12.4.3

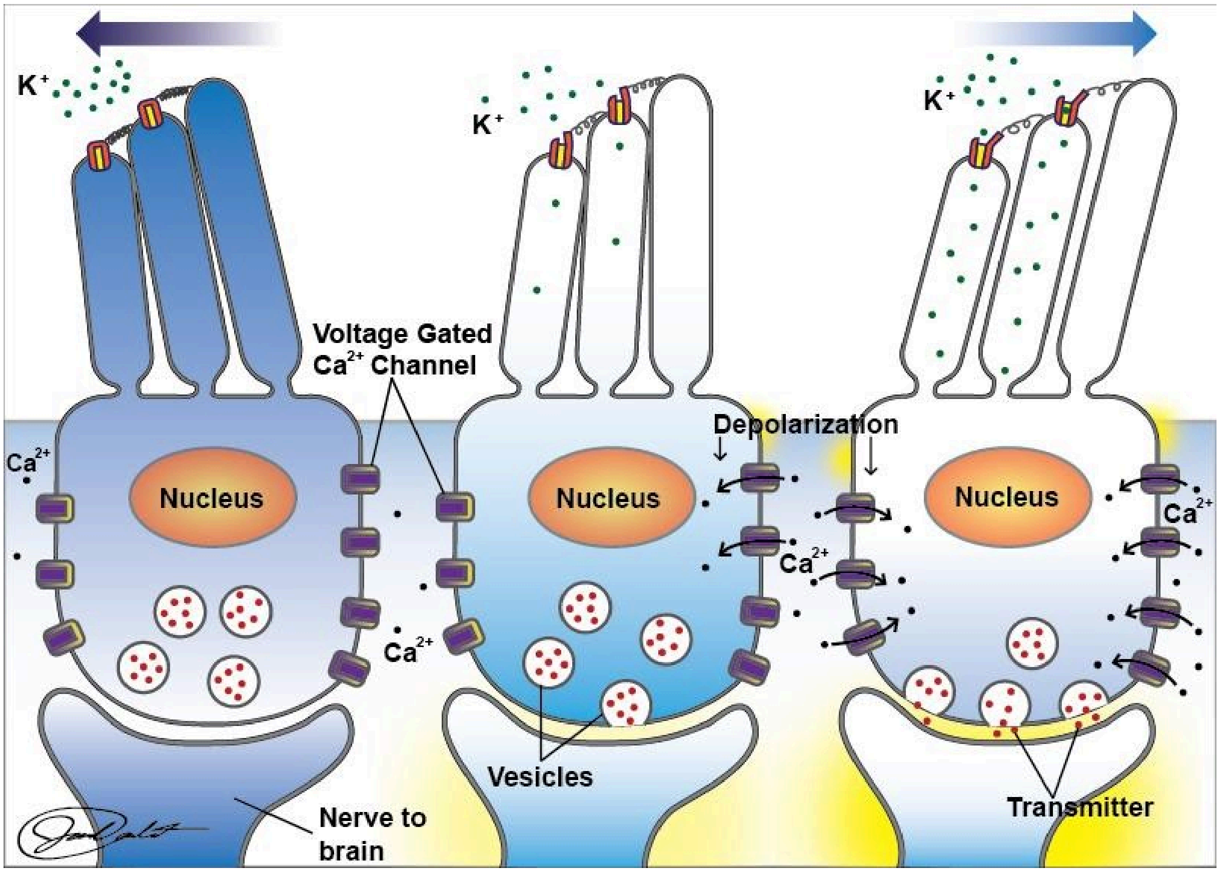
Sound Vibrations to Action Potentials

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 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 row of hair cells in the cochlea. Recall that the apical end of the hair cell contains the 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). When the stereocilia bend toward the longest stereocilium the tension in the tip link increases, pulling the gates on the ion channels open, and when they bend in the opposite direction the tension decreases and the gates close. The stereocilia are bathed in the endolymph of the cochlear duct. Endolymph is similar to intracellular fluid and has a high K^+ concentration. When the gates on the cation channels open, K^+ rushes into the cell, depolarizing the membrane. This depolarization opens voltage gated Ca^{2+} channels on the basal membrane of the hair cell allowing Ca^{2+}

to enter. The influx of Ca^{2+} stimulates the release of neurotransmitter by the hair cell triggering an action potential in the neuron that synapses with the hair cell. 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).



Conversion of Sound Wave to Action Potential. *Produced 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.

Other Factors Influencing Our Perception of Sound: There are several other factors that impact what we hear. An important consideration is the function of the three outer rows of hair cells. About 90% of the neurons of the cochlear nerve arise from the inner row of hair cells and these are thought to be key to communicating with the auditory cortex. The outer hair cells, on the other hand, are implicated in a process called cochlear amplification. These hair cells have special proteins in their plasma membranes that allow the cell to actively lengthen and shorten. This action can either enhance or reduce the movement of specific regions in the cochlea. The outcome of this action is thought to help focus the sound to specific regions of the spiral organ so that we can better detect the different frequencies of sound waves. Also, recall that only the stereocilia of the outer three rows of hair cells are embedded in the tectorial membrane, those of the inner hair cells are not. What then causes the stereocilia in the inner hair cells to bend? The structure of the spiral organ allows the basilar membrane and the tectorial membrane to function like a bellows. The two membranes form a pocket, the inner sulcus, behind the inner row of hair cells. When the basilar membrane moves up it squeezes the bellows and endolymph flows out of the inner sulcus bending the stereocilia one way and when the basilar membrane moves down the bellows enlarges pulling endolymph into the inner sulcus bending the stereocilia the opposite way.

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 where high energy / high pitch sound waves are experienced.