9.01 Introduction to Neuroscience
Fall 2007

Hearing

Sebastian Seung

Outer, middle, and inner ear

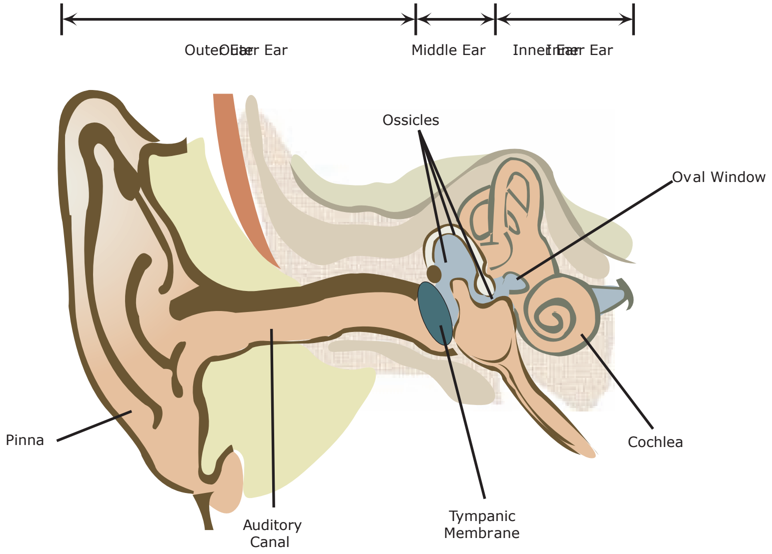


Figure by MIT OpenCourseWare. After figure 11.3 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Sound in air is mostly reflected when it meets fluid.

- This is why it’s so quiet underwater.
- Sound penetrates very little, because fluid is more difficult to move than air.
- This is a special case of a general phenomenon called impedance mismatch.
- The middle ear dramatically reduces reflection at the air/fluid interface.

Auditory nerve

- 8th cranial nerve
- about 30,000 fibers in humans
- “output” of the ear

Pure tones

- pitch ≈ frequency
- loudness ≈ intensity

- 20 to 20,000 Hz
- 12 decades

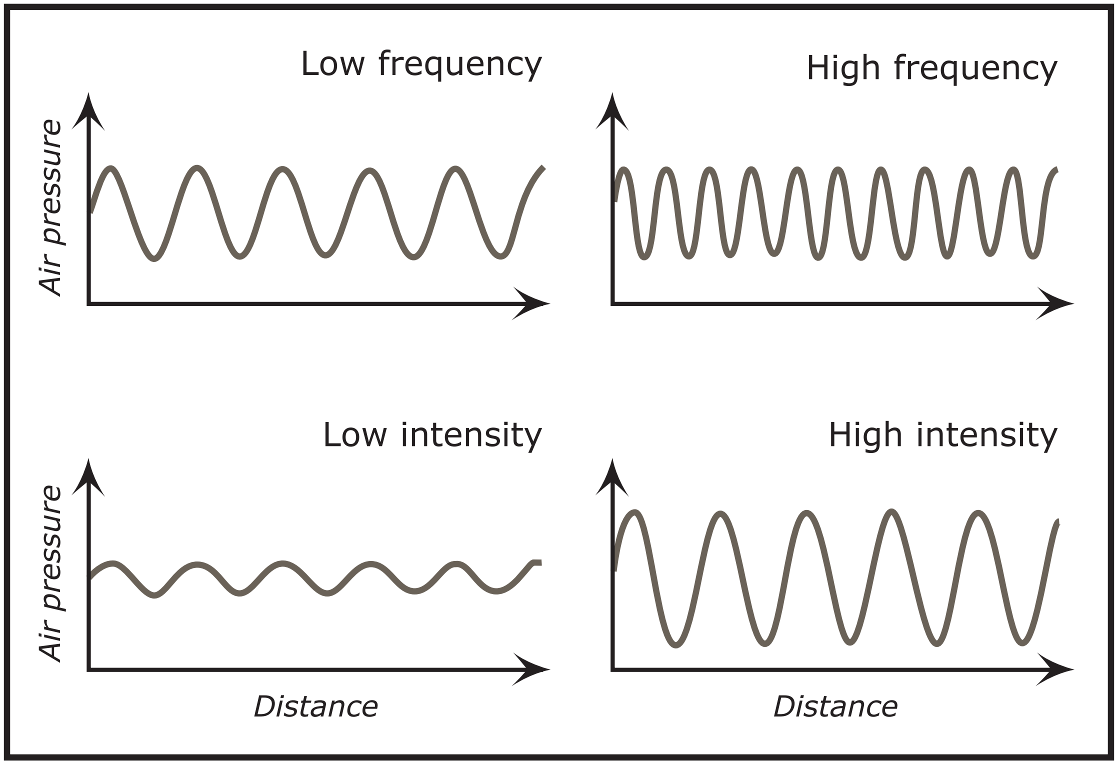


Figure by MIT OpenCourseWare. After figure 11.2 in: Bear, Mark F., Barry W.Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Auditory nerve responses are frequency-tuned

- For a given intensity, the firing rate is maximal at some “characteristic” frequency.

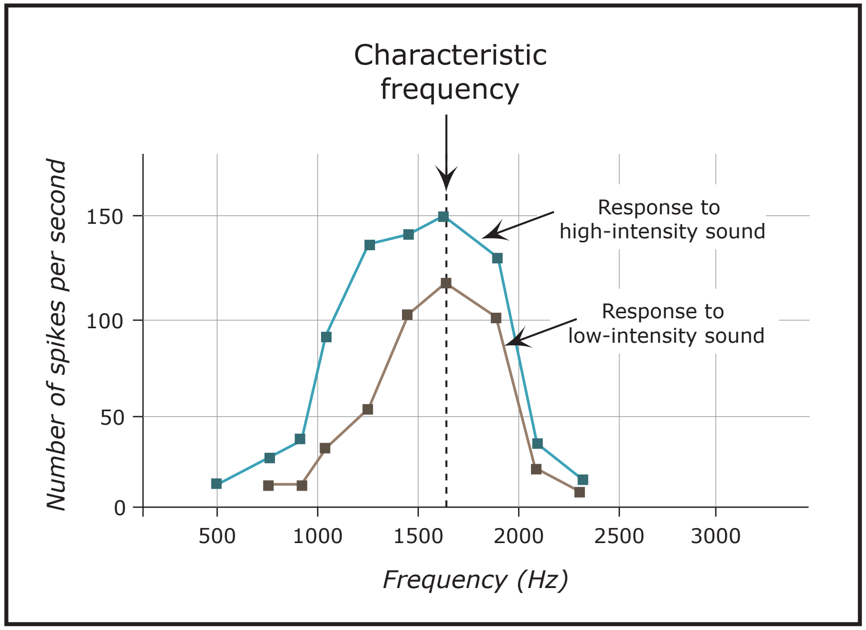


Figure by MIT OpenCourseWare. After figure 11.19 in Bear, Mark F., Barry W.Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001.

ISBN: 9780683305968.

Sound waves travel along the basilar membrane

Image removed due to copyright restrictions.
See Figure 11.8 in Bear, Connors, and Paradiso. *Neuroscience: Exploring the Brain*. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

The properties of the basilar membrane vary along its length

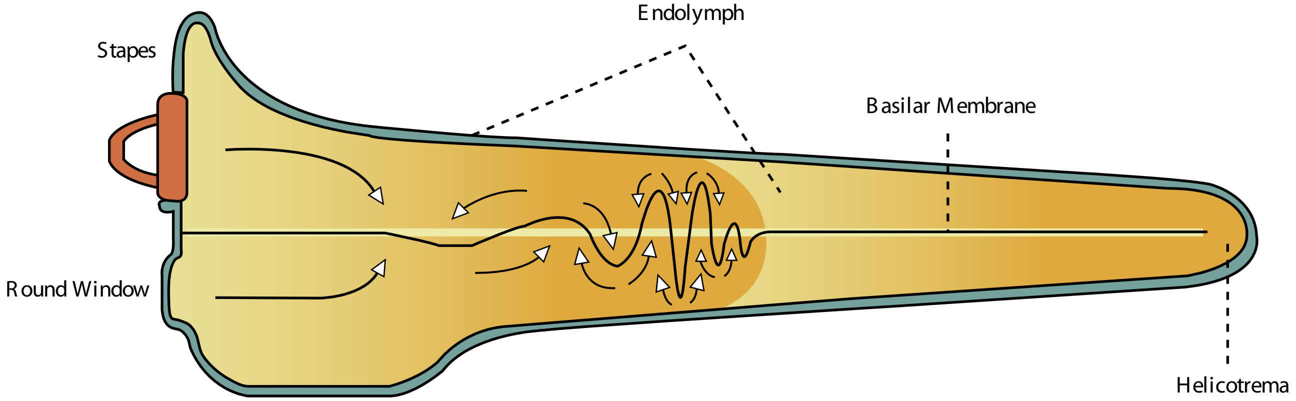


Figure by MIT OpenCourseWare. After figure 11.9 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

- The base is stiffer than the apex.
- The base is narrower than the apex.
- As a result, the amplitude of a wave varies as it travels along the membrane.

Place code for frequency

- The location of the peak amplitude of the wave is a function of its frequency

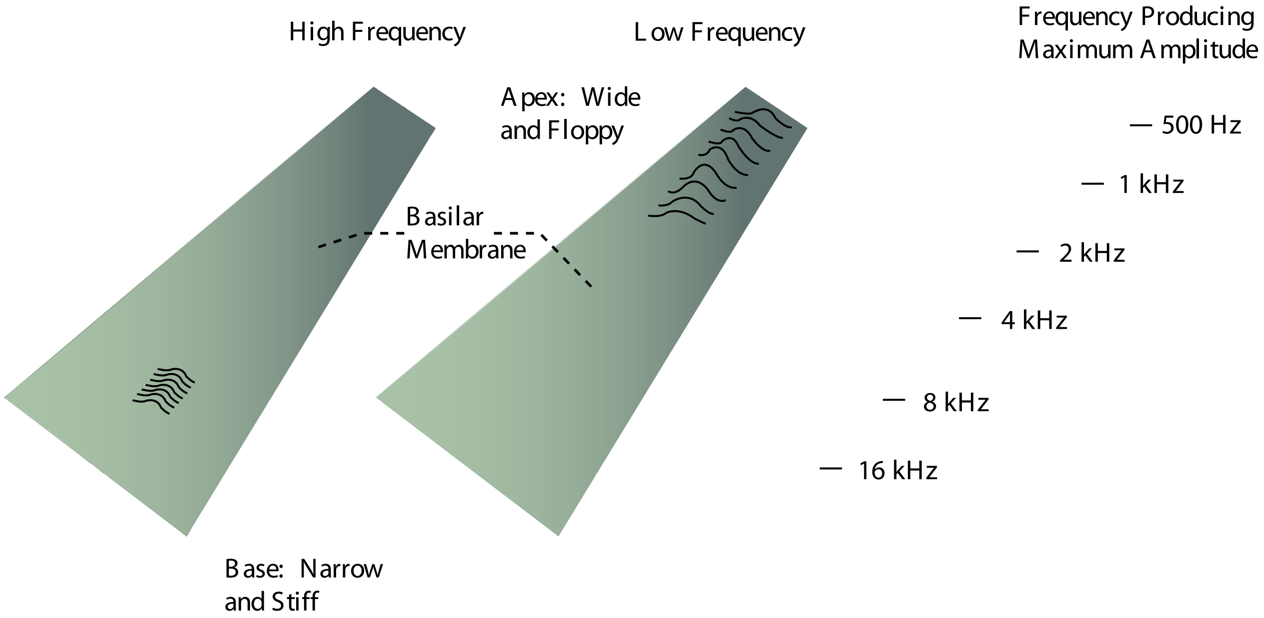


Figure by MIT OpenCourseWare. After figure 11.10 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Neurons are sensitive to places on the basilar membrane

Image removed due to copyright restrictions.
See Figure 11.20 (tonotopic maps) in Bear, Connors, and Paradiso.
Neuroscience: Exploring the Brain. 3rd ed. Baltimore, MD: Lippincott
Williams & Wilkins, 2007.

- much as visual neurons are sensitive to particular locations on the retina.

Fourier analysis

- Any signal can be expressed as a sum of sine waves
- Each sine wave has three parameters
  - frequency
  - intensity
  - phase

Measures of frequency content

- Spectrum
  - Graph of intensity versus frequency
- Spectrogram
  - Spectrum as a function of time
  - Intensity vs. frequency and time
- Software for spectral analysis
  - http://www.speech.kth.se/wavesurfer/

A periodic signal contains multiples of one frequency.

- This frequency is called the “fundamental.”
- Multiples are called “harmonics.”
- The fundamental plus its harmonics are called a “harmonic stack.”

Three scalae run the length of the cochlea

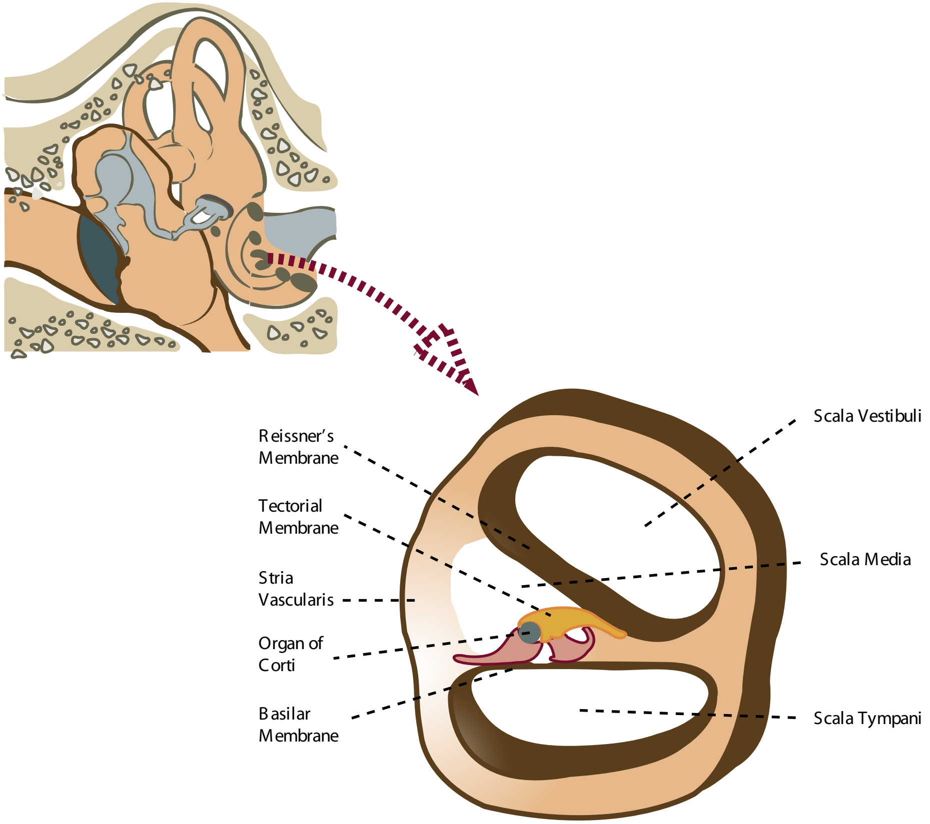


Figure by MIT OpenCourseWare. After figure 11.7 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed.
Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Hair cells sit on the basilar membrane

- in the organ of Corti

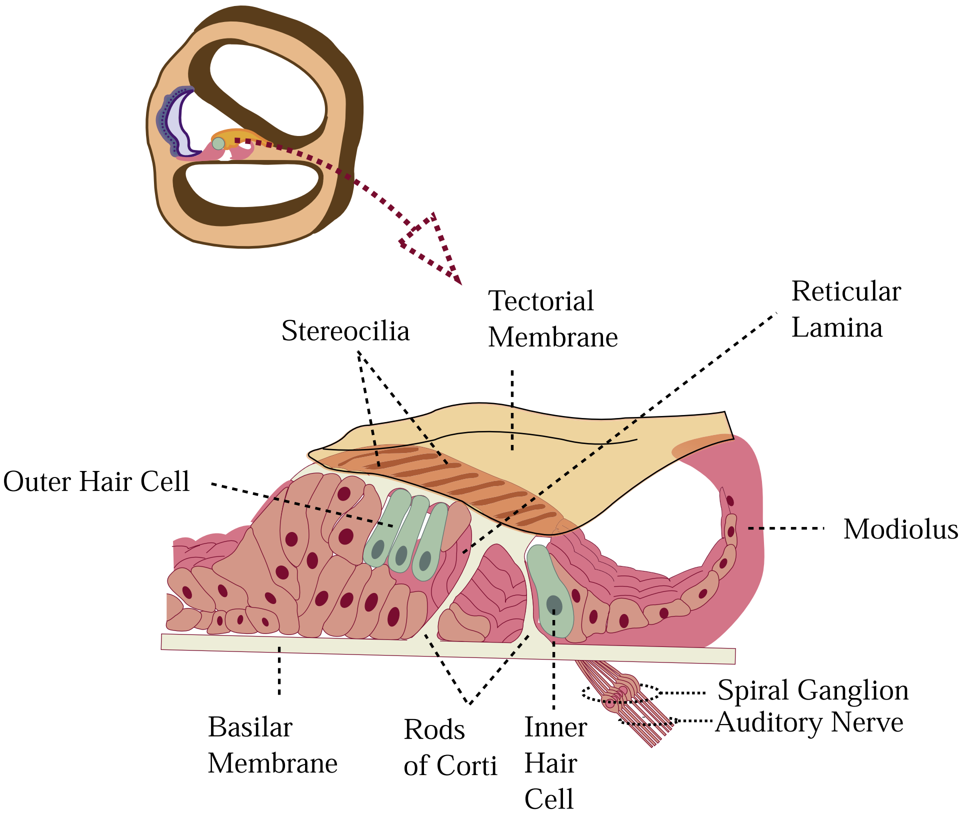


Figure by MIT OpenCourseWare. After figure 11.12 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed.
Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Hair cells are mechanosensors

- Displacement relative to the tectorial membrane causes bending of the stereocilia

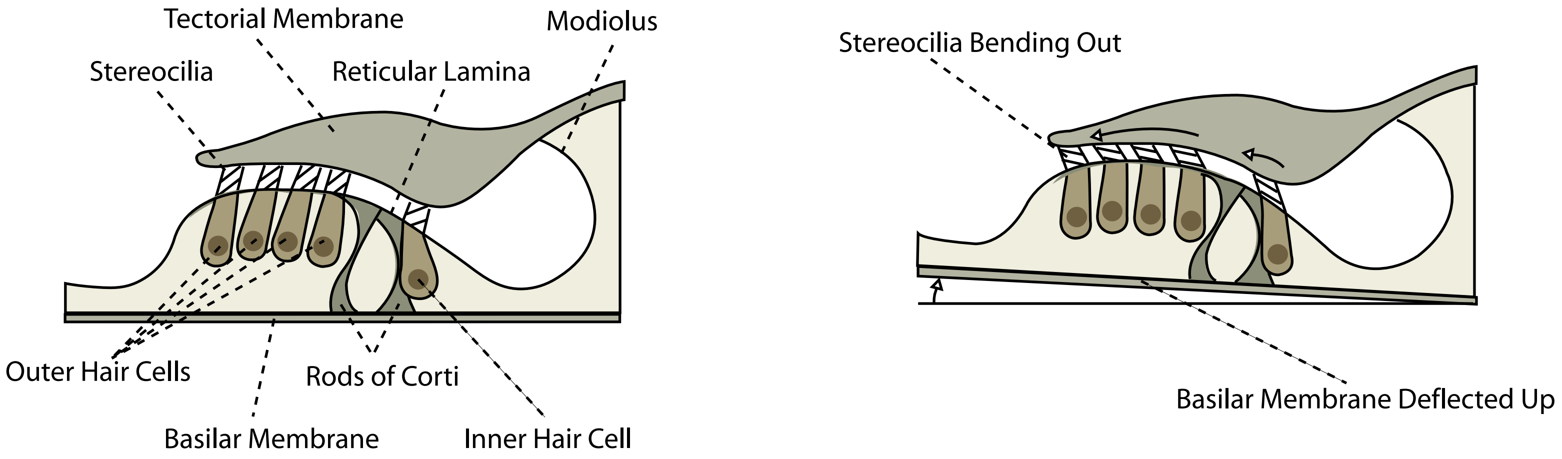


Figure by MIT OpenCourseWare. After figure 11.13 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Hair cells have stereocilia

Two photos removed due to copyright restrictions.

- Each hair cell has about 100 stereocilia
- Auditory transduction involves bending of cilia

The TRPA1 channel senses stereocilia movement

- potassium channel
- opened by stereocilia movement
- potassium influx causes depolarization

Image removed due to copyright restrictions.
See Figure 11.15a (hair cell ion channels) in Bear, Connors, and Paradiso.
Neuroscience: Exploring the Brain. 3rd ed. Baltimore, MD: Lippincott Williams
& Wilkins, 2007.

The receptor potential encodes stereocilia displacement

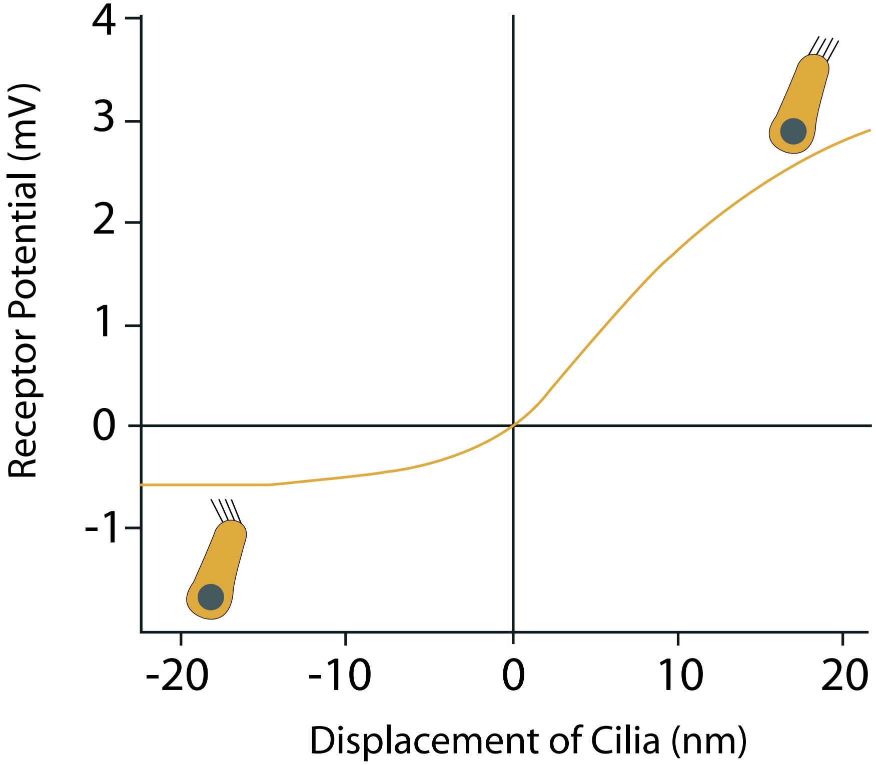


Figure by MIT OpenCourseWare. After figure 11.14 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Hair cells synapse onto neurons in the spiral ganglion

- Depolarization leads to calcium influx through voltage-gated calcium channels
- Calcium causes release of neurotransmitter.

Image removed due to copyright restrictions.
See Figure 11.15b (hair cell ion channels) in Bear, Connors, and Paradiso. *Neuroscience: Exploring the Brain*. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

There are two kinds of hair cells

- Outer hair cells (OHC)
  - three rows of 5000 each
  - attached to tectorial membrane
- Inner hair cells (IHC)
  - single row of 3500
  - not attached to tectorial membrane

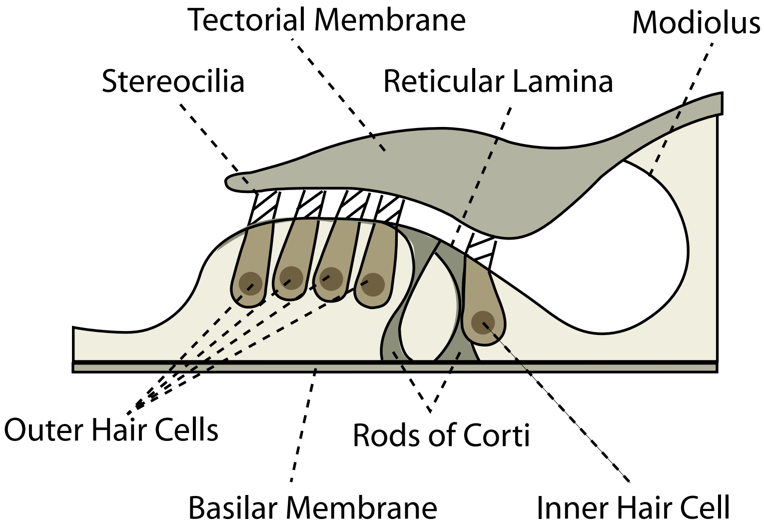


Figure by MIT OpenCourseWare. After figure 11.13 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Inner hair cells dominate cochlear output

- There are fewer inner hair cells
- But less than 5% of spiral ganglion cells receive synapses from outer hair cells
- The fan-out of an inner hair cell is 1 to 10.

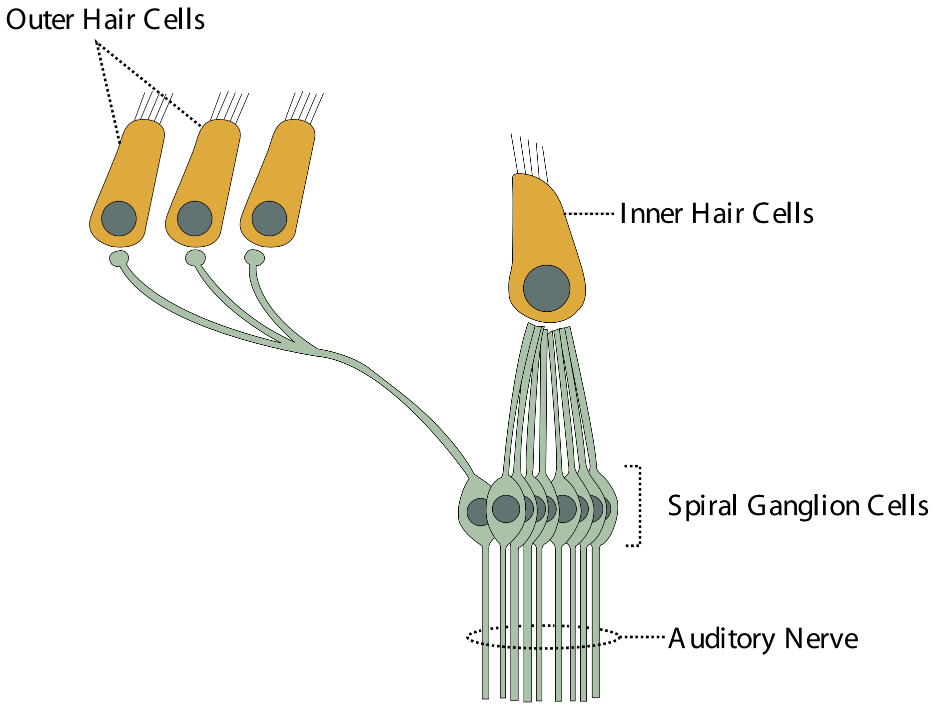


Figure by MIT OpenCourseWare. After figure 11.16 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001. ISBN: 9780683305968.

Outer hair cells amplify basilar membrane deflections

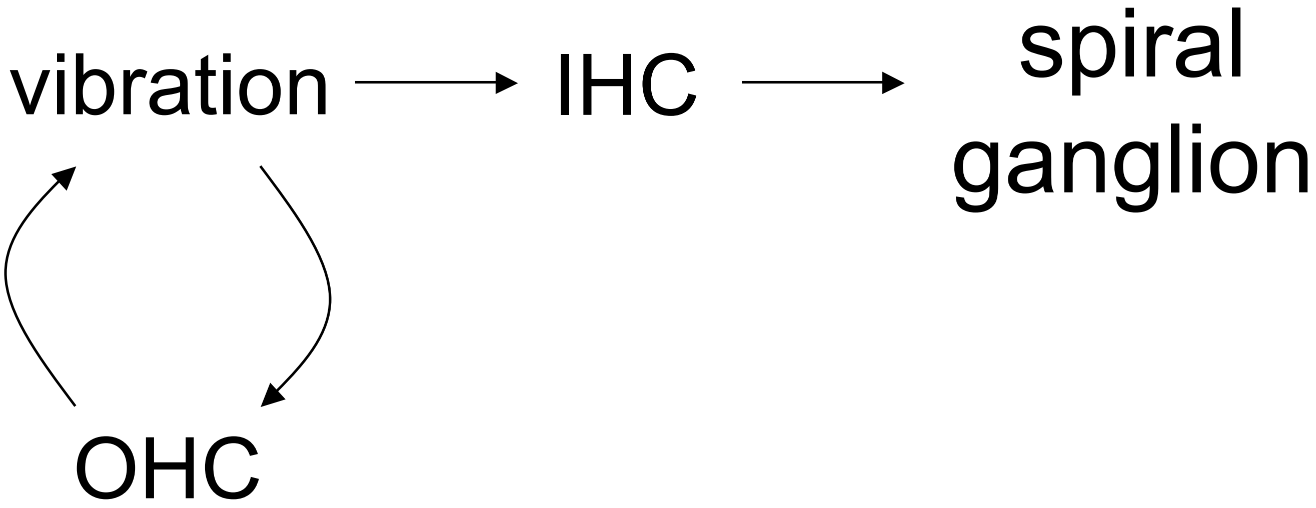
- They respond to membrane deflections by deflecting the membrane more.
- Antibiotics that damage outer hair cells lead to deafness.
- Furosemide decreases transduction, and reduces basilar membrane deflection dramatically.

Prestin is the motor protein in outer hair cells

- Prestin changes the length of outer hair cells in response to sound.

Image removed due to copyright restrictions.
See Figure 11.17a (motor proteins in outer hair cells) in Bear, Connors, and Paradiso. *Neuroscience: Exploring the Brain*. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

The outer hair cells mediate a feedback loop



vibration → IHC → spiral ganglion

vibration → OHC → vibration

- This loop is sometimes called the “cochlear amplifier.”

The ear can make sounds

- Otoacoustic emissions
  - play a click into the ear
  - an “echo” is produced by the cochlear amplifier
- Tinnitus
  - spontaneous otoacoustic emissions
  - instability of the cochlear amplifier

The spiral ganglion projects ipsilaterally to the medulla

- two cochlear nuclei
  - dorsal
  - ventral

Image removed due to copyright restrictions.
See Figure 11.18 (auditory pathways) in Bear, Connors, and Paradiso. *Neuroscience: Exploring the Brain*. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

Ascending pathways converge on the inferior colliculus

- The ventral cochlear nucleus projects bilaterally to the superior olive,
- which projects to the inferior colliculus through the lateral lemniscus.
- There are also longer pathways.

The inferior colliculus connects to a thalamocortical pathway

- The inferior colliculus projects to the medial geniculate nucleus (MGN)
- The MGN projects to auditory cortex.

Image removed due to copyright restrictions.
See Figure 11.18 (auditory pathways) in Bear, Connors, and Paradiso. *Neuroscience: Exploring the Brain*. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

Summary of one auditory pathway

- Spiral ganglion

auditory nerve

- Ventral cochlear nucleus
- Superior olive

lateral lemniscus

- Inferior colliculus
- MGN
- Auditory cortex

Tonotopic maps

- Nearby neurons have similar characteristic frequencies.
- found in many auditory brain areas
  - brainstem auditory nuclei
  - MGN
  - auditory cortex

Primary auditory cortex

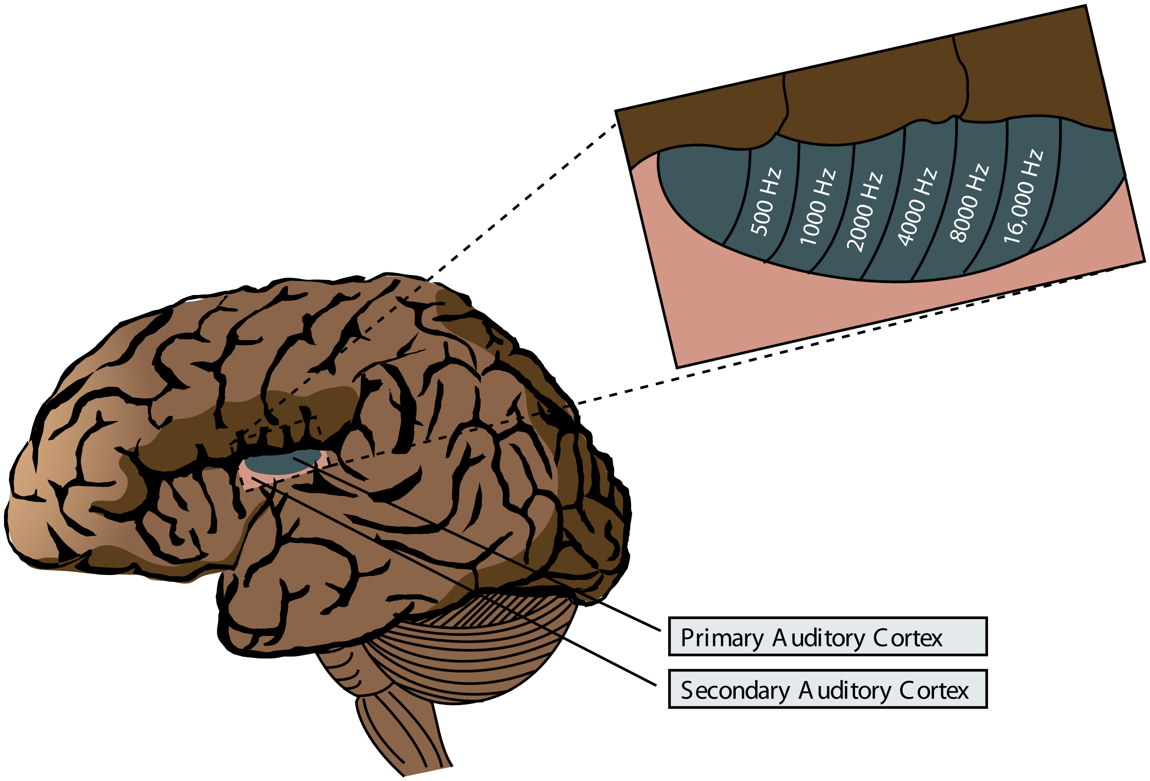


Figure by MIT OpenCourseWare. After figure 11.29 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 2nd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2001.

Prey capture by the barn owl

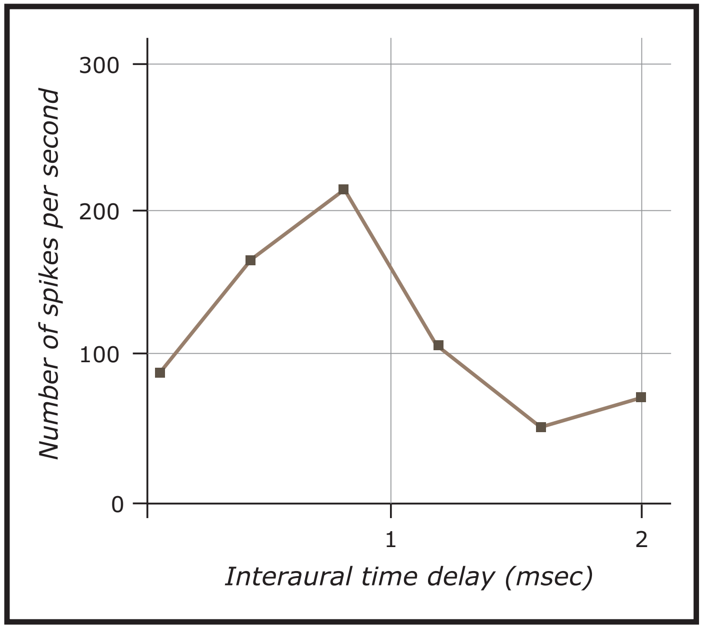
Image removed due to copyright restrictions.
Flying barn owl in the dark, approaching a mouse.

Interaural time delay

Image removed due to copyright restrictions.
See Figure 11.22 in Bear, Connors, and Paradiso.
Neuroscience: Exploring the Brain. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

- Sound reaches the closest ear first.
- Not useful at high frequencies
  - Then the wavelength of sound is smaller than the distance between the ears.

Superior olive neurons encode time delay in firing rate



- Superior olive has binaural neurons
- Inputs from left and right ventral cochlear nuclei
- Selective for interaural time delay.

Figure by MIT OpenCourseWare. After figure 11.24 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

Axonal delay lines

Image removed due to copyright restrictions.
See Figure 11.25 in Bear, Connors, and Paradiso.
Neuroscience: Exploring the Brain. 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

- Coincidence detection
- Phase locking is necessary, so only low frequencies are relevant.

Vertical localization

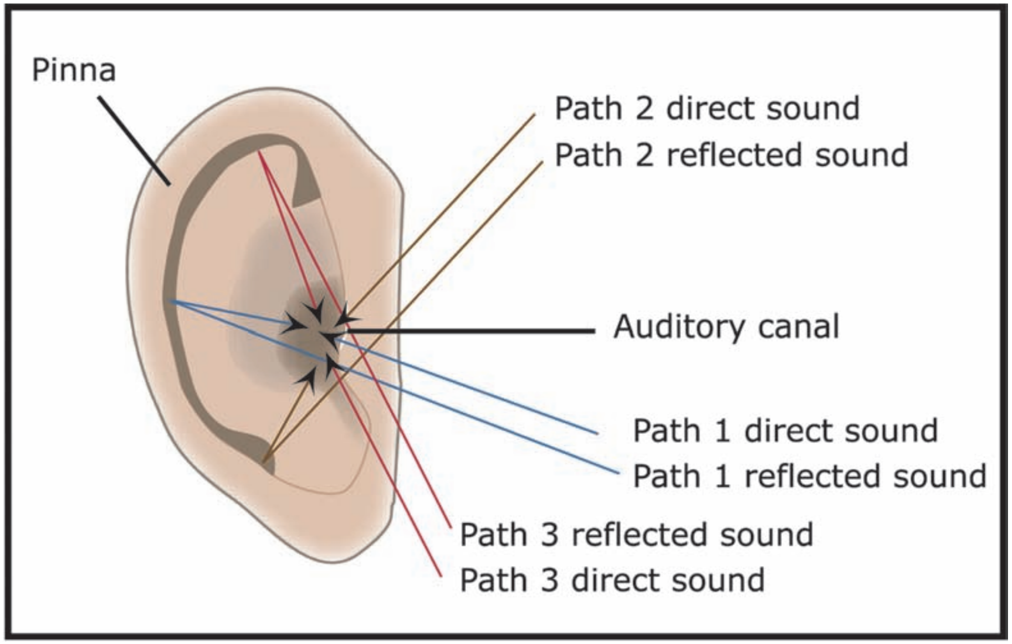


Figure by MIT OpenCourseWare. After figure 11.28 in Bear, Mark F., Barry W. Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain.* 3rd ed. Baltimore, MD: Lippincott Williams & Wilkins, 2007.

- Impairment if the pinna is bypassed with a tube in the auditory canal.
- Reflections off the pinna are important.