Chapter

Structure and Physiology of Human Ear Involved in Hearing

Alishbah Sheikh, Bint-e-Zainab, Kanwal Shabbir and Ayesha Imtiaz

Abstract

Hearing is the fundamental sense based on the normal functioning of the hearing organ “the ear,” which plays a vital role in social interaction and the ability of learning. The human ear is divided into three parts: the outer, middle, and inner ear. Defects in outer and middle ear can cause conductive hearing loss, while the defective inner ear may lead to sensorineural hearing loss. So, it is important to study the structure and physiology of the human ear. When a sound of particular frequency enters the outer ear, it passes through the auditory canal and strikes the tympanic membrane. It vibrates and passes these vibrations to three ossicles present in the middle ear. The ossicles amplify the vibrations of sound and send them to the cochlea in the inner ear. Cochlea contains organ of Corti, which converts these vibrations into electrical signals by its hair cells. The neural signals in turn are interpreted by the brain, which one can hear and understand. The aim of this chapter is to review the basic structure and physiology of different parts of the human ear that are involved in the hearing process.

Keywords: hearing, human ear, organ of Corti, auditory system

1. Introduction

Sound is a mechanical energy wave which can travel through in air or any other physical medium (gas, liquid and solid). These longitudinal waves consist of alternating compressions and refractions. When sound waves travel through a medium, the particles of that medium vibrate parallel to the direction of sound wave that explains the longitudinal wave nature of sound. A human speaker or any other sound source produces the specific vibration patterns that are converted into appropriate auditory signals by the ear [1].

Hearing is the fundamental sense that allows one to perceive the sound. It also helps the person to communicate and detect different environmental signals. Human ear converts the physical vibration (sound) into a nerve impulse which is further processed by central auditory pathway of the brain. This mechanism of the sound interpretation is complex [2]. This chapter will mainly discuss the structure of different parts of the ear and their physiological interplay in hearing.
The hearing organ “the ear” is a paired organ, located one on each side of the head. Each ear contains the cochlea, a snail-shaped coiled moiety, as the sense organ. A human ear has hearing range of 20–20,000 Hz through the air conduction while this range is greater for much higher frequencies in case of bone conduction. The former part of the ear deals with conducting the sound to the sense organ cochlea and then the cochlea is responsible for the transduction of vibrations, which is performed by delicate hair cells. The ear is structurally and functionally partitioned into three parts that are required for normal hearing: the outer inner, middle ear, and the inner ear—the latter is further divided into the vestibular labyrinth and cochlea (Figure 1). These are discussed in detail below.

### 2. Structure and physiology of outer ear

The outer ear comprises the pinna and the auditory canal both of which transmit the focused sound signal on the tympanic membrane which separates the outer ear and middle ear. For functional hearing, proper development of the outer ear is essential. As outer ear defects are involved in a number of syndromic and non-syndromic conditions of conductive deafness, it is very crucial to understand the structure of the outer ear [3].
2.1 Pinna

The pinna protruding from the side of the skull is comprised of cartilage and is completely covered with skin. It is responsible for collecting the sound vibrations and funneling them to the auditory canal. The pinna is helpful in localizing the sound as it catches the sounds, which are more efficiently coming from the front than those coming from behind because of its angle. But this effect is applicable only in the case of high frequencies because of the wavelength of audible sound vibrations and also the relative size of the head. The head itself has a role in localizing the sound as it casts a shadow of sound in the case of middle frequencies, and in lower frequencies, the phases of sound arrival between the ears are responsible for localizing the sound.

2.2 Auditory Canal

The auditory canal is about 4 cm in length and the outer part with hairy skin and the inner thinner part (Figure 1). The outer hairy part has sebaceous and sweat glands [4, 5], both of which together with keratin form ear wax. The ear wax and the hair growth in the outer part of the canal serve as a disinfectant and provide a protective barrier for the ear. Moving inward, the skin of the auditory canal is thin and it is firmly attached to the deeper ear canal bone, which is a hard cavity that absorbs faint sound and then directs it to the tympanic membrane at its base.

2.3 Tympanic membrane

The tympanic membrane has an outer layer of skin that is continuous with the auditory canal and an inner layer called the endoderm [6]. The outer ectodermal layer is made of stratified and squamous epithelium, which displays lateral unique migration of cells from the center to the edges of the tympanic membrane where these epidermal cells can then exfoliate [7]. This process is referred to as the self-cleaning property of the outer ear. The inner layer of the tympanic membrane comprises of a simple squamous epithelium [8].

The tympanic membrane is divided into two main regions based on its morphology (Figure 2); firstly, the tense structure appropriate for the vibration known as the ventral pars tensa, and second the more elastic one the dorsal pars flaccida.

![Figure 2.](image)

The structural morphology of the tympanic membrane. Schematic of tympanic membrane, which is partitioned into two parts based on morphology: One the pars flaccida and second the pars tensa.
The pars flaccida also called as Shrapnell’s membrane is in the upper part of the tympanic membrane above the malleolar fold and is a relatively more fragile region than the other larger part of the tympanic membrane, the pars tensa [8, 9]. Both of these regions are tri-layered structures containing an inner layer of neural crest cells, which are in the arrangement of loose connective tissue, and this middle layer is sandwiched between two epithelium layers. The inner layer of pars tensa is the lamina propria consisting of further two collagen-rich connective tissue layers [10]; the outer radiative layer and an inner circular layer. While in pars flaccida there is no regular arrangement of extracellular matrix in the inner layer. So, both these regions of the tympanic membrane, the pars tensa and pars flaccid, are different from each other at a cellular and gross level. These structural and functional differences explain why retraction pocket (a condition in which the tympanic membrane is pulled more deeply into the middle ear cavity and may cause pain) more commonly occurs in pars flaccida [11].

The whole tympanic membrane structure has a thickness of about 0.1 millimeters and in the middle ear cavity, it covers an opening (round) of about 1 cm in diameter. Although the tympanic membrane is generally referred to as the eardrum, technically the middle ear cavity is the eardrum with the tympanic membrane acting as the drum skin [12].

3. Structure and physiology of middle ear

The middle ear, an air-filled cavity is associated with the back of the nose by a long and thin tube known as the Eustachian tube (Figure 1). In the middle ear, the outer wall is the tympanic membrane while the cochlea is the inner wall. The middle ear floor is a thin bony plate that covers the beginning of the jugular bulb, a great vein that drains the blood from the head. At the upper limit of the middle ear, it forms the bone beneath middle lobe of the brain. At the middle ear front end, there is the opening of the Eustachian tube, and at its posterior end lies a passageway to mastoid cells, which are a group of air cells present within temporal bone [12]. The middle ear, lined with the respiratory membrane, is basically an extension of respiratory air spaces of the sinuses and the nose. This respiratory membrane, thick at the Eustachian tube and thin when passing through mastoid, can produce mucus [13]. The Eustachian tube is a bony structure as it leaves the middle ear but, in the nasopharynx, comprises of cartilage and muscle. The tube is opened by active contraction of muscles which also allows to equalize the air pressure in both the middle ear and nose.

3.1 Auditory ossicles

The middle ear contains three small bones: malleus, incus, and stapes (also commonly known as hammer, anvil, and the stirrup, respectively, (Figure 1)). These ossicles conduct the sound from the ear drum to the inner ear. The malleus is club-shaped with its handle buried in the tympanic membrane, running along its center to upward, and its head lying in the middle ear cavity above the tympanic membrane where it is suspended through a ligament from a bone that forms brain covering. Here, the head of a club articulates with a cone-shaped incus. The base of cone articulates with the malleus head, above the tympanic membrane. The incus, present between two other ossicles, has a thin projection protruding out from it called
as its long process. It freely hangs in the middle ear and is connected to stapes at its tip which has a bend of right-angle. The third ossicle stapes is an arch-shaped bone comprising a footplate and an arch. The footplate is articulated by the joint of the stapedio-vestibular as it covers the oval window which is an opening into the vestibular system of inner ear or cochlea [14].

4. **Function of outer and middle ear**

To understand the role of the outer and middle ear in hearing physiology, it is important to first study the conducting mechanism of sound. The audible sound range is about 10 octaves from somewhere between 16 and 32 Hz to somewhere between ~16,000 and 20,000 Hz. The sensitivity of sound is above 128 Hz to ~4000 Hz and this range of maximum audibility and sensitivity decreases with age. As mentioned earlier, the head itself forms a natural barrier between the two ears. This plays a role in sound localization based both on the intensity and the difference in time of arrival of sound. Moving to the pinna, its crinkle shape catches and funnels the high frequency sounds to the auditory canal, which acts as a resonating tube since it amplifies the sounds falling between 3000 and 4000 Hz to increase sensitivity of the ear at these respective frequencies. The ear responds to very low-intensity sounds owing to its sensitivity. The equal pressure of air on both sides of the tympanic membrane also enables this sensitivity. The Eustachian tube provides this equalized pressure by opening for short intervals with every 3rd or 4th swallow. If it remained open all the time, one could even hear the sound of his or her own breath. If the Eustachian tube is closed for too long; it can absorb oxygen and carbon dioxide from the air in the middle ear. As the middle ear comprises lining of a respiratory membrane that can absorb gases, this process produces negative pressure. This may cause pain as is the case during descent of an airplane if the Eustachian tube is not unblocked. The middle ear cavity is quite small, containing mastoid air cells which act as air reservoirs to provide the cushion effects to pressure change. If the negative pressure remains for too long then the fluid is secreted by the middle ear cavity, which can cause conductive hearing loss [12, 15].

The outer and middle ears amplify the sound signal since the pinna has a relatively large surface area and funnels the sound to smaller tympanic membrane which has in turn large surface area as compared to the stapes footplate. This results in hydraulic amplification [16] i.e., a smaller movement over a large area is being converted into larger movement to a smaller area. The ossicular chain acting as a lever system amplifies the sound. Overall, both the outer and middle ears amplify the sound by about 30 dB on its passage from outside to the inner ear.

5. **Inner ear**

The human inner ear is present between the middle ear and acoustic meatus and is labeled as a labyrinth of ear that can be a bony or membranous labyrinth that each is further divided into three portions. Bony labyrinth comprises of semicircular canals, the vestibule, and the cochlea whereas the membranous labyrinth comprises of the semicircular duct, two sac-like structures of the vestibule; namely the saccule and the utricle and the cochlear duct (Figure 1). The space between the membranous and bony labyrinth is filled with watery fluid named perilymph that is obtained from...
the lymphatic system, and it is similar but not identical to the aqueous humor of
eyes and cerebrospinal fluid. It is poor in potassium and rich in sodium ions [17, 18].
Membranous labyrinth also has enclosed fluid named endolymph, which has a high
potassium concentration, and its composition is different from that of perilymph.
Endolymph is produced by vestibular dark cells that have a resemblance with stria
vascularis, which is part of the cochlea [18]. Endolymph within the membranous
labyrinth of inner ear interacts with hair cells and causes depolarization of hair cells by
providing high potassium gradient, resulting in afferent nerve transmission [19]. These
structures form two systems of inner ear, a vestibular system involved in maintaining
equilibrium and the cochlear system only part of the ear that participates in hearing.
The vestibular system is proprioceptive (feedback loop between sensory organs and
nervous system, external stimuli is not involved in it), whereas the cochlear system is
exteroceptive (sensation in cochlea is caused by external stimuli e.g., sound).

5.1 Vestibular system

Many hearing loss disorders are accompanied by vestibular defects, which necessi-
tate some description when considering the auditory system. The vestibular system is
a sensory system of inner ear that is important for postural equilibrium maintenance
and helps develop coordination between the position of the head and eye movements.
It comprises of five organs; three semicircular canals that are present at right angles to
each other and control angular (Head) rotation and two otolith organs that play a vital
role in linear acceleration (straight line movement) [20]. Semicircular canals based on
their position are designated as superior, posterior, and horizontal. Each canal opens
into the vestibule through its expanded end known as Ampulla. Sensory neuroepi-
thelium in ampulla is known as crista ampullaris consisting of ridge of tissues. From
cristae arises a gelatinous protein-polysaccharide structure, cupula that divides the
ampulla into equal parts and is important to keep hair cells in place [21]. Rotational
acceleration causes endolymph to displace cupula which results in bending of hair
cells in direction opposite to acceleration [22]. It is the middle part of bony labyrinth
that is connected posteriorly with the semicircular canal and anteriorly with the
cochlea and separated through the oval window from the middle ear.

Two membranous structures of the vestibule are the utricle and saccule are desig-
nated as otolith organs [22]. A single patch of sensory neuroepithelium in the vestibu-
lar system is called macula, which is present on the inner surface of a membranous sac.
It lies in the utricle in the horizontal plane and originates from the anterior wall of the
tubular sac. Whereas in saccule it is in the vertical plane and covers the bone of the
vestibular inner wall. Gelatinous otolithic membrane (macula) of utricle and saccule
contains thousands of otoconia (calcium carbonate crystals) embedded in a protein
matrix [23]. In mammals, these otoconia are arranged to form various layers that help
the hair cells to respond to endolymph drag. The sensory cells in vestibular region are
hair-like cilia that project out from the apical end that are flexible motile kinocilia and
stiff non-motile stereocilia. The stereocilia are arranged according to curvilinear line
called striola [24], the area of thickening of saccule and thinning of utricle [25]. If the
endolymph pressure is toward the kinocilium; it causes opening of cation channel and
potassium influx resulting in depolarization of hair cells. This depolarization of hair
cells results in release of glutamate to afferent nerve receptors and neurotransmis-
sion. Various signals from the vestibular nucleus are sent to the cortex, thalamus, and
cerebellum that in return send efferent signals to the ocular and postural muscles [26].
5.2 Cochlea

Cochlea is a coiled hollow bony structure that is lined by epithelial tissue. Despite being a bone, it is requisite for hearing and transduction as part of the auditory system. It is named after the Greek word 'kokhliās', meaning snail, due to its coiled shape (Figure 3A). This spiral shape of the cochlea helps it to differentiate between different frequencies because the different but specific region of the cochlear spiral detects different frequencies. Cochlea consists of three canals lined by epithelial cells that are filled with fluids. It also has the organ of Corti, which is a sensory organ that converts sound energy into neural signals that are conducted through the nerve fibers to the brain [29–31].

5.2.1 Canals of cochlea

Cochlea consists of three canal systems (Figure 3C); the scala vestibuli, the scala media and the scala tympani which envelop the modiolus. These three scala wind around the bony axis in a spiral stairway.

Figure 3.
Cochlear anatomy. A. Cochlea Structure. B. Cross-section of cochlear duct showing fluid-filled cavities around the modiolus. C. Three main canals: Scala vestibuli, scala tympani, and scala media along with Reissner’s membrane, stria vascularis and the organ of Corti in middle. D. Magnified view of the organ of Corti, containing outer and inner hair cells, stereocilia and supporting cells with tectorial and basilar membranes (taken from [27, 28] with permission).
5.2.1.1 Scala vestibuli

Scala vestibuli is the exterior lymph-filled canal and it is connected to the vestibules of the inner ear. The oval window is present at the base of the scala vestibuli. It is the part of cochlea that receives vibrations from the middle ear (stapes). Scala vestibuli and scala tympani sense the change in pressure that is caused by the different frequencies of sound.

5.2.1.2 Scala tympani

Scala tympani is the inferior canal and it connects to the tympanic membrane forming the two-and-half coiled structure of cochlea. Its superior end is connected to the scala vestibuli, while its inferior end separates the cochlea from the round window. The point at cochlear apex where scala vestibuli and scala tympani meets is known as the helicotrema.

5.2.1.3 Scala media

Scala media is present between the scala vestibuli and the scala tympani and has the organ of Corti and the basilar membrane. A basilar membrane is present between the scala media and the scala tympani, thus separating them. Scala media also contains the spiral ganglions that are extended neurons from the hair cells. The stria vascularis of scala media is involved in the regulation of K\(^+\) into scala media, thus maintaining the potential of endo-cochlea [32].

5.2.2 Fluids of cochlea

The chambers of the cochlea are filled with three types of fluids: perilymph, endolymph, and intrastrial fluid. These fluids maintain the endo-cochlear potential which is important for sensory transduction. The intrastrial fluid only fills the cavities present in stria vascularis.

5.2.2.1 Perilymph

Perilymph is present in scala vestibuli and scala tympani, and its fluid composition is similar to the extracellular fluid of the body. It has a high sodium concentration (140 mM) and low concentration of calcium (1.2 mM) and potassium (5 mM). The perilymph present in scala media is continuation from CSF while that in scala media is from plasma of blood.

5.2.2.2 Endolymph

Endolymph is present only in the scala media and has a unique ionic composition i.e., high K\(^+\) concentration (150 mM), which is not found anywhere in the body. This high concentration of K\(^+\) helps to maintain the endo-cochlear potential. Hence, endolymph is a noteworthy characteristic of the cochlea. It has considerably low concentration of sodium (1 mM) and calcium (0.002 mM) [32–34].

5.2.3 Reissner's membrane

Reissner’s membrane is present between the scala vestibuli and scala media and is involved in the regulation of ions. The membrane along with the basilar membrane
creates a cavity in the cochlear duct that is filled with endolymph. It is an avascular membrane that is made up of two types of cells. The part of Reissner’s membrane cells that lines the scala vestibuli are fibroblasts, while the cells that line scala media are epithelial cells. This cavity also contains the sensory organ i.e., the organ of Corti. Two types of ion channels are present on Reissner’s membrane: potassium ion channel and non-selective cation channel. These channels maintain the pressure between endolymph and perilymph [35, 36].

5.2.4 Organ of Corti

The organ of Corti is the organ for audition and is present on the basilar membrane. It consists of outer and inner hair cells (mechanosensory cells) and supporting cells (Figure 3D). The organ of Corti hair cells also has stereocilia that attach it to the tectorial membrane (soft ribbon-like structure on the top of organ of Corti). Alterations in basilar and tectorial membrane help in the movement of stereocilia that stimulates the hair cell receptors [37–39].

5.2.4.1 Tectorial membrane

The tectorial membrane covers the mechanosensory and supporting cells of organ of Corti. It has a viscous structure consisting of collagen and non-collagen proteins (glycoproteins and proteoglycans). The membrane helps in storing the calcium ions for the sensory organs of the inner ear. The stereocilia present in the organ of Corti are embedded in the tectorial membrane [40].

5.2.4.2 Mechanosensory cells

The hair cells are erect and contain micro-projections at their apical ends, known as stereocilia, that are filled with F-actin. The arrangement, size, and toughness of the hair cells in the cochlea are responsible for responding to different ranges (low to high) of sound frequencies. The cochlea shows a fundamental effect of tonotopy. Tonotopy refers to the orderly coding of sound based on high to low frequencies by hair cells and their afferents (spiral ganglion neurons). The hair cells residing at the apex of cochlea reciprocate to lower frequencies while the ones at the base, near to oval window reciprocate to a higher range of frequencies, thus creating a tonotopic gradient all over the cochlea. The hair cells convert the sound energy into neural signals.

5.2.4.2.1 Outer hair cells

Outer hair cells are oblong cells containing myosin and actin protein, which help these cells contract in rhythmic movement in response to sound stimuli from the middle ear. There are about 12,000 outer hair cells that are arranged in three rows. At the top of these cells are stereocilia that are embedded in the tectorial membrane. These cells are present on the basilar membrane area where the largest frequencies would be received [41]. These cells play a role in mechanoelectrical stimulation as well as in the feedback mechanism for low-frequency sounds for its amplification. They can amplify the faint sound by the inversion transduction through the positive feedback mechanism i.e., conversion of electrical signals to mechanical (sound) signals. The outer membrane of outer hair cells has a unique motor protein known as prestin, which is involved in the generation of movements that couple back to the
wave produced in a fluid membrane. In this way, weak sounds are amplified by the ‘active amplifier’ mechanism [42, 43].

5.2.4.2.2 Inner hair cells

The primary organ for the audition is the bundle of inner hair cells. These cells have pear-shaped morphology, and their stereocilia make weak connections with the tectorial membrane. There are about 3500 inner hair cells arranged in just a single row that is surrounded by supporting cells. These hair cells transmit the electrical signal to the auditory cortex of the brain through the nerve fibers. About 95% of auditory nerve projection to the brain is through inner hair cells. The outer hair cells help inner cells in the generation of synaptic nerve conduction to cochlear nerve fibers [37].

5.2.4.2.3 Supporting cells

Supporting cells are rigid sensory epithelial cells, organized in a mosaic manner that during the head movement and stimulation of sound maintain the integrity of the sensory hair cells. These cells play a vital role in maintaining the microenvironment for the proper functioning of hair cells. There are different types of these cells that are arranged in a row on the basilar membrane. They are Hensen’s cells, Deiters’ cells (phalangeal cells), pillar cells, Claudius cells, Boettcher cells, and border cells. These are arranged from the outer edge to the inner edge of an organ of Corti. These cells maintain the structure of the organ of Corti as well as the composition of the endolymph in the scala media. Supporting cells have negative resting potential so these cells tend to transport Na⁺ out and K⁺ into the scala media through the channels present in these cells [44, 45].

Figure 4.
Structure of stereocilia on hair cells. The stereocilia are made of F-actin protein and these stereocilia are linked to each other through the tip links. When the largest stereocilium moves due to the pressure at the tectorial membrane, the shorter ones move as well and mechanotransduction channels (MET channels) open and influx of ions takes place.
5.2.5 Mechatransduction in cochlea

A small number of transduction channels present in the stereocilia are open at the resting state. The stereocilia consist of shafts of F-actin protein, which has upper and lower tip link densities that help in linking the long and short stereocilia through tip links (Figure 4) [46]. These stereocilia are arranged in ascending order of their height. When the largest stereocilium embedded in the tectorial membrane is displaced, the ones with shorter lengths also move. These movements of stereocilia open the mechatransduction channels present at the tips of the stereocilia, leading to an influx of $K^+$. As a result, the voltage-gated calcium ion channel opens and uptake of $Ca^{2+}$ into the cells takes place. This depolarization of cells excites the cochlear nerves and in turn, results in the release of glutamate from the hair cells into the auditory nerves. The sound wave signal is then conveyed to the brain. Both the apical and basal regions of the cochlea are separated by membranes and their extracellular ionic environments are tightly regulated. These regulations of ions are important for converting the sound signals into electric impulses that are sent to the brain [47].

6. Conclusion

The human ear, one of the most developed sensing organs, has structurally and functionally divided into three parts. Firstly, the outer part, containing pinna and auditory canal, passes the sound vibrations to the tympanic membrane which separates the outer and middle ear. The middle ear containing the three ossicles (malleus, incus, and stapes) receives these vibrations and amplifies them. Traveling through middle ear, the vibrations are passed to inner ear which contains the spiral-shaped cochlea as the sense organ. In cochlea, the hair cells present in the organ of Corti contain stereocilia whose rhythmic movements open the mechatransduction channels, which send the nerve signal to the brain. In this way, these vibrations are converted into understandable sound.

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