Pathway of Sound and Components of the Ear

Frequency Selectivity of the Pinna
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The pathway of sound begins at the pinna, which is responsible for collecting frequencies around 5000Hz. The pinna aids in (1) horizontal sound localization and (2) the convolutions aid in spectral cues for vertical localization. The pinna also acts as a resonator for high frequency sounds due to its convolutions and depressions.

After the pinna the sound enters to the ear canal which is a tunnel into the temporal bone from the concha to the tympanic membrane. Due to the structure of the ear canal being closed on one end and open on the other, it is considered a quarter wavelength resonator and it resonates best with sound wavelength that is 4x that of the ear canal, being 2-5kHz.

At the end of the ear canal the tympanic membrane is composed of three layers, (1) the outer epithelial layer, (2) the middle connective layer and the (3) medial mucosal layer. The umbo on the tympanic membrane is the most depressed point. The tympanic membrane has many functions such as (1) transmitting acoustic vibrations from the outer ear to the middle ear, (2) protecting the middle ear by preventing reflux or insufflation of secretions through the eustachian tube and (3) the buckling effect in sound transmission.

Right after sound passes through the tympanic membrane it goes through the three ossicles of the middle ear; the malleus, incus and stapes. The resonance of the ossicles is about 2000 Hz. When the tympanic membrane vibrates, the vibrations move the manubrium of the malleus, which then moves the incus and in turn the stapes onto the cochlea.

The middle ear has a resonance of 900-1000Hz and demonstrates an impedance mismatch correction to make up for the loss of energy due to the impedance mismatch caused by the transmission of vibration from the air to the cochlear fluids, this gain totals out to be about 30dB. The middle ear transformer is a result of the (1) area ratio of the tympanic membrane to the stapes footplate (TM:Stapes), the ratio is about 17:1. Pressure is a result of force divided by area (P=F/A) so the force that is on the tympanic membrane during vibrations becomes concentrated on the stapes footplate which creates a ~25dB gain making up about 85% of the energy that would be lost due to the impedance mismatch. The next step of the transformer mechanism is the (2) ossicular level ratio, which results due to the manubrium of the malleus being larger than the long process of the incus. This difference in length creates more force onto the incus than the manubrium with a ratio of 1:3:1, resulting in a 2.5dB gain. The last part of the transformer mechanism is the (3) buckling effect of the tympanic membrane or the curved membrane ratio. This ratio results from the conical shape of the tympanic membrane causing a buckling action at the umbo resulting in the umbo being the least displaced when compared to the rest of the tympanic membrane. Since the manubrium of the malleus is on the umbo the malleus is also the least displaced which leads to an increase in force by 2 times, contributing to a 3dB gain. The overall gain of the middle ear transformer mechanism is about 25-30dB in total. If the mechanism did not exist, over 99% of sound energy would be lost due to the fact that sound would arrive to the oval and round window at the same time and cancel each other out (Bekesy, 1934). The gain increase from the middle ear transformer is frequency dependent, for example at 1000 Hz there is a maximum of 25dB increase, and for every octave frequency above that there is a 6dB decreasing rate. If there was a break in the chain of ossicles or a stiffening of the ossicles, this would result into a conductive hearing loss due to the sound cancelation.

The middle ear also contains the acoustic reflex which results from to middle ear muscles, the tensor tympani and the stapedius. The tensor tympani muscle inserts onto the malleus and the stapedius muscle inserts on the neck of the stapes. The primary function of the contraction of these muscles is to attenuate sound. The tensor tympani contributes to the acoustic reflex mainly in the higher frequencies in such that when vibrations hit the last of the ossicles, the stapes, it then hits the oval window of the cochlea where sound is transmitted into mechanical energy and then electrical.

The cochlea itself has three main chambers; (1) scala media, (2) scala vestibuli, and (3) scala tympani. The tapping on the oval window produces fluid displacement within the cochlea starting with the scala vestibuli. This instantly causes the basilar membrane in the scala media to vibrate in up/down motion. The basilar membrane analyzes the sound by performing Fourier spectral analysis by breaking down sound into frequency components so that shearing action of the hair cells will occur at optimal placement. The cochlea is tonotopic in such a way that the basal end of the cochlea is stimulated by high frequencies and the apical end is stimulated by low frequencies. Different frequencies cause maximum vibration amplitudes along the different points of the cochlea. The Organ of Corti is a structure of the cochlea that lies on top of the basilar membrane and it is attached to the tectorial membrane. There are two types of hair cells that are embedded in the Organ of Corti, (1) inner hair cells and (2) outer hair cells. The inner hair cells are organized in a single row with about 3500 hair cells and are supported by the Claudius and Boettcher cells. The outer hair cells are organized in 3 rows with about 13500 hair cells in which their cell tips are attached to the tectorial membrane. The outer hair cells are different from the inner hair cells in such a way that they are motile (lengthen and shorten) in response to mechanical displacement and they are in contact with the tectorial membrane. At the point where the amplitude of a traveling wave is at maximum vibration on the basilar membrane, a shearing action of the OHCs occurs causing the stereocilia of the OHCs to bend towards the IHCs causing ion channels to open and an electrical current of K+ ions to flow into the hair cells causing a voltage change. This voltage change results in a neurotransmitter release from the IHCs eliciting a response in the central auditory nervous pathway to the primary auditory cortex.

The lengthening or shortening of the OHCs generates a force which changes the motion of the traveling wave and increases mechanical input to the IHCs. The change in the direction of the traveling wave and the increased input to the IHCs causes an action potential to the auditory nerve fibers, this is known as the cochlear amplifier. The cochlear amplifier causes a (1) increase in input that improves the sensitivity of the basilar membrane by lowering thresholds and an (2) increase frequency selectivity by sharpening tuning curves.

There are two types of nerves that innervate at the Organ of Corti (1) afferent nerves and (2) efferent nerves. Afferent nerves are ascending from the cochlea to the brain and efferent nerves are descending from the brain to the cochlea. Type I radial afferent nerve fibers represent about 95% of the spiral ganglion neurons that only innervate the IHCs. One radial afferent fiber is in contact with one IHC and each IHC has more than one radial afferent fiber attached to it (innervated by). Type II spiral afferent nerve fibers make up 5% of the spiral ganglion neurons that only innervate the OHCs. The nerve fibers are not myelinated and traverse along the length of the cochlea to reach the OHCs. The efferent nerves descend from the olivocochlear branch and the superior olivary complex (SOC) to the cochlea. The spiral efferent nerve fibers enter the habenula and branch off to 3000 nerve fibers, these types of nerves make up the homolateral/ipsilateral pathway that travels from the lateral SOC to the cochlea on the same side (hence ipsilateral pathway). These spiral efferent fibers innervate the afferent nerves that are on the IHCs (not on the IHCs), so one spiral efferent fiber can innervate more than one IHC. Radial efferent fibers enter through the habenula and branch off to 8000 nerve fibers at the Organ of Corti which hen branch off to 40,000 nerve endings directly. These radial efferent fibers travel from the medial SOC and cross over to the cochlea on the contralateral side. Radial efferent fibers make up for about 80% of all efferent fibers and synapse directly onto the OHCs, so that one radial efferent fiber innervates multiple OHCs

The classic afferent pathway that begins that the auditory nerve first travels to the cochlear nucleus (CN) where frequency, intensity, duration, and onset is processed. It then travels to the superior olivary complex (SOC) which is comprised of three nuclei; (1) trapezoid body, (2) medial superior olivary complex (MSO), and (3) lateral superior olivary complex (LSO). The MSO is responsible for decoding timing differences between the ears and the LSO decodes intensity differences between the ears. Next, the signal travels to the lateral lemniscus (LL) where sound input from both ears is combined and processed to the inferior colliculus (IC) where directionality of sound is integrated. The signal then goes to the medial geniculate body (MGB) which has three divisions that are responsible for further auditory processing and lastly to the primary auditory cortex (A1). The primary auditory cortex is located on the temporal lobe of the brain in the transverse gyrus of Heschel. The descending pathway projects from the auditory cortex to the cochlear nucleus (CN) in the cochlea. The olivocochlear system projects from the SOC to the ipsilateral and contralateral cochleae. The efferent pathway modulates sensitivity and activity of the cochleae.