Psych 1XX3 – Audition Notes – Mar 18, 2010

Auditory Mechanisms of Different Species:

- Auditory mechanisms vary across different species according to specific needs.

Sound Frequency:

- One way that the hearing abilities of various species differ is the range of frequencies that can be detected.
- Blowing a dog whistle: you know that blowing the whistle doesn't produce any audible sound to your own ears, but you will certainly have a dog's attention! The dog whistle produces a sound at a high frequency that is beyond the range of human ears but well within the range of the dog's auditory system.

Sound Frequency Perception in Vertebrates:

- Humans can perceive sounds that lie anywhere between 20 and 20,000 Hz, a respectable auditory range. Relatively speaking, whales, dolphins and dogs have a wider hearing range, while frogs and birds have a much narrower range of frequencies that they can detect.
- At the lower frequency detection extreme are fish, while at the higher frequency detection extreme are bats and rodents.

Environmental Impacts on Auditory Structure:

- Audible frequency range is determined in part by the evolution of the structures of the auditory system.
- One key structure is the **basilar membrane** which contains the hearing receptors; sounds of different frequencies are processed along different areas of the basilar membrane.

The Basilar Membrane:

- The basilar membrane varies in length across species; it is shortest in amphibians and reptiles, longer in birds, and longest in mammals.
- A longer basilar membrane allows processing of a wider range of frequencies. And so, mammals can discriminate the widest range of frequencies while most other species cannot discriminate frequencies over 10000 Hz.

The Stimulus: Sound Waves
Introduction:

- Like light, sound travels in waves, although sound waves travel much slower and require some medium to travel through.
- Sound waves are initiated by either a vibrating object, like our vocal cords or a guitar string, a sudden burst of air, like a clap, or by forcing air past a small cavity, like a pipe organ.
- This causes the air molecules surrounding the source of the sound to move which causes a chain reaction of moving air particles.

Responding to Changes in Air Pressure:

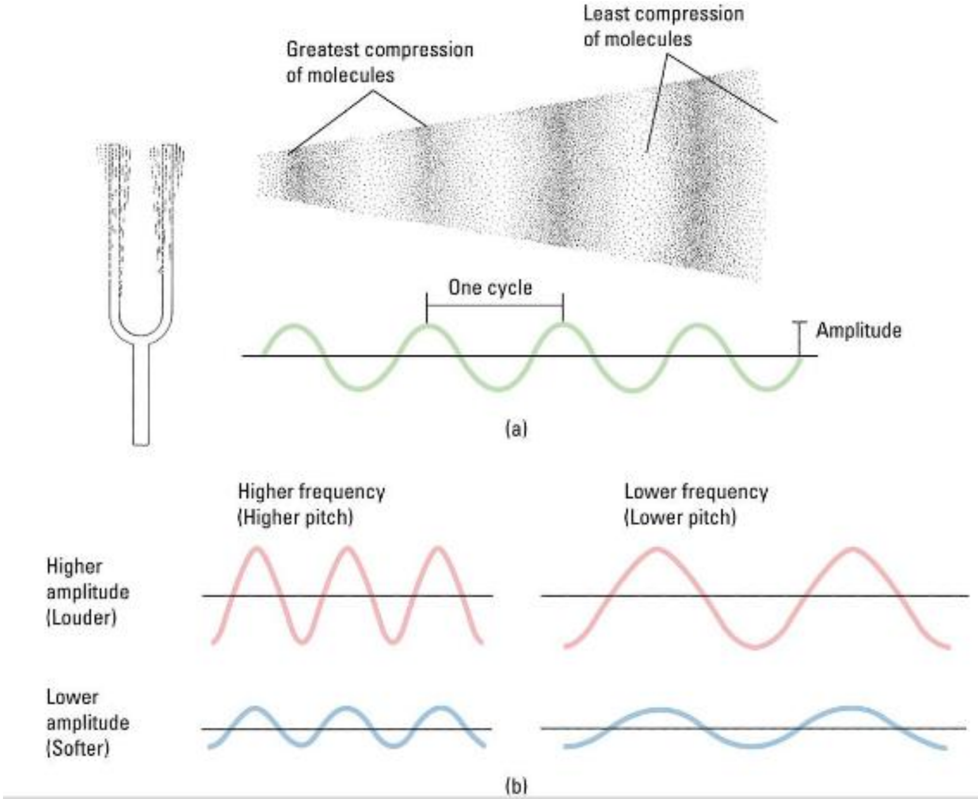
- This chain reaction is much like the ripples you observe when you throw a stone into a pond. The point where the stone hits the pond produces waves that travel away in all directions, much like the alternating bands of more and less condensed air particles that travel away from the source of a sound.

The Eardrum Responds to Air Pressure Changes:

- These alternating bands of more and less compressed air molecules interact with the eardrum to begin auditory processing.
- A band of compressed air molecules causes your eardrum to get pushed slightly inwards, whereas a band of less dense air particles causes the eardrum to move outwards.

Sine Waves:

- The changes in air pressure over time that make up a sound wave can be graphed as a sine wave, as shown here below.



- In our survey of the neurophysiology of vision, we examined three physical characteristics of a wave: **amplitude, wavelength**, and **purity**.
- In audition, the same three physical characteristics, when applied to sound waves, translate into the three psychological properties of **loudness, pitch**, and **timbre**.

Amplitude: Measure of Loudness

- Variations in the **amplitude** or height of a sound wave affect the perception of **loudness**.
- Since waves of greater amplitude correspond to vibrations of greater intensity, higher waves correspond to louder sounds.
- Humans are sensitive to a very wide range of different sound amplitudes, and because of this, loudness is measured using a logarithmic scale of decibels (dB).
- In this scale, the perceived loudness of a sound doubles for every 10 dB increase.
- A normal conversation takes place at around 60 dB, a whisper at around 17 dB, and sitting in the front row at a rock concert means you get to hear the music at around 120 dB.

Frequency: Measure of Pitch

- Sound waves also vary in the distance between successive peaks; this is called the wavelength or **frequency** of the sound and this property affects the perception of **pitch**.
- Pitch is measured in Hertz (Hz), which represents the number of cycles per second, or the number of times in a second that a sound wave makes one full cycle from one peak to the next.
- If many wave peaks are condensed into one second, then this sound will be of a high frequency, and result in the perception of a high pitched sound.
- We learned that what we call the visible spectrum of light is only a small portion of the total spectrum of light waves; similarly, the audible zone of frequencies that humans can detect represents only a portion of the possible frequencies that can be produced.

Timbre: Measure of Complexity/Purity

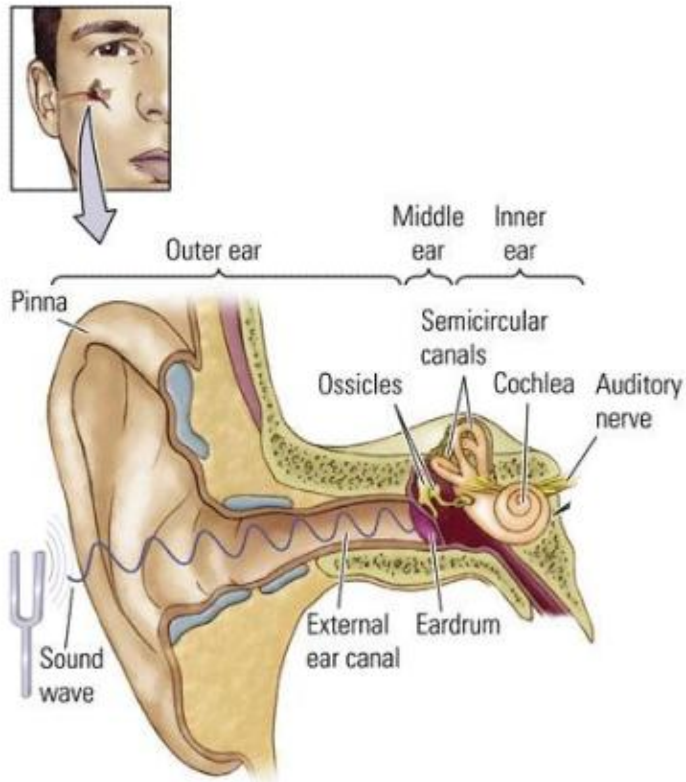
- The third physical property of sound is **purity**, which affects our perception of **timbre**.
- Most of the sounds we hear everyday are complex sounds that are composed of multiple sound waves that vary in frequency.
- Timbre refers to the complexity of a sound.
- When you pluck a guitar string, it vibrates as a whole which is the fundamental tone, but it also vibrates at shorter segments along the string, called the overtones.
- The final sound you hear is a mixture of the fundamental tone and all the overtones, and this combination is timbre. So a piccolo and a Bassoon may both play the same note, but because each instrument produces a unique combination of the fundamental frequency and overtones, they still sound different to us, even though each instrument is producing the same frequency and amplitude.

The Ear:

- The **ear** can be divided into the external, middle, and inner ear and each area conducts sound in a different way.
- Incoming changes in air pressure are channelled through the external ear, onto the middle ear, and amplified so that it can be detected as changes in fluid pressure by the inner ear.
- These changes in fluid pressure are then finally converted to auditory neural impulses.

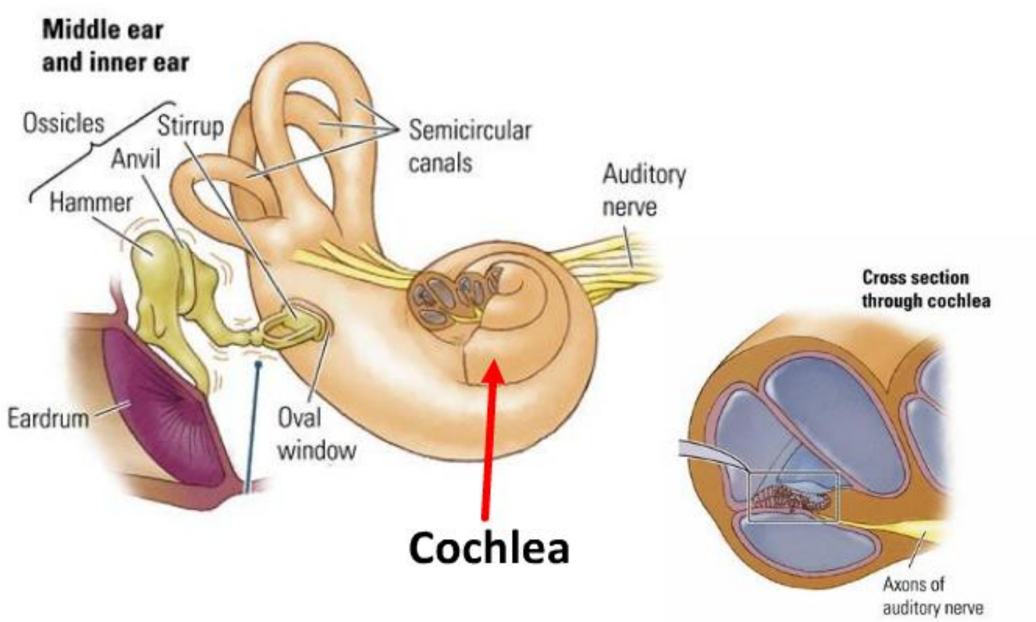
The External Ear:

- Let's begin this journey by examining the **external ear**, which is made up of the **pinna**, **the ear canal**, and **the eardrum**.
- The **pinna** is what you probably think of when referring to your ears; it is the folded cone that collects sound waves in the environment and directs them along the **ear canal**.
- Since the ear canal narrows as it moves towards the eardrum, it functions to amplify the incoming sound waves, much like a horn.
- The **eardrum** is a thin membrane vibrating at the frequency of the incoming sound wave and forms the back wall of the ear canal.
- See image on next page



The Middle Ear:

- The **middle ear** begins on the other side of the eardrum, which connects to the **ossicles**, the three smallest bones in the body.
- These ossicles are named after their appearance and consist of the **hammer**, **anvil**, and **stirrup**.
- The amplification of the vibrating waves continues here in the middle ear.
- The vibrating ossicles are about 20 times larger than the area of the oval window to which they connect to create a lever system that amplifies the vibrations even more.
- This additional amplification is necessary because the changes in air pressure originally detected by the external ear are about to be converted to waves in the fluid-filled inner ear. (See image below.)



The Inner Ear:

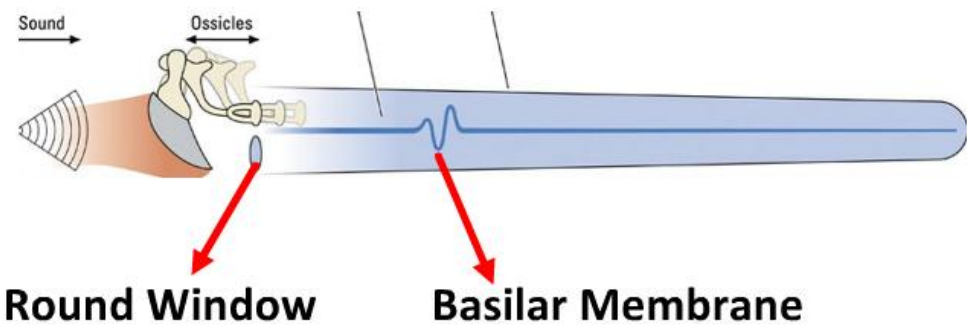
- The vibrating **oval window** connects to the **cochlea** of **the inner ear**.
- The cochlea is a fluid-filled tube, about 35 mm long, coiled like a snail shell. The cochlea contains the neural tissue that is necessary to transfer the changes in fluid to neural impulses of audition.

The Cochlea:

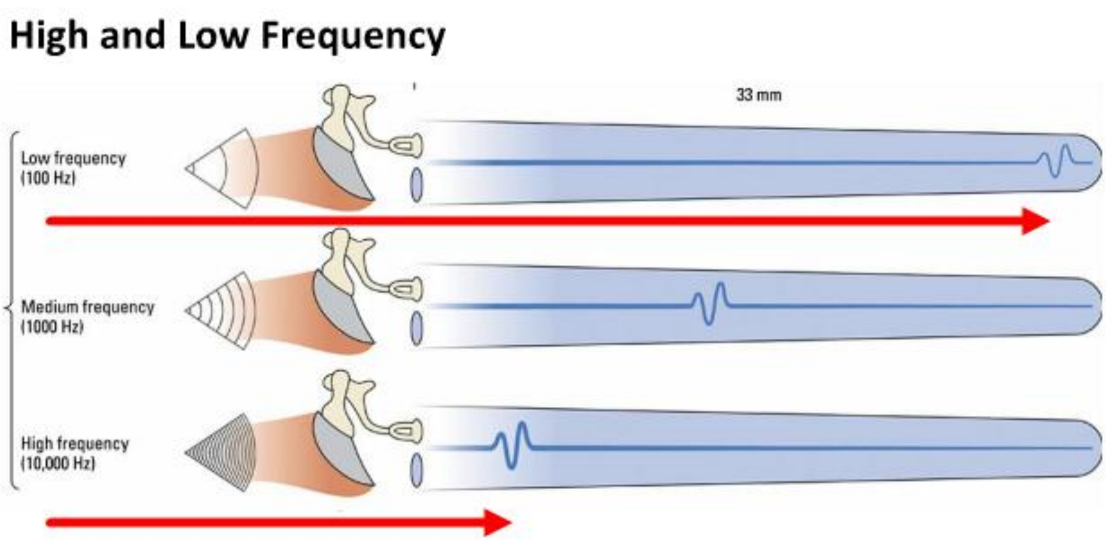
- The oval window is actually a small opening in the side of the cochlea, and when the oval window is made to vibrate, it causes the fluid inside the cochlea to become displaced.
- The round window, located at the other end of the cochlea, accommodates for the movement of the fluid by bulging in and out accordingly.

Basilar Membrane:

- Inside the cochlea is a flexible membrane, called the basilar membrane that runs the length of the cochlea like a carpet.
- When the basilar membrane is pushed downwards, the fluid inside the cochlea causes the round window to bulge out, and when the basilar membrane is forced upwards, the round window bulges inwards. (See image below.)

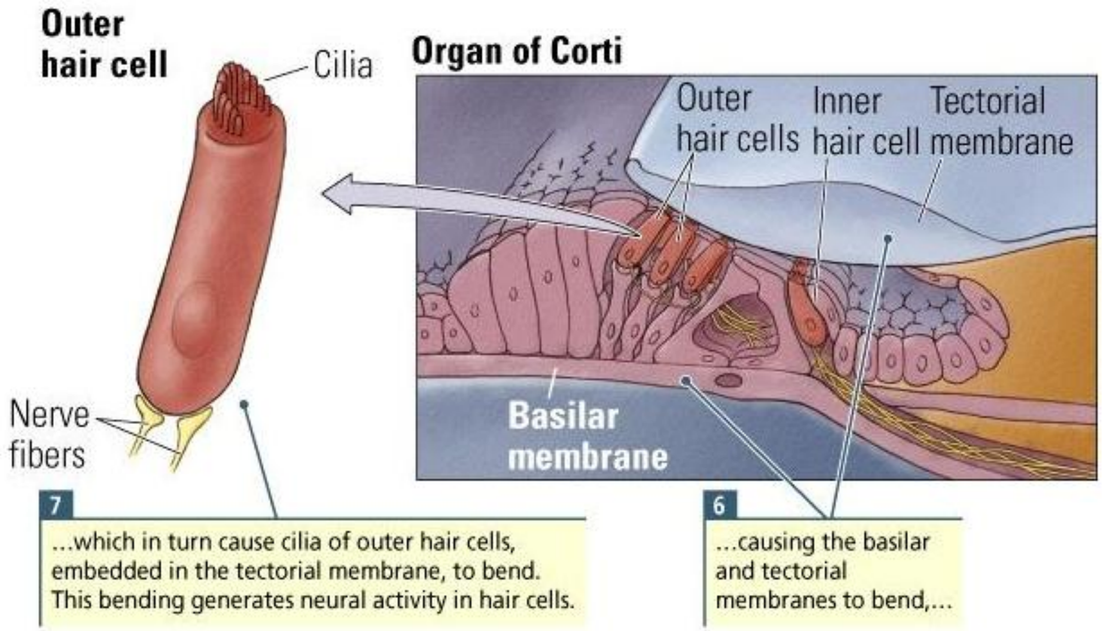


- Although the cochlea itself gets narrower towards the end, the basilar membrane actually gets wider towards the end.
- Because the length of the basilar membrane varies in both flexibility and width, sounds of different frequencies cause different regions of the membrane to vibrate.
- Higher frequency sounds cause the end nearest the oval window to vibrate whereas lower frequency sounds cause the end nearest the round window to vibrate. (See image below.)



Hair Cells:

- The basilar membrane houses the auditory receptors, which are called **hair cells**.
- As the membrane moves in response to the waves in the fluid, the hair cells also move, and this movement is finally converted to neural impulses that the brain can understand. (See image below.)



Auditory Pathway: From Receptors to Auditory Cortex

Introduction:

- When activated, the hair cells along the basilar membrane release a neurotransmitter. The hair cells form synapses with bipolar cells, whose axons make up the cochlear nerve, a branch of the main auditory nerve.
- Although the outer hair cells outnumber the inner hair cells by about 4 to 1, it is the inner hair cells that mainly contribute to the signal in the cochlear nerve.

Cochlea Nerve and Hair Cells:

- There are some important differences between the **inner hair cells** and **outer hair cells**. Each inner hair cell communicates with roughly 20 afferent fibres, which means that the signal from each inner hair cell has exclusive rights to 20 direct links to the brain.
- The outer hair cells, on the other hand have to share one direct link to the brain with about 30 other outer hair cells.
- The axons that synapse with the **outer hair cells** are **thin and unmyelinated**, whereas the axons that carry information from the **inner hair cells** are **thick and myelinated**.
- The arrangement of these connections suggests that even though there are far fewer inner hair cells than outer hair cells, the inner hair cells are primarily responsible for transmitting the auditory signal to the brain.

Cochlear Nucleus:

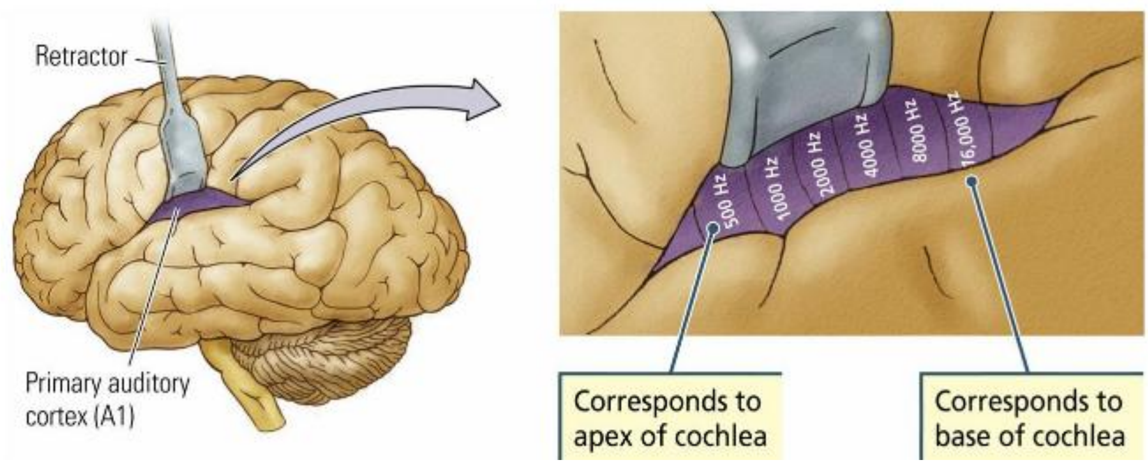
- The neurotransmitter released by the hair cells is capable of triggering EPSPs in the cochlear nerve fibres, which then sends this signal to the **cochlear nucleus** in the hindbrain.
- The cochlear nucleus has separate dorsal and ventral streams.

Dorsal and Ventral Stream:

- This dorsal and ventral stream is reminiscent of the way that information is processed by our visual system.
- In the visual system, we learned that the ventral stream processes object recognition and the dorsal stream processes the location of an object.
- Similar processes occur with the auditory system. Another similarity in how the brain processes visual and auditory information has to do with how the raw information is organized along the neural pathways.
- Recall that the spatial organization of our visual world is maintained at all levels along our visual pathway.
- So, for example, neighbouring locations in space fall on neighbouring regions on our retinas, and this spatial organization is still true at the level of our LGN, primary visual cortex, and extrastriate cortex.
- We learned that this type of organized neural representation of our visual world is called topographical.

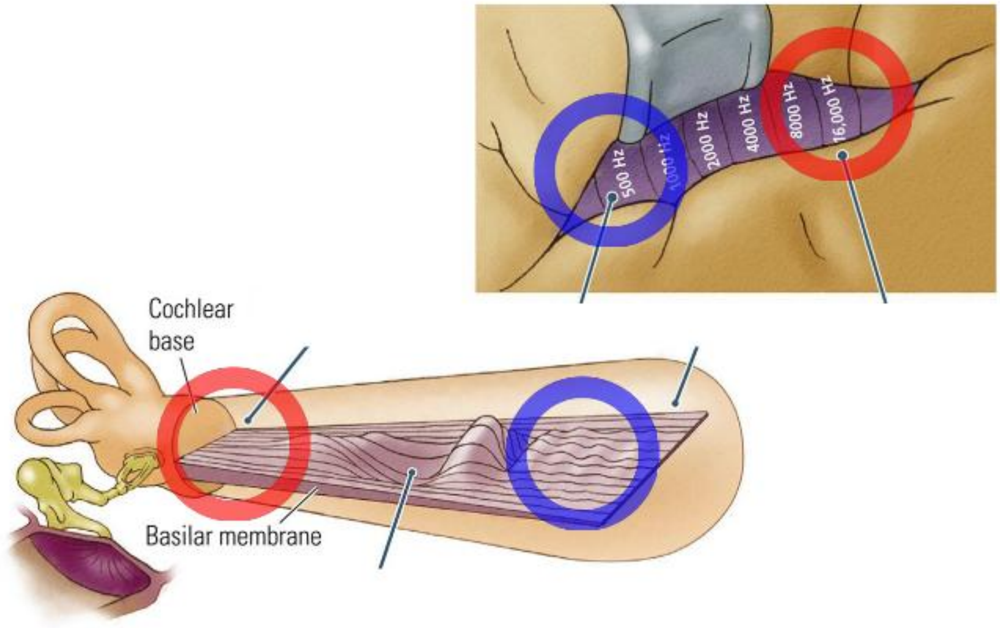
Tonotopic Organization:

- Well, the same principle applies with our auditory sense, only it is called a **tonotopic organization**.
- Recall that frequency is coded along different regions of the basilar membrane because sounds of different frequencies displace the hair cells in these different regions.
- The hair cells connect to the cochlear nerve such that neighbouring regions of hair cells remain together, and this organization is maintained all the way through the auditory pathway to the primary auditory cortex.



Frequency and the Basilar Membrane:

- How does the primary auditory cortex respond to sounds of different frequencies?
- The region of the basilar membrane that is closest to the oval window and responds the most to low frequency sounds is represented at one end of area A1, whereas the other end of the basilar membrane that is closest to the round window and responds best to high frequency sounds is represented at the other end of area A1.
- With this type of organization, information about similar frequencies is processed together.
- See image on the next page.

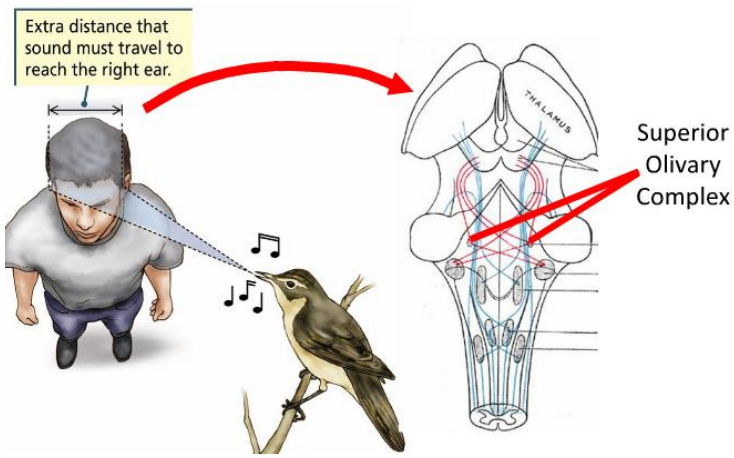


Auditory Localization:

- In addition to being able to identify what the source of a sound is, we are also able to localize where a sound is coming from in space through **auditory localization**.
- Like the depth perception component of visual localization, our skills in auditory localization rely on the fact that our sense organs are separated in space.
- The process is a little different from visual localization. In vision, we learned that the location of an object in the environment directly corresponds to the image of the object on the retina.
- In audition, there is no such direct representation of the spatial arrangement of objects. Auditory localization is calculated from the neural representations of incoming sound.
- With vision, we saw that retinal disparity occurs because each eye sees a slightly different image, which gives us cues for the perception of depth.
- Similarly, the fact that our ears are located on the opposite sides of our head results in interaural differences in sound that give us cues for auditory localization.
- The first interaural cue is the difference in time it takes for the sound to reach each ear.

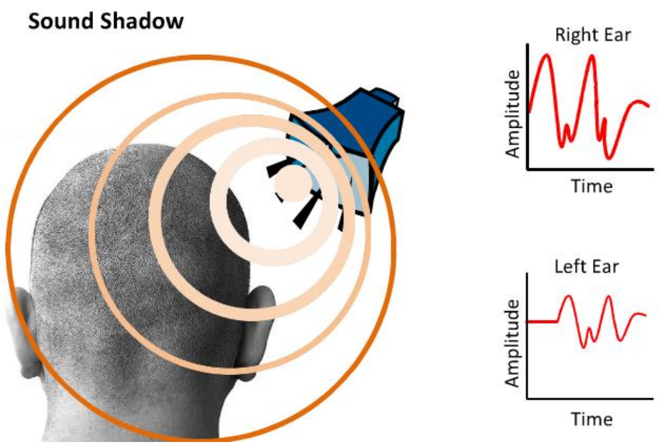
Time Difference to Arrive at Each Ear:

- The slight difference in time it takes for a sound to arrive in each ear can be measured in the sub-milliseconds.
- This may seem like a trivial difference, but it is dependent on the direction of the incoming sound
- Specific neurons in the **superior olivary complex** respond to these slight differences in the timing of arrival of the action potentials from each ear in response to the same sound.
- See image on next page.

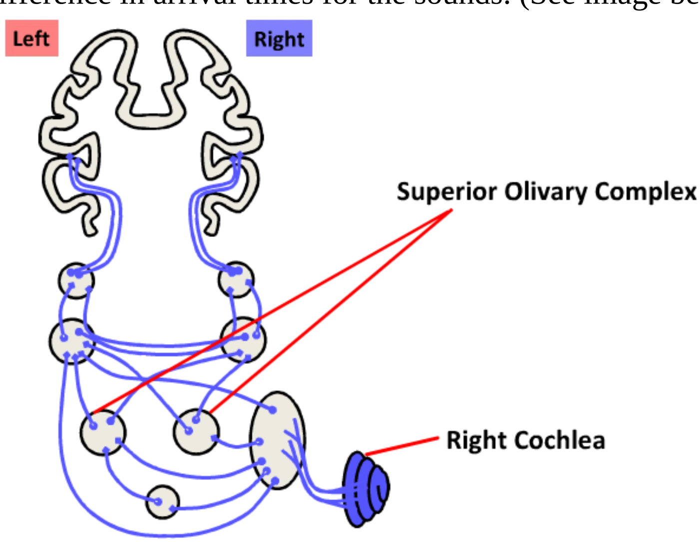


Intensity Difference at Each Ear:

- For very close sounds, there is a detectable loss of intensity because the sound wave has to travel farther to reach one ear than the other.
- However, for sounds that are further ways this difference is less detectable; instead the ears rely on the difference in intensity caused by the head which casts a "sound shadow" which diminishes the intensity at the distal ear much as light is diminished within the shadow you cast in sunlight. (See image below.)



- Since input from each ear travels to both sides of the brain, these differences in intensity can be directly compared to calculate the location of the sound.
- Some neurons in the superior olivary complex respond specifically to these intensity differences from each ear while others respond specifically to the interaural difference in arrival times for the sounds. (See image below)



Sounds in Front / Behind have Little Difference:

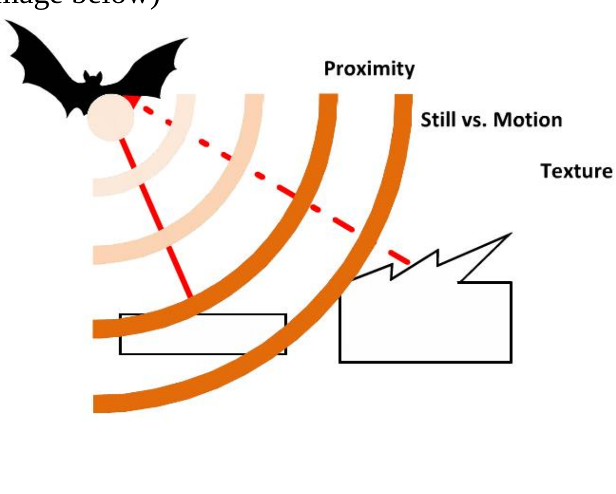
- When a sound is directly in front or directly behind you, it strikes both ears at the same time and you will have difficulty locating the source of the sound.
- In this case, rotating your head will cause slight changes in the sound intensity reaching each ear, and you will once again be able to localize the sound.

Pinna Cues:

- Another type of acoustical cue is the sound direction produced by the characteristics folds and ridges of our pinnae.
- The pinna diffracts incoming sound waves to make significant changes to the frequency content of the sound that reaches the inner ear: some frequencies become amplified, while others are attenuated.
- These changes are collectively called pinna cues and are required for accurately localizing the elevation of a sound source.
- Because everyone has a unique ear shape, pinna cues are particular to the individual, and are sometimes called 'earprints‘.
- When pinna cues are altered (by placing plastic molds into the pinna cavities) there is a dramatic disorienting effect on localization ability, despite the fact that the interaural difference cues are still available.
- Interestingly, over the course of weeks, subjects can adapt to the new pinna cues, and localization becomes normal again.

Echolocation in Bats:

- Most bats are able to use an entirely different system that is based on hearing.
- How can bats hunt and navigate so successfully without using their sense of vision? They use a system of **echolocation**, through which a bat is able to form a perceptual "image" of the objects in the surrounding environment by emitting a sound and then analyzing the time and frequency information that is contained in the returning echoes.
- The bat first emits a burst of sound waves of a very high frequency which bounces off the object and returns to the hat's ears.
- The bat's brain analyzes the slight differences in the frequency content and timing of the returning sound waves to determine the characteristics of objects in its environment.
- An object that is close to the bat will return echoes sooner in time than objects that are farther away; objects that are moving will have echoes that are Doppler-shifted compared to stationary objects; and objects that are textured will produce echoes that vary slightly in their return times relative to echoes from objects that are smooth, much as a textured object alters the reflection of light in the visual world. (See image below)



Evolution at Work:

- Bats have evolved a very efficient system for navigation and prey detection in an environment they may otherwise he unable to exploit.
- In response to the selective pressure exerted by the bat's abilities at echolocation. some prey have evolved a sense of hearing designed especially for the detection of bat calls.

Co-Evolution:

- Def'n of **Co-Evolution**: The process by which the evolution and adaptation of traits of one species can directly affect the evolution of traits in another species.

Echolocation in Bats and Moths:

- Across many generations of predation and selection by echolocating bats, moths have evolved the ability to hear sounds that match the frequency range used by most bats when they're hunting insects using echolocation.
- Being able to detect the bat has certainly helped the moth, because their chance of survival increases significantly when they can hear the bat coming in advance and can respond by engaging in a defensive flight pattern.
- Because our experience with the world is so heavily dominated by vision, we often fail to consider the important role of audition. Audition helps us to localize objects in the environment and focus our attention to important events.