ENDINGS OF THE DORSAL AND VENTRAL SPINOCEREBELLAR TRACTS IN THE WHITE RAT

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I should like to express my appreciation to Dr. R. S. Dow for his helpful criticism and his wise and learned counsel.

INTRODUCTION

The terminations of the tracts of Flechsig and Gower have been studied histologically in the cat, dog, monkey and man. These tracts have not been previously traced in the white rat. This study seems desirable because of recent work in which action potentials were led from the rat's cerebellum in response to exteroceptive and proprioceptive stimulation, Dow and Anderson(1942). These two modalities of sensation appeared to activate different regions of the cerebellum. Proprioceptive stimulation produced impulses of greatest amplitude in the pyramis. Impulses of lesser magnitude were found in the middle lobe of the vermis and the hemispheres but almost never in the anterior lobe. Stimulation of tactile endings by moving the hair on the rat's back produced impulses which were more widely scattered. However, the largest surface positive impulses could be picked up in the culmen with impulses of lesser magnitude in the pyramis and occassionally in the lobulus simplex. Impulses led from other parts of the cerebellum appeared at a greater latency and were surface negative.

The endings of the dorsal and ventral spinocerebellar pathways have been studied here in order to correlate them with the lobes in which the impulses produced by physiological stimulation of proprioceptive and exteroceptive endings were found.

It is difficult to review the literature regarding the endings of the spinocerebellar pathways without including the closely allied problems of the origin of these fibers in the cord and their pathway through the cord, medulla and pons. In the excellent reviews of MacMalty and Horsley(1909) and Beck(1927) all of these problems were covered. This review has been limited to the reports concerning the terminations of these fiber tracts.

These two tracts in the lateral border of the cord were first noticed by Fouville(1844) in myelinization studies. Later Bastian (1867) described ascending degeneration in the anterolateral region while studying a case of paraplegia and suggested their afferent nature to the cerebellum. Gower(1880) described this tract also in a case of paraplegia and suggested that it conducted pain impulses from the opposite side of the body. Flechsig(1876) studying myelinization in the cord, described this ascending tract and followed it into the cerebellum.

Löwenthal(1885) (as translated by Mott(1892))working on dogs severed the left lateral column of the cord and found degenerating fibers passing into the medulla. The ventral tract arched back over the superior cerebellar peduncle and the dorsal tract passed up the restiforme body into the cerebellum. He did not trace these fibers to their folial termination.

Auerbach (1890) destroyed the dorsal part of one half of the cord of dogs and found de enerated fibers in the direct cerebellar and ventrolateral tracts of both sides. He traced the dorsal tract to the dorsal part of the superior vermis and the ventral tract to the ventral part of the superior vermis.

Edinger(1890) who worked on fishes, reptiles and amphibians, came to the same conclusions as Auerbach from comparative morphological data.

Testut(1893) is ordinarily credited with first dividing the lateral ascending fibers into the dorsal and ventral groups. He suggested that they were long cerebellar connections from Clarke's column.

Mott(1892, 1895) selectively sectioned the anterolateral tracts both unilaterally and bilaterally in the monkey. He traced the dorsal fibers from Clarke's column to the dorsal portion of the superior vermis and the ventral fibers in their circuitous route around the fifth nerve to the ventral part of the superior vermis.

Tooth(1892) confirmed Mott's report on the course and endings of the two tracts.

Grünbaum(1894) working on monkeys and cats followed the two paths into the cerebellum and assumed that they went to the superior vermis as described by Auerbach(1890).

Bruce(1898) reported his study of the degeneration that resulted from a sarcomatous tumor pressing on the human spinal cord. The dorsal tract was found to end on both sides of the lobulus centralis, monticulus (lobulus simplex), lingula, nodulus and the uvula. No fibers were found in the cerebellar hemisphere. The ventral tract was traced to the homolateral portion of the lingula. This report agreed very closely with Patrick(1898).

VanGehuchten(1900-1901) in degeneration experiments traced the dorsal fibers into the posterior portion of the superior vermis and the ventral fibers into the anterior portion of the superior vermis.

Collier and Buzzard(1903) reported the findings on traumatized human cords. They traced the dorsal fibers to all parts of the cerebellar cortex particularly the lower part of the lateral lobes and to the flocculus. They found ventral fibers going chiefly to the contralateral superior vermis and to the hemispheres.

Schäfer and Bruce(1907) and A. H. Bruce(1910) traced degenerated fibers into the monkey cerebellum but they were interested in the origin of the fibers and did not record their folial terminations.

Bing(1907) studying degeneration on dogs followed the dorsal tract into the anterior superior part of the superior vermis and the ventral tract into the anterior inferior part of the superior vermis.

MacMalty and Horsley(1909) working on monkeys traced the dorsal fibers to the culmen, lobulus centralis, folium tuber, declive and pyramis chiefly on the same side. They traced the ventral fibers to the lobulus centralis, culmen and pyramis but none to the lingula. These fibers were distributed ipsilateral to contralateral in the ratio of 4:1.

Horrax(1915) working on dogs traced the dorsal fibers to the posterior vermis, lobulus simplex and medial parts of the hemispheres. He traced the ventral fibers to the anterior vermis only.

Ingvar(1918) studying degeneration on cats traced the ventral fibers to the lobulus centralis and culmen. None ended posterior to the fissura prima. The dorsal tract ended in the anterior lobe and in the pyramis and uvula and a few in the paraflocculus of the posterior lobe.

Beck(1927) working on cats corroborated Ingvar's findings. In addition he concluded that the ventral tract was distributed chiefly to the opposite side of the vermis while the dorsal fibers were distributed mainly on the same side of the vermis lateral to the midline.

Pass(1933) confirmed the previous work of Beck.

Brodal and Jansen(1941) studying the degeneration following chordotomy in a human reported fibers ending in the anterior lobe, pyramis, uvula and a few in the lobulus simplex. They did not distinguish between the endings of the two tracts.

Grundfest and Campbell(1942) applied electrical methods to the study of the dorsal tract in the cat. From stimulation of localized points on the cord they recorded impulses chiefly ipsilateral in the culmen and lobulus centralis but none were found in the posterior lobe or the hemispheres.

An intermediate cerebellar tract has been recorded by Pellizzi (1895), Rothman(1909), MacNalty and Horsley(1909), A. N. Bruce (1910), Beck (1927). It is difficult however to separate this from the dorsal or ventral tracts.

MATERIAL AND METHODS

Degeneration experiments were successfully performed on eight white rats. The animals were anaesthetized with nembutal 0.1 cc of 6% solution per Kg. body weight. An appropriate midline incision was made, the spinous processes and laminae of one or two vertebrae removed and the dura opened. With a fine hooked wire lesions were made either at the lower cervical, the upper thoracic or the lower thoracic segments of the cord. The lesions ranged from destruction of the lateral funiculus to complete hemisection of the cord. It was not possible to localise the lesion to the dorsal or ventral tract in any one animal. After 14 days the animals were killed with an excess of ether. The cord and brain were removed and fixed and stained according to Marchi method, Allen(1919). The brain stem, cerebellum and selected portions of the cord, where the lesion was placed, were sectioned at 60 microns and mounted.

In addition to these eight animals one cerebellum was borrowed from Dr. Robert Dow's material. While studying the vestibular fibers in the white rat Dow(1936) accidentally sectioned the ventral tract as it passed over the brachium conjunctivum without involving the dorsal tract.

Serial drawings of four brains are presented. Three of these brains, sectioned in three different planes (horizontal, transverse and sagittal) are from my own preparations. The fourth, borrowed from Dr. Dow's material, was cut sagittally and may be compared with my own sagittal series to contrast the differences between the degeneration resulting from a lesion of both dorsal and ventral tracts and of the ventral tract alone.

RESULTS

The typical course of the fibers in the cord, brain stem and cerebellar peduncles has been confirmed. The two tracts lie in close proximity in the cord but separate at the lower end of the medulla. The dorsal tract swings posteriorly to enter the cerebellum through the restiforme body (Figs. A, D, M, N, U, V, W). The ventral tract ascends through the pons. Superior to the fifth nerve it bends dorsally over the superior cerebellar peduncle to pass dorsomedially into the cerebellum just lateral to the lingula (Figs. B, C, D, E, F, J, M, N, W, X).

The lesion involving only the ventral tract was made through the juxtarestiforme body just before the ventral tract bends dorsomedially into the cerebellum. (Figs. B, C). Just beyond this point the ventral tract receives a small group of fibers from the dorsal tract which is inseparably distributed with the ventral tract (Figs. M, O).

The ventral tract bends sharply to the midline to be distributed to all parts of the anterior lobe (lobulus centralis, culmen and lingula) and to the pyramis of the posterior lobe (Figs. D, G, M, O, P, V, W). A few fibers may be seen to enter the most central part of the lobulus simplex (Fig. M). The ventral tract ends chiefly near the midline of the vermis. (Figs. G, M.).

As the dorsal tract bends dorsomedially in the cerebellum its fibers become less compact (Figs. O, P). Its medial fibers pass across the mid-line and are inseparable from those of the ventral tract (Figs. M, O, P, Q). The laterally placed fibers of the dorsal tract pass to the pyramis and medial parts of the lobulus paramedianus and to the lobulus simplex on the same side (Figs. O, P, Q, R, S). A few fibers appear to enter the most central part of the uvula (Fig. K).

The very fine degeneration in the nodulus and uvula (Figs. C, G, K, I) is a result of damage to the vestibulo-cerebellar fibers and can be distinguished from the coarser degeneration of the spino-cerebellar tracts. Where only the latter tracts are cut no degeneration can be seen in the nodulus and uvula (Figs. I, J, K, L).

DISCUSSION

Among all of the conflicting evidence recorded in the literature the work of MacNalty and Horsley(1909), of Ingvar(1918), and of Beck(1927), seems to find acceptance by contemporary authorities, (Kappers, Huber and Crosby,1936; Larsell,1937; 1942; Fulton and Dow,1937; Ranson,1939; Dow,1942). They all conclude that the ventral spinocerebellar tract passes anteriorly around the fifth nerve and over the brachium conjunctivum to be distributed to the midline of the anterior lobe only. The dorsal tract is said to be distributed to the anterior lobe, the lobulus simplex, the pyramis and uvula and the lobulus paramedianus. They all agree that no spinocerebellar fibers pass to the flocculonodular lobe, the hemispheres, the paraflocculus or tuber vermis.

Ordndfest and Campbell(1942) in their electrophysiologic experiments stimulated the dorsal tract in the cat and found these impulses confined wholly to the anterior lobe, chiefly near the midline and homolateral. They state that their findings are in keeping with the histological findings of Ingvar and Beck. Their findings would agree well with the endings of the ventral spinocerebellar tract rather than the dorsal.

With the exception of Mott's paper(1892) there is no report in which a single spinocerebellar tract was unilaterally sectioned and its degeneration traced to its folial termination. Grünbaum(1894), A. Bruce(1896), Collier and Buzzard(1902), MacNalty and Horsley(1909), Morrax(1913), Ingvar(1918), Beck(1927), Brodal and Jansen(1941), all studied the degeneration to the cerebellum from both the dorsal and ventral spinocerebellar tracts. One who is familiar with the technical

details can understand the difficulty of sectioning selectively only one tract.

Schäfer and A. N. Bruce (1907) and A. N. Bruce (1910) were evidently able to section these tracts selectively in the monkey but they were interested in studying their origin by chromotolysis rather than their termination my Marchi staining.

The findings in this report on the folial terminations of the dorsal tract in the rat would agree with the generally accepted views on this subject.

The above findings on the folial terminations of the ventral tract are in agreement likewise except that there is definite evidence in the rat that a few fibers of the ventral spinocerebellar tract terminate in the pyramis.

This work indicates that the chief difference between the cerebellar distribution of the dorsal and ventral spinocerebellar fibers is in the relation of their endings to the midsagittal plane. The ventral fibers are distributed in a narrow band at the midline while the majority of the dorsal fibers are distributed to the lateral parts of the vermis. Both tracts send fibers to the lingula, lobulus centralis, culmen, lobulus simplex, pyramis and uvula. The dorsal tract alone goes to the lobulus paramedianus.

There are a few fibers in the rat which seem to correspond to the intermediate cerebellar tract in the cat and monkey as reported by previous workers. Nothing new can be said regarding their course other than that they seem to be inseparably distributed with the ventral tract.

SUMMARY

1. This experiment was undertaken to determine by means of the Marchi technic the folial distribution of the endings of the dorsal and ventral spinocerebellar tracts in the white rat.

2. In all, nine specimens were studied. Eight of these animals had both tracts cut on one or both sides of the cord. One had only the ventral tract sectioned on one side.

3. The two tracts followed the course described as typical in other animals through the upper cord and the medulla into the cerebellum.

4. The dorsal tract terminated in all parts of the anterior lobe (culmen, lobulus centralis, lingula), in the lobulus simplex of the middle lobe and in the pyramis of the posterior lobe. A few fibers ended in the most medial parts of the lobulus paramedianus and the uvula. None went to any other parts of the vermis, to the paraflocculus, to the flocculus or to the hemispheres. The fibers were distributed ipsilaterally to contralaterally in the proportion of 3:1 on either side of the midline of the vermis.

5. The ventral tract was found to be distributed to the anterior lobe (culmen, lobulus centralis, lingula) and the pyramis of the posterior lobe. There were a few degenerated fibers in the most central part of the lobulus simplex. No degenerated fibers were found in any other parts of the vermis, in the paraflocculus, flocculus or the hemispheres. The fibers were found in greatest numbers near the midline.

6. There were some fibers in the rat which might correspond to the intermediate fibers described by other workers. In the cord these

fibers are indistinguishable from either tract but in the medulla at the point where the ventral tract bends dorsally over the brachium conjunctivum there is a small group of the fibers from the dorsal tract which joins it to be distributed indistinguishably with it.

7. There appears to be no correlation between the cerebellar endings of these two fiber tracts and lobular distribution of impulses following proprioceptive and exteroceptive stimulation.

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ABBREVIATIONS USED IN FIGURES

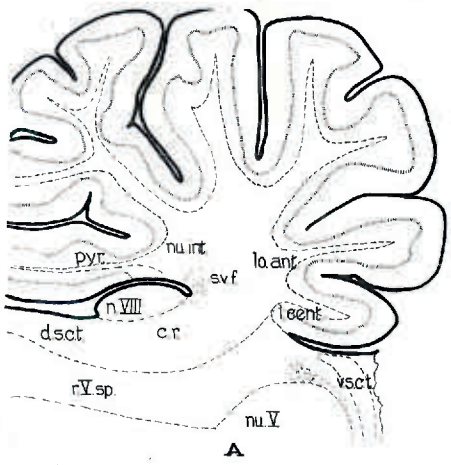
br. conj., brachium conjunctivum
br. p., brachium pontis
c.j.r., corpus juxtarestiforme
c.p., choroid plexus
c.r., corpus restiforme
d.s.c.t., dorsal spinocerebellar tract
d.s.c.f., dorsal spinocerebellar fibers
fis. ppd., fissura prepyramidalis
fis. pr., fissura prima
floc., flocculus
inf. col., inferior colliculus
l. a., lobulus ansiformis
l. cent., lobulus centralis
l. cul., lobulus culmenatis
l.p. med., lobulus paramedianus
l. simp., lobulus simplex
ling., lingula
lo. ant., lobus anterior
lo. med., lobus medius (Ingvar)
n. VIII, acoustic nerve
nod., nodulus
nu. dent., nucleus dentatus
nu. fast., nucleus fastigii
nu. int., nucleus interpositus
nu. V., nucleus of the trigeminal nerve
pyr., pyramis
r.V.sp., spinal root of the trigeminal nerve
s.v.f., secondary vestibulo-cerebellar fibers
uv., uvula
v.s.c.t., ventral spinocerebellar tract
v.4., fourth ventricle

This plate shows comparable sagittal sections of two rat cerebella; one (no. 55, figs. A, B, C) in which only the ventral tract was cut and the other (no. 7, figs. D, E, F) in which both the dorsal and ventral tract had been cut. (x12.5)

Figs. A and D--plane through the restiforme body. Note the complete absence of degenerated fibers in the dorsal tract in A. There is a small area of the dorsal fibers in D that are not stained but a study of other serial sections shows the continuity of these fibers.

Figs. B and E--plane through the juxtarestiforme body. Note the lesions in the ventral tract in B just before it enters the cerebellum. In E note the degenerated fibers in the lateral planes of the vermis. These fibers are from the dorsal tract.

Figs. C and F--plane through the medial part of the juxtarestiforme body. Note the most inferior part of the lesion in C. The fine degeneration in the uvula and nodulus in C is due to section of the vestibular fibers. Note the absence of these degenerated fibers in F.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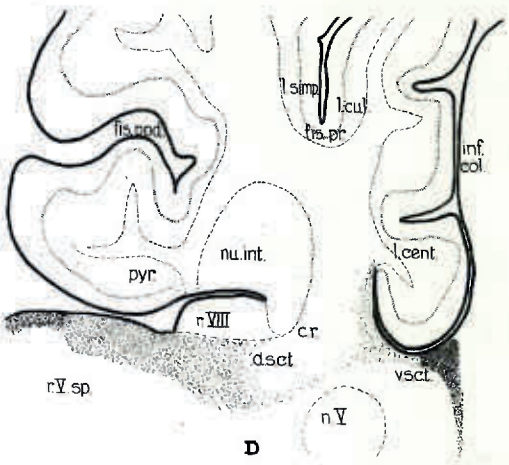
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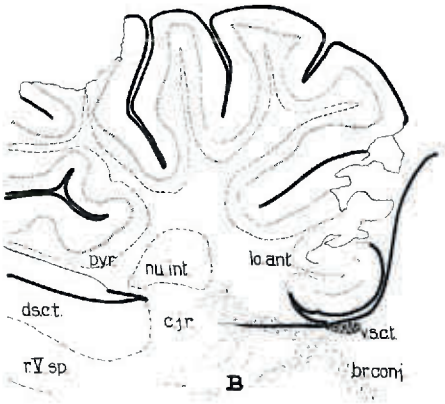
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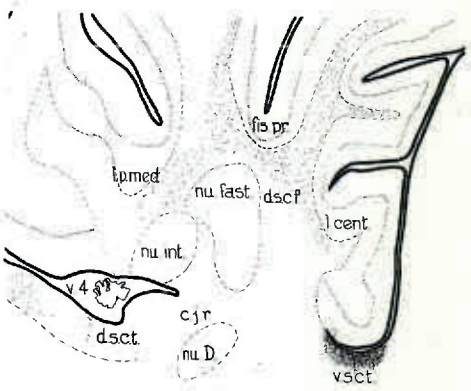
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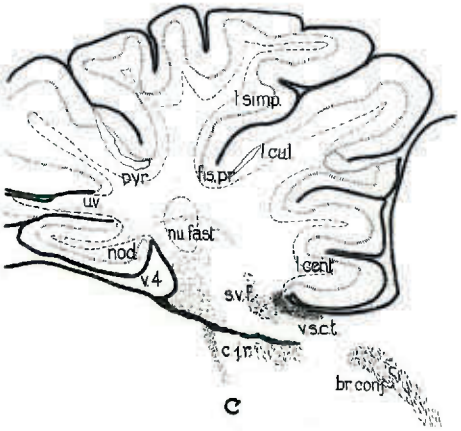
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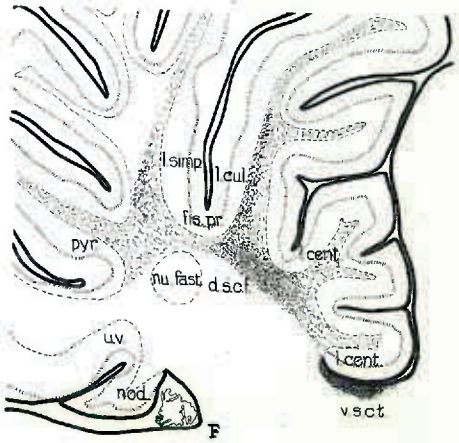
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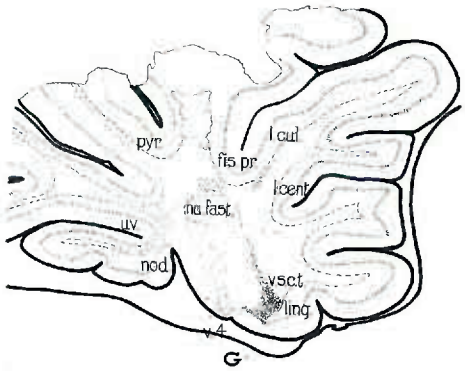
PLATE II

This is a continuation of Plate I. (x12.5)

Figs. G and J--paramedian plane. Note the fibers of the ventral tract in G, and the absence of degenerated fibers in the anterior lobe, lobulus simplex and pyramis. In J note the heavy concentration of the dorsal fibers in the same parts of the vermis.

Figs. H and K--mid-sagittal plane. In H note the ventral tract fibers fanning out to the lobulus centralis, culmen and pyramis. A few can be seen entering the most proximal part of the lobulus simplex. In K note the fibers from the dorsal and ventral tracts fanning out indistinguishably to all parts of the anterior lobe, the lobulus simplex and the pyramis with a few entering the most proximal part of the uvula.

Figs. I and L--plane through the contralateral juxtarestiforme body. In I note that the only degeneration is fine vestibular fibers in the nodulus and the secondary vestibular tract. In L note the moderate amount of degeneration due to the decussated dorsal tract fibers.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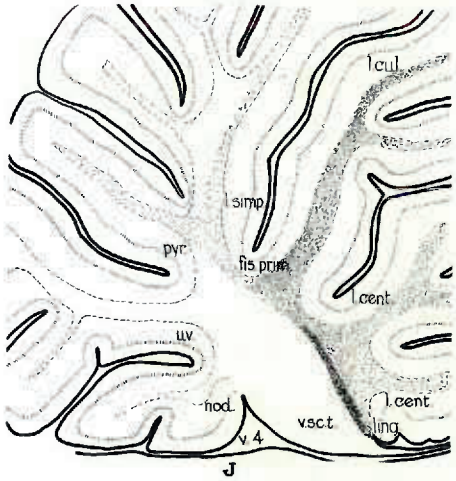
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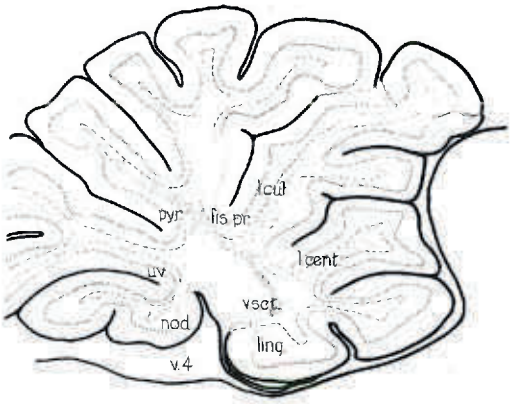
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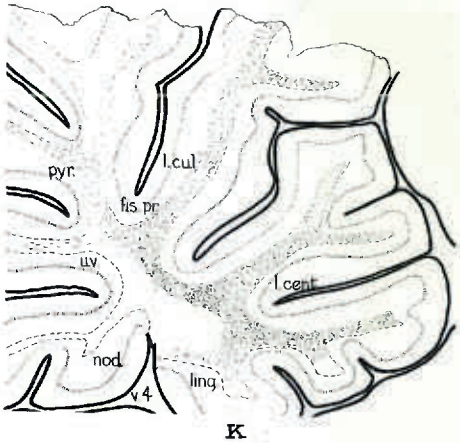
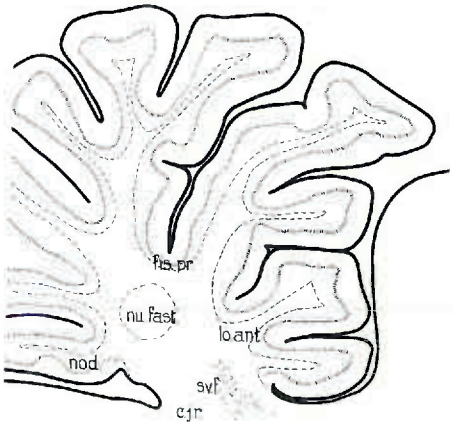
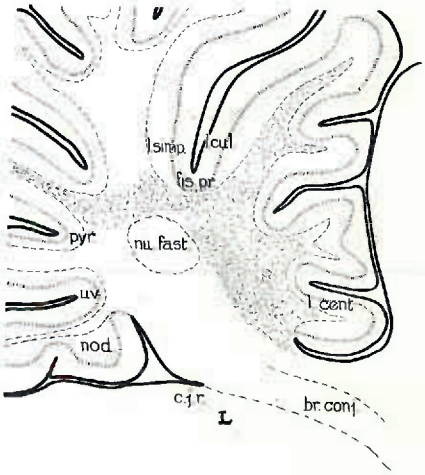

pyr
l cul
fis pr
uv
l cent
nod
ling
v 4

K


fis pr
nu fast
lo ant
nod
svf
c.j.r

I


l simp
l cul
fis pr
pyr
nu fast
uv
l cent
nod
c.j.r
br conj

L

PLATE III

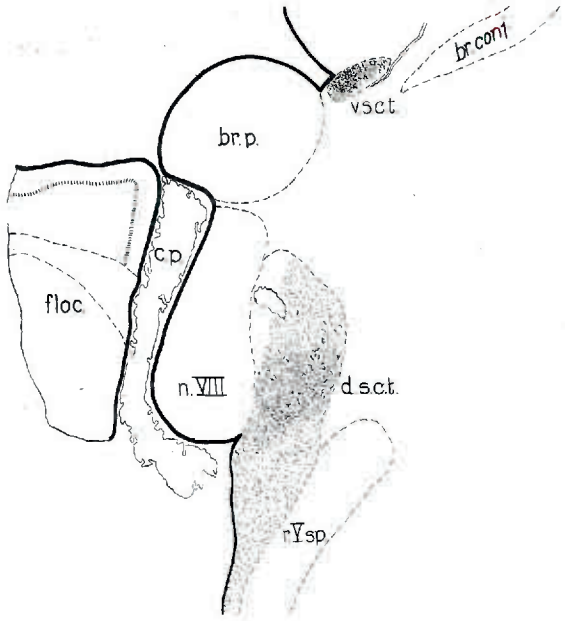
These are horizontal sections taken through rat cerebellum no. 9 in which the dorsal and ventral tracts had been cut on the left side in the cord. Each section starting at the level of the eight nerve shows a higher dorsal plane. (x16.6)

Fig. M. Note the complete separation of the dorsal and ventral tracts. The dorsal tract is passing up the restiforme body and the ventral tract is passing dorsal over the brachium conjunctivum. It is at this level that the ventral tract was cut in rat 53 (see Figs. B, C.).

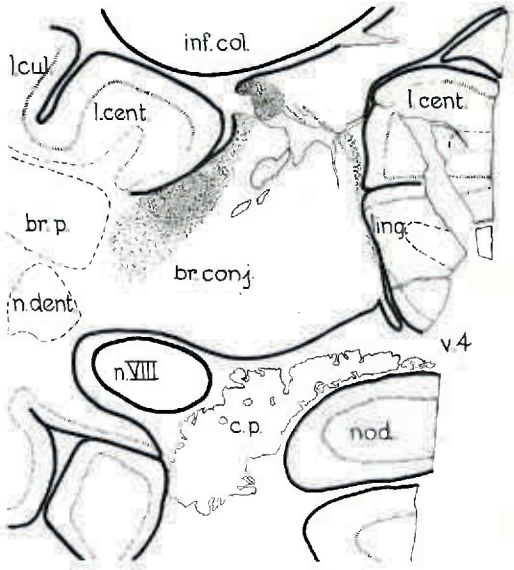
Fig. N. Note the few fibers from the dorsal tract that are joining with the ventral tract.

Fig. O. Note that the ventral tract bends sharply in a medial direction to enter the cerebellum just lateral to the lingula.

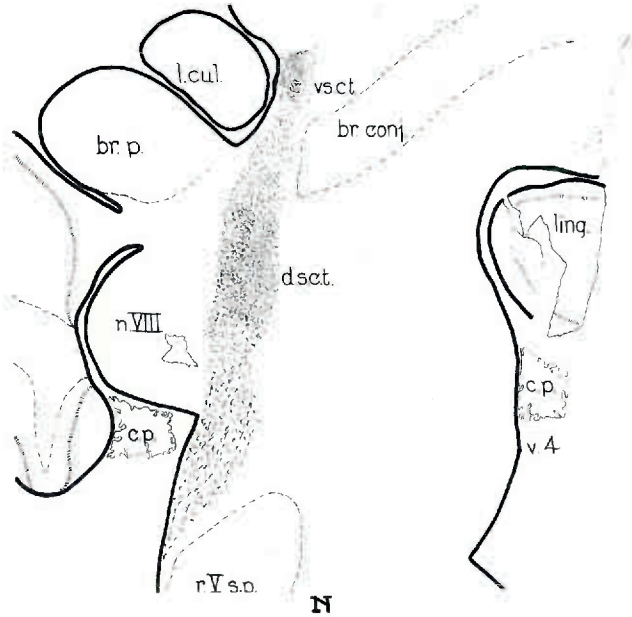
Fig. P. In this diagram the ventral tract along with the most medial part of the dorsal tract have passed to and across the midline to be distributed to the lobulus centralis.


br. conj.
v.s.c.t.
br. p.
floc.
c.p.
n. VIII
d.s.c.t.
r V sp.

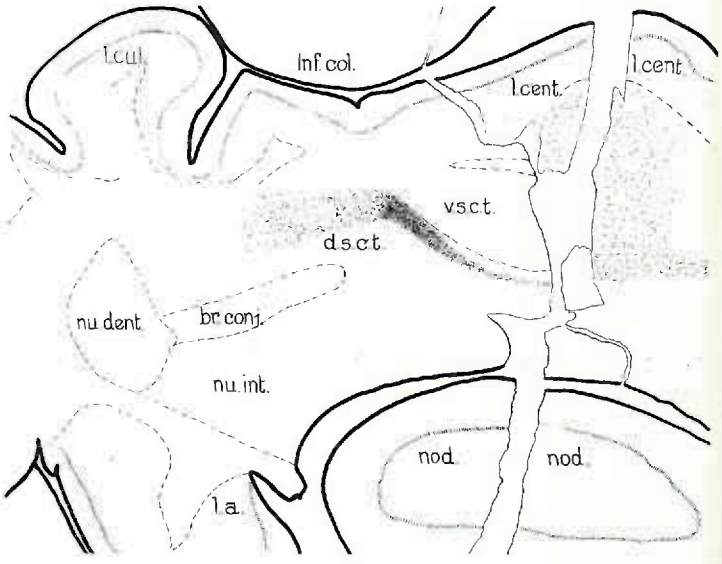
M


inf. col.
l.cul.
l.cent.
l.cent.
br. p.
ling.
br. conj.
n. dent.
v.4
n. VIII
c.p.
nod.

O


l.cul.
v.s.c.t.
br. conj.
br. p.
ling.
d.s.c.t.
n. VIII
c.p.
c.p.
v.4
r V s.p.

N


l.cul.
Inf. col.
l.cent.
l.cent.
v.s.c.t.
d.s.c.t.
nu. dent.
br. conj.
nu. int.
nod.
nod.
l.a.

P

PLATE IV

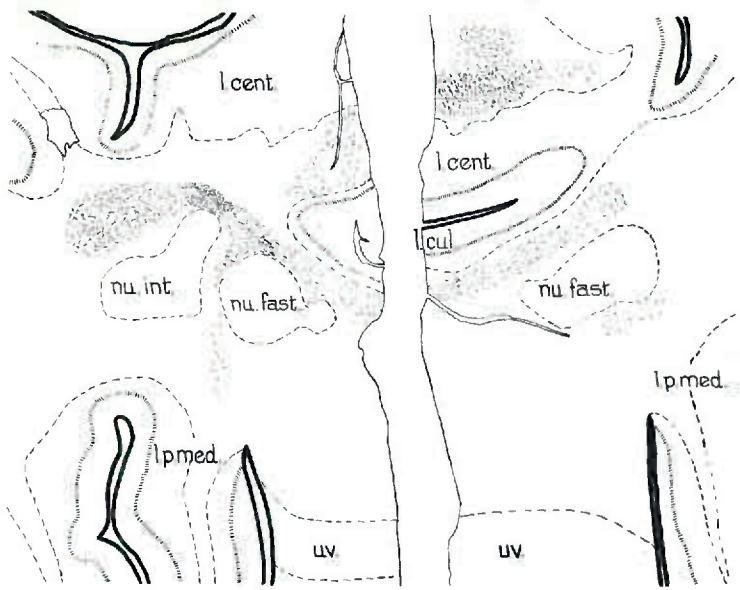
This is a continuation of Plate III.

Fig. Q. Note the degenerated fibers in lobulus centralis and some passing towards the posterior lobe.

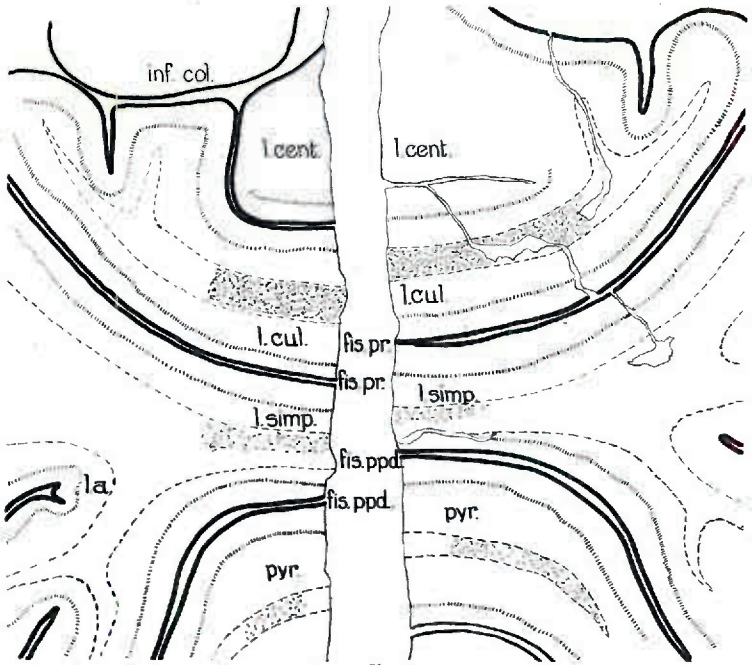
Fig. R. Note the degenerated fibers in the lobulus centralis, culmen, lobulus simplex and the most proximal parts of the lobulus paramedianus.

Fig. S. Note the degeneration in the culmen, lobulus simplex and the pyramis.

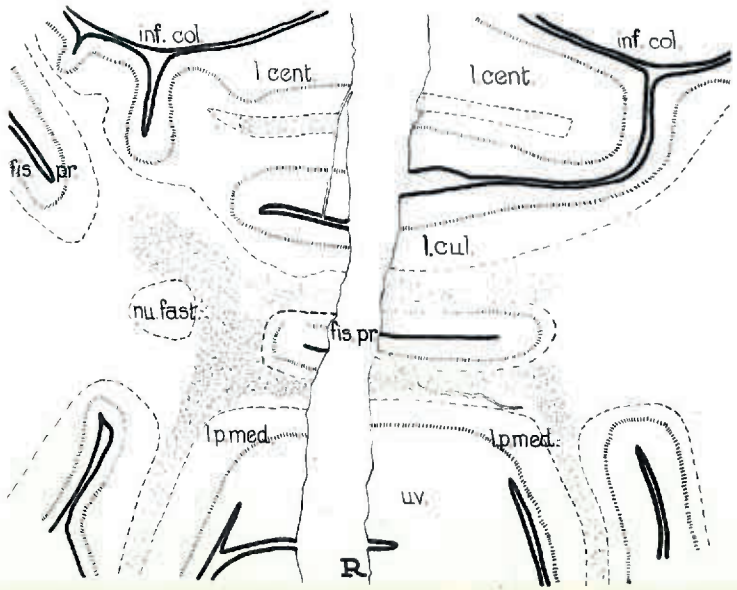
Fig. T. Note the small number of degenerated fibers in the culmen and lobulus simplex.


l.cent.
nu. int.
nu. fast.
l.p.med.
uv.
l.cent.
l.cul.
nu. fast.
l.p.med.
uv.

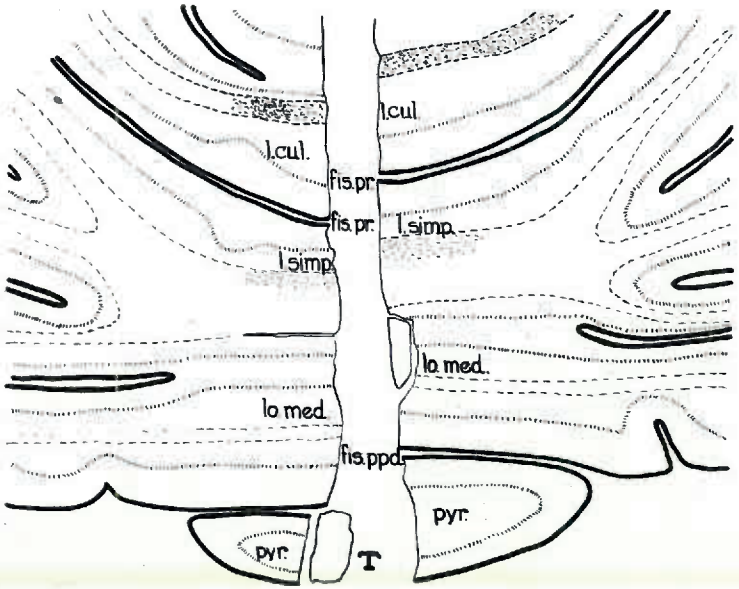
Q


inf. col.
l.cent.
l.cent.
l.cul.
l.cul.
fis.pr.
fis.pr.
l.simp.
l.simp.
fis.ppd.
l.a.
fis.ppd.
pyr.
pyr.

S


inf. col.
l.cent.
fis. pr.
l.cul.
nu. fast.
fis. pr.
l.p.med.
uv.
inf. col.
l.cent.
l.cul.
l.p.med.
uv.

R


l.cul.
l.cul.
fis.pr.
fis.pr.
l.simp.
l.simp.
lo.med.
lo.med.
fis.ppd.
pyr.
pyr.

T

PLATE V

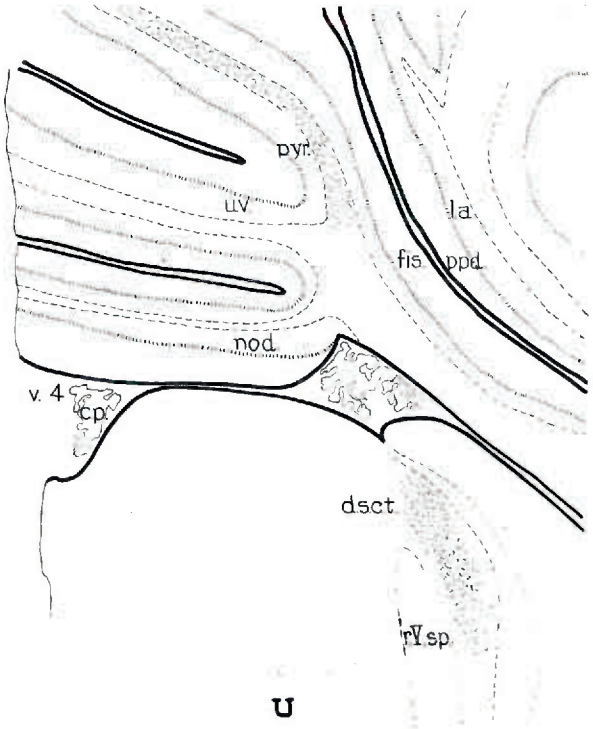
These are diagrams taken transversley through rat cerebellum no. 4. Both the dorsal and ventral tracts were cut on the right side in the cord. (x16.6)

Fig. U. The dorsal tract can be seen swinging posterior to enter the restiforme body.

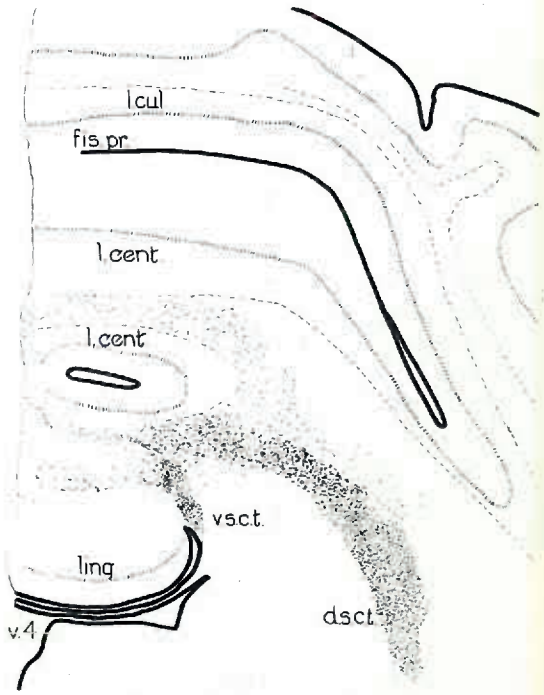
Fig. V. This diagram shows the dorsal tract passing up the restiforme body and fanning out across the midline of the cerebellum.

Fig. W. This diagram, anterior to V, shows the ventral tract entering the midline of the cerebellum to mingle indistinguishably with the dorsal tract.

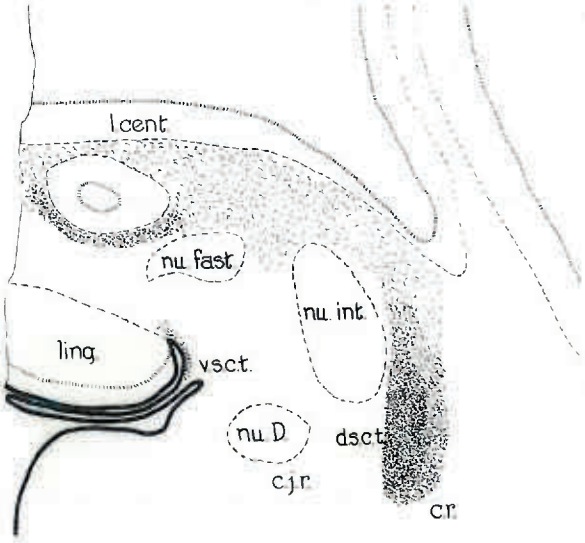
Fig. X. This diagram shows the ventral tract as it bends anteriorly over the brachium conjunctivum before entering the cerebellum.


pyr.
LIV
la.
fis. ppd.
nod.
v. 4
cp.
dsct.
rV sp.

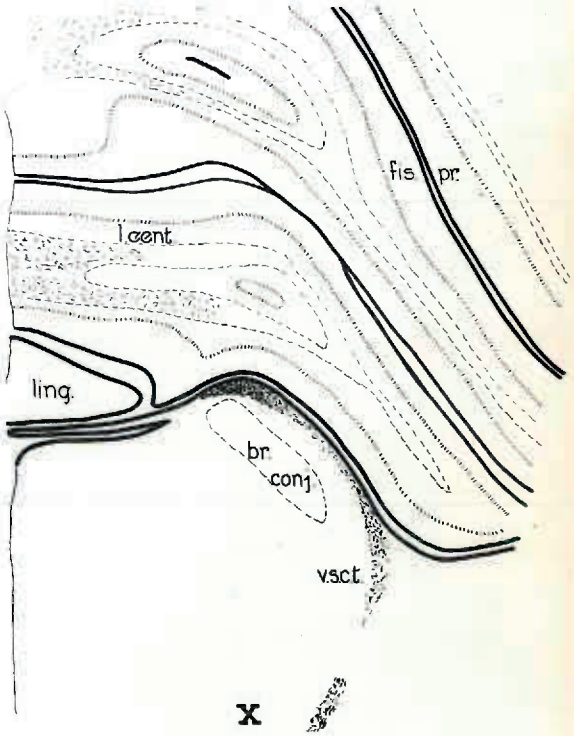
U


lcul
fis. pr.
l. cent.
l. cent.
vsct.
ling.
v. 4
dsct.

W


l. cent.
nu. fast.
nu. int.
ling.
vsct.
nu. D.
dsct.
c.j.r.
cr.

V


fis. pr.
l. cent.
ling.
br.
conj.
vsct.

X