

The Vestibular Apparatus

While discussing physiology of hearing, we deliberately ignored a part of the inner ear which is not concerned with hearing. Now the time has come to discuss that part, known as the vestibular apparatus. Vestibule is a hall between the outer door and the interior of a building, for example the lobby of a hotel. The vestibular apparatus is so called because it may be considered an entrance to the cochlea. However, in terms of function it is more than a passage hall. It is a sensory organ in its own right. It detects position and motion of head. Since the head generally moves with the rest of the body, we might say that it informs us about the position and movement of the body. It is stimulated by acceleration—both linear and angular. When stimulated, the vestibular apparatus initiates postural and ocular reflexes. The postural reflexes help maintenance of equilibrium while the ocular reflexes help in achieving reasonable stability of visual images in spite of the body being in motion. We are not much conscious of vestibular sense, but its importance becomes obvious when it is not in good order. Disorders of the vestibular system often lead to dizziness, nausea and impaired ability to maintain postural balance.

FUNCTIONAL ANATOMY

As in case of the auditory apparatus, the vestibular apparatus also consists of a membranous labyrinth which is enclosed in a bony labyrinth. The membranous labyrinth contains endolymph, the composition of which resembles that of the intracellular fluid in that it has a high concentration of potassium. The space between the membranous labyrinth and the bony labyrinth contains perilymph, which resembles any other extracellular fluid in its composition.

The vestibular apparatus consists of the *otolith organs* and three *semicircular canals* or ducts (Fig. 13.11.1). ‘Otolith organs’ is the name given to two sac-like structures, one called the *sacculus*, and the other the *utricle*. The sacculus communicates with the cochlea via the ductus reuniens. The three semicircular canals are arranged in the three different mutually perpendicular planes. The canals are named, respectively, the horizontal, anterior and posterior canals. If the head is tilted down by 30°, the horizontal canals lie exactly in the horizontal plane. The anterior canals lie in a plane that points anteriorly at about 45° from the sagittal plane. The posterior canals lie in a plane

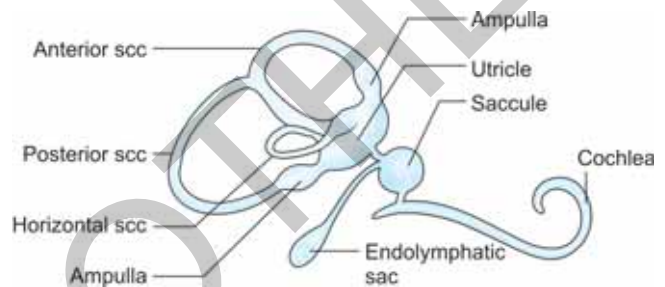


Fig. 13.11.1: A schematic diagram of the vestibular apparatus and cochlea. Only the membranous labyrinth has been shown. scc, semicircular canal.

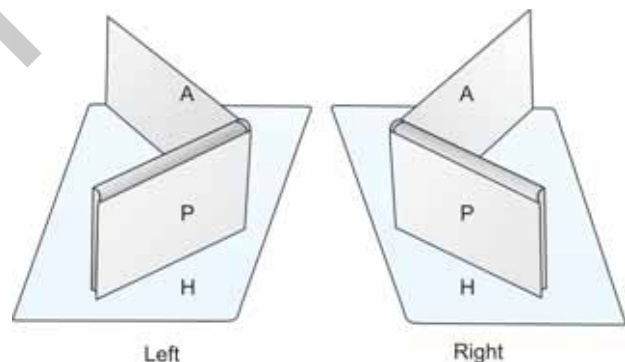


Fig. 13.11.2: Orientation of the semicircular canals as visualized from above the head. H, horizontal; A, anterior; P, posterior semicircular canal. Note that A on the left side is in the same plane as P on the right side, and vice versa. The horizontal canal is exactly horizontal only when the head is bent forwards about 30°.

that points posteriorly at about 45° from the sagittal plane. Thus the right anterior semicircular canal lies in the same plane as the left posterior canal. And, the right posterior canal lies in the same plane as the left anterior canal. To understand it more clearly, place a closed book parallel to the floor, and imagine it passing through both ears. The book lies roughly in the plane of the horizontal canals. Then place two partially open books on it as shown in Figure 13.11.2. The covers of these books lie in the planes of the anterior and posterior canals.

The epithelium of the membranous labyrinth is specialized at a few places to form sensory cells, known as the *hair cells*. Hair cells of the sacculus and utricle are located on a thickened

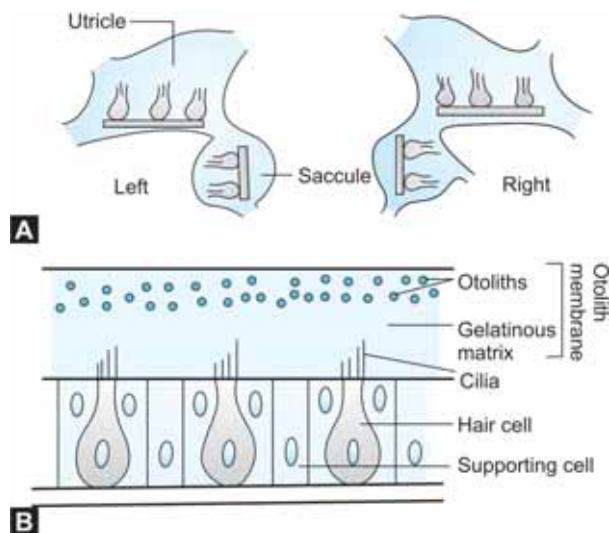


Fig. 13.11.3: The otolith organs. A. The sensory cells in the otolith organs are located on maculae, and their orientation has been diagrammatically shown. B. Schematic diagram of microscopic structure of the macula.

portion of their walls, known as the *macula* (Fig. 13.11.3). The macula is covered with a gelatinous mass containing crystals of calcium carbonate, known as *otoliths*. The cilia of the hair cells project into the gelatinous mass. Hair cells of otolith organs are stimulated by linear acceleration and change in position of the head with respect to gravity. The macula of the saccule is oriented vertically. Therefore its hair cells respond to vertically directed linear acceleration, e.g. the type of acceleration experienced while travelling in a lift (in USA, an elevator). The macula of the utricle is oriented horizontally. Therefore its hair cells respond to tilting of the head or horizontally directed linear acceleration, e.g. the type of acceleration experienced while travelling in a car.

Hair cells of the semicircular canals are located in a dilated end of each canal, known as an *ampulla*. Thus, the three canals have three ampullae. The ampullae open into the utricle. Each ampulla has a semi-elastic pendular hillock (i.e. 'a small hill') called *crista*, on which are lodged the hair cell (Fig. 13.11.4). The cilia of the hair cells, in the ampullae are also embedded in a gelatinous mass known as *cupula*. The cupula is like an inverted cup, and forms a water—tight seal between the canal and the utricle. However, the cupula *does not* contain any otoliths. The disposition of the canals ensures that angular acceleration in any plane will stimulate at least one pair of ampullae.

The hair cells of the vestibular apparatus are furnished with large number of stereocilia of graded length, and a kinocilium which is next to the longest stereocilium (Fig. 13.11.5). The stereocilia and kinocilia of the vestibular sensory cells are arranged in a very orderly fashion. The geometrical arrangement is important because the cells are directionally sensitive; bending of cilia towards the kinocilium leads to excitation, and bending away from the kinocilium leads to inhibition. Change in the activity of hair cells is conveyed to the central nervous system by afferent fibres which are a part of the eighth cranial nerve. In turn, the activity of hair cells is also influenced by efferent nerve fibres which originate in the ipsilateral lateral

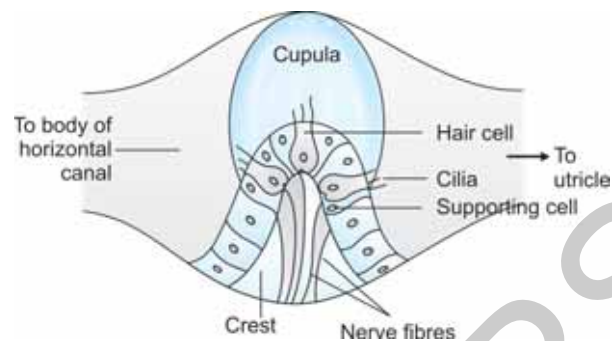


Fig. 13.11.4: Schematic diagram of the interior of the ampulla of the horizontal canal. There is no essential difference between the ampulla of the horizontal canal and those of the vertical canals except for the orientation of the kinocilia of hair cells. In the horizontal canals the kinocilia are towards the utricular opening while in the vertical canals the kinocilia are towards the other opening of the semicircular canal.

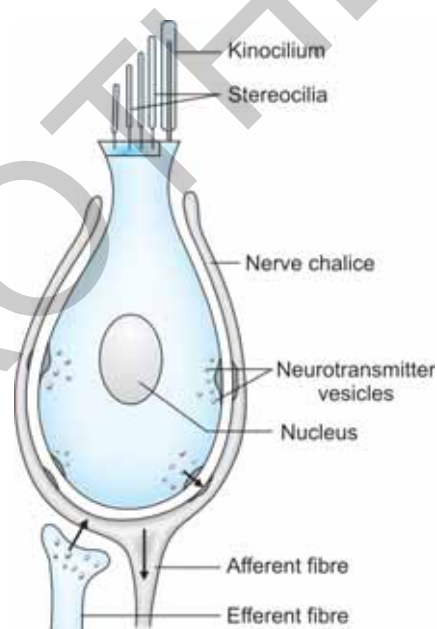


Fig. 13.11.5: Diagrammatic representation of a hair cell. The neurotransmitter involved in transfer of information from hair cells to afferent fibres is possibly either glutamate or aspartate.

vestibular nucleus and in the reticular formation near the sixth cranial nerve.

Connections

The cell bodies of afferent fibres innervating the vestibular sensory cells are located in the vestibular ganglion (Scarpa's ganglion). These cells are bipolar cells. Their central axons travel in the vestibular division of the vestibulocochlear nerve (VIIIth cranial nerve). The VIIIth cranial nerve enters the brain at the level of the pons. The central axons of vestibular afferent fibres project to the vestibular nuclei (Fig. 13.11.6). The vestibular nuclear complex has four divisions. The *lateral vestibular nucleus* receives afferent fibres from the utricle. In addition, it also receives inputs from the cerebellum and spinal cord. Efferent fibres arising from the lateral vestibular nucleus exert a facilitatory influence on alpha and gamma motor neurons supplying antigravity muscles of limbs. The *medial and*

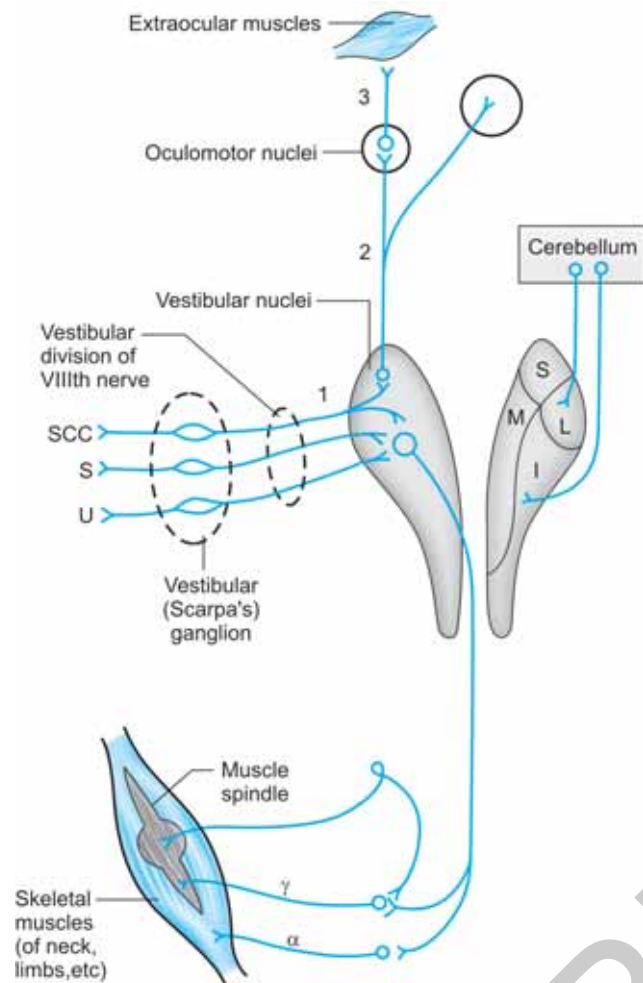


Fig. 13.11.6: A simplified diagram of major vestibular pathways. SCC, semicircular canals; S, saccule; U, utricle. 1, 2 and 3, the three neurons involved in vestibulo-ocular reflex.

superior vestibular nucleus receives afferent fibres from the saccule and utricle, as well as the semicircular canals. In addition, it also receives inputs from the cerebellum. Some vestibular afferents also project, directly to the flocculonodular lobe of the cerebellum.

To summarize, changes in position or movement of the head, which are detected by the vestibular apparatus, are conveyed to (a) the cerebellum, so that the cerebellum can use this information for better coordination of postural muscles, (b) the oculomotor muscles, so that eye movements can be coordinated with bodily movement, and (c) motor neurons of head, neck and other postural muscles, so that postural stability may be achieved during bodily movement.

PHYSIOLOGY OF VESTIBULAR RECEPTORS

Receptor function in the vestibular apparatus is performed by the hair cells. Hair cells are slowly-adapting mechanoreceptors with a very high degree of directional sensitivity. Their activity is altered by the bending of their hair, or cilia. If the cilia bend towards the kinocilium, there is a depolarizing receptor potential, and the frequency of discharge in the afferent nerves increases. Bending of cilia away from the kinocilium leads to changes in the opposite direction (Fig. 13.11.7). The next question which naturally comes to our mind is: how does movement or acceleration of the head bend cilia of sensory cells in the vestibular apparatus? The mechanism is somewhat different for the otolith organs and the semicircular canals.

Otolith Organs

The cilia of hair cells of the otolith organs are embedded in a gelatinous mass (otolith membrane) containing crystals of calcium carbonate. Therefore the specific gravity of the otolith

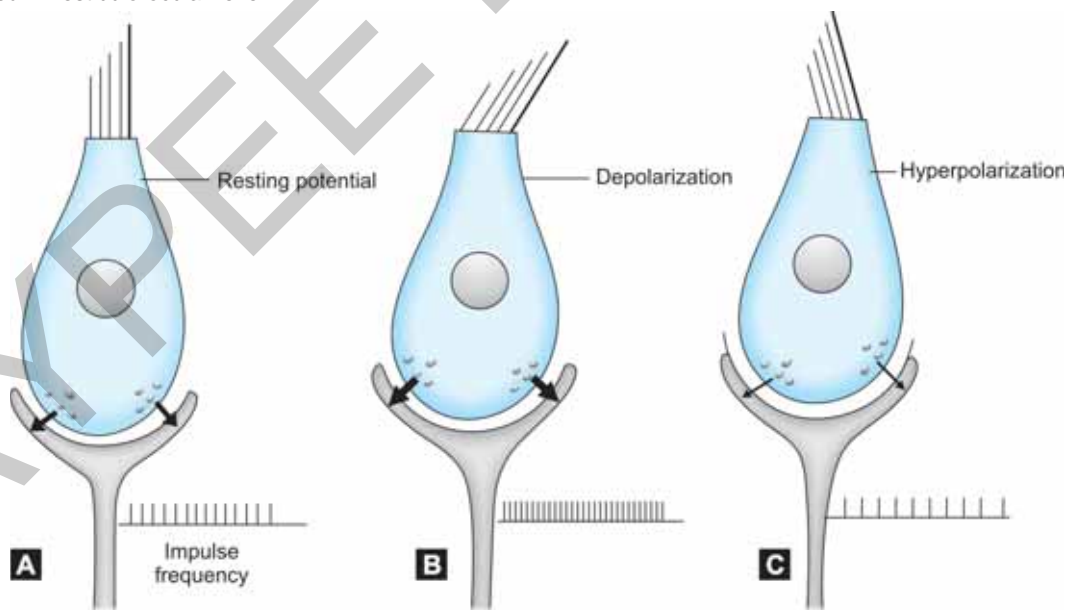


Fig. 13.11.7: Directional sensitivity of vestibular hair cells. A. Resting cell. The receptor potential as well as afferent nerve fibre impulse frequency show a resting value. B. Bending of cilia towards the kinocilium leads to a depolarization type of receptor potential, and hence an increase in the quantity of neurotransmitter released at the synapse between the hair cell and afferent nerve fibre. Consequently, there is an increase in the afferent nerve fibre impulse frequency. C. Bending of cilia away from the kinocilium leads to a hyperpolarization type of receptor potential, and hence a decrease in the release of neurotransmitter by the receptor cell. Consequently, there is a decrease in the nerve fibre impulse frequency.

membrane is greater than that of the endolymph. Therefore a change in the direction of the gravitational pull exerted on the otolith membrane bends the cilia of hair cells.

Detecting a Change in Position of the Head

The macula of the utricle is horizontal when the body is erect and the head is held normally. Therefore any tilt in the head from this position alters the direction of the gravitational pull exerted on its otolith membrane (Fig. 13.11.8). The macula of the saccule is in the sagittal plane. Therefore its hair cells may be affected more when the position of the head is changed while a person is lying down.

In both the utricle and the saccule, the kinocilia of the hair cells are oriented in relation to a curved ridge, called the striola. Therefore they do not all point in any single direction. Therefore a head tilt bends the cilia of some of them towards the kinocilium, and of the others away from the kinocilium. Therefore any movement of the head excites some hair cells and inhibits others to varying degrees. Therefore the information conveyed to the central nervous system is in terms of a change in the pattern of excitation rather than simple excitation or inhibition.

Detecting Linear Acceleration

The saccule and utricle can detect also linear acceleration of the head because the higher specific gravity of the otolith membrane imparts to it greater inertia than the surrounding fluids. Therefore when the head accelerates, the otolith membrane lags behind the surrounding endolymph. That creates a shearing stress which bends the cilia embedded in the otolith membrane.

Semicircular Canals

In order to understand the function of the semicircular canals, it will be useful to note that:

- the canals are filled with endolymph
- the hair cells are located in dilatations, called ampullae, at the ends of the canals,
- the cilia of the hair cells are embedded in a gelatinous mass, the cupula, the specific gravity of which is the same as that of the endolymph, and
- the cupula forms a water-tight seal between the semicircular canal and the utricle.

Let us consider what happens in the horizontal canals when the head is rotated to the right in the horizontal plane. Imagine as if you are looking at the canals from above the head (Fig. 13.11.9). When the head rotates to the right, the canals (which are a part of the head) naturally turn to the right. But the endolymph in the canals, due to inertia, does not move immediately, and then moves slower than the head. It is only after 20–30s that the endolymph also moves at the same speed as the head. Let us concentrate on the initial phase when the movement of the endolymph lags behind. This phenomenon is equivalent to the endolymph moving in a direction opposite to that in which the canal moves. Thus *when the head rotates to the right, initially the endolymph effectively rotates to the left.*

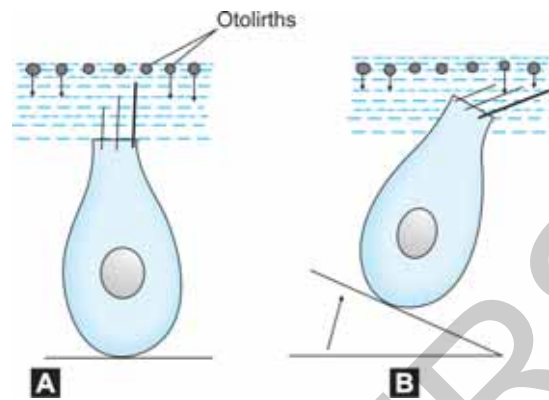


Fig. 13.11.8: Stimulation of hair cells in otolith organs. A. Resting position. B. Head tilted to the right. Because of the presence of otoliths, the force of gravity bends the cilia of hair cells considerably more than the tilt in the hair cell itself. As a result, the hair cell activity changes. In the figure, the hair have been shown to bend towards the kinocilium. Hence the hair cell activity would increase.

Since the cupula has the same specific gravity as the endolymph, it moves along with the endolymph. Since the cupula forms a water tight seal, its movement bends the cilia of the hair cells. As a matter of detail, it might be added that *in the horizontal canals*, the kinocilia are located towards the utricle. Therefore, if the cupula bends towards the utricle, the cilia bend towards the kinocilia, and therefore the hair cells are stimulated. By the same token, if the cupula bends away from the utricle, the hair cells are inhibited. In the *anterior and posterior canals*, the kinocilia are located away from the utricle. Therefore, in these canals, bending of the cupula away from the utricle leads to stimulation of the hair cells. The above discussion shows that when the head rotates, *in the beginning* there is a change in the stimulation pattern of the hair cells of semi-circular canals. We have learnt to interpret this change as rotation of the head in the direction in which the head actually rotates. After about 30s of rotation, however, the head, the canals, and the endolymph all rotate in the same direction at the same speed. The cupula returns to its elastic position by virtue of its elasting recoil. The hair cell activity also returns to its resting level, and we are no longer conscious of rotation, at least on the basis of information from the semicircular canals.¹

Now let us consider what happens when the head *stops* rotating. The head, and naturally also the semicircular canals, stop rotating together. But due to inertia, the endolymph continues to rotate for some time in the same direction in which the head was rotating. For example in the case which we have considered, *if the head was rotating to the right, after stopping the rotation, initially the endolymph continues to rotate to the right.* Therefore the bending of the cupula and change in the pattern of stimulation of hair cells is opposite to that which takes place when the rotation was begun. Therefore we interpret this change as rotation of the head in a direction which is opposite to that in which the head was actually rotating. Within about 30s, however, the endolymph comes to rest, the cupula returns to its resting position, and the hair cell activity also

¹ We may still be conscious of rotation on the basis of visual information.

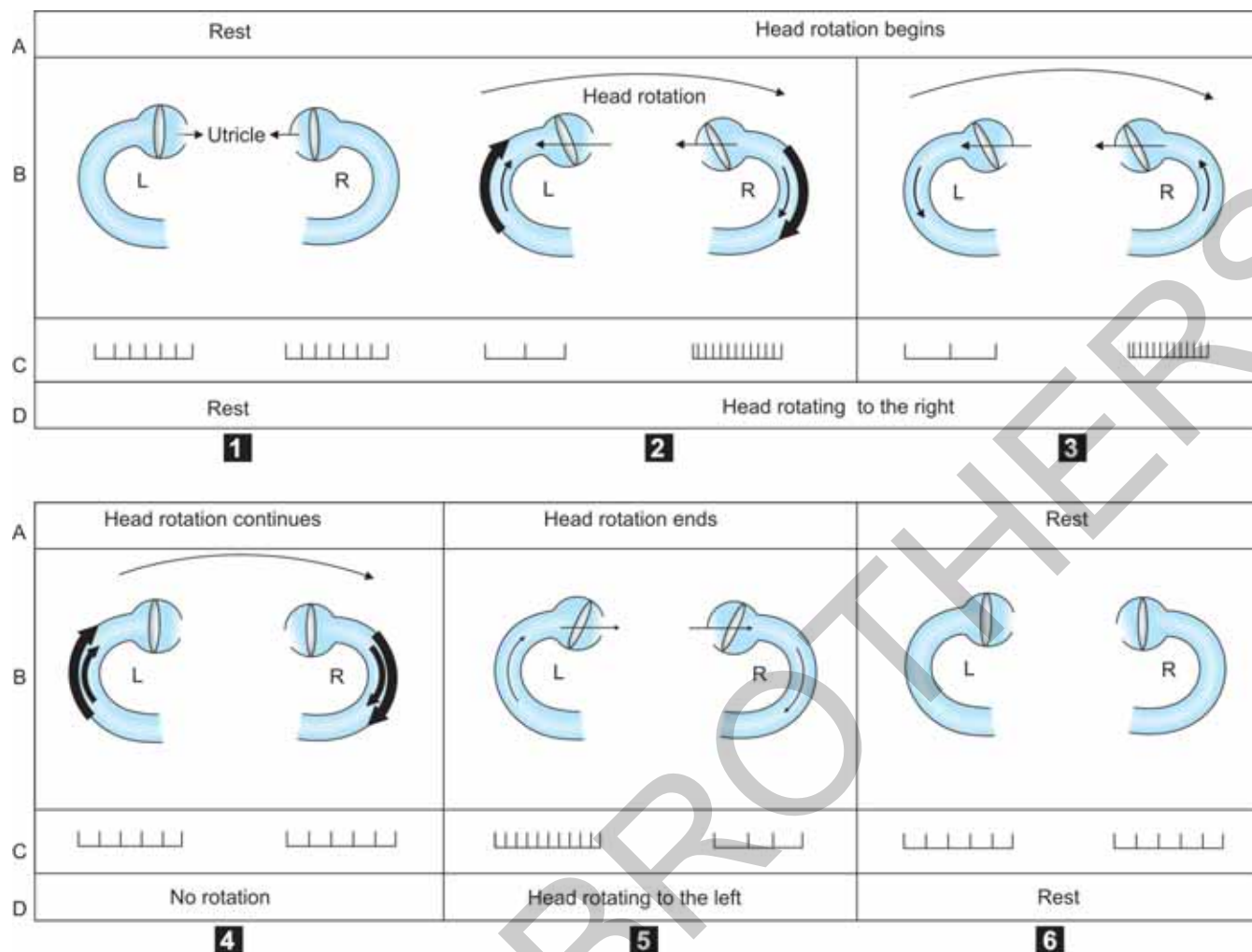


Fig. 13.11.9: Mechanism of action of semicircular canals. The example chosen for illustration is that of the horizontal canals when the head rotates to the right in the horizontal plane. A. Actual state of rest or motion of the head; B. Schematic representation of events in the semicircular canals; C. Frequency of nerve impulses in afferent nerve fibres; D. Conscious interpretation of the neural message.

(1) Rest. L, left; R, right. (2) Head rotation to the right just begins. The walls of the canal move at the same rate as the head but the endolymph moves slowly due to inertia. The difference in velocity has been shown by arrows. (3) The situation in 2 is equivalent to what has been shown in 3. Since the endolymph moves slowly, it is equivalent to its moving in the opposite direction, i.e. to the left. If this concept of relative motion is grasped, it becomes easy to understand the direction in which the cupulae bend. Cilia of the hair cells bend in the same direction as the cupulae. Thus the cilia in the right ampulla bend towards the utricle. In the horizontal canals, the kinocilia are towards the utricle. Therefore in the right ampulla, the cilia bend towards the kinocilium. Hence the firing frequency in the afferent nerve increases on the right side. (4) If the head rotation continues beyond about 30 s, the endolymph also starts rotating at the same speed as the head. This is equivalent to no motion. Therefore the cupula returns to the resting level, and so does the afferent nerve fibre activity. Therefore the brain interprets the neural message to mean that there is no rotation of the head going on. (5) When the rotation of the head just stops, the endolymph continues to move for some time due to inertia. Since the movement of endolymph is in a direction opposite to that in 3, the neural message is also reversed. Therefore the brain interprets the message to mean that the head is rotating to the left. (6) Finally, the endolymph also stops moving and the resting state is restored.

returns to the resting level. Correspondingly, we no longer feel that the head is moving.²

Although we have considered only the events in the horizontal canals, the basic mechanism underlying the function of the anterior and posterior semicircular canals is the same. The net result of having three pairs of canals is that no matter in which direction the head rotates, there is some change in the pattern of discharge from some hair cells in some canals, and the body is able to respond appropriately.

VESTIBULAR REFLEXES

The information collected by vestibular apparatus leads mainly to reflex adjustments in posture and eye movements. Both these functions are also affected by information from other sensory structures. In the intact organism the regulation of posture and of the eye movements are the integrated result of contributions made by various reflexes, only some of which originate in the vestibule. But it is possible to show through experiments that

²The semicircular canals thus detect only the beginning and end of rotation of the head. Therefore it is more appropriate to say that the canals detect angular acceleration.

vestibular apparatus makes a specific, considerable and sometimes very significant contribution to these functions.

Postural Reflexes

Vestibular postural reflexes contribute to stability when the position of the head is changed or the body suddenly experiences acceleration—positive or negative, linear or angular.

Tonic Labyrinthine Reflexes

If a decerebrate animal is placed supine, it displays maximal tone in antigravity (extensor) muscles of its limbs. On the other hand, if it is placed prone with the snout about 45° below the horizontal plane, the tone in extensor muscles decreases to a very low level.

If the head of a decerebrate animal is dorsiflexed (i.e. bent backwards), it shows extension of all the four limbs. To visualize the possible utility of this reflex imagine an animal who has seen food somewhere high up. It looks up (by dorsiflexing the head), and extends the limbs to jump at the food.

Afferents for the tonic labyrinthine reflexes originate in the otolith organs. The information is processed in vestibular and reticular nuclei. The efferents travel in the vestibulospinal and reticulospinal tracts to the motor neurons in the spinal cord.

Labyrinthine Righting Reflex

In a decorticate animal, if the head is held in the lateral position, the animal tends to assume the upright posture. The pressure receptors (which are stimulated more on the side which is in contact with the floor) and visual information also contribute to the righting reflex. But if the animal is pressed with a board on the side which is not in contact with the floor (so that pressure receptors are stimulated equally on both sides) and the animal is blindfolded (so that there is no visual information), the animal is still able to right itself due to the labyrinthine righting reflex.³

Visual Reflex

The visual reflex of vestibular origin is called the *vestibulo-ocular reflex* (VOR). VOR enables the eyes to fixate on the same object when there is a rotation of the head.⁴ If the head rotates to the left, eyes move an appropriate distance at the same rate to the right so that the retinal image remains constant. However, if the rotation exceeds 60°, rapid movement of the eyes in the same direction as the rotation of the head takes place. This rapid movement (saccadic movement) leads to fixation on a new object. Thus VOR also, like the optokinetic reflex (OKR), gives rise to nystagmus, i.e. a slow movement of the eyeballs alternating with a rapid movement in the opposite direction. However, only the slow component is attributable to

information originating in the vestibular apparatus. The rapid component depends on visual information and is integrated in visual centres such as the superior colliculi and prepontine reticular formation.⁵

The pathway for VOR is extremely short, involving only three sets of neurons, and accounts for its short latency (about 12 ms). The first order neurons are vestibular afferents which terminate in the vestibular nuclei. The second order neurons project from vestibular nuclei to oculomotor nuclei. The third order neurons project from oculomotor nuclei to extraocular muscles. (Fig. 13.11.6).

APPLIED VESTIBULAR PHYSIOLOGY

We shall now discuss one disorder which is believed to be due to vestibular malfunction, and a few tests for assessment of vestibular function.

Motion Sickness

Motion sickness occurs in susceptible individuals when travelling in a fast moving vehicle. It is more likely to occur when travelling in a ship. It is associated with palpitation, sweating, dizziness and vomiting. It is believed to be due to strong stimulation of the vestibular apparatus. Discrepancy between information conveyed to the central nervous system by the vestibular apparatus and that conveyed by the eyes is likely to contribute much to motion sickness. That is why closing the eyes might help in reducing the symptoms of motion sickness.

Postrotatory Nystagmus

Vestibular nystagmus may be tested by having the patient sit in a chair which can rotate. If the subject is seated with the head bent about 30° forwards the horizontal semicircular canals are exactly horizontal and can be stimulated most effectively by rotation around a vertical axis. With the subject thus seated, the chair may be revolved at the rate of one revolution per two seconds for 10 revolutions, and then suddenly stopped. If vestibular function is normal, nystagmus will be observed for 20-30 s. If the chair is rotated to the right, in which direction will the postrotatory nystagmus be? Work out the answer yourself before turning to Figure 13.11.10.

By altering the posture of the patient in the chair appropriately, the vertical semicircular canals may be stimulated.

In the postrotatory nystagmus test, the observations may be complicated by the simultaneous operation of visual reflexes (e.g. the optokinetic reflex). This may be avoided by giving the patient glasses having very strong convex lenses to wear. Some of these glasses are also fitted with an inbuilt source of

³Although the tonic labyrinthine reflexes are best studied in a decerebrate animal and the labyrinthine righting reflex in a decorticate animal, these reflexes operate also in intact animals (and humans!). The simplified preparations used in experiments only show the reflexes more clearly because in the intact animal the reflexes are masked and complicated by voluntary motor activity.

⁴Be careful to distinguish VOR from the optico-kinetic reflex (OKR). OKR enables the eyes to fixate on the same object when there is a movement of the scenery to which eyes are exposed, as when travelling in a train. VOR has a very short latency (only about 12 ms) whereas OKR has a latency of about 80 ms.

⁵The convention regarding naming the nystagmus is controversial. According to Hutchison's Clinical Methods, a standard British book which is widely used in India, nystagmus is named according to the direction of the quick component. That is, if the head rotates to the left, the quick component of the nystagmus is to the left, and the nystagmus is called "left nystagmus".

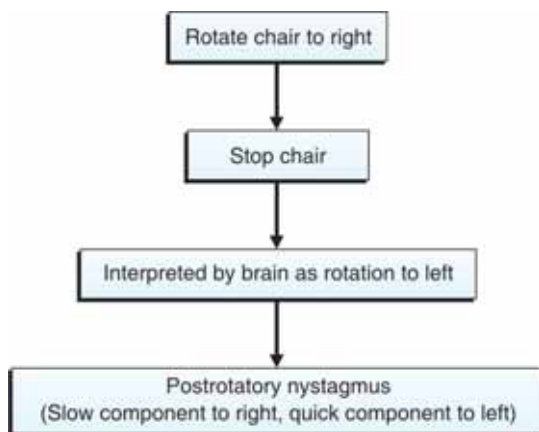


Fig. 13.11.10: Direction of postrotatory nystagmus. When the chair stops, why the brain interprets it as rotation in the opposite direction has been explained in Fig. 13.11.9

light. Such glasses prevent visual reflexes (because the patient cannot see anything clearly) and also facilitate examination for nystagmus (How?).

Caloric Nystagmus

This test is based on stimulating the semicircular canals using an unnatural stimulus, i.e. cold or warm water in the ear. The test is based on Barany's theory that when the endolymph gets warm, its specific gravity falls, and as a result convection currents are set up which produce movement of endolymph comparable to that which occurs during angular acceleration. However, Barany's theory is doubtful because the test works also in conditions of weightlessness, where specific gravity of endolymph should not matter. Therefore the test may be working because change of temperature is perhaps an unnatural but suitable stimulus for hair cells of semicircular canals. Be that as it may, to perform the test, the patient may be seated or may lie down supine. If the patient is seated, the head is tilted backward by 60° ; if lying down supine, the head is raised by 30° . Either manoeuvre makes the horizontal semicircular canal vertical. Then the external auditory meatus is syringed gently with either cold or warm water. The procedure leads to nystagmus if

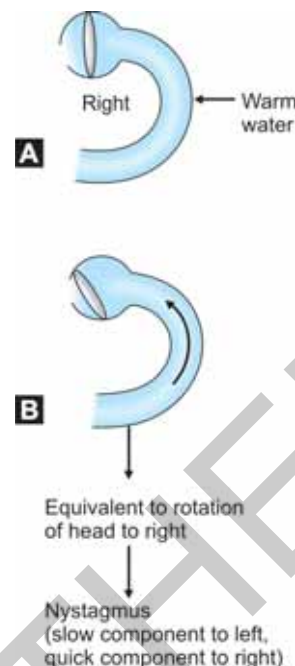


Fig. 13.11.11: Caloric nystagmus. Rinsing the right ear with warm water (A) makes the endolymph in the right horizontal canal, which is oriented vertically during the test, rise (B). The situation in B is comparable to that in the right horizontal canal in Fig. 13.11.9(3). Therefore the neural message corresponds to the rotation of the head to the right. That explains the direction of the nystagmus.

semicircular canal function is normal. The direction of nystagmus when warm water is introduced into the right ear has been worked out in Figure 13.11.11.

CONCLUSION

Vestibular sense is not considered a special sense. It does not even normally figure prominently in our consciousness. But it has been considered in this section because its receptors are extremely close to the receptors for hearing. In any case, there is no radical difference in the physiology of senses which are considered special and those which are not.