THE EAR: EQUILIBRIUM

Equilibrium is a state of balance, whether the word is used to describe ion concentrations in body fluids or the position of the body in space. In body positioning, sensory information from the inner ear and from joint and muscle proprioceptors tells our brain the location of different body parts in relation to one another and to the environment. Visual information also plays an important role in equilibrium, as you know if you have ever gone to one of the 360° movie theaters where the scene tilts suddenly to one side and the audience tilts with it!

Our sense of equilibrium is mediated by hair cells lining the fluid-filled vestibular apparatus and semicircular canals of the inner ear. These non-neural receptors respond to changes in rotational, vertical, and horizontal acceleration. The hair cells function just like those of the cochlea, but gravity and acceleration rather than sound waves provide the force that moves the stereocilia.

The Vestibular Apparatus Is Filled with Endolymph

The **vestibular apparatus** consists of two saclike **otolith organs**—the **utricle** and the **saccule**—along with three **semicircular canals** (Fig. 10-23a ■). The semicircular canals connect to the utricle at their bases. They are oriented at right angles to one another, like three planes that come together to form the corner of a box (Fig. 10-23b).

At one end of each canal is an enlarged chamber, the **ampulla** [bottle], which contains a sensory receptor known as a **crista** [a crest; plural *cristae*]. The crista consists of a gelatinous mass, the **cupula** [small tub], that stretches from floor to ceiling of the ampulla, closing it off (Fig. 10-23c). Embedded in the cupula are the cilia of hair cells. The basal membranes of the hair cells synapse on the sensory neurons of the **vestibular nerve** (a branch of the VIII cranial nerve).

The sensory receptors of the utricle and saccule, the **maculae**, are different from those of the cristae (Fig. 10-23d). Each macula consists of a gelatinous mass known as the **otolith membrane** on which mineral and protein particles called **otoliths** are embedded [*oto*, ear + *lithos*, stone]. Otoliths form when calcium carbonate crystals precipitate and bind to matrix proteins. Underneath the otolith membrane are hair cells whose cilia are embedded in the membrane.

The vestibular apparatus, like the cochlear duct, is filled with endolymph secreted by epithelial cells. Like cerebrospinal fluid, endolymph is secreted continuously and drains from the inner ear into the venous sinus in the dura mater of the brain. If endolymph production exceeds the drainage rate, buildup of fluid in the inner ear may cause *Ménière's disease*. This condition is marked by episodes of dizziness and nausea, apparently as a result of changes in fluid pressure within the vestibular apparatus. It may also cause hearing loss if the organ of Corti in the cochlear duct is damaged.

The Vestibular Apparatus Provides Information About Movement and Position in Space

The special sense of equilibrium has two components: a dynamic component that tells us about our movement through space, and a static component that tells us if our head is displaced from its normal upright position. The three semicircular canals sense *rotational acceleration* in various directions. The otolith organs tell us about *linear acceleration* and head position.

Hair cells in both the semicircular canals and the otolith organs function just like the hair cells of the organ of Corti. When the cilia bend in one direction, they depolarize, and when they bend in the opposite direction, they hyperpolarize (see Fig. 10-21). Vestibular hair cells, like cochlear hair cells, have one kinocilium located at one side of the ciliary bundle. The kinocilium creates a reference point for the direction of bending.

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The Semicircular Canals Sense Rotational Acceleration

How is rotation sensed? As the head turns, the bony skull and the membranous walls of the labyrinth move, but the fluid within the labyrinth cannot keep up because of inertia. In the ampullae of the vestibular apparatus, the drag of endolymph bends the cupula and its hair cells in the direction opposite to the direction in which the head is turning.

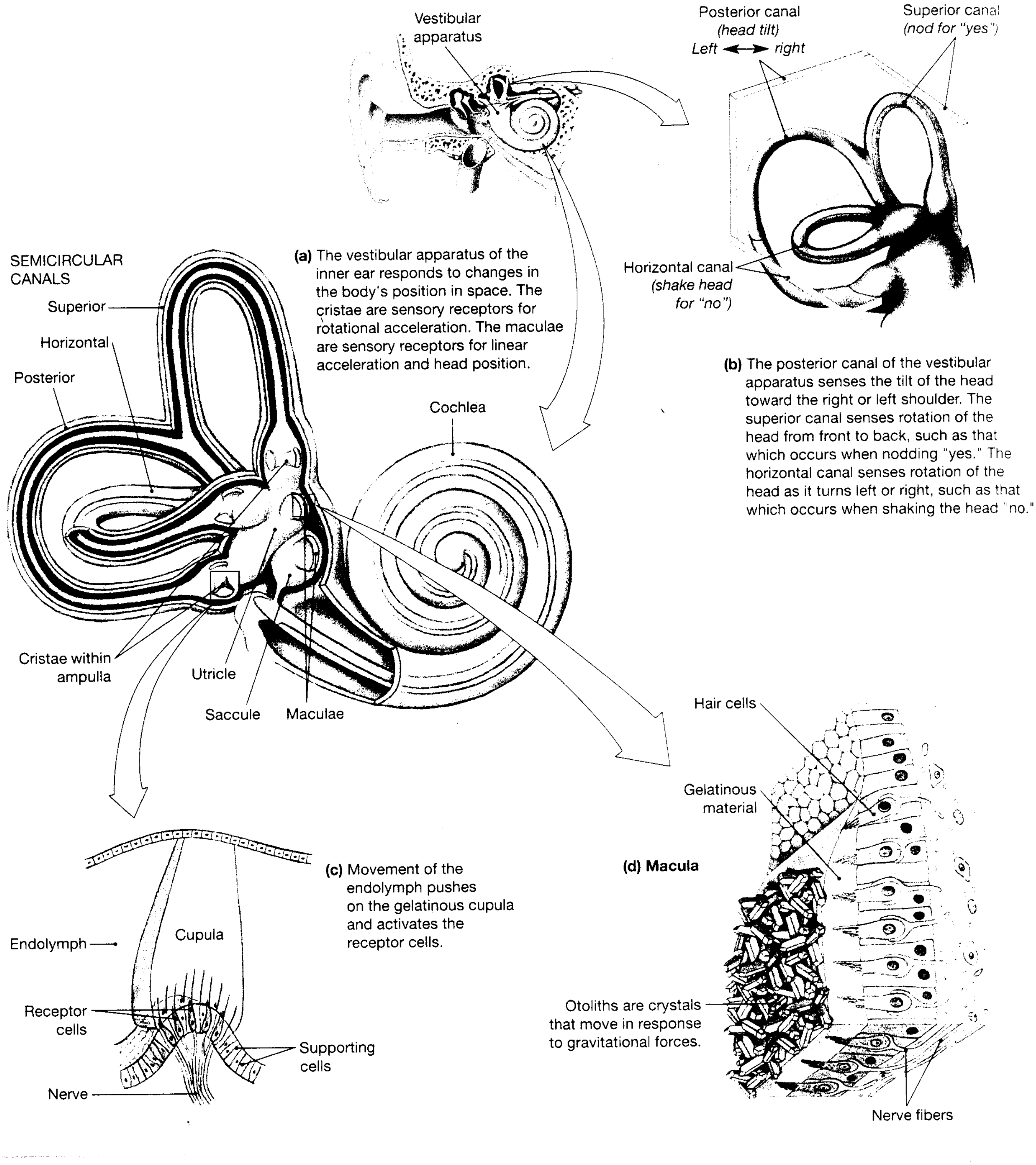
For an analogy, think of pulling a paintbrush (a cupula attached to the wall of a semicircular canal) through sticky wet paint (the endolymph) on a board. If you pull the brush to the right, the drag of the paint on the bristles bends them to the left (Fig. 10-24 ■). In the same way, the inertia of the fluid in the semicircular canal pulls the cupula and the cilia of the hair cells to the left when the head turns right.

If rotation continues, the moving endolymph finally catches up. Then if head rotation stops suddenly, the fluid has built up momentum and cannot stop immediately. The fluid continues to rotate in the direction of the head rotation, leaving the person with a turning sensation. If the sensation is strong enough, the person may throw his or her body in the direction opposite the direction of rotation in a reflexive attempt to compensate for the apparent loss of equilibrium.

The Otolith Organs Sense Linear Acceleration and Head Position

The otolith organs of the utricle and saccule are arranged to sense linear forces. The maculae of the utricle are horizontal when the head is in its normal upright position. If the head tips back, gravity

ANATOMY SUMMARY
THE VESTIBULAR APPARATUS



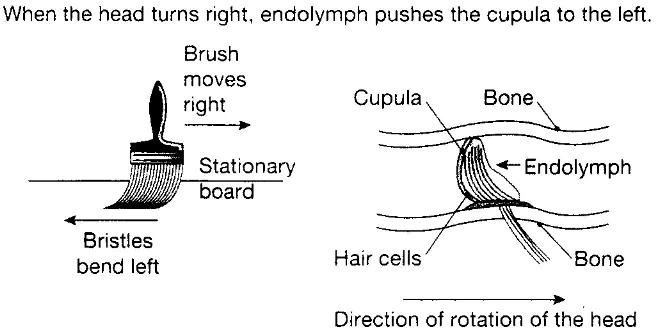
(a) The vestibular apparatus of the inner ear responds to changes in the body's position in space. The cristae are sensory receptors for rotational acceleration. The maculae are sensory receptors for linear acceleration and head position.

(b) The posterior canal of the vestibular apparatus senses the tilt of the head toward the right or left shoulder. The superior canal senses rotation of the head from front to back, such as that which occurs when nodding "yes." The horizontal canal senses rotation of the head as it turns left or right, such as that which occurs when shaking the head "no."

(c) Movement of the endolymph pushes on the gelatinous cupula and activates the receptor cells.

(d) Macula

■ **FIGURE 10-23**



■ **FIGURE 10-24** ***Rotational forces in the cristae***

When the head turns, inertia keeps endolymph inside the ampulla from moving as rapidly as the surrounding cranium.

causes the otoliths in the gelatinous otolith membrane to slide backward (Fig. 10-25 ■). The cilia of the hair cells bend and set off a signal.

The maculae of the saccule are oriented vertically when the head is erect and are sensitive to vertical forces, such as dropping downward in an elevator. The brain analyzes the pattern of depolarized and hyperpolarized hair cells in order to compute head position and direction of movement.

RUNNING PROBLEM

Although many vestibular disorders can cause the symptoms Anant is experiencing, two of the most common are positioning vertigo and Ménière's disease. In *positioning vertigo,* calcium crystals normally embedded in the otolith membrane of the maculae become dislodged and float toward the semicircular canals. The primary symptom of positioning vertigo is brief episodes of severe dizziness brought on by a change in position. People with this condition often say that they cannot go to sleep because they feel dizzy when they turn over in bed.

Question 3:

When a person with positioning vertigo changes position, the displaced crystals float toward the semicircular canals. Why would this cause dizziness?

Question 4:

Compare the symptoms of positioning vertigo and Ménière's disease. On the basis of Anant's symptoms, which condition do you think he has?

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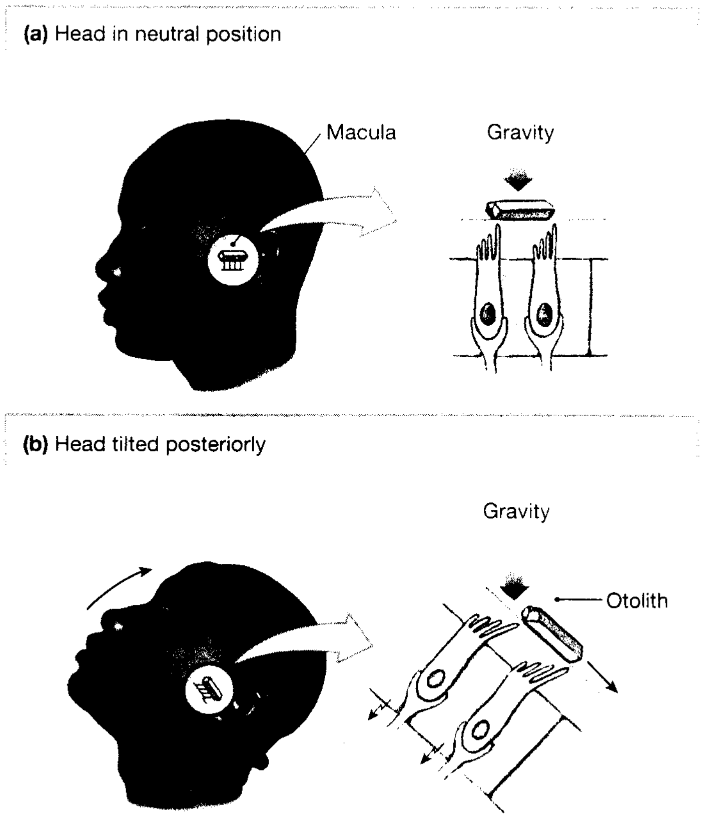

■ **FIGURE 10-25** ***Otolith organs***

Equilibrium Pathways Project Primarily to the Cerebellum

The hair cells of the vestibular apparatus stimulate primary sensory neurons in the vestibular nerve. Those neurons either synapse in the vestibular nuclei of the medulla or run without synapsing to the cerebellum (Fig. 10-26 ■). Collateral pathways run from the medulla to the cerebellum or upward through the reticular formation and thalamus. There are some poorly defined pathways to the cerebral cortex, but most integration for equilibrium comes from the cerebellum. Descending pathways from the vestibular nuclei go to certain motor neurons involved in eye movement. These pathways help keep the eyes locked on an object as the head turns.

CONCEPT CHECK

20. The stereocilia of hair cells are bathed in endolymph, which has a very high concentration of K^+ and a low concentration of Na^+. When ion channels in the stereocilia open, which ions move in which direction to cause depolarization?
21. Why does hearing decrease if an ear infection causes fluid buildup in the middle ear?
22. When dancers perform multiple turns, they try to keep their vision fixed on a single point ("spotting"). How does spotting keep a dancer from getting dizzy?

Answers: p. 375