

# Auditory System

## The physical stimulus

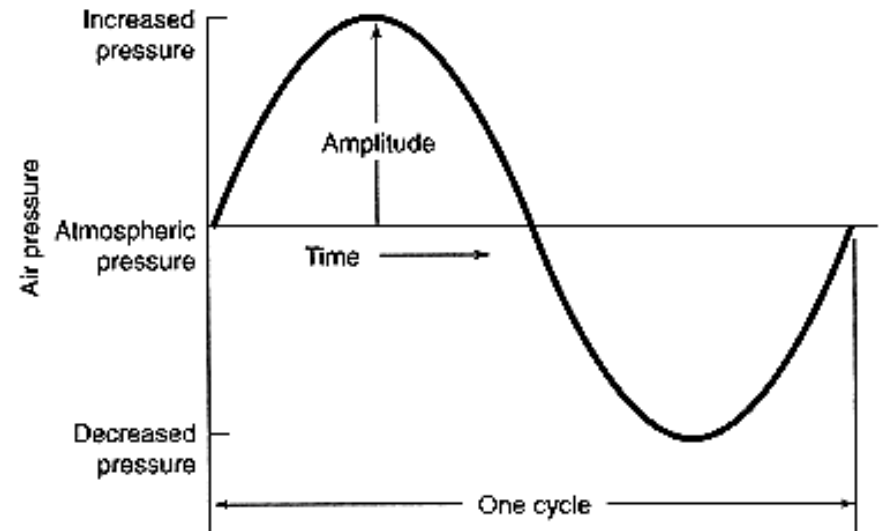
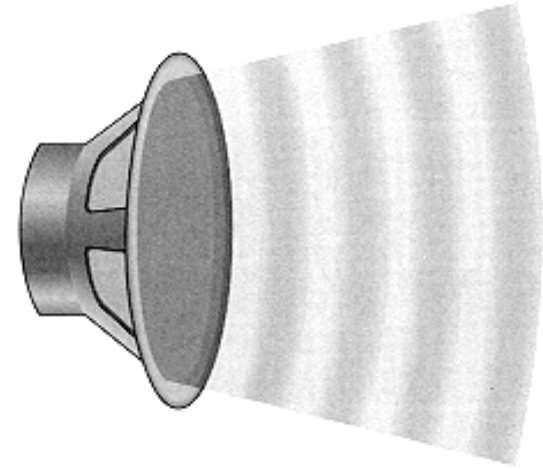
- physical stimulus for audition is time-varying changes in air pressure that propagate through space in wave-like manner

- e.g., pure tone played by speaker: sinusoidal variation in air pressure

- characterize in terms of frequency content, amplitude, and phase

- amplitude measured in decibels (dB), a logarithmic measure: 20dB increment equals 10-fold change

- humans are only sensitive to sound frequencies in the range from 20-20kHz



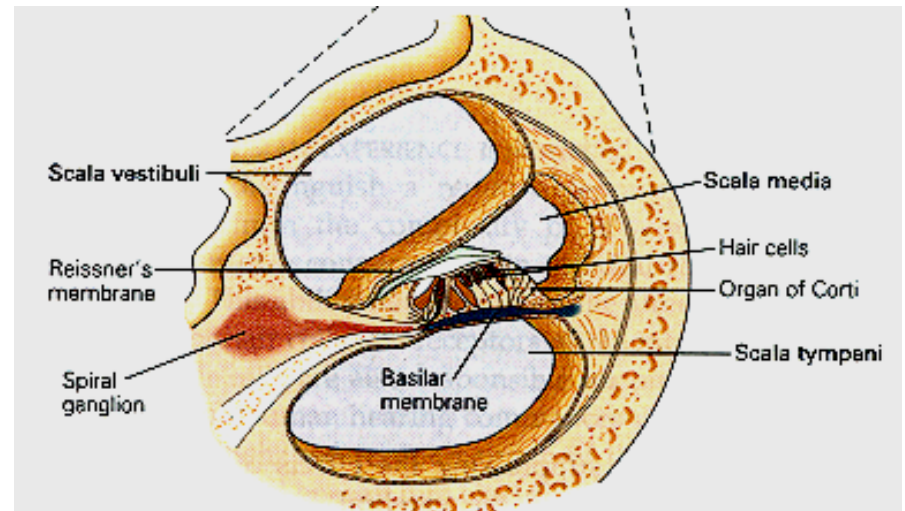
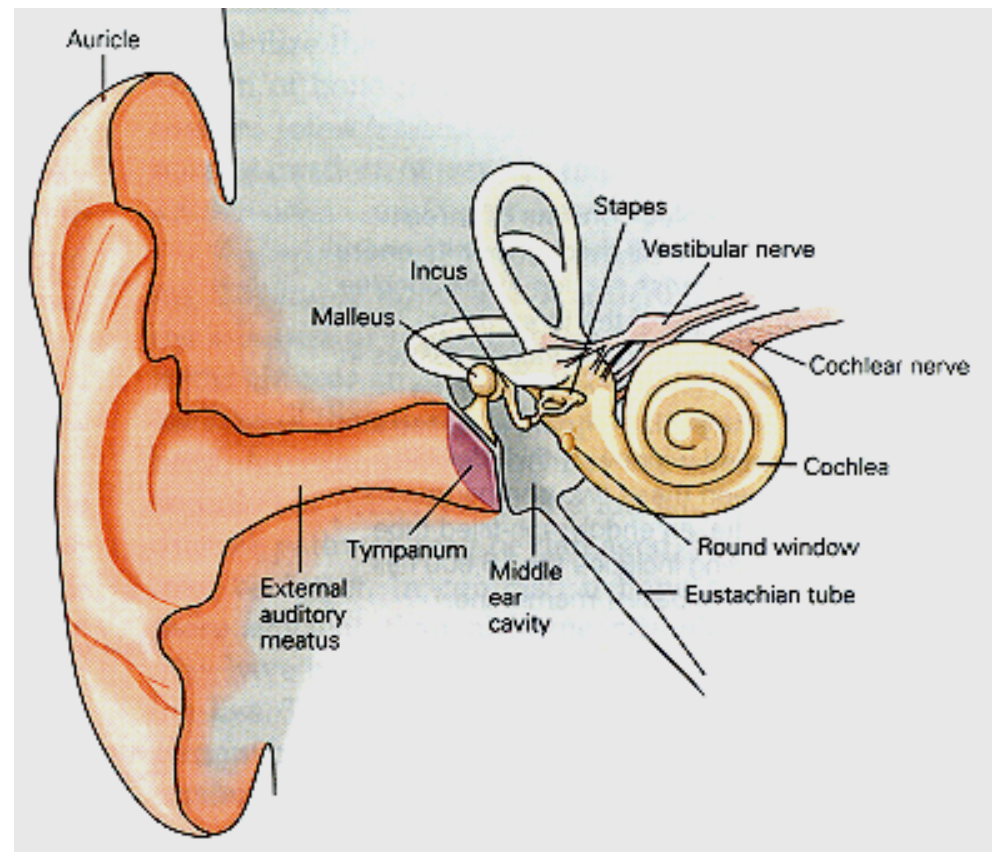
## Auditory transduction

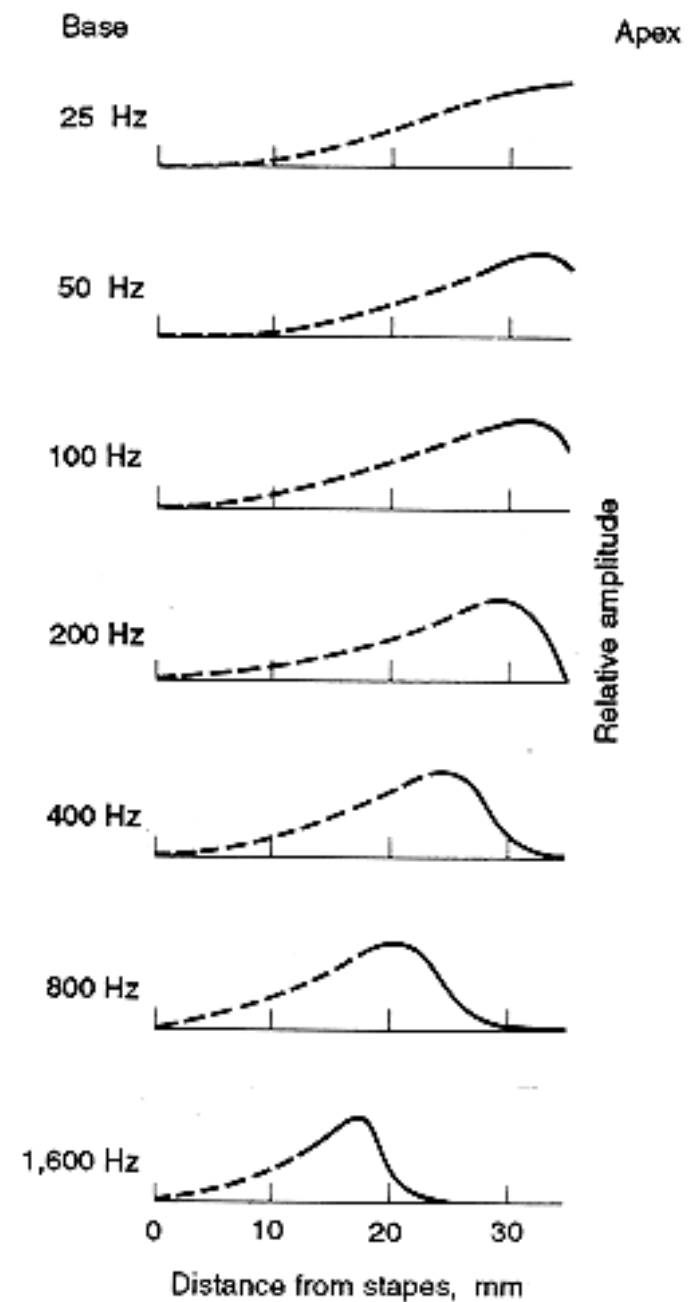
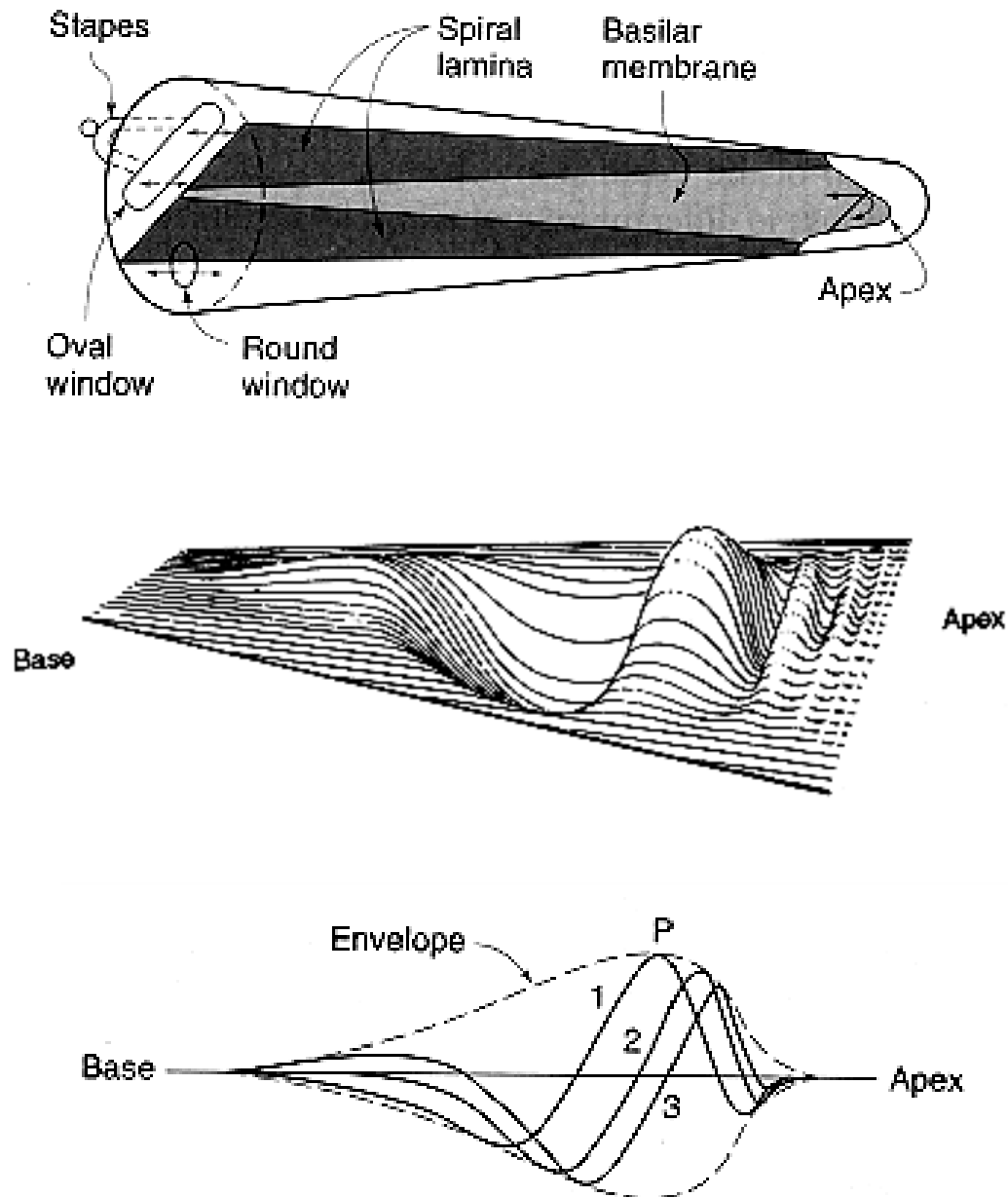
-External ear (pinna) funnels sound into the auditory canal, which has a resonance in frequency range of speech (2-5 kHz)

-Sound waves vibrate the tympanic membrane and these vibrations are transmitted to the oval window of the cochlea via the bones of the middle ear: malleus, incus, stapes. Why needed?

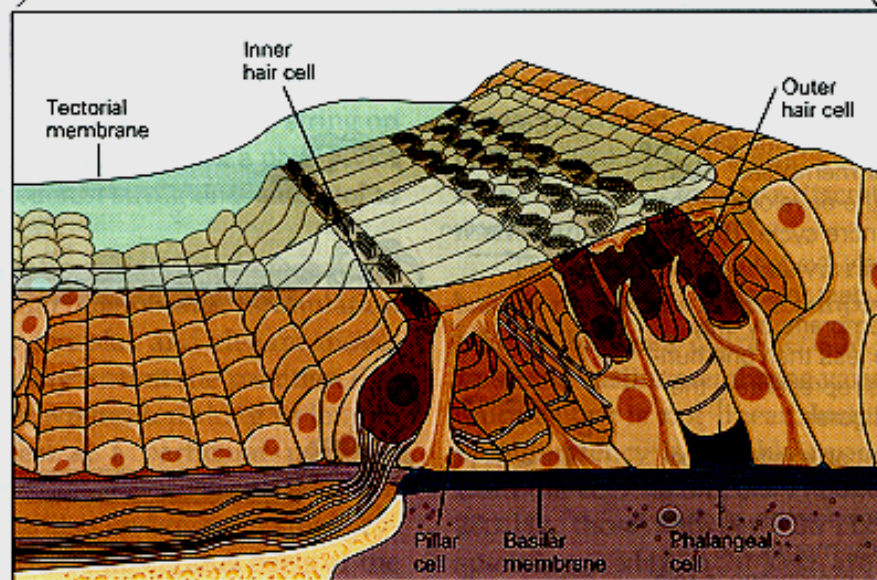
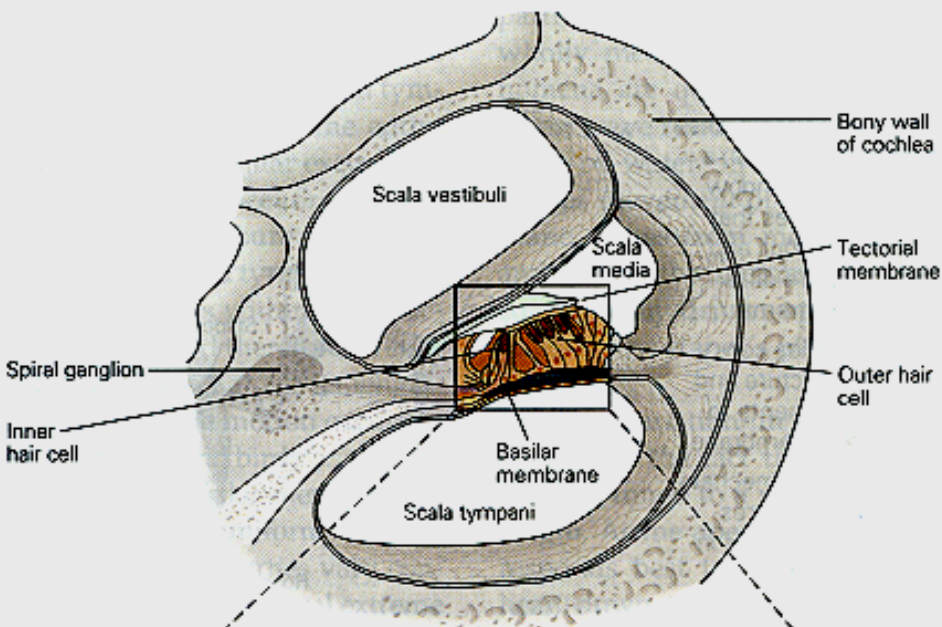
-In cross-section, cochlea has 3 chambers: scala vestibuli, scala media, and scala tympani.

-Basilar membrane sits at base of the organ of Corti. Mechanical properties of basilar membrane change along its length; this makes the *resonant frequency* vary along the length of the cochlea.





Georg von Békésy

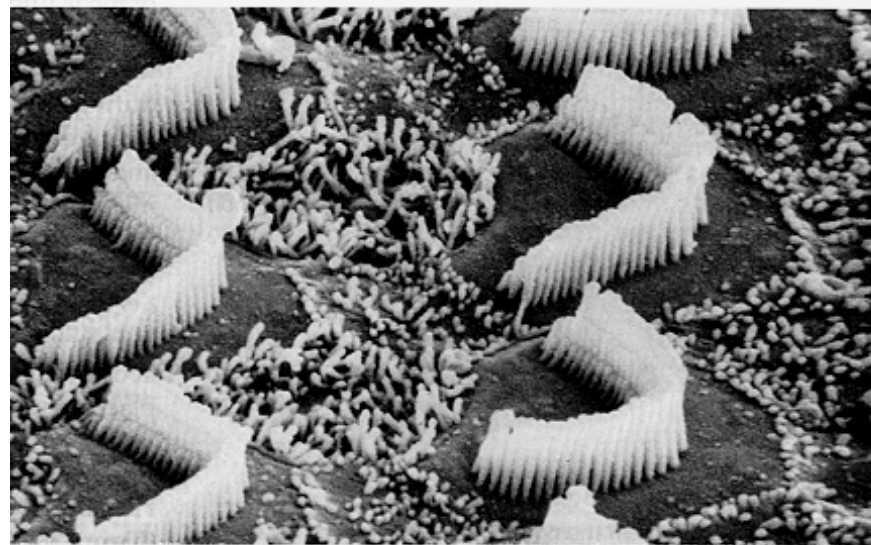


-vibrations are transduced by hair cells in the organ of Corti, which resides atop the basilar membrane

-inner hair cells – send signals to the cochlear nuclei about sound frequency and amplitude

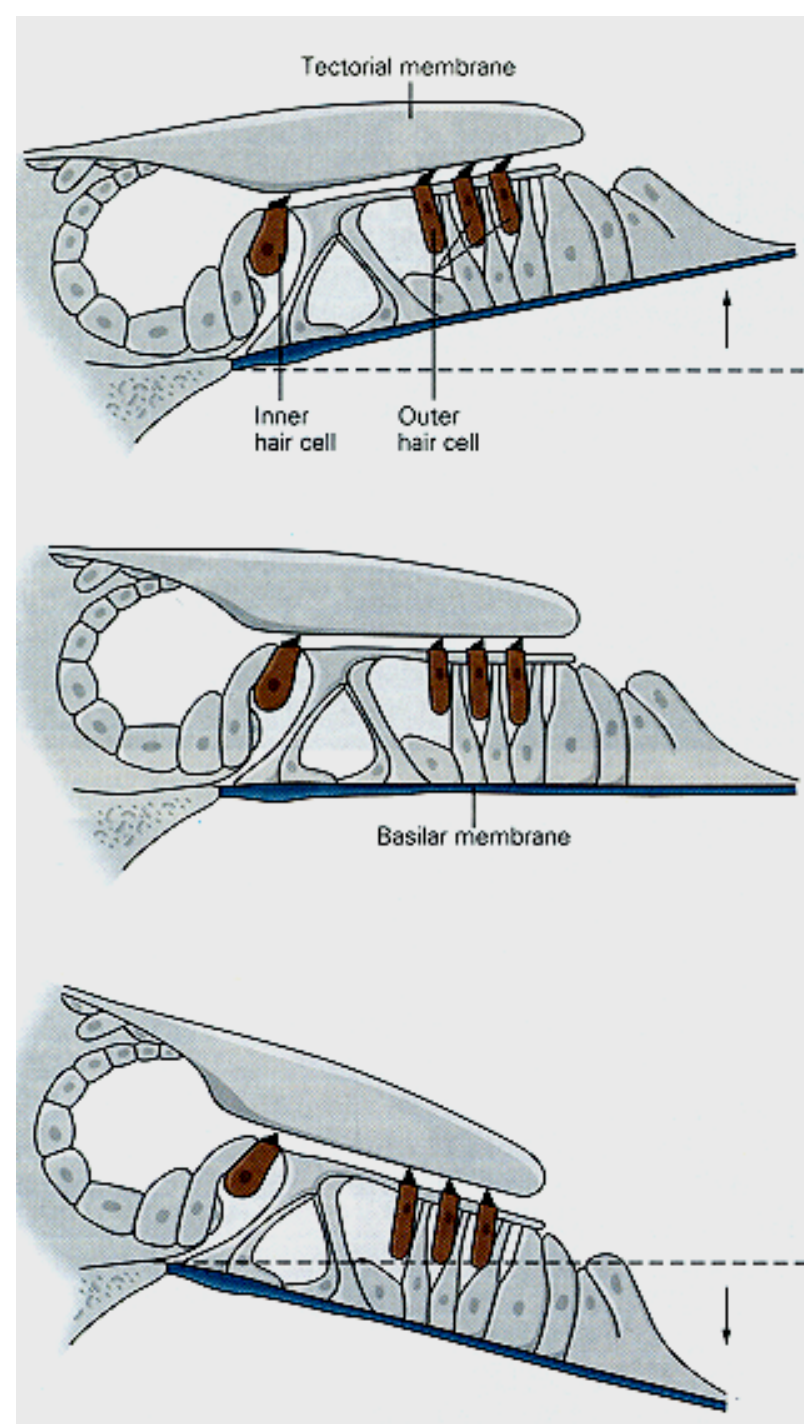
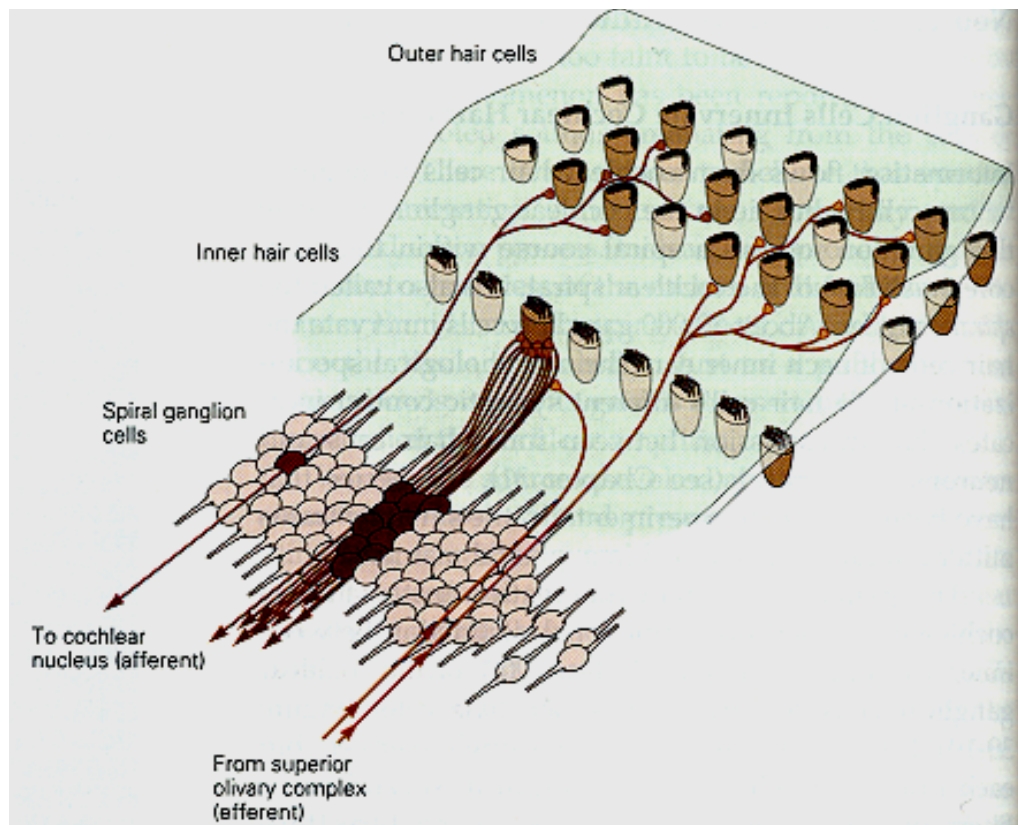
-outer hair cells – serve as tunable amplifiers

-30,000 hair cells per cochlea vs. 120 million photoreceptors per retina. Why such a big difference?



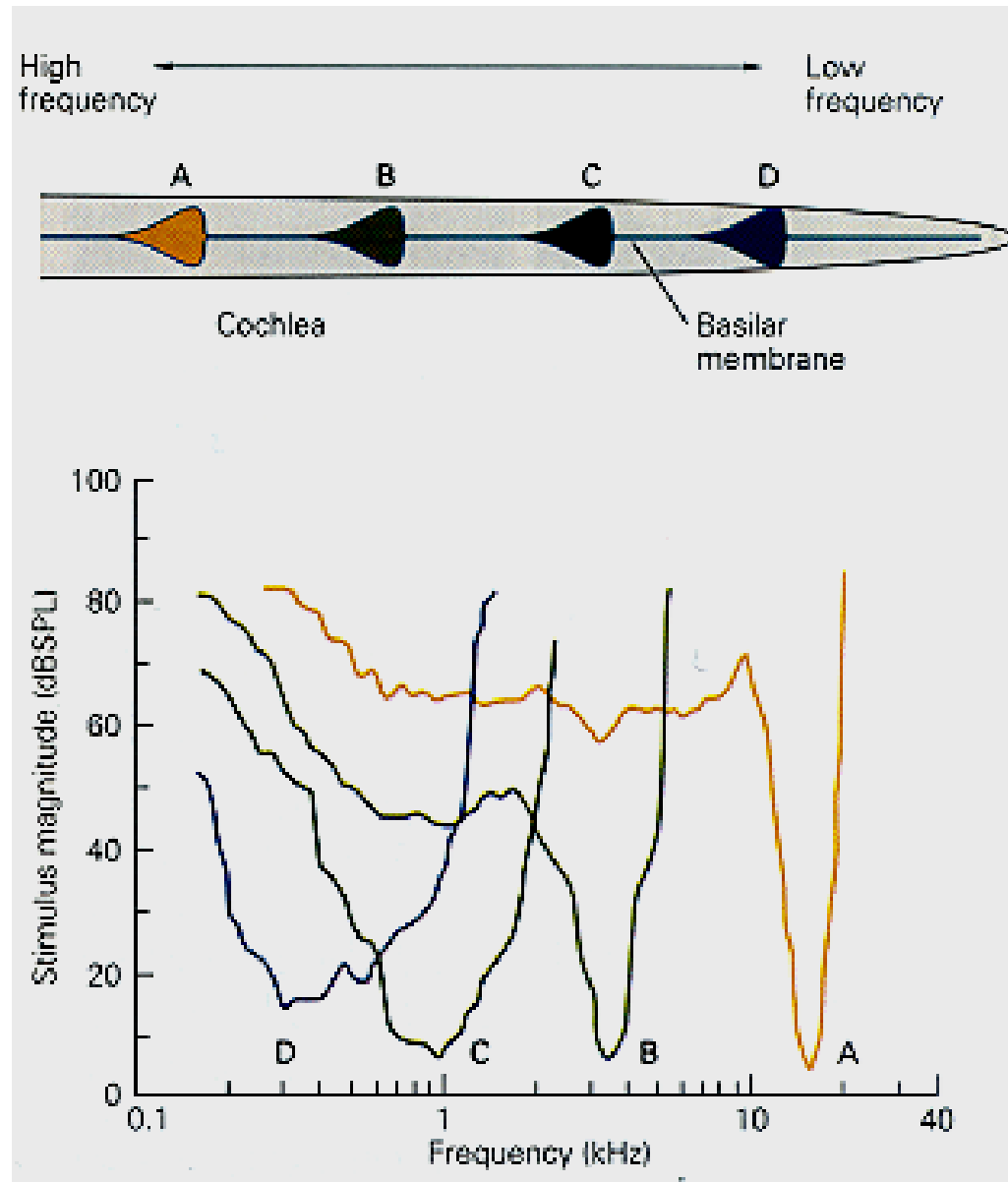


- upward movement of the basilar membrane causes stereocilia to be bent (toward largest) by the tectorial membrane and depolarizes the hair cell, thus activating afferents to the cochlear nucleus
- downward movement causes opposite shear and hyperpolarizes hair cell
- bending of stereocilia causes opening of ion channels through mechanical mechanism. Why direct mechanical mechanism?



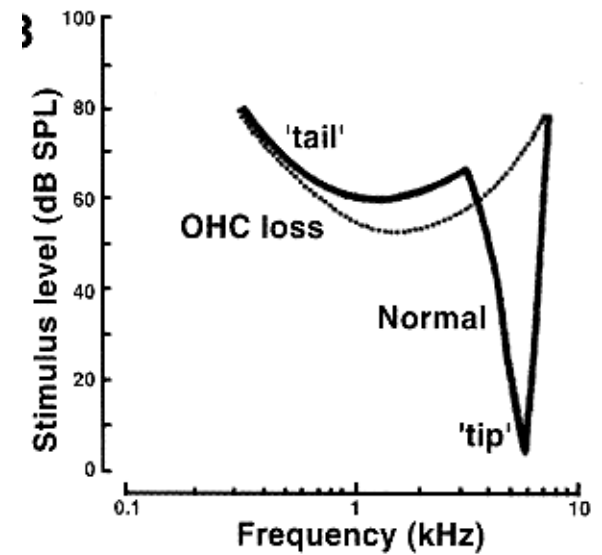
# Frequency coding

- due to properties of basilar membrane, each hair cell is tuned to a particular frequency of sound, called its 'characteristic frequency' (CF)
- CFs vary from high to low along cochlea (**place code**). Tonotopic map.
- relative activity of hair cells along cochlea specifies the frequency content of a sound stimulus. Cochlea essentially performs a Fourier transform of the sound (analogous to a spectrum analyzer)
- For low frequency tones, action potentials of cochlear afferents are phase-locked to the input (**temporal code**). Not so for high frequencies. How high?



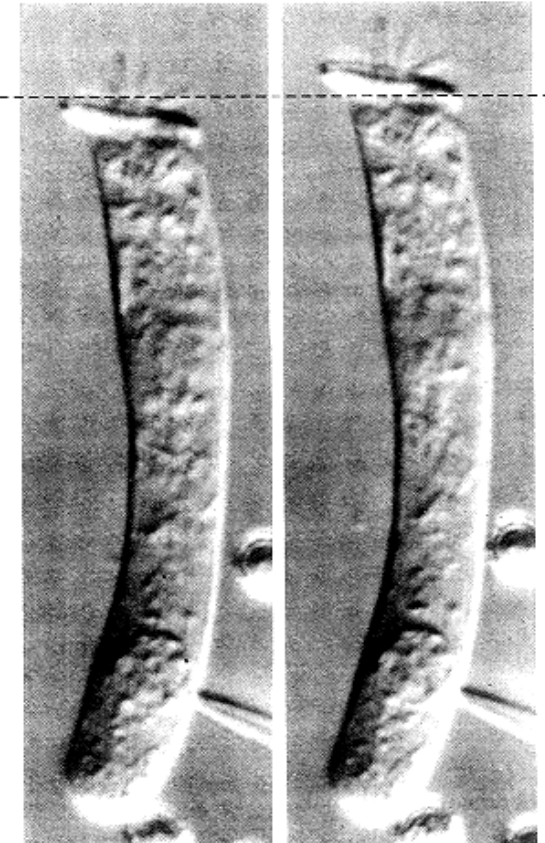
## Outer hair cells and amplification

- can detect vibrations of ear drum of  $10^{-11}$  cm; 10dB more sensitivity would detect random movements of air molecules!
- cannot be explained by passive mechanics of cochlea; basilar membrane vibrates much more at low SPL than expected.
- this implies active amplification, which appears to involve outer hair cells (OHCs); tuning of 8<sup>th</sup> nerve fibers (afferents from inner hair cells) is much broader without them (right).



### -Some probable mechanisms

- electrically induced motility of OHCs: each OHC has a resonant frequency matched to the location along the basilar membrane
- direct sound pressure-induced motility of *isolated* OHCs. Frequency specificity related to length of OHCs which varies smoothly along the length of cochlea.
- > OHCs themselves help to 'push' the basilar membrane and amplify weak oscillations, especially at low SPLs
- OHCs receive extensive efferents from higher auditory centers, which adjust the amount of amplification.
- Unlike retina, where there is no feedback from above (why?)







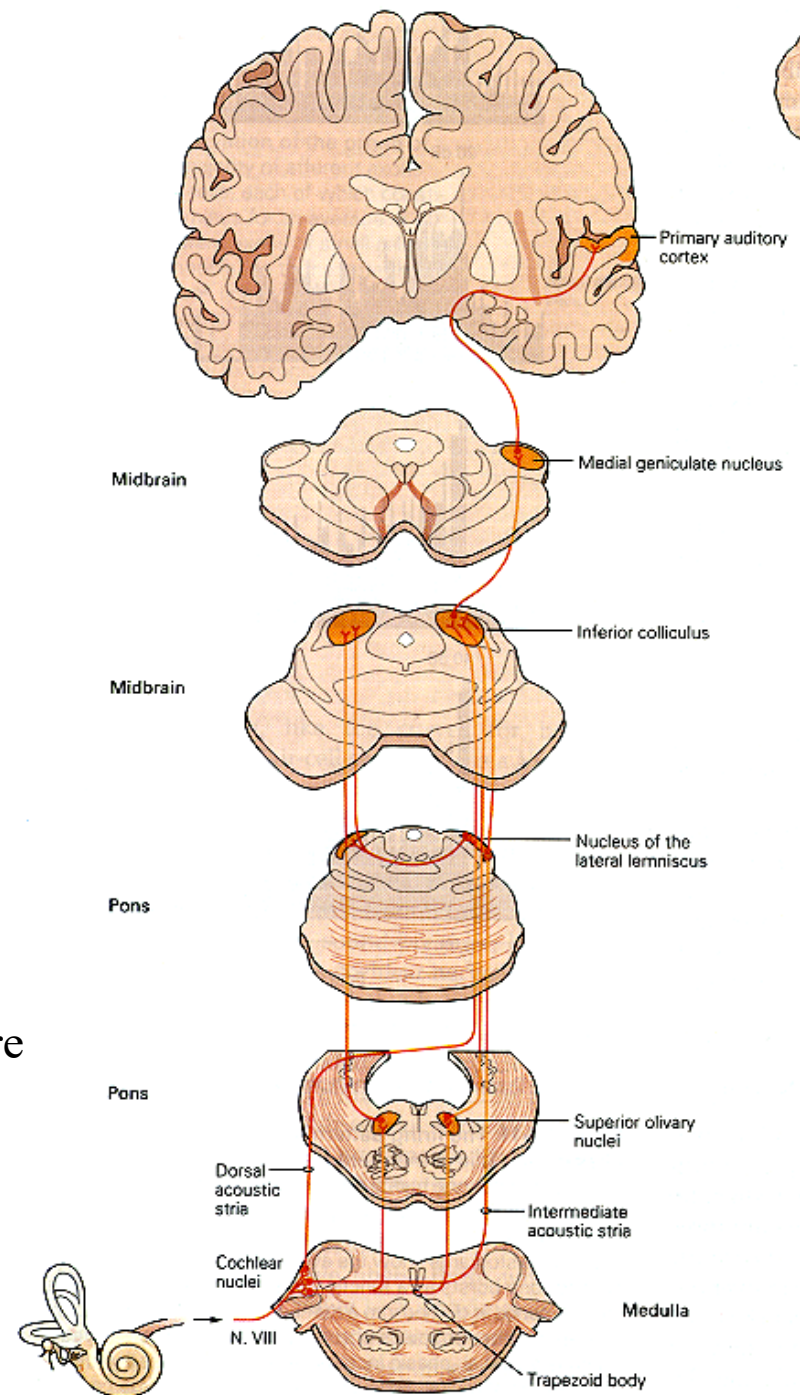
# Central auditory pathways

- major stages include cochlear nuclei (medulla), superior olivary nuclei (pons), inferior colliculi (midbrain), medial geniculate nucleus (thalamus), and auditory cortex.

- frequency selective neurons and tonotopic maps are found at all levels

- functions of the higher stages are active areas of research, and relatively little is known about the functions of different parts of auditory cortex.

- note that neurons of primary auditory cortex are several synapses away from outputs of cochlea, whereas (some) primary visual cortical neurons are only two synapses away.



# Auditory Sound Localization

## Cues

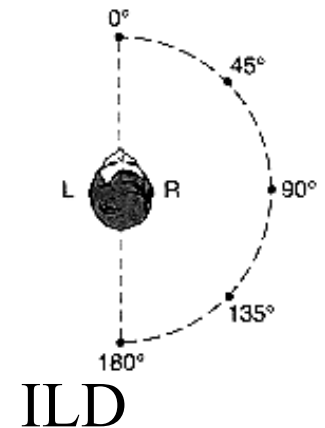
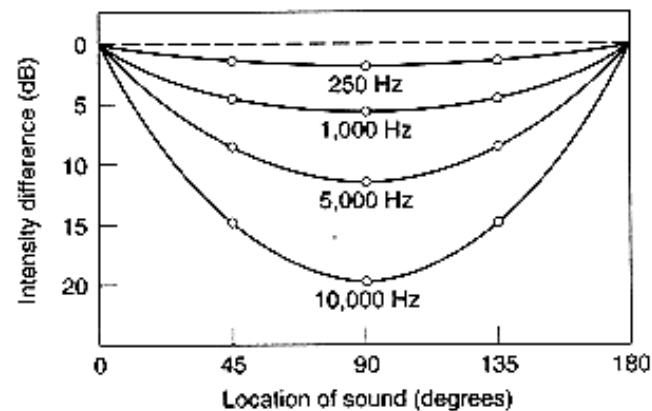
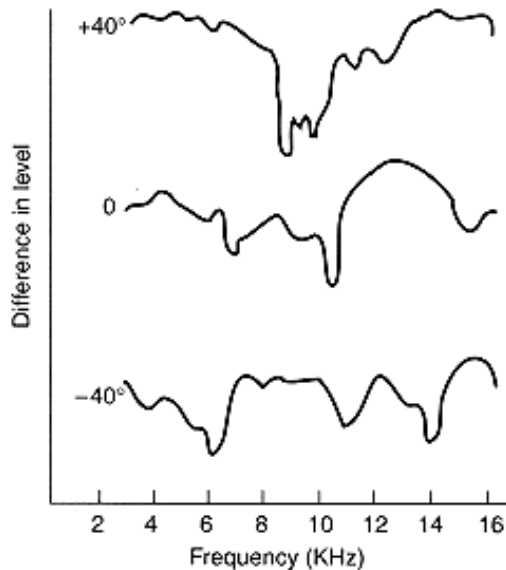
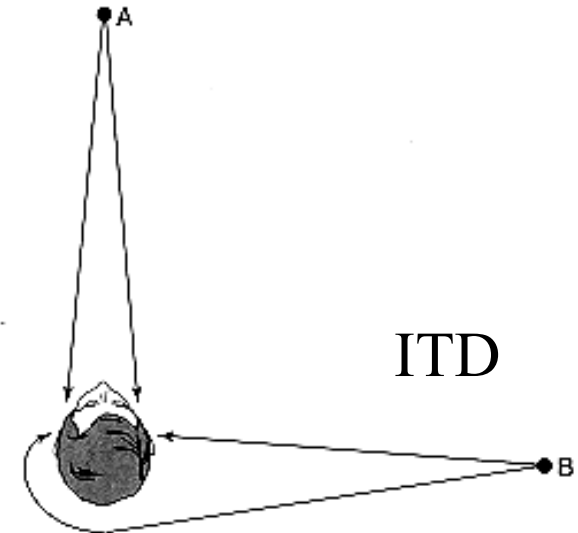
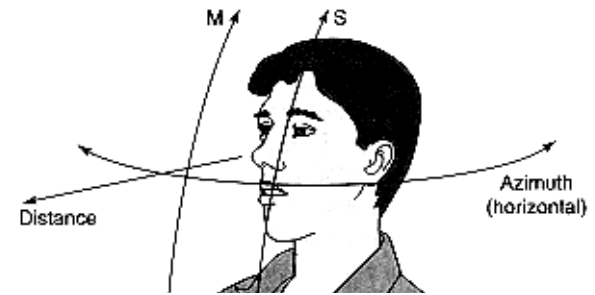
-Unlike visual and somatosensory systems, no direct mapping of physical space onto receptor space

-Have to reconstruct all 3 axes of space:

**Azimuth:** Interaural time difference (ITD) for low frequencies, interaural level difference (ILD) for high frequencies

**Elevation:** Changes in sound spectrum due to shape of external ear and head (some animals use ILD due to pinnae orientation)

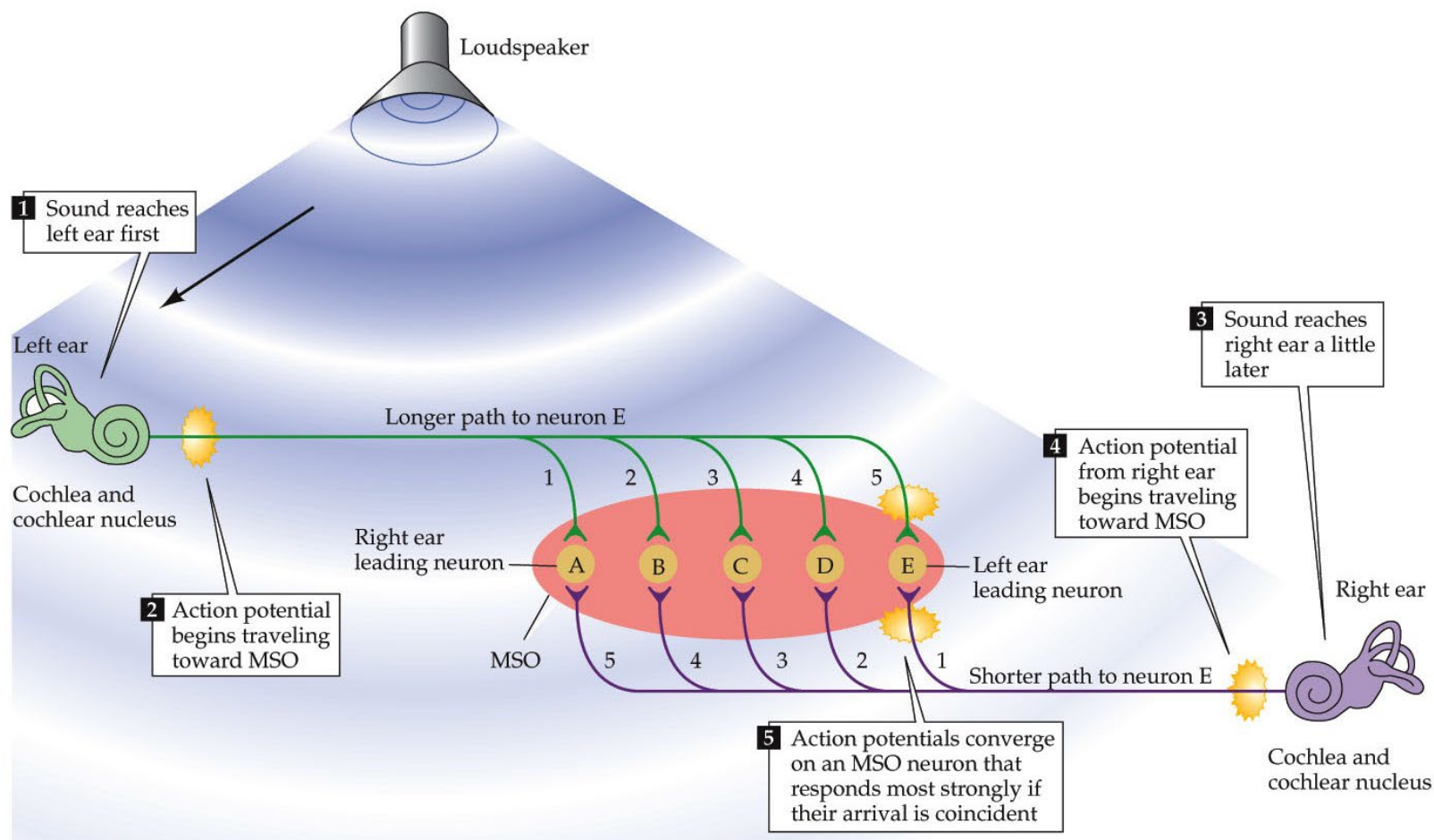
**Distance:** Many subtle factors, including sound level, frequency dulling, reflections.



# Neural coding of azimuth

-neurons in the medial superior olivary nucleus (MSO) can discriminate ITDs of a few microseconds (as can humans). How is this possible??

-afferents of varying length from the ipsi- and contra-lateral cochlear nuclei make orderly connections and MSO neurons only fire if spikes from both sides arrive near simultaneously. Axons serve as delay lines to give sub-millisecond resolution.



# Jeffress (1948) Coincidence model



Medial superior olive



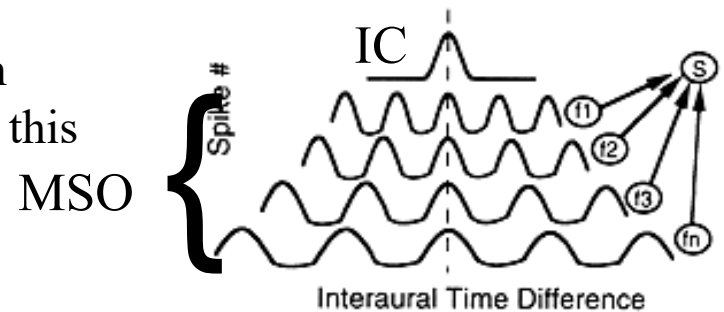
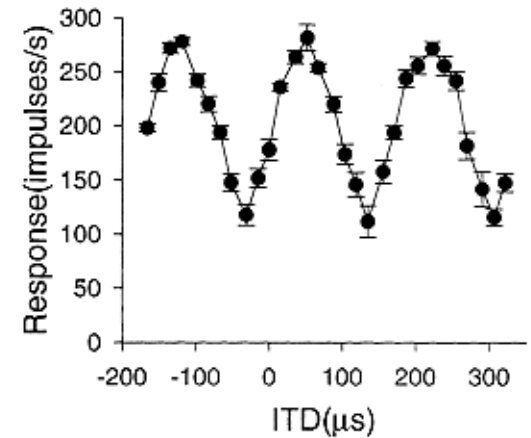
By virtue of different axon lengths from the two cochlear nuclei, different cells come to be tuned for different ITDs. So we have a place code for ITD.

BUT...

MSO neurons have multi-peaked ITD curves for tones and even for broadband sounds (why?). Problem of *phase ambiguity*.

MSO units are tuned for both ITD and frequency.

Neurons in inferior colliculus combine responses from MSO units tuned to different frequencies to overcome this phase ambiguity



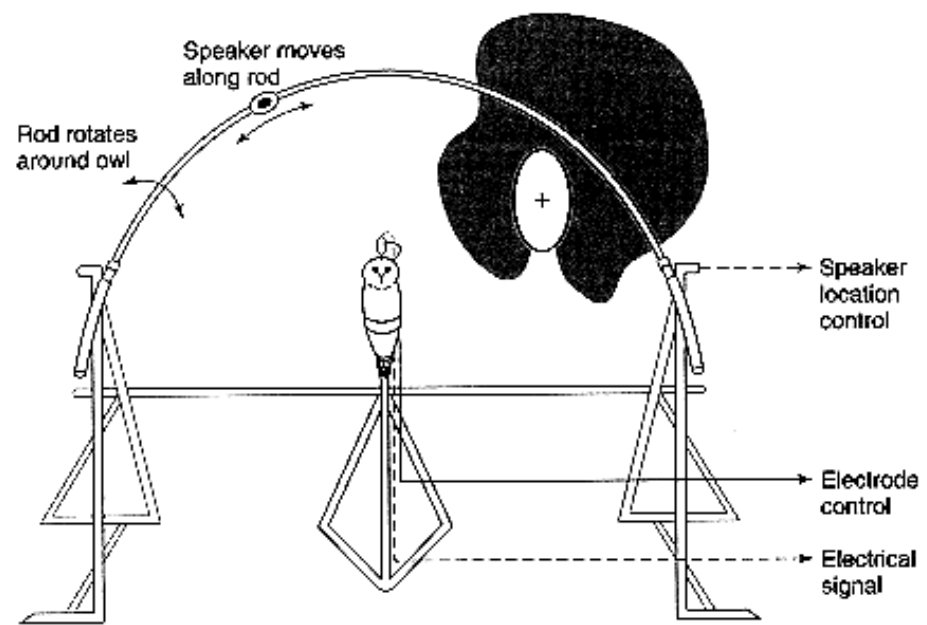
-neurons in the lateral superior olive (LSO) are tuned for ILD and provide azimuth information at high frequencies.

-spectral cues to elevation may be processed in the dorsal cochlear nuclei

- Inferior colliculus neurons combine azimuth, elevation (and perhaps distance) cues to create a map of auditory space.

- some auditory receptive fields have an inhibitory surround

- spatial receptive fields are generally narrower in azimuth than elevation (why?), a result which parallels behavioral measurements of sound localization (bottom left)



Knudsen and Konishi

- neurons in superior colliculus (optic tectum) have both auditory and visual receptive fields, aligned in space.

- If the visual input is shifted with prisms, the ITD tuning of neurons in optic tectum gradually shifts so that the auditory and visual receptive fields become aligned again (Eric Knudsen, Stanford Univ)

