Vestibular Pathways and their Central Connections

—A Framework of the Review of Recent Developments in this Field—

Toru SEKITANI M. D.

Department of Otolaryngology
Yamaguchi University School of Medicine,
Ube, Japan

CONTENTS

I. General View of the Vestibular System.

The vestibular system, in wide sense, consists of, as follows; 1) the sensory hair cells of the peripheral labyrinthine organs, 2) Vestibular ganglion cells and their fibers, 3) vestibular nuclei; and the following main connections and organs (Fig. 1 and Fig. 26) ,i.e., 4) vestibulospinal reflex system, 5) vestibulo-oculomotor system, 6) vestibulocerebellar reflexes system, 7) reticular formation in the brain stem, relating to the various vestibular responses, 8) cerebrum, relating to the vestibular functions, and 9) vestibulo-autonomic nervous systems and their peripheral effector organs.

These complex structures and functions of the vestibular system are multipurposely and meticulously integrated and acting as a whole body. Each parts of their pathways will contain the afferent nerve fibers and the efferent nerve fibers, those which are forming the feedback and feedforward systems. No one has doubt that the necessity of the fundamental knowledge about the vestibular system will be emphasized for understanding the neuro-pathological condition in the patient with dizziness.

Although their course, distributions and/or their neurophysiological meanings are not clarified yet in a whole, the recent rapid advances of the neuro-anatomical and neurophysiological investigations in this field are noteworthy in the individual problem but the knowledge are rather

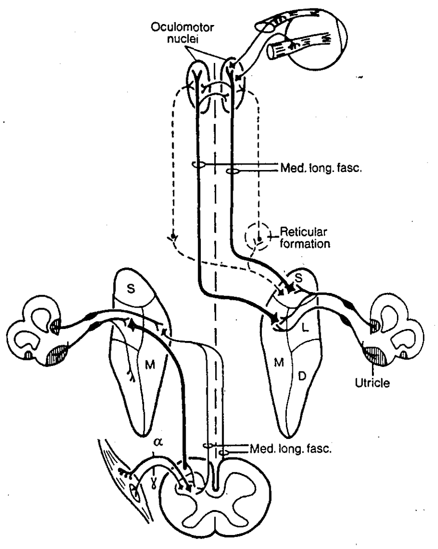

Fig. 1.

Simplified diagrams of two reflex arcs involving the vestibulr nuclei. (Brodal, 1967)
Above to the right a diagram of the vestibuloocular reflex arc.
Below to the left there is a diagram of the elementary vestibulospinal arc.
Note that ascending fibers to the nuclei of the extrinsic ocular muscles come only from the superior nucleus and rostral part of the medial vestibular nucleus. The former ascend ipsilaterally, the latter contralaterally.

scattered or complicated for the medical students and for the graduates of medicine, even for the otolaryngologists.

Therefore, this description on the vestibular pathways and their central connections will be made from the clinico-anatomical standpoint of view and mentioned the framework of a review of recent development in this field, comprehensively.

VESTIBULAR NERVE.

The primary vestibular nerve fibers are the processes of the bipolar neuron of the vestibular ganglia cells.

The dendrit, a peripheral process of the ganglion cell, reaches at the base of the peripheral endorgans in the labyrinth (Fig. 2). The neurit, a central process of the ganglion cell, runs centrally to the vestibular nucleus in the brainstem.

On the pathways (Fig. 3), the nerve fibers (Table 1) leaving from the vestibular sensory hair cells on the macula of the utricie and the cristae ampullaris of the anterosuperior and horizontal canals, run through the macula cribrosa superior (Fig. 3); the nerve fibers from the saccule pass through the macula cribrosa media. And the fibers from the posterior vertical canal pass through the macula cribrosa inferior. The vestibular nerves occupy the posterior part of the porus acousticus internus (Fig. 4). They all enter the vestibular ganglia (Scarpa's ganglion) located on the floor of the internal auditory meatus. Vestibular ganglion is the tropic center of the peripheral neuron. The ganglion consists of bipolar cells, having so-called dendrit and neurit.

Table 1. Cell populations in and Nerve fibers to the sensory epithelium (Tabulated from data of Engström, H. el, 1974)

	"Normal" man	"Elderly" man (above 40 years)
No. of Cells		
Macula sacculi	18. 800	14. 200
M. utriculi	33. 100	26. 100
Cristae (each average)	7. 600	4. 600(40%)
No. of Nerve fibers		
Saccular nerve	4. 046	2. 589
Utricular nerve	5. 952	3. 600
Ampullar nerve	2. 782	1. 570

*Diameter reduced with increasing age

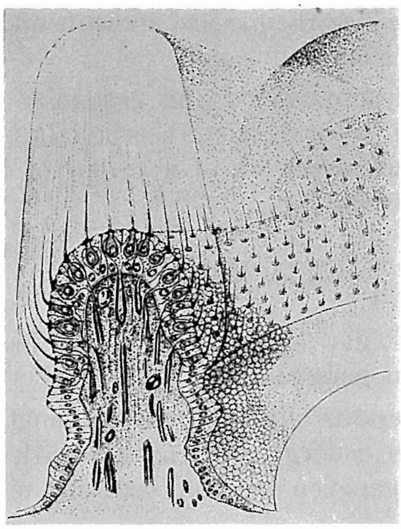

Fig. 2.

Innervation of the sensory epithelium of the crista ampullaris (Schematic drawing of the ultrastructure of the one half of a crista ampullaris) (Wersäll, 1956)

Thick nerve fibers forming nerve calyces round type I hair cells at the summit of the crista, medium calibre fibers innervating type I hair cells on the slope of the crista; medium calibre and fine nerve fibers forming a nerve plexus innervating hair cells of type II.

The sensory hairs pass from the hair cells into fine canals in the cupula. The hairs protrude into the gelatinuous cupula filling out the space between the epithelial surface and ampullar wall.

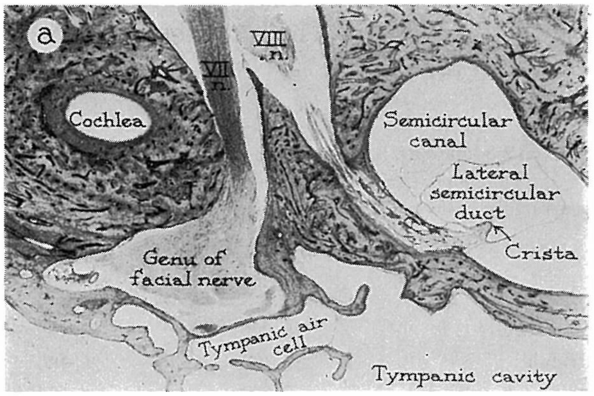

Fig. 3.

Passageway of the vestibular nerve (Anson & Donaldson, 1973, by courtesy of authors)

Note the passageway for the lateral ampullary branch of the vestibular nerve, showing from the superior vestibular area of the fundus of the meatus to the superior cribrose macula of the vestibule, and then to the crista of the semicircular duct.

And also demonstrating the relationship between the vestibular nerve and the facial nerve, and the tympanic cavity.

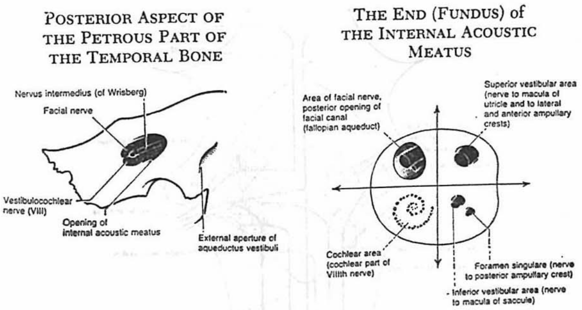

Fig. 4.

Internal Acoustic Meatus (Bossy, 1970):

Each nerve fibers occupy the internal acoustic meatus in a definite order of localization. In the superior vestibular area, the nerves to macula of utricle and to lateral and anterior ampullary crests pass through. And in the inferior vestibular area, the nerve to macula of saccule. The nerve to posterior ampullary crest, in the foramen singulare.

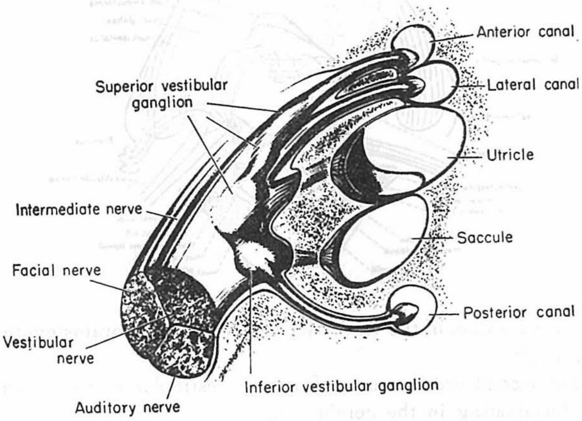

Fig. 5.

The vestibular ganglia and peripheral branches. (Stein and Carpenter, 1967)

Semischematic drawing of the vestibular ganglia and the peripheral branches innervating anatomically distinctive portions of the labyrinth.

Cells of the superior vestibular ganglion are arranged in a spiral fashion.

The distal portion of the superior vestibular ganglion supplies fibers innervating the cristae of the anterior and lateral canals. Cells in the broader, proximal part of this ganglion innervate the macula of the utricle.

The superior and inferior vestibular ganglia are joined by an isthmus of cells. Cells of the infer or vestibular ganglion innervate the macula of the saccule and the crista of the posterior canal.

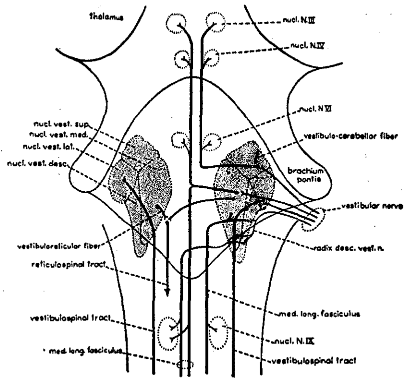

Fig. 6.
Vestibular nuclei and pathways in the brainstem (Bast and Anson, 1949) Diagrammatic representation of their localization.

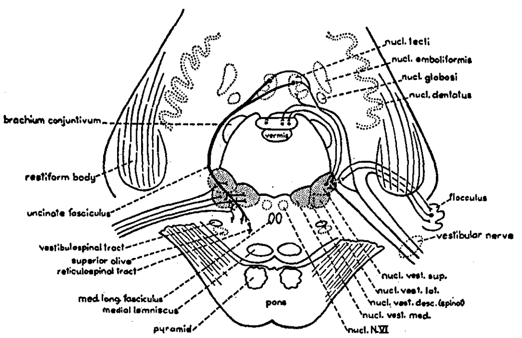

Fig. 7.
Diagrammatic representation of the vestibular pathways in the brainstem to the cerebellum. (Bast and Anson, 1949)
In addition to the second order neurons from the vestibular nuclei, a primary neuron is indicated here as terminating in the cerebellum.

From the ganglion, the fibers relay and join the fibers from the cochlea and together they enter the medulla. The fibers from the saccule, posterior vertical canal and some from the cochlea, travel together as a group, but the cochlear fibers are not related functionally, eventually joining the other cochlear fibers without being associated in Scarpa's ganglion (Fig. 5).

Leaving Scarpa's ganglion, the fibers of central process enter the medulla at the lateral angle of the fourth ventricle, so-called cerebellopontine angle.

Within the medulla they run dorsomedially until they have traversed about two-thirds of the distance to the lateral angle of the fourth ventricle

(Fig. 6 and 7). Here, each bifurcates into ascending and descending branches. These branches ternimate in four vestibular nuclei. The vestibular nuclei are subdivided into four major nuclei (Fig. 1 and 6):

1) the superior vestibular nucleus (SVN, nucleus of von Bechterew, or angular n.)

2) the lateral vestibular nuclus (LVN, Deiters'n)

3) the medial vestibular nucleus (MVN, principal or triangular nucleus) (n. of Schwalbe)

4) the inferior vestibular nucleus (IVN, spinal or descending nucleus)

In addition to these major nuclei, 5) small cell groups (interstitial nucleus of the vestibular nerve, group x, y, and z of Brodal's, and nucleus supravestibularis) are known to be related to the vestibular nuclei, and to function much than the priviously imagined.

Some fibers from the peripherals go directly to the cerebellum without joining a nucleus; these go through the restiform body to the nodule and the flocculus of the cerebellum--- the vestibuloflocculonodular tract (tractus vestibulofloccularis) (Fig. 7).

III. Vestibular Nuclei.

1. Lateral Vestibular Nucleus (Deiters' Nucleus, LVN).

The LVN is characterized by the presence of large, multipolar cells. The cells of the LVN are among the largest of the nervous system. Some of the LVN is 70 μ in diameter, so-called as Nucleus vestibularis magnocellularis.

The border of the LVN from other vestibular nuclei are clear, except where the ventral border fuses with the rostral part of th e inferior vestibular nucleus.

A restricted area of the dorsoventral part of the LVN receives primary fiber terminations, but the number of the primary fiber terminations are few (Fig. 8).

The cells of the LVN give the origin to the fibers of the direct (uncrossed) vestibulospinal tract, and terminate in the ventral fasciculus proprius of the spinal cord, descending through the entire length of the cord.

The fibers end in the motor cells of the ventral horn. This, the direct vestibulospinal tract, exercises a constant motor influence on the extensor muscles.

The LVN receives primarily from the cerebellum, and has fiber connections with the reticular formation and the spinal cord. In addition, its

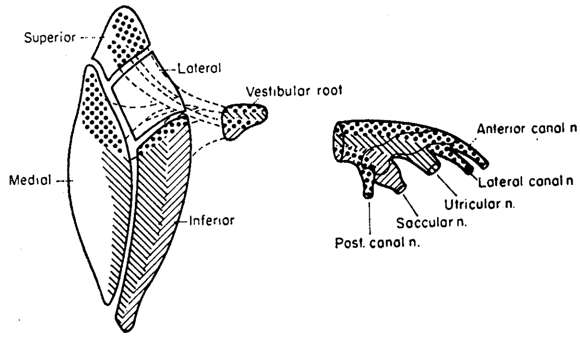

Fig. 8.

Diagrammatic representation of relationship between portions of the vestibular ganglia and central projecting fibers within the vestibular nuclear complex. [Redrawn from Stein & Carpenter (1967) by Brodal (1972)]

The vestibular ganglia and peripheral branches are shown on the right. The canal nerves and portions of the ganglia innervating the canal nerves are shown in each different drawings

Portions of the vestibular ganglia innervating the cristaeof the semicircular canals project primar ly to the superior vestibular nucleus and oral parts of the medial vestibular nucleus. Portions of the vestibular ganglia innervating the macula of the utricle project primarily to parts of the medial and inferior vestibular nuclei. Central fibers from the saccular ganglion project mainly to dorsolateral parts of the inferior vestibular nucleus.

ventralmost part receives fibers from the contralateral vestibular nuclei via commissural fibers and some fibers from the frontal and parietal cortex.

2. Superior Vestibular Nucleus (Bechterew's N. ,SVN)

The nucleus is the most superiorly located of all vestibular nuclei in the brainstem.

The SVN is distinguished by being composed of rather loosely scattered cells, chiefly medium and small in size. Along its rostrocaudal extent the SVN is capped dorsally by the superior cerebellar peduncle.

The mesencephalic trigeminal nucleus is situated dorsomedial to its rostral two-thirds. The border against the lateral vestibular nucleus is fairly distinct based on cytoarchitectonic criteria.

The main input to the SVN is from the vestibular endorgans, especially from the cristae ampullaris of the semicircular canals (Fig. 8 and 9).

Gacek (1969) found that the large calibre fibers terminating in the superior vestibular nucleus were distributed around large cell in the center of the nucleus, while the small diameter fibers ended more predominantly in the same nucleus, where small cell predominate. And he suggests that such findings indicate different functional properties for type I and type II vestibular hair cells.

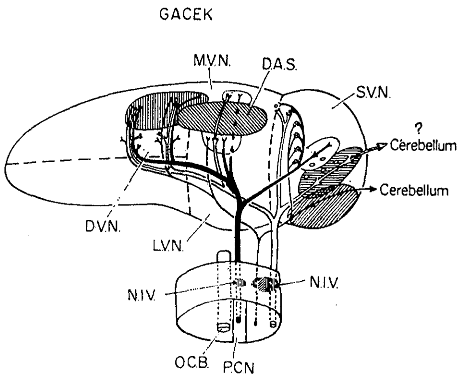

Fig. 9.

Diagram showing the distribution of the nerve fibers from the semicircular canals to the various parts of the vestibular nuclei (From Gacek, 1969).

The neurons supplying the cirstae have their fibers in the rostal two-thirds of the vestibular nerve, those coming from the maculae occupy the caudal portion.

Furthermore, the neurons from the cristae after giving off collaterals to the interstitial nucleus of Cajal, proceed into the brain stem where the axons bifurcate into an ascending and a descending branch.

The ascending branch terminates in the superior vestibular nucleus and in the cerebellum, hile the descending branch passes medially into the lateral, medial and descending vestibular nucleus.

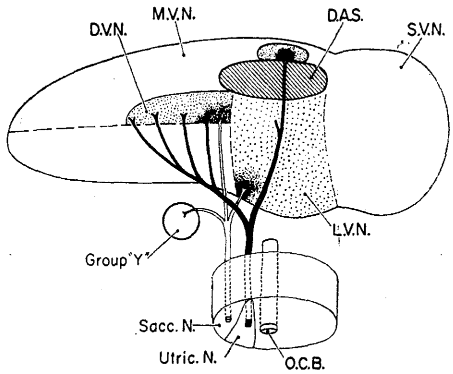

Fig. 10.

Distribution of the macular nerves passing through the nerve bundle to the termination in the vestibular nuclei (Gacek, 1969, in cat)

The ascending branches of the utricular neurons terminate in the rostroventral part of the lateral vestibular nucleus, and in the rostral part of the medial vestibular nucleus.

Their descending branches give off collaterals to the caudal part of the medial vestibular nucleus and the rostral part of the descending vestibular nucleus.

Gacek found no projection from the maculae to the interstitial nucleus of Cajal or to the superior vestibular nucleus.

The fibers coming from the saccular macula projected mainly to the cell-group y and to a lesser ext ent to the la eral and descenidng vestibular nuclei.

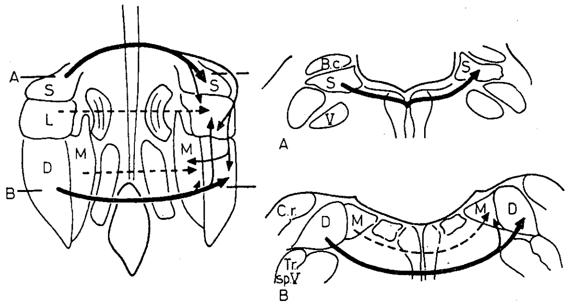

Fig. 11.

Internucleal commissural fibers (Ladpli and Brodal, 1968, in cat)
Commissural fibers between the vestibular nuclei on both sides are demonstrated.
Figure on left showed the horizontal section of the brainstem. Figure A and B on the right showed the transection of the brainstem at the level A and B shown in left figure.
One originates in the SVN and ends in the contralateral SVN and the ventral part of the other three vestibular nuclei. Other origintates in the IVN (DVN) and ends in the ventral part of the contralateral vestibular nuclei.

The ipsilateral SVN is heavily connected to the contralateral SVN via the commissural fibers. Restricted area in the SVN receive fibers from the cerebellum, the reticular formation, the medial accessory olive and higher centers, but none from the spinal cord. The fibers join the medial longitudinal fasciculus of the same side, oculomotor nuclei of the same side, abducens nucleus of the opposite side (direct vestibulo-mesencephalic tract).

According to Gacek (1969, in cat) there was no projection of the fiber from the maculae utriculi et sacculi to the SVN (Fig. 10).

3. Medial Vestibular Nucleus (Schwalbe's, triangular; MVN)

The MVN contains cells of different sizes; most of them are medium-sized, triangular or multiform, while smaller cells are usually round. The MVN is more tightly packed with cells than the other vestibular nuclei and its borders are usually easily identifiable.

The oral and rostrodorsal half receive fibers from the cristae of the three semicircular canals, and its dorsolateral part receives fibers from the macula of the utricle. The MVN also have fiber connections with reticular formation; i. e., the fibers run across to the medial longitudinal fasciculus of the opposite side (crossed vestibulo-mesencephalic tract). The fibers of the MVN connects with the abducens nucleus of the same side, and with the trochlear and oculomotor nuclei of its opposite side (Fig. 12-A, 12-B and 13). The fiber connection with the contralateral vestibular nuclei via commissural fibers (Fig. 11) will be existed.

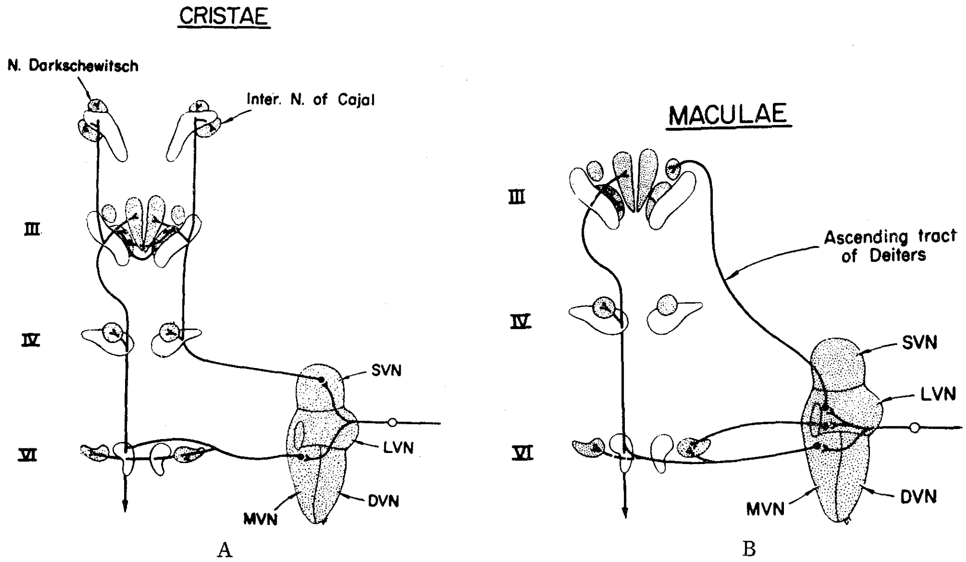

Fig. 12-A. and-B.
Vestibulo-ocular Projections (Gacek, 1971, cat)

a: Diagram summarizing the ascending pathways that may be activated by first order neurons from the semicircular canal cristae.

b: Diagram summarizing the ascending pathways that may be activated by first order neurns from the maculae of utricle or saccule.

In Figure A, the primary neuron from a semicircular canal crista is represented as a bifurcating fiber sending an ascending branch to the superior vestibular nucleus and a descending branch to the rostal porion of the medial vestibular nucelus These two nuclei connect the semicircular canal neurons through the IIIrd, IVth and VIth nuclei by way of the ipsilateral and contralateral ascending systems in the medial longitudinal fasciculi.

In Figure B, the fibers from the otolithic sense organs (utricle and saccule) could be represented by a fiber which has an ascending branch terminating in the ventral division of the lateral vestibular nucleus and a descending one terminating in the rostral portion of the medial vestibular nucleus. Compensatory eye movements whether they be horizontal or vertical from utricular stimulation or the theoretical vertical movements from saccular stimulation could be carried out by the the systems in this diagram.

The dorsolateral portion of the MVN has fiber connections with higher centers, and receive the fibers from the ipsilateral LVN; but no fiber from the vermis reaching to the MVN was observed.

This nucleus communicates with the nuclei of the muscles of the neck, also with the vegetative centers in the medulla oblongata.

4. Inferior Vestibular Nucleus (Descending V. N.) (IVN)

The inferior vestibular nucleus is located at the ventrolateral portion of the vestibular nuclei zone.

The IVN is the largest and longest in contour among the vestibular

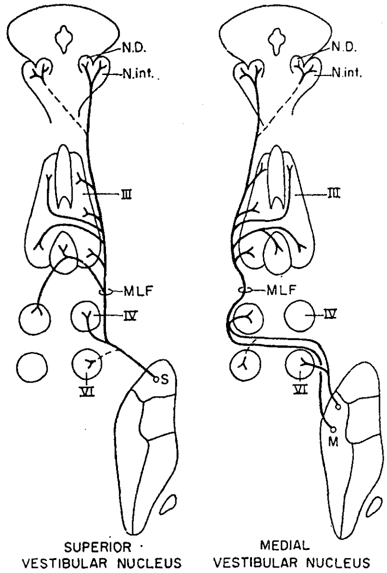

Fig. 13.
Diagramatic representation of the vestibulo-ocular nerve fiber connections (Tarlov, 1970)

nuclei (Fig. 8,9 and 10).

The cells of the inferior vestibular nucleus are resembling those of the medial vestibular nucleus. The IVN, which is fused with the ventral border of the LVN, contains a certain number of large multipolar cells. The border between the IVN and the LVN is not sharply devided cytoarchitectually, but there are significant differences in the fiber patterns between them.

The fibers run to the medial longitudinal fasciculus on the opposite side, and descend as the crossed vestibulospinal tract. They descend throughout the entire length of the cord and probably end in the intermediate nucleus.

Anatomical studies show that the dorsomedial part of the IVN receives fibers mainly from the utricular macula, the dorsolateral part receive fibers from the saccular macula and the rostromedial part receives fibers from the semicircular canal (Fig. 8,9 and 10).

The caudalmost portion of the IVN receives a relatively modest number of spinal afferents and fibers from the cerebellum. The medial portion receives fibers from the higher centers and ventral portion receives commissural fibers mainly from the contralateral IVN and some fibers from the remaining contralateral vestibular nuclei (Fig. 11).

In addition, the IVN also has fiber connections with the reticular formation, the mandibular nerve, the glossopharyngeal nerve and the cranialmost cervical dorsal roots.

This nucleus exercises an inhibtory effect on the extensor muscles of the opposite side of the body.

5. Scattered Small Groups of the Vestibular Nucleus.

Several of the small groups of the vestibular nucleus are characterized and can be identified, for example the group x and the minute group y. And also group z and group f are identified and named. A particularly clear example of a subunit within a greater nucleus is the group f, described first by Meesen and Olszewski (1949) in the rabbit.

Group x is located at the lateral portion of the inferior vestibular nucleus.

Group z is located at the caudal part of the vestibular nuclei, in continuity with group y.

Group f is located at the caudal-ventral portion of the inferior vestibular nucleus.

Group y is located at the dorsolateral part of the lateral vestibular nucleus, and at the rostalmost than the group x, closely to the restiform body (inferior cerebellar peduncle).

These small cell groups located in and around the major four vestibular nuclei and will play some important role in the neuronal control mechanism, feedback or feedforward, in the reflex arc system between the vestibular nuclei and the relating nuclei which include the cerebellum and the reticular formation.

IV. Primary Vestibular Fiber Connections

Primary vestibular fibers are consisted of principally the peripheral and central processes of bipolar neurons of the vestibular nerve ganglia, the superior and inferior vestibular ganglia (Fig. 5 and 1).

First, the peripheral processes dendrit of the superior vestibular ganglion innervate;

1) the cristae of the superior and horizontal (lateral) semicircular canals,
2) the macula utriculi,
3) a small dorsal part of the macula sacculi.

The inferior vestibular ganglion innervate;

1) the crista of the posterior semicircular canal,
2) the major portion of the macula sacculi.

Next, the central processes neurit of the vestibular ganglia have more complicate projection to the vestibular nuclei and other parts of the central nervous system.

Most of the primary vestibular fibers terminate at the vestibular nuclei in the brainstem. Each fibers from the peripheral endorgans of the vestibular system terminate at each specifically localized portions of the vestibular nuclei; i. e., primary afferent nerve fiber from the cristae ampullaris of three semicircular canals terminate in the superior vestibular nucleus and oral part of the medial vestibular nucleus (Fig. 8,9 and 10).

Primary afferent nerve fiber from the macula utriculi terminate in the inferior vestibular nucleus and the medial vestibular nucleus. Fiber from the macula sacculi terminate in the dorsolateral part of the inferior vestibular nucleus.

According to Stein and Carpenter's description based on their experimental study on the monkeys, the primary vestibular fibers from the cristae ampullaris and the macula utriculi et sacculi did not show any definite termination in the lateral vestibular nucleus.

Gacek also explained that a few termination of primary fibers from the ascending branch of the macula utriculi and from the descending branch of the crista ampullaris was observed but scarcely.

There are some direct projection of the primary vestibular nerve fibers to other nucleus in a higher center; i e., a fiber of the ascending branch of the crista ampullaris reaches directly to the cerebellum through the juxtrarestiform body. Localizations of terminations to the cerebellum are at the vermis, nodulus, lingula cerebelli, nuclues fastigii and bilateral flocculus (Fig. 7).

Anatomical studies show that a scanty of primary vestibular fiber reaches in the ipsilateral region of the tractus solitarius and the nucleus dorsalis n. vagi and the medullary reticular formation.

But, no projection into the Fasciculus longitudinalis medialis, or spinal cord was observed.

And it is generally believed that there is no primary vestibular nerve fiber reaching further above the mesencephalon.

V. Vestibular Commissural Fibers between the Bilateral Vestibular Nuclei.

Some commissural fibers connecting both vestibular nuclei through the midline of the brainstem were found and described (Fig. 11).

The function of these commissural fibers will be noticeably important, though their neurophysiological activities were not completely clarified yet.

There are two definite commissural connections between two sets of the vestibular nuclei on both sides (Fig. 11, by Ladpli and Brodal, 1968).

One main commissural fibers originate in the superior vestibular nucleus and end chiefly inthe contralateral SVN and the ventral parts of the three vestibular nuclei.

Other main commissural fibers originate in the inferior (descending) vestibular nucleus and end chiefly in the ventral part of the contralateral inferior vestibular nucleus and end partly in the medial vestibular nucleus and in the lateral vestibular nucleus.

Commissural fibers between both lateral vestibular nuclei are scanty. And commissural fiber from the MVN is scanty and the originating area is still unknown.

The change in the neuronal activity of the ipsilateral vestibular nuclei may influence the activities in the contralateral vestibular nuclei via these commissural fibers, but the exact interaction mechanism is still beyond some imagination and will be required further investigation in this field.

VI. Vestibulo-ocular Connections.

Some of the secondary vestibular nerve fibers emerging from the vestibular nuclei terminate the oculomoter nuclei ascending through the medial longitudinal fasciculus (Vestibulo-ocular projections) (Fig. 12 and 19).

i) Ascending pathways relating to the semicircular ampullary nerve. (Fig. 12-A)

First, figure 12-A shown by Gacek (1971) is the diagram summarizing the ascending pathways that may be activated by first order neurons from the cristae ampullaris of the semicircular canals. The primary neuron from a semicircular canal is represented as a bifurcating fiber sending an ascending branch to the superior vestibular nucleus and a decsending branch to the rostal portion of the medial vestibular nucleus.

These two nuclei connect the semicircular canal neurons through the III rd, IVth nuclei by way of the ipsilateral and contralateral ascending systems in the medial longitudinal fasciculi.

Ipsilateral ascending pathway originates in the superior vestibular nucleus and passing through the outer lateral part of the MLF, it reaches at the ipsilateral trochlear nucleus and reaches bilateral oculo-moter nucleus (except for the dorsolateral part). It terminates further in the ipsilateral nucleus of Darkschewitsch and nucleus interstitials of Cajal.

Contralateral ascending pathway originates in the MVN, and ascending through the contralateral MLF (inner half), it terminates in the contralateral trochlear nucleus, oculomotor nuclei, nucleus of Darkschewitsch and nucleus of Cajal.

Bilateral abducens nuclei receive the projection fibers from the ascending branch through this ascending pathway.

A part of the ascending branch to the abducens nuclei comes from the ventral part of the LVN.

ii) Ascending Pathways relating to the maculae.

The fibers from the otolithic sense organs (utricle and saccule) (Fig. 12-B) could be represented by a fiber which has an ascending branch terminating in the ventral division of the LVN and a descending one terminating in the rostral portion of the medial vestibular nucleus.

"Ascending tract of Deiters" arises from the LVN. This ipsilateral ascending pathway arises from the ventral portion of the LVN and ascending through the lateral part of the MLF, the fibers terminate at the ipsilateral oculomotor nuclei (dorsal part). This fiber acts as the inferior rectus muscle control.

Ipsilateral direct innervation fiber to the trochlear nucleus originates from the ventral portion of the LVN. There is some fibers to the ipsilateral and contralateral trochlear nuclei via the MVN.

According to Tarlov, an ascending fiber from the SVN terminate at the bilateral extrinsic ocular muscle nuclei, passing through the ipsilateral MLF. (Fig. 13, left) Fibers to the contralateral oculomotor and trochlear nuclei are crossing the midline of the brainstem in the oculomotor nuclei.

Fibers originated in the MVN cross over the midline at the level of the trochlear and abducens nuclei.

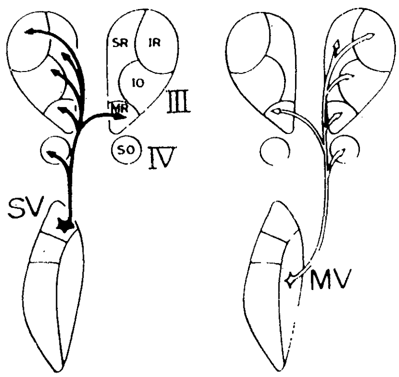

Fig. 14.

Synaptic connection between the vestibular nuclei and the nuclei of the oculomotor and trochlear nerve. (Diagram by Ito, 1972, in rabbit)

Black line showed an inhibitory projection, and the white line showed excitatory projection.

Ascending fibers from the SVN and the MVN to the oculomotor nuclei show the symmetrical distribution (Tarlov, 1970) suggesting the inhibitory activity against the ipsilateral oculomotor system and excitatory action to the contralateral oculomotor nuclei.

Synaptic connections between the vestibular nuclei and the nuclei of oculomotor and trochlear nerves was diagramatically summarized by Ito (1972), showing some neuronal mechanism of simultaneous (synchronuous) eye movement of each eyeballs. (Fig. 14)

VII. Connections between the Vestibular Nuclei or the Vestibular primary fibers and the reticular formation.

Projection of the fibers from the vestibular nuclei to the reticular formations are shown in Fig. 15 and 16. Complex projection of the nerve from the vestibular nuclei to the ipsilateral and contralateral reticular formation was observed, predominantly in the superior vestibular nucleus.

There is no definite origin of projection fiber from the medial vestibular nucleus, though the termination of it was suspected to be in the similar area where the projection fibers from the inferior vestibular nucleus terminated.

A few of the primary afferent vestibular fibers from the peripheral endorgan will directly terminate in the reticular formation (Fig. 15).

This pontomesencephalic reticular formation spreaded upward to the hypothalamus, giving the branches to the oculomotor nuclei, trochlear nucleus, the abducens nucleus, the thalamus, the cerebellum, the hypothalamus and the cerebral cortex.

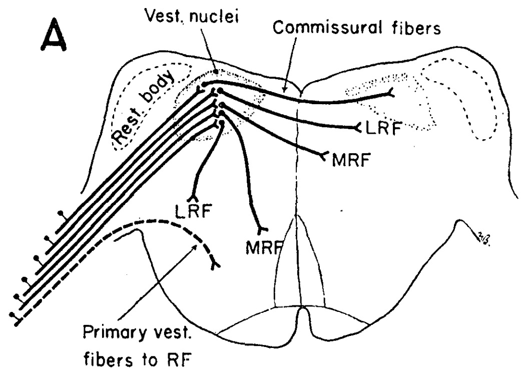

Fig. 15.

Connection between the vestibular nuclei or the vestibular primary fibers and the reticular formation.

In otherwords, the fibers of the vestibular nuclei have some complex connections with the most parts of the central nervous system via these networks of the reticular formation.

Physiological responses in the reticular formation is believed as the fascilitatory action in most of the area (bulbo-reticular fascilitatory area). Stimulation of these area produced the increase of the muscular tonus in whole body or a part of the body.

In other place, i. e. a small area close to the midline of the ventral portion of the medulla oblongata respond as inhibitory (bulboreticular inhibitory area). Stimulation of this small area yield the decrease of the muscular tonus of the whole body.

Meanwhile, the predominant fascilitatory activity in the reticular formation will be suppressed and controlled by a constant inhibitory activity from the cerebral cortex or basal ganglia. These harmonious and well balanced integration mechanism will be one of the most important functions of the reticular formation, but individual processes remained unknown.

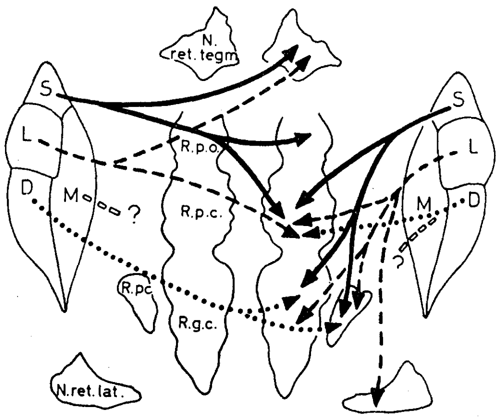

Fig. 16.

Main projection of the nerve connection from the vestibular nuclei to the reticular formation (Brodal, 1968; Brodal & Pompeiano, 1972)

Complex projection of the nerve from the vestibular nuclei to the ipsilateral and contralateral reticular formation are shown. Note the predominant projection from the superior vestibular nucleus.

N. ret. lat: Nucleus reticularis lateralis pontis
N. ret. tegm.: N. reticularis tegmenti pontis
R. g.c.: N. reticularis giganto-celluaris in the medulla.
R. pc.: N. reticularis parvicellularis. R.p.o.&
R. p.c.: N. reticularis pontis and caudalis, respectively.

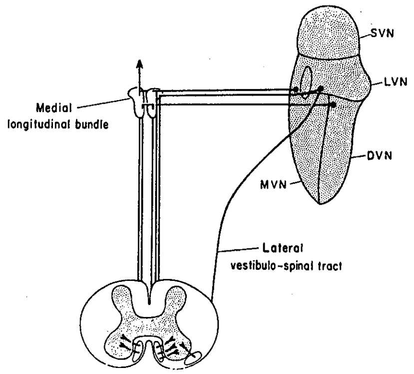

Fig. 17.
Descending spinal tract from the vestibular nuclei. (Gacek, 1971, in cat)
Note that the superior vestibular nucleus does not contribute to the descending pathways to the cervical and lower cord region, in this diagram.

VIII. Descending Spinal Pathways.

Descending spinal pathways emerging from the vestibular nuclei are devided into two main tracts; i. e., tractus vestibulospinalis lateralis and tractus vestibulospinalis medialis.

Lateral vestibulospinal tract originating from the lateral vestibular nucleus runs ipsilaterally down and terminate the anterior horn cells of whole length of the spinal cord, transmitting the impulses from the LVN to the spinal motor neurons distributing whole body and extremities (Fig. 17).

Medial vestibulospinal tract pass the fibers originating from the medial vestibular nucleus and the inferior vestibular nucleus, and descend through the medial longitudinal fasciculus.

The majority of the fibers of this tract is crossing but a part of them terminates uncrossly in the anterior horn cells of the cervical spinal cord. This descending fibers send the impulses affecting the labyrinthine tonus over the neck muscles contributing much for maintaining the head position and postures. In other words, there is close relationship between the labyrinthine neck reflexes and the head positions.

Note: Gacek (1971) denied the previously prevailing opinion that there was no fiber originating from the MVN and IVN in the vestibulospinal tract.

Note: Since the LVN receives the fibers from the nucleus fastigii of the cerebellum, the neuronal activity of the nucleus fastigii will affect the whole spinal cord.

IX. Vestibular Nuclei and the Cerebellum.

—Vestibulocerebellar Pathways—

i) Primary vestibulocerebellar Fibers.

Course and termination of the primary vestibulocerebellar fibers: Afferent,primary vestibular fibers having entered into the brainstem, that fibers continue dorsomedially as a fairly well circumscribed bundle. A great number of the fibers penetrate the SVN. Others pass just dorsal to it.

The primary vestibulocerebellar fibers terminate in the nodulus, the adjoining ventral folia of the uvula, the paraflocculus and the ventral paraflocculus (Fig. 19 and 20)

Within the intracerebellar nuclei terminations have been established in small-celled ventral part of the lateral (dentate) nucleus, but a termination in the fastigial nucleus is still unclear.

It appears that most primary vestibular fibers ending in the cerebellum are derived from the semicircular ducts.

The primary vestibular fibers end as mossy fibers (Fig. 19).

ii) Secondary vestibulocerebellar fibers.

Secondary vestibular fibers take origin from restricted parts of the

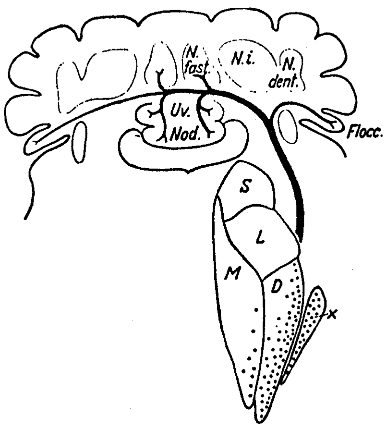

Fig. 18.

The secondary vestibulo-cerebellar projection. (Dow, 1936. Brodal and Torvik, 1957)
The dotted areas indicate the sites of origin of secondary vestibular fibres , as projected on a horizontal section through the vestibular nuclei (of the cat). Note the site of termination of the fibers.

Floc: Flocculus	Uv: Uvula
N. dent.: Nucleus dentatus	Nod.: Nodosa
N. i.: Nucelus interstitialis	N. fast.: Nucleus fastigii.

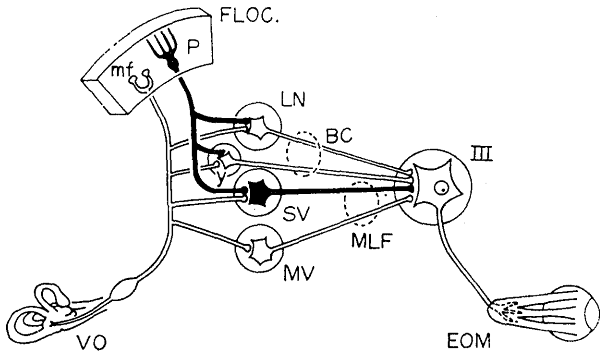

Fig. 19.

Neuronal connections in the vestibulo-ocular reflex arcs related to the flocculus. (Ito, 1972)

VO: vestibular organ,
Floc: flocculus,
mf: mossy fiber terminal,
P: Purkinje cell,
LN: Lateral cerebellar nucleus.
Y: goup y of the vestibular nuclear complex.
SV: superior vestibular nucleus.
MN: medial vestibular nucleus,
BC: brachium conjunctivum,
MLF: medial longitudinal fasciculus
III: the IIIrd nucleus
EOM: extra-ocular muscles.

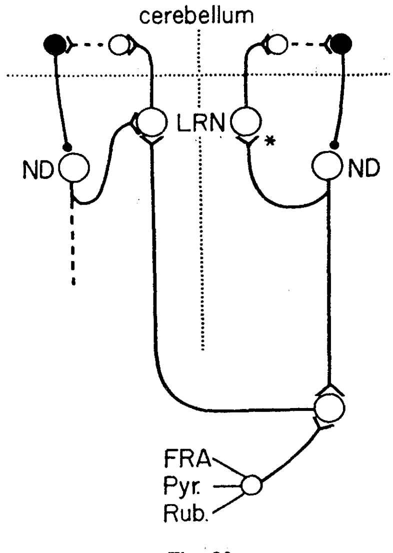

Fig. 20.

Relationship between the vestibulospinal control in the vestibuloreticulocerebellar tract and the cerebellum (Grillner & Hongo, 1972)

Black dot (large and small): Inhibitory neuron and synapses, respectively.
White circle and Y-shape line: Excitatory neuron and its synapses, respectively.
ND: Deiters Nucleus
LRN: Nucleus lateralis reticularis
FRA: Flexor reflex afferent, i. e., cutaneous and high threshold muscle and joint afferents.
Pyr.: Pyramidal tract.
Rub.: Rubrospinal tract.

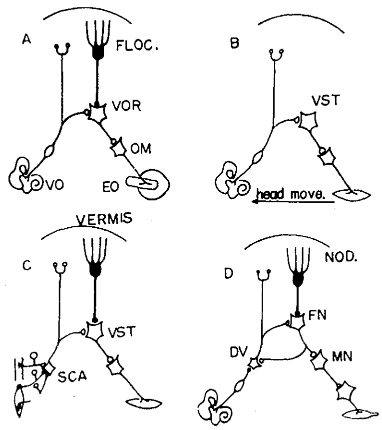

Fig. 21.
Prototype description of the vestibulo-cerebellar connections (Ito, 1972)
A: Vestibular feed-forward control system.
B: Vestibular feed-back control system.
C: Spinal feed-forward control system
D: Indirect control by the N. fastigii.

vestibular complex only: group x and ventrolateral part of the IV N. with a few fibers from the ventral part of the medial nucleus.

Fibers from the vestibular nuclei to the cerebellum were described by many authors, (Fig. 20 and 21) concluding that the site of termination of the secondary vestibular fibers is the same as that of the primary vestibulocerebellar fibers.

Secondary vestibulocerebellar fibers end ipsilaterally in the nodulus, the adjoining folia of the uvula, the flocculus and the fastigial nucleus (Fig. 18).

A termination of secondary vestibular fibers bilaterally in the fastigial nucleus was advocated by Carpenter et al (1959 and 1960).

There may well be further details of this kind which so far remain unknown.

X. Vestibular Nuclei and the Cerebrum

—Cerebral Connections—

Since the dizzy sensation is induced by the stimulation to the peripheral labyrinthine endorgans, there might be some definite transmission route for impulses from the vestibular system to the cerebral cortex.

Penfield and Gaze (1933) reported that a sensation of giddiness was induced by the stimulation of the posterior part of the temporal lobe in the human.

These connections have been studied by many investigators from the various standpoint of view.

The ascending fibers are derived from all four vestibular nuclei and Brodal's cell group x. These fibers from the vestibular nuclei pass to levels rostral to the oculomotor nucleus. The superior vestibular nucleus appears to give off all its efferent fibers in the ascending direction, and they are uncrossed.

The lateral vestibular nucleus gives off crossed and uncrossed ascending fibers, and they show the largest contingent of ascending vestibular fibers.

The MVN and IVN also originate crossed and uncrossed ascending fibers. The fibers of the medial longitudinal fasciculus end in or give off collaterals to the nuclei of the abducens, trochlear and oculomotor nerves. Some of these fibers continue rostrally beyond the oculomotor nuclei and end in several different parts of the central nervous system (i e., the interstitial nucleus of Cajal, the red nucleus, the thalamus, etc).

There is disagreement as to the location of the cortical vestibular area and whether the projection is homolateral or bilateral. Fredricksen, Scheid and Kornhuber explained, based on their experimental study on the monkey brain (Fig. 22), that the predominant vestibular evoked responses

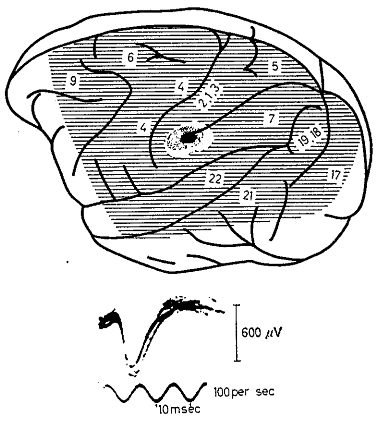

Fig. 22.

Localization of the vestibular evoked responses on the brain cortex, following contra-lateral vestibular nerve stimulation. (Fredricksen, Scheid & Kornhuber, 1966)

Responses are located in the parietal lobe of Macaca mularta brain at the foot of the intraparietal sulcus.

Numbers show approximate location of Brodmann's cytoarchitectonic areas.

occurred at and near the foot of the intraparietal sulcus. However, some investigators believe that the cortical vestibular area will be around the Brodmann's area I includes the anterior suprasylvian and anterior ectosylvian gyri, and area II includes the middle and posterior ectosylvian gyri.

Further researches relating much more to the vestibular system are required.

XI. Efferent Vestibular Fibers.

As shown by Wersäll (1956) and by Engström (1958) based upon their electron microscopical investigations of the inner ear sensory organs, some vestibular fibers form a complicated system of branching fibers partly ending at the sensory cells and partly at the afferent nerve fibers.

This was the peripheral efferent vestibular fibers.

In mammals, the hair cell of type I, which is enclosed in an afferent nerve chalice, has no direct contact with the efferent endings which form synapses with the nerve chalices or the afferent fibers and terminals. The hair cell of type II has synaptic contacts with both afferent and efferent endings.

The efferent presynaptic fibers are slender elements (0.18–0.3 μm in diameter) which run among the suporting cells parallel to the basement membrane. They seem to form a sort of horizontal nerve plexus there.

They contain a few filaments, some elongated mitochondria and small (300–600 A°) round vesicles. The precise physiological properties of the efferent pathways to the inner ear has not yet been definitely clarified. Iurato (1972) condensed to explain that some evidence about the efferent nerve is in favour of an inhibitory activity. The vestibular efferent system functions as a mechanism for balancing the output from the afferent nerve in two ways: by ditect presynaptic action on hair cell of type II, an d by postsynaptic action on the nerve chalices and afferent fibers.

The number of efferent fibers is small, only 2 percent (200 fibers against a total of 12,000 in the entire vestibular nerve of the cat, caliculated), but they show extensive terminal branching.

An afferent component of the vestibular nerve in the nerve route along the fibers of first order neuron and in the brainstem was demonstrated by Rasmussen and Gacek (1958) and by Gacek (1960).

Rossi and Cortesina (1962) did state on the basis of cell changes and cell loss following vestibular nerve section in the guinea pig that they could demonstrate the origin of the vestibular efferent bundles. They found two bundles, one arising from the LVN and a more ventral bundle

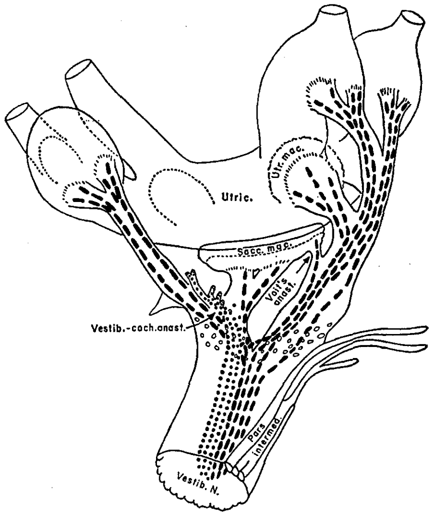

Fig. 23.

The efferent vestibular fibers in the vestibular nerve. (Gacek, 1960)

Diagram showing the course and peripheral distribution in the cat of the efferent (dashed lines) and afferent vestibular fibers (Abbr: Vestib. N.).

Efferent cochlear fibers are shown as dotted lines.

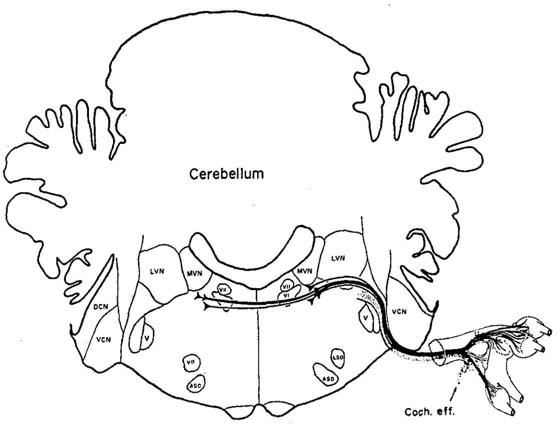

Fig. 24.

Origin, course and termination of the efferent vestibular nerve pathway (Gacek, 1974, in kitten).

The drawing depicts the origin, course and termination of the vestibular efferent pathway and its relationships to the efferent cochlear bundle.

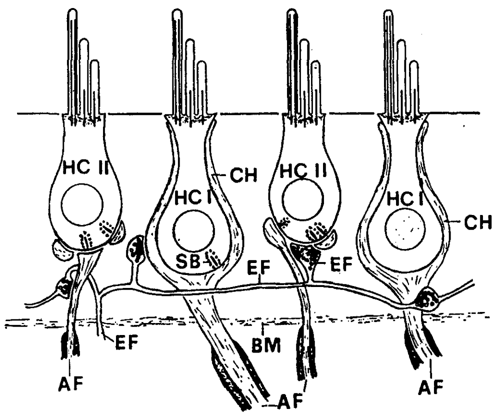

Fig. 25.

Relationship of efferent fibers and their vesiculated endings to hair cells. (Smith and Rasmussen, 1968, slightly modified by Iurato, 1972)

Schematic drawing showing relationship of the efferent fibers and their vesiculated endings (EF) to hair cells type II (HC II), afferent nerve chalices (CH) and afferent fibers and endings (AF).

BM—basement membrane, SB—synaptic bar;

The e ferent nerves form a sort of horizontal plexus.

which arise from a nucleus called the "nucleus interpositus". This small nucleus was located between the LVN and the descending trigeminal root.*

*Note: There is some discrepancy (Gacek).

The present location of the efferent vestibular neurons is further supported by the acetylcholinestrase localization technique, where an area of the vestibular activity has been noted medial and ventral to the lateral vestibular nucleus.

The origin, course and termination of the vestibular efferent pathway and its relationship to the efferent cochlear bundle were drawn in Fig. 23, 24 and 25.

At their location, ventral to the medial and lateral vestibular nuclei, these neurons originate in an area where the descending branches of first order neurons from the cristae and maculae converge. The opportunity is present, therefore, for direct termination of the afferent neurons from all vestibular sense organs into the efferents.

The efferent vestibular system forms part of a closed feedback loop system between the labyrinthine receptors and the vestibular nuclei or other centers.

The efferent system plays an important role of the inhibitory actions related to the vestibular mechanism.

XII. Vestibular Nuclei and the Autonomic Nervous System.

Various types of stimulation to the labyrinth produce vegetative reactions, such as paleness, nausea and vomit, or cold sweat, etc; but very little is known about the localization of the groups of neurons in the vestibular nerve system.

Direct connection of the fibers from the vestibular nuclei to the sympathetic nerve system was reported by Ban (1966), in rabbits. He divided these connection fibers to two groups; i. e., i) fibers originating the vestibular nuclei enter the ipsilateral dorsal longitudinal fasciculus, thenafter branching ascending and descending parts. ii) fibers originating the vestibular nuclei, passing through the MLF, trochlear and oculomotor nuclei and the central grey matter, and then connect to the dorsal longitudinal fasciculus.

In this point, the dorsal longitudinal fasciculus is one of the major fibers entering in the area of B-sympathetic system of SPH system.

General sympathetic nerve responses will be easily induced by the vestibular stimulations through these fiber connections in the brainstem as the "vestibulo-vegetative reactions".

The possible role played by the vestibular nuclei and their efferent projections in the transmission of cerebellar and reticular effects on the vegetative apparatus and motion sickness should be further investigated from the anatomical and physiological standpoint to the vestibular nuclei and their central or peripheral connections, too.

SUMMARY

The complex structures and complicated functions of the vestibular system are miraculously formed and are working with some harmonious integration beneath our consciousness (Fig. 26).

The description on this vestibular pathways and their central connections was made after reviewing the recent development in this field, as comprehensively as possible; but it was very hard to go through.

Even though a large number of anxious investigations and numerous papers are issued, there are still abundant gaps among the individual results and comments, and lacks of our knowledge on it.

Author concluded with the deepest wishes and hope for further advances and contributions in this fundamental problems of a life.

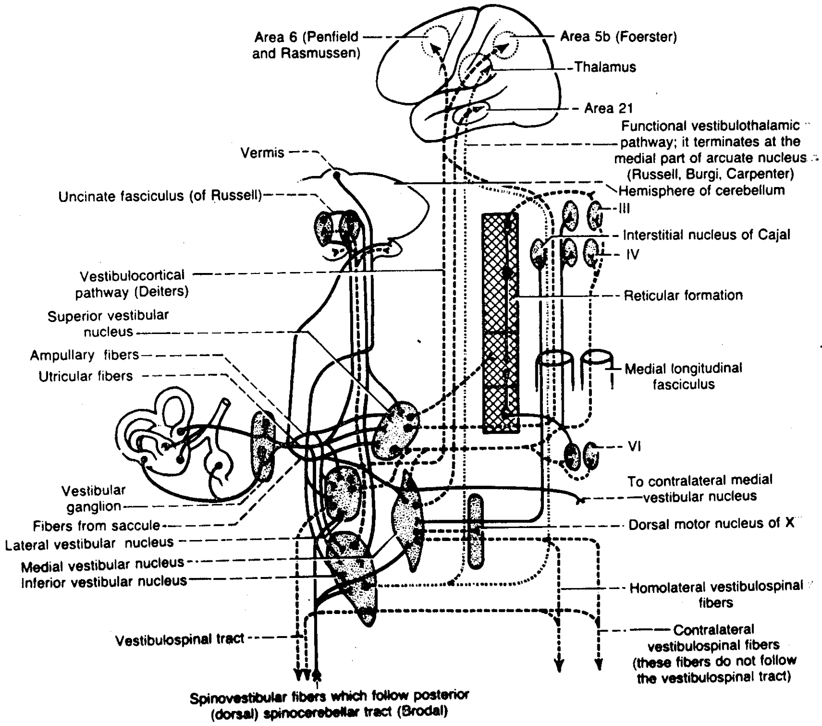

Fig. 26.

Vestibular pathways and Centers (Bossy. 1970)

Schematic representation of the nerve passways and centers relating to the vestibular system

ACKNOWLEDGEMENT:

Author has no word to express his grateful acknowledgement to Professor Shoichi Honjo for his constant interest and continuous encouragement to finish the framework of reviewing the latest confirmed knowledges in this developing field of neurotology.

REFERENCES

1) Anson, H. J. and Donaldson, J. A.: *Surgical Anatomy of the Temporal Bone and Ear* (2nd Ed), W. B. Saunders Co., Philadelphia, 1973.

2) Bast, T. H. and Anson, B. J.: The Temporal Bone and the Ear, Springfield, Ill., Charles C Thomas, 1949.
(Cited by Maloney (Ed): *Otolaryngology, Vol. I,* Chapter 3, Harper & Row, Publisher, New York, 1970.

3) Ban, T.: Interrelationship between the vestibular nuclei and SPH system. Reports on Researches by Grantees Ministry of Education—*Medicine (1)*—, p. 215, 1966.

4) Brodal, A. and Pompeiano, O. (Editors): Basic Aspects of Central Vestibular Mechanisms (*Progress in Brain Res.*, *Vol. 37*, Elsvier Publish. Co., Amsterdam/London/New York., 1972.
5) Brodal, A., Pompeiano, O. and Walberg, F.: *The Vestibular Nuclei and their Connections*, Anatomy and Functional Correlations, Oliver & Boyd, London, 1962.
6) Brodal, A.: Anatomical Observations on the Vestibular Nuclei with Special Reference to their Relations to the Spinal Cord and the Cerebellum. *Acta Oto-Laryng.*, *Suppl.* 192, 1962.
7) Brodal, A.: *Neurological Anatomy in relation to Clinical Medicine.* (2nd Ed) New York, Oxford University Press, 1969.
8) Bossy, Jean; *Atlas of Neuroanatomy and Special Sense Organs.* W. B. Saunders Co. Philadelphia, 1970.
9) Brodal, A. and Torvik, A.: *Arch. Psychiat. Z. ges. Neurolog.*, 195 : 550, 1957.
10) Engström, H., Bergström, B. and Rosenhall, U.: Vestibular Sensory Epithelia. *Arch. Otolaryng.*, 100 : 411–418, 1974.
11) Forester, O.: The Cerebral Cortex in Man, *The Lancet*, 2 : 309–312, 1931.
12) Fredrickson, J.: Afferent Integration in the Central Vestibular System. *Proc. Canada Oto. Soc.*, 20 : 15–46, 1966.
13) Fredrickson, J. M., Figg, U., Scheid, P. & Kornhuber, H. H.: Vestibular Nerve Projection to the Cerebral Cortex of the PheususMonkey. *Exp. Brain Res.*, 2 : 318–327, 1966.
14) Gacek, R. R.: Anatomical Demonstration of the Vestibuloocular Proje ctions iL the Cat. *Laryngoscope*, 81 : 1559–1595, 1971.
15) Gacek, R. R. and Lyon, M.: The Localization of Vestibular Efferent Neurons in the Kitten with Horseraddish Peroxydase. *Acta Oto-Laryng.*, 77 : 92–101, 1974.
16) Gillingham, K. K.: A Primer of Vestibular Function, Spatial Disorientation and Motion Sickness, Review 4–66, USAF School Of Aerospace Medicine, Brooks Air Force Base, Texas, 1966.
17) Goto, T et al (Ed): Sasaki, K.: *Oto-rhino-laryngology*, Vol. I, Igaku Shoin, Ltd. Tokyo, 1968.
18) Goto, T. et al (Ed), Watanabe, I.: *Oto-rhino-Laryngology*, Vol. I, Igaku Shoin, Ltd. Tokyo, 1968.
19) Haymaker (Ed): *Bing's Local Diagnosis in Neurological Diseases* (15th Ed) The C. V. Mosby Company, St. Louis, 1969.
20) Honjo, S.: Dizzines —*Examinations and Treatments*— Kanehara Shuppan, Tokyo, 1960.
21) Kornhuber, H. H.: translated by Sakata, E. et al,: *Neurotology —Physilologie* Physilologie und Klinik des zentral vestibularen Systems (Blick-und Stutzmoto rik). Ishiyaku Shuppan Co., Tokyo, 1973.
22) Krieg, W. J. S.: *Functional Neuroanatomy*, The Blakiston Co Inc., New York/Toronto., (2nd Ed.), 1953.
23) Maloney (Ed): *Otolaryngology*, Vol. 1, Chapter 3, Harper & Row, Publisher, New York, 1970.
24) McMasters, R. E., Weiss, A. H. and Carpenter, M. B.: Vestibular Projections to the Nuclei of the Extraocular Muscles, *Am. J. Anat.*, 118 : 163–194, 1966.
25) Meesen, H.and Olszewski, J.: *A Cytoarchitectonic Atlas of Rhomboencephalon of the Rabbit*, Karger,Basel., 1949.
26) Mori, Hirazawa, Ogawa, and Mori,: *Anatomy*, Vol. II (Vascular and Nervous System), Nihon Isho Co., Tokyo, 1953.
27) Penfield, W. and Rasmussen, T.: *The Cerebral Cortex of Man*, New York, The Macmillan Co., 1950.
28) Sano, Y.: *Neuroanatomy*, Nanzando, Tokyo, 1974.
29) Stein, B. M. and Carpenter, M. B.: Central Projection of Portions of the Vestibular Ganglio innervating Specific Parts of the Labyrinth in the Rheusus monkey. *Amer. J. Anat.*, 120 :

281-318, 1967.
30) Uemura, T. Suzuki, J-I, and Hozawa, J.: *Neurotological Examination,* with Special reference to Vestibular Function Tests, Igaku Shoin, Ltd., Tokyo, 1968.
31) Warnick, R.: Representation of the Extraocular Muscles in the Oculomotor Nuclei of the Monkey, *J. Comp. Meur.*, 98 : 449-504, 1953.
32) Wersäll, J.: Studies on the Structure and Innervation of the Sensory Epithelium of the Cristae ampullaris in the Guinea Pig, *Acta Oto-Laryng., Suppl.* 126 : 1-85, 1956.