2.8.3

Sound Vibrations to Action Potentials

Transfer of Vibrations in Air to Vibrations in Fluids: The first challenge that our ears face is transferring the vibrations in the air, to vibrations in a fluid. Because the density of the fluid in the inner ear is much greater than the density of air it requires more energy to generate sound waves in the fluid than in the air. Think of being underwater at a swimming pool and listening to people talk, it is very hard to hear and understand. It is the middle ear's responsibility to amplify the sound waves so that their energy is not lost. This is accomplished in two ways. First, the arrangement of the ear ossicles amplifies the sound. Second, and probably more importantly, the tympanic membrane has about 20 times more surface area than the oval window. This size difference results in concentrating the energy on the oval window. Think of how you might move a large rock with a pry bar. You would place the fulcrum close to the stone to gain the maximal mechanical advantage of the bar. The long end of the bar would be analogous to the tympanic membrane and the short end would be analogous to the oval window. These mechanisms are so effective that very little, if any, energy is lost as it is transferred from air waves in the external ear to fluid waves in the internal ear.

Detection of Sound Waves of Different Frequencies: As explained earlier, sound waves of different frequencies are perceived as different pitches. Therefore, the inner ear needs a way of detecting the different frequencies. The structure in the inner ear tasked with this responsibility is the basilar membrane. Recall the design of the basilar membrane; it is narrow (thick) and stiff near the oval window and gradually gets wider and more limber as it progresses toward the helicotrema. Think of the example of the xylophone mentioned earlier. When you strike a key on a xylophone it always sounds the same because it always vibrates at the same frequency. Another analogy might be a guitar string. As you tighten a guitar string making it stiffer, it vibrates at a faster rate and produces a sound of a higher pitch. Also on the guitar as you shorten the string by pressing on a fret with your finger the pitch gets higher. At a given tension and length the guitar string always vibrates at the same rate so we always perceive it as the same pitch. The basilar membrane functions in much the same way. Each segment of the membrane has an innate frequency. If it were a guitar string and you plucked it at a certain point along its length it would always vibrate at the same rate at that point. A different point on the basilar membrane would vibrate at a different rate. When a vibration in the fluid reaches the segment of the basilar membrane that has the same innate frequency, it will cause the basilar membrane to vibrate. This phenomenon is known as resonance. Based on this principle of resonance the basilar membrane is able to respond to all of the different frequencies in the sounds we hear, within the range of human hearing.

Conversion of a Sound Wave to an Action Potential: The function of any sensory organ is to convert a sensory stimulus to an action potential that can then be transmitted to the brain. In this case, the sensory signal is the sound wave. The responsibility of converting vibrations into action potentials falls upon the inner hair cells in the cochlea.

Recall that the apical end of the hair cell contains stereocilia and that they are arranged in order of ascending lengths from one side of the cell to the other. The membranes of the stereocilia contain mechanically gated cation channels. Extending from the gate of the ion channel to the adjacent, taller, stereocilium is a fibrous protein called a tip link (see image below). In response to a fluid wave (caused by the stapes pressing against the oval window) the unique section of the basilar membrane moves. Since the outer hair cells are connected to the tectorial membrane, this movement causes the stereocilia to bend toward the longest stereocilium and creates tension. The resultant tension from the

bending acts to pull the gates on the ion channels open. Consequently, when sterocilium bend in the opposite direction the tension decreases and the gates close.

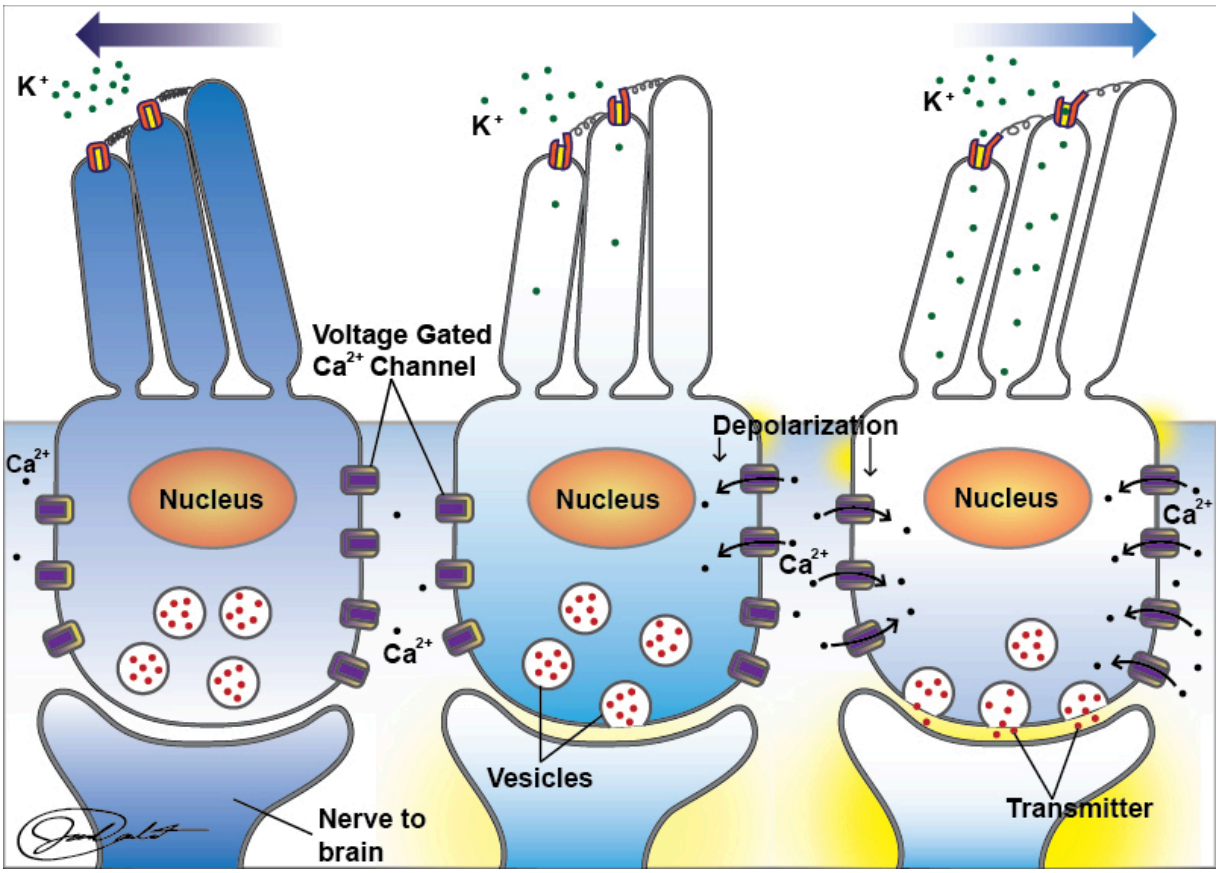
Since the sterocilia are bathed in endolymph, when the gates on the cation channels open, K^+ rushes into the cell, depolarizing the membrane. The resultant depolarization also activates a motor protein called **prestin**. Prestin is a contractile protein that when active causes the sterocilia to shorten, thus pulling on the tectorial membrane and at the same time accentuating the upward movement of the basilar membrane. The actions of prestin serve to amplify the signal, the result of which greatly enhances the sensitivity of the signal.

In addition, the up and down movement of the basilar membrane and associated outer hair cells forces endolymph fluid to flow within the organ of corti. This flow then causes the inner hair cells (not connected to the tectorial membrane) to bend. The bending induces depolarization of the inner hair cells. In contrast to activating prestin for amplification, the inner hair cell depolarization causes voltage gated Ca2+ channels to open and subsequent fusion of synaptic vesicles which then release the neurotransmitter glutamate. Glutamate induces an EPSP in the associated neuron. Thus, the outer hair cells serve to amplify movement while the inner hair cells release neurotransmitter sending action potentials to the brain.

The axons of these neurons form the cochlear nerve that transmits the action potential to the auditory cortex of the brain. In hair cells at rest, about 10% of the K+ ion channels are open resulting in a low frequency of action potentials traveling to the brain when it is perfectly quiet. This allows for both an increase in action potential frequency when hair cells bend toward the longest stereocilium and a decrease in frequency of action potentials when the hair cells bend the other way (see image below).

It may seem odd that K+ instead of Na+ is used to depolarize the hair cells, but in the case of hair cells the driving force for K+ to enter the hair cells is very large. This is because of a specialized structure called the **stria vascularis** which actively secretes K+ from the perilymph into the endolymph. The active transport involves the Na+/K+ ATPase pump and a secondary active transport protein that moves in Na+, K+ and 2Cl- molecules into the cell.

Since the cochlea of the inner ear is essentially filled with two extracellular fluids, perilymph and endolymph, the directional driving force for potassium to enter the cells needs to allow K+ to move into the hair cells (from endolymph) through the apical surface and then exit the hair cell (into perilymph) through the basolateral surface so that it can be recycled back to the endolymph. This can be a bit complicated to understand because the concentrations of K+ in the endolymph match the concentrations of K+ in the cytoplasm, essentially eliminating any movement due to concentration differences. So why does the driving force favor K+ to move into the cell, even though concentrations gradients are nearly equivalent? The answer lies in the **endocochlear potential**. The endocochlear potential is derived from the sum of two potentials: a potential between the endolymph and perilymph formed by active secretion of the K+ into the endolymph by the stria vascularis (80mV), and a potential formed between the cytoplasm of hair cells and the perilymph as K+ passively diffuses out of the hair cell (40mV). Thus the endocochlear potential is about 120mV between the endolymph and the perilymph. This potential drives K+ from the endolymph into the cytoplasm of the hair cell (depolarization) and then to the perilymph only to be recycled by the stria vascularis back to the endolymph. Loss of this endocochlear potential appears to be a frequent cause of hearing loss.



Conversion of Sound Wave to Action Potential

Image by BYU-Idaho student Jared Cardinet Fall 2014

Hair Cells of the Spiral Organ

Perception of Sound: Once the action potential is generated and sent to the brain it is the function of the auditory cortex to convert that action potential into a perception. Each region of the cochlea is hardwired to its own specific region of the auditory cortex. When that particular region of the brain receives input from the ear we perceive the unique pitch associated with that frequency of the sound wave. It's kind of like a piano where each key is like a different segment of the cochlea. That key is linked to a specific string in the piano such that each time the key is struck we hear the same sound. In this case, the strings would be like a specific region in the auditory cortex. Each time an action potential reaches that specific segment of the auditory cortex we perceive the same sound. Therefore, the pitch is determined by the region of the brain that receives input from the cochlea. Loudness, on the other hand, is determined by the number of action potentials that reach the brain. Recall that the loudness of a sound is a function of the amplitude of the sound wave. Sound waves of higher amplitude cause the hair cells to vibrate more vigorously, which would cause more ion channels to open. This would result in a greater depolarization of the hair cell, more Ca^{2+} entry through the voltage-gated ion channels and more neurotransmitter release. The end result is a greater frequency of action potentials going to the auditory cortex, which is perceived as a louder sound. A common misconception is to equate the frequency of action potentials with the frequency of the sound waves. The frequency of action potentials is a function of the amplitude of the sound wave whereas the frequency of the sound waves determines which portion of the auditory cortex receives the action potentials.

In addition, the brain can actually “fine” tune hearing by controlling action potential frequency via efferent neurons. That’s right, the brain can actually send signals (via efferent neurons) from the auditory cortex in addition to just receiving them (afferent neurons). The efferent neurons sent by the brain synapse on the outer hair cells and some afferent axons. When the brain uses these efferent neurons, they act to suppress the responsiveness of the hair cells connected to the efferent neuron in use. These efferent neurons use acetylcholine to open up nonselective cation channels, triggering the entry of Ca++. In this case, the Ca++ acts to open Ca++ activated K+ channels, causing a

hyperpolarization event. Dampening frequency allows the brain to filter out unwanted sounds and focus on sounds that we are wanting to hear in noisy environments. They may also be important during sleep to help dampen all sounds.

Hearing Loss

There are three forms of hearing loss: conductive, central, and sensorineural. Conductive hearing loss is a result of sound waves being unable to move from the external ear to the inner ear. This can be caused by a plugged ear canal (excessive ear wax), infection of the middle ear or calcification of the stapes to the oval window. Anything that prevents conduction of sound through the external ear or proper vibration of the middle ear bones is termed conductive hearing loss. Central hearing loss results from damage to the auditory cortex, usually caused by a stroke. Sensorineural hearing loss is caused by damage to the structures of the inner ear (hair cells, cochlear neurons, viscous fluid). A common cause of sensorineural hearing loss is exposure to loud sounds. In humans, this loss is irreversible at present. Interestingly, birds have the ability to regenerate hair cells after complete destruction. Study of hair cells in birds may one day lead to the ability to replace damaged hair cells in humans.

It is interesting to note that as we age, we tend to lose the ability to hear very high frequency sounds. This appears to be from a lifetime of wear and tear to the hair cells located closer to the oval window end of the cochlea. This is where the basilar membrane length is shorter and thicker, and where high energy / high pitch sound waves are experienced.

Here is a link to a video that goes through a lot of what you have read so far. It is one of the best hearing physiology videos we have ever seen. It was made in 2002 and continues to be a favorite to show in physiology classes. We encourage you to check it out!

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