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
Békésy’s 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
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

![Diagram of auditory system](image)
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*. 

[Diagram showing the Cochlea's process of breaking down complex tones into their component frequencies.]
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.

(a) 400 800 1,200 1,600 2,000 2,400

(b) 800 1,200 1,600 2,000 2,400

(c) 1,600 2,000 2,400
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.