

CHAPTER 20

TRANSDUCTION, TONOTOPIC MAPS AND THE CENTRAL AUDITORY SYSTEM

20.1. TRANSDUCTION IN THE AUDITORY SYSTEM

20.1.1. Mechanical basis of transduction.

As shown in the previous section, the tops of the hair cells contact the tectorial membrane so that the motion of the traveling wave in the cochlear fluids creates shearing forces on the hair cells. The resulting movement of the stereocilia activates transduction mechanisms that convert mechanical energy into electrochemical activity.

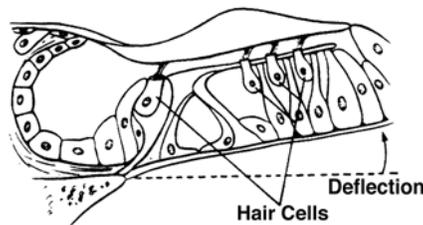


Figure 20-1. The traveling wave in the cochlear fluids causes the basilar membrane to move alternately upward and downward around its resting position (dashed line). The tectorial membrane moves in a different pattern, resulting in a shearing motion of the stereocilia between the tops of the hair cells and the tectorial membrane.

20.1.2. Biophysical basis of transduction.

When the stereocilia bend in one direction, the hair cell *depolarizes*. When they bend in the other direction, the hair cell *hyperpolarizes*. These changes in electrical potential result from opening and closing of *mechanically-gated K^+ channels* on the tips of the stereocilia.

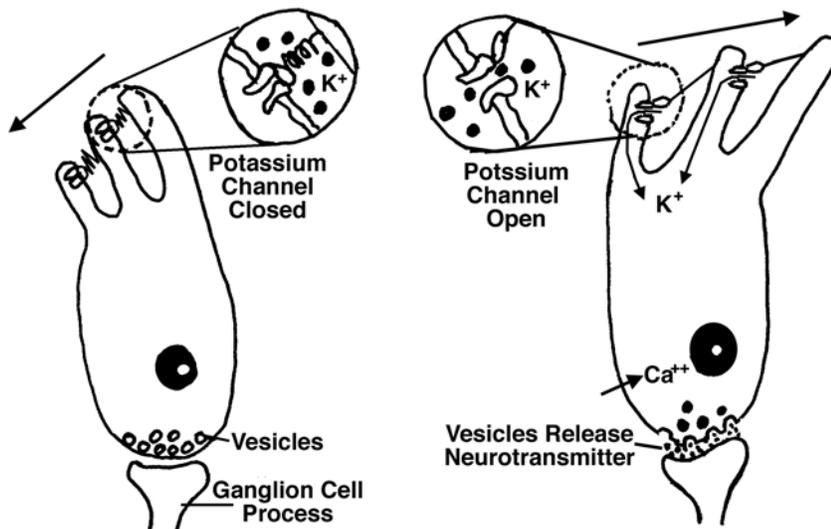


Figure 20-2. Transduction in hair cells takes place by means of mechanically-gated ion channels in the stereocilia. When the stereocilia are bent in one direction (left), the tension on the tip-links is minimal and the ion channels are

closed. When the stereocilia are bent in the opposite direction (right), tension on the tip-links causes them to open, allowing potassium (K^+) to enter the cell and depolarize it.

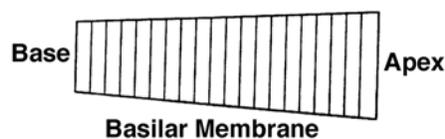
It is thought that the ion channels are linked through an elastic filament, the "*tip-link*", to the wall of the adjacent cilium. The tip-link, when stretched, provides mechanical energy that pulls on a part of the ion channel and "unplugs" the opening of the channel allowing positively charged ions to enter the hair cell. Displacement in the direction that increases tension on the tip-link opens the channel and allows K^+ to enter the cell (remember that there is an unusually high potassium concentration in the endolymph). Displacement in the opposite direction releases tension and allows the channel to close, preventing entry of K^+

The depolarization of the hair cell triggers neurotransmitter release (probably glutamate) from the base of the hair cell onto the dendrite-like processes of spiral ganglion cells. If depolarization is great enough, the spiral ganglion cell produces an action potential that is transmitted via the auditory nerve to the brain.

20.2 The inner ear as a frequency analyzer.

Vibrations transmitted by the stapes to the oval window cause displacement of the fluid in the cochlea toward a second small membrane-covered opening, the *round window*, located between the scala tympani and the middle ear cavity. This flow causes a *traveling wave*, or alternating upward and downward displacement of the basilar membrane that propagates from the base to the apex in much the same way that a wave of motion would propagate along a rope if it were shaken at one end.

The basilar membrane is wider and less tightly stretched at the apical end, causing this part to resonate most strongly to low frequencies. It is narrower and stiffer at the basal end, causing it to resonate maximally to high frequencies.



20-3. Schematic drawing showing how the width of the basilar membrane changes from the basal (high frequency) to apical (low frequency) end.

Because of the mechanical properties of the basilar membrane and cochlear fluids, different frequencies cause maximum vibration amplitude at different points along the membrane. For high frequencies, the maximal displacement is near the base. For low frequencies it is near the apex.

Vibration of the basilar membrane is the mechanical stimulus that leads to transduction in the cochlear hair cells, the receptor cells for hearing. Because the part of the basilar membrane that vibrates most strongly varies as a function of sound frequency, hair cells on the basal part of the membrane are stimulated by high frequencies while hair cells on the apical part of the membrane are stimulated by low frequencies.

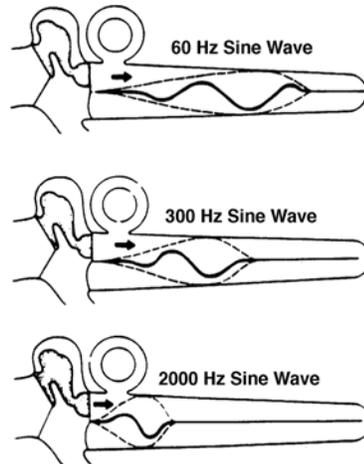


Figure 20-4. For a low frequency sound (top), the traveling wave peaks near the apex of the cochlea; for a mid-frequency sound, the peak is near the middle, and for a high frequency sound (bottom), the peak is near the base of the cochlea.

20.3. TONOTOPIC REPRESENTATION IN THE AUDITORY SYSTEM

The fact that hair cells in different parts of the cochlea are maximally stimulated by different frequencies results in a spatial representation of sound frequency (or pitch) across the array of hair cells in much the same way that visual space is represented across the array of photoreceptors on the retina. The difference is that in the visual system, a spatial parameter is mapped directly onto a spatial array of cells, whereas in the auditory system a non-spatial parameter (frequency, or cycles per second) is converted to a spatial representation.

The resulting representation is a *topographic map of sound frequency*, also called a *tonotopic representation or tonotopic map*.

The tonotopic map is the fundamental principle of organization in the auditory system. Like the retinal map of visual space, it is maintained at every level of the auditory system through the auditory cortex. In parallel auditory pathways, each pathway contains a tonotopic map.

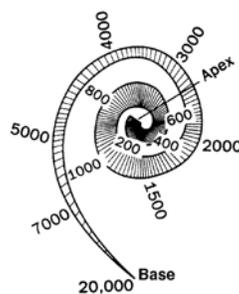


Figure 20-5. Hair cells at different places along the basilar membrane are maximally stimulated by different frequencies, with those at the base activated by high frequencies and those at the apex activated by low frequencies.

20.4. THE SPIRAL GANGLION CELLS AND AUDITORY NERVE.

Each inner hair cell *diverges* to many ganglion cells. Spiral ganglion cells are the first neurons in the auditory system. Their cell bodies are located in the spiral ganglion, in the center part of the cochlea. Each spiral ganglion cell has a process that contacts one or more hair cells and an axon that projects to the brain. This axon is the *auditory nerve fiber*.

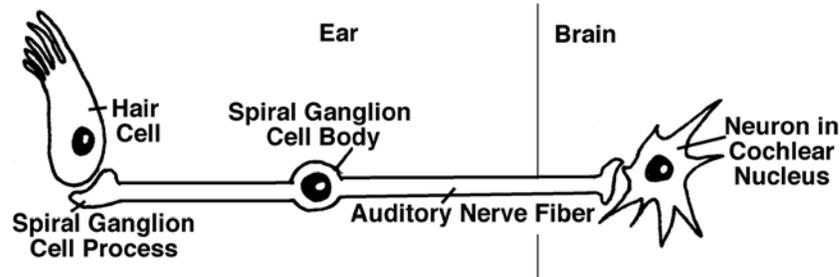


Figure 20-6. The cochlear hair cell is contacted by the distal (away from the brain) process of a spiral ganglion cell. The proximal process (axon) projects in the auditory nerve to the first part of the central auditory system, the cochlear nucleus.

20.4.1. Frequency tuning of auditory nerve fibers.

The frequency sensitivity of an auditory nerve fiber (or neuron in the central auditory system) is usually limited to a single frequency at threshold, but broadens to include higher and lower frequencies as sound level is increased. Each auditory nerve fiber can be assigned a *best frequency* (frequency at which threshold is lowest) and a frequency *tuning curve*. The tuning curve is somewhat analogous to a visual receptive field, except that it represents those combinations of frequency and amplitude that cause a change in the activity of the spiral ganglion cell or central auditory neuron.

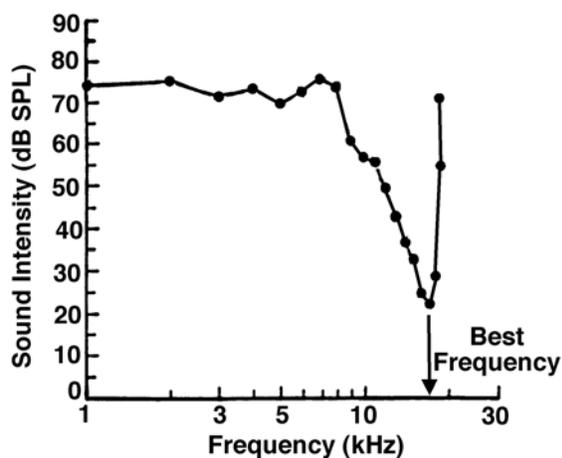


Figure 20-7. Tuning curve of a typical auditory nerve fiber. The curve represents the lowest sound intensity that evokes a response from the neuron as a function of frequency. There is one frequency (the best frequency) at which sensitivity is highest (i.e., threshold is lowest). At higher and lower frequencies, the threshold is higher. Note that as sound becomes louder, the fiber responds to progressively broader ranges of frequencies.

20.4.2. Phaselocking in auditory nerve fibers.

For low frequency tones (< 5000 Hz), action potentials always occur at the same phase angle of the sine wave. This means that the nerve fiber fires "in time with" the waveform of the sound.

20.4.3. Sources of information about pitch

The range of frequencies to which auditory neurons respond varies as a function of sound intensity. However, the same number (or rate) of spikes can be evoked by a low-intensity sound at best frequency or a high intensity sound at a lower frequency. Therefore, there is not an unambiguous labeled line code for pitch. The information on which we base pitch judgements takes the form of a spatially -distributed population code as well as a temporal code.

The place code for pitch. For any given sound frequency, auditory nerve fibers from a specific part of the cochlea are active. Information about pitch can be derived from knowing *which* fibers are active, especially the relative amounts of activity in different fibers across the population.

The temporal code for pitch. For any given sound frequency up to about 5000 Hz, auditory nerve fibers fire action potentials that are phaselocked to the waveform of the sound. By examining the distribution of action potentials over time, it is possible to derive a good estimate of the pitch of the sound. Information about pitch can also be derived from patterns of amplitude modulation of a high-frequency sound because auditory nerve fibers phaselock to the modulation cycle.

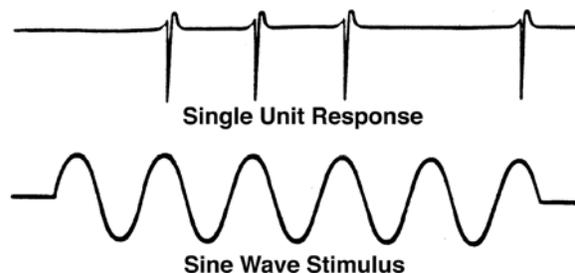


Figure 20-8. The phaselocked response of an auditory nerve fiber (top) to a pure tone (bottom). Action potentials always occur at a specific time relative to a cycle of the sine wave that represents the tone. The nerve fiber may not respond to every cycle (e.g., the 1st and 5th in the example shown), but whatever action potentials occur are always correlated in time with a particular phase angle (the peak in this example).

An auditory illusion - periodicity pitch. Interestingly, we not only perceive the frequency of a sine wave (pure tone) - if that sine wave is amplitude modulated (or turned on and off) in a regular fashion we also perceive a pitch corresponding to the frequency at which the tone is modulated. Technically, there is no energy present at the modulation frequency, so neurons sensitive to that frequency would not be active. The illusion of the modulation pitch is presumably due to phaselocked responses to the amplitude peaks in the stimulus.

20.4.4. Sources of information about sound intensity

For a given auditory neuron, the same level of activity can be elicited by a faint stimulus at its best frequency or a loud stimulus at a frequency far from that at which its sensitivity is highest. Therefore, the rate of firing of any individual auditory neuron cannot unambiguously signify sound intensity. For a low intensity sound, few fibers will be active. For a high intensity sound, many fibers will be active. This means that information about sound intensity takes the form of a population code in which it is necessary to know the number of fibers active, and their relative rates of activity.

Thought question: The perceived loudness of a sound depends on sound pressure level, but is also strongly influenced by frequency. Why does the frequency of a sound affect our perception of its loudness?

20.5. THE CENTRAL AUDITORY SYSTEM

20.5.1. General characteristics of the central auditory system

The auditory system is *tonotopically organized* at all levels.

The auditory system is divided into multiple *parallel pathways* below the thalamus.

The auditory system includes special circuits for *computing location* of a sound source in space.

The auditory system includes special circuits for analyzing and *selecting temporal patterns* of sound.

20.5.2. Structure of the central auditory system

Unlike most other sensory systems, the auditory system comprises a multitude of complex parallel pathways below the level of the thalamus.

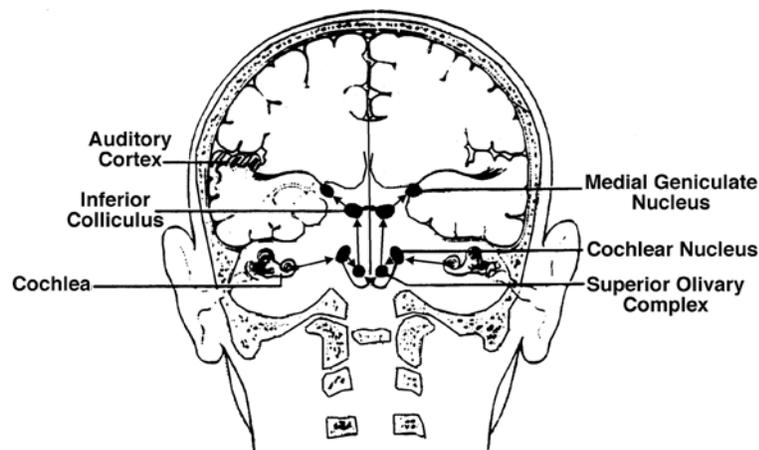


Figure 20-9. Diagram of the auditory system showing the main pathways as they would appear in a section through the center of the head cut from ear to ear.

20.5.2.1. The cochlear nucleus. The first target of the auditory nerve is located in the lower brainstem. It is called the *cochlear nucleus*. Each auditory nerve fiber diverges to three divisions of the cochlear nucleus. Each auditory nerve fiber makes different types of synaptic endings on different cell types in the cochlear nucleus.

Cells in the cochlear nucleus (and other brainstem auditory nuclei) may *transform* the incoming signal by changing the *response pattern* (distribution of action potentials over time), *increasing the range of latencies*, and *changing excitatory input to inhibitory output*. These transformations are necessary for the different analytical and computational tasks that are performed at higher levels.

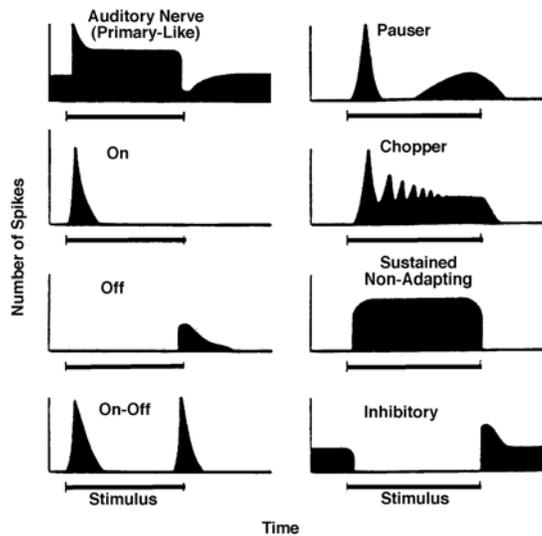


Figure 20-10. In response to a tone or noise burst, distribution of action potentials over time follows approximately the same pattern in every auditory nerve fiber (upper left). In the absence of sound, auditory nerve fibers discharge continually at a low rate (spontaneous activity). At the onset of a sound, the firing rate increases abruptly to reach a peak, then quickly decays to a lower steady state that is maintained for as long as the sound is present. At the offset of the sound, the firing rate drops below spontaneous rate, but soon recovers. Neurons in the cochlear nucleus exhibit a variety of different discharge patterns in response to the same sound ("on", "off", and "on-off" on left, and the four patterns on the right). The changes in discharge pattern are due to differences in the types of ion channels present in the membranes of different cell types, as well as other factors.

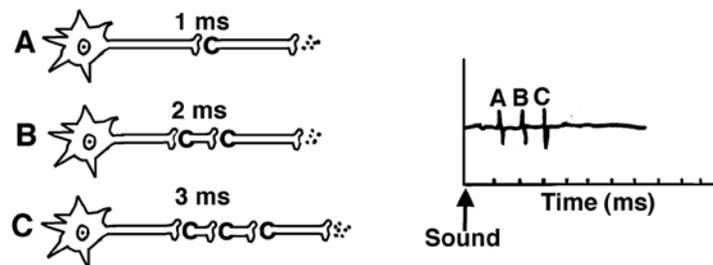


Figure 20-11. The latency of a given neuron's response (the time that elapses between stimulus onset and firing of the neuron) is determined by different factors, one of which is the number of synapses through which input must

pass before reaching the neuron in question. If neurons A, B and C (left) were all stimulated at the same time, their outputs would be separated in time as shown in the diagram on the right.

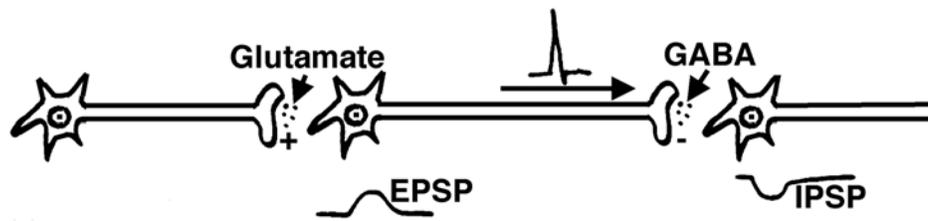


Figure 20-12. Excitatory input from terminals of auditory nerve fibers activates neurons in the cochlear nucleus that may be excitatory or inhibitory, as shown here. In this case, the target neuron in the cochlear nucleus manufactures and releases the inhibitory neurotransmitter GABA, so whenever it is excited it releases a substance that hyperpolarizes and inhibits the neuron(s) to which it projects.

17.5.2.2. Parallel pathways in the brainstem. The subdivisions of the cochlear nucleus are the source of a number of ascending pathways which, as in the visual system, can be roughly classified as "where" pathways and "what" pathways. The major targets of the cochlear nucleus are:

The superior olive (the "where" pathway): The superior olivary complex is a set of cell groups in the lower brainstem that receive direct or indirect input from both ears. The nuclei of the superior olive are important for comparing sound at the two ears, in order to localize the sources of sounds in the environment. We will discuss in some detail the mechanisms for comparing sound at the two ears because this system is a good example of a network specialized for *neural computation*.

The nuclei of the lateral lemniscus (the "what" pathway): Another set of nuclei in the lower brainstem, the nuclei of the lateral lemniscus, receive inputs from one ear only, but relayed through different pathways. The nuclei of the lateral lemniscus are important for analyzing temporal patterns of sound in order to identify what type of sound it is and, ultimately, what it means.

The inferior colliculus: The inferior colliculus is located in the midbrain. It receives direct input from the cochlear nucleus as well as from the nuclei of the superior olive and lateral lemniscus. The inferior colliculus is a major center for integration of auditory sensory information. It is important for selecting specific features of sound and for activating pathways that provide output to motor systems. It also projects to the auditory portion of the thalamus.

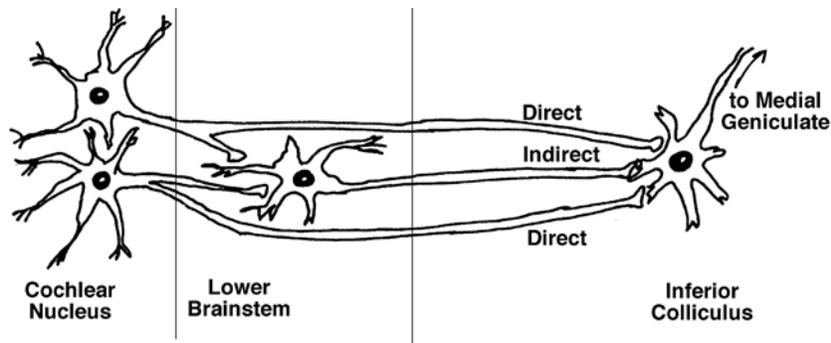


Figure 20-13. The inferior colliculus receives input via direct (straight-through) pathways from the cochlear nucleus as well as multisynaptic (indirect) pathways.

20.5.2.3. The auditory thalamus and cortex. The inferior colliculus projects to the auditory thalamic area, the medial geniculate nucleus. The medial geniculate nucleus projects, in turn, to the primary auditory cortex. In addition to the primary auditory cortical area, there are several secondary auditory areas as well as polysensory areas that receive input from the auditory system as well as the visual and/or somatosensory system.

Thought question: When we listen to complex auditory stimuli such as speech or music, we need to analyze sequences of information distributed over time. What role do you think neural delay lines might play in this type of analysis?
