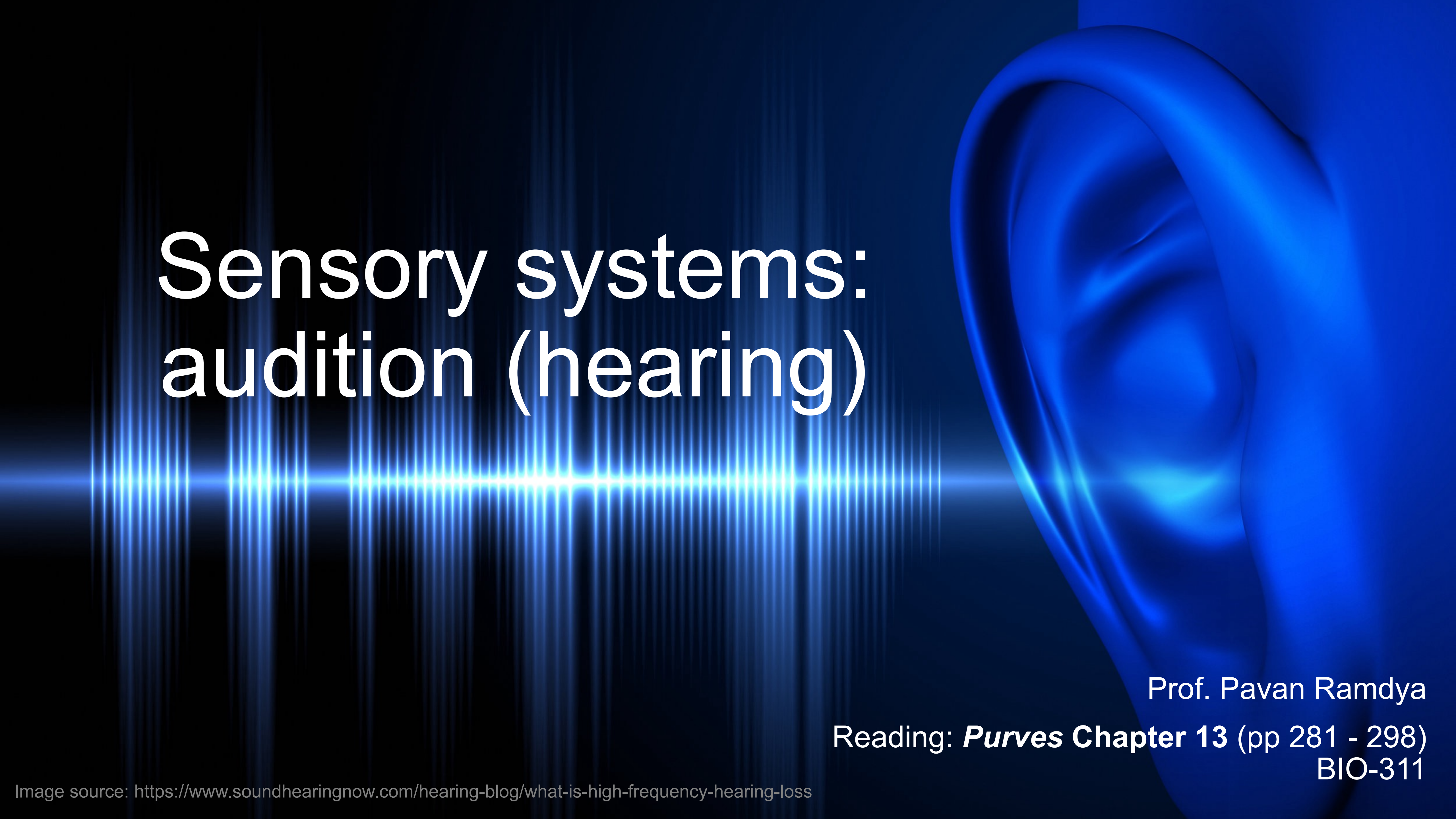


Sensory systems: audition (hearing)

Prof. Pavan Ramdya

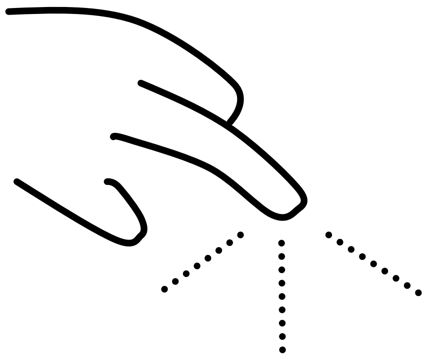
Reading: ***Purves* Chapter 13** (pp 281 - 298)
BIO-311

Image source: https://www.soundhearingnow.com/hearing-blog/what-is-high-frequency-hearing-loss

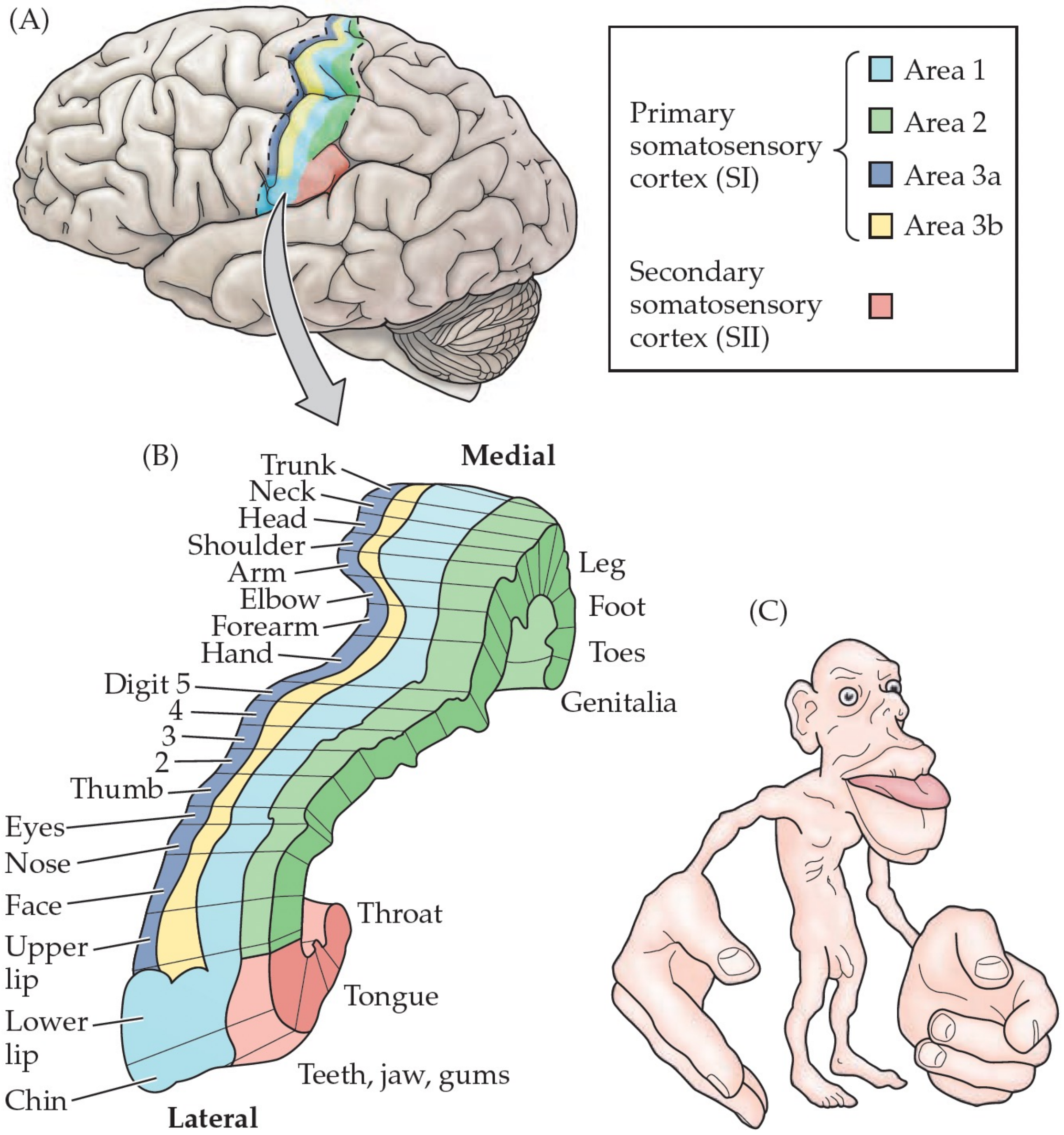
What are the sensory systems?

The different sensory systems enable different kinds of percepts

Somatosensation (sense of touch)



Detecting mechanical deformation of the body's surface

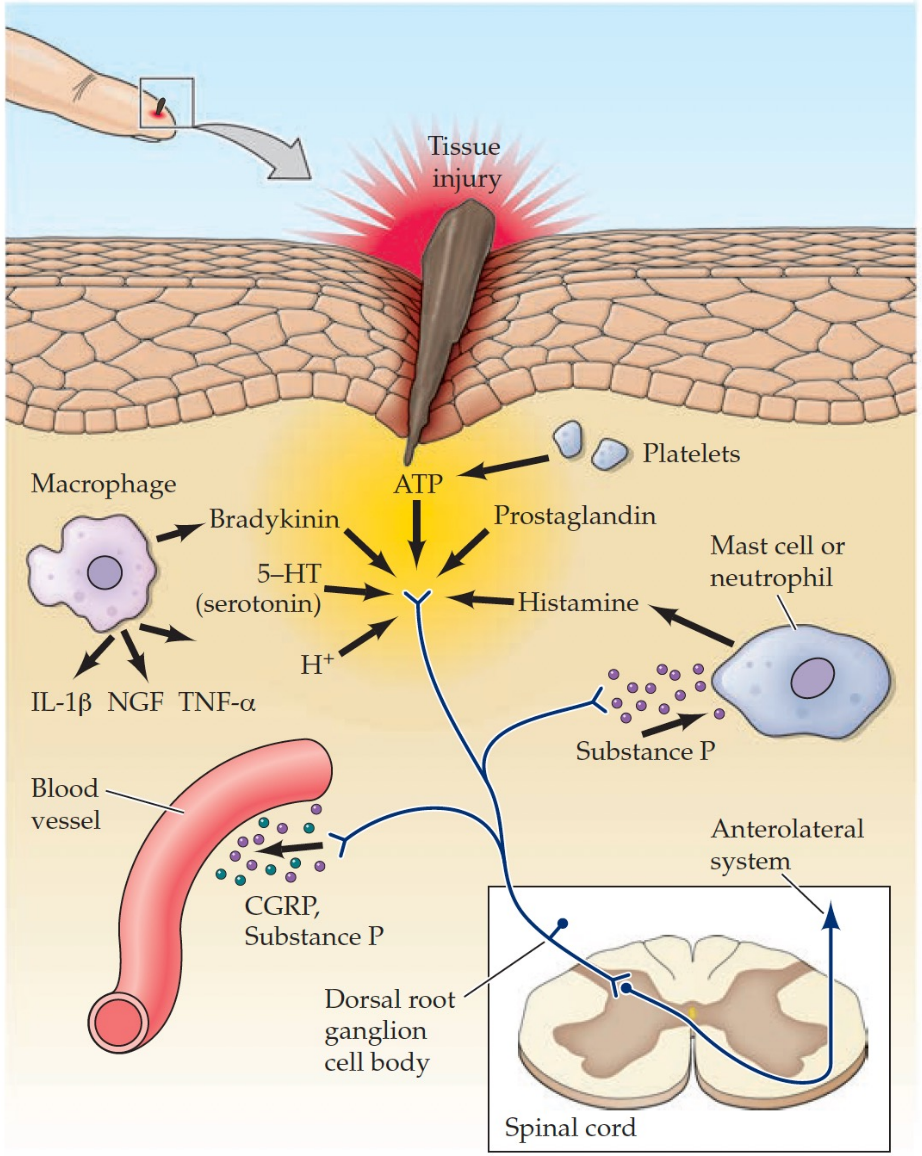


Purves, Figure 9.11

The different sensory systems enable different kinds of percepts

Nociception (sense of pain)

Detecting the byproducts of injury and painful stimuli

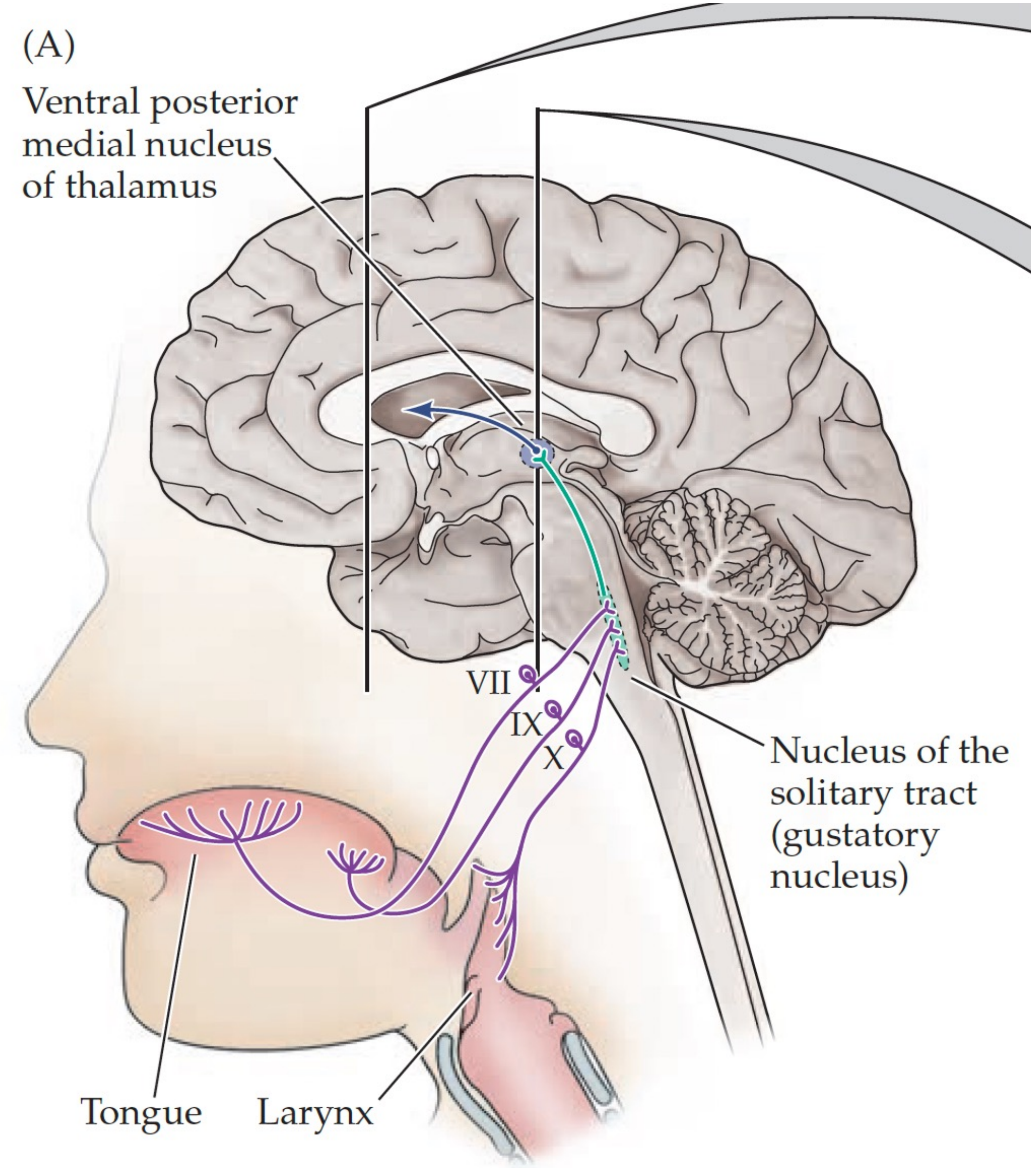


Purves, Figure 10.7

The different sensory systems enable different kinds of percepts

Gustation (sense of taste)

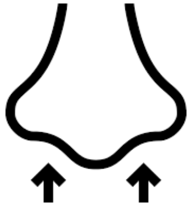
Detecting contact with chemicals and molecules



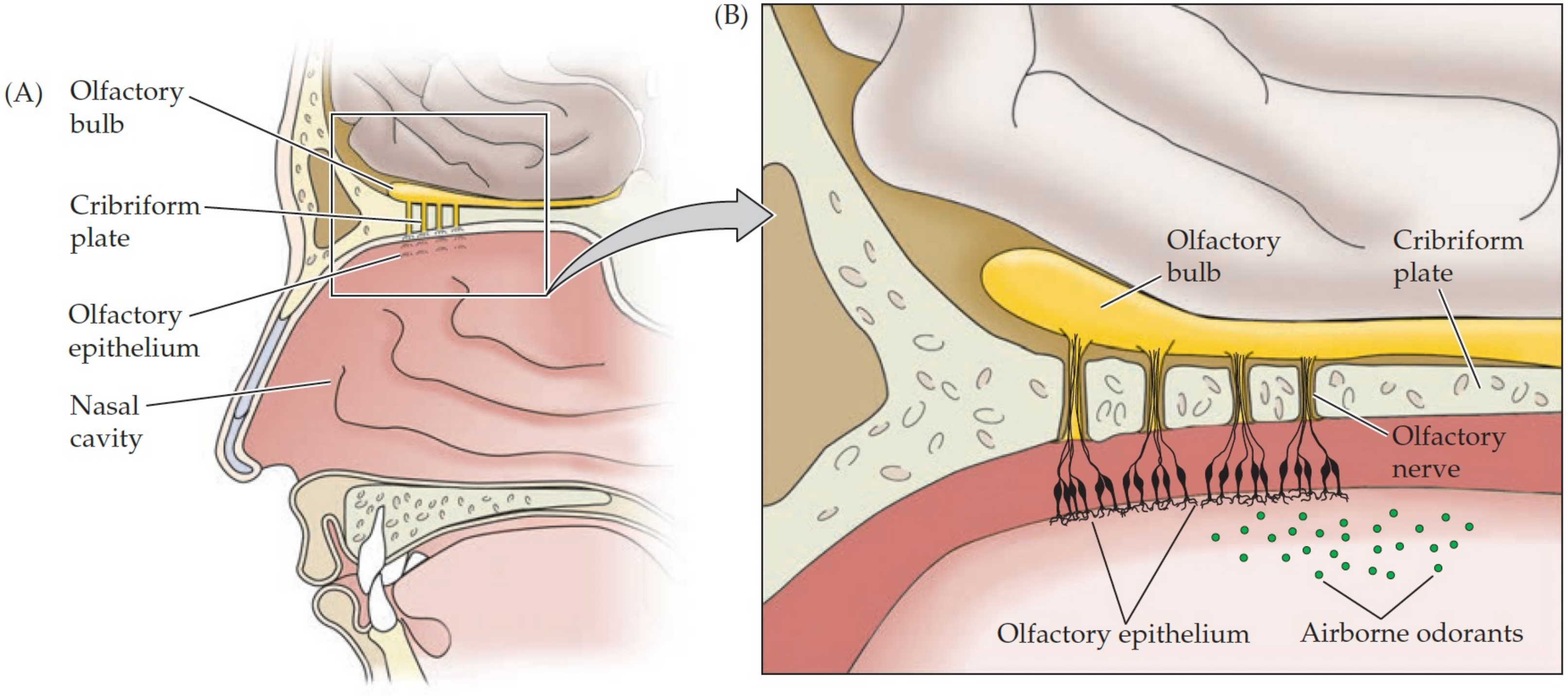
Purves, Figure 15.20

The different sensory systems enable different kinds of percepts

Olfaction (sense of smell)



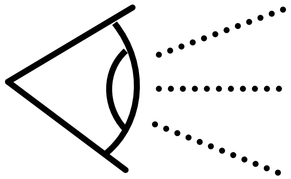
Detecting volatile airborne chemicals



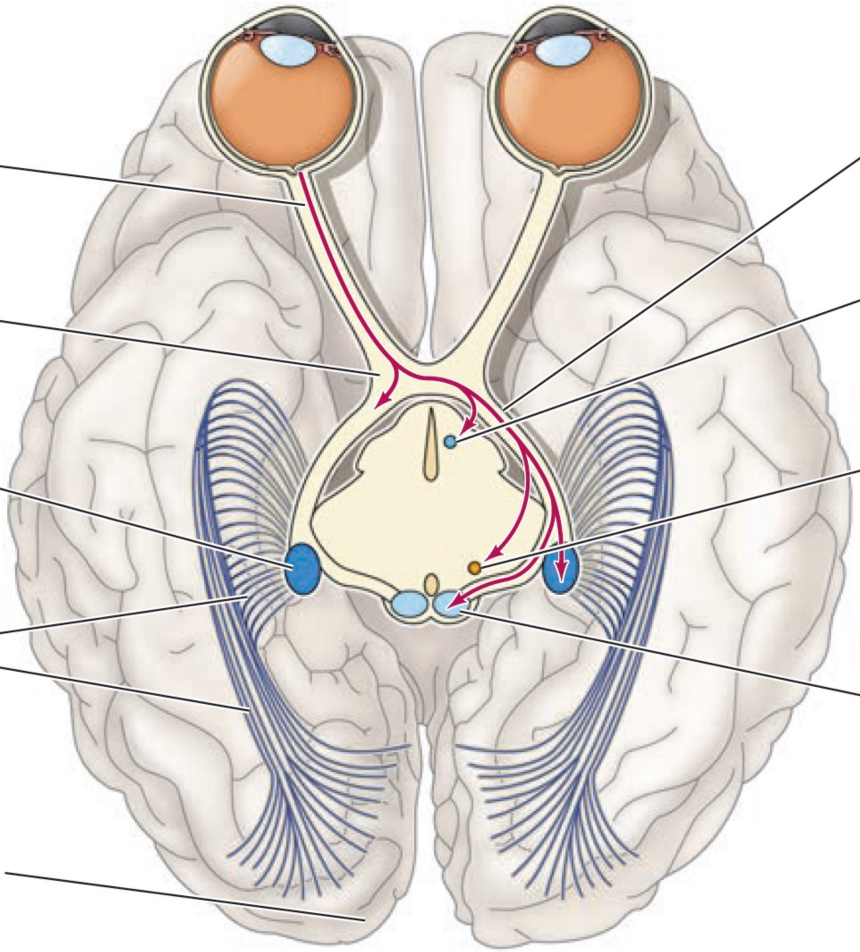
Purves, Figure 15.1

The different sensory systems enable different kinds of percepts

Vision (sense of sight)



Detecting photons

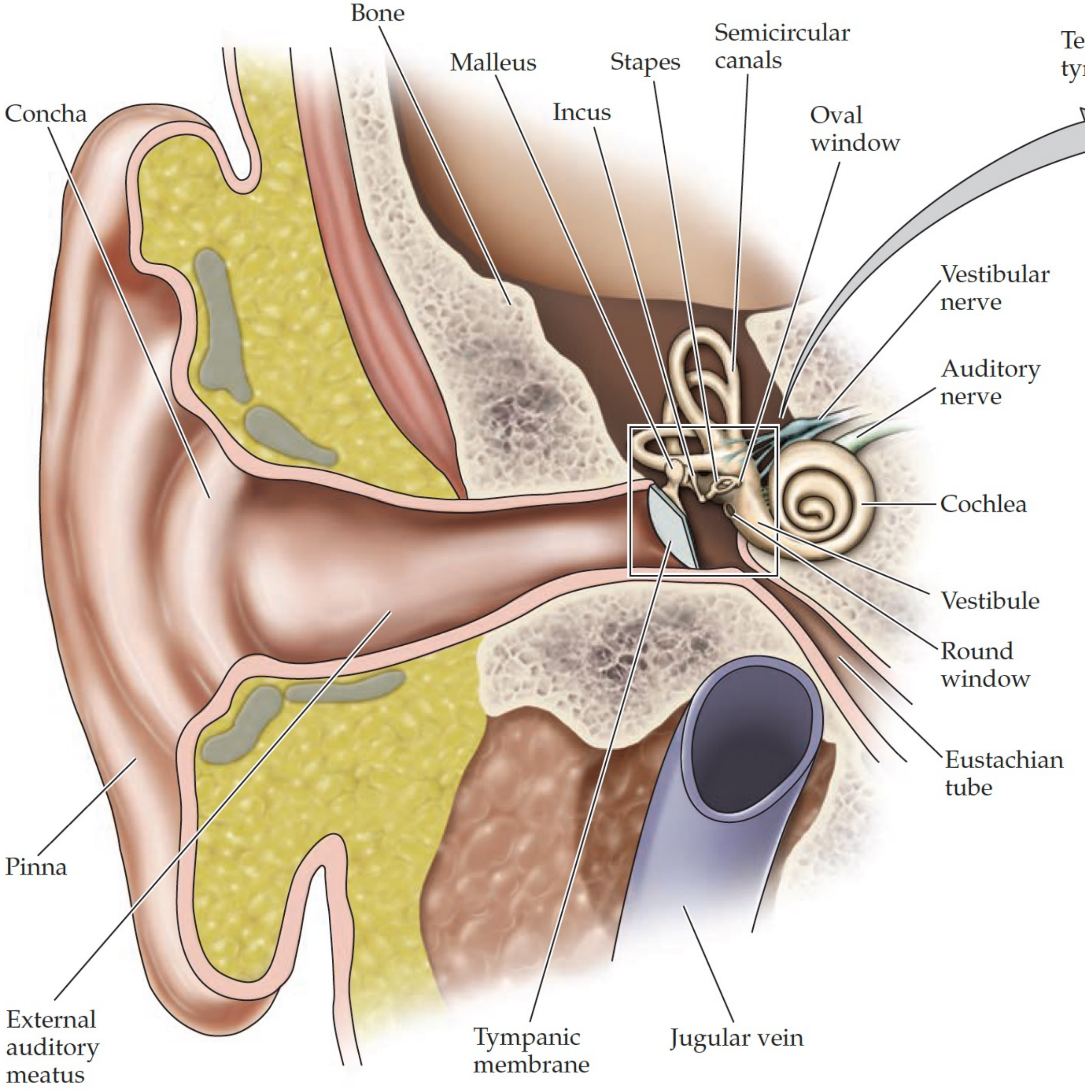


Purves, Figure 12.1

The different sensory systems enable different kinds of percepts

Audition (sense of hearing)

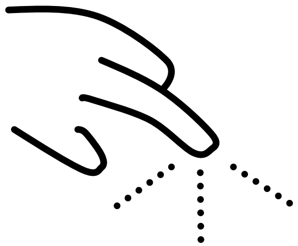
Detecting airborne pressure waves



Purves, Figure 13.4

The different sensory systems enable different kinds of percepts

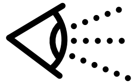
Proximal (near) sensing


Somatosensation

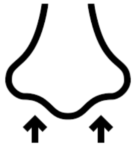

Nociception


Gustation

Distal (far) sensing


Vision

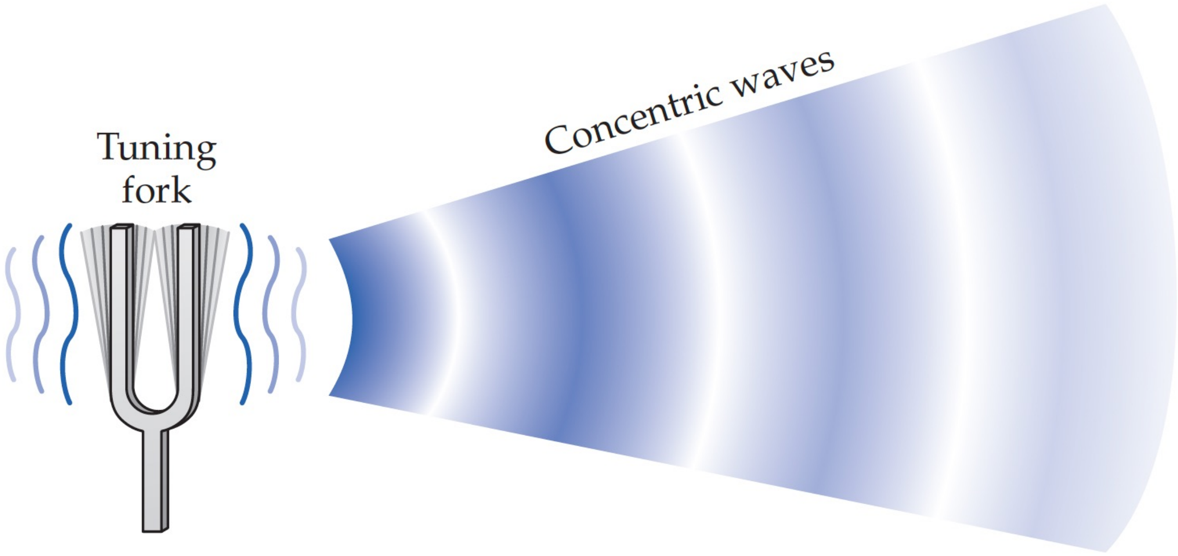

Audition


Olfaction

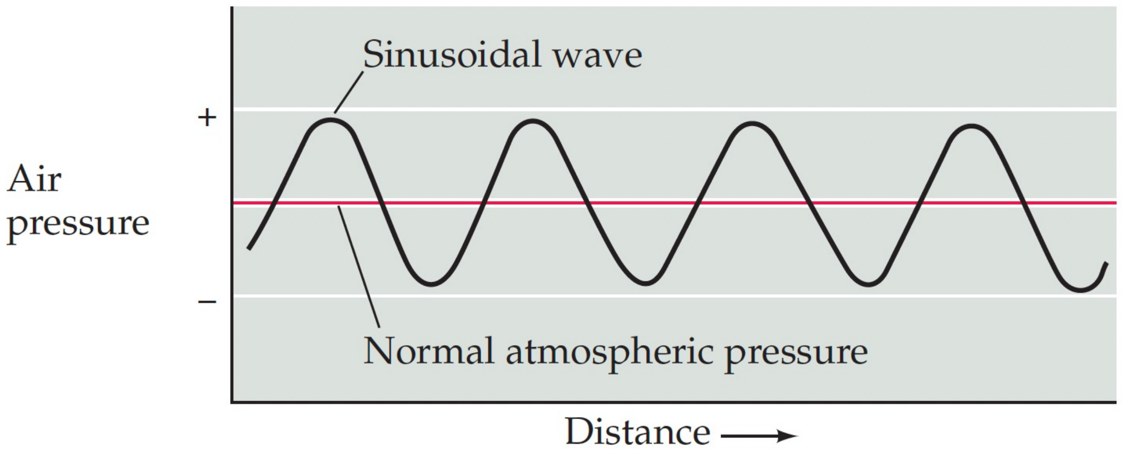
What is sound and what can we hear?

What is sound?

Condensation and Rarefaction of air molecules



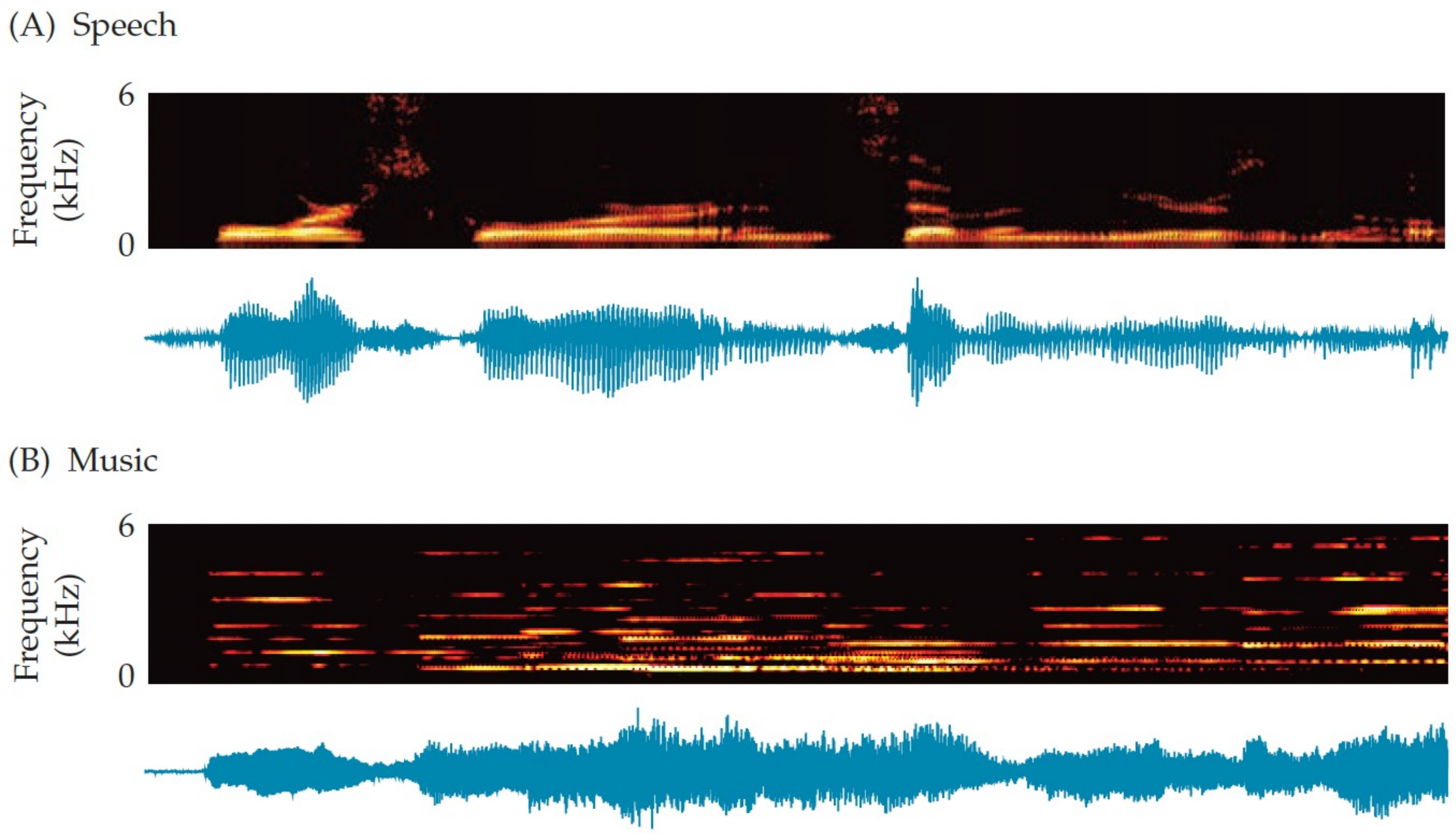
A pure tone is a periodic oscillation of air pressure at a single frequency



Characterized by amplitude (dB) and frequency (Hz)

Purves, Figure 13.1

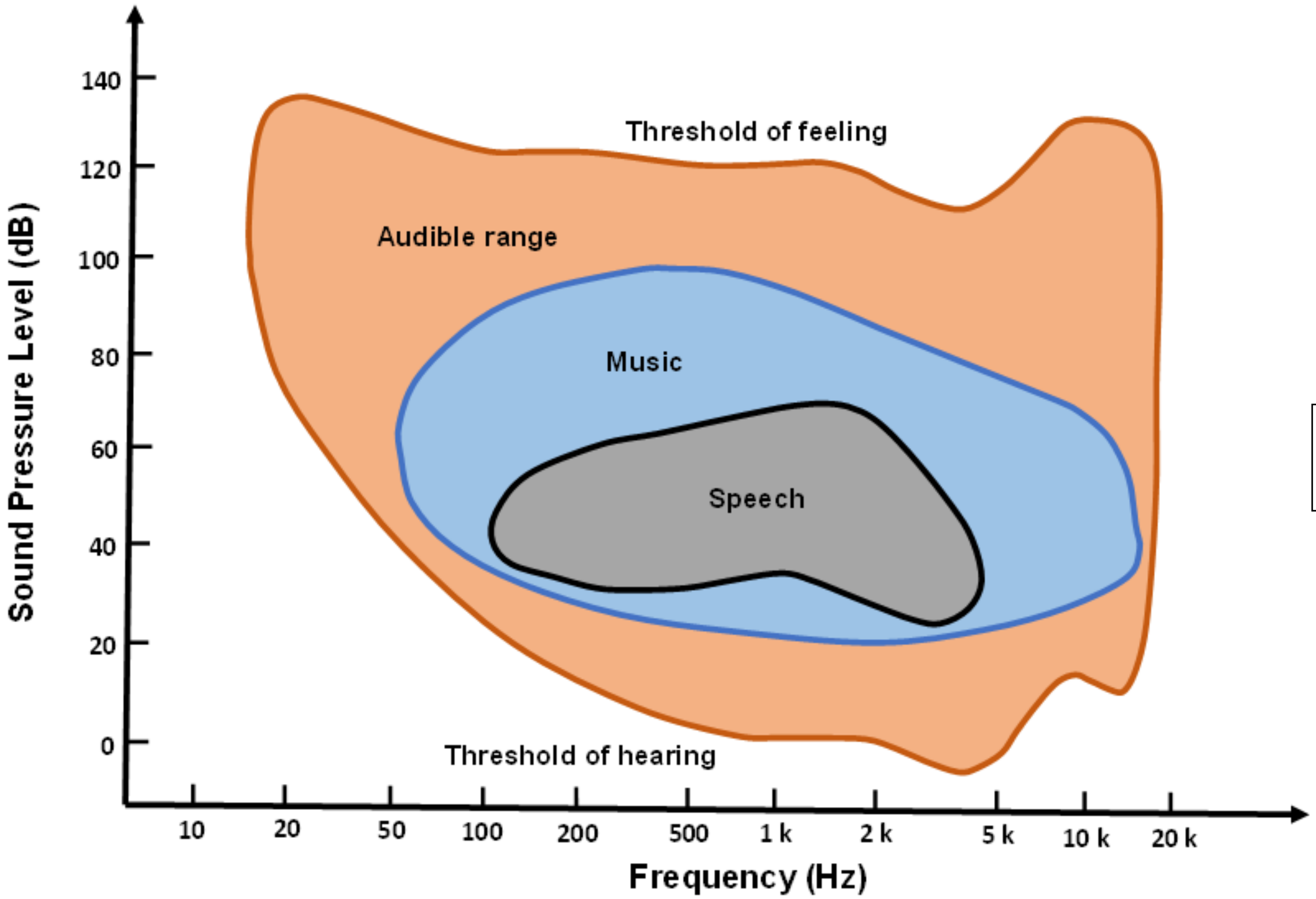
Complex sounds like speech and music



- Complex sounds are a superimposition of numerous "pure" sounds
- This superimposition of various sine waves is decomposed by the inner ear

Purves, Figure 13.3

The intensity and frequency range of hearing in humans

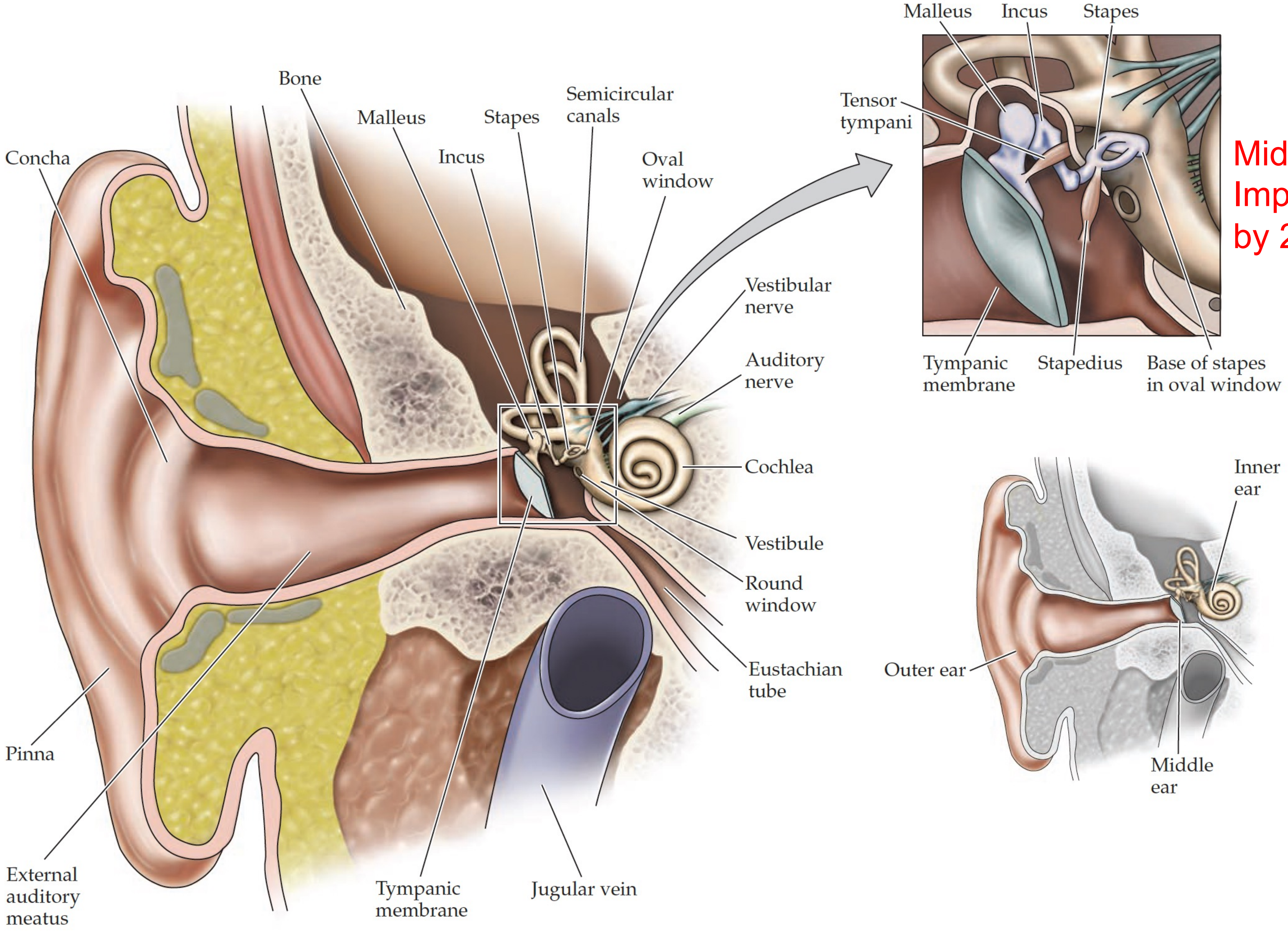


Human hearing ranges between 20 Hz – 20 kHz

https://www.sound2020.org/sound/audible/

What is the structure of the ear?

The outer and middle ear transmit sound wave energy to the inner ear

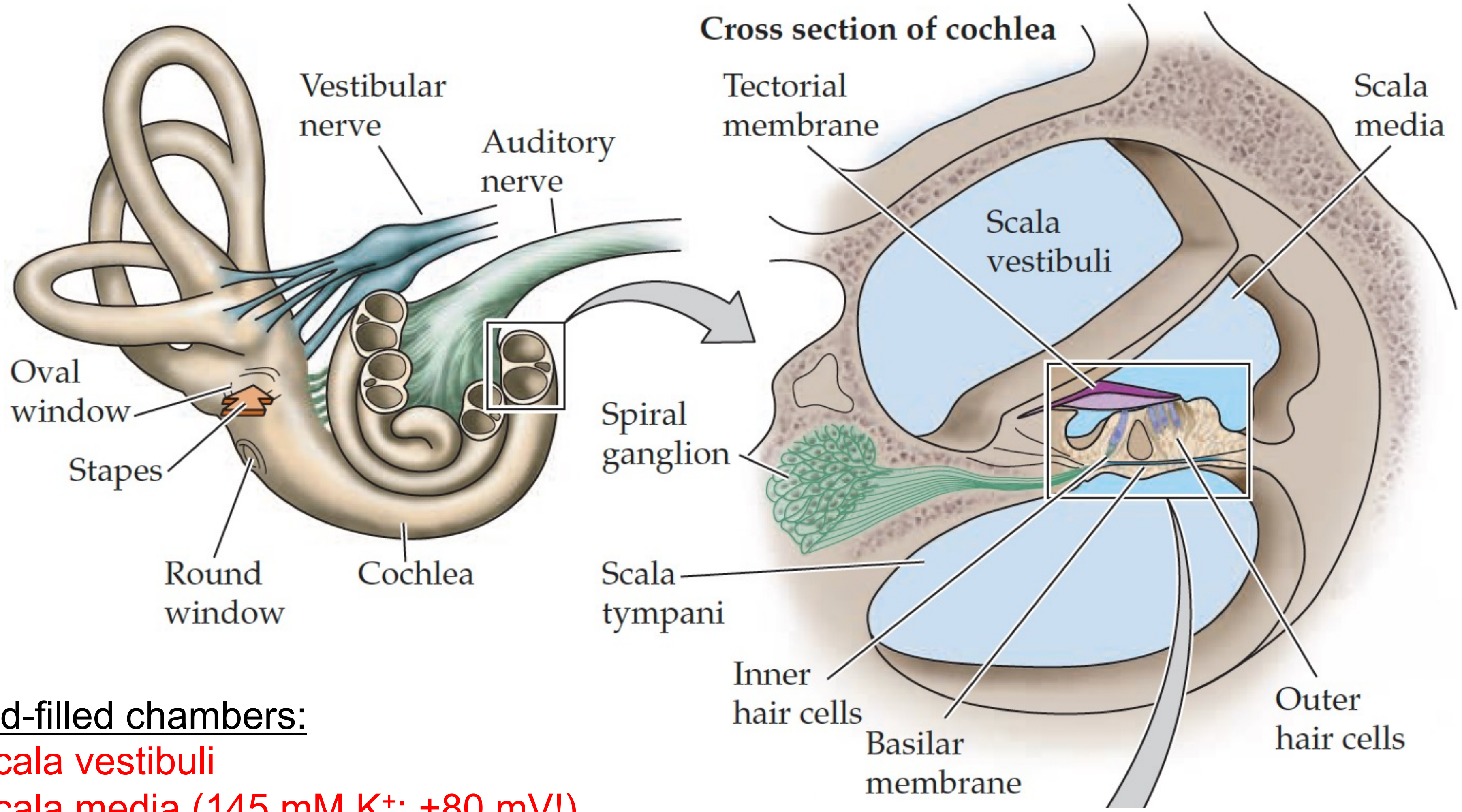


Middle ear: Impedence matching by 200x boost

Outer ear: focuses sound

Purves, Figure 13.4

The inner ear's cochlea

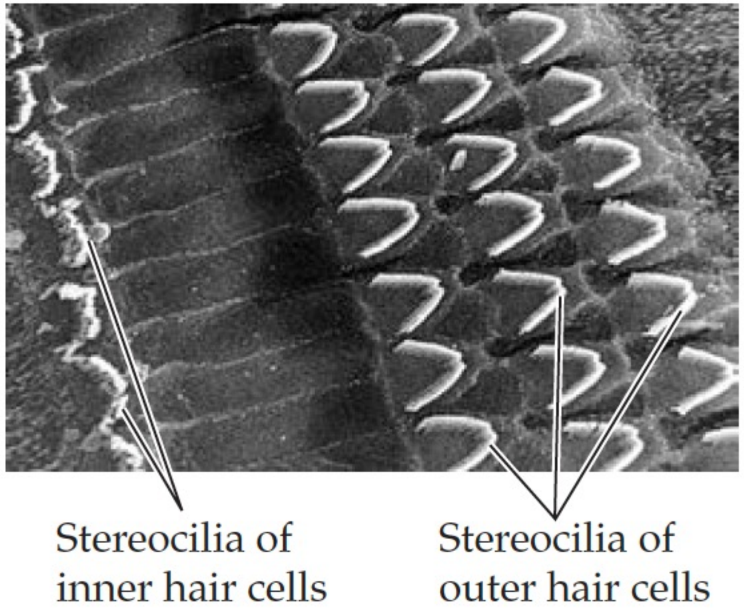


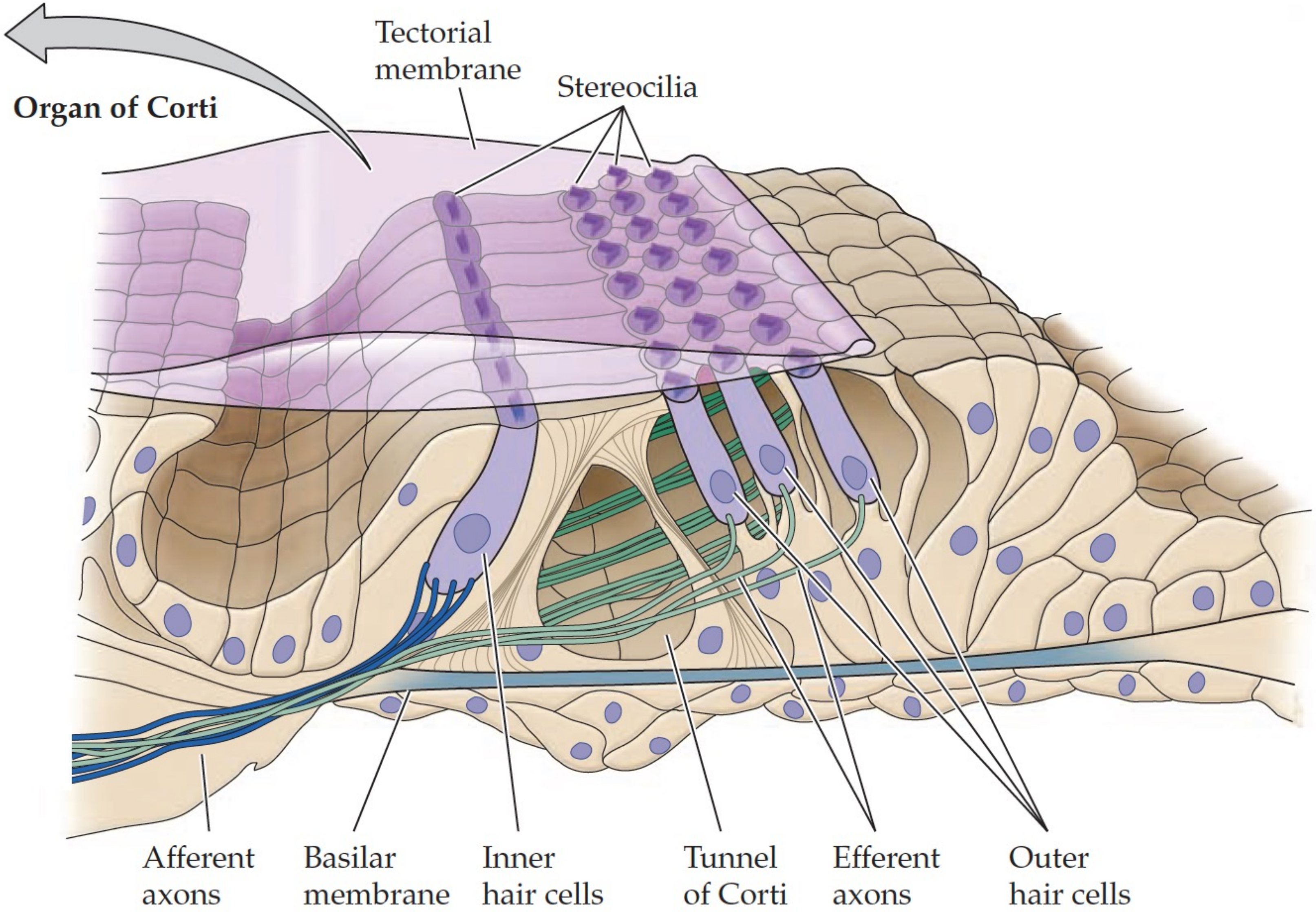
<u>3 fluid-filled chambers:</u>

- Scala vestibuli
- Scala media (145 mM K^+; +80 mV!)
- Scala tympani

Purves, Figure 13.5

Cochlea: Organ of Corti





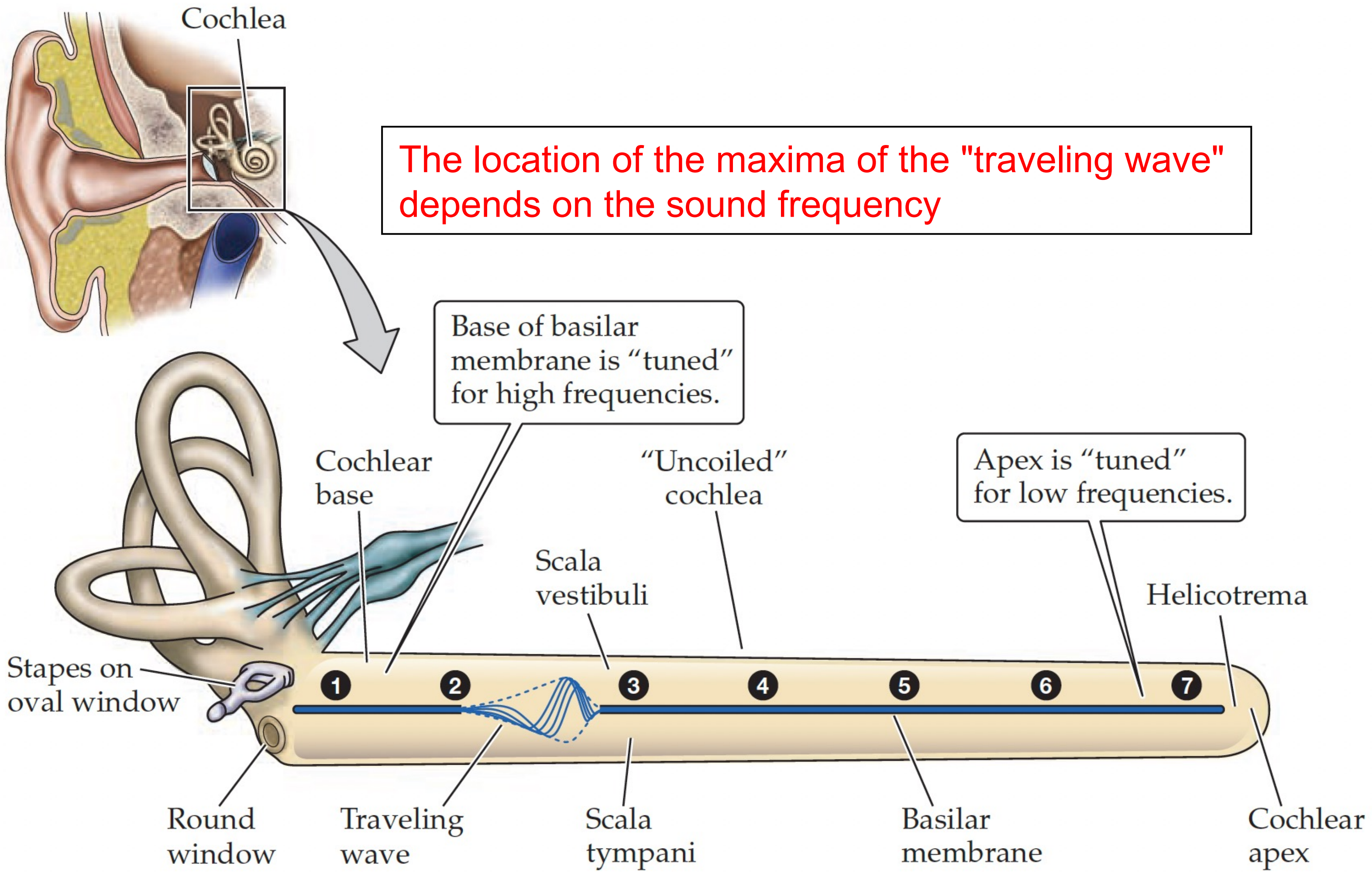
Hair cells are located within the Organ of Corti, between the Basilar and Tectorial membranes

Purves, Figure 13.5

How is sound mechanically transmitted to the inner ear?

Sound energy transmitted from the middle ear via the stapes produces a "travelling wave" in the cochlea

The location of the maxima of the "traveling wave" depends on the sound frequency

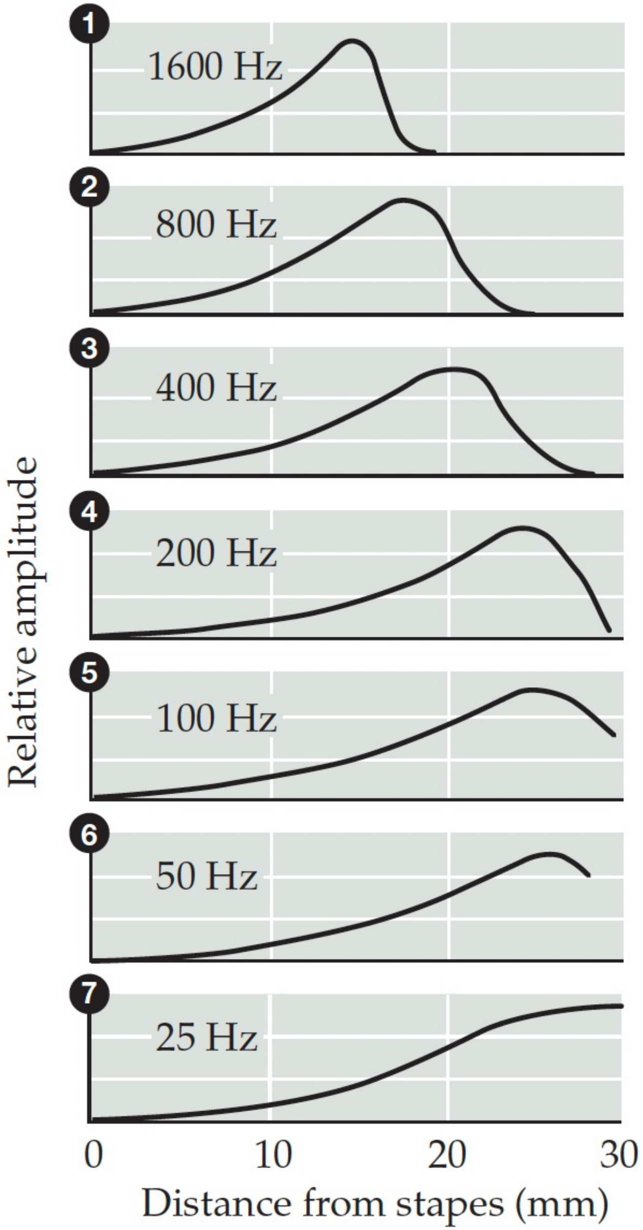


Base:
High frequency sounds

Apex:
Low frequency sounds

Purves, Figure 13.6

Location of maximum activity on the cochlea depends on sound frequency



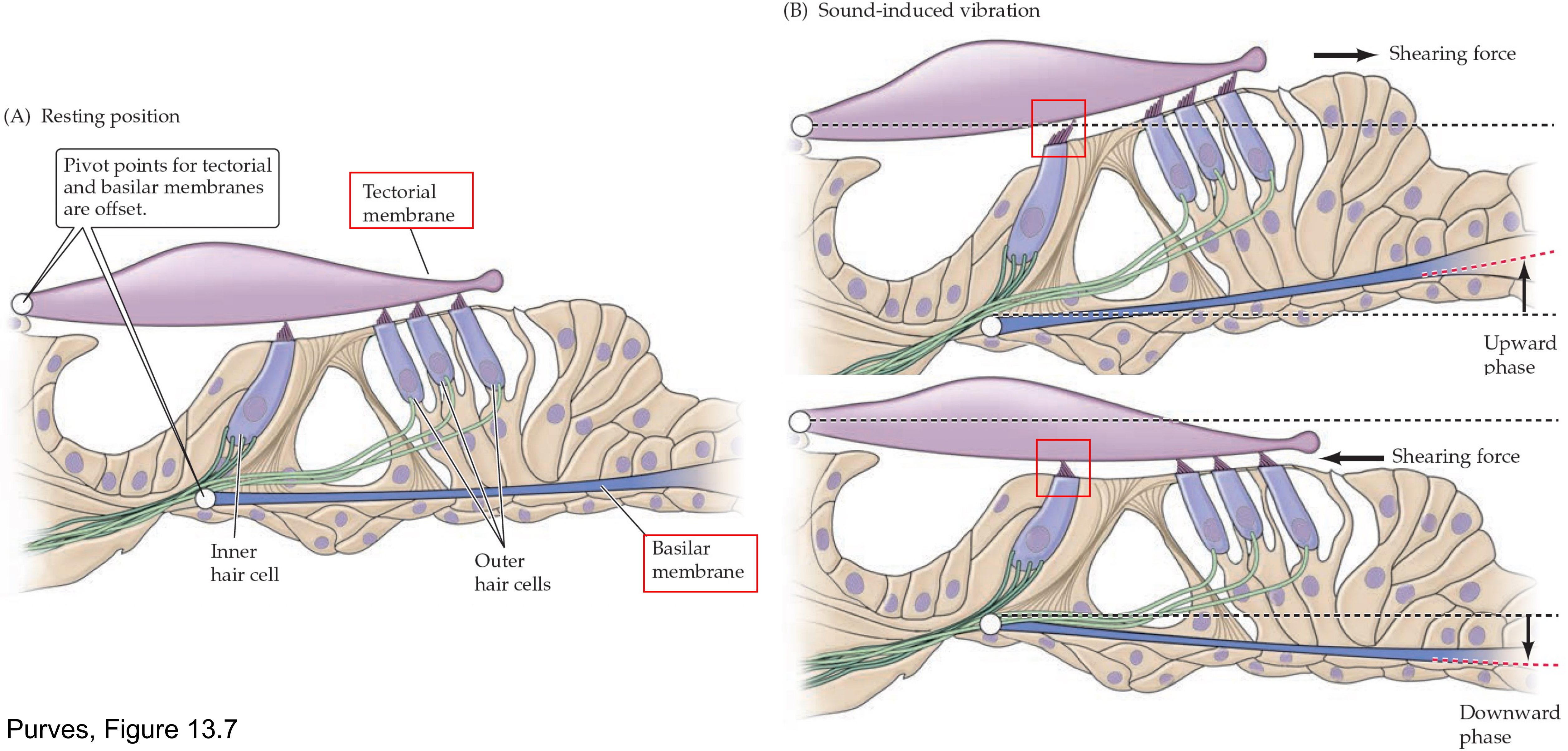
Purves, Figure 13.6

A “tonotopy" for decoding sound frequencies in the cochlea

Georg von Békésy
Cochlea model

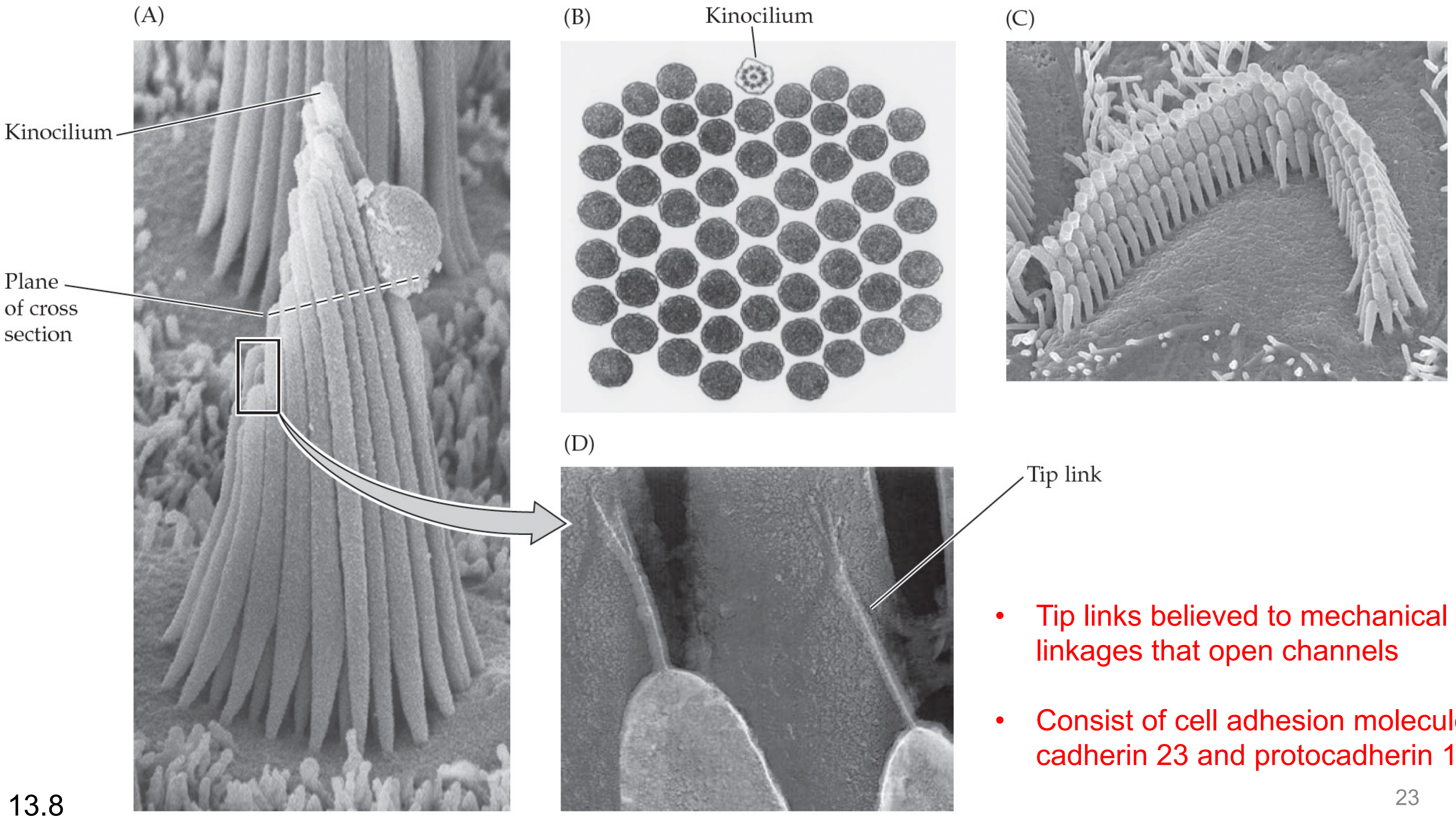
How are these sound waves
transformed into electrical potentials?

Basilar membrane movement creates a shearing force that bends hair cell stereocilia



Purves, Figure 13.7

The structure and function of the hair bundle in cochlear and vestibular hair cells



- Tip links believed to mechanical linkages that open channels
- Consist of cell adhesion molecules cadherin 23 and protocadherin 15

Purves, Figure 13.8

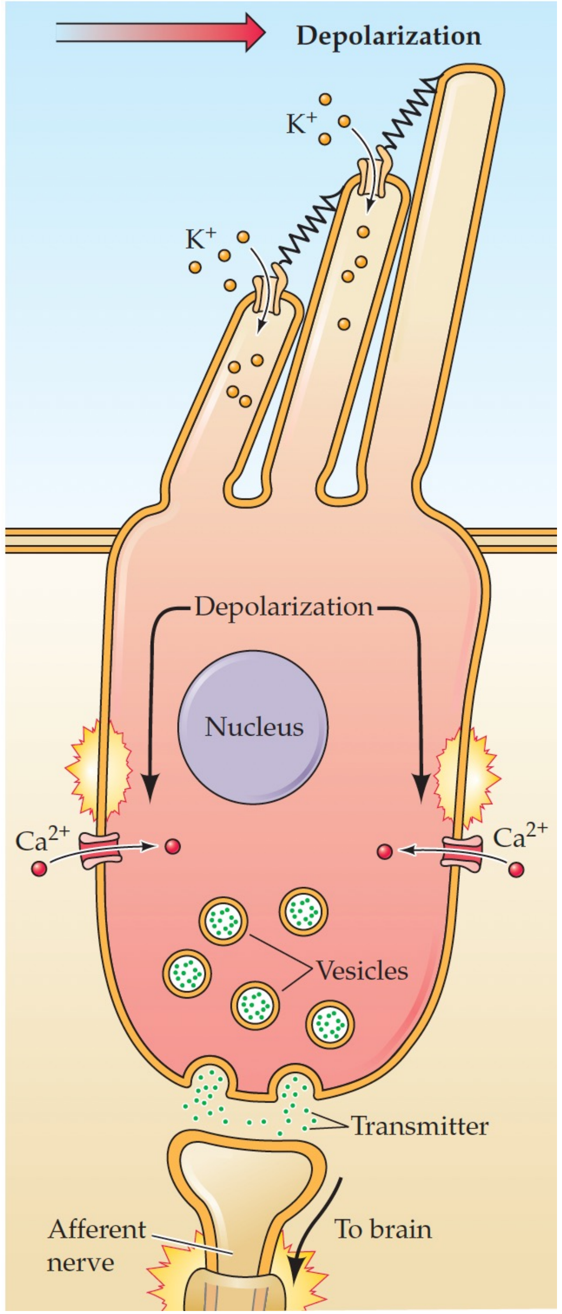
The "*primary sensory transduction*“ process in inner hair cells

<u>Signalling events in the inner hair cell (IHC)</u>:

- Stereocilia bend
- Tip links stretch
- Transduction channel opens

Note: the mechanosensitive ion channel: cation-selective hcMET channel is unknown!

- Depolarization of IHC (Scala media high K^+!)
- Ca^{2+} channel opening at the base of the IHC
- Local Ca^{2+} influx,
- Transmitter release at the base

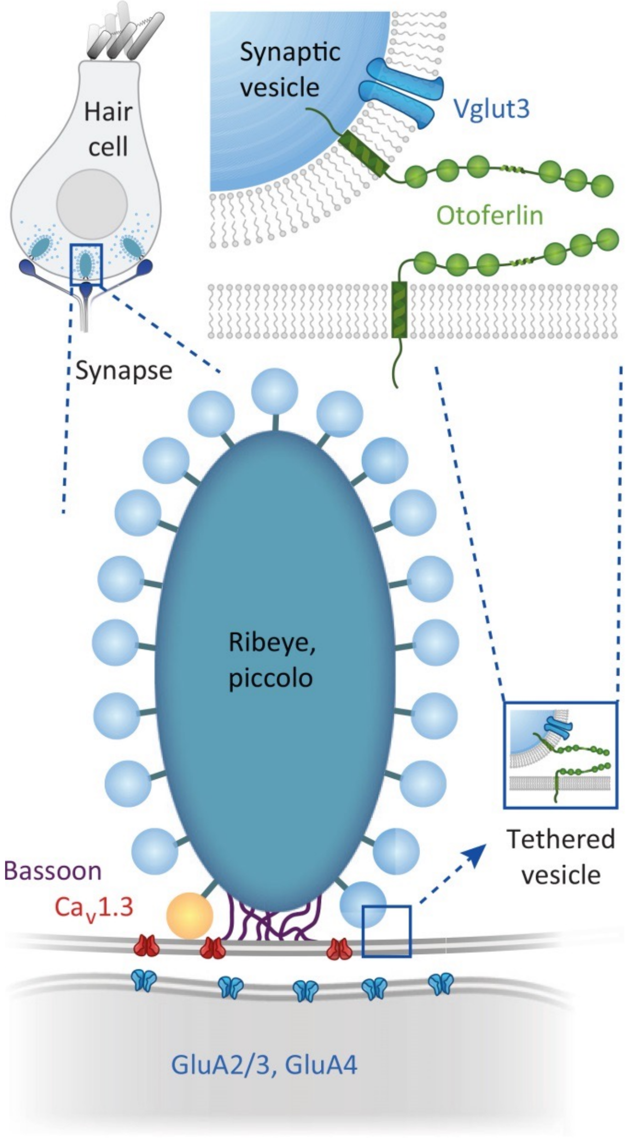


0.3 nm movements – the diameter of gold atom – can be detected!

Glutamate is the transmitter at the IHC – afferent nerve synapse

Purves, Figure 13.9

Proteins and structure of the **ribbon synapse** in inner hair cells (compared to regular CNS excitatory synapses)



- **Inner hair cells (IHCs) of the cochlea have ribbon-synapses to release glutamate**
- "Ribbon-type synapses" are also found in photoreceptor cells and bipolar cells of the retina to release glutamate
- These neurons have another commonality: graded membrane potential (V_m) signaling, and no action potentials

Pangrsic et al. 2012 *TINS*

Receptor potentials generated by a single IHC in response to pure tones

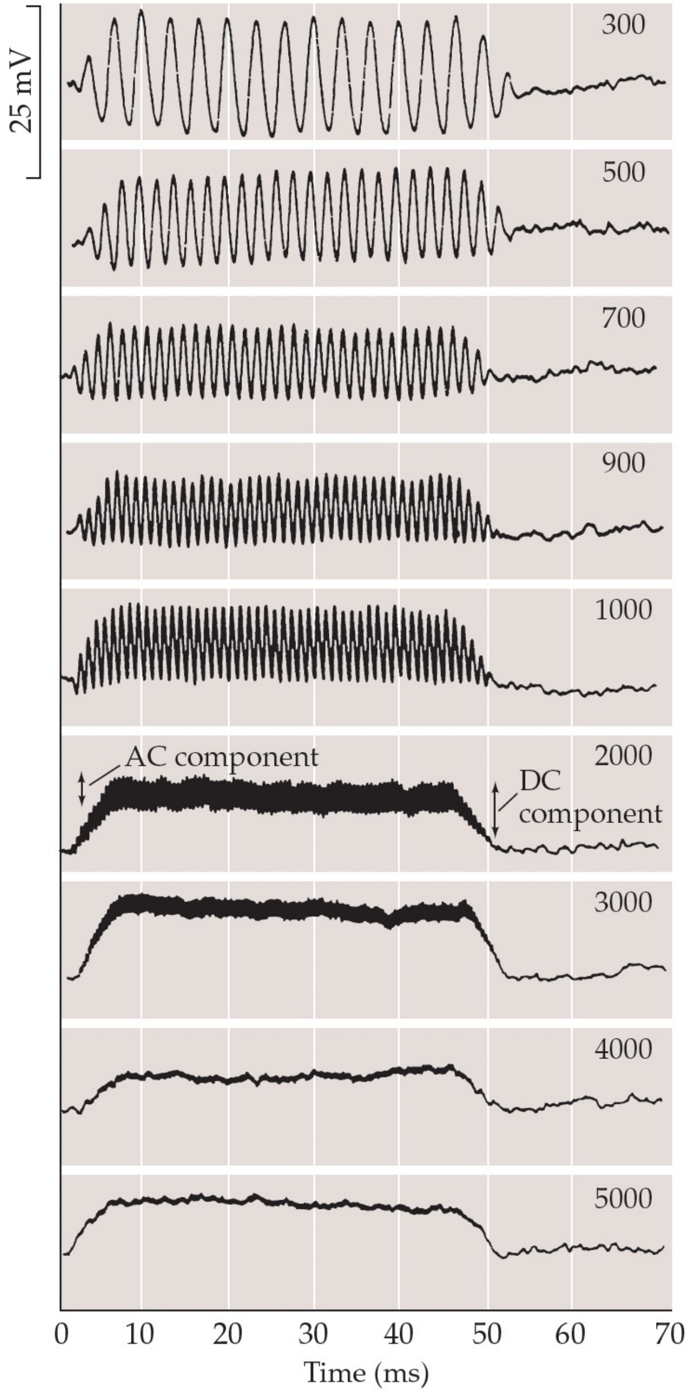
Methods:
- Guinea pig, *in-vivo* intracellular recording of inner hair cells
- Pure sound stimulation 80 dB, at indicated frequency

Note:

(1) "Phase locking" of IHC membrane potential at up to ~2 kHz

(2) Hair cells do not generate APs

(3) For sounds above 2 kHz, frequency is only encoded by “tonotopy“

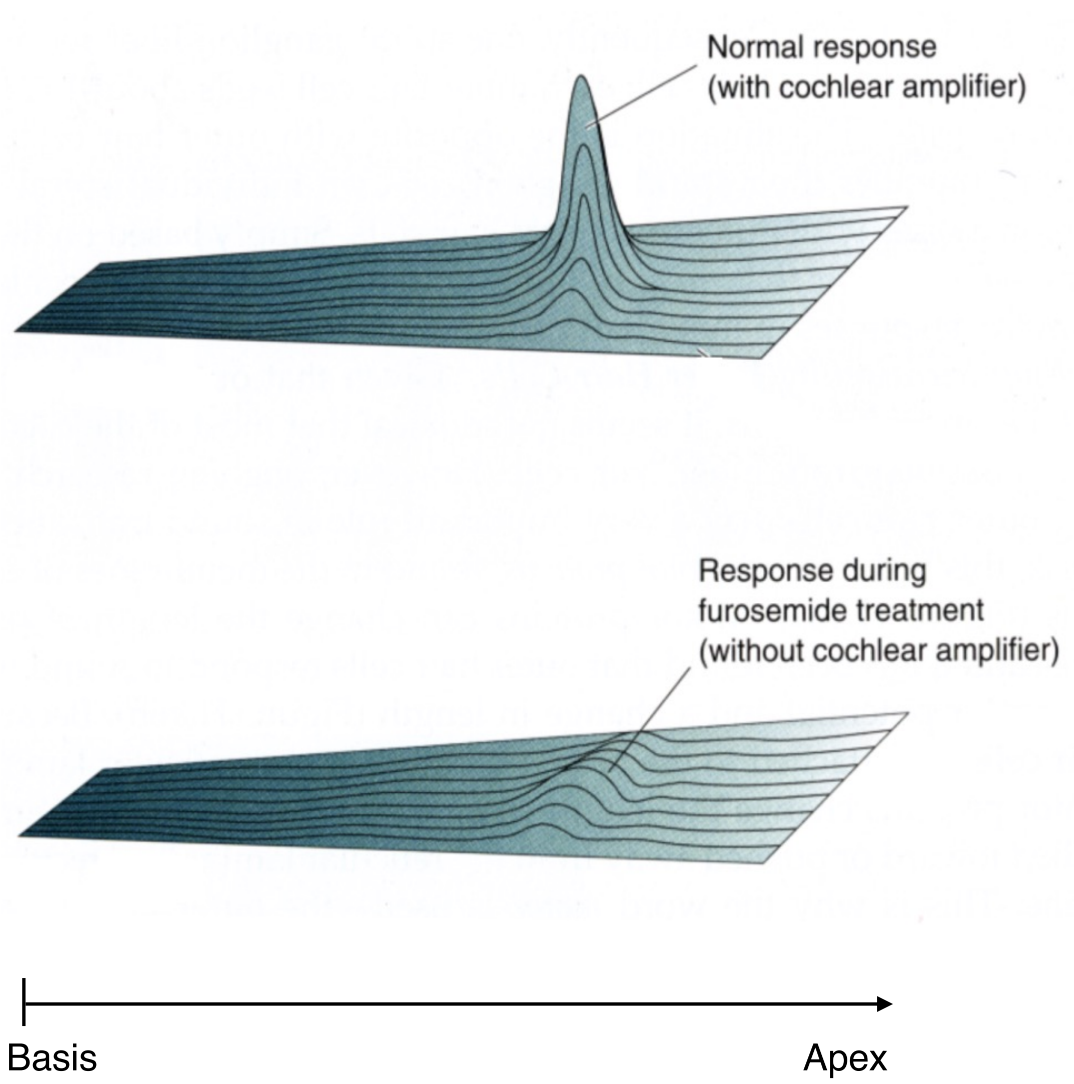


Tone frequency (Hz)

Purves, Figure 13.10

What do the outer hair cells do?

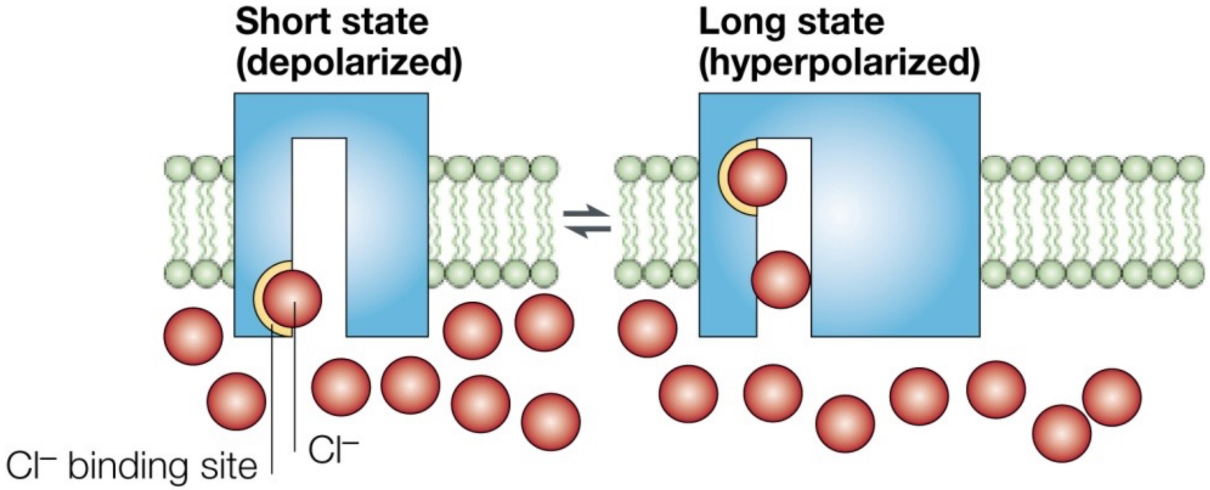
Outer hair cells function as "cochlear amplifiers"



OHC active movements
amplify the deflection of the cochlear partition

A possible cause of “tinnitus“ (ringing in the ears)

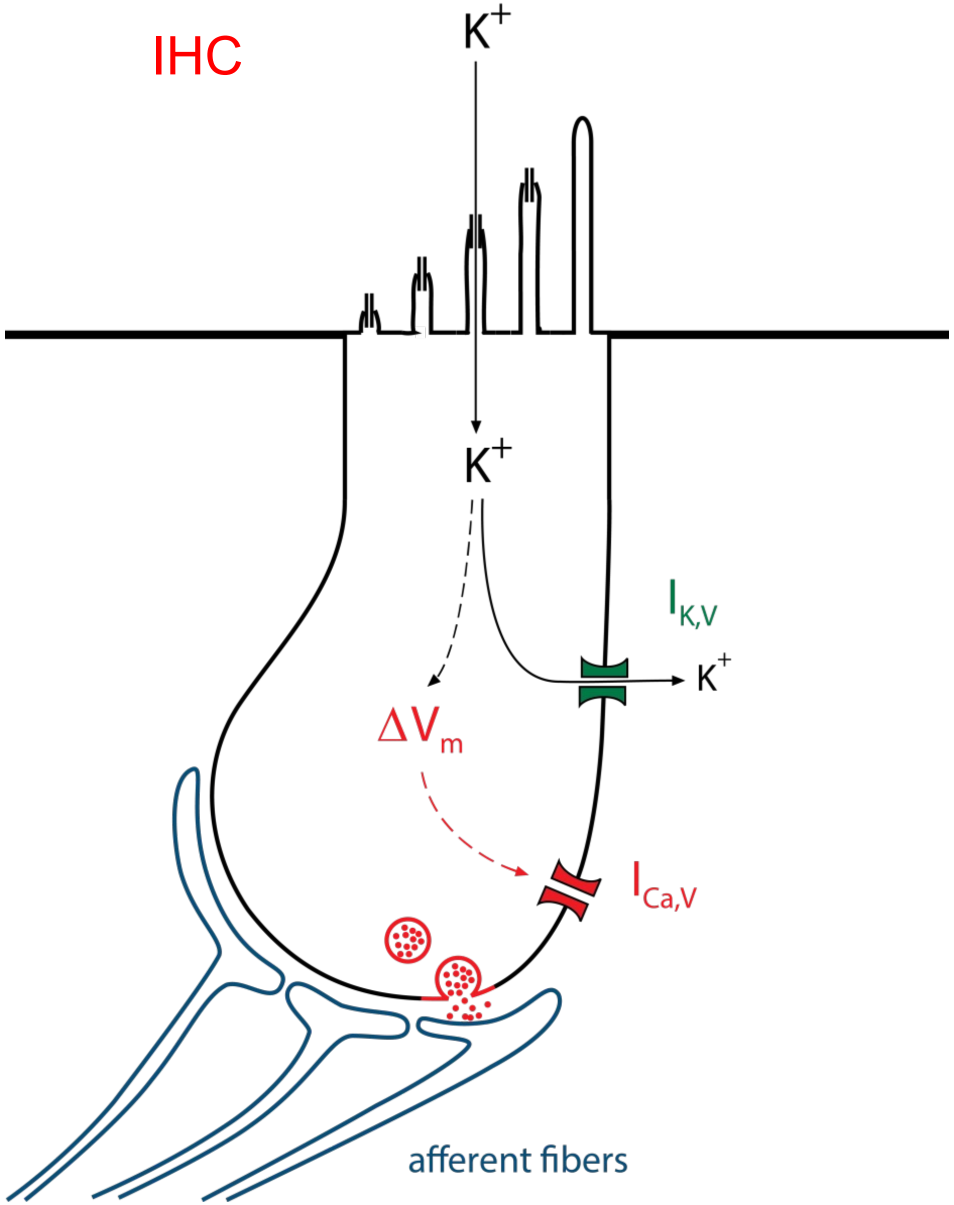
Fast changes in length of outer hair cells are caused by **prestin**, a voltage-dependent motor protein in the OHC membrane

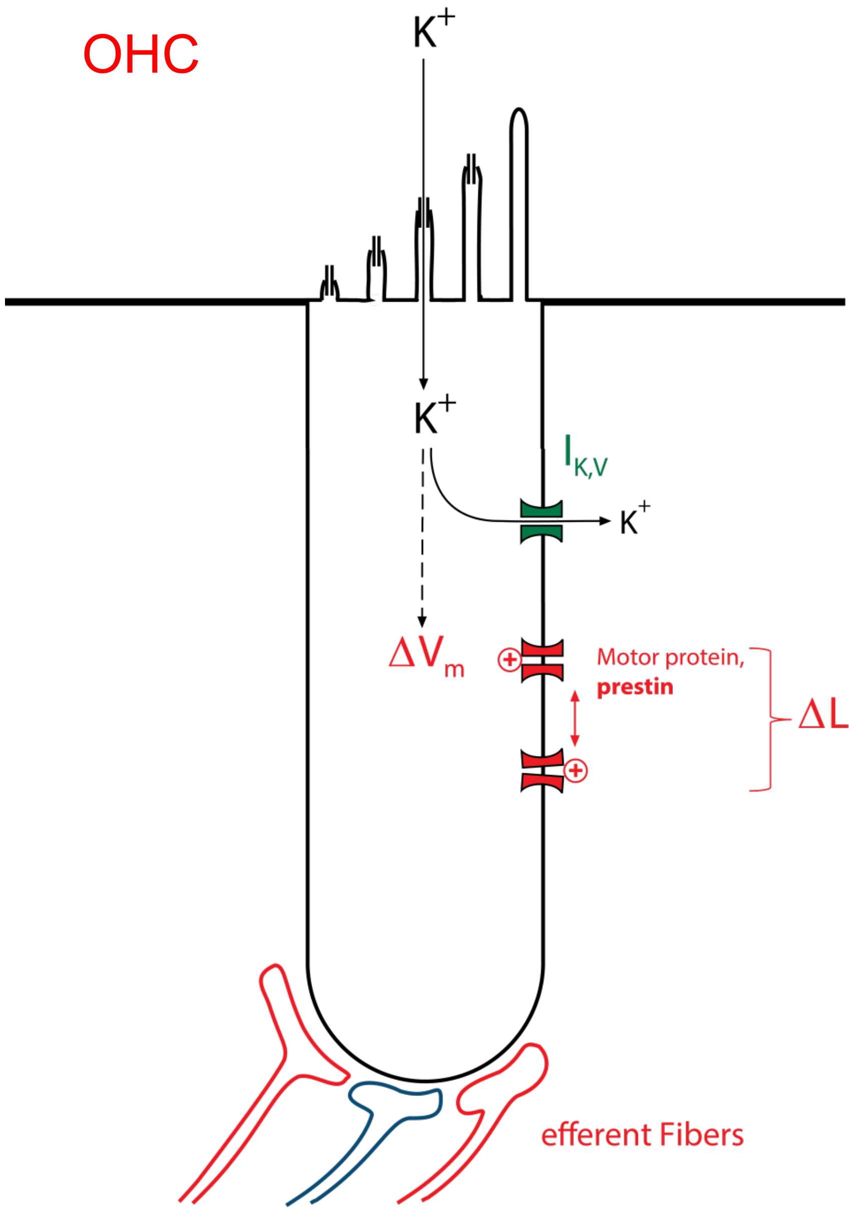


Zenner et al. (1985) *Hearing Research*

Ashmore (1987) *J. Physiology*

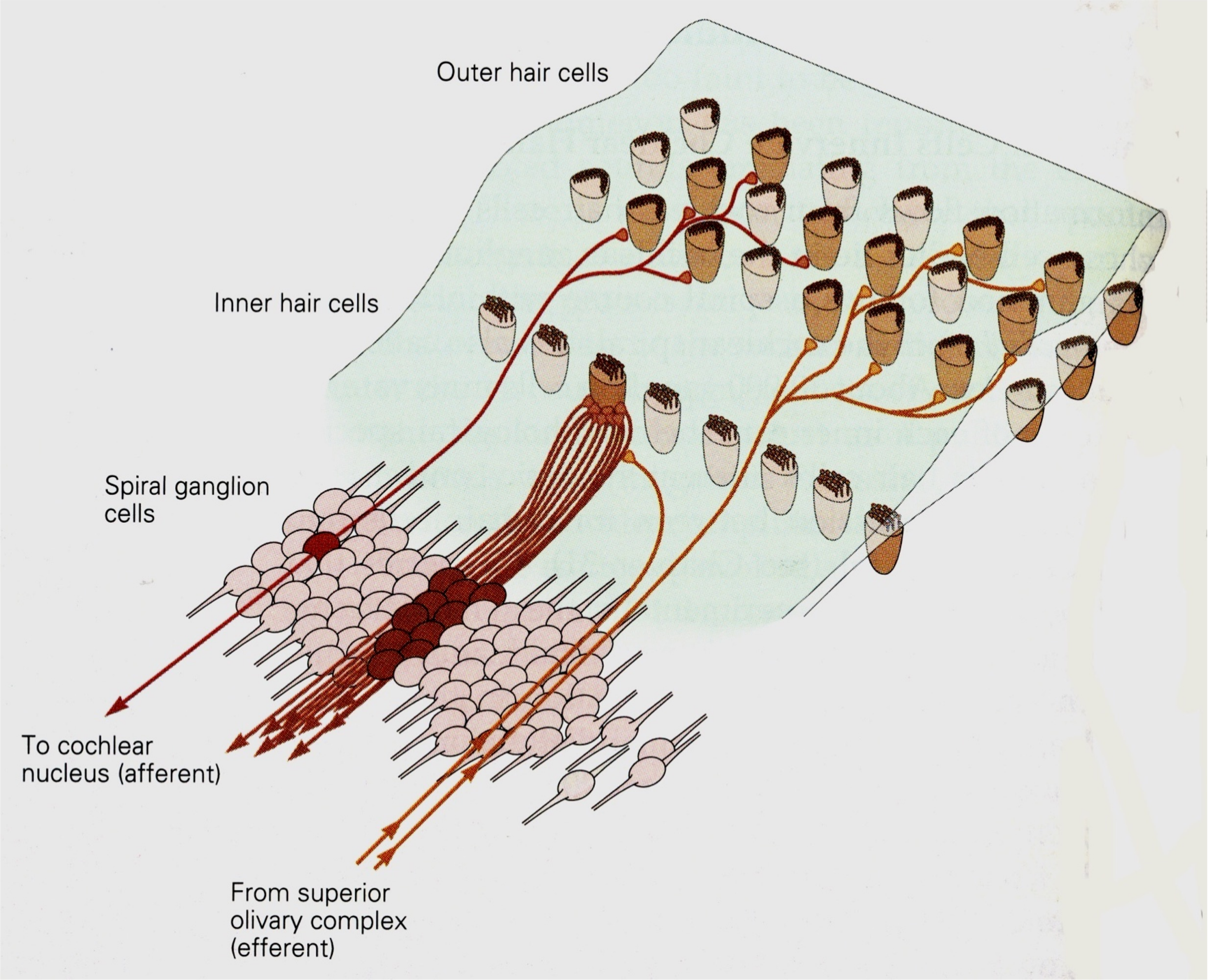
Summary of inner and outer hair cell function





How does information travel from inner hair cells
to the central nervous system?
(the auditory nerve fiber synapse)

Innervation of inner hair cells (and outer hair cells)



<u>IHC</u>:
Innervated by 8 – 10 *afferent* fibers (dendrites of spiral ganglion cells)

<u>OHC</u>:
Innervated by *efferent* fibers from auditory brainstem (superior olivary complex)

Also innervated by a few *afferent* fibers

Summary of inner hair cell to spiral ganglion neuron connectivity

IHC — Releases glutamate, is contacted by ***several*** SGN dendrites

- Has **1 dendrite** which contacts a single IHC
- AMPA receptors, and **generation of an AP**

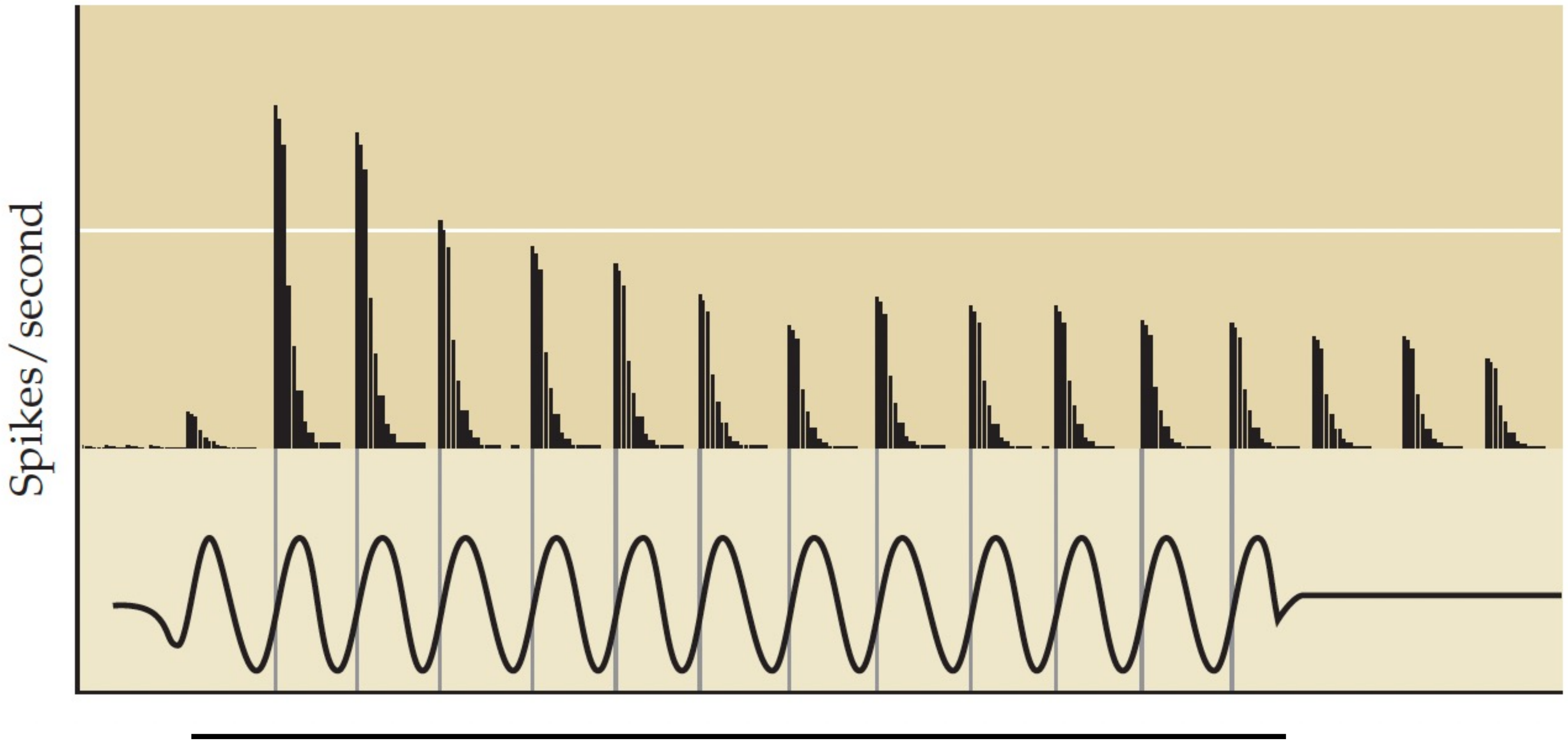
Spiral Ganglion Neuron (SGN)

- Has **1 axon, or auditory nerve fiber**
- Leaves the cochlea & projects to brainstem
- Innervates neurons in cochlear nucleus; transmitter: glutamate

Brainstem (Cochlear Nucleus)

How do auditory nerve fibers along the cochlea represent sound?

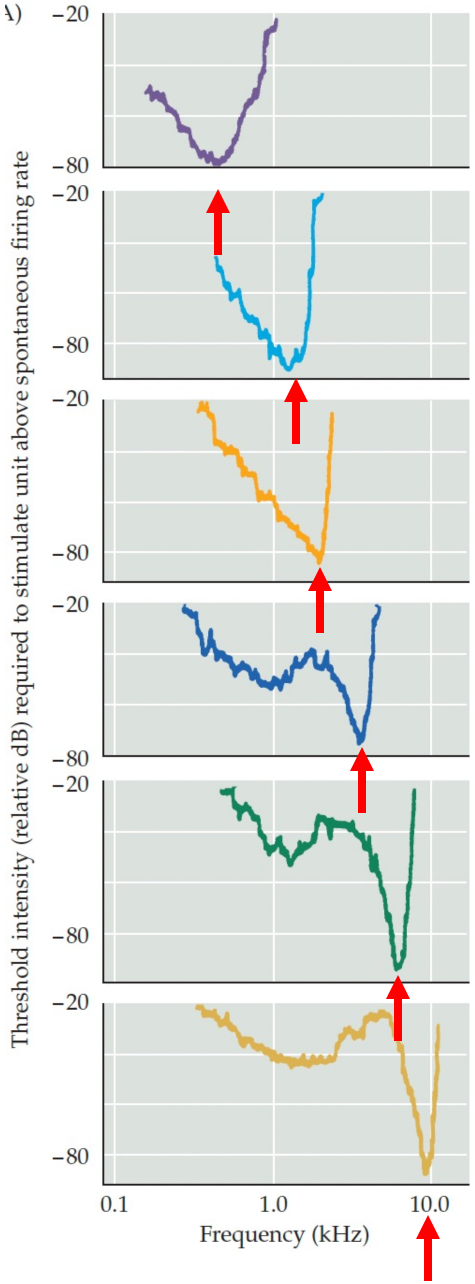
Action potentials in a low-frequency auditory nerve fiber are "phase locked"



Duration of the tone (= 50 ms)
260 Hz tone

Purves, Figure 13.12

Frequency tuning curves of auditory fibers

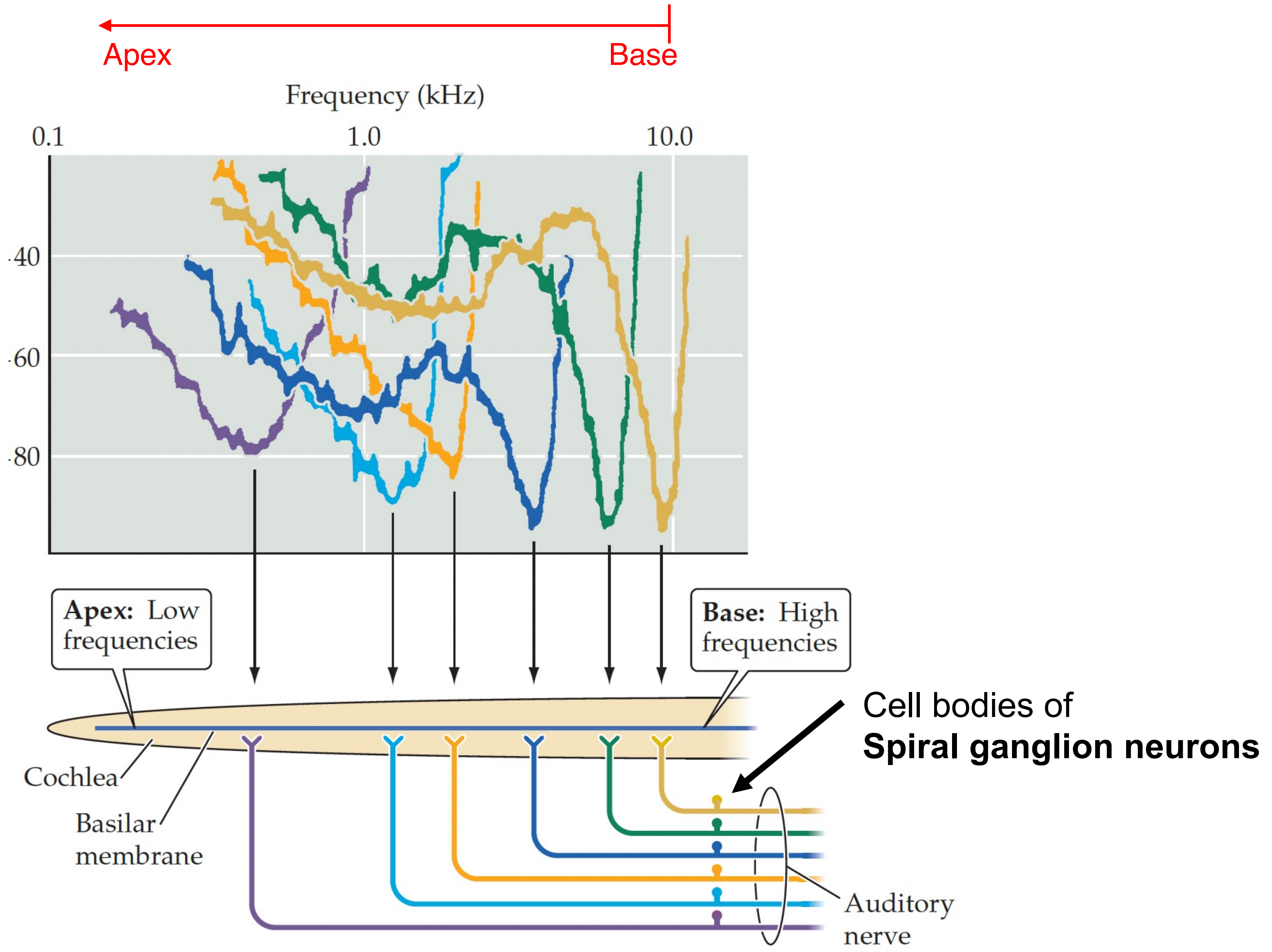


Weakest sound intensity
to which the neuron will respond

- The firing frequency of six different auditory nerve fibers was recorded
- Each fiber has a "characteristic" sound frequency at which it fires with a **minimal threshold**

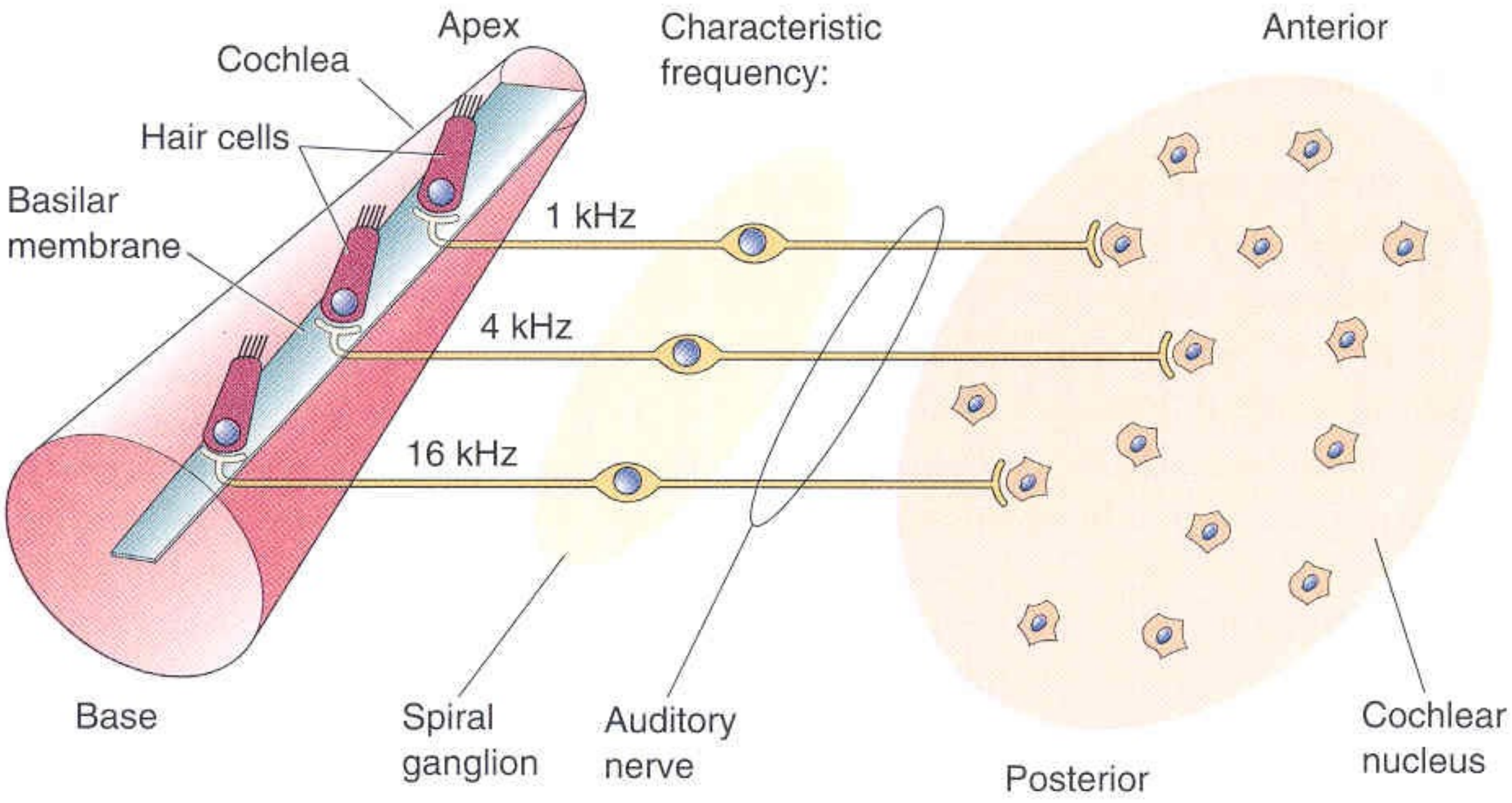
Purves, Figure 13.12

"Tuning" of auditory nerve fibers to sound frequencies depends on the location along the cochlea (“tonotopy“)



Purves, Figure 13.12

Tonotopic representation of sound frequency in the cochlea, spiral ganglion and cochlear nucleus



The tonotopic map is carried through to the **cochlear nucleus** and up to **primary auditory cortex** A1!

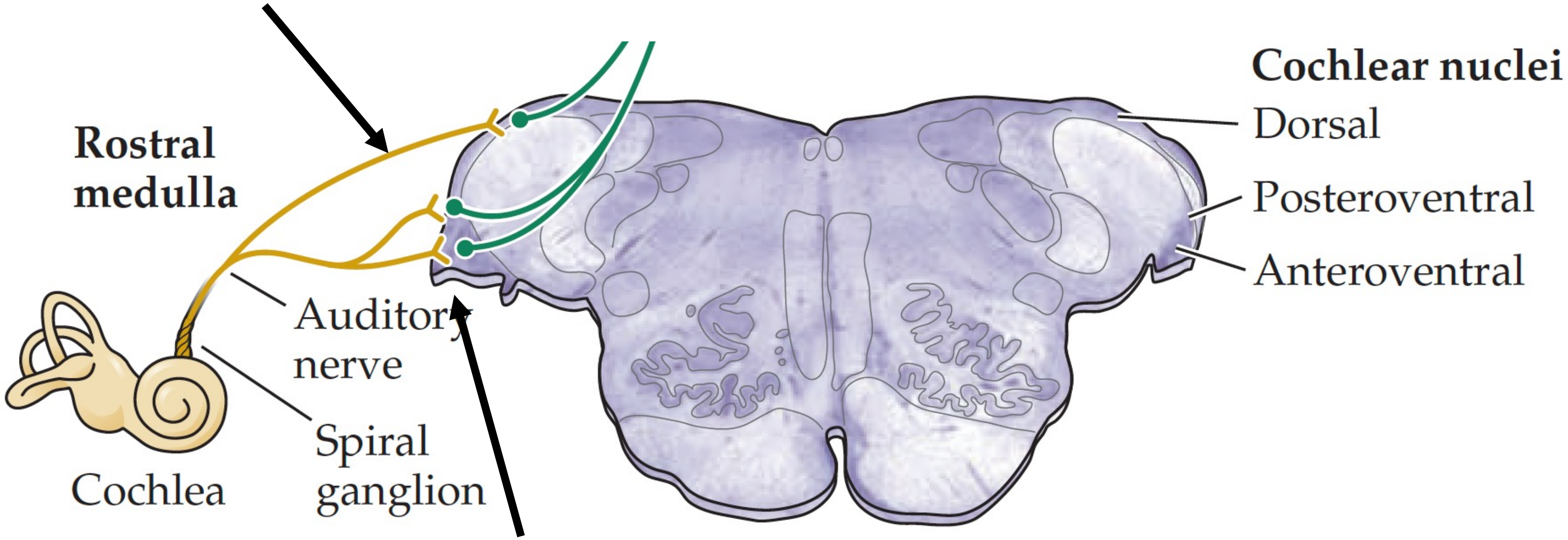
A “Labeled line” coding mechanism

Bear, "Exploring the Brain"

How does the central nervous system (CNS) process sound?

Auditory nerve fibers project to the brainstem‘s **cochlear nucleus**

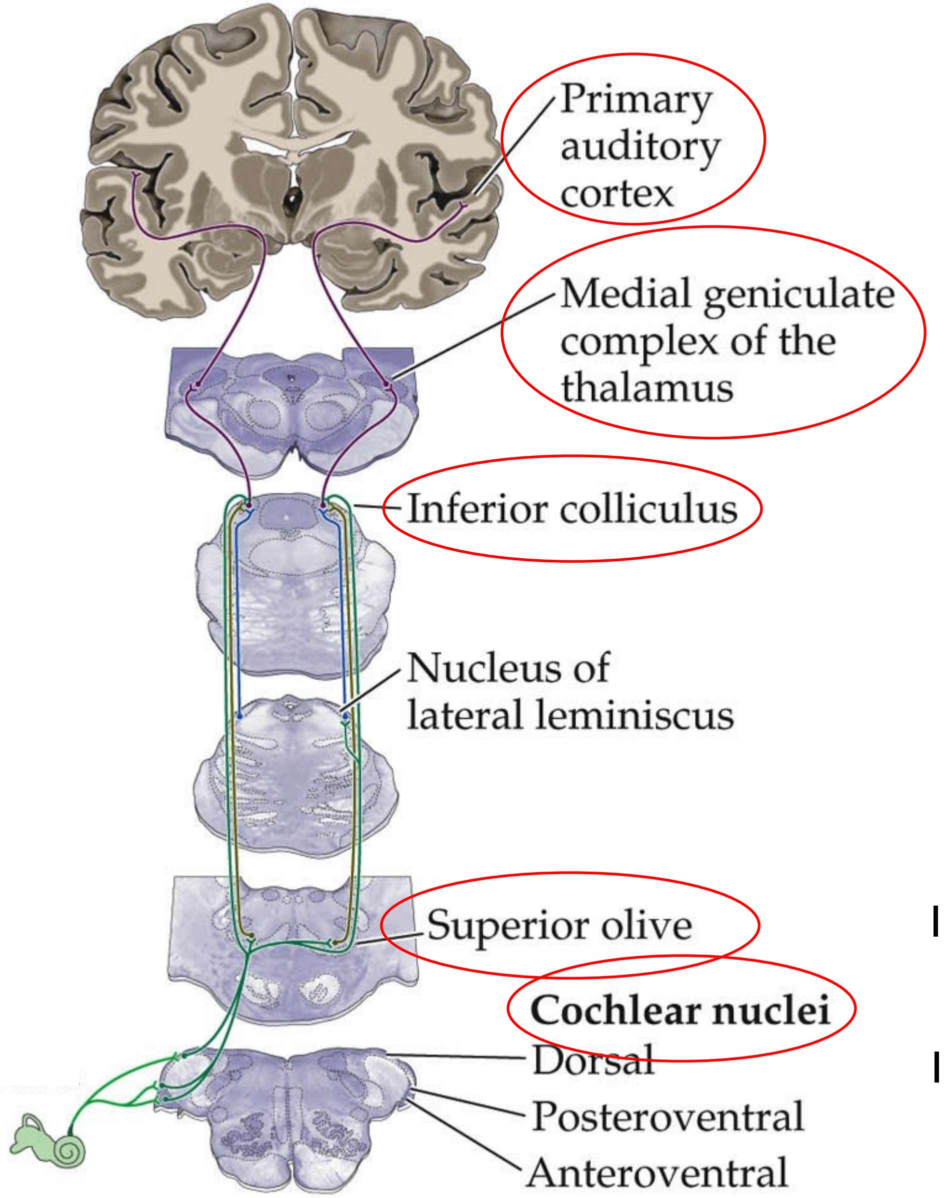
Axons of spiral ganglion neurons (i.e., auditory nerve fibers)



Excitatory (glutamate) synapse between auditory nerve fibers and neurons of the **cochlear nucleus**

Purves, Figure 13.13

The major auditory nuclei and ascending auditory pathways



I.e., Auditory thalamus

In midbrain – spatial topography map

In pons - localization

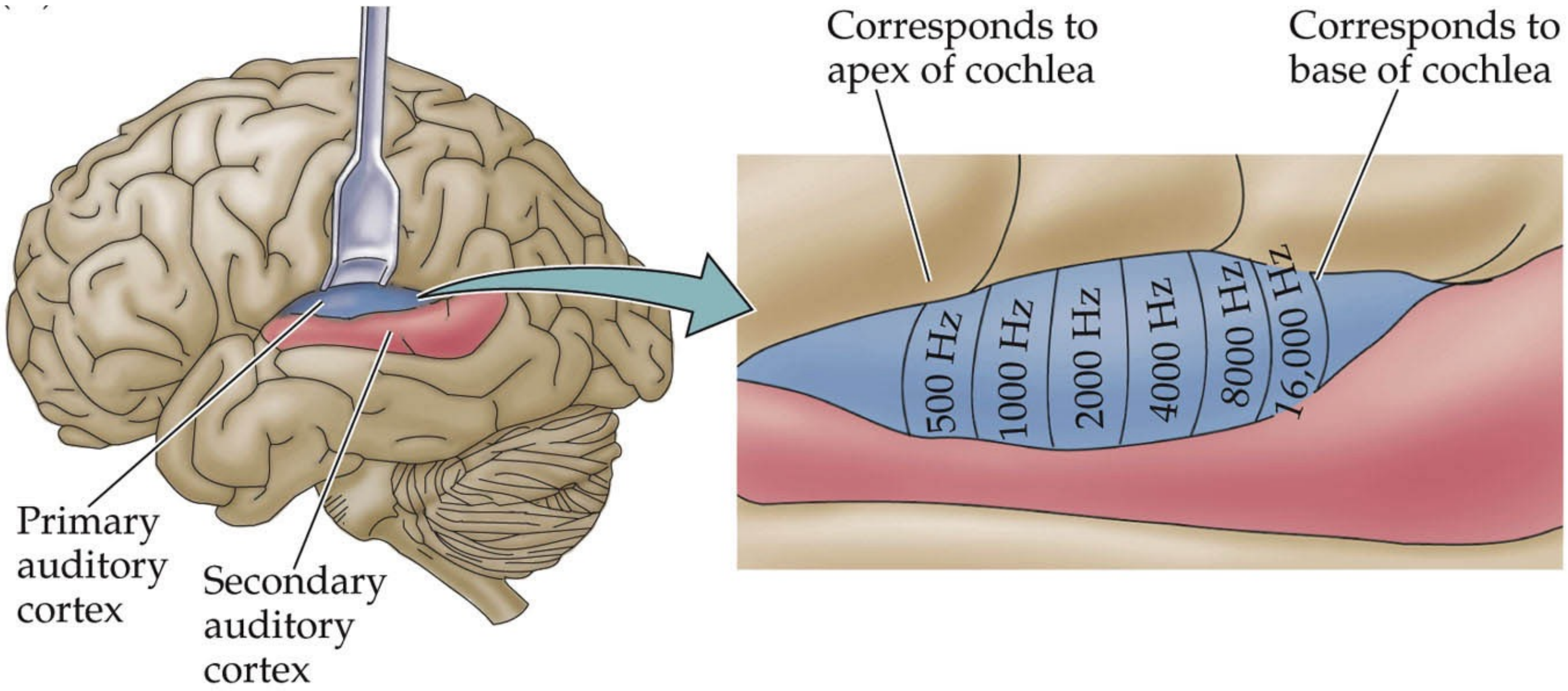
In medulla

Hindbrain

Note:
- Mutliple parallel pathways
- Bilateral projections

Purves, Figure 13.13

The human auditory cortex



- There is also a "tonotopic map" in the primary auditory cortex ("A1")
- This implies that tonotopic information is correctly wired from all lower auditory brain nuclei

Purves (older version), Figure 13.16

Sound source localization: a demonstration

Sound source localization

Because the location of sounds in the environment are *not* mapped onto the surface of the sensory epithelium (instead, sound frequency is mapped there)

Sound location must be computed from several cues:

(1) Interaural Timing Difference of sound arrival ("ITD") – below 3 kHz phase-locked signals

(2) Interaural Intensity Difference (“IID“) – above 3 kHz

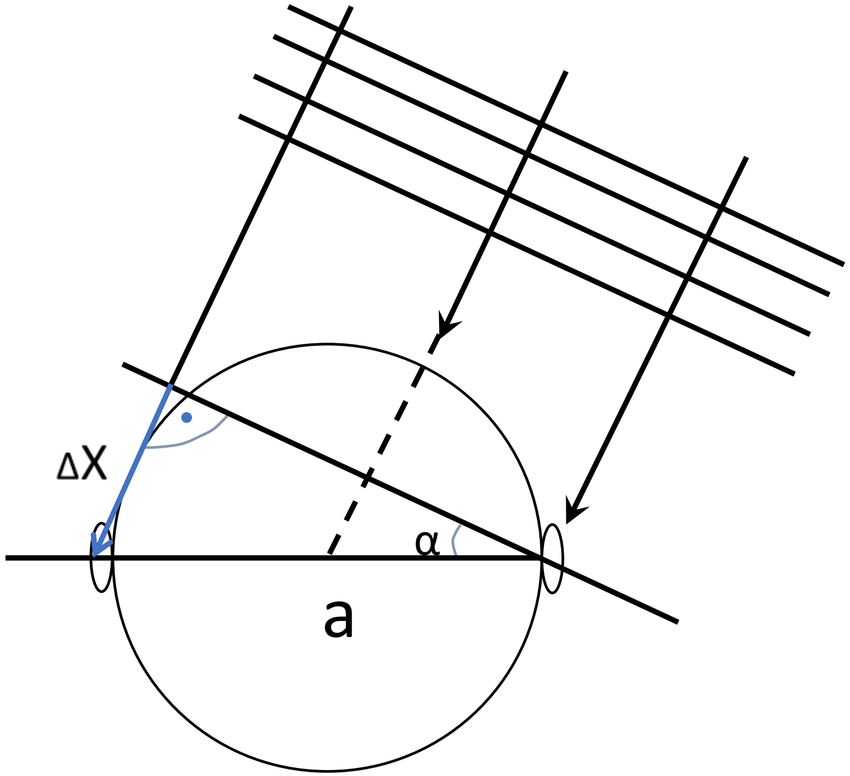
These computations occur in a brain area called the "superior olivary complex" (SOC), which receives input from the ventral cochlear nucleus (VCN)

Two important structures in the SOC:

(1) Medial Superior Olive (MSO) uses ITD cues

(2) Lateral Superior Olive (LSO) uses IID cues

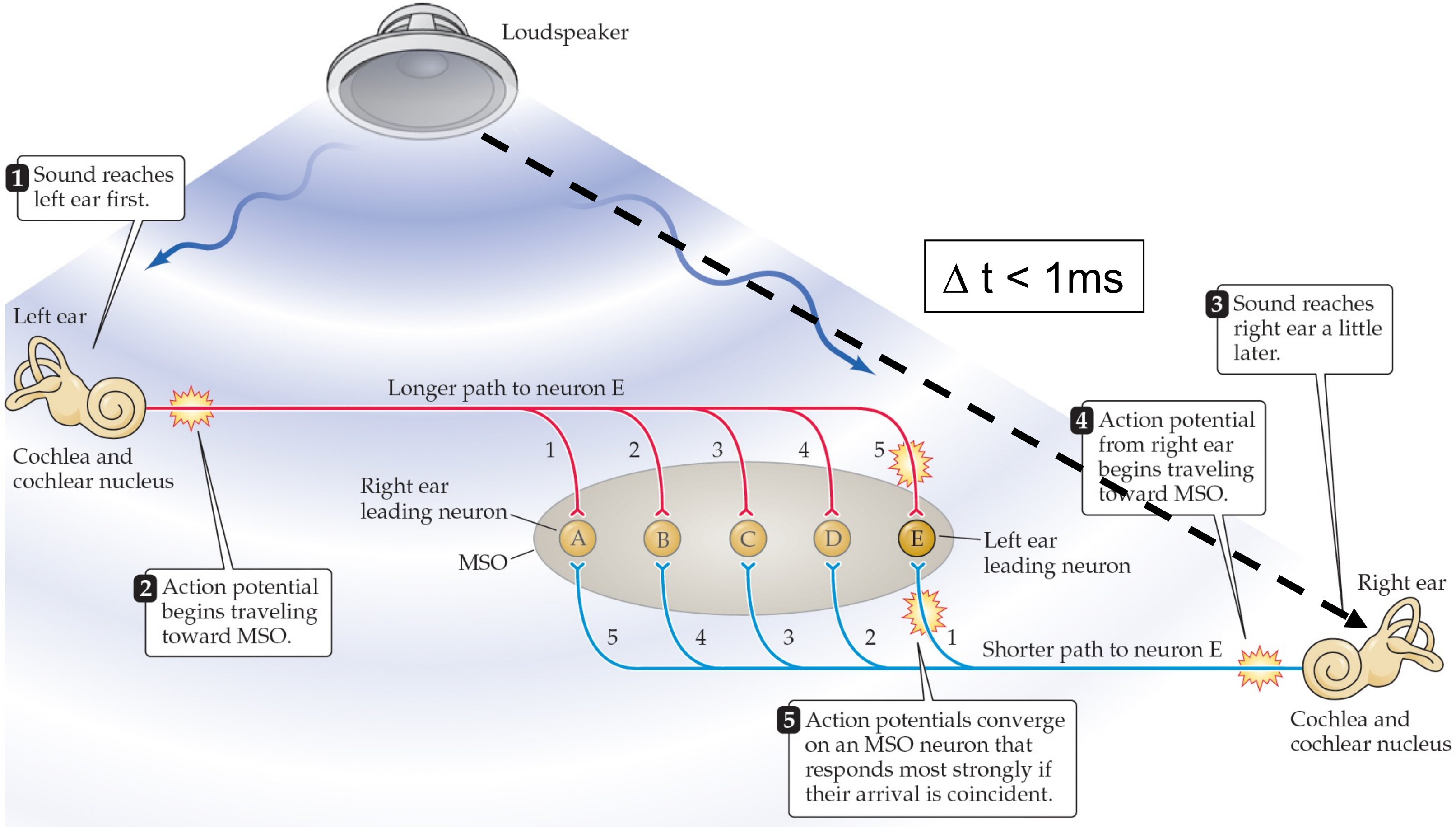
ITD depends on small differences in sound arrival time at each ear



head diameter: a = 15 cm = 150 mm
speed of sound: c = 340 m/s (= 340 mm/ms)
$\Delta X = a * sin\alpha$ = 150 mm * sin 10° = 26 mm
$\Delta t = \Delta X / c$ = 26 [mm] / 340 [mm/ms] = 0.077 ms

This is calculated as a function of head width and incoming sound angle.
In practice it is well below 1ms (!) even for a large angle of α = 10°

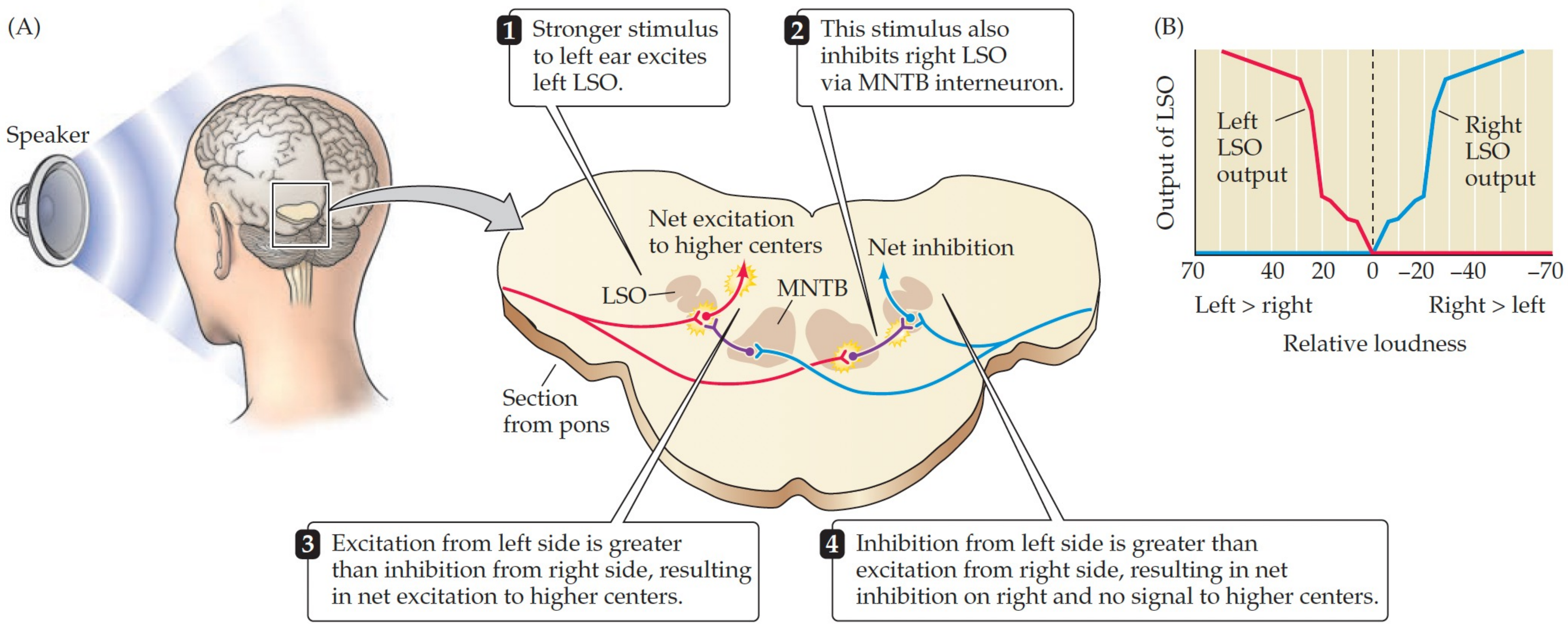
The MSO (*medial superior olive*) nucleus in the superior olive computes the **interaural time differences (ITD)**



Coincidence detection of excitatory inputs: Postsynaptic neuron fires AP **only** when the two EPSPs arrive within << 1 ms!

Purves, Figure 13.14

The Lateral Superior Olive (LSO) and MNTB nuclei in the superior olive compute **Interaural intensity difference (IID)**



Purves, Figure 13.15

Summary of sound source localization

- The MSO calculates Interaural Time Difference (ITD)

- The LSO calcultes Interaural Intensity Difference (IID)

- Many "basic" computations take place at "lower centers"
like the superior olive (hindbrain) and inferior colliculus (midbrain)

Congenital deafness can be treated using a cochlear implant

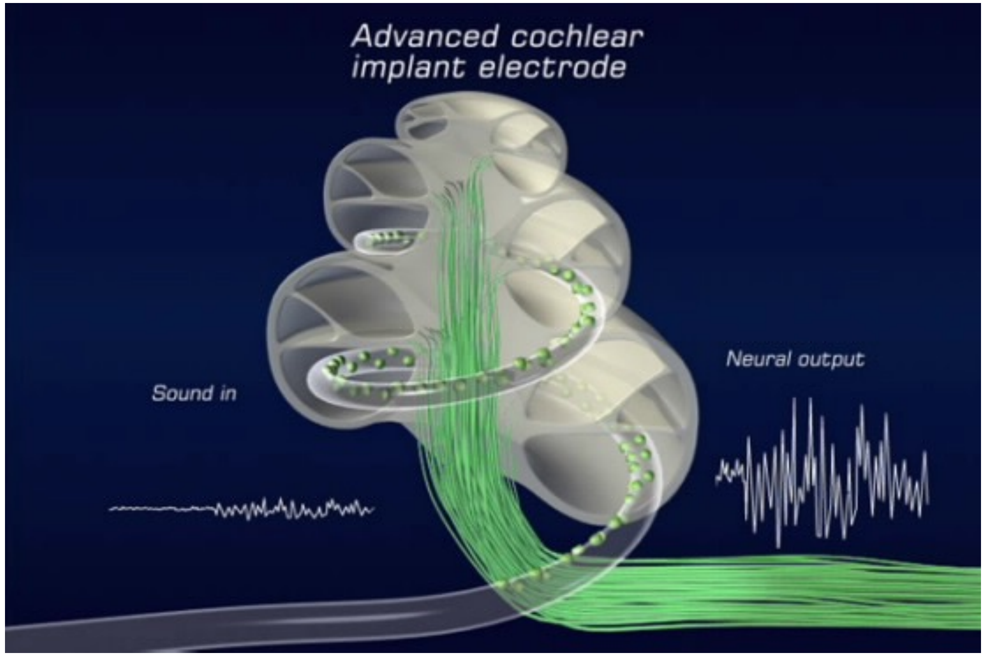
- Around 1 child in 1000 is born deaf or has severe hearing loss.
- Around 400 known syndromes involve severe hearing loss
- Hair cell function is highly specialized (mechano-electrical transduction) and highly sensitive to minute displacements

Thus, mutations in a single gene can jeopardize the entire transduction mechanism

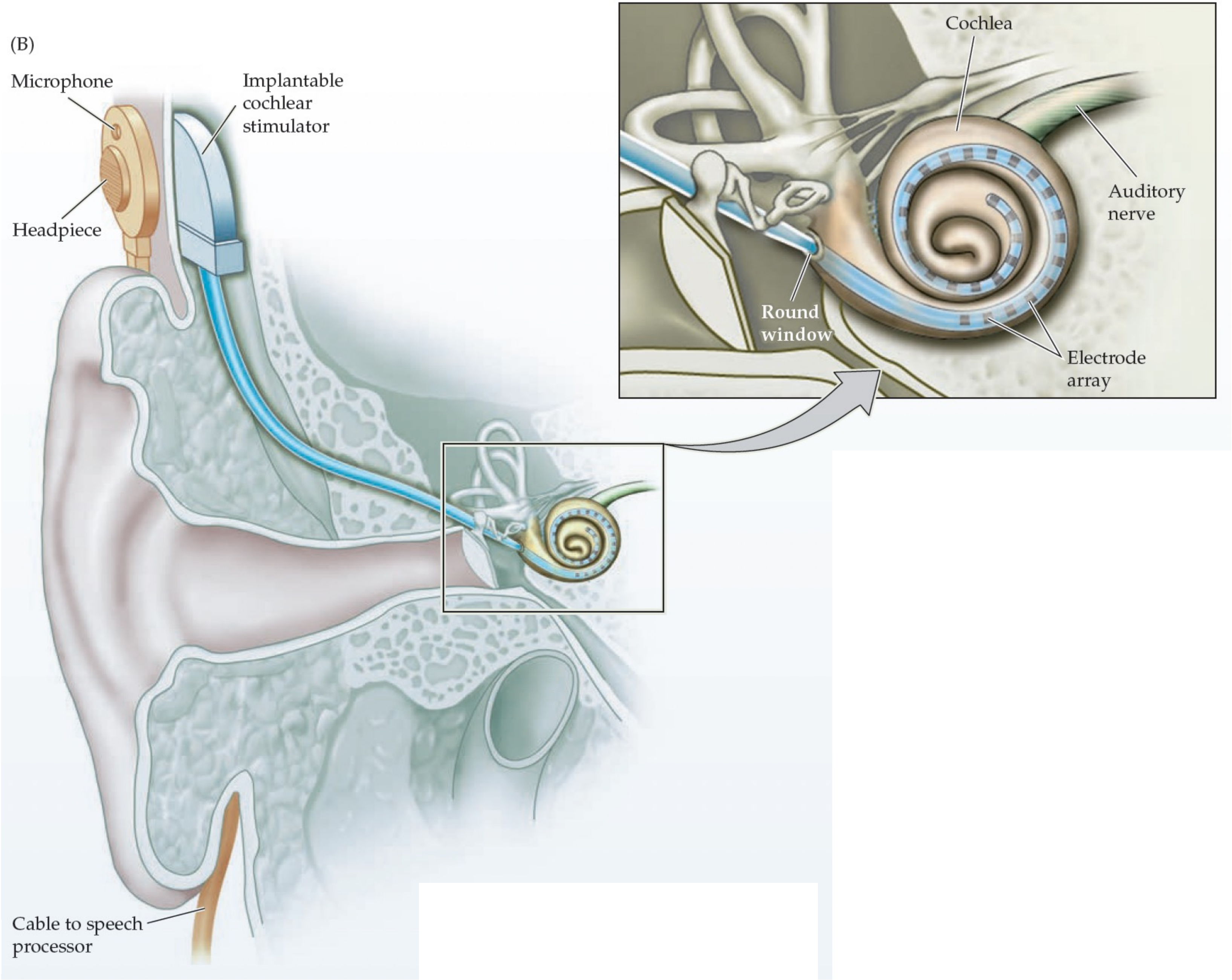
see also a review by
Richardson, de Monvel, Petit 2011
Annu. Rev. Physiol. 2011. 73:311 - 334

One treatment: the cochlear implant

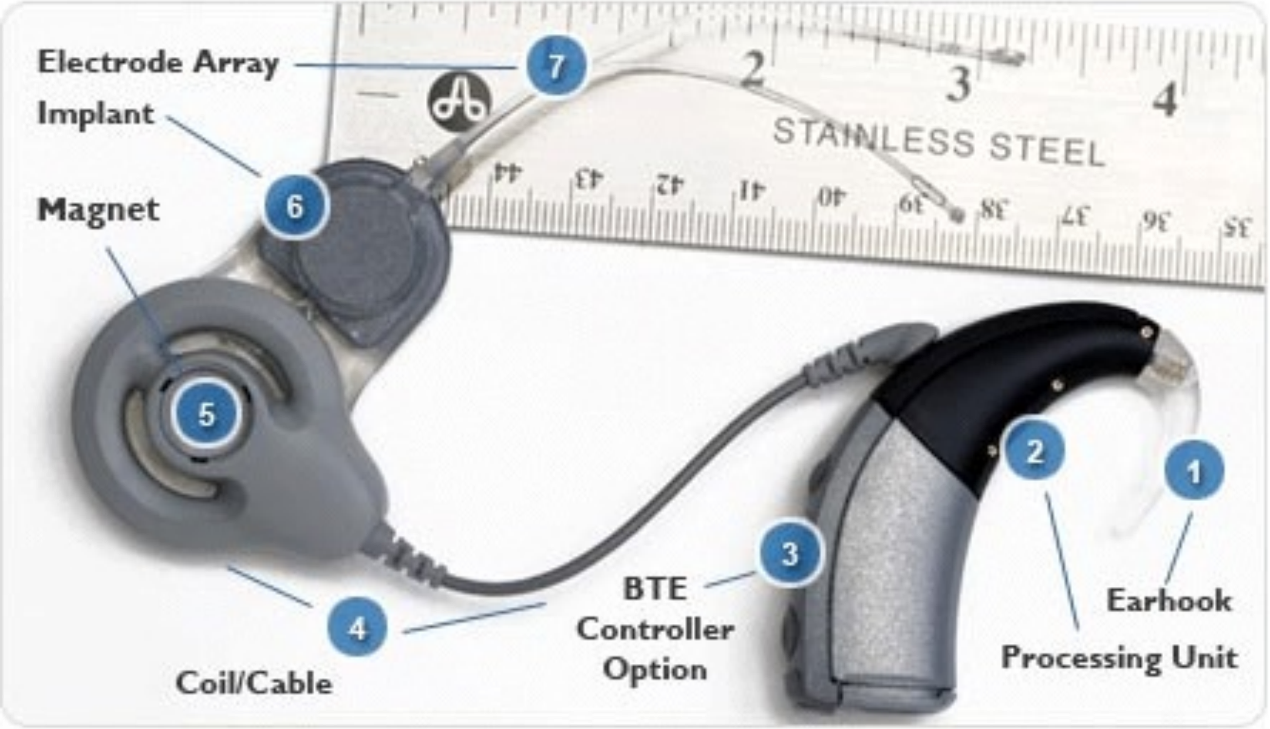
- Consists of a series of electrodes in parallel (up to 32) that are inserted into the cochlea.
- The auditory nerve is stimulated by electrical stimulations at specific sites depending on the sound frequency components
- Cochlear implants can be used as long as the auditory nerve is intact



The cochlear implant uses the tonotopic organization of the cochlea



Purves, Box Clinical Applications



<u>Perception of words in deaf children with cochlear implants:</u>

- A few months after implantation: perception of the characteristics of single words
- 1-2 years after implantation: perception of words and simple sentences
- 2-6 years: perception of words and sentences without immediate context
- 6 years: ability to lead a conversion without "lip-reading" for ~ 80% of patients

Summary: Audition - Important concepts and keywords

- Structure of the cochlea: scala vestibule, scala tympani, scala media (with unusually high K^+).
- Principle of “tonotopy” (on cochlea) of sound frequency
- Inner hair cell: primary transduction mechanism, ions, synapse function
- Role and mechanisms of Outer hair cell function
- Innervation of Inner hair cells
- Principle anatomical pathway from cochlea to auditory brainstem
- Tonotopic organization of auditory brainstem nuclei.
- Sound source localization is calculated in which brain regions using which cues?
- Processing centers of auditory information in the brain
- Treating congenital deafness with a cochlear implant