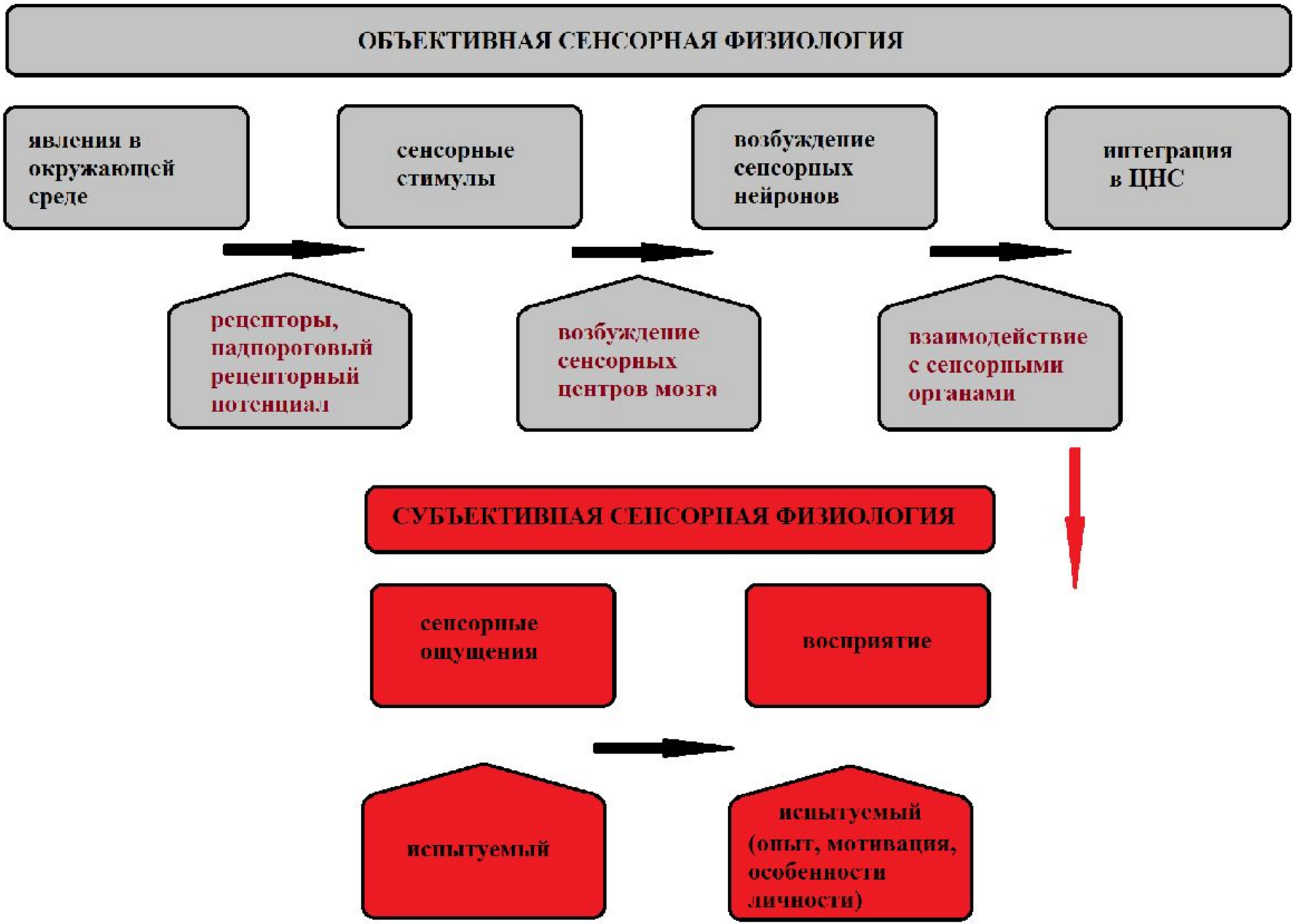
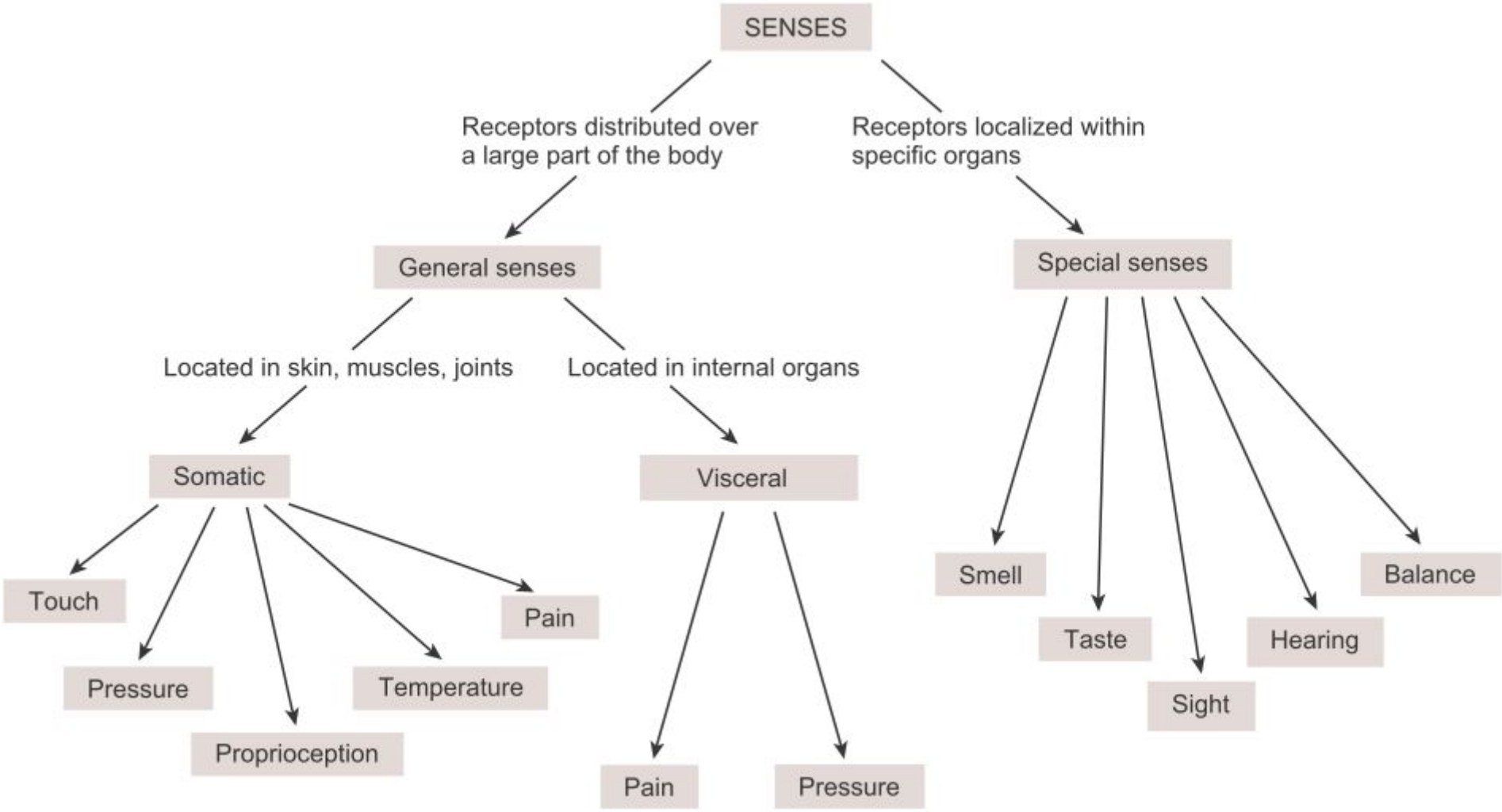
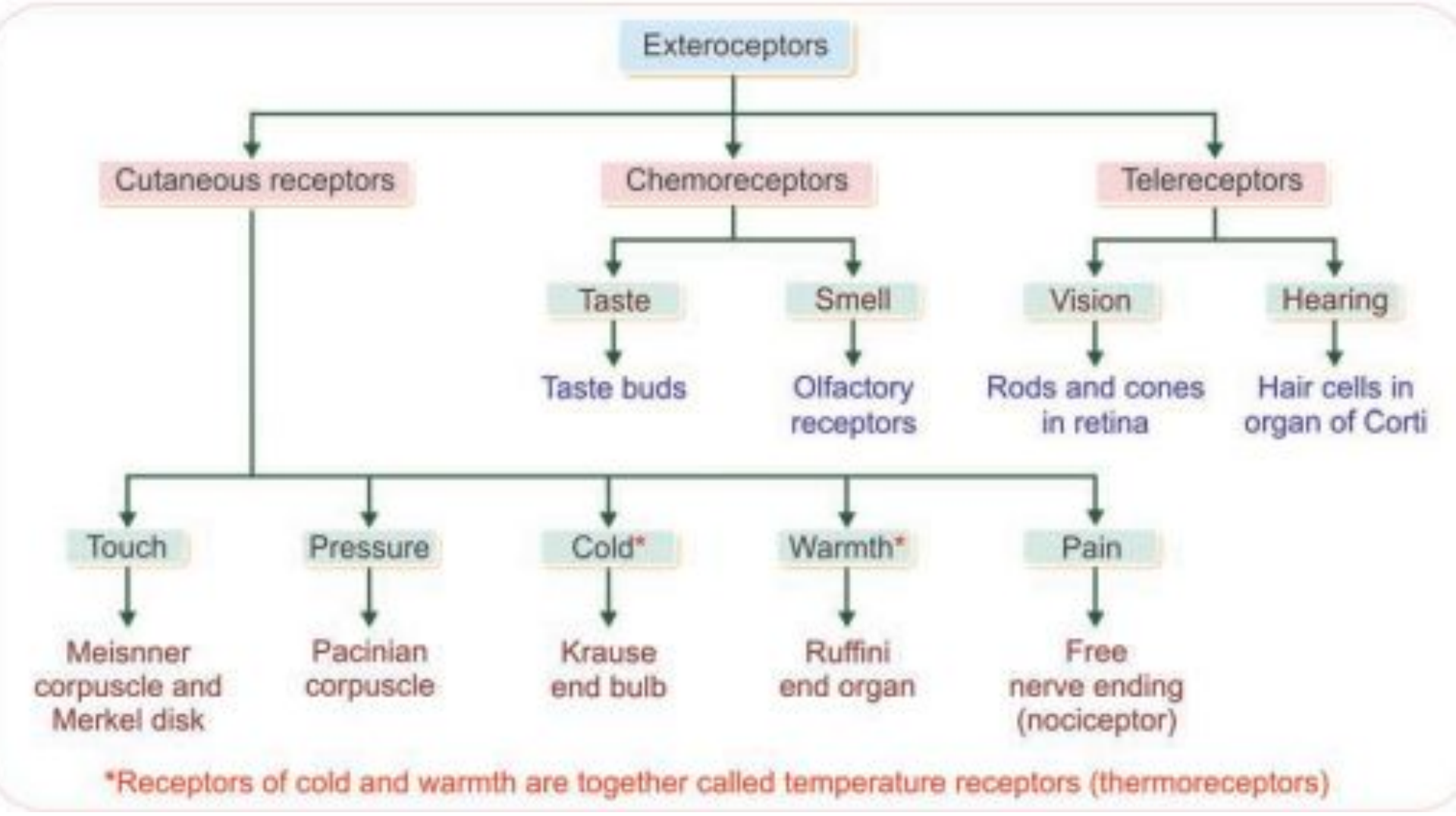
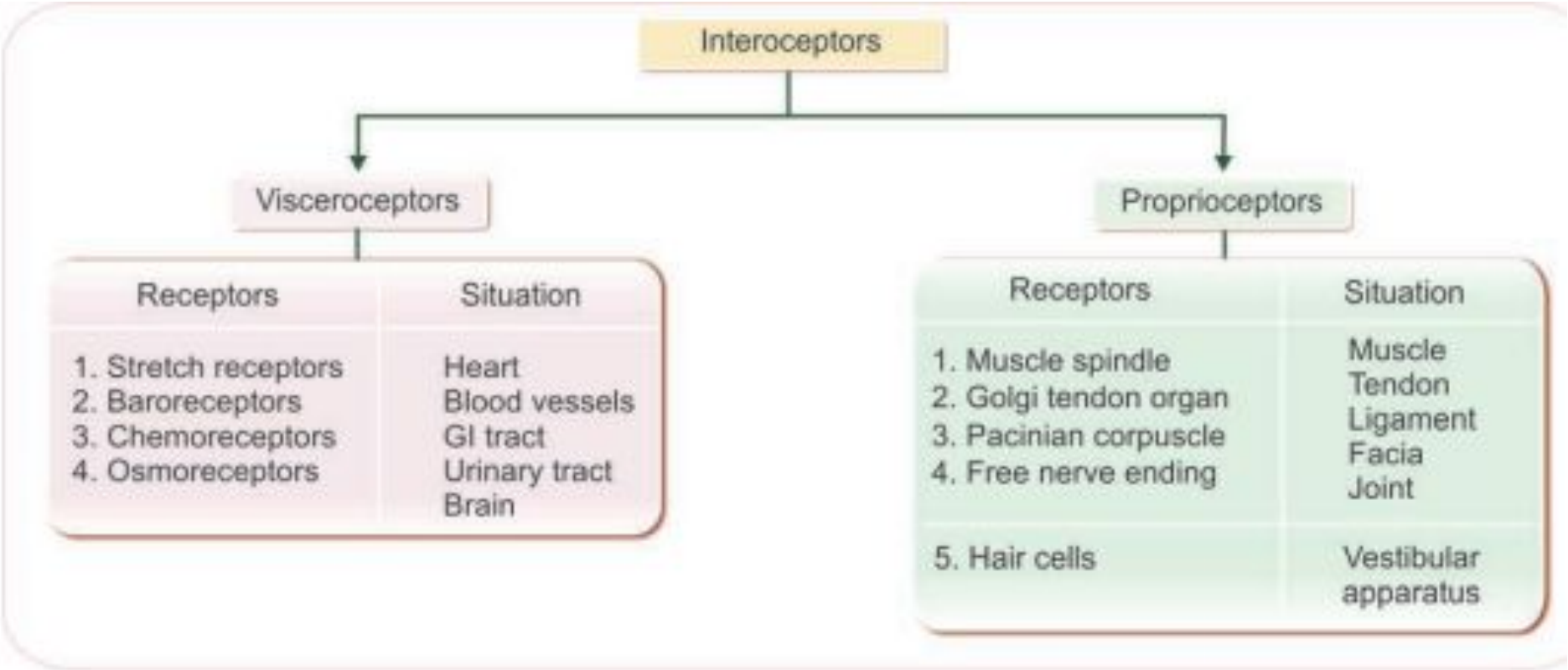
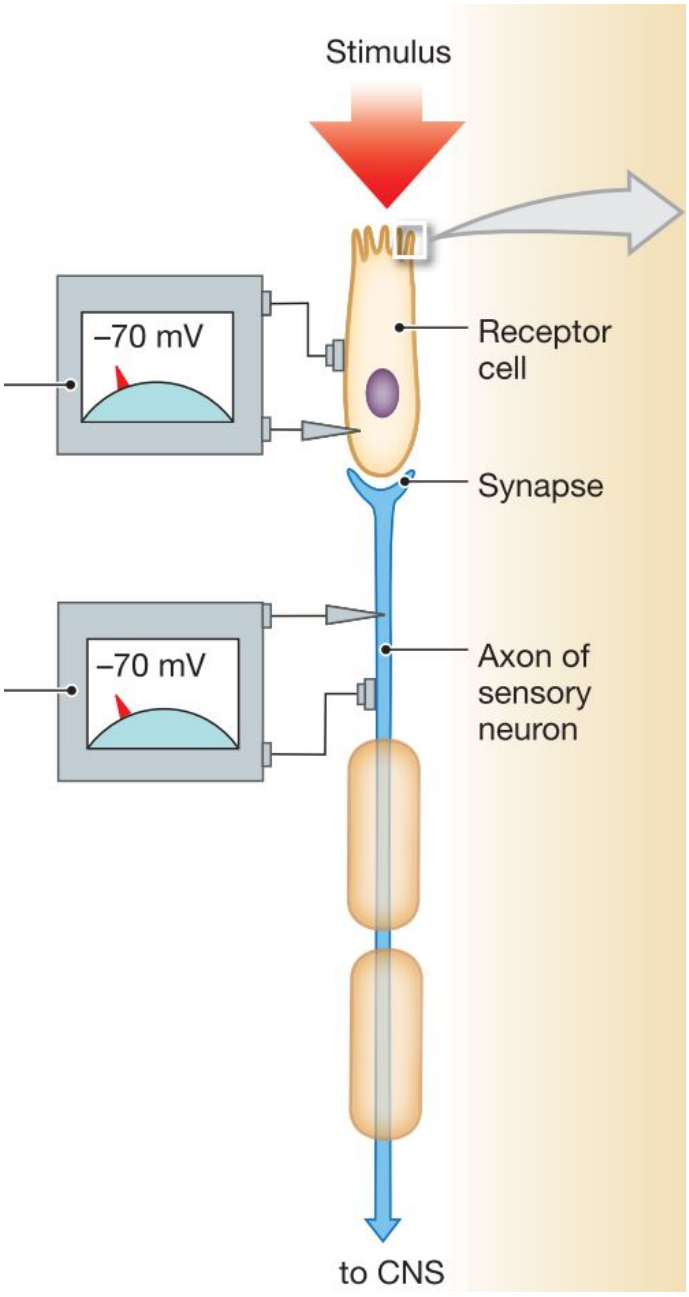
# Общая физиология сенсорных систем. Слуховой анализатор

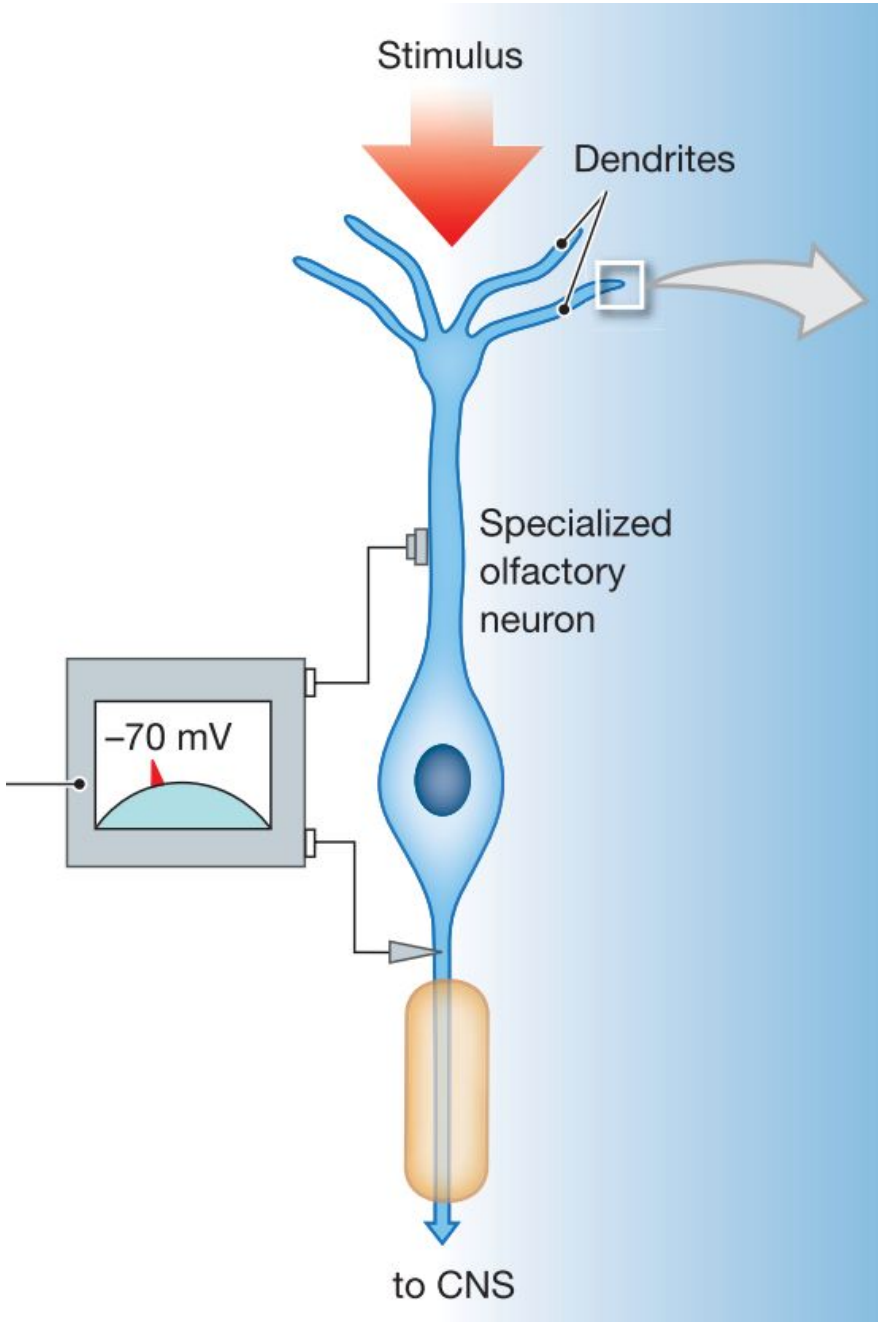

ОБЪЕКТИВНАЯ СЕНСОРНАЯ ФИЗИОЛОГИЯ
явления в окружающей среде
сенсорные стимулы
возбуждение сенсорных нейронов
интеграция в ЦНС
рецепторы, надпороговый рецепторный потенциал
возбуждение сенсорных центров мозга
взаимодействие с сенсорными органами
СУБЪЕКТИВНАЯ СЕНСОРНАЯ ФИЗИОЛОГИЯ
сенсорные ощущения
восприятие
испытуемый
испытуемый (опыт, мотивация, особенности личности)

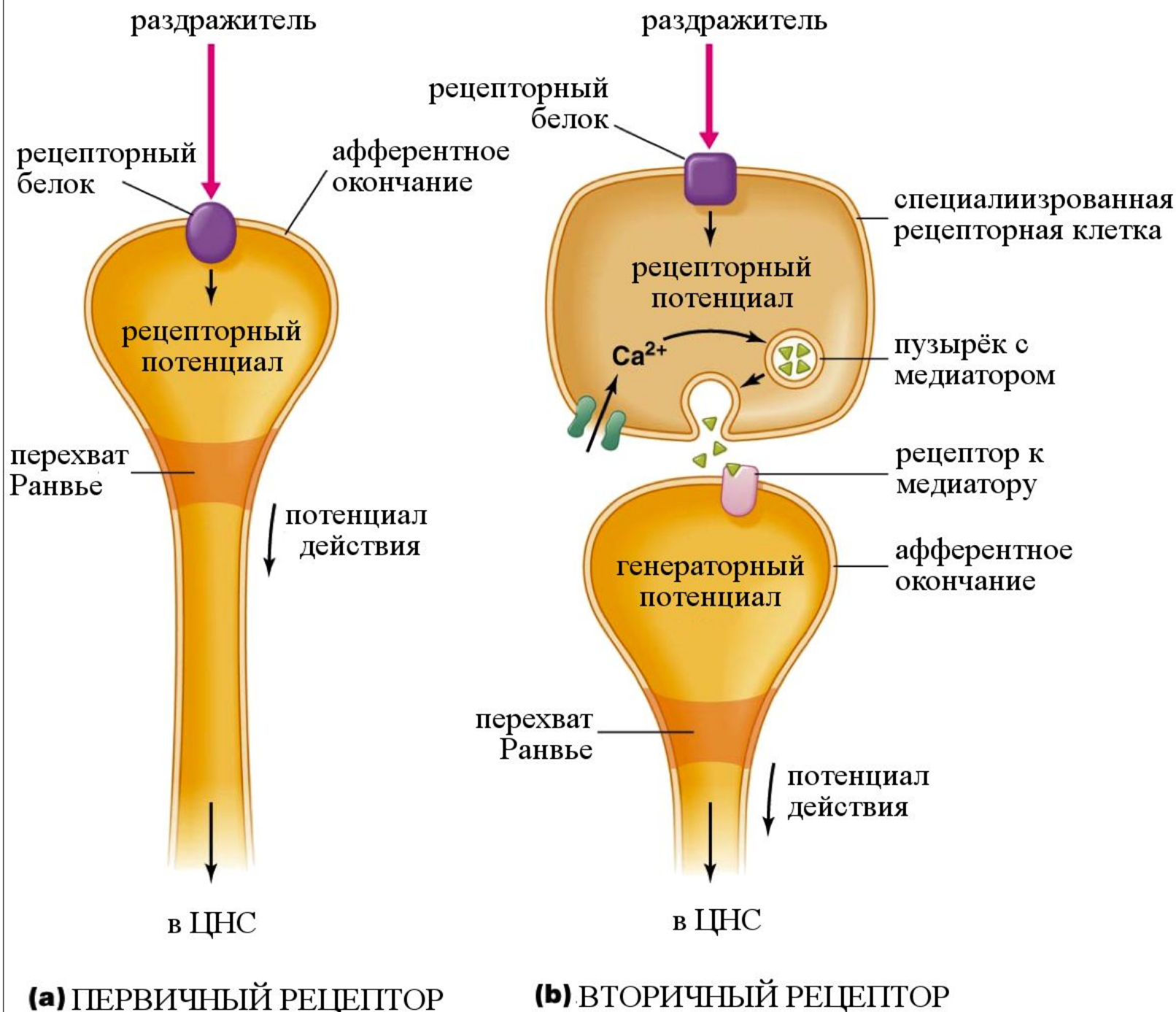

SENSES
Receptors distributed over a large part of the body
Receptors localized within specific organs
General senses
Special senses
Located in skin, muscles, joints
Located in internal organs
Somatic
Visceral
Touch
Pressure
Proprioception
Temperature
Pain
Pain
Pressure
Smell
Taste
Sight
Hearing
Balance

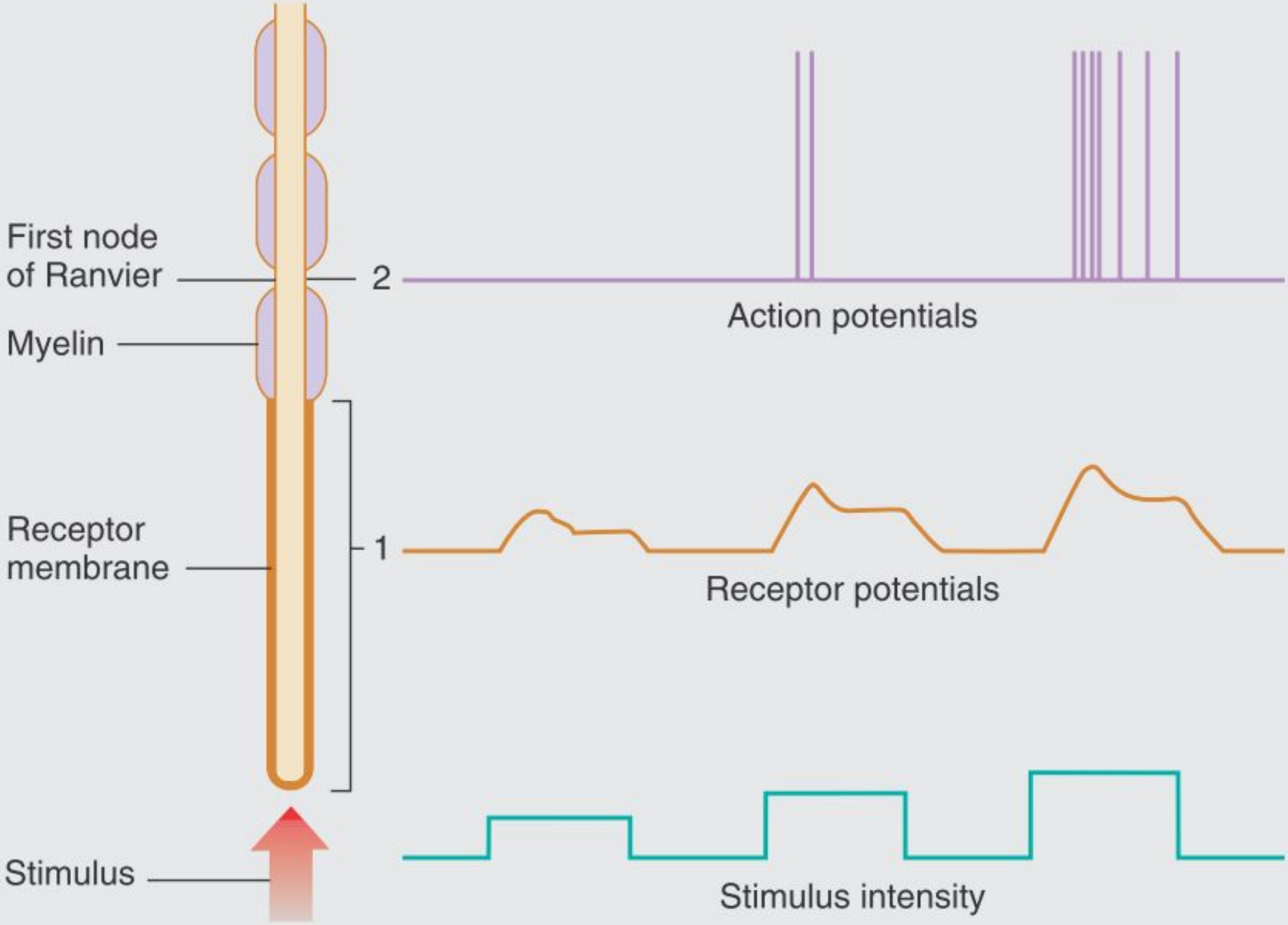

Exteroceptors
Cutaneous receptors
Chemoreceptors
Telereceptors
Taste
Smell
Vision
Hearing
Taste buds
Olfactory receptors
Rods and cones in retina
Hair cells in organ of Corti
Touch
Pressure
Cold*
Warmth*
Pain
Meisnner corpuscle and Merkel disk
Pacinian corpuscle
Krause end bulb
Ruffini end organ
Free nerve ending (nociceptor)
*Receptors of cold and warmth are together called temperature receptors (thermoreceptors)

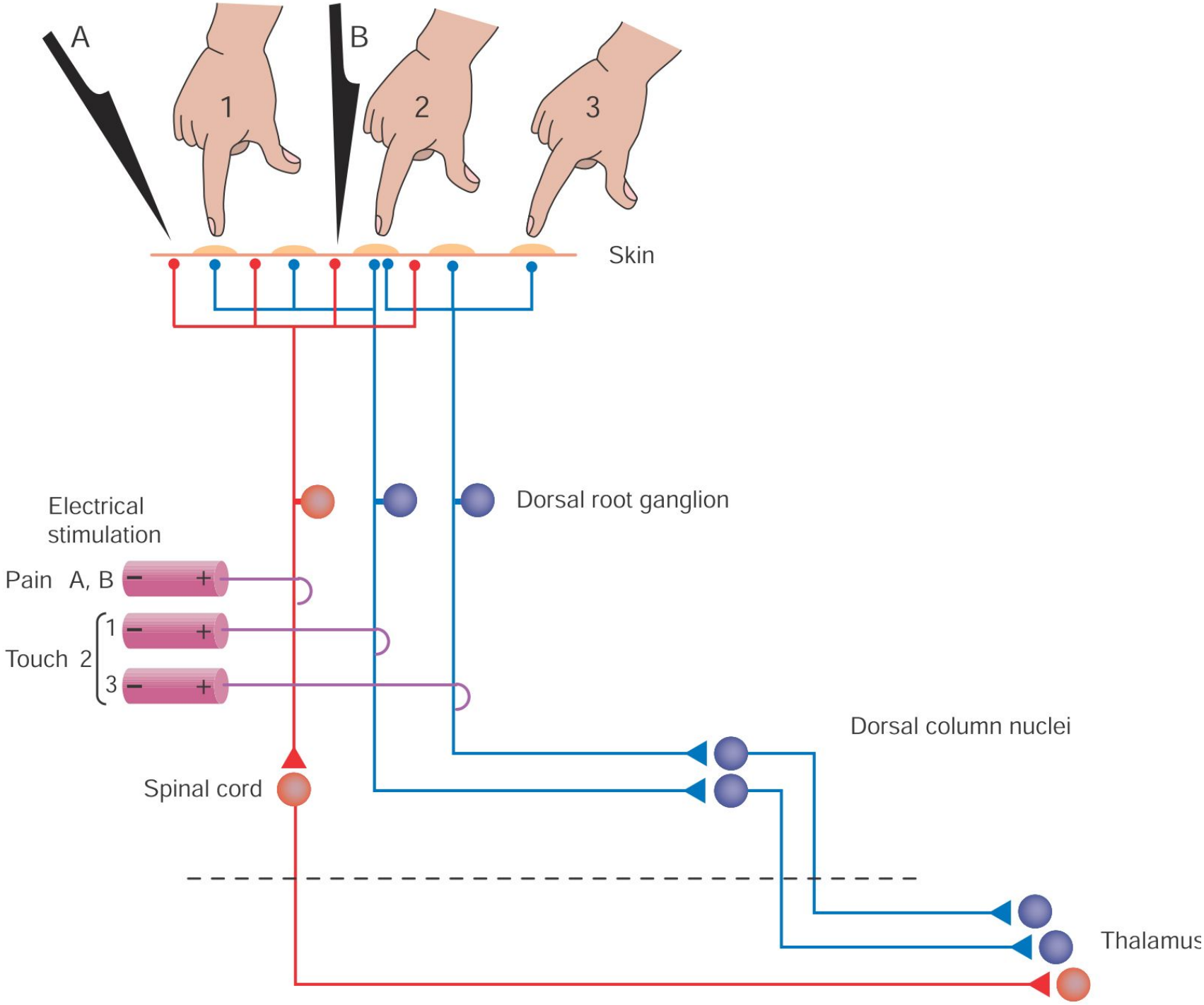

Interoceptors
Visceroceptors
Receptors
Situation
1. Stretch receptors
2. Baroreceptors
3. Chemoreceptors
4. Osmoreceptors
Heart
Blood vessels
GI tract
Urinary tract
Brain
Proprioceptors
Receptors
Situation
1. Muscle spindle
2. Golgi tendon organ
3. Pacinian corpuscle
4. Free nerve ending
Muscle
Tendon
Ligament
Facia
Joint
5. Hair cells
Vestibular apparatus

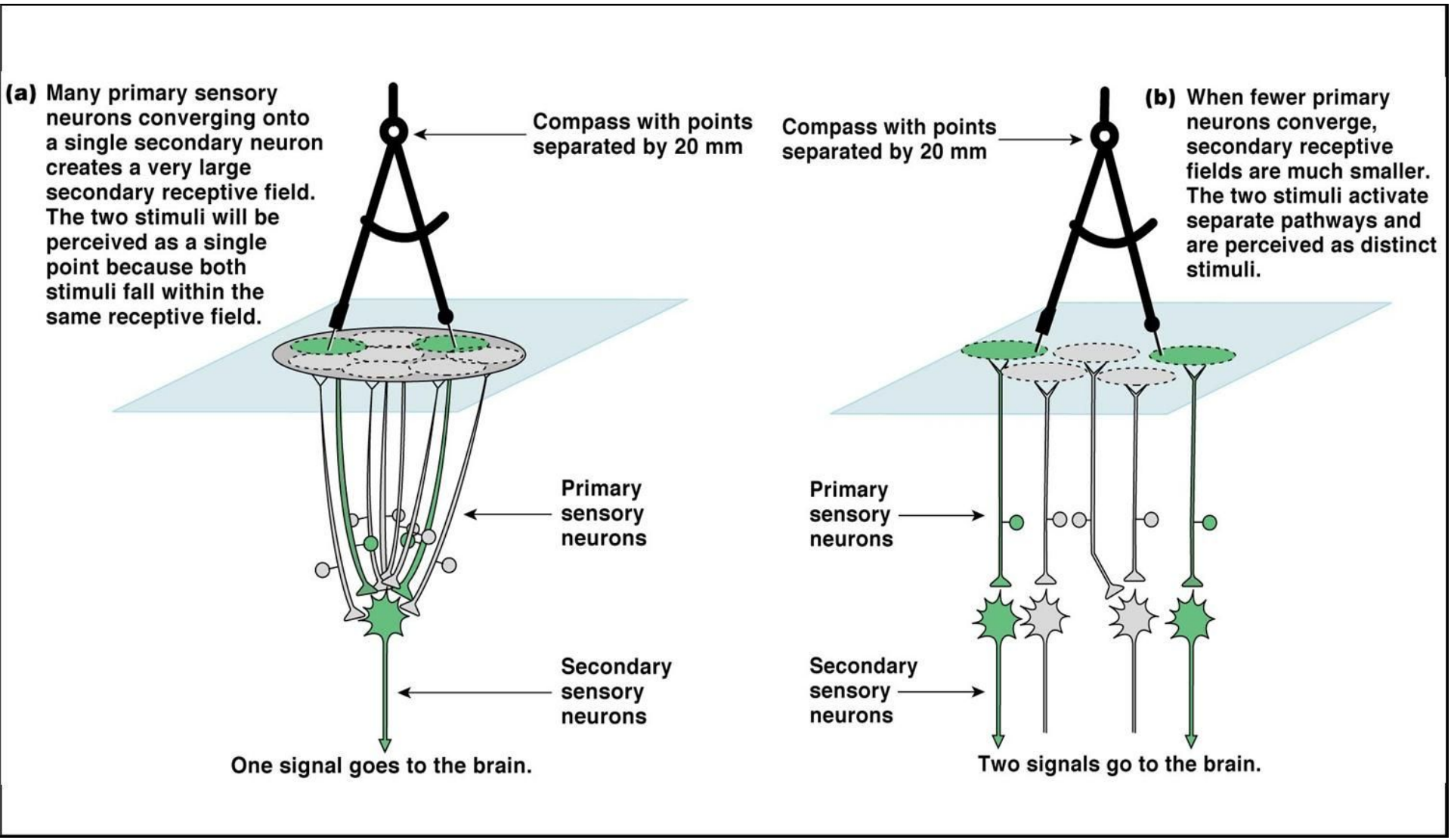

Stimulus
–70 mV
Receptor cell
Synapse
–70 mV
Axon of sensory neuron
to CNS


Stimulus
Dendrites
Specialized olfactory neuron
–70 mV
to CNS

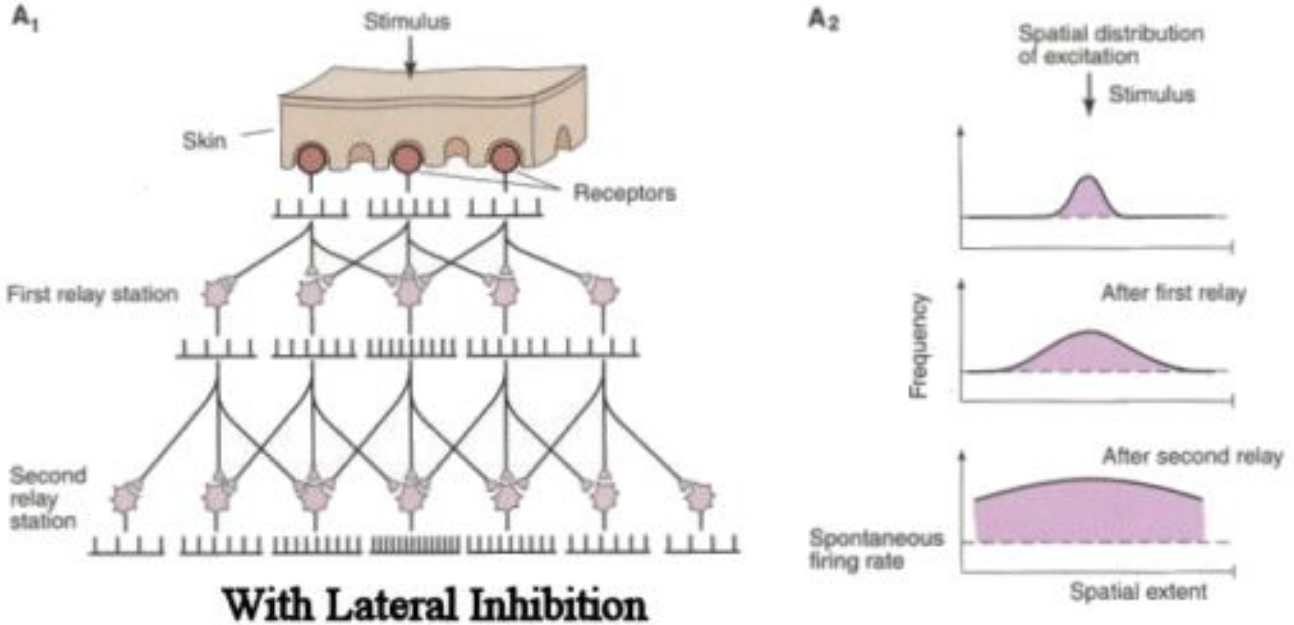

раздражитель
рецепторный белок
афферентное окончание
рецепторный потенциал
перехват Ранвье
потенциал действия
в ЦНС
(a) ПЕРВИЧНЫЙ РЕЦЕПТОР
раздражитель
рецепторный белок
специалиизрованная рецепторная клетка
рецепторный потенциал
Ca2+
пузырёк с медиатором
рецептор к медиатору
генераторный потенциал
афферентное окончание
перехват Ранвье
потенциал действия
в ЦНС
(b) ВТОРИЧНЫЙ РЕЦЕПТОР


First node
of Ranvier
2
Myelin
Receptor
membrane
1
Stimulus
Action potentials
Receptor potentials
Stimulus intensity

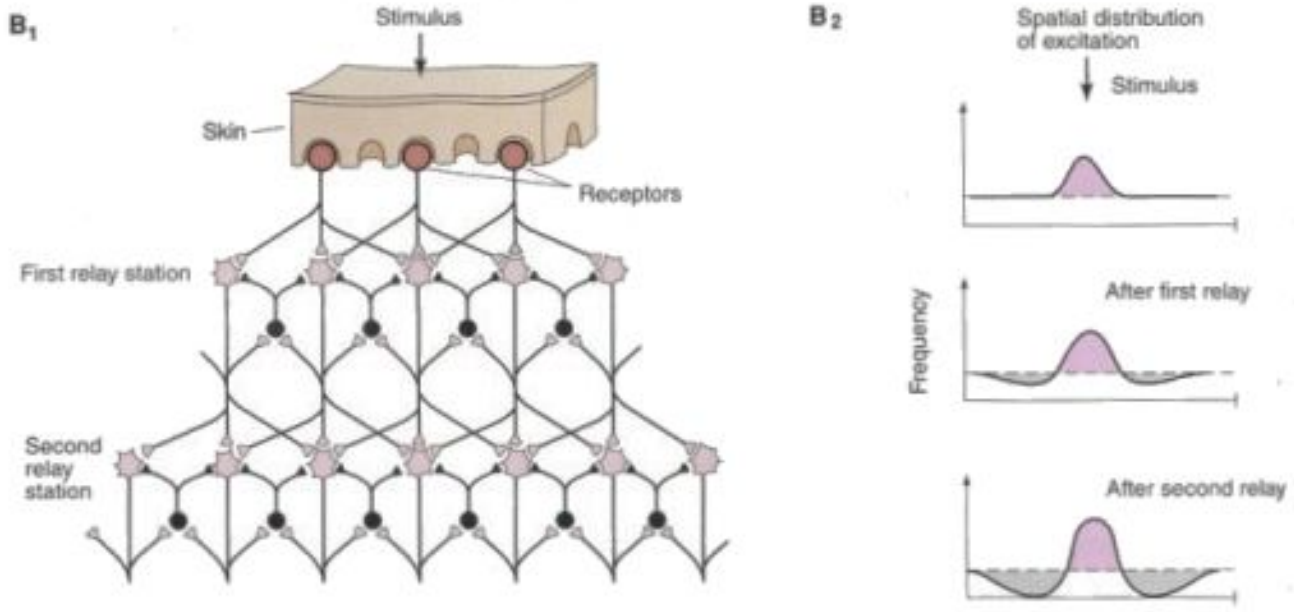

A
B
1
2
3
Skin
Electrical stimulation
Dorsal root ganglion
Pain A, B
Touch 2
1
3
Dorsal column nuclei
Spinal cord
Thalamus


(a) Many primary sensory neurons converging onto a single secondary neuron creates a very large secondary receptive field. The two stimuli will be perceived as a single point because both stimuli fall within the same receptive field.
Compass with points separated by 20 mm
Primary sensory neurons
Secondary sensory neurons
One signal goes to the brain.
Compass with points separated by 20 mm
(b) When fewer primary neurons converge, secondary receptive fields are much smaller. The two stimuli activate separate pathways and are perceived as distinct stimuli.
Primary sensory neurons
Secondary sensory neurons
Two signals go to the brain.

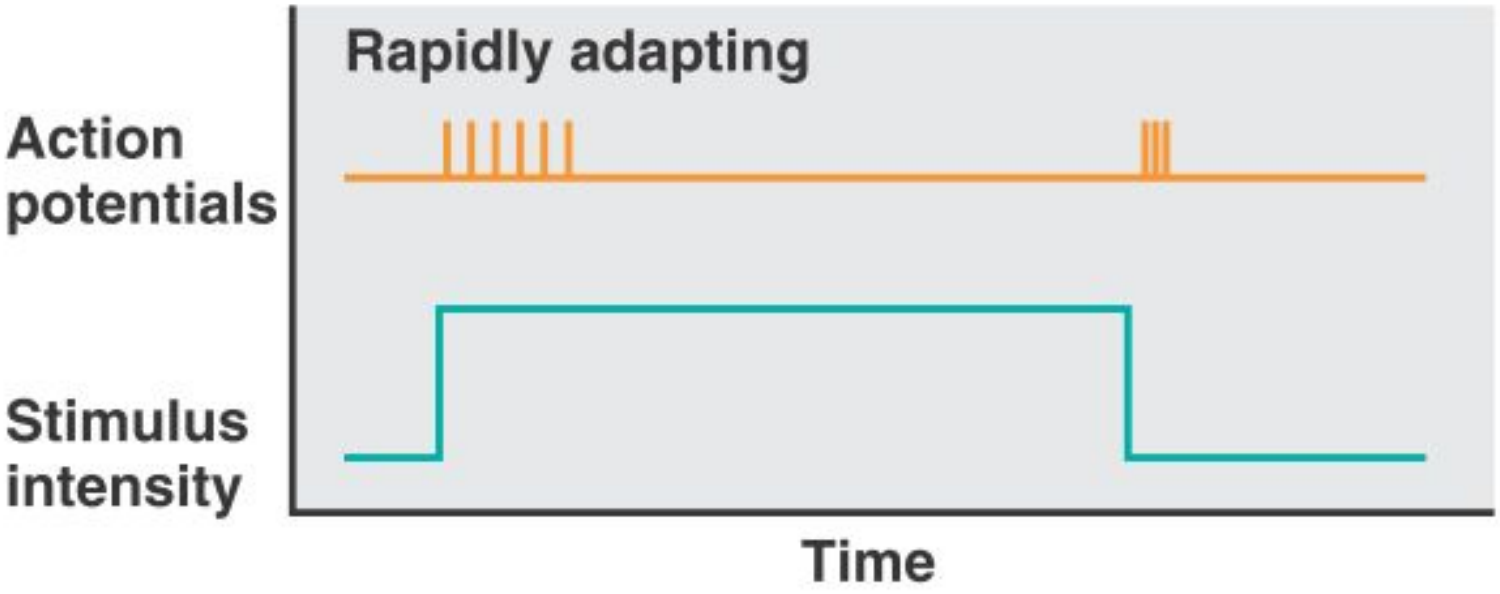
## Without Lateral Inhibition

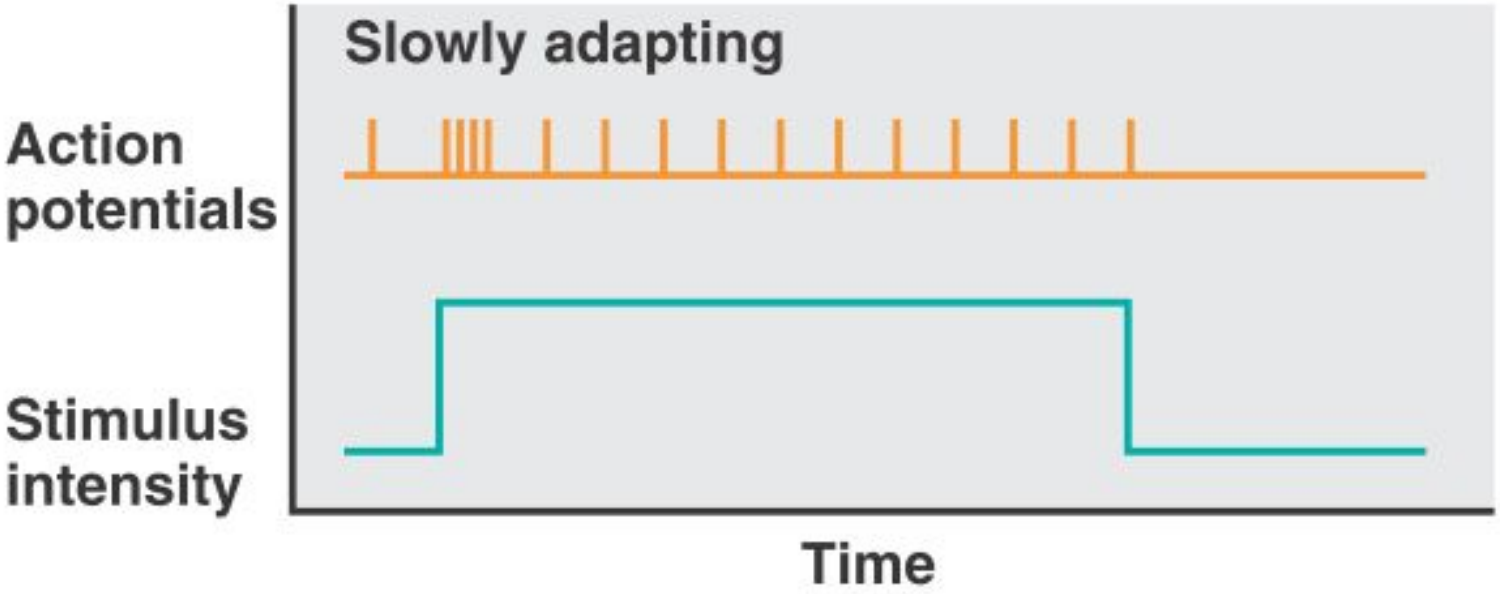


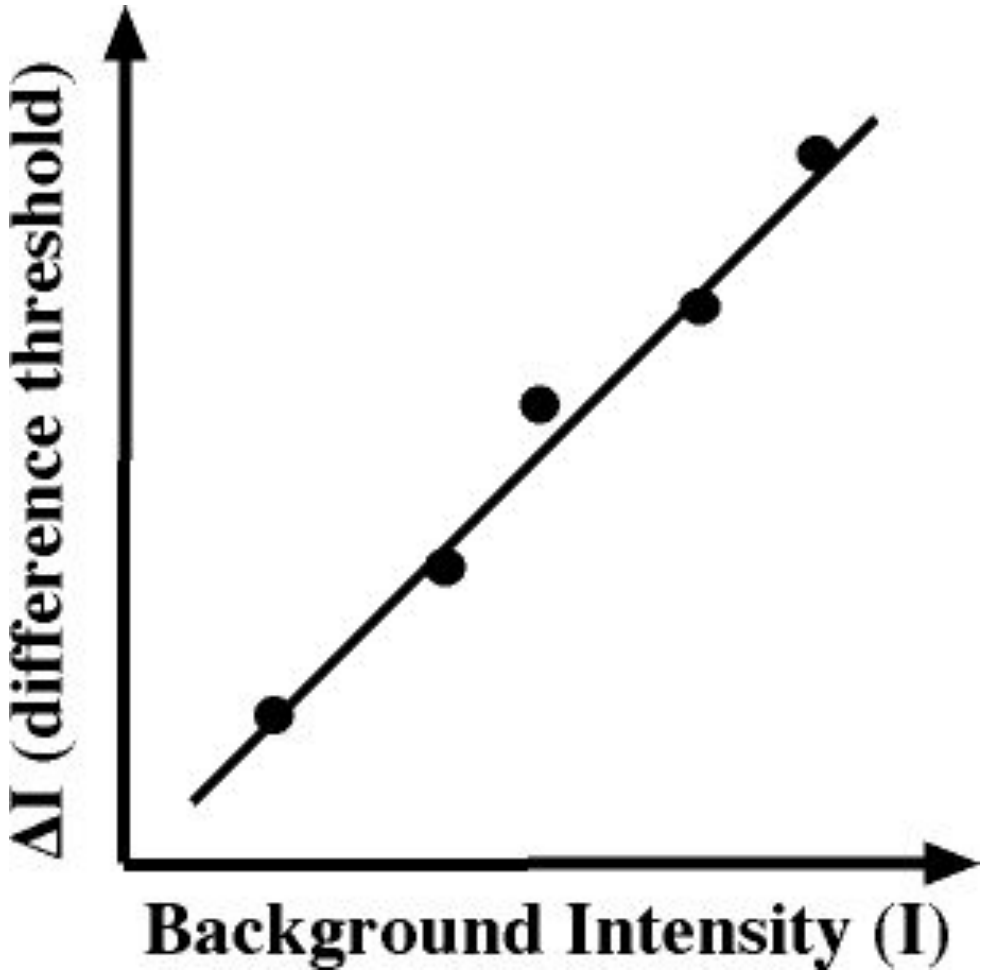

## With Lateral Inhibition



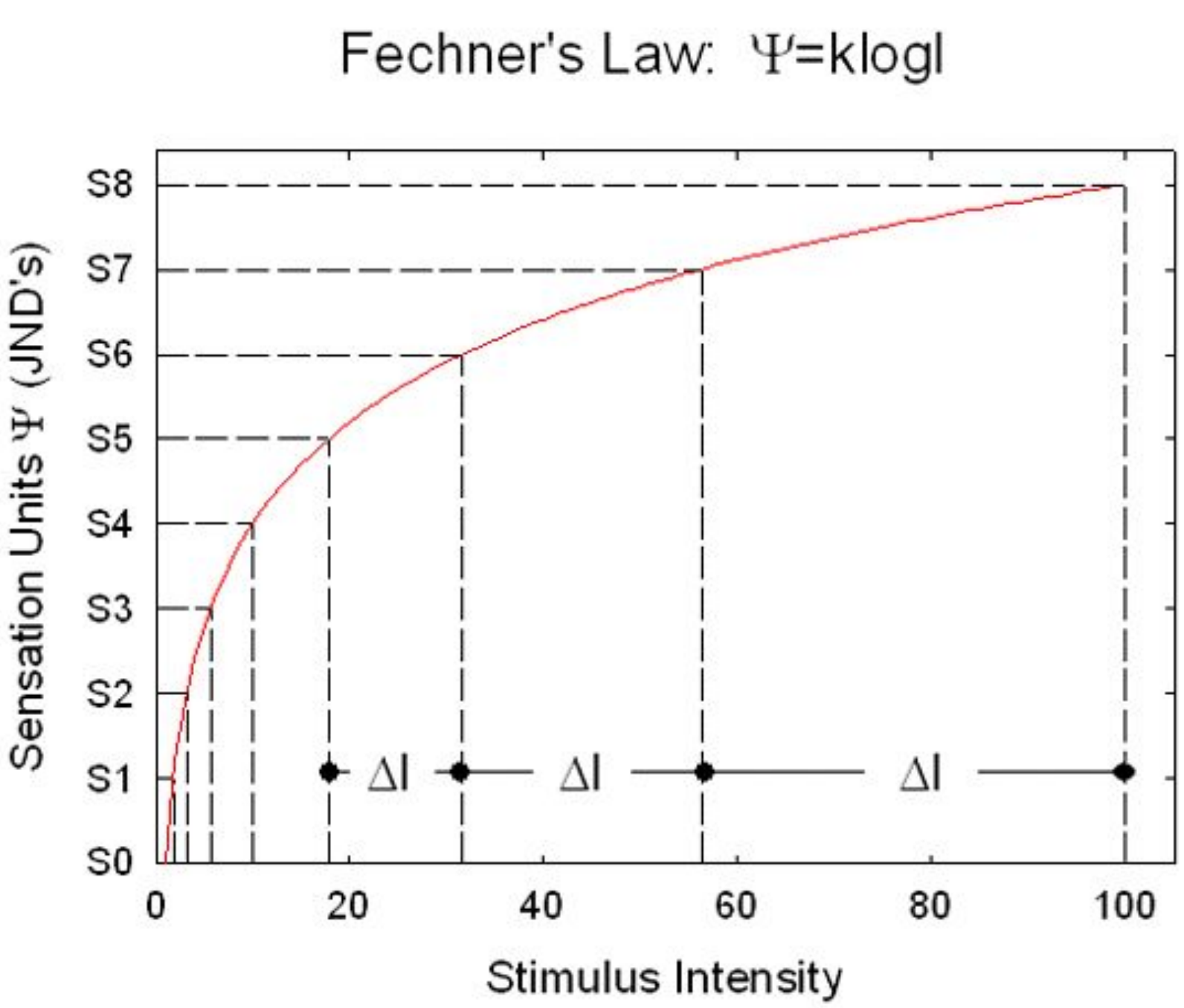

**Adapted from Kandel, E. R., Schwartz, J. H. , et al. (1995). Essentials of neural science and behavior. Stamford, CT, Appleton & Lange.**


Rapidly adapting
Action potentials
Stimulus intensity
Time


Slowly adapting
Action potentials
Stimulus intensity
Time




$$\frac{\Delta I}{I} = \text{const.}$$


Fechner's Law: Ψ=klogI
Sensation Units Ψ (JND's)
S8
S7
S6
S5
S4
S3
S2
S1
S0
ΔI
ΔI
ΔI
0
20
40
60
80
100
Stimulus Intensity

# Закон Вебера - Фехнера

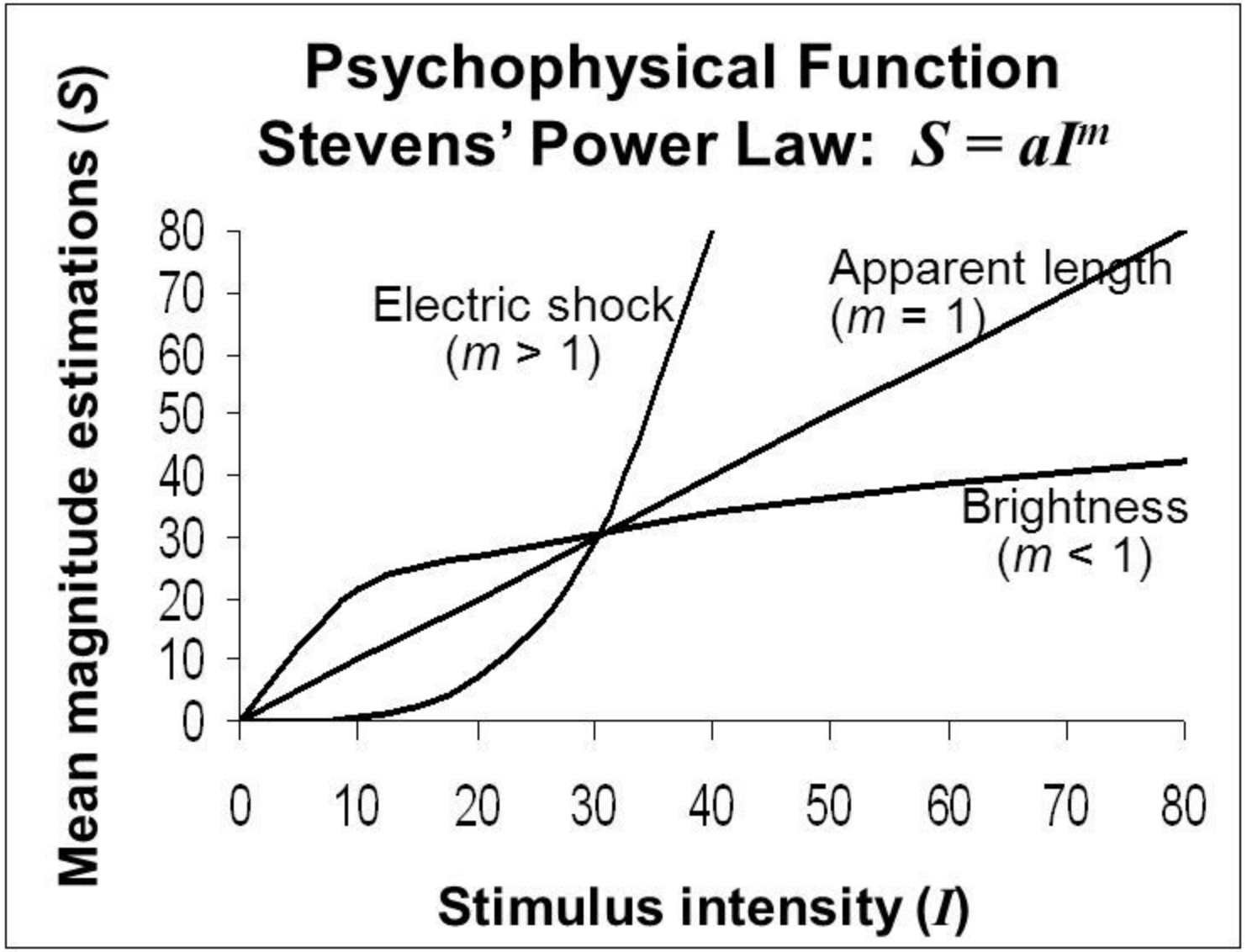
$$S = k \cdot \lg(J/J_0)$$

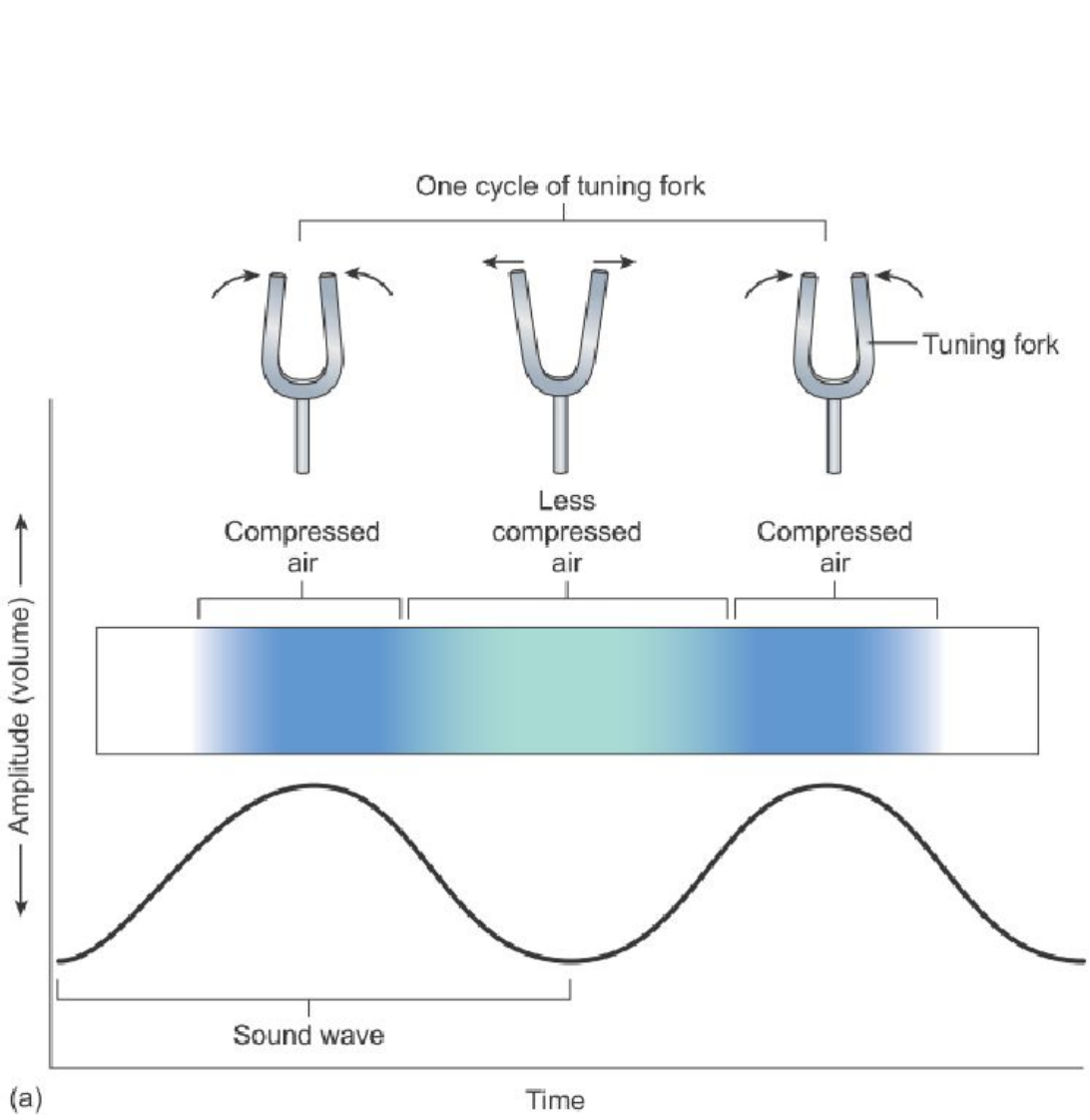
S – величина ощущения человека (интенсивность ощущения)

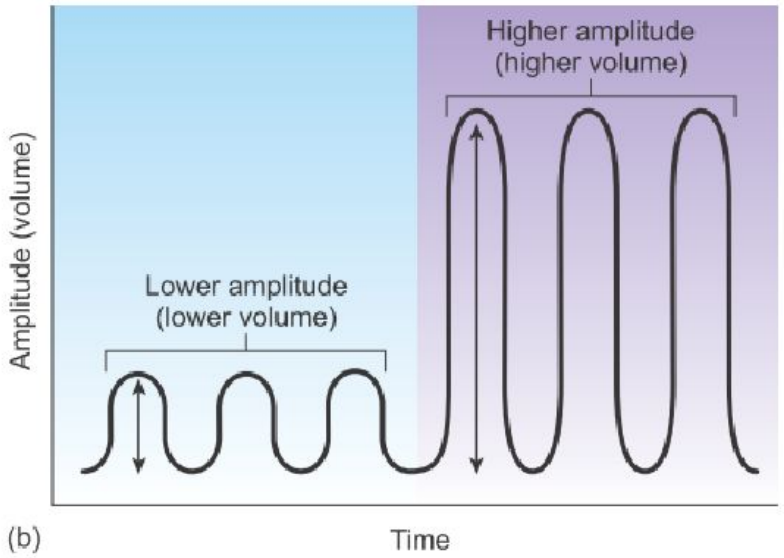
k – коэффициент пропорциональности

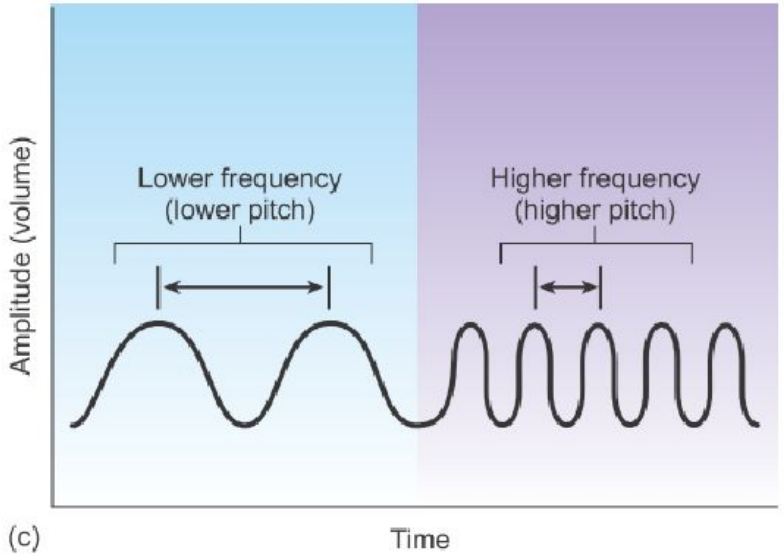
J – уровень (значение) раздражителя

$J_0$ – пороговый ощутимый уровень раздражителя

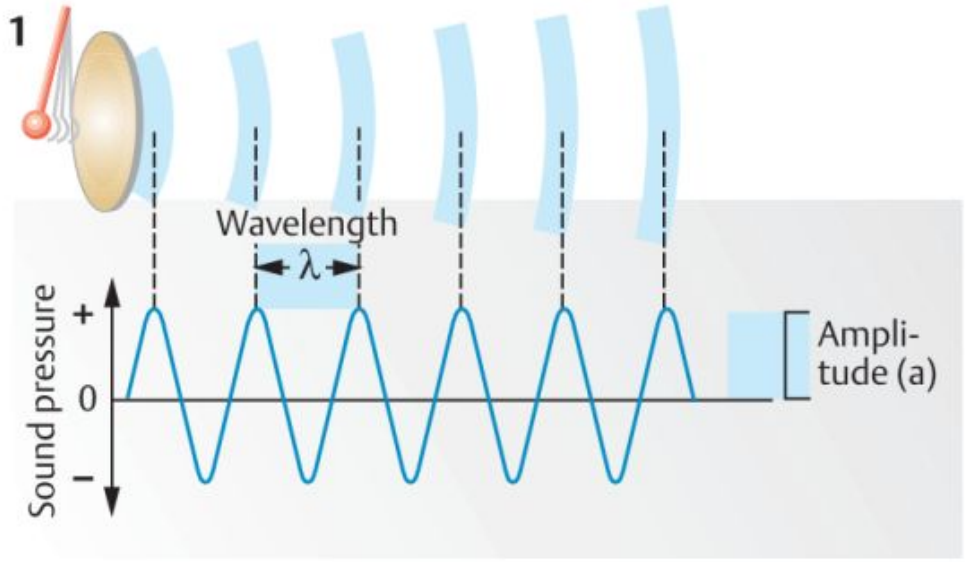

Psychophysical Function
Stevens' Power Law: $S = aI^m$
Mean magnitude estimations (S)
80
70
60
50
40
30
20
10
0
Electric shock
($m$ > 1)
Apparent length
($m$ = 1)
Brightness
($m$ < 1)
0
10
20
30
40
50
60
70
80
Stimulus intensity ($I$)

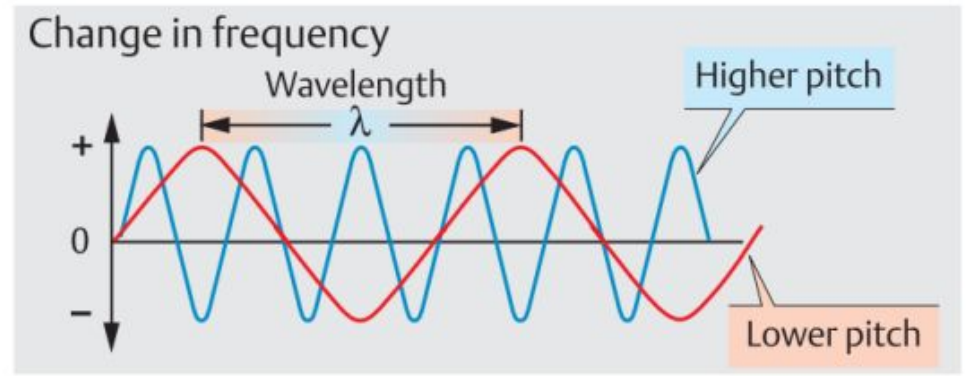

One cycle of tuning fork
Tuning fork
Compressed air
Less compressed air
Compressed air
Amplitude (volume)
Sound wave
(a)
Time

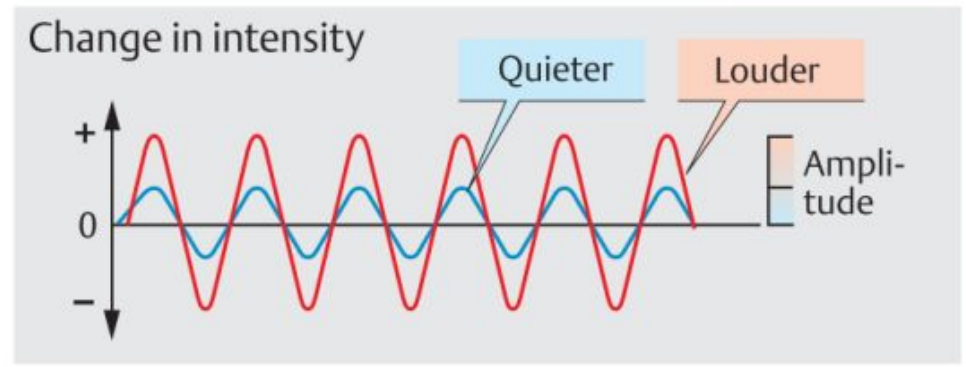

Higher amplitude (higher volume)
Lower amplitude (lower volume)
Amplitude (volume)
(b)
Time

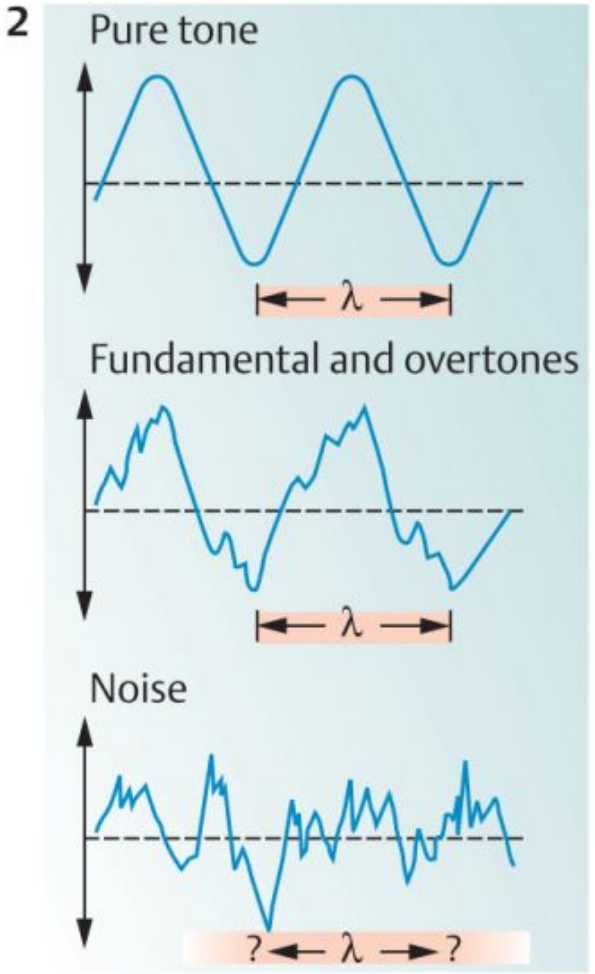

Lower frequency (lower pitch)
Higher frequency (higher pitch)
Amplitude (volume)
(c)
Time

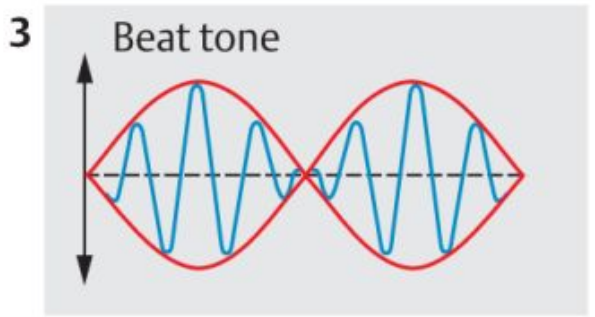
## A. Wavelength, wave amplitude and wave types

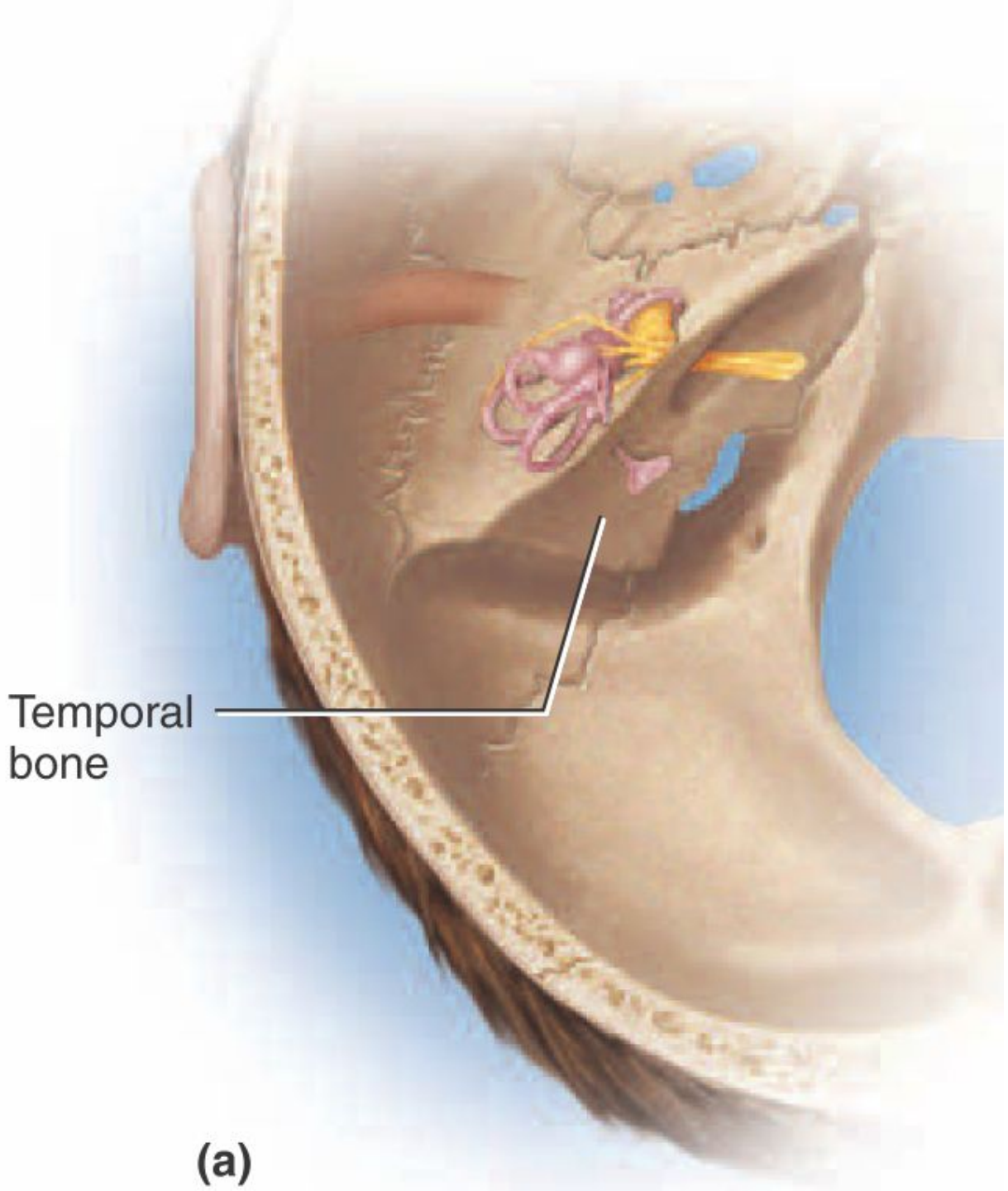


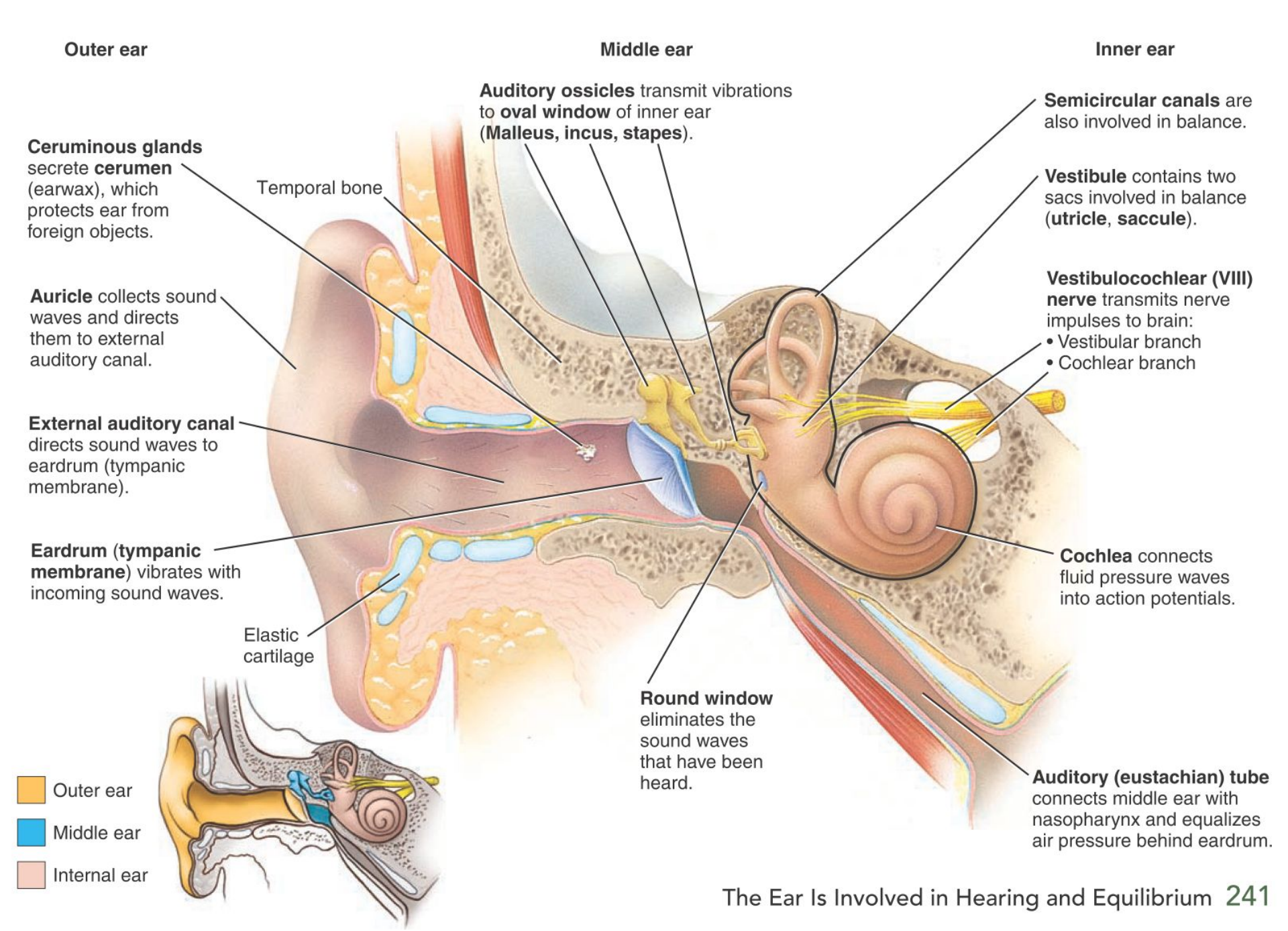



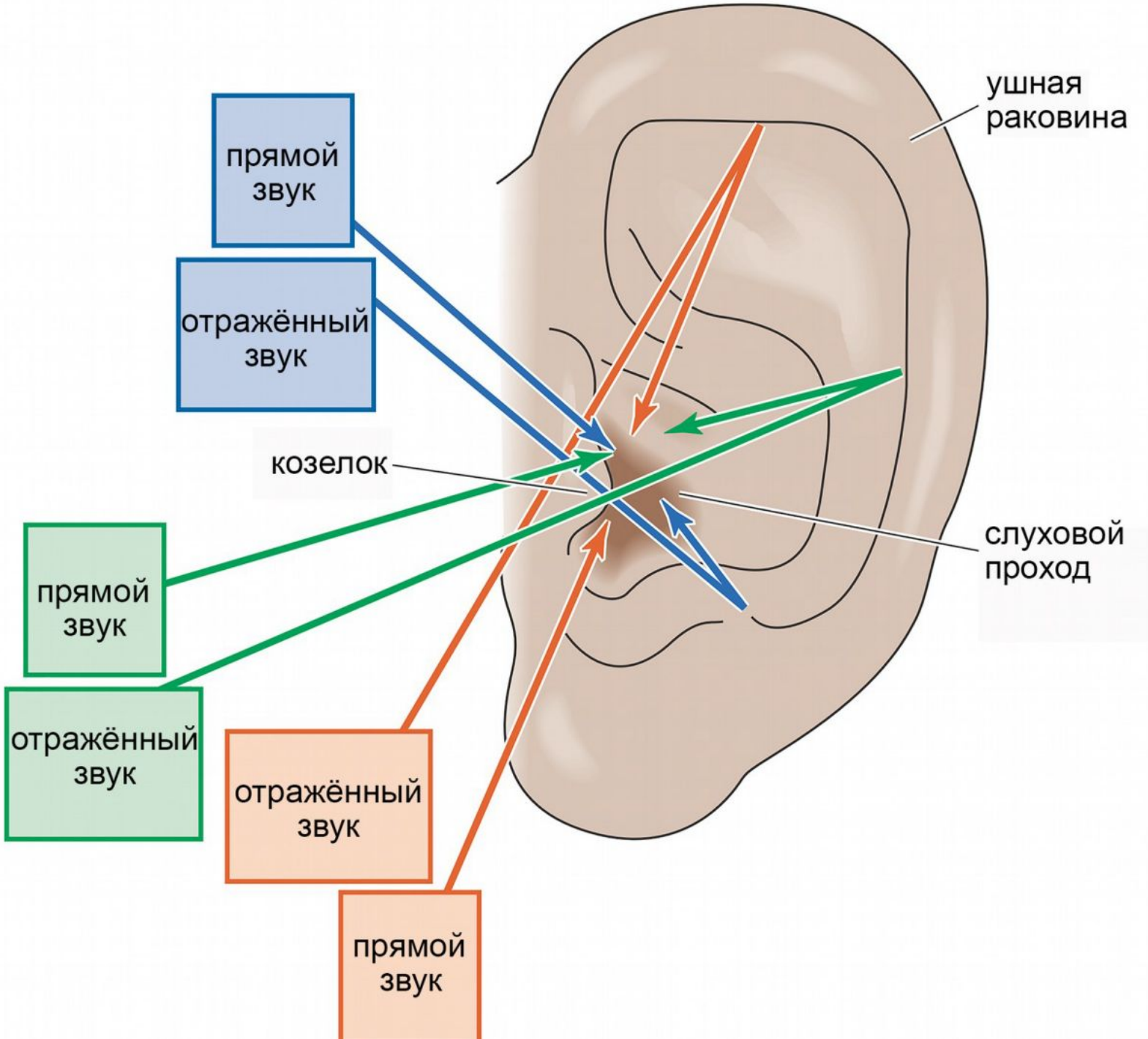



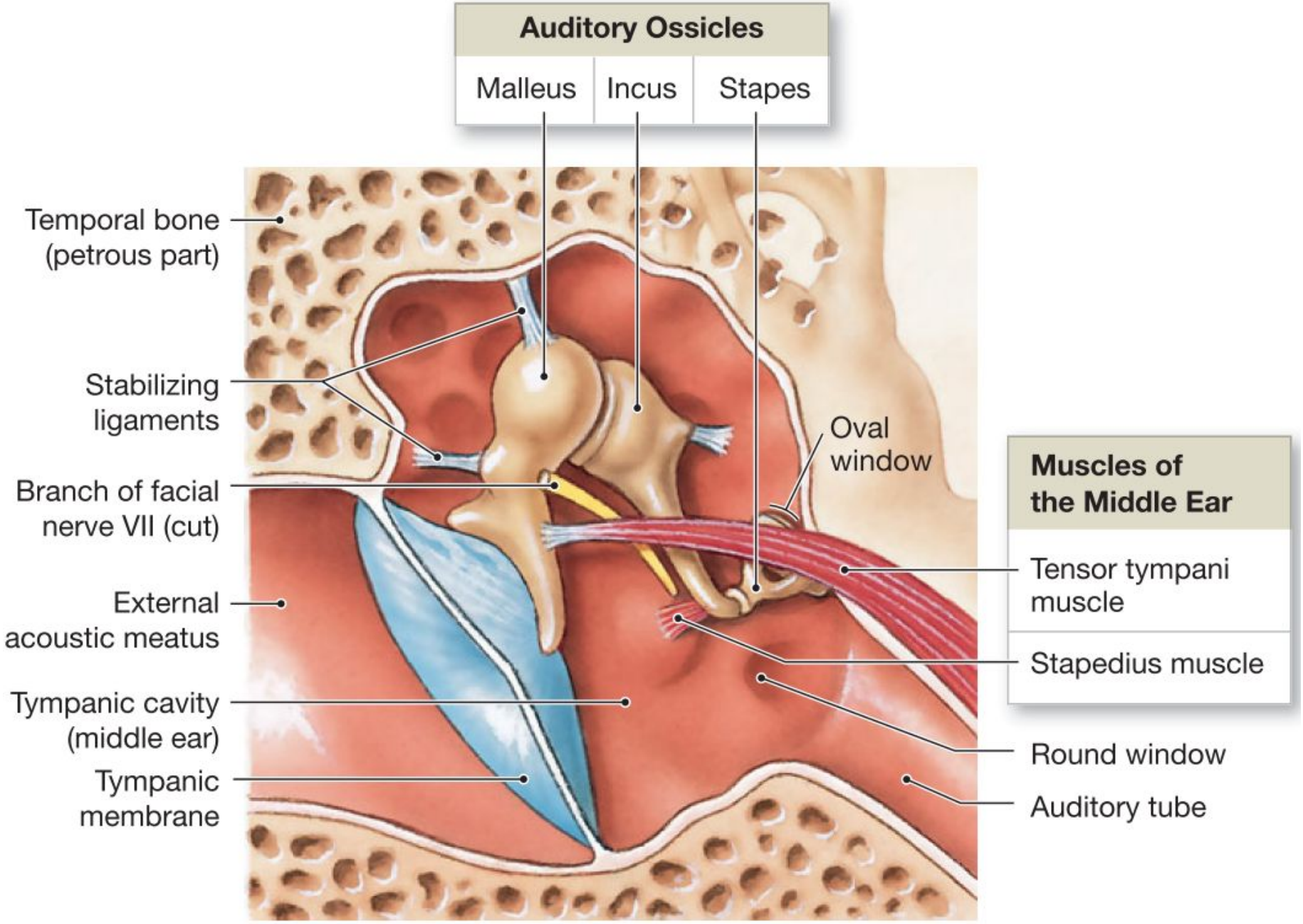



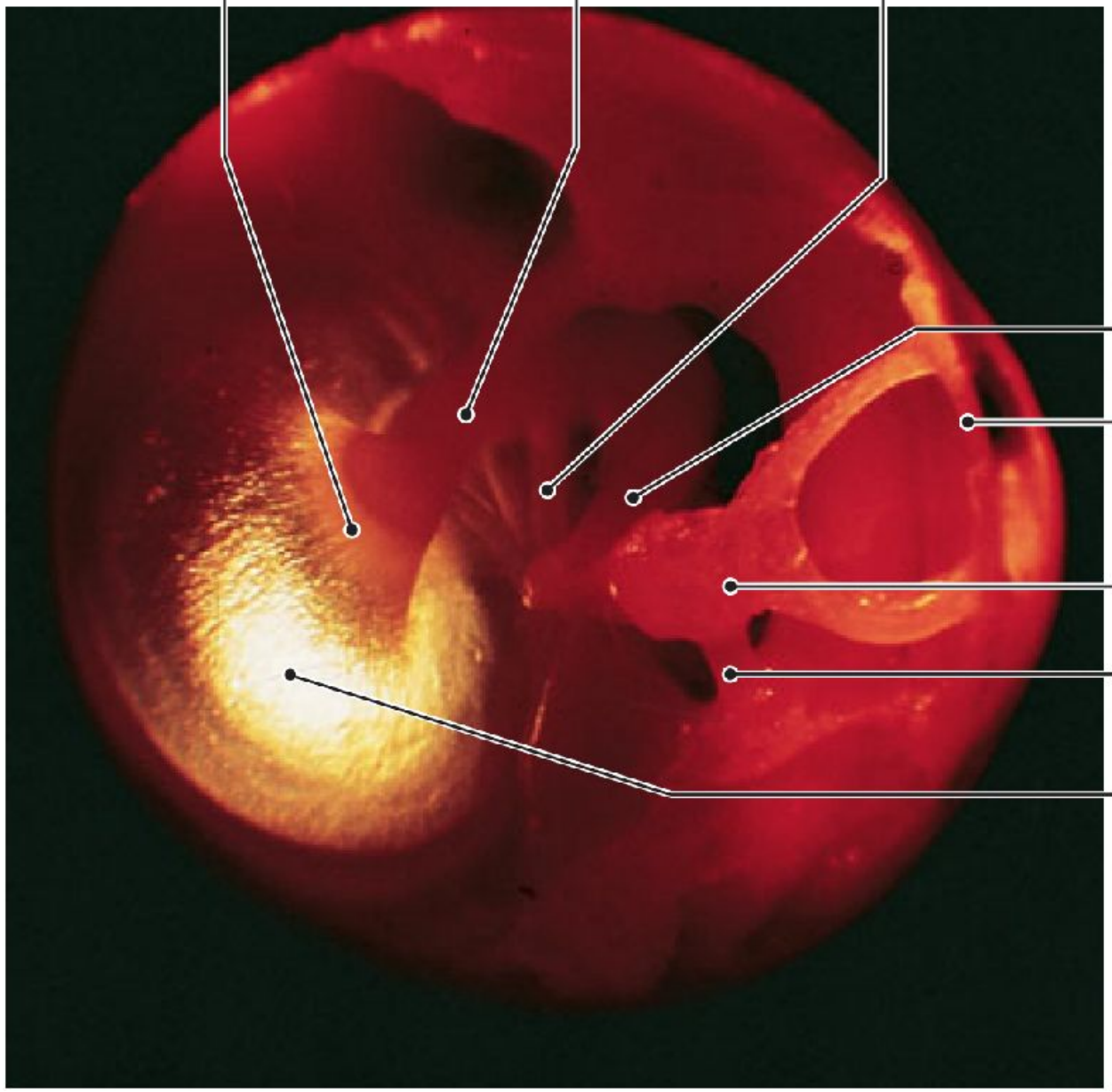


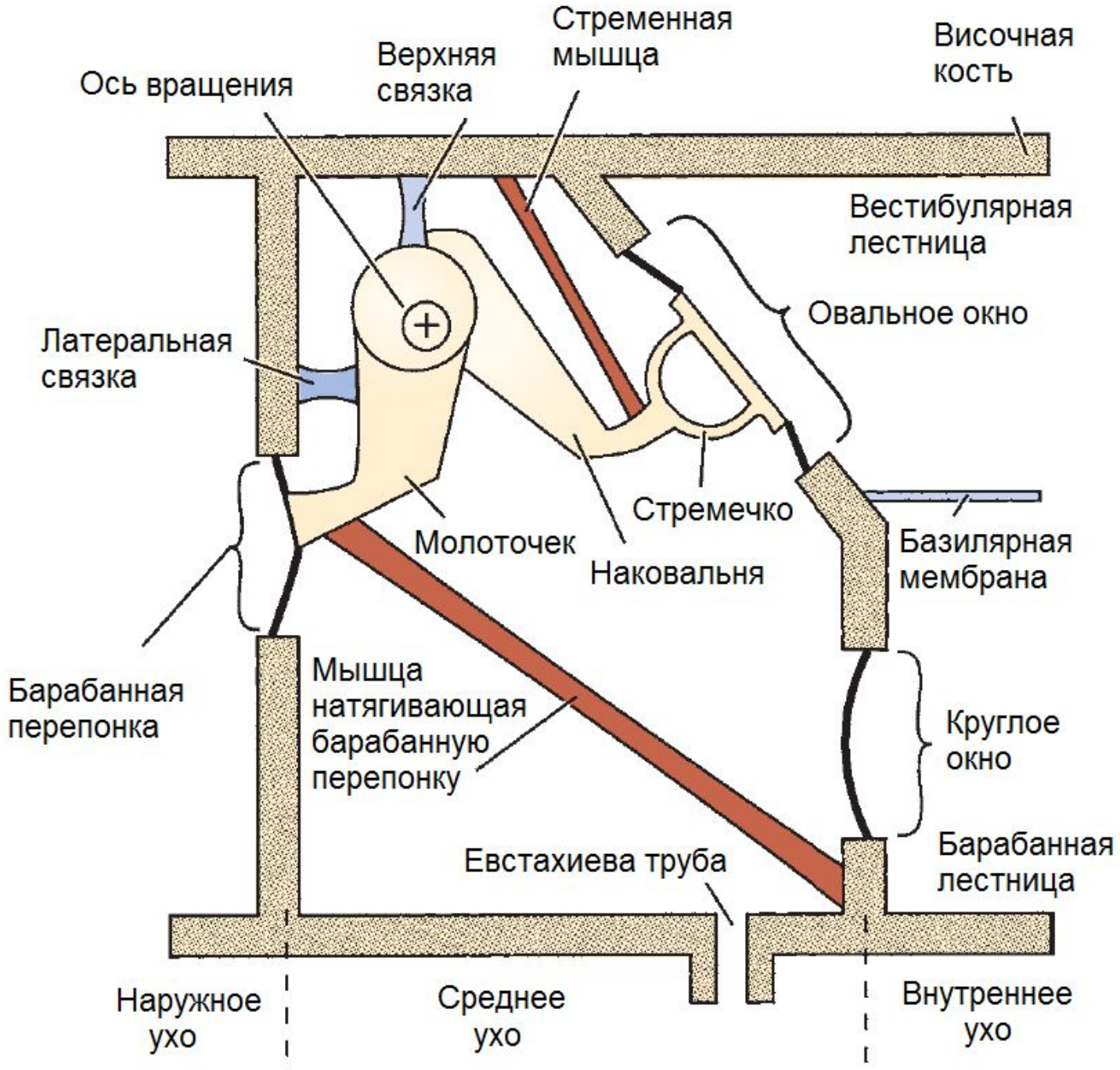

(a)

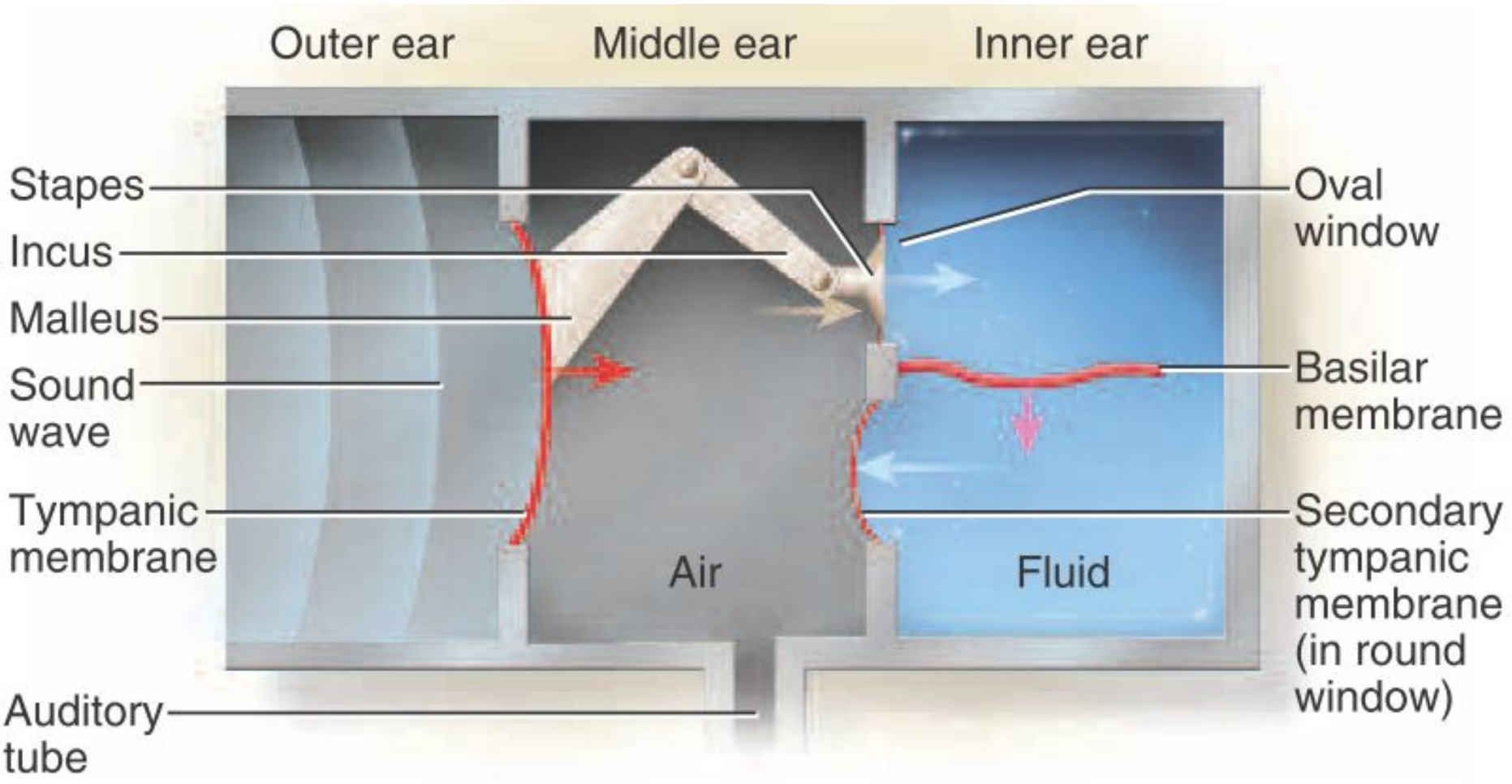

Outer ear
Middle ear
Inner ear
Auditory ossicles transmit vibrations to oval window of inner ear (Malleus, incus, stapes).
Semicircular canals are also involved in balance.
Ceruminous glands secrete cerumen (earwax), which protects ear from foreign objects.
Temporal bone
Vestibule contains two sacs involved in balance (utricle, saccule).
Auricle collects sound waves and directs them to external auditory canal.
Vestibulocochlear (VIII) nerve transmits nerve impulses to brain:
• Vestibular branch
• Cochlear branch
External auditory canal directs sound waves to eardrum (tympanic membrane).
Eardrum (tympanic membrane) vibrates with incoming sound waves.
Cochlea connects fluid pressure waves into action potentials.
Elastic cartilage
Round window eliminates the sound waves that have been heard.
Auditory (eustachian) tube connects middle ear with nasopharynx and equalizes air pressure behind eardrum.
Outer ear
Middle ear
Internal ear

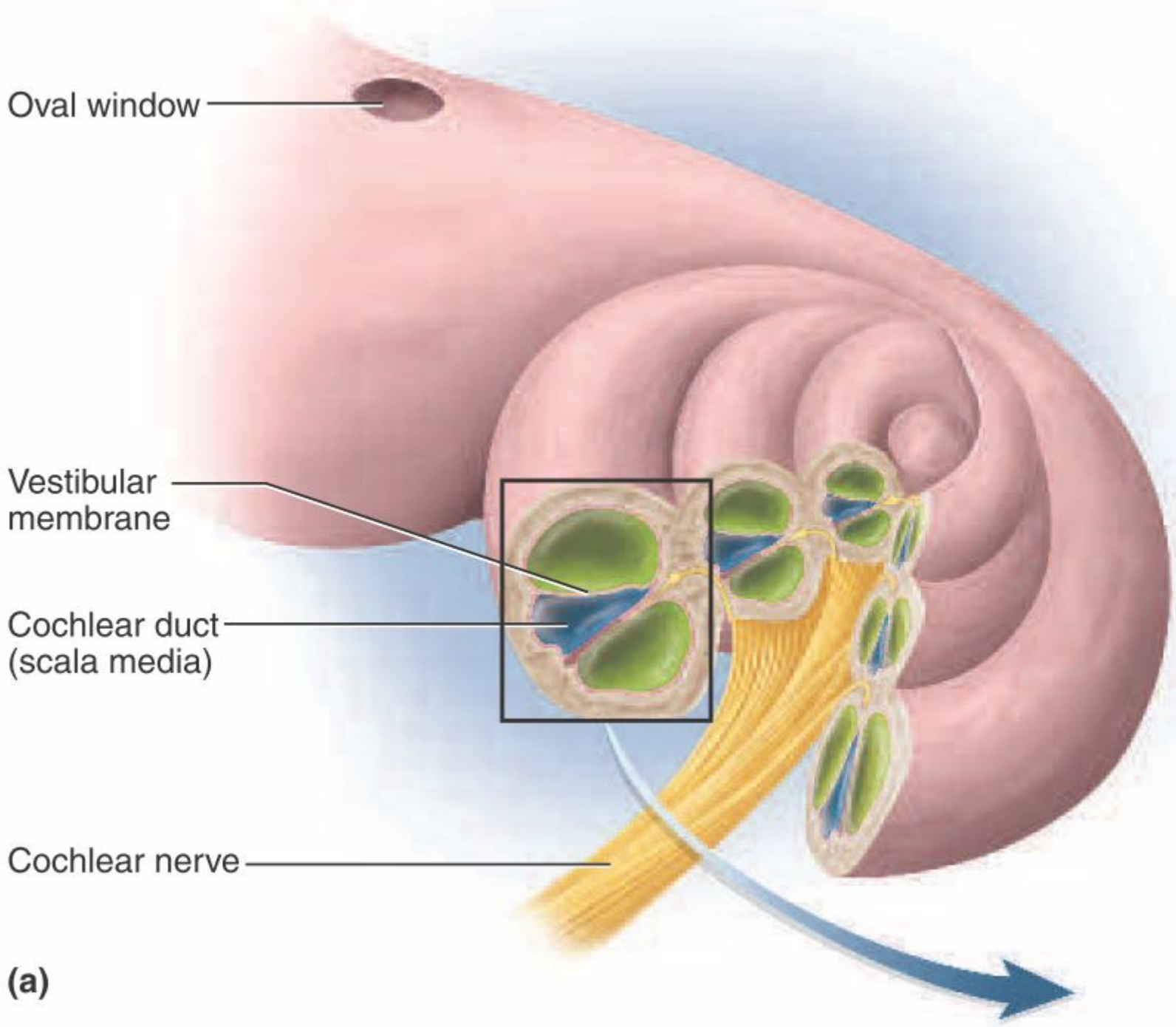

прямой звук
отражённый звук
козелок
прямой звук
отражённый звук
отражённый звук
прямой звук
ушная раковина
слуховой проход

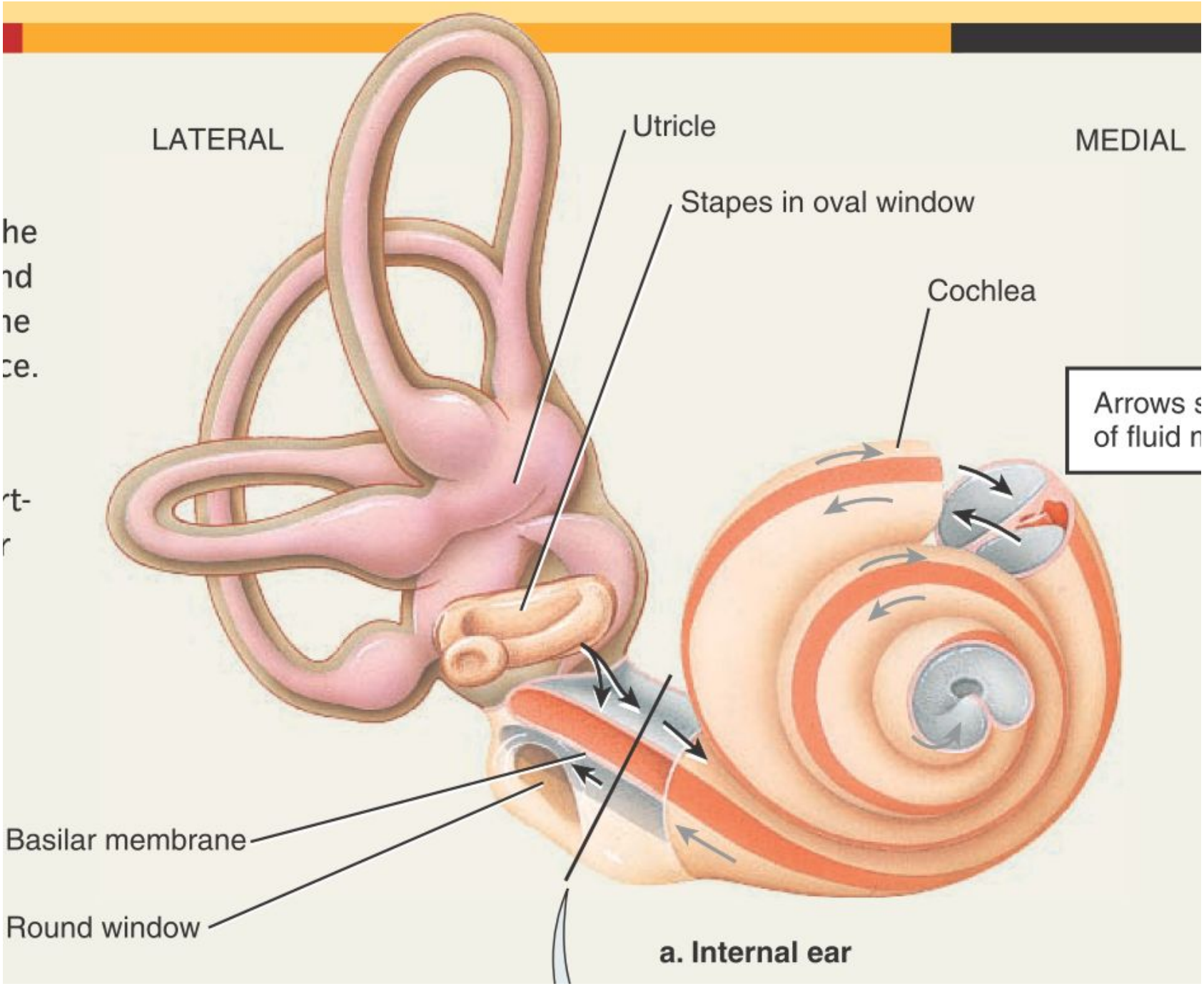

Auditory Ossicles
Malleus
Incus
Stapes
Temporal bone (petrous part)
Stabilizing ligaments
Branch of facial nerve VII (cut)
External acoustic meatus
Tympanic cavity (middle ear)
Tympanic membrane
Oval window
Muscles of the Middle Ear
Tensor tympani muscle
Stapedius muscle
Round window
Auditory tube


Malleus attached to tympanic membrane
Malleus
Tendon of tensor tympani muscle
Incus
Base of stapes at oval window
Stapes
Stapedius muscle
Inner surface of tympanic membrane

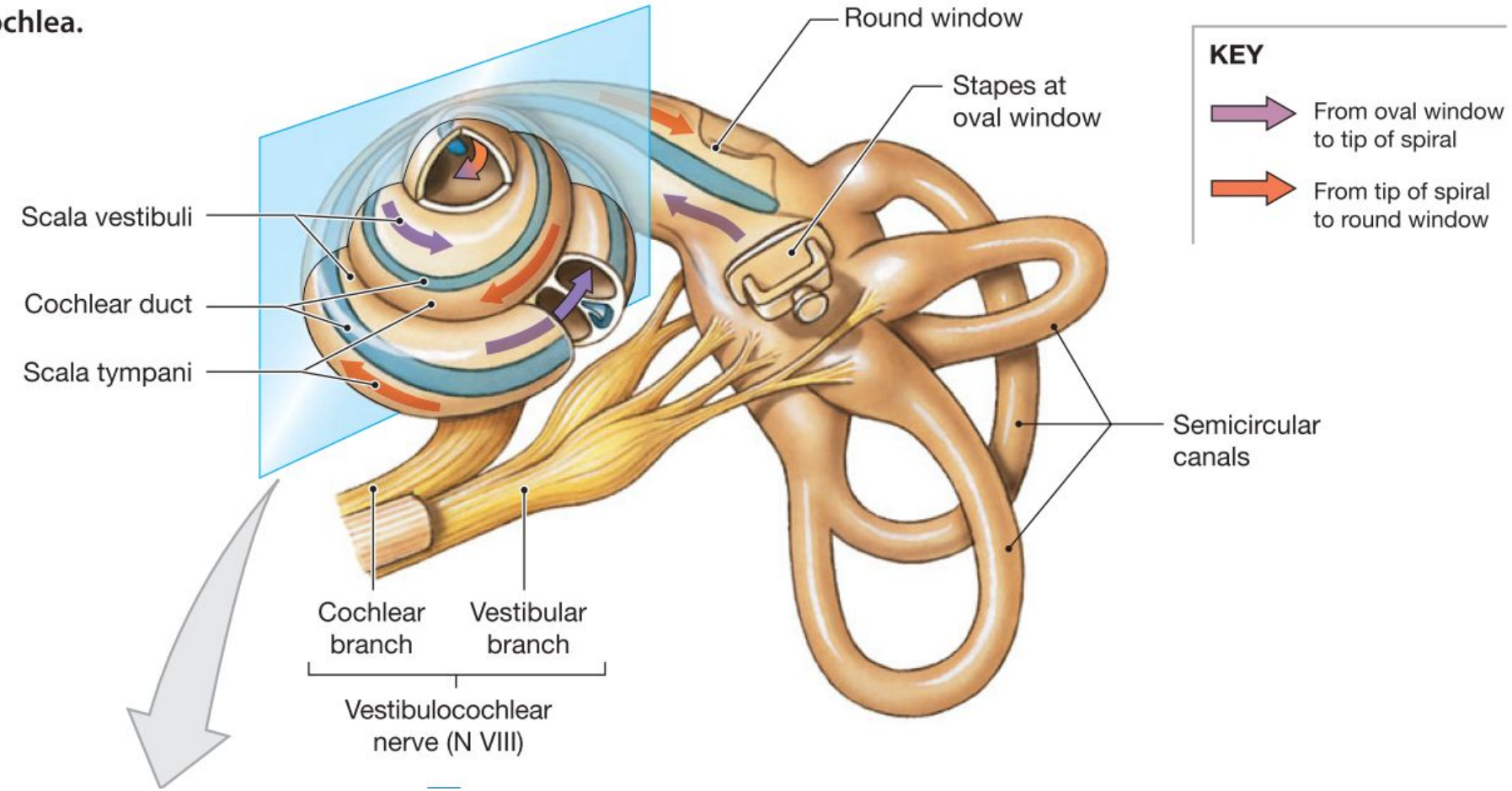

Ось вращения
Верхняя связка
Стременная мышца
Височная кость
Вестибулярная лестница
Овальное окно
Латеральная связка
Стремечко
Молоточек
Наковальня
Базилярная мембрана
Барабанная перепонка
Мышца натягивающая барабанную перепонку
Круглое окно
Барабанная лестница
Евстахиева труба
Наружное ухо
Среднее ухо
Внутреннее ухо

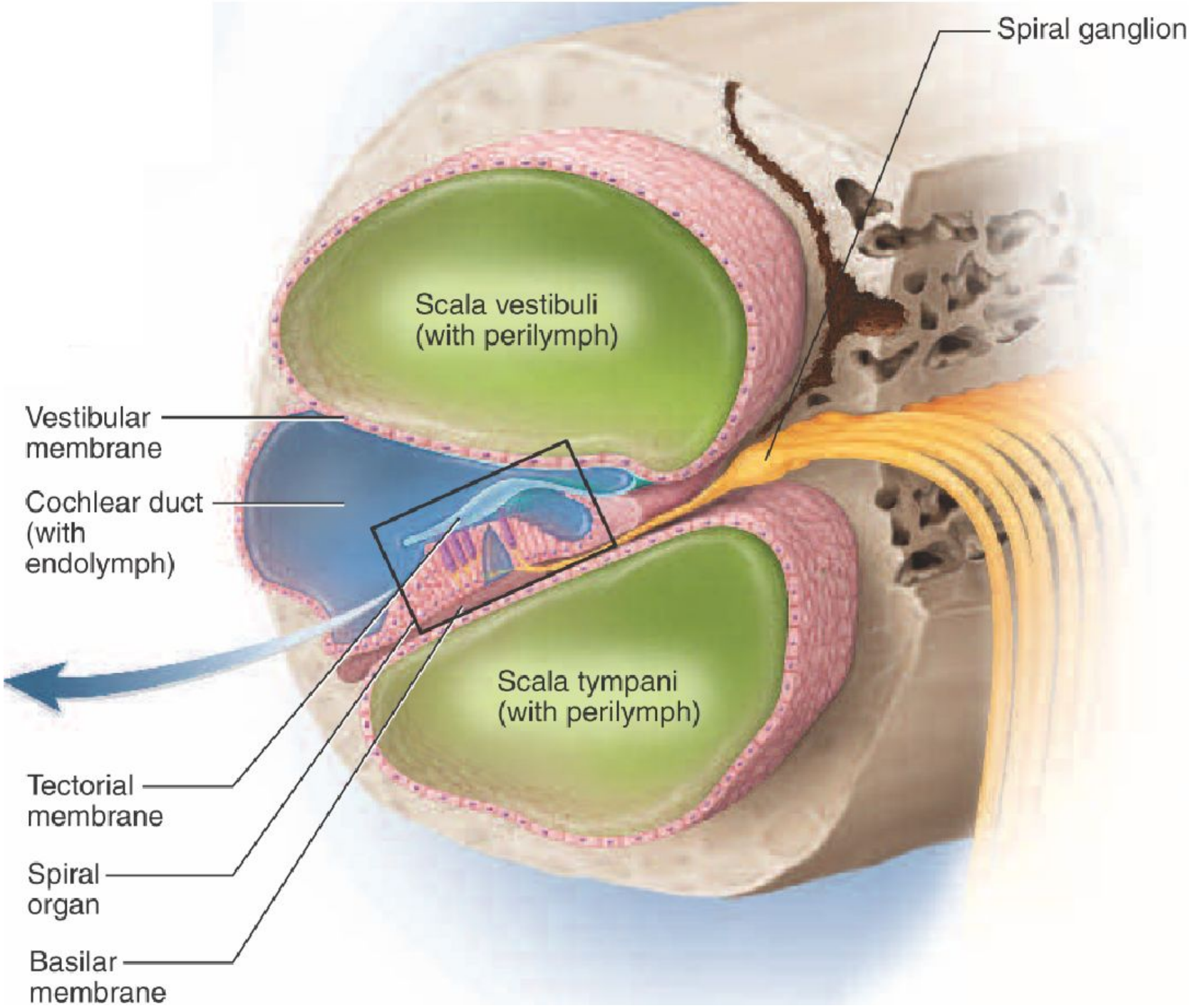

Outer ear
Middle ear
Inner ear
Stapes
Incus
Malleus
Sound wave
Tympanic membrane
Auditory tube
Oval window
Basilar membrane
Secondary tympanic membrane (in round window)
Air
Fluid

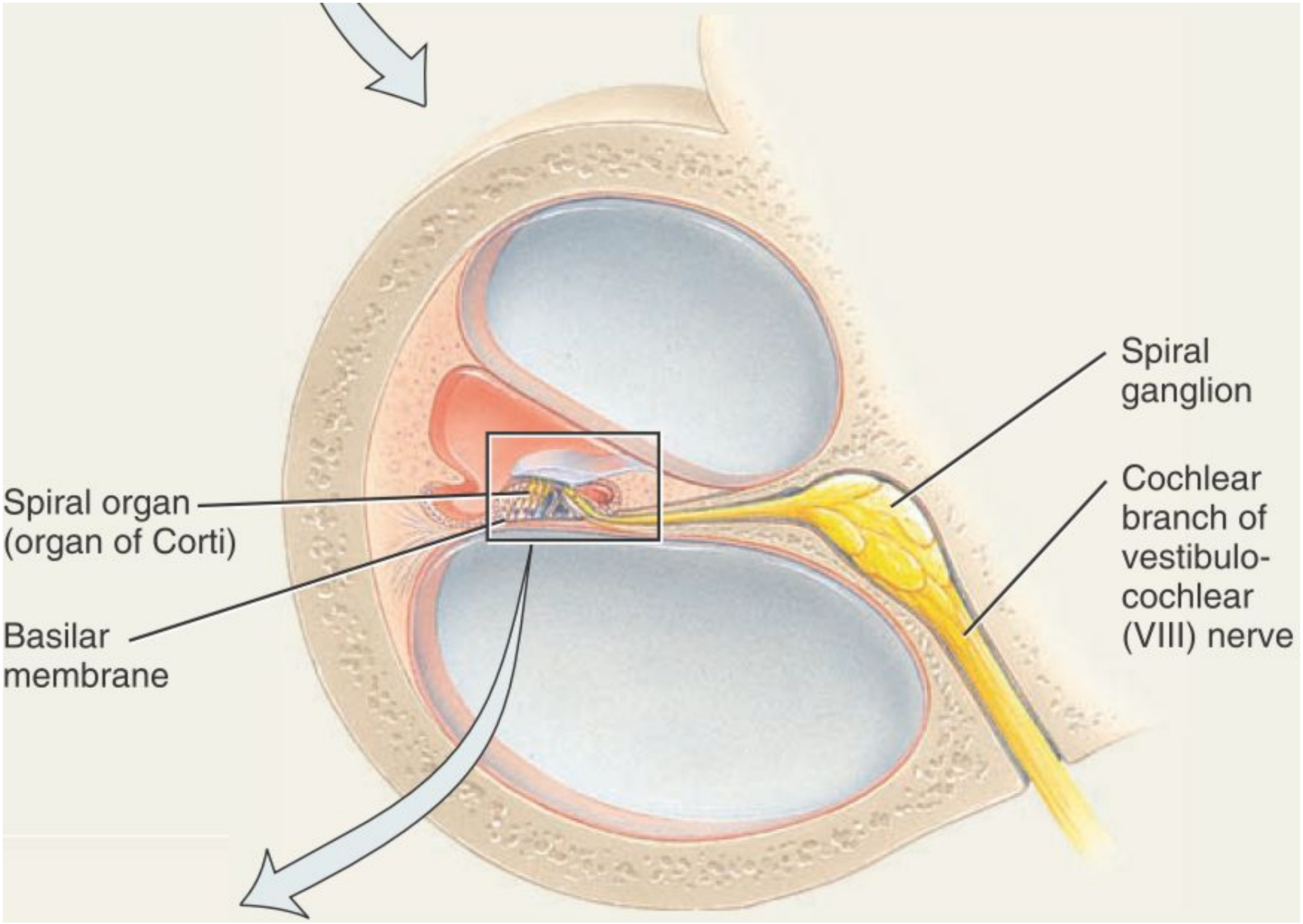

Oval window
Vestibular membrane
Cochlear duct (scala media)
Cochlear nerve
(a)

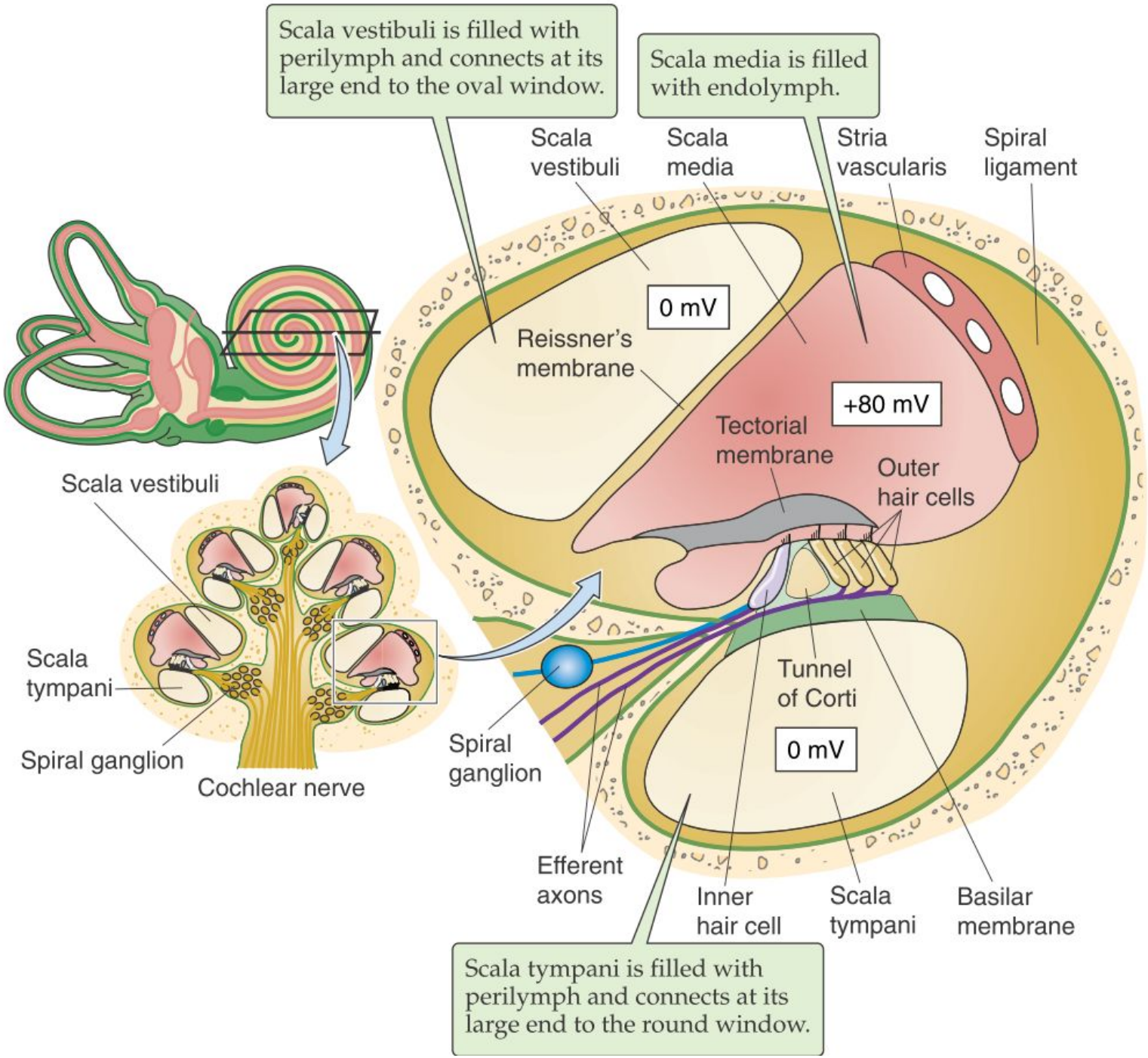

LATERAL
Utricle
MEDIAL
Stapes in oval window
Cochlea
Arrows s
of fluid m
Basilar membrane
Round window
a. Internal ear

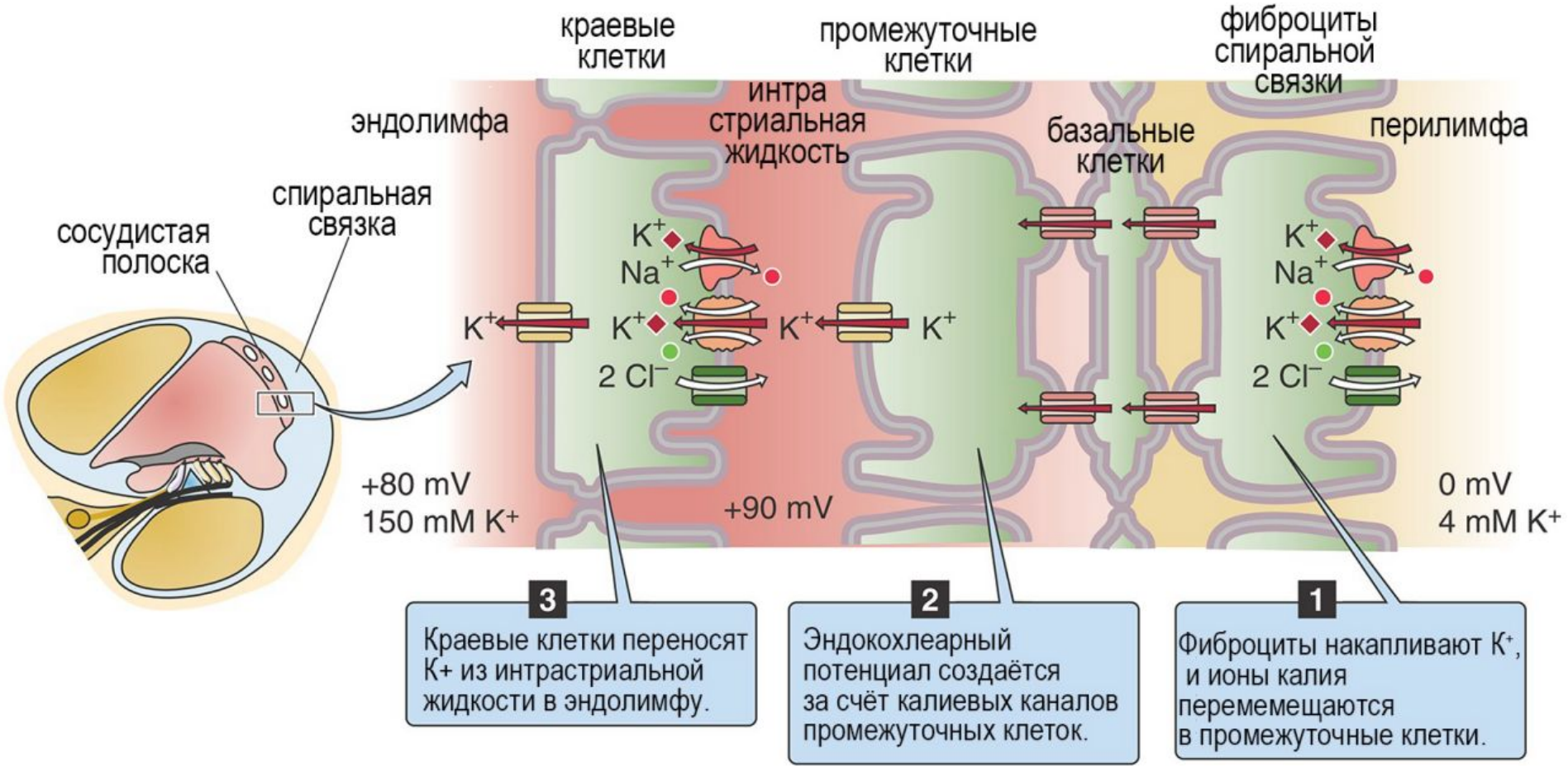
**The Cochlea.**

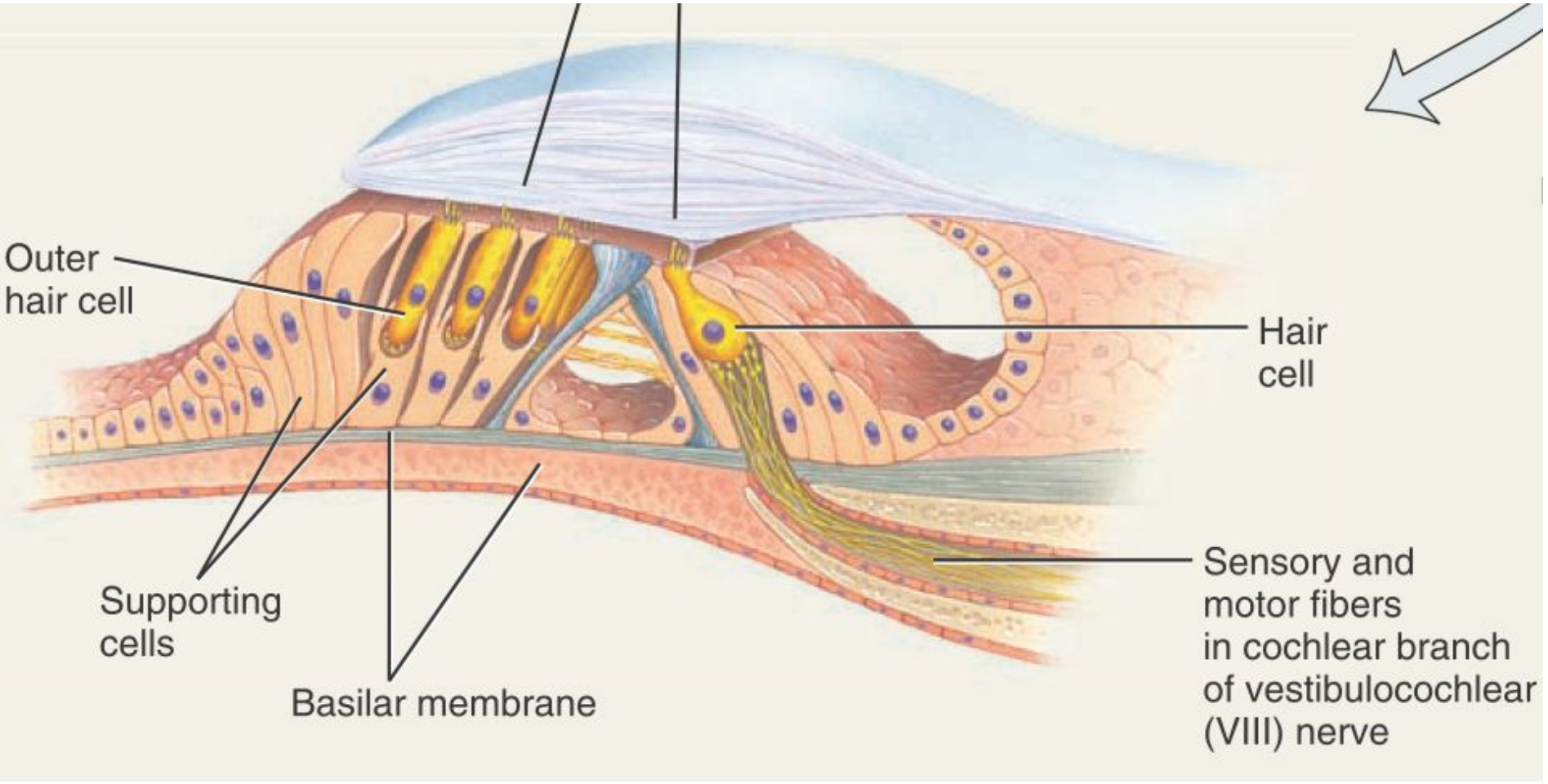

Round window
Stapes at oval window
KEY
From oval window to tip of spiral
From tip of spiral to round window
Scala vestibuli
Cochlear duct
Scala tympani
Semicircular canals
Cochlear branch
Vestibular branch
Vestibulocochlear nerve (N VIII)

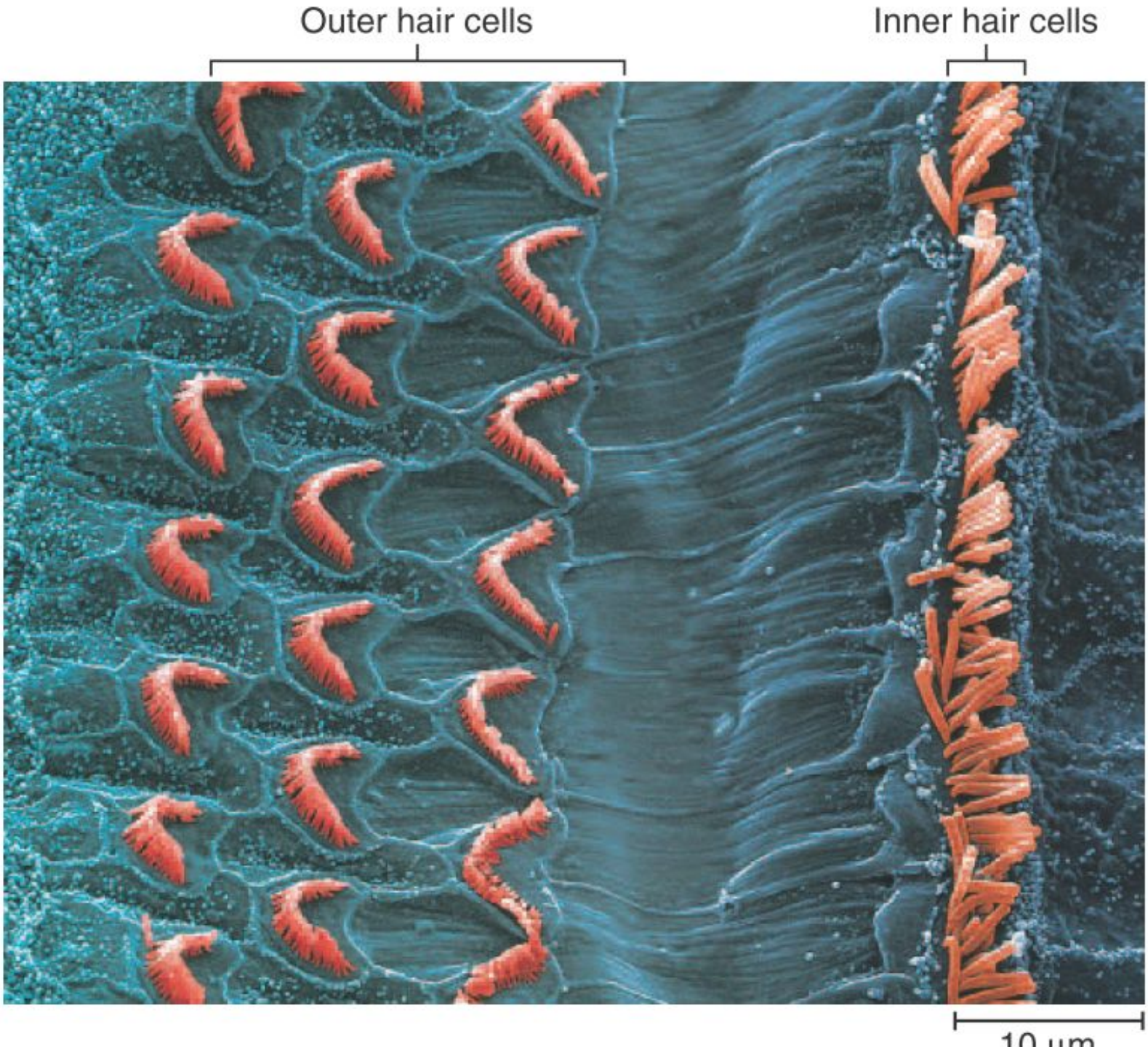

Spiral ganglion
Scala vestibuli
(with perilymph)
Vestibular
membrane
Cochlear duct
(with
endolymph)
Scala tympani
(with perilymph)
Tectorial
membrane
Spiral
organ
Basilar
membrane

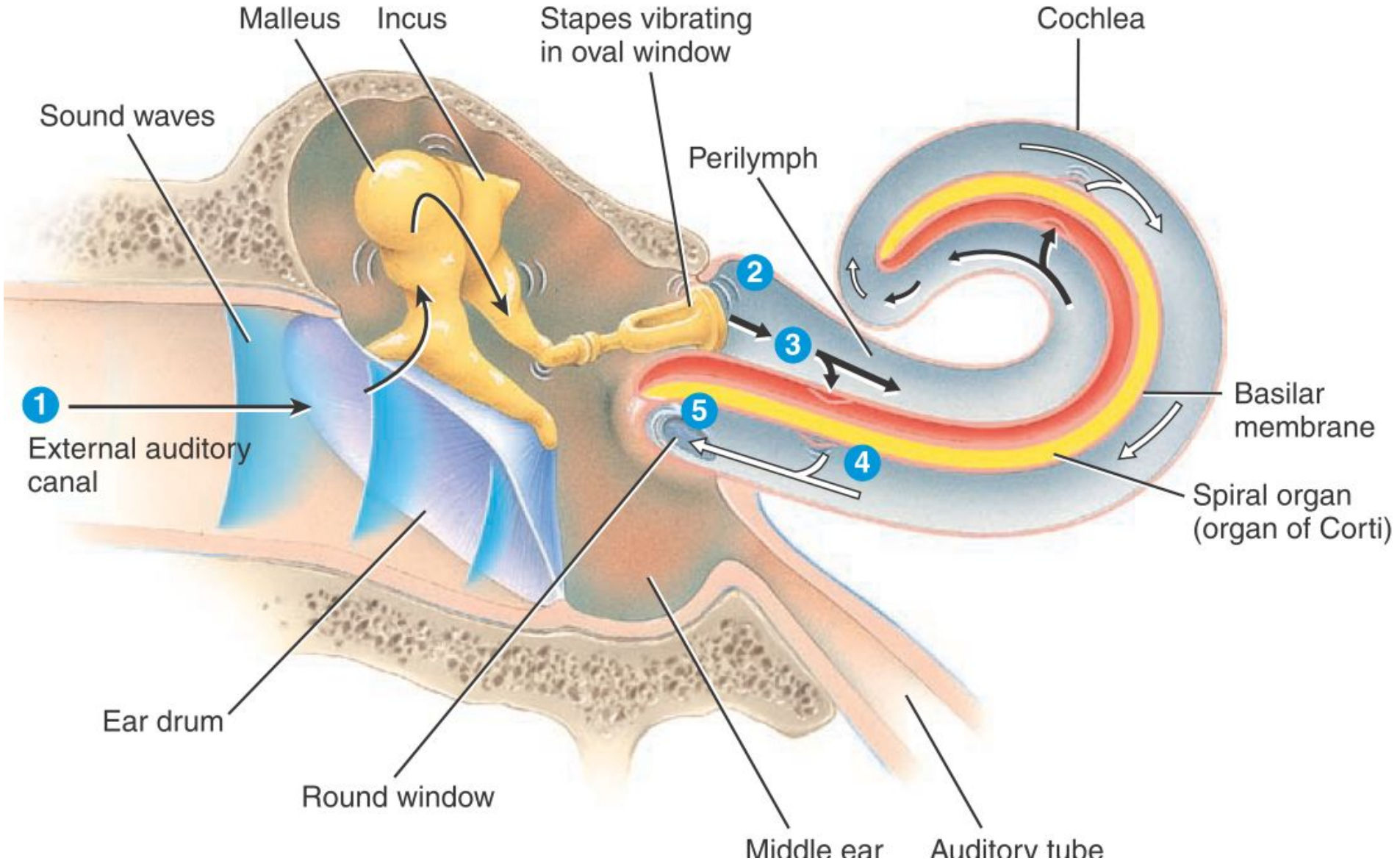

Spiral ganglion
Cochlear branch of vestibulo-cochlear (VIII) nerve
Spiral organ (organ of Corti)
Basilar membrane

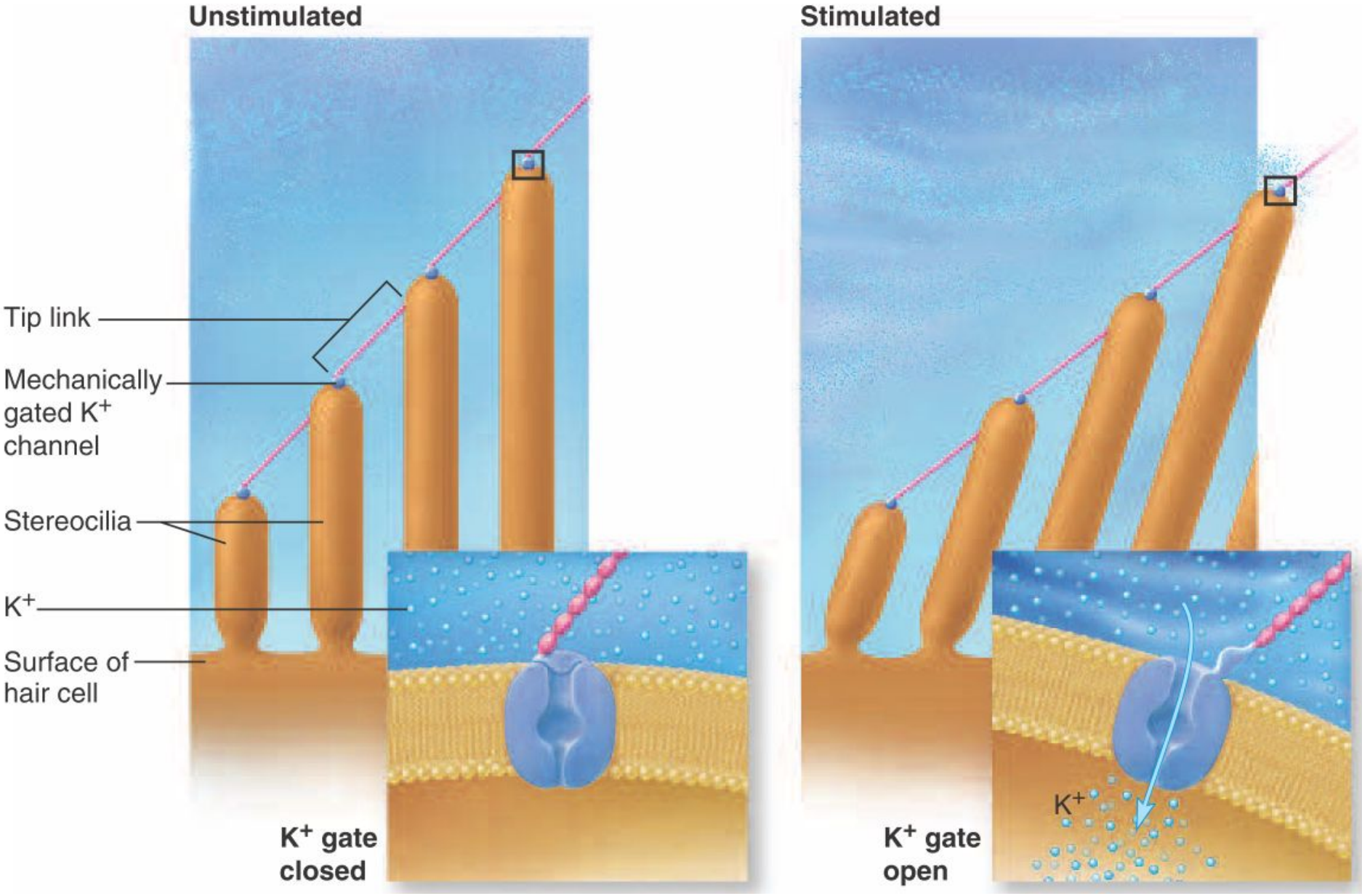

Scala vestibuli is filled with perilymph and connects at its large end to the oval window.
Scala media is filled with endolymph.
Scala vestibuli
Scala media
Stria vascularis
Spiral ligament
0 mV
Reissner's membrane
+80 mV
Tectorial membrane
Outer hair cells
Scala vestibuli
Scala tympani
Spiral ganglion
Cochlear nerve
Spiral ganglion
Tunnel of Corti
0 mV
Efferent axons
Inner hair cell
Scala tympani
Basilar membrane
Scala tympani is filled with perilymph and connects at its large end to the round window.

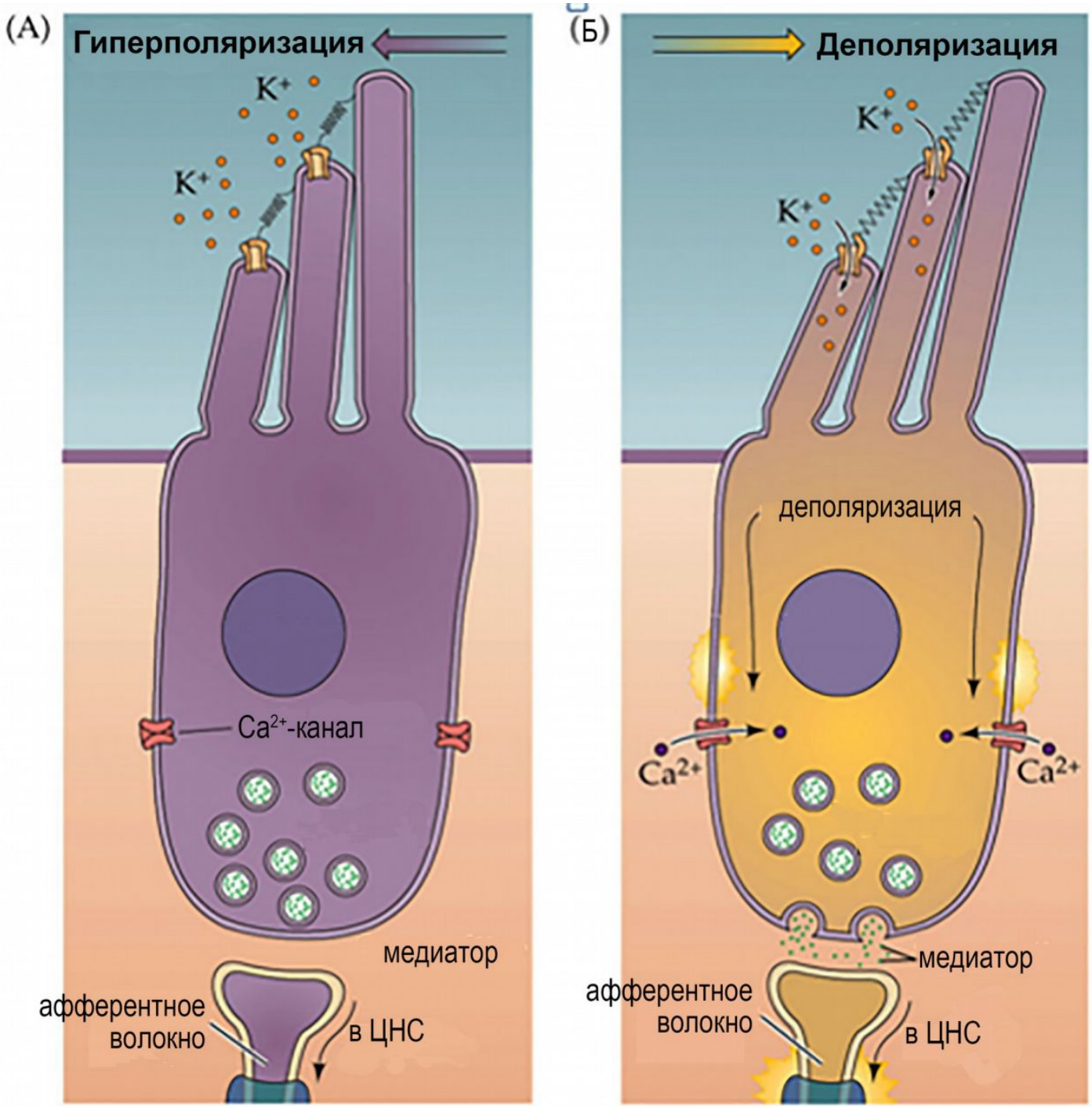

краевые клетки
промежуточные клетки
фиброциты спиральной связки
эндолимфа
интра стриальная жидкость
базальные клетки
перилимфа
спиральная связка
сосудистая полоска
K+
Na+
2 Cl−
+80 mV
150 mM K+
+90 mV
0 mV
4 mM K+
3
Краевые клетки переносят К+ из интрастриальной жидкости в эндолимфу.
2
Эндокохлеарный потенциал создаётся за счёт калиевых каналов промежуточных клеток.
1
Фиброциты накапливают К+, и ионы калия перемемещаются в промежуточные клетки.

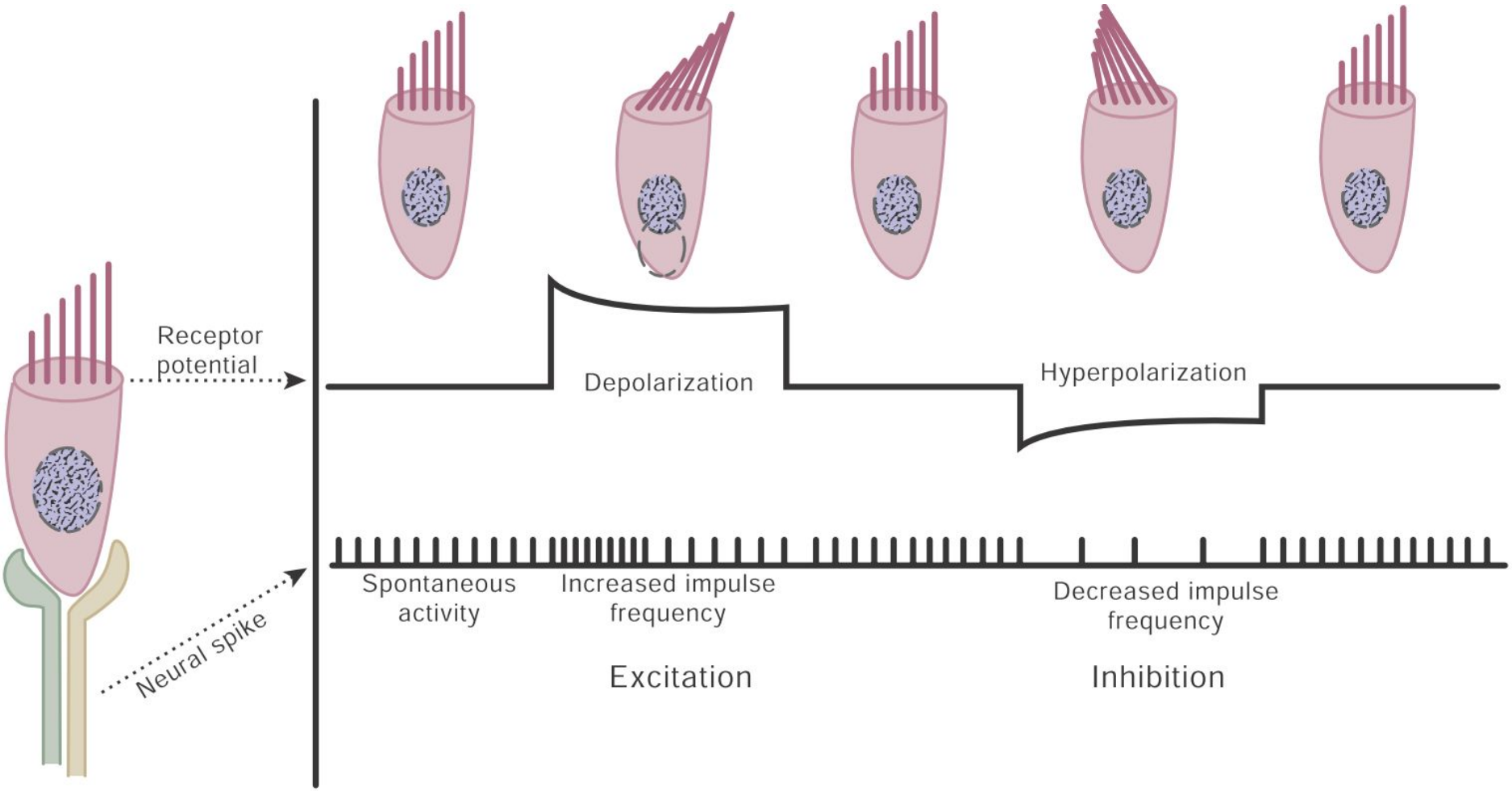

Outer
hair cell
Hair
cell
Supporting
cells
Basilar membrane
Sensory and
motor fibers
in cochlear branch
of vestibulocochlear
(VIII) nerve


Outer hair cells
Inner hair cells
10 µm

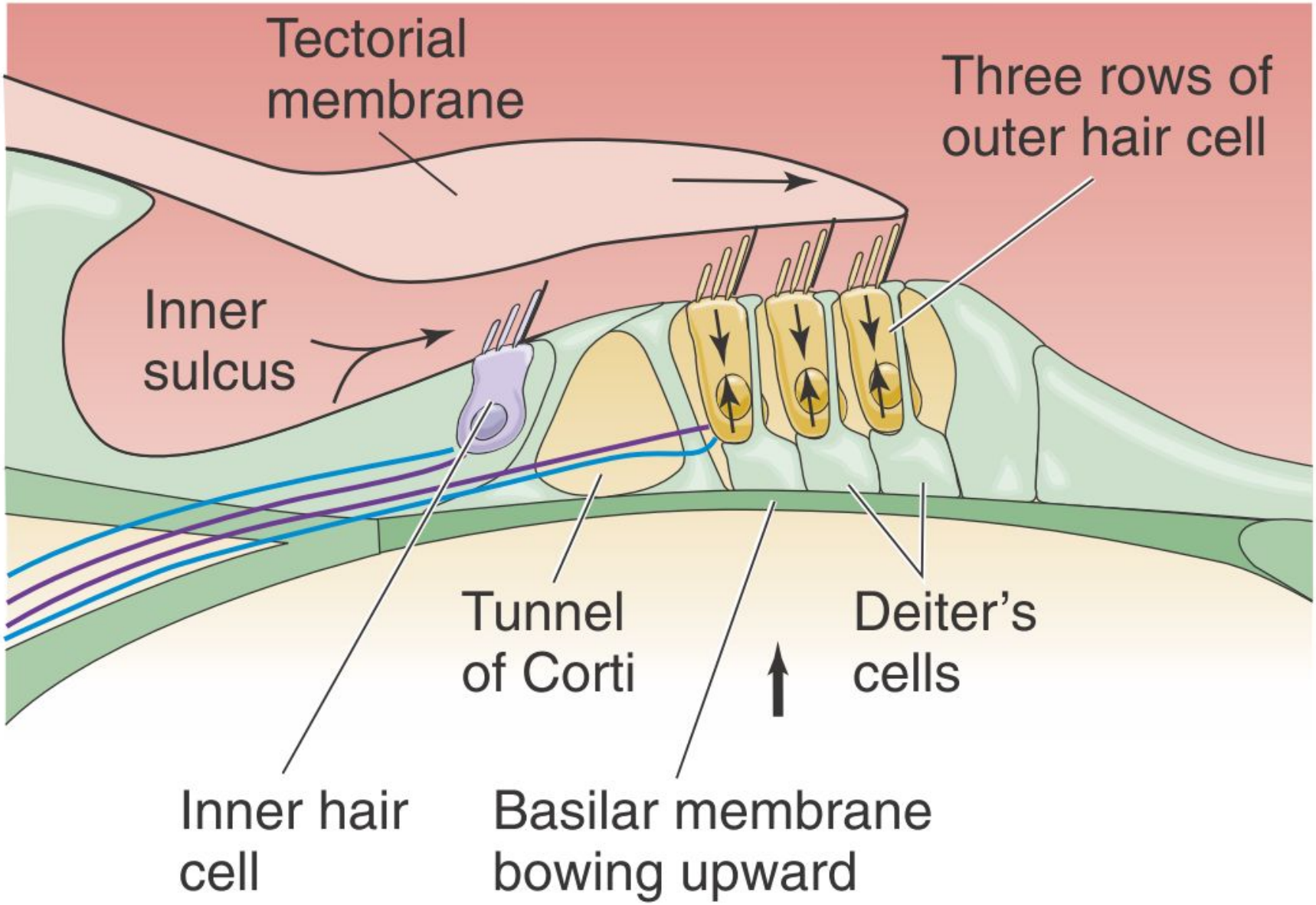

Malleus
Incus
Stapes vibrating in oval window
Cochlea
Sound waves
Perilymph
2
3
1
5
4
Basilar membrane
External auditory canal
Spiral organ (organ of Corti)
Ear drum
Round window
Middle ear
Auditory tube

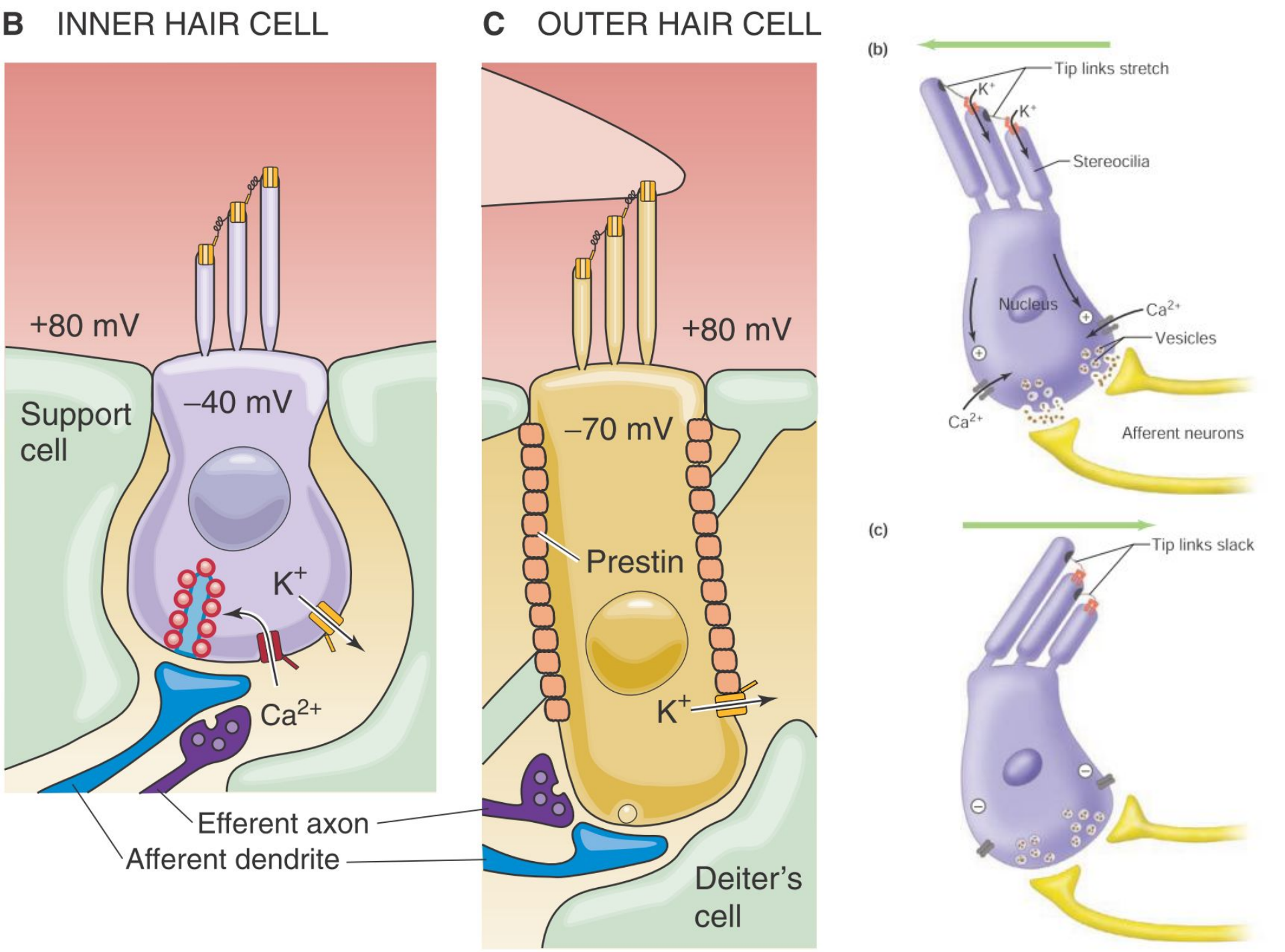

Unstimulated
Stimulated
Tip link
Mechanically gated K+ channel
Stereocilia
K+
Surface of hair cell
K+ gate closed
K+ gate open
K+

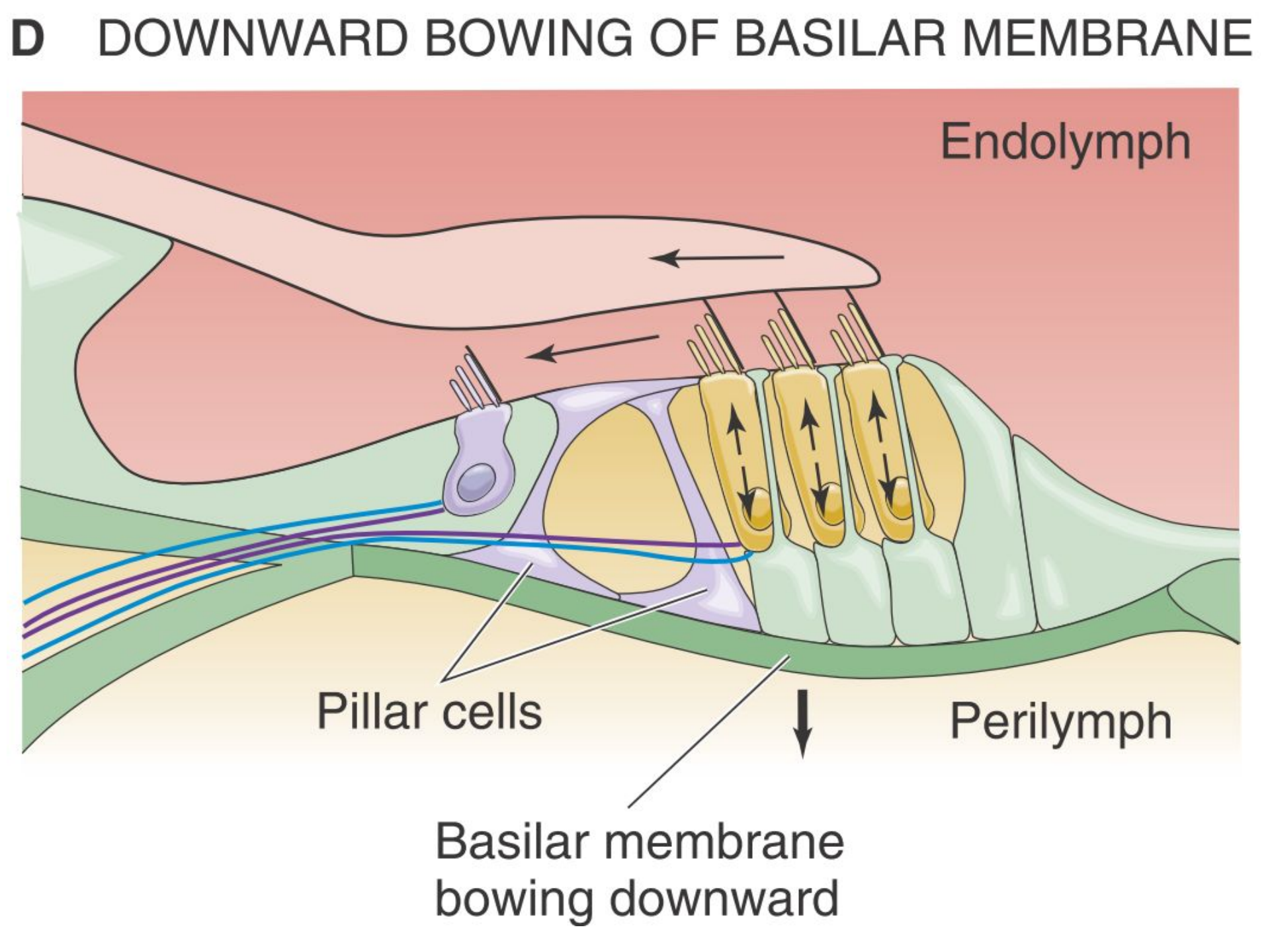

(А)
Гиперполяризация
K+
K+
Ca2+-канал
медиатор
афферентное волокно
в ЦНС
(Б)
Деполяризация
K+
K+
деполяризация
Ca2+
Ca2+
медиатор
афферентное волокно
в ЦНС

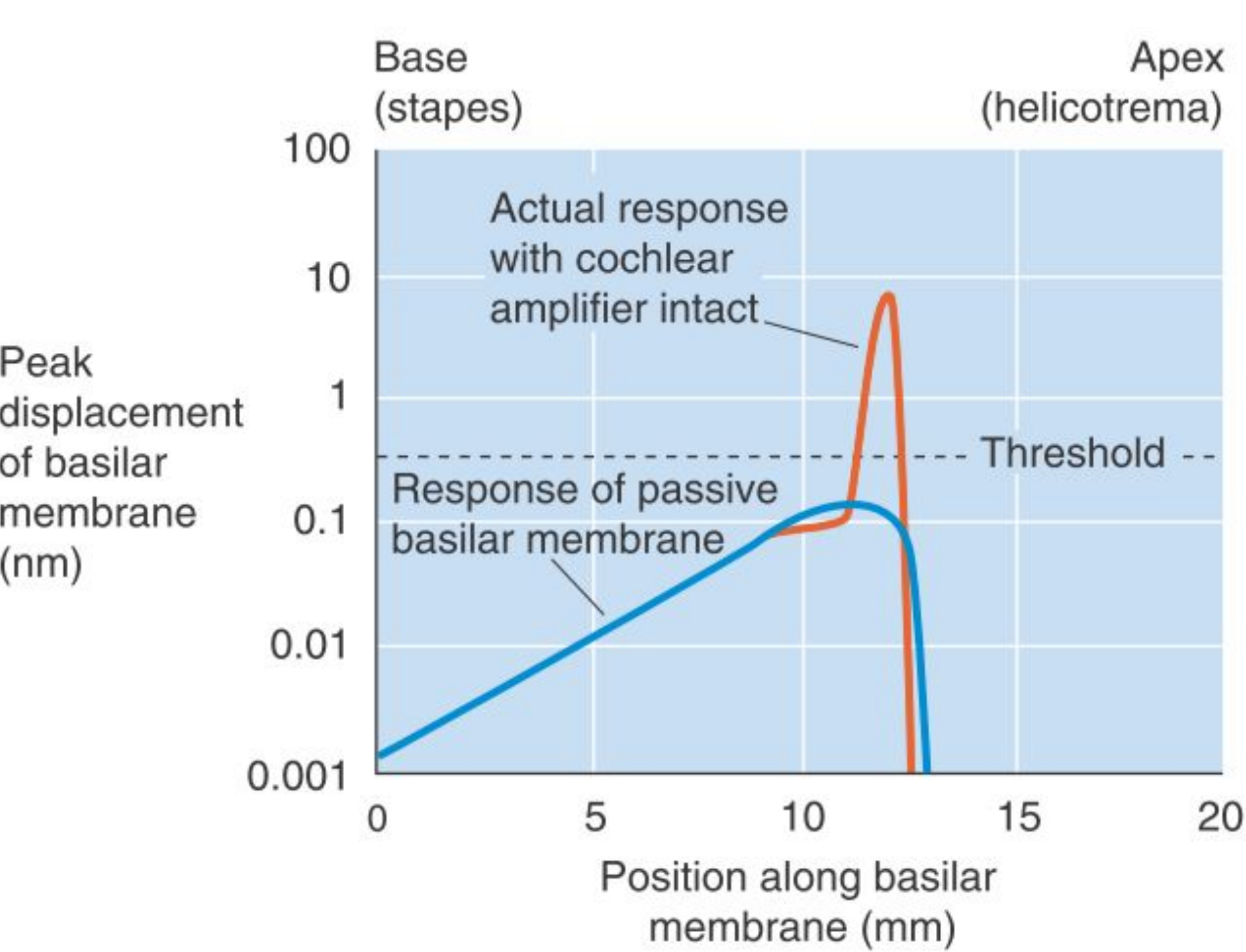

Receptor potential
Depolarization
Hyperpolarization
Neural spike
Spontaneous activity
Increased impulse frequency
Decreased impulse frequency
Excitation
Inhibition

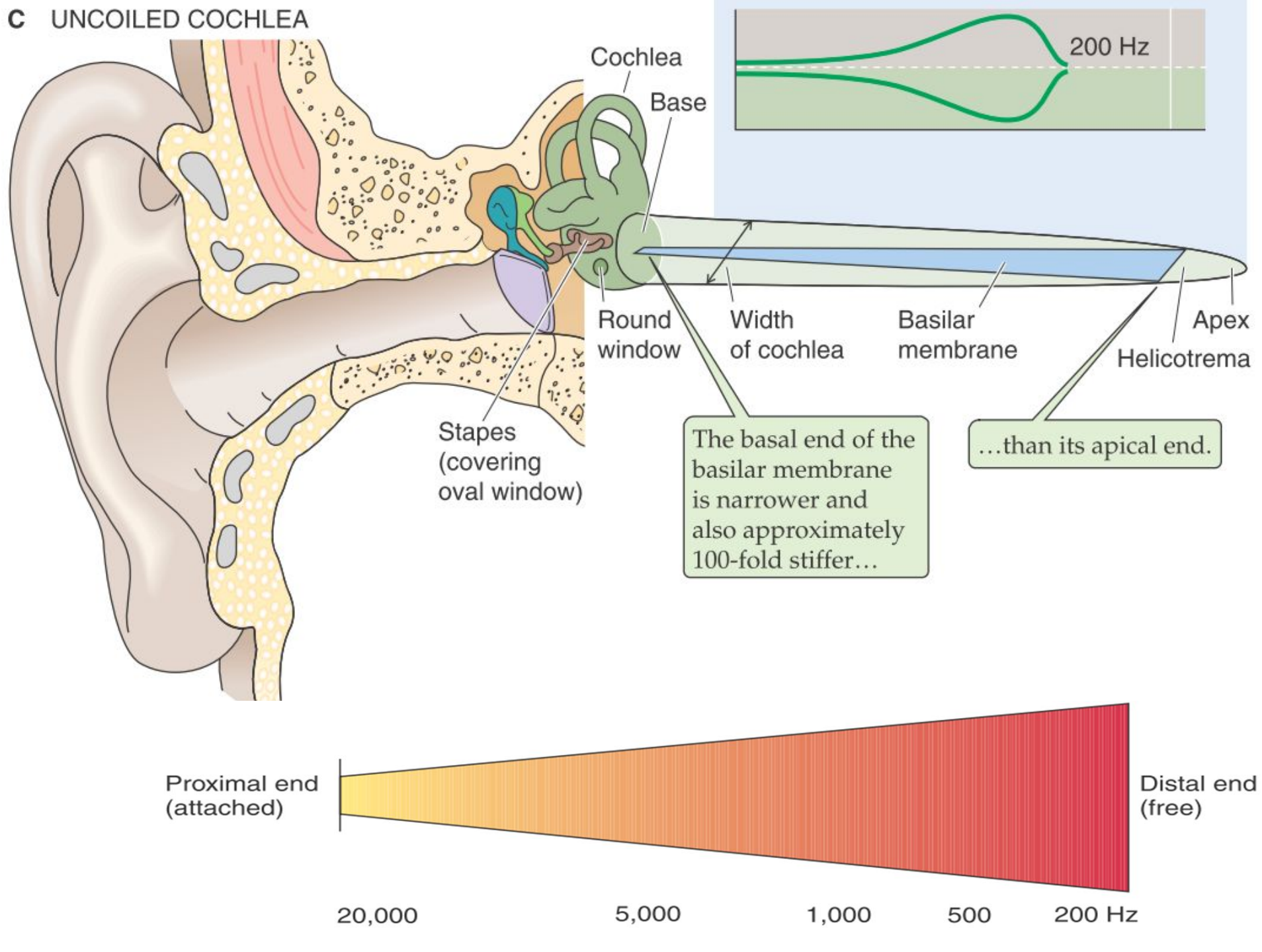
# A UPWARD BOWING OF BASILAR MEMBRANE

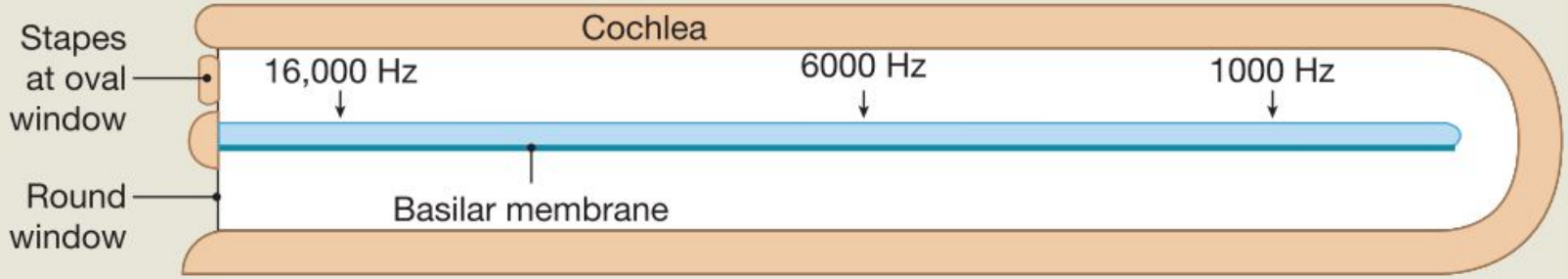



B INNER HAIR CELL
C OUTER HAIR CELL
+80 mV
Support cell
–40 mV
K+
Ca2+
Efferent axon
Afferent dendrite
+80 mV
–70 mV
Prestin
K+
Deiter's cell
(b)
Tip links stretch
K+
K+
Stereocilia
Nucleus
Ca2+
Vesicles
Ca2+
Afferent neurons
(c)
Tip links slack

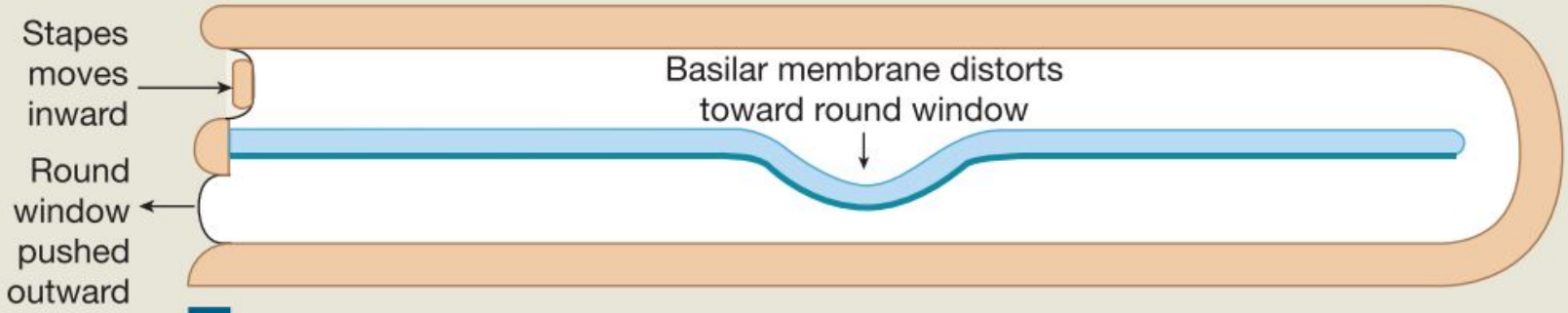

D DOWNWARD BOWING OF BASILAR MEMBRANE
Endolymph
Pillar cells
Perilymph
Basilar membrane
bowing downward


Base
(stapes)
Apex
(helicotrema)
100
10
1
0.1
0.01
0.001
Peak displacement of basilar membrane (nm)
Actual response with cochlear amplifier intact
Threshold
Response of passive basilar membrane
0
5
10
15
20
Position along basilar membrane (mm)

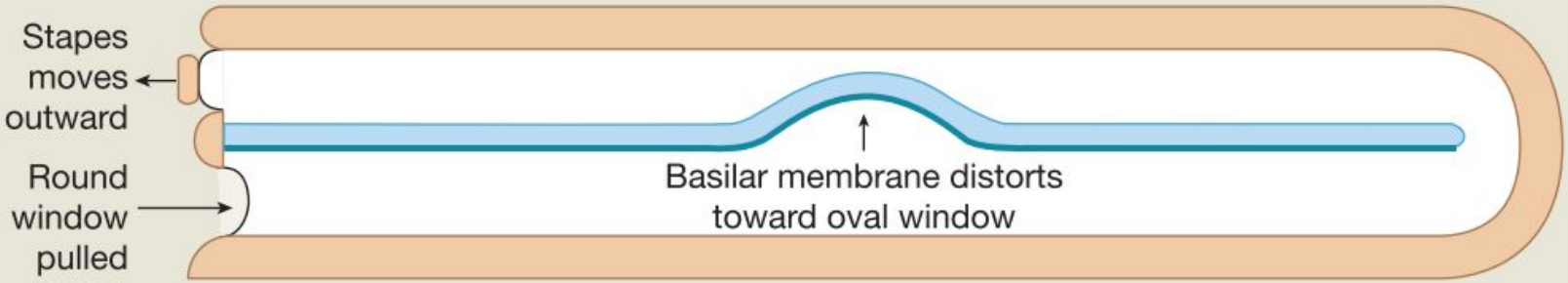

C UNCOILED COCHLEA
200 Hz
Cochlea
Base
Round window
Width of cochlea
Basilar membrane
Apex
Helicotrema
Stapes (covering oval window)
The basal end of the basilar membrane is narrower and also approximately 100-fold stiffer…
…than its apical end.
Proximal end (attached)
Distal end (free)
20,000
5,000
1,000
500
200 Hz



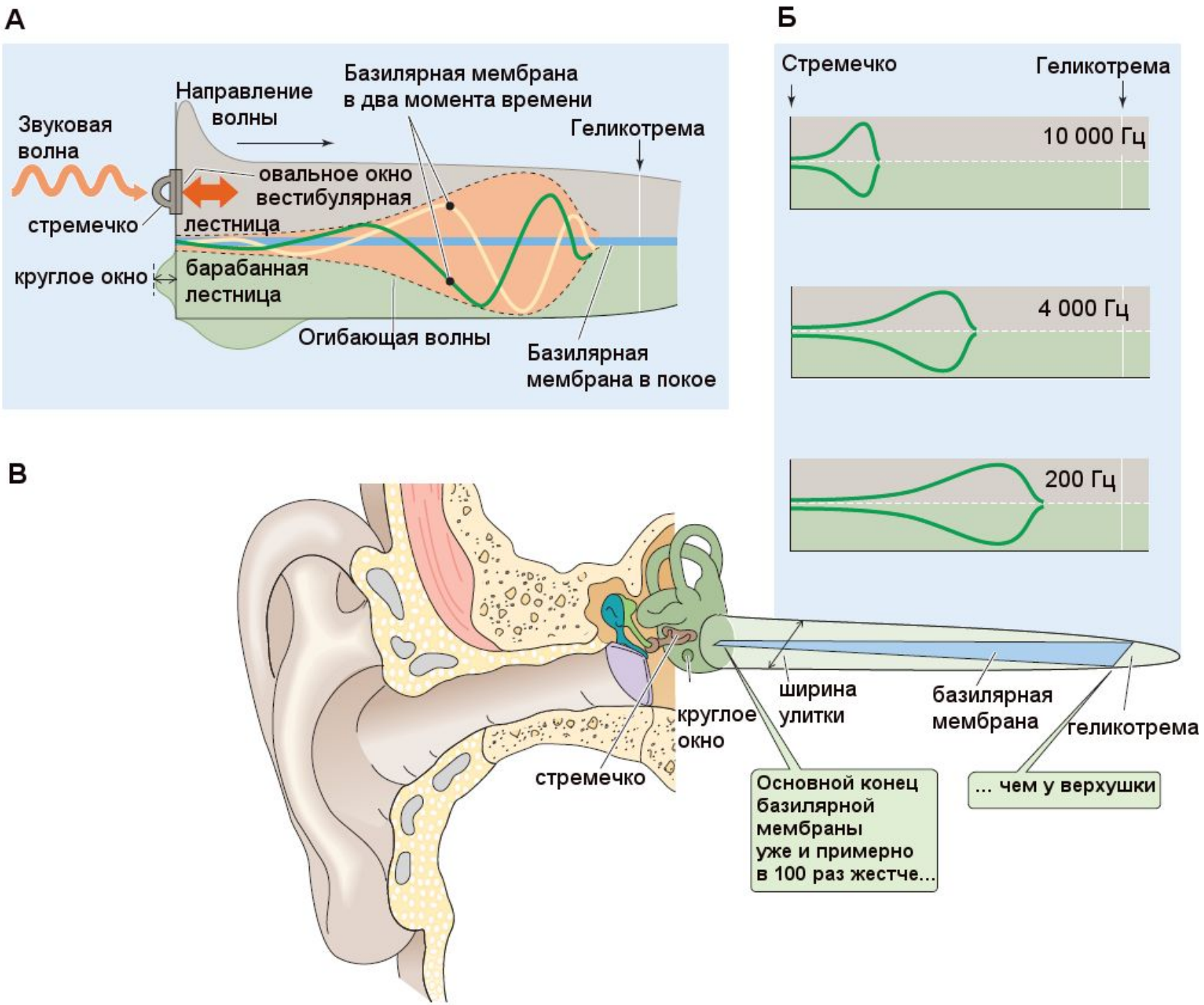

**a** The flexibility of the basilar membrane varies along its length, so presure waves of different frequencies affect different parts of the membrane.

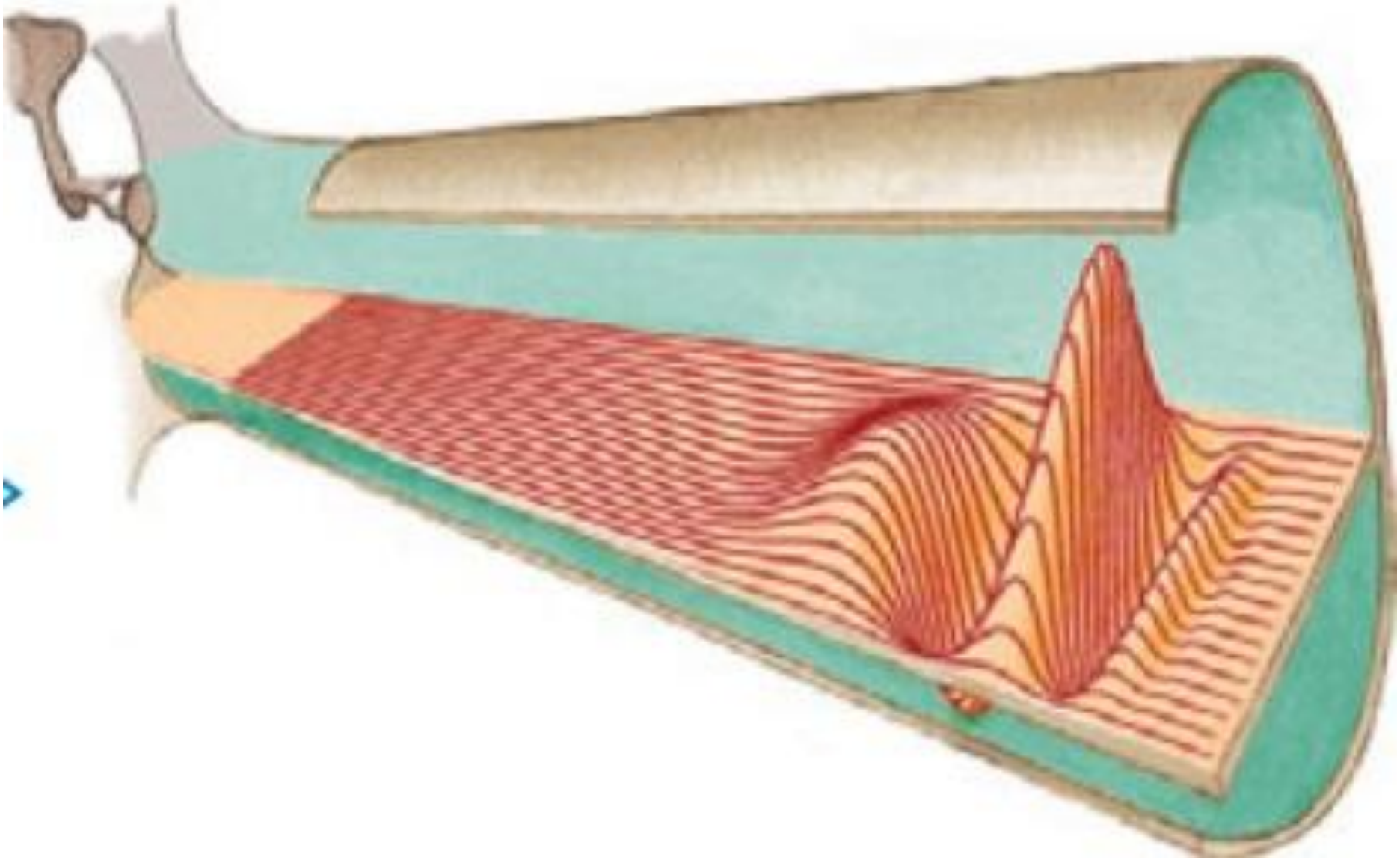


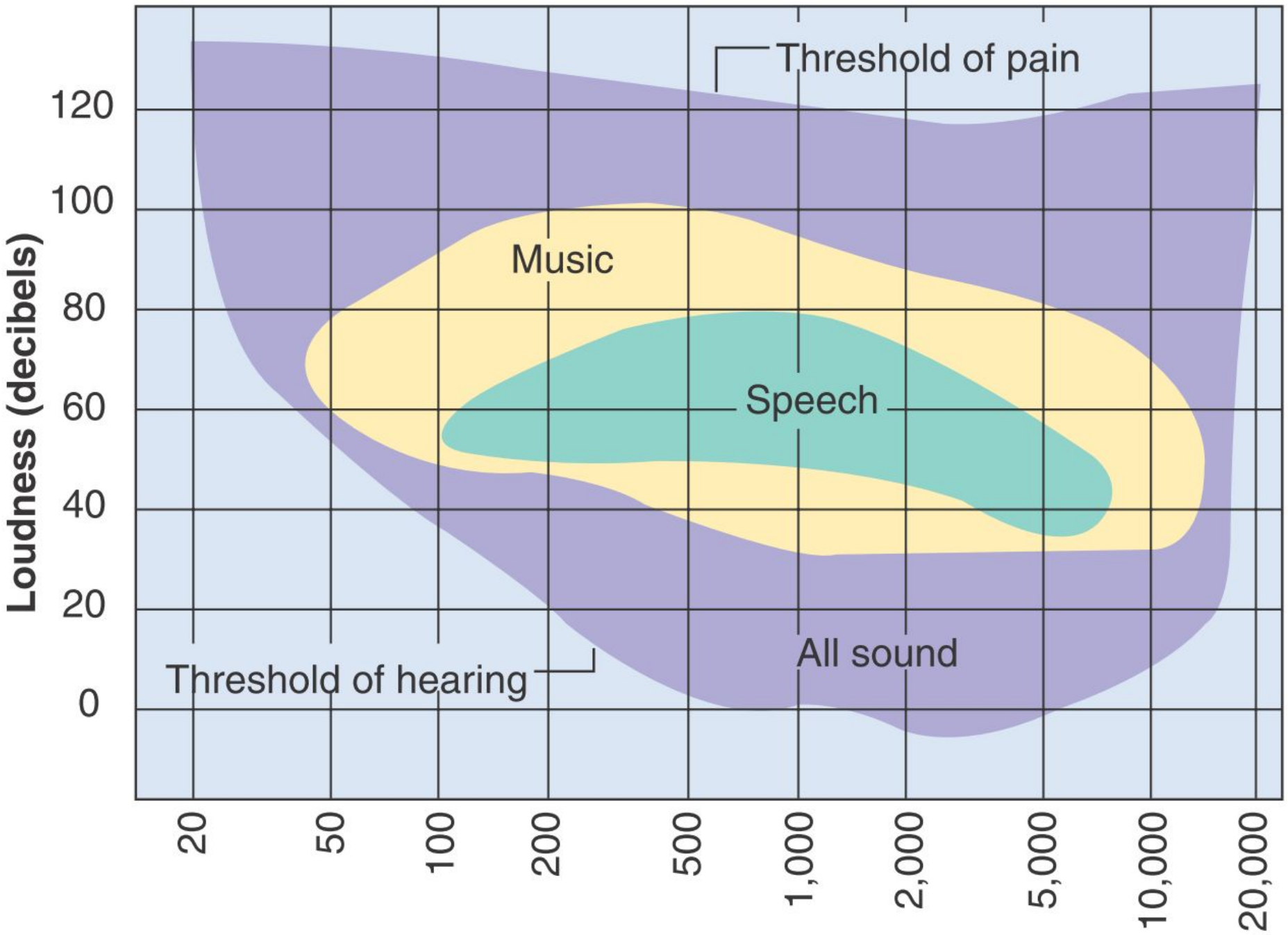

**b** The effects of a vibration of the stapes at a frequency of 6000 Hz. When the stapes moves inward, as shown here, the basilar membrane distorts toward the round window, which bulges into the middle-ear cavity.

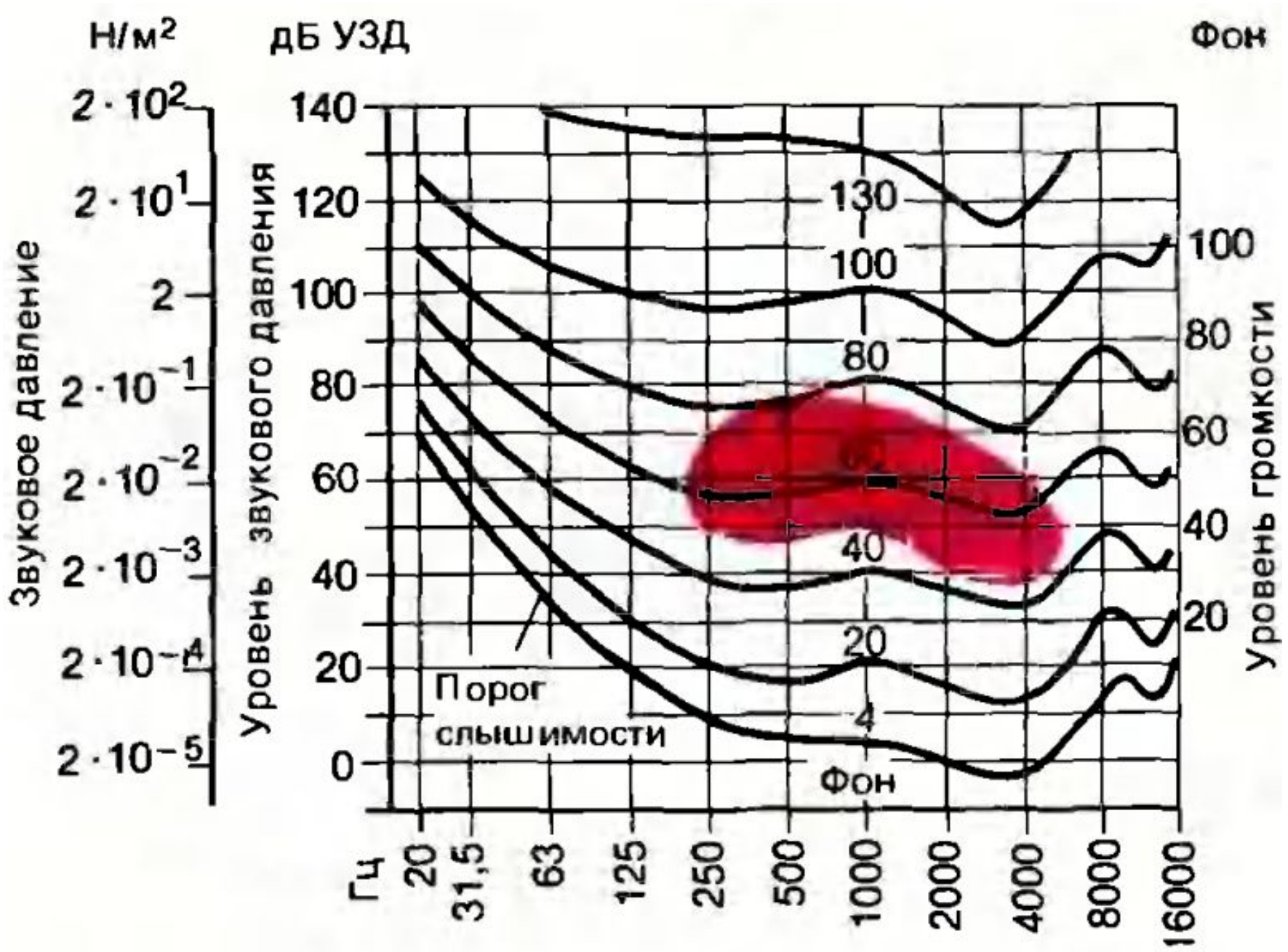


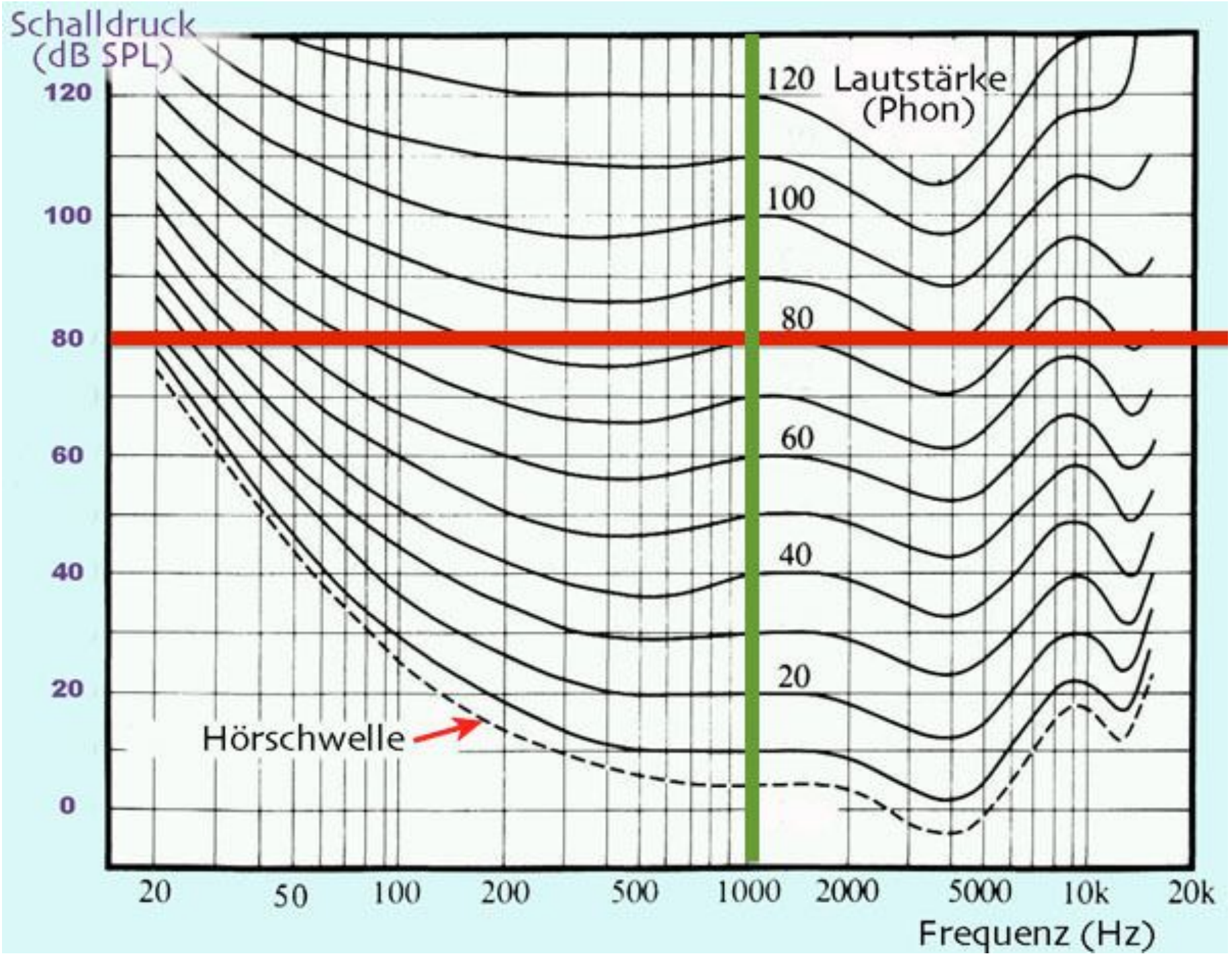

**c** When the stapes moves outward, as shown here, the basilar membrane rebounds and distorts toward the oval window.


А
Звуковая волна
Направление волны
Базилярная мембрана в два момента времени
Геликотрема
овальное окно
вестибулярная лестница
стремечко
круглое окно
барабанная лестница
Огибающая волны
Базилярная мембрана в покое
Б
Стремечко
Геликотрема
10 000 Гц
4 000 Гц
200 Гц
В
ширина улитки
базилярная мембрана
геликотрема
круглое окно
стремечко
Основной конец базилярной мембраны уже и примерно в 100 раз жестче...
... чем у верхушки




Threshold of pain
120
100
Music
80
Speech
60
40
20
All sound
Threshold of hearing
0
Loudness (decibels)
20
50
100
200
500
1,000
2,000
5,000
10,000
20,000

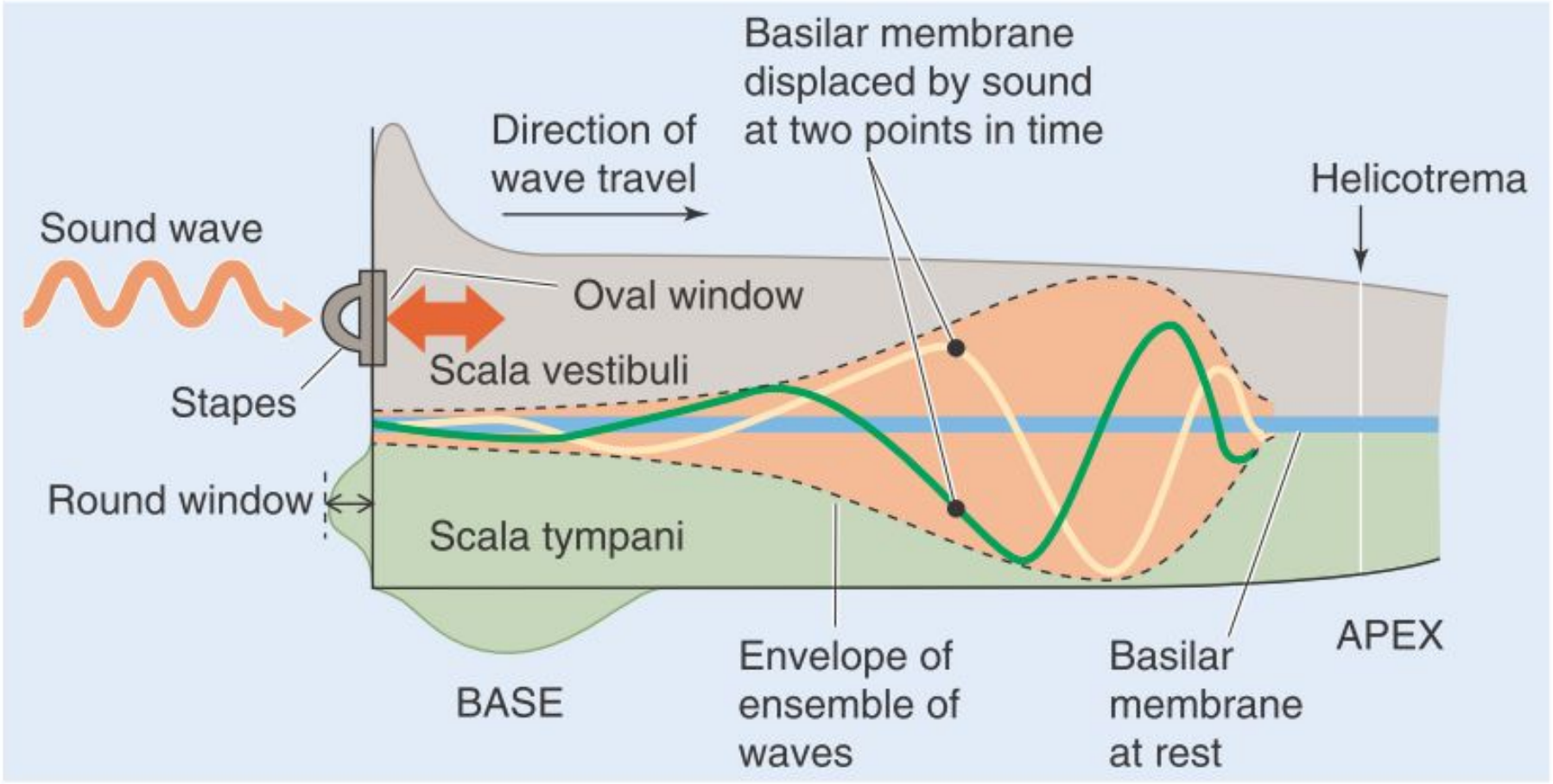

Н/м²
дБ УЗД
Фон
Звуковое давление
Уровень звукового давления
Уровень громкости
2·10²
2·10¹
2
2·10⁻¹
2·10⁻²
2·10⁻³
2·10⁻⁴
2·10⁻⁵
140
120
100
80
60
40
20
0
130
100
80
60
40
20
4
Фон
Порог слышимости
Гц
20
31,5
63
125
250
500
1000
2000
4000
8000
16000

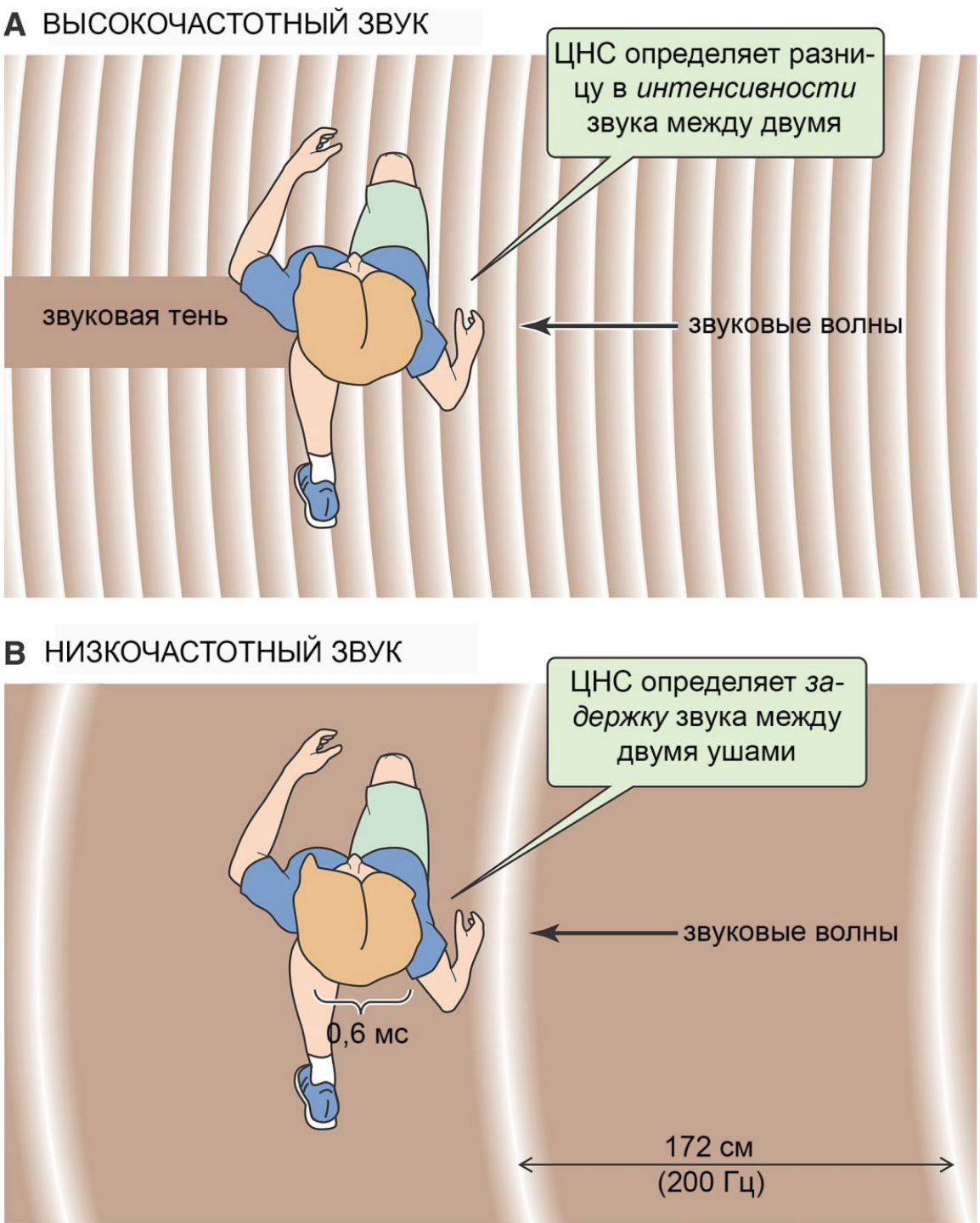

Schalldruck
(dB SPL)
120
100
80
60
40
20
0
120 Lautstärke
(Phon)
100
80
60
40
20
Hörschwelle
20
50
100
200
500
1000
2000
5000
10k
20k
Frequenz (Hz)

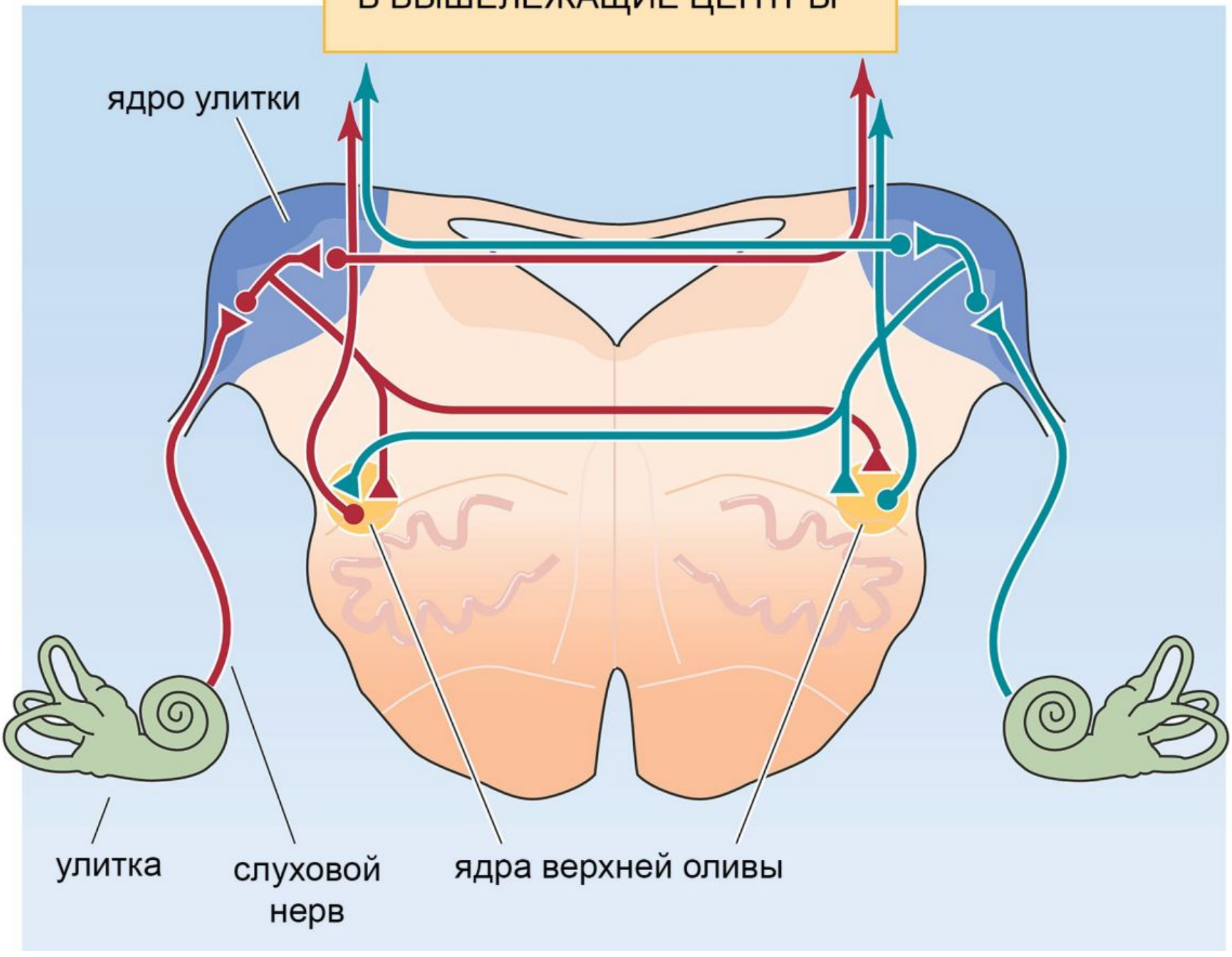
$$\text{УЗД} = 20 \cdot \lg \frac{p_x}{p_o} [\text{дБ}].$$

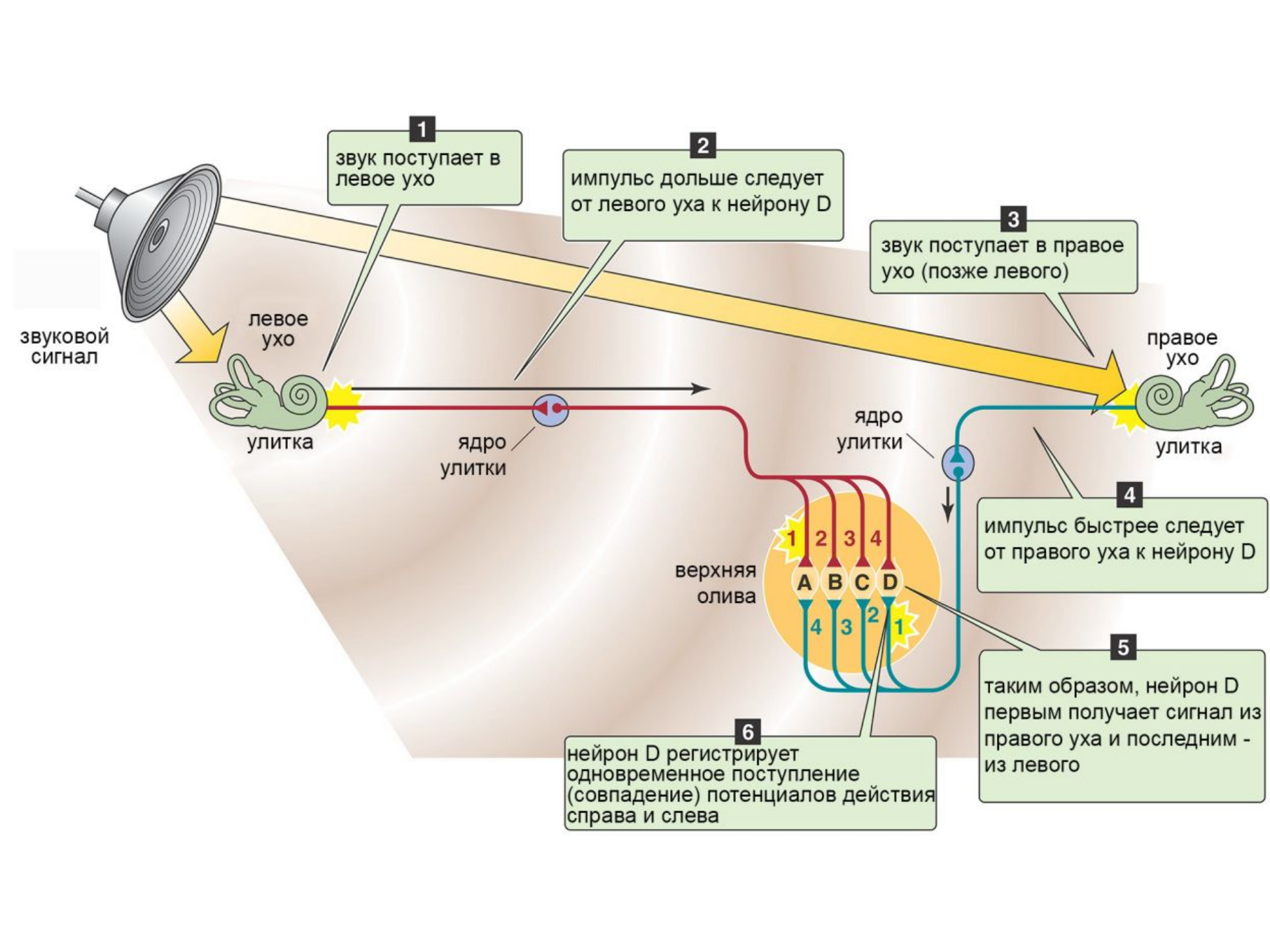
$$\frac{p_x}{p_o} = \frac{2 \cdot 10^{-1}}{2 \cdot 10^{-5}} = 10^4, \quad \text{УЗД} = 20 \lg 10^4 = 20 \cdot 4 = 80.$$

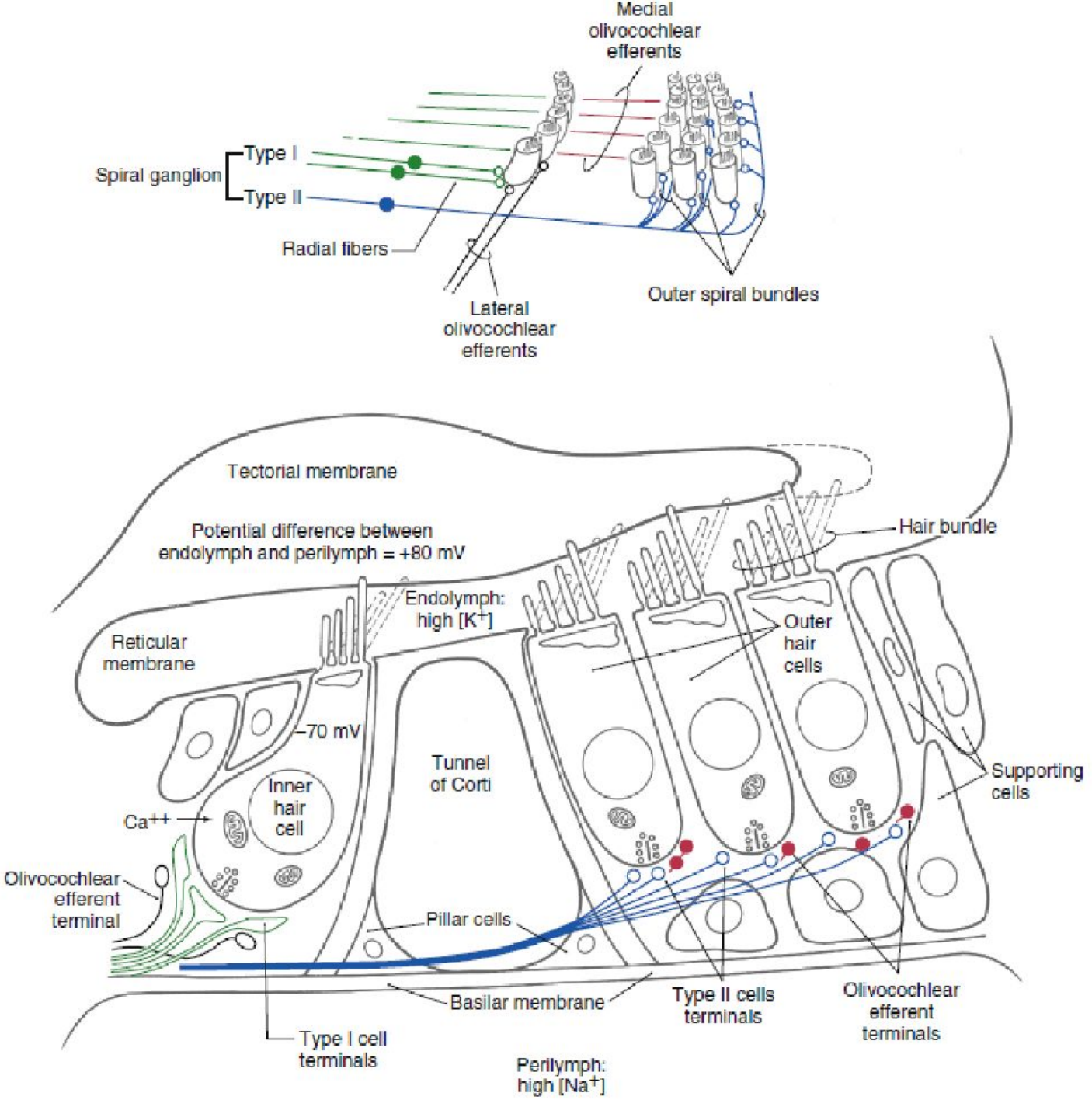
**A** ENVELOPE OF MAXIMUM WAVE AMPLITUDES

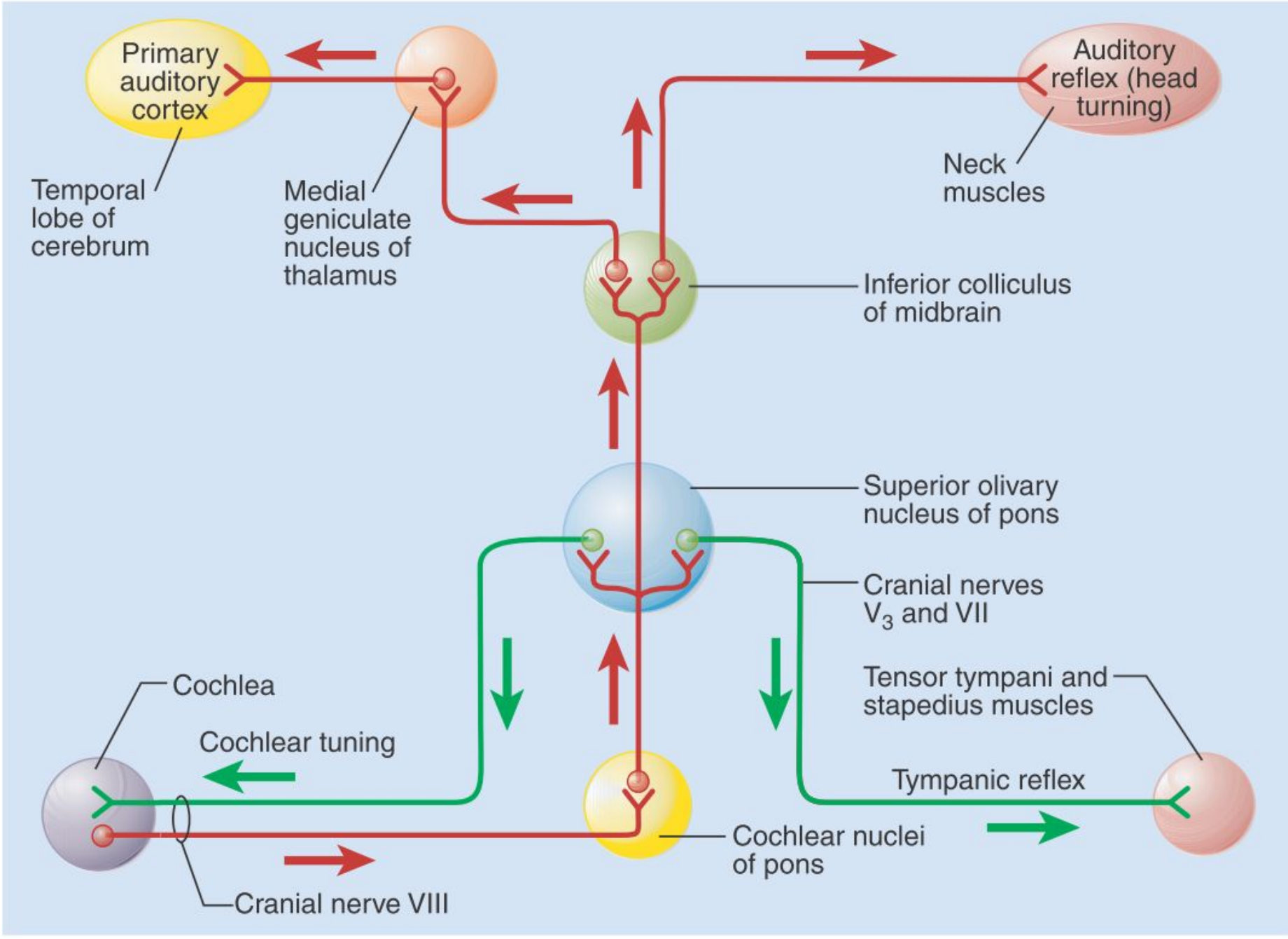


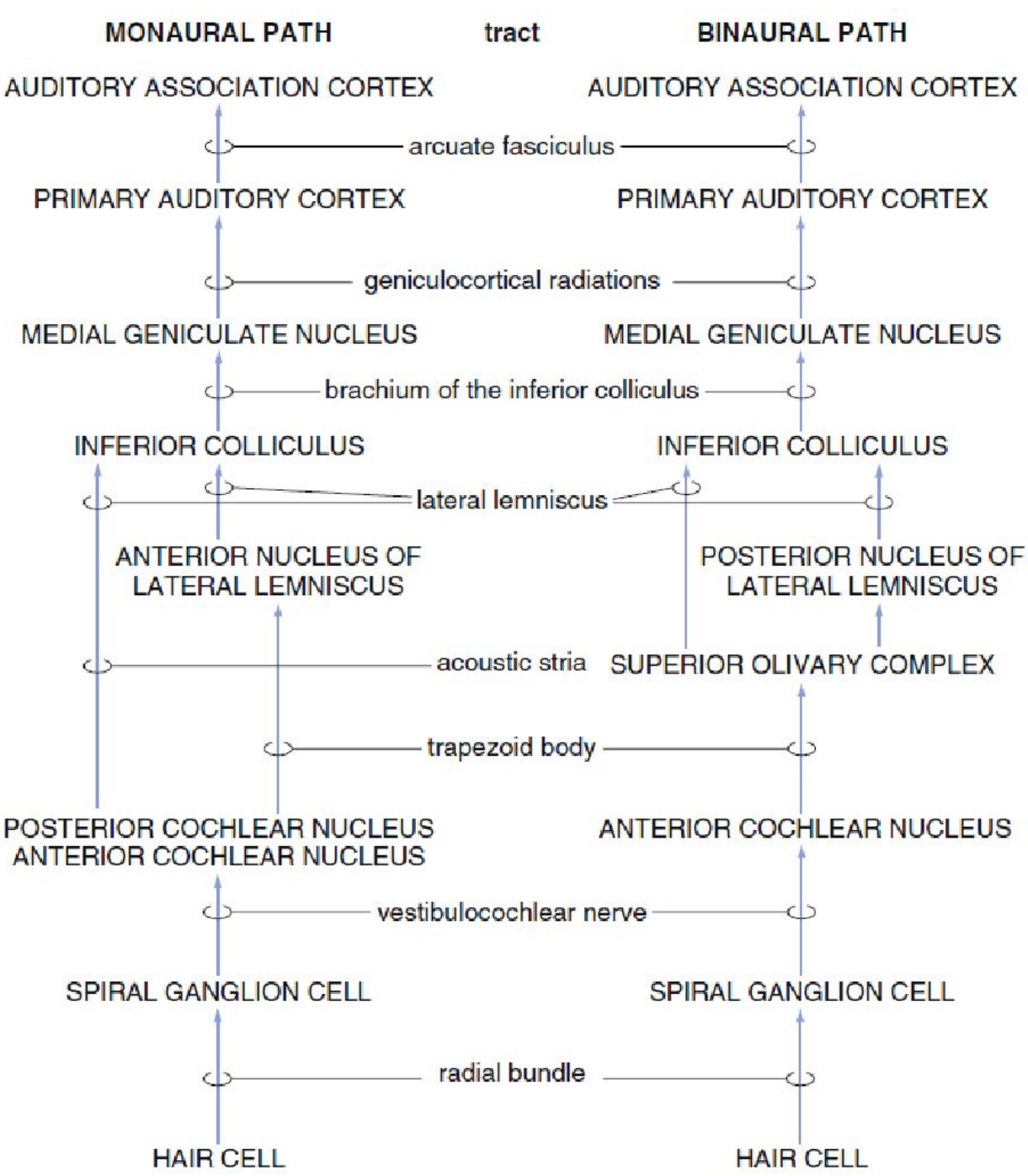

A ВЫСОКОЧАСТОТНЫЙ ЗВУК
ЦНС определяет разницу в *интенсивности* звука между двумя
звуковая тень
звуковые волны
B НИЗКОЧАСТОТНЫЙ ЗВУК
ЦНС определяет *задержку* звука между двумя ушами
звуковые волны
0,6 мс
172 см
(200 Гц)


В ВЫШЕЛЕЖАЩИЕ ЦЕНТРЫ
ядро улитки
улитка
слуховой нерв
ядра верхней оливы


1
звук поступает в левое ухо
2
импульс дольше следует от левого уха к нейрону D
3
звук поступает в правое ухо (позже левого)
звуковой сигнал
левое ухо
правое ухо
улитка
ядро улитки
ядро улитки
улитка
верхняя олива
A B C D
1 2 3 4
4 3 2 1
4
импульс быстрее следует от правого уха к нейрону D
5
таким образом, нейрон D первым получает сигнал из правого уха и последним - из левого
6
нейрон D регистрирует одновременное поступление (совпадение) потенциалов действия справа и слева


Medial olivocochlear efferents
Spiral ganglion
Type I
Type II
Radial fibers
Lateral olivocochlear efferents
Outer spiral bundles
Tectorial membrane
Potential difference between endolymph and perilymph = +80 mV
Hair bundle
Endolymph: high [K+]
Reticular membrane
Outer hair cells
−70 mV
Tunnel of Corti
Supporting cells
Inner hair cell
Ca++
Olivocochlear efferent terminal
Pillar cells
Basilar membrane
Type II cells terminals
Olivocochlear efferent terminals
Type I cell terminals
Perilymph: high [Na+]


Primary auditory cortex
Temporal lobe of cerebrum
Medial geniculate nucleus of thalamus
Auditory reflex (head turning)
Neck muscles
Inferior colliculus of midbrain
Superior olivary nucleus of pons
Cranial nerves $V_3$ and VII
Tensor tympani and stapedius muscles
Tympanic reflex
Cochlea
Cochlear tuning
Cochlear nuclei of pons
Cranial nerve VIII


MONAURAL PATH
tract
BINAURAL PATH
AUDITORY ASSOCIATION CORTEX
AUDITORY ASSOCIATION CORTEX
arcuate fasciculus
PRIMARY AUDITORY CORTEX
PRIMARY AUDITORY CORTEX
geniculocortical radiations
MEDIAL GENICULATE NUCLEUS
MEDIAL GENICULATE NUCLEUS
brachium of the inferior colliculus
INFERIOR COLLICULUS
INFERIOR COLLICULUS
lateral lemniscus
ANTERIOR NUCLEUS OF LATERAL LEMNISCUS
POSTERIOR NUCLEUS OF LATERAL LEMNISCUS
acoustic stria
SUPERIOR OLIVARY COMPLEX
trapezoid body
POSTERIOR COCHLEAR NUCLEUS
ANTERIOR COCHLEAR NUCLEUS
ANTERIOR COCHLEAR NUCLEUS
vestibulocochlear nerve
SPIRAL GANGLION CELL
SPIRAL GANGLION CELL
radial bundle
HAIR CELL
HAIR CELL

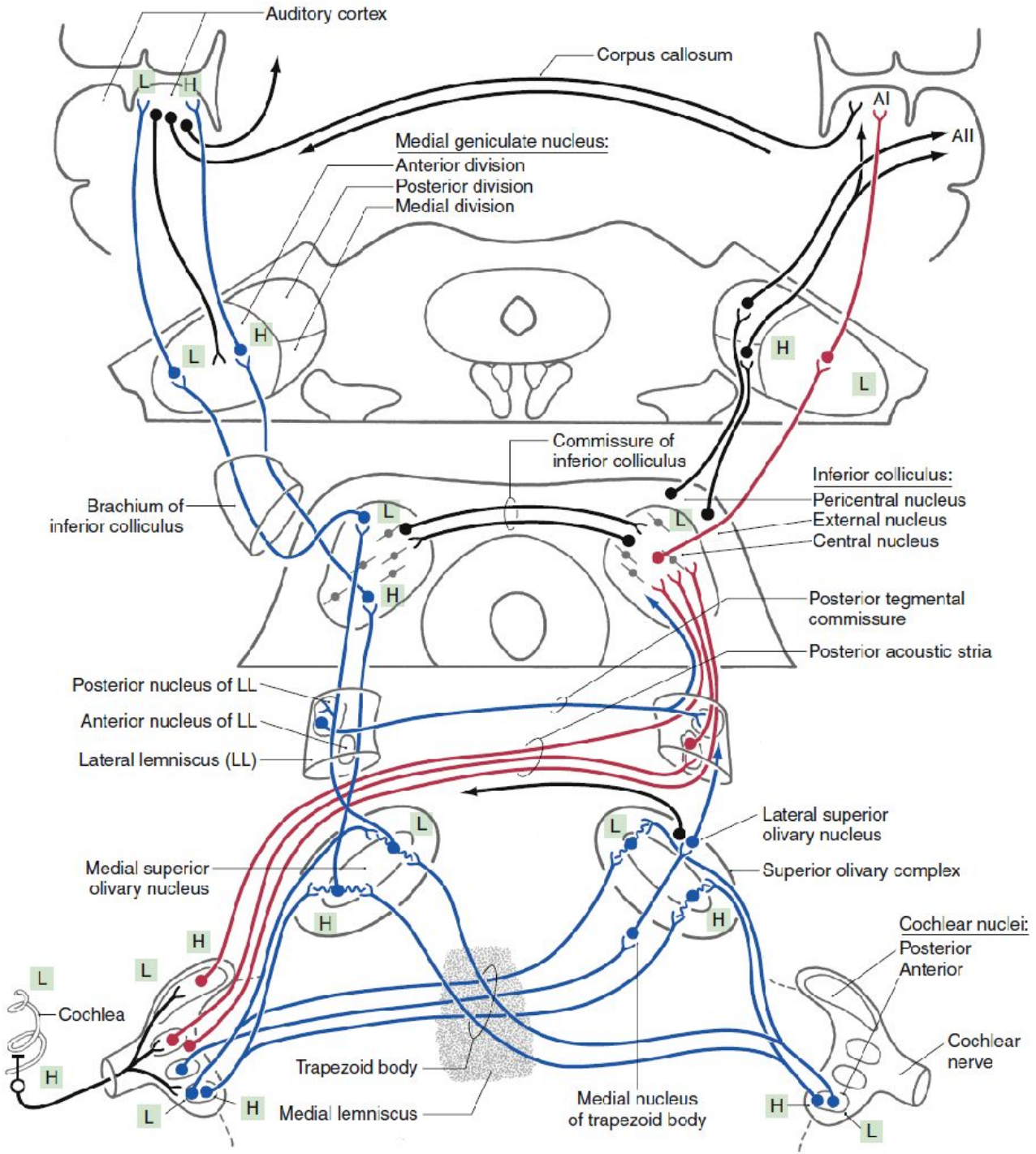
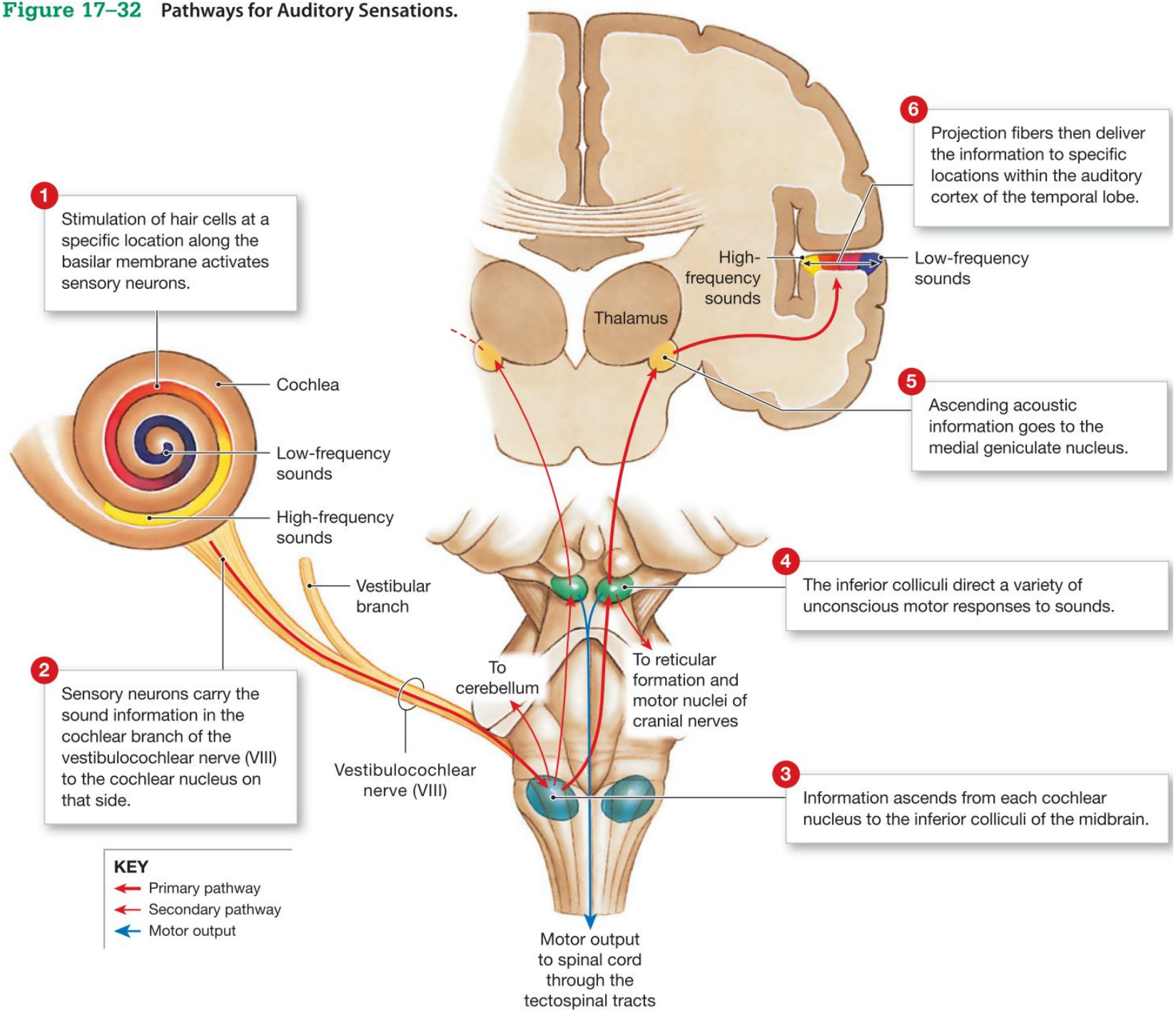
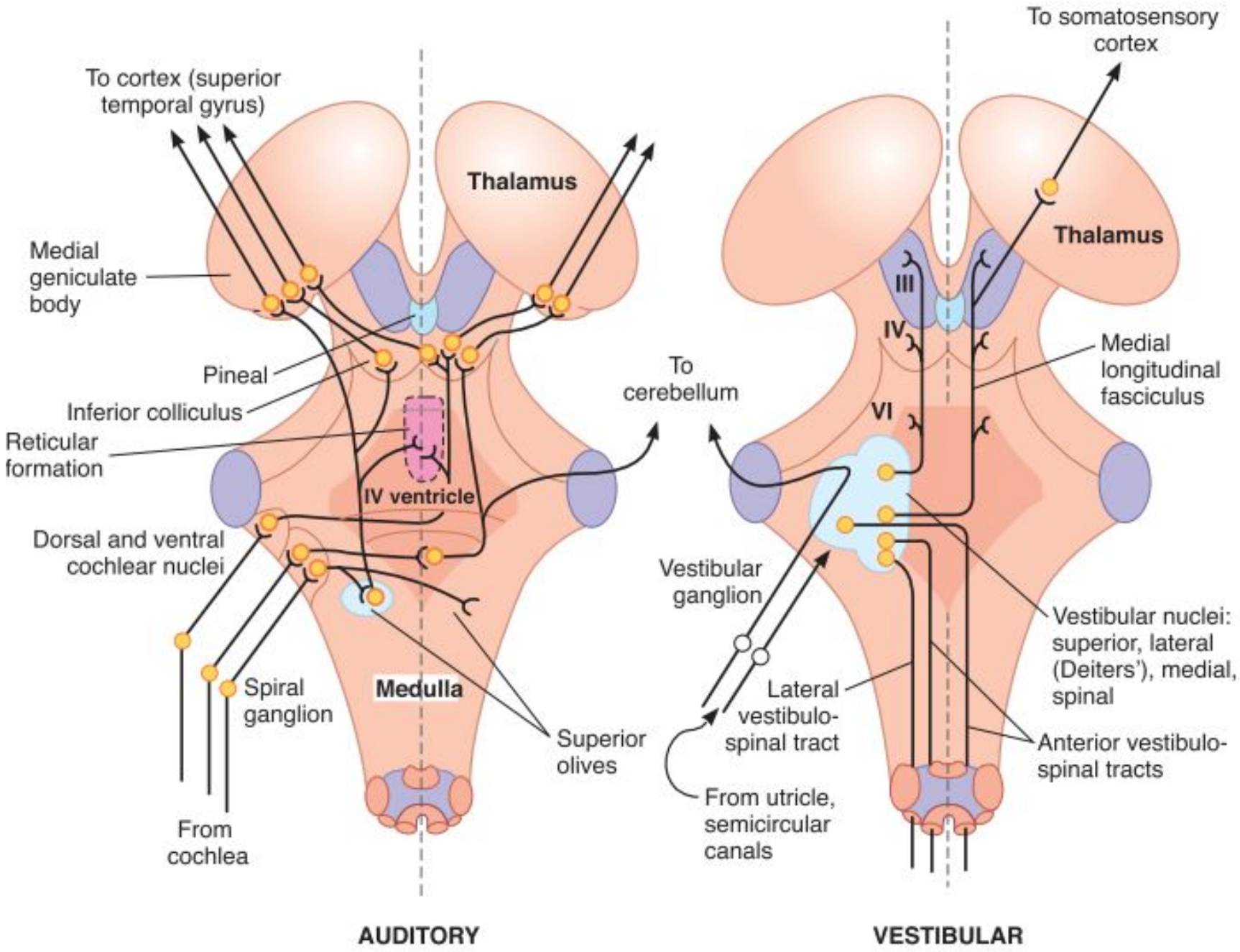

Auditory cortex
Corpus callosum
Medial geniculate nucleus:
Anterior division
Posterior division
Medial division
AI
AII
L
H
Commissure of inferior colliculus
Brachium of inferior colliculus
Inferior colliculus:
Pericentral nucleus
External nucleus
Central nucleus
Posterior tegmental commissure
Posterior acoustic stria
Posterior nucleus of LL
Anterior nucleus of LL
Lateral lemniscus (LL)
Lateral superior olivary nucleus
Superior olivary complex
Medial superior olivary nucleus
Cochlear nuclei:
Posterior
Anterior
Cochlea
Cochlear nerve
Trapezoid body
Medial lemniscus
Medial nucleus of trapezoid body

**Figure 17–32** Pathways for Auditory Sensations.




To cortex (superior temporal gyrus)
Thalamus
Medial geniculate body
Pineal
Inferior colliculus
Reticular formation
IV ventricle
Dorsal and ventral cochlear nuclei
Spiral ganglion
Medulla
Superior olives
From cochlea
AUDITORY
To somatosensory cortex
Thalamus
III
IV
VI
Medial longitudinal fasciculus
To cerebellum
Vestibular ganglion
Vestibular nuclei: superior, lateral (Deiters'), medial, spinal
Lateral vestibulo-spinal tract
Anterior vestibulo-spinal tracts
From utricle, semicircular canals
VESTIBULAR