

# BIOPHYSICS OF SENSORY RECEPTORS

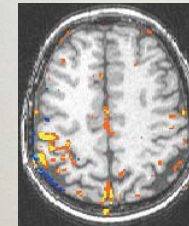
## Theories about sensing



Cardiocentric sensing  
(Medieval reconstruction)

Aristotle (384-322 BC)  
cardiocentric sensing.

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



fMRI recording during  
sensorimotor function



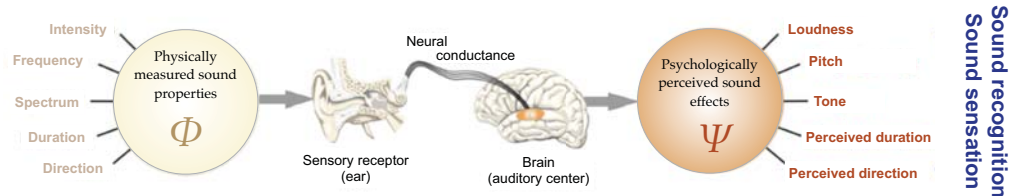
Sensory homuncle

Today:

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

## 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 initiate 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 pressure	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...

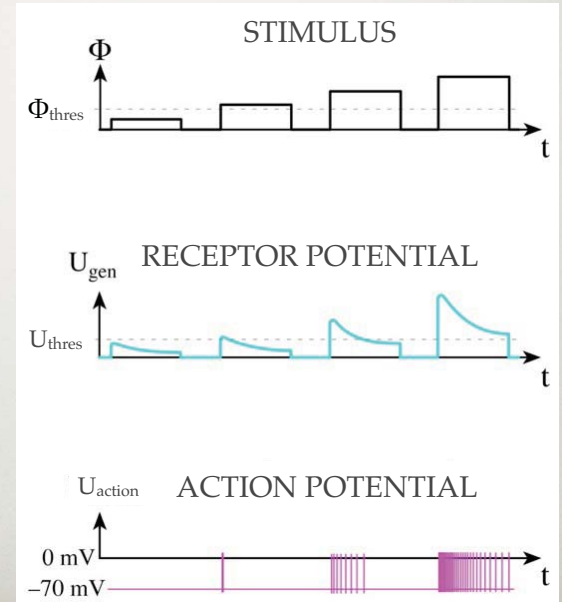
## Steps of signal transduction

Environment  
(physical-chemical effects)

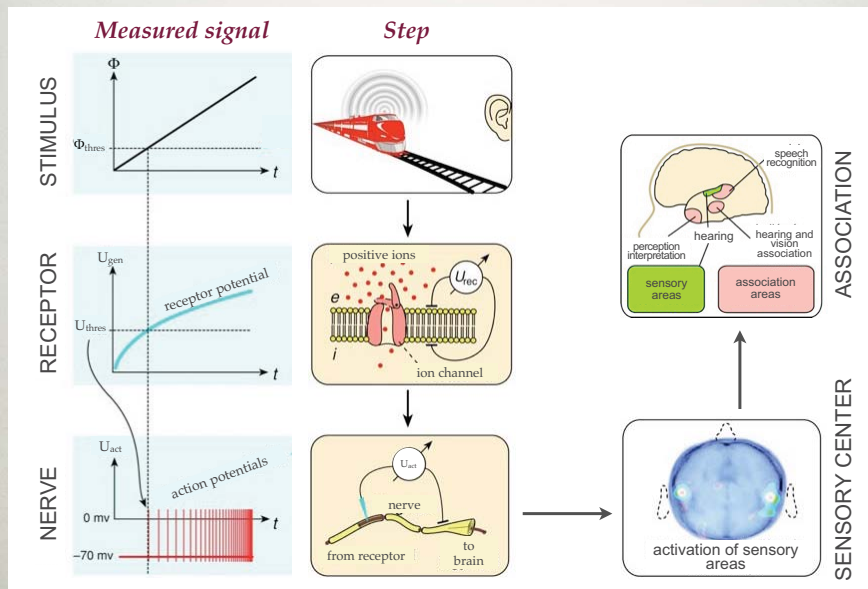
Receptor

Neuron

Central nervous system



## 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!

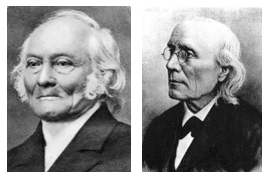
## 2. Intensity

Which parameters carry information about stimulus strength?

- frequency of action potentials
- number of activated receptor cells

Weber-Fechner  
psychophysical law

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



Weber (1795-1878) Fechner (1801-1887)

Stevens' law

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



Stevens (1906-1973)

$\psi$  = sensation strength  
 $\phi$  = background intensity  
 $\phi_0$  = 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

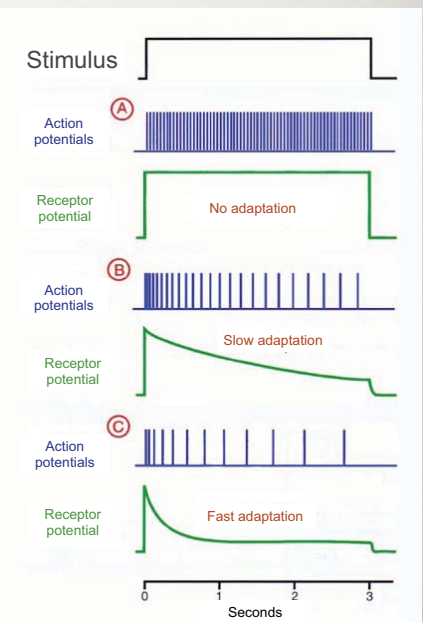
**Adaptation.** During constant stimulus the frequency of action potentials gradually decreases.

*Rapidly adapting (phasic) receptors*

E.g., pressure, smell, heat

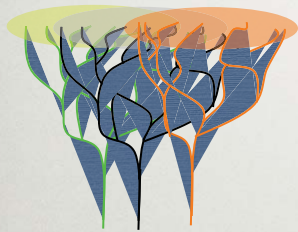
*Slowly and partially adapting (tonic) receptors*

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

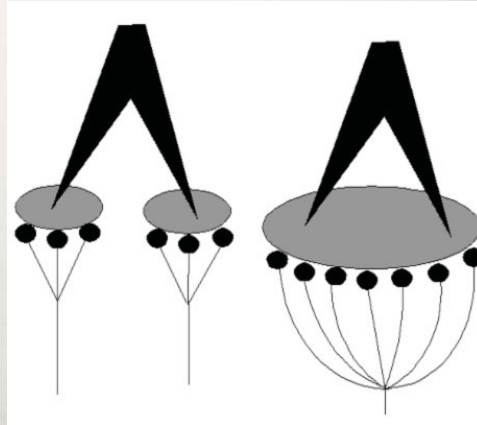


## 4. Localization, receptor fields

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

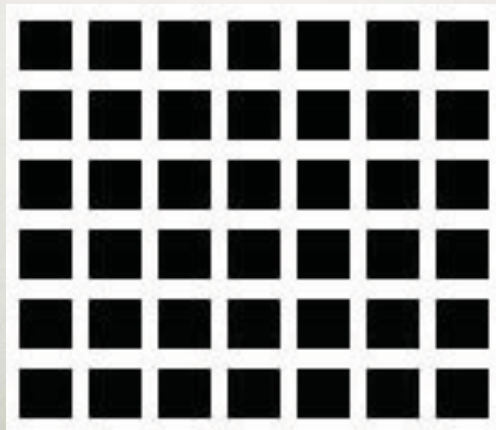


Receptor fields with overlap

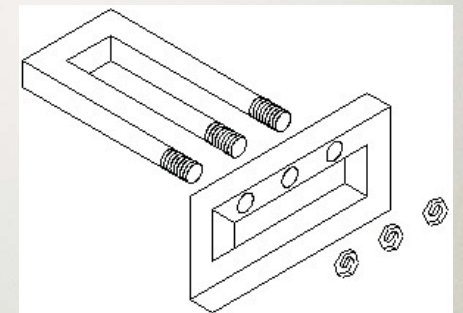
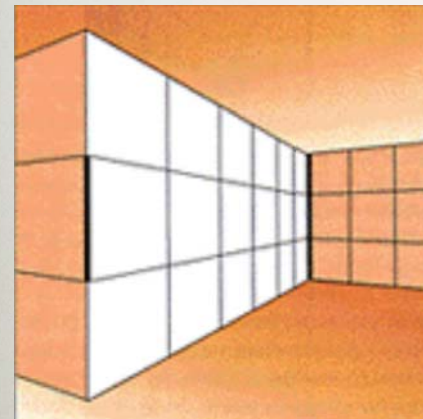


## BIOPHYSICS OF THE EYE

### Optical illusions – intensity

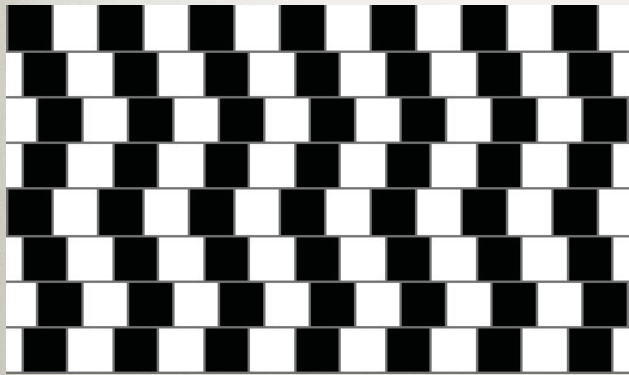


### Optical illusions – space

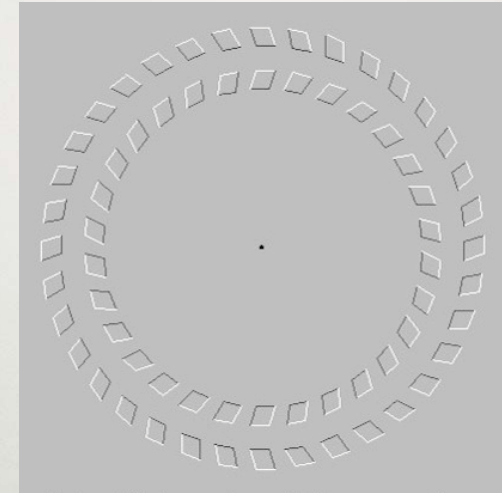




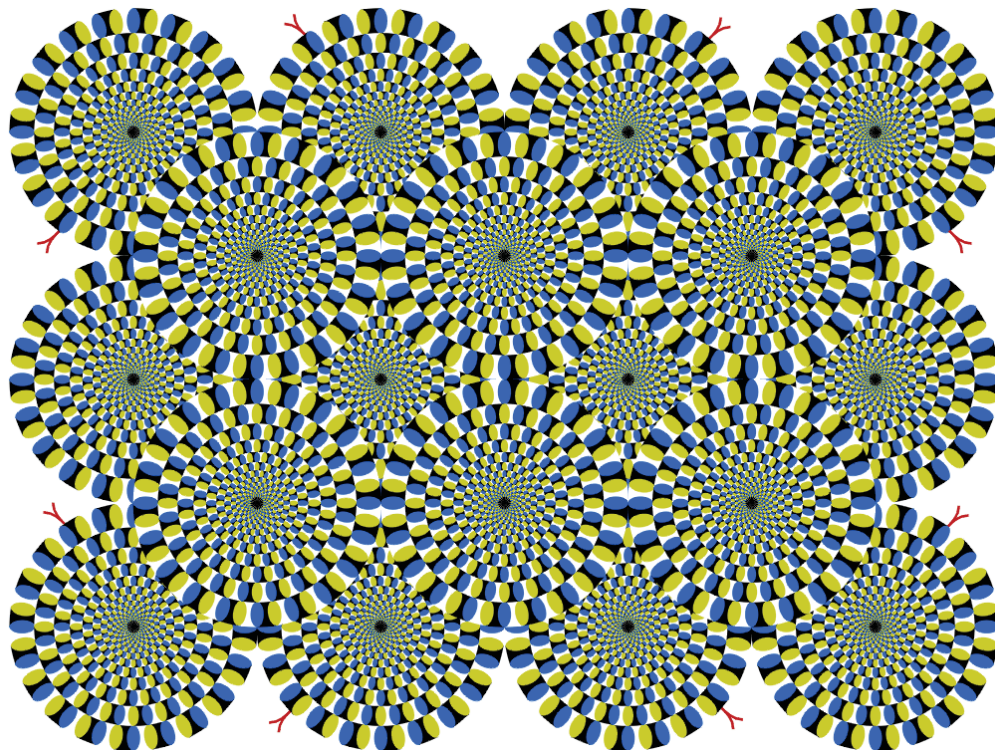
## Optical illusions - direction



## Optical illusions - motion

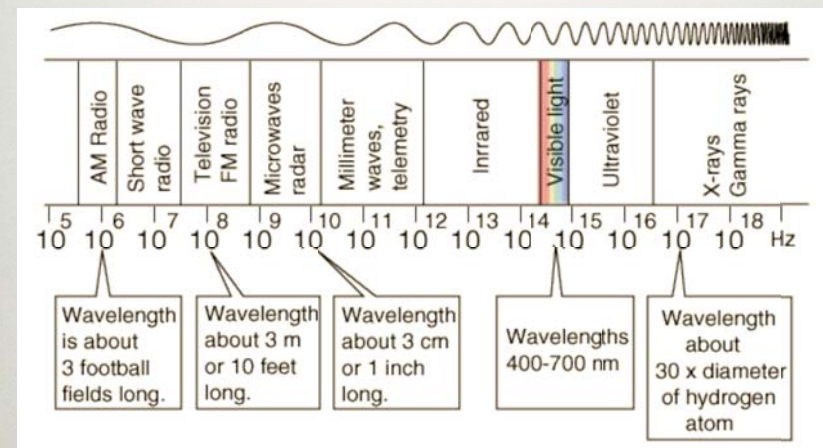


Optical illusions point out the remarkable and unusual processing power of the visual system.



## Stimulus: light

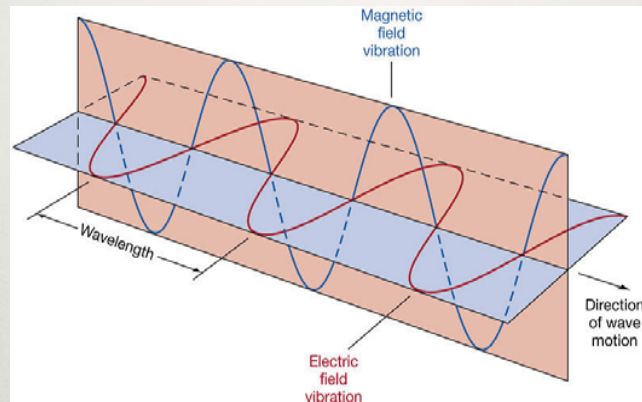
### Electromagnetic wave





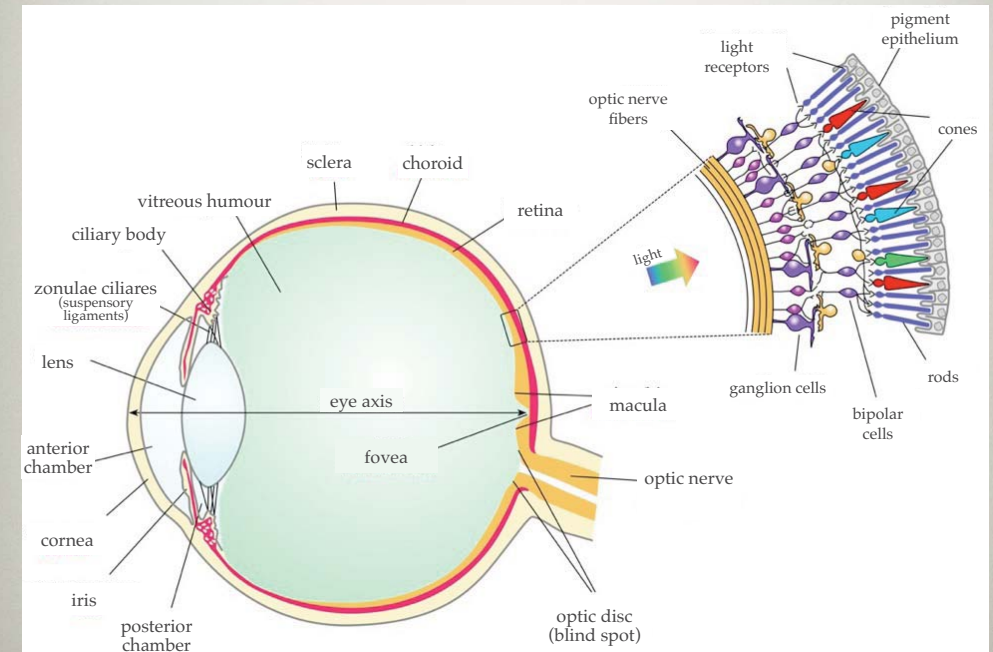
# Stimulus: light

## Transverse wave

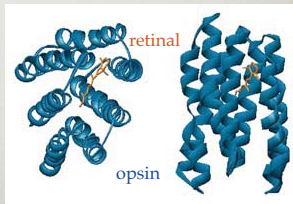
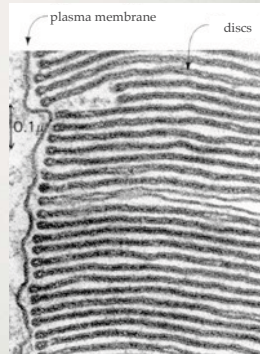
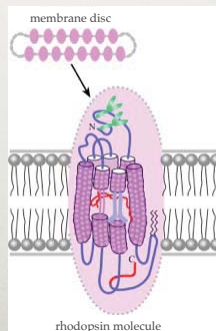
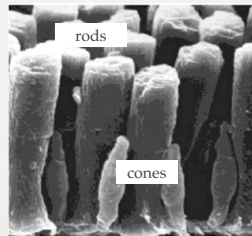
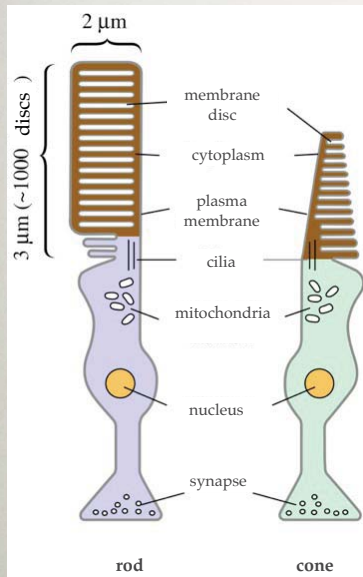


The eye is sensitive to: wavelength and amplitude (~intensity)  
The eye is insensitive to: phase and polarization

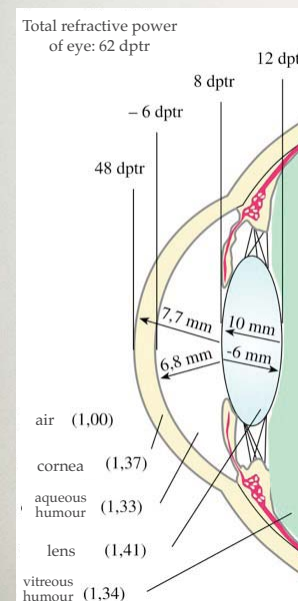
# "Receptor-organ": eye



## Photoreceptors



## Optics of the eye



Optical power entering the eye (P)

$$P = J\pi\left(\frac{d}{2}\right)^2$$

J=intensity (W/m<sup>2</sup>)  
d=pupil diameter

$$\frac{P_{\max}}{P_{\min}} = \left(\frac{d_{\max}}{d_{\min}}\right)^2 = 16$$

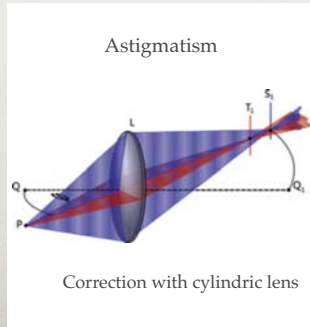
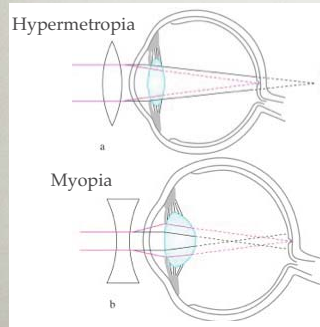
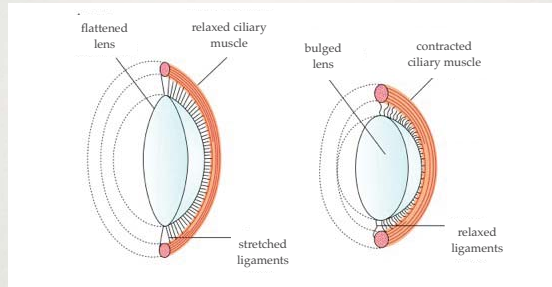
d<sub>max</sub>=8 mm  
d<sub>min</sub>=2 mm

Refractive power of surfaces (D)

$$D = \frac{n - n'}{r}$$

n-n'=refractive index difference between refractive media  
r=radius of curvature of refractive surface

## Accommodation and refractive problems



## Spatial resolution of the eye

**visual angle:** the smallest angle at which two object points can be distinguished.

For a healthy eye: 1' (angular minute, 1/60 degree)

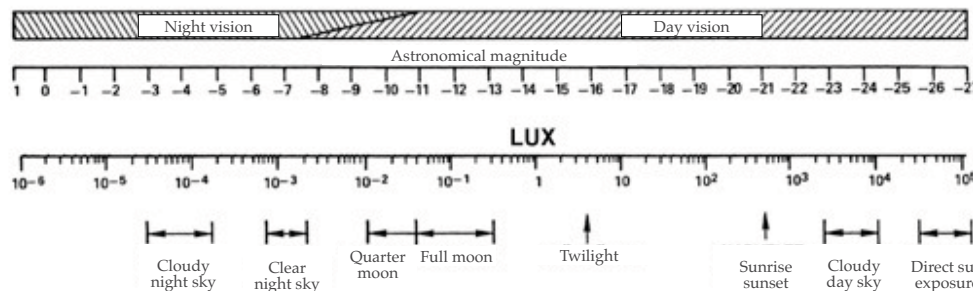
$$\text{visual\_acuity} = \frac{1'}{\alpha} 100\% \quad \alpha = \text{experimental visual angle}$$

Resolution has wave optics (diffraction) and biological (receptor density) limitations.

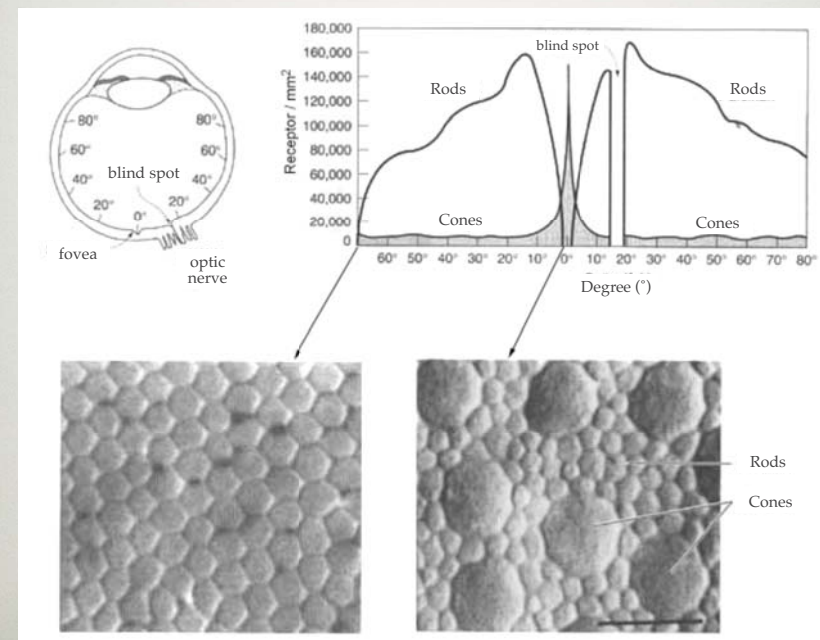
Object	Image on receptors	Sensation

## Generation of visual stimulus

### Sensitivity of the human eye



## Photoreceptor distribution in retina

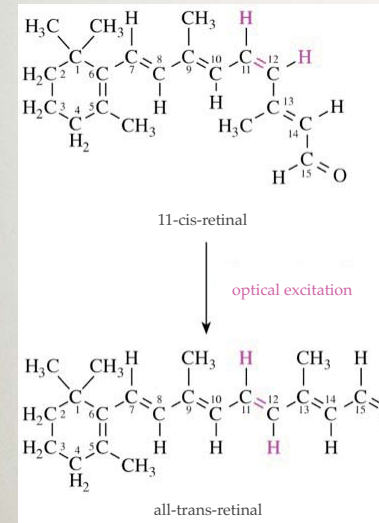




## Properties of receptor cells

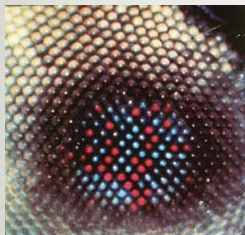
Rod	Cone
Stimulated by very small intensity (optimally 1 photon!)	Smaller sensitivity, but functions at high intensities
Saturates at average intensities	No saturation
Found mainly in the peripheral retina	In the fovea, mainly central fovea
Many rods per ganglion (convergence); greater sensitivity, smaller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

## Photochemical reaction

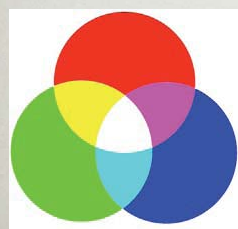


1 rhodopsin absorbs 1 photon  
 ↓  
 500 transducin molecules activated  
 ↓  
 500 phosphodiesterase molecules activated, and  
 ↓  
 10<sup>5</sup> cGMP molecules hydrolyzed  
 ↓  
 250 Na<sup>+</sup>-channels closed  
 ↓  
 Entrance of 10<sup>6</sup>-10<sup>7</sup> Na<sup>+</sup> ions/s inhibited  
 ↓  
 cell hyperpolarized (1 mV)  
 ↓  
 transmitter release reduced (glutamate: inhibitory neurotransmitter).

## Color vision

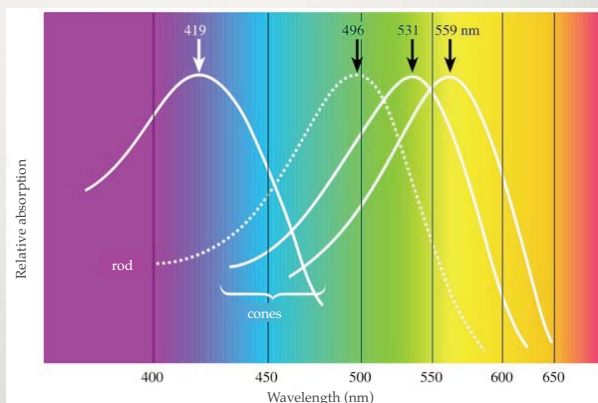


Light reflection from butterfly retina. The different receptors reflect different colors.



Additive color mixing

In human: 3 types of receptors. Each senses different colors - absorbs at different wavelengths (R=64%, G=32%, B=2%).



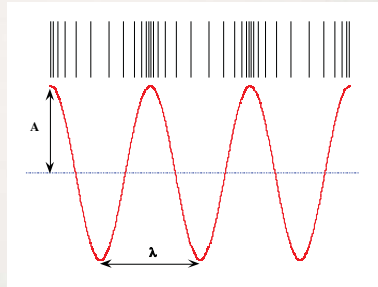
$$X = rR + gG + bB$$

## BIOPHYSICS OF HEARING



# Stimulus: sound

Longitudinal  
mechanical wave  
(pressure wave)



Longitudinal wave

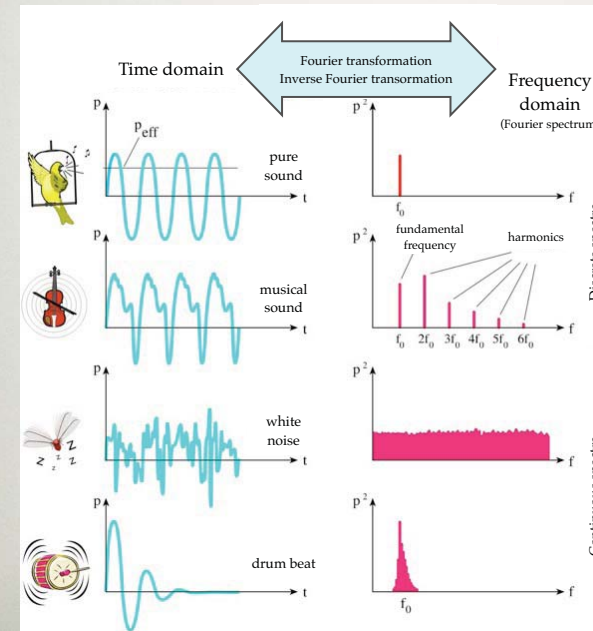


Transverse wave

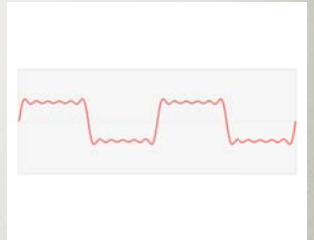
**Harmonic oscillation:**  $y(t) = A \sin(ft + \phi)$

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

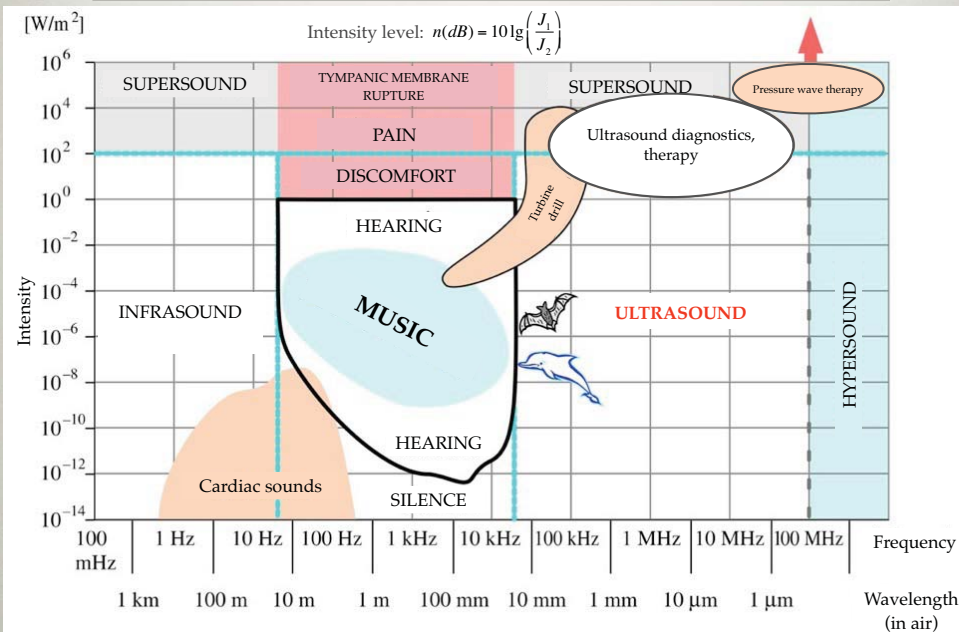
# Sounds and their spectra



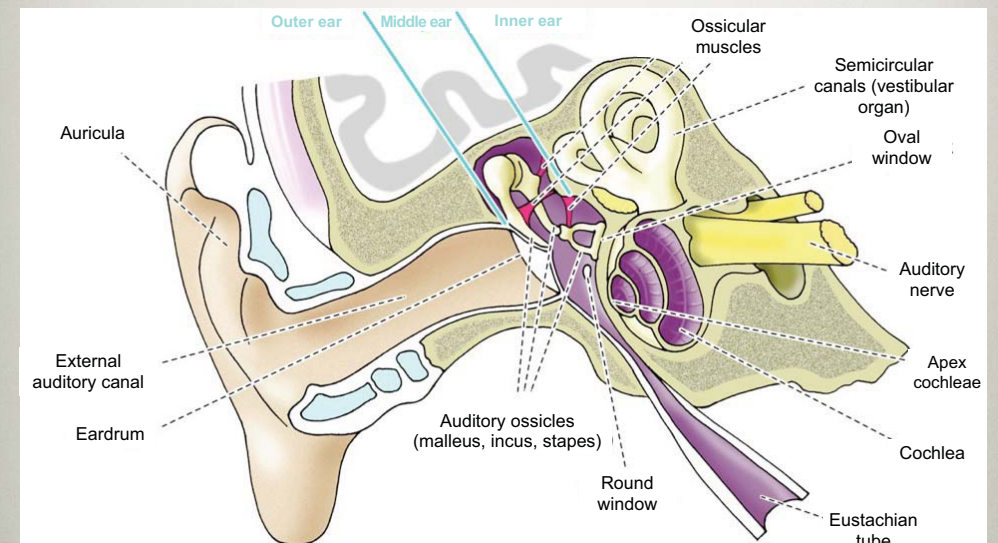
Steps of Fourier transformation:



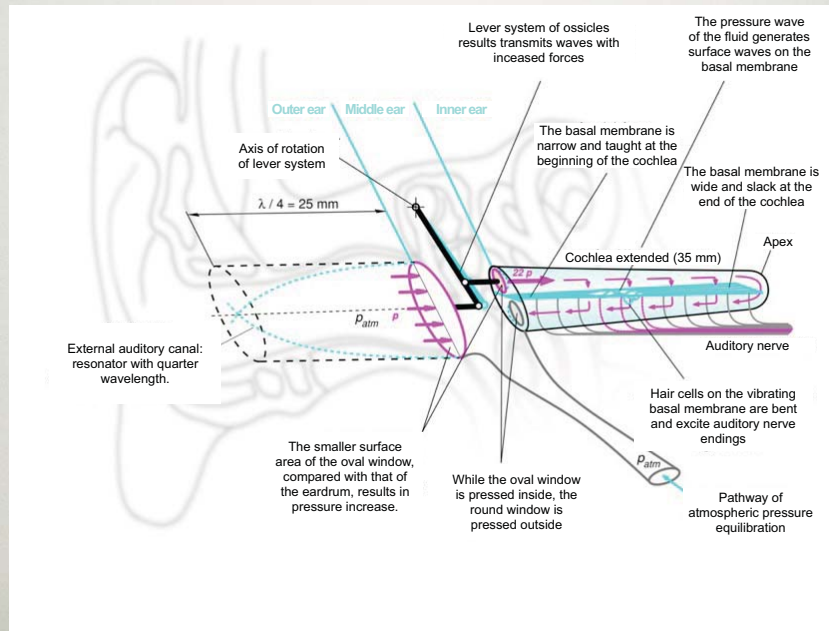
# Frequency and intensity of sounds



# “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 frequency range (2000-5000 Hz).

### Eardrum

Brought into resonance by sound waves.

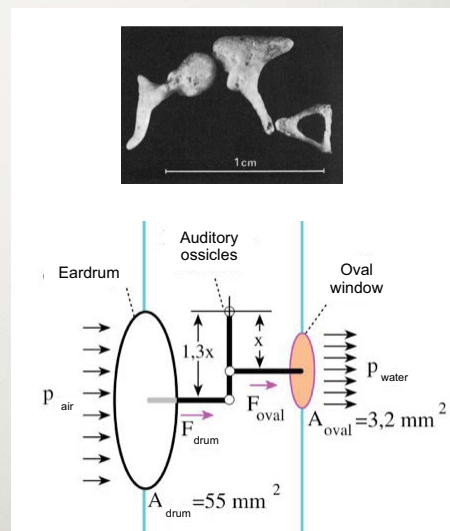
## Middle ear: mechanical amplifier

**Auditory ossicles** (malleus, incus, stapes)

They amplify eardrum resonance and transmit it to the oval window.

**Amplification:**  
due to area ratio:  $17 \times$   
due to lever action:  $1,3 \times$

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



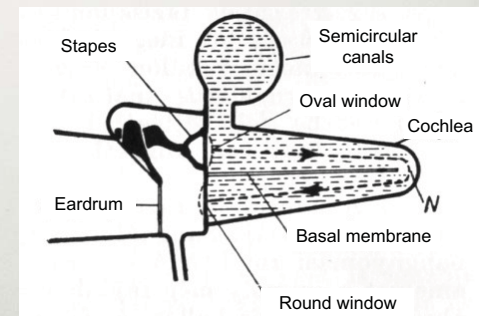
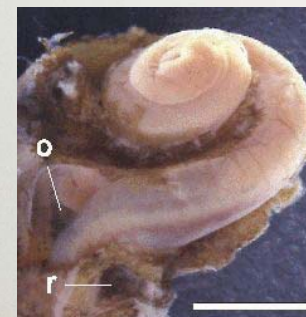
## Inner ear: sensor

**Vestibular organ:** semicircular canals

**Cochlea:** 2.5-pitch, 35-mm-long fluid-filled channel.

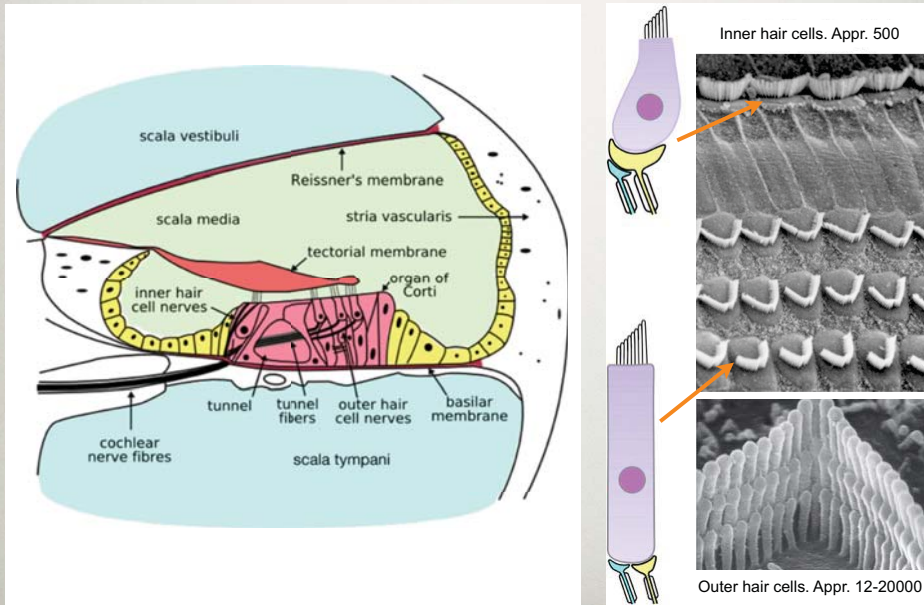
It is halved in length partly by an osseous, partly by a membranous wall, the *basal membrane*.

Sensory organ of sound.

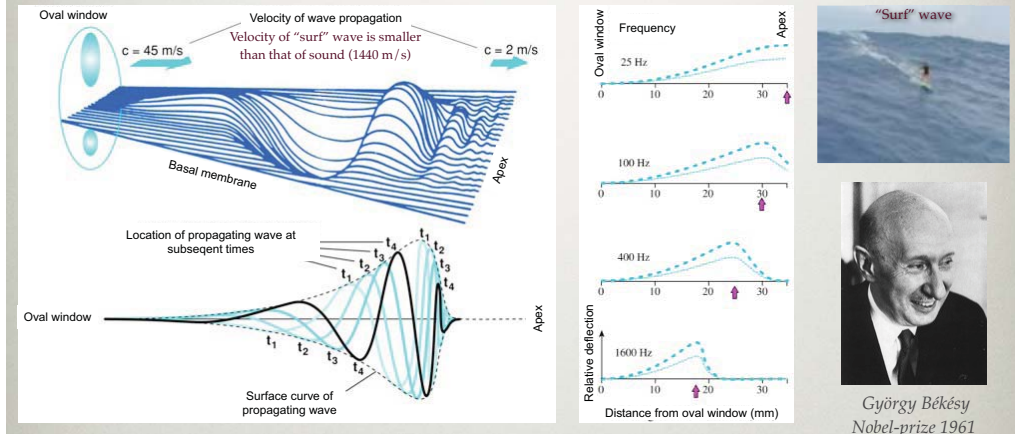




# Ultrastructure of the inner ear



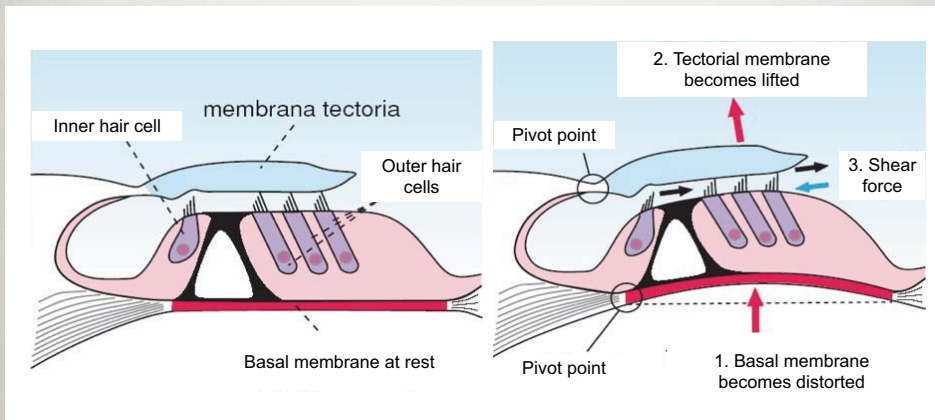
# Békésy: propagating surface waves on basal membrane



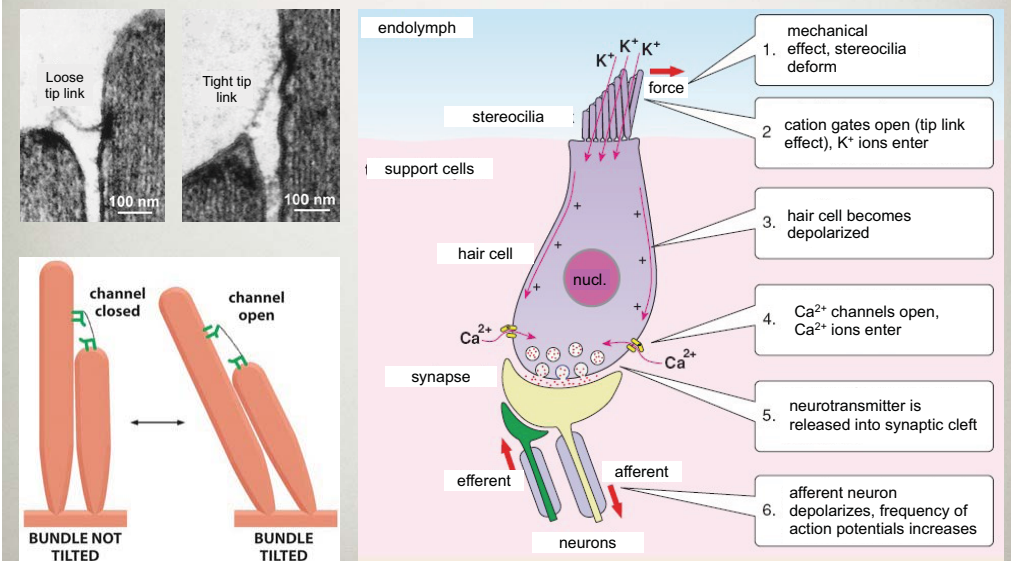
The frequency-dependence of the location of propagating wave maxima provide a rough frequency-discrimination.

# Function of the organ of Corti

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



# Inner hair cells: 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).

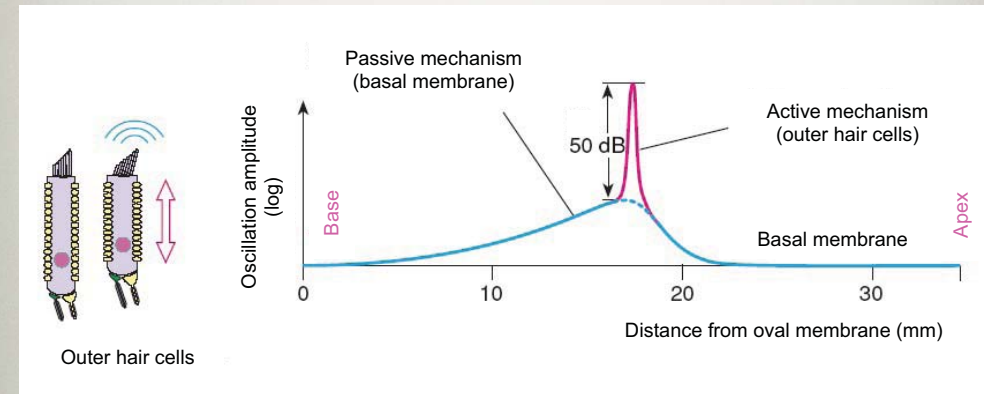
## Active detection (Energy is pumped into the system at the resonance frequency)

- T. Gold (1948): analogy 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



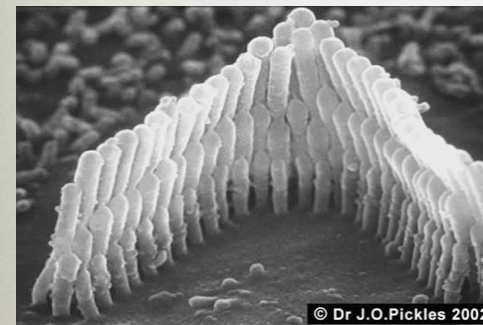
**Regenerative amplifier:** positive feedback mechanism (Large amplification in narrow frequency range. Only the dissipated energy is regenerated, otherwise ringing may occur)

## Amplification function of outer hair cells

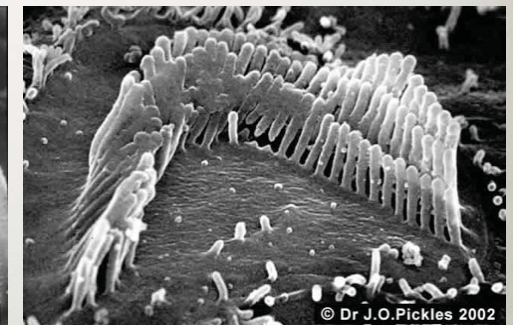


Responsible protein - **prestin**, transmembrane motor protein  
mechanoelectric and electromechanical transduction

## ACOUSTIC DAMAGE



Outer hair cells (normal state)



Outer hair cells (damaged state)



# Coding of acoustic information

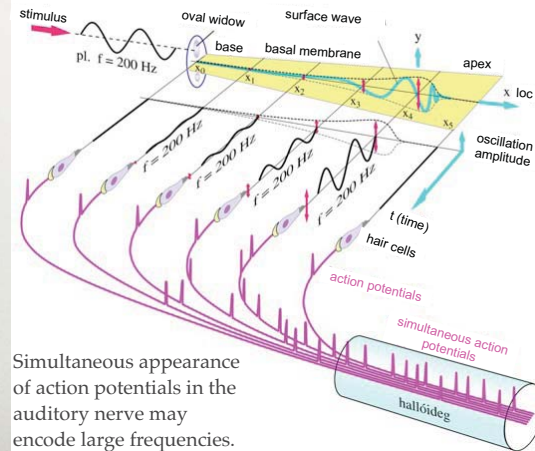
## Location theory

Frequency sensing coded spatially.

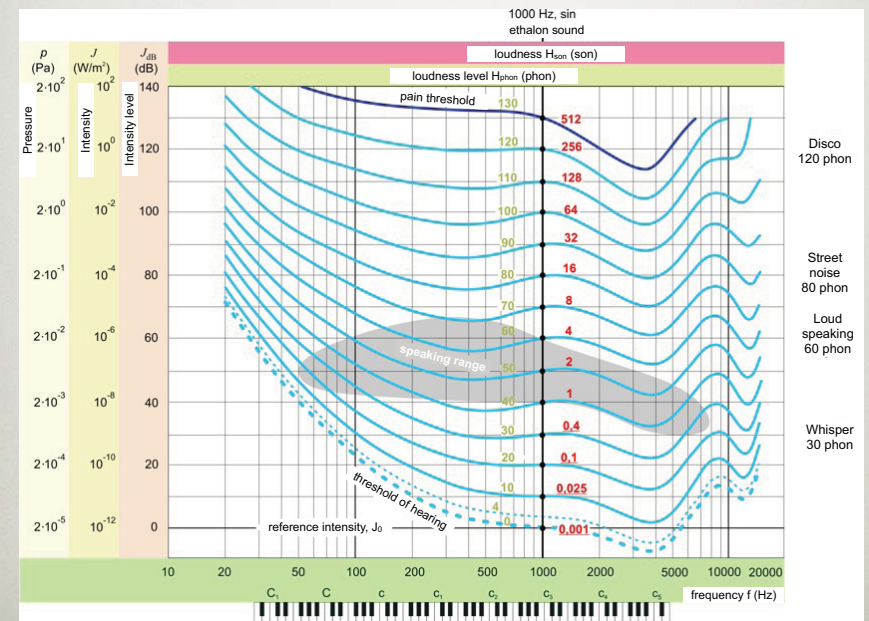
Basis:

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".

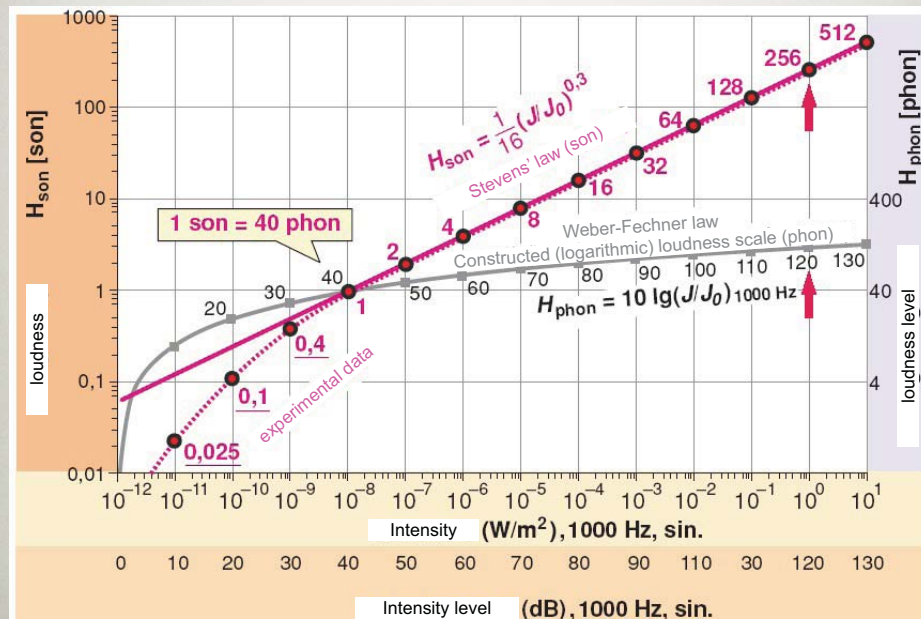
## Volleyball theory



## Psychoacoustics: loudness (Fletcher-Munson)

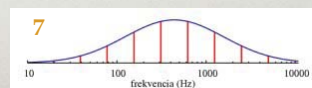
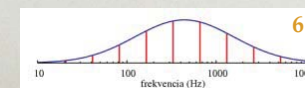
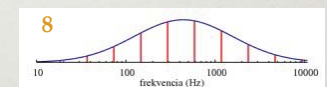
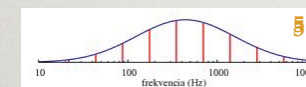
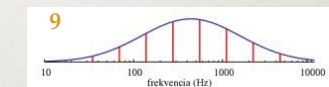
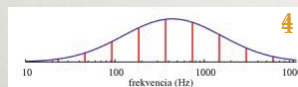
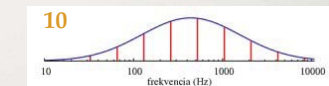
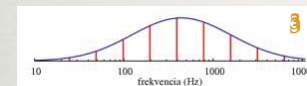
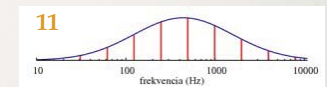
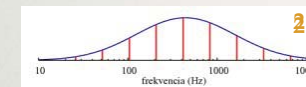
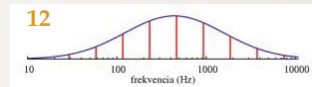
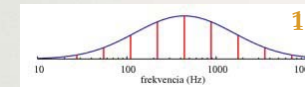


## Phon and son scales



## Acoustic illusion?

Shepard tone:  
sine waves  
separated by  
octaves

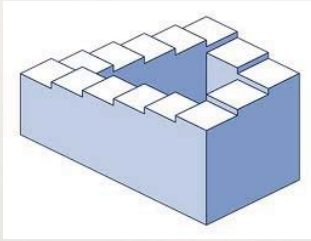


# Acoustic illusion?

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Maurits Cornelis Escher  
(1898-1972)



Escher staircase

