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# The Vestibular System

## The Vestibular Labyrinth in the Inner Ear Contains Five Receptor Organs

Hair Cells Transduce Acceleration Stimuli Into Receptor Potentials

The Semicircular Canals Sense Head Rotation

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## Central Vestibular Nuclei Integrate Vestibular, Visual, Proprioceptive, and Motor Signals

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## Highlights

**M**ODERN VEHICULAR TRAVEL ON EARTH and through extraterrestrial space relies upon sophisticated guidance systems that integrate acceleration, velocity, and positional information through transducers, computational algorithms, and satellite triangulation. Yet the principles of inertial guidance are ancient: Vertebrates have used analogous systems for 500 million years and invertebrates for even longer. In these animals, the inertial guidance system, termed the vestibular system, serves to detect and interpret motion through space as well as orientation relative to gravity.

Through extensive research over many decades, it is apparent that most, if not all, organisms on Earth have evolved to sense one of the most prevalent “forces” in our universe, gravity. The mechanisms for the sensory transduction are as diverse as nature could devise. Gravity is most precisely referenced as gravito-inertial acceleration (GIA), a distinct form of linear acceleration directed toward the core of our planet. In truth, gravity varies systematically by as much as 0.5% between the equator and the poles; it increases over mineral-dense regions and decreases over mineral-light regions of the Earth’s surface. Yet every single behavior that animals perform is referenced to the GIA, and all of our actions and cognitive directives depend

upon knowledge of our motion and orientation relative to it. The first developments of what we refer to as a vestibular system were actually gravity sensors; as behavior became increasingly mobile, sensory organs evolved to process rotational accelerations as well.

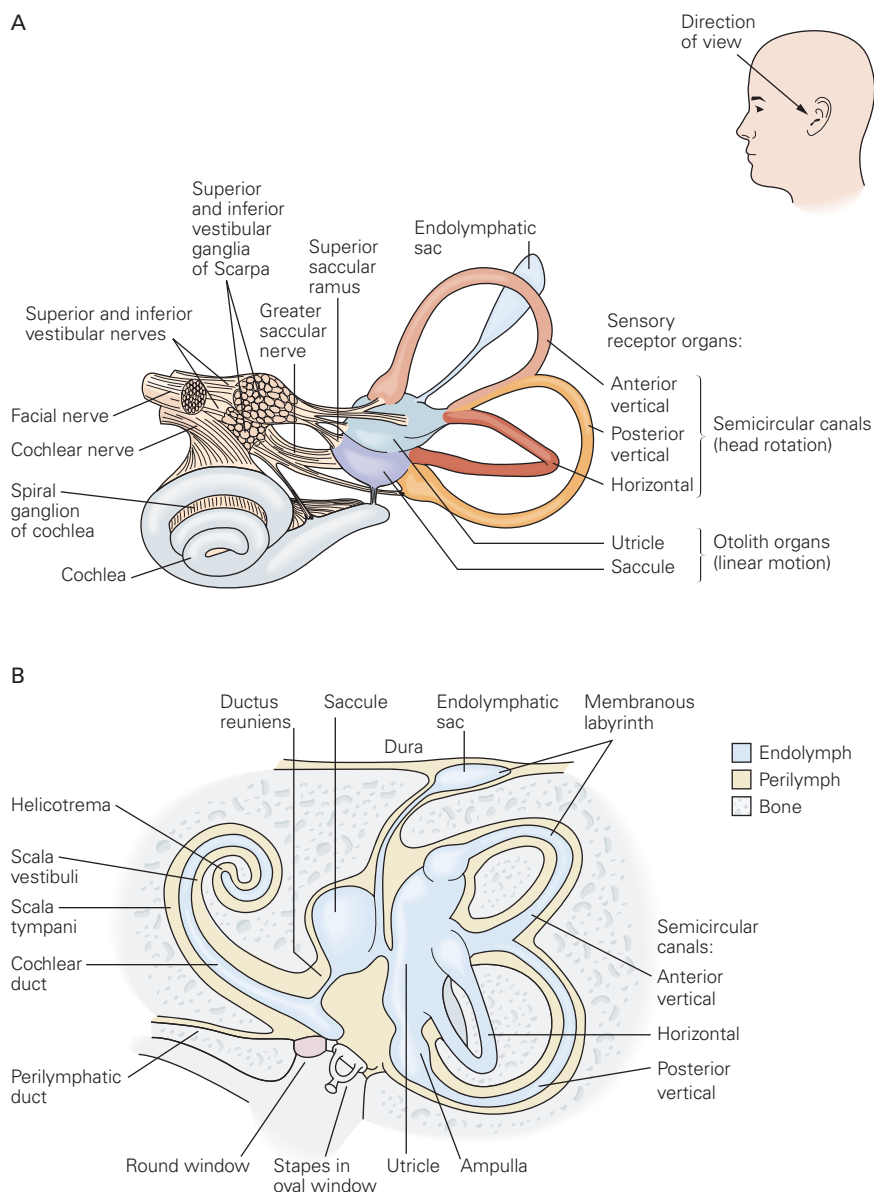
In this chapter we will concentrate on the vestibular system of vertebrates, which has remained highly conserved across many species. Vestibular signals originate in the labyrinths of the internal ear (Figure 27–1B). The *bony labyrinth* is a hollow structure within the petrous portion of the temporal bone. Within it lies the *membranous labyrinth*, which contains sensors for both the vestibular and auditory systems.

The vestibular receptors consist of two parts: two otolith organs, the utricle and saccule, which measure linear accelerations, and three semicircular canals, which measure angular accelerations. Rotational motion (angular acceleration) is experienced during head turns, whereas linear acceleration occurs during walking, falling, vehicular travel (ie, translations), or head tilts relative to gravity. These receptors send vestibular information to the brain, where it is integrated into an appropriate signal regarding direction and speed of motion, as well as the position of the head relative to the GIA. Many of the central vestibular neurons at the first junction with receptor afferent fibers also

**Figure 27–1** The vestibular apparatus of the inner ear.

**A.** The orientations of the vestibular and cochlear divisions of the inner ear are shown with respect to the head.

**B.** The inner ear is divided into bony and membranous labyrinths. The bony labyrinth is bounded by the petrosal portion of the temporal bone. Lying within this structure is the membranous labyrinth, which contains the receptor organs for hearing (the cochlea) and equilibrium (the utricle, saccule, and semicircular canals). The space between bone and membrane is filled with perilymph, whereas the membranous labyrinth is filled with endolymph. Sensory cells in the utricle, saccule, and ampullae of the semicircular canals respond to motion of the head. (Adapted from Iurato 1967.)



receive convergent signals from other systems such as proprioceptors, visual signals, and motor commands. Central processing of these multimodal signals occurs very rapidly to ensure adequate coordination of visual gaze and postural responses, autonomic responses, and awareness of spatial orientation.

### The Vestibular Labyrinth in the Inner Ear Contains Five Receptor Organs

The membranous labyrinth is supported within the bony labyrinth by a filamentous network of connective tissue. The vestibular portion of the membranous labyrinth lies lateral and posterior to the cochlea. Vestibular receptors are contained in specialized enlarged regions of the membranous labyrinth, termed the ampullae for the semicircular canals and maculae for the otolith organs (Figure 27-1B). Both of the otolith organs lie in a central compartment of the membranous labyrinth, the vestibule, which is surrounded by the bony labyrinth of the same name.

The membranous labyrinth is filled with endolymph, a  $K^+$ -rich (150 mM) and  $Na^+$ -poor (16 mM) fluid whose composition is maintained by the action of ion pumps in specialized cells. Endolymph bathes the surface of the vestibular receptor cells. Surrounding the membranous labyrinth, in the space between the membranous labyrinth and the wall of the bony labyrinth, is *perilymph*. Perilymph is a high- $Na^+$  (150 mM), low- $K^+$  (7 mM) fluid similar in composition to cerebrospinal fluid, with which it is in communication through the cochlear duct. Perilymph bathes the basal surface of the receptor epithelia and the vestibular nerve fibers. Two fluid-tight partitions in the bony labyrinth, the oval and round windows (Figure 27-1B), connect the perilymphatic space to the middle ear cavity. The oval window is connected to the tympanic membrane by the middle ear ossicles. These windows are important

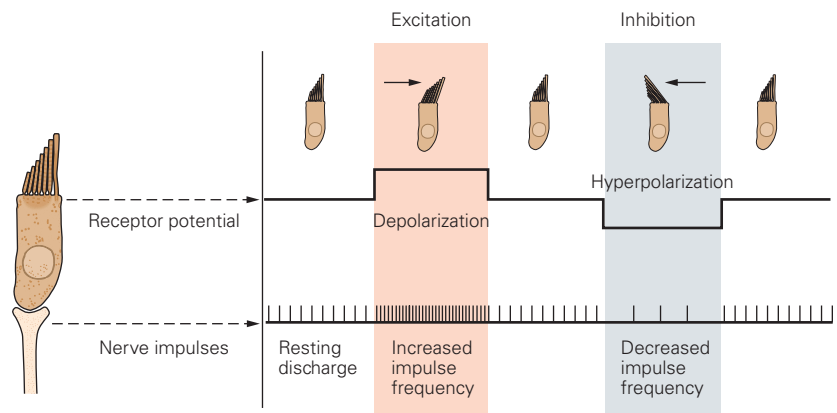
for sound transduction (Chapter 26). The endolymph and perilymph are kept separate by a junctional complex of support cells that surrounds the apex of each receptor cell. Disruption of the balance between these two fluids (by trauma or disease) can result in vestibular dysfunction, leading to dizziness, vertigo, and spatial disorientation.

During development, the labyrinth progresses from a simple sac to a complex set of interconnected sensory organs, but retains the same fundamental topological organization. Each organ originates as an epithelium-lined pouch that buds from the otic cyst, and the endolymphatic spaces within the several organs remain continuous in the adult. The endolymphatic spaces of the vestibular labyrinth are also connected to the cochlear duct through the ductus reuniens (Figure 27-1B). In addition, the membranous labyrinth contains a small tube, the endolymphatic duct, which extends through a space in the sigmoid bone, the vestibular aqueduct, to end in a blind sac adjacent to the dura in the epidural space of the posterior cranial fossa. It is thought that the endolymphatic sac has both absorptive and excretive functions to maintain the ionic composition of the endolymphatic fluid.

### Hair Cells Transduce Acceleration Stimuli Into Receptor Potentials

Each of the five receptor organs has a cluster of hair cells responsible for transducing head motion into vestibular signals. Hair cells are so named due to an array of nearly 100 staggered height stereocilia. The shortest stereocilia are at one end of the cell and the tallest at the other, ending with the only true cilium of the hair cell, termed the kinocilium. The kinocilium is typically the tallest of all stereocilia. Angular or linear acceleration of the head leads to a deflection of the stereocilia, which together compose the hair bundle (Figure 27-2).

**Figure 27-2** Hair cells in the vestibular labyrinth transduce mechanical stimuli into neural signals. At the apex of each cell are the stereocilia, which increase in length toward the single kinocilium. The membrane potential of the receptor cell depends on the direction in which the stereocilia are bent. Deflection toward the kinocilium causes the cell to depolarize and thus increases the rate of firing in the afferent fiber. Bending away from the kinocilium causes the cell to hyperpolarize, thus decreasing the afferent firing rate. (Adapted, with permission, from Flock 1965.)



Specialized ion channels in the tips of the hair bundle stereocilia allow  $K^+$  to enter or be blocked from the surrounding endolymph (Chapter 26). This action allows hair cells to act as mechanoreceptors, where deflection of the stereocilia produces a depolarizing or hyperpolarizing receptor potential depending on which direction the hair bundle moves (Figure 27-2). These depolarizations and hyperpolarizations of the receptor membrane lead to excitation and inhibition, respectively, in the firing rate of the innervating afferent (Figure 27-2). In each vestibular receptor organ, hair cells are arranged so that movement directional specificity is defined by excitation in some cells and inhibition in other cells.

Vestibular signals are carried from the hair cells to the brain stem by branches of the vestibulocochlear nerve (cranial nerve VIII), which enter the brain stem and terminate in the ipsilateral vestibular nuclei, cerebellum, and reticular formation. Cell bodies of the vestibular nerve are located in Scarpa's ganglia within the internal auditory canal (Figure 27-1A). The *superior vestibular nerve* innervates the horizontal and anterior canals and the utricle, whereas the *inferior vestibular nerve* innervates the posterior canal and the saccule. The labyrinth's vascular supply, which arises from the anterior inferior cerebellar artery, travels with nerve VIII. The anterior vestibular artery supplies the structures innervated by the superior vestibular nerve, and the posterior vestibular artery supplies the structures innervated by the inferior vestibular nerve.

All vertebrate receptor hair cells receive efferent inputs from the brain stem. The function of the efferent innervation of vestibular receptors is still a subject of debate. Stimulation of the efferent fibers from the brain stem changes the sensitivity of the afferent axons from the hair cells. It increases the excitability of some afferents and hair cells while inhibiting others, and varies across species.

### The Semicircular Canals Sense Head Rotation

An object undergoes angular acceleration when its rate of rotation about an axis changes. Therefore, the head undergoes angular acceleration when it turns or tilts, when the body rotates, and during active or passive locomotion. The three semicircular canals of each vestibular labyrinth detect these angular accelerations and report their magnitudes and motion directions to the brain.

Each semicircular canal is a semicircular tube of membranous labyrinth extending from the vestibule. One end of each canal is open to the vestibule, whereas at the other end, the ampulla, the entire lumen of the

canal is traversed by a fluid-tight gelatinous diaphragm, the cupula. The stereocilia and the kinocilium protrude into the gelatinous cupula, while the hair cells are located below in a receptor epithelium, the crista, along with the innervating afferent terminals (Figure 27-3).

The vestibular organs detect accelerations of the head because the inertia of endolymph and cupula results in forces acting on the stereocilia. Consider the simplest situation, a rotation in the plane of a semicircular canal. When the head begins to rotate, the membranous and bony labyrinths move along with it. Because of its inertia, however, the endolymph lags behind the surrounding membranous labyrinth, thus pushing the cupula in a direction opposite that of the head (Figure 27-3B).

The motion of endolymph in a semicircular canal can be demonstrated with a cup of coffee. While gently twisting the cup about its vertical axis, observe a particular bubble near the fluid's outer boundary. As the cup begins to turn, the coffee tends to maintain its initial orientation in space and thus counter-rotates in the cup. If you continue rotating the cup at the same speed, the coffee (and the bubble) eventually catches up to the cup and rotates with it. When the cup decelerates and stops, the coffee keeps rotating, moving in the opposite direction relative to the cup.

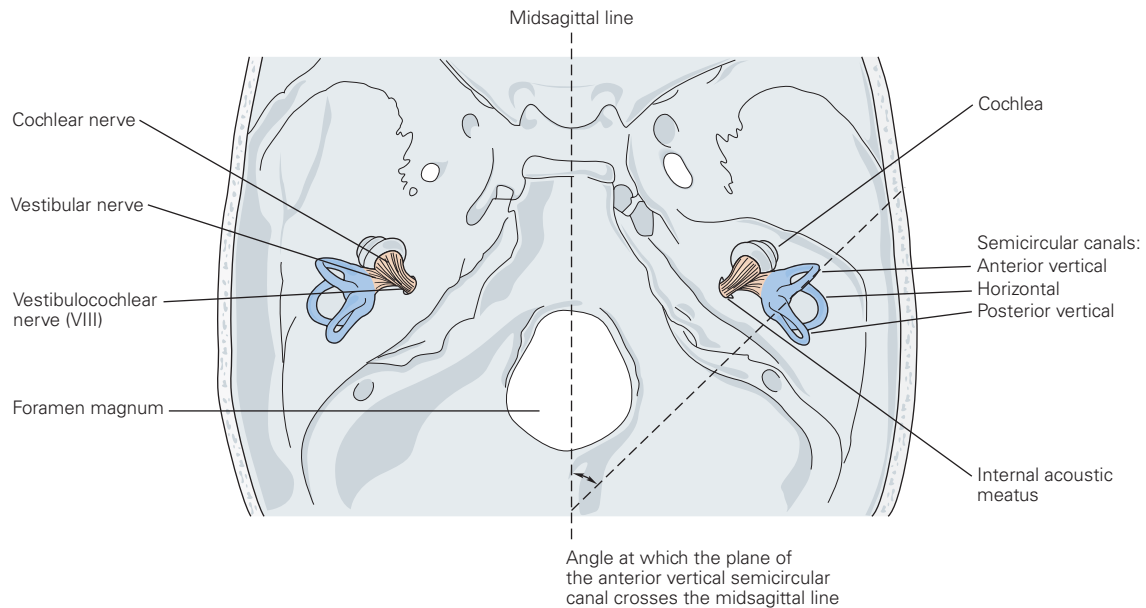
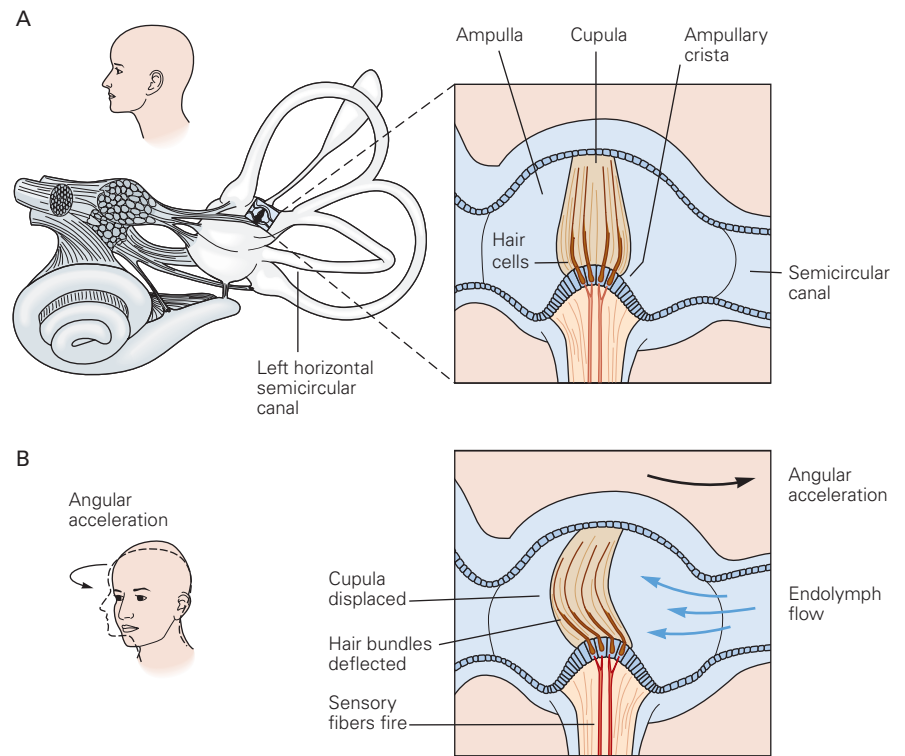
In the ampulla, this relative motion of the endolymph creates pressure on the cupula, bending it toward or away from the adjacent vestibule, depending on the direction of endolymph flow. The resulting deflection of the stereocilia alters the membrane potential of the hair cells, thereby changing the firing rates of the associated sensory fibers. Each semicircular canal is maximally sensitive to rotations in its plane. The horizontal canal is oriented approximately  $30^\circ$  elevated above the naso-occipital axis (roughly in the horizontal plane as a person walks and looks at the ground ahead) and thus is most sensitive to rotations in the horizontal plane. The stereocilia are arranged so that leftward rotational motion is excitatory for the left horizontal canal and inhibitory for the right horizontal canal. The anterior and posterior canals are oriented more vertically in the head, at an angle of approximately 45 degrees from the sagittal plane (Figure 27-4). Similar rotational motion downward in the plane of the anterior canals is excitatory for anterior canal hair cells, while upward head motion is excitatory for posterior canals.

Because there is approximate mirror symmetry of the left and right labyrinths, the six canals effectively operate as three coplanar pairs. The two horizontal canals form one pair; each of the other pairs consists of one anterior canal on one side of the head and the contralateral posterior canal. Further, the three

**Figure 27–3** The ampulla of a semi-circular canal.

**A.** A thickened zone of epithelium, the ampullary crista, contains the hair cells. The stereocilia and the kinocilia of the hair cells extend into a gelatinous diaphragm, the cupula, which stretches from the crista to the roof of the ampulla.

**B.** The cupula is displaced by the relative movement of endolymph when the head turns. As a result, the hair bundles are also displaced. Their movement is greatly exaggerated in the diagram.



**Figure 27–4** The bilateral symmetry of the semicircular canals. The horizontal canals on both sides lie in approximately the same plane and therefore are functional pairs. The bilateral vertical canals have a more complex relationship. The anterior canal on one side and the posterior canal on the

opposite side lie in parallel planes and therefore constitute a functional pair. The vertical semicircular canals lie nearly  $45^\circ$  from the midsagittal plane. Each of the semicircular canals on one side of the head lie in approximately orthogonal planes to each other.



semicircular canals on each side of the head lie roughly orthogonal to each other (Figure 27–4). When the head moves toward the receptor hair cells (eg, leftward head turns for the left horizontal semicircular canal), the stereocilia are bent toward the tall kinocilium, thus exciting (depolarizing) the cell. Head motion in the opposite direction causes bending away from the kinocilium and toward the smallest stereocilia, thus closing the channels and inhibiting (hyperpolarizing) the cell.

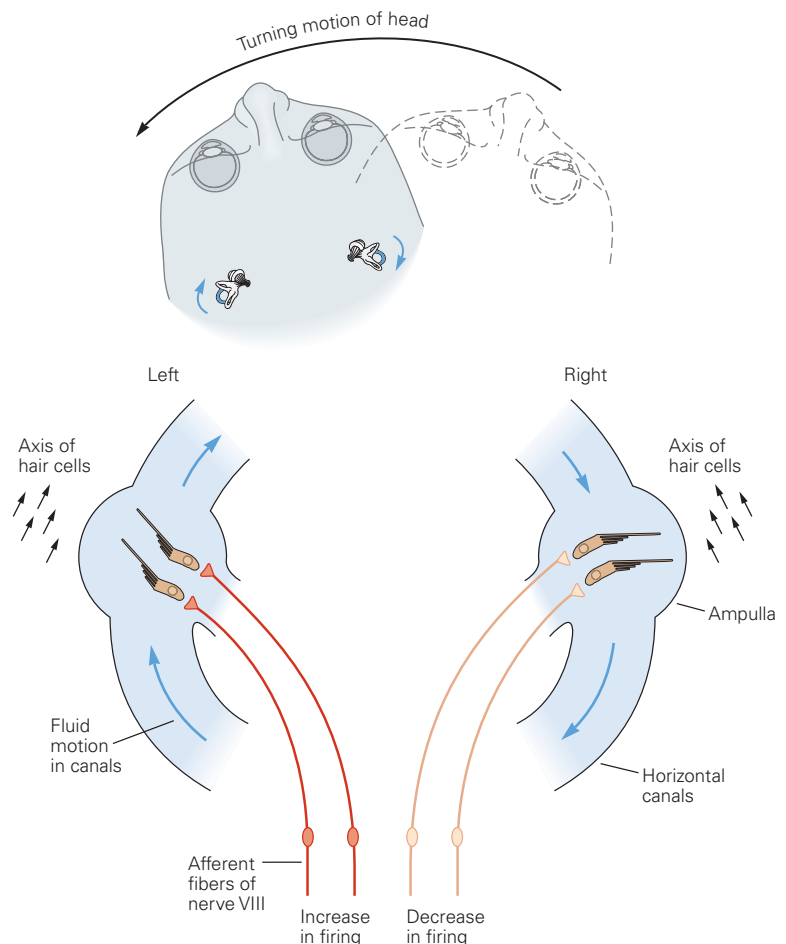
The left and right ear semicircular canals have opposite polarity; thus, when you turn your head to the left, the receptors in the left horizontal semicircular canal will be excited (increased firing rate), whereas right horizontal canal receptors will be inhibited (decreased firing rate; Figure 27–5). The same relationship is true for the vertical semicircular canals. The canal planes are also roughly aligned to the pulling planes of specific eye muscles. The pair of horizontal canals lies in the pulling plane of the lateral and medial rectus muscles. The left anterior and right posterior canal pair lie in the pulling plane of the left superior

and inferior rectus and right superior and inferior oblique muscles. The right anterior and left posterior pair occupies the pulling plane of the left superior and inferior oblique and right superior and inferior rectus muscles.

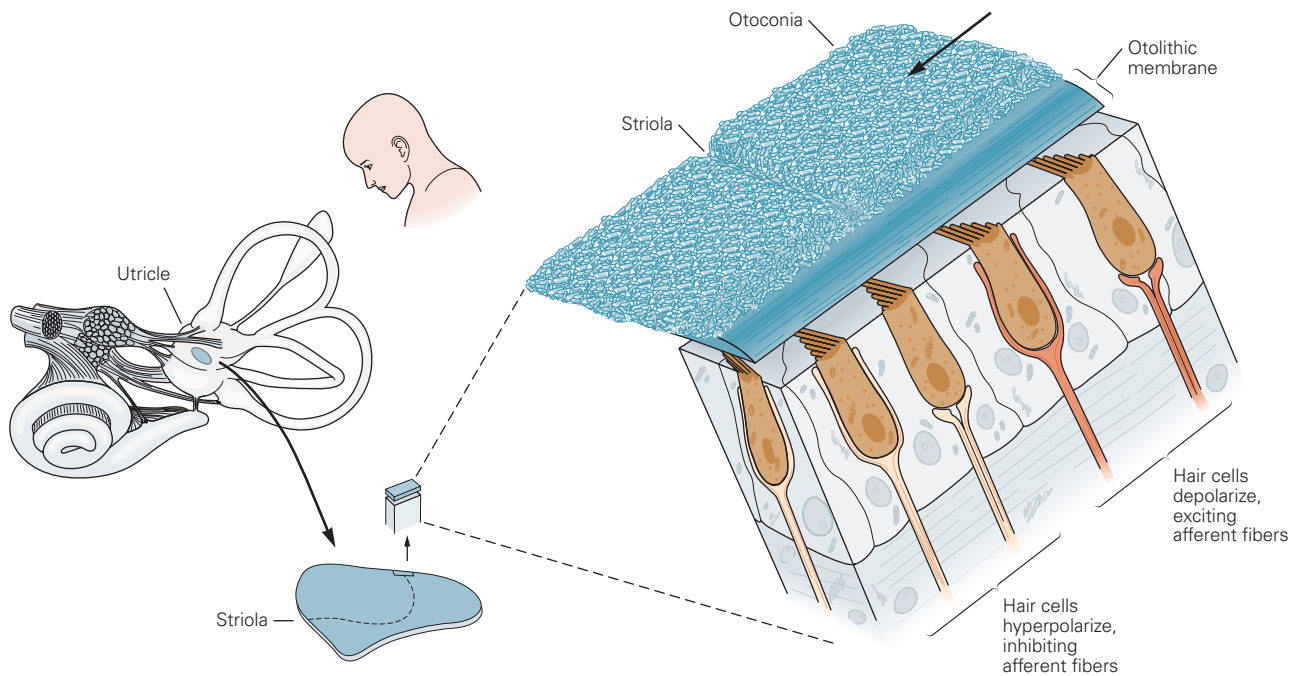
### The Otolith Organs Sense Linear Accelerations

The vestibular system must compensate not only for head rotations but also for linear motion. The two otolith organs, the utricle and saccule, detect linear motion as well as the static orientation of the head relative to gravity, which is itself a linear acceleration. Each organ consists of a sac of membranous labyrinth approximately 3 mm in the longest dimension. The hair cells of each organ are arranged in a roughly elliptical patch called the *macula*. The human utricle contains approximately 30,000 hair cells, whereas the saccule contains some 16,000.

The hair bundles of the otolithic hair cells extend into a gelatinous sheet, the *otolithic membrane*, which



**Figure 27–5** The left and right horizontal semicircular canals work together to signal head movement. Because of inertia, rotation of the head in a counterclockwise direction causes endolymph to move clockwise with respect to the canals. This deflects the stereocilia in the left canal in the excitatory direction, thereby exciting the afferent fibers on this side. In the right canal, the afferent fibers are hyperpolarized so that firing decreases.



**Figure 27-6** The utricle detects tilt of the head. Hair cells in the epithelium of the utricle have apical hair bundles that project into the otolithic membrane, a gelatinous material that is covered by millions of calcium carbonate particles (otoconia). The hair bundles are polarized but are oriented in different directions. The directional polarity of each hair cell is organized relative to a reversal region running through the center of the utricle, termed

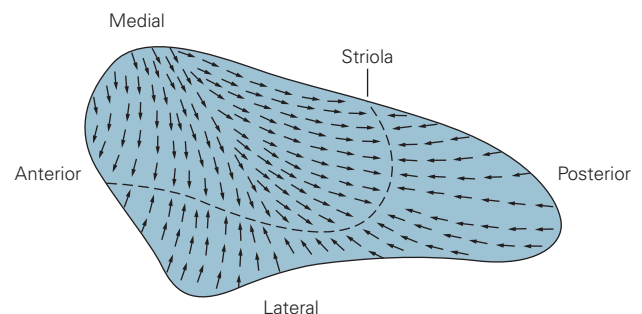
the striola (see Figure 27-7). Thus, when the head is tilted, the gravitational force on the otoconia bends each hair bundle in a particular direction. When the head is tilted in the direction of a hair cell's axis of polarity, that cell depolarizes and excites the afferent fiber. When the head is tilted in the opposite direction, the same cell hyperpolarizes and inhibits the afferent fiber. (Adapted from Iurato 1967.)

covers the entire macula (Figure 27-6). Embedded on the surface of this membrane are fine, dense particles of calcium carbonate called *otoconia* (Greek root translates to “ear dust”), which give the otolith (“ear stone”) organs their name. Otoconia are typically 0.5 to 30  $\mu\text{m}$  long; thousands of these particles are attached to the otolithic membranes of the utricle and saccule.

Gravity and other linear accelerations exert shear forces on the otoconial matrix and the gelatinous otolithic membrane, which can move relative to the membranous labyrinth. This results in a deflection of the hair bundles, altering activity in the vestibular nerve to signal linear acceleration owing to translational motion or gravity. The orientations of the otolith organs and the directional sensitivity of individual hair cells are such that a linear acceleration along any axis can be sensed. For example, with the head in its normal position, the macula of each utricle is raised above the naso-occipital axis by approximately  $30^\circ$ , similar to the horizontal semicircular canal. In normal resting head position, the utricle is deviated to bring the utricle approximately equal to an Earth horizontal plane. Any acceleration in the horizontal plane excites some hair cells in each

utricle and inhibits others, according to their orientations (Figures 27-6 and 27-7).

The operation of the paired saccules resembles that of the utricles. The hair cells represent all possible



**Figure 27-7** The axis of mechanical sensitivity of each hair cell in the utricle is oriented toward the striola. The striola curves across the surface of the macula containing the hair cells, resulting in a characteristic variation in the axes of mechanosensitivity (arrows) in the population of hair cells. Because of this arrangement, tilt in any direction depolarizes some cells and hyperpolarizes others, while having no effect on the remainder. (Adapted, with permission, from Spoendlin 1966.)



orientations within the plane of each saccular macula, but the maculae are oriented vertically in nearly parasagittal planes. The saccules are therefore especially sensitive to vertical accelerations. Certain saccular hair cells also respond to accelerations in the horizontal plane, in particular those along the anterior–posterior axis.

### Central Vestibular Nuclei Integrate Vestibular, Visual, Proprioceptive, and Motor Signals

The vestibular nerve projects ipsilaterally from the vestibular ganglion mainly to four vestibular nuclei (medial, lateral, superior, and descending) in the dorsal part of the pons and medulla, in the floor of the fourth ventricle. Many vestibular nerve fibers also bifurcate, sending a direct projection to the fastigial nucleus, the nodulus and uvula, and the reticular formation (Figure 27–8A). These nuclei integrate signals from the vestibular organs with signals from the spinal cord, cerebellum, and visual system.

The vestibular nuclei project, in turn, to many central targets, including the oculomotor nuclei, reticular and spinal centers concerned with gaze and postural movement, and the thalamus (Figure 27–9). Many vestibular nuclei neurons have reciprocal connections with the cerebellum, primarily in the flocculo-nodular lobe, that form important regulatory mechanisms for eye movements, head movements, and posture (Figures 27–8 and 27–9). The vestibular nuclei receive inputs from the premotor cortex, the accessory optic system (nucleus of the optic tract), the neural integrator nuclei (nucleus prepositus hypoglossi and interstitial nucleus of Cajal), and the reticular formation (Figure 27–8). Further projections from the vestibular nuclei reach the rostral and caudal lateral medulla nuclei that are involved in regulation of blood pressure, heart rate, respiration, and bone remodeling, as well as the parabrachial nucleus for homeostasis modulation. Finally, there are projections from the vestibular nuclei to the medial geniculate (auditory) nuclei, as well as the supragenual nucleus and dorsal tegmental nucleus, which contribute to spatial orientation (Figure 27–9).

The superior and medial vestibular nuclei receive fibers predominantly from the semicircular canals in the medial regions and some otolith input in the lateral regions (Figure 27–8). They send fibers predominantly to the cerebellum, reticular formation, thalamus, oculomotor centers, and spinal cord (Figure 27–9). Oculomotor center outputs include the three oculomotor nuclei (abducens, oculomotor, trochlear), as well as the neural integrators for converting head velocity into head position signals in the nucleus hypoglossi

(horizontal eye movements) and interstitial nucleus of Cajal (vertical eye movements). These nuclei are described in some detail later.

Another major output pathway concerned with gaze control arises from the medial vestibular nucleus (as well as lesser projections from the descending and lateral vestibular nuclei) and projects bilaterally to the cervical spinal cord through the medial vestibulospinal tract (Figure 27–9; see Chapter 35). There are two categories of medial vestibulospinal fibers. Vestibulospinal neurons project only to the spinal cord to control neck musculature. Vestibulo-ocular neurons project to both the spinal cord and the oculomotor nuclei and are involved in coordinated eye and head movements to maintain gaze stability.

The lateral vestibular nucleus (Deiters' nucleus) receives fibers from the semicircular canals medially and the otolith organs laterally. There is a major output to all levels of the ipsilateral spinal cord through the lateral vestibulospinal tract that is concerned principally with postural reflexes through modulation of limb and axial musculature (Figure 27–9). Lateral vestibular nuclei neurons also project heavily to the reticular formation. The descending vestibular nucleus receives predominantly otolithic input, but also receives semicircular canal fibers medially, and projects to the cerebellum, reticular formation, and spinal cord (medial vestibulospinal tract). The primary neurotransmitters for excitatory vestibular nuclear projections include glutamate, whereas the inhibitory projections are either glycine or  $\gamma$ -aminobutyric acid (GABA). Vestibular projections to the spinal systems are discussed in more detail in Chapter 36.

### The Vestibular Commissural System Communicates Bilateral Information

Many of these vestibular nuclei neurons receive convergent motion information from the opposite ear through an inhibitory commissural pathway that uses GABA as a neurotransmitter (Figure 27–8B). The commissural pathway is highly organized according to the type of receptor from which information is received. For example, cells receiving signals from the ipsilateral horizontal excitatory canal will also receive signals from the contralateral horizontal canal through an inhibitory interneuron. Due to the directional selectivity of the receptors in each ear, the contralateral horizontal canal input will always be decreased during an ipsilateral head turn, in effect “disinhibiting” the inhibitory input from the contralateral side.

The effect of the commissural system is to increase the response of the vestibular nuclei neuron and