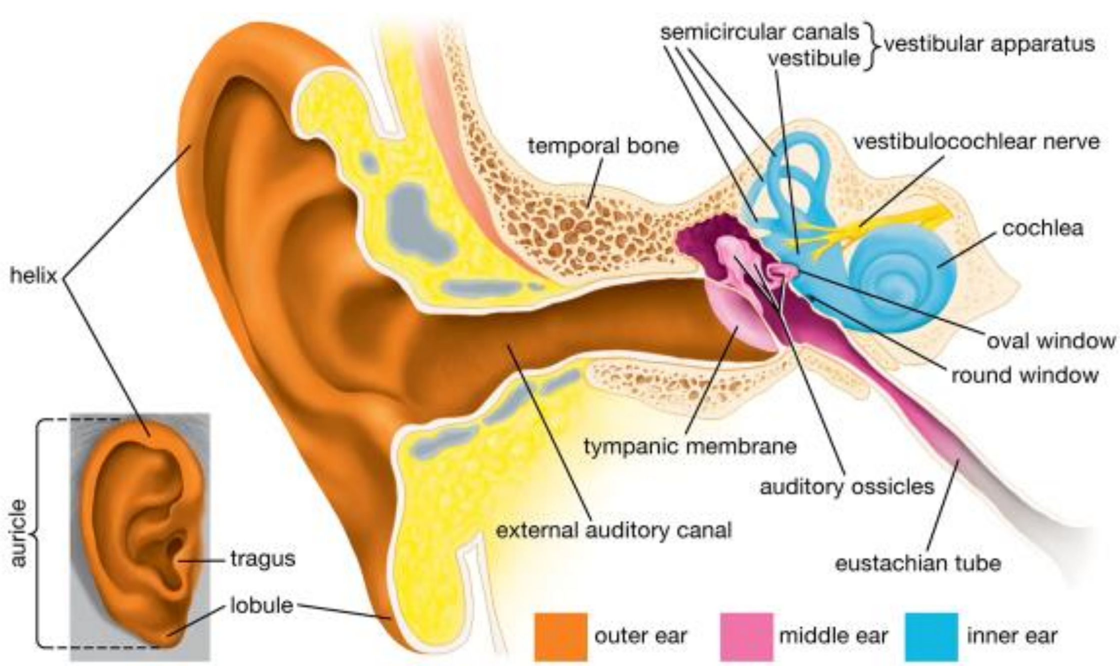
The Special Senses

Physiology of Hearing

The Tympanic Membrane and Ossicular System

The process of hearing begins when sound waves in air strike the tympanic membrane, or eardrum. The tympanic membrane is a thin, cone-shaped structure whose central portion is attached to the handle of the malleus—the first of the three ossicles of the middle ear. The malleus articulates with the incus, which in turn connects to the stapes. The stapes footplate is anchored to the oval window of the cochlea, forming the mechanical link between air vibrations in the external auditory canal and fluid vibrations within the inner ear.

The tensor tympani muscle, attached to the malleus, maintains tension on the tympanic membrane, ensuring effective vibration transmission. This mechanical linkage transforms the relatively weak air vibrations into amplified pressure changes sufficient to set the dense cochlear fluids into motion.



Impedance Matching by the Ossicular Chain

A critical function of the ossicular system is impedance matching—the process of overcoming the resistance difference between air in the external auditory canal and fluid in the cochlea. Without this mechanism, most of the sound energy would be reflected at the air–fluid boundary, and hearing would be inefficient.

The ossicular system achieves impedance matching through two mechanisms. First, the ossicles act as a lever system that increases the force of vibration by about 1.3 times. Second, because the area of the tympanic membrane (≈55 mm^2) is much larger than that of the oval window (≈3.2 mm^2), the pressure applied to the cochlear fluid increases approximately 22-fold. Together, these factors make the ear capable of transmitting sound waves efficiently from air to the inner ear fluid. In the absence of a functional ossicular chain, as occurs in ossicular discontinuity or otosclerosis, normal sounds become barely audible.

Protective Reflexes of the Middle Ear

Two small muscles within the middle ear—the stapedius and tensor tympani—provide a protective mechanism against excessively loud sounds. In response to loud auditory stimulation, these muscles contract reflexively, increasing the rigidity of the ossicular chain. This reflex, known as the attenuation reflex, particularly reduces the transmission of low-frequency vibrations, thereby preventing damage to the cochlea and enhancing speech discrimination in noisy environments. The reflex is also activated during one's own speech, minimizing the perception of self-generated sounds.

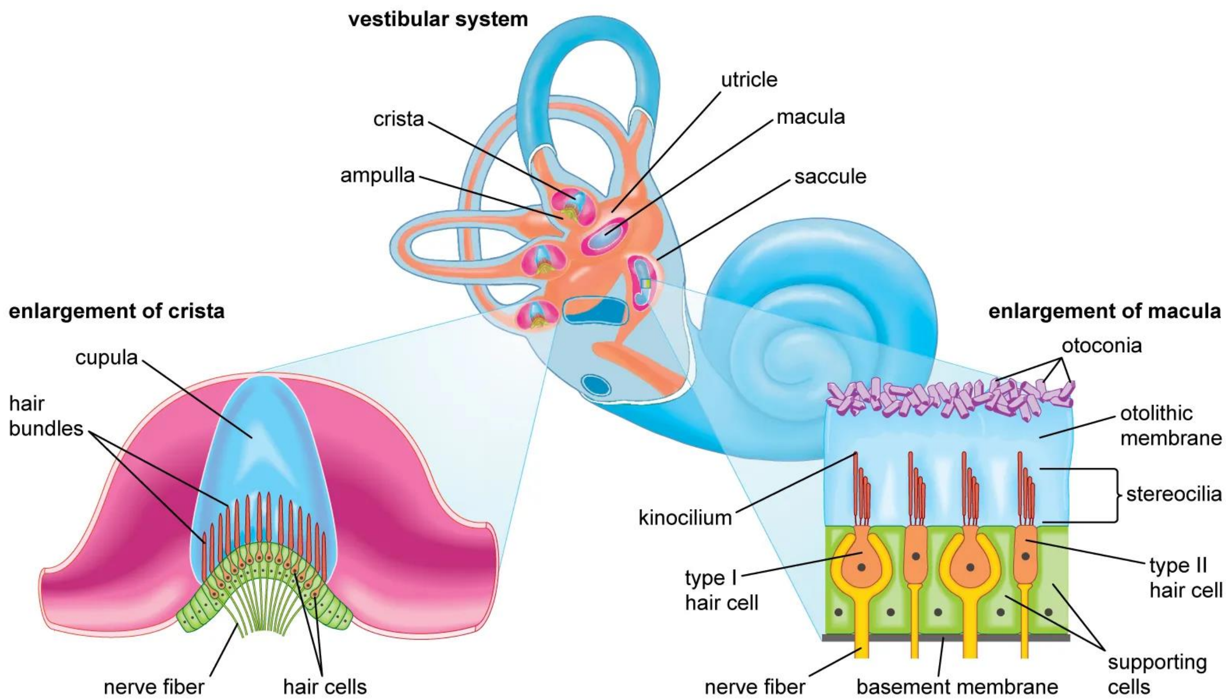
Bone Conduction of Sound

Although air conduction is the primary mode of hearing, vibrations of the skull bones can also stimulate the cochlea—a phenomenon known as bone conduction. This can be demonstrated by placing a vibrating tuning fork against the skull, such as on the forehead or mastoid process. Under normal conditions, however, the contribution of bone conduction to everyday hearing is minimal because air-transmitted sounds dominate.

The Cochlea

The cochlea is a spiral-shaped structure composed of three parallel compartments: the scala vestibuli, scala media, and scala tympani. The scala vestibuli and scala media are separated by Reissner's membrane, while the scala media and scala tympani are divided by the basilar membrane. Sitting atop the basilar membrane is the organ of Corti, the sensory organ for hearing. The roof of the organ of Corti is formed by the tectorial membrane.

At the apex of the cochlea, the scala vestibuli and scala tympani communicate through an opening called the helicotrema. The basilar membrane varies in stiffness along its length—it is narrow and stiff near the oval window (base) and wide and flexible near the helicotrema (apex). Consequently, high-frequency sounds cause maximal vibration near the base, while low-frequency sounds stimulate the apical region.

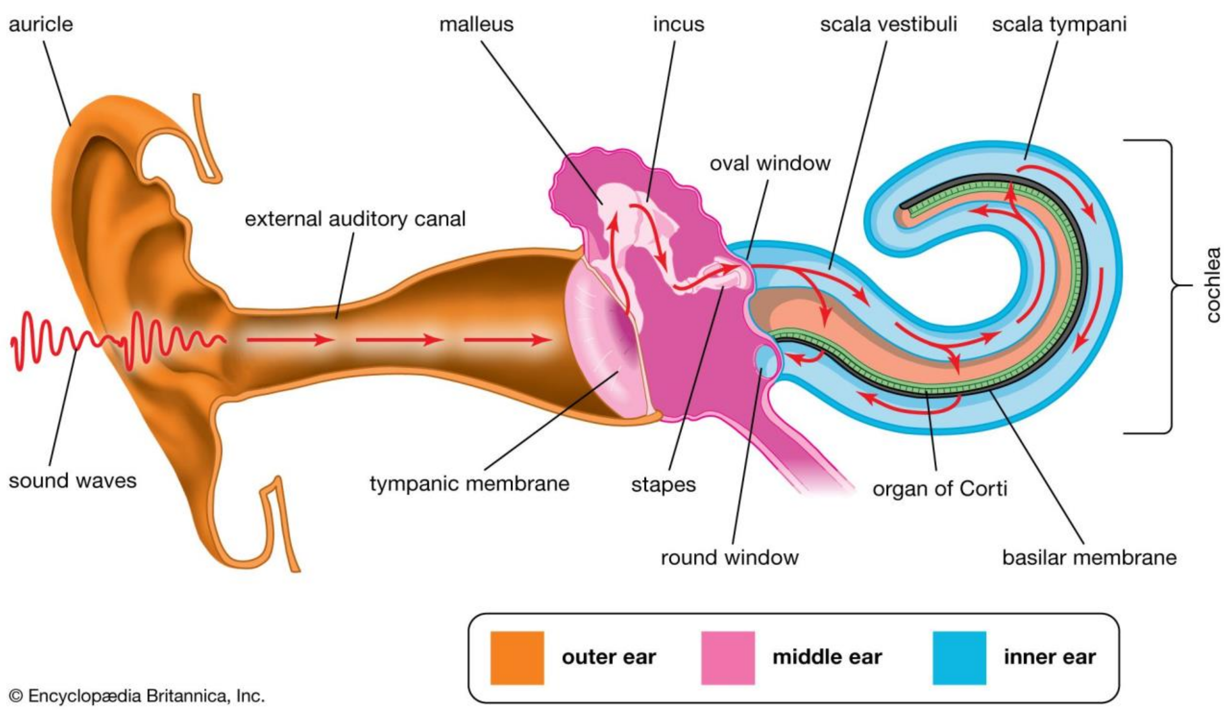


Transmission of Sound Waves in the Cochlea: The Traveling Wave

When the stapes footplate pushes against the oval window, it generates a pressure wave in the perilymph of the scala vestibuli. This pressure wave travels along the cochlea, causing a traveling wave to form on the basilar membrane.

Each segment of the basilar membrane resonates maximally at a specific sound frequency—its characteristic frequency. Thus, high-pitched sounds produce peak displacement near the base, whereas low-pitched sounds resonate closer to the apex. The wave amplitude increases until it reaches the point corresponding to its frequency, where it dissipates rapidly. This mechanical frequency analysis forms the basis of tonotopic organization in the auditory system.

The amplitude of vibration also varies with sound intensity: louder sounds produce larger displacements of the basilar membrane, activating more sensory hair cells.



Function of the Organ of Corti

The organ of Corti contains two main receptor cell types—inner hair cells and outer hair cells. Approximately 3,500 inner hair cells are arranged in a single row, while about 12,000 outer hair cells form three to four parallel rows. Nearly 95% of afferent fibers in the cochlear (auditory) nerve synapse with inner hair cells, emphasizing their primary sensory role.

The apical surface of each hair cell bears bundles of stereocilia and one kinocilium projecting into the tectorial membrane. As the basilar membrane moves in response to sound, shearing forces bend these cilia. Bending toward the kinocilium opens mechanically gated potassium channels, allowing K^+ influx from the endolymph (a potassium-rich fluid secreted by the stria vascularis). This depolarizes the cell and triggers neurotransmitter release onto afferent nerve terminals. Bending in the opposite direction closes the channels, leading to hyperpolarization.

The endocochlear potential, approximately +80 mV relative to perilymph, combined with the hair cell's resting potential of −70 mV, produces an effective potential difference of about 150 mV across the ciliary membrane. This large voltage difference enhances the sensitivity of the hair cells to minute mechanical displacements.

Frequency and Loudness Coding

The "Place" Principle

The auditory system identifies sound frequency primarily through the place principle—the specific location of maximal vibration along the basilar membrane. High-frequency tones stimulate the basal end near the oval window, while low-frequency tones activate the apical end near the helicotrema.

For very low frequencies (below 200 Hz), frequency discrimination depends not on place but on the volley principle, in which groups of auditory nerve fibers fire in synchrony with the sound wave frequency.

Determination of Loudness

1- Loudness perception depends on several factors:
2- Increased amplitude of basilar membrane vibration.

3- Recruitment of a greater number of hair cells (spatial summation).

Activation of outer hair cells at high vibration amplitudes, enhancing sensitivity and signaling high-intensity sounds.

Because sound energy varies over an enormous range (up to a trillionfold between a whisper and a loud explosion), the auditory system expresses intensity on a logarithmic scale, measured in decibels (dB). The human hearing range typically spans 20–20,000 Hz, but sensitivity varies with intensity—most acute hearing occurs between 500 and 5,000 Hz at moderate sound levels.

Central Auditory Pathways

Ascending Pathway

Primary afferent fibers arise from the spiral ganglion and enter the brainstem to synapse in the dorsal and ventral cochlear nuclei. From these nuclei, fibers project bilaterally—though with contralateral predominance—to the superior olivary complex, which serves as the first site of binaural interaction. Ascending fibers then travel via the lateral lemniscus to the inferior colliculus, continue to the medial geniculate body of the thalamus, and finally terminate in the primary auditory cortex (Brodmann areas 41 and 42) located in the transverse temporal gyrus of Heschl.

Throughout these pathways, the auditory system maintains tonotopic organization, preserving frequency mapping from the cochlea to the cortex.

Auditory Cortex Function

The primary auditory cortex processes the basic attributes of sound, including pitch and intensity. Surrounding it, the secondary auditory cortex (area 22) integrates these features into complex auditory perceptions such as speech and music. Bilateral lesions of the primary auditory cortex do not abolish hearing but impair sound localization. Lesions of the secondary area cause receptive aphasia, an inability to comprehend spoken words despite preserved hearing.

Sound Localization and Descending Modulation

The superior olivary complex determines sound direction by comparing input from both ears. The lateral nucleus detects differences in sound intensity, while the medial nucleus measures time differences in sound arrival between ears. These computations allow precise localization of sound sources in space.

Descending fibers from higher auditory centers project back to lower nuclei and even to the cochlea itself. These centrifugal pathways enable selective auditory attention—enhancing relevant sounds while suppressing background noise.

Part of Ear	Major Function	Key Structure	Type of Signal
External Ear	Collects sound	Pinna, auditory canal	Sound waves
Middle Ear	Transmits & amplifies	Ossicles, tympanic membrane	Mechanical vibration
Inner Ear (Cochlea)	Transduces sound to nerve impulse	Organ of Corti	Electrochemical signal
Vestibular Apparatus	Detects balance & movement	Semicircular canals, utricle, saccule	Electrochemical signal