AN EXPERIMENTAL INVESTIGATION OF THE ORIGIN OF EFFERENT FIBER PROJECTIONS TO THE VESTIBULAR NEURO-EPITHELIUM OF THE CAT

By

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A THESIS

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INTRODUCTION

Recent trends in anatomical and physiological research have demonstrated a keen interest on the part of many workers in establishing the possibility of the existence of an efferent group of nerve fibers leading to the neuro-epithelium of the internal ear (Rasmussen[1]; Galambos[2]; Fernandez[3]). Other afferent systems have also been investigated with the purpose of demonstrating efferent connections to a specific receptor. Adey[4] has demonstrated central efferents in the olfactory bulb, Granit[5] recently revealed the presence of central efferents to the retinal neuro-epithelium, and the existence of gamma efferents to the neuro-muscular spindle has been demonstrated by a large group of investigators including Granit and Kaada[6]; Kuffler, Hunt and Quilliam[7] and Leksell[8].

In the widespread pre-occupation with the classical afferent pathway between the end-organ epithelium and its central connections, the numerous anatomical reports of a parallel efferent system have curiously received little attention. This descending efferent pathway has been followed, particularly, in the auditive system from the receptive cortex to the cochlear end organ. Observations by Held[9], Cajal[10], Dejerine[11], Morgan[12], Nissl[13], Ohnishi[14] and Papez[15] have pointed to the existence of pathways from the cortex to the medial geniculate body. Ades[16] has described connections from the cortex to the inferior colliculus, lateral lemniscus and trapezoid body. Held[9] defined connections from the inferior colliculus to the lateral lemniscus and from the superior olive to the cochlear nuclei and cochlea. More recently, the discovery of the olivo-cochlear bundle by Rasmussen[1,17,18,19] in connection with his work on the

olivary peduncle has pointed toward the existence of an efferent fiber bundle running with the cochlear division of the eighth nerve. Further study of efferent projections to the organ of Corti has been, and is being done, by Fernandez[3], Portmann, Portmann, and Portmann[20,21,22]. These studies, because of their implications, should arouse considerable interest among anatomists and physiologists, but many of the observations deserve further confirmation.

Shortly after the turn of the century many detailed descriptions of the neuroanatomy of the internal ear were made available. The afferent nerve fibers from the organ of Corti with their cells of origin in the spiral ganglion and the afferent fibers from the vestibular neuro-epithelium with their cells of origin in Scarpa's ganglion were meticulously described by Cajal[23], Retzius[24], Kolmer[25], and Poljak[26]. These authors have also described the existence of fine fibers within the elements of the vestibular neuro-epithelium. These fine fibers were uniformly considered as part of the afferent system.

No substantial information has, as yet, been offered which might elucidate the extent of distribution, or function of these fine fibers. Nor has it been shown where the cells of origin for these fibers might be located. The purpose of this investigation was to attempt to do so by the experimental method.

MATERIAL AND METHOD

To establish a normal control, the internal ears of a series of fourteen cats and two monkeys were studied. The monkeys were invluded in order to eliminate the possibility that the observations might be confined to the peculiarity of a single species.

The cats were healthy young adult animals weighing between 1.4 and 2.0 kg.. Lethal doses of intraperitoneal Nembutal were administered and in each case immediate intracardiac perfusion with 15% formalin was carried out. The petrous portion of the temporal bone was then separated from the sphenoid and occipital bones. The tympanic, squamous and mastoid portions of the temporal bones were also chipped away leaving a neuro-osseous unit containing the cochlear and labyrinthine end organs with their respective nerves. The internal ears, thus separated from each side of the skull, were immersed in 15% formalin for an additional period of at least 7 days. Fourteen to twenty-one days were required for decalcification of the internal ears and was accomplished with the use of a solution containing 10% formic acid in 15% formalin. After decalcification the internal ears were dehydrated, imbedded in paraffin blocks, sectioned at 15 u., mounted serially, and stained according to the intensified Protargol technique described by Stotler(27). The sections were extensively studied under oil immersion with particular emphasis on the vestibular neuro-epithelium represented in the cristae of the ampullae of the three semi-circular canals and in the maculae of the saccule and utricle.

Healthy young cats of the same weight and age group as the normal controls were also employed as the experimental animal. Using intraperitoneal Nembutal for anesthesia, the following manual lesions were made with a small

slender knife: (1) unilateral section of the eighth nerve in a series of eight cats; (2) median sagittal section in the floor of the fourth ventricle in the region of the facial genu in a series of five cats. Additional electrocoagulative lesions in the tegmentum were made with the use of the Horsely-Clarke stereotaxic instrument.

An appropriate period, varying from ten to twenty-one days, depending upon the type and amount of neuronal reaction desired, was allowed for degeneration. The animals were sacrificed and prepared according to the same technique employed in the study of the normal preparations.

Studies previously mentioned in the introduction have relied on the accepted Weigert, Marchi, and Nissl type preparations for analysis of their material. The use of the silver staining techniques has been extensively applied by Cajal[10,23] in his investigations of the normal nervous system and by Glees and Le Gros Clark[28], Brodal[29], Stotler[30] and Nauta[31] in experimental studies of the optic, auditory, and other major fiber systems. The use of the silver stained preparations in this study was prompted by the acknowledged superiority of this method for the demonstration of axonal, fine fiber, and terminal ending degeneration.

OBSERVATIONS

The description of the normal anatomy of the vestibular neuro-epithelium has been drawn from observations upon the entire series of normal cats and monkeys. The end organs of the experimental animals have been studied in detail and the histological analysis of the results of six typical lesions will be described to illustrate the results of this investigation.

Study of the normal silver stained preparations revealed the presence of fine unmyelinated fibers as well as the usually described coarse fibers. In accordance with calssic descriptions offered by Cajal[10] and Kolmer[25], the coarse fibers were observed as the peripheral processes of bipolar cells situated in Scarpa's ganglion. These heavily myelinated fibers had an average diameter of 4 to 5 u. and were seen to end in calyx-like structures embracing the lower five-sixths of the hair cells. The central processes of the coarse fibers were also heavily myelinated with an average diameter of about 5 to 6 u.. Characteristically, the peripheral processes of the bipolar cells lose their myelin sheaths immediately before passing through the basement membrane of the vestibular neuro-epithelium. The majority of the fibers appear to end on a single hair cell, but in some instances they may divide to supply two or three cells. In this instance the division occurs near the basement membrane at the point of loss of the myelin sheath.

The fine fibers were observed as undulating unmyelinated fibers whose thickness averaged about 1 to 1.5 u.. These fibers are enveloped in a thin neurolemma and the nuclei of the neurolemmal cells may be seen spaced along the course of the fibers as they run a parallel course to the coarse fibers and in some instances spiral about them. After penetrating the basement

membrane these fine fibers bend at near-right angles giving off collaterals which join the peripheral processes of other fine fibers in forming a plexus at the base of the hair cells. At no time were the constituents of this plexus seen to penetrate beyond the lower one-sixth of the hair cells. Fine fibers were found to be present in all portions of the vestibular nerve both proximal and distal to the ganglion of Scarpa. They undulated parallel to the coarse fibers and were particularly prominent in Scarpa's ganglion, in the cristae of the ampullae of the three semicircular canals and in the maculae of the saccule and utricle, Fig. 1 & 2.

In the histological study of the silver stained preparations, early primary degeneration of the efferents appeared as swollen, darkly staining, grossly fragmented fibers. In those preparations with increasing length of survival period the degeneration appeared as faint linear aggregations of argyrophilic debris lying along the course of the persisting neurolemmal sheath. In those of longest survival, only the neurolemmal sheath could be followed faintly.

Cat 8S. Manual lesion; 20 day degeneration.

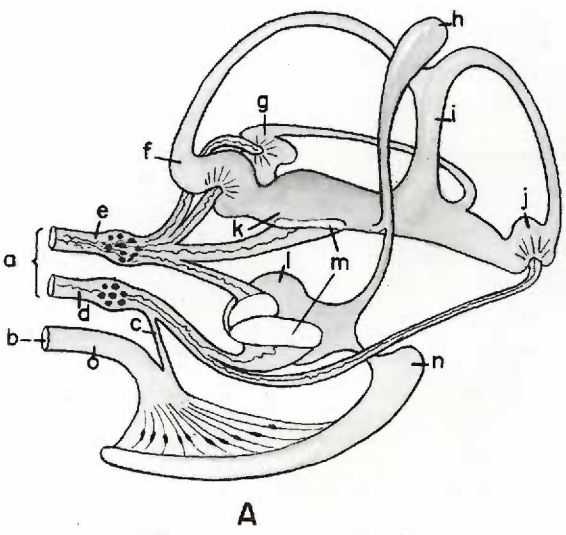
This lesion completely severed the seventh and eighth nerves on the left side leaving a slight amount of hemorrhage manifested by the presence of a small amount of organized antemortem thrombus.

No degeneration could be detected in the cochlear division of the eighth nerve. The intraganglionic spiral bundle of the cochlea remained intact. No loss of ganglion cells occurred in the ganglion of Scarpa or in the spiral ganglion. Since the seventh nerve had been sectioned as well as the eighth, its degenerated fibers could be followed in the facial canal running through the petrous bone. Coarse fibers to the vestibular and

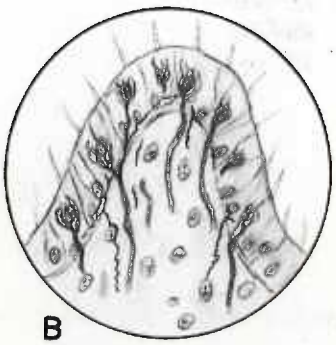
Figure 1. The double innervation of the vestibular neuro-epithelium. Drawing (A) is a schematic representation of the double innervation of the vestibular end organ. The wavy line within all branches of the vestibular division of the eighth nerve (a) represents the efferent fiber system demonstrated in this investigation.

(a) Vestibular division of the eighth nerve.
(b) Cochlear division of the eighth nerve.
(c) Oort's vestibulo-cochlear anastamosis.
(d) Ramus inferior.
(e) Ramus superior.
(f) Ampulla of the anterior semi-circular canal.
(g) Ampulla of the lateral semi-circular canal.
(h) Saccus endolymphaticus.
(i) Common crus.
(j) Ampulla of the posterior semi-circular canal.
(k) Utricle.
(l) Saccule.
(m) Maculae of the utricle and saccule.
(n) Ductus cochlearis.
(o) Cochlear nerve.

Drawing (B) shows the typical appearance of a section of the crista of an ampulla of a semi-circular canal. The fine and coarse fibers course toward the neuro-epithelium in parallel. Coarse fibers end in calyx-like formations about the hair cells while fine fibers ramify in an extensive plexus beneath the hair cells. Drawing (C) shows the typical appearance of the macular epithelium seen in the saccule and utricle. The morphology is similar to that found in the cristae.



A



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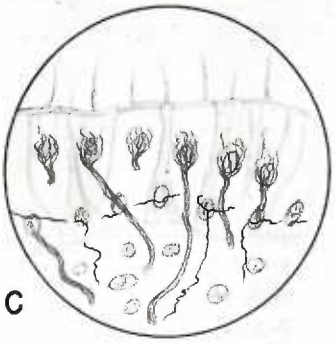
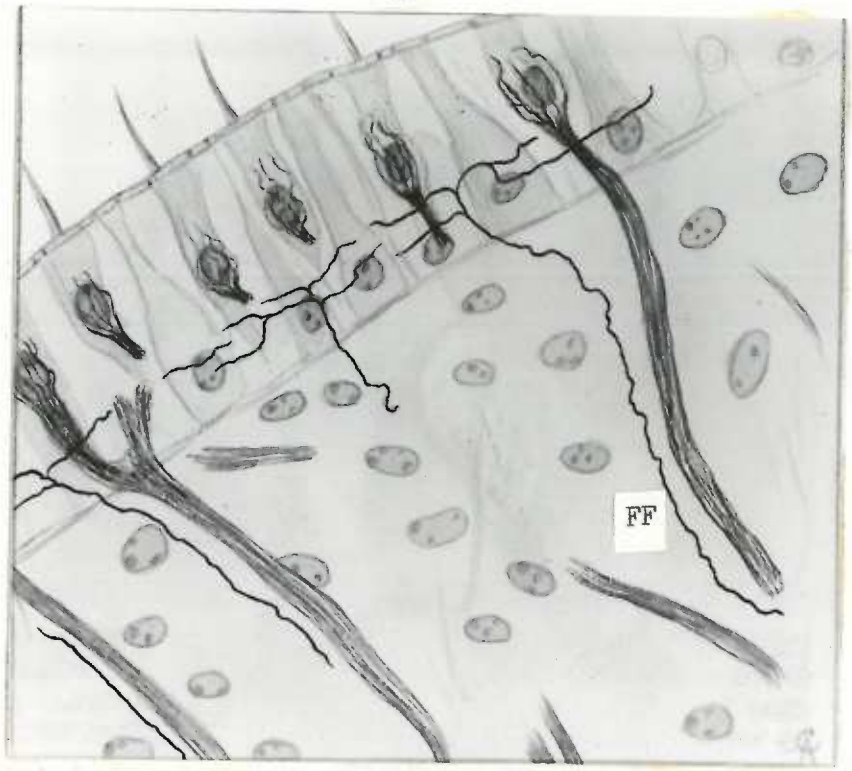


C

1

Figure 2. Two drawings made from representative sections of the macula of the saccule (A) and the crista of an ampulla of a semi-circular canal (B). Note the fine fibers (FF) coursing parallel to the coarse fibers (CF). The coarse fibers embrace the lower five-sixths of the hair cells (HC) in a calyx-like formation as the fine fibers ramify in an extensive plexus (P) beneath the hair cells.

2



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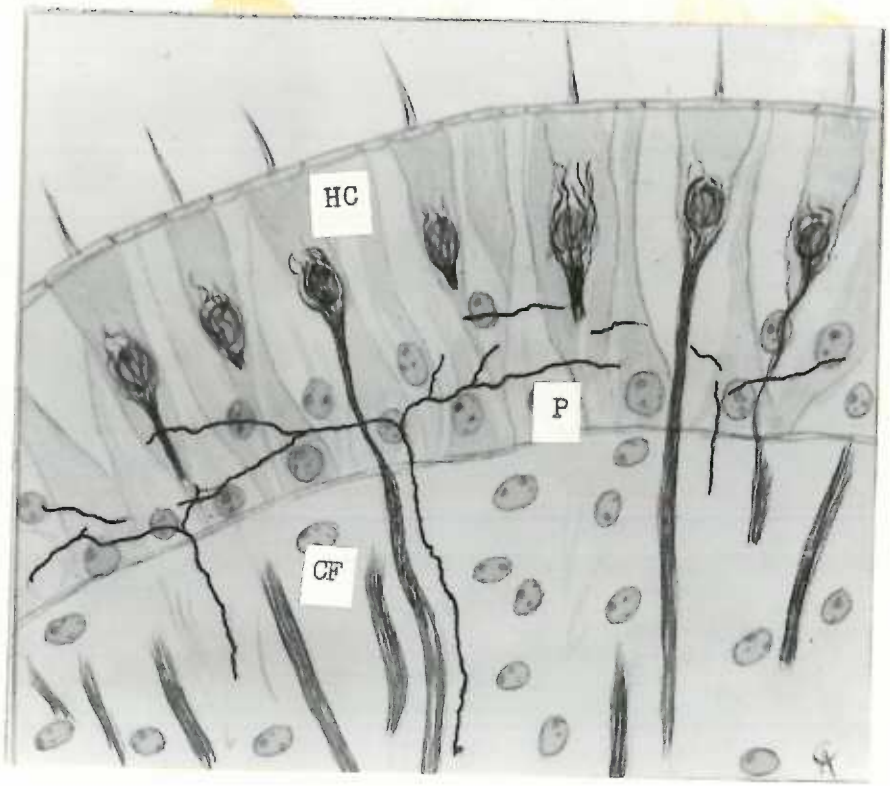

B

cochlear neuro-epithelium remained normal in appearance as in the normal control.

There appeared to be a loss of fine fibers within the vestibular nerve which could be followed peripherally to the cristae of the ampullae of the three semi-circular canals and to the maculae of the utricle and saccule. No intact fine fibers were found supplying the neuro-epithelium of the cristae or maculae of the vestibular end-organ and their original course could be traced as fine argyrophilic debris lying along persistent neurolemmal sheaths.

The internal ear of the right side was unharmed and was identical to the control preparations in every way (Plate VII., Figs. 16 and 17).

Cat 8S2. Manual lesion; 13 day degeneration.

The destructive lesion in this animal was identical to that in Cat 8S.

The coarse fibers to the cochlear and vestibular neuro-epithelium appeared unaltered. No fiber loss could be detected in the cochlear division of the eighth nerve or in the intraganglionic spiral bundle. Terminal fibers ending on the internal and external hair cells of the organ of Corti were intact.

Active primary degeneration of the fine fibers could be detected in the cristae of the ampullae of the three semi-circular canals and in the maculae of the saccule and utricle. Linear aggregations of argyrophilic debris within remnant neurolemmal sheaths marked the former existence of fine fibers. The degenerating fine fibers could be detected both proximal and distal to Scarpa's ganglion as well as within the ganglion itself.

The internal ear of the right side was unharmed and was identical to the control preparations.

Cat MS. Manual lesion; 13 day degeneration.

This lesion was a sagittal section through the floor of the fourth ventricle at the level of the genu of the facial nerve. It was placed slightly to the left of the median raphe and involved the fibers of the seventh nerve. This paramedian sagittal section had an antero-posterior extent of 3 mm. and extended 2.5 mm. rostral and caudal to the area marked by the facial genu. Degeneration could be seen bilaterally in the brain-stem as the crossing fibers in the median raphe had been cut.

Examination of sections from preparations of the right and left internal ears revealed the degeneration of fine fibers occuring bilaterally. Active primary degeneration was visualized in both right and left ears and was specifically found in the vestibular end-organs. These changes were similar to those found in Cat 8S2. except that the single central lesion caused a fiber loss to occur in both right and left internal ears.

The coarse fibers to the vestibular end-organs and the cochlear apparatus did not undergo any detectable morphologic change.

On the left side the degeneration of the facial nerve could be seen within the petrous bone and persistent fibers whose cell bodies lay in the geniculate ganglion could be identified. The seventh nerve was intact on the right side. (See Plate VIII., Figs. 18 & 19 and Plate IX., Fig. 20)

Cat MT. Electrocoagulation lesion; 15 day degeneration.

This lesion was placed slightly to the left of the median raphe involving the rostromedial portion of the abducens nucleus and some of the egressing fibers which form the genu of the facial nerve. The lesion was discreet having a diameter of only 2.5 mm.. Degeneration of fibers crossing in the median raphe extended noticeably to the right of the raphe.

The left internal ear exhibited a loss of fine fibers noted prominently in the cristae and the maculae of the vestibular end-organ. Argyrophilic debris within remnant neurolemmal sheath cells indicated the previous existence of fine fibers. Vestibular coarse fibers and the cochlear apparatus remained intact.

The internal ear of the right side appeared similar to the left except that a few fine fibers remained intact due to the location and limited extent of the lesion. (See Plate IX., Fig. 21)

Cat Tp234. Electrocoagulation lesion; 15 day degeneration.

The Horsely-Clarke stereotaxic instrument was employed to place this lesion in the rostral portion of the left lateral pontine and medullary tegmentum. Coordinate settings of posterior 2, 3 and 4 were used. Parts of the vestibular nuclei and adjacent reticular formation were involved.

This resulted in the partial degeneration of fine fibers occuring bilaterally. Coarse fibers to the vestibular neuro-epithelium and cochlea remained intact as did the intraganglionic spiral bundle. (See Plate X., Fig. 22)

Cat Tp8910. Electrocoagulation lesion; 15 day degeneration.

This lesion was made by setting the coordinates of a Horsely-Clarke stereotaxic instrument at posterior 8, 9 and 10 which resulted in the destruction of an area in the caudal portion of the left lateral pontine and medullary tegmentum involving the vestibular nuclei and the adjacent reticular formation.

Fine fiber losses could be detected as argyrophilic debris distributed along faintly persisting neurolemmal sheaths. These fiber losses occurred

bilaterally, but were not complete as a few intact fine fibers could be be detected. However, the loss of fine fibers was more complete in this caudal lesion than it was in Cat Tp23¼. (See Plate X., Fig. 23)

DISCUSSION

The presence of fine fibers as a component of the innervation of areas of the vestibular neuro-epithelium has been indicated by the work of Cajal[23], Retzius[24], Kolmer[25], and Poljak[26]. Their observations did not indicate whether the presence of fine fibers was a constant occurrence in all areas of the vestibular end organ; and the polarity of the fibers was generally conceded to be afferent as related to the central nervous system.

Observations of serial sections of the internal ear and vestibular nerve have shown that a dual innervation consisting of fine and coarse components exists within the three cristae of the ampullae of the semicircular canals and the maculae of the saccule and utricle. The fine fibers could be traced within the vestibular nerve both proximal and distal to Scarpa's ganglion from the brain stem to the neuro-epithelium of the end-organ.

The examination of individual ganglion cells reveals that the peripheral processes of the bipolar cells of Scarpa's ganglion are of slightly smaller diameter (4.0 - 4.5 u.) than the central processes which have a diameter range of 5.0 - 6.0 u.. However, the diameter of the fine fibers falls into a distinctly lower category with a range of 1.0 - 1.5 u.. The liklihood of the fine fibers taking origin from the cells of Scarpa's ganglion is precluded by the uniform morphology of these cells.

Observations of all areas of the end-organ show a consistent dual innervation without deviation of the normal population of coarse and fine fibers in any specific area of the neuro-epithelium. The coarse fibers are seen to end upon from one to three hair cells with the usual mode

being to one alone. The type of termination is a calyx-like formation which engulfs the lower five-sixths of the cell. This arrangement constitutes a very specific point to point relationship between these components of the nerve and the receptor. On the other hand, the fine fibers form a plexus within the neuro-epithelium of the end-organ which parallels the epithelial surface and lies at the level of the bases of the hair cells. Its terminations upon the hair cells are in the form of varicosities and free endings. The individual fine fibers of the plexus extend for considerable distances so that large numbers of cells are innervated by a single fiber and each cell is related to numerous fine fibers. This is in distinction to the parallel system in which the mode is the termination of one coarse fiber upon a single receptor cell. The small areas of contact of the fine fibers contrast strongly with the enveloping character of the calyx-like formations of a large fiber terminal.

The observations of normal material have revealed two contrasting types of innervation to the hair cells; one very specific and one of a diffuse, generalized character. The fact that the fine fibers could be followed as far as the brain-stem indicated that their cells of origin might be found there rather than in Scarpa's ganglion. The experimental lesions performed in this investigation were directed toward the objective of locating the cells of origin which supply the fine fibers to the end organ epithelium.

One series of eight cats sustained unilateral lesions in which the eighth nerve was severed proximal to Scarpa's ganglion. Following survival periods of varying lenths of time, depending upon the degree

of axonal reaction desired, it was noted that degeneration of the fine fibers took place distal to the lesion in every case. On the other hand, the coarse fibers distal to the lesion showed no morphologic deviation from the control preparations. This indicated that the fine fibers which innervate all areas of the vestibular neuro-epithelium have their cells of origin within the brain stem and have an efferent relationship to the central nervous system.

To further clarify the location of the cells which supply fine unmyelinated fine fibers to the vestibular end-organ, shallow longitudinal sections were made in the floor of the fourth ventricle in a series of five cats. This resulted in bilateral degeneration of fine fibers innervating the vestibular end organ. Degenerative changes of these fine fibers could be traced from the central portion of the vestibular nerve to its terminations in the end organ. Areas of chromatolysis were noted in the vestibular nuclei. This would seem to indicate that the origin of the cells supplying fine fibers to the vestibular end organ are located either in the vestibular nuclear group of the opposite side or in the adjacent reticular formation. Electrocoagulative lesions made in the midline of the tegmentum resulted in similar degenerations of fine fibers occurring bilaterally. The rostro-caudal extent of single lesions of this variety was not as great as the manual sagittal sections and as was expected, fine fibers leading toward the neuro-epithelium occasionally escaped injury.

Unilateral electrocoagulative lesions made in the tegmentum resulted in partial losses of fine fibers occurring bilaterally. These lesions were made in an area of the pontine and medullary tegmentum extending

from the inferior colliculus to the obex. The observation that partial destruction of fine fibers occurred following lesions which were made over a wide area of the brain stem serves to indicate that a nuclear group of considerable rostro-caudal representation in the tegmentum must be the site where the cells supplying fine fibers to the end-organ are located.

Although the exact location of the cells supplying fine fibers to the vestibular neuro-epithelium is not conclusively known, the origin from the contralateral brain stem and the peripheral distribution of fine fibers within the neuro-epithelium of the vestibular end organ has been demonstrated in this investigation. Chromatolytic changes which occur in the cells of the vestibular nuclei of the opposite side following unilateral section of the eighth nerve suggest that this might be the location of the cells of origin of the fine fibers. However, the reaction may be from overactivity of the cells of the intact side. Another possibility is the adjacent reticular formation.

Median sagittal section and median tegmental electrocoagulative lesions (Cats MS and MT) were placed in such a way that the olivo-cochlear bundle described by Rasmussen[1,17,18,19] was involved. It was not possible to detect fiber loss within the cochlear division of the eighth nerve. Fernandez[3] has traced the olivo-cochlear bundle through the vestibular nerve and describes it crossing in Oort's vestibulo-cochlear anastamosis to be eventually represented as the intraganglionic spiral bundle which terminates on the hair cells of the organ of Corti. The intraganglionic spiral bundle did not degenerate in preparations obtained from animals who had sustained lesions of the so called olivo-cochlear bundle which crosses

the median raphe in the region of the facial genu.

The presence of an efferent bundle to the cochlea was not substantiated in this investigation. It was not the purpose of this investigation to prove or disprove its existence, but findings have pointed to the more striking efferent innervation of the vestibular division of the internal ear. The possibility that a parallel system of efferent fibers to the cochlear epithelium may exist is of course intriguing, but was without confirmation in our observations.

Flourens[32] has been credited with the initial physiological investigations on the semi-circular canals. His studies involved selective destruction of individual semi-circular canals in the pigeon followed by careful recording of the disturbed states of muscle tone. His findings touched off a spark of interest that has given us some extremely detailed knowledge of labyrinthine function. Mach[33] and Breuer[34,35,36] presented their theories which proposed that the flow of endolymph in the semi-circular canals deforms the cupola with its underlying hair cells resulting in nerve impulses being transmitted to secondary connections in the brain stem. Ewald[37] described the semi-circular canals as the seat of tonic function of the labyrinth. Later, especially under the influence of Magnus and de Kleijn[38], the otolith apparatus came to be regarded as the main source of labyrinthine tone. However, a number of workers, (Maxwell[39]; Lorente de No[40]; Tait and McNally[41,42] and Lowenstein[43]) have furnished conclusive evidence that the semi-circular canals have an important share in the influence which the labyrinth exercises on muscle tone. Steinhausen's[44] photographic recordings, which were shown at the sixteenth International Congress of Physiology at Zürich in 1938,

conclusively showed the pendulous swinging of the cupola in obedience to the flow of endolymph. Ross[45] (1936) obtained oscillographic records of single fiber discharges from the eighth nerve of a frog, but did not analyse them quantitatively. During the same year, Lowenstein and Sand[46] made their first attempt to obtain oscillographic records from the nerve branch to the horizontal ampulla of the dogfish. These authors obtained evidence that the ampulla discharges impulses spontaneously when at rest, and that this discharge is augmented during ipsilateral rotation and diminished during contralateral rotation. They stated that their records gave only an additive picture of asynchronous activity in the whole nerve branch and that their results were necessarily no more than qualitative. In 1940 Lowenstein and Sand[47] obtained oscillographic records of single fiber action potentials in the ray (Raja clavata). They were able to quantitatively analyse the "resting discharge" obtained from a single fiber preparation of an isolated labyrinth. Large potentials were clearly derived from the activity of a single unit. Their records showed a spontaneous frequency of discharge from the stationary labyrinth which was augmented by ipsilateral rotation and diminished by contralateral rotation. They explained that the fundamental property of this "resting discharge" is to maintain a permanent state of excitation which gives rise to a persistent, spontaneous rhythm, the origin of which must remain, for the present, a matter of conjecture. The essential fact is that the rhythmical excitation is there when no deforming force operates on the cupola.

In addition to these large potentials, their records showed a background of smaller potentials whose frequency of discharge did not vary with angular acceleration. At no time were they able to note that the background

discharges would vary while the large potentials would remain stationary during angular acceleration. This finding led them to explain that the ampulla, in addition to its principal innervation, is supplied with fibers of relatively small diameter which are not concerned with response to totation and whose function remains unknown.

The fine fiber system postulated by the preceding authors would apparently lie in an afferent relationship to the brain stem as its activity could be observed in an isolated preparation. The results of the present investigation provide adequate anatomical demonstration of a dual system of nerve fibers in the vestibular neuro-epithelium. The fact that isolated labyrinthine preparations yielded evidence of a spontaneous rhythmicity on the part of the resting cupola does not preclude the possibility of central modification of an excitatory state maintained in the labyrinthine neuro-epithelium. The probable origin of these efferent fibers from the contralateral vestibular nuclei or tegmental reticular formation opens the possibility that the activity of one end organ might secondarily affect the other following relay through multiple synaptic connections in the brain stem. Central modification of vestibular end organ activity and an extensive bilateral representation of the vestibular system are suggested by the results of this investigation.

SUMMARY AND CONCLUSIONS

The study of serial sections of the internal ear of the cat and monkey revealed the presence of a system of fine fibers in addition to the better known coarse fibers innervating the vestibular neuro-epithelium. A series of normal preparations were studied to determine the extent of distribution of these fine fibers within the neuro-epithelium of the intact vestibular apparatus.

The present series of experiments was undertaken to differentiate the point of origin of the fine fiber system, i.e. central or peripheral. In one series of cats the eighth nerve was sectioned proximal to Scarpa's ganglion and in another series a mid-sagittal section was made in the floor of the fourth ventricle. Additional unilateral electrocoagulative lesions were made in the pontine and medullary tegmentum extending from the inferior colliculus to the obex involving portions of the vestibular nuclei and the adjacent reticular formation. After survival periods of ten to twenty-one days, the animals were sacrificed and serial sections of the internal ears were prepared using the intensified Protargol technique.

Sectioning of the eighth nerve resulted in the degeneration of these fine fibers in all areas where they had been previously observed indicating their central origin. Mid-sagittal section in the floor of the fourth ventricle resulted in identical changes occurring bilaterally indicating an origin from the contralateral brain stem. Unilateral tegmental electrocoagulative lesions resulted in bilateral partial degeneration of these fine fibers which occurred primarily in the contralateral vestibular end-organ. Partial degeneration which occurred in the ipsilateral end-organ

was interpreted as arising from lesions involving the crossed efferent fibers. Active primary degeneration was observed in preparations where the survival time was relatively short. The coarse fibers also seen in the normal preparation remain unchanged as their cells of origin are situated in Scarpa's ganglion.

Analysis of the normal and experimental material has yielded the following information:

1. The vestibular neuro-epithelium has been shown to have a double innervation which is characteristic of all areas of the end-organ.

2. A group of large myelinated fibers originate from Scarpa's ganglion and terminate in a calyx-like formation about one or more hair cells. These fibers lie in an afferent relationship to the central nervous system.

3. A fine unmyelinated fiber group originates from the contralateral brain stem and terminates in an extensive plexus at the base of the hair cells. These fibers lie in an efferent relationship to the central nervous system.

4. The partial degeneration which occurred following tegmental electrocoagulative lesions suggests that the possible locus of the cells supplying fine fibers to the vestibular neuro-epithelium is in the contralateral vestibular nuclei or the adjacent reticular formation.

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TABLE OF ABBREVIATIONS

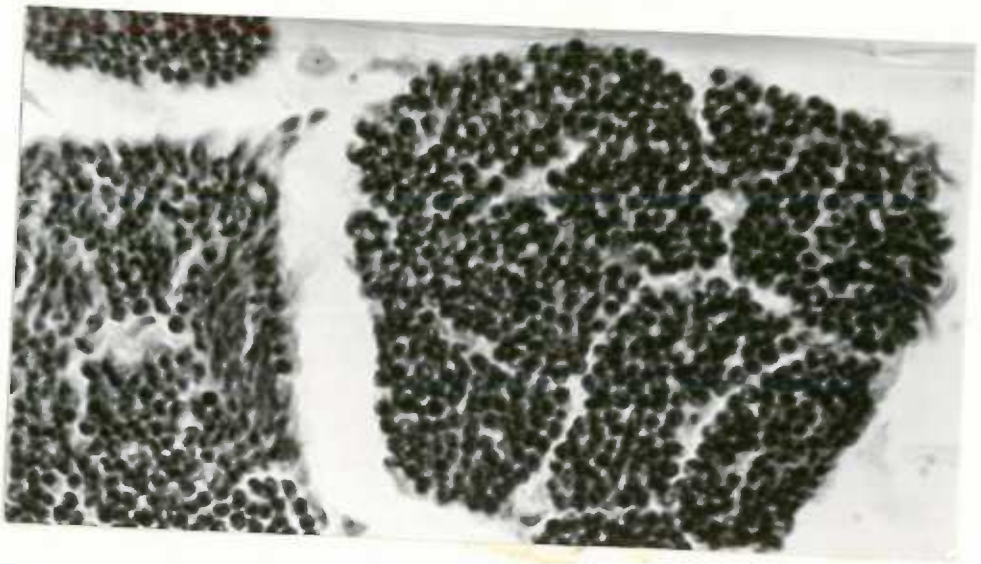
C	Cilia of hair cells
HC	Hair cell
VN	Vestibular neuro-epithelium
CX	Calyx-like formation
P	Plexus of fine fibers
CF	Coarse fiber
FF	Fine fiber
FV	Fourth ventricle
MR	Median Raphe
AN	Abducens nucleus
G7	Genu of the facial nerve

PLATE I.

Figure 3. A crossection of the cochlear nerve of a cat. Note the remarkable uniformity of nerve fiber caliber. (low power)

Figure 4. A crossection of the vestibular division of the eighth nerve in a normal cat showing some bipolar cells in Scarpa's ganglion and a variety in nerve fiber caliber. (low power)

Figure 5. A higher power view of a crossection of the branch of the superior division of the vestibular nerve leading toward the crista of the ampulla of the lateral semi-circular canal. Note that two sizes of fibers predominate; fine fibers (FF) and coarse fibers (CF).



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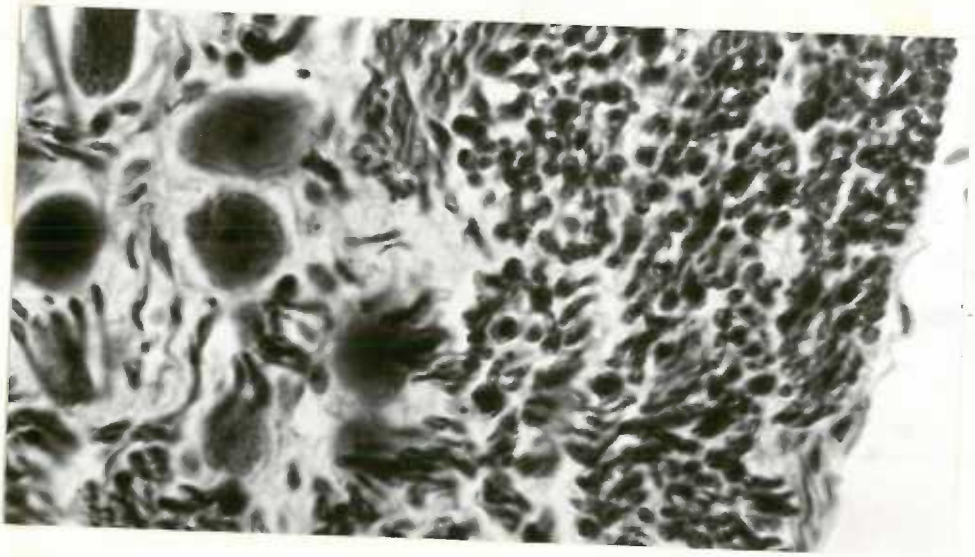

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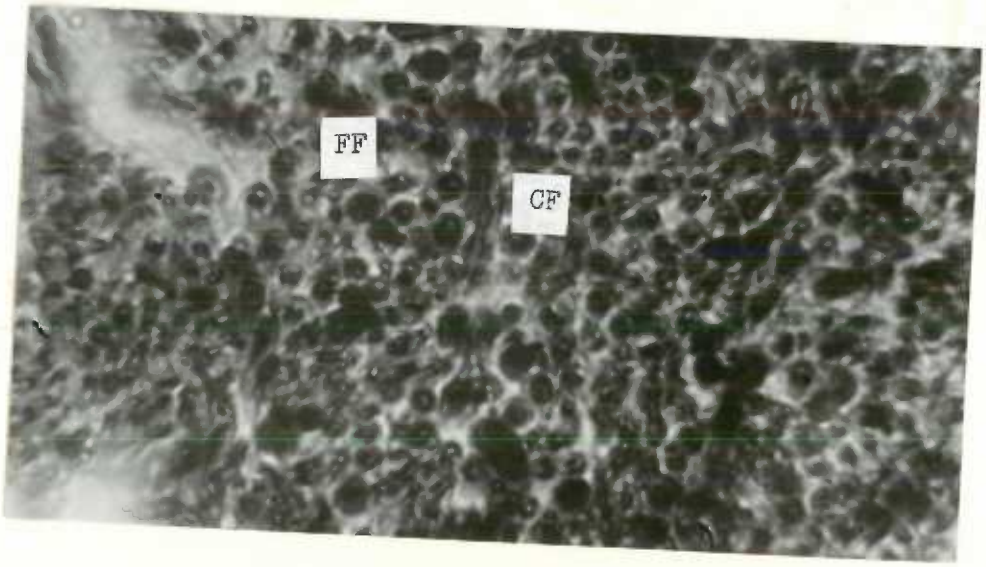

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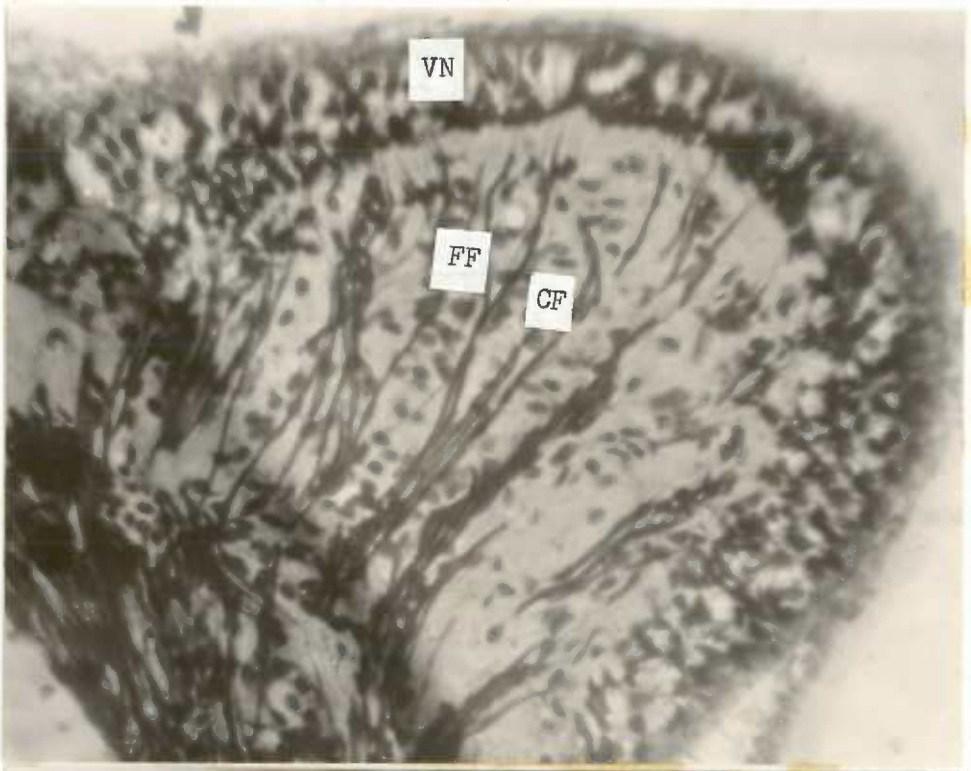
PLATE II.

Figure 6. This is a section through the crista of the ampulla of the posterior semi-circular canal of a normal cat showing the presence of fine fibers (FF) and coarse fibers (CF) running in parallel toward the vestibular neuro-epithelium (VN). (low power magnification)

Figure 7. This is a high-power magnification of the same section shown in the previous figure. Note the fine (FF) and coarse fibers (CF) in parallel.



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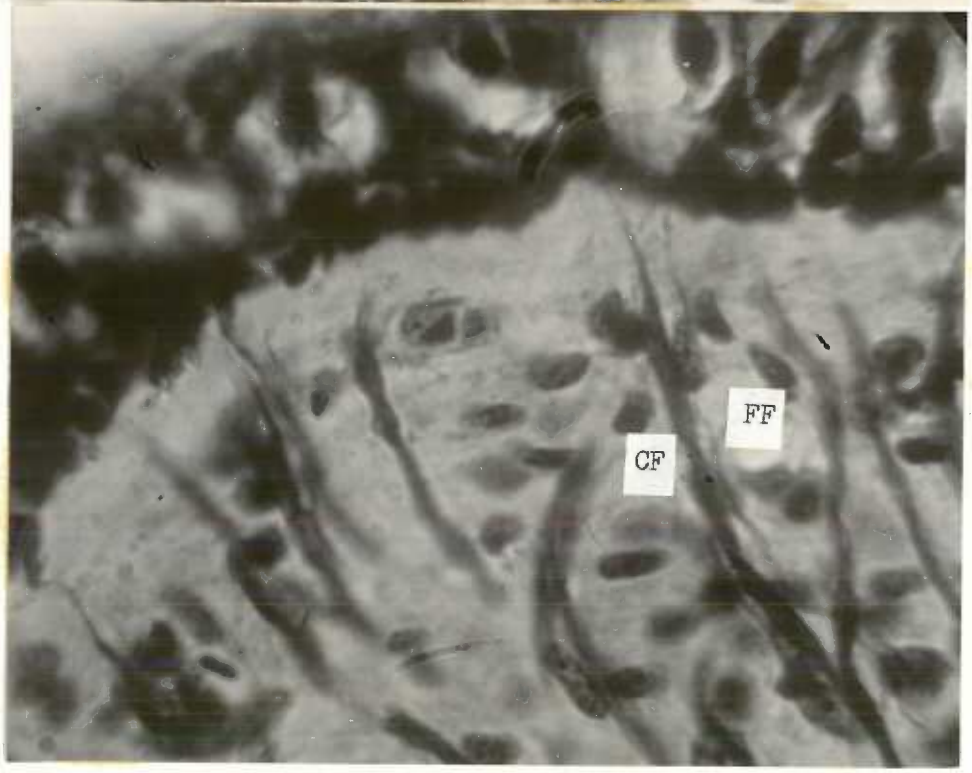

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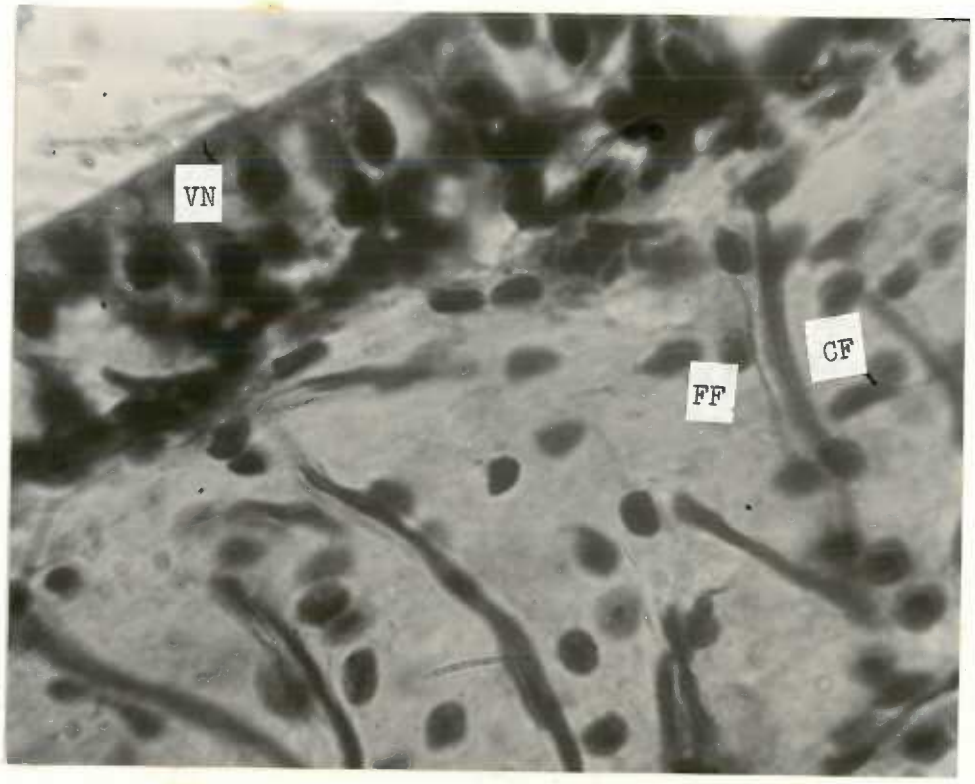
PLATE III.

Figure 8. A high-power photomicrograph of a section through the macula of the saccule in a normal cat showing a coarse (CF) and fine fiber (FF) coursing toward the neuro-epithelium (VN).

Figure 9. A high-power magnification of a section through the crista of the ampulla of the lateral semi-circular canal showing a fine fiber (FF) running parallel to the plane of the neuro-epithelium (VN) just below the hair cells (HC).



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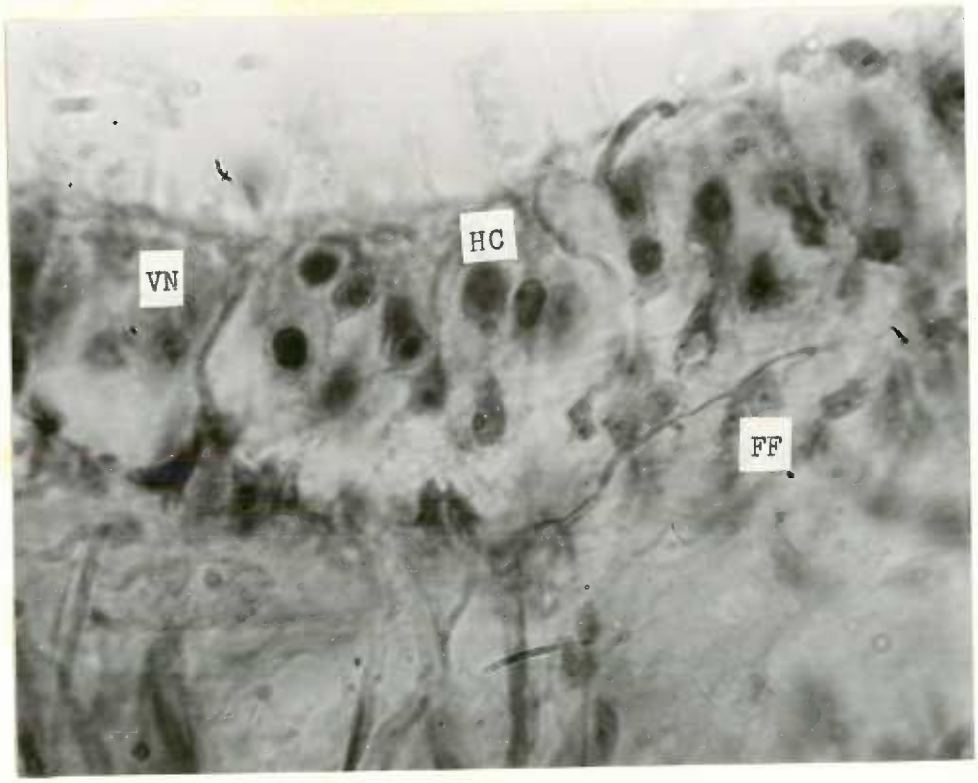

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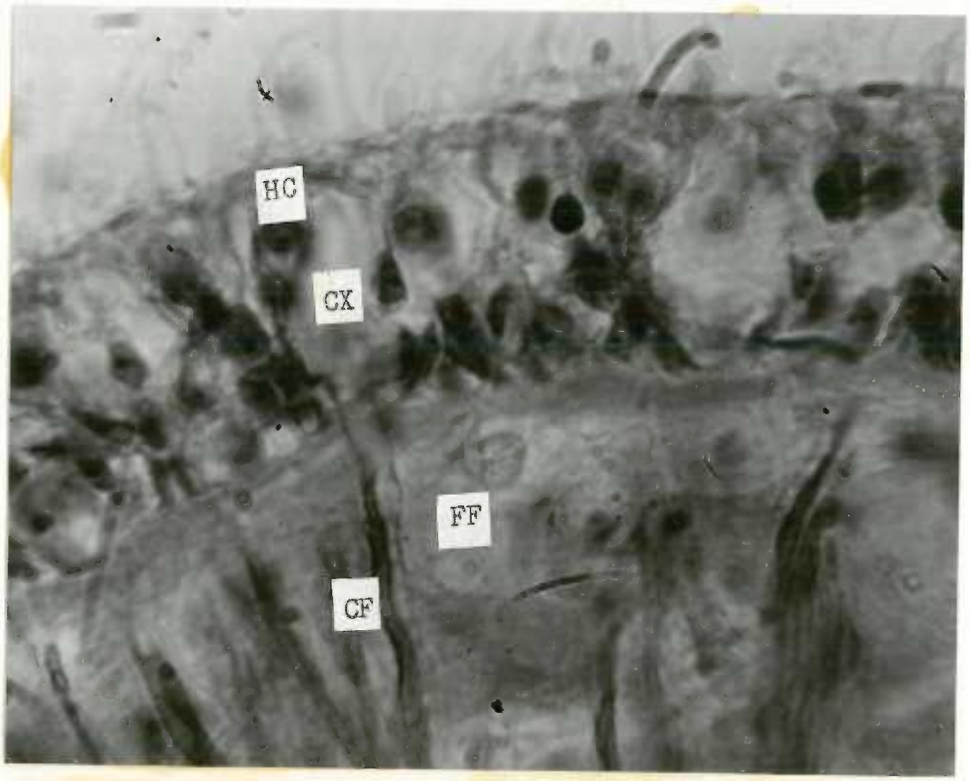
PLATE IV.

Figure 10. A photomicrograph of the crista of the ampulla of the lateral semi-circular canal showing a coarse fiber (CF) with its calyx-like formation (CX) embracing the hair cell (HC) and a fine fiber (FF) beside it.

Figure 11. This photomicrograph of a section through the macula of the utricle of a normal cat shows a portion of the plexus (P) formed by the fine fibers at the base of the hair cells.



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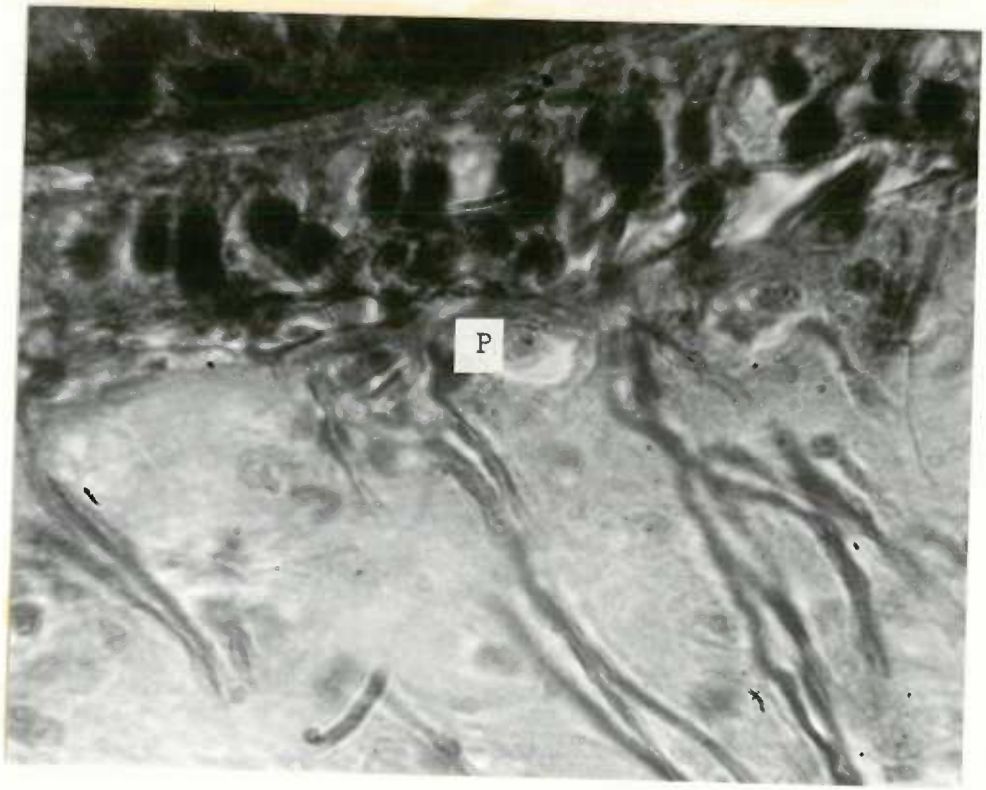

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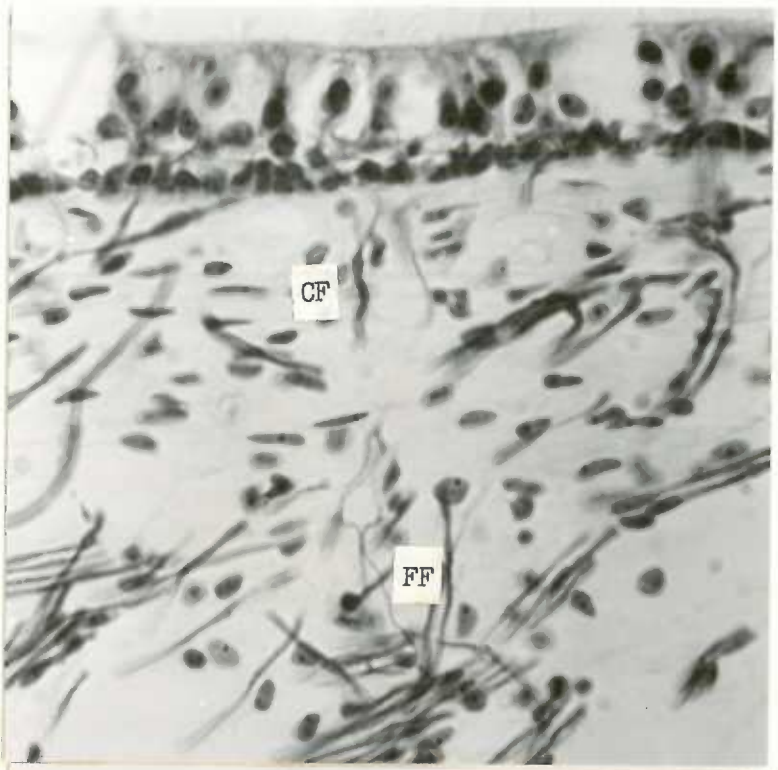
PLATE V.

Figure 12. A photomicrograph of a section through the macula of the utricle in a normal monkey showing fine (FF) and coarse fibers (CF).

Figure 13. The macula of the saccule in a normal monkey showing fine (FF) and coarse fibers (CF).



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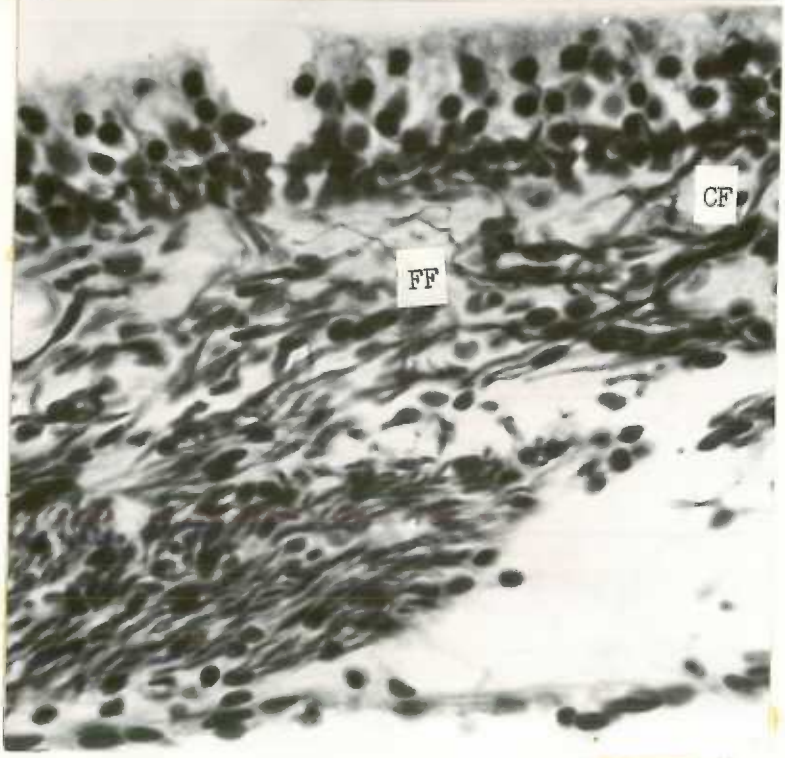

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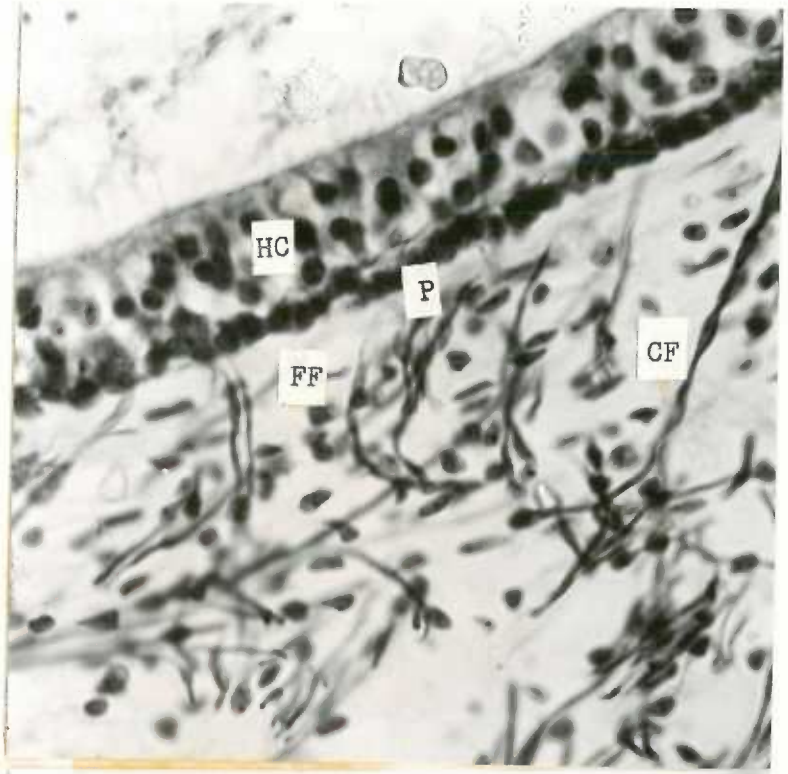
PLATE VI.

Figure 14. The crista of the ampulla of the anterior semicircular canal of a normal monkey showing fine (FF) and coarse fibers (CF). Note the fine fiber plexus (P) just beneath the hair cells (HC).

Figure 15. The crista of the ampulla of the lateral semicircular canal of a normal monkey showing fine (FF) and coarse fibers (CF).



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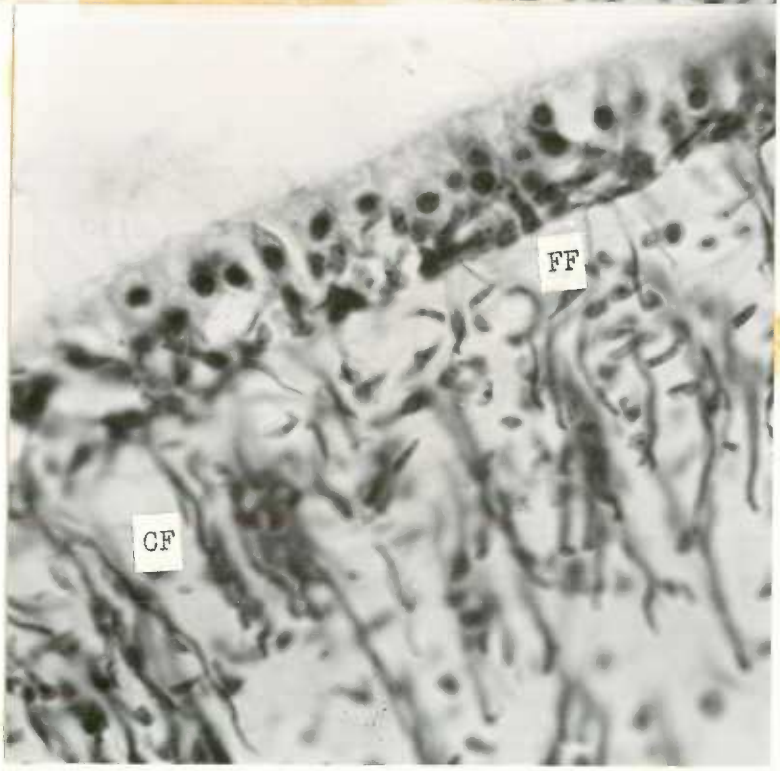

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PLATE VII.

Figure 16. Cat 8S. A photomicrograph of a section through the crista of the ampulla of the lateral semi-circular canal in a cat following sectioning of the eighth nerve. Note that fine fibers are absent and that coarse fibers (CF) retain their normal morphology.

Figure 17. A high power view of the same section shown in Figure 16. Note the absence of fine fibers in the presence of intact coarse fibers (CF).

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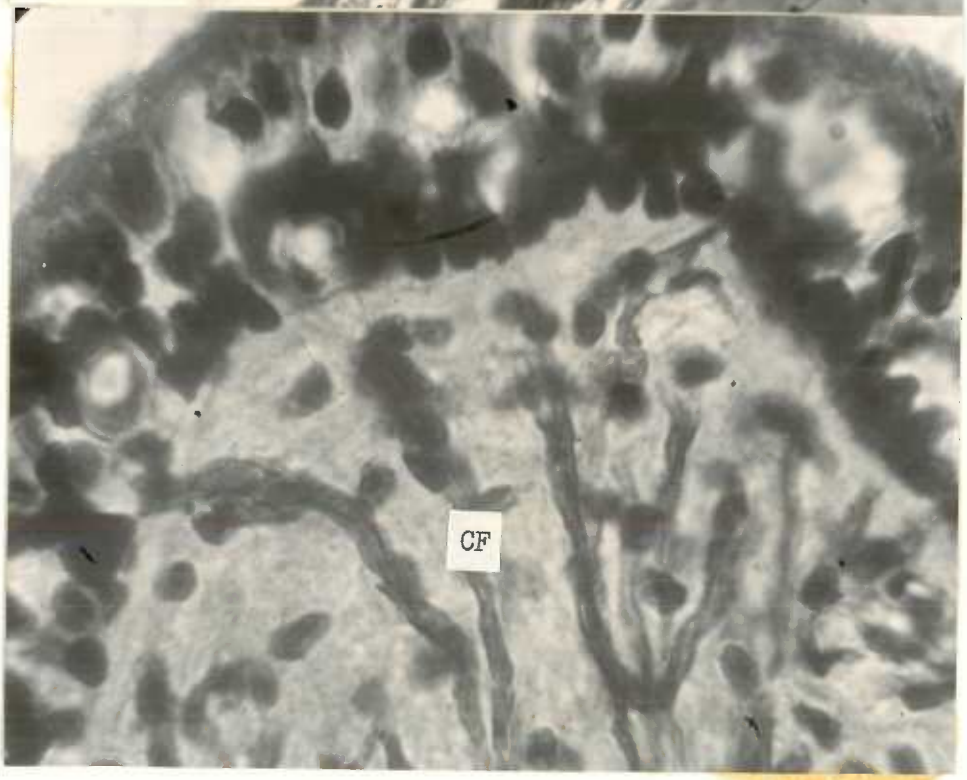

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PLATE VIII.

Figure 18. Cat MS. This is a section through the crista of the ampulla of the posterior semi-circular canal taken from the left internal ear. This animal sustained a median sagittal section in the floor of the fourth ventricle. Fine fibers are absent wheras coarse fibers (CF) are intact.

Figure 19. Cat MS. This is a section of a crista of the ampulla of the lateral semi-circular canal taken from the right internal ear of the same animal shown in the previous figure. This crista also shows the absence of fine fibers as does the previous figure. Coarse fibers (CF) are intact.

18

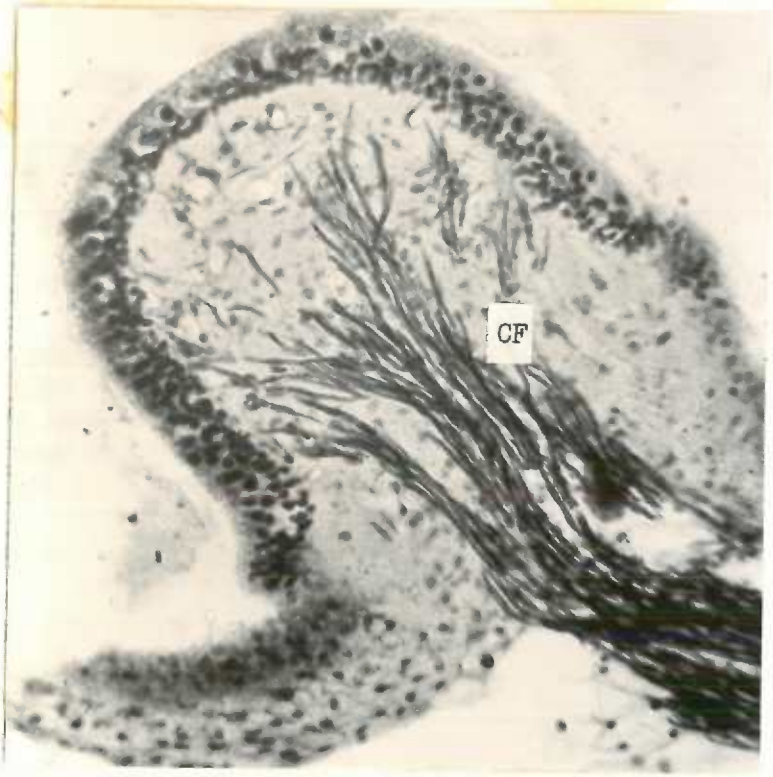

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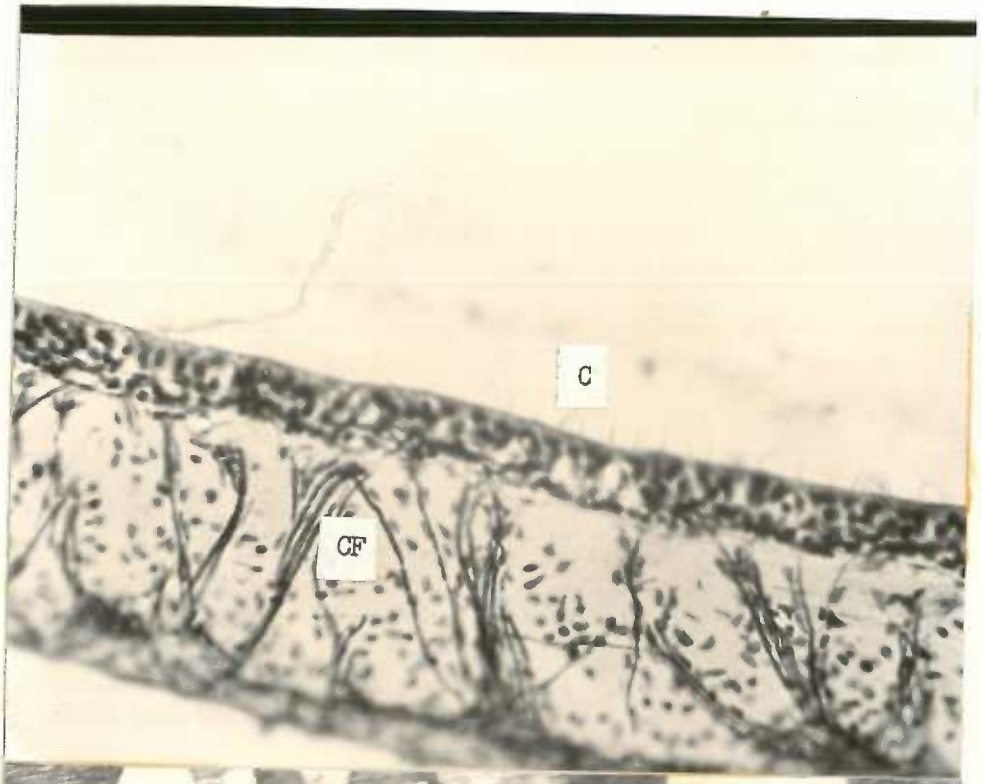
PLATE IX.

Figure 20. Cat MS. This is a photomicrograph of a section through the macula of the saccule of the left internal ear taken from the same animal shown in the previous two figures. Note the absence of fine fibers with the presence of unharmed coarse fibers (CF). Note the cilia (C) projecting from the hair cells.

Figure 21. Cat MT. An electrocoagulative lesion in the floor of the fourth ventricle (FV) showing the extension of degeneration accross the median raphe (MR) to the opposite side. Note the abducens nucleus (AN) and the genu of the seventh nerve (G7).



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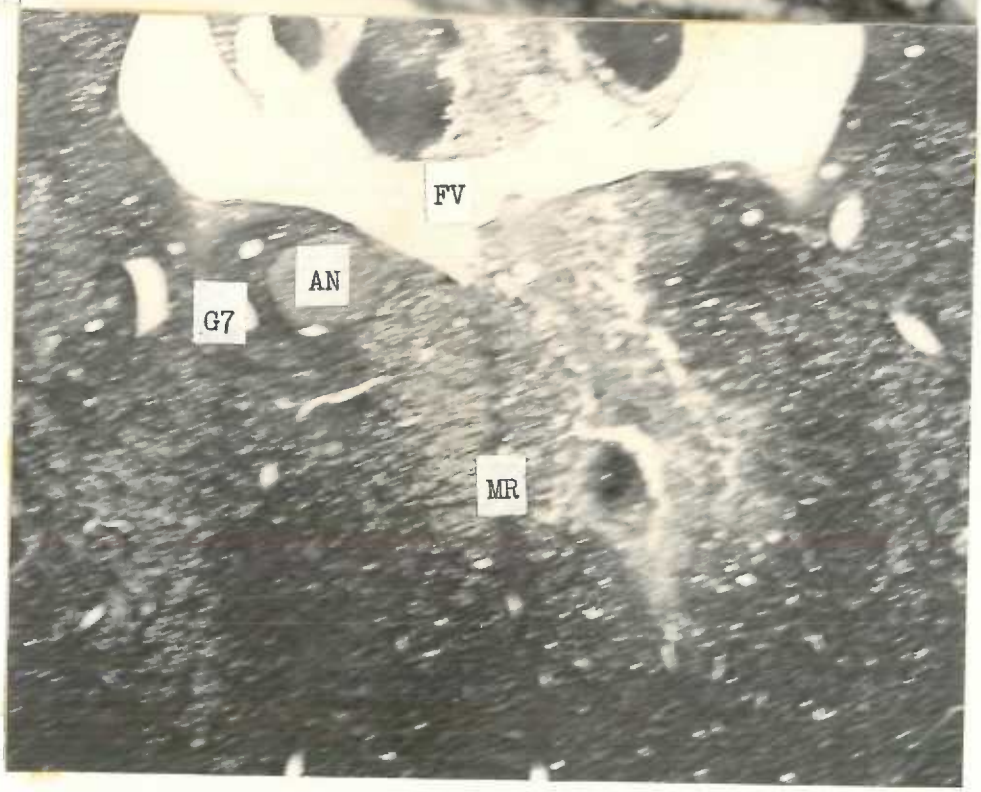

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PLATE X.

Figure 22. Cat Tp234. This is a low power view of a section through the crista of the anterior semi-circular canal. Note that the coarse fibers (CF) are intact in the presence of a marked reduction of fine fibers.

Figure 23. Cat Tp8910. A low power view of a section through the crista of the ampulla of the lateral semi-circular canal showing intact coarse fibers (CF) with a distinct reduction in the number of fine fibers (FF).

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