



Sixth lecture

Auditory System

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Auditory system

The Vertebrate Hair Cell: Mechanoreceptor Mechanism, Tip Links, K^+ and Ca^{2+} Channels

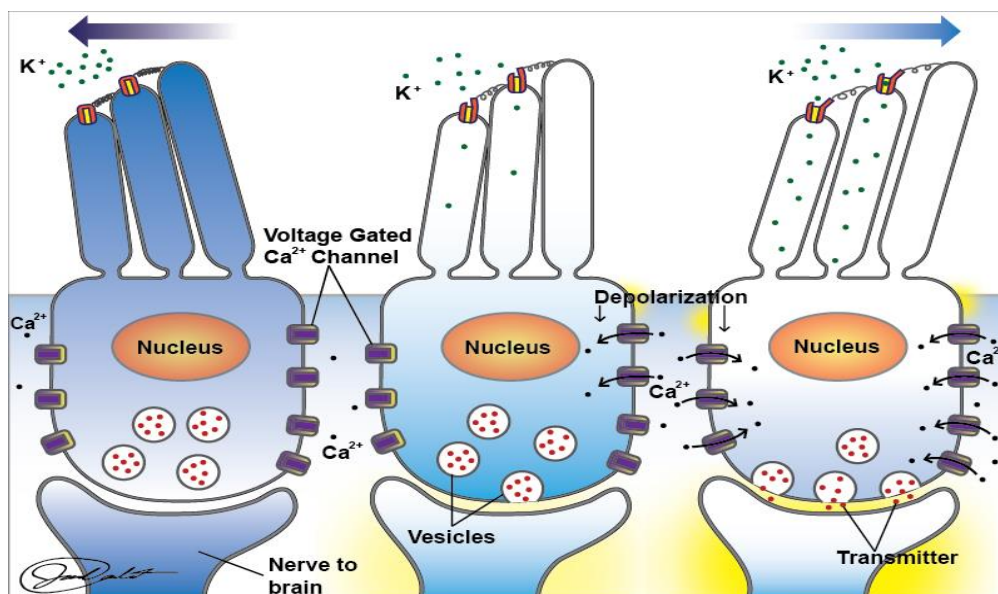


Figure 12.1 illustrates the process of mechanical transduction at the tips of the hair cell cilia.

The key structure in the vertebrate auditory and vestibular systems is the hair cell. The hair cell first appeared in fish as part of a long, thin array along the side of the body, sensing movements in the water. In higher vertebrates the internal fluid of the inner ear (not external fluid as in fish) bathes the hair cells, but these cells still sense movements in the surrounding fluid. Several specializations make human hair cells responsive to various forms of mechanical stimulation. Hair cells in the Organ of Corti in the cochlea of the ear respond to sound. Hair cells in the cristae ampullares in the semicircular ducts respond to angular acceleration (rotation of the head). Hair cells in the maculae of the

sacculle and the utricle respond to linear acceleration (gravity). (See the chapter on Vestibular System: Structure and Function). The fluid, termed endolymph, which surrounds the hair cells is rich in potassium. This actively maintained ionic imbalance provides an energy store, which is used to trigger neural action potentials when the hair cells are moved. Tight junctions between hair cells and the nearby supporting cells form a barrier between endolymph and perilymph that maintains the ionic imbalance.

Cilia emerge from the apical surface of hair cells. These cilia increase in length along a consistent axis. There are tiny thread-like connections from the tip of each cilium to a non-specific cation channel on the side of the taller neighboring cilium. The tip links function like a string connected to a hinged hatch. When the cilia are bent toward the tallest one, the channels are opened, much like a trap door. Opening these channels allows an influx of potassium, which in turn opens calcium channels that initiates the receptor potential. This mechanism transduces mechanical energy into neural impulses. An inward K^+ current depolarizes the cell, and opens voltage-dependent calcium channels. This in turn causes neurotransmitter release at the basal end of the hair cell, eliciting an action potential in the dendrites of the VIIIth cranial nerve.

Hair cells normally have a small influx of K^+ at rest, so there is some baseline activity in the afferent neurons. Bending the cilia toward the tallest one opens the potassium channels and increases afferent activity. Bending the cilia in the opposite direction closes the channels and decreases afferent activity. Bending the cilia to the side has no effect on spontaneous neural activity.

The auditory system changes a wide range of weak mechanical signals

into a complex series of electrical signals in the central nervous system. Sound is a series of pressure changes in the air. Sounds often vary in frequency and intensity over time. Humans can detect sounds that cause movements only slightly greater than those of Brownian movement. Obviously, if we heard that ceaseless (except at absolute zero) motion of air molecules we would have no silence.

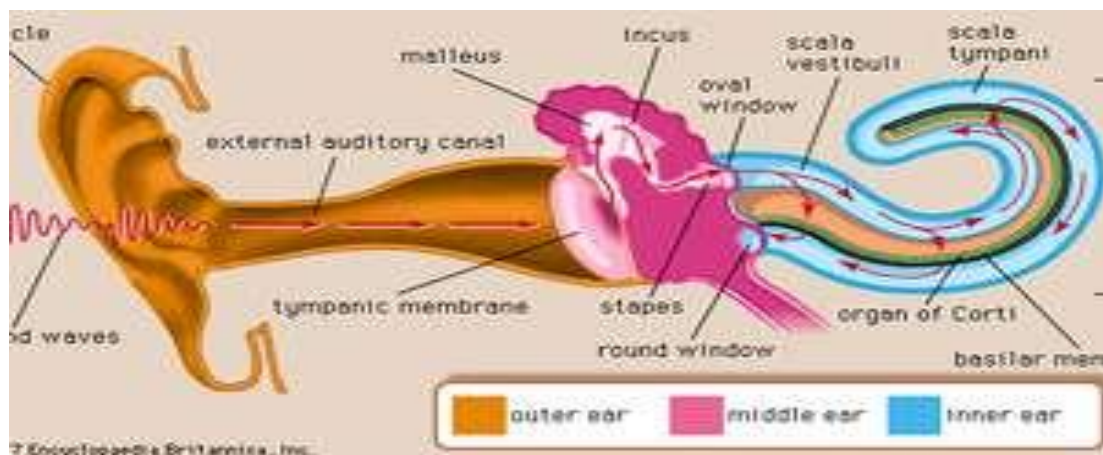


Figure 12.2 depicts these alternating compression and rarefaction (pressure) waves impinging on the ear. The pinna and external auditory meatus collect these waves, change them slightly, and direct them to the tympanic membrane. The resulting movements of the eardrum are transmitted through the three middle-ear ossicles (malleus, incus and stapes) to the fluid of the inner ear. The footplate of the stapes fits tightly into the oval window of the bony cochlea. The inner ear is filled with fluid. Since fluid is incompressible, as the stapes moves in and out there needs to be a compensatory movement in the opposite

direction. Notice that the round window membrane, located beneath the oval window, moves in the opposite direction.

Because the tympanic membrane has a larger area than the stapes footplate there is a hydraulic amplification of the sound pressure. Also because the arm of the malleus to which the tympanic membrane is attached is longer than the arm of the incus to which the stapes is attached, there is a slight amplification of the sound pressure by a lever action. These two impedance matching mechanisms effectively transmit air-borne sound into the fluid of the inner ear. If the middle-ear apparatus (ear drum and ossicles) were absent, then sound reaching the oval and round windows would be largely reflected.

The Cochlea: three scalae, basilar membrane, movement of hair cells

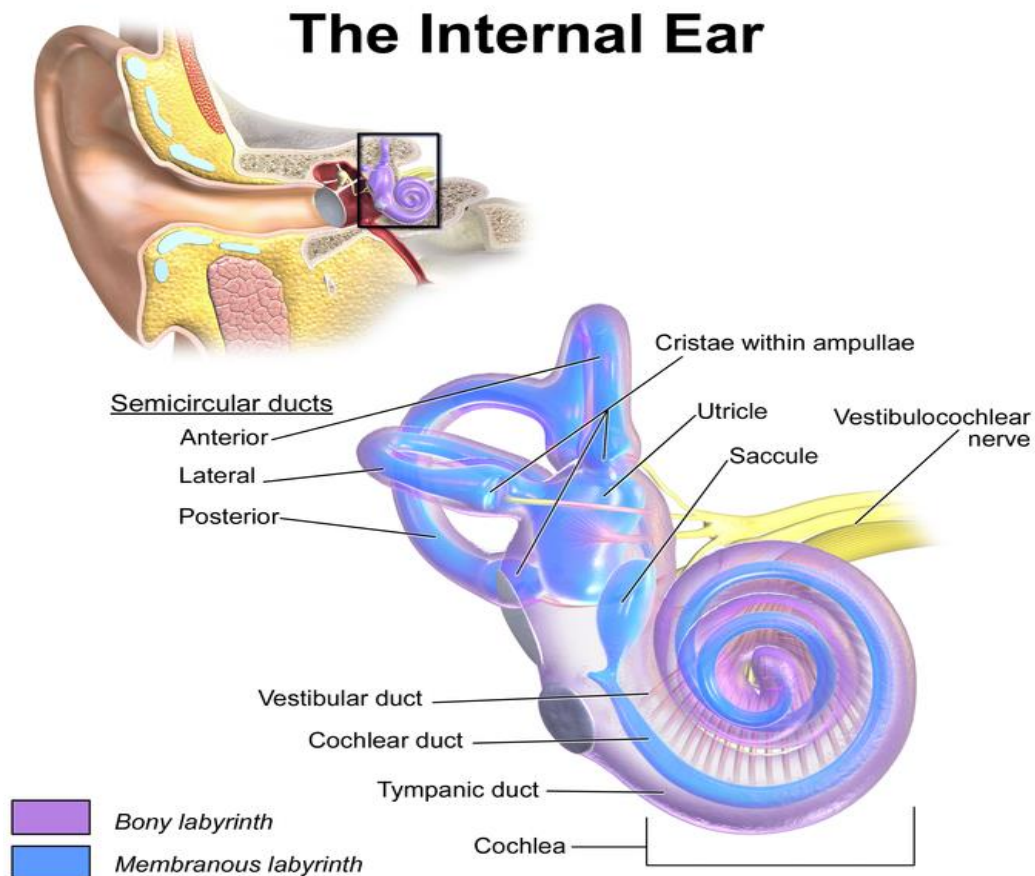


Figure 12.3 illustrates a cross section through the cochlea.

The **cochlea** is a long coiled tube, with three channels divided by two thin membranes. The top tube is the **scala vestibuli**, which is connected to the oval window. The bottom tube is the **scala tympani**, which is connected to the round window. The middle tube is the **scala media**, which contains the **Organ of Corti**. The Organ of Corti sits on the basilar membrane, which forms the division between the **scala media** and **scala tympani**.

The three **scalae** (**vestibuli**, **media**, **tympani**) are cut in several places as they spiral around a central core. The cochlea makes 2-

1/2 turns in the human (hence the 5 cuts in midline cross section). The tightly coiled shape gives the cochlea its name, which means snail in Greek (as in conch shell). As explained in Tonotopic Organization, high frequency sounds stimulate the base of the cochlea, whereas low frequency sounds stimulate the apex. This feature is depicted in the animation of Figure 12.3 with neural impulses (having colors from red to blue representing low to high frequencies, respectively) emerging from different turns of the cochlea. The activity in Figure 12.3 would be generated by white noise that has all frequencies at equal amplitudes. The moving dots are meant to indicate afferent action potentials. Low frequencies are transduced at the apex of the cochlea and are represented by red dots. High frequencies are transduced at base of the cochlea and are represented by blue dots. A consequence of this arrangement is that low frequencies are found in the central core of the cochlear nerve, with high frequencies on the outside.

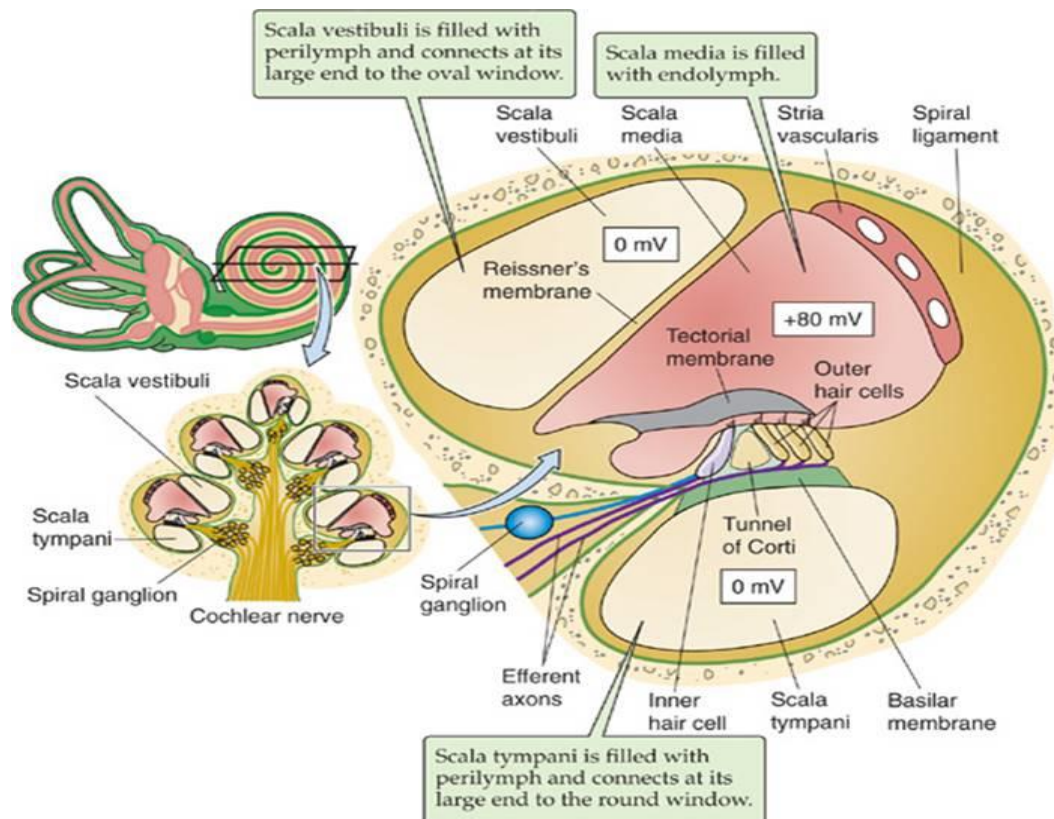


Figure 12.4 illustrates one cross section of the cochlea. Sound waves cause the oval and round windows at the base of the cochlea to move in opposite directions (See Figure 12.2). This causes the basilar membrane to be displaced and starts a traveling wave that sweeps from the base toward the apex of the cochlea (See Figure 12.7). The traveling wave increases in amplitude as it moves, and reaches a peak at a place that is directly related to the frequency of the sound. The illustration shows a section of the cochlea that is moving in response to sound.

Figure 12.5 illustrates a higher magnification of the Organ of Corti. The traveling wave causes the basilar membrane and hence the Organ of Corti to move up and down. The organ of

Corti has a central stiffening buttress formed by paired pillar cells. Hair cells protrude from the top of the Organ of Corti. A tectorial (roof) membrane is held in place by a hinge-like mechanism on the side of the Organ of Corti and floats above the hair cells. As the basilar and tectorial membranes move up and down with the traveling wave, the hinge mechanism causes the tectorial membrane to move laterally over the hair cells. This lateral shearing motion bends the cilia atop the hair cells, pulls on the fine tip links, and opens the trap-door channels (See Figure 12.1). The influx of potassium and then calcium causes neurotransmitter release, which in turn causes an EPSP that initiates action potentials in the afferents of the VIIIth cranial nerve. Most of the afferent dendrites make synaptic contacts with the inner hair cells.

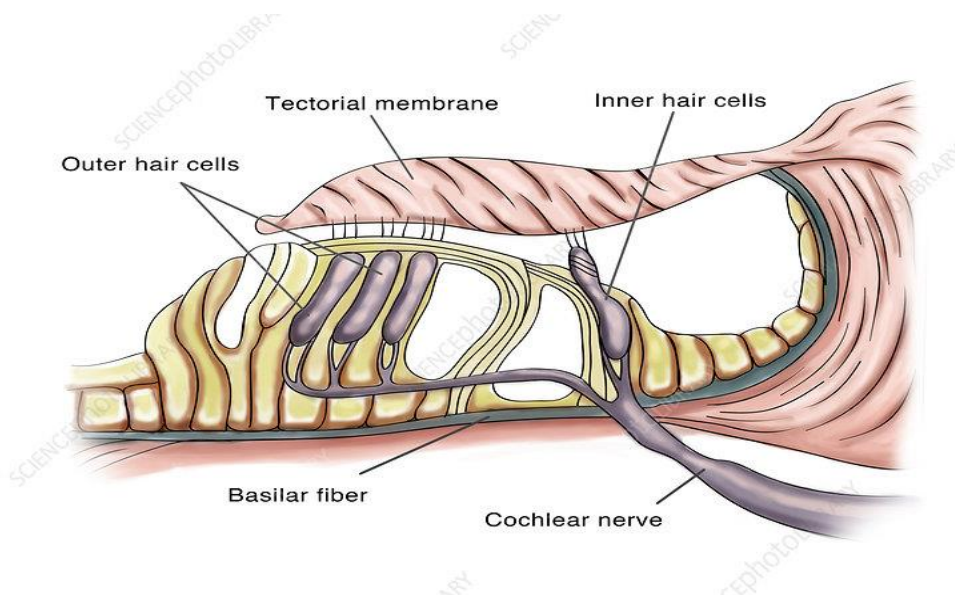


Figure 12.6 looks down on the Organ of Corti. There are two

types of hair cells, inner and outer. There is one row of inner hair cells and three rows of outer hair cells. Most of the afferent dendrites synapse on inner hair cells. Most of efferent axons synapse on the outer hair cells. The outer hair cells are active. They move in response to sound and amplify the traveling wave. The outer hair cells also produce sounds that can be detected in the external auditory meatus with sensitive microphones. These internally generated sounds, termed otoacoustic emissions, are now used to screen newborns for hearing loss. Figure 12.6 shows an immunofluorescent whole mount image of a neonatal mouse cochlea showing the three rows of outer hair cells and the single row of inner hair cells. The mature human cochlea would look approximately the same. Superimposed schematically-depicted neurons show the typical pattern of afferent connections. Ninety-five percent of the VIIIth nerve afferents synapse on inner hair cells. Each inner hair cell makes synaptic connections with many afferents. Each afferent connects to only one inner hair cell. About five percent of the afferents synapse on outer hair cells. These afferents travel a considerable distance along the basilar membrane away from their ganglion cells to synapse on multiple outer hair cells. Less than one percent (~0.5%) of the afferents synapse on multiple inner hair cells. The below micrograph is courtesy of Dr. Douglas Cotanche, Department of Otolaryngology, Children's Hospital of Boston, Harvard Medical School. Reprinted with permission.

