

The Physiology of the Senses

Lecture 9 - Hearing

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Objectives

1. Explain how the ossicles act like a lever to enhance the ear's ability to hear sounds.
2. List the chain of events that transforms vibrations of the basilar membrane into action potentials in the 8th nerve.
3. Design a good cochlear implant. Provide an explanation for your design features.
4. Explain how the location of a sound is determined.
5. Differentiate the role of each of the early auditory cortical areas in processing the sound of words.
6. Specify how the exposure to one language in infants alters their perception of another language later in life.
7. Contrast the functions of Wernicke's and Broca's areas.

The Importance of Hearing

Our sense of hearing is often underappreciated. If you had to choose, which would you give up, hearing or vision?

People who lose hearing feel very isolated from the world, and most importantly the company of people. Imagine what life would be like if at dinner you were unable to participate in conversation with your friends and family. Children who are hard of hearing are often misdiagnosed as cognitively impaired. The sound of approaching cars can save your life. A ringing in your ears, tinnitus, can drive you crazy.

What are sound waves?

Sound is produced when something vibrates, like the speaker in your stereo. When the speaker pushes on the air, it compresses it. The vibrating speaker produces a series of pressure waves that travel, at a speed faster than most jets, to the ear causing the eardrum to vibrate. But you do not hear the speaker vibrate, nor the sound waves move through the air. It is only when the sound waves move your ear drum and activity reaches your cortex that you perceive a sound. How this occurs is the subject of this lecture.

If one plots air pressure, then the peaks correspond to points of maximum compression, and the troughs, points of maximum rarefaction (Figure 9.1). The amplitude is the difference between minimum and maximum pressure and is perceived as loudness. Frequency or pitch is the number of peaks that go by a fixed point in one second. The normal range of frequencies audible to humans is 20 to 20,000 Hz (the number of waves per second). We are most sensitive to frequencies between 2000 to 4000 Hz, the frequency range of the spoken words.

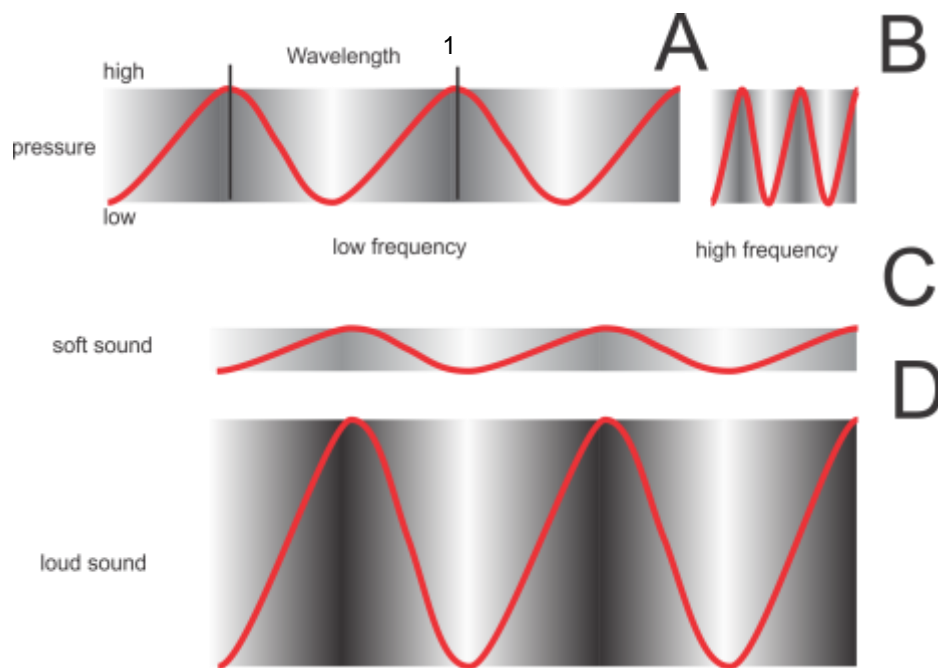


Figure 9.1 Sound Waves **A:** low frequency or low pitch. **B:** high frequency. **C:** soft sound. **D:** loud sounds.

The Conversion of Sounds to Action Potentials

1) Sound waves pass through the air filled outer ear canal (Figure 9.2).

2) Sound vibrates the ear drum and the vibration is conveyed across the air-filled middle ear by three bones called the ossicles. The ossicles pass vibrations to the oval window, a membrane that seals the opening to the cochlea.

3) Finally, vibrations reach the fluid filled inner ear where, inside a snail shell shaped cochlea, neurons are activated.

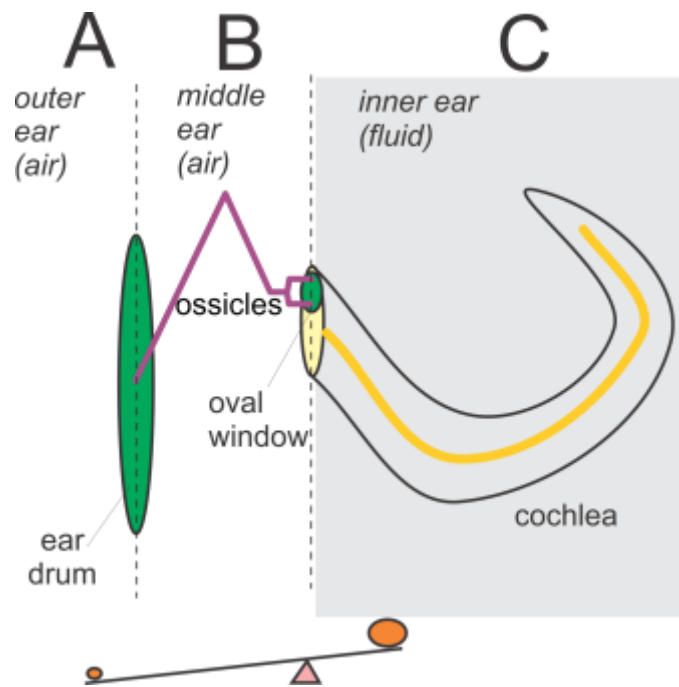


Figure 9.2 The Three Chambers of the Ear A: the air filled outer ear canal. B: the middle ear bones. C: The snail shell shaped cochlea

Why such a complicated chain of transmission?

The middle ear has two functions:

1. **Impedance matching.** You may recall while snorkelling how quiet it is underwater, how little of the sound in the air reaches under water. This is because most of the sound wave bounces off the water surface. Likewise, fluid in the cochlea is much harder to vibrate than air. If sound waves in the air struck the oval window directly, they would mostly bounce off. The eardrum picks up weak vibrations over a large area. The ossicles then act like a lever system, concentrating these movements to more forceful vibrations over the smaller area of the oval window. These more forceful vibrations are able to displace the oval window against the cochlear fluid. Without the ossicles, your hearing would be similar to that when swimming underwater and you would require a hearing aid which amplifies the volume of sounds.

2. **Gating.** Muscles attached to the ossicles in the middle ear are able to reduce the leverage of the ossicles in order to protect the inner ear from loud noise. These muscles prevent you from being deafened by the sound of your own voice. These muscles are activated before you speak (a preprogrammed response) or after a sustained loud noise such as at a rock concert (a reflexive response).

What is the function of the round window?

The final goal of this complex system is to displace the basilar membrane. This membrane stretches the length of the cochlea and is imbedded with hair cells, whose motion is converted into electrical activity. This membrane is surrounded by fluid, which cannot be compressed. When the oval window is pressed in, the initial portion of the pliable basilar membrane also bulges (Figure 9.3). This in turn produces a bulge in the round window into the middle ear. Thus pressure waves are transmitted across the basilar membrane to the round window, which acts as a pressure outlet. Without it, the oval window could not move fluid behind it because fluid cannot be compressed.

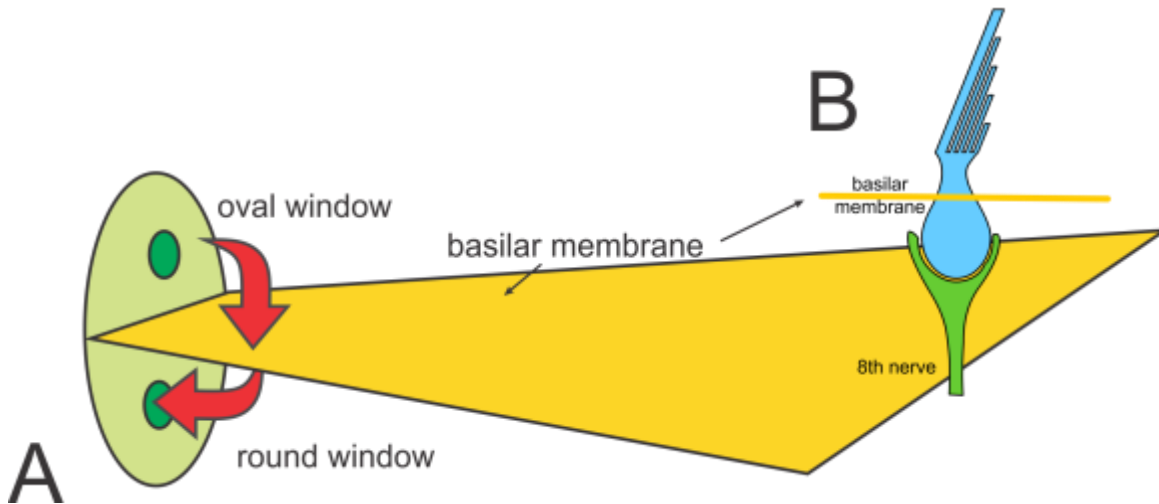
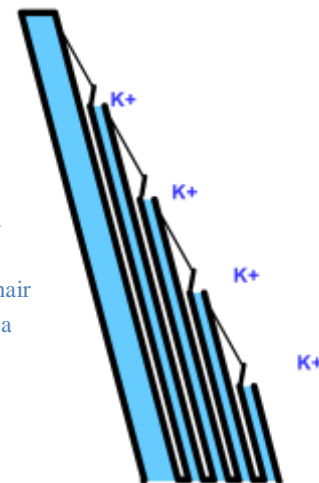


Figure 9.3 The Inner Ear **A:** The basilar membrane, inside a cochlea that is unrolled, holds hair cells. **B:** One of these hair cells is shown with hairs that bend when a wave travels down the basilar membrane.

How does deformation of the basilar membrane activate auditory afferents?

The hair cell, located in the basilar membrane, is a very delicate structure, which can be easily damaged by loud sounds. When the basilar membrane bends, the hairs on the hair cell are also bent. A tiny filament between adjacent hairs opens a flap allowing K^+ to enter the hair cell causing it to depolarize (Figure 9.4). This mechanical opening of the K^+ channel is very fast (less than a few microseconds) a precision that is necessary for sensing high frequencies or locating the source of a sound. The hair cell releases a neurotransmitter, increasing the firing rate in the 8th nerve.

Figure 9.4 The hairs of a hair cell have a crew cut for a reason. Tiny filaments, from one hair to the next lower one, pull open a flap when the hair is bent allowing K^+ to enter the cell.



The Traveling Wave

Georg von Békésy, in the 1920's, made the direct observation that a traveling wave sweeps down the basilar membrane starting near the oval window. Figure 9.5 shows 2 "snapshots" of such a wave taken an instant apart.

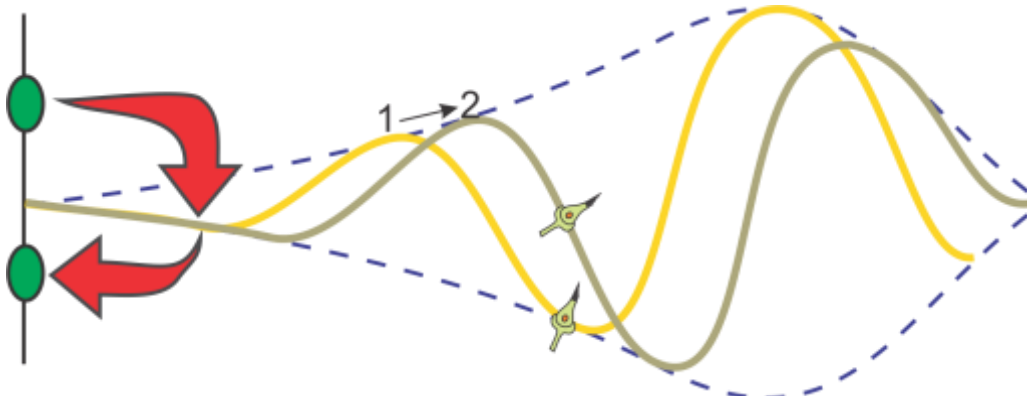


Figure 9.5 A sound's pressure wave deflects the inner ear's basilar membrane (viewed edge on) and sends a traveling wave down the membrane rocking the hair cells. This wave becomes larger, then smaller. The dashed line shows the wave's maximum displacement.

You can mimic this by taking a heavy cord, about 5 meters long, and attaching one end to something to something solid. Holding the end, flick your hand down. You should see a wave travel the length of the cord. The cord has the same properties throughout. So the size of the wave remains fairly constant. The basilar membrane mechanical properties change, somewhat like a bull whip, and so the wave changes its size as it flows down the length of the membrane.

How is the frequency of a sound coded?

Hermann von Helmholtz noted, in the 1860's, that the basilar membrane is narrow and stiff (like a high string on a piano) near the oval window, and wide and floppy (like a low string) at the other end (Figure 9.6). Because of this, each portion of the basilar membrane vibrates maximally for a particular frequency of sound. High frequency sounds maximally displace the hair cells near the oval window, while low frequency sounds maximally displace hair cells at the other end. Thus sound frequency is topographically represented on the basilar membrane (place coding) by the place at which it maximally vibrates. Frequency is coded by which of about 16,000 hair cells are maximally activated, not by their firing rate. This is like labeled lines in the sense of touch. The tone you hear is coded by which cell is firing.

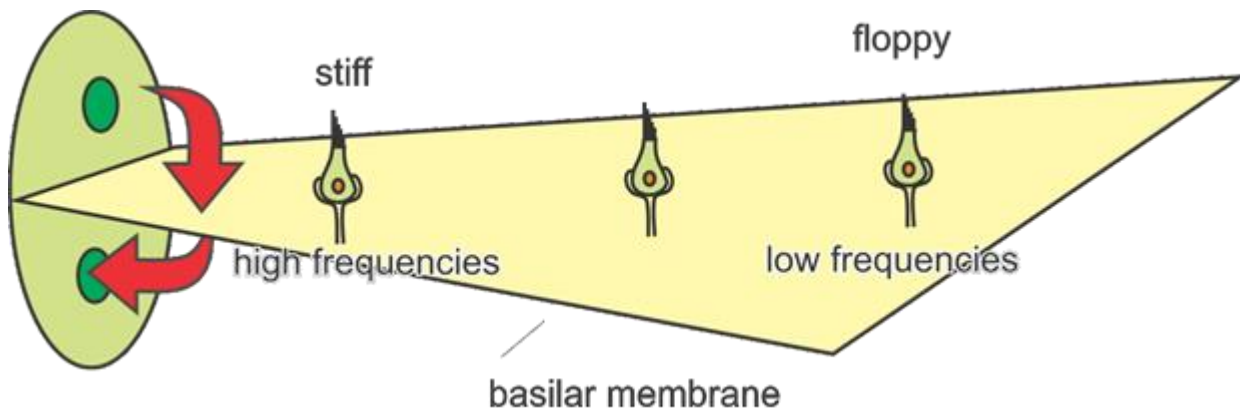


Figure 9. 6 Three of 16,000 hair cells are located on the basilar membrane and code the frequency of sound by their location.

How is loudness coded?

Loud sounds produce a larger amplitude vibration of the basilar membrane than soft sounds. The large vibration produces more displacement of the hair cells and a larger change in potential inside these cells. Thus loudness **is** encoded by the frequency of action potentials that travel down a particular afferent fiber.

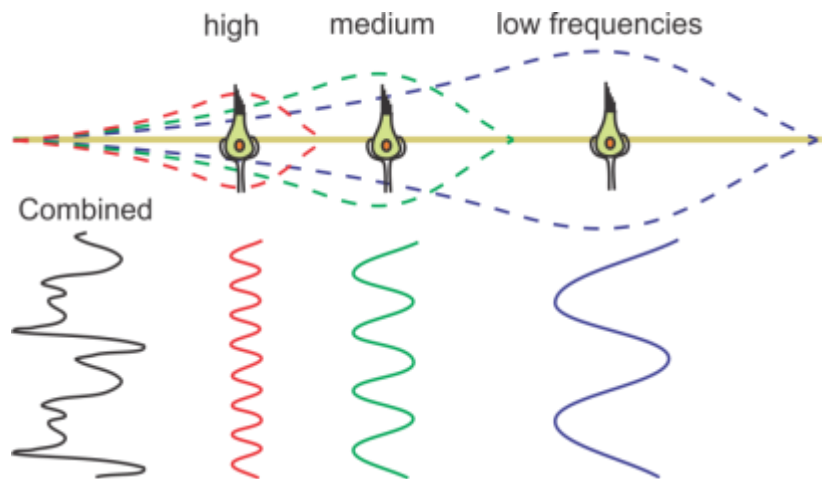


Figure 9. 7 The clarinet produces a complex wave that activates three groups of hair cells.

Most every day sounds, such as that of a clarinet, are complex because they contain multiple waves at different frequencies (Figure 9.7). This is what makes the sound of a clarinet different from another instrument. The hair cells decompose this sound into its different frequencies, as does a synthesizer, with each hair cell encoding the loudness of a particular frequency.

Four Major Causes of Hearing Loss

1. Loud sounds break parts in the ear.

Extremely loud sounds from explosions and gunfire can rupture the ear drum, break the ossicles, or tear the basilar membrane.

Hair cells are very fragile and once damaged, do not recover. Loud sounds common around the house, such as lawnmowers or loud music on headphones, can shear the hairs off the hair cells or break the filaments that open the ion channels.

2. Infections

Middle ear infections, in rare cases, rupture the ear drum. Inner ear infections can damage hair cells.

3. Toxic Drugs

Toxins can enter hair cells through the open channels and poison the hair cells (Figure 9.8). Some early antibiotics caused poisoning in this way and deafness.

4. Old Age

The parts simply wear out with time. In old age, blockage in the blood supply kills cells.

Hair cells are not replaced and must last a life time.

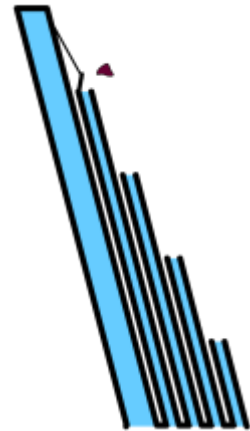


Figure 9.8 A toxic molecule enters the hair cell through the opened ion channel.

What are the cues to sound direction?

Besides frequency and loudness the auditory system computes a third sound quality, the direction from which a sound originates. There are two methods for detecting this direction. Both involve a comparison between the ears.

The first cue involves sound **intensity differences**. Think of the head as casting a shadow in the airborne sound waves (Figure 9.9). The sound striking the ear facing away from its source will be muffled by the head. This method works best for high frequencies over 3000 Hz. Low frequency sounds wrap around the head and do not cast a shadow.

The second cue is **timing difference**. The peak of a sound wave strikes the ear facing the source before it strikes the other ear (Figure 9.10). The timing difference is least for sounds coming from in front and most when coming from one or the other side. Timing differences are most accurately measured in low frequency sounds.

Humans can resolve direction with an accuracy of about 1 deg. This corresponds to a remarkable timing difference of 1/100,000 sec.

The shape of the earlobe, besides amplifying sound, helps in distinguishing sounds coming from in front from those coming from behind (and also above vs. below). Because the earlobe acts like a directional antenna, one can also localize sound by turning ones head to where the sound is loudest. Also, other sensory modalities, especially vision, team up with audition to localize the sound source. When watching a movie with two actors talking, one senses that the sound is coming from the one whose mouth is moving. The same occurs when we think we hear a ventriloquist's dummy speak because we see its lips move.

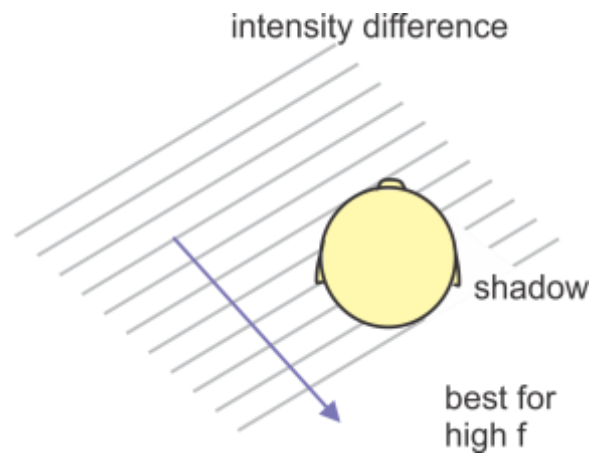


Figure 9. 9 High frequency sound waves pass the head forming a shadow over the right ear.

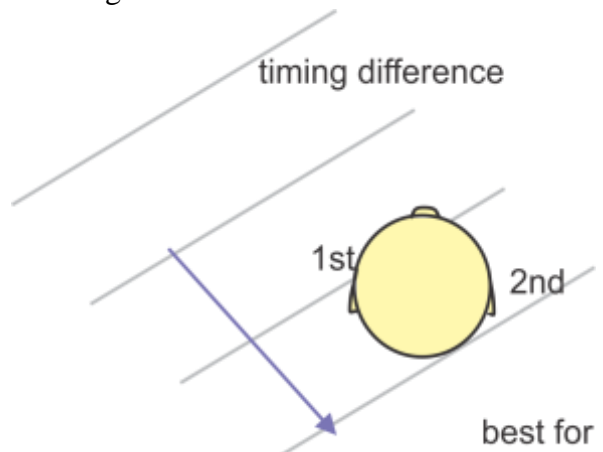


Figure 9. 10 Low frequency sound waves pass the head striking the left ear first and the right second.

The Auditory Pathways

The Role of the Superior Olive in Sound Localization

The **superior olivary nucleus** (Figure 9.11), in the brainstem, is the first place where signals from the two ears come together and can be compared. It is here that one can first measure the sound's location. Cells in the **lateral** superior olive encode differences in sound intensity. Cells in the **medial** superior olive encode timing differences.

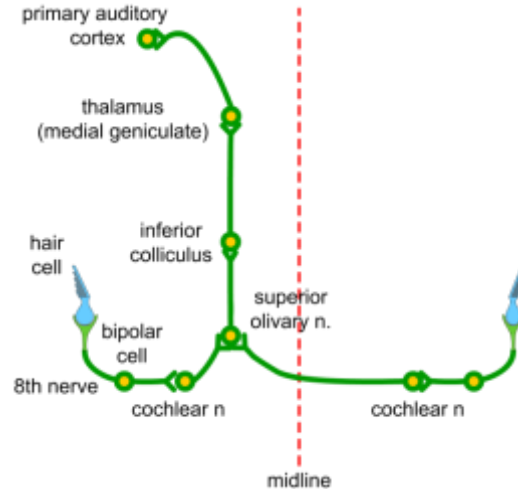


Figure 9.11 The brainstem pathways include the superior olivary nucleus, and inferior colliculus. Not shown is a mirror symmetric pathway on the right side.

The Central Pathways

Auditory information is then sent

1) to the inferior colliculus which codes the location of a sound. Here a topographic neuronal map codes sound location with respect to the head. This location is coded by which group of neurons on the map are activated. The inferior colliculus then signals the superior colliculus to generate orienting movements of the eye and head towards a sound.

2) to the medial geniculate nucleus of the thalamus and then to the primary auditory cortex, which is the first relay involved in the conscious perception of sound.

The primary auditory cortex has a columnar organization.

The basilar membrane is remapped in the **primary auditory cortex**, topographically with low frequencies at one end and high frequencies at the other. The cells in each column are tuned to the same frequency (Figure 9.12).

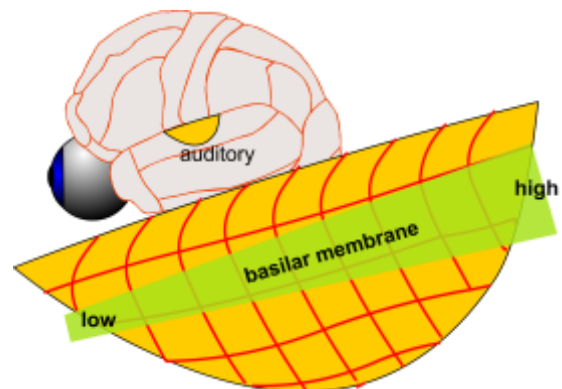


Figure 9.12 The primary auditory cortex is located on the top of the temporal lobe tucked into the Sylvian fissure. Each column shares neurons activated by a similar frequency. Low frequencies (f) are coded at the anterior end.

Beyond the Primary Auditory Cortex

Sounds are processed first by the primary auditory cortex (A1) (Figure 9.13). They are further processed by higher order areas (A2). A2 is best-activated by sounds called phonemes that are the building blocks of words (e.g. ba, ga, r, l). A1 is also called the core area and A2 the belt. Together these two areas have been found to contain several mirror-image tonotopic representations (Saenz & Langers 2014) (Moerel et al 2014) similar to visual areas V1, V2, and V3. Next, the sounds that are words are processed by Wernicke's area. This area is important for word comprehension.

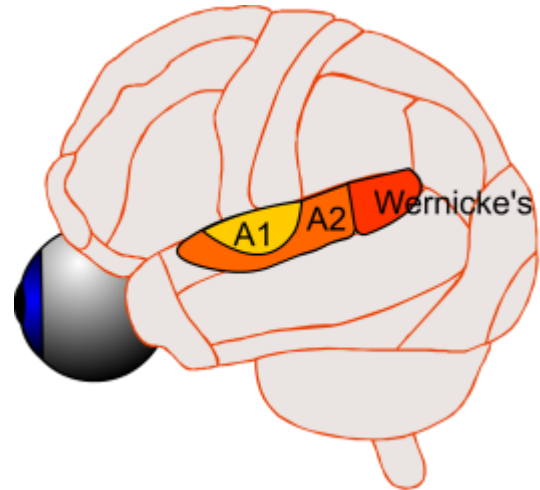


Figure 9.13 Cortical Auditory Areas A1 is activated by all sounds. A2 is best activated by phonemes. Wernicke's area is best activated by the sound of words.

Newborns, regardless of where they are born, initially all have the ability to distinguish a common set of phonemes. We are born citizens of the world.

And how does one ask babies whether they can differentiate between ba and pa? In 1974 Peter Eimas found, using an electronically monitored pacifier, that babies habituated to the repetition of the same sound (ba, ba, etc.) and that they started sucking much more rapidly when the sound changed (ba to pa). Patricia Kuhl and her students took recorded phonemes and a similar pacifier around the world testing babies of different ages and backgrounds. She found that after the age of 6 months, the auditory system starts to filter phonemes. These filters act like magnets (Figure 9.14) which

- 1) attract phonemes that are similar to make them sound like the more familiar phonemes, and
- 2) produce a clear boundary between different and familiar phonemes.

Experiment. Make an "R" sound and then an "L". Move your tongue back and forth to change one into the other. Note that you hear either an "R" or an "L", not some third sound.

Because of this filter, we start losing the ability to distinguish phonemes that are not part of our culture. For example, in Japan, adults cannot distinguish between "R" and "L", while infants can. Likewise, someone raised in an English environment will not distinguish phonemes indigenous to Japan.

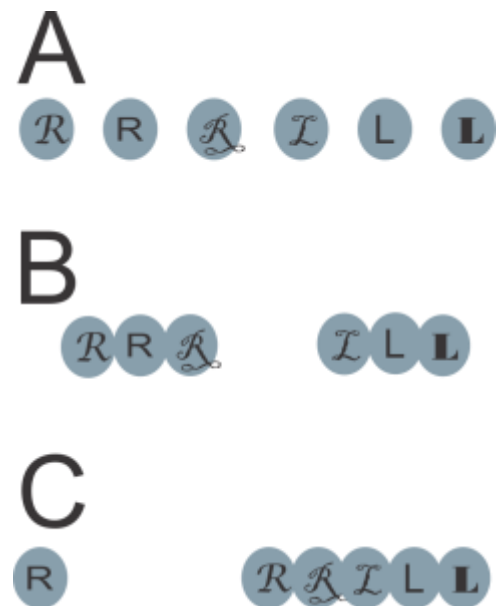


Figure 9.14 Perceptual Filters for Phonemes in Area A2. Each circle represents a different "R" sound, either a different person's "R" or with a different tongue position. A: A newborn's filter. B: That of a 6 month baby raised in England. (Different "R"'s elicit a similar percept which is different from "L"'s) C: That of a 6 month baby raised in Japan. ("R" and "L" elicit the same percept.)

The Sequence of Activity When Reading Out Loud

Wernicke-Geschwind Model

When reading, the primary and higher order visual cortex detect simple features such as the line elements of a letter (Figure 9.15).

The **Visual Word Form Area (VWFA)** is activated by letters that form familiar words. Neurons here are oblivious to the same words with their letters scrambled, just as those of the Fusiform Face Area (FFA) are to a face with its features scrambled. The VWFA is located posterior to where one would expect to find the FFA on the left side. The FFA allows us to quickly recognize a familiar face while the VWFA allows us to quickly recognize a familiar word. Normally the ability to recognize faces develops automatically while reading requires extensive training. This is perhaps because we are rewiring a part of FFA for novel function. Recall that a lesion of right FFA results in prosopagnosia, the inability to recognize faces visually. Similarly, a lesion of VWFA produces dyslexia, a reading disability.

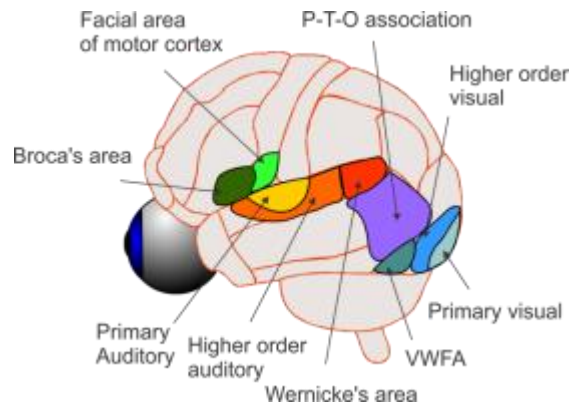


Figure 9.15 The Cortical Areas Involved in Reading Out Loud: primary visual cortex (V1), higher order visual areas (V2, V3 and others), visual word form area (VWFA), PTO association area, Wernicke's area, Broca's area, facial area of motor cortex.

In the PTO association area there is convergence of visual, auditory and tactile information and the object is recognized. The object "apple" can be recognized by the written word or picture of the apple, the sound of the spoken word, the feel of an apple through touch and of course, by taste.

Wernicke's area is involved in verbal understanding and associating the object with the sound of a word. Recall that biological motion produced by lip movements is analyzed here in the superior temporal sulcus (STS). This can override what we hear. For example, hearing "ba" while seeing the lips form "ga" leads to the perception of "ga". **Vision predominates.** [For demo of the McGurk effect see video by Prof Lawrence Rosenblum.](#)

Broca's area is responsible for language production. This area is involved in grammatical rules and verbal expression. This is part of the frontal working memory. Working memory is used to order words in a sentence. Finally, the facial area of motor cortex contracts the correct muscles to produce the required sound. Broca's area is also used for writing language. In this case it activates the arm and hand area of motor cortex.

Compare the deficits caused by lesions in Broca's and Wernicke's areas:

Lesion	Patient cannot	Patient can
Wernicke's aphasia	understand language	say words (often nonsense)
Broca's aphasia	say the right word or grammar	understand language

The deaf use **American Sign Language (ASL)** hand gestures to communicate. As in spoken language, lesions of Broca's area produce deficits in expression with hand gestures, while lesions of Wernicke's, a deficit in the comprehension of these gestures. Thus, these areas are not limited to the understanding or production of language through sounds.

Auditory “What” and “Where” Streams

In the last decade “what” and “where” streams, similar to that seen in the visual and touch pathways, have been proposed for the auditory pathways (Figure 9.16).

The **auditory “What” stream** flows into the anterior temporal lobe and then to the prefrontal cortex. This path is used to identify the sound object: a bird from its chirping, a car from its passing sound, grandma from her voice. With the visual system, you can recognize the same object from a variety of views. Similarly, in the auditory “What” stream you can recognize a violin in a variety of musical pieces (Bizley & Cohen 2013).

The **auditory “Where” stream** flows in a posterior direction through Wernicke’s area to the parietal lobe and then to the prefrontal cortex. This path is used to identify the sound’s location, its temporal properties and if a word, its meaning.

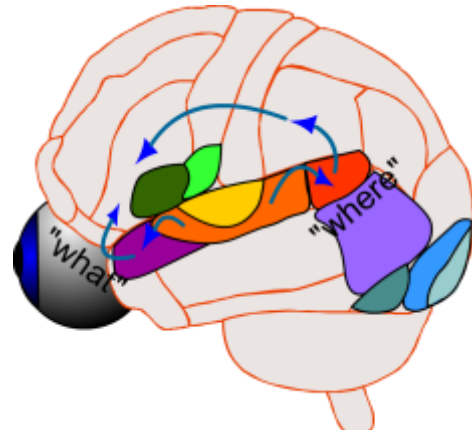


Figure 9.16 The Auditory “What” and “Where” Streams

See problems and answers posted on

<http://www.tutis.ca/Senses/L9Auditory/L9AuditoryProb.swf>

References

- Bizley JK, Cohen YE. 2013. The what, where and how of auditory-object perception. *Nature Reviews Neuroscience* 14: 693-707
- Moerel M, De Martino F, Formisano E. 2014. An anatomical and functional topography of human auditory cortical areas. *Frontiers in Neuroscience* 8
- Saenz M, Langers DRM. 2014. Tonotopic mapping of human auditory cortex. *Hear. Res.* 307: 42-52