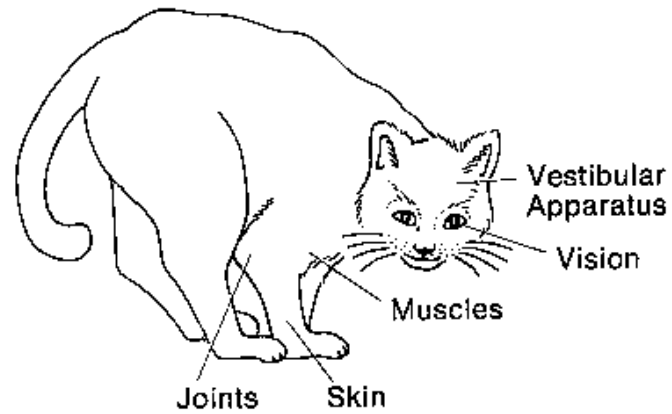


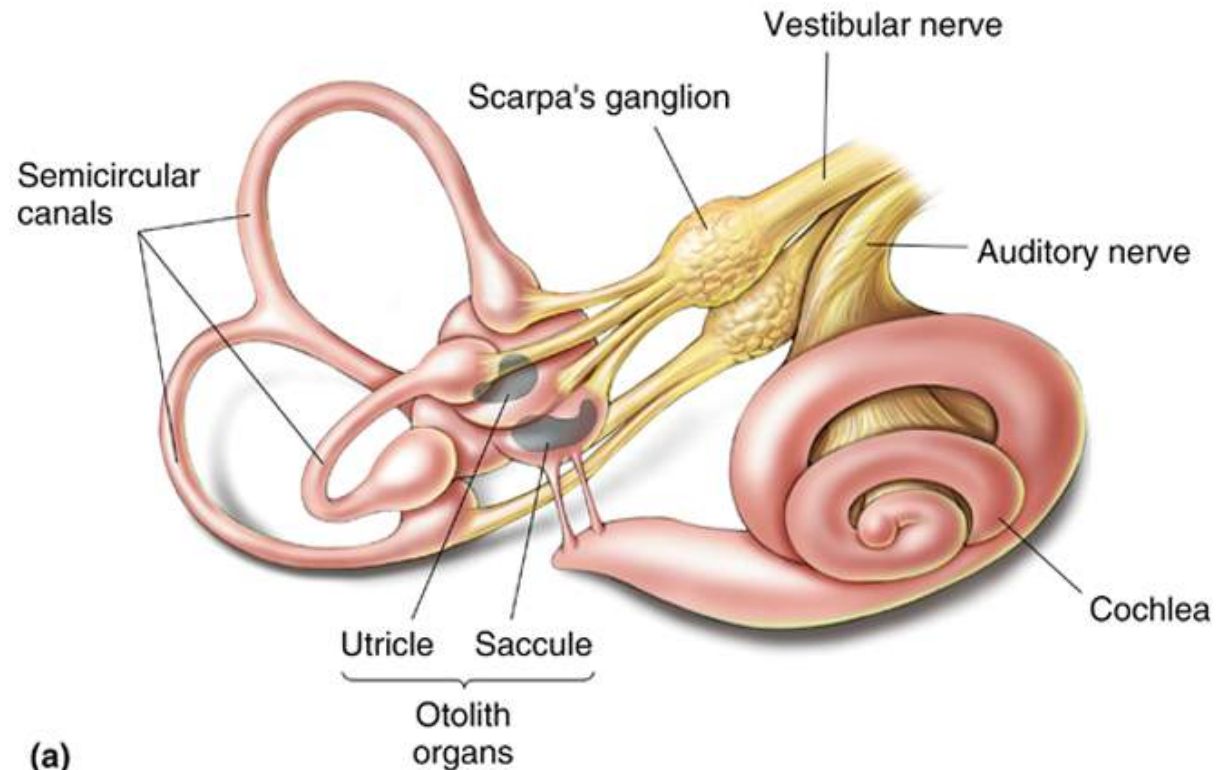
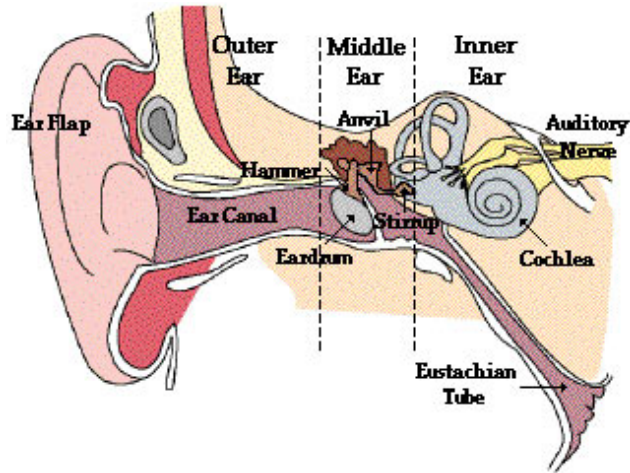
The sense of balance



Sense of balance consists of sense of linear and angular acceleration. But different kinds of sensory information are used in maintaining balance as indicated in the figure.



The vestibular system (labyrinth)

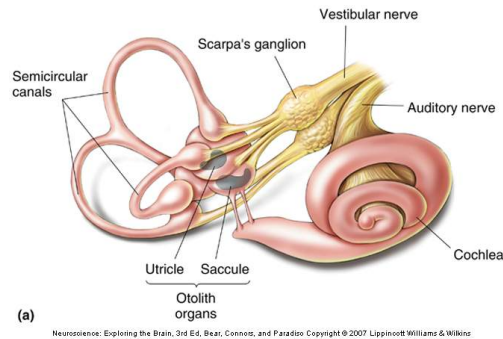


(a)

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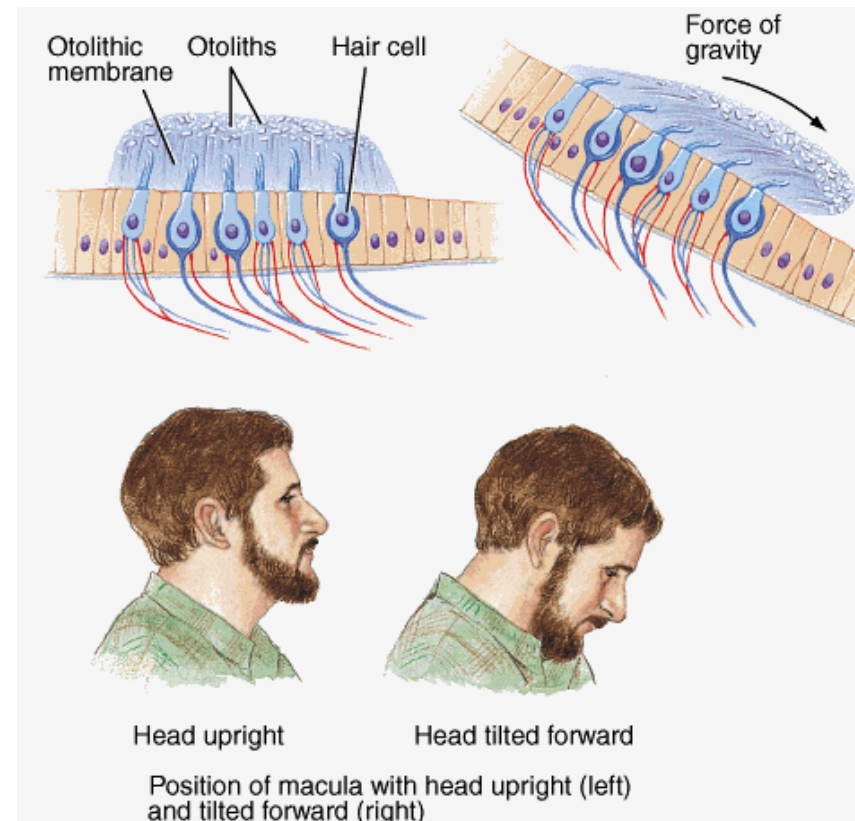
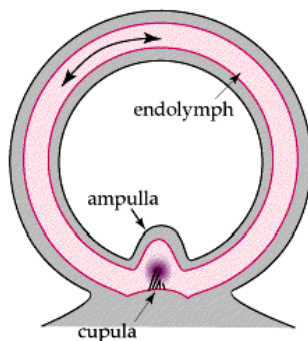
The inner ear is divided into vestibular division, which contains the organs of equilibrium (the utricle, saccule, and semicircular canals) and cochlear division, which contains the organs of hearing (the cochlea).

The vestibular system (labyrinth)



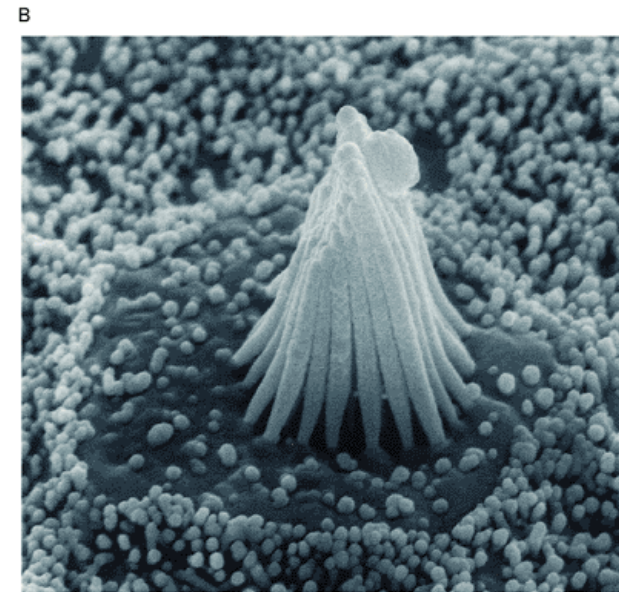
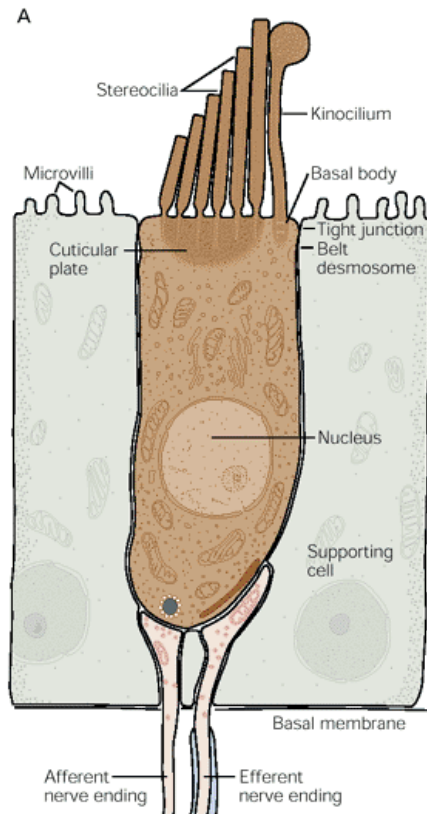
The otolith organ is detecting linear acceleration. It consists of two sacs and the receptors are grouped in a macula in each sac.

Three semicircular canals are detecting rotation (angular acceleration). Each semicircular canal has an enlargement (ampulla) within which the sensory cells are grouped.



Hair cells

Hair cells are receptors responsible for the sense of equilibrium and for audition. The hair cells of the receptor organs in the human internal ear are of similar form and function. They transduce mechanical stimuli into receptor potential.



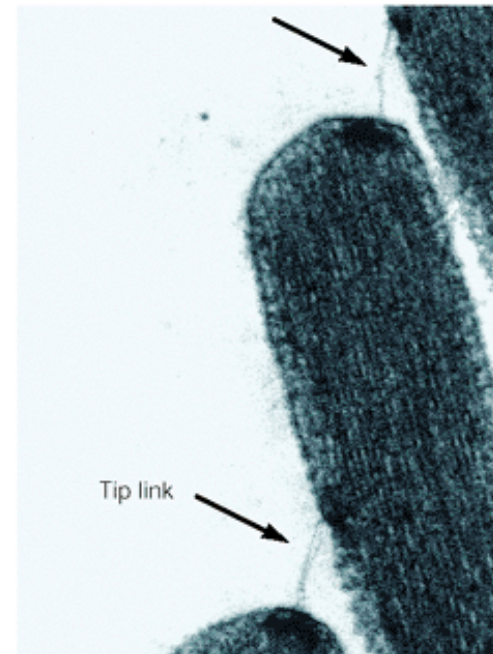
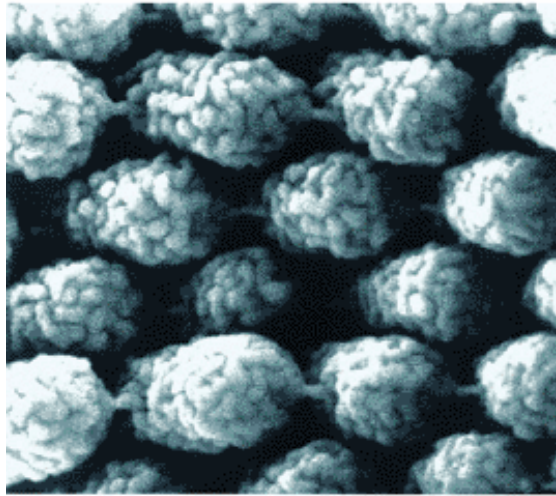
From the cell's apical surface extends the hair bundle, the mechanically sensitive organelle. Afferent (from receptors) and efferent (to receptors) synapses occur upon the basolateral surface of the plasma membrane.

This scanning electron micrograph of a hair cell's apical surface. The hair bundle comprises some 60 stereocilia, arranged in rows of varying length and the single kinocilium at the bundle's tall edge. Deflection of the hair bundle to the right, the positive stimulus direction, depolarizes the hair cell; movement in the opposite direction elicits a hyperpolarization.

Tip links

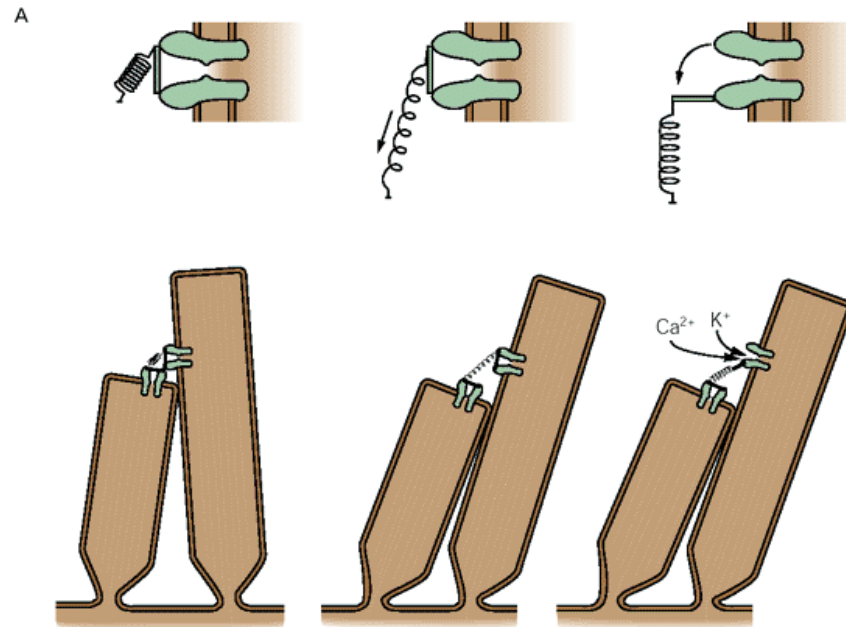
Stereocilia are connected with each other by elastic structures within the hair bundle called tip links.

B

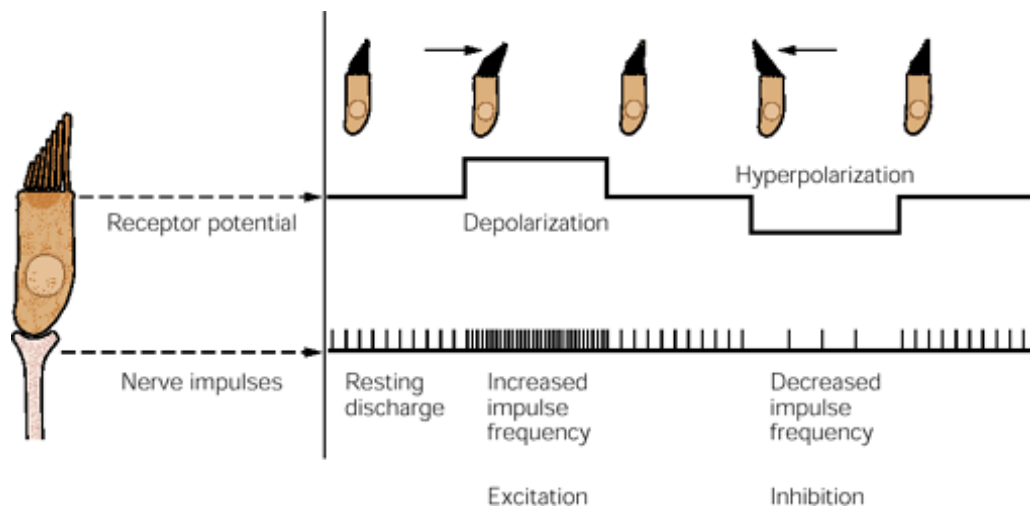


The scanning electron micrograph of a hair bundle's top surface. The links that connect each stereociliary tip to the side of the longest adjacent stereocilium are visible.

A model for the mechanism of mechano-electrical transduction by hair cells

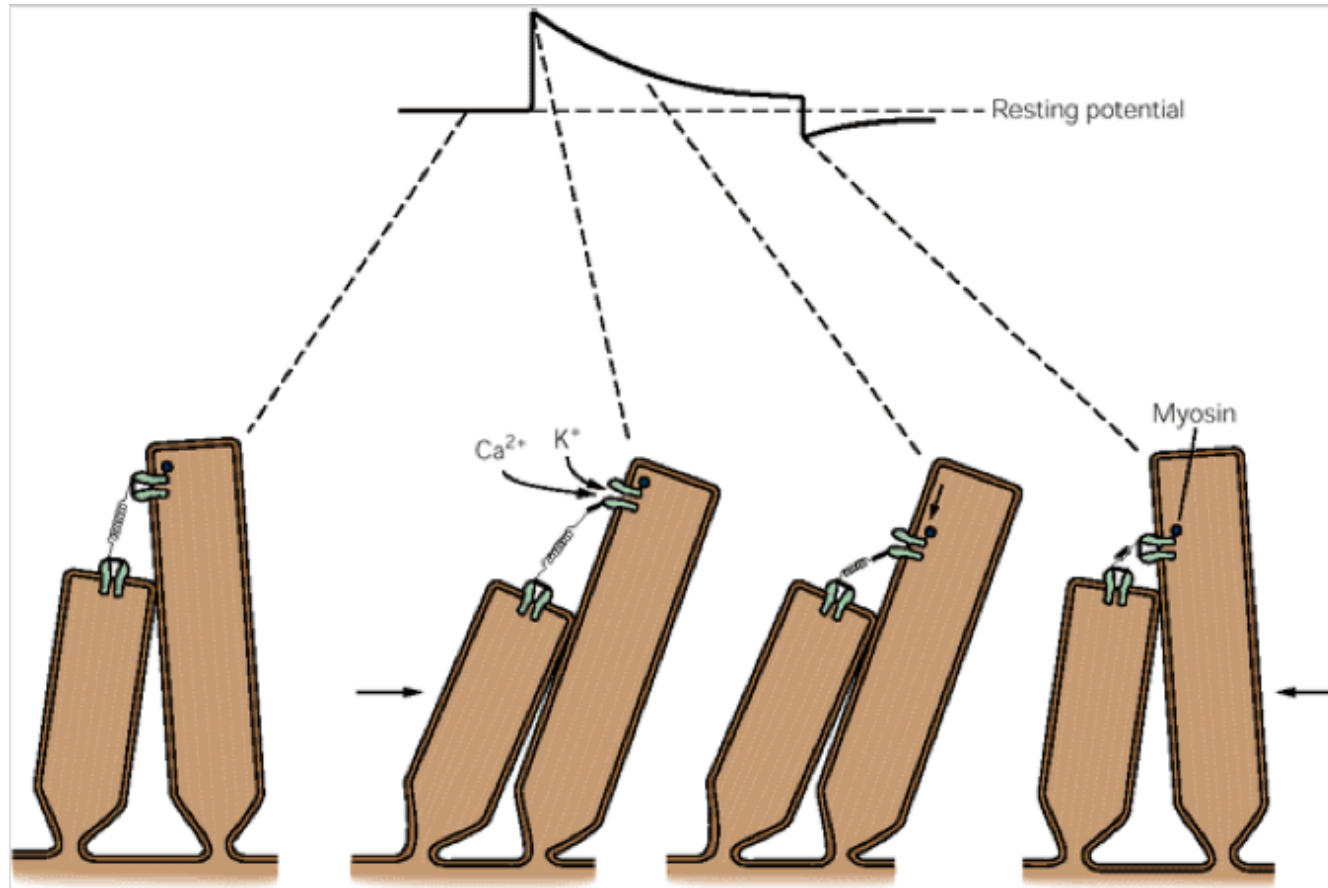


The ion channels that participate in mechano-electrical transduction in hair cells are gated by elastic structures in the hair bundle. Opening and closing of these channels is controlled by the tension in the gating spring, that senses hair-bundle displacement.



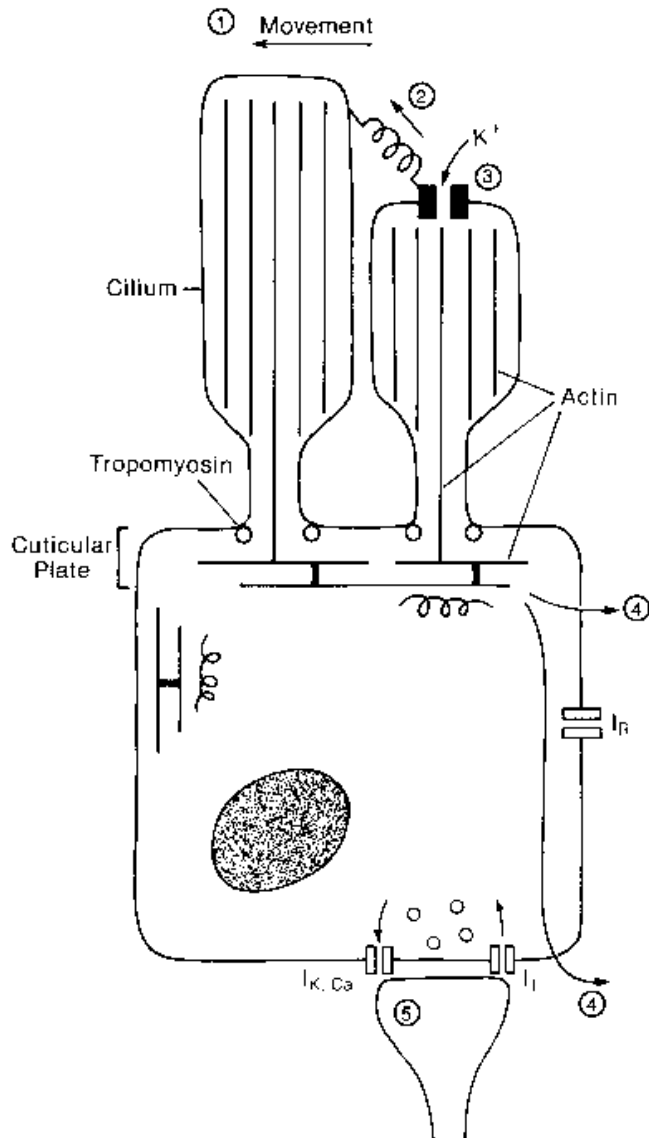
The membrane potential of the receptor cell depends on the direction in which the hair bundle is bent. Deflection toward the kinocilium causes the cell to depolarize and thus increases the rate of firing in the afferent fiber. Bending away from the kinocilium causes the cell to hyperpolarize, thus decreasing the afferent firing rate.

Adaptation in the hair cells



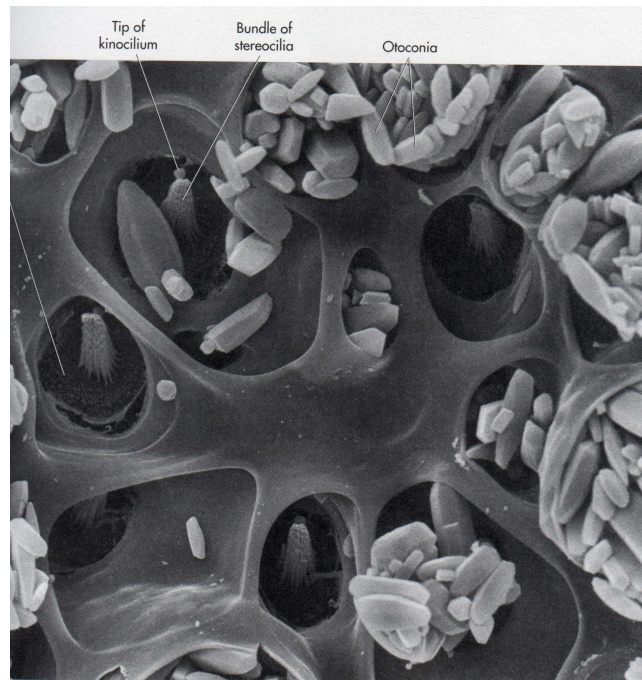
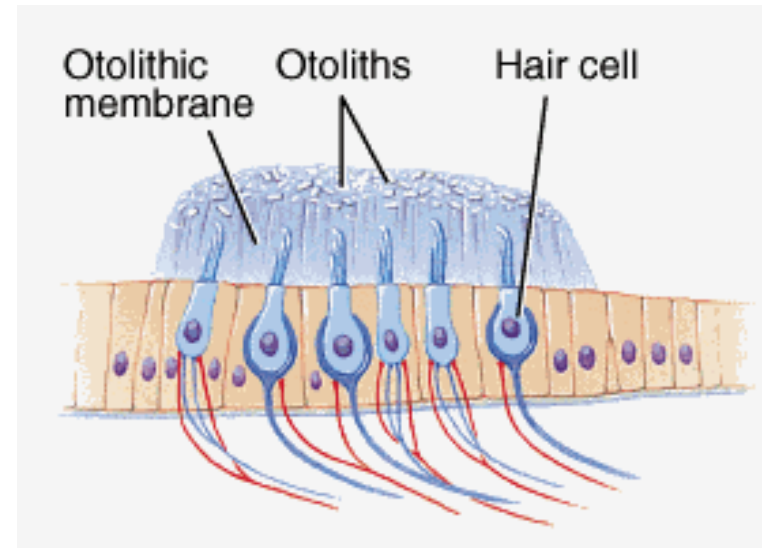
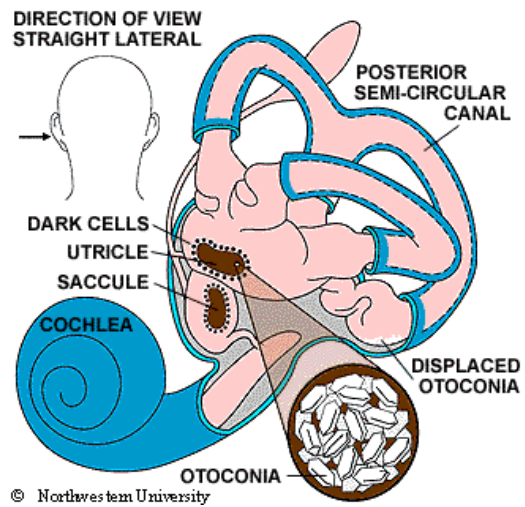
The electrical response to a positive stimulus displays an initial depolarization, followed by a decline to a plateau and an undershoot at the cessation of the stimulus. Negative stimulation elicits a complementary response. Bundle movement in response to positive stimulation increases tip link tension and opens transduction channels. As stimulation continues, the tip link's upper attachment moves down the stereocilium, allowing each channel to close during adaptation. During negative stimulation tension is restored to the initially slack tip link by active ascent of the link's upper insertion.

Mechanism of transduction



1. Movement
2. Stretching of the gating string
3. Increase membrane conductance to K⁺
4. Influx of K⁺ ions into the cell, the depolarization spreads into the cell
5. Release of neurotransmitter at the hair cell synapse onto vestibular nerve sensory terminal.

The Otolith Organs

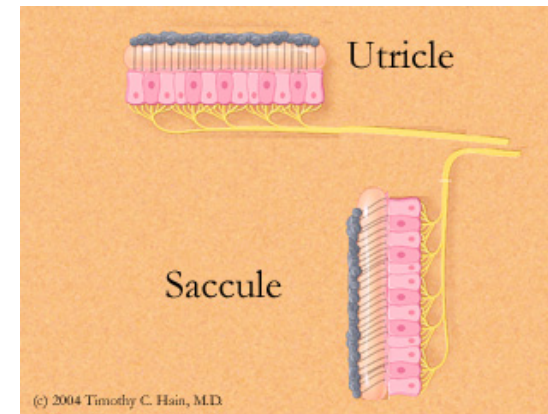
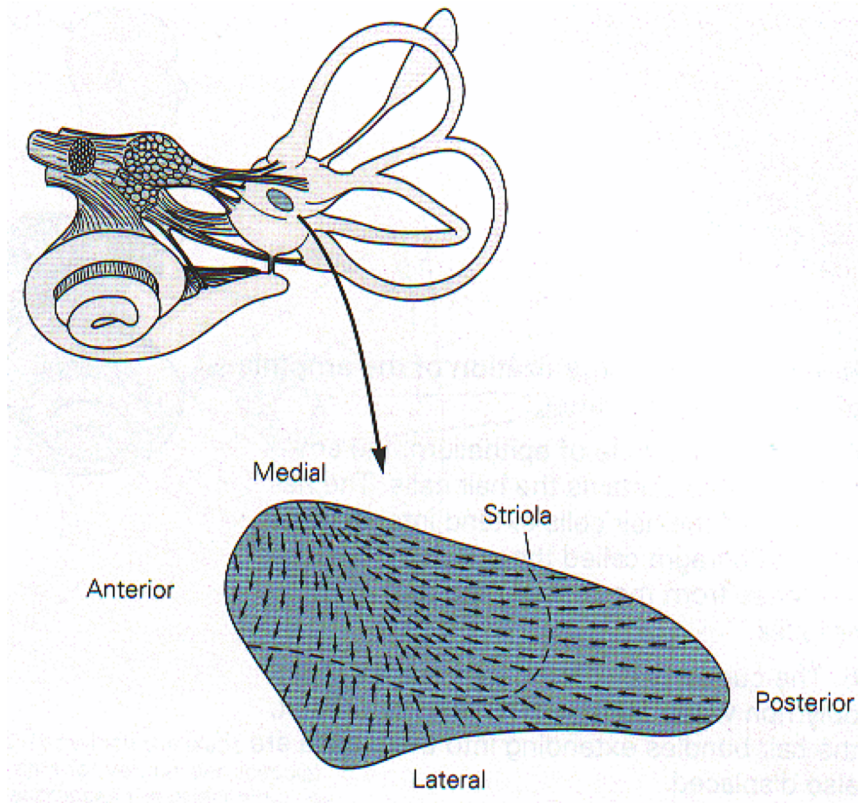


Otolithic membrane

In the otolith organs, the sensory epithelium is overlain with a sheet of gelatinous extracellular matrix, the otolith membrane. Embedded in this structure are otoconia, rocklike crystals of calcium carbonate.

When the head undergoes linear acceleration the otoconial mass lags behind movement of the head, because of its inertia. The motion of the otoconia is communicated to the otolith membrane, which thus shifts with respect to the underlying epithelium. This motion in turn deflects the hair thus exciting an electrical response in the hair cells.

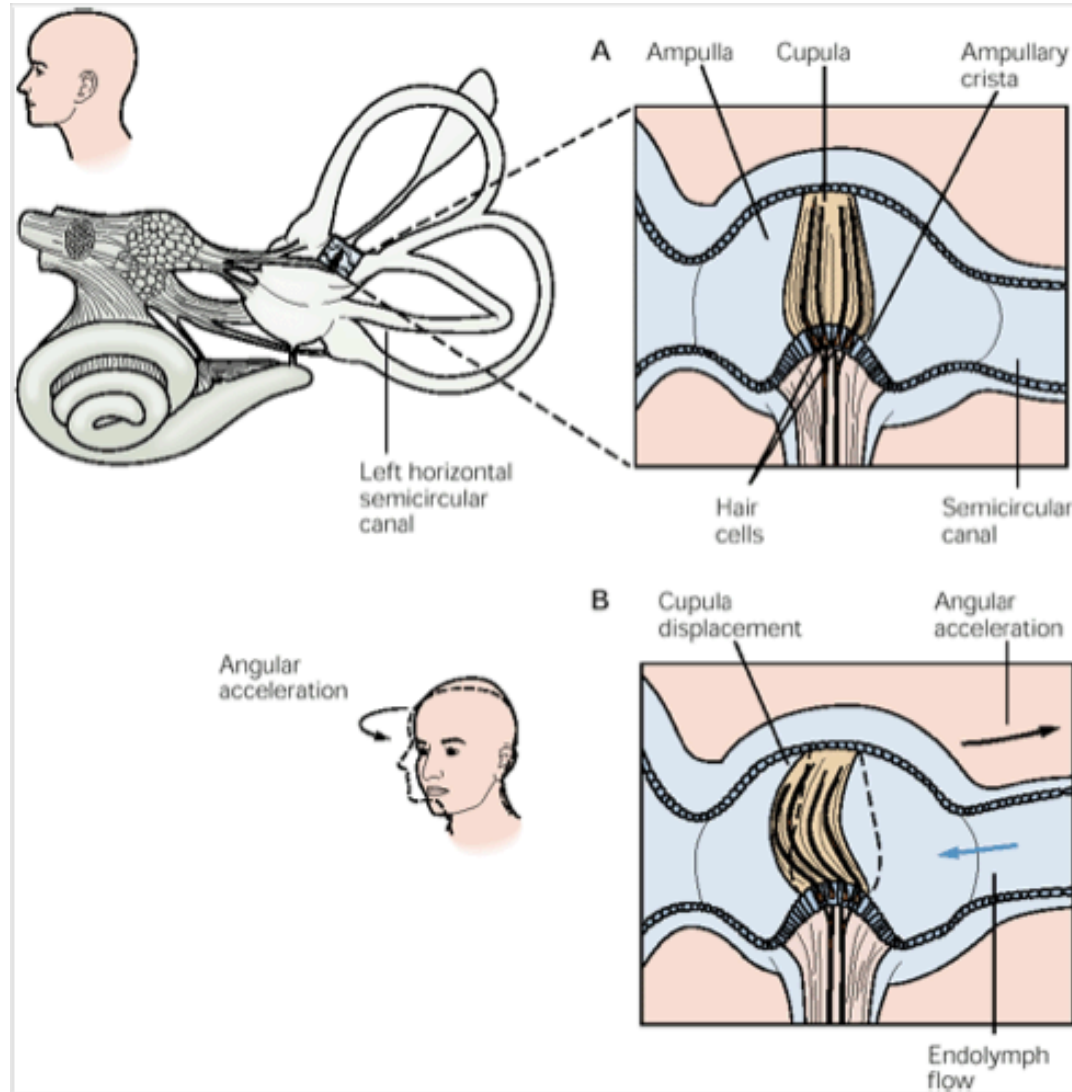
Spatial organization of the otolith organs



The hair cells in each organ are localized to a roughly elliptical patch, called the *macula*. The hair bundles are oriented orthogonally to a curving midline (the striola). This arrangement allows for detection of all possible stimulus orientations within the plane of the macula. Any particular horizontal acceleration maximally depolarizes one group of hair cells and maximally inhibits a complementary set. Because the organs are bilateral, the brain receives additional information from the contralateral labyrinth.

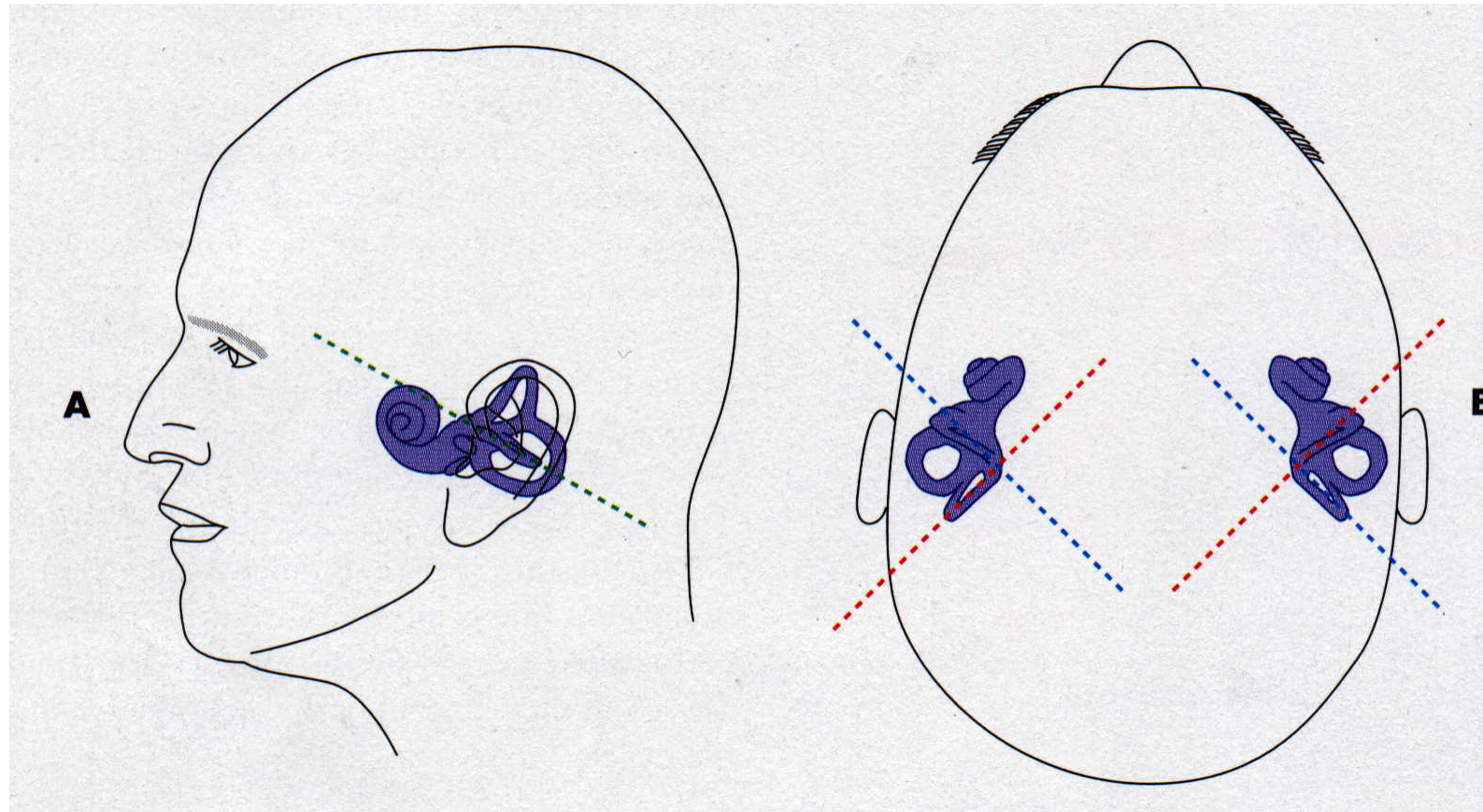
The utricles are oriented horizontally, the saccules are oriented vertically. The hair cells in the utricles respond to accelerations in the horizontal plane; saccules are especially sensitive to vertical accelerations, of which gravity is the most important.

The semicircular canals



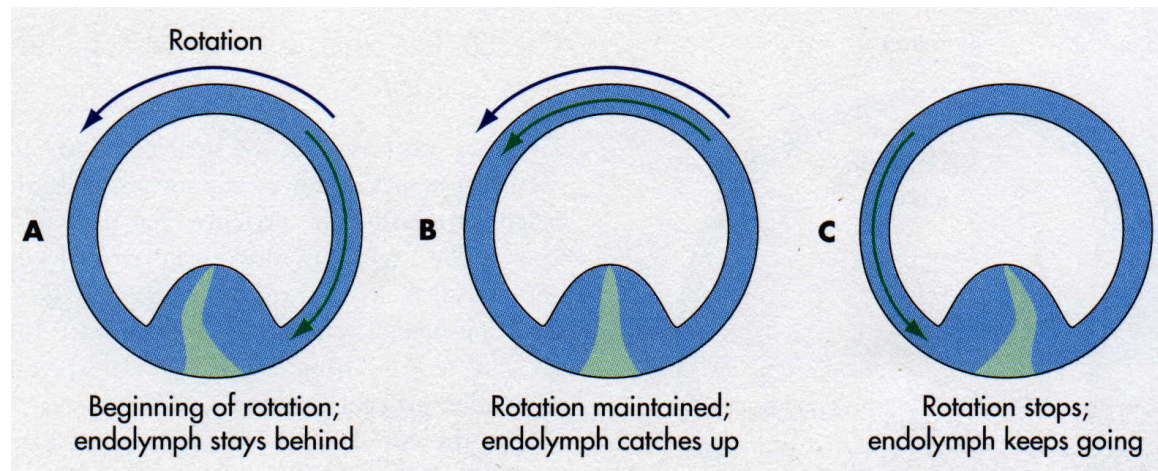
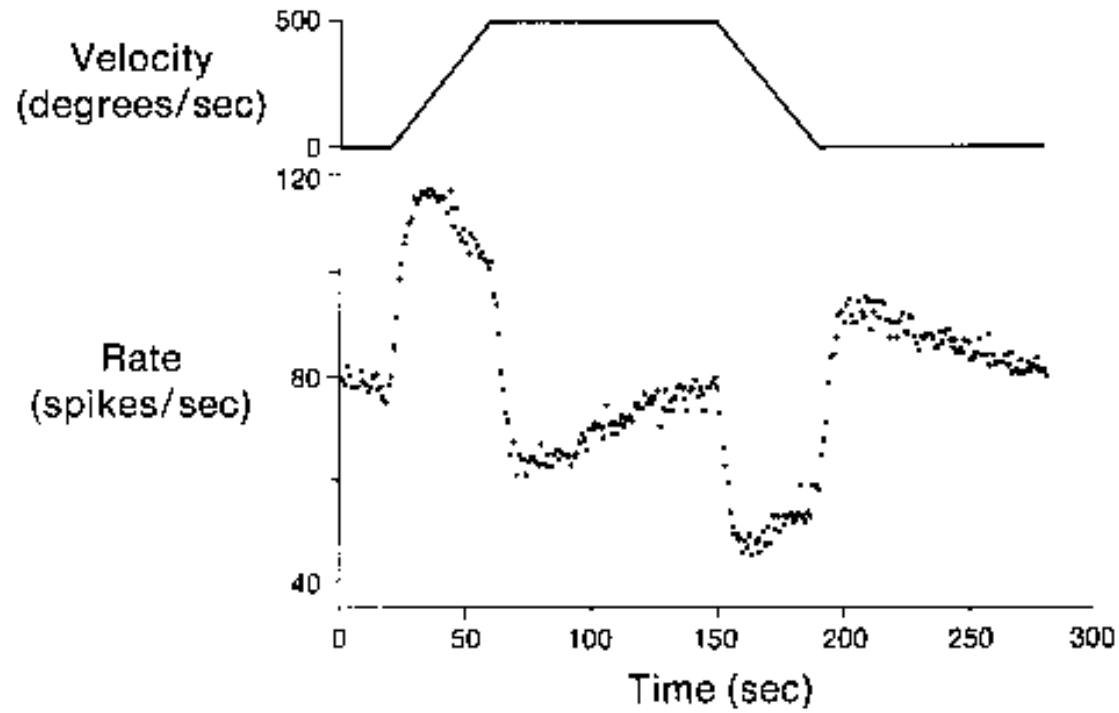
A thickened zone of epithelium, the ampulla, contains the hair cells. The hair bundles of the hair cells extend into a gelatinous cupula, which stretches from the crista to the roof of the ampulla. The cupula is displaced by the flow of endolymph when the head moves. As a result, the hair bundles extending into the cupula are also displaced. Because all the hair bundles in each semicircular canal share a common orientation, angular acceleration in one direction depolarizes hair cells while acceleration in the opposite direction hyperpolarizes the receptor cells and diminishes spontaneous neural activity.

Orientation of the semicircular canals



In each labyrinth the three canals are almost precisely perpendicular to one another, so that the canals represent accelerations about three mutually orthogonal axes. The planes in which the semicircular canals lie do not, however, correspond with the head's major anatomical planes.

Responses of receptors in semicircular canals



Menière Disease

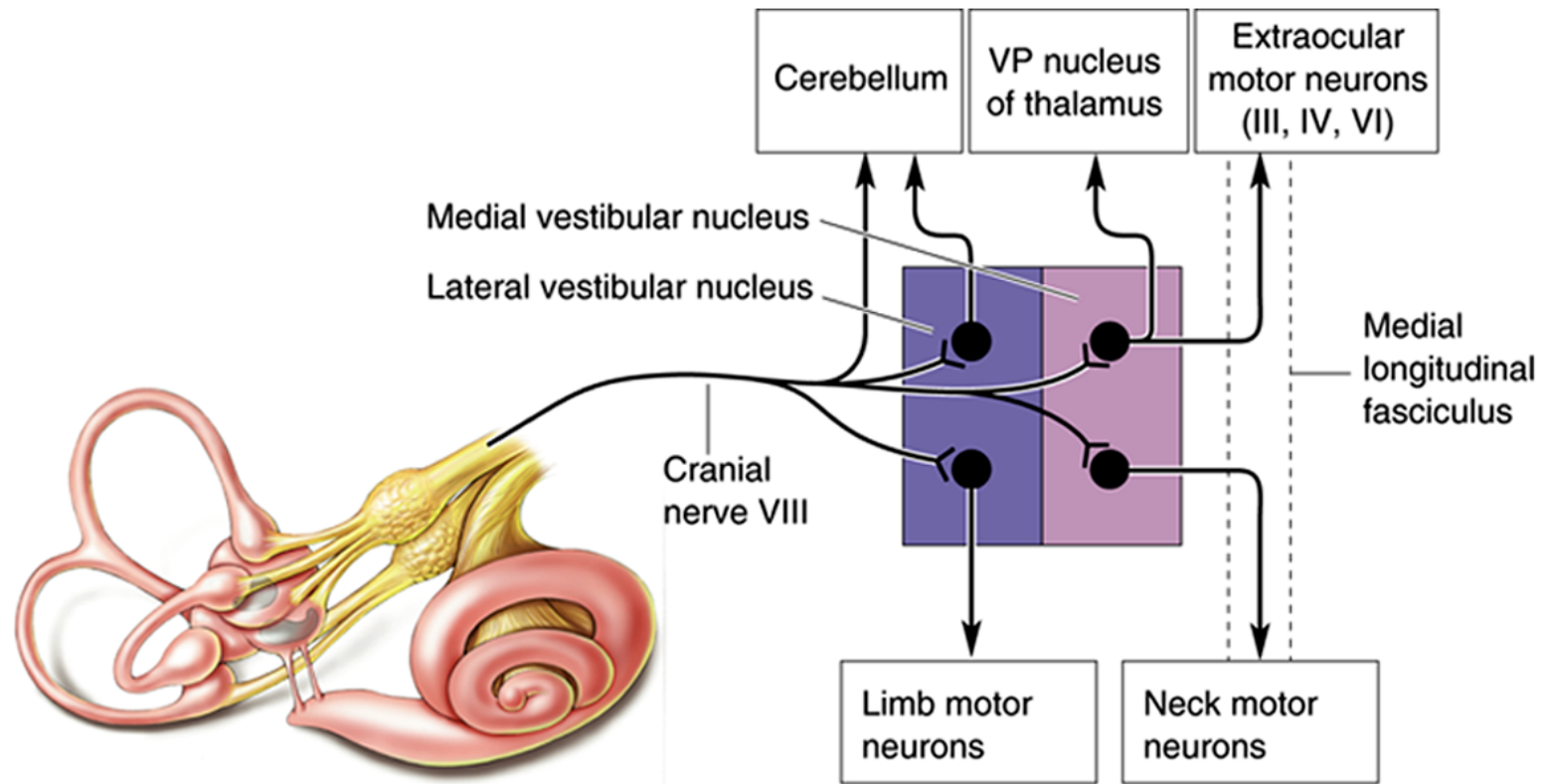
- Menière disease affects the vestibular labyrinth.
- It is characterized by relapsing vertigo (dizziness), with attacks lasting from tens of minutes to tens of hours. The vestibular symptoms are often accompanied by noise in the ears (*tinnitus*) and distorted hearing.
- It is believed to be linked to an excess of endolymph in the inner ear.
- Removal of the affected labyrinth surgically may relieve severe vertigo.
- Vincent Van Gogh may have suffered from Menière disease.



Vincent van Gogh, Selfportrait, 1889

K. Arenberg, L. F. Countryman, L. H. Bernstein and G. E. Shambaugh Jr, Van Gogh had Meniere's disease and not epilepsy, JAMA, Vol. 264 No. 4, July 25, 1990
Arnold, Wilfred N. (1992). "Vincent van Gogh: Chemicals, Crises, and Creativity". *Birkhäuser Boston*.

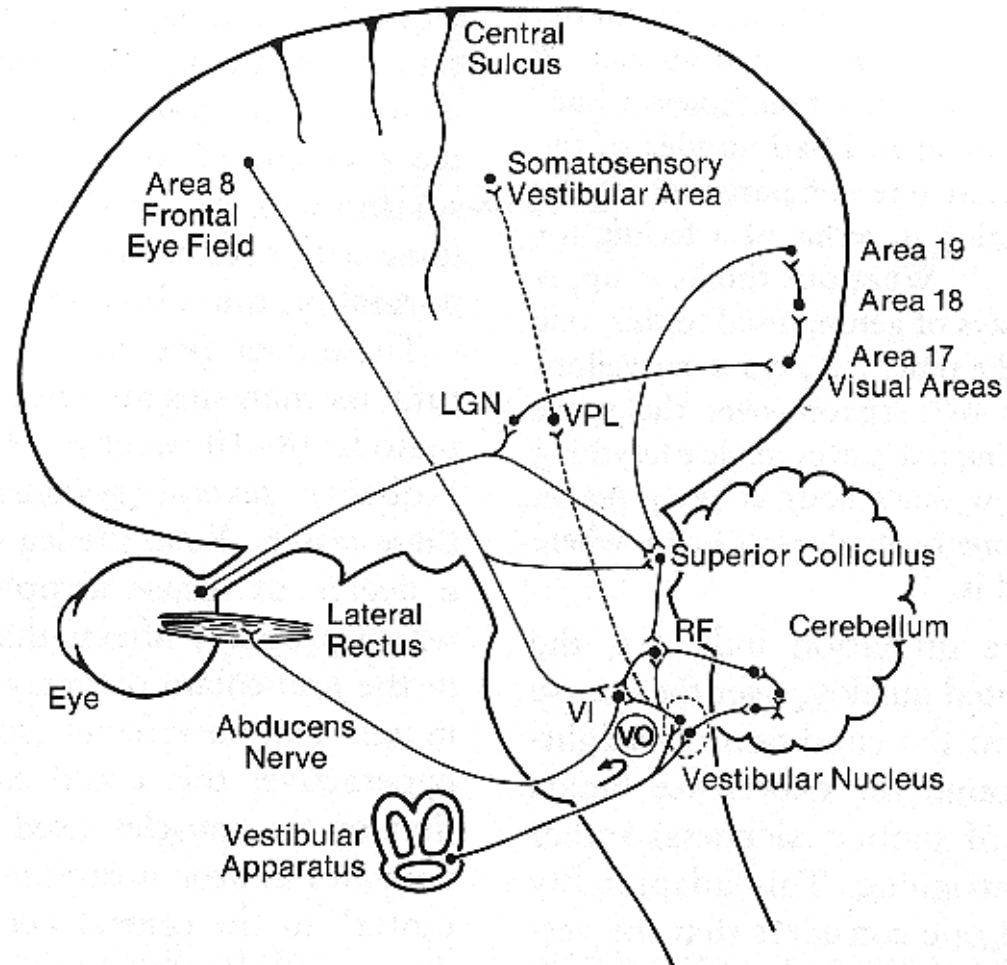
Vestibular pathways



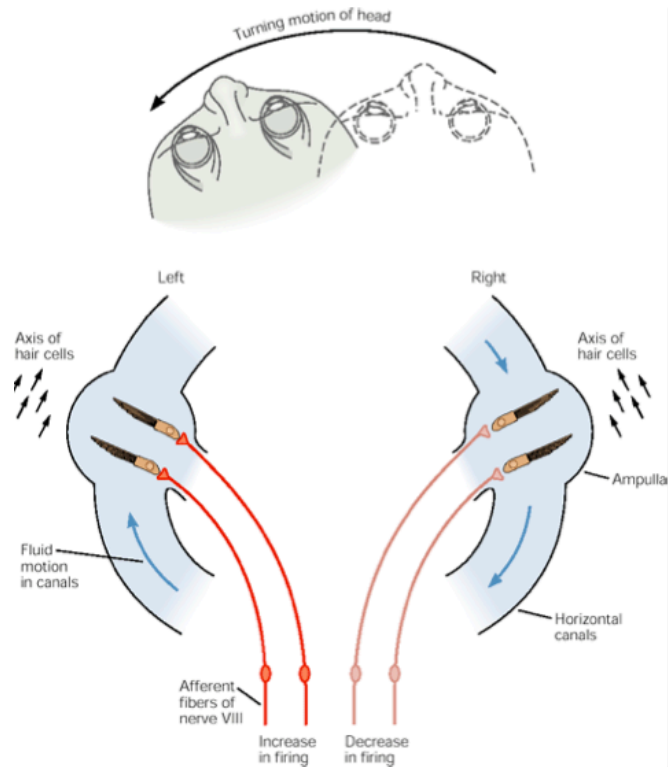
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The axons that carry the hair cells responses to the central nervous system terminate in several large cell groups (vestibular nuclei) in the brainstem. From there the signals go to neck and trunk motoneurons, to limb motoneurons, to cerebellum, thalamus and extraocular motoneurons. This network of vestibular connections is responsible for the various reflexes that the body uses to compensate for head movement and the perception of motion in space.

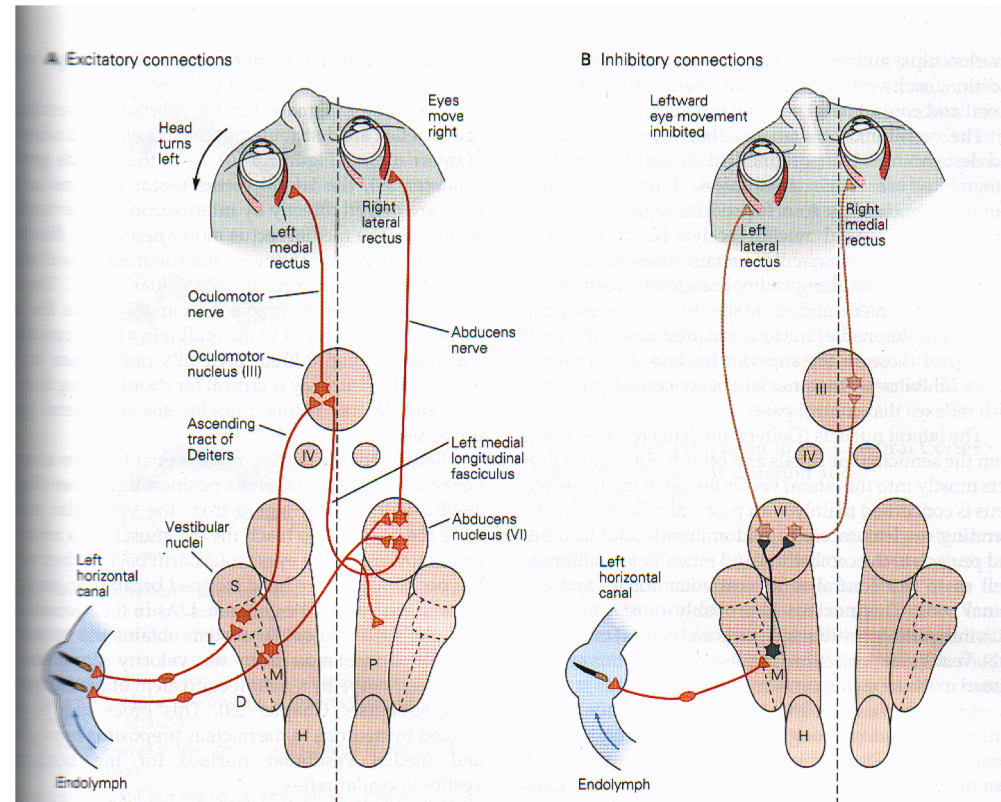
Circuits involved in control of eye movements



The vestibulo-ocular reflex

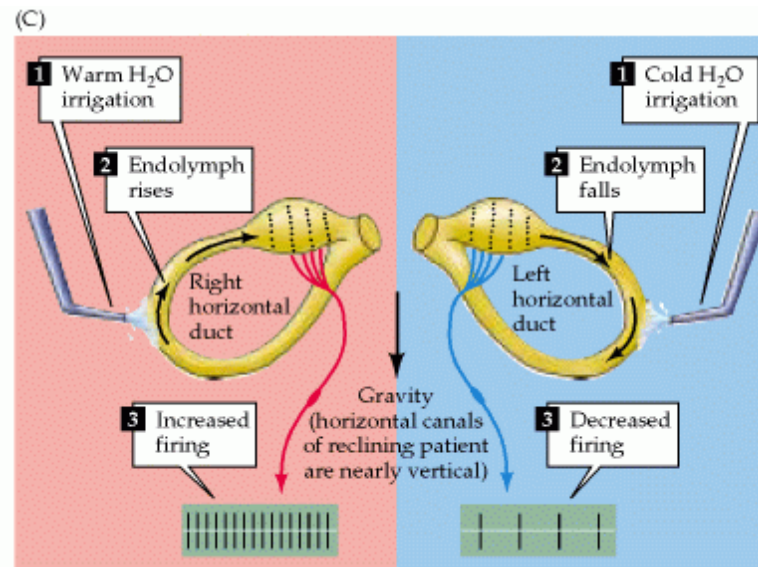


Rotation of the head in a counterclockwise direction causes endolymph to move clockwise with respect to the canals. This reflects the stereocilia in the left canal in the excitatory direction, thereby exciting the afferent fibers on this side. In the right canal the hair cells are hyperpolarized and afferent firing there decreases.

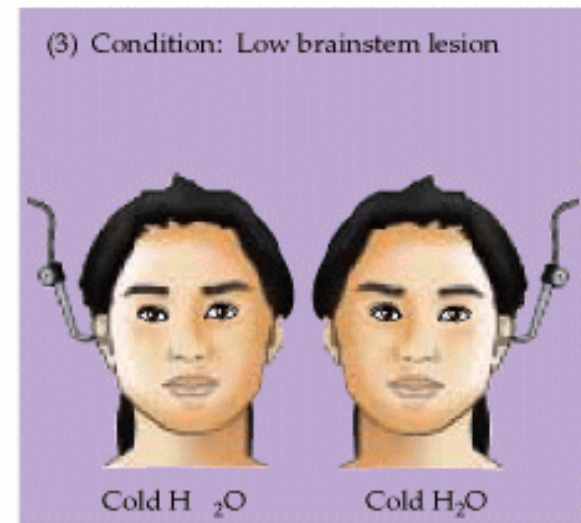
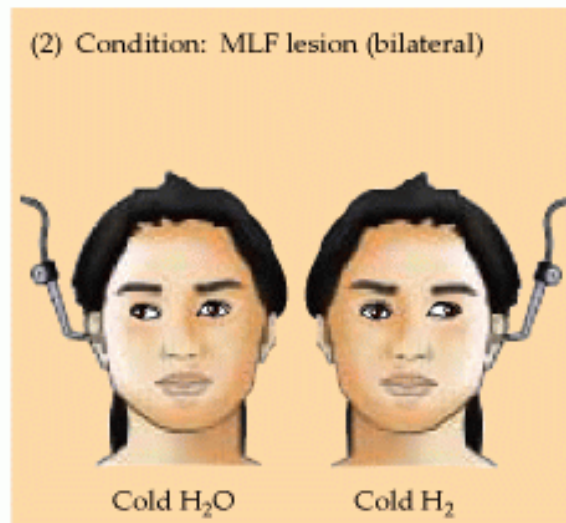
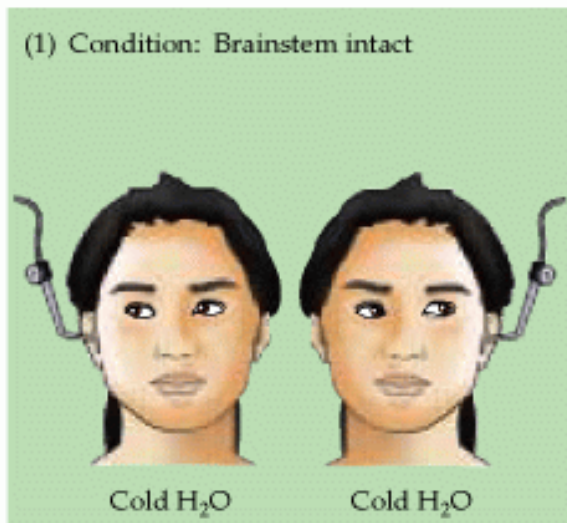


The vestibulo-ocular reflex keeps the visual images fixed on the retina, by moving the eyes when the head moves. Vestibular nerve signals head velocity to the vestibular nuclei and motoneurons that control ocular muscles. E.g., counterclockwise head rotation excites the left horizontal canal, which then excites neurons that evoke rightward eye movement.

Caloric stimulation



(D) Ocular reflexes in unconscious patients



Zero gravity



1. Pleasant and intriguing experience.
2. Space adaptation syndrome (SAS) – vomiting, headache, nausea.
3. Fast adaptation (< 72 hours)
4. Upon return to Earth after long-term weightlessness, slow adaptation, e.g., in maintaining standing balance with eyes closed.
5. After more than 1 month flights astronauts experience vision problems due to redistribution of fluids and increased pressure on the eyeballs, causing optic nerve crush.