# EXPERIMENTAL STUDIES OF VESTIBULAR AND CEREBELLAR INTERCONNECTIONS IN THE CAT

by

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(Professor in Charge of Thesis)

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(Chairman, Graduate Council)

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To Dr. William A. Stotler, who has extended to me an enjoyable and valuable educational experience.

# INTRODUCTION

The initial impetus was given to vestibular investigation in 1825 when Flourens (14) first demonstrated that the entire internal ear was not solely auditory in function as previously supposed. By disturbing the semicircular canals, certain signs of cerebellar excitation could be elicited suggesting a functional relationship between the ear and the cerebellum. The demonstration of this relationship has subsequently resulted in an imposing volume of experimental papers.

The vestibular nuclei were classically divided into four major components; the superior (nucleus of Becterew), lateral (nucleus of Deiter), medial (nucleus of Schwalbe), and inferior (descending) nucleus by Fuse (16). Brodal and Pompeiano ( 3 ) have described subdivisions and additional small cell groups in close proximity to the four major vestibular nuclei. Cajal ( 5 ) felt that the interstitial nucleus situated among the fibers of the vestibular nerve was an aberrant part of the lateral vestibular nucleus.

Larsell (23) has shown that the flocculo-nodular lobe of the cerebellum is intimately related to the vestibular apparatus. Although Lorente de Nó (24) had not observed primary vestibular fibers passing to the cerebellum, these fibers have been described by Cajal ( 5 ) in Golgi material

and by Larsell (21) and Whitlock (40) using silver impregnated material. In Marchi preparations, primary vestibular fibers projecting to the flocculus, nodulus, and the fastigial nucleus have been described by Ingvar (18) in the cat, Dow (10) in the rat and cat, and Whitlock (40) in birds. Dow (10) also made the further observation that there existed a homolateral projection to the uvula.

Studies of secondary vestibulo-cerebellar fibers employing normal silver impregnated material in the opossum, bat, and man by Larsell (21, 22, 23), in reptiles by Westen (39), and in birds by Whitlock (40) have shown the areas of termination to be the same as those of primary vestibular fibers. Larsell (21) working with the opossum was of the opinion that the superior and lateral vestibular nuclei are the major sources of secondary vestibular fibers, whereas Vores and Hoerr (36) working with the same animal indicate that the inferior and medial vestibular nuclei are the origins of these fibers. Brodal, Pompeiano, and Walberg (4) using kittens, made lesions involving the entire vermis of the cerebellum and both fastigial nuclei. They found no retrograde changes in the superior or lateral vestibular nuclei although changes were present in the medial and inferior vestibular nuclei. Carpenter, Bard and Alling (7) worked on adult cats and came to the same conclusions.

It has been well extablished for several decades that the fastigial nucleus projects upon the vestibular nuclei. Allen (1), Rasmussen (28), and other investigators using

the Marchi method had noted the bilaterality of the fastigial efferents. The efferent projections of the fastigial nucleus reach the vestibular nuclei via the fastigio-bulbar fibers in the juxtarestiform body homolaterally and be means of the uncinate fasciculus (hook bundle of Russell) contralaterally. Cohen, Sprague, and Chambers ( 9 ) using silver impregnation techniques to show terminal degeneration and Jansen and Jansen ( 20) employing the modified Gudden method to follow retrograde degeneration concluded that the fastigio-bulbar fibers were derived largely from the rostral half of the fastigial nucleus, while the uncinate fasciculus fibers were derived predominantly from the cells of the caudal half of the fastigial nucleus. Although no conclusive evidence of the presence of an afferent component to the vestibular nuclei from the interpositus or dentate nuclei has been offered, Cohen, Sprague, and Chambers ( 9 ) have indicated that the homolateral vestibular and reticular nuclei receive a small projection from the interpositus and dentate nuclei.

Neuroanatomists have known for many years that a major part of the "vestibular system" consisted of cerebellar components (30, 8 ). The majority of investigators feel that the cerebellum influences the vestibular nuclei by two distinct means; the cortico-vestibular fibers which are axones of Purkinge cells, and fastigio-vestibular fibers which arise from the deep cerebellar nucleus. Probst (26) suggested in 1902 that corticofugal fibers of the cerebellar

cortex pass to the lateral vestibular nucleus, although Clarke and Horsley ( 8 ) felt that all fibers leaving the cerebellum by way of the peduncles have their origin in one or the other of the deep cerebellar nuclei. With the exception of the studies by Dow (10, 11) on the efferent connections of the flocculo-nodular lobe, most authors have focused their attention on the efferent cortical projections to the deep cerebellar nuclei and have largely ignored the terminations in the vestibular nuclei. Relying on the Marchi method in the rat, cat, and monkey, Dow concluded that fibers from the nodulus project to all vestibular nuclei, while efferent floccular fibers terminate in the superior vestibular nucleus and the dorsal lateral aspect of the lateral vestibular nucleus. The publications of Allen ( 1 ), Rasmussen (28), Jansen and Brodal (19), and Eager (12) all indicate that such fibers emanating from the entire vermis and flocculus exist.

In Golgi material, Lorente de Nó ( 25) and Scheibel and Scheibel ( 31) found the vestibular nuclei to project upon the reticular formation. Following lesions of the vestibular Nuclei in cats, Szentágothai ( 34) was able to discern by means of the silver impregnation method degenerating fibers which terminate on cells in the reticular formation, chiefly homolateral in the pons and contralateral in the mesencephalon.

## MATERIAL AND METHODS

The brains of forty-four healthy adult cats were investigated. Operations were done employing aseptic conditions under light intraperitoneal pentobarbital anesthesia. Both electrocoagulative and clean surgical lesions were placed sterotaxically. Lesions were unilateral or bilateral and involved the following areas: cerebellar cortex, fastigial nucleus, interfastigial area, interpositus nucleus, brachium conjunctivum, uncinate fasciculus, juxtarestiform body, and vestibular nuclei.

The post-operative period allowed for degeneration to occur varied between four and nine days except in one instance when the post-operative period was twenty days. The cats were sacrificed with a lethal dose of intraperitoneal pentobarbital immediately followed by thoracotomy and pulsatile transcardiac perfusion with 1.5 liters of 15 per cent formalin through a Turner perfusion machine. The brains were then removed and immersed in 15 per cent formalin for a minimum period of four weeks.

Blocks of tissue cut in the coronal plane were dehydrated and embedded in paraffin. Serial sections, twenty microns thick, were cut with a rotatory microtome. Every fifth or tenth section was mounted and stained with

the Stotler intensified Protargol® method (33) and additionally in some instances with the Nissl method employing cresyl fast violet. Prior to employing the Stotler method, mounted sections were treated with potassium permanganate to potentiate the staining of both normal and degenerated element or were treated with potassium dichromate to enhance the staining quality of the degenerated elements while supressing the normal elements.

The silver impregnation method was excellent for demonstration of neuronal elements including normal and degenerated axones and boutons. Retrograde degeneration was characterized by chromatolysis, eccentric or absent nuclei, and a swollen homogeneous hyaline-like cytoplasm. Degenerated axones were swollen, fragmented, and abnormally argyrophilic and the degenerated preterminal and terminal fibers appeared as argyrophilic, finely granular stippled lines. Degenerated boutons appeared as black swollen dots or rings terminating on cells or their processes.

The Nissl stained material was originally employed to differentiate types of cells and to delineate nuclear boundaries as well as minor subdivisions of nuclei on a cytoarchitectonic basis. An additional use of the Nissl method was for observing retrograde changes in the neuron soma, which were characterized by eccentrically placed nuclei, swollen cytoplasm, and loss or alteration of Nissl substance.

While the presence of retrograde changes in a cell was

indicative of injury to its axone, the converse was not necessarily true; i.e. it was possible for an axone to be sectioned without resultant retrograde changes. This was especially true of certain resistant nuclear groups and may have been due to sustaining collaterals. Dark shrunken cells were interpreted as being the result of changes in osmolarity either in the agonal state, from functional effects or fixations artifact and were not accepted as evidence of retrograde degeneration (15).

## RESULTS

In each cat, the position and extent of the lesion and degeneration are illustrated by superimposition on representative sections of Weigert stained preparations.

Cat 431X Bilateral lesion; four day degeneration.

The lesion and resulting degeneration are summarized in Figure 1. The lesion extends horizontally through approximately the anterior half of the vermian cerebellar cortex. The deep cerebellar nuclei are not involved in the lesion.

Bilaterally, fine degenerating fibers appear chiefly in the lateral vestibular nuclei (Fig. 22), while the superior, medial, and inferior vestibular nuclei receive fewer fibers (Figs. 23, 24, 25). No large degenerating fibers are observed in the vestibular nuclei. In the anterior vermian cerebellar cortex there is a loss of many Purkinge cells and some of the Purkinge cells show chromatolytic changes. The fine cortico-vestibular projections exhibit degenerating fibers as well as a loss of fibers as they pass to the brain stem predominantly in the rostral-lateral area of the fastigial nucleus (Fig. 20, 21) and then disperse diffusely through the juxtarestiform body as the fibers approach the vestibular nuclei. Although

many fine degenerating fibers are present in close relationship primarily with the processes of the larger vestibular cells, no degenerating terminal boutons are demonstrable. A varying degree of degeneration of fine fibers in the vestibular nuclei is also seen in cats T12Y, 360, T9X, 353, 354, T7, and 297. No retrograde changes are seen in any of the vestibular nuclei.

The fastigial and interpositus nuclei contain many degenerating terminals, but exhibit no retrograde degeneration.

No degenerating fibers are observed leaving the cerebellum via the brachium conjunctivum. The interstitial nucleus of the vestibular nerve, medial longitudinal fasciculus, and reticular formation contain no degeneration.

Cat T12Y Unilateral lesion; five day degeneration.

The lesion and resulting degeneration are summarized in Figure 2. The anterior and posterior limits of the lesion are the brachium conjunctivum and cerebellar cortex respectively. Between these areas the fastigial nucleus, interpositus nucleus, inferior cerebellar peduncle, dorsal third of the superior vestibular nucleus, and the uncinate fasciculus are included in the lesion.

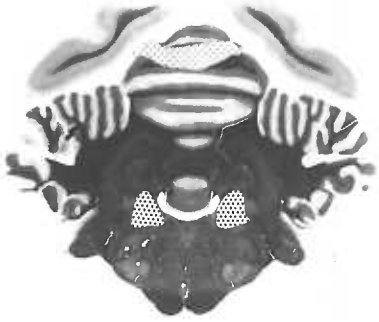
Degenerating fibers are found in all vestibular nuclei homolateral to the lesion. Both large and fine degenerating fibers are present in the lateral, superior, and inferior vestibular nuclei. A fine argyrophilic debris is seen in the medial vestibular nucleus. From the area of the

Figure 1

A series of eight photographs illustrating representative sections of cat 431X. The extent of the lesion is shown in A, B, C, D, E, F, and G. Note bilateral degeneration in all vestibular nuclei except the interstitial nucleus of the vestibular nerve. Cross hatching represents lesions. Stippling represents degeneration.

A

E



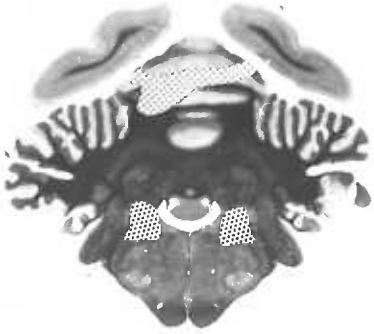
B

F

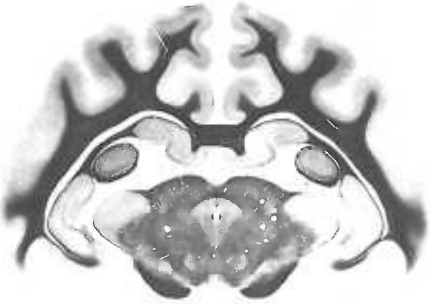
C

G

D



H



LESION

DEGENERATION

lesion occupied by the fastigial and interpositus nuclei, large degenerating fastigio-bulbar and interposito-bulbar fibers can be followed serially to the superior vestibular nucleus. Degeneration of the fastigio-bulbar tract with no degeneration of the interposito-bulbar tract is seen in cats 353, 354, and 352. Degeneration of the interposito-bulbar tract without accompanying degeneration of the fastigio-bulbar tract occurs in cat 360. Degeneration of both tracts concomitantly is present in cats T12Y, T9X, and 297.

The large degenerating fibers of the uncinate fasciculus which terminate in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus can be traced serially in a superior and cephalad direction as it courses just lateral to the vestibular nuclei to reach the area of the lesion at the level of the brachium conjunctivum. Degeneration of the uncinate fasciculus homolateral to the lesion is also seen in cats 360, T9X, T7, and 297.

The fine degenerating fibers which occur in all homolateral vestibular nuclei are similar to the type of degenerating fibers seen following lesions of the vermian cerebellar cortex as in cat 431X (Fig. 1), and may be due to interruption of the cortico-vestibular fibers as they pass through the area of the deep cerebellar nuclei. A similar interruption of cortico-vestibular fibers resulting in degeneration of fine fibers in the vestibular nuclei

to varying degrees is present in cat 431X, 360, T9X, 353, 354, T7, and 297.

That vestibulo-cerebellar fibers have been interrupted by the lesion is indicated by the presence of marked chromatolysis in the inferior vestibular nucleus. Retrograde degeneration following a lesion incorporating the vestibulo-cerebellar fibers is seen in the lateral and inferior vestibular nuclei in cat 297 and in the lateral vestibular nucleus in cat T9X. No retrograde changes are seen in the superior or medial vestibular nuclei.

On the contralateral side the large degenerating fibers can be followed serially from the interfastigial area where the uncinate fasciculus is dispersed widely to the superior cerebellar peduncle where it occupies its position as a discrete bundle of fibers just dorsal to the brachium conjunctivum. In Figure 13 the uncinate fasciculus shows degeneration and a loss of fibers as it occupies this position. The uncinate fasciculus is closely applied to the dorsal convexity of the brachium conjunctivum and from its lateral margin courses obliquely in a ventral and caudal direction along the lateral aspect of the vestibular nuclei. The large degenerating fibers of the uncinate fasciculus then sweep medially to terminate in the ventral portion of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus (Fig. 14). Degeneration of the uncinate fasciculus contralateral to the side of the lesion also seen in cat T9X

and 352. No degeneration is observed in the superior, medial, dorsal part of the lateral, and caudal part of the inferior vestibular nuclei. No retrograde degeneration is noted in the contralateral vestibular nuclei.

The large degenerating fibers of the brachium conjunctivum can be traced through the decussation of the brachium conjunctivum from the superior cerebellar peduncle to the contralateral red nucleus. At this level a few large degenerating fibers of the brachium conjunctivum turn dorsally to enter the oculomotor nuclei of the contralateral side (Fig. 15). The degenerating fibers of the brachium conjunctivum can also be traced to the contralateral red nucleus in cats 360, T9X, and T7, but in only cat 360 can degenerating fibers be found in the oculomotor nuclei.

An isthmus of cells between the lateral vestibular nucleus and the interstitial nucleus of the vestibular nerve serves to make these two nuclear groups continuous (Fig. 16).

No changes are evident in the interstitial nucleus of the vestibular nerve, medial longitudinal fasciculus, or the reticular formation bilaterally.

Cat 360 Unilateral lesion; nine day degeneration.

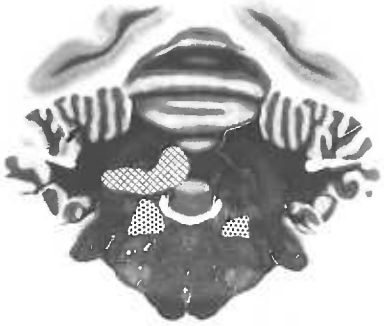
The lesion and resulting degeneration are summarized in Figure 3. The lesion (Fig. 17) includes a small needle tract through the posterior cerebellar cortex, the interpositus nucleus, the brachium conjunctivum, and the

Figure 2

A series of eight photographs illustrating representative sections of cat T12Y. The extent of the lesion is shown in A, B, C, D, E, F, and G. Note degeneration in the vestibular nuclei bilaterally (A-F), in the homolateral superior vestibular nucleus (G), and in the contralateral red nucleus and oculomotor nuclei (H).

A

E



B

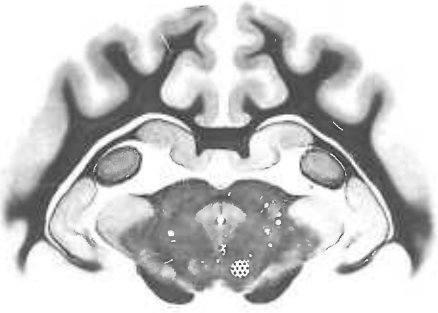
F

C

G

D

H



LESION

DEGENERATION

uncinate fasciculus.

The degeneration in the vestibular nuclei is limited to the homolateral side, where a minimal amount of fine argyrophilic debris is present in all vestibular nuclei. The large degenerating fibers are found in the superior vestibular nucleus, dorso-lateral part of the lateral vestibular nucleus, ventral part of the lateral vestibular nucleus, and rostral part of the inferior vestibular nucleus. From the area of the lesion occupied by the interpositus nucleus, large degenerating interposito-bulbar fibers can be traced to the dorso-lateral part of the lateral vestibular nucleus. The dorso-medial portion of the lateral vestibular nucleus is free of degeneration of large fibers, however there is marked degeneration in the dorso-lateral aspect of the lateral vestibular nucleus (Fig. 18). In cats 353, 354, and 352 the fastigio-bulbar tract is degenerated and the interposito-bulbar fibers are intact. In these cases the dorso-medial part of the lateral vestibular nucleus shows degenerating terminals and the dorso-lateral part of the lateral vestibular nucleus contains no degenerating terminal fibers. The fastigial nucleus and fastigio-bulbar tract in this case are spared by the lesion and are free of degeneration.

The large degenerating fibers of the uncinate fasciculus which terminate in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus can be followed serially in a

superior and cephalad direction as it courses just lateral to the vestibular nuclei to reach the area of the lesion at the level of the brachium conjunctivum.

The presence of fine degenerating fibers is chiefly limited to the lateral vestibular nucleus and is similar to the type of degenerating fibers seen following lesions of the vermian cerebellar cortex as in cat 431X (Fig. 1). The lesion apparently does not disrupt as many cortico-vestibular fibers as they pass the area of the deep cerebellar nuclei as do lesions which extend more medially into the fastigial nucleus (Figs. 20, 21). The relatively long period allowed for degeneration to occur may also be a factor accounting for the sparseness of fine degenerating fibers because the fine terminal degeneration is cleared more rapidly than the coarse degenerating fibers. No retrograde degeneration is noted in the vestibular nuclei of either side.

The degenerating fibers of the brachium conjunctivum can be followed through the decussation of the brachium conjunctivum from the lesion in the superior cerebellar peduncle to the contralateral red nucleus. Although a continuity of degenerating fibers from the brachium conjunctivum is not demonstrable, degenerating fibers appear in the contralateral oculomotor nuclei (Fig. 19).

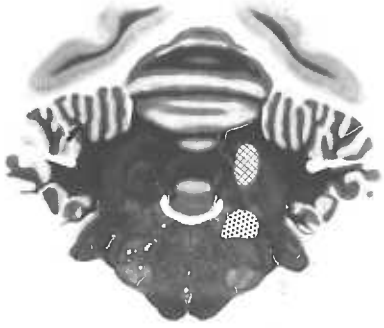
No alteration of normal cytoarchitecture is seen in the interstitial nucleus of the vestibular nerve, reticular formation, or medial longitudinal fasciculus of either side.

Figure 3

A series of eight photographs illustrating representative sections of cat 360. The extent of the lesion is shown in A, B, C, D, E, F, and G. Note degeneration in the homolateral vestibular nuclei (A-G) and contralateral red nucleus and oculomotor nuclei (H).

A

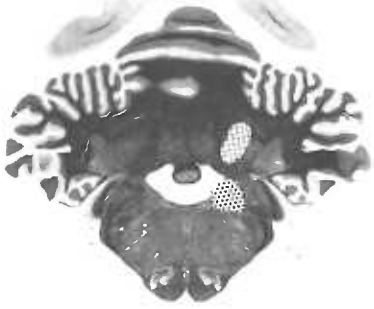
E



B

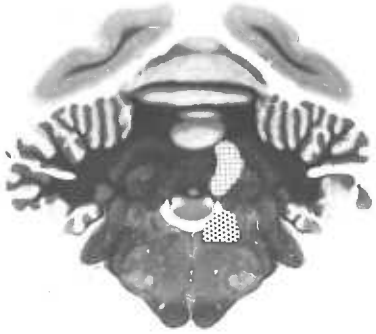
F

C

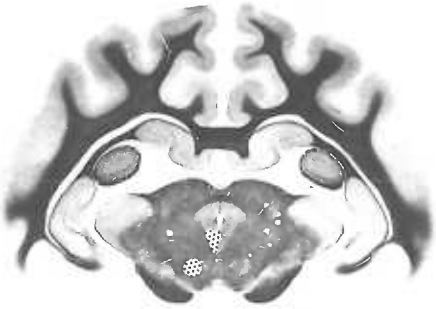


G

D



H



LESION

DEGENERATION

Cat T9X Unilateral lesion; nine day degeneration.

The lesion and resulting degeneration are summarized in Figure 4. The lesion was made through the posterior cerebellar vermis and involves the fastigial nucleus, interpositus nucleus, uncinate fasciculus, and brachium conjunctivum.

Homolaterally, both large and fine degenerating fibers are present in the lateral (Fig. 11), superior, and inferior vestibular nuclei, whereas only fine degenerating fibers occur in the medial vestibular nucleus (Fig. 12). The course of the large degenerating fastigio-bulbar and interposito-bulbar fibers can be traced serially through the juxtarestiform body from the area of the fastigial and interpositus nuclei involved in the lesion to the superior vestibular nucleus and the dorsal part of the lateral vestibular nucleus. A similar pattern of degeneration obtains in cats T12Y, T9X, and 297.

The large degenerating fibers in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus can be followed in a superior and cephalad direction along the lateral side of the vestibular nuclei to the area of the lesion. These fibers have the same pattern of distribution as the fibers of the uncinate fasciculus of the contralateral side.

The fine degenerating fibers found in all homolateral vestibular nuclei are similar to the type of degenerating fibers seen following lesions of the vermian cerebellar

cortex as in cat 431X (Fig. 1), and may be due to interruption of the cortico-vestibular fibers as they pass through the area of the deep cerebellar nuclei. A varying degree of degeneration of fine fibers in the vestibular nuclei following interruption of the cortico-vestibular fibers is seen in cats T12Y, 360, T9X, 353, 354, T7, and 297.

Some of the axones of the vestibulo-cerebellar tract which originate in the lateral vestibular nucleus are included in the lesion and the lateral vestibular nucleus (Fig. 10) exhibits the resultant chromatolysis. Retrograde degeneration resulting from a lesion involving the vestibulo-cerebellar fibers is seen in both the lateral and inferior vestibular nuclei in cats T12Y and 297. The superior, medial, and inferior vestibular nuclei do not show retrograde changes.

On the contralateral side large degenerating fibers can be followed serially from the interfastigial area where the uncinate fasciculus is dispersed widely to the superior cerebellar peduncle where it occupies its position as a discrete bundle of fibers just dorsal to the brachium conjunctivum. The uncinate fasciculus is applied closely to the dorsal convexity of the brachium conjunctivum and from its lateral margin courses obliquely in a ventral and caudal direction along the lateral aspect of the vestibular nuclei. The large degenerating fibers of the uncinate fasciculus then sweep medially to terminate in the ventral

portion of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus. Degeneration of the uncinate fasciculus contralateral to the lesion is also present in cats T12Y and 352. No degeneration is observed in the superior, medial, dorsal part of the lateral, and caudal half of the inferior vestibular nuclei. No retrograde degeneration is seen in the contralateral vestibular nuclei.

The degenerating fibers of the brachium conjunctivum on the side of the lesion can be traced to the contralateral red nucleus.

No degenerative changes are observed in the interstitial nucleus of the vestibular nerve, reticular formation, medial longitudinal fasciculus, or oculomotor nuclei of either side.

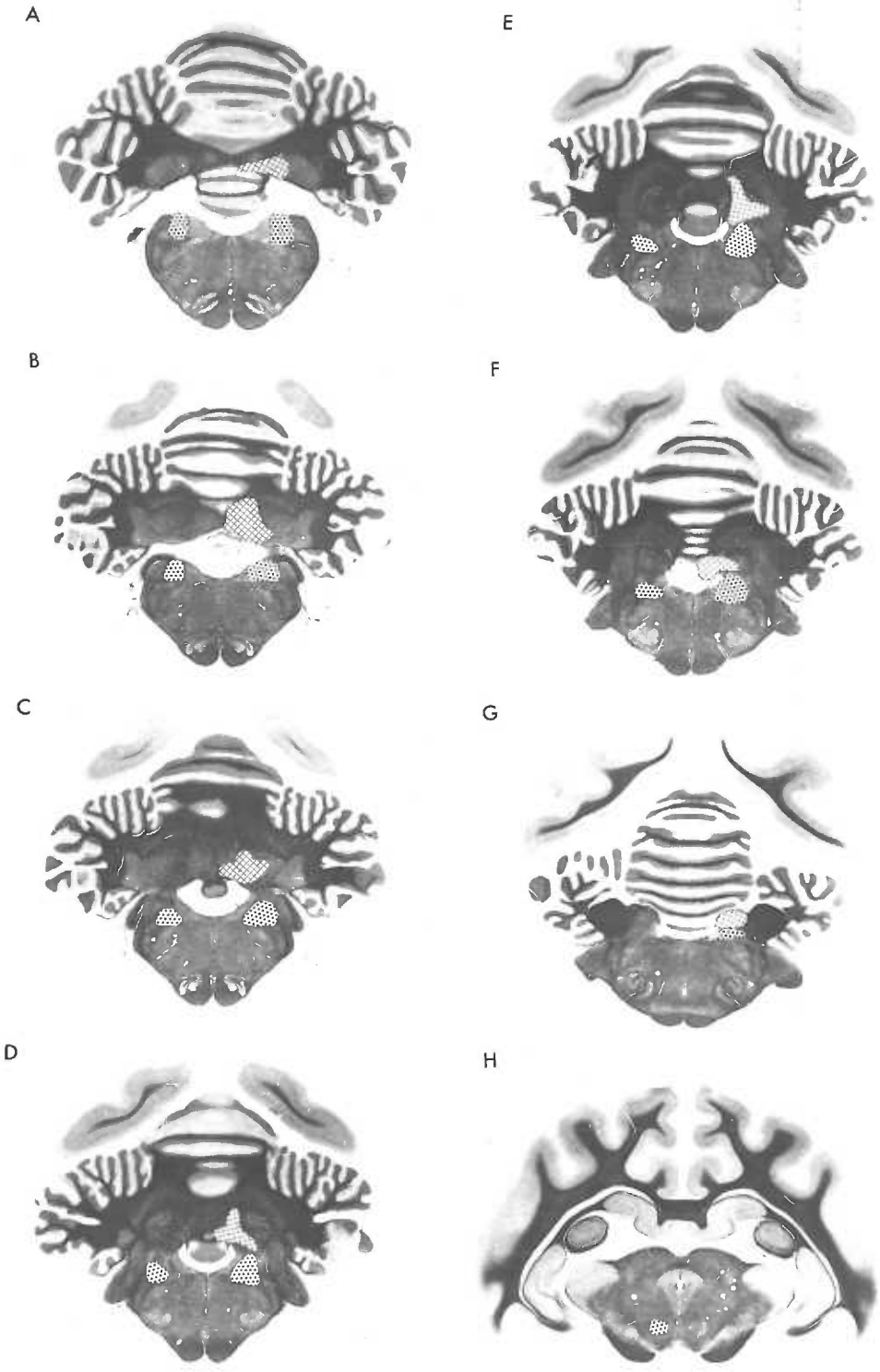
Cat 353 and 354 Unilateral lesion; eight and six day degeneration respectively.

The lesion and resulting degeneration of these two cats are summarized in Figure 5 and are sufficiently similar to be considered together. A small needle tract through the posterior cerebellar cortex and the juxtarestiform body are involved in the lesion (Fig. 26).

The degeneration is limited to the homolateral vestibular nuclei. Large as well as fine degenerating fibers occur in the superior (Fig. 27) and dorso-medial portion of the lateral vestibular nucleus (Fig. 28). The dorso-lateral part of the lateral vestibular nucleus

Figure 4

A series of eight photographs illustrating representative sections of cat T9X. The extent of the lesion is shown in A, B, C, D, E, F, and G. Note degeneration in the vestibular nuclei bilaterally (A-F), in the homolateral superior vestibular nucleus (G), and in the contralateral red nucleus (H).




LESION

DEGENERATION

is free of degeneration in contrast to the abundant degeneration present in the dorso-medial part of the lateral vestibular nucleus (Fig. 28). The interpositus nucleus and the interposito-bulbar fibers are spared by the lesion. When the interposito-bulbar fibers are degenerated and the fastigio-bulbar fibers spared of degeneration as in cat 360, the dorso-medial part of the lateral vestibular nucleus is free of degeneration and the dorso-lateral part of the lateral vestibular contains numerous degenerating terminal fibers. The uncinate fasciculus is not involved in the lesion and consequently no large degenerating fibers can be seen in the ventral part of the lateral vestibular nucleus or in the inferior vestibular nucleus. A few fine degenerating fibers are also seen in the medial vestibular nucleus, but not in the inferior vestibular nucleus. The presence of fine degenerating fibers is chiefly limited to the dorso-medial part of the lateral vestibular nucleus and the medial vestibular nucleus. These degenerating fibers are similar to the type of degenerating fibers seen following lesions of the vermian cerebellar cortex as described in cat 431X (Fig. 1) and may be due to the interruption of the cortico-vestibular fibers as they pass through the juxtarestiform body. No retrograde changes are noted in the vestibular nuclei. Degeneration of the "retraction ball type" is seen in the lateral vestibular nucleus near the lesion (Fig. 29) and is similar to the "retraction ball type" of

degeneration which occurs when axones of the Purkinge cells are interrupted in the cerebellum (Fig. 30).

No terminal degeneration is seen in the fastigial nuclei. No changes are noted in the medial longitudinal fasciculus, adjacent reticular formation, or interstitial nucleus of the vestibular nerve.

Cat 352 Unilateral lesion; six day degeneration.

The lesion and resulting degeneration are summarized in Figure 6. The lesion is small, well localized in the fastigial nucleus, and extends just to the rostral pole of the fastigial nucleus (Fig. 31).

Degenerating fibers of the fastigio-bulbar tract predominantly of the large type are noted originating from the area of the fastigial nucleus involved in the lesion and traversing the juxtarestiform body to terminate in the homolateral superior vestibular nucleus and the dorso-medial part of the lateral vestibular nucleus (Fig. 32). The dorso-lateral portion of the lateral vestibular nucleus shows no terminal degeneration. The homolateral medial, inferior, and ventral part of the lateral vestibular nuclei show no degeneration. No retrograde degeneration is noted in the homolateral vestibular nuclei.

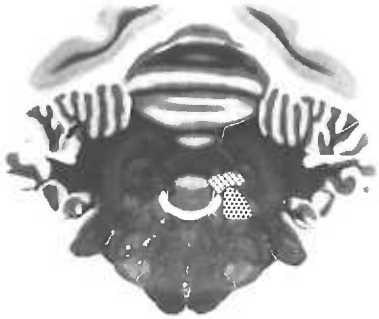
On the contralateral side the large degenerating fibers can be followed from the area of the lesion involving the fastigial nucleus where the uncinate fasciculus crosses the midline as widely dispersed fibers, to the

Figure 5

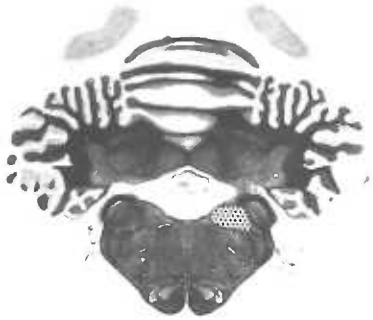
A series of eight photographs illustrating representative sections of cat 353 and 354. The extent of the lesion is shown in C, D, E, and F. Note degeneration in the homolateral vestibular nuclei (A-G).

A

E

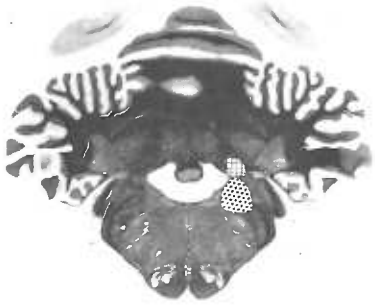


B



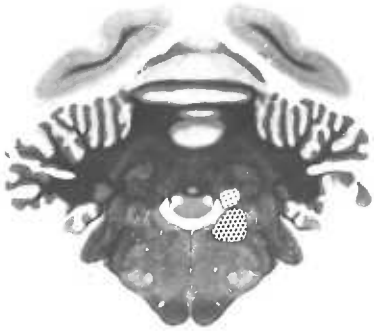
F

C

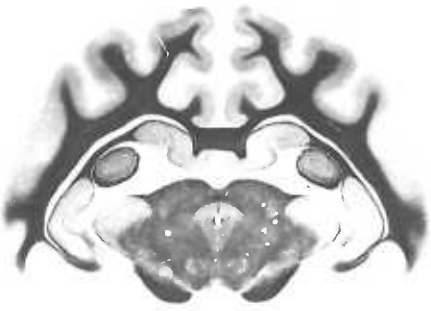


G

D



H



LESION

DEGENERATION

superior cerebellar peduncle where it occupies its position as a discrete bundle of fibers just dorsal to the brachium conjunctivum. The uncinate fasciculus is closely applied to the dorsal convexity of the brachium conjunctivum and from its lateral margin courses obliquely in a ventral and caudal direction along the lateral aspect of the vestibular nuclei. The large degenerating fibers of the uncinate fasciculus than sweep medially to terminate in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus (Fig. 33). Degeneration of the uncinate fasciculus contralateral to the side of the lesion is also observed in cats T12Y and T9X. No degeneration is observed in the superior , medial, dorsal part of the lateral, and caudal part of the inferior vestibular nuclei. No retrograde degeneration is noted in the contralateral vestibular nuclei.

No degeneration is observed in the medial longitudinal fasciculus, reticular formation, or interstitial nucleus of the vestibular nerve.

Cat T7 Unilateral lesion; eight day degeneration.

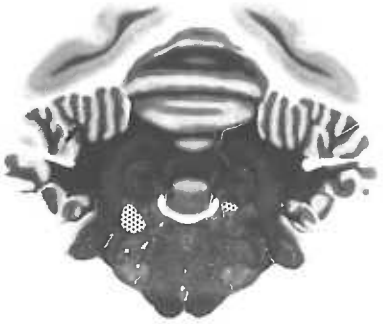
The lesion and resulting degeneration are summarized in Figure 7. The following structures are involved in the lesion; a needle tract in the posterior cerebellar cortex, juxtarestiform body, dorsal part of the superior vestibular nucleus, ventral part of the interpositus nucleus, brachium conjunctivum, and uncinate fasciculus.

Figure 6

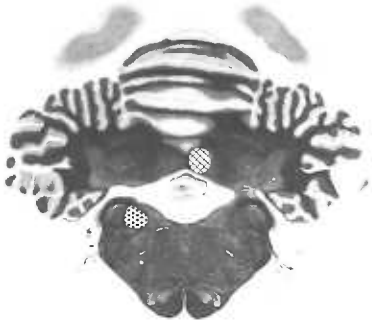
A series of eight photographs illustrating representative sections of cat 352. The extent of the lesion is shown in A, B, C, and D. Note degeneration in the vestibular nuclei (A-G).

A

E



B

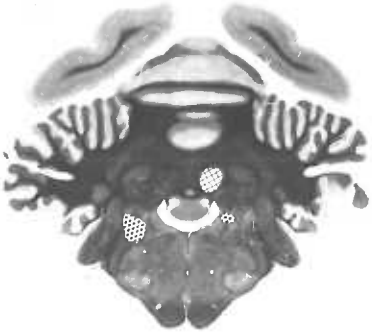


F

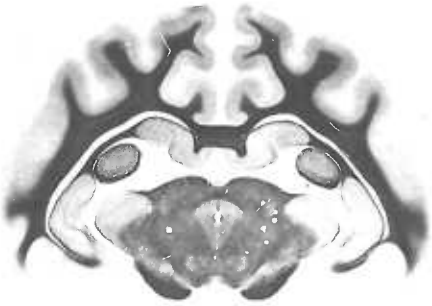
C

G

D



H



LESION

DEGENERATION

Homolaterally, large and fine degenerating fibers and terminal boutons are seen in the superior, lateral (Figs. 34, 35), and inferior vestibular nuclei. A moderate amount of argyrophilic debris is present in the medial and inferior vestibular nuclei. The course of the large degenerating fibers can be followed from the superior vestibular nucleus and the dorsal part of the lateral vestibular nucleus dorsally to the lesion. The large degenerating fibers of the uncinate fasciculus in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus can be followed serially in a superior and cephalad direction along the lateral aspect of the vestibular nuclei to the area of the lesion at the level of the brachium conjunctivum.

The fine degenerating fibers found in all vestibular nuclei are similar to the type of degenerating fibers seen following lesions of the vermian cerebellar cortex as in cat 431X (Fig. 1) and may be due to the lesion involving the cortico-vestibular fibers just dorsal to the vestibular nuclei. No retrograde degeneration is seen in the vestibular nuclei of this cat.

The vestibular nuclei of the contralateral side appear free of degenerative changes.

The contralateral medial longitudinal fasciculus show a few degenerating fibers. The large degenerating fibers of the brachium conjunctivum can be traced through the

decussation of the brachium conjunctivum from the lesion in the superior cerebellar peduncle to the contralateral red nucleus. No degenerating fibers of the brachium conjunctivum or medial longitudinal fasciculus are seen to enter the oculomotor nuclei in this case.

No degeneration is exhibited by the reticular formation nor the interstitial nucleus of the vestibular nerve.

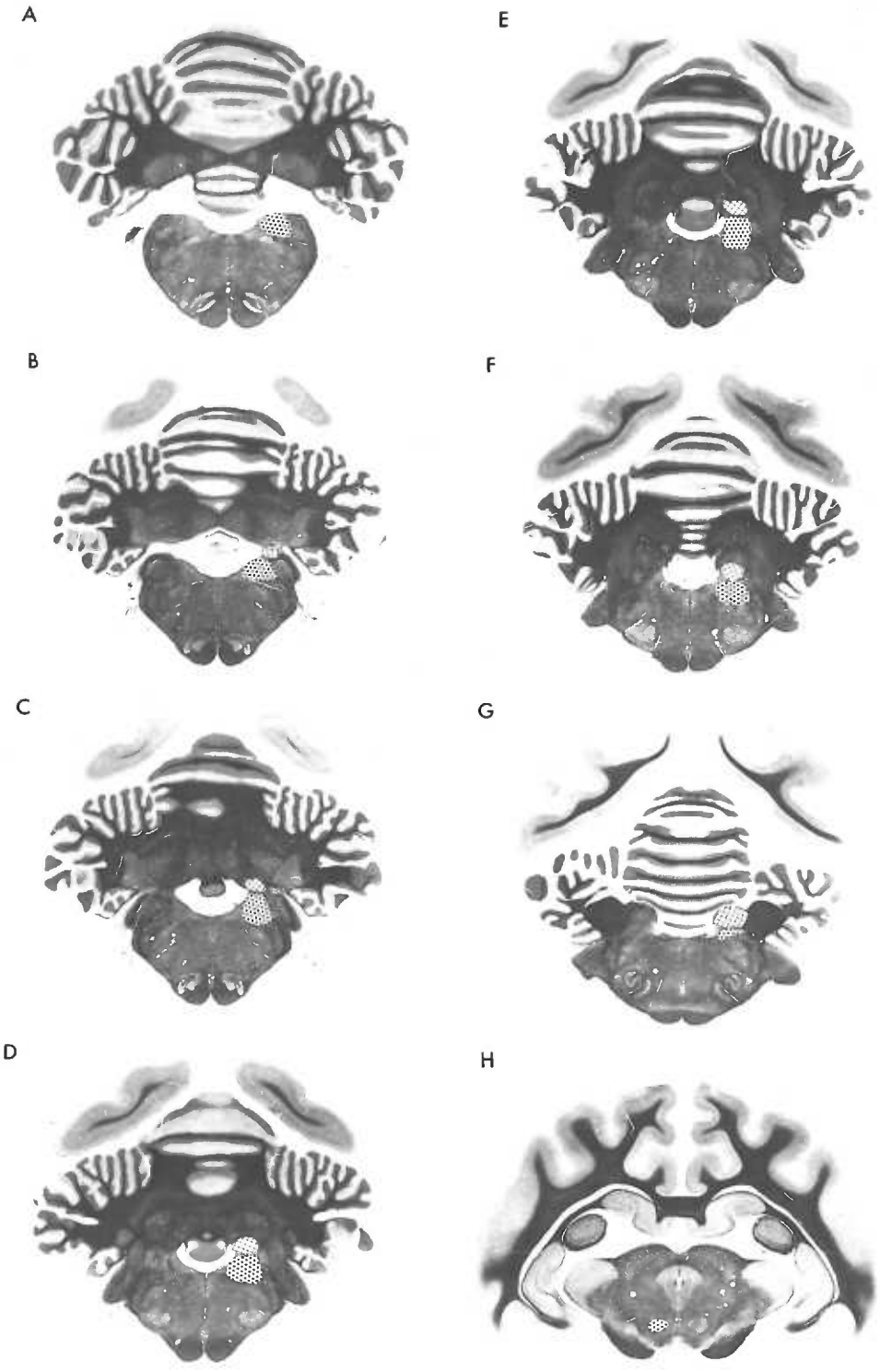
Cat 297 Unilateral lesion; six day degeneration.

The lesion and resulting degeneration are summarized in Figure 8. The lesion involves the posterior cerebellar cortex, interpositus nucleus, juxtarestiform body, uncinate fasciculus, and cortico-vestibular fibers.

Degenerating fibers occur in all vestibular nuclei homolateral to the lesion. Both large and fine degenerating fibers are seen in the lateral, superior, and inferior vestibular nuclei. The medial vestibular nucleus contains a fine argyrophilic debris. From the area of the vertically placed lesion through the interpositus nucleus, large degenerating fastigio-bulbar and interposito-bulbar fibers can be traced serially to the superior vestibular nucleus and the dorsal part of the lateral vestibular nucleus. The large degenerating fibers of the uncinate fasciculus which terminate in the ventral part of the lateral vestibular nucleus and the rostral part of the inferior vestibular nucleus can be traced serially in a superior and cephalad direction as it runs just lateral to the vestibular nuclei to reach and swing over the dorsal convexity of the brachium

Figure 7

A series of eight photographs illustrating representative sections of cat T7. The extent of the lesion is shown in B, C, D, E, F, and G. Note degeneration in the homolateral vestibular nuclei (A-G), and contralateral red nucleus (H).




LESION

DEGENERATION

conjunctivum to gain the area of the lesion.

The fine degenerating fibers which occur in all homolateral vestibular nuclei are similar to the type of degenerating fibers seen following lesion of the vermian cerebellar cortex as in cat 431X (Fig. 1) and may be due to involvement of the cortico-vestibular fibers as they pass through the lateral fastigial area (Figs. 20, 21).

That fibers of the vestibulo-cerebellar tract have been interrupted by the lesion is indicated by the presence of marked chromatolysis in the lateral vestibular nucleus (Figs. 36, 38) and inferior vestibular nucleus (Figs. 37, 38). Chromatolytic cellular changes following a lesion incorporating the vestibulo-cerebellar projections are also seen in the lateral and inferior vestibular nuclei in cat T12Y and in only the lateral vestibular nucleus in cat T9X. The lateral extent of the chromatolytic cells in the vestibular nuclei is shown in Figure 39.

The contralateral vestibular nuclei are entirely free of degeneration.

Retrograde degeneration of the cells in the contralateral fastigial nucleus following section of the uncinate fasciculus is manifested by the alteration of Nissl substance (Fig. 40). The cells of the fastigial nucleus which demonstrate this retrograde change are diffusely scattered throughout the entire extent of the nucleus. Retrograde degeneration is limited principally to the rostral half of the fastigial nucleus on the homolateral side.

No changes are noted in the medial longitudinal fasciculus, adjacent reticular formation, and interstitial nucleus of the vestibular nerve.

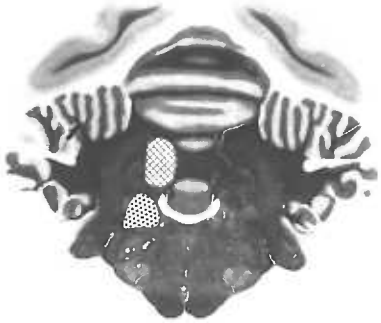
A diagrammatic partial summary of the results of this study is shown in Figure 9.

Figure 8

A series of eight photographs illustrating representative sections of cat 297. The extent of the lesion is shown in A, B, C, D, E, F, and G. Note the degeneration in the homolateral vestibular nuclei (A-G).

A

E



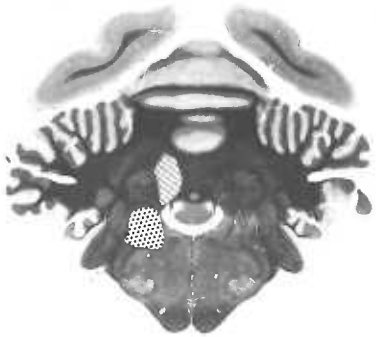
B

F

C

G

D



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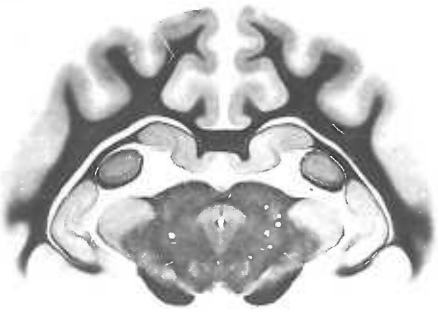


LESION

DEGENERATION

Figure 9

A schematic diagram representing a partial summary of the vestibular and cerebellar interconnections in the cat. Unbroken lines represent large fibers and broken lines represent fine fibers.

TABLE OF ABBREVIATIONS

D Dentate nucleus

F Flocculus

FA Fastigial nucleus

I Inferior vestibular nucleus

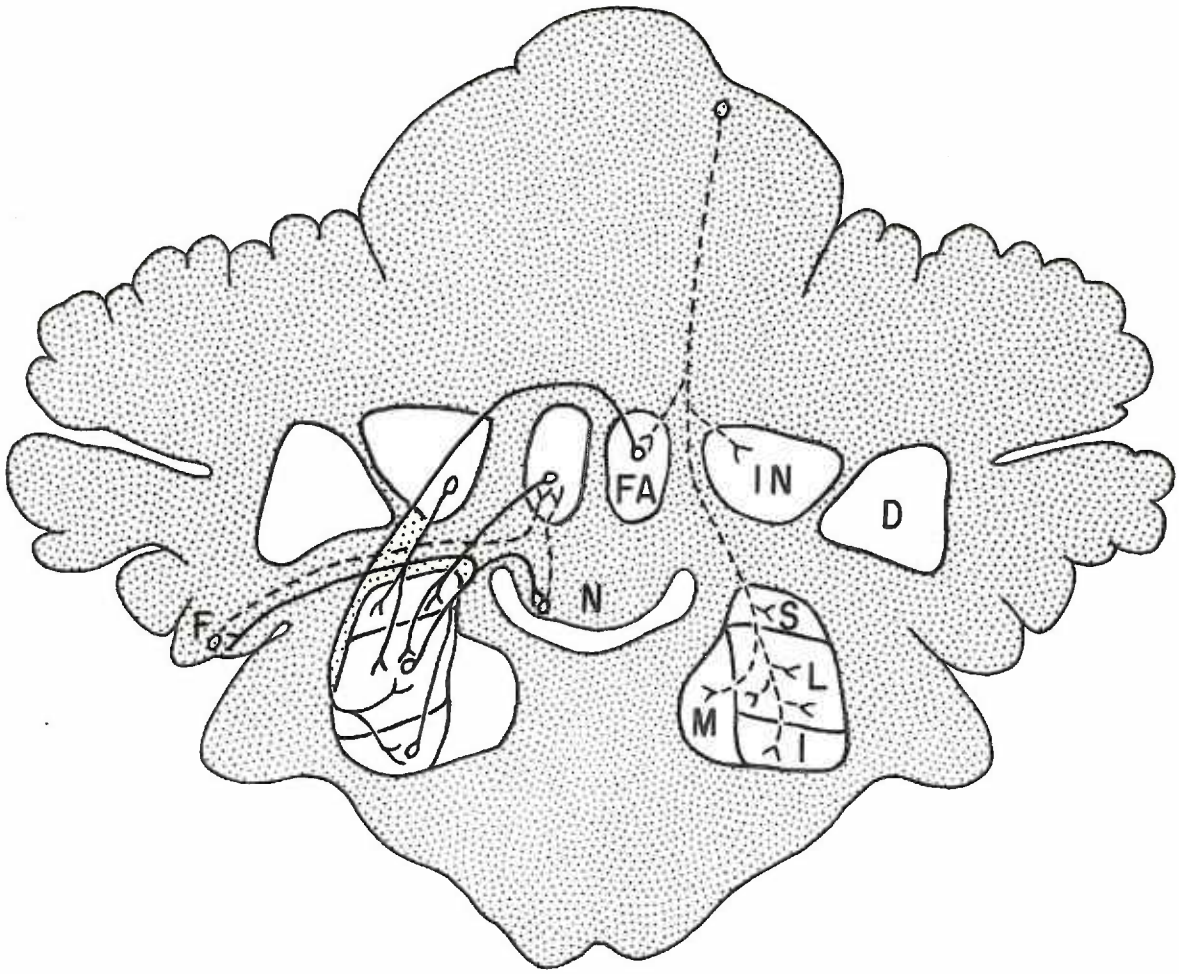
IN Interpositus nucleus

L Lateral vestibular nucleus

M Medial vestibular nucleus

N Nodulus

S Superior vestibular nucleus


FA
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I

# DISCUSSION

## Cortico-Vestibular Connections

Clarke and Horsley ( 8 ) concluded from their anatomical investigations in 1905 that axones of the cerebellar cortex make synaptic connections with one or another of the deep cerebellar nuclei and that none of the axones of the cerebellar cortex leave the cerebellum. However, the later experimental works of Allen ( 1 ), Bender ( 2 ), Rasmussen (28), Dow (10, 11), Jansen and Brodal (19), and Eager (12) have shown that the vermis and Flocculus project direct fibers to the vestibular nuclei. It is the concensus among most investigators in this field that the cortico-vestibular fibers pass to the brainstem via the inferior cerebellar peduncle, and with the exception of the flocculus no cortico-vestibular fibers arise from the cerebellar hemispheres.

From studying Marchi preparations of the guinea pig, Allen ( 1 ) reported that all of the efferent cerebellar cortex fibers are distributed to the deep cerebellar nuclei except for a few fibers from the vermis which pass medial to the restiform body to reach the lateral vestibular nucleus in what was designated as the "inner cerebellar funiculi". Cerebellar cortex fibers were also found to

pass to the dorsal reticular formation. A few fibers as well were said to pass to the medial longitudinal fasciculus.

Employing the Marchi method in cats, Rasmussen (28) noted that the vermis discharged many fibers into the fastigial nucleus and some fibers into the vestibular nuclei. Cerebellar cortical lesions caused no degeneration in the brachium conjunctivum.

Walberg and Jansen (37) and Brodal, Pompeiano, and Walberg ( 4 ) noted that a considerably larger contribution of cortico-vestibular fibers are derived from the anterior lobe than is derived from the posterior lobe. The cortico-vestibular fibers were found to be homolateral projections which terminate in the dorsal half of the lateral vestibular nucleus. In the inferior vestibular nucleus the heaviest concentration of degenerating terminals was found in the rostral portion. In the ventral half of the lateral vestibular nucleus no degenerating fibers were found. In the superior vestibular nucleus a few pericellular arborizations of fine degenerating fibers were observed on some cells. These authors reported that the cortico-vestibular fibers terminate on all types of cells, but the majority make contact with the large cells, especially their dendrites. No degenerating fibers were seen in the medial vestibular nucleus, interstitial nucleus of the vestibular nerve, brachium conjunctivum, or reticular formation.

Some of the cortico-vestibular fibers were thought to be bilateral projections by Eager (12) who reported

that following unilateral vermal cerebellar cortex lesions, bilateral degeneration appeared in the fastigial nuclei and lateral vestibular nuclei. When lesions involved the paravermal cortex, degenerating fibers appeared in the interpositus nucleus throughout its rostral-caudal extent and also in the lateral vestibular nucleus of the same side. Degeneration of fibers was said to occur in the dentate nucleus and in the homolateral lateral vestibular nucleus following lesions in the lateral cerebellar cortex. Eager also found that vermal cerebellar cortex lesions of the anterior lobe resulted in degenerating terminals in the anterior part of the fastigial nuclei, but that vermal lesions of the posterior lobe resulted in terminal degeneration throughout the fastigial nucleus. The vermis of the anterior lobe appeared to contribute a much larger quantity of cortico-vestibular fibers than the vermis of the posterior lobe (12, 37, 4).

The present experimental studies indicate that cortico-vestibular fibers exist (Figs. 22, 23, 24, 25) and that these fibers are actually axones of the Purkinge cells of the cerebellum. Cajal ( 6 ) observed that degeneration of the peripheral stump of Purkinge axones suffering from traumatic degeneration become varicose, and at a variable distance from the lesion, ends in a "retraction ball". That the free balls resulting from autonomy of the portion that is degenerated traumatically are preserved for many days near the lesion was also reported by Cajal.

In cat 354 the lesion was located near the dorsal portion of the lateral vestibular nucleus resulting in the formation of prominent "retraction ball type" of degeneration (Fig. 29). This indicated that axones of Purkinge cells are present in the vestibular nuclei. The "retraction ball type" of degeneration was typically found near lesions in the cerebellum and was easily observed because of the numerous Purkinge axones present in the cerebellum as in cat 388 (Fig. 30).

In cat 431X following a lesion in the anterior vermal cerebellar cortex, the majority of degenerating fibers passing to the fastigial nucleus and the brainstem were seen occupying a region in the rostro-lateral part of the fastigial nucleus (Figs. 20, 21). Because all cerebellar cortex lesions were placed bilaterally in this study, the homolateralarity or bilateralarity of the cortico-vestibular fibers could not be determined.

Because of the fine caliber of the cortico-vestibular projections, they were thought to be part of a collateral system of the Purkinge axones.

Only fine degenerating fibers were found in all vestibular nuclei, but the vast majority were restricted to terminations in all parts of the lateral vestibular nucleus (Figs. 22, 23, 24, 25). Although numerous fine degenerating fibers could be found in close relationship to the larger vestibular cells and especially their processes, no degenerating terminal boutons could be

demonstrated. The inability to demonstrate degenerating boutons may be due to their relatively small size as compared to terminal boutons of larger fibers.

Degenerating fibers were not found in the brachium conjunctivum, medial longitudinal fasciculus, reticular formation, or interstitial nucleus of the vestibular nerve.

Fastigio-Bulbar Connections

It has been established for a considerable length of time by Russell (30) and other investigators (1, 28) that the fastigial nucleus gives rise to the homolateral fastigio-bulbar tract which runs through the juxtarestiform body to the vestibular nuclei.

Cohen, Sprague, and Chambers ( 9 ), and Walberg, Pompeiano, Brodal, and Jansen (38) using the silver impregnation technique to show terminal degeneration and Jansen and Jansen (20) employing the modified Gudden method to follow retrograde degeneration concluded that the fastigio-bulbar fibers were derived largely from the rostral half of the fastigial nucleus.

The areas of termination of the fastigio-bulbar fibers have been studied by Thomas, Kaufman, Sprague, and Chambers (35) using the silver impregnation method. They found that the fastigio-bulbar fibers terminate in the superior vestibular nucleus and dorso-medial part of the lateral vestibular nucleus.

Walberg, Pompeiano, Brodal, and Jansen (38) found the terminations of the fastigio-bulbar fibers to be

restricted to certain regions within each of the four vestibular nuclei; the superior vestibular nucleus, the dorso-medial part of the lateral vestibular nucleus, the medial vestibular nucleus except for its ventral strip, and the inferior vestibular nucleus except for its ventro-lateral region.

Carpenter (29) was of the opinion that the fastigial nuclei project bilateral efferent fibers to the labyrinths and that homolateral fastigial efferent fibers passing in the juxtarestiform body are distributed chiefly to the lateral and inferior vestibular nuclei.

Because the cortico-vestibular fibers pass through and in close proximity to the antero-lateral part of the fastigial nucleus (Figs. 20, 21) and are inevitably injured in lesions of the fastigial and interpositus nuclei, interpretation of the present studies were made difficult. Although the presence of fine fibers arising from the deep cerebellar nuclei and passing to the vestibular nuclei could not be ruled out, large degenerating fibers as well as fine degenerating fibers were always present when the lesion involved the deep cerebellar nuclei or their tracts (Figs. 18, 27, 34). Only fine degenerating fibers were seen in the vestibular nuclei following anterior vermal cerebellar cortex lesions.

In cat 297 the majority of chromatolytic cells in the fastigial nucleus homolateral to a lesion interrupting the fastigio-bulbar tract were found in the anterior

part of the nucleus indicating that the fastigio-bulbar tract arises large from the anterior part of the fastigial nucleus.

In cat 352 a small well localized lesion was placed in the fastigial nucleus (Fig. 31) and in cats 353 (Fig. 26) and 354 small lesions were placed in the juxta-restiform body. Large degenerating fibers of the fastigio-bulbar tract were found to terminate in these cases in the superior vestibular nucleus and the dorso-medial part of the lateral vestibular nucleus. No degeneration was noted in the interstitial nucleus of the vestibular nerve or in the vestibular nerve itself.

Uncinate Fasciculus Connections

Allen ( 1 ) and Rasmussen (28), employing Marchi preparations, have shown that the majority of the uncinate fasciculus fibers originate from the caudal part of the fastigial nucleus. In experiments using the modified method of Gudden to detect retrograde cellular changes, Jansen and Jansen (20) felt that the uncinate fasciculus originates primarily from cells in the caudal two-thirds of the fastigial nucleus and decussates in the cerebellum to join the contralateral superior cerebellar peduncle. The observations of Cohen, Chambers, and Sprague ( 9 ) concurred with that of Jansen and Jansen.

Rasmussen (28) and Cohen, Chambers, and Sprague ( 9 ) were of the opinion that the uncinate fasciculus terminates largely either in the vestibular nuclei or in the

reticular formation of the pons and the upper half of the myelencephalon. According to Carpenter (29) bilateral fastigial efferent fibers running in the uncinate fasciculus project to all vestibular nuclei and to the paramedian area of the pontine and medullary reticular formation.

Thomas, Kaufman, Sprague, and Chambers (35) studied efferent projections of the fastigial nuclei using the silver impregnation technique in the cat and found that total contralateral fastigial nucleus lesions did not cause terminal degeneration in the superior vestibular nucleus and the dorso-medial part of the lateral vestibular nucleus. They found terminal degeneration located predominantly ventro-laterally in the lateral vestibular nucleus and in the inferior vestibular nucleus. The observations of Walberg, Pompeiano, Brodal, and Jansen (38) also working with silver impregnated preparations of the cat following total contralateral fastigial nucleus ablation differed markedly. They reported the presence of terminal degeneration in the superior vestibular nucleus, in the ventral part of the lateral vestibular nucleus, in the ventral most strip of the medial vestibular nucleus, and in the lateral half of the inferior vestibular nucleus as well as along its ventral strip. No terminal degeneration was observed in the interstitial nucleus of the vestibular nerve. The terminal fibers of the uncinate fasciculus were also

felt to be present in the nucleus parasolitarius, nucleus praepositus hypoglossi, nucleus intercalatus, and the nucleus of Roller.

In this study it was noted that following transection or electrocoagulative lesions involving fibers emanating from the deep cerebellar nuclei, a considerable number of neurones of the deep cerebellar nuclei retained their normal appearance in both Nissl stained and silver impregnated sections. This relative resistance to retrograde degenerative changes as compared to other nuclear groups such as the vestibular nuclei is undoubtedly due to various factors. One of these factors may be the presence of sustaining collaterals. Jansen and Jansen (20) seemed to favor the hypothesis that some of the neurons in the cerebellar nuclei are intrinsic cerebellar elements.

A lesion involving the uncinate fasciculus in cat 297 shows retrograde degeneration in the contralateral fastigial nucleus (Fig. 40). The degenerative changes in the cells are diffusely scattered throughout the rostral-caudal extent of the fastigial nucleus indicating that the uncinate fasciculus takes origin from all parts of the fastigial nucleus, although the fastigio-bulbar tract arises predominantly from the rostral portion of the same nucleus.

After decussating in the cerebellum the uncinate fasciculus passes dorsal to the contralateral brachium conjunctivum. (Fig. 13).

The uncinate fasciculus enters the vestibular nuclei from the lateral aspect and sweeps medially to terminate approximately in the ventral half of the lateral vestibular nucleus and in the rostral part of the inferior vestibular nucleus (Figs. 14, 33).

The uncinate fasciculus was not noted to terminate in any areas other than those mentioned above. No fine degenerating fibers were present in the vestibular nuclei contralateral to the lesion.

Lesions of the fastigial nucleus in the cat resulted in a disorder of equilibrium, in which the cat circled to the side of the lesion. Its homolateral limbs were abducted and exhibited extensor hypertonus, and its contralateral limbs were adducted and exhibited flexor hypertonus.

The demonstration that the contralateral uncinate fasciculus projects to the ventral part of the lateral and rostral part of the inferior vestibular nuclei while the homolateral fastigio-bulbar and interposito-bulbar tracts project to the dorsal part of the lateral and superior vestibular nuclei may be functionally correlated with a somatotopic arrangement of flexor and extensor activity within the vestibular nuclei.

## Interposito-Bulbar Connections

Although conclusive evidence that fibers from the interpositus and dentate nuclei project on to the vestibular nuclei has not been obtained in previous experimentation,

Cohen, Chambers, and Sprague ( 9 ) using the silver impregnation technique evidently felt that such fibers existed. Evidence of projections to the vestibular nuclei were said to be found following homolateral ablation of various parts of the interpositus and dentate nuclei. From their paper it can not be determined whether the degeneration observed actually resulted from damage to fibers coming from other cerebellar areas.

The study of the interposito-bulbar fibers was made difficult by the presence of inevitable damage to cortico-vestibular fibers. According to Dow (10) in the cat, degenerating fibers from a lesion in the flocculus arch above and between the posterior fibers of the restiform body and end in the lateral part of the lateral vestibular nucleus. In cat 360 the restiform body is spared and the lesion is fairly well localized in the interpositus nucleus (Fig. 17). The lesion is placed too dorsally to disrupt the flocculo-vestibular projections and yet large degenerating fibers are seen to stream ventrally from the area of the lesion in the interpositus nucleus to the superior vestibular nucleus and the dorso-lateral part of the lateral vestibular nucleus (Fig. 18).

The dorso-lateral part of the lateral vestibular nucleus is free of large degenerating terminal fibers following lesions of the fastigial nucleus (Fig. 31), or from lesions of the medial part of the juxtarestiform body involving the fastigio-bulbar fibers (Fig. 26). In these

cases numerous degenerating terminal fibers are seen in the dorso-medial part of the lateral vestibular nucleus.

In summary the interposito-bulbar fibers take origin from the homolateral interpositus nucleus and terminate in the superior vestibular nucleus and the dorsal lateral part of the lateral vestibular nucleus.

Topography of Cerebello-Vestibular Projections: a Summary

A diagram of the cerebello-vestibular projections is presented in Figure 9.

The cortico-vestibular fibers originate from the flocculo-nodular lobe and the vermal cerebellar cortex of the anterior lobe. These fibers terminate as fine fibers in the superior, lateral, medial, and inferior vestibular nuclei. The vast majority of cortico-vestibular fibers terminate in the lateral vestibular nucleus.

The fastigio-bulbar fibers arise predominantly from the rostral part of the homolateral fastigial nucleus and traverse the medial part of the juxtarestiform body to terminate in the superior vestibular nucleus and the dorso-medial part of the lateral vestibular nucleus.

The uncinate fasciculus takes origin equally from the rostro-caudal extent of the fastigial nucleus and terminates contralaterally in the ventral part of the lateral vestibular nucleus and the rostral portion of the inferior vestibular nucleus.

The interposito-bulbar fibers arise from the interpositus nucleus, traverse the lateral part of the

juxtarestiform body, and terminate in the homolateral superior vestibular nucleus and the dorso-lateral part of the lateral vestibular nucleus.

Thus it would appear that the superior and the dorsal portion of the lateral vestibular nuclei receive homolateral projections from the interpositus and fastigial nuclei in addition to the direct cerebellar cortical projections, while the ventral portion of the lateral and the rostral portion of the inferior nucleus receive a contralateral projection from the fastigial nucleus by way of the uncinate fasciculus in addition to their cortical afferents. The homolateral projections from the fastigial and interpositus nuclei differ in projecting to the medial and lateral areas of the dorsal part of the lateral vestibular nucleus respectively.

Vestibulo-Cerebellar Connections

Although primary vestibular fibers passing to the cerebellum were not observed by Lorente de Nó (24) in Golgi preparations of the mouse, Cajal ( 5 ) also using Golgi material has described such fibers. The observation of these fibers have been confirmed by Larsell (21) and Whitlock (40) using silver impregnated material. In experimental studies employing the Marchi method, primary vestibular fibers projecting to the flocculus, nodulus, and the fastigial nucleus have been described by Ingvar (18) in the cat, Dow (10) in the rat and cat, and Whitlock (40) in birds.

In this study no lesions were made in the vestibular nerve, however in lesions involving the vestibular nucleus or juxtarestiform body (Cat 353, 354) no terminal degeneration was noted in the fastigial nuclei.

Secondary vestibulo-cerebellar fibers have been studied in normal silver impregnated material be Larsell (21, 22, 7) in the opossum, bat, and man, by Westen (39) in reptiles, and by Whitlock (40) in birds. These investigators have shown the areas of termination of fibers passing from the vestibular nuclei to the cerebellum to be the same as those given above for the primary vestibulo-cerebellar fibers.

Larsell (21) working with the opossum felt that the superior and lateral vestibular nuclei were the major sources of secondary vestibulo-cerebellar fibers, whereas Voris and Hoerr (36) working with the same animal indicated that the inferior and medial vestibular nuclei were the origins of these fibers. Brodal, Pompeiano, and Walberg (4) using kittens and Carpenter, Bard, and Alling (7) working on adult cats concluded that the nuclei of origin of secondary vestibulo-cerebellar fibers were the medial and inferior vestibular nuclei.

Evidence in the present study points to the lateral and inferior vestibular nuclei as being the sources of vestibulo-cerebellar fibers. Chromatolytic cells appeared in the lateral and inferior vestibular nuclei following cerebellar lesions in cat T12Y and 297 (Figs. 36, 37, 38)

and in the lateral vestibular nucleus in cat T9X (Fig. 10).

No vestibulo-cerebellar fibers were observed to terminate in the fastigial nuclei, however vestibulo-cerebellar fibers were not followed to their areas of termination in the cerebellar cortex in the present study.

Brachium Conjunctivum Afferents to the Oculomotor Nuclei

Allen ( 1 ) observed in Marchi preparations of the guinea pig that a number of brachium conjunctivum fibers branch off dorsally to enter the oculomotor nuclei. These fibers were said to enter the oculomotor nuclei from behind and from the side. The observation was made by Rasmussen (28) using the Marchi method in the cat that the brachium conjunctivum terminates to a slight extent in the region of the oculomotor nuclei and adjacent reticular formation.

Cohen, Chambers, and Sprague ( 9 ) working with the silver impregnation method reported that no efferent fibers from the cerebellar nuclei of the cat terminate on the somatic motor cells of the brainstem or spinal cord.

The brachium conjunctivum was involved in many lesions in this study. In cat T12Y a few large fibers of the degenerating brachium conjunctivum appeared to turn dorsally at the level of the red nucleus to enter the contralateral oculomotor nuclei from below (Fig. 15). The medial longitudinal fasciculus was free of degenerating fibers.

Although a continuity of degenerating fibers from the

brachium conjunctivum was not demonstrable in cat 360, a few degenerating fibers were seen in the contralateral oculomotor nuclei (Fig. 19). The medial longitudinal fasciculus was free of degeneration.

Although a few fibers of the brachium conjunctivum may terminate in the oculomotor nuclei, the degeneration did not occur consistently in this study. Following lesions of the brachium conjunctivum, degenerating fibers in the oculomotor nuclei were found to be absent more often than they were present. From the evidence of the material analyzed in these experiments, the existence of these fibers is still a conjectural matter.

## SUMMARY AND CONCLUSIONS

The interconnections of the vestibular nuclei and cerebellum have been studied in the cat brain by the experimental method. Lesions were produced in various regions of the cerebellum, vestibular nuclei, and their associated tracts. Following a survival period of four to twenty days, the animals were sacrificed and sections prepared by the intensified protargol and Nissl methods.

Analysis of the histologic preparations yielded the following results:

1. The majority of cortico-vestibular fibers originate from the Purkinge cells of the vermal cerebellar cortex of the anterior lobe. These fibers pass through or in close proximity to the rostro-lateral part of the fastigial nucleus and then disperse diffusely through the juxtarestiform body to terminate as fine fibers in the superior, lateral, medial, and inferior vestibular nuclei. The vast majority of cortico-vestibular fibers terminate in the lateral vestibular nucleus. The fibers end predominantly in relationship to the large vestibular cells, expecially their processes. No cortico-vestibular fibers are found in the brachium conjunctivum, medial longitudinal fasciculus, reticular formation, or interstitial nucleus of the vestibular nerve.

2. The fastigio-bulbar fibers arise predominantly from the rostral part of the homolateral fastigial nucleus and traverse the medial part of the juxtarestiform body to terminate in the superior vestibular nucleus and the dorso-medial part of the lateral vestibular nucleus.

3. The uncinate fasciculus takes origin equally from the rostro-caudal extent of the fastigial nucleus, and decussates in the cerebellum to reach the superior cerebellar peduncle where it occupies a position as a discrete bundle of fibers just dorsal to the brachium conjunctivum. The uncinate fasciculus is closely applied to the dorsal convexity of the brachium conjunctivum, and from its lateral margin courses obliquely in a ventral and caudal direction along the lateral aspect of the vestibular nuclei. The large fibers of the uncinate fasciculus turn medially to terminate in the ventral part of the lateral vestibular nucleus and the rostral portion of the inferior vestibular nucleus. There are no fine fibers running with the uncinate fasciculus. No fibers of the uncinate fasciculus were found to terminate in the superior vestibular nucleus, medial vestibular nucleus, reticular formation, interstitial nucleus of the vestibular nerve, nucleus parasolitarius, nucleus praepositus hypoglossi, nucleus intercalatus, or nucleus of Roller.

4. The interposito-bulbar fibers arise from the interpositus nucleus, traverse the lateral part of the juxtarestiform body, and terminate in the homolateral

superior vestibular nucleus and the dorso-lateral part of the lateral vestibular nucleus.

5. The lateral and inferior vestibular nuclei are the sources of the vestibulo-cerebellar projections. No primary or secondary vestibulo-cerebellar fibers terminate within the fastigial nuclei.

6. The interstitial nucleus of the vestibular nerve is connected to the main vestibular nuclear mass by an isthmus of cells, and receives no fiber projections from the cerebellum.

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PLATE I

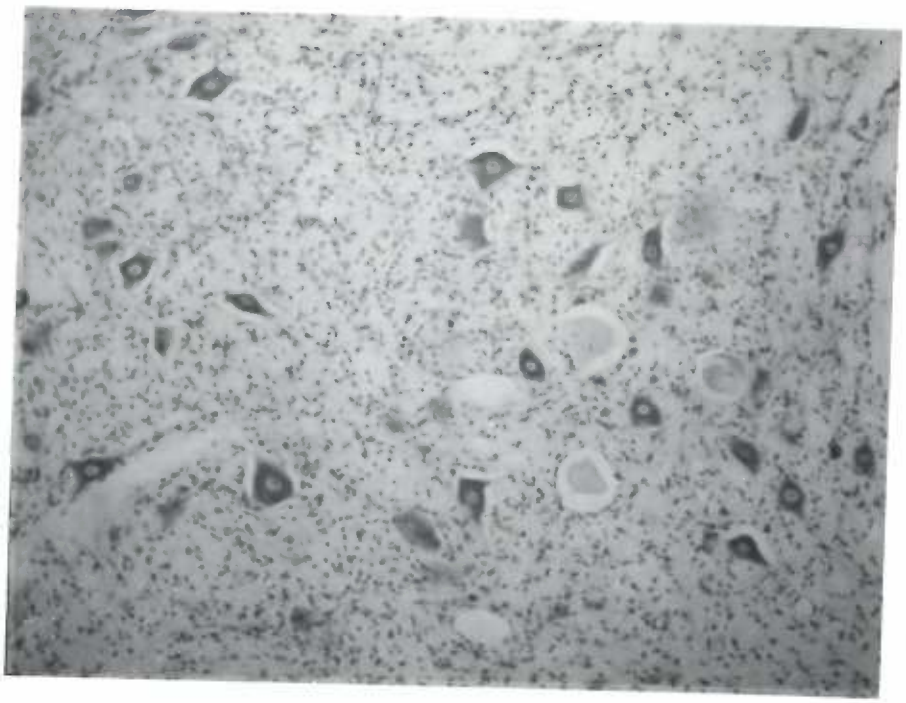
Figure 10

Cat T9X. Photomicrograph of the lateral vestibular nucleus. Note chromatolytic cells. Nissl stain. 100X.

Figure 11

Cat T9X. Photomicrograph of a cell in the lateral vestibular nucleus. Note heavy degeneration of terminal boutons on the soma and dendrite. Intensified protargol stain. 430X.

10



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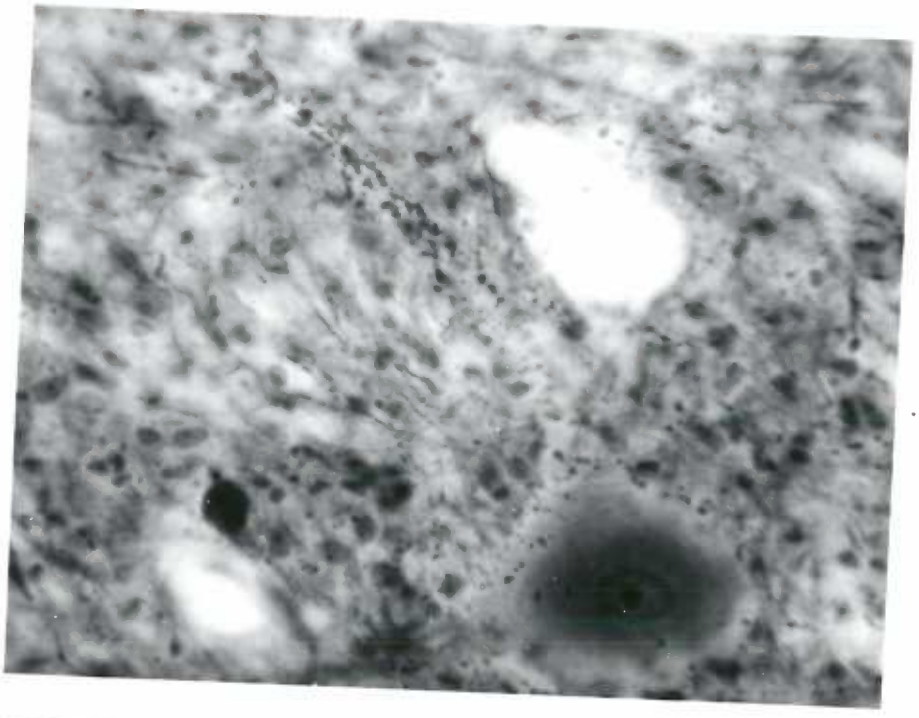


PLATE II

Figure 12



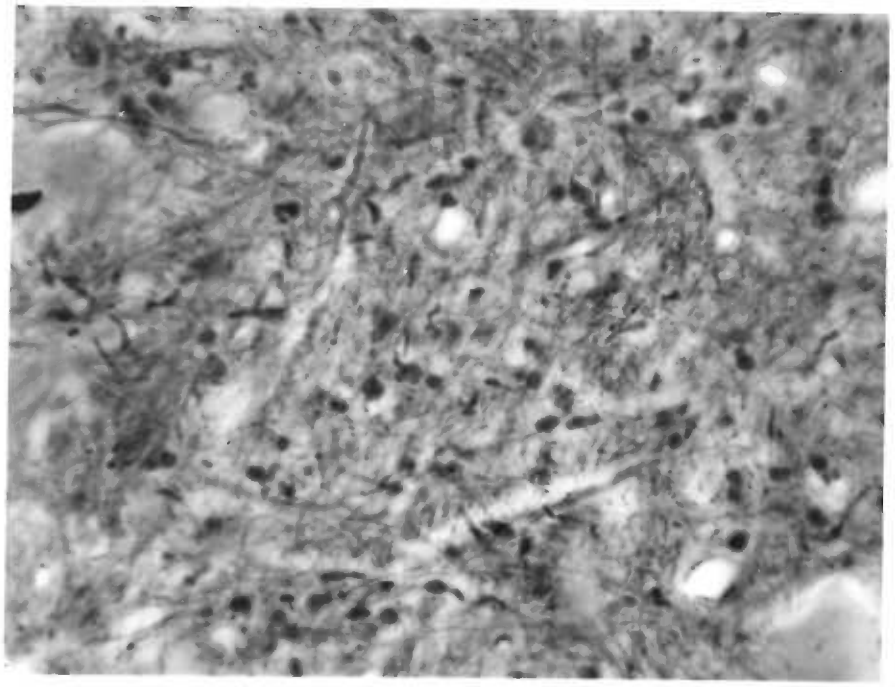
Cat T9X. Photomicrograph of the medial vestibular nucleus. Note fine degenerating argyrophilic debris. Intensified protargol stain. 430X.

Figure 13



Cat T12Y. Photomicrograph of the uncinate fasciculus. Note loss of fibers and the large degenerating fibers. Intensified protargol stain. 430X.

12



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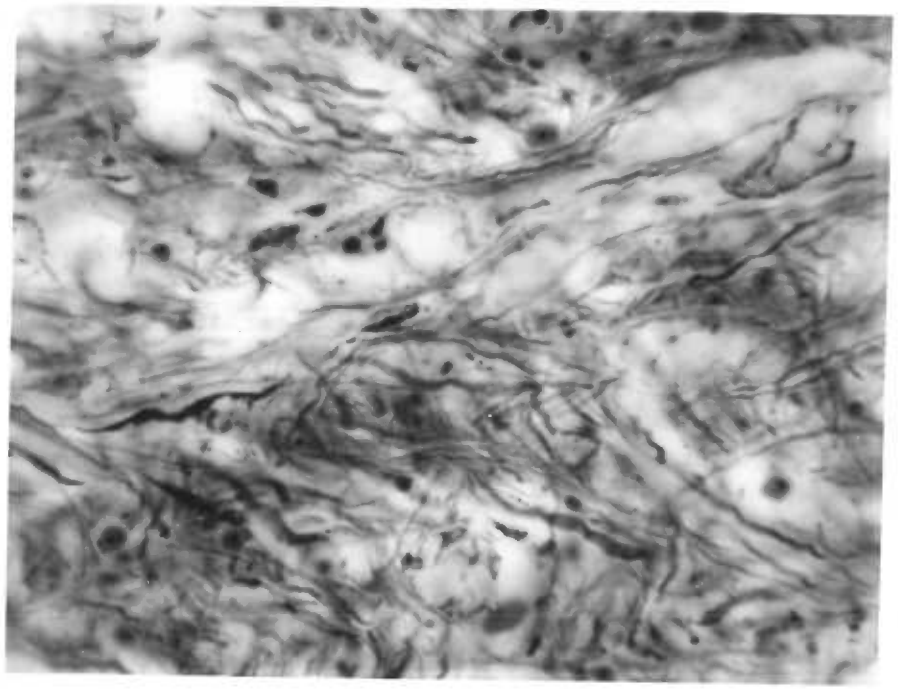


PLATE III

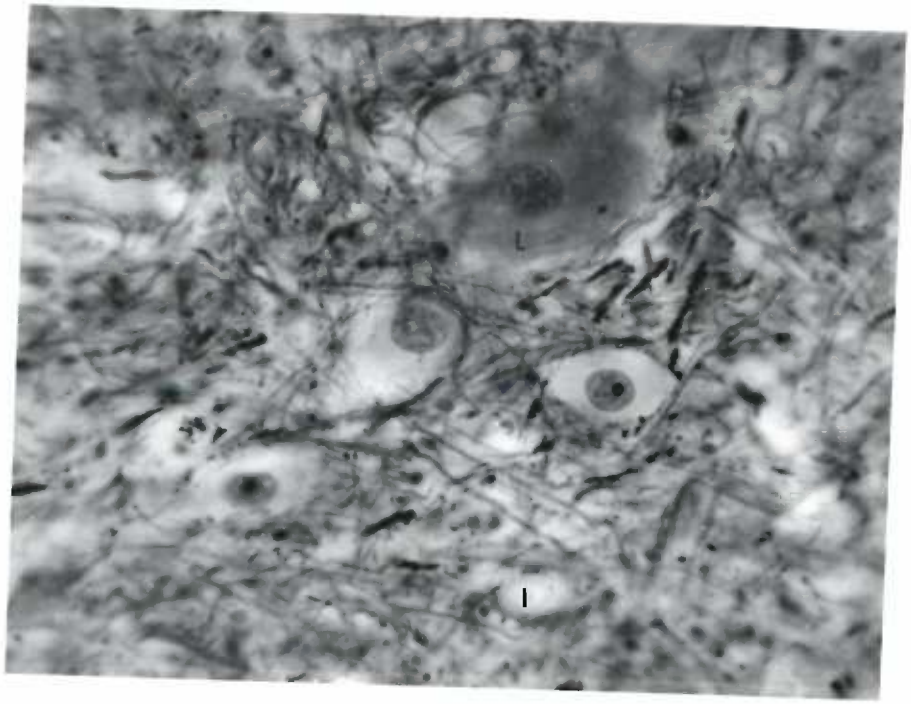
Figure 14

Cat T12Y. Photomicrograph of the ventrolateral part of the lateral vestibular nucleus (L) and the dorsal aspect of the inferior vestibular nucleus (I). Note the large degenerating fibers of the uncinate fasciculus. Intensified protargol stain. 430X.

Figure 15

Cat T12Y. Photomicrograph of the oculomotor nucleus. Note the large degenerating fiber. Intensified protargol stain. 430X.

14



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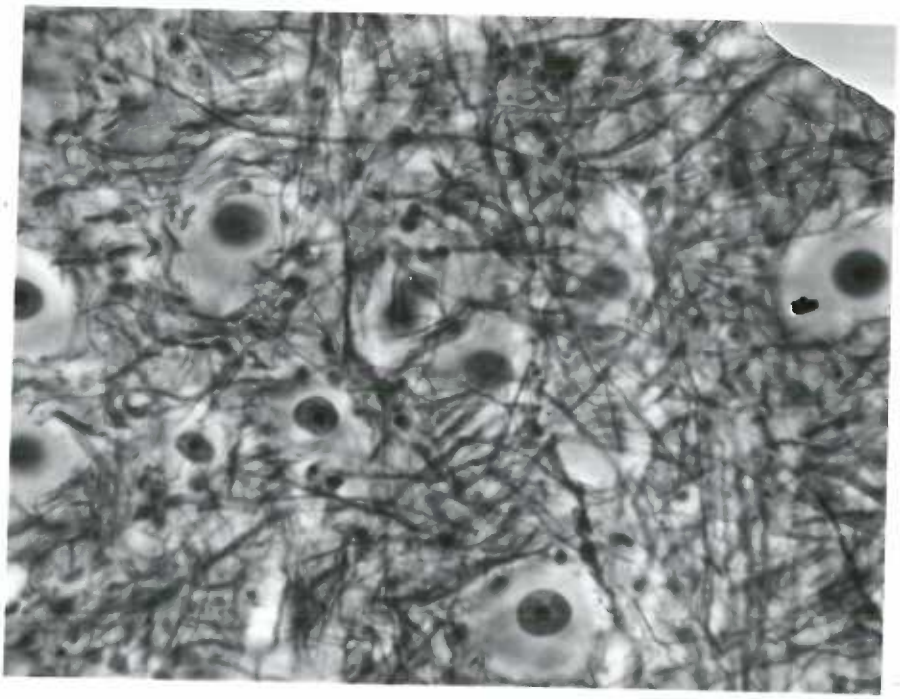


PLATE IV

Figure 16



Cat T12Y. Photomicrograph of the interstitial nucleus of the vestibular nerve (I) and lateral vestibular nucleus (L). Note the isthmus of cells (C) connecting the two nuclear groups. Intensified protargol stain. 35X.

Figure 17



Cat 360. Photomicrograph illustrating the position of the lesion. Note fourth ventricle and vestibular nuclei. Intensified protargol stain. 35X.

16


17

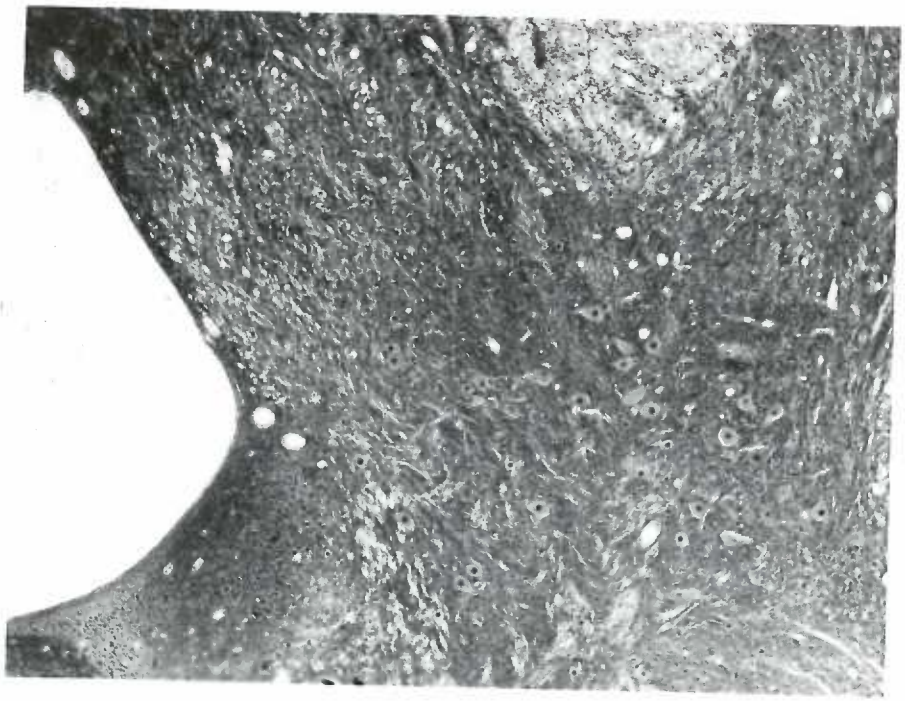


PLATE V

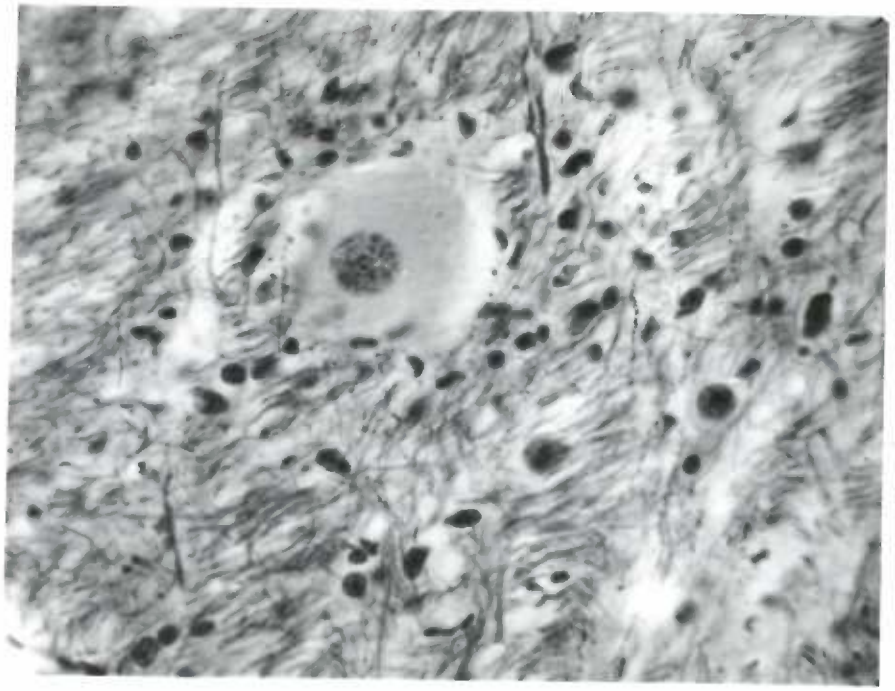
Figure 18

Cat 360. Photomicrograph of a cell in the dorso-lateral portion of the lateral vestibular nucleus. Note degenerating fibers in the area. Intensified protargol stain. 430X.

Figure 19

Cat 360. Photomicrograph of oculomotor nucleus. Note degenerating fiber. Intensified protargol stain. 970X.

18



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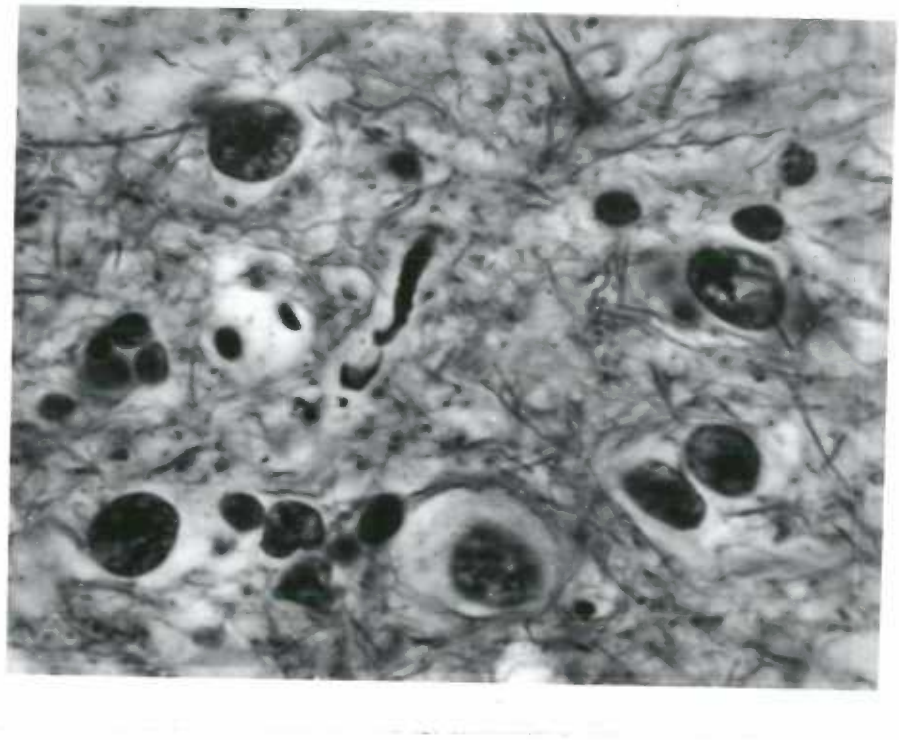


PLATE VI

Figure 20



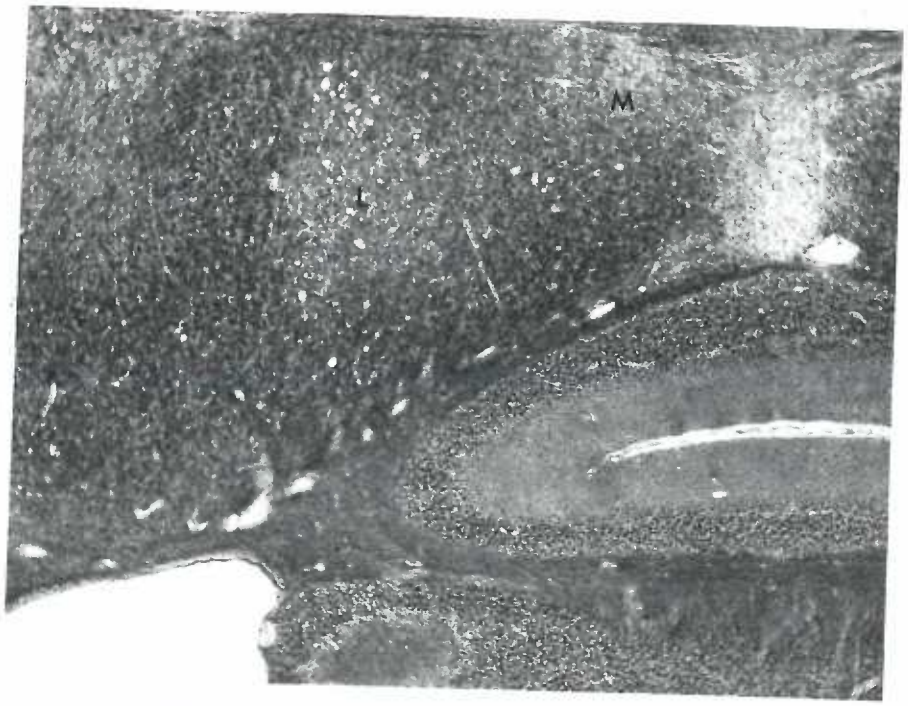
Cat 431X. Photomicrograph of the medial deep cerebellar nuclei. Note that there is no loss of fibers in the medial part of the fastigial nucleus (M), whereas the antero-lateral part of the fastigial nucleus (L) shows a loss of fibers. Intensified protargol stain. 35X.

Figure 21



Cat 431X. Photomicrograph of the fastigial nucleus shown in Figure 20. Note there is no loss of fibers in the medial part of the fastigial nucleus (M), whereas the antero-lateral part of the fastigial nucleus (L) shows a loss of fibers. Intensified protargol stain. 100X.

20

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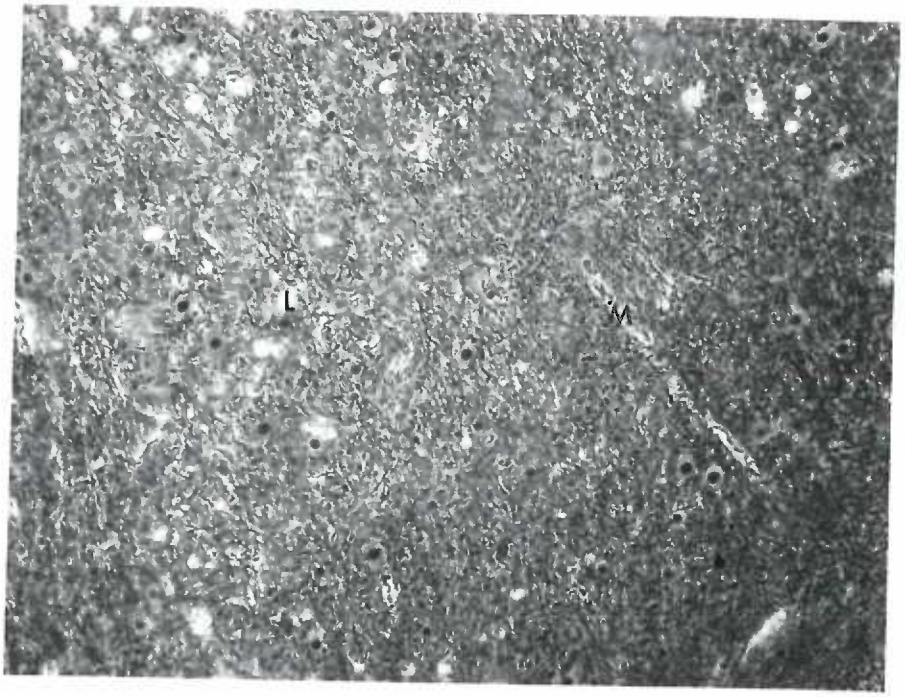


PLATE VII

Figure 22



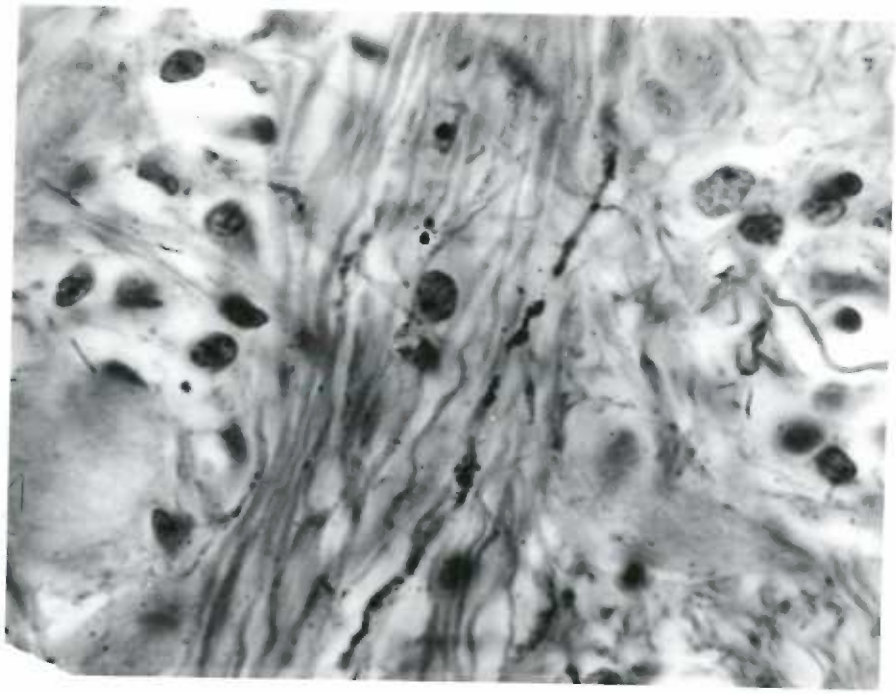
Cat 431X. Photomicrograph of the lateral vestibular nucleus. Note the abundant fine degenerating fibers. Intensified protargol stain. 970X.

Figure 23



Cat 431X. Photomicrograph of the superior vestibular nucleus. Note the fine degenerating fibers are not as abundant as in the lateral vestibular nucleus (Fig. 22). Intensified protargol stain. 970X.

22



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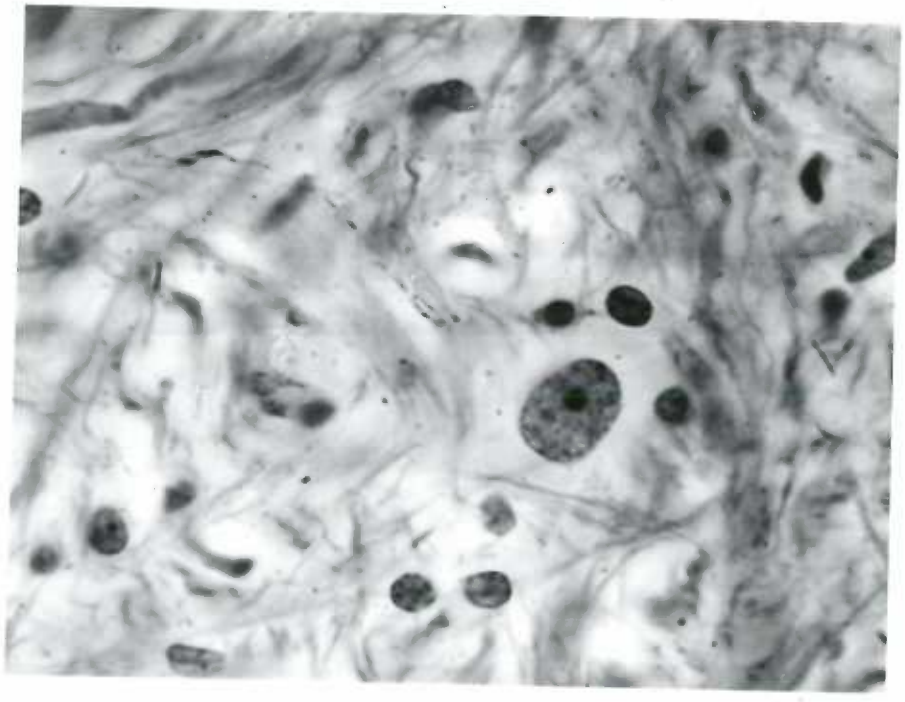


PLATE VIII

Figure 24



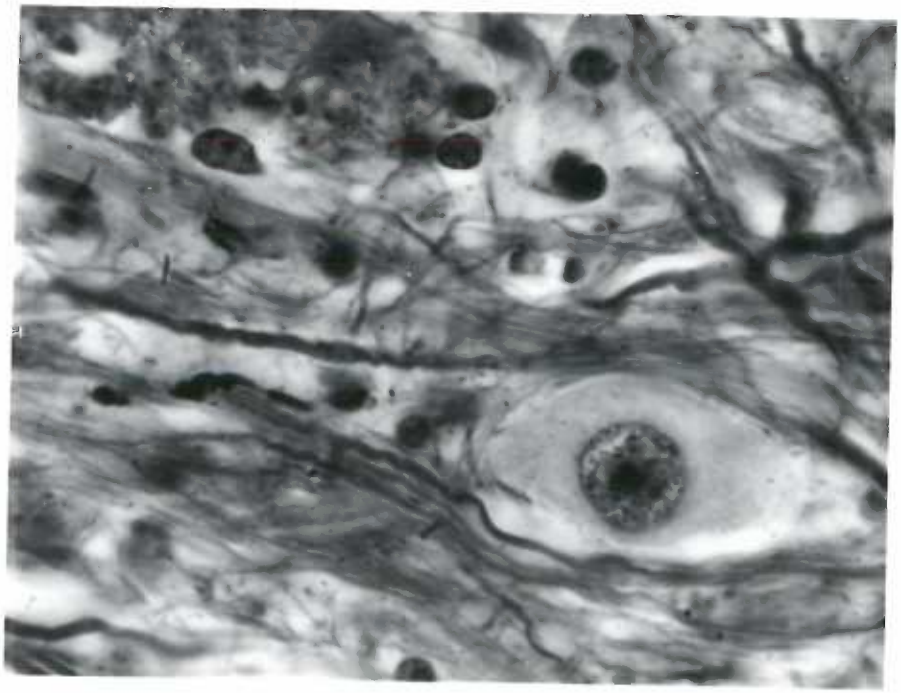
Cat 431X. Photomicrograph of the inferior vestibular nucleus. Note degenerating fibers are not as abundant as in the lateral vestibular nucleus (Fig. 22). Intensified protargol stain. 970X.

Figure 25



Cat 431X. Photomicrograph of the medial vestibular nucleus. Note degenerating fibers are few in comparison with the lateral vestibular nucleus (Fig. 22). Intensified protargol stain. 970X.

24



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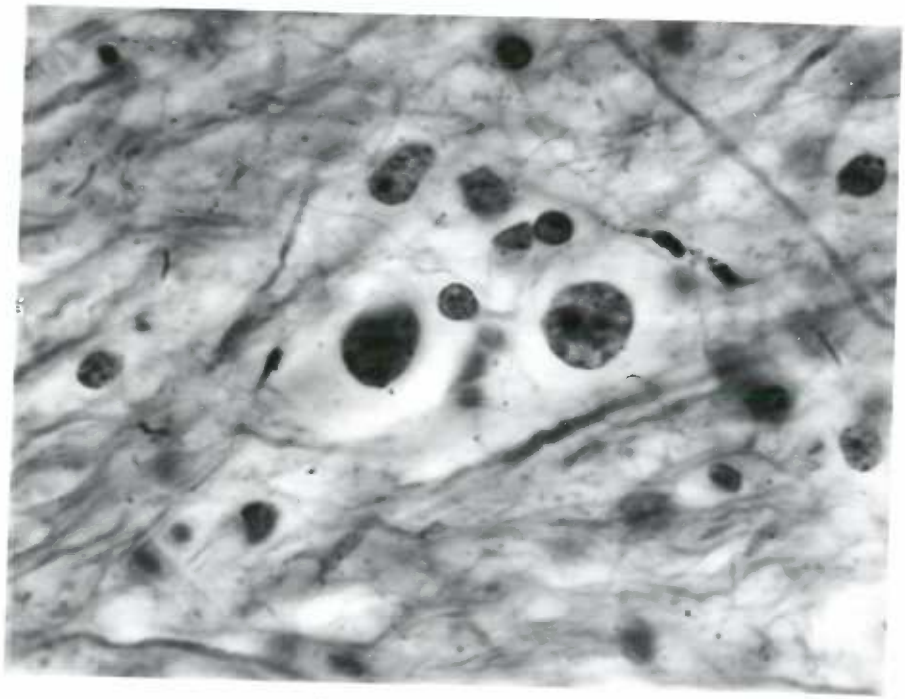


PLATE IX

Figure 26



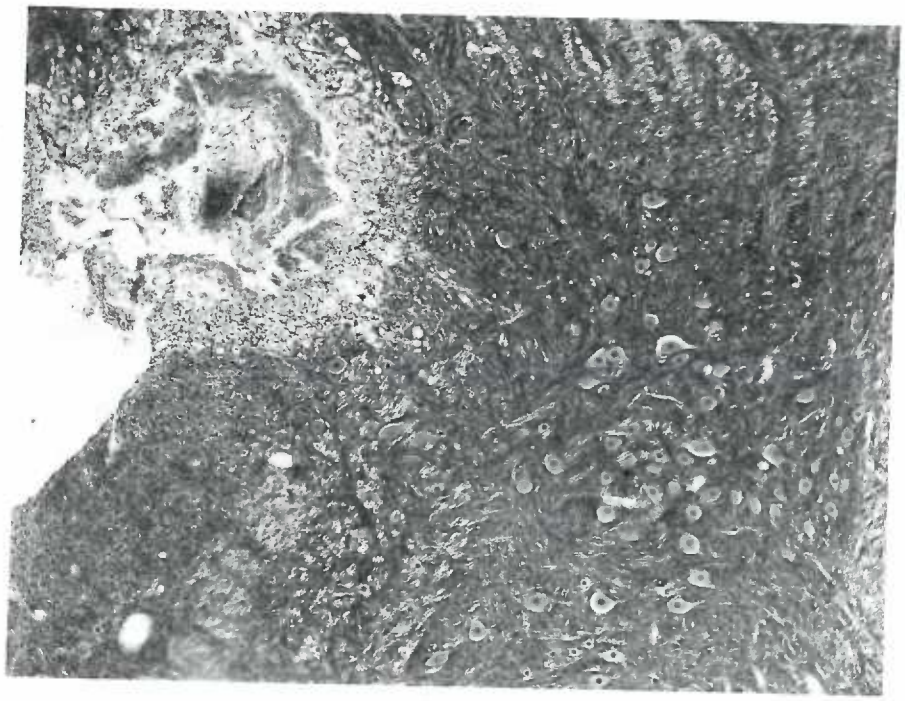
Cat 353. Photomicrograph showing the extent of the lesion in the juxtarestiform body. Note lateral vestibular nucleus. Intensified protargol stain. 35X.

Figure 27



Cat 353. Photomicrograph of the medial part of the lateral vestibular nucleus. Note the large and fine degenerating fibers. Intensified protargol stain. 970X.

26



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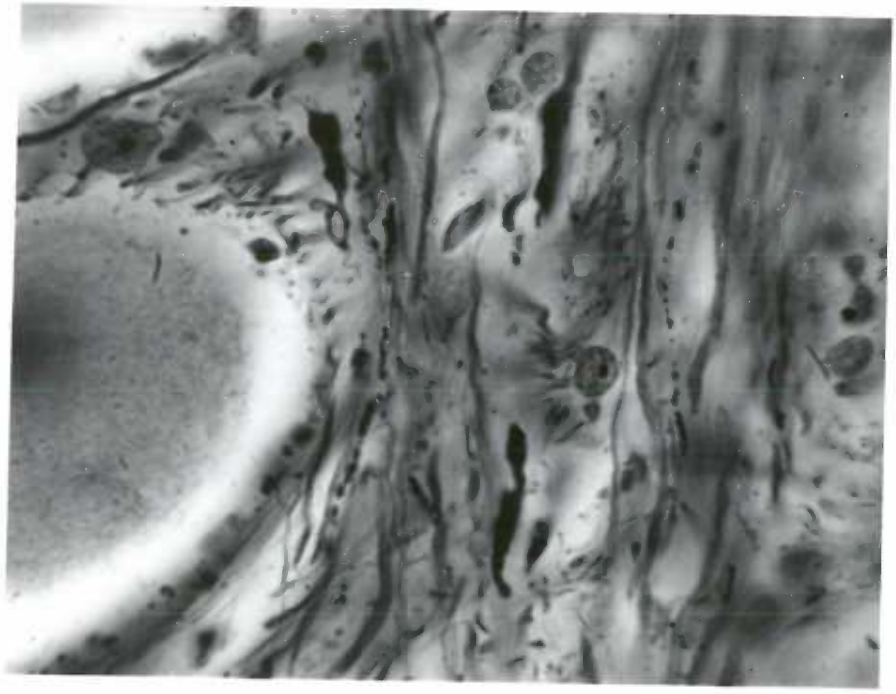


PLATE X

Figure 28



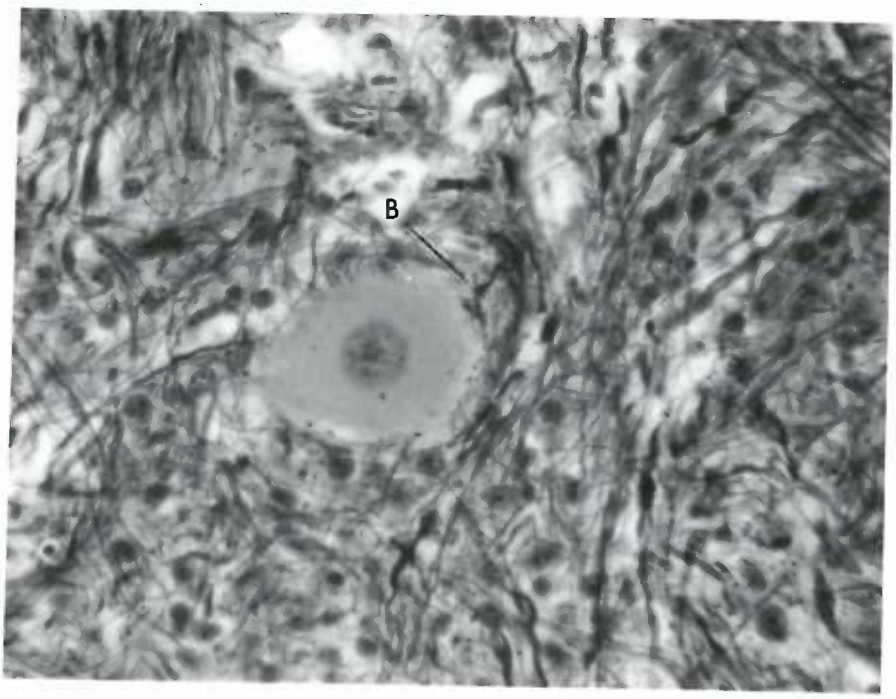
Cat 353. Photomicrograph of the dorso-medial part of the lateral vestibular nucleus. Note swollen argyrophilic degenerating terminal bouton (B). Intensified protargol stain. 430X.

Figure 29



Cat 354. Photomicrograph showing the lesion near the dorsal portion of the lateral vestibular nucleus. Note "retraction ball type" of degeneration (T) is similar to that in Figure 30. Intensified protargol stain. 100X.

28




29

PLATE XI

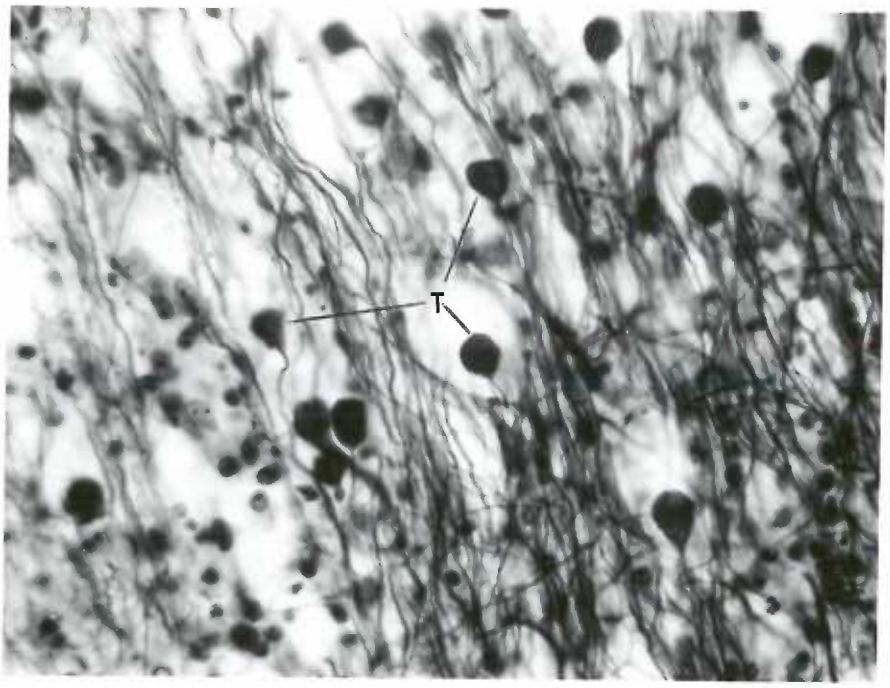
Figure 30

Cat 388. Photomicrograph near the lesion in the cerebellum. Note "retraction ball type" of degeneration (T) of Purkinge axones is similar to that in Figure 29. Intensified protargol stain. 430X.

Figure 31

Cat 352. Photomicrograph of the lesion in the fastigial nucleus. Intensified protargol stain. 35X.

30

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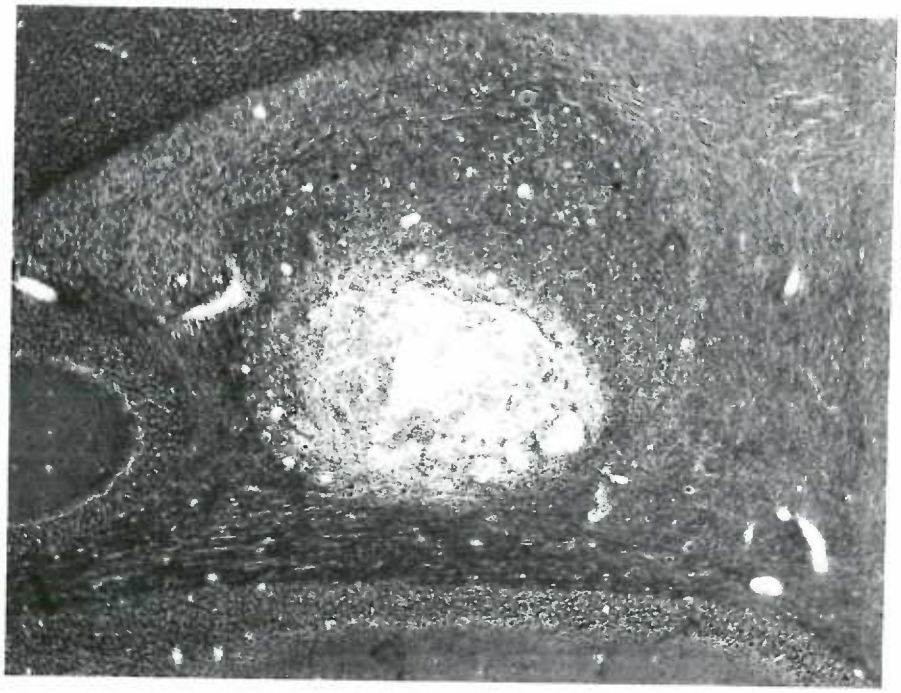


PLATE XII

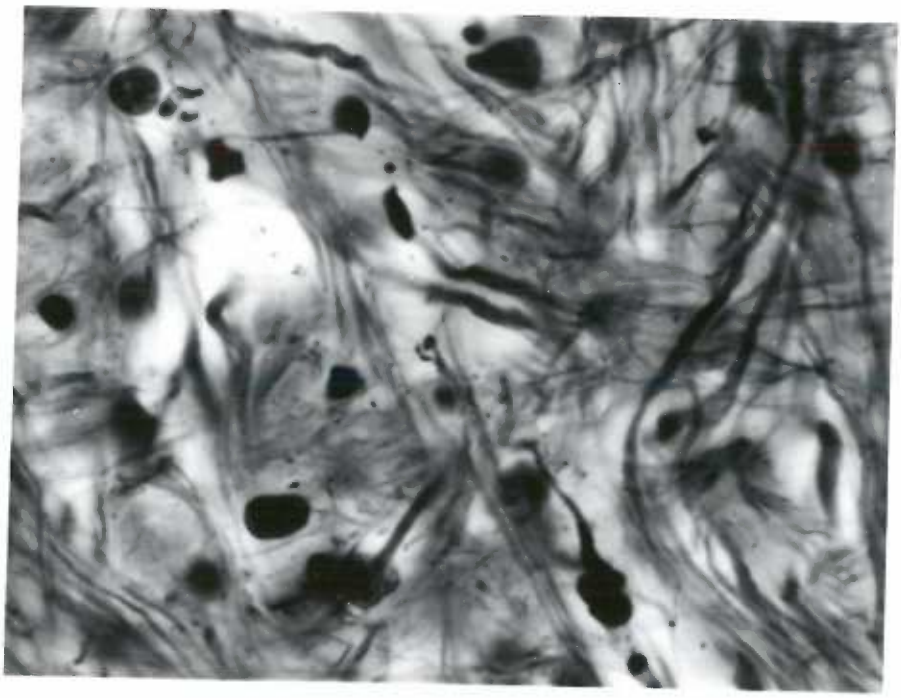
Figure 32

Cat 352. Photomicrograph of large degenerating fibers in the dorso-medial part of the lateral vestibular nucleus. Intensified protargol stain. 970X.

Figure 33

Cat 352. Photomicrograph of the dorsal part of the inferior vestibular nucleus. Note degenerating fibers. Intensified protargol stain. 100X.

32



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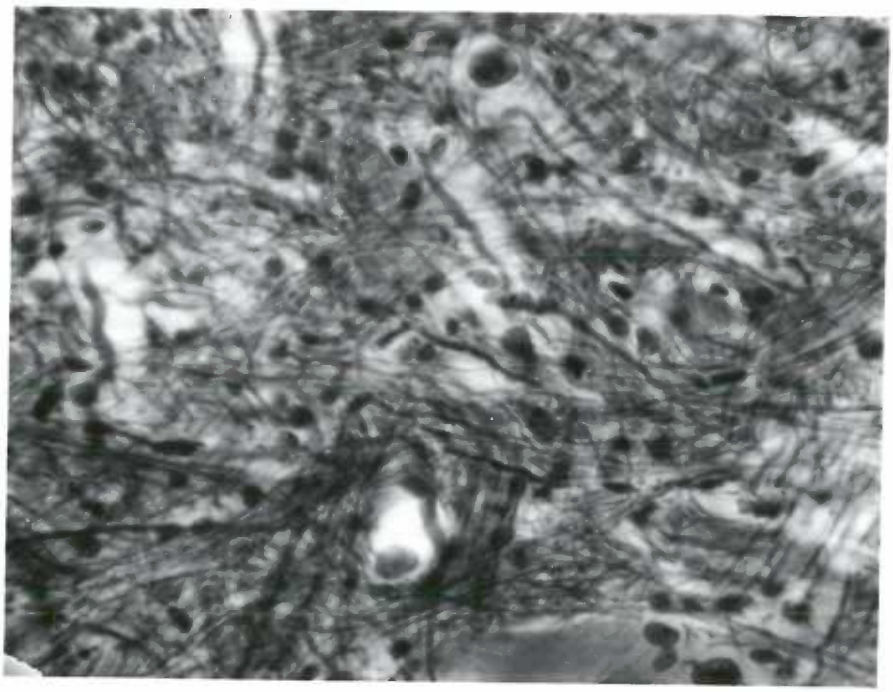


PLATE XIII

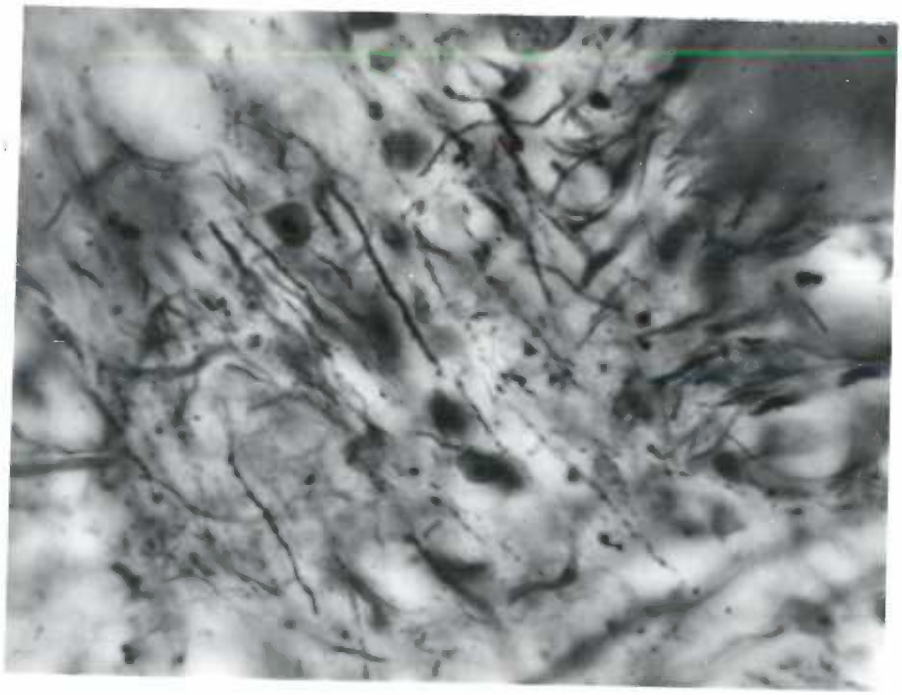
Figure 34

Cat T7. Photomicrograph of the lateral vestibular nucleus. Note fine and large degenerating fibers. Intensified protargol stain. 970X.

Figure 35.

Cat T7. Photomicrograph of the dorsal part of the lateral vestibular nucleus. Note the degenerating fibers and boutons. Intensified protargol stain. 430X.

34



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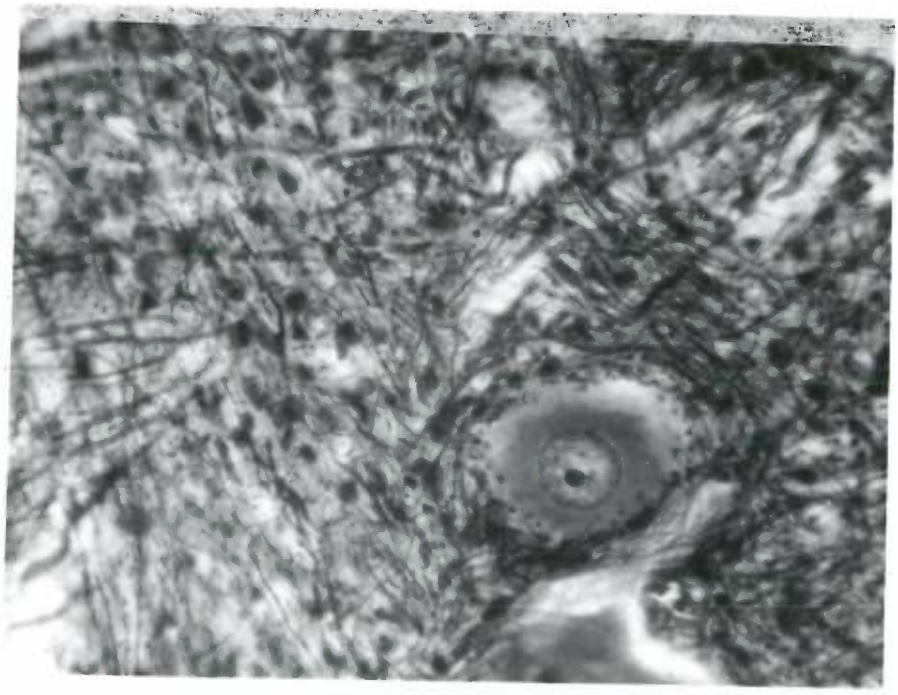


PLATE XIV

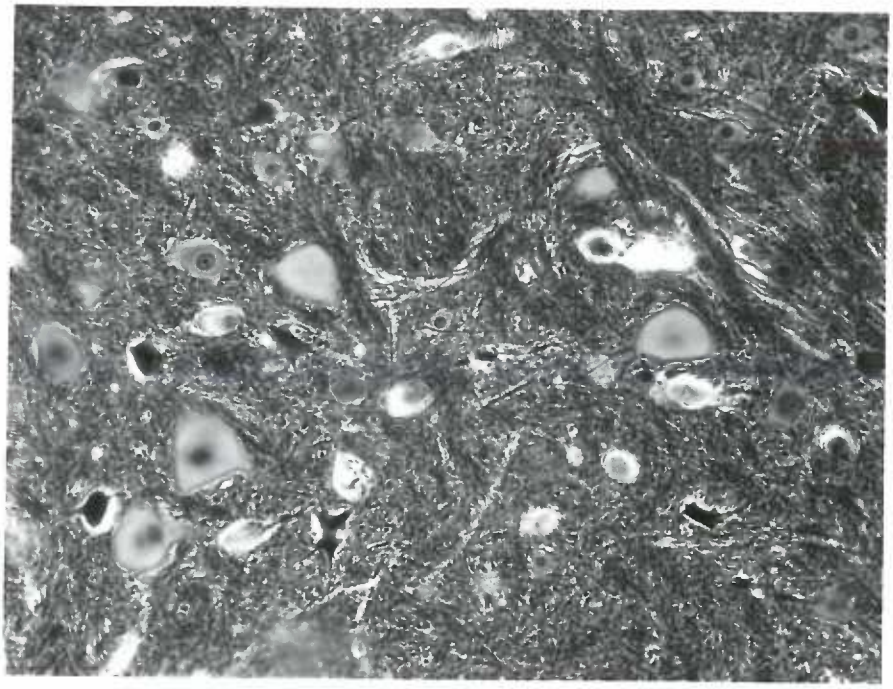
Figure 36

Cat 297. Photomicrograph of the lateral vestibular nucleus. Note chromatolytic cells. Intensified protargol stain. 100X.

Figure 37

Cat 297. Photomicrograph of the inferior vestibular nucleus. Note chromatolytic cells (C). Intensified protargol stain. 100X.

36



37

PLATE XV

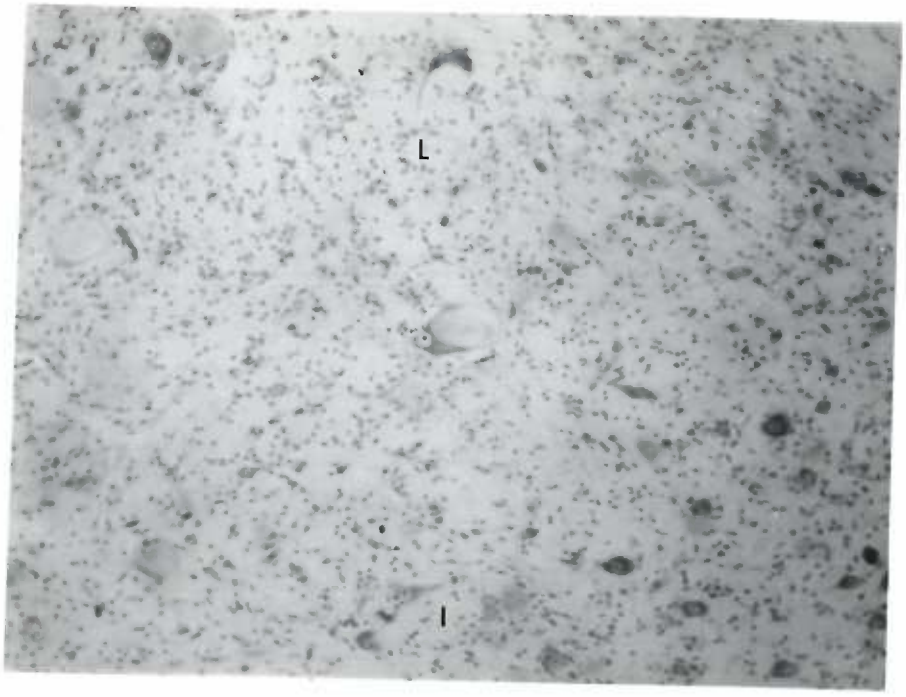
Figure 38

Cat 297. Photomicrograph of the ventral part of the lateral vestibular nucleus (L) and the dorsal part of the inferior vestibular nucleus (I). Note chromatolytic cells. Nissl stain. 100X.

Figure 39

Cat 297. Photomicrograph of the vestibular nuclei. Note the lateral extent of chromatolytic cells (X). Intensified protargol stain. 35X.

38

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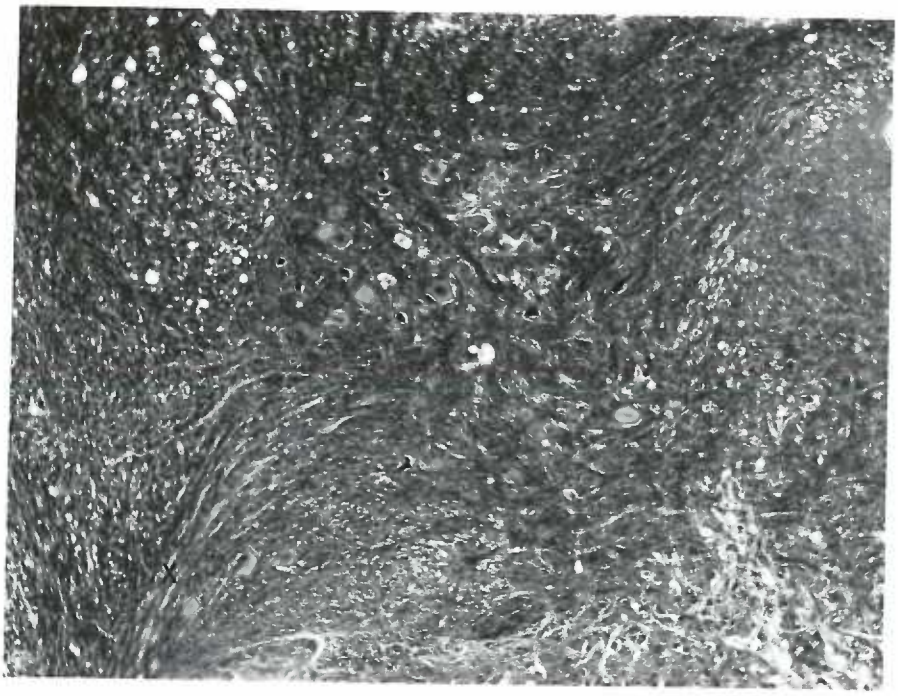

PLATE XVI

Figure 40

Cat 297. Photomicrograph of the anterior part of the fastigial nucleus. Note alteration of Nissl substance (N). Nissl stain. 430X.

40