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APPROVAL SHEET

Title of Thesis: Primary and Secondary Vestibular Connections in the Brain Stem and Cerebellum

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ABSTRACT

Title of Dissertation: PRIMARY AND SECONDARY VESTIBULAR CONNECTIONS IN THE BRAIN STEM AND CEREBELLUM: An Axoplasmic Transport Study in the Monkey and Cat

Steven Craig Carleton, Doctor of Philosophy, 1983

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The projections of the vestibular ganglion were explored in the monkey by anterograde transport of tritiated amino acids from the labyrinth. The central connections of the principal vestibular nuclei (VN) were studied by retrograde and anterograde axoplasmic transport technics in the monkey and cat.

Primary vestibular fibers terminate in virtually all parts of the superior (SVN) and medial vestibular nuclei (MVN). Projections to the inferior vestibular nucleus (IVN) terminate in all areas except cell group "f", while peripheral inputs to the lateral vestibular nucleus (LVN) are restricted to its ventral part. Of the small cell groups associated with the VN, only the interstitial nucleus of the vestibular nerve and cell group "y" receive primary vestibular fibers. Primary vestibular fibers project beyond the VN to terminate in the ipsilateral accessory cuneate nucleus, subtrigeminal lateral reticular nucleus and reticular formation (RF). Primary vestibulocerebellar projections terminate as mossy fibers in the ipsilateral nodulus, uvula, flocculus, lingula and deep folia of vermal lobules V and VI; no primary fibers terminate in the fastigial nuclei (FN).

The most impressive central afferents to the VN are commissural projections from the contralateral MVN, SVN, IVN and cell group "y". Other brain stem afferents are derived from the perihypoglossal nuclei (PH), the interstitial nucleus of Cajal (INC), the visceral nuclei of the oculomotor nuclear complex (OMC) and the RF. Spinovestibular projections arise from the contralateral central cervical nucleus (CCN). Cerebellovestibular projections differ for LVN, IVN and MVN. LVN receives cortical inputs from the ipsilateral anterior lobe vermis, and bilateral projections from rostral FN. IVN receives fewer fibers from the anterior lobe, but has substantial inputs from the nodulus, uvula and middle portions of FN. MVN receives cortical projections primarily from the ipsilateral flocculus.

The largest contingent of efferent fibers from the VN are commissural projections. MVN contributes the greatest number of commissural fibers. MVN also projects bilaterally to the spinal cord, the PH, the abducens nuclei and the OMC, and contralaterally to the CCN, trochlear nucleus (TN), INC and rostral interstitial nucleus of the medial longitudinal fasciculus. IVN projects bilaterally to the spinal cord via the medial longitudinal fasciculus (MLF); en route, fibers terminate in the paramedian reticular nuclei and PH. IVN also has impressive ipsilateral projections to nucleus β of the inferior olive. The commissural projections of IVN are similar to those of MVN, but smaller. Ascending projections from IVN reach the TN and OMC with the same distribution as crossed fibers from MVN. LVN has ipsilateral projections that descend in the vestibulospinal tract (VST); collaterals of the VST terminate in the lateral reticular nucleus and medial RF. In the cat, LVN also projects to the OMC via the ipsilateral ascending tract of

Deiters. SVN has contralateral projections to the VN, ipsilateral projections to the TN and INC, and bilateral projections to the OMC. Ipsilateral fibers from SVN ascend in the MLF; crossed ascending projections pursue a ventral course and decussate in the caudal mesencephalon.

Secondary vestibulocerebellar projections are outnumbered by primary vestibulocerebellar fibers. LVN does not appear to project to the cerebellum, and none of the VN project to the FN.

PRIMARY AND SECONDARY VESTIBULAR CONNECTIONS IN THE BRAIN STEM AND CEREBELLUM
An Axoplasmic Transport Study in the Monkey and Cat

by
Steven Craig Carleton

Dissertation submitted to the Faculty of the Department of Anatomy
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for Margie

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INTRODUCTION

The central projections of the labyrinth and the connections of the vestibular nuclei reflect the importance of the vestibular system in postural reflexes, the maintenance of a stable visual field, and the subjective sensations of equilibrium and orientation in three dimensions. Primary vestibular projections are the only primary afferents with terminations in both brain stem nuclei and the cerebellar cortex. They represent the greatest contingent of afferents to the vestibular nuclei which, in turn, distribute secondary fibers more widely in the neuraxis than any other special sensory system.

Because distinctive secondary vestibular projections arise from particular regions within individual vestibular nuclei (VN), the pattern of termination of primary vestibular fibers has particular functional significance. Information concerning the pattern of termination of primary vestibular fibers has been based almost entirely upon classic Golgi and silver degeneration technics. Golgi studies indicate that primary vestibular fibers reach parts of each of the principal VN, but do not end in dorsal portions of the lateral vestibular nucleus (LVN) (Lorente de Nó, '33; Hauglie-Hanssen, '68). Silver degeneration studies corroborate these findings, but are inconsistent in descriptions of terminals in other VN, the so-called accessory vestibular nuclei, the cerebellar cortex and the deep cerebellar nuclei. The majority of authors using silver impregnation methods report a restricted and differential distribution of primary vestibular fibers in the VN. Portions of the vestibular nuclei described as not receiving primary vestibular inputs, in addition to the dorsal half of LVN, include: (1) peripheral portions of the superior vestibular nucleus (SVN) (Walberg et al., '58), (2) caudal

parts of the medial vestibular nucleus (MVN) (Walberg, et al., '58; Carpenter, '60; Stein and Carpenter, '67), and (3) cell group "f" in caudal and ventrolateral parts of the inferior vestibular nucleus (IVN) (Walberg et al., '58; Carpenter, '60; Stein and Carpenter, '67; Gacek, '69). In contrast, a recent degeneration study demonstrated terminals in all parts of SVN and MVN (Korte, '79). Projections to the accessory vestibular nuclei appear to reach only cell group "y" and the interstitial nucleus of the vestibular nerve (NIVN) (Walberg et al., '58; Carpenter, '60; Stein and Carpenter, '67; Gacek, '69; Korte, '79).

In the cat and monkey primary vestibular fibers enter the accessory cuneate nucleus (ACN) (Stein and Carpenter, '67; Gacek, '69) and specific portions of the pontomedullary reticular formation (RF) (Carpenter, '60; Gacek, '69). Golgi studies have demonstrated collaterals of vestibular root fibers terminating in portions of the RF immediately adjacent to the VN, and in areas of the dorsolateral RF beyond the dendritic ramifications of vestibular neurons (Lorente de Nô, '33; Hauglie-Hanssen, '68). In a preliminary autoradiographic study in the monkey, primary vestibular fibers were identified in portions of the RF (Batton and Carpenter, '78). In the cat, primary vestibular projections to the abducens nucleus (AN) have been described by anterograde and retrograde axoplasmic transport methods (Lang and Kubik, '79; Gacek, '79).

Primary vestibulocerebellar (VC) projections have been described to the cortex of the nodulus, uvula, flocculus, lingula and paraflocculus in degeneration studies (Brodal and Høivik, '64; Carpenter et al., '72); a more restricted distribution of a smaller number of fibers has been reported using similar methods (Korte and Mugnaini, '79).

Physiological data suggest that portions of vermal lobules V and VI may also receive a primary input (Precht et al., '77), while a recent horseradish peroxidase (HRP) study suggests that the entire cerebellar vermis receives primary vestibular fibers (Kotchabhakdi and Walberg, '78). Primary projections to the deep cerebellar nuclei, considered to terminate in the fastigial nucleus (Carpenter, '60; Furuya et al., '75) and in the ventral parvicellular dentate nucleus (Brodal and Høivik, '64), have been disputed (Korte and Mugnaini, '79).

Secondary vestibular projections have been described extensively using degeneration technics (Pompeiano and Brodal, '57; Brodal and Torvik, '57; Carpenter et al., '59; Carpenter, '60a; Nyberg-Hansen, '64; Nyberg-Hansen and Mascitti, '64; McMasters et al., '66; Erulkar et al., '66; Petras, '67; Ladpli and Brodal, '68; Tarlov, '70; Gacek, '71). These studies are subject to methodological limitations because the principal VN are traversed by: (1) primary afferents, (2) fastigial efferents, and (3) projections from adjacent vestibular nuclei (Ladpli and Brodal, 68; Brodal, '74). Basic data from degeneration studies have been refined using axoplasmic transport methods. Autoradiographic studies indicate that portions of the vestibular nuclear complex project in a specific pattern to the oculomotor complex, the accessory oculomotor nuclei, the thalamus and the inferior olivary nucleus (Raymond et al., '74; Raymond et al., '76; Lang et al., '79; St. Cyr and Courville, '79). Projections to the contralateral VN, the spinal cord, and the abducens and trochlear nuclei were confirmed, but detailed descriptions were not provided (Lang et al., '79). Retrograde transport studies have defined the origin of vestibular projections to the spinal cord (Kuypers and Maisky, '75; Kneisley et al., '78; Castiglioni et al., '77; Peterson

and Coulter, '77), the contralateral VN (Pompeiano et al., '78), the perihypoglossal nuclei (Mergner et al., '77), the inferior olive (St. Cyr and Courville, '79), the cerebellum (Gould and Graybiel, '76; Precht et al., '77; Ruggiero et al., '77; Kotchabhakdi and Walberg, '78a) , the various extraocular motor nuclei (Graybiel and Hartweig, '74; Maciewicz et al., '77; Gacek, '77, '79. '79a; Büttner-Ennever, '77) and the thalamus (Condé and Conde´, '78; Kotchabhakdi et al., '80).

Although the vestibular nerve provides the largest contingent of afferents to the VN (Walberg et al., '58; Stein and Carpenter, '67; Gacek, '69; Korte, '79), considerable input to these nuclei is derived from the cerebellum, a variety of brain stem nuclei and the spinal cord. Projections from the cerebellum appear to constitute the greatest source of central afferents to the VN (Brodal, '74). Cerebellovestibular fibers are derived from: (1) the flocculonodular lobe and uvula, (2) the anterior lobe vermis, and (3) the fastigial nuclei. Projections of the "vestibulo-cerebellum" (i.e., flocculus, nodulus and uvula) are largely to SVN and MVN (Angaut and Brodal, '67; Haines, '77), while fibers from the anterior lobe are more closely related to IVN and LVN (Walberg and Jansen, '61; Haines, '76; Corvaja and Pompeiano, '79). The fastigial nuclei provide a link between Purkinje cells in all portions of the vermal cortex (Courville and Diakiw, '76) and the vestibular nuclei on both sides (Carpenter, '59; Walberg et al., '62). Fastigiovestibular fibers are distributed nearly symmetrically to LVN, IVN and cell groups "f" and "x" (Batton et al., 77).

Commissural vestibular projections have been described in degeneration (Carpenter, '60a; Ladpli and Brodal, '68) and retrograde transport studies (Pompeiano et al., '78; Gacek, '78), and provide an

anatomical substrate for short latency potentials recorded in the VN with stimulation of the contralateral vestibular nerve (Shimazu and Precht, '66; Wilson et al., '68; Mano et al., '68; Kashahara et al., '68; Kashahara and Uchino, '74). The VN also receive brain stem projections from the pontomedullary RF (Lorente de Nó, '33a; Scheibel and Scheibel, '58; Hoddevik et al., '75; Pompeiano et al., '78), the perihypoglossal nuclei (Pompeiano et al., '78) and the ipsilateral interstitial nucleus of Cajal (Pompeiano and Walberg, '57; Nyberg-Hansen, '66). Modest spinal projections to the VN end in restricted areas which do not receive primary vestibular inputs (Pompeiano and Brodal, '57a; Brodal and Angaut, '67; Rubertone and Haines, '82). The most significant spinovestibular projections terminate in dorsal LVN and cell group "x". Lesser projections reach caudal portions of IVN and MVN, areas which do not appear to receive primary vestibular fibers.

The axoplasmic transport technics have demonstrated the capability to define both major and subtle aspects of vestibular connectivity with a sensitivity unavailable in degeneration studies. However, these methods have yet to be applied in a comprehensive investigation of the primary vestibular projection or the central connections of individual vestibular nuclei. The present study examines central termination of neurons innervating the labyrinth, and the central connections of each of the principal vestibular nuclei, using the autoradiographic and horseradish peroxidase methods.

MATERIALS AND METHODS

Material for the current study was taken from 50 normal adult animals, including 18 squirrel monkeys (Saimiri sciureus), 10 macaques (M. rhesus and M. cynomologous) and 22 cats. In seven squirrel monkeys tritiated amino acids (proline and/or leucine) were introduced into the crista ampullaris of individual semicircular ducts. The labyrinth was exposed transmastoidally using small bone curettes. Once exposed and identified, a small hole was cut into an individual duct with a dental drill, the membranous labyrinth was opened with a needle, and the interior of the canal was dried with a cottonoid wick. Small gelfoam pledgets saturated with [^{3}H] amino acid (40 μCi/μl) were placed in the opening in the duct and pushed into the ampulla with a fine wire. The opening in the canal was then sealed with bone wax, the defect in the mastoid bone was packed with gelfoam, and the muscle and skin incisions were closed.

Following survivals of 2 to 25 days, animals were anesthetized and perfused through the left ventricle of the heart with a liter of physiological saline followed by a liter of 10% buffered neutral formalin. Brains were removed and blocked in planes either transverse, sagittal or horizontal to the long axis of the brain stem. Tissue was postfixed in 10% neutral formalin, washed, dehydrated and embedded in paraffin. Blocks of tissue were cut serially at 15 μm and every fifth section was mounted on slides. In order to evaluate the end-organ, the petrous portions of the temporal bones were removed, decalcified and subjected to the same histological treatment as brain tissue. Ear bones were sectioned in either the long or transverse axis of the vestibular

nerve. Selected sections of the brain and ear bones were deparaffinized, dipped in Kodak NTB-2 nuclear track emulsion, air dried and sealed in opaque plastic boxes with a dehydrating agent. Slides exposed for 10 to 14 weeks at 4° C were developed for three minutes in undiluted Kodak D-19 at 15° C. Developed autoradiographs were fixed, washed, counterstained with cresyl violet and examined under bright and dark field illumination.

Autoradiographic material also included seven macaques used in a preliminary study (Batton and Carpenter, '78). In five animals the labyrinth was approached extradurally via the middle cranial fossa (Stein and Carpenter, '67). The labyrinth in one animal (C-1430) was exposed by a transmastoidal approach. Isotope (20 to 40 μCi/μl) was injected in the direction of the ampulla in volumes of 2 to 4 μl with a 10μl Hamilton syringe, and the bony labyrinth was resealed with bone wax. In one control monkey (C-1440) 2 μl of [^{3}H] leucine was injected into the middle turn of the cochlea (Table I).

In four squirrel monkeys attempts were made to label primary vestibular fibers by transganglionic transport of horseradish peroxidase (HRP). Gelfoam pledgets saturated with 20% HRP or 2% wheat germ agglutinin conjugated to HRP (WGA-HRP), or small pellets of dry HRP, were implanted into the ampulla of the lateral semicircular duct by the method described above for squirrel monkeys (Table II). Following postoperative survivals of 2 to 5 days, animals were anesthetized with Nembutal and injected intracardially with 500 units of heparin and 0.5ml of 1% sodium nitrite solution; animals were perfused through the left ventricle of the heart with a liter of physiological saline followed by 2

liters of fixative containing 1.25% paraformaldehyde and 2.5% glutaraldehyde in 0.1M phosphate buffer (pH 7.4). Brains and vestibular ganglia were removed, and brains were cut into sagittal blocks 2-4mm thick. Tissue was post-fixed for 24 hours at 4° C, then transferred to 30% sucrose in phosphate buffer for an additional 24 hours. The vestibular ganglia and blocks of the brain stem were cut serially on a freezing microtome at 40 µm. Groups of 5 adjacent sections were collected in compartments of plastic trays filled with cold phosphate buffer. Selected sections from each compartment were reacted by the method of Mesulam ('78) using tetramethylbenzidine (TMB) as a chromagen. Reacted sections were mounted, counterstained with neutral red and examined by bright and dark field microscopy.

In 14 cats and 1 squirrel monkey central afferents to the vestibular nuclei (VN) were studied. Small volumes of 10-15% HRP, either alone or mixed with 2-4% WGA-HRP, were injected into the MVN, IVN, and LVN. The VN were approached stereotaxically via the posterior fossa in the cat, while a transtentorial approach was used in the monkey. Coordinates were determined from dissections of formalin fixed heads with brains in situ (Carpenter and Whittier, '52). Tracers were injected in volumes of 0.10µl to 0.20µl through glass micropipettes with inside tip diameters of 20-25µm. Injections were made using a metal plunger from a 10µl Hamilton syringe inserted into the shaft of the pipette. After survivals of 48 hours, animals were sacrificed and perfused. Brains and spinal cords were removed and blocked in the transverse plane. Blocks of the brain stem and samples of spinal cord from multiple cervical, thoracic and lumbar levels were cut at 40 µm on a freezing microtome.

Selected sections were treated by the method described above for HRP histochemistry (Table III).

The efferent projections of the vestibular nuclei were studied in 8 cats and 6 squirrel monkeys in which small volumes of [^{3}H] leucine and/or proline were injected into MVN, SVN, IVN or LVN (Table IV). Isotope was concentrated to 40 μCi/μl and injected either hydraulically or by iontophoresis. For iontophoresis a fine silver wire was inserted into a glass micropipette filled with isotope and attached to the positive terminal of a constant-current source (Midgard, Model C-3). The indifferent electrode was attached to muscle. An anodal current of 2μA was applied in 7 second on/off pulses for 30 minutes. At the conclusion of the iontophoresis, the polarity was reversed and the pipette was withdrawn from the brain. Hydraulic injections were accomplished by the method described earlier. Stereotaxic approaches used for the VN were identical to those in HRP experiments.

In two rhesus monkeys, tritiated proline and leucine were injected unilaterally into the abducens nucleus in order to compare abducens internuclear projections with vestibular projections to the oculomotor complex. Following postoperative survivals of 2 and 14 days, animals were anesthetized with Nembutal and perfused with one liter of normal saline followed by a liter of 10% buffered neutral formalin. Brains were blocked perpendicular to the axis of the brain stem. Blocks of tissue were subjected to the same histological procedures as described previously for the autoradiographic method. Resultant autoradiographs were studied microscopically under bright and dark field illumination. Vestibulo-ocular projections also were examined in the brain stem of a rhesus monkey (C-668) with a electrolytic lesion

discretely localized in MVN and stained by the Nauta technic (from McMasters et al., '66).

The cytoarchitecture and nuclear boundaries of the primate VN correspond closely to detailed descriptions provided by Brodal and Pompeiano ('57a) for the cat, and their terminology was used. The atlases of Emmers and Akert ('63) and Berman ('68) were used to identify brain stem structures in the primate and cat, respectively. The cerebellar atlas of Madigan and Carpenter ('71) was used to delineate cortical lobules and folia, and descriptions provided by Igarashi ('64) were used in interpreting the labyrinth in section.

TABLE I

Isotope Injections of the Labyrinth

Animal No.	Species	Semicircular duct injected	[^{3}H] amino acid	Survival time (days)
U-55	S. sciureus	R lateral	proline & leucine	15
U-55	S. sciureus	L posterior	proline & leucine	7
U-63	S. sciureus	L lateral	proline	25
U-70	S. sciureus	R posterior	proline	16
U-70	S. sciureus	L lateral	proline & leucine	7
U-71	S. sciureus	R posterior	proline	17
U-71	S. sciureus	L lateral	proline & leucine	8
U-73	S. sciureus	L anterior	proline & leucine	7
U-91	S. sciureus	R posterior	leucine	2
U-119	S. sciureus	L posterior	leucine	7
C-1427	M. rhesus	R anterior	proline & leucine	8
C-1430	M. cynomologous	R lateral	proline & leucine	11
C-1443	M. cynomologous	L anterior	proline & leucine	12
H-1461	M. rhesus	R anterior	leucine	8
H-1472	M. cynomologous	R lateral	proline & leucine	14
H-1484	M. cynomologous	L anterior	proline & leucine	7

R and L refer to right and left.

TABLE II

HRP Injections of the Labyrinth

Animal No.	Species	Injected duct	Tracers	Survival time (days)
U-109	S. sciureus	L lateral	20% HRP	3
U-110	S. sciureus	L lateral	2% WGA-HRP	3
U-111	S. sciureus	L lateral	HRP pellet	5
U-113	S. sciureus	R lateral	2% WGA-HRP	3

R and L refer to right and left.
HRP, Horseradish peroxidase.
WGA-HRP, Wheat germ agglutinin-Horseradish peroxidase.

TABLE III

HRP Injections of the Vestibular Nuclei

Animal No.	Species	Nucleus	Tracers	Survival time (days)
U-118	Cat	IVN	2% WGA-HRP/20% HRP	2
U-122	Cat	MVN, IVN	2% WGA-HRP/10% HRP	2
U-123	Cat	MVN	2% WGA-HRP/10% HRP	2
U-125	Cat	IVN	2% WGA-HRP/10% HRP	2
U-127	Cat	IVN	2% WGA-HRP/10% HRP	2
U-133	S. sciureus	LVN	4% WGA-HRP/10% HRP	2
U-145	Cat	MVN	4% WGA-HRP/10% HRP	2
U-146	Cat	MVN	4% WGA-HRP/10% HRP	2
U-148	Cat	MVN	25% HRP	2
U-158	Cat	LVN	4% WGA-HRP/17.5% HRP	2
U-188	Cat	LVN	20% HRP	2

HRP, Horseradish peroxidase.
WGA-HRP, Wheat germ agglutinin-Horseradish peroxidase.

TABLE IV

Isotope Injections of the Vestibular Nuclei

Animal No.	Species	Nucleus	Isotope	Survival time
U-112	S. sciureus	IVN	leucine	8
U-115	S. sciureus	IVN	leucine	6
U-116	S. sciureus	IVN-LVN	leucine	6
U-126	S. sciureus	MVN*	leucine	7
U-129	Cat	IVN-LVN	leucine	6
U-135	Cat	MVN	leucine	5
U-138	Cat	MVN	leucine	4
U-160	Cat	IVN-LVN	leucine	7
U-161	Cat	IVN-LVN	leucine	7
U-164	Cat	IVN-LVN	leucine	6
U-176	S. sciureus	All VN	Pro-Leu	15
U-177	S. sciureus	All VN	Pro-Leu	7
U-193	Cat	SVN	Pro-Leu	11
U-196	Cat	SVN	Pro-Leu	13

Pro-Leu, Proline and leucine.
*Injection encroached upon the abducens nucleus.

RESULTS

Primary Vestibular Afferents

Tritiated amino acids were introduced into the ampullae of individual semicircular ducts in 13 monkeys. In three squirrel monkeys (U-55, U-70, and U-71) isotope was introduced bilaterally, yielding a total of 16 sides. In two squirrel monkeys (U-91 and U-119) gelfoam pledgets saturated with [^{3}H] leucine were implanted unilaterally. In the remaining animals injections or gelfoam implantations containing proline, or both proline and leucine, were made into individual ampullae. Table I contains data relative to the individual semicircular ducts injected or implanted, the [^{3}H] amino acids used and the post-operative survival times. When tritiated proline was used alone or in combination with leucine, transneuronal transport was consistently seen with survivals exceeding two weeks. The only exception was monkey C-1443 which showed transneuronal transport following a 12 day survival. In the control animal (C-1440) [^{3}H] leucine injected into the cochlea and labeling cells of spiral ganglion demonstrated profuse bilateral transneuronal transport only in the auditory system. Survivals of 8 days or less did not produce transneuronal transport in either vestibular or auditory pathways. Transneuronal transport in both vestibular and auditory pathways was seen in five monkeys (U-55R, U-63, U-70R, U-71R and C-1443). Commissural transneuronal transport was not seen and results obtained in bilaterally injected animals were not compromised.

Introduction of [^{3}H] amino acids into one ampulla resulted in uptake and central transport of isotope by ganglion cells innervating all receptive elements of the labyrinth on 11 sides (Fig. 1A,B). In

these animals variable isotope uptake also was seen in the cochlea and spiral ganglion. In 5 animals isotope introduced into a single ampulla labeled the cristae of all semicircular ducts and corresponding parts of the vestibular ganglion (Stein and Carpenter, '67); only scant label was seen in ganglion cells which innervate the maculae of the utricle and saccule. Isotope implantation in the ampulla of the posterior semicircular duct in one animal selectively labeled only ganglion cells innervating the crista of that duct (Fig. 1C,D).

Data from this portion of the study was separated into six categories: (1) transport from all parts of the vestibular ganglion, (2) transport from ganglion cells innervating primarily the semicircular ducts, (3) transport from ganglion cells innervating only the posterior semicircular duct, (4) primary and transneuronal transport from the entire vestibular ganglion, (5) control, and (6) horseradish peroxidase (HRP) transport from the labyrinth. Because of the similarity of axoplasmic transport within each group, results in each category will be described synthetically.

Projections of the vestibular ganglion. In six animals (U-55L, U-70L, U-71L, U-73, C-1430, H-1472) tritiated amino acids labeled the cristae of all semicircular ducts, the utricular and saccular maculae, and the basal turns of the cochlea. Autoradiographs of temporal bone sections revealed isotope uptake by bipolar neurons in all parts of the vestibular ganglia, and in portions of the spiral and geniculate ganglia (Fig. 1A,B). Central transport of the tracer was evident in the vestibulocochlear nerve and in fibers of the intermediate nerve. The density of label was uniform in all parts of the vestibular root which in

sagittal section formed flattened, obliquely oriented plates separated by intervening septa (Fig. 2A).

Vestibular root fibers penetrated the ventrolateral aspect of LVN near its caudal border, and immediately divided into ascending and descending branches. Ascending root fibers passed dorsomedially and rostrally, bisecting SVN obliquely from its ventrolateral and caudal pole to its rostral and dorsomedial border. Labeled fibers of the ascending vestibular root continued into the cerebellum along the ventral and dorsal margins of the superior cerebellar peduncle (SCP) (Fig. 2C,F). At the level of vestibular root entry, numerous densely labeled axons traversing ventral portions of LVN were distributed to the rostral third of MVN (Fig. 2B). Descending root fibers entering IVN traveled in the longitudinal axis of this nucleus (Fig. 2C). The principal bundle of descending root fibers occupied the ventromedial quadrant of IVN; smaller fascicles of labeled axons descended parallel to this bundle in ventrolateral portions of the nucleus, while relatively few descending fibers were noted in its central and dorsal parts.

Terminal label in the vestibular nuclear complex was dense and widespread. While there were regional variations in the density of silver grains, only the most medial border of SVN was devoid of primary vestibular terminals (Fig. 2F). Transport was massive to the central, larger-celled portion of SVN, but terminations also were evident throughout the peripheral parts of this nucleus, including its caudolateral extension on the dorsolateral aspect of LVN (Fig. 3D).

Within LVN, both the volume and distribution of labeled terminals were restricted. Silver grains were most notable over cells in ventrolateral and rostral portions of the nucleus. While labeled fibers

traversed dorsal and caudal portions of LVN, no terminals were evident in these parts of the nucleus (Figs. 2B and 3D). Cell group "l", an island of medium-sized cells in dorsolateral portions of the feline LVN (Brodal and Pompeiano, '57a), was not identified in the monkey.

Terminal labeling in IVN formed two distinct pools of dense silver grains: one was in rostral portions of the nucleus surrounding the proximal fibers of the descending root, and the other filled the caudal third of the nucleus (Fig. 3B). In both locations terminals were most numerous dorsally. In the middle third of IVN, terminals were relatively sparse. Cell group "f", an area of large cells in ventrolateral and caudal IVN, was the only part of the nucleus entirely free of silver grains (Fig. 2E).

Projections to MVN filled the nucleus to its boundaries and were distributed homogeneously (Fig. 2C,D,E). No mediolateral or rostrocaudal differences in terminal density were seen within MVN, except for a small circular area of conspicuously sparse terminals evident on the ventral margin of the nucleus medially (Fig. 2D). No remarkable cytological features distinguished this area from adjacent more heavily labeled regions of MVN.

Projections to the accessory vestibular nuclei were confined to the interstitial nucleus of the vestibular nerve (NIVN) and cell group "y" (Fig. 2A). Terminal density was massive in NIVN and distributed equally over all subgroups. Labeled fibers distributed throughout cell group "y" were somewhat less dense than in the VN and most prominent in its caudal part (Fig. 2A). Primary vestibular projections in the brain stem are summarized in Figure 4.

Labeled fibers and terminals were noted in several brain stem nuclei outside the boundaries of the vestibular nuclear complex. Axons of the descending vestibular root emerged caudolaterally from IVN to terminate in punctate islands in lateral portions of the accessory cuneate nucleus (ACN) (Fig. 3A,B). This projection was more prominent in the macaque than in the squirrel monkey. Rostral to ACN, a small but distinct projection from the ventral border of IVN terminated in medial portions of the subtrigeminal lateral reticular nucleus (SLRN) (Figs. 3C and 4). Axons en route to this structure traversed lateral portions of the spinal trigeminal nucleus. In all animals of this group, labeled fibers projected toward caudal portions of the ipsilateral nucleus prepositus (NPP), but were not observed to terminate within it; terminals were found in the nucleus intercalatus (NIC) in one animal (H-1472). While labeled axons approached the lateral margin of the ipsilateral abducens nucleus (AN), they could not be followed to terminations within its borders. Weak reticular projections noted along the ventral margins of the vestibular nuclei extended into: (1) dorsolateral portions of the nucleus reticularis parvicellularis (NRpc) at the level of the vestibular root, and (2) dorsomedial portions of the nucleus reticularis gigantocellularis (NRgc) immediately caudoventral to the abducens nucleus (Figs. 3D,4 and 5A). In these locations, label was found primarily in fibers. Labeled axons were never observed to enter the medial longitudinal fasciculus (MLF) or cross the midline. With the exception of vestibular projections to ACN, brain stem transport beyond the vestibular nuclear complex was an order of magnitude less than that seen to the VN.

Isotope implantation in these animals produced abundant transport to the cochlear nuclei, and moderate labeling of the nucleus of the

solitary tract. Weak projections also descended in the spinal trigeminal tract. A control animal (C-1440) also demonstrated these projections. Transport to the latter structures appeared related to the intermediate nerve.

Primary vestibular fibers entered the cerebellum by: (1) the juxtarestiform body (Fig. 2B), (2) scattered fibers surrounding the SCP both dorsally and ventrally (Fig. 2C,F), and (3) coarse axons traversing dorsal portions of LVN (Fig. 3D). Labeled fibers associated with the SCP constituted a surprisingly large proportion of primary VC fibers. En route to the vermal cortex, large numbers of labeled fibers traversed portions of the ipsilateral fastigial nucleus (FN), but no terminals were noted in this structure. A patch of faint, finely granular terminals, noted in ventrocaudal portions of the ipsilateral dentate nucleus (U-55L), was distinct from cell group "y". Projections to the cerebellar cortex terminated in the granular layer in globular clusters of silver grains interpreted to represent mossy fiber rosettes (Fig. 5F). Cortical terminations were most numerous in the nodulus and in portions of the uvula adjacent to the posterolateral fissure (Fig. 5E). Mossy fiber terminals in these areas extended from the lateral margins of the vermis only to the midline. Distinct terminals also were noted in the deepest folia of vermal lobules V and VI adjacent to the primary fissure (Fig. 5E). These terminals were restricted to three folia (folia "e" and "f" of lobule V, and folium "f" of lobule VI, Madigan and Carpenter, '71). Only a few terminals were noted in the lingular cortex. In the flocculus, labeled terminals were surprisingly sparse and identified primarily in ventral folia. There was no evidence of terminations in the molecular layer in any of these cortical areas.

Projections related to the semicircular ducts. Tritiated amino acids in four monkeys (U-119, H-1427, H-1461, H-1484) labeled the cristae of all semicircular ducts and corresponding portions of the vestibular ganglia. Scant isotope uptake was seen in ganglion cells associated with the utricle and saccule. The geniculate ganglion and portions of the spiral ganglion innervating the basilar turn of the cochlea also contributed to central transport of the tracer. Silver grains overlying the vestibular root were distributed differentially; portions of the root corresponding to the areas of macular afferents (Gacek, '69; Stein and Carpenter, '67) were poorly labeled, while root fibers in other locations were densely labeled.

With a few important exceptions, the pattern of terminal labeling in the brain stem and cerebellum corresponded to that seen in animals where all elements of the labyrinth contributed to central transport. Terminals in NIVN were not uniformly distributed but were labeled commensurate to the volume of transport in associated portions of the vestibular root (i.e., caudal subdivisions were sparsely labeled while rostral subdivisions were densely labeled). Transport to IVN had the same distribution as described earlier, but the volume of terminal label was reduced, particularly in caudal portions of the nucleus. There was no obvious difference in the character or volume of transport to the other principal VN. Projections to cell group "y" were less numerous than in animals where the entire labyrinth was involved, and reached only caudoventral portions of the nucleus. While occasional descending fibers approached the ACN, none terminated in any part of this nucleus. Isotope transport was evident in dorsomedial portions of NRgc caudal to the abducens nucleus, but not in other reticular nuclei.

Primary vestibulocerebellar fibers terminated in the nodulus, uvula and flocculus, but not in the lingula or deep folia of lobules V and VI. No terminals were found in any of the deep cerebellar nuclei.

Transport related to the posterior semicircular duct. Tritiated leucine implanted into the ampulla of the posterior semicircular duct in squirrel monkey U-91 resulted in isotope uptake and transport by cells of the inferior vestibular ganglion associated with the posterior duct nerve (Fig. 1C,D). While silver grains were present over all receptive elements of the labyrinth, only bipolar cells in ventral portions of the inferior vestibular ganglion contributed to central transport. Labeling in the vestibular root was confined to a central band of fibers corresponding to descriptions of posterior duct afferents (Gacek, '69; Stein and Carpenter, '67) (Fig. 3E). Labeled root fibers pursued a rostromedial and dorsal course to reach the ventrolateral aspect of LVN, where fibers divided into ascending and descending branches. Labeled terminals were dense in central portions of SVN medial to the ascending vestibular root (Fig. 3F). A small bundle of ascending root fibers continued into the cerebellum along the ventromedial border of the SCP, but no terminals were evident in any part of the cerebellar cortex or the deep nuclei. Descending branches of the vestibular root passed caudomedially, and moderate numbers of labeled terminals were noted in the rostral pole of IVN. Labeling in MVN was present in the rostral third of the nucleus and in a lateral strip extending into its central region (Fig. 3F). No projections were noted to brain stem nuclei beyond the borders of the vestibular nuclear complex and no label was present in the cochlear nerve or nuclei.

Primary and transneuronal transport from the vestibular ganglion. In five animals (U-55R, U-63, U-70R, U-71R, C-1443) isotope uptake by all labyrinthine receptors, the cochlea, and the geniculate ganglion produced labeling in both primary and secondary vestibular and auditory pathways. No transneuronal transport related to the intermediate nerve was identified.

The distribution of terminals in the vestibular nuclei was similar to that seen in animals demonstrating only primary transport but the volume of transport was much greater. With the exception of dorsal LVN and cell group "f", all parts of all four VN were heavily labeled, including middle portions of IVN and the ventral island in mid-portions of MVN. Cell group "x" was unlabeled, while group "y" was blanketed with silver grains. Transport was evident to the same reticular nuclei as in primary studies, but was more intense; projections to dorsomedial portions of NRgc caudoventral to the AN (paragigantocellularis dorsalis) were particularly impressive (Fig. 5B). The location of label in the ACN and SLRN was identical to that described earlier, but greater in density (Fig. 3B,C). Terminals also were found in the caudal half of the ipsilateral nucleus prepositus (NPP).

Cerebellar projections were heavy to the nodulus and basal folia of the uvula, and moderate to the flocculus, the deep folia of vermal lobules V and VI, and the lingula. The greatest increase in terminal density, over animals with only primary transport, was observed in the flocculonodular lobe and ventral uvula. Although tremendous numbers of fibers traversed the ipsilateral FN, no terminals were identified in this nucleus. Projections to the ventral dentate nucleus were noted bilaterally in one animal (U-55), and were indistinguishable in volume

and distribution on the two sides, suggesting that ipsilateral transport (right) probably was not transneuronal.

Transport via established secondary vestibular pathways was distinct, but faint. Spinal projections descended in the MLF and the vestibulospinal tract (VST) into upper cervical spinal segments. Labeling in the descending MLF was noted only on the side of the injection except for one animal (U-63). Terminals of descending projections were found in caudomedial portions of the ipsilateral medial accessory olive (dorsal cap, nucleus β). Commissural projections were not seen.

The most impressive example of transneuronal labeling occurred in the ipsilateral abducens nucleus (AN). Fibers projected medially from rostral portions of MVN to terminate in all parts of AN; in several animals, suggestive transport was noted in ipsilateral abducens root fibers (Fig. 5B). Projections to the contralateral AN were evident in medial parts of the nucleus only in one animal (U-63). Labeled ascending fibers, mainly in the contralateral MLF, reached the trochlear and oculomotor nuclei (OMC). The distribution of isotope in fibers of the MLF differed on the two sides; contralateral fibers traveled in medial portions of the bundle, while ipsilateral projections coursed in its lateral wing. Labeled terminals in the trochlear nuclei were faint, and almost entirely contralateral. Projections to the OMC were greatest contralaterally but were not seen in the ventral cell column (Warwick, '53) (Fig. 5C). Scant terminations in the ipsilateral OMC favored dorsal locations. Suggestive projections to the thalamus, evident in U-70R, surrounded cells near the ventral margin of the ipsilateral ventrobasal complex in the ventral posterior inferior thalamic nucleus.

FIGURE 1

Squirrel monkeys U-55 (A,B) and U-91 (C,D). A,B: bright field (A) and dark field (B) photomicrographs of the same autoradiograph of a temporal bone section through the vestibular ganglia and cochlea. All parts of the superior (SVG) and inferior (IVG) ganglia show uptake of radioactive label. Less isotope uptake is seen in the basal turn of the cochlea (C), the cochlear nerve (CN) and in the facial nerve (N. VII). C,D: bright field (C) and dark field (D) autoradiographs of a section through the vestibular ganglia cut in the same plane as in A and B. Selective uptake of [^{3}H] leucine is seen in the nerve of the posterior semicircular duct (PSD) and in the related part of the IVG. No radioactive uptake is evident in the SVG, the CN or N. VII. Cresyl violet; magnification: X5.

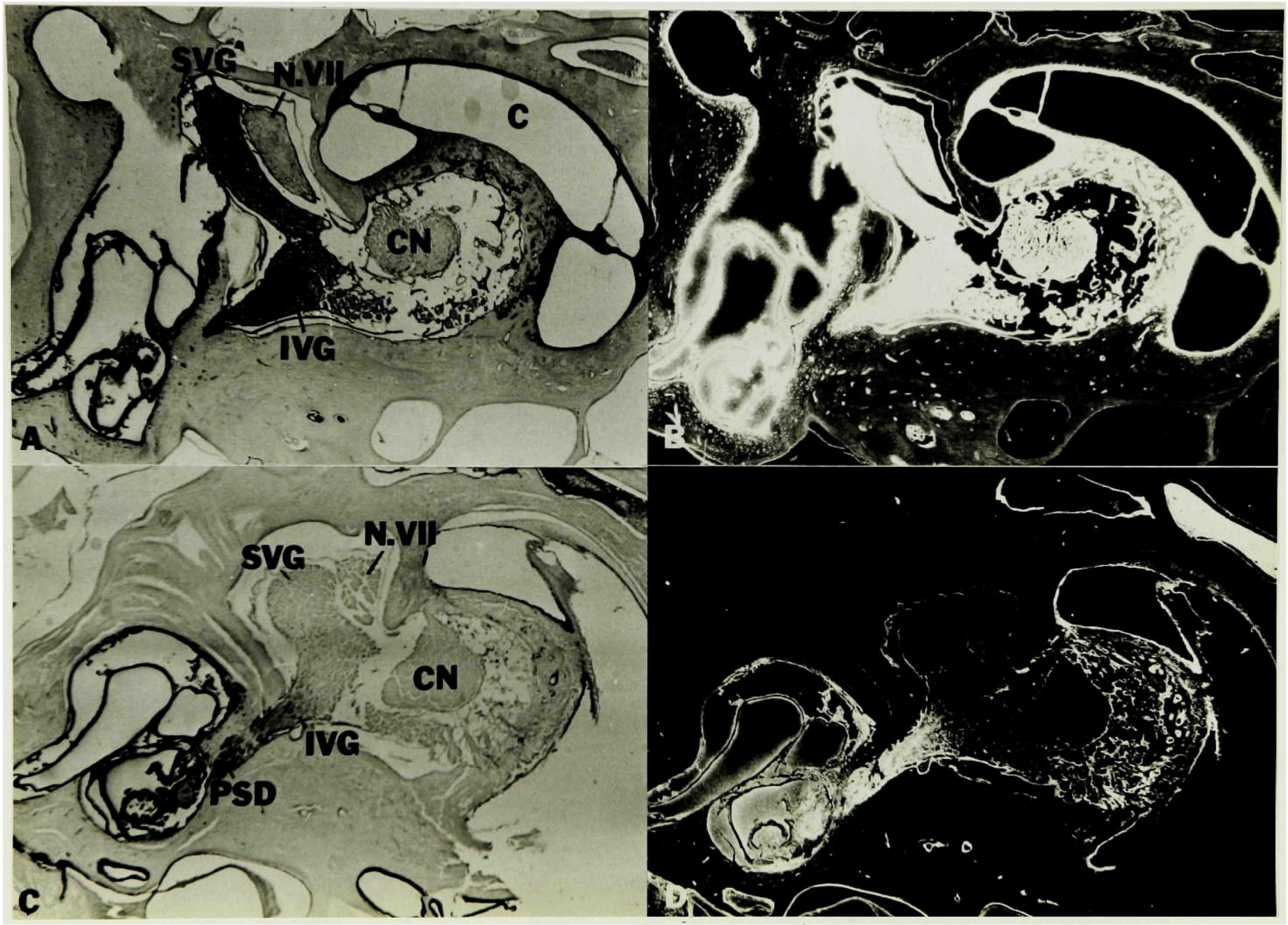

SVG
N.VII
C
CN
IVG
A
B
N.VII
SVG
CN
IVG
PSD
C
D

FIGURE 2

Monkeys C-1430 (A), H-1472 (B,F), U-71 (C), U-70 (D) and U-73 (E). A: Sagittal autoradiograph through the vestibular nerve root (VNR) showing fibers traversing parts of the inferior cerebellar peduncle to terminate most profusely in caudal parts of cell group "y". B: Transverse autoradiograph through the VNR demonstrating terminations in the medial vestibular nucleus (MVN), in fibers and terminals in the ventral parts of lateral vestibular nucleus (LVN) and in portions of the superior vestibular nucleus (SVN). C: Sagittal autoradiograph of fibers and terminals in parts of all left vestibular nuclei as well as primary vestibulocerebellar (VC) fibers. I, indicates inferior vestibular nucleus; M, indicates MVN; S, indicates SVN and VNR indicates vestibular nerve root. D: Sagittal autoradiograph demonstrating uniform primary vestibular terminations in all parts of left MVN except for the small circular zone (indicated by arrows) on the ventral border of the nucleus which receives sparse terminations. E: Transverse autoradiograph of primary vestibular terminations in MVN and IVN showing fibers projecting towards the accessory cuneate nucleus (ACN). Note absence of terminals in cell groups "f" and "x", and VC fibers in the ipsilateral nodulus. F: Transverse autoradiograph of primary vestibular fibers and terminals in SVN and VC fibers coursing dorsal to the superior cerebellar peduncle. Only the most medial part of SVN is free of fiber terminations. Cresyl violet; dark field photomicrographs; magnifications: A, C-F, X5; B, X2.5.

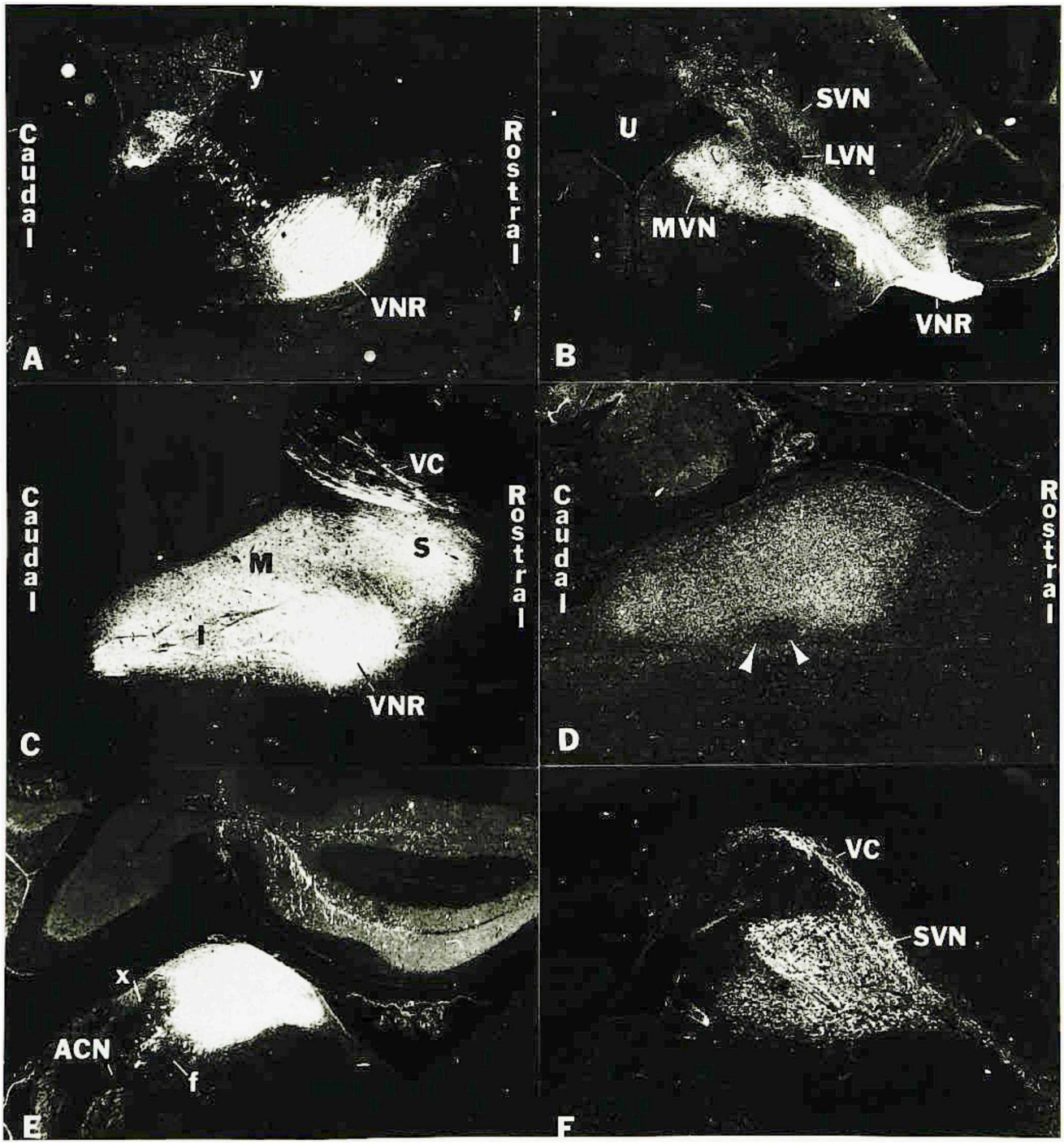

y
Caudal
Rostral
VNR
A
SVN
U
LVN
MVN
VNR
B
VC
Caudal
S
M
Rostral
l
VNR
C
Caudal
Rostral
D
x
ACN
f
E
VC
SVN
F

FIGURE 3

Monkeys H-1472 (A), C-1443 (B), U-55 (C,D) and U-91 (E,F). A,B: Transverse (A) and sagittal (B) autoradiographs of primary vestibular fibers projecting beyond the inferior vestibular nucleus (IVN) to discrete terminations within the accessory cuneate nucleus (ACN). These projections to ACN arise from vestibular ganglion cells innervating the maculae of the otoliths, particularly the utricle. C,D: Transverse autoradiographs demonstrating primary vestibular projections to the right subtrigeminal lateral reticular nucleus (SLRN) (C) and to portions of the reticular formation (NRgc) along the ventral border of the left vestibular nuclei (D). E,F: Autoradiographs of horizontal sections of the brain stem showing transport of isotope from vestibular ganglion cells innervating the crista of the posterior semicircular duct. E demonstrates a band of labeled fibers in the VNR and F shows the regions of termination in rostral MVN and in medial SVN. Cresyl violet; dark field photomicrographs; magnifications: A,C, X9; B,D,E,F, X5.

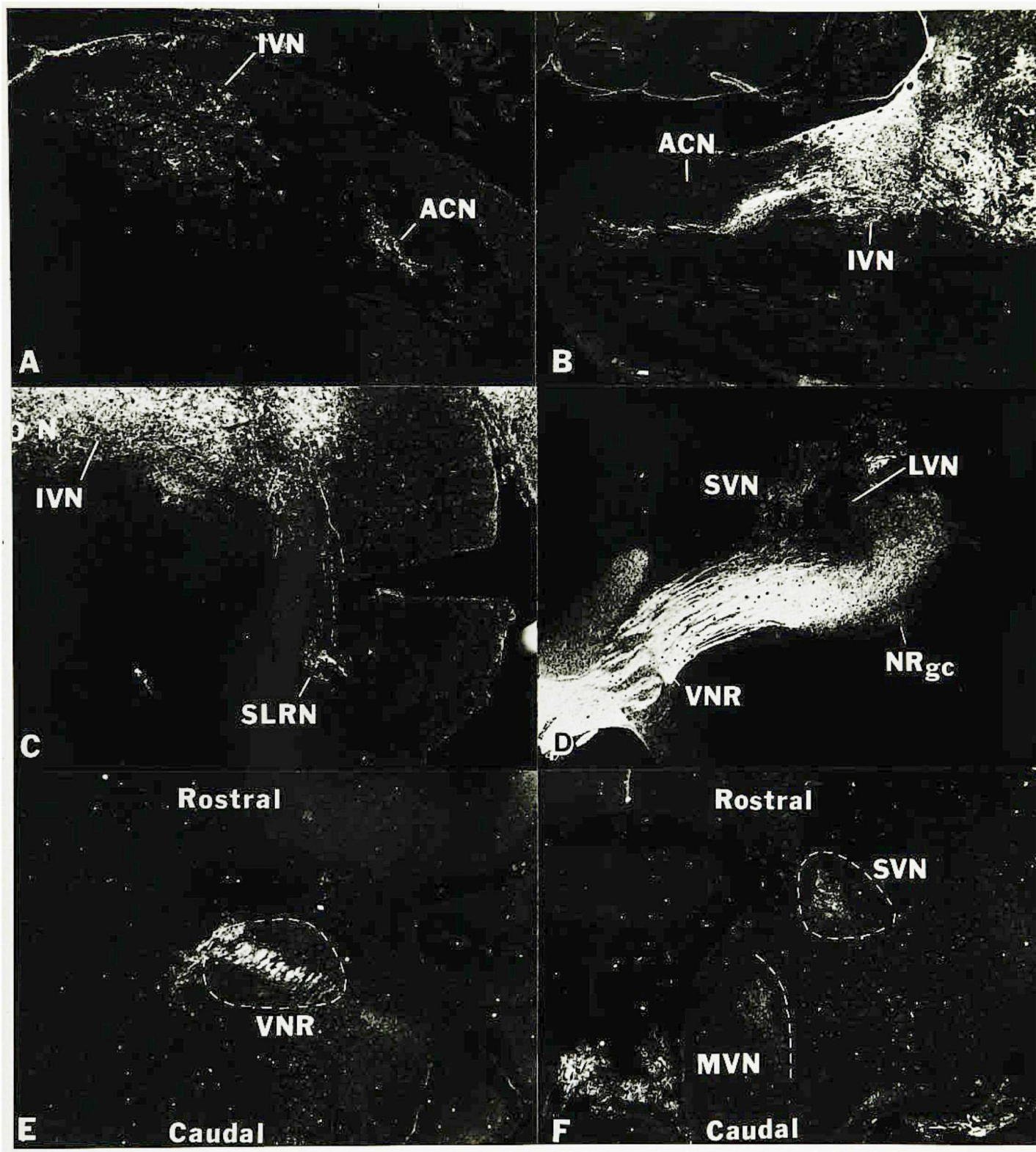
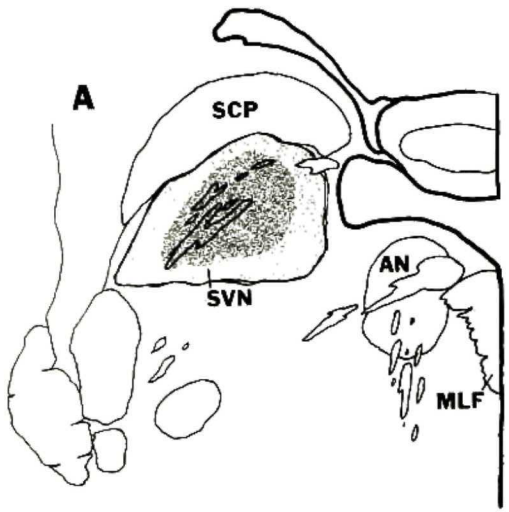
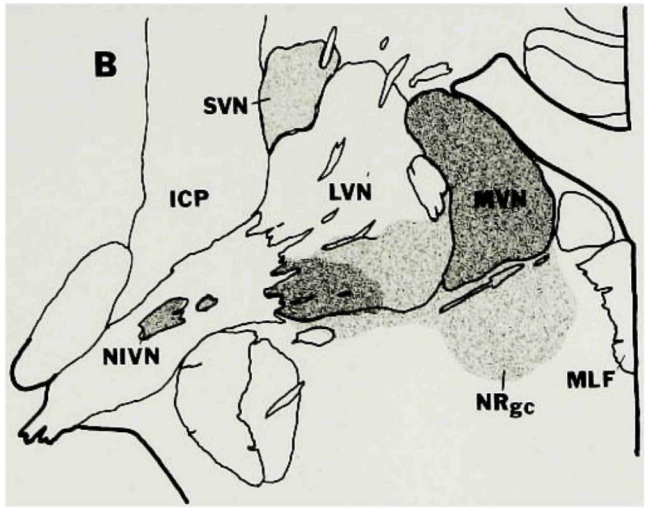
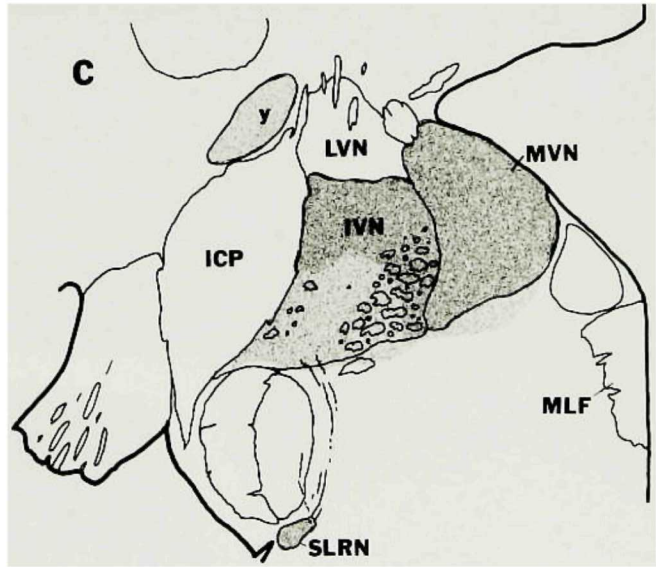

IVN
ACN
A
ACN
IVN
B
IVN
SLRN
C
SVN
LVN
NRgc
VNR
D
Rostral
VNR
E
Caudal
Rostral
SVN
MVN
F
Caudal

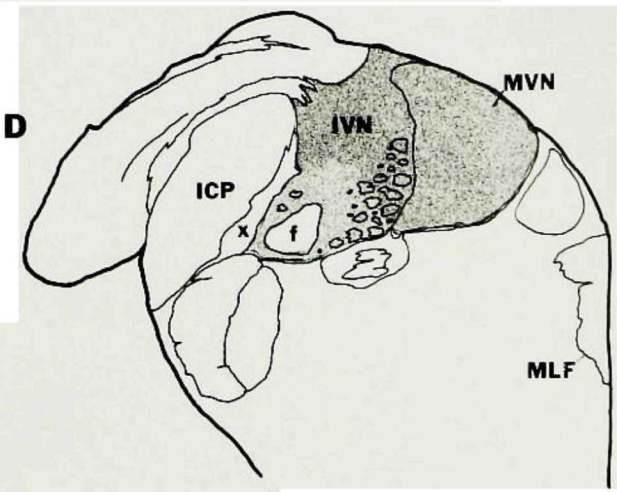
FIGURE 4

Diagrammatic summary of primary vestibular projections in the brain stem. E represents a sagittal section through the vestibular nuclear complex indicating the planes of section in panels A (rostral) through D (caudal). Shading covers the areas receiving primary vestibular fibers. For abbreviations, see text.


A
SCP
AN
SVN
MLF


B
SVN
ICP
LVN
MVN
NIVN
NRgc
MLF


C
y
LVN
MVN
IVN
ICP
MLF
SLRN


D
MVN
IVN
ICP
x
f
MLF

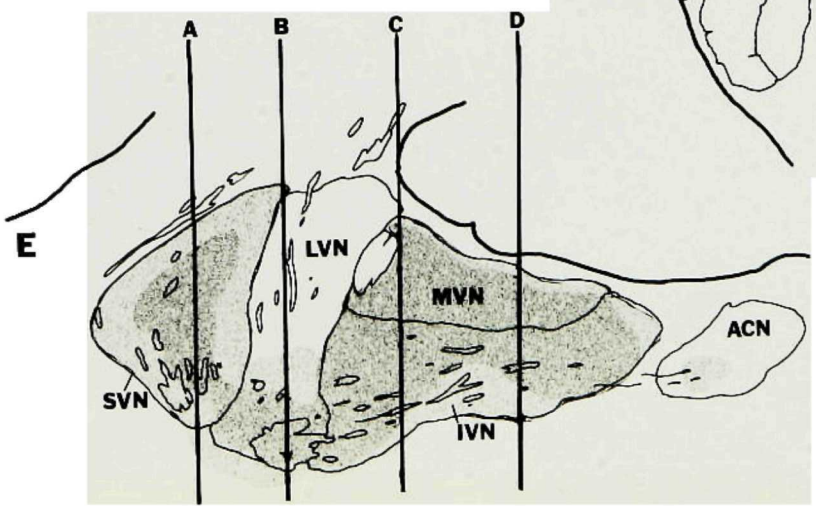
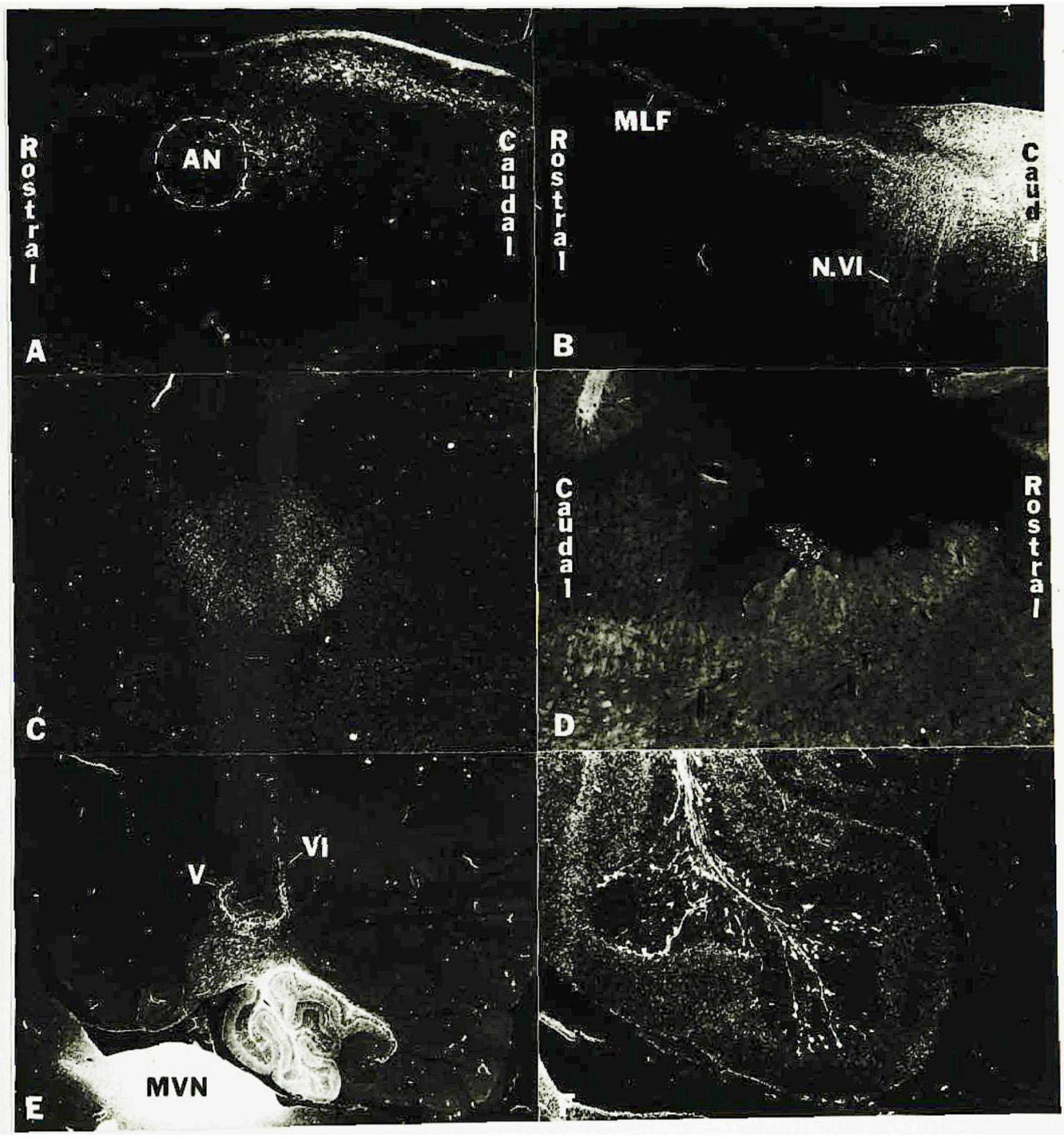

E
A
B
C
D
LVN
MVN
ACN
SVN
IVN

FIGURE 5

Monkeys C-1443 (A), U-70 (B,E,F), U-63 (C) and U-111 (D). A: Sagittal autoradiograph demonstrating primary vestibular fibers in the reticular formation caudal and ventral to the abducens nucleus (AN). B: Sagittal autoradiograph showing transneuronal transport on the right side in secondary vestibular projections to the ipsilateral AN, the reticular region caudal and ventral to the AN, and the ipsilateral MLF. C: Transverse autoradiograph of bilateral transneuronal transport from the left labyrinth to the oculomotor complex via the MLF. D: Efferent vestibular neurons labeled retrogradely with HRP from the crista of one lateral semicircular duct. These cells were labeled bilaterally and symmetrically along the lateral border of the AN. E,F: Sagittal autoradiographs of vestibulocerebellar (VC) projections from the right vestibular ganglion showing terminations in the granular layer of the nodulus, ventral part of the uvula and deep folia of lobules V and VI on each side of the primary fissure (E). In the right nodulus (F), and all other locations within the cerebellar cortex, VC fibers terminated in formations resembling those described for mossy fibers. Dark field photomicrographs; cresyl violet, A-C, E,F; neutral red, D; magnifications: A,B, X5; C,D, X9; E, X2.5; F, X15.


Rostral
AN
Caudal
A
MLF
Rostral
Caudal
N.VI
B
C
Caudal
Rostral
D
V
VI
MVN
E

Control. In one monkey (cynomolgous C-1440), tritiated leucine injected into the middle turn of the cochlea was taken up by cells in all parts of the spiral ganglion and in portions of the geniculate ganglion. There was no isotope uptake by receptive elements of the labyrinth or by cells of the vestibular ganglia. Central transport of isotope was confined to fibers of the cochlear and intermediate nerves. Fibers of the cochlear nerve terminated massively in all parts of the dorsal and ventral cochlear nuclei (Carpenter et al., '78). Labeled axons also were found in the ventral and intermediate acoustic stria, the trapezoid body and the contralateral lateral lemniscus. Weak terminals were evident bilaterally in portions of the superior olivary complex, and contralaterally in the nuclei of the lateral lemniscus and the central nucleus of the inferior colliculus.

Fibers of the intermediate nerve terminated in dorsal portions of the principal sensory nucleus of the trigeminal nerve, and diffusely along the entire length of the nucleus of the solitary tract. Labeled fibers also descended in the dorsal part of the spinal tract of V. No labeled fibers entered the cerebellum or terminated in the VN.

Retrograde transport from the labyrinth and cochlea. In four monkeys (U-109, U-110, U-111, U-113) HRP or WGA-HRP implanted into the ampulla of the lateral semicircular duct retrogradely labeled efferent vestibular and cochlear neurons (Table II). Sections of the vestibular ganglia showed scant or no labeling of bipolar cells, and no anterograde transport via primary vestibular afferents. Bilateral retrograde transport to the brain stem was confined to: (1) a tight knot of small, heavily labeled cells rostroventral to MVN and lateral to the AN near the facial nerve (Fig. 5D), (2) a diffuse array of faintly labeled cells

on the dorsal aspect of the lateral superior olivary nucleus, and (3) several neurons within the medial superior olivary nucleus. Labeled cells of the efferent cochlear bundle (Rasmussen, '60) were most numerous contralaterally and less numerous than efferent vestibular neurons. Cells lateral to the AN were symmetric in number and distribution on the two sides, and correspond to efferent vestibular neurons described by Goldberg and Fernández ('80).

Central Afferents to Vestibular Nuclei

Unilateral HRP injections worthy of detailed analysis in 9 cats selectively involved MVN, IVN and LVN. Injections in another cat involved portions of both IVN and MVN. In one squirrel monkey an HRP injection was confined to LVN. Information concerning tracer substances and survival times used are summarized in Table III.

Medial vestibular nucleus. Four HRP injections involved cells and terminals within parts of the MVN. The injection in cat U-123 involved ventral and caudal parts of MVN. In two cats (U-145 and U-146) similar HRP injections stained large portions of the MVN throughout its caudorostral extent (Fig. 6A). HRP injected iontophoretically in the MVN (U-148) involved medial regions of the nucleus in its central part and portions of the nucleus prepositus (NPP). Although these HRP injections varied in size and spatial disposition, the resulting axoplasmic transport was similar.

The upper cervical spinal cord revealed labeling of a few cells in the contralateral central cervical nucleus (CCN) in only one cat (U-146). In the medulla labeled cells were found contralaterally in the nucleus prepositus (NPP) and in the nucleus intercalatus (NIC).

Commissural transport of HRP was profuse in all parts of MVN with the most intense label in regions corresponding to the greatest concentration of HRP (Fig. 6B). Labeled neurons were seen in all parts of cell group "y" (Fig. 6B), in ventrolateral parts of the superior vestibular nucleus (SVN) (Fig. 6C) and sparsely in caudal IVN. No labeled cells were seen in LVN.

Sections rostral to the VN revealed labeling in the ipsilateral interstitial nucleus of Cajal (INC) and in a surprising number of visceral neurons within the oculomotor nuclear complex (OMC). Midline visceral neurons labeled in the OMC were especially great in cat U-145, but were seen in all animals in this group (Fig. 6D). In one animal a few cells of the ipsilateral nucleus subparafascicularis (subPF) were labeled (Barmack et al., '79). In the cerebellum labeled Purkinje cells (PCs) were noted in a central band of the flocculus and in portions of the ipsilateral nodulus and uvula. Cells in the contralateral fastigial nucleus (FN) were sparsely labeled in caudal regions. Afferent projections to MVN are summarized in Figure 7.

Inferior vestibular nucleus. HRP injections in IVN were made in three cats. In cat U-118 an injection of the caudal half of nucleus included cell groups "f" and "x" (Fig. 8A). Similar injections in two other cats (U-125 and U-127) also involved rostral parts of IVN. Retrograde cellular labeling at spinal levels was scant, but consistent in the contralateral CCN in upper cervical segments and at the spinomedullary junction (Fig. 8B). No cells were labeled at other spinal levels. At medullary levels, enzyme was detected in neurons of the PH in all animals. Cells were labeled bilaterally in ventrocaudal portions of the NPP with contralateral dominance. Two cats demonstrated labeling of

neurons in the contralateral NIC and the nucleus of Roller (NR). Transport of HRP to cells of the ponto-medullary RF was bilateral and sparse.

Labeled neurons in VN adjacent to the injection suggested interruption of axons in passage or direct uptake of the tracer. HRP cells in peripheral parts of the ipsilateral SVN were spatially removed from the injection. Transport of HRP to cells of the contralateral VN was much greater and occurred in a consistent pattern. The nucleus most heavily labeled was MVN; cells were clustered along its caudal border with IVN, while rostral portions of the nucleus contained larger numbers of labeled cells. Retrograde transport was seen in cells of SVN along its ventral and lateral borders. Labeled cells in IVN were sparse and occupied caudomedial portions of the nucleus. No cells were labeled in LVN. Among the small cell groups of the contralateral vestibular complex, only cell group "y" demonstrated retrograde transport (Fig. 8C). There was no enzyme transport to cell groups "f" or "x".

Retrograde labeling in the visceral cell columns of the OMC was less impressive than that associated with MVN. Sparse retrograde labeling of cells in the ipsilateral INC was seen only in cat U-127. Retrograde labeling in the cerebellar cortex was restricted to the ipsilateral nodulus, uvula, and anterior lobe vermis (Fig. 8E). Within the anterior lobe, labeled PCs most frequently were encountered in deep folia. Labeled fastigial neurons were found ventrolaterally in the central third of the FN with contralateral dominance (Fig. 8F). Afferent projections to IVN are summarized in Figure 9.

Inferior and medial vestibular nuclei. A large HRP injection in cat U-122 involved virtually all parts of IVN and MVN, without encroaching upon other VN. The upper cervical spinal cord revealed labeled

cells in the contralateral CCN. Discrete label was present in cells of the contralateral NIC and NPP (Fig. 6E), but no labeled cells were seen in the inferior olivary complex on either side.

Labeled cells in the ipsilateral VN were seen in fringe areas of IVN and MVN and in large numbers in cell group "y". Commissural neurons were prominent in MVN, cell group "y" and in parts of SVN. Nearly all cells of contralateral MVN and cell group "y" were labeled, while those in the SVN were labeled in ventrolateral regions. No labeled cells were seen in LVN or cell groups "f" and "x".

Rostral to the VN, HRP was transported retrogradely to: (1) visceral neurons in the OMC and (2) neurons throughout the ipsilateral INC (Fig. 6F). A small collection of labeled cells found ipsilaterally near the fasciculus retroflexus, designated as the subPF, appeared to form part of the INC.

Sections of the cerebellum revealed labeled PCs in the ipsilateral nodulus, uvula, anterior lobe vermis and parts of the flocculus. In the flocculus labeled cells formed a central band 4 or 5 cells wide which extended through all folia (Fig. 10). Both FN contained labeled cells ventrolaterally in caudal and central parts of the nucleus.

Lateral vestibular nucleus. In two cats (U-158 and U-188) HRP injected into the center of LVN spread beyond the borders of the nucleus. The pattern of retrograde cellular labeling in the brain stem reflected variable transport from other VN. The absence of labeled cells in the contralateral LVN was the most significant observation.

The major locus of retrograde transport was the ipsilateral cerebellar cortex, where labeled PCs were found 5 to 20 abreast in all

vermal folia of the anterior lobe (Fig. 11C). The number of labeled cells progressively declined in vermal lobules VIII, IX and X. Retrograde transport to the deep cerebellar nuclei (DCN) was restricted to the FN. In cat U-158, HRP cells were found in the rostral third of the ipsilateral FN. A greater number of labeled cells was found bilaterally in the rostral third of the FN in cat U-188.

In a squirrel monkey (U-133) HRP injected into the center of the LVN labeled the entire nucleus selectively (Fig. 11A). Upper cervical spinal segments revealed a small number of labeled cells in the contralateral CCN, but no labeled cells were identified at other spinal levels. Enzyme transport to reticular neurons was sparse, bilateral and confined to a few cells in the dorsomedial RF. Labeling in the contralateral VN was limited to a few cells in lateral parts of MVN and SVN. No label was present in the opposite LVN or cell group "y".

The principal retrograde transport of HRP was seen in the cerebellar cortex and in the FN. A continuous band of labeled PCs, five or six across, was noted in all folia of the ipsilateral anterior lobe vermis. A less distinct band containing fewer cells was seen in the nodulus and uvula. HRP cells in the FN were localized to ventrolateral and rostral regions ipsilaterally, and scattered in rostral regions contralaterally (Fig. 11B). Afferent projections to LVN are summarized in Figure 12.

Projections of the Vestibular Nuclei

Efferent connections of the vestibular nuclei were studied in 14 animals in which injections of [^{3}H] amino acids were made into individual or multiple VN. Information concerning the species and tracers

FIGURE 6

Cats U-145 (A-D) and U-122 (E,F). A: bright field photomicrograph showing an HRP injection in the left medial vestibular nucleus (MVN). B-D: dark field photomicrographs showing retrograde transport of HRP from the injection site in A to neurons in the contralateral cell group "y" and the MVN (B), in peripheral portions of the contralateral superior (SVN) vestibular nucleus (C) and in the midline visceral nuclei of the oculomotor complex (D). E: dark field photomicrograph showing retrograde and anterograde transport of HRP from an injection involving both the medial and inferior vestibular nuclei to cells and terminals in the nucleus intercalatus (NIC) on both sides. Contralateral transport is predominantly retrograde while ipsilateral transport is mainly anterograde. F: dark field photomicrograph of retrograde label in cells of the ipsilateral interstitial nucleus of Cajal (INC). Neutral red; magnifications: A, X2.5; B, X5; C,E,F, X9; D, X15.

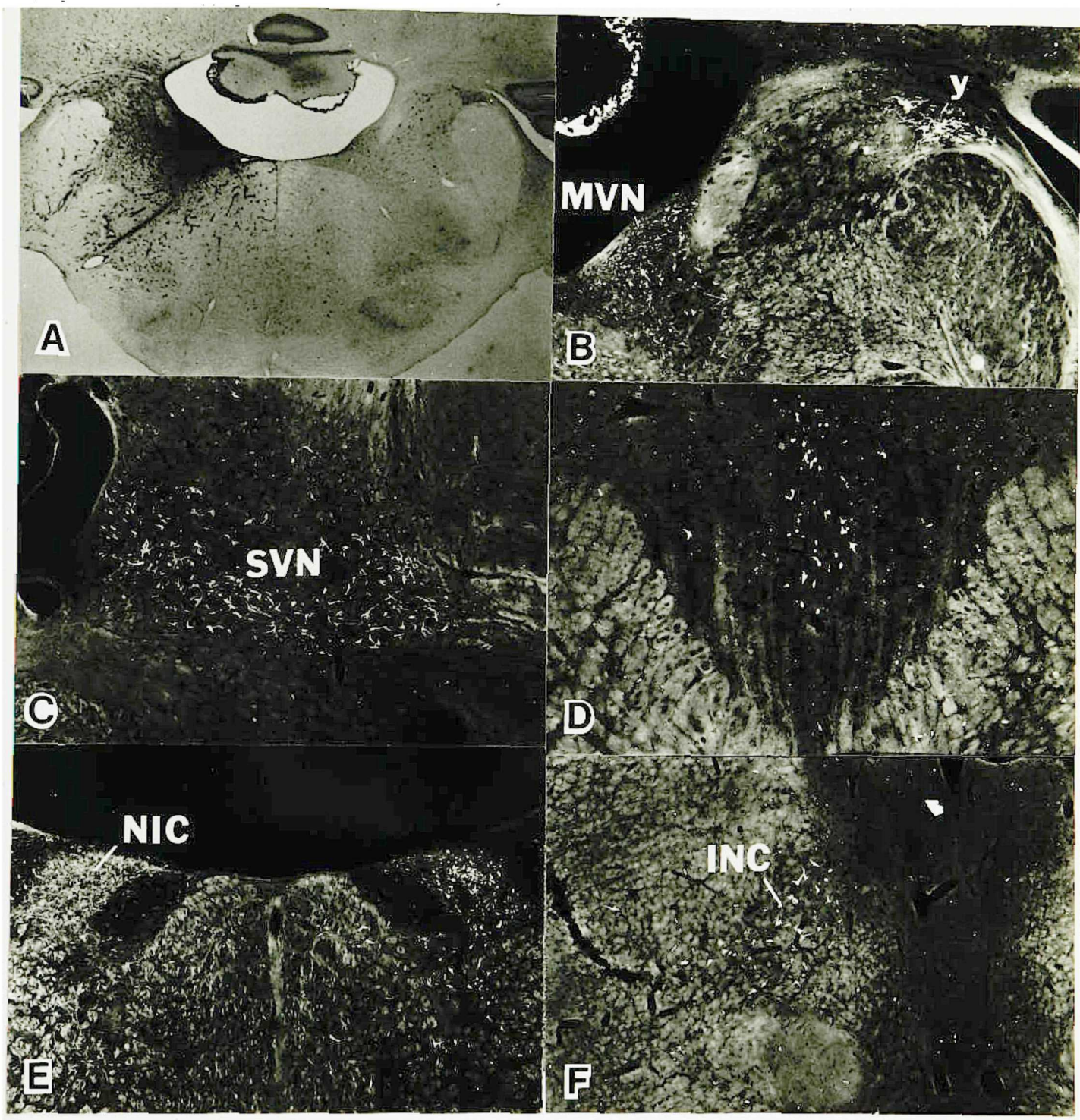
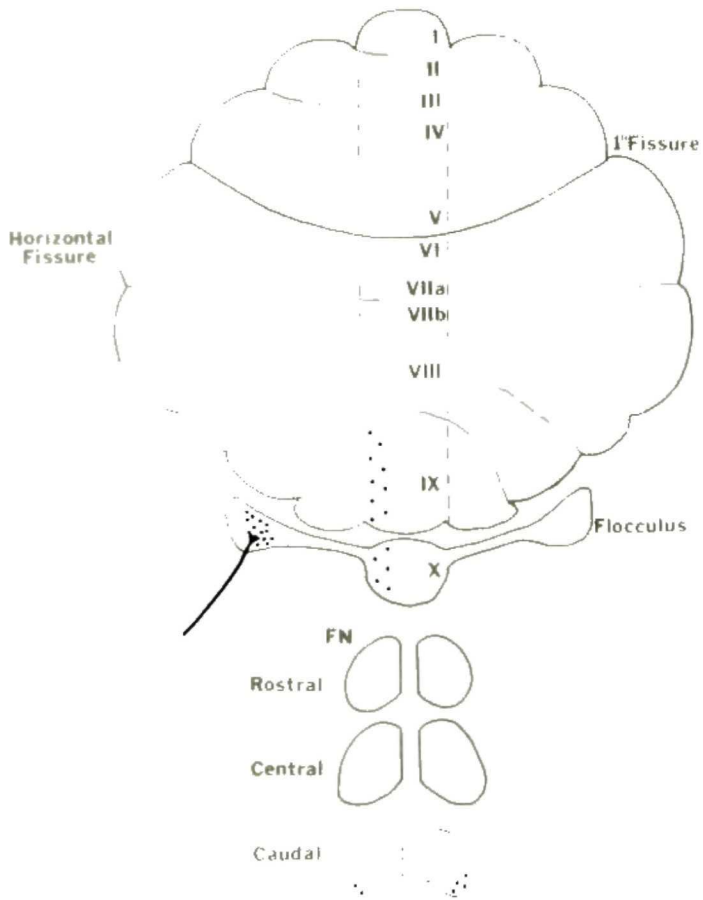

A
B
MVN
y
C
SVN
D
E
NIC
F
INC

FIGURE 7

Schematic diagram of the brain stem and cerebellum summarizing the afferent and efferent connections of the medial vestibular nucleus (MVN). Neurons projecting to the MVN are shown as small dots. The injection site (HRP or [^{3}H] amino acid) is represented in black and projections of the MVN are shown by black lines. The major ascending projections from MVN are to: (1) the ipsilateral VI nucleus, (2) the opposite IV nucleus and (3) the opposite OMC.


I
II
III
IV
1°Fissure
V
VI
VIIa
VIIb
VIII
Horizontal Fissure
IX
Flocculus
X
FN
Rostral
Central
Caudal

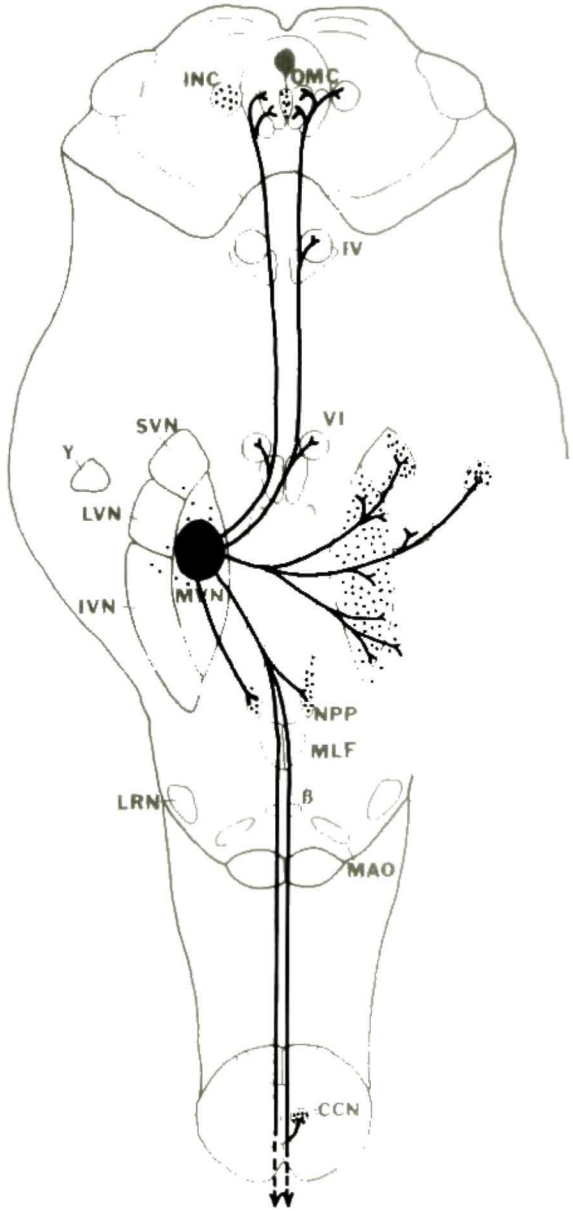

INC
OMC
IV
SVN
VI
Y
LVN
IVN
MVN
NPP
MLF
LRN
β
MAO
CCN

FIGURE 8

Cats U-118 (A) and U-127 (B-F). A: dark field photomicrograph showing an HRP injection confined to the inferior vestibular nucleus (IVN). B,C,E and F: dark field photomicrographs of retrograde transport of HRP from the IVN to cells of the contralateral central cervical nucleus (CCN) (B), the contralateral cell group "y" (C), the ipsilateral cortex of the nodulus (E) and the fastigial nuclei (FN) on both sides (F). D: dark field photomicrograph of anterograde transport of HRP to terminals in the ipsilateral nucleus β. Neutral red; magnifications: A, X2.5; B, X15; C, X9; D, X25; E,F, X5.

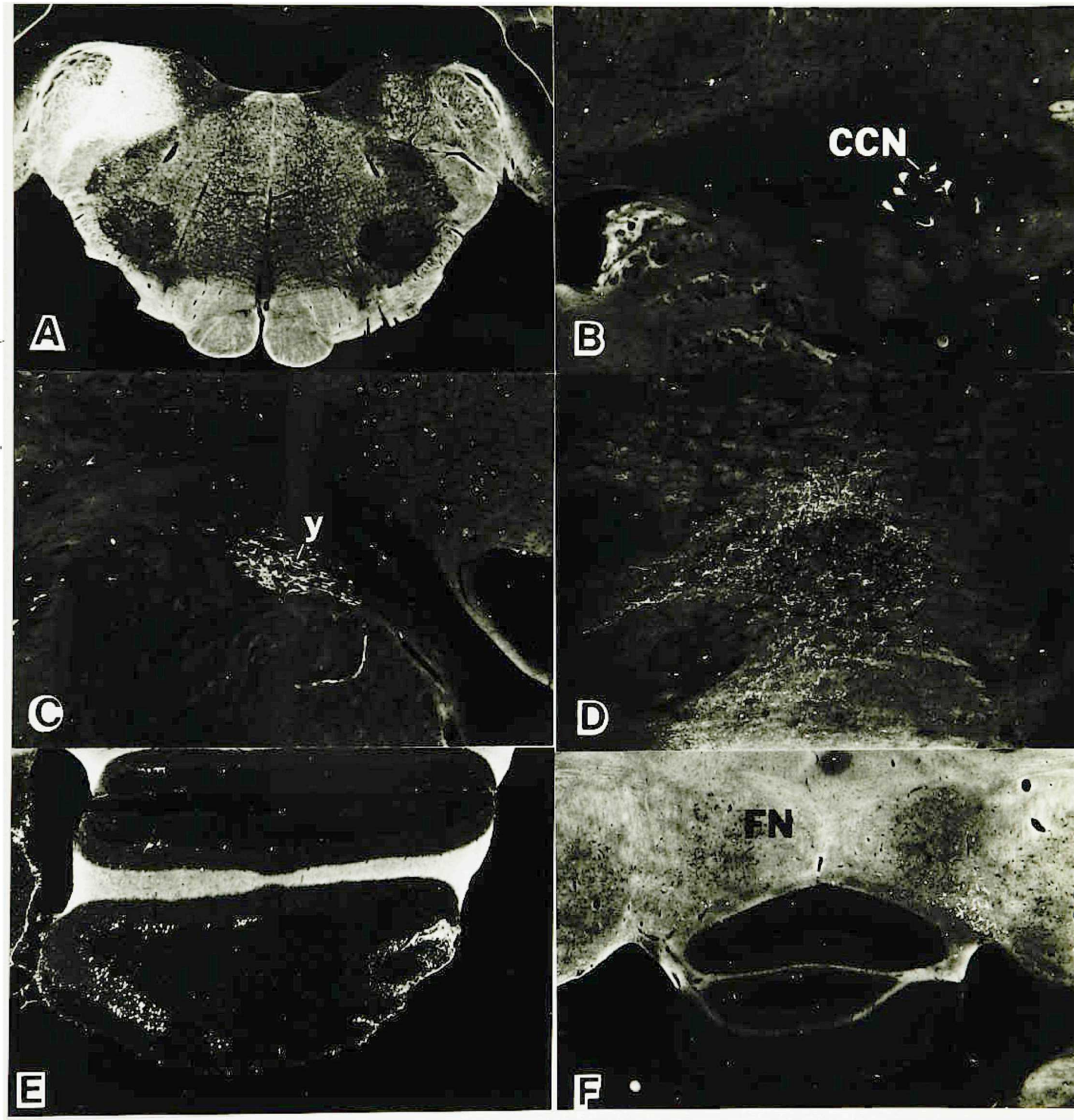

A
B
CCN
C
y
D
E
F
FN

FIGURE 9

Schematic diagram of the afferent and efferent projections of the inferior vestibular nucleus (IVN) in the brain stem and cerebellum. Neurons projecting to IVN are shown as small dots. The injection site (HRP or [^{3}H] amino acid) is represented in black and projections from IVN are shown by black lines. Projections to the paramedian reticular nuclei are not shown.

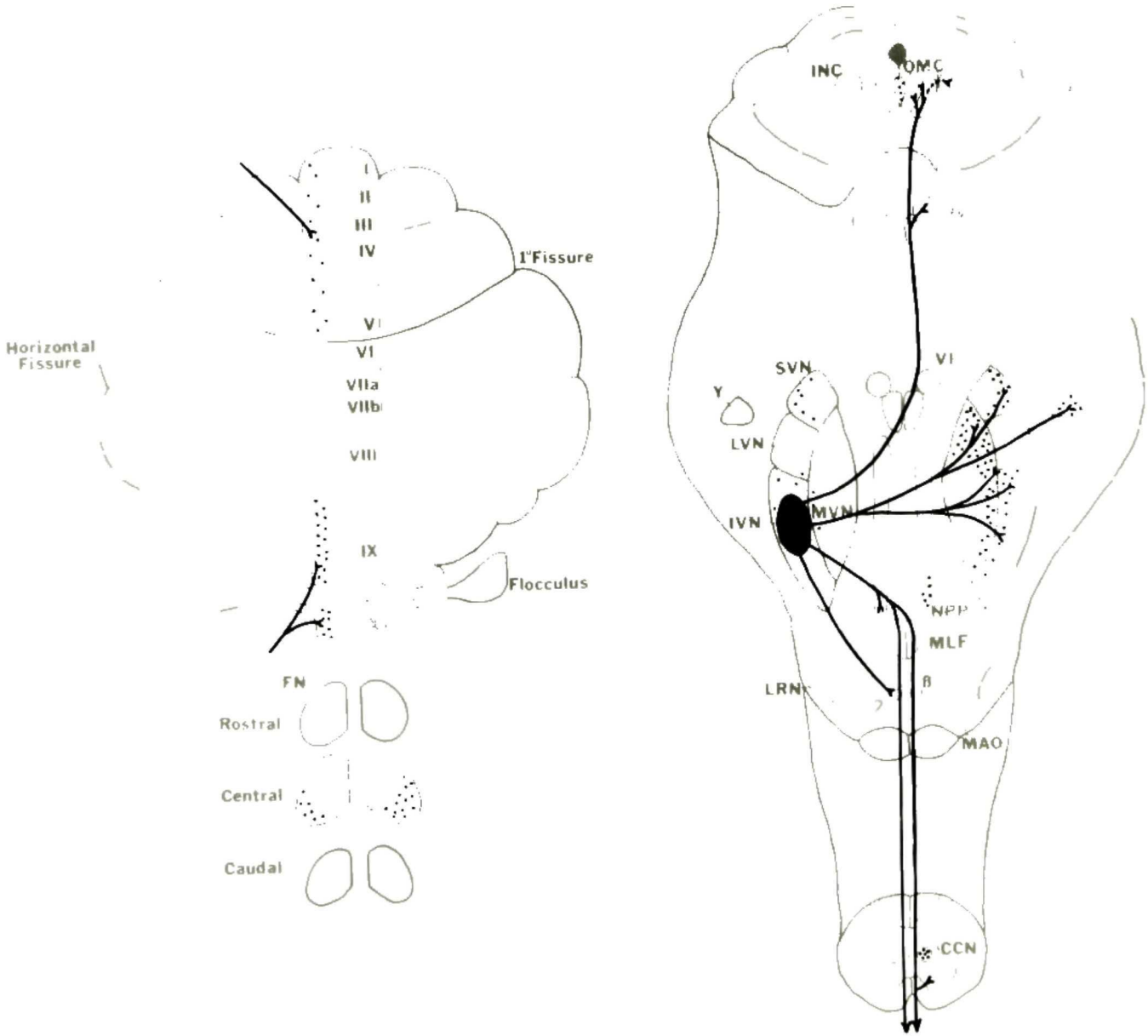

Horizontal Fissure
I
II
III
IV
1°Fissure
V
VI
VIIa
VIIb
VIII
IX
Flocculus
FN
Rostral
Central
Caudal
INC
OMC
SVN
VI
Y
LVN
IVN
MVN
NPP
MLF
LRN
ß
MAO
CCN

FIGURE 10

Cat U-122. Dark field photomicrograph of retrograde transport of HRP to Purkinje cells in a central band in the ipsilateral flocculus. Neutral red; magnification: X9.

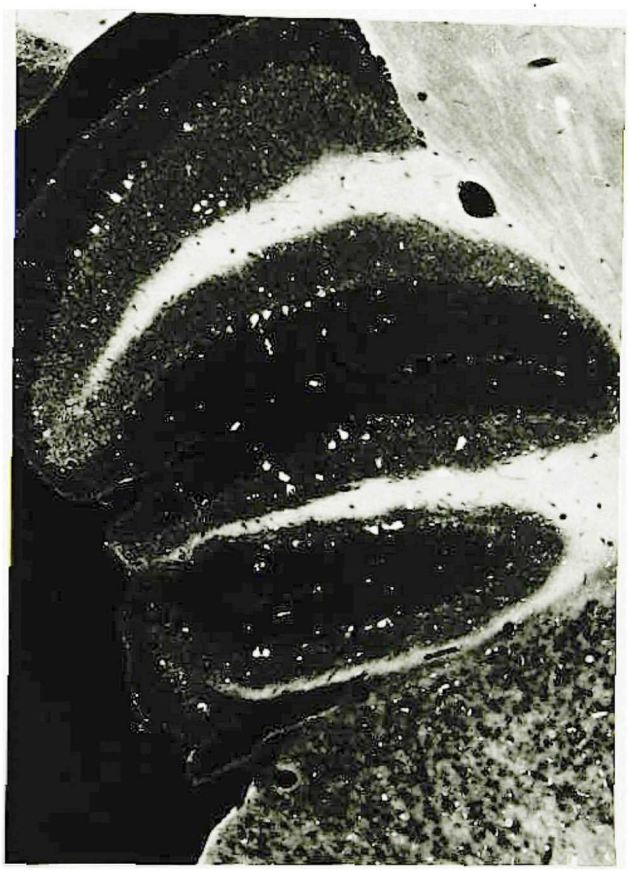


FIGURE 11

Squirrel monkeys U-133 (A,B) and U-116 (E). Cats U-188 (C) and U-161 (D,F). A: dark field photomicrograph of an HRP injection confined to the left lateral (LVN) vestibular nucleus. B: bright field photomicrograph of retrograde transport of label from the injection in A to the cells of the fastigial nuclei (FN). C: dark field photomicrograph of retrograde transport of HRP from the LVN to Purkinje cells of the ipsilateral anterior lobe vermis. D: dark field autoradiograph of an [^{3}H] leucine injection into the lateral (LVN) and inferior (IVN) vestibular nuclei showing transport via the vestibulospinal tract (VST, from LVN) and the contralateral ascending medial longitudinal fasciculus (MLF, from IVN). E: dark field autoradiograph showing transport via the left VST and the MLF on both sides from an isotope injection involving both LVN and IVN. Transport to nucleus β arises from IVN. F: dark field autoradiograph of terminal label in the ipsilateral dorsal paramedian reticular nucleus (DPRN) and descending fibers in the MLF on both sides following the isotope injection shown in D. A-C: neutral red. D-F: cresyl violet; magnifications: A,D, X2.5; B, X9; C,E, X5; F, X5.

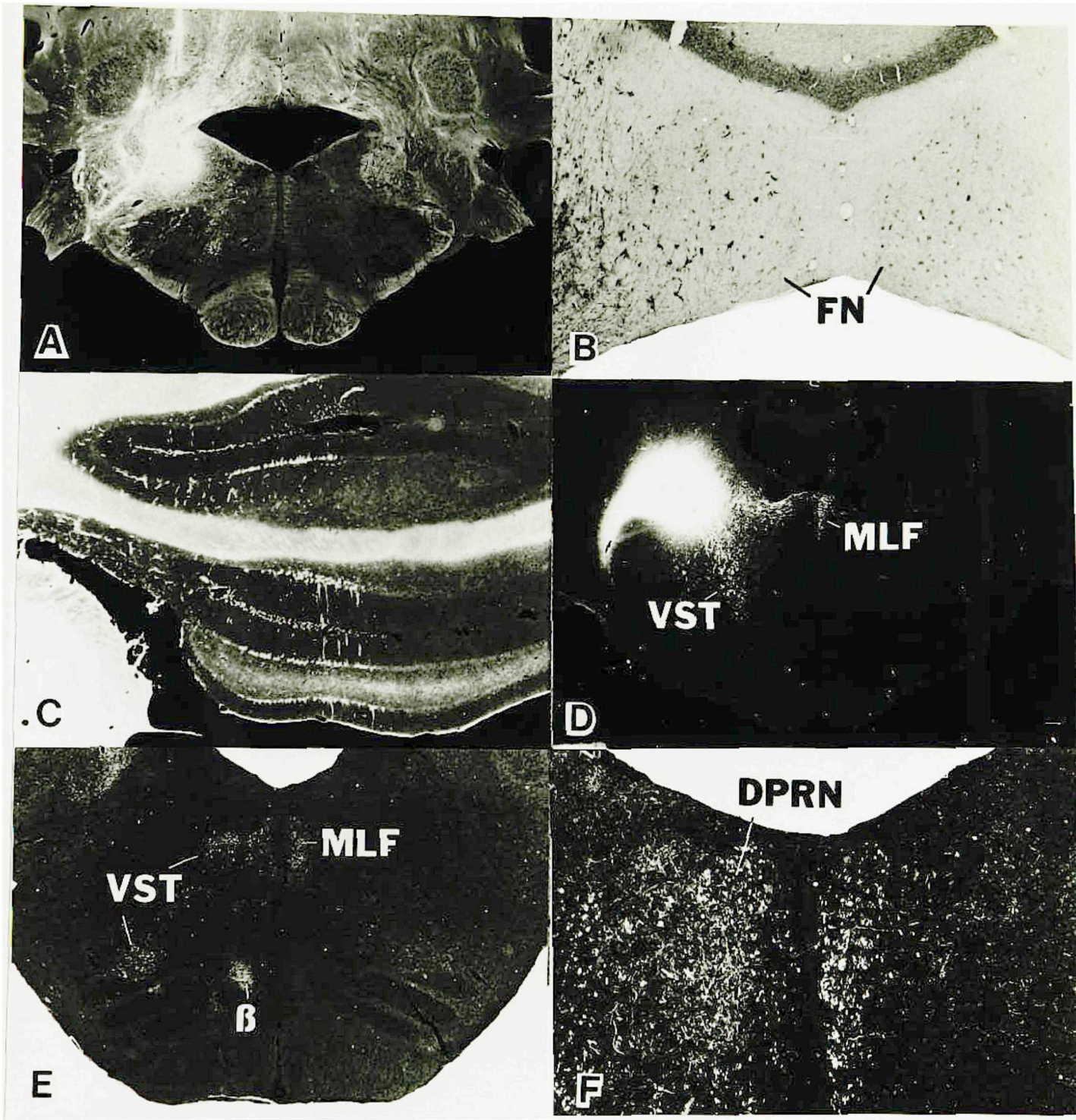
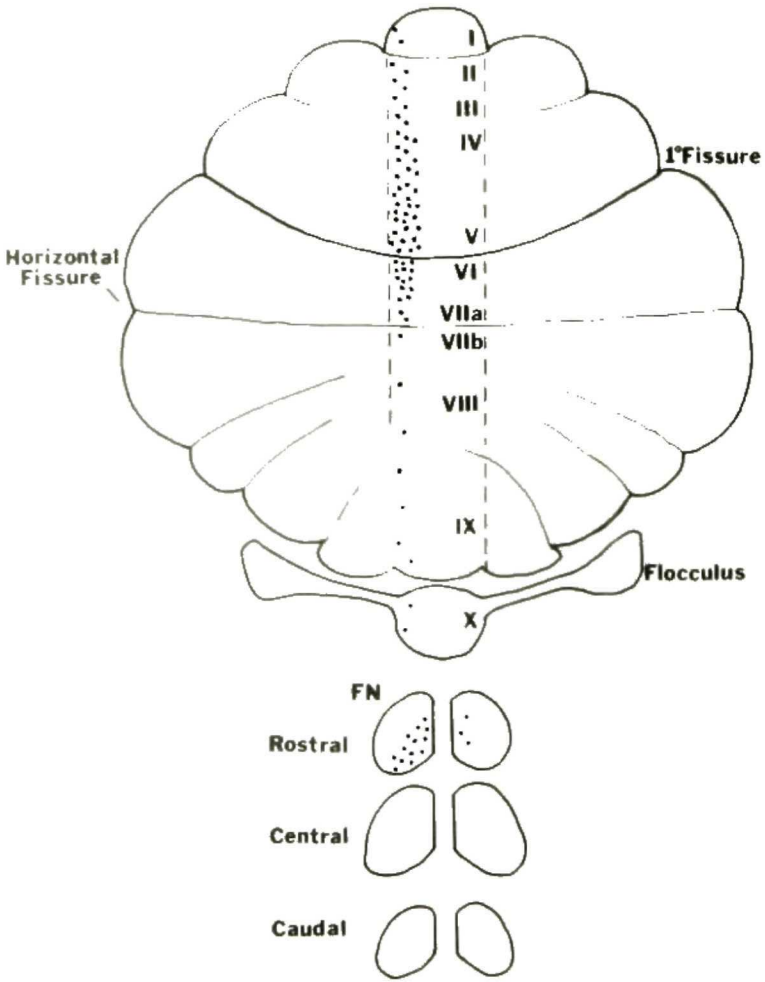
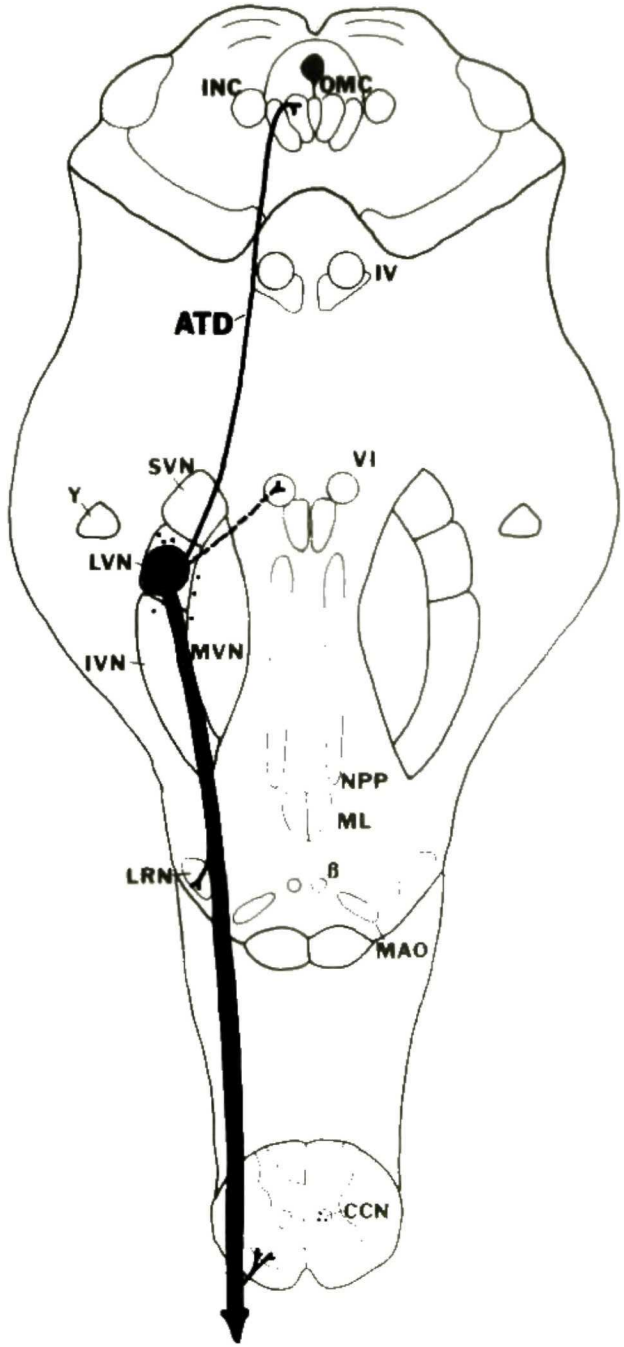

A
B
FN
C
D
MLF
VST
E
MLF
VST
ß
F
DPRN

FIGURE 12

Schematic summary of the afferent and efferent connections of the lateral vestibular nucleus (LVN). Neurons projecting to the LVN are shown as small dots. The region of the injection site (HRP or [^{3}H] amino acid) is shown in black and projections from LVN are represented by black lines. Terminals of the ascending tract of Deiters' (ATD) were identified in the medial rectus subdivision of the oculomotor complex only in the cat.


I
II
III
IV
V
VI
VIIa
VIIb
VIII
IX
X
1°Fissure
Horizontal Fissure
Flocculus
FN
Rostral
Central
Caudal


INC
OMC
IV
ATD
SVN
VI
Y
LVN
IVN
MVN
NPP
ML
LRN
β
MAO
CCN

used, the nuclei injected, and the survival times allowed appears in Table IV. Degeneration resulting from an electrolytic lesion in MVN, and anterograde transport of HRP from the injections described previously, provided supportive evidence. Injections of [^{3}H] amino acids into the abducens nuclei in two monkeys allowed comparisons between vestibular and abducens internuclear projections to the primate OMC.

Medial vestibular nucleus. Injections of [^{3}H] leucine into the MVN in two cats (U-135 and U-138) selectively involved the rostral half of the nucleus (Fig. 13D). The pattern of isotope transport was the same in both animals. Descending fibers from MVN entered the medial longitudinal fasciculus (MLF) on both sides. Terminals were seen in nearly all parts of NPP ipsilaterally; contralaterally a smaller number of terminals were confined to caudal parts of NPP. Bilateral transport also was evident in the NIC with ipsilateral dominance. Descending fibers in the MLF were asymmetrically disposed; ipsilaterally labeled axons were confined to a dorsolateral location, while contralateral fibers were located ventromedially. Descending fibers diminished bilaterally as they passed caudally and all crossed fibers in the MLF disappeared near the corticospinal decussation. Ipsilateral fibers entered the supraspinal nucleus (SSN) but terminals did not preferentially surround large motor neurons. Contralaterally terminals were noted only in the CCN. Because of discontinuities in labeling, it was not possible to determine whether terminals in the opposite CCN descended in the contralateral MLF, or crossed within the spinal cord. No fibers or terminals were noted at more caudal spinal levels.

Commissural fibers emerged from the MVN, arched ventromedially through the RF and entered the opposite VN (Fig. 13D). Contralateral

terminations were distributed to all but the most caudal parts of MVN. Less impressive terminals were present in medial parts of IVN and ventrolateral parts of SVN. A weak crossed projection terminated in rostroventral LVN and in cell group "y".

Fibers emerging from rostral portions of MVN entered the abducens nuclei (AN) and dorsomedial parts of the opposite MLF. Terminals were profuse in all parts of the ipsilateral AN, but endings were seen only in dorsomedial regions of the opposite AN (Fig. 13E). Ascending projections in the opposite MLF were followed into the trochlear nucleus (TN) and OMC (Fig. 13F); in the OMC fibers terminated in nuclear subdivisions innervating the medial rectus and inferior rectus muscles (Akagi, '78).

A few fibers ascending in the lateral wing of the ipsilateral MLF bypassed the TN and entered the OMC. Most of these fibers terminated in dorsal and lateral regions of the OMC considered to innervate the medial and inferior rectus muscles. In addition, labeled fibers were seen crossing within the OMC from the opposite side (Fig. 13F), an observation never made in the monkey. No terminals were identified in the visceral nuclei. Fibers bypassing the OMC were seen only contralaterally; these projected weakly to a small ventral part of the nucleus of Darkschewitsch and profusely to the INC (Fig. 14A). Sections of the cerebellum in these animals did not reveal isotope transport to any part of the cerebellar cortex or to the FN.

Data concerning efferent projections of the MVN also were obtained from the study of anterograde transport of HRP in 4 cats previously described. Observations in these animals confirmed the pattern of vestibular projections to the PH, the contralateral VN, and the

nuclei of the extraocular muscles seen in isotope studies. No fibers from MVN could be traced to terminations in the cerebellum.

In one squirrel monkey [^{3}H] leucine injected into the MVN (U-126) demonstrated maximal uptake in central and rostral portions of the nucleus (Fig. 15A). The rostral tip of the injection spread into the dorsolateral part of the AN and produced transport in root fibers of that nerve. Descending transport of isotope by fibers of the MLF was bilateral and asymmetrical but could not be followed into the spinal cord. At upper cervical spinal levels a distinct collection of silver grains was present about cells of the contralateral CCN (Fig. 13C).

In the medulla fiber terminations were seen ipsilaterally in the NR, NIC and in caudal portions of NPP. Fibers from MVN coursing through the RF and the MLF projected to the contralateral NPP, MVN, cell group "y" and SVN. Commissural projections were massive to all parts of the opposite MVN. Although no terminals were noted in IVN, sparse commissural projections terminated in rostroventral LVN. Projections to SVN were restricted to peripheral portions of this nucleus. Some laterally projecting fibers traversed portions of IVN and LVN on both sides and passed peripherally into the vestibular root. These were considered to be the vestibular efferent fibers described by Goldberg and Fernández ('80).

Ascending fibers entered the MLF near the AN. Because the injection involved part of the left AN, it was difficult to interpret all observations. Fibers projecting through the MLF to the opposite AN terminated throughout its extent. Ascending transport via the MLF was bilateral, asymmetrical and much greater on the side opposite the injection. Fibers in the contralateral MLF ascended in medial parts of

the bundle to terminate in all parts of the contralateral TN (Fig. 14B), and in the OMC in: (1) all nuclear subdivisions caudally, and (2) the intermediate (ICC, inferior oblique muscle) and ventral (VCC, medial rectus muscle) cell columns rostrally (Figs. 14C and 15B). Fibers of the ipsilateral MLF, ascending in the lateral wing of the bundle, ended mainly in the ICC. Terminals also were seen in the VCC in rostral portions of the complex, and in the dorsal cell column caudally (Fig. 15B).

A number of fibers in the contralateral MLF continued rostrally and terminated on cells in the INC (Fig. 14D) and ND; no similar projections were seen ipsilaterally. Fibers also passed dorsally through the contralateral INC to terminate in the rostral interstitial nucleus of the MLF (RiMLF) (Büttner-Ennever, '77). Terminals in this structure were scant, but distinct. Crossed fibers ascending to the level of the fasciculus retroflexus projected laterally along the ventral margin of the ventral posteromedial nucleus of the thalamus. Although these fibers could not be followed to terminations, they appeared to represent a vestibulothalamic bundle.

Fibers passing laterally from the area of isotope uptake projected to folia of the ipsilateral flocculus, where terminations were seen in the granular layer. Most of these fibers terminated in a central band in the flocculus. No terminations were seen in any of the DCN.

In a single rhesus monkey (C-668), a discrete electrolytic lesion confined to the rostral two-thirds of the right medial vestibular nucleus (MVN) (Fig. 15C) produced anterograde degeneration which ascended bilaterally in the MLF to the oculomotor complex (OMC) (McMasters et al., '66). Terminal degeneration was observed bilaterally

and symmetrically in the abducens nuclei, contralaterally in the trochlear nucleus, and bilaterally and asymmetrically in the OMC. Degeneration in the ipsilateral OMC had the same distribution as described for squirrel monkey U-126. Contralateral degeneration in the OMC was greatest over cells of the ICC at all levels, and in the dorsal cell column (DCC) in rostral portions of the nuclear complex. Few, if any, degenerated terminals were evident in the VCC on the side opposite the lesion (Fig. 15D).

Inferior vestibular nucleus. While no isotope injections were confined to the IVN in any cat, HRP injections in three cats provided information concerning efferent projections. Injection sites and retrograde transport in these animals has been described. Labeled axons from IVN descended bilaterally via the MLF to upper cervical spinal segments, but terminations could not be detected in the spinal gray. Descending fibers from the IVN terminated: (1) bilaterally in the dorsal paramedian reticular nuclei (DPRN) with ipsilateral dominance and (2) in specific parts of the ipsilateral inferior olivary complex. In all animals, nucleus β contained a dense plexus of fine granular terminals (Fig. 8D). Lesser projections were noted to the dorsal cap (dc) of Kooy and the dorsomedial cell column (dmcc).

Commissural projections traversed broad regions of the RF and terminated: (1) about the border of IVN and MVN caudally, (2) throughout rostral MVN, (3) in ventrolateral regions of SVN and (4) sparsely in cell group "y". No terminals were identified in LVN or in cell groups "f" or "x". Fibers ascending in the contralateral MLF terminated in the opposite TN and in the inferior and medial rectus subdivisions of the

OMC. Labeled fibers in the medullary core of the cerebellum could not be followed to terminations.

In two squirrel monkeys (U-112 and U-115) injections of [^{3}H] leucine labeled the caudal half of IVN. These injections differed primarily in laterality, in that the injection in U-112 involved cell groups "f" and "x", while that in U-115 excluded these cell groups. Although both injections involved other structures, it was possible to identify projections from IVN.

Vestibular fibers descending bilaterally in the MLF were followed into the upper cervical spinal cord, but not to terminations. At medullary levels fibers terminated in: (1) nucleus β, (2) the dmcc and (3) the dc of the principal olive. These projections were largely ipsilateral.

Commissural vestibular projections were the same as described for anterograde HRP studies in the cat. Ascending fibers from IVN projected through the ipsilateral AN without evidence of terminations and entered the opposite MLF. All ascending isotope transport was via the contralateral MLF. These fibers terminated in the opposite TN and primarily the dorsal somatic cell column of the OMC; lesser projections were evident in the intermediate cell column. Secondary vestibulocerebellar projections from IVN were limited to the ipsilateral vermal cortex of the nodulus, uvula and anterior lobe where fibers ended in mossy fiber rosettes.

Inferior and medial vestibular nuclei. A large HRP injection involving portions of both IVN and MVN in a cat (U-122, p. 38) provided information concerning vestibular projections. Anterograde transport of enzyme reflected the combined projections of both nuclei as seen in

isotope studies. Terminal label in the ipsilateral nucleus β, the PH (Fig. 6E) and the contralateral INC was impressive.

Lateral vestibular nucleus. Selective isotope injections in the LVN were not obtained in cats, but HRP injections into this nucleus in two cats (U-158 and U-188) provided information concerning efferent projections. The principal anterograde transport was seen ipsilaterally in the vestibulospinal tract (VST). Coarse axons of the VST formed a broad, loosely organized, oblique band in the brain stem, but could not be followed into the spinal cord. Distinct branches of VST axons entered the ipsilateral LRN where they formed islands of terminals in the magnocellular and parvicellular divisions. No commissural projections were evident and no fibers could be traced into the nuclei of the extraocular muscles or the cerebellar cortex.

An HRP injection in the LVN (Fig. 11A) in a monkey (U-133) resulted in similar anterograde transport. No terminals were seen in the contralateral VN and no labeled fibers descended in the MLF on either side. A small number of ascending fibers entered the lateral wing of the ipsilateral MLF but none could be traced into nuclei of the extraocular muscles. Labeled fibers seen in the white matter of the cerebellum did not terminate in the cortex or the DCN.

Lateral and inferior vestibular nuclei. Nearly identical injections of [^{3}H] leucine in four cats (U-129, U-160, U-161 and U-164) labeled the LVN and dorsorostral portions of IVN (Fig. 11D). Labeling was seen in the VST ipsilaterally (Fig. 11D) and in the MLF bilaterally (Fig. 11F). Collaterals from the VST terminated in the LRN (Fig. 13A). The VST was followed caudally to the cervical enlargement.

Descending transport in the MLF was bilateral and asymmetrical. Collaterals from the MLF terminated in the dorsal (DPRN) (Fig. 11F) and ventral (VPRN) paramedian reticular nuclei bilaterally with ipsilateral dominance. Axons in the MLF were traced in the sulcomarginal area to the cervical enlargement, and terminals were noted bilaterally in the anterior horn of upper cervical spinal segments. Because of concomitant labeling in the VST and MLF on the injected side, ipsilateral terminals could not be assigned to either tract. Contralateral terminals in lamina VIII and medial parts of lamina VII clearly were related to the MLF. In the medulla descending fibers terminated ipsilaterally in NPP and weakly in nucleus β. Commissural projections to the contralateral VN were the same as described in the monkey for IVN, except that no terminals were seen in cell group "y".

Ascending projections entered the contralateral MLF and also projected rostrally via the uncrossed ATD. Terminal label was sparse in parts of the ipsilateral AN. Crossed ascending fibers in the MLF terminated weakly in the opposite TN and continued rostrally to end in lateral and dorsal cell columns of the OMC which innervate the inferior and medial rectus muscles (Fig. 14E,F). A few crossed ascending fibers in the MLF ended in parts of the INC. Axons forming the ATD became incorporated into the lateral process of the MLF and terminated about neurons in dorsal parts of the OMC innervating the medial rectus muscle (Fig. 14E,F). No terminals were found in the cerebellar cortex or the DCN.

Observations in a squirrel monkey (U-116) in which [^{3}H] leucine was injected into LVN and parts of IVN were similar to those described above for the cat. Terminal arborizations in nucleus β (Fig. 11E), DPRN and portions of the contralateral VN were the same as described for IVN

(monkeys U-112 and U-115). Ascending transport in the contralateral MLF and terminations in the opposite TN and OMC were the same as described for IVN. Ipsilateral fibers in the ATD were followed only to isthmus levels. No terminals were seen in the cerebellar cortex or in the DCN.

Superior vestibular nucleus. In two animals (cats U-193, U-196), injections of [^{3}H] proline and leucine labeled all parts of SVN and dorsal portions of LVN (Fig. 16A). In U-193, isotope also diffused to include dorsolateral and rostral portions of MVN and a small medial part of cell group "y". Neither injection involved any of the deep cerebellar nuclei, nor areas of the reticular formation adjacent to the VN.

Scant descending transport was evident in fibers of the ipsilateral VST, and in the descending vestibular root. In U-193, a few fibers also were labeled in the dorsolateral part of the ipsilateral MLF. These were presumably derived from portions of MVN involved by the injection in this animal. Projections were noted in the VST but were followed only to the first cervical spinal segment. No terminations related to the VST and descending MLF were observed in the spinal cord or any nuclei of the brain stem. Faint terminations related to the descending vestibular root were visible in dorsal portions of MVN and IVN ipsilateral to the injection.

Commissural projections crossed the midline in the dorsal pontine tegmentum at levels coextensive with SVN. Labeled terminals were most pronounced in the contralateral SVN, where silver grains were distributed primarily in the periphery of the nucleus (Fig. 16B). Fewer terminals were observed in the central, large-celled portion of SVN. Crossed projections to MVN terminated in dorsal and lateral portions of

the nucleus in its rostral two-thirds. Terminations in IVN were sparse, and none were seen in LVN or any of the small cell groups of the vestibular nuclear complex.

Ascending axons from SVN projected rostrally via two routes: (1) the ipsilateral MLF, and (2) a crossed bundle outside of the MLF. Ipsilateral ascending projections passed rostromedially to enter the lateral wing of the MLF at isthmus levels. These fibers terminated heavily in the ipsilateral TN (Fig. 16C,D) and in the inferior rectus and inferior oblique cell columns of the OMC (Fig. 16G). Fibers projecting rostral to the OMC terminated in all parts of the ipsilateral INC (Fig. 16H). Ascending fibers outside of the MLF projected rostroventrally from SVN along the medial margin of the ipsilateral lateral lemniscus. This bundle crossed the midline through the superior central nucleus of the raphe caudoventral to the decussation of the SCP (Fig. 16C). Rostral to TN labeled fibers passed dorsally through the SCP and MLF to terminate in the medial cell column (superior rectus subdivision) of the OMC in its caudal two-thirds (Fig. 16E,F). No label was found in the AN, the contralateral INC or the thalamus in either animal.

Cerebellar projections were evident in the cortex of the ipsilateral flocculus, nodulus and uvula. Fibers terminated in globular arrays suggestive of mossy fiber rosettes in the granular layer. Fibers entered the cerebellum in small bundles surrounding the SCP, and via the juxtarestiform body. No terminals were noted in any of the deep cerebellar nuclei.

All vestibular nuclei. In two squirrel monkeys (U-176, U-177), large injections of [^{3}H] proline and leucine centered in LVN involved virtually the entire vestibular nuclear complex unilaterally (Fig.

15E). Areas of isotope uptake included cell group "y" and ventral portions of the interposed nuclei of the cerebellum; the only parts of the vestibular complex not fully labeled were caudal and medial areas of MVN. No part of the nucleus prepositus (NPP) was involved by the injection, but isotope diffusion was present in portions of the reticular formation immediately subjacent to the VN.

Descending transport of isotope was evident ipsilaterally in the VST and bilaterally in the MLF. Coarse labeled axons of the VST traversed the pontomedullary reticular formation as a broad band extending from the lateral margin of the MLF to the ventrolateral aspect of the brain stem. En route to the spinal cord, the VST provided branches to the lateral reticular nucleus (LRN) and portions of the nucleus reticularis gigantocellularis (NRgc) medial to the tract. Terminals in LRN were found in punctate islands in both the magnocellular and parvicellular portions of the nucleus. At the spinomedullary junction, the VST condensed into a compact bundle and passed into the ventral part of the lateral funiculus. In the spinal cord, the tract formed a dense flattened band that was followed to the second lumbar spinal segment (Fig. 13B). Spinal terminations of the VST were noted in medial portions of laminae VIII and VII, and were not observed to form preferential contacts with large motor neurons.

Descending fibers in the MLF were asymmetrically disposed on the two sides; ipsilateral fibers occupied dorsolateral portions of the bundle, while more numerous contralateral projections descended in medial and ventral parts of the bundle. Fibers in the MLF branched to terminate in both the DPRN and VPRN with strong ipsilateral dominance. The volume of isotope transport in the MLF declined in the caudal

medulla, and few fibers entered the sulcomarginal area of the spinal cord. Spinal terminations related to the MLF were identified with certainty only on the contralateral side; these were restricted to the supraspinal nucleus (SSN) and medial portions of lamina VII at upper cervical spinal segments.

At levels co-extensive with the vestibular nuclear complex terminals were identified in the perihypoglossal nuclei and in specific subdivisions of the inferior olivary complex. These had the same distribution as described previously (see p. 59) for injections involving the inferior vestibular nucleus.

Vestibular commissural projections were heavily labeled; fibers arched ventromedially from the injection site to traverse the pontomedullary reticular formation along the entire length of the vestibular nuclear complex. Terminal label was not seen in portions of the RF traversed by these fibers. Commissural projections terminated massively in MVN, SVN, IVN and cell group "y". The nucleus most heavily supplied with commissural fibers was MVN; terminals seen in all but the medial extremes of MVN were most numerous in dorsolateral locations. Heavy projections to SVN terminated in peripheral portions of the nucleus, particularly ventrally and laterally. Terminals in IVN were faint and uniformly distributed in the caudal half of the nucleus. In rostral IVN, terminals were predominantly in ventral areas. Only faint terminations were seen rostroventrally in LVN. All portions of cell group "y" were labeled. Fibers projecting medially from rostral portions of the vestibular nuclear complex terminated bilaterally with strong ipsilateral dominance in the AN. Terminals in the ipsilateral AN were

distributed evenly, while contralateral projections were restricted to its dorsomedial part.

Ascending projections were labeled bilaterally and asymmetrically in the MLF; ipsilateral fibers traveled in the lateral wing of the bundle, while crossed fibers ascended in its medial portion. Labeled fibers also ascended outside of the MLF and crossed to the contralateral side in the ventral mesencephalic tegmentum at isthmus levels. Projections in the MLF terminated bilaterally in the TN and were greatest on the side opposite the injection. Terminals in the OMC were distributed differentially on the two sides. Contralaterally, the heaviest projection was seen in the medial cell column (MCC, superior rectus subdivision) in the caudal two-thirds of the OMC (Fig. 15F). The majority of fibers to the MCC entered this subdivision from the ventral bundle of fibers which crossed through the superior central nucleus of the raphe in a decussation distinct from that of the SCP. In their course, these fibers traversed the contralateral SCP, MLF and ventral cell column (VCC) in slender fascicles (Fig. 15F). Crossed projections contained in the MLF terminated in the intermediate (ICC) and dorsal cell columns (DCC) of the OMC, innervating the inferior oblique and inferior rectus muscles, respectively (Fig. 17A,B,C). The VCC was free of silver grains at all levels of the OMC and its dorsal border was sharply demarcated by terminations in other cell columns (Fig. 17A,B,C). Labeled terminals also were found in large numbers in the contralateral INC, and sparsely in the nucleus of Darkschewitsch. Vestibular projections in the lateral wing of the ipsilateral MLF terminated most profusely in the ICC (Fig. 17A). Moderate projections ended in the DCC (Fig. 15F) VCC (Fig. 17C).

A number of fibers, presumably from the SVN, terminated in the ipsilateral INC (Fig. 17C). The most striking observation in these animals was the difference in the projection to the VCC on the two sides.

Fibers passing rostral to the mesencephalon terminated bilaterally in the rostral interstitial nucleus of the MLF (RiMLF) (Büttner-Ennever, '77), then passed laterally over the zona incerta to terminate in portions of the ventrobasal complex on both sides. Contralateral fibers projected to portions of the ventral posterior lateral nucleus, pars oralis (VPLo), and to the ventral lateral nucleus, pars caudalis (VL). Because of involvement of the deep cerebellar nuclei by portions of the injection, it was not possible to ascribe all of these crossed projections to the vestibular nuclei. Ipsilateral projections terminated in moderate volume in all parts of the ventral posterior intermediate nucleus (VPI).

Labeled fibers entered the cerebellum via two principal routes: (1) the juxtarestiform body and (2) in association with the SCP. Fibers surrounding the SCP formed a large proportion of these projections. These were not fibers intrinsic to this peduncle, but traveled dorsal and ventral to it. Involvement of the interposed nuclei by the injections made it impossible to determine the sources of terminations seen in the cerebellar cortex, but mossy fiber terminals in the ipsilateral nodulus, uvula and flocculus were suggestive of vestibulocerebellar projections.

Projections of the Abducens Nucleus.

In two rhesus monkeys (U-30, U-31), nearly identical injections of [^{3}H] proline and leucine labeled cells in all parts of the right

abducens nucleus, and some adjacent fibers of the ipsilateral MLF and facial genu (Fig. 17D). Anterograde transport of the tracer was evident only in ipsilateral abducens root fibers and in medial portions of the contralateral MLF. Terminal label was limited to several discrete locations in the contralateral oculomotor complex (OMC). Dense terminals were found in all parts of the VCC, while a lesser collection of silver grains was evident in a circular cluster in caudal portions of the DCC (Fig. 17E,F). The areas of termination in the contralateral OMC corresponded closely to descriptions of the location of medial rectus motor neurons provided by Büttner-Ennever and Akert ('81); terminations in the VCC can be equated with their group A, while those in the DCC are the equivalent of cell group B. Cell group C was not labeled or identified in the current study.

FIGURE 13

Cats U-161 (A) and U-138 (D-F). Squirrel monkeys U-176 (B) and U-126 (C). A: dark field autoradiograph of fibers of the vestibulospinal tract (VST) and terminal collaterals in the lateral reticular nucleus (LRN) after the isotope injection shown in Fig. 11D. B: dark field autoradiograph of isotope transport via the VST at C4 after an injection involving the left lateral vestibular nucleus. C: dark field autoradiograph of terminal labeling in the central cervical nucleus (CCN) at C2 following an isotope injection in the contralateral medial vestibular nucleus (MVN). D: dark field autoradiograph of an [^{3}H]-leucine injection into the left MVN showing commissural projections to the contralateral medial and inferior vestibular nuclei. E and F: dark field autoradiographs of isotope transported from the injection in D to terminals in the abducens (E) and oculomotor nuclei (F). In E terminals are distributed differently on the two sides. In F terminals are mainly contralateral in the oculomotor complex but some fibers cross the midline. Cresyl violet; magnifications: A-C, X15; D, X2.5; E,F, X9.

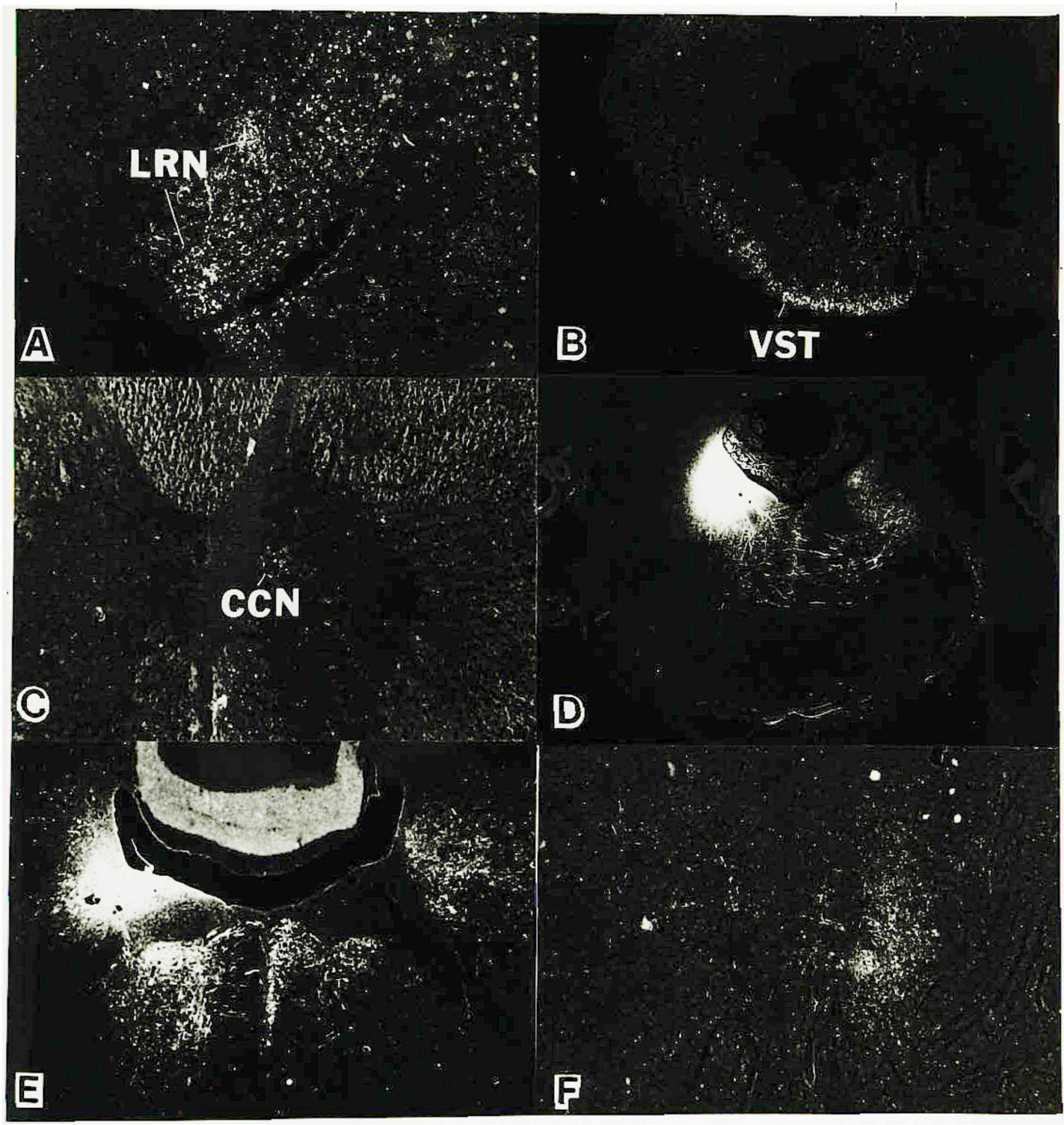

LRN
A
B
VST
CCN
C
D
E
F

FIGURE 14

Cats U-135 (A) and U-129 (E,F). Squirrel monkey U-126 (B,C,D). A. dark field autoradiograph of isotope transport from the medial vestibular nucleus (MVN) to the contralateral interstitial nucleus of Cajal (INC). B, C and D: dark field autoradiographs of isotope transport from MVN to the opposite trochlear nucleus (B), the oculomotor complex (OMC) (C) and the contralateral INC (D). E and F: dark field autoradiographs of caudal (E) and rostral (F) regions of the OMC showing the distribution of terminals following an isotope injection involving the lateral and inferior vestibular (IVN) nuclei. Ipsilateral transport is via the ascending tract of Deiters (ATD) while contralateral fibers ascending in the MLF arise from portions of IVN. Cresyl violet; magnification: A-F, X9.

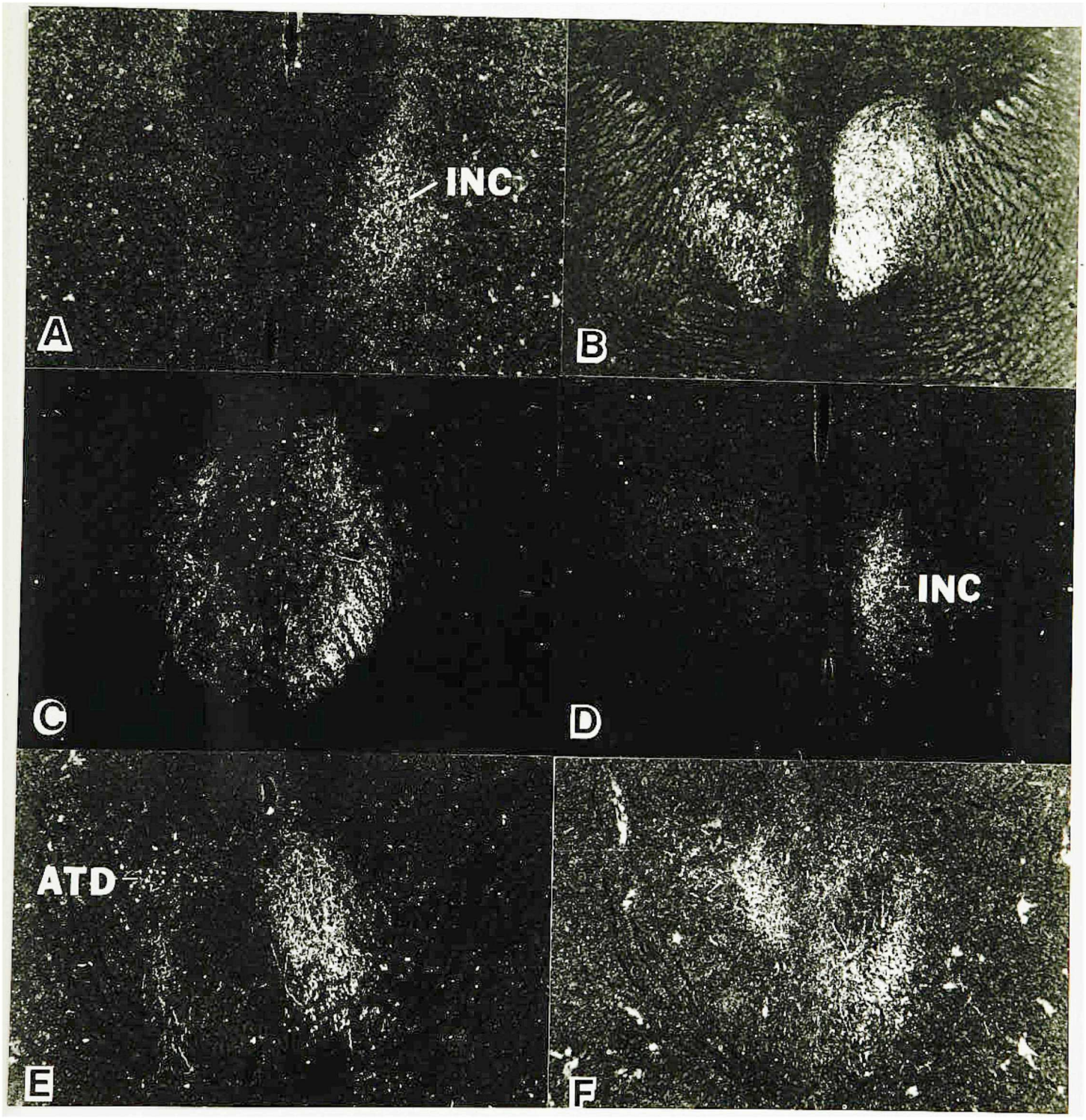
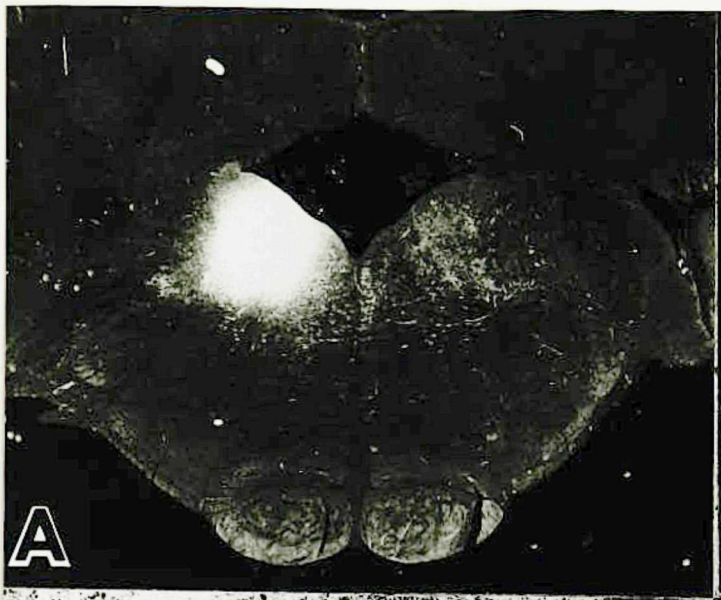
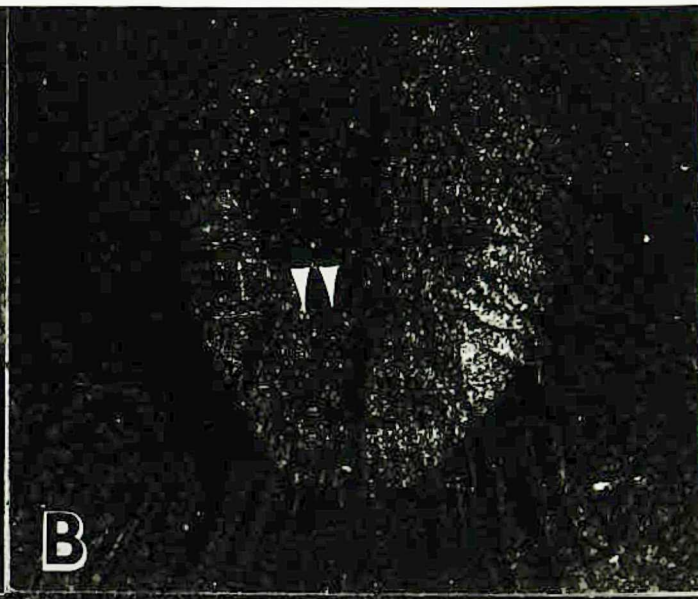
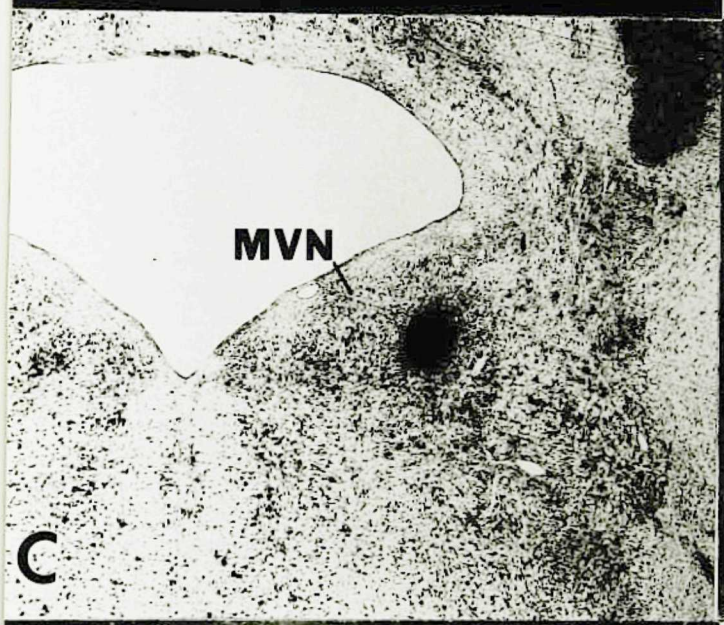

INC
A
B
C
INC
D
ATD
E
F

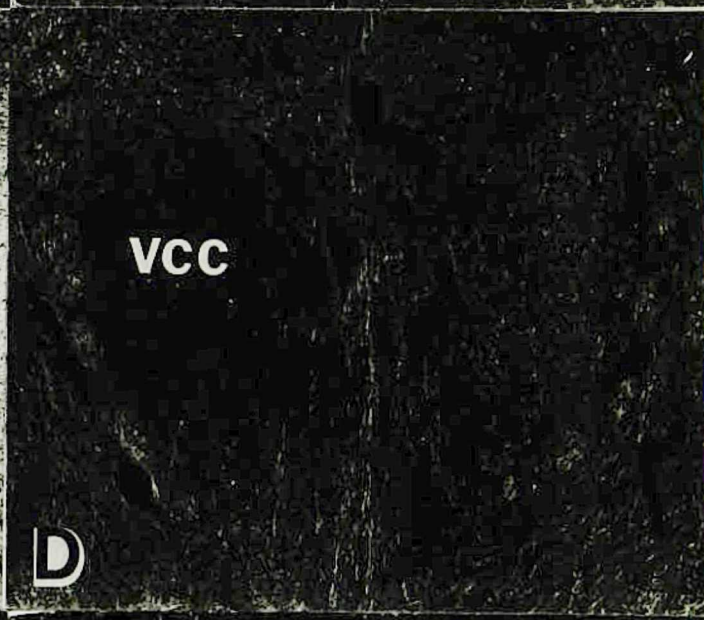
FIGURE 15

Squirrel monkeys U-126 (A,B) and U-177 (E,F). Rhesus monkey C-668 (C,D). A: dark field autoradiograph of an isotope injection in the medial vestibular nucleus (MVN) which rostrally also involved portions of the ipsilateral VI nerve nucleus. B: dark field autoradiograph of labeled terminals in the oculomotor nuclear complex (OMC); ipsilateral terminals in the OMC arise only from MVN and end in the VCC (medial rectus subdivision, below paired arrows) and in the intermediate cell column (ICC, inferior oblique subdivision). C: bright field photomicrograph of a discrete lesion in the right MVN. D: dark field photomicrograph of silver degeneration in the ipsilateral VCC; virtually no degeneration is present in this nucleus contralaterally. E: dark field autoradiograph of an isotope injection involving all vestibular nuclei, cell group "y" and ventral portions of the interposed nucleus. F: dark field autoradiograph of labeled terminals in the caudal third of the OMC; contralaterally terminals are profuse in the medial cell column (MCC, superior rectus subdivision) and in the ICC. Virtually no labeled terminals are present in the contralateral VCC, although fascicles of labeled fibers ascending from the superior cerebellar peduncle pass through this nucleus to end in the SRS. A modest number of terminals are present in the ipsilateral VCC and in the ICC. A, B, C, E, F: cresyl violet; D: Nauta-Gygax; magnifications: A,E, X2.5; B,F, X9; C, X5; D, X15.


A


B


MVN
C


VCC
D


E

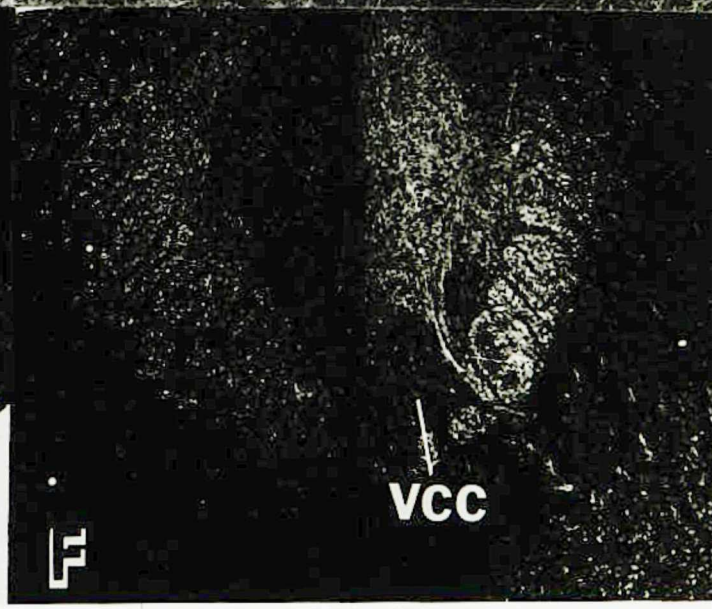

VCC
F

FIGURE 16

Cats U-193 (B,C,D and H) and U-196 (A,E,F and G). A: dark field autoradiograph showing an injection of tritiated amino acids in the left superior vestibular nucleus. B: dark field autoradiograph showing terminations of commissural projections in SVN from an injection similar to that shown in A. Note that the majority of transport is to peripheral portions of the nucleus. Medial collection of silver grains is artifactual. C: dark field autoradiograph showing anterograde transport of tritiated amino acids from an injection in SVN to the ipsilateral trochlear nucleus, and via crossing fibers dorsal to the basilar pons (denoted by "+"). D: higher magnification view of the section shown in C demonstrating terminations in the ipsilateral TN. Note the absence of transport in fibers of the contralateral MLF. E: dark field autoradiograph showing transport of tritiated amino acids from the injection in A to the superior rectus subdivision (SRS) in the caudal half of the contralateral OMC. F: high magnification view of the section shown in E demonstrating terminations in the SRS, and crossed fibers from SVN (denoted by "+"). G: dark field autoradiograph from the rostral half of the OMC in the same animal showing terminations in the ipsilateral inferior rectus subdivision (IRS) from the injection in A. H: dark field autoradiograph demonstrating anterograde transport of tritiated amino acids in the left SVN to terminals in the ipsilateral INC. Cresyl violet; magnifications: A,C, X2.5; B,E,G, X5; D,E,H, X9.

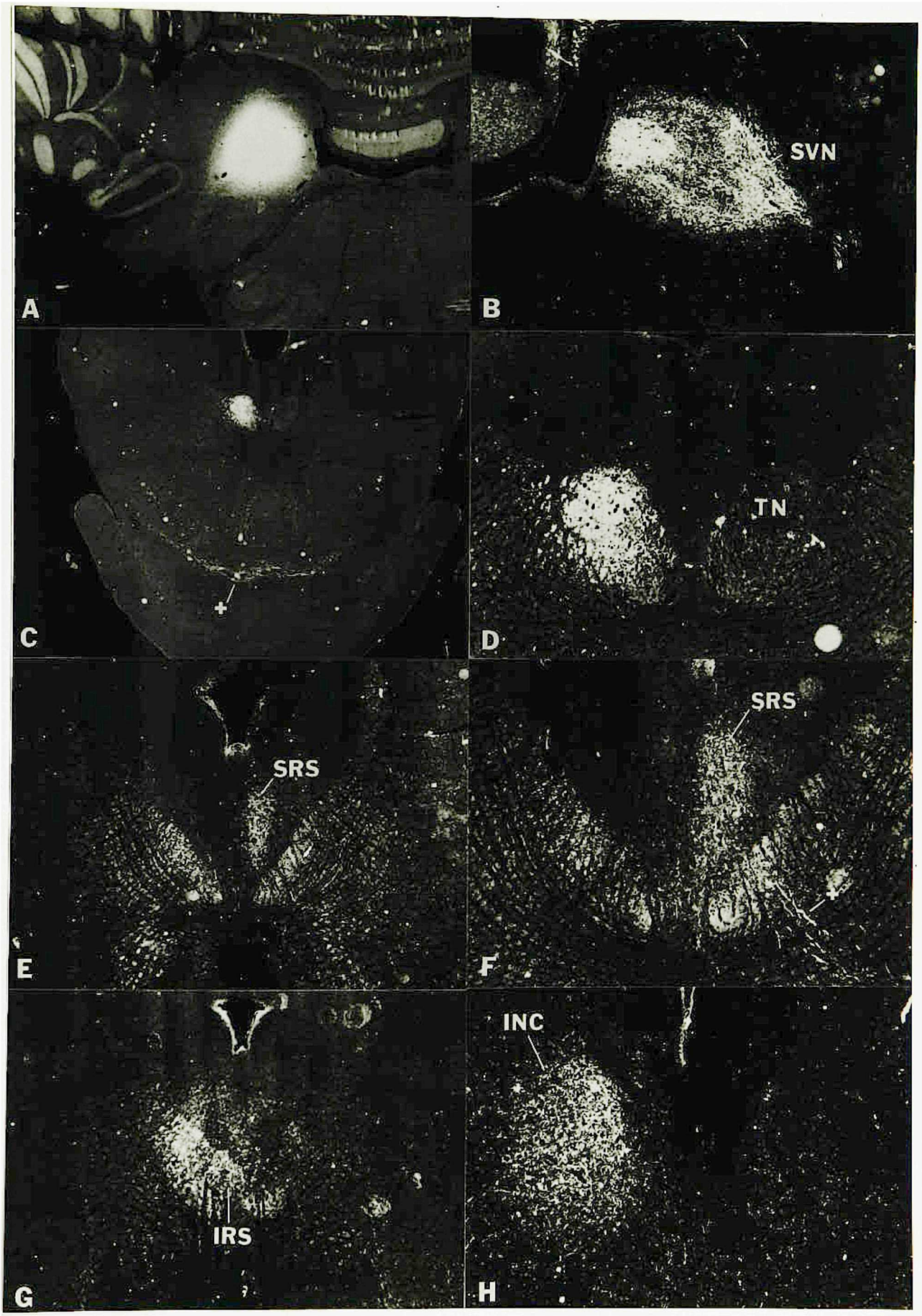
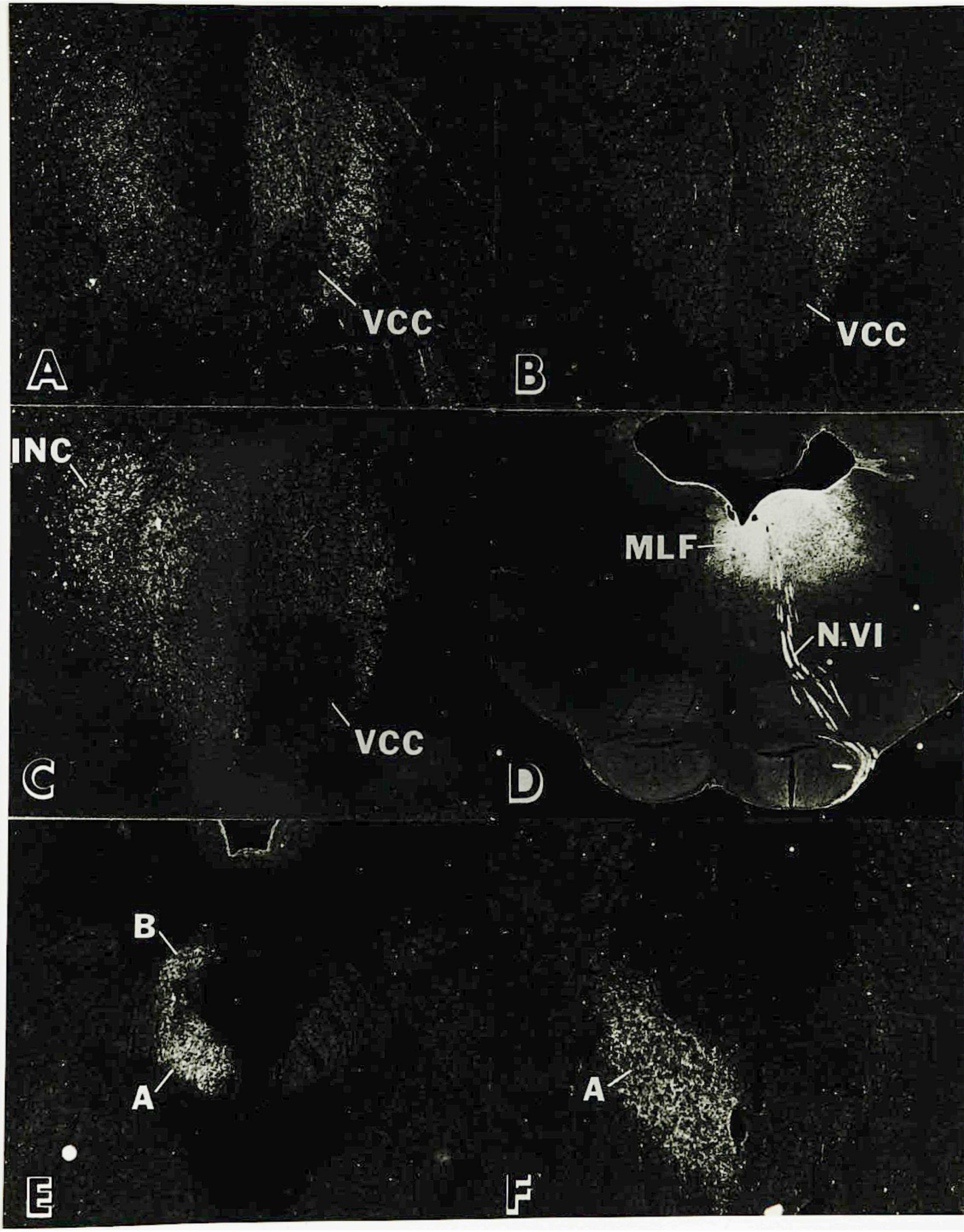

A
B
SVN
C
D
TN
E
SRS
F
SRS
G
IRS
H
INC

FIGURE 17

Squirrel monkeys U-177 (A,B) and U-176 (C). Rhesus monkey U-30 (D,E,F). A,B: autoradiographs through the middle (A) and rostral (B) thirds of the OMC showing the virtually absence of labeled terminals in the contralateral (right) VCC (medial rectus subdivision) and modest terminals in the same subdivision ipsilaterally. C: autoradiograph of the OMC in another monkey in which all vestibular nuclei on the left were injected with [^{3}H] amino acids. In the VCC (medial rectus subdivision) all labeled terminals were ipsilateral. D: autoradiograph of an isotope injection of the right VI nucleus. Isotope was transported only via the ipsilateral root fibers and the contralateral MLF. E,F: autoradiographs of labeled terminals in the OMC; in caudal parts of the OMC (E) terminals surround cells in the contralateral VCC (cell group A) and in group B, located dorsally, both of which innervated the medial rectus muscle. In rostral parts of the OMC (F) terminals of abducens internuclear neurons are confined to the contralateral cell group A. A-F: cresyl violet; magnifications: A,B,C,F, X9; D, X2.5; E, X5.


VCC
A
VCC
B
INC
MLF
N.VI
VCC
C
D
B
A
A
E
F

DISCUSSION

Primary Vestibular Afferents

Although it had been thought that selective labeling of the crista ampullaris of individual semicircular ducts might provide autoradiographic evidence concerning the central projections of vestibular ganglion cells innervating distinctive receptor elements of the labyrinth, this occurred in only one animal. The circulation of endolymphic fluid disseminates injected and implanted isotope to virtually all parts of the labyrinth and some parts of the cochlea. Two exceptions to this generalization were noted, in that: (1) selective labeling occurred in the crista of the posterior semicircular duct in one of five animals, and (2) in several animals not all ganglion cells innervating the maculae of the otoliths transported isotope centrally. Thus, the present study provides data concerning primary vestibular afferents and some information relative to the central distribution of fibers from vestibular ganglion cells that innervate particular parts of the labyrinth.

Projections to the vestibular nuclei. Primary vestibular afferents can be separated into two patterns of termination within the vestibular nuclei (VN). Projections to SVN and MVN terminate within virtually the entire territory of these nuclei, although each nucleus has a small zone of sparse or no terminations. In the SVN few terminations were noted medially near the ependymal border and the junctional zone with MVN. In MVN sparse terminations were noted in a small circular zone on its ventral border in central regions. Neither of these areas exhibiting weak primary vestibular inputs corresponds to any previously described cytological subdivision of the vestibular nuclear

complex (Brodal and Pompeiano, '57a), and both represent minute portions of these nuclei. Primary vestibular projections to LVN and IVN have more restricted terminations in these nuclei. The observation that the dorsal half of LVN is devoid of primary endings has been reported repeatedly (Lorente de Nó, '33; Walberg et al., '58; Carpenter, '60; Stein and Carpenter, '67; Hauglie-Hanssen, '68; Gacek, '69; Sugawara, '78; Korte, '79) and was confirmed autoradiographically. Those portions of IVN which receive major primary vestibular inputs are its rostral part near the root entry zone and a dorsomedial area near the caudal pole of the nucleus. As in most other studies no terminals were found in cell group "f", located ventrolaterally in caudal regions of IVN (Walberg et al., '58; Carpenter, '60; Stein and Carpenter, '67; Gacek, '69; Korte, '79). In the present study relatively few terminals were seen in central parts of IVN, suggesting an additional differential feature. The pattern of termination of primary vestibular projections to IVN corresponds closely to the terminal fields of cerebellar cortico-vestibular fibers from the nodulus and ventral uvula (Haines, '77). Primary vestibular afferents terminating in cell group "y", considered to be specifically related to ganglion cells innervating the saccule (Gacek, '69), were identified but appeared less dense than endings in the VN. No labeled primary vestibular afferents were found in the accessory vestibular nuclei identified as cell groups "x", "z" and "g" (Gacek, '69).

Although primary vestibular terminations in peripheral parts of SVN were not described in most degeneration studies (Walberg et al., '58; Stein and Carpenter, '67; Gacek, '69; Sugawara, '78), terminals noted in this part of SVN have important functional implications. Cells

in the periphery of SVN receive afferents from the nodulus and uvula (Angaut and Brodal, '67; Haines, '77) and the contralateral VN (Ladpli and Brodal, '68; Carleton and Carpenter, '83), and constitute the portion of the nucleus giving rise to commissural fibers (Pompeiano et al., '78; Carleton and Carpenter, '83). Commissural vestibular neurons are known to relay disynaptic inhibition to the contralateral VN (Shimazu and Precht, '66), and must, therefore, receive primary vestibular projections. Physiological studies have only recently shown this to be the case for SVN (Mitsacos et al., '83a). The current study gives anatomical confirmation of primary vestibular projections to portions of SVN involved in commissural interactions. Primary vestibular fibers would thus appear to activate the commissural system from SVN as it does for other VN (Wilson and Melvill-Jones, '79), while cerebellar input to this nucleus probably provides inhibitory modulation.

Caudal portions of IVN and MVN have been described as receiving spinovestibular inputs (Pompeiano and Brodal, '57a; Brodal and Angaut, '67), and are a major source of projections from the VN to the cerebellar cortex (Brodal and Torvik, '57). Because these regions of IVN and MVN have been largely excluded as targets of primary vestibular fibers, Brodal ('74) concluded that the cerebellar projections of the VN are only remotely related to the labyrinth. Present findings indicate that primary vestibular projections are homogeneously distributed throughout the rostrocaudal extent of MVN, and are particularly dense to dorsal and caudal portions of IVN. These findings, and those of Korte ('79), suggest that caudal areas of IVN and MVN transmit primarily vestibular impulses to the cerebellum. This conclusion is reinforced by current evidence based on retrograde axoplasmic transport and by recent

degeneration studies indicating that spinovestibular fibers are meagre (Rubertone and Haines, '82).

The small zone on the ventral border of MVN which receives only sparse primary vestibular projections previously has not been described. However, most studies of primary vestibular fibers have been done in the cat (Walberg et al., '58; Gacek, '69; Korte, '79), and this area may thus represent a feature unique to primates.

Data from this study indicate that primary vestibular fibers have a widespread distribution and probably establish synaptic contacts with cells in the VN which give rise to virtually every major secondary projection. The somatotopic features in the origin of the vestibulospinal tract, however, suggest that only portions of this tract destined for cervical spinal segments are directly influenced by the ipsilateral labyrinth (Pompeiano and Brodal, '57).

Selective primary transport. Both Golgi (Lorente de Nó, '33) and degeneration studies (Stein and Carpenter, '67; Gacek, '69) suggest that primary vestibular afferents innervating the maculae reach IVN and ventral portions of LVN, while ganglion cells innervating the cristae terminate primarily in MVN and SVN. In the current study, selective central transport was observed in several animals in which isotope uptake was relatively scant in ganglion cells associated with the saccule and utricle. Comparisons between these animals and those in which the entire ganglion was labeled revealed no obvious differences in the density of terminals in SVN, LVN and MVN, but projections to caudal IVN, the accessory cuneate nucleus (ACN) and cell group "y" were reduced. It is extremely difficult to evaluate the ventral part of LVN because of the large number of fibers passing through this area to other loci.

These negative findings suggest that caudal IVN, ACN and cell group "y" receive afferents from the maculae. No separation between utricular and saccular afferents was possible in this study. In degeneration studies afferents associated with the otoliths were the dominant vestibular input to caudal parts of IVN and ACN (Stein and Carpenter, '67). Gacek ('69) demonstrated in the cat that primary vestibular projections to cell group "y" were related exclusively to the saccule. Few if any afferent fibers conveying impulses from the semicircular ducts appear to reach cell group "y". Projections from cell group "y" reach the contralateral VN (Pompeiano et al., '78; Carleton and Carpenter, '83) and the OMC (Graybiel and Hartweig, '74; Gacek, 77; Steiger and BUttner-Ennever, '79; Stanton, '80) and may participate in both commissural inhibition and vestibulo-ocular reflexes. Macular afferents also appear to terminate in caudal portions of the NIVN as reported by Stein and Carpenter ('67), suggesting that this nucleus samples afferents from the maculae as well as the semicircular ducts.

The only portion of the labyrinth and vestibular ganglion selectively labeled was that related to the posterior semicircular duct in one animal. Terminal label was localized to three regions: (1) medial SVN, (2) lateral portions of rostral MVN and (3) oral parts of IVN. This pattern of central termination was nearly identical with that described in degeneration studies in the monkey and cat (Stein and Carpenter, '67; Gacek, '69). Physiological evidence also suggests that afferents from the ampulla of the posterior duct end in medial parts of SVN and do not overlap the zone of termination of afferents from other ducts (Abend, '77).

Projections to the reticular formation and relay nuclei. Primary vestibular fibers projecting beyond the borders of the VN terminated in several areas of the reticular formation (RF), in the subtrigeminal lateral reticular nucleus (SLRN), and in portions of the ACN and perihypoglossal nuclei. The most impressive reticular projections end in rostrodorsal portions of NRgc immediately caudoventral to the AN. Fibers to this area also have been described in preliminary autoradiographic studies (Batton and Carpenter, '78) and in degeneration studies (Korte, '79). Autoradiographic and HRP evidence suggests that neurons in this part of NRgc project to the contralateral AN (Graybiel, '77; Graybiel, '77a; Maciewicz et al., '77; Gacek, '79). Primary vestibular projections to this area might explain imbalances between modest crossed secondary vestibular projections to AN (Carpenter and Carleton, '83), and potent vestibular effects noted upon the contralateral AN (Baker et al., '69; Precht et al., '69; Highstein, '73a). Primary vestibular projections observed in portions of the RF immediately adjacent to the VN confirm Golgi studies (Hauglie-Hanssen, '68). Remmel and Skinner ('79) suggest that neurons in this region of the RF may transmit vestibular impulses to extraocular motor neurons via the contralateral MLF.

Primary vestibular projections to ACN, SLRN and NIC probably represent indirect pathways conducting vestibular impulses to the cerebellar cortex. Projections to ACN, the largest and most discrete, arise from the macular regions and terminate in several small islands within the nucleus. Degeneration studies based on selective lesions of the vestibular ganglion (Stein and Carpenter, '67; Carpenter et al., '72) suggest that projections to ACN are related primarily to the utricle.

Projections to the SLRN were observed in animals with both short and long survival times, but were most evident in monkeys showing profuse central transport. It seems unlikely that projections to this nucleus are transneuronal, because isotope injections of individual VN in this study never resulted in label traced into the SLRN. Primary vestibular projections to SLRN were most obvious after long survivals. The SLRN has been demonstrated to project to the flocculonodular lobe of the cerebellum (Brodal, '43; Gould, '80). Terminals in the NIC were sparse and ipsilateral. This nucleus has been found to project: (1) bilaterally to the VN (Pompeiano et al., '78; Carleton and Carpenter, '83), (2) to the nuclei of the extraocular muscles (Steiger and BÜttner-Ennever, '79), and (3) to the cerebellar cortex (Kotchabhakdi et al., '78; Gould, '80).

Transneuronal transport. Isotope transport beyond the vestibular and auditory nuclei occurred in six animals. Transneuronal transport was always most intense in the secondary auditory pathways (Carpenter et al., '78). The wide dispersion of secondary vestibular projections, compared with the discretely focused auditory pathways, might be a factor accounting for the greater density of label in that system. Data also suggest that transneuronal transport tends to occur at an earlier time in the auditory system and may be independent of the [^{3}H] amino acid used. Massive transneuronal transport beyond the cochlear nuclei was evident after a 10 day survival in monkey C-1440 in which [^{3}H] leucine was injected into the cochlea; no primary or secondary vestibular fibers were labeled in this animal. Transneuronal transport in both auditory and vestibular pathways occurred in five animals with survival periods of 12 days or longer in which [^{3}H] proline, or

[^{3}H] proline and leucine, were injected into the ampulla of a single semicircular duct. There was one exception (H-1472) in which a 14 day survival did not produce transneuronal transport. No evidence suggests that transneuronal transport is more likely to occur if a particular duct is labeled. The volume and density of transneuronal labeling in secondary vestibular fibers appears related to survival times and distance from the vestibular nuclei. Proximal portions of major vestibular pathways such as the VST and the MLF were particularly well labeled. An exception to this generalization was the commissural vestibular projection, which was not labeled in any animal. This observation is inconsistent with the massive commissural projections evident in animals with isotope injections in the VN (Carleton and Carpenter, '83). The absence of transneuronal transport in commissural vestibular projections also has been reported in the pigeon (Correia et al., '83). These authors also noted a paucity of transneuronal transport in secondary vestibular pathways in the ipsilateral MLF. Physiological studies have demonstrated that commissural vestibular fibers and some ascending ipsilateral projections in the MLF are inhibitory and appear to have γ-aminobutyric acid (GABA) and/or glycine as their neurotransmitter (Ito et al., '70; Precht et al., '73; Precht, '78). These observations suggest that inhibitory secondary vestibular projections, particularly those utilizing GABA, are less likely to participate in transneuronal transport of isotope, although the reason for this is not known. This may also account for predominant contralateral transneuronal transport in the ascending MLF.

Physiological studies have shown that tonic vestibular neurons in the VN are multisynaptically activated by stimulation of the

ipsilateral labyrinth (Precht and Shimazu, '65) and suggest that either internuncial neurons or recurrent collaterals are responsible for this effect. Golgi studies have not demonstrated local interneurons in the VN (Lorente de Nó, 33a; Zhukova, '65; Hauglie-Hanssen, '68), but support the existance of recurrent collaterals from cells in MVN and IVN (Hauglie-Hanssen, '68). In the current study, the volume of labeled terminals in the ipsilateral VN was greatly increased in animals demonstrating transsynaptic transport. Areas of increased transport included the central third of IVN and ventral island in MVN, regions only sparsely labeled in other animals. This greater terminal density may result from transneuronal labeling of neurons with axons which branch in the vicinity of the cell body and supply adjacent areas. Thus, few portions of the vestibular nuclear complex are free of either monosynaptic or multisynaptic inputs from the ipsilateral end-organ. However, even in animals showing marked transneuronal transport of isotope, no terminal labeling was evident in dorsal parts of LVN or in cell groups "f" or "x", reinforcing the concept that these structures do not receive primary or secondary vestibular afferents (Walberg et al., '58; Brodal, '74).

Primary vestibulocerebellar projections. Comparative anatomical studies indicate that primary vestibulocerebellar (VC) fibers reach the flocculus and nodulus in a variety of reptiles, birds and mammals (Larsell, '36; Larsell, '36a; Weston, '36; Whitlock, '52). In the cat Brodal and Høivik ('64) described primary vestibular projections terminating as mossy fibers in the ipsilateral nodulus, ventral folia of the uvula, flocculus and ventral paraflocculus. Attempts to determine the distribution of primary VC fibers arising from cell groups of the

vestibular ganglion innervating distinctive parts of the labyrinth revealed that: (1) cells from all parts of the vestibular ganglion project ipsilaterally and indistinguishably to the nodulus, ventral part of the uvula and lingula and (2) ganglion cells innervating the cristae of the semicircular ducts and the maculae of the utricle and saccule project to distinct, but overlapping regions of the flocculus (Carpenter et al., '72). Although most primary VC fibers terminated as mossy fibers, some fibers in the flocculus arborized about Purkinje cell somata within the molecular layer, suggesting they might represent climbing fibers. Recent silver degeneration studies in the cat emphasized the relatively small number of primary VC fibers and their ipsilateral distribution only to the nodulus, uvula and flocculus (Korte and Mugnaini, '79). In Golgi preparations vestibular fibers were followed into the nodulus and uvula, but not to terminations (Hauglie-Hanssen, '68); in similar material Lorente de Nó ('24) denied the existence of primary VC fibers.

Retrograde transport studies using HRP stand in sharp contrast to the above data in suggesting that the vestibular ganglion projects to virtually the entire cerebellar vermis (Kotchabhakdi and Walberg, '78). Observations in the present autoradiographic study indicate that primary VC fibers are entirely ipsilateral and terminate most profusely in all parts of the nodulus and in ventral folia of the uvula. These fibers terminate in the granular layer in formations which resemble mossy fiber rosettes (Fox et al., '67). Significantly smaller numbers of terminals were found in the granular layer of the ipsilateral flocculus and lingula. A number of labeled fibers traversed the fastigial nucleus (FN) and regions dorsal to it to enter the granular layer in deep folia

of lobules V and VI on both sides of the primary fissure. These fibers ended in apparent mossy fiber rosettes. Terminals in these lobules were encountered in animals in which nearly all cells of the vestibular ganglion were labeled with isotope. This locus in the cerebellar vermis corresponds to the sites where vestibular single unit and field potentials have been recorded at monosynaptic latencies (Precht et al., '77). A primary vestibular projection to these deep folia of the vermis was postulated because potentials: (1) had the same characteristics as those recorded in the nodulus and (2) were not affected by lesions in the lateral reticular nucleus of the medulla, which receives ipsilateral fibers from the LVN (Ladpli and Brodal, '68; Carleton and Carpenter, '83). Thus, physiological evidence for a primary vestibular projection to deep vermal folia of lobules V and VI is strengthened by the present autoradiographic findings. Retrograde transport of HRP indicates that these same vermal folia also receive secondary vestibular projections from MVN and IVN (Precht et al., '77).

In the older Marchi literature there are numerous references describing primary vestibular projections to the FN (see Brodal and Høivik, '64). In contrast, silver staining studies have failed to confirm this cerebellar termination (Brodal and Høivik, '64; Carpenter et al., '72), or considered it to be very sparse (Korte and Mugnaini, '79). Physiological data demonstrate that stimulation of both the vestibular nerve and nuclei evoke EPSPs in the FN with monosynaptic latencies (Furuya et al., '75). Responses recorded in the FN upon stimulation of the VN were facilitated by stimulation of the vestibular nerve. Although autoradiographs in the current study revealed large numbers of primary vestibular fibers traversing nearly all parts of the

FN, no terminals were identified within the nucleus. Most of the fibers passing through the FN terminated in parts of the nodulus and uvula. In contrast to data from HRP studies indicating that secondary vestibular fibers project to the FN (Kotchabhakdi and Walberg, '78; Ruggiero et al., '77), autoradiographic data do not reveal projections to the FN from any of the principal VN. HRP injections of the FN almost invariably interrupt corticopetal fibers projecting to the nodulus and uvula.

Apparent primary vestibular projections to the parvicellular ventral part of the dentate nucleus (DN) have been described in cat, rabbit and monkey in degeneration studies (Brodal and Høivik, '64; Carpenter et al., '72; Sugawara, '78). Degeneration in a similar site in the DN has been reported following lesions in primary auditory fibers (Rasmussen, '58) and selective lesions of the cochlea (Carpenter et al., '72). In more recent degeneration and axoplasmic transport studies no primary vestibular fibers were noted to terminate in any part of the DN (Kotchabhakdi and Walberg, '78; Korte, '79). The presence of isotope transport to the ventral parvicellular part of the ipsilateral DN in one animal (U-55) remains unexplained. No similar isotope transport was found in our control animal (C-1440) in which virtually all parts of the spiral ganglion showed uptake and central transport of radioactivity.

Evaluation of data with respect to possible transneuronal transport of isotope by secondary vestibular fibers is more difficult to assess in the cerebellum than in the brain stem because these fibers terminate in the same regions as primary vestibular fibers. Comparison of primary and secondary VC fibers leaves no doubt that primary fibers are more numerous and establish more impressive terminations in the cerebellar cortex. Nevertheless, it is our impression that some

transneuronal transport occurred in secondary VC fibers; this was evidenced by unusually dense fibers and cortical terminals in animals with long survivals.

The results of this study indicate that primary vestibular fibers project ipsilaterally only to specific and restricted regions of the cerebellar cortex. These cortical regions include the nodulus, ventral folia of the uvula, the flocculus, the lingula and deep folia of lobules V and VI in the floor of the primary fissure. The term "vestibulocerebellum" as defined by Brodal and Høivik ('64) includes those regions of the cerebellar cortex which receive primary vestibular afferents. Since primary and secondary vestibular fibers have essentially the same distribution within the cerebellar cortex, it seems proper to use the term "vestibulocerebellum" to designate those regions of the cerebellar cortex that receive predominantly a vestibular input. This concept is strengthened by observations that indicate that the principal brain stem projections of the "vestibulocerebellum" are to the vestibular nuclei (Angaut and Brodal, '67; Brodal, '74; Haines, '77). The major exception to this generalization is the dorsal half of the LVN, which receives its major input from the ipsilateral anterior lobe vermis (Walberg and Jansen, '61).

Efferent Vestibular Neurons

The pattern of retrograde labeling of efferent vestibular neurons was the same as that reported by Goldberg and Fernández ('80) in the squirrel monkey. Efferent vestibular fibers in the cat appear to have a broader origin (J. Ito et al., '83), suggesting fundamental species differences. In spite of the tremendous volumes of HRP used in

the present study, there was no evidence of transganglionic transport of the tracer, and retrograde labeling of vestibular ganglion cells was minimal and of poor quality. The relatively large HRP molecule (40,000 daltons) apparently cannot traverse the synapse between hair cells and peripheral processes of vestibular ganglion cells (Wersäll, '60), while [^{3}H] amino acids do so readily.

Central Afferents to the Vestibular Nuclei

Injections of HRP into individual vestibular nuclei (VN) and groups of VN provide an opportunity to determine the sources of central afferents to the vestibular nuclei. Although the cerebellar vermis and the so-called "vestibulocerebellum" (as defined by Angaut and Brodal, '67) have been regarded as the major source of central input to the VN (Brodal, '74), these projections were found to be modest in comparison to commissural projections. Cerebellovestibular fibers appear to constitute the greatest source of central afferents only to LVN. Reticular projection to the VN, implicated in labyrinthine nystagmus and conjugate eye movements (Pompeiano et al., '78), appear meagre.

Spinal cord. Degeneration studies suggest that spinovestibular fibers are sparse, distinct from the spinocerebellar tracts, arise largely from caudal levels of the spinal cord and project to portions of the VN which do not receive primary vestibular afferents (Pompeiano and Brodal, '57a; Brodal, '74; Rubertone and Haines, '83). The only spinal nucleus retrogradely labeled after HRP injections in the VN was the contralateral central cervical nucleus (CCN). Labeled cells in CCN were most numerous after injections involving IVN, but were also noted after injections of MVN and LVN. Initially it was thought that transport to

CCN neurons was related to involvement of cell groups "x" or "f", or fibers of the inferior cerebellar peduncle, by the injection. Consistent labeling in this nucleus following injections not including the above structures suggested that cells of CCN project to the VN. It is well established that CCN receives dorsal root afferents (Shriver et al., '68; Petras and Cummings, '72), and projects crossed fibers to the cerebellar cortex (Wiksten,'75; Cummings and Petras, '77; Matsushita and Ikeda,'75; Matsushita et al., '79). Although it has been claimed that all cells of this nucleus project to the cerebellum, present evidence also indicates a projection to the VN; it is possible that dichotomizing axons project to both the cerebellum and the VN. Physiological studies suggest that CCN neurons are activated by dorsal root afferents concerned with joint capsules and ligaments of the upper cervical vertebrae (Hirai et al., '78). Thus, CCN may transmit information related to the position of the neck to the vestibular nuclei. The anatomical demonstration of a crossed projection from MVN to CCN in the current study supports observations of short latency potentials recorded in CCN after stimulation of the contralateral vestibular nerve (Hirai et al., '78). These results indicate a close relationship between CCN and the vestibular system.

Medulla and pons. One source of afferents to the VN which has been given little attention arises from the perihypoglossal nuclei (PH) (Pompeiano et al., '78). Cells in the caudal half of the nucleus prepositus (NPP), nucleus intercalatus (NIC) and nucleus of Roller (NR) project to both MVN and IVN. These projections are bilateral, with the largest number of fibers being crossed and related to MVN (Figs. 6E and 7). No afferents from the PH were found to project to LVN. Anterograde

transport in the present study indicates that MVN and IVN project bilaterally to NPP and NIC with ipsilateral dominance, suggesting an unequal, bilateral and reciprocal relationship between these nuclei. This observation is strengthened by retrograde transport studies demonstrating bilateral and unequal projections from the VN to NIC (Mergner et al., '77). Physiological data indicate that the perihypoglossal nuclei receive disynaptic inputs from the vestibular nerves that exhibit ipsilateral inhibition and contralateral excitation (Baker and Berthoz, '75).

Commissural connections. Physiological evidence indicates that the VN on the two sides function in an integrated manner, even though primary vestibular fibers are entirely ipsilateral (Shimazu and Precht, '66; Mano et al., '68; Markham, '68; Wilson et al., '68a). The anatomical substrate for this integrative function is a system of commissural fibers interconnecting portions of the VN. Demonstration of vestibular commissural projections by degenerative methods is complicated by interruption of passing fibers (Brodal, '74). Using silver degeneration technics, Ladpli and Brodal ('68) concluded that the SVN are most closely interrelated, but that significant projections also interconnect IVN and MVN. Although retrograde transport studies also may be complicated by passing fibers, autoradiography provided confirmatory evidence of the vestibular commissural projection. Because this system represents both an afferent and efferent connection of the VN, results obtained by retrograde and anterograde methods will be discussed together.

Neurons projecting to the contralateral VN were identified in MVN, SVN, IVN and cell group "y". Commissural projections fall into two categories: (1) projections interconnecting corresponding regions of the

same vestibular nucleus, and (2) non-corresponding projections interconnecting different VN on the two sides. The nucleus projecting and receiving the largest number of commissural fibers is MVN (Fig. 7). HRP injections of MVN label cells in all parts of the contralateral nucleus with the greatest density corresponding to the area of the injection site. MVN also receives impressive non-corresponding afferents from the contralateral SVN (peripheral parts) and cell group "y". Commissural projections to MVN from IVN are modest, and originate primarily from caudal parts of the nucleus. MVN projects commissural fibers back upon areas of the vestibular complex from which it receives inputs and, in addition, projects weakly to the contralateral ventral LVN. This was the only commissural connection noted for LVN.

With several exceptions, the commissural connections of IVN are similar to those of MVN, but are less numerous (Fig. 9). IVN does not project to LVN, and commissural afferents to IVN from MVN originate primarily in rostral parts of the nucleus; interconnections between the MVN arise throughout the rostrocaudal extent of the nuclei.

The commissural projections of SVN were demonstrated by both retrograde and anterograde technics, but data concerning other central afferent connections of SVN were not obtained in the present study. SVN has profuse projections to its contralateral fellow, and substantial non-corresponding connections with MVN and IVN. The commissural connections of SVN originate and terminate in the peripheral small-celled portion of the nucleus. Current evidence confirms primary vestibular terminations in all parts of SVN, and supports physiological observations indicating that commissural projections from SVN are influenced by primary afferents (Mitsacos et al., '83a). SVN also contributes

ipsilateral fibers to IVN, suggesting a special relationship between these nuclei. Projections intrinsic to the vestibular nuclear complex also have been demonstrated in the rat using retrograde methods (Rubertone et al., '83).

Of the small cell groups associated with the vestibular complex, only cell group "y" projects and receives commissural fibers. This small nucleus, known to project bilaterally to the OMC (Graybiel and Hartweig, '74; Steiger and Büttner-Ennever, '79; Stanton, '80), has reciprocal connections with MVN and IVN on the opposite side. With the exception of cell group "y", the small cell groups of the vestibular complex appear to have no functional relationship with the labyrinth.

Findings of other authors concerning commissural fibers largely correspond with current observations (Gacek, '78; Pompeiano et al., '78), but because their studies were based solely on retrograde transport, the reciprocal nature of these connections was not obvious. In most instances, neurons that project fibers to the contralateral VN receive fibers from the same nuclear subdivision. Connections between the VN on the two sides are far more massive and complex than prior studies have suggested, and constitute the greatest source of central afferents to the VN.

Reticular formation. Reticulovestibular fibers as described in Golgi material enter the VN directly and via the MLF, and probably constitute collaterals of reticular projections to other locations (Cajal, '09-11; Lorente de Nó, '33a; Scheibel and Scheibel,'58; Hauglie-Hanssen, '68). Investigation of reticular projections to the VN based upon lesions indicate that most fibers: (1) arise from the nuclei reticularis gigantocellularis (NRgc) and pontis caudalis (RPC), and (2) project

bilaterally and diffusely with ipsilateral dominance to all four of the principal VN (Hoddevik et al., '75). Silver degeneration studies indicate no vestibular afferents arise from portions of the reticular formation (RF) rostral to the pons, except those from INC (Pompeiano and Walberg, '57). Because vestibular commissural fibers traverse broad areas of the RF and are necessarily interrupted with most reticular lesions, it is difficult to interpret degeneration studies on reticulovestibular fibers. Hoddevik et al. ('75) were unable to confirm their silver degeneration studies on the reticulovestibular projection autoradiographically, suggesting that this fiber system is very small. This conclusion is supported by retrograde transport data from the present study. HRP injections in the VN revealed only small numbers of labeled cells in dorsomedial portions of the RF at the junction between NRgc and RPC. Labeling was bilateral with contralateral dominance. No cells were labeled rostral to the vestibular complex in the region of the pontine paramedian reticular formation (PPRF). This result is in contrast to observations from a prior study in which HRP injections of VN produced substantial reticular labeling in widespread areas of the RF (Pompeiano et al., '78). Because diaminobenzidine (DAB) was used as the chromagen in this study, it is possible that the extent of the injection sites were underestimated, and that the cells of origin of reticuloreticular projections were labeled (Hoddevik et al., '75). No conclusions are possible in the current study concerning reticulovestibular projections to SVN.

Descending vestibular afferents. The only established descending brain stem projections to the VN arise from the interstitial nucleus of Cajal (INC) (Pompeiano and Walberg, '57), descend in the MLF and

project collaterals into the ipsilateral MVN (Nyberg-Hansen, '64; Carpenter et al., '70). HRP injections in the MVN retrogradely labeled neurons in the ipsilateral INC and in the midline visceral nuclei of the OMC. The number of labeled neurons in the INC associated with discrete injections in MVN was not as great as had been expected. The greatest volume of retrograde labeling in INC (Fig. 6F) followed an injection involving nearly all parts of both the MVN and IVN (Cat U-122). This observation suggests that INC may project descending fibers to both of these nuclei. One recent study suggests that the MVN receives a modest projection from cells near the fasciculus retroflexus, designated as the nucleus subparafascicularis (subPF) (Barmack et al., '79). These same cells, noted in the present study, appeared to be within the rostral part of INC.

The large number of midline visceral neurons labeled in the OMC after HRP injections in the VN was unexpected. Visceral neurons in the OMC have been retrogradely labeled by spinal HRP injections, indicating that these cells distribute fibers widely (Loewy et al., '78). The extent of this distribution has been demonstrated autoradiographically (Loewy and Saper, '78). It is difficult to understand how a small collection of cells gives rise to such an extensive descending fiber system. Fibers from visceral neurons in the OMC were described as descending both in the MLF and lateral regions of the brain stem. Although terminations were not described in the VN, diagrams suggested fibers of passage bilaterally in the LVN, MVN and IVN (Loewy and Saper, '78). Present data seem more specific in that retrograde labeling in visceral neurons was greatest in association with injections in the MVN, a nucleus traversed by few fibers.

Cerebellar projections to the vestibular nuclei. Except for primary vestibular fibers, the largest number of afferents to the VN are considered to arise from the "vestibulocerebellum" (flocculonodular lobe and uvula, after Angaut and Brodal, '67), the cerebellar vermis and the fastigial nuclei (Brodal, '74). Components of the "vestibulocerebellum" have similar, but not identical, projections to the VN (Voogd, '64; Angaut and Brodal, '67; van Rossum, '69; Haines, '77). The nodulus and uvula project ipsilaterally to peripheral parts of SVN, caudal and lateral portions of IVN and to cell group "x"; the nodulus has additional projections to MVN and cell group "f" (Angaut and Brodal, '67; Haines, '77). Ipsilateral projections of the flocculus are greatest to MVN and central parts of SVN (Angaut and Brodal, '67; Haines, '77). Purkinje cells (PCs) of the flocculus, arranged in zones, project in a specific manner to the MVN and SVN (Balaban et al., '81).

Corticovestibular projections from the cerebellar vermis to LVN arise from all lobules of the ipsilateral anterior lobe (Figs. 11C and 12), are most numerous in lobules IV and V, and progressively diminish in the posterior vermis. The longitudinal zone of labeled PCs in the ipsilateral vermal cortex of the anterior lobe was the same as described by Corvaja and Pompeiano ('79) and Haines ('76). Because retrograde transport technics do not differentiate between terminal projections and fibers of passage, some of the labeled PCs seen after HRP injections of LVN may represent cells projecting beyond this nucleus to parts of IVN.

Corticovestibular projections to IVN are similar to those of LVN, but differ quantitatively in two important aspects. IVN receives a smaller projection from the ipsilateral anterior lobe vermis, but its input from the nodulus and uvula is greater. These data confirm earlier

studies (Walberg and Jansen, '61; Voogd, '64; Angaut and Brodal, '67; van Rossum, '69; Haines, '76, '77).

Corticovestibular projections to MVN are restricted in origin. Purkinje cells in the ipsilateral nodulus and uvula projecting to MVN are less numerous than those to IVN. The part of the flocculus related specifically to the MVN is a central band extending through all folia (Fig. 10) as described in prior reports (Yamamoto and Shimoyama, '77; Balaban et al., '81). Projections from the cerebellar cortex to SVN were not examined in the present study, but are reported to originate from the vestibulocerebellum. Afferents to vestibulo-ocular neurons in central SVN are considered to arise in the flocculus (Haines, '77; Yamamoto and Shimoyama, '77; Balaban et al., '81) while projections to peripheral portions of SVN involved in commissural interactions take orgin from the nodulus and uvula (Haines, '77).

Part of the input to VN from the cerebellar vermis is relayed via the fastigial nucleus (FN), which receives an orderly corticonuclear projection from all parts of the cerebellar vermis (Courville and Diakiw, '76). Because the FN are traversed by corticovestibular fibers and crossed fastigial efferents, degeneration studies probably have overestimated the fastigiovestibular projection (Cohen et al., '58; Walberg et al., '62). Present findings based upon retrograde transport of HRP are consistent with autoradiographic observations (Batton et al., '77; Carpenter and Batton, '82), and indicate that projections to LVN arise preferentially from rostral parts of the ipsilateral FN (Figs. 11B and 12) while fibers projecting to IVN arise largely from central regions of the contralateral nucleus. The MVN receive only a few afferents from FN.

Cerebellar afferents to the VN are distributed selectively. The LVN and IVN receive direct projections from the anterior lobe vermis, with LVN receiving the greatest proportion. Indirect vermal connections to LVN and IVN via the FN are bilateral, arise from different parts of the nucleus and vary in the proportion of crossed fibers. Both IVN and MVN receive projections from the nodulus and uvula, but the major cortical input to MVN is from a central zone of the flocculus.

Projections of the Vestibular Nuclei

Because inputs to the vestibular nuclei (VN) from various sources are distributed differentially, it might be expected that individual VN would have distinctive projections reflecting unique functions. Although axoplasmic transport technics offer the best method for determining the course and terminations of vestibular efferents, this method is dependent upon injections limited to specific nuclear subdivisions.

Spinal cord. Vestibular pathways projecting to the spinal cord are the vestibulospinal tract (VST) and the medial longitudinal fasciculus (MLF). The VST is a somatotopically organized, ipsilateral projection originating exclusively from LVN that descends the length of the spinal cord (Pompeiano and Brodal, '57a; Nyberg-Hansen and Mascitti, '64; Petras, '67; Castiglioni et al., '77; Kneisley et al., '78). Fibers of this tract terminate in medial portions of the anterior horn, particularly in laminae VIII and VII, and form excitatory synapses with α- and γ-motor neurons, as well as interneurons (Nyberg-Hansen and Mascitti, '64; Erulkar et al., '66; Lund and Pompeiano, '68; Grillner et al., '69; Wilson and Yoshida, '69; Grillner et al., '70; Hultborn et

al., '76). Fibers of the VST labeled by HRP injections of LVN could not be followed beyond the spinomedullary junction, but transport of isotope by the VST usually could be traced to the cervical enlargement. With large injections of both [^{3}H] leucine and proline, fibers of the VST were followed to the second lumbar level. Terminals of the VST, found in medial portions of the anterior horn, corresponded to descriptions in degeneration studies (Nyberg-Hansen and Mascitti, '64).

Although degeneration studies suggest that descending vestibular projections in the MLF originate only from the MVN (Pompeiano and Brodal, '57; Carpenter, '60a; Carpenter and Hanna,'62; Nyberg-Hansen, '64), physiological (Wilson et al., '67; Kawai et al., '69; Wilson et al., '70; Rapoport et al., '77) and HRP studies (Kuypers and Maisky, '75; Castiglioni et al., '77) indicate origins from both the MVN and the IVN. Isotope injections of either nucleus labeled fibers which descended into upper cervical spinal segments. These findings support physiological data in which spinal stimulation antidromically activated neurons in rostral parts of both nuclei (Wilson et al., '67, '68). Descending vestibular axons in the MLF are bilateral and asymmetrically disposed (Ferraro et al., '40; Busch, '64); contributions from MVN and IVN are quantitatively similar. Spinal projections from MVN and IVN, considered to relay impulses from the semicircular ducts and the otoliths (Wilson et al., '67; Rapoport et al., '77), are described as having monosynaptic actions upon axial cervical motor neurons, most of which are inhibitory (Wilson et al., '70). Although no terminal label was seen in the anterior horn after injections of MVN, it was seen following injections involving IVN. These projections were evident in the medial parts of laminae VIII and VII in contralateral cervical

spinal segments. Descending projections from MVN were found ventromedially in the ipsilateral supraspinal nucleus (SSN), and in the contralateral central cervical nucleus (CCN). Cells of the CCN can be driven by stimulation of the vestibular nerve (Hirai et al., '78) and are considered to project crossed fibers to the cerebellum (Matsushita and Ikeda, '75). The observation that CCN receives crossed fibers from MVN and projects back upon the opposite VN suggests that this nucleus may interact with vestibular nuclei as well as with the cerebellum.

Medulla and pons. Excepting commissural fibers, the most impressive vestibular projections at medullary and caudal pontine levels are to precerebellar relay nuclei. Injection of HRP and isotope into various VN produced anterograde labeling of terminals in the lateral reticular nucleus (LRN), the paramedian reticular nuclei (PRN), the perihypoglossal nuclei (PH) and the inferior olivary complex. These projections were also noted in degeneration studies (Brodal and Gogstad, '57; McMasters et al., '66; Ladpli and Brodal, '68; Brodal, '74). Projections to LRN are wholly ipsilateral, while those to other precerebellar nuclei are bilateral with strong ipsilateral dominance. Vestibular inputs to LRN are derived from collaterals of the vestibulospinal tract (VST), and terminate in punctate islands in both the magnocellular and parvicellular portions of the nucleus. Projections to LRN from LVN probably account for the activation of LRN neurons recorded during static tilts of the head (Ghelarducci et al., '74). The LRN projects to broad areas of the cerebellar cortex (Clendenin et al., '74; Künzle, '75; Matsushita and Ikeda, '76), including the anterior lobe vermis (P. Brodal, '75; Dietrichs and Walberg, '79), and may be involved in feedback regulation of VST neurons.

Vestibular projections to PRN are related primarily to IVN, and reach both the dorsal (DPRN) and ventral (VPRN) divisions of this nucleus. Like LRN neurons, cells of the PRN respond to static head tilts (Ghelarducci et al., '74) and project to the cerebellum (Somona and Walberg, '78; Ruggiero et al., '77). This projection represents another indirect vestibulocerebellar pathway that may integrate macular and spinal impulses.

Physiological studies suggest that vestibular projections to the PH transmit impulses related to the semicircular canals rather than the maculae (Blanks et al., '77). Current data and prior retrograde transport studies (Mergner et al., '77) indicate that this pathway originates from MVN and IVN. MVN contributes the greatest number of fibers. All portions of the nucleus intercalatus (NIC) receive this projection, while terminals in nucleus prepositus (NPP) are restricted to its caudal half. Stimulation of the vestibular nerve produces disynaptic responses in NPP which exhibit ipsilateral inhibition and contralateral excitation (Baker and Berthoz, '75). The NPP has multiple inputs from a wide variety of sources (Brodal, '52; Walberg, '61; Angaut and Brodal, '67; Carpenter et al., '70; Sousa-Pinto, '70) in addition to the VN, and projects fibers to the ipsilateral flocculus (Alley et al., '75; Gould and Graybiel, '76; Fuchs, '77), the abducens nuclei (Gacek, '79) and the oculomotor complex (Graybiel and Hartweig, '74; Baker and Berthoz, '75; Gacek, '77; Steiger and Büttner-Ennever, '79; Carpenter and Batton, '80). Cells in NPP are considered to exert monosynaptic excitatory influences upon OMC neurons concerned with vertical eye movements (Baker, '77; Fuchs, '77). Graybiel ('77a) has suggested that rostral NPP is involved in direct guidance of individual eye movements, while

caudal NPP is related to the control of gaze in response to integrated information from spinal and vestibular inputs (Yingcharoen and Rinvik, '82).

Recent autoradiographic data indicate that MVN and IVN project to specific subdivisions of the inferior olivary complex (St. Cyr and Courville, '79; Martin et al., '80). These projections are considered to terminate ipsilaterally in nucleus β, and bilaterally in the dorsomedial cell column (dmcc). The present study suggests that vestibulo-olivary fibers arise primarily from caudal parts of IVN. Terminals of this pathway are profuse in nucleus β, while the dmcc and dorsal cap of Kooy (dc) receive lesser projections. These projections are predominantly ipsilateral, and are distinct from those rising in multiple regions of the medullary RF (Walberg, '82; Courville et al., '83).

Anatomical data suggest that nucleus β receives inputs from the pretectal area (Mizuno et al., '73; Walberg et al., '82) and the INC (Cintas et al., '80). Projections claimed to nucleus β from deep layers of the superior colliculus (Graham, '77) are not supported by critical studies (Frankfurter et al., '76; Weber et al., '78; St. Cyr and Courville, '80). Non-vestibular projections to the dmcc arise in the accessory oculomotor nuclei, including INC and the nucleus of Darkschewitsch (ND) (Cintas et al., '80). The dc of Kooy receives both cervical and pretectal afferents (Mizuno, '66; Mizuno et al., '73; Mizuno et al., '74) in addition to vestibular fibers. Nucleus β and the dmcc are considered to project crossed fibers to the uvula (Brodal, '76), while the dc projects to the contralateral flocculonodular lobe (Groenwegen et al., '79). Interpretation of these data suggests that

the VN have: (1) direct, ipsilateral projections to the vestibulocerebellum that terminate as mossy fibers, and (2) indirect, crossed projections to the contralateral vestibulocerebellum that are relayed from the inferior olive as climbing fibers. Fibers from IVN to nucleus β, which projects to the contralateral uvula, are quantitatively the most important. Vestibular projections to the inferior olive would appear to be integrated with functionally related inputs from the mesencephalon and spinal cord.

Vestibuloreticular projections have been especially difficult to define by lesion technics because portions of the VN are traversed by fastigial efferents, and vestibular commissural fibers pass through the RF. In spite of these difficulties, Brodal ('72) suggested that secondary fibers from all VN pass to the RF. The LVN and SVN were considered to project respectively to the LRN and the reticulotegmental nucleus (Ladpli and Brodal,'68). However, the majority of secondary vestibuloreticular fibers were considered to terminate in the NRgc and RPC. Such terminations are equally difficult to identify in autoradiographs. After large isotope injections involving multiple VN, diffuse terminals were noted in areas of NRgc medial to the VST. Cells in the medial pontomedullary RF have been shown physiologically to receive monosynaptic excitatory and inhibitory projections from the VN on both sides (Peterson and Abzug, '75). Nonetheless, vestibuloreticular fibers, like reticulovestibular fibers, appear to be scant.

Ascending projections. Retrograde chromatolytic studies suggest that all four principal vestibular nuclei project to the nuclei of the extraocular muscles (Brodal and Pompeiano, '57; Carpenter and McMasters, '63), while HRP studies have both supported (Graybiel and Hartweig, '74)

and denied contributions from IVN (Gacek, '77). Anterograde degeneration studies also have failed to reveal vestibulo-ocular projections from IVN (Gacek, '71), or both IVN and LVN (Tarlov, '70). In the current study, MVN, SVN, IVN and LVN were all found to project fibers to the nuclei of the extraocular muscles.

Projections from MVN to the AN terminate bilaterally with ipsilateral dominance. Physiological studies indicate that vestibular inputs to AN end upon both motor and internuclear neurons without apparent preference (Baker and Highstein, '75; Highstein and Baker, '78). HRP studies have demonstrated bilateral projections from MVN to the AN that are greatest ipsilaterally (Maciewicz et al., '77; Gacek, '79). Projections from MVN ascend bilaterally and asymmetrically in the MLF; crossed fibers reach the contralateral TN, OMC and INC, while lesser numbers of ipsilateral fibers project exclusively to the OMC. Vestibulotrochlear projections from MVN have been found to be entirely crossed in degeneration studies in the cat (Tarlov, '70; Gacek, '71). Stimulation of the posterior semicircular duct or the utricle produces disynaptic excitation of contralateral superior oblique motor neurons mediated through a relay in MVN (Highstein, '73).

In the monkey, determination of projections from MVN to the OMC was complicated by involvement of AN in the only isotope injection of MVN in this study (U-126). Because all internuclear projections from AN to the OMC are crossed (Baker, '77; Steiger and Büttner-Ennever, '79; Carpenter and Batton, '80), it was possible to conclude that ipsilateral projections from MVN terminate in cell columns innervating the medial rectus, inferior rectus, and inferior oblique muscles. In U-126, no conclusions were possible concerning the termination of crossed

projections to the OMC. Following a lesion restricted to MVN (C-668), preterminal degeneration was evident only in the dorsal (DCC) and intermediate cell columns (ICC) of the contralateral OMC. Isotope injections involving all VN but avoiding AN (U-176, 177) also failed to label the ventral cell column (VCC) on the contralateral side. These results indicate that in the monkey, crossed projections from MVN to the OMC reach only subdivisions innervating the inferior rectus and inferior oblique muscles, and avoid the cell column which contributes the largest number of fibers to the medial rectus muscle (Warwick, '53; Büttner-Ennever and Akert, '81).

Projections from MVN to the OMC differ in the cat. Fibers ascend bilaterally in the MLF, but also cross within the OMC to innervate ipsilateral neurons. MVN projects ipsilaterally to the caudal half of the medial rectus subdivision (MRS) column; contralateral projections reach all somatic cell columns in caudal portions of the OMC, and the MRS and inferior rectus subdivision (IRS) in its rostral part (Fig. 14F). Fibers crossing within the feline OMC have been reported earlier (Tarlov, '70).

Fibers projecting beyond the OMC terminate in the contralateral INC in both cat and monkey (Fig. 16A,D). The INC has projections through the posterior commissure to the contralateral TN and all somatic cell columns of the opposite OMC, except those innervating the medial rectus and levator palpebrae muscles (Carpenter et al., '70). In the monkey, MVN also was found to project fibers rostral to INC to terminals in the contralateral RiMLF. Neurons in this area project bilaterally to the OMC (Graybiel, '77) and have been implicated in vertical eye movements (Büttner-Ennever, '77; Büttner et al., '77; Büttner-Ennever and

Büttner, '78). Thus, MVN has direct and indirect pathways to the extraocular motor nuclei involved in the horizontal and vertical eye movements. Indirect pathways involved in horizontal eye movements are relayed via the AN while those underlying vertical and rotatory eye movements may be mediated by the INC and RiMLF.

Vestibulo-ocular projections from IVN are similar in both cat and monkey; no projections reach the AN, and only crossed fibers ascend in the MLF to terminate in the contralateral TN and OMC. However, projections to the contralateral MRS noted in the cat were not found in the monkey. In agreement with HRP studies, ascending projections from IVN to the OMC originate from rostral portions of the nucleus (Graybiel and Hartweig, '74; Steiger and Büttner-Ennever, '79). Crossed projections from IVN and MVN to TN and the OMC are similar in distribution, suggesting that these nuclei interact in vestibulo-ocular reflexes.

Ascending projections from LVN in the cat terminate sparsely in the ipsilateral AN, and substantially in the ipsilateral OMC. LVN does not project to the TN on either side. Retrograde HRP studies in the cat have demonstrated both ipsilateral (Maciewicz et al., '77) and bilateral (Gacek, '79) projections from LVN to the AN, but no projections to the TN (Gacek, '79a). In the older literature, several authors describe in the cat ipsilateral ascending projections from LVN to the OMC (Muskens, '14; Winkler, '21; Buchanan, '37). Terminals of this pathway, designated the ascending tract of Deiters (ATD), were restricted to the dorsal portions of the feline OMC (Gacek, '71), an area demonstrated to innervate the medial rectus muscle (Naito et al., '74; Gacek, '74; Akagi, '78). The course and termination of the ATD were seen after isotope injections involving LVN only in the cat (Figs. 12 and 16E,F).

While ipsilateral projections from MVN terminate primarily in caudal portions of the MRS, projections of the ATD are to its rostral part. HRP studies in the cat suggest that the ATD originates from cells in the ventral part of LVN (Graybiel and Hartweig, '74). In the monkey a few ascending fibers were noted in the ipsilateral MLF, but none were followed into the OMC. Physiological characterization of ATD cells indicate excitatory responses to ipsilateral horizontal angular acceleration (Baker and Highstein, '78) and contralateral disynaptic inhibitory responses (Reisine and Highstein, '79). Present data suggest that MVN may be the source of the contralateral inhibition in LVN. Although the projection from MVN to LVN is small, it appears to be the only contralateral vestibular input to this nucleus. ATD neurons have an excitatory effect on ipsilateral medial rectus motor neurons (Baker and Highstein, '78).

Current observations indicate that SVN projects ascending fibers: (1) ipsilaterally via the lateral wing of the MLF, and (2) contralaterally via a pathway crossing in the ventral mesencephalic tegmentum caudal to the decussation of the superior cerebellar peduncle, and distinctly separate from it. Crossed projections terminate exclusively in the superior rectus subdivision (SRS) of the OMC. After lesions involving SVN in the monkey, McMasters et al. ('66) noted ascending projections in "ventral parts of the brachium conjunctivum" which terminated in this same subdivision, but attributed these fibers to damage of the SCP. Autoradiographic demonstration of this pathway confirms its origin from SVN. Degeneration studies in the cat failed to demonstrate this projection (Gacek, '71), or ascribed contralateral terminals in the OMC to fibers crossing from the ipsilateral MLF (Tarlov,

'70). Projections with the same course and termination were observed in monkeys after isotope injections involving all four VN, but were absent when injections excluded SVN.

Ipsilateral ascending projections from SVN terminate heavily in the TN, the IRS and inferior oblique subdivisions of the OMC, and the INC. No fibers from SVN terminate in the AN on either side. Retrograde transport studies support bilateral projections from SVN to the OMC (Graybiel and Hartweig, '74; Gacek, '77; Steiger and BUttner-Ennever, '79), and indicate that SVN does not project to the AN (Maciewicz et al., '77; Gacek, '79). HRP data suggesting bilateral projections from SVN to TN (Gacek, '79a) are not substantiated.

The anatomical organization of ascending projections from SVN indicates a role in vertical, but not horizontal, vestibulo-ocular reflexes. The predominant primary vestibular inputs to SVN are from the anterior and posterior semicircular canals (Abend, '77), and SVN is known to have both inhibitory (Uchino et al., '78; Wilson and Melvill-Jones, '79) and excitatory (Yamamoto et al., '78) effects on extraocular motor neurons involved in vertical and torsional eye movements (Precht, '78).

The total pattern of ascending vestibular projections was revealed in two monkeys (U-176, U-177) with large isotope injections involving all four VN. The most striking observations in these animals was the virtual absence of vestibulo-ocular terminations in the ventral cell column (VCC) of the contralateral OMC. The VCC is known to be the principal location of motor neurons innervating the medial rectus muscle, although two small groups of cells in the dorsal cell column also participate (BUttner-Ennever and Akert, '81). Injections of

individual VN in the monkey also failed to label the VCC on the contralateral side; only moderate ipsilateral projections to the VCC were demonstrated after injections or lesions in MVN. In the cat, terminals were found in the MRS of the OMC after isotope injections of the MVN on either side, the ipsilateral LVN, or the contralateral IVN. These observations indicate fundamental differences in the organization of horizontal vestibulo-ocular reflexes in these two species.

The vestibular nuclei can influence medial rectus motor neurons indirectly via abducens internuclear neurons (Baker and Highstein, '75; Highstein and Baker, '78). Massive, crossed abducens internuclear projections terminate in all cell columns innervating medial rectus motor neurons (Büttner-Ennever and Akert, '81; Carpenter and Carleton, '83). These projections are much greater than ipsilateral vestibular projections reaching the VCC in the monkey, indicating that the abducens internuclear pathway is the principal projection transmitting vestibular signals to the medial rectus subdivision of the OMC. Projections from MVN to the AN inhibit ipsilateral motor and internuclear neurons, while contralateral projections are excitatory (Baker and Highstein, '75). Current data, and prior studies (Maciewicz et al., '77; Carleton and Carpenter, '83), indicate that crossed secondary vestibular projections to AN are small relative to ipsilateral fibers, and do not match the massive ascending projection of internuclear neurons to the contralateral medial rectus cell column. These findings suggest that vestibular inputs to the contralateral AN must either exert powerful excitatory drives upon abducens internuclear neurons, or that these neurons receive additional excitation (or release of inhibition) by indirect pathways related to the opposite vestibular complex.

Vestibulothalamic projections are considered to terminate bilaterally to portions of the ventrobasal complex of the thalamus (Condé and Condé, '78; Lang et al., '79; Kotchabhakdi et al., '80), particularly the ventroposterolateral nucleus, pars oralis (VPLo), the ventroposterior inferior nucleus (VPI), and the ventral lateral nucleus, pars caudalis (VLc) (Lang et al., '79). Cells of origin of these projections have been identified in all four principal VN (Kotchabhakdi et al., '80), but are greatest from MVN and SVN (Condé and Condé, '78). Isotope injections involving all VN produced terminal labeling in the thalamus in two animals. Scant ipsilateral terminals were found in VPI, and greater contralateral projections ended in VPLo and VLc. Involvement of the interposed nuclei by the injections made it impossible to identify the source of crossed projections. While ipsilateral vestibulothalamic projections to VPI were confirmed, the vestibular nucleus from which they originate could not be identified.

Secondary vestibulocerebellar fibers. The cerebellum receives primary vestibular fibers from cells of the vestibular ganglion which traverse portions of LVN and SVN and terminate in the ipsilateral nodulus, uvula and flocculus (Brodal and Høivik, '64; Carpenter et al., '72; Korte and Mugnaini, '79). A smaller number of fibers from the VN are thought to terminate in the same cortical regions and in the FN (Carpenter, '60a). Secondary vestibulocerebellar (VC) fibers are considered to arise from centrolateral parts of IVN, cell group "f", cell group "x" and caudal parts of MVN (Brodal and Torvik, '57). Identification of the regions of termination of secondary vestibular fibers present problems in degeneration studies because lesions in the VN may involve both primary and secondary VC fibers. Axoplasmic transport

technics would seem to circumvent these problems, but they show discrepancies. Retrograde transport studies in the cat suggest that parts of all VN project fibers to all of the cerebellar vermis, the flocculus, the FN and the anterior and posterior interposed nuclei (Kotchabhakdi and Walberg, '78a). Similar studies report no evidence of a projection from LVN to any part of the cerebellar cortex (Yamamoto, '79; Gould, '80; Rubertone and Haines, '81). Although the SVN has been demonstrated to project to the flocculus, its fibers have not been traced to portions of the vermis other than the nodulus (Gould, '80; Rubertone and Haines, '81). Folia adjacent to the posterolateral fissure, which receive large numbers of primary VC fibers, also receive projections from neurons in MVN and IVN (Carpenter et al., '72; Rubertone and Haines, '81).

The present study provides no evidence that cells of LVN project to any part of the cerebellar cortex. Cerebellar projections from MVN were followed into mossy fiber rosettes in the ipsilateral flocculus only in the monkey. Higher concentrations of isotope and longer exposure times might have revealed bilateral terminations in the flocculus as described by others (Kotchabhakdi and Walberg, '78a; Kawasaki et al., '81; Rubertone and Haines, '81). Bilateral terminations in the flocculus were evident after large isotope injections of multiple VN, but could not be ascribed to MVN. Projections from MVN to the nodulus and uvula could not be confirmed in this study.

While secondary VC projections from IVN were greater than those from MVN, they were surprisingly modest; terminals in the cerebellar vermis were limited to the anterior lobe, the uvula and the nodulus. Because cell groups "f", "x" and portions of IVN projecting to the cerebellum were considered to receive inputs primarily from the spinal cord,

this cerebellar pathway was regarded as only remotely related to the vestibular apparatus (Brodal, '74). This hypothesis is weakened by data indicating a broader distribution of primary vestibular afferents in IVN, and a paucity of spinal inputs to the VN.

Vestibulocerebellar projections from SVN terminate ipsilaterally in the nodulus, ventral uvula and flocculus. This pattern is in general agreement with prior studies (Kotchabhakdi and Walberg, '78a; Yamamoto, '79; Gould, '80; Rubertone and Haines, '81). SVN neurons projecting to the cerebellum have been shown in anatomico-physiological studies to originate in both the central and peripheral parts of the nucleus (Mitsacos et al., '83, '83a). Thus, both vestibulo-ocular and commissural neurons in SVN may feedback on the specific areas of the cerebellum from which they receive afferents.

Although Dow ('36) suggested that secondary VC fibers outnumbered primary vestibular projections by a factor of three, present data indicate that secondary vestibulocerebellar afferents form a smaller contingent. Reciprocal connections between the VN and the cerebellar cortex seem very lopsided in that IVN and MVN receive more fibers than they project, while LVN appears to have no cerebellar projections.

There was no evidence that any of the VN project to the FN. Although prior studies of fastigial afferents (Ruggiero et al., '77) suggested bilateral inputs to FN from MVN and IVN, present data do not support this conclusion. Labeling of cells in the VN after HRP injections of FN probably was a consequence of retrograde transport by fibers projecting to both the nodulus and uvula.

SUMMARY

The patterns of termination of primary vestibular afferents from the whole vestibular ganglion and from portions of the ganglion innervating particular receptors of the labyrinth were explored using the autoradiographic technic in the monkey. Central connections of the principal vestibular nuclei were examined using both retrograde and anterograde axoplasmic transport methods in the monkey and cat. Conclusions concerning the primary and secondary connections of the vestibular system follow:

1. Primary vestibular projections are the greatest source of afferents to MVN, SVN and IVN. Massive projections to MVN and SVN terminate in virtually the entire territory of these nuclei, and are related primarily to ganglion cells innervating the semicircular ducts. Within each nucleus, the area supplied by posterior duct afferents is limited. Large proportions of primary afferents to IVN are derived from ganglion cells innervating both duct and macular receptors. No primary vestibular fibers terminate in cell group "f" in caudal and ventrolateral portions of IVN, and projections to the middle third of the nucleus are relatively sparse. Primary afferent projections to LVN are restricted to ventral portions of the nucleus. Cell group "y" receives primary afferents that are largely related to the maculae. No other small cell groups associated with the vestibular complex receive peripheral inputs from the labyrinth.

2. Primary vestibular fibers project beyond the vestibular nuclear complex to terminate ipsilaterally in the accessory cuneate nucleus, the subtrigeminal lateral reticular nucleus, the nucleus intercalatus and the dorsomedial gigantocellular reticular formation.

3. Primary vestibulocerebellar projections terminate as mossy fibers in the ipsilateral cortex of the nodulus, uvula, flocculus, lingula and deep folia of vermal lobules V and VI. No projections from the labyrinth were found to terminate in the fastigial nuclei, and terminations in the ventral dentate nuclei are equivocal.

4. Few areas of the vestibular nuclear complex are free of either monosynaptic primary or multisynaptic inputs from the ipsilateral vestibular ganglion. Nonetheless, primary and transneuronal transport of isotope failed to label dorsal LVN and cell groups "f" and "x", indicating that these structures have little functional relationship to the labyrinth.

5. The largest source of central afferents to MVN and IVN are commissural projections originating in the contralateral MVN, SVN, IVN and cell group "y". LVN receives only scant commissural inputs from the contralateral MVN and does not project commissural fibers. Commissural fibers also are the largest contingent of efferents from MVN, SVN and IVN, and project in a reciprocal fashion upon VN from which these nuclei receive afferents.

6. Cerebellovestibular projections from the ipsilateral anterior lobe vermis constitute the principal source of central afferents to LVN. LVN also receives bilateral inputs from rostral portions of the fastigial nuclei. Lesser corticovestibular projections from the anterior lobe reach IVN, but IVN receives large numbers of fibers from the ipsilateral nodulus and uvula. Projections to IVN from the fastigial nuclei are largely crossed from the middle part of the FN. MVN receives substantial afferents from a central band of Purkinje cells in the

ipsilateral flocculus, and modest inputs from the posterior vermis. Few fibers reach MVN from the FN.

7. Projections from the vestibular nuclei to the cerebellar cortex are much less numerous than primary vestibulocerebellar fibers. IVN contributes the largest number of fibers, which terminate in the anterior lobe vermis, nodulus and uvula. MVN projects to central portions of the ipsilateral flocculus and has few projections to the caudal vermis. SVN projects to the ipsilateral nodulus, uvula and flocculus. LVN, which receives massive inputs from the cerebellar cortex, does not project to the cerebellum. None of the VN have projections to any of the deep cerebellar nuclei.

8. Brain stem afferents to the VN, other than commissural fibers, are derived from the perihypoglossal nuclei, the dorsomedial pontomedullary reticular formation, the interstitial nucleus of Cajal and the visceral nuclei of the OMC. Vestibular afferents from the perihypoglossal nuclei are predominantly crossed, arise mainly from caudal portions of the nucleus prepositus and terminate in MVN and IVN. Descending afferents from INC terminate ipsilaterally in MVN, while fibers from the visceral nuclei of the OMC appear to reach MVN, IVN and LVN. Reticulovestibular projections are scant.

9. MVN, IVN and LVN receive spinovestibular projections from the contralateral central cervical nucleus. If spinovestibular projections from more caudal levels of the spinal cord exist, they are probably sparse.

10. LVN has massive projections to the spinal cord via the ipsilateral vestibulospinal tract. The VST descends the length of the spinal cord to terminate in laminae VIII and VII of the ventral and

intermediate spinal gray. Secondary vestibular fibers descending in the MLF project bilaterally to cervical segments of the spinal cord. Projections from MVN terminate in the contralateral central cervical nucleus and ipsilateral supraspinal nucleus. IVN projects to medial portions of laminae VIII and VII.

11. The vestibular nuclei have impressive projections to medullary precerebellar relay nuclei including the lateral reticular nucleus, the paramedian reticular nuclei, the perihypoglossal nuclei and specific subdivisions of the inferior olivary complex. Projections to the ipsilateral LRN arise as collaterals of the VST and terminate in both magnocellular and parvicellular portions of the nucleus. Vestibular projections to the inferior olive and PRN take origin primarily from IVN, while projections to the perihypoglossal nuclei are derived largely from MVN. Projections from the VN to precerebellar relay nuclei offer additional pathways by which vestibular impulses may reach the cerebellar cortex and deep nuclei. Vestibular efferents to brain stem nuclei coextensive and caudal to the VN also include diffuse projections to portions of the nucleus reticularis gigantocellularis medial to the VST.

12. Vestibulo-ocular projections to the abducens nuclei terminate bilaterally with ipsilateral dominance; these fibers originate almost exclusively from MVN, although LVN contributes small numbers of fibers to the ipsilateral AN. Vestibular projections to the contralateral AN do not match the massive, crossed abducens internuclear projection which subserves the horizontal vestibulo-ocular reflex.

13. Vestibulo-ocular projections to the trochlear nuclei ascend bilaterally in the MLF. Ipsilateral projections originate from SVN, while more numerous crossed fibers take origin from both MVN and IVN.

14. Vestibulo-ocular projections to the oculomotor nuclear complex arise from all four principal VN in the cat. Projections from MVN ascend bilaterally in the MLF, but also cross back within the OMC to innervate ipsilateral neurons. Contralateral projections terminate in all somatic cell columns in caudal parts of the OMC, and in the inferior and medial rectus subdivisions rostrally. Ipsilateral fibers reach caudal portions of the medial rectus subdivision. Fibers from IVN are wholly crossed and terminate in the OMC with the same distribution as projections from MVN. Ascending projections from LVN travel outside of the MLF via the ascending tract of Deiters to terminate in rostral portions of the ipsilateral medial rectus subdivision. SVN has bilateral ascending projections to the OMC in the lateral wing of the ipsilateral MLF, and via a bundle that crosses in the ventral mesencephalic tegmentum caudal to the decussation of the superior cerebellar peduncle. Ipsilateral fibers terminate in cell columns innervating the inferior rectus and inferior oblique muscles. Crossed fibers terminate exclusively in the superior rectus cell column.

15. Vestibulo-ocular projections to the monkey OMC differ from those in the cat. No equivalent to the feline ATD appears to exist in primates. Ascending projections from MVN terminate ipsilaterally in cell columns innervating the inferior rectus, inferior oblique and medial rectus muscles, while crossed fibers reach the inferior rectus and inferior oblique cell columns. Ascending fibers from IVN are the same as crossed projections from MVN. While SVN was not selectively involved in any isotope injection in the monkey, indirect evidence suggests that SVN projects crossed fibers outside of the MLF to the contralateral superior rectus cell column of the OMC. None of the

primate vestibular nuclei project to the contralateral medial rectus cell column.

16. Ascending vestibular fibers project beyond the OMC to terminate in preoculomotor nuclei implicated in the control of vertical and rotatory eye movements. MVN has crossed projections to the interstitial nucleus of Cajal and rostral interstitial nucleus of the MLF, while SVN projects to the INC on the ipsilateral side. Vestibulothalamic projections terminate in the ipsilateral ventral posterior inferior (VPI) nucleus of the thalamus. Projections to other thalamic nuclei could not be confirmed.

APPENDIX

List of Abbreviations

A	Cell group A (medial rectus subdivision of the oculomotor complex)
ACN	Accessory cuneate nucleus
AN	Abducens nucleus
ATD	Ascending tract of Deiters
B	Cell group B (medial rectus subdivision of the oculomotor complex)
β	Nucleus β (inferior olive)
C	Cochlea
CCN	Central cervical nucleus
CN	Cochlear nerve
dc	Dorsal cap of Kooy (inferior olive)
DCC	Dorsal cell column of the oculomotor complex (innervates inferior and medial rectus muscles)
DCN	Deep cerebellar nucleus .
dmcc	Dorsomedial cell column (inferior olive)
DN	Dentate nucleus
DPRN	Dorsal paramedian reticular nucleus
f	Cell group "f" (vestibular nuclear complex)
FN	Fastigial nucleus
HRP	Horseradish peroxidase
ICC	Intermediate cell column of the oculomotor complex (innervates inferior oblique muscle)
ICP	Inferior cerebellar peduncle
IRS	Inferior rectus subdivision of the oculomotor complex
INC	Interstitial nucleus of Cajal
IVG	Inferior vestibular ganglion

IVN	Inferior vestibular nucleus
L	Left
LRN	Lateral reticular nucleus
LVN	Lateral vestibular nucleus
MCC	Medial cell column of the oculomotor complex (innervates superior rectus muscle)
MLF	Medial longitudinal fasciculus
MRS	Medial rectus subdivision of the oculomotor complex
MVN	Medial vestibular nucleus
NIC	Nucleus intercalatus
NIVN	Interstitial nucleus of the vestibular nerve
NPP	Nucleus prepositus
NR	Nucleus of Roller
NRgc	Nucleus reticularis gigantocellularis
NRpc	Nucleus reticularis parvicellularis
N.VI	Nerve VI (abducens)
N.VII	Nerve VII (facial)
OMC	Oculomotor nuclear complex
PCs	Purkinje cells
PH	Perihypoglossal nucleus
PPRF	Paramedian pontine reticular formation
PSD	Posterior semicircular duct nerve
PRN	Paramedian reticular nuclei
R	Right
RF	Reticular formation
RiMLF	Rostral interstitial nucleus of the medial longitudinal fasciculus
RPC	Nucleus reticularis pontis caudalis
SCP	Superior cerebellar peduncle

SLRN	Subtrigeminal lateral reticular nucleus
SRS	Superior rectus subdivision of the oculomotor complex
SSN	Supraspinal nucleus
subPF	Nucleus subparafascicularis
SVG	Superior vestibular ganglion
SVN	Superior vestibular nucleus
TN	Trochlear nucleus
V	Cerebellar vermal lobule V
VC	Vestibulocerebellar
VCC	Ventral cell column of the oculomotor complex (innervates medial rectus muscle)
VI	Cerebellar vermal lobule VI
VN	Vestibular nuclei
VNR	Vestibular nerve root
VPRN	Ventral paramedian reticular nucleus
VST	Vestibulospinal tract
WGA-HRP	Wheat germ agglutinin-horseradish peroxidase
x	Cell group "x" (vestibular nuclear complex)
y	Cell group "y" (vestibular nuclear complex)

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