BIOPHYSICS OF SENSORY RECEPTORS

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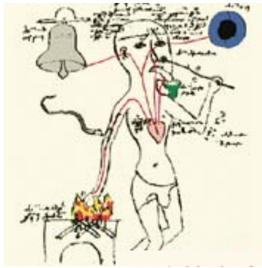
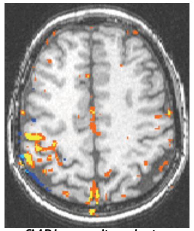
Theories about sensing



Cardiocentric sensing (Medieval reconstruction)

Aristotle (384-322 BC) cardiocentric sensing.

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



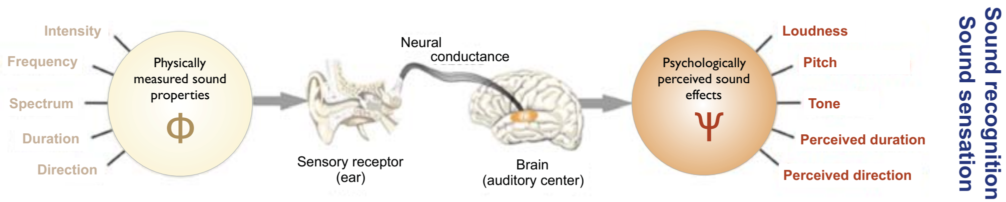
fMRI recording during sensomotoric function

Sensory homuncle

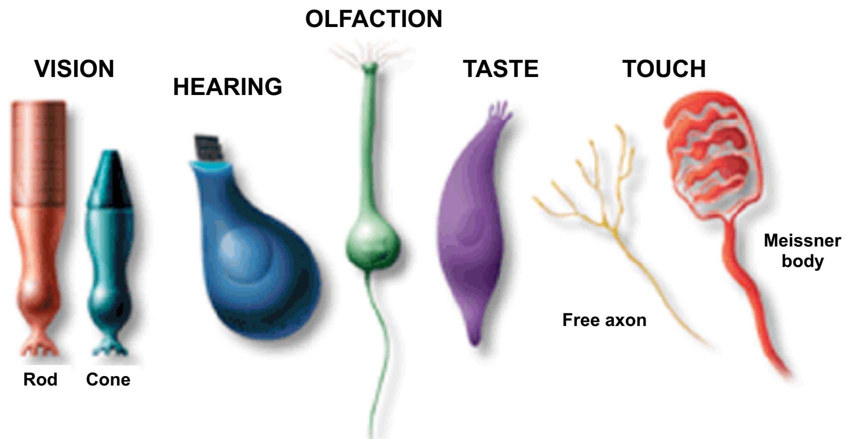
Today:
stimulus ➛
➛ sensory receptors ➛
➛ receptor potential ➛
➛ neuron/nerve ➛
➛ action potential ➛
➛ central nervous system ➛
➛ signal processing ➛
➛ sensation

Steps of sensing

Case of hearing



Sensory receptors



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.

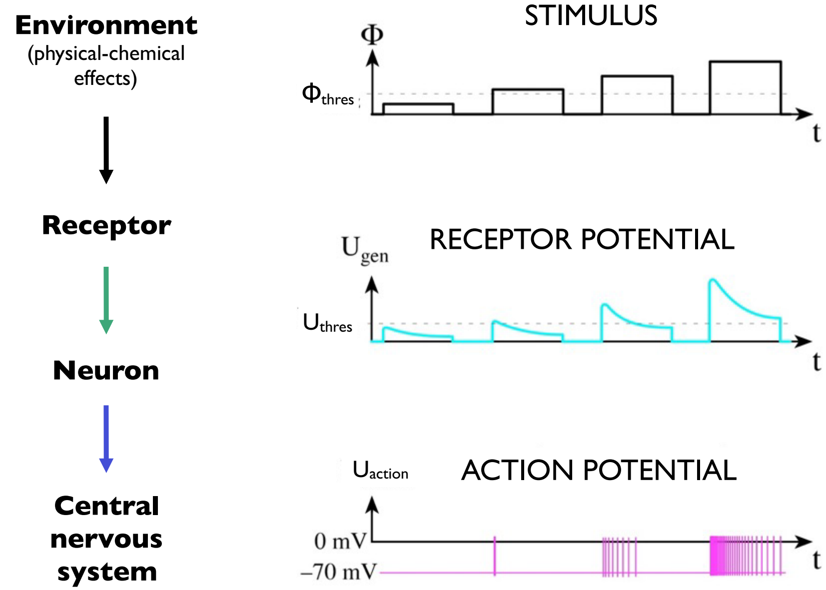
Cell surface receptor (different meaning!): Proteins which specifically bind hormones, neurotransmitters and other molecules, and thus iniate specific cellular reactions.

Five senses?

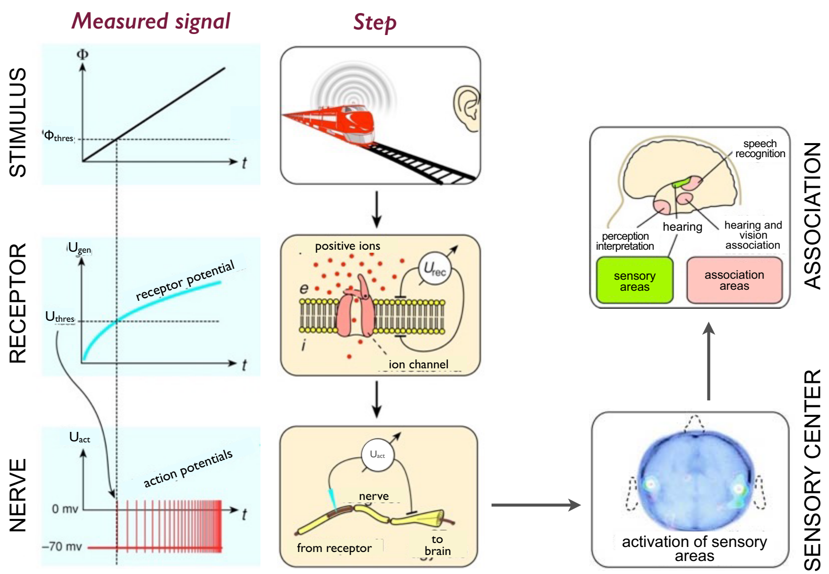
Most important sensory modalities (First 11: perceived modalities)

	Modality	Receptor	Organ
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	...
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...

Steps of signal transduction



From stimulus to sensation



Sensitivity

eV - size stimulus is sufficient for evoking action potential:

- sound receptors: thermal motion of the molecules of air
- light receptors: 1-2 photons

What is coded by the action potential?

- modality (type)
- intensity (strength)
- duration
- localization

of the **stimulus**

1. Modality

Adequate stimulus

Type of energy for which the receptor is most sensitive (e.g., light for the eye).

Action potentials are identical in all nerves. How do we know, for example, whether an action potential codes for touch and not cold?

Principle of specific sensory energies

Sensation is determined by the stimulated cortical region!

2. Intensity

Which parameters carry information about stimulus strength?

- frequency of action potentials
- number of activated receptor cells

Weber-Fechner psychophysical law

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

Stevens' law

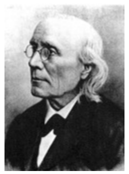
$$\psi = const \cdot \left(\frac{\phi}{\phi_0}\right)^n$$

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

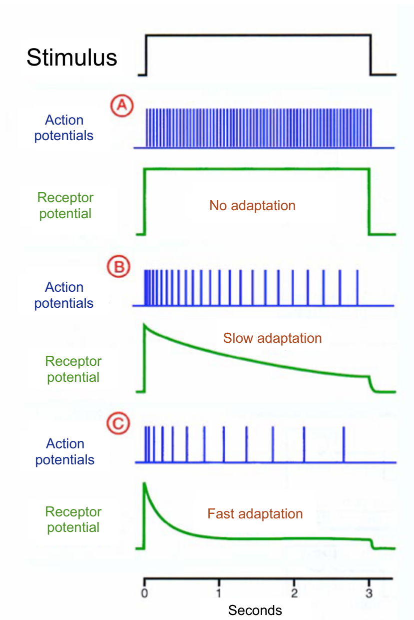
Adaptation. During constant stimulus the frequency of action potentials gradually decreases.

Rapidly adapting (phasic) receptors

E.g., pressure, smell, heat

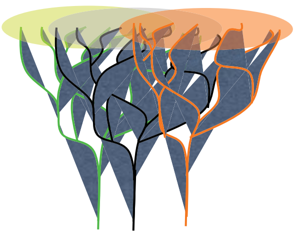
Slowly and partially adapting (tonic) receptors

E.g., cold, pain (dental pain)

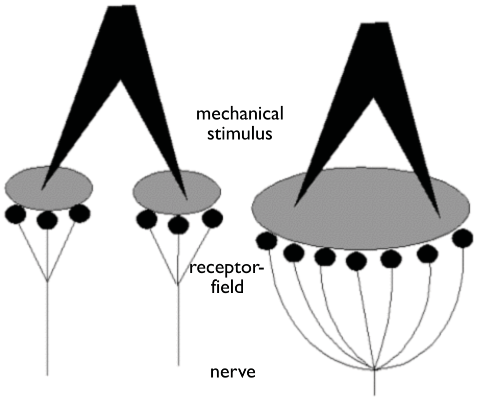


4. Localization, receptor fields

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

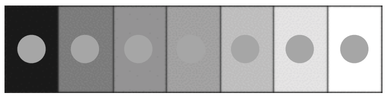


Receptor fields with overlap

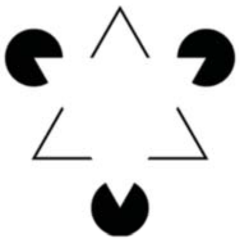


Biophysics of the eye

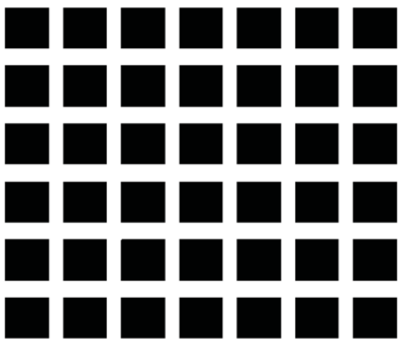
Optical illusions - intensity

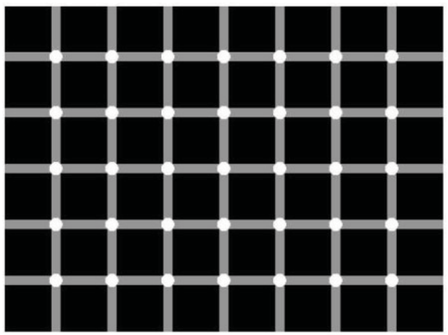


Mach bands



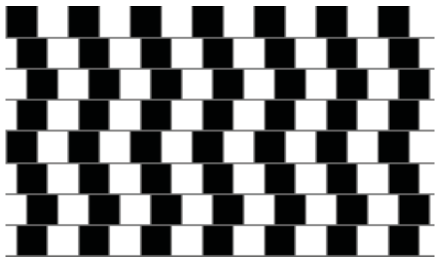
Kanizsa triangle



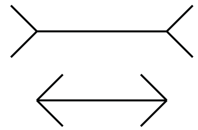


How many black circles can we count?

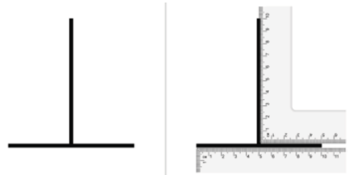
Optical illusions – direction, size



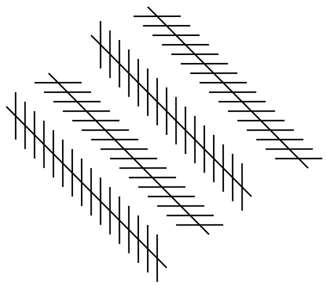
Café Wall illusion



Müller-Lyer illusion

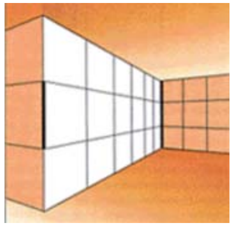


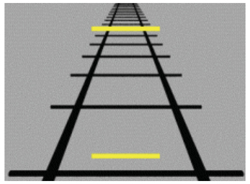
Vertical-horizontal illusion



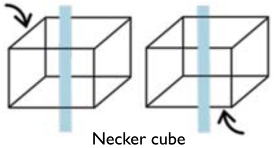
Ebbinghaus illusion

Optical illusions – space





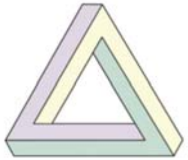
Ponzo illusion



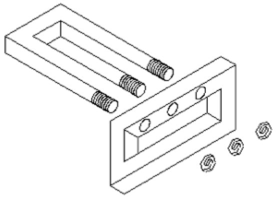
Necker cube

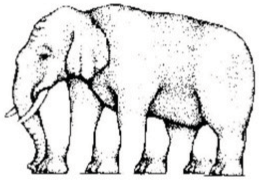
Necker cube effect on a Roman mosaic

"Impossible" geometries

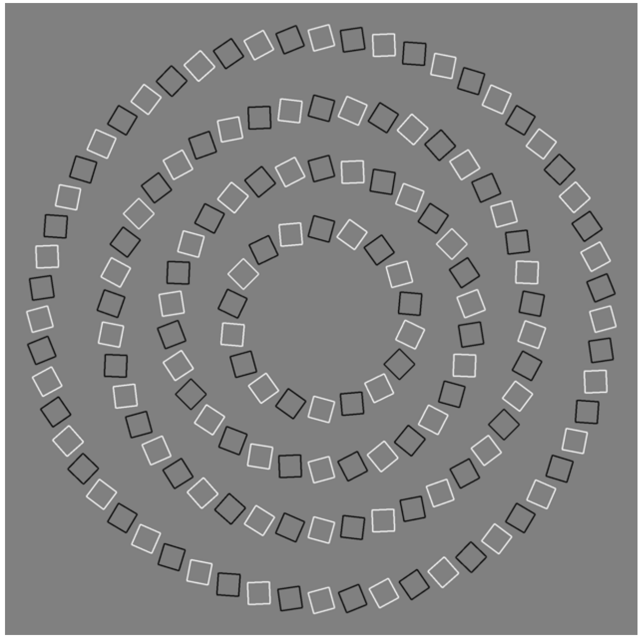


Penrose triangle





Optikai illusions – geometry

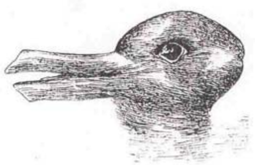


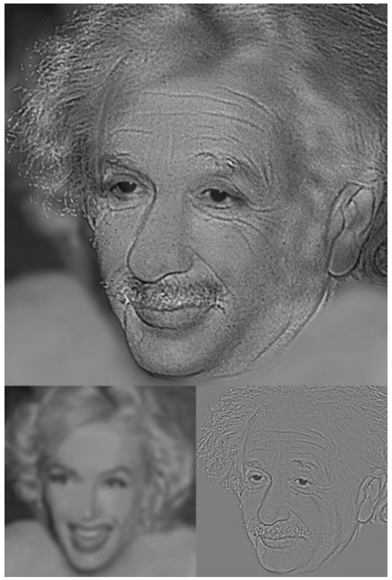
Pinna illusion: Spiral, or concentric rings?

Optikai illusions – shape

Reverzible shapes, complementary shapes

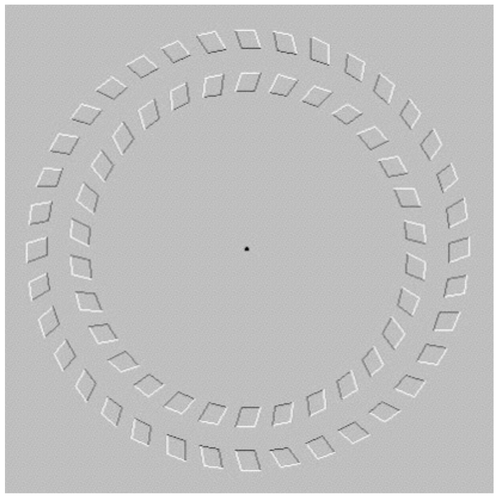
Rubin vase illusion



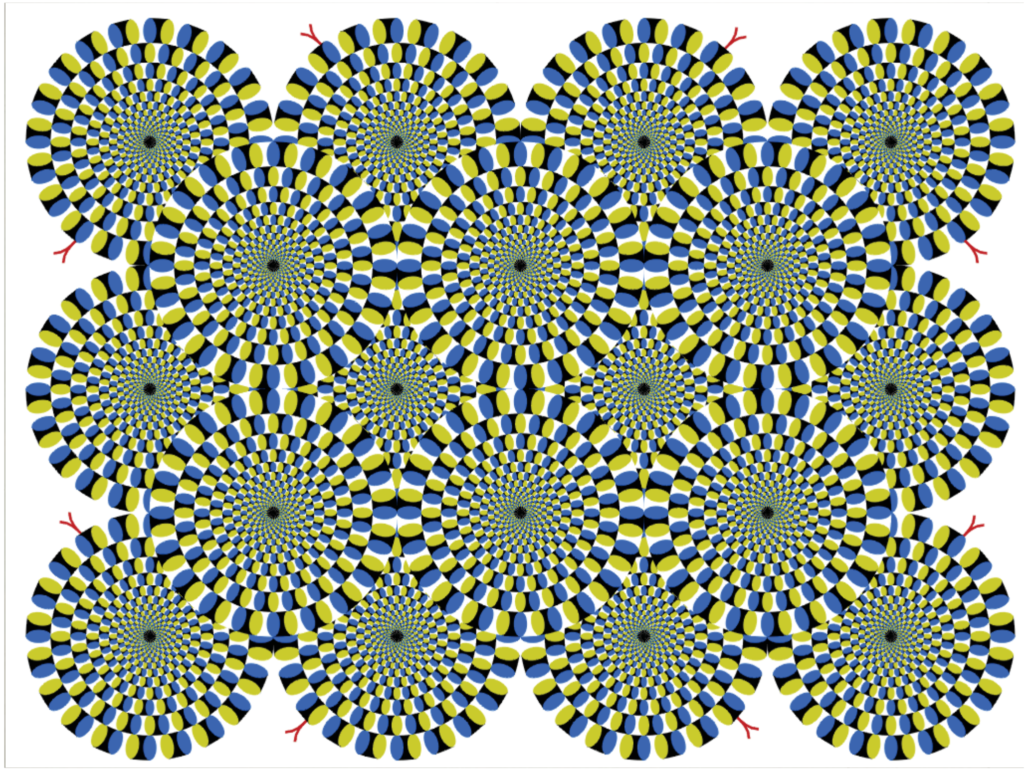


"Gestalt" Contour

Optical illusions – motion

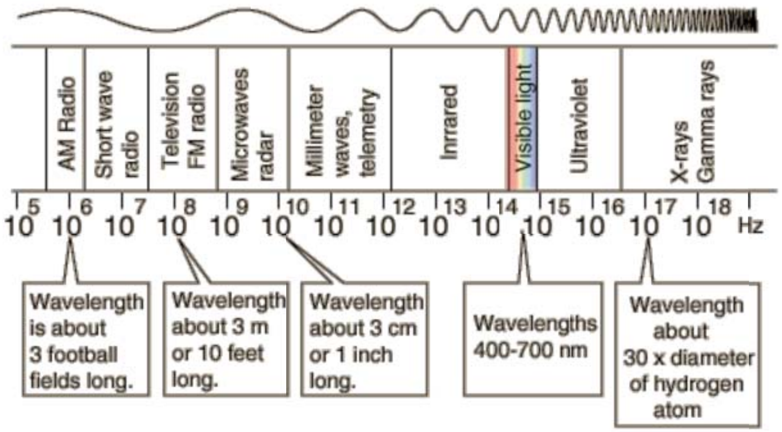


Optical illusions point out the remarkable and unusual processing power of the visual system.



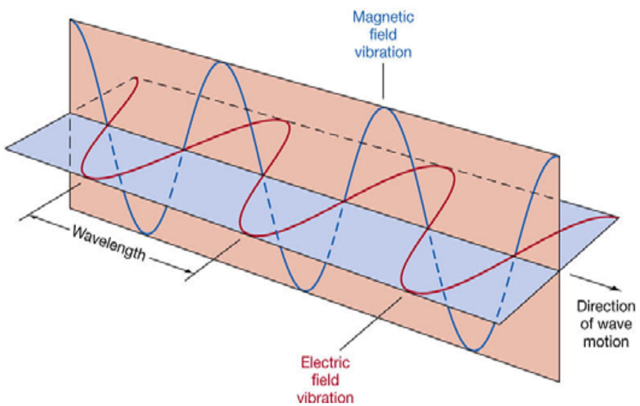
Stimulus: light

Electromagnetic wave



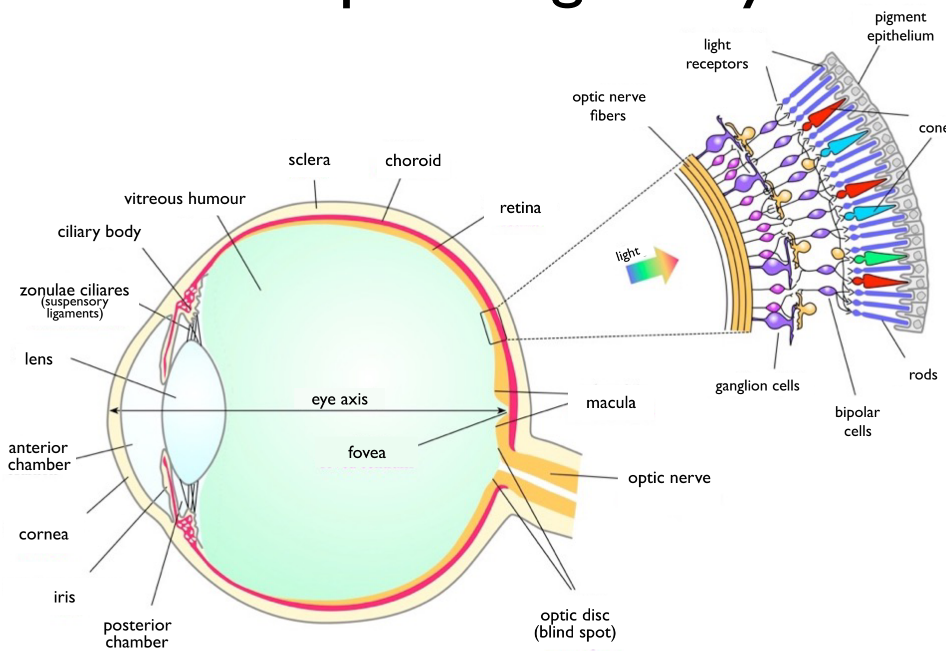
Stimulus: light

Transverse wave

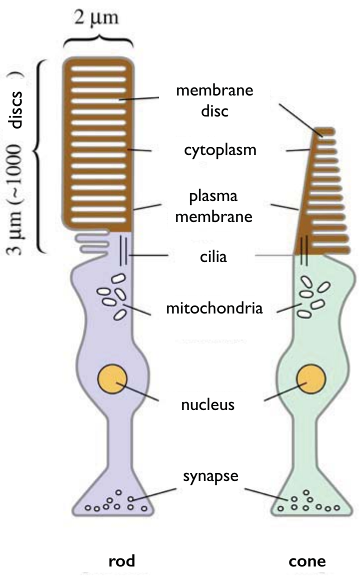


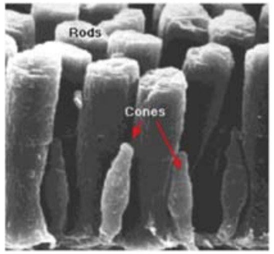
The eye is sensitive to: wavelength and amplitude (~intensity)
The eye is insensitive to: phase and polarization

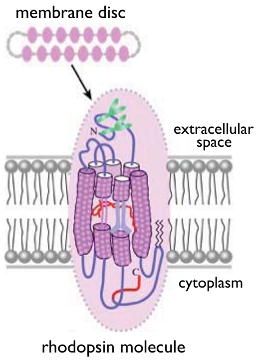
“Receptor-organ”: eye

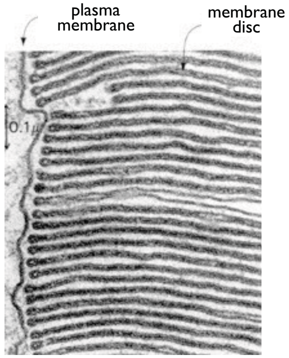


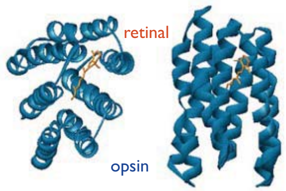
Photoreceptors







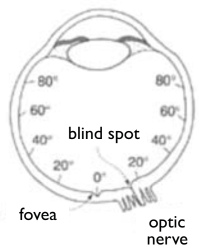


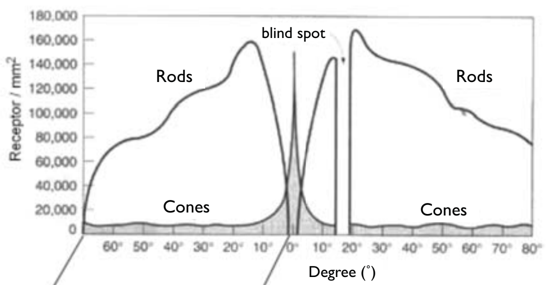


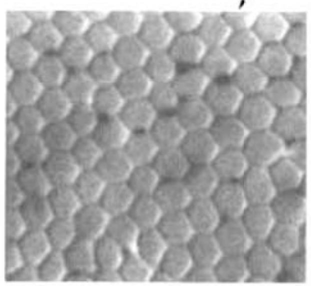
Properties of receptor cells

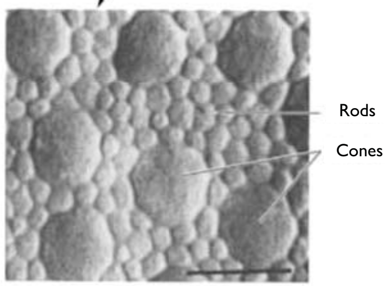
Rod	Cone
Stimulated by very small intensity (optimally 1 photon!)	Smaller sensitivity, but functions at high intensities
Saturates at average intensities	No saturation
Found mainly in the peripheral retina	In the fovea, mainly central fovea
Many rods per ganglion (convergence); greater sensitivity, smaller spatial resolution	Small convergence; greater spatial resolution
No color sensitivity	Sensitivity to colors

Photoreceptor distribution in retina

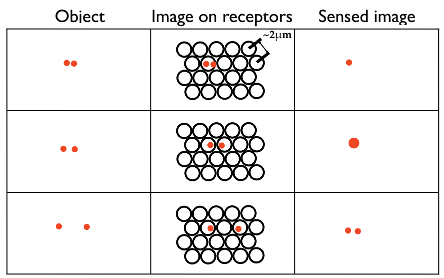








Photoreceptor density determines the biological resolution of the eye



- Condition of resolution: at least one inactivated receptor cell falls in between two activated ones. The limiting angle of view under this condition is (α_B)≈ **0.8'**
- The diffraction and biological limits of the human eye are **comparable**!

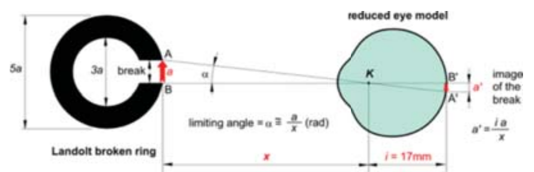
Visual Acuity ("visus", vision):

$$visual\_acuity = \frac{1'}{\alpha} 100\%$$

α = experimental (measured) visual angle

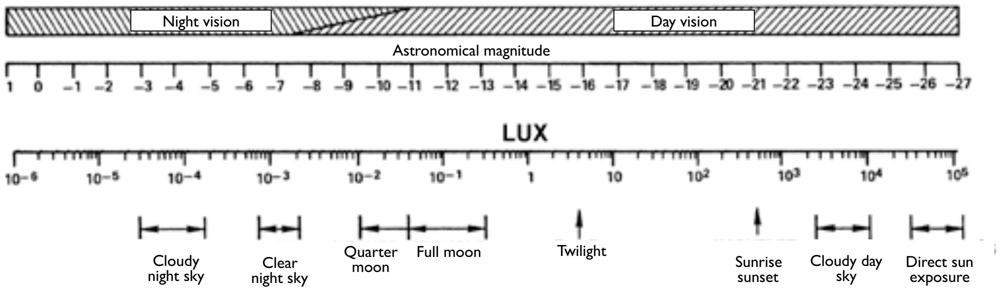
Average visual angle in healthy humans:
1' (= 100% vision)

Measurement of visual acuity

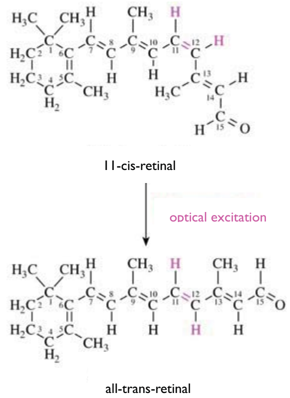


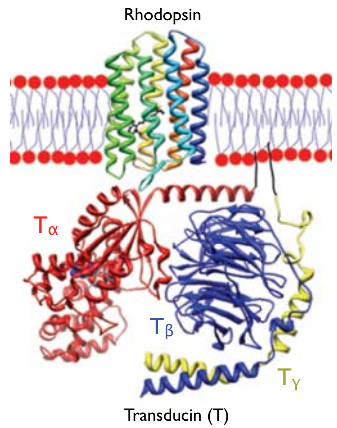
Generation of visual stimulus

Sensitivity of the human eye:
10^{-9} - 10^{5} lux!



Basis of light sensing: photochemical reaction





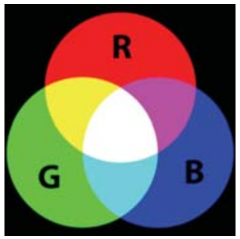
1 rhodopsin absorbs 1 photon
↓
metarhodopsin
↓
transducin molecule activated (T_α subunit dissociates from the $T_{\beta\gamma}$ subunit)
↓
500 phosphodiestherase molecules activated
↓
10^5 cGMP molecules hydrolyzed
↓
250 Na^+-channels closed
↓
Entrance of 10^6-10^7 Na^+ ions/s inhibited
↓
cell hyperpolarized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

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

n: change in number of Na ions
e: elementary charge
Δφ: membrane p otential
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)

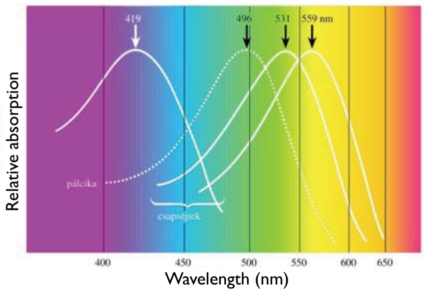


Additive color coding

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

$$X = rR + gG + bB$$

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

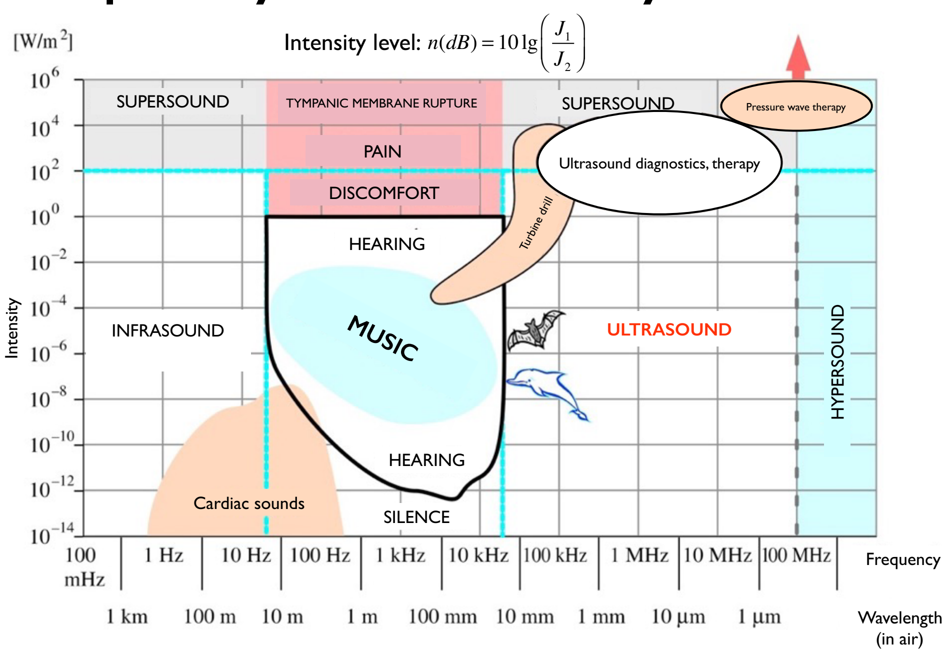


In the human eye:

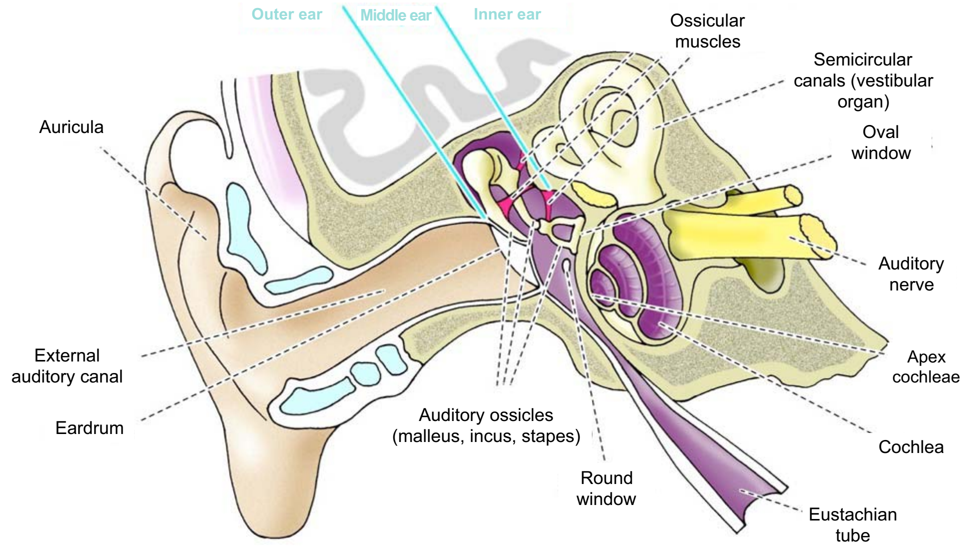
- 3 different color-sensitive receptors.
- Each receptor absorbs in different regions of the visible spectrum (R=64%, G=32%, B=2%).

Biophysics of hearing

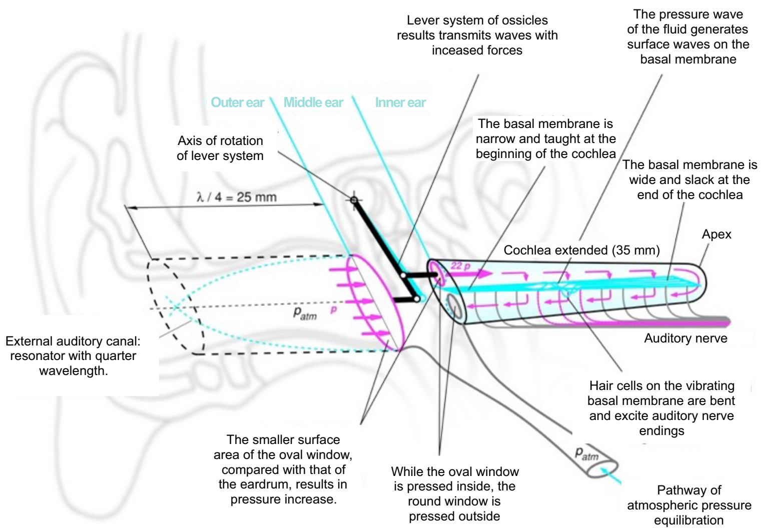
Frequency and intensity of sounds



"Receptor-organ": ear



Physical schematics of the ear



Outer ear: sound collector

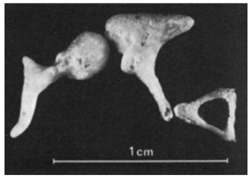
Auricula
Sound is steered into the external auditory canal.

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

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

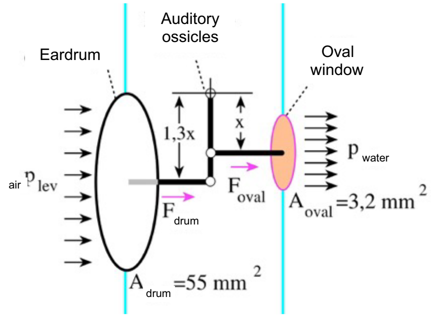
Auditory ossicles
(malleus, incus, stapes)



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 ×

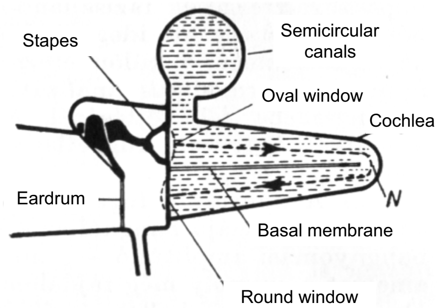
Total amplification: 22× (pressure increase)



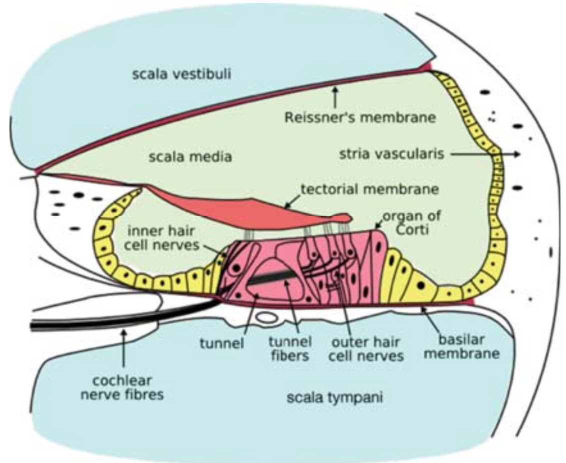
Inner ear: sensor

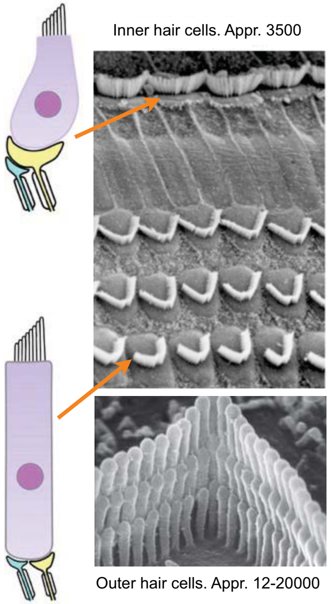
Vestibular organ: semicircular canals

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.

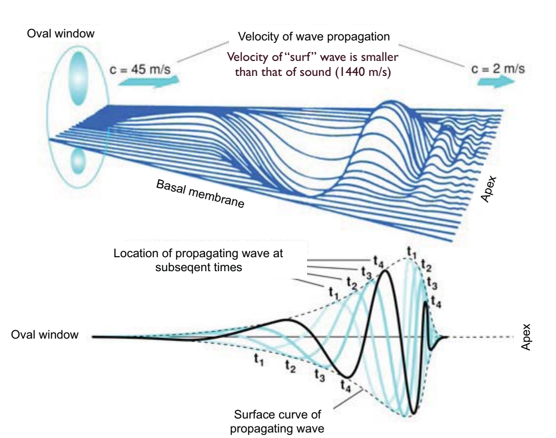


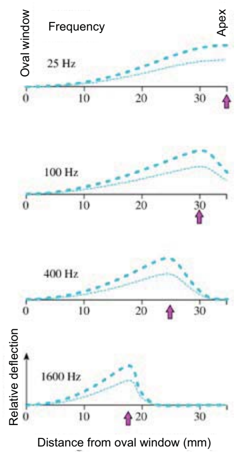
Ultrastructure of the inner ear





Békésy: propagating surface waves on basal membrane



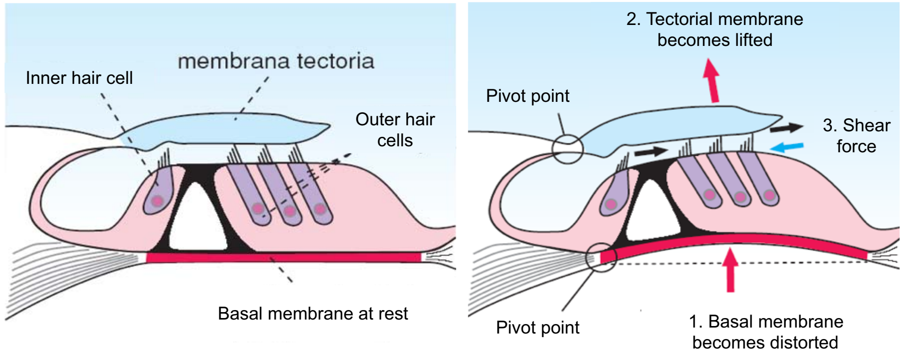


György Békésy
Nobel-prize 1961

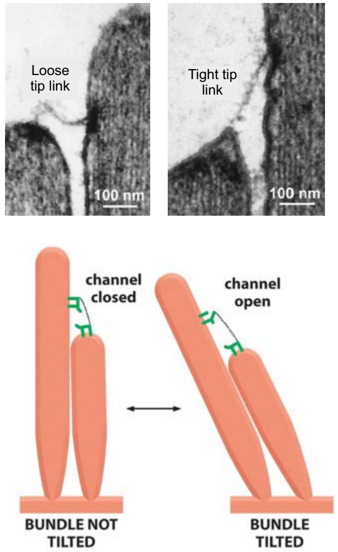
The frequency-dependence of the location of propagating wave maxima provide a rough frequency-discrimination.

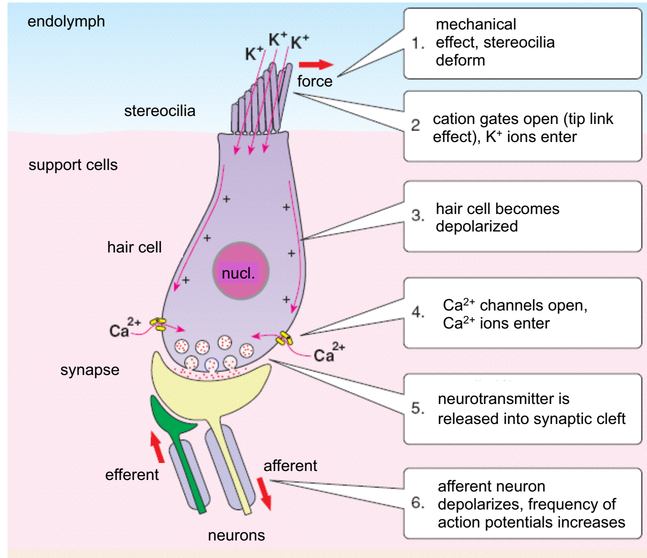
Function of the organ of Corti

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



Inner hair cells: Mechanoelectric transducers





Passive versus *active* detection

Passive detection (Problem: too large damping)

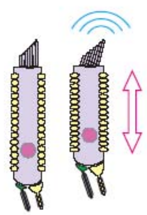
- H. Helmholtz (1857): resonating strings.
- Békésy Gy. (1930-40's): basalmembrane resonates (position coding).

Active detection (Energy is pumped into the system at the resonance frequency)

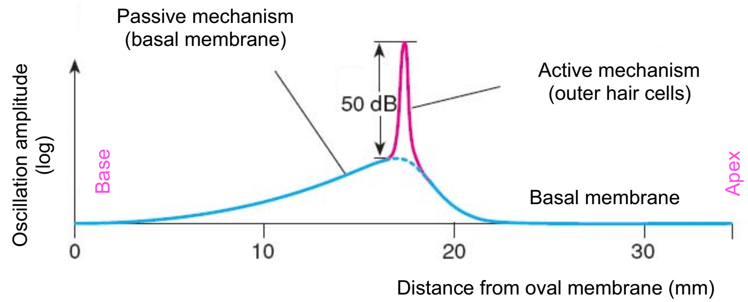
- T. Gold (1948): abalogy with the regenerative radio receivers (positive feedback at a given frequency: selectivity + sensitivity).
- W. Rode (1971): living ear is more sensitive.
- D. Kemp (1979): the ear generates sound (otoacoustic emission).

Tuned to the critical point the hair cells become highly sensitive to small stimuli (similarly to bending at the critical load)

Outer hair cells: amplifiers



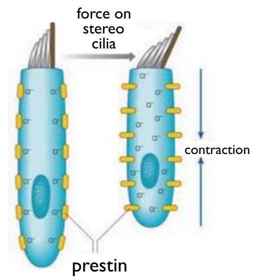
Outer hair cells



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

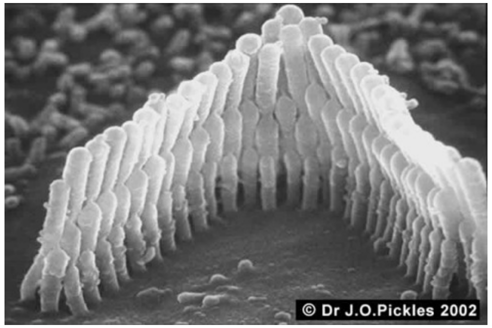
Amplification function of outer hair cells

Outer hair cell

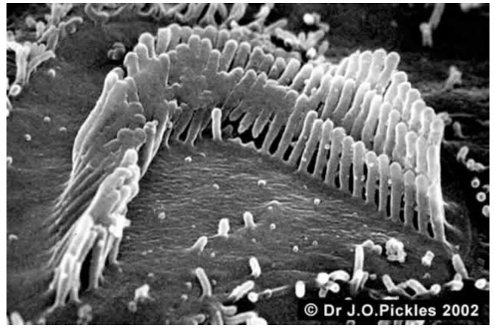


Responsible protein - **prestin**, transmembrane motor protein
mechanoelectric and electromechanical transduction

Acoustic damage



Outer hair cells (normal state)



Outer hair cells (damaged state; e.g., after a concert)

Coding of acoustic information

Location theory

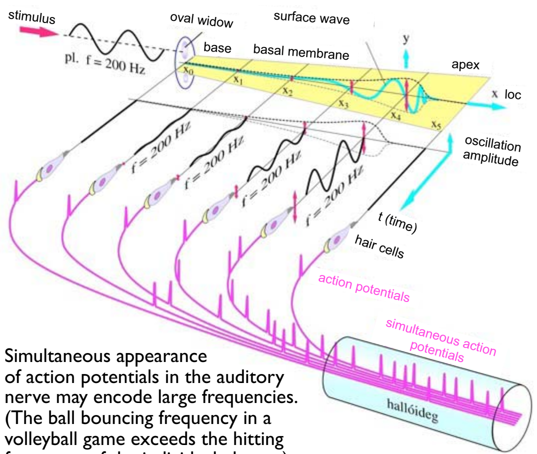
Frequency sensing coded spatially (in the cortex).

Basis:

1. Weak frequency-dependence of the amplitude maxima of propagating surface waves.
2. Active amplification.
3. Frequency sensitivity of afferent neurons innervating the inner hair cells.
4. Cortical projection of afferent neurons is spatially different - "coded by location".

Volleyball theory

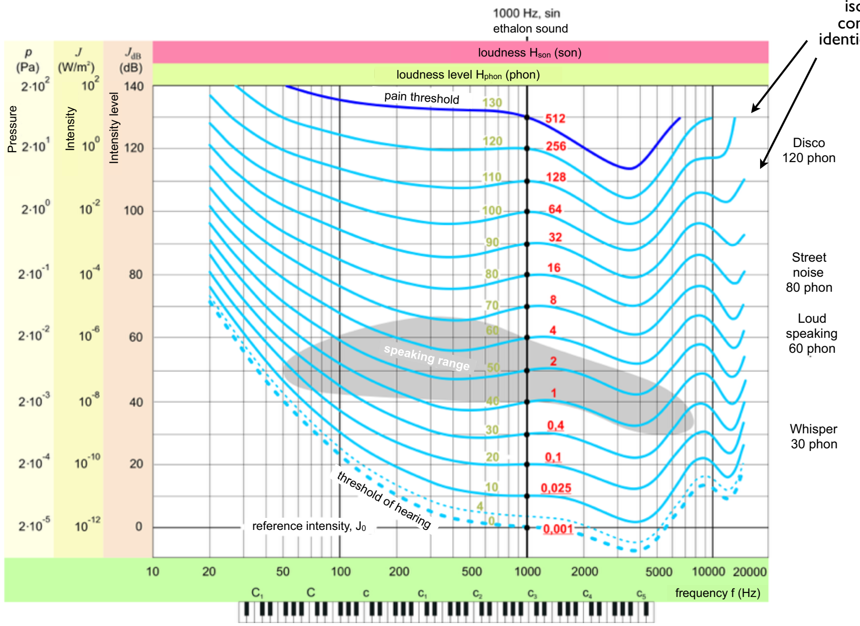
Problem: frequency of action potential is limited (cca. 1 kHz).



Simultaneous appearance of action potentials in the auditory nerve may encode large frequencies. (The ball bouncing frequency in a volleyball game exceeds the hitting frequency of the individual players.)

Psychoacoustics: loudness
(Fletscher-Munson)

isophon curves: connect points of identical loudness level

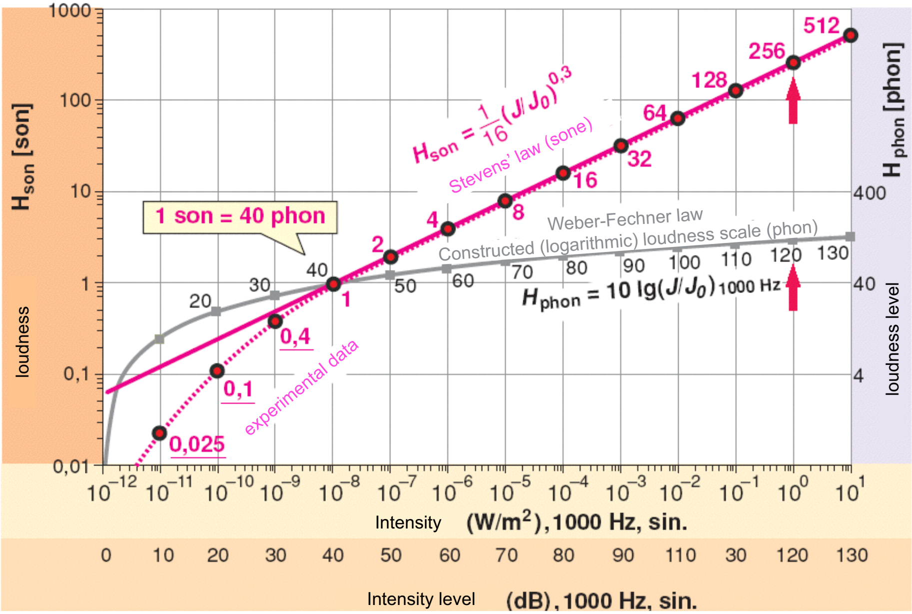


N.B.: The loudness level of a sound, in phon, is the dB value of a 1000 Hz sound with which we hear it identically loud.

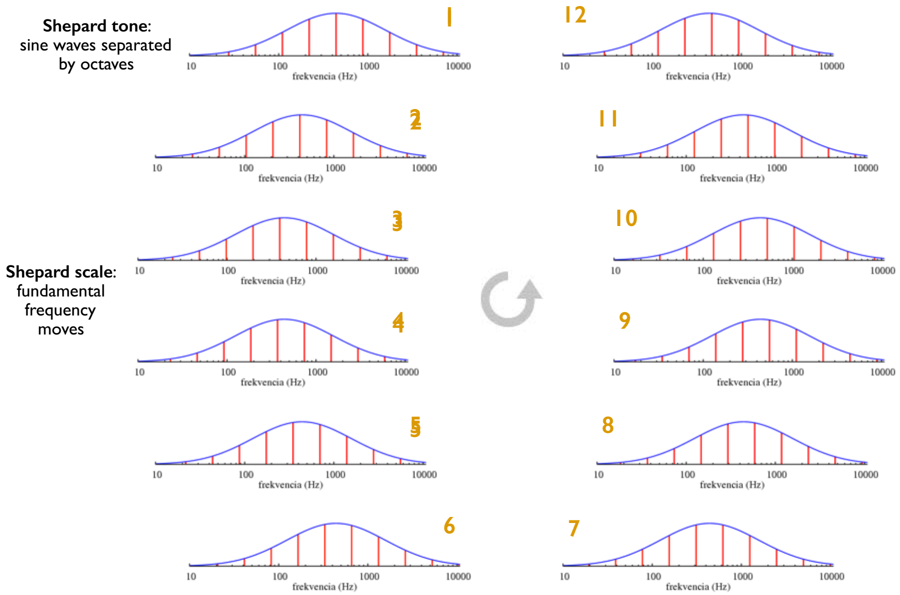
Subjective loudness (son scale): 10 dB increase in loudness level is perceived as doubling of loudness.

Phon and son scales

Stevens' law describes psychoacoustics more precisely



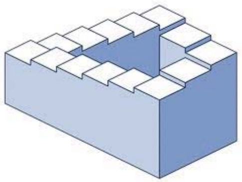
Acoustic illusion?

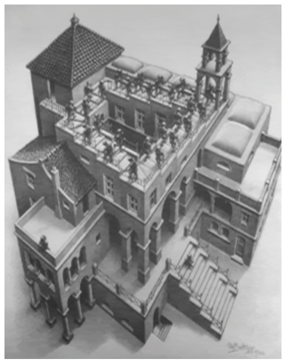


Acoustic illusion?

Visual analogs of the Shepard scale:

Maurits Cornelis Escher
(1898-1972)





Escher staircase

Barber's pole