

# BIOPHYSICS OF SENSORY RECEPTORS VISION, HEARING

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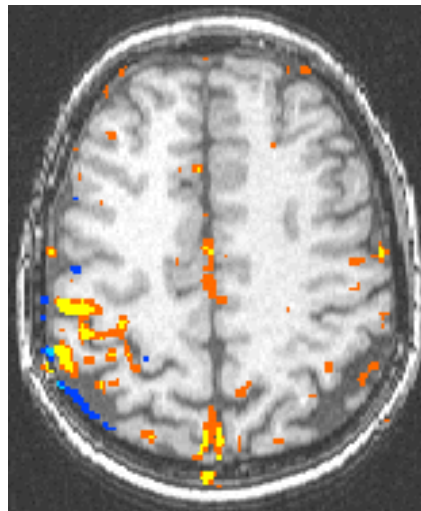
# Theories about sensing

Cardiocentric sensing  
(Medieval reconstruction)



Aristotle (384-322 BC)  
cardiocentric sensing.

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



fMRI recording during  
sensomotoric function



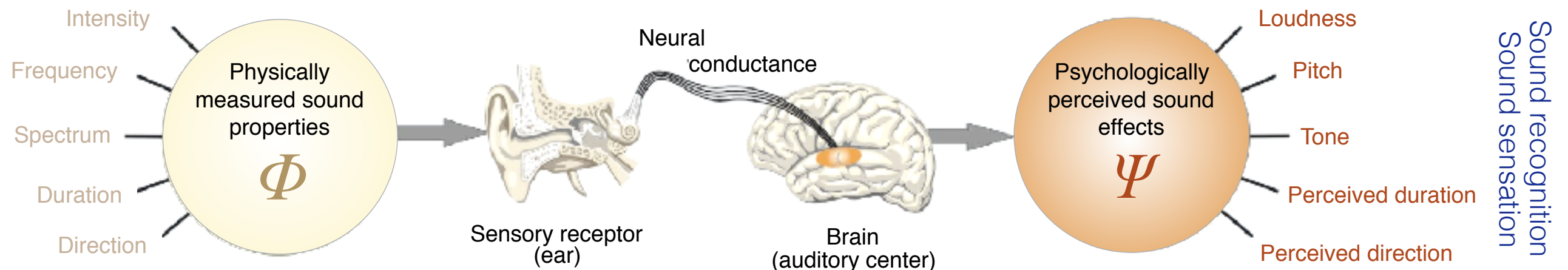
Sensory homuncle

Today:

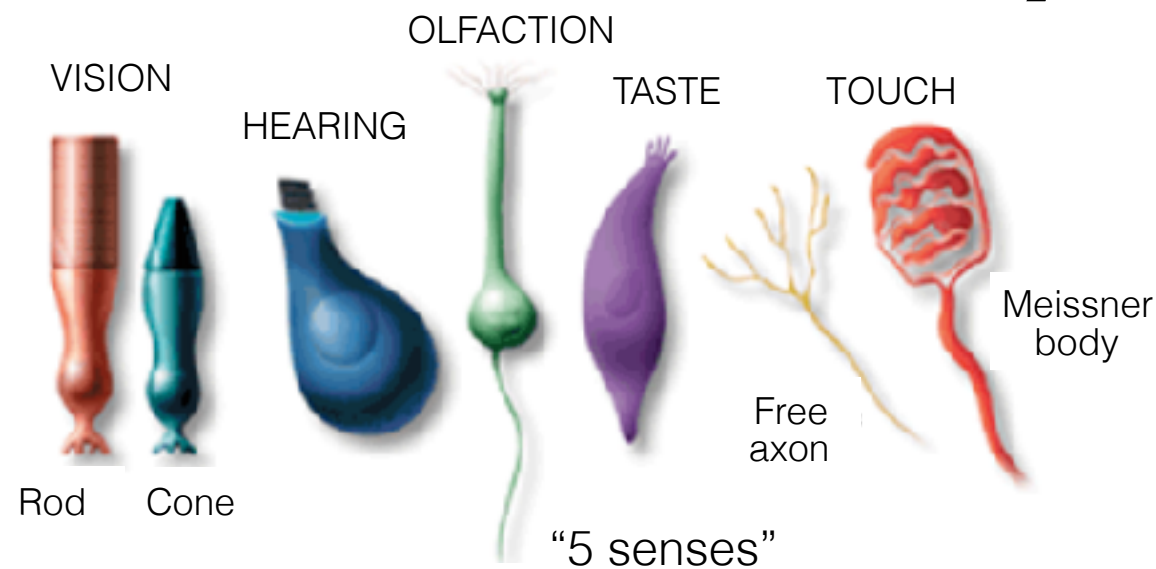
**stimulus** →

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

## 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 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...

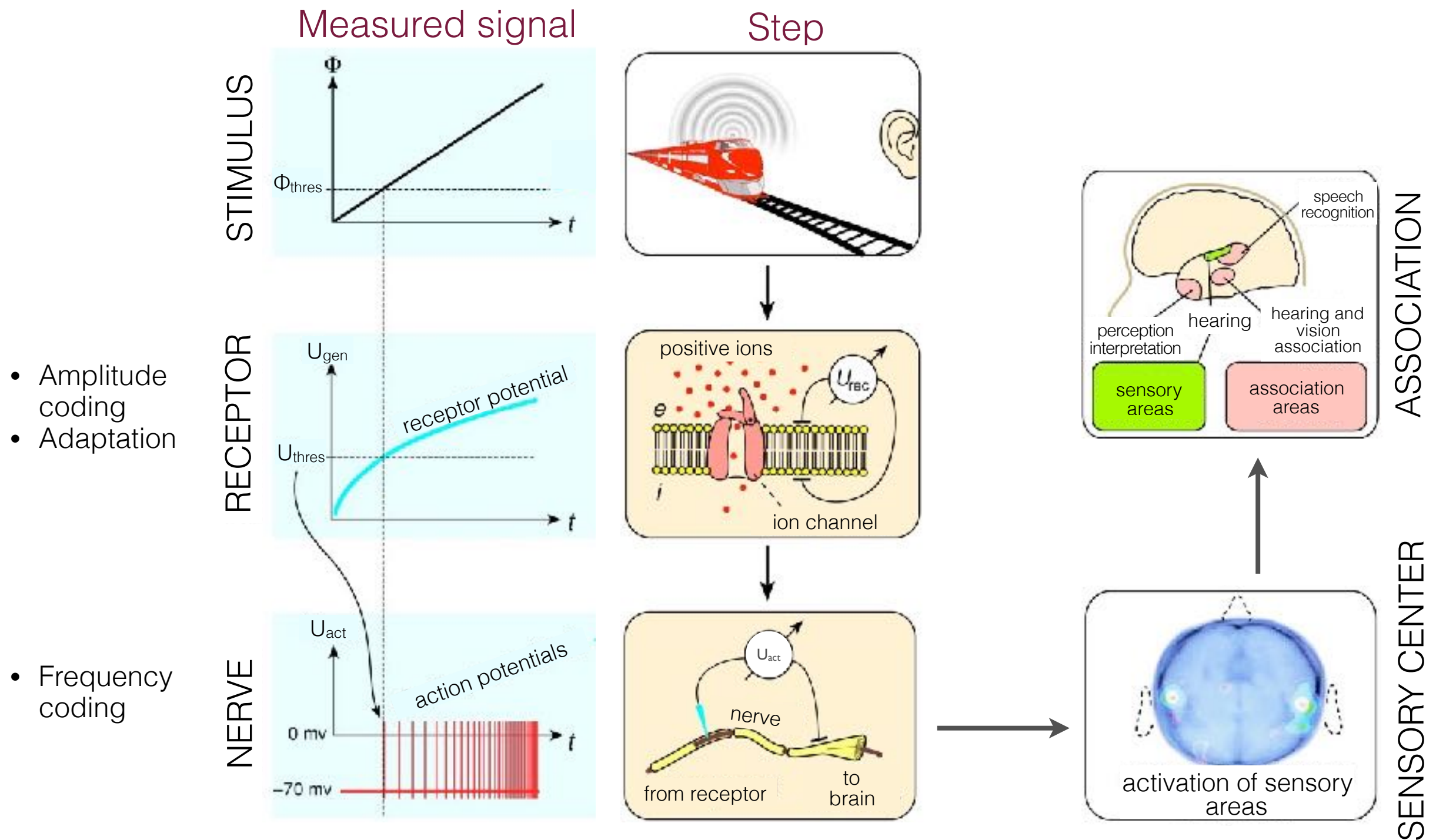
## Sensitivity of sensory receptors

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

# I. 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

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



Weber (1795-1878)



Fechner (1801-1887)

Stevens' law

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



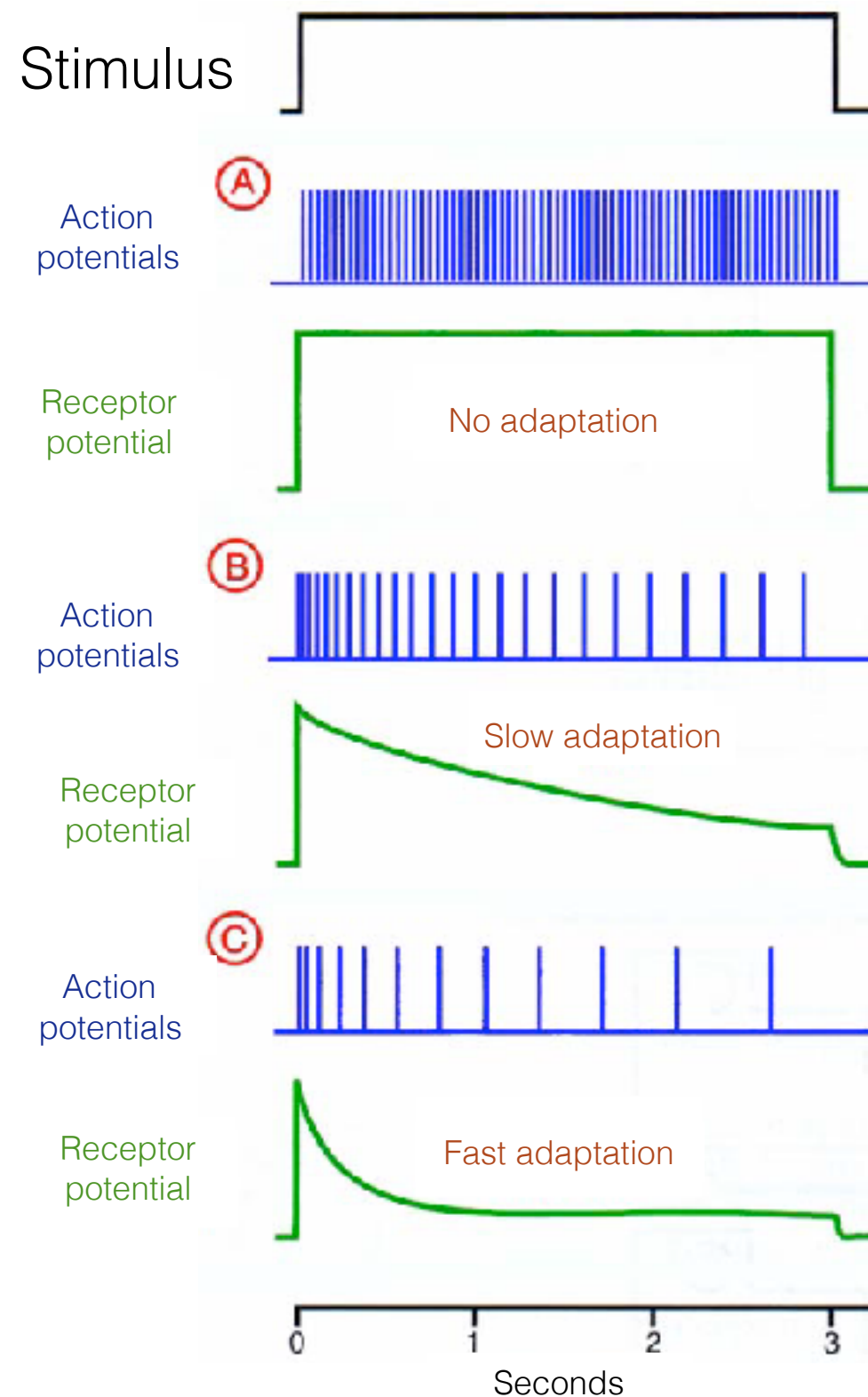
Stevens (1906-1973)

$\psi$  = 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



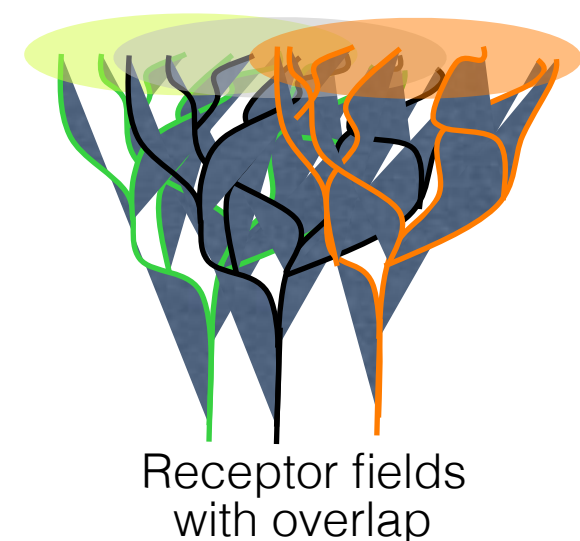
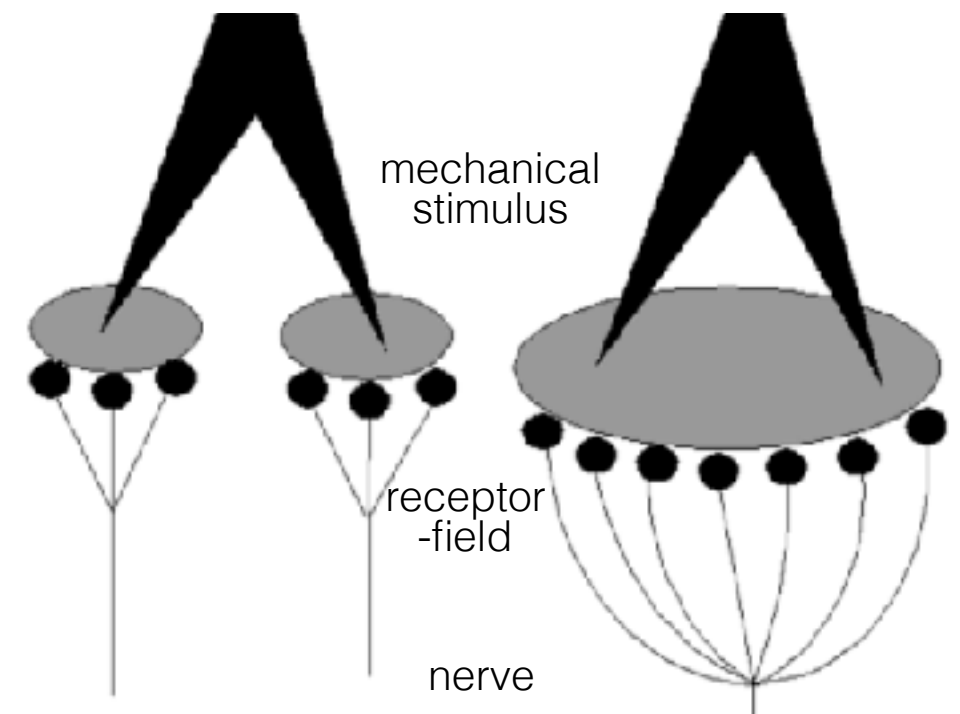
Adaptation: during constant stimulus the frequency of action potentials gradually decreases.

Rapidly adapting (phasic) receptors: 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).



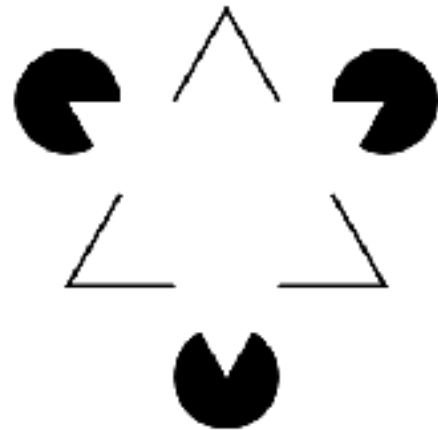
# Biophysics of vision

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

Optical illusion - intensity

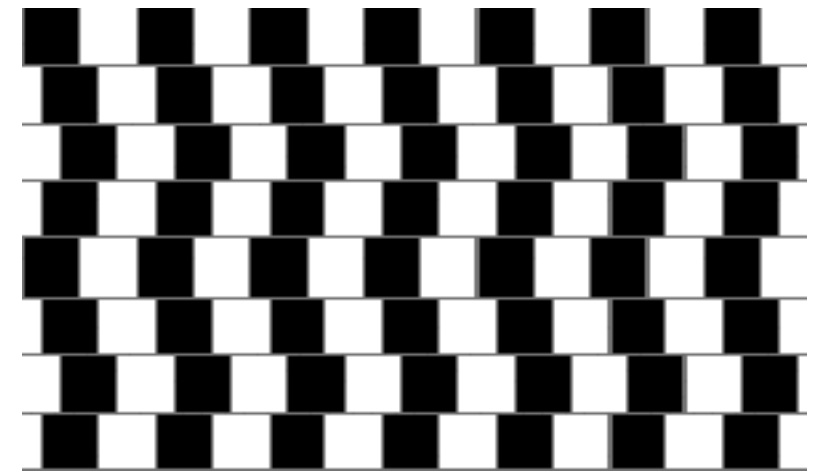


Mach bands

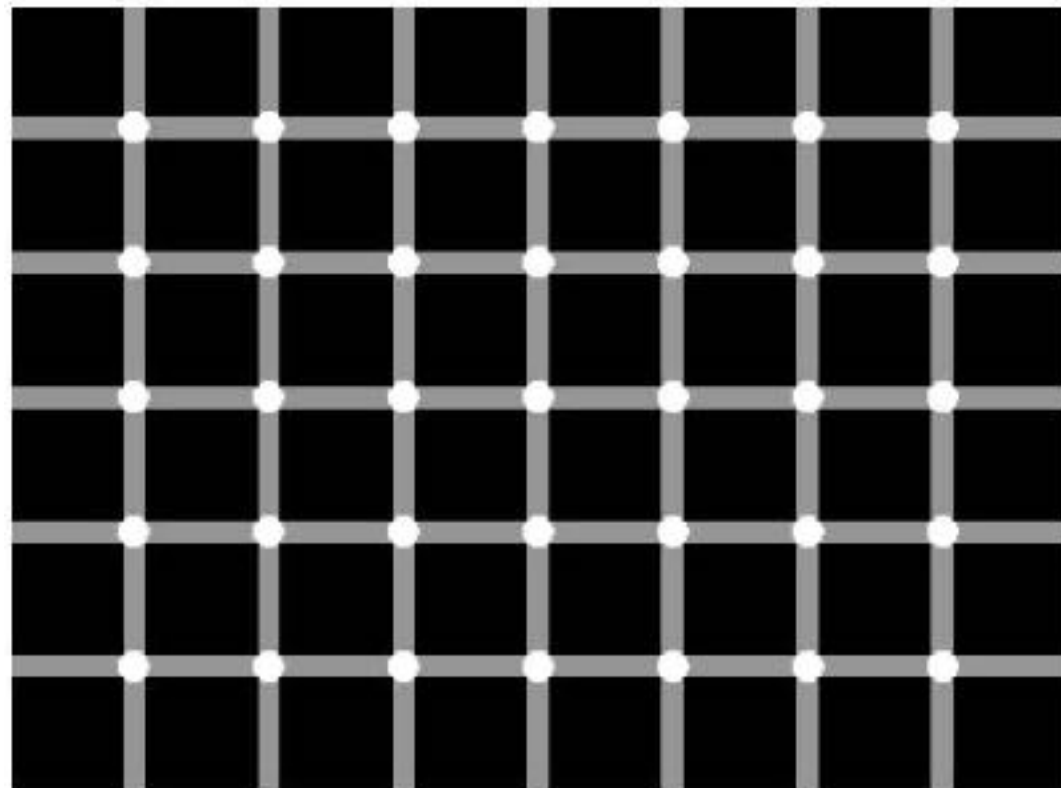


Kanizsa triangle

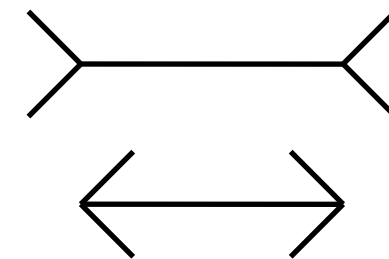
Optical illusion - direction, size



Café wall illusion



How many black circles can we count?



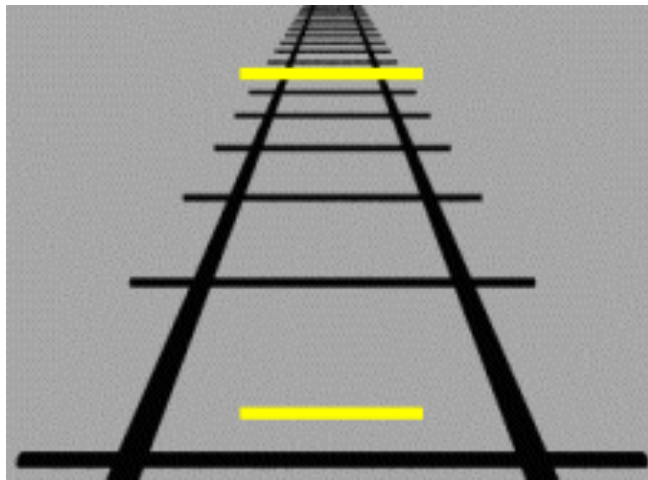
Müller-Lyer illusion



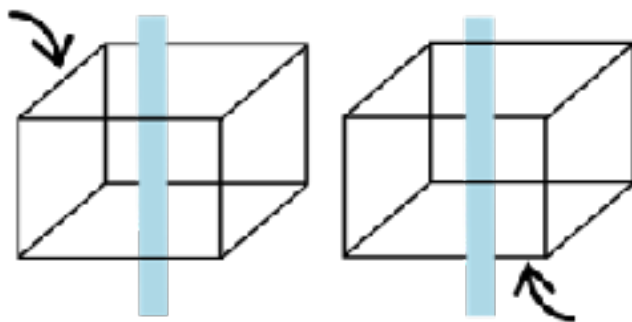
Ebbinghaus illusion



# Optical illusions – space, shape



Ponzo illusion



Necker cube

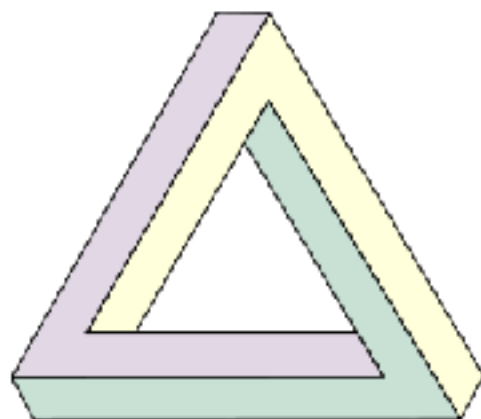


Necker cube effect on a roman mosaic

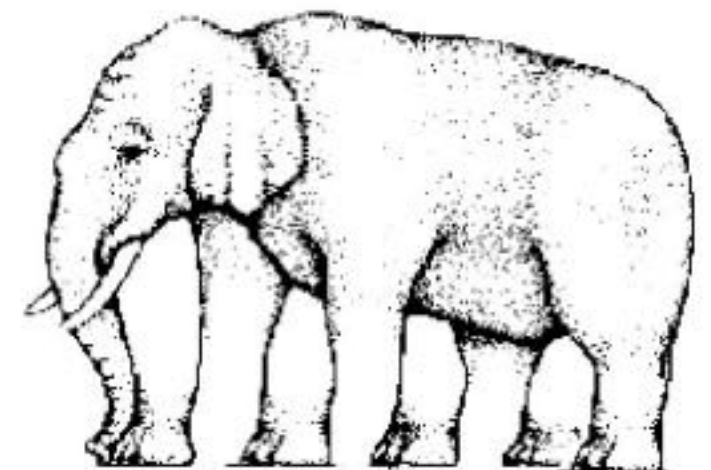
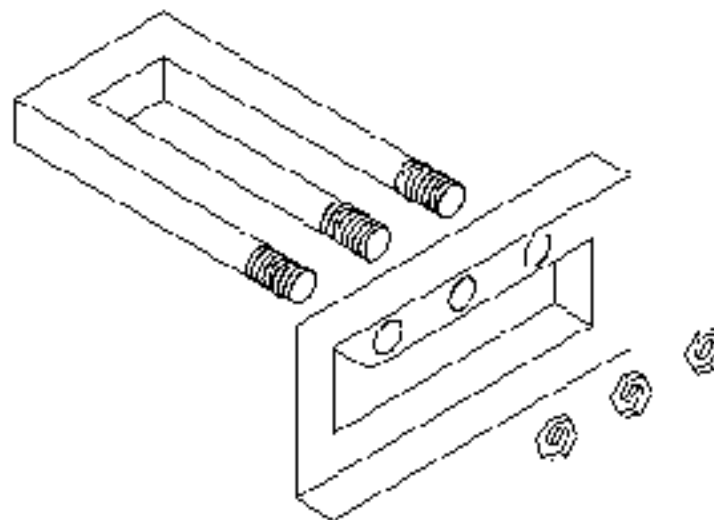


Rubin vase illusion

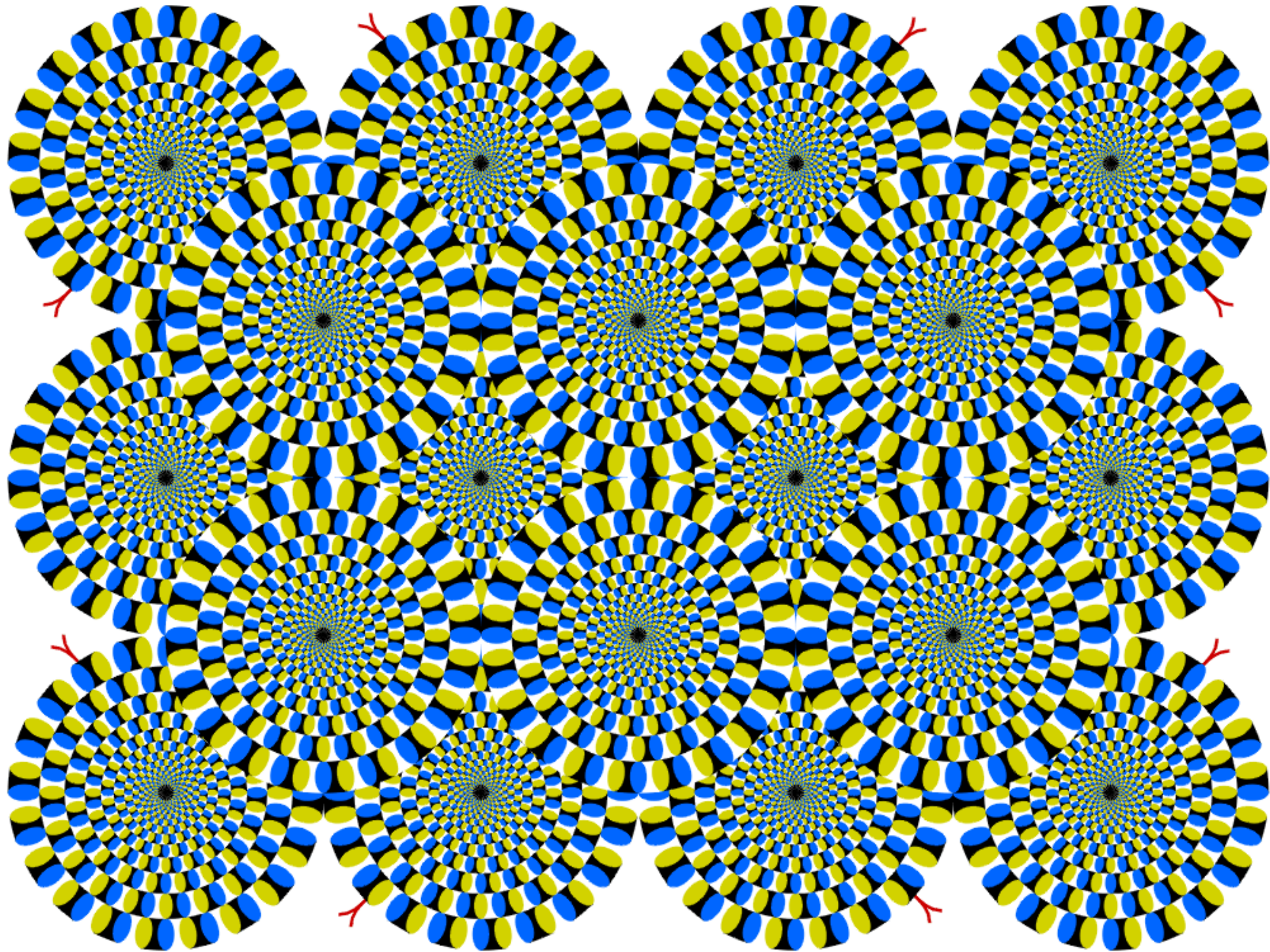
“Impossible”  
geometries



Penrose triangle



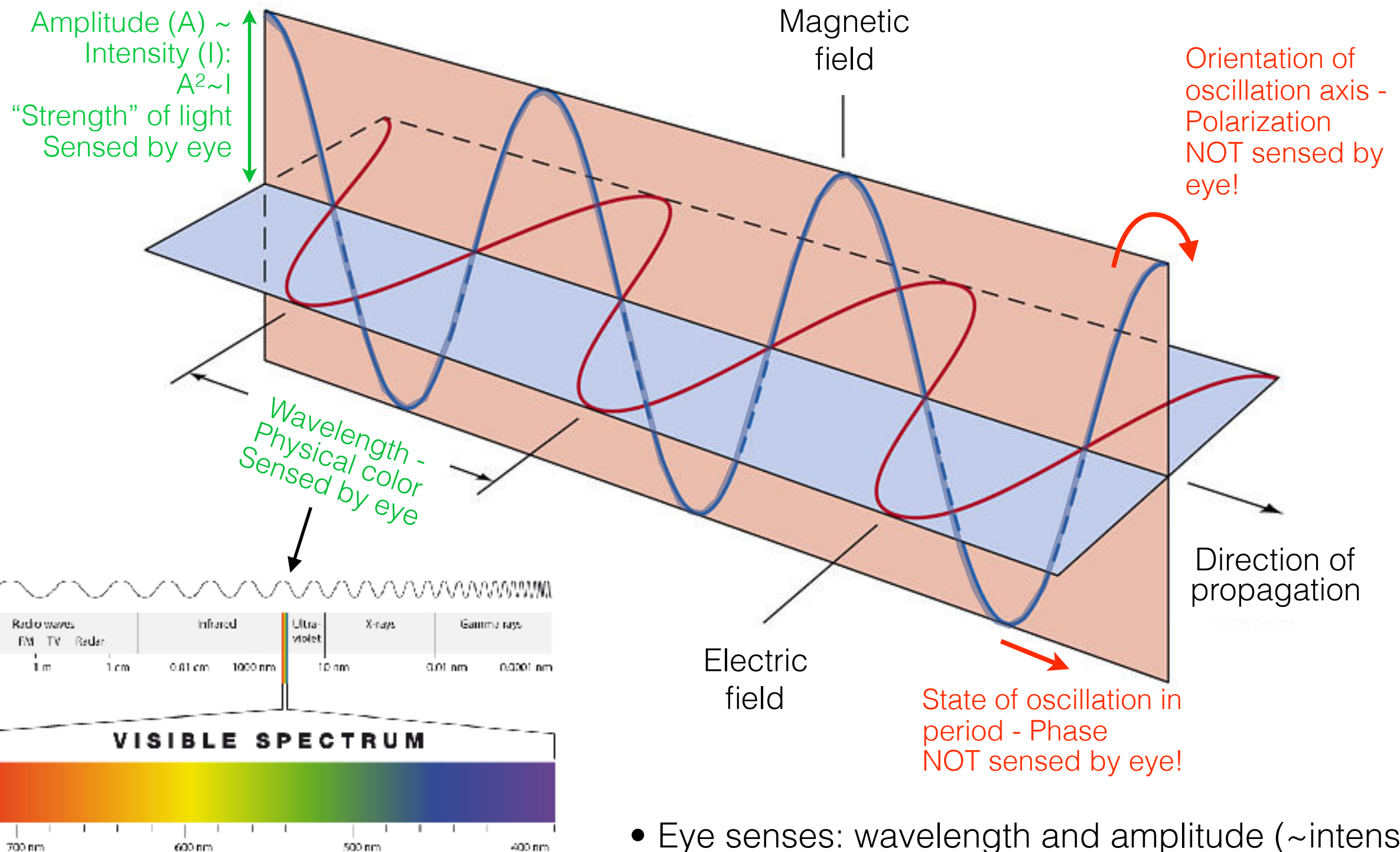






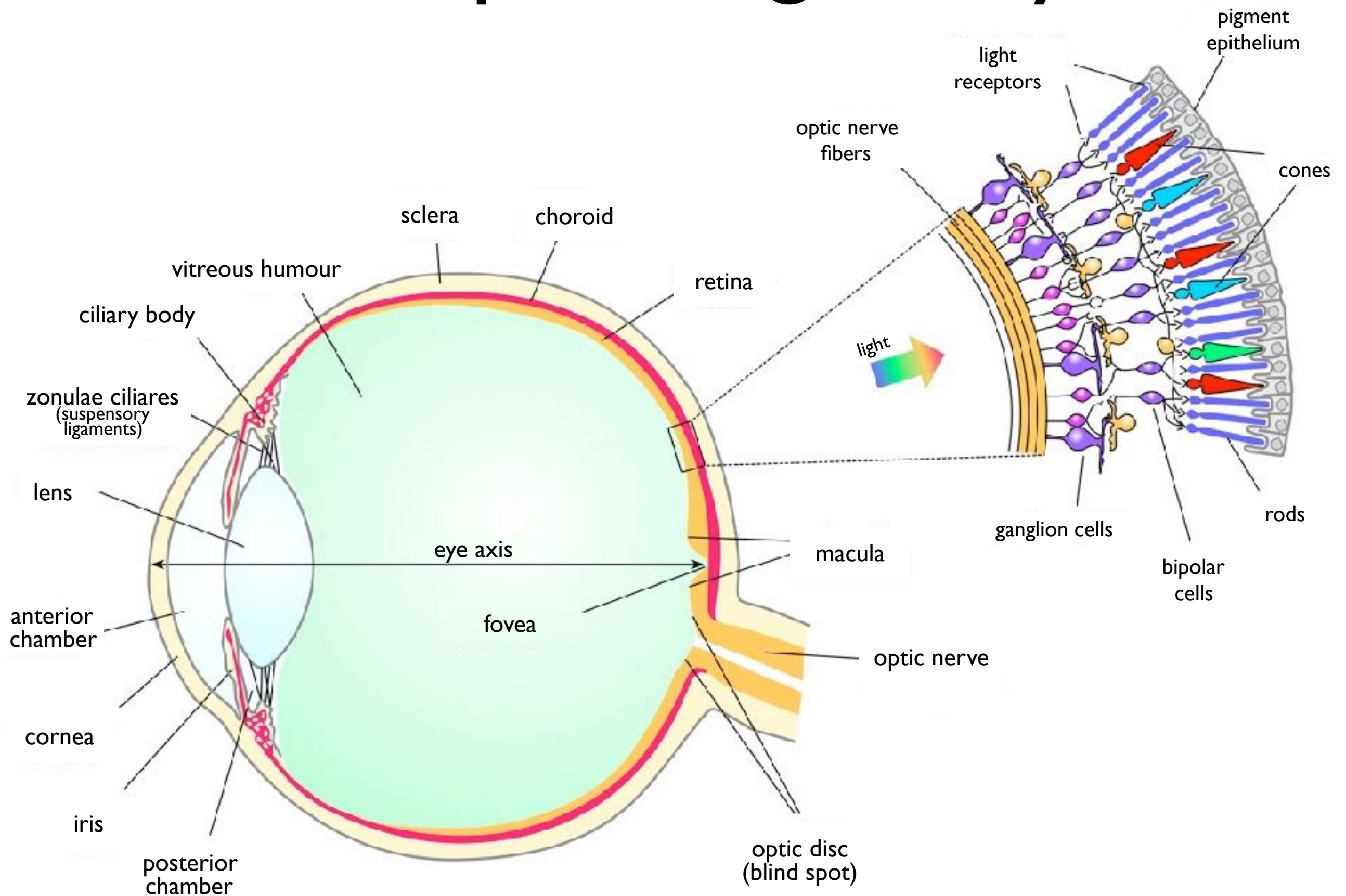
# Stimulus of vision: light

Electromagnetic (transverse) wave



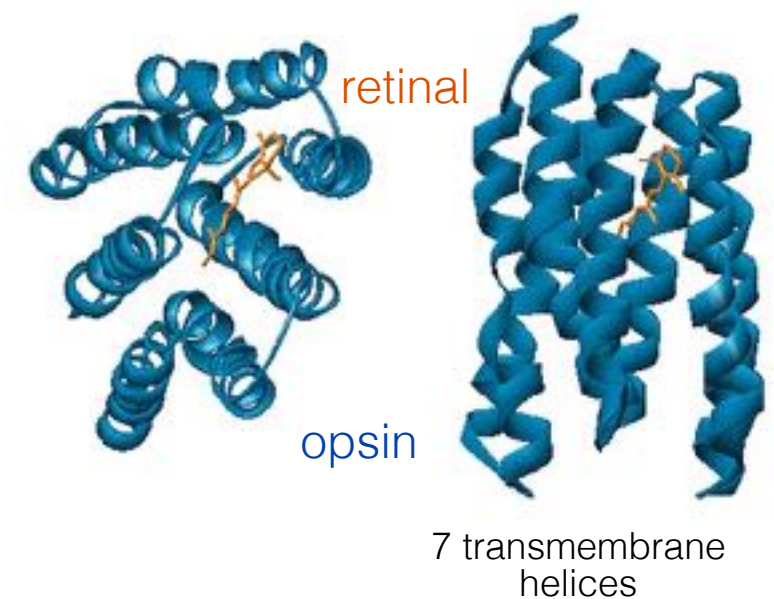
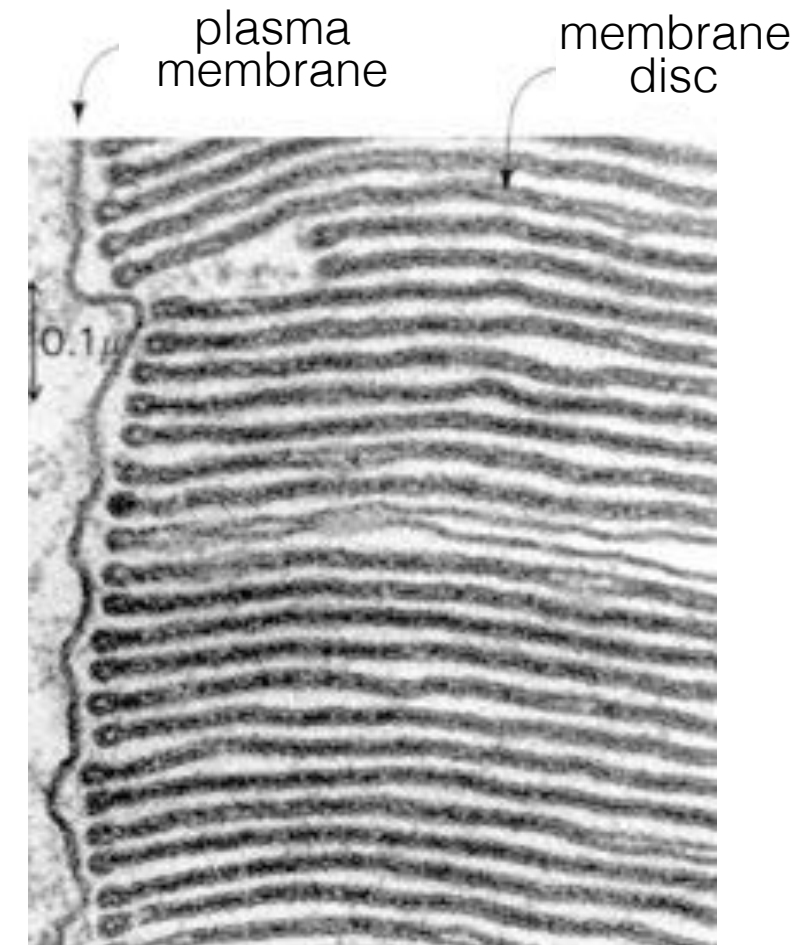
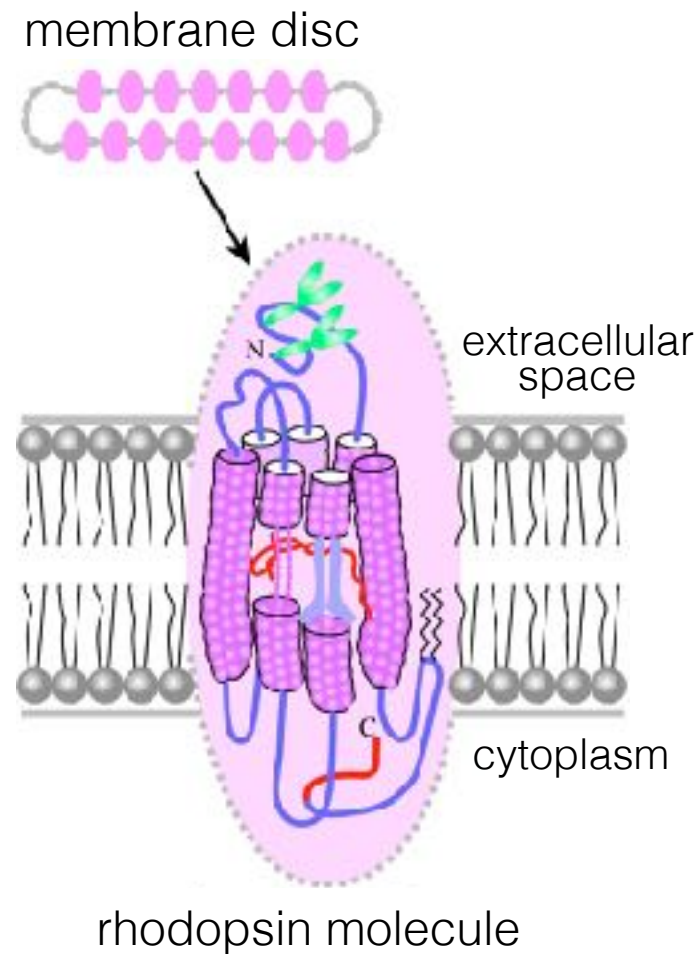
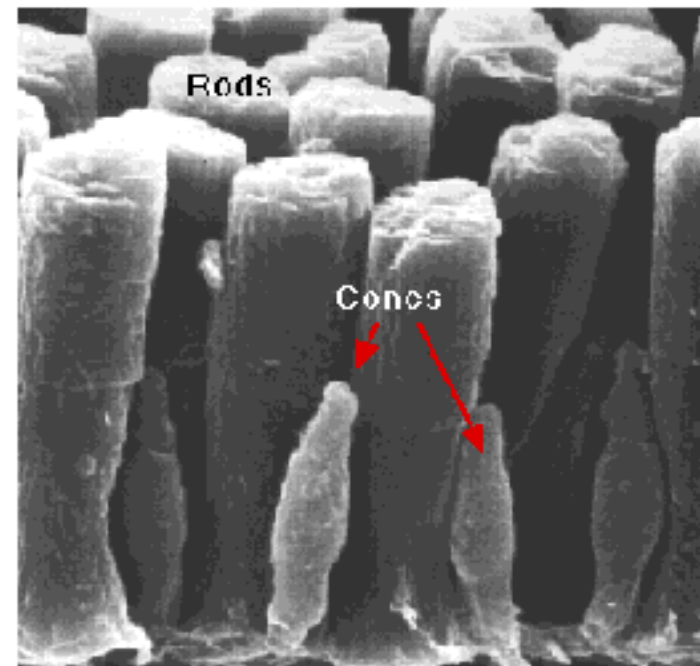
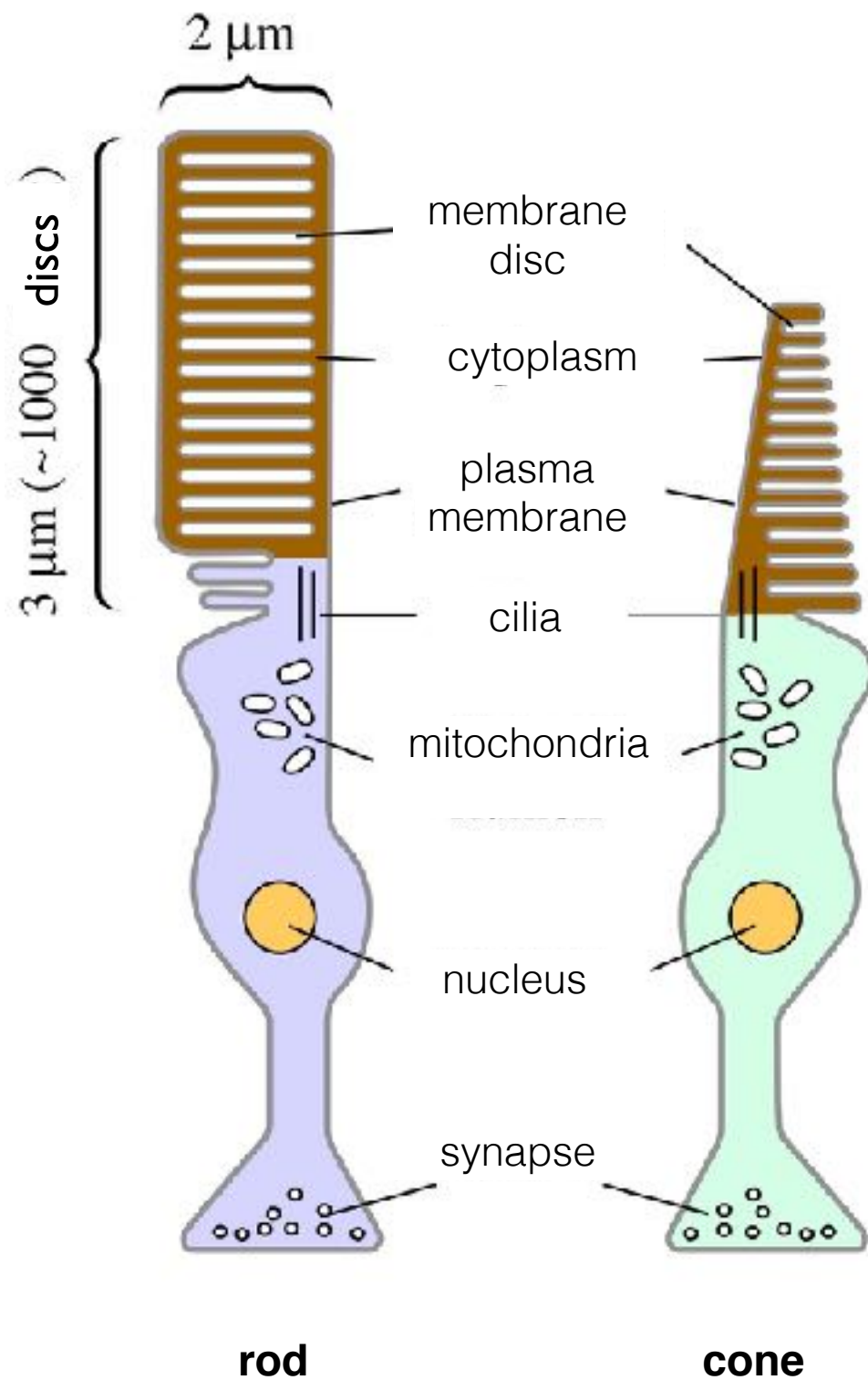
- Eye senses: wavelength and amplitude (~intensity)
- Eye is insensitive to: phase and polarization

# “Receptor-organ”: eye





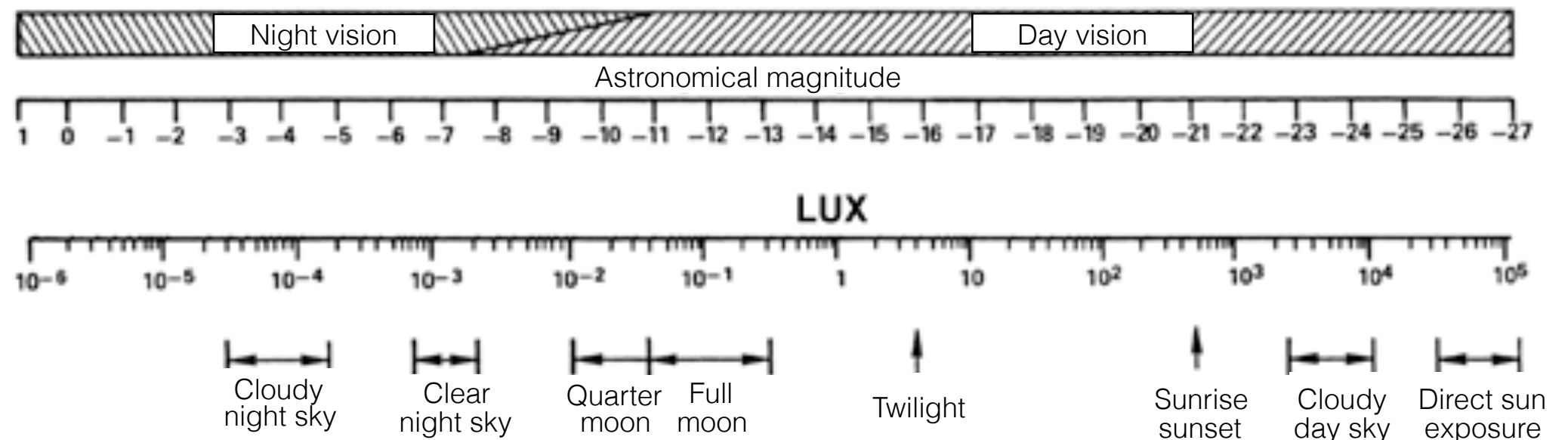
# Photoreceptors



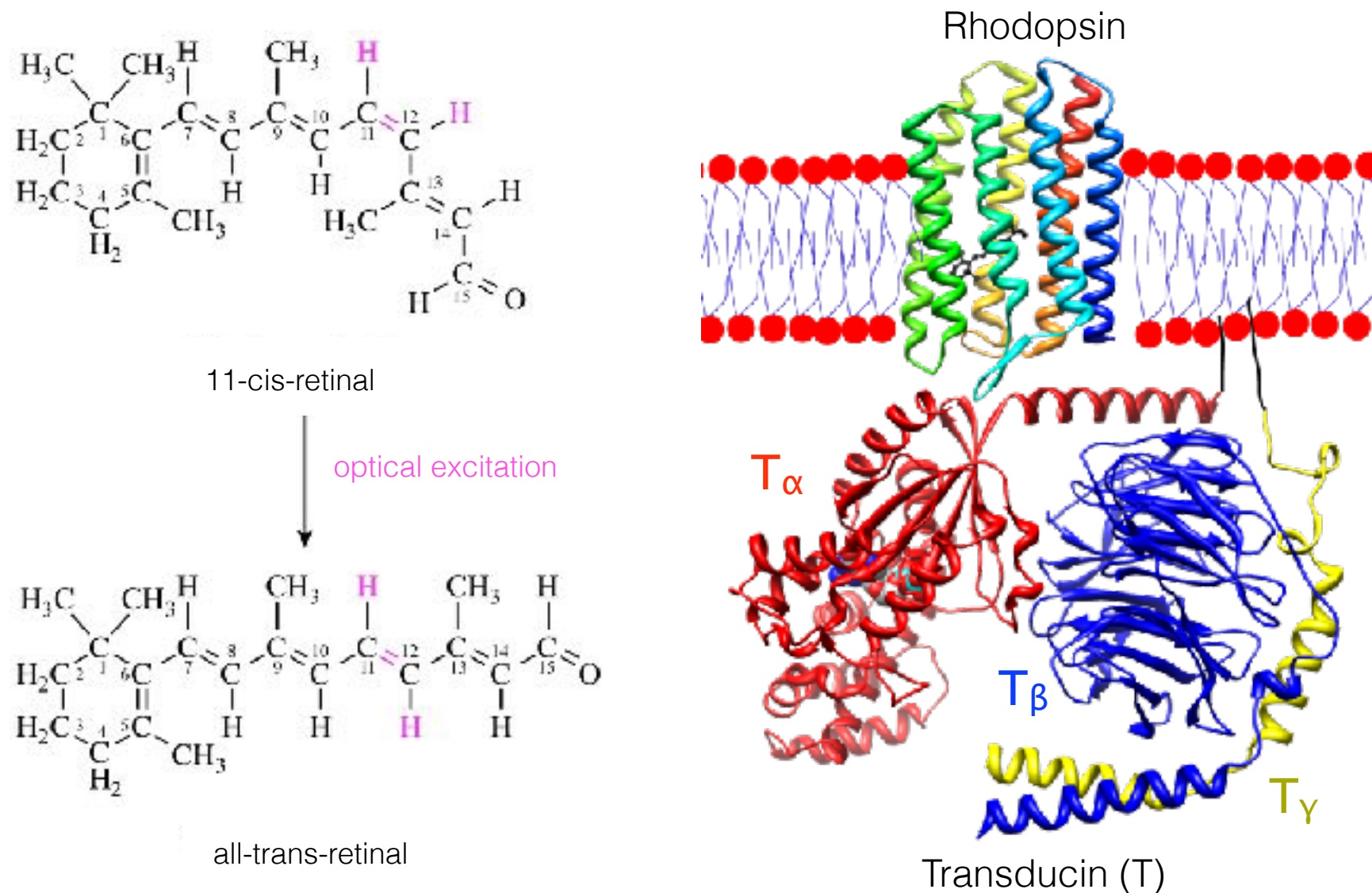
# Properties of receptor cells

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

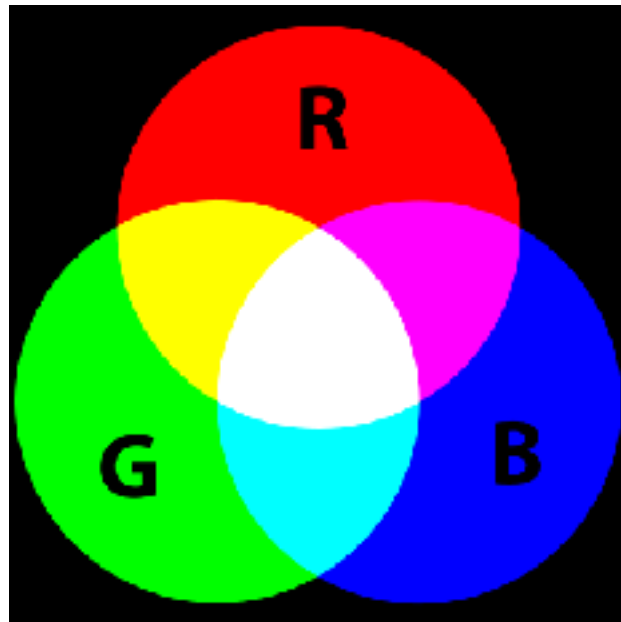
Amplification: 
$$A = \frac{E_{ion}}{E_{photon}} = \frac{ne\Delta\varphi}{hf}$$

$n$ : change in number of Na ions  
 $e$ : elementary charge  
 $\Delta\varphi$ : 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

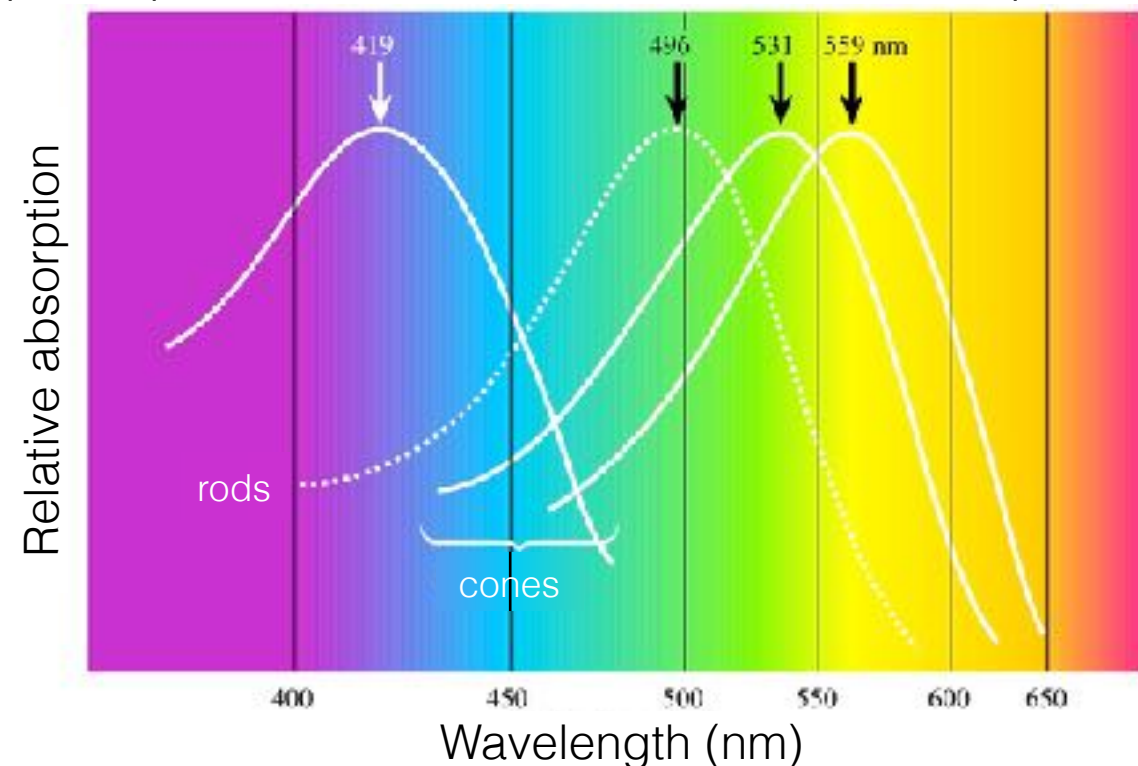
Any color ( $X$ ) may be generated by mixing three basic colors ( $R$ =red,  $G$ =green,  $B$ =blue) with varying weighing factors ( $r$ ,  $g$ ,  $b$ ):

$$X = rR + gG + bB$$

In the human eye:

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

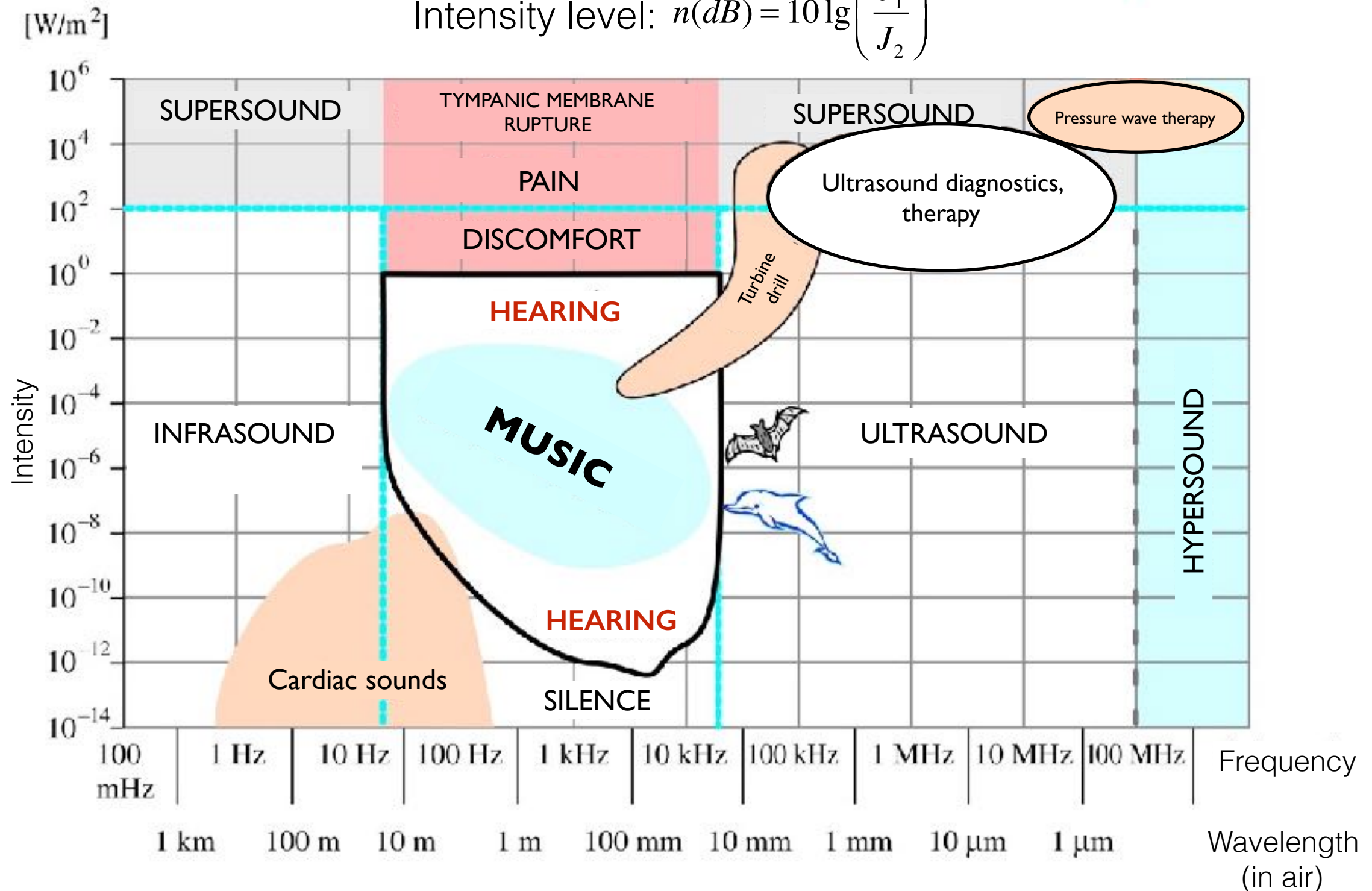
Absorption spectra of the human color-sensitive receptors (cones)



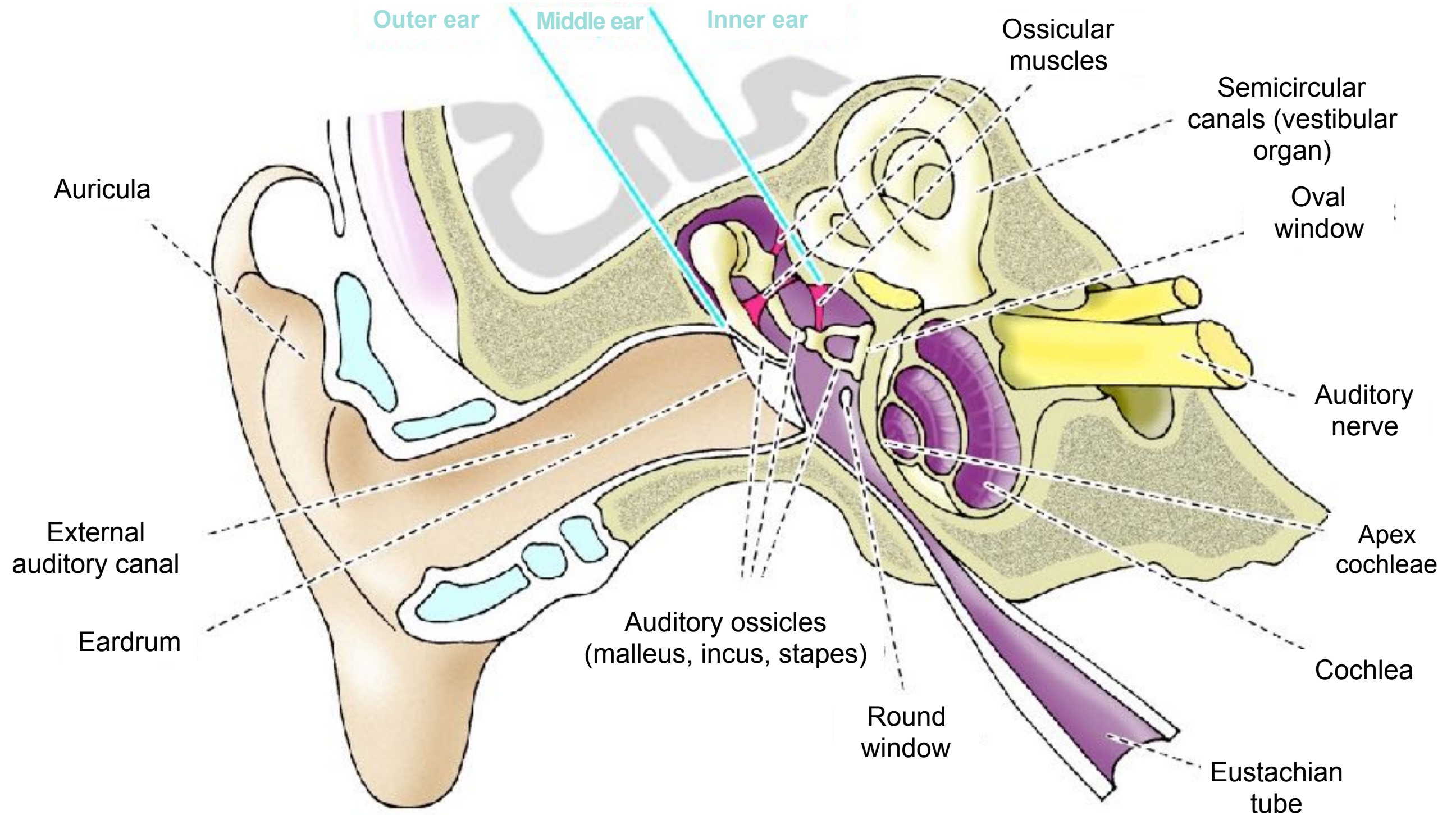
# Biophysics of hearing

Stimulus: sound - mechanical wave

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



# “Receptor-organ”: ear





# Physical schematics of the ear

## Outer ear:

### 1. Auricula

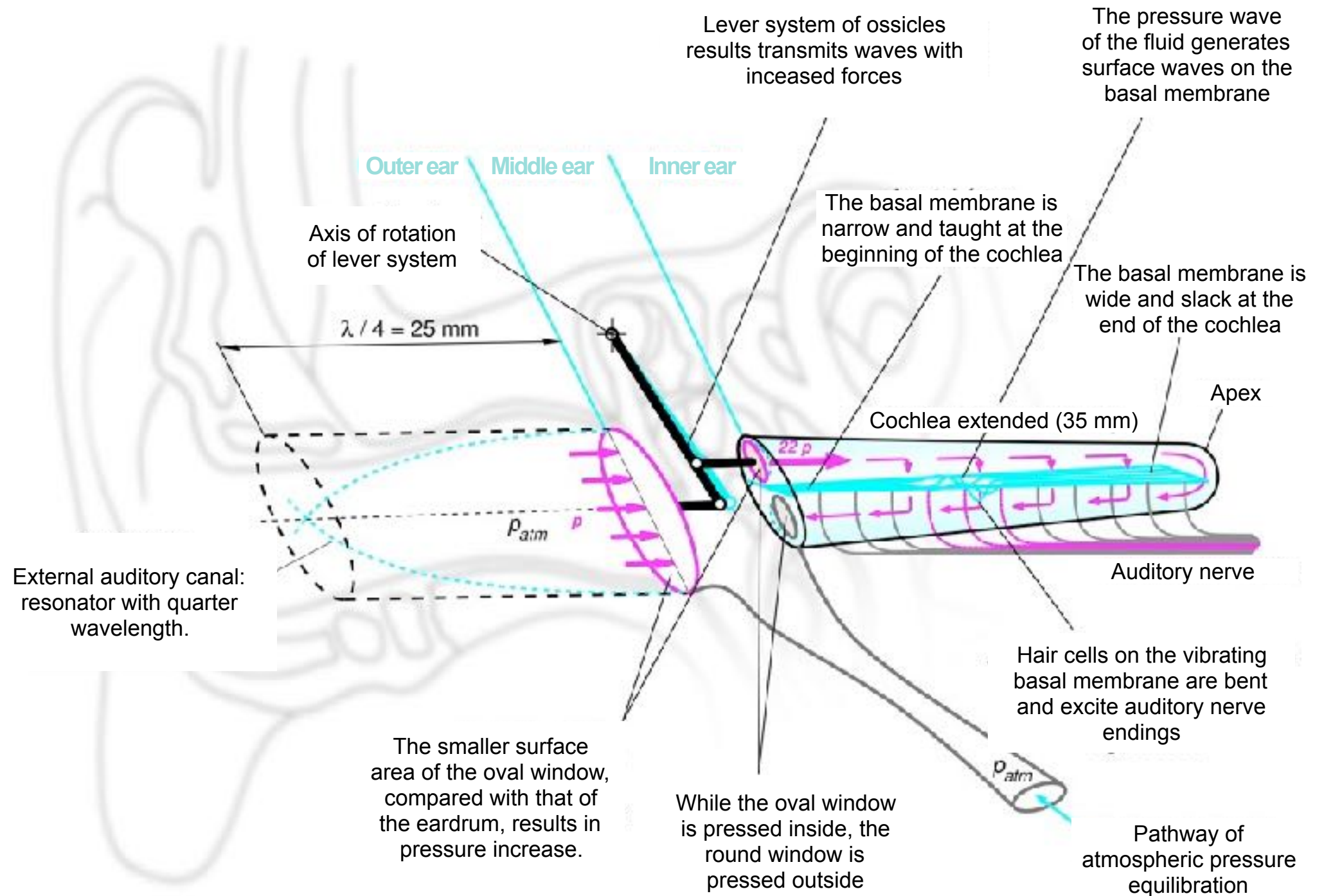
Sound is steered into the external auditory canal.

### 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)

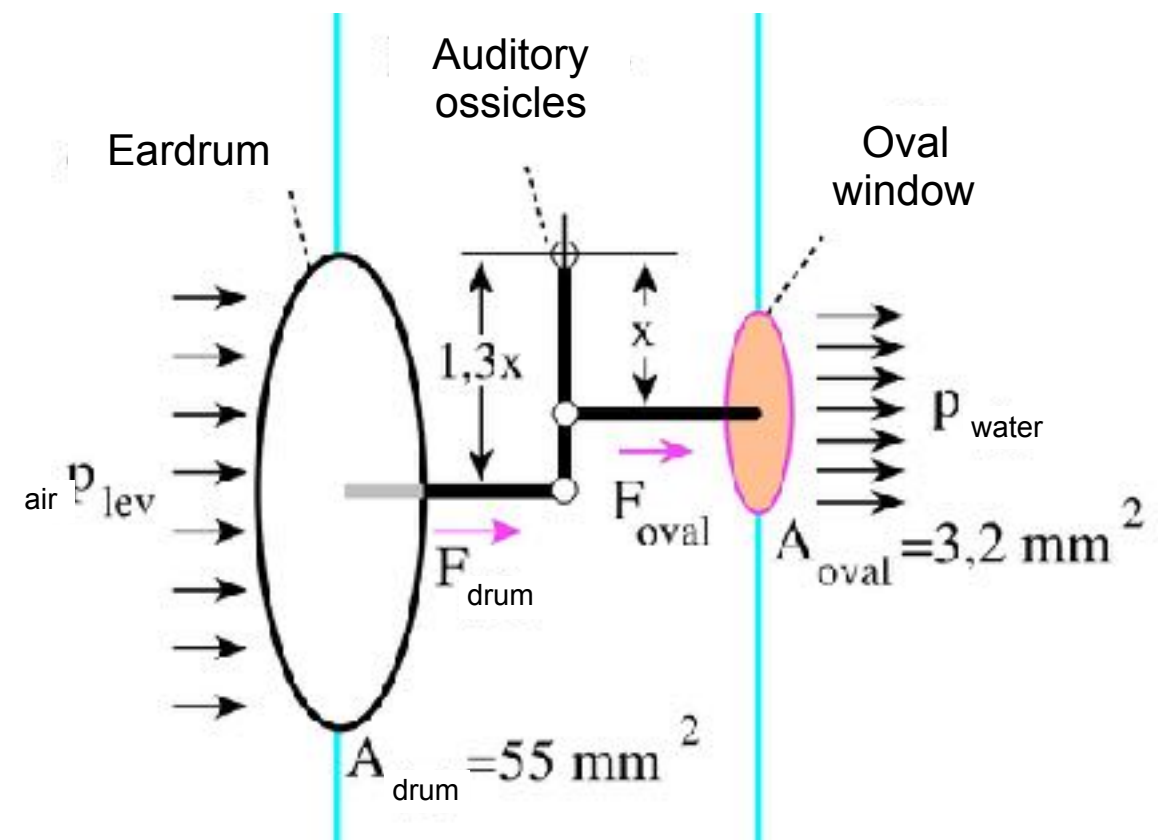
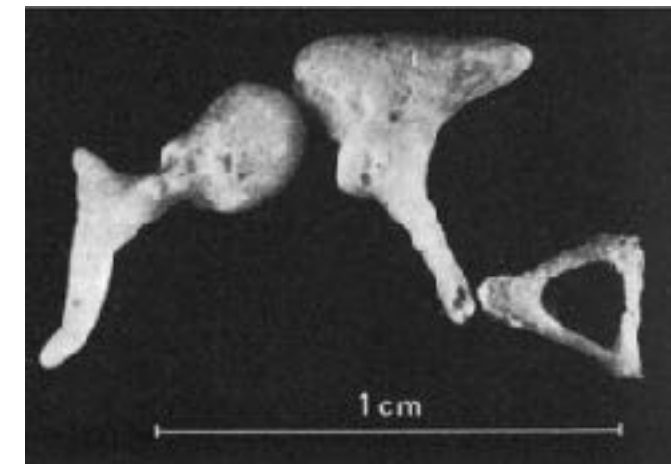
They **amplify** eardrum resonance and transmit it to the oval window. (N.B.: due to the difference in the acoustic impedance of air and water, total reflection would occur!)

**Amplification:**

due to area ratio:  $17 \times$

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

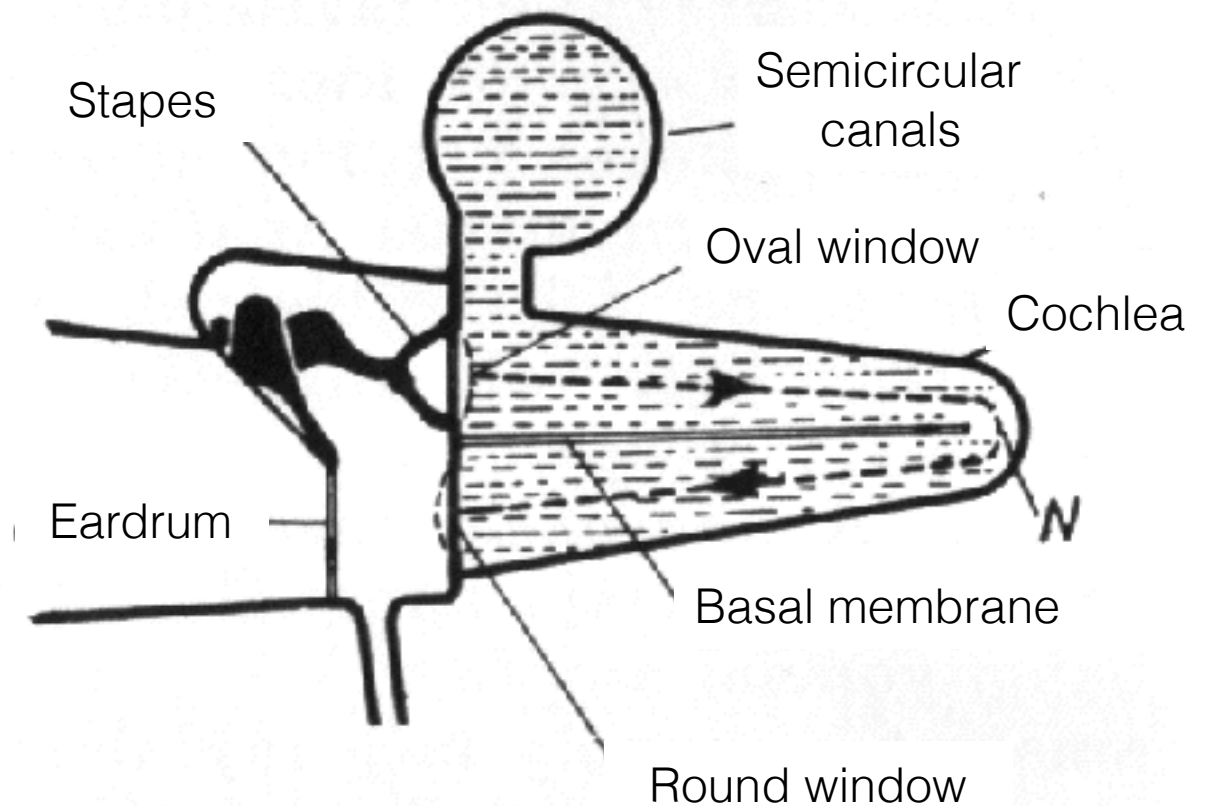
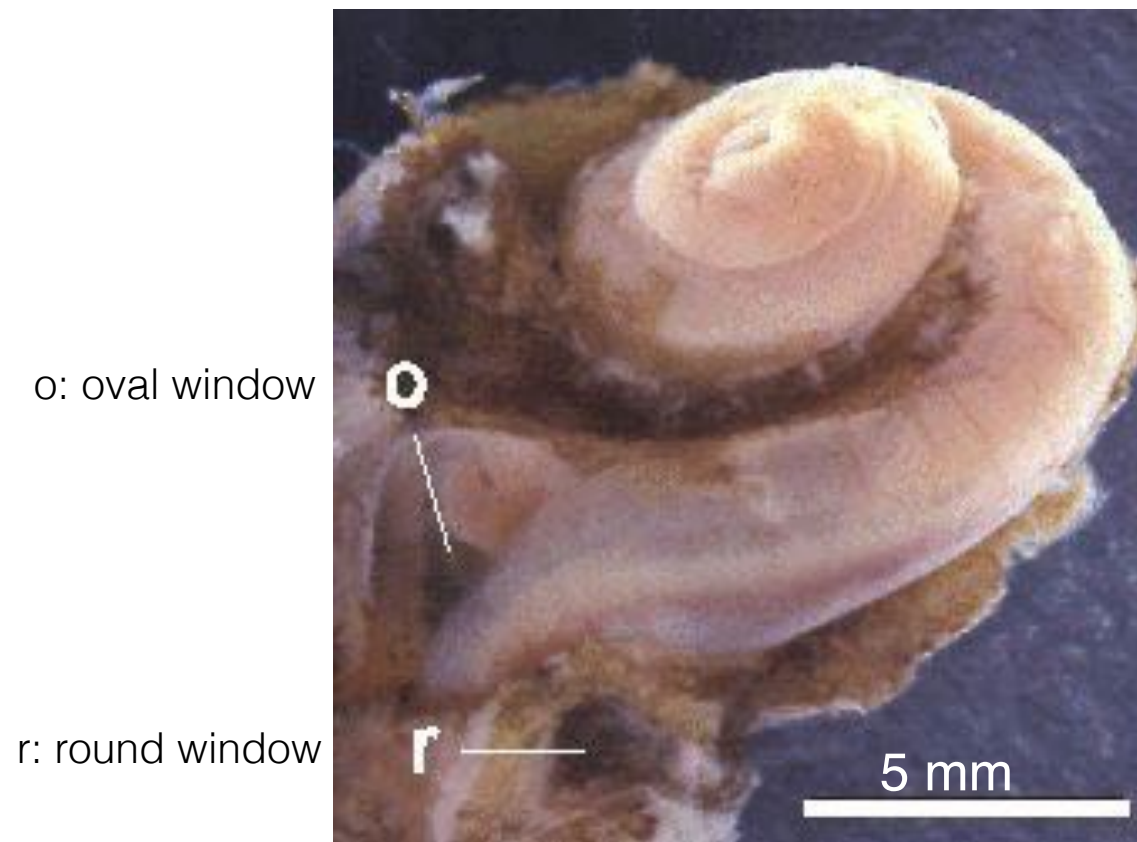
**Total amplification:**  $22 \times$  (pressure increase)



# Inner ear: sensor

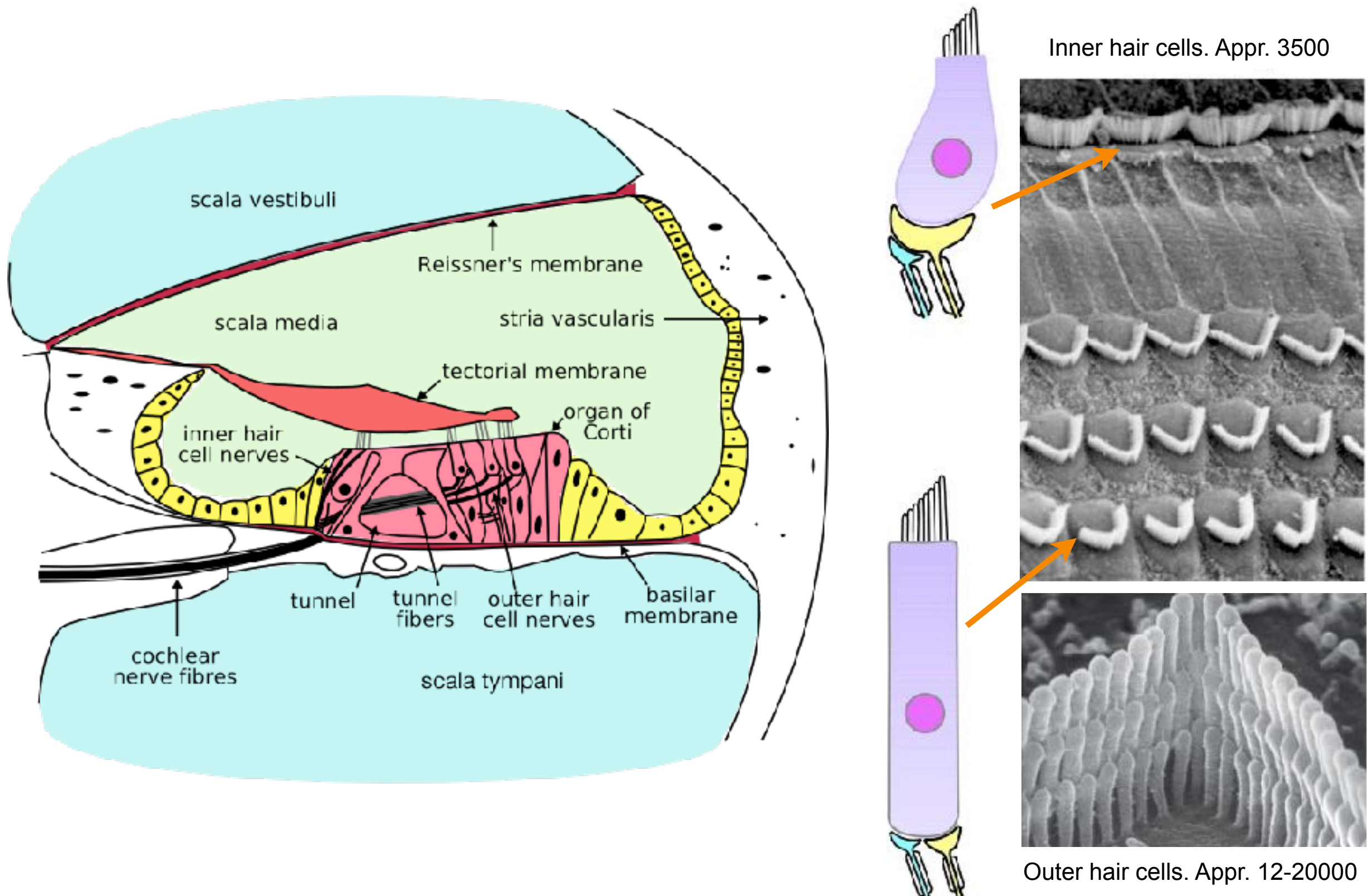
Vestibular organ: semicircular canals

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

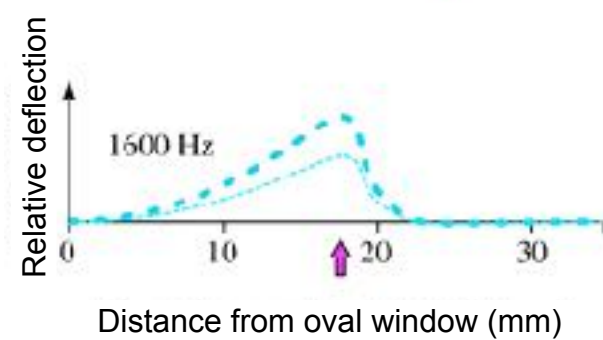
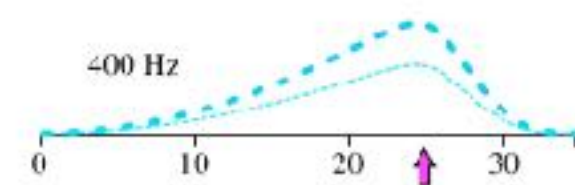
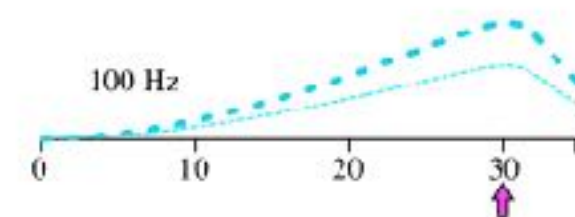
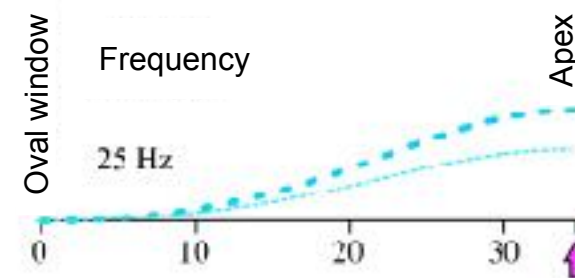
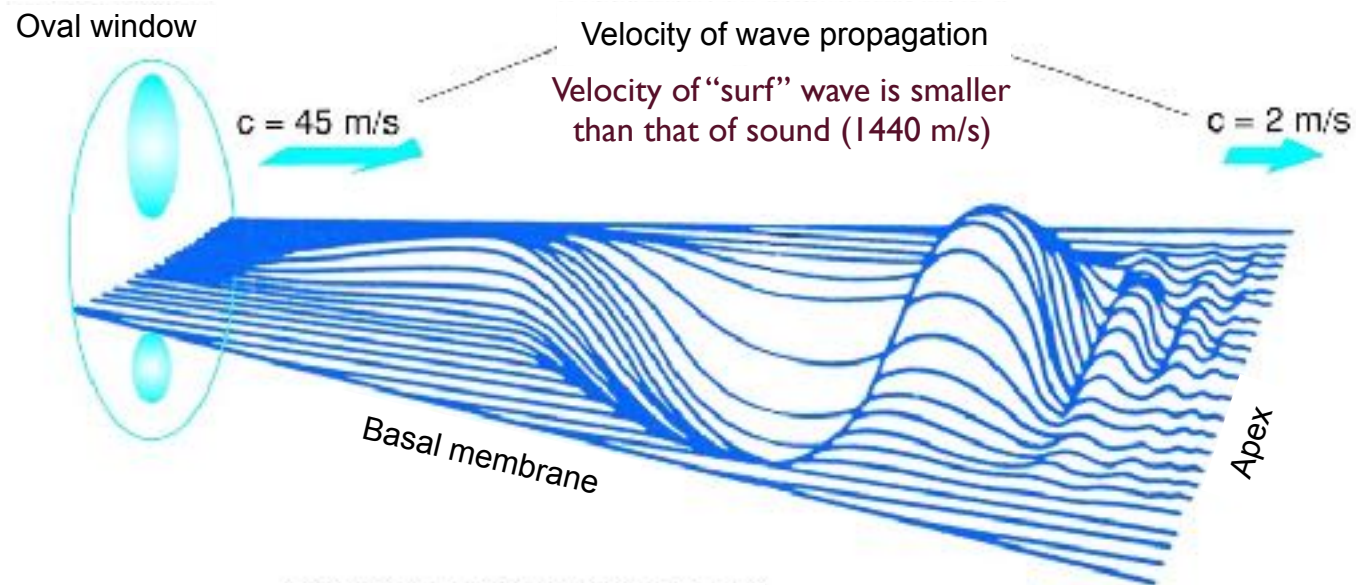




# Ultrastructure of the inner ear



# Békésy: propagating surface waves on basal membrane

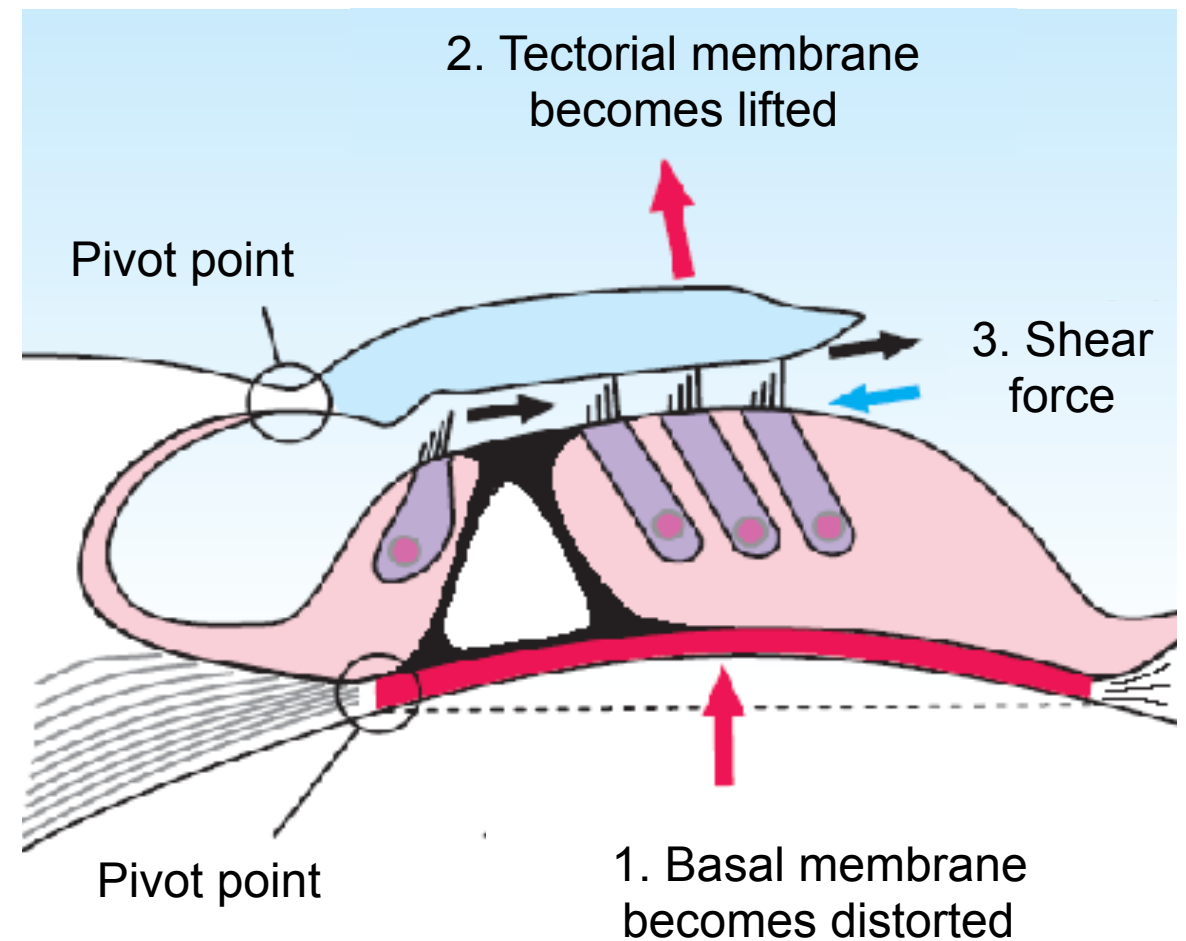
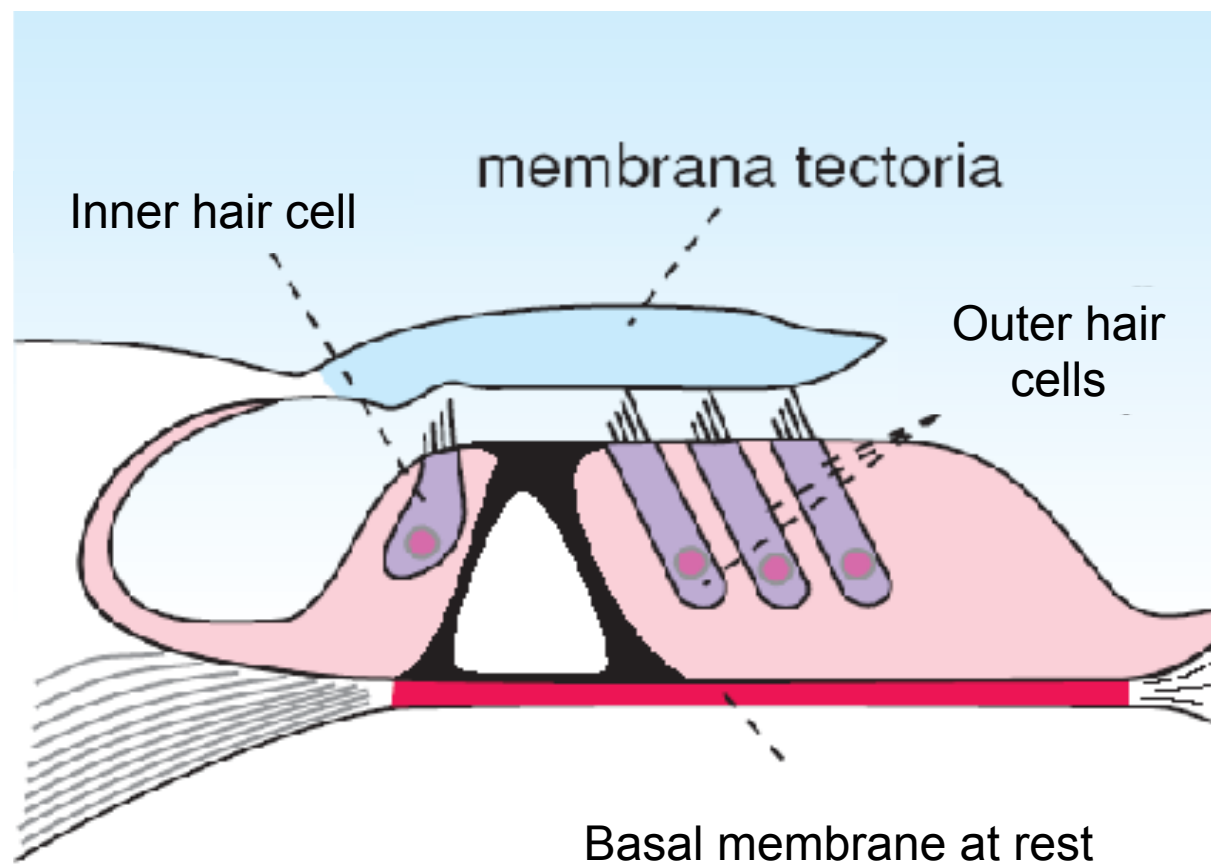


György Békésy  
Nobel-prize 1961

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

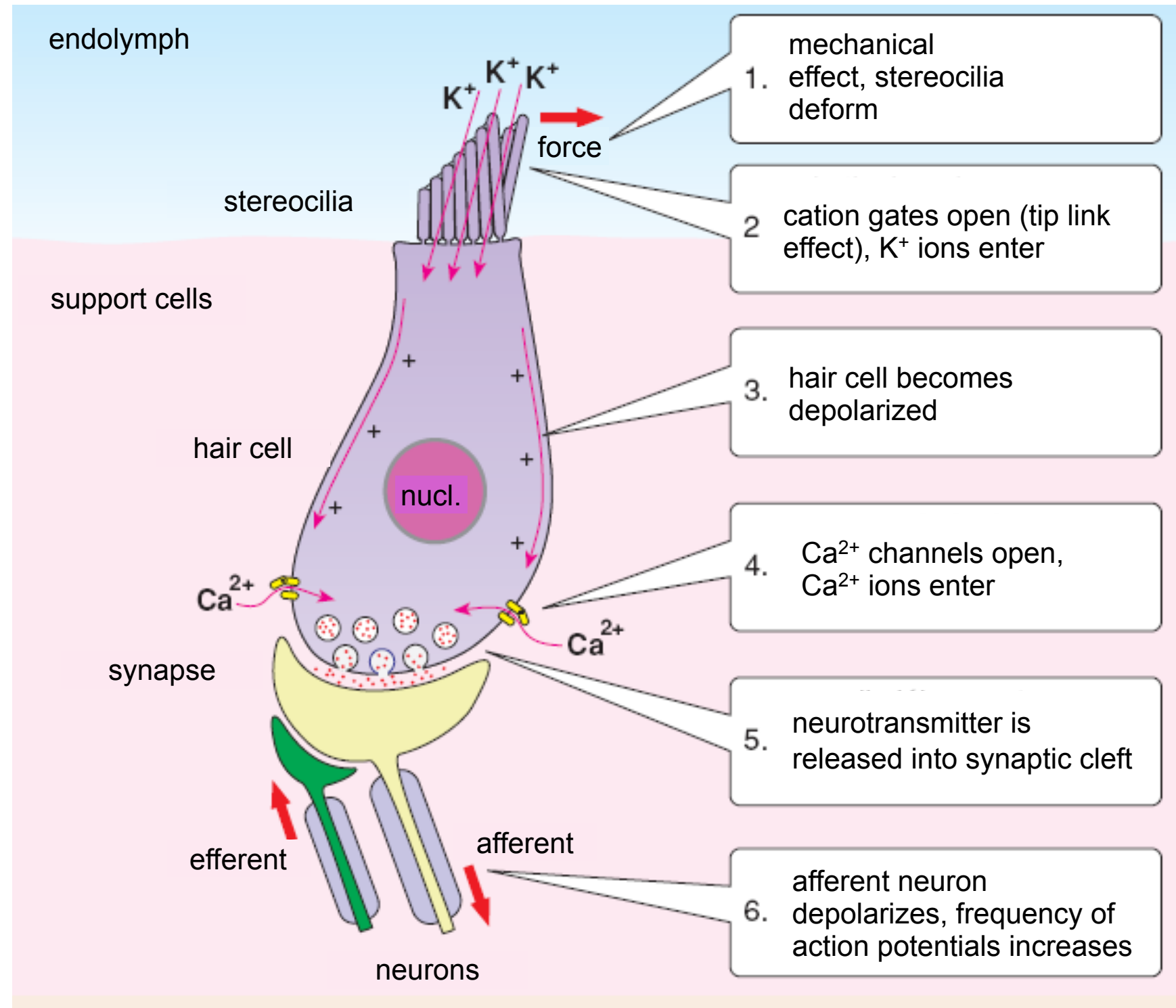
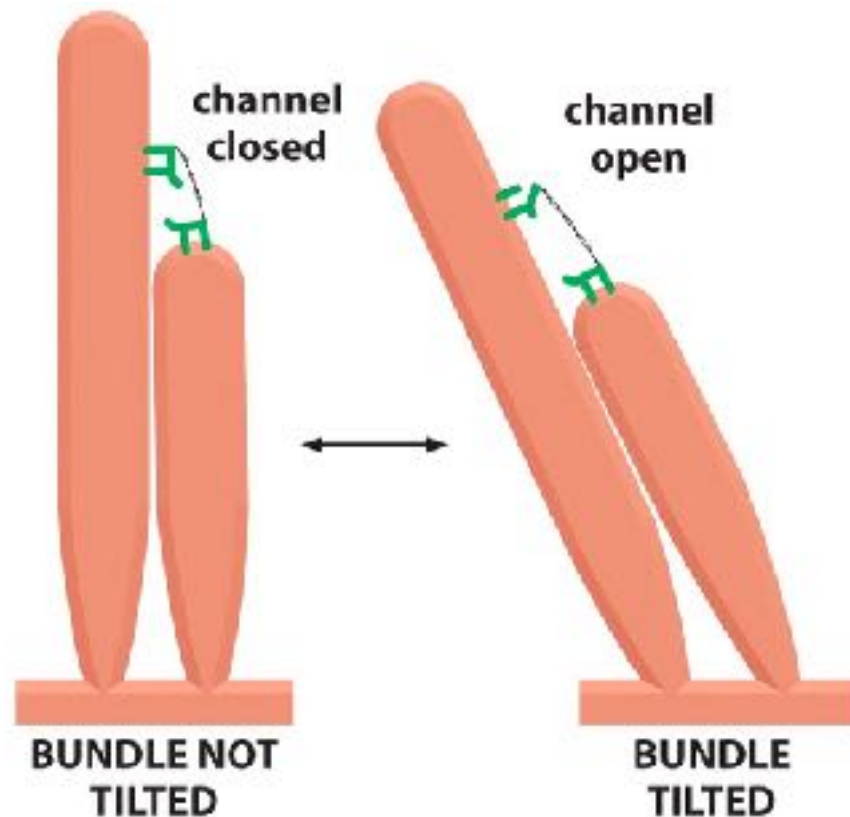
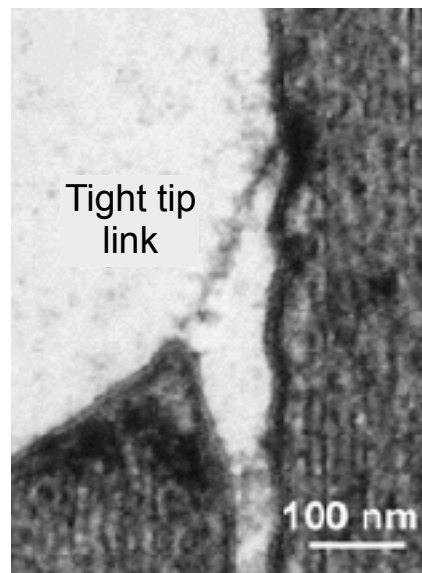
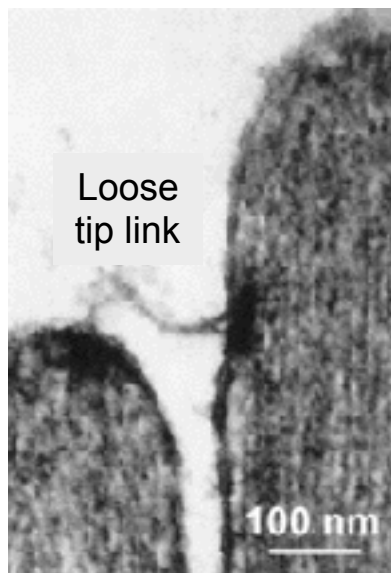
# Function of the organ of Corti

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

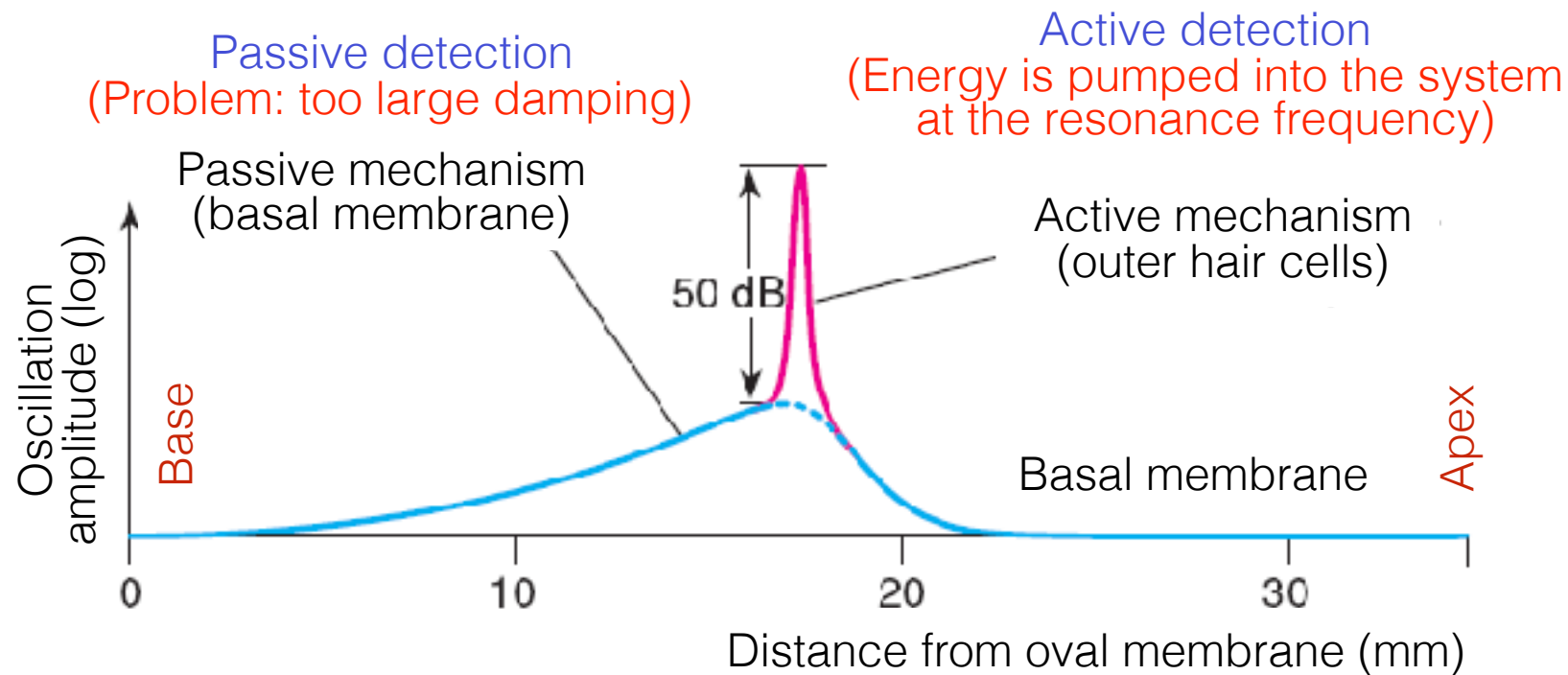




# Inner hair cells: Mechanoelectric transducers



# Outer hair cells: amplifiers

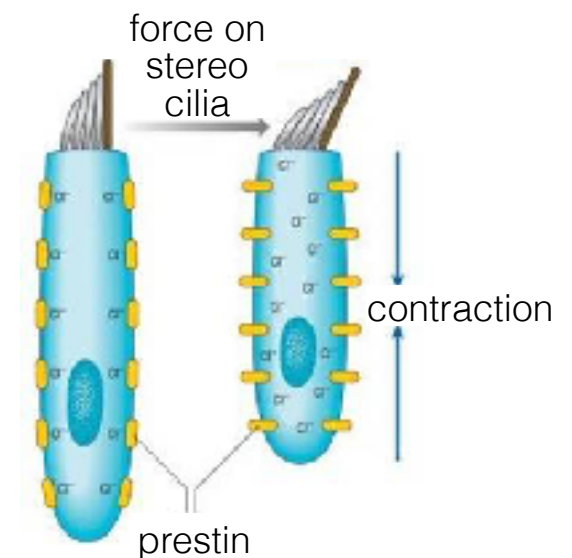


Observations pointing at active detection:

- 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

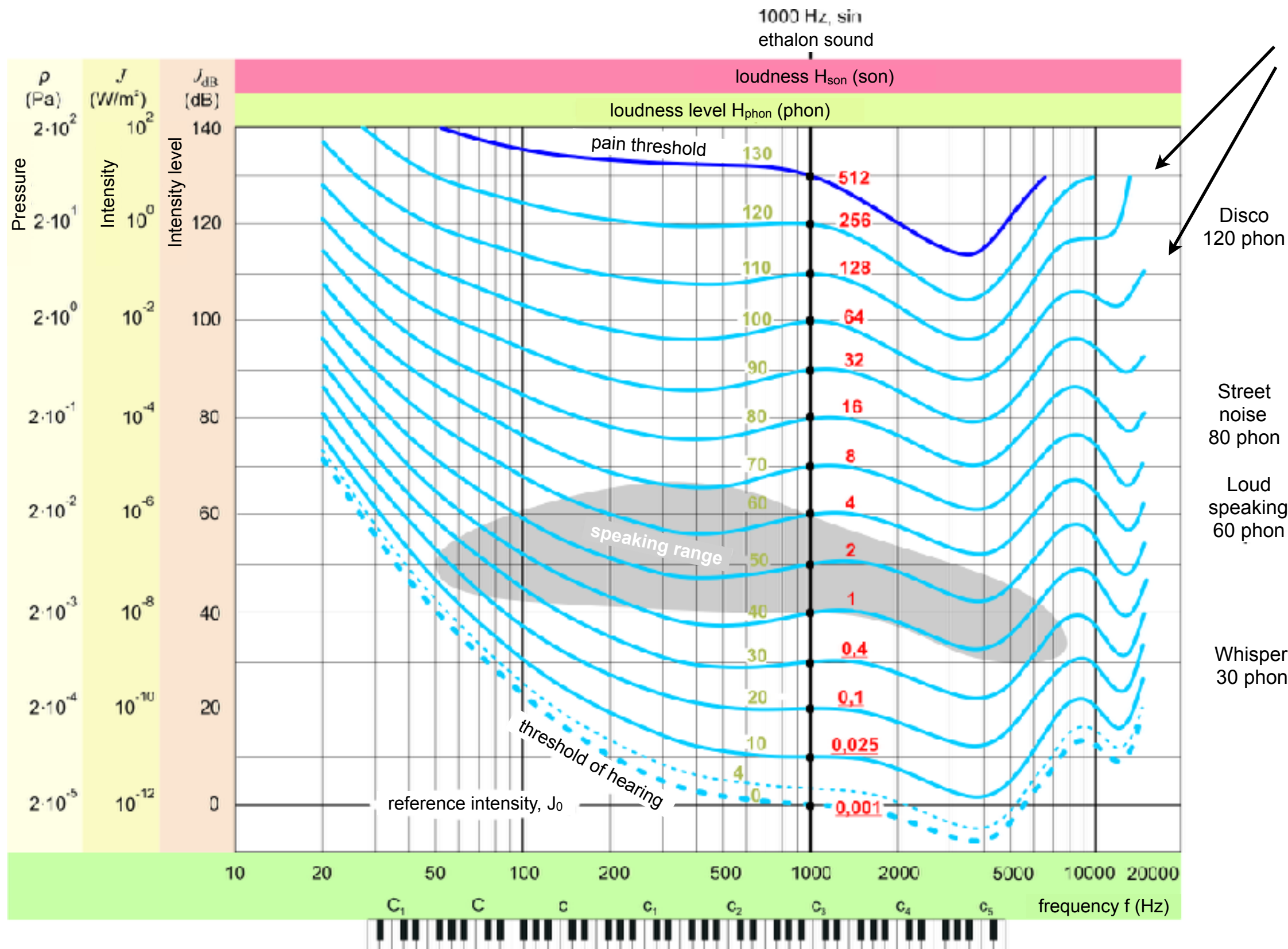


# Stimulus intensity and sensing - psychoacoustics

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

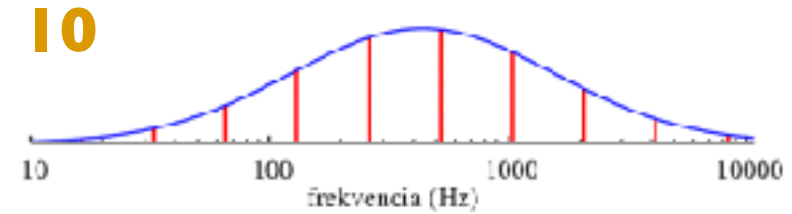
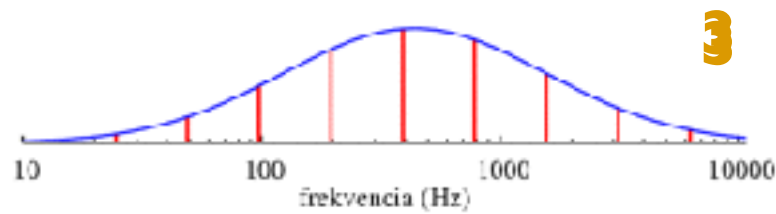
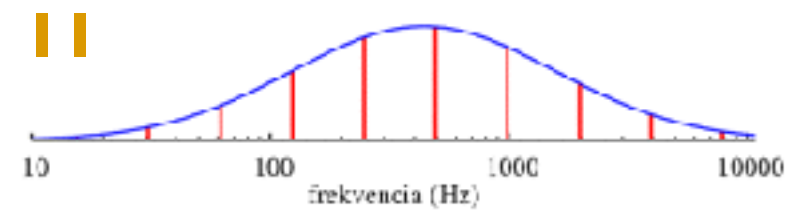
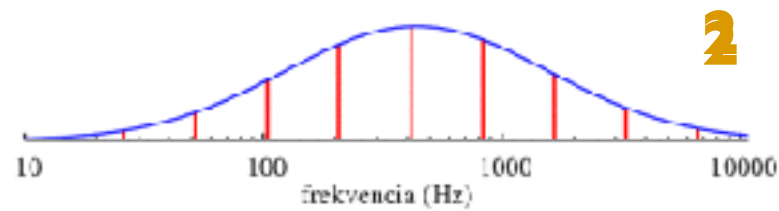
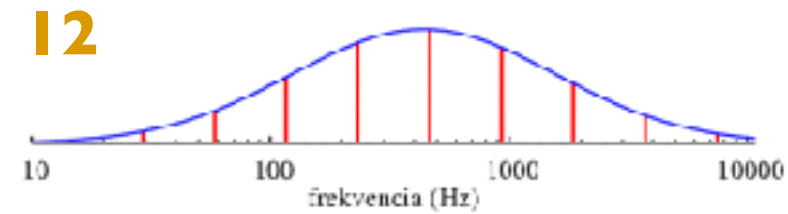
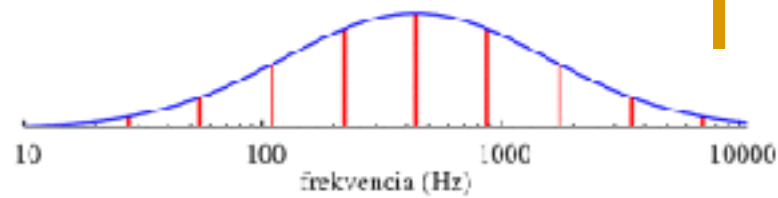
N.B.: The  
loudness level  
of a sound, in  
phon, is the dB  
value of a 1000  
Hz sound with  
which we hear it  
identically loud.

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

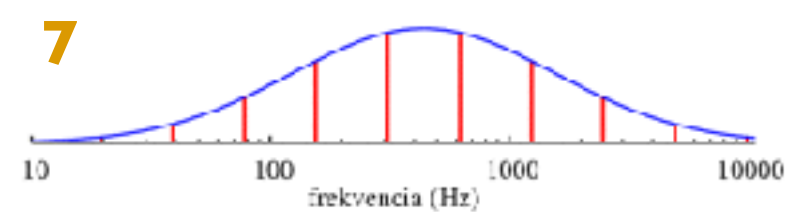
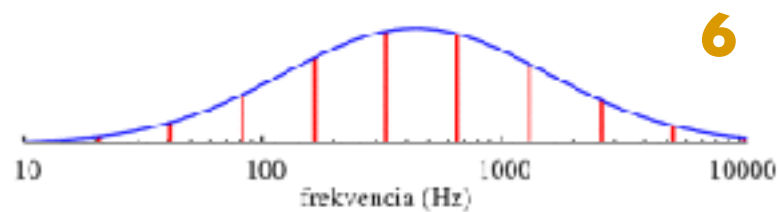
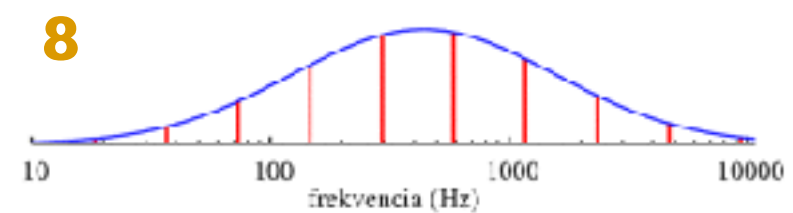
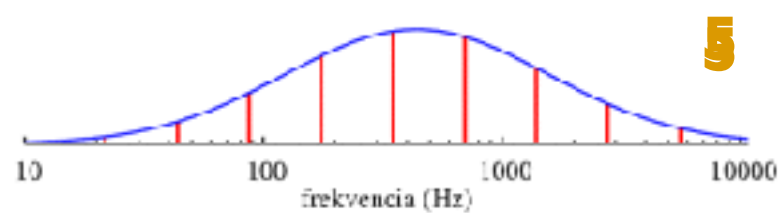
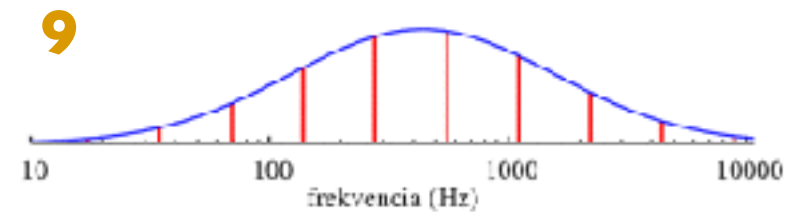
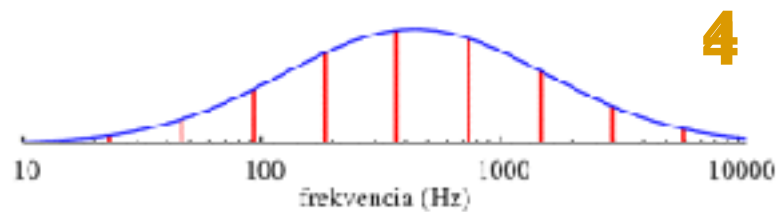


# Acoustic illusion?

Shepard tone:  
sine waves  
separated by  
octaves



Shepard  
scale:  
fundamental  
frequency  
moves



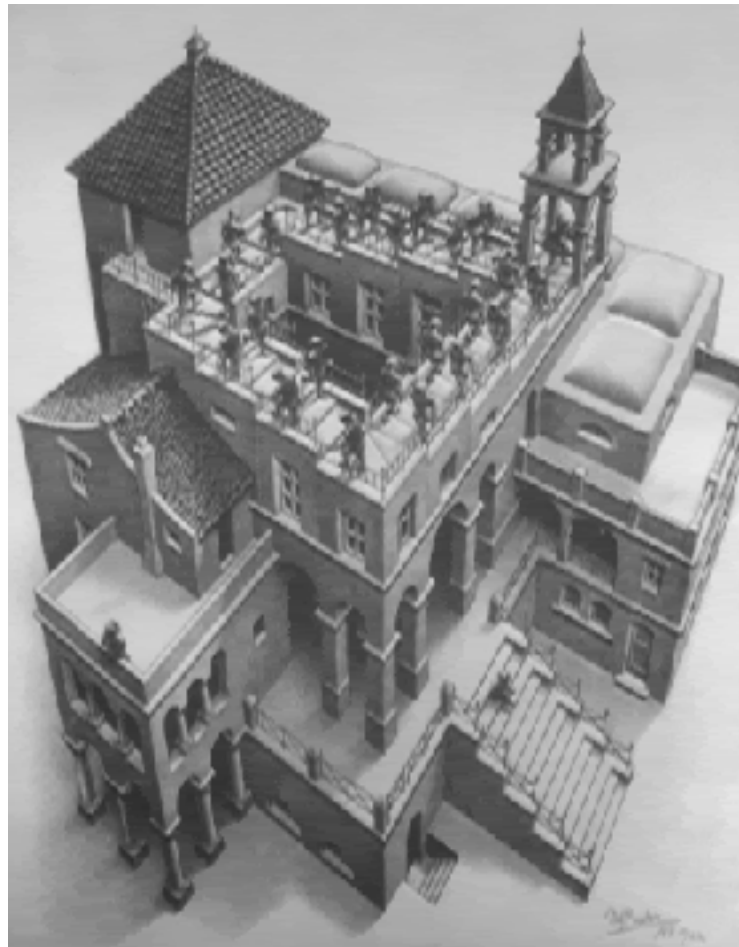
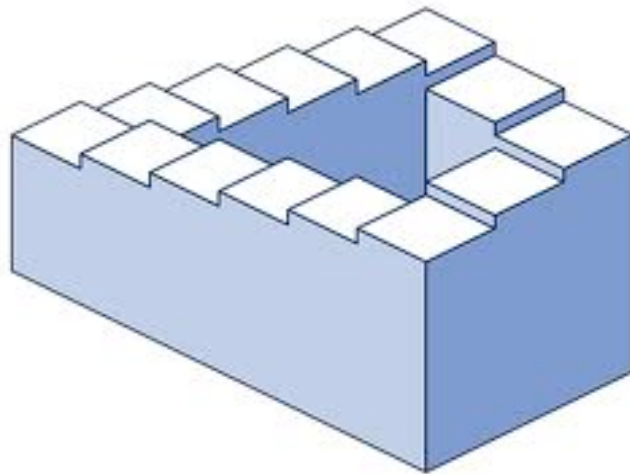


# Acoustic illusion?

Visual analogs of the Shepard scale:



Maurits Cornelis Escher  
(1898-1972)



Escher staircase



Barber's pole