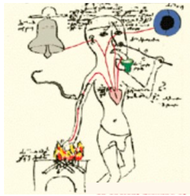
Biophysics of sensory receptors
Vison, Hearing

Miklós Kellermayer

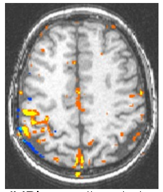
Theories about sensing

Cardiocentric sensing
(Medieval reconstruction)



Aristotle (384-322 BC)
cardiocentric sensing.

Galenus (129-200 AD) raised doubts about cardiocentric sensing.

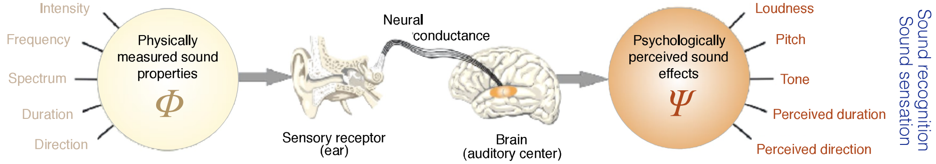


fMRI recording during sensomotoric function

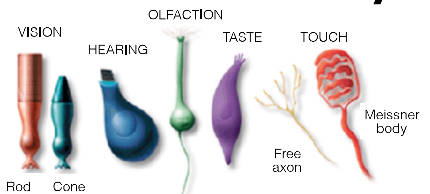
Sensory homuncle

Today:
stimulus ➛
➛ sensory receptors ➛
➛ receptor potential ➛
➛ neuron/nerve ➛
➛ action potential ➛
➛ central nervous system ➛
➛ signal processing ➛
➛ sensation

Process of sensing - example of hearing



Sensory receptors



"5 senses"

Sensory receptor: Specialized sensory cell, which responds to a given stimulus (e.g., light, sound, chemicals) and relays the information to the central nervous system.

Cell surface receptor (different meaning!): Proteins which specifically bind hormones, neurotransmitters and other molecules, and thus iniate specific cellular reactions.

		Modality	Receptor	Organ
Perceived	1	Vision	Rods and cones	Eye
	2	Hearing	Hair cells	Ear (organ of Corti)
	3	Olfaction (smelling)	Olfactory neuron	mucus membrane
	4	Taste	Taste receptor cells	Taste buds
	5	Angular acceleration	Hair cells	Ear (semicircular canals)
	6	Linear acceleration	Hair cells	Ear (utricle and saccule)
	7	Touch, pressure	Nerve endings	Multiple types
	8	Heat	Nerve endings	Multiple types
	9	Pain	Nerve endings	Multiple types
	10	Cold	Free nerve endings	...
Not perceived	11	Joint position and motion	Nerve endings	Multiple types
	12	Muscle length	Nerve endings	Muscle spindle
	13	Muscle stress	Nerve endings	Golgi's tendon organ
	14	Arterial presure	Nerve endings	Sinus caroticus stretch receptors
	15	Central venous pressure	Nerve endings	Venous, atrial stretch receptors
	16	Lung stress	Nerve endings	Pulmonary stretch receptors
	17	etc...	etc...	etc...

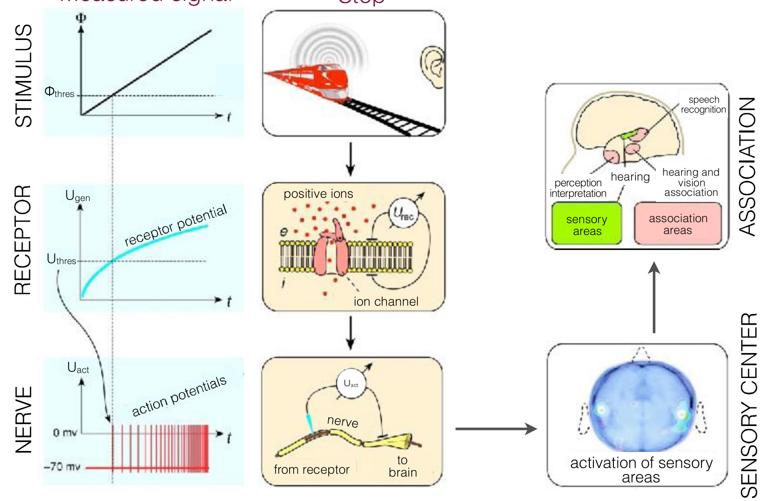
Sensitivity of sensory receptors

eV-size stimulus is sufficient for evoking action potential:
- sound receptors: thermal motion of the molecules of air
- light receptors: 1-2 photons

Steps of signal transduction

- Amplitude coding
- Adaptation

- Frequency coding



Action potential codes the…
- modality (type)
- intensity (strength)
- duration
- localization

…of the stimulus

1. Modality

Physical characteristic of the stimulus

Adequate stimulus: type of energy for which the receptor is most sensitive (e.g., light for the eye).

Principle of specific sensory energies: sensation is determined by the stimulated cortical region!

2. Stimulus intensity and sensation

Weber-Fechner psychophysical law

$$\psi = const \cdot \lg \frac{\phi}{\phi_0}$$

Stevens' law

$$\psi = const \cdot \left(\frac{\phi}{\phi_0} \right)^n$$

ψ= sensation strength
φ=background intensity
φ_0=absolute threshold intensity
n=constant specific for the type of sensation

n<1: compressive function (hearing, vision)

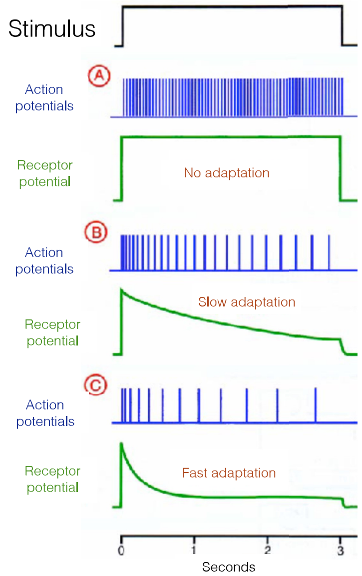
n>1: expansive function (pressure, taste)


Weber (1795-1878)


Fechner (1801-1887)


Stevens (1906-1973)

3. Duration, adaptation



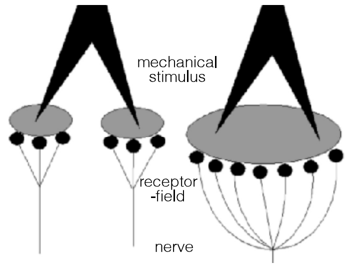
Adaptation: during constant stimulus the frequency of action potentials gradually decreases.

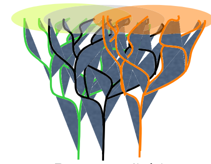
Rapidly adapting (phasic) receptors: pressure, smell, heat

Slowly and partially adapting (tonic) receptors: cold, pain (dental pain)

4. Localization

Branched nerve endings define receptor fields (convergence). Such can be found in the skin (touch) and in the peripheral retina (rods).



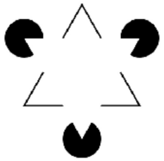

Receptor fields with overlap

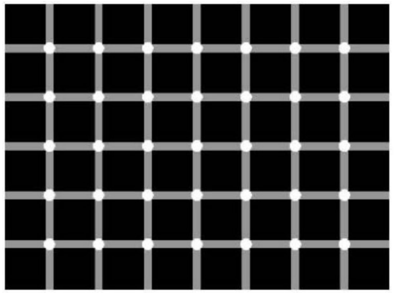
Biophysics of vision

The visual system displays a remarkable and unusual processing power. This is demonstrated by optical illusions.

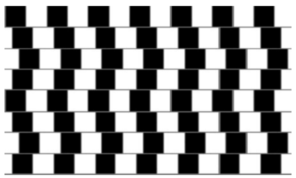
Optical illusion - intensity

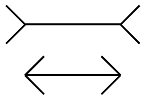

Mach bands


Kanizsa triangle


How many black circles can we count?

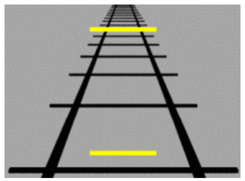
Optical illusion - direction, size

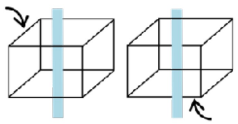

Café wall illusion

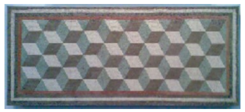

Müller-Lyer illusion


Ebbinghaus illusion

Optical illusions – space, shape

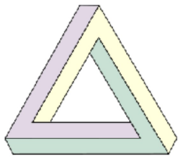

Ponzo illusion

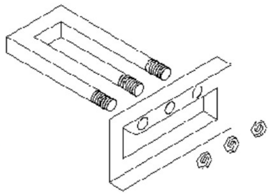

Necker cube

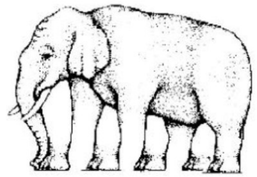

Necker cube effect on a roman mosaic

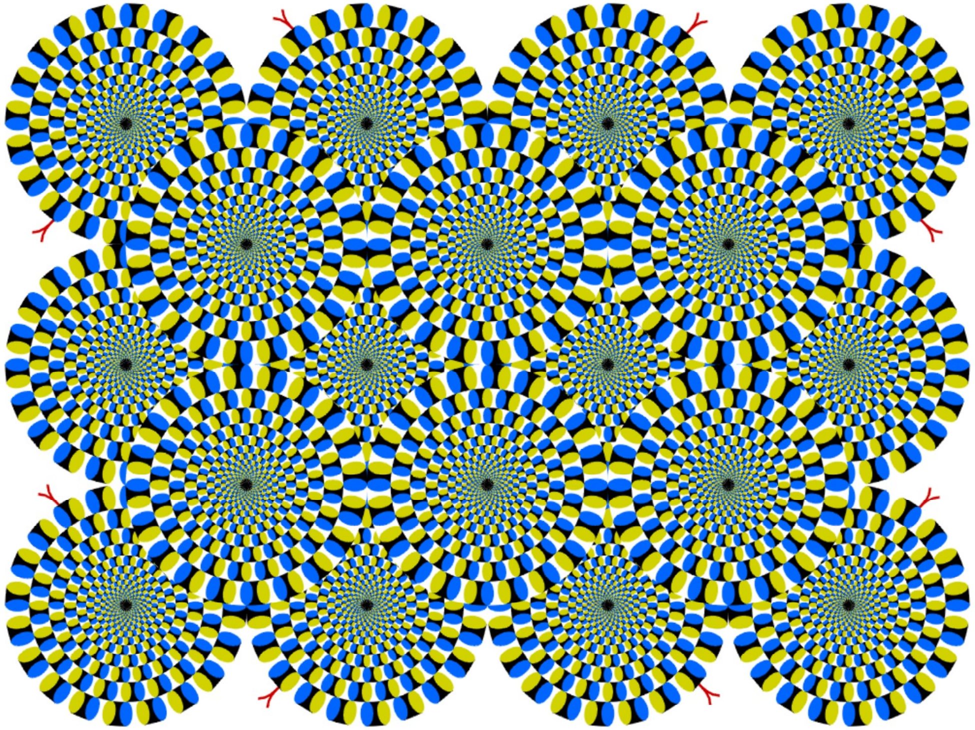

Rubin vase illusion

"Impossible" geometries


Penrose triangle

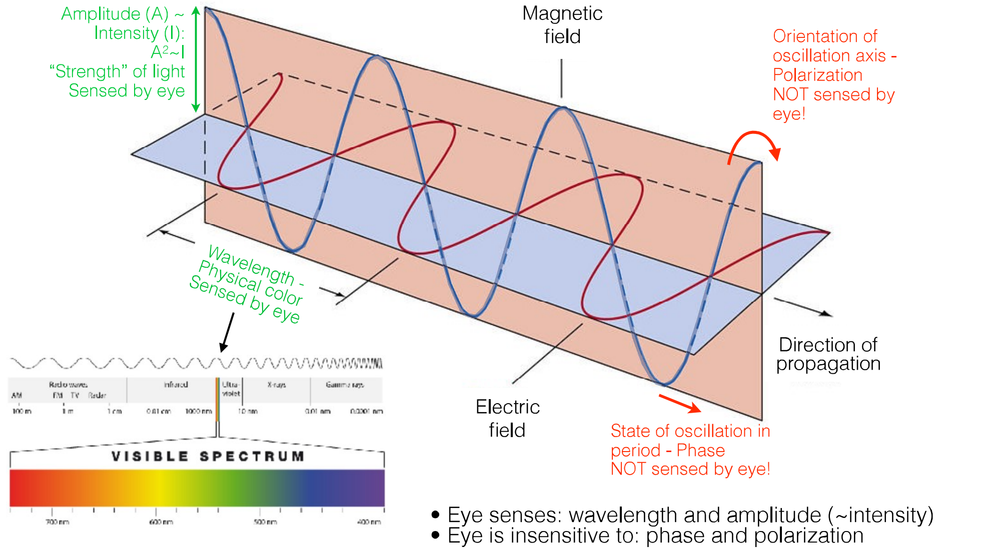






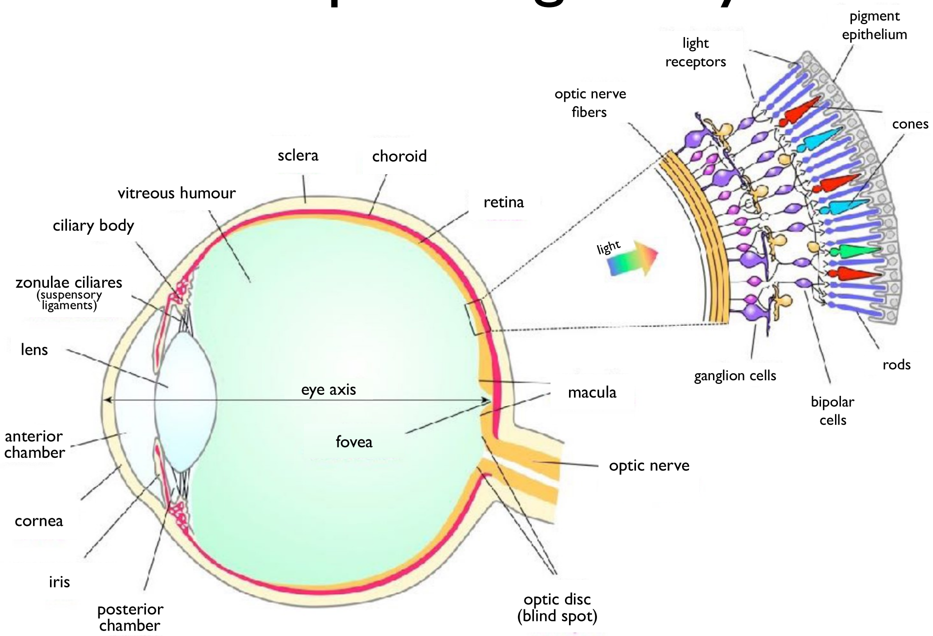
Stimulus of vision: light

Electromagnetic (transverse) wave

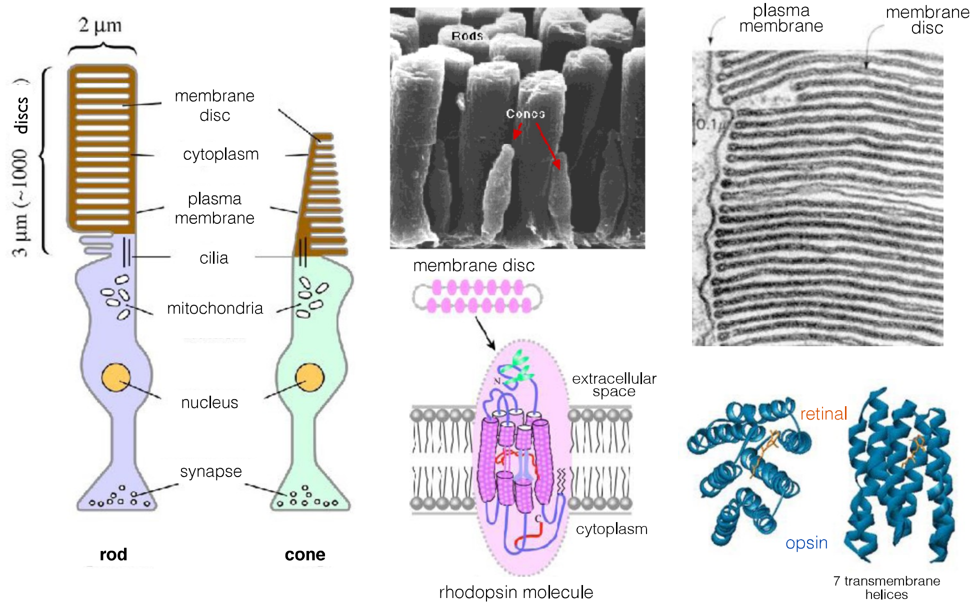


- Eye senses: wavelength and amplitude (~intensity)
- Eye is insensitive to: phase and polarization

"Receptor-organ": eye



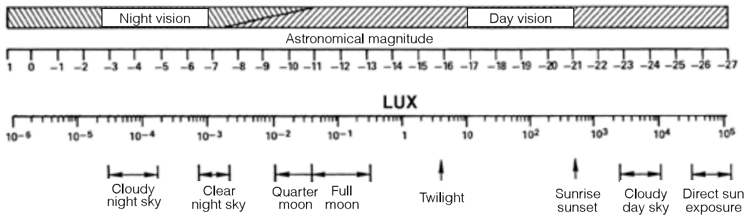
Photoreceptors



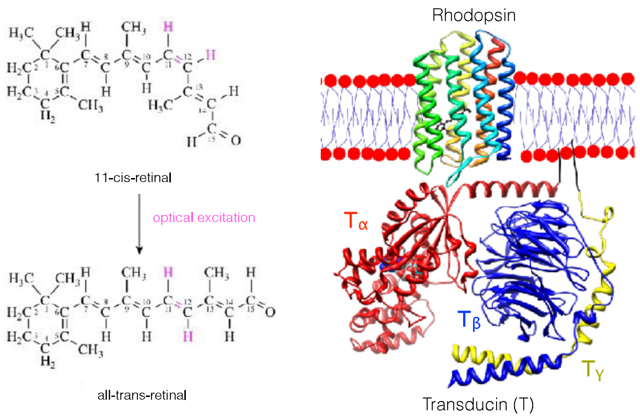
Properties of receptor cells

Rods	Cones
Stimulated by very small intensity (down to 1 photon!)	Smaller sensitivity, but is able to function at high intensities
Saturates at average intensities	No saturation
Found mainly in the peripheral retina	In the fovea, mainly the central fovea
Many rods per ganglion (convergence); greater sensitivity, smaller spatial resolution	Small convergence; greater spatial resolution
No color sensitivity	Sensitivity to colors
Large frequency sensitivity	Flow frequency sensitivity (~20 hz)

Combined sensitivity of the receptors: 10^{-9} - 10^{5} lux!



Basis of light sensing: photochemical reaction



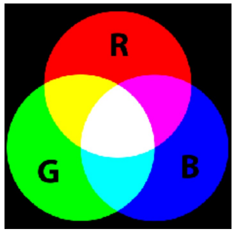
1 rhodopsin absorbs 1 photon
↓
metarhodopsin
↓
transducin molecule activated (T_α subunit dissociates from the $T_{\beta\gamma}$ subunit)
↓
500 phosphodiesthérase molecules activated
↓
10^5 cGMP molecules hydrolyzed
↓
250 Na^+-channels closed
↓
Entrance of 10^6-10^7 Na^+ ions/s inhibited
↓
cell hyperpolarized (1 mV)
↓
transmitter release reduced (glutamate: inhibitory neurotransmitter).

Amplification: $A = \dfrac{E_{ion}}{E_{photon}} = \dfrac{ne\Delta\varphi}{hf}$

n: change in number of Na ions
e: elementary charge
$\Delta\varphi$: membrane potential
h: Planck's constant
f: frequency of light

Color sensing

Color: sensation and not a physical property (not all colors can be defined by a wavelength)



Additive color coding

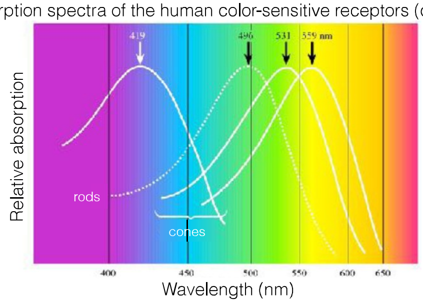
Any color (X) may be generated by mixing three basic colors (R=red, G=green, B=blue) with varying weighing factors (r, g, b):

$$X = rR + gG + bB$$

In the human eye:

- 3 different color-sensitive receptors.
- Each receptor absorbs in different regions of the visible spectrum (R=64%, G=32%, B=2%).

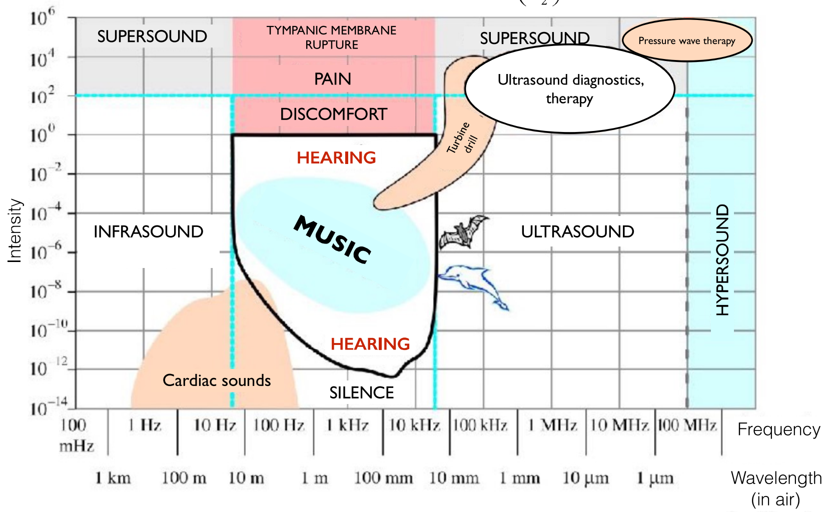
Absorption spectra of the human color-sensitive receptors (cones)



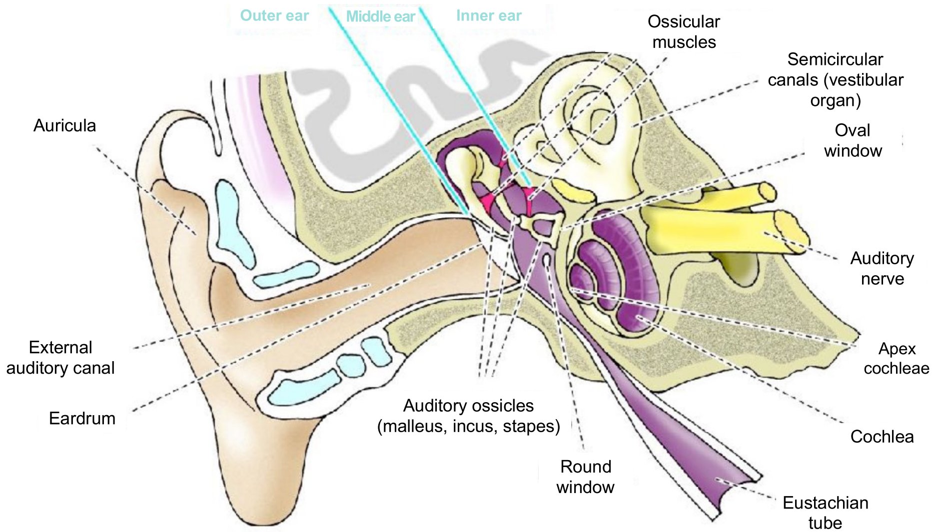
Biophysics of hearing

Stimulus: sound - mechanical wave

Intensity level: $n(dB) = 10\lg\left(\dfrac{J_1}{J_2}\right)$



“Receptor-organ”: ear



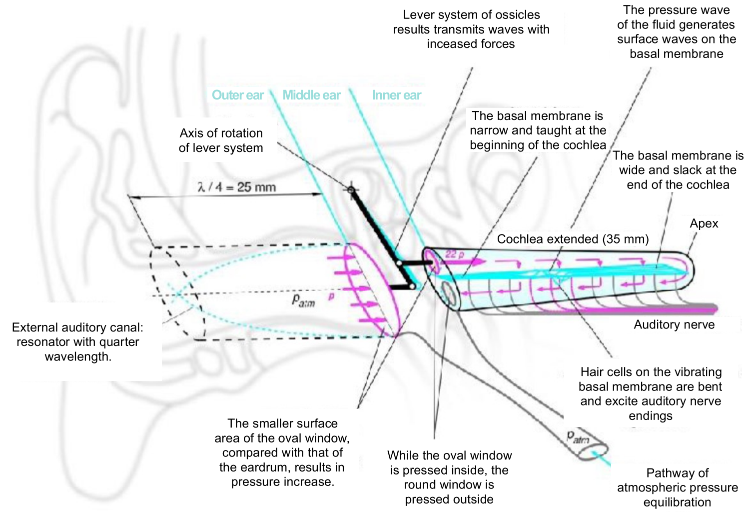
Physical schematics of the ear

Outer ear:

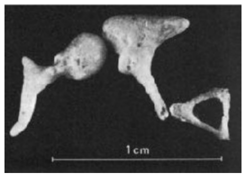
1. Auricula
Sound is steered into the external auditory canal.

2. External auditory canal
Conducts pressure waves towards the eardrum. More efficient in certain freqency range (2000-5000 Hz).

3. Eardrum
Brought into resonance by sound waves. Its oscillation amplitude at the stimulus threshold: 10^{-11} m (slightly exceeds that caused by thermal noise)!



Middle ear: mechanical transmitter and amplifier

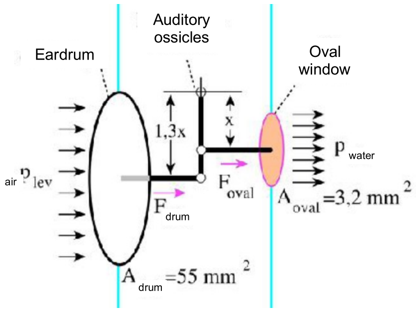


Auditory ossicles
(malleus, incus, stapes)

They **amplify** eardrum resonance and transmit it to the oval window. (N.B.: due to the difference in the acoustic impedance of air and water, total reflection would occur!)

Amplification:
due to area ratio: 17 ×
due to lever action: 1,3 ×

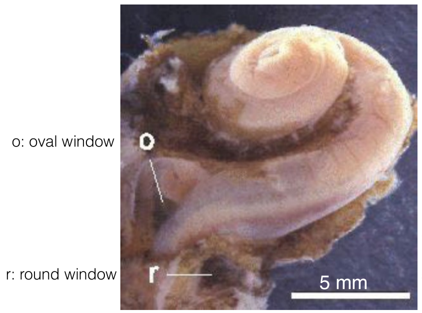
Total amplification: 22× (pressure increase)

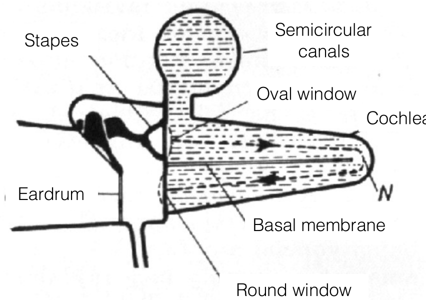


Inner ear: sensor

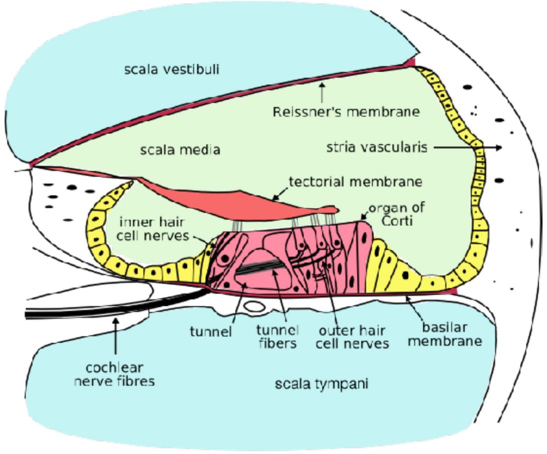
Vestibular organ: semicircular canals

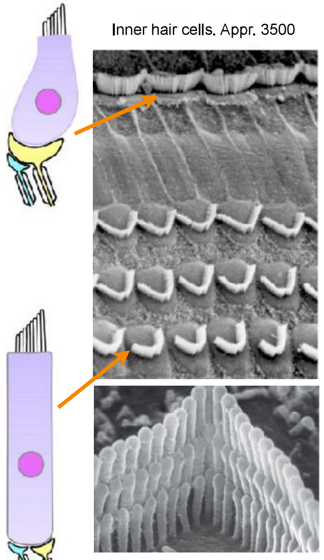
Cochlea: 2.5-pitch, 35-mm-long fluid-filled channel.
It is halved in length partly by an osseous, partly by a membranaeous wall, the basal membrane.
Sensory organ of sound.





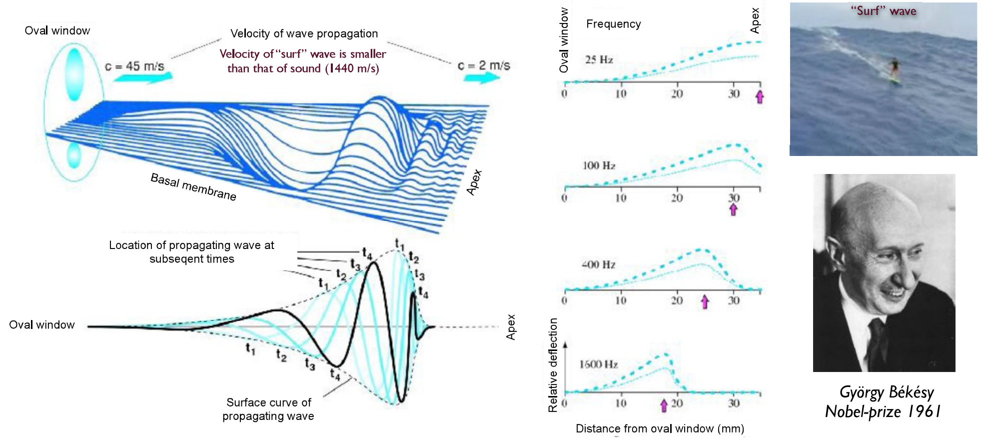
Ultrastructure of the inner ear




Inner hair cells. Appr. 3500

Outer hair cells. Appr. 12-20000

Békésy: propagating surface waves on basal membrane

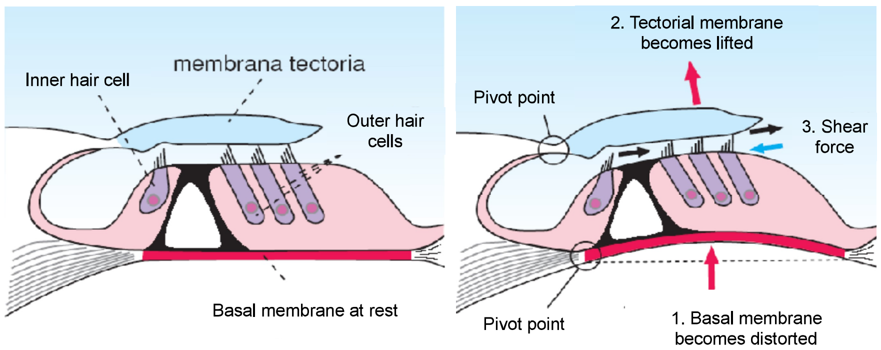


György Békésy
Nobel-prize 1961

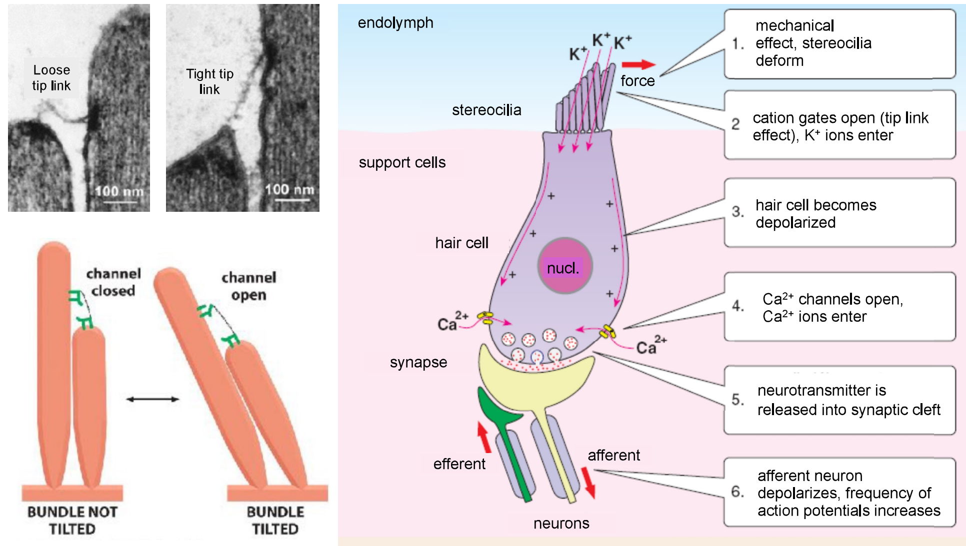
The frequency-dependence of the location of propagating wave maxima provide a rough frequency-discrimination.

Function of the organ of Corti

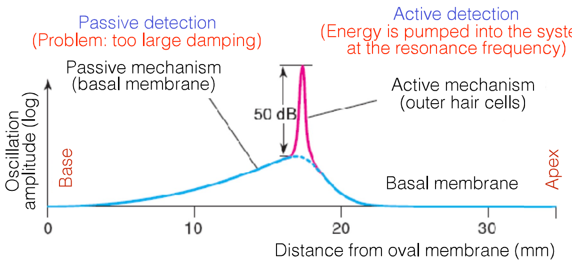
Due to the bending of the basal membrane, hair cells become tilted and depolarized.



Inner hair cells: Mechanoelectric transducers



Outer hair cells: amplifiers

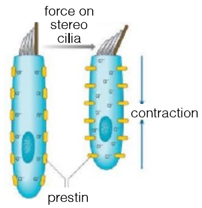


Observations pointing at active detection:

- T. Gold (1948): analogy with regenerative radio receivers (positive feedback at a given frequency: selectivity + sensitivity).
- W. Rode (1971): living ear is more sensitive.
- D. Kemp (1979): the ear generates sound (otoacoustic emission).

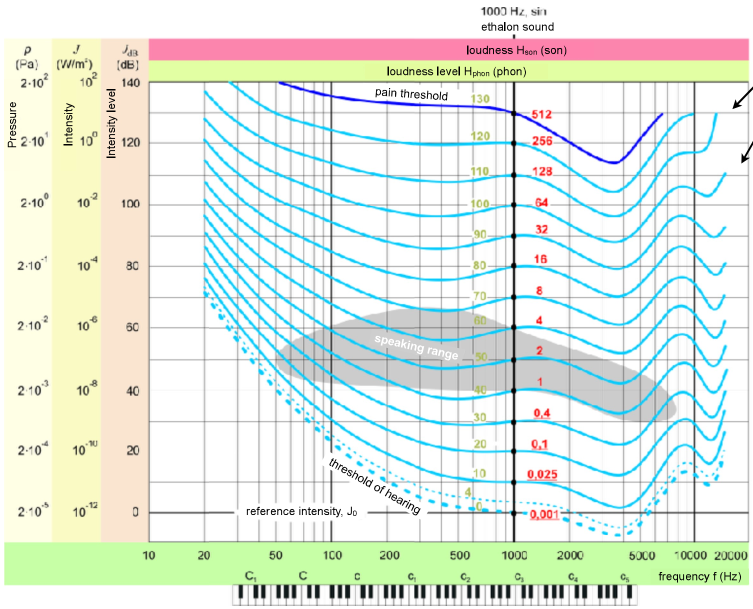
Regenerative amplifier: positive feedback mechanism (Large amplification in narrow frequency range. Only the dissipated energy is regenerated, otherwise ringing occurs)

Amplification: sound-induced contraction in outer hair cells



Prestin - transmembrane motor protein. Mechano-electric and electromechanical transduction

Stimulus intensity and sensing - psychoacoustics



Isophon curves: connect points of identical loudness level
Fletscher-Munson curves

Disco 120 phon

Street noise 80 phon

Loud speaking 60 phon

Whisper 30 phon

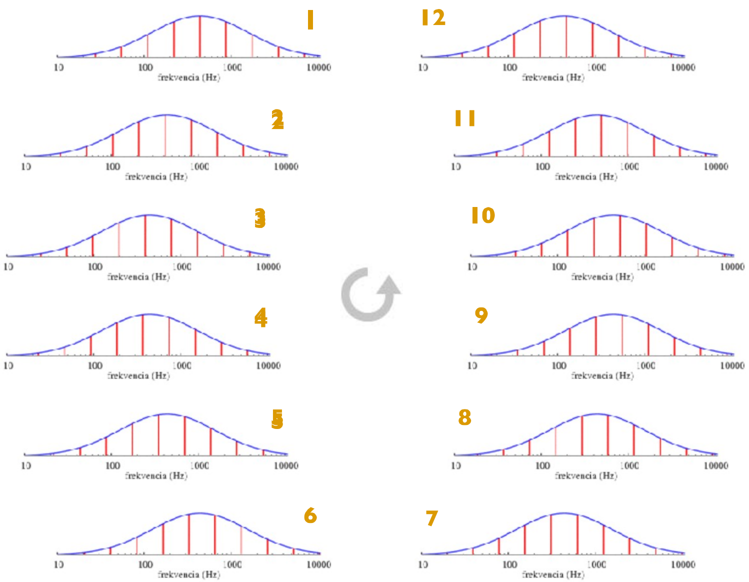
N.B.: The loudness level of a sound, in phon, is the dB value of a 1000 Hz sound with which we hear it identically loud.

Subjective loudness (son scale): 10 dB increase in loudness level is perceived as doubling of loudness. (Stevens law)

Acoustic illusion?

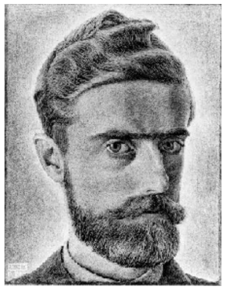
Shepard tone: sine waves separated by octaves

Shepard scale: fundamental frequency moves

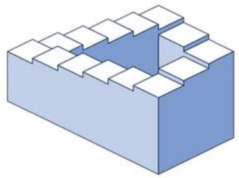


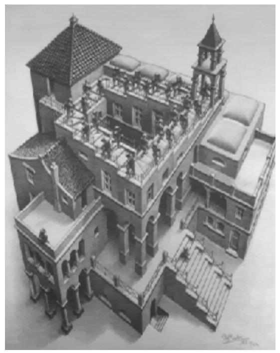
Acoustic illusion?

Visual analogs of the Shepard scale:



Maurits Cornelis Escher
(1898-1972)





Escher staircase

Barber's pole