AN EXPERIMENTAL ANATOMICAL INVESTIGATION
OF THE PROJECTIONS OF THE CEREBELLAR
NUCLEI IN THE CAT

By

Mark A. Melgard, B. A.

A THESIS

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(Professor in Charge of Thesis)

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ACKNOWLEDGEMENT

To Dr. William A. Stotler, the professor in charge of this thesis, I express my most sincere appreciation and friendship for his kind and patient instruction during the past few years.

INTRODUCTION

Although investigations of the cerebellum date back to the middle of the 19th century, one of the foremost discoveries was that of Marchi (1) who first suggested that the brachium conjunctivum had its origin in the dentate nucleus and its termination in the contralateral red nucleus and thalamus. Further studies by Russell (2), Thomas (3), Probst (4), Van Gehuchten (5, 6), Lewandowsky (7), Bechterew (8), Luna (9), and others agreed in the majority with the general course of this complex bundle.

Cajal (10, 11) using a silver impregnation method described the direct and crossed descending limbs of the brachium conjunctivum, in addition to elucidating the various components of the efferent cerebellar connections. Detailed and extensive investigations followed by Winkler (12), Clark and Horsley (13), Mussen (14), Allen (15), Rasmussen (16), Fuse (17), Ranson and Ingram (18), Hohman (19), Sachs and Fincher (20) which served to explain certain elements of the problem but provided considerable dissension in the literature.

More recently, Mettler and others (21, 22, 23, 24, 25, 26) have exhaustedly studied the brachium conjunctivum and its descending limb in the cat and monkey. Their work professes the existence of an uncrossed ascending limb of the brachium, and further that the descending route traverses the spinal cord to sacral segments. Carpenter and Stevens (27), Ranson and Ingram (18), McMasters (28), have not concurred with these findings. Rand (29) has demonstrated previously undescribed terminations of the brachium in the posterior midline thalamic regions in addition to tracing the descending component to the inferior olivary complex.

Jansen and Brodal (30) in their book on the cerebellum have reviewed the literature on the cerebellar efferent projections in connection with their investigations of cerebello-fugal tracts using the modified Gudden method.

Observations by Chambers and Sprague, et al (31), using the Nauta-Laidlaw technique have been concerned with the fastigio-vestibular system and its relation to the brachium conjunctivum. However, no other workers have studied cerebellar efferent systems using silver preparations of experimental material.

These apparent variations of opinion demonstrate that the total picture of the structural relationships between the efferent pathways and the deep cerebellar nuclei has not been completed. Disagreement exists in interpretation of practically all of these relationships.

The purpose of this investigation was to attempt to clarify these matters by experimental methods using the intensified Protargol silver technique.

MATERIAL AND METHODS

Healthy adult cats, weighing between 1.4 and 2.0 Kg. were employed as the experimental animal. Using intraperitoneal Nembutal for anesthesia, electrocoagulative lesions were made unilaterally with the Johnson-Krieg modification of the Horsley-Clark stereotaxic instrument. Lesions included electro-coagulation of the deep nuclei of the cerebellum involving varied portions of nucleus interpositus and lateralis, and mesencephalic electrocoagulation of the brachium conjunctivum varied in dorso-ventral position.

The period allowed for degeneration ranged from eight to thirty days, depending on the amount and type of neuronal reaction desired. Following the administration of a lethal dose of Nembutal, the animals were immediately perfused with 15% Formalin in order to insure adequate fixation. The brains were immersed in 15% Formalin for ten days, dehydrated and embedded in paraffin. Blocks were serially sectioned at twenty microns, every tenth or twentieth section mounted, and stained according to the intensified Protargol method described by Stotler (32). A control series was done using accepted procedure for staining with the Marchi method.

The courses of the pathways involved by the experimental lesions were studied by observation of the alterations occurring primary to direct lesions of the tracts and secondary to destruction of their cells of origin. By this method axones were seen to degenerate in a typical fashion; first showing a pronounced argyria as contrasted with the normal fibers when stained by the intensified Protargol method. Animals in which the period of survival exceeded ten days the alteration consisted of loss of axones and their preterminal branches and terminal structures, and their replacement by argyrophilic degeneration products. These products consisted of short lengths of beaded fibers and large and small granules. In the animals with longer terms of survival, many of the elements involved in the degeneration have been removed and the observations contrasted the resultant fallout of afferent neuropil with that present in the corresponding normal nuclear areas. It was observed that different portions of the pathways seemed to degenerate at different rates and that in general, the more distal elements disappeared first, and that the fine fiber tracts seemed more resistant than those consisting of coarse elements.

In the evaluation of the amount of involvement present in tracts such as the brachium conjunctivum, recourse was had to percentage figures, which were merely the subjective judgement of the investigator as applied for purely descriptive purposes.

Extent of lesions and resultant patterns of degeneration have been pictured on a series of stereotyped drawings of representative sections of the cat brain.

The terminology of the "Nomina Anatomica" as revised by the International Anatomical Nomenclature Committee in Paris in 1955 has been used in thalamic nomenclature, in which the term ventral intermediate has been substituted for ventral lateral, making a subdivision of the ventro-lateral complex consist of ventral posterior, ventral intermediate and ventral anterior nuclei.

Nearly all studies previously mentioned in the introduction have relied on the accepted Weigert, Marchi and Nissl type preparations for analysis of their material. Cajal (11), in his investigations of the normal nervous system, has extensively applied the silver techniques. Chambers and Sprague et al (31) have used the Nauta-Laidlaw silver method. Glees and Le Gros Clark (33), Brodal (34), and Stotler (32) have used silver methods on experimental studies of the optic, auditory and other major systems. The use of the silver stained preparations in this study was prompted by the superiority of this method for the simultaneous demonstration of degenerated axones, fine preterminal fibers, and terminal endings.

While a larger series of animals were used in the course of this investigation, the histological analysis of only eleven lesions will be described to illustrate the results.

OBSERVATIONS

Cat D-15

The lesion in this case is located in the pontine tegmentum and includes the ventro-lateral third of the brachium conjunctivum. It extends caudally however to include a portion of the uncinate fasciculus, the vestibular root, a portion of the lateral vestibular nucleus, and the motor nucleus and descending tract of the trigeminal nerve. At the level of the brachium conjunctivum, the lateral lemniscus, the nucleus of lateral lemniscus, the rubro-spinal tract, the lateral reticular nucleus, and the tegmento-olivary bundle are also involved. Some fine granulation of degeneration is present in the region of median longitudinal fasciculus. A small amount of degeneration is present in the inferior olive, presumably due to interruption of rubro-olivary homolateral fibers. The descending root of the brachium conjunctivum is seen crossing over the interpeduncular area and contralateral degeneration products are present in the ventral lateral tegmental nucleus of Bechterew. Granules are present in the regions of the crossed and uncrossed vestibulo-mesencephalic tracts. The main decussation shows minimal changes in the ventral one fourth, with dispersion throughout the magnocellular portion of the red nucleus. Fibers seen rostral to the pre-rubral field, however, are few and course upwardly to the ventral part of the nucleus ventralis intermedius of the thalamus. Uncrossed dentato-thalamic fibers are not seen, nor are there any contributions from the uncinate fasciculus to the thalamus.

Cat D-4

The lesion in this case occupies the middle of the interpositus nucleus with some sparing in the caudal dorsal portion of the nucleus and in the rostral ventral portion. Nearly the entire dentate nucleus is destroyed along with dorsal and ventral spino-cerebellar tracts and the medial portion of the restiform body. The uncinate fasciculus in this case is not markedly involved, nor is the direct fastigio-bulbar tract.

Degeneration in the brachium consists of degeneration in the middle and lateral ventral thirds. The amount of degeneration in the dorsal one third is small, approximately 20-30%. The degeneration in the intermediate portion is slightly more pronounced medially, but generally approximates 60%. The most distal extremity of the ventro-lateral brachium shows 40-50% degeneration along with the remainder of the lower third.

In examination of the decussation, the first fibers to decussate (the slender ventral portion) show some granulation on the contralateral side. This is associated with granularity of the ventral tegmental nucleus of Bechterew. No granularity is seen in the ponto-tegmental area, superior central nucleus, nucleus mesencephali profundus, inferior olive, trapezoid body, or III cranial nerve nuclei. The homolateral regions show no granularity. The ventral one half of the decussation is most severely involved with fibers from the dorsal part of the intermediate one third of the brachium decussating first after the small ventral decussation, and followed by the more ventral portion of the brachium. No discrete decussating fibers are noted dorsally. No associated abnormalities are found in cranial nerves V or VII. Distribution in the red nucleus is primarily in the large cell portion that appears postero-laterally. No terminations are found in the nucleus of Darkschewitsch, nucleus of Cajal, the periaqueductal gray, the periventricular gray, or nucleus mesencephali profundus. Degenerating granules are seen in the parvacellular portion of the red nucleus more rostrally. The crossed vestibulo-mesencephalic tract appears to be involved.

No thalamic terminations are present in the midline nuclei (centre median, parafascicular). The degenerating area lies lateral to the habenular-interpeduncular tract and flares outwardly and upwardly through the fasciculus thalamicus, and ventrally through the ventralis posterior terminating in the ventralis intermedius. No fibers enter the subthalamic body nor do they enter the globus pallidus.

Cat D-2

Two extensive lesions have been made in this case involving the ventral portions of the lateral and interpositus nuclei. The lesions begin directly over the roof of the fourth ventricle and extend both directly and through vascular infarction to include the total neuronal composition of these nuclei. The fastigial nucleus is not involved. No neurons are present in the ventro-lateral extremity of the nucleus lateralis. Fibers of the homolateral fastigio-bulbar tract are partially destroyed along with the inner edge only of the uncinate fasciculus. Homolaterally, Deiters nucleus shows some disruption and granularity, however, the other vestibular nuclei demonstrate no significant findings. The origin and pathway of the descending root is well demonstrated here as a slender band of fascicles leaving the ventro-lateral angle of the brachium and curving downward and medially in an arching manner. A more rostral section shows this ventrally arching pattern to curve upwardly and cross dorsal to the interpeduncular nucleus and, following decussation, circle back ventrally. Previously more caudal sections show granulation along this pathway in the ventral median reticular formation. The descending root terminates in the nucleus of Bechterew, but no other of the previously reported terminations could be found. The brachium conjunctivum is involved to the extent of approximately 70% in both intermediate and ventral thirds. The dorsal one third shows some sparing in the median portion of this third and minimal degeneration in the remaining area. Decussation, arrangement, and distribution in the red nucleus is similar to that found in Cat D-4. The periaqueductal gray and periventricular gray substances are negative for degeneration, however, the uncrossed vestibulo-mesencephalic tract seems to have some degenerating type granulation. Thalamic terminations are similar to Cat D-4. No ascending uncrossed brachium is noted nor are connections seen to the lentiform nuclei.

Cat D-14

The involvement is in the dorsal two thirds of the nucleus lateralis, the nucleus interpositus, and in a small degree the lateral portion of the fastigial nucleus. A small amount of sparing has occurred rostrally in the intermediate nucleus in its ventral component. Also a very small ventro-lateral portion of the nucleus lateralis has been spared rostrally. The fastigial nucleus is nearly intact in its most rostral extent. A few direct fastigio-bulbar fibers are interrupted along with some degree of damage to the restiform body. A small amount of granulation appears in the lateral vestibular nucleus, and a few fibers in the uncinate fasciculus appear to be involved. Superior and lateral vestibular nuclei are also involved to a minor degree on the homolateral side. The trigeminal nerve nuclei do not show abnormalities.

More rostrally we find that the lesion has extended to involve the downward radiating fibers of the brachium conjunctivum and presumably has interrupted them at the area where these fibers congregate before forming the brachium conjuctivum proper. Fallout in the brachium is primarily in the dorso-lateral portion, and especially lateral in the intermediate one third. Some granular material is present in the ventral one third but it is certainly not remarkable.

Percentage-wise the dorsal and intermediate thirds have probably experienced between 65-85% fallout degeneration. Looking at the brachium in a more rostral section gives the impression that the degeneration is more diffuse rostrally than as previously described and that most areas without fibers are present in the medial one half of the dorsal and intermediate thirds of the brachium with some small amount of scattered degeneration in the ventro-lateral portions.

This series shows no apparent degeneration in the descending root of the brachium. Starting at the decussation we find no degeneration in the ponto-tegmental nuclei, central reticular nuclei, nucleus of Bechterew, cranial nerves, or the inferior olive. The nuclei of Cajal, Darkschewitsch, the periaqueductal gray, the periventricular gray, and nucleus mesencephali profundus are similarly free from degeneration.

The decussation shows fine granularity throughout and hence a specific pattern of crossing is difficult to obtain. However, it is felt that a few ventral fibers decussate first, followed by the most dorsal part and subsequently the entire brachium. No ascending homolateral tract is seen which may correspond to the so-called uncrossed ascending brachium conjunctivum of Carrea and Mettler. Neither are there any apparent fascicles emmanating from the uncinate fasciculus and coursing to the thalamus. The III cranial nerve does not appear to be involved in degeneration either in the nucleus or degenerating fascicles in the nerve proper. Degeneration is present around the magnocellular portion of the red nucleus with a general spread laterally passing through the parvacellular portion. Midline nuclei are negative for degenerating terminations as is the globus pallidus and subthalamic body. Fibers course upwardly through the fasciculus thalamicus and go medial toward the external medullary lamina and enter the ventralis lateralis of the thalamus. No terminations are seen rostral to this.

Cat D-13

The lesion in this case was made in the basal cerebellar nuclei and involved the lateral nucleus with slight sparing of that nucleus ventro-laterally. This sparing occurred in the ventral commissural component between the lateral and interpositus nucleus. The interpositus proper was spared in its most caudal extent, but the rostral portion was completely destroyed with exception of those cells described previously in the commissure. The medial portion of the restiform body was minimally involved. There is little damage in the region of the direct fastigio-bulbar or the uncinate fasciculus. The fastigial nucleus is not significantly involved. Examination of the vestibular nuclei fails to show degeneration. Cranial nerves V and VII are not involved. The distribution of degeneration-type granules and axonal fallout in the brachium proper is approximately 60-70% in the middle third and 30-40% in the dorsal third. Although more fallout appears in the medial portion of the intermediate third this pattern does not persist in the remainder of the brachium. The ventral third, including the narrow ventro-lateral extremity fibers, shows minimal degeneration with only 15-20% fiber fallout in its most dorsal region. No degenerating terminations of the descending root of the brachium are seen. Comparison of contrasting sides fails to reveal any difference in the median longitudinal fasciculus. No ascending or descending components, which may have arisen from the uncinate fasciculus, are seen. The organization in the decussation is in agreement with that of other experimental animals in that the degenerating granulation is scattered primarily in the middle third of the crossing with a minimal amount of degeneration in the dorsal portion of that decussation in the more caudal sections. The fine ventrally arching fibers believed to be those which become the descending root are free of axonal change. The nucleus of Darkschewitsch and the nucleus of Cajal are negative for degeneration, as is the periventricular gray. No fibers are seen in the region of the vestibulo-mesencephalic tract. Granulation within the red nucleus is confined most extensively to the ventral medial portion of magnocellularis, with diffusion spreading upwardly and laterally. The third nerve nucleus and its fibers are free from change. More rostrally, products of degeneration are present in the parvacellular portion of the red nucleus. Distribution rostrally follows the customary pattern, terminating via the fasciculus thalamicus in the nucleus ventralis intermedius of the thalamus. No fibers are seen to enter or pass through the ventralposterior nor does any connection appear with the globus pallidus or subthalamic body. Nucleus parafascicularis is free of degeneration. No uncrossed homolateral degeneration is present in either the ventralis intermedius nucleus or other nuclei such as centre median, subthalamic nucleus of Luys, or the lentiform nuclei.

Cat D-6

The lesion in this case occupies the most caudal extent of the interpositus nucleus. The more rostral and medial portion of the lateralis is partially involved but the lateral extremity is grossly intact. The lesion has partially included the uncinate fasciculus of Russell, direct fastigio-bulbar fibers, the restiform body, and possibly the most dorsal and rostral part of the lateral vestibular nuclei (Deiters). The fastigial nucleus is not involved.

The brachium conjunctivum appears to be approximately 60-70% degenerated in its middle one third, both lateral and medial components. The dorsal one third is intact as is the ventral one third. No degeneration is present in association with cranial nerve V and VII, nor in fibers of the uncinate fasciculus. No degeneration is present in the nucleus mesencephali profundus, superior central nucleus (central reticular nucleus), ponto-tegmental nucleus, nor the ventral-tegmental nucleus of Bechterew. The inferior olivary complex is also free of degenerating fibers. The most dorsal portion of the homolateral median longitudinal fasciculus suggests very minimal axonal fallout. Degenerating fibers of the brachium appear to be fairly equally distributed throughout the decussation, but appear only after the large body of fibers of the dorsal part of the brachium has already crossed. The small ventral component which crosses first is free of degeneration, therefore the descending root is probably not degenerated. It appears that the decussation is complete and that the droplets are confined primarily to the central lateral portion of the red nucleus among the magnocellular portion. No fibers appear to join the III cranial nerve. No degeneration appears on the homolateral side either directly in front of the red nucleus or rostrally in the thalamus. Thalamic projections are similar to Cat D-13.

Cat D-5

The lesion involves the lateral one half to two thirds of the interpositus nucleus and the dorsal two thirds of the lateral nucleus. The lesion does not include uncinate fasciculus nor does it include any of the radiating fibers of the direct fastigio-bulbar tract as it courses down toward the vestibular nuclei. Significantly the cells in the ventro-lateral one third of the nucleus lateralis are not involved. As expected therefore, no degeneration is seen in the previously described course of the descending root of the brachium. The vestibular nuclei are similarly uninvolved. The brachium itself is degenerated primarily in the intermediate one third and a fraction of the dorsal portion of the ventral third. This degeneration is estimated at approximately 60%. Dorso-medial cap and ventro-lateral angle are intact. No significant differences occur in the red nucleus with terminations apparently occurring in the magnocellular portion. Further, an even smaller granulation pathway appears somewhat diffusely in the upper lateral parvacellular red nucleus. Epi-thalamic terminations are not seen and thalamic projections also follow earlier descriptions. The ventral posterior is free of degeneration. Again, no uncrossed ascending component is apparent in this series.

Cat D-M

Destruction in this animal includes the entirety of nucleus lateralis and interpositus. Surrounding areas damaged either directly or secondary to vascular interference are: portion of the uncinate fasciculus, direct fastigio-bulbar fibers, superior and lateral vestibular nuclei, portion of the restiform body, nucleus and tract of V cranial nerve, and spino-cerebellar tracts. Associated with the primary lesion there appears to have been pressure interference with the ipsilateral dorsal column of the medulla with subsequent degeneration in the medial lemniscus. More rostrally electrocoagulative changes involve the entire brachium conjunctivum and adjoining vestibular and trigeminal areas. The median longitudinal fasciculus shows bilateral scattered degeneration somewhat more pronounced contralaterally. No fibers are seen terminating in the inferior olive, medial vestibulo-spinal, or reticulo-spinal tracts extending to the lower medulla or upper cervical areas. Although typical fine granular degeneration is present in the ventral tegmental nucleus of Bechterew no other descending root terminations are seen. A few scattered granules are seen along the midline in the region of the central reticular nucleus but are probably not significant. The descending root as it leaves the ventro-lateral portion of the brachium conjunctivum and decussates over the interpeduncular nucleus is readily discernible in this series.

Decussation takes place as was previously described; the small ventral portion crossing first, followed by the dorsal third, middle third and finally the upper portion of the ventral third. Both crossed and uncrossed vestibulo-mesencephalic tracts are involved, in addition to some granulation in the central tegmental fasciculus and lateral to the periaqueductal gray. It has been suggested that the latter two pathways may be associated with the trigeminal nerve. The nucleus mesencephali profundus is free of degeneration bilaterally.

In the region of the red nucleus the more typical and heaviest granulation is present in the magnocellular portion but diffuses upward and laterally. Further, the posterior commissure shows some degeneration along with a lesser degree of granulation in the periaqueductal gray and periventricular gray. This evidence of degeneration, however, fails to impress this investigator as being valid. No other epi-thalamic granulation is seen. Some degeneration is also seen in the III cranial nerve contralateral to the involved red nucleus. In addition to the arching pathway to the nucleus ventralis intermedius, degenerated fascicles are found in the ventralis posterior which are evidence of the involved projections from nucleus gracilis and cuneatus. No subthalamic or pallidal connections are noted, nor are there any uncrossed ascending pathways terminating in the thalamic area.

Cat D-01

The nucleus interpositus and the nucleus lateralis are nearly totally destroyed in this case. The fastigial nucleus is apparently not involved; however, the medial projection of the interpositus nucleus seems to be damaged. The ventro-lateral portion of the lateral nucleus is directly involved with no intact cells seen. The direct fastigio-bulbar tract has been interrupted with associated granulation in the homolateral vestibular nucleus. The uncinate fasciculus has been partially destroyed. The lesion extends forward and includes the area between the fourth ventricle and the restiform body (superior vestibular nuclei, associated white matter, and the converging fibers of the brachium conjunctivum.) The brachium shows degeneration throughout its extent; however, the greatest amount appears to be in the upper third. Some sparing occurs medially in that segment, but less than has been previously encountered. The intermediate and ventral thirds are involved to approximately 60%. Terminal degeneration in the nucleus of Bechterew is less than previously encountered; although some is present. No other terminations of the descending root are seen. The pattern of decussation again agrees with the previous observations. Distribution in the red nucleus is as previously described with maximum endings in the magnocellular portion. Thalamic terminations include the nucleus ventralis intermedius and possibly some arching fibers to the ventral posterior from the dorsal portion of the fasciculus thalamicus. The subthalamic nucleus does not receive any terminations. No ascending homolateral components are seen.

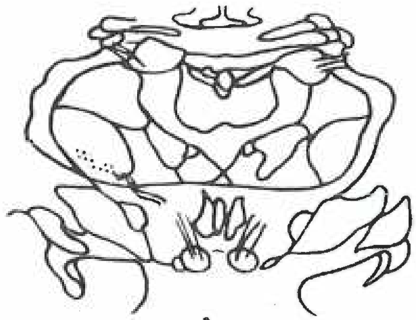
Cat D-30S

In this animal the lesion includes nearly the total extent of the nucleus interpositus with some sparing medially and cephalad. The more lateral lesion has included nearly all of the nucleus lateralis. The degeneration extends rostrally and includes a portion of the cerebellar vermis and the restiform body. The ventro-lateral portion of the lateral nucleus is also involved, with portions of the fastigio-bulbar tract and the uncinate fasciculus. Degeneration is present homolaterally in the superior and lateral vestibular nuclei. A small upper portion of the descending spinal root of the trigeminal nerve is also involved. The brachium conjunctivum shows degeneration in all but the dorsal most tip. The upper and middle thirds are involved to approximately 55% while the inferior lateral extent of the brachium is involved to approximately 45%. Degeneration is present in the ventral tegmental nucleus of Bechterew. As described in other animals no other terminations of the descending root are seen. A small homolateral vestibulo-mesencephalic component is degenerated. Degeneration distributed in the red nucleus and at the thalamic terminations (ventral intermediate nucleus) are as previously described.

Cat D-3

The lesion in this case is rather extensive, in that it includes portions of interpositus and lateralis, in addition to specific damage in the brachium conjunctivum as it is formed at the level of the V cranial nerve. The electrolytic lesion in the interpositus destroyed most of the nucleus, while the second lesion is localized in the ventral lateral one fourth of the nucleus lateralis. More rostrally the lesion extends into the lower half of the nucleus with sparing of the dorsal portions (approximately 60% of the nucleus intact). The lesion extends forward and includes the intermediate and dorsal parts of the brachium as they are being formed. The ventro-lateral portion of the brachium is degenerated in the same section. In examining pontine sections through the brachium it is shown that nearly the entire fiber bundle is damaged. Again, some fibers may be spared in the dorsal cap, especially in the dorso-median area. The descending root appears to be involved by this lesion and degeneration of axone terminals is present in the contralateral nucleus of Bechterew. No other terminations are seen. The fastigial nuclei and the uncinate fasciculus are undamaged, but direct fastigio-bulbar pathways are probably interrupted, accounting for minimal granulation in the lateral vestibular necleus on the homolateral side. The course of the brachium in the red nucleus and decussation follow the pattern previously described. Epi-thalamic terminations are not seen and thalamic projections also follow earlier descriptions. The ventral posterior is free of degeneration. Again, no uncrossed ascending component is apparent in this series.

Figure 1. A series of six drawings made at representative levels. Cat D-15. Drawing (D) shows the area of the lesion involving the ventral brachium conjunctivum (vertical lines.) Drawings (E and F) show caudal extent of the lesion and adjoining degeneration (stipple). Drawings (A, B and C) show resulting degeneration in the decussation (C), red nucleus (B), and nucleus ventralis intermedius of the thalamus (A). Note the involvement of crossed descending limb of the brachium conjunctivum pathway and termination (C and D). The crossed and uncrossed vestibulo-mesencephalic tracts (C), fibers in the median longitudinal fasciculus (D), and vestibular nuclei and trigeminal nerve (E) are involved.



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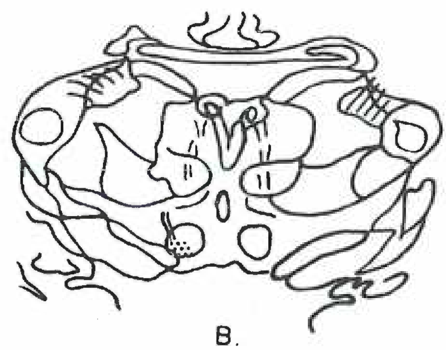

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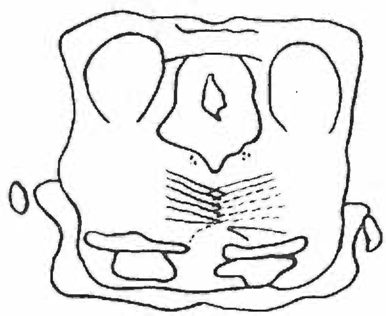

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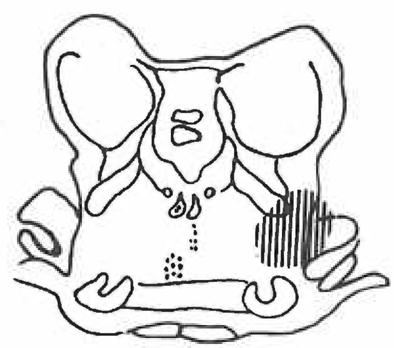

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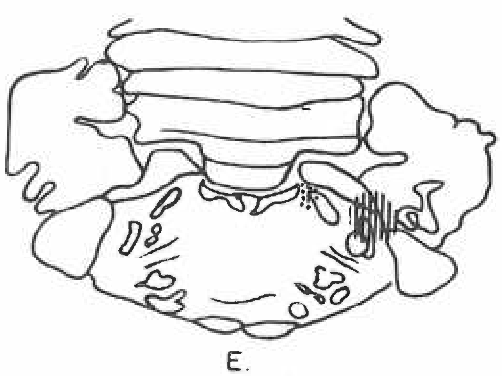

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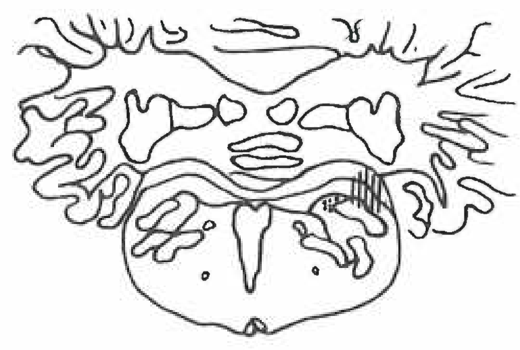
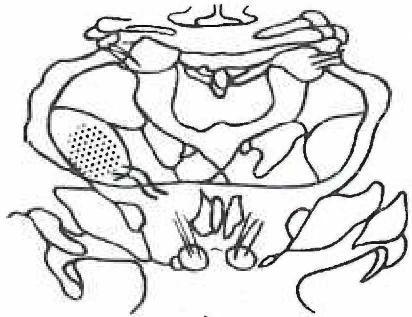


F.

Figure 2. A series of six drawings made at representative levels. Cat D-4. Drawing (F) shows the cerebellar nuclear lesions (vertical lines). The resulting degeneration (stipple) is seen in drawings (A-E); noting that the ventral two thirds of the brachium conjunctivum is involved (D) and the ventral tegmental nucleus of Bechterew is involved (D). The crossed descending limb of the brachium conjunctivum pathway and termination is also involved (C and D). Drawings (A-C) show thalamic (A), rubral (B) and decussation degeneration (C).



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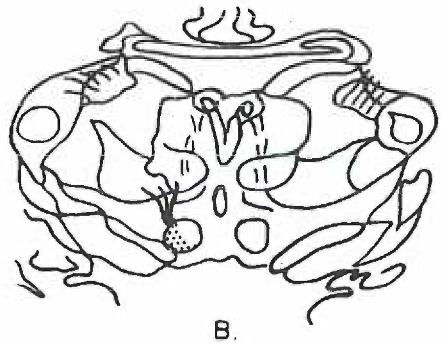

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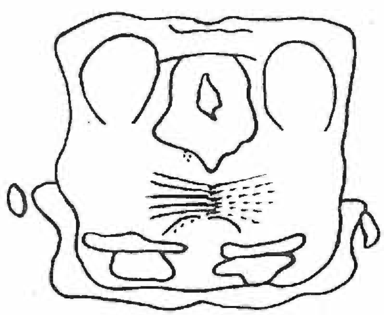

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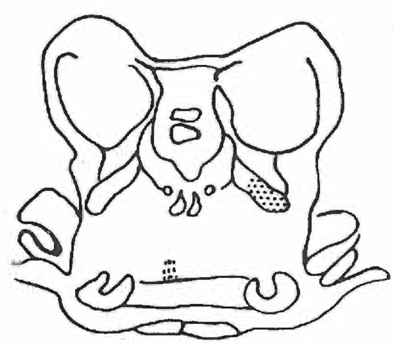

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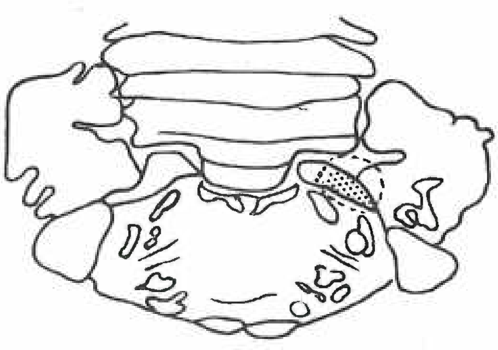

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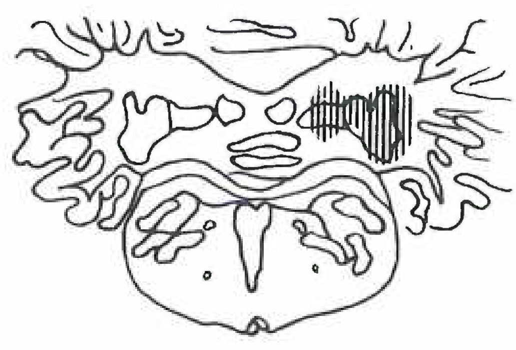
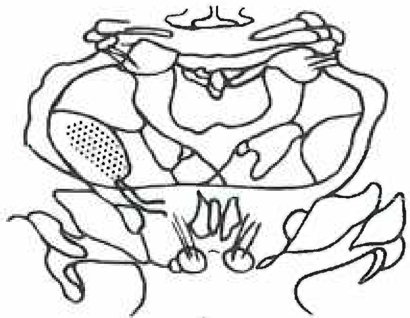
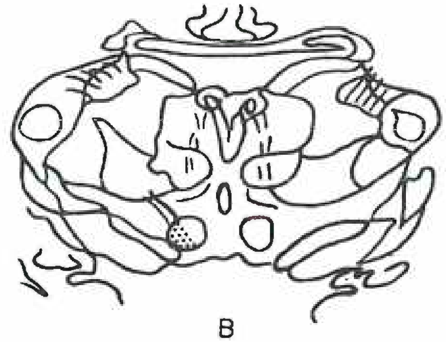


F.

Figure 3. A series of six drawings made at representative levels. Cat D-2. Drawing (F) shows the cerebellar nuclear lesions (vertical lines). The resulting degeneration (stipple) is seen in the brachium conjunctivum (D-E), the descending limb of the brachium conjunctivum (C-D), and uncrossed vestibulo-mesencephalic fibers (C). Additional degeneration (A-E) is similar to Cat D-4.



A.



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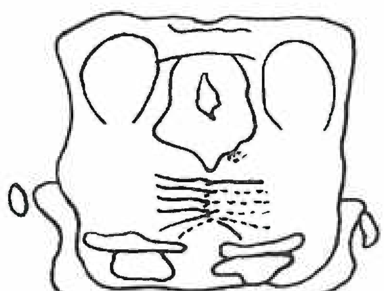

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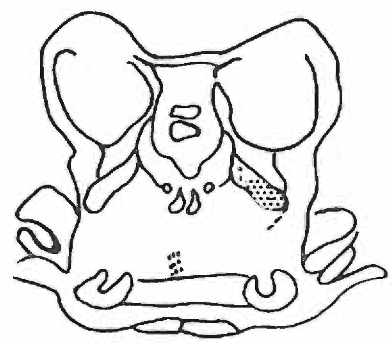

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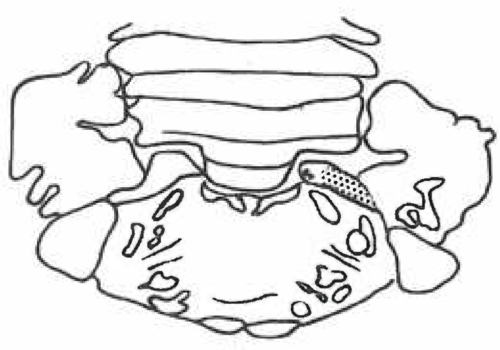

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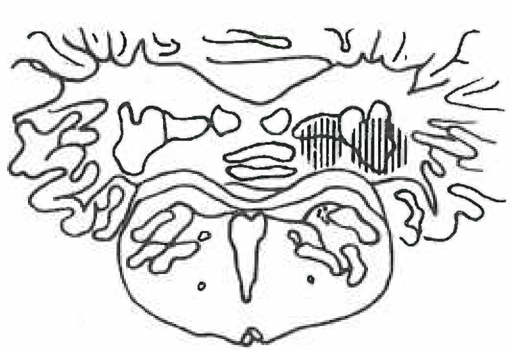
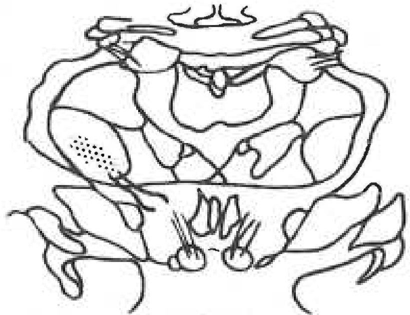
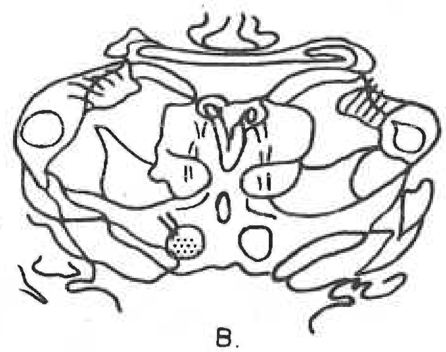


F.

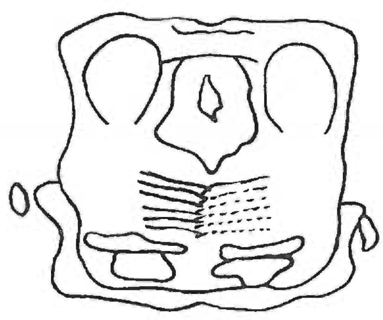
Figure 4. A series of six drawings made at representative levels. Cat D-14. Drawing (F) shows the cerebellar nuclear lesions (vertical lines) and degeneration in the homolateral vestibular nuclei (stipple). Drawings (D-E) show degeneration primarily in the dorsal two thirds of the brachium conjunctivum. Drawings (A-C) show degeneration in thalamic (A), red nucleus (B) and decussation (C).



A.



B.



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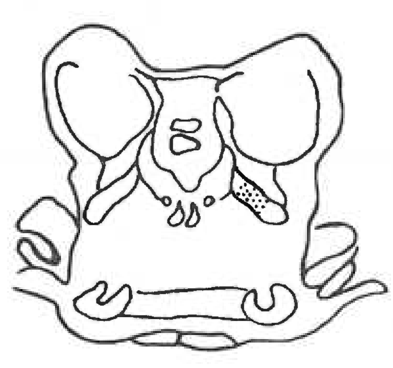
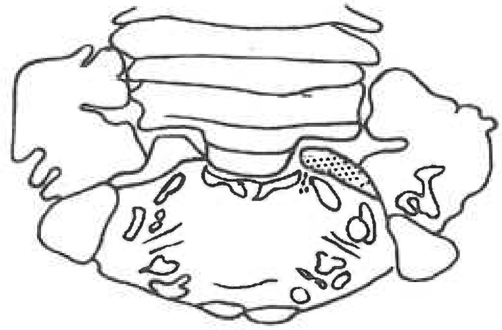


D.



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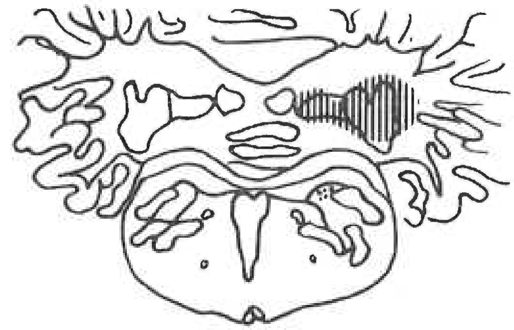
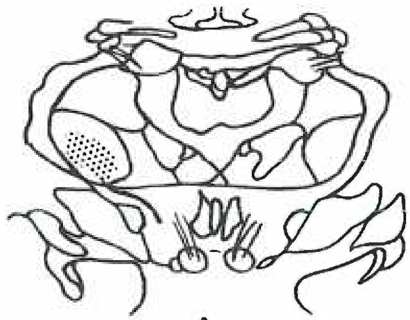
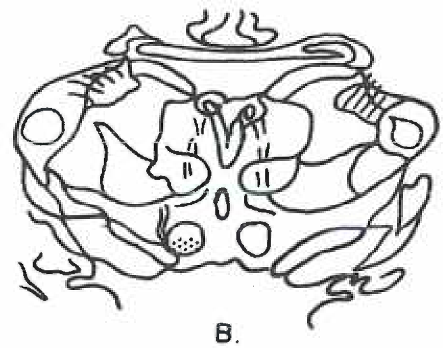
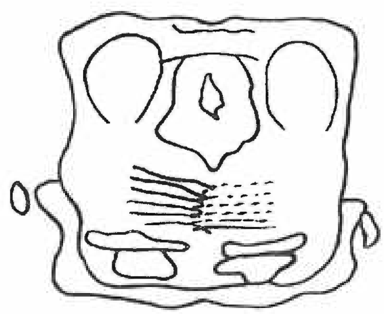


F.

Figure 5. A series of six drawings made at representative levels. Cat D-13. Drawing (F) shows the cerebellar nuclear lesions (vertical lines). Resulting degeneration in the brachium (E-F) is seen. Additional degeneration (A-C) is similar to that of cat D-14.


A.


B.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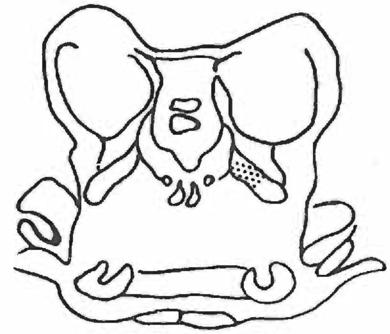
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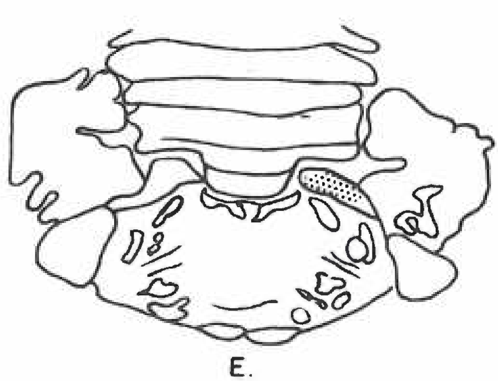
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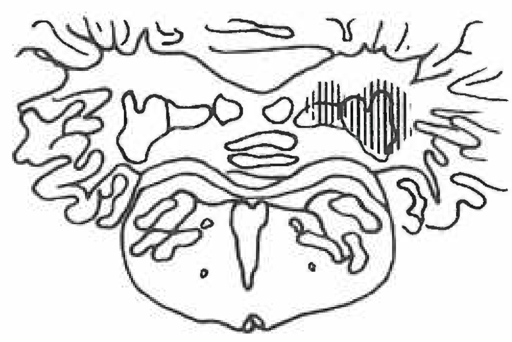

F.

Figure 6. A series of six drawings made at representative levels. Cat D-6. Drawing (F) shows the cerebellar nuclear lesion (vertical lines). The resulting degeneration (stipple) is seen in the medial one third of the brachium conjunctivum (D and E), vestibular nucleus (E), homolateral median longitudinal fasciculus (D), and the uncrossed vestibulo-mesencephalic tract (C). Additional degeneration (A-C) is similar to cat D-14.

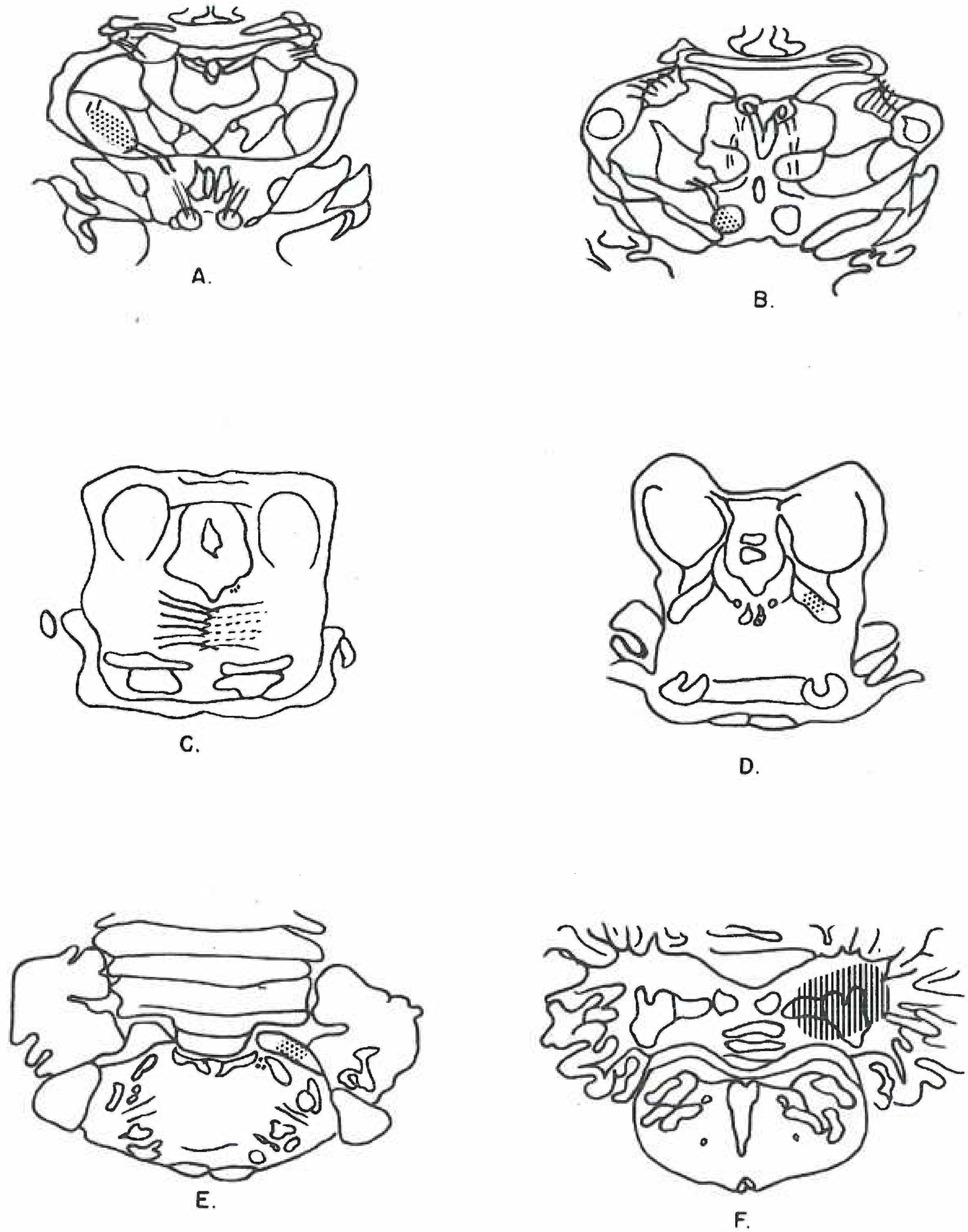
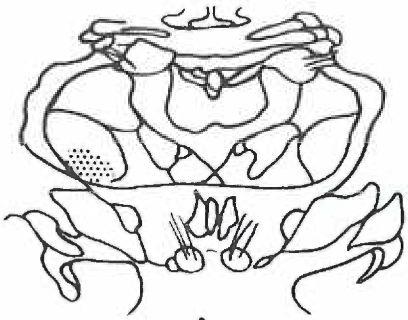
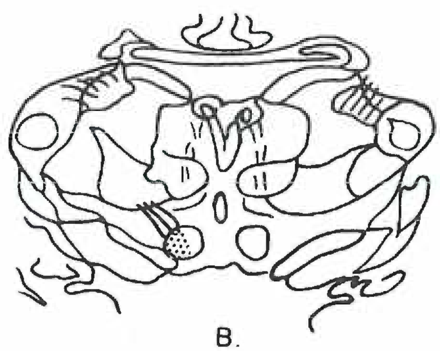

A.
B.
C.
D.
E.
F.

Figure 7. A series of six drawings made at representative levels. Cat D-5. Drawing (F) shows the cerebellar nuclear lesion (vertical lines). The resulting degeneration (stipple) is seen in the middle one third of the brachium conjunctivum (D and E) with accompanying vascular encroachment of the lesion (E). Additional degeneration (A-C) is similar to D-6.



A.



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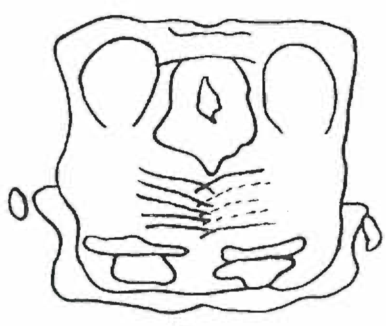
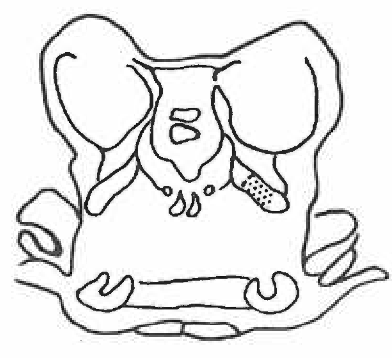


C.



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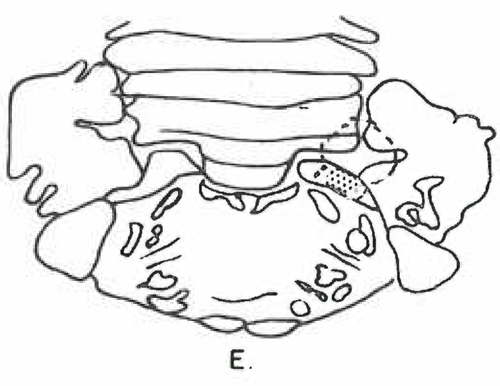

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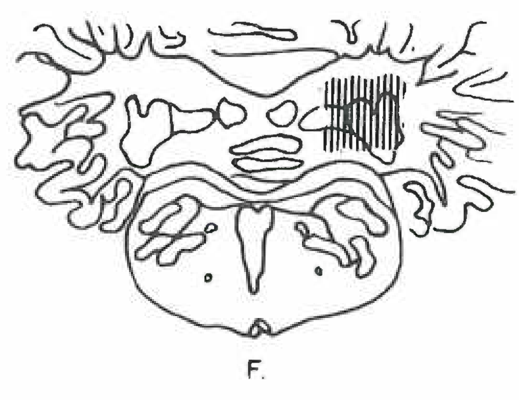
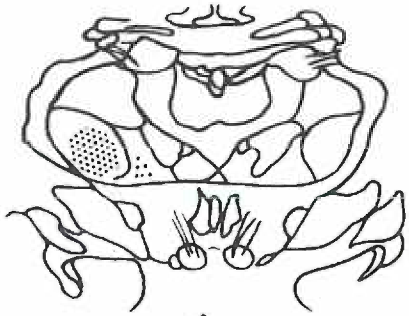
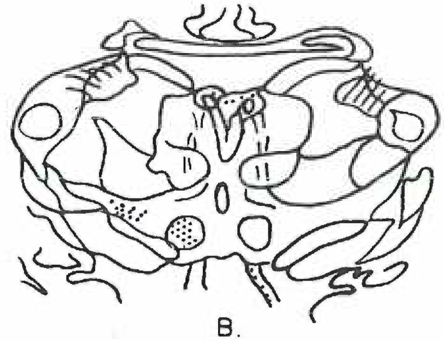


F.

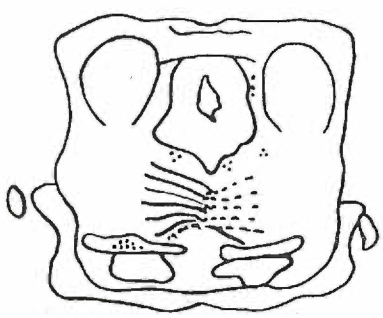
Figure 8. A series of six drawings made at representative levels. Cat D-M. Drawings (E and F) show the cerebellar nuclear lesions (vertical lines) and associated vascular encroachment. Important degeneration (stipple) is seen in the crossed descending limb of the brachium conjunctivum pathway and termination (C and D). Inadvertant damage to dorsal medullary area (F) is seen in addition to the involvement of the medial lemniscus (A-E). Further drawings (E and F) show involvement of the vestibular nuclei, medial and lateral vestibulo-spinal tracts and the nucleus and tract of V cranial nerve. Drawing (C) illustrates involvement of crossed and uncrossed vestibulo-mesencephalic tracts, central tegmental fasciculus, and periaqueductal gray area. Drawing (B) in addition to rubral degeneration illustrates pseudo-degeneration in the posterior commissure, and ipsilateral III nerve. In addition to ventral intermediate termination in drawing (A), involvement is seen in the ventral posterior nucleus.



A.



B.



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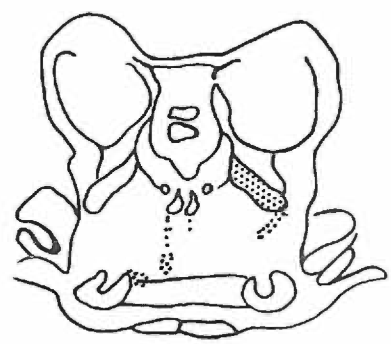

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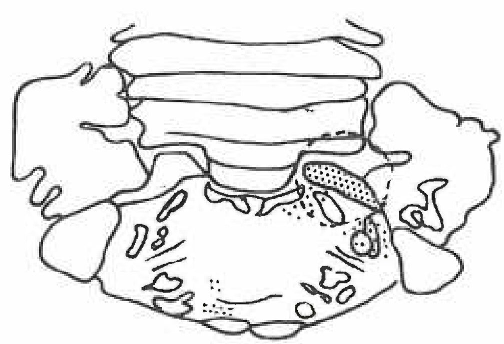
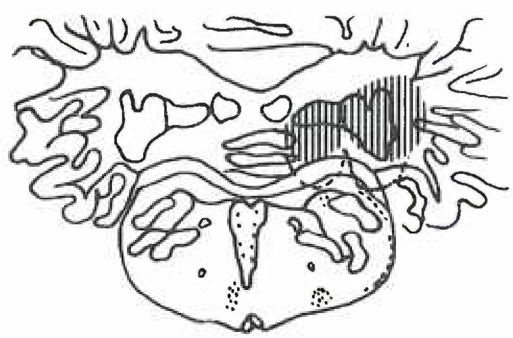
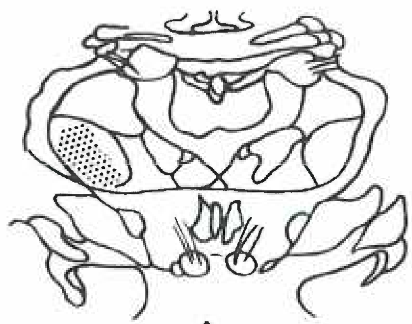


E.

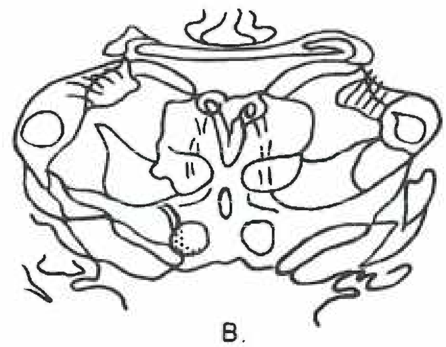


F.

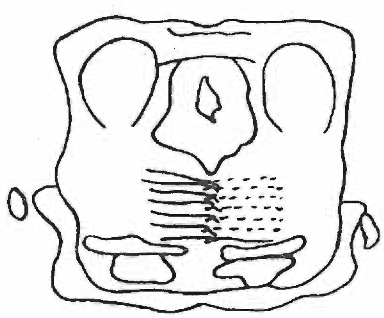
Figure 9. A series of six drawings made at representative levels. Cat D-3. Drawing (F) shows the cerebellar nuclear lesions (vertical lines) with associated direct brachial involvement (E) and adjoining vascular (broken lines) encroachment. Drawing (D) shows near total involvement of the brachium conjunctivum with some sparing in the dorsal most cap, plus degeneration of the ventral tegmental nucleus of Bechterew. Additional degeneration (A-C) is similar to Cat D-13; although slightly more extensive in regard to the thalamic termination (A).



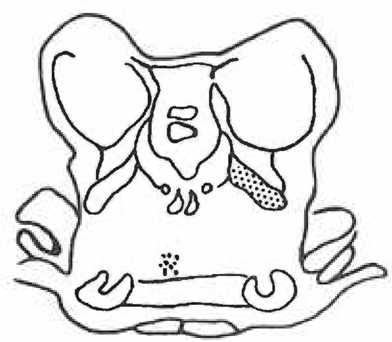
A.



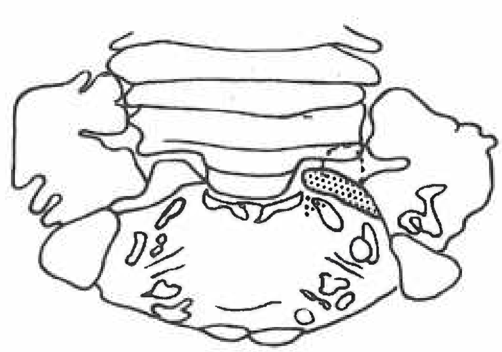
B.



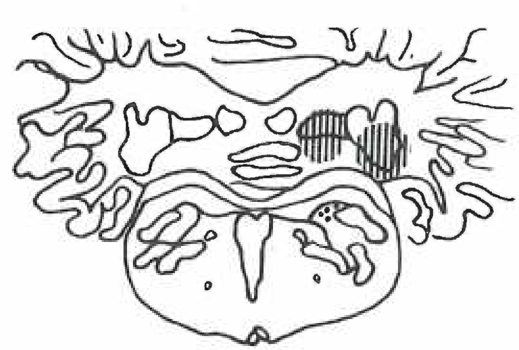
C.



D.

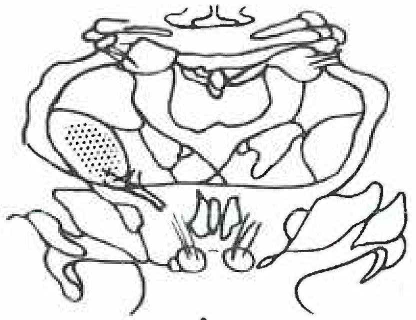


E.

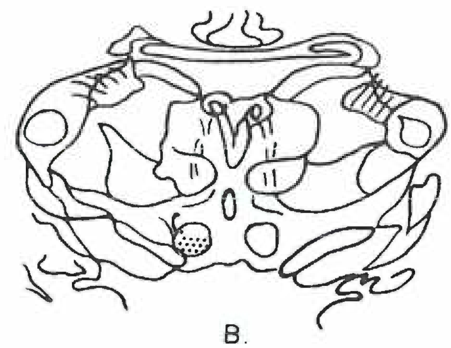


F.

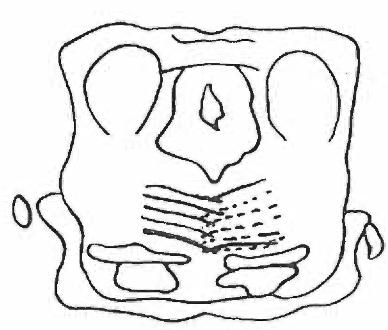
Figure 10. A series of six drawings made at representative levels. Cat D-01. Drawing (F) shows the cerebellar nuclear lesions (vertical lines) with associated direct brachial involvement (E) and adjoining vascular encroachment. Drawing (F) shows involvement (stipple) of the homolateral vestibular nucleus. Drawing (A-D) are similar to cat D-3 with the exception that there is less involvement of the ventral tegmental nucleus of Bechterew and that in addition a few arching fibers are seen in the ventral posterior of the thalamus (A).



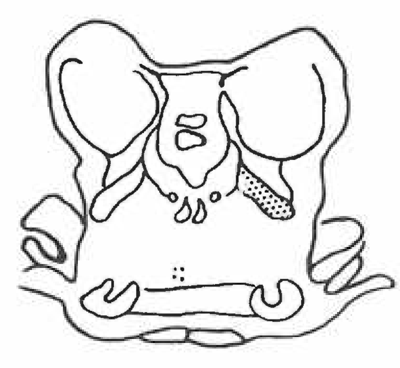
A.



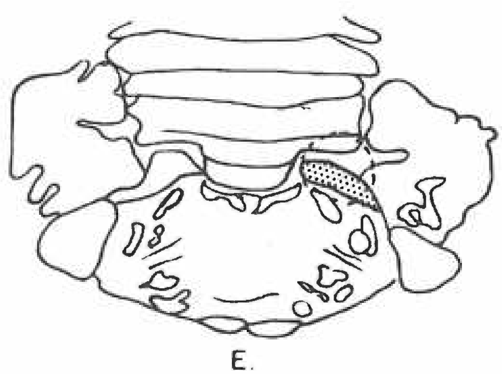
B.



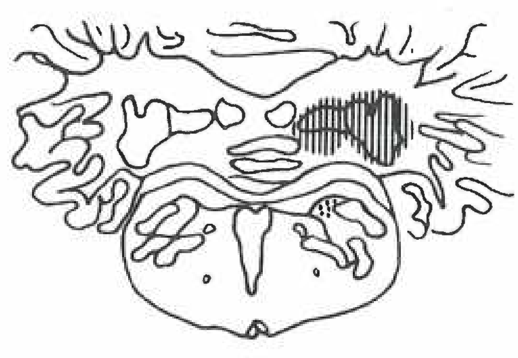
C.



D.

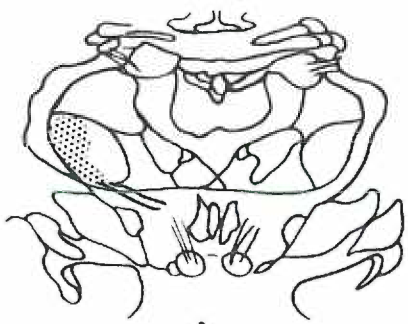


E.



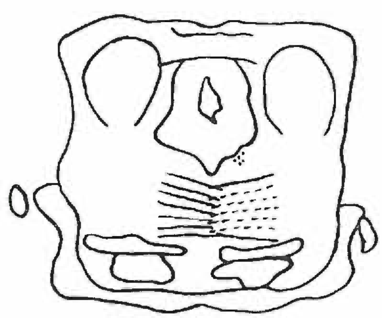
F.

Figure 11. A series of six drawings made at representative levels. Cat D-30S. Drawing (F) shows the cerebellar nuclear lesions (vertical lines) with associated direct (stipple) and vascular brachial involvement (E). Drawings (D and E) show degeneration in all but the dorsal most tip of the brachium conjunctivum and involvement of the ventral tegmental nucleus of Bechterew. Additional degeneration (A-C) is similar to Cat D-3.

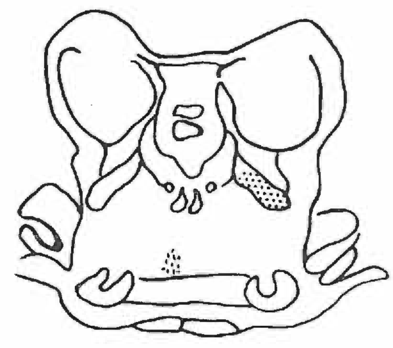


A.

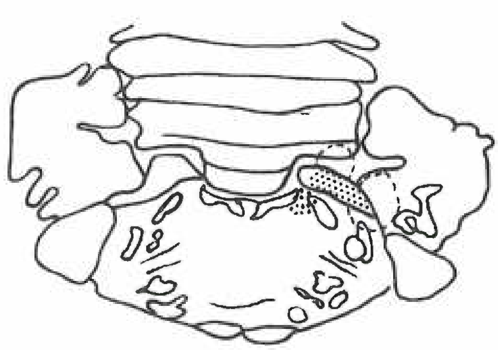
B.



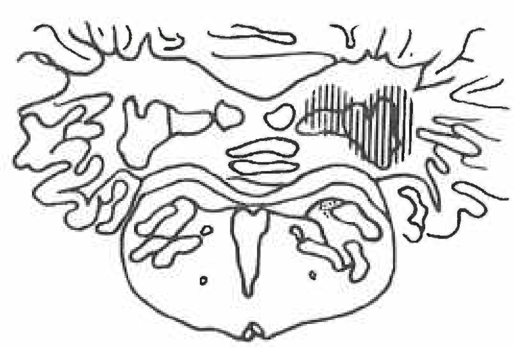
C.



D.



E.



F.

DISCUSSION

Cerebellar Nuclei

The configuration and terminology of the deep nuclei of the cerebellum has long been a subject of much consideration. Various descriptions have been made of the homology involved between the human brain and various experiment animals. Undoubtedly the most complete work has been done by Jansen and Brodal (30), augmented by Allen (15), Clark and Horsley (13), Snider (35), and Tilney (36).

A). Nucleus Fastigius

This nuclear complex has been known also as the roof nuclei or the medial nuclei in the various animals, and is generally accepted as being concerned primarily with the vestibular system. Jansen and Brodal (30) have felt that cerebello-fugal fibers from the fastigial nucleus leave the cerebellum via the superior and inferior cerebellar peduncles. Using retrograde analysis, they found ipsilateral dentate and interpositus changes in addition to bilateral fastigial changes after section of superior and inferior peduncles. They felt justified further to state that all the cerebellar nuclei contribute fibers to the brachium conjunctivum. This was in agreement with Winkler (12) and Rasmussen (16). The above investigations have shown that only fibers originating in the fastigial nuclei decussate in the cerebellum.

B). Nucleus Interpositus

Snider (37) has shown that this nuclear group is homologous to the nucleus globosus and emboliformis in the primate. Although this investigation has been entirely devoted to cats in which this nucleus is fairly discrete, comparisons may be drawn between interpositus and its primate homologes. Commissural connections are present between both nucleus interpositus and fastigius and between interpositus and lateralis. Fuse (17) has inferred that all cerebellar nuclei except the dentate contribute to the inferior peduncle. Although Winkler (12) and Rasmussen (16) have been similarly impressed, Allen (15) and Jansen and Jansen (38) have supported the concept that no fibers from the interpositus leave via the inferior or middle peduncles. The main contribution of the interpositus is via the brachium conjunctivum with those fibers from the lateral cerebellar nuclei.

C). Nucleus Lateralis

In close association with the interpositus nucleus lies the lateral nuclear group. This nucleus is homologous, (Jansen and Brodal (30)) to the dentate nucleus of primates; in the human developing into an increasingly larger and more complex structure. Gans (39), Demole (40), and others have described developmental and structural components of this nucleus in the higher forms, but due to the histological homogeneity in the cat, we will consider it as a single area. As was described above, the most accepted viewpoint is that the bulk of the fibers from the lateral nucleus exit from the cerebellum via the brachium conjunctivum. As with the interpositus, Jansen and Jansen (38) have felt that few, if any, fibers from the lateral nucleus contribute to the inferior peduncle.

This investigation has not been concerned with cortical distributions to the various cerebellar nuclei; however, the relationship suggested by Jansen and Brodal (30) should be observed. They have stated that there are three cortical zones: a median projecting to the fastigial nucleus, an intermediate projecting to the nucleus interpositus, and a lateral area associated with the nucleus lateralis. Chambers and Sprague (41) have found physiologic agreement with this distribution in relating the vermian cortex with fastigial nuclei and the paravermian cortex with nucleus interpositus.

The terminology used in the publication of Snider (37) on the deep nuclei of the cat has been used in this investigation, and his descriptions of the morphology and histology of the deep nuclei have been correlated with the observations in the present work.

<u>Efferent Pathways</u>

Most of the known cerebellar efferent fibers are found in the brachium conjunctivum along with fibers from the medulla that, at present, are poorly understood. The former portion of the brachium conjunctivum, pars cerebellar (Jansen and Brodal (30)), is the primary concern of this investigation.

Following the initial description of the distribution of the brachium by Marchi (1), Cajal (10) has stated that the dentate nucleus was the major site of origin of the brachium, and that the axones bifurcated, one limb entering the superior peduncle and the other descending down into the medulla of spinal cord as the "via descendente de Marchi". Clark and Horsley (13) have felt that no fibers from the cerebellar cortex entered the superior peduncle, which was in complete disagreement with the findings of Thomas (3) and Cajal (10). Sachs and Fincher (20) have described fibers to the basal ganglia and red nucleus, while the work of Hohman (19) demonstrated that the only cerebellar cortical efferent was from the anterior vermis to Deiters nucleus. Hohman has further shown that there are no pons, midbrain, or spinal cord efferents from the cerebellar cortex. This confusing question has been considered extensively by Jansen and Brodal (30) who have classified cerebellar cortical fugal fibers into long and short types. The long fibers pass beyond the cerebellar nuclei and terminate primarily in Deiters' (lateral) vestibular and Bechterew's (superior) vestibular nuclei. The short cortico-fugal fibers project to the deep cerebellar nuclei in the general topographical manner previously described. Nevertheless, complete classification of these fibers is far from finished.

The earliest study of the composition of the brachium conjunctivum was done by Bechterew (8) who employed myelogenetic analysis of human embryos. Bechterew divided the brachium into four parts: dorsal part emmanating from the roof nuclei and homolateral vermian cortex pcI, pcII from globosus and emboliformus situated in the middle third of the lateral part, pcIII from dentate and adjoining cortex running medial to pcII, and the ventral portion, pcIV, which has been associated with the "accessorische bindearmbundel" of Probst (4) and reportedly ascended homolaterally to the red nucleus and thalamus.

It is generally agreed that we owe the most extensive analysis of the composition of the brachium conjunctivum to Winkler (12). Although his work follows Bechterew rather closely, important additions were noted. Winkler found that the dorsal third of the brachium was composed of fibers from nuclei fastigius and globosus and from the juxta-restiform body. The middle third, lateral portion was derived from nucleus emboliformus while the median portion of the middle third was formed by fibers from the dentate nucleus. The lower third in this case is occupied by fibers from the vestibular and sensory fifth nucleus and here presents the question as to whether these fibers are truly within the limits of the bounderies of the brachium conjunctivum. Comparisons of the various analysis of the composition of the brachium conjunctivum lead one to believe that the lower third described above is not commonly included.

Further work by Allen (15) and Mussen (14) has shown that few fibers emmanating from the medial nuclei enter the brachium conjunctivum. According to their findings the dorsal part of the superior peduncle is composed largely of fibers from the dentate, while the dorsal two-thirds is supplied by interpositus. Fibers from the dentate appear to be lateral while the interpositus components are medial. Rand (29) in the macaque has felt that the ventral portions of the nucleus interpositus contribute fibers to the ventral part of the brachium conjunctivum, while the ventral and lateral portions are supplied by the dentate nucleus. Carpenter and Stevens (27) in the monkey have supported the aforementioned findings and have demonstrated that destruction of the ventral lateral portion of the dentate nucleus leads to degeneration in the ventral lateral portion of the brachium. They summarize by saying that the medial cerebellar nuclei tend to occupy more dorsal and medial areas of the superior peduncle, while lateral and ventral fibers are derived from the more lateral and ventral portions of the deep cerebellar nuclei.

McMasters (28), using Marchi technique in the cat, has found that the interpositus nucleus projects via the medial brachium conjunctivum and the lateral nucleus proper contributes fibers to the mid and ventral two-thirds of the superior peduncle. The caudo-lateral portion of the dentate seems to ascend ventro-laterally in the brachium. Although McMasters has found fibers of the uncinate fasciculus infiltrating through the superior peduncle he has denied fastigial efferent contributions to the conjunctival "arm".

It is interesting to note that Carpenter and Stevens (27) have noted no twisting or crossing of fibers within the cerebellum and suggest an orderly arrangement in the brachium. This finding would not be in keeping with the concepts professed by Winkler (12) and Bechterew (8).

In this study, observations are in general agreement with the work of Carpenter and Stevens (27). Lesions (cats D-15, D-4, and D-2) involving the ventro-lateral portion of the dentate lead to degeneration in the ventro-lateral portion of the brachium conjunctivum. Degeneration in the middle third of the superior cerebellar arm (cats D-14, D-6, and D-5) seem to follow destruction of all the dentate except the ventro-lateral portion and the lateral one-half to two-thirds of the interpositus nucleus.

Whenever the fastigial nucleus or its projections are involved, (cats D-M, D-3, D-01, D-30S, and D-14) we see various degeneration in the dorsal cap of the brachium.

No medio-lateral spacial configurations in the brachium corresponding to nuclear lesions are seen in this investigation.

In summary, the lateral nuclear areas project via the ventro-lateral brachium and are distributed dorso-medially both in relation to nuclei and the superior cerebellar arm, with fastigial components apparently occupying the dorsal cap area.

Decussation

Logically, further discussion would concern the anatomical relationships of the decussation of the brachium (the commissure of Wernekink). This midbrain crossing of the cerebellar outflow system should be considered in two sections: spacial relations of the decussation, and enumeration and discussion of pathways radiating both caudally and rostrally. The arbitrary zone differentiation (Carrea and Mettler (26)) of the brachium seems of little import here, both anatomically and functionally.

A). Spacial Relations

Allen (15), in 1924, has stated that most descriptions up to that time dismissed the decussation with the assertion that the fibers crossed to the contralateral midbrain. Using human material, Probst (4), has found that the matter was not as simple as this and reported that the decussation of the brachium was divided into dorsal and ventral parts. Carpenter and Stevens (27) have felt that this description is in agreement with the arrangement found in the Rhesus monkey where the ventral brachial fibers appear to cross the midline in a straight course, while the fibers of the dorsal portion curve ventrally. Central peduncular fibers were found to cross obliquely at a higher level by these investigators. Van Gehuchten (5) and Allen (15) have maintained that the ventral fibers of the decussation are primarily cephalad; while the dorsal fibers appear to cross more caudally. Cajal (10) on using various animals, believed that the more dorsal fibers cross first, while Rand (29) on the other hand, states that the brachium decussates ventrally at first, then proceeds medio-cephalad. Further he has added that the dorsal region crosses in a step like fashion as it proceeds cephalad; and the central portion crosses last. His work has verified that the superior peduncle is dispersed in its ventral third but compact dorsally.

Carrea and Mettler (26), in their extensive study of the decussation, although somewhat confusing verbally, have described thusly: the arc of the dorsal median brachial fibers as they proceed ventrally is greater than that of those fibers coursing in the ventro-lateral part of it. The decussation is an oblique one with dorsal caudal fibers decussating first and rostral ventral fibers decussating last.

The fastigial component of the brachium must be mentioned here in relation to the question of complete or incomplete decussation. Allen (15), Mussen (19), Lewandowsky (7) and Van Gehuchten (5) all have maintained that the fibers cross completely. Probst (4), however, has described fibers coursing in what is now described as the direct ascending brachium conjunctivum (Carrea and Mettler (26)). Notable disagreement by Rand (29) is exemplified in his observations that the decussation is complete in confirmation of earlier workers. Carpenter and Stevens (27) have concurred with this. Carrea and

Mettler (26), in support of Cajal (10), have found that there is a component from the fastigial nucleus which decussates caudally and dorsally, and hence, are the only fibers to give rise to the descending limb and the uncrossed ascending component of the brachium. Finally, Jansen and Brodal (30) have mentioned that this component may be absent when the fastigial nucleus is left undamaged. The association of this fiber bundle with the ascending limb of Carrea and Mettler will be discussed further in a later section.

The present series suggests that decussation is ventral initially, followed by dorsal arching fibers which cross dorsoventrally as one proceeds cephalad until the dorsal portion of the lower one third of brachium conjunctivum finally crosses. The most ventral parts of the first portion of the decussation are believed to represent the crossed descending limb of the brachium.

Although some early investigators have been concerned with the description of fibers prior to the decussation (Allen (15)), little apparent interest has prevailed and its importance seems questionable. However, its mention in this reviewis made for the sake of completeness. The various nuclear groups which have been reported as being supplied by fibers from the conjunctival arm include pars lateralis, pars intermedius, pars dorsalis, and pars ventralis of the nucleus mesencephali profundus (Rand (29)) located in the tegmentum of the midbrain. Allen (15) described, prior to decussation, fibers which entered the dorsal and lateral reticular formation. Present material has failed to reveal such connections, although the crossed and uncrossed vestibulo-mesencephalic tracts are commonly involved. In addition to these tracts, it is the opinion of this author that the inconstant distribution of degenerated fibers in the MLF was due primarily to partial damage of the fastigio-vestibular system.

At this point, it seems necessary to state that the degeneration of the spino-cerebellar tracts, the gracilis, cuneatus, V nerve nuclear damage, and the vestibular involvement is allowable since the Marchi control series had to be done on a nearly complete lesion of the brachium conjunctivum. The subsequent degeneration (in central tegmental fasciculus and periaqueductal gray area) in the animal (D-M) cannot be evaluated in the face of the other lesions however, and we must rely on the more restrictive areas of distribution.

B). Radiating Pathways

In discussing the subsequent pathways the larger component will be discussed first; the crossed ascending brachium.

First and foremost of the pathways diffusing from Wernekink's commissure is that portion commonly referred to as the crossed ascending component of the brachium conjunctivum. Probably no portions of these tracts are more well known than this segment which finds its way rostrally to the red nucleus and thalamus. Fractional representation of brachial endings in the red nucleus and their proportionate relation to ascending thalamic fibers has long been a matter of some dispute. Cajal (10) and Rasmussen (16) have suggested rubral terminations while Probst (4) has felt that the main body of fibers project to the thalamus. Mussen (14), and Ariens Kappers, et al (42) in their quantitative analysis of the fiber contributions to the nucleus ruber, have stated that "generally one half of the fibers (in the superior cerebellar arm) in the cat or monkey terminate in the magno-cellular portion, one fourth in parvacellularis, and one fourth in the thalamus." The work of Jansen and Jansen (38) has supported the hypothesis that one third of the fibers pass rostrally to the red nucleus. Two thirds of these fibers are derived from nucleus lateralis and one third originate equally from interpositus and fastigius. Carpenter and Stevens (27), in the main, have agreed with the fiber counts of Mussen (14) and Jansen and Jansen (38) in stating that fibers originating in the dentate nucleus contribute primarily to the diencephalic terminations. Rand (29), on the other hand, has found fibers from the medial portion of the dentate ending in both portions of the red nucleus. He has emphasized also that the fastigial nucleus does not contribute connections to either part of the red nucleus.

Carrea and Mettler (26) have found that the fibers lying dorsolaterally in the red nucleus constitute the dorsal component of the brachium, and intermediate components apparently go through the central portion of the red nucleus in a more diffuse manner. These authors have implied further that ventral brachial components terminate chiefly in the small cell portion of the nucleus ruber.

In this investigation all lesions lead to degenerated fascicles in the red nucleus. Generally the magnocellular portion showed fine granularity associated with terminal degeneration; however, the parvacellular portion was not free of changes. Also, the proportion of axones terminating in the nucleus ruber are difficult to designate by this method, but certainly at least one half of the brachium projects upward to diencephalic terminations. Further, no specific distribution was noted in the red nucleus corresponding to cerebellar nuclear areas, although lesions involving the middle one third of the brachium conjunctivum are usually associated with predominate rubral degeneration and some decrease in thalamic terminations.

The evaluation here of the fibers passing through the mesencepalon must include the possibility of fiber termination in the III cranial nerve nucleus. A great body of investigators (Van Gehuchten (6), Winkler (12), Allen (15), Rasmussen (16) and Clark (43))have traced fibers to this site. Ranson and Ingram (18) and Carpenter and Stevens (27) have found no fibers to the III nerve nucleus which, according to Jansen and Brodal (30), is probably due to restricted lateral nucleus lesions. Indirect connections via the

the median longitudinal fasciculus have been described however.

Rand (29) has described "terminations in the interstitial nucleus of the medial longitudinal fasciculus, the nucleus of Darkschewitsch, the nucleus of the posterior commissure, the nucleus parvocellularis aqueductus annuli, the Edinger-Westphal nucleus (caudal portion), and the region of the dorsal longitudinal fasciculus." In describing this distribution, Rand (29) feels that most anatomists would agree that fascicles from the nucleus lateralis commonly have a coincident dispersal with the fibers from the interpositus nucleus. Mehler, Vernier, and Nauta (44) have described connections with s. reticularis mesencephali, n. posterior commissure and pretectal region, and others terminating in the central gray, interstitial n. of Cajal and Darkschewitsch.

In this study, most lesions were confined to the two lateral nuclear areas in the cat, and hence no fiber terminations were noted in the interstitial nucleus of Cajal and Darkschewitsch, nuclei of any cranial nerves, pretectal region, central gray, or the reticular nucleus of the mesencephalon. In cat D-M a few fibers were noted in the posterior commissure and III nerve but these are not deemed significant since other areas such as the medial lemniscus, and trigeminal ascending pathways were involved besides the brachium conjunctivum.

Early investigations of this system were simple in their explanation of thalamic terminations. Since that time however, many authors have added concepts of end stations for the cerebellar efferent fibers throughout the thalamus and adjoining areas. To mention only a few: Probst (4) stated the termination to be in the ventral nucleus, Clark and Horsley (13) to the lateral thalamic nucleus, Cajal (10) to the anterior part of the ventral nucleus, Sachs and Fincher (20) to the center median nucleus, and Mussen (14) to the arcuate nucleus. Further, Ranson and Ingram (18) found terminations in the arcuate nucleus and the pars externa of the ventral nucleus. Clark (43) has agreed with arcuate termination and points out that the arcuate nucleus in the cat is not directly homologous to the macaque nucleus, and only the most caudal portion of the feline arcuate nucleus is homologous. Little degeneration is found there by Ranson and Ingram (18). Rand (29) has described in addition to fiber endings in the ventralis intermedius, fascicles distributing through centromedian dorso-medial, and midline nuclei. Crouch and Thompson (29) inadvertently destroyed the brachium conjunctivum and found, using Marchi method, thalamic terminations only in the nucleus ventralis intermedius.

Dow (46) has stated that difficulties concerned with the fixing of definite terminations in the thalamus is complicated by the varieties in the nomenclature and the wide-range of animals used. Although some order as to thalamic terminations is difficult, the major contributions should be considered separately. Jansen and Brodal (30) have stated that "considering the fan-like course of the brachium conjunctivum within the thalamus, it is no wonder that in the literature a variety of thalamic nuclei figures as end stations for fibers belonging to this system." Allen (15) and Ranson and Ingram (18) have described fibers passing to the subthalamic region and possibly ending in the nucleus of Forel's Field H_1. Winkler (12) and others have described fibers to the periventricular gray and to the medial thalamic nucleus. Allen (15) has been in agreement with this and has traced fibers to the zona incerta. Rand (29) has described crossed and uncrossed fibers to periventricular gray throughout the lower brain stem and crossed and uncrossed fibers to all parts of the nucleus mesencephalus profundus.

Allen (15) has divided thalamic fibers into the dorsal brachium conjunctivum which terminates in the nucleus "medialis thalami" at the same level as the thalamic termination of the medial lemniscus in the nucleus lateralis thalami. The main bundle continues upward to the ventral reticular formation, the subthalamic region, and the zona incerta. Thence the fibers radiate through the ventral nucleus and terminate in the larger lateral portion of that nucleus. Carpenter and Stevens (27) have agreed with the more common interpretation that thalamic fibers course through the prerubral field, enter the thalamic fasciculus, and terminate in the nucleus ventralis intermedius of the thalamus. Their work suggests, however, that an additional component courses via the dorsal division of the ansa lenticularis to the globus pallidus and that these fibers are derived principally from the ventro-lateral portion of the brachium conjunctivum. This area in turn receiving from the ventral lateral dentate nucleus. Other authors discussing subthalamic terminations (Allen (15) and Mussen (14)) have described similar pathways. Sachs and Fincher (20) were first to state that cerebellar fibers project to the basal ganglia. Gerebtzoff (47) felt that these subthalamic fibers come predominantly from the ventro-lateral portion of the brachium conjunctivum. Carrea and Mettler (26) have confirmed these observations concerning globus pallidus terminations via the lenticular fasiculus. Foltz and Matzke (48) have described projections to the corpus striatum in the opossum. Carpenter (49) has stated that lesions in the red nucleus provoked pallidal degeneration. However, this type of conclusion seems unwarranted in the face of more recent work on rubrol-pallidal connections.

Carrea and Mettler (26) have also believed that fibers of the "uncrossed ascending brachium conjunctivum" project to the globus pallidus ipsilaterally but have denied specific terminations in the subthalamic nucleus. Rand (29) has separated thalamic fibers into four bundles. Of the two larger components, one courses to the nucleus intermedius while the other projects to the central median and dorso-median nuclei. Clark (43) has stated that these fibers were fibers of passage on their way to the nucleus ventralis lateralis. The other bundle passes through H1 and into the nucleus ventralis lateralis. A smaller third group enters the dorsal midline gray, substantiating the postulation by Ranson and Ingram (18) that such terminations exist. McMasters (28), in studying the cat with the Marchi method, has also described some interlaminar thalamic terminations. The relationship of these fibers to hypothalamic centers is certainly not clear. The fourth bundle is abruptly described as terminating in the zona incerta with no further distribution.

Other investigators, Snider (50, 51) and Combs (52, 53), have incorporated electro-anatomical methods in describing terminations of the brachium conjunctivum. Snider (50) has recorded impulses in the nucleus ventralis posterior medialis and ventralis posterior lateralis following cerebellar cortical stimulation. Snider (51) has recorded responses in centrum medianum, centralis medialus and occasionally centralis lateralis following cerebellar cortical stimulation, but states that these latencies are longer than those found in the nucleus ventralis lateralis. His work with Whiteside (54) has demonstrated some short latency responses in the "fan" region of the prerubral field but has failed to conclusively demonstrate short latencies in the caudate or lentiform nuclei.

Combs (53), using electro-stimulation to the culmen, Crus I, and tuber vermis, explored the brain stem between the red and caudate nuclei. Recordings in the "fanning area" of the prerubral field were near the habenulo-interpenduncular tract. The remainder of the impulses were from ventralis medialis and ventralis lateralis.

Only occasional ipsilateral activity was noted by that investigator. In an earlier study Combs (52) had also recorded along the pathway of the descending root of the brachium conjunctivum in addition to contributions in the median longitudinal fasciculus.

Mehler, Vernier and Nauta (44), using primates and the Nauta-Laidlaw silver technique, have recently described multiple thalamic terminations. These include, in addition to small intralaminar fibers, a "compact subthalamic component" coursing in Forel's Field H_1 and terminating in ZI, VPL_o, VL_o, VA and most densely in VL."

The work of this investigator agrees with the classic description of thalamic terminations in that the main fiber distribution was in the nucleus ventralis intermedius. Lesions did not generally involve the fastigial nucleus and hence its representative distribution in the thalamus cannot be evaluated. It would not seem inordinant to state that the "minor fascicles of the brachium conjunctivum" (Jansen and Brodal (30)) are primarily related to the fastigial nucleus. This would be in keeping with the lack of terminations found in the following areas: oculomotor nucleus, interstitial nuclei of Cajal and Darkschewitsch, the peri-aqueductal gray, periventricular gray, parafasicular nucleus, and the center median nucleus.

After leaving the red nucleus, degenerated fascicles course through the prerubral field, zona incerta and subthalamic area to enter the fasciculus thalamicus and terminate in the ventral intermediate nucleus. Some fiber bundles course more caudal and medial through the ventral posterior, however, these fibers are not constant nor do they have a specific relation to the cerebellar lesion. Cat DM, using the Marchi technique, shows degeneration in the ventral posterior but this is secondary to an inadvertent pressure lesion of the dorsal columns and subsequent degeneration of the medial lemniscus. No particular arrangement was present in the thalamus in relation to partial lesions in the cerebellar nuclei. No terminations were seen in the globus pallidus (Carpenter and Stevens (27), and Carrea and Mettler (26)).

Uncrossed Ascending Brachium Conjunctivum

The previous discussion concerning thalamic terminations immediately brings to mind the relations of the so-called "uncrossed ascending brachium conjunctivum" of Carrea and Mettler (26). This fiber bundle reportedly arises from the brachium conjunctivum near its decussation and passes upward in a region lateral to the central gray to terminate in the ipsilateral arcuate nucleus. Jansen and Brodal (30) put forth the explanation that the intermediate and lateral nuclei of the cerebellum plus the contralateral fastigial nucleus make up the brachium conjunctivum. The fastigial components give rise to the uncinate fasciculus and the fibers in the dorsal most cap of the brachium conjunctivum. Therefore the terms "ascending limb of the uncinate fasciculus" (Rasmussen (16)), fasciculus retropeduncularis (Thomas (3)), "accessorische Bindearmbundel"

(Probst (4)), and finally the uncrossed ascending brachium conjunctivum (Carrea and Mettler (26)) are probably equivalent. Since this work has not involved the fastigial nucleus, nor have the lesions of the cerebellar nuclei and brachium extended to a point medially to include the upward coursing uncinate fascicles, we cannot find disagreement with this explanation. Lesions in the intermediate and lateral nuclei however show no homolateral mesencephalic or thalamic degeneration.

Allen (15) and Van Gehuchten (5) have interpreted Probst's accessory brachium as a portion of the fifth nerve. Carpenter and Stevens (27) have believed that this uncrossed component is the dorsal trigeminal tract and terminates in the arcuate nucleus of the thalamus. At another point Carpenter further has stated that these fibers terminate in center median nucleus. Although some animals (D-30S, D-15, and DM) involved subtotally the trigeminal area, no ascending homolateral component was noted. McMasters (28) has stated that fibers from the uncinate fasciculus infiltrate the brachium conjunctivum in its more dorsal portion and extend up into the approximate region of the central tegmental fasciculus and furnish some fibers to the intralaminar nuclei of the thalamus.

Little light can be shed on the "brachium conjunctivum pars bulbaris" (Jansen and Brodal (30)) in this work. Although some direct and vascular damage was present in the region of the reported noncerebellar fibers, few conclusions can be made. The vestibular correlation will be considered later.

As one considers the possibility of the ascending uncinate components, Jansen and Brodal (30) suggest the interesting concept that Cajal (10) in his initial explanations of the direct descending brachium conjunctivum was in reality describing the descending component of the uncinate fasciculus. The direct or dorsal descending brachium conjunctivum seems to explain the incompatibility between the views of Allen (15), Mussen (14), and Gerebtzoff (47) who have supported total decussation of the brachium and Jansen and Brodal (30) and Carrea and Mettler (26) who have found uncrossed components. This investigation which, like Allen (15), Mussen (14), and Gerebtzoff (47), has failed to include the fastigial nucleus in the cerebellar lesions, can certainly find little disagreement with this concept. Jansen and Jansen (38) have shown definitely that all fibers from the fastigial nucleus definitely cross in the cerebellum. Jansen and Brodal (30) conclude that this direct descending limb terminates in the reticular formation of the medulla oblongata and gives off collaterals to the motor nuclei of the V and VII cranial nerves.

Descending Root of the Brachium Conjunctivum

By way of introduction into the descending root of the brachium which, in this work, occupies one of the most significant findings, we should refer back to the primary work of Cajal (10) and his initial description of this bundle. The "voie olivo-spinali croisee" arose, according to Cajal (10), as the descending portion of the bifurcating axones of the brachium and spreads inferiorly in the cord. Although Marchi (1) first noticed the descending root, he had remarked that fibers from the brachium conjunctivum reach the anterolateral column of the spinal cord. Thomas (3), Probst (4), Lewandowsky (7), Van Gehuchten (6), and Luna (9) all have described descending pathways of the brachium to the medulla. Probst (4) has suggested that the descending root leaves the main brachium before the superior arm leaves the cerebellum, while Von Monakow (55) has found that descending fibers pass caudally before the decussation of Wernekink occurs. Van Gehuchten (6), in addition to demonstrating only crossed descending fibers has recorded that fibers, after crossing in the decussation, bifurcate and the caudal portions form the descending root. Wallenberg (56) has thought that these fibers are not formed at the decussations but are a separate bundle, which was confirmed by Allen (15). The latter author along with Mussen (14), Rasmussen (16), and Van Gehuchten (6) has stated that the descending limb is completely crossed. Mettler and Zimmerman (21) have described two portions of the crossed descending limb: a small ventral portion, exiting from the brachium conjunctivum, which crosses the midline first and terminates in the ventral tegmental nucleus of Bechterew, and the other portion arising from the dorsal cap of the brachium conjunctivum, sending rostrally an ascending limb and then descending to terminate in the tegmental nucleus of Gudden, the superior central nucleus, ventral tegmental nucleus of

Bechterew, the ponto-tegmental nucleus, and finally to lie in the ventral column of the cord down to lumbar levels. Mettler, Oriole, and Grundfest (23) have attempted to corroborate this spinal course using physiological methods. They show primarily a contralateral pathway of rapid conducting fibers but failed to show specific spinal connections.

More recently, McMasters (28), Foltz and Matzke (48) have described the descending root in the cat and opossum respectively. McMasters (28) has felt that the small descending portions of the brachium takes its origin from the dentate nucleus and decussates in the ventral midline below Wernekink's commissure. Using the Marchi method, he was unable to trace this pathway caudal to the lower medulla. Foltz and Matzka (48) were able to trace these fibers to the upper cervical region in the opossum.

Other authors, Van Gehuchten (5) and Ranson and Ingram (18) have traced descending root fibers only to the border of the pons, while Allen (15), using the guinea pig, has reported fibers in the reticular formation of the pons and medulla. Inferior olivary connections have been described by Lewandowsky (7) and Rasmussen (16). Carpenter and Stevens (27) have followed this tract to the upper medulla and in one case to the cervical cord in the Rhesus, and have stated that the cervical degeneration follows a discrete lesion in the dorsal third of the brachium conjunctivum. These authors have described the descending root as taking origin primarily from the nucleus interpositus and the dorsal part of the dentate, and sending fibers to the median longitudinal fasciculus, superior central nucleus, reticulo-tegmental nucleus, and possibly the inferior olive. Further, these workers have described components of the ventral third of the brachium conjunctivum (juxtarestiform body fibers, fibers of the lateral lemniscus, and trigeminal fibers) which are not generally described as part of that bundle. They have however, stated that the ventral lateral portion of the dentate nucleus probably gives rise to the ventral lateral third of the brachium. These investigators support the relationship of the cerebellar nuclei to the brachium conjunctivum but do not include the other noncerebellar pathways. Carpenter and Stevens (27) also have divided the descending limb into the portion from the interpositus nucleus descending in the spinal cord, while those from the dentate nucleus terminate in the pons,medulla. One would question here the possible confusion between the spinal fibers and the more classic vestibulo-spinal tract. The origin of this tract could be damaged by cerebellar fulgeration or secondarily by vascular interference.

Confusion certainly exists in relation to the olivary terminations; however, this investigator feels that vestibular and reticular vascular ischemia which so often accompanies these lesions in the cerebellar roof may cause degeneration in the median extrapyramidal group and hence may simulate these olivary terminations (Rasmussen

(16), Lewandowsky (7), and R nd (29)). Mehler, Vernier and Nauta (44) have traced the crossed descending brachium to the nucleus papillioformis (nomenclature: Olszewski, 1952), abducens rootlets and the median reticular area. The discussion of Carrea and Mettler (26) as to the philogenetic development of the descending root and its relation to the median longitudinal fasciculus, III, IV, and VI cranial nerve nuclei is interesting, however, this author can give little substantiation to these findings anatomically.

Allen (15) has emphasized that no portions of the descending limb terminate in the motor nuclei of the cranial nerves, in contradiction to the work of Cajal (10). These fiber terminations more logically may be related to the descending portion of the uncinate fasciculus.

As has been mentioned before, disagreement exists concerning the origin of the crossed descending limb and further as to its position in the superior arm as it proceeds from the cerebellum. Carrea and Mettler (26) have stated that the descending limb originates only in the dorsal median two thirds of the brachium conjunctivum contralaterally and therefore apparently taking its origin from the fastigial and intermediate nuclei. Rand (29), however, has described a cephalo-caudal distribution pattern to the descending root and states that the more dorsal components of the brachium from the dorsal portions of nucleus interpositus and dentatus, end in the pons. Also that the ventral lateral portion of the descending limb, from the ventral lateral portions of the two cerebellar nuclei extends down to medullary levels.

This work has attempted to more clearly describe the origin, course and terminations of the crossed descending limb of the brachium conjunctivum. Both in animals with total lesions of the brachium conjunctivum and in animals with restrictive destruction in the ventral lateral portion of the brachium, degeneration is present in the descending limb. It is felt that the axones originate in the ventral lateral portion of the dentate nucleus and lie in the ventral lateral portion of the brachium conjunctivum. This relationship would be in keeping with the work of Carrea and Mettler (26), Rand (29), McMasters (28) and Carpenter and Stevens (27). However, in contradiction to these authors this work suggests that these ventral lateral fibers course ventrally and medially just prior to the decussation of Wernekink, circle beneath the reticular formation, and cross the midline caudal to the interpeduncle nucleus (see fig. 8). These fibers are entirely crossed and extend caudally to terminate in the ventral tegmental nucleus of Bechterew. No terminations are found in the nucleus of Gudden, the superior central nucleus, the ponto-tegmental nucleus, cranial nerve nuclei, nor any portion of the inferior olivary complex. It is the contention of this author that this pathway terminates at the level of Bechterew's nucleus (ventral tegmental) and that no fibers pass caudally into the spinal cord. As was previously mentioned, involvement of the descending portion of the uncinate fasciculus and/or dorsal medullary nuclei (vestibular, reticular) may serve to explain the terminations described by other authors.

Fastigial Vestibular System

The pertinant relationships of this system to the present work have been considered above. However, a few further statements are necessary. Since the lesions have included only partial destruction of both the uncinate fasciculus and the direct fastigio-bulbar tract, further postulations in this system would be unfounded. As might be expected, destruction of portions of the direct fastigio-bulbar tract led to rather consistent change in the vestibular nuclei (superior and lateral). Also important was the damage to the lateral vestibulo-spinal tract in cat D-M. Nuclear connections and terminations in this system, therefore, cannot be determined by this work.

The work of Thomas, Kaufman, Sprague and Chambers (57) and others (58) using the Nauta-Laidlaw technique substantiates the majority of these findings in that their work with fastigial nucleus lesions has led to the following observations. Both crossed and uncrossed uncinate fasicles traverse in the dorsal portion of the brachium conjunctivum and ascend through the mesencephalon bilaterally in the "so-called uncrossed ascending limb of the brachium." They find, in agreement with Jansen and Brodal (30), that all decussation of the fastigio-bulbar tracts occur in the cerebellum except that portion in the posterior commissure. Extensive degeneration is found from the rostral thalamus through the brain stem down to upper cervical segments of the spinal cord. No degenerations are found in the cranial nuclei. Supramedullary degeneration includes the following nuclear masses: Edinger-Westphal, interstitial of Cajal and Darkschewitsch, posterior commissure, tegmental reticular formation, pretectal superior colliculus, Forel's Field H_1, ventral posterior, (lateral and medial) ventral lateral, subparifascicular, centralis lateral, centre median, reuniens, and ventral anterior. These extensive degenerations following fastigial lesions in addition to the present work seem to resolve some of the previous confusion of the efferent cerebellar system. The conclusions would certainly suggest that at least in the cat the lateral and intermediate nuclei constitute a more restrictive system than previously described. The fastigio-vestibular system therefore occupies a more separate entity.

The functional and physiological ramifications of this problem are certainly worthy of extensive work. This study, however, has been concerned with the anatomical components of the cerebellar efferent system, and physiological considerations are beyond the scope of this investigation.

SUMMARY AND CONCLUSIONS

The efferent projections of the cerebellum have been studied in the cat brain using selective destruction of various portions of the cerebellar nuclei and brachium conjunctivum, followed by a histological analysis of the resulting degeneration. In a series of cats, unilateral lesions were made in nucleus interpositus and lateralis, and the mesencephalic brachium conjunctivum. Following a survival period of eight to thirty days, the animals were sacrificed and histological sections were prepared by the intensified Protargol and Marchi methods.

Analysis of the experimental material has yielded the following information:

1. Lesions in the cerebellar nuclei produce degenerations in the brachium conjunctivum which have a characteristic distribution. The lateral nuclear area projects to the ventro-lateral brachium conjunctivum, the intermediate nuclei and medial portion of the lateral project to the intermediate brachium conjunctivum, while the more medial nuclei occupy the dorsal brachium conjunctivum.

2. Lesions producing various amounts of degeneration in the brachium conjunctivum demonstrate a specific reproducible pattern of distribution in the decussation of Wernekink.

a). The small ventral component is first to cross the midline decussating immediately dorsal to the interpeduncular nucleus. This is the element which is indicated to be the descending limb of the brachium conjunctivum. b). The dorsal component decussates next passing in a dorso-ventrad direction. c). The most rostral element of the decussation is made up of the intermediate component of the brachium conjunctivum of which the ventral portion is the last to cross the midline.

3. The crossed ascending limb of the brachium conjunctivum following decussation distributes itself to both the magnocellular and parvacellular portions of the red nucleus. Although more terminations are seen in the magnocellular portion some degenerated endings are seen in the parvacellular area. The pathway courses upward through the prerubral field, medial to the zona incerta, and subthalamic nucleus to enter the fasciculus thalamicus and terminate in the nucleus ventralis intermedius of the thalamus. No other thalamic terminations are seen nor do fibers reach the globus pallidus.

4. No degeneration in an uncrossed ascending limb of the brachium conjunctivum follows intermediate or lateral cerebellar lesions.

5. No degeneration is noted in the interstitial nucleus of Cajal and Darkschewitsch, nuclei of any cranial nerves, pre-tectal region, central gray, or the reticular nucleus of the mesencephalon following these cerebellar lesions.

6. No degeneration is seen in a direct or uncrossed descending limb of the brachium conjunctivum following these lesions.

7. Lesions in the ventro-lateral portion of the nucleus lateralis produce degeneration in the ventro-lateral portion of the brachium conjunctivum, in the initial ventral portion of the decussation of Wernekink, and terminal degeneration in the ventral tegmental nucleus of Bechterew. This is taken to correspond with the origin and course of the crossed descending limb of the brachium conjunctivum. Destruction of this pathway produces no terminal degeneration in the superior central nucleus, ponto-tegmental nucleus, cranial nerve nuclei, or inferior olivary nucleus.

8. No lesions were made in the fastigial nuclei in this investigation.

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TABLE OF ABBREVIATIONS

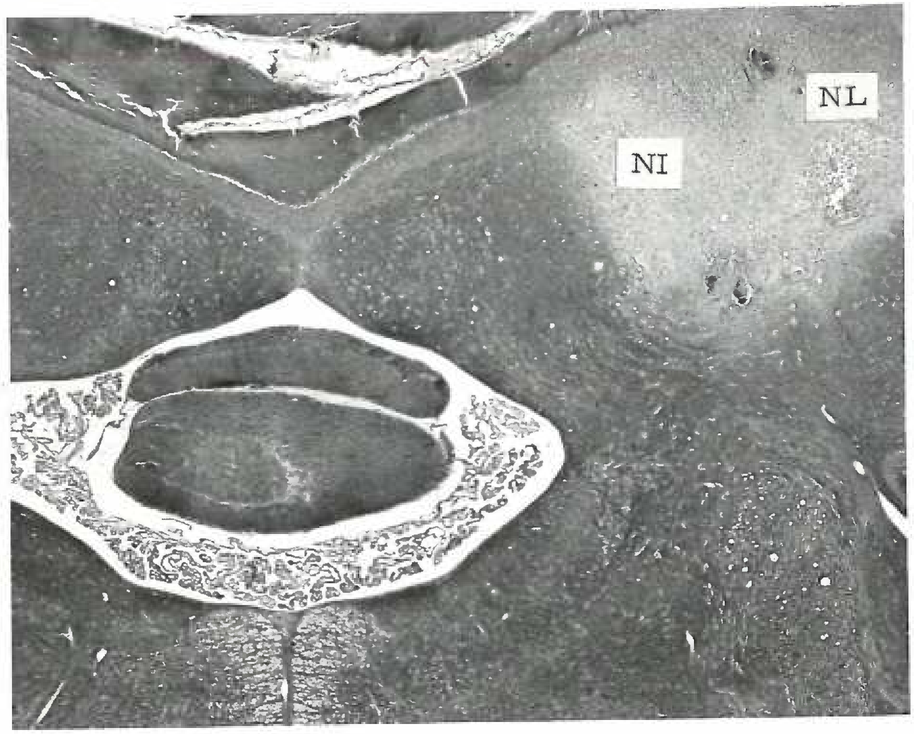
NL	Nucleus Lateralis
NI	Nucleus Interpositus
BC	Brachium Conjunctivum
N	Normal
D	Degenerated
DO	Dorsal
MD	Medial
VT	Ventral
RN	Red Nucleus
VI	Ventralis Intermedius
--DA	Destroyed Axon Termination
--CDL	Crossed Descending Limb
IPN	Interpeduncular Nucleus
NB	Nucleus of Bechterew
--IA	Intact Axon
--DPA	Deafferented Pericellular Area

PLATE I.

Figure 12. Cat D-5. Electrocoagulative lesion in nucleus lateralis (NL) and nucleus interpositus (NI). Note sparing of ventro-lateral portion of nucleus lateralis (NL). Magnification 13 X. Intensified Protargol stain.

Figure 13. Cat D-5. Cross-section through mesencephalic brachium conjunctivum (BC). Note that this distribution of degenerated fibers is found in animal with lesion pictured in Figure 12. Compare with normal appearance in Figure 14. Magnification 75 X. Intensified Protargol stain.

12.



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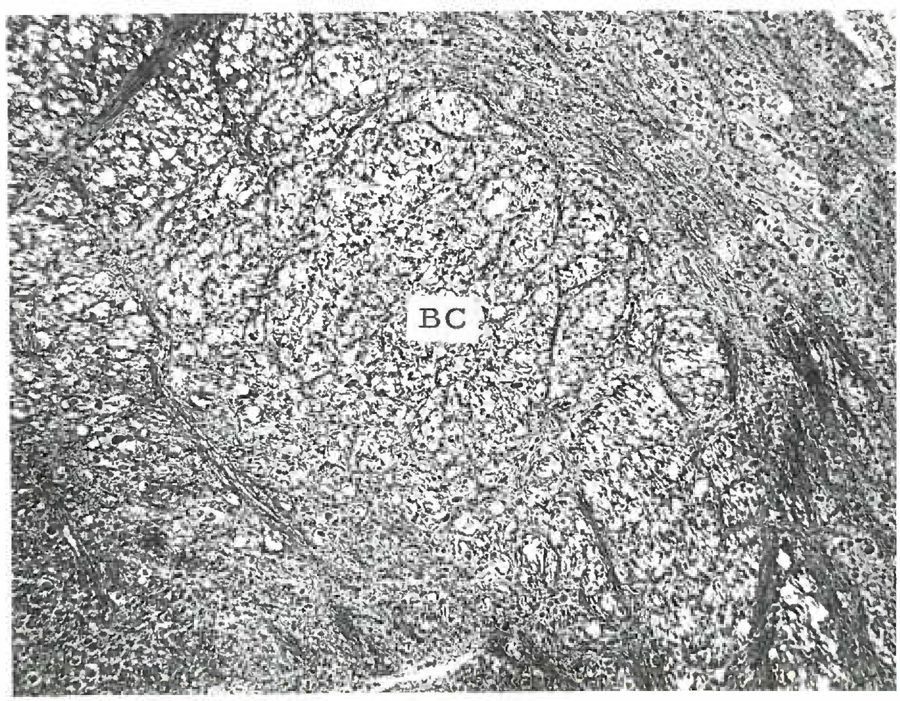
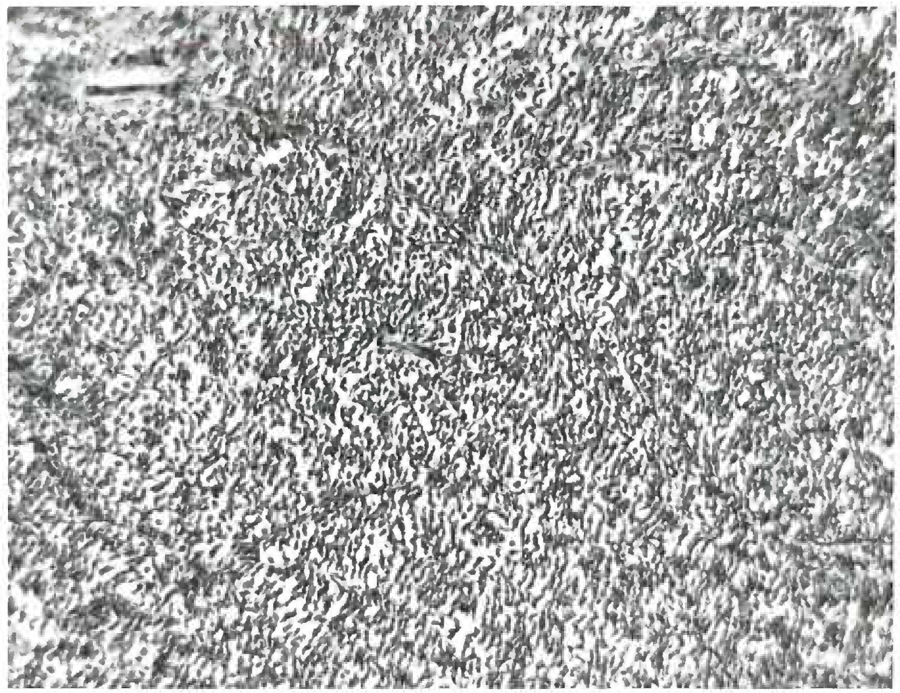


PLATE II.

Figure 14. Cat D-4. Photomicrograph of the histological pattern of normal brachium conjunctivum. Note uniformity of nerve fibers. Magnification 200 X. Intensified Protargol stain.

Figure 15. Cat D-4. Photomicrograph of the contralateral brachium conjunctivum showing degeneration in the median and ventral thirds. Magnification 150 X. Intensified Protargol stain.

14.



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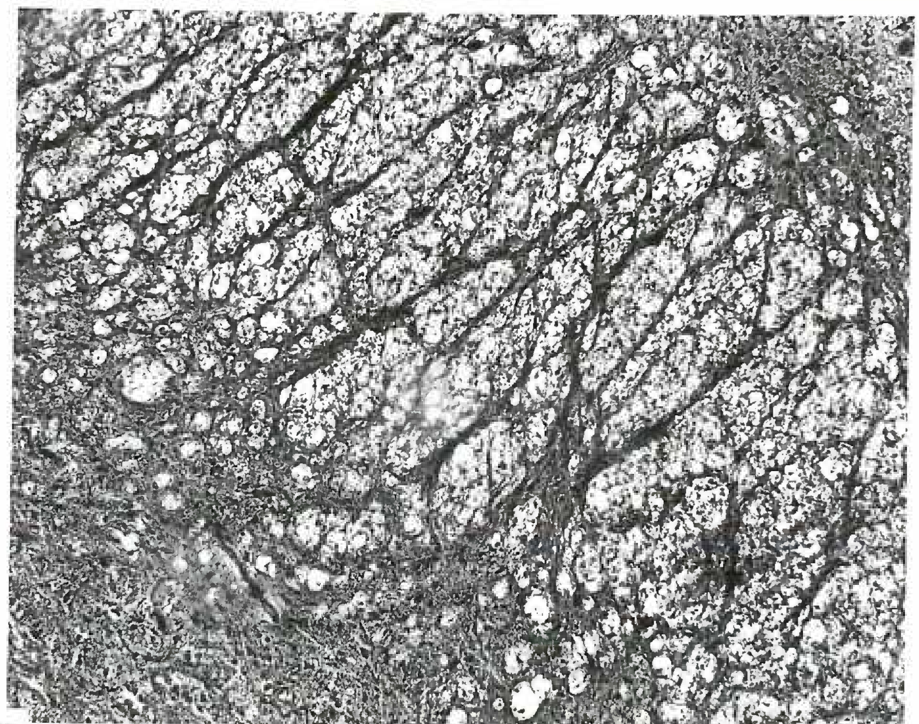

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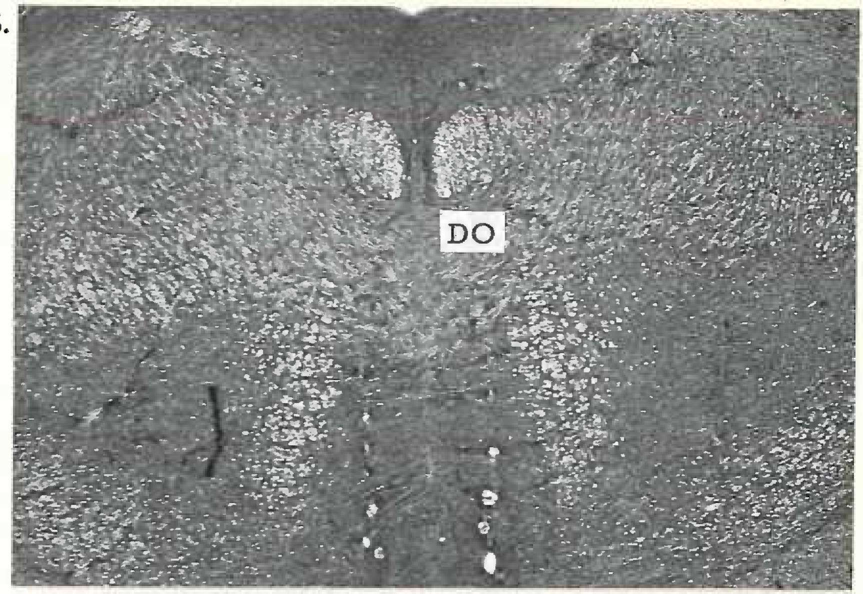
PLATE III.

Figure 16. Cat D-4. Photomicrograph of the decussation of the brachium conjunctivum. Degeneration is seen in the most dorsal (DO) fibers. Ventral decussation of crossed descending limb of the brachium conjunctivum has already taken place. Magnification 22 X. Intensified Protargol stain.

Figure 17. Cat D-4. Photomicrograph of the decussation of the brachium conjunctivum cephalad to the section shown in Figure 16. Degeneration is seen in the medial (MD) fibers. Magnification 22 X. Intensified Protargol stain.

Figure 18. Cat D-4. Photomicrograph of the decussation of the brachium conjunctivum cephalad to the section shown in Figure 17. Degeneration is seen in the ventral (VT) fibers. Magnification 22 X. Intensified Protargol stain.

16.



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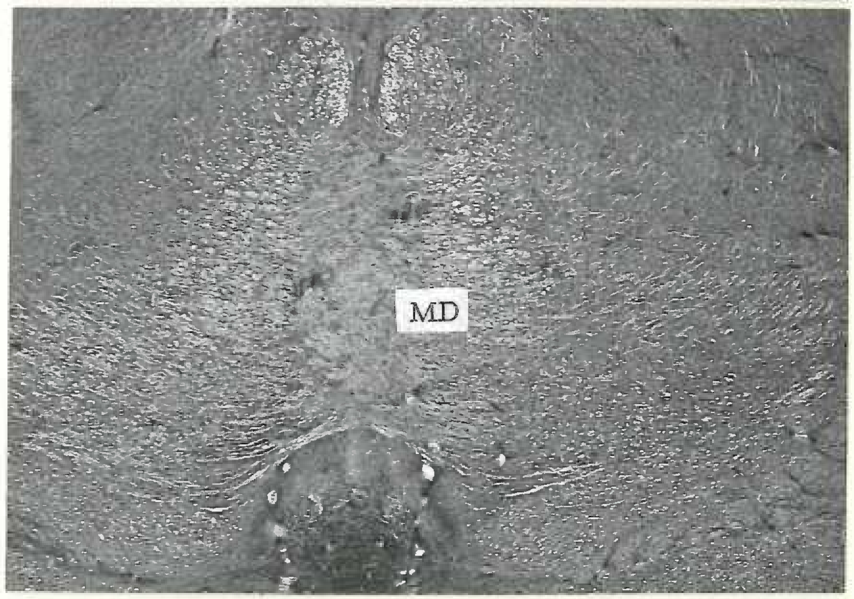

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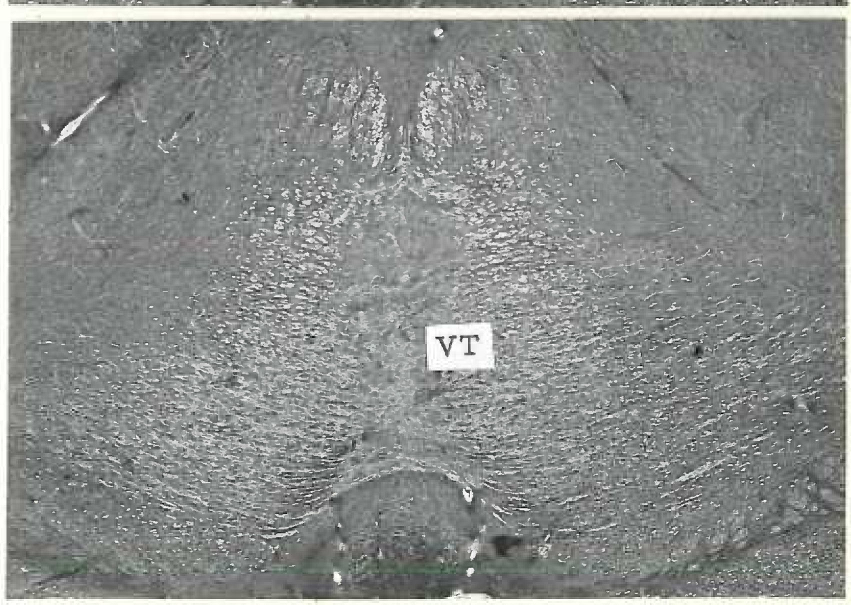
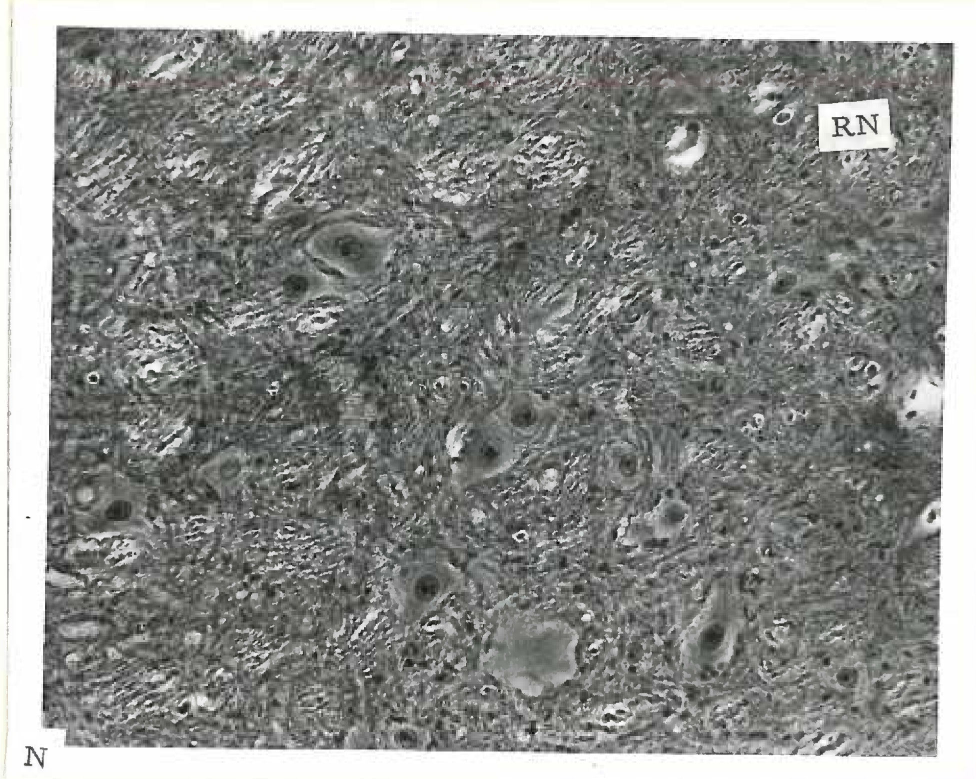


PLATE IV.

Figure 19. Cat D-3. Photomicrograph of the histological pattern of normal red nucleus (RN). Magnification 300 X (medium power). Intensified Protargol stain.

Figure 20. Cat D-3. Photomicrograph of the involved contralateral red nucleus (RN). Magnification 300 X. Intensified Protargol stain.

19.



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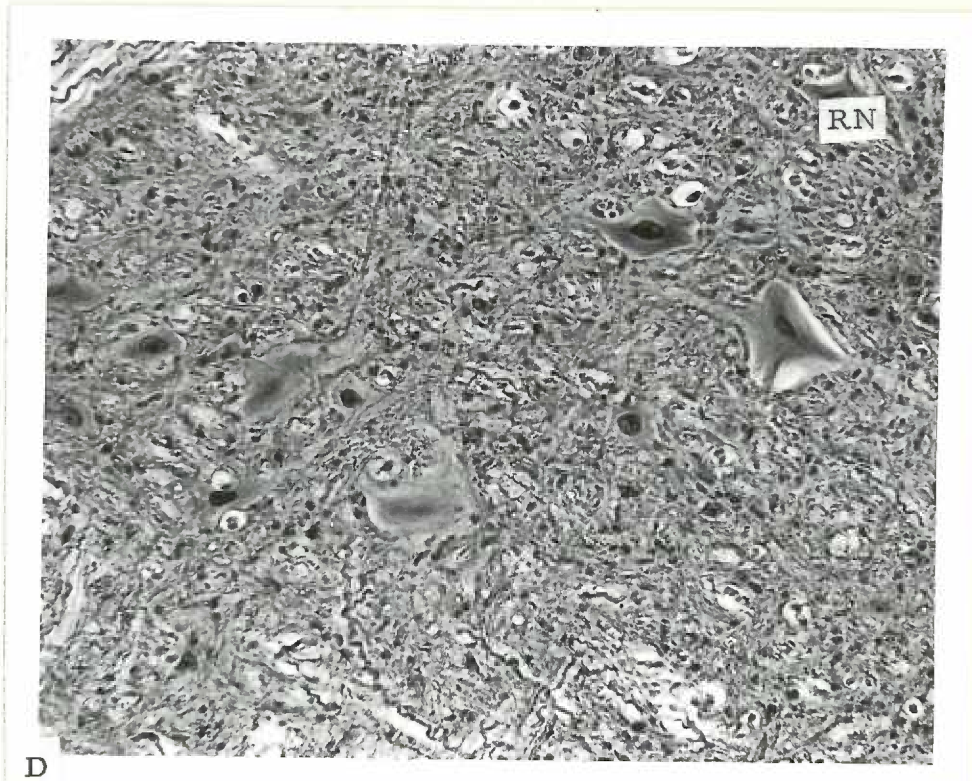
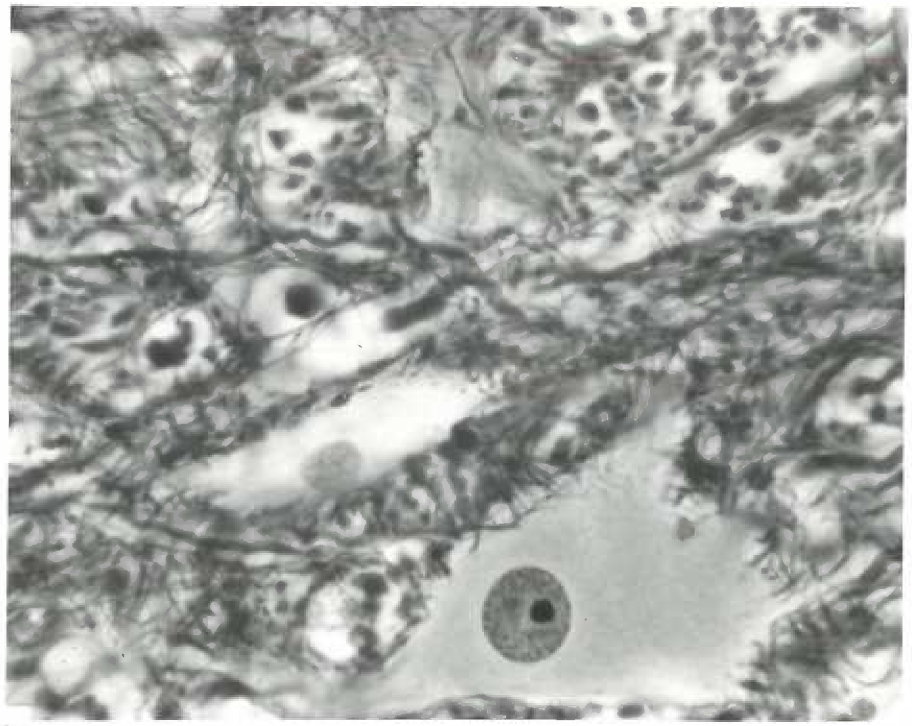


PLATE V.

Figure 21. Cat D-4. Photomicrograph of the histological pattern of normal red nucleus. Note presence of preterminal axons and terminals on cell bodies and adjacent neuropil. Magnification 500 X (high power). Intensified Protargol stain.

Figure 22. Cat D-4. Photomicrograph of the involved contralateral red nucleus. Note absence of preterminal afferents to cell bodies. Magnification 500 X (high power). Intensified Protargol stain.

21.



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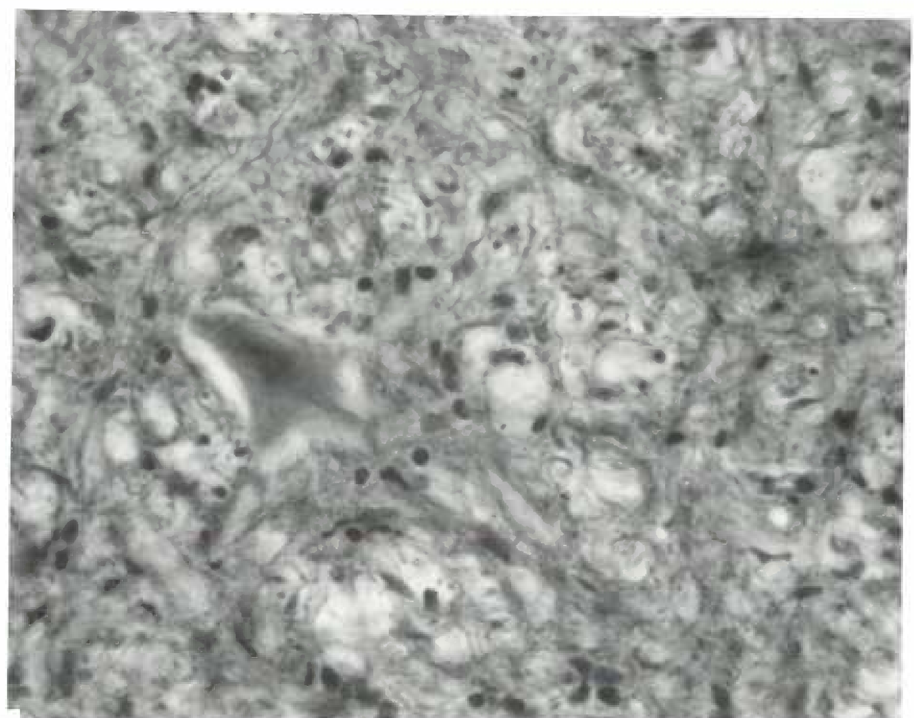

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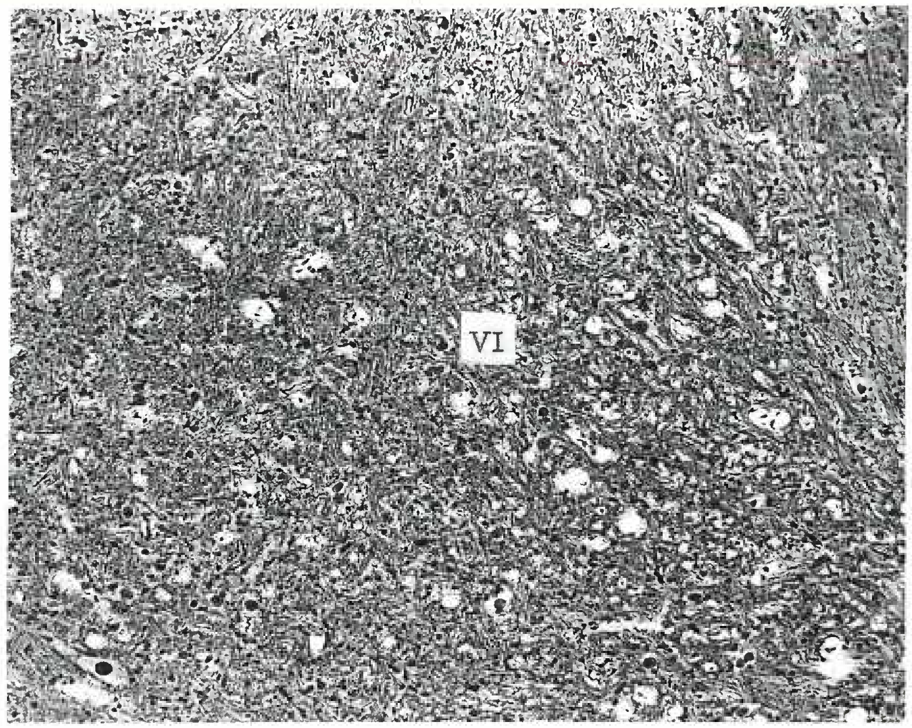
PLATE VI.

Figure 23. Cat D-13. Photomicrograph of the histological pattern of degenerated nucleus ventralis intermedius (VI). Note the axon fallout present throughout the nucleus. Magnification 150 X (low power). Intensified Protargol stain.

Figure 24. Cat D-13. Photomicrograph of the histological pattern of degenerated nucleus ventralis intermedius (VI). Note axon fallout with decrease in terminal fibers (DA). Magnification 500 X (high power). Intensified Protargol stain.

23.



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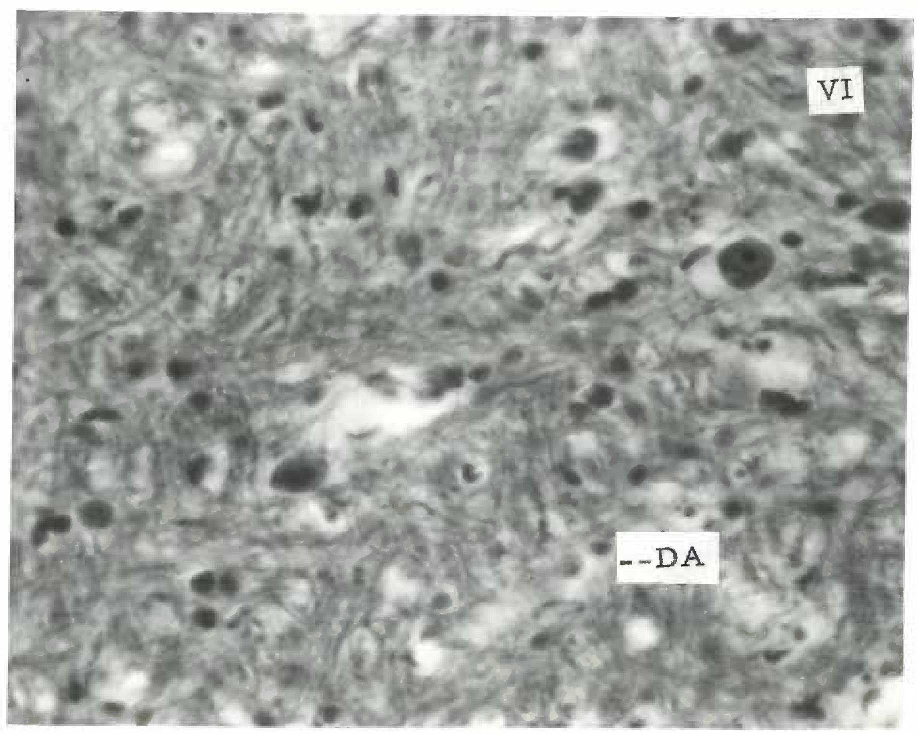


PLATE VII.

Figure 25. Cat D-M. Section through mesencephalic brachium conjunctivum showing degeneration throughout extent of tract. This destruction resulted from contralateral cerebellar nuclear lesions. Magnification 13 X. Marchi stain.

Figure 26. Cat D-M. Section just caudal to main decussation of brachium conjunctivum showing ventrally decussating fibers of crossed descending limb of brachium conjunctivum (CDL). Magnification 13 X. Marchi stain.

25.

26.

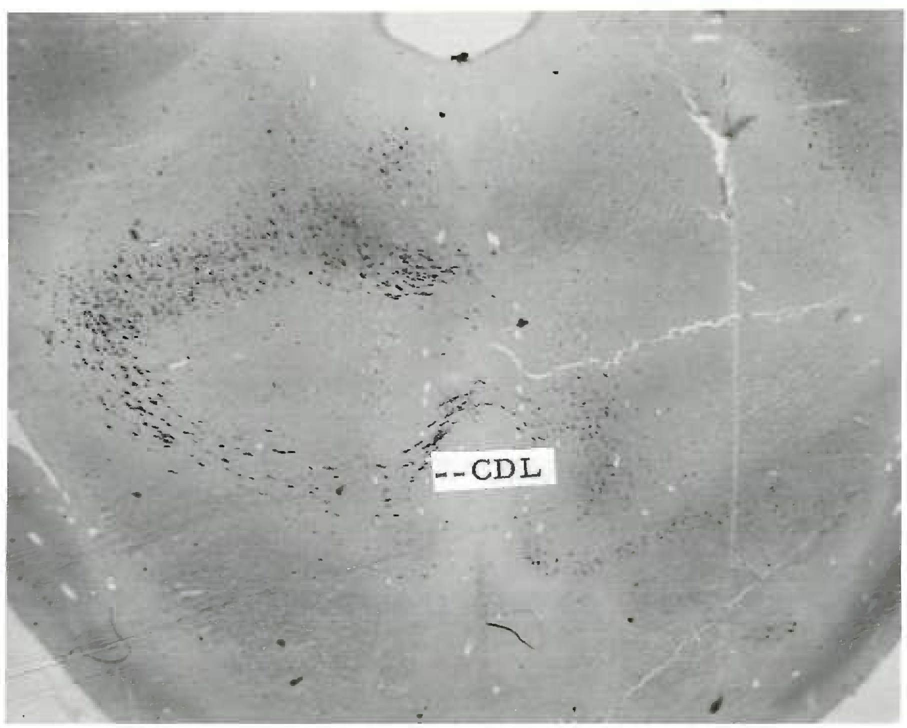
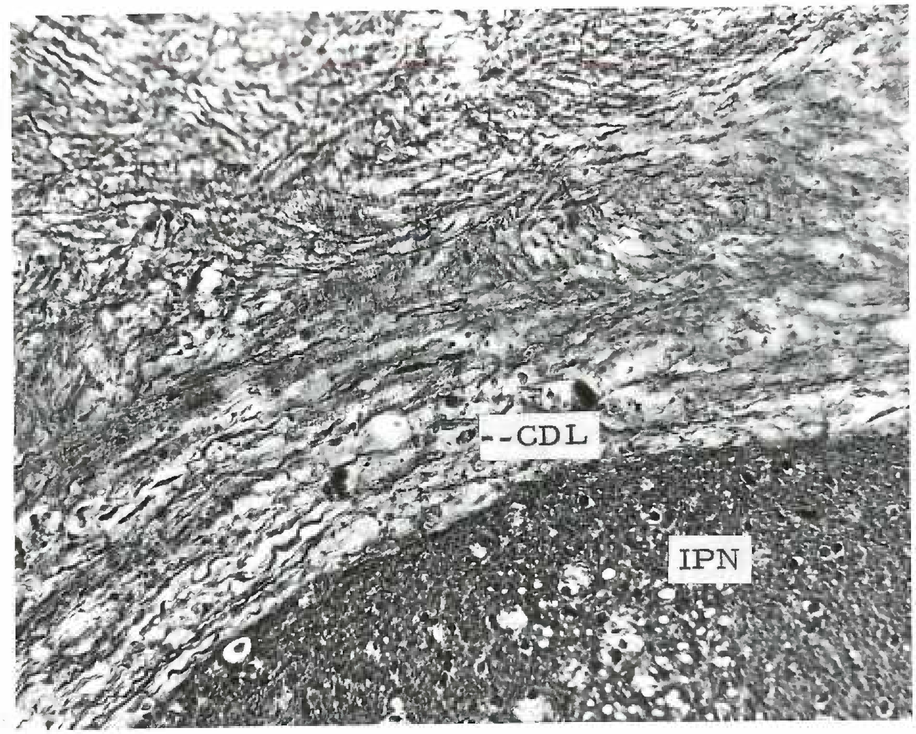


PLATE VIII.

Figure 27. Cat D-2. Photomicrograph of the ventral portion of the decussation of the brachium conjunctivum. Degeneration is seen in the crossed descending limb of the brachium conjunctivum (CDL) as it courses over the interpeduncular nucleus (IPN). Magnification 300 X. Intensified Protargol stain.

Figure 28. Cat D-2. Photomicrograph of the ventral portion of the decussation of the brachium conjunctivum. Degeneration is seen in the crossed descending limb of the brachium conjunctivum (CDL). Magnification 300 X. Intensified Protargol stain.

27.



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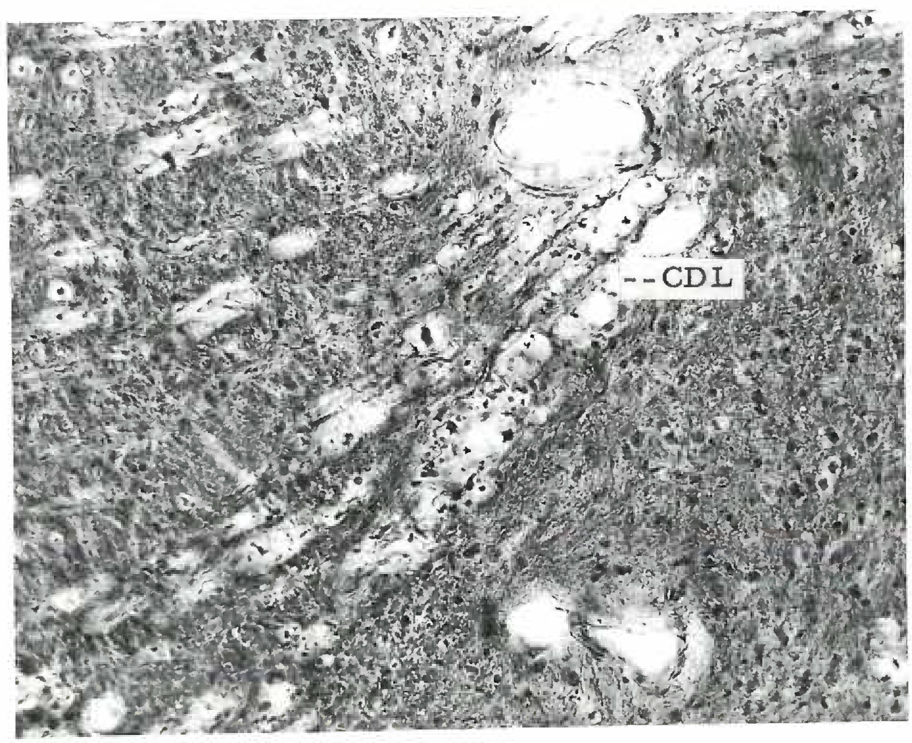


PLATE IX.

Figure 29. Cat D-2. Photomicrograph of the ventro-lateral portion of the brachium conjunctivum (X) correlating with degeneration in the crossed descending limb of the brachium conjunctivum seen in Figures 27 and 28. Magnification 150 X. Intensified Protargol stain.

29.

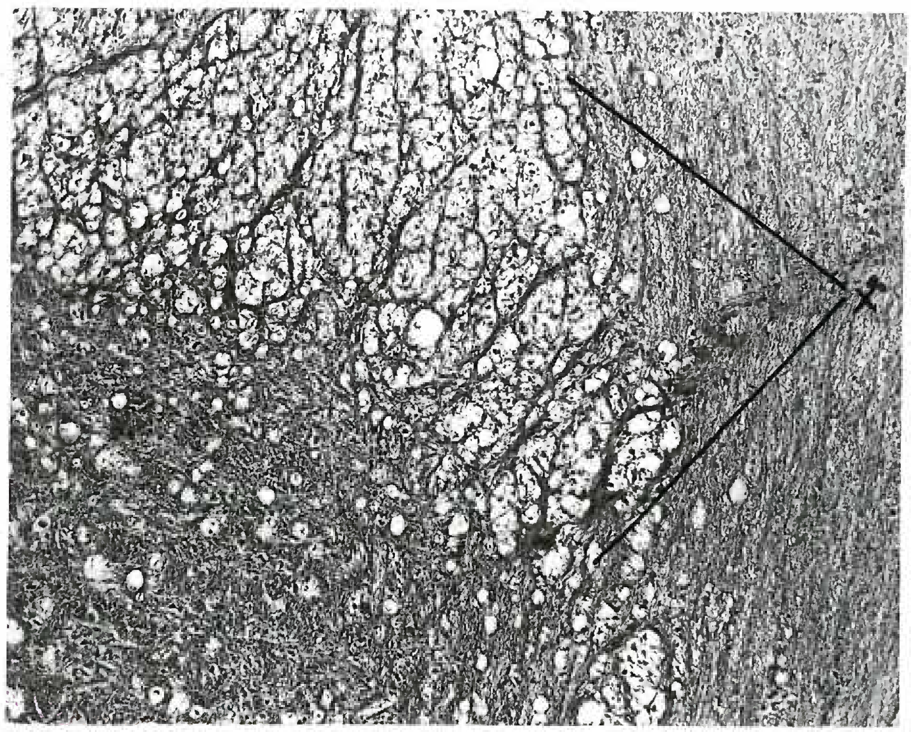
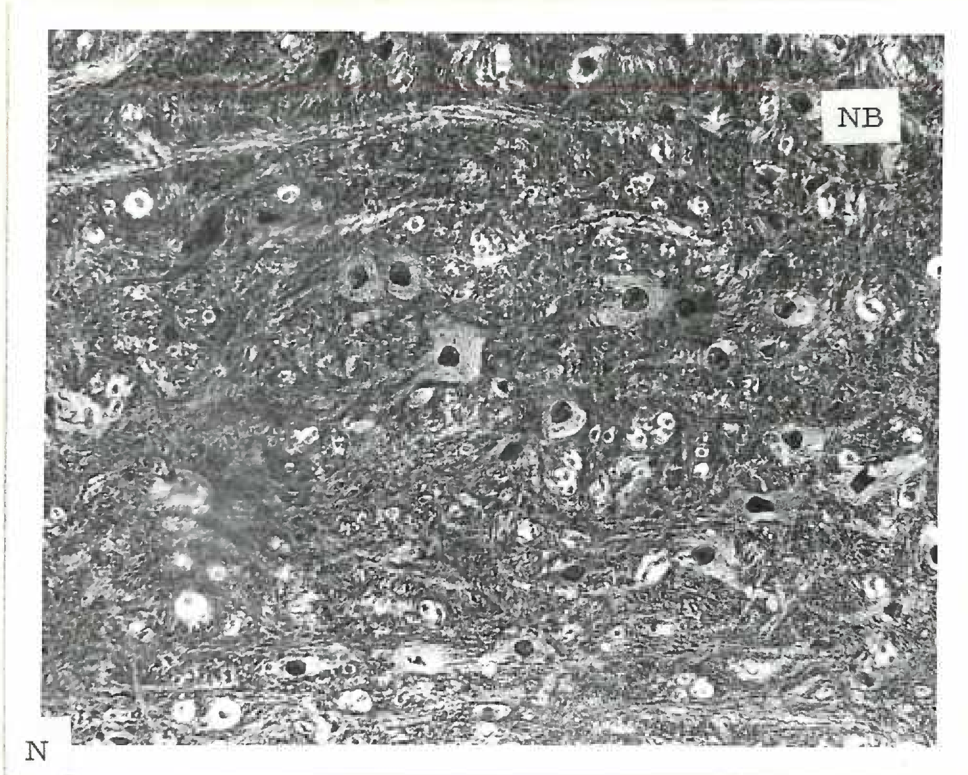


PLATE X.

Figure 30. Cat D-2. Photomicrograph of histological pattern of normal ventral tegmental nucleus of Bechterew (NB). Magnification 300 X. Intensified Protargol stain.

Figure 31. Cat D-2. Photomicrograph of deafferented contralateral ventral tegmental nucleus of Bechterew (NB). Note decrease in preterminal and terminal axons, shrunken appearance of cell bodies. Magnification 300 X. Intensified Protargol stain.

30.



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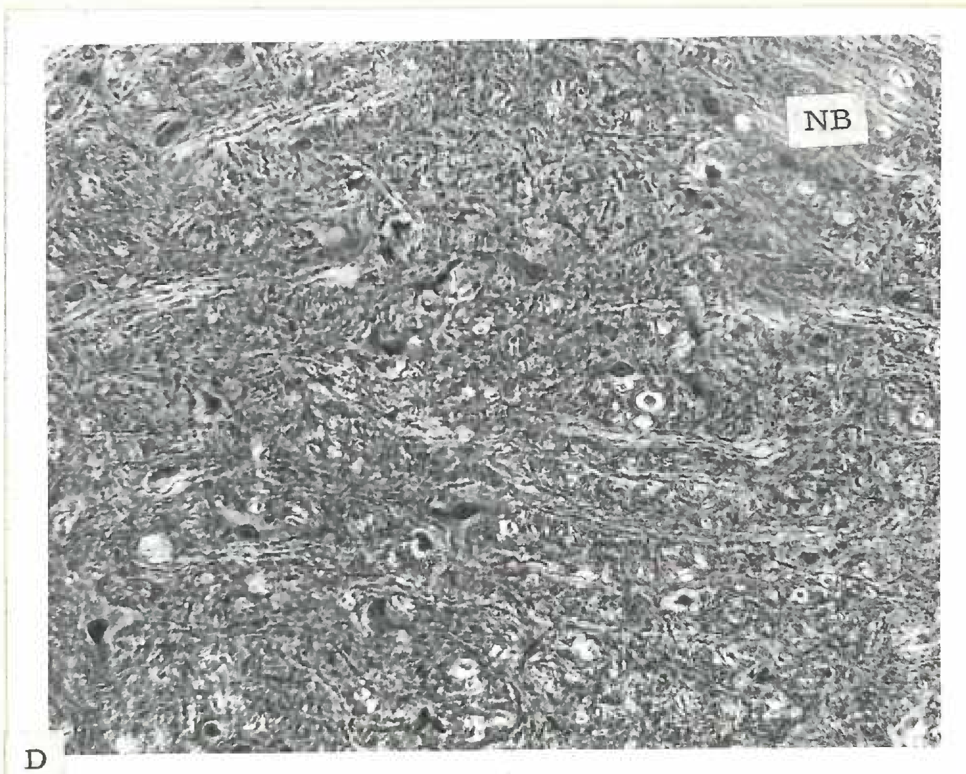
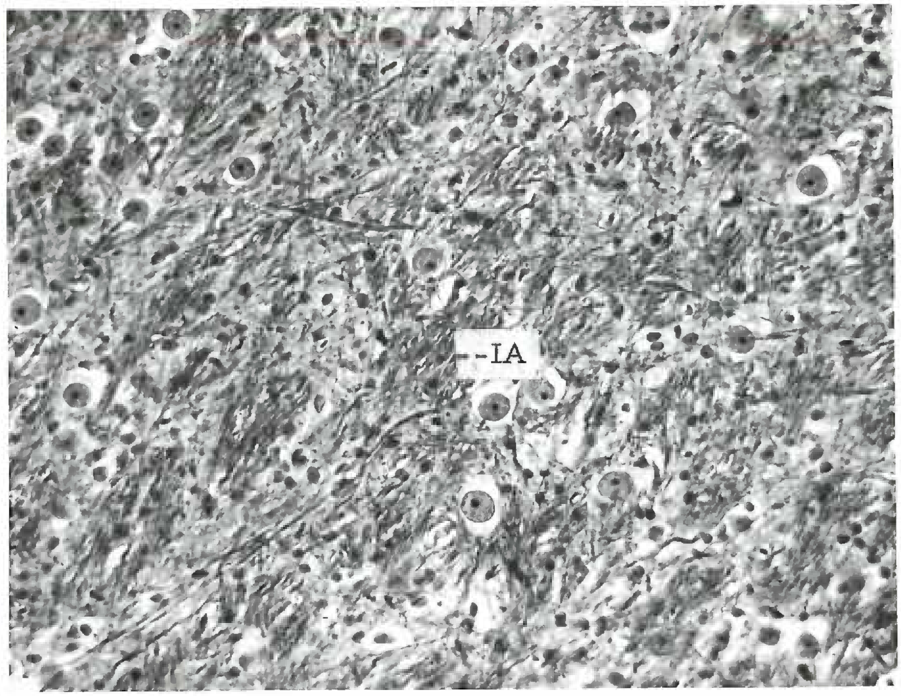


PLATE XI.

Figure 32. Cat D-2. Photomicrograph of histological pattern of normal ventral tegmental nucleus of Bechterew. Note presence of bundles of intact afferent axons (IA), and normal preterminal fibers. Magnification 300 X. Intensified Protargol stain.

Figure 33. Cat D-2. Photomicrograph of deafferented contralateral ventral tegmental nucleus of Bechterew. Note absence of preterminal afferents to cell bodies, and decrease in pericellular terminals (DPA), associated with degeneration of afferent bundles of descending root (clumps) (DA). Magnification 300 X. Intensified Protargol stain.

32.



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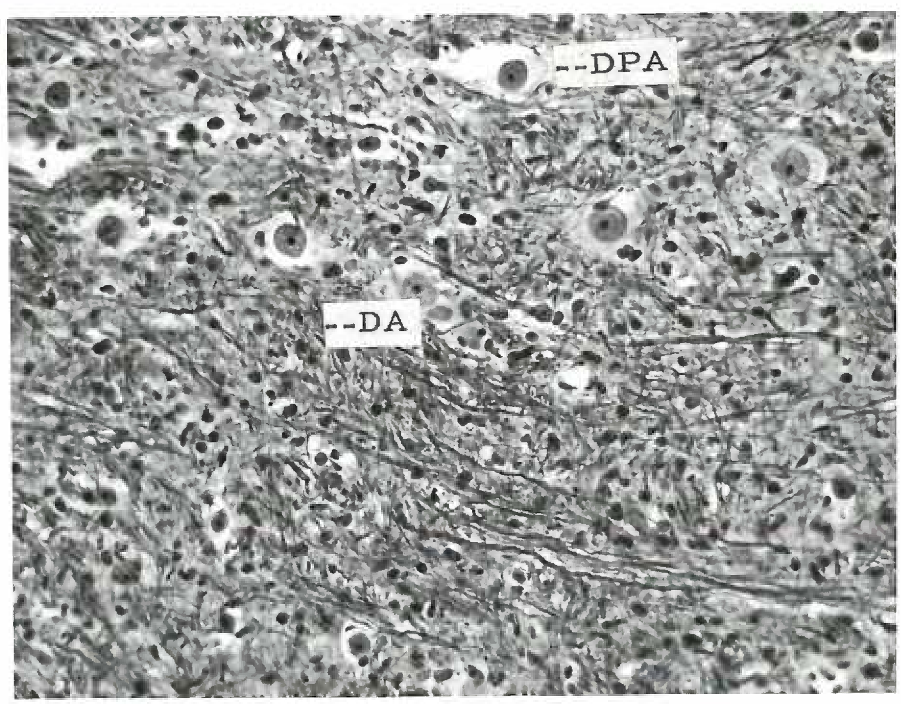

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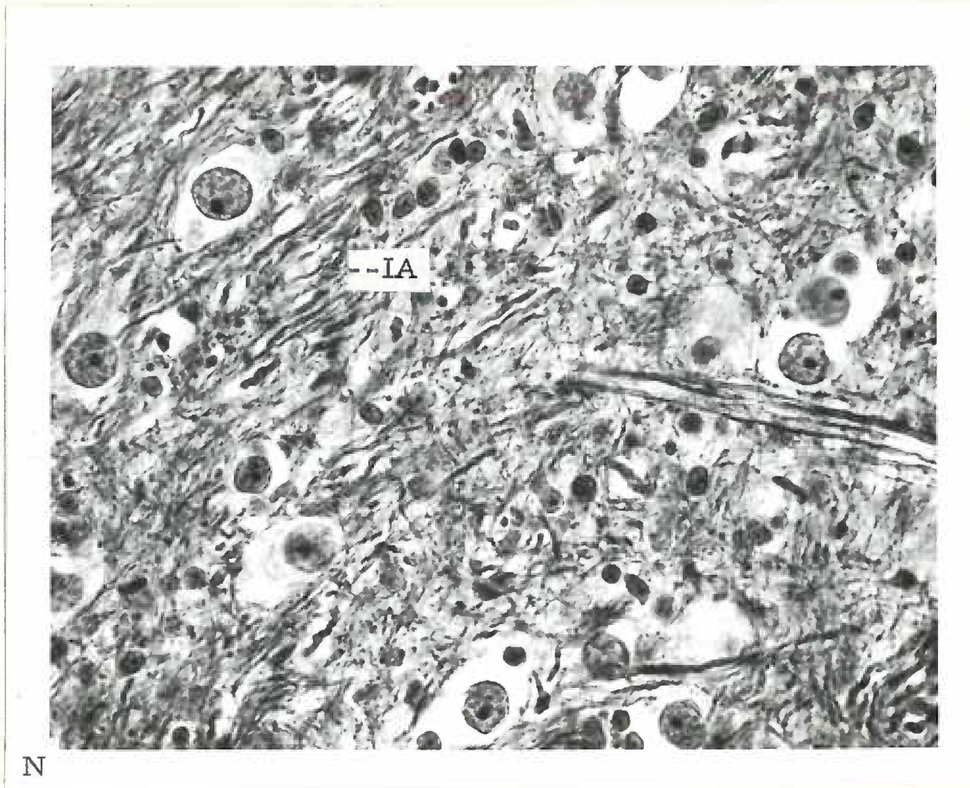
PLATE XII.

Figure 34. Cat D-2. Photomicrograph of histological pattern of normal ventral tegmental nucleus of Bechterew. Note presence of intact afferent terminations (IA). Magnification 500 X. Intensified Protargol stain.

Figure 35. Cat D-2. Photomicrograph of degenerated contralateral ventral tegmental nucleus of Bechterew. Note absence of preterminal afferents (DA), and abundance of terminal axon granular debris. Magnification 500 X. Intensified Protargol stain.

34.



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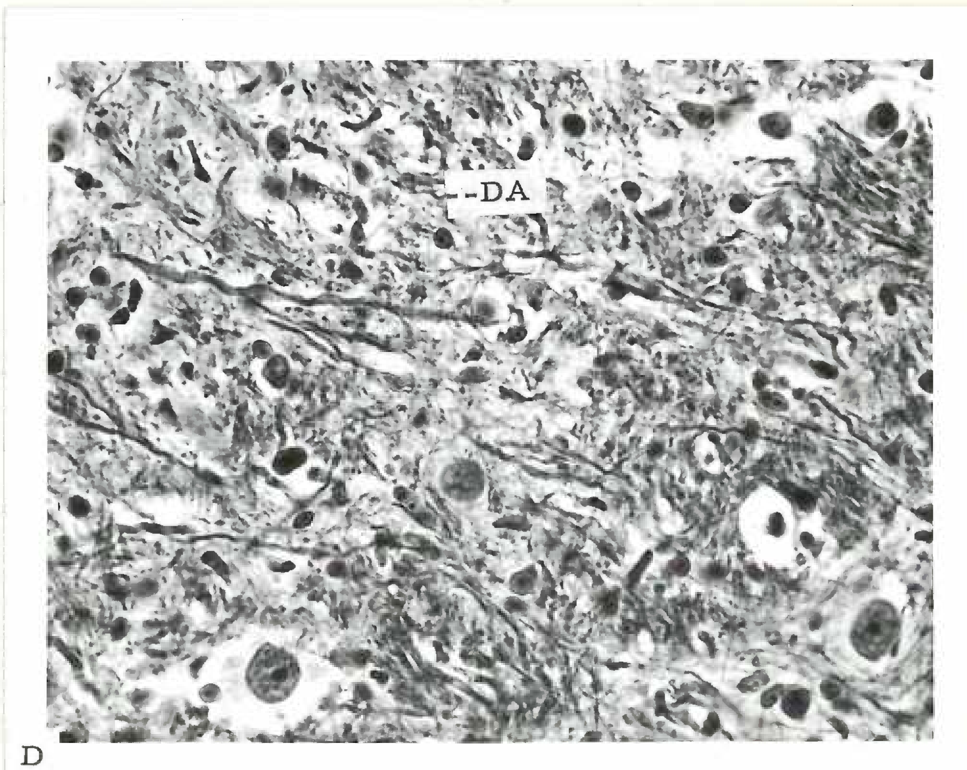
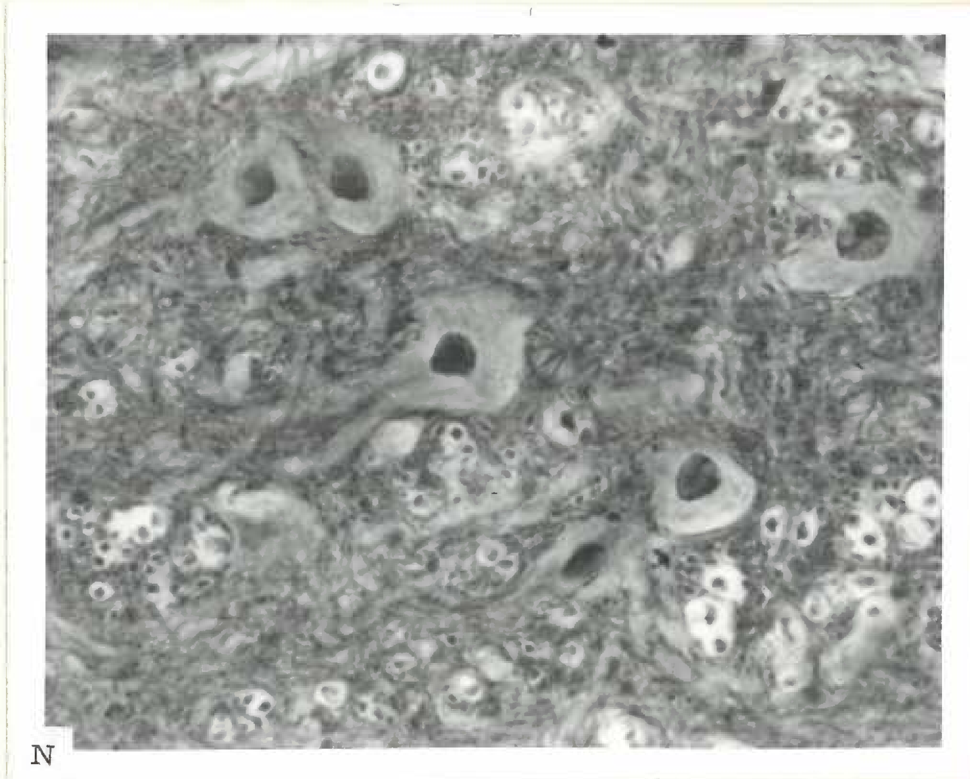


PLATE XIII.

Figure 36. Cat D-2. Photomicrograph of histological pattern of normal ventral tegmental nucleus of Bechterew. Note intact neuropil and cell bodies. Magnification 500 X. Intensified Protargol stain.

Figure 37. Cat D-2. Photomicrograph of degenerated contralateral ventral tegmental nucleus of Bechterew. Note terminal axon granular debris, and shrunken appearance of cell bodies. Magnification 500 X. Intensified Protargol stain.

36.



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