Chapter 11
The Auditory System

This chapter begins a new aspect of the science of acoustics, the study of the human listener. We continue to proceed in an analytical way by studying the physiology of hearing. The physiology begins with anatomy—the science of where things are in the body, what they look like, how they are connected, and how these facts give clues about physiological function.

Overall, the auditory system consists of peripheral elements and central elements. The peripheral elements are near the skull and comprise what is commonly called "the ear." The central elements are located in the brain—the brainstem, midbrain, and cortex. The peripheral part of the auditory system is shown in Fig.11.1—a complicated figure.

11.1 Auditory Anatomy

The anatomy of the peripheral auditory system has three main divisions: (1) outer ear, (2) middle ear, and (3) inner ear, as shown in Fig. 11.2. Figure 11.2 is a simplified version of Fig. 11.1. Please try to identify the parts of Fig. 11.1 that belong to the divisions shown in Fig. 11.2.

11.1.1 The Outer Ear

The outer ear is the part that you can see. It consists of the *pinna* and the ear canal. The pinna is the fleshy, horn-like protuberance from the side of the head—often used for hanging decorations. The ear canal (*external auditory meatus*) is a duct, about 2.5 cm long, running from the pinna to the eardrum. It sometimes accumulates ear wax. The eardrum, or *tympanic membrane*, is the end of the outer ear; it is the beginning of the middle ear.

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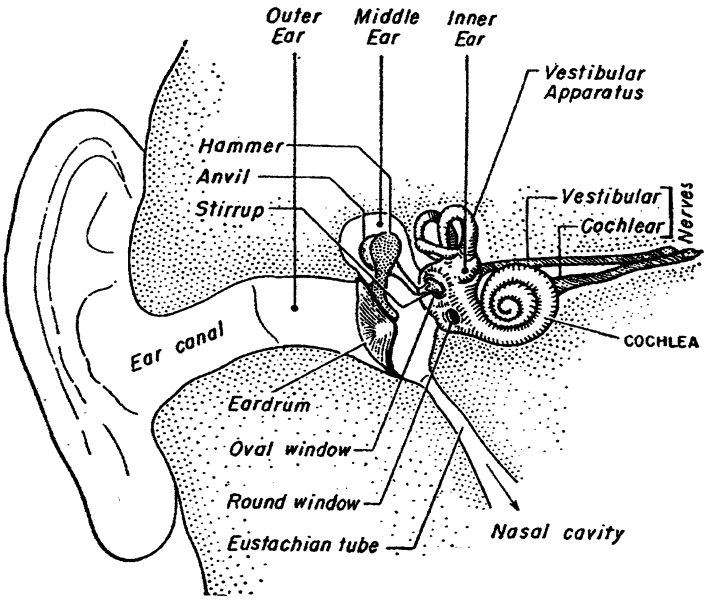


Fig. 11.1 The entire peripheral auditory system, plus the semicircular canals

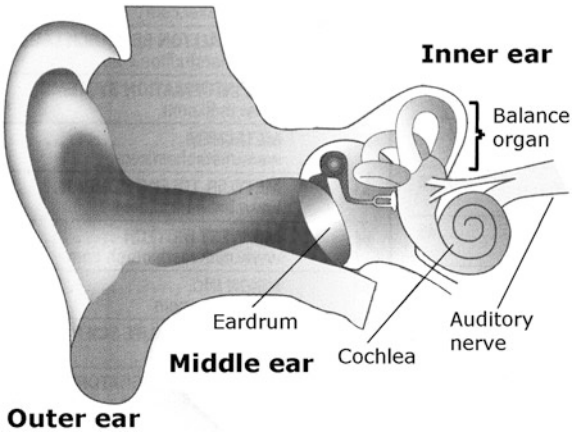


Fig. 11.2 A simpler figure of the outer, middle, and inner ear

11.1.2 The Middle Ear

The middle ear consists of three bones and several muscles in a small cavity in the temporal bone. The bones act as a lever that conducts sound vibrations from the eardrum to the *oval window*. The oval window is the point of contact with the inner ear. The three bones are called *ossicles*, meaning "little bones." They are appropriately named because they are the smallest bones in the body. From the eardrum to the oval window, the bones are, in order, the *malleus*, the *incus*, and the *stapes*—translated: the hammer, the anvil, and the stirrup.

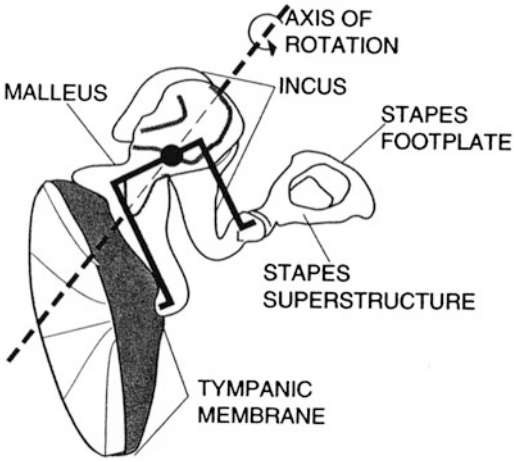


Fig. 11.3 The middle ear has three bones, hammer, anvil, stirrup, connecting the eardrum (tympanic membrane) to the oval window. The stirrup (stapes) pushes on the oval window

The middle ear cavity is normally filled with air, but it is sealed off at one end by the eardrum and at the other by the oval window and round window. When the outside pressure changes (perhaps because you are going up in an airplane), there would be painful pressure on the eardrum if it were not for the *eustachian tube* that connects the middle ear cavity to the nasal cavities, which, in turn, are open to the outside air. The eustachian tube allows the pressure in the middle cavity to become equal to the atmospheric pressure outside. This is a good thing. However, infections, such as a common cold, that affect the nasal cavities can make their way up to the middle ear cavity. This is a bad thing. Infants are particularly susceptible to middle ear infections. When an infection does reach the middle ear, it causes the eardrum to be inflamed. Because the eardrum is translucent, it is possible to see this inflammation by looking down the ear canal with an otoscope. That is what the physician is looking for when he or she inspects your ear canals.

The last bone in the chain, the stapes, presses on the oval window and transmits vibrations to the inner ear (Fig. 11.3).

11.1.3 The Inner Ear

The inner ear is where the real action takes place. It is possible to hear without an outer ear. It is possible to hear without a middle ear. But it is not possible to hear without an inner ear. The inner ear is responsible for converting acoustical signals into signals that the brain can understand.

The inner ear is a cavity in the skull's temporal bone called the "cochlea." It is curled up into a snail shape and divided into three canals by two membranes as shown by the cross section in Fig. 11.4. The canals are filled with fluid, not unlike sea water. The main membrane is the *basilar membrane*. The other membrane is *Reissner's membrane*, and it is so light as to be unimportant mechanically. It does

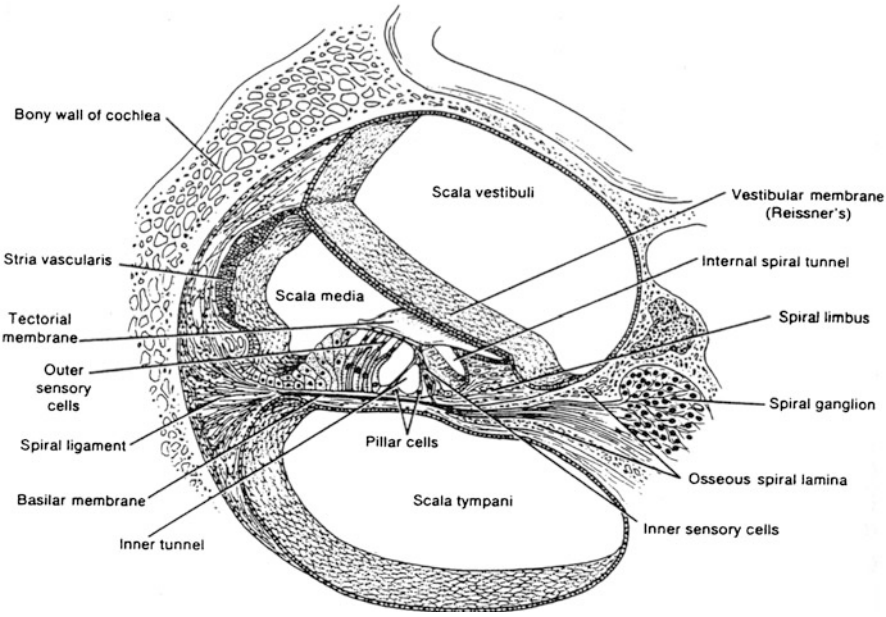


Fig. 11.4 A cross section of the cochlea showing the three canals

not affect the way the fluids move in the cochlea. But Reissner's membrane *is* important electrically. It separates the ions in the canal called "scala media" from the ions in the *scala vestibuli.* The differences in ionic concentration provide the energy source for the action of the hair cells. The ionic differences serve as the ear's battery—a source of electrical energy.

A pressure pulse from the oval window travels down the duct made from scala vestibuli and scala media to the end of the snail shell cavity where there is a small opening called the "helicotrema." There the pulse can turn around and come back on the other side of the basilar membrane through the scala tympani. At the end of the scala tympani is the *round window*, another membrane that acts as a pressure relief mechanism. The response to a pressure pulse at the oval window is shown in Fig. 11.5 by dashed lines.

Motion of the fluids in the canals causes the basilar membrane to move. On the basilar membrane is the *Organ of Corti* (Fig. 11.6), which is filled with hair cells that play a most vital role in hearing. The hair cells are transducers that convert mechanical motion into neural impulses. The neural impulses are electrical spikes that are essentially the language of the brain.

Communication within the nervous system is by means of such electrical *spikes*. Impulses from the hair cells travel along the *auditory nerve* to higher centers. The auditory nerve is sometimes called the "eighth (VIII-th) cranial nerve," or "cochlear nerve."

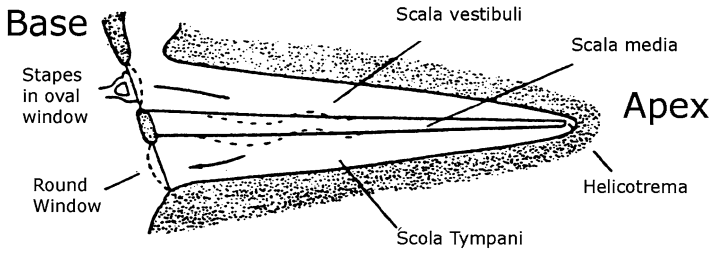


Fig. 11.5 A lengthwise X-ray cartoon of the inside of the cochlea as though it were uncoiled. What you see here is actually coiled up two and a half turns in the human head. The *dashed lines* show the response to a positive pressure pulse

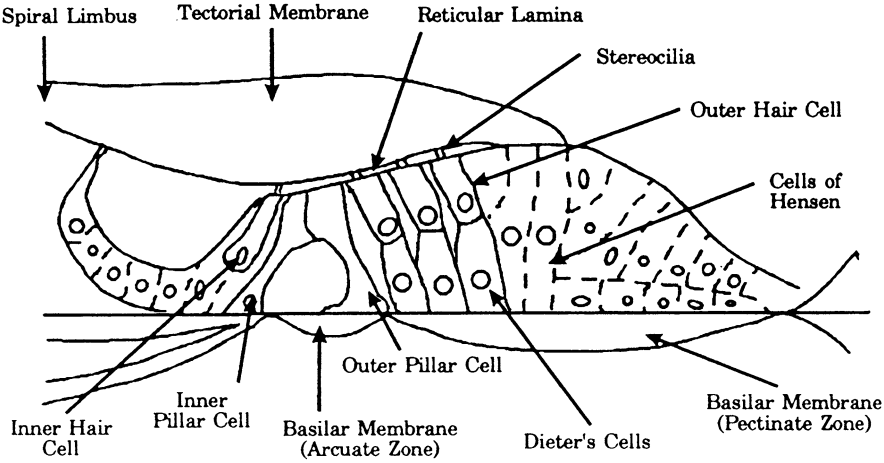


Fig. 11.6 The organ of Corti, sitting on the basilar membrane

11.1.4 The Semicircular Canals

The *semicircular canals* are contiguous with the cochlea and share the same fluids. However, they have nothing to do with hearing. They are the origin of our sense of balance (*vestibular system*). In fact, the semicircular canals work rather like the cochlea in that motion of fluids result in neural spikes that are sent to higher centers of the nervous system. However, the mechanism of the semicircular canals is sensitive only to the low frequencies of whole head motion, mostly below 10 Hz. The cochlea is sensitive to the high frequencies of the auditory world, 20–20,000 Hz.

The neural messages from the semicircular canals also travel on the VIII-th nerve. Diseases, such as Meniere's disease, that affect the vestibular system also affect the auditory system. Sometimes the cochlea and semicircular canals are jointly referred to as the "inner ear," but only the cochlea merits further study as part of the hearing system.

11.2 Auditory Function

Knowing the auditory anatomy gives you strong clues about the functions of the divisions of the auditory periphery.

11.2.1 Outer Ear Function

The pinna gathers sound and directs it into the ear canal. Its peculiar shape gives it an uneven frequency response. It captures some frequencies better than others, though this unevenness only has a big effect on high frequencies above 5 kHz. Furthermore, the frequency response depends on the direction that the sound is coming from. That is not the sort of behavior one would expect from a high-fidelity sound transmitting system. That would seem to be a bad thing. However, we humans have learned to use the asymmetry of this frequency response to help us localize the sources of sound, and so it turns out to be a good thing in the end.

The ear canal is about 2.5 cm long and it looks like a tube that is open at one end and closed at the other. It is closed by the ear drum. An exercise at the end of the chapter will ask you to show that such a tube has a resonance at about 3,400 Hz. Because of this resonance one might expect that the auditory system is most sensitive to frequencies between 3,000 and 4,000 Hz. This is actually true, as will be seen in Chap. 12 on loudness.

11.2.2 Middle Ear Function

Sound waves in the *ear canal* are pressure waves in the air inside that canal. Sound waves in the *inner ear* are pressure waves in the fluids of the cochlea—similar to seawater. The function of the middle ear is to form an efficient coupling of the waves in the air to the fluids. If it were not for the bones of the middle ear, most of the waves in the air of the ear canal would be reflected from the denser fluids of the cochlea, and little of the sound energy would be coupled into the motion of the fluids. In fact, the mismatch between the air and fluids is so bad that only 1 % of the sound energy would be transmitted from the outer ear into the inner ear. The middle ear solves that problem.

At the same time, the middle ear can reduce the efficiency of the coupling between outer and middle ear by using two muscles, the *stapedius muscle* and the *tensor tympani.* These muscles contract to make the coupling less efficient in the presence of loud sounds. This serves as a form of automatic volume control to protect the delicate inner ear. Unfortunately this is a system that is incompletely evolved and is rather slow in its action. It is too slow to react to impulsive sounds like

the banging of a hammer, the explosion of gunfire, or the beat of a drum. However, it works well on sustained amplified guitar.

The muscles also contract to make the middle ear coupling less efficient when you begin to vocalize. This defends your inner ear against your own voice.

11.2.3 Inner Ear Function

As described above, the function of the inner ear, or cochlea, is to convert sound vibrations into neural impulses that the brain can understand. The action of the cochlea is one of the most fascinating stories in physiology. The cochlea is an incredibly sensitive mechanical system that gains sensitivity and sharp frequency tuning from internal electromechanical feedback. It appears that the feedback coupling can also be modulated by higher centers of the system. The cochlea is responsible for encoding signals sent to the brain, and this encoding is done in two very different ways.

Place Encoding The basilar membrane is caused to vibrate by the vibrations of the fluids in the cochlea. The basilar membrane is heavier near the apex than at the base and it vibrates maximally at different places for tones of different frequency.

A high-frequency sine tone causes vibration of the membrane near the base. (Note where the base is in Fig. 11.5.) There is little vibration anywhere else. As a result, the hair cells near the base are caused to fire, and hair cells elsewhere on the membrane are silent. This specific activity of the hair cells near the base provides a way to encode the fact that the frequency is high. The information about the *location* of active hair cells is transmitted to the brain because each hair cell is connected to higher auditory centers by about ten nerve fibers in the auditory nerve that are dedicated to that hair cell. Therefore, the brain can recognize the frequency of a tone just by knowing which hair cells are active and which are inactive.

A low-frequency sine tone causes vibration of much of the basilar membrane, but the maximum vibration occurs near the apex. The brain can recognize a low-frequency tone because hair cells near the apex are the most active. Thus, every location on the basilar membrane is best excited by a particular frequency; this is called the "characteristic frequency" of the location. A plot showing the characteristic frequency of a place on the basilar membrane for each location is given in Fig. 11.7.

The pattern of vibration is not symmetrical on the basilar membrane. The peak of the pattern is given by Fig. 11.7, but the pattern decreases abruptly on the apex side and decreases slowly on the base side when the tone has a moderate or high level. Figure 11.8 shows the responses of the basilar membrane to two separate tones with different frequencies.

For a complex tone with many frequencies, the low-frequency components cause activity in hair cells near the apex and the high-frequency components cause activity

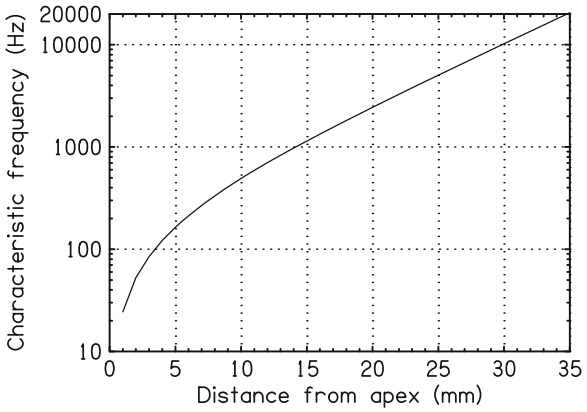


Fig. 11.7 Frequency map of the basilar membrane according to the Greenwood equation (see Exercise 8). The *horizontal axis* shows the location of the peak of the vibration pattern for a sine tone whose frequency is given on the *vertical axis*

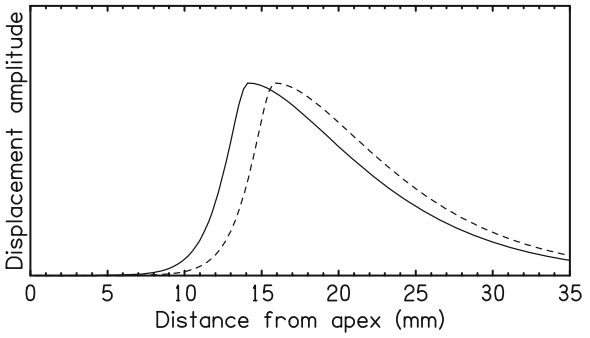


Fig. 11.8 A cartoon showing the vibration amplitude of the basilar membrane for two separate tones. A 1,000-Hz tone leads to a vibrational peak at 14.1 mm, and a 1,300-Hz tone leads to a peak at 15.8 mm. The patterns extend more toward the base (high-frequency side) than to the apex

in hair cells near the base. Thus, the basilar membrane performs a spectral analysis (Fourier analysis) of the incoming wave. Different neurons transmit the signals from the various sine components. The analysis by frequency that begins in the cochlea is maintained at higher levels of the auditory system.

Timing Encoding A hair cell encodes information about the frequency of a tone in yet another way, by synchronizing the pulses it generates with the tone itself. When a hair cell is excited by a tone it fires more frequently, but the spikes are not generated at random times. Instead, the hair cell tends to produce a spike at a particular phase of the sine waveform as shown in Fig. 11.9. As a result, the firing tends to preserve the period of the waveform. The time between successive spikes might be equal to a period, or two periods, or three, or four, ... Therefore, frequency information is passed to the brain by means of the regular firing of the neurons. In order to transmit information in this way the neurons must be able to synchronize to the signal. The nervous system cannot keep up with a signal having a frequency greater than 5,000 Hz, but it can faithfully follow a signal with a frequency of 2,000 Hz and below. More about time encoding and neural synchrony appears in Chap. 13 on pitch perception.

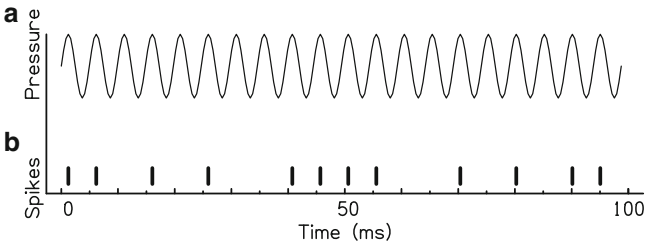


Fig. 11.9 Part **a** shows the pressure in the cochlear ducts caused by a 200-Hz sine tone. Part **b** shows the electrical spikes recorded from an auditory nerve that is tuned to a frequency near the sine tone frequency. The spikes occur on peaks of the pressure waveform, though not on every peak. In this way, the spikes are synchronized with the sine tone

How Do We Know About the Cochlea? For all its complexity, the cochlea is extremely small. It is deeply embedded in the hardest bone in the body and is also very delicate. Perhaps you are wondering how anyone could learn about the action of the cochlea, about the place encoding and timing encoding, in view of the difficulties of studying it. For instance, how could one do experiments on the cochlea without seriously affecting its action? How does one know that the experiments show the real action? Questions like these frequently arise in many different sciences. Fortunately, in the case of the cochlea there is a multi-pronged approach that has been successful.

First are experiments that open the cochlea. The opening allows the experimenter to view the basilar membrane with a high powered microscope, or to insert electrical or optical probes, or to place radioactive particles on the membrane to measure velocity [footnote 1]. These experiments can demonstrate the tuning of the cochlea, from base to apex as described above, but obviously one must be concerned about damage to the cochlea that affects the very process that one is trying to measure.

Second are experiments that allow an experimenter to infer the action of the cochlea without actually opening the cochlea to see it directly. The key to these experiments lies in the fact that individual nerve fibers in the auditory nerve are connected to particular hair cells on the basilar membrane. It is possible to insert an electrical probe into the auditory nerve and pick up the firing of a *particular* nerve, connected to a particular place on the basilar membrane. That kind of experiment demonstrates the sharp frequency tuning of the cochlea. It also shows the synchrony between the neural spikes and the signal that is presented. Experiments probing the auditory nerve also give evidence of the active feedback mechanism that is responsible for the high sensitivity and sharp tuning of the cochlea. Because the feedback process is active, it requires oxygen from the blood. Depriving an experimental animal of oxygen while monitoring the tuning and sensitivity via the auditory nerves shows that the tuning becomes much broader and the system becomes less sensitive. The cochlea seems to be acting much like the cochlea of a person whose hair cells have been damaged by a drug. Restoring normal oxygen brings back the normal tuning and sensitivity.

Third are experiments that measure cochlear emissions. Because the cochlea is electromechanically active it actually generates acoustical signals of its own. These signals propagate back along the basilar membrane, back through the middle ear, and back into the ear canal where they can be measured by microphones placed in the canal. The signals that return from the cochlea in this way are delayed compared to sounds that excite the cochlea into action. The delay makes it possible to recognize the emissions and to study them. While the open-cochlea and auditory-nerve experiments can only be done on animals, the experiments that measure otoacoustic emissions can be done on human beings. They are even part of infant screening tests.

11.2.4 Beyond the Cochlea

The hair cells on the basilar membrane in the cochlea convert sound waves into neural impulses, or electrical spikes. Higher stages of the auditory system process these impulses. The auditory nerve transmits impulses from the hair cells to a collection of neural cells called the cochlear nucleus. The cochlear nucleus is in the brainstem, part of the brain just above your neck. After the cochlear nucleus comes half a dozen stages of neural processing which include millions of neurons and an elaborate cross-linking between left- and right-hand sides. The processing proceeds by excitation, where a spike in one neuron causes a spike in another, and by inhibition where a spike on one neuron inhibits spike generation by another. The auditory pathway ascends through the processing stages to the auditory cortex, located near your left and right temples. In addition to the ascending pathway are descending pathways by which the higher auditory centers send neural messages to lower stages, even into the cochlea! The descending pathways are a form of feedback by which the processing of lower centers is controlled by the higher. The complexity of the auditory nervous system has kept psychoacousticians and auditory physiologists busy for years. They are still hard at work. One aspect of the system that seems clear is that frequency tuning, originally established by the basilar membrane is retained throughout the higher stages. At every stage, it is possible to locate a 1,000-Hz place, differently located from, say, a 200-Hz place.

11.2.5 Hearing Impairments

Ringing in the Ears Ringing in the ears is an everyday name for *subjective tinnitus,* a sound that you hear that does not have an external physical origin. Many people have the experience that while doing nothing in particular, they suddenly hear a high-pitched ping. Often it is lateralized to one side of the other. This sound lasts a

few seconds and then goes away. Such experiences are minor curiosities and so far as one knows they have no particular implications for the health of the ear or brain. Unfortunately, there are many people for whom the sound does not go away. It is a persistent tone, or buzzing, or hissing sound—usually tonal, meaning that it has a pitch. For such people, and they are perhaps as much as 20 % of the population, tinnitus can become a serious disturbance, significantly reducing the quality of life.

Tinnitus is so common that you might expect it to have a simple explanation. Surprisingly, there is no simple single explanation. Tinnitus can originate in the external ear, with an accumulation of ear wax, or in the middle ear with infection or otosclerosis, wherein a bony mass grows within the middle ear cavity and impedes the motion of the stapes. It can originate in the inner ear, especially in connection with hair cell loss caused by an acoustical trauma such as a nearby explosion. It can apparently originate in the auditory nerve, especially in the case of an acoustic neuroma, a slow-growing tumor that presses on the nerve. It may originate in the brain.

Tinnitus can be caused by common drugs, aspirin or non-steroidal anti-inflammatory drugs such as ibuprofen, or by aminoglycocides, potentially highly ototoxic antibiotics used to treat systemic bacteriological infections. Drug-induced tinnitus often ceases when the drug regimen is changed.

In some cases, tinnitus can be a warning of other disorders such as anemia, an aneurysm, or a tumor, but most of the time it seems that tinnitus has no other health implication beyond the annoyance of the tinnitus itself. There is no recognized cure for the problem. People who suffer from tinnitus are encouraged to avoid loud noises, which may aggravate the problem. Paradoxically many sufferers gain relief from masking noise, either from a loudspeaker or from a hearing aid. For most tinnitus patients, masking noise that is 14 dB above threshold is adequate to obscure the tinnitus. In some cases, masking noise may even provide relief for minutes, hours, or days after it is turned off. Programs that use biofeedback or relaxation techniques have proved helpful to some. For some individuals nothing helps, and they are required to learn to live with the problem. In summary, although tinnitus would seem to be a simple and common phenomenon, it turns out to be surprisingly complicated.

Hearing Loss and Hearing Aids Hearing loss can be classified as one of two types: conductive loss or sensorineural loss. Conductive loss occurs when the normal acoustical path to the inner ear is blocked in some way. An accumulation of ear wax can block the ear canal. Otosclerosis can prevent normal conduction of sound by the ossicles. Conductive loss can often be cured surgically. If not, conductive loss responds well to hearing aids because hearing aids essentially solve the problem of conductive loss, namely insufficient acoustical intensity arriving at the inner ear. A hearing aid consists of a microphone to pick up the sounds, an amplifier which requires battery power, and a tiny loudspeaker that fits in the ear canal. The amplifier may include filtering and other signal processing to try to tailor the hearing aid to the individual patient.

Sensorineural loss is usually a deficit in the inner ear. Normal hair cells are essential for normal hearing. Unfortunately, hair cells are vulnerable to ageing, to intense noises, to ototoxic drugs, and to congenital abnormalities. The classic case of impaired hearing results from poorly functioning hair cells. Because the hair cells are responsible for sensitivity, tuning, and timing, people who are hearing impaired may have deficits in some or all of these functions.

There is a tendency to think about hearing aids as analogous to eyeglasses, and for people with conductive hearing loss the analogy is not bad. But for the large number of people with sensorineural loss the analogy is not accurate. For the great majority of visually impaired individuals, eyeglasses (or contact lenses) solve the problem. The optical defects of an eyeball that does not have exactly the correct shape are readily compensated by passing the light through corrective lenses—end of story. Hearing impaired individuals do not normally gain the same kind of benefit from hearing aids. Hearing impairments, resulting from poor hair cell function, are as complicated as the hair cells themselves. A better analogy with the visual system would compare abnormal hair cells in the cochlea with an abnormal retina in the eyeball.

Cochlear Implants In order to benefit from hearing aids, an impaired person needs to have some residual hair cell activity. Some people however are totally deaf with no hair cell function at all. But such people often still have functioning auditory nerves. The nerve endings come to the cochlea in the normal way, but they don't find normal hair cells there to excite them.

Thousands of people who are totally deaf because of hair cell loss have regained some auditory function by the use of cochlear implants. The implant consists of a microphone that picks up sounds like a hearing aid, but the resemblance to hearing aids stops there. Instead, an electrode is inserted in the cochlea via surgery through the middle ear's round window. The electrode excites the auditory nerve directly by an electrical representation of the wave from the microphone.

Early cochlear implants were not a great success. Although they restored some sense of hearing, they did not make it possible to understand speech. These implants had only one electrode. From the place-encoding principle, however, it is known that nerve endings near the base of the cochlea normally receive high-frequency signals and nerve endings near the apex receive low-frequency signals. A modern cochlear implant has many electrodes, as many as 24, all along its length, encoding different frequency regions. Sounds with different frequencies can be sent to the correct fibers of the auditory nerve. Thus, the implant itself performs the Fourier analysis that is normally performed by the basilar membrane. Implants like this, retaining the normal frequency analysis of the cochlea, have enabled deaf persons to understand speech, even over the telephone where they cannot gain anything from lip reading.

Cochlear implants and the encoding of information sent to the electrodes have been optimized for speech. The sounds perceived by implanted patients are very different from normal speech—they have been compared to the quacking of ducks. Nevertheless, people who learned to speak and to understand speech prior to

deafness have been able to make the transition and decipher the quacking. Initially, implants were restricted to people who were post-lingually deaf because it was reasoned that there was no point in providing degraded speech information to a patient who had never heard any normal speech in the first place.

Eventually, implants were tried on deaf children, and the results were surprisingly good. Further, it was found that the younger the child, the better the results! Now, infants are implanted, often so successfully that the child learns to speak and understand essentially like a normal hearing child. An important philosophical take-home message from that experience is that those of us who have normal hearing and perceive speech in the usual way, do so because our brains have learned to interpret the signals sent by the periphery. Marvelous though the peripheral auditory system may be, there is no need for it to encode signals in one specific way or another; the young brain can learn to cope with a wide variety of inputs from the periphery.

There are some drawbacks to cochlear implants. The present encoding strategy that has proved to be so successful in encoding speech removes timing information from the input signal and the patient receives no normal timing encoding. This has the effect of eliminating most musical pitch information. Implantees, even young ones, don't perceive music normally at all. Also, the surgery that implants electrodes wrecks whatever normal features there may be in the cochlea. If someday a drug is found that causes normal hair cells to grow and restore hearing to deaf people, implantees are unlikely to benefit. For the present, cochlear implants have given normal speech perception to individuals who would otherwise be as deaf as bricks. Implants represent a strikingly successful collaboration between medical practice and fundamental research in human hearing.

Cochlear Nucleus Implants A cochlear implant can restore hearing to individuals who have a functioning auditory nerve, but what if there is no functioning auditory nerve? The obvious answer is to put an implant into the next stage of auditory processing, the cochlear nucleus. A procedure that has recently been developed places electrodes in the cochlear nucleus. Although the concept of electrodes implanted in the brain stem may seem spooky, it's not the only bionic brain technology. Electrodes can be implanted in the thalamus to control the tremors of Parkinson's disease.

Exercises

Exercise 1, The ear canal as a pipe

(a) Given the description of the ear canal in the section on the outer ear, show that the resonant frequency of the ear canal (first mode) is about 3,400 Hz.
(b) What is the frequency of the second mode for air in the ear canal?

Exercise 2, Inside the canals

The speed of sound in cochlear fluid is about five times the speed of sound in air. If the cochlear duct is 35 mm long show that it takes a sound pulse about 40 μs to go from the oval window, down the duct, and back to the round window opening to the middle ear. However, the mechanical traveling wave on the basilar membrane is much slower. That wave takes about 10 ms to go from the base to the apex.

Exercise 3, Acoustic reflex

The action of middle ear muscles in response to a loud sound is called the "acoustic reflex." Describe loud sounds that you expect to trigger the action of the acoustic reflex.

Exercise 4, The "place" model of hearing.

(a) Use Fig. 11.7 to find where the basilar membrane most excited for a frequency of 440 Hz.
(b) Where are the hair cells that are most activated by the second harmonic of 440 Hz?

Exercise 5, In sync

If you were able to probe the firing of a neuron in the VIII-th nerve, what time intervals between spikes would you expect to see if the ear receives a 440-Hz tone?

Exercise 6, Place encoding

As human beings age, we lose the ability to hear high frequencies. This effect is attributed to the loss of hair cells. Where on the basilar membrane are these hair cells?

Exercise 7, Tone-on-tone masking

Intense tones of one frequency interfere with the perception of weaker tones of other frequencies. Given what you know about the mechanics of the basilar membrane, which to you expect to reveal more interference?

(a) An intense 1,000-Hz tone and a weak 1,300-Hz tone.
(b) An intense 1,300-Hz tone and a weak 1,000-Hz tone.

See Fig. 11.8 for a cartoon showing basilar membrane displacement for these two frequencies in the case of equal levels.

Exercise 8, The Greenwood equation.

The mapping of characteristic frequency (f_C) vs distance (z) along the basilar membrane was plotted using an equation published in 1961 by Donald Greenwood. This equation says,

$$f_C = 165\,(10^{az} - 1), \tag{11.1}$$

where distance z is measured from the apex, and constant a is 0.06 inverse millimeters. Use this equation to show that the frequencies corresponding to 5, 10, 15, 20, 25, and 30 mm places are, respectively, 164, 492, 1,146, 2,450, 5,053, and 10,246 Hz.

Exercise 9, Inverse Greenwood

(a) Invert the Greenwood equation to show that the distance along the basilar membrane as a function of characteristic frequency is given by

$$z = \frac{1}{a} \log_{10}(1 + f_C/165). \tag{11.2}$$

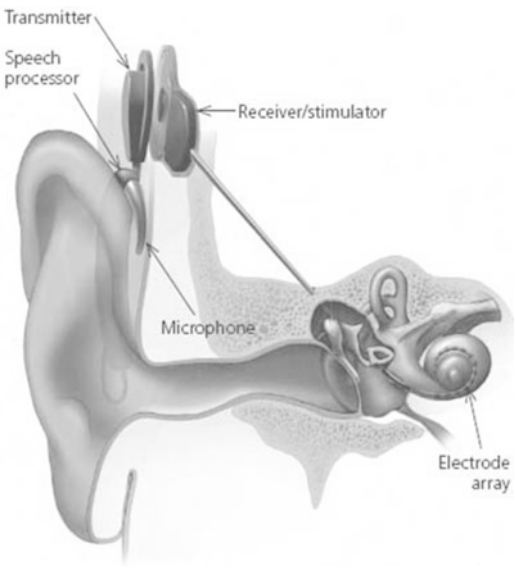
(b) Use Eq. (11.2) to work Exercise 4(a) more precisely.

Exercise 10, The cochlear nucleus implant

Cochlear implants have multiple electrodes dedicated to different frequency bands. In this way they simulate the action of the basilar membrane—analyzing sound by frequency and sending different bands along different neural channels. Would you expect that the cochlear nucleus implant would also have multiple electrodes so that multiple frequency bands can be transmitted?

Exercise 11, The cochlear implant

The insertion of a cochlear implant is shown in the figure below. (a) Where is the conversion from acoustical to electrical? (b) What parts can be seen by an outside observer? (c) How many turns of the cochlea have been implanted?



Footnote 1, Mössbauer effect: Radioactive nuclei like iron with an atomic mass of 57 units decay by emitting gamma radiation. The frequency of this radiation is amazingly precise, one part in ten billion. Because the frequency is determined so precisely, it is possible to measure small velocities of the radioactive particles by measuring the Doppler shift in the frequency of the radiation. The effect that makes this possible is known as the Mössbauer effect.