the removal of the "formatio vermicularis" in the rabbit two bundles of degenerated fibers leaving the "flocculus". These leave the cerebellum via the brachium conjunctivum and the brachium pontis, both ascend and eventually reach the region of the red nucleus.

Clark and Horsley ('05, p.25) concluded that the flocculus and paraflocculus send fibers to the fastigial nucleus. They differentiate between these parts in their diagrams and explanations but only in one animal was the paraflocculus damaged without also involving the flocculus. In this animal, the parafloccular lesion was only incidental to the main lesion which was on the "anterior pennate lobe".

Van Gehuchten ('06, p.652) denies the presence of commissural fibers between the cortex of the two cerebellar hemispheres or the two "flocculi".

Lowy ('16), in rabbits and guinea-pigs, traced the degeneration following injury of the "formatio vermicularis". The lesions probably centered on the paraflocculus and, from the degeneration described, probably also involved the flocculus. From a "cortical lesion" he traced fibers to the flocculus proper, to the neighboring folia above, to the dentate nucleus and a few fibers to the contralateral oculomotor nucleus via the brachium conjunctivum. He also described an "angular bundle" which passes medially inferior to the brachium conjunctiva and arches over the restiform body as a close fitting cap, then ascends along the fourth ventricle in the angle between the cerebellum and the medulla to the region of Bechterew's nucleus and up as far as the mesencephalic root of the trigeminus. A deeper lesion involving the dentate nucleus, as well, produced the degeneration as described above as well as additional fibers in the brachium conjunctivum and also fibers passing down the brachium pontis to the nuclei of the III and IV cranial nerves. Fibers were also traced to the abducens nucleus but none into the posterior longitudinal bundle.

De Villaverde ('20, p.143) reported the results of operations on the "flocculus" in 19 rabbits of which only 5 lived the required 12 to 14 days after operation. His lesions, as he states, were not what he had hoped for and involved not only large areas of the cerebellum but extra-cerebellar structures as well. From his description of the "flocculus", on p.185, one must conclude he refers to that part which we would designate as the paraflocculus. He concluded (p.198) that all the fibers from the cortex synapse in the dentate nucleus; that no fibers go to the abducens nucleus. Other beliefs expressed were that fibers go from the dentate nucleus out the brachium pontis to the pontine nuclei of the same and opposite side and that the "flocculus" of the rabbit is homologous to the human cerebellar hemisphere.

Brouwer and Coenen ('21) removed the "flocculus", probably paraflocculus, in 5 rabbits with more or less injury to the dentate nucleus. The degeneration described in the homolateral brachium conjunctivum was present in proportion to the extent of the injury to the dentate nucleus and was said to be absent entirely when the injury was minimal. They found no direct connection between the "flocculus" and the dorsal longitudinal bundle, the abducens nucleus or the medulla oblongata. They did trace degenerated fibers to the middle and dorsal part of the vermis. Their lesions, as Jansen ('33, p.395) has pointed out were of sufficient depth to probably involve incoming fibers to the vermis.

Allen ('24, p.402) reported the results of cortical injuries to the "lobulus petrosus" as well as other parts of the cortex of vermis and hemisphere without causing degeneration in any of the recognised efferent paths from the cerebellum. He did observe degenerated fibers from the vermis to the lateral vestibular nucleus.

Marburg ('24, p.14; '24a, p.314) fails to differentiate flocculus and paraflocculus. He shows fibers from what he has labeled "flocculus" going to the dentate nucleus, out the brachium conjunctivum and possibly to Deiter's nucleus.

Kusume ('26, p.107; '27, p.138) following lesions of the "flocculus" in rabbits found degenerated fibers in the lobus medianus, central nuclear area, the lobus paramedianus, the lobus anterior, the lobus ansiformis, the uvula, and the lingula, principally on the side of the lesion. Extra-cerebellar fibers were found in the dorso-lateral portion of the corpus restiformis, in the region of the facial genu, in the anterior medullary velum on both sides. There was also perceptible degeneration in the posterior longitudinal bundle and in the homolateral brachium conjunctivum. He also found degenerated fibers in the homolateral brachium pontis or to the region of the nucleus of the III or VI cranial nerves.

Hohman ('29, p.460), recognizing fully the dangers of false interpretation in the use of the Marchi technique, found that lesions restricted to the cortex of the paraflocculus in cats produced degeneration only to the homolateral dentate nucleus. He did not injure the flocculus in any case.

Mussen ('30, p.448) stated that the paraflocculus in rabbits was destroyed without injury to the dentate nucleus and an obvious tract of degenerated fibers passed directly into the superior cerebellar peduncle and on to the red nucleus. He then stated that a loss of the paraflocculus results in a loss of the righting reflex on the side of the lesion. He cites earlier work by himself ('27, p.344) where he had made the statement that the destruction of the flocculus produced such a loss of function.

Jansen ('33) has described the degeneration of arcuate fibers resulting from lesions of the paraflocculus in rabbits. These, he found, to extend only to the folia of the uninvolved portions of the paraflocculus and to the flocculus. From his diagrams one would assume that the other degenerated fibers ended only in the lateral deep cerebellar nuclei. He does not show the results of any injuries to the flocculus.

The following observations have been made concerning the afferent supply to the parts of the cerebellum with which we are chiefly concerned. Vestibular root fibers to the cerebellum of mammals are mentioned as follows: to the cerebellar cortex by Cajal ('09, p.763, '11 p.141), Camis ('30, p.24), Ingvar ('19, p.366), Dusser de Barenne ('24, p.594), Grey ('26, p.353), Miller ('26, p.128), and Abbie ('34, p.23); to the deep nuclei, especially the festigial nuclei, by Andre-Thomas (1898, '12, p.80), Winkler ('19, p.475), A. Van Gehuchten

('06, p.566 and p.857), Leidler ('16, p.199), Sachs ('21, p.144), Grey ('26, p.353), Ingvar ('18, p.386), Dusser de Barenne ('24, p.594), Miller ('26, p.128), and P. Van Gehuchten ('27). According to Marburg (24a, p.286) primary root fibers to the cerebellum have been found by Probst ('02) and Tschermak (1898) while Lewandowsky ('04) is quoted as being unable to find them. Winkler ('21, p.305) denies that direct root fibers of the vestibular nerve go to either the cerebellar cortex or nuclei in the higher mammals although he previously stated ('19, p.475) that they ended in the nucleus fastigii in the rabbit. The exact projection of the root fibers has been shown by Ingvar in the cat ('18, p.386). He describes the fibers as ending in the fastigial nucleus of both sides, the dentate nucleus of the homolateral side and in the cortex of the nodulus, the uvula, the flocculus and in the lowermost folia of the anterior vermian lobes chiefly the lingula.

Secondary vestibulo-cerebellar fibers are described by Van Gehuchten ('00a, p.182) originating in Deiter's and Bechterew's nuclei and passing to the roof nuclei. Such connections are not mentioned, however, by Van Gehuchten ('04 to '06), Rasmussen ('32), Miller ('26) nor Grey ('26). Paul Van Gehuchten ('27) concludes that there are apparently no important afferent connections of the vestibular nuclei with the cerebellum.

It has been assumed by several authors that these secondary vestibulo-cerebellar fibers go to most parts of the cerebellum. A careful search of the literature has failed to disclose any evidence for such an assumption. Winkler ('19), always emphasizing the features which the cochlear and vestibular divisions of the VIII nerve have in common especially in their central course, states (p.477) that secondary octavo-cerebellar fibers originate in Deiter's nucleus, the ventral cochlear nucleus and the tuberculum acousticum and end in all the deep cerebellar nuclei. Later Winkler ('21, p.305) changed his schema and shows secondary octavo-cerebellar fibers originating from the ventral cochlear nucleus and the triangular vestibular nucleus.

Kappers ('20, p.420 and '21, p.726) quotes Bruce and Winkler, Hatschech and Schlesinger, and Bruce, to the effect that there are afferent cerebellar connections from the triangular vestibular nucleus and states that there is some evidence to support the contention that these end largely in the uvula and nodulus. Insert (see opposite page) Kuzume ('26, p.92 and '27, p.138) has attempted to solve this problem by the use of the Nissl stain for chromatolysis. Following destruction of the "flocculus", probably paraflocculus, he found chromatolysis in the following nuclei: the dentate nucleus, the fastigial nuclei, the middle sized cells of Deiter's nucleus and the abducens nucleus. The dorsal part of the oculomotor nucleus also showed some chromalytic change. Bechterew's nucleus and the nucleus dorsalis of the acoustic were entirely spared.

Yoshida ('24) has described chromatolysis in Deiter's nucleus following lesions in various parts of the cerebellar cortex.

A review of the literature on the termination of spino cerebellar fibers will not be attempted here. The literature is summarized by McNalty and Horsley ('09) and Beck ('27). Ingvar ('18, p.400) has traced a few fibers from the dorsal spinocerebellar tract to the paraflocculus, especially shown in one specimen. He found no fibers to the flocculus or nodulus. The remainder of the fibers of both the spinocerebellar tracts were shown to be distributed to the uvula, pyramis, all of the anterior lobe and the lobulus simplex. Beck ('27, p.84) traced a small bundle of the dorsal spinal cerebellar tract to the stalk of the "flocculus" but the exact course could not be determined. He did not distinguish between flocculus and paraflocculus. Klimoff in his schema ('99, p.112) shows no fibers coming in the inferior peduncle to the flocculus. Collier and Buzzard ('03, p.580) applied Marchi technique to transverse lesions of the cord in humans. They observed degenerated fibers through the restiform body to the stalk of the flocculus in every case.

The projection of the olivo cerebellar fibers are less well known. Holmes and Stewart ('08) give no information concerning olivary fibers to the flocculus.

Lewandowski ('04) describes olivo-cerebellar fibers to the "flocculus" but Kappers ('21, p.730) is of the opinion that they probably go to the paraflocculus. Wilson ('33, p.474) has expressed the opinion that the huge size of the medial accessory olive in the whale may be related to the enormously developed paraflocculus in this animal. Kooy ('18, p.663) has also expressed this opinion.

Ponto-cerebellar fibers are distributed to the hemisphere only, according to Andre-Thomas ('12, p.24) and Masuda ('14), but to the vermis as well according to Spitzer and Karplus ('08) and Besta ('13). Kappers ('21, p.731) states that they have never been found going to any part of the "flocculus". Wilson ('33, p.443) estimates that in the whale 60% of the incoming fibers to the paraflocculus originate in the pontine nuclei. Klimoff ('99, p.218) describes fibers to the "flocculus" following lesions of the brachium pontis. The description of the operation would suggest that he possibly injured secondary vestibulo-cerebellar fibers.

Ingvar ('18) considers that ponto-cerebellar fibers end chiefly in the lobulus ansiformis, paramedianus and middle lobe of the vermis. He has done no degeneration experiments in this connection. He has observed (p.404) that in the brain of a cat, showing a congenital atrophy, the middle lobe of the "vermis", the lobulus ansiformis, the lobulus paramedianus and also the paraflocculus showed developmental defects.

The importance of the trigeminal nerve in the cerebellum is becoming more and more apparent. Edinger ('08, p.484) mentions the Vth nerve along with other cranial nerves as having connections with the cerebellum. Kappers ('21, p.726) states that the presence of such a connection is becoming more and more substantiated. The work of Herrick and Larsell, as mentioned above, has demonstrated the importance of the trigeminus in the phylogeny of the cerebellum. Abbie ('34, p.33) states that in Echnida aculeata the Vth nerve is very large and has many cerebellar connections chiefly to the paraflocculus. He concludes (p.17) that the cerebellum receives direct root fibers and also fibers from the chief and spinal Vth nuclei, and states that the size of the Vth nerve and the paraflocculus is well correlated in Echidna, Ornithorhynchus, Zeuglodonts and monotremes. Ingvar ('23, p.318) makes the suggestion that the fact that the paraflocculus regresses so strikingly in man may be related "to the fact, that owing to the erect gait, the trigeminal region has not the same importance in motility in man as it has in the quadrupeds, where it is a very important organ for grasping, defense, etc."

Other medullary centers send afferent connections to the cerebellum according to Edinger ('08, p.484) and Krause ('30). The latter, using the Marchi method, followed degenerated fibers from lesions involving the sensory nuclei of the vagus and glossopharyngeal nerves into the opposite restiform body to end in the lobus medianus anterior and in the uvula and lingula. Russell (1897, p.437) and Ferrier and Turner (1895) denied the presence of such connections when they were advocated by Edinger.

Reticulo-cerebellar fibers have been described by Van Gehuchten ('02, p.42 and '04, p.138) and by Papez ('30, p.18). The latter investigator traced them to the "flocculer lobes".

Jensen ('33) has recently summarized the work of Clark and Horsley ('05), Brouwer and Coenen ('21), and Saito ('23) on the arcuate fibers of the cerebellum. Variable results have been obtained as to their extent and distribution. Kusume ('26, '27) and Bender ('32) have also studied this problem. As Jensen has pointed out, unless the lesions are superficial and restricted to a single part of the cortex, the results are inconclusive. So far no lesions have been reported on the flocculus or nodulus without involvement of other parts of the cerebellum. Many have used the term flocculus but on analysis, it is clear that they have always referred to the paraflocculus.

Practically nothing is known concerning the connections of the nodulus, considered separately from other parts of the cerebellum. Klimoff (1899), Clark and Horsley ('05), Allen ('24), Hohman ('29) and others have each observed the connections of the vermis to the festigial nuclei. They also have described fibers, especially from the anterior part of the vermis, to the vestibular nuclei. Bender, ('32, p.24) in a study on dogs following lesions of the basilar parts of the cerebellum, is able to trace fibers to the roof nuclei. By so-called long cortico-fugal fibers, the basal cerebellar folia are said to be connected with the vestibular nuclei and adjacent reticular formation of the same and the opposite sides. From an analysis of her lesions it is difficult to exclude possible injury to tracts originating in cerebellar and para-cerebellar nuclei. She describes association bundles to all parts of the paleo-cerebellum (vermis and flocculi). The fibers to the flocculus, found in dog 17, may be secondary vestibulo-cerebellar fibers. The lesion in this animal involves, in addition to the cortex of the uvula, nodulus, and lingula, the medial surface of the left inferior peduncle. All other lesions were obviously even more extensive and could hardly have avoided deep cerebellar structures. She states that the nodulus receives fewer association bundles than any other part of the vermis.

Ingvar ('18, p.402) in his schema of the efferent supply to the cerebellum puts the flocculus and the nodulus in a separate class from all other parts of the cerebellum. These two lobules are shown to be the only parts of the cerebellum which receive purely vestibular efferent connections.

More information is needed concerning the possible differences in the efferent cortical connections of specific parts of the so-called "vermis".

DESCRIPTION

The Paraflocculus

In the experimental procedure on which the present study is based, the paraflocculus, alone was damaged only in rat 17 (figs. 20, 21 and 22); deep lesions of the paraflocculus and flocculus, including incoming fibers to a greater or less extent, were made in rats 5, 10, 31 and 32 (figs. 26 and 27); the paraflocculus and lobulus ansiformis were damaged in rat 21 and cat 9 (figs. 1 and 2); the lobulus ansiformis, the paraflocculus and flocculus in rat 4 and cat 11 (figs. 3, 4, 5, 6, 7 and 8); and the lobulus ansiformis, paraflocculus and vestibular nerve in cat 13 (figs. 12, 13, 14, and 15). All of these specimens were stained by the Marchi method.

Degenerated fibers from lesions of the cortex of the paraflocculus in both the cat and the rat can be followed to the ventrocaudal portion of the dentate nucleus and to the lateral extremity of the nucleus interpositus where it is continuous with the dentatus (fig. 53). In rat 17, the fibers pass medially from the paraflocculus into its stalk (fig. 23) and then caudal to the incoming pontine fibers to end in the ventrocaudal portion of the dentate nucleus (fig. 24). Some of the fibers extend farther medially to end in the basilar portion of the nucleus interpositus (fig. 25). In cats 9, 11, and 13, lesions in the paraflocculus were followed by similar degenerated tracts (figs. 1 to 19). No fibers from the paraflocculus could be traced in either the cat or the rat to the fastigial nucleus or the vestibular nuclei. The findings are quite in close agreement with those of Hohman ('29).

Arcuate fibers from the paraflocculus pass to the three or four folia adjacent to the lesion and in lesser numbers to the flocculus (figs. 2, 4, 5, 6, 13, 14, 15, 21, 22 and 23). None were found connecting the paraflocculus and lobulus ansiformis. In rats 31 and 32 in which the entire paraflocculus was destroyed, fibers could be traced passing to the uvula and pyramis (figs. 26, 27 and 29). These appear to have their origin in the medial portions of the paraflocculus since none are found after lesions confined to the lateral region (fig.21). These fibers all terminated in the lateral parts of the uvula and pyramis. The pyramis and uvula are continuous with the paraflocculus in the young rat (Larsell and Dow '35). These arcuate fibers in the rat appear to agree well with those found by Jansen ('33) in the rabbit. He does not describe any experiments in which the medial portion of the cortex of the paraflocculus was destroyed.

Incoming fibers to the paraflocculus are not well known. Spino-cerebellar fibers, (Ingvar '18), trigeminal connections (Abbie '34), and (Ingvar '23), olivary connections (Kooy '16) and (Wilson '33), pontine fibers (Klimoff 1899) and (Wilson '33), and possibly reticulo-cerebellar connections (Papez '30) have all been described or suggested as being incoming fibers to the paraflocculus. In this study no primary or secondary vestibular fibers were found to end in the paraflocculus (figs. 16, 40, 43 and 52). Experiments using the Nissl method following paraflocculer lesions in 3 rats show no chromatolysis in the vestibular nuclei, the deep cerebellar nuclei, the inferior olive, the pontine nuclei, the sensory Vth nucleus including the dorsomedial portion of sensory V, nucleus of the cerebellar commissure of Larsell ('35), into which according to Allen ('19, p.190) the mesencephalic V root sends collaterals. The lack of chromatolysis does not eliminate the possibility of a connection between some of the nuclei mentioned and the paraflocculer cortex in view of the small size of the lesion compared to the wide areas of cerebellar cortex into which many of these nuclei are known to send fibers. We are unable to corroborate Kuzume's ('26) description of extensive chromatolysis following similar lesions in the rabbit.

The Lobulus Ansiformis

The lobulus ansiformis was damaged in cats

9, (figs. 1 and 2) 11, (figs. 3, 4, 5, 6 and 7) and 13, (figs. 12, 13, 14 and 15) and in rats 16, 21, and 4. The degeneration can be traced in all cases to the nucleus dentatus (figs. 8, 9, and 16), with fibers from the more anterior portions of Crus I and the lobulus simplex also going to the nucleus interpositus (fig. 9). Although no figures are given to show this degeneration in the rat, the distribution in this animal is identical to that found in the cat. Arcuate fibers connect Crus I lobulus ansiformis to Crus II lobulus ansiformis and vice versa. Fibers from Crus II can be traced to neighboring folia of the lobulus paramedianus. No fibers were traced to the midline unless the lesion was deep enough to involve incoming fibers, probably pontine. This differs from the conclusion reached by Jansen ('33, p.399).

The Flocculus

The flocculus alone was damaged in rat 30 (figs. 31, 32 and 33). It was damaged, together with the paraflocculus, in rats 5 and 10; with the paraflocculus and lobulus ansiformis rat 4 and cat 11 (figs. 3, 4 and 7); with the paraflocculus and brachium pontis in rats 12, 31 and 32 (figs. 26 and 27).

Degeneration in the cat. From the lesion on the cat's flocculus (fig. 7) fibers of degeneration pass medially above and rostral to the lateral recess of the fourth ventricle and just caudal and below the brachium pontis (fig. 8). Some of the fibers ascend into a cradle-like bundle of fibers beneath the nucleus dentatus (fig. 9) which is part of the brachium conjunctivum. Here they intermingle with fibers from the lobulus ansiformis, which descend and apparently terminate in the neighboring portion of nucleus dentatus (fig. 9). Some of the fibers retain a more basal position rostrally of the dorsal cochlear nucleus. These fibers from the flocculus pass between the upper fibers of the corpus restiforme (fig. 10) to terminate in the lateral part of the Deiter's nucleus (fig. 11). Those which pass medially in company with fibers to the brachium conjunctivum end in the superior vestibular nucleus of Bechterew (fig. 11). None can be followed to the fastigial nucleus proper, although the vestibular nuclei and the basal portions of both the nucleus interpositus and fastigii are, at many points, continuous.

Degeneration in the rat. The fibers from the lesions on the flocculus (figs. 27 and 33) pass medially along the rostral apex of the lateral recess of the fourth ventricle and are well separated from the fibers of the paraflocculus (figs. 28 and 34). Although a few degenerated fibers are seen in the basal portion of the adjacent dentate nucleus, the bulk of the fibers terminate in the vestibular nuclei, as in the cat. After arching over the restiform body, the majority of the floccular fibers terminate in the lateral portion of Deiter's nucleus (fig. 29) which lies just medial to the restiform body. The remainder of the fibers forms a small compact bundle at the angle between the base of the cerebellum and the medulla. This bundle passes into the medial portion of the juxta-restiform body. In the sagittal plane at which the dorsal cochlear root fibers pass deep into the substance of the medulla, this tiny "angular bundle of Löwy" turns sharply rostrally to terminate in the superior vestibular nucleus of Bechterew (fig. 30). No fibers pass to the fastigial nuclei. There is no doubt that these fibers come exclusively from the flocculus and not from any other part of the so-called "formatio vermicularis" from which they are said to be derived by Löwy. It is difficult to compare these findings with previous experimental work because of the lack of details given concerning the exact location of the lesions. There probably has been no previous experiments where the lesion was confined to the flocculus proper.

The afferent fibers to the flocculus are entirely vestibular and will be described below.

The Nodulus, Uvula and Pyramis

Lesions to study the connections of nodulus, uvula and pyramis have been made in rats 14 and 15 (fig. 35), in which the uvula and nodulus were damaged; rat 18 (figs. 37 and 38) in which the pyramis and uvula were damaged; and rat 23 in which all three lobules were damaged, together with the nuclei fastigii and interpositus. All of the above have been stained with the Marchi method and are of value in demonstrating the efferent connections of these parts. The afferent supply to the nodulus and uvula is discussed later under vestibular connections. The stain for chromatolysis has been used in the left half of the cerebellum of rats 14 and 15, and the whole cerebellum of rats 20 and 22. This procedure has given meager results.

Fibers from the nodulus and the uvula end in the fastigial nucleus and in all the vestibular nuclei of the same side (figs. 35 and 36). From the medial part of the pyramis, fibers pass to the fastigial nucleus (fig. 37), but no degeneration is found in the bundles of the cerebello-vestibulo fibers (c.v.f.)(fig. 38). The lateral part of the pyramis, which is closely associated with the lobulus paramedianus, sends fibers to the medial part of the nucleus interpositus (fig. 38). There is no evidence from this study that fibers, in any significant number, cross the midline to end in any of the controlateral nuclei. Arcuate fibers between the lobules are not numerous. None are found from the uvula to the nodulus (fig. 37) nor from the uvula to the pyramis in rats 14 or 15 (fig. 35). No lesion has as yet been made entirely restricted to the nodulus, so arcuate fibers from it have not been studied. Interconnections are observed between the lesion and the cortex of the same lobule medial and lateral to the lesion. These occasionally cross the midline if the original lesion was placed quite medially. If the lesion involves the base of the taenia between the uvula and the para-flocculus, a small amount of degeneration may be observed to extend as far as the medial part of the para-floccular cortex and some degeneration is observed to the flocculus, the latter presumably largely due to involvement of secondary vestibular fibers (see page no. 30). Connections similar to those of the nodulus and uvula have been described by many previous workers but few have differentiated between the specific lobules of the posterior part. Most of the fibers to the vestibular area are described as being from the vermis or from the anterior part of the vermis.

The afferent connections of nodulus, uvula, and pyramis are discussed in the description of the vestibular system.

Vestibulo-cerebellar Fibers

Root fibers of the vestibular nerve are involved in the lesions in rats 6, 29, 27 (figs. 39, 40, and 41), and cat 13 (figs. 12 and 13). The latter two probably represent incomplete severing of the vestibular nerve, judging from the absence of vestibular symptoms following the operation. In rats 8 and 28 the vestibular ganglion is not destroyed and consequently the degeneration is confined to the distribution of the cochlear division. This has been useful as a control in interpreting some of the other lesions which were more extensive.

In cat 13, the fibers are traced into the flocculus lateral to the corpus restiforme (fig. 16). Ingvar ('18, p.386) shows fibers from the vestibular nerve coming into the flocculus around the restiform body. Sagittal series clearly show that this is not the case (figs. 17 and 18). The remaining vestibular fibers pass medially between the restiform body and the spinal Vth root (fig. 17) to terminate in the vestibular nuclei (fig. 18). The vestibular fibers which ascend toward the cerebellum pass through Deiter's and Bechterew's nuclei and the basilar portion of the fastigial nucleus (figs. 18 and 19). They terminate in part in these nuclei but some fibers continue on to end in the cortex of the nodulus and the lower folia of the uvula of the same side (fig. 19). In this cat the lesion of the vestibular nerve was incomplete, but no degenerated root could be traced to the lingula or to any other parts of the anterior lobe. Also none could be traced to the deep nuclei or to the cortex of the opposite side.

These results were confirmed in the rat except that direct fibers to the flocculus were not demonstrated with certainty (figs. 39, 40, 41 and 42). The results in this particular phase of the work were somewhat unsatisfactory because the lesions when they involved the VIII nerve in its entirety always involved adjacent medullary structures, and the lesions in rat 29 and cat 13 were probably incomplete. From these experiments alone, no conclusion is possible as to whether the degeneration described is the result of injury of the vestibular root (Ingvar '18) or of the ventral cochlear nucleus (Winkler '19 and '21). The major part of previous work would, however, indicate that they are truly vestibular root fibers.

Secondary vestibulo-cerebellar connections have been studied by means of fortunate lesions in the juxta-restiform body of the rats 33, 34 and 35. In rat 33 (figs. 46 and 47), the lesion was a complete division of the juxta-restiform body without involving the restiform body proper. There was a very small lesion on the under surface of the nodulus and a slight bruising of the left posterior longitudinal bundle (fig. 48). The main lesion unfortunately extends far enough rostrally to sever the ventral spino-cerebellar tract (fig. 46). Rats 34 and 35 have similar, though more extensive, lesions. The degeneration found, however, is in harmony in all particulars with that from the almost ideal lesion in rat 33 (figs. 46 and 47).

The secondary vestibulo-cerebellar fibers to the homolateral side (fig. 47) pass to the nodulus and uvula by the same course as was taken by the root fibers (fig. 42). The fibers to the homolateral flocculus are divided into dorsal and ventral groups by the restiform body (fig. 45). The dorsal division arches above the restiform taking a course parallel to the efferent fibers from the flocculus, while the ventral division passes between the chief sensory nucleus of the trigeminus and the fibers of the brachium pontis (fig. 45). As the sections are read laterally these two groups come together (fig. 44) and terminate entirely in the flocculus (fig. 43). None are found in the paraflocculus (fig. 43).

The secondary vestibular fibers to the contralateral parts of the cerebellum pass across the midline both caudally and rostrally of the fastigial nuclei. The majority of the fibers to the uvula and nodulus cross at the base of these lobules. At the lateral extremity of the contralateral part of the nodulus a few fibers are present at the base of the taenia of the fourth ventricle. They pass into the flocculus (figs. 48, 49, 50, 51 and 52). These fibers appear to represent the lateral commissure of Larsell. The majority of fibers to the contralateral flocculus take a more rostral course and cross the mid-sagittal plane in company with the undegenerated fibers which make up the uncinate fasciculus of Russell (figs. 48 and 49). A few turn medially to terminate in the vestibular nuclei. Those destined for the contralateral flocculus continue laterally taking a course rostral and ventral to the opposite restiform body and caudal to the brachium pontis (fig. 50) to enter the flocculus at its rostromedial extremity (fig. 51). They end only in the flocculus (fig. 52). These vestibulo-cerebellar connections agree quite well with those described by Shimazono ('12) in the birds. From this material it is impossible to tell whether secondary vestibular fibers go to the anterior cerebellar lobe or not, because the ventral spino-cerebellar tract was also severed, and the degenerated fibers to anterior folia can be accounted for on this basis. However, the course of the crossed fibers at the base of these folia and the presence of efferent vestibular connections from this region, pointed out by Allen ('24, p.438), Bender ('32, p.24) and others, makes it probable that there are secondary vestibulo-cerebellar connections to the folia of the anterior lobe. The degeneration to the flocculus, nodulus and uvula is not due to injury of the ventral spino-cerebellar fasciculus is shown by the fact that this bundle was also accidently severed in rat 11, and in this series its distribution is limited to the anterior lobe of the cerebellum. This is in agreement with the results of MacNalty and Horsley ('09), Ingvar ('18) and others on the termination of the ventral spino-cerebellar tract. The lingula is said to be free of spino-cerebellar fibers according to MacNalty & Horsley ('09, p.250) while Ingvar finds that a few fibers of the ventral spino-cerebellar tract end in the lingula ('18, p.400).

The number of degenerated fibers to the contralateral flocculus appears to be only slightly less than those to the homolateral flocculus. So far as conclusions from these experiments are justified as to the ratio of secondary fibers to root fibers in a given area, the homolateral secondary vestibular fibers are about three times as numerous as the root fibers. When those from the opposite side are included, all secondary vestibular fibers are about five times as numerous as the root fibers.

Marchi preparations are inadequate to determine specifically which of the vestibular nuclei give rise to nucleo-cerebellar fibers and the experiments made, using the Nissl method have been unsatisfactory. The review of the literature (see above p.12) gives very little information bearing on this point. In the schema (fig. 53) I have purposely omitted a cell body on the secondary vestibulo-cerebellar fibers.

SUMMARY AND CONCLUSIONS

1. The literature concerning attempts to learn, by experimental methods, the connections of the flocculus, paraflocculus, nodulus and uvula is reviewed. Careful attention is given to the previous work done on the direct and secondary vestibulo-cerebellar connections.

2. The importance of considering the flocculus and paraflocculus separately in determining their fiber connections is emphasized. Attention is called to the lack of such a distinction in much of the previous work and the difficulty therefore of properly interpreting the results.

3. The material used in this study consists of 13 cats and 35 rats. The experiments on 4 cats and 28 rats were sufficiently successful to be used in this study.

4. The material was either stained by a standard Marchi method for degenerated fibers or by the Nissl stain for chromatolysis of nerve cells.

5. What are believed to be direct vestibular root fibers, are traced to the vestibular nuclei, the fastigial nucleus, the flocculus, the lateral half of the uvula and nodulus all on the same side.

6. A lesion confined to the juxta-restiform body in the rat involves incoming fibers to the

cerebellum. The majority of these fibers are believed to be secondary vestibulo-cerebellar fibers. Their exact origin is not known. They are distributed to both fastigial nuclei and the cortex of both the flocculi, the nodulus and the uvula. They probably also end in the basilar parts of the anterior lobe. Their distribution resembles the vestibulo-cerebellar connections in lower forms. In mammals, however, the course of these oldest cerebellar connections has been modified and pushed aside by the extensive development of spino-cerebellar and ponto-cerebellar systems. No secondary vestibulo-cerebellar fibers were studied in the cat.

7. The paraflocculus in both the rat and the cat sends efferent fibers to the ventrocaudal border of the dentate nucleus and into the lateral part of the basilar portion of the nucleus interpositus. The fibers are sharply limited from the efferent fibers from the flocculus in their course and distribution. No fibers from the cortex of the paraflocculus leave the cerebellum by any of its peduncles. Little information was gained concerning the afferent supply to the paraflocculus. Lesions involving primary and secondary vestibulo-cerebellar fibers cause no degeneration in the paraflocculus. Lesions confined to the paraflocculus followed by stain for chromatolysis failed to disclose the origin of its incoming fibers. From lesions confined to a few folia of the paraflocculus in the cat, arcuate fibers pass to neighboring

folia within the paraflocculus and a few pass into the homolateral flocculus. In the rat the same condition is found except that when the medial extremity of the paraflocculus is damaged, arcuate fibers pass to the lateral part of the pyramis and uvula.

8. The flocculus sends efferent fibers, in both the rat and the cat, to Deiter's and Bechterew's nuclei. None end in the fastigial nuclei. The flocculus receives direct root fibers of the vestibular nerve in the cat and probably also in the rat. These fibers enter the flocculus lateral to the restiform body. In the rat the flocculus receives secondary vestibulo-cerebellar fibers from the vestibular nuclei of the same and opposite sides. Arcuate fibers connect the cortex of the flocculus with the nearest portions of the parafloccular cortex.

9. The lobulus ansiformis sends fibers to the dentate nucleus in both the cat and the rat. The anterior part of Crus I lobulus ansiformis and the lobulus simplex send fibers to the nucleus interpositus also. Crus I and Crus II of the lobulus ansiformis are interconnected by arcuate fibers. Crus II sends arcuate fibers to the nearer folia of the lobulus paramedianus. No true arcuate fibers pass to the "vermis" from the lobulus ansiformis in either the cat or the rat nor are the two cerebellar "hemispheres" connected by arcuate fibers.

10. In the rat, fibers pass from the medial part

of the pyramis to the fastigial nucleus. The lateral part of the pyramis is connected to the nucleus interpositus. It sends no fibers to the vestibular nuclei. Neither direct nor secondary vestibular fibers end in the pyramis. Arcuate fibers from the lateral part of the pyramis pass to the nearer folia of the lobulus paramedianus. None go to the lobus medius.

11. In the rat the uvula and nodulus send fibers to the fastigial nucleus on the same side as the lesion. The nodulus and to some extent the uvula also, send cerebello-vestibular fibers through the fastigial nucleus into the juxta-restiform body where they terminate in the homolateral vestibular nuclei. The nodulus and uvula receive primary root fibers of the vestibular nerve in their homolateral halves. They receive secondary vestibulo-cerebellar fibers both crossed and uncrossed. No arcuate fibers pass from the uvula to the nodulus or pyramis. The arcuate fibers of the nodulus were not determined.

12. Ample evidence is presented to indicate the necessity for differentiating between the flocculus and the paraflocculus in all future experiments on these parts of the cerebellum. The fiber connections of these lobules do not justify their classification into a single lobe.

13. This work indicates, as Ingvar has shown,

that the cerebellar vermis consists of separate parts with different connections. It re-emphasizes the fallacy of considering the vermis as a single anatomical entity.

14. This study shows, by experimental methods, that the division between the flocculo-nodular lobe and the corpus cerebelli is fundamental in the morphology of the cerebellum.

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ABBREVIATIONS USED IN FIGURES.

br. conj.	brachium conjunctivum
br. p.	brachium pontis
c. j. r.	corpus juxta-restiforme
c. p.	cerebral peduncle
c. r.	corpus restiforme
c. tr.	trapezoid body
c. v. f.	cerebello-vestibulo fibers
cr. I., l.a.	crus I lobulus ansiformis
cr. II., l.a.	crus II lobulus ansiformis
ex. arc. f.	external arcuate fibers
fis. po. lat.	fissura posterolateralis
fis. ppd.	fissura prepyramidalis
fis. pr.	fissura prima
floc.	flocculus
floc. f.	fibers from the flocculus
l. a.	lobulus ansiformis
l. a. f.	fibers from the lobulus ansiformis
l. cent.	lobulus centralis
l. cul.	lobulus culmenatis
l. p. med.	lobulus paramedianus
l. r. v. 4	lateral recess of 4th ventricle
l. simp.	lobulus simplex
ling.	lingula
lo. ant. (1,2,3 and 4)	lobus anterior and divisions (Riley)
lo. med.	lobus medius (Ingvar)

med. obl.	medulla oblongata
mes.	midbrain
mes. V	mesencephalic root of the trigeminus
mes. V f.	fibers of the mesencephalic root of the trigeminus
n. IV	trochlear nerve
n. V.	trigeminal nerve
n. VIII	acoustic nerve
nod.	nodulus
nu. B.	Becterew's nucleus (superior vestibuler nucleus)
nu. c.	cochlear nucleus
nu. L.	Deiter's nucleus (lateral vestibuler nucleus)
nu. dent.	nucleus dentatus
nu. fast.	nucleus fastigii
nu. int.	nucleus interpositus
nu. m. V	motor nucleus of the trigeminus
nu. ol. sup.	superior olivary nucleus
nu. parol. sup. med.	nucleus paroliveris superior medianus
nu. s. V	sensory nucleus of the trigeminus
nu. tr.	triangular nucleus
p.	pons
p. f.	pontine fibers
p. long. fas.	posterior longitudinal bundle
pfl.	parafloeculus
pfl. f.	fibers from the parafloeculus

pyr.	pyramis
r. V.	root of the trigeminal nerve
r. V M.	motor root of the trigeminal nerve
r. V sp.	spinal root of the trigemial nerve
r. VII	root of the facial nerve
r. VIII	root of the acoustic nerve
r. d. c. VIII	root of the dorsal cochlear portion of the acoustic nerve
r. d. c. VIII f.	fibers from the dorsal cochlear root of the acoustic nerve
r. v. VIII	root of the vestibular part of the acoustic nerve
r. v. VIII f.	fibers from vestibular root of the acoustic nerve
s. v. f.	secondary vestibulo-cerebellar fibers
un. fac.	uncinate bundle of Russell
uv.	uvula
v. s. c. t.	ventral spino-cerebellar tract
v. 4	fourth ventricle

Fig. 1 -- Lateral view of the cerebellum of cat no. 9.
Lesion in solid black. 1.5x

Fig. 2 -- Schema of the cat cerebellum modified from
Riley ('29). Lesion in cat no. 9 in solid
black with distribution of the arcuate
fibers shown by stippling.

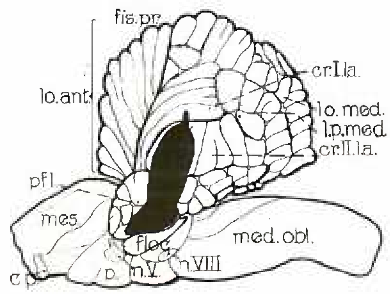

fis.pr.
cr.I.la.
lo.ant.
lo.med.
l.p.med.
cr.II.la.
pfl
mes
floc
med.obl.
n.VIII
n.V.

Fig. 1

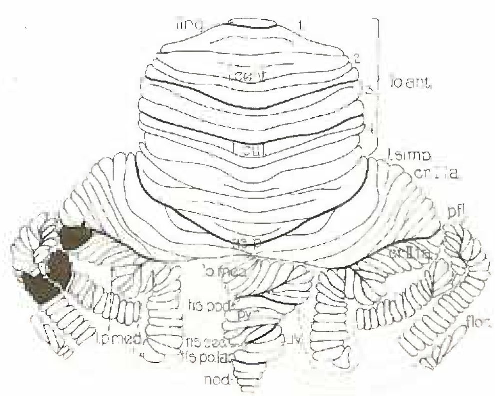

1
2
3
lo.ant.
pfl
py
l.p.med.
nod

Fig. 2

Fig. 3 -- Lateral view of the cerebellum of cat no. 11. Lesion in solid black. 1.5x.

Fig. 4 -- Schema of the cat cerebellum modified from Riley ('29). Lesion in cat no. 11 in solid black with the distribution of the arcuate fibers shown by stippling.

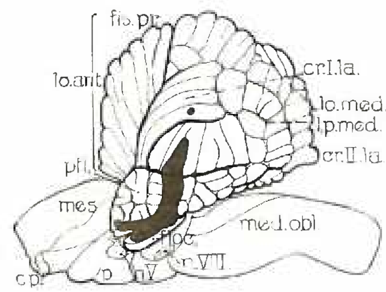

fis.pr
lo.ant
cr.I.la.
lo.med.
l.p.med.
cr.II.la.
pfl.
mes
med.obl
floc
c.p.
p
n.V
n.VII.

Fig. 3

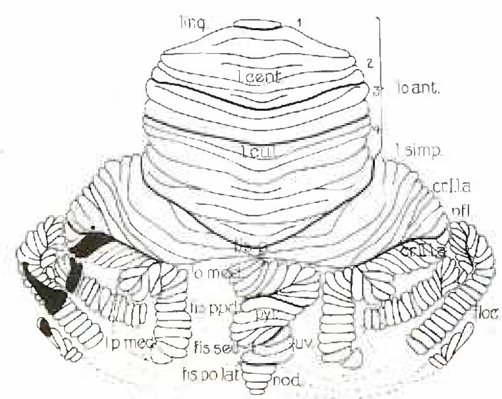

ling.
1
2
l.cent
3
lo.ant.
l.cul
l.simp.
cr.I.la
pfl.
cr.II.la
lo.med.
fis.ppd.
pyr.
floc
l.p.med.
fis.sec.
uv.
fis.po.lat.
nod.

Fig. 4

Fig. 5 -- Sagittal section of the lateral part of the cerebellum of cat no. 11. 3.75x. Note the lesion and the arcuate fibers to adjacent folia. (11 L, 2-2-2).

Fig. 6 -- Sagittal section of the cerebellum of cat no. 11 medial to fig. 5. 3.75x. (11 L, 5-1-1).

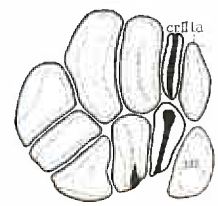


Fig. 5

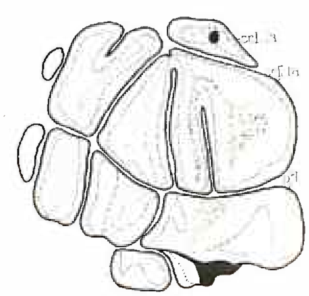


Fig. 6

Fig. 7 -- Sagittal section of the cerebellum of the cat no. 11, medial to fig. 6. 3.75x. (11 L, 7-2-1).

Fig. 8 -- Sagittal section of the cerebellum of cat no. 11, medial to fig. 7. 3.75x. Shows fibers from lobulus ansiformis and paraflocculus separated by the incoming pontine fibers. The fibers from the flocculus are isolated from the others being located just above the fourth ventricle. (11 L, 13-1-3).

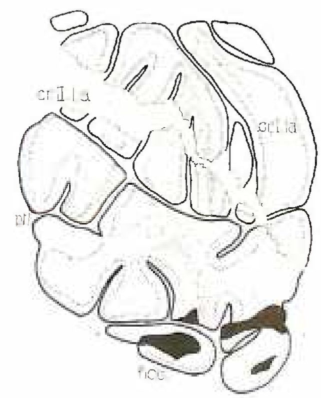

cr II a
pfl
flcc

Fig. 7

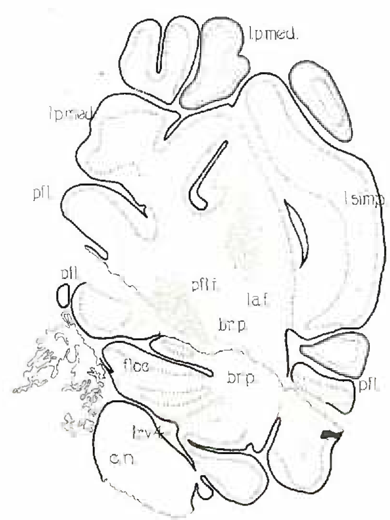

l.p.med.
l.p.med.
pfl
l.simp.
pfl
pfl.i.
la.f.
br.p.
flcc
br.p.
pfl.
c.n.

Fig. 8

Fig. 9 -- Sagittal section of the cerebellum of cat no. 11, medial to fig. 8. 3.75x. The fibers from the lobulus ansiformis and paraflocculus have terminated in the nucleus dentatus. A part of the parafloccular fibers end in the nucleus interpositus. The fibers from the flocculus are moving upward to lie among the fibers just beneath the nucleus dentatus. (11 L, 17-2-3).

Fig. 10 - Sagittal section of the cerebellum of cat no. 11, medial to fig. 9. 3.75x. The fibers from the paraflocculus and lobulus ansiformis have practically all terminated. The fibers from the flocculus are seen passing medially by two routes; one between the incoming fibers of the corpus restiforme, and the other among the fibers of the brachium conjunctivum. (11 L, 24-2-2).

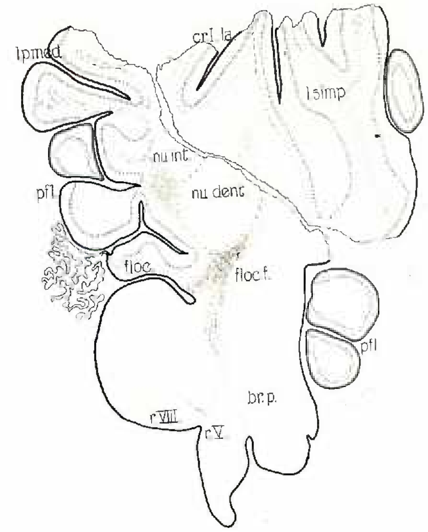

l.p.med.
cr.I la
l.simp
nu.int.
nu.dent.
pfl.
floc.
floc.f.
pfl
br.p.
r.VIII
r.V

Fig. 9

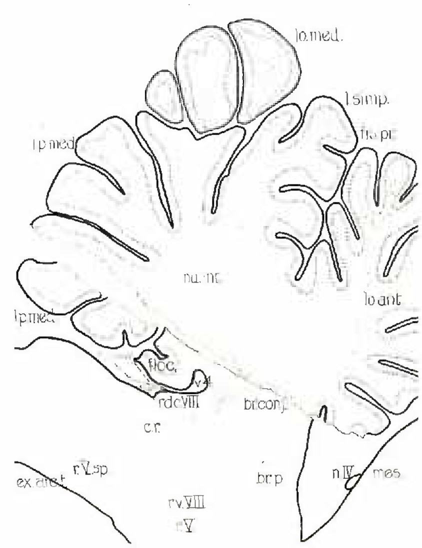

lo.med.
l.simp.
l.p.med.
nu.int.
lo.ant
l.p.med.
floc.
v.4
rdc.VIII
br.conj.
c.r.
r.V.sp
br.p
n.IV
mes
r.v.VIII
r.V

Fig. 10

Fig. 11 -- Sagittal section of the cerebellum of cat no. 11, medial to fig. 10. 3.75x. The fibers from the flocculus are seen terminating in Deiters' and Bechterew's nuclei. (11 L, 30-2-1).

Fig. 12 -- Lateral view of the cerebellum of cat no. 13. Lesion in solid black. 1.5x.

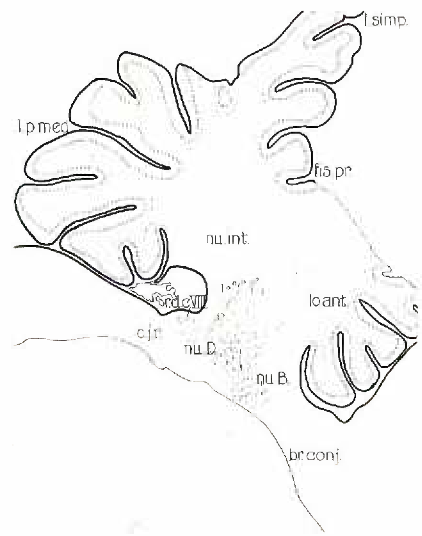

l simp.
l p med
fis pr
nu int.
lo ant.
c j r
nu D.
nu B.
br conj.

Fig. 11

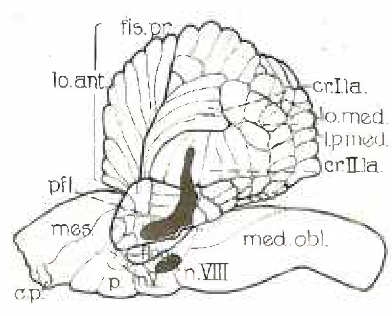

fis.pr.
lo.ant.
cr.I.la.
lo.med.
l.p.med.
cr.II.la.
pfl.
mes.
med.obl.
n.VIII
p.
c.p.

Fig. 12

Fig. 13 -- Schema of the cat cerebellum modified from Riley ('29). Lesion in cat no. 13 in solid black with distribution of the arcuate fibers shown by stippling. (The stippling seen on the lower part of the nodulus does not indicate arcuate fibers, but shows a part of the cerebellar cortical area supplied by the vestibular root fibers).

Fig. 14 -- Sagittal section of the lateral part of the cerebellum of cat no. 13. 3.75x. Note the lesion and arcuate fibers to adjacent folia. (13 L, 1-2-4).

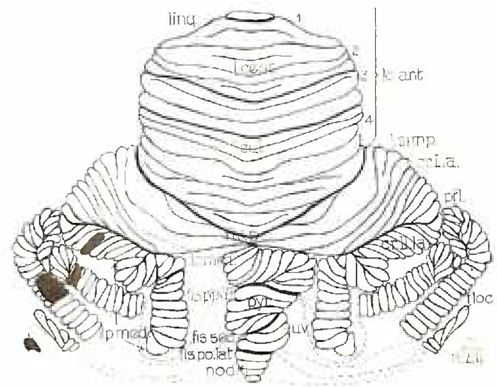


Fig. 13

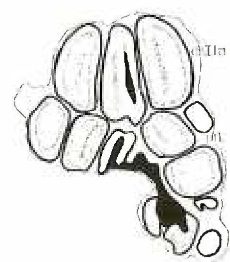


Fig. 14

Fig. 15 -- Sagittal section of the cerebellum of cat no. 13, medial to fig. 14. 3.75x. (13 L, 2-2-4).

Fig. 16 -- Sagittal section of the cerebellum of cat no. 13, medial to fig. 15. 3.75x. The fibers from the paraflocculus and lobulus ansiformis are seen to terminate in their respective parts of the nucleus dentatus. Root fibers of the vestibular nerve are seen passing into the flocculus. (13 L, 9-3-1).

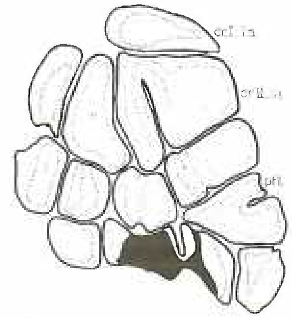

pfl

Fig. 15

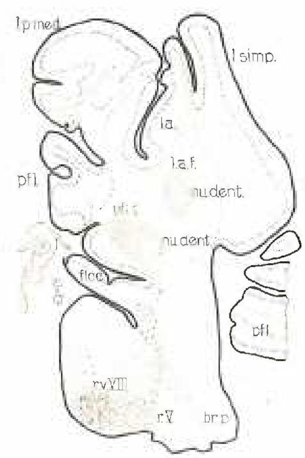

l p med
l simp.
la
l.a.f.
pfl
nu dent.
nu dent
flcc
pfl
r v VIII
r V
br p

Fig. 16

Fig. 17 -- Sagittal section of the cerebellum of cat no. 13, medial to fig. 16. 3.75x. The fibers from the paraflocculus are seen to end, in part, in the nucleus emboliformis. The vestibular root is not shown. Note the absence of VIII root fibers coming into the flocculus around the restiform body. (13 L, 13-2-2).

Fig. 18 -- Sagittal section of the cerebellum of cat no. 13, medial to fig. 17. 3.75x. The section passes through the juxta restiform body - (c.j.r.) and shows the distribution of vestibular root fibers to the vestibular nuclei. The fibers which have passed medially in the dorsal cochlear root of the acoustic nerve - (r.d.c. VIII f.) descend through this same vestibular area. (13 L, 23-2-1).

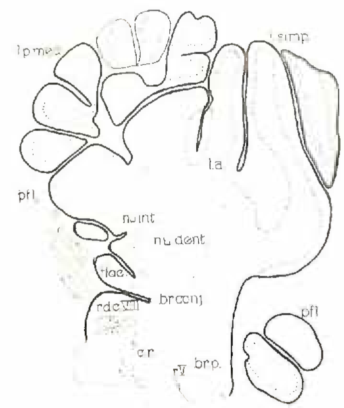

l simp
l p med
l a
pfl
nu int
nu dent
floc
br conj
rdc VIII
pfl
c r
r V
br p.

Fig. 17

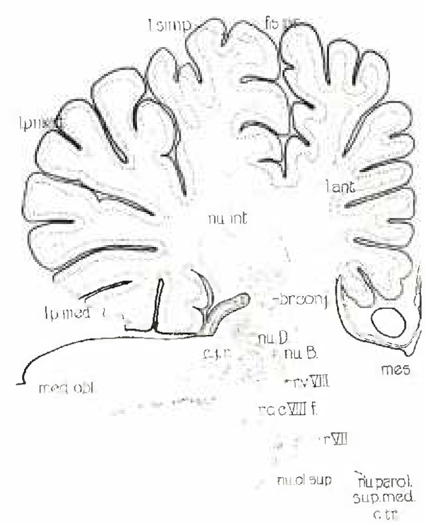

l simp
l ant
nu int
br conj
l p med
nu D
c.j.r.
nu B.
mes
med obl
rd c VIII f.
r VII
nu ol sup
nu parol.
sup.med.
c tr.

Fig. 18

Fig. 19 -- Sagittal section of the cerebellum of cat no. 13, medial to fig. 18. 3.75x. Root fibers of vestibular nerve are seen in the basal part of the nucleus fastigii and in the nodulus and uvula. (13 M, 6-1-1).

Fig. 20 -- Lateral view of the cerebellum of rat no. 17. Lesion in solid black. 3x.

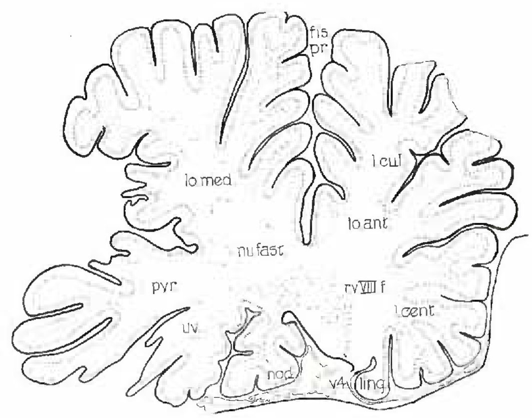

fis.
pr.
lo.med.
l.cul.
lo.ant.
nu.fasc.
pyr.
rvVIII f.
l.cent.
uv.
nod.
v4.
ling.

Fig. 19

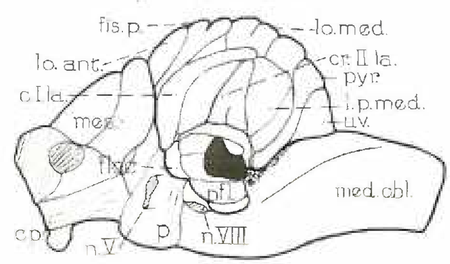

fis.p.
lo.med.
lo. ant.
cr.II la.
pyr.
c.I la.
l.p.med.
uv.
mes.
flc.
pfl.
med.obl.
p.
n.VIII
n.V

Fig. 20

Fig. 21 -- Schema of the rat cerebellum. Lesion in rat no. 17 shown in solid black with the distribution of the arcuate fibers shown by stippling.

Fig. 22 -- Sagittal section of the lateral part of the cerebellum of rat no. 17. 7.5x. The lesion is seen here. (17 L, 19-5-4).

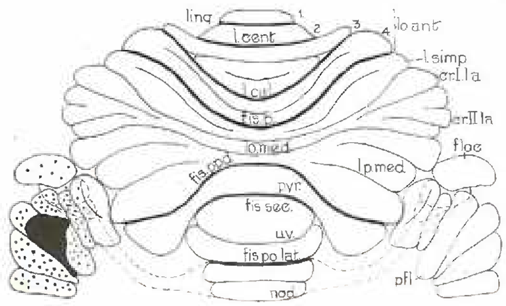

ling
l.cent
1
2
3
4
lo ant
l.simp
cr.I la
cr.II la
l.cul
fis.p
lo.med
floc
l.p.med
fis.ppd
pyr.
fis sec.
uv.
fis po lat.
pfl
nod

Fig. 21


pfl

Fig. 22

Fig. 23 -- Sagittal section of the cerebellum of rat no. 17, medial to fig. 22. 7.5x. The degeneration is seen in the stalk of the paraflocculus and a few arcuate fibers to the flocculus. (17 L, 17-3-4).

Fig. 24 -- Sagittal section of the cerebellum of rat no. 17, medial to fig. 23. 7.5x. The fibers from the paraflocculus are seen to end along the ventrocaudal border of the nucleus dentatus. (17 L, 15-2-3).

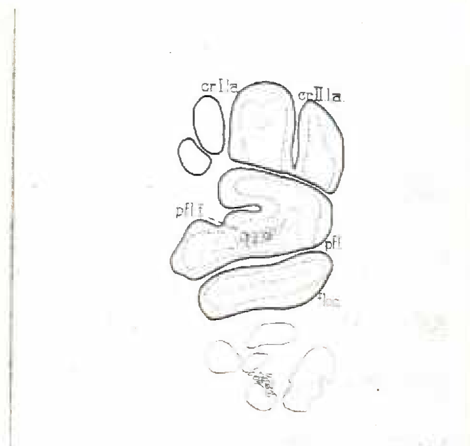


Fig. 23

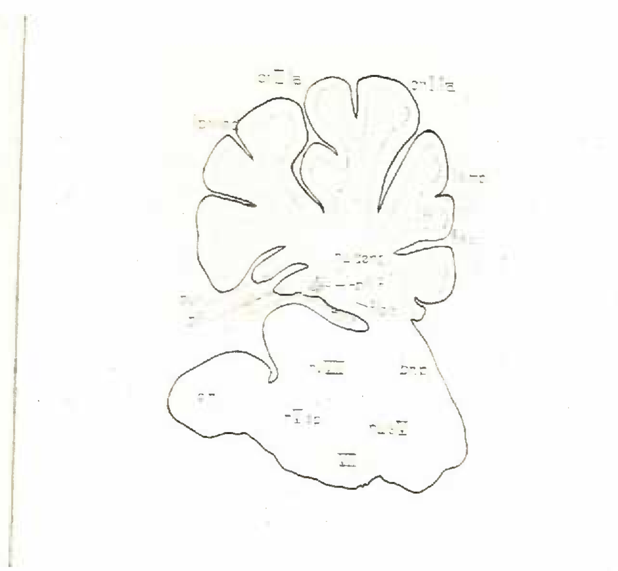


Fig. 24

Fig. 25 -- Sagittal section of the cerebellum of rat no. 17, medial to fig. 24. 7.5x. The fibers from the paraflocculus end, in part, in the nucleus interpositus.

Fig. 26 -- Schema of the rat cerebellum. Lesion in rat no. 32 shown in solid black with the distribution of the arcuate fibers shown by stippling. Degeneration to other cortical areas shown in subsequent figures is caused by the involvement of the brachium pontis in the lesion. (see fig. 27).

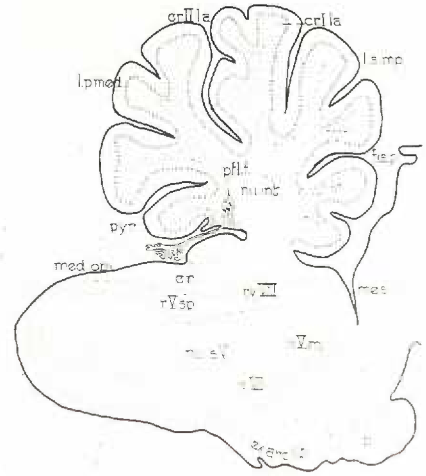

crII la
crI la
l.p med
l simp
pfl.f
nu.int
pyr
med obl
rV sp
rv VII
mes
Vm

Fig. 25

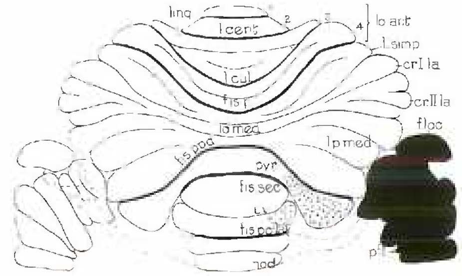

ling
l cent
2
4
lo ant
l simp
crI la
crII la
floc
l cul
fis p
lo med
l p med
fis pod
pyr
fis sec
fis po
nod

Fig 26

Fig. 27 -- Sagittal section of the lateral part of the cerebellum of rat no. 32. 7.5x. The lesion involves the whole stalk of the flocculus and paraflocculus and a part of the brachium pontis. (32 R, 9-1-5).

Fig. 28 -- Sagittal section of the cerebellum of rat no. 32, medial to fig. 27. 25x. The degeneration is from both the flocculus and the paraflocculus. Compare with fig. 24, in which only the paraflocculus is damaged and fig. 34 in which the flocculus alone is damaged. (32 R, 7-4-6).

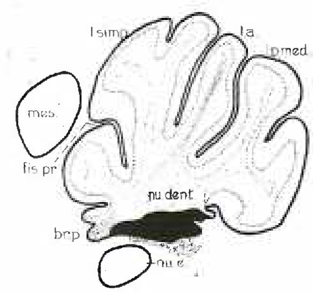

l simp
l a
l p med
mes.
fis pr
nu dent
brp
nu e

Fig. 27

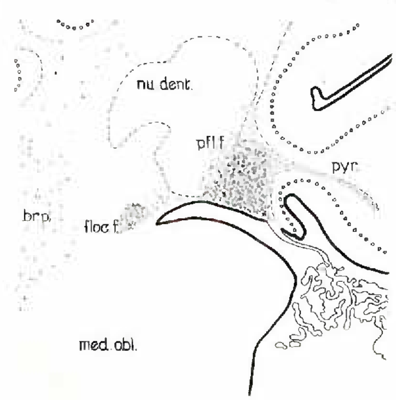

nu dent.
pfl f
pyr.
brp.
floc f.
med. obl.

Fig. 28

Fig. 29 -- Sagittal section of the cerebellum of rat no. 32, medial to fig. 28. 25x. Arcuate fibers from the medial part of the paraflocculus are near their termination in the lateral part of the uvula. The majority of the fibers from the flocculus are seen in Deiter's nucleus.

Fig. 30 -- Sagittal section of the cerebellum of rat no. 32, medial to fig. 29. 25x. The "angular bundle of Löwy" is seen ending in Bechterew's nucleus. (32 R, 4-1-3).

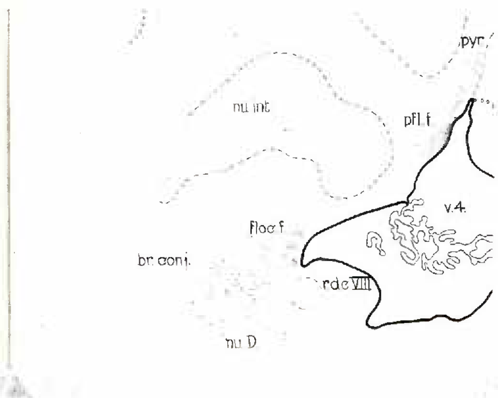

pyr.
nu int
pfl f
v.4
floc f
br conj.
rd c VIII
nu D

Fig. 29

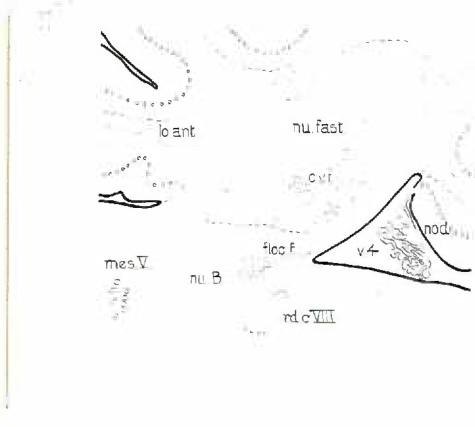
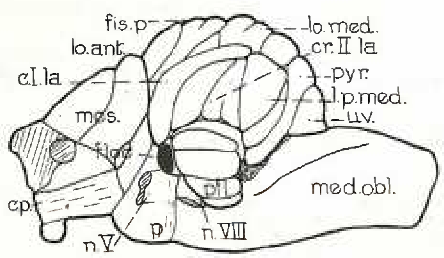

lo ant
nu fast
nod
mes V
floc f
v4
nu B
rd c VIII

Fig.30

Fig. 31 -- Lateral view of the cerebellum of rat no. 30. Lesion shown in solid black. 3x. The lesion is confined to the flocculus.

Fig. 32 -- Schema of the cerebellum of rat no. 30. The lesion is shown in black and the distribution of the arcuate fibers is shown by stippling.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lo.ant.
c.I.la
mes.
cp.
n.V
p
n.VIII
lo.med.
cr.II la
pyr.
l.p.med.
uv.
med.obl.

Fig.31

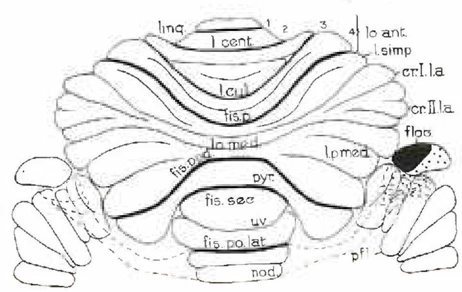

linq.
l.cent.
1
2
3
4
lo.ant.
l.simp
cr.I.la
cr.II.la
floc.
l.cul.
fis.p.
lo.med.
l.p.med.
pyr.
fis.sec
uv
fis.po.lat
nod.
pfl

Fig. 32

Fig. 33 -- Sagittal section of the cerebellum of rat no. 30 to show the extent of the lesion. 7.5x. Note the arcuate fibers to the nearer portions of the paraflocculus. (30 R, 10-3-4).

Fig. 34 -- Sagittal section of the cerebellum of rat no. 30, medial to fig. 33. 25x. Note the difference in degeneration resulting from a lesion confined to the flocculus to that resulting from damage of both the flocculus and paraflocculus, fig. 28; and from the paraflocculus alone, fig. 24. (The termination of these fibers is identical to the floccular fibers shown in figs. 29 and 30.) (30 R, 9-2-2).

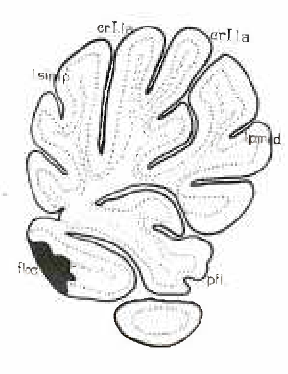


Fig. 33

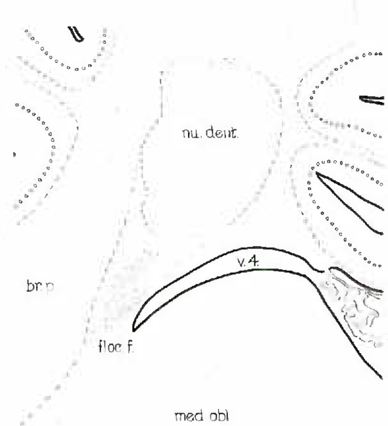


Fig. 34

Fig. 35 -- Sagittal section of the cerebellum of rat no. 15. Lesion on the nodulus and uvula shown in solid black. 7.5x. Note the degeneration to the fastigial nucleus. (15 L, 1-3-1).

Fig. 36 -- Sagittal section of the cerebellum of rat no. 15, lateral to fig. 35. 18.75x. Note the cerebello-vestibular fibers (c.v.f.) which are collected into bundles. They descend to the vestibular nuclei. (15 L, 5-1-5).

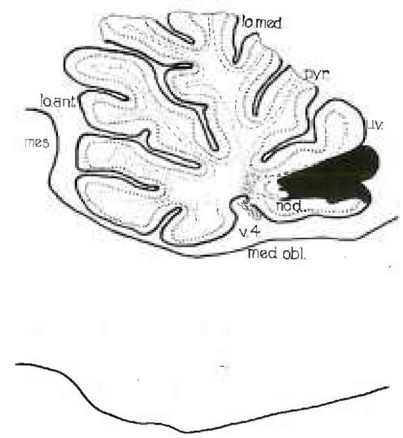

lo.med.
pyr.
lo.ant.
uv.
mes.
nod.
v.4
med obl.

Fig. 35

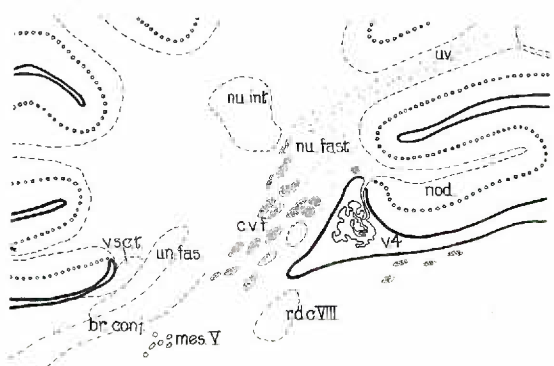

uv.
nu int.
nu fast.
nod.
c.v.f.
v4
v.sc.t.
un fas.
rd.c.VIII
br.conj.
mes.V

Fig. 36

Fig. 37 -- Sagittal section of the cerebellum of rat no. 18. Lesion on pyramis and uvula shown in solid black. 7.5x. Note degeneration to fastigial nucleus. (18 L, 6-2-3).

Fig. 38 -- Sagittal section of the cerebellum of rat no. 18, lateral to fig. 37. 18.75x. Note the distribution of fibers from the pyramis to the nucleus interpositus, and the absence of degeneration in the small bundles of cerebello-vestibular fibers (c.v.f.). Compare with fig. 36 in which these bundles are filled with fine granules. (18 L, 7-2-3).

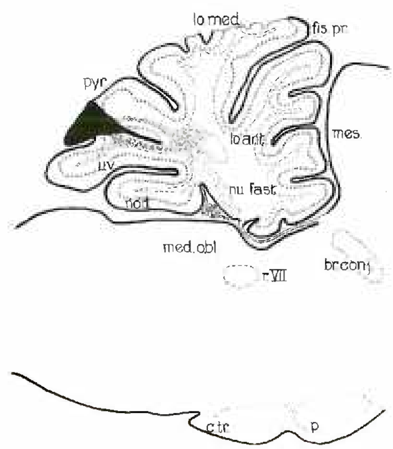

lo med
fis pr
pyr
lo ant
mes
uv
nu fast
nod
med obl
r VII
br conj
ctr
p

Fig. 37

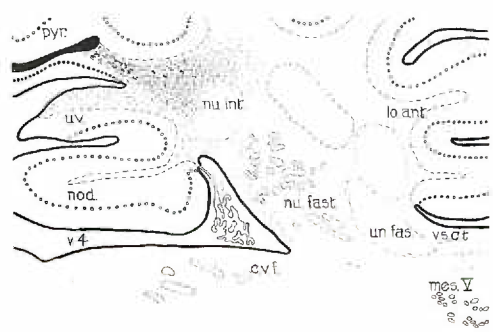

pyr
nu int
lo ant
uv
nod
nu fast
un fas
vs ct
v 4
cvf
mes. V

Fig. 38

Fig. 39 -- Lateral view of the cerebellum of rat no. 27. Lesion shown in solid black. 3x.

Fig. 40 -- Sagittal section of the cerebellum of rat no. 27. 7.5x. Note the slight degeneration to the flocculus. The degenerated fibers in the brachium pontis result from damage to that tract farther medial. (27 L, 14-1-2).

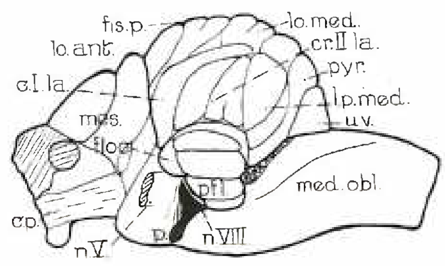

fis.p.
lo.med.
lo.ant.
cr.II la.
pyr.
c.I la.
l.p.med.
mes.
u.v.
floc.
pfl.
med. obl.
cp.
nV.
nVIII

Fig.39

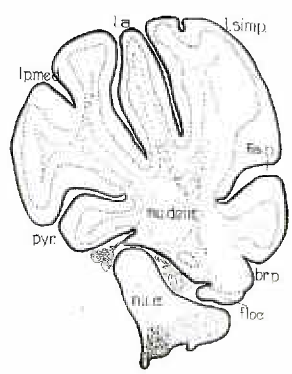

l.a.
l.simp.
pyr.
brp
floc

Fig. 40

Fig. 41 -- Sagittal section of the cerebellum of rat no. 27, medial to fig. 40. 7.5x. The lesion involves the V root with resulting degeneration in the spinal V tract and its sensory nucleus. The region of the vestibular nuclei is further medial. (27 L, 11-3-2).

Fig. 42 -- Sagittal section of the cerebellum of rat no. 27, medial to fig. 41. 7.5x. The cerebellum alone is shown. The vestibular root fibers terminate in the vestibular nuclei as well as the nucleus fastigii, the nodulus and uvula. (27 L, 7-3-1).

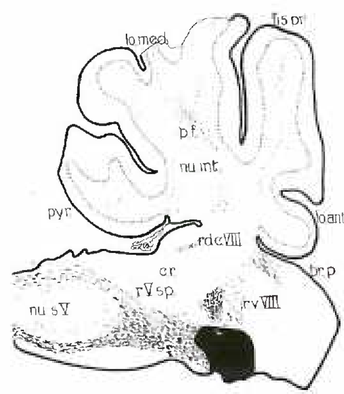

fis pr
lo med
p f
nu int
pyr
lo ant
rdcVIII
cr
br p
rV sp
nu sV
rv VIII

Fig. 41

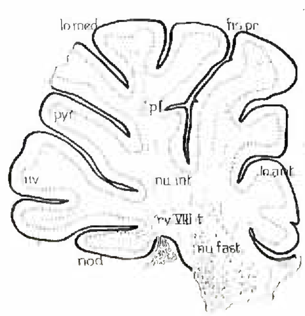
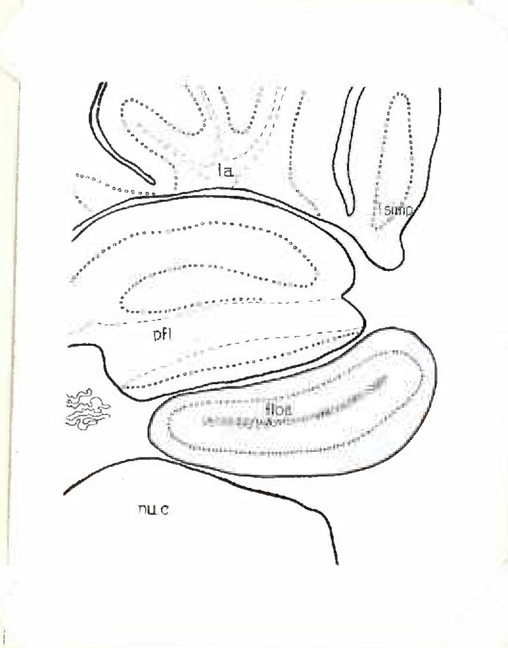

lo med
fis pr
pf
pyr
lo ant
nu int
rv VIII t
nu fast
nod

Fig. 42

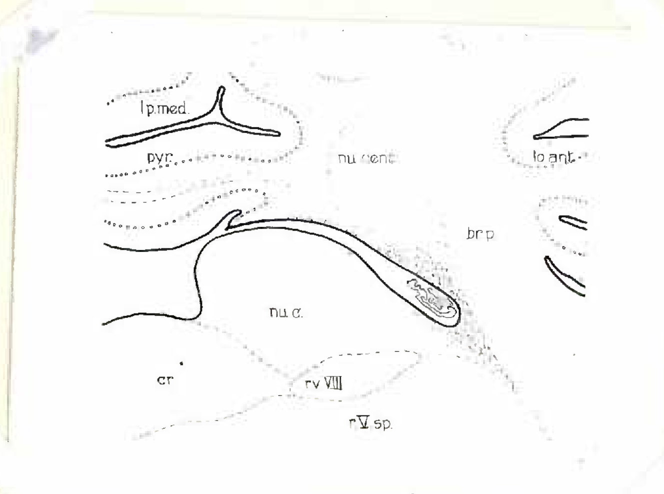
Fig. 43 -- Sagittal section of the lateral part of the left half of the cerebellum of rat no. 33. 18.75x. Secondary vestibulo-cerebellar fibers are seen ending in the flocculus. (33 L, 14-2-4).

Fig. 44 -- Sagittal section of the left half of the cerebellum of rat no. 33, medial to fig. 43. 18.75x. Note the secondary vestibulo-cerebellar fibers entering the region of the flocculus. (33 L, 13-1-5).



la
sump
pfl
floc
nu c

Fig. 43

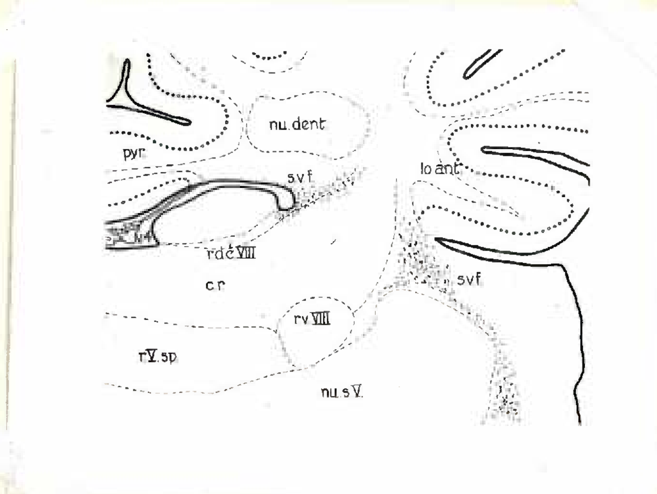


l p med
pyr
nu cent
lo ant
br p
nu c
cr
rv VIII
r V sp

Fig. 44

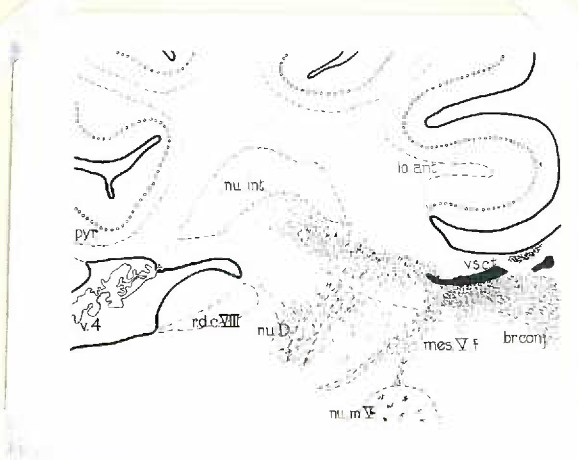
Fig. 45 -- Sagittal section of the left half of the cerebellum of rat no. 33, medial to fig. 44. 18.75x. Note the secondary vestibulo-cerebellar fibers (s.v.f.) passing to the homolateral flocculus both dorsal and ventral to the restiform body (c.r.). (33 L, 12-2-5).

Fig. 46 -- Sagittal section of the left half of the cerebellum of rat no. 33, medial to fig. 45. Lateral edge of the lesion is shown in solid black. 18.75x. Note the involvement of the ventral spino-cerebellar tract (v.s.c.t.), the brachium conjunctivum (br. conj.), the mesencephalic root of the trigeminus (mes.V.f.) and the fastigio-bulbar fibers ending in Deiter's nucleus (nu.D.). (33 L, 9-26).



nu.dent
pyr.
s.v.f.
lo.ant
rdc.VIII
c.r.
s.v.f.
r.v.VIII
rV.sp.
nu.s.V.

Fig. 45

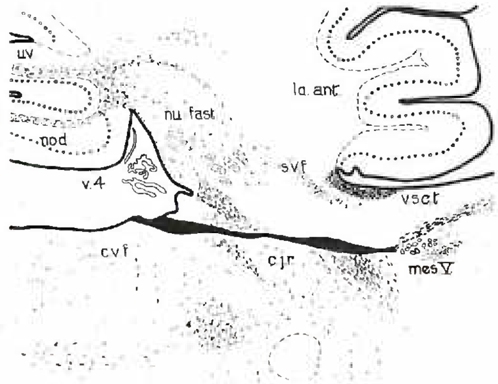


lo.ant
nu.int
pyr.
v.s.c.t.
v.4
rd.c.VIII
nu.D.
mes.V.f.
br.conj.
nu.m.V

Fig. 46

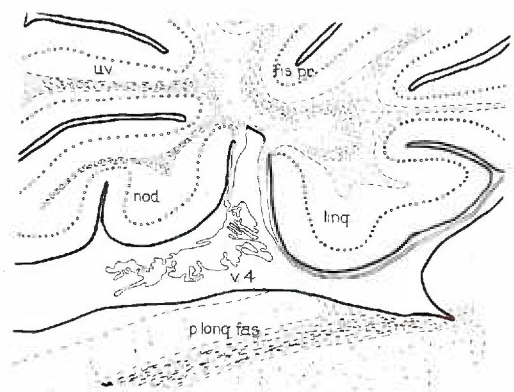
Fig. 47 -- Sagittal section of the left half of the cerebellum of rat no. 33, medial to fig. 46. Medial part of the lesion shown in solid black. 18.75x. Note the complete division of the juxta-restiform body (c.j.r.). Primary and secondary vestibulo-cerebellar fibers are seen ending in the uvula and nodulus. (33 L, 6-2-6).

Fig. 48 -- Mid-sagittal section of the cerebellum of rat no. 33. 18.75x. The fibers terminating in the nodulus and uvula are almost entirely secondary vestibulo-cerebellar fibers. Fibers crossing more rostrally are mixed secondary vestibular fibers and fibers from the ventral spino-cerebellar tract. (33 L, 2-2-3).



uv
la. ant.
nu. fast.
nod
svf
v.4
vsct
cvf
cjr
mes V

Fig. 47



uv
fis pr.
nod
ling.
v.4
p.long.fas.

Fig. 48

Fig. 49 -- Sagittal section of the right half of the cerebellum of rat no. 33 lateral to fig. 48. 18.75x. Note the secondary vestibulo-cerebellar fibers terminating in the nodulus and uvula. They are seen both caudal to the nucleus fastigii at the base of the uvula and nodulus, and also along with fibers in the uncinate fasciculus dorsal to the brachium conjunctivum. These secondary vestibulo-cerebellar fibers terminate in the contralateral flocculus (fig. 52). (33 R, 4-1-3).

Fig. 50 -- Sagittal section of the right half of the cerebellum of rat no. 33, lateral to fig. 49. 18.75x. Note the secondary vestibulo-cerebellar fibers passing to the flocculus by two routes; one at the base of the taenia of the choroid plexus and the other continuing laterally from the uncinate fasciculus. (33 R, 7-1-2).

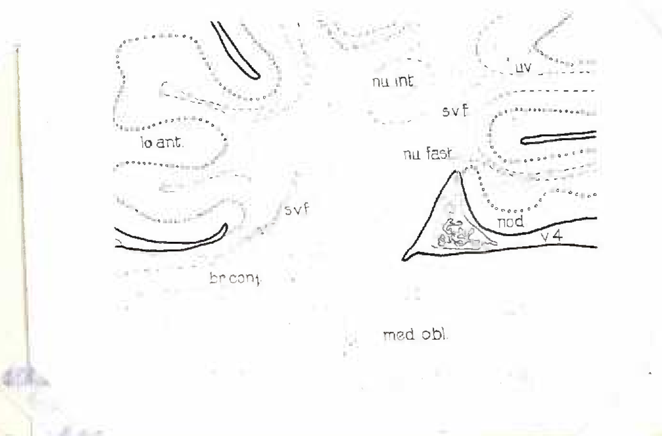

nu int
uv
svf
lo ant
nu fast
svf
nod
v4
br conj
med obl

Fig. 49

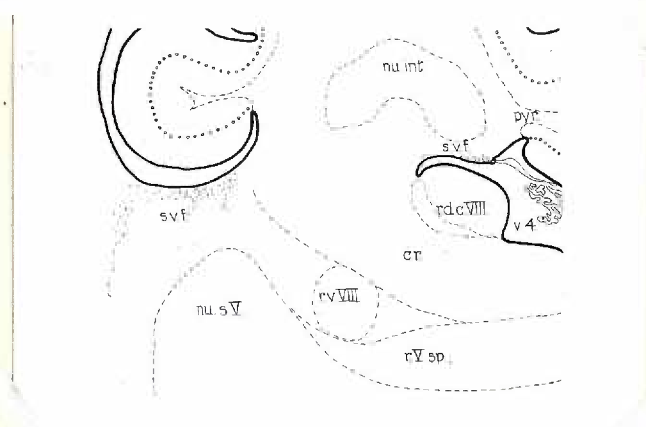

nu int
pyr
svf
rdcVIII
v4
svf
cr
nu s V
rvVIII
rV sp

Fig. 50

Fig. 51 -- Sagittal section of the right half of the cerebellum of rat no. 33, lateral to fig. 50. 18.75x. Note the secondary vestibulo-cerebellar fibers approaching the medial extremity of the flocculus. (33 R, 8-3-4).

Fig. 52 -- Sagittal section of the right half of the cerebellum of rat no. 33, lateral to fig. 51. 18.75x. Note that the secondary vestibulo-cerebellar fibers are restricted to the flocculus. (33 R, 10-1-4).

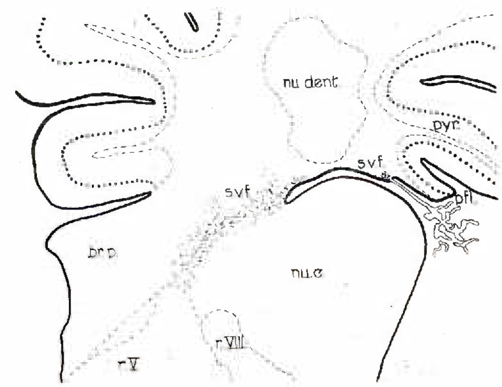


Fig. 51

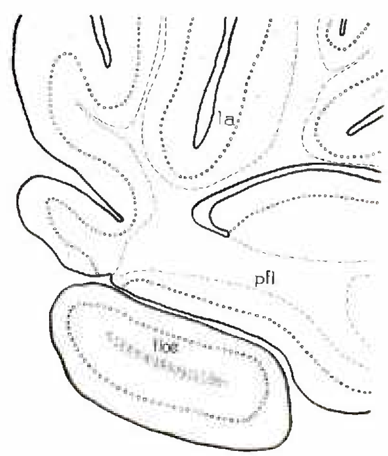
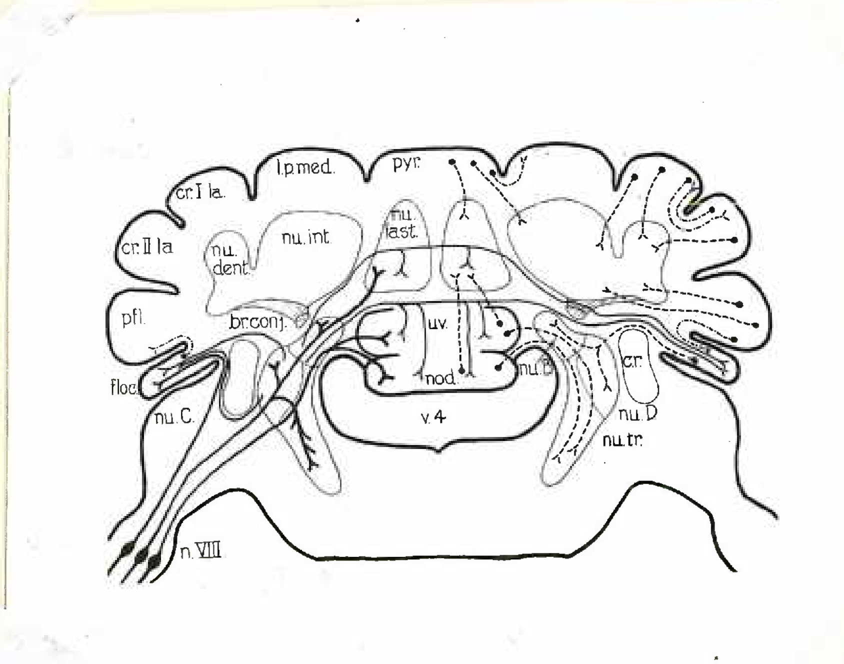


Fig. 52

Fig. 53 -- Schematic diagram to show the cerebellar and vestibular fiber connections which were determined in this study. The cells of origin of the secondary vestibulo-cerebellar fibers are purposely omitted because no information as to the exact origin of these fibers was obtained.

▬▬▬▬▬▬▬▬	Vestibular root fibers.
————————	Secondary vestibulo-cerebellar fibers.
- - - - - - - - - - - - - - -	Cortico-nuclear fibers.
-·-·-·-·-·-·-·-	Arcuate fibers.



l.p.med.
pyr.
cr.I la.
cr.II la.
nu. dent.
nu. int
nu. fast.
pfl.
br.conj.
uv.
floc.
nod.
nu.B
cr.
nu.C.
v.4
nu.D
nu.tr.
n.VIII

Fig. 53