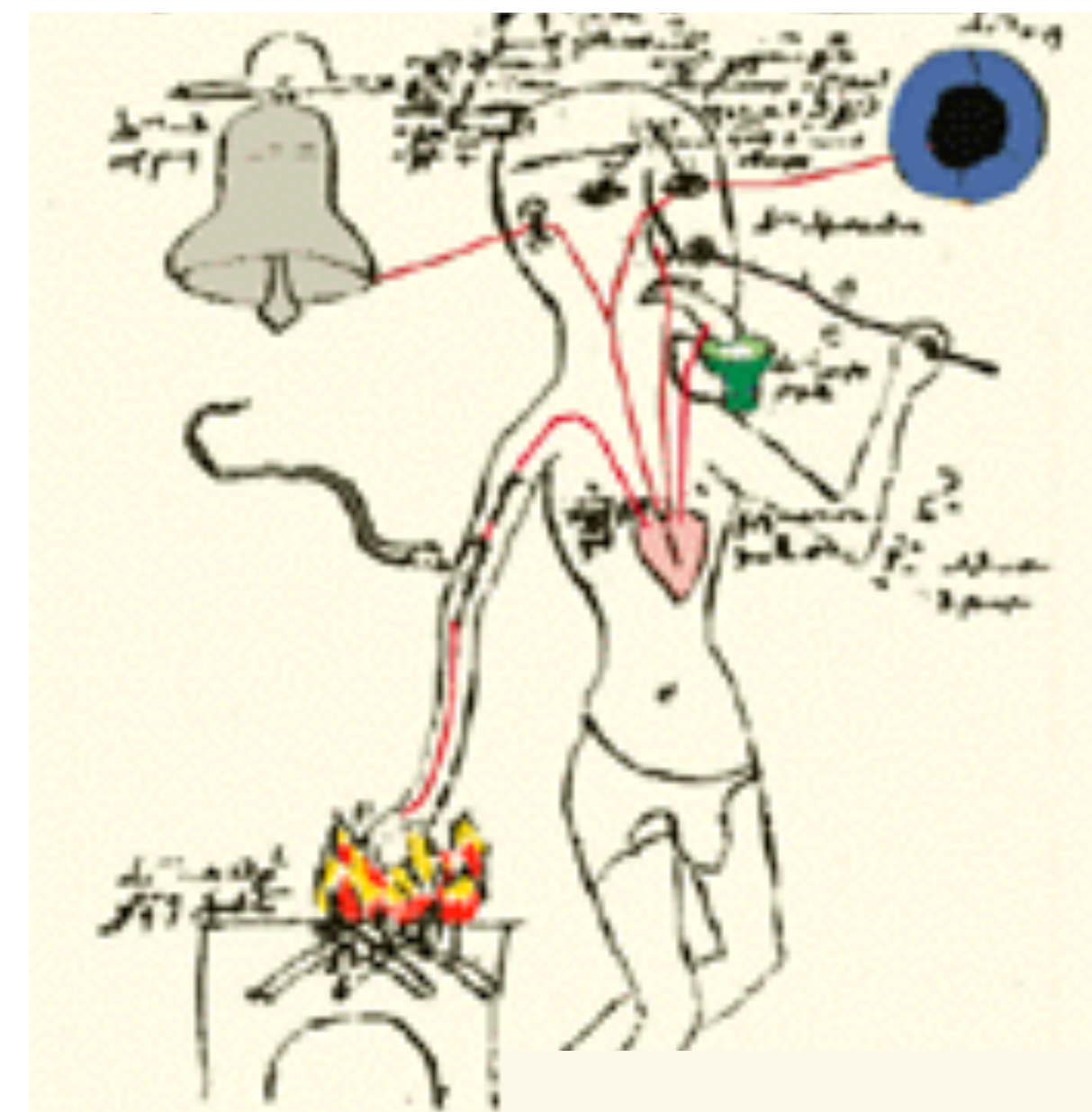


BIOPHYSICS OF SENSORY
RECEPTORS
VISION, HEARING

MIKLÓS KELLERMAYER

Theories about sensing

Cardiocentric sensing
(Medieval reconstruction)



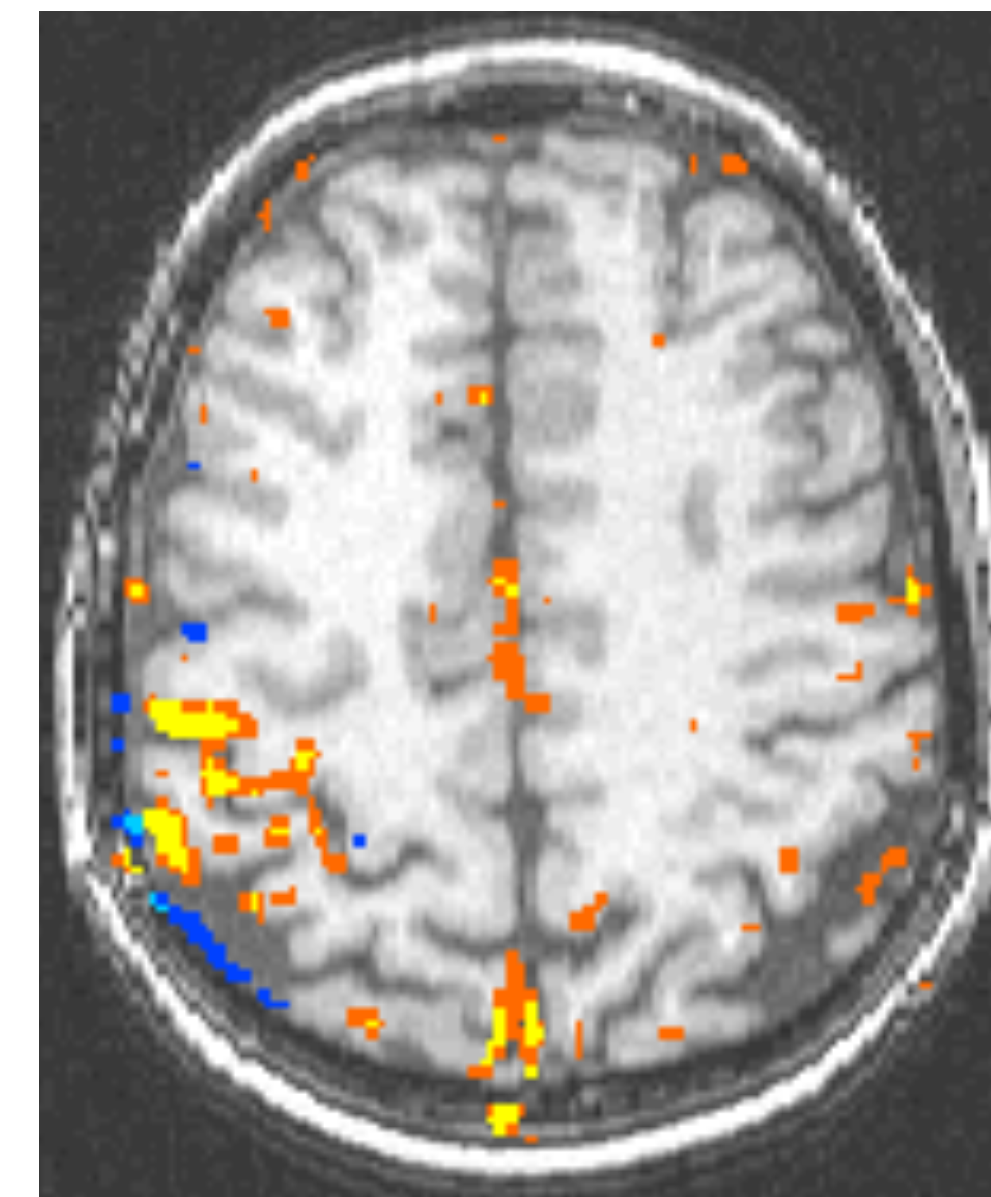
Aristotle (384-322 BC)
cardiocentric sensing.

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

Today:

stimulus →

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

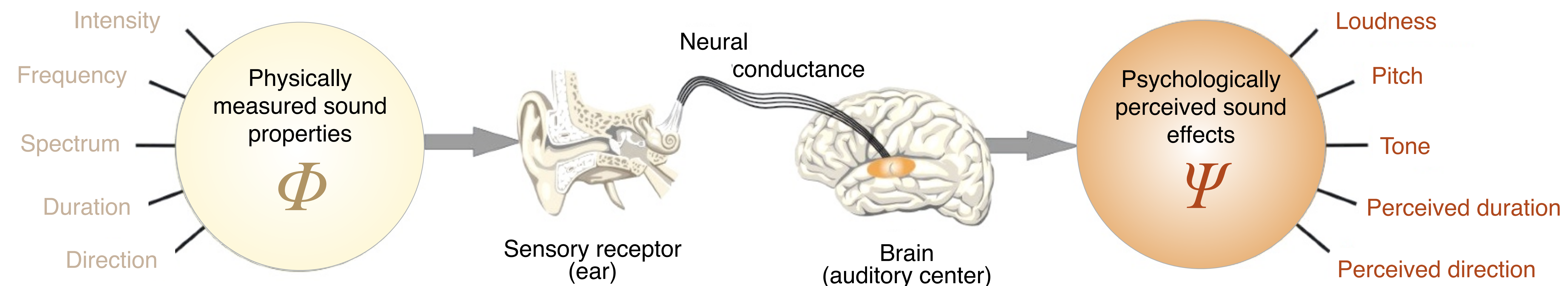


fMRI recording during
sensomotoric function



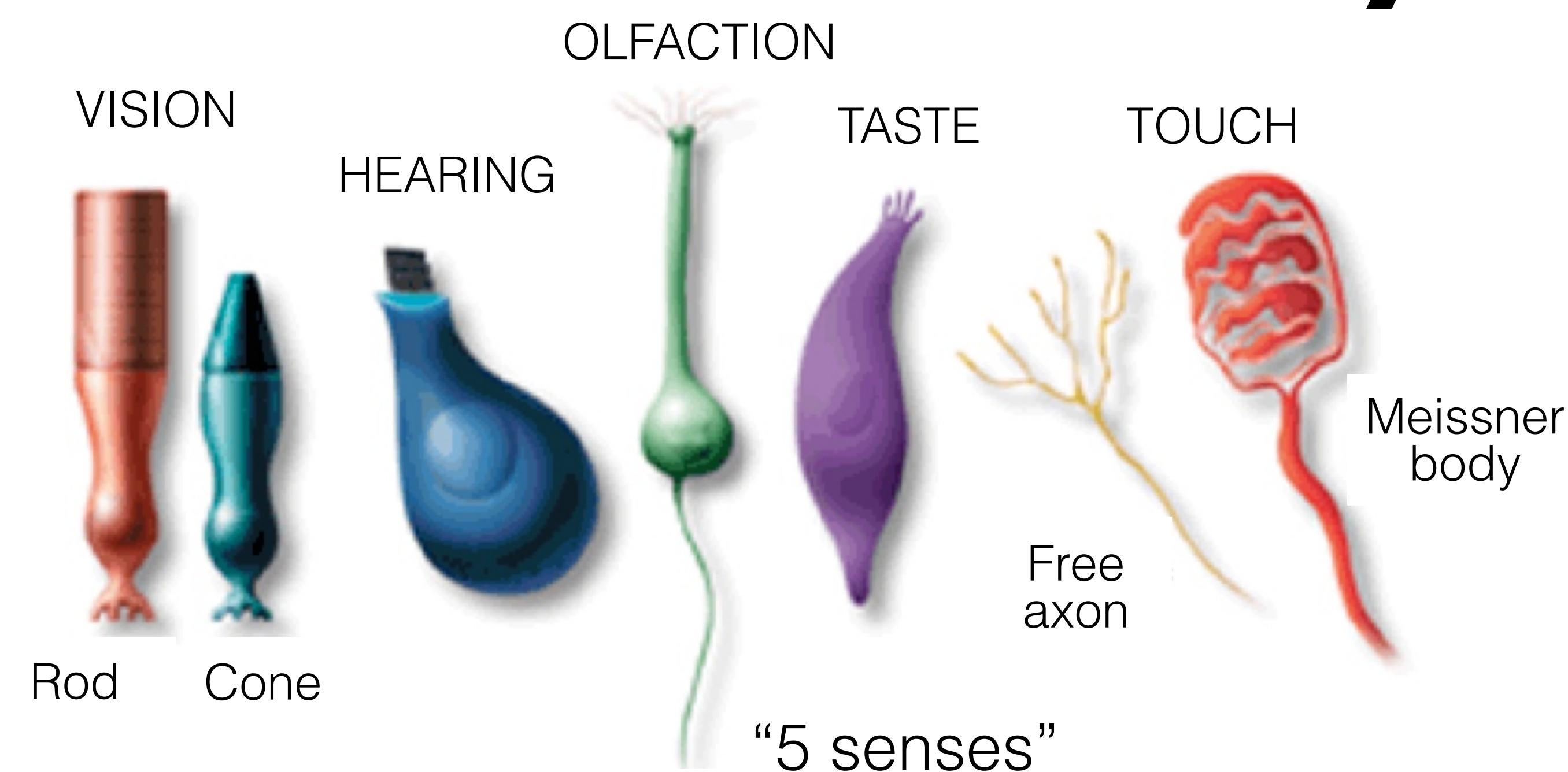
Sensory homuncle

Process of sensing - example of hearing



Sound recognition
Sound sensation

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.

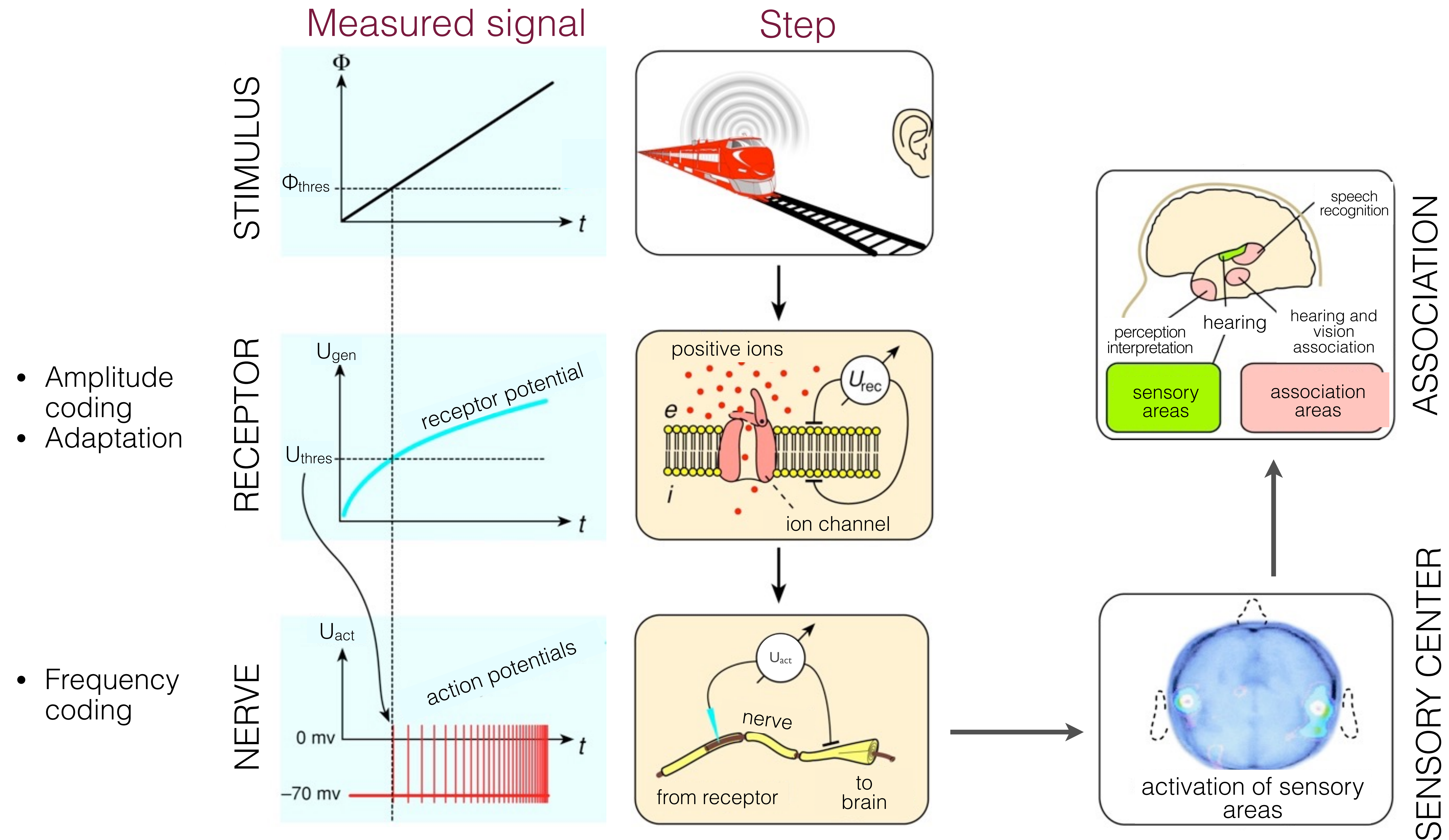
	Modality	Receptor	Organ
↑ Perceived	1 Vision	Rods and cones	Eye
	2 Hearing	Hair cells	Ear (organ of Corti)
	3 Olfaction (smelling)	Olfactory neuron	mucus membrane
	4 Taste	Taste receptor cells	Taste buds
	5 Angular acceleration	Hair cells	Ear (semicircular canals)
	6 Linear acceleration	Hair cells	Ear (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 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

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!

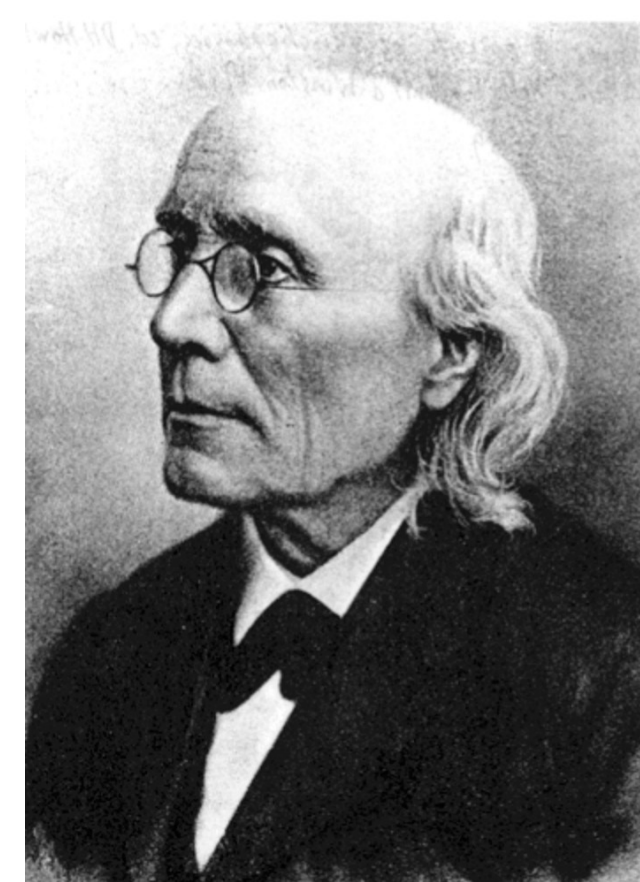
2. Stimulus intensity and perception strength

Weber-Fechner
psychophysical law

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



Ernst Weber
(1795-1878)



Gustav Fechner
(1801-1887)

Stevens' power law

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



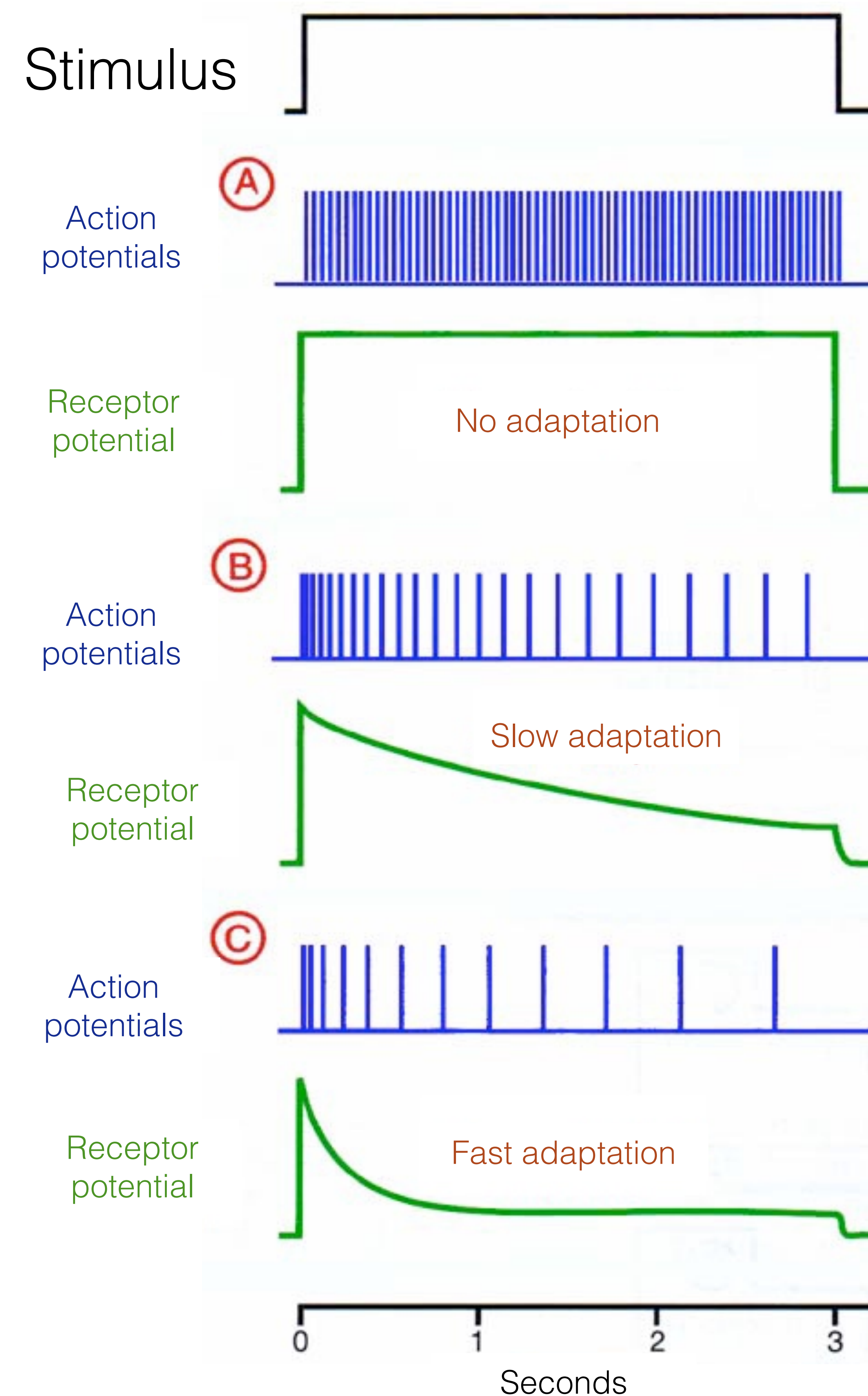
Stanley Smith Stevens
(1906-1973)

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



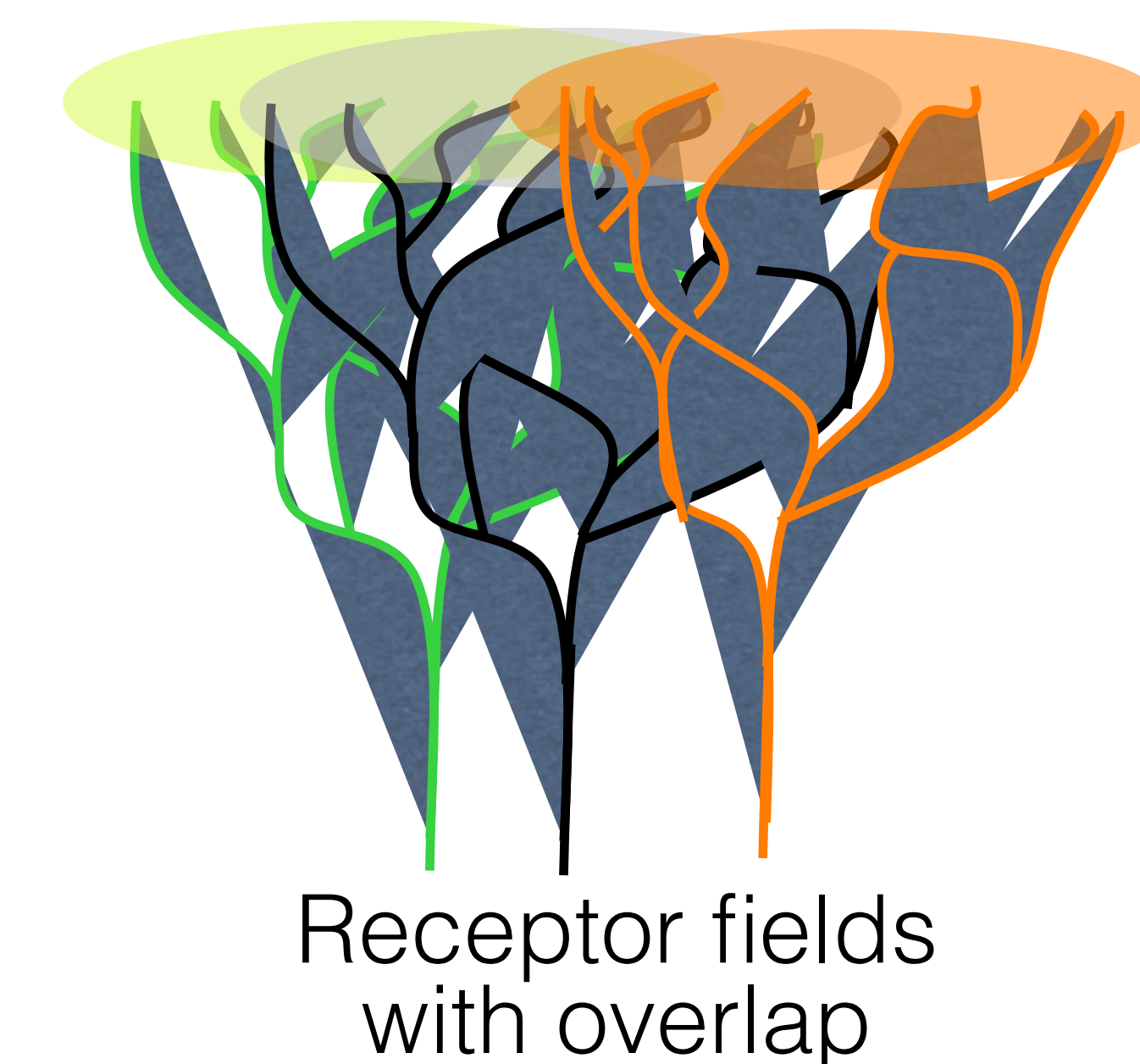
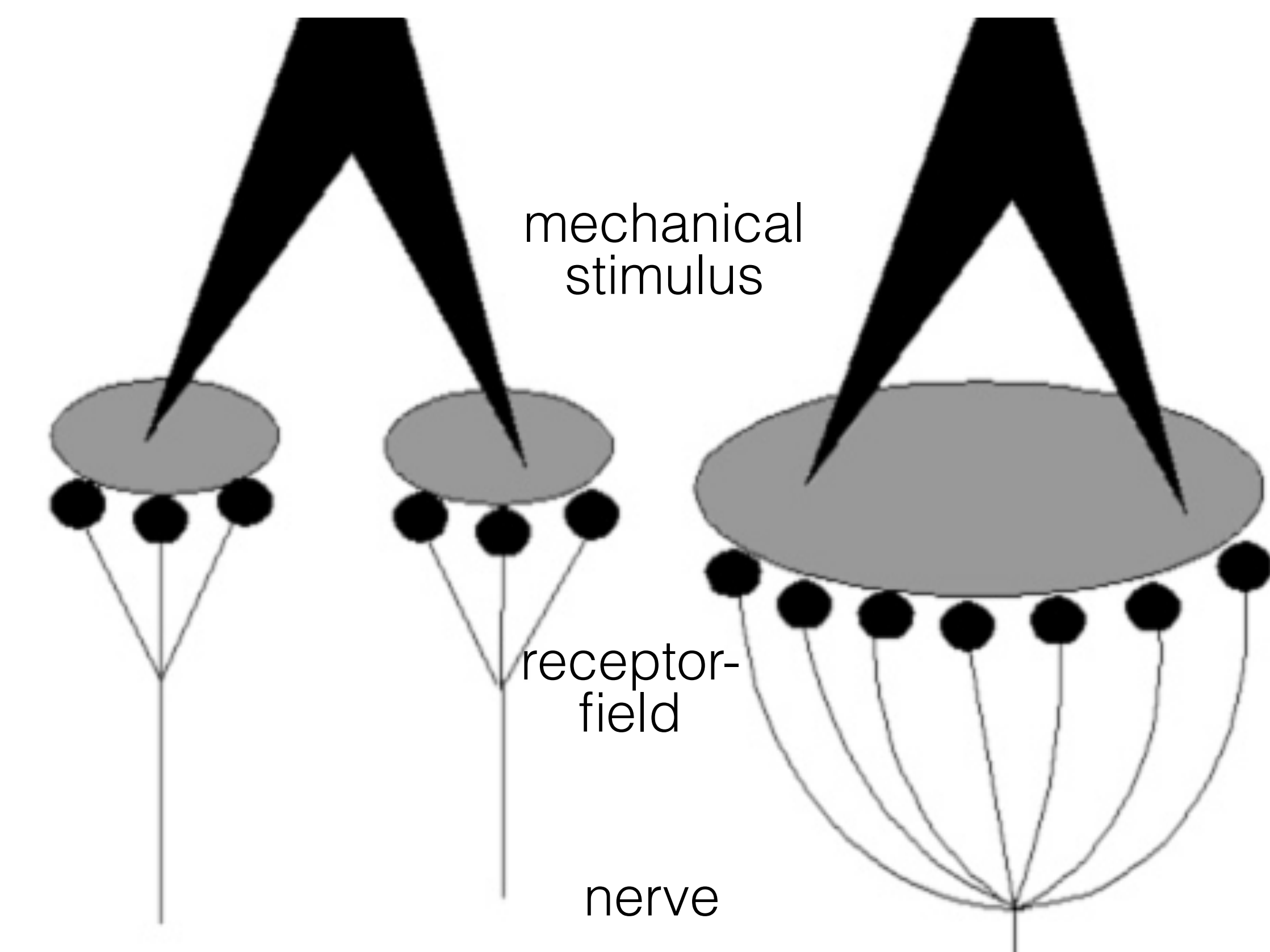
Adaptation: during constant stimulus the frequency of action potentials gradually decreases.

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

MIKLÓS KELLERMAYER

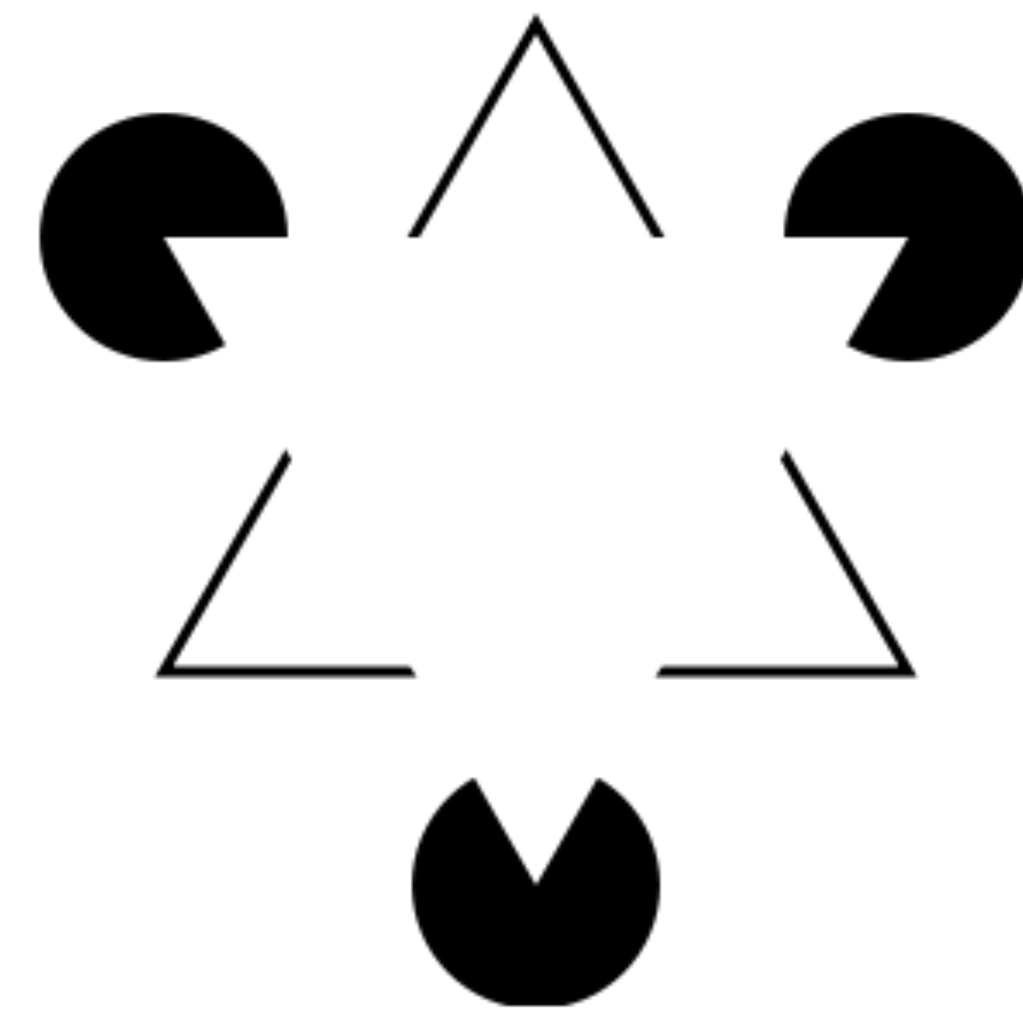
Biophysics of vision

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

Optical illusion - intensity

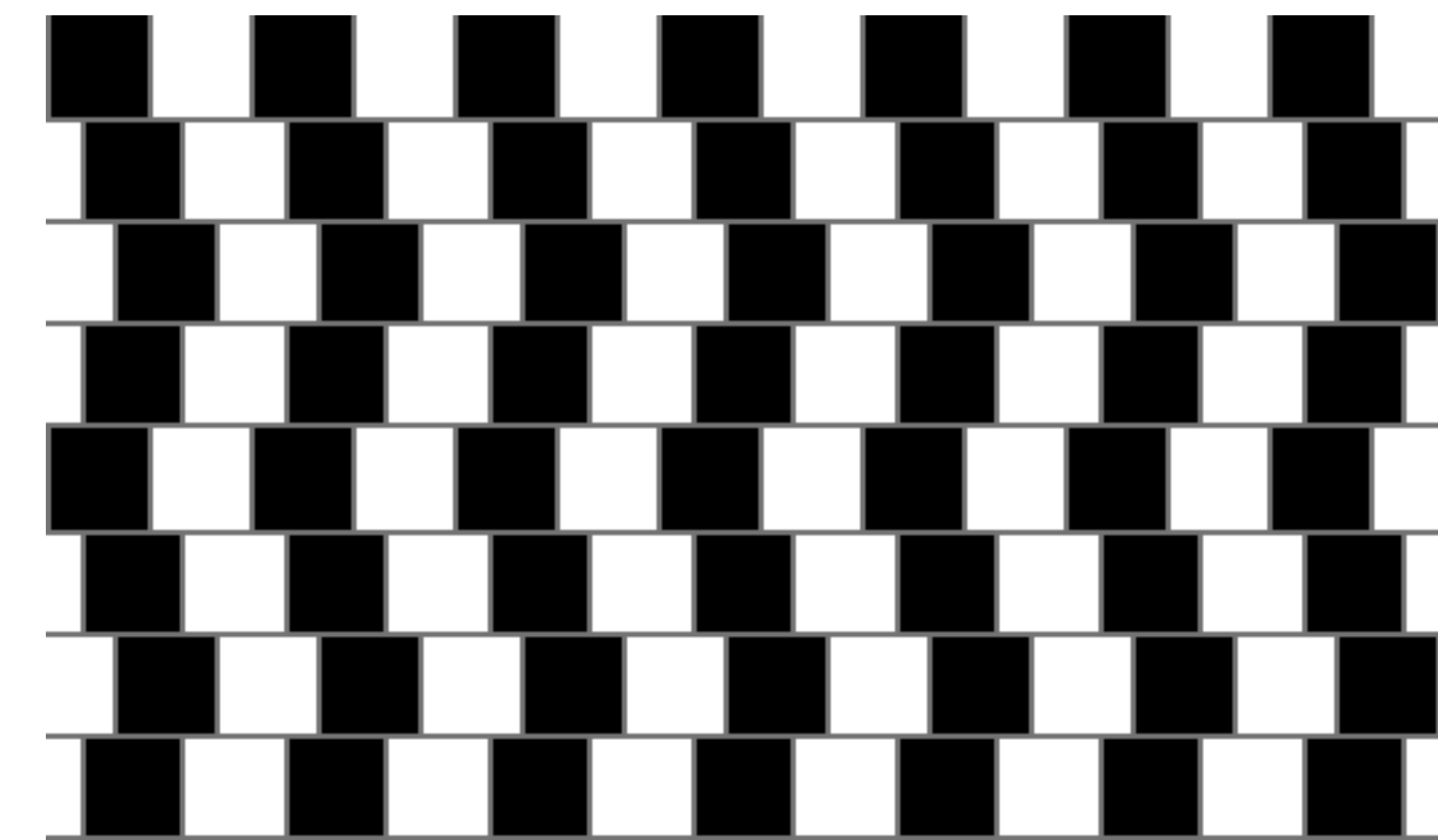


Mach bands

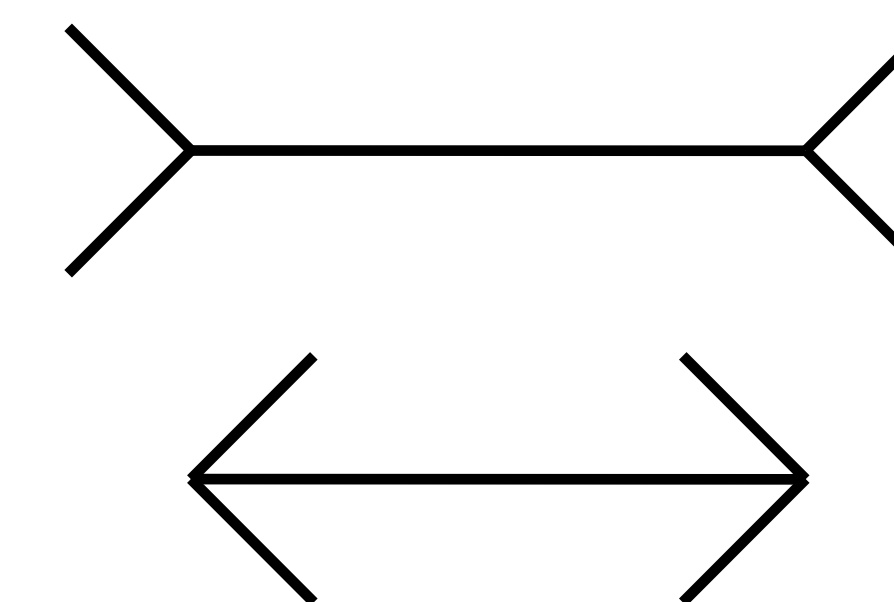


Kanizsa triangle

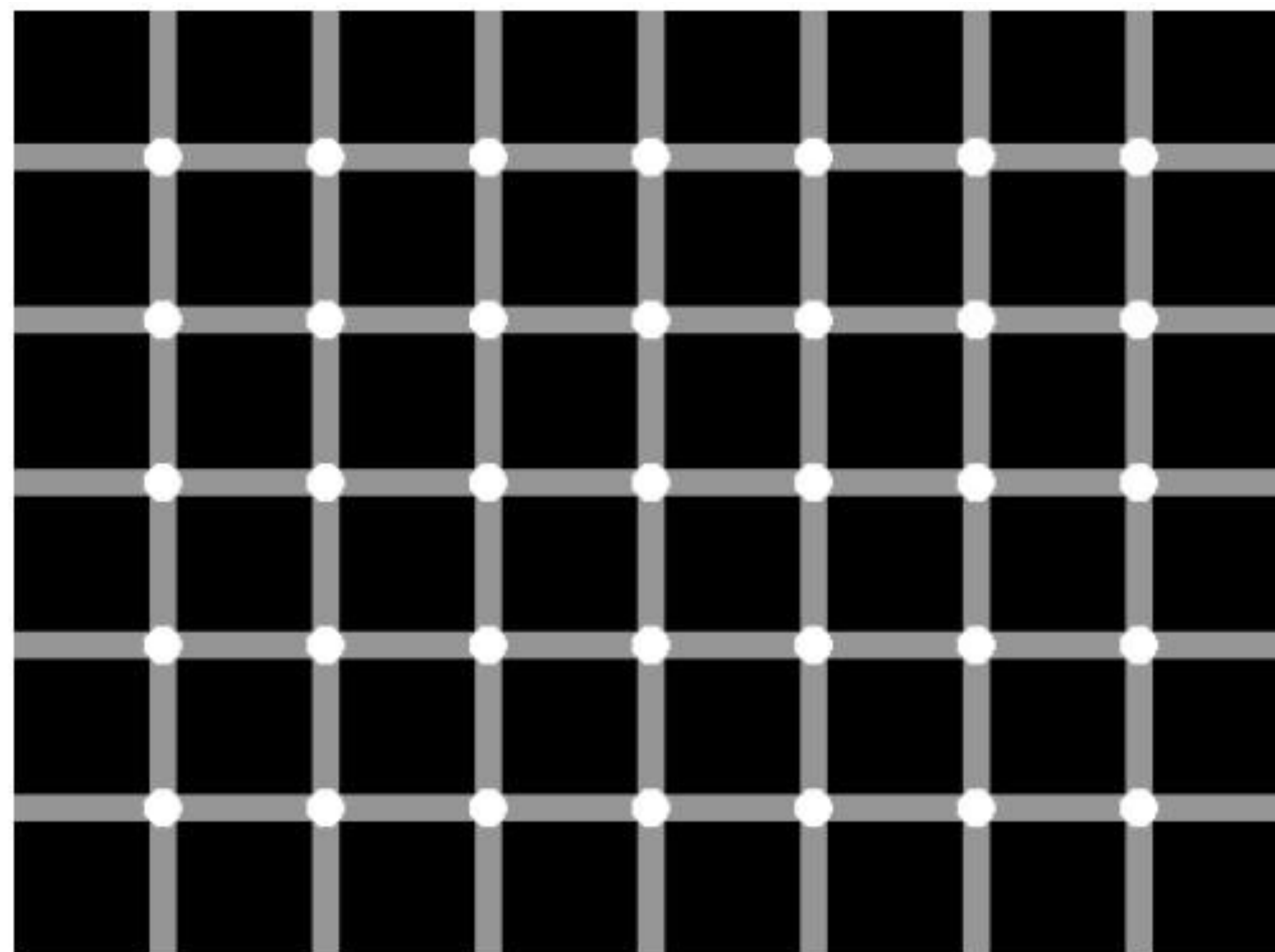
Optical illusion - direction, size



Café wall illusion



Müller-Lyer illusion

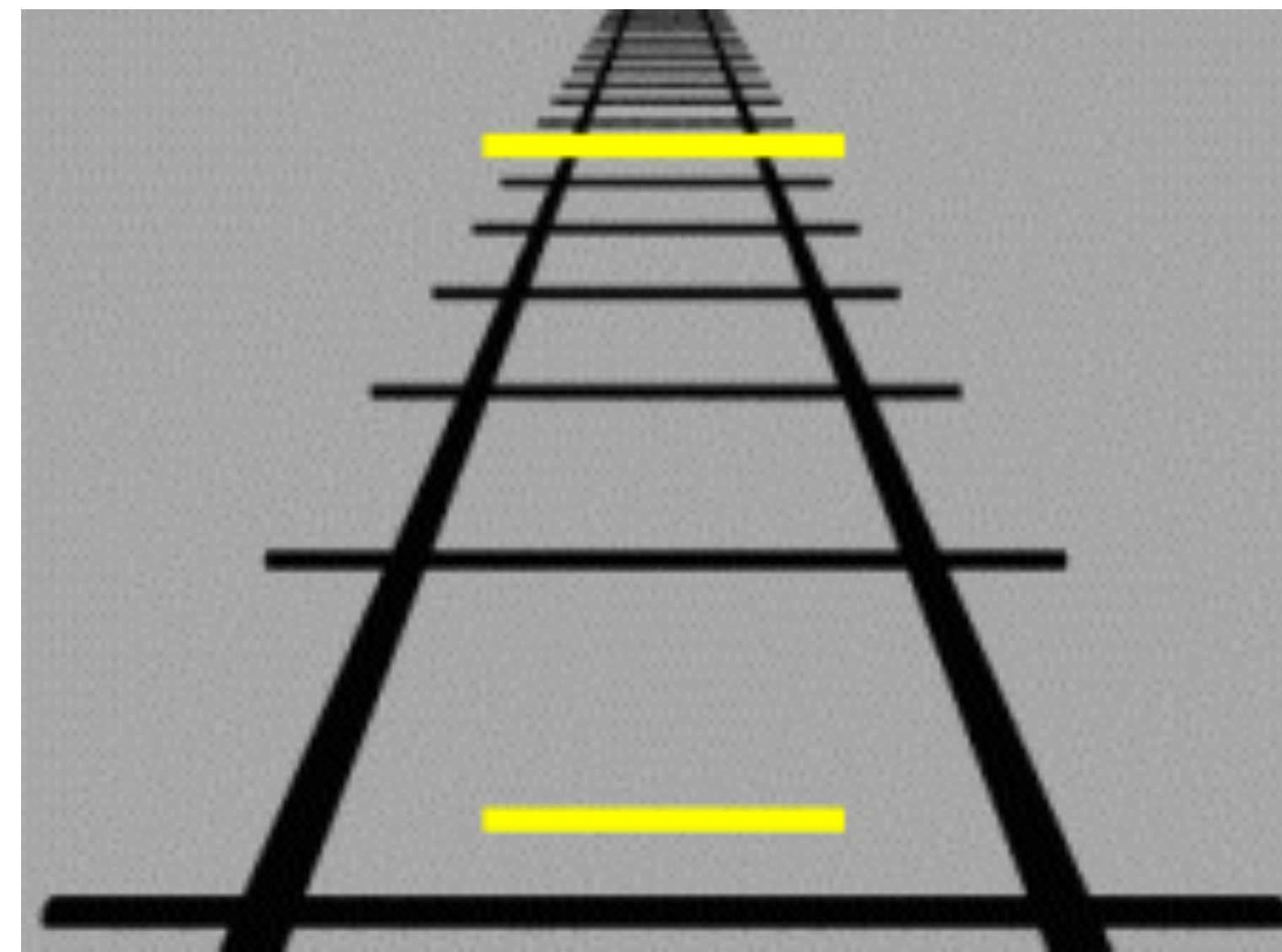


How many black circles can we count?

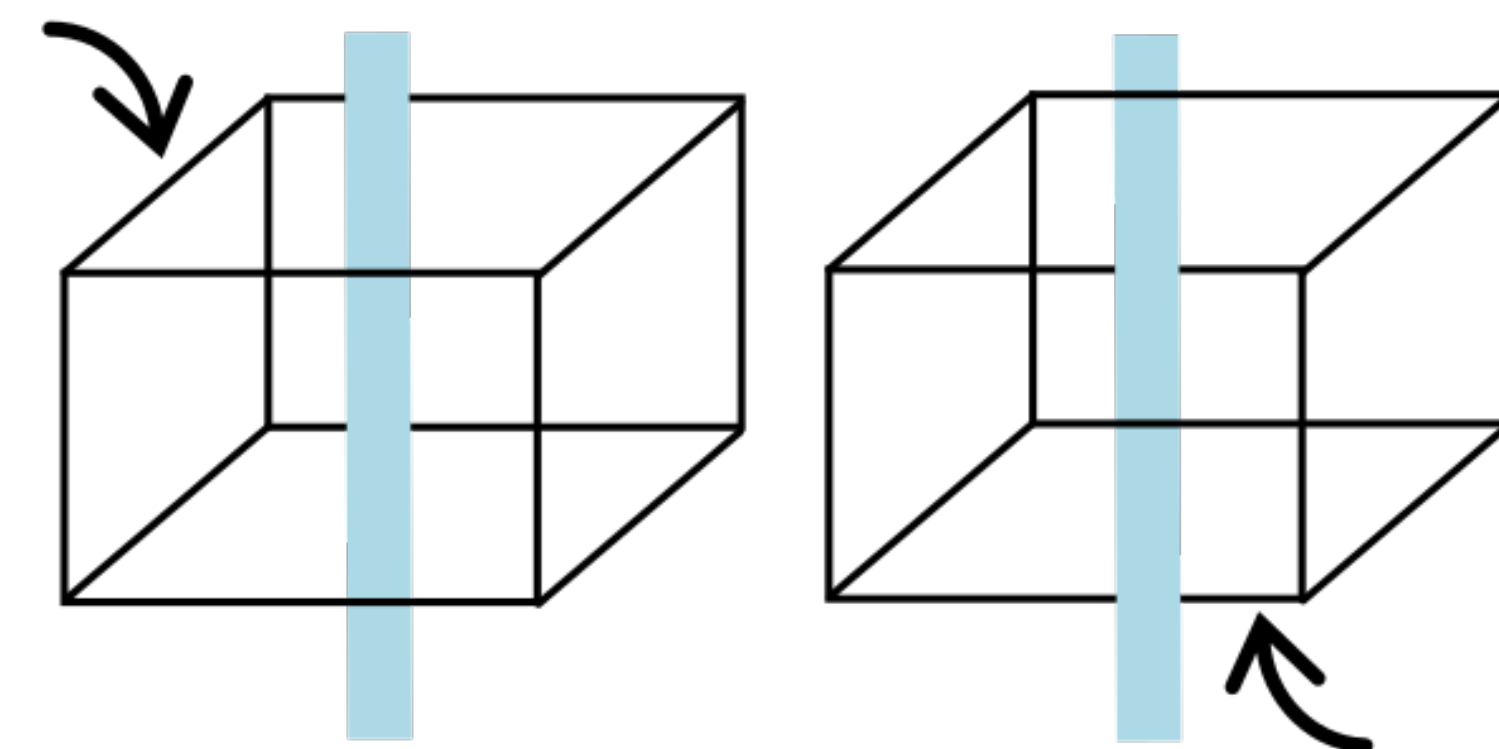


Ebbinghaus illusion

Optical illusions – space, shape



Ponzo illusion



Necker cube

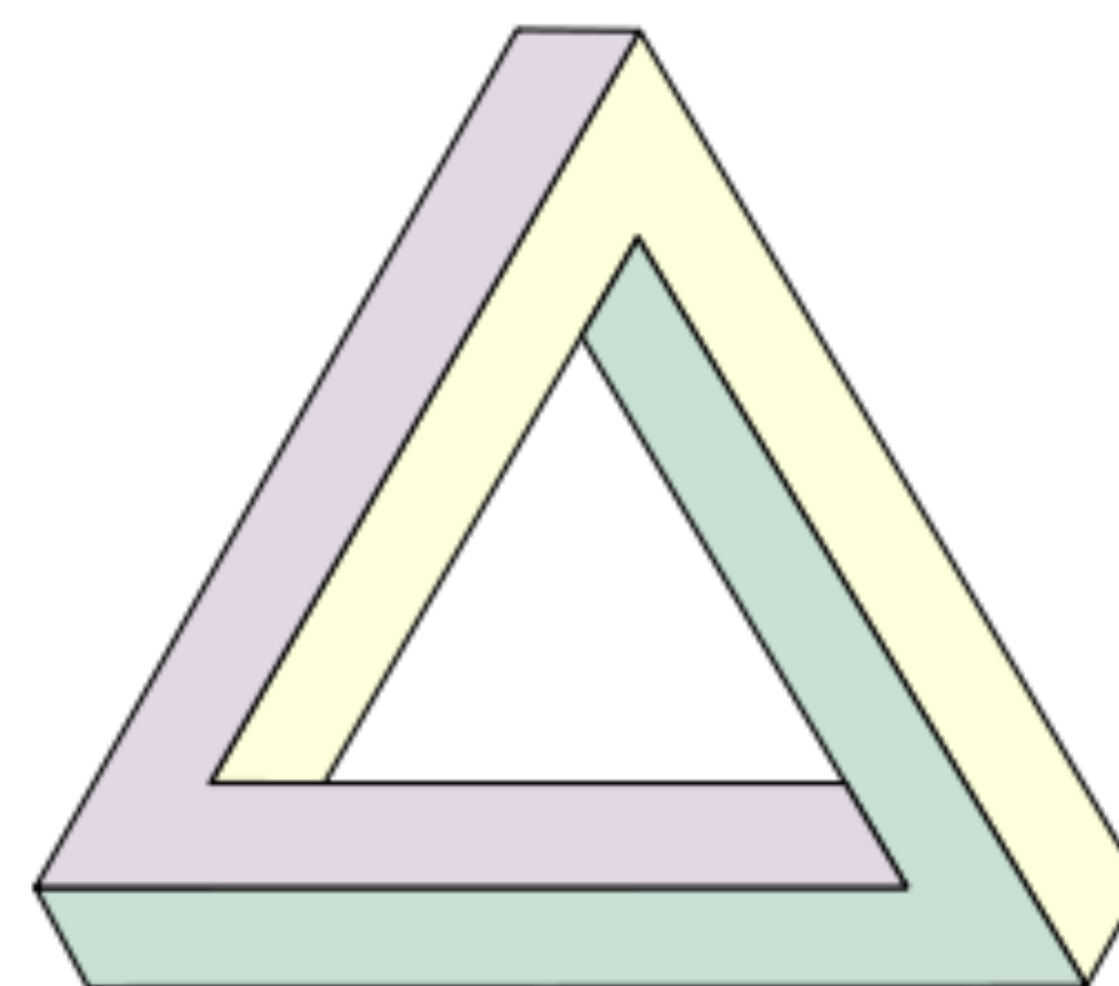


Necker cube effect on a roman mosaic

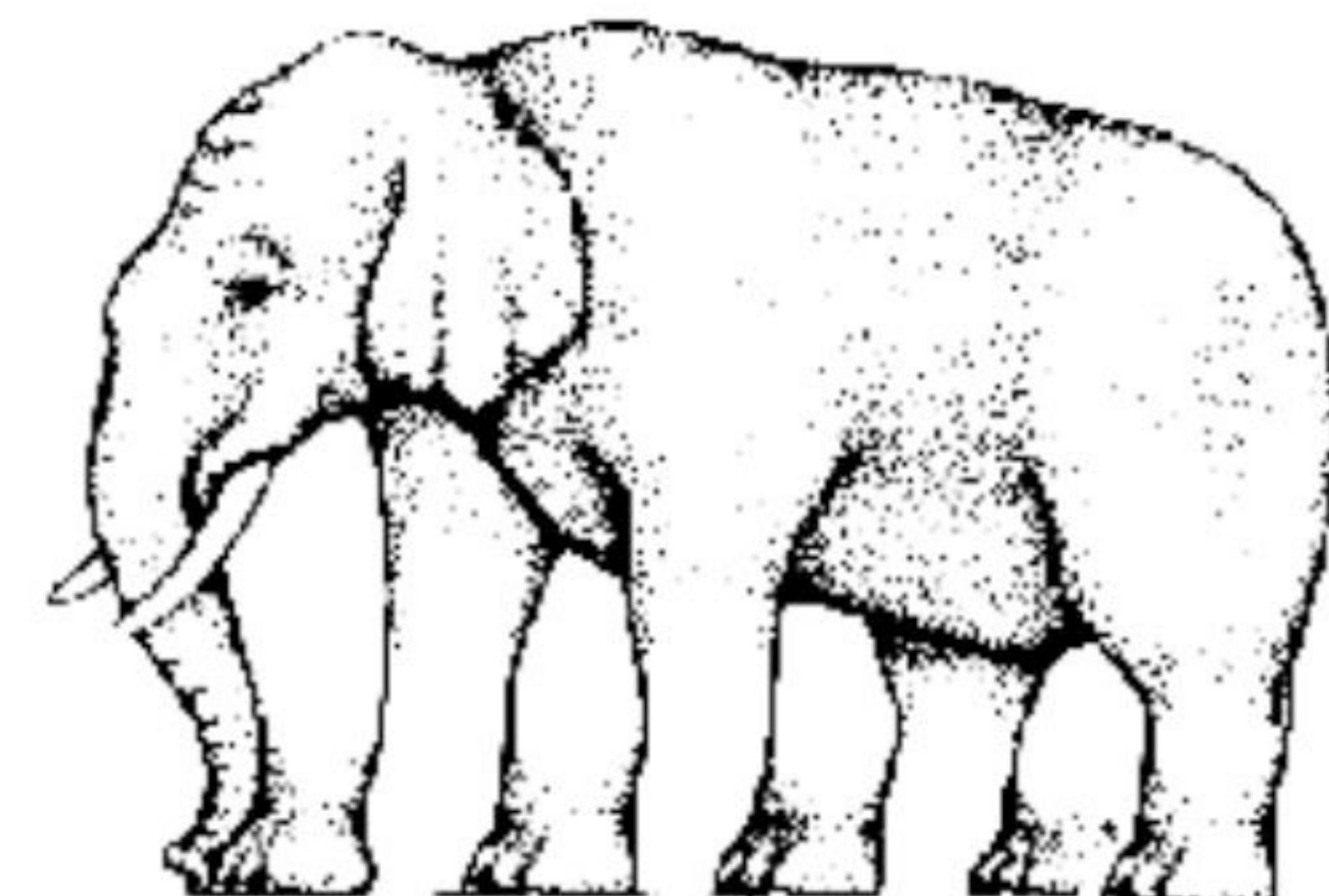
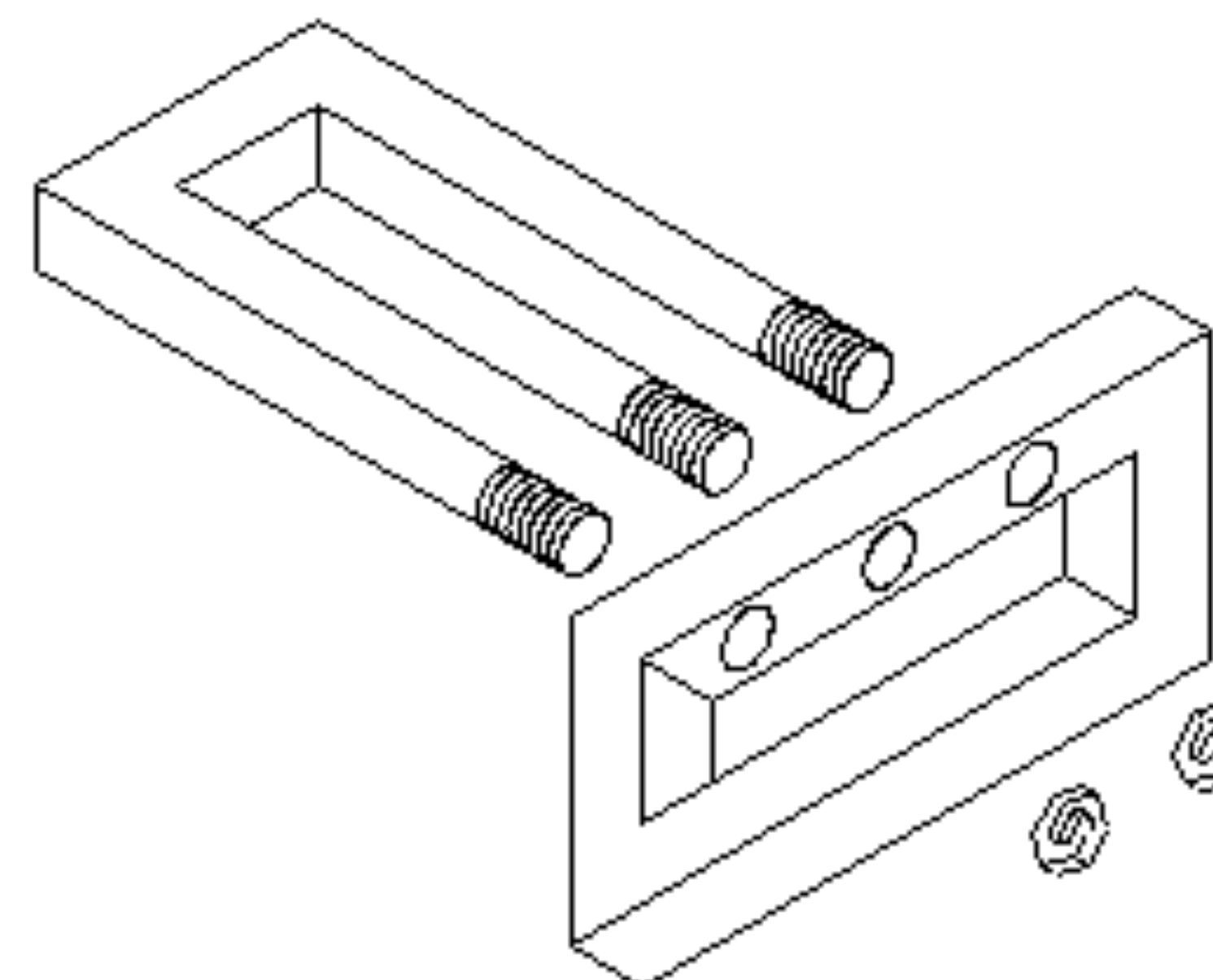


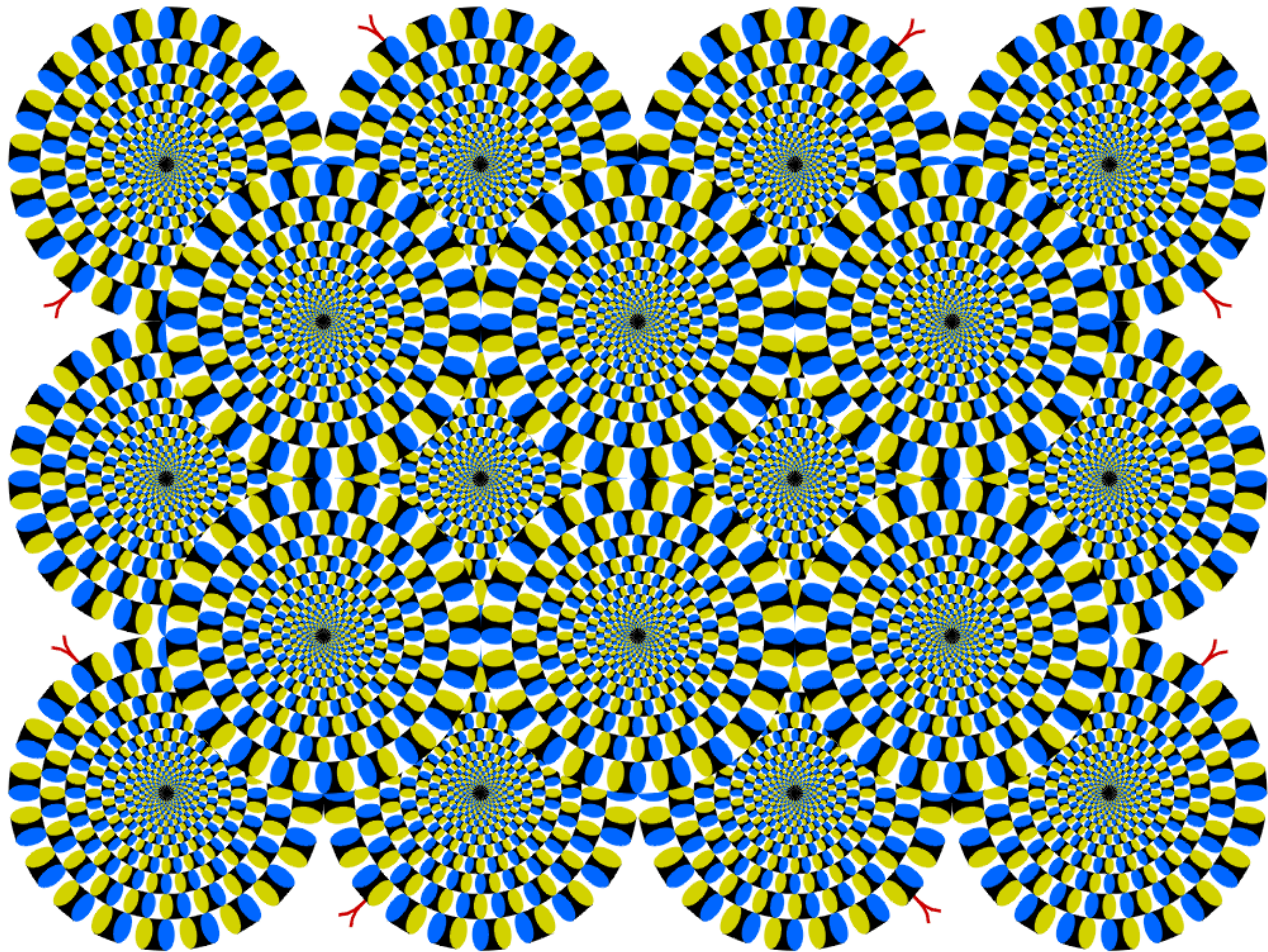
Rubin vase illusion

“Impossible”
geometries



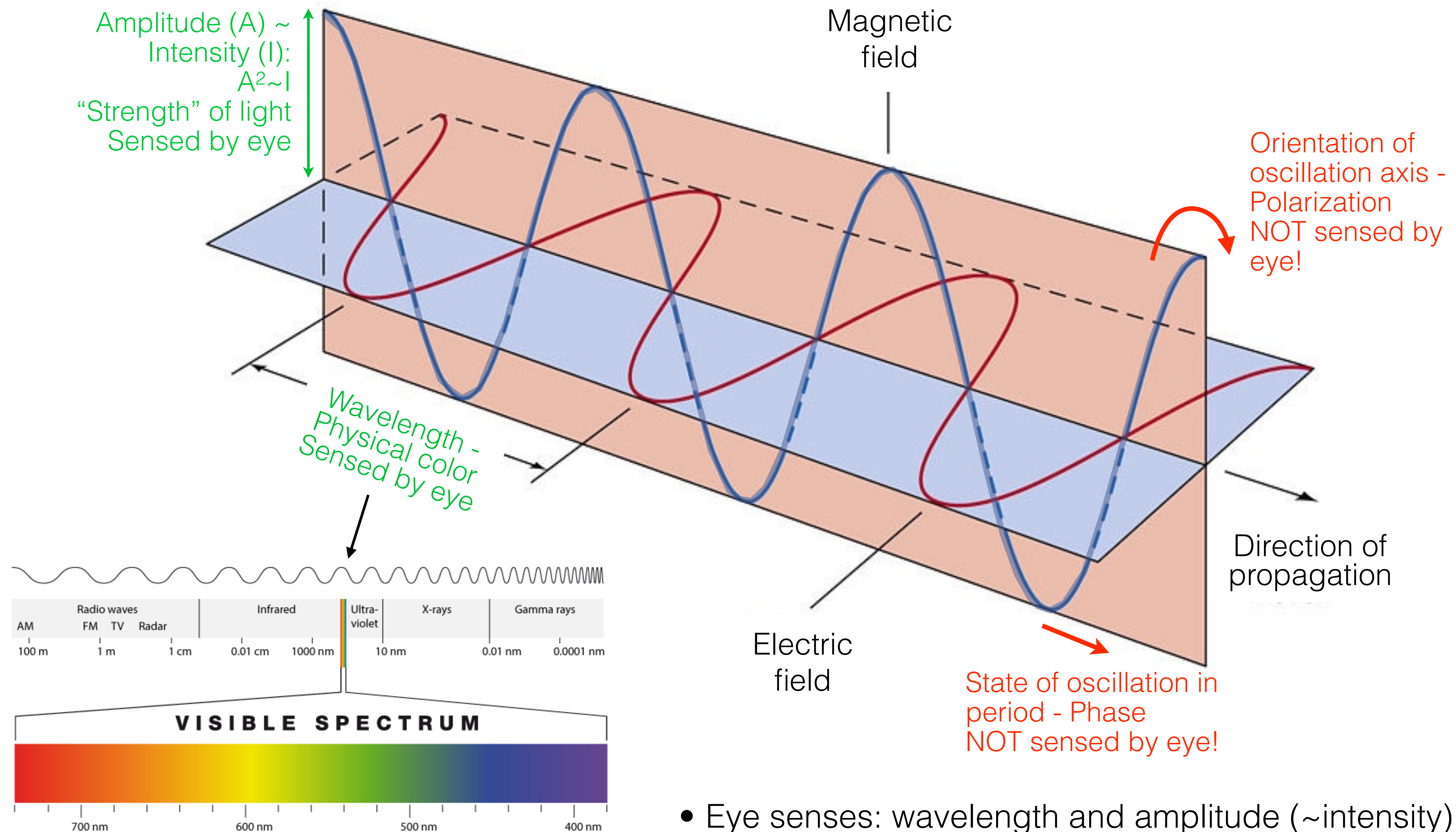
Penrose triangle





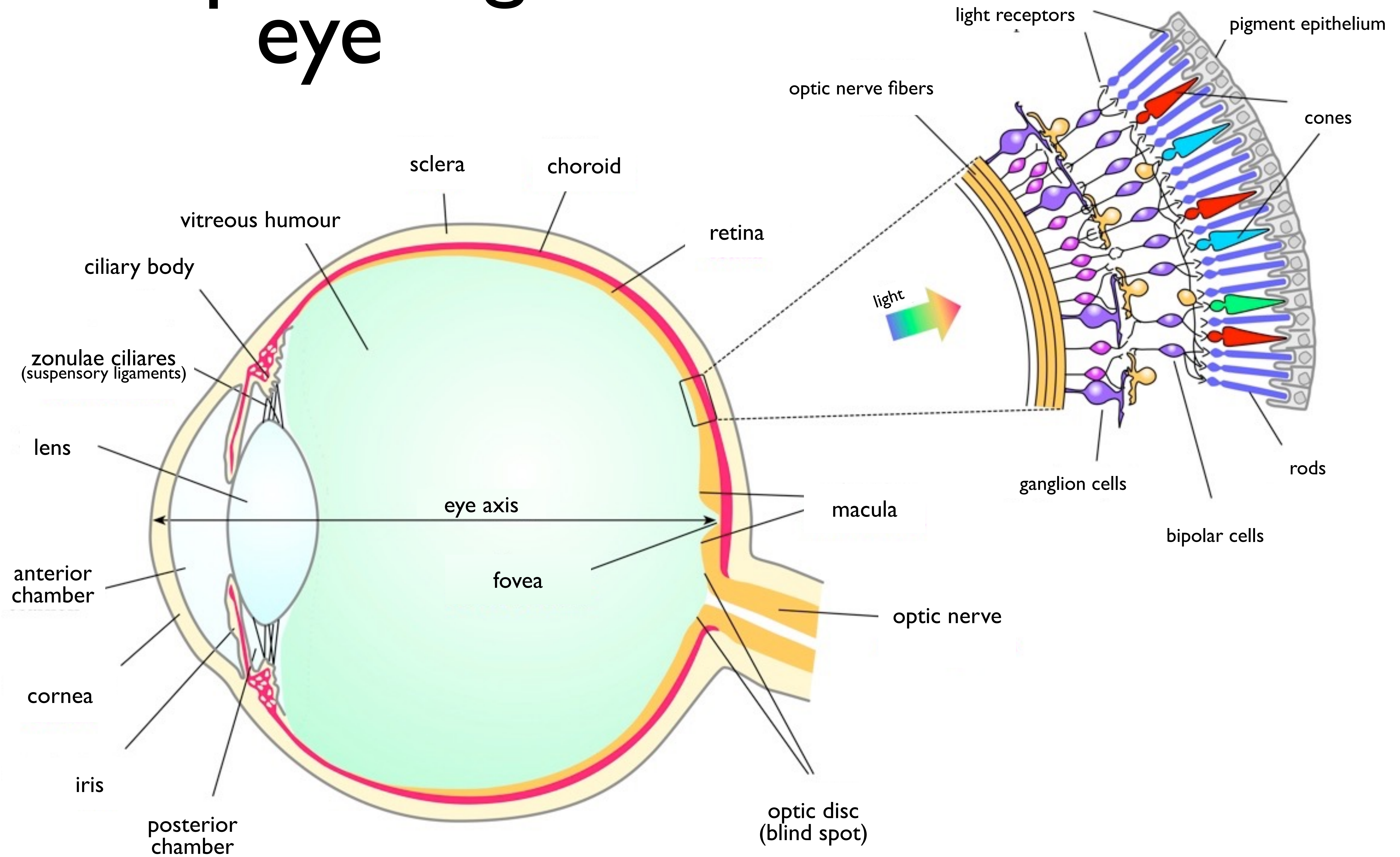
Stimulus of vision: light

Electromagnetic (transverse) wave

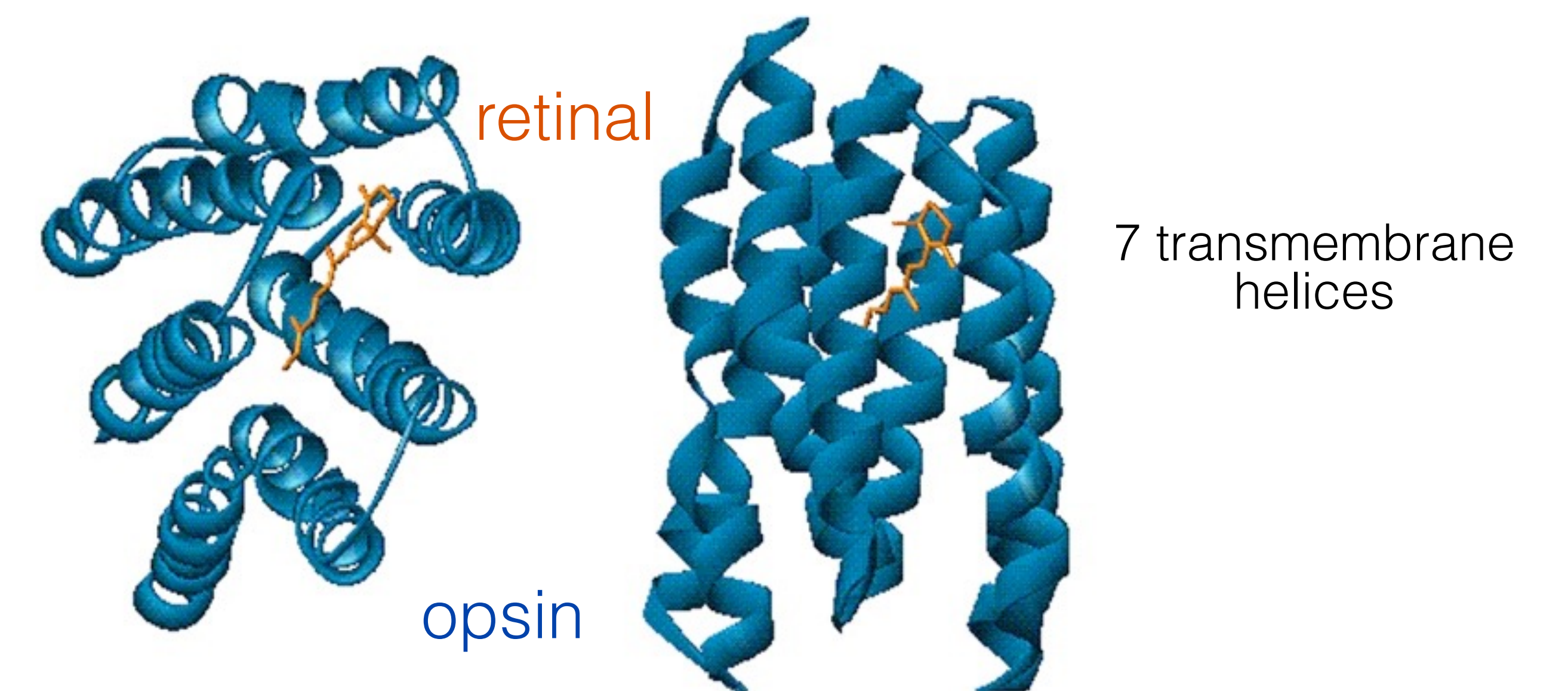
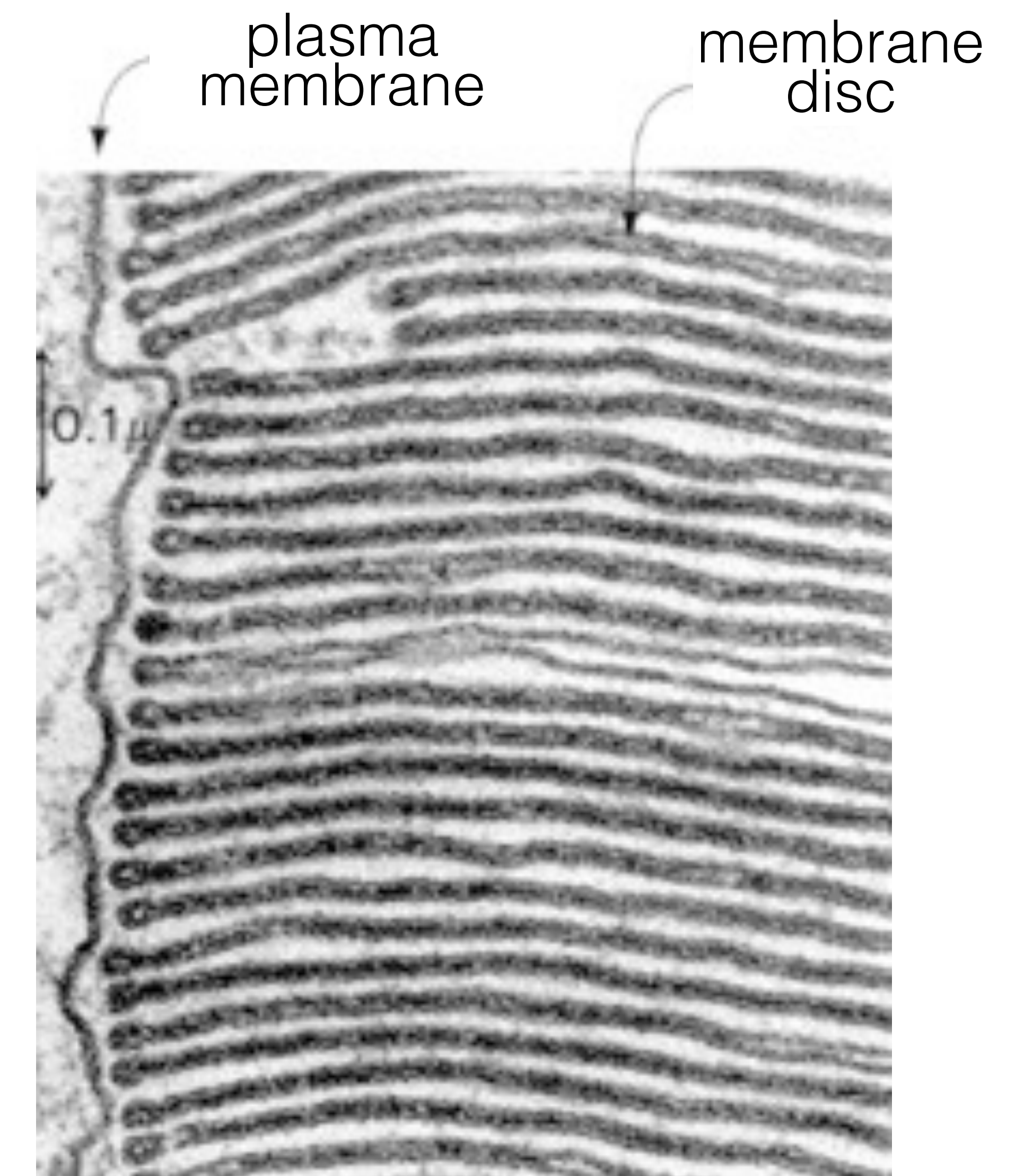
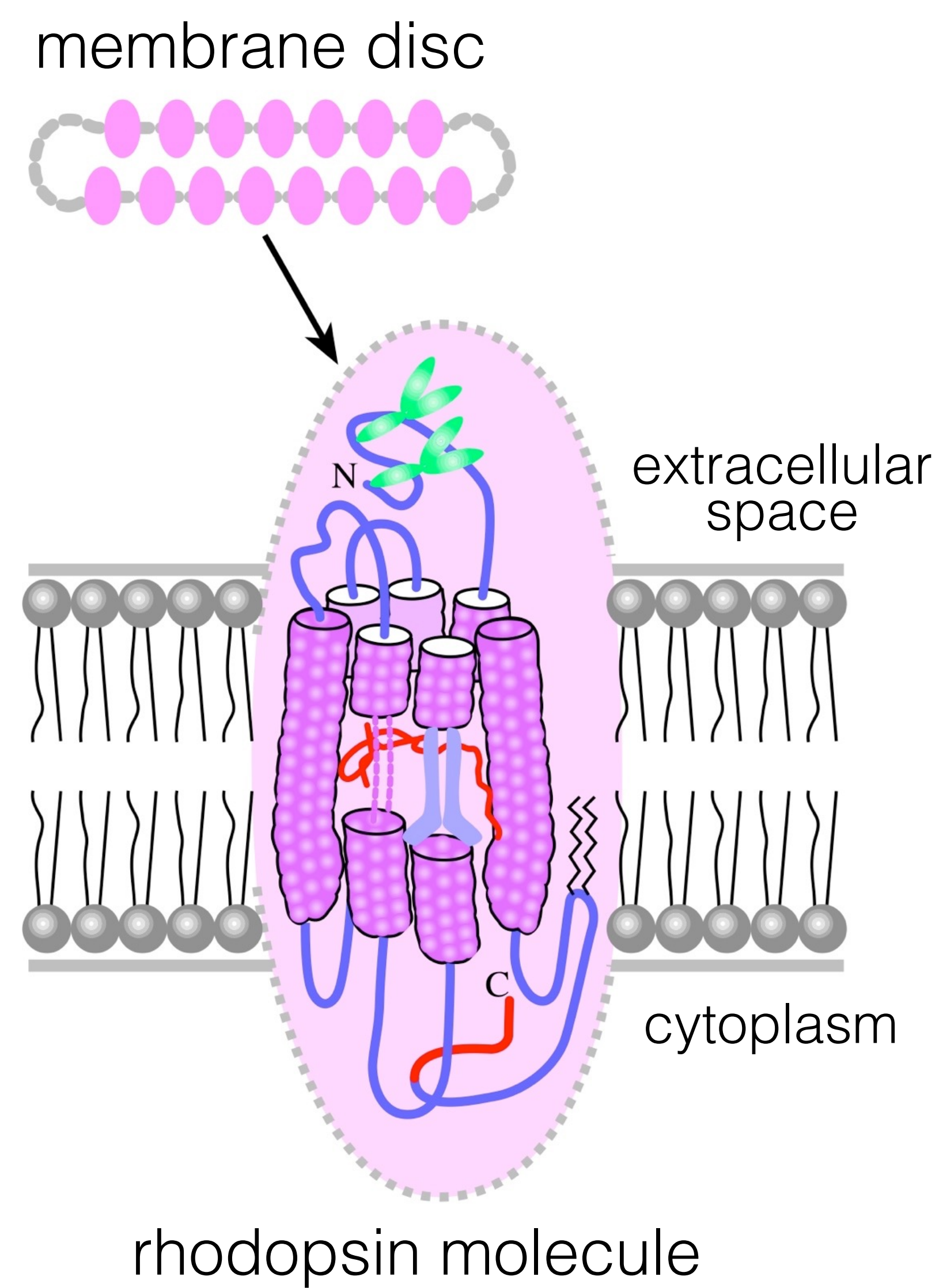
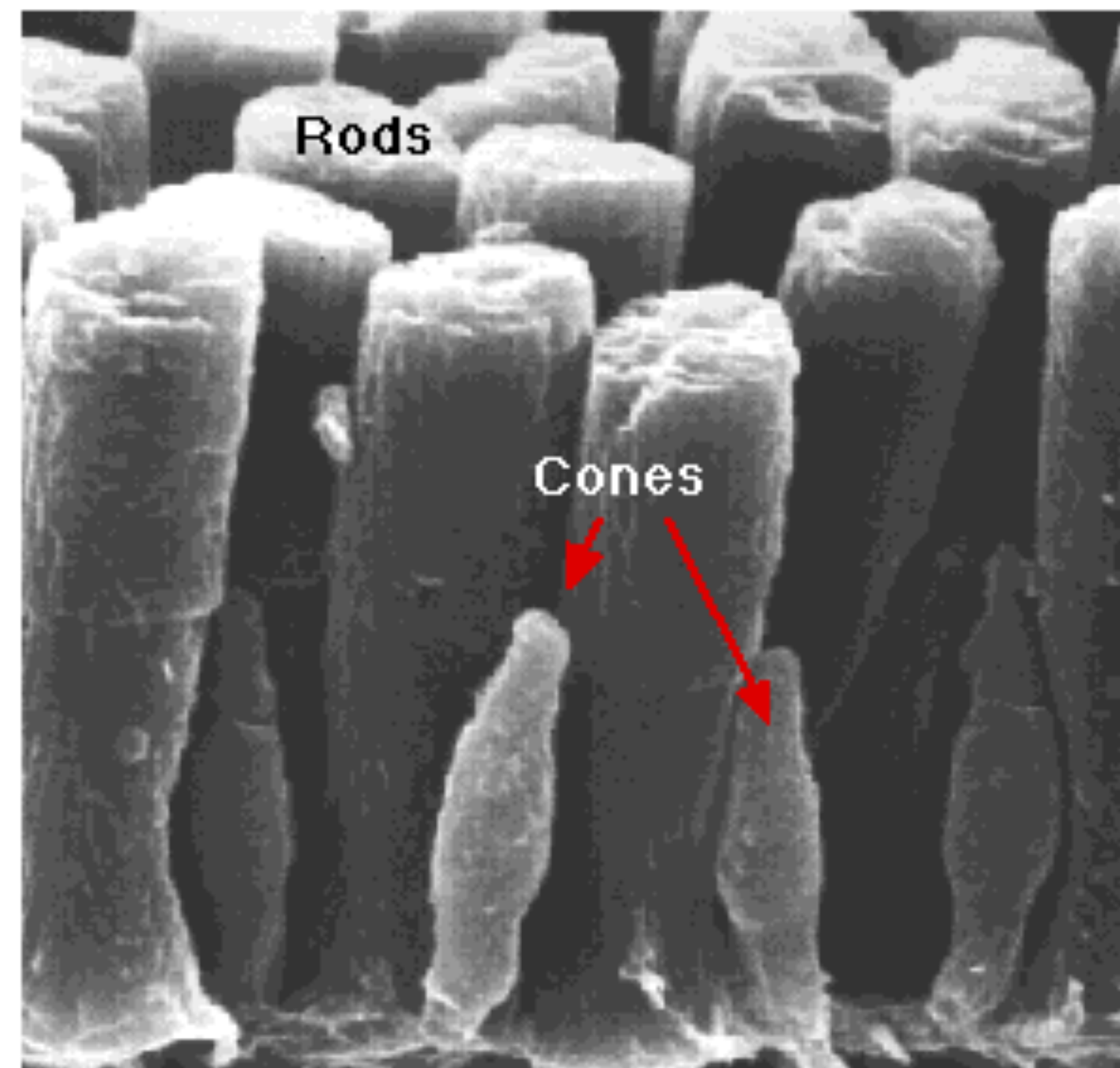
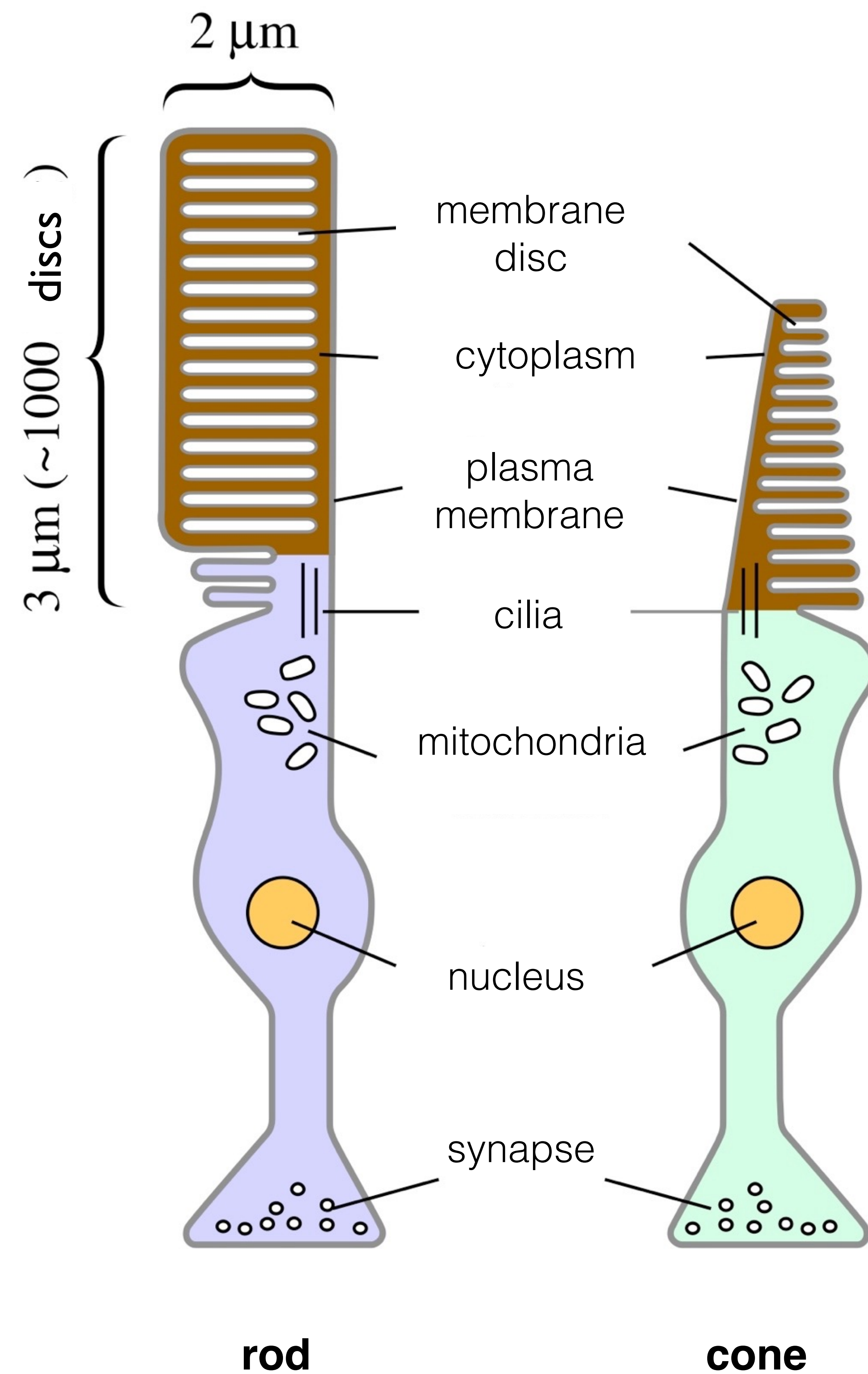


- Eye senses: wavelength and amplitude (~intensity)
- Eye is insensitive to: phase and polarization

“Receptor-organ”: eye



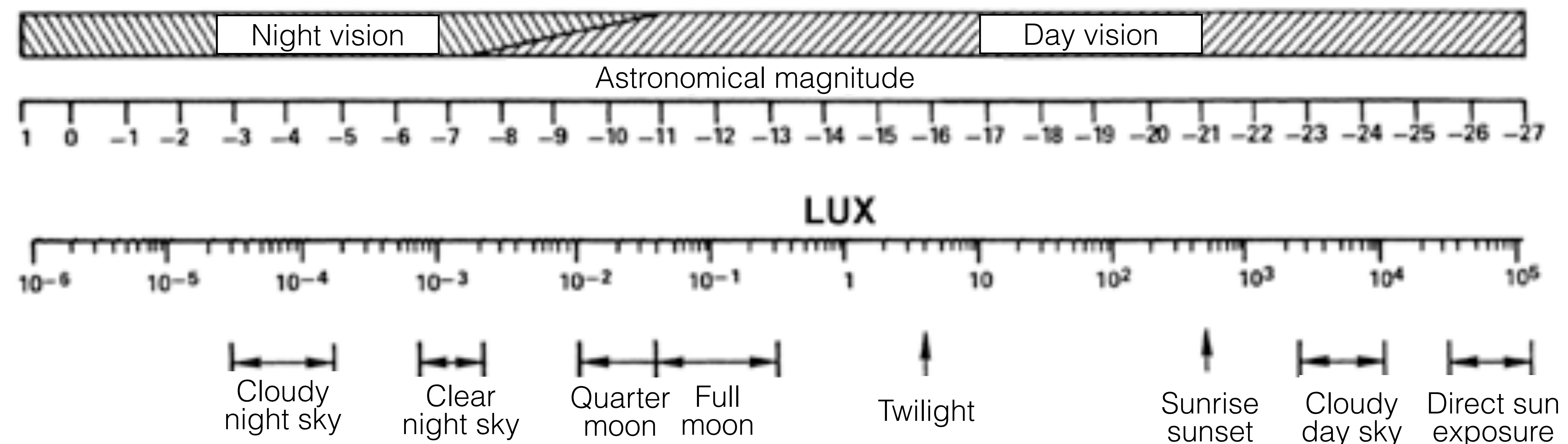
Photoreceptors



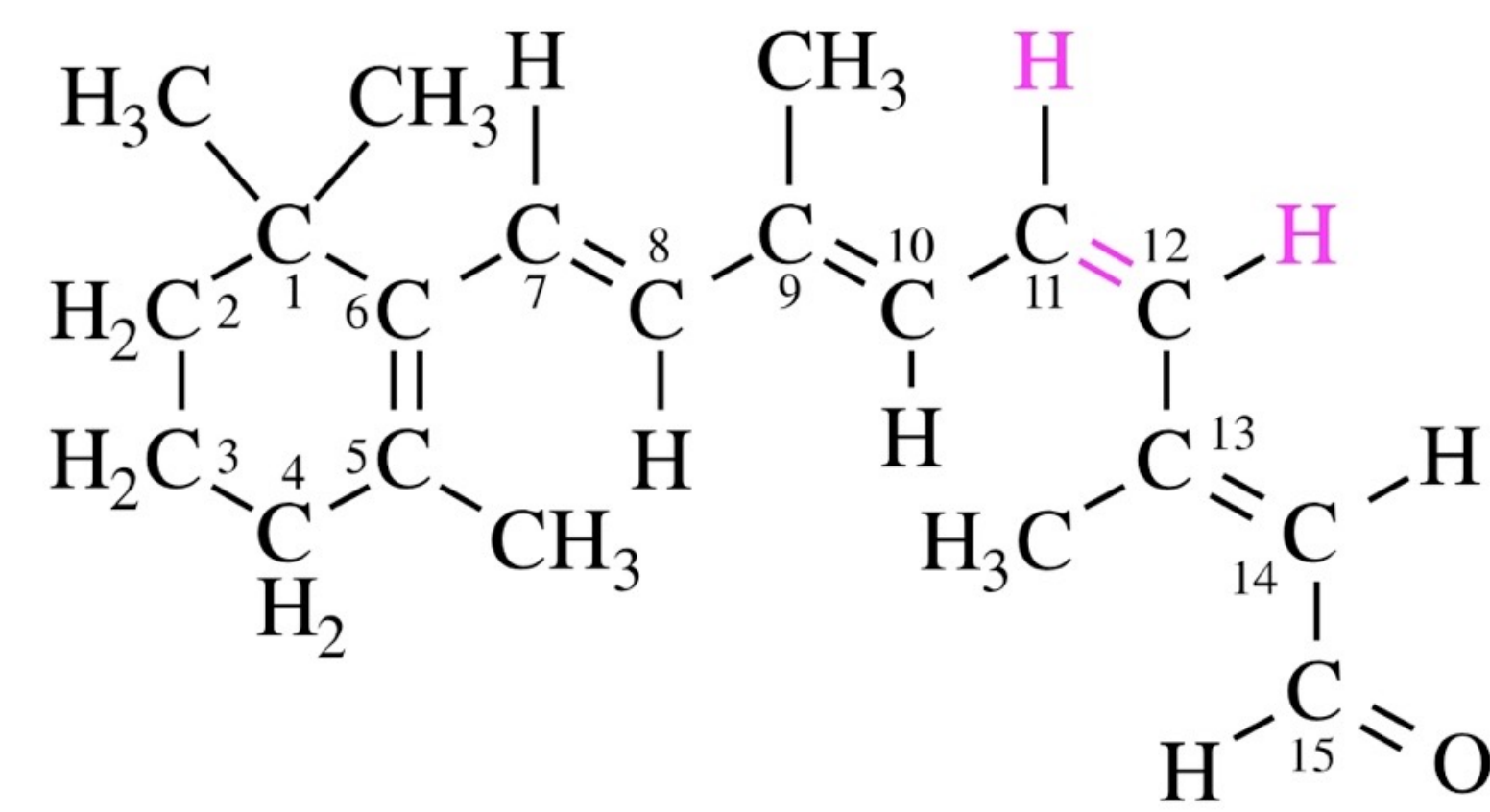
Properties of receptor cells

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!

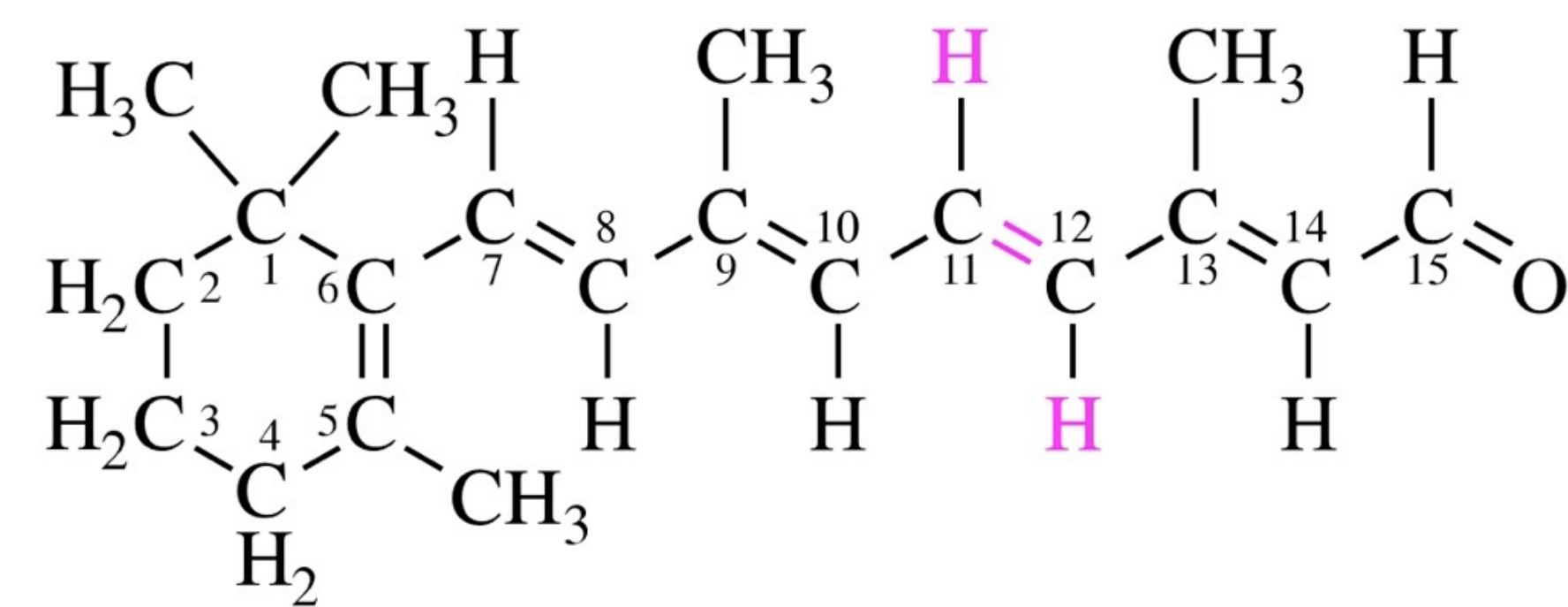


Basis of light sensing: photochemical reaction

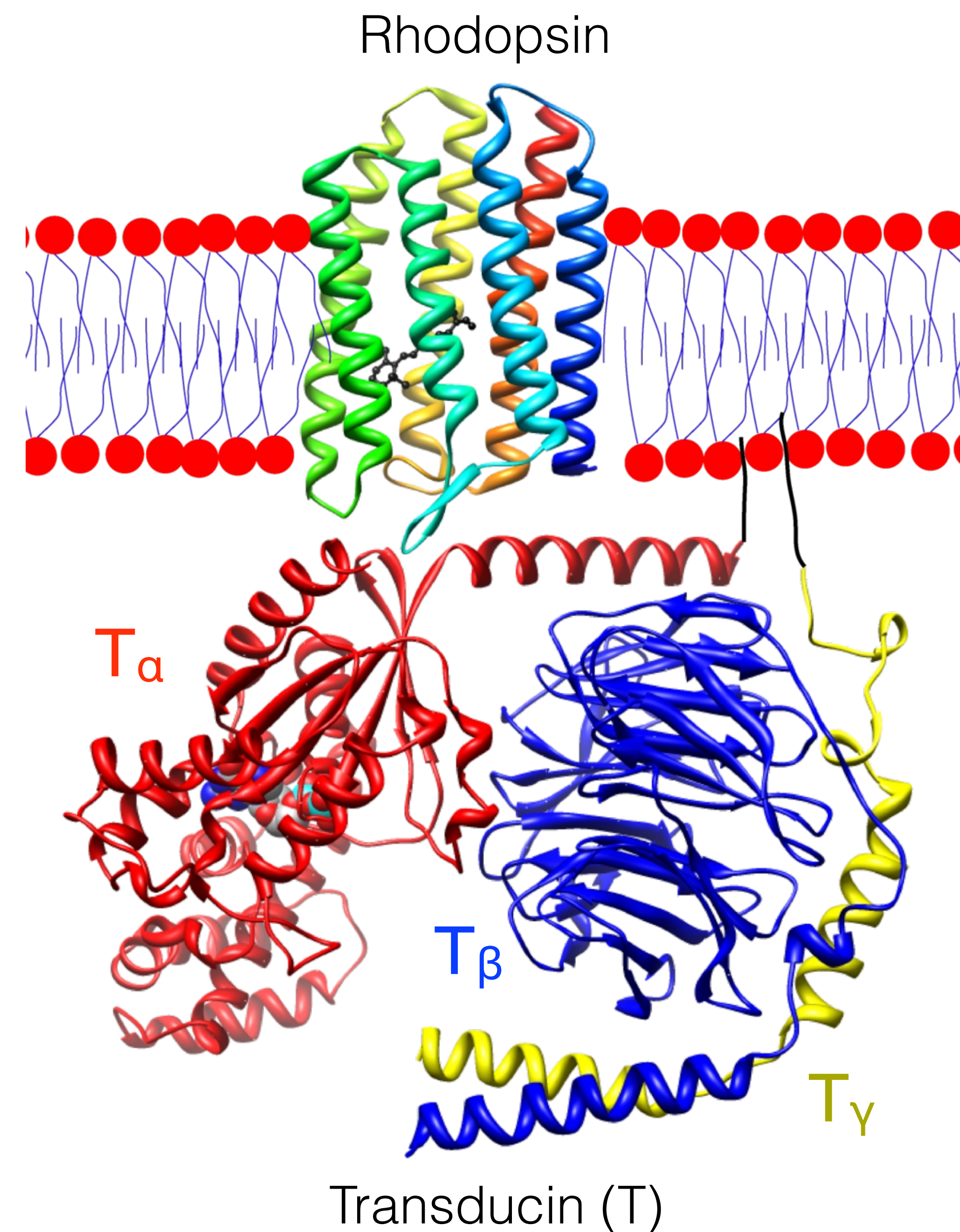


11-cis-retinal

optical excitation



all-trans-retinal



1 rhodopsin absorbs 1 photon

↓
metarhodopsin

↓
transducin molecule activated (T_α subunit dissociates from the $T_{\beta\gamma}$ subunit)

↓
500 phosphodiesterase 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).

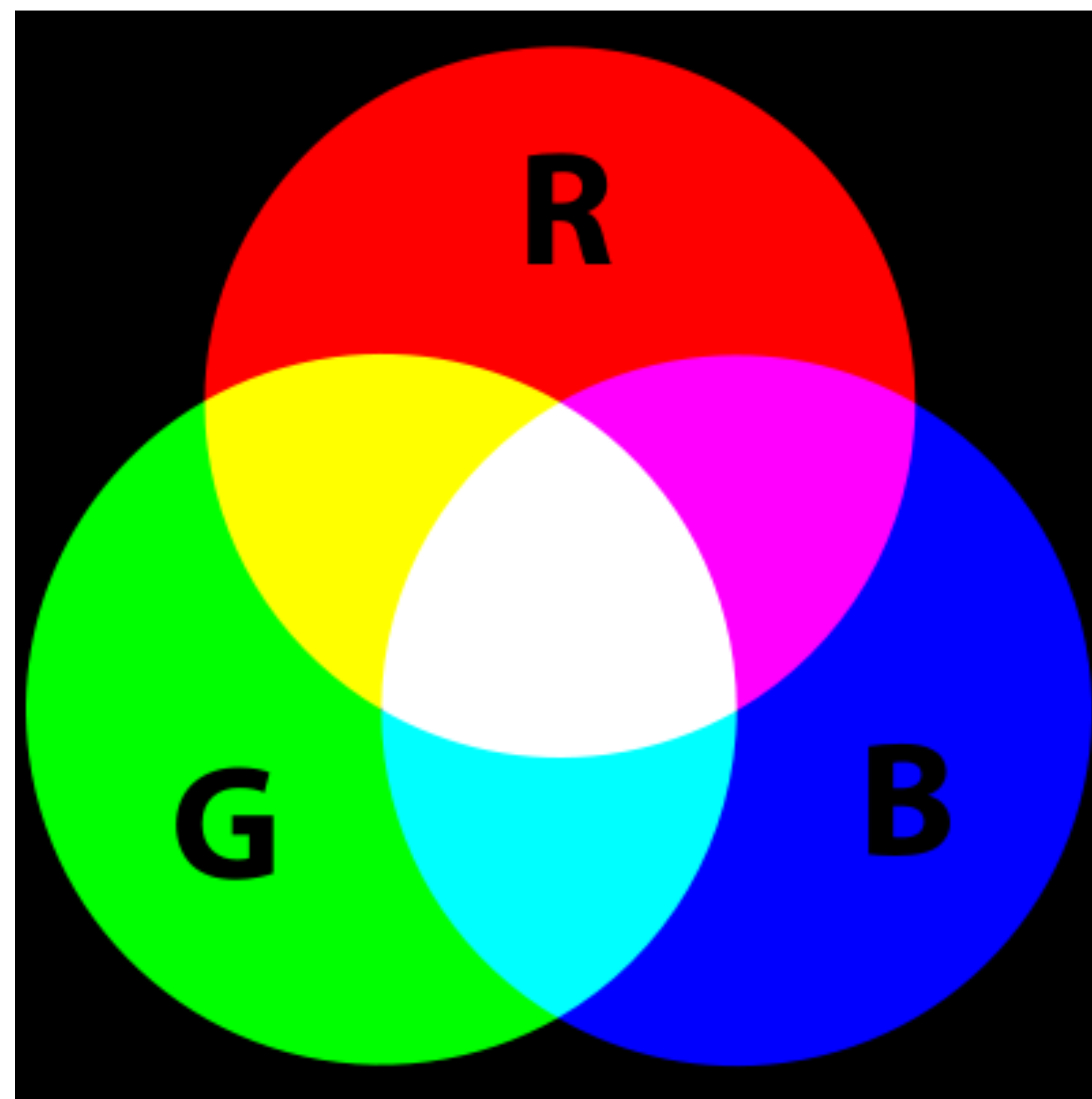
Amplification: ($\sim 10^4$)

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

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

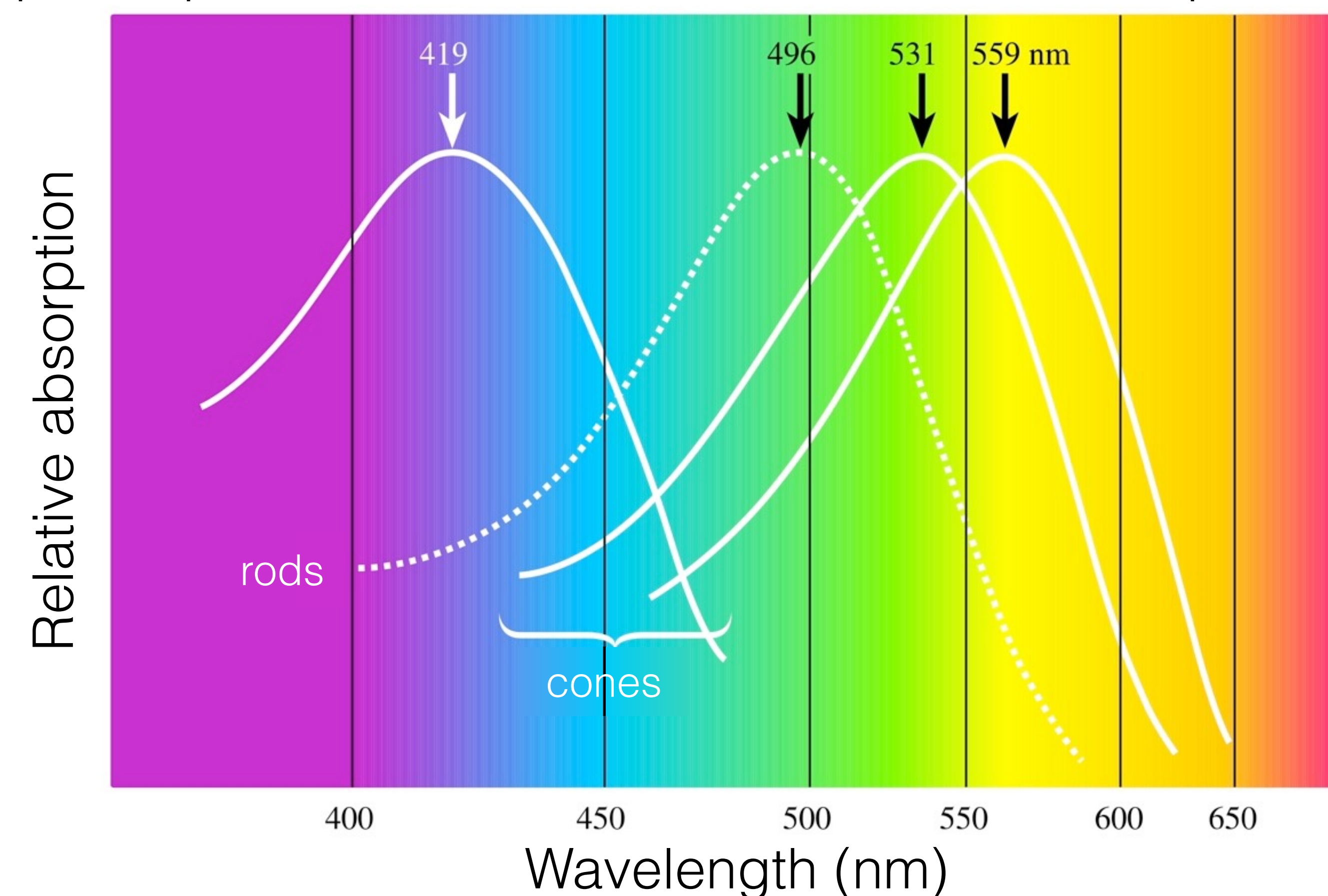
Any color (X) may be generated by mixing three basic colors (R =red, G =green, B =blue) with varying weighing factors (r , g , b):

$$X = rR + gG + bB$$

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)

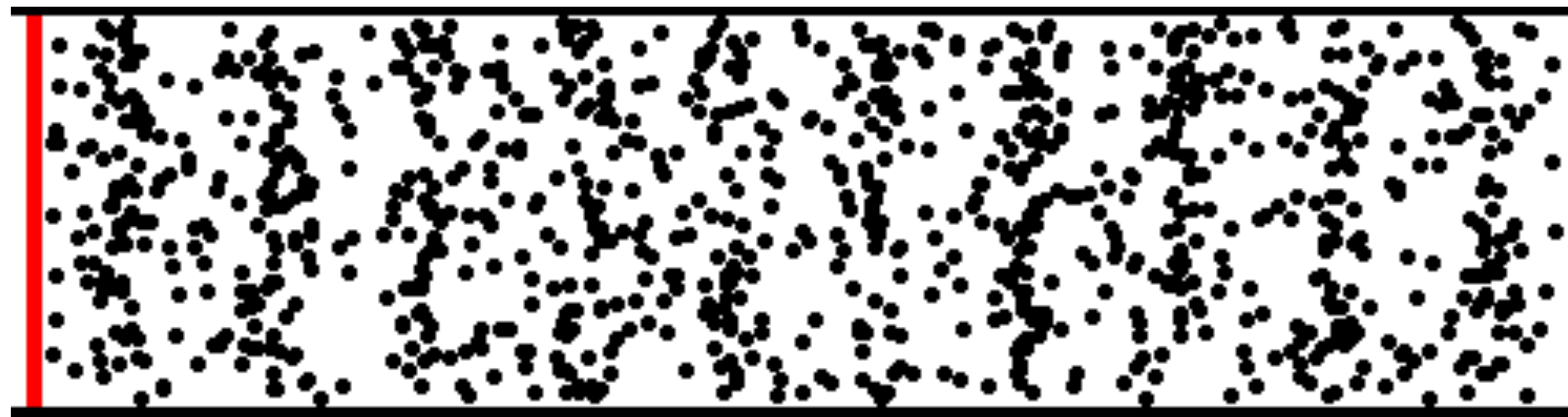
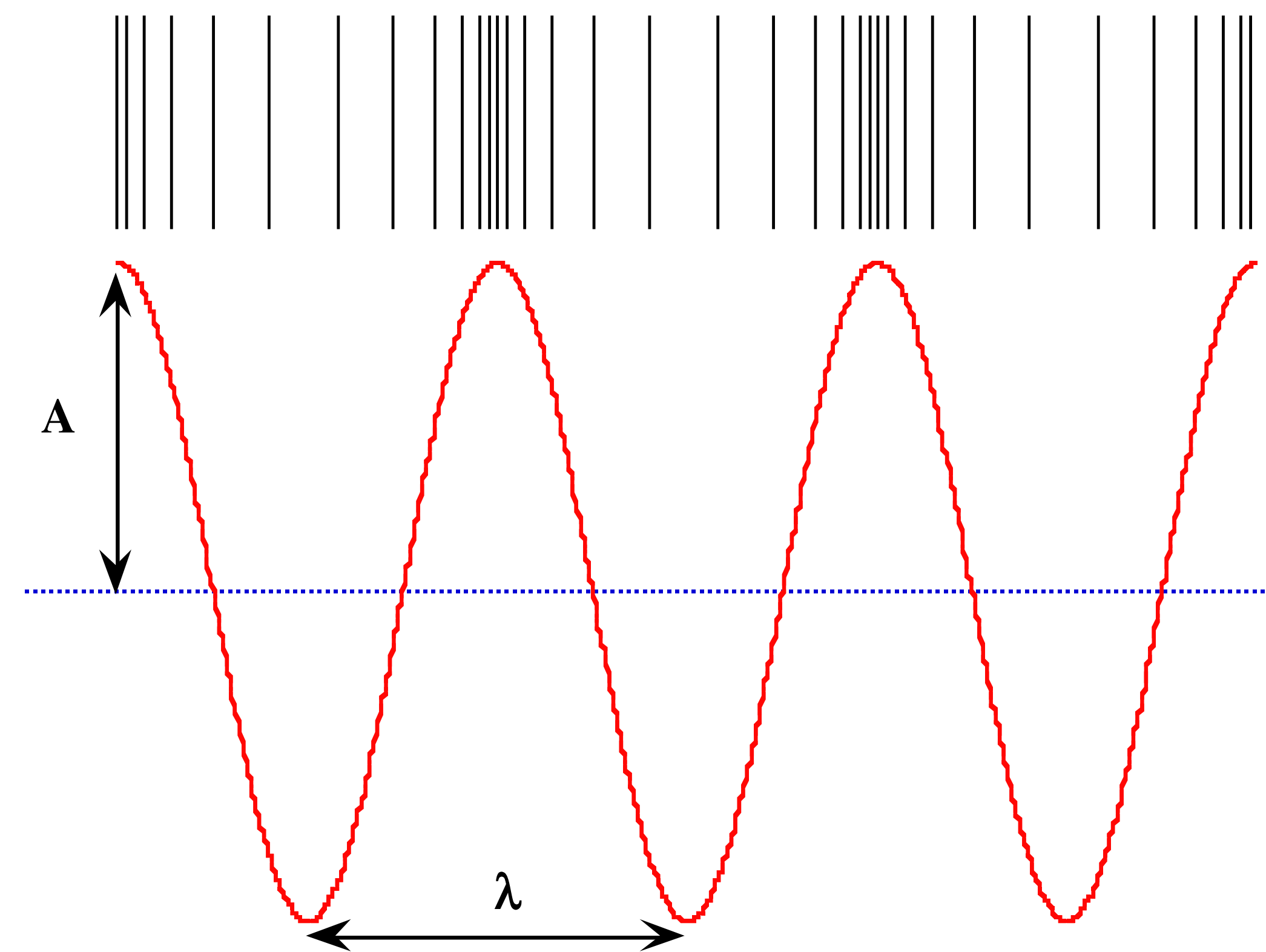


BIOPHYSICS OF HEARING

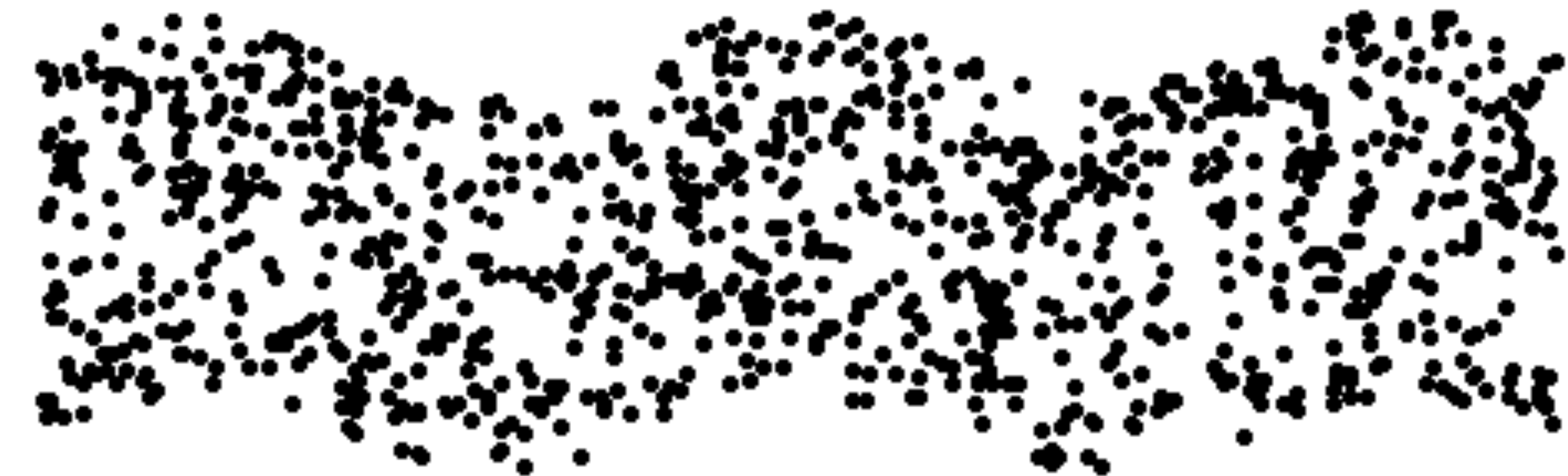
MIKLÓS KELLERMAYER

Sound

Longitudinal
mechanical wave
(pressure wave)



Longitudinal wave

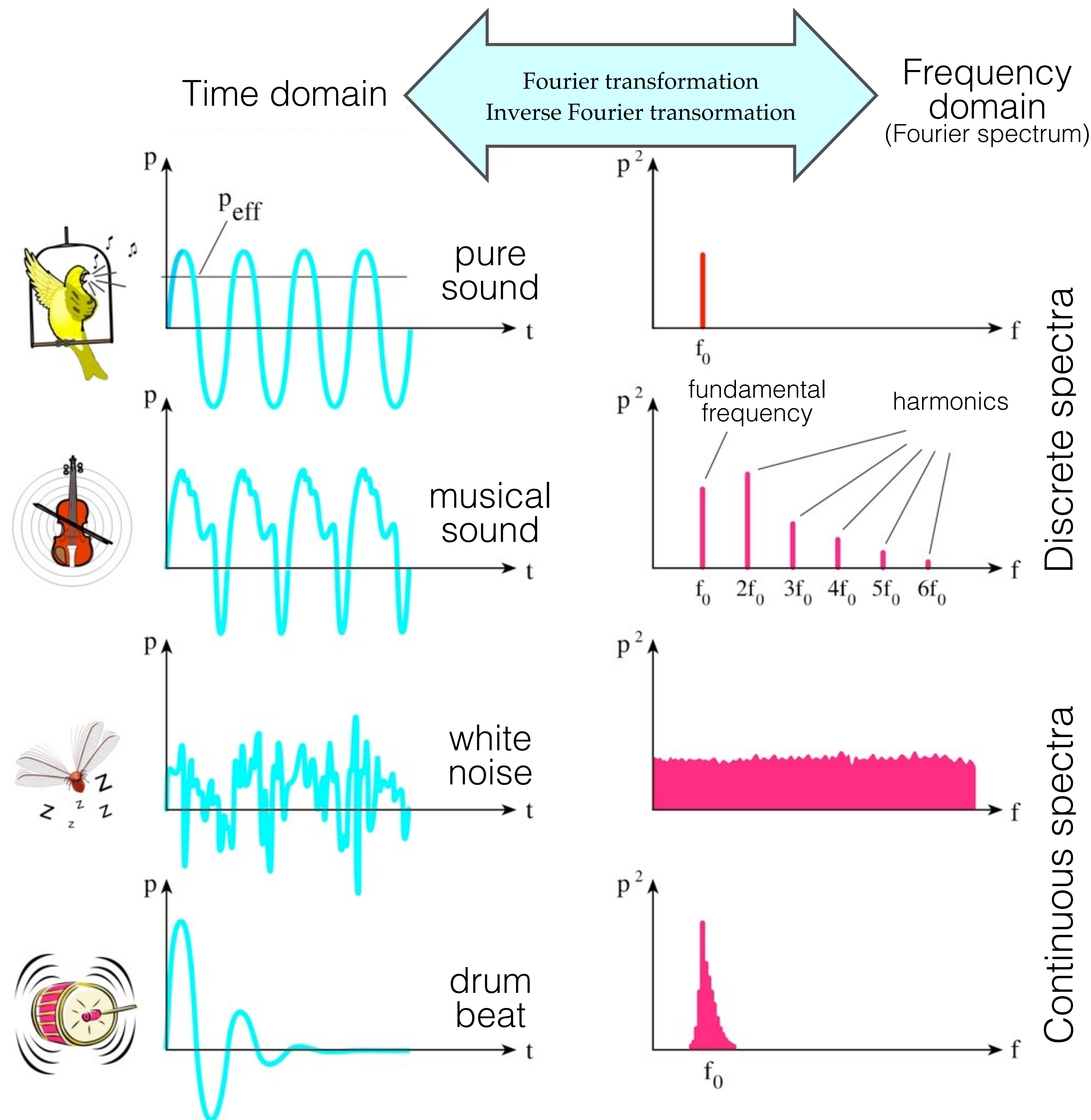


Transverse wave

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:

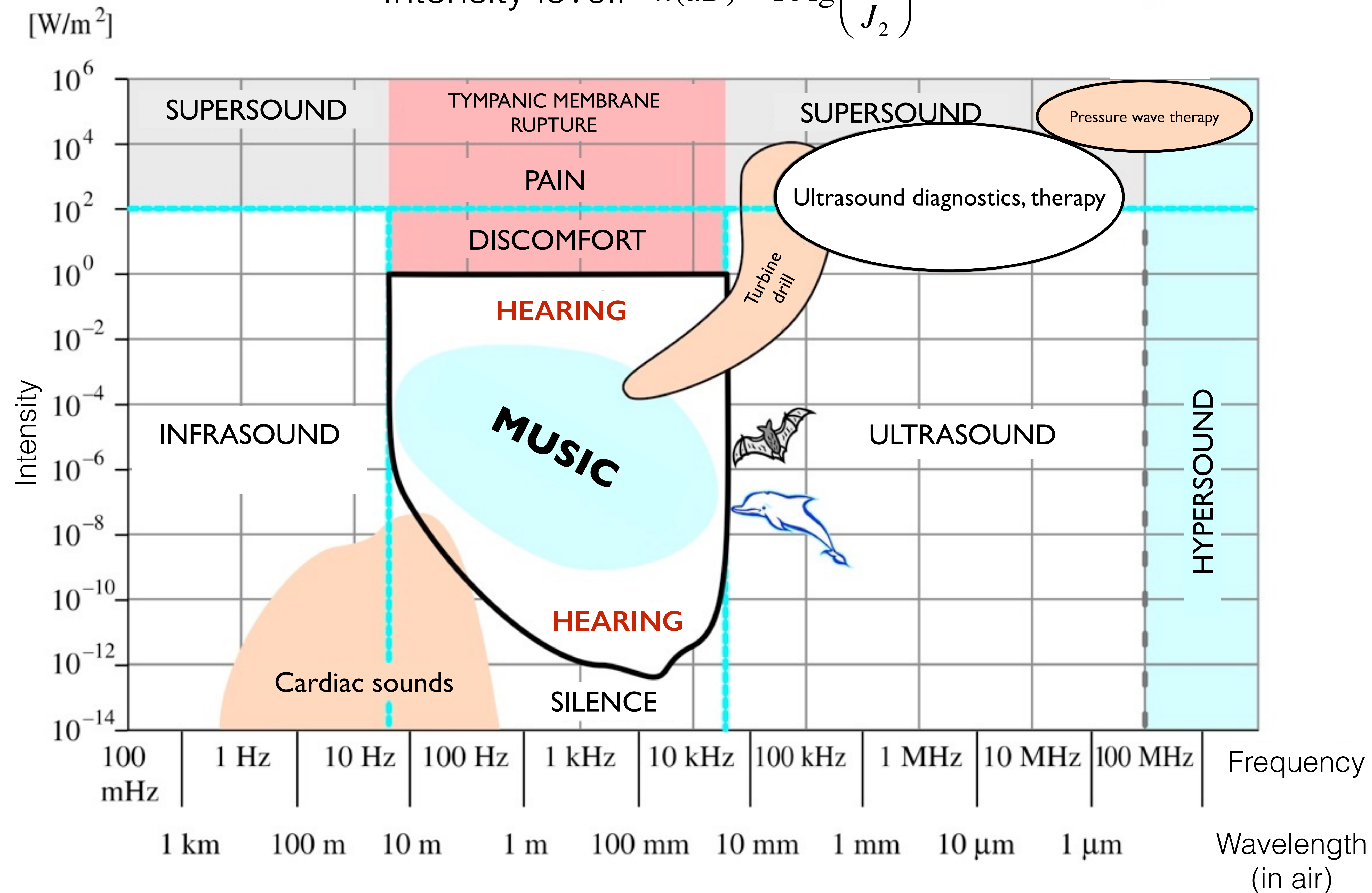


Octave - frequency difference with a 2:1 ratio

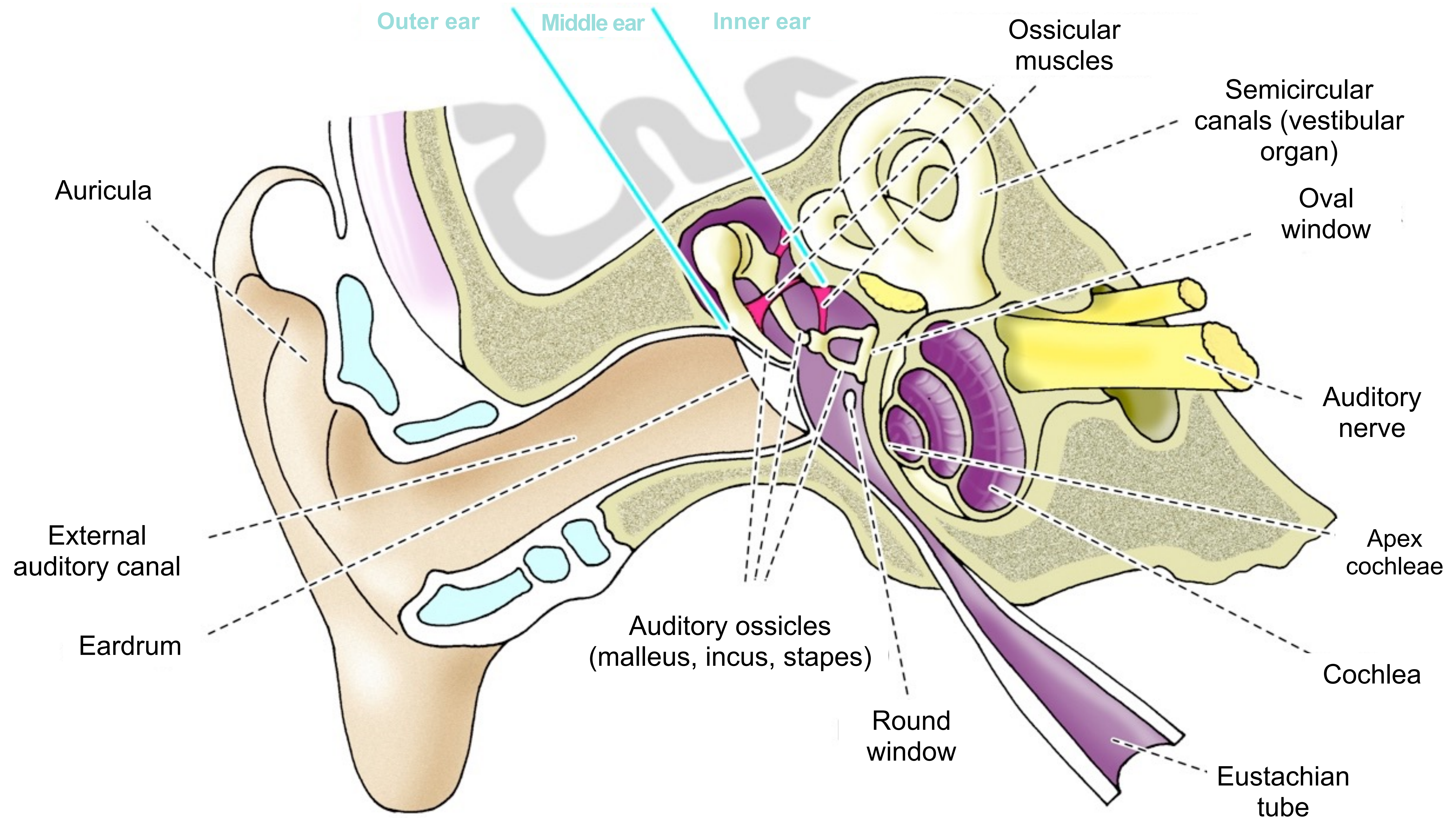
Sound intensity and frequency

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

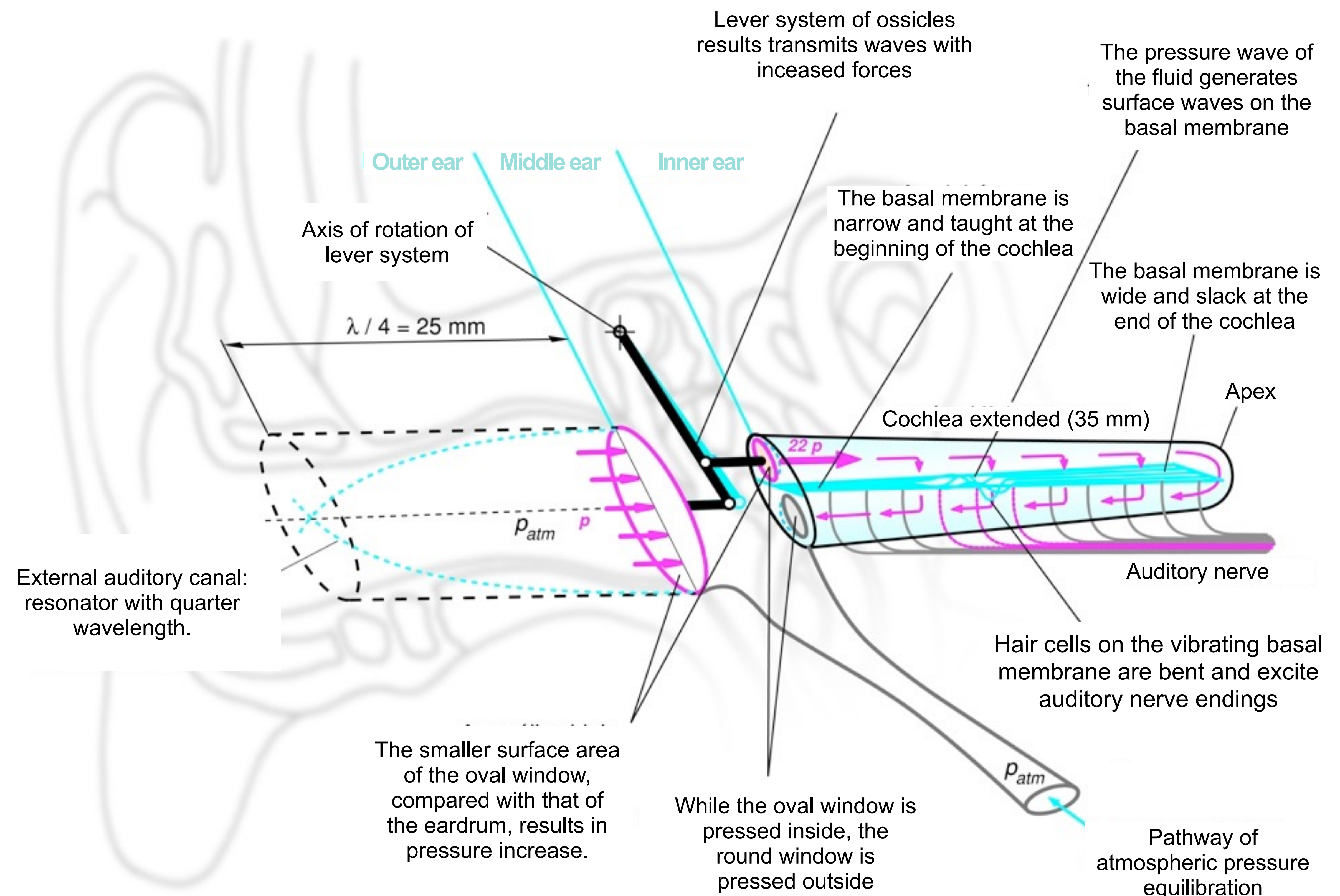
Sound is steered into the external auditory canal.

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)

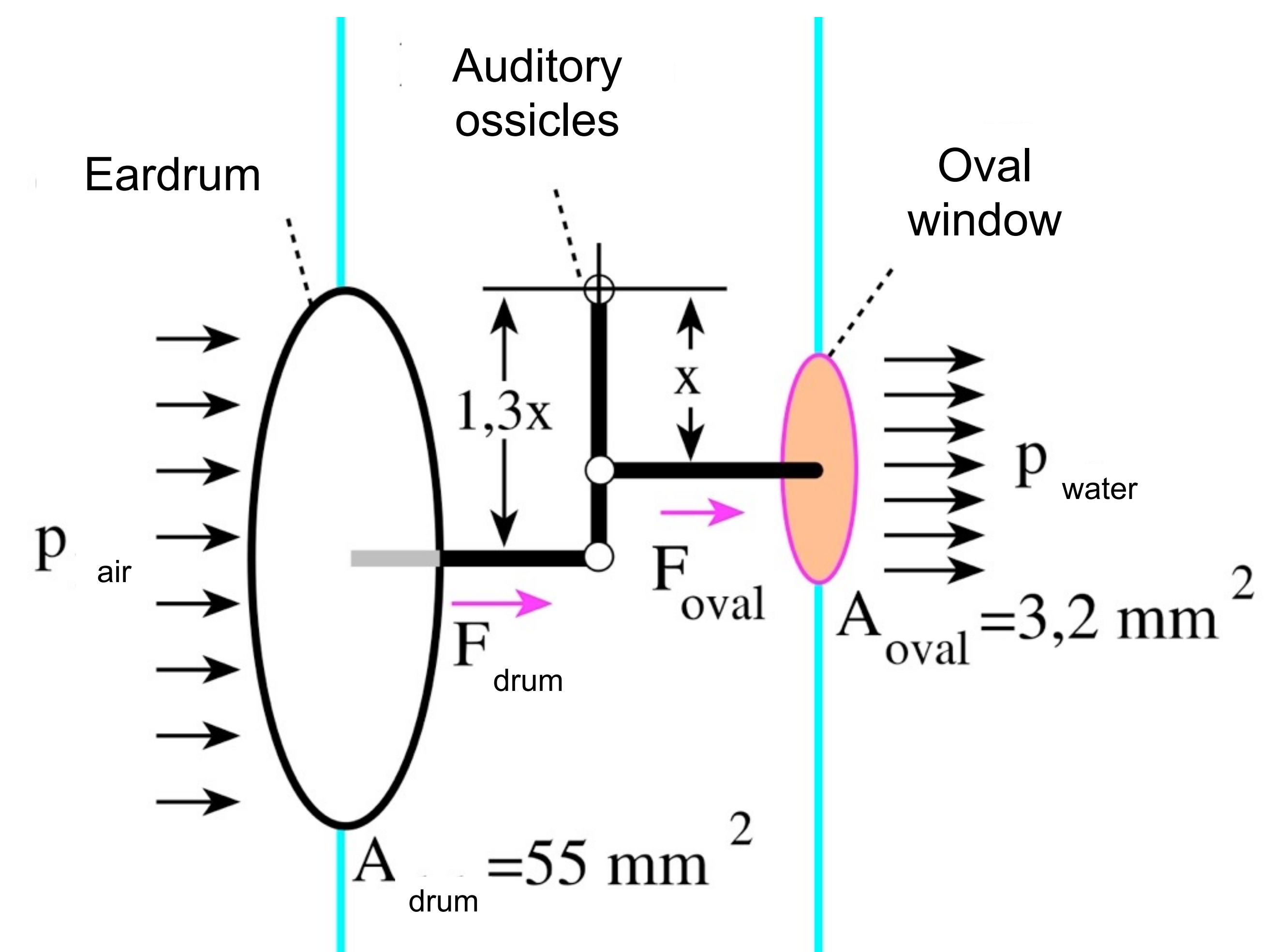
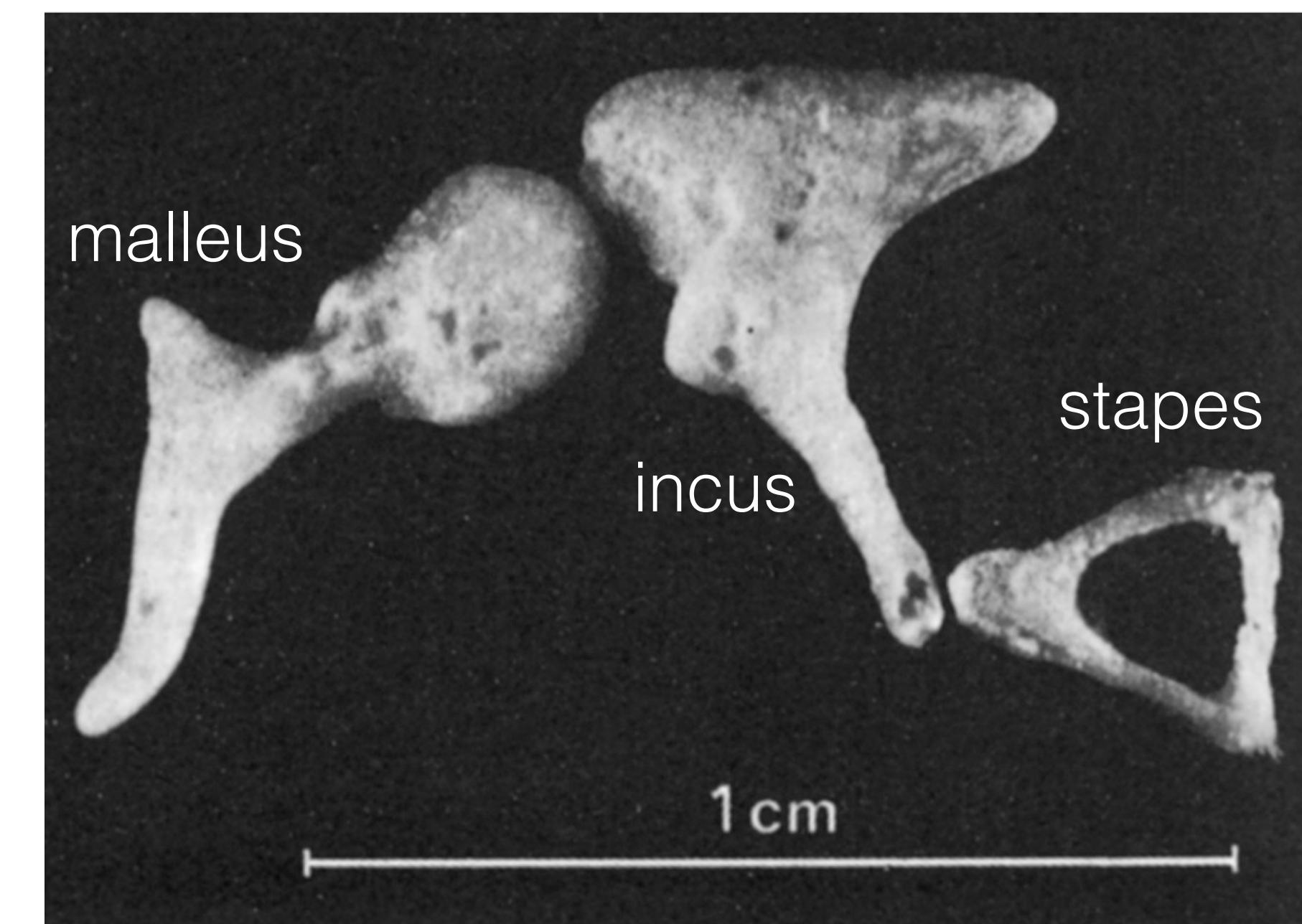
They **amplify** eardrum resonance and transmit it to the oval window. (N.B.: due to the difference in the acoustic impedance of air and water, total reflection would occur!)

Amplification:

due to area ratio: $17 \times$

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

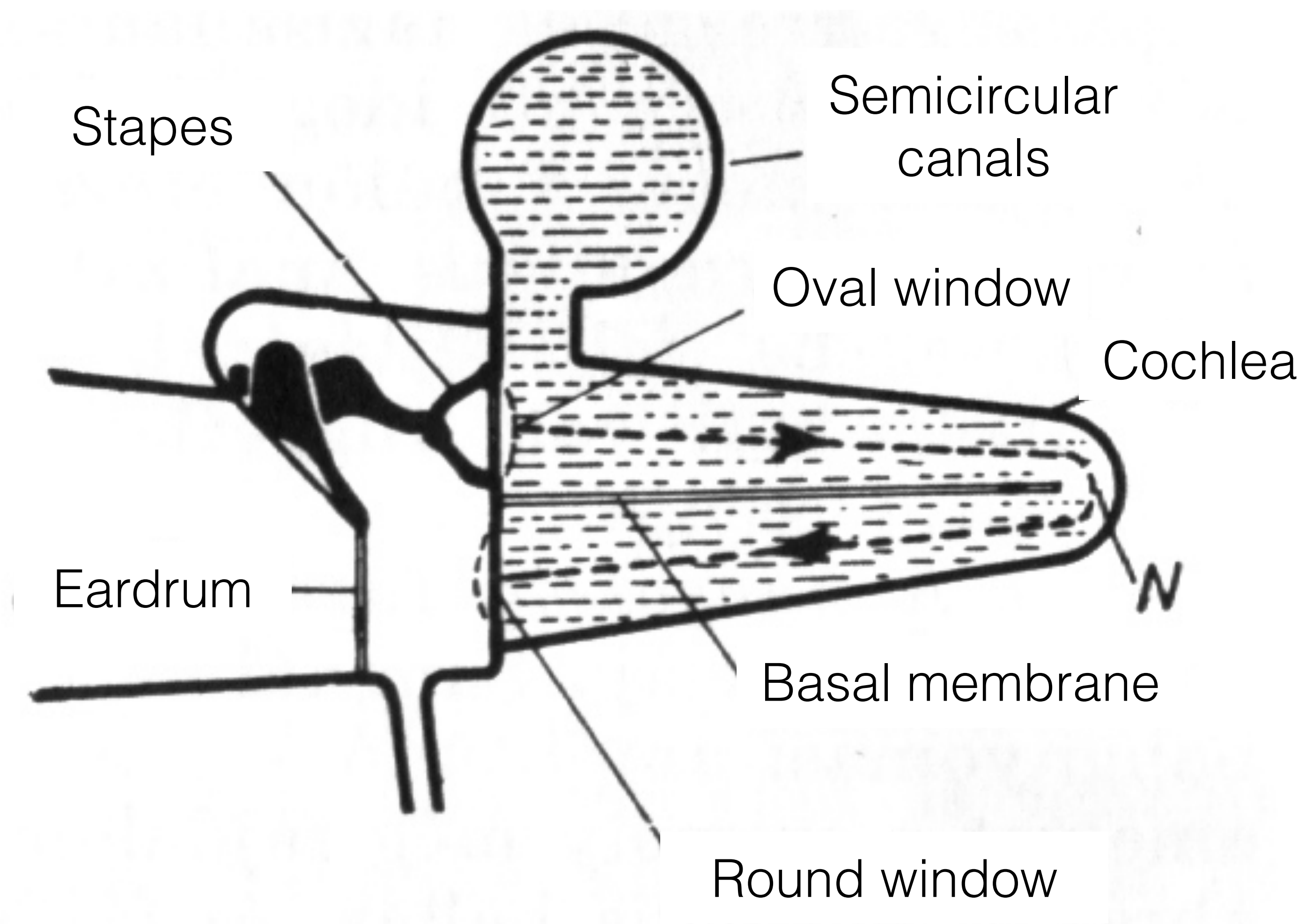
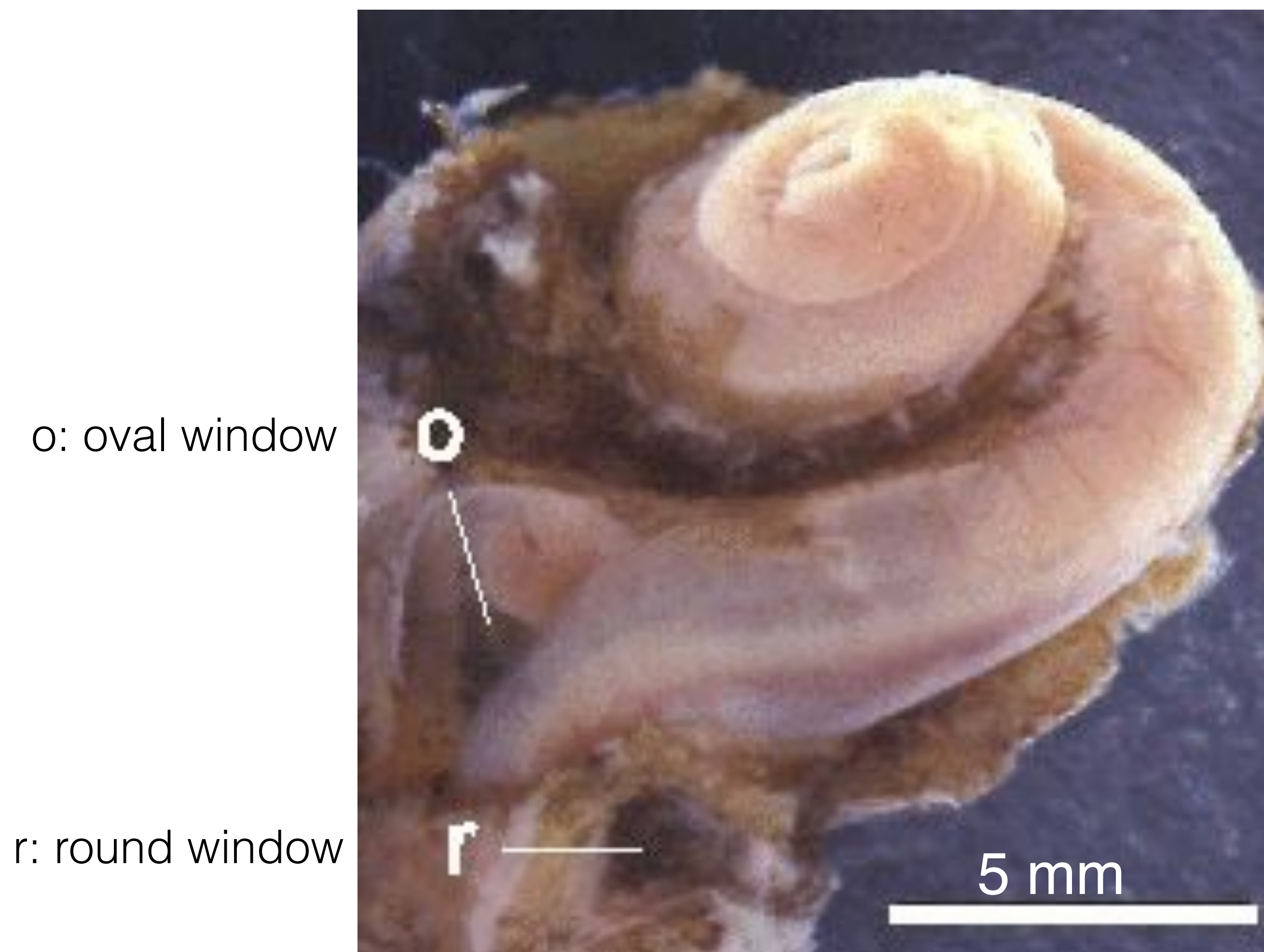
Total amplification: $22 \times$ (pressure increase)



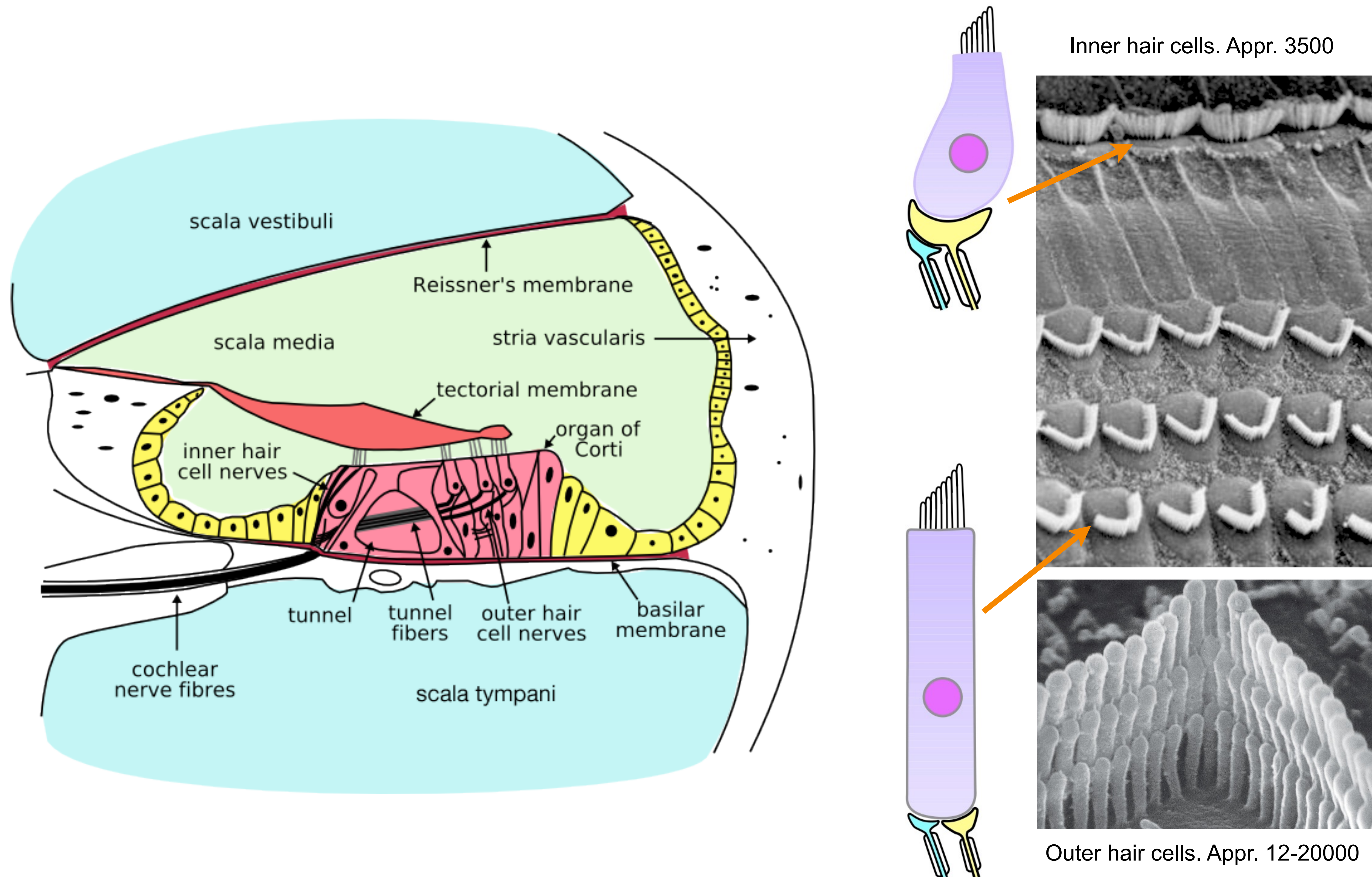
Inner ear: sensor

Vestibular organ: semicircular canals

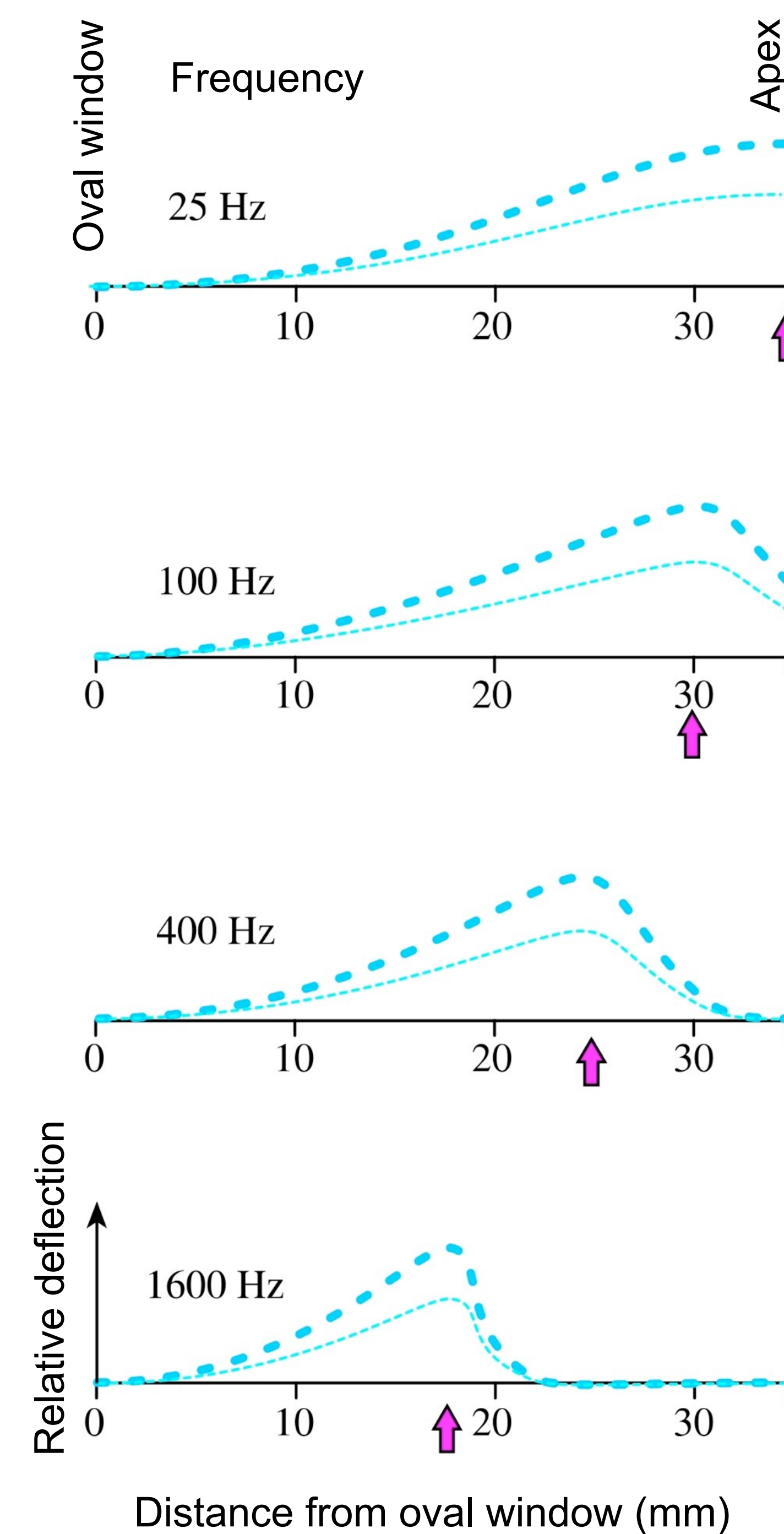
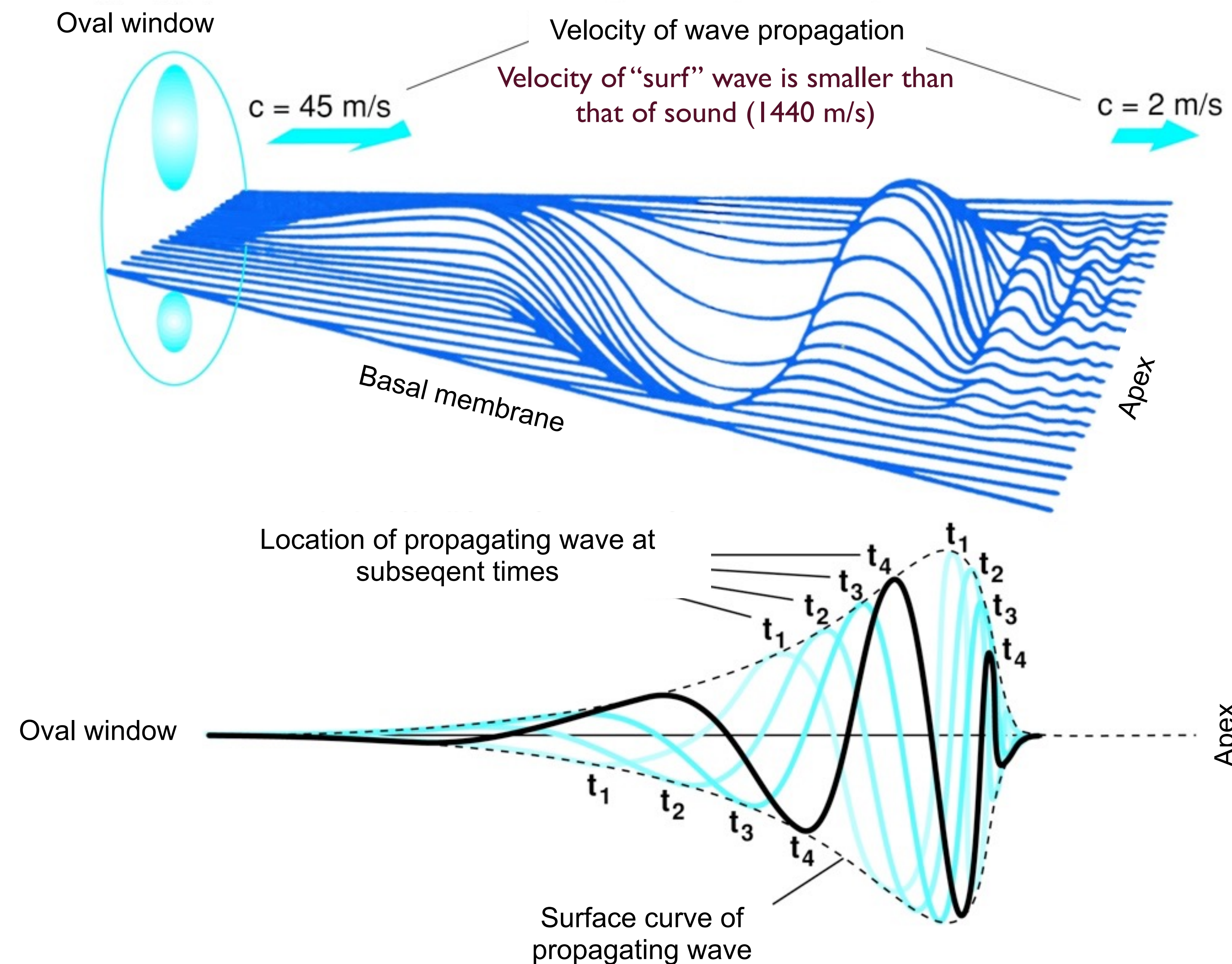
Cochlea: 2.5-pitch, 35-mm-long fluid-filled channel.
It is halved in length partly by an osseous, partly by a membranaceous wall, the basal membrane.
Sensory organ of sound.



Ultrastructure of the inner ear



Békésy: propagating surface waves on basal membrane

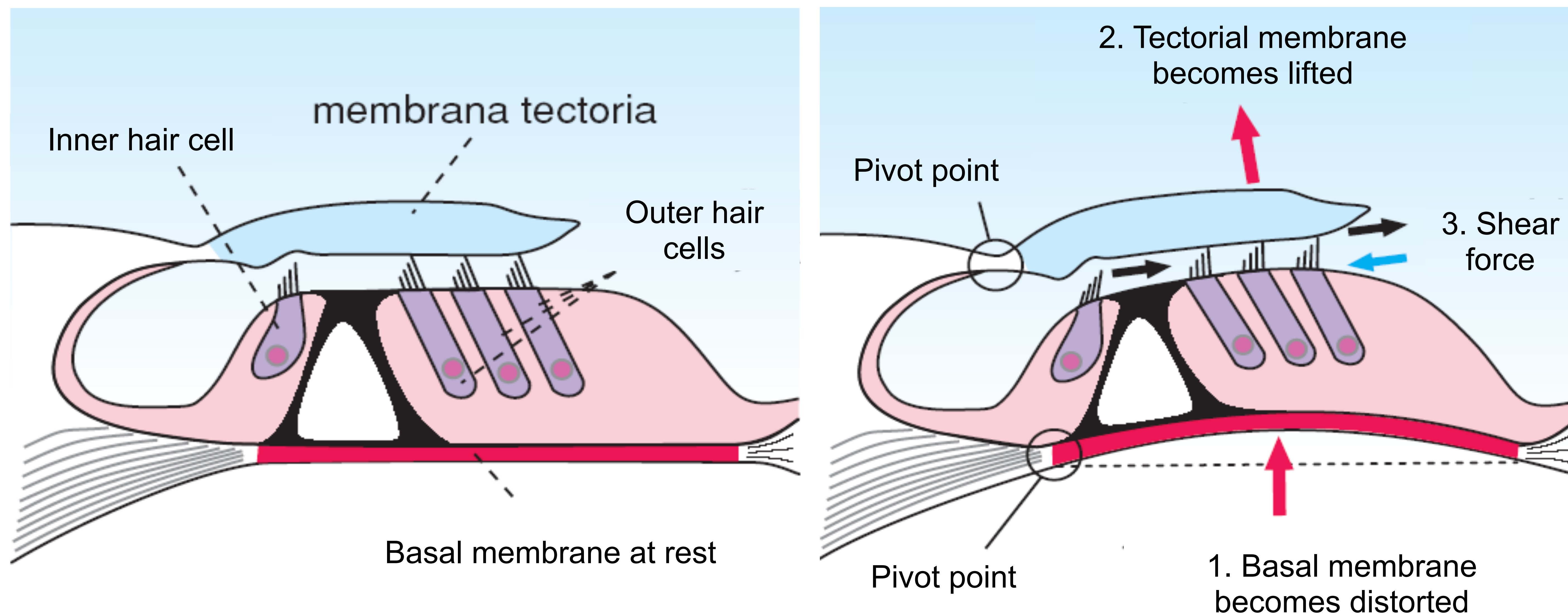


György Békésy
Nobel-prize 1961

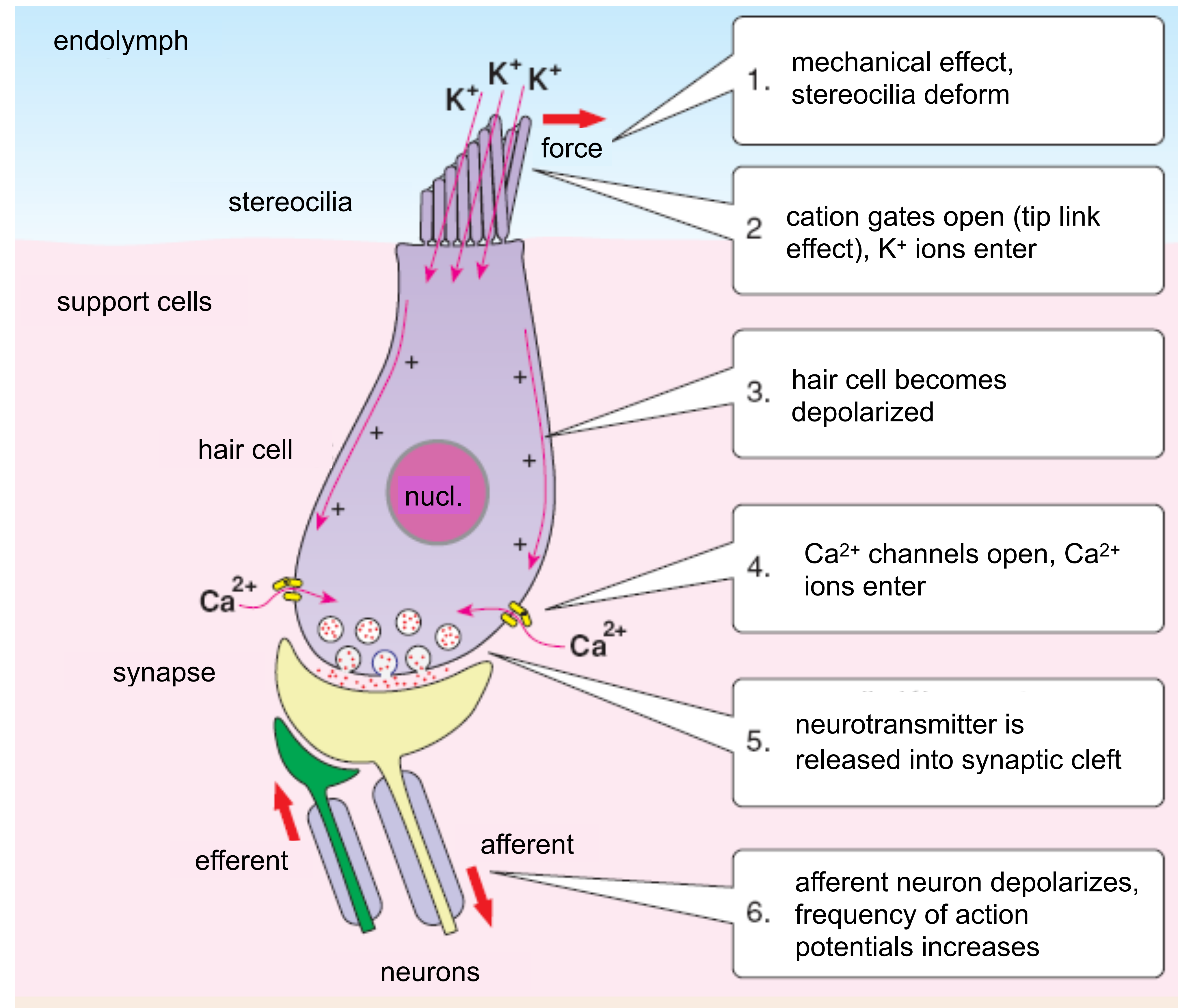
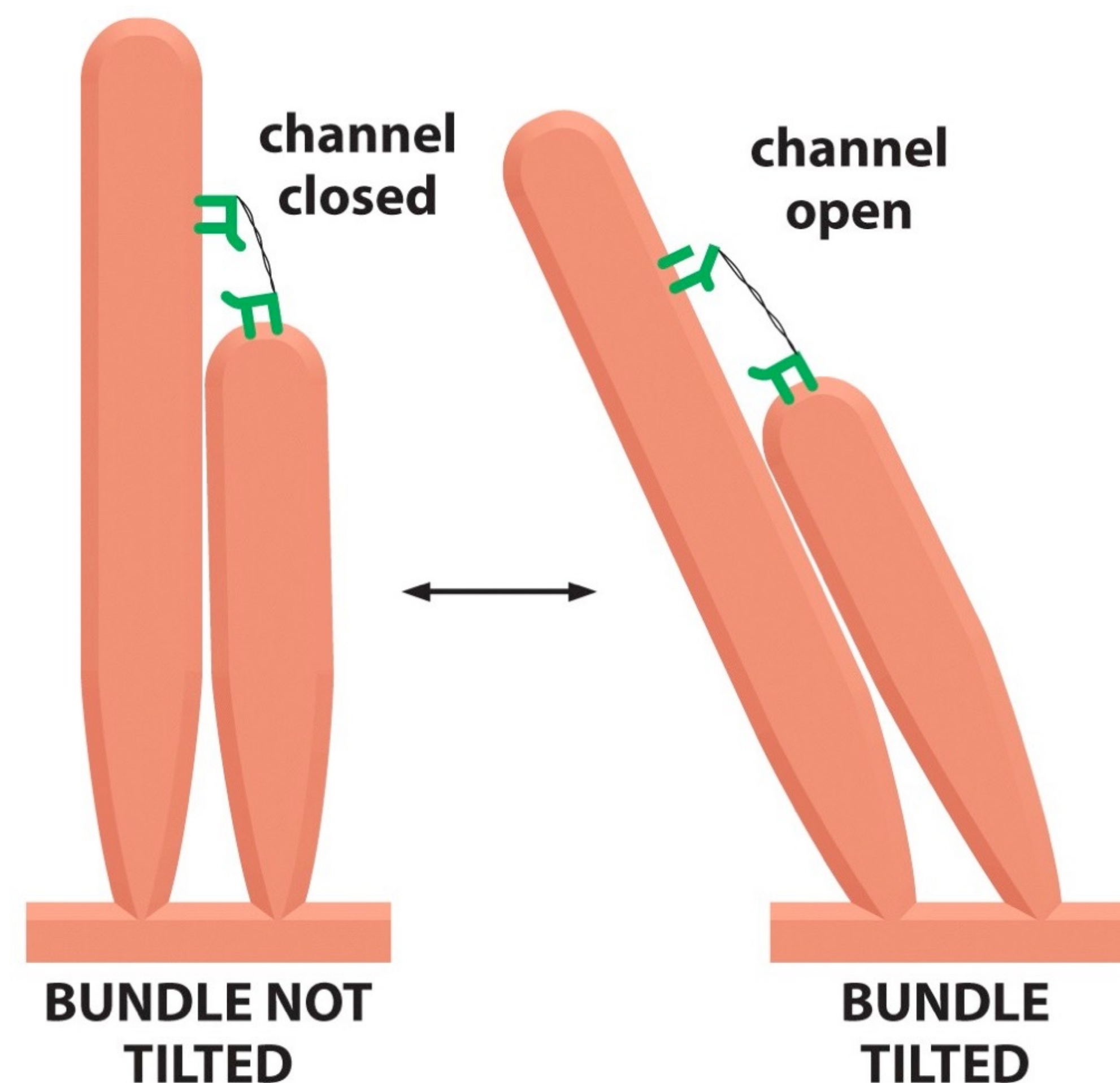
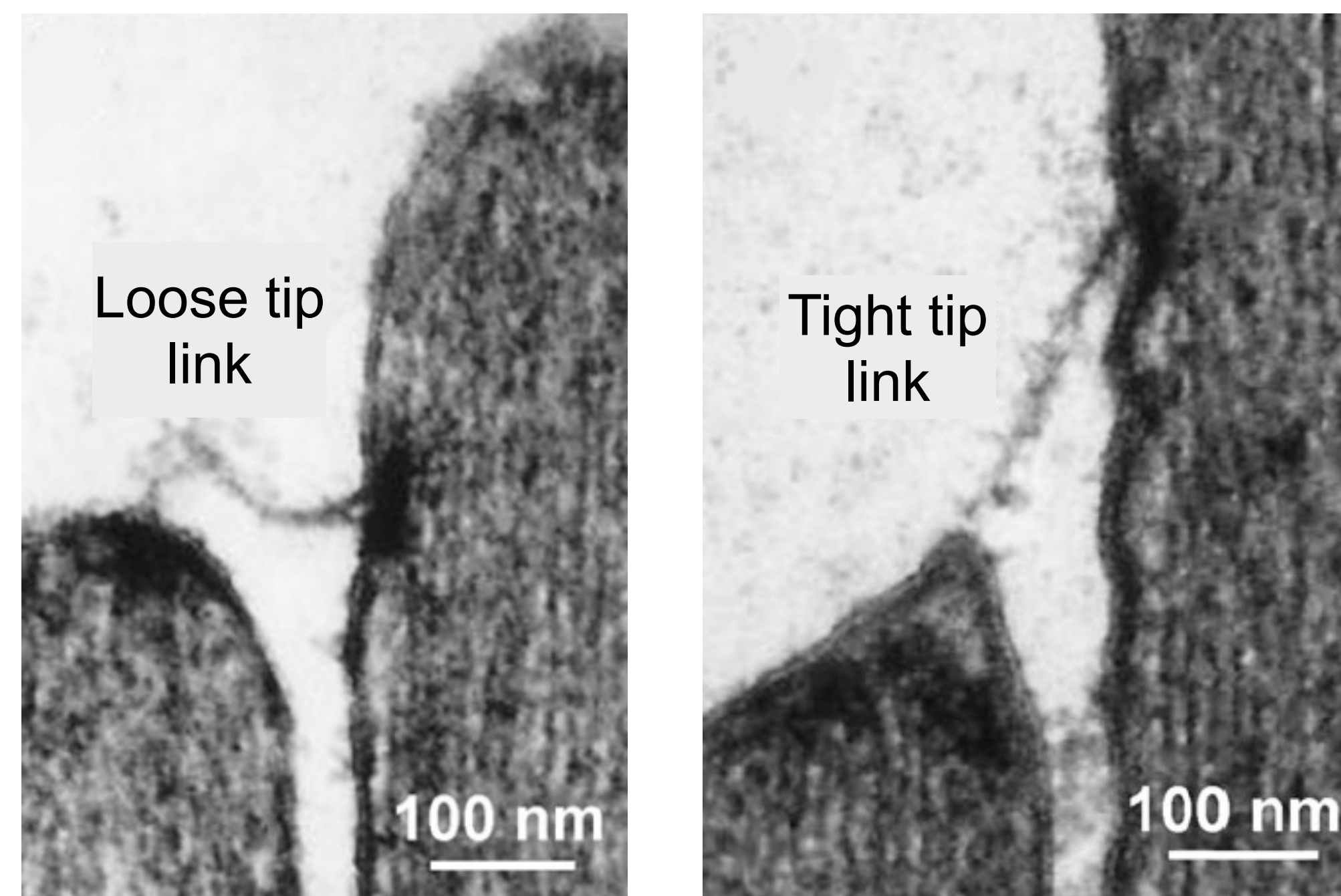
The frequency-dependence of the location of propagating wave maxima provide a rough frequency-discrimination.

Function of the organ of Corti

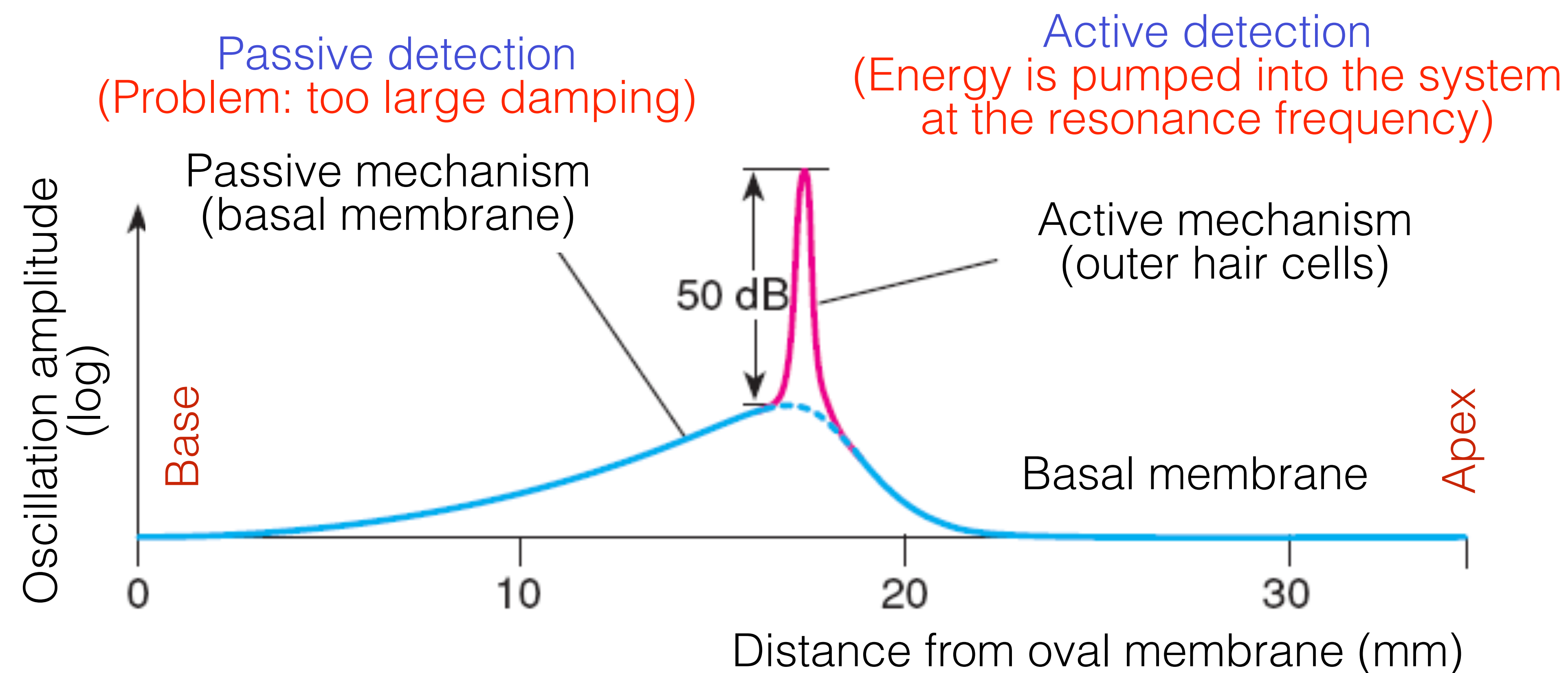
Due to the bending of the basal membrane, hair cells become tilted and depolarized.



Inner hair cells: Mechanoelectrical transducers



Outer hair cells: amplifiers

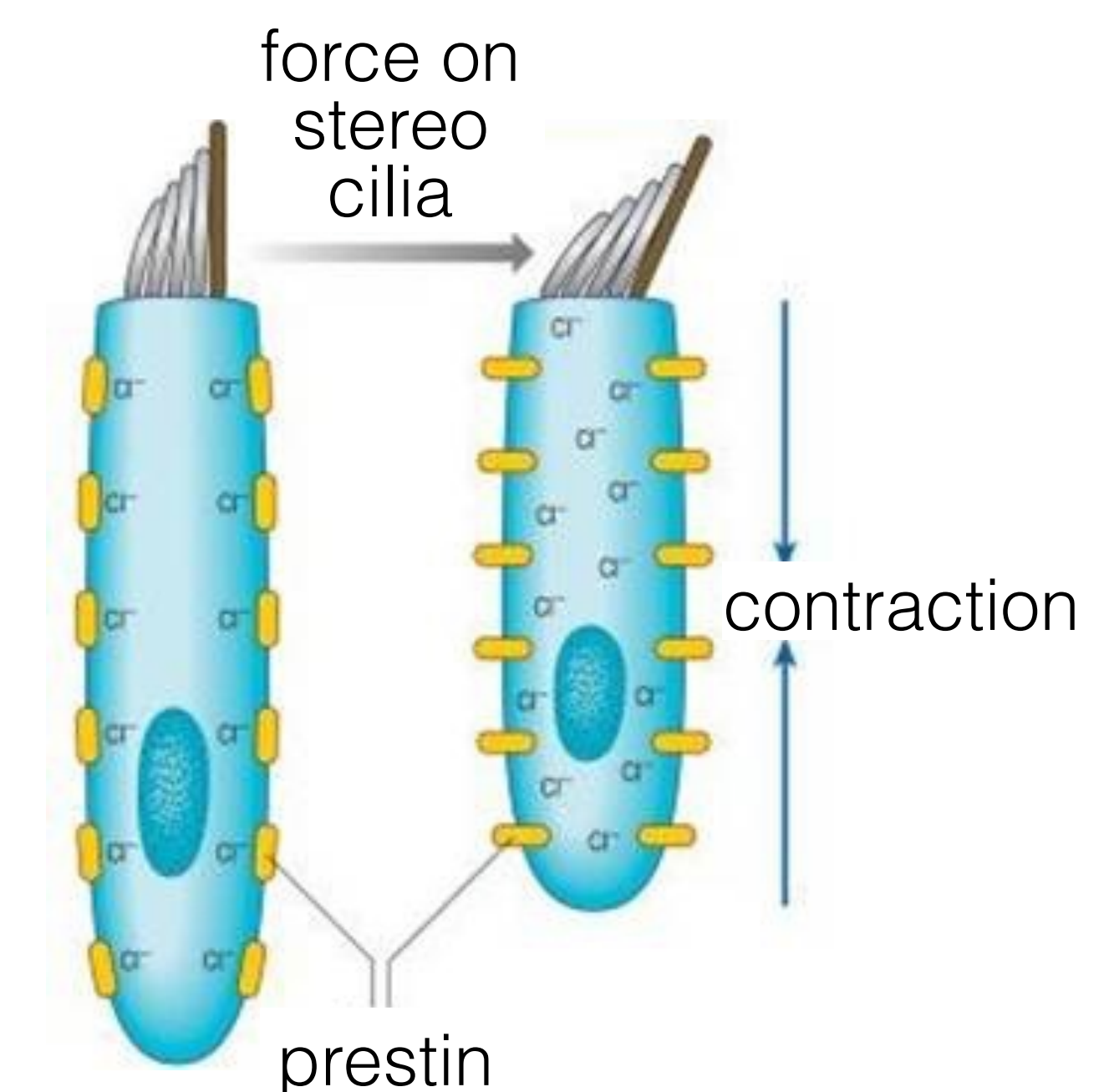


Observations pointing at active detection:

- 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).

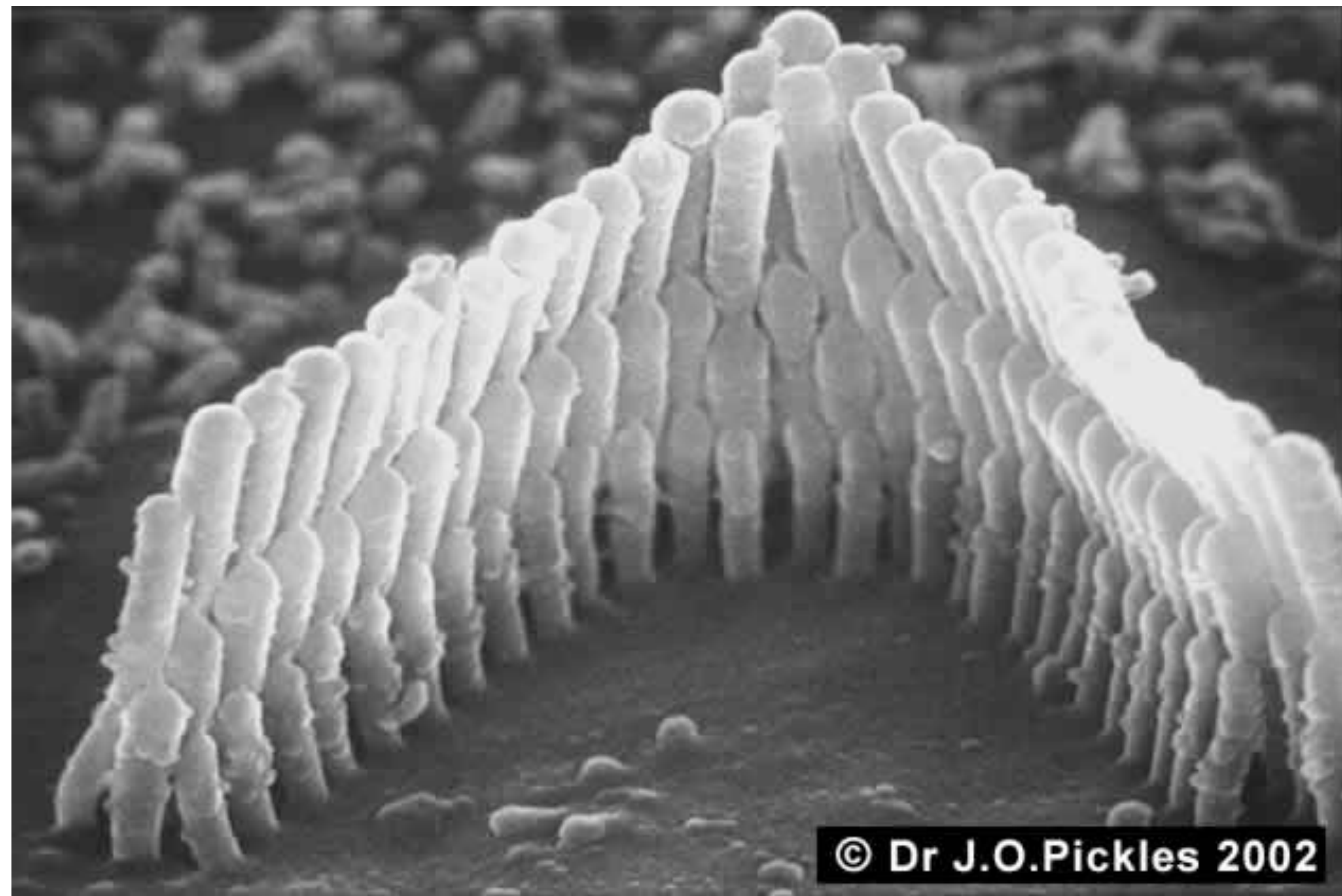
Regenerative amplifier: positive feedback mechanism (Large amplification in narrow frequency range. Only the dissipated energy is regenerated, otherwise ringing occurs)

Amplification:
sound-induced
contraction in outer
hair cells

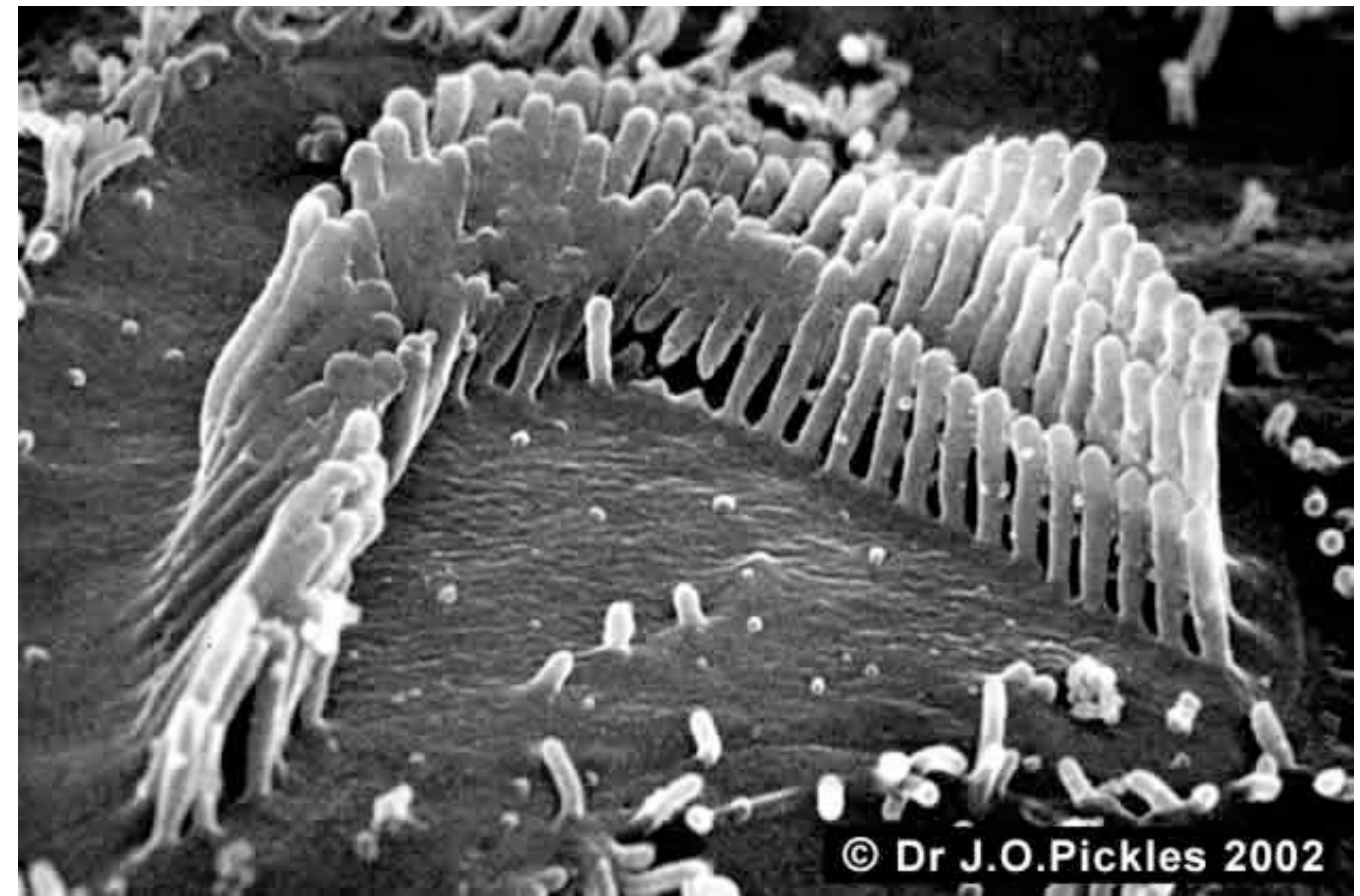


Prestin - transmembrane motor protein.
Mechano-electric and
electromechanical transduction

Acoustic damage



Outer hair cells (normal state)



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

Coding of acoustic information

Location theory

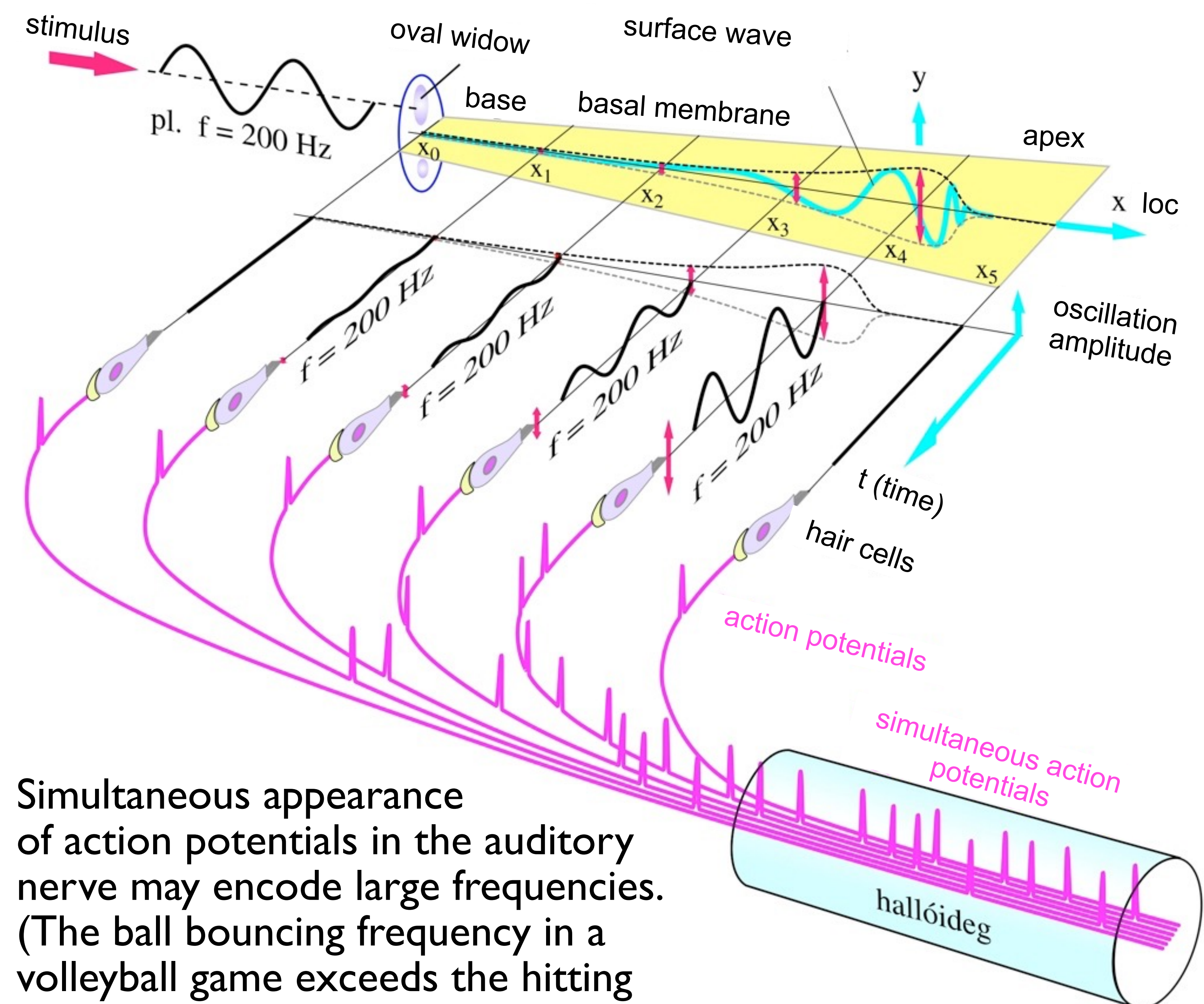
Frequency sensing coded spatially (in the cortex).

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".

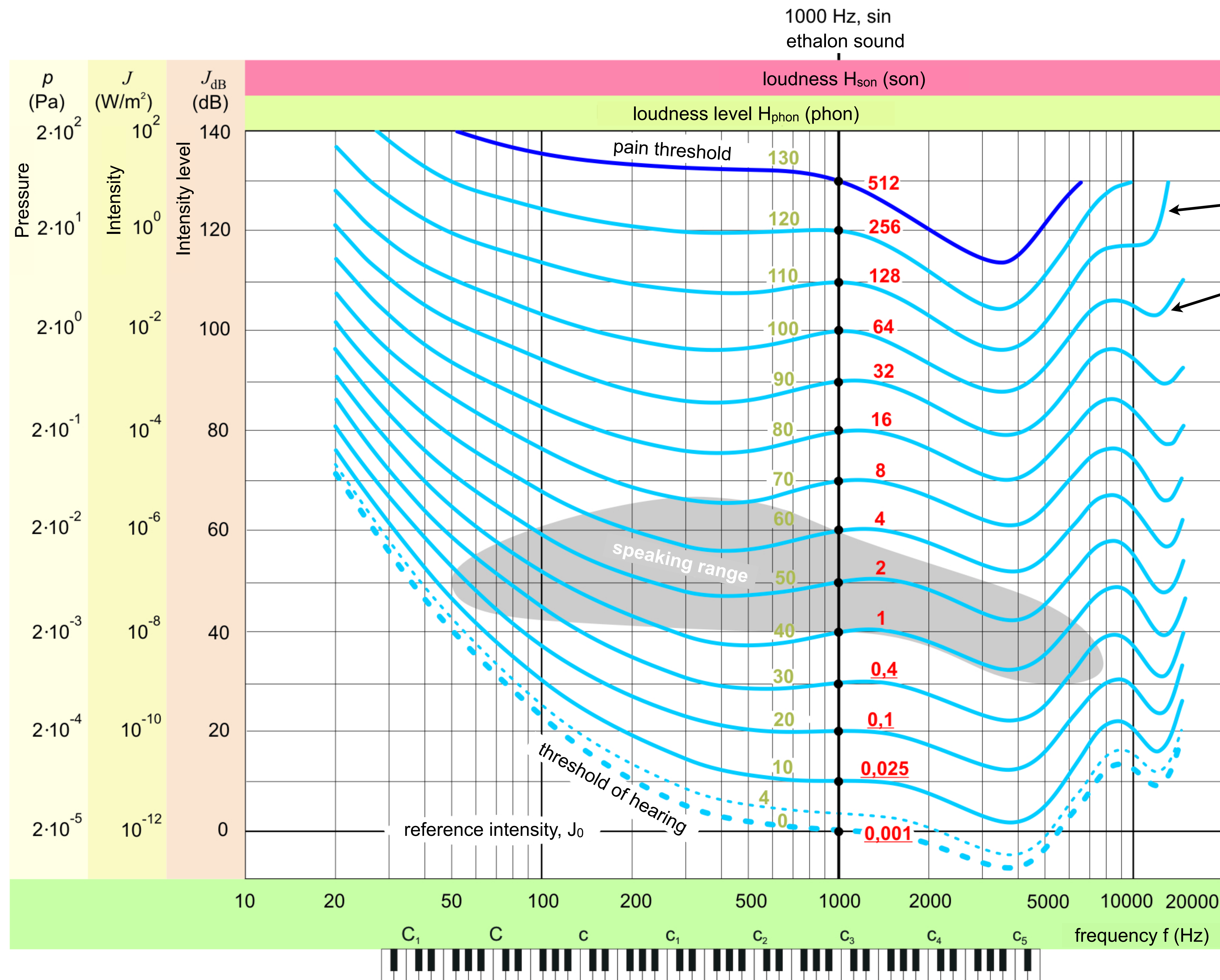
Volleyball theory

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.)

Stimulus intensity and sensing - psychoacoustics



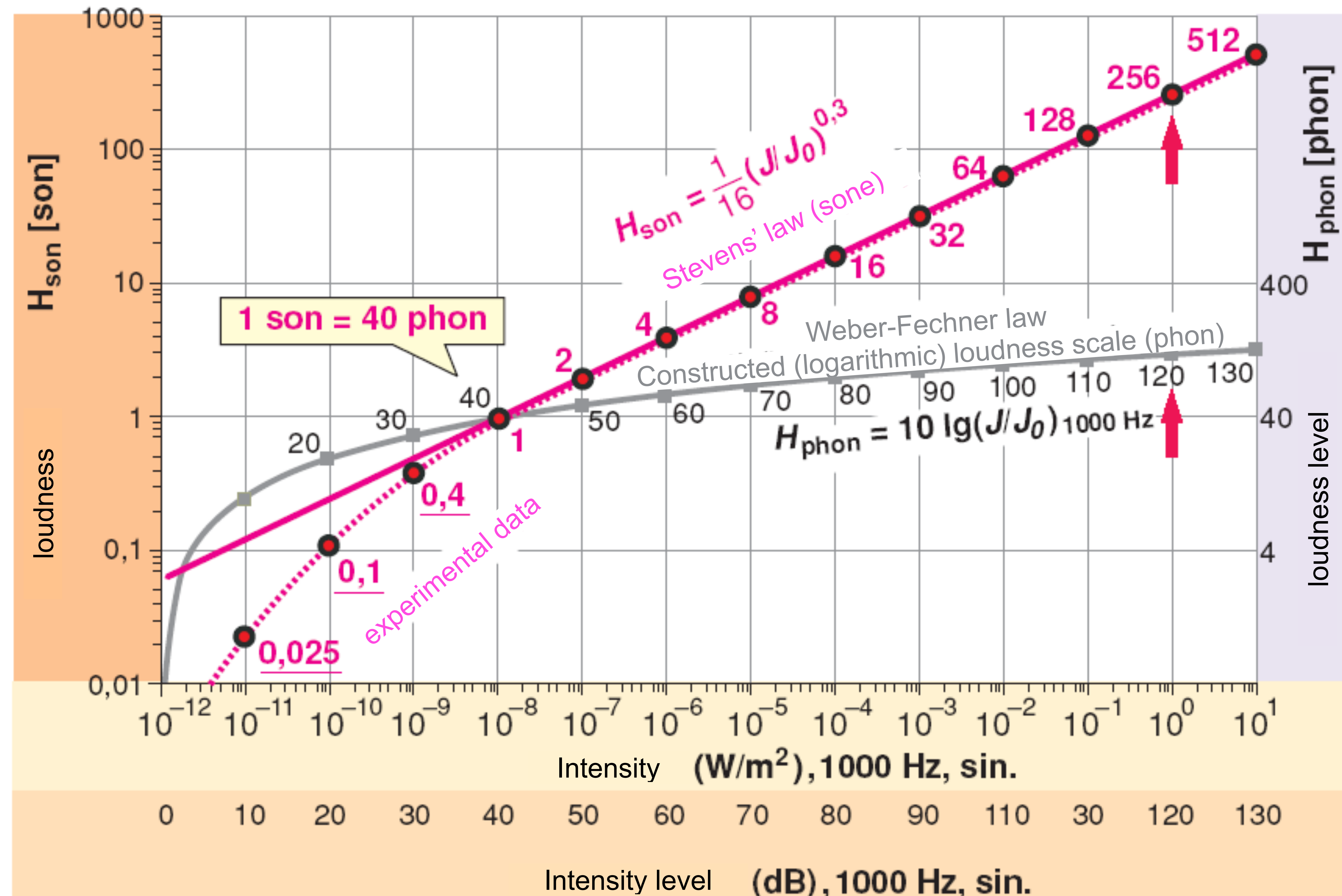
Isophon curves:
connect points of
identical loudness
level
Fletcher-Munson
curves

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

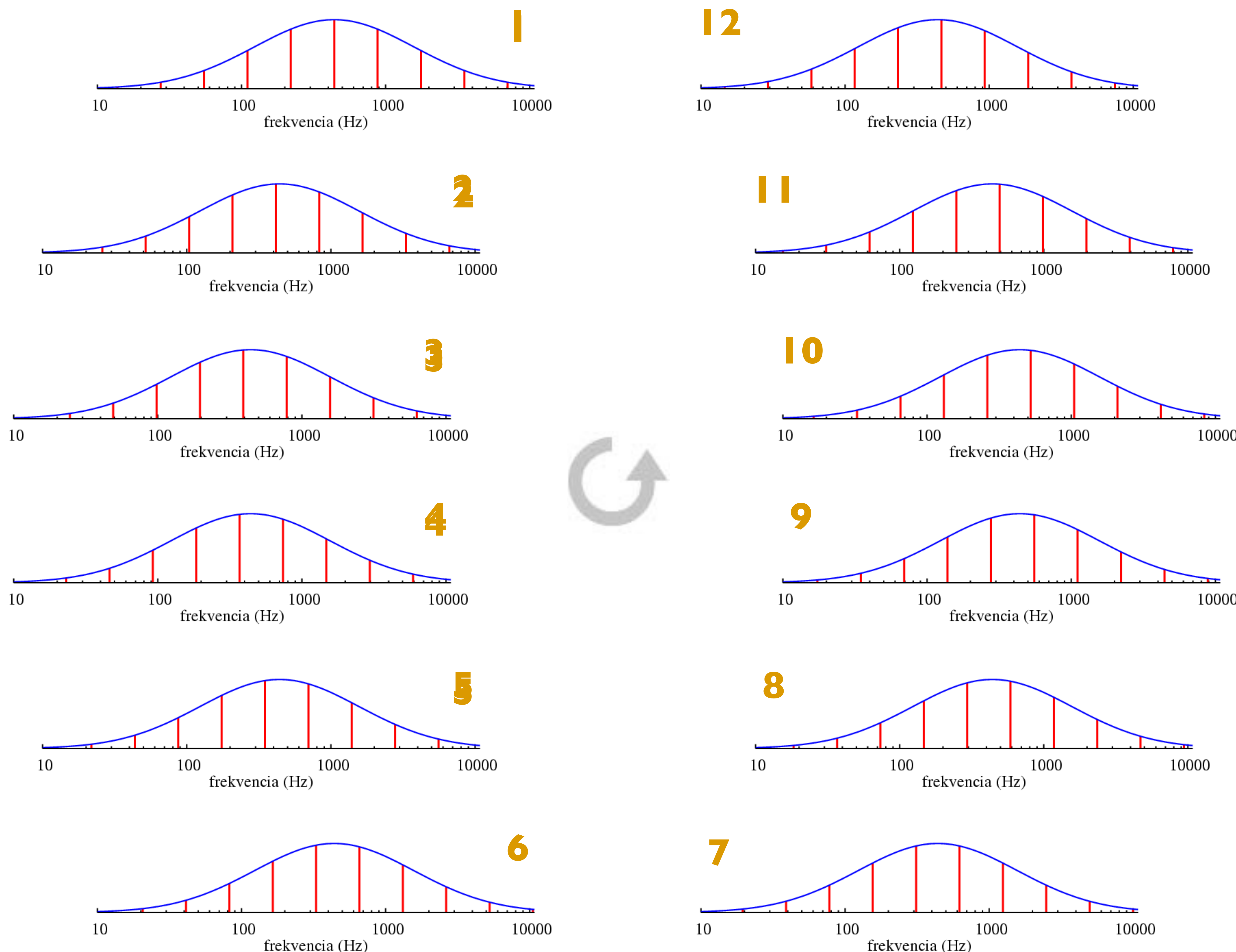
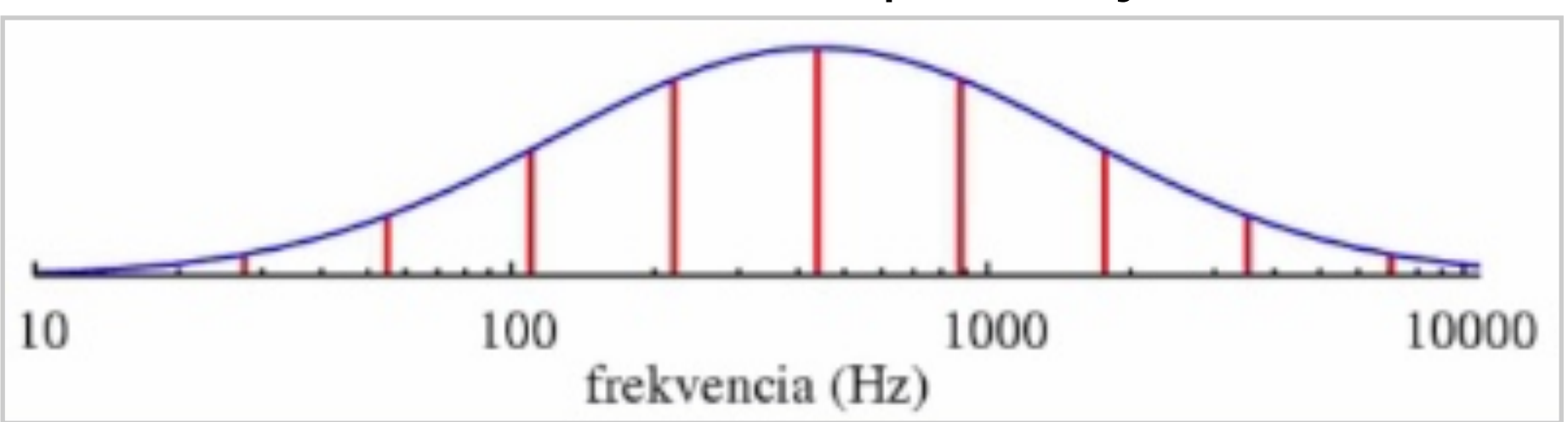
Stevens' law describes
psychoacoustics more precisely



Acoustic illusion?

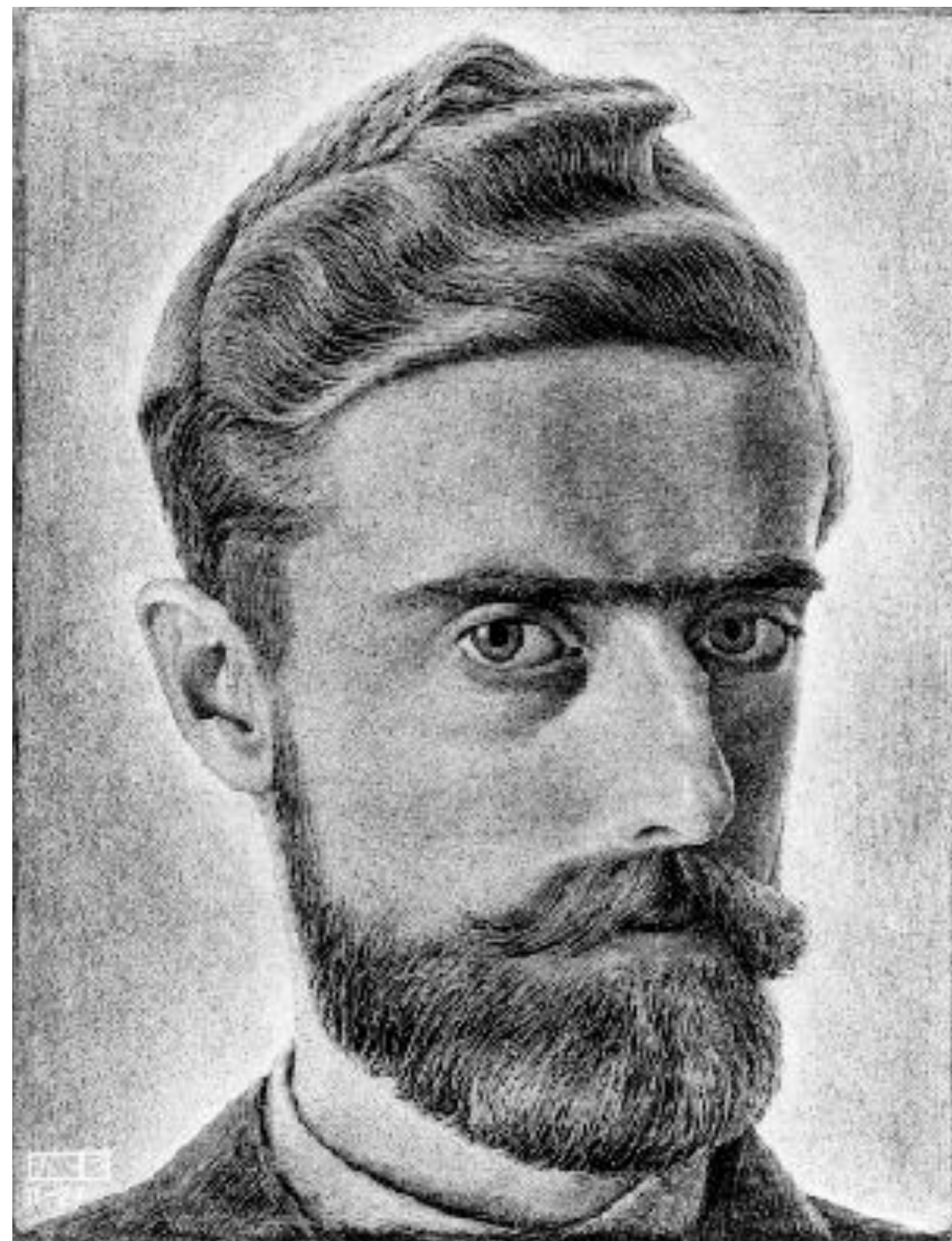
Shepard tone:
sine waves
separated by
octaves

Shepard scale:
fundamental frequency moves

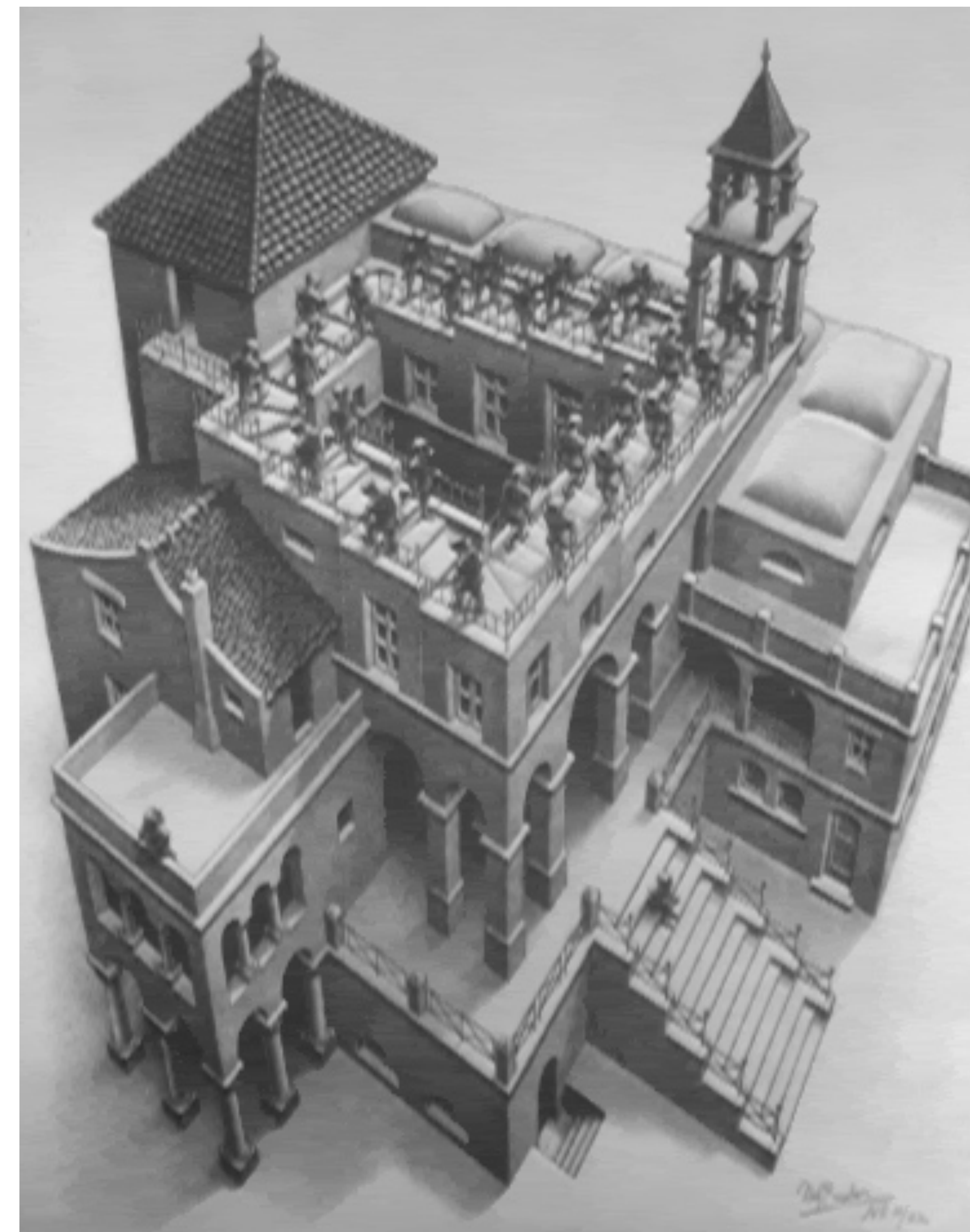
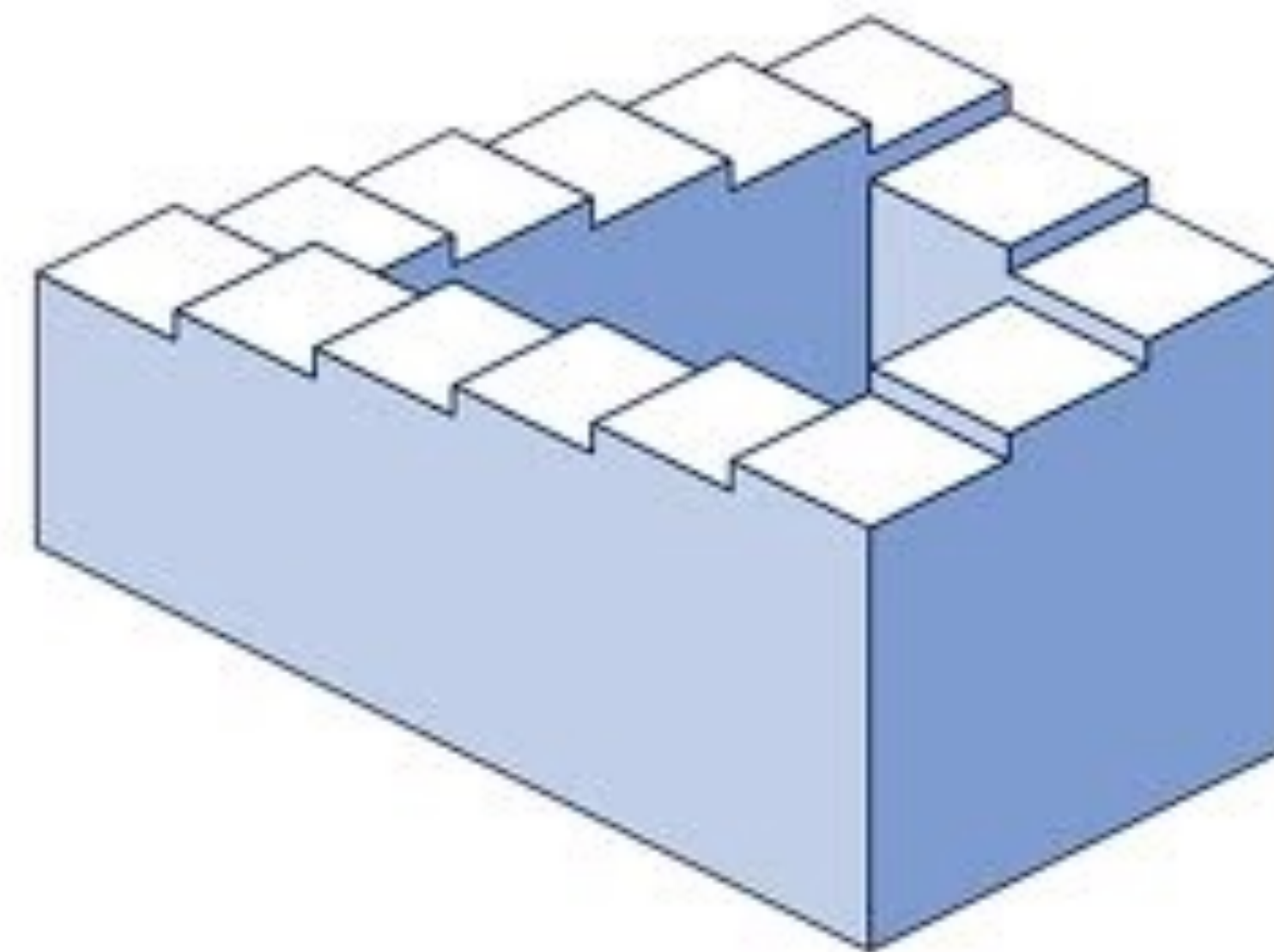


Acoustic illusion?

Visual analogs of the Shepard scale:



Maurits Cornelis Escher
(1898-1972)



Escher staircase



Barber's pole

Feedback



<http://report.semmelweis.hu/linkreport.php?qr=X5K33IXDKNKNF89U>