

The Physiology of the Senses

Transformations For Perception and Action

Lecture 9 - Hearing

Tutis Vilis <http://www.physpharm.fmd.uwo.ca/undergrad/sensesweb/>

Hearing

Our sense of hearing is often underappreciated. If you had to choose, which would you give up, hearing or vision?

People who lose hearing feel very isolated from the world, and most importantly the company of people.

Imagine what life would be like if at dinner you were unable to participate in conversation with your friends and family.

What are sound waves?

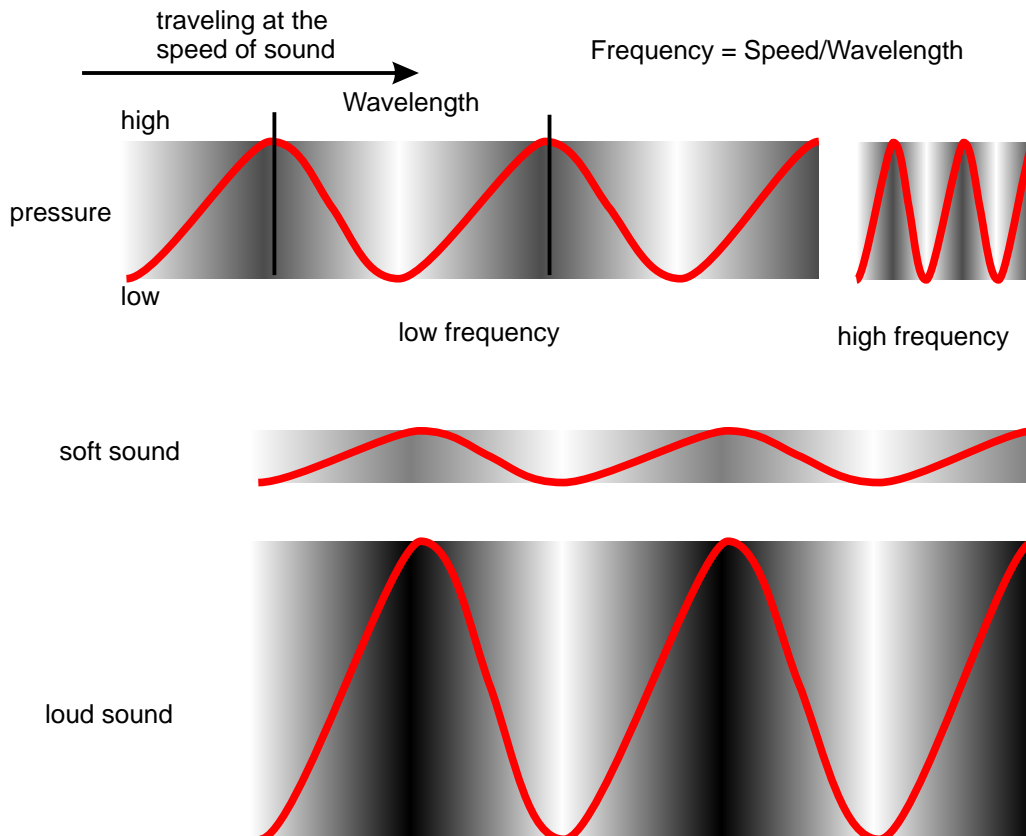
~ Sound waves are waves of air pressure.

~ If one plots air pressure, then the peaks correspond to points of maximum compression, and the troughs, points of maximum rarefaction.

~ Amplitude is the difference between minimum and maximum pressure and is perceived as loudness.

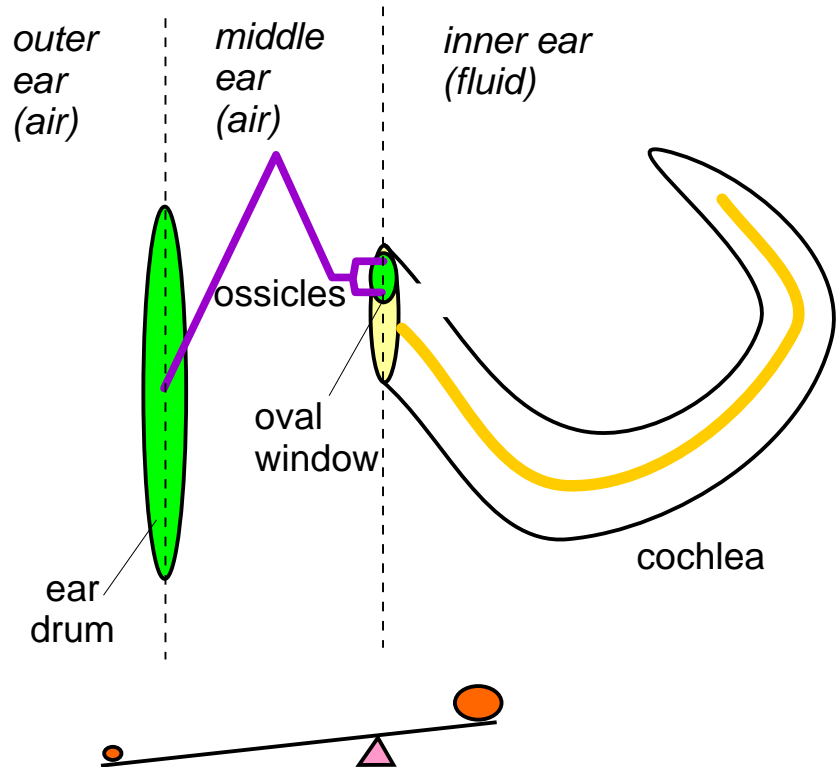
~ Frequency is the number of peaks that go by a fixed point in one second.

~ The normal range of frequencies audible to humans is 20 to 20,000 Hz (the number of waves per second). We are most sensitive to frequencies between 2000 to 4000 Hz, the frequency range of the spoken words.



How does sound energy reach the inner ear?

- 1) Sound passes down the air filled outer ear canal.
- 2) Sound vibrates the ear drum and the vibration is conveyed to across air-filled middle ear by three bones called the ossicles. The ossicles vibrate the oval window, a membrane which seals the opening to the cochlea.
- 3) Finally vibrations reach the fluid filled inner ear where, inside a coiled shaped cochlea, neurons are activated.



Why such a complicated chain of transmission?

The middle ear has two functions:

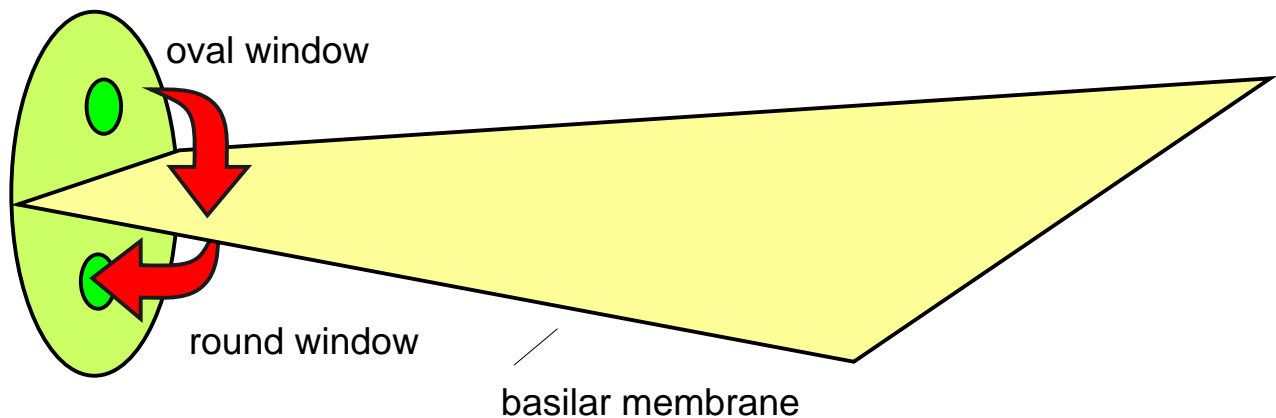
1. Impedance matching. Fluid in the cochlea is much harder to vibrate than air. If sound waves in the air struck the oval window directly, they would mostly bounce off. The ear drum picks up weak vibrations over a large area. The ossicles then act like a lever system, concentrating these movements to more forceful vibrations over the smaller area of the oval window. These more forceful vibrations are able to displace the oval window against the cochlear fluid.
2. Gating. Muscles in the middle ear are able to reduce the transmission efficiency of the ossicles in order to protect the inner ear from loud noise. These muscles are activated before you speak (a preprogrammed response) or after a sustained loud noise such as at a rock concert (a reflexive response).

What is the function of the round window?

The idea is to displace the basilar membrane. But this membrane is surrounded by fluid which cannot be compressed. This problem is solved by the round window.

When the oval window is pressed in, some portion of the pliable basilar membrane also bulges. This in turn produces a bulge in the round window into the middle ear.

Thus pressure waves are transmitted across the basilar membrane to the round window which acts as a pressure outlet. Without it, the oval window could not move.



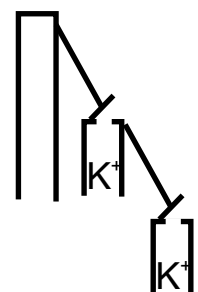
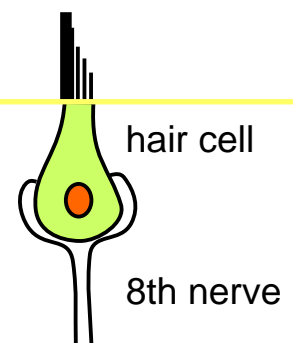
How does deformation of the basilar membrane activate auditory afferents?

Hair cells are located on the basilar membrane.

When the basilar membrane bends, the hairs on the hair cells are also bent.

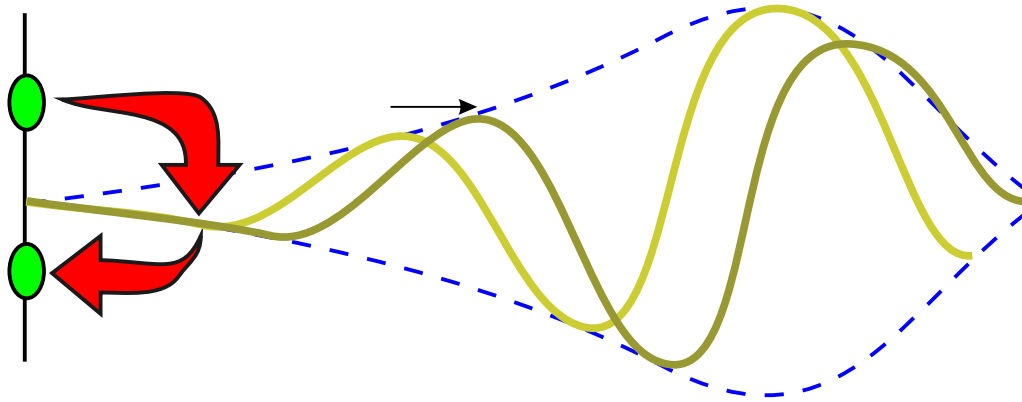
A filament between adjacent hairs opens ion channels allowing K^+ to enter the hair cell causing it to depolarize.

Neurotransmitter is released, increasing the firing rate in 8th nerve neurons.



Describe the traveling wave theory.

Von Békésy made the direct observation that a traveling wave sweeps down the basilar membrane starting near the round window and ending at the helicotrema. The figure shows "snapshots" of such a wave taken an instant apart.



You can mimic this by taking a heavy cord, about 5 meters long, and attaching one end to something at the end of the room. Holding the other end, flick your hand down. You should see a wave travel the length of the cord. The cord has the same properties throughout. So the size of the wave remains fairly constant. The basilar membrane properties change, so a low frequency would cause the wave to build in size, whereas at a high frequency, the wave shrinks in size.

How is the frequency of a sound coded?

Helmholtz noted that the basilar membrane is narrow and stiff (like a high string on a piano) near the oval window, and wide and floppy (like a low string) at the other end.

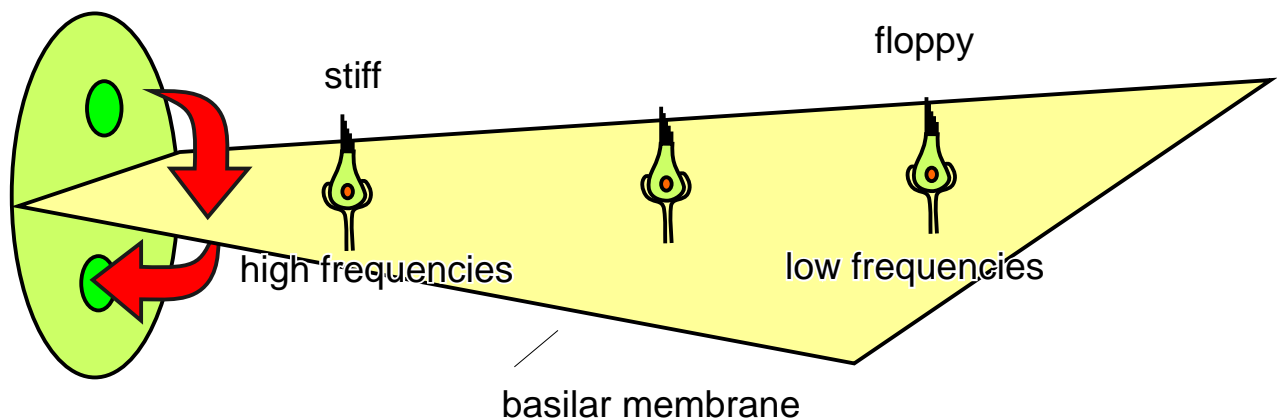
Because of this, each portion of the basilar membrane vibrates maximally for a particular frequency of sound.

High frequency sounds maximally displace the hair cells near the oval window while low frequency sounds maximally displace hair cells at the other end.

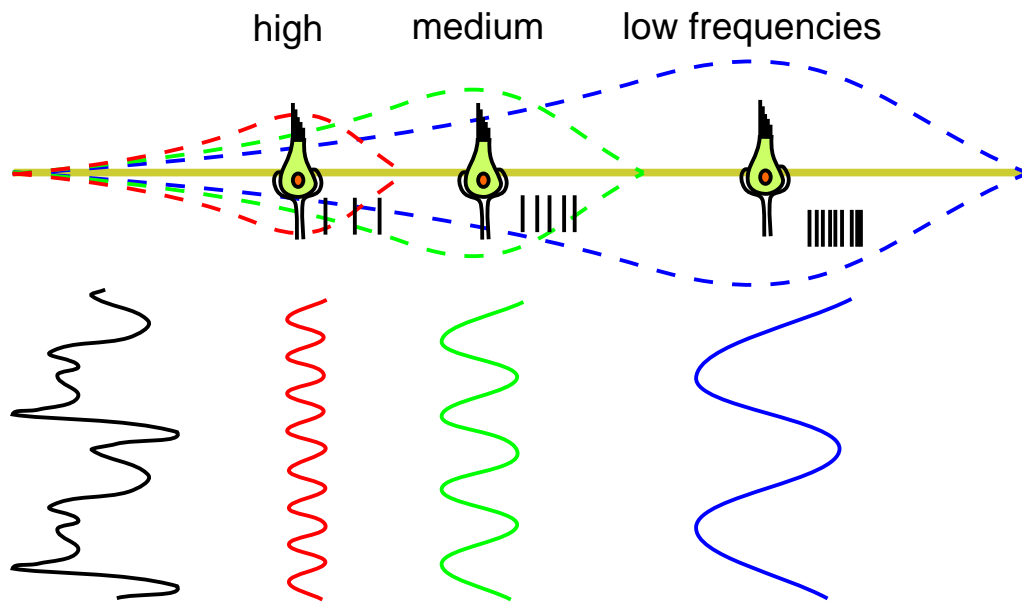
Thus sound frequency is topographically represented on the basilar membrane (place coding). (i.e. frequency is coded by which neuron is activated, not necessarily by its firing rate. This is like labeled lines in the sense of touch)

How is loudness coded?

Loud sounds produce a larger amplitude vibration of the basilar membrane more than soft sounds. The large vibration produce more activation of the hair cells. Thus loudness is encoded by the frequency of ap's in a particular afferent fibre.



Most every day sounds, such as that of a clarinet, are complex because they contain multiple frequencies. This is what makes the sound of a clarinet different from another instrument. The hair cells decompose this sound into its different frequencies, each hair cell encoding the loudness of a particular frequency.



Four Major Causes of Hearing Loss

1. Loud sounds break parts in the ear.

Extremely loud sounds from explosions and gunfire can rupture the ear drum, break the ossicles, or tear the basilar membrane.

Loud sounds common around the house such as lawnmowers or loud music can shear the hairs off the hair cells.

2. Infections

Middle ear infections in rare cases rupture the ear drum.

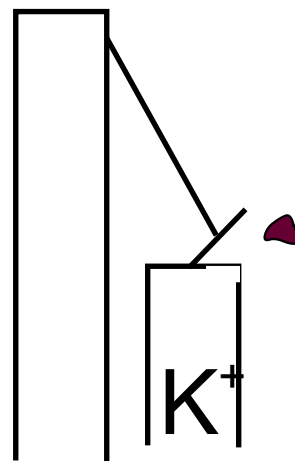
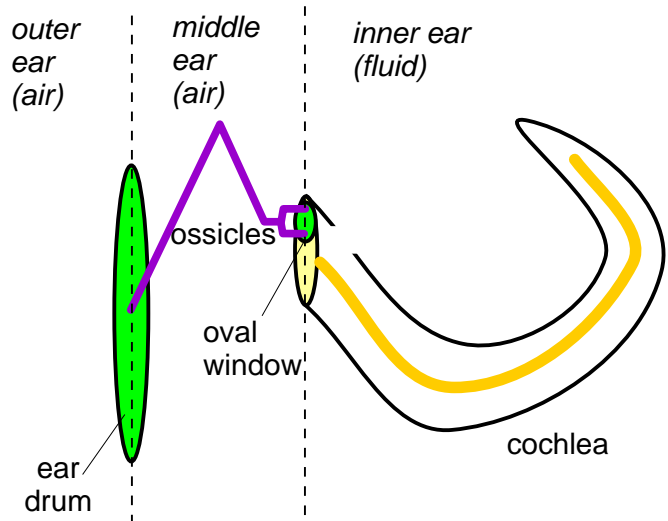
Inner ear infections can damage hair cells.

3. Toxic drugs

Toxins and some antibiotics can enter hair cells through the open channels and poison them.

4. Old Age

The parts simply wear out with time. In old age, blockage in the blood supply kills cells.



What are the cues to sound direction?

There are two methods for detecting the direction of sound. Both involve a comparison between the ears.

The first cue involves sound intensity differences. Think of the head as casting a shadow in the airborne sound waves. The sound striking the ear facing away from its source will be muffled by the head. This method works best for high frequencies over 3000 Hz. Low frequency sounds wrap around the head and do not cast a shadow.

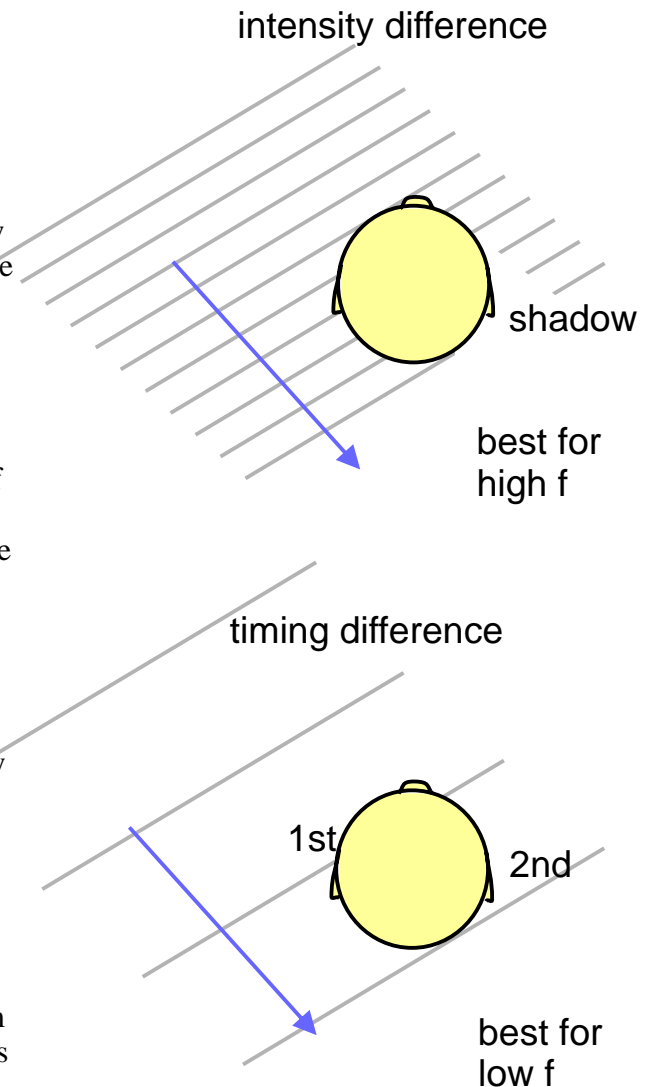
The other cue is timing difference. The peak of a sound wave strikes the ear facing the source before it strikes the other ear. The timing difference is least for sounds coming from in front and most when coming from one or the other side. Timing differences are used to localize low frequency sounds.

Humans can resolve direction with an accuracy of about 1 deg. This corresponds to a remarkable timing difference of 10/1000000 sec.

The shape of the ear lobe, besides amplifying sound, helps in distinguishing sounds coming from in front vs. those coming from behind (and perhaps above vs. below). One can also localize sound by turning one's head to where the sound is loudest.

Also, other sensory modalities, especially vision, team up with audition to localize the sound source.

Sometimes vision can mislead us, such as when we think we hear a ventriloquist's dummy speak.

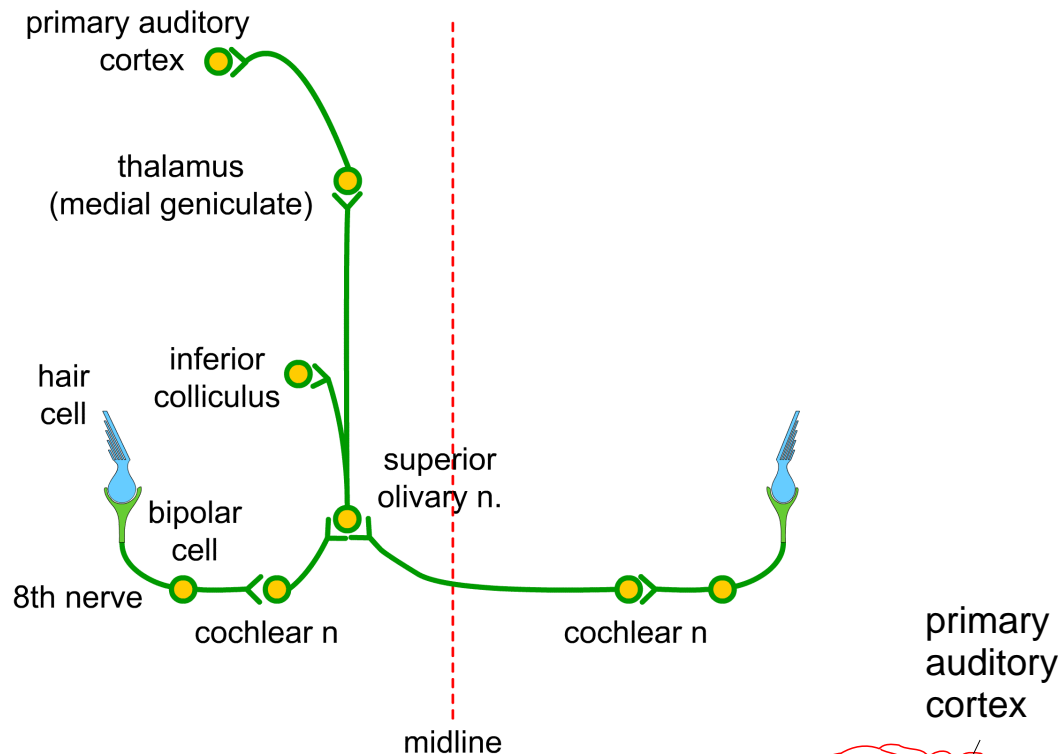


The role of the superior olive in sound localization.

The superior olive is the first place where signals from the two ears come together and can be compared.

Cells in the lateral superior olive look for differences in sound intensity.

Cells in the medial superior olive look for particular timing differences.



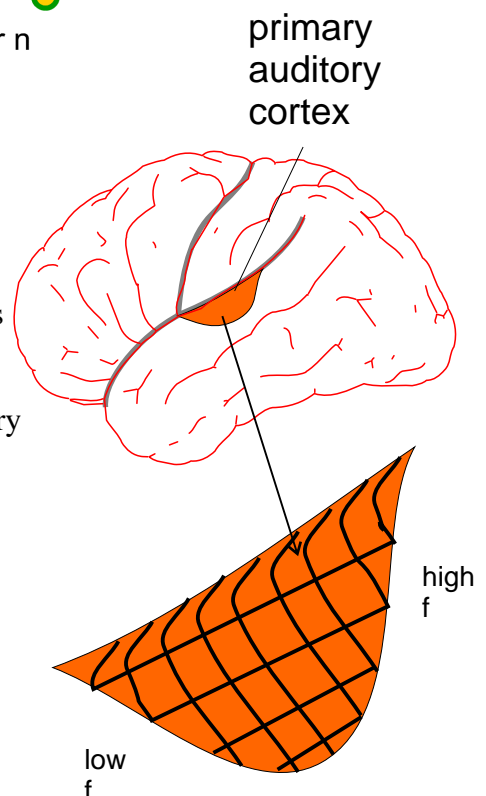
The central auditory pathways

Auditory information is then sent

- 1) to the inferior colliculus which mediates orienting movements towards a sound and
- 2) via the medial geniculate nucleus of the thalamus to the primary auditory cortex which is the first relay involved in the conscious perception of sound.

The primary auditory cortex has a columnar organization.

The basilar membrane is mapped topographically in a strip of columns (low frequencies at one end and high frequencies at the other). The columns have a tonotopic representation.



What happens beyond the primary auditory cortex?

Sounds processed first by the primary auditory cortex (A1) are further processed by higher order areas (A2).

Then the sounds that are words are processed by Wernicke's area (W).

The building blocks of the sounds of words are called phonemes (e.g. ba, ga, r, l).

Newborns, regardless of where they are born, initially all have the ability to distinguish a common set of phonemes. We are born citizens of the world.

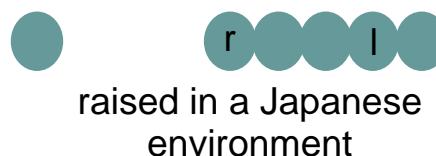
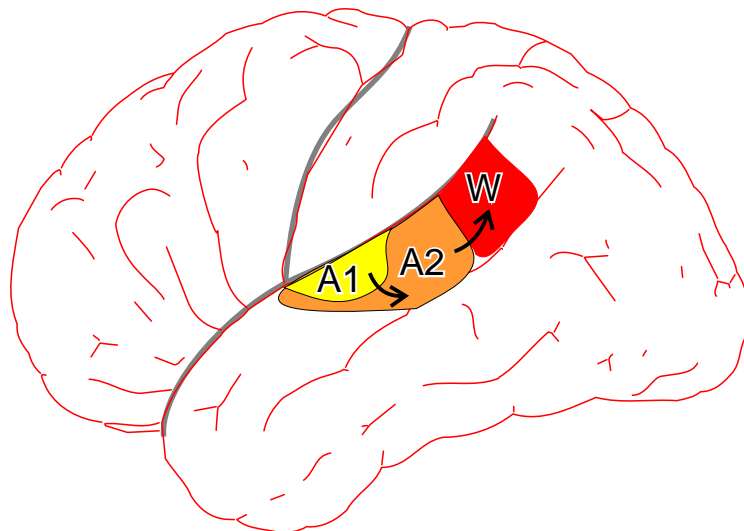
And how does one ask babies whether they can differentiate between ba and pa? In 1974 Peter Eimas found that babies habituated to the repetition of one sound (ba,ba, etc) and that they started sucking much more rapidly, on an electronically monitored pacifier, when the sound changed (pa, pa etc). Patricia Kuhl and her students took recorded phonemes and a similar pacifier around the world testing babies of different ages and backgrounds. She found that after the age of 6 months, the auditory system starts to filter phonemes. These filters act like magnets which

- 1) attract phonemes that are slightly different to make them sound like familiar phonemes
- 2) produce a clear boundary between different familiar phonemes

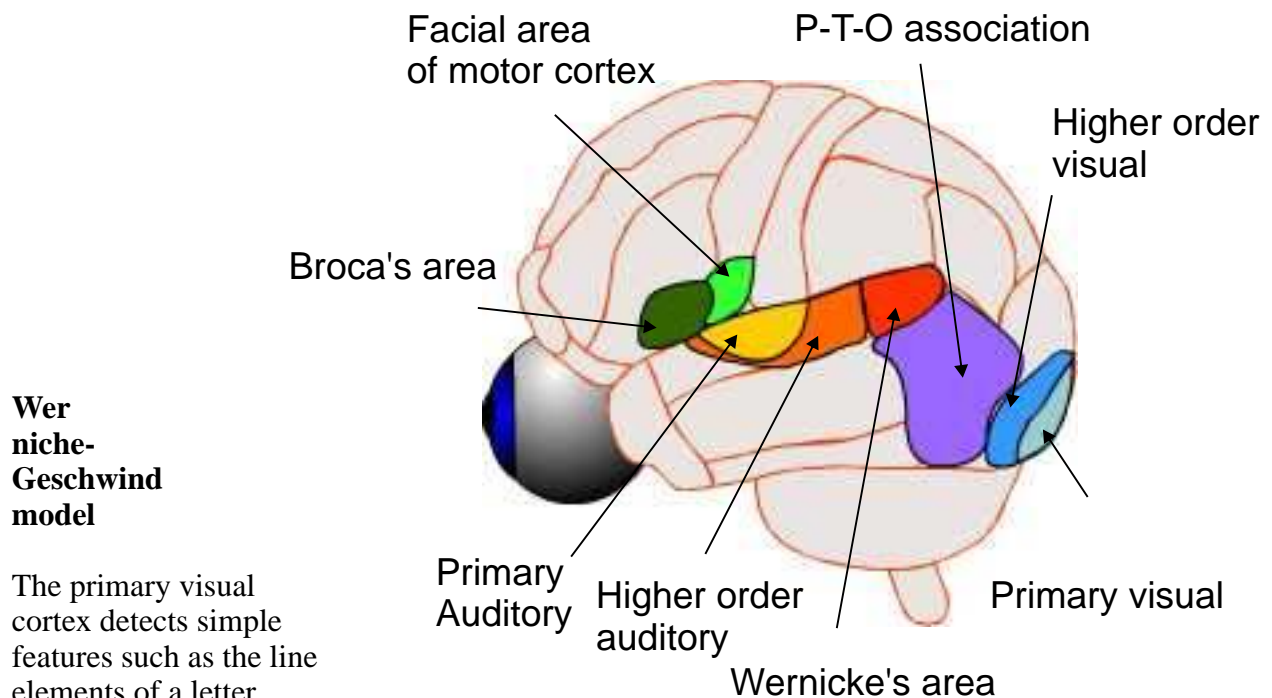
Experiment. Make an “R” sound and then an “L”. Move your tongue back and forth to change one into the other. Note that you hear either an “R” or an “L”, not some third sound.

Because of this filter, we start losing the ability to distinguish phonemes that are not part of our culture. For example, in Japan, adults cannot distinguish between “R” and “L”, while infants can.

Likewise someone raised in a English environment will not distinguish phonemes indigenous to Japan.



The probable sequence of activity that occurs when a person repeats a written word.



Higher order visual areas detect complex features.

In the PTO association area there is convergence of visual, auditory and tactile information. Here the left and right side of the word is put together and the object is recognized.

Wernicke's area is involved in verbal understanding and associating the object with the sound of a word.

Broca's area is involved in verbal expression, the production of the sound. This is part of frontal working memory. Working memory is required to order words in a sentence.

Finally the facial area of motor cortex contracts the right muscles to produce the required sound.

Note. When reading out loud, Wernicke's area may be bypassed and information sent directly from PTO to Broca's area. Perhaps this occurs when one is reading without understanding.

Use this model to compare the deficits caused by lesions in Broca's and Wernicke's areas.

Lesion of
Wernicke's
Broca's

Subject cannot
understand language
say the right word or grammar

Subject can
say words (often nonsense)
understand language