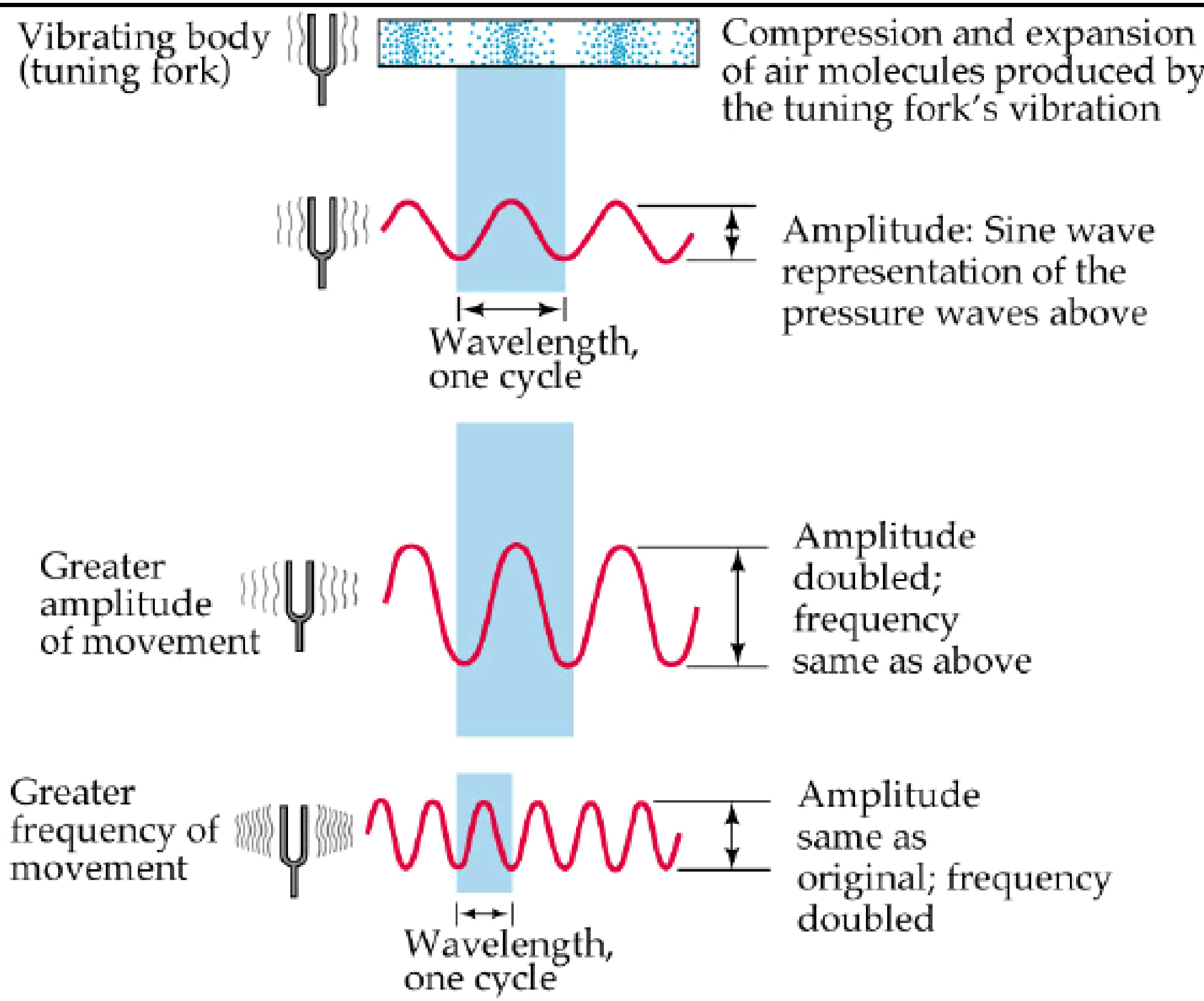
Systems Neuroscience

Oct. 16, 2018

Auditory system

http: www.ini.unizh.ch/~kiper/system_neurosci.html

The physics of sound



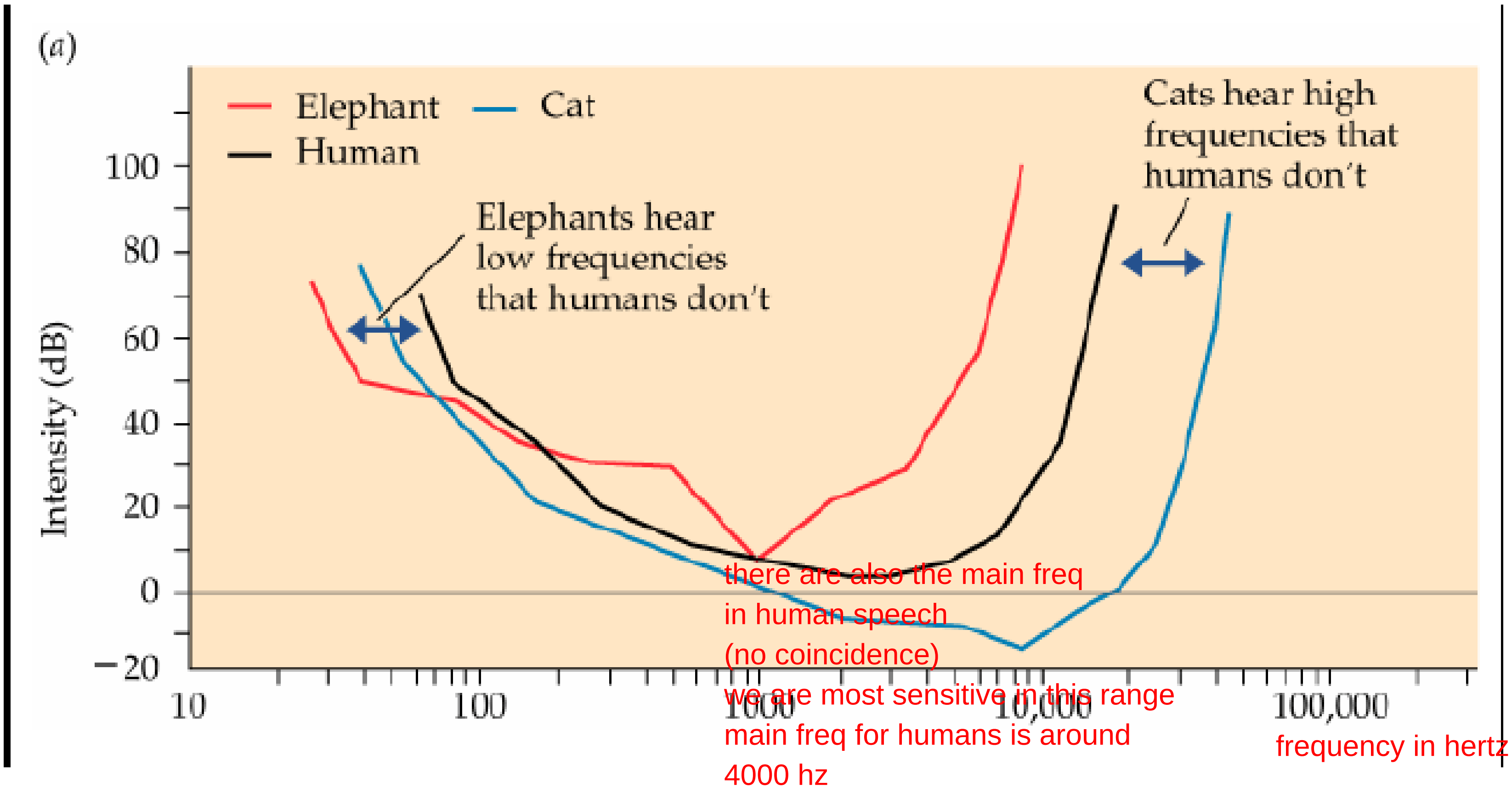
P1 := sound pressure of particular sound
P2 := 20 micropascal

Measuring sound intensity

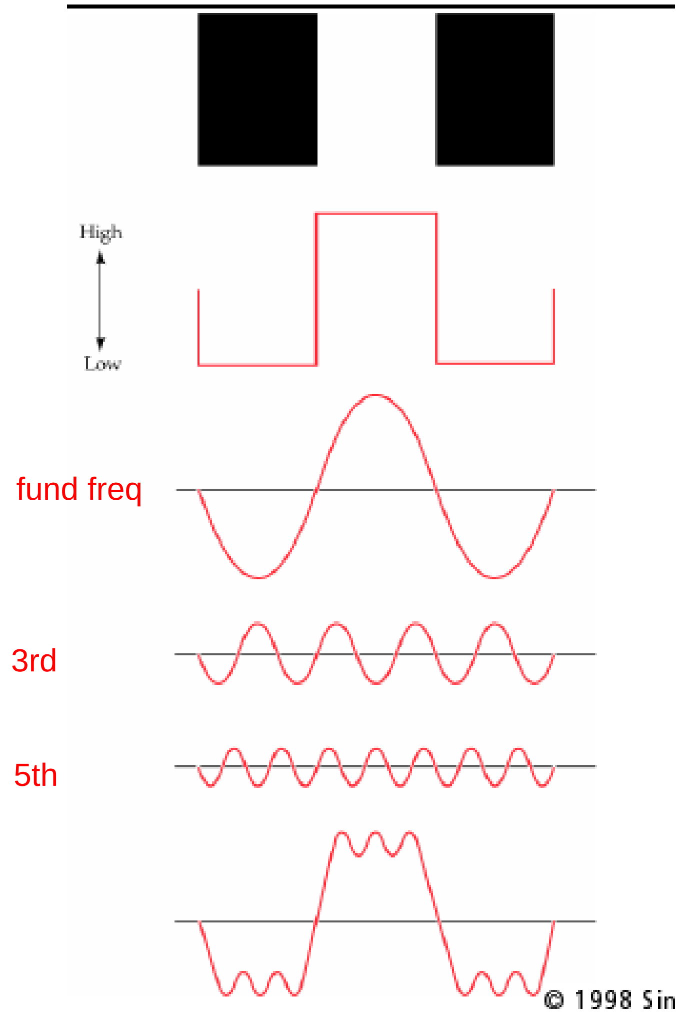
- We are sensitive to an enormous range of intensities, so a logarithmic scale works well
- intensity in dB=20 x log (P1/P2)
  - where P2 is 20 Micropascal
- remember log(1)=0, log(10)=1, log(100)=2
  - (and also, log(.1)=-1)

relative measure to the faintiast sound a human observer can hear (has no units by definition)

Remember this….



Fourier analysis



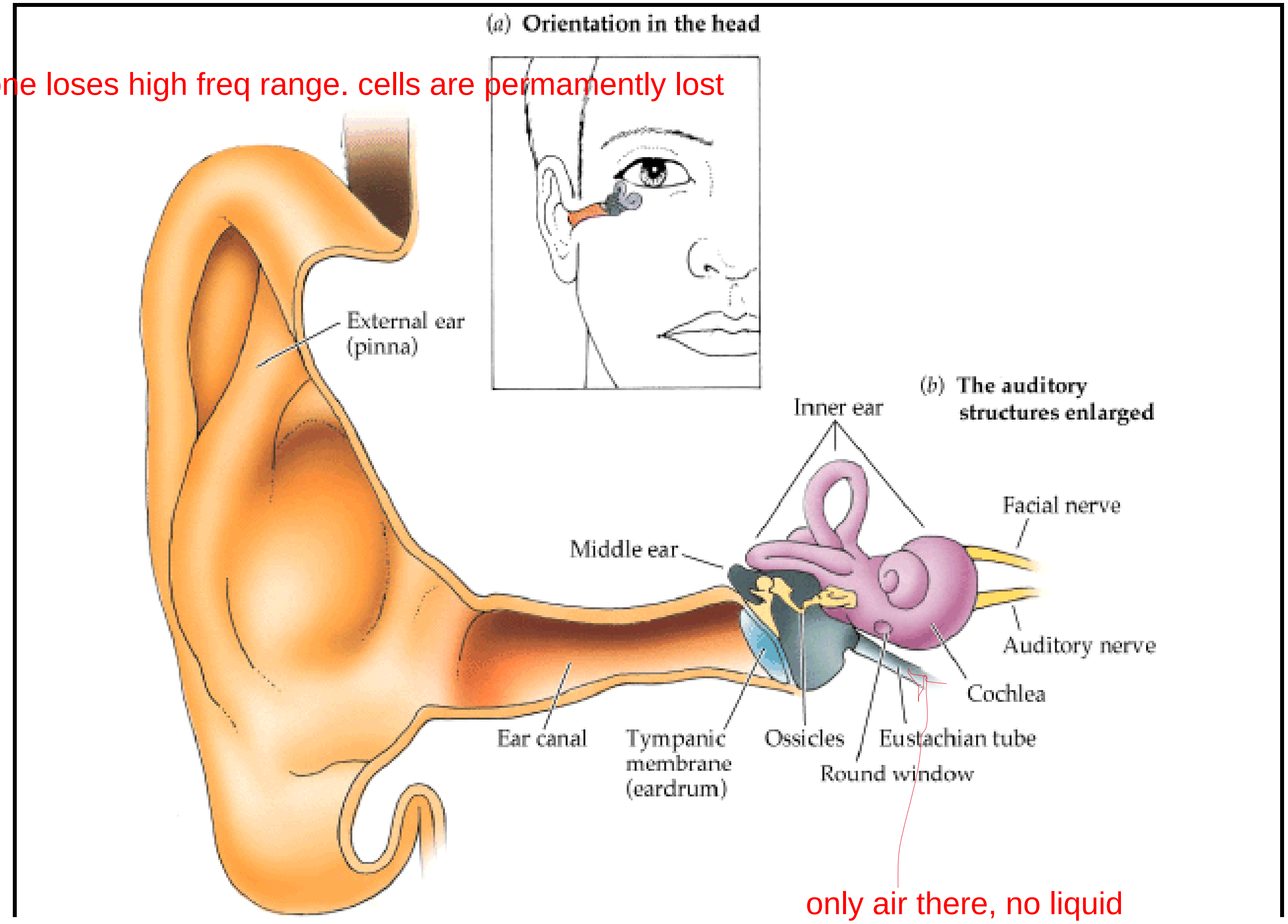
Any complex waveform can be represented as the sum of a series of sine waves of different frequencies and amplitudes

add only all (infinitely many) odd frequencies (sine waves) to obtain the square frequency

The human ear

shaped to catch language signals best, also needed to identify place of a sound

as one gets older, one loses high freq range. cells are permamently lost

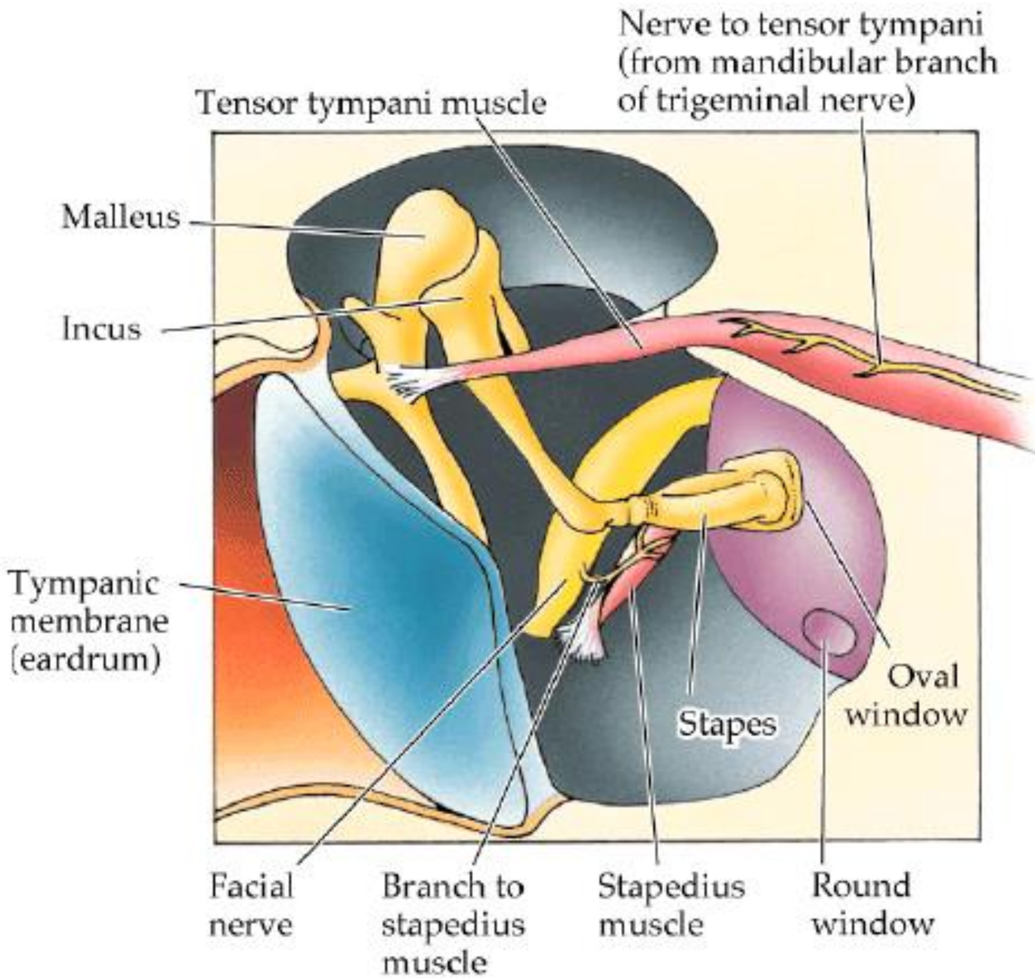


only air there, no liquid

sounds are changes in air pressure.
cochlea has a liquid inside, the ossicles match the impedance of air and liquid in cochlea, such that transduction can even happen. ossicles also play a protective role.

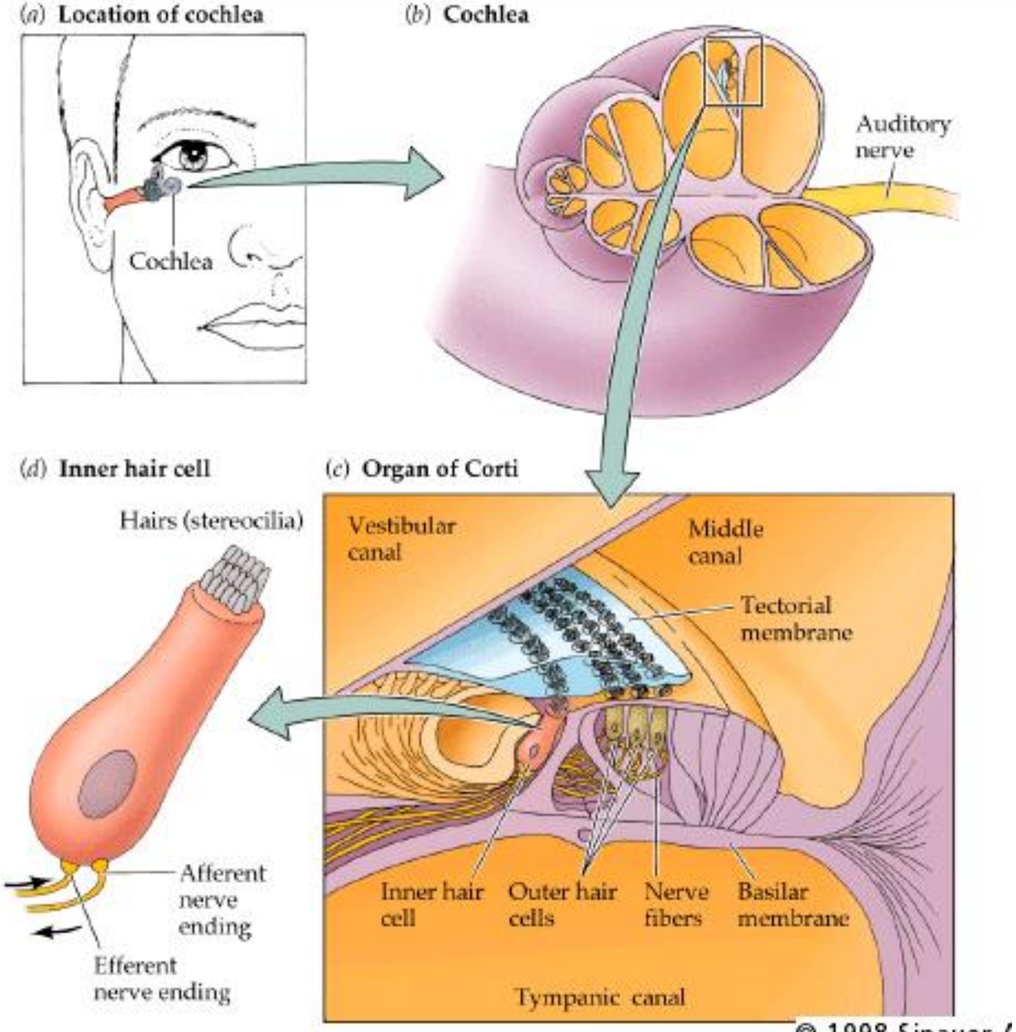
(not so interesting for us, didnt go in detail at all, mostly skipped)

The middle ear



without the liquid, actually the cochlea could be destroyed

The inner ear



depending on how the HC (cilia) is bent, it changes also the electric potential accordingly.

Tympanic membrane & ossicular system

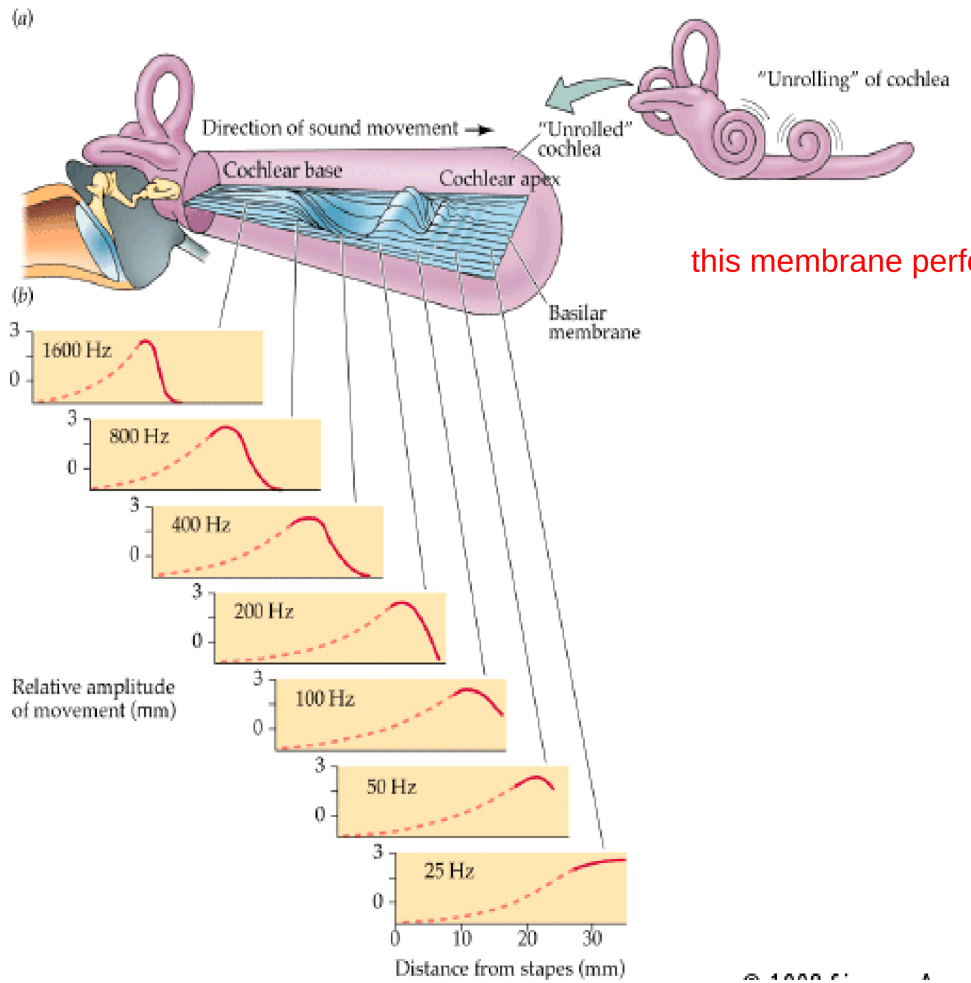
Sound stimuli pass through pinna and ext aud canal to strike TM, causing it to vibrate.

The **ossicular system** conducts sound from the TM through the middle ear to the cochlea.

The *faceplate* of the stapes pushes forward on the cochlear fluid (oval window) everytime the TM and malleus move inward.

Impedance matching is provided by the ossicular system between sound waves in air and sound vibrations in the cochlear fluid (fluid has a greater inertia than air). Most amplification occurs because the area of the TM is 17x greater than the stapes/oval window surface area.

The mechanics of the basilar membrane

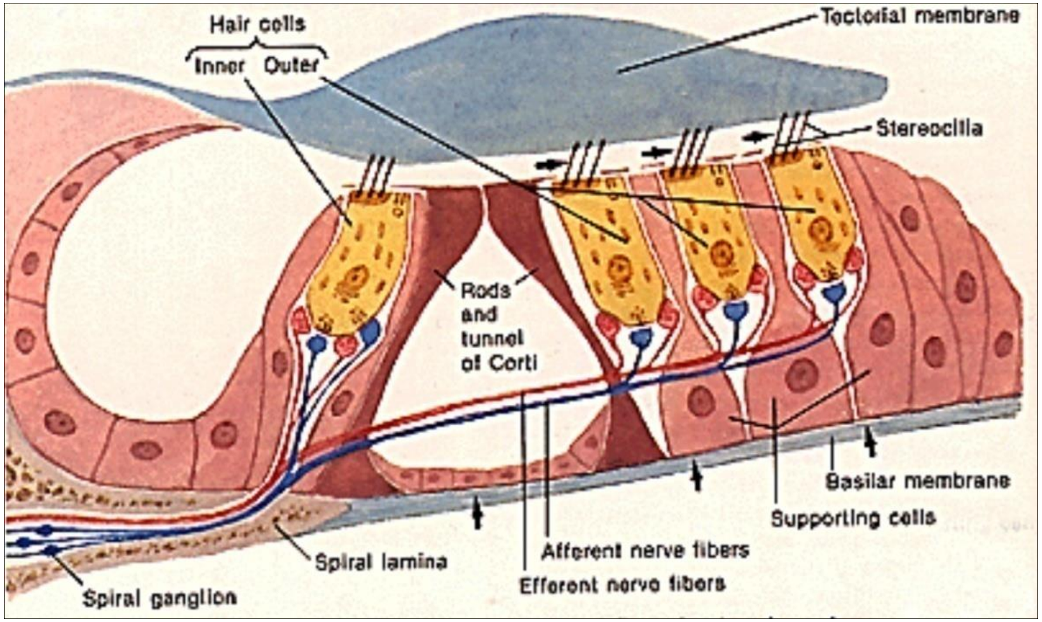


this membrane performs "fourier analysis" movement of cilia can be modulated by OHC, such that relative movements are not too big, which would cause damage to the membranes

The **organ of Corti**, which is situated on top of the basilar membrane, contains **hair (auditory receptor) cells….**

Inner hair cells - single row; provide fine **auditory discrimination**. 90% of auditory nerve fibres innervate these cells.

Outer hair cells - three rows; detect the **presence of sound.**
and also protective roles

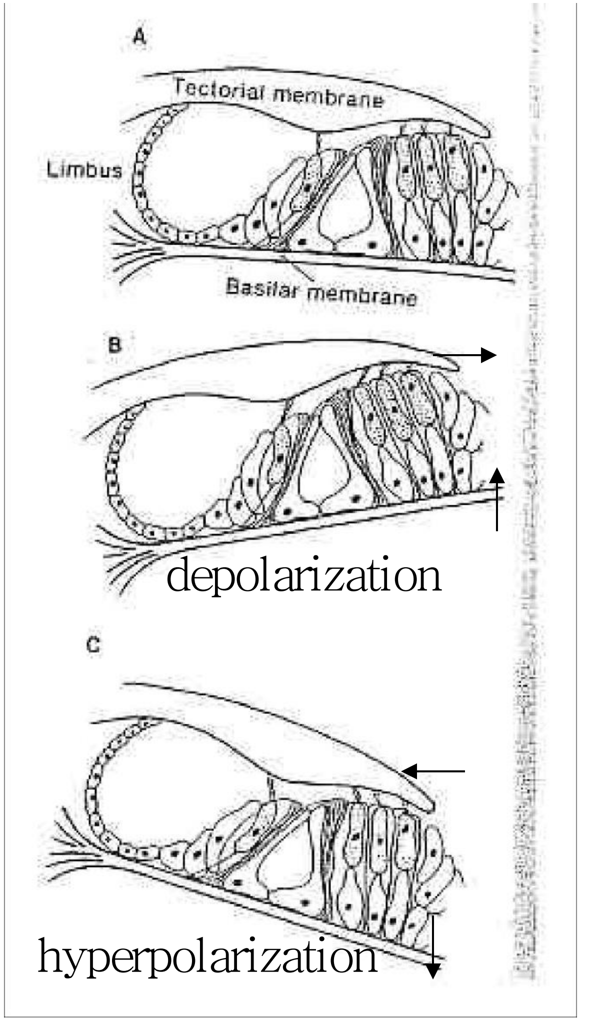


The hair cells contain **stereocilia**, which protrude into the overlying **tectorial membrane.**

…these generate **nerve impulses** in response to vibration of the basilar membrane.

Auditory transduction

The **up-and-down** motion of the basilar membrane causes the organ of Corti to vibrate up-and-down, which, in turn causes the stereocilia to bend **back-and-forth.**

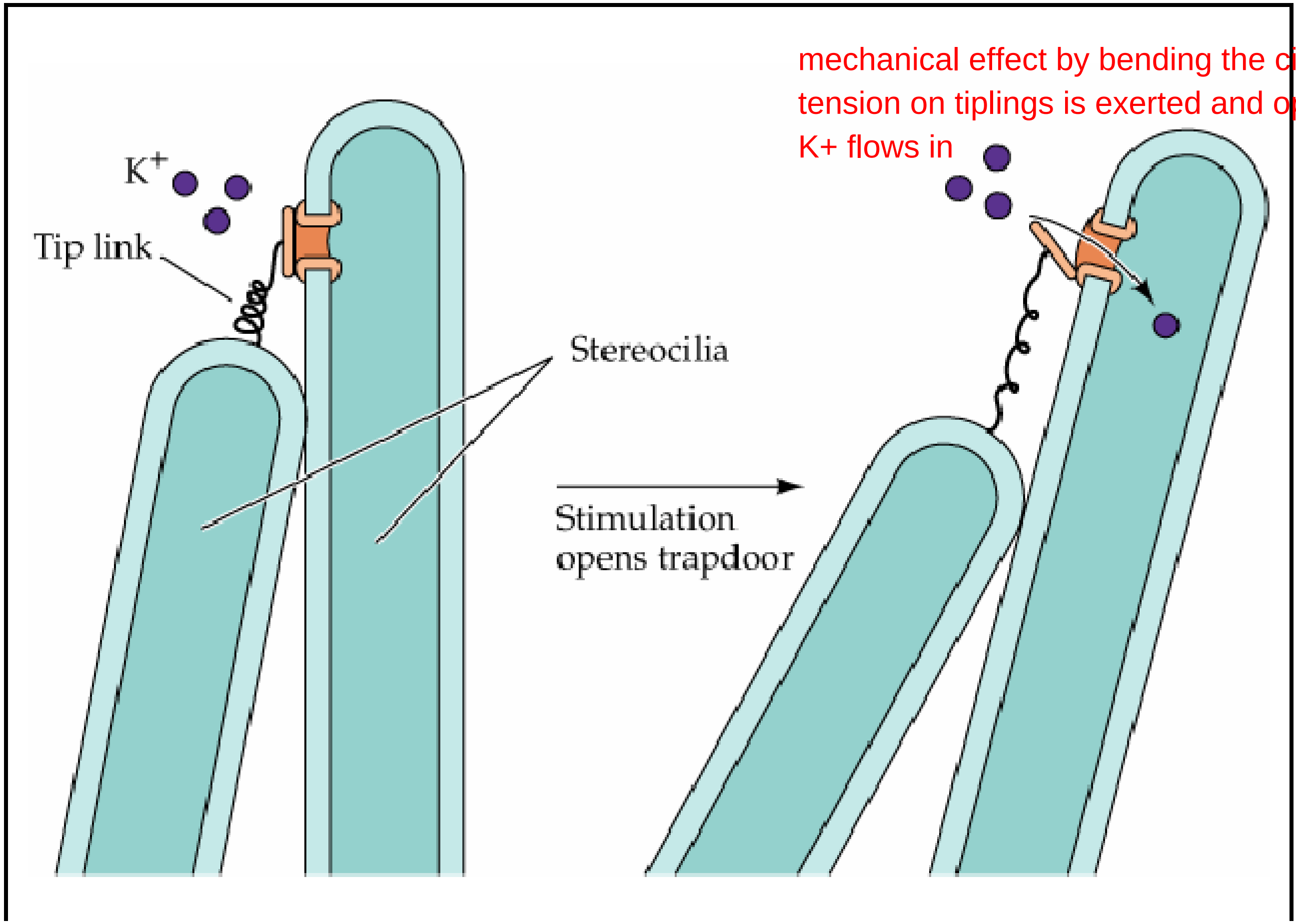


Polarization of the stereocilia

(B) When the organ of Corti moves **upward**, the stereocilia bend **away** from the limbus and they **depolarize**.

(C) When the organ of Corti moves **downward**, the stereocilia bend **toward** the limbus and they **hyperpolarize**.

Transduction at hair cells



mechanical effect by bending the cilia, mechancal tension on tiplings is exerted and opens the channel and K+ flows in

Auditory transduction

Receptor potential. The hair cells are depolarized by the movement of K+ ions into the cell:

1. The **endolymph** contains a high K+ and is **electrically positive.** The **hair cells** also contain a high K+ but are **electrically negative** (Na/K pumps). Hence driving force for **K+ into cells.**

2. When the **stereocilia bend away** from the limbus, they cause K channels to **open.** K+ then flows into the cell and the **hair cell depolarizes.**

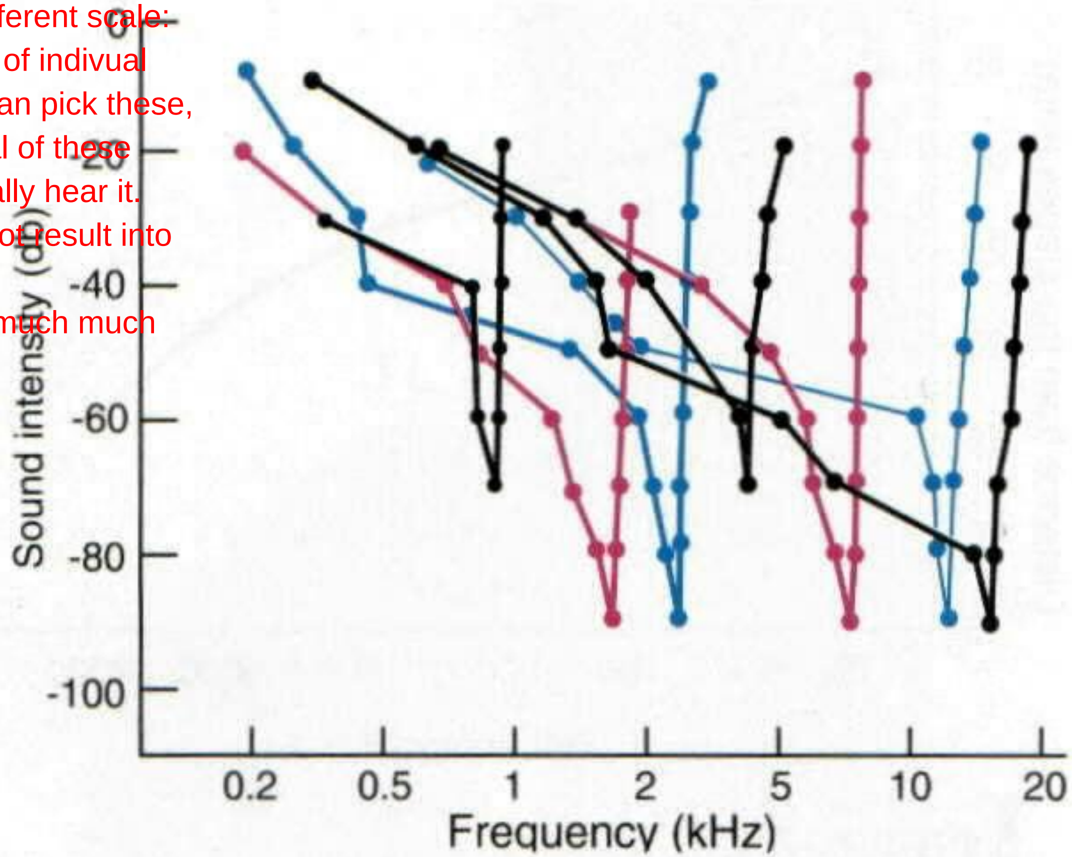
3. When the **stereocilia bend towards** the limbus, they cause K channels to **close** and the **hair cell hyperpolarizes.**

Auditory transduction

Release of synaptic transmitter

1. When the hair cell depolarizes, a Ca channel opens, allowing **calcium** to enter the cell. Calcium initiates the release of synaptic transmitter, which stimulates the auditory nerve fiber.
2. The cell bodies of the auditory nerve fibers are located within the **spiral ganglion**. Their axons join those from the vestibular apparatus to form the **vestibulocochlear nerve**.

y axis has a completely different scale:
they measured the activity of indivual
nerve fibers. the cochlea can pick these,
but a human needs several of these
active nerve fibers to actually hear it.
a single nerve fiber does not result into
a conscious experience.
theoretically, we could be much much
more sensitive to sounds



Tuning curves of single units in the cochlear nerve. dB = decibel; kHz = kilohertz (1000 Hz).

(From Katsuki, Y. in *Sensory Communication*, edited by W.A. Rosenblith. Copyright 1961 by MIT Press.)

Encoding

1. Place principle of *f* determination. The *f* of a sound that activates a particular hair cells depends on the location of the hair cell along the basilar membrane. This spatial organization is maintained all the way to the cerebral cortex.

The auditory cortex shows that specific brain neurons are activated by specific sound *f*. **(tonotopic organization)**

2. Volley principle of *f* determination. Low *f* are discriminated by firing of the auditory nerve fibers at the same *f* as the sound wave.

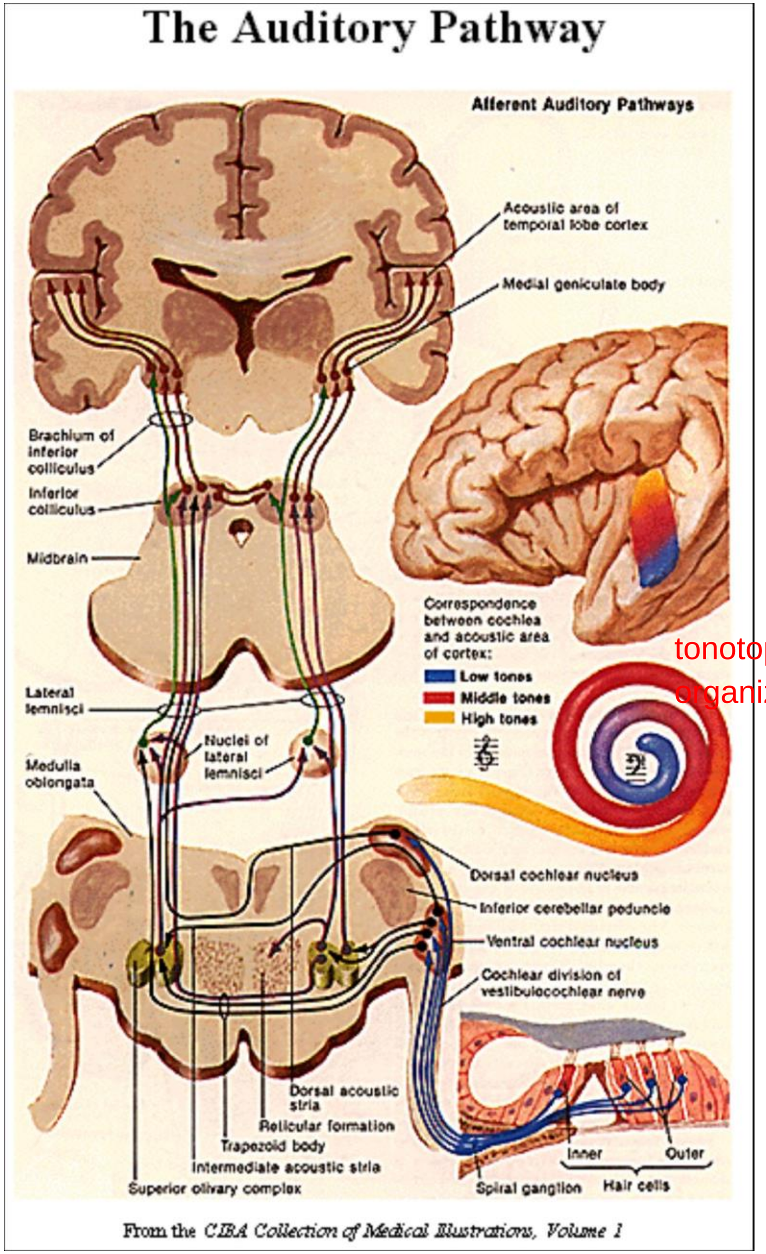
3. Loudness. As the amplitude of vibration increases, a larger proportion of the basilar membrane vibrates, causing more and more of the hair cells to move. This leads to **spatial summation** of impulses and transmission through a greater number of nerve fibers.

Signals from both ears are transmitted to both sides of the brain, with preponderance to contralateral pathway.

Many collateral fibers to RAS of brain stem (loud sound)

Tonotopic organization is maintained from cochlea to auditory cortex. Where high *f* sounds excite neurons at one end, whereas low *f* sounds excite neurons at the opposite end.

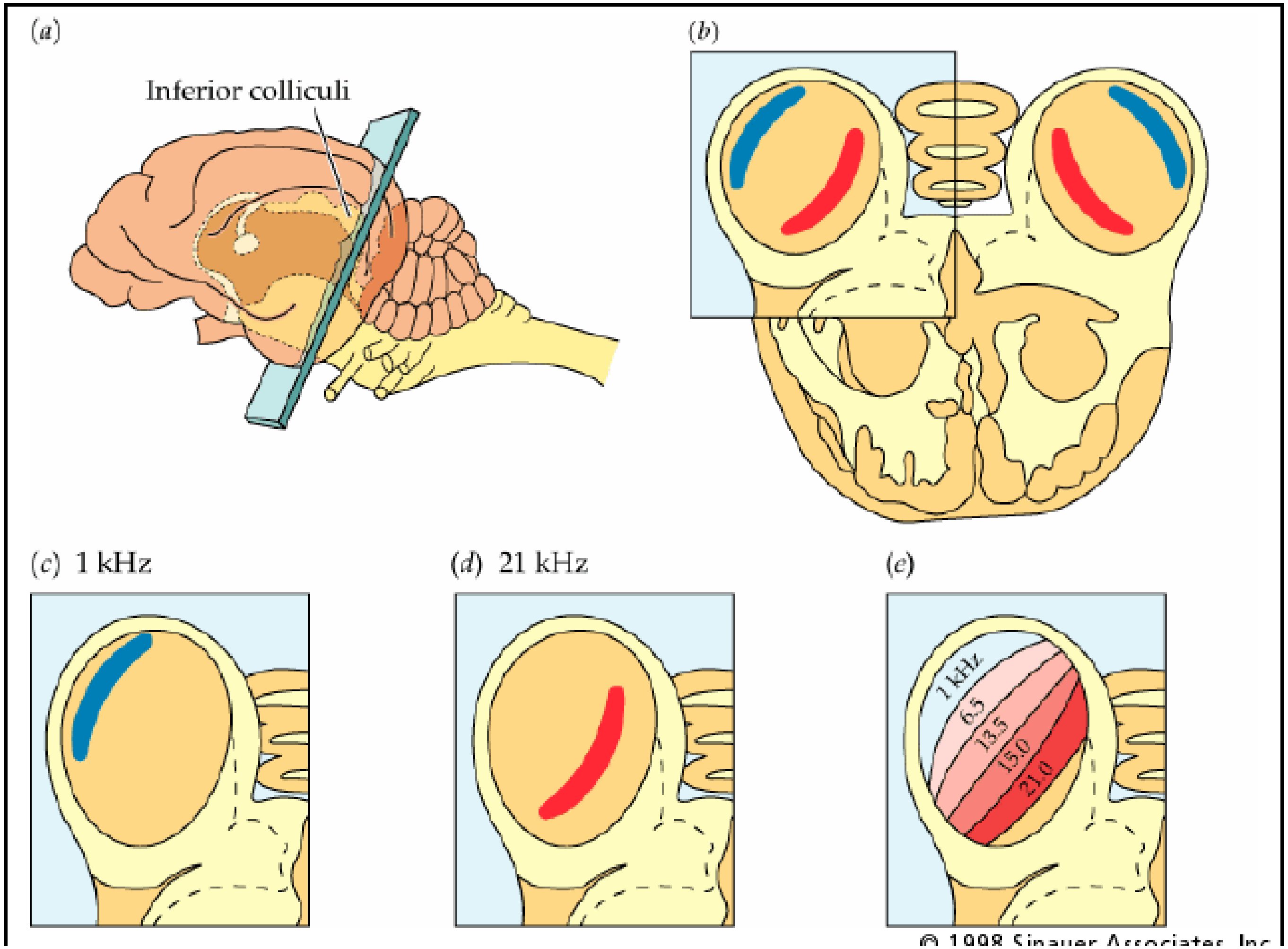
The 1 aud cortex is excited by the MGN, whereas the aud association areas are excited secondarily by impulses from the 1 aud cortex.



tonotopic organization

differences is in the range of microseconds

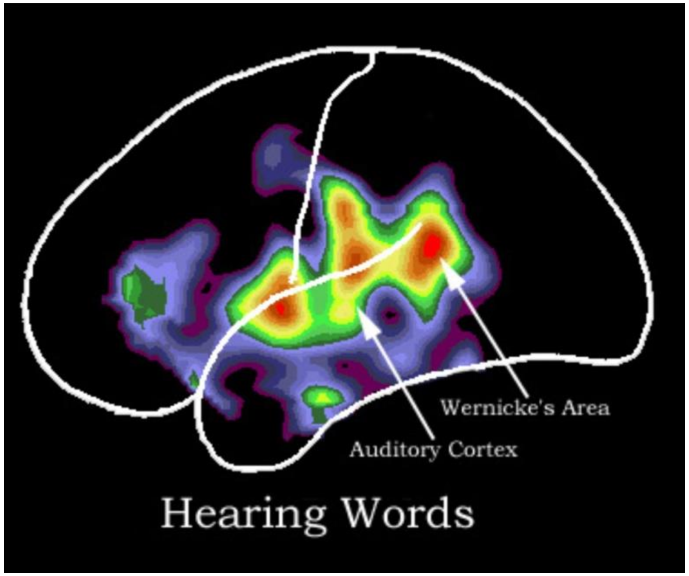
Tonotopic organization



aphasia: trouble understanding or producing language

Discrimination of “sound patterns” by the 1& 2 auditory cortex.
Destruction of both (but not one) 1 aud cortices will reduce greatly one’s sensitivity to hearing.

Interpretation of the *meanings and sequence of sound tones* in the auditory signals - 2 aud cortex .



Physiology and psychophysics

- Cochlea performs mechanical spectral analysis of sound signal
- Pure tone induces traveling wave in basilar membrane.
  - maximum mechanical displacement along membrane is function of frequency (place coding)
- Displacement of basilar membrane changes with compression and rarefaction (frequency coding)

Perception of pitch

- Along the basilar membrane, hair cell response is tuned to frequency
  - each neuron in the auditory nerve responds to acoustic energy near its preferred frequency
  - preferred frequency is place coded along the cochlea. Frequency coding believed to have a role at lower frequencies
- Higher auditory centers maintain frequency selectivity and are ‘tonotopically mapped’

- Pitch is related to frequency for pure tones.
- For periodic or quasi-periodic sounds the pitch typically corresponds to inverse of period
- Some have no perceptible pitch (e.g. clicks, noise)
- Sounds can have same pitch but different spectral content, temporal envelope … *timbre*

timbre: combination of different frequencies - same note does not sound the same in different instruments.each insturment produces many different freq. there is a dominating pitch, but there are side freq that also influence the final experience of that sound and therefore they shape the final outcome, even if the same note is played on both instruments

Perception of loudness

- Intensity is measured on a logarithmic scale in decibels
- Range from threshold to pain is about 120 dB-SPL
- Loudness is related to intensity but also depends on many other factors (attention, frequency, harmonics, …)

Spatial hearing

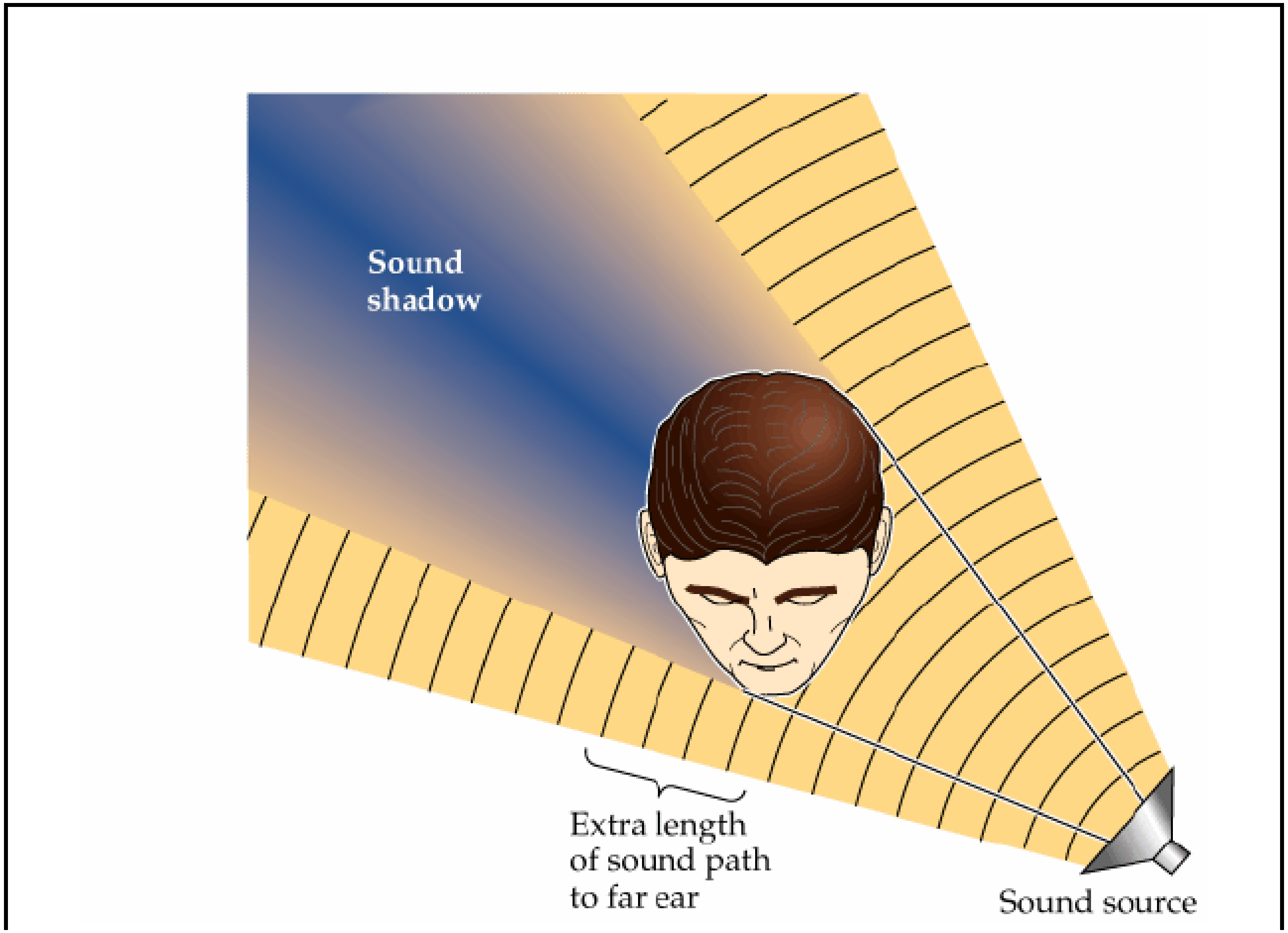
- Auditory events can be perceived in all directions from observer
- Auditory events can be localized internally or externally at various distances
- Audition also supports motion perception
  - change in direction
  - Doppler shift

during a party, we can focus to some conversation and ignore all others and only listen to that conservation

Cocktail party effect

- In environments with many sound sources it is easier to process auditory streams if they are separated spatially
- Spatial sound techniques can help in sound discrimination, detection and speech comprehension in busy immersive environments

Auditory localization - sources of information

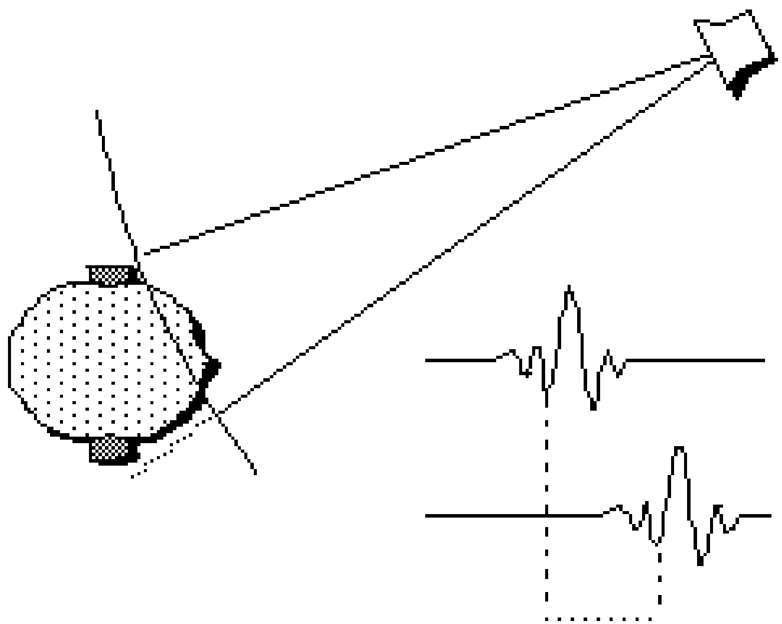


Spatial Auditory Cues

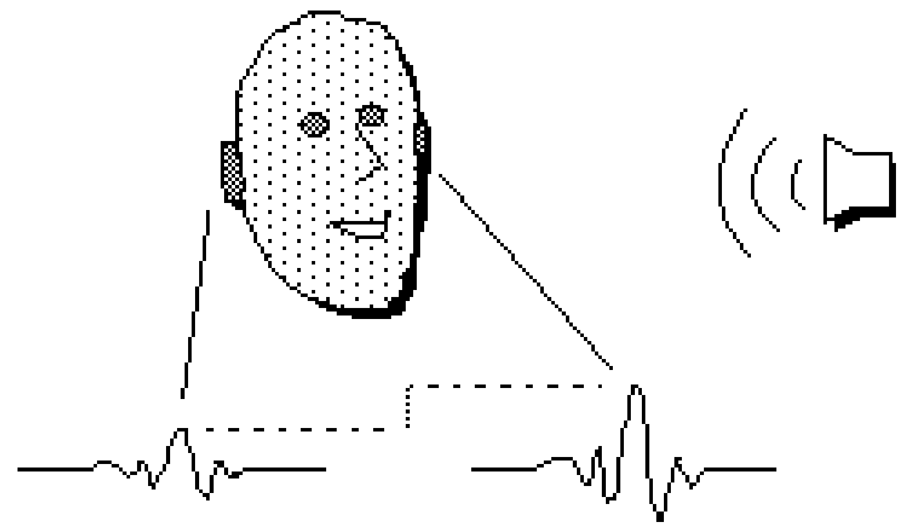
- Two basic types of head-centric direction cues
  - binaural cues
  - spectral cues

Binaural Directional Cues

- When a source is located eccentrically it is closer to one ear than the other
  - sound arrives later and weaker at one ear
  - head ‘shadow’ also weakens sound arrive at opposite ear
- Binaural cues are robust but ambiguous



interaural time difference (ITD)



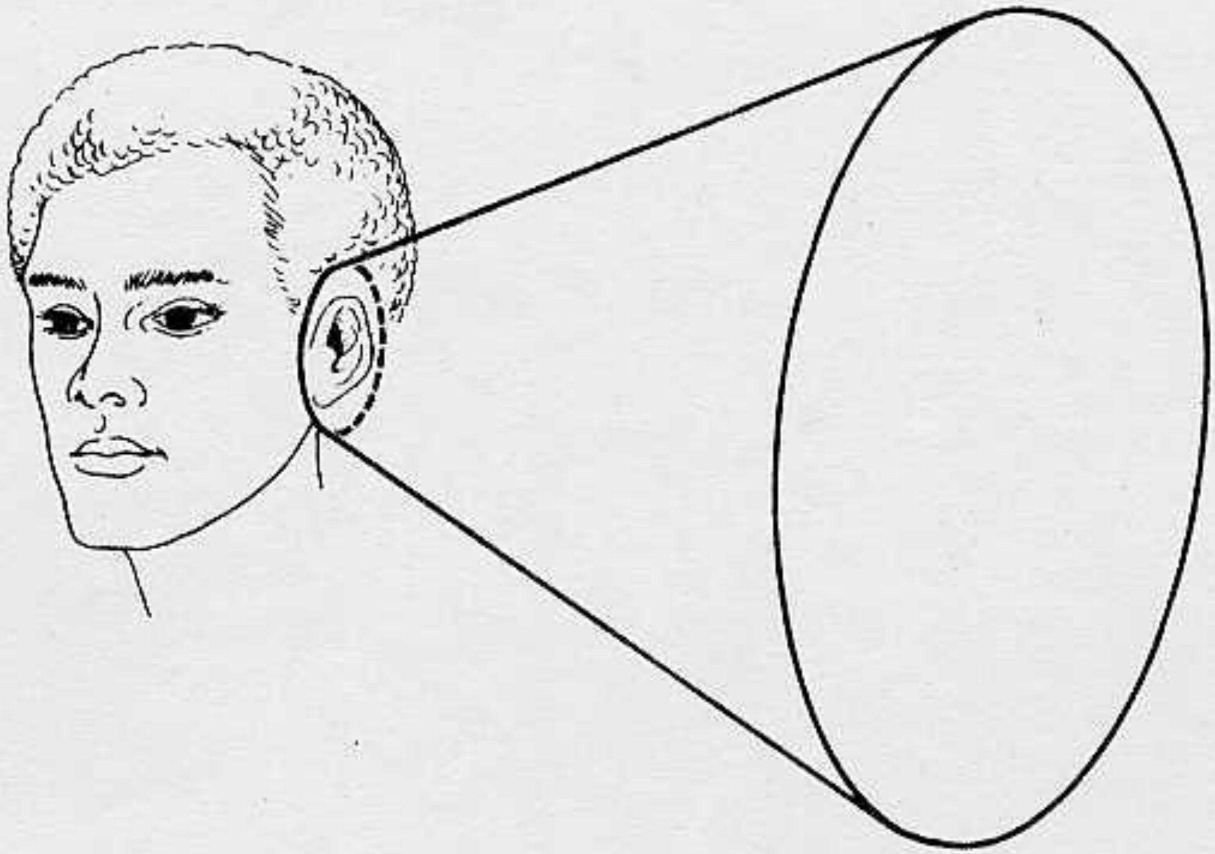
interaural intensity difference (IID)

- Interaural time differences (ITD)
  - ITD increase with directional deviation from the median plane. It is about 600 μs for a source located directly to one side.
  - Humans are sensitive to as little as 10 μs ITD. Sensitivity decreases with ITD.
  - For a given ITD, phase difference is linear function of frequency
  - For pure tones, phase based ITD is ambiguous

- At low to moderate frequencies phase difference can be detected. At high frequencies can use ITD in signal envelope.
- ITD cues appear to be integrated over a window of 100-200ms (binaural sluggishness, Kollmeier & Gillkey, 1990)

- Interaural intensity differences (IID)
  - With lateral sources head shadow reduces intensity at opposite ear
  - Effect of head shadow most pronounced for high frequencies.
  - IID cues are most effective above about 2000 Hz
  - IID of less than 1dB are detectable. At 4000 Hz a source located at 90° gives about 30 dB IID (Matlin and Foley, 1993)

Ambiguity and Lateralization



The "cone of confusion." Without moving the head, it is difficult to localize tones originating

Ambiguity and Lateralization

- These binaural cues are ambiguous. The same ITD/IID can arise from sources anywhere along a ‘cone of confusion’
- Spectral cues and changes in ITD/IID with observer/object motion can help disambiguate
- When directional cues are used in headphone systems, sounds are *lateralised* left versus right but seem to emanate from inside the head (not localised)

- also for near sources (less than 1 m) there is significant IID due to differences in distance to each ear even at lower frequencies (Shinn-Cunningham et al 2000)
- Intersection of these ‘near field’ IID curves with cones of confusion constrains them to toroids of confusion

Spectral Cues

- Pinnae or outer ears and head shadow each ear and create frequency dependent attenuation of sounds that depend on direction of source
- Pinnae are relatively small, spectral cues are effective predominately at higher frequencies (i.e. above 6000 Hz)

- Direction estimation requires separation of spectrum of sound source from spectral shaping by the pinnae
- Shape of the pinnae shows large individual differences which is reflected in differences in spectral cues