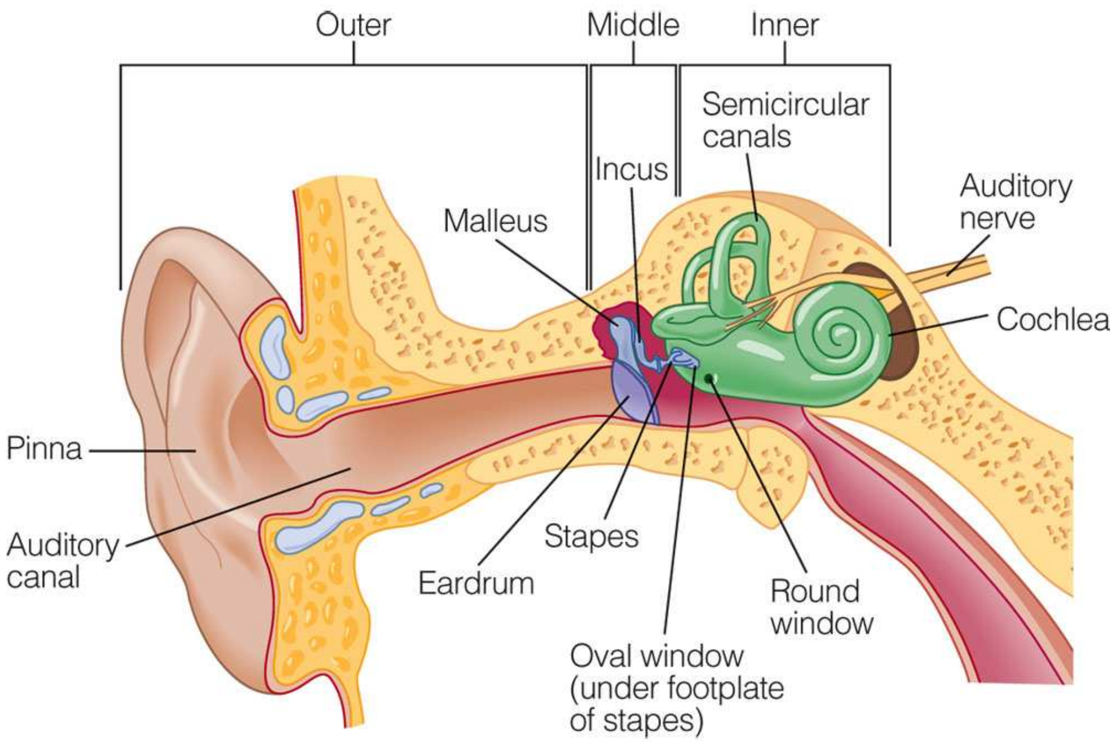
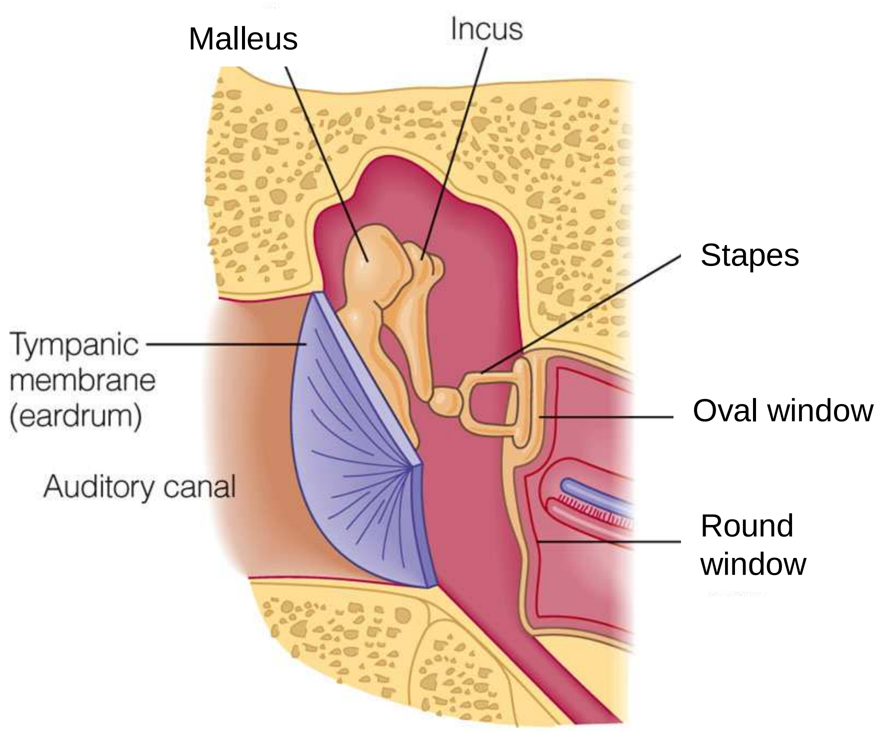
The Ear

- **Outer ear** - pinna and auditory canal
  - Pinna helps with sound location
    - Holds glasses on your head.
  - Auditory canal - tube-like 3 cm long structure
    - Protects the tympanic membrane at the end of the canal
    - Resonant frequency of the canal amplifies frequencies between 2,000 and 5,000 Hz



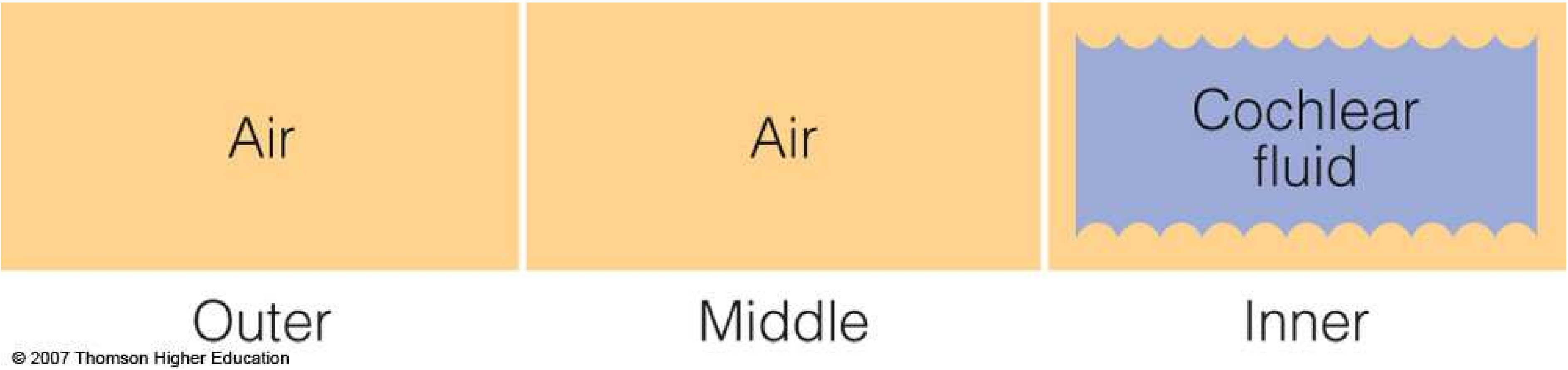
The Middle Ear

- 2 cubic centimeter cavity separating inner from outer ear
- It contains the three ossicles (the smallest bones in the body!)
  - **Malleus** - moves due to the vibration of the tympanic membrane
  - **Incus** - transmits vibrations of malleus
  - **Stapes** - transmit vibrations of incus to the inner ear via the oval window of the cochlea

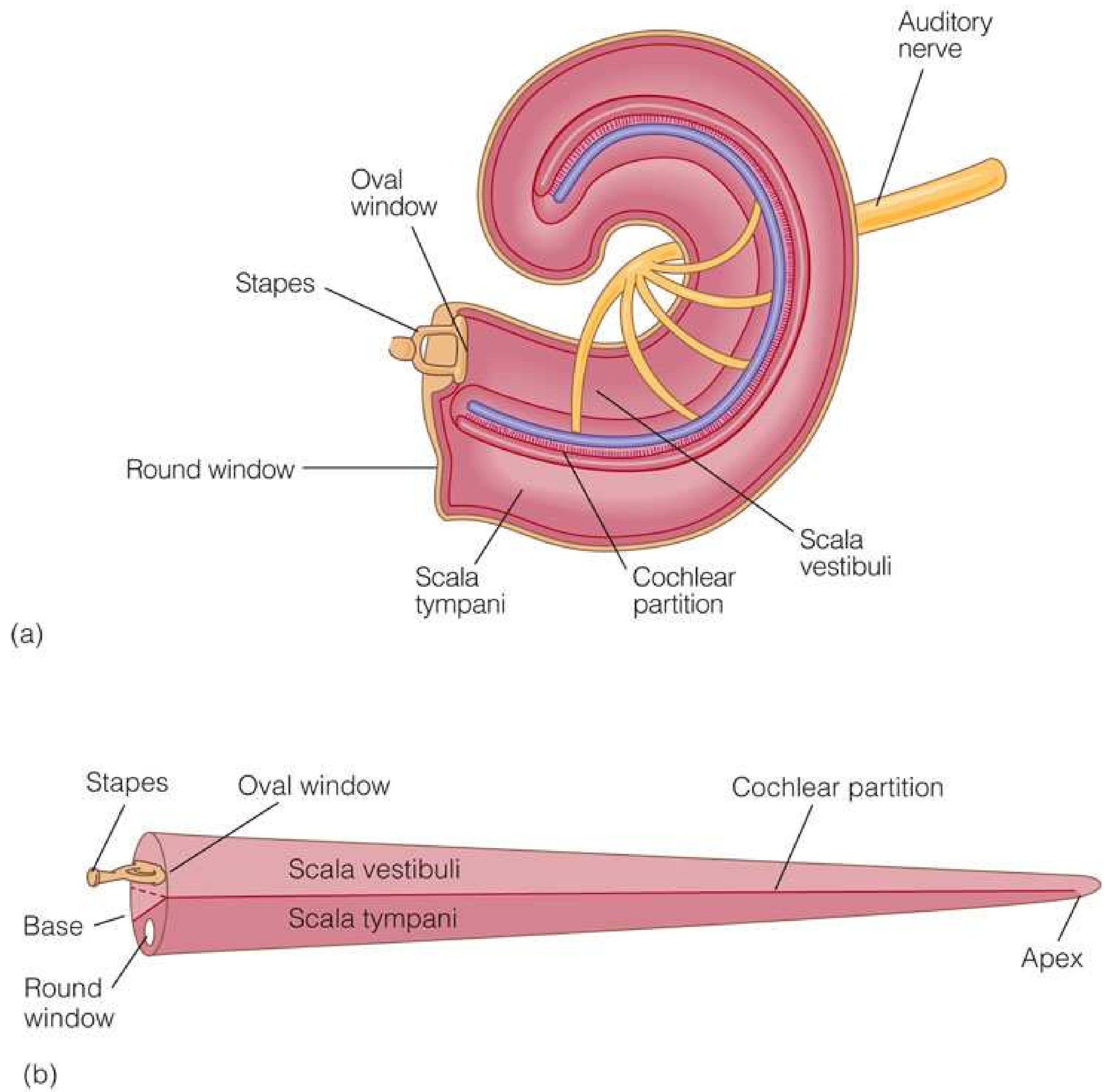


Function of Ossicles

- Outer and inner ear are filled with air
- Inner ear filled with fluid that is much denser than air
- Pressure changes in air transmit poorly into the denser medium
- Ossicles act to amplify the vibration for better transmission to the fluid

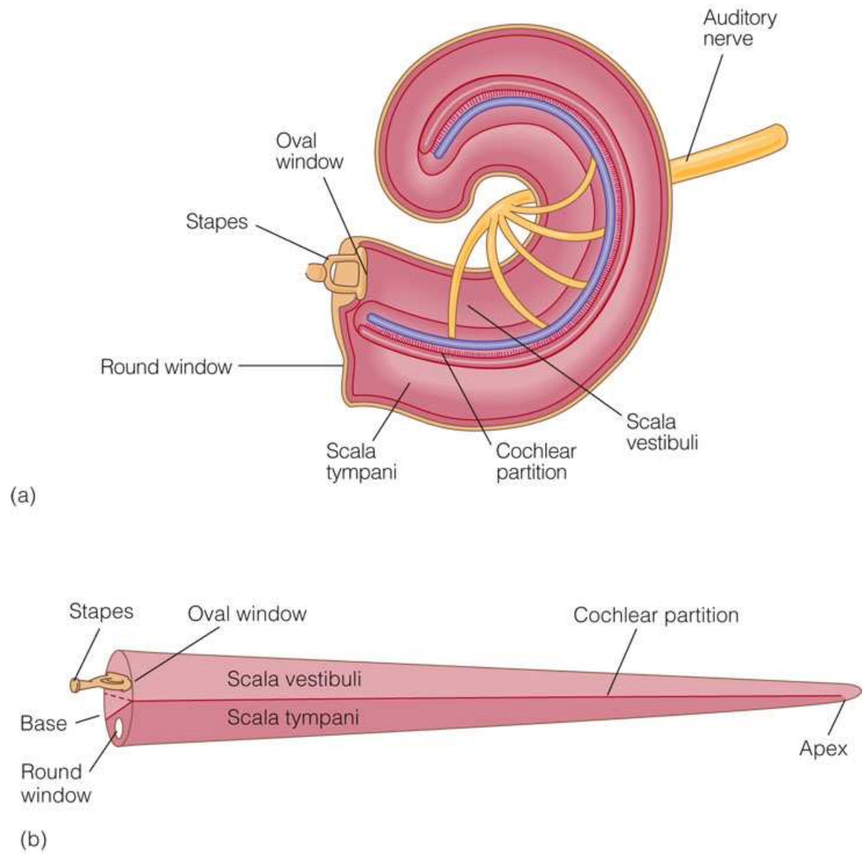


The Inner Ear



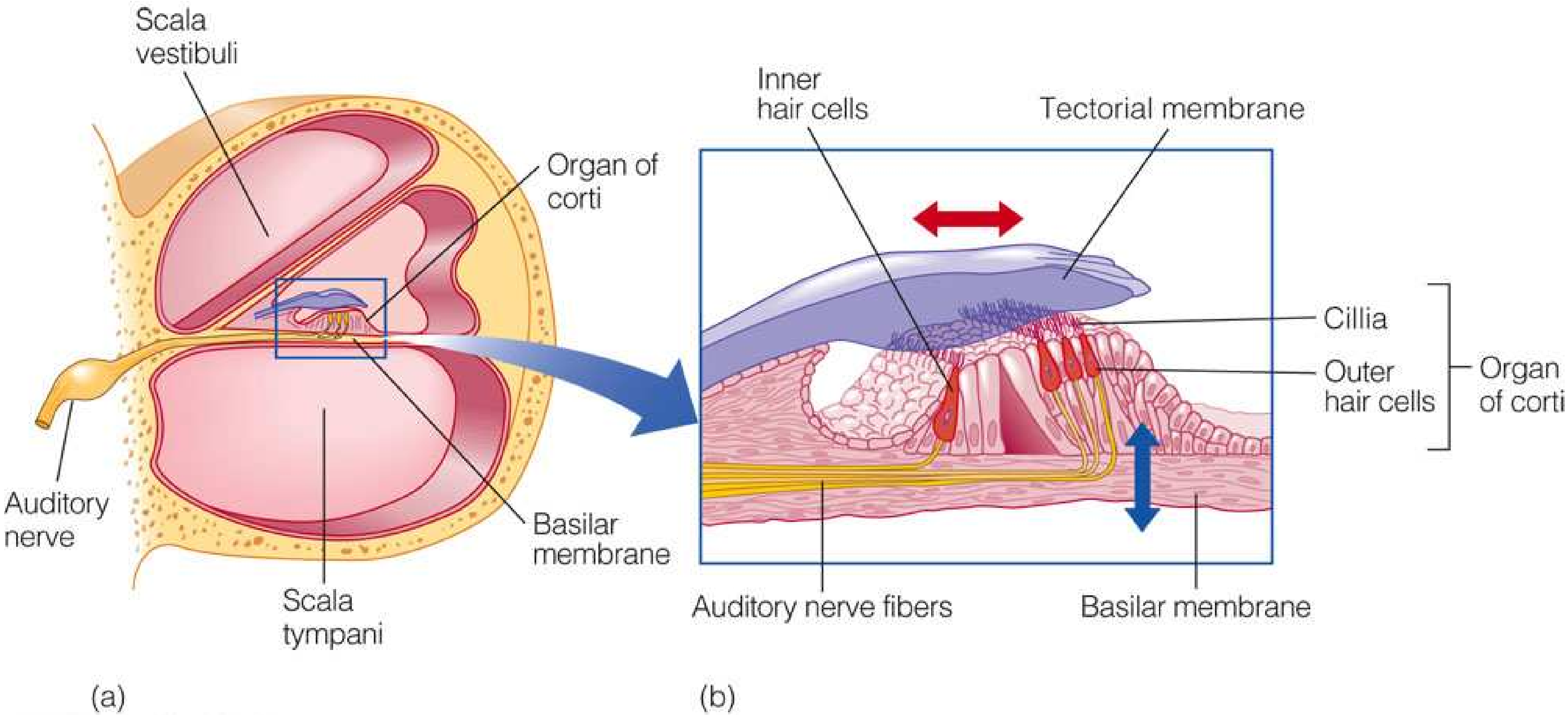
The Cochlea

- Fluid-filled snail-like structure set into vibration by the stapes
- Divided into the scala vestibuli and scala tympani by the cochlear partition
- Cochlear partition extends from the base (stapes end) to the apex (far end)
- Organ of Corti contained by the cochlear partition



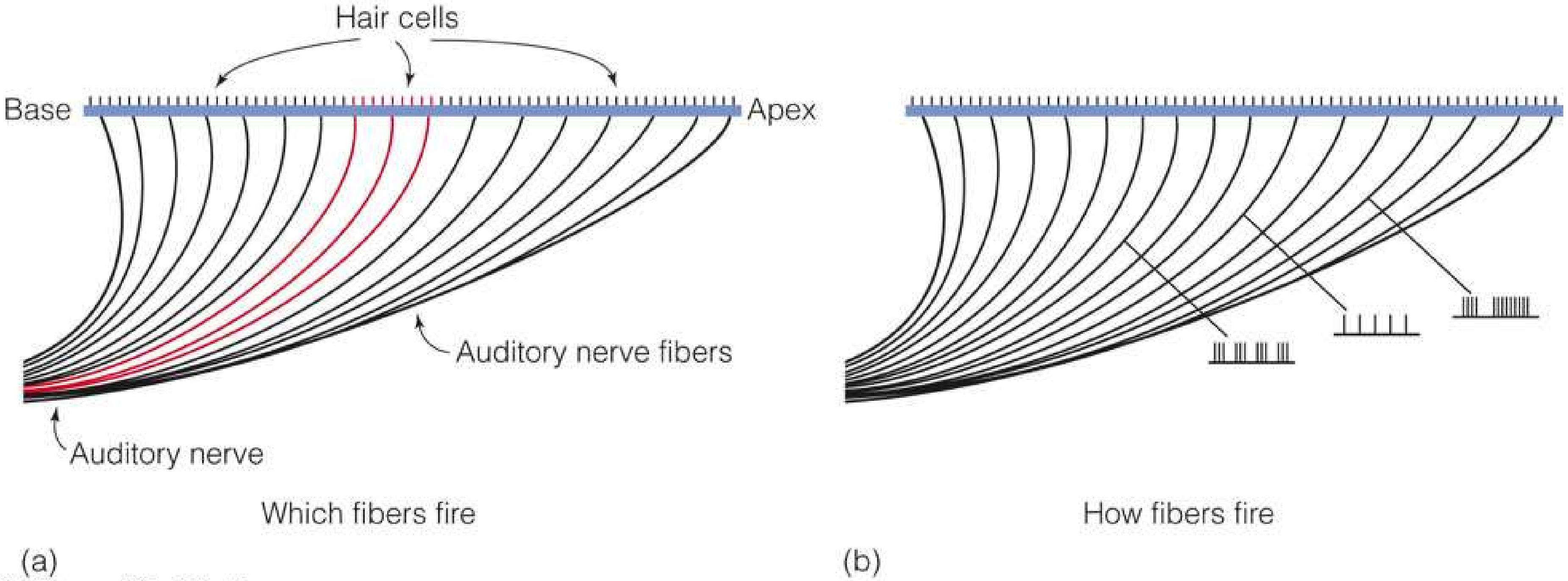
The Organ of Corti

- Key structures
  - Basilar membrane vibrates in response to sound and supports the organ of Corti
  - Inner and outer hair cells are the receptors for hearing
  - Tectorial membrane extends over the hair cells
- Transduction at the hair cells takes place due to the interaction of these structures



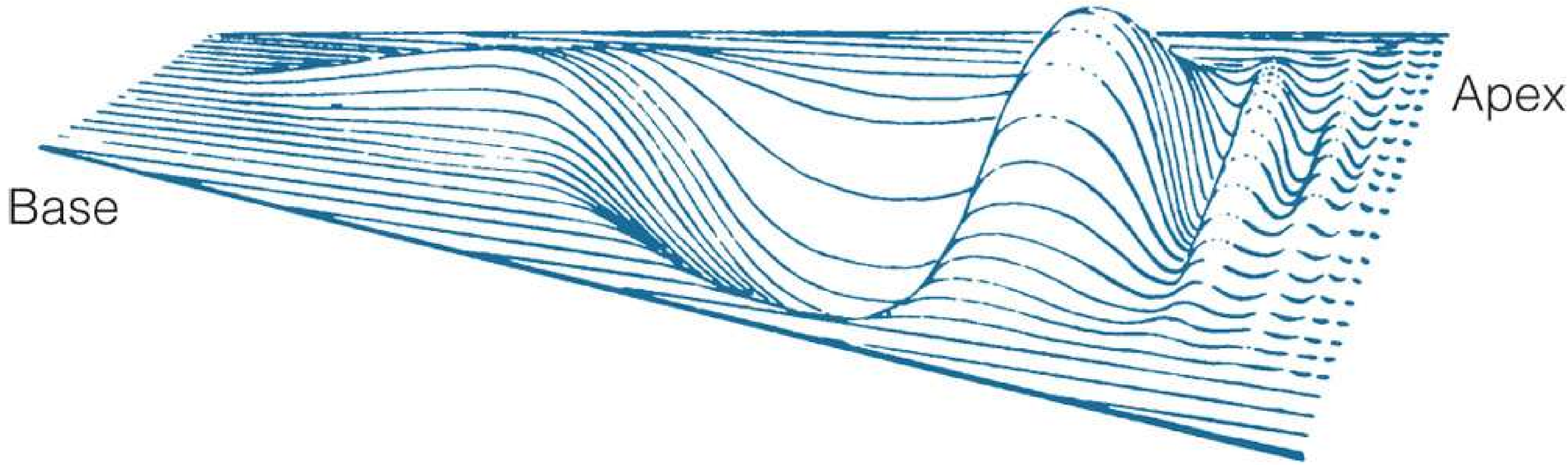
Neural Signals for Frequency

- There are two ways nerve fibers signal frequency
  - ***Which*** fibers are responding
    - Specific groups of hair cells on basilar membrane activate a specific set of nerve fibers
  - ***How*** fibers are firing
    - Rate or pattern of firing of nerve impulses



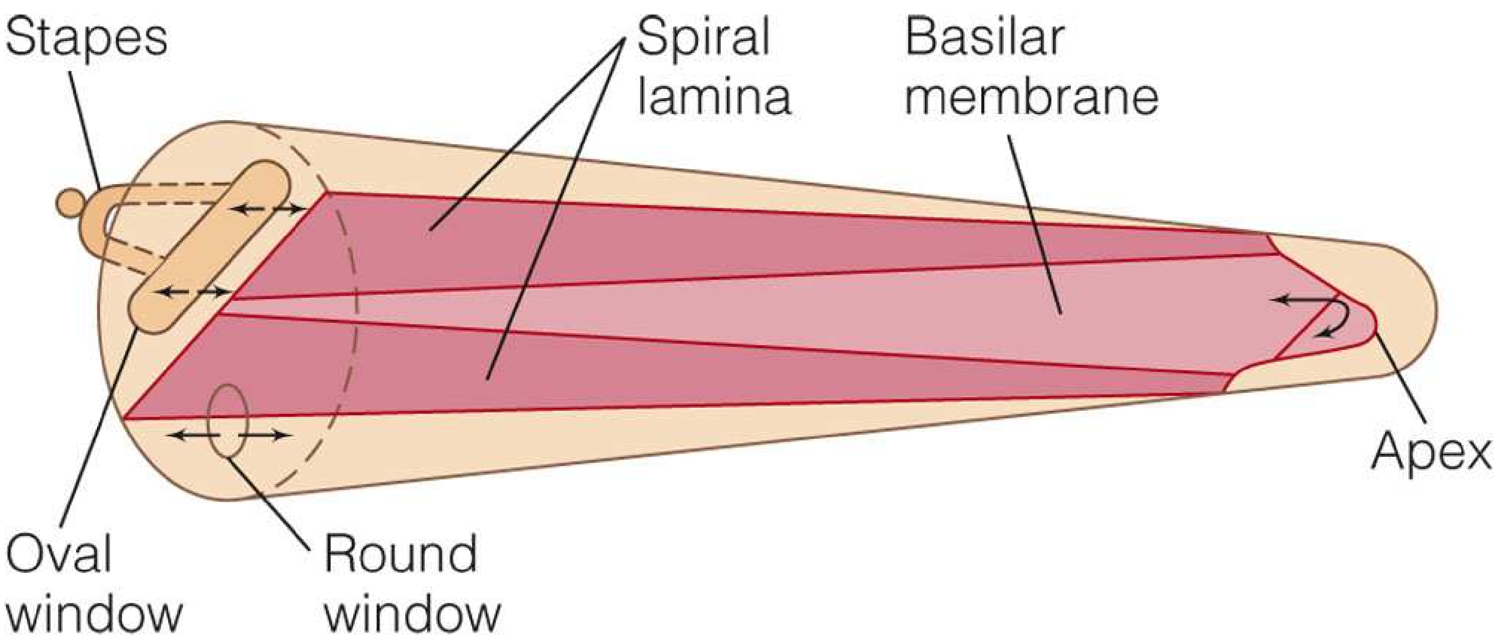
Békésys' Place Theory of Hearing

- Frequency of sound is indicated by the place on the organ of Corti that has the highest firing rate
- Békésy determined this in two ways
  - Direct observation of the basilar membrane in a cadaver
  - Building a model of the cochlea using the physical properties of the basilar membrane



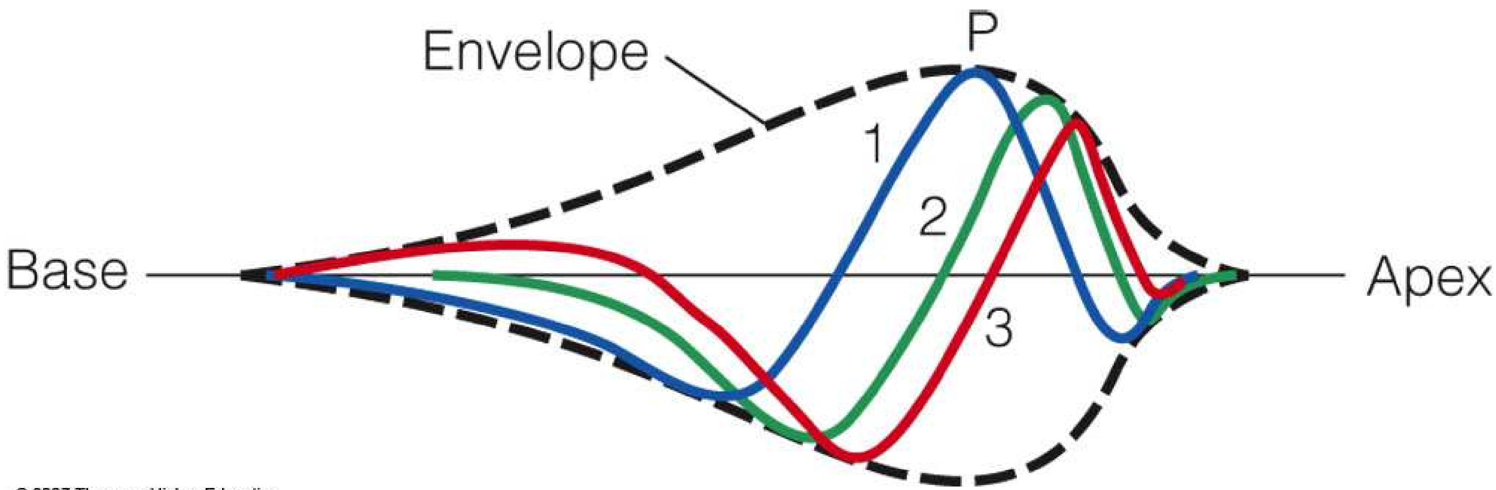
Békésys' Place Theory of Hearing

- Physical properties of the basilar membrane
  - Base of the membrane (by stapes) is
    - 3 to 4 times narrower than at the apex
    - 100 times stiffer than at the apex
- Both the model and the direct observation showed that the vibrating motion of the membrane is a traveling wave



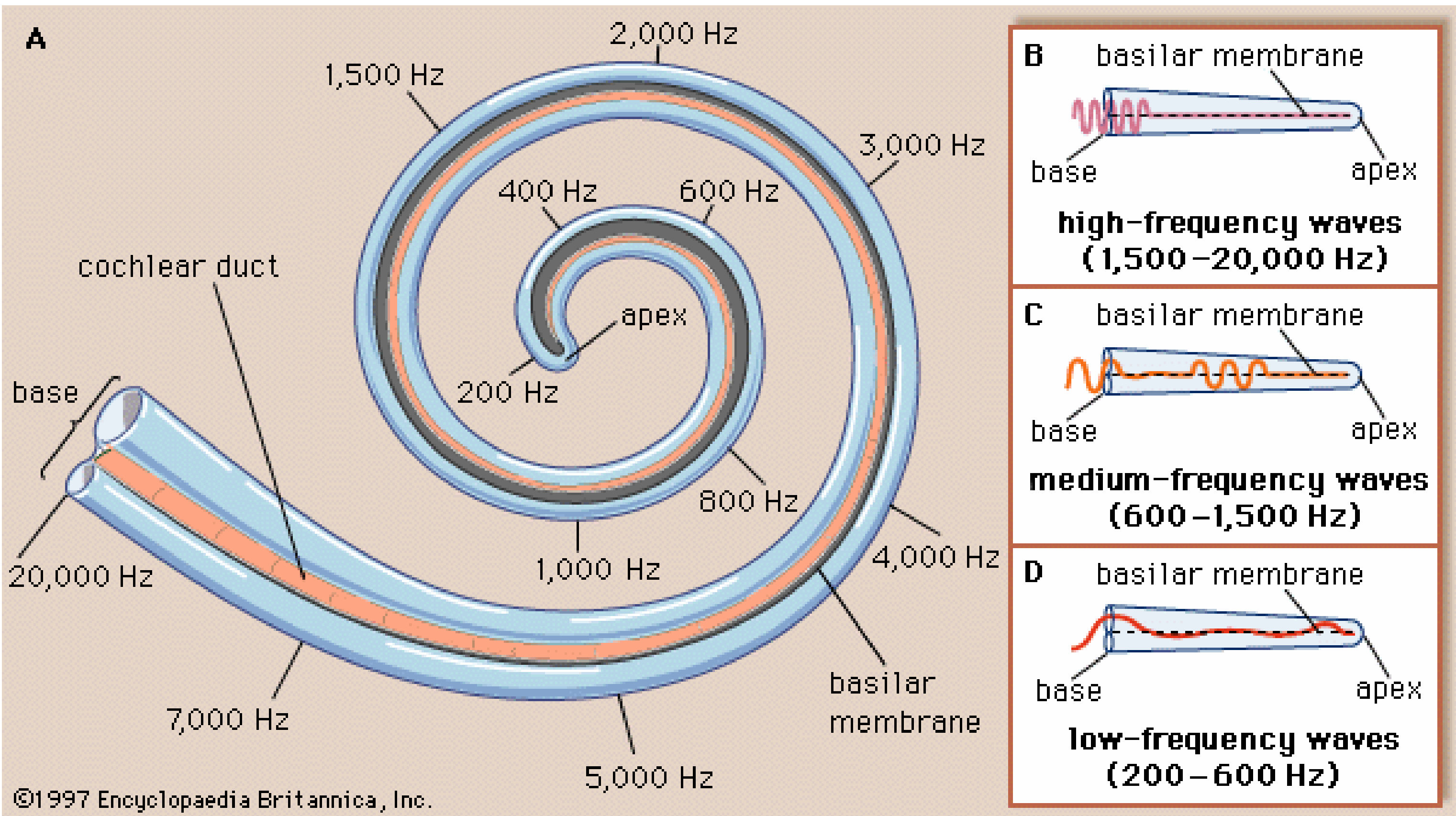
Békésys' Place Theory of Hearing

- Envelope of the traveling wave
  - Indicates the point of maximum displacement of the basilar membrane
  - Hair cells at this point are stimulated the most strongly leading to the nerve fibers firing the most strongly at this location
  - Position of the peak is a function of frequency



Evidence for Place Theory

- Tonotopic map
  - Cochlea shows an orderly map of frequencies along its length
    - Apex responds best to low frequencies
    - Base responds best to high frequencies



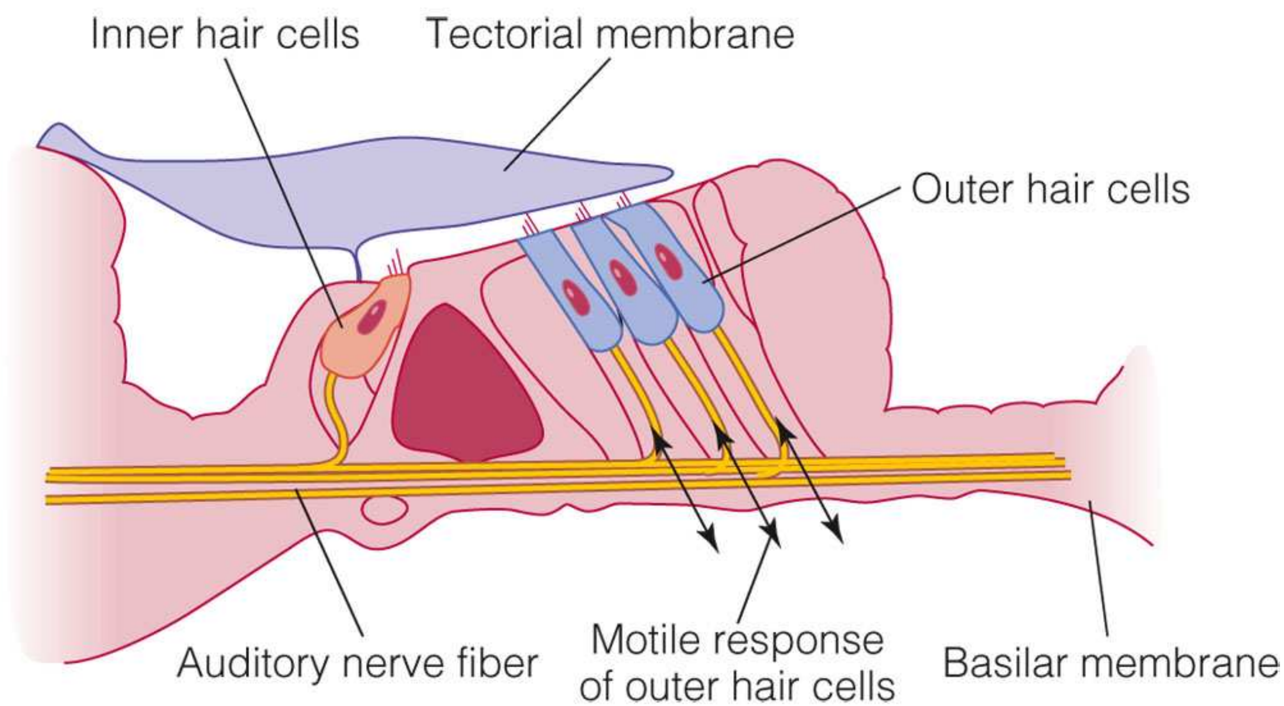
Tonotopic map of the guinea pig cochlea.

Evidence for Place Theory

- Neural frequency tuning curves
  - Pure tones are used to determine the threshold for specific frequencies measured at single neurons
  - Plotting thresholds for frequencies results in tuning curves
  - Frequency to which the neuron is most sensitive is the characteristic frequency

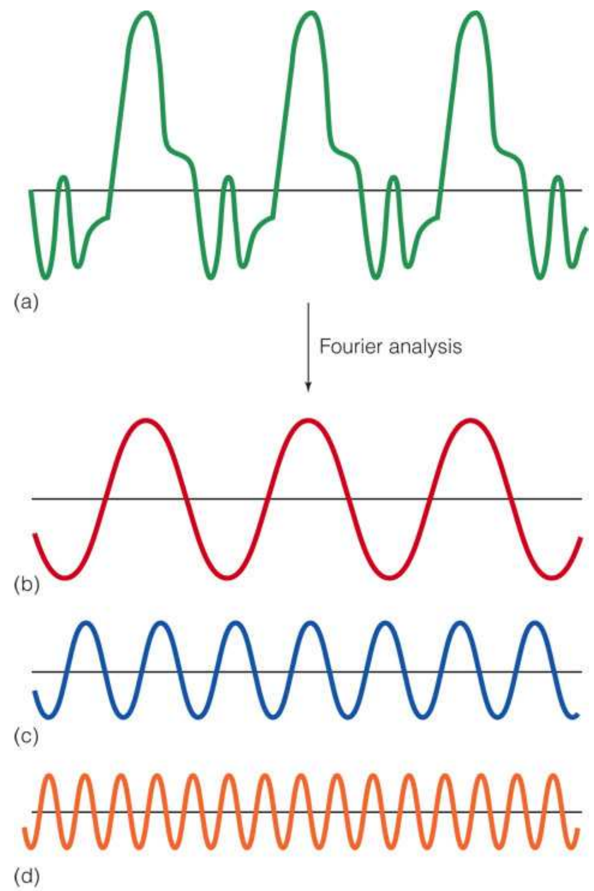
Updating Békésy's Place Theory

- Békésy used unhealthy basilar membranes and his results showed no difference in response for close frequencies that people can distinguish.
- New research with healthy membranes show that the entire **outer hair cells** respond to sound by slight tilting and a change in length
  - This is called the *motile response* and helps to amplify action on the membrane

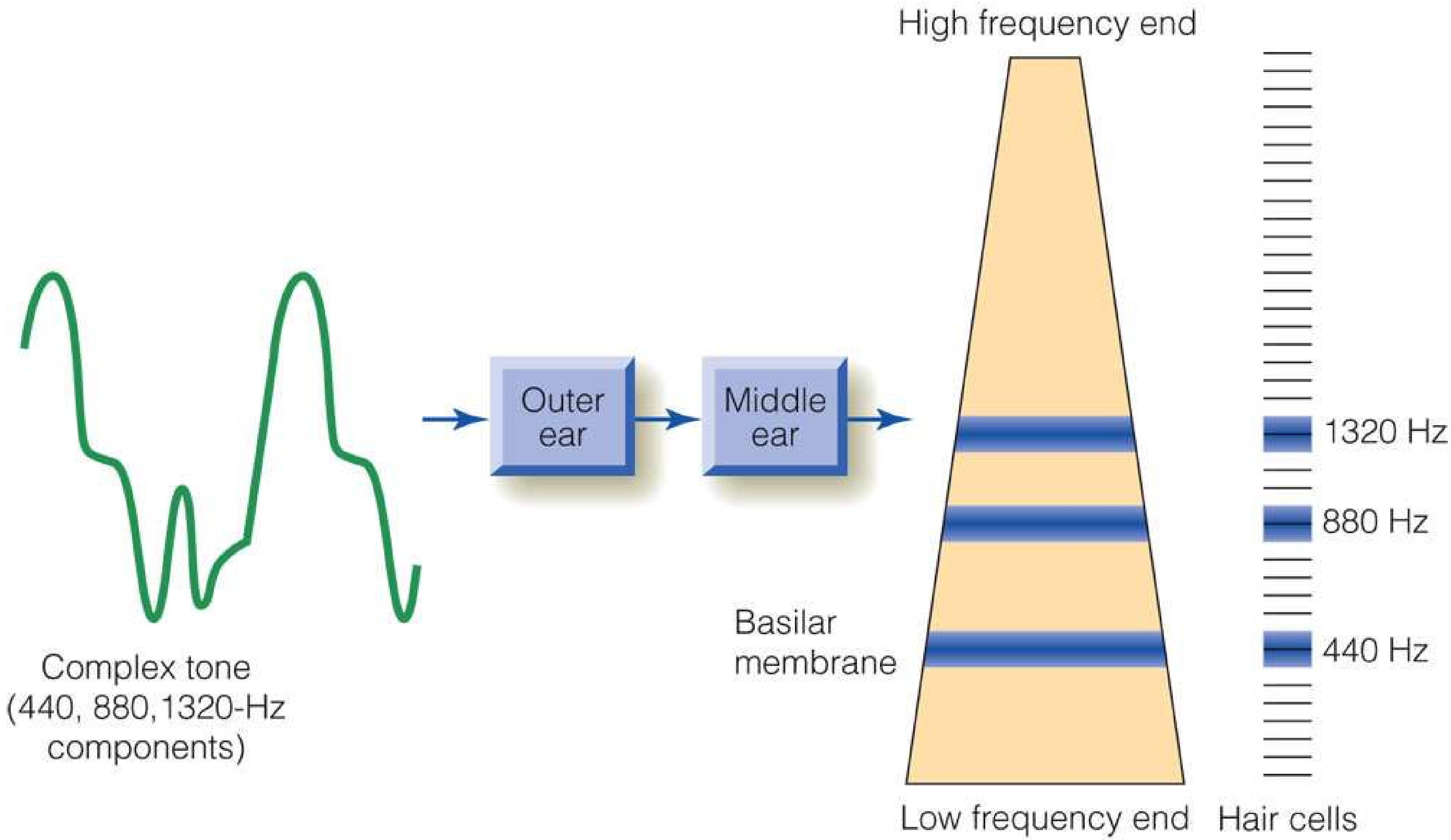


Response of Basilar Membrane to Complex Tones

- Fourier analysis - mathematic process that separates complex waveforms into a number of sine waves
- Research on the response of the basilar membrane shows the highest response in auditory nerve fibers with characteristic frequencies that correspond to the sine-wave components of complex tones
- Thus the cochlea is called a frequency analyzer

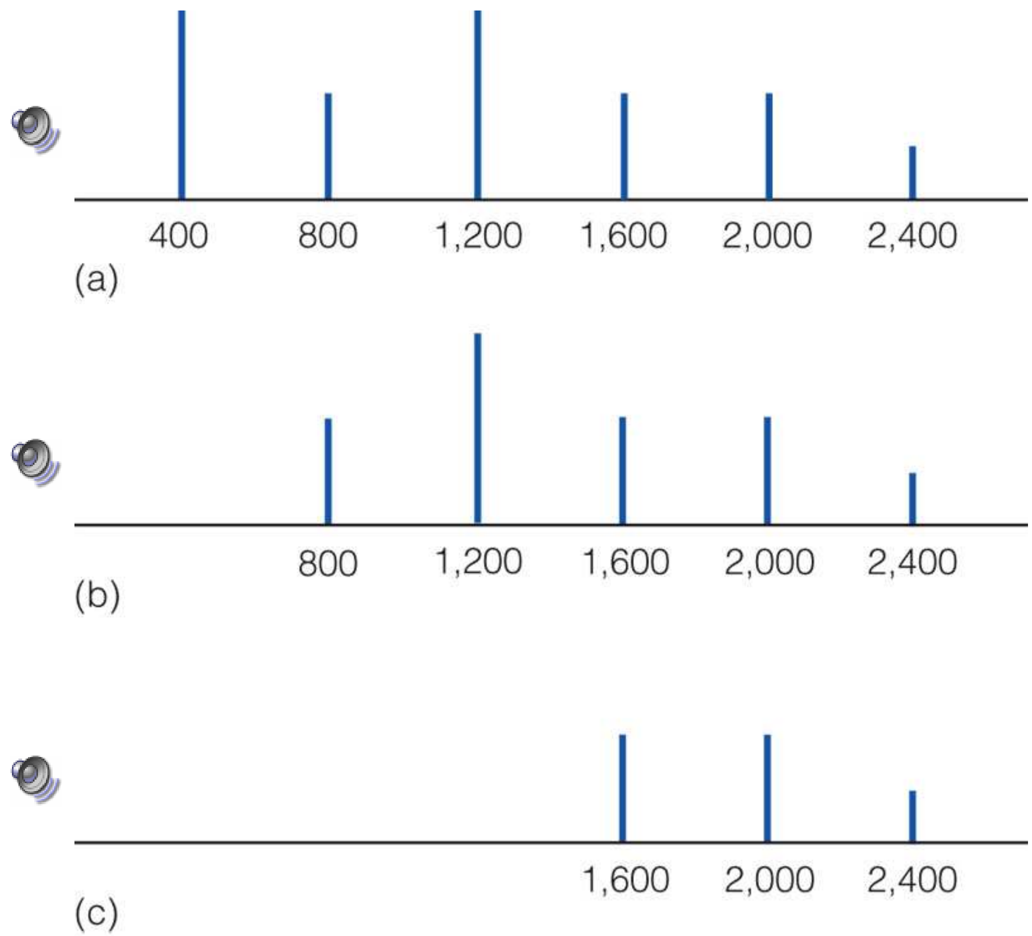


The Cochlea automatically breaks down complex tones into their component frequencies – it's performing *Fourier Analysis*.



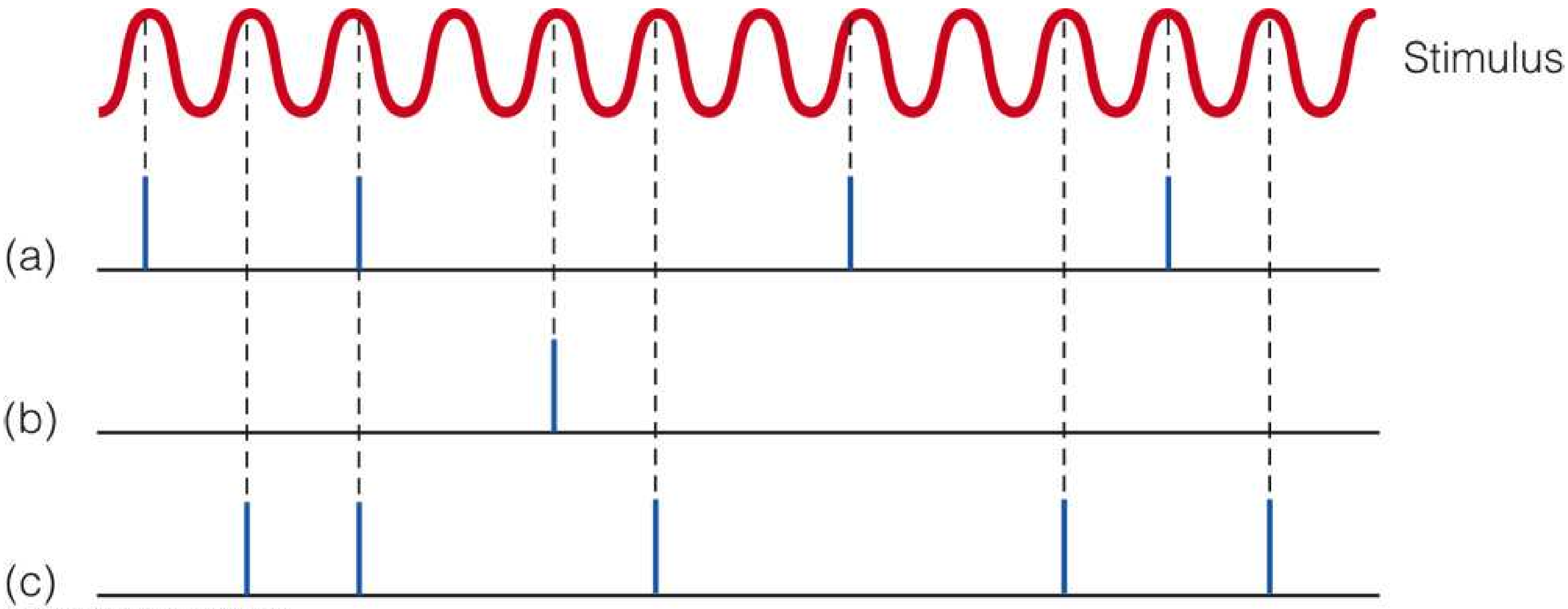
Missing Fundamental: evidence against Place Theory

- Pattern of stimulation on the basilar membrane cannot explain this phenomenon since removing the fundamental and harmonics creates different patterns
- Periodicity pitch is perceived even when the tones are presented to two ears



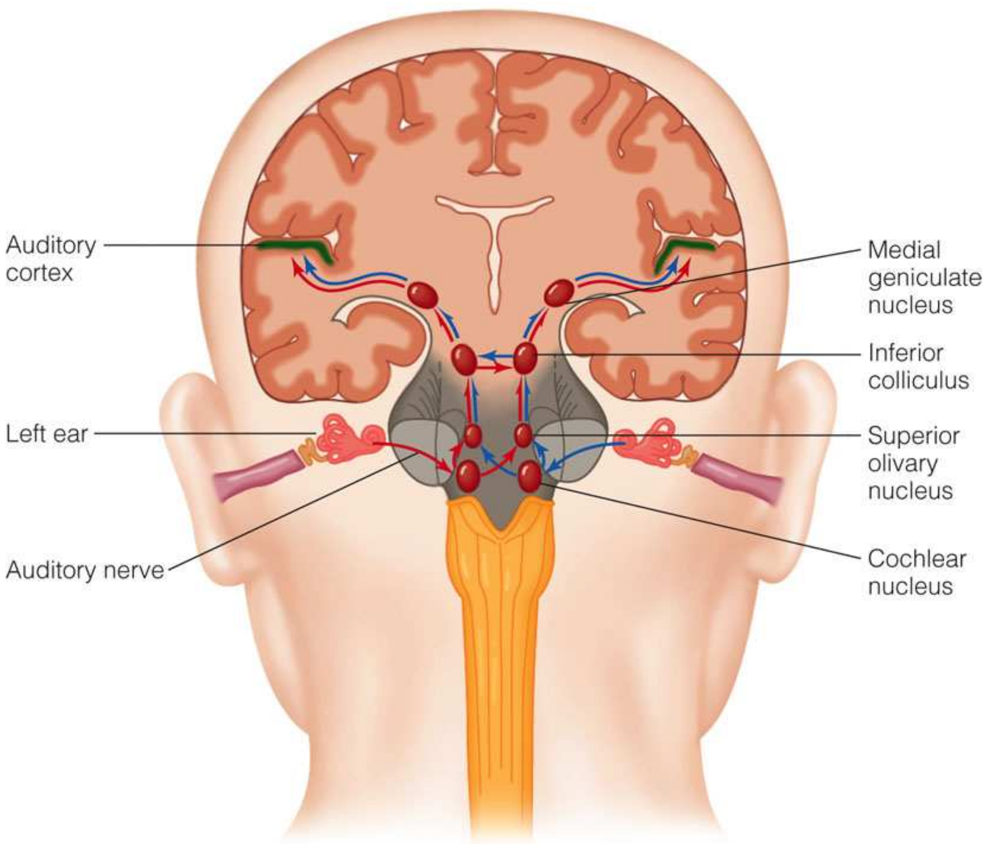
Timing of Neural Firing and Frequency

- ***Phase locking***
  - Nerve fibers fire in bursts
  - Firing bursts happen at or near the peak of the sine-wave stimulus
  - Thus, they are "locked in phase" with the wave
  - Groups of fibers fire with periods of silent intervals creating a pattern of firing



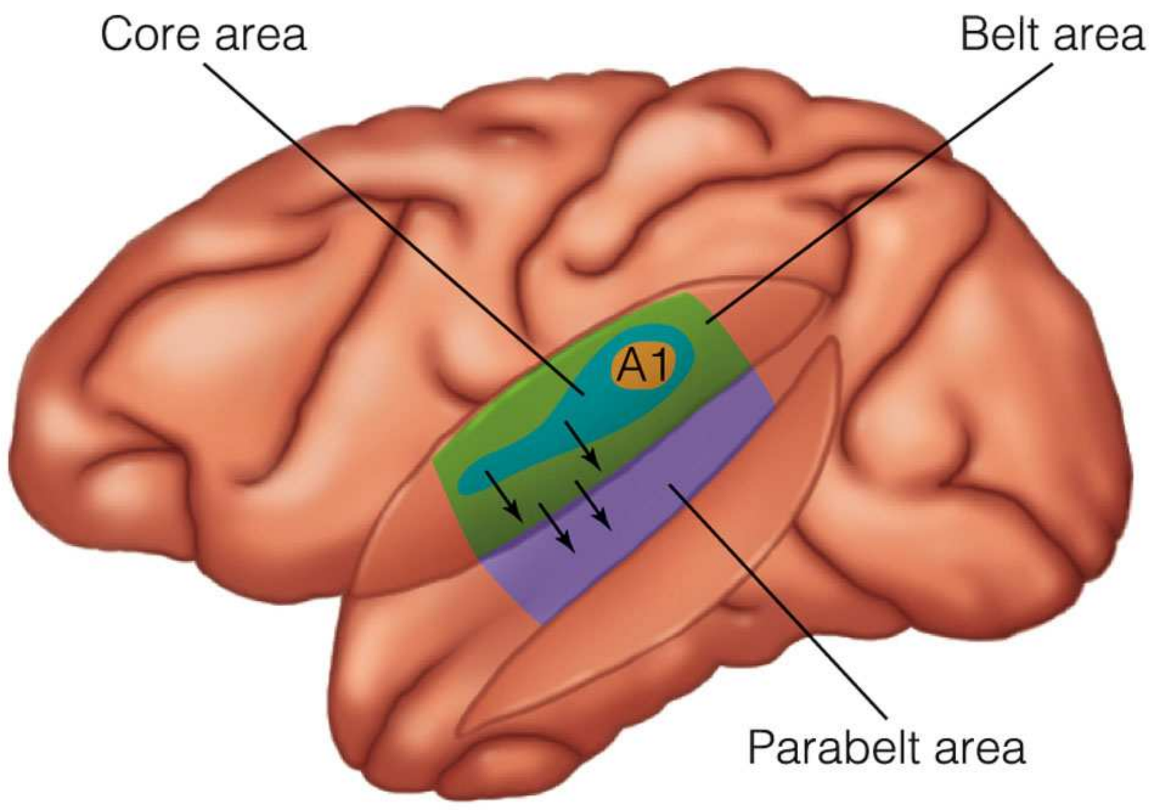
Pathway from the Cochlea to the Cortex

- Auditory nerve fibers synapse in a series of subcortical structures
  - Cochlear nucleus
  - Superior olivary nucleus (in the brain stem)
  - Inferior colliculus (in the midbrain)
  - Medial geniculate nucleus (in the thalamus)
  - Auditory receiving area (A1 in the temporal lobe)



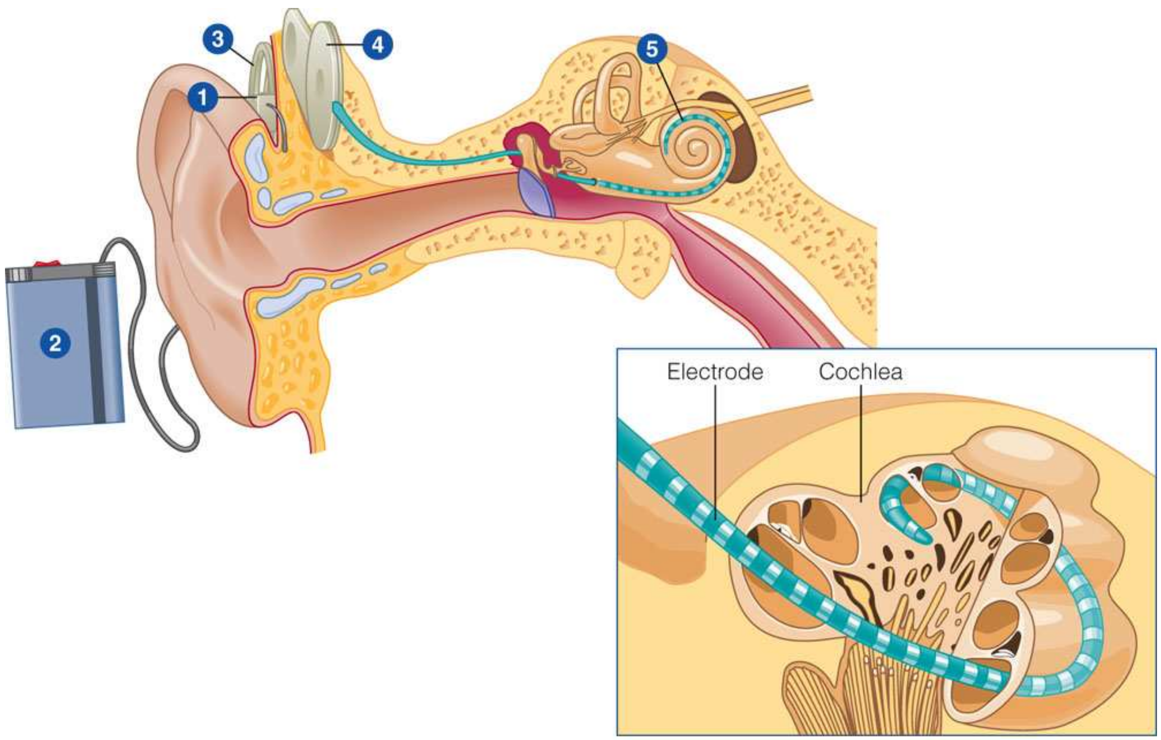
Auditory Areas in the Cortex

- Hierarchical processing occurs in the cortex
  - Neural signals travel through the core, then belt, followed by the parabelt area
  - Simple sounds cause activation in the core area
  - Belt and parabelt areas are activated in response to more complex stimuli made up of many frequencies



Cochlear Implants

- Electrodes are inserted into the cochlea to electrically stimulate auditory nerve fibers
- The device is made up of
  - A microphone worn behind the ear
  - A sound processor
  - A transmitter mounted on the mastoid bone
  - A receiver surgically mounted on the mastoid bone



Cochlear Implants

- Implants stimulate the cochlea at different places on the tonotopic map according to specific frequencies in the stimulus
- These devices help deaf people to hear some sounds and to understand language
- They work best for people who receive them early in life or for those who have lost their hearing, although they have caused some controversy in the deaf community