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# DISTRIBUTION OF THE FIBERS ORIGINATING FROM THE DIFFERENT BASAL CEREBELLAR NUCLEI

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## INTRODUCTORY

Since completing the second report ('23) on the central visceral system of the guinea-pig and finding no evidence of any secondary visceral fibers going to the cerebellum, it seemed advisable to enlarge the original scope of this paper to include the distribution of the fibers originating from each and all of the basal cerebellar nuclei.

Considerable work of an experimental nature has been done on the distribution of the fibers arising from the basal nuclei as a whole or limited more or less to the nucleus dentatus or nucleus fastigii, but so far as can be ascertained the intermediate nuclear mass, nucleus globosus et emboliformis, has received no especial attention. There are also some discrepancies in the literature concerning the origin and distribution of the tracts having their source in the basal cerebellar nuclear mass which require further study. No separate review of the literature will be attempted, for the reason that van Gehuchten and Luna have fulfilled this requirement. Occasional reference to the literature, however, will be made throughout the text.

It is apparent from any transverse section through the guinea-pig's cerebellum that the general arrangement of the basal nuclear mass conforms to the descriptions of Weidenreich and Brunner for the lower Mammalia, namely, that this nuclear mass can be separated into three or four different, but connected nuclei. In the guinea-pig it is possible to recognize a median, a lateral, and an intermediate nucleus. The median is the nucleus fastigii or tecti; the solid lateral, nucleus lateralis, is probably phylogenetically and ontogenetically related to the hollow nucleus dentatus of man; while the intermediate nucleus or nucleus interpositus of Brunner can be separated only with great difficulty, if at all, into the N. globosus and N. emboliformis or into the N. lateralis anterior and the N. lateralis posterior of Weidenreich.

This investigation has been restricted largely to a study of certain Marchi series where the lesion was confined well within the limits of one or more of the left cerebellar nuclei. In one instance recourse is made to a Nissl series where the left brachium conjunctivum was severed directly behind its decussation. The cerebellar lesions were all made with an electric cautery or by the rotation of a chisel as described in the previous paper and the same Marchi and Nissl technique were also employed.

### DISTRIBUTION OF THE CEREBELLAR CORTICAL FIBERS

In this problem it is of considerable importance at the outset to determine if the Purkinje cell fibers take any part in the formation of the outgoing tracts, especially the brachium conjunctivum and the tractus cerebello-bulbaris (tractus arcuatus Russell). After the investigations of Probst, and Clarke and Horsley it appeared settled that no cortical fibers supply the above-mentioned tracts. Probst, however, found degenerated cortical fibers passing to Deiters' and to the pontine nuclei; while Clarke and Horsley explicitly state that all fibers leaving the cerebellum by way of the peduncles originate in one of the cerebellar nuclei and, in other words, that "No fibers issuing from the cortex cerebelli enter any of the cerebellar peduncles." Nevertheless, Rothmann, K. Schaffer, Luna, and Saito have recently reopened the question. Rothmann obtained degenerated cerebello-pontine fibers in the middle peduncle as a result of experimental lesions in the cerebellar cortex of dogs that were allowed to live several months after the operations. Schaffer describes cerebellar fibers supplying the inferior olive. Luna states in his microscopical findings for cats A and B, where the lesions were said to be cortical, that degenerated fibers are present in the brachium conjunctivum, in the brachium pontis, in the fasciculus uncinatus, and as tractus cerebello-spinalis fibers. Saito records two distinct groups of degenerated fibers resulting from a lesion which involved the caudal part of the lobus paramedianus and a small part of the lobus medianus in the rabbit; the first group follow ventrally in the corpus restiforme to the inferior olive and ventral part of the medulla, while the second group traverse the inner portion of the brachium pontis to end in the lateral part of the pons.

The writer has not attempted any comprehensive study of this subject, but possesses two Marchi series which have a general bearing on this phase of the problem. In series no. 96 practically all of the superficial and deep dorsal and caudal cortex, including the lobus petrosus, of the left side was destroyed with an electric cautery. So far as could be determined from a microscopical examination, none of the basal cerebellar nuclei were injured, although laterally, where the cortex is thinnest, the lesion approximated the nucleus dentatus. In series 112 the lesion was confined to the superficial cortex of the vermis (lobus medianus).

It is clear from a microscopical study of these series that there is no more than the normal number of degenerated fibers in either brachium conjunctivum, in either corpus restiforme and in either tractus cerebello-bulbaris (tractus arcuatus Russell) caudal to the nucleus nervi vestibularis lateralis. On the other hand, there are in both series more than the normal number of degenerated fibrae cerebello-bulbares going from the vermis to end in the nucleus nervi vestibularis lateralis, which is in agreement with Saito's findings. There are also many fine black granules in the brachia pontis and in the nucleus pontis medialis. This granulation recalled similar granules that were recorded in the previous paper for certain superficial tracts, namely, the tractus opticus and the pedunculus corporis mamillaris, and which are present in equal numbers in those tracts in these series. It also suggested an examination of the brachia pontis in several series where the lesion was confined to the spinal cord. All of these series exhibited a variable number of granules in the brachia pontis, which in some instances were as numerous as in these two cortical lesion series. Therefore these minute black granules in the brachia pontis do not appear to be associated with degenerated cortical cerebellar fibers.

The presence of not more than the normal number of degenerated cortical fibers in the cerebellar peduncules of the above-mentioned series is in agreement with the findings of Clark and Horsley. In series 96, where the lesion involved most of the left cortex of the cerebellum, the degenerated cortical fibers are distributed mainly to the cerebellar nuclei of the left side and to the nucleus fastigii of the opposite side; while in series 112, in which the lesion was confined to the superficial cortex of the vermis, the degenerated fibers terminate chiefly in the fastigial nuclei. A few degenerated cortical fibers in both series pass ventrally, median to the corpora restiformia and end in the vestibular nuclei. It is probable that the length of time Luna allowed his cats to live after the operations, three weeks or more, would account for some retrograde degeneration in the brachia pontis as a result of the chromatolysis of the cells of the pontine nuclei. The long time Rothmann kept his dogs living—several months—certainly would result in considerable retrograde degeneration of the ponto-cerebellar fibers.

## DISTRIBUTION OF DEGENERATED FIBERS RESULTING FROM THE DESTRUCTION OF ALL OF THE LEFT BASAL CEREBELLAR NUCLEI

Marchi series 103 is selected as illustrative of a lesion which destroyed all of the basal cerebellar nuclear mass of the left side, and figure 1 is from a transverse section through the

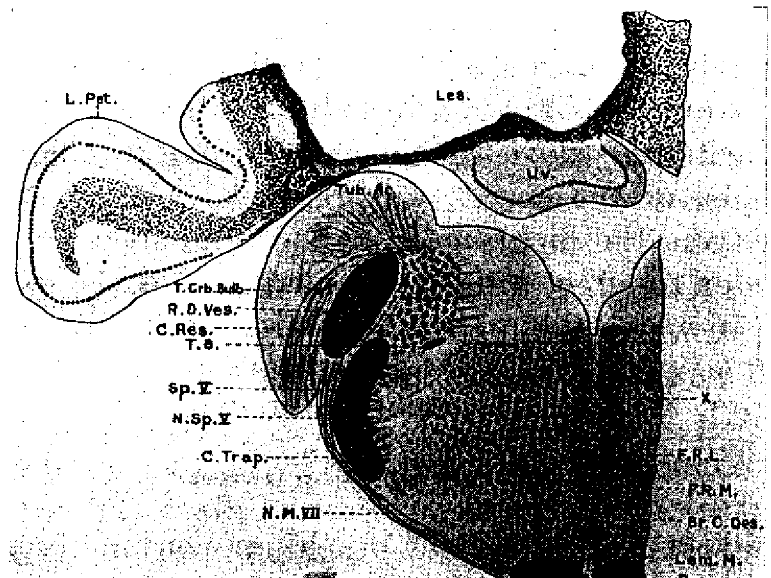
### EXPLANATION OF THE FIGURES

All drawings from transverse sections were made with the aid of a projection drawing apparatus, using a Leitz 42 mm. apochromatic lens. In every instance degenerated fibers are represented as black dots. The drawings of isolated cells were first sketched with a camera lucida, using a Leitz 4 mm. apochromatic objective and a no. 9 periplan eyepiece.

#### ABBREVIATIONS

*Aq.*, aquaeductus cerebri (Sylvii)
*Arc.E.*, fibrae arcuatae externae
*Arc.I.*, fibrae arcuatae internae
*Br.C.*, brachium conjunctivum
*Br.C.D.*, brachium conjunctivum dorsalis
*Br.C.Des.*, brachium conjunctivum descendens
*Br.P.*, brachium pontis
*C.C.*, canalis centralis
*C.Gen.M.*, corpus geniculatum mediale
*Col.I.*, colliculus inferior
*Col.S.*, colliculus superior
*C.M.*, corpus mammilare
*C.Post.*, commissura posterior
*Crb.Bulb.*, fibrae cerebello-bulbares
*C.Res.*, corpus restiforme
*C.Trap.*, corpus trapezoideum
*D.Br.C.*, decussatio brachii conjunctivi
*D.For.*, decussation of the columna descendens fornicis
*D.R.IV*, decussatio radicis nervi trochlearis
*F.L.M.*, fasciculus longitudinalis medialis
*F.M.T.*, fasciculus mamillo-thalamicus or bundle or Vicq d'Azyr
*For.*, fornix or columna descendens fornicis.
*F.R.*, formatio reticularis

*F.R.(a)*, formatio reticularis dorsalis (thalamic region)
*F.R.(b)*, formatio reticularis ventralis (thalamic region)
*F.R.L.*, formatio reticularis lateralis
*F.R.M.*, formatio reticularis medialis
*G.Gen.L.*, ganglion geniculatum laterale
*G.Intp.*, ganglion interpedunculare
*I.Crb.F.*, inner cerebellar funiculus
*Inf.*, infundibulum
*Lam.M.M.*, lamina medullaris medialis
*Lam.M.V.*, lamina medullaris ventralis
*Lem.L.*, lemniscus lateralis
*Lem.M.*, lemniscus medialis
*Lem.M.D.*, lemniscus medialis dorsalis
*Les.*, lesion
*L.Pet.*, lobulus petrosus of Bolk
*N.Cun.*, nucleus fasciculi cuneati
*N.D.*, nucleus nervi vestibularis lateralis (Deiter's)
*N.D.Br.C.*, nucleus dorsalis brachii conjunctivi of Winkler
*N.Den.*, nucleus dentatus
*N.Emb.*, nucleus emboliformis
*N.F.*, nucleus fastigii (tecti)
*N.Glob.*, nucleus globosus
*N.Grac.*, nucleus fasciculi gracilis
*N.Hab.*, nucleus habenulae
*N.Intc.*, nucleus intercalatus Staderini
*N.Lat.T.*, nucleus lateralis thalami (b division of Winkler)
*N.Lem.L.*, nucleus lemnisci lateralis
*N.Med.T.*, nucleus medialis thalami (a and b divisions of Winkler)
*N.Mon.*, nucleus Monakow of Winkler
*N.M.VII*, nucleus motorius nervi facialis
*N.Pon.L.*, nucleus pontis lateralis of Winkler
*N.Pon.M.*, nucleus pontis medialis of Winkler
*N.Pon.V.*, nucleus pontis ventralis of Winkler
*N.Res.*, nucleus proprius corporis restiformis
*N.Rub.*, nucleus ruber
*N.Sp.V.*, nucleus tractus spinalis nervi trigemini
*N.T.S.*, nucleus tractus solitarii
*N.V.Br.C.*, nucleus ventralis brachii conjunctivi of Winkler
*N.Ven.T.(a)*, lateral division, nucleus ventralis thalami
*N.Ven.T.(b)*, central median division, nucleus ventralis thalami
*N.Ven.T.(c)*, median division, nucleus ventralis thalami
*N.III*, nucleus nervi oculomotorii
*N.IV*, nucleus nervi trochlearis
*N.XI*, nucleus nervi accessorii or caudal continuation of the nucleus motorius dorsalis nervi vagi
*N.XII*, nucleus nervi hypoglossi
*Ol.I.*, nucleus olivaris inferior
*Ped.Cer.*, pedunculus cerebri
*Ped.C.M.*, Pedunculus corporis mammillaris
*Pyr.*, pyramis or tractus cerebrospinalis
*R.D.Ves.*, radix descendens nervi vestibularis
*R.Mes.V.*, radix mesencephalica trigemini
*R.Subt.*, regio subthalamica
*R.Ves.*, radix nervi vestibularis
*R.III*, radix nervi oculomotorii
*R.IV*, radix nervi trochlearis
*S.Gr.C.*, substantia grisea centralis
*S.Nig.*, substantia nigra
*Sp.V.*, radix spinalis nervi trigemini
*St.Med.*, stria medullaris thalami
*T.Crb.Bulb.*, tractus cerebello-bulbaris
*T.Hab.Ped.*, tractus habenulo-peduncularis
*T.Op.*, tractus opticus
*T.S.*, tractus solitarius
*Tub.Ac.*, tuberculum acusticum
*Uv.*, uvula
*Ves.Crb.*, fibrae vestibulo-cerebellares
*X.*, fasciculus cerebello-bulbaris, pars medialis
*Z.Inc.*, zona incerta of Winkler
*III Ven.*, ventriculus tertius
*IV ven.*, ventriculus quartus

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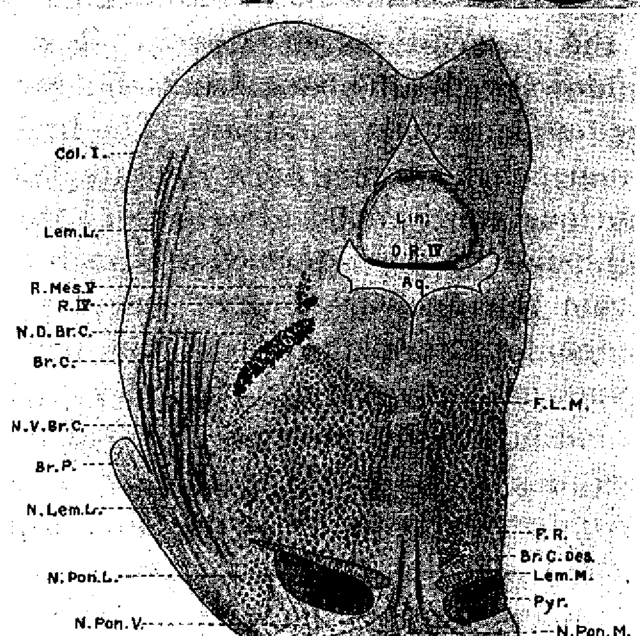


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Fig. 1 Left half of a transverse section from Marchi series no. 103 through the center of a cerebellar lesion which involves all of the left basal cerebellar nuclei, showing some of the resultant degeneration. A large part of the cerebellar cortex was removed during fixation. × 6.6.

Fig. 2 Left half of a section through the caudal end of the colliculus inferior segment from the same series as figure 1. Observe degenerated fibers in the brachium conjunctivum, in the fasciculi longitudinales mediales and in the right brachium conjunctivum descendens. × 6.6.

center of the destroyed area (*Les.*). A microscopical study of this and other sections demonstrates that all of the cells of the left cerebellar nuclei are destroyed, and that few, if any, of the right or opposite nuclear cells are affected. The reason for not including more of the cerebellum in the figure is because most of the cortex was removed while transferring the brain from the bichromate to the osmic-bichromate solution in order to effect a deeper infiltration of the osmic acid. Series 77, in which the proximal portion of the brachium conjunctivum was severed, serves as a control.

### *Brachium conjunctivum*

The general course of the brachium conjunctivum up to and including its decussation in the guinea-pig conforms in the main to the descriptions of Marchi, Russell, Thomas, Probst, Lewandowsky, Wallenberg, van Gehuchten, Luna, and others for various mammals and man. The first appearance of the brachium conjunctivum as a definite tract is at the level of the nucleus nervi abducentis, in the basal part of the cerebellum cephalad of the intermediate nucleus. Degenerated fibers from the nucleus dentatus unquestionably pass through the cephalic lateral portion of this nucleus, namely, through the nucleus emboliformis part of it. At its source the brachium conjunctivum presents an oval appearance in transverse section; its long axis extending from the corpus restiforme medially nearly to the uvula, being separated from the latter by the fasciculus uncinatus (tractus arcuatus Russell) and the tractus spino-cerebellaris ventralis. It is dorsal to the nucleus nervi vestibularis lateralis and is more or less roofed by the corpus restiforme fibers. In its general cephalic course the brachium conjunctivum gradually acquires a more ventral position, and at the same time its long axis in cross-section rotates slowly to a dorso-ventral plane, the dorsal end acting as a pivot. Upon entrance into the brain stem the brachium conjunctivum rests on the motor and sensory nuclei of the nervus trigeminus, is arched dorsally by the tractus spino-cerebellaris ventralis, is median to the brachium pontis and lateral to the lingula. Within the colliculus inferior segment the rotation of the axis of the brachium conjunctivum is pronounced and at the level of figure 2 the long axis has not only almost reached a dorso-ventral plane, but the tract has taken on a half-moon shape and, as was noted by van Gehuchten, resembles the radix spinalis nervi trigemini in transverse section.

It is obvious from figure 2 that the brachium conjunctivum forms a base for the radix mesencephalica trigemini (*R.Mes.V.*). In this region Probst and Luna describe and figure an accessory brachium conjunctivum bundle situated as a cap on the main brachium conjunctivum. This bundle is said to come from the roof nuclei of the cerebellum and to cross in the cerebellum instead of in the decussation of the brachium conjunctivum. Probst portrays some of the degenerated fibers from the accessory bundle as ending in the posterior corpora quadrigemina. Also Russell's figures 1, 7, and 15 suggest a similar bundle. Since the position of this accessory bundle is identically the same as the radix mesencephalia trigemini and inasmuch as this bundle usually contains a few degenerated fibers in any Marchi series, the writer agrees with van Gehuchten that the so-called accessory brachium conjunctivum of Probst and Luna is nothing more than the radix mesencephalica trigemini.

Throughout its entire course, up to the point of its decussation, numerous degenerated brachium conjunctivum fibers are distributed to the adjacent formatio reticularis of the brain stem. At the exit of the brachium conjunctivum from the cerebellum, a number of small bundles of degenerated fibers pass ventrally between the nucleus motorius nervi trigemini and the brachium pontis, to accompany the radix motorius nervi trigemini ventrally and caudally between the motor and sensory trigeminal nuclei and terminate in the formatio reticularis between the ventral median corner of the radix spinalis nervi trigemini and the cephalic lateral border of the nucleus olivaris superior. In the colliculus inferior segment (fig. 2) many degenerated brachium conjunctivum fibers appear in the formatio reticularis, dorsally and laterally to the brachium conjunctivum in Winkler's nucleus dorsalis brachii conjunctivi (*N.D.Br.C.*) and ventrally to the extreme ventral corner of the brachium conjunctivum, but few or none are present median to this tract in a mass of cells which Winkler has labeled as the nucleus ventralis branchii conjunctivi.

*Decussation.* Most of the descriptions of the brachium conjunctivum dismiss the decussation with a statement that the fibers cross to the opposite side in the midbrain region. A few fibers are mentioned by von Monakow as continuing caudad without decussating. Probst states that experimental lesions in dogs and cats demonstrate a few degenerated brachium conjunctivum fibers going to the 'Marklamelle' without decussating in the commissure of Wernekink. In his human Marchi series Probst also describes a few degenerated brachium conjunctivum fibers which do not decussate in the posterior corpora quadrigemina, but pass to the nucleus ruber of the same side, where they pursue an identical course to the crossed fibers. These fibers are said to originate from the nucleus fastigii and to cross in the cerebellum. In cat E, Luna observes that the median fibers of the brachium conjunctivum are the first to cross, the dorsal are next and the ventral last.

Van Gehuchten presents a most detailed description of the commissure of Wernekink, which is illustrated by five transverse sections and several frontal sections. The author notes the dorsal fibers as being the first to assume a median course, and indicates that the dorsal fibers have a different mode of crossing than the ventral fibers. The ventral fibers are said to be little massed and to describe concentric arcs in crossing to the opposite side of the raphé; while the dorsal fibers pass directly median and cross the raphé as a fasciculus. Cephalad, the décussation consists mainly of ventral fibers.

The writer's observations on the decussation of the brachium conjunctivum in the guinea-pig are in the main confirmatory of van Gehuchten's descriptions for the rabbit. It is certain that all of the brachium conjunctivum fibers which reach the level of Wernekink's commissure cross. This commissure (fig. 3A, *D.Br.C.*) is situated directly above the ganglion interpedunculare (*G.Intp.*) and a little below the

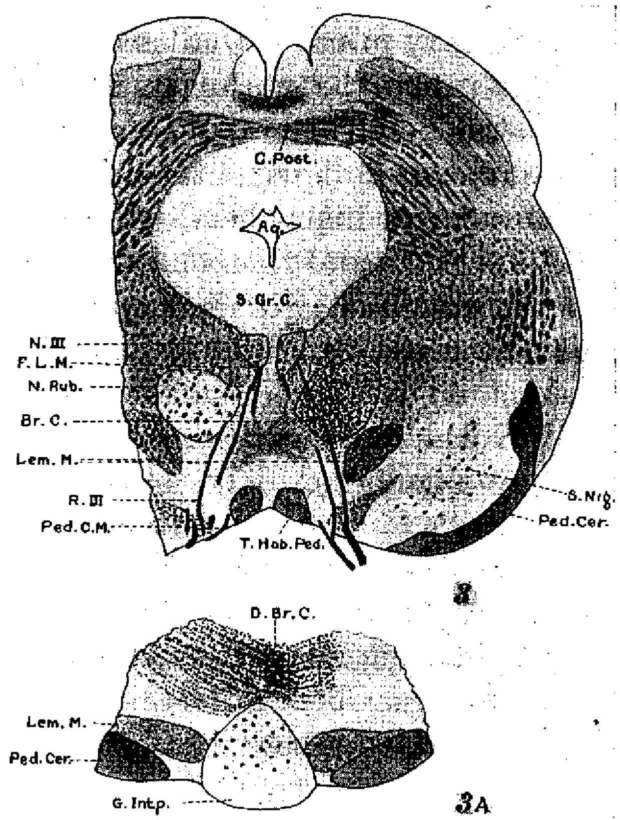



Fig. 3 Right half of a section at the level of the nucleus ruber and the nucleus nervi oculomotorii from the same series as figure 1, demonstrating degenerated fibers in the fasciculi longitudinales mediales and the distribution of the brachium conjunctivum fibers to the nucleus ruber and dorsally. × 6.6.

Fig. 3A Section through the decussation of the brachium conjunctivum or Wernekink's commissure from the same series as figure 1. × 6.6.

fasciculi longitudinales mediales in section. The crossing of these fibers occupies a considerable caudo-cephalad space, and is barely completed when the nucleus ruber is reached. So far as could be determined, the dorsal and ventral fibers start medially about the same level, but the dorsal fibers are the first to reach the raphé in large numbers. A section through the center of the decussation (fig. 3A) confirms the characteristic differences noted by van Gehuchten for the dorsal and ventral fibers, namely, that the dorsal fibers pass horizontally to the raphé as a fasciculus, while the ventral fibers, fewer in number, are very much arched. It will be seen from figure 3A that the dorsal fibers pass to the raphé in small bundles, closely approximating each other, while the ventral fibers run in very minute bundles or as isolated fibers. Upon reaching the raphé the majority of the dorsal fibers make a sharp ventral bend after passing the midline, while the ventral maintain a more horizontal line. Figure 3A also shows some of the ventral fibers bending ventrally below the ganglion interpedunculare and then curving dorsally to cross the raphé above the ganglion. No degenerated brachium conjunctivum fibers enter the ganglion interpedunculare at any point. Van Gehuchten is correct in his statement that the cephalic fibers of Wernekink's commissure are chiefly ventral brachium conjunctivum fibers. It is obvious, then, that the dorsal fibers of the brachium conjunctivum exhibit a general tendency to decussate earlier than the ventral fibers.

*Brachium conjunctivum descendens.* Thomas, Probst, Lewandowsky, Wallenberg, van Gehuchten, von Monakow, and Luna have each described a descending brachium conjunctivum extending into the medulla. Probst portrays this trunk as being given off ventrally from the brachium conjunctivum at the point where the peduncle leaves the cerebellum, and that it passes caudally in the angle between the raphé and the lemniscus medialis. Von Monakow also records descending brachium conjunctivum fibers as not crossing in Wernekink's commissure, but passing caudad before the commissure is reached. The others maintain that the brachium conjunctivum fibers separate into cephalic and caudal fasciculi after decussation takes place, but there is some disagreement as to the manner in which this is accomplished. Van Gehuchten and Luna are of the opinion that some of the fibers after crossing in Wernekink's commissure bifurcate and that the caudal divisions form the descending brachium conjunctivum. Wallenberg, on the other hand, believes that some of the brachium conjunctivum fibers after decussating bend cephalad to form the ascending brachium conjunctivum and others bend caudad to form the descending brachium conjunctivum. According to Wallenberg, the brachium conjunctivum descendens is situated directly above the lemniscus medialis and passes caudad to the level of the inferior olive. Many collaterals are distributed to the dorso-lateral pons nuclei, to the nucleus reticularis tegmenti, and a few to the nucleus of the nervus hypoglossus. Van Gehuchten shows essentially the same course for this trunk as Wallenberg.

In the guinea-pig there is no question but that the brachium conjunctivum descendens is formed from fibers that have decussated in the commissure of Wernekink. The writer saw no evidence of any bifurcation of these fibers after decussation, but admits that van Gehuchten, in possessing a frontal series, was in a better position for determining this point. Figure 2, taken from an inferior colliculus section a short distance behind the decussation, shows the brachium conjunctivum descendens (*Br.C.Des.*) as a more or less circular bundle situated dorsally to the median portion of the lemniscus medialis (*Lem.M.*). It is obvious from this section that degenerated fibers are radiating in all directions from the brachium conjunctivum descendens to the formatio reticularis (*F.R.*), especially dorsally and laterally. Figure 1, which is from the level of the caudal end of the nucleus motorius nervi facialis and not far from the caudal end of the brachium conjunctivum descendens, demonstrates this tract (*Br.C.Des.*) to be composed of a few fibers, situated dorsally to the lemniscus medialis and close to the median line. Furthermore, it is apparent from series 103 and 77 that the brachium conjunctivum descendens is distributed solely to the formatio reticularis of the pons and medulla. There is no evidence of any of its fibers in the guinea-pig going to the pontine nuclei or to any motor nuclei of the medulla. It therefore supplies a region of the formatio reticularis that is not supplied by the main brachium conjunctivum or the tractus cerebello-bulbaris to be described later.

*Brachium conjunctivum ascendens.* Any section cephalad of the decussation of the brachium conjunctivum will show the brachium conjunctivum ascendens or main brachium conjunctivum trunk to be located at a decidedly more ventral level than the original brachium conjunctivum before decussation. In transverse section it is cylindrical in outline, occupying a much greater area than before decussation, due in part, to the fact that its fibers are cut up by normal vertical fibers as well as by normal horizontal fibers, thereby taking on the appearance of the formatio-reticularis. Like the corresponding brachium conjunctivum descendens, it is dorsal to the lemniscus medialis and but a short distance from the midline. The writer is able to confirm the observations of Klimoff and van Gehuchten that a number of brachium conjunctivum fibers branch off dorsally to the nucleus nervi oculomotorii. These fibers begin leaving the ascending brachium conjunctivum at the level where the last fibers are decussating and are continued to be given off until the nucleus ruber is reached. In both series 103 and 77 these fibers enter the right nucleus nervi oculomotorii from behind and from the side, and singularly there are more degenerated brachium conjunctivum fibers in the dorsal small-celled Edinger-Westphal nucleus than there are in the more ventral somatic area. These fibers also penetrate the adjacent central gray, and some of them undoubtedly end in the formatio reticularis dorsad of the nucleus ruber. There are also a few degenerated fasciculi longitudinales mediales fibers supplying the III nuclei, which will be shown later to originate from the fastigial nuclei. In more cephalic sections through the III nuclei there are no more degenerated fibers in the right nucleus than in the left (fig. 3, *N.III*), which in both instances are indicative of fasciculi longitudinales mediales origin. Klimoff thought that the other eye muscle nuclei might receive brachium conjunctivum fibers, but the writer found no evidence in series 103 and 77 of degenerated brachium conjunctivum fibers supplying these nuclei.

With the exception of Sand, who believes that some of the brachium conjunctivum fibers go to the cerebral cortex, all of the investigators agree that the brachium conjunctivum ascendens fibers terminate cephalad in the nucleus ruber and in the thalamus.

Marchi, Russell, Thomas, Wallenberg, van Gehuchten, von Monakow, and Luna state that brachium conjunctivum fibers both end in and pass through the nucleus ruber. In man Probst records more brachium conjunctivum fibers in the ventral than in the dorsal part of the nucleus ruber. He finds no degenerated conjunctivum fibers in the dorsal cord of this nucleus, while the lateral cord or Flechsig's 'Haubenstrahlung' is made up entirely of brachium conjunctivum fibers.

Concerning the ending of the brachium conjunctivum-thalamic fibers, there is considerable vagueness in many of the descriptions and some difference of opinion as to the actual endings. Marchi and Russell simply record the brachium conjunctivum fibers as terminating in the optic thalamus. Thomas places their endings in the corpus subthalamicum and von Monakow in the median thalamic nucleus. Wallenberg found degenerated brachium conjunctivum fibers supplying the gray of the hypothalamus below the nucleus ruber, the gray of Forel's field, and going by way of the lamina medullaris interna to the median thalamic nucleus and to the corresponding nucleus of the opposite side. Van Gehuchten is of the opinion that no brachium conjunctivum fibers cross to the opposite side in the posterior commissure. In both transverse and frontal sections van Gehuchten portrays the cerebellar thalamic fibers of the rabbit as separating into an outer and inner bundle after crossing the lateral surface of the tractus habenulo-peduncularis. The outer bundle is represented as supplying the inner parts of the optic thalamus of the same side and the outer bundle, the inner portion of the opposite optic thalamus. Luna observed degenerated brachium conjunctivum fibers in the gray of Forel's field and in the outer medullary lamina, and states that a number vanished in the median and lateral thalamic nuclei.

Probst not only has furnished us with a detailed account of the endings of the brachium conjunctivum-thalamic fibers in the cat, dog, and man, but in addition has shown the relation of these fibers to the lemniscus medialis. In general the brachium conjunctivum fibers were represented as occupying a more dorsal and median position in the caudal part of the thalamus and to have a more cephalic termination. Probst ('01) figures six sections through the thalamic region of his human Marchi series. In the caudal sections Probst found cerebellar-thalamic fibers ending in the more medial of the ventral thalamic nuclei (*ven.b.*) and in the subthalamic region. Also a few fibers were traced through the nucleus (*ven.b.*) to enter the central part of the more lateral of the median thalamic nuclei (*med.b.*). No degenerated brachium conjunctivum fibers were found in the caudal end of the more lateral of the ventral thalamic nuclei (*ven.a.*), where the lemniscus medialis fibers were said to terminate. Farther cephalad, Probst represents the cerebellar-thalamic fibers as acquiring a more lateral course, being bounded dorsally by the lamina medullaris interna, and ventrally by the lamina medullaris externa. They terminate in the cephalic end of the more lateral of the ventral thalamic nuclei (*ven.a.*) and in the lateral thalamic nucleus. Probst contends that no brachium conjunctivum fibers are distributed to the zona incerta, to the corpus Luysi, to the formatio reticularis 'Gitterschichte,' or to the capsula interna.

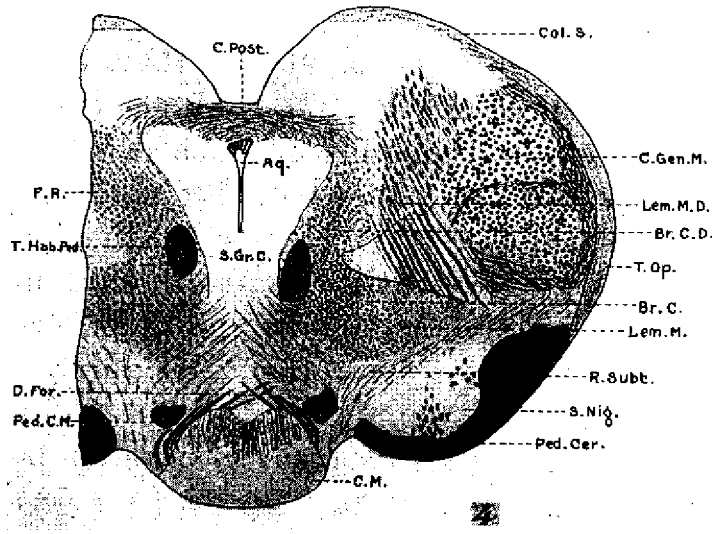
In the dog and cat Probst would divide the brachium conjunctivum fibers into dorsal and ventral fasciculi before the decussation occurs. The ventral tract is said to travel more ventrally in the nucleus ruber and regio subthalamica, to end in the ventral and probably also in the median thalamic nucleus. The dorsal or main fasciculus forms the lateral striations to the ventral thalamic nuclei situated between the outer and inner lamina medullaris. Furthermore, isolated degenerated brachium conjunctivum fibers were observed in the inner half of the lamina medullaris that supplies the median thalamic nuclei.

Regarding the distribution of the brachium conjunctivum fibers in the nucleus ruber, the writer has little to add to Probst's description. A caudal section through the nucleus ruber (fig. 3, *N.Rub.*) shows this nucleus a little ventro-laterad of the corresponding fasciculus longitudinalis medialis (*F.L.M.*) and a little dorso-mesad of the corresponding lemniscus medialis (*Lem.M.*). Its large cells are median and ventral and its small cells are dorsal and lateral. Throughout, the nucleus is filled with degenerated brachium conjunctivum fibers, more ventrally than dorsally. These fibers have every indication of being both collaterals and trunk fibers, also of terminating in and passing through the nucleus.

Upon leaving the nucleus ruber, the thalamic portion of the brachium conjunctivum (fig. 4, *Br.C.*) is situated a little lateral to the center of the section, between the tractus habenulo-peduncularis (*T.Hab.Ped.*) and the lemniscus medialis (*Lem.M.*), placing it dorso-mesad of the lemniscus medialis as located by Probst. After comparing figure 4 with figure 5, a section at the same level from a series in which the lemniscus medialis is shown in degeneration, it is clear that the main thalamic fasciculus of the brachium conjunctivum (*Br.C.*) and its dorsal bundle (*Br.C.D.*) occupy a general position median to the main lemniscus fasciculus (*Lem.M.*) and its dorsal bundle (*Lem.M.D.*). In so far as could be determined no brachium conjunctivum fibers cross in the commissura posterior as Probst described for the dog and cat. Figure 4 demonstrates similar small black granules in the commissura posterior (*C.Post.*) to those described in the previous paper for the pedunculus corporis mamillaris and the tractus opticus and earlier in this paper for the brachium pontis (see this paper, fig. 4, *Ped.C.M.* and *T.Op.;* fig. 2, *Br.P.*). For the reasons previously stated on page 402, the writer is not warranted in classifying these fine black granules as degenerated posterior commissure fibers. Since the brachium conjunctivum dorsalis pursues a general cephalic course, its distribution will be described along with the main thalamic bundle of the brachium conjunctivum.

A section through the caudal end of the thalamus (fig. 6), including that region of the lateral division of the nucleus ventralis thalami (*N.Ven.T.*(*a*)) and the nucleus lateralis thalami (*N.Lat.T.*) in which the lemniscus medialis fibers were shown to terminate in the previous paper, discloses the brachium conjunctivum dorsalis fibers as being distributed to the nucleus medialis thalami (*N.Med.T.*). It also reveals the main thalamic tract of the brachium conjunctivum (*Br.C.*) as a conspicuous bundle of degenerated fibers situated medially to the large lateral division of the nucleus ventralis thalami (*N.Ven.T.*(*a*)), and directly dorsad of the fasciculus mamillo-thalamicus (*F.M.T.*) and a dense median portion of the ventral formatio reticularis designated as the zona incerta (*Z.Inc.*). Furthermore, a few degenerated brachium conjunctivum fibers are distributed to the gray above the ventriculus tertius, but few, if any, cross to the opposite side, certainly nothing like a commissural tract such as van Gehuchten described for this level.

It is apparent that a considerable number of degenerated brachium conjunctivum fibers pass ventro-laterally through the zona incerta and the median portion of the lamina medullaris ventralis to the regio subthalamica (*R.Subt.*) dorsad of the median portion of the corresponding pedunculus cerebri. It will be recalled that Probst described brachium conjunctivum fibers supplying the subthalamic region, but, contrary to Probst, there are apparently degenerated fibers in the guinea-pig ending in the zona incerta and in the median portion of the ventral formatio reticularis (*F.R.*(*a*)). In fact, a large part of the fibers of the zona incerta appear to be of brachium conjunctivum origin. Nevertheless, none of these degenerated brachium conjunctivum fibers extend laterally to any great distance in the ventral formatio reticularis. The number and size of the degenerated fibers bear every evidence of being collaterals rather than trunk fibers. There is absolutely no trace of degenerated brachium conjunctivum fibers in any of the sections through the caudal ends of the most lateral division of the nucleus ventralis thalami (*N.Ven.T.*(*a*))



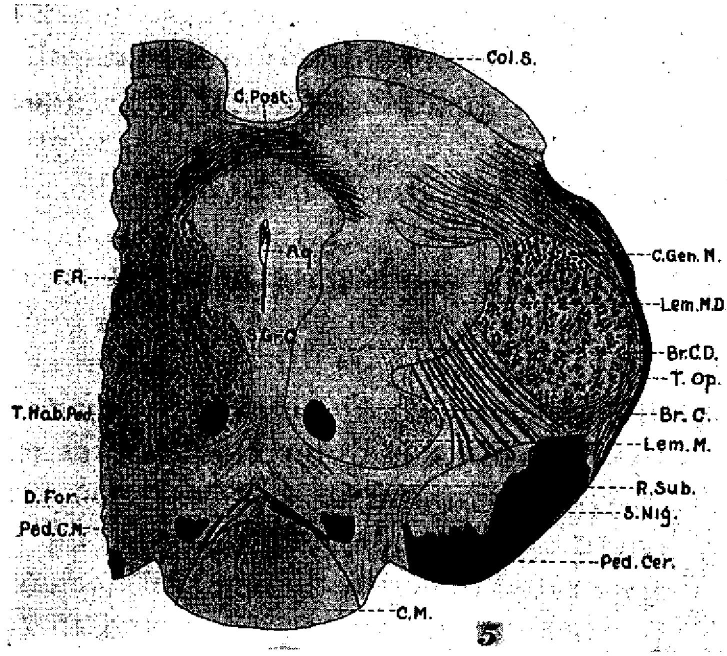




Fig. 4 Right half of a section directly cephalad of the nucleus ruber from the same series as figure 1, illustrating the branching off of the brachium conjunctivum dorsalis and the relation of the thalamic portion of the brachium conjunctivum to the lemniscus medialis. × 6.6.

Fig. 5 Similar section to figure 4 from series 140, showing the branching off of the dorsal fasciculus of the lemniscus medialis and the relation of the lemniscus to the thalamic portion of the brachium conjunctivum. × 6.6.

and the nucleus lateralis thalami (*N.Lat.T.*), which regions were shown in the previous paper to be the chief terminals for the lemniscus medialis fibers.

A large percentage of the cerebellar-thalamic fibers continue cephalad in the main brachium conjunctivum trunk until the cephalic end of the thalamus is reached, where they terminate in the guinea-pig somewhat, but not entirely, after the manner described by Probst. Instead of the fibers bending laterally to be distributed to the cephalic ends of the most lateral of the ventral thalamic nuclei and the lateral thalamic nucleus as represented by Probst, they pass dorsally (fig. 6A), in company with many normal fibers, through an intermediate nucleus of large cells (*N.Ven.T.*(*b*)), situated between the outer and inner ventral thalamic nuclei (*N.Ven.T.*(*a*)) and (*N.Ven.T.*(*c*)). The great majority of these degenerated brachium conjunctivum fibers eventually bend laterally, to enter the lamina medullaris medialis (*Lam.M.M.*), inner thalamic lamina of Probst, whence they are distributed ventrally to the cephalic end of the large lateral division of the nucleus ventralis thalami (fig. 6A, *N.Ven.T.*(*a*)). A few degenerated brachium conjunctivum fibers pass medially in the lamina medullaris medialis above the median division of the nucleus ventralis thalami (*N.Ven.T.*(*c*)) to end in the central gray dorso-mesad of this nucleus. An occasional degenerated fiber may cross to the opposite side to terminate in the corresponding central gray, but nothing in any way comparable to a fasciculus. There appeared to be no more than the normal number of degenerated fibers in the median nucleus ventralis thalami, in the nucleus medialis thalami, and in the nucleus lateralis thalami at this level. It was not determined whether the brachium conjunctivum fibers end in or simply pass through the intermediate nucleus ventralis thalami (*N.Ven.T.*(*b*)), but it is likely that some fibers terminate in this nucleus.

It is obvious, then, that the cephalic end of the large lateral nucleus ventralis thalami (fig. 6A, *N.Ven.T.*(*a*)) is the terminal for most of the thalamic brachium conjunctivum fibers, and the caudal part of this nucleus is the terminal for most of the lemniscus medialis fibers. A dorsal fasciculus of the brachium conjunctivum was described as ending in the caudal part of the nucleus medialis thalami, and a corresponding dorsal fasciculus of the lemniscus medialis terminates in the

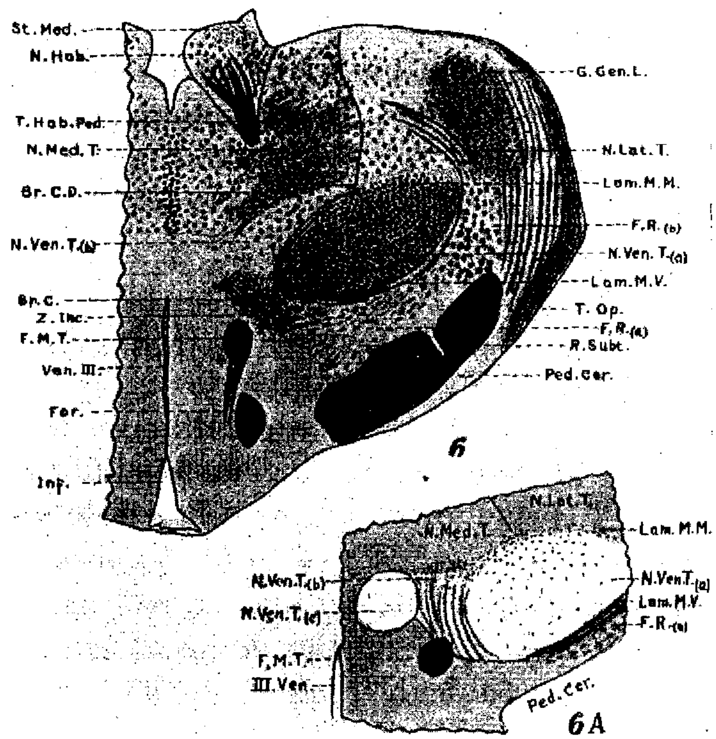



Fig. 6 Right half of a section through the caudal end of the thalamus from the same series as figure 1, demonstrating the position of the thalamic portion of the brachium conjunctivum and the termination of its dorsal fasciculus in the nucleus medialis thalami. × 6.6.

Fig. 6A From a section through the cephalic end of the thalamus, from the same series as figure 1, showing the main ending of the thalamic portion of the brachium conjunctivum. × 6.6.

caudal part of the nucleus lateralis thalami. Furthermore, the lemniscus medialis fibers are lateral to the brachium conjunctivum fibers at the caudal end of the thalamus, and all terminate laterally in the caudal end of the thalamus. Hence it is apparent that there is little or no overlapping or mixing of the fibers of these two great thalamic bundles.

Although having no especial bearing on this problem, it is of general interest to record that Thomas, von Monakow, Marie et Guillain, and others have described descending fibers in the brachium conjunctivum originating from cells in the nucleus ruber. On the other hand, van Gehuchten and others have denied the existence of such fibers. The writer has nothing to contribute to this subject, but is rather skeptical of the positive evidence, for the reason that most of these results were obtained from pathological lesions or from animals that were killed a long time after the operation, so that there would be a chance for the appearance of retrograde degeneration as a result of the chromatolysis of the nucleus dentatus cells.

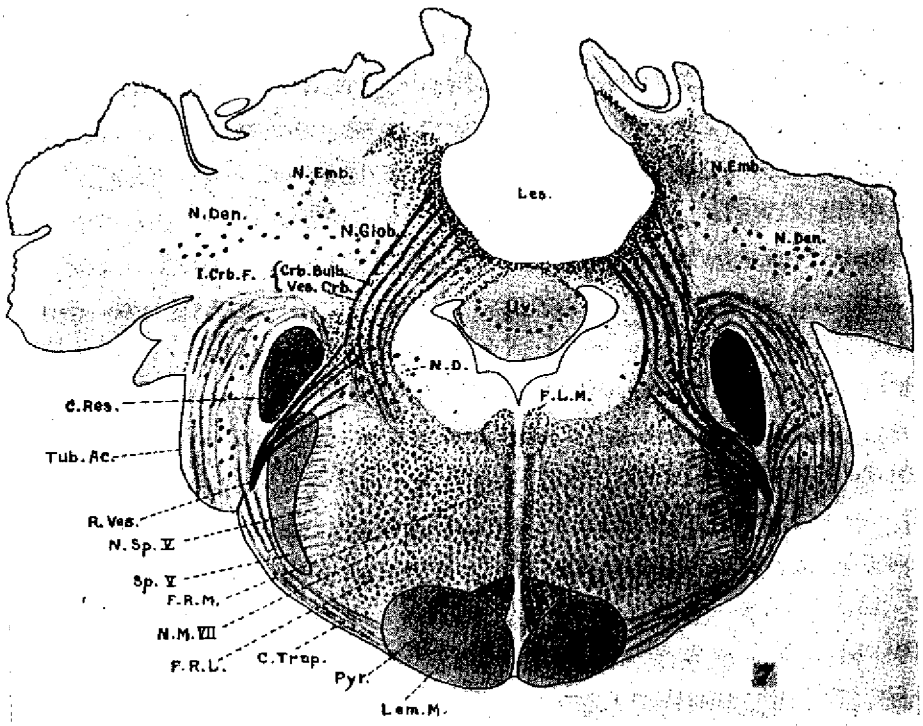
### *Fibrae cerebello-bulbares or fastigio-bulbares*

Series 103, in which the basal cerebellar nuclei of the left side were destroyed, shows many degenerated fibers median to each corpus restiforme in what may be designated as the *inner cerebellar funiculus* (I.A.K. of Meynert and Fuse). It should be noted, however, that there are many more on the left or lesion side than on the opposite side. No figure was made of these funiculi in series 103 for the reason that they appear practically the same as in figure 7, from series 79. It is obvious from figure 7 that the inner cerebellar funiculus (*I.Crb.F.*) is composed largely of small bundles of afferent and efferent vestibular fibers. The afferent fibers (*Ves.Crb.*) are normal fibers from the radix nervi vestibularis and from the nucleus nervi vestibularis lateralis; while the efferent fibers are degenerated fibrae cerebello-bulbares (*Crb.Bulb.*), which will be shown later to originate chiefly from the nucleus fastigii of the same and opposite side and the degeneration of which, according to Rothmann, causes the atrophy of the cells of the median cerebellar nuclei. It is clear from figure 7 and Luna's figure 6 that that these degenerated cerebello-bulbar fibers enter the nucleus nervi vestibularis lateralis (*N.D.*) from above. Farther cephalad a number of degenerated fibrae cerebello-bulbares, known as the fasciculus arcuatus Russell, fasciculus uncinatus or 'faisceau cérébello-bulbaire,' encircle the proximal end of the brachium conjunctivum dorsally and laterally, to follow ventrally along the median surface of the corpus restiforme and enter the nucleus nervi vestibularis, laterally, where they mix with the more median previously described fibrae cerebello-bulbares. The fasciculus uncinatus has not been figured for the reason that van Gehuchten's and Luna's illustrations for the rabbit and cat will apply equally well for the guinea-pig.

Van Gehuchten notes that the cerebello-bulbar fibers form two distinct tracts in the medulla. First, a posterior fasciculus is portrayed as passing caudally between the corpus restiforme and the radix descendens nervi vestibularis, and a second or anterior fasciculus as being formed in the dorsal part of the formatio reticularis from bifurcating median fibers. The second tract is said to extend as far caudad as the posterior tract. Luna describes three cerebello-bulbaris et spinalis tracts. First, the fasciculus uncinatus which follows the radix descendens nervi vestibularis; second, the 'fascio cerebello spinale laterale,' which is undoubtedly the same as van Gehuchten's anterior fasciculus, and, third, the 'fascio cerebello-spinale mediale,' situated dorsally close to the median line. Luna traced both of his cerebro-spinal tracts to the lumbar region of the spinal cord, and the fasciculus uncinatus is said to send some of its fibers into these cerebello-spinal tracts.

As previously stated, all of the fibrae cerebello-spinales enter the nucleus nervi vestibularis lateralis, and Thomas is undoubtedly correct in his statement that some of these fibers end in this nucleus. Many of the fibrae cerebello-bulbares, however, continue caudad as described by van Gehuchten and Luna, but in the guinea-pig they are scattered throughout the entire width of the radix descendens nervi vestibularis (fig. 1, *T.Crb.Bulb.*) and not confined to the extreme outer surface, as van Gehuchten portrays them for the rabbit. A section from the spinal part of the medulla below the termination of the radix descendens nervi vestibularis fibers (fig. 8) demonstrates a considerable number of degenerated tractus cerebello-bulbaris fibers (*T.Crb.Bulb.*) directly lateral to the tractus solitarius (*T.S.*). In series 103 the last of the tractus cerebello-bulbaris fibers appeared at about the level of the decussation of the pyramids. Throughout its entire course (figs. 1 and 8) numerous degenerated fibers can be traced to the dorsal part of the formatio reticularis lateralis et medialis (*F.R.L.* and *F.R.M.*), but so far as could be determined no degenerated tractus cerebello-bulbaris fibers terminate in the nucleus tractus solitarii or in any of the motor nuclei of the medulla.

Figure 7 discloses many degenerated fibrae cerebello-bulbares (*Crb.Bulb.*) passing medially through the nucleus nervi vestibularis lateralis to the dorsal part of the formatio reticularis lateralis et medialis, some of which enter and travel cephalad in the fasciculi longitudinales mediales. These degenerated cerebellar fibers are shown in the colliculus inferior region (fig. 2, *F.L.M.*) and can be traced to end in the nucleus nervi oculomotorii (fig. 3, *N.III*). Throughout the entire cephalic end of the medulla there is an accumulation of degenerated cerebello-bulbaris fibers (fig. 1, *X*) in the dorsal part of the formatio reticularis lateralis, which suggests van Gehuchten's anterior 'faisceau cérébello-bulbaire' and Luna's 'fascio cerebello spinale laterale.' This mass of fibers gradually becomes less dense caudally, but can be recognized throughout most of the medulla. Its more lateral and dorsal position prevents it from being confused with the brachium conjunctivum descendens (fig. 1, *Br.C.Des.*). There appears to be no overlapping in the distribution of the fibers from the tractus cerebello-bulbaris and the brachium conjunctivum descendens. Figure 8 divulges no massing of degenerated fibers in the dorsal part of the formatio reticularis lateralis and consequently no suggestion of a descending cerebellar tract in the spinal portion of the medulla. In connection with the previous statement that the tractus cerebello-bulbaris



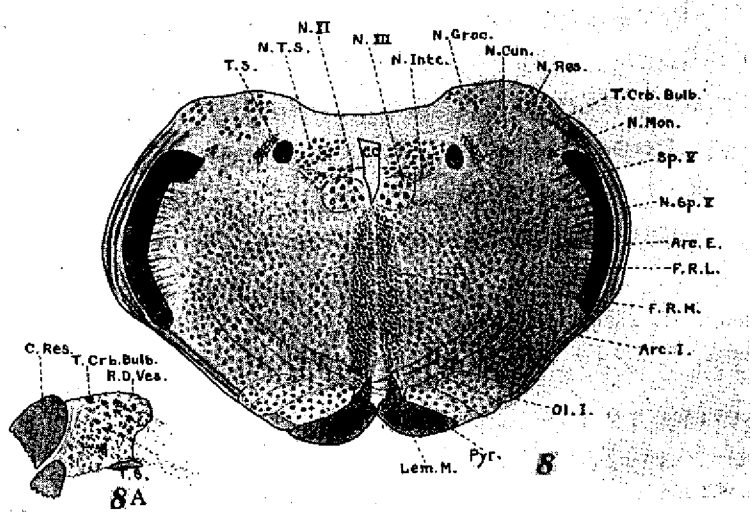




Fig. 7 Transverse section through the center of a cerebellar lesion, which included the fastigial nuclei and the median and caudal portions of the right intermediate nucleus (N. emboliformis and N. globosus), from series 79 and disclosing resulting degeneration. × 6.6.

Fig. 8 Section through the spinal portion of the medulla from the same series as figure 7, illustrating position and distribution of the tractus cerebello-bulbaris fibers. × 6.6.

Fig. 8A Section through the proximal end of the tractus cerebello-bulbaris, showing its degenerated fibers scattered through the radix descendens nervi vestibularis. × 6.6.

is constantly sending off degenerated fibers to the dorsal part of the formatio reticularis throughout its entire course, there exists the possibility that the accumulation of degenerated fibers shown in figure 1 (*X*) may not represent a descending tract, even though it possesses a number of the characteristics of such a tract. In series 103 there is no evidence of any condensation of degenerated fibers in the formatio reticularis medialis that might correspond to Luna's 'fascio cerebello spinale mediale.'

Series 103 and other series in which all or nearly all of the left basal cerebellar nuclei were destroyed demonstrate no more than the normal number of degenerated fibers in the corpora restiformia. Luna describes such fibers, but it is possible, since his cats were not killed for three weeks or more after the operations, that he obtained some retrograde degeneration as a result of the disintegration of some of the cells of the ascending corpus restiforme fibers. Furthermore, series 103 discloses the same kind of minute black granules in the brachium pontis that were recorded for this peduncle in the cortical lesions of the cerebellum and also for other superficial tracts. Hence, for the reasons enumerated on pages 402 and 415, the writer doubts if these black granules represent degenerated brachium pontis fibers.

### DEGENERATION RESULTING FROM THE EXTIRPATION OF BOTH FASTIGIAL NUCLEI AND PART OF ONE INTERMEDIATE NUCLEUS

This series is the outcome of one successful attempt to destroy the medial and caudal portions of an intermediate basal cerebellar nucleus (Nucleus interpositus of Brunner or the N. globosus plus the N. emboliformis), without injuring in any way the nucleus dentatus or its fibers which radiate through the cephalic lateral portion of this nucleus. To attempt destroying all of this nucleus or even a large part of it would invalidate the results through severing some of the nucleus dentatus fibers. It is obvious from figure 7, a section through the center of this lesion, that the nucleus fastigii of each side is destroyed completely and the right half of the intermediate nucleus, nucleus interpositus, is involved, but that the outer portion (*N.Emb.*) is uninjured. A thorough microscopical study of this lesion demonstrates no more damage to the intermediate nucleus than is shown in figure 7 and that the lesion does not extend into the extreme cephalic portion of this nucleus. The writer is convinced that the nucleus dentatus (*N.Den.*) and its fibers are left intact on the right side and that both the dentate and intermediate nuclei and their fibers are normal on the left side of this series.

### *Fibrae cerebello-bulbares*

A section from the internal cerebellar funiculus region of this series (fig. 7) discloses more degenerated fibrae cerebello-bulbares on the left side than are present in a similar section from series 103, where the lesion involved all of the left basal cerebellar nuclei. This is accounted for on page 420 by the fact that the chief source of the cerebello-bulbar fibers for either side is from both of the fastigial nuclei. There is exactly the same distribution of these fibers as was shown for series 103. A comparison of the tractus cerebello-bulbaris of figure 8A with figure 1, taken from series 103, shows a similar distribution of their degenerated fibers to the vestibular nucleus and to the dorsal formatio reticularis. Figure 8, which is from series 79, was used to illustrate the position and distribution of the degenerated tractus cerebello-bulbaris fibers in the spinal part of the medulla for series 103. Figure 9, taken from the colliculus inferior region of series 79, demonstrates more degenerated cerebello-bulbar fibers in the fasciculi longitudinales mediales (*F.L.M.*) than are present in a similar section (fig. 2) from series 103, which is explainable on the ground that each of these bundles receives fibers from both sides of the cerebellum. Likewise, there are no degenerated cerebellar fibers in the fasciculi longitudinales mediales supplying either nucleus nervi trochlearis (fig. 9, *N.IV*), the majority of them end in the nucleus nervi oculomotorii (fig. 9A, *N.III*) as in series 103.

*Brachium conjunctivum*

Any section through the midbrain region before the decussation is reached (fig. 9) discloses the left (side in which the lesion did not involve the intermediate cerebellar nucleus) brachium conjunctivum (*Br.C.*) as possessing no more than the normal number of degenerated fibers; while the opposite or right brachium conjunctivum (side in which the lesion involved the median and caudal portions of the right intermediate nucleus) exhibits a number of degenerated fibers scattered uniformly throughout the trunk. Occasional degenerated fibers from the right brachium conjunctivum (fig. 9) are distributed ventrally to the formatio reticularis of the pons. Farther cephalad in series 79 the decussation takes place normally. In the first few sections immediately behind the decussation there are a few degenerated brachium conjunctivum fibers in the area of the reformed brachium conjunctivum descendens. These could only be followed for a short distance, and at the level of figure 9 there are no more degenerated fibers in this area on one side than on the other. No degenerated brachium conjunctivum fibers could be traced to the nucleus nervi oculomotorii in this series, although some are present in the formatio reticularis ventrolaterad of this nucleus. Most of the degenerated fibers in the ascending brachium conjunctivum of series 79 terminate in the left nucleus ruber. Degenerated fibers are present in every part of this nucleus and they appear to be both trunk fibers and collaterals. Sections cephalad of the nucleus ruber demonstrate a few fibers in the main brachium conjunctivum thalamic bundle, which has been shown to be distributed chiefly to the cephalic end of the lateral nucleus ventralis thalami (*N.Ven.T.(a)*), and in its dorsal fasciculus, which terminates in the nucleus medialis thalami. Unfortunately, series 79 did not extend sufficiently cephalad to include the terminal endings of these fibers. There is, however, every reason to believe that the degenerated fibers observed in the abovementioned thalamic bundles terminated as corresponding fibers do in series 103 and 77.

It is of interest to record briefly that series 100, in which the lesion was confined to the median portions of both fastigial nuclei, shows exactly the same arrangement, distribution, and number of fibrae cerebello-bulbares as series 79, but there are no more than the normal number of brachium conjunctivum fibers in either brachium conjunctivum.

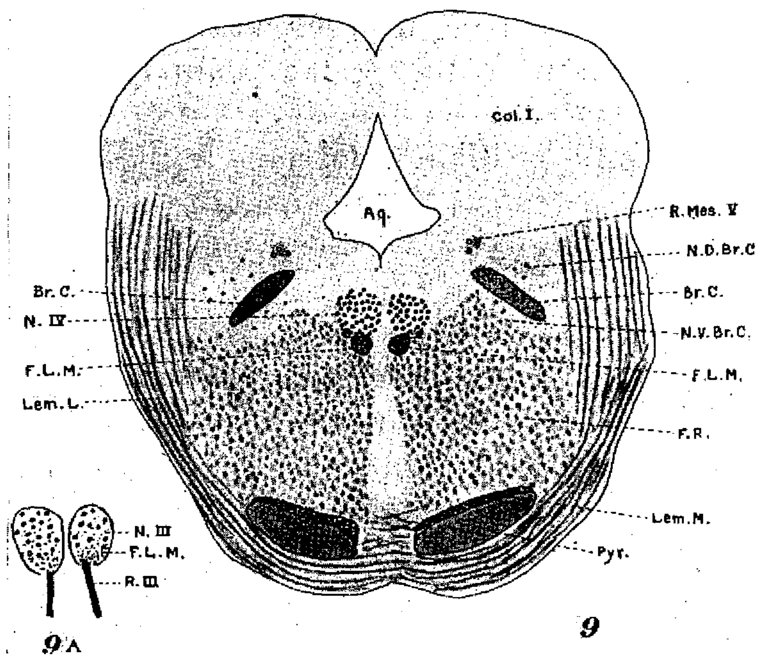



Fig. 9 From a section at the level of the nucleus nervi trochlearis from the same series as figure 7. Observe degenerated fibers in the right brachium conjunctivum and in both fasciculi longitudinales mediales. × 6.6.

Fig. 9A Represents ending of degenerated fasciculi longitudinales mediales fibers in the III nuclei from the same series as figure 7. × 6.6.

## DEGENERATION EFFECTED FROM THE DESTRUCTION OF THE LEFT NUCLEUS DENTATUS

In this series the lesion destroyed the left nucleus dentatus without injuring the intermediate nucleus (nucleus interpositus). Unfortunately, it also severed the more ventrally situated root fibers of the nervus vestibularis, but to destroy this nucleus without injuring these root fibers would probably require more time and animals than the experiment justified.

A microscopical study of this series demonstrates a large number of degenerated fibers in the left brachium conjunctivum, but not as many as are present in series 77, where the left brachium conjunctivum was severed, and in 103, where all of the left cerebellar nuclei were destroyed. At the outset it can be stated that the course, distribution, and decussation of the degenerated fibers in the brachium conjunctivum, including the brachium conjunctivum descendens, of this series is identical to the description previously given for series 103 and 77. On the contrary, there are absolutely no degenerated fibrae cerebello-bulbares on the right side, none in the fasciculi longitudinales mediales, and none in the lateral cephalic bundle of cerebello-bulbar fibers, usually designated as the fasciculus uncinatus or tractus arcuatus Russell. There are degenerated fibers in the left internal cerebellar funiculus and in the left radix descendens nervi vestibularis. The writer, however, is of the opinion that these are not cerebello-bulbar fibers, but solely root fibers of the nervus vestibularis. Therefore, the results obtained from this experiment are in accord with the general view entertained that the nucleus dentatus furnishes the main supply of fibers for the brachium conjunctivum.

## CHROMATOLYSIS PRODUCED THROUGH SEVERING THE LEFT BRACHIUM CONJUNCTIVUM

In series 147 the left brachium conjunctivum was severed a short distance behind its decussation in the midbrain, without damaging the cerebellum or the fasciculi longitudinales mediales. This was accomplished in identically the same manner as the lemniscus medialis was severed as described in the previous paper. The animal was killed fourteen days after the operation—a longer time being allowed on account of the larger cells and fibers involved. The brain was fixed in the formalin-alcohol-acetic mixture mentioned in the previous paper, and sectioned and stained after the same manner.

An examination of any section through the basal cerebellar nuclei of this series discloses the interesting fact that the left nucleus dentatus or lateralis and the left nucleus intermedius or interpositus (N. globosus plus the N. emboliformis) are full of chromatolytic cells while the left fastigii or tecti and all of the right cerebellar nuclei contain no more than the normal number of chromatolytic cells. Figure 10a shows the left nucleus intermedius or interpositus to be full of cells undergoing early and median stages of chromatolysis. They exhibit a diffuse staining of the protoplasm, little or no differentiation of the eccentrically placed nuclei, with some disin-

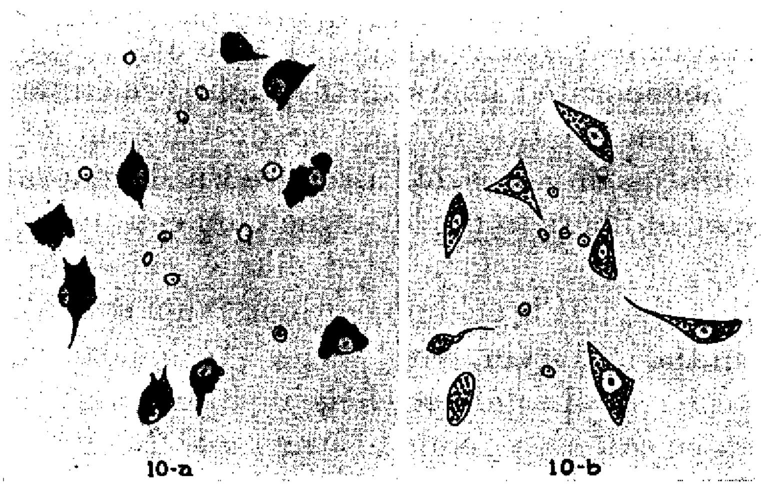



Fig. 10a Chromatolytic cells from the left intermediate nucleus (N. emboliformis and N. globosus) from Nissl series 147, in which the left brachium conjunctivum was severed directly behind its decussation. × 127.

Fig. 10b Normal cells from the left nucleus fastigii from the same series as figure 10a. × 127.

tegration of the outer cytoplasm. On the other hand, figure 10b, which is from the left nucleus fastigii, presents perfectly normal cells.

## DISCUSSION

Van Gehuchten's experiment, in which the basal cerebellar nuclei of one side were severed from the corresponding nuclei of the opposite side, demonstrated an equal number of degenerated fibers in the most lateral and cephalic bundle of the fibrae cerebello-bulbares (tractus arcuatus Russell or 'faisceau cérébello-bulbaire') on either side. The writer's series 103 in which the lesion involved all of the basal cerebellar nuclei of the left side without injuring the corresponding nuclei of the opposite side, disclosed degenerated fibrae cerebello-bulbares on both sides, but in greater number on the left than on the right. There is an equal number of degenerated fibrae cerebello-bulbares on either side with none in either brachium conjunctivum in series 100, where the lesion involved the nucleus fastigii of each side. Series 79, in which the lesion extirpated both fastigial nuclei together with the medial and caudal portions of the right nucleus intermedius (N. emboliformis and N. globosus), showed an equal number of fibrae cerebello-bulbares on either side and a considerable number of degenerated fibers in the right brachium conjunctivum with none in the left. The destruction of the left nucleus dentatus in series 142 produced a degeneration of a large number of fibers in the left brachium conjunctivum, with no evidence of any degenerated fibrae cerebello-bulbares. After cutting the left brachium conjunctivum caudal to its decussation in the midbrain, Nissl series 147 demonstrated chromatolytic cells in the left nucleus dentatus and in the left nucleus intermedius (N. emboliformis and N. globosus), but none in the left nucleus fastigii or in any of the opposite cerebellar nuclei. Rothman found that degeneration of the cerebello-bulbar tract brought about atrophy of the median (fastigial) cerebellar nuclei. The two series in which the cortex of the vermis and the greater part of the cortex of the left side of the cerebellum was destroyed portrayed a few degenerated fibrae cerebello-bulbares supplying each nucleus nervi vestibularis lateralis, but with the great majority going to the basal cerebellar nuclei. It can be concluded from these facts that, aside from the few cortical cerebellar fibers that go to the vestibular nucleus, the fibrae cerebello-bulbares originate from the fastigial nuclei, the larger number coming from the nucleus of the same side, and consequently they might appropriately be designated as fibrae fastigio-bulbares.

Furthermore, since it was demonstrated in Marchi series 142, where a destruction of the left nucleus dentatus brought about a degeneration of a large proportion of the left brachium conjunctivum fibers, but not as complete obliteration of this tract as is shown in series 77, where the brachium conjunctivum was severed, or in series 103, where all of the left cerebellar nuclei were destroyed; that an extirpation of both fastigial nuclei and the inner and caudal portions of the right intermediate nucleus in series 79 produced a number of degenerated fibers in the right brachium conjunctivum, but none in the left brachium conjunctivum; that the two cortical lesions (series 112 and 96) disclosed no degenerated fibers in either brachium conjunctivum; that Nissl series 147 in which the left brachium conjunctivum was severed directly behind its decussation in the midbrain showed a complete chromatolysis of the cells of the left nucleus dentatus and the left nucleus intermedius, but no chromatolysis of the cells of the left nucleus fastigii or of the opposite cerebellar nuclei, it is evident that the source of the brachium conjunctivum must be from both the nucleus dentatus and the nucleus intermedius or interpositus (N. emboliformis and N. globosus) of the same side. Hence it is reasonable to suppose that the nucleus globosus and the nucleus emboliformis of the higher Mammalia sustain about the same relation to the nucleus dentatus that the accessory olives do to the main inferior olive.

Finally, it was shown that the distribution of the degenerated brachium conjunctivum fibers in series 79, where the lesion involved the nucleus intermedius (N. emboliformis and N. globosus), and in series 142, where the lesion destroyed the nucleus dentatus, were apparently both identical to the distribution of the brachium conjunctivum fibers in series 103 where all of the basal cerebellar nuclei of one side were extirpated; hence they are the same. In other words, the axones from the nucleus intermedius (interpositus) and the nucleus dentatus probably supply the same regions.

## SUMMARY AND CONCLUSIONS

From the description of the results of the previous experiments and discussion, the following conclusions seem warranted for the brain of the guinea-pig:

1. All of the efferent cortical cerebellar fibers are distributed to the basal cerebellar nuclei, except a few from the vermis, which pass medially to the corpora restiformia, in what was designated as the inner cerebellar funiculi, to the lateral vestibular nuclei. The majority of the vermis fibers supply the fastigial nuclei; while those from the hemispheres go principally to the nucleus intermedius (nucleus interpositus or N. globosus and N. emboliformis) and to the nucleus dentatus.

2. A varying amount of very fine black granules has been recorded in this and in the previous paper for certain peripheral tracts, namely, the brachium pontis, commissura posterior, tractus opticus, pedunculus corporis mamillaris, radix nervi trochlearis, and other motor roots. Since similar minute granules appeared in equal number in other Marchi series in which no injury could have happened to these fibers, it is the opinion of the writer that these minute black granules may be a precipitate that has nothing to do with the degeneration of these fibers.

3. The brachium conjunctivum originates solely from the nucleus dentatus (lateralis) and the nucleus intermedius (nucleus interpositus or N. globosus and N. emboliformis); the distribution of fibers from either nucleus is apparently the same. There is no evidence of any Purkinje cell fibers entering the brachium conjunctivum.

4. In the colliculus inferior segment all of the brachium conjunctivum fibers which reach the level of the decussation decussate, forming the commissure of Wernekink directly dorsad of the ganglion interpedunculare, but send no fibers to this nucleus. Before decussating, the brachium conjunctivum supplies the dorsal and lateral formatio reticularis with a number of fibers. After decussation the brachium conjunctivum separates into a main cephalic bundle and a minor

caudal bundle, the latter according to van Gehuchten is formed from the bifurcation of some of the commissural fibers.

5. The brachium conjunctivum descendens in passing caudad, dorsal to the lemniscus medialis, to the level of the nucleus olivaris inferior, conforms to Wallenberg's and van Gehuchten's descriptions of the course of this tract for the rabbit. In the pons region it is distributed to the ventral and median formatio reticularis—a region not supplied by the opposite brachium conjunctivum, and in the medulla it continues to supply the same region of the formatio reticularis. There is no evidence of any of the brachium conjunctivum descendens fibers being distributed to any of the pontine nuclei or to any of the motor nuclei of the medulla.

6. Fibers from the main or ascending brachium conjunctivum permeate every part of the nucleus ruber, where many trunk fibers and collaterals end. That part of the brachium conjunctivum situated between the decussation and the nucleus ruber sends off numerous fibers to the formatio reticularis dorsad of the nucleus ruber, some of which enter the nucleus nervi oculomotorii as described by Klimoff and van Gehuchten, while others enter the dorsal small-celled portion of the nucleus, namely, the Edinger-Westphal nucleus, and the adjacent central gray. Many fibers continue through the nucleus ruber to become the brachium conjunctivum thalamic fibers. Some of these fibers form a fasciculus, the brachium conjunctivum dorsale, which terminates in the nucleus medialis thalami at the same level that the corresponding dorsal fasciculus of the lemniscus medialis ends in the caudal portion of the nucleus lateralis thalami. The main bundle of the brachium conjunctivum thalamic fibers continues cephalad in its median position, giving off fibers en route to the zona incerta, median portion of the formatio reticularis ventralis and to the regio subthalamica. Ultimately the main brachium conjunctivum thalamic fasciculus fibers radiate dorsally through the central median division of the nucleus ventralis thalami (*N.Ven.T.*(*b*)) to enter the lamina medul-

laris medialis (internus of Probst), where a few fibers pass medially to end in the gray dorsad of the most median division of the nucleus ventralis thalami (*N.Ven.T.(c)*), but the great majority pass laterally and ventrally to terminate in the cephalic end of the largest and most lateral division of the nucleus ventralis thalami (*N.Ven.T.(a)*, which nucleus Probst is correct in placing as the chief terminal for the cerebellar thalamic fibers.

7. There is apparently no overlapping of the fibers of the brachium conjunctivum with those of the lemniscus medialis, either in their cephalic course or at their terminal endings. As noted by Probst, the cephalic course of the brachium conjunctivum is distinctly median and dorsal to that of the lemniscus medialis. Very few, if any, of the lemniscus medialis fibers are distributed to the nucleus ruber, formatio reticularis, and to the regio subthalamica, while a large number of the brachium conjunctivum fibers end in the nucleus ruber, formatio reticularis and in the regio subthalamica. The great mass of lemniscus medialis fibers terminate in the caudal end of the most lateral of the ventral thalamic nuclei (*N.Ven.T.(a)*), while the majority of the brachium conjunctivum thalamic fibers continue cephalad median to the caudal end of this nucleus to finally end in the same nucleus, but entirely cephalad of the termination of the lemniscus medialis fibers. Both the thalamic brachium conjunctivum and the lemniscus medialis send off dorsal fasciculi at the caudal end of the thalamus; the more median brachium conjunctivum bundle ends in the nucleus medialis thalami and the more lateral lemniscus bundle terminates in the caudal end of the nucleus lateralis thalami. There is no evidence of any brachium conjunctivum fibers ending in the nucleus lateralis thalami.

8. The destination of the main outgoing tract from the cerebellum, namely, the brachium conjunctivum, is to the formatio reticularis of the brain stem, especially the nucleus ruber, and to the median and ventro-cephalic portions of the thalamus.

9. With the exception of the few fibers which originate in the cortex of the vermis and go to the nucleus nervi vestibularis lateralis, all of the fibrae cerebello-bulbares of one side take origin from the nucleus fastigii of the same and opposite sides (though chiefly from the same side) and might well be designated as fibrae fastigio-bulbares. In passing ventrally to the nucleus nervi vestibularis lateralis, they follow the corpus restiforme, medially, in what was designated as the internal cerebellar funiculus. A lateral cephalic bundle of these fibers, which encircles dorsally the proximal end of the brachium conjunctivum, the fasciculus uncinatus or the fasciculus arcuatus Russell, enters the nucleus nervi vestibularis lateralis, laterally, but soon becomes mixed with the more median fibrae cerebello-bulbares. A number of the fibrae cerebello-bulbares end in the nucleus nervi vestibularis lateralis, but many continue caudally in the radix descendens nervi vestibularis as the tractus cerebello-bulbaris to the level of the decussation of the pyramids, and en route distribute many fibers to the vestibular nuclei and to the dorsal formatio reticularis. It was recorded that many fibrae cerebello-bulbares pass medially through the nucleus nervi vestibularis lateralis to the dorsal formatio reticularis; a few enter the fasciculi longitudinales mediales and were traced to the nuclei nervi oculomotorii. There is a condensation of these fibers in the dorsal part of the formatio reticularis lateralis, which suggests van Gehuchten's posterior cerebello-bulbar tract and Luna's 'fascio cerebello spinale laterale.' No cerebello-bulbar fibers were traced to the spinal cord, and nothing corresponding to Luna's 'fascio cerebello spinale mediale' was observed in the medulla region. Also there is no evidence of any cerebellar fibers ending in the inferior olive.

10. Functionally there are apparently two distinct cerebellar nuclei in mammals, a lateral one composed of the nucleus dentatus and nucleus intermedius or interpositus (N. emboliformis and N. globosus) and a median one, the nucleus fastigii (tecti). The lateral nucleus receives no direct spinal or cranial nerve roots and no fibers from the spinal cord and

medulla. Its afferent supply is from the cerebellar cortex, chiefly from the hemispheres. It gives origin to the brachium conjunctivum. Its function as suggested by this relationship appears to be mainly one of correlation and strengthening. The connections of the median nucleus are chiefly with the vestibular system. It receives both direct vestibular root fibers and fibers from the vestibular nuclei. It may receive spino-cerebellar fibers, has cortical connections from the vermis and probably from the basal vestibular cortex. It gives rise to most of the fibrae cerebello-bulbares. This relationship suggests both a reflex and correlating vestibular center.

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