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The Ear & Mechanism of Hearing

The ear is one of the most important sensory organ in the vertebrates. Receptors for two sensory modalities :- i) hearing & ii) equilibrium are housed in this organ. Hearing involves the participation of the external ear, middle ear & the cochlea of the inner ear while semicircular canals, utricule and saccule serves as sensory receptors in each case.

Anatomy of ear (Mammalian)

The mammalian ear is divisible into 3 well defined regions from outer to inner :—

i) External ear
ii) Middle ear &
iii) Inner ear.

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A) External ear

Comprises two parts :—

1) Pinna

i) A cartilaginous, flattened, convoluted & expanded part, covered by skin.
ii) Outer rim of pinna is called Helix.
iii) A curved and rim like prominance infront of pinna is called Anti-helix.
iv) A depression infront of helix is called Concha.
v) A non-cartilagenous, soft & muscular structure present from the lower end of antihelix & helix is called Earlobe.

2) External auditory meatus & auditory canal

i) Meatus is present at the junction of pinna and auditory canal.

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ii) ~~Ae~~ Auditory canal is a hollow rounded passage passes from the meatus inward to the tympanic membrane (eardrum).

iii) The canal slants ~~forwar~~ downward, forward & medially.

iv) Ceruminous glands in the skin of meatus secretes cerumen.

Function

Collects & funnels soundwaves inward to the middle ear.

B) Middle ear

This air filled cavity also called tympanic cavity comprises :—

1) Tympanic membrane/eardrum

Located at the junction b/w external & middle ear.

2) Three auditory ossicles

These bony structures are —

Malleus, Incus & Stapes.

Malleus

i) This hammer like ossicle remains attached by its manuberium (the handle) to the back of the eardrum.

ii) Its head remains attached to the wall of middle ear.

iii) By the short process it remains attached with Incus.

Incus

i) More or less triangular in shape

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ii) Head attached with malleus.

iii) Lower end articulates with the head of stapes.

Stapes

i) It resembles a stirrup.

ii) Compriseses of a head, a neck, an anterior crus, a posterior crus, a foot plate.

iii) Foot plate remains attached with the wall of oval window.

Function

These chain of ear-ossicles vibrate as a single unit when the soundwaves impinge on the eardrum.

1) The Tensor Tympany - that on contraction pulls the manubrium medially to decrease the ~~air~~ viberation of the tympanic membrane

2) The Stapedius - that on contraction pulls the foot plate of stapes out of the oval window

Two windows in the median wall

1) Oval window/ Fenestra ovalis

Opening into the inner ear to which foot plate fits.

2) Round window/ Fenestra rotunda/ Cocklea

that remains closed by a membrane.

Eustachian tube

1) This tube opens the air-filled cavity of middle ear into the nasopharynx.

2) This tube remains usually closed, but opens during chewing, swallowing and yawning.

Function

To keep the air pressure equalized on the two sides of the eardrum.

2) Inner ear (or Labyrinth)

Comprises two parts one within the other :-

1. Bony labyrinth

this is a series of channels filled with a fluid called perilymph rich in Na^+

2. Membranous labyrinth

This is a series of closed channels within the bony labyrinth. It is filled with a fluid called endolymph rich in K^+

Malleus, Incus & Stapes.

Bony labyrinth comprises three parts:— Cochlea, vestibules & 3 semicircular canals.

Cochlea

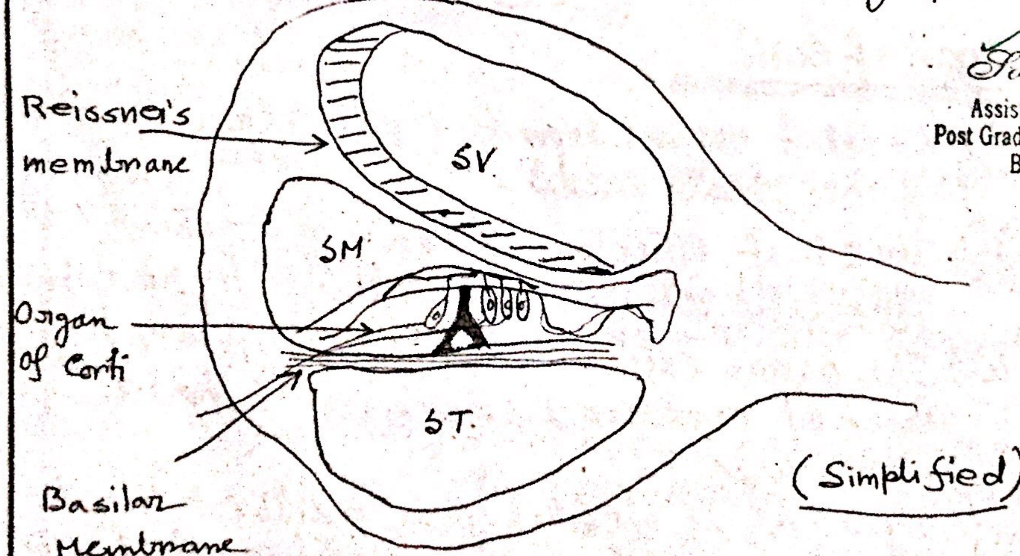
i) This is the coiled part of bony labyrinth.

ii) 20-35 mm in length & ~~turns~~ takes 2$\frac{3}{4}$ turns like conch ~~coil~~ shell.

iii) Cochlear nerves pass through the axis of modiolus — a central bony pillar.

iv) Throughout its length two membranes called Reissner's membrane & Basilar membrane divide it into 3 distinct chambers:—

Upper chamber :— Scala vestibuli
Middle chamber :— Scala media
Lower chamber :— Scala tympani



(Simplified)

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v) Scala ~~media~~ vestibuli & scala tympani contain perilymph & remain connected with each other at the apex of the cochlea through a small opening called Helicotrema.

vi) Scala vestibuli opens at oval window while scala tympani opens at the round window.

2 scalas.

viii) Basilar membrane is present b/w scala tympani & scala media and contains the actual organ of sense ~~or~~ <u>organ of corti</u>.

ix) Reissner's membrane is present b/w scala media & scala vestibuli.

Organ of corti

i) Located on the basilar membrane & projecting into scala media.

ii) The chief structure of hearing contains Hair cells which serve as auditory receptors.

iii) The organ extends from the apex to the base of cocklea & consequently has a spiral shape.

iv) Two rods of ~~cocklea~~ corti meets at the apex to form a tunnel called tunnel of corti.

v) Hair cells are arranged in 4 rows:—

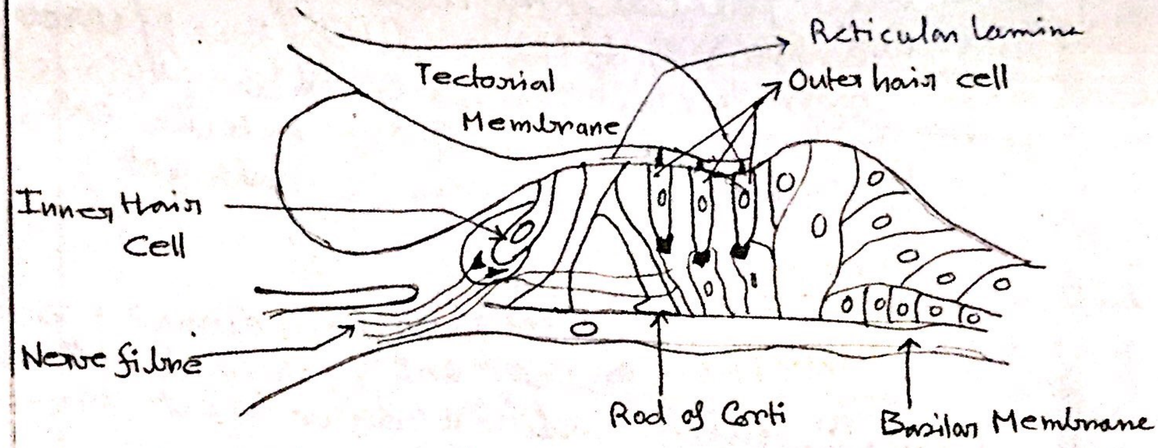
a) 3 rows of outer hair cells lateral to the tunnel and

b) 1 row of inner hair cells medial to the tunnel.

c) No:— 20,000 outer hair cells & 3,500 inner hair cells in each ~~of corti~~ cocklea (human)

called endolymph ... in K+

d) Minute processes of Stereocilia projects upward from the hair cells.



e) Processes of hair cells pierce a rigid membrane like plate called Reticular membrane, supported by the rods of corti.

f) Covering the rows of ~~hair~~ hair cells is an overlying thin, viscous but elastic membrane called Tectorial membrane composed of glycoproteins.

g) Tips of hairs of outer hair cells are embedded on the tectorial membrane but not the inner hair cells.

h) Supporting cells of outer hair cells are:–
- Deiter's cells – ~~outside the~~ in b/w the hair cells
- Hensen's cells – outside the hair cells
- Cells of Claudius – outerside of the hensen's cells.

i) Neurons of spiral ganglion innervates hair cells. Most of the afferent neurons innervate inner hair cells while efferent neurons innervate outer hair cells.

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Mechanism of hearing

Ear converts the soundwaves into action potential in the auditory nerve, which on transmission to the auditory zone of cerebral cortex develop hearing sensation (This is a complex process is accomplished involving the external ear; middle ear and cochlea of inner ear.)

1) **External ear**

Pinna collects soundwaves from the external environment & forward it through the external auditory meatus to put pressure on tympanum.

2) **Middle ear**

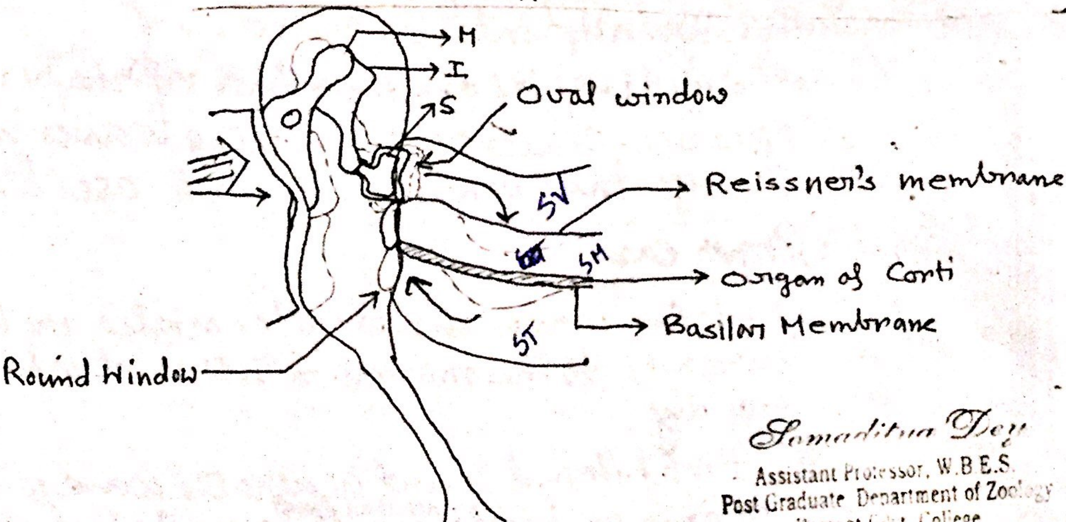
In the middle ear tympanum acts as a Resonator and the ear - ossicles functions as Lever system and increases the sound pressure arriving at oval window. This performs in following steps:-

i) In response to the pressure changes ~~in the~~ produced by the soundwaves at ~~the~~ its external ~~outer~~ surface, tympanum moves in and out & this functions as a Resonator.

ii) It stops vibrating almost immediately when soundwaves stop.

iii) Motions of the tympanic membrane are imparted to the manubrium of Malleus.

iv) Malleus rocks on an axis through the junction of its long and short processes, so that the short processes transmitt the vibration of the manubrium to Incus.



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v) Incus moves in such a way that the vibrations are transmitted to the head of the stapes.

vi) Movement of the head of stapes swings the foot plate to & fro like a door hinged at the posterior edge of the oval window.

vii) Auditory ossicles thus functions as a lever system that converts the resonant vibration of tympanum into the movement of stapes against the perilymph filled scala vestibuli of cochlea.

viii) This lever system increases the sound pressure that arrives at the oval window because the lever action of malleus and incus multiplies the force 1.3 times and the area of the tympanum is much greater (13 times) than the area of the foot plate of stapes.

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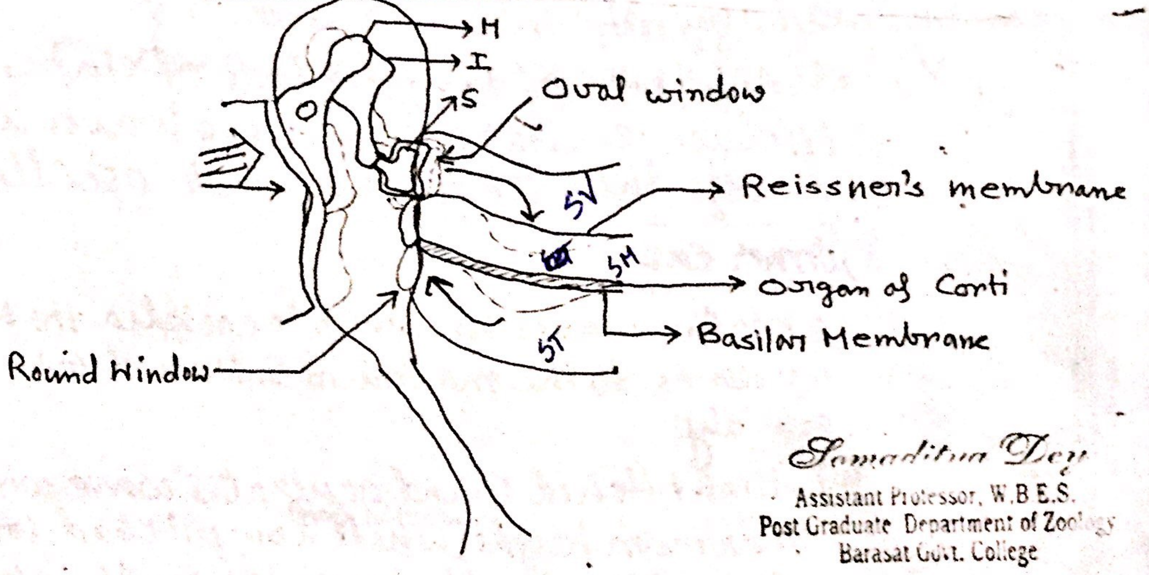

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ix) Muscles of middle ear plays an important role in hearing. Tensor tympany on contraction pulls the manuberium and tympanum inwardse Stapedium on contraction pulls the foot-plate outwards. Contraction of muscles checks the movements of ear-ossicles and protect the ear against intense sound.

x) Movement of the footplate of stapes produce series of travelling waves which brings the cochlea duct into oscillation.

3) **Inner ear**

i) As the waves moves up to cockhea its height increases to the maximum & then drops off rapidly.

ii) High pitched sound generates wave with maximum height near the base while low pitched sound generates wave that peak near the apex of cochlea.

iii) Travelling waves results in the displacement of fluid of scala vestibuli ~~into scala tympani~~ which in turn causes the movement of Reissner's membrane.

by the peaks of waves into scala vestibuli.

v) This leads to the displacement of fluid in the scala tympani that are dissipated into air at the round window.

vi) Sound, thus produces distortion of the basilary membrane and the site at which the distorti-on is maximum is determined by the frequency of soundwaves. Thus, basilary membrane acts as frequency analyser of the ear.

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vii) The vibrations of the basilar membrane ~~causes~~ distort its overlying sensory hair cells of organ of corti ~~by the move~~ which are apparently bent by fluid running b/w the tectorial membrane & the underlying hair cells.

viii) The inner hair cells are stimulated by the fluid movement.

ix) The outer hair cells are motile and improve hearing by influencing vibration pattern of the basilar membrane

Genesis of action potential

i) There is a potential difference b/w the endolymph and perilymph of the hair cells due to high conc. of K^+ & low conc. of Na^+ in endolymph against high conc. of Na^+ & low conc. of K^+ in perilymph.

ii) The membrane potential of the haircell is about -60 mv; when stereocilia are displaced towards kinocilium the potential ~~difference~~ is decreased to -50mv and the haircells become depolarised.

iii) When the stereocilia are displaced away from kinocilium, repolarisation of haircells occur.

iv) Action potentials ~~is~~ are then transmitted through the auditory pathway to
Auditory nerve → ~~basal & lateral~~ dorsal & ventral cochlear nuclei → superior olivary nucleus → lateral lumniscus nucleus → Inferior colliculi → median geniculate body → auditory cortex of cerebrum, where the hearing sensation develops.

Hearing & Equilibrium 9

INTRODUCTION

Receptors for two sensory modalities, hearing and equilibrium, are housed in the ear. The external ear, the middle ear, and the cochlea of the inner ear are concerned with hearing. The semicircular canals, the utricle, and the saccule of the inner ear are concerned with equilibrium. Receptors in the semicircular canals detect rotational acceleration, receptors in the utricle detect linear acceleration in the horizontal direction, and receptors in the saccule detect linear acceleration in the vertical direction. The receptors for hearing and equilibrium are hair cells, and there are six groups of hair cells in each inner ear: one in each of the three semicircular canals, one in the utricle, one in the saccule, and one in the cochlea.

ANATOMIC CONSIDERATIONS

External & Middle Ear

The external ear funnels sound waves to the **external auditory meatus.** In some animals, the ears can be moved like radar antennas to seek out sound. From the meatus, the **external auditory canal** passes inward to the **tympanic membrane** (eardrum) (Figure 9–1).

The middle ear is an air-filled cavity in the temporal bone that opens via the **auditory (eustachian) tube** into the nasopharynx and through the nasopharynx to the exterior. The tube is usually closed, but during swallowing, chewing, and yawning it opens, keeping the air pressure on the two sides of the eardrum equalized. The three **auditory ossicles,** the **malleus,**

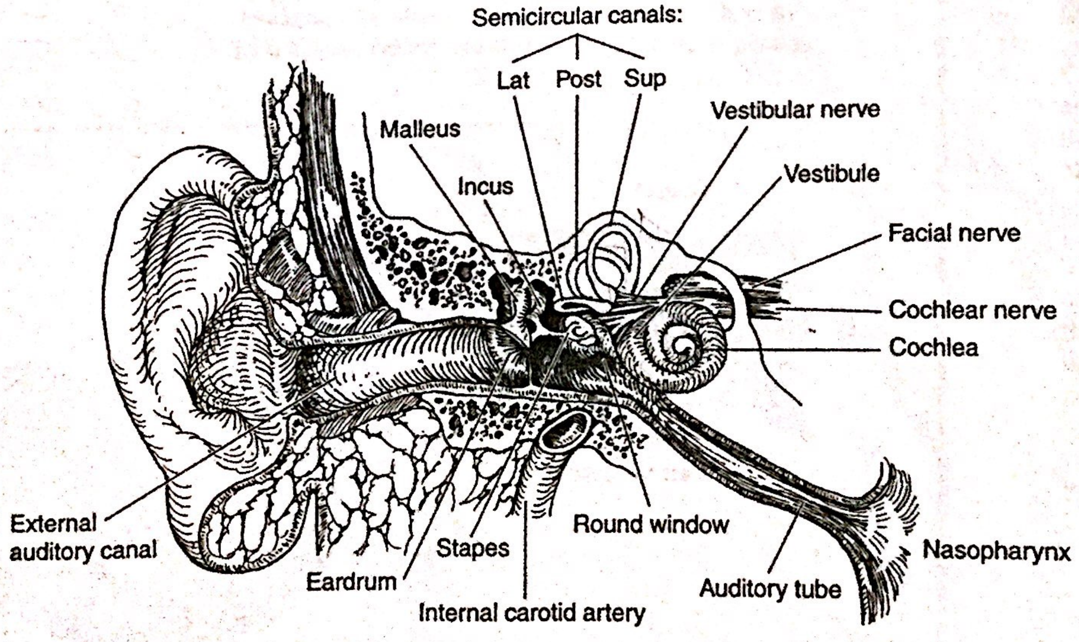

Figure 9–1. The human ear. To make the relationships clear, the cochlea has been turned slightly and the middle ear muscles have been omitted. Sup, superior; Post, posterior; Lat, lateral.

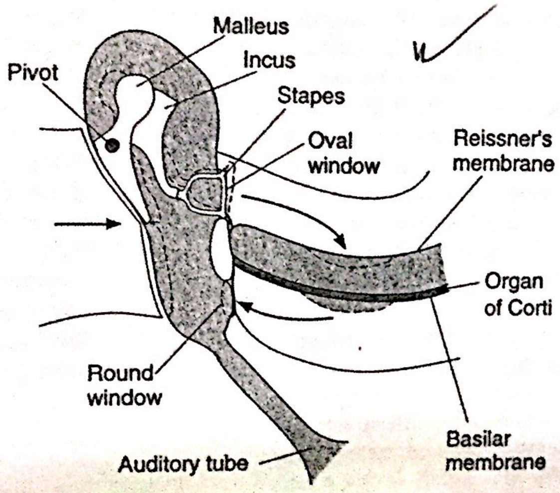

Figure 9–2. Schematic representation of the auditory ossicles and the way their movement translates movements of the tympanic membrane into a wave in the fluid of the inner ear. The wave is dissipated at the round window. The movements of the ossicles, the membranous labyrinth, and the round window are indicated by dashed lines.

incus, and **stapes,** are located in the middle ear. The **manubrium** (handle of the malleus) is attached to the back of the tympanic membrane. Its head is attached to the wall of the middle ear, and its short process is attached to the incus, which in turn articulates with the head of the stapes. The stapes is named for its resemblance to a stirrup. Its **footplate** is attached by an annular ligament to the walls of the **oval window** (Figure 9–2). Two small skeletal muscles, the **tensor tympani** and the **stapedius,** are also located in the middle ear. Contraction of the former pulls the manubrium of the malleus medially and decreases the vibrations of the tympanic membrane; contraction of the latter pulls the footplate of the stapes out of the oval window.

Inner Ear

The inner ear (**labyrinth**) is made up of two parts, one within the other. The **bony labyrinth** is a series of channels in the petrous portion of the temporal bone. Inside these channels, surrounded by a fluid called **perilymph,** is the **membranous labyrinth** (Figure 9–3). This membranous structure more or less duplicates the shape of the bony channels. It is filled with a fluid called **endolymph,** and there is no com-

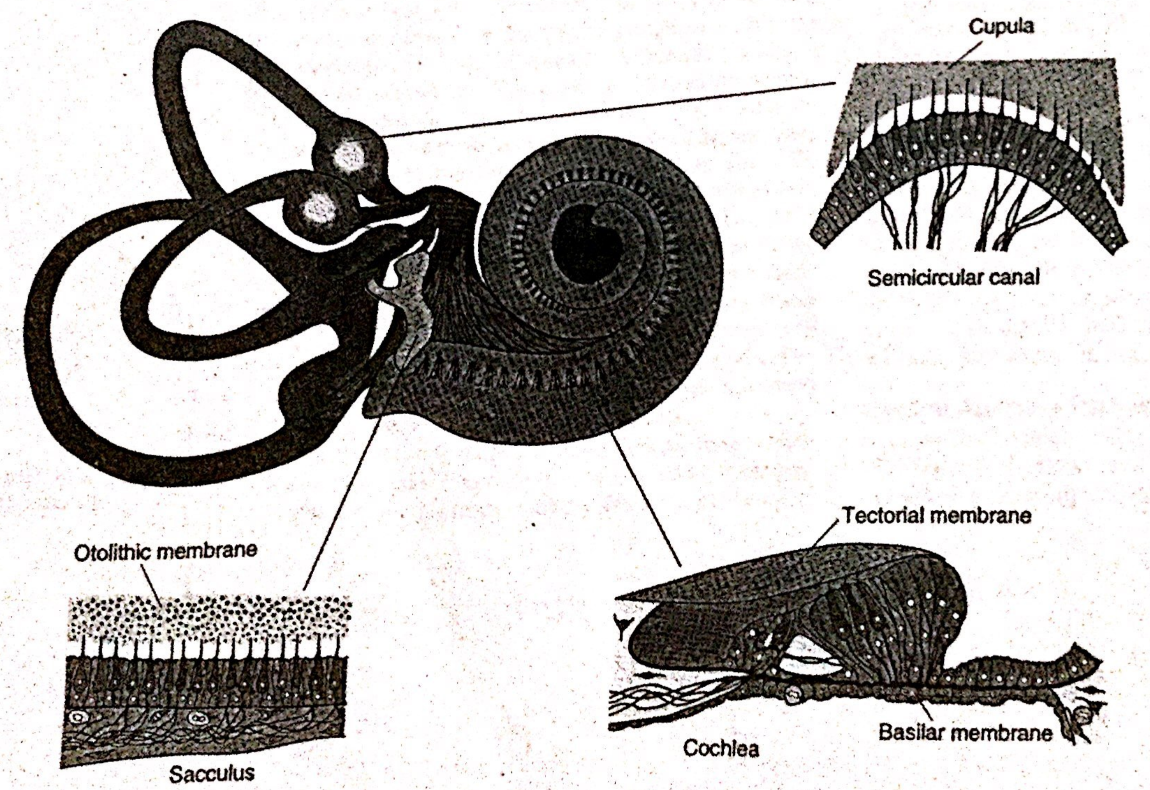

Figure 9–3. Human membranous labyrinth, with enlargements of the structures in which hair cells are embedded. (Reproduced, with permission, from Hudspeth AJ: How the ear's works work. Nature 1989;341:397. Copyright © 1989 by Macmillan Magazines Ltd.)

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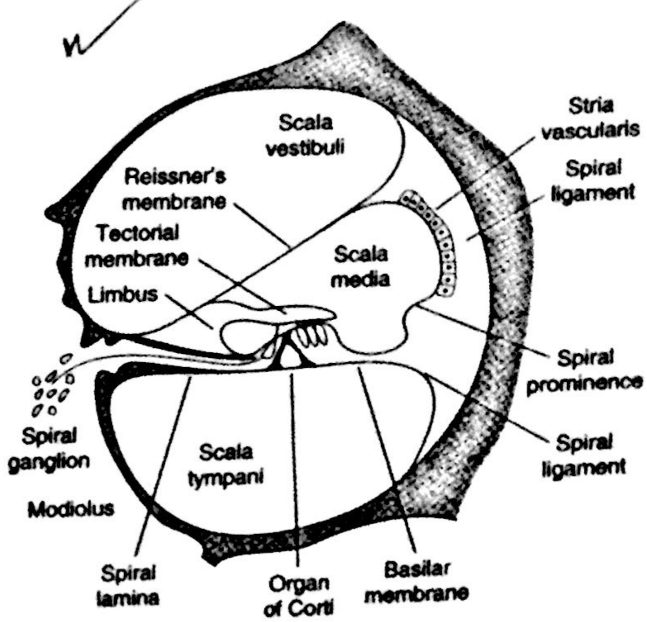
Cochlea

The cochlear portion of the labyrinth is a coiled tube which in humans is 35 mm long and makes 2 3/4 turns. Throughout its length, the basilar membrane and Reissner's membrane divide it into three chambers (**scalae**) (Figure 9–4). The upper **scala vestibuli** and the lower **scala tympani** contain perilymph and communicate with each other at the apex of the cochlea through a small opening called the **helicotrema.** At the base of the cochlea, the scala vestibuli ends at the oval window, which is closed by the footplate of the stapes. The scala tympani ends at the **round window,** a foramen on the medial wall of the middle ear that is closed by the flexible **secondary tympanic membrane.** The **scala media,** the middle cochlear chamber, is continuous with the membranous labyrinth and does not communicate with the other two scalae. It contains endolymph (Figures 9–3 and 9–4).

Organ of Corti

Located on the basilar membrane is the **organ of Corti,** the structure that contains the hair cells which are the auditory receptors. This organ extends from the apex to the base of the cochlea and consequently has a spiral shape. The processes of the hair cells pierce the tough, membrane-like **reticular lamina** that is supported by the **rods of Corti** (Figure 9–4). The hair cells are arranged in four rows: three rows of **outer hair cells** lateral to the tunnel formed by the rods of Corti, and one row of **inner hair cells** medial to the tunnel. There are 20,000 outer hair cells and 3500 inner hair cells in each human cochlea. Covering the rows of hair cells is a thin, viscous, but elastic **tectorial membrane** in which the tips of the hairs of the outer but not the inner hair cells are embedded. The cell bodies of the afferent neurons that arborize around the bases of the hair cells are located in the **spiral ganglion** within the **modiolus,** the bony core around which the cochlea is wound. Ninety to 95 percent of these afferent neurons innervate the inner hair cells; only 5–10% innervate the more numerous outer hair cells, and each neuron innervates several of these outer cells. By contrast, most of the efferent fibers in the auditory nerve (see below) terminate on the outer hair cells rather than on the inner hair cells. The axons of the neurons that innervate the hair cells form the auditory (cochlear) division of the vestibulocochlear acoustic nerve and terminate in the **dorsal** and **ventral cochlear nuclei** of the medulla oblongata. The total number of afferent and efferent fibers in each auditory nerve is approximately 28,000.

In the cochlea, there are tight junctions between the hair cells and the adjacent phalangeal cells; these prevent endolymph from reaching the bases of the cells.



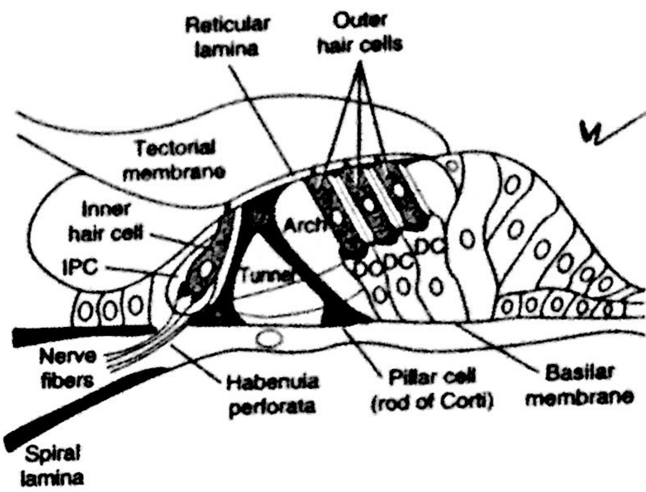


Figure 9–4. **Top:** Cross section of the cochlea, showing the organ of Corti and the three scalae of the cochlea. **Bottom:** Structure of the organ of Corti, as it appears in the basal turn of the cochlea. DC, outer phalangeal cells (Deiters' cells) supporting outer hair cells; IPC, inner phalangeal cell supporting inner hair cell. (Reproduced, with permission, from Pickels JO : *An Introduction to the Physiology of Hearing,* 2nd ed. Academic Press, 1988.)

However, the basilar membrane is relatively permeable to perilymph in the scala tympani, and consequently, the tunnel of the organ of Corti and the bases of the hair cells are bathed in perilymph. Because of similar tight junctions, the arrangement is similar for the hair cells in other parts of the inner ear; ie, the processes of the hair cells are bathed in endolymph, whereas their bases are bathed in perilymph.

Central Auditory Pathways

From the cochlear nuclei, auditory impulses pass via a variety of pathways to the **inferior colliculi,** the centers for auditory reflexes, and via the **medial**

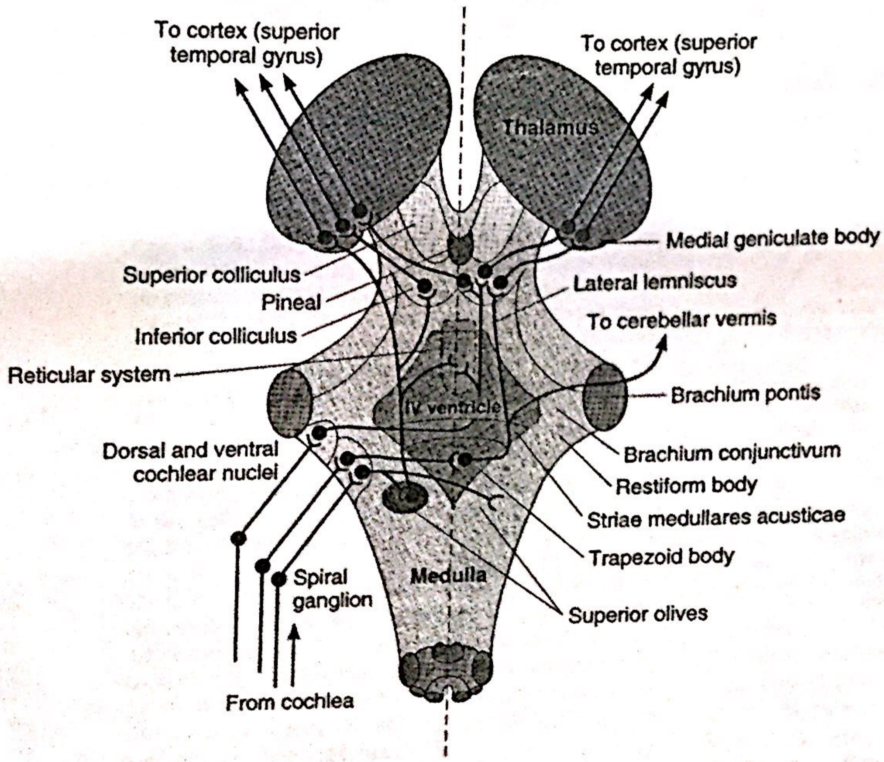


Figure 9–5. Simplified diagram of main auditory pathways superimposed on a dorsal view of the brain stem. Cerebellum and cerebral cortex removed.

geniculate body in the thalamus to the **auditory cortex.** Others enter the reticular formation (Figure 9–5). Information from both ears converges on each superior olive, and at all higher levels most of the neurons respond to inputs from both sides. The primary auditory cortex, Brodmann's area 41, is in the superior portion of the temporal lobe. In humans, it is located in the sylvian fissure (see Figure 7–4) and is not normally visible on the surface of the brain. There are several additional auditory receiving areas, just as there are several receiving areas for cutaneous sensation (see Chapter 7). The auditory association areas adjacent to the primary auditory receiving area are widespread, extending onto the insula. The **olivocochlear bundle** is a prominent bundle of efferent fibers in each auditory nerve that arises from both the ipsilateral and the contralateral superior olivary complex and ends primarily around the bases of the outer hair cells of the organ of Corti.

Semicircular Canals

On each side of the head, the semicircular canals are perpendicular to each other, so that they are oriented in the three planes of space. Inside the bony canals, the membranous canals are suspended in perilymph. A receptor structure, the **crista ampullaris,** is located in the expanded end **(ampulla)** of each of the membranous canals. Each crista consists of hair cells and sustentacular cells surmounted by a gelatinous partition **(cupula)** that closes off the ampulla (Figure 9–6). The processes of the hair cells are embedded in the cupula, and the bases of the hair cells are in close contact with the afferent fibers of the vestibular division of the vestibulocochlear nerve.

Utricle & Saccule

Within each membranous labyrinth, on the floor of the utricle, there is an **otolithic organ (macula).** Another macula is located on the wall of the saccule in a semivertical position. The maculas contain sustentacular cells and hair cells, surmounted by an otolithic membrane in which are embedded crystals of calcium carbonate, the **otoliths** (Figure 9–3). The otoliths, which are also called **otoconia** or **ear dust,** range from 3 to 19 μm in length in humans and are more dense than the endolymph. The processes of the hair cells are embedded in the membrane. The nerve fibers from the hair cells join those from the cristae in the vestibular division of the vestibulocochlear nerve.

Neural Pathways

The cell bodies of the 19,000 neurons supplying the cristae and maculas on each side are located in the

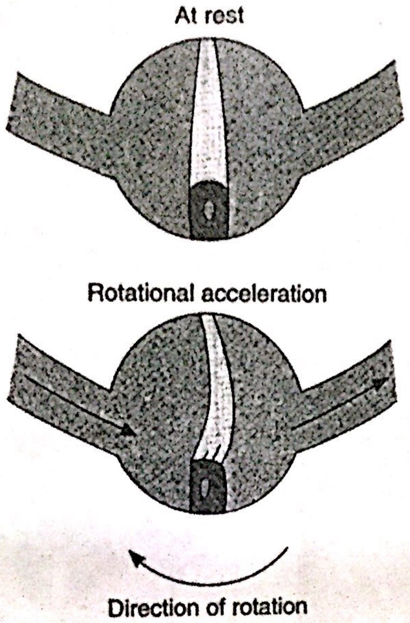


Figure 9–6. Diagrammatic representation of the ampullar crista. The cupula on the top of the crista closes off the ampulla and is flexible. Because of its inertia, the endolymph is displaced in a direction opposite to the direction of rotation during rotational acceleration. This bends the hair cell processes, altering their permeability and changing the membrane potential of the hair cells.

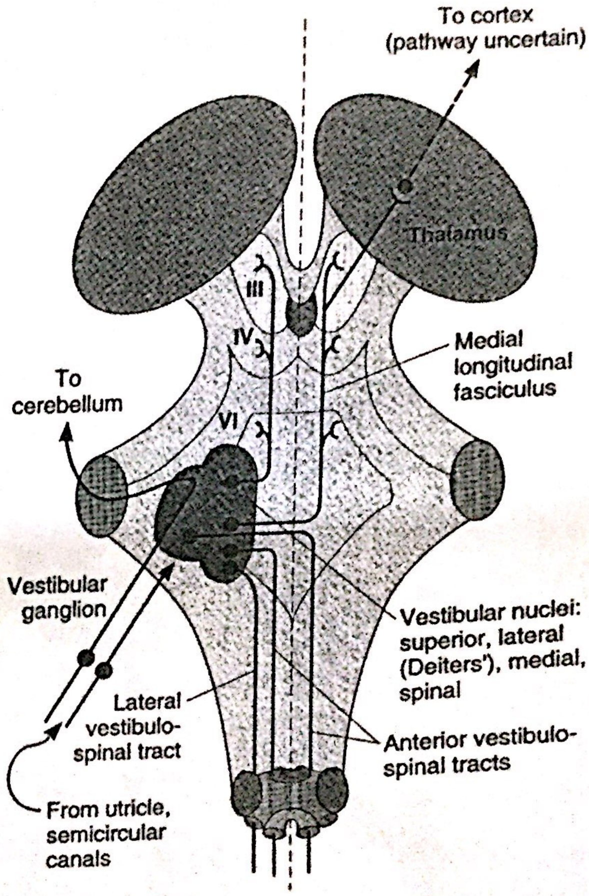


Figure 9–7. Principal vestibular pathways superimposed on a dorsal view of the brain stem. Cerebellum and cerebral cortex removed.

vestibular ganglion. Each vestibular nerve terminates in the ipsilateral four-part vestibular nucleus and in the flocculonodular lobe of the cerebellum. Second-order neurons pass down the spinal cord from the vestibular nuclei in the vestibulospinal tracts and ascend through the **medial longitudinal fasciculi** to the motor nuclei of the cranial nerves concerned with the control of eye movement. There are also anatomically poorly defined pathways by which impulses from the vestibular receptors are relayed via the thalamus to the cerebral cortex (Figure 9–7).

HAIR CELLS

Structure

The hair cells in the inner ear have a common structure (Figure 9–8). Each is embedded in an epithelium made up of supporting or sustentacular cells. The basal end is in close contact with afferent neurons. Projecting from the apical end are 30–150 rod-shaped processes, or hairs. Except in the cochlea, one of these, the **kinocilium,** is a true but nonmotile cilium with nine pairs of microtubules around its circumference and a central pair of microtubules (see Chapter 1). It is one of the largest processes and has a clubbed end. The kinocilium is lost in the hair cells of the cochlea in adult mammals. However, the other processes, which are called **stereocilia,** are present in all hair cells. They have cores composed of parallel filaments of actin. The actin is coated with various isoforms of myosin. Within the clump of processes on each cell, there is an orderly structure. Along an axis toward the kinocilium, the stereocilia increase progressively in height; along the perpendicular axis, all the stereocilia are the same height.

Electrical Responses

The membrane potential of the hair cells is about –60 mV. When the stereocilia are pushed toward the kinocilium, the membrane potential is decreased to about –50 mV. When the bundle of processes is pushed in the opposite direction, the cell is hyperpolarized. Displacing the processes in a direction perpendicular to this axis provides no change in membrane potential, and displacing the processes in directions that are intermediate between these two directions produces depolarization or hyperpolarization that is proportionate to the degree to which the direction is toward or away from the kinocilium. Thus, the hair processes provide a mechanism for generating changes in membrane potential proportionate to the direction of displacement.

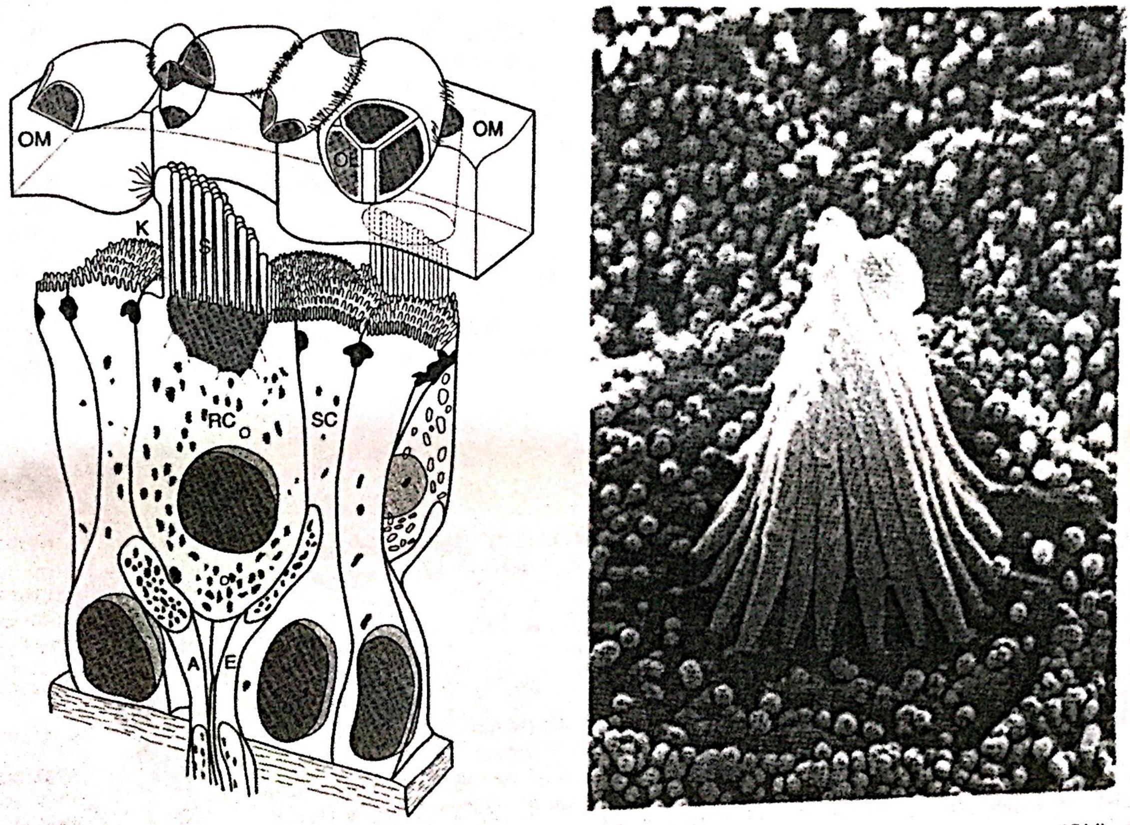


Figure 9–8. **Left:** Structure of a hair cell in the saccule of a frog, showing its relation to the otolithic membrane (OM). K, kinocilium; S, stereocilia; RC, hair cell with afferent (A) and efferent (E) nerve fibers; OL, otolith; SC, supporting cell. (Reproduced, with permission, from Hillman DE: Morphology of peripheral and central vestibular systems. In: Llinas R, Precht W [editors]: *Frog Neurobiology.* Springer, 1976.) **Right:** Scanning electron photomicrograph of processes on a hair cell in the saccule of a frog. The otolithic membrane has been removed. The small projections around the hair cell are microvilli on supporting cells. (Courtesy of AJ Hudspeth.)

Genesis of Action Potentials in Afferent Nerve Fibers

As noted above, the processes of the hair cells project into the endolymph whereas the bases are bathed in perilymph. This arrangement is necessary for the normal production of generator potentials. The perilymph is formed mainly from plasma. Entry of mannitol and sucrose from plasma into perilymph in the scala tympani is slower than entry into the perilymph in the scala vestibuli, and there are small differences in composition between the fluids in these two scalae, but both resemble extracellular fluid. On the other hand, endolymph is formed by the stria vascularis and has a high concentration of K^+ and a low concentration of Na^+ (Figure 9–9). Cells in the stria vascularis have a high concentration of Na^+-K^+ ATPase. In addition, it appears that there is a unique electrogenic K^+ pump in the stria vascularis, which accounts for the fact that the scala media is electrically positive relative to the scala vestibuli and scala tympani.

Very fine processes called **tip links** (Figure 9–10) tie the tip of each stereocilium to the side of its higher neighbor, and at the junction there appear to be mechanically sensitive cation channels in the higher process. When the shorter stereocilia are pushed toward the higher, the open time of these channels increases. It is postulated that tension on each of the channels is adjusted by an "adaptation motor" made up of myosin in the higher stereocilium. Displacement of the stereocilia in the opposite direction reduces channel open time. The α subunit of the epithelial sodium channel may be involved because this subunit can form a relatively nonselective cation channel by itself (see Chapter 1), and amiloride is bound to a junction-like structure at the points of contact between the shorter and taller stereocilia. In any case, the channels are relatively nonspecific cation channels, but since they are bathed in endolymph, which has a high K^+ concentration, K^+ enters the hair cell when they are open, producing depolarization. Ca^{2+} also enters, and a synaptic transmitter is released that depolarizes the afferent neuron or neurons in con-

auditory canal

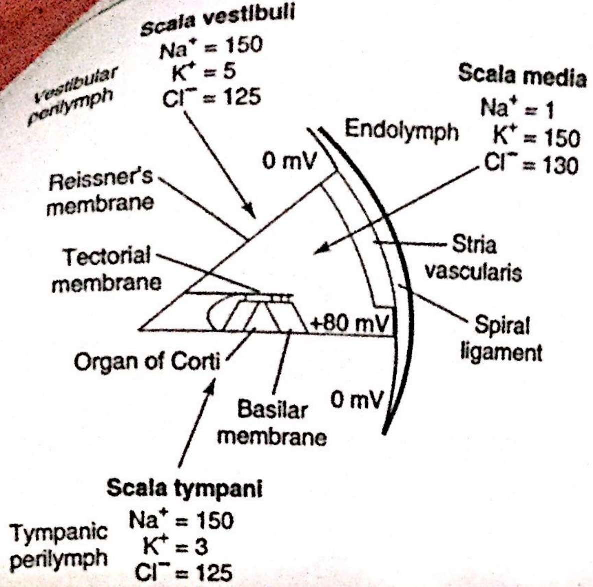


Figure 9–9. Composition of perilymph in the scala vestibuli, perilymph in the scala tympani, and endolymph. Values for Na^+, K^+, and Cl^- are in mmol/L. (Modified and reproduced, with permission, from Sterkers O, Ferrary E, Amiel C: How are inner ear fluids formed? News Physiol Sci 1987;2:176.)

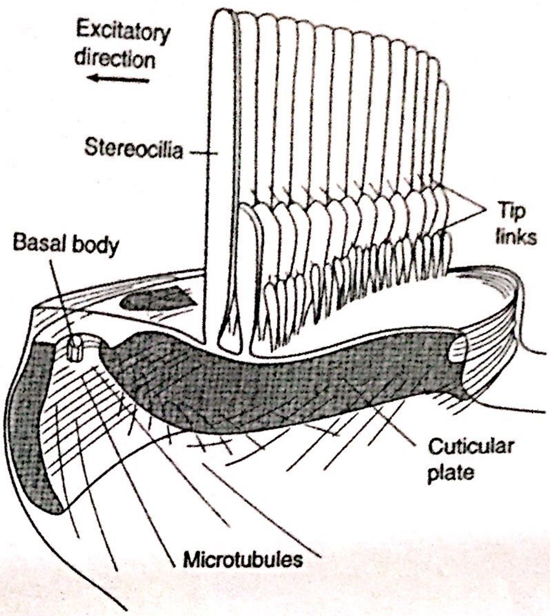


Figure 9–10. Structure of hair cell apex. Note the tip links between rows of stereocilia. Arrow indicates the direction in which pushing the cilia increases ion influx into the hairs. (Reproduced, with permission, from Hackney CM, Furness DN: Mechanotransduction in vertebrate hair cells: Structure and function of the stereociliary bundle. Am J Physiol 1995;268:C1.)

tact with the hair cell. The identity of the transmitter has not been established, but it is probably glutamate.

HEARING

Sound Waves

Sound is the sensation produced when longitudinal vibrations of the molecules in the external environment, ie, alternate phases of condensation and rarefaction of the molecules, strike the tympanic membrane. A plot of these movements as changes in pressure on the tympanic membrane per unit of time is a series of waves (Figure 9–11), and such movements in the environment are generally called sound waves. The waves travel through air at a speed of approximately 344 m/s (770 miles/h) at 20 °C at sea level. The speed of sound increases with temperature and with altitude. Other media in which humans occasionally find themselves also conduct sound waves but at different speeds. For example, the speed of sound is 1450 m/s at 20 °C in fresh water and is even greater in salt water. It is said that the whistle of the blue whale is as loud as 188 decibels (see below) and is audible for 500 miles.

Generally speaking, the **loudness** of a sound is correlated with the **amplitude** of a sound wave and its **pitch** with the **frequency** (number of waves per unit of time). The greater the amplitude, the louder the sound; and the greater the frequency, the higher the pitch. However, pitch is determined by other poorly understood factors in addition to frequency, and frequency affects loudness, since the auditory threshold is lower at some frequencies than others (see below). Sound waves that have repeating patterns, even though the individual waves are complex, are perceived as musical sounds; aperiodic nonrepeating vibrations cause a sensation of noise. Most musical sounds are made up of a wave with a primary frequency that determines the pitch of the sound plus a number of harmonic vibrations **(overtones)** that give the sound its characteristic **timbre** (quality). Variations in timbre permit us to identify the sounds of the various musical instruments even though they are playing notes of the same pitch.

The amplitude of a sound wave can be expressed in terms of the maximum pressure change at the eardrum, but a relative scale is more convenient. The **decibel scale** is such a scale. The intensity of a sound in **bels** is the logarithm of the ratio of the intensity of that sound and a standard sound. A decibel (dB) is 0.1 bel. Therefore,

$$\text{Number of dB} = 10 \log \frac{\text{Intensity of sound}}{\text{Intensity of standard sound}}$$

Sound intensity is proportionate to the square of sound pressure. Therefore,