

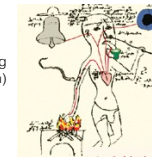
BIOPHYSICS OF SENSORY RECEPTORS

VISION, HEARING

MIKLÓS KELLERMAYER

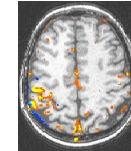
Theories about sensing

Cardiocentric sensing
(Medieval reconstruction)



Aristotle (384-322 BC)
cardiocentric sensing.

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



fMRI recording during
sensorimotor function

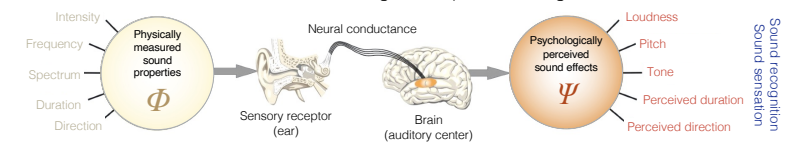


Sensory homuncle

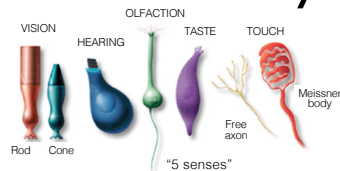
Today:

- stimulus
- sensory receptors
- receptor potential
- neuron/nerve
- action potential
- central nervous system
- signal processing
- sensation

Process of sensing - example of hearing



Sensory receptors



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.

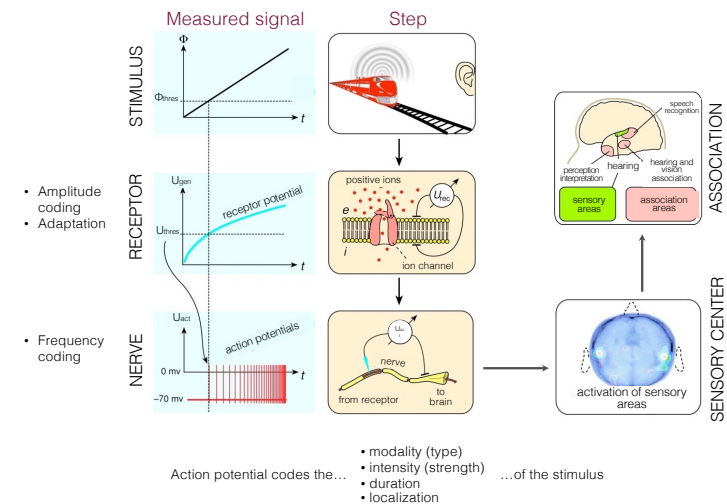
Cell surface receptor (different meaning!): Proteins which specifically bind hormones, neurotransmitters and other molecules, and thus initiate specific cellular reactions.

	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 pressure	Nerve endings	Sinus carotid 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



I. Modality

Sensory modality refers to the way information is encoded. Thus, it corresponds to the physical and chemical 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 perception strength

Weber-Fechner psychophysical law

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



Ernst Weber
(1795-1878)



Gustav Fechner
(1801-1887)

Stevens' power law

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



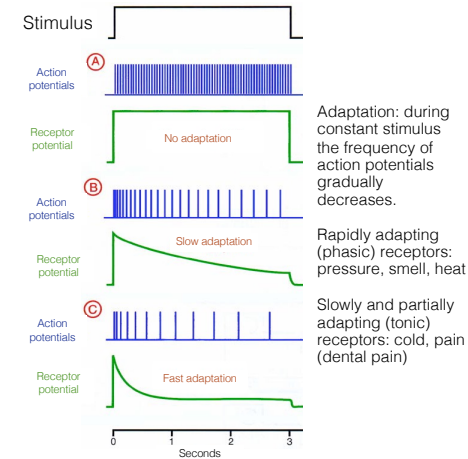
Stanley Smith Stevens
(1906-1973)

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

$n < 1$: compressive function (hearing, vision)

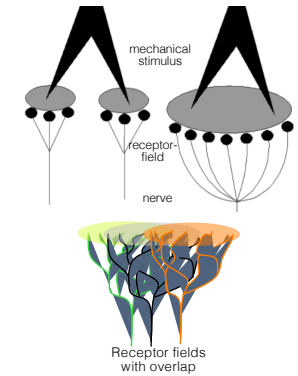
$n > 1$: expansive function (pressure, taste)

3. Duration, adaptation



4. Localization

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



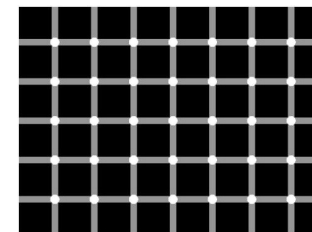
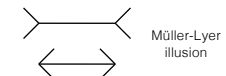
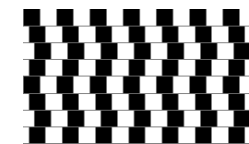
Biophysics of vision

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

Optical illusion - intensity



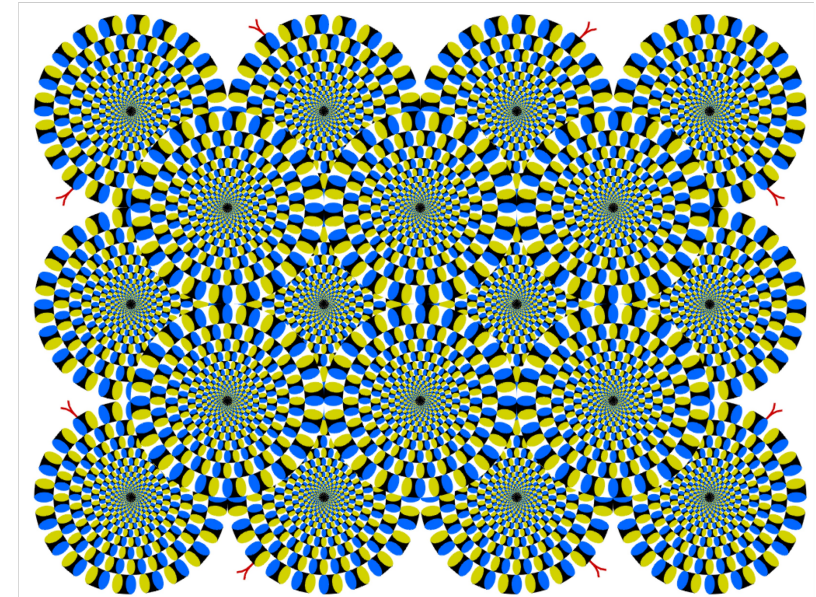
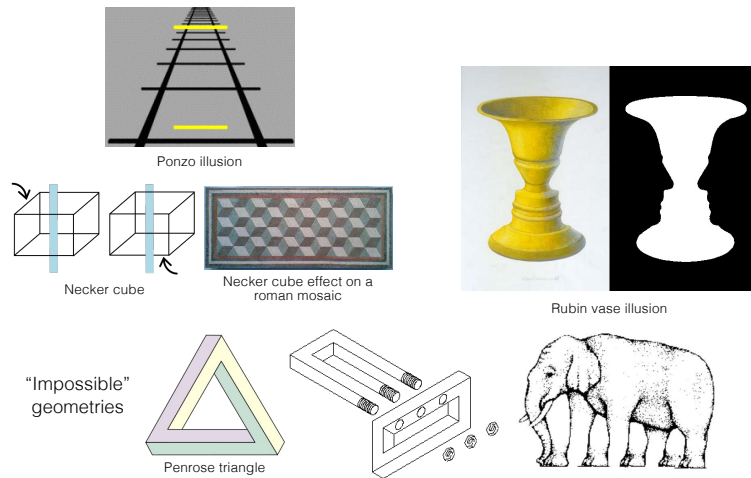
Optical illusion - direction, size



BIOPHYSICS OF VISION

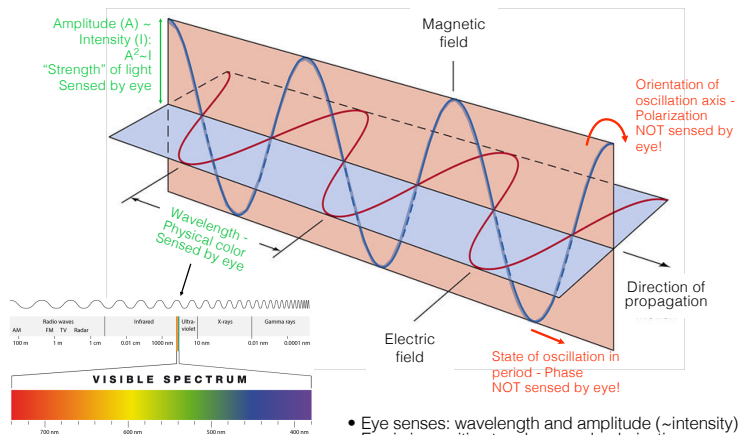
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Optical illusions – space, shape



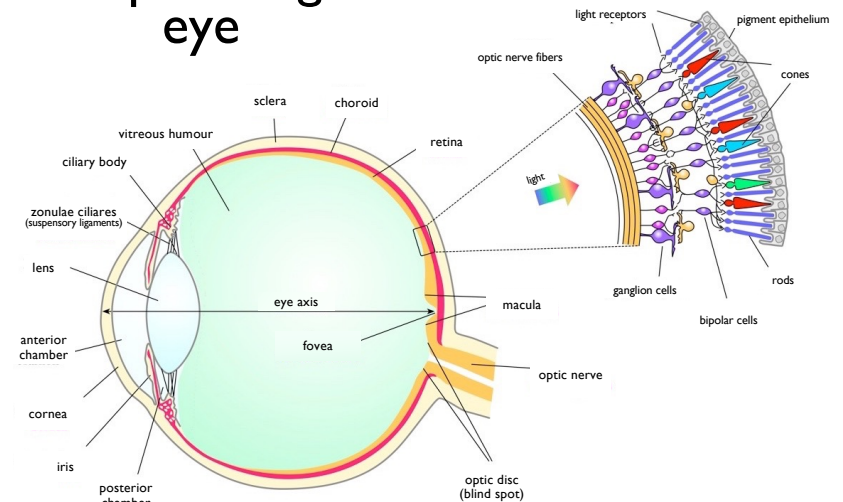
Stimulus of vision: light

Electromagnetic (transverse) wave

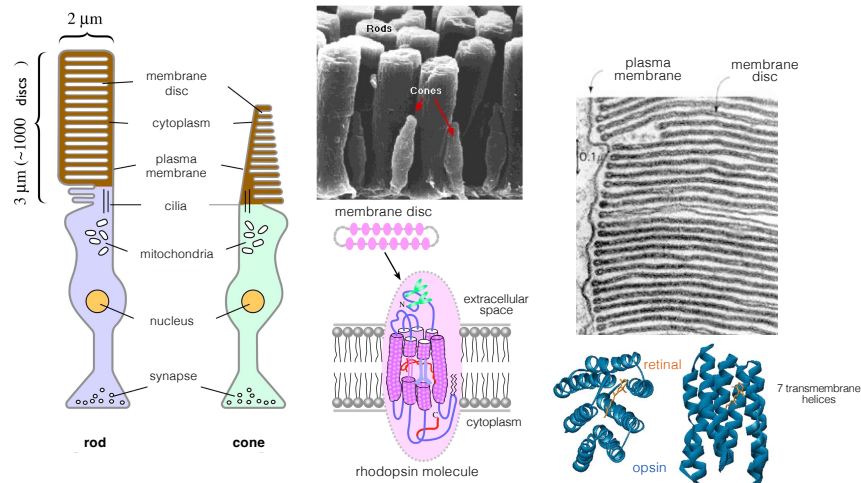


- Eye senses: wavelength and amplitude (~intensity)
- Eye is insensitive to: phase and polarization

"Receptor-organ": eye

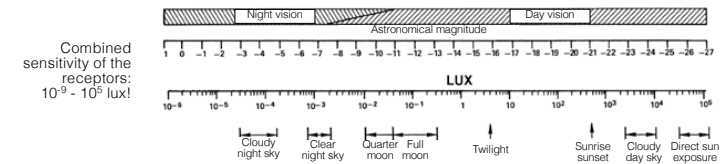


Photoreceptors

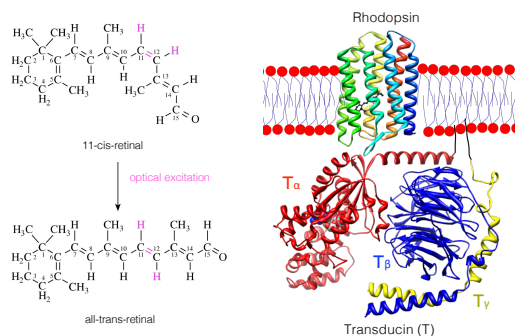


Properties of receptor cells

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	Low frequency sensitivity (~20 hz)



Basis of light sensing: photochemical reaction



Amplification: $A \approx 10^4$

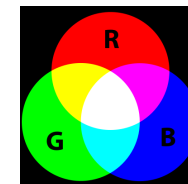
$$A = \frac{E_{ion}}{E_{photon}} = \frac{ne\Delta\phi}{hf}$$

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

1 rhodopsin absorbs 1 photon
 ↓
 metarhodopsin
 ↓
 transducin molecule activated (T_α subunit dissociates from the $T_\beta\gamma$ subunit)
 ↓
 500 phosphodiesterase molecules activated
 ↓
 10⁵ cGMP molecules hydrolyzed
 ↓
 250 Na⁺-channels closed
 ↓
 Entrance of 10⁶-10⁷ Na⁺ ions/s inhibited
 ↓
 cell hyperpolarized (1 mV)
 ↓
 transmitter release reduced (glutamate: inhibitory neurotransmitter).

Color sensing

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

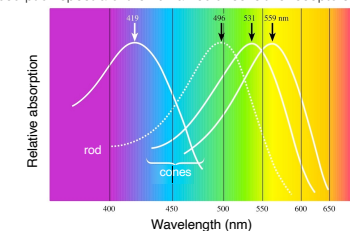


Additive color coding

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

$$X = rR + gG + bB$$

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



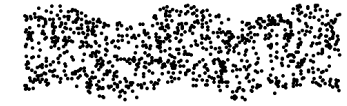
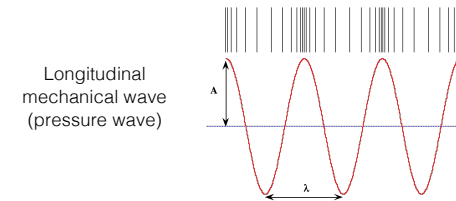
In the human eye:

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

BIOPHYSICS OF HEARING

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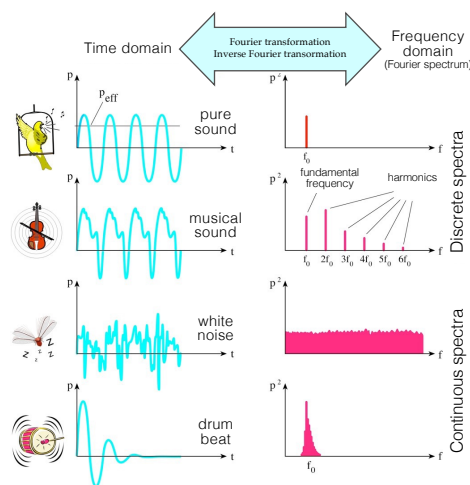
Sound



Harmonic oscillation: $y(t) = A \sin(ft + \varphi)$

y =actual pressure; t =time
 f =frequency (Hz); A =amplitude
 φ =phase shift

Sounds and their spectra



Fourier theorem:
 any function can be expressed as the sum of a fundamental sine wave and its harmonics

Steps of Fourier transformation:

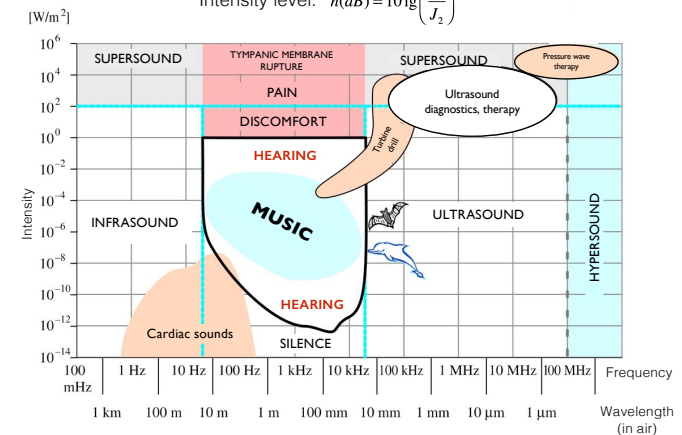


Octave - frequency difference with a 2:1 ratio

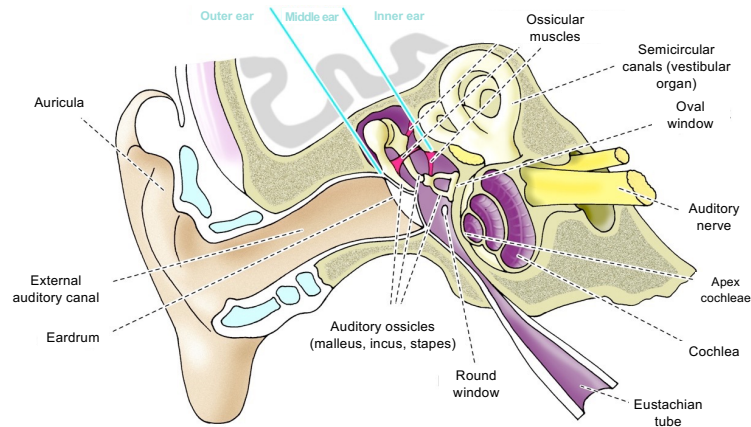
Sound intensity and frequency

Stimulus: sound - mechanical wave

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



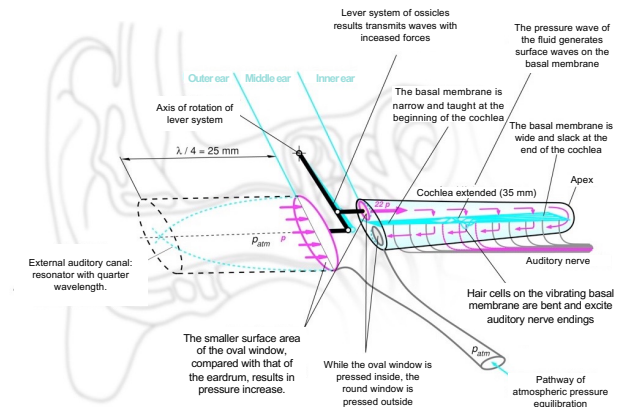
“Receptor-organ”: ear



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 frequency 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!)



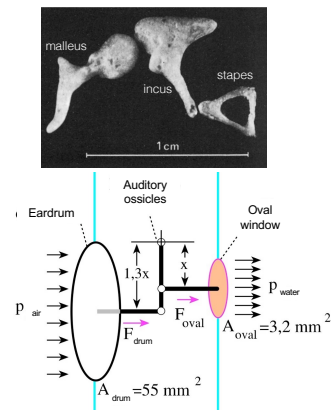
Middle ear: mechanical transmitter and amplifier

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: $17 \times$
due to lever action: $1,3 \times$

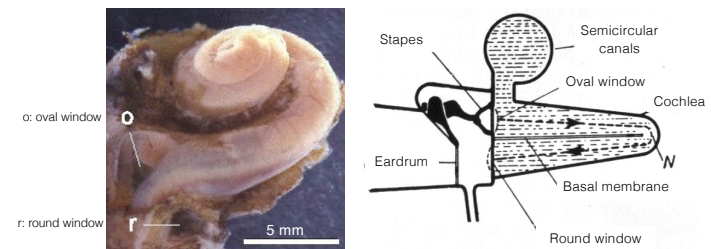
Total amplification: $22 \times$ (pressure increase)



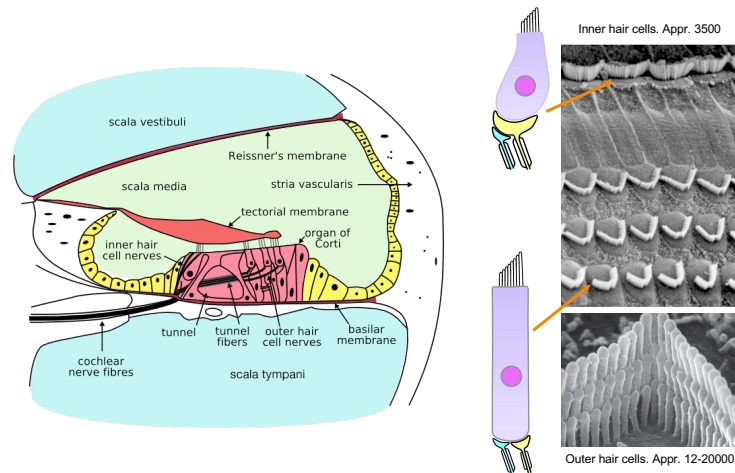
Inner ear: sensor

Vestibular organ: semicircular canals

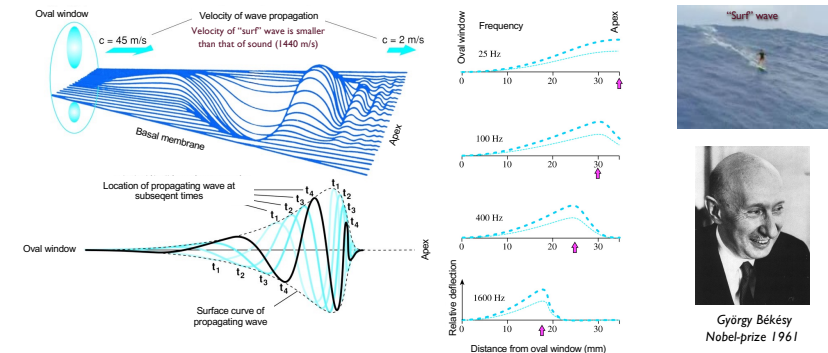
Cochlea: 2.5-pitch, 35-mm-long fluid-filled channel. It is halved in length partly by an osseous, partly by a membranous wall, the basal membrane. Sensory organ of sound.



Ultrastructure of the inner ear



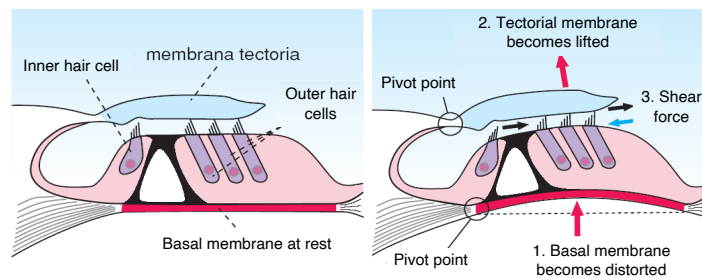
Békésy: propagating surface waves on basal membrane



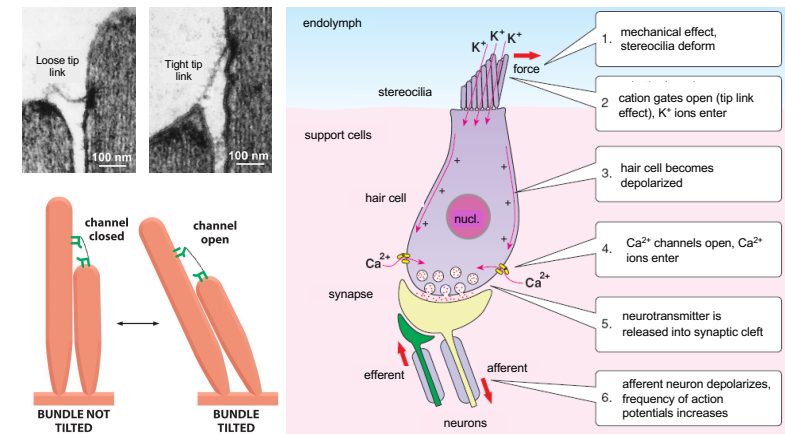
The frequency-dependence of the location of propagating wave maxima provide a rough frequency-discrimination.

Function of the organ of Corti

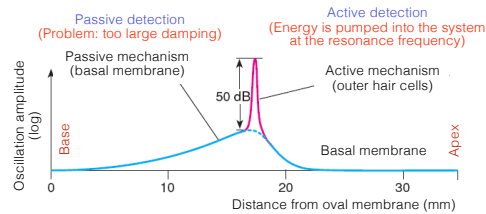
Due to the bending of the basal membrane, hair cells become tilted and depolarized.



Inner hair cells: Mechanoelectrical transducers



Outer hair cells: amplifiers

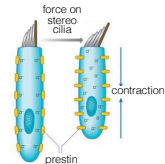


Amplification: sound-induced contraction in outer hair cells



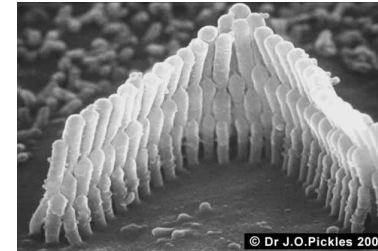
- Observations pointing at active detection:
- T. Gold (1948): analogy with regenerative radio receivers (positive feedback at a given frequency: selectivity + sensitivity).
 - W. Rode (1971): living ear is more sensitive.
 - D. Kemp (1979): the ear generates sound (otoacoustic emission).

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

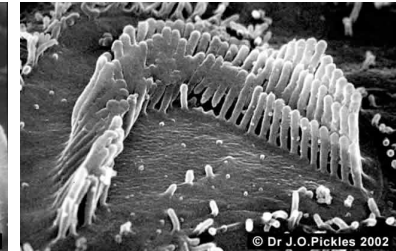


Prestin - transmembrane motor protein. Mechano-electric and electromechanical transduction

Acoustic damage

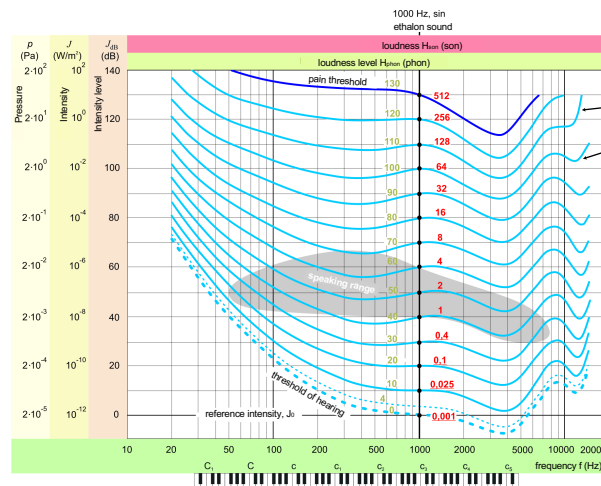


Outer hair cells (normal state)



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

Stimulus intensity and sensing - psychoacoustics



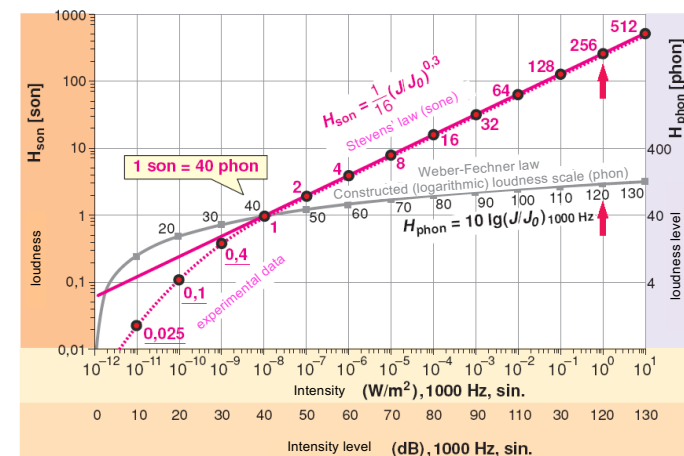
Isophon curves: connect points of identical loudness level
Fletcher-Munson curves

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.

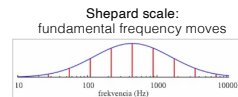
Subjective loudness (son scale): 10 dB increase in loudness level is perceived as doubling of loudness. (Stevens' law)

Phon and son scales

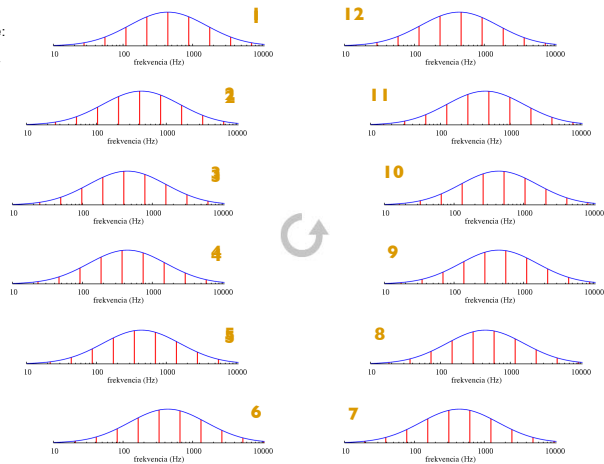
Stevens' law describes psychoacoustics more precisely



Acoustic illusion?



Shepard tone:
sine waves
separated by
octaves



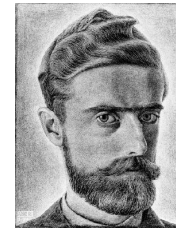
Feedback



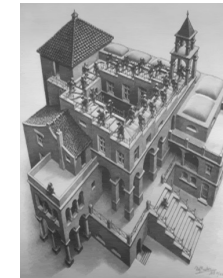
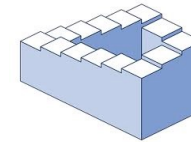
<https://feedback.semmelweis.hu/feedback/pre-show-qr.php?type=feedback&qr=3D773BQ2ESC6ER5W>

Acoustic illusion?

Visual analogs of the Shepard scale:



Maurits Cornelis Escher
(1898-1972)



Escher staircase



Barber's pole