Physiology of auditory system

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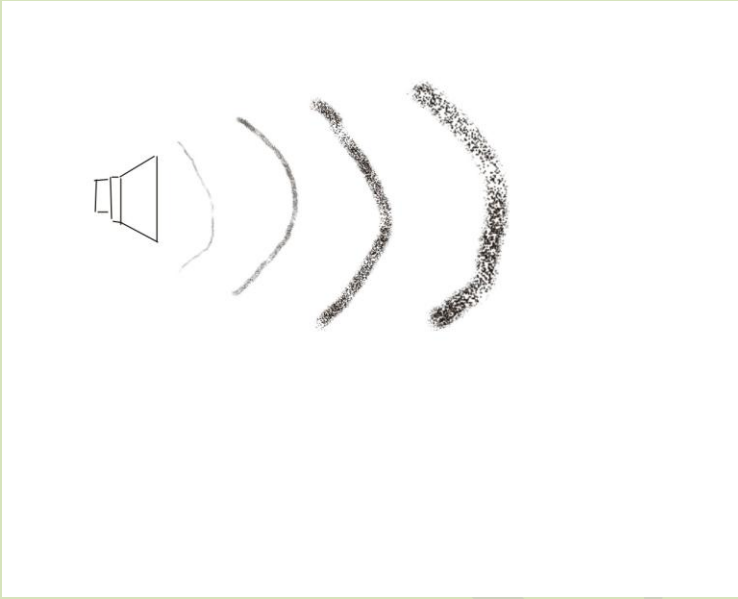
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Physiology of auditory system

By

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Introduction: Before dwelling into the exact physiology of hearing it will be better to refresh the physics of sound. Understanding the basic physical properties of sound is a prerequisite for better understanding of the physiology.

Figure showing sound being transmitted from a speaker

Sound wave travels in air by alternating compression and rarefaction of air molecules. These compressions and rarefactions are said to be adiabatic. When the pressure of sound wave is at a maximum then the forward velocity of the air molecules would also be the maximum. Displacement of air molecules lags by one quarter of a cycle. The displacement usually occurs around the mean position. Sound wave does not cause any net flow of air in the direction of motion, and air pressure variations are very small.
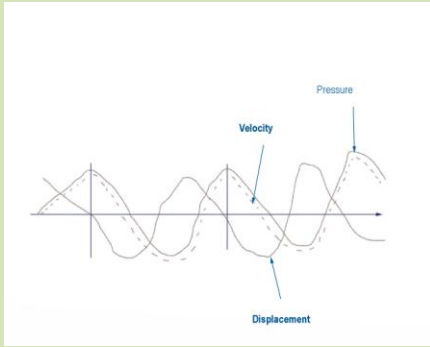
Figure showing pressure velocity & displacement of sound wave

Sound which is loud enough to cause pain i.e. 130 dB produces pressure variation of just 0.2% of resting atmospheric pressure.

Physical properties of sound:
   Sound has two basic properties: intensity and frequency. Intensity has the subjective correlate of loudness.   Frequency infact has the subjective correlate of pitch.
Intensity – is defined as power transmitted by sound waves through a unit area.

Pressure & Intensity of sound waves:
   Peak pressure of sound wave (P) is related to peak velocity of air molecules (V) by a constant of proportionality R.

P = RV ("R" is the impedance of the medium).

Impedance is the resistance offered by the medium for sound transmission.

Intensity = Peak pressure x Peak velocity / 2. Factor 2 is the function of the shape of the wave form. The factor 2 which depends on the exact shape of sound wave can be removed by measuring not the peak velocities and pressures but by measuring Root Mean Square values (RMS). The RMS value is calculated by taking the value of the pressure / velocity at each moment in the wave form, squaring it and then taking thee average of all the squared values over the wave form. The RMS value is very useful because

the same relation between intensity, pressure and velocity holds good for all shapes of sound wave forms.

If intensity of the sound wave is constant, the peak velocity and peak pressure are also constant. This relationship does not depend on the frequency of the sound wave; on the contrary displacements produced by sound waves do vary with frequency if the sound intensity is constant. Displacements usually vary in inverse proportion to the frequency. For example for a constant intensity, low frequency vibrations produce greater displacements.

Decibel:

Sound pressure levels are usually measured in decibels. This is the logarithmic unit of measurement that expresses the magnitude of the physical quality of sound, relative to a reference level.

A difference of 1 dB is the minimum perceptible change in the volume of sound.

Properties of sound:

i. Frequency / wavelength / velocity of sound:

Velocity of sound waves in air is independent of its frequency. At sea level the speed of sound in air is about 330m/s. This means that if the frequency of a wave is f cycles / sec (Hz) then f waves must pass any point in one second.

Length of one wave is 330/f metres. Wave lengths become shorter with increasing sound frequency.

ii. Sound gets attenuated by distance. In an ideal situation, the sound wave front will not lose / gain energy with time. The energy in each unit area of wave front decreases with distance. Another factor that plays a role in sound attenuation with distance is that when air is compressed at the peak of sound pressure wave, its temperature raises, and some of the energy of sound wave is stored as heat. The process gets reversed, and the energy is passed back to the wave during the trough phase. This passage of heat from the warmer to the cooler regions of sound wave can cause some loss of energy in the wave. This particular factor is very important for high frequency waves, where the short wavelength allows flow of heat between the peaks and troughs of the wave.

iii. Sound transmission in different media: Sound transmission in different media depends on the impedance values of the media concerned. When sound traverses through media of differing impedance values, majority of sound waves get reflected from the interface between the two media.

Fourier analysis:

Analysis of a complex sound into its constituent sinusoids is known as Fourier's analysis. This analysis makes study of sound waves really simple as mathematical tools can be easily applied. A sinusoidal wave behaves in a simple manner in complex environments like the reflecting environment of external auditory canal, or in complex mechanical environments like the middle ear. Cochlea uses Fourier analysis of sound in order to process it. These sinusoidal waves can easily be projected in an oscilloscope.

Role of external ear in sound transmission mechanism:

Figure showing the external ear

The external ear components that play an important role in sound transmission are:

a. Pinna
b. Concha
c. External auditory meatus

External ear has two main influences on the incoming sound:

1. It increases the pressure at the ear drum level in a frequency sensitive way by acting as a resonator.
2. It increases the pressure in a way that depends on the direction of the sound source. This particular feature plays an important role in sound localization function of the ear. It also plays a very important role in sound localization in difficult situations, especially front to back and high to low distinctions, where interaural time differences donot help.
3. The Pinna Concha system acts like a trumpet, catching sound over a large area and concentrating it in the smaller area of external meatus. This increases the total energy available to the ear drum.

Resonating function of external ear: Resonance of sound at the external auditory canal changes the sound pressure at the ear drum level in a frequency selective way.

Role of external ear in sound localization:
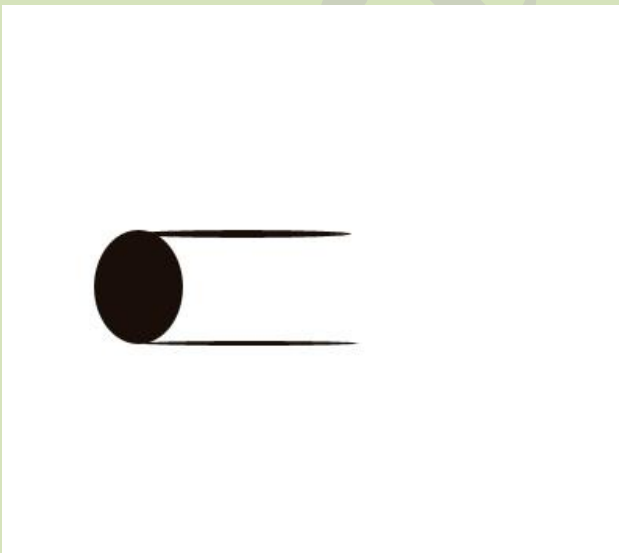
Figure showing a tube of quarter wave length

If a tube of quarter wavelength long, blocked at one end and open at the other is placed in a sound field, the pressure will be high at the closed end and low at the open end. The tube also adds resonance to the incident sound making the sound frequencies of 3 kHz stronger. This phenomenon is seen in the human external ear. This particular resonance is known as "Quarter wave resonance". The meatal quarter wave resonance can develop only if the meatus is terminated by a boundary with higher impedance than the air in the canal. This feature adds to the clarity of hearing to spoken sounds. The external ear by dampening low frequency sounds serves to block out the endogenous noises produced by the body (air inside the lungs, blood flowing inside blood vessels etc).
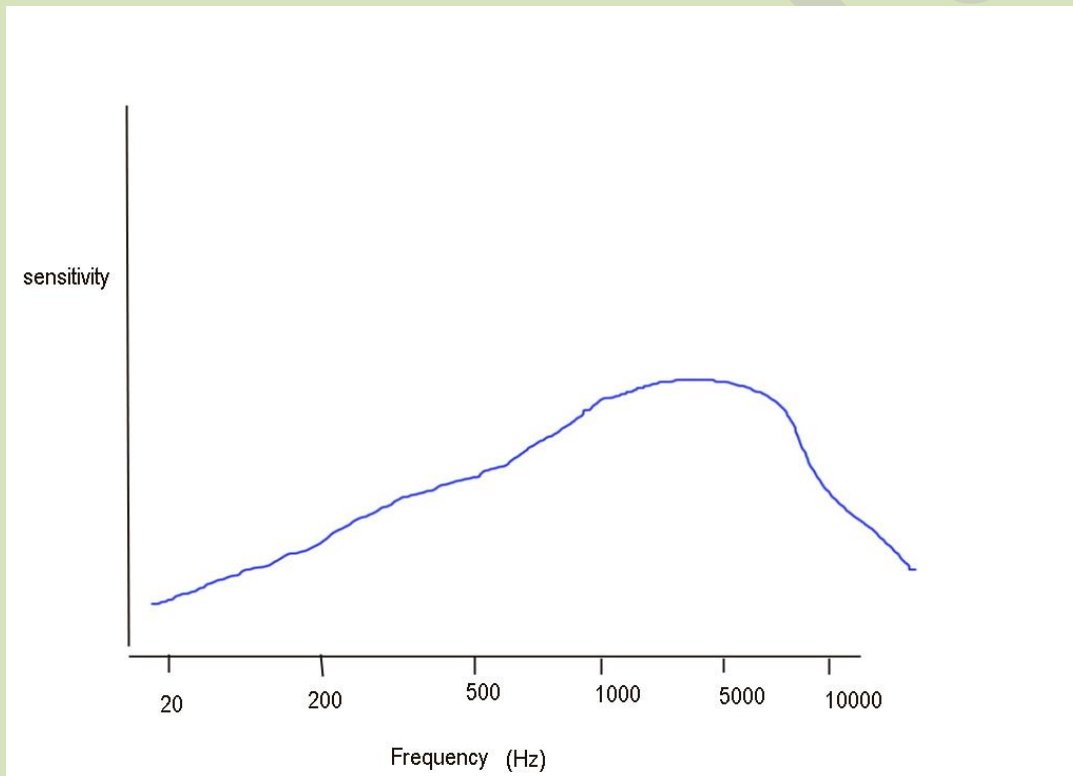

Figure showing the effects of quarter wave resonance

Another important resonance which is present in the external is termed as the "Broad resonance". This particular resonance adds about 10dB for sound frequencies around 5 kHz. These two resonances are complimentary

as they increase the sound pressure relatively uniformly over a frequency range between 2 – 7 kHz.

When a sound source is moved around the head, beginning in front and moving round to the side, main change which occurs is an attenuation of up to 10 dB in the frequency range between 2 – 7 kHz. This is due to the interference between the wave transmitted directly, and the wave that is scattered off the pinna.
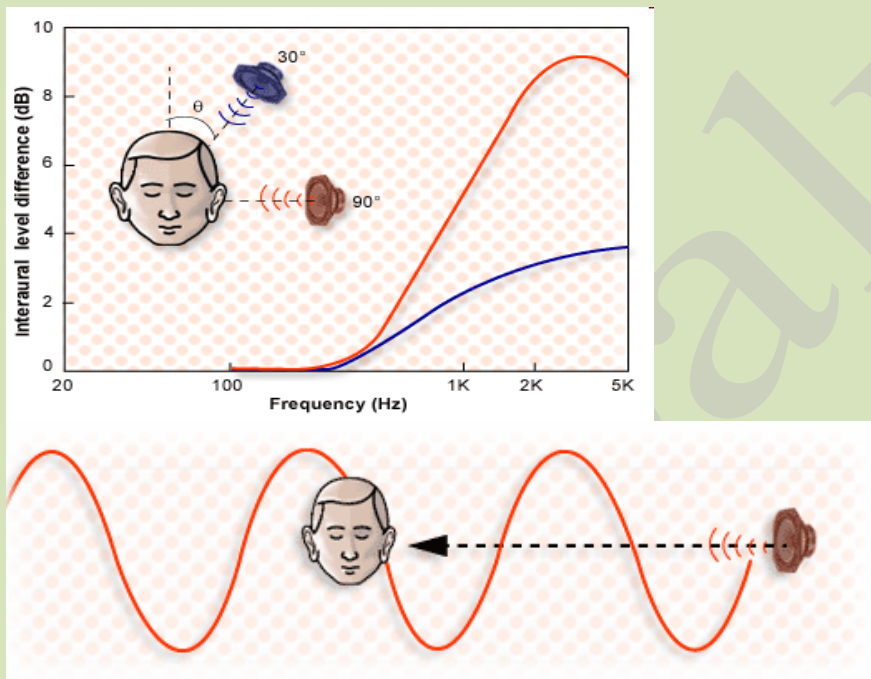
Figure showing the sound localization function of external ear

Both sound pressure levels and phase of acoustic waves are important determinants of sound localization function of external ear.

When the sound source is raised above the horizontal plane, the low frequency edge of the dip moves to higher frequencies as seen in the frequency gain curve. This phenomenon occurs due to cancellation between multiple out of phase reflections off the back wall of the pinna and concha. At very high frequencies, the wave length is short compared to the dimensions of the pinna. The pinna is highly directional and produces high gain on a narrow axis.
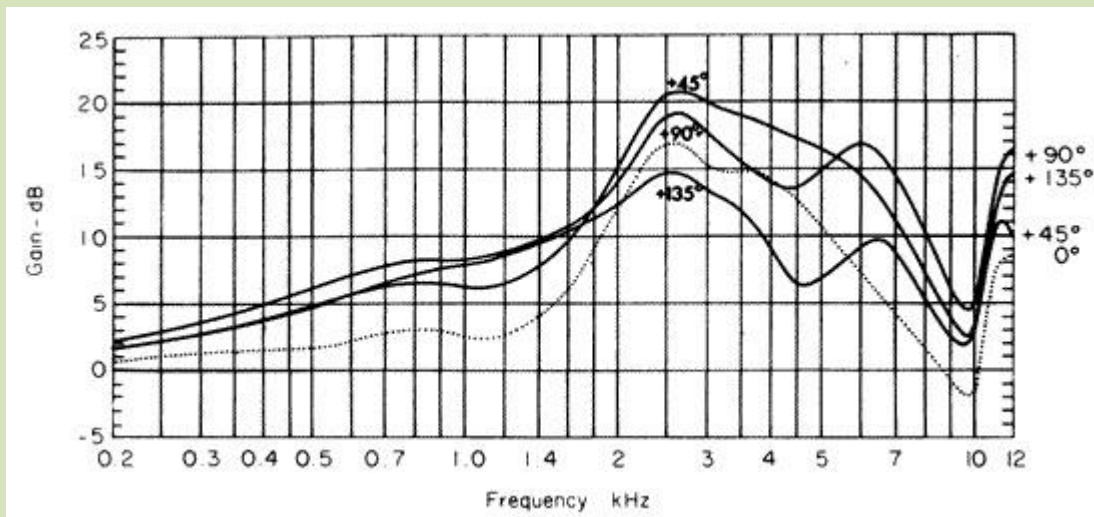
Figure showing pressure gain of the human external ear for different frequencies of sound source. 0° is straight ahead.

Role of ear drum in sound conduction:

The ear drum conducts sound from the external ear to the middle ear. Bekesy postulated that the ear drum moved like a stiff plate up to frequencies of 2 kHz. He also suggested that the inferior edge of the drum is flaccid and moves the most. At frequencies above 6 kHz the vibrating pattern becomes more complex and chaotic. This reduces the efficiency of sound transfer mechanism.
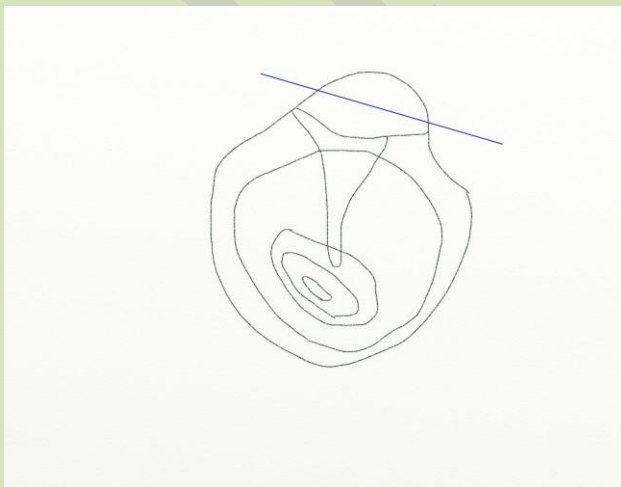
Figure showing ear drum vibration

The handle of the malleus is attached to the centre of the ear drum. This allows sound vibrations on any portion of the ear drum to be transmitted to the ossicles.


Role of Middle ear in sound conduction:

   The middle ear couples sound energy to the cochlea. It also acts as an acoustic transformer, facilitating impedance matching between the external and internal ear structures. The impedance of cochlear fluids is much higher when compared to that of air. Middle ear is an efficient impedance transformer. This will convert low pressure, high displacement vibrations into high pressure of the air into, low displacement vibrations suitable for driving cochlear fluids.
Middle ear also protects the cochlea from the deleterious effects of environmental agents.
The middle ear apparatus couples sound preferentially to only one window of the cochlea thus producing a differential pressure between the round and oval windows. This differential pressure causes movement of cochlea fluid. The movement of cochlear fluid is perceived by the hair cells of the cochlea.

The ossicles of middle ear are suspended by ligaments in such a way that the combined malleus and incus acts a single lever, having its fulcrum approximately at the border of the ear drum.
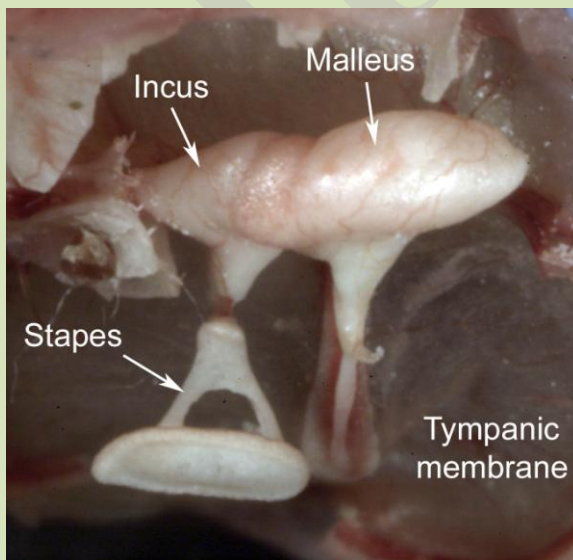
Picture showing middle ear structures

Components of impedance transformer:

1. The surface area of ear drum is about 55 mm^2; where as the surface area of the stapes is about 3.2 mm^2. The difference between these surface areas works out to be 17 fold. This causes an increase in the pressure at the level of foot plate of stapes. The forces collected over the ear drum are concentrated on a smaller area, so that the pressure at the oval window is increased.
2. Ossicular lever ratio (2.1 times). The incus is shorter than that of malleus. This is the reason for the lever action of the ossicles. This lever action increases the force and decreases the velocity at the level of stapes.
3. Buckling effect of ear drum: The ear drum curves from its rim to its attachment to the manubrium. The buckling effect causes greater displacement of the curved ear drum and less displacement for the handle of the malleus. This causes high pressure low displacement system.
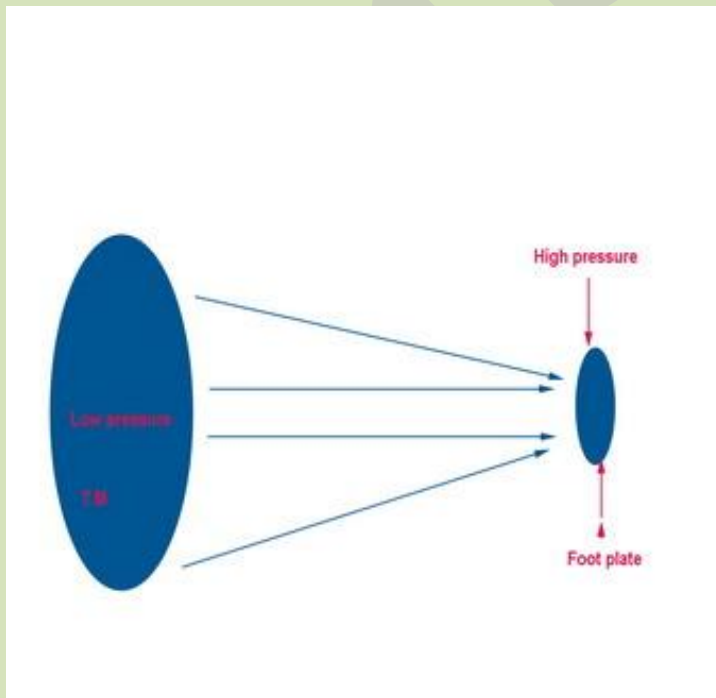
Figure showing the area ratio between the ear drum and foot plate
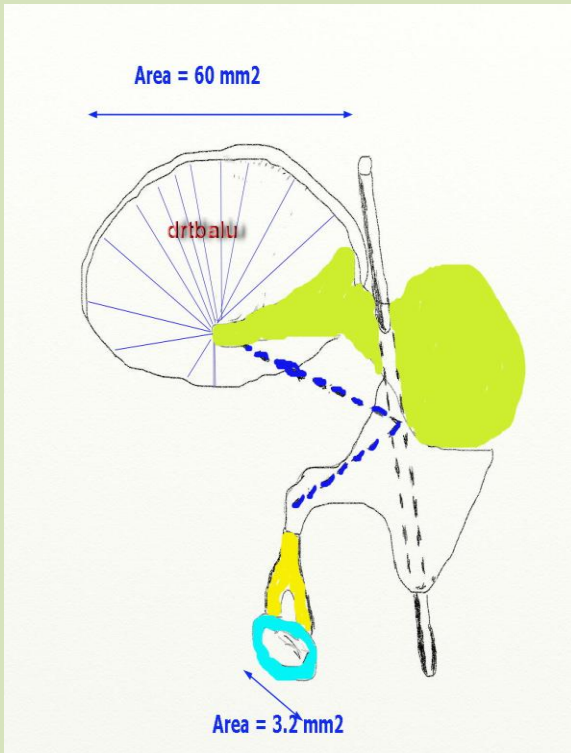
Figure showing the area ratio and ossicular lever ratio
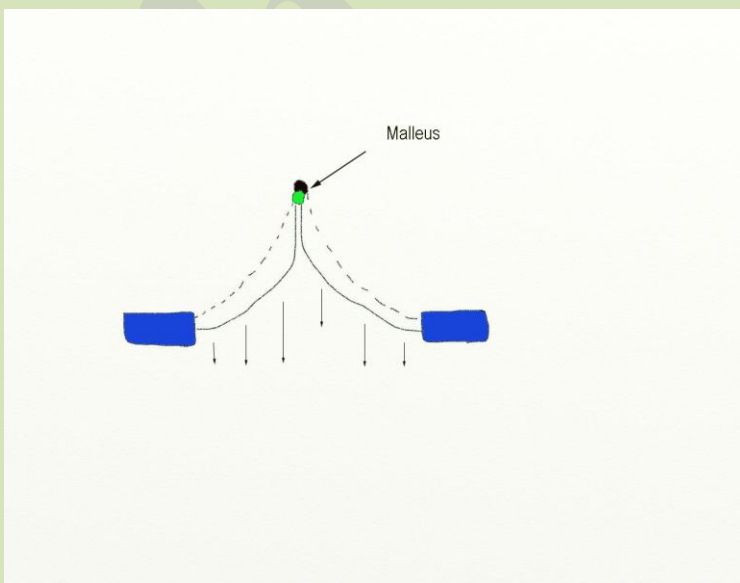
Figure showing the buckling effect of ear drum

The middle ear transformer mechanism ensures that up to 50% of the incident sound energy is transmitted to the cochlea. This value is applicable for one frequency only i.e. 1 kHz. At other frequencies additional factors come into play.

The malleus incudal joint is fixed in contrast to incus Stapedial joint which is flexible. The incudo malleolar joint moves as a single unit, where as the foot plate of stapes rocks in and out of oval window.

Frequency resolution effect of middle ear cavity:

Low frequency transmission in the middle ear is affected by the elastic stiffness of various components of the middle ear cavity. The elastic stiffness of middle ear cavity is contributed by various ligaments holding the ossicles in place. One important ligament which contributes the maximum to the middle ear stiffness component is the annular ligament. This ligament fixes the circumference of the foot plate of the stapes in the oval window. This ligament has been found to cause stiffness of the system to sound waves below 500 Hz. Presence of air in the middle ear cavity also adds to the stiffness component. When the ear drum moves in response to sound waves, air inside the middle ear cavity is compressed thereby reducing the movement of the ear drum. This in effect reduces conduction of low frequency sounds. If grommet is inserted, it improves low frequency sound wave conduction.

Mass effect is important in limiting ossicular movements in high frequencies. The mass effect increases during oedematous conditions of middle ear cavity, which in turn depresses conduction of high frequency sounds.

Above 2 kHz frequency the motion of ear drum breaks up into separate zones. As the frequency raises this break up becomes more pronounced causing a reduction in the coupling of vibrations of ear drum to the malleus. It has also been demonstrated that the effective ossicular lever ratio also changed with frequency of the incident sound wave. It is largest around 2 kHz to fall progressively at higher frequencies. At high frequencies a relative motion occurs between the malleus and incus there by causing a reduction in the ossicular chain lever ratio.

Role of middle ear muscles in sound transmission of middle ear:

Two muscles are found in the middle ear cavity: Tensor tympani and the Stapedial muscle. The tensor tympani muscle inserts onto the top of the handle of malleus. When it contracts, it pulls the malleus medially and anteriorly. This is nearly at right angles to the normal direction of vibration of the ossicles. It increases the stiffness of the middle ear cavity.
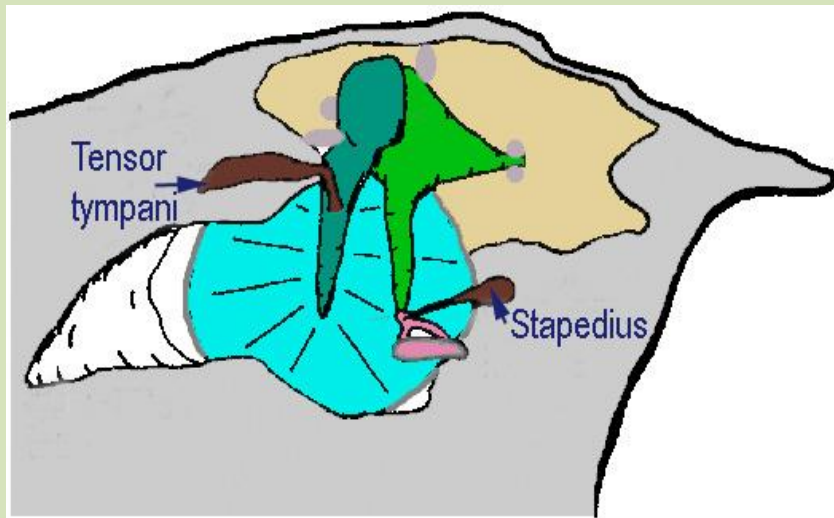
Figure showing the middle ear muscles

Stapedius muscle inserts to the posterior aspect of stapes. Contraction of Stapedius rocks the stapes to the oval window reducing its pumping action in response to sound. Contraction of these middle ear muscles reduces the conduction of low frequency sound. It also decreases the patient's hearing sensitivity to his / her speech. Contraction of these muscles also changes the direction of vibration of ossicles so that the movement is less effectively coupled to the cochlea.

Contraction of Stapedius muscle occurs reflexively to loud noises. This reflex protects the inner ear from deleterious effects of loud noise to the inner ear. The latency of Stapedial reflex is about 6 – 7 ms. This reflex may be too slow to protect the ear from sudden explosive noise. This reflex may play a protective role during prolonged exposure to loud noises.

Stapedius contractions can reduce transmission by up to 30 dB for frequencies less than 1 – 2 kHz. For higher frequencies this is limited to 10 dB.

Sound transmission through damaged middle ear:

Middle ear damage can lead to sound transmission problems due to:

1. Inadequate coupling to the tympanic membrane
2. Loss of impedance transformer
3. Reduction of the ability of the ossicles to move
4. Differential sound pressure levels at the oval and round windows may be affected (Round window baffle)

The loss of middle ear transformer mechanism alone can lead to an increase of 15 dB in auditory threshold levels of mid range frequencies. In patients with no middle ear apparatus, the pressure level delivered by sound is more or less equal in both round and oval windows. Pressure differential between both these windows is very important to set the cochlear fluids into motion. Only the moving cochlear fluid can stimulate the hair cells of the cochlea. Tondroff by his classic experiments was able to demonstrate that sound transmission is still possible without any pressure differential between the two windows. He postulated that pressure release through cochlear aqueduct could cause pressure differential. Other factors that could facilitate sound conduction in the absence of middle ear are:

1. Lower compliance of annular ligament of stapes, in comparison to that of round window membrane. This will facilitate differential movement of cochlear fluids
2. Scala vestibuli is more yielding than Scala tympani. This could facilitate differential movement of cochlear fluids.

Physiology of bone conduction:
    Sound conduction via bone is one important way in which one hears his/her voice. It also maintains some level of residual hearing in patients with conductive hearing losses. Bone conducted sound can be used for diagnostic purposes (Bone conduction audiometry).
    Cochlea is embedded in a bony cavity in the temporal bone. Vibrations of the entire skull can cause fluid vibrations within the cochlea itself. Vibrations of the skull could vibrate the CSF. Cochlear fluids are in continuity with the CSF via the cochlear aqueduct. Vibrations from CSF can

be transmitted via the cochlear aqueduct causing movement of cochlear fluids. Bone vibrations may also be transmitted by the air inside the external canal which in turn could cause vibrations of the ear drum.

Direct vibration of osseous spiral lamina can excite the hair cells of the cochlea.

The centre of inertia of middle ear ossicles does not coincide with their attachment points. Translational vibrations of skull will cause rotational vibration of bones, which can be coupled to the internal ear.

The middle ear acts like a broadly tuned filter with peak transmission of sound waves of frequencies 1 – 2 kHz. If the resonance of middle ear is hampered by fixation of foot plate of stapes, main loss would be seen in this frequency. This explains the presence of Carhart's notch in patients with mild stapes fixation. This dip appears around 2 kHz in bone conduction curve.

Cochlea: could be assumed to be a system of coiled tube.   It consists of three tubes coiled side by side. They are Scala vestibuli, Scala media and Scala tympani. The Scala vestibuli and Scala tympani contains perilymph while the Scala media contains endolymph.   The Scala vestibuli and Scala media are separated from each other by Reissner's membrane.
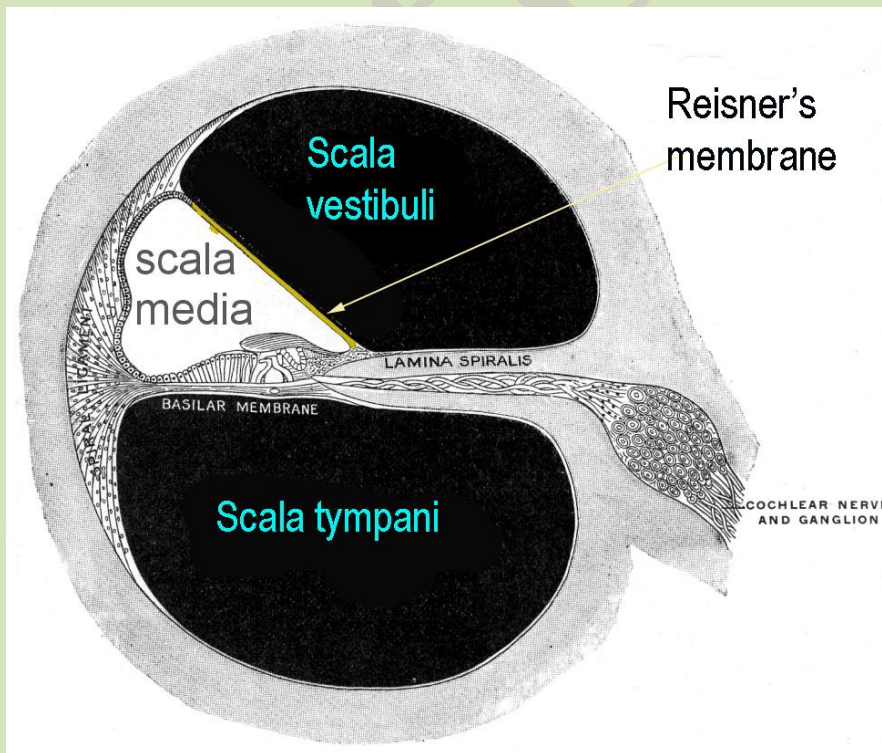
Figure showing cross section of cochlea

The Scala vestibule and Scala media are separated from each other by the basilar membrane. On the surface of basilar membrane lies the organ of Corti. Organ of Corti contains a series of electromagnetically sensitive cells i.e. hair cells. These hair cells are the end organs of hearing.

The Reissner's membrane is very thin and hence easily moves. It also does not obstruct the passage of sound vibrations from the Scala vestibuli to Scala media. As far as the conduction of sound is concerned, the Scala vestibuli and Scala media can be considered to act like a single chamber. The major function of Reissner's membrane is to maintain a special kind of fluid in the Scala media that is required for normal function of the end organs of hearing.

Perilymph: The perilymphatic space surrounding the membranous labyrinth opens into the CSF by way of the cochlear aqueduct. This space is continuous between the vestibular and cochlear divisions.
Site of production:

1. Ultra filtrate of plasma – This is not acceptable these days because none of the ions distribute between plasma and perilymph according to a Gibbs – Donnan equilibrium.
2. From CSF – Because the perilymphatic space is continuous with that of CSF by way of cochlear aqueduct. The concentration of K+, glucose, amino acids and proteins are higher in the perilymph of Scala vestibuli than in the CSF. When the cochlear aqueduct is mechanically blocked, the concentration of solutes in the Scala tympani rises towards the levels found in the Scala vestibuli.
3. Perilymph of Scala vestibuli originates primarily from the plasma, while the perilymph of the Scala tympani originates from both plasma and CSF.

The ionic concentration of perilymph resembles that of extra cellular fluid. Only notable difference being that the K+ concentration in Scala vestibuli is slightly higher than in the Scala tympani. The electrical potential of Scala tympani is +7mV and Scala vestibuli is +5mV.

Endolymph: The Scala media of cochlea contains endolymph. This is secreted by stria vascularis. Microscopically the cells of stria vascularis can be divided into superficially located darkly staining cells, known as the marginal cells, and more lightly staining basal cells. Under electron

microscope the marginal cells have long infoldings on their basal edge. These infoldings contain mitochondria.   The endolymphatic fluid component is joined to the endolymphatic sac by means of endolymphatic duct.
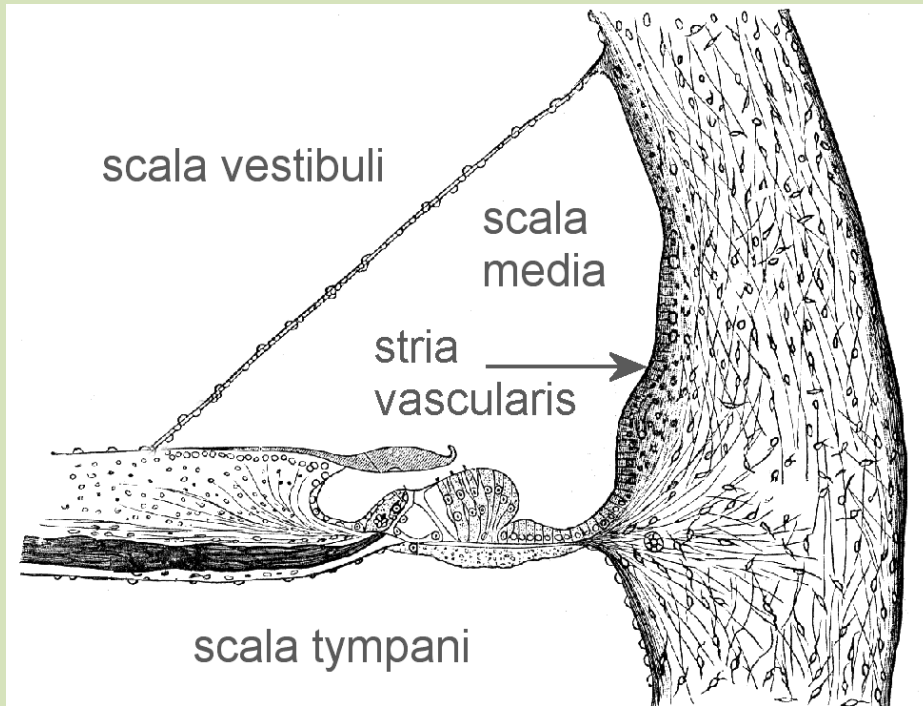
Figure showing stria vascularis

The vestibular labyrinth
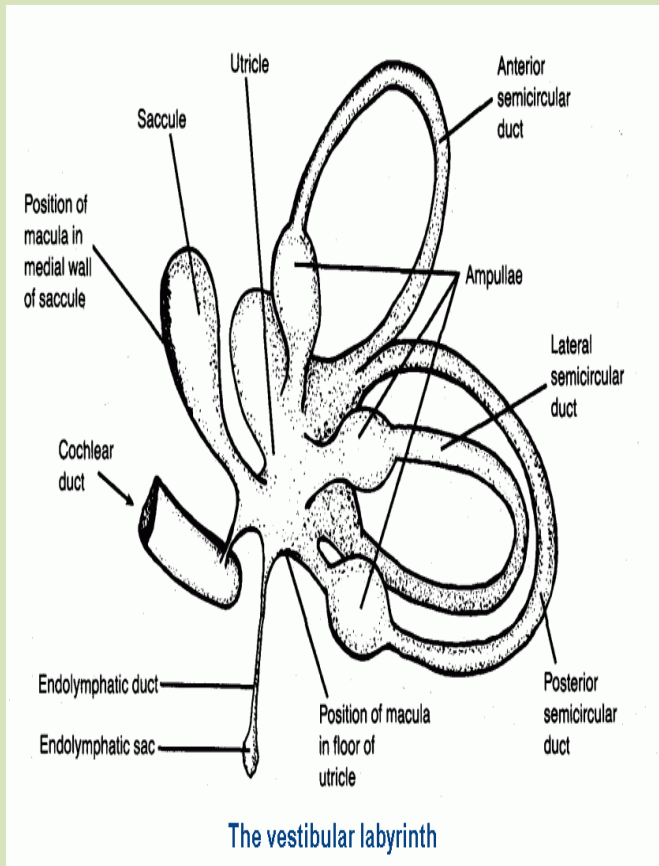
Figure of vestibular labyrinth

The stria vascularis contain a high concentration of Na+/K+ - ATPase, adenyl cyclase and carbonic anhydrase. These enzymes are associated with active pumping of ions and transport of fluid into the endolymph. Endolymph contains higher levels of potassium ions. Endolymph is unique among extracellular fluids of the body in that it has a high K+ content and a low Na+ content resembling intracellular fluid. These ions are cycled through the cochlea. Endolymphatic potential is about +50 – 120 mV. This is also known as endocochlear potential. The theory of this endocochlear potential maintenance was first proposed by Wangemann et al.

The potassium ions of the endolymph flow into sensory hair cells through the mechanotransduction channels and then into the perilymph via basolateral K+ channels in the hair cells. The potassium ions are then taken up by fibrocytes in the spiral ligament and transported via gap junctions into strial intermediate cells before being secreted into the endolymph again. There are three types of potassium channels in the hair cells:

1. KCNQ1

2. KCNE1
3. KCNQ4

Genetic mutations involving these channels can lead to defects in K+ recycling causing sensorineural hearing losses.

Abnormalities involving gap junctions could also cause defective recycling of K+ ions causing sensorineural hearing losses. Three types of proteins are involved in these gap junctions. They include connexin – 26, connexin – 30 and connexin – 31. Genetic mutations involving the genes coding these proteins also cause sensorineural hearing losses. Mutations in the gene for connexin – 26 account for half of all cases of autosomal nonsyndromic prelingual hearing impairment.
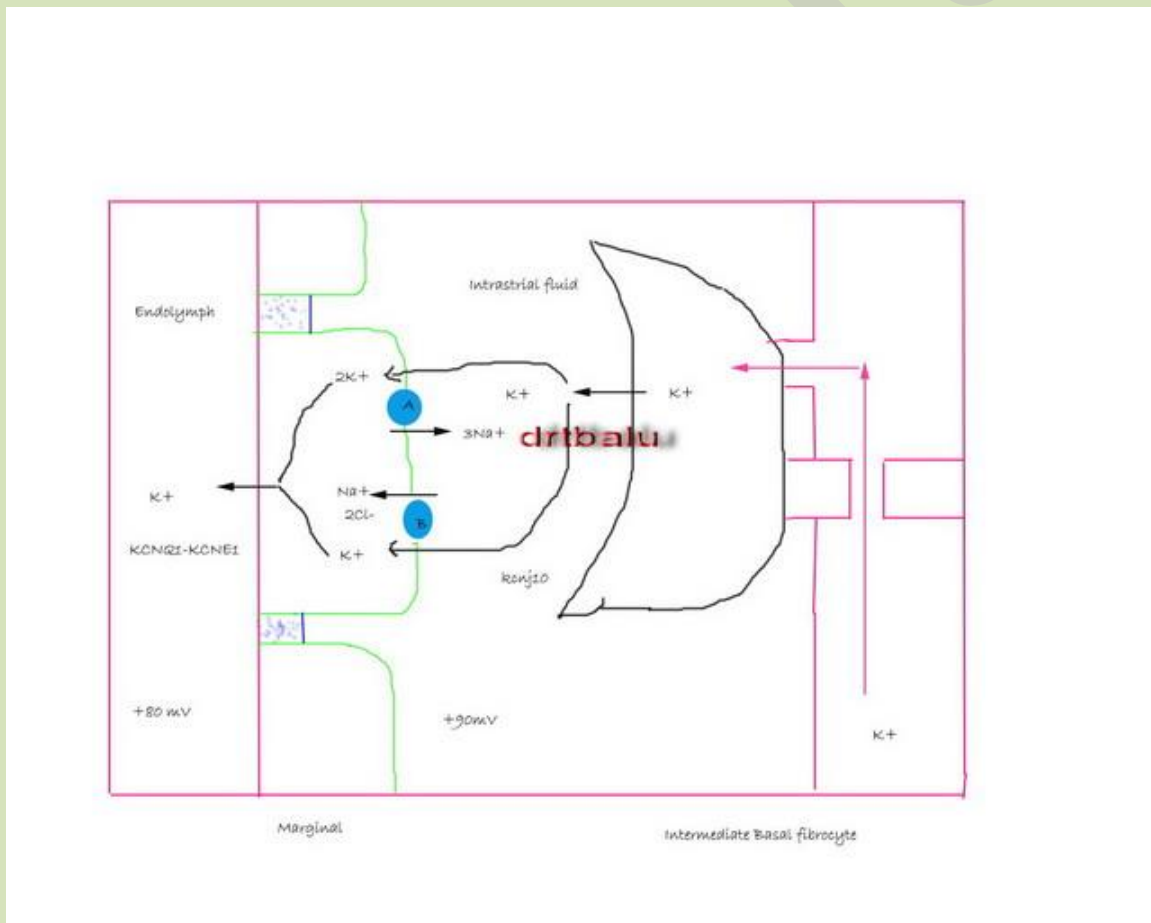

Figure showing Wangemann theory of endolymphatic ionic maintenance

The endolymphatic sac contributes to the homeostasis of the endolymph. It is capable of both increasing and decreasing its volume, rather than simply

absorbing endolymph. Obliteration of the endolymphatic sac and duct causes endolymphatic hydrops.

Basilar membrane: The basilar membrane is a fibrous membrane that separates the Scala media from the Scala tympani. This membrane contains 20,000 – 30,000 basilar fibers that project from the bony center of the cochlea (modiolus) towards the outer wall. These fibers are stiff, elastic and reed like structures that are fixed at their basal ends in the central bony structure (modiolus) of the cochlea. They are not fixed at their distal ends. The distal ends are embedded in the loose basilar membrane. Since these fibers are stiff and free at one end, they can vibrate like the reeds of a harmonica.

The lengths of the basilar fibers increase progressively beginning at the oval window and going from the base of the cochlea to the apex, increasing from a length of about 0.004 mm near the oval and round windows to 0.5 mm at the tip of the cochlea (Helicotrema). This constitutes a 12 fold increase in length.

The diameters of these fibers however decrease from the oval window to the Helicotrema, so that their overall stiffness decreases more than 100 fold. The stiff, short fibers near the oval window vibrate best at very high frequency, while the long limber fibers near the tip of the cochlea vibrate best at a low frequency.

The high frequency resonance of the basilar membrane occurs near the base, where the sound waves enter the cochlea through the oval window. Low frequency resonance occurs near the Helicotrema, mainly because of the less stiff fibers.

Cochlear mechanics:

The mechanical travelling wave in the cochlea is the basis of frequency selectivity. A normal travelling wave is fundamental to normal auditory function, while a pathological wave, which occurs in cases of cochlear sensorineural hearing loss, can cause severe sensori neural deficit.

The cochlear travelling wave was first described by Bekesy.

Features of cochlear travelling wave:

1. The wave travels along the cochlea, comes to a peak and dies away rapidly.
2. The basilar membrane vibrates with constant frequency for all low frequency waves, until above a certain frequency the response drops abruptly.

3. According to Bekesy, the capacity of the basilar membrane for frequency filtering is very poor indeed.
4. As the travelling wave moves up the cochlea towards its peak, it reaches a region which is mechanically active. In this region the membrane starts putting more energy in to the wave. The amplitude hence rises rapidly and falls rapidly.
5. The travelling wave has two components. The first component is a broadly tuned small component. This component depends on the mechanical properties of the membrane. The second component is caused by active input from the cochlea. This component is prominent for low intensity sounds.
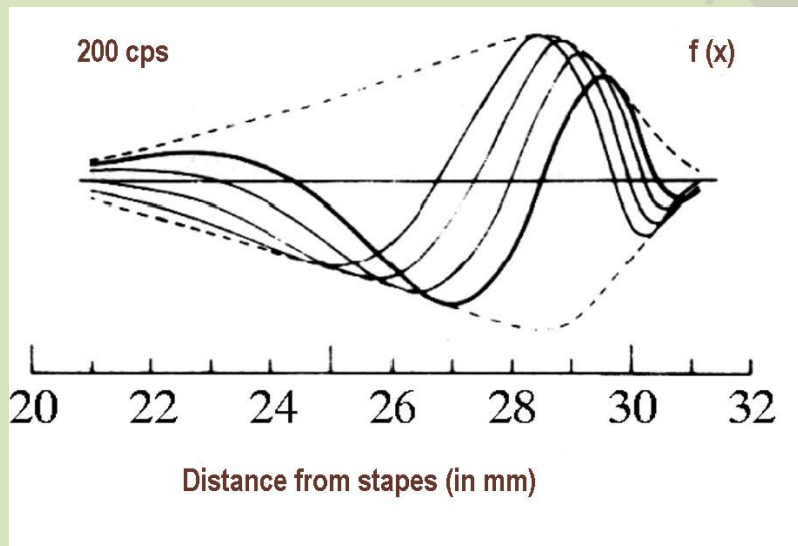

Figure showing travelling wave of Bekesy. Base of cochlea is to the left, and the apex towards right. Solid lines show displacements at four successive instants. Dotted lines show the envelope which is static

It has been shown that the relative amplitude of basilar membrane vibration is the largest for low intensity stimulus. As the stimulus amplitude is increased, the relative response becomes smaller and smaller.

Experimental evidence has shown that high frequency tones produce greater effect near the base of the cochlea, while low frequency tones had a similar effect closer to the apex, with a gradation for in between for intermediary frequencies.

It has also been shown that the basilar membrane tuning becomes less selective at high stimulus intensities. This has been accounted for by the non linearity of the basilar membrane.
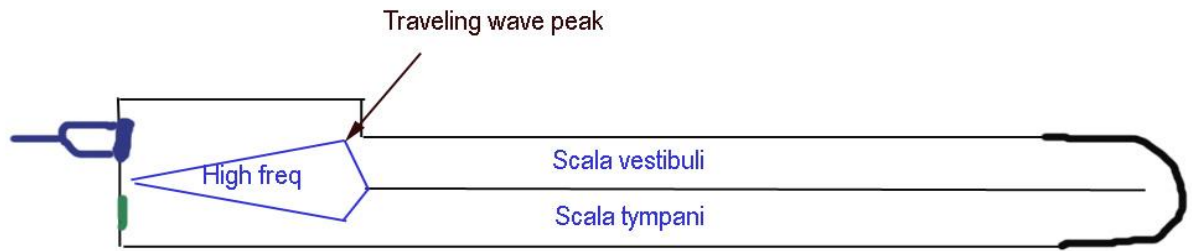
Figure showing basal turn of cochlea's response to high frequency sounds
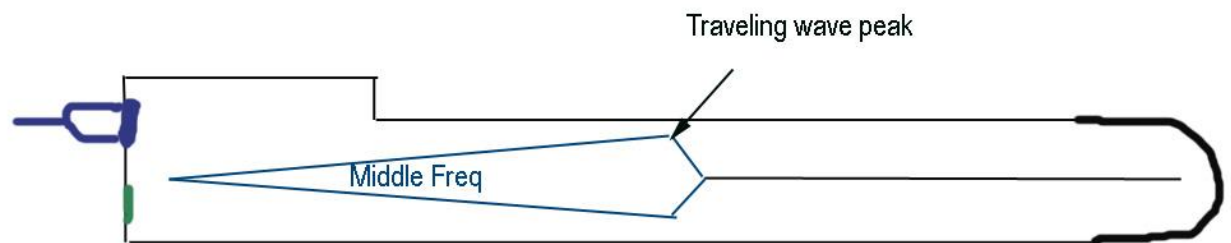
Figure showing the cochlea's responsive area to middle tone frequencies

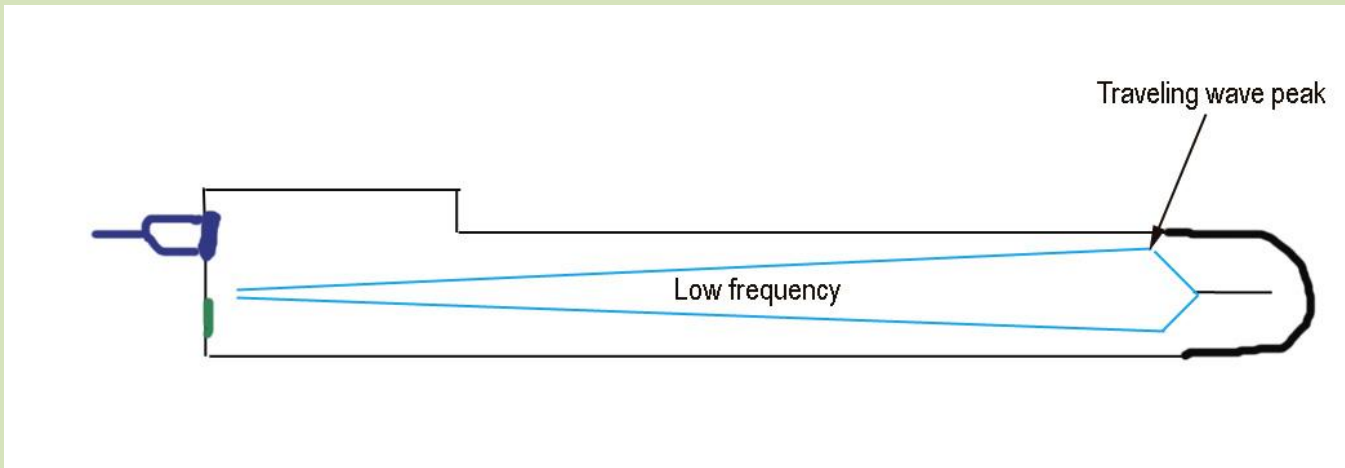*Figure showing the response of apex of the cochlea to low frequency sounds*

Transduction of hair cells:

The individual sterocilia on the apical surface of the hair cell are mechanically rigid. They are braced together with cross links so that they move as a stiff bundle. When this bundle gets deflected, the different rows of stereocilia slide relative to one another.
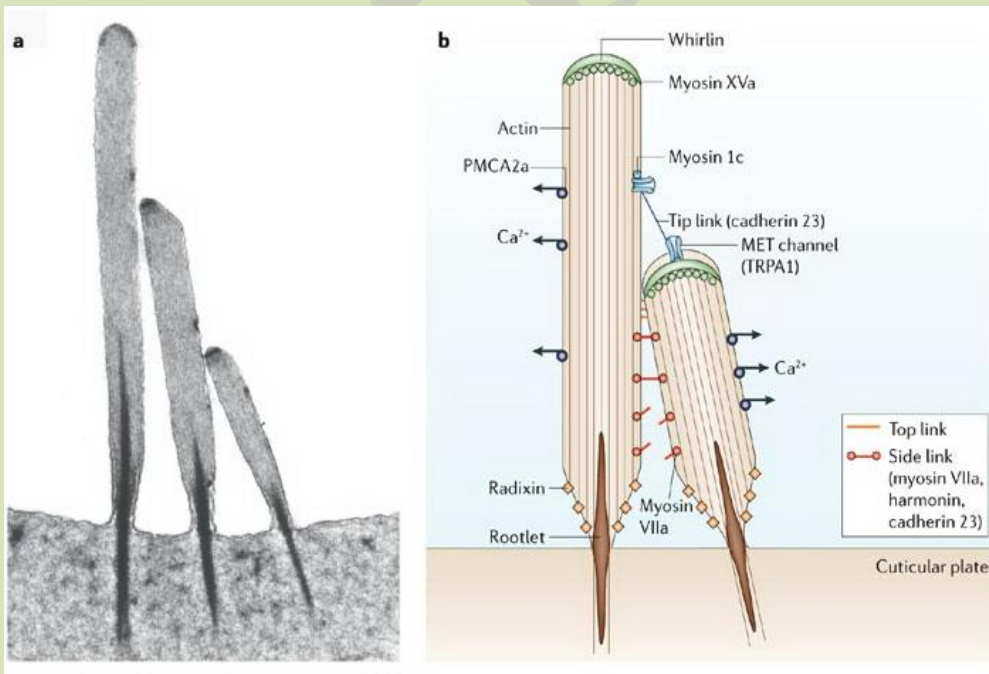

Figure showing the ultrasturcture of hair cells

There are fine links running upwards form the tips of the shorter stereocilia on the hair cell, which join the adjacent taller stereocilia of the next row. When the stereocilia are deflected in the direction of the tallest stereocilia, the links are placed under tension. This opens up the ion channels in the cell membrane.

The stimulus is coupled to the stereocilia by means of a shear / relative motion between the tectorial membrane and the reticular lamina. As the basilar membrane and organ of Corti are driven upwards and downwards by a sound stimulus, the stereocilia are moved away from and towards the modiolus. Since the tallest stereocilia is situated on the side of the hair cell furthest away from the modiolus, upward movement of the basilar membrane is translated into a movement of the stereocilia in the direction of the tallest hair cell. This movement opens up the ion channels.

There are two types of hair cells in the cochlea. These hair cells are the ultimate end organs of hearing.

Inner hair cells: 95% of the afferent auditory fibers make contact with the inner hair cells. Each inner hair cell has terminals from approximately 20 afferent fibers.   It has been assumed that the role of inner hair cell is to detect the movement of the basilar membrane and transmit it to the auditory nerve. The potential on the inside of inner hair cell is about -45 mV.

Each hair cell has about 100 stereocilia on its apical border. These cilia are driven by the viscous drag of endolymph. The inner hair cells respond to the velocity rather than the displacement of basement membrane.

Outer hair cells: There are 3-4 times more outer hair cells than inner ones. Only `10% of auditory nerves synapses with the outer hair cells. It has been shown that extensive damage of outer hair cells in the presence of functioning inner hair cells still cause significant amount of sensorineural hearing loss. It has hence been proposed that the outer hair cells in someway control the sensitivity of inner hair cells to sound. This phenomenon is also known as "Tuning". The potential on the inside of outer hair cell is about -70 mV.   The cochlear microphonic potentials are derived from the outer hair cells.

Electrical potentials of cochlea:

By placing electrodes in the vicinity of cochlea electrical potentials generated by it in response to sound waves can be recorded. These potentials can be divided into three components. They are:

1. Cochlear microphonics – A/C potential
2. Summating potential – D/C potential
3. Negative neural potentials – N_1 & N_2.

The cochlear microphonics is derived almost exclusively from outer hair cells. This helps in the magnification of the traveling wave. This is an A/C response following the waveform of the stimulus. Superimposed on this is a D/C shift in the baseline. This is known as the summating potential. The summating potential could either be negative / positive depending on the stimulus conditions. The summating potential takes sometime to reach the maximum after the onset of stimulus. It is mostly generated as a distortion component of the outer hair cell response, with perhaps a small contribution from the inner hair cells. At the beginning of sometimes at the end, a series of deflections in the negative direction can be seen. These are also known as neural potentials. The first one is known as N1, and the second smaller one which is not always visible is known as N2 potential.

Determination of loudness of sound:

Loudness is determined by the auditory system in the following three ways:

1. As the sound becomes louder, the amplitude of vibration of the basilar membrane and hair cells also increases, so that the hair cells excite the nerve endings at more rapid rates.
2. As the amplitude off vibration increases, it causes more and more of the hair cells on the fringes of the resonating portion of the basilar membrane to become stimulated, causing spatial summation of impulses i.e. transmission through many nerve fibers rather than through only a few.
3. The outer hair cells do not become stimulated significantly until vibration of the basilar membrane reaches high intensity and

stimulation of these cells appraises the nervous system that the sound is loud.

Auditory nerve fibers response to stimuli:

In response to stimulus, neurotransmitter is released in the synapses at the base of inner hair cells. This gives rise to action potentials in the auditory nerve fibers. Single auditory nerve stimuli are always excitatory, and never inhibitory. Transmitter release occurs due to depolarization of inner hair cells. For low frequency stimuli, the transmitter will be released in packets concentrated during the depolarization phases of the hair cell response. These events take place in synchrony with the sound stimulus, transmitter release and action potential generation is also in synchrony with individual cycles of the stimulus. This is known as phase locking. Phase locking takes place only at low frequencies. Phase locking is one way in which information about the sound stimulus is transmitted via the auditory nerve. For stimulus frequencies below 5 kHz, the timing of action potentials play a vital role in frequency discrimination. This is known as temporal coding of the stimuli. Frequency specificity is another method by which frequency discrimination occur at the level of auditory nerve. This is also known as "Place coding". Fibers responding best to different frequencies arise from different places in the cochlea.

Theories of hearing:

Various theories of hearing have been proposed. They are:

1. Place theory of Helmholtz
2. Telephone theory of Rutherford
3. Volley theory of Weaver
4. Place volley theory of Lawrence
5. Travelling wave theory of Bekesy

Place theory of Helmholtz: Also known as resonance theory. It was first proposed by Helmholtz. He proposed that the basilar membrane was constructed of different segments that resonated in response to different frequencies. These segments are arranged according to the location along the length of basement membrane. For this tuning process to occur the

segments in different locations would have to be under different degrees of tension. According to this theory, a sound entering the cochlea causes the vibration of the segments that are tuned to resonate at that frequency. Pitfalls: This theory has various pitfalls. Sharply tuned resonators dampen rather slowly. This could lead to constant after ringing long after the stimulus has ceased. This theory also fails to explain why a stream of clicks of frequencies ranging from 1220, 1300 and 1400 Hz is heard as 100 Hz pitch.

Telephone theory of Rutherford: According to this theory proposed by Rutherford the entire cochlea responds as a whole to all frequencies instead of being activated on a plate by place basis. Here the sounds of all frequencies are transmitted as in a telephone cable and frequency analysis is performed at a higher level (brain).

Pitfalls: Damage to certain portions of cochlea can cause preferential loss of hearing certain frequencies i.e. like damage to the basal turn of cochlea causing inability to hear high frequency sounds. This cannot be explained by telephone theory.

Temporal theory supposes that the auditory nerve conducts sounds containing the whole range of frequencies and discrimination takes place at higher centers.

The neurons respond to stimulus obeying the all or none law. They either fire or stop firing. They should be provided with a latent interval of atleast 1 millisecond before the next stimulus is presented. The auditory nerves will have no problems conducting sounds up to 900 Hz. Conduction of sounds above 1000 Hz will become a problem and this theory doesn't explain how this frequency gets conducted and perceived by the brain.

Volley theory of Wever: Wever proposed that several neurons acting as a group can fire in response to high frequency sound, even though none of them could do it individually. This could be possible if one neuron could fire in response to one cycle and another neuron fires in response to the next cycle, while the first neuron is still in its refractory period.

Place volley theory of Lawrence: Lawrence combined both volley and place theory to explain sound transmission and perception.

Travelling wave theory of Bekesy: Bekesy proposed that frequency coding took place at the level of cochlea. Contrary to resonance theory, Bekesy

found that basilar membrane is not under tension and elasticity is uniform throughout. Anatomically the basilar membrane gets wider towards the top resulting in a gradation of stiffness along its length, going from stiffest at the base, close to the stapes and least stiff at the apex (helicotrema). As a result of this stiffness gradient sound transmitted to the cochlea develop a special kind of wave pattern which travels from base towards the apex.

This wave is known as the travelling wave. The travelling wave involves a displacement pattern that gradually increases in amplitude as it moves up the basilar membrane; it reaches a peak at a certain location, decays in amplitude rather quickly beyond the peak. The location of the traveling wave peak along the basilar membrane depends on the frequency of the sound. In other words traveling wave is the mechanism that translates signal frequency into place of stimulation along the basilar membrane. High frequencies are represented towards the base of the cochlea, and successively lower frequencies are represented closer and closer to the apex.

Central auditory pathways: Nerve fibers from the spiral ganglion of corti enter the dorsal and ventral cochlear nuclei. These nuclei are located in the upper portion of the medulla. Here all the fibers synapse, and the second order neurons pass mainly to the opposite side of brain stem to terminate in the superior olivary nucleus. A few second order neuron fibers also pass to the superior olivary nucleus on the same side. From the superior olivary nucleus, the auditory pathway passes upwards through the lateral lemniscus. Some of these fibers terminate in the nucleus of lateral lemniscus, but many fibers bypass this nucleus and travel to the inferior colliculus, where almost all of the auditory fibers synapse. From here, almost all the fibers synapse at the medial geniculate nucleus. From here auditory fibers pass via auditory radiation to the auditory cortex located in the superior gyrus of the temporal lobe.

- Signals from both ears are transmitted through the pathways of both sides of the brain, with a preponderance of transmission in the contralateral pathway
- Crossing over occurs in three places in the brain stem. Usually in the trapezoid body, in the commissure between the two nuclei of the lateral lemnisci and in the commissure connecting the two inferior colliculi.
- Many collateral fibers from the auditory tract passes directly into the reticular activating system of the brain stem
- Other collaterals go to the vermis of the cerebellum.

- A high degree of spatial orientation is maintained in the fiber tracts from the cochlea all the way to the cortex.
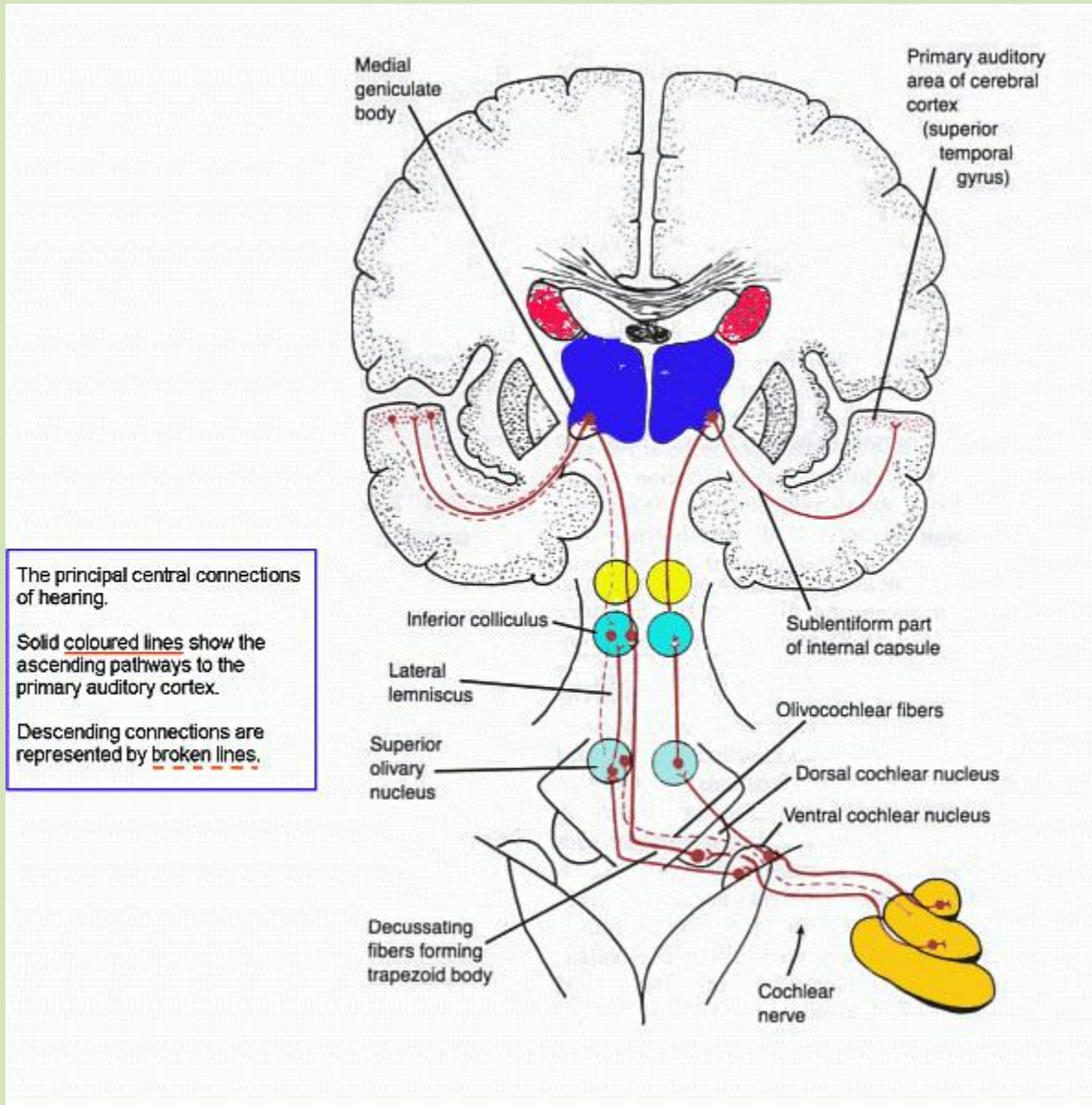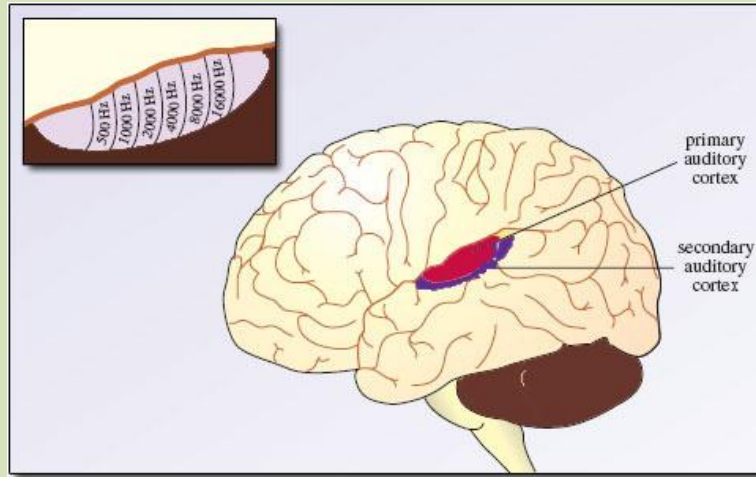

Figure showing central auditory pathway

Figure showing cortical centre for hearing

Central functions:

Sound localization and lateralization
· Auditory discrimination
· Temporal aspects of audition including
» temporal resolution
» temporal masking
» temporal integration
» temporal ordering
· Auditory performance with competing acoustic signals
· Auditory performance with degraded signals