Behavioral Neuroscience A
9: Audition

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https://youtu.be/qpipLPFDR9k

Lecture Video at above link.

Hearing!

Audition

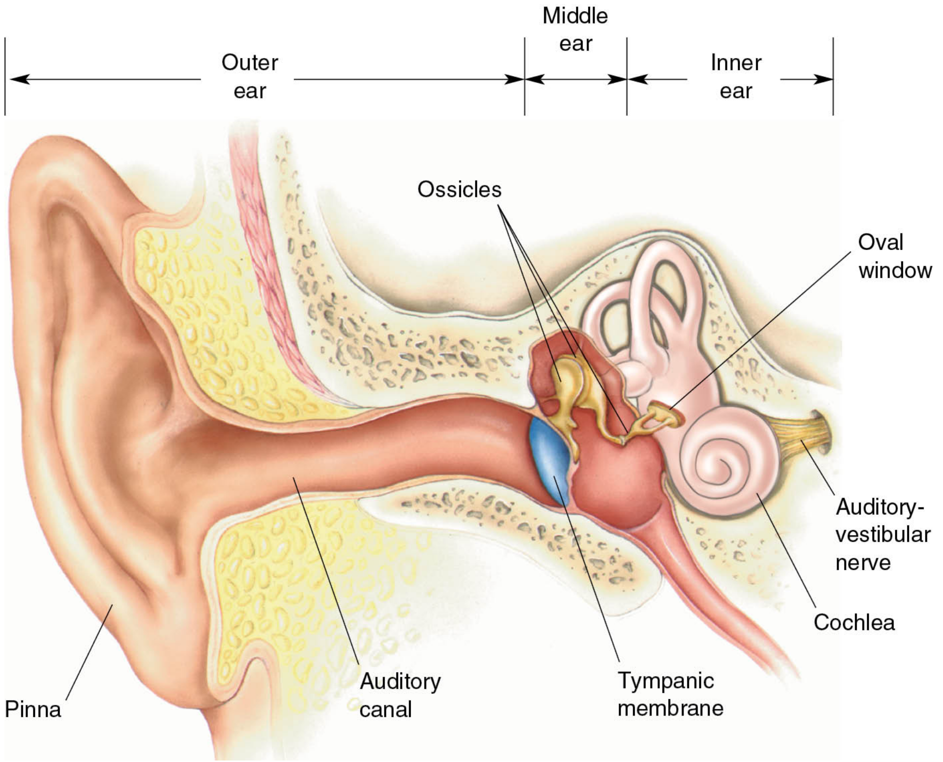
- To understand how **sound** entering our ears is converted into **nerve excitation**.

- To understand how our **acoustic** environment is interpreted by the brain.

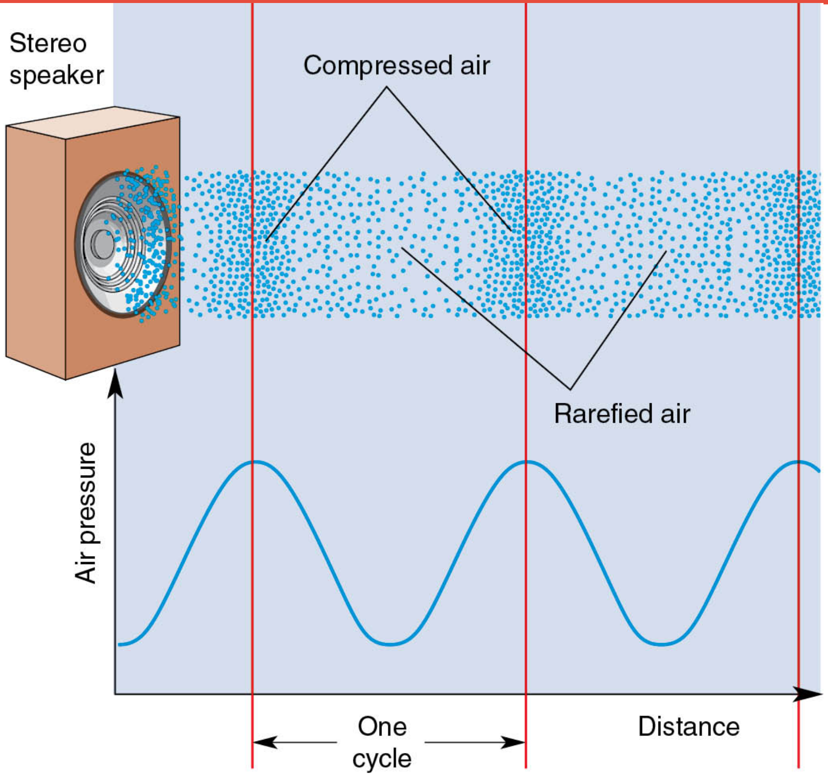
Today

Audition – or how we hear…

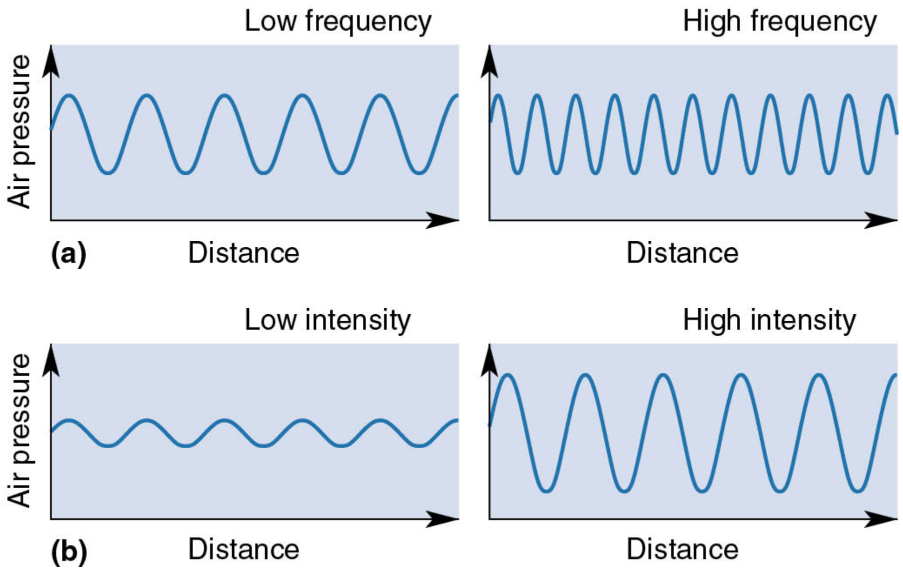
1) The ear
2) Sound receptors
3) Auditory pathway
4) Auditory cortex
5) Sound localization
6) Echolocation



Sound waves



Sound waves are variations in air pressure; we can hear them from about 20 µPa (0 dB sound pressure level) to 200 Pa (140 dB SPL, damage to auditory system). Standard atmospheric pressure is 101,325 Pa.
Speed of sound in air is about 340 m/s.



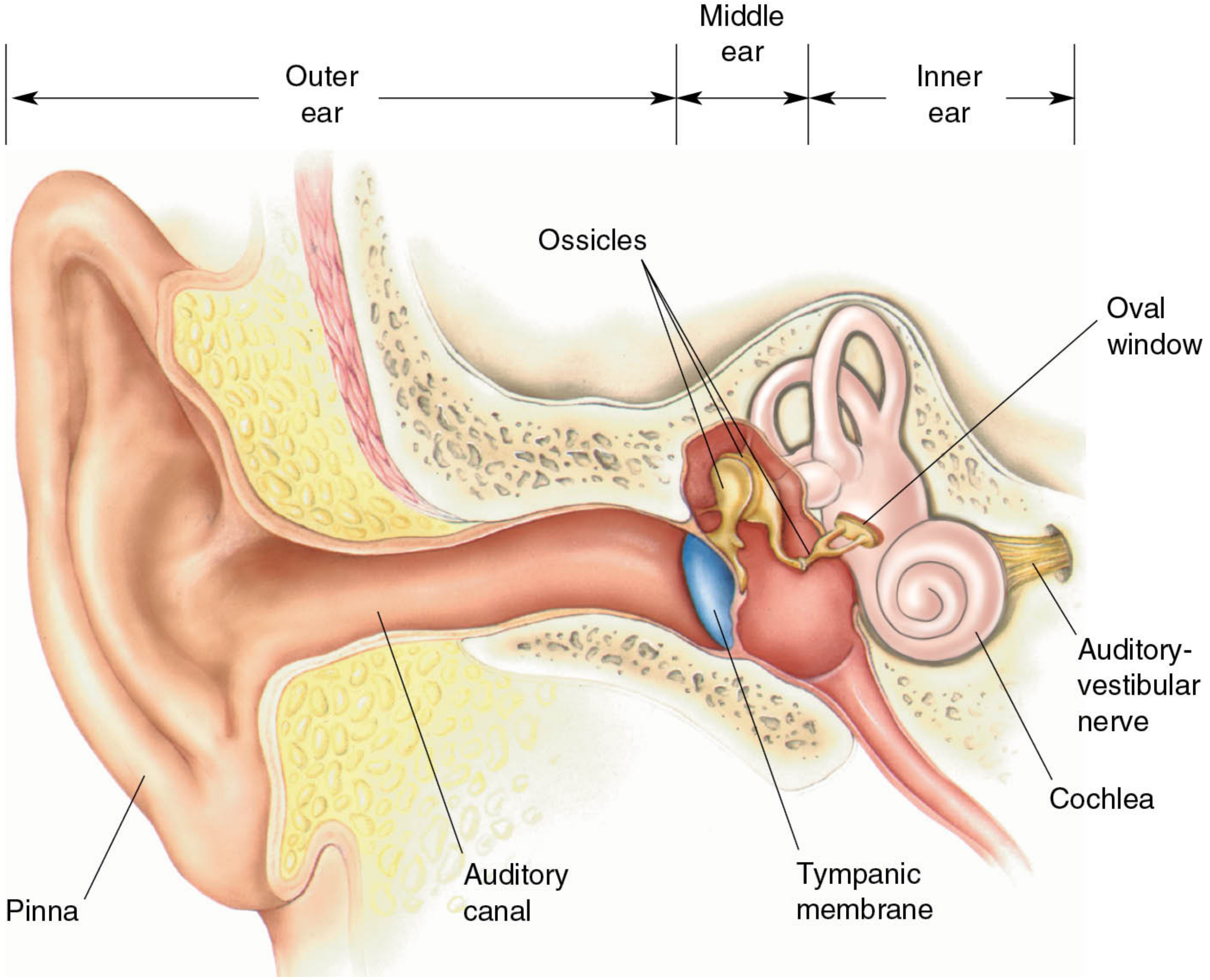
Low-frequency sound waves appear low-pitched, high-frequency sounds high-pitched. The amplitude of pressure changes determines their loudness (high amplitude-> loud sounds). Audible frequency range for humans is about 20-20,000Hz.

Bear, Neuroscience

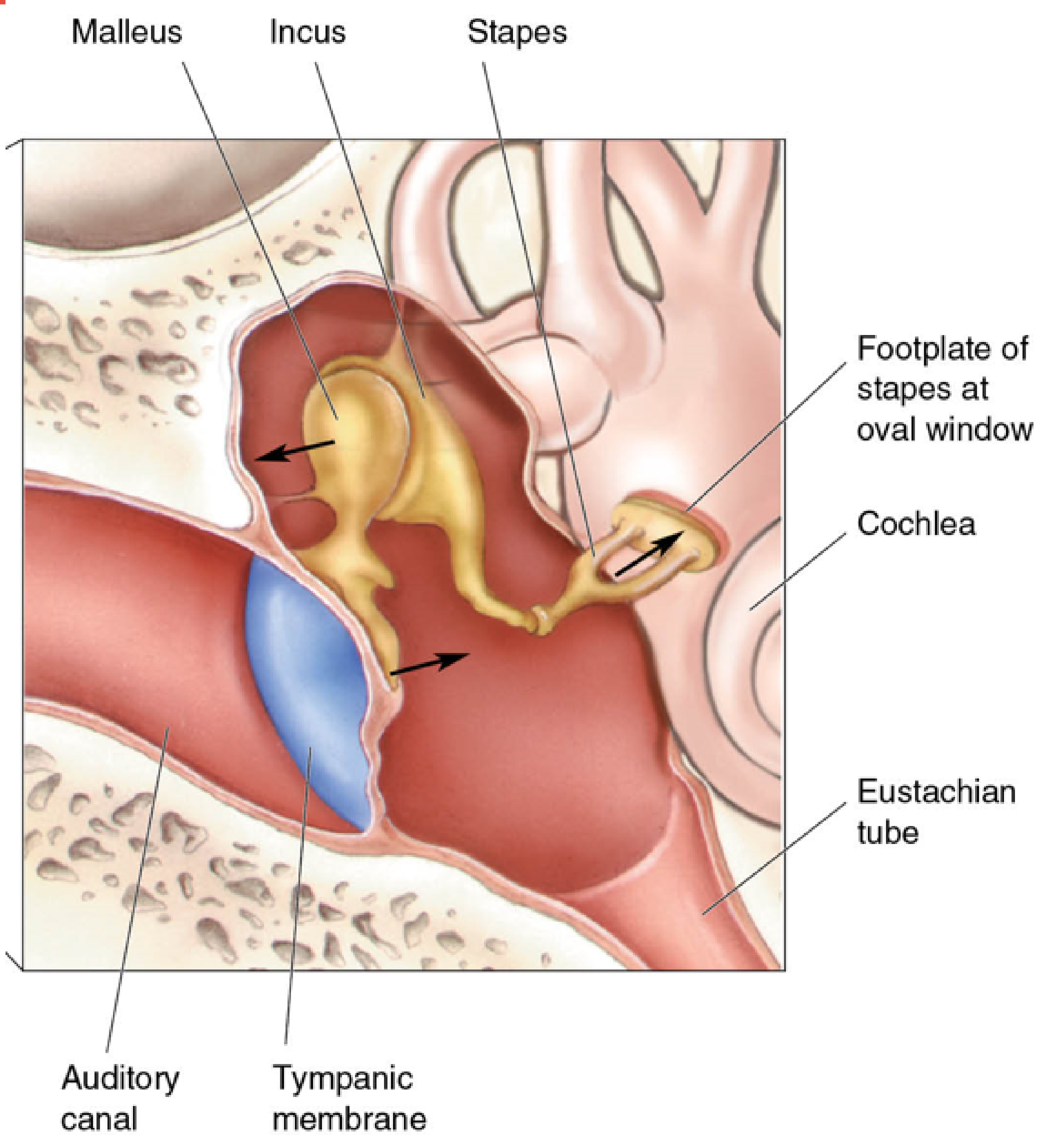
The ear

→ See movie
"Auditory Transduction" by Brandon Pletsch

https://youtu.be/PeTriGTENoc



The middle ear



Sound waves move the tympanic membrane.

→

The middle ear (air-filled cavity) ossicles malleus, incus, and stapes transmit sound to the oval window and amplify it.

→

Movement of the oval window will move the fluid in the cochlea.

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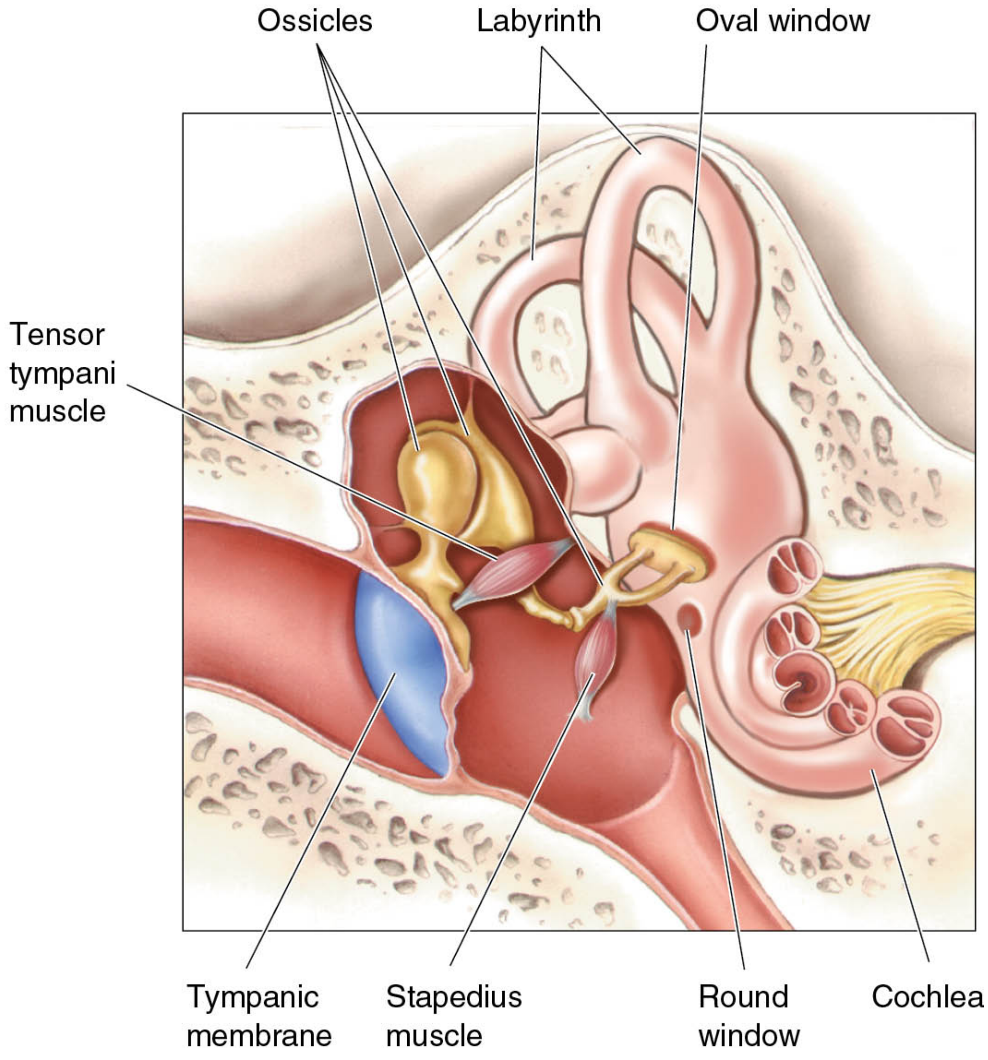
The middle ear (2)



To allow for movement of the fluid inside the cochlea (the perilymph), there is a second elastic membrane, the round window.

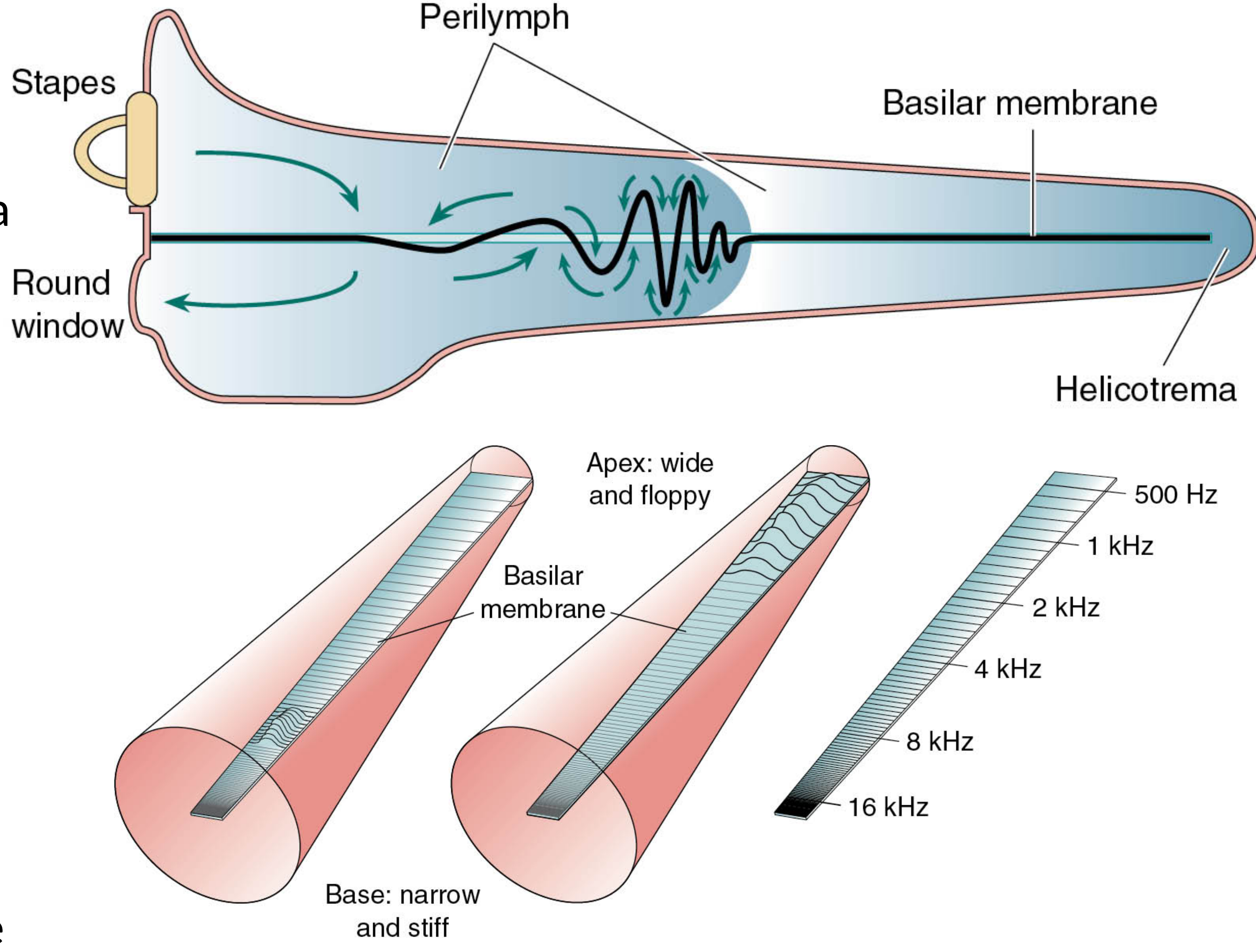
Two muscles in the middle ear can actively attenuate sound transmission, e.g., in response to very loud sounds: Stapedius muscle (contraction stiffens the stapes) and Tensor tympani muscle (can stiffen the tympanic membrane).

Bear, Neuroscience

The inner ear

Movement of the <u>perilymph</u> in the cochlea will create a traveling wave along the <u>basilar membrane</u>.

Due to the properties of the basilar membrane (wide and floppy at the apex) <u>higher frequencies</u> will create maximum vibration amplitudes at the <u>base</u>, <u>lower</u> frequencies at the <u>apex</u>.



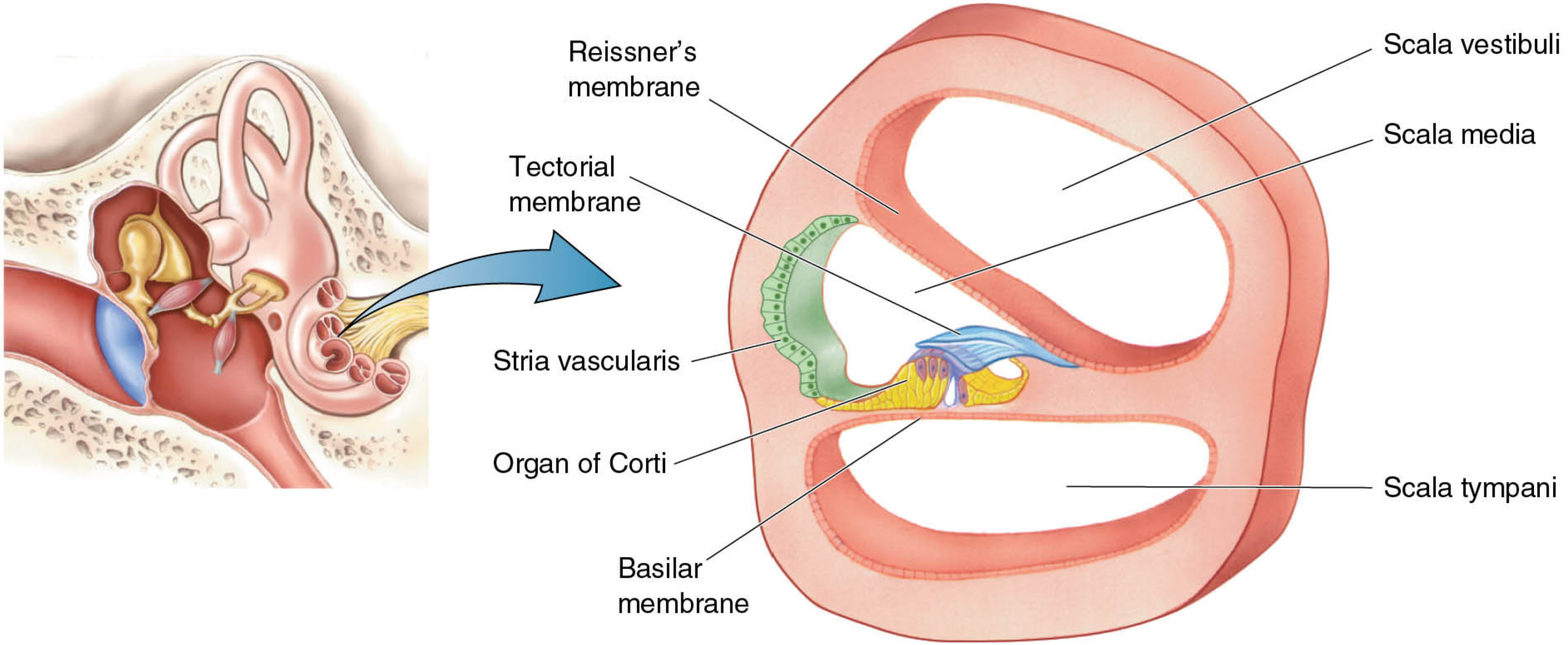
(a) High frequency (b) Low frequency (c) Frequency producing maximum amplitude

Bear, Neuroscience

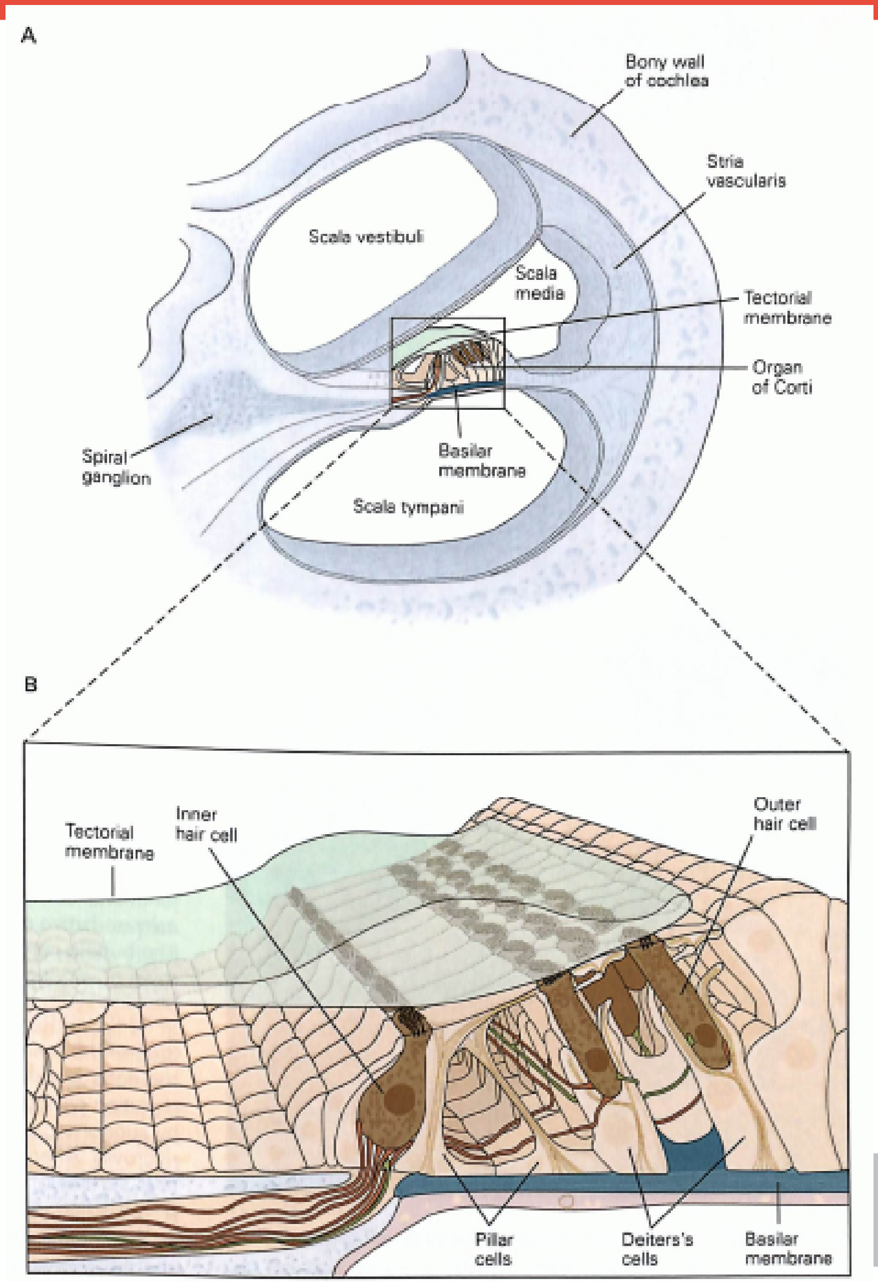
The inner ear (2)

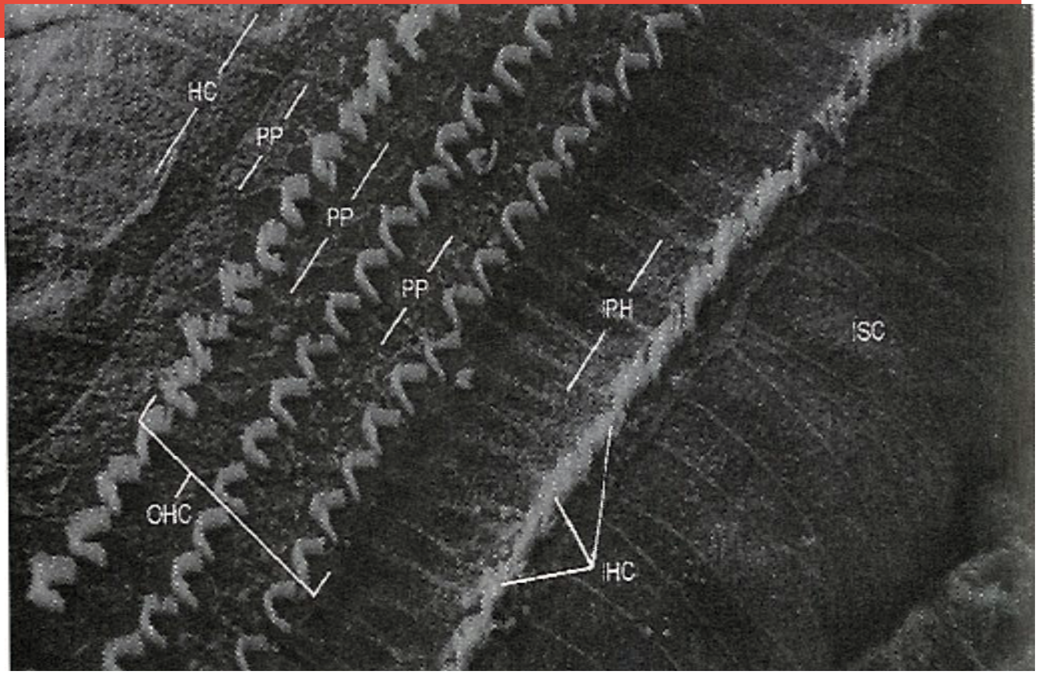
The cochlear has a spiral shape with 2.5-3 turns (32mm long).
Two compartments (connected at the helicotrema) are filled with <u>perilymph</u>:
<u>Scala vestibuli</u> and <u>Scala tympani</u>.
The <u>Scala media</u> (cochlear duct) is between them and filled with <u>endolymph</u>.

The <u>endolymph</u> has high K^+ and low Na^+ concentration, unlike other extracellular fluid.
Within the Scala media, two important structures are responsible for the generation of nerve impulses: <u>Organ of Corti</u> and <u>Tectorial membrane</u>.



The inner ear (3)





The auditory receptor cells – hair cells – are situated in the organ of Corti. **Inner hair cells** (IHC) are arranged in one row, **outer hair cells** (OHC) in three rows. Their “hair” (stereocilia) extends into the endolymph, touching the tectorial membrane (OHC) or ending just below it (IHC).

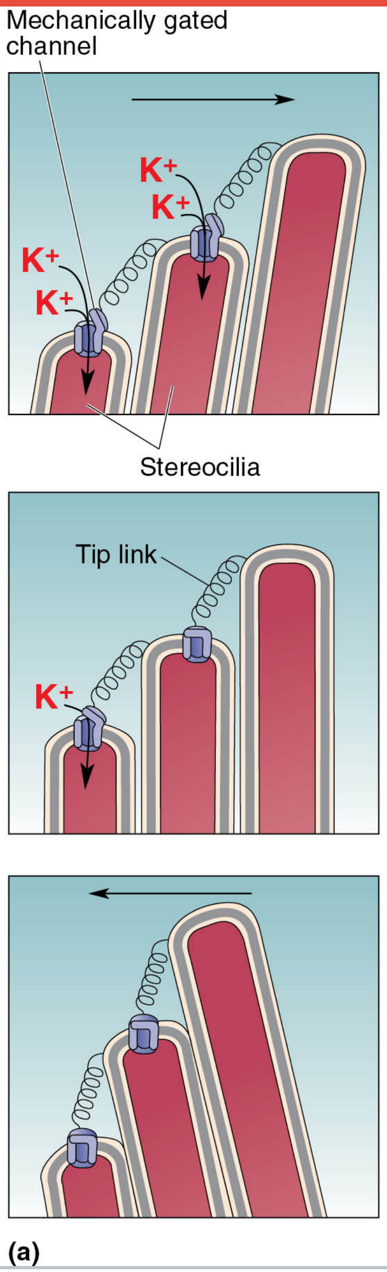
Kandel, Principles of Neuroscience

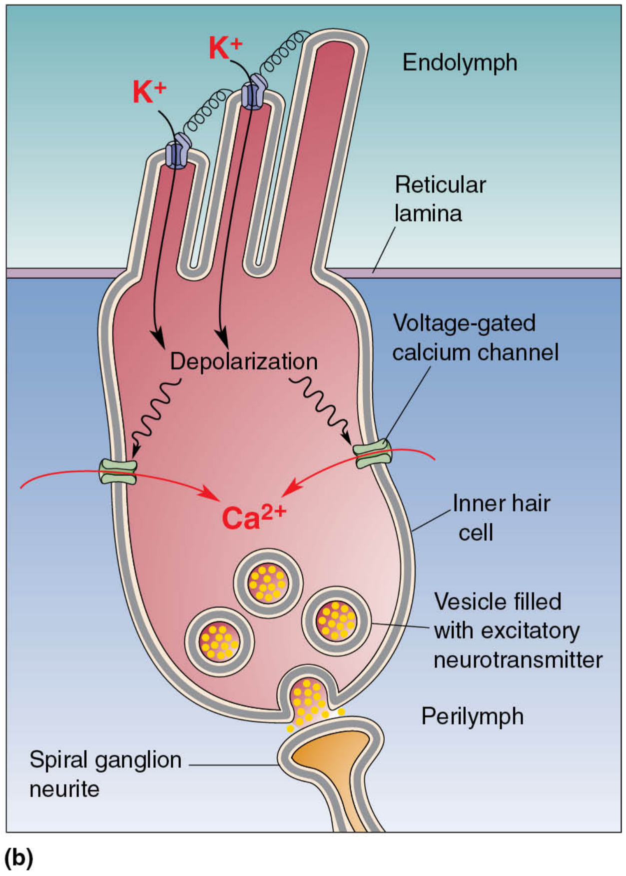
Mechanotransduction – Physical movement → Electricity

Hair cells have <u>stereocilia</u> stretching into the endolymph. During vibration, they are bent and because their tips are connected by <u>cross-link filaments</u> they move as a unit.

The tips of the stereocilia have mechanically gated K^+ channels connected via tip links to an adjacent cilium. They open when the cilium is bent in one and close when bent in the other direction.

K^+ ions flow into (!) the hair cell and depolarize it. This is possible, because the endolymph has a high concentration of K^+.

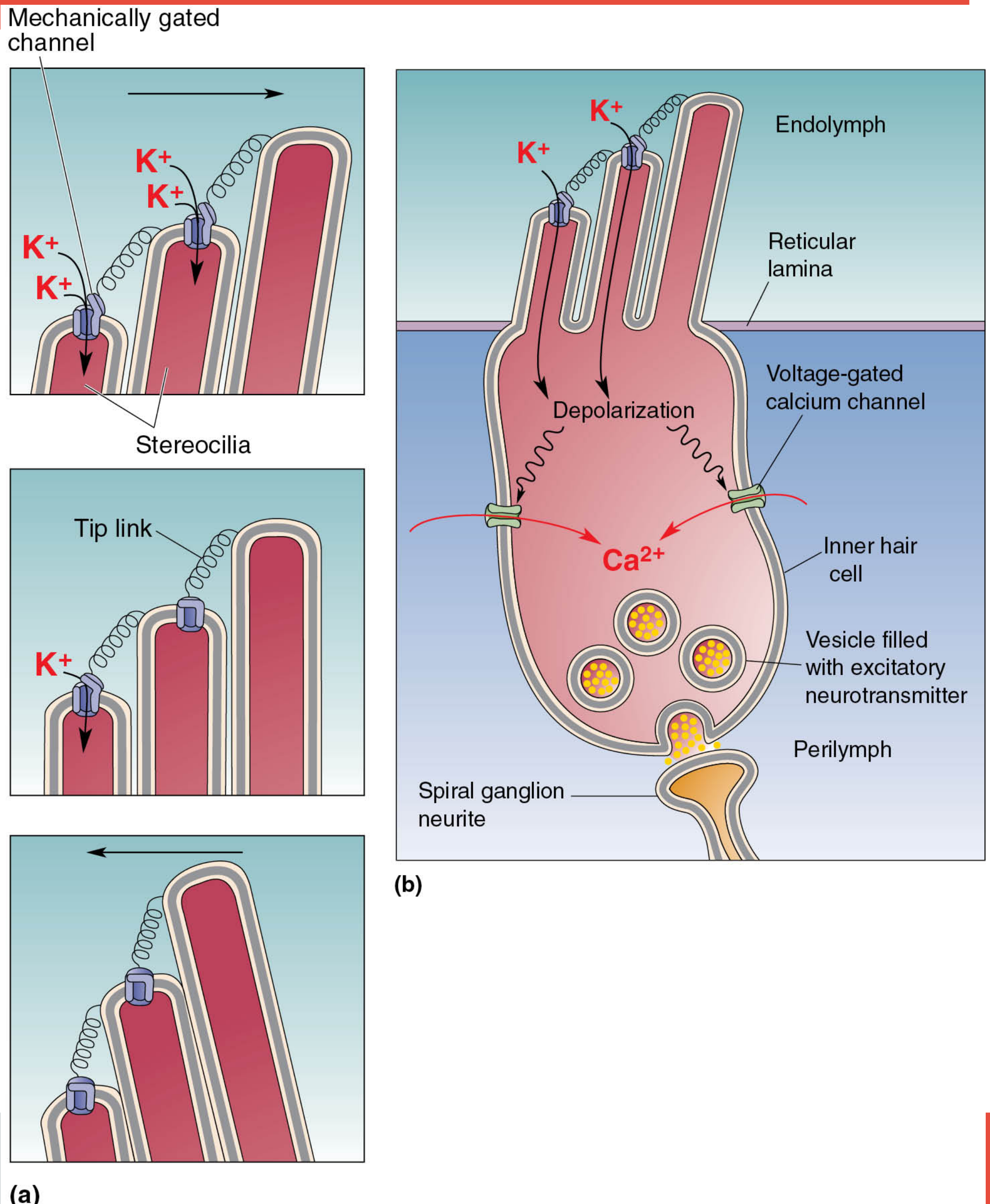




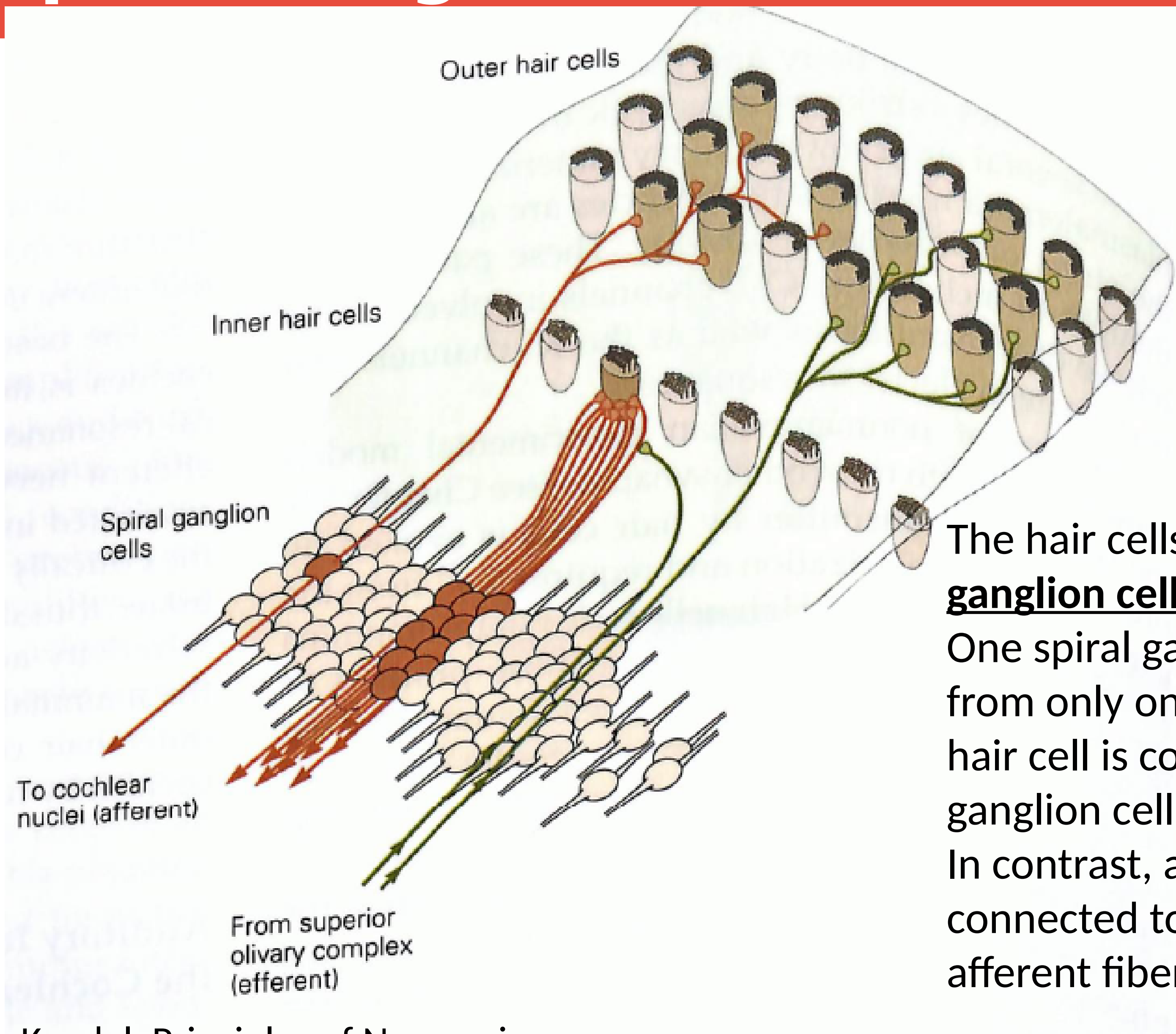
Mechanotransduction (2) – Physical movement → Electricity

The depolarization will cause voltage-gated Ca^{2+} channels to open and let Ca^{2+} into the hair cell.

This will lead to a release of the neurotransmitter glutamate. Synaptic receptors of spiral ganglion cells respond to glutamate and the spiral ganglion cell will fire an action potential.



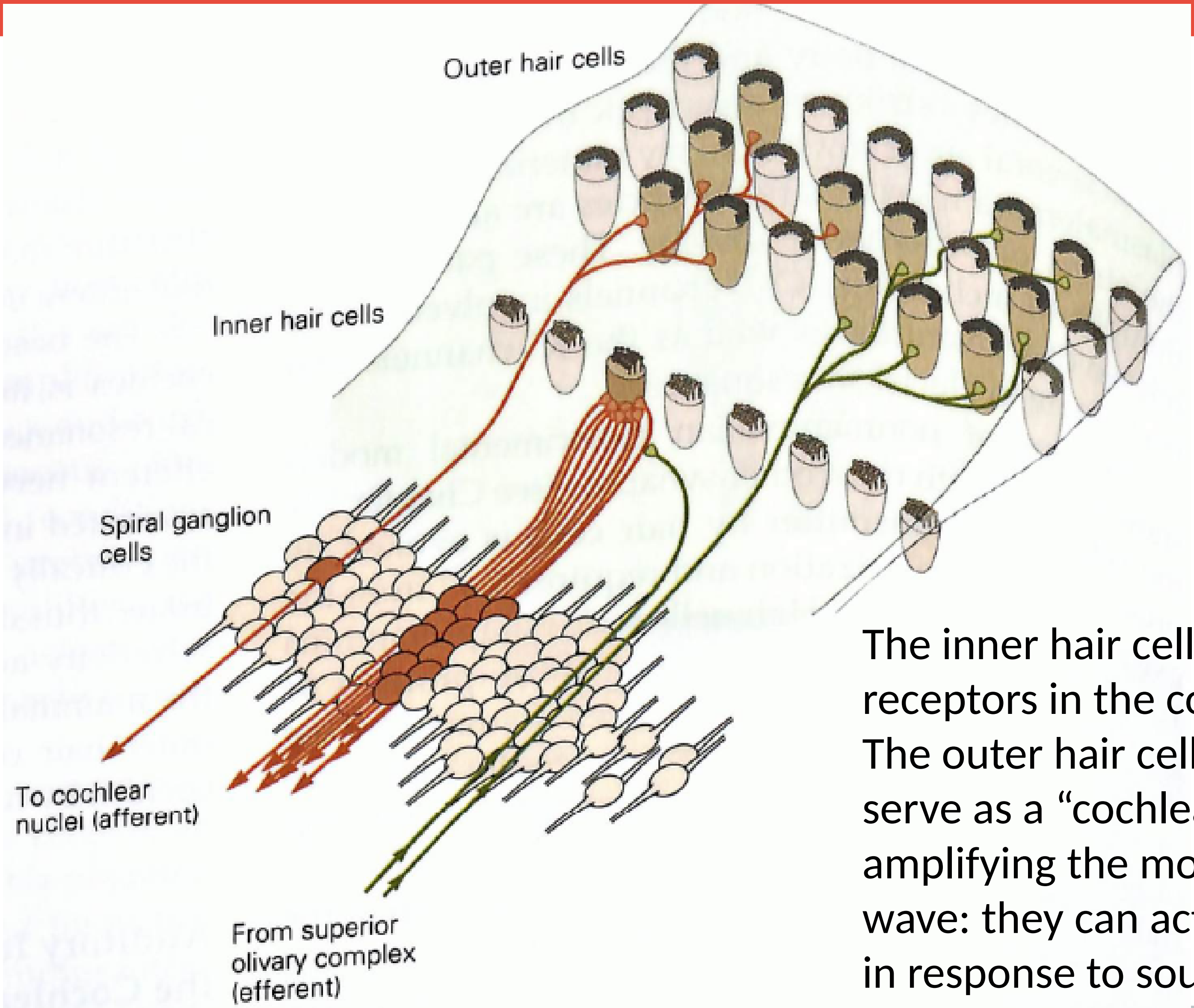
Spiral Ganglion Cells in Cochlea



The hair cells are innervated by **<u>spiral ganglion cells</u>** of the cochlea.
One spiral ganglion cell receives input from only one inner hair cell. One inner hair cell is connected to about 10 spiral ganglion cells.
In contrast, about 10 outer hair cells are connected to a spiral ganglion cell via an afferent fiber.

Kandel, Principles of Neuroscience

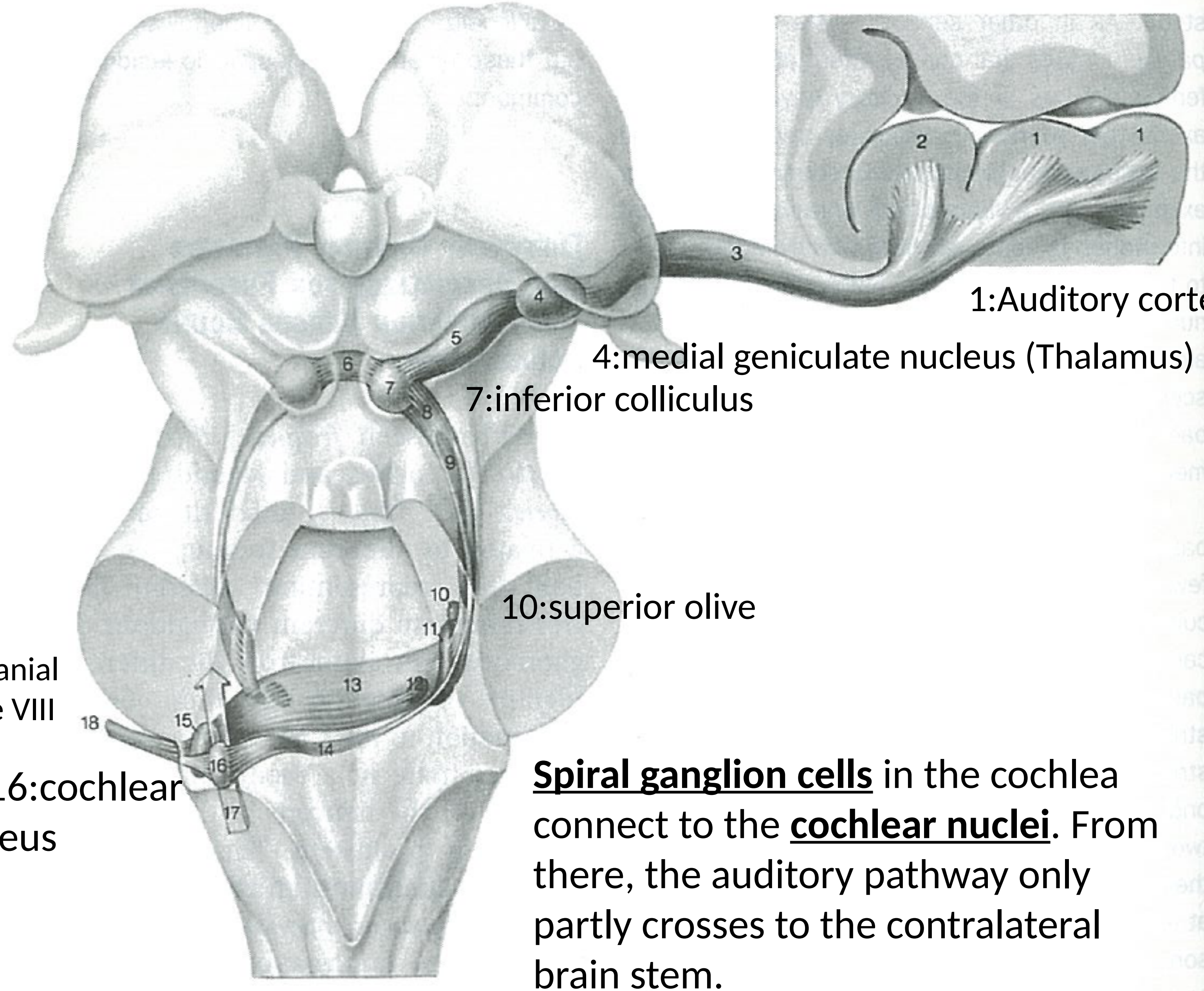
Outer Hair Cells – Cochlear Amplifier?



The inner hair cells are the primary sound receptors in the cochlea.
The outer hair cells have been proposed to serve as a “cochlear amplifier” by amplifying the movement of the travelling wave: they can actively change their length in response to sound.

Kandel, Principles of Neuroscience

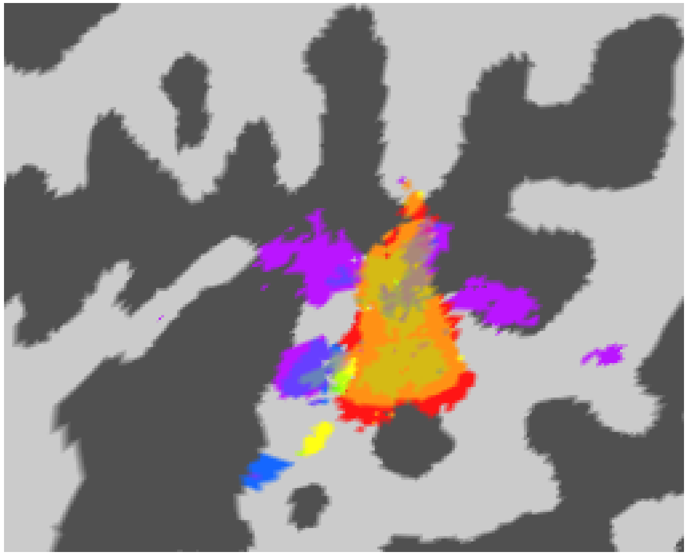
Auditory Pathway



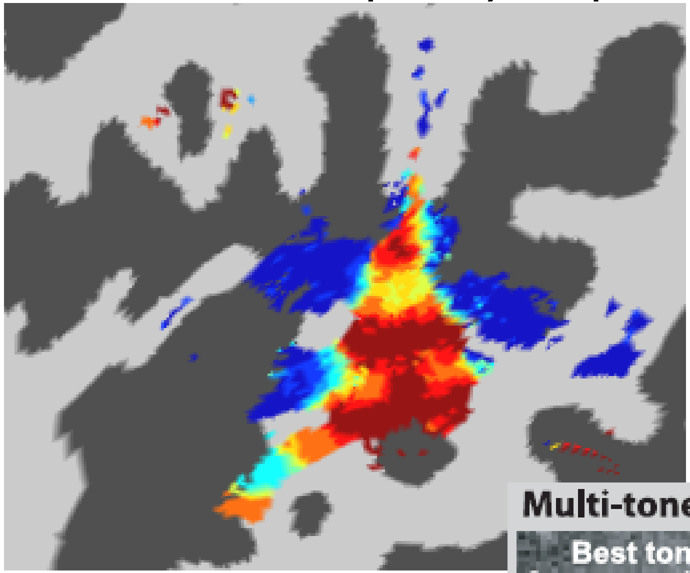
Spiral ganglion cells in the cochlea connect to the **cochlear nuclei**. From there, the auditory pathway only partly crosses to the contralateral brain stem.

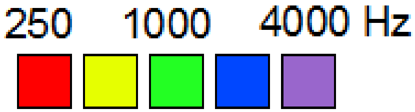
Primary Auditory Cortex (A1) “Tonotopic”

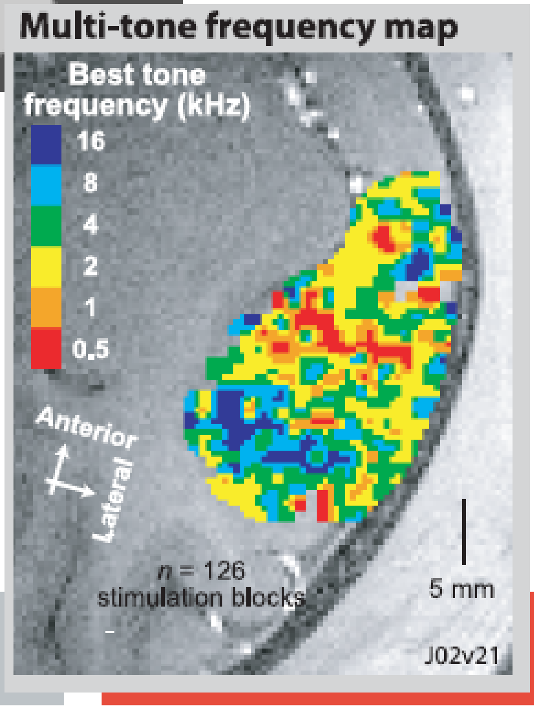
Response to specific Frequency



Preferred Frequency Map

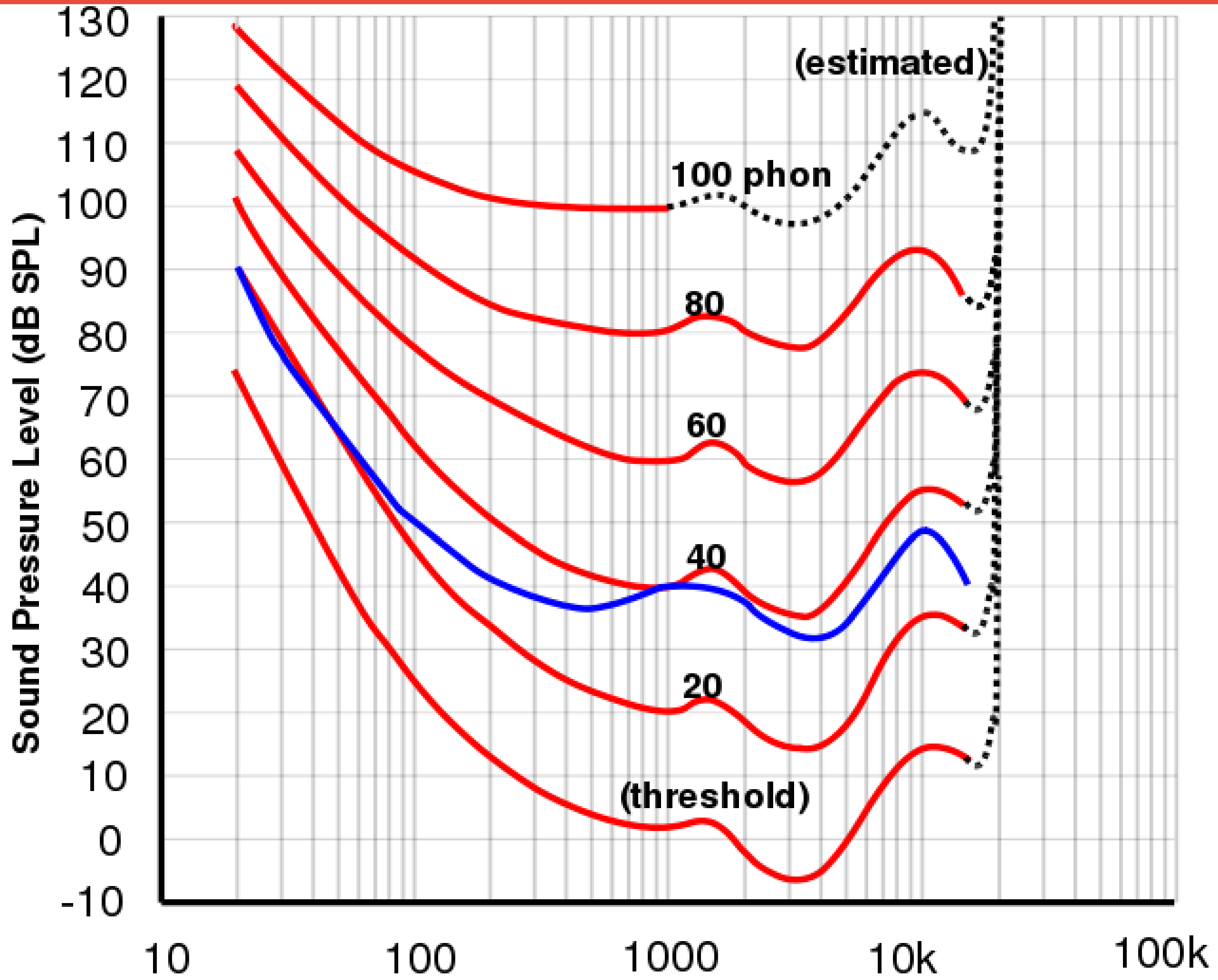






Rhesus Monkey:
Petkov, PLOS One, 2006

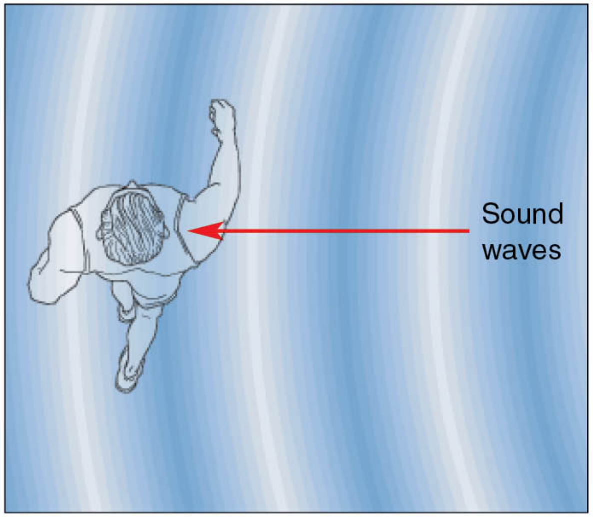
Frequency selectivity



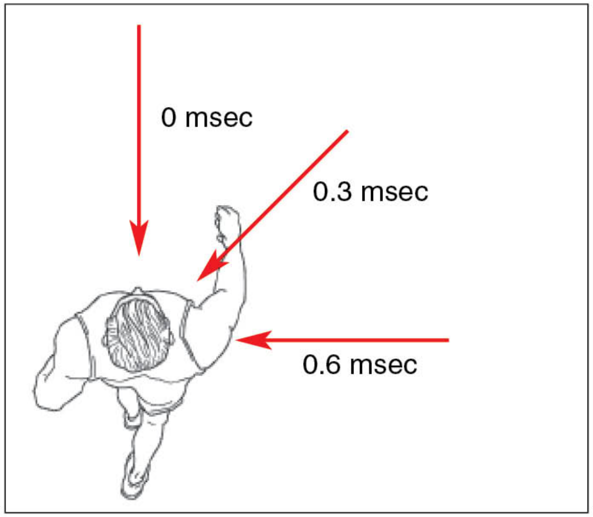
Equal-loudness contours (red) (from ISO 226:2003 revision)
Original ISO standard shown (blue) for 40-phons

http://newt.phys.unsw.edu.au/jw/hearing.html

Sound localization: ITD
Timing difference between ears



(a)



(b)

Sound localization in the horizontal plane ("azimuth") (left-right) is achieved mainly by two cues:
Interaural time delay (ITD) and interaural intensity difference (IID).

Interaural time delay (ITD): sound waves from a sound to the right will first hit the right, then the left ear (a).
Time delays between the two ears are up to around 0.6 ms (b).

For higher frequencies (>2000 Hz), this cue cannot be used, because correspondence between sound peaks cannot be resolved.

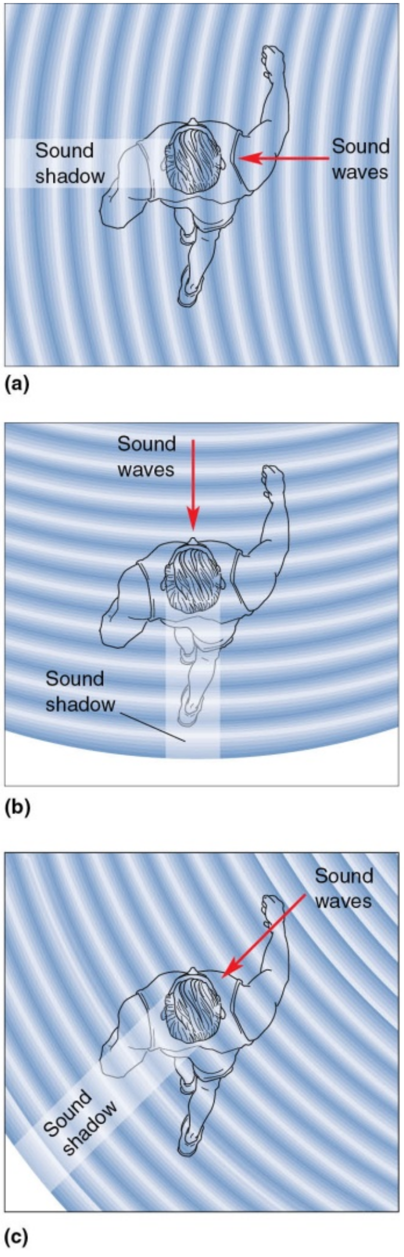
Bear, Neuroscience

Sound Localization: IID
Volume difference between ears

<u>Interaural intensity difference (IID)</u>: sound waves are blocked by our own head, so sound from the right will be louder in the right compared to left ear (a).

This shadowing effect is small for lower frequencies (<2000 Hz), because low-frequency sound diffracts (bends) around the head.

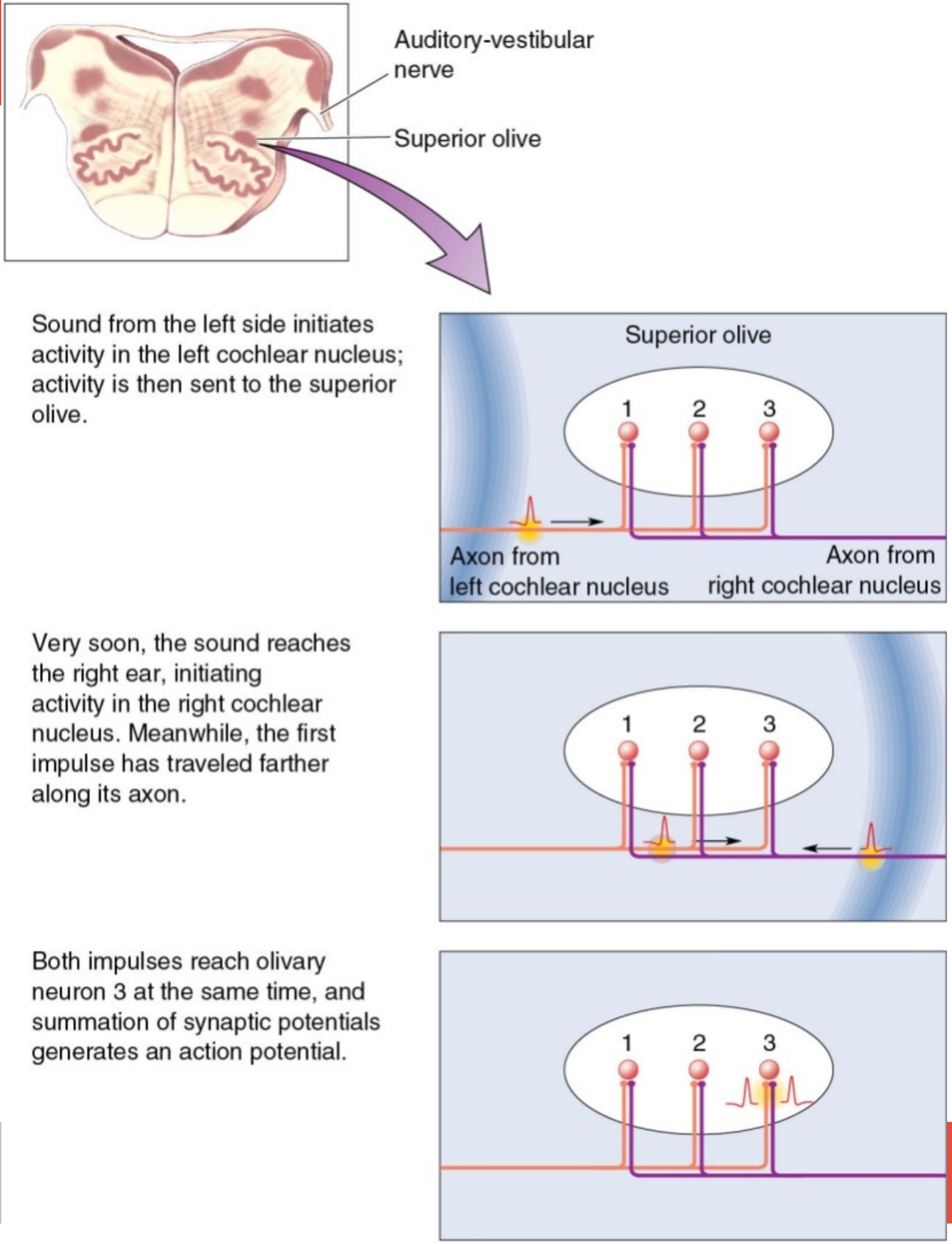
Thus, ITD can be used at lower (<2000 Hz), IID at higher frequencies.



Neural Circuit for Sound Localization

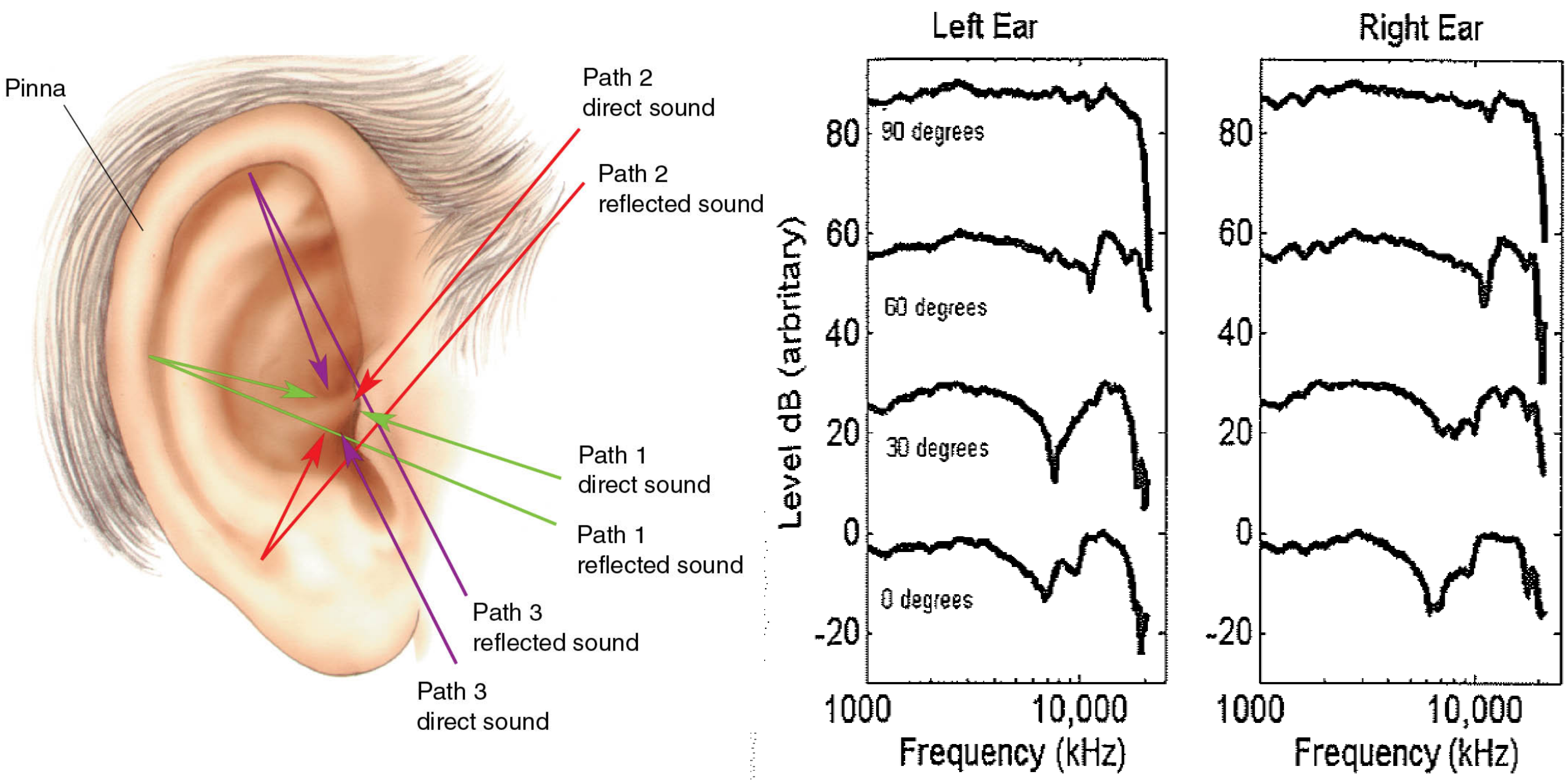
The **superior olive** is a brain stem structure where monaural input from the cochlear nuclei is integrated in binaural neurons.

Sensitivity of binaural neurons to interaural time delay could be based on **delay lines**: longer axons from one side delay signal conduction such that a neuron (3) is activated only when there is a time delay between sound impact on left and right ear.



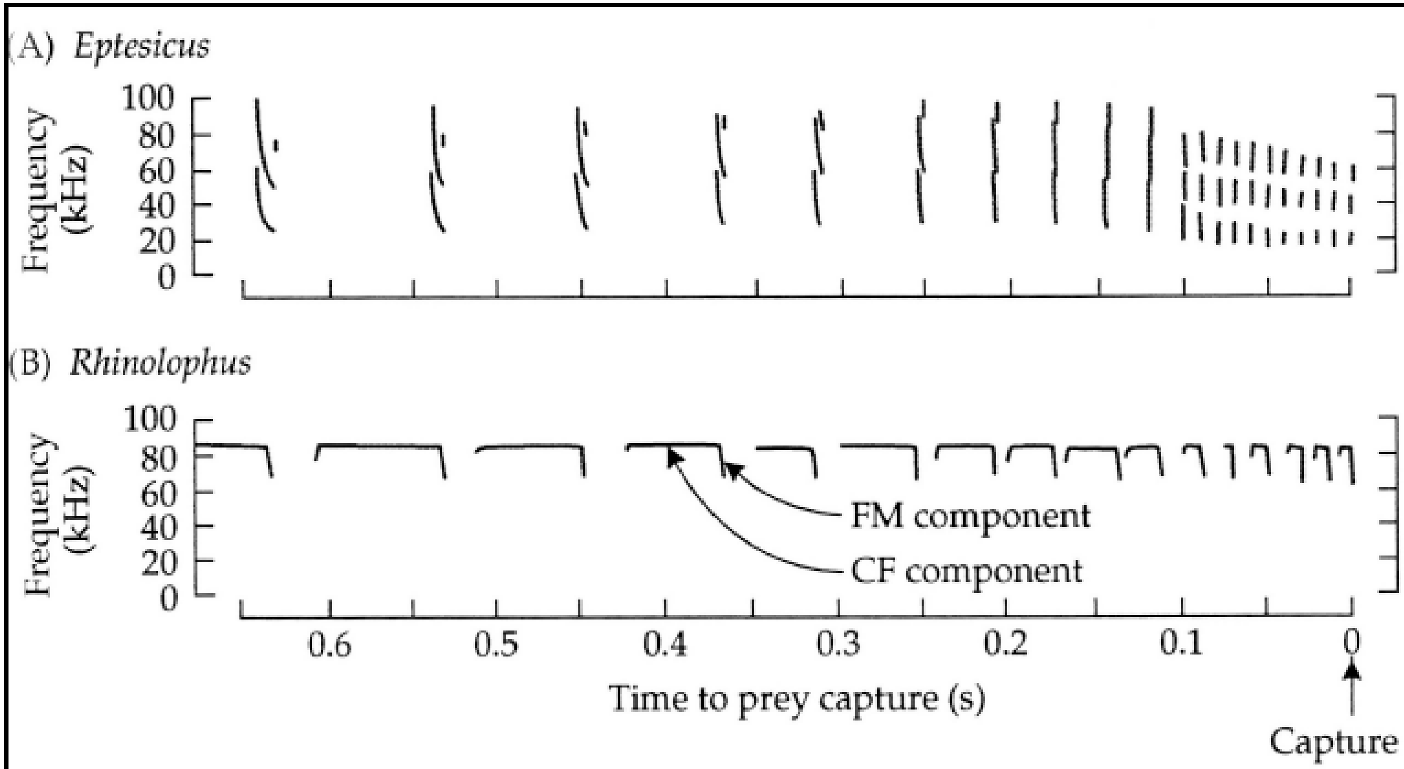
Sound Localization:
What about vertical (elevation)?

Localization in the **vertical plane** (up/down):



Sounds from different elevations undergo different filtering by the **pinnae**. These typical notch patterns (dent in the spectrum) tell us the sound's vertical position.

Bat Echolocation



2.2 Bats emit ultrasonic signals
The ultrasonic signals that bats emit can be recorded and plotted as shown. Here bat cries were measured as bats approached and captured their prey. (A) Some bats, like *Eptesicus*, use primarily FM signals. (B) Other bats, like *Rhinolophus*, use a combination of FM and CF signals. Note how the rate of the cry goes up dramatically as the bats near their prey. After Camhi 1984; data from Simmons, Fenton, and O'Farrell 1979.

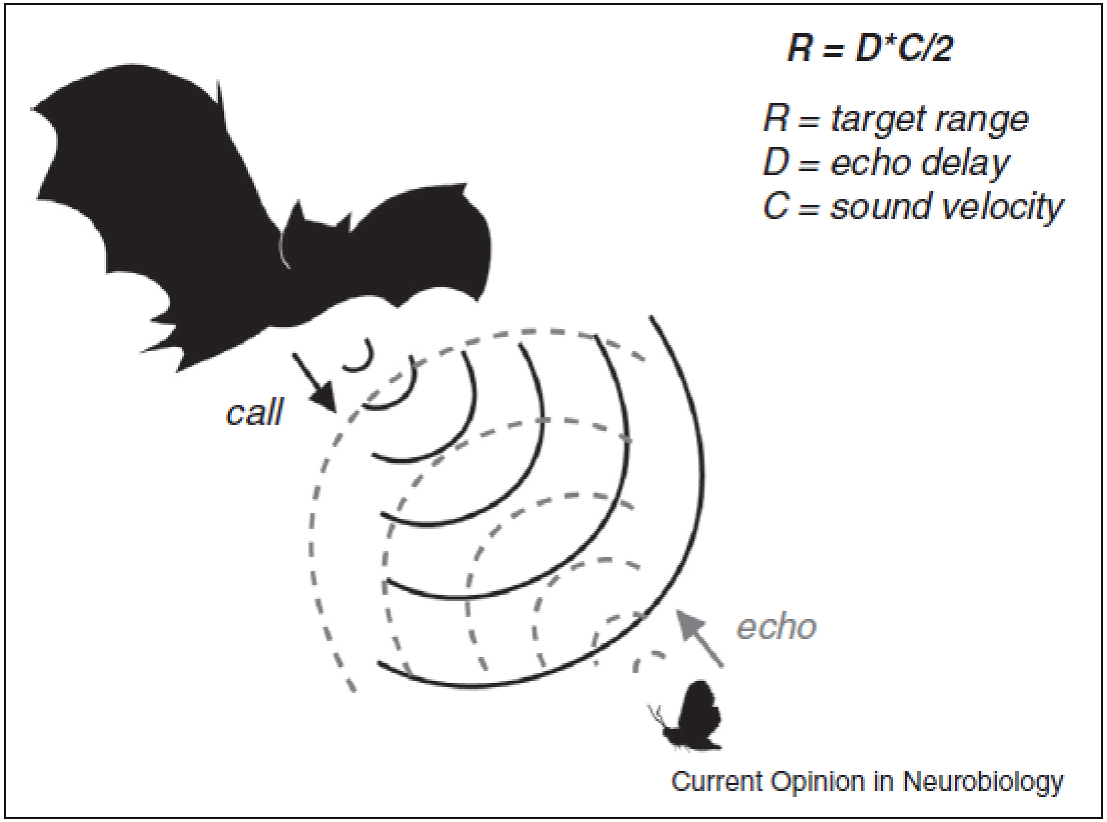
FM: frequency-modulated

CF: constant-frequency

Bat Echolocation

Bats can compute target range from echo delay, because the sound will take a longer time to return from a distant object.

Increased cry rate allows for faster information update, but leads to limited range.

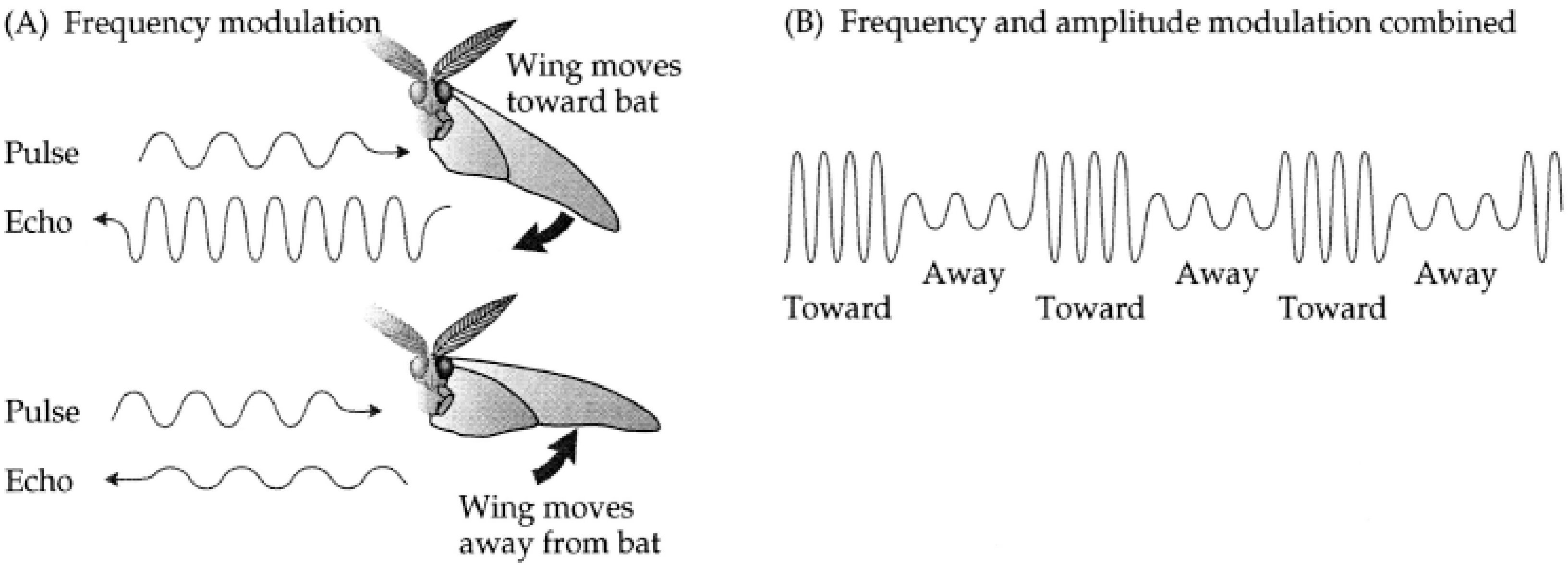


Echolocating bat that computes target range (*R*) from the echo delay (*D*).

Kössl et al., Current Opinion in Neurobiology, 2014

Bat Echolocation

Bats can compute target velocity from Doppler shift (the change of sound frequency due to motion of the sound source).



2.6 Using Doppler shift to determine flutter
Doppler shift provides a mechanism for determining the amount of flutter an object exhibits. (A) Part of flutter determination is derived from frequency modulation of the cry: As the wing of prey such as a moth moves toward the bat, the echo increases in frequency; the opposite is true as the wing moves away from the bat. (B) Flutter can also be determined by amplitude modulation of the echo: As the wing moves toward the bat, the echo will be slightly louder than as the wing moves away from the bat. Amplitude and frequency modulation are combined in flutter analysis.

→movie: BBC – bats hunting their prey. https://youtu.be/p08Y0oRAX3g

Human echolocation?

Humans (even non-blind) can learn to use click sounds for active echolocation.

(movie: Daniel Kish)
https://youtu.be/A8lztr1tu4o

Summary...

- Sound is converted to neural signals by mechanoreceptors (inner hair cells).

- Hearing has a wide range between 20-20,000 Hz in frequency and 20 µPa-200 Pa in sound pressure.

- Tonotopy means that representation of sound frequency is arranged as a spatial map and it is preserved along the auditory pathway from cochlear up to auditory cortex.

- Main cues for spatial localization of sounds in the horizontal plane are interaural time and level differences.