**CLINICAL VIGNETTE**

**Case History**

Sabina Ketter is a 51 year-old female who complains of decreased hearing in her right ear. She says it has been getting progressively worse over the past two years so that she now has to use her left ear when talking on the telephone. She also notes an occasional high pitched ringing (tinnitus) in her ear. For several years, she has suffered from headaches, which had recently become worse and which occasionally awaken her from sleep. Her speech is normal, and she denies problems with dizziness, swallowing or vision. She had no recollection of ever having an ear infection.

**Past Medical History**

There are no previous neurologic problems or serious illnesses. She is not taking any medications other than an occasional aspirin or ibuprofen for pain. She has no allergies.

**Social History**

Mrs. Ketter is married and works with her husband and 3 children on the family farm. She does not smoke and drinks moderate amounts of alcohol.

**Family History**

There is no family history of hearing loss. A brother was diagnosed recently with Parkinson’s disease. Her father and a maternal aunt have glaucoma.

**Physical Examination**

**General:** This is an alert person in no distress.

**Vital signs:**

- Temperature = 97.8°F
- Blood Pressure = 125/77
- Pulse = 67 and regular
- Respiration = 13
- Height = 5’6”
- Weight = 152 lbs.

**Neurologic:**

Fundoscopy revealed normal optic nerves. Visual acuity and visual fields, determined by confrontation, are normal. There was no response in either eye when the right cornea was stimulated. Both eyes blinked upon stimulation of the left cornea. There was subtle lower facial weakness when she grimaced. Right plantar response was flexor. Left plantar response was extensor. Tympanic membranes were normal. The Weber test lateralized to the left. The Rinne test showed better sensitivity via air than bone conduction bilaterally.
Laboratory tests:

Audiological:
Pure tone audiograms showed sensorineural loss at high frequencies in the right ear. The left was normal. Speech discrimination was 41% in the right ear, 100% in the left ear. Abnormal auditory brain stem response on right side. Waves III and V were diminished with increased latency.

Vestibular:
0/2 cc ice water in left ear produced nystagmus for > 2min. 0/4 cc icewater in right ear produced no response.

MRI: A golf ball-sized mass was evident at the right ponto-medullary junction.

FIND THE DIAGNOSIS AT THE END OF THE HEARING TESTS SECTION
(JUST BEFORE THE CLINICAL CORRELATION SECTION OF AUDITION)
Close your eyes for a moment and listen. Even in a quiet environment, you can hear sounds. You can hear the low pitch of thunder in the distance, the high pitch of notes on a flute. You can distinguish the gender and age of unknown speakers, understand the meaning of words, and recognize instantly the voice of a friend on the telephone. You can identify the source of the sounds as well. We take for granted our ability to learn a language as children.

In this first section on Audition, Dr. Uhlrich will introduce you to the structures in the ear and to the auditory pathways that underlie our ability to hear. We divide the auditory system into the peripheral auditory system, which receives sound and transforms it into electrical nerve impulses, and the central auditory system, which accepts the coded neural messages from the inner ear and processes them for perception.

In the second part of the Audition module, Dr. Pasic will discuss common clinical tests of auditory function and the predominant clinical issues and diseases affecting hearing.

**Quick introduction to sound**

The sounds that we hear are the result of vibrations— for example from a speaker’s vocal cords or from the strings on a violin. The vibrations result in sound waves that propagate through space and into your ears. The fundamental physical descriptors of a sound wave for our purposes are its **frequency** and its **intensity**. These translate into the psychological attributes of **pitch** and **loudness**, respectively.

**The frequency of a sound corresponds to its pitch**

The *frequency* of a pure tone is the number of cycles (or complete oscillations of air condensation and rarefaction) in one second. The unit of measurement is Hertz (Hz). A pure tone, such as the sound from a tuning fork, can be represented as a sine wave. A pure tone that goes through 1000 cycles per second has a frequency of 1000 Hz, or 1 kHz. Human hearing spans the frequency range from 40 Hz to 20,000 Hz, although we use a much narrower range in practice. For example, the greatest energy of human speech sounds is between 400 and 3000 Hz.

Low frequencies sound like low pitch sounds (think of the keys on the far left on the piano) and high frequencies sound like high pitch sounds (the keys on the far right on the piano).
The intensity of a sound corresponds to its loudness

In depictions of sound waves, the amplitude of the sine wave corresponds to its maximum change in air pressure, or intensity. Higher amplitudes correspond to louder sounds; smaller amplitudes correspond to quieter sounds. In audition, the amplitude of pressure waves, sound pressure, is measured with the decibel scale (dB), a normalized logarithmic scale. The log scale is useful because the ear operates over an enormous range of sound pressures (its dynamic range). The loudest sound that can be heard without pain is a million times greater pressure than the quietest sound that the ear can detect.

Sound pressure at the threshold of hearing, which means sounds that are just barely detectable by a normal listener under optimal conditions, is designated as 0 dB sound pressure level, or 0 dB SPL. The accompanying chart shows on a dB scale the approximate sound pressure levels of events in our everyday environment. The sound pressure levels of the loudest sounds we can hear, such as jet plane engines, cause not only discomfort, but damage to the sensory apparatus.

<table>
<thead>
<tr>
<th>Sound pressure level (dB)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pain threshold</td>
<td>140</td>
</tr>
<tr>
<td>Jet aircraft</td>
<td>130</td>
</tr>
<tr>
<td>Loud organ</td>
<td>120</td>
</tr>
<tr>
<td>Rock concert</td>
<td>110</td>
</tr>
<tr>
<td>Concert hall seat</td>
<td>100</td>
</tr>
<tr>
<td>Heavy traffic</td>
<td>90</td>
</tr>
<tr>
<td>Ordinary conversation</td>
<td>80</td>
</tr>
<tr>
<td>Quiet conversation</td>
<td>70</td>
</tr>
<tr>
<td>Soft background music</td>
<td>60</td>
</tr>
<tr>
<td>Whisper</td>
<td>50</td>
</tr>
<tr>
<td>Average residence</td>
<td>40</td>
</tr>
<tr>
<td>Hearing threshold (young males)</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

The accompanying chart shows on a dB scale the approximate sound pressure levels of events in our everyday environment. The sound pressure levels of the loudest sounds we can hear, such as jet plane engines, cause not only discomfort, but damage to the sensory apparatus.
The sensitivity of hearing

Think of the adjacent graph as a *map of hearing space*. It shows how acute our hearing is for different sounds. The pitch (frequency) of pure tone sounds of varied frequency is plotted along the bottom on the X axis, progressing from low pitch to high pitch pure tones from left to right. The intensity (dB) of those sounds is plotted along the Y axis on the left, with the quietest sounds near the bottom and the loudest sounds towards the top.

The thick, sort of tipped U shaped, black curve indicates the sound pressure level at the threshold of detection for human hearing across the range of frequencies and intensities of sounds. *We can hear everything above the curve*, from the soft sounds represented just adjacent to the curve, to the region where conversational speech lies in the middle of the graph, to the top of the graph where the loudest sounds produce pain and inner ear damage (above the dashed line).

Notice that *the absolute threshold of hearing depends on the frequency* of the particular sound, so we’re not equally sensitive to all frequencies. *We are most sensitive to the middle range of frequencies plotted* (think of the middle range of piano keys), and in particular at that notch around 4 kHz. Notice also that the corresponding amplitude of motion of the tympanic membrane in the ear, the eardrum, which moves in response to incoming sound waves (more about this coming up soon), is plotted along the Y axis on the right side of the figure for each sound. The amplitude of motion of
the eardrum is about $10^{-9}$ cm at the frequency where we’re most sensitive, which is about 1/10 the diameter of a hydrogen atom. So the ear is extraordinarily sensitive to sound vibration, operating in the range of atomic motion.

**The Audiogram**

The auditory threshold curve provides detailed information about how quiet a sound we can detect. In practice, however, we’re usually more concerned about how well or poorly a person’s hearing might be, relative to normal, so such data as these are converted to a different and clinically more useful graph of auditory sensitivity called an audiogram. An audiogram plots how well a person hears compared to the clinical normative data, and also normalizes the data to take into account normal differential sensitivity to different pure tone frequencies. Notice in the adjacent model audiogram that the y-axis is flipped compared to that of the auditory threshold curve (in which the loudest sounds were at the top). The intensity of sound is plotted on the Y axis of the graph with quieter sounds towards the top and louder sounds towards the bottom. Pure tone sounds are shown on the X axis, ranging from low to high frequencies.

The audiogram indicates *how much louder* a certain sound needs to be, compared to normal, in order to be detected. So, after audiometric testing of a person with normal hearing, the audiogram curve would be a flat line (at 0 dB intensity) near the top of the graph. No increase in dB level was required in order for the person to hear the normally detectable sounds at any of the frequencies tested. A *hearing loss* is represented by points plotted below this normal level. The further below the 0 dB straight line, the worse the hearing.

When the audiogram curve is plotted in the 20-30 dB range, that’s generally called a *mild degree of hearing loss* (despite the fact that a person with such a hearing loss may be unable to function well in life without intervention). Curves reaching the 40-60 dB range are called a *moderate degree of hearing loss*, and greater hearing loss than that this, when none but the strongest sounds can be heard, is termed a *severe* or *profound loss*. Dr. Pasic and your small groups will discuss audiograms and their clinical application in detail later.
The ear can be divided into three major parts: the external, middle and inner ear. We’ll start externally and work our way inward. First, as concise as possible, here are the really remarkable events that lead to activation of the auditory nerve:

- **Sound waves enter** the external ear and travel through the external ear canal until they **strike the eardrum**;

- **Vibration** of the eardrum is **transferred through tiny bones** in the middle ear to vibration of a membrane at the inner ear;

- Vibration of the inner ear membrane **causes a pressure wave** in the fluid-filled ducts of the inner ear;

- The pressure wave causes movement of the structures in the inner ear and the **motion activates the cilia of hair cells**, which are the receptor cells of hearing.

- The hair cells are connected to the **8th nerve**, which carries auditory information to the brain.

The highly schematized adjacent figure of the ear illustrates the major structures and relations of the external, middle and inner ear.
THE EXTERNAL EAR

The external (outer) ear consists of the **auricle** (or **pinna**), which is the portion of the ear that projects out from the side of the head, and the **external auditory meatus**, or **ear canal**. The shape of the auricle helps to collect soundwaves. The external auditory meatus, lined with skin, winds inward to the **tympanic membrane**, or **ear drum**. The depth of the ear canal and its tortuous shape and rigid walls provide protection for the tympanic membrane and the middle ear beyond from direct injury.

Although Charles Darwin had concluded in 1907 that the human external ear is vestigial and of no functional significance and Van Gogh had no respect for it, this structure does play a useful role in hearing.

**Acoustic functions of the external ear**

The external ear alters the amplitude of incoming sound waves and, in doing so, *aids in hearing human speech*. The external ear also contributes to the *spatial localization of sound*—the ability to judge the source of a sound.

The curves in the adjacent figure are referred to as **transfer functions**. A transfer function is obtained by measuring the **sound pressure level of sounds of different frequencies at the eardrum** using a miniature microphone. These sound pressure levels are then compared to the sound pressure levels of **the same sounds measured outside the ear in open, uncluttered space**. The resulting transfer functions represent the filtering contributions of the external ear. In other words, **the transfer functions indicate how sound level is increased or decreased at each frequency because of the presence of the external ear** (and head and torso). The adjacent figure shows a family of such transfer functions for sound sources varying in elevation along the midsagittal plane (above to below the midline).

At zero on the Y axis is a horizontal line that represents the transfer function that would be obtained with no difference in sound pressure between the two measurements (amplitude of sound at the ear drum vs. amplitude of the same sound outside the ear). An increase in the amplitude of the sounds (+ dB values) or decreases in amplitude (- dB values) at the eardrum, relative to outside the ear, is plotted as a function of the frequency of each test sound.
The outer ear performs two functions that are important for hearing. First, the **outer ear amplifies speech sounds**. Notice that most of the curves are plotted above the “0” line, so the external ear amplifies tones of almost all frequencies shown. Sounds around 4 kHz and 14 kHz, for example, were 10 dB more intense because of the presence of the external ear. Most importantly, the major amplification occurs across the range from about 2-7 kHz, which is the range in which speech sounds occur.

A second important function of the **outer ear** is to help with sound localization. The amount of amplification in the transfer function figure depended upon the location of the source of the tone. The pure tones were presented in front of a person, either level with the ears (0°), below the ears (-15°), or above the ears (+15°). The pattern of sound modulation varies systematically, depending on the direction from which it came, from up high, from straight ahead, or from down low (compare the systematic change in the shapes of the three curves). While sounds coming from all three positions were amplified at frequencies from 2-6 kHz and 12-18 kHz, a sharp dip of inhibition in sound is present and varying systematically from around 6.5 kHz for 15 degrees below the ears, to almost 7 kHz for straight ahead, to 8 kHz for 15 degrees above the ears. This provides cues to the brain, which it interprets to judge the source of a sound. So, the external ear acts as a **directional amplifier of sound**. The shifts in the shape of the transfer function with changes in sound direction can provide the brain with cues for sound localization.

**ANATOMY OF THE MIDDLE EAR**

The **middle ear**, or **tympanic cavity**, is a narrow, air-filled chamber lined with mucous membrane and situated between the external acoustic meatus (bounded by the tympanic membrane) and the inner ear. Within the middle ear are the auditory **ossicles**, a chain of three small bones (the **malleus**, **incus**, and **stapes**, otherwise known as the hammer, anvil, and stirrup). The **ossicles connect the tympanic membrane with the inner ear**. The handle of the malleus attaches to the tympanic membrane. The incus is attached to the malleus and to the stapes, which in turn is attached via its footplate to the membranous **oval window**, the gateway to the inner ear.
FUNCTION OF THE MIDDLE EAR

The tympanic membrane moves in and out under the influence of the incoming, alternating sound pressure. Motion of the eardrum causes the malleus and incus to rotate as a unit about a pivot point. Rotation of the long process of the incus about this pivot causes the stapes to rock back and forth in the oval window. This sets up a wave of sound pressure in the fluid of the inner ear.

The movement of the footplate of the stapes corresponds to the frequency and amplitude of the incoming sound wave. The higher the frequency of the sound wave, the faster the stapes rocks back and forth in the oval window. The greater the amplitude of the sound wave, the more the stapes footplate deflects the oval window.

The middle ear functions to transmit sound efficiently from air to fluid

The middle ear provides an important mechanism to increase auditory sensitivity, or more accurately, to prevent a loss of sensitivity to sound. As you will learn, the auditory receptors of the inner ear operate in a fluid-filled environment, and the inner ear is really an “underwater” sound receiver. When sound in air strikes a fluid boundary, there is a theoretical loss of 99.9% of the energy (or 30 dB) in a sound wave in air due to reflections. (That’s why yelling at your fish has so little effect...) The mechanics of the middle ear are designed to overcome this mismatch in the impedance of air and fluid. The process is referred to as impedance matching.

Impedance matching

The middle ear acts as a kind of hydraulic press in which the effective area of the eardrum is about 21 times that of the stapes footplate. So, the force caused by sound pressure in the air acting on the eardrum is concentrated through the ossicles and focused onto the small area of the footplate, resulting in a pressure increase proportional to the ratio of the areas of the two structures (about 21:1). Also, the lever arm formed by the malleus in rotating about its pivot is somewhat longer than that of the incus, providing an additional 1.3x pressure increase.

The 21x ratio of the drum/footplate area, multiplied by the 1.3x lever arm factor, yields about a 27.3x increase in pressure, which is 29 dB. This very nearly overcomes the theoretical 30 dB loss due to the air/liquid interface. The important point is that the middle ear matches the acoustic impedance between the air and the fluid, thus maximizing the flow of energy from the air to the fluid of the inner ear.
Reflex contractions of the middle ear muscles

Two muscles in the middle ear, the tensor tympani and the stapedius tensor muscles, help regulate the sensitivity of the ear to sound. These muscles contract reflexively in response to loud sounds. The tensor tympani muscle (innervated by cranial nerve V = motor V) acts on the malleus to regulate the tension on the tympanic membrane. The stapedius muscle (innervated by cranial nerve VII = motor VII) regulates the range of motion of the stapes. (In fact, notice in your diagram the facial nerve passing very close to the middle ear chamber.)

The two muscles regulate sensitivity to sound by increasing the stiffness of the ossicular chain. This can reduce sound transmission by 15 dB, depending on the frequency. The reflexes are generally thought to be primarily a protective mechanism to shield the inner ear from damage due to intense sound but, because the latency of muscle contraction is at least 10 milliseconds, the reflexes cannot protect against impulsive sounds, like a gun shot. The reflexes primarily reduce the transmission of low frequencies, so they also improve the discrimination of speech sounds in the presence of loud, low frequency background noise.

Attributes of a vibrating system - mechanical resonance in the middle ear

Movement of the ossicles is also affected by clinical conditions. To better understand the effects of pathology in the middle ear, it is helpful to consider the basic properties of a vibrating mechanical system- in this case, keeping in mind the middle ear ossicles.

1) A vibrating system generally includes three elements: mass, stiffness (or ‘springiness’) and friction (or damping).

2) When such a system is subjected to a sinusoidal driving force of constant magnitude, but varying in frequency, the resulting plot of vibration amplitude versus driving frequency is referred to as a resonance curve, which gives the frequency response of the system. The amplitude of vibration is maximum at a frequency known as the resonant frequency.

3) If the stiffness of the system is increased (and mass and friction remain unchanged), the resonant frequency is increased and the amplitude is reduced for frequencies below the resonant frequency. Conversely, if the mass is increased (and the stiffness of the original system is unchanged), the resonant frequency is lowered, as well as the vibration amplitudes of frequencies above the resonant frequency.
Imagine how this would work in other mechanical systems, with a weight hanging on a spring, or on the strings of a piano or harp. A spring or string will oscillate at its resonant frequency when vibrated. If you increase the mass of the weight or the string itself, the resonant frequency will decrease accordingly to a lower frequency. If you decrease the mass of the weight or the string, the resonant frequency will increase accordingly to a higher frequency. Similarly, if you increase or decrease stiffness, the resonant frequency will increase or decrease, accordingly.

What does this mean for the ear?? The point of all this is that events in the middle ear affect the stiffness and mass of vibrating bones and membranes. Changes in the stiffness and functional mass of structures in the middle ear produce predictable changes in the perception of sound and in the audiogram. For example, contraction of the middle ear muscles or decreased middle ear air pressure makes the ossicular chain stiffer, which suppresses sound transmission especially for low frequency sounds. In contrast, the accumulation of thick, purulent material in the middle ear due to infection, or the pathological growth of bone around the stapes in otosclerosis increases the functional mass of middle ear structures and results predictably in decreased transmission of high frequency sound.

Impairment in the transmission of sound through the middle ear creates a conductive hearing loss. This means that vibration is not being transmitted normally via the tympanic membrane to the ossicles to the inner ear. The clinical aspects of conductive hearing loss will be discussed in the second half of the Audition module.

**The Eustachian tube functions to equalize pressure**

The tympanic cavity of the middle ear communicates with the nasopharynx via the Eustachian (auditory) tube. The Eustachian tube provides an important mechanism for equalizing external and internal pressures on two sides of the tympanic membrane. This enable us to adapt to and hear in situations with different atmospheric pressures.

The middle ear operates normally when it is filled with air at atmospheric pressure—so pressure is equal on both sides of the tympanic membrane. The Eustachian tube opens and closes periodically to insure that the static pressure in the middle ear will remain the same as atmospheric pressure.

When the Eustachian tube fails to open, a negative pressure immediately begins to build in the middle ear cavity due to absorption of the trapped air by the middle ear mucosa. The tympanic membrane basically gets sucked into the inner ear. This results in increased stiffness (just discussed!) in the middle ear mechanics. The stiffer elements won’t vibrate normally, so sound transmission through the middle ear is reduced, especially at low frequencies.
You may experience such a pressure difference when your Eustachian tube fails to open while traveling in an airplane. Sounds have a tinny, high frequency character. But what happens when your ears “pop?” As the pressure across the tympanic membrane equalizes, stiffness is suddenly reduced, and you notice an increase in sound level and a “roar” as the relative sensitivity to low frequency sounds is regained.

The Eustachian tube plays a second role as well. It provides a convenient path for infections of the pharynx to invade the middle ear, and you will certainly hear more about this later.
PRACTICE QUESTIONS: SOUND, EXTERNAL, AND MIDDLE EAR

1. Which of the following statements is FALSE?
   A. the strength or loudness of an auditory stimulus is expressed in decibels sound pressure level
   B. the ear is most sensitive to frequencies around 1,000 Hz
   C. at the threshold of hearing, the amplitude of motion of the tympanic membrane is smaller for a pure tone of 4 kHz than for a pure tone of 1,000 Hz
   D. the more intense the sound, the greater the amplitude of the motion of the tympanic membrane
   E. to be just perceivable, the amplitude of a 200 Hz tone needs to be greater than the amplitude at which a 4000 Hz tone is just perceivable

2. Which of the following statements is TRUE regarding decibel notation as it applies to sound?
   A. is used because the ear operates over a wide range of sound intensity
   B. is a measure of the frequency of a sound wave
   C. is the measure used on the X axis of an audiogram
   D. is rarely used in modern audiology or otology
   E. two are true

3. Which of the following statements is FALSE regarding the external ear?
   A. the external ear amplifies sounds in the frequency range of speech sounds
   B. the external ear amplifies sound in a direction dependent manner
   C. the external ear consists of the auricle and the internal auditory meatus
   D. the external ear canal ends at the tympanic membrane
   E. the external ear has both acoustic and non-acoustic functions

4. Which of the following statements is TRUE regarding the middle ear or structures within the middle ear?
   A. lies external to the tympanic membrane
   B. communicates with the pharynx via the external auditory meatus
   C. stapes is attached to the tympanic membrane
   D. Eustachian tube helps equalize external and internal pressure on the tympanic membrane
   E. is normally fluid filled

5. Which of the following statements is FALSE regarding the middle ear or structures within the middle ear?
   A. when sound traveling in air hits a fluid environment, most of the sound energy is transmitted to the fluid
   B. when sound traveling in air hits a fluid environment, about 99.9% of the sound energy (30dB) is reflected back into the air
   C. the main function of the middle ear is to transfer sound energy from air to cochlear fluid
   D. the force acting on the tympanic membrane is concentrated into the small area of the footplate of the stapes
   E. the relative lengths of the ossicles helps overcome the mismatch in the impedance of air and fluid
6. Which of the following statements is **FALSE**?
   A. reflex contraction of the tensor tympani and stapedius muscles may protect the inner ear by decreasing sound transmission
   B. increased stiffness of the ossicular chain can reduce transmission of sounds, especially at low frequencies
   C. contraction of the tensor tympani and stapedius muscles are unable to protect the ear from high intensity impulsive sound (e.g. gun shots)
   D. contraction of the stapedius muscle may decrease the stiffness of the ossicular chain
   E. changes in stiffness and mass within the middle ear can yield a conductive hearing loss

7. Which of the following associations is **correct**?
   A. C=incus
   B. A=longer lever arm than C
   C. D=can be culprit in middle ear problems
   D. B=controlled by cranial nerve 5
   E. E=contraction increases amplitude of vibration of eardrum
SOUND, EXTERNAL, AND MIDDLE EAR: ANSWERS TO PRACTICE QUESTIONS

1. B
2. A
3. C
4. D
5. A
6. D
7. C
THE INNER EAR

The inner ear is called the *labyrinth* because of its complex shape. The *bony* (or *osseous*) *labyrinth* is the *hollow* in the temporal bone. Within the osseous labyrinth and ensconced protectively within the temporal bone is the *membranous labyrinth*, a series of communicating, membrane-bound sacs and ducts. The membranous labyrinth is comprised of six mechanoreceptive structures. Five of these structures contain sensory structures that serve the sense of equilibrium (=balance): the three *semicircular canals*, a *utricle*, and a *saccule*). The sixth structure, the *cochlea*, is our focus here. The cochlea contains the sensory elements specialized for the detection of sound waves.

Two kinds of fluid are found in the inner ear. The space between the temporal bone and the membranous labyrinth is filled with a liquid called *perilymph*. Within the membranous labyrinth, and flowing between the interconnected sensory structures, is liquid *endolymph* produced by the *stria vascularis*.

**Structure of the cochlea**

The *cochlea* (L. snail shell) is the coiled, fluid-filled structure that contains the receptor organ of hearing. The cochlea resembles a long tube that is coiled with increasing sharpness upon itself in *two and one half to two and three quarters turns*. Two partitions that run the length of the coiled tube of the cochlea. These membranous partitions divide the cochlea into three separate compartments that are seen in the cross section of the cochlea. *Reissner’s membrane* separates the *scala vestibuli* and the *scala media* (cochlear duct). The *basilar membrane* (together with the *osseous spiral lamina*, a delicate bony shelf) divide the *scala media* from the *scala tympani*. 
At the basal end of the cochlea there are two membrane-covered openings to the middle ear: the oval and the round windows. The **oval window** is in contact with the stapes foot plate on the middle ear side and with the scala vestibuli on the inner ear side. The **round window** is in contact with no structure on the middle ear side and with the scala tympani on the inner ear side.

The fluid-filled *scala vestibuli* and *scala tympani* are actually *continuous* and connected by a small opening at the very apex of the cochlea, called the **helicotrema**. So, when inward pressure is applied to the stapes footplate, it is transmitted through the oval window into the fluid of the scala vestibuli, and on through the helicotrema to the scala tympani. This results in outward pressure on the round window membrane because movement of the oval window by the stapes footplate is met with equal and opposite action of the round window. The **round window allows for fluid displacement in the cochlea**. Because fluid of the inner ear is non-compressible, inward movement of the stapes footplate increases the pressure within the fluid-filled cochlear ducts, and this pressure is taken up by the yielding of the thin, membranous round window.
An increasingly higher magnification view of the cochlea, progressing from showing its location in the head in A, to taking an imaginary slice through the entire cochlea in B, to taking a slice through one turn of the cochlea in C, to showing the organ of Corti in its position on the basilar membrane in D.

In between the scala vestibuli and scala tympani lies the third and separate fluid filled chamber, the scala media. The receptor organ of hearing, the organ of Corti, lies within the scala media and sits on the basilar membrane. It contains the auditory receptors, which are called hair cells because of their cilia (more on hair cells later). Hair cells within the organ of Corti are distributed along the entire length of the basilar membrane. When pressure waves make their way around the fluid-filled chambers of the cochlea, the basilar membrane vibrates, as well, and that activates the hair cells.
Cochlear mechanics and the Traveling Wave

Georg von Bekesy, a Hungarian physicist, was the first to study the mechanical vibration patterns of the inner ear by a series of ingenious experiments in human cadavers in the 1920’s, a feat that earned him the Nobel Prize. This is what we now know takes place in the cochlea after a sound wave enters the inner ear:

1. Sound waves (we’ll presume they’re all pure tones) normally enter the inner ear via stapedial displacement of the oval window and are transmitted rapidly through the cochlear fluid.

2. The basilar membrane deflects in response to this fluid pressure. This deflection of the basilar membrane is called a **traveling wave**, and this propagates along the basilar membrane from base to apex.

**The figure below shows a three dimensional rendition of the traveling wave envelope at one moment in time.**

**The figure above shows a traveling wave at four successive instants in time, together with the envelope of the peaks of the displacement. The displacement constitutes a traveling wave of deformation that progresses along the basilar membrane from base to apex.**
3. The **basilar membrane** varies systematically along the length of the cochlea. At the **base** of the cochlea, the basilar membrane is **narrow** (about 0.1 mm). At the **apex** the basilar membrane is 5 times **wider** (about 0.5 mm). This change in width translates into a systematic change in effective stiffness, which is high at the base and decreases toward the apex. Consequently, **the resonance of the basilar membrane varies**, and its response to particular frequencies of sound varies systematically across its length.

The important point is that **high frequency sounds** cause **maximal deflection at the base of the cochlea** and **low frequencies** cause **maximal deflection towards the apex**. Thus, the basilar membrane is **tonotopically organized**. Remember that hair cells are found along the entire length of the basilar membrane, and the response of any given hair cell depends upon what the basilar member underneath it is doing. Thus, different sound frequencies activate different groups of hair cells. The “spiral” figure illustrates in more detail the relationship between cochlear location and the regions of best frequency sensitivity, in other words, cochlear tonotopy. Tonotopic organization will be conveyed to the auditory nerve fibers that innervate the hair cells.
Hair cells are the receptor cells of the inner ear

**Hair cells** are the actual receptor cells of hearing, found within the organ of Corti. Hair cells, whether vestibular or cochlear, are all similar morphologically.

The hair cell is cylindrical or flask-shaped and equipped at its apical end with a bundle of sensory hairs called **stereocilia**. The stereocilia uniformly increase in length from one edge of the hair bundle to the other. An extra big **kinocilium** is present early in development, but absent in the adult. Stereocilia are linked together near their apex by protein filaments, called ‘**tip links**’. Consequently, the stereocilia on a given hair cell move as a bundle.
Inner and outer hair cells

There are two kinds of hair cells in the organ of Corti: **inner hair cells (IHC)** and **outer hair cells (OHC)**. Usually, there is one row of inner hair cells and three to four rows of outer hair cells. (There are approximately 3,500 inner hair cells and 12,000 outer hair cells in each cochlea.) It is the **inner hair cells** that are the primary sensory organ of the cochlea. **Outer hair cells** act to control the function of the **inner hair cells**. Outer hair cells change shape in response to efferent activation, which in turn alters the micromechanical action of the tectorial membrane and its effect on inner hair cells. Outer hair cells are much more vulnerable than inner hair cells to ototoxic (ear damaging) chemicals, drugs, and and the effects of overstimulation.

**Mechano-electrical transduction by hair cells**

The hair cell is a mechanoreceptor, producing an electrical signal, or **receptor potential**, in response to movement of its hair bundle. Each stereocilium behaves like a stiff rod that pivots at its base. The adequate stimulus for the hair cell is displacement of the hair bundle. **Excitation** occurs when the deflection is toward the tall stereocilia (or kinocilium), and **inhibition** occurs when the deflection is toward the short stereocilia (and thus away from the kinocilium).

Hair cells are extraordinarily sensitive to cilia displacement. If the height of one cilium is scaled to the height of Chicago’s Sear’s Tower, the movement of the tip of the cilium at the threshold of hearing is equivalent to a two-inch displacement of the top of the Tower!
As in neurons, the electrical signals in the hair cell originate from the flow of ionic currents across the cell membrane through specific pores, or ion channels. Movement of the hair bundle toward the tallest cilium increases membrane conductance, so the membrane becomes more permeable to positively charged ions (K\(^+\) and Ca\(^{++}\)), leading to depolarization and neurotransmitter release. Movement of the hair bundle in the opposite direction, away from the tallest cilium, closes ion channels, thereby stemming the flow of ionic current and stopping neurotransmitter release.

So, what moves the stereocilia? The tectorial membrane lies above, and is in contact with, the hair bundles of the auditory receptor cells. Actually, the tectorial membrane connects with the stereocilia of the outer hair cells, but it appears not the inner hair cells.

When sound energy is introduced into the inner ear, the resultant up-and-down motion of the basilar membrane produces shearing motion between the stereocilia projecting from the apical surfaces of hair cells and the tectorial membrane. Shearing occurs because of the relative positions of the hinge points for the basilar membrane and the tectorial membrane. This shearing action displaces the stereocilia which, in turn, results in cellular depolarization or hyperpolarization through the transduction mechanisms.
Otoacoustic Emissions

The cochlea of the healthy ear creates naturally occurring vibrations in response to sound. The cochlear vibrations themselves can produce a measurable sound that can be recorded by a specialized microphone fitted to the ear. Such sounds are called otoacoustic emissions - they are sounds that “come out of the ear”.

Otoacoustic emissions are believed to arise from the movements of those many rows of outer hair cells. (Think of the vibrating hair cells as producing their own tiny, reverse traveling wave back to the oval window and out to the ossicles.) Our ability to record otoacoustic emissions in response to test sounds in the clinic forms the basis for recently developed non-invasive tests of the integrity of cochlea. These tests are becoming commonplace in screening hearing in newborns and infants. When active otoacoustic emissions are found, it demonstrates that the hair cell processes of the cochlea are present and working. If otoacoustic emissions are not produced, it is an indication of cochlear dysfunction that can be detected in the first days after birth.

Innervation of the organ of Corti by the 8th nerve

The auditory or eighth nerve cells make synaptic contact with the base of hair cells. A change in hair cell receptor membrane potential associated with movement of the hair bundles results in release of neurotransmitter at the base of the hair cell and produces change in the discharge of eighth-nerve afferent axons. As you just read, depolarization of the hair cell leads to increased firing of the fiber, while hyperpolarization results in decreased firing. This relation between the direction of motion of the hair cells and the resulting changes in receptor potentials in the hair cells and their eighth-nerve discharge patterns is referred to as functional polarization.
There are two types of eighth nerve fibers that innervate hair cells in the organ of Corti: afferent and efferent:

**Afferent** (from cochlea to brain) innervation arises from the peripheral processes of bipolar neurons with cell bodies in the spiral ganglion. The central processes of the spiral ganglion neurons form the auditory component of the eighth nerve and project to the brainstem cochlear nuclei. They account for about 95% of the axons in the auditory nerve.

The peripheral processes of the afferent fibers contact primarily inner hair cells— with little divergence. Each auditory nerve fiber contacts just one inner hair cell. Each inner hair cell innervates as many as 20 auditory nerve fibers.

**Efferent** (from brain stem to cochlea) innervation arises in the superior olivary complex of the brain stem. These axons travel in the olivocochlear bundle and synapse mainly on the base of outer hair cells.

So, keep in mind that in addition to the sound-related signals traveling along the eighth nerve to the brain, there are also feedback signals traveling along the eighth nerve from the brain to the organ of Corti.

The efferent system, working through the outer hair cells, is thought to play a role in helping us to hear better. Roles proposed for the efferent system include 1) enhancing signal-to-noise ratio in noisy environments (for example, helping you understand your dinner companion in a noisy, echo-filled restaurant); 2) controlling the sensitivity of the cochlea to boost the dynamic range (in other words, helping you hear equally well and comfortably in the Med
School’s noisy lounge and in the quiet lounge); 3) suppressing auditory responses during selective attention to other sensory modalities (for example, helping you pay more attention to vision, rather than hearing); and 4) preventing damage to the auditory structures as a consequence of intense sound.

**The Place Principle of Hearing**

Different parts of the basilar membrane vibrate maximally in response to different frequencies of sound. Auditory nerve cells also exhibit selectivity for particular frequencies of sound and they mirror the mechanical tuning of the basilar membrane. *Each auditory nerve cell contacts a single inner hair cell,* so an auditory nerve fiber is most sensitive to the frequency that reflects the position of the contacted hair cell along the basilar membrane. An auditory nerve fiber is said to have a **characteristic frequency** of sound to which it responds best or is “tuned”. Since the characteristic frequency of a nerve fiber is directly related to its ‘place’ along the basilar membrane, this is referred to as a **Place Code**. Thus, the terms **tonotopy** and **cochleotopy** are both used to describe the relation between location and sound frequency in the organization of the cochlea. And again, **high frequencies are represented towards the narrow base** and **low frequencies towards the wider apex of the cochlea.**

**Auditory codes**

Auditory signals are encoded in trains of action potentials in the eighth nerve that link the hair cells in the organ of Corti with target neurons in the brainstem. We know that certain information is especially important to brainstem and cortical auditory cells.

1. **The auditory nerve conveys sound frequency information:** Auditory nerve fibers exhibit “frequency tuning”, meaning they respond to a restricted range of sound frequency. This sound frequency coding is important for frequency discrimination and pitch perception. Central auditory neurons are also tuned to sound frequency.

2. **The auditory nerve conveys precise timing information:** Timing is a very important feature in the auditory system. The auditory nerve axons carry extremely precise timing information in the timing of their action potentials, conveying information about many aspects of sound. This is used by central auditory neurons to aid in pitch perception, speech recognition, and for localizing the source of sounds (more later).

**Sensorineural hearing loss**

We mentioned earlier that pathology in the external or middle ear can result in a **conductive hearing loss.** A different term is used to describe pathology in the **inner ear** that results in hearing loss or deafness. Disease of, or damage to, the cochlea, including the hair cells, the cochlear division of the eighth cranial nerve, or the cochlear produces a **sensorineural hearing loss,** or **sensorineural deafness.**
INNER EAR: PRACTICE QUESTIONS

1. Which of the following statements is **FALSE** regarding the inner ear?
   A. consists of osseous and membranous labyrinths
   B. osseous labyrinth contains no fluid
   C. membranous labyrinth filled with endolymph
   D. consists of semicircular canals, cochlea, utricle and saccule
   E. the round window opens into the scala tympani

2. Which of the following statements is **FALSE** regarding the inner ear?
   A. the helicotrema is a connection between the scala tympani and the scala media
   B. the round window is associated with scala tympani
   C. the scala media is closed at the apex of the cochlea
   D. the oval window connects to the scala vestibuli
   E. the apical end of the cochlea contains the helicotrema

3. Which of the following statements is **FALSE** regarding the inner ear?
   A. the cochlear duct is the same thing as the scala media
   B. the organ of Corti lies in the scala media
   C. the scala vestibuli is filled with endolymph
   D. the basilar membrane is narrower at its base than at its apex
   E. the tectorial membrane contacts the stereocilia of the outer hair cells

4. Which of the following statements is **FALSE** regarding auditory hair cells?
   A. they are the receptor cells of the organ of Corti
   B. they have a kinocilium early in development
   C. those at the apex encode low frequencies
   D. movement of the stereocilia away from the kinocilium results in depolarization of the hair cell, an increase in transmitter release, and more action potentials in the fibers of C.N. VIII
   E. there are three times as many outer hair cells as inner hair cells

5. Which of the following statements is **TRUE** regarding the inner ear?
   A. Reissner’s membrane separates scala media from scala tympani
   B. the basilar membrane separates scala media from scala vestibuli
   C. the basilar membrane is widest at the base of the cochlea
   D. the basilar membrane is the stiffest at the apex
   E. the tectorial membrane overlies the hair cells
6. Which of the following statements is **TRUE** regarding the inner ear?
   A. most auditory nerve fibers innervate multiple inner hair cells
   B. about 95% of the auditory nerve afferent fibers destined for the brain originate at the base of outer cells
   C. information destined for the central nervous system is conveyed primarily by the outer hair cells
   D. inner hair cells receive most of the efferent input from the central nervous system
   E. movement of the basilar membrane results in shearing of the hair cells by the tectorial membrane

7. Which of the following statements is **TRUE**?
   A. a traveling wave is a deformation of the basilar membrane caused by sound
   B. sound waves reaching the inner ear cause the part of the basilar membrane near the apex to move first. This is followed by movement of more basal segments of the membrane
   C. a low frequency tone will result in maximum deflection of the basilar membrane at its base
   D. high frequency tones produce maximal deflection of the basilar membrane near the apex
   E. two of these statements are correct

8. Which of the following statements is **FALSE**?
   A. the characteristic frequency of an eighth nerve fiber is directly related to its location along the basilar membrane
   B. the characteristic frequency of an eighth nerve fiber depends upon the location on the basilar membrane of the hair cell to which it is attached
   C. the efferent auditory nerve fibers synapse on the base of the outer hair cells
   D. inner hair cells control the mechanics of the tectorial membrane
   E. outer hair cells can regulate the sensitivity to both low and high intensity sounds

9. Which of the following associations are **FALSE**?
   A. D=inner hair cell
   B. D=receives efferent information from the superior olive
   C. C=vesicle release results in firing of eighth nerve fiber
   D. A=supporting cell
   E. B=tectorial membrane
10. Which of the following associations are **TRUE**?

A. B=scala tympani  
B. C=scala media  
C. A=basilar membrane  
D. D=scala vestibuli  
E. E=Reissner’s membrane

11. Which of the following statements about otoacoustic emissions is **TRUE**?

A. Otoacoustic emissions are thought to be generated by the inner hair cells as they innervate eighth nerve fibers.  
B. Otoacoustic emissions can be evoked by sound, and they can occur spontaneously.  
C. Infants normally do not produce otoacoustic emissions.  
D. The presence of an otoacoustic emission indicates a hearing loss.  
E. Two statements are true.

**INNER EAR: ANSWERS TO PRACTICE QUESTIONS**

1. B  
2. A  
3. C  
4. D  
5. E  
6. E  
7. A  
8. D  
9. A  
10. B  
11. B
The central auditory system is comprised of a number of nuclear groups within the medulla, pons, midbrain, thalamus, and cerebral cortex. The accompanying figure shows the major pathways carrying information about the acoustic environment that reaches higher order auditory cortex. Unlike the visual system, where there is just one nucleus (the lateral geniculate nucleus) interposed between the sensory organ and the cortex, many auditory nuclei lay between the cochlea and the auditory cortex. These nuclei are very well interconnected by fiber tracts that ascend in an array of uncrossed, crossed, and bilateral projections.
The cochlear nuclei are the first synaptic stations in the auditory pathway

As you remember from the brainstem module, there are two major divisions of the cochlear nuclear complex, the **dorsal cochlear nucleus** (DCN) and the **ventral cochlear nucleus** (VCN). Auditory nerve fibers bifurcate and send a branch to each nucleus. All information transmitted from the ear to the brain passes through at least one synapse in the cochlear nuclei, so the cochlear nuclei are ‘obligatory’ synaptic stations.

The two cochlear nuclei are not homogeneous structures. Cells in these two nuclei have different properties and their input from the auditory nerve differs. **Timing** information is carefully and in a straight-forward fashion conveyed from the eighth nerve to the ventral cochlear nucleus. Auditory signals dealing with **frequency and timing** information are more **radically transformed** in the dorsal cochlear nucleus.

**Tonotopic organization is a fundamental feature of the cochlear nuclei and other ascending auditory nuclei**

There is an orderly arrangement of eighth nerve axons entering the cochlear nuclei. This preserves the tonotopic organization of auditory nerve fibers in the cochlear nuclei in the spatial arrangement of the cells in the nuclei.

Recall that the characteristic frequency of an auditory nerve axon is related to its base-to-apex place of origin along the basilar membrane in the cochlea (with high frequency sounds represented in the cochlear base and low frequency sounds located in the cochlear apex). This is a **tonotopic organization**. Because of the orderly spatial distribution of eighth nerve terminals, each of the cochlear nuclei is also tonotopically organized (as indicated by the direction of arrows in the accompanying figure). In fact, all of the major auditory nuclei are tonotopically arranged.

The tonotopic/cochleotopic organization can be viewed in much the same way as retinotopic organization in the visual system and somatotopic organization in the somatic sensory system: it is a spatial representation of the receptor surface.
OUTPUT OF THE COCHLEAR NUCLEI -

The major targets of the cochlear nuclei are the superior olive and the inferior colliculus. The major pathways are the trapezoid body and lateral lemniscus. (These structures should sound familiar from the brainstem portion of the course.)

Higher Auditory Centers:

Superior Olivary Complex
There are a number of crossed pathways in the lower brain stem. One of these, trapezoid body, provides massive input to nuclei of the superior olivary complex (SOC) on both sides of the brainstem. Hence, the superior olivary complex occupies a pivotal position in the central auditory pathway for it is here that information from the two cochlear nuclei first converges and where interaural cues used by listeners for sound localization are first detected (more on this later). Key message: information from the two ears is first combined here.

The superior olivary complex includes a number of closely grouped nuclei that span the ventrolateral regions of the pons. Two nuclei that we will return to later are the Medial Superior Olivary Nucleus (MSO), and the Lateral Superior Olivary Nucleus (LSO).

Inferior Colliculus The inferior colliculus receives major inputs from many auditory regions of the brainstem, including the cochlear nuclear complex, superior olivary complex, nuclei of the lateral lemniscus and inferior colliculus on the opposite side. All fibers ascending in the lateral lemniscus synapse in the inferior colliculus. A neat representation of the
contralateral sound field (a computational map of auditory space) is present for the first time at the level of the inferior colliculus and is then present at all higher levels in the auditory system. The inferior colliculus is tonotopically organized, contains a neural map of auditory space, and it sends its axons to the ipsilateral medial geniculate body.

**Medial Geniculate Body** Neurons in the inferior colliculus send most of their axons by way of the *brachium of the inferior colliculus* to the medial geniculate nucleus or body (MGB), which is the auditory relay nucleus of the thalamus. Medial geniculate body neurons project in an orderly fashion to the auditory areas of the cerebral cortex by way of the sublenticular portion of the internal capsule. The medial geniculate body is tonotopically organized, contains a neural map of auditory space, and sends axons to the ipsilateral auditory cortex.

**Auditory Cortex** The primary auditory cortical areas are located in the temporal lobe on the superior bank of the superior temporal gyrus (area 41 and 42 of Brodmann). Auditory cortex occupies one or more of the transverse gyri of Heschl on the dorsal, inner surface of the temporal lobe (you’ve got to peak inside the gyri on the superior side of the temporal lobe to see the transverse gyri). The blood supply to auditory cortex is provided by the middle cerebral artery.
Auditory cortex consists of a primary receiving area (AI), which is tonotopically organized and which has a relatively uniform cellular structure throughout, and several other auditory cortical fields (not shown) surrounding AI. Each auditory cortical area has complex afferent and efferent connections with nearby cortical fields and with auditory areas in the contralateral hemisphere. The multiple cortical regions are believed to process different aspects of the acoustic stimulus.
‘WHERE IS THAT SOUND COMING FROM?’
Listening with two ears - mechanisms of directional hearing

The auditory system also shows organization for some other features of sound in addition to tonotopy. One of these is location. We can discriminate the sources of two stationary sounds that are only a few degrees apart on the horizontal plane. This marvelous ability to localize sound no doubt aids in survival. Remember the earlier discussion on the external ear? We said that it functions as a directional amplifier of sound, providing cues that aid in localizing sounds along a vertical plane. The spectral properties of the external ear provides one of the major cues for sound localization. However, there are three major cues for sound localization. A schematic representation of the physical situation that accounts for the other two cues, interaural time difference and interaural level difference, is shown below. These cues are made possible by the placement of the ears on either side of the head.

The superior olivary complex, the first place in the brainstem where inputs from the two ears converge, has subdivisions that are involved in these different aspects of processing binaural (= two ears) acoustic signals.

**Interaural time difference (ITD)**

The auditory system uses the difference in the time for a sound reach one ear, relative to the other ear, to determine the source of the sound in space. If a source of sound is off to one side of the head, the sound reaches the farther ear some 30 µsecs later than the nearer ear for each additional centimeter it must travel (velocity of sound = 343 meters/sec). For the average human head, the maximum interaural time difference (ITD) is about 800 µsecs. The maximum ITD will occur when the stimulus is located directly to one side and thus as far as possible from the opposite ear. The ability of the auditory system to detect ITDs is quite remarkable. Under optimal conditions, the just noticeable time difference is 6 µsecs!! (This is accomplished in a nervous system that uses action potentials whose width and synaptic delays are over 100 times longer!)

How does the auditory system do this? Clearly, preserving timing information is an important task for the central auditory system. Cells important for encoding ITDs are located in the medial superior olive (MSO). The MSO cells convey detailed information about the timing of low frequency sound. The MSO receives its major bilateral excitatory input from the left and the right ventral cochlear nuclei. This sensitive timing information has been transmitted with high fidelity via the auditory nerve to the ventral cochlear nuclei and on to the MSO. Since auditory nerve fibers are not able to convey this kind of timing information for frequencies greater than about 4000 Hz (too many action potentials to distinguish one from another!), ITDs are effective cues for low, but not for high frequencies.

The MSO neuron serves as a sharply tuned coincidence detector. This means that the output of an MSO cell depends critically on the relative time at which action potentials from the left and right ventral cochlear nuclei converge upon it. Furthermore, the MSO neural circuitry is set up to handle a range of timing delays, to take into account the time required for sound to reach the far ear, relative to the near ear, when sounds arise from more and more laterally-placed sources. The end result of this circuitry is that the MSO generates a map of the contralateral sound space. The MSO then relays this information to the ipsilateral inferior colliculus.
**Interaural level difference (ILD)**

The auditory system also neurally compares the difference in sound pressure level for a given sound at the two ears and uses this cue to aid in sound localization. The head acts as an ‘acoustic shadow’ for high frequency sounds off the midline. The far ear lies in a sound shadow whose depth depends upon the direction of the source and upon the wavelength of the sound. The head acts as an effective acoustic shadow only if the wavelength of the sound is not larger than the size of the head. For the size of human heads, interaural intensity differences are negligible at low frequencies, but may be as great as 20 dB at higher frequencies. Thus, interaural level differences (ILDs) are only effective cues at high frequencies.

---

**TWO MAJOR CUES USED BY LISTENERS FOR LOCATING THE DIRECTION OF A SOUND ON THE HORIZONTAL PLANE**

**Interaural Time Difference**

**Interaural Intensity Difference**

---

Cells important for encoding ILDs are found in the lateral superior olive (LSO). Neural determinations of ILDs depend on the interaction of excitation produced by the ipsilateral ear and inhibition by the contralateral ear. As a result, LSO cells are excited when sounds are in the ipsilateral sound acoustic hemifield and inhibited when sounds are displaced to the contralateral hemifield. The LSO cells then project across the midline to the contralateral inferior colliculus, which means that cells in the inferior colliculus are excited by sounds in the contralateral sound field. As a result, the inferior colliculus (and MGB and cortex) contains a spatial (location) map of the contralateral auditory field.
Therefore, for low frequency tones (below about 1500 Hz), a listener relies upon ITD cues for sound localization. For higher frequency tones, the listener relies upon ILDs. This dichotomy between the cues used for localizing high and low frequency tones is known as the \textit{duplex theory of sound localization}.

\textbf{EFFECTS OF LESIONS IN AUDITORY PATHWAYS}

You’ve heard about conductive hearing loss and sensorineural hearing loss, but you can also have a central hearing loss. Because information from the two ears is combined at the superior olivary complex, a complete lesion at the level of the superior olive or in structures higher in the auditory pathway will not result in complete deafness unless both sides of the brain are damaged. However, higher order analysis of auditory signals can be damaged.

The \textit{major effect of extensive damage to auditory cerebral cortical areas} appears to be in the \textit{ability to discriminate complex sound patterns} and in \textit{sound localization}. Deficiencies are commonly seen in \textit{discrimination of changes in the temporal order or sequence of sounds, their duration, and in the ability to localize sounds in space}. Damage to cortical areas has little effect on the ability to discriminate between tones of different frequencies or intensities. After a period of time following bilateral lesions of the auditory cortex, the pure tone hearing threshold (= sound sensitivity) returns toward normal.

If a cortical lesion includes the areas surrounding auditory cortex on the superior temporal gyrus or frontal operculum, then \textit{speech and language are affected specifically}. These conditions are referred to as \textit{aphasias}. You will hear more about this when you study cerebral cortex.

Finally, it is important to recognize that even minimal damage in any auditory structures can produce serious consequences in communication- without causing deafness. Speech and language depend critically upon hearing. Even with mild hearing loss, speech and language may not develop normally.
OPTIONAL READING

Processing Speech

Perhaps the most complex and most important sounds to be recognized are those of human speech. We have a remarkable ability to process speech very rapidly and to identify the speaker after hearing just a few utterances. How do we do this? Little is known about the detailed processing of speech sounds, but it is instructive to consider the encoding of speech sounds by the auditory periphery. Let’s briefly analyze the components of simple speech. The accompanying figure compares two similar, but distinguishable, speech sounds, the utterances /tu/ (pronounced as in “to”) and /du/ (as in “do”), as depicted in both the time and frequency (or spectral) domain. In the time domain we plot the sound pressure of the sound as a function of time; this would be the waveform recorded by a microphone. Both sounds begin with a burst of high frequency noisy sound associated with a burst of air in the vocal tract (called aspiration) followed by the vowel, which is associated with the more periodic vibration of the vocal cords (or voicing). The major distinction between the two sounds is the so-called voice onset time, the time before voicing begins. In /tu/ the voice onset time is about 60 msec, whereas in /du/ it is very short, less than 10 msec. These are the types of cues that enable us to distinguish sounds and comprehend language!

The frequency domain representation is shown by a spectrogram, which is a three dimensional plot: the x axis is time, the y axis is frequency, and the darkness of the dot represents the energy in the sound at that frequency-time point. A spectrogram of a pure tone would be a single horizontal line since the pure tone has only a single frequency component.
Most sounds will be more complex and have many components. For example, musical notes have higher order harmonic frequencies that are at multiples of the fundamental frequency. In speech sounds the frequency components vary with time and thus are not simple horizontal lines, and this can be seen in the darkened regions of the spectrograms. During the vowel sound, there are clear peaks in the spectrum that are called formants. Four distinguishable formants, F1, F2, F3, and F4, are marked. In the spectrogram, it is clear that the F2 formant has a downward trajectory, decreasing in frequency, through the course of the vowel. Clearly, the speech sounds themselves are a complex waveform, and the obvious question arises “How does the auditory system encode such signals?”

When the responses of auditory nerve fibers are represented in a spectrogram, the major features of the sound are also represented. The responses are shown to the utterance /tu/ in the form of spectrograms of three auditory nerve fibers of different characteristic frequencies. The characteristic frequency of each fiber is indicated on the frequency axis by the solid line to the right. In these response spectrograms, dark spots indicate that there is significant energy at that frequency (y axis) at a specific point in time (x axis), which means that the fiber is phase-locking at that frequency. The strength of the response on the spectrogram depends on two factors: the degree of phase-locking and the discharge rate.

The response of each auditory nerve fiber reflects the three important properties: frequency tuning, coding by discharge rate, and phase-locking at low frequencies. In the second figure, which shows auditory nerve responses, we can see that each fiber responds to the components of the speech stimulus that lie near its characteristic frequency and not to components that are displaced in frequency. For example, the fiber with a characteristic frequency of 1535 Hz follows the falling trajectory of the F2 formant during voicing but does not respond to either F1 below it or F3 above it. The fact that the fiber is responding shows that it is following the temporal pattern or waveform at that frequency, and thus is phase-locked.

Therefore, to reconstruct the whole spectrum of the speech sound, the auditory system needs to look over a population of nerve fibers, which is shown by part D, where the responses of eight nerve fibers to the same sound are summed. By comparing the composite spectrogram with the original stimulus spectrogram in part E, we can see that the major features of the stimulus are evident in the response of these auditory nerve fibers. However, there are disparities between the stimulus and response: the major difference is that the onset of the stimulus itself and of voicing are more strongly represented in the neural responses than they are in the stimulus. This is also expected from the adaptation of auditory nerve fibers to a pure tone: their response at stimulus onset is greater than that during the sustained portion of the tone.

Thus, we can see from this example that the phase-locking of auditory nerve fibers to low frequency sounds allows them to encode the temporal waveform of low frequency speech and ensemble averaging over the population of fibers allows reconstruction of the entire stimulus waveform. From this, one gets a sense of the way in which complex waveforms such as speech can be encoded neurally.
PRACTICE QUESTIONS: CENTRAL AUDITORY SYSTEM

1. Which of the following statements is TRUE. The major interaural cues for sound localization are:
   A. first detected at the auditory cortex
   B. first detected by the cochlea
   C. detected first by cells of the medial geniculate nucleus
   D. detected first by cells of the superior olivary complex
   E. detected first by cells in the spiral ganglion of the auditory nerve

2. Which of the following statements is FALSE.
   A. the lateral superior olivary nucleus detects mainly interaural sound intensity difference
   B. the external ear provides cues to auditory neurons in the brain for localizing sounds that vary in elevation
   C. the medial superior olivary nucleus detects mainly interaural time difference, providing cues for localization along the horizontal plane
   D. the medial superior olivary nucleus receives low frequency sound information from the ventral cochlear nuclei of the two sides of the brainstem
   E. the lateral superior olivary nucleus mainly handles low-frequency information

3. Which of the following is FALSE regarding the ascending auditory pathways:
   A. there is a spatial map of the contralateral sound field along the basilar membrane
   B. the superior olivary complex is the first level at which input from the two ears is combined
   C. the tonotopic organization of the cochlear nucleus is preserved at all levels up to and including the primary auditory cortex
   D. the principal projection of the inferior colliculus is to the medial geniculate body
   E. the response properties of auditory nerve fibers can undergo considerable transformation in the dorsal cochlear nucleus

4. The ability to localize the source of a sound:
   A. depends upon interaural time differences at high frequency
   B. depends upon the medial superior olive at high frequencies.
   C. depends upon interaural level differences at low frequencies
   D. depends upon filtering of the external ear for sounds varying in horizontal position
   E. can depend upon interaural time differences; the smallest ITD we can detect is on the order of 6 microseconds

5. Which of the following is FALSE with regard to binaural hearing, i.e., the ability to hear with both ears?
   A. it enables us to detect signals in a noisy acoustical environment
   B. it helps us in sound localization
   C. auditory information would only reach the contralateral cortex if we could suddenly hear with only one ear
   D. it helps us to detect interaural time differences
   E. it helps us to detect interaural level differences
6. What is **FALSE** with regard to the primary auditory cortex (AI)?
   A. It is located in the postcentral gyrus.
   B. It is tonotopically organized, i.e. there is a systematic map of best frequencies.
   C. It receives thalamic input from the medial geniculate body.
   D. Cells can be influenced by stimulation of either ear.
   E. It is located on the superior bank of the temporal lobe in Brodmann’s area 41 and 42.

7. The following statement is **FALSE**. The cochlear nuclei:
   A. are the first synaptic stations in the central auditory pathway
   B. are homogeneous in their afferent input, efferent output, and cellular structure
   C. direct their axonal output through the lateral lemniscus and the trapezoid body
   D. are obligatory synaptic stations for auditory nerve fibers
   E. are cochleotopically organized

8. The following statement is **FALSE**. Tonotopic organization:
   A. refers to the orderly arrangement of neurons within a central auditory structure according to their characteristic frequency
   B. is related to the location on the basilar membrane from which auditory nerve fibers are derived
   C. is related to the resonant properties of the basilar membrane
   D. is the functional counterpart of cochleotopic organization
   E. refers to the temporal coding mechanisms of neurons in the ventral cochlear nucleus

9. Which of the following statements is **TRUE**?
   A. the terminals of auditory nerve axons are in the superior olive
   B. the auditory nerve innervates only the dorsal cochlear nucleus
   C. the neural processing of auditory nerve signals that takes place in the cochlear nuclei is very similar in dorsal and ventral nuclei
   D. the dorsal cochlear nucleus is more devoted to preserving precise timing information than is the ventral cochlear nucleus
   E. eighth nerve fibers and cells of the ventral cochlear nucleus are specialized to transmit temporal information to higher auditory centers

10. Which of the following statements is **FALSE**?
    A. the superior olivary complex receives crossed input from the ventral cochlear nucleus
    B. the cochlear nuclei send axons through the eighth nerve to the superior olive
    C. the superior olivary complex is located in the ventrolateral portion of the pontine tegmentum
    D. the inferior colliculi receive massive converging input from many auditory nuclei in the brain stem and midbrain
    E. the medial geniculate body is the auditory portion of the thalamus
11. The following statement is **FALSE**. The auditory cortex:
   A. is located on the superior temporal gyrus of the temporal lobe
   B. is the first location in the auditory pathways where a map of auditory space is present
   C. when damaged may result in deficits in processing complex sound and in sound localization
   D. makes connections with other cortical fields on the same and opposite hemisphere
   E. is supplied by the middle cerebral artery

12. Which of the following statements is **TRUE**?
   A. listeners are very poor at discriminating the locations of sound sources
   B. the shape of the external ears and their placement on the two sides of the head provide the major cues for sound localization
   C. auditory cortex is found only on the left side of the brain
   D. damage to peripheral auditory structures is unlikely to effect speech and language acquisition
   E. two of the statements above are true

**RE-REVIEW OF EXTERNAL AND INNER EAR**
(Remember this?)

Make sure you can still describe the general functions of the outer, middle, and inner ear. Describe the sequence of events from sound waves entering the outer ear to the excitation of auditory nerve fibers in the cochlea.

1. Which of the following is **FALSE** with regard to auditory nerve fibers?
   A. auditory nerve fibers synapse on cells in the dorsal and ventral cochlear nuclei
   B. hyperpolarization of a hair cell leads to an increase in the action potentials in the associated 8th nerve afferent fiber
   C. auditory nerve fibers carry information from a single hair cell and have a characteristic frequency
   D. approximately 95% of auditory nerve fibers carry afferent information from inner hair cells to the cochlear nuclei
   E. some fibers traveling in the auditory nerve are carrying information from the central nervous system back to the cochlea

2. Which of the following statements about the **middle ear** is **FALSE**?
   A. its main components are the three ossicles: hammer, anvil and stirrup
   B. it serves as an impedance matching device for coupling air-borne sounds to the fluid-filled cochlea
   C. the stapedius muscle helps to dampen loud sounds
   D. it amplifies the pressure of sound chiefly by virtue of the difference in area of the tympanic membrane and oval window
   E. it provides a cue for sound localization by enhancing the difference in sound pressure level between the two ears
3. Your patient was involved in a brawl in which a blow to the head severed the linkage between the ossicles of the middle ear on the left side. The right side is normal. Which of the following would you expect to be **TRUE** when comparing the left and right sides?
   A. the patient has greater sensitivity in detecting sounds coming from his/her left side
   B. audiometric testing will show a conductive hearing loss on the left side, but not the right
   C. speech is not as distinct or easily understood in the right ear
   D. the cochlea of the left ear is still organized tonotopically
   E. two of the above statements are true

4. Which of the following statements about the **external ear** is **FALSE**?
   A. the acoustical filtering properties help us to localize sounds in the vertical dimension
   B. it helps to collect more sound, thereby acting as an amplifier
   C. it is designed to protect the tympanic membrane
   D. its sound filtering properties are the basis for the tonotopic organization of the organ of Corti
   E. it plays a negligible or minor role in encoding interaural time disparities

5. Which of the following statements about **hair cells in the inner ear** is **FALSE**?
   A. there are three rows of outer hair cells
   B. there is a single row of inner hair cells
   C. the overwhelming majority of auditory nerve fibers innervate the outer hair cells
   D. high frequency tones result in deflection of the basilar membrane at its base
   E. a change in receptor membrane potential associated with movement of the stereocilia results in release of neurotransmitter at the base of the hair cell and changes in the discharge of eighth nerve afferent axons
CENTRAL PATHWAYS PRACTICE QUESTIONS: ANSWERS

1. D 7. B
2. E 8. E
3. A 9. E
4. E 10. B
5. C 11. B

OVERALL REVIEW QUESTIONS: ANSWERS

1. B
2. E
3. E (B, D)
4. D
5. C  Ask me about my summer job!!
HEARING TESTS

The audiogram is THE standard hearing test, but there are times when it's useful to have a quick and easy test: Introducing the tuning fork!

TUNING FORK TESTS

Simple, easily portable tuning forks have been used for centuries and can still tell us a lot about a person's hearing. A qualitative assessment of hearing loss can be carried out with a tuning fork to help determine the nature of the hearing loss, conductive versus sensorineural.

Remember:
- **Conductive hearing loss** refers to a defect in the ability of the outer or middle ear to conduct sound to the cochlea.
- **Sensorineural hearing loss** is due to a defect in the cochlea or in the auditory division of the 8th nerve.

Tuning fork tests exploit the ability of sound to be conducted through the bones of the skull, as well as through the ear. Bear in mind that vibration of the bones of the skull can pass vibration on to the fluid of the cochlea. Normally, air conduction works better than bone conduction (ears weren't invented for nothing!), but both air and bone conduction can do the job. The tuning fork on the bone provides a second sound pathway to the inner ear, bypassing the external ear and, in particular, bypassing the ossicles and the stapes-oval window interface.

Once vibration adequately “shakes up” the fluids within the cochlea, the basilar membrane starts moving, and all the processes that lead to hair cell deflection and neural signals being directed centrally to the brain then follow, regardless of whether the process was initiated by sound waves coming through the ear canal, or by a metal tuning fork applied to the mastoid bone. As long as those hair cells get deflected, hearing sound can result.

**WEBER TEST**

For the Weber test, the stem of a vibrating tuning fork is simply placed on the patient’s forehead, and the examiner asks in which ear the person hears it. The tuning fork is typically placed on the skull in the midline (but but can be heard even better if it’s placed on a tooth!). When testing by bone conduction, the examiner should not forget to have the patient remove his or her eyeglasses: the earpiece can interfere with proper placement of the stem of the tuning fork or contribute to inappropriate conduction or vibration.

The Weber Test is helpful to test for a unilateral hearing loss. If hearing is normal in both ears, the sound will be heard equally well in both ears.

If a sensorineural lesion is present in one ear, the person will localize the sound (will say “it sounds louder”) in the opposite (the “better” or “normal”) ear, than in the affected ear. It will sound louder in the ear in which the inner ear and afferent pathways are functioning normally and weaker on the damaged side.
However, if a conductive defect is present, the person will localize the sound in the “worse” ear— the ear with the conductive defect. This is because that ear is protected from interference by extraneous sounds (i.e., better signal-to-noise ratio), so the tuning fork vibrations delivered by means of bone conduction sound louder because no or few other extraneous background sounds are also entering through that ear. This simple test has been a valuable aid in the diagnosis of otosclerosis for many years.

**RINNE TEST**

The vibrating tuning fork is placed on the mastoid process for the Rinne test, and the person being tested is asked to report when the sound of the tuning fork is no longer heard. The fork stem should be placed firmly on the mastoid, as near to the postero-superior edge of the ear canal as possible. The patient should cover his untested ear with his/her hand. The examiner then removes the fork immediately after the patient reports hearing the sound and holds the prongs close to the open ear canal. The normally functioning ear continues to hear the sound of the tuning fork for about 45 seconds by means of air conduction. However, a conductive deficit of greater than 15 db reverses the normal tuning fork responses, so that bone conduction becomes better than air conduction. The person with a conductive hearing loss hears the vibrating tuning fork poorly through air conduction. With such a “negative” result, the tuning fork is heard better by bone conduction than by air conduction. The patient reports hearing the sound only a short time, and a conductive type of hearing loss is determined to be present.

In the case of a sensorineural hearing loss, air conduction would be better than bone conduction, but sensitivity to both would be reduced in the affected ear compared to normal.

**SUMMARY: TUNING FORK TESTS**

Indication: Differentiate Normal Hearing from Sensorineural Hearing Loss and Conductive Hearing Loss
Equipment: Tuning fork (512 Hz - 1024 Hz)

**Weber Test** (For patient with unilateral hearing loss)

Technique: Place tuning fork at forehead midline
Normal: Sound radiates to both ears equally
Abnormal: Sound louder in one ear than the other
   Which ear sounds louder?
      a. Ipsilateral ear - Conductive hearing loss (pathology is on same side as “louder ear”)
      OR  
      b. Contralateral - Sensorineural hearing loss (pathology is on opposite side from “louder” ear)
**Rinne Test**

Technique:
1st Bone Conduction
   a. Vibrating tuning fork place on mastoid
   b. Patient covers opposite ear with hand
   c. Patient signals when sound ceases

2nd Air Conduction
   a. Vibrating tuning fork moved immediately over ear canal (not touching the ear)
   b. Patient indicates when the sound ceases

Normal: **Air Conduction is better** than Bone Conduction
   Patient hears the tuning fork through the ear.
   Air conduction usually persists twice as long as bone conduction

Abnormal: **Bone Conduction is better** than Air Conduction
   Patient doesn’t hear or hears only momentarily through the ear via Air Conduction.
   Suggests Conductive Hearing Loss
Sometimes it’s necessary to evaluate the integrity of the auditory pathways using methods other than standard hearing tests, for example in infants, comatose patients, uncooperative persons, or in the determination of brain death. Also, assessment of the physiology of the auditory pathways may be required in diagnosing specific pathology. The brainstem auditory response, or auditory evoked potential has long been used in these circumstances.

In this test, conventional scalp electrodes are applied to the head to record the electroencephalogram (EEG) along the auditory pathways in response to brief pulses of sound. As the neural signal that is created as a consequence of the sound is delivered successively from the inner ear to the cochlear nuclei and on up through the brainstem nuclei to cortex, the anatomical stations of the auditory pathways generate consecutive waves of electrical activity. The auditory evoked brainstem response records these temporally related waves of electrical activity along the auditory pathways that you have learned. The timing of particular positive and negative electrical waves measured in response to sound delivered to one ear is compared to those in response to sound delivered to the other ear and to clinical normative measures.

The auditory evoked brainstem response is divided into early-, middle-, and long-latency components. The earliest brainstem components, seen in the first 10 milliseconds following presentation of an auditory stimulus, are the most consistent and most relied upon. Wave I is believed to arise from the cochlea and the distal portion of the 8th nerve adjacent to the cochlea; Wave II is may arise from a combination of the cochlea, the 8th nerve, and the cochlear nuclei; Wave III is generated at the level of the superior olive; Waves IV and V are generated in the rostral pons and/or in the midbrain near the inferior colliculus.

**AUDITORY BRAINSTEM RESPONSES**

![Auditory Brainstem Response to a Brief Sound](image)
The later occurring middle- and long-latency negative (N0, Na, Nb, N1, N2) and positive (P0, Pa, P1, P2) components represent a mixture of activity that is more difficult to distinguish in the brainstem, thalamus, and higher auditory centers, including the temporal lobe.

Auditory brainstem waves that are markedly delayed or missing are cues that something is wrong in the ascending auditory pathways. Because the auditory system is so precise time-wise, any delays in the timing of the EEG are significant.

Waves can be delayed (i.e., they exhibit a longer latency) for a number of reasons. For example, lack of synchrony in the firing of individual fibers of a nerve, or slowed nerve conduction because of damage to the nerve would produce a longer latency response. Also, as you learned in Physiology, stronger signals generally have a shorter latency of response, while weaker signals take a longer time to build up and result in longer latency of response. So, a weaker signal coming out of the cochlea, for instance because many hair cells are not functioning or because of a serious problem with the ossicles, can yield a delay in the brainstem response compared to normal. The absence of all waves should not occur unless a severe hearing loss exists due to pathology at the earliest sites in the auditory pathways.

Despite being a gross measure of auditory neuron activity, the auditory evoked response can help to differentiate cochlear pathology from 8th nerve pathology and help to diagnose patients with brainstem tumors, including acoustic neuromas (auditory nerve tumors). Patients with demyelinating diseases such as multiple sclerosis may show abnormalities of the brainstem auditory evoked response before symptoms of brainstem dysfunction become apparent. Increased absolute latencies of all waves may signify a conductive deficit. The most sensitive evoked potential abnormality is an increase in the interwave interval—a longer time between waves. For example, longer interwave latencies (I-III or I-V) are seen with cerebellopontine angle tumors. The absence of waves III and V has been seen in patients with vestibular schwannoma and in cerebellopontine angle meningiomas.
HEARING TESTS: PRACTICE QUESTIONS

1. A person has excessive ear wax buildup in the right, but not the left, ear. Which of the following statements is FALSE?

   A. the Weber test localizes (is heard louder) in the right ear
   B. the Rinne test shows better air conduction in the left ear
   C. the Rinne test shows better bone conduction in the right ear
   D. the patient has a conductive hearing loss in the right ear
   E. all statements are true

2. Which of the following statements about the brainstem auditory evoked response is FALSE?

   A. the early component (wave I) is generated by the distal part of the eighth nerve
   B. a conductive hearing loss is indicated by normal latency for wave I and increased latencies for waves II to V
   C. brainstem damage can result in an increased latency or decreased amplitude of the later evoked components
   D. an acoustic neuroma (tumor of the eighth nerve) affects waves II and III
   E. a conductive hearing loss may lead to an increase in latency of all waves in the auditory brainstem response

HEARING TEST PRACTICE QUESTIONS: ANSWERS

1. E
2. B

Clinical Vignette Diagnosis (from the first two pages of the AUDITION section):
Acoustic Neuroma (technically, a schwannoma on the vestibular division of the eighth cranial nerve). This explains the vestibular signs. As the tumor grows, it involves the Auditory division of the Eighth Nerve (sensorineural hearing loss) as well as the nearby Facial (weakness) and Trigeminal (abnormal blink reflex) Nerves. Large tumors compress the brainstem and are often associated with long tract signs (Babinski).

Learn more about Acoustic Neuromas at:
http://itsa.ucsf.edu/~rkj/IndexAN.html