4 The auditory system

PREVIEW

This is the first chapter of the set of two on the auditory system. The ear is a fascinating piece of machinery. It is composed of tiny bones and membranes, with spiral-shaped tubes filled with fluid. When sound waves arrive at the ear, they are directed down precisely shaped passageways through a complex series of membranes and bones, which transform the sound waves to pressure variations in a liquid-filled cavity. These pressure variations cause bulges in a membrane, and the bulges act on a set of hairs that run along the length of the membrane. Each hair is connected to a cell, and when the hair is bent, the cell sends a signal along the acoustic nerve into the brain. Thus, what we hear is determined by which hairs are bent.

By comparison with the ear, all the other sensory systems are much simpler. In the eye, for example, the mechanical parts are fairly straightforward, and all the complexity resides in the interactions of the nerve cells at the back of the eye, in the retina. With the ear, the neural connections in the ear itself are relatively simple, and all the complexity is put into the mechanical structures that transform sound waves into particular patterns of bulges along the basilar membrane. (The neural circuits for hearing in the brain are quite sophisticated, of course. But the neural circuits within the ear are relatively simple.)

This chapter discusses the operation of the ear, starting with a simple explanation of the physics of sound, then describing in some detail the construction of the ear, and finally concluding with a discussion of the electrical responses to sounds. The next chapter will cover the resulting perceptual experiences of hearing.

To start with, you have to understand something of the nature of sound, of the way in which it is measured, and of the physics of sound. The concept of decibels (dB) is important, and those of you who detest mathematics should not be frightened by the concept. Decibels are pretty simple, and you really do not have to know much about them for these chapters. Decibels will not be too important in this chapter, but they will be used extensively in the next.

In reading the section on the ear, there is no need to learn all the details of the anatomy. The critical terms that you should know are listed at the end of the chapter (as usual), and maybe you ought to refer to them as you go through the chapter. You should know the distinctions among the outer, middle, and inner ear, the ear drum, the round and oval windows, and the three middle ear bones (and their associated muscles). The cochlea is important, and here you should try to understand the mechanics of the thing. Get a picture of a membrane vibrating with a bulge traveling from one end to the other. The shape and location of the bulge is very important for hearing.

The next chapter will try to piece all this information together, illustrating the applications of the details that you read in this chapter. Conceivably, you may wish to skim both chapters rapidly, then back up to read this one with more care, after you have an idea of how the concepts will be used.

THE EAR

The human ear is surprisingly complicated. From outward appearances, it consists mainly of a tube between the outside world and a small internal membrane, the eardrum. Vibrations in the air cause the eardrum to vibrate. These outermost parts of the ear, the pinna, the ear canal, and the eardrum, however, are the least important components for the ear's successful operation. The vibration of the eardrum in response to changing air pressure is only the beginning of a long chain of events, which ultimately produces our perception of sound.

The process of getting the sound through the ear to create neurological signals involves a rather intricately detailed set of steps. Examine Figures 4-1 and 4-2. First, the sound wave arriving at the ear travels down the auditory canal and causes the membrane at the end—*the eardrum*—to vibrate. This vibration is transmitted through the three small bones

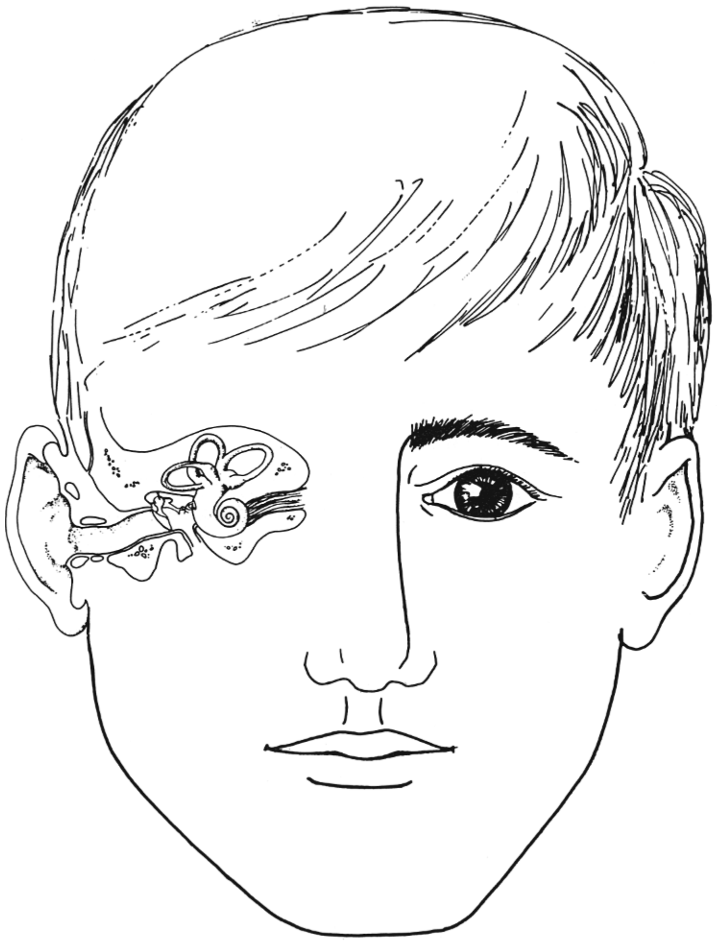
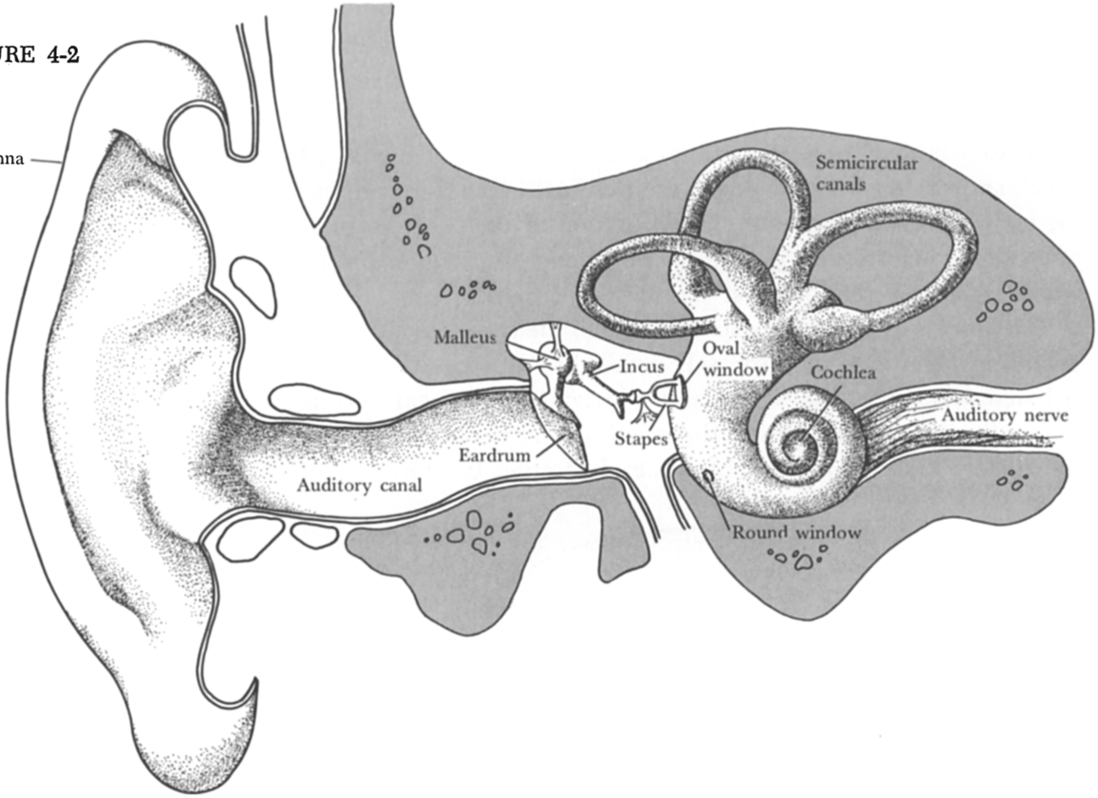


FIGURE 4-1

FIGURE 4-2



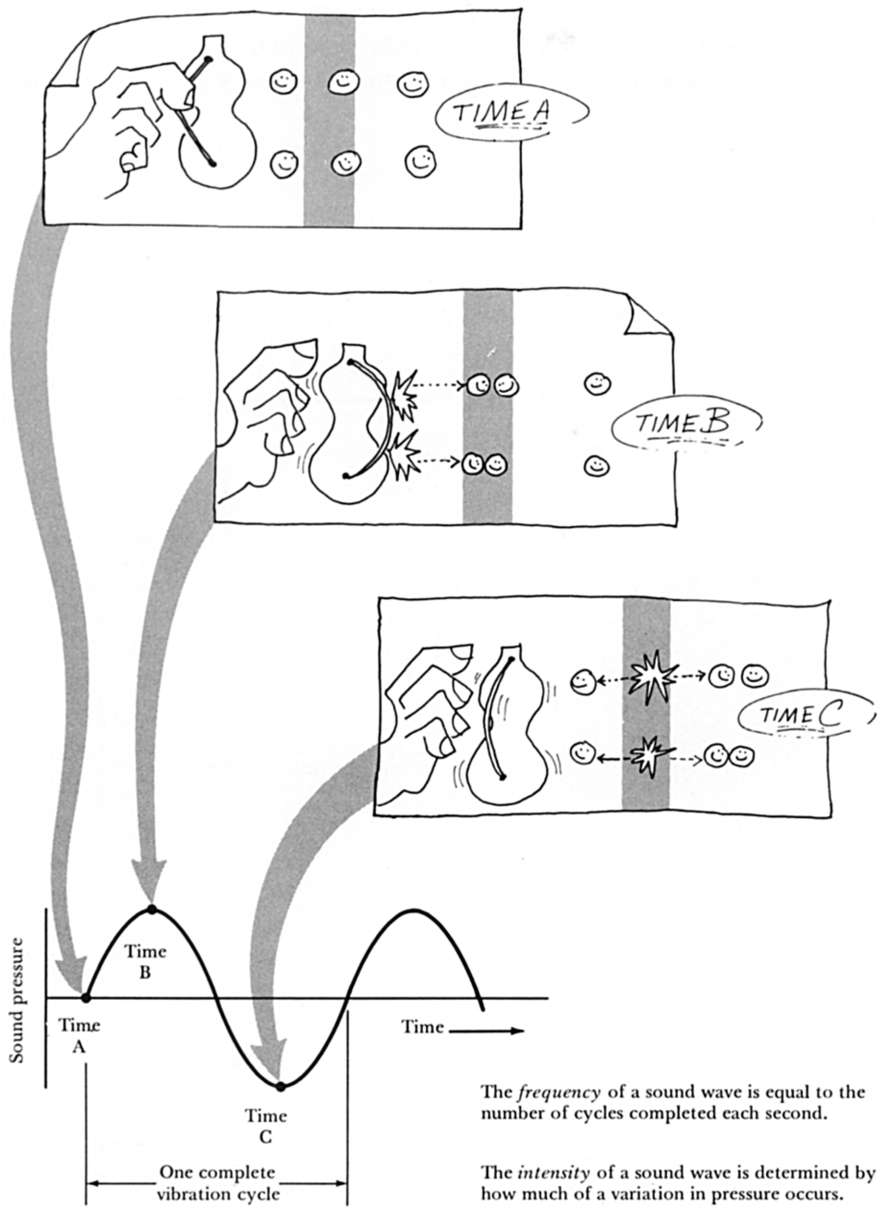
of the middle ear to another membrane, the *oval window.* This window is the opening into the bony, spiral shaped structure of the inner ear, *the cochlea.* Fluids in the cochlea are set into motion by the movements of the oval window and, in turn, cause a membrane that lies along the spiral inside the cochlea to vibrate. The vibration pattern of this last membrane, *the basilar membrane,* is sensed by several rows of hairs that line the membrane, causing the cells to which they are connected to create the neural impulses that carry the acoustic information to the brain. Each component in this strange path has a good reason for its presence. Our task is to discover how each of these components contributes to the development of the neural message sent along the auditory nerve to the brain and then, how that message is decoded into the psychological experiences of sound, of music, and of speech.

THE PHYSICS OF SOUND

Sound consists of pressure variations. When an object "makes a sound" it causes pressure waves to propagate out through the surrounding medium. The sound pressures measured some distance away from the sound source create an imperfect image of the sound pressures initially generated. In part this is because the wave has been attenuated by its travel through the air and, in part, because of various types of reflections and refractions caused by objects encountered in the path of the wave.

The frequency of sound

For the simplest kind of sound, the pressure variations in the air over time produce a waveform that looks like that in Figure 4-3. To describe this waveform (a *sine wave*) three things must be specified: how rapidly it is varying (its *frequency*); how great a pressure it produces (its *amplitude*); when it starts (its *phase*). In general (with exceptions



The graph shows the pressure measured at the shaded (gray) area in each of the panels. FIGURE 4-3 that will be described later), the larger the amplitude of the sine wave, the louder it sounds; the higher the frequency, the higher the pitch. A sine wave with a frequency of 261.63 cycles per second, for example, has a pitch of middle C on the musical scale. One *cycle per second* is called one *hertz* (Hz).[1]

Although the description of the variations in sound pressure with time produce a complete description of the sound, it is often more convenient to describe the wave in an entirely different fashion. Look at the sound pressure patterns shown in Figures 4-4 and 4-5. These complex

FIGURE 4-4

From Denes and Pinson (1963).

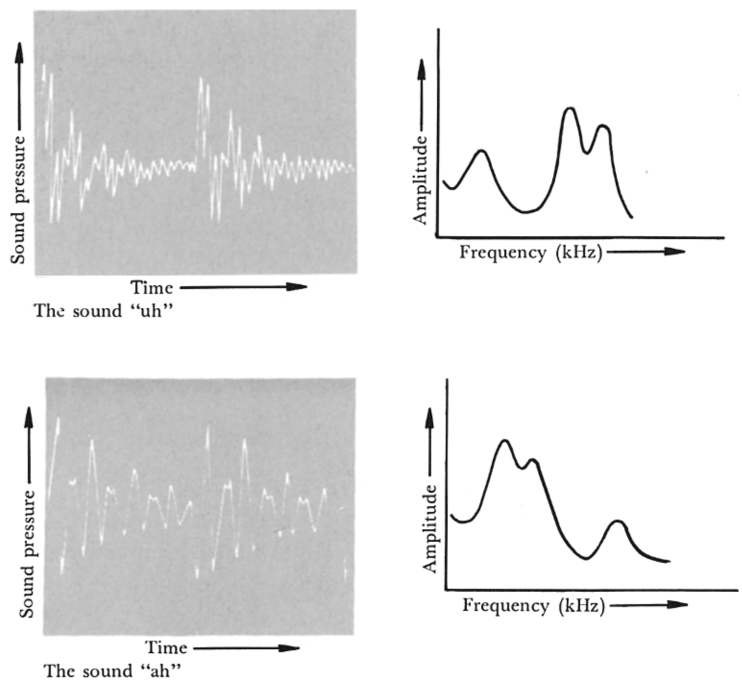
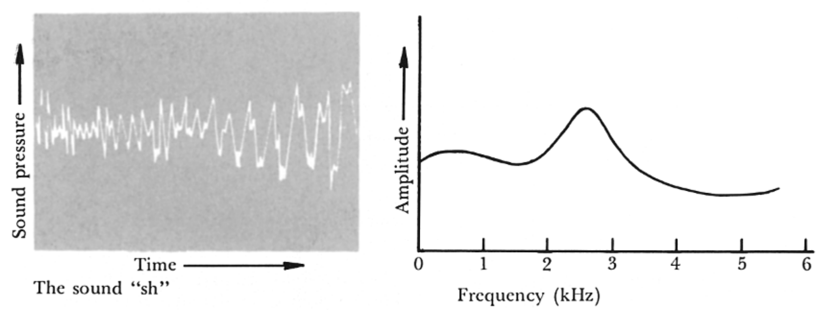


FIGURE 4-5

From Denes and Pinson (1963).



[1] The unit of frequency comes from the name of the German physicist, Heinrich R. Hertz (1857–1894). Frequency is often specified in *kilohertz* (*kHz*), where 1 kHz is equal to 1000 Hz.

time waves are awkward to handle. They can be dealt with more easily by breaking up the complex wave into simple elementary components, namely, the sine waves just discussed. The rationale is based on a theorem by the mathematician *Fourier* (1768–1830), who proved that any complex waveform (with certain restrictions) can be represented by a combination of sinusoidal waves of specific frequencies, intensities, and starting times: The decomposition of a waveform into its individual component frequencies is called *Fourier analysis.* Figure 4-6

Representing complex waves by their sinusoidal components seems also to be most compatible with the way the ear actually deals with sounds. In fact, the ear appears to do a rough Fourier analysis of the incoming signal. If a 440-Hz tone (A above middle C) is played together with a 698-Hz tone (an F), it is still possible to hear the two individual notes in the resulting combination. This fact first impressed the German physicist Georg Ohm (1787–1854), and the correspondence between what is heard and the representation of sounds in terms of the separate frequency

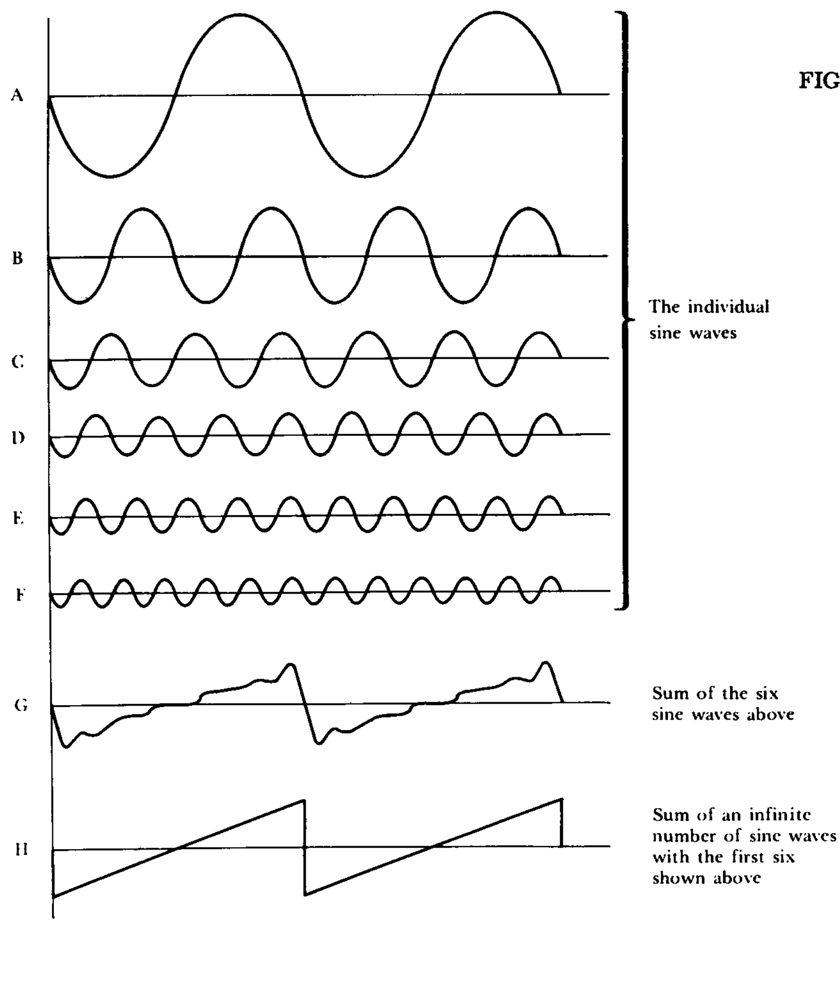


FIGURE 4-6

components has come to be known as Ohm's Law. (This is the Ohm who proclaimed the Ohm's Law of electricity; same Ohm, different law.) Things are quite different with light. When a light of a frequency that looks red (a wavelength of 671 nm) is mixed with a light of a frequency that looks green (a wavelength of 536 nm), the resulting mixture is a light that looks yellow (a wavelength of 589 nm). Unlike the auditory system, the visual system does not keep separate the different frequencies

Table 4-1

Sound	*Intensity (dB)*
	200
Manned spacecraft launch (from 150 feet)	• 180
	160
Pain threshold	•
	140
Loud thunder: rock band	•
	120
Shouting	• 100
Conversation	• 80
	60
	40
Soft whisper	•
	20
Threshold of hearing at 1000 Hz	• 0

Sound	*Frequency (Hz)*
Lowest note on piano	27.5
Lowest note of bass singer	100
Lowest note on clarinet	104.8
Middle C on piano	261.6
Standard tuning pitch (A above middle C)	440
Upper range of soprano	1,000
Highest note on piano	4,180
Harmonics of musical instruments	10,000
Limit of hearing for older persons	12,000
Limit of hearing	16,000–20,000

impinging upon it: Visual waveforms are combined by the eye, leaving no trace of the individual components.

The intensity of sound

As is true with light intensities, the difference in sound intensity between the weakest sound that can be heard and a sound producing physical pain is immense. At 2000 Hz, for example, the most intense sound that is tolerable is about one thousand billion times more intense than the weakest detectable sound. This enormous range of intensities makes it inconvenient to describe sound intensities directly. The range is compressed by describing sound intensities in *decibels*.

Table 4-1

DECIBELS[2]

To compress the very large range of physical intensities of sound, we use the trick of expressing intensities in terms of how many powers of ten one intensity is greater than another. This procedure is named after the inventor of the telephone, Alexander Graham Bell, although his last name has been shortened. Thus, if one intensity is a million times another (10^6 times greater), it is 6 bels more than the other. If an intensity is 1/1000 of another (10^{-3}), it is 3 bels less than the other. This is the same as having the number of bels between two intensities be given by the logarithm of their ratios. Actually, it turns out there are not enough bels in the span of sound intensities, so intensity ratios are usually specified in terms of the number of *tenths of bels* they contain. These are called *decibels*, abbreviated *dB*. In the two examples above, the intensities are 60 and −30 dB apart. The number of decibels that separate two intensities I and I_0 is:

$$\text{Number of dB} = 10 \log (I/I_0)$$

1. Doubling (or halving) the ratio of signal intensities adds approximately (subtracts) 3 dB.
2. Multiplying (or dividing) the ratio of signal intensities by 10 adds (subtracts) 10 dB.
3. If two sounds are separated by $10n$ dB, their intensity ratio is 10^n. For example, a 60 dB difference in the intensities of two sounds means that one sound is 10^6 (1 million) times more intense than the other.
4. Since decibels refer to the ratio of two intensities, to say that a sound has a level of 65 dB is completely meaningless unless the comparison sound is known. Generally, whenever you see statements of this form, it means that the sound is 65 dB more intense than the international standard reference level of 0.0002 dynes/cm². This standard is a very low sound pressure. It is, approximately, the weakest sound that can be detected by a human listener for a sound of 1000 Hz.

[2] Although this box is similar to the box on decibels in Chapter 2, please look it over long enough to notice the differences between the standard references for sound and light.

In this book, we will usually refer to sound levels by *dB spl*, for *sound pressure level*. This means that we are using the standard reference level of 0.0002 dynes/cm^2. When you read the technical literature, you might also encounter *dB sl* and *dBA*. These are measures of sound intensity designed to be relevant to the human ear: *dB sl* is *sensation level*—the reference level is the minimum detectable sound; *dBA* has the sensitivity curve of the human (Figure 5-2) built into the measuring instrument.

Decibels

Number of dB = 10 log (I/I_0)

I/I_0	*dB*	I/I_0	*dB*
0.0001	−40	10000.0	40
0.001	−30	1000.0	30
0.010	−20	100.0	20
0.032	−15	31.6	15
0.10	−10	10.0	10
0.13	−9	7.9	9
0.16	−8	6.3	8
0.20	−7	5.0	7
0.25	−6	4.0	6
0.32	−5	3.2	5
0.40	−4	2.5	4
0.50	−3	2.0	3
0.63	−2	1.6	2
0.79	−1	1.3	1
1.00	0	1.0	0

THE MECHANICS OF THE EAR

The inner ear

To the psychologist, the most important part of the ear is the tiny snail-shaped bony structure in the inner ear called the *cochlea*. The cochlea is a tube, coiled up 2½ times (in the human) and filled with a saline solution. In the human, the cochlea is about the size of a sugar cube—about 0.2 inches long and 0.4 inches wide (0.5 cm long, 1 cm wide).

There are two openings in the bone that encloses the cochlea. One, a small membrane called the *oval window* is connected to the last bone in the lever chain of the middle ear. Vibrations from the eardrum via the middle ear bones pass into the cochlea through this membrane. Because the cochlea is filled with an incompressible fluid, some means must be found for relieving the pressures generated at the oval window. This is done with another small opening in the bone structure, also covered by a thin membrane. This is the opening at the rear of the cochlea—the *round window.* [You can remember which window is which by a simple mnemonic device: The *O*pening into the cochlea is the *O*val window (**O**); the window at the *R*ear is the *R*ound window (**R**).]

Figures 4-7 & 4-8

Inside the cochlea is a highly sophisticated mechanism for converting the incoming pressure variations into the electrical signals that travel along the many thousand fibers of the auditory nerve. It is easier to examine this mechanism if we unwind the cochlea (which is possible artistically, but not physically) so that you can see inside, as is done in Figure 4-9.

The two membranes running the length of the cochlea divide it into three different regions, each of which is filled with fluid. The membrane that has most importance for our discussion is the *basilar membrane.* This membrane extends all the way from the start of the cochlea (the *base*), where the middle ear bone vibrates the oval window, to very near the end of the inner tip (the *apex*) of the coil. At the apex there is a small space between the membrane and the walls of the cochlea. When stretched out, the basilar membrane is about 1.4 inches long (3.5 cm), with a width that increases from the oval window to the apex. This increase in width plays an important role in its operation. Note several things about the basilar membrane. First, it starts out by the oval

Figure 4-10

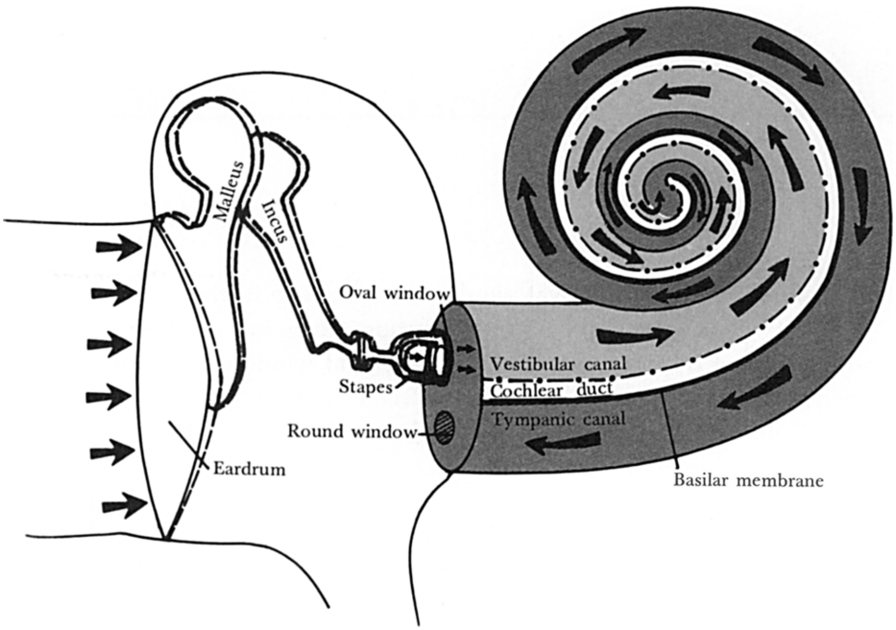


FIGURE 4-7

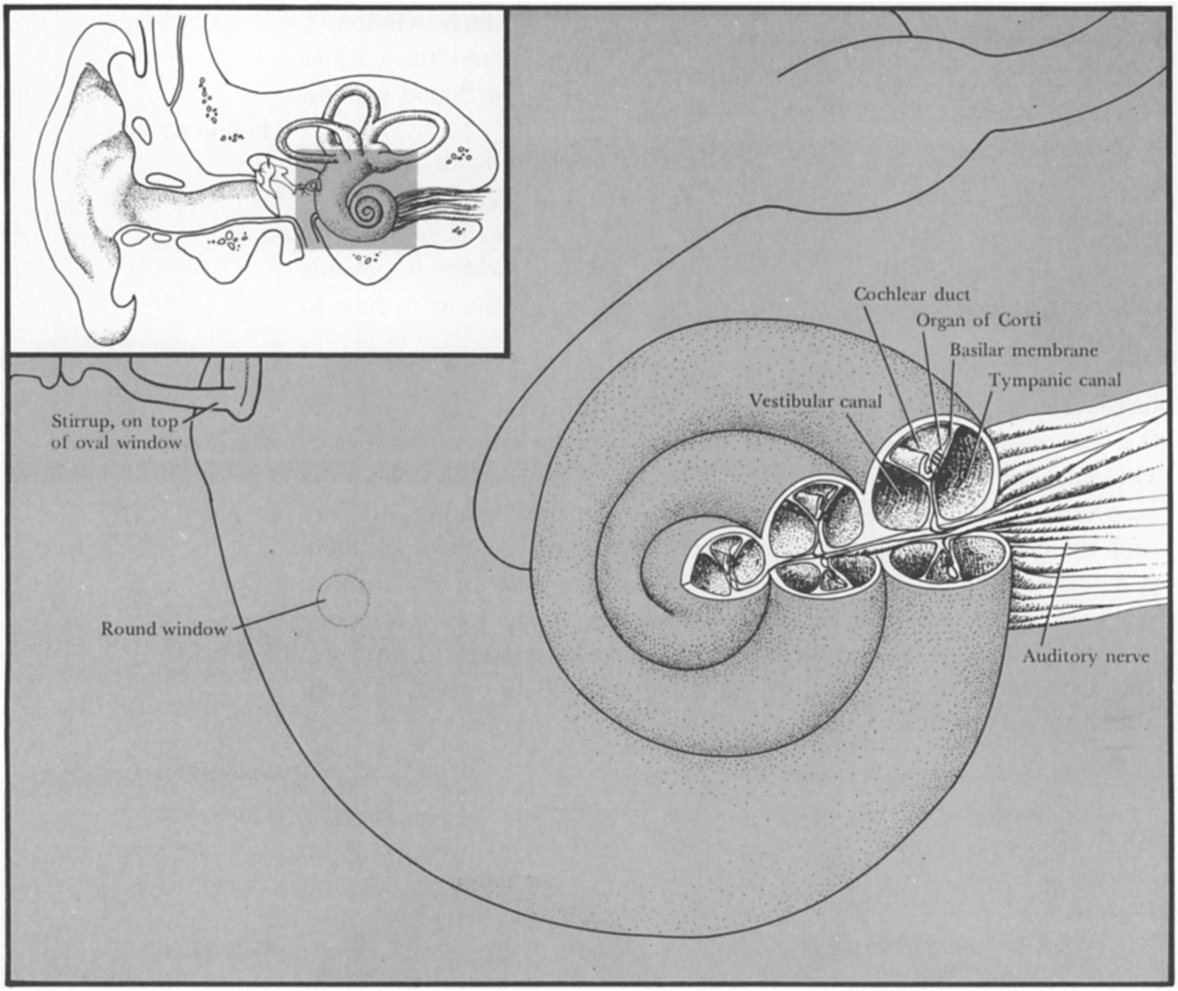


FIGURE 4-8

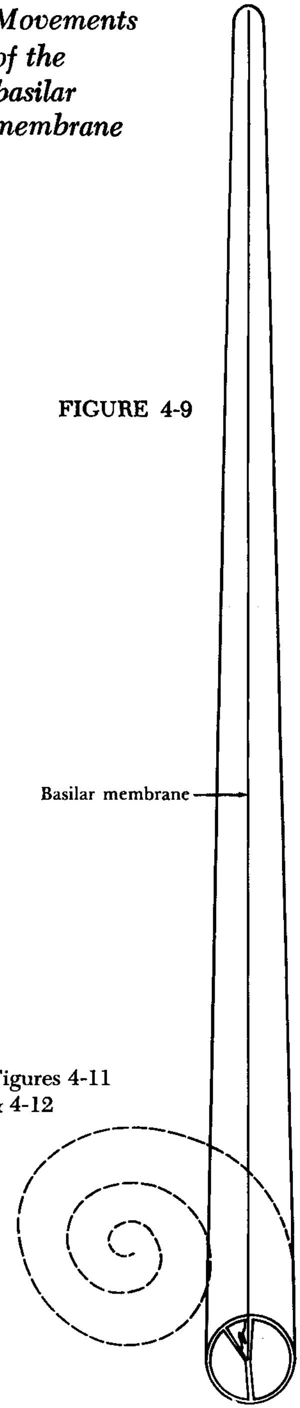
and round windows, the oval window being above it, the round window below it. Thus, when we describe position along the membrane, we do so in terms of distance from the round or oval window and also distance from the apex. Second, although the cochlea itself gets narrower as it goes from the window end toward the apex, the membrane does the opposite: the membrane is wider near the apex than near the windows. Finally, the membrane decreases in stiffness towards the apex. All these factors—a widening of the membrane, an increase in mass, and a decrease in stiffness—make the part at the apex more responsive to low-frequency sounds, and the part at the oval and round windows more responsive to high frequencies.

Movements of the basilar membrane

Pressure exerted inward at the oval window produces a pressure in the fluids above the basilar membrane that is applied, essentially, instantaneously across the whole length of the membrane. (The pressure wave requires only about 20 millionths of a second to travel the length of the cochlea.) Thus, the pattern of activity produced in the basilar membrane does not depend upon which end of the cochlea is stimulated. If the system were set into motion at the apex rather than the oval window it would work just as well.

The basilar membrane itself does not react immediately to the pressure that is applied to it. As one watches the membrane where the oval window begins vibrating there appears to be a traveling wave: First it bulges at the end by the oval window, then the bulge gradually travels up the membrane toward the apex. It takes several milliseconds for the bulge to go from one end of the basilar membrane to the other. The distance it travels depends upon the frequency of the sound wave. The height of the wave is directly proportional to the amplitude of the sound: as the sound level increases there is a corresponding increase in the height of the traveling wave.

FIGURE 4-9



The traveling bulge results from the elastic properties of the membrane. Remember that the membrane increases in width as it goes from the oval window toward the apex and decreases in stiffness, being some 100 times stiffer at the oval window end than at the apex. These factors, combined with the geometry of the cochlea itself, cause the size of the bulge produced by a sound wave to increase gradually as the wave moves out from the oval window. The point along the membrane at which it reaches its maximum size depends on the frequency of the sound. The displacement then drops off rapidly as the wave continues on to the end of the membrane. For high-frequency tones, the maximum displacement of the basilar membrane occurs near the oval window, and there is very little activity in the remainder of the membrane. For low-frequency tones, the bulge travels all the way to the apex, reaching its peak just before the end of the membrane.

Figures 4-11 & 4-12

The vibration pattern converts different sound frequencies into activity at different locations along the basilar membrane. This recoding of the frequency of an acoustic signal into a particular place of vibration along the basilar membrane is what is meant by the statement earlier in the chapter, "The ear appears to perform a rough Fourier analysis of the incoming signal."

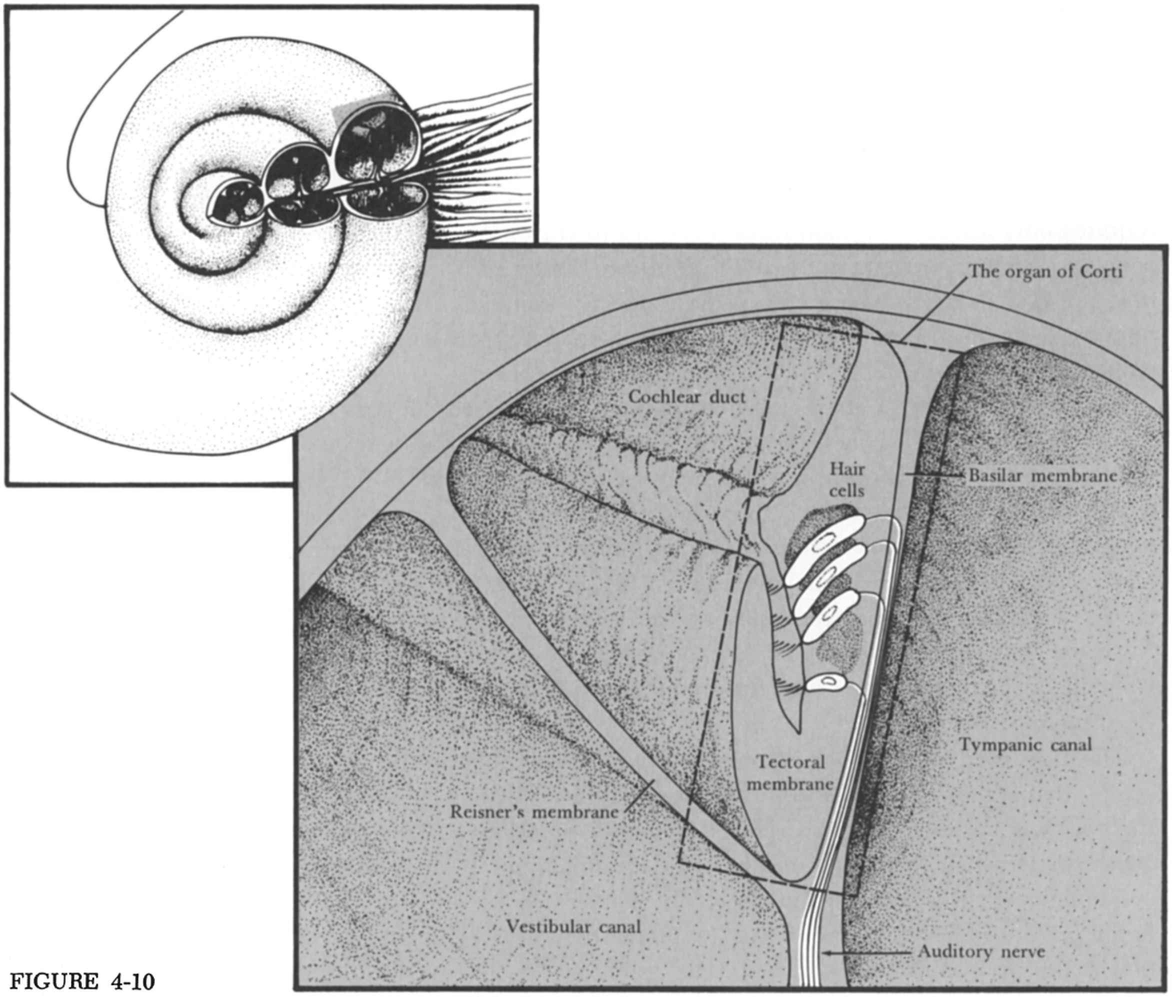


FIGURE 4-10

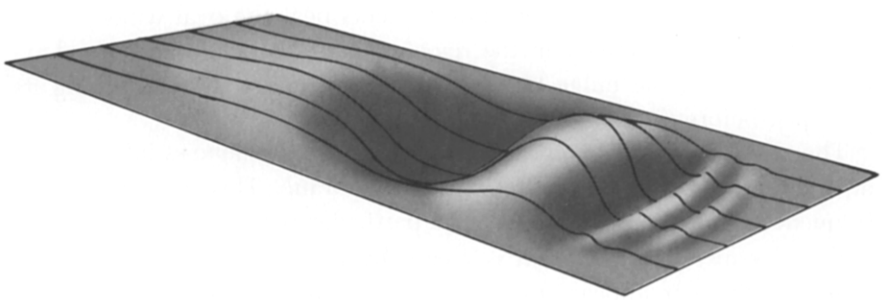
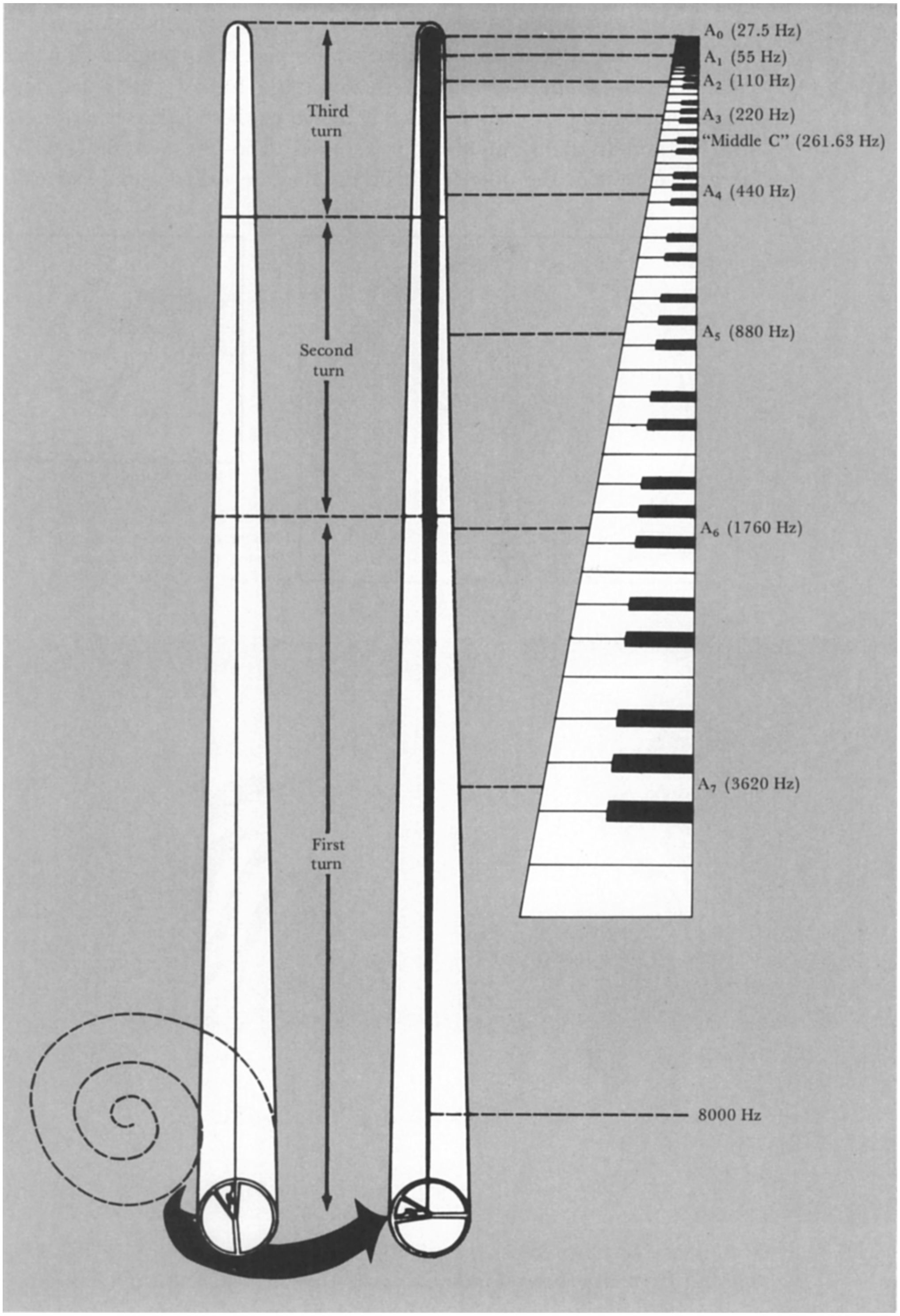


FIGURE 4-11 *After G. L. Rasmussen and W. F. Windle (Eds.),* Neural mechanisms of the auditory and vestibular systems, *1960. Courtesy of Charles C Thomas, Publisher, Springfield, Illinois.*



Third turn
Second turn
First turn
A_0 (27.5 Hz)
A_1 (55 Hz)
A_2 (110 Hz)
A_3 (220 Hz)
"Middle C" (261.63 Hz)
A_4 (440 Hz)
A_5 (880 Hz)
A_6 (1760 Hz)
A_7 (3620 Hz)
8000 Hz

FIGURE 4-12

The hair cells

Figure 4-13

The basilar membrane is really a piece of skin and, like skin, it has hair cells attached to it. These hair cells are part of a complex structure called the *organ of Corti,* located along the top of the membrane. In the human, there are approximately 23,500 of these hair cells arranged into two subdivisions, divided by an arch. The cells on the side of the arch closest to the outside of the cochlea are called *outer hair cells*

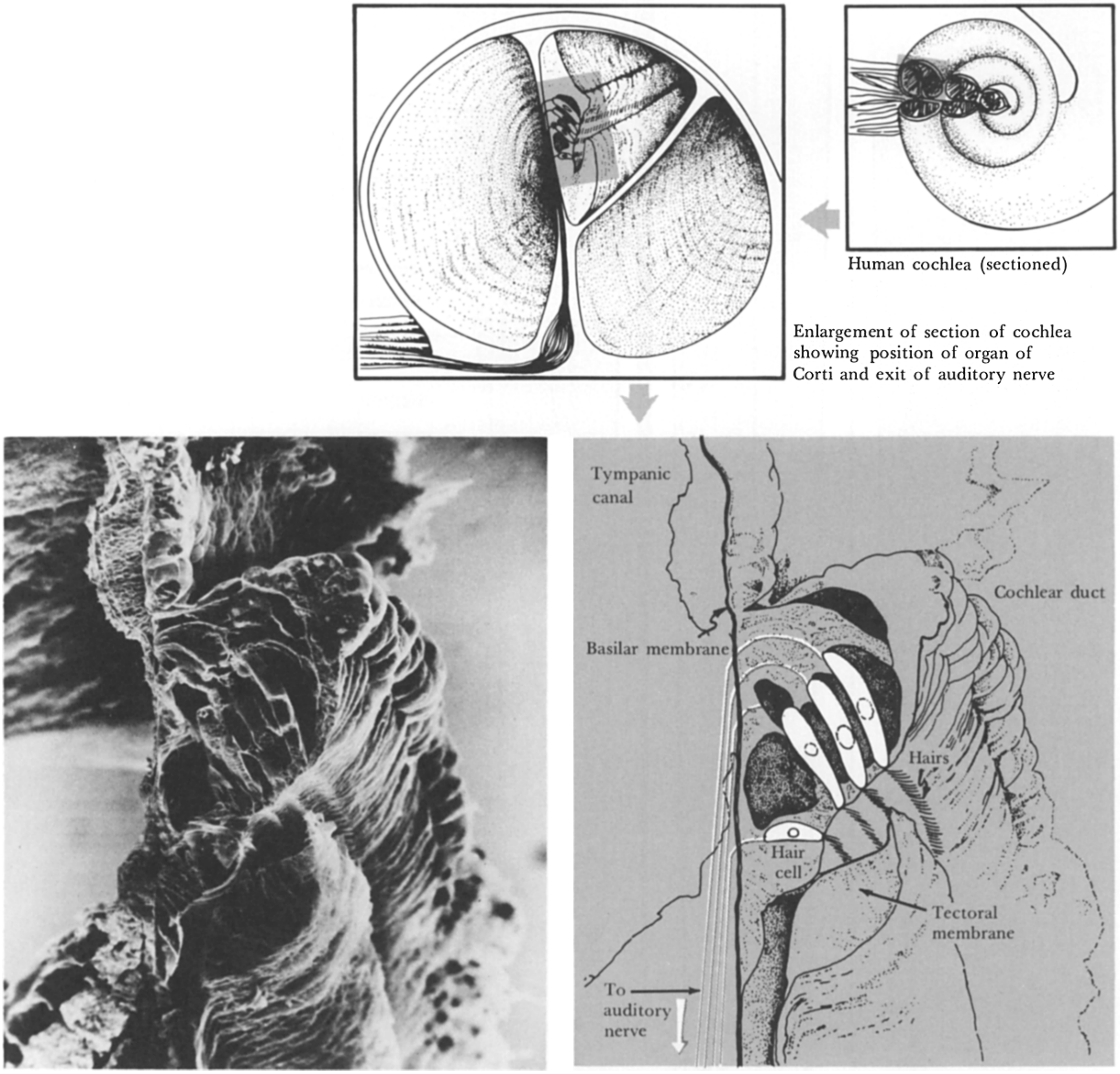


FIGURE 4-13 *Scanning electron microscope photograph of organ of Corti. ×370. Photograph from Bredberg, Lindeman, Ades, West, and Engström (1970).*

and are arranged in rows three to five abreast. The hair cells on the other side of the arch are called *inner hair cells*. They are usually in a single row. There are some 20,000 outer cells, and any given cell may have as many as a hundred hairs protruding from it. There are only about 3500 inner hair cells. There are around 30,000 nerve fibers that connect these hair cells to the brain.

As you can see from the way they are sandwiched between the two membranes in the organ of Corti, any movement in the basilar membrane causes the hair cells to twist and bend. Moreover, since the membranes are anchored, there will be more movement associated with the outer hair cells than with the inner cells. The stresses and strains exerted on the hair cells initiates neural activity in the fibers connected to them, starting the flow of electrical impulses up the auditory nerve.

ELECTRICAL RESPONSES TO SOUND

No matter how elegant the mechanical responses of the ear, they would be of no value unless there were some way of converting this activity into signals that can be used by the nervous system. The mechanical responses convert auditory frequency and intensity into vibration patterns along the basilar membrane. This information must now be analyzed by the nerve cells, which carry the signal along the pathway to the brain.

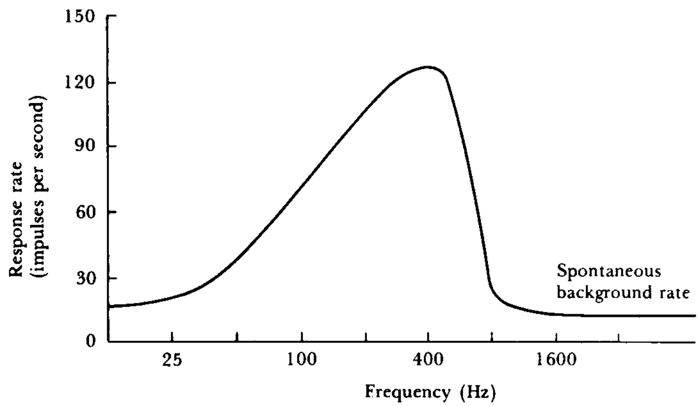
In a later chapter (Chapter 6) we examine the physiological mechanisms of the brain in some detail. For the present purposes, it is only necessary to know that the various parts of the nervous system are interconnected by neurons, the cells that form the basic building block of the brain. For the moment, simply consider the neuron to be a cell that has two parts: a cell body and a nerve fiber. The fiber carries information from one neuron to another, and it can range in length from microscopic dimensions up to several feet. Nerve fibers can be thought of as wires that carry the basic signals of the nervous system from one location to another. The signals conveyed by neurons are electrical impulses that last around a millisecond in duration and have an amplitude of a few microvolts.

Tuning curves

With a careful surgical preparation, a tiny electrode can be inserted into the auditory nerve so that it records the impulses flowing down a single auditory fiber. The first thing that is noticed is that this fiber is not quiet. Even when no sounds are presented it responds sporadically at anywhere up to 150 impulses per second. This *background* or *spontaneous* firing in the absence of any external signal is a characteristic of almost all types of sensory neurons.

The first step in investigating the neuron is to determine what kind of signal makes it respond. We start by presenting a pure tone of moderate intensity and some high frequency, say 10,000 Hz, and then we slowly lower the frequency. At first, the neuron does not seem to notice the tone at all; it continues firing at its spontaneous rate. As the frequency comes within a certain critical range, the neuron's response will increase, reaching a peak at a particular signal frequency called the *critical frequency.* As we continue to lower the frequency, the activity of the neuron again becomes less vigorous, until it finally goes back to its spontaneous background rate. The response of the unit to different frequencies is called a *tuning curve*. It looks like this:

FIGURE 4-14



This particular unit appears to be most sensitive to a tone whose frequency is 400 Hz. For frequencies higher than 400 Hz, its response rate drops off rather rapidly. For lower frequencies, the response rate changes more slowly with changing frequencies.

This is the response pattern we expect if the neuron being monitored is reacting directly to the amount of activity in a local region of the basilar membrane. Suppose that the neuron is recording the responses of hair cells in a region about 24 mm from the oval window. The maximum vibration of the membrane occurs at this point when a 400-Hz tone is presented. But there will be some activity at this point when frequencies other than 400 Hz are presented. Here is a diagram of the amplitude of the vibration for frequencies ranging from 25 to 1600 Hz. On the right, the amplitude on the membrane is shown as a function of frequency.

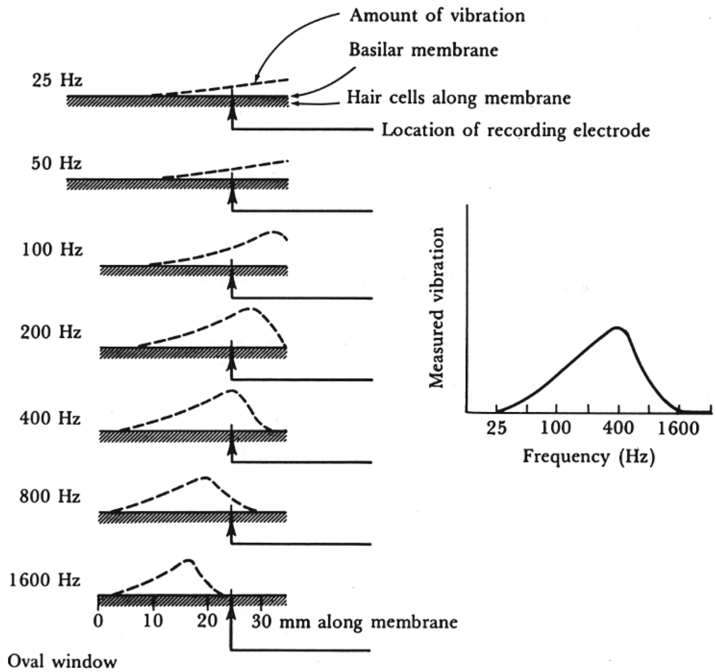


FIGURE 4-15

Temporal coding in neural responses

So far, we have been concerned only with the number of neural impulses produced by a given signal. The temporal patterns in the activity of individual neurons are also important. Consider a neural cell with a critical frequency of 500 Hz. This signal goes through a complete cycle of sound pressures in 2 msec. The impulses from the cell mirror the time properties of the critical frequency: The interval between pulses is approximately 2 msec: The cell fires in synchrony with its signal. Sometimes a pulse will fail to appear at the right time, but when it does reappear, it will again be in synchrony with the repeated cycles of the external signal. In short, a 500-Hz tone tends to produce a regular response of 500 impulses per second.

Even if the cell cannot fire as rapidly as its critical frequency, it still maintains synchrony. Suppose a cell with critical frequency of 500 Hz can only manage a maximum of 250 or 125 impulses per second. It will respond at some frequency that is a rational divisor of the signal frequency, say at 250, 125, or even 67.5 impulses per second. It will not respond to a 500-Hz tone at 73 or 187 impulses per second.

This synchronized firing might be expected from a consideration of the vibration pattern of the basilar membrane. When the membrane is moving up in response to a pressure change, it bends the hair cells sandwiched between it and the membrane above, initiating the neural impulse. No response occurs when the membrane moves down. Upward movement is produced when the pressure in the fluids above the membrane is reduced, which happens as the oval window is pulled out by the low-pressure (rarefaction) phase of the signals.

The ability of individual neurons to follow the pressure changes of an incoming signal suggests a way of coding frequency. Signal frequency can be determined directly from the impulse rate or from the average interval between pulses. The fact that individual fibers may not be able to keep up with the pressure changes in a given signal (particularly at higher frequencies) is no problem. A large number of fibers are involved in monitoring any given region of the basilar membrane. An individual nerve may miss a few cycles, but its neighbors that are responding to the same frequency will probably respond to these missing components. When the responses of all the units are considered together, there should be a burst of impulses for every rarefaction phase of the signal.

This is precisely what is seen in physiological recordings. The activity rises and falls regularly and in synchrony with the pressure changes in the signal. The auditory nerve seems to be able to follow signals with frequencies as high as 3000–4000 Hz; such frequencies are well above the response rate that can be achieved by any individual unit. Beyond 4000 Hz, the regular cyclic response in the auditory nerve breaks down into a disorganized, continuous impulse flow.

Figure 4-16

Coding of intensity information

Responses of neurons in the acoustic nerve to changing intensities are much less complex than their response patterns to changing frequency. Basically, if the frequency is held constant while intensity increases, the response rate of the units goes up. Of course, it cannot go up indefinitely. In fact, an individual cell may start off at a spontaneous level of some 200 responses per second, increase its rate to, say, 300 responses per second when the intensity is changed by 10 dB, but show no further increases in rate with additional increases in intensity. Thus, the range over which most cells code intensity in the signal is relatively small compared to the total range of hearing. Moreover, there is an enormous variability in both the baseline rates and the reactions of individual cells to increases in the intensity of the signal.

Of course, a cell's increase in its firing rate must still maintain synchrony with the sound wave. Thus, if an individual cell has a spontaneous firing rate of 200 impulses per second, it will react to a sound first by changing the spontaneous, random firing into one synchronized

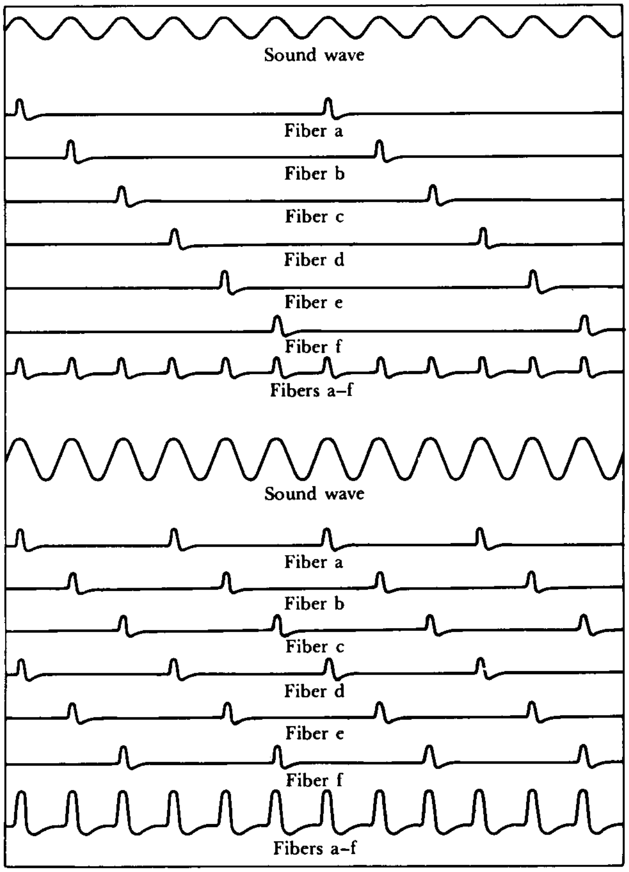


FIGURE 4-16 *The "volley" theory. Each cycle of the sound wave elicits a response in at least one fiber in the array, so that the stimulus frequency is represented in the combined pattern. At higher stimulus intensities (below), more than one fiber responds at a given cycle. From Wever (1970).*

with the signal, and then by increasing the number of neural impulses it produces to the sound—always, however, maintaining synchrony.

When the basic frequency and intensity information has been encoded by the auditory nerves, the signal is finally on its way to the brain. Several different things are done as the signal makes its way up. Specific auditory information is extracted, localization of the sound source takes place, and a rough determination of the sound's loudness and pitch components are extracted. A discussion of the physiological structures and neural responses of the auditory system can be found in Chapter 6, "Neural Information Processing."

REVIEW OF TERMS AND CONCEPTS

In this chapter, the following terms and concepts that we consider to be important have been used. Please look them over. If you are not able to give a short explanation of any of them, you should go back and review the appropriate sections of the chapter.

Terms and concepts you should know

The parts of the ear
- the outer ear
  - pinna
- the middle ear
  - malleus (the hammer)
  - incus (the anvil)
  - stapes (the stirrup)
  - eardrum
- the inner ear
  - cochlea
  - oval window
  - round window
  - basilar membrane
  - apex
  - how the cochlea is unwound
- the basilar membrane
  - the traveling wave: what it looks like
  - hair cells
  - tuning curves
  - critical frequency
  - how frequency is represented along the membrane
  - synchronization of neural impulses with the sound wave

Sound
- sound waves
- amplitude
- frequency
- decibels
- hertz
- Fourier analysis

SUGGESTED READINGS

The two volumes of *Foundations of modern auditory theory* provide a good summary of much work (Tobias, 1970, 1972). Dallos (1973) provides a good description of the auditory periphery (which is also the title of his book). And Carterette and Friedman's (1976) *Handbook* volume on *Hearing* is probably the best place to start for more advanced treatments.

The works of Georg von Békésy won him a Nobel Prize for his studies of the operation of the inner ear. Anyone who intends to do work in the field of hearing will sooner or later come upon his material. Most of his important articles on hearing are reprinted in Békésy's *Experiments in hearing* (1960). Békésy's papers are delightful to read because he never sticks to a simple topic, but rather delights in demonstrating how the topic he is discussing relates to a wide variety of other phenomena.

The major readings for this chapter are listed at the end of the next; see the Suggested Readings for Chapter 5.