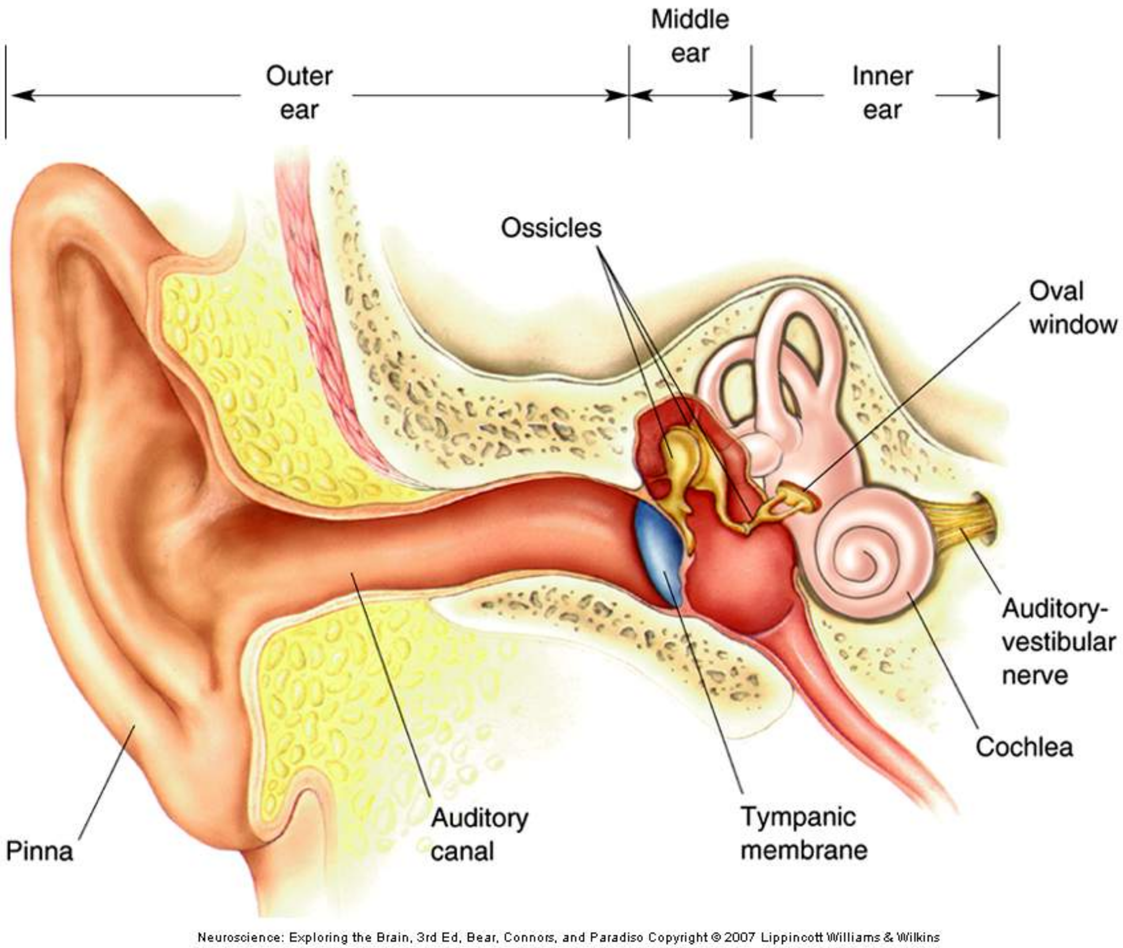
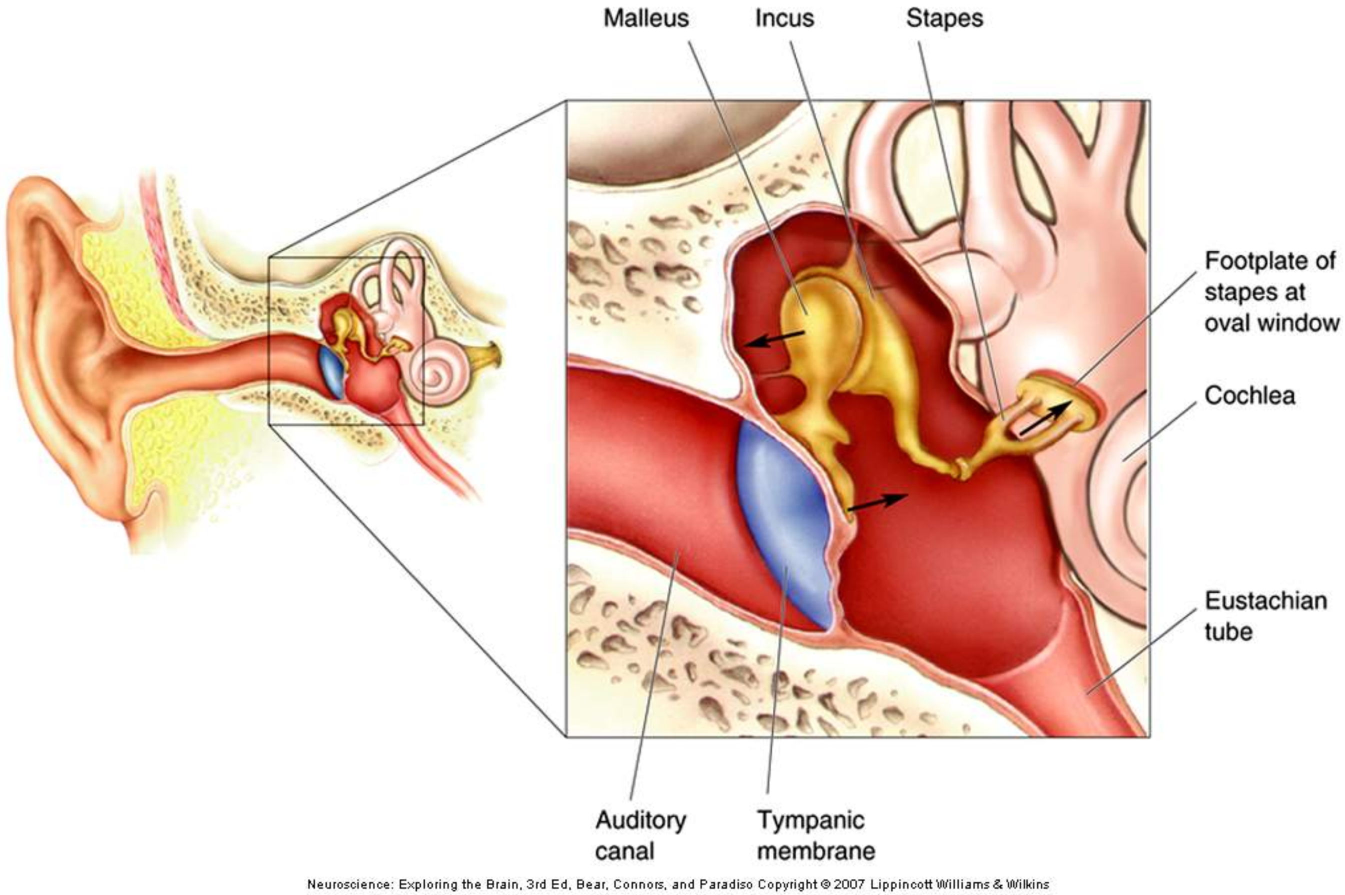
Hearing

Outer ear



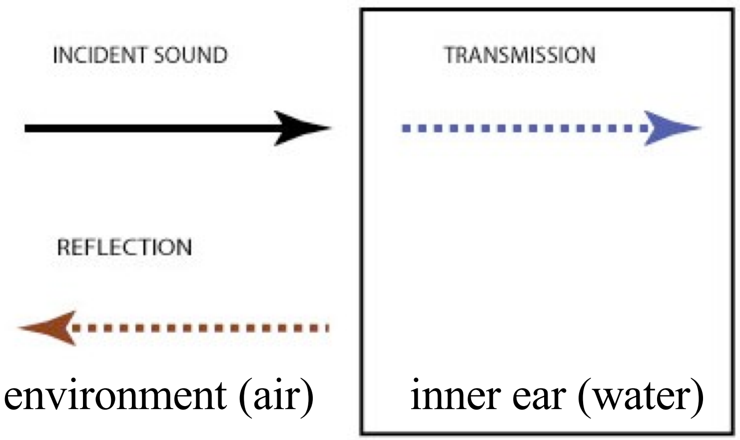
The ear has three functional parts. The main part of the external ear, the auricle, captures sound efficiently and sends it into the ear canal. Our capacity to localize sounds in space, especially along the vertical axis, depends critically upon the sound - gathering properties of the external ear.

Middle ear



Middle ear transmits mechanical energy to the ear's receptive organ. The three tiny ossicles, or bones: the malleus, or hammer; the incus, or anvil; and the stapes, or stirrup pass the motions of the tympanic membrane (eardrum) to the oval window – the bony covering of the cochlea.

Reflection and transmission at the eardrum



Amplitude reflection and transmission coefficients:

$$r_{12} = \frac{B}{A} = \frac{Z_1 - Z_2}{Z_1 + Z_2}$$

$$t_{12} = \frac{C}{A} = \frac{2Z_1}{Z_1 + Z_2}$$

Energy reflection and transmission coefficients:

$$R = r^2$$

$$T = t^2$$

Z – mechanical impedance (= ρv)
ρ - density
v – wave propagation speed

Reflection and transmission at the eardrum

$\rho_{air} = 1.21\ kg/m^3$
$v_{air} = 340\ m/s$

$\rho_{water} = 10^3\ kg/m^3$
$v_{water} = 1480\ m/s$

This values yield energy reflection and transmission coefficients:

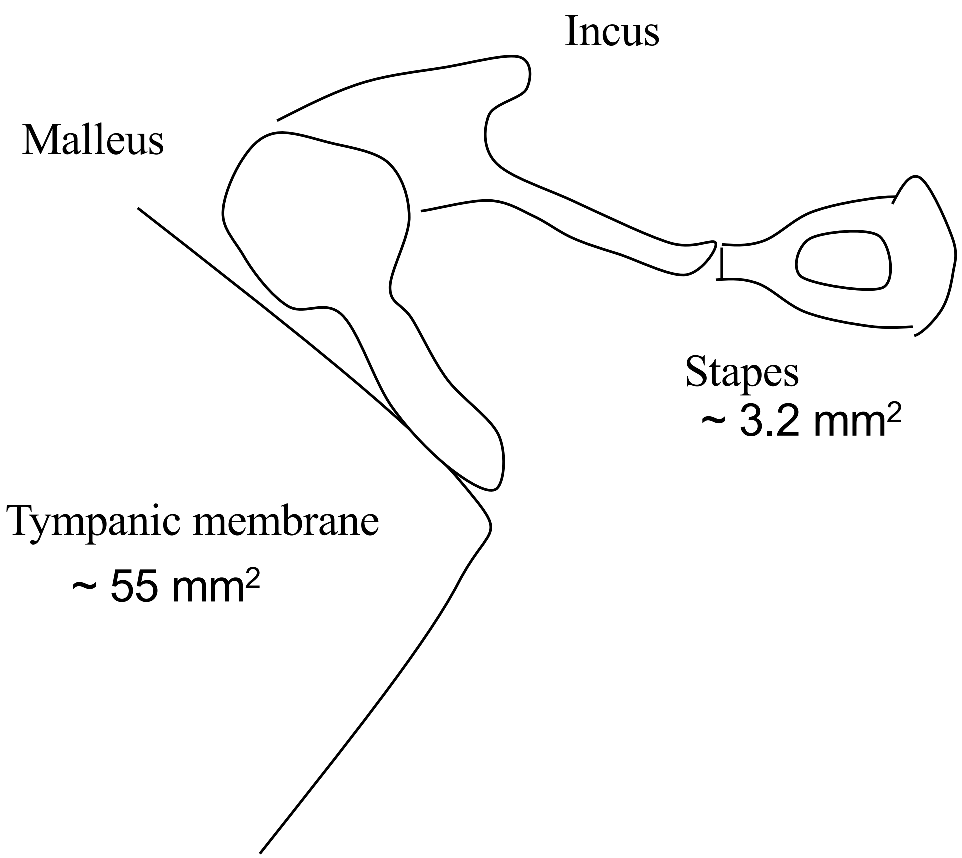
$T = 1 - R = 0.0011$ 0.1% energy transmitted
$R = 0.9989$ ~99.9% is reflected

If only 1 part in 1000 makes it through, the loss is:

$10\log_{10} 1/1000 = -30\ dB$

The middle ear

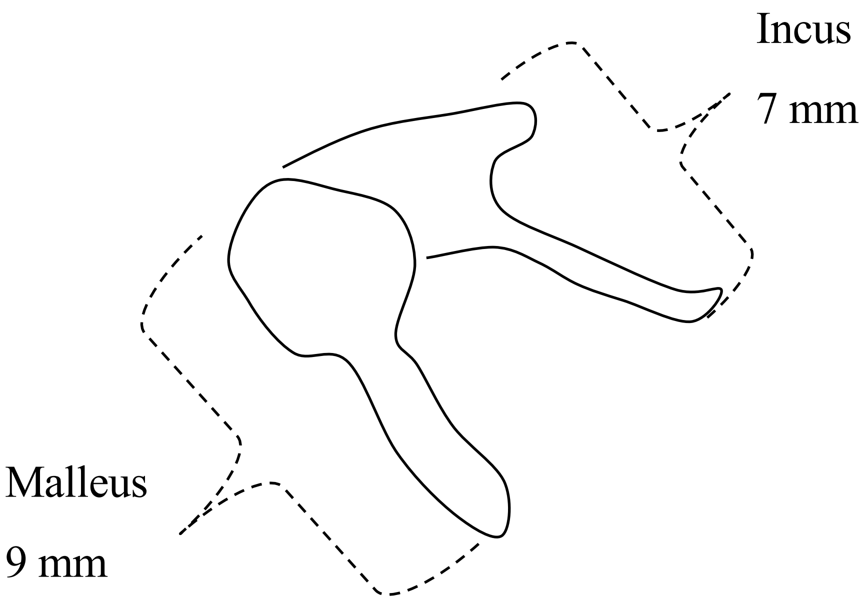
Purpose of the bones in the middle ear is to serve as amplifying system for the transmission of the eardrum vibrations towards the inner ear.



p = F/S, hence area ratio about 17:1 gives 17-fold sound pressure increase. It represents an increase in decibels of:

$$20\log_{10}17/1 = 25\text{dB}$$

The middle ear



Malleus/Incus length ratio is 9:7 so force and hence the pressure is increased by 1.3:1

Sound pressure level increase is approximately:

$20\log_{10}9/7 = 2$ dB

Eardrum displacement at threshold of hearing

$$\Psi(x,t) = A\cos(kx - \omega t)$$

Acoustic travelling wave

$$\Delta E = 2\frac{1}{2}\rho \Delta x S\left(\frac{\partial \Psi}{\partial t}\right)^2 = \rho \Delta x S A^2 \omega^2 \sin^2(kx - \omega t)$$

Total wave energy

($E_{pot} = E_{kin}$)

$$I = \left\langle \frac{dE}{dtS} \right\rangle = \frac{\rho v dt S A^2 \omega^2}{dtS} \left\langle \sin^2(kx - \omega t) \right\rangle = \frac{1}{2}\rho v A^2 \omega^2$$

Wave intensity

$$I = I_0 = 10^{-12} \ \mathrm{W/m^2}$$

Wave intensity at the threshold of hearing 0 dB

$$A = \frac{1}{2\pi\nu}\sqrt{\frac{2I}{\rho v}}$$

Wave amplitude

$$A = \frac{1}{2764}\sqrt{\frac{2*10^{-12}}{1.29*340}} = 1.26*10^{-11} \ \mathrm{m}$$

Wave amplitude at 440 Hz

$$D = 1.06*10^{-10} \ \mathrm{m}$$

Hydrogen atom diameter

The eardrum displacement at threshold of hearing is ~ 1/10 the diameter of a hydrogen atom!

The threshold of hearing

At a threshold of 3000 Hz (the frequency to which we are most sensitive – important for speech) the eardrum displacement is about one tenth of the diameter of a single hydrogen atom.

In a very quiet setting, blood can actually be heard flowing through the vessels near the ear. If ears were much more sensitive, we would be hearing noise generated by air molecules colliding with the eardrum.

A threshold vibration deflects auditory receptors in an inner ear (stereocilia) through an angle of only about 0.003 degree. Bending the Empire State Building (380 m) through such an angle would deflect its top by less than 2.5 cm.

From this threshold we can hear over a 10 million–fold range of sound pressure levels before sounds become painfully loud. Because it is cumbersome to keep track of all the zeros in such large numbers, a logarithmic decibel scale was introduced.

Sound Intensity and Sound Pressure Levels

Human ear responds to sound intensities in the range of 10^{-12}– 10^{0} W/m^2. Sound intensity level is defined as:

$$\beta = (10dB)\log\frac{I}{I_0}$$

where:

β – sound intensity level

I – sound intensity

I_0 – standard reference sound intensity 10^{-12} W/m^2

In such scale 10-fold increase in sound intensity, gives 10 dB increase in sound volume (intensity level).

Sound pressure level (SPL) or sound level is a logarithmic measure of the effective sound pressure of a sound relative to a reference value:

$$L = (20dB)\log\frac{p}{p_0}$$

Sound Intensity and Sound Pressure Levels

Intensity	dB	Pressure	Examples
10^8 W/m^2	200	$2*10^5$ Pa	Volcano erruption
10^2 W/m^2	140	$2*10^2$ Pa	Jet aircraft, 50 m
1 W/m^2	120	$2*10^1$ Pa	Rock concert
10^{-2} W/m^2	100	2 Pa	Disco, 1m from the speaker
10^{-4} W/m^2	80	$2*10^{-1}$ Pa	Highway, 5 m
10^{-6} W/m^2	60	$2*10^{-2}$ Pa	Speech, 1 m
10^{-8} W/m^2	40	$2*10^{-3}$ Pa	Background in quiet library
10^{-10} W/m^2	20	$2*10^{-4}$ Pa	Background in TV studio
10^{-12} W/m^2	0	$2*10^{-5}$ Pa	Hearing threshold

Threshold of pain 130 dB

Discomfort threshold, hearing damage possible 120 dB

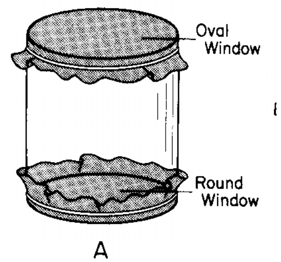
EU sound limit of music players and mobile phones 85 dBA

Sound Intensity and Sound Pressure Levels

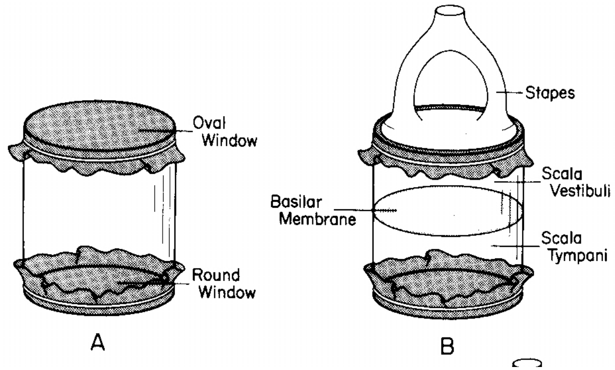
A-weighted decibels, abbreviated dBA, or dBa, or dB(a), are an expression of the relative loudness of sounds in air as perceived by the human ear. Low and very high frequencies are given less weight than on the standard decibel scale. This correction is made because the human ear is less sensitive at very high and low audio frequencies. In computer systems, dBA is often used to specify the loudness of the fan used to cool the microprocessor. Many regulatory noise limits are specified in terms of dBA, based on the belief that dBA is better correlated with the relative risk of noise-induced hearing loss.

Sound intensity monitoring in Hydrozagadka club in Warsaw

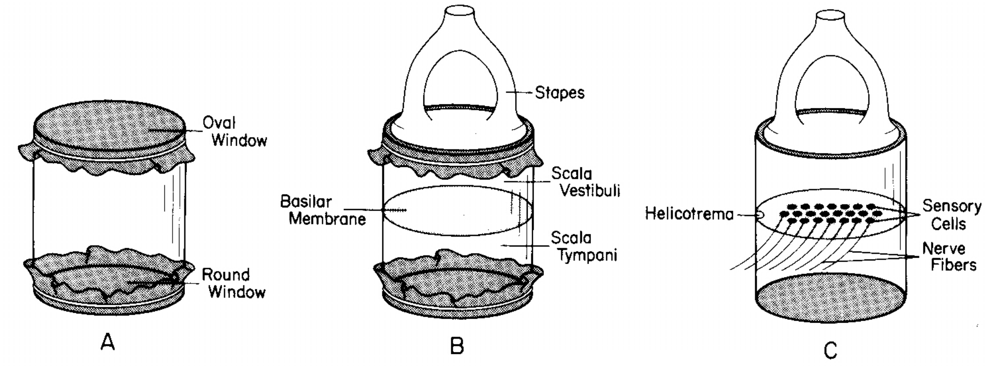
Building a cochlea



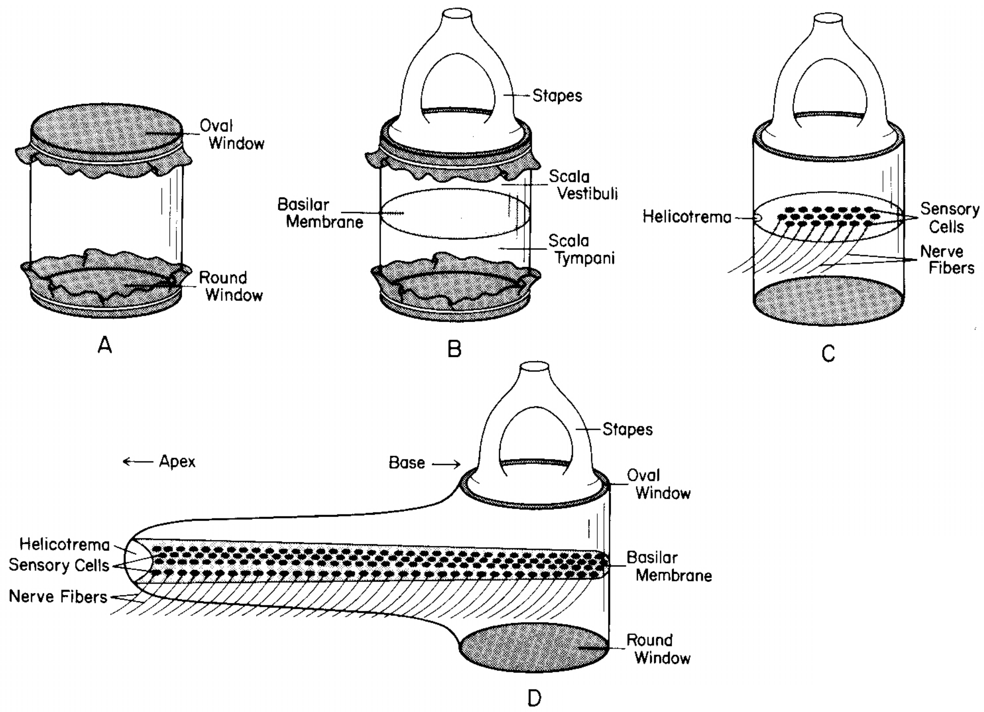
Building a cochlea



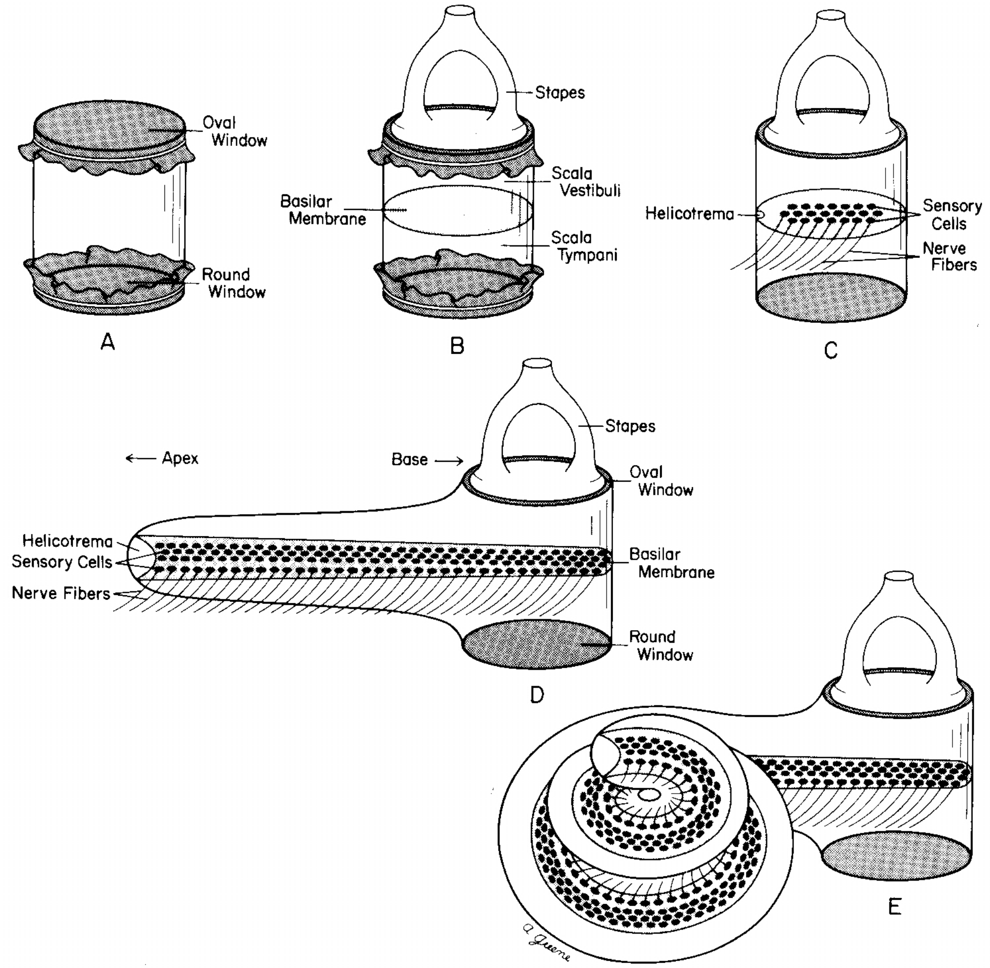
Building a cochlea



Building a cochlea

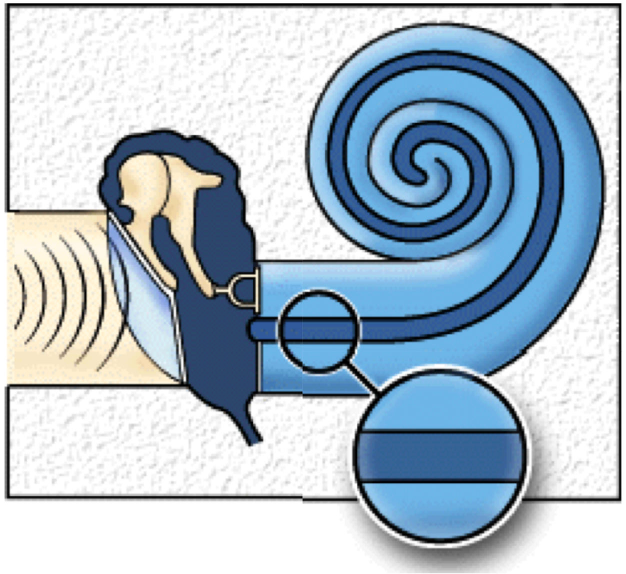


Building a cochlea

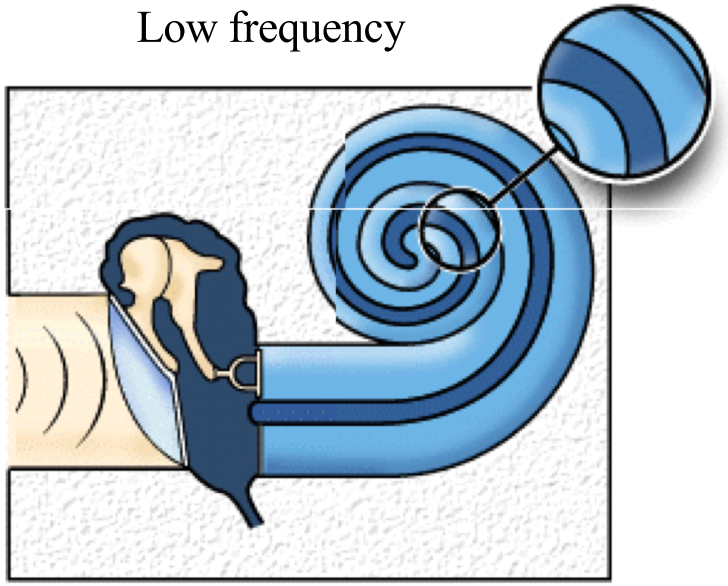


How cochlea works?

High frequency

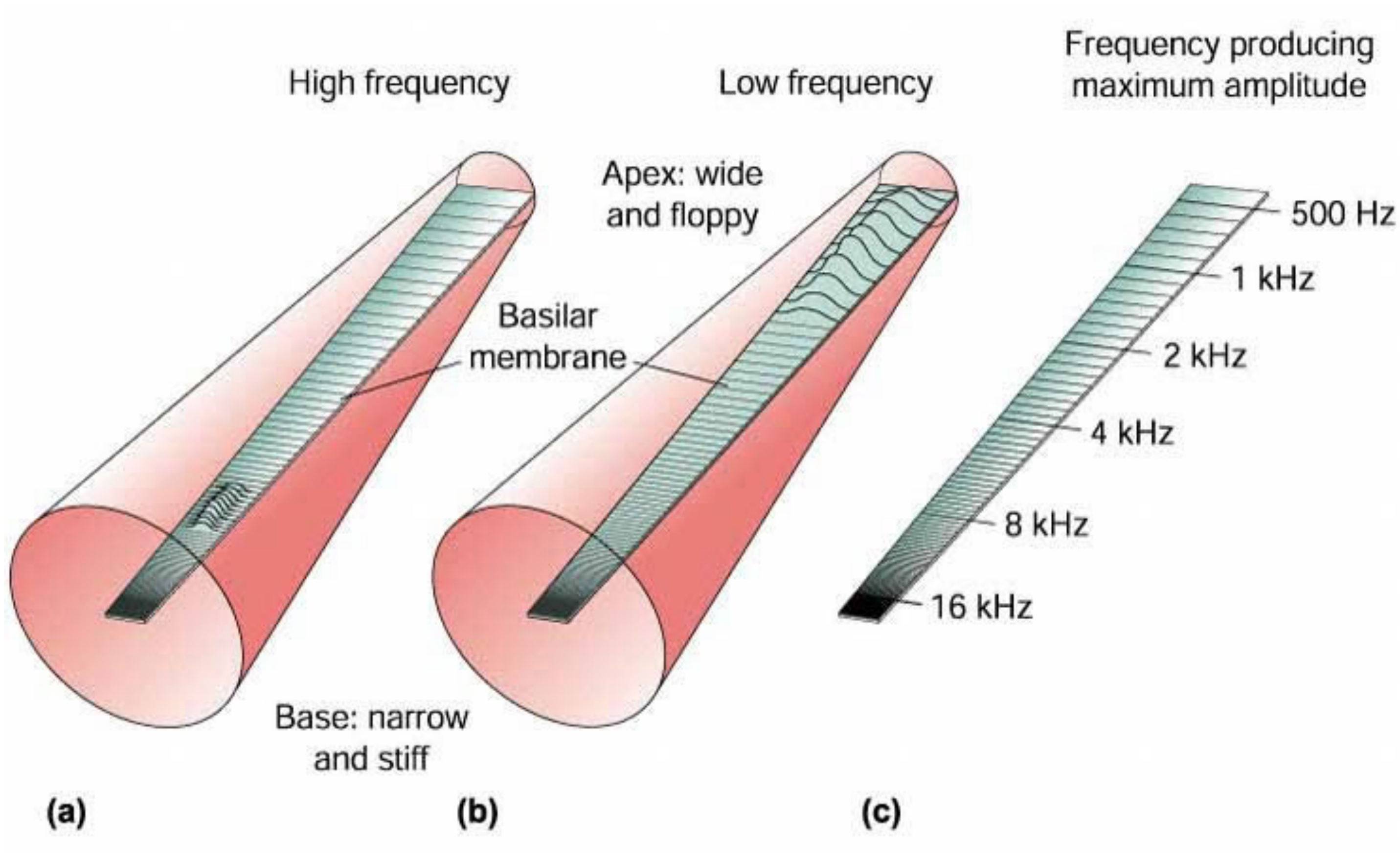


Low frequency



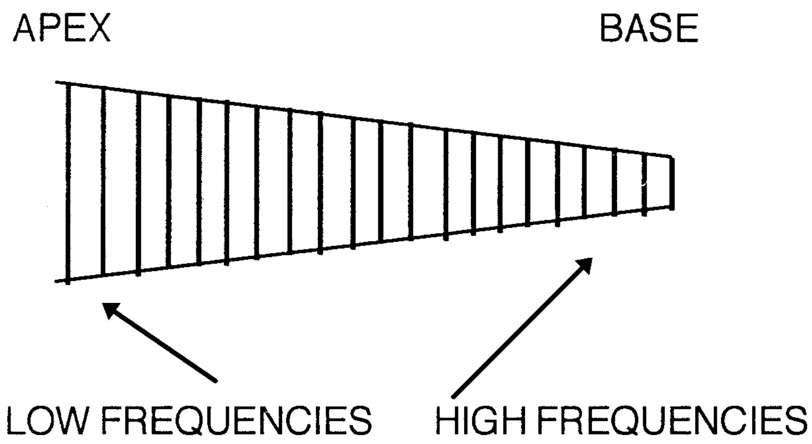
Cochlea in the inner ear is shaped like a snail shell. It contains inner ear fluid which moves in response to the vibrations coming from the middle ear. Cochlea's spiral shape effectively boosts the strength of the vibrations caused by sound, especially for low frequencies.

Cochlea and basilar membrane



Cochlea contains basilar membrane, which is narrow at the base and widens at the tip. Different frequencies are coded by the position along the membrane – high frequencies displace the membrane at the base, low frequencies displace the membrane at the apex.

Helmholtz's resonance theory of hearing



$$\Psi(x,t) = (A\sin kx + B\cos kx)\cos(\omega t + \varphi)$$

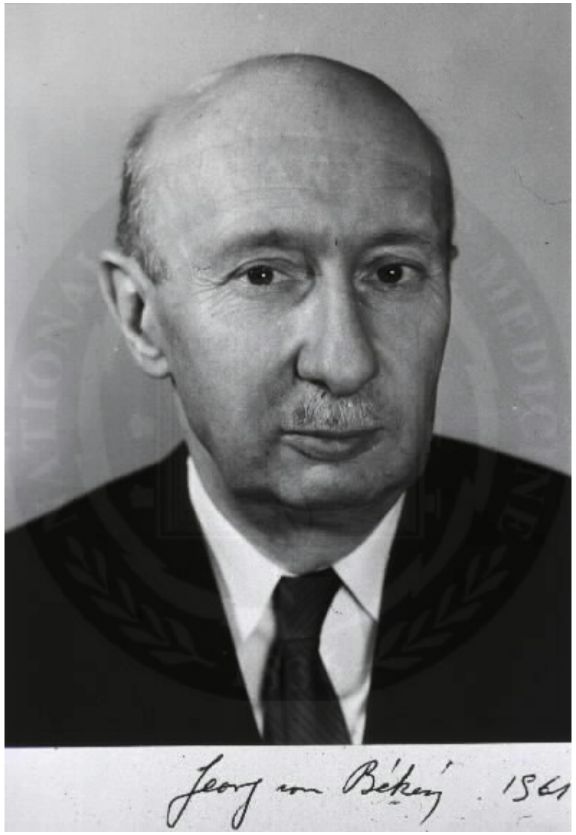
$$\Psi(0,t) = 0 \Rightarrow B = 0$$

$$\Psi(L,t) = 0 \Rightarrow kL = \pi$$

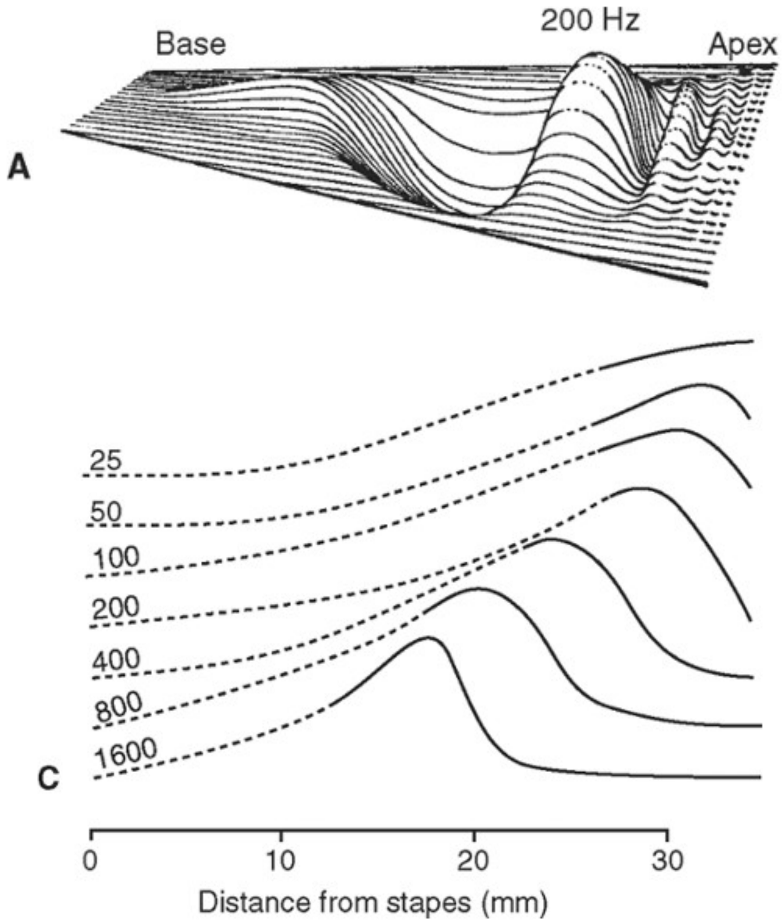
$$\omega = kv = \frac{\pi v}{L}$$

Different frequencies of sound are encoded by their precise position along the basilar membrane. Short strings at the base would resonate in response to high notes, and the long strings (at the apex) to low notes.

The travelling wave theory - Von Bekesy (1928). Nobel 1961



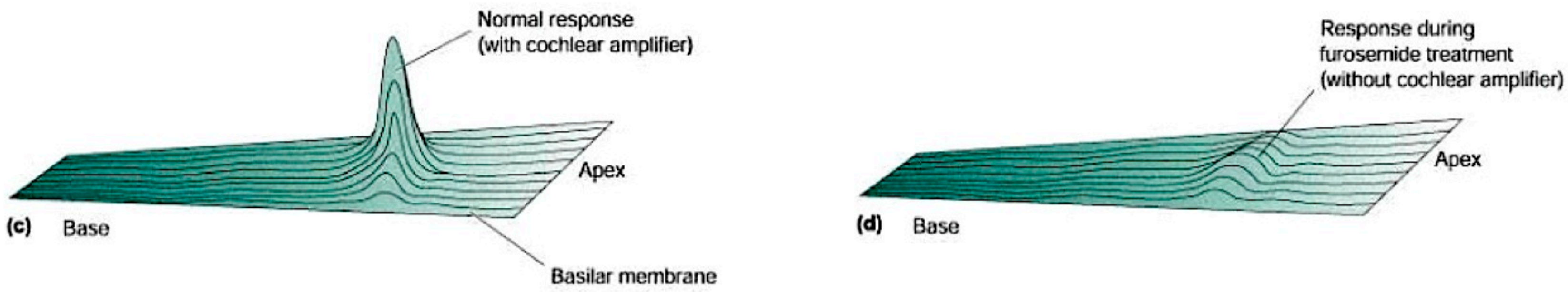
Georg von Békésy (1899 – 1972)



A. The sound pressure applied to the oval window produces travelling wave along the basilar membrane. C. The peak displacements for high frequencies are toward the base, and for low frequencies are toward the apex.

Evidence for active amplification mechanism

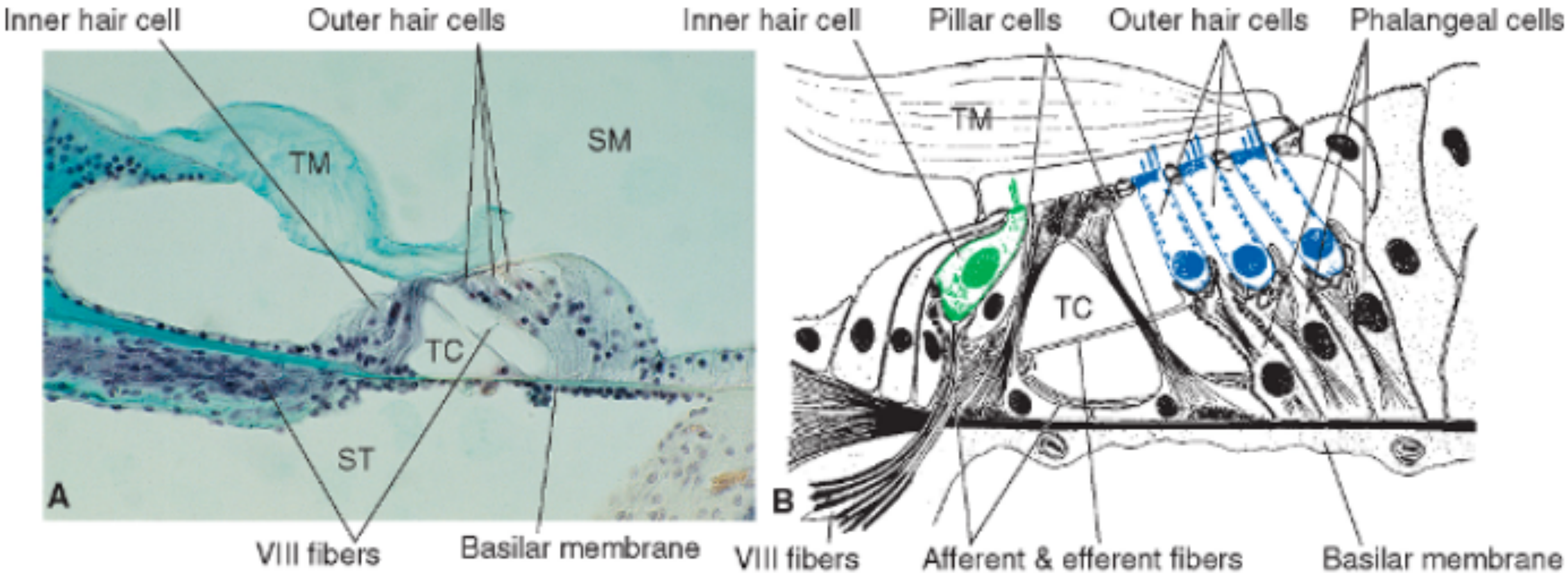
Theory of van Bekesy contradicts our daily experience. Envelopes of the travelling waves are wide while we are able to hear pure tones. There must be some additional mechanism for tunning of the auditory system to the sound frequency. The frequency response of individual cochlear nerve fibers depends on a combination of the mechanical properties of the basilar membrane and an active amplification mechanism.



Effect of cochlear amplifier. (c) The peak due to cochlear amplifier.(d) Amplitude of the passive movement of basilar membrane with metabolic block applied of the cochlear amplifier.

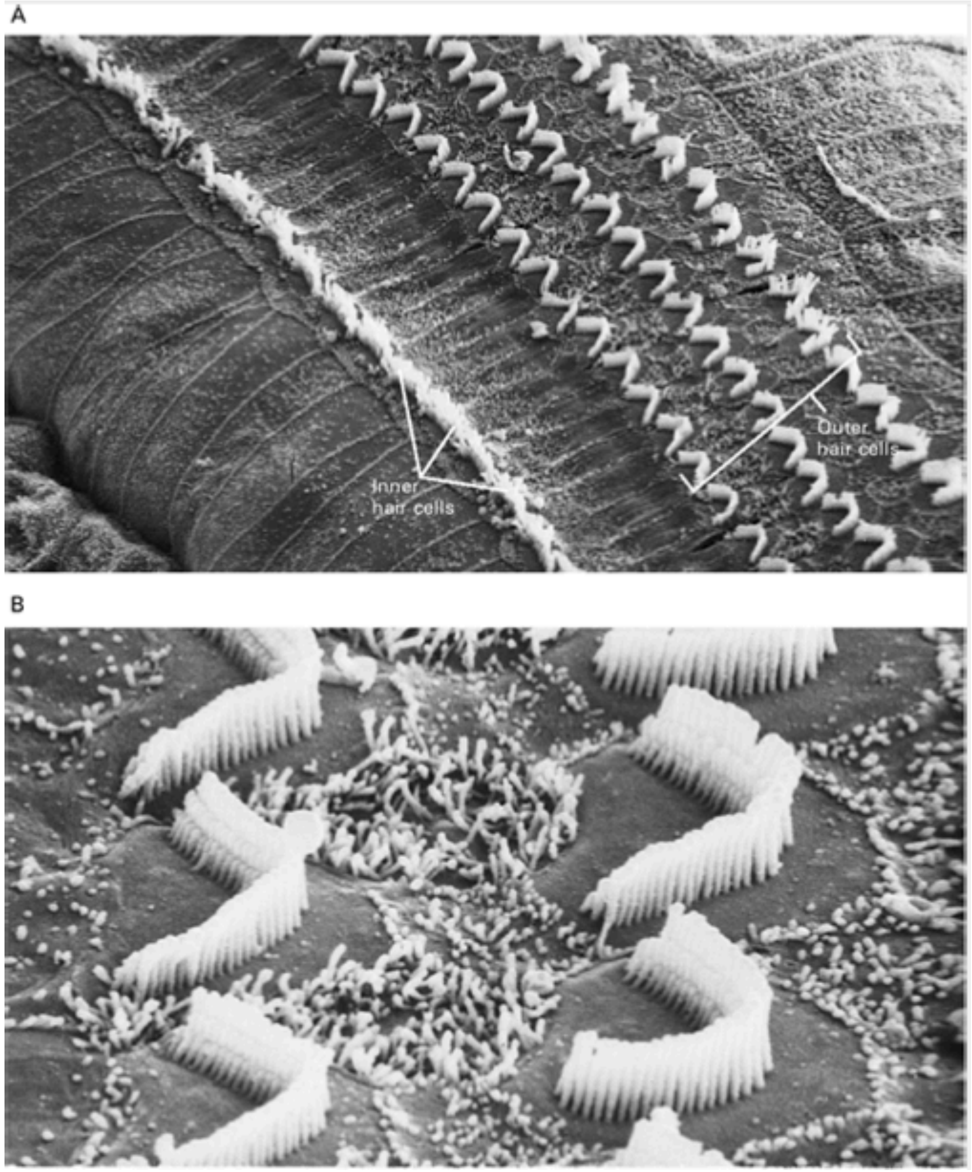
The Organ of Corti

The organ of Corti is the receptor organ of the inner ear, which actively amplifies the travelling wave. It contains the hair cells and a variety of supporting cells.



A. Light micrograph of a human organ of Corti. B. Drawing of a cross section of the organ of Corti.

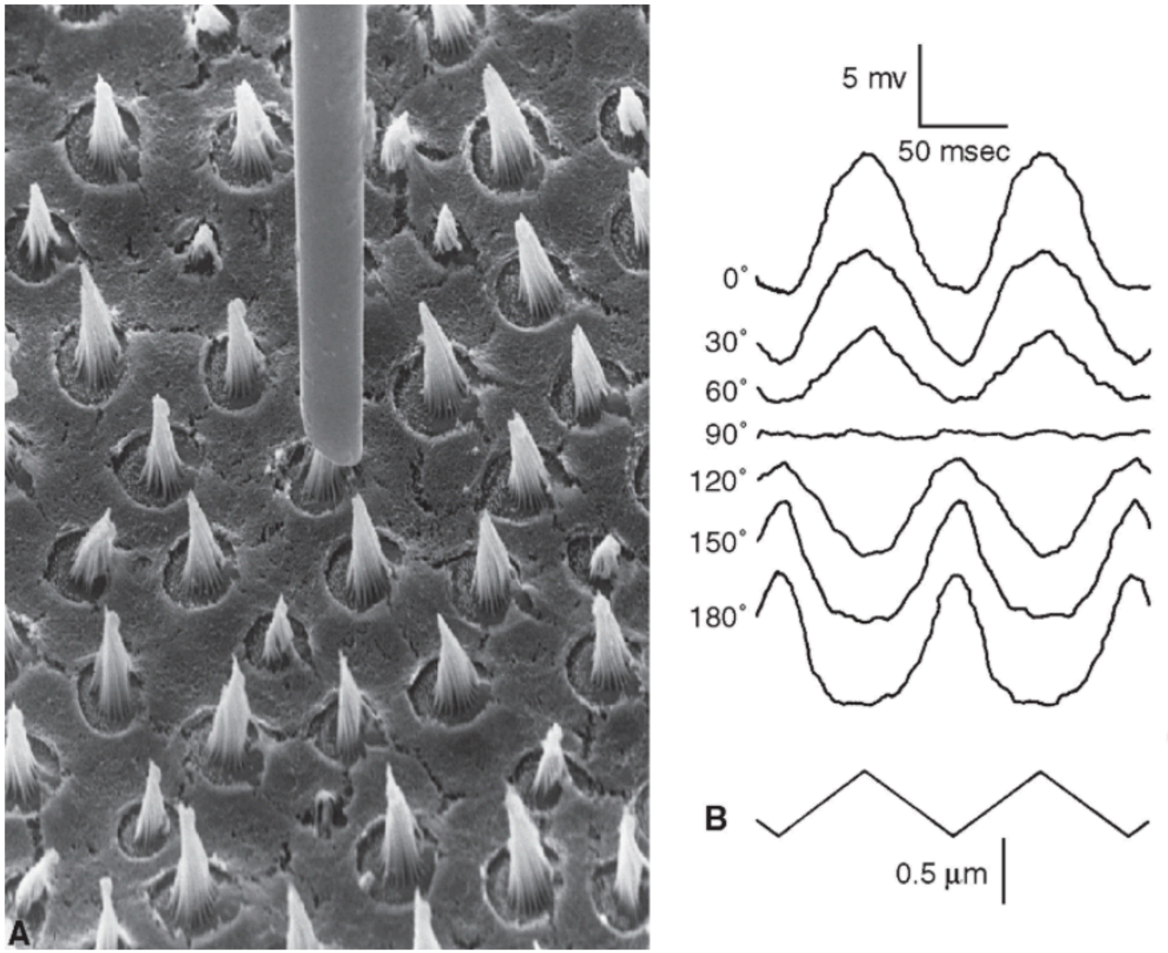
Two types of hair cells



Scanning electron micrographs of the organ of Corti after removal of the tectorial membrane. Inner hair cells are arranged in the single row. Outer hair cells are arranged in the three rows and the stereocilia of each cell are arranged in a V configuration.

Hair cells respond to displacement of the stereocilia

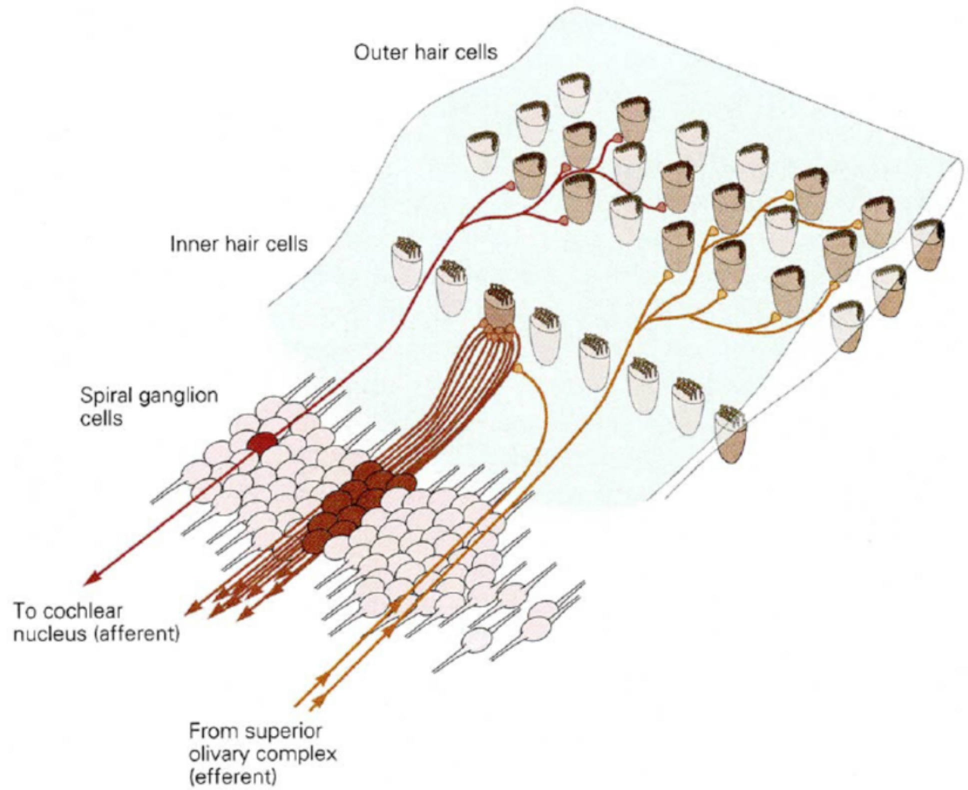
Hair cells are transforming vibrational energy into an electrical signal.
Mechanical displacement of the hair bundle produces electrical response.



A. A glass micropipette used to wiggle cilia bundle in various directions. B. Electrical response of the cell.

Inner hair cells are sensory cells; outer hair cells are amplifiers

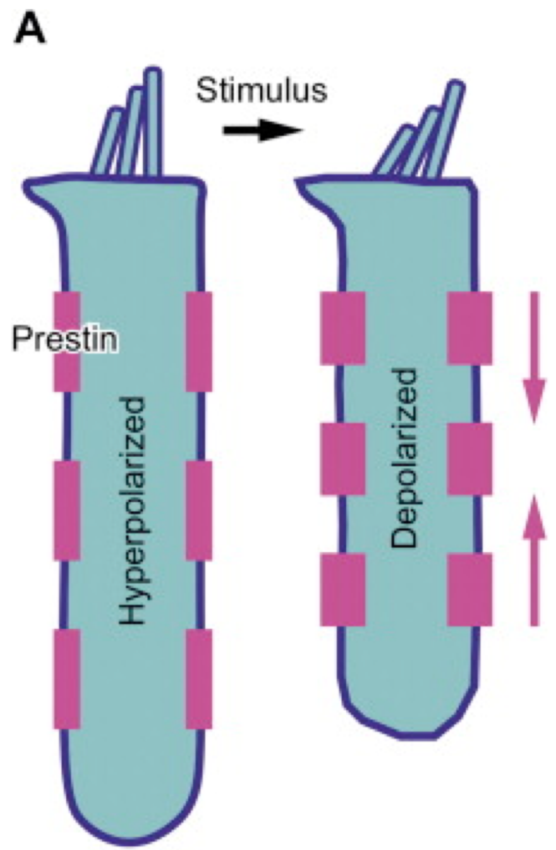
95 % of the fibers of the auditory nerve arise from the inner hair cells. It suggests that the inner hair cells are actual sensory receptors.



Innervation pattern: 20000 nerve fibers connect to the 3500 IHC, while 1000 nerve fibers connect to the 20000 OHC. The IHC are the main sites of auditory transduction.

Outer hair cells

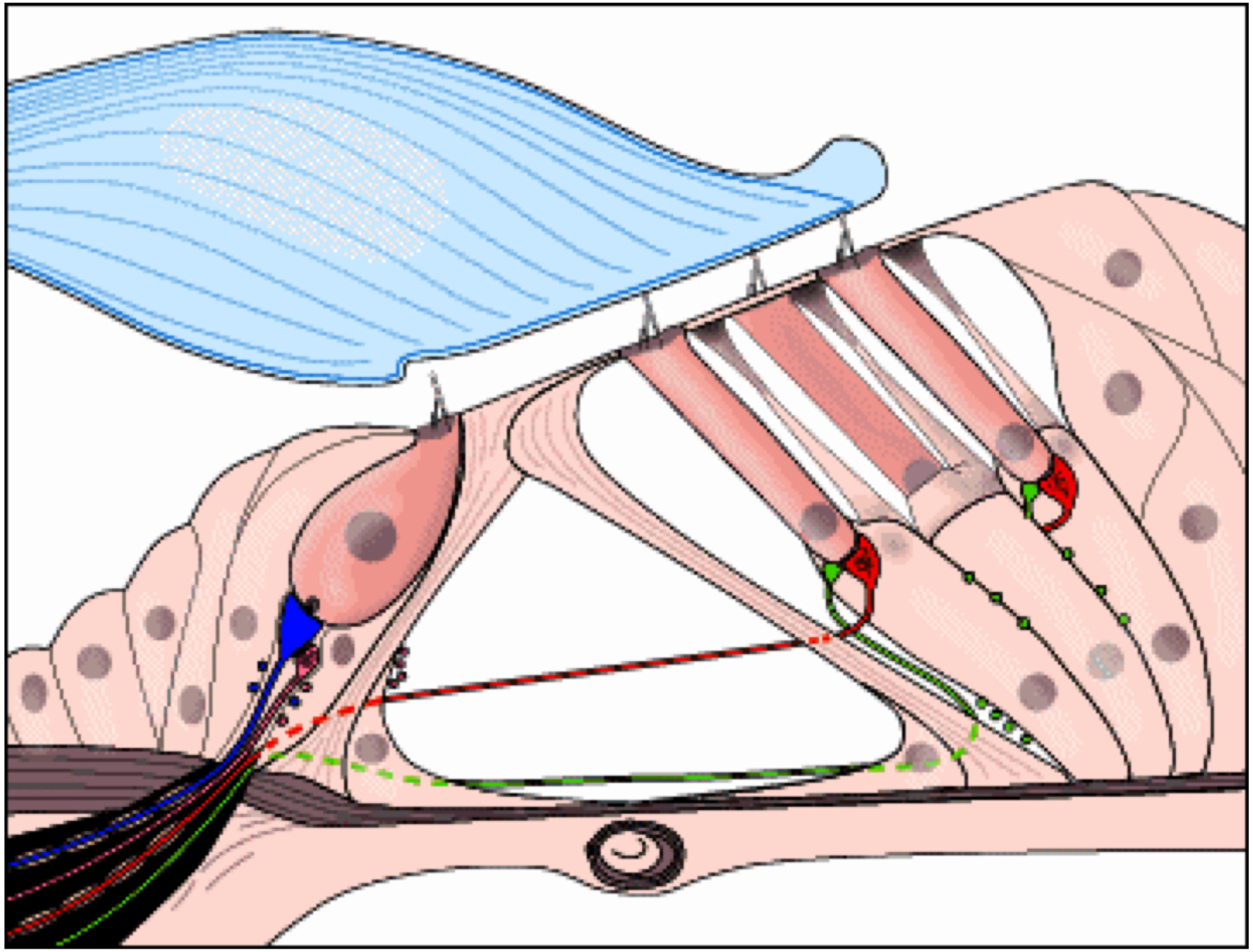
Outer hair cell may change its length in response to stimulus. The ‘motor’ is a transmembrane protein that mechanically contracts and elongates the cell. The molecule, discovered in 2000 is called ‘prestin’.



Rock Around the Clock Hair Cell

An outer hair cell is being stimulated electrically by a patch pipette which enters from the lower left. The cell's potential is changed by by plugging Walkman into the input socket of the electrophysiology amplifier.
(from: http://www.ucl.ac.uk/ear/research/ashmorelab)

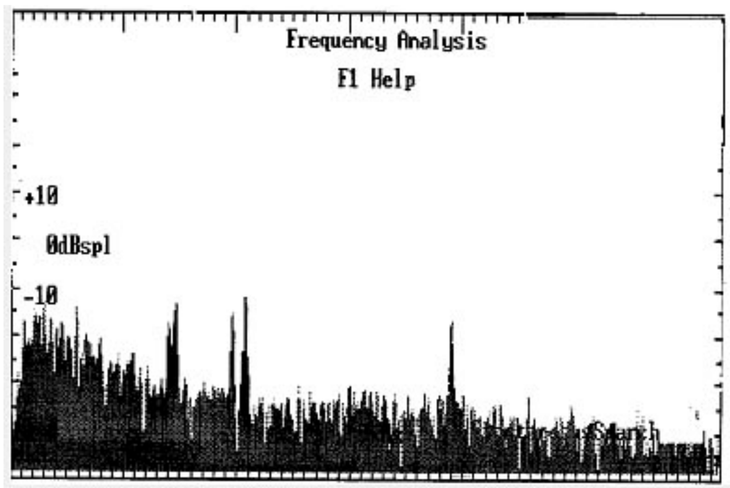
The cochlear amplifier



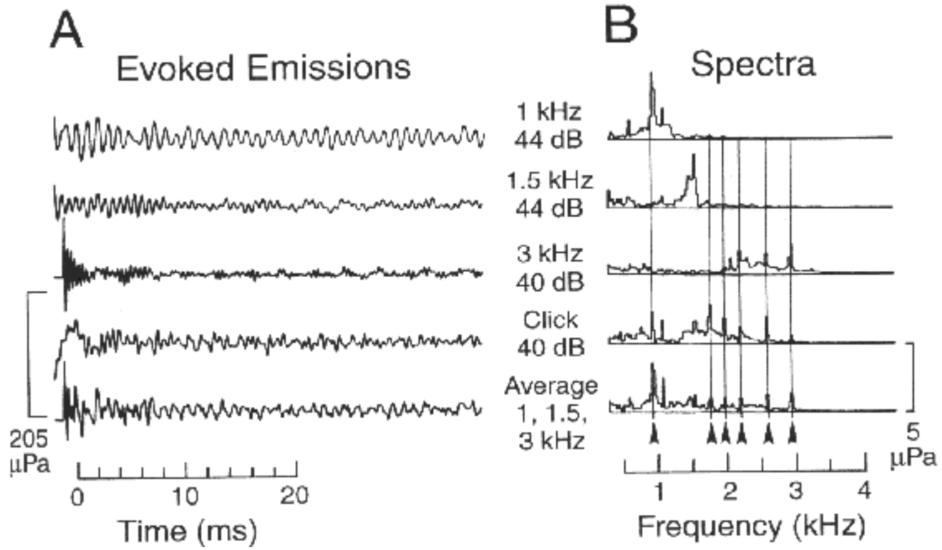
Shape changes of the outer hair cells due to rapidly oscillating membranne potential contribute to movement of the tectorial and basilar membranes. Inner hair cells are stimulated by the relative movements between these membranes. It is presumed that this mechanism contributes to the active tunning of hair cells responses.

Otoacoustic emission

An otoacoustic emission (OAE) is a sound which is generated from within the inner ear. There are two types of otoacoustic emissions: spontaneous otoacoustic emissions, which can occur without external stimulation, and evoked otoacoustic emissions, which require an evoking stimulus. Most probably, otoacoustic emissions are produced by the cochlear outer hair cells as they expand and contract. Otoacoustic emissions are the basis of a simple, non-invasive, test for hearing defects in newborn babies.

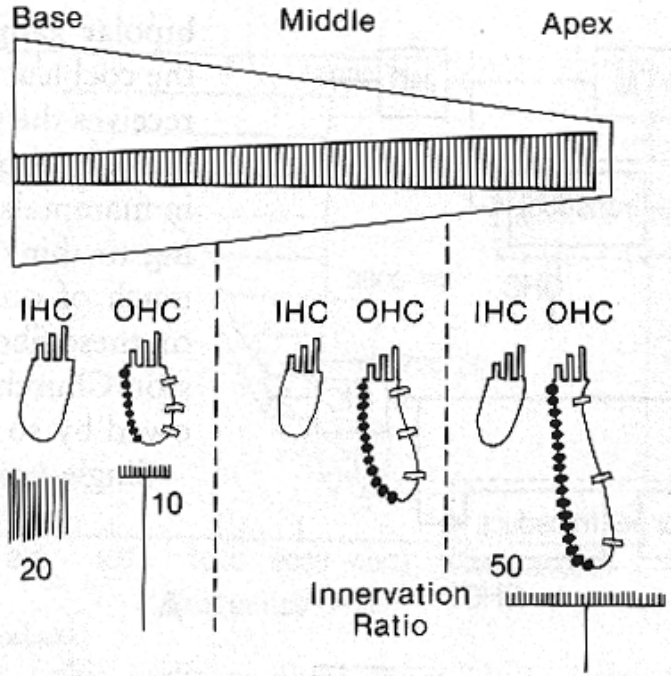


An example of multifrequency spontaneous otoacoustic emissions recorded from a 48-year-old woman with normal hearing. The black spikes represent the response above the noise floor.



An example of evoked otoacoustic emissions and their spectra. Evoked otoacoustical emissions are evidence for a cochlear amplifier.

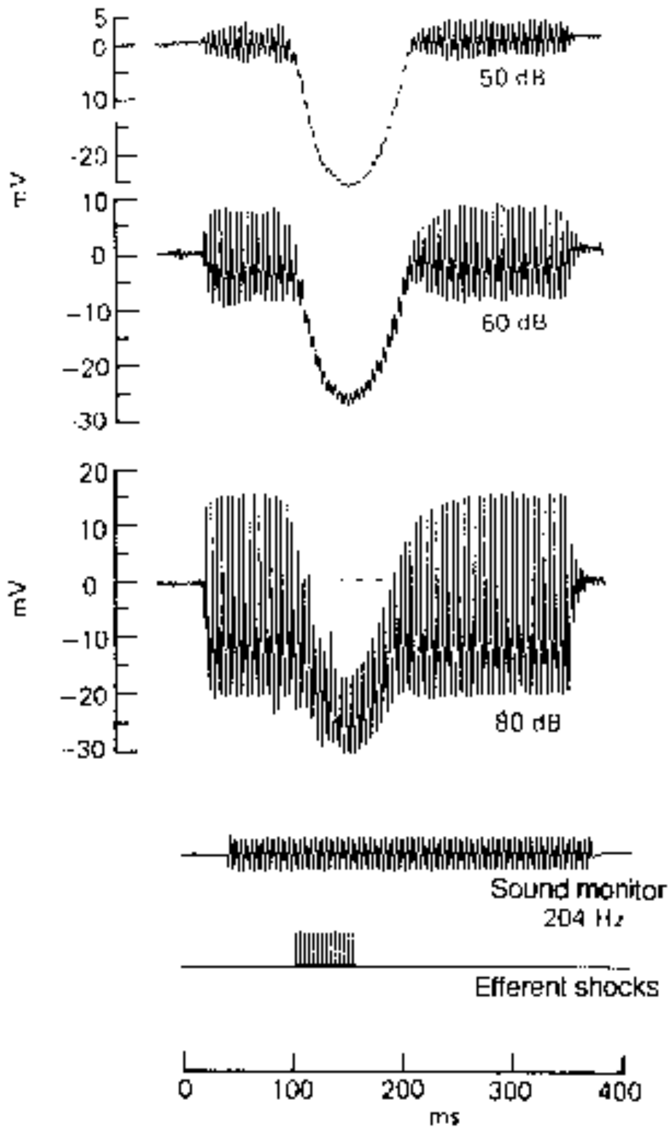
Mechanism of frequency tunning 2 – dependence on the location



OHC	Base	Middle	Apex
Input Conductance (G_N)	50 ns		10 ns
Time Constant (τ)	200 μs		1 ms
Channel Density	60 μm^{-2}		6 μm^{-2}
Gating Charge Density	5000 μm^{-2}		5000 μm^{-2}
Innvervation Ratio	10		50
Cell Length	30 μm	50 μm	70 μm

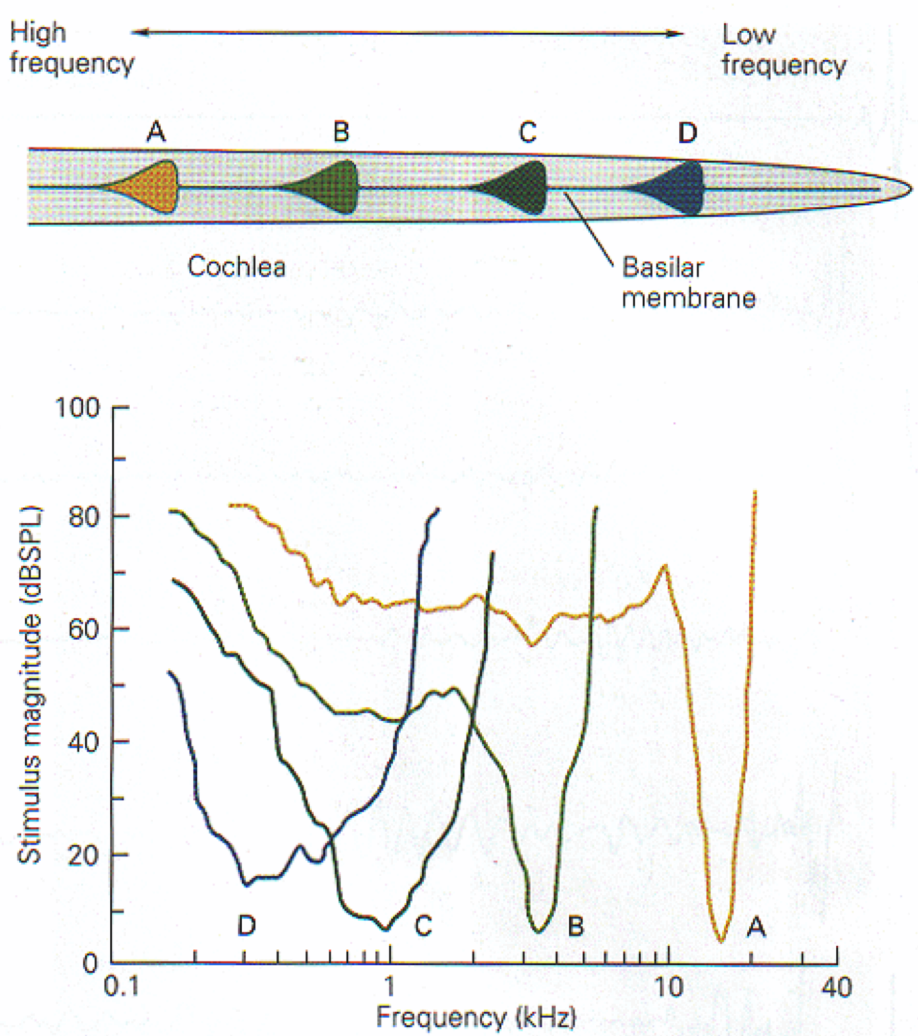
Many properties of IHC and OHC vary with the position along the cochlea. These differences are likely to be correlated with the differing frequencies that are processed along the cochlea, but the significance of these changes is still not understood.

Efferent fibers



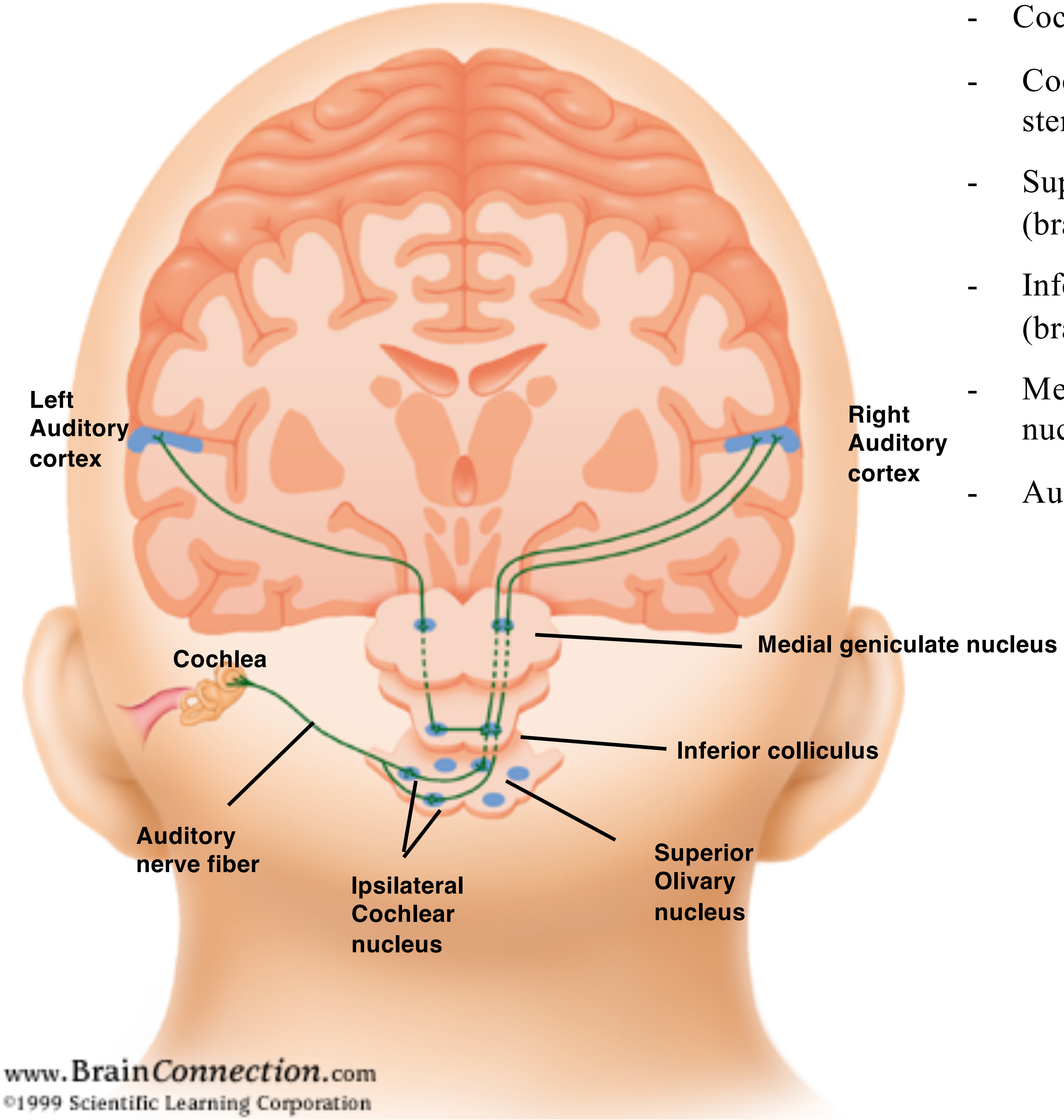
In addition to afferent fibers, the auditory nerve also contains efferent fibers, which arises from cells in the brain-stem. Efferent fibers inhibit mainly outer hair cells by hyperpolarizing the hair cells membrane. It reduces the motor output of the outer hair cells and reduces the movement of the tectorial and basilar membranes and the sensory response of the inner hair cells. Its role is assumed to be a protection against overstimulation.

Tunning curves



Tuning curves for cochlear hair cells. To construct a curve, the experimenter presents sound at each frequency at increasing amplitudes until the cell produces a criterion response, here 1 mV. The curve thus reflects the threshold of the cell for stimulation at a range of frequencies. Each cell is most sensitive to a specific frequency. The threshold rises briskly (sensitivity falls abruptly) as the stimulus frequency is raised or lowered.

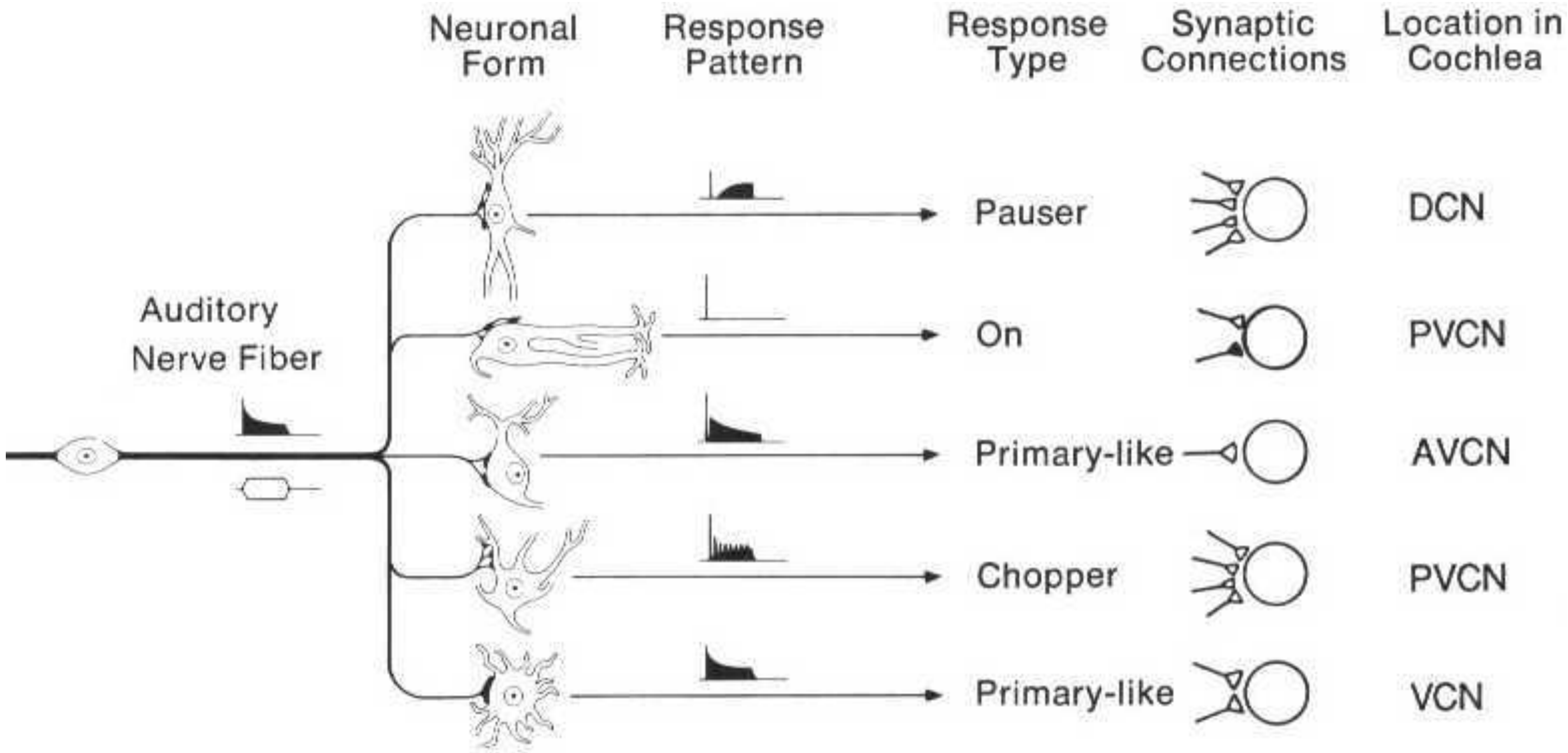
Auditory pathways



Auditory pathways:

- Cochlea
- Cochlear nuclei (brain-stem)
- Superior olivary nuclei (brain-stem)
- Inferior colliculus (brain-stem)
- Medial geniculate nuclei (thalamus)
- Auditory cortex

Types of cells in the cochlear nuclei

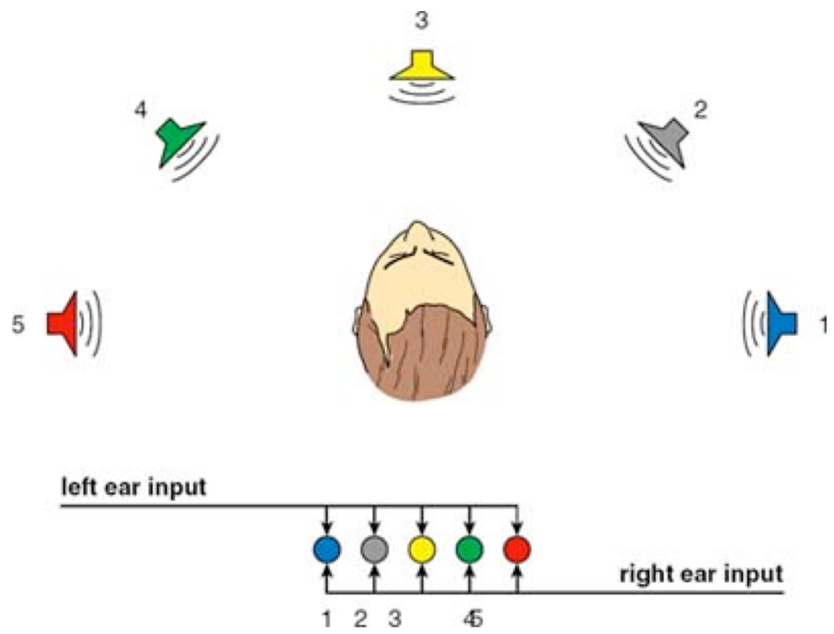


Auditory nerve fibers terminate in the cochlear nuclei (CN) on different types of cells with different response properties. Responses to a tone burst of 50 ms are shown. The ‘Primary-like’ preserve the envelope of the input signal, the ‘Pauser’ and the’Chopper’ provide for differentation between onset and ensuing phases of the tone, the ‘On’ cells signal the onset or timing of a sound. Each cell type represents an abstraction of one particular feature of the input. Different functional properties are processed and transmitted in **parallel** pathways. In humans, the receptor potentials of certain hair cells and the action potentials of their associated auditory nerve fiber can follow stimuli of up to about 3 kHz in a one-to-one fashion.

Founding sound in space

In the brainstem, the brain computes the location of a sound by interaural time differences:

- When distance to each ear is the same, there are no differences in time
- When the source is to the side of the observer, the times will differ

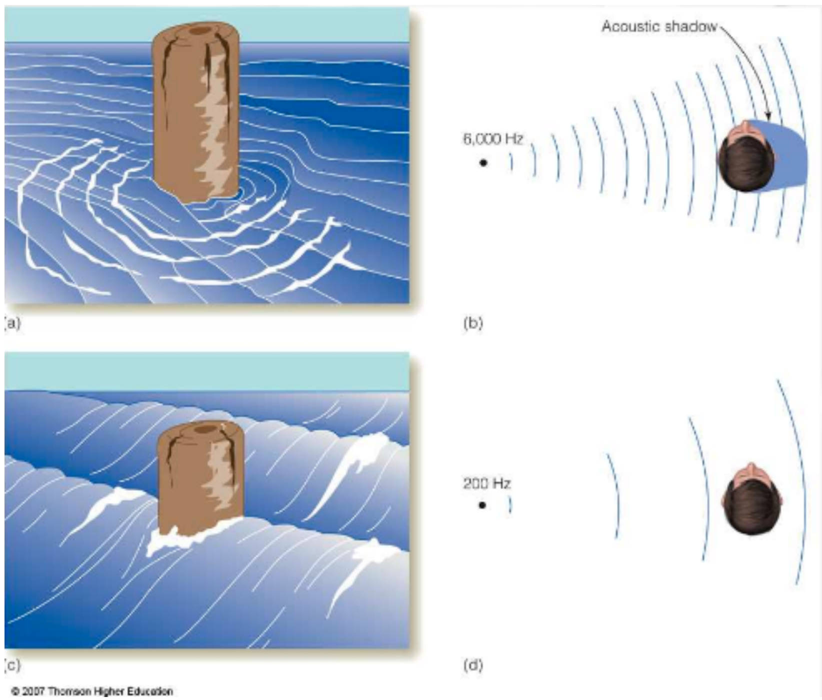


Each coincidence detector responses best to a particular time difference corresponding to sound arriving from a specific direction. Based on the activation of the detectors the brain ‘knows’ position of the sound source. Psychophysical experiments show that humans can actually detect interaural time differences as small as 10 microseconds; This sensitivity translates into an accuracy for sound localization of about 1° . Interaural time differences are used to localize the source for frequencies below 3 kHz .

Founding sound in space 2

The brain computes the location of a sound also by interaural level differences.

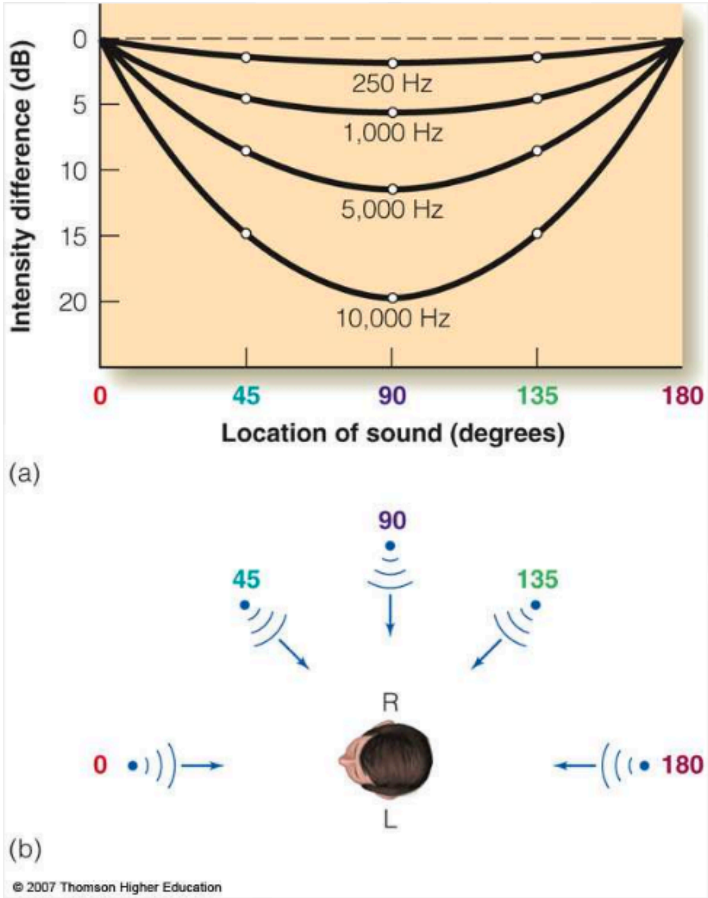
Interaural level difference is best for high frequency sounds because low frequency sounds are not attenuated much by the head.



The head casts an acoustic shadow for high frequency sounds. Low frequency sounds are able to bend around the head and therefore have no significant interaural intensity differences.

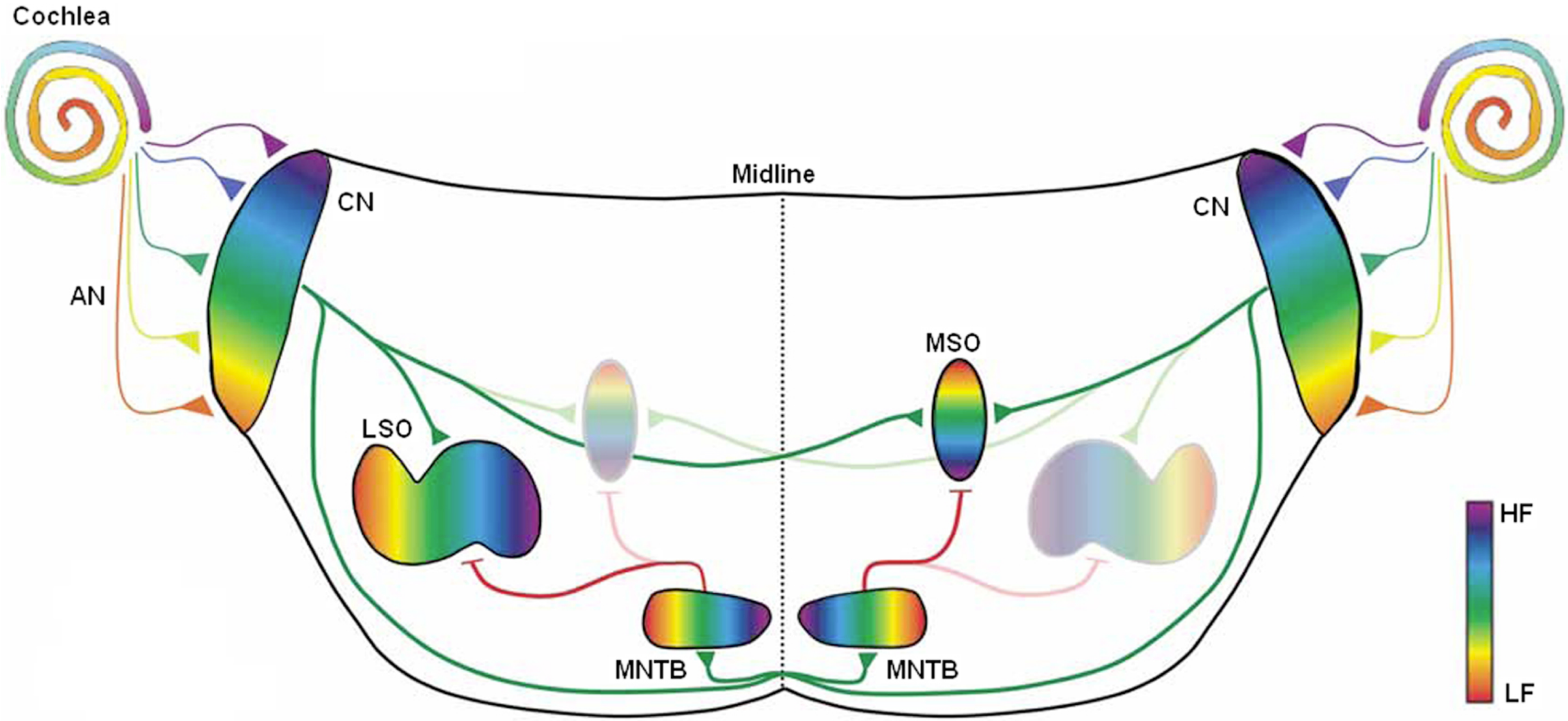
Founding sound in space 2

Interaural level difference is best for high frequency sounds (>3 kHz).



Based on intensity difference the brain may compute position of the sound source.

Tonotopic organisation



The basilar membrane in the cochlea is tonotopically organized. The tonotopic organization is retained at all levels of the central auditory system.

The auditory cortex

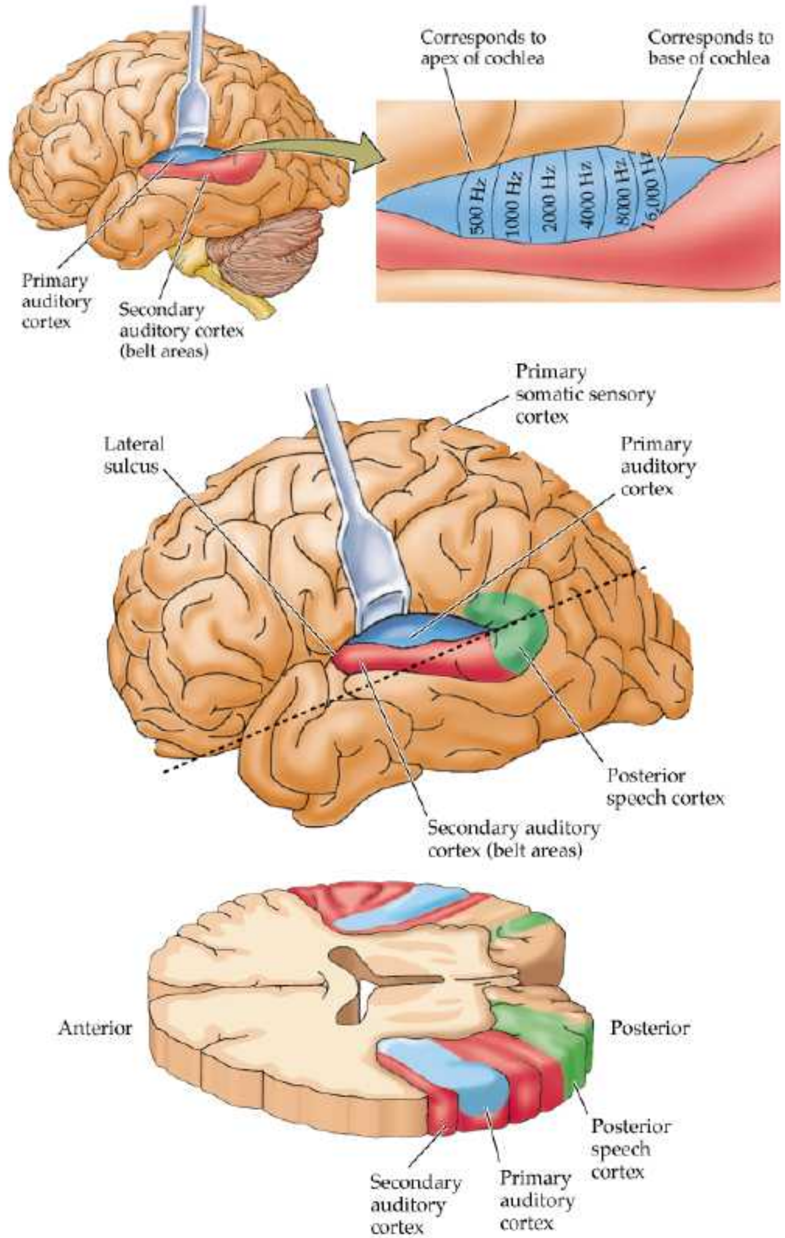
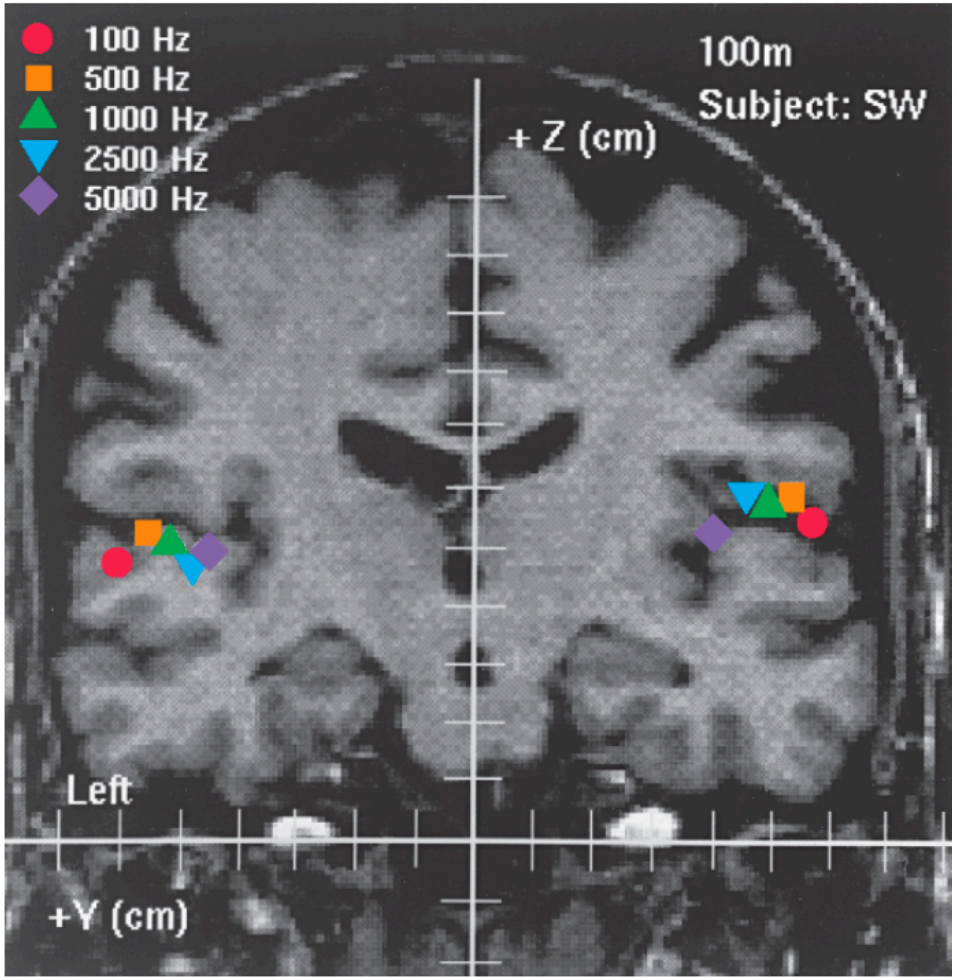


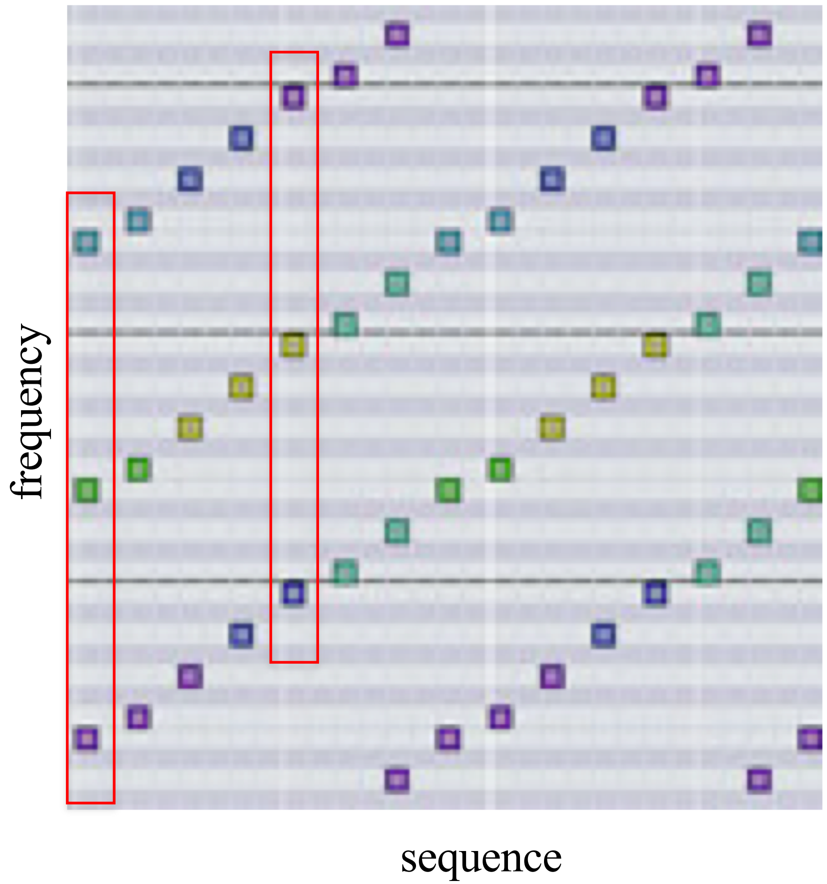
Diagram showing the brain in left lateral view, including the depths of the lateral sulcus, where part of the auditory cortex occupying the superior temporal gyrus normally lies hidden. The primary auditory cortex (A1) is shown in blue; the surrounding belt areas of the secondary auditory cortex are in red. The primary auditory cortex has a tonotopic organization, as shown in the blowup diagram of a segment of A1. The Wernicke's area shown in green is a region important in comprehending speech. It is just posterior to the primary auditory cortex.

Tonotopic mapping in auditory cortex



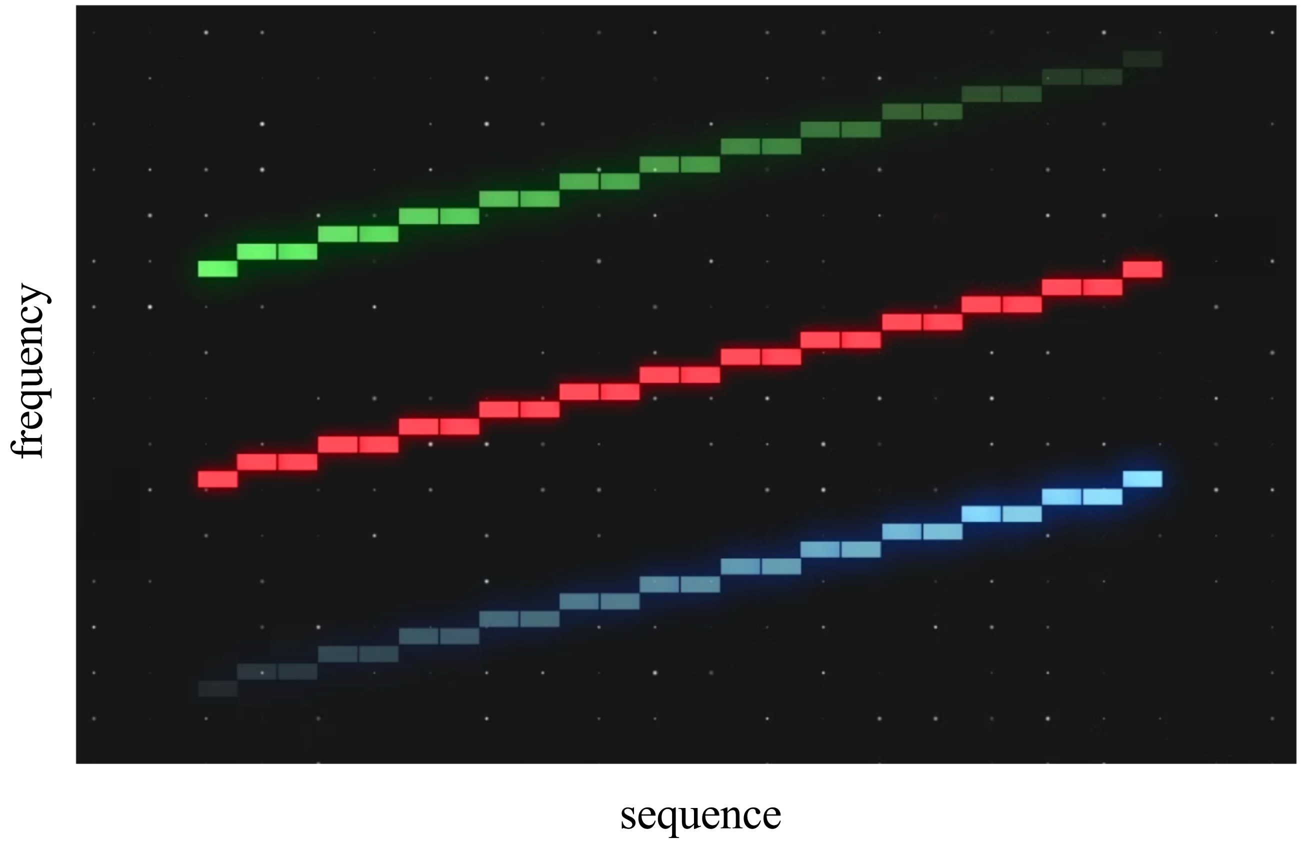
Tonotopic mapping in human primary auditory cortex, demonstrated by applying 500-msec tone bursts at five different sound frequencies to one ear while mapping the magnetic field changes produced by neuronal current flow in primary auditory cortex. Location of the primary auditory cortex in the transverse temporal gyri is visible.

Tritone paradox



Shepard tones. Each square in the figure indicates a tone, with any set of squares in vertical alignment together making one Shepard tone. The color of each square indicates the loudness of the note, with purple being the quietest and green the loudest. Overlapping notes in one Shepard tone are exactly one octave apart. A pair of Shepard tones separated by an interval of a tritone (half an octave) produces the tritone paradox. They may be heard as either descending or ascending and constitute a bistable figure in auditory domain.

Shepard-Risset glissando



Each square in the figure indicates a tone, with notes in one octave apart making one Shepard tone. The color of each square indicates the loudness of the note. The high pitch fades away, the middle pitch is constant and the low pitch becomes audible. We can hear at least two notes rising in pitch at the same time, what makes the brain to perceive constant ascending tone. When looped together, it may last infinitely long.

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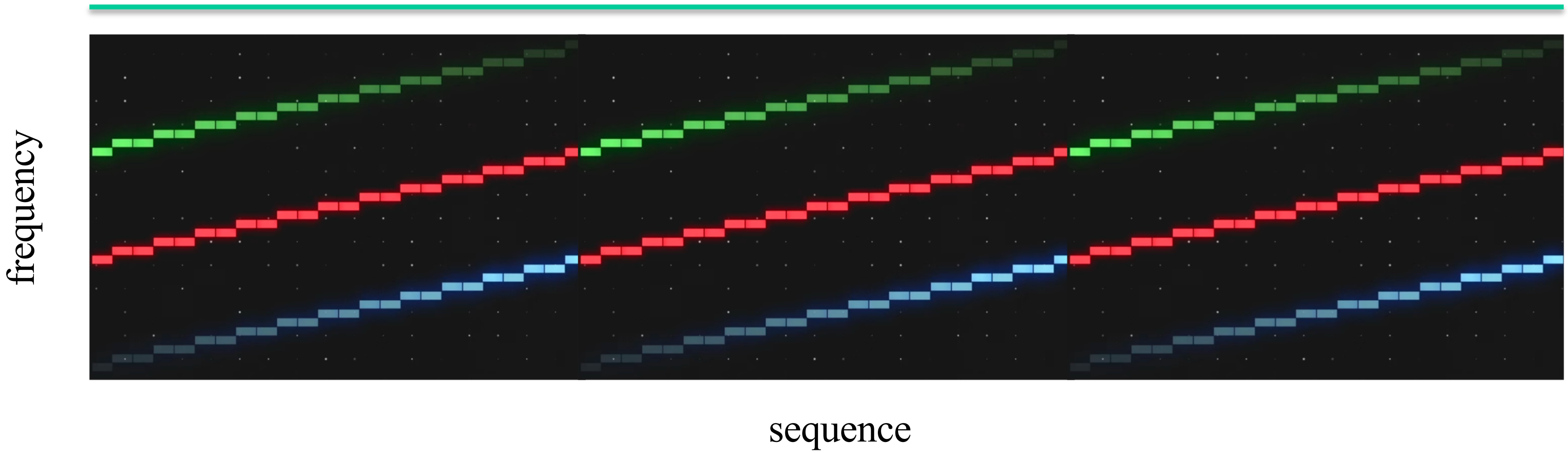

Shepard-Risset glissando has been used in soundtracks of computer games and movies, e.g. Dunkirk, Dark Knight The Prestige.