# Lecture 31. The Auditory System

*Professor Nilay Yapici*

## Pre-lecture preparation – Posted on the course website before the lecture

## Reading – Chapter 11- Pages 369-403

## Optional Readings- Posted on the black board site before the lecture

## Lecture Objectives

- To understand the basic function of the auditory system.
- Be able describe the structure of the cochlea and the basilar membrane.
- Be able to describe the process of auditory transduction in inner hair cells on the basilar membrane of the cochlea.
- Be able to discuss how the auditory nerve cells (and beyond) encode sound intensity and frequency using tonotopic mapping, rate coding, and phase-locking.
- Be able to discuss models for horizontal sound localization in the auditory brainstem.

## Lecture outline

This lecture will discuss the anatomical and functional structures of the auditory system and how auditory information is transmitted to the central nervous system.

1) What are the structural compartments of the ear: outer ear, middle ear and inner ear

   a. The outer ear is made up of the pinna (important for funneling and directing sound), and the auditory canal (the pathway towards the tympanic membrane).

   b. The middle ear is the air-filled cavity between the larger tympanic membrane and the smaller oval window which houses the ossicles. The ossicles act as a piston to amplify sound from the air to be transmitted into the liquid-filled inner ear.

   c. The inner ear is the part of the ear that is medial to the oval window which contains the cochlea. The cochlea is a spiral structure with three parallel chambers (Figure 11.7). When stretched out (Figure 11.8), the oval window is located at the base of the scala vestibuli, which is continuous with the scala tympani eventually through a hole in the apex of the cochlea (far end). Importantly, the central scala media contains the basilar membrane. This is the membrane that houses the organ of corti, which contains the auditory hair cells.

2) How is the auditory stimuli transmitted in hair cells:

   a. The hair cells have stereocilia that are linked together. When pressure waves enter the inner ear via the oval window, this produces a wave of movement which originates at the base of the flexible basilar membrane. Because of the properties of the basilar membrane (narrow and stiff at the base, wide and floppy at the apex), there is a tonotopy on the basilar membrane (Figure 11.10). This tonotopy (frequency map) is fed through the auditory nerve to downstream auditory brain areas.

   b. If sound activates a portion of the basilar membrane, mechanoreceptor in the hair cell produces an ionotropic current responsible for transduction (Figure 11.5). This mechanoreceptor is located at the tip of the stereocilia. Tip links keep these channels physically *mostly* closed at rest, open when the basilar membrane moves up, and more closed when the basilar membrane goes down. This mechanosensor is an ionotropic receptor permeable to potassium. In the endolymph surrounding the hair cells, the potassium is higher than inside of the hair cells, causing potassium to rush in and depolarize the cell (unlike most normal neurons!). This leads to opening of voltage-gated calcium channels and subsequent release of glutamate onto neurons of the auditory nerve (spiral ganglion neurites).

3) How is auditory information encoded in the brain?

   a. Sound intensity can be encoded by rate (the more action potentials, the more intense the sound) as well as number of active neurons (more neurons, higher intensity)

   b. Coding for frequency information of the sound takes at least two forms in auditory nerve cells, cochlear nuclei, and up to at least the auditory cortex: Tonotopy and phase locking.

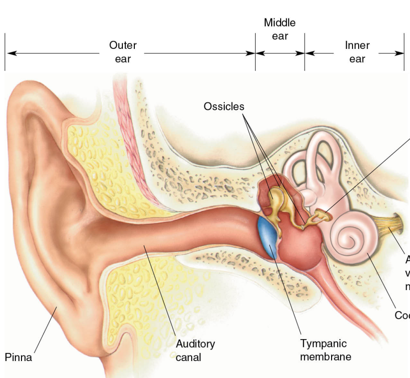
4) Sound localization in the horizontal environment

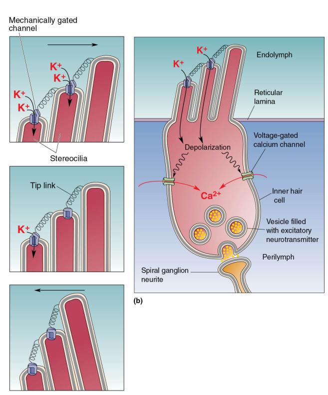
   a. Interaural Time Delay (ITD) relates to the time difference that a sound (or phase of a sound wave) takes to the two different ears (**Figure 11.22**). If a sound is directly in front of you, the ITD is 0, but if it is to your right, for instance, it gets to your right ear faster than your left. This method only works when the frequency of the sound is low enough.

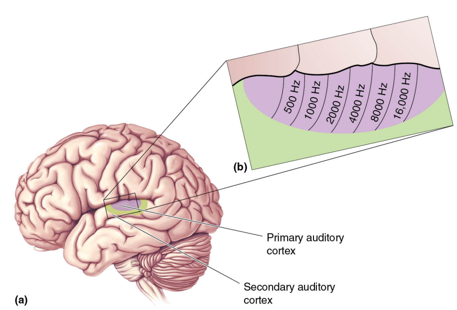
   b. Interaural Intensity Difference (IID) relates to the phenomenon that the head itself can act as a sound shield, so that if a sound comes from one side of the head, it is louder on that side than the other side (**Figure 11.23**). This can't work for very low frequency sounds, because the head doesn't cast a shadow for long wave lengths.

## Study questions:

1) What would happen to auditory transduction in the hair cells if the endolymph had an ionic composition like that of the perilymph (which is similar to normal extracellular fluid)?
2) Cochlear implants do a pretty good job at treating deafness caused by abnormalities in the ear. Would it do as good of a job if there were damage to the auditory nerve? Why or why not?
3) Humans can localize sound very well along the horizontal environment, but less so in the vertical environment. Other animals such as bats and owls can locate sounds much better than humans. Why are humans not so great at localization in the vertical world, and what makes these other animals better?



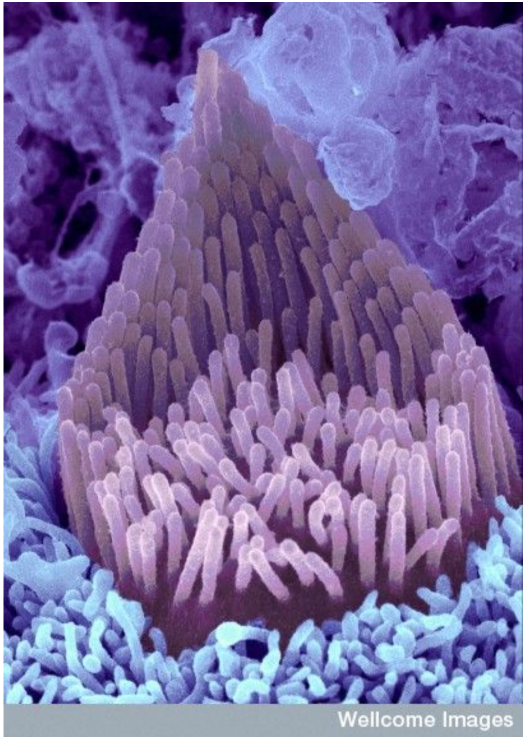



# Lecture 31: Auditory System

Nilay Yapici (ny96@cornell.edu)

Office Hours: Wednesdays 2PM-5PM

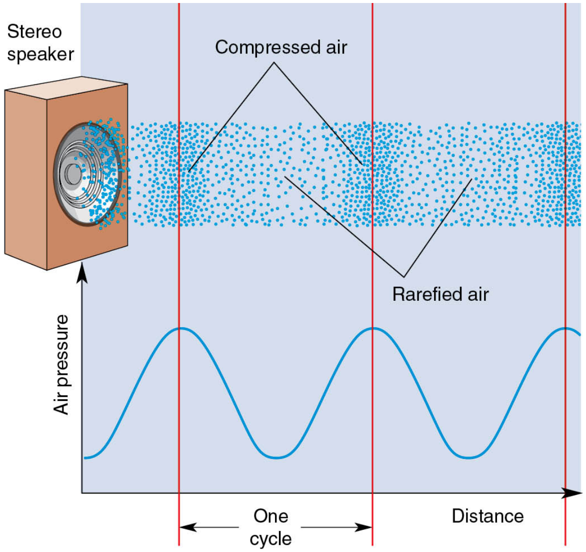


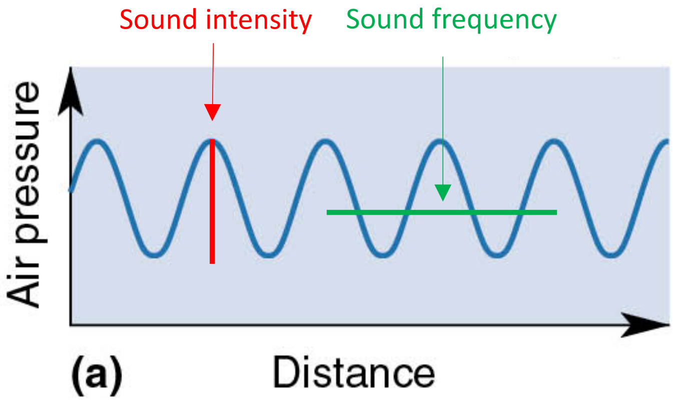
# Learning objectives

- Be able describe the structure of the cochlea and the basilar membrane.
- Be able to describe the process of auditory transduction in inner hair cells on the basilar membrane of the cochlea.
- Be able to discuss how the auditory nerve cells (and beyond) encode sound intensity and frequency using tonotopic mapping, rate coding, and phase-locking. (Important!)
- Be able to discuss models for horizontal sound localization in the auditory brainstem; interaural time difference and interaural intensity difference.

# What is sound?

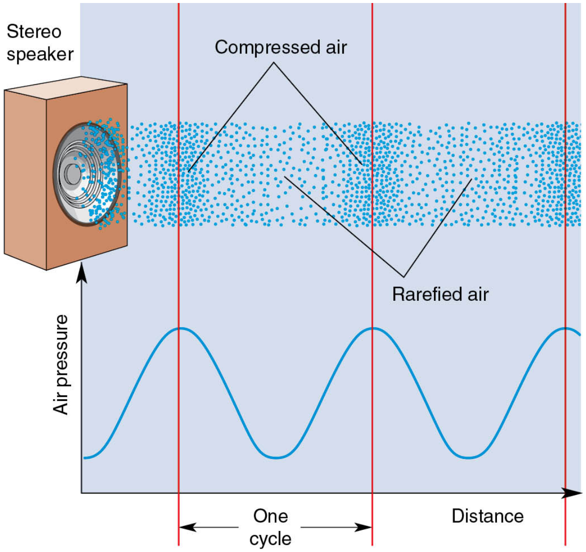
Sound waves are produced by pressure, compressing air molecules in a particular medium within our auditory range.

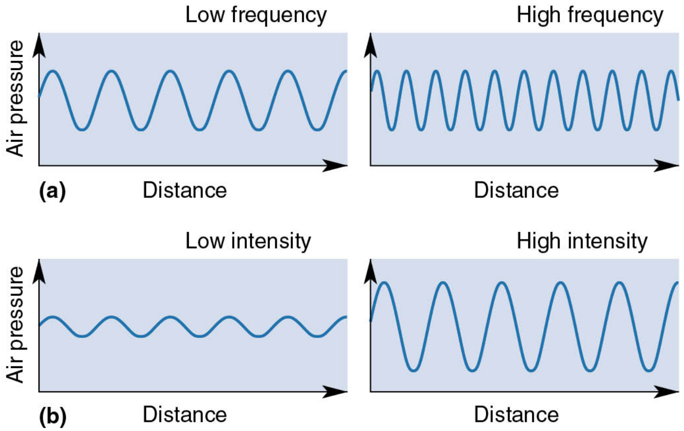


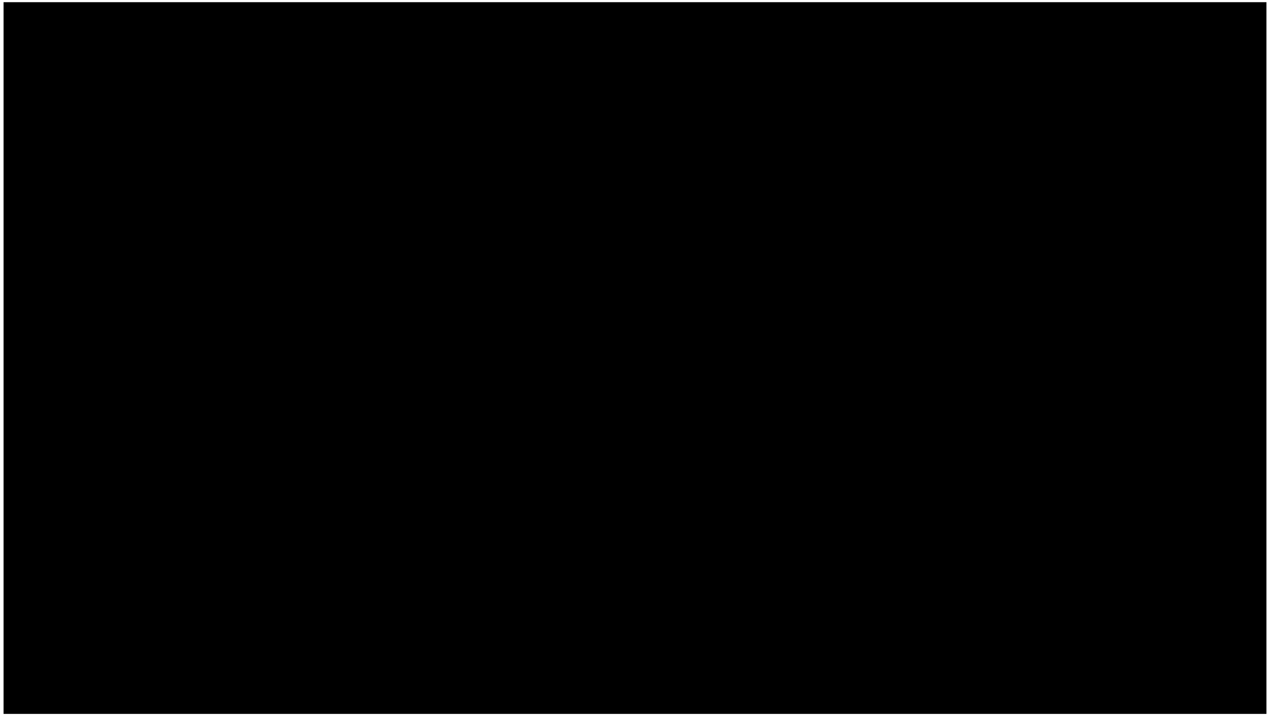
# What is sound?

Sound waves are produced by pressure, compressing air molecules in a particular medium within our auditory range.

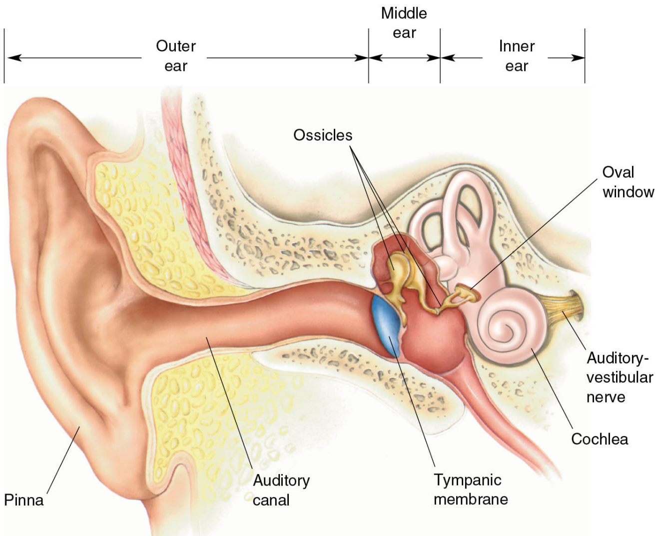


Human auditory system can respond to sound waves ranging from 20Hz to 20,000Hz.



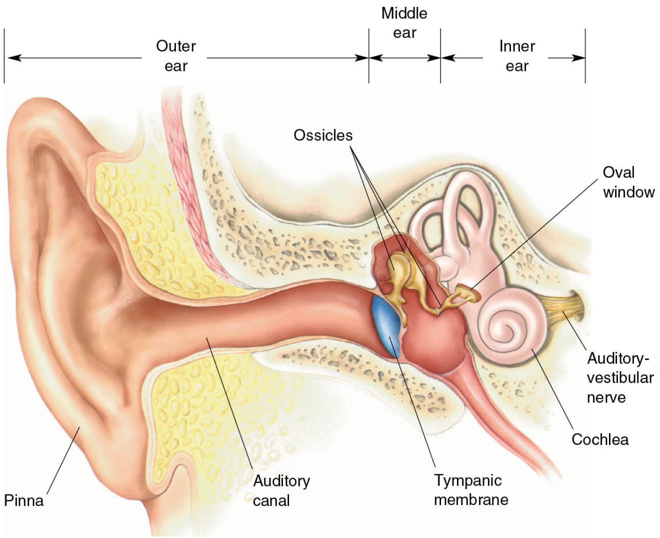
# Auditory System




- Ear has three compartments:

1. Outer ear
2. Middle ear
3. Inner ear

# Auditory System

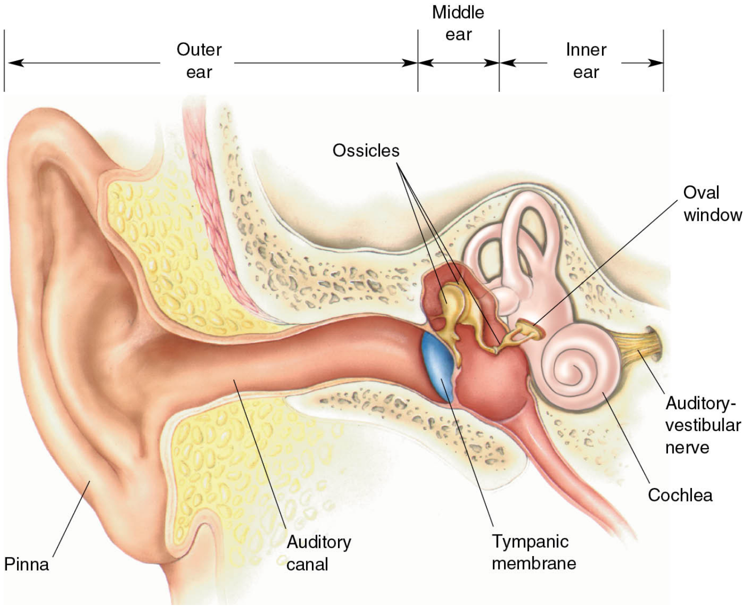



- Ear has three compartments:

1. Outer ear
   - Auditory canal
   - Tympanic membrane
2. Middle ear
   - Three bone structure called Ossicles
     a. Malleus
     b. Incus
     c. Stapes
   - Oval Window
3. Inner ear
   - Vestibule
   - Cochlea

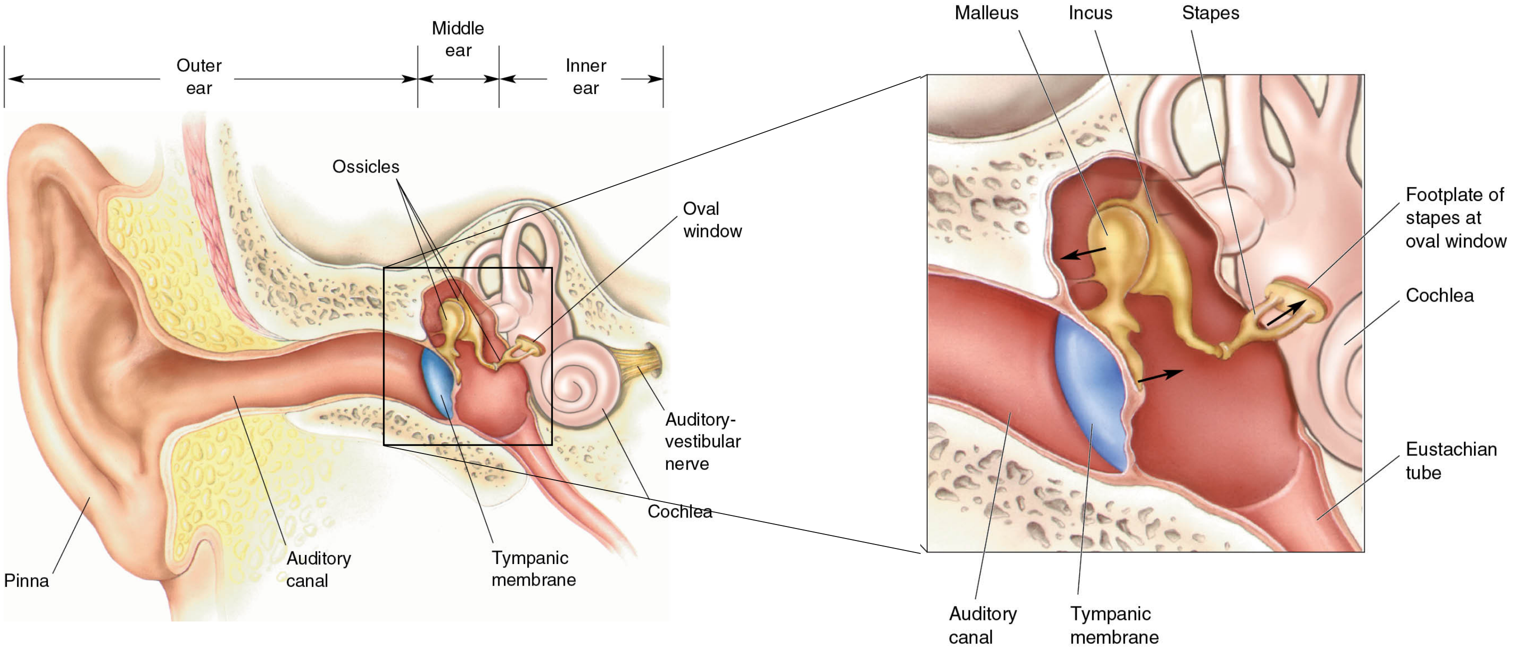
# Components of the Outer and Middle Ear

The ear is structured to transfer sound waves to the cochlea

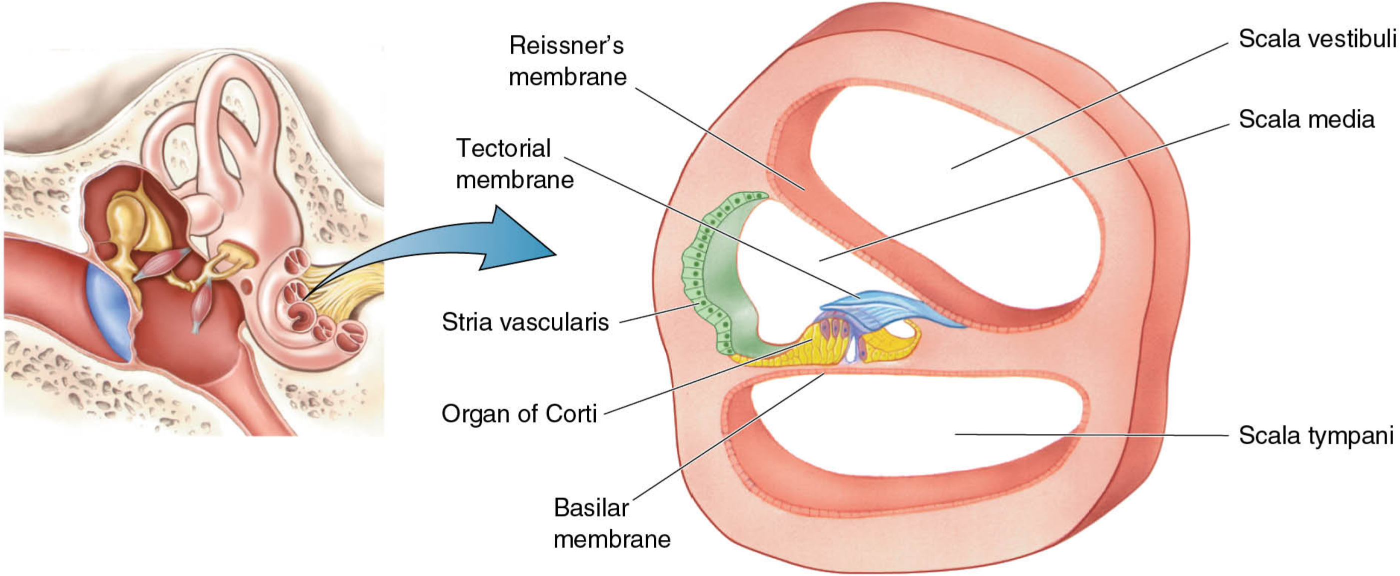


# Components of the Outer and Middle Ear

The tympanic membrane vibrates with sound, causing the ossicles to amplify sound waves and transfer them to the inner ear through the oval window



# Cochlea (in the inner ear) is a critical part of the auditory system

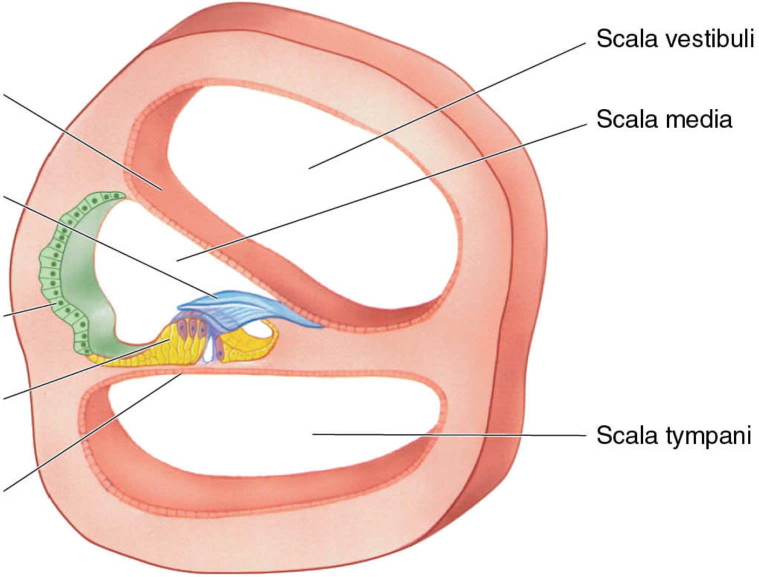


# Cochlea (in the inner ear) is a critical part of the auditory system

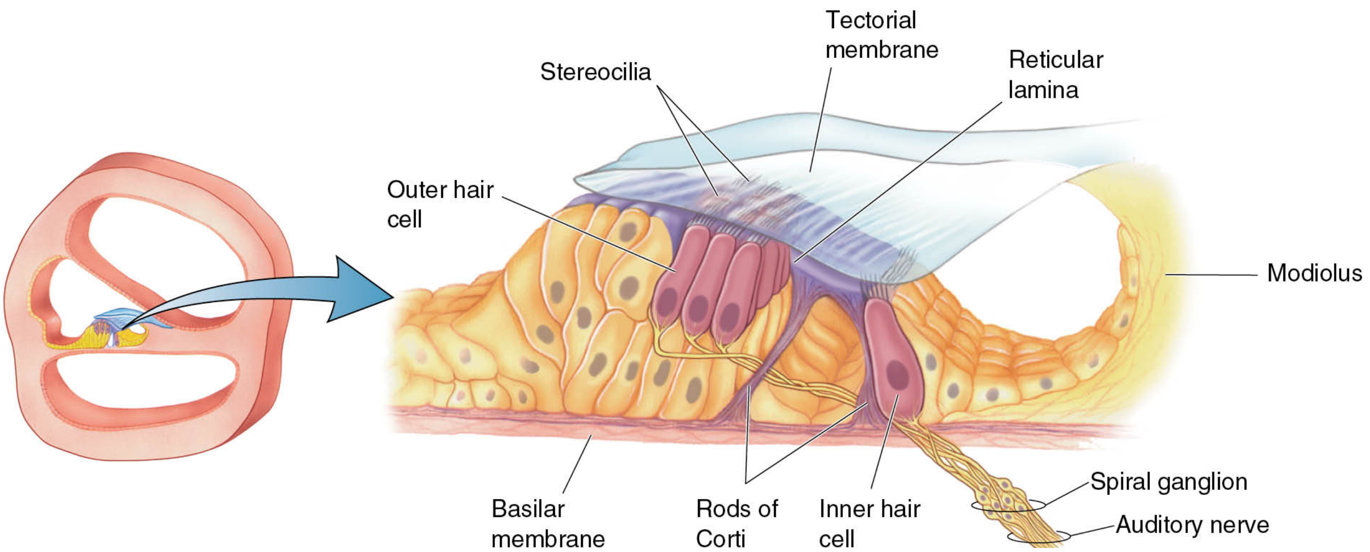
The cochlea has three chambers

- Scale vestibuli
- Scale media
- Scala tympani

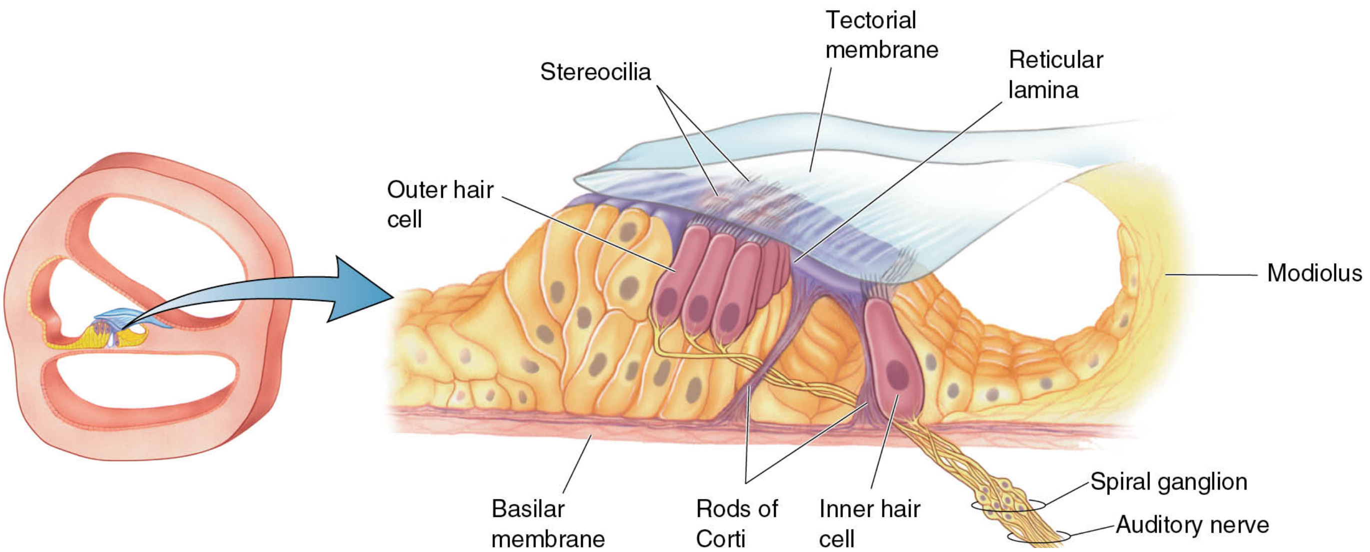
The organ of corti which detects sound is in the scala media.



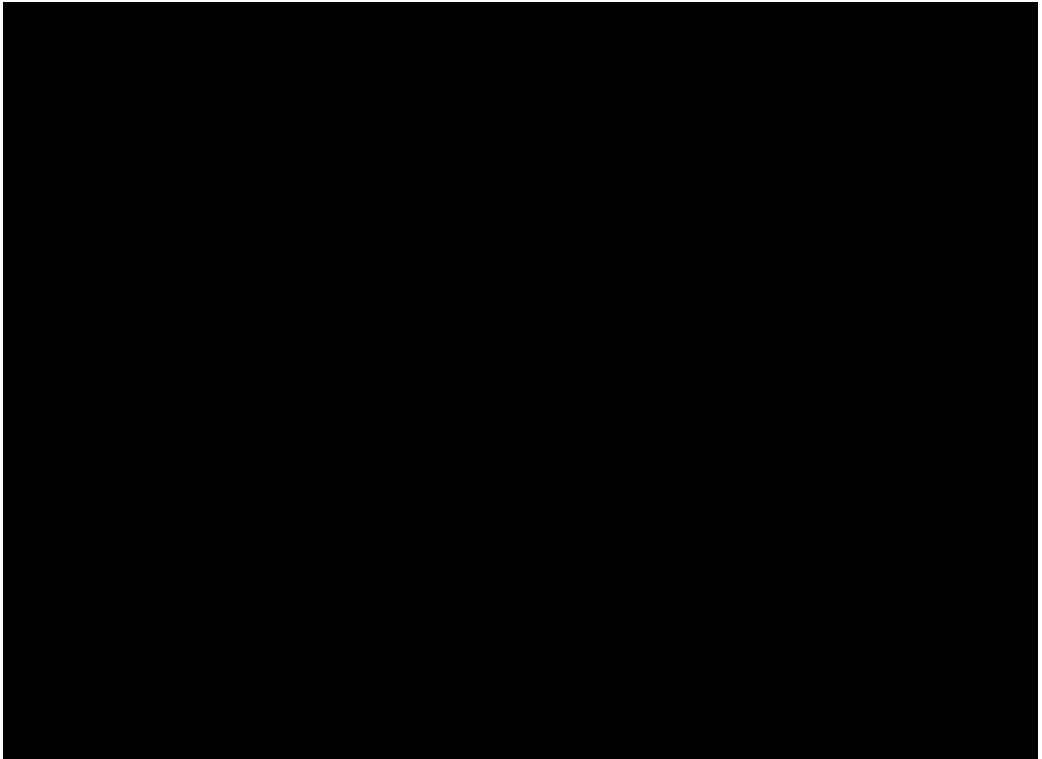
# The organ of corti is located on the basilar membrane



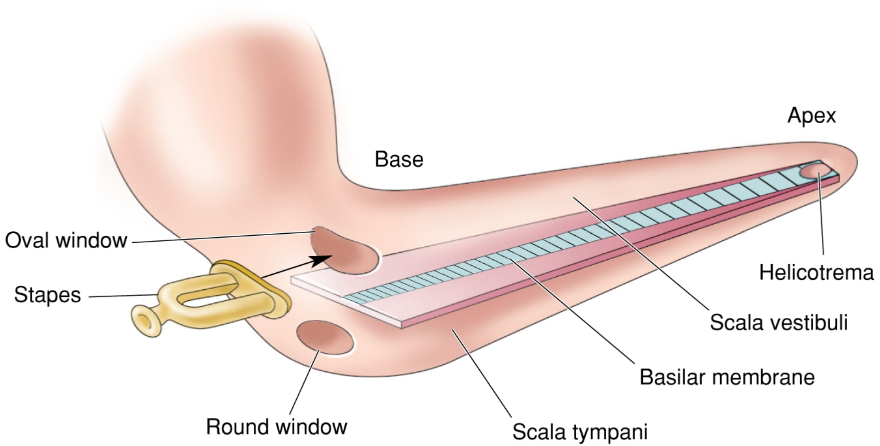
# Hair cells are imbedded in the organ of corti on the basilar membrane



# Travel of sound waves through the ear compartments and the tonotopic map of the inner ear.



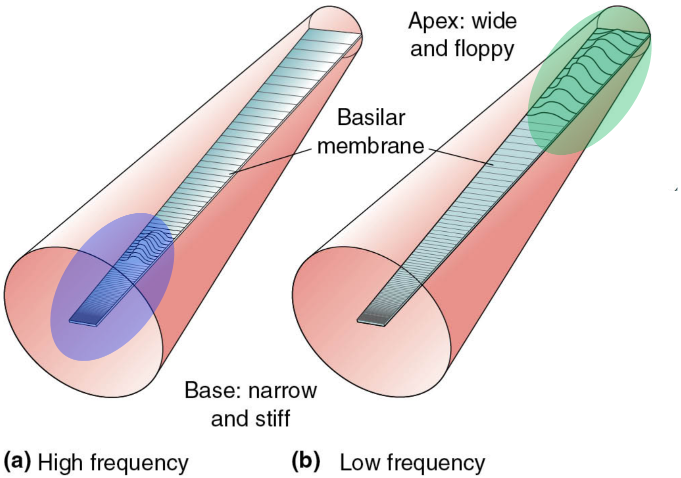
# Tonotopy in the basilar membrane of cochlea



# Tonotopy in the basilar membrane of cochlea

- If the frequency is high, the stiffer base of the membrane will vibrate, and wave will not propagate further.

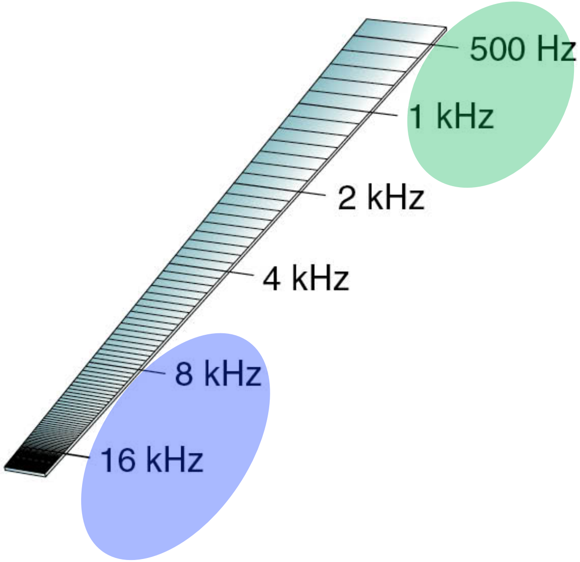
- If the frequency is low it will travel all the way to the apex.



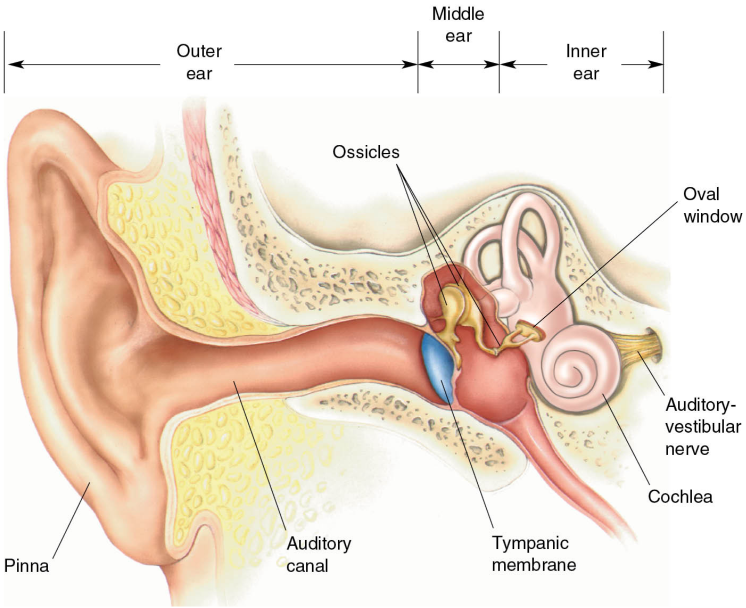
# Tonotopy in the basilar membrane of cochlea

- If the frequency is high, the stiffer base of the membrane will vibrate, and wave will not propagate further.

- If the frequency is low it will travel all the way to the apex.



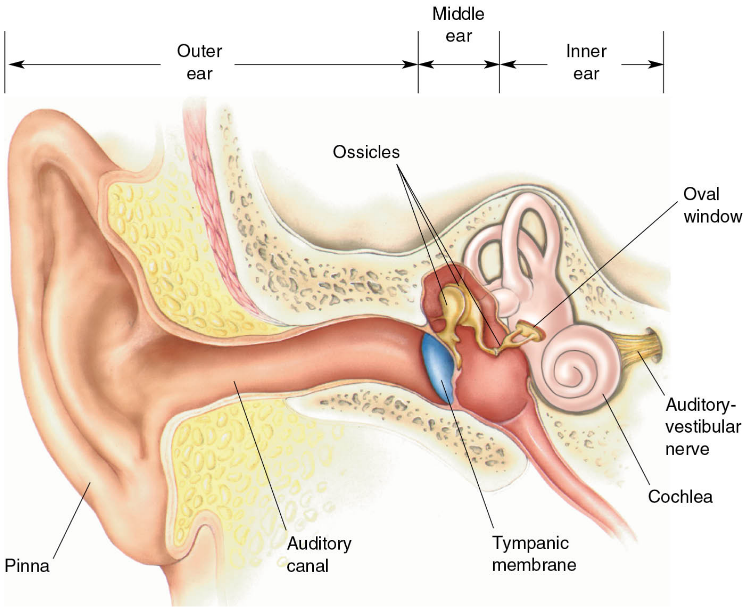
# Clicker Question 1




Which part of the auditory pathway does the tonotopic map originate?

A. Ear canal
B. Tympanic membrane
C. Cochlea basilar membrane
D. Ossicles
E. Vestibular nerve

# Clicker Question 1

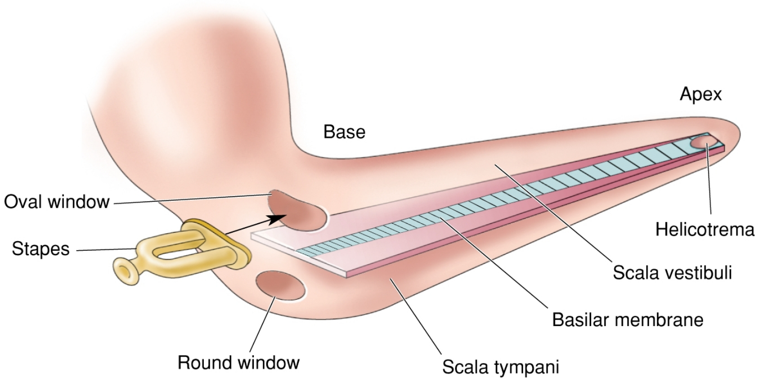



Which part of the auditory pathway does the tonotopic map originate?

A. Ear canal
B. Tympanic membrane
C. Cochlea basilar membrane
D. Ossicles
E. Vestibular nerve

# Clicker Question 2

Which of part of the basilar membrane does a 8kHz sound wave stimulate?






A. at the apex of the cochlea

B. at the base of the cochlea

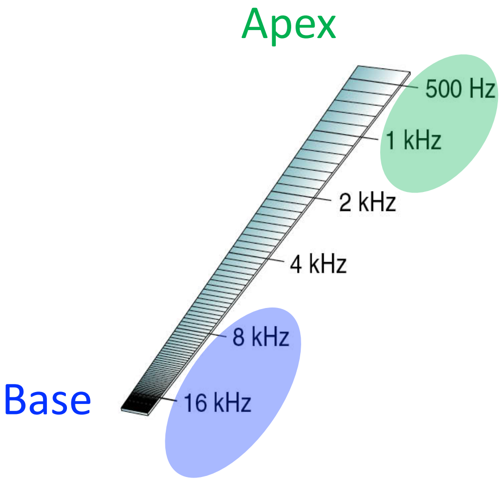
C. throughout the cochlea

D. by vibrations of the stapes

E. at the middle of cochlea

# Clicker Question 2

Which of part of the basilar membrane does a 8kHz sound wave stimulate?




A. at the apex of the cochlea

B. at the base of the cochlea

C. throughout the cochlea

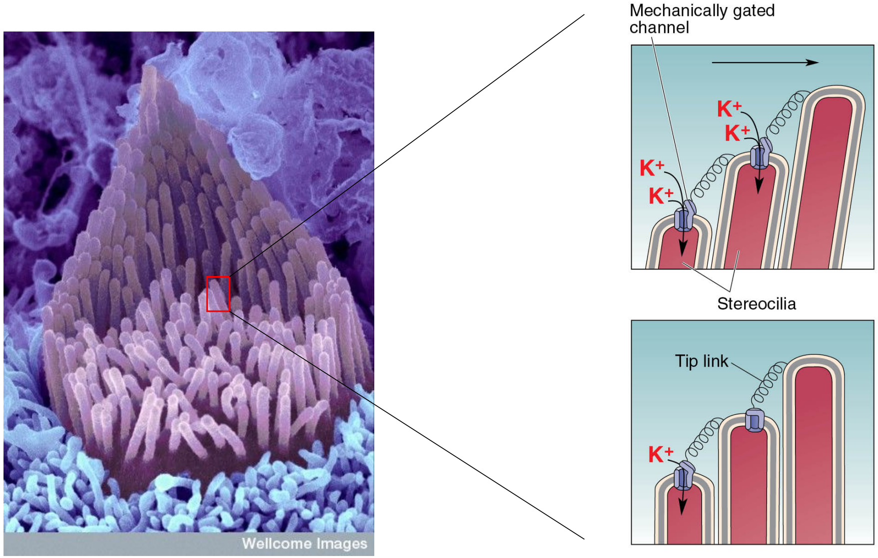
D. by vibrations of the stapes

E. in the middle of the cochlea

# Hair cells

# Hair cells have mechanoreceptors

- $K^+$ channels at the tip links are mechanically activated.
- Opening of these channels depolarize the hair cell because of $K^+$ influx in to the cell



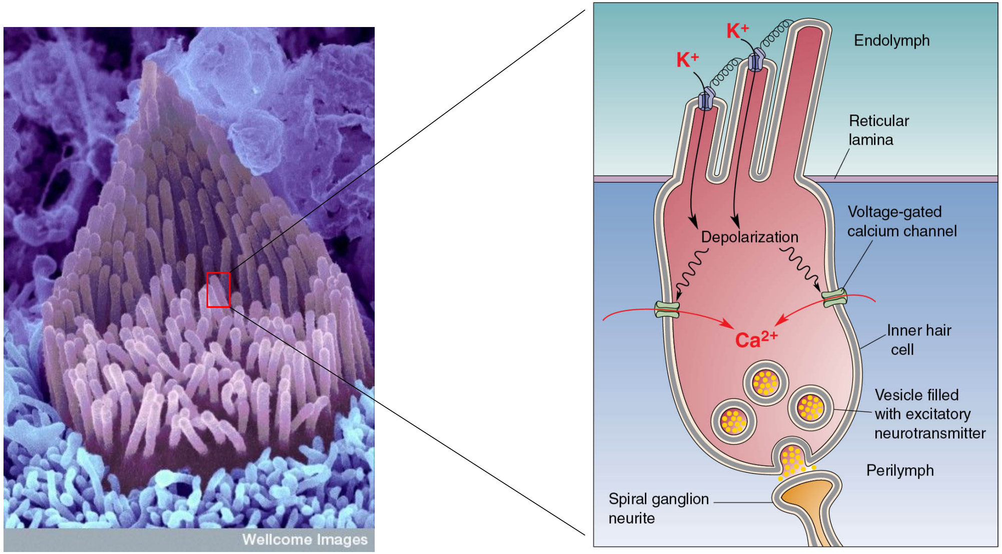

**High K+ in endolymph**

↓

Relatively low K+ in hair cell

# Auditory hair cell physiology

- Depolarization of the hair cell triggers voltage gated $Ca^{2+}$ channels to open.
- Incoming $Ca^{2+}$ leads to the release of synaptic vesicles carrying neurotransmitters, which activates the auditory sensory neuron

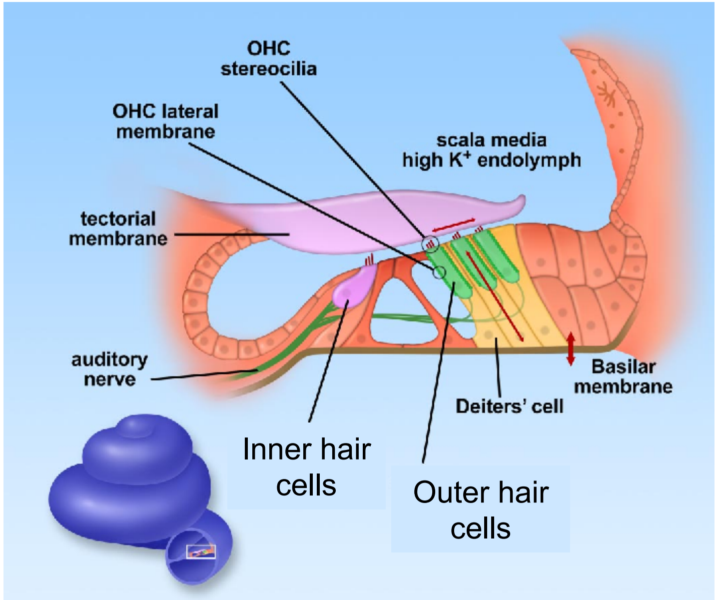



**High K+ in endolymph**

↓

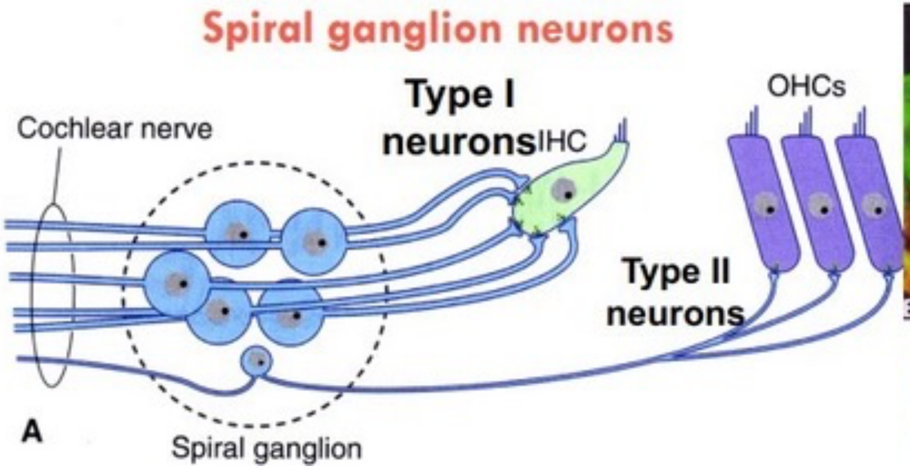
Relatively low K+ in hair cell

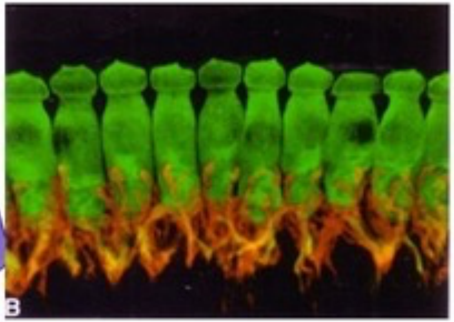
# There are two types of hair cells




- Hair cells are innervated with auditory neurons from the spiral ganglion.
- 95% of the auditory neurons communicate with the Inner hair cells.

# Hair cells can be innervated by single auditory neurons or multiple auditory neurons

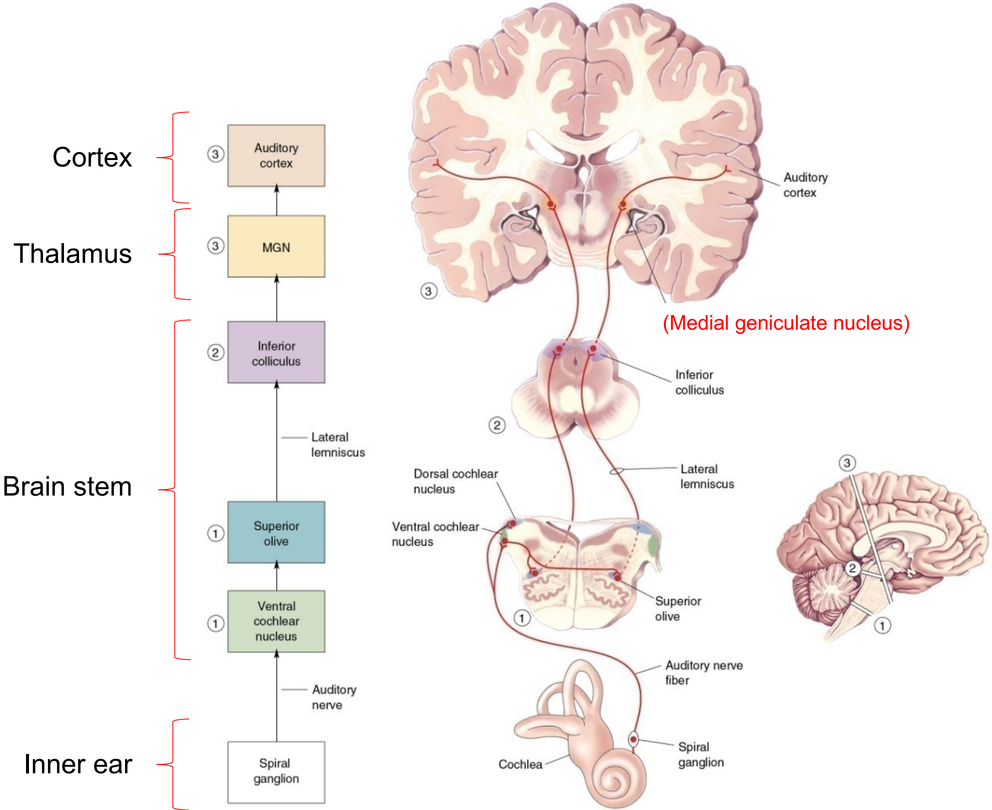



Mouse inner hair cell innervation.
IHCs: green, afferent spiral ganglion cell innervation: orange

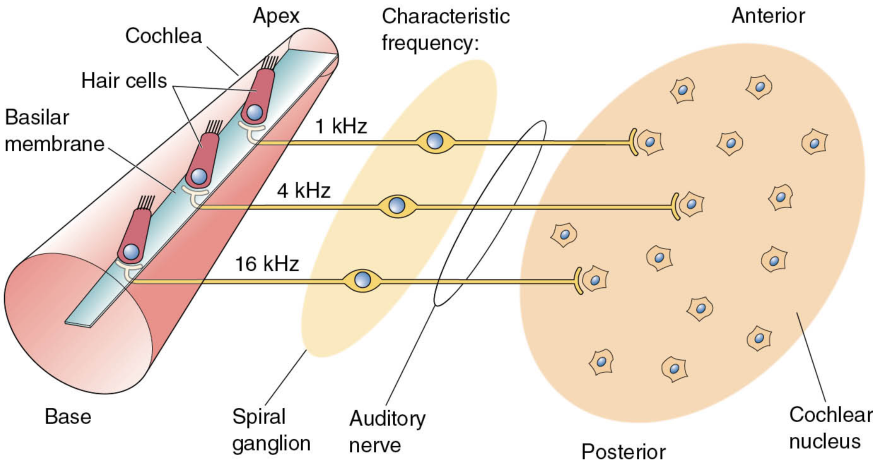
# Central auditory pathways

Neural signals travel from the spiral ganglion to auditory cortex through the brain stem and thalamus



# Coding for sound frequency: Tonotopy

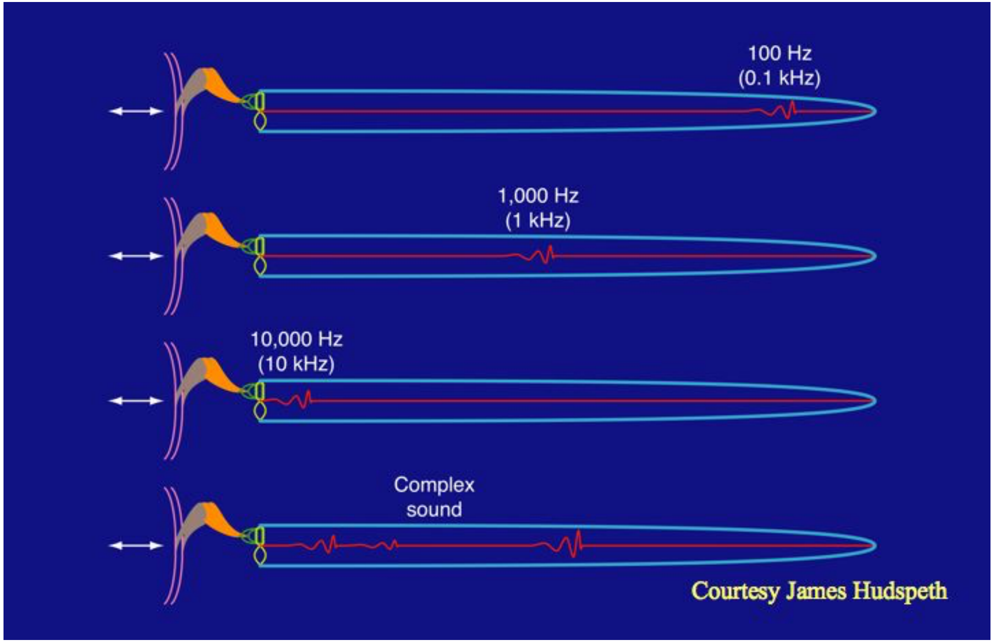
Tonotopy is largely conserved across auditory brain areas, except for low frequencies




There is a map of basilar membrane within the cochlear nuclei except for low frequencies!

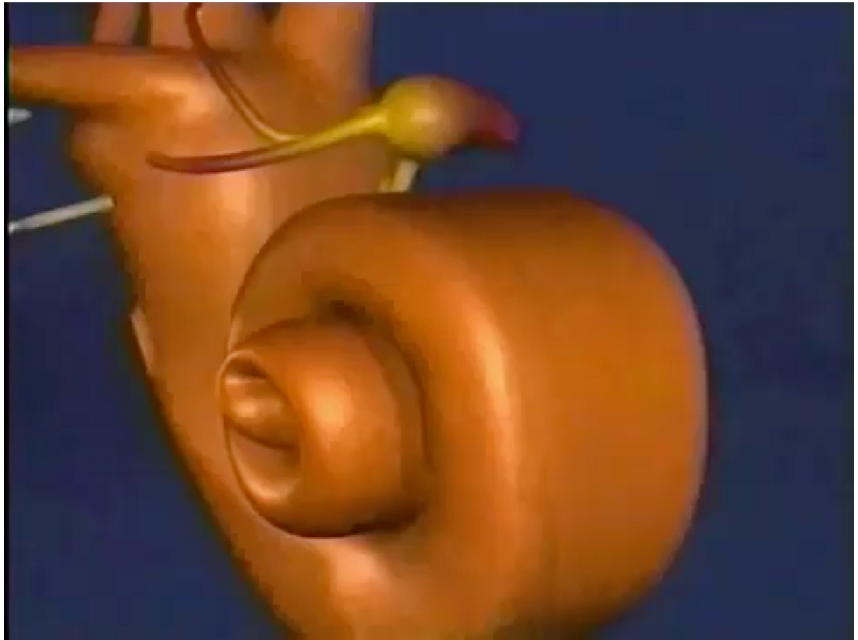
# Coding for sound frequency: Tonotopy

The motion in response to a complex sound is just the sum or the responses to the pure tone components of that complex sound.



# Coding for sound frequency: Tonotopy

The motion in response to a complex sound is just the sum or the responses to the pure tone components of that complex sound.



# Encoding sound intensity and frequency

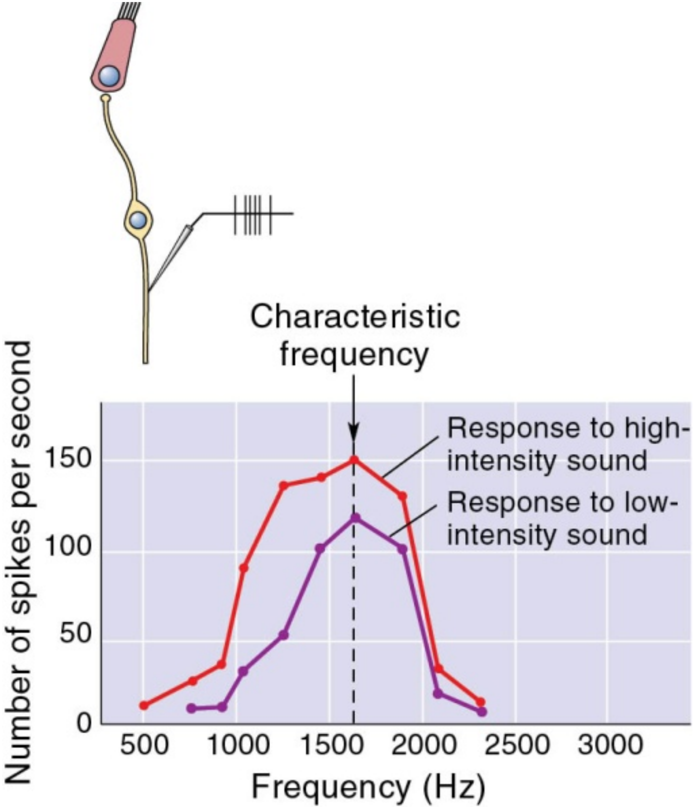
Stimulus intensity is coded in two interrelated ways:

1. Firing rates of neurons
2. Number of active neurons

Stimulus frequency is coded in two interrelated ways:

1. Tonotopy
2. Phase locking

# Encoding sound intensity and frequency

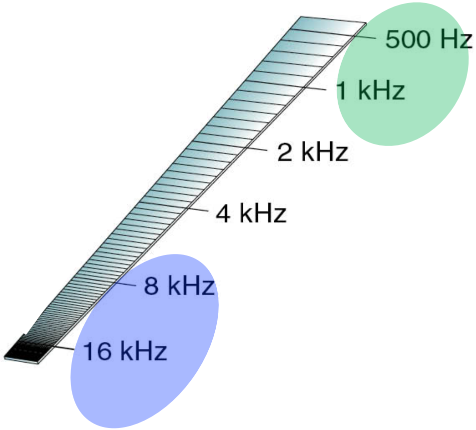



- Example of a frequency tuned auditory neuron.
- This neuron's characteristic frequency is ~1600Hz, but it also changes firing based on intensity of the sound.

# Coding for low frequency sounds: Phase locking

No tonotopy at low frequencies…(below 200Hz)

So how does the brain perceive low frequency sounds?




The timing of neural firing provides and additional information

# Coding for low frequency sounds: Phase coding

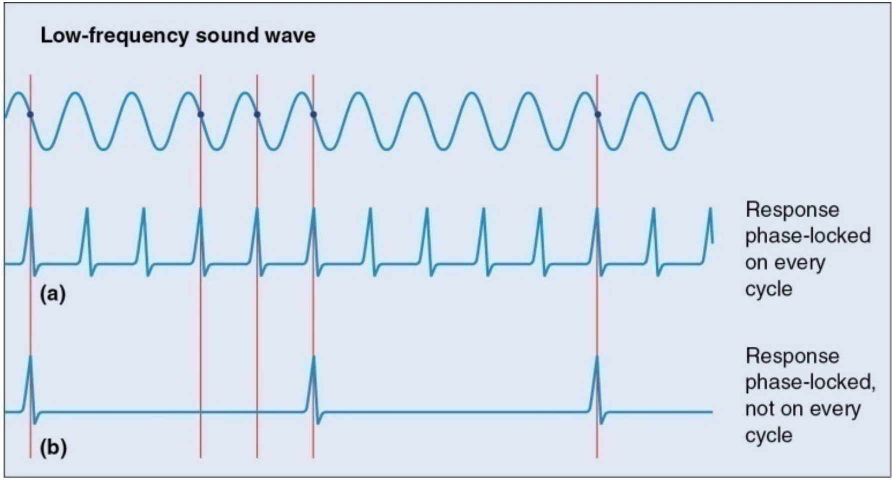
No tonotopy at low frequencies…(below 200Hz)

So how does the brain perceive low frequency sounds?

By measuring the firing rate of auditory neurons

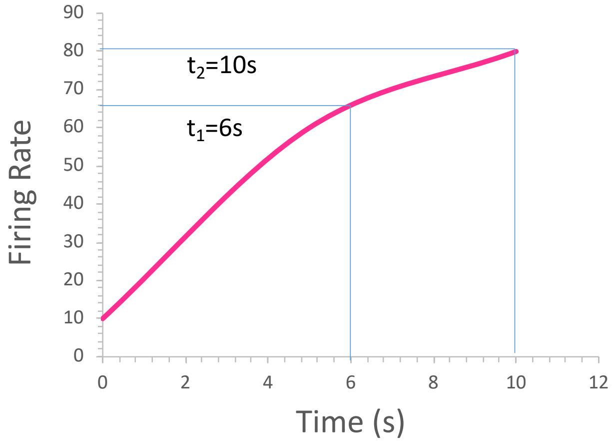
Example neuron firing on every sound cycle at the same phase

Example neuron firing on every 5 sound cycles at the same phase



# Clicker Question 3

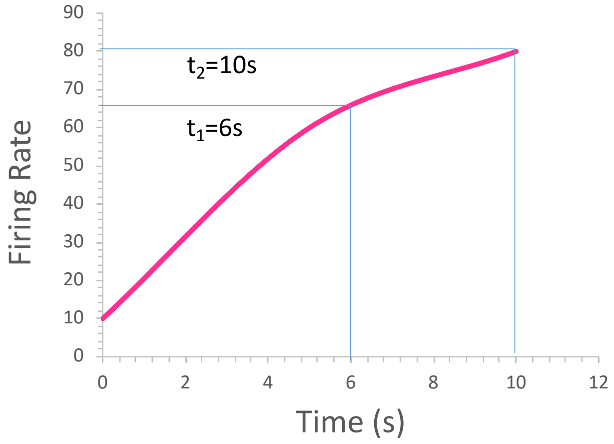
Auditory cortex is trying to decode auditory information from an auditory neuron. First, firing rate increases from 10 to 65. Next, it increases from  65 to 80. What might have changed between $t_1$ and $t_2$?




A. The stimulus intensity increased.
B. The frequency of the stimulus changed so that it is closer to the center of its preferred frequency.
C. A and/or B.
D. None of the above

# Clicker Question 3

Auditory cortex is trying to decode auditory information from an auditory neuron. First, firing rate increases from 10 to 65. Next, it increases from  65 to 80. What might have changed between $t_1$ and $t_2$?




A. The stimulus intensity increased.
B. The frequency of the stimulus changed so that it is closer to the center of its preferred frequency.
C. A and/or B.
D. None of the above

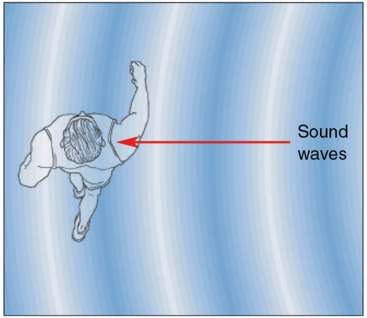
# Mechanisms of Sound Localization

While the interpretation of sounds by frequency and intensity is critical, sound localization is equally important for survival!

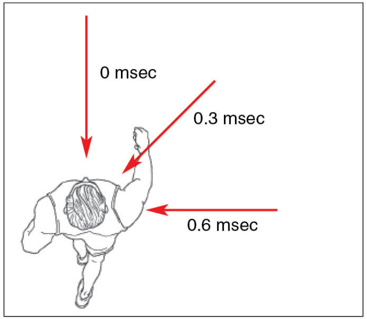
There are two distinct ways our brain localize sound

- Horizontal plane ( left-right):
- Vertical plane (up-down):

# Localization of Sound in the Horizontal Plane




(a)

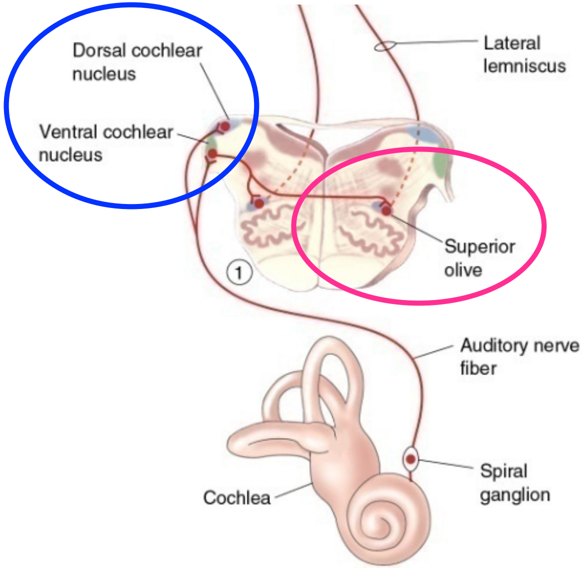



(b)

## Interaural Time Difference (Range 20-2000 Hz)

- If sound wave is coming from one side (for example right), there will be a delay of sound reaching the left ear (0.6 msec).
- If sound wave is coming from straight a head there is no delay in either ear.
- People can discriminate the direction of a sound source up to $2^o$ which means they can discriminate the $11\mu$sec difference.

# Localization of Sound in the Horizontal Plane



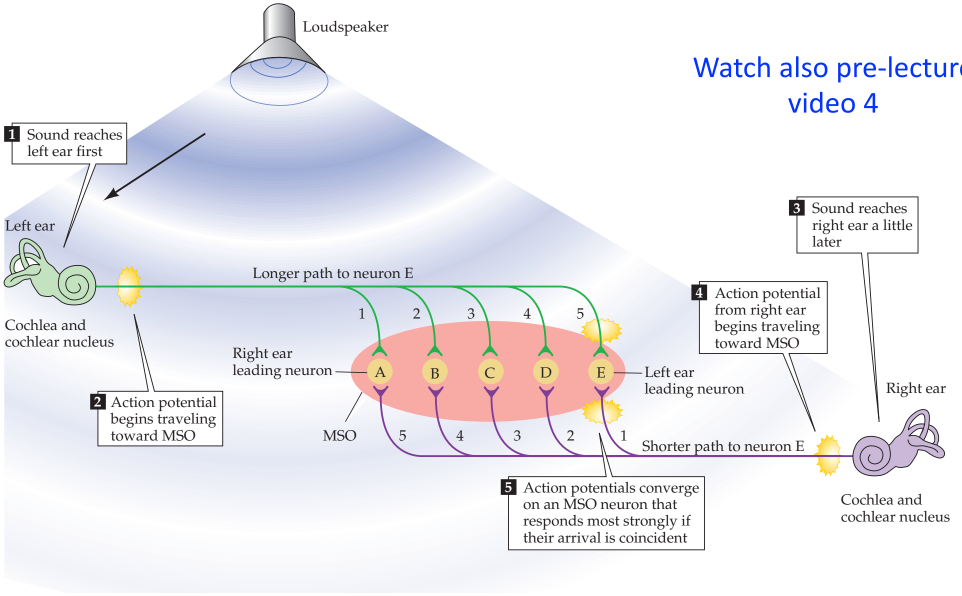

There are two types of auditory neurons;

- Monaural neurons receive afferents only from the ipsilateral auditory nerve, meaning they only respond to sound from one ear. The neurons are present in **cochlear nucleus**.

- Binaural neurons respond to sound stimuli coming from both ears. Because of their response profiles they are critical in sound localization. They are present in superior olive and further auditory centers.

# Localization of Sound in the Horizontal Plane

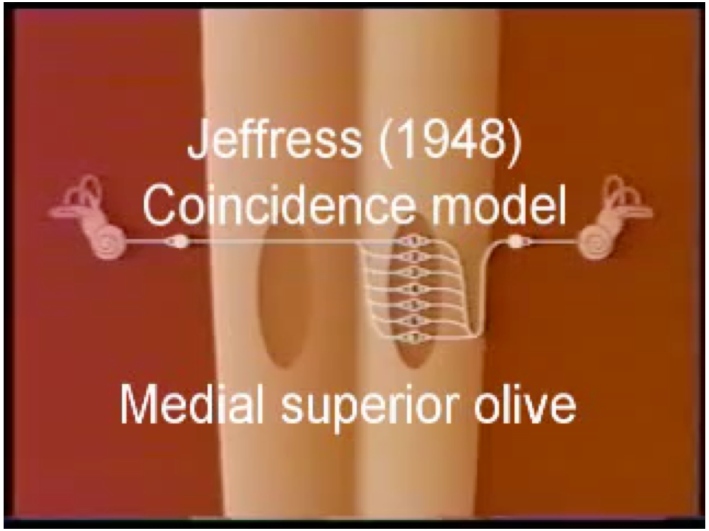
Medial Superior Olive binaural neurons are coincidence detectors!



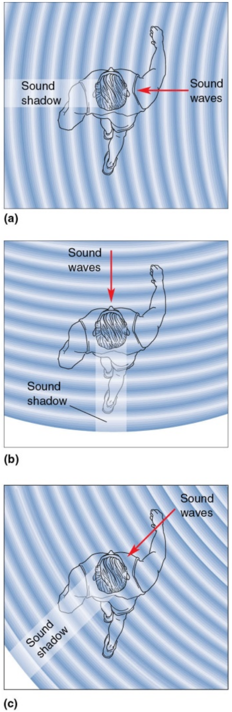

Watch also pre-lecture video 4

# Localization of Sound in the Horizontal Plane

Medial Superior Olive binaural neurons are coincidence detectors!



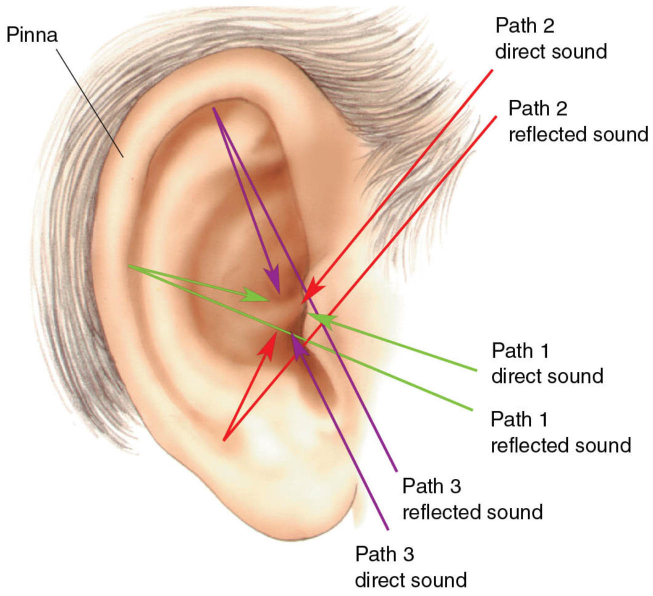
# Localization of Sound in the Horizontal Plane




## Interaural Intensity Difference (Range 2000-20,000 Hz)

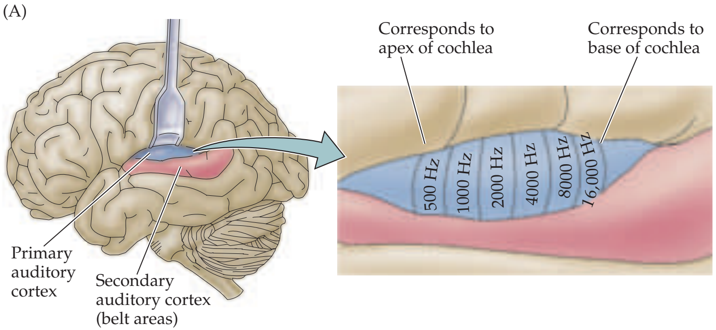
- At frequencies higher than about 2 kHz, the human head begins to act as an acoustical obstacle, as a result an acoustical "shadow" is created at the far ear.
- The intensity difference because of the head shadow provide a second cue about the location of a sound.
- Auditory neurons sensitive to differences in intensity can use this information to locate sound (processing in lateral superior olive).

# Localization of Sound in the Vertical Plane




- Vertical sound localization is based on reflections from the pinna.
- The bumps and ridges produce reflections of the entering sound.
- The delay between the direct path and reflected path change as sound moves vertically.

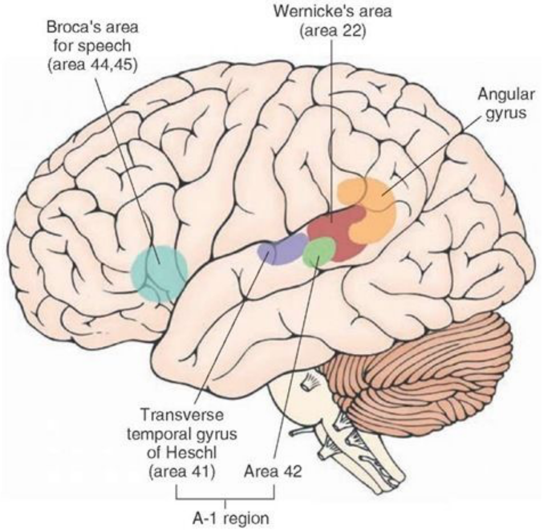
# Auditory Cortex



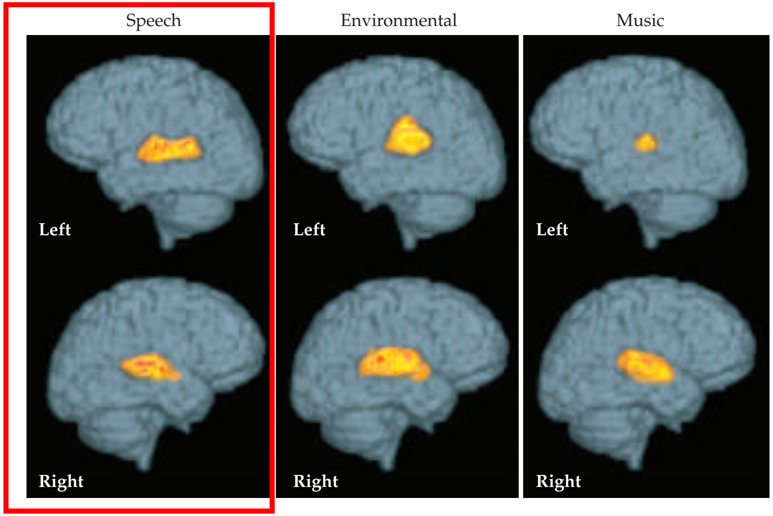

- The ultimate target of afferent auditory information is the auditory cortex.
- The **primary auditory cortex** (**A1**) is located on the superior temporal gyrus in the temporal lobe and receives point-to-point input from the ventral division of the medial geniculate complex; thus, it contains a precise **tonotopic map.**
- The **primary auditory cortex (A1**) has a topographical map of the cochlea, just as the **primary visual cortex (V1)** and the **primary somatic sensory cortex (S1)** have topographical maps of their respective sensory stimuli.

# Other Sound Responsive Cortical Areas

Natural sounds are complex and their representation within the sensory cortex tends to be asymmetric across the two hemispheres.

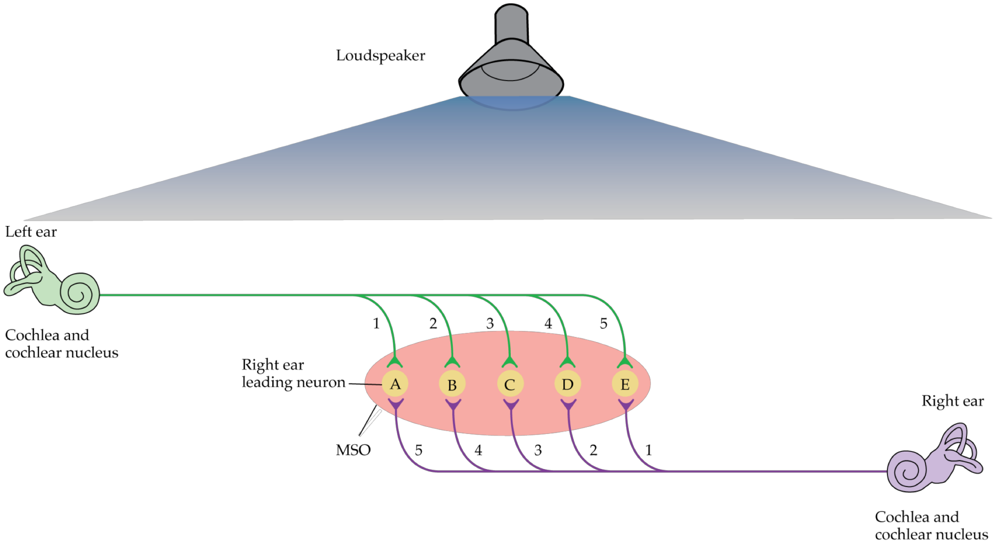



**Lecture 38**



# Clicker Question 4

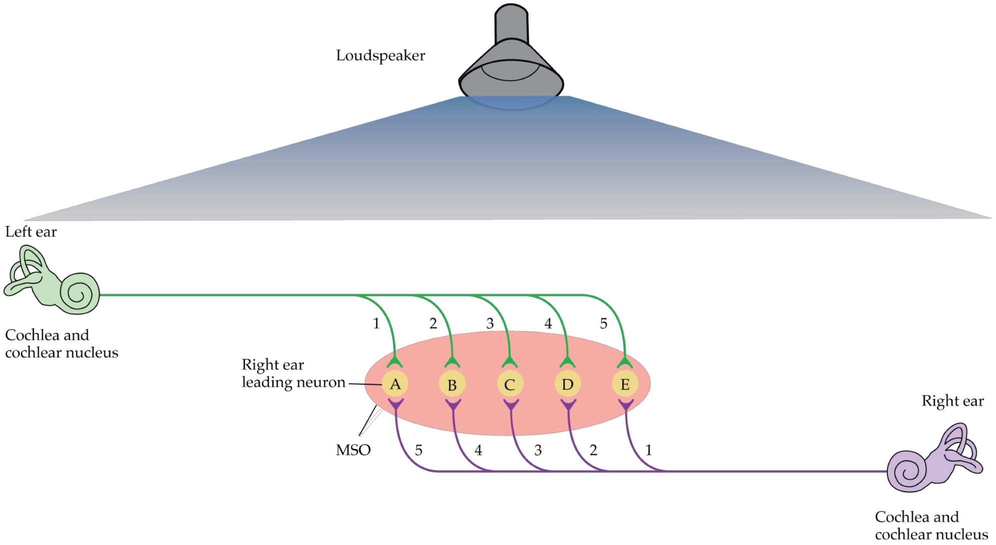
If the sound is coming from in front of you which of the superior olive neuron will fire as a coincidence detector?




a) A
b) B
c) C
d) D
e) E

# Clicker Question 4

If the sound is coming from in front of you which of the superior olive neuron will fire as a coincidence detector?




a) A
b) B
c) C
d) D
e) E

# Interaural TIME difference in barn owls

# Take home messages

- Pressure waves are transferred via the outer and middle ear to the cochlea. The cochlea contains the basilar membrane which selectively resonates to form a tonotopic map.
- Movement  in the basilar membrane displaces tip links of hair cells, opening +K channels which DEPOLARIZE the membrane due to a reversed K gradient between hair cells and the endolymph. Hair cells synapse onto spiral ganglion neurites of the auditory nerve.
- Sound intensity is coded by rate coding. Frequency is encoded by a mixture of tonotopic mapping and phase-coding.
- In birds, ITD pathways have been well worked out via the Jeffress delay line models. IID pathways work using contralateral inhibition and ipsilateral excitation.

# Take home messages

- There are tonotopic maps on the basilar membrane, spiral ganglion, and cochlear nucleus
- From the base to apex, basilar membrane resonates with increasingly lower frequencies.
- Tonotopy is preserved in the auditory nerve and cochlear nucleus.
- In cochlear nucleus, bands of cells with similar characteristic frequencies; characteristic frequencies increase progressively from anterior to posterior.

# Lecture 32: Visual System I-The Eye

Nilay Yapici (ny96@cornell.edu)

Office Hours: Wednesdays 2PM-5PM