Chapter 2

Sound and Sound Signal Production

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Overview

Most humans are born into a world in which sound communication is a dominant activity. While we tend to take the mechanisms that allow vocal exchanges for granted, the production of useful sound signals presents significant hurdles, and most animals dispense with sound communication altogether. In this chapter, we outline the basic physical constraints within which we, and animals, must operate if we are to communicate with sound, and describe some of the techniques that different species use to mitigate and even take advantage of these constraints.

Properties of Sound

The media of sound communication

In contrast to the vacuum of outer space, every cubic meter of our planet is filled with matter. Matter consists of atoms that are largely bound together into molecules. When animals want to communicate with each other, their signals must pass through some type of intervening matter. We call the matter linking sender and receiver the **medium** of the communication process. Different media impose different constraints on the kinds of signals that senders can create and receivers can detect and process. For sound, the different states of matter constitute quite different media.

STATES OF MATTER We can initially categorize a medium according to whether it is a **fluid** or a **solid**. In turn, we can divide fluids into **gases** and **liquids**. To understand the differences, note first that all molecules on the Earth are moving at least slightly. A number of types of motion are possible, including internal vibrations within each a molecule, molecular rotations, or translational movements of a molecule from one location to another. The total energy in all such movements is the **kinetic energy** of the molecule. The **temperature** of a medium is a measure of the average kinetic energy of its molecules.

Molecules and atoms can be attracted to each other through a number of forces. Whereas kinetic movements tend to separate molecules, the attractive forces bring them closer together. When the kinetic energy of molecules is high relative to the attractive forces between them, the matter occurs as a gas (such as air). Air molecules occur at low densities, which means they can travel considerable distances before they collide with another molecule. When they do collide,

they bounce and do not stick to each other. In a liquid (such as water), the attractive forces between molecules are high relative to kinetic energies; molecules thus remain much closer together and at higher densities than air. A water molecule can move, but not very far, before it collides with another, and water molecules tend to cohere (stick together) when they do collide. Air and water are both considered fluids because they can assume any shape. In contrast to fluids, solids tend to retain their shape when perturbed. The attractive forces in a solid are so much stronger than the kinetic energy of the molecules that molecules can make only tiny translational movements. Internal vibrations may also be limited by the proximity of nearby molecules, and molecular rotations are usually prevented by the strong linkage between neighbors.

PRESSURE If we were to map the translational movements of individual air or water molecules, we would see that the directions moved in any small neighborhood were random. Suppose we place a small square surface inside such a neighborhood. When a molecule collides with that surface, it exerts a small force on it. Over a short period, many different molecules will collide with that surface, exerting a combined force on it. This total force divided by the area of the surface is known as the **ambient pressure** of the medium. Since molecular movements are random, similar numbers of collisions occur over time in any given direction. We would record the same pressure whether we aimed the surface upward, to the side, or even diagonally. Pressure is nondirectional.

In a neighborhood with a higher density of molecules than our first sample, there would be more molecules available to collide with the square, and the net force, and thus the measured pressure, would be higher. Similarly, if we examined another neighborhood with the same density of molecules as the first sample but at a higher temperature, the higher kinetic energy per molecule would result in a greater force per collision, and again, a higher recorded pressure. Ambient pressure is thus positively correlated with both molecular density and temperature.

The nature of sound

GENERATING SOUNDS Suppose we insert a large flat circle of a hard material into a fluid medium such as air or water. After the molecules settle down to their usual random movements, we can use the disk to measure the ambient pressure in the medium. Once we have this measurement, we rapidly move the flat side of the disk forward by one centimeter (Figure 2.1). As the front side of the disk moves forward, it pushes all the air molecules in front of it forward as well. This creates a higher-than-average density of molecules (a **condensation**) on the front side of the disk, and a lower-than-average density of molecules (a **rarefaction**) on the back side of the disk. The condensation layer of molecules will show a pressure that is higher than the ambient pressure we measured earlier, and the rarefaction layer will show a lower-than-ambient pressure.

FIGURE 2.1 Generation of a sound by movement of a disk in an air-filled tube If the disk is immobile, air pressures will be identical throughout the tube. As we move the disk suddenly to the right, we collect air molecules and create a condensation ahead of it. At the same time, we create a rarefaction behind the disk. The disturbances created on each side of the disk are then transferred to successive layers of molecules further away from it even though individual molecules do not move very far. We will have created a propagating sound.

In addition to altering local pressures, the movement of the disk transfers additional kinetic energy and a relatively cohesive forward direction of motion to each of the molecules in the condensation. These molecules move forward and collide with the next layer of molecules. These collisions transfer both the forward direction and extra kinetic energy to the molecules in the second layer, while bouncing the first layer back toward the disk. This process continues to transfer the condensation to successively distant layers while individual molecules move no further than the 1-cm displacement caused by the disk movement. Behind the disk—the area of rarefaction—a similar process takes place. In this case, molecules just outside the rarefaction encounter more collisions from molecules farther from the disk than from those close to it. They thus get bounced into the rarefaction and fill it up. However, this leaves a rarefaction layer behind them, and this causes the next layer to move into that zone and fill it up. In this way, the rarefaction also radiates away from the disk.

The net effect of moving the disk forward is to generate two disturbances (a condensation and a rarefaction), both of which radiate away from the source over time. While the molecules closest to the disk are forced to move distances much larger than they would have traveled given no disk movement, successive layers of molecules acquire the forward kinetic energy not from the solid disk but from collisions with other molecules. Their subsequent direction of movement will be a combination of the random movement they would have undergone after any normal collision plus

FIGURE 2.2 Waveform of English-speaking human child saying the word *are* It is easy to see that even though there is considerable variation in successive peaks of this waveform, there is a clear pattern that repeats every fourth peak. This signal is thus periodic.

the forward motion of the disturbance. As a result, molecules farther from the disk pass on the forward disturbance, but their actual net displacement gets smaller and smaller with distance from the disk. Eventually at long distances from the disk, it is only the disturbances that change location, and not individual molecules. A radiating disturbance in the pressure of a medium is called a **sound**.

Web Topic 2.1 ***Measuring sound pressure***
Microphones are used to measure the variations in pressure caused by a propagating sound. Specialized types of microphones exist for sound propagation in air, water, and solid substrates. These microphones work by converting pressure variation into electrical signals that can then be measured, stored, and characterized.

GENERATING WAVES IN A FLUID A single sudden disturbance in the pressure of a medium generates an **impulse** sound. What if, instead of creating a single impulse, we repeatedly move the disk back and forth along some fixed axis? Let us further ensure that the movement of the disk is **periodic**: that is, that it repeats the same motion over and over. This will generate successive condensations and rarefactions on both sides of the disk. Instead of a single radiating layer of condensations around the sound source, we now have a series of successive condensation (and intervening rarefaction) layers. The inner layers reflect the most recent disk movements and the outer layers reflect earlier movements.

If we use a fixed microphone to record the successive condensations and rarefactions as they radiate past us, we can generate a graph of pressure versus time. Depending on the way we move the disk back and forth, this graph might appear as in Figure 2.2. Because the pressure measurement in this graph rises and falls around the ambient pressure average, we say that the sound propagates as **waves**, and the graph of pressure versus time is thus called the sound's **waveform**. In our example, the shared direction of movement that molecules pass on to each other as the disturbance spreads is the same direction in which the condensations and rarefactions are moving. When molecular movements and sound disturbances travel in the same direction, we say that the sound consists of **longitudinal waves**. This is the primary process for sound propagation inside large volumes of fluids such as air and water (Figure 2.3A).

Web Topic 2.2 ***Visualizing sound waves***
The best way to understand the differences between different types of sound waves is to view an animation that shows how the molecules move as the sound propagates. We list a number of websites where you can watch visualizations of most of the basic acoustic processes described in this chapter.

GENERATING WAVES IN A STRING If we tie a rope to a tree, add just a bit of tension, and make a small flip in our end, a wave of displacement will move down the rope until it hits the tree. This is another example of a propagating wave. Note that each segment of the rope does not move toward or away from the tree, as would the molecules propagating a longitudinal wave, but instead oscillates along a line perpendicular to the rope axis. A similar type of oscillation is generated in the strings of a guitar or harp when they are plucked. This oscillation is called a **transverse wave** (Figure 2.3B). Light signals are propagated as transverse waves of electromagnetic energy. As we shall see, spiders and some insects communicate by sending transverse waves along strands of silk, and some fish species pluck tightened tendons like guitar strings to make sounds.

GENERATING WAVES ON A WATER SURFACE Unlike air, water is a relatively sticky medium: water molecules are strongly attracted to each other. Below the surface of a body of water, the forces experienced by each water molecule include the downward pull by gravity and the attractive forces from all directions exerted by nearby molecules. At

the surface, gravity continues to pull down on the molecules; but now, attractive forces only pull the molecules downward and to the sides. Unless disturbed, the result is a flat surface with a strong surface tension. When we toss a rock into a pond, the ripples radiate out as circular waves from the impact point. These waves propagate with both longitudinal and transverse components (Figure 2.3C). In a ripple moving from left to right, a molecule near the surface moves in a clockwise trajectory, rising and moving in the same direction as the ripple when the crest passes, and then descending and moving opposite to the direction of ripple movement while in the trough (see Web Topic 2.2 for an animated example). When ripples are close together, surface tension (capillarity) dominates ripple behavior, and the resulting **capillary waves** radiate more slowly as the distance between them is increased [39, 119, 161, 230]. When the ripples are far apart (at least 1.7 cm or more), gravity affects the ripple behavior more than surface tension does. The resulting **gravity waves** radiate more quickly from the source as the distance between ripples is increased.

GENERATING WAVES IN A SOLID In a solid, molecules cannot move very far before they collide with adjacent molecules. As a result, one often finds both longitudinal waves (also called compression waves) and transverse waves (also called shear waves) propagating inside a solid at the same time. In cylindrical solids such as plant stems, a third category, called **bending waves**, may also be present. These are similar to transverse waves but propagate in more complicated ways [254]. One may also find waves propagated on the surfaces of solids. These are similar to the ripples described above for water surfaces, except that surface molecules in solids move in an elliptical counterclockwise trajectory as the sound propagates from left to right (Figure 2.3D). In **Rayleigh waves**, the transverse component moves on a vertical line perpendicular to the surface, (see animation at Web Topic 2.2), and in **Love waves**, the transverse component is a side-to-side motion parallel to the surface. As one moves into the interior of a solid, the elliptical trajectories of molecules near the surface gradually lose their longitudinal component and become entirely transverse.

FIGURE 2.3 Types of propagating sound waves In all examples, sound propagates from left to right, and the dark arrows indicate the trajectory of motion of propagating molecules. (A) Longitudinal waves such as one finds in air or water far from any boundaries. Molecular motion is parallel with the direction of sound propagation. (B) Transverse waves as in a vibrating guitar string. Molecular motion here is perpendicular to the direction of sound propagation. (C) Surface waves on a body of water. Surface molecules propagate the ripples by moving in a clockwise (relative to direction of propagation) elliptical trajectory. (D) Rayleigh waves on the surface of a solid substrate. Molecules on the surface move along a counter-clockwise elliptical path. Love waves (not shown) are similar to Rayleigh waves except that they move the substrate side to side in a transverse motion, whereas Rayleigh waves move the substrate up and down. In solids, one may find any combination of these wave types as well as additional types such as bending waves.

The characterization of sounds

Sound is a propagated disturbance in the density and pressure of a medium. This means that characterizing any given sound requires that we specify both how sound pressure might vary at a fixed location over time (temporal properties) and how sound pressure might vary over space at any given time (spatial properties). We take up each of these perspectives in turn.

BASIC TEMPORAL PROPERTIES OF SOUNDS We now return to the use of a moving disk to generate sound waves in air or water, only this time we place a single microphone at some moderate distance from the disk to record pressure variations at that site over time. Let us begin with a sound source that moves in a simple **sinusoidal pattern**. This is the movement pattern that we would record if we tracked the oscillating position of a child on a playground swing or a bouncing weight suspended from a spring. In each case, the object being tracked moves rapidly in one direction, gradually slows down, and then reverses direction and moves the other way, building up speed as it passes the midpoint, and then gradually slows down to reverse its movement again. If we move our disk in

FIGURE 2.4 Time recording of varying pressure due to passage of sinusoidal sound waves past a microphone Amplitude is a measure of the deviation of the passing sound pressures relative to the ambient level (here marked as 0). A typical songbird would produce a sound amplitude of about 0.16 Pa recorded 1 m away. The period is the amount of time it takes to record one complete cycle of the sound. Here, the period is about 0.001 sec. The frequency of the sound is the reciprocal of the period and in this example would be about 1000 Hz.

such a sinusoidal way, it will generate successive condensations and rarefactions in the medium that will pass by our microphone. A graph of the corresponding pressure recorded by the microphone over time would appear as in Figure 2.4.

There are several obvious measures we could make on this graph to characterize the sound. We see that the pattern of pressure variation repeats in a regular fashion. One obvious measure that we could extract from the graph is the interval we have to wait before the same part of the sound wave repeats. This interval, measured in seconds, is called the **period** of the wave. We could also measure how many complete cycles occur per second, which is called the **frequency** of the sound. Because wave frequencies are important measures throughout physics, the fundamental unit of frequency, one cycle per second, has been named the **Hertz** (abbreviated **Hz**), after the German physicist Heinrich Hertz. In practice, we need to measure only period or frequency, since one is the reciprocal of the other. For example, if we find the period of a sinusoidal wave to be 0.001 seconds (or 1 msec), the frequency can easily be computed as 1/0.001 = 1000 Hz (or 1 kHz). The only other time measurement we might want to make on this graph is *when*, relative to some reference time, the wave achieves a specific part of the cycle, such as a peak or valley. This is known as the **phase** of the wave. Phase is not very important when there is only a single frequency present in a sound. But as we shall see, it can become very important when multiple sine waves are present in the same sound or at the same location.

In addition to the time measurements, this graph allows us to measure the degree to which the passing sound waves differ from ambient pressure levels. One obvious measure is the difference between the peak (or valley) pressure and the ambient pressure (shown as the midline of the graph). This difference is one measure of the **amplitude** of the sound wave, measured as a standard unit of pressure, the **Pascal** (abbreviated **Pa**). While the difference between the peak and ambient pressure is a useful amplitude measure for single sine waves, it may not be very representative for more complicated sounds. The most common alternative is a weighted average of the differences between each part of the wave and the ambient level called **RMS** amplitude. Details can be found at Web Topic 2.3. Finally, whether one measures peak or RMS amplitude, most publications on sound will not report these absolute values, but instead will report the ratio between the measured amplitude and a reference sound. The most common reference is the pressure difference between the measured sound and the softest sound an average human can hear (called SPL). Because humans can hear over a very wide range of amplitudes, these ratios can get very large. The practical solution is to use the logarithm of the ratio, properly scaled, to report amplitudes. This relative unit of amplitude is called the **decibel** (abbreviated **dB**). See Web Topic 2.3 for details on computing amplitudes in dB. However measured, the amplitude of a sound signal is usually referred to as its **sound pressure**.

Web Topic 2.3 ***Quantifying and comparing sound amplitudes***

A variety of methods are available for measuring and comparing sound amplitudes. Here we define some of these methods, show how they are computed, and discuss when each might be most useful.

One might wonder why we don't use ambient pressure as the reference point and then refer to different sound levels as the percentage change from ambient pressures. There are several reasons why this is not done. The first is that ambient pressures change with altitude, the weather, local exposure to sunlight or wind, and many other factors. Having a fixed reference standardizes sound measurements. The second reason is that the change in pressure created by a passing sound wave is extremely small. Even a sound with an amplitude so high that it reaches the pain threshold in humans would only change local pressures by 0.02% as it passed. This is another reason why the instruments for measuring ambient pressure and sound pressures require quite different designs.

An additional temporal measure of sound propagation that will be important in later chapters is **particle velocity**. Velocity is defined as the distance an object moves per

unit time. If we focus on an infinitesimal volume of fluid as a sound propagates, this "particle" of fluid will move back and forth at the same frequency as the sound. At low-fluid densities, this particle will be able to move some distance before it turns around and moves back in the other direction; at higher densities, it will encounter more resistance to its movements and the displacement will be less. Since the frequency is the same in both media, the time available for movement in a given direction has to be the same. Thus, the particle velocity in the lower-density medium will be higher than that in the higher-density medium. We shall see that this has important implications for how animals emit and capture ambient sounds.

TEMPORAL PATTERNS OF SOUNDS: INTERFERENCE AND BEATS The prior example considered a sound source moving in a sinusoidal manner. What if the movement of the disk is best described as the sum of two sine waves? Alternatively, what if our microphone responds simultaneously to sine waves radiated from two different nearby disks? In either case, any medium molecule near the microphone is going to be receiving kinetic energy and directions of motion from two different sine waves at the same time. What would we record? In fact, what we record is simply the sum of the pressures predicted at each moment for the two waves. Suppose the two sine waves have exactly the same frequencies and amplitudes. If they arrive at the medium molecules near the microphone so that they are in exactly the same part of their cycle, we say that they are **in phase**. When both peak at the same time, the total pressure at the microphone is twice what it would be if only one sine wave were present. Now consider the opposite possibility that the two waves are completely **out of phase**: when one has its peak near the microphone, the other is in its valley. The condensation caused by one wave will be countered by the rarefaction caused by the other. The result will be no deviation from ambient sound pressures at all: the two waves simply cancel each other out. When two sine waves with the same frequencies and amplitude are in phase, we say that they experience **positive interference**; when they are out-of-phase, they experience **negative interference**.

What if the two sine waves do not have the same amplitude or frequency? They can still interfere with one another. As the two waves become more dissimilar in amplitude, the higher-amplitude wave will dominate the combination and the second wave will have a decreasing effect on the first (whether positive or negative). If they have the same amplitude, but differ slightly in frequency, then the behavior of the sum is a bit more complicated. At first, one may have its peaks when the other is having its valleys and the interference will be negative, reducing the amplitude of the sum. However, after several more cycles, the wave with a higher frequency will begin to catch up with the other wave, they may interfere more positively, and the amplitude of the sum will increase. The higher-frequency wave then moves ahead of the slower one again, and they return to the out-of-phase state.

FIGURE 2.5 Generation of beats (A) Waveform of pure sinusoidal tone at 1 kHz. (B) Waveform of pure sinusoidal tone at 1.2 kHz. (C) Waveform of combination of first two tones producing beats. Combination waveform is periodic but nonsinusoidal; the pattern repeats at a rate equal to the frequency difference between the original two pure tones (1.2 kHz – 1.0 kHz = 200 Hz).

The summed result of two waves with slightly dissimilar frequencies is a sine wave whose frequency is the average of the two components, and whose amplitude rises and falls with a regular pattern (Figure 2.5). The frequency of this rise and fall in amplitude equals the difference between the frequencies of the two original sine waves, and the resulting variations in amplitude are called **beats**. An animated example can be found at Web Topic 2.2.

TEMPORAL PATTERNS OF SOUNDS: COMPLEX WAVEFORMS In practice, it is very difficult for most physical systems (or animals) to produce a sinusoidal sound in air or water. The waveform recorded at a single microphone will not be sinusoidal but some other more complicated pattern. To complicate this further, many animal sounds are not really **periodic**: the same waveform pattern is not present throughout the entire sound, and so we see a series of different waveforms during the course of the sound signal. How can we possibly measure and compare such sounds?

Luckily, several mathematicians, particularly J. B. J. Fourier (1768–1830) and J. P. G. L. Dirichlet (1805–1859), showed that most periodic and continuous waveforms can be decomposed into an infinite sum of simple sine waves. Because the amplitudes of the high-frequency components tend to be very small, (see Web Topic 2.4 for reasons), we really need to consider only a limited range of low-frequency sine waves to adequately characterize most periodic signals. This characterization would specify the frequency, amplitude, and relative phase of each component of the sound signal, measures that we already know how to make. Because most animal ears perform this kind of **Fourier analysis** on

sound signals before sending information to the brain, this approach also provides an excellent way to compare sounds similarly to the way an ear would do it. Even better, most animal ears ignore the relative phase information except when two components are very similar in frequency. This allows us to focus largely on the component differences in frequency and amplitude when we compare two animal sound signals.

How do we handle animal sounds that are not periodic throughout the signal? Fortunately, most animal signals can be divided into consecutive segments that are sufficiently periodic that we can perform a separate Fourier decomposition on each segment and then string the results together to see the overall pattern. The cost of this segmentation is that the ability to discriminate between adjacent frequencies declines as segments get shorter. But in practice, we can usually find a suitable segmentation of a complex sound that tells us most of what we need to know.

The most common way to characterize animal sound signals is with a **spectrogram** (also called a **sonogram**). This is a plot with time on the *x*-axis running from left (earlier) to right (later), and frequency on the *y*-axis (running from low frequencies near the origin and extending upward). Each point in the plot corresponds to a specific time segment within the signal and a particular band of frequencies. If the Fourier decomposition indicates a high amplitude for frequencies in a given band at a given time, the plot shows one extreme of color or darkness; but if that band of frequencies is not present or is at low amplitude at that time, the plot shows an opposite color or darkness at that point. A variety of computer programs are now available (many for free) that generate spectrograms quickly and effectively. Since where the segmentation cuts are made is arbitrary, several sophisticated techniques are used to smooth out these plots so that junctions between adjacent segments are not visible. Some programs also allow the user to extract and view the Fourier composition of any segment that they wish to examine. Such a plot is called a **power spectrum** or **section**.

As an example of this approach, consider a single call of a male túngara frog (*Engystomops pustulosus*). The overall waveform of this call is shown in Figure 2.6. We can see that the call is fairly explosive, with a rapid onset at high amplitude and then a gradual diminution in amplitude during the call. Variation in amplitude during the course of a signal is called **amplitude modulation**. If we expand the waveform

FIGURE 2.6 Waveform of single call by male túngara frog (*Engystomops pustulosus*) Both plots show varying sound pressure relative to ambient pressure (middle line) on the vertical axis and time on the horizontal axis (events on left occurred prior to events on right). The waveform in the dashed section of the top plot is expanded along the time axis in the lower plot to show the wave details. Inset shows a male túngara frog with his throat sac filled with air while calling.

FIGURE 2.7 Three different visualizations of túngara frog call (A) Waveform (same as in Figure 2.6). (B) Spectrogram of same sound aligned and on same time scale as waveform in (A). Brighter (yellow) colors in the spectrogram indicate that a given frequency at that time has a high amplitude, and darker colors indicate low-amplitude components. Spectrogram shows that the beginning of call is quite noisy, with many different frequencies contributing to this portion. Subsequently, the major components are evenly spaced bands. These start at higher frequency values early in the call and gradually decrease in frequency over the course of the call. We note also a band of background noise between 4–5 kHz that extends through the entire recording. (C) A power spectrum slice at the point of the white line in the spectrogram. This shows that the bands of frequencies are harmonically related: the lowest component (the fundamental) has a frequency of about 0.7 kHz, and all higher frequency bands are integer multiples of this frequency. Note that the component amplitudes tend to decrease with frequency. This pattern of harmonically related bands is very common in the spectrograms of animal sound signals.

along the time axis at any point after the initial onset, we see that it is not a simple sine wave, but is periodic within short segments: the same basic shape repeats at regular intervals. At the point shown in Figure 2.6, the wave pattern repeats every 0.00143 seconds or at a rate of about 0.7 kHz.

The Fourier decomposition of a nonsinusoidal but periodic waveform is fairly easy to predict: if the rate at which the waveform pattern repeats is w, then the major components in the spectrogram will have frequencies that are integer multiples of w. In our example, the waveform repeats at a rate of 0.7 kHz (Figure 2.7A). We would thus expect the spectrogram to show major components at 0.7 kHz, 1.4 kHz, 2.1 kHz, 2.8 kHz, and so forth. As we can see in Figure 2.7B, this is exactly what we find. This spectrogram shows evenly spaced bands throughout the course of the call. The power spectrum for the segment indicated by the vertical white line in the spectrogram is shown in Figure 2.7C. Here we plot the

relative amplitude of each frequency component on the vertical axis against the frequencies of possible components. We see that there is a series of peaks in this plot with each peak corresponding to the band at that frequency in the spectrogram. If we measure the frequency at the top of each peak, we find that these are all integer multiples of 0.7 kHz, the repeat rate for the waveform. Frequencies that are integer multiples of a reference frequency are called **harmonics** and the entire suite of them is called a **harmonic series**. The reference frequency is called the **fundamental**, the component at twice the reference is called the **second harmonic**, and so on. For most animal sounds, all harmonics will be present. In cases where the repeating wave pattern is very symmetrical, only the fundamental and the odd-numbered harmonics are present; however, this happens only rarely with animal sounds.

In the spectrogram in Figure 2.7B, we see that the fundamental and the harmonics all seem to decrease in frequency as the call proceeds. This is because the repeat rate of the basic pattern actually slows down during the call, and thus the frequency components must all decrease accordingly. We hear this as a slightly descending pitch during each frog's call. Variation in frequency composition during the course of a signal is called **frequency modulation**. Note that if we had performed the Fourier decomposition on the entire sound, we would not be able to detect these slow frequency modulations during the call. Segmenting the call into sections and performing Fourier analysis on each provides us with some ability to detect such changes during the course of a signal.

This is a very useful example because the majority of animal sounds in air or water are nonsinusoidal waves but are almost periodic within short segments. We should thus expect to see harmonics in the spectrograms of such animals' signals. Where we see only single pure frequencies, the animal has probably gone to a lot of work to filter out all but a few components in what was initially a harmonically rich sound. As we shall discuss later, animals have an easier time generating nearly sinusoidal sounds in solid media.

Web Topic 2.4 ***Fourier analysis of animal sounds***
Here we provide an introduction to the logic behind Fourier decomposition of animal sounds, including links to several excellent software packages for creating spectrograms and introductions on how to use these packages. We also provide links to sites where one can use such methods to compare archived animal sounds.

SPATIAL PATTERNS OF SOUNDS: THE SPEED OF SOUND As we have seen, a sound disturbance is passed from molecule to molecule at successive distances from the source. The speed with which a layer of molecules can hand off the pressure disturbance to the next layer, and thus the speed at which the sound propagates in that medium, depends on two properties of the medium (Figure 2.8). The first property is the density of the medium. This is a function of the mass of the molecules (larger masses result in higher densities), and the average distance between the molecules (more tightly packed molecules result in higher densities). All other factors being equal, the speed of sound is inversely related to medium density. This is because it takes longer for an activated layer to get the next layer moving if the second layer has many molecules in it or if those molecules have large masses. Water is about 800 times as dense as air; and a solid, such as steel, is about 8 times as dense as water. Based on density alone, we might expect sound speed to be highest in air, intermediate in water, and least in solids. In fact, the reverse is true. This is due to a second factor that must be considered.

FIGURE 2.8 Stiffness, density, and speed of sound in some sample media Stiffness is measured as bulk modulus for fluids and Young's modulus for solids (Mpa), density in tens of kg/cubic meter, and sound speed in m/second. The speed of sound increases with stiffness, but decreases with medium density. Because both measures tend to increase together as one switches between media, the range of sound speeds is much less than might be expected given independent variation in stiffness and density.

The second factor affecting sound speed is the **stiffness** of the medium. For fluids such as air and water, stiffness is the relative resistance to compression: water resists being compressed much more than air does. For solids, stiffness refers both to incompressibility and to the solid's resistance to distortion in shape. All other properties held constant, the speed of sound in a medium is positively correlated with its stiffness. This is because a pressure disturbance passing through a stiff medium spends less time in compression and distortion than a disturbance moving through a non-stiff medium does. Water is about 10,000 times as stiff as air, and steel is about 100 times as stiff as water. Although the differences in density bias the speed of sound in these media in one

FIGURE 2.9 The acoustic spectrum The plot shows the sound frequencies used by different animals, including humans; the wavelengths of those frequencies in air; and whether the resulting sounds are propagated in air, water, or solid substrates. Note that wavelengths for a given frequency in water will be 4.4 times as long as those in air, and those in solids roughly 14–15 times as long as those in air. Microbaroms are low-frequency airborne sounds created by large-scale movements of the ocean that compress or rarefy the layer of air above. Microseisms are low-frequency vibrations propagated in the Earth from distant earthquakes, volcano action, fault movements, and explosions.

direction, the differences in stiffness more than compensate. As a result, the speed of sound is about 344 m/sec in air, 1500 m/sec in water, and 5100 m/sec in a bar of steel. Actual sound speeds will differ a bit from these values depending on local temperatures, ambient pressures, and the composition of the medium. Humidity can change the speed of sound in air, and salinity can alter the speed of sound in water. Although the speed of sound is independent of frequency within fluids like air or water, it can be very frequency-dependent inside solids and at boundaries between media. For example, the speed with which ripples spread on the surface of a pond will vary depending on the frequency being propagated. Sounds in solids can also show frequency-dependent propagation speeds.

SPATIAL PATTERNS OF SOUNDS: WAVELENGTH The speed of sound plays a major role in determining the spatial pattern of a sound. Consider a sound wave with a frequency of 1 kHz in air. It will take 0.001 seconds (the period) to generate one complete cycle of this sound. By the time the sound source has finished generating this single cycle, the leading edge of the wave will have radiated 0.34 m (about 1 foot) away from the sound source. If we had created this same 1-kHz sound in water, the initial part of the wave would be 1.5 m away from the final part. The spatial length of a single cycle of a sound wave in a particular medium is known as its **wavelength**.

Because it takes longer to create a sound with a longer wavelength, we see that the wavelength and frequency of a sound are inversely related: high frequencies have small wavelengths, and low frequencies will have large wavelengths (Figure 2.9). Wavelength will also depend critically on the speed of sound of the medium. A given frequency of sound in water will have a wavelength about 4.4 times as long as that same frequency in air because of the difference in the speeds of sound in the two media. Sounds in solids will have wavelengths 14–15 times as long as the same sounds in air. Why does wavelength matter? As we shall see later, it is difficult for most animals to generate an intense sound with a wavelength more than twice their body size. Given the effects of different speeds of sound, this constraint will be greater for aquatic animals than for terrestrial ones.

SPATIAL PATTERNS OF SOUNDS: DOPPLER EFFECTS Consider a male bird that is flying toward its perched mate and emitting a call in flight (Figure 2.10). As successive waves radiate from its beak toward its mate, the male follows in the same direction. This means that the leading edge of a wave will travel a shorter distance by the time the trailing edge is emitted than would be the case if the caller were not moving. The wavelengths of all frequencies in the male's call will thus be shortened because of his motion toward his mate. Because successive peaks and valleys of the sound waves arrive at the female's ear with reduced delays, she perceives his call as being shifted to higher frequencies. If the male were flying away from the female, then the wavelengths of his emitted sounds would lengthen, and she would perceive his call as being shifted to lower frequencies. The same effects would be created if the male were to call from a perch and the female receiver were to fly toward or away from him during his calling. If both birds were to fly in the same direction, then the changes in wavelengths and frequencies would cancel out. Shifts occur only when the sender and receiver have different relative motions.

The change in propagated frequencies when either the sender or the receiver is moving relative to the other is called a **Doppler shift**. The magnitude of the shift in sound frequencies depends on the ratio of the speed of the moving individual to the speed of sound in the relevant medium. Birds and bats are among the fastest fliers in terrestrial environments. Their speeds rarely exceed 10 m/sec, although a stooping falcon might achieve a speed of nearly 50 m/sec. In air, a perched receiver attending to a call emitted by a sender flying directly toward or away from the receiver at 10 m/sec will experience a Doppler shift of about 3% in all song frequencies. The speed of movement of most animals sending and receiving sound signals in air—and thus the Doppler shifts they experience—will be less than this, and animals typically ignore the slight shifts in frequency. Foraging bats

FIGURE 2.10 Doppler shift when calling sender is moving relative to receiver Calling bird is flying from left to right. This causes successive waves in its emitted call to crowd together in front of it and spread out behind it. A receiver to the right of the flying bird will hear all components in the flyer's call at slightly higher frequencies. A receiver positioned behind the flying bird will hear the call at slightly reduced frequencies.

are an exception. They emit calls and listen for echoes from possible food targets. Slight shifts in the frequencies of the outgoing sound and returning echoes provide information to the bat on its speed relative to an edible target. We discuss this strategy further in Chapter 14. In water and solids, the speed of sound is so much higher than the velocities of moving animals that Doppler shifts are much less likely to be biologically relevant. See an animation of Doppler shifts at Web Topic 2.2.

SPATIAL PATTERNS OF SOUNDS: NEAR FIELD VERSUS FAR FIELD We noted that near a sound source, medium molecules get moved over distances larger than they would normally travel if no sound were being propagated. However, as a disturbance radiates away through successive layers of molecules, the distances traveled by the molecules quickly become little more than they would have been without a disturbance present. This does not mean that molecular movements are the same whether a sound is being propagated or not. What differs during sound propagation is that adjacent molecules in a layer will all have a component of their movement in the same direction and in sufficient concert that they increase pressure in the next layer. It is not *how far* they move, but *where and when* they move that distinguishes the movements of molecules that are propagating sounds from their movements when no sound is present.

The zone around the sound source where the distances that propagating molecules travel are greater than usual is called the **near field** of the sound, and the outer zone where molecular translocations return to normal is called the **far field** of the sound (Figure 2.11). In acoustics, the outer boundary of the near field is usually defined as a distance of 1/6 of a wavelength from the source or 1/3 the diameter of the source, whichever is larger. However, it should be remembered that the transition is actually gradual and not

FIGURE 2.11 Plot of sound pressure and molecular velocity as a function of the distance (in wavelengths of the sound) from a point source Pressure values have been standardized relative to the characteristic acoustic impedance of the medium. Both pressure and velocity decrease with distance from the source, but velocity begins at a much higher value close to the source and decreases more rapidly with increasing distance. The two eventually converge at about one wavelength's distance. Although the transition is clearly gradual, the convention is to consider the region between the source and the distance marked with the dashed line the near field of the sound, and all greater distances the far field.

sharp, so this guideline is only approximate. In practice, a distance of 1/3 of a wavelength from the source or 2/3 the diameter of the source is required before near field effects become negligible. The ability of a receiver to detect a sound signal may depend significantly on whether it is located in the near or the far field of a sound source. A receiver in the near field could perceive the sound through some delicate sensor that is dragged by the tidal movements of the surrounding medium. In the far field, it is unlikely that tidal movements of the medium will be sufficient to cause stimulation of the sensor. In this situation, the receiver can at best try to monitor variations in pressure. Even this strategy can be challenging: by the time a sound propagates into the far field, the pressure variations due to the sound may only be about 0.02% or less of the ambient pressure of the medium.

The propagation of sound

One cannot hear a sound once one gets far enough away from the source. Sound signals get fainter with distance and eventually drop below the level of ambient noise. To understand this process, we now examine the various factors that erode a sound disturbance as it propagates and thus limit the range over which the sound can be detected by a receiver.

SPREADING LOSSES Each time a sound source moves, it must expend energy to push the adjacent medium molecules ahead of it. The stiffer and denser the medium, the more energy the sound source has to expend to move the molecules a given distance. Because most animal sound sources move repeatedly to produce waves, the best measure of this process is the amount of energy expended per unit time. This is known as the **power** spent by the sound source. By forcing adjacent medium molecules to move in a given direction, the sound source transfers some of its kinetic energy to the molecules. This transfer is never very efficient: in animals, less than 1% of the energy expended by the sound source ends up in the pressure wave radiating away from the sound source [119].

A sound source first transfers kinetic energy to the first layer of molecules. This layer then passes this energy on to the second layer which in turn passes it on to the third layer. The successive layers of molecules propagating a sound are concentrically arrayed around the sound source: the first layer is enclosed by the second layer which is, in turn, enclosed by the third layer. If the layers are truly concentric, then it must be the case that an outer layer constitutes a larger surface area and consists of more molecules than an inner layer. It follows that as the sound radiates away from the sound source, the initial kinetic energy supplied to the first layer gets spread out over more and more molecules as it moves to successively more distant layers (Figure 2.12). The amount of energy each molecule acquires will thus decrease with distance from the sound source. As the kinetic energy per molecule decreases, the difference between the peak sound pressure and the ambient pressure must also decrease. This **spreading loss** causes the pressure of a sound signal propagating into three dimensions to decrease with the reciprocal of the distance between the sender and the receiver. Because spreading losses arise simply from geometrical considerations, they occur at the same rate for all frequencies.

FIGURE 2.12 Spreading losses in a sound signal's pressure as it propagates away from its source Reddish spheres show the location of the leading portion of a single call element at successive times after the cricket made the sound. Because the same initial energy is spread over larger and larger spherical surfaces as the sound radiates away from the source, the pressure at any point on a larger and later sphere is less than that on a smaller and earlier one.

Water striders and other aquatic insects signal by sending ripples outward on the surface of the water. In this case, the sound energy is largely spread in two dimensions instead of three. This reduces the rate of spreading loss; in fact, pressure decreases with the square root of the distance from the source for sound waves moving on a surface. Tree hoppers and spiders that live on thin-stemmed plants can communicate by introducing sound waves into the plant tissues. Receivers that are some distance away from the sender detect these waves as they pass under their feet. Because such stems and branches are essentially one-dimensional media, there is *no* spreading loss as these sounds propagate [32].

HEAT LOSSES In addition to spreading losses, sound energy can be lost each time that molecules collide with each other. Such losses are largest when a molecule collides with another that has different physical properties. For example, air is largely composed of oxygen and nitrogen molecules. When one layer of these molecules is moved forward by a propagating sound wave and collides with the next layer, most (though not all) of the kinetic energy is passed on to the next layer, since nitrogen and oxygen gas molecules have similar properties. If, however, there are water vapor molecules in the next layer, they may convert the kinetic energy passed to them by nitrogen or oxygen molecules into internal vibrations and molecular rotations. This reduces some of the translational kinetic energy needed to sustain the sound wave and eventually converts it to heat (random movements of the molecules). The amount of heat loss in air is a complicated function of frequency, temperature, and relative humidity. At a temperature of 20° C, heat losses are maximal at relative humidities of 4–20% for frequencies of 1–10 kHz, respectively, and less for lower and higher humidities. As the frequency is increased, the relative humidity at which peak heat losses occur also increases. In seawater, dissolved salts such as magnesium sulfate and boric acid are very dissimilar to water molecules and thus have a similar effect on sound propagation. Here too, attenuation depends on frequency, temperature, dissolved salt concentrations, and pressure.

Since **heat losses** (also known as **excess attenuation**) occur with each successive collision between layers of molecules propagating the sound, their effect is cumulative. The drop in sound pressure during propagation due to heat losses alone will thus be roughly proportional to the distance between sender and receiver. Also, since adjacent layers collide more frequently when propagating a high-frequency sound wave than when propagating a low-frequency one, high frequencies lose more sound energy to heat losses than do low frequencies. In most media, heat losses increase with the square of the sound frequency. This means that the maximum distance over which two animals can communicate by sound will be shorter if they use high frequencies than if they use low frequencies. We discuss this principle in more detail in Chapter 3.

The type of medium significantly affects the rate of heat losses (Figure 2.13). For example, a 1-kHz sound propagating 500 m in fresh water will lose about 0.001% of its energy due to heat losses. The same sound propagating the same distance in seawater would lose 0.5% of its initial energy, and in air the heat losses would reduce the signal amplitude by 44%. Sounds are detectable at much greater distances in water than in air. Excess attenuation is very complicated in solids, in part because most solids have bounded surfaces that also affect sound propagation. We take up such boundary effects in the next sections.

FIGURE 2.13 Heat losses of propagating sound as a function of frequency and medium Heat losses need to be combined with spreading losses and any scattering effects to compute actual sound pressures at a distance from a source. As a rough rule, heat losses increase with the square of the frequency in all media. Deviations from this rule depend on humidity and temperature effects in air, and dissolved salts and temperature in water. Note that for a given frequency in the range typically used by animals for communication, heat losses in salt water are about 100 times as high as those in fresh water, and those in air are 100 times as high as those in salt water. (After [323].)

ACOUSTIC IMPEDANCE When a layer of medium molecules propagating a sound pushes against the adjacent layer, the latter will resist being compressed and distorted. This resistance by the medium to having its current behavior altered is called its **acoustic impedance**. When a large volume of medium is far from sound sources and also from objects consisting of different media, its acoustic impedance is approximately equal to the product of its current density and speed of sound. This product is called the **characteristic acoustic impedance** of the medium. Since the speed of sound depends largely on the stiffness of the medium, characteristic acoustic impedance is essentially the product of medium density and stiffness. Both factors will make it harder for a given sound pressure to move a given volume of medium. In fact, the higher the characteristic acoustic impedance of a medium, the shorter the distance that one layer of medium can move the next when propagating a sound. As we noted earlier, water is about 800 times as dense as air, and also has a sound propagation speed that is 4.4 times as high. As a result, the characteristic acoustic impedance of water is about 3500 times as great as that of air. Most solids, such as wood, have characteristic acoustic impedances 5000 times as great as that of air. This has very important implications for how sound propagates in each medium, and what happens at boundaries between different states of matter.

We have seen that the energy imparted to a medium by a sound source becomes spread over larger and larger areas of medium as the sound propagates away from the source (spreading losses). It follows that the amount of energy per unit area of medium, known as the **intensity** of the sound, must decrease as the distance from the source increases. Sound intensity is equal to the product of the sound pressure

and the particle velocity of the propagating sound wave. The low characteristic acoustic impedance in air means that it does not require very much sound pressure to generate substantial molecular and particle velocities. That same sound pressure in water, however, would generate only a small increase in particle velocities. As a result, a sound of a given intensity will be represented by high particle velocities and low sound pressures in air, but low particle velocities and high sound pressures in water. Put another way, the energy of a sound is carried for the most part by the particle velocities in air, and by local sound pressures in water. In solids, which usually have higher characteristic acoustic impedances than either air or water, the energy in sound waves is almost entirely conveyed by the sound pressure, and molecules are barely able to move at all.

In practice, the actual acoustic impedance for sound propagation is often different from that predicted by the medium's characteristic acoustic impedance value. For example, consider a tube with walls consisting of some solid material and a hollow filled with air. When sound waves propagate along the air-filled hollow of the tube, the air molecules in the center of the tube largely encounter only other air molecules, while those at the boundary of the hollow space will also collide with the incompressible and unmoving molecules that make up the tube wall. This will create a drag or friction that resists the passage of the sound waves close to the tube wall. The acoustic impedance will be closest to the characteristic value for air in the center of the hollow but higher at its margins. Overall, the average acoustic impedance inside a tube filled with air will be higher than that for an unbounded volume of air at the same temperature and humidity. Similarly, the acoustic impedance of air close to the surface of a body of water will be higher than the acoustic impedance of air high above this surface: air molecules close to the surface will not be able to move as freely as those with no water molecules nearby. Conversely, the acoustic impedance for water near a pond's surface will be lower than that deeper into the pond since water molecules on the surface will meet much less resistance to movement upwards than they would if surrounded on all sides by water molecules. While we can easily compute the characteristic acoustic impedance for a medium using its density and sound speed, we often have to modify this value up or down when considering that same medium near a boundary with another medium.

REFLECTION AND REFRACTION What happens when sound traveling in one medium encounters a boundary with another medium? The answer depends critically on the relative acoustic impedances of the two media at the boundary. Because sound energy is conveyed largely by molecular velocities in air, but by high sound pressures in water, a sound wave traveling in one of these media will face a difficult time crossing a boundary into the other medium. Instead, nearly all of the incident sound energy will be **reflected** back into the initial medium at the surface of the boundary (Figure 2.14). The angle of travel of the reflected waves will be determined by

FIGURE 2.14 Reflection and refraction of sound at a boundary between two media In this example, sound initially traveling in the white medium along line A strikes the surface of the blue medium at an angle. If the acoustic impedances of the two media differ, some of the incident sound energy will likely be reflected from the surface and back into the white medium along line B. Note that the angles of the incident and reflected sound waves are the same relative to the boundary surface. If the acoustic impedances of the two media are not too different, some incident sound energy may also be transmitted through the boundary and into the blue medium. If the speed of sound (C) in the blue medium is higher than that in the white medium, the transmitted sound will be refracted (bent) away from the dashed line perpendicular to the surface as shown in line C_{higher}. If the blue medium has a slower sound speed, the transmitted sound's trajectory will be refracted toward the dashed perpendicular line as shown in line C_{lower}.

the angle of the incident waves. For example, if the incident sound waves were traveling from left to right at an angle of 30° relative to the surface of the boundary, then the reflected waves would also travel from left to right at an angle of 30° relative to the surface. Depending on the two media and the incident angle of the sound waves before reflection, the reflected sound waves may experience a phase shift: what were peaks in the incident sound wave can become valleys and vice versa in the reflected wave.

Reflections can have a major effect on sound propagation within a medium. For example, if two animals that are both in air are communicating by sound close to the ground, some of the sound waves arriving at the receiver will travel on a straight-line trajectory from the sender, but others will arrive at the receiver after being reflected off of the ground. If these are out of phase with the directly transmitted waves, the two can cancel and the receiver will hear nothing. Reflections within a small volume of medium such as inside a solid or small body of water can also produce very complicated interference patterns and thus modify the efficacy of sound communication significantly.

When the acoustic impedances of the two media are more similar than those of air and water, then some sound energy will traverse the boundary and continue propagating in the second medium. The direction of travel of the sound waves will likely be shifted: if the speed of sound is slower in the second medium, the travel direction of sound waves in the second medium will be bent closer to a line perpendicular to the surface than was the incident wave direction; if the speed of sound in the second medium is higher than the first, then the waves in the second medium will be bent upward so that their direction is more parallel to the surface than was the incident sound wave. This bending of the waves after crossing a boundary between media is called **refraction**. It is most likely to affect animal communication when sound is traveling in a single medium and encounters adjacent regions of medium with different temperatures, pressures, or compositions. Both water and air often exist in vertically stacked layers. These layers are usually insufficiently different in acoustic impedance to generate reflections, but are sufficiently different in sound speed to cause refraction. For useful animations demonstrating reflection and refraction, see Web Topic 2.2.

Web Topic 2.5 ***Reflection and refraction***
The fraction of sound energy reflected or refracted at a boundary is a complicated function of incident angle, relative acoustic impedances, and relative sound speeds. Here we present the equations for several different cases, and provide some real physical examples.

DIFFRACTION Consider a solid wall separating two large air-filled spaces. Sound traveling in one of the air-filled spaces will be reflected at the wall and no sound will appear on the other side. Suppose we then open up a circular window in the wall. Now some of the incident sound can pass through the hole and propagate in the second space. One might expect the sound field in the second space to be cylindrical in shape, given the circular shape of the hole. This is true only when the hole is large relative to the wavelengths of the incident sound. As the hole is made smaller relative to the sound wavelengths, the sound waves emerging from the hole will form a cone of sound. The angle of the cone increases as the relative size of the hole decreases, and for a small enough hole, emerging sound waves will radiate into all parts of the second space. The bending of sound waves after passing through or around an obstruction is called **diffraction**. Diffraction is a consequence of the wave nature of sound and explains why we can hear someone speaking around the corner of a building or detect a sound with both ears when the source is located on only one side of our heads. See an animated example at Web Topic 2.2.

SCATTERING A special case of reflection occurs when many objects consisting of one medium are distributed throughout a second one. Examples include trees and bushes sticking into the air space above the ground, and the air-filled swim bladders of fish scattered about in seawater (e.g., over a coral reef). If the acoustic impedances of the two media are sufficiently different, each object will constitute an individual reflector of incident sound waves. If the reflecting objects are situated between a sender and a receiver, this **scattering** of the sound during propagation can be another significant source of signal attenuation. The amount of scattering, and thus the amount of reduction in sound energy reaching the receiver, will depend on the abundance of such objects, their size relative to the wavelengths of the sound, and the location of the receiver relative to the source of sound and the objects. When wavelengths are much larger than the scattering objects, they simply bend around these obstacles, and very little sound energy is scattered. This is called **Rayleigh scattering** (Figure 2.15). As the wavelengths decrease in size, the fraction of incident sound energy that is scattered back toward the source gradually increases. Rayleigh scattering thus prevents higher-frequency components in a sound signal from reaching the receiver. Once wavelengths get down to about six times the size of the scattering objects, a more complicated behavior, **Mie scattering**, takes over. In this case, part of the incident sound energy arriving at a scattering object is directly reflected backward, whereas another part is diffracted around the object. Interference between the diffracted and reflected components can be positive or negative depending on the circumference of the object relative to the sound wavelengths and the relative location of the receiver. At even smaller wavelengths of sound, diffraction is negligible and all sound energy that strikes the object is reflected and lost to the receiver. See animation at Web Topic 2.2. We shall discuss the consequences of sound scattering in more detail in Chapter 3.

Sound Signal Generation

Sound signals begin with the production of some sort of vibration. There are dozens of ways that animals might generate a vibration, and nearly every mechanism has been used by at least one species. Given this, we might expect sound communication to be widespread among animal taxa. In fact, sound communication is largely restricted to arthropods and vertebrates, and even among these, modalities other than sound often predominate in their signaling repertoires. The major constraint that limits the use of sound for communication is not the generation of a vibration but the efficient coupling of that vibration into the propagating medium. In species that need to communicate over distances smaller than a body length, inefficient sound radiation can often be tolerated, and it is here that we see the widest variety of vibration mechanisms being used. However, animals that use sound to communicate over larger distances either use only those vibration sources that radiate efficiently or they feed the vibrations into secondary structures that are designed specifically for efficient sound radiation. In the following sections, we first examine the many ways in which animals

FIGURE 2.15 Sound scattering by a rigid sphere in a fluid medium Vertical axis is the ratio of reflected to incident sound pressure measured at a location about one-half wavelength away from the sphere along the line joining the sphere and the source. Horizontal axis indicates ratio of sphere diameter (here held fixed) to varying wavelengths of incident sound. At low ratios, sound waves sweep around the sphere and there is little reflection. Increasing the ratio (by decreasing the wavelengths) initially creates a smooth increase in reflected sound pressures, an effect called Rayleigh scattering. Above this ratio, reflection processes can become very complex, an effect called Mie scattering. For a sphere, reflection pressures rise and fall as the ratio is increased and eventually asymptote to a fixed value by a ratio of 6:1. While sound is reflected roughly equally in all directions for Rayleigh scattering, Mie scattering is increasingly asymmetric as the ratio is increased. Each blue plot shows the sum of incident and reflected sound pressure at the surface of the sphere for a given sphere/wavelength ratio; the sound source is located to the left of each plot, and the radius of the plot for any given angle around the sphere indicates the overall sound pressure in that direction. The dashed circle shows what that pressure would be if there were no sphere at that location. As the ratio increases, incident and reflected sound pressure add up positively in front of the sphere, whereas they interfere to form a "sound shadow" with lower-than-incident pressure on most of the rear side of the sphere.

generate vibrations and then look at the various devices that have allowed arthropods and vertebrates to improve the efficiency of sound radiation.

Producing vibrations

The production of a vibration usually entails an animal moving one part of itself relative to a nearby volume of medium or moving the nearby medium relative to some part of its body. There are four broad categories of movement that we encounter in animal sound production:

1. movement of a solid body part against another solid;
2. movement of a body part to create surface waves at a boundary between media;
3. movement of a body part to produce waves within a fluid medium; and
4. movement of a fluid medium against a body part.

We discuss each of these mechanisms in more detail below.

MOVING A BODY PART AGAINST ANOTHER SOLID There are several ways in which an animal can generate a vibration by moving a body part against another solid. The simplest method is **percussion**, in which the animal strikes two solid objects together with a rapid motion (Figure 2.16). The two most commonly used targets for percussion are nearby substrates and another body part. In arthropods, substrate percussion is known in crabs (Decapoda), stoneflies (Plecoptera), grasshoppers (Orthoptera), katydids (Orthoptera), crickets (Orthoptera), termites (Isoptera), booklice (Psocoptera), true bugs (Hemiptera), lacewings (Neuroptera), alderflies (Megaloptera), snakeflies (Raphidioptera), scorpion flies (Mecoptera), beetles (Coleoptera), caddis flies (Trichoptera), caterpillars (Lepidoptera), ants and wasps (Hymenoptera), and spiders (Araneae) [1, 15, 23, 62, 66, 92, 189, 243, 303, 331, 390]. Body parts used by arthropods to strike the substrate include the head, antennae, mouthparts, two or more legs, wings, the abdomen, or the entire body. Vertebrate examples of substrate percussion include head slaps against the substrate by benthic fish such as the mottled sculpin [399], vocal sac and foot drumming against the substrate in frogs [51, 232, 233, 269], rapid bill drumming of many woodpecker species against anything that will reverberate [90, 94, 196, 351, 406], beating a drumstick against a hollow

FIGURE 2.16 Vibration generation by drumming on external substrates (A) Like most members of their taxon, Pileated woodpeckers (*Dryocopus pileatus*) drum their beaks against tree trunks. Typical drums consist of 10–30 strikes at rate of 15/sec. (B) Male palm cockatoo (*Probosciger aterrimus*) holding the branch he used to drum against an advertised nesting cavity in a tree. (C) Lacewings (*Chrysoperla agilis*) vibrate their body and strike the vegetation substrate with a curved abdomen. (D) American beavers (*Castor candadensis*) strike the water's surface with their tails as an alarm signal to conspecifics.

log by male palm cockatoos [407], foot stamping by a wide variety of mammals [311], thumping of the head against burrow walls by mole rats [272], and the loud drumming against tree buttresses by chimpanzees [6, 7].

Mouthparts and wings are the most common anatomical tools for body–body percussive actions (Figure 2.17). Among vertebrates, many birds pop or snap their bills together as a threat; storks, herons, and the roadrunner perform more elaborate bill clacking as an integral part of their displays [347, 401]. Arthropods such as caterpillars and grasshoppers also click their mandibles to make sounds [92]. Wings can be struck against each other or against some other part of the body to produce sounds. Avian examples include owls [402], nightjars [252], manakins [42-45, 306], and flappet larks [38, 293]. Arthropod examples of wing clapping include grasshoppers [92] and whistling moths; the latter have hardened "castanets" on each wing to increase the intensity of the percussive sound

FIGURE 2.17 Vibration generation by striking body parts together (A) Male ruddy duck (*Oxyura jamaicensis*) drumming bill against water trapped in feathers and air-filled sac on breast. (B) White stork (*Ciconia boyciana*) performing bill clacking display at nest. (C) Male red-capped manakin (*Pipra mentalis*) striking wing against leg to make sound during courtship display. (D) Eastern diamond-backed rattlesnake (*Crotalus adamanteus*) coiled and rattling dry buttons on tail tip as a threat. Rattle is not in focus in the photo because it was vibrating back and forth at about 60 times/sec.

[2]. Rattlesnakes whip the hard multiple segments at the ends of their tails back and forth at a very rapid rate, resulting in a percussive staccato [76, 325, 411]. The displaying male stiff-tailed duck drums its bill against an inflated air sac on its breast [202, 203], and gorillas beat air-filled sacs on their breasts as a threat.

Instead of percussive striking, some species rub two solids together to produce more continuous vibrations. This is called **stridulation**. In the simplest case, simple friction between the two surfaces generates a repetitive cycle of sticking and slipping (see analysis of relevant physics in [119]). Fish such as grunts (Haemulidae) grind their pharyngeal teeth together, producing noisy vibrations with little periodic structure [50]. However, most stridulating species have accentuated this process by providing bumps, hairs, spines, ridges or ribs, on one or both of the rubbing surfaces. The most efficient system is a row of carefully spaced teeth on one surface (called a **file**) and a sharp edge or single tooth on the other (called a **plectrum**). The animal either moves the plectrum across the file or vice versa to generate a steady sequence of nonsinusoidal but relatively periodic vibrations. Thus spectrograms of stridulation signals can range from broadband smears across a wide range of frequencies (grunt tooth grinding) to stable harmonic series (orthopteran wing stridulation and catfish spine stridulation).

Given their hard exoskeletons and multi-jointed bodies, many arthropods (Figure 2.18) use stridulation to generate vibrations [99]. Almost every pair of juxtaposed or nearby body parts has been used for this purpose by some arthropod [92]. Insect examples include rubbing one segment of an antenna or leg against another segment of the same appendage, one wing against another wing, wings against legs, head against thorax, thorax against abdomen, legs against thorax, legs against abdomen, proboscis against thorax, etc. Crustaceans are a bit less inventive, but examples include rubbing

FIGURE 2.18 Example of arthropod stridulatory organ All members of the scorpion genus *Rhopalurus* are known to produce sounds. (A) Dorsal view of an adult *Rhopalurus abudi*. (B) Ventral view of *R. agamemnon* showing one of the paired toothed structures called pectines (singular *pecten*) that have both chemosensory and mechanosensory functions. The pecten on the left is shown in its normal position, while the other has been removed to reveal the dense field of bumps on the ventral side of the body. (C) *Rhopalurus* species have rows of fine ridges on the surface of each pecten tooth where it faces the body, and (D) an extensive field of small bumps on the opposing ventral surface. By moving the pectines appropriately, the pecten tooth ridges are dragged over the ventral surface bumps producing a steady stridulation. (After [236].)

antenna against cephalothorax, uropods against each other, one segment of a claw or leg against another segment of the same appendage, legs against carapace, claw against legs, and legs against legs. Spiders stridulate using pairs of mouthparts, legs against the body, or the cephalothorax against the abdomen. Scorpions use their claws and legs against each other or against the body, body segments against adjacent body segments, and some even use their sting as the plectrum against a file on a more basal segment of the tail. Other arachnids such as amblypygids, solpugids, and harvesters usually stridulate using mouthparts. Not surprisingly, millipedes and centipedes put their stridulation structures on adjacent legs. There is a very large literature on arthropod stridulation. Sample publications include studies on lobsters [290, 291], hermit, ghost, and fiddler crabs [1, 62, 195, 303, 331], orthopteran insects [82, 84, 103, 235, 264, 265, 298, 329], hemipteran insects [69, 242, 296, 322, 336, 418], beetles [77, 129, 193, 205, 237, 283, 284, 287], butterflies, moths, and caterpillars [75, 89, 117, 223, 409], caddis flies [197], ants and wasps [68, 158, 183, 189, 321, 382], spiders [23, 96, 98, 102, 201, 297, 308, 355, 379, 385], and scorpions [236].

Stridulation also occurs in vertebrates. Fish stridulate by grinding their teeth together [16, 50, 109, 222, 267], grating adjacent bones [73, 108, 378], or rubbing bony spines against adjacent bones, scales, or other spines [41, 105, 182, 335, 339]. Spine stridulation is used for sound production by hundreds of species of catfish [107, 217]. Some gekko lizards whip their tails so that adjacent scales rub and produce a rasping sound [130]. The elaborately barbed structure of bird feathers facilitates stridulatory rustling when plumes are rubbed or shaken together [147]. Male sage grouse rub the hard leading edge of the folded wings against rows of stiff breast feathers to produce swishing sounds during their display strut [188]. The small mammals called tenrecs can produce sound vibrations by rustling the spines on their back [55].

A third mechanism for vibration production involves the bending of a highly elastic plate of cuticle by body muscles until the plate buckles and snaps into a different configuration producing impulsive vibrations (Figure 2.19). The plate usually snaps back when the pressure on it is released, and this may produce an additional vibration. Such **buckling** is largely restricted to insects in the orders Hemiptera and

FIGURE 2.19 Insect tymbals (A) Bladder cicada (*Cystosoma saundersii*). (B) Dorsal view of male bladder cicada with wings removed to show ribbed tymbals on each side of body (arrows). (C) Successive stages in buckling of cicada tymbal (left to right). Each tymbal is viewed from the side with the anterior end on the left. Brown area is central plate. As plate is pulled towards anterior end by muscles, it, and then successive ribs, buckle and produce a sequence of sounds. (D) Arctiid moth (*Bertholdia trigona*) and (E) SEM photo of one of the tymbals located on its thorax. Note ridges along side of tymbal similar to ridges in cicada tymbal. Male moths use these tymbals to produce ultrasonic sounds that jam the sonar of attacking bats (see Chapter 14).

Lepidoptera. Auchenorrhynchan Hemiptera such as cicadas (Cicadidae), leafhoppers (Cicadellidae), froghoppers (Cercopidae), treehoppers (Membracidae), and planthoppers (Delphacidae) typically possess a convex cuticular plate called a **tymbal** covering an air space on each side of the abdomen [57, 66, 286]. Except for cicadas, tymbals are present in both sexes. Muscles rooted at the center of the body attach to each tymbal either directly or through a levered rod called an **apodeme**. As the muscles contract, a force is exerted on one portion of the convex tymbal plate until it suddenly pops into a concave state with a sudden generation of vibrations. Some cicadas have elaborated this scheme with a series of parallel ribs at successive distances from the apodeme insertion point. Instead of a single buckling of the entire tymbal, these ribbed tymbals buckle in steps, producing a longer series of initial vibrations [33, 35, 123, 178, 344, 354, 356, 416]. Cicadas typically buckle and relax the tymbals repeatedly at rates up to 100 times/sec. In some cicada species, the two tymbals are buckled repeatedly at this high rate but out-of-phase, producing even higher rates of buckling cycles [124, 231]. Tymbals also occur in Prosorrhynchan Hemiptera such as stink bugs (Pentotomidae), burrowing bugs (Cydnidae), and assassin bugs (Reduviidae) [390].

Lepidopteran tymbals are used to generate ultrasonic vibrations by a variety of nocturnal moths. Tiger moths (Arctiidae) have paired muscle-activated tymbals on the thorax; some owlet moths (Noctuidae), such as the Australian *Amyna natalis*, have tymbals on each forewing that are activated by twisting the wings; many waxmoths (Pyralidae) have tymbals at the base of each wing that are buckled by wing movements; and male *Symmoracma minoralis* (Pyralidae) have a single large tymbal on the ventral side of their abdomen [40, 75, 93, 160, 200, 268, 334, 346, 348, 349]. Many of these species have ribbed tymbals like those of the cicadas to produce longer bursts of vibrations. Neotropical butterflies in the genus *Hamadryas* (Nymphalidae) typically produce audible "cracking" sounds in flight. Although it was initially thought that this was due to percussion between the wings [263], recent work shows that a single wing can produce the sound and that some form of buckling vibration is the most likely source [408].

One group of fish, the croaking gouramis (Osphronemidae), has evolved a unique mechanism of sound production. Two enlarged tendons attached to each pectoral fin are stretched as the fin is moved in an anterior direction. The tendons are adjacent to bony processes of the fin rays that trap the tendons momentarily until further tension releases them with a snap. The effect is rather like the plucking of a guitar string. Each forward fin movement produces two short pulses of sound, and the two fins often move in opposite directions, producing long series of double pulses. Both sexes use these sounds when interacting with conspecifics [212, 213, 216, 221].

A final mechanism for generating vibrations using solids is **tremulation**. This involves rocking the entire body (or large parts of it) and transmitting the resulting vibrations into a solid substrate through the legs or some other appendage. It has been reported in insects in the orders Plecoptera, Orthoptera, Hemiptera, Megaloptera, Rhapidioptera, Neuroptera, Mecoptera, Trichoptera, Diptera, and Hymenoptera [14, 184, 390]. This is also the likely source of vibrations induced in plant stems by chameleons [21]. Such motions may also generate vibrations in the surrounding fluid medium (air or water), a mechanism that will be discussed in a later section.

Web Topic 2.6 ***Sample animal sounds***
Visit this website to hear examples of the kinds of animal vibrations discussed in this and following sections of the chapter. You will also be able to see the waveform and spectrogram of each example.

MOVING A BODY PART TO CREATE SURFACE WAVES As we have seen, the layer of medium closest to a boundary is likely to have somewhat different acoustic properties than a layer of the same medium farther from the boundary. Acoustic impedance is one property that is likely to vary in this manner. Various animal species have taken advantage of these differences to produce sound vibrations that then propagate on the boundary surface [230].

Some aquatic animals living on or near the surface of a body of water communicate by generating surface ripples that radiate away from the initial disturbance (Figure 2.20). Insect examples include Hemipteran water striders (Gerridae), which generate radiated ripples using vertical movements of the legs [403], and waterbugs (Belostomatidae), which pump the entire body up and down under water but

FIGURE 2.20 Calling signal of male water strider Repetitive motion of a male of this North American species (*Rhagadotarsus anomalus*) generates regular ripples that radiate out in concentric circles. The male is the tiny object at the center of the concentric ripples.

FIGURE 2.21 Alternative mechanisms for vibrating the swim bladder in catfish In all cases, the relevant muscles are rooted on one end to a structure other than the swim bladder. Examples from four catfish families are shown with details of representative swim bladder, relevant muscles, and elastic spring. (After [220].)

near the surface [214]. Male Siamese fighting fish signal to small fry feeding near the water's surface by pulsing water with their fins to generate surface ripples [215]. American alligators slap the water's surface with their heads [391], and a variety of whales and porpoises either perform tail slaps or leap out of the water and fall back to produce a massive splash [241, 395, 400]. It is not clear in either case whether the relevant vibrations are propagated at the surface or instead in the body of water as a whole.

Many of the percussive actions on substrates noted earlier are designed to create vibrations in the substrate instead of, or in addition to, vibrations in the nearby air or water. Where the wavelengths of the resulting vibrations are shorter than the thickness of the substrate, propagation will be limited largely to surface waves. Where wavelengths are larger than the thickness of the substrate (for example, when the substrate is a leaf or stem of a plant), the entire structure will propagate the vibrations. At intermediate wavelengths, both surface and interior waves may be propagated. We discuss these processes in further detail in the next chapter.

MOVING A BODY PART INSIDE A FLUID MEDIUM Many animals move a solid object to create vibrations and waves in their surrounding fluid medium. In some cases, these body parts are simply passing on vibrations generated elsewhere in the body. We take up this type of process in a later section. Here, we focus on movements of body parts that are the initial sources of sound vibrations in fluid media. There are at least four ways that animals initiate these sound vibrations.

The first method, **pulsation**, is to alternately contract and expand the surface of a closed but flexible object, so that medium is forced to move in concert with the surface. American lobsters [179] and mantis shrimp [292] expand

and compress their cephalothoracic carapace in this manner. Most bony (teleost) fishes maintain buoyancy using a gas-filled sac called a **swim bladder** in the center of their bodies. Because the gas is more compressible than any fluid-filled tissue, the swim bladder can be compressed, stretched, or struck to produce relatively large vibrations over its surface. These are then radiated into the surrounding medium as sounds [52, 81, 104, 175, 176, 218-220, 288, 289, 377, 378].

In many fish, the relevant **sonic muscles** are attached to the back of the skull, the backbone, or the sides of the body and are used to move, stretch, or compress the swim bladder relative to that base attachment point. There is an amazing diversity of designs (Figure 2.21). In the simplest case—naked catfish (Pimelodidae), some rockfish (Sebastidae), and tiger perch (Terapontidae)—the muscles attach directly to the swim bladder. In thorny catfish (Doradidae), ocean catfish (Ariidae), and upside-down catfish (Mochokidae), an intervening bony plate or lever, called an elastic spring, is attached both to the swim bladder and to the muscles. Tension on the muscles pulls the elastic spring and the bladder in one direction, and muscle relaxation allows the elastic spring to snap the bladder back to its original position. In squirrelfish (Holocentridae), the muscles move flattened ribs that are attached to the sides of the swim bladder and thus compress and expand the swim bladder walls indirectly. The muscles in some rockfish (Sebastidae) connect first to the pectoral girdle and then terminate on ribs or vertebrae, allowing for overall contractions and expansions of the cavity containing the swim bladder. Piranhas (Characidae) have a flattened tendon enveloping the lower half of the swim bladder that can be pulled upward by muscles attached to one of the ribs. The reverse system is used in drums and croakers (Sciaenidae), which have a flattened tendon over the top of the swim bladder attached to muscles in the ventral body walls that can pull downward on the swim bladder. Cusk eels (Ophidiidae) and pearl fish (Carapidae) have one pair of muscles that stretches the anterior end of the swim bladder perpendicular to the body axis while a second set pulls the anterior end forward. Because the posterior end of the swim bladder is attached to vertebrae, these muscles stretch the anterior end of the swim bladder in two directions at once. Some mormyrid electric fish make sounds with muscles attached to the posterior end of the swim bladder [81]. Finally, the relevant muscles in toadfish and midshipman fish (Batrachoididae), sea robins (Triglidae), flying gunards (Dactylopteridae), dories (Zeidae), wasp fishes (Apistidae), cod and haddock (Gadidae), and other mormyrid electric fish are unattached to any skeletal component (Figure 2.22). This allows for rapid and repetitive excitations of the swim bladder at rates up to 300 contractions/sec in toadfish and midshipman fishes. Interestingly, the sonic muscles in toadfish and midshipman fishes are among the fastest-oscillating muscles known in vertebrate animals [106, 325]. The vibrations generated by these species are usually periodic but nonsinusoidal in waveform. The resulting spectrograms typically show a harmonic series with

FIGURE 2.22 Examples of fish in which vibratory muscles are attached only to the swim bladder Swim bladders are drawn with anterior end to the left. Differences in geometry and shape reflect functional differences. For example, muscles (dark red) surround the sides and rear of the toadfish swim bladder, whereas they are found only on the sides of the midshipman's organ. This allows sufficient posterior flexibility for the midshipman to inflate its swim bladder before drumming. (After [220].)

a fundamental identical to the contraction rate of the sonic muscles [220].

A second mechanism, **fanning**, involves moving a flat solid object cyclically along a line perpendicular to its surface to produce a parallel movement of the nearby fluid medium. The wings of insects provide a classic example, as they may be vibrated (with or without flight) at rates up to several hundred Hz (Figure 2.23). In nearly all cases, little far-field sound is produced, but in the near field, air movements can be quite large and easily detected at distances of several centimeters by nearby receivers. Examples include the courtship dances of male *Drosophila* (Drosophilidae) [28, 32, 375, 376], large fruit flies (Tephritidae) [4, 48, 49, 240, 260] and sand flies (Psychodidae) [85, 86, 285]; the waggle dances of honeybees [256, 257]; and the wing-flicking displays of cave crickets (Phalangopsidae) [88, 177]. Male mosquitoes (Culicidae) are attracted to the near-field wing sounds of flying females, and females signal their interest by matching their wing-beat frequencies to that of the approaching male [146].

A third method, **fluid compression**, remains poorly understood but seems to involve such a rapid modification of local pressure in a fluid medium that it generates far-field sounds. In air, the rapid wing flicks of displaying male manakins produce loud snaps and pops that are easily heard in the far field [44, 45]. One possible mechanism is a sonic boom: this is produced whenever a solid object moves faster than the speed of sound in that medium, and is the cause of

FIGURE 2.23 Near-field waveforms of sine and pulse songs generated by wings of courting male fruit fly (*Drosophila melanogaster*) Sine song is a nearly sinusoidal waveform with a repeat rate of about 130 Hz. Pulse song consists of sudden bursts of waves. The two kinds of songs are interspersed sequentially in normal courtship song. (A) Broad time scale showing 10 seconds of continuous courtship song. (B) Expanded portion of A showing 0.5-second portion. (After [204].)

FIGURE 2.24 Snapping by snapping shrimp (*Alpheus* sp.) (A) Dorsal view of snapping shrimp with enlarged right claw. (B) Detailed view of enlarged right claw propus, and the moveable dactyl on which is a specially shaped plunger. Claw is currently open in the "cocked" position. (C) Plot of sound pressure amplitude relative to ambient levels versus time during one complete "snap" by the shrimp. After the claw is cocked (1), the plunger on the dactyl is moved extremely rapidly into a socket on the propus creating a cavitation bubble (2). Shortly thereafter, the bubble collapses (3), producing the large peak of pressure (the snap) and subsequent reverberations from nearby objects. (C after [387].)

the loud snap when one cracks a whip. Whether manakins can move the tips of their wings fast enough to produce a whip-crack remains unknown. Male ruffed grouse produce an accelerating series of low (40 Hz) thumping sounds by repeatedly bringing their partially extended wings toward each other very rapidly [8, 188]. High-speed films have eliminated the possibility of percussive effects in this behavior. The male sage grouse produces two loud "pops" during his strut display that are associated with a sudden expansion and oscillation of the two air sacs on his breast. While the pops might be generated in part by percussion between the two expanding sacs, it is also likely that each sac produces very rapid pressure changes near the sac surfaces [83]. Finally, very rapid movements in water can generate sufficiently extreme pressures around the moving object that nearby layers turn into a gas and form a bubble. The subsequent collapse of the bubble then generates a loud sound. This process, which can occur only in liquids, is called **cavitation**, and is the source of bubbles behind boat propellers. Snapping shrimp (Alpheidae) have an enlarged claw in which one of the two terminal segments can be locked, stressed, and then released very rapidly (Figure 2.24). The loud sound is the result of cavitation and not percussion [101, 387]. The shrimp use snapping as a defense against predators, to stun prey, during intraspecific contests, and to rally neighbors to eject intruders from a group territory [180, 209, 338, 381]. Because snapping shrimp are common throughout most of the world's oceans, they constitute the major source of high-frequency noise in most marine environments [10, 37, 56, 304, 309, 312].

The fourth mechanism, **streaming**, occurs when the signaler moves sufficiently rapidly through a fluid medium that the flow over its appendages generates vibrations. Several groups of birds produce whistling, winnowing, or humming vibrations while in flight. Among shorebirds, the woodcock

(*Scolopax minor*) has special feathers in the tips of its wings that can be spread to produce vibrations while in flight [299], whereas several species of snipe (genera *Gallinago* and *Coenocorypha*) have similar adaptations in their tails [53, 259, 383, 386]. Wing feathers specialized to produce flight sounds also occur in honeyeaters (Meliphagidae) [78], and several nighthawks in the genus *Chordeiles* perform an aerial dive display that ends with a booming sound when wing feathers are angled into the airflow [166, 258]. Hummingbirds also have specialized tail or wing feathers that generate display sounds during particular modes of flight [59, 60, 192]. Many pigeons and doves produce a whistling sound with their wings when startled into sudden flight, and this sound functions as an alarm signal attended to by both conspecifics and heterospecifics [72, 186].

MOVING FLUID MEDIUM OVER BODY PARTS Although some fish produce sounds by forcing bubbles out of their mouth or anus [393, 405], sound production using a forced flow of medium is largely restricted to terrestrial air-breathing animals. In the latter case, vibrations are generated when air present in the respiratory system is forced down a tube and through a narrow orifice. There are two basic types of vibrations that might be generated: vocalizations and aerodynamic sounds.

In a **vocalization system**, a tube used to move air into and out of the body is blocked by a valve. When the animal is breathing through this tube, the valve is kept open and out of the airflow. To produce vibrations, muscles close the valve, and other respiratory muscles increase the air pressure behind the valve. At some point, the air pressure behind the valve, (the upstream side) exceeds whatever muscle forces are holding the valve closed, and the valve pops open. This allows a sudden pulse of air to flow through the valve, decreasing the pressure difference between the upstream and downstream portions of the tube, and generating a suction on the valve lips called a **Bernoulli force**. The continued tension on the valve-closing muscles, the reduced pressure difference across the valve, the Bernoulli suction, and differential latencies in the movements of different masses in this system then cause the two lips of the valve to close and stop the airflow [87, 181, 380]. Upstream pressure starts to build up again, and the cycle repeats. Such a system will usually produce vibrations that are periodic but nonsinusoidal. A spectrogram of the resulting sound will show a harmonic series whose fundamental frequency is equal to the rate at which the valve pops open and closed. This rate will depend on the size, mass, and elastic properties of the valve lips, the muscle force used to close them, any tension applied to them by other muscles, and the pressure exerted by the upstream respiratory system prior to valve opening [119].

All terrestrial vertebrates have similar respiratory plumbing (Figure 2.25). Each of the two lungs is connected to a tube called a **bronchus**. The two bronchi join at some point to form a single tube called the **trachea**, which connects to the outside via the mouth and nasal cavities. Even though all terrestrial vertebrates share this basic design, their vocal sound production mechanisms are quite varied. This variation is due in part to different strategies for ventilating the respiratory system: those taxa with more sophisticated controls over ventilation are the ones most likely to produce vocal sounds, and the finer that control, the more complex the vocalizations.

FIGURE 2.25 The basic elements of a terrestrial vertebrate respiratory system Air is inspired through the nostrils or mouth into the nasal or pharyngeal cavities, respectively. It then passes through the larynx (originally evolved to keep food out of the trachea) into the trachea, which consists of bone or cartilage rings joined by membranes. The trachea then joins the two bronchi (the junction elaborated into the syrinx in birds), which convey the air into the lungs. During sound emission, the reverse process occurs, with air moving through vibrating valves in the upper bronchi or syrinx junction (birds), or in the larynx (amphibians, reptiles, and mammals).

Frogs and toads acquire air by expanding a throat sac while all other openings except the nostrils are closed. Once partially inflated, the sac is contracted, forcing air into the lungs. This is called **buccal pumping**. Air is expelled by the contraction of muscles in the body wall. Lizards and snakes, unlike frogs, have ribs and muscles that allow expansion of the thoracic cavity. Turtles' ribs are attached to their shells. Turtles, crocodiles, and alligators all have special muscles that move their viscera backward and forward to facilitate inhalation. Birds, like lizards and snakes, use muscles in their rib cages to expand and contract their thoracic cavities. Birds' lungs, unlike those of most other vertebrates, are not elastic and do not inflate or deflate with breathing. Instead, inhalation fills a set of air sacs that can subsequently pass the air through the lungs (Figure 2.26). This system stores large amounts of air needed for the high metabolic costs of flight. Mammals have augmented their thoracic musculature with a diaphragm that contracts to expand the thoracic cavity and draw air into the lungs. Whereas relaxed birds have relatively

FIGURE 2.26 Air sac system in birds Diagram shows typical distribution of sacs using budgerigar (parrot) as example. There is a pair of sacs, one for each lung, for all but the clavicular air sac. Only one lung and one example of each paired set of sacs is shown in the figure. While there is a single clavicular air sac, it is divided into two lobes that encircle the syrinx and may be involved in vocalization. (After [100].)

As might be expected given their relatively simple ventilation systems, many modern reptiles do not vocalize. Exceptions include some turtles and tortoises, most gecko lizards, and most crocodilians [130, 266, 319, 326, 328]. In contrast, the more sophisticated ventilation system in mammals has made vocalization extremely common in this group. The roars of lions, rumbles of elephants, lowing of cattle, screams of the tree hyrax, howls of monkeys, and human speech are all examples of vocalization sounds. In a variation on this theme, some bats have a very thin ribbon of tissue just downstream from the free margin of each vocal cord. These membranes, which are thinner than full air sacs and must work to *exhale*, relaxed mammals have empty lungs and must work to *inhale*. The consequent differences in neuromuscular control of breathing may be partly responsible for the greater abundance of complex vocalizations in birds than in mammals.

All terrestrial vertebrates except birds position the valve for production of vocal vibrations at the top of the trachea [270]. This valve, called the **glottis**, likely first served functions other than vocalization. Possibilities include preventing food from entering the trachea, generation of internal pressures for egg laying or defecation, or prevention of air loss during diving [208]. When used to produce sounds, the glottal lips are called **vocal cords** (Figure 2.27). The glottis, along with its associated cartilages and muscles, is part of the **larynx**. In most vocalizing mammals and reptiles, sound vibrations are produced when the laryngeal muscles move the vocal cords into a laryngeal cavity at the top of the tracheal passageway. Upstream air pressure is then increased by contracting the muscles used for exhalation. At some point, the vocal cords begin to open and close, letting small puffs of air flow through the larynx. Additional muscles are often present that can vary tension on the vocal cords. This tension will help to determine the rate at which the vocal cords oscillate open and closed: increased tension usually leads to more rapid rates of vibration, and a spectrogram of the sound will thus show a higher fundamental frequency and a greater spacing between harmonics. Varying the tension during a call is often used to modulate both the fundamental and the harmonic structure in the resulting sound.

FIGURE 2.27 Mammalian larynx View from mouth of top of human larynx (A) and human larynx with soft tissues removed to show cartilages and ligaments (B). (C) Simplified diagram of essential working parts in mammalian larynx. Separate muscles open, close, and put tension on the vocal cords by moving them relative to attached cartilages. Cords are closed just prior to vocalization.

the vocal cord base, can vibrate independently and at much higher frequencies than the thicker part of the cords [164, 361]. Bats with these membranes typically echolocate by emitting short pulses of ultrasonic sounds in the dark and using the echoes to avoid obstacles and to locate food items (see Chapter 14). It has been proposed that the thicker bases of their vocal cords open and close to begin and end each pulse, and that airflow during the open phase causes the thinner membranes to vibrate independently at ultrasonic frequencies. Similar membranes are also known in some primates, cats, pigs, and llamas, but their function in these species is not yet clear [253].

Diving mammals present another special case. Because it is inefficient for these animals to release stored air when they are deep underwater, they need a way to trap and recycle air after it has passed through the vibratory valve during vocalization. Baleen whales (mysticete cetaceans) appear to generate vibrations in the larynx like other mammals, but pass the air into expandable nasal passages or a vocal sac attached to the larynx [9]. Toothed whales and porpoises (odontocete cetaceans), however, move air back and forth between nasal sacs situated between the larynx and the blowhole. A new valve, called **sonic lips**, has evolved in the passage between these sacs to produce the requisite vibrations [79, 80, 238, 239]. Seals, sea lions, and walruses also turn out to be highly vocal underwater (**Figure 2.28**). The loud and complex advertisement calls of male bearded seals (*Erignathus barbatus*), Weddell seals (*Leptonychotes weddellii*), ribbon seals (*Histriophoca fasciata*), and walruses (*Odobenus* spp.) are particularly striking [324, 345, 353]. Several of these species have special sacs attached to the trachea or the pharynx (the throat region between the larynx and the mouth), and the usual bony rings on one entire side of the trachea in the bearded seal have been replaced with a soft and expansible membrane [384]. These specializations contribute to underwater sound production, but the details are not yet understood. Tracheal sacs may provide air for long-duration vocalizations, and pharyngeal sacs, such as those found in frogs, may store air after vocalization for reuse.

Modern frogs and toads also produce sounds with a larynx at the top of their trachea, but like echolocating bats, most species use the glottis to turn airflow on and off. When on, the airflow passes over secondary membranes that are set into vibration and insert higher frequency components into the call (**Figure 2.29**). These membranes, unlike the ones in bats, are not attached to the margins of the glottis, but protrude into the airflow upstream (closer to the lungs) from the glottis [244–246, 337, 340]. In fire-bellied toads (*Bombina* spp.), the vibrating structures are thickened ridges on the sides of the larynx. These animals produce sounds on both inspiration and exhalation, and setting the ridges to vibrate with airflow in either direction requires symmetrical attachments. In contrast, common toads (*Bufo* spp.) have thin membranes, aimed downstream, that are set into vibration when the glottis pops open and airflow begins. In many toads, glottis oscillation is produced by mechanisms similar

FIGURE 2.28 Modifications of trachea for vocalization by phocid seals (A) Incomplete tracheal and bronchial rings and associated membrane in bearded seal (*Erignathus barbatus*). (B) Tracheal air sac in male ribbon seal (*Histriophoca fasciata*). There is only one sac, located on the seal's right side. Females usually lack the sac and in males, it appears to get larger with body size or age. (After [384].)

to that in mammals: upstream pressure, airflow, elasticity, and muscle tension combine to produce repetitive glottal opening and closing at rates of several hundred Hz [244, 245]. When the glottis is open, the vocal membranes then oscillate at fundamental frequencies of 1–2 kHz. In some toads, the vocal membrane oscillations are nearly sinusoidal and display little energy at higher harmonics in spectrograms.

Amphibian genera with more complex laryngeal structures include common frogs (*Rana* spp.), cricket frogs (*Acris* spp.), and tree frogs (*Hyla* spp.), which have perpendicular ridges at the end of the vocal membranes (forming a T in cross section). The glottis is usually opened and closed by muscles in these species. When it opens, air pressure first pushes the flattened edges of the two vocal membranes together to close the airflow, and then forces them open again, setting them to vibrate [337, 340, 394]. The decrease in pressure and Bernoulli forces then pull them back together, and the cycle repeats as long as the glottis is held partially open. The result is a long call consisting of successive pulses of high-frequency vibrations [144]. The duration of the call (up to many seconds) is determined by how long the muscles hold the glottis open; the pulse rate (usually several hundred Hz) is set by the physical structure and properties of the vocal membranes and the airflow; and the vibration of the membranes when open (usually one to several kHz) is also determined by physical properties of the membranes and the

FIGURE 2.29 Some common frogs and toads and their larynges Glottal opening is at the top of each diagram, and arrow shows direction of airflow during vocalization. Blue area below the glottis indicates the tracheal and laryngeal air space; white area above the glottis is the pharyngeal cavity. (A) Cricket frog (*Acris crepitans*). Vocal membranes are T-shaped with a slight thickening at midpoint. (B) European common frog (*Rana temporaria*). T-shaped vocal membranes are considerably enlarged on their ends relative to cricket frog. (C) African toad (*Bufo regularis*). These vocal membranes are very enlarged before the filamentous tip and incorporate an ossicle that is heavy enough to depress the fundamental frequency considerably. Note that toads often have two pairs of vocal membranes, one upstream from the other. (After [145, 248, 340].)

airflow. Whether harmonics are present in spectrograms of the vibrations within a pulse depends on how sinusoidally the membranes can vibrate when not touching.

Many frogs and toads attach fibrous masses to the upstream side of the vocal membranes. These masses often lower the fundamental frequency of the membrane vibrations, and they can significantly affect the movement of the membranes and thus the presence or absence of harmonic structure in the sound [247, 248, 404]. In the túngara frog (*Engystomops pustulosus*), unusually large masses are present in cavities adjacent to the vocal membranes. Air flows not only between the edges of the vocal membranes, but also laterally through these cavities. The masses are also attached to the wall of the larynx and to the vocal cords in ways that allow them to vibrate at about half the fundamental frequency of the vocal cords. Male túngara frogs can vary laryngeal tensions and airflows either to prevent oscillation of the large masses, producing the obligatory "whine" component of the call, or to allow the masses to vibrate interactively with the vocal membranes, producing the facultative "chuck" component after the whine [91, 162, 198, 327].

Perhaps because they have such sophisticated neuromuscular control over exhalation, birds exhibit the most diverse and complex vocalization patterns. Unlike frogs, reptiles, and terrestrial mammals, birds do not have a sound-producing valve at the top of the trachea, but instead have one or more vibrating valves near the junction of the trachea and the bronchi. The specialized cartilages and muscles associated with these valves are called the **syrinx**. Normally, the trachea and bronchi of vertebrates consist of bony or cartilaginous rings linked by connective tissue to form tubes. Many birds create a vibration-producing valve in the syrinx by expanding the soft tissues linking the bony rings into large **tympaniform membranes** [5, 26, 207]. In some cases, these membranes are created using incomplete C-shaped rings in which the missing bony tissue is replaced with soft tissues. In other cases, several adjacent rings are converted into flattened and flexible elements that are embedded in the softer tissues. As a third option, the distance between a pair of adjacent rings is increased and filled with a much larger patch of membrane. However created, pulling the syrinx toward the head or tail, rotating particular rings, or expanding the air pressure in the interclavicular air sac that surrounds the syrinx can cause the tympaniform membranes to buckle into the center of the tube where airflow will set them vibrating. Avian syringes have classically been divided into three categories based on where these membranes are located.

FIGURE 2.30 Example of bird tracheal syringes All figures are ventral views with mouth at top and lungs below. (A) Syrinx of blue-and-gold macaw (*Ara ararauna*). (B) Cross section of macaw syrinx showing lateral tympaniform membranes buckled into airflow (vertical arrows) by external muscles. (C) Syrinx of domestic chicken (*Gallus gallus*). Horizontal arrows indicate which membranes are buckled into tracheal cavity to create vibrating valve. (D) Syrinx of imperial pigeon (*Ducula latrans*). (After [26, 46, 207, 227].)

In birds with **tracheal syringes** the tympaniform membranes are located at the base of the trachea just before the junction with the two bronchi (Figure 2.30). Because these membranes form part of the outer wall of the trachea, they are called **lateral tympaniform membranes**. In many of these species, such as parrots and tyrannid flycatchers, but not pigeons and doves, the last 2–8 tracheal rings are fused into a single bony chamber called a **tympanum**. This appears to serve as a firm base against which the tension in adjacent membranes can be adjusted. In chickens and some relatives (Galliformes), doves and pigeons (Columbiformes), parrots (Psittaciformes), and some wading birds (Ciconiiformes), a tympaniform membrane exists on each side of the trachea just above the junction with the bronchi. In furnarioid suboscines (Passeriformes) such as woodcreepers, ovenbirds, gnateaters, antpipits, and antbirds, and in whistling ducks (genus *Dendrocygna*), a single tympaniform membrane is positioned centrally on the ventral side of the trachea. Physiological studies have demonstrated that these tracheal tympaniform membranes are indeed the source of vocal vibrations [46, 47, 95, 132–135, 138, 139, 153, 226, 227]. In pigeons and parrots, the tympaniform membranes are already partially buckled into the tracheal cavity during normal respiration. To create sounds, muscles move the syrinx toward the head, buckling the membranes further until they form a thin slit. Airflow through this slit generates the vocal vibrations, and adjacent muscles vary tension on the membranes to alter fundamental frequencies.

Birds with **bronchial syringes** have 1–2 tympaniform membranes on each bronchus below the junction of the trachea and bronchi (Figure 2.31). Examples include oilbirds, pauraques, and frogmouths (Caprimulgiformes), cuckoos, coucals, and guiras (Cuculiformes), penguins (Sphenisciformes), and some owls (Strigiformes). Oilbirds vocalize by relaxing the tension between the trachea and the syrinx, thus causing the lateral (external) tympaniform membranes in each bronchus to buckle into the bronchial cavity until each is very close to the corresponding medial (internal) tympaniform membrane. Airflow then generates vibrations in the tympaniform membranes [363, 371]. Note that these birds have a vibration generator on each bronchus and can theoretically produce two independent (i.e., not necessarily harmonically related) sounds at once. Penguins use unique combinations of the two sounds for individual recognition [12].

FIGURE 2.31 Example of bird bronchial syringes (A) Syrinx of ground cuckoo (*Carpococcyx renauldi*). (B) Syrinx of oilbird (*Steatornis caripensis*). Note that there are tympaniform membranes on both sides of each bronchus in both species. (A after [26]; B after [207].)

FIGURE 2.32 Example of bird tracheobronchial syrinx External view with relevant muscles attached (A) and cross section (B) of mockingbird syrinx when not vocalizing. Arrows show direction of airflow when exhaling and vocalizing. Medial and lateral labia are moved into airflow during vocalization by rotating third bronchial cartilage (B3). (C) Diagrammatic cross section of songbird syrinx when breathing, showing quiescent position of labia and B3 cartilages. (D) Configuration of songbird syrinx when producing high-frequency notes. Third bronchial cartilages (B3) are rotated forcing lateral labia into airflow. For high-frequency notes, left side is closed completely and right side pulses open and closed. (E) Configuration of songbird syrinx when producing low-frequency notes: right side is closed and left side pulses open and closed. (After [358].)

The majority of birds have **tracheobronchial syringes** in which the main expanses of elastic tissue are the **medial tympaniform membranes** located on the insides of each bronchus just below the junction of the trachea and the bronchus (Figure 2.32). Examples include ratites such as cassowaries (Struthioformes); most ducks and geese (Anseriformes); gulls and shorebirds (Charadriiformes); woodpeckers, barbets, and toucans (Piciformes); trogons, hornbills, and kingfishers (Coraciiformes); and perching birds (Passeriformes, with the exception of the furnarioid suboscines noted earlier). For many years, indirect evidence suggested that the medial tympaniform membranes were buckled into each bronchial cavity and set into vibration by concomitant exhalation [118, 139, 159, 352]. Subsequent work on songbirds (the Oscine Passeriformes) showed that vibrations are generated not by tympaniform membranes but by a pair of soft tissue pads, called the **lateral** (outside) and **medial** (inside) **labia**, located opposite each other in each bronchus [152, 155, 199, 226–228, 370]. A similar mechanism may operate with analogous structures in echolocating swiftlets [362]. In songbirds, each lateral labium is attached to a syringeal ring that can be rotated. Each medial labium is connected directly to the medial tympaniform membranes below it. Rotation of the ring behind a lateral labium and movement of the entire syrinx toward the head forces the two labia into the bronchial cavity. Such a syrinx thus has two independently vibrating valves (one in each bronchus). As with the other two types of syringes, vibrations generated by each valve are typically periodic but nonsinusoidal.

Web Topic 2.7 ***Animations of vocalizing birds***
Dr. Roderick Suthers and his team at Indiana University have pioneered our understanding about how the avian syrinx works. His lab has conveniently produced several animated clips demonstrating key steps in song production by northern cardinals and brown-headed cowbirds.

While all songbirds have labia and appear to use them to create vibrations, other taxa with a similar syrinx (e.g., gulls) appear to lack labia [132, 207]. All taxa with tracheobronchial syringes have medial tympaniform membranes, and it is possible that these contribute to sound production when labia are absent. Some species also show thinned membranes, (often called lateral tympaniform membranes but not to be confused with the lateral membranes in tracheal syringes), in the outer wall of the bronchi where songbirds would have a labium. Other species appear to have intermediate types of syringes in which tracheal lateral membranes extend down past the junction with the bronchi, and medial membranes that extend further toward the head than in songbirds [207]. Male sage grouse (*Centrocercus urophasianus*) have thin

membranes on the external top sides of each bronchus and apparently can use these independently to produce two different and unrelated sounds at once [211]. An extreme case occurs in some geese and swans in which nearly the entire top section of each bronchus consists of membranous tissues. Sound production in geese is clearly an effective process, but the exact mechanisms remain to be studied.

Although both bronchial and tracheobronchial syringes allow for concurrent production of vibrations from two independent sources, the songbirds have taken most advantage of this opportunity [149–151, 154, 228, 274, 276, 278, 359, 366, 368–371, 373, 374]. With their sophisticated syringeal musculature, songbirds can move the labia into or out of the airflow at will. They can also use the labia to close off the airflow in a bronchus. This allows songbirds to produce rapid and complex songs by alternating between the two sides of the syrinx for successive syllables. Because the two sides of the syrinx are largely independent (except perhaps in very small songbirds; [277]), the successive syllables in a song can have quite different amplitude and frequency patterns. Many species have adopted a division of labor, producing low-frequency syllables on the left side of the syrinx and high-frequency syllables on the right. Male cardinals (*Cardinalis cardinalis*) combine these tricks by producing frequency-modulated syllables in which the first half is generated by one side of the syrinx, and the second half is added nearly seamlessly by the other side (Figure 2.33). In addition to using the two sides of the syrinx to produce successive syllables or successive parts of syllables, species such as brown thrashers (*Toxostoma rufum*) may use the two sides to produce two concurrent notes that are not harmonically related. This, combined with a specialization of the right side of the syrinx for rapid modulations, allows this group to produce some very complicated sounds.

Many songbird males include trills in their songs. These are very rapid and long duration bursts of successive notes. At lower trill rates, the singers can take **mini-breaths** between syllables to maintain sufficient air to continue the trill over long periods; at higher rates, no inhalation is possible and the birds simply pulse the labial valve on one side of the syrinx until they run out of air [171, 172]. As a result, there is often an inverse relationship between trill duration and the trill rate, with larger birds having to switch to pulsatile trills at a lower trill rate than smaller birds [374]. A similar trade-off occurs between the frequency range over which a trill syllable can be swept and the trill rate [18]. Many songbirds thus appear to have pushed vibration production to a point where any further increase in one property (e.g., trill rate) degrades another concurrent property (e.g., trill duration or frequency range of each syllable). These

FIGURE 2.33 Two examples of frequency-modulated syllables in cardinal song (*Cardinalis cardinalis*) In each example, the horizontal dashed white line in the spectrogram shows the break point (at about 2.7 kHz) at which one side of the syrinx takes over from the other to produce a nearly continuous single syllable. (A) Male song showing upswept syllables. Very faint break can be seen in spectrogram at 2.7 kHz as the left side of the syrinx takes over from the right side, but no break is visible in the waveform. (B) Female song showing downswept syllables. Note the visible break in both spectrogram and waveform when the right side of syrinx takes over from the left side.

trade-offs will be of relevance later when we discuss the role of song in avian mate choice.

The final mechanism involving fluid flow over solid parts is called **aerodynamic vibration** [119]. In contrast to the vocalizations just discussed, the solid parts remain immobile as fluid passes over them and do not themselves vibrate. Instead, the flow of fluid through an aperture or against a hard obstacle will generate local turbulence in the medium. Turbulence takes the form of eddies or vortices that spiral away from the aperture or obstacle; their size determines the frequencies of any far-field sounds produced [119, 392]. There are three general types of aerodynamic sounds. Streaming of fluid through an aperture in a solid barrier will generate a wide range of vortex sizes; the resulting sounds will have many different frequencies present and be noisy and atonal like a hiss. This is an inefficient process, and the resulting sounds are likely to be useful at close range only. It is how humans generate many of their consonants. A second method involves aiming a steady stream of fluid against a small or sharp obstacle. This is more likely to produce vortices of similar size than is an aperture, and thus produces somewhat tonal sounds that can be heard at a distance. An example is the musical wail generated by wind against the outside corners of a building. Finally, positioning an aperture or obstacle to an airstream near a cavity can result in selective amplification (resonance; see next sections) of a limited number of vortex frequencies, resulting in a relatively pure-tone whistle. It is the most efficient of the three aerodynamic mechanisms and can generate sounds heard at significant distances. Humans whistle using the oral cavity in this manner.

A number of insects force air (or in grasshoppers, foam) out of their respiratory spiracles to produce hissing sounds [92, 271, 357]. In a similar manner, various reptiles force air through a partially closed and immobile glottis or through their mouths or nostrils to produce hisses [130, 410, 412–414]. Similar oral or nasal hisses are produced by some birds and mammals. More whistle-like mechanisms have been described in the death's-head hawkmoth (*Acherontia atropos*), which draws air into and out of its pharynx creating a squeaky sound in each direction [92, 330], and the king cobra (*Ophiophagus hannah*), which "growls" using tracheal air spaces to amplify vortices generated as air passes through its glottis [410]. While it was initially suggested that some bird vocalizations might be whistles [54, 136, 137, 275], this proposition has since gained no experimental support [155, 374].

Web Topic 2.8 *Linear versus nonlinear systems*

Although animal sound vibrators typically change frequency and amplitude linearly as the forces on them are changed, most will adopt less predictable nonlinear behavior at extreme force values. Some animals such as parrots, zebra finches, and canids use nonlinear vibration behavior to increase their vocal diversity.

Modification and coupling of sound signals

Clearly, there are several ways that arthropod and vertebrate animals can generate vibrations. It is not so easy, however, to convert these initial vibrations into useful sound signals. There are two problems. First, many of the initial vibrations are of such low amplitude that by the time they are coupled to the propagating medium, they are no longer detectable at the required distances. Second, many mechanisms for coupling vibrations from animals into a propagating medium can be hopelessly inefficient. The obvious solution is to amplify the vibrations before coupling, and then use those mechanisms that provide the most efficient coupling. As so often happens in physics and biology, the best amplifiers are not necessarily compatible with the best coupling mechanisms, and sound production is necessarily compromised. Below, we examine each of these options in principle, and conclude this chapter with some of the compromises that animals have adopted in practice.

MODIFICATION OF SOUND SIGNALS: RESONANCE AND FILTERING The vast majority of vibrations generated by animals have periodic but nonsinusoidal waveforms, and thus will consist of many different frequencies. Noisy sounds (e.g., hisses) also contain many different frequency components. When a vibrational pattern is introduced into an object such as a wing, swim bladder, or pharyngeal cavity, some of the component frequencies will have wavelengths that fit within the dimensions of the object, and some will not. If the acoustic impedance of the object is similar to that of the adjacent medium, this fit does not matter, as all frequencies will simply propagate across the boundary and into the medium. If there *is* a significant impedance difference between the object and the medium, then much of the sound energy inside the object will be reflected back at its boundary and the object will store successive energy inputs cumulatively. The result is a series of superimposed waves for each frequency component in the vibration: some will have just entered the object from the vibrational source, some will have already traversed the object and bounced back the other way, and still others will have been reflected multiple times between opposite sides of the object. Given the right ratio between the wavelength of a frequency component and the dimensions of the object, both incoming and reflected waves will be in phase; successive waves will combine their sound pressures additively; and over time, the amplitude of the original vibrations will be amplified. This is known as **resonance** and those frequencies that fit and are amplified are called **normal modes** of the object. At the same time, those components that do not have the appropriate wavelength-to-object ratio, (e.g., do not fit), will produce reflected waves that are out-of-phase with incoming waves, and the resulting destructive interference will reduce the amplitudes of these components. This is known as **filtering**. See the examples of resonant systems at Web Topic 2.2.

Whether a given frequency component is amplified by resonance or reduced by filtering depends on the object's size, shape, speed of sound, and acoustic impedance relative

FIGURE 2.34 Frequency and time responses of resonators (A) Two resonators with a resonance at 2000 Hz but differing in their Q (quality) factor. The high-Q resonator is a better amplifier than the low-Q resonator at their shared resonant frequency. Q values can be estimated from such a graph by finding those frequencies on either side of the resonant frequency for which the pressure amplitude is 70.7% (–3 dB) of the peak value. (These will also be the frequencies at which the power is *half* of the peak value). The –3 dB bandwidth is the difference between these two frequencies and is marked with arrows on the graphs. Q is then the ratio of the resonant frequency to this bandwidth. (B) Damping properties of the same two resonators at their resonant frequency. Graphs show the amplitude of successively radiated cycles once the source of sound vibrations ends. The high-Q resonator is poorly damped, and continues to radiate for many cycles after stimulation ceases. The highly damped low-Q resonator, on the other hand, quickly loses all prior sound energy and becomes silent. Damping and Q are inversely related.

to the nearby medium. Small objects cannot accommodate large wavelengths; thus any resonant amplification will be limited to higher frequencies. However, if a given fundamental frequency of the introduced vibration fits within an object, most of the higher harmonics in a periodic nonsinusoidal vibration will also fit and can be amplified. The natural modes are then likely to be integer multiples of some fundamental value. If the fundamental frequency of the introduced vibrations is less than the lowest natural mode of the object, the latter will filter out the fundamental, amplify subsets of adjacent harmonics (called **formants**), and filter out intervening subsets. Nonsymmetrical objects may be able to accommodate several unrelated frequencies and thus can have normal modes that are not necessarily harmonics of the same fundamental frequency. The speed of sound in the object is important because this determines the wavelength of each frequency component in the introduced vibrations. Where the object is a solid, (e.g., a cricket wing), the relevant speed of sound is that of the relevant tissues. Many animals use gas-filled cavities either in their bodies or in a substrate for resonance. The relevant value in such **cavity resonators** is the speed of sound of gas in the cavity.

If the acoustic impedance of the object is sufficiently similar to that of the medium, introduced sound energy is quickly lost through the boundary. A sudden short pulse of vibrations will cause only a few cycles of successive wave overlap before the signal has completely moved into the medium. We say that such a system is **highly damped**. Because only a few recent waves will overlap in this object even with sustained stimulation, there is less opportunity to produce significant resonance or filtering, and thus the frequency selectivity of the object will be low (Figure 2.34). We say that the object supports a **wide bandwidth** (of frequencies). Objects with wide bandwidths and high damping are said to have a **low Q** (quality of resonance). In contrast, an object with an acoustic impedance very different from the medium will be very slow to transfer sound energy to the medium. Many successive waves will build up inside it, allowing for very strong resonance and filtering. Such an object generally will have a very narrow bandwidth around each normal mode frequency. A prior signal may continue to reflect back and forth inside the object long after the input source has halted. This is called **ringing** and reflects very low damping. An object that loses sound energy slowly and has a narrow bandwidth and low damping is said to have a **high Q**.

While a high-Q resonator can significantly amplify a narrow bandwidth of frequencies if these are present in the introduced vibrations, it will smear and distort any rapid amplitude and frequency modulations of those vibrations. Similarly, a low-Q resonator can track and replicate rapid modulations accurately, but it will result in much lower levels of amplification. There is thus a trade-off between amplification and accurate temporal tracking when using secondary objects to amplify signals. In general, animals communicating

over long distances, such as cicadas, are more likely to use high-Q resonators to maximize signal range. The cost is that they will lose any rapid temporal patterns in the signal. At shorter distances, animals need less amplification, and one expects—and finds—sound signals with greater temporal complexity.

COUPLING TO THE MEDIUM: LIMITS ON EFFICIENCY At some point, an animal's vibrations must be radiated into the propagating medium (air, water, a solid substrate, or some boundary between two media). If the medium is a fluid (e.g., air or water) the surface of a vibrating radiator forces a layer of medium away from itself during part of each cycle, and causes medium to flow toward it during the rest of the cycle. If the medium is a solid, the pressure forces of the radiator generate corresponding pressure waves in the solid with little if any movement of medium molecules. The efficiency of this vibrational transfer is critically dependent on the size of the radiating organ, the way in which the organ moves, and the organ's acoustic impedance relative to that of the medium.

For fluid media, a larger radiator is better than a small one, because larger radiating surfaces will move more fluid per cycle. Another way to see this advantage is to consider two spheres differing in diameter by a factor of ten and both pulsating in air or water at the same rate. Suppose each sphere expands and contracts the same small distance per pulsation. The amount of medium moved *per unit area of sphere surface* will be very similar for the two spheres, and thus the initial energy provided per unit area will be similar. However, by the time the sound generated by the small sphere travels a distance from its center equal to the radius of the large sphere, its pressure will have decreased significantly due to spreading loss. It follows that at any further location equidistant from the two spheres, the larger sphere's sound pressures will always be greater. As a result, larger radiators produce more intense sounds for all frequencies.

Efficiency can also be affected by *how* the radiator moves, especially at low frequencies. A **monopole** radiator, like the spheres in the example above, simply expands and contracts equally in all directions. It thus changes its size to couple its vibrations to the medium. A **dipole** radiator, in contrast, is coupled to the medium by moving back and forth along an axis. The simple disk that we discussed at the beginning of this chapter is a good example of a dipole radiator. Finally, a **quadrupole** radiator maintains its location and size but changes its shape. A fish swim bladder that is compressed at one end and balloons out on the other is a good example of a quadrupole radiator. While there are additional radiators used by animals, nearly all of these behave like one or some combination of these three basic types. For example, the open mouth of a vocalizing bird or mammal radiates sound in a manner similar to a monopole placed close to a solid reflecting surface [119].

The coupling of vibrations to a medium becomes increasingly inefficient as the wavelengths of the sounds being radiated grow larger than the diameter of the radiator. This is true regardless of which type of motion is used. However, whenever the radiators are smaller than the wavelength, monopoles are much more efficient than dipoles, which in turn are more efficient than quadrupoles [119, 167]. In part, the increased inefficiency of dipoles and quadrupoles, when compared to monopoles, arises from acoustic **short-circuiting**. Because these radiators create rarefactions and condensations in different locations but at the same time, sufficiently slow oscillations (e.g., low frequencies) allow the condensation enough time to propagate to the rarefaction and cancel it out [255]. Once the radiator is at least one-third the size of the wavelength or larger, short-circuiting is minimal, efficiency becomes dependent only on the absolute size of the radiator (as noted earlier), and the type of motion is largely irrelevant.

Web Topic 2.9 ***Radiation efficiency and sound radiator size***

Monopoles, dipoles, and quadrupoles all show reduced efficiency when the wavelengths being produced are larger than the sound source. Here we explain in more detail why this happens.

These effects essentially limit sounds useful for long-distance communication to those with wavelengths no greater than 1–2 times the sender's body size. For animals smaller than 30 cm, this requires vibration frequencies of 0.5 kHz or more in air, and 2–3 kHz in water. The fastest muscles known in vertebrates are those used to generate repetitive vibrations in toadfish swim bladders; their maximal contraction rate is several hundred Hz [325]. Insect flight muscles just reach the minimal value of 1 kHz for 15 cm animals, but can barely generate the 5 kHz rate required for a 3 cm katydid [388]. Some cicadas achieve vibration rates twice that of their maximal muscle contractions by buckling their two tymbals out-of-phase with separate muscles [124]. Sea robins achieve doubling by alternating contractions of the muscles on each side of their swim bladder [74]. However, the more widespread solution to this problem is a **frequency multiplier**: a device that produces many vibratory cycles for every muscle stroke. Stridulation and vocalization are two vibration-generating mechanisms that act as frequency multipliers: each stroke of a katydid's wings causes many successive teeth in its file to pass over the corresponding plectrum, and each expelled breath by a vertebrate produces many successive vibrations of its glottis, labia, or tympaniform membranes. Without devices for frequency multiplication, most small animals would be unable to send sound signals or be limited to very short-range acoustic communication.

In addition to creating differences in low-frequency efficiency, different radiator motions also produce different distributions of sound pressure in the medium. The spatial pattern of pressure around a sound source is called its **sound field**. For example, a spherical monopole far from any boundaries produces the same pressure at all points

equidistant from its center. A dipole, however, suffers negative interference between radiating condensations and rarefactions at points midway between its ends and perpendicular to its vibrational axis. Points closer to one or the other end of the vibrational axis show only minor interference and thus higher pressures. A graph connecting all locations at a given pressure around a dipole will show two large **lobes**, one radiating from each end of the vibrational axis. These lobes become narrower at higher frequencies. A quadrupole typically shows a sound field graph with four lobes (see Web Topic 2.2 for animated examples). Note that proximity between a radiator and a reflecting surface can change the sound-field shape. A monopole near to a reflecting surface will generate lobes similar to those of a dipole in open space; a dipole close to a surface will reduce acoustic short-circuiting and act more like a monopole. The significance of sound fields for communicating animals is that sounds from monopole radiators can be detected at equal distances in all directions, whereas the range of detection of a dipole can be highly dependent on the relative angle of sender and receiver.

The final factor affecting radiation efficiency is the relative acoustic impedance of the radiator and the propagating medium. Ideally, the impedance of the radiator would be identical to that of the medium to ensure complete transfer of the vibrations across the boundary. Aquatic organisms consist largely of water, and sounds are easily radiated into the medium. A hippopotamus lying at the water's surface is an interesting case: when it vocalizes to produce airborne signals, its submerged tissues also vibrate, coupling the same sounds to the surrounding water, where submerged conspecifics can detect them [19, 20]. More commonly, a terrestrial radiator has an acoustic impedance that is quite different from the medium. The acoustic impedance is much higher within a tracheal tube than in the outside air, causing sound vibrations to be reflected back into the trachea when they reach the mouth opening. The solution to this problem is to provide an **impedance matching device** at the boundary to ease the transition.

One impedance-matching device used by many terrestrial vertebrates is an inflated air sac. The thin membrane of the sac and the contained air create a combination that has an acoustic impedance intermediate between ambient air and solid living tissues. If sufficiently inflated, it can also produce a much larger radiating surface than any other part of the animal. Examples include the throat sacs of most frogs and toads, and the esophageal sacs of doves and pigeons.

Another common impedance-matching device is a **horn** like the bell on a trumpet: its narrow end matches the high acoustic impedance of the attached tube, and as the bell flares, it provides a gradual match to the acoustic impedance of open air. Horns can greatly improve the efficiency of radiation. The cost is that, like most acoustic tools, they can only radiate sound efficiently over a limited frequency range that depends on their shape and size. In addition, the resulting sound fields are usually very directional, with one or more lobes [119]. Despite these constraints, many birds and mammals use an opened mouth or beak as a horn, and some species even elaborate the opening to produce a flared bell like a trumpet (Figure 2.35).

Horns made of living tissue will not work underwater because sound will pass through the horn walls without any channeling. Toothed whales (Odontocete Cetacea) have

FIGURE 2.35 Horns on bats for sound emission (A) Flared bell around the mouth of a male hammer-headed bat (*Hypsignathus monstrosus*). These bats produce loud calls to attract females for mating. (B) African leaf-nosed bat (*Hipposideros cyclops*). This bat emits its echolocation calls through its nostrils, which are surrounded by a horseshoe-shaped horn. (C) Neotropical leaf-nosed bat (*Mimon crenulatum*). This bat also emits its echolocation calls through its nostrils, but in contrast with the prior species, hosts a vertically elongated horn that can be moved in concert with pulse emission.

FIGURE 2.36 Resonance and impedance matching devices in toothed (Odontocete) cetaceans (A) Diagram of acoustic radiation structures in the spinner dolphin (*Stenella longirostris*). Phonic lips are a presumed source of vibrations and are interposed between lungs and blowhole. The skull is a partial reflector aiming sounds forward, where they are focused and radiated by the melon, which consists of a layered mixture of oils and fats. (B) Diagram of acoustic radiation structures in adult male sperm whale (*Physeter macrocephalus*). Vibrations are thought to arise in phonic lips located at the junction of the right nasal passages and the vestibular air sac. They may then follow several concurrent paths involving direct radiation into the water, reflections back and forth between the vestibular and nasofrontal air sacs, reflections and modification inside the oil-filled spermaceti organ, and absorption and radiation from the fatty material (called junk by whalers) just below the spermaceti organ.

evolved an aquatic equivalent, however (Figure 2.36). The **melon** on the whale's forehead consists of multiple layers of special oils and fats that form a graded sequence of acoustic impedances. Sounds generated by phonic lips are reflected off of the bony skull and then focused and radiated forward through the melon [11, 61, 131, 190, 210, 260–262, 273, 419].

Balancing amplification and efficiency

Some animals do not require special modification or coupling devices for their vibrations. The beating wings of displaying fruit flies are dipoles, and the wavelengths of the sounds produced are several thousand times as large as the insects themselves. They are thus very inefficient as sources of far-field sounds. However, because female receivers are within a body length of a displaying male, the strong near-field flows are sufficient stimuli at that close distance. Certain arthropods [15, 23, 58, 62, 64, 65, 67, 69–71, 96, 97, 148, 185, 194, 254, 308, 320, 390] and elephants [165, 279–282] transfer vibrations through their appendages into solid substrates. Because the vibrating animal legs (and insect proboscises) are also solid, impedances between the animals and the medium are not sufficiently different to require elaborate modification and coupling devices. However, some filtering and resonance in the appendages themselves probably affect which frequencies are most apparent in the substrates.

Crickets and katydids produce stridulations by rubbing their forewings together. The file and plectrum are both small and thus inefficient sound radiators. However, they transfer the vibrations to adjacent areas of the forewings, (called the *harp* in crickets and the *mirror* in katydids), that act as resonant radiators [31, 34]. Cricket harps have low damping and radiate a highly amplified narrow band of frequencies. Katydid mirrors are more highly damped but produce a wider bandwidth of sound. In both groups, the sound-radiating wings act as dipoles, which makes them susceptible to acoustic short-circuiting at low frequencies. Because low frequencies propagate further, this poses a problem for long-distance signalers. Tree crickets (Oecanthinae) deal with this problem by calling near the edge of a leaf or putting their bodies in a hole or notch in a leaf (Figure 2.37A,B); by increasing the distance between concurrent condensations and rarefactions, they can radiate low-frequency sounds at reasonable amplitudes [125, 126]. The short-tailed cricket (*Anurogryllus muticus*) excavates a horn-shaped depression in the ground and positions itself in the cavity so that reflections of its stridulations from the cavity walls minimize short-circuiting and turn the cavity into a directional monopole [30, 125]. Mole crickets also create a horn in the ground surface, but then connect it through a narrow tunnel to a bulbous cavity below (Figure 2.37C). The combination of horn and cavity results in a complex

FIGURE 2.37 Insect strategies to maximize radiated sound pressures *Oecanthus fultoni* (A) and *Neoxabea bipunctata* (B), both tree crickets, reduce acoustic short-circuiting by placing their bodies in notches or holes that they have chewed in leaves. By the time a pressure condensation has propagated away from one side of the body and around both sides of the leaf, it is too attenuated to interfere significantly with a rarefaction. (C) Mole cricket (*Scapteriscus acletus*) stridulating at a critical location in its burrow that provides both a resonant amplification of its vibrations in the nearby bulb and enhanced radiation efficiency due to the funnel dug into the opening. (C after [29].)

resonance structure that is carefully tuned to the insect's fundamental stridulation frequency [27, 29, 31, 34].

Most cicadas have a large air-filled sac in the center of their abdomen that acts as a tuned cavity resonator for the vibrations produced by the two nearby tymbals [33–35, 305, 332, 333, 354, 389]. The amplified sound is radiated through two large eardrums located on either side of the body. In contrast, the gas-filled swim bladders of fish [106, 220] and inflated throat sacs of frogs and toads [145, 198, 307, 310] do not appear to function as cavity resonators. The walls of both types of structures do not differ sufficiently in acoustic impedance from the medium to retain successive waves inside their respective cavities, and are thus heavily damped. However, the properties of the vocal sac tissues in frogs appear to be adjusted to act as filters that emphasize particular harmonics produced by the larynx [163]. In fish, the temporal pattern of acoustic signals is key to species identity, and low-Q swim bladders may thus be advantageous. Frog and toad throat sacs have acoustic impedances intermediate between solid tissue and free air, and thus should be good radiators. However, many frogs and toads also radiate sound from their entire bodies, and like cicadas, some species such as bullfrogs even radiate sound from their eardrums [307]. A number of frogs, like mole crickets, create burrows with cavity resonances tuned to their calls [13, 294, 295], and one Asian species, *Metaphrynella sundana*, adjusts the frequency and temporal characteristics of its calls to match the cavity resonance of the tree hollow in which it lives [224, 225].

The opened mouths or beaks of reptiles, birds, and mammals function as monopole radiators and are thus relatively efficient. However, most species exploit resonant properties of their vocal tracts to modify the patterns in the initial vibrations and to increase coupling further. Even when the beak or mouth is used as an impedance-matching horn, the acoustic impedance inside the vocal tract is sufficiently higher than outside that some sound energy is reflected at the opening back into the tract. The reflected sound waves then interfere with subsequent waves moving toward the mouth to produce resonance. Since the vocal tract is roughly tubular, its normal modes depend primarily on the length of the tract and whether the ends are open or closed. If the tube is open on both ends, the lowest normal mode will have a wavelength approximately equal to twice the length of the tube; if it is closed on one end, the first mode's wavelength will be four times the length of the tube. Thus closing one end decreases the frequency of the lowest normal mode by a factor of two. Since most birds and mammals produce vibrations with a fundamental frequency lower than the lowest normal mode of their vocal tract, the upper vocal tract acts as a resonator and filter to emphasize some vibrational frequencies over others. Attaching additional cavities to the vocal tract can both alter and accentuate the normal modes of the vocal

FIGURE 2.38 Elongated tracheae in birds (A) Trumpeter swan (*Cygnus buccinator*) showing coiling of elongated trachea inside hollowed breastbone. (B) Magpie goose (*Anseranas semipalmata*). Elaborate tracheal coils are located just under skin of breast. (C) Spoonbill (*Platalea leucorodia*). The tracheal coils lie above the breastbone (sternum). (D) Manucode bird-of-paradise (*Manucodia keraudrenii*). Highly convoluted trachea is also arrayed just under skin of breast. (E) Capercaillie grouse (*Tetrao urogallus*). Single loop lies just under skin of breast. (F) Crested guinea fowl (*Guttera edouardi*) with single loop stored in special hollow of clavicle bones. (G) Helmeted curassow (*Crax pauxi*). Elongated coil lies along breastbone just under skin. (H) Whooping crane (*Grus americana*). Sternum is hollowed out to accommodate extensive tracheal coils. (B after [113]; A, C–H after [251].)

tract. As a general rule, males are more likely than females to have such additional cavities or to have larger ones; however, there are exceptions, such as painted snipe (*Rostratula* spp.), in which females have the more elaborated vocal tracts [251].

The basic avian vocal tract consists of the beak, pharyngeal cavity, trachea, and syrinx when the vibrating valve(s) are closed. When the vibrating valve(s) are open, the upstream respiratory components, including the bronchi, lungs, and air sacs, are similar in acoustic impedance and must be included in the calculation of the length of the vibrating column of air. Thus a typical bird may have two sets of normal modes: one in which the vibrating valves are open, and another in which they are closed. As long as damping in the vocal tract is low relative to the vibration rate of the valves, both sets of normal modes can contribute to the formants in the radiated sound [119].

Birds have multiples ways to adjust the normal modes of their vocal tracts (Figure 2.38). A permanent mechanism is to elongate the trachea beyond a direct connection between syrinx and mouth. This will lower the frequencies of all normal modes. Elongated tracheae are found in curassows and their allies, grouse, and guinea fowl (Galliformes); swans and magpie geese (Anseriformes); limpkins and cranes (Gruiformes); painted snipe (Charadriiformes); spoonbills and wood ibises (Ciconiiformes); and manucode birds-of paradise (Passeriformes) [26, 63, 110, 113, 128, 140, 251]. Oilbirds have

FIGURE 2.39 Syringeal bullae in ducks Males of many species of ducks have a cartilaginous bulla on the left side of their syrinx or just above the syrinx on their trachea. The shape and complexity differs among species, and the bulla is often a useful character for taxonomy. (A) Dorsal view of tracheal bulla, trachea, and upper bronchi of male mallard duck (*Anas platyrhynchos*). (B) Cut-away view of mallard syrinx showing presumed airflow during vocalization. A valve in the right bronchus can block airflow on that side while airflow on the left is routed through the bulla before rejoining the trachea (arrows). (After [207].)

asymmetrical bronchial syringes with the valves on the two bronchi situated at different distances from the junction with the trachea. This results in different normal modes for the two sides of the vocal tract [367]. An additional permanent mechanism is the attachment of a fixed resonant cavity at a location along the vocal tube. This is largely found in male ducks (Anseriformes), which have one or more bony **bullae** (Figure 2.39) attached just above or to the side of the syrinx [26, 202, 207].

A more customizable approach is to open or close the oral end of the vocal tract with the beak or tongue: closing lowers the frequencies of all the normal modes in the tract; opening increases these modes [187]. The greatest effect will be on higher modes and thus on the higher harmonics in the syringeal vibrations [120]. Many birds vary their beak and tongue positions in synchrony with the amplitude and frequency modulations of their syringeal vibrations [25, 156, 157, 191, 300–302, 398]. Cardinals (*Cardinalis cardinalis*) coordinate beak gape with a muscular expansion and contraction of the pharyngeal cavity and upper esophagus to remove all but the fundamental component in their syringeal vibrations before radiating the songs [122, 318]. Because many syllables of these songs are rapidly frequency modulated, the volume of the cavity must be altered just as quickly to track the changing fundamental frequency of the vibrations. See the animation at Web Topic 2.6.

Other birds use air-filled chambers to modify, amplify, and even radiate their vocalizations (Figure 2.40). Doves keep their beaks closed during vocalization; airflow toward the head picks up vibrations in the syrinx, and then passes through the glottis into an inflatable esophageal chamber. The wall of this chamber, enveloping the trachea and puffing up the breast of the bird, acts both as a filter/resonator and as the main radiator of the dove's vocalizations [24, 121]. Many species of grouse (Tetraonidae, Galliformes) inflate esophageal sacs and use them for modifying and radiating vocalization as well as for eversion of colored skin patches on the sides of the head or body [188]. Other birds that use inflatable sacs for vocalization resonance and radiation include emus (Struthioniformes), bustards (Gruiformes), musk ducks (Anseriformes), the kakapo parrot (Psittaciformes), the American bittern (Ciconiiformes), and button quail (Charadriiformes) [83, 207, 250, 251].

In mammals, the acoustic impedance of the respiratory tract upstream from the glottis is sufficiently greater than that downstream that even when the valves are open, the upstream tubes have little effect on resonance and filtering [119]. This excludes the trachea as a possible resonant cavity, and limits most terrestrial mammals to the short space between the glottis and the mouth or nostrils for any resonance, filtering, or coupling devices. Despite these constraints, many mammalian species rely heavily on these processes during sound emission.

The open mouths of many mammals, as well as special nose-leaf structures around the nostrils in some echolocating bats, can easily function as impedance-matching horns [119, 168, 170]. Certain body positions may accentuate this effect and modify normal modes [174]. Pharyngeal and nasal cavities are often used as resonance- and impedance-matching devices [110–112, 114, 313-315, 317]. To make these cavities large enough to accommodate lower frequencies, some mammals depress their larynx away from the mouth, either permanently or when vocalizing, to increase the cavity dimensions. Examples include dogs, roaring cats (lions, tigers, jaguars, and leopards), pigs, goats, and tamarin monkeys [110, 114, 115, 173, 249, 397]. In humans, particularly adult males, the larynx is positioned away from the mouth to facilitate the resonant filtering of vowel sounds [234]. Pharyngeal and nasal cavities in many echolocating bats filter out all but certain harmonics in their echolocation calls [169, 170, 364, 365]. For those species emitting the sounds through the nostrils, nasal sacs may also function as impedance-matching devices [168, 169]. Males of the non-echolocating hammer-headed bat (*Hypsignathus monstrosus*) have exaggerated nasal

FIGURE 2.40 Vocal air sacs in birds (A) Male ring dove (*Streptopelia risoria*) with inflated esophagus (pink) enveloping trachea (blue) during emission of "coo" call. (B) Same bird viewed from the front. (C) Waveforms (top) and spectrograms (bottom) of ring dove "coo" recorded from outside the bird (left) and inside the bird at the syringeal end of the trachea (right). The inflated esophagus acts as a resonance device to filter out all but the fundamental frequency in the syringeal vibrations before emission. (D) Paired sacs on chest of strutting male sage grouse (*Centrocercus urophasianus*) during sound emission. (E) Male greater prairie chicken (*Tympanuchus cupido*, another species of grouse), showing one of paired vocal sacs on sides of head. (A–C after [316].)

cavities that appear to function as resonators and filters of their sharp honking calls (Figure 2.41). These bats also have an enlarged and cartilaginous larynx that fills nearly two-thirds of their body cavity [342].

Other mammals have air-filled sacs located just downstream from the glottis or in adjacent tissues and cartilages [206, 270, 341]. Reindeer and muskoxen have a single inflatable sac in their throat used to amplify their calls [127, 270]. Other taxa such as bears and epomophorine bats have paired pharyngeal pouches that function in a similar way [396, 417]. Resonant and impedance-matching air sacs are widespread in primates [110, 111, 141, 142, 206, 270, 350]. Males of forest species such as the African De Brazza's monkey (*Cercopithecus neglectus*) and the neotropical howler monkeys (*Alouatta* spp.) have particularly well-developed vocal sacs and produce calls that can be detected at great distances [141, 343]. Perhaps the most spectacular mammalian air sacs occur on the male hooded seal (*Cystophora cristata*), which can inflate a dark

FIGURE 2.41 Longitudinal section of male hammer-headed bat (*Hypsignathus monstrosus*) Diagram shows relative locations of internal organs (brown) and enormous size of larynx and trachea (blue). (From [3].)

nasal sac on the top of its head as well as a bright red septal sac that is extruded through one nostril (Figure 2.42). Sac inflation is part of a combined visual and acoustic display directed toward competing males during the breeding season. Interestingly, males perform the display in the same way whether in the air or underwater [17, 36, 229, 384]. How the sacs might modify sound radiation in each medium remains unknown.

FIGURE 2.42 Vocalizing male hooded seal (*Cystophora cristata*) Male with black nasal hood inflated and red nasal septum inflated so that it protrudes out of nostrils. Males can inflate either sac or both when performing combined visual and acoustic display to opponent males.

SUMMARY

1. Sound propagation requires a material **medium** containing atoms or molecules. The atoms or molecules may be in the form of a **fluid** (such as a gas or liquid), a **solid**, or an interface between two of these phases of matter. **Pressure** is a measure of the degree to which the motions of atoms and molecules affect the motions of other nearby atoms and molecules.
2. **Sound** is the propagation of a perturbation in local pressure away from an initial location. It thus consists of alternating regions of higher-than-average pressure (molecular **condensations**) and lower-than-average pressure (molecular **rarefactions**).
3. Inside fluids, the molecules that pass on a pressure disturbance tend to move back and forth along the same axis on which the sound is propagating. The pattern of successive condensations and rarefactions moving away from the source of the disturbance is called a **longitudinal wave**. The molecules of a vibrating string propagate sounds along the string's length, but they do so by vibrating on a line perpendicular to the direction in which the sound is propagating. This is called a **transverse wave**. The molecules on the surface of a body of water that is propagating ripples move elliptically and thus have both longitudinal and transverse components in their motion. Solids can also propagate sounds, but the molecules can move only tiny distances, if at all. Solids can support longitudinal and transverse waves, as well as a variety of elliptical and more complex patterns such as **Rayleigh**, **Love**, and **bending waves**.
4. A **periodic wave** repeats the pattern of pressure variation over time. The **period** of the wave is the amount of time

(seconds) required to produce one complete cycle. The simplest type of periodic wave shows a **sinusoidal pattern** in pressure over time. The **frequency** of such a wave is equal to the number of times the pattern is repeated per second, and is measured in **Hertz** (abbreviated **Hz**). The part of the cycle that occurs at some reference time is called the **phase** of the wave. Finally, a wave's deviations of pressure from ambient levels provide a measure of its **amplitude**. Amplitudes are usually measured on a logarithmic scale relative to some reference value. The units are called **decibels** (abbreviated **dB**).

5. Two waves of the same sinusoidal frequency passing through the same location are **in phase** if they have maxima and minima at the same time and **out of phase** otherwise. Waves that are in phase will show positive **interference** by creating a composite wave of similar frequency but enhanced amplitude; waves that are out of phase interfere negatively and tend to cancel each other out. Two sinusoidal waves that are similar but not identical in frequency will drift in and out of phase, creating **beats**.
6. Most animal sounds are periodic but not sinusoidal. In most cases, they can be decomposed into the sum of a set of pure sine waves (called a **harmonic series**) with frequencies that are integer multiples (called **harmonics**) of the lowest frequency in the set (called the **fundamental**). The decomposition (called **Fourier analysis**) can also be performed on aperiodic signals, but the sine wave components then tend to be more numerous, and their frequencies are not integer multiples of a single fundamental. Where the periodicity varies within animal sounds, one can usually break the sound into roughly periodic segments and perform a Fourier analysis on each segment. A plot of the Fourier decomposition of successive segments in an animal sound is called a **spectrogram**.
7. Inside fluids, all frequency components of a complex sound propagate at the same speed. In air, the speed of sound is about 344 m/sec (with variation depending on temperature and humidity). The speed of sound in water is about 4.4 times as fast as that in air, and the speed of sound in solids is about 15 times as fast as that in air. On the surface of a body of water and in certain solids, different frequency components may propagate at different speeds.
8. The spatial distance between the beginning and end of one cycle of a propagating sinusoidal wave is called its **wavelength** and is measured in meters. Wavelengths are inversely related to the wave frequency and directly related to the speed of sound in the medium. Wavelengths for a given frequency are thus longer in water than in air. Wavelengths may also be decreased, (and the effective frequency increased), if a sender and receiver are moving toward each other; wavelengths will increase if they are moving apart. This is called a **Doppler shift**.
9. Close to a sound source, medium molecules flow back and forth in unison. This is called the **near field** around the source. At distances of about 1/3 of the wavelength of the sound (or 2/3 the diameter of the source), medium molecules pass on the pressure disturbance without taking part in a cohesive tidal flow back and forth. The propagating medium at this and further distances from the source constitutes the **far field** of the sound.
10. Sound amplitudes decrease with distance from the source. Inside fluids such as water or air, the pressure of a sound radiating away from the source decreases with the reciprocal of the distance from the source. This is called **spreading loss**. Spreading losses are less severe for ripples on the water's surface or inside the solid stems of plants. In addition to spreading losses, propagating high frequencies cause molecules to collide more often, and thus lose pressure to **heat losses** faster than propagating low frequencies. Spreading losses are the same in air and water, but heat losses are much higher in air.
11. **Acoustic impedance** is the resistance of a medium to a change in its molecular behavior. Away from interfaces between media, acoustic impedance depends on the density and speed of sound of that medium. Media with low acoustic impedances (e.g., air) propagate sound with weak pressures but significant molecular velocities; high-impedance media (e.g., water and solids) propagate sounds with high pressures and low molecular velocities. At an interface between two media with different acoustic impedances, most of the sound traveling in one medium will be **reflected** back into the same medium at the boundary. If the impedances are not too different, then some sound energy will pass into the second medium, but its direction of travel will likely be bent (**refraction**).
12. In addition to spreading and heat losses, a propagating sound can be attenuated by reflective **scattering** from objects that have acoustic impedances different from that of the medium, and by refraction that bends sound waves out of the path connecting sender and receiver.
13. Most animals produce sound signals in three steps: generation of vibrations, vibration modification, and coupling of the modified vibrations to the medium. Generation of vibrations can be achieved in many ways. Hard-bodied animals can use **percussion** (striking a body part against a substrate or another body part); **stridulation** (rubbing a file over a plectrum); **buckling** (of flat plates); or **tremulation** (vibrating the whole body on the surface of water or solid substrates). Animals in fluid media can also use **pulsation**, **fanning**, **fluid compression**, or **streaming** as vibrational sources. Finally, animals can force respiratory system air through openings to create **aerodynamic vibrations** in the form of hisses or single-frequency whistles, or through a valve like a **glottis** to create periodic but nonsinusoidal vibrations. Frogs, reptiles, and mammals have their vocalization valves in a **larynx** at the top of their trachea, whereas birds may have one valve at the bottom of the trachea (parrots and chickens), or a separate valve on each bronchus (songbirds, oilbirds, and woodpeckers). Wherever the bird valve is located, the associated tracheal-bronchial junction is called the **syrinx**. Birds with a valve on each bronchus can produce two different sounds at once, or more commonly, assign high frequencies to one valve and low frequencies to the other.

14. **Modification** usually involves linking the vibrational source to a flat surface or cavity with an acoustic impedance sufficiently different from the medium that successive vibrations overlap and can interfere. This facilitates positive interference and amplification (**resonance**), and negative interference (**filtering**) depending on the sound frequencies. **High-Q** modifiers provide strong amplification of a few select frequencies (**normal modes**), but have **low damping** that muddles rapid temporal patterning in the sound. **Low-Q** modifiers track temporal patterns accurately, but are much less selective for frequency and provide only minimal amplification.
15. Effective **coupling** of vibrations to the propagating medium depends in part on the size of the radiating surface, and in part on how it moves: **monopoles** expand and contract in all directions at once, **dipoles** oscillate along a single axis, and **quadrupoles** change shape by moving along two axes at the same time. Unlike monopoles, dipoles and quadrupoles produce directional **sound fields**. All three mechanisms are inefficient when the wavelengths of the radiated sounds are larger than the radiator, and the latter two are even more inefficient due to acoustic **short-circuiting**. These effects limit small animals communicating over moderate or greater distances to high frequencies. To create sufficiently high frequencies given limits on muscle contraction rates, small animals often resort to **frequency multipliers**. Examples include stridulation and vocalization mechanisms. Terrestrial animals can also improve radiation efficiency with acoustic horns or inflated sacs, which have acoustic impedances intermediate between that inside their bodies and that of the outside air.
16. Different species have evolved different compromises between elaborated sound structure and amplitude. Adaptations such as elongated tracheae in cranes and currasows, or cartilaginous vessels in ducks and howler monkeys, allow great amplitude at the cost of severely constraining what kinds of sounds can be produced and radiated. Species such as frogs, tree crickets, and mole crickets excavate or select calling sites that dramatically increase the resonance or radiation efficiency of the sounds they produce. Finally, species such as cardinals and humans actively vary the dimensions of their internal resonant cavities dynamically to amplify different frequency combinations during the production of a given sound.

Further Reading

Readers interested in more detailed treatments of biological acoustics should consult Fletcher [119] and Michelsen [255]. Additional explanations of monopole, dipole, and quadrupole radiator efficiencies can be found in Harris [167] and Kalmijn [204]. Most other reviews or general treatments of the topics in this chapter are taxon-specific. Suggested resources include: Bailey [14], Bennet-Clark [30-34], Gerhardt and Huber [145], Greenfield [161], and Virant-Doberlet and Čokl [390] for insects; Barth [22, 23] for spiders; Ladich [219] and Ladich and Fine [220] for fish; Gerhardt [143] and Gerhardt and Huber [145] for amphibians; Young [415], Kirchner [208] and Gans [130] for reptiles; Goller and Larsen [155, 227] and Suthers [360, 372, 374] for birds; Fitch and Hauser[111], Fitch et al. [116], and Frey et al. [127] for terrestrial mammals; and Tyack [384] for marine mammals.

COMPANION WEBSITE
sites.sinauer.com/animalcommunication2e

Go to the companion website for Chapter Outlines, Chapter Summaries, and References for all works cited in the textbook. In addition, the following resources are available for this chapter:

Web Topic 2.1 *Measuring sound pressure*
Microphones are used to measure the variations in pressure caused by a propagating sound. Specialized types of microphones exist for sound propagation in air, water, and solid substrates. These microphones work by converting pressure variation into electrical signals that can then be measured, stored, and characterized.

Web Topic 2.2 *Visualizing sound waves*
The best way to understand the differences between different types of sound waves is to view an animation that shows how the molecules move as the sound propagates. We list a number of websites where you can watch visualizations of most of the basic acoustic processes described in this chapter.

Web Topic 2.3 *Quantifying and comparing sound amplitudes*
A variety of methods are available for measuring and comparing sound amplitudes. Here we define some of these methods, show how they are computed, and discuss when each might be most useful.

Web Topic 2.4 *Fourier analysis of animal sounds*
Here we provide an introduction to the logic behind Fourier decomposition of animal sounds, including links to several excellent software packages for creating spectrograms and introductions on how to use these packages. We also provide links to sites where one can use such methods to compare archived animal sounds.

Web Topic 2.5 *Reflection and refraction*
The fraction of sound energy reflected or refracted at a boundary is a complicated function of incident angle, relative acoustic impedances, and relative sound speeds. Here we present the equations for several different cases, and provide some real physical examples.

Web Topic 2.6 *Sample animal sounds*
Visit this website to hear examples of the kinds of animal vibrations discussed in this and following sections of the chapter. You will also be able to see the waveform and spectrogram of each example.

Web Topic 2.7 ***Animations of vocalizing birds***
Dr. Roderick Suthers and his team at Indiana University have pioneered our understanding about how the avian syrinx works. His lab has conveniently produced several animated clips demonstrating key steps in song production by northern cardinals and brown-headed cowbirds.

Web Topic 2.8 ***Linear versus nonlinear systems***
Although animal sound vibrators typically change frequency and amplitude linearly as the forces on them are changed, most will adopt less predictable nonlinear behavior at extreme force values. Some animals such as parrots, zebra finches, and canids use nonlinear vibration behavior to increase their vocal diversity.

Web Topic 2.9 ***Radiation efficiency and sound radiator size***
Monopoles, dipoles, and quadrupoles all show reduced efficiency when the wavelengths being produced are larger than the sound source. Here we explain in more detail why this happens.

Chapter 3

Sound Signal Propagation and Reception

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Overview

In Chapter 2, we described the properties of sound and the various ways that senders create and modify vibrations before sending them on their way to a receiver. In this chapter, we pick up the communication sequence by following the emitted sound signals as they propagate through the medium. It turns out to be a complex journey in which the signal can be significantly altered. Once a sound signal arrives at a receiver, it must be captured and processed. We shall see that the physical processes underlying sound reception are generally the same as for sound signal production, but reversed in order. Finally, we look at how combining the physics of sound generation, propagation, and reception helps explain why different animals use different sound frequencies for communication.

Sound Propagation

As we have seen, animals can put a lot of effort into producing a sound with a particular set of properties: a well-equipped sender can fine-tune its signal's amplitude, frequency composition, temporal pattern, and directionality. However, once the sound enters the medium, the sender has no further control over it. Signals are invariably altered during propagation between sender and receiver; how they are changed and to what degree will depend on the medium, the distance traveled, and the original properties of the sound [117, 218, 219, 242, 243, 250, 279, 307, 309, 310, 364, 371].

Animals that can anticipate likely changes during propagation are able to modify their communication strategies accordingly. How they do so depends upon the context. For example, sound is often used for long-distance communication. The volume of medium within which a receiver can detect and recognize a sender's signal is called the **active space** of that signal. Sound production, propagation, and reception will each affect the size of a signal's active space. A sender can increase the active space of its signal by modifying its properties to minimize potential propagation effects. Receivers can increase active space by focusing on those signal properties that are least affected by propagation. The proposition that evolution favors those acoustic signals that suffer minimal propagation losses and noise overlap is called the **acoustic adaptation hypothesis** [132, 250, 313, 372]. However, while some species show some of the adaptations predicted by this hypothesis [6, 14, 62, 77, 81, 95, 120, 132, 151, 174, 202, 231, 259, 261, 327, 346, 356, 372], others show only minor adjustments,

suggesting that in some cases, the potential benefits may be outweighed by other selective forces [31, 33, 44, 165, 197, 277, 318, 344]. Some senders (e.g., those living in the constant presence of predators) may not benefit by maximizing their active space, and may instead favor signals that are easily attenuated or degraded by propagation.

Most animal sound signals suffer some degradation during propagation. Many species exploit this fact by using the amount of degradation in a received signal to estimate the distance to calling senders. This information can then be a key determinant of subsequent receiver behavior. Estimation of sender distances from acoustic degradation is called **ranging** (Figure 3.1) and is widespread in birds [251, 254, 271, 373]. In this and in other ways, acoustic degradation can play much more complex roles in animal social interactions than simply limiting active spaces.

There are four types of degradation that a sound signal might experience during propagation: (1) overall attenuation; (2) distortion of its frequency composition; (3) distortion of its temporal pattern; and (4) masking by noise. While the basic principles are similar in all media, the details often differ depending on whether the sound is propagating in air, water, or a solid substrate. Below, we discuss each of these types of potential change, compare effects in the three types of media, and note strategies that senders and receivers might pursue to enhance or minimize that type of modification during propagation.

FIGURE 3.1 Degradation in song of male cardinal (*Cardinalis cardinalis*) due to long-distance propagation (A) Waveform (top) and spectrogram (bottom) of male song recorded close to bird. (B) Waveform and spectrogram of the same song recorded several hundred meters away in the forest. White lines in each spectrogram indicate 2 kHz intervals. Degradation includes overall reduction in amplitude, filtering out of higher frequencies, and addition of reverberations (echoes) that blur the temporal pattern. These effects can be used by other males to estimate their distance from the singer (ranging).

Overall attenuation

Two main processes that result in decreasing overall signal amplitudes with distance from the sender are spreading losses and refraction. Both are largely frequency-independent and over usual communication distances produce minimal changes in the temporal pattern of a signal. However, both processes play major roles in determining the active space of a sound signal.

SPREADING LOSSES As we saw in Chapter 2, the pressure of a sound signal decreases with the reciprocal of the distance from the source due to spreading losses. In the far field, there will be a 6 dB decrease in signal amplitude for each doubling of distance. Spreading losses are the same for all frequencies of sound and for all media as long as no boundaries with other media are nearby. If there are nearby boundaries, then spreading losses may be altered. We noted in Chapter 2 that waves on the water's surface spread into two dimensions, not in three as in open air or deeper water, and thus sound pressures decrease much more slowly with distance. Similarly, sound propagating inside a narrow stem of a plant may show little spreading loss at all because the sound is essentially propagating along one dimension (Figure 3.2).

REFRACTION Large bodies of air or water often contain gradients or vertically stacked layers in which the speed

FIGURE 3.2 Spreading losses during sound propagation Red line shows drop in sound pressure with increasing distance from the sound source in a free field with spherical (3-dimensional) spreading. Pressure decreases by 6 dB for every doubling of distance. Blue line shows slower drop for cylindrical spreading. This occurs for ripples on the surface of water, surface waves on the ground, and when sounds in air or water propagate between two or more boundaries. Pressure here decreases 3 dB for every doubling of distance.

of sound varies. Speeds of sound can differ between layers because of different temperatures (sound usually moves faster in warmer layers); different pressures (sound usually moves faster under higher pressure); different current velocities in the medium (sound moving with a current moves faster than sound moving against it); or some combination of these. Sound traveling in a layer with one sound speed will be refracted if it crosses a boundary into another layer with a different sound speed: if the second layer has a lower sound speed, the sound's trajectory will be bent into the second layer (e.g., toward a line perpendicular to the layer surface). If the new layer has a higher sound speed, the trajectory of the propagating sound will be bent back toward the initial layer.

Refraction can exacerbate or reduce spreading losses by changing the volume into which a sound is radiating. Whether the active space of a sound decreases or increases depends on how the medium gradients or layers are arranged and upon the locations of the sender and receiver with respect to the layers. As an example, consider two birds communicating near the ground on a sunny day (Figure 3.3). The sunlight heats the ground and causes the air immediately above it to be warmer than the air higher above the ground. As a result, the speed of sound is highest close to the ground and decreases with increasing height above the ground. Sound waves traveling from the sender to the receiver will be refracted up and into the higher and cooler layers of air. At a sufficiently large distance, this can create a **sound shadow** close to the ground within which signal amplitudes are minimal. On hot and sunny days in open country, refraction can significantly reduce the active space of sound signals. This may explain why many birds sing only sporadically in such contexts.

The opposite situation can occur on a cold clear night or subsequent dawn (Figure 3.4). During the night, as the Earth radiates its accumulated heat back into the clear night sky, the ground becomes colder than the air. Air closest to the ground will then be cooled relative to the air somewhat higher above the ground. (This is called a **temperature inversion**.) Sound waves propagating between two animals close to the ground will now be refracted downward into the cooler layer and thus kept near the ground. Sound waves that otherwise would have radiated upward will be refracted and now arrive at the receiver. In this case, refraction due

FIGURE 3.3 Refraction of sound waves for a receiver close to the ground on a hot day The warm ground heats the immediately adjacent layer of air, and this generates a gradient of decreasing air temperatures, (and thus sound speeds), with increasing height above the ground. Sound traveling parallel to the ground is refracted up and away from potential receivers. At a sufficient distance from the sender, a sound shadow may be created within which receivers cannot detect the sound. The active space of a sender is reduced in this context.

FIGURE 3.4 Refraction of sound waves for a receiver close to the ground on a clear night or at dawn The earth radiates its heat back into the sky on a clear night, generating a gradient of increasing temperatures, (and thus sound speeds), with increasing height above the ground. Sound that would have radiated above a receiver is refracted downward toward it. Sounds directed at the receiver are initially refracted downward away from the receiver, but are reflected by the ground and travel back up along curved refracted paths toward the receiver. The active space of a sender is increased in this context.

to a temperature gradient can increase the active space of sound signals. Many species of animals vocalize intensively at dawn, a phenomenon called the **dawn chorus** [142, 186]. One explanation for this intense period of sound emission at, or for nocturnal animals just prior to, dawn is the potential for a greater active space due to refraction.

Refraction can also be generated by currents in media, such as wind (Figure 3.5). Wind speeds are typically lowest near the ground and increase with height above it. If a receiver is upwind from a sender, the speed of a sound traveling between them is highest near the ground, (where reductions in sound speed due to wind are minimal), and decreases at successively greater heights, since sound propagation is opposed by the increasing wind velocities. This situation is analogous to that of a sunny day: sound will be refracted up and into higher layers of air where sound

FIGURE 3.5 Refraction of sound waves near the ground due to wind In this figure, wind is blowing from left to right. When a receiver is upwind from the sender, wind slows down the propagation speed. Because wind speed is least near the ground and increases with increasing height above the ground, sound speeds will be highest near the ground and increasingly slowed down by wind at greater heights. Refraction of upwind sounds thus bends them up into the layers of slower sound speed, and away from distant receivers. It may even generate a sound shadow at sufficient distances. Sound speeds traveling downwind are lowest at the ground and highest higher above the ground. Refraction here bends radiating sounds back down toward the receiver and thus enhances signal range.

FIGURE 3.6 Refraction of sound waves inside a forest The canopy traps incident sunlight and heats up, whereas shade and evaporation leave the ground and understory cool. Air temperatures and thus sound speeds increase along a gradient between the ground and the underside of the canopy. Bird sounds emitted under the canopy are refracted down, as in propagation over cold ground. This extends the active space. Sounds emitted above the canopy are refracted up and into the atmosphere. Like sounds propagated near the ground on a hot day, their range is reduced.

speeds are low. Given a sufficient distance between sender and receiver, winds can generate an upwind sound shadow just as temperature layering does. If the receiver is downwind from the sender, sound speeds will be lowest near the ground (where wind has minimal effects) and increase at successively greater heights due to increasing wind speeds. In this case, sounds will be refracted back down toward the lower-speed layer near the ground, enhancing detection range and active space. The magnitude of wind effects will depend on wind speed relative to the speed of sound in air. Even on a blustery day, one might expect at most a change of 5% in sound speeds due to wind. As we know from experience, this can be sufficient to make it hard to hear a downwind speaker, but much easier to hear an upwind one. Note that mild winds may combine with temperature effects, but stronger winds create eddies that tend to mix air layers and thus eliminate contributions to refraction due to temperature differences.

Complex environments, such as mature forests, may consist of vertical stacks of layers with *alternating* sound speeds (Figure 3.6). For example, a forest canopy typically absorbs the sun's rays during the day and becomes hot on its top side, whereas the understory is kept cool not only by the shade of the canopy but also by the evaporation of moisture in the forest litter. The air beneath a forest canopy thus tends to be coolest close to the ground and somewhat warmer as one approaches the canopy. The resulting refraction of sounds near the ground and in the understory favors long-range sound propagation. The warmed canopy vegetation heats the air layer immediately above it, so sound speeds are greater immediately above the canopy than in the higher air layers. Thus sounds generated in the canopy will refract up and away from a receiver in or on the canopy. Of course, the situation can change at dawn, when the canopy foliage may be cooler than the ambient air, or when the wind is blowing. Wind velocity is usually higher above the canopy than below it.

We find very similar principles at work in water (Figure 3.7). Near the surface, a critical factor influencing the speed of sound is the relative temperature of the air and the water. When the air temperature is higher than the average water temperature, (as in summer at intermediate and low latitudes), water closest to the surface will be warmed and have a higher sound speed than water just a bit deeper. The active space for sound-producing fish close to the surface will be reduced, because sound waves traveling between them will be refracted down and into the deeper and cooler water. If the air above the surface is colder than the water, (as in winter), then the reverse will be found: water near the surface will be colder and have a slower sound velocity than deeper water. Active spaces near the surface will be enhanced due to refraction. In principle, currents in streams, waves, or tidal flows could produce layered sound speeds in water just as wind does in air. However, the magnitude of these differences in water will be much smaller, because although the velocity of water flow is quite similar to that of air, the speed of sound is much greater in water than it is in air.

FIGURE 3.7 Refraction in water near the surface (A) Conditions in summer. The water nearest the surface is warmed by the atmosphere, while deeper waters remain cold. This creates a gradient of decreasing sound speed with depth. Sounds emitted near the surface are refracted down into the slower-speed regions of deeper water and lost to receivers near the surface. (B) Conditions in winter. Cold air cools the water surface to temperatures lower than deeper layers. Sound speeds now show a gradient of increasing speed with depth. Sounds emitted near the surface that begin to radiate downward are refracted back up toward the surface.

Like terrestrial forests, large bodies of water may consist of multiple layers with alternating sound speeds. As with most fluids, ocean sound speeds increase with pressure and with temperature. In the open ocean, temperature decreases with increasing depth until it reaches 3–4° C (in nonpolar regions, at a depth of about 1000 m); it then shows only minimal reductions in temperature for subsequent depths. Taken alone, this temperature gradient would result in decreasing sound speeds with increasing depth down to a minimal value and then remain constant at greater depths. However, pressure increases with depth continuously and by itself, would generate increasing sound speeds with increasing depth. The result of the interaction between the two is a layer at intermediate depths where the water is cold but pressure is still moderate. Sound speeds are low in this layer and higher either above or below this depth (**Figure 3.8**). Sounds propagated in this SOFAR (*So*und *F*ixing *a*nd *R*anging) channel are restrained by refraction from radiating into either upper or lower layers. The result is very long-range propagation for sounds emitted in the channel. The SOFAR layer typically begins at about 600–1200 m depths in the tropics and warmer temperate oceans, and varies from 100–1500 m in thickness. It moves closer to the surface in polar regions, and its thickness varies with temperature profiles, salinity, and ocean current patterns. In the North Atlantic in early spring, there may be two depths at which sound speeds are minimal: one at the usual SOFAR depth of 1000 m, and a second due to cold water at the ocean's surface [35]. While it has been suggested that baleen whales could exploit the deep SOFAR channel for very long-distance communication [276, 351, 375], current data suggest that most baleen whales actually vocalize at shallower depths (20–40 m) [340, 357].

FIGURE 3.8 Refraction in deep ocean SOFAR channel in summer Graph on right shows typical deep ocean sound speed profile with increasing depth. Sound speed depends on water temperature (which is highest near surface and decreases to minimum value with depth) and water pressure (which is least at the surface, and increases with depth). Sound speed is high near the surface (because high temperature compensates for low pressure), and again high in very deep water (because high pressure compensates for low temperature). At intermediate depths, sound speed is low because neither temperature nor pressure is sufficiently high. Sound emitted in this channel can travel long distances due to refraction both above and below.

Frequency pattern distortion

Changes in the frequency composition of a sound result in changes in its waveform, and changes in a waveform imply changes in its frequency composition. Spectrograms and waveforms thus provide similar information about a sound, with the exception that phase relationships between frequency components contribute to waveforms but are ignored in spectrograms. As we shall see later, phase relationships are often ignored by animal ears unless components of a sound have very similar frequencies. In this section, we discuss changes in the spectrographic view of a sound signal as it propagates through different media.

TRANSFER FUNCTIONS Let us begin with a sound that has just been emitted by a sender and characterize that sound with its spectrogram. For the moment, consider the block of medium between the sender and the receiver as a "black box." Sounds are introduced into one side of the black box and emerge after propagation from the other side (Figure 3.9). What do we need to know to be able to predict the spectrogram of the signal as it emerges from the far side of the black box and arrives at a receiver?

Luckily, each sound frequency propagates independently of the others in fluids such as air or water, a property called **linearity**; see Web Topic 2.8. If we know the initial amplitude of each frequency component in the emitted signal, and we can determine what happens to that amplitude during propagation in the black box, we can easily predict that

FIGURE 3.9 Frequency response of a linear black box This example shows the initial waveform, spectrogram, and frequency spectrum (at a point marked by the vertical white line in the waveform and spectrogram) for a parrot call (input). Horizontal lines in spectrograms indicate 5 kHz intervals, and vertical lines in frequency spectra indicate 2 kHz intervals. The call propagates through the air in the forest (the black box). During this passage, the amplitude of each frequency component in the original signal is decreased by the amount specified by the red line on the black box graph. This red line is the frequency response of this particular propagation path. Note that there is no resonance in this example and thus there are no increases in component frequency amplitudes (e.g., no positive values for the red line). The waveform, spectrogram, and frequency spectrum (for the same point in the signal) after propagation are shown as the output signal. The phase response of this system, which together with the frequency response forms the transfer function for this propagation path, is not shown here, but the same logic would apply.

component's amplitude when it emerges. The spectrogram of the propagated signal will consist of each original frequency component in each time segment but with a new amplitude. A graph that displays the changes in the amplitude of a signal component caused by the box on the vertical axis and the frequency of that component on the horizontal axis is called the **frequency response** of the box. The vertical axis is usually scaled in dB and centered at a value of zero, which means no change in amplitude. If a given frequency in this graph has a positive vertical axis value, then its amplitude has been enhanced (probably by resonance, echoes, or addition of noise) during propagation; a negative value means that amplitude is being filtered out during propagation. The frequency-response graph is one of two graphs engineers use to characterize the way in which a black box converts an input signal into an output signal. The second is the **phase response** which shows, for each frequency, whether its phase is advanced or retarded as the signal passes through the black box. When combined into a three-dimensional graph, the frequency and phase responses define the **transfer function** of the box. As noted earlier, when dealing with animal sounds, we can usually ignore the phase-response graph and concentrate on the frequency-response graph. In the following sections, we shall examine several sources of frequency distortion during propagation and show how these contribute to the overall frequency response of the medium.

FIGURE 3.10 Frequency- and distance-dependent heat losses during sound propagation Black line shows decrease in dB of the amplitude of a sound due to spherical spreading alone during propagation over different distances. Red line shows expected decrease in amplitude due to spreading combined with heat losses for a 1 kHz sound in air. Blue line shows equivalent losses in air for a 10 kHz signal, and green line shows losses for a 100 kHz signal. In seawater, spreading losses are the same, but heat losses are lower. Amplitudes of frequencies in the range of 100 Hz to 10 kHz would decrease at rates similar to the red line; losses for ultrasonic sounds of 50–100 kHz in seawater would be more similar to the blue line. (After [112].)

Web Topic 3.1 *Transfer functions*
Here we discuss methods for measuring transfer functions of black boxes in general, and blocks of propagation medium specifically. What assumptions have to be met to make these measurements, and what happens if they are not met?

HEAT LOSSES As we saw in Chapter 2, sound signals lose energy to heat losses during propagation. Heat losses increase monotonically with the distance between the sender and the receiver (Figure 3.10), and are dependent upon the type of medium; heat losses are a hundredfold greater for seawater compared to fresh water, for air compared to seawater, or for solid substrates compared to air [112, 185, 216, 217, 307, 371]. They are also highly frequency-dependent: as a rough rule, heat losses increase with the square of sound frequency. This produces a strong filtering effect in the frequency response graphs for all media: the higher the frequency of a component in a sender's signal, the lower its amplitude will be when it arrives at a receiver. For signals with broad ranges of component frequencies, heat losses during propagation can seriously distort the signal pattern.

What can a sender do to minimize heat losses? In water or within plant material, there is little it can do to increase active spaces except to favor lower frequencies in its sounds. As we have seen in Chapter 2, body size limits the lowest frequencies that can be radiated efficiently, so for small animals, this option is limited. In air, heat losses are more variable than in water, as they are sensitive to fluctuating temperature and humidity. In principle, this should allow terrestrial species to select a time of day when heat losses are low to broadcast their sounds. In practice, diurnal temperature and humidity often have opposite effects on heat losses [371], and the best times for minimizing heat losses often coincide with the maximal constraints on active space due to refraction. These complex interactions make prediction of optimal transmission times difficult.

SCATTERING Although a completely different process from heat loss, scattering also distorts propagating signals by filtering out higher frequency components. Scattering occurs whenever there are objects or regions in the propagating medium with a different acoustic impedance from that of the rest of the medium. This process is highly frequency dependent. When the wavelengths of the incident sounds are larger than the objects encountered, most energy sweeps around the objects and continues on to the receiver. As the ratio of object size to incident sound wavelength increases, increasing amounts of sound energy striking the object will be backscattered toward the source and likely lost to the receiver. At sufficiently large object-to-wavelength ratios, sound shadows with no transmitted sound may exist between the objects and the receiver. Most media will contain more small reflectors than large ones: a summer forest consists of some tree trunks but many more leaves and branches. The result is that there are many more objects that scatter high frequencies than ones

FIGURE 3.11 Scattering and heat losses in temperate terrestrial habitats Frequency response graphs for sound propagation in air across a distance of 100 m (A) over an open field, (B) in a coniferous forest, (C) in a deciduous forest without leaves, and (D) in a deciduous forest with leaves. All samples have spreading losses removed and are taken 10 m above the ground to exclude boundary effects. Note the significantly higher losses at high frequencies when a deciduous forest has leaves. This difference is largely due to scattering effects. (After [218].)

that scatter low frequencies. The frequency response graph will again show a drop in amplitude that becomes more severe with increasing frequency.

In forested environments, trees and foliage are the main sources of scatter [13, 218-220]. Significant scattering with sound shadows can occur at frequencies as low as 1–2 kHz (Figure 3.11). In open terrestrial sites, rising pockets of heated air or wind vortices may generate similar frequency-dependent scatter [367, 368]. In the open ocean, the main sources of scatter are the air-filled swim bladders of fish and the air bubbles and fat globules carried by various zooplankton. Marine animals with acoustic impedances similar to but still not equal to that of water (e.g., shrimp and squid [159]) can also generate significant backscatter when aggregated in sufficient numbers. Surf turbulence near the shore can create vortices full of air bubbles that also serve as scattering sites. Because wavelengths for any frequency in water are 4.4 times as large as those of the same frequencies in air, whereas the size distributions of objects are similar in air and water, scattering in water only becomes important for component frequencies of 10 kHz or higher [146]. This exceeds the frequencies used by most marine animals, excepting toothed whales and porpoises, for sound communication. Over the same frequency ranges, scattering losses are thus much less of a problem for aquatic animals than they are for terrestrial ones. Inside a solid substrate such as a plant, the speed of sound is sufficiently high that potential obstacles would have to be larger than the entire plant to produce scatter. However, as we shall see in the next section, the plant boundaries themselves become important reflectors, and this leads to a similar filtering out of higher frequencies.

BOUNDARY EFFECTS A boundary is a large expanse of interface between two media with significantly different acoustic impedances. There are three basic situations in which boundaries affect sound propagation: (1) when a sender and receiver exchange sound signals in one medium that is near a boundary with another medium; (2) when sender, receiver, and sounds exchanged between them are confined between two or more boundaries; and (3) when sender and receiver are located in one medium but communicate with signals propagating along or through a boundary with another medium. We take up each case in turn.

Sounds emitted by a sender close to a boundary with another medium may reach a receiver by multiple paths (Figure 3.12). Assuming no intervening obstacles, a **direct wave** will propagate along the straight line connecting the two animals. In addition, some of the sound that normally would not reach the receiver now encounters the boundary and is reflected toward it. This is a **reflected wave**. The arrival of two or more concurrent waves at the receiver sets the scene for interference between them [99, 100, 102, 371]. If the direct and reflected waves arrive at similar amplitudes but out of phase, they will cancel each other out, and the receiver will detect little sound. If they arrive at similar amplitudes but in phase, then the receiver will hear the sound at a greater amplitude than if there were no boundary nearby. Whether the two waves do or do not arrive with similar amplitudes depends on the strength of the reflection and on how far

FIGURE 3.12 Interference between direct and reflected waves near a boundary When sender or receiver are located in one medium, but one or both are close to a boundary with another medium of quite different acoustic impedance, sound waves that would otherwise have missed the receiver can now reach it due to reflections at the boundary. Such reflected waves can interfere (positively or negatively) with the direct wave that has traveled on a straight line between sender and receiver.

above the boundary the two parties are located (**Figure 3.13**). If one or both are high above the boundary, the reflected wave must travel much farther than the direct wave, suffer greater spreading, heat, and scattering losses, and thus arrive at a sufficiently lower amplitude that any interference will be negligible. When both parties are close to the boundary, the reflected wave will travel only slightly farther than the direct wave and interference can be significant.

Whether the direct and reflected waves are in or out of phase is more complicated. All other factors being equal, the

(A)

(B)

FIGURE 3.13 Effects of sender and receiver height on boundary interference If one or both parties are high above a nearby boundary (A), the path taken by the direct wave will be significantly shorter than that taken by the reflected wave. As a result, the amplitude of the reflected wave will be much lower than that of the direct wave, and interference will be minimal. When both animals are on the ground (B), the paths taken by the direct and reflected waves will be very similar and interference can be maximal.

FIGURE 3.14 Boundary interference for airborne sounds over a hard surface For a very hard surface, such as asphalt, and any biologically likely incident angle, the reflected wave from the nearby hard surface will be large in amplitude and without any phase shifts at reflection. Reflected and direct waves thus interfere positively at low frequencies, but interfere negatively for that frequency where the reflected wave travels 1/2 of a wavelength further than the direct wave, (here, 3.2 kHz), and again when the reflected path length is 3/2 of a wavelength further than the direct wave (here, 9.6 kHz). (After [101].)

two waves will cancel each other out when the reflected wave has to travel an odd number of half-wavelengths (e.g., 1/2, 3/2, 5/2, etc., of a wavelength) farther than the direct wave. The two waves will interfere positively if the reflected wave travels 0, 1, or more full wavelengths farther than the directed wave (Figure 3.14). At very low frequencies, the difference in direct and reflected travel distances will be only a small fraction of a wavelength, and the two waves will be almost in phase. The frequency response graph for a signal propagating near a boundary would thus exhibit:

- high amplitudes for very low frequencies;
- a decline to a minimum at a frequency with a wavelength twice the difference in direct and reflected wave travel distances;
- an increase to a maximum at the frequency with a wavelength equal to the distance difference;
- a decline to a second minimum for a wavelength equal to 2/3 of the distance difference, etc.

When the boundary is between air and the ground, this oscillating pattern of negative and positive interference is usually lost at higher frequencies, because each blade of grass or pebble becomes a separate sound reflector once it is larger than the incident wavelengths of sound. This creates many out-of-phase reflected waves instead of one cohesive one, and thus no consistent pattern of interference with the direct wave.

All factors are rarely equal in natural contexts. If both the speed of sound and the acoustic impedance of the first medium are greater than those in the second medium, (as happens when sound is traveling in water and hits an air–water boundary), all component frequencies in the incident sound will be phase-shifted by one-half of a cycle at reflection. This generates a frequency-response graph that is the exact opposite of the one described above: low frequencies are now heavily cancelled out, a maximum arises for that frequency with a wavelength twice the difference in direct and reflected wave distances, a minimum occurs for the frequency with a wavelength equal to this distance, and so on (Figure 3.15).

A similar phase shift can occur when the speed of sound is higher in the second medium, (as with sound in air striking the ground), if the angle at which the sound strikes the boundary is lower than a **critical angle**. The angle at which the sound strikes the boundary depends on the distance between the two parties (greater distances mean lower incident angles), the height of the sender above the boundary (lower heights mean lower incident angles), and the height of the receiver above the boundary (lower heights again mean lower incident angles). The value of the critical angle depends on the relative speeds of sound in the two media. If they are very different (as with sound in air striking an asphalt or cement surface), the critical angle is close to zero, and only animals very far apart or very close to the ground will experience a phase shift in reflected sound waves. If the sound speeds are not so different, as with sound in air striking soft ground, grassy turf, or new snow, the critical angle can be quite high and phase shifts at reflection will be the more common situation. As with sound in water striking the surface, phase shifts cause lower frequencies to be severely attenuated during propagation. Note that the angle of incidence can also affect the amplitude of the reflected wave, and this will also modulate the degree of interference. For more details on phase shifts, go to Web Topic 2.5.

Interference between direct and reflected waves can clearly impose major changes in the frequency composition of sound signals propagating near a boundary. For underwater animals near the water's surface, there is no recourse. For

FIGURE 3.15 Boundary interference for airborne sounds at low incident angles The boundary surface is here assumed to be hard enough to produce a reflected wave of large amplitude, soft enough that the critical angle is larger than the incident angle defined by the proximities of sender and receiver to the boundary, and no ground wave is present. This results in a full (180°) phase shift at reflection. The frequency response is the mirror image of that shown in Figure 3.14: direct and reflected waves now interfere negatively for low frequencies, but show positive interference for those wavelengths equal to 1/2 and 3/2 of the path difference. (After [101, 102].)

FIGURE 3.16 Boundary interference for airborne sounds at low incident angles and over soft substrates Frequency responses for propagation over ground covered with fresh snow (black) and soft earth inside a woodland (red). As in Figure 3.15 direct and reflected waves interfere negatively for low frequencies and certain higher frequencies. But here ground and surface waves restore the propagation of the lowest frequencies, leaving a "notch" at intermediate frequency values. Such soft boundaries also exhibit varying strengths of reflection and amount of phase shift as a function of frequency. This rounds and broadens the curves seen over hard surfaces. (After [101, 102].)

terrestrial animals, two processes can minimize these changes if the boundary is sufficiently soft and porous [8, 102, 279]. When sound from a distant source strikes a very hard surface such as asphalt, most of the sound energy is reflected toward the receiver from a single point on the surface. However, reflection from a softer and more porous boundary occurs in a more diffuse region on the surface. While that part of the sound wave reflected from a central point forms the reflected wave described above, incident sound reflected from other nearby points will differ from the reflected wave in both amplitude and relative phase. The ensemble of reflected contributions from these adjacent points is called a **ground wave** and constitutes a third path by which a signal might reach a receiver (Figure 3.16). Ground waves are detectable only at low heights above the boundary, and attenuate least when propagating low frequencies: whereas a 200 Hz ground wave must propagate 200 m before its amplitude has dropped by 3 dB, an 800 Hz ground wave will decrease by the same amount after propagating only 8 m. Over sufficiently soft terrain, ground waves can restore some of the lowest frequencies in a signal that might otherwise be filtered out at low incident angles. Propagation for frequencies that are too low to avoid negative interference and too high to be restored by ground waves cannot be improved. This results in a conspicuous **notch** in the frequency responses of most terrestrial habitats. Ground waves can also provide low levels of sound that persist in refractive sound shadow zones. If the ground is sufficiently porous, incident sound can also be trapped in a thin layer just above a boundary, and continue propagating as a **surface wave**. This fourth path linking sender and receiver attenuates less slowly than the ground wave, but is also limited to lower frequencies.

FIGURE 3.17 Measured frequency response curves near ground in temperate terrestrial habitats These graphs show the same four contexts of Figure 3.11. The frequency response for each habitat with both sender and receiver 10 m above the ground (red) is compared to response when both are at ground level (black). Ground level measurements show high attenuation at lower frequencies due to direct and reflected wave interference and some restoration of certain low frequencies due to ground and surface waves leaving a notch at intermediate values. All plots show complex patterns of frequency dependent scattering at intermediate frequencies; and a gradual drop in amplitudes at high frequencies due to heat and scattering losses. (After [218].)

In most terrestrial environments, scattering, boundary interference, ground waves, and surface waves all combine to produce an overall frequency response graph generating

outputs with moderate-amplitude low frequencies, low amplitudes for the notch (200–700 Hz), and a gradual rise to a maximum near 1–2 kHz (Figure 3.17). At higher frequencies, boundary interference, ground waves, and surface waves have diminishing roles, and signal amplitudes decrease with increasing frequency due to heat and scattering losses. Ground-living animals that wish to communicate over long distances using sound must use either low frequencies (assuming they are large enough to do so efficiently) or high frequencies (at the cost of higher heat and scattering losses). The only alternative is to move sufficiently far above the ground that boundary reflections are negligible [84, 145, 230].

We now turn to the second type of boundary effect: that created when sender and receiver are both located between two parallel boundaries. For signals propagating in caves, water of intermediate or shallow depths, the SOFAR channel, or between the ground and a forest canopy, sound can be reflected (or refracted) back and forth between multiple parallel boundaries. Because sound is trapped between these boundaries, the propagating environment is called a **waveguide**. The direct wave and multiple reflections inside a waveguide interfere in complicated ways, just as multiple reflections interact inside a resonant structure [35, 106, 237]. As a result, certain frequencies (normal modes) are accentuated in waveguides, and others are filtered out (Figure 3.18). The lowest mode is called the **cutoff frequency** of the waveguide, since lower frequencies cannot propagate within it. As a rule of thumb, the cutoff frequency has a wavelength about four times the thickness of the waveguide. Shallow bodies of water are a good example of a waveguide. The water's surface and the bottom form the two parallel reflecting surfaces. The depth of the sender in the water body, the acoustic properties of the bottom, whether the water's surface is choppy or smooth, and the temperature profile as a function of depth all play contributing roles in determining the cutoff frequency and the frequencies of normal modes. Cutoff frequencies for water bodies can be as high as 500–1000 Hz for a sender in a 1 m deep pool, and drop to 30–200 Hz for a 10 m deep lake or near-shore zone [307]. The low-frequency sounds exchanged by many shallow water fish are often below the ambient cutoff frequency; this limits their acoustic communication to very short ranges. Above the cutoff value, there is usually an **optimal frequency** whose amplitude is maximized during propagation; signal components with frequencies below and above this optimal value will tend to be filtered out with increasing propagation distances. The optimal frequency generally decreases as the depth of the sender is increased, and for a given location, there is usually an optimal depth and frequency combination that produces the maximal active space [155]. Male humpbacked whales (*Megaptera novaeangliae*) may take these factors into account in selecting both singing sites and singing depth during the mating season [237].

The third type of boundary effect occurs when both sender and receiver live in one medium but transmit and detect sound signals propagated across a boundary in another medium. For example, many small insects and hunting spiders communicate by exchanging sounds that propagate through their host plants [19, 22, 67, 68, 71, 152, 361]. Percussion, tremulation, tymbal buckling, or stridulation are used to generate vibrations that pass directly into the plant through the sender's appendages. In principle, such sounds could be propagated in a solid substrate such as a plant as longitudinal, transverse, Rayleigh, Love, or bending waves [217]. In practice, the signals used by these small arthropods appear to be propagated largely by bending waves [242]. Bending waves travel along the major axes of the plant, and unlike other substrate wave types, cause the entire cross section of

FIGURE 3.18 Predicted frequency response in a marine waveguide Low-frequency sounds propagating in a waveguide created by the ocean surface and bottom. The examples assume 60 m total water depth and positioning of the sender and receiver (e.g., humpbacked whales) at 15 m depth. Dashed lines indicate no change in signal amplitude; all points below this line are decrements in signal amplitude. Distances between sender and receiver: (A) 1 km; (B) 3 km; (C) 5 km. Note rise and fall of curves at increasing distance due to excitation of normal modes for this waveguide configuration. Cutoff frequency for this depth would be about 6 Hz and is thus barely visible in the graphs (After [237].)

FIGURE 3.19 Frequency response of sound propagating plant stems Plots show frequency dependence of sound propagation over a 3 cm distance (red) and a 17 cm distance (blue) within the stems of the plant *Thesium bavarum*, a common host for substrate-signaling shield bugs (Cydnidae, Hemiptera). Interference between direct and multiple reflected waves inside the plant generates complex frequency response patterns that differ depending on where the receiver is located on plant. (After [242].)

a stem or leaf at a given location to oscillate in concert along a line perpendicular to the direction of propagation. Bending waves suffer little attenuation or damping during propagation, and are reflected at the root and branch tips back into the plant. Interference between direct and persistent reflected waves accentuates those frequencies that are compatible with the plant dimensions (normal modes) and filters out others. At normal-mode frequencies, bending waves cause some locations along the plant (acoustic internodes) to experience major oscillatory movements, while just a half-wavelength away (an acoustic node), there will be little motion at all. The locations of acoustic nodes and internodes along a plant vary with the frequency of the sound. Frequency-response graphs for plants show strong propagation of low frequencies (below 100 Hz), complex patterns of reduced propagation at intermediate frequencies (100–2000 Hz), and smoother variation at decreasing amplitudes for higher frequencies [20, 72, 164, 205, 242] The frequency response graph for plants thus shows the same kinds of peaks and valleys seen in other boundary contexts, but the better-propagated frequencies are largely compressed into the lower end of the bioacoustic spectrum (**Figure 3.19**).

Boundary propagation of animal signals also occurs at the water's surface (water striders and spiders), at the surface of the ground (fiddler crabs, snakes, rodents, and elephants), and on spider webs. Each of these two-dimensional boundaries has its own frequency-dependent properties. Propagation of ripple signals on the water's surface attenuates higher frequencies faster than it does low frequencies [20, 30, 112, 127, 191, 217]. Seismic signals in the ground can propagate in various ways, but those used by animals for communication are usually Rayleigh surface waves [3, 46, 257]. This is even true for burrowing animals, in which the relevant boundary is the surface of their tunnels [224]. As with ripple propagation on the water's surface, high-frequency Rayleigh waves tend to attenuate faster during propagation than do low-frequency waves [7, 46], although the degree of difference varies with soil type [98]. And, as with waveguides, certain frequencies may be optimal for maximizing range and active space. Dry sand, for example, shows optimal propagation at 300–400 Hz, with lower values at lower and higher frequencies [3, 46]. In contrast with animals that signal via water and ground boundaries, spiders can design their webs to have favored acoustic properties. The multiple threads in a typical orb web can vibrate as longitudinal waves and as transverse waves (either parallel or perpendicular to the plane of the web). Optimal propagation in orb webs appears to occur via longitudinal vibrations in the radial threads of the web, and there is little frequency dependence up to 9–10 kHz [184, 228, 229]. Sheet webs of other spiders likely show some resonance and thus frequency dependence, but computations suggest that this resonance enhances propagation and normal modes are sufficiently close together to provide a nearly flat frequency response [253].

Temporal pattern distortion

As noted above, any change in the frequency composition of a signal will likely produce a corresponding change in the signal's waveform. Thus all of the processes outlined in the previous section can result in changes in the temporal pattern of a signal. Three additional propagation processes can modify temporal pattern directly: reverberation, added modulation, and dispersion. We take up each below.

REVERBERATION We discussed earlier how a sound propagating in one medium can be scattered by intervening objects of appropriate size and acoustic impedance. Leaves and branches constitute the main source of scattering in forested habitats, and the swim bladders of schooling fish act similarly in aquatic environments. Depending upon the relative locations of the sender, receiver, and the scattering objects, one or more reflected versions of the signal can arrive at the receiver. These are called **reverberations** (or echoes).

Because scattering is frequency-dependent, a reverberation may emphasize different frequency components than does the original signal. It may also represent only a portion of the original signal. Depending on the duration of the original signal and the proximity of the scattering objects to the line connecting sender and receiver, reverberations may arrive after receipt of the direct signal and thus create a separate echo, or they may overlap and sum with the latter portion of the direct signal. An overlapped combination is invariably longer in duration than the original signal, and exhibits a "tail" that

FIGURE 3.20 Reverberations in forests (A) Waveform of the song of a male lark sparrow (*Chondestes grammacus*) before (top) and after (below) propagation in a thick forest. This species normally lives in open habitats where reverberations are rare and thus has adopted none of the specializations used by forest birds to minimize song distortion due to reverberation. Note blurring of successive notes due to overlapping echoes and addition of long "tail" to song. (B) The length of added "tails" and blurring of successive notes are both greater when the rate of echo decay is low. This plot shows the rates of echo decay for different frequencies and different sender-receiver distances in a box-ironbark forest in Australia. At short distances, intermediate frequencies (1–3 kHz) reverberate longest and suffer the worst blurring of successive elements; at long distances, intermediate frequencies should experience the least blurring and minimal tail additions. (After [272].)

decays in amplitude with time (**Figure 3.20**). The duration of this reverberation "tail" has been measured in several terrestrial forests, and depends on the distance between sender and receiver, the component frequencies in the original signal, the density and sizes of scattering objects, and to a lesser degree, the height of the sender above the ground [150, 272, 300]. For distances less than 100 m, reverberation tails in forest are longest for frequencies with wavelengths similar to the dimensions of nearby leaves and branches, and shorter for either higher or lower frequencies. Longer distances result in longer tails. Reverberation tails are diminished if the sender moves higher above the ground; receiver height appears to have little effect on reverberation. Senders with more directional sound fields also produce less scatter and shorter tails [300].

Overlap of reverberation and a direct signal is bound to distort the temporal pattern that reaches the receiver. Longer or more rapidly repeated signals and longer tails are the most vulnerable combinations. Reverberations can fill in the initially silent intervals between successive syllables in a bird trill; a rapid and broad frequency sweep, such as that of a male cardinal, will be broadened in each time segment by overlapping the original segment with slightly lagging copies of it. Senders faced with "blurring" of a temporal pattern due to reverberations can select emission heights, component frequencies, and sound-field directionalities that generate minimal tails; limit the rates of amplitude or frequency modulations to values much shorter than the decay rates of tails; or avoid modulations and temporal patterns altogether.

FIGURE 3.21 Correlations between habitat and temporal patterns in birdsong The horizontal axis in this graph indicates the percentage of 120 North American songbird (Oscine) species in each of 6 habitat types that space successive elements in their songs at intervals of 10 msec or more (abscissa). The vertical axis plots the fraction of those same species in each habitat that exhibit significant modulations in their songs (as evidenced by significant sidebands in spectrograms). As expected, if songbirds avoid song distortion due to reverberation, songs of forested species (deciduous forest, conifer forest, and parkland) are unlikely to show modulations and the shortest intervals between successive song elements are quite long. Songbirds of open country habitats (marsh, grassland, and shrubland) should have to worry less about reverberations, and they indeed show significantly higher fractions of species whose songs include amplitude and/or frequency modulations with very short intervals between successive song elements. These patterns remained statistically significant even after corrections for inclusion of bird families with many similar species. (After [372].)

The latter strategy can even turn reverberation into an advantage: echoes that overlap with a direct signal contain the same frequencies and can thus enhance the received signal against background noise [260, 330]. The risk of signal reverberations perhaps explains the widespread observation that forest birds include fewer and less dramatic modulations in their vocalizations than do birds that live in open habitats where reverberant scatter is minimal (Figure 3.21) [14, 27, 34, 43, 44, 129, 130, 156, 315, 332, 337, 355, 372].

ADDED MODULATION In open terrestrial environments and under water, turbulence and eddies can make the medium quite heterogeneous. Large eddies typically spin off smaller eddies from their margins, these spin off even smaller ones, and so on, creating a series of different eddy sizes. As a sound signal propagates through such a medium, different segments encounter different densities and vortex patterns. The result is additional amplitude modulation of the signal waveform with greater distortion at higher frequencies and greater sender-receiver distances [279].

In terrestrial habitats, the major source of turbulence is wind which creates vortices that can modulate propagating sounds. In addition, bubbles of air rising from the ground on a hot day generate heterogeneities in the medium that can also add amplitude modulations to signals passing through them. Animal sounds produced at dawn and dusk usually have the least risk of added modulations, whereas midday winds and heat effects can produce significant alterations in the waveforms of propagating sounds. Richards and Wiley [300] reported up to 40 dB variations in amplitude imposed on propagating sounds in even mildly windy conditions. They also noted that this process modulated the envelope of waveforms at rates of 10–50 Hz over a wide range of conditions. Senders would have to modulate the amplitude of their emitted signals at rates higher than 50 Hz to avoid temporal distortion during propagation in these contexts.

DISPERSION In bulk volumes of air or water, and in strings (e.g., spider webs), all sound frequencies propagate at the same speed. As a result, the alignment between a signal's frequency components is preserved during propagation even if their amplitudes are altered. This is not the case for bending waves in plants, waves on boundary surfaces (water ripples, Rayleigh and Love waves on solid substrates), or sound inside waveguides. In these situations, different frequencies propagate at different speeds, resulting in their temporal and spatial **dispersion**. Even if propagation does not change the relative amplitudes of a signal's frequency components, its waveform can become drastically altered if their alignment is changed due to dispersion. Propagation speeds increase with frequency in bending waves [217], but usually decrease with frequency for Rayleigh and Love waves [189]. In wave guides, propagation speed also decreases with frequency at least above the cutoff frequency [35]. The most complex situation is on the water's surface, where propagation velocity increases monotonically both below and above a minimum at 13 Hz [19, 29, 112]. In each of these contexts, a signal's

waveform will be increasingly altered as it propagates farther away from the sender.

Web Topic 3.2 ***Dispersive sound propagation***
Sound propagation with dispersion can result in major changes in a signal's waveform and in the speed with which the signal propagates as a whole. Here we provide more details on dispersive sound propagation for each of the contexts in which communicating animals are likely to encounter it.

Noise masking

Noise is any concurrent sound that obscures receipt of a sound signal by a receiver. At high intensities, noise can hinder receiver detection of a signal; at lower intensities, the receiver can detect the signal but noise hinders signal recognition (i.e., assignment of the received signal to an expected category). In many cases, noise, more than receiver sensitivity, sets the limits of active space size. The degree to which noise masks signals depends upon its amplitude, frequency, spatial distribution, and temporal pattern. Signals with a high amplitude relative to ambient noise—which create a high signal-to-noise ratio—are more likely to be detected and recognized by receivers. Signals with frequency compositions different from that of ambient noise will be favored in those species whose ears are tuned to a limited band of frequencies or can decompose sound signals into their frequency components (see later sections). A receiver may be able to ignore noise generated by a nearby directional sound source if its receiving organs are also sufficiently directional. The temporal properties of noise vary along a continuum ranging from fully continuous to sporadically intermittent. Continuous noise usually poses a greater problem for sound communication than intermittent noise. Below, we summarize the patterns of background noise in each type of environment, and outline the special challenges presented by noise from nearby conspecifics.

BACKGROUND NOISE In both terrestrial (Figure 3.22) and aquatic environments, noise levels tend to be greatest at the two ends of the biologically relevant spectrum [39, 49, 167, 168, 250, 307, 315, 331, 332, 335, 364, 365]. In air, the turbulence generated by wind creates low-frequency noise (100–1000 Hz). Intensities are highest in the lower end of this range, with values for moderate winds (1 m/sec) of 30–40 dB above the threshold of human hearing, (a reference called SPL; see Web Topic 2.3), and 60–70 dB (SPL) for strong winds (8 m/sec). Wind noise is generally greater in open habitats than in forested ones [250, 315]. Airborne noise can also be significant close to running streams and waterfalls and during heavy rainfall. While lower frequencies also

FIGURE 3.22 Frequency dependence of ambient noise in terrestrial habitats (A) Low tropical forest: low-frequency band due to wind; high-frequency band due to forest insects and birds. (B) Open grassland: high wind noise similar to (A) but reduced animal noise. (C) High tropical rainforest: very low wind noise; high-frequency noise due to cicadas and birds. (D) Coastal forest: similar to (C), but with wind noise and high-frequency bands shifted due to different cicada and bird species. (E) Patchy (gallery) tropical forest: similar to (D), but cicadas producing higher frequency noise. (F) Riparian scrub near a rushing stream. (G) Wind noise over a meadow. (H) Vehicular traffic noise. (A, B (Panama) after [315]; C–E (Cameroon), F (California Sierra Mountains), G (Colorado Rocky Mountains), and H (San Francisco, CA) after [335].)

FIGURE 3.23 Frequency dependence, relative amplitude, and sources of ambient noise in the ocean Natural nonbiological sources of noise: (1) undersea earthquakes; (2) sea floor volcanic eruptions; (3) lightning strikes; (4) heavy rain and storm winds on sea surface; (5) seismic noise; (6) calm surface wave noise; (7) thermal (molecular) noise. Biological sources of noise: (8) blue and fin whale calls; (9) humpback whale songs; (10) bowhead, right, and gray whale calls; (11) sperm whale echolocation clicks; (12) dolphin whistles and other social sounds; (13) dolphin echolocation clicks; (14) fish choruses; (15) snapping shrimp. Human sources of noise: (16) seismic airguns; (17) naval low-frequency active sonar; (18) ATOC and successor ocean temperature measurements using sound; (19) supertanker noise; (20) drilling rigs and dredgers; (21) large naval ships; (22) echo-sounding sonars; (23) side-scan sonars; (24) submarines; (25) general shipping noise. (After [65].)

tend to dominate these types of noise, noticeable amplitudes may persist up to 5–6 kHz [194, 335]. An increasing source of lower-frequency noise throughout the terrestrial world is vehicular traffic, which has a frequency spectrum and amplitudes not unlike those of wind [334, 335]. The major sources of ambient noise inside plants [57] or on the water's surface are wind and rain.

The major sources of continuous noise at the higher end of the terrestrial spectrum are advertising frogs, cicadas, crickets, and katydids [39, 335]. This band of noise begins to be significant around 2 kHz and can extend, particularly in the tropics, far into ultrasonic frequencies. All of these taxa can produce relatively continuous noise levels. Some cicadas alternate calling and silent periods, but often stimulate each other to call as a chorus, making for very intense bouts of noise. Frogs are more likely to call at night and can also chorus. The frequency zone between the upper margins of wind noise and the lower limits of frog and insect noise, (approximately 500–2000 kHz), is relatively quiet with respect to continuous noise. This is a band favored by many birds and mammals for their vocalizations. However, few species of either group produce the continuous chorusing of frogs or insects, and their songs and calls constitute at most intermittent noise for other species. The major exceptions are breeding colonies [11] and the dawn chorus, which is a period of maximal avian and primate vocalization in many habitats [45, 58, 142].

We have seen that sound signals attenuate much more slowly in water than in air. Unfortunately for communicating animals, ambient noise also attenuates more slowly (Figure 3.23). This is especially true for low frequencies. In large bodies of water, very low-frequency noise (10–100 Hz) is generated by the Earth's seismic activity and lightning strikes. In polar regions, sea ice adds additional low-frequency sounds. Natural noise in the 100–5000 Hz range is mostly generated at the surface through wave action, breaking surf, and rainfall [235, 301]. Much of this surface noise is due to the entrapment of air bubbles that vibrate and then burst [87, 88, 190]. Wind is the major driving force for wave action in the open ocean, and noise levels in calm seas decrease with increasing frequency above 300 Hz. In stormy weather, surface wave noise can increase by 30 dB or more. Between 1 kHz and 100 kHz, snapping shrimp are the dominant sources of continuous marine noise [9, 28, 60, 289], although barnacles, sea urchins, and mussels contribute to the din [110]. Since these invertebrates live on the sea bottom, their noise is most intense in shallow coastal waters. This habitat also suffers high noise due to surf and breaking waves. Fish contribute only moderately to ambient noise levels. Most species use low-to-intermediate frequencies for communication (100–900 Hz) and call intermittently [232, 252]. A few species chorus, but usually during limited periods each day and in sufficiently shallow water that the sounds propagate only short distances. The calls and songs of baleen whales may also make a significant contribution to background noise in the ocean [83].

As with vehicular and airplane traffic in terrestrial environments, human activities are a major source of ocean noise [328]. Shipping produces noise in the 10–100 Hz range due to propeller cavitation; very large (supertanker) and very small but fast (jetski) vessels are of particular import. Modern mineral exploration uses reverberations from air guns above the sea floor to assess geological structure and content. Drilling, pile driving, and trench digging also produce intense local noise levels, and both military (<100 Hz) and fishing (>100 kHz) sonars contribute additional frequency bands. For each of the taxa of aquatic animals that use sound for communication, there is now a significant overlap between the frequencies used for communication and dominant

frequencies of ambient anthropogenic noise [4, 32, 51, 78, 82, 85, 103, 116, 192, 198, 204, 215, 233, 285, 286, 308, 317, 321, 322, 328, 338, 339, 359, 363, 377, 379].

Web Topic 3.3 ***Animal communication and anthropogenic noise***
To what degree does noise generated by human activities interfere with sound communication in animals? Recent studies in both terrestrial and marine environments suggest that there are increasing problems, but animals can sometimes adapt.

Communicating animals faced with ambient noise at frequencies overlapping their signals have limited options [49]. Where noise is not too intense, senders tend to try to maintain communication by increasing signal amplitude—the **Lombard Effect** [47, 48, 207, 288, 293]. They may also increase their signal durations [48] or signal repetition rates [191, 275, 285]. If the noise is sufficiently intermittent, senders can limit sound emission to the more quiescent periods [122]. Reciprocal acoustic exchanges between senders and receivers are used by many insects to confirm receipt of a signal despite noise [17]. Where noise is both intense and relatively continuous, the sole option is to shift signal frequencies to reduce overlap with the ambient noise. Such spectral shifts might occur over evolutionary time when noise spectra are sufficiently predictable, or within a generation, given sufficient flexibility in a species' sound-production mechanisms. A variety of animal species have evolved dominant signal frequencies that fall within a low-level "window" in the natural patterns of ambient noise [38, 40, 49, 81, 86, 201, 202, 315, 332, 365]. Short-term spectral shifts have also been reported in a number of avian and mammalian species living in urban areas with significant human noise (Figure 3.24) [160, 274, 294, 295, 333, 336, 362, 376].

CONSPECIFICS Special problems can arise when a sender is surrounded by other sound-producing senders of the same species. In a breeding colony of penguins or other seabirds, calling is largely random and there is no overt attempt by neighbors to mask a given sender's calls. This is not the case in mating choruses of insects or anurans (frogs and toads), where males monitor each other's calling and attempt to call earlier, faster, or louder than nearby competitors. At high calling rates or with many nearby males calling concurrently, male calls overlap in time, and females have a difficult time assigning specific calls to specific caller locations. Faced with call overlap, females often invoke a **precedence effect** in which overlapping calls are assigned to the location of the first caller [386]. This sets up a competition in which males either jockey to call first or wait until a cluster of males has called and then follow with their own non-overlapping call. The typical outcome of this competition is either a high level of synchronous calling by neighboring male callers (e.g., full overlap), or completely alternate calling (e.g., no overlap) [26, 127, 128, 247]. In the first case, noise is maximized for the receiver females, and in the second it is minimized. We shall return to the evolutionary implications of these adjustments to conspecific competition in later chapters.

FIGURE 3.24 Shifts in minimum song frequencies in the songs of great tits (*Parus major*) for urban versus nearby forest populations For each of 10 European cities and towns, an average of 30 great tit songs were recorded in the urban environment, and another 30 songs were collected in a nearby forested site. (A) Average minimum frequencies for songs in each pair of sites (linked by lines). In every case, the average minimum frequencies are higher in the urban setting. (B) The same data plotted to show that there are no underlying geographical correlates to the minimal frequencies found in the songs. In each case, the urban population has shifted to a minimum frequency somewhat higher than that of the nearest forest population. If there had been no shift, points would fall on the dashed line in the graph. (After [336].)

Sound Reception

Animals use their ears to detect, identify, evaluate, and localize ambient sound sources. As with other sensory modalities, communication is only one of several possible tasks mediated by hearing organs. The monitoring of parasites, predators,

prey, and nearby obstacles (e.g., echolocation) can be more important functions for hearing than is conspecific signal exchange. As a result, the design of auditory organs is often a compromise determined by the relative importance to the animal of each of these potential hearing tasks. In addition, while an ideal ear would identify source locations accurately, and operate equally efficiently in near and far fields, over all frequencies and amplitudes, and with unlimited temporal and frequency resolution, the relevant physics makes such simultaneous perfection impossible. There are always trade-offs in which increasing scope or resolution for one type of acoustic data results in a decrease in the scope or resolution of another. The results are ears that are good at some measurements and poor at others, with different weightings in different taxa. In the remainder of this chapter, we examine the causes and consequences of a number of these compromises.

Fortunately, most of the principles and trade-offs outlined in Chapter 2 for sound production apply, in reverse, to sound reception. Just as small animals are limited to wavelengths smaller than their bodies when using horns or resonance structures to modify and radiate sounds, the same constraints apply to using horns or resonant structures to capture and amplify a sound signal. This ability to replace senders with receivers and vice versa, (at least within linear systems), is called the **reciprocity theorem of acoustics** [112], and it will simplify our task in the remainder of this chapter. Reversing our sequence from Chapter 2, we can break down the process of sound-signal reception into three successive tasks: (1) the coupling of sound in the medium to the receiver; (2) modification (including filtering, amplification, and impedance matching); (3) and analysis (characterization and interpretation of the perceived signal's temporal and frequency patterns).

Coupling between medium and the receiver

The auditory organs of animals have two major design constraints. First, all receptors used to detect sounds are derived from generalized mechanoreceptors. As a result, animals can detect a sound signal only if it moves some body part relative to the rest of the receiver's body. As we saw in Chapter 2, the energy in a propagating sound is divided between locally coordinated movements of molecules and local variations in pressure. In the near field close to a sound source, the contribution of molecular movement is dominant, and the propagating medium will exhibit a cohesive tidal surge back and forth. If a receiver can insert a flexible hair or filament into this tidal oscillation, and not have its entire body also move in concert, the differential movement of the hair and the body can be used to detect and even track the direction of the passing sound waves. In the far field, molecular movements are no greater than when no sound is present, and the major indication that a sound is passing is pressure variation. Far-field sound detection is thus more complicated, because a receiver will be able to detect passing sound waves only if the variations in pressure can be converted into relative movement of several body parts. Animals have evolved various devices to perform this conversion, and we humans rely on one such device for our own hearing.

The second and related problem is that a receiver's ability to capture a detectable amount of passing sound energy is dependent upon the relative acoustic impedances of the receiver and the propagating medium. If the two impedances are very different, as is the case for most terrestrial animals communicating through air, most of the incident sound energy at the receiver's ears will be reflected. Devices are thus needed to bridge the impedance differences and enhance sound energy capture. If the acoustic impedances of receiver and medium are very similar, as with crustaceans and fish in water, then the opposite problem arises: incident sound is fully absorbed into the receiver, causing its entire body to vibrate. Unless it can devise a way to make one part vibrate out of phase with the rest, it will be unable to detect much less track the incident sound waves. Below, we describe the common solutions to these coupling problems in four different acoustic situations.

NEAR-FIELD SOUNDS Near-field sound detection poses somewhat different challenges in water and air. In water, the near field for a given frequency extends 4.4 times farther from the sender than it would in air. This makes near-field sound detection potentially more useful in water than in air. On the other hand, because the acoustic impedance of receivers and the medium are so similar, the animal must employ a coupling device that will vibrate in a sound field with a different phase or amplitude from that of the remainder of the body. The coupling device used by most aquatic animals is a fine hair, seta, or cilium that either projects from a sensory neuron or is connected to a sensory neuron. Such hairs are usually thin and stiff but have a flexible attachment to the receiver's body. Many display a fine feathering or other elaboration near the tip to increase friction with a moving medium. As the medium surges back and forth during the passage of a near-field sound, it drags the free tip of the hair with it. This rotates the base of the hair and stretches or compresses the attached sensory neurons. The neurons then send electrical signals to the brain for processing. Note that the hair tip must move either to a greater degree or with a different lag relative to any movements induced in its base and the whole animal by the sound. If all tissues move in concert, there will be no rotation of the hair and no electrical signals. Differential movement is guaranteed by making the mass and inertial properties of the hair significantly different from those of the animal. Since the animal is much larger than the hair, this is usually not difficult. Note also that the hair must be stiff: if it simply bends in the middle as the sound passes, there will be no rotation at the attachment point and no stimulation of the neuron. Aquatic arthropods and cephalopods (squids and octopuses) have many such receptor hairs on the surfaces of their bodies [37, 52-54, 89, 94, 131, 154, 284, 349, 360, 367]. Some are used to monitor the animal's movement and water currents, but others play important roles in the reception of near-field sounds (Figure 3.25).

FIGURE 3.25 Sensory hairs on exoskeletons of aquatic crustaceans (A) Filiform hairs on carapace of rock lobster (*Palinurus vulgaris*). (B) Hair-fan receptor on carapace of European lobster (*Homarus gammarus*). (C) Hair-pit organs on claws of young crayfish (*Cherax destructor*), and (D) similar organs on adult crayfish of same species.

Sense organs called **statocysts** are a variation on the same theme. These are typically fluid-filled capsules in which heavy masses called **statoliths** (sand, calcareous secretions, or a protein matrix) sit over the tips of an array of sensory hairs (Figure 3.26). Statocysts are widely employed by animals to distinguish up from down using gravity [50]. They have interesting dynamic properties that make them useful for additional functions, as well. If the animal changes its velocity or direction, or if its tissues are set into oscillation by an incident near-field sound, the soft tissues respond at a more rapid rate than the statoliths, and as a result of the discrepancy, the sensory hairs are rotated. Whereas exoskeleton hairs described earlier continue to be rotated and produce nerve impulses as long as there is a steady flow of medium over them, statolith hairs remain rotated only until the statoliths can catch up with the rest of the body's new motion. Put another way, free hairs on the animal's surface measure the velocity of the nearby medium relative to the animal whereas statocysts monitor acceleration of the animal's tissues. Given their dynamic properties and the transparency of most aquatic animals to ambient sound, statocysts can easily serve as effective couplers and detectors of near-field sounds. It has been suggested that statocyst reception may account for the widespread startle response of cephalopods to sudden underwater sounds [54, 131]. Statocysts are also the likely receptor organs for conspecific sound signals in many marine crustaceans [53, 109, 143, 198, 199, 273, 284, 323].

FIGURE 3.26 Crustacean statocysts These organs can be located at the base of the antennules (in crabs, lobsters, and crayfish), on the head (in amphipods), or on the tail (in mysid shrimp and isopods). They consist of open or closed capsules embedded in the exoskeleton. The capsules of crayfish and lobsters contain many small statoliths (A), whereas those of most other taxa host a single amalgamated mass (B). The statoliths sit on hairs (setae) that can rotate in their sockets just like the exoskeleton hairs shown in Figure 3.25. When the statoliths and the rest of the body move with different accelerations, the base of the hair moves relative to its socket, stimulating attached sensory neurons. The number of hairs per statocyst can range from 3 in isopods to over 400 in lobsters.

FIGURE 3.27 Inner ear of bony fish (A) One of paired inner ears from inside the head of a bony fish. The three orthogonal semicircular canals monitor movements in the three dimensions. Most fish rely in part on the saccule and lagena for hearing, and some species also use the utricle or macula neglecta. (B) The saccule, lagena, utricle, and macula neglecta each have a structure similar to that of the statocysts of Figure 3.26: a fluid-filled cavity is lined with sensory cells (called hair cells) and a single large otolith. Whereas crustacean statoliths rotate setae that in turn stretch or compress sensory cells, a fish otolith directly contacts the kinocilia and stereocilia of the hair cells. Hair cells do not have axons, but are innervated by auditory neurons. (C) Sample otoliths from different bony fish species (left column from top): New England hake (*Merluccius bilinearis*), morid cod (*Halargyreus johnsonii*), and opah (*Lampris guttatus*); (right column from top) white hake (*Urophycis tenuis*), and tilefish (*Lopholatilus chamaeleonticeps*).

Since statocysts are present in larvae of both invertebrates and fish, they may account for reports that pelagic larvae of many marine species find suitable settling sites by moving toward loud sound sources [248].

Most fish also use a statocyst design for the paired ears in their heads (Figure 3.27). In addition to three semicircular canals used to monitor a fish's movement in each of three directions, a typical fish ear contains three adjacent capsules (the **saccule**, the **lagena**, and the **utricle**), each of which has hair cells and a calcareous statolith (called an **otolith** in fish) with a density at least three times that of surrounding tissues. Sharks, rays, and some bony fish have a fourth capsule called the **macula neglecta**, in which a gelatinous mass replaces the calcareous otoliths of the other organs. In the majority of bony fish, the saccule and lagena appear to be the main acoustic sensors, and the utricle functions as a gravity monitor [104, 182, 200, 283, 378]. However, some catfish use the utricle for low-frequency hearing [280], and several herring species use it to detect the ultrasonic sounds of predatory cetaceans [287]. Sharks and rays rely on a combination of inputs from their enlarged macula neglecta and one or several of the other three organs [75, 76, 206].

In air, the near field for a given frequency ends very close to the sender, and the large impedance difference between the receiver and the medium seriously limits the transfer of energy into any sound-receiving organ. Despite these constraints, many terrestrial arthropods rely on surface hairs to detect near-field sounds (Figure 3.28). The body hairs of some caterpillars can detect the flight-generated airflow of hymenopteran predators at up to 70 cm [347]. The legs of spiders have arrays of specialized sensory hairs (**trichobothria**) that respond to nearby air currents. Away from a surface, detection ranges are limited to 15 cm; but close to surfaces, where near-field airflows are more channeled, ranges of 50–70 cm are possible [20]. Crickets and cockroaches have dense arrays of sensory hairs on their cerci that are highly sensitive to any type of air current [55, 136, 158, 326]. Female flies, male mosquitoes and midges, and worker honeybees have elaborate and often plumose antennae (Figure 3.29). Each antenna is attached to a mass of sensory cells (over 30,000 in male mosquitoes) called a **Johnston's organ** [23, 166, 234, 304]. These organs act as receivers of conspecific near-field sounds over distances of several body lengths, and usually have properties such that resonant modes of the antenna match species-specific sound frequencies.

Some terrestrial vertebrates also appear to communicate with near-field sounds. Elephants produce group coordination calls of very low frequency. Members of a typical herd are often well within the 20 m near-field limit of each others'

FIGURE 3.28 Near-field sensory hairs of terrestrial arthropods (A) Filiform sensory hair on cercus of cockroach (*Periplaneta* spp.). (B) Filiform sensory hair on cercus of cricket (*Gryllus bimaculatus*). (C) Grooved sensory hair on thorax of bottle fly (*Calliphora* spp.). (D) Leg segment of *Nephila* spider showing trichobothria hairs, as well as tactile and chemosensory hairs.

sounds. Although human ears do not respond to these low-frequency sounds in the far field, one can feel induced body vibrations when close enough to communicating elephants. It appears likely that elephants also use these near-field effects to exchange signals when sufficiently close together [275, 299].

FAR-FIELD SOUNDS IN AIR All terrestrial animals with ears use some form of thin membrane, called a **tympanum**, to couple airborne far-field sounds into their ears. There are two basic designs for tympana. In the first design, called a **pressure detector**, the tympanum is stretched over a closed cavity containing air at the same pressure as the silent ambient medium (Figure 3.30). Because the membrane is very thin and pliable, the combined acoustic impedance of the membrane and the air cavity is not very different from that of the medium; the similarity allows some incident sound energy to be absorbed. When incident sound waves raise the air pressure outside the

FIGURE 3.29 Near-field antennae of insects (A) Plumose antenna of male mosquito used to detect wingbeats of nearby female. (B) Antennal arista of female fruit fly used to detect near-field song created by courting male's wings.

FIGURE 3.30 Pressure detector ears Diagrammatic cross section through head of a typical mammal with a pressure detector ear on each side of the head. Each ear is structurally and dynamically independent of the other. A thin tympanic membrane is stretched over a closed cavity in head. This membrane is bent inward when ambient sound pressure is higher than the resting pressure inside the cavity, and outward when outside pressure falls below inside level. A structural linkage (here, three articulated bones) connects movement of the tympanum to sensory cells in the inner ear. Each ear cavity connects by a Eustachian tube to the pharyngeal cavity. These tubes are normally closed during hearing but can be forced open to equilibrate cavities with ambient air pressure during silent periods.

membrane above that inside the cavity, the membrane is bent inward, and when the outside pressure falls below the cavity value, the membrane is bent outward. Incident sound waves thus create a synchronized inward and outward oscillation of the tympanum that can then stimulate attached motion sensors. Pressure detection works only if the tissues surrounding the cavity do not absorb enough sound energy to vibrate in concert with the tympanum: if they did, there would be no relative motion to stimulate the sensors. Given the large difference between the acoustic impedances of air and most animal tissues, this condition is easily met. Note that sensors attached to a tympanum change its impedance. As we shall discuss later, the sensors and attachments must minimize any increased reflection at the tympanum while transferring some sound energy to the sensors. Mammals typically have one pressure detector tympanum (eardrum) on each side of the head. Tympanal pressure detectors are also found in mantids, moths, lacewings, and beetles, in which they are largely used to perceive echolocating bats [16, 381, 382].

The second design also relies on differences in pressure on the two sides of the tympanum to bend it inward or outward. But here, the cavity behind the membrane is not closed: it is connected to a tube whose other end is exposed to the medium at another point on the body (Figure 3.31). Such a **pressure differential detector** allows the animal to sample the impinging sound field at two locations. When the pressure outside the tympanum is higher than that at the tube opening, the tympanum is bent inward, and when the reverse is true, it bends outward. Pressure differences on the two sides of the tympanum can arise because one side experiences higher peak values than the other, or even if peak pressures are similar, because the two samples are out of phase. This design is widely found in insects, frogs, and birds. For example, locusts and grasshoppers have a tympanum on each side of the anterior part of their abdomen. Behind each tympanum is an air space bounded by a thin tissue wall. This wall abuts two air sacs in the center of the abdomen. The tissue walls for the cavity and air sacs are sufficiently thin and flexible that they propagate low- and intermediate-frequency sounds easily. Within this frequency range, each tympanum acts as the second source of pressure sampling for the other [246]. A functionally similar situation occurs in cicadas, which have a large central air sac acoustically coupled to the tympana on each side of the body [115]. Frogs, lizards, and birds have equivalent cavities connecting the air spaces behind the tympana on the two sides of their heads, and frogs may receive additional far-field input through the vocal sac and body wall [61, 63, 169, 176, 195, 255].

Katydids and crickets have two tympana on each foreleg. In crickets, the posterior membrane appears to be the major sound coupler [187], whereas in katydids, both membranes can respond to incident sound [244, 246]. The air space behind the tympana in each leg connects to a tracheal tube that winds through the upper leg and opens to the air through a spiracle on the same side of the thorax. In the katydid, each tympanum thus samples the sound field at two points. In crickets, however, the tracheal tubes from the left and right forelegs abut in the middle of the body before

FIGURE 3.31 Pressure differential ears (A) Tympanic ears on opposite sides of body joined by one or more air sacs in center (grasshoppers, cicadas). Arrows show paths delivering sound to each side of left-hand tympanum. The same pattern occurs at the other ear. The tympanum moves when the pressures or phases of sounds on the two sides of its surface are different. (B) Tympanic ears on opposite sides of head connected by an interaural canal (most birds) or open Eustachian tubes and the pharynx (lizards and some birds). (C) Tympanic ears on the head connecting through large open Eustachian tubes and the pharynx with additional sound paths from the lungs, vocal sac, and body wall (frogs and toads). (D) A pair of tympana (one anterior and one posterior) on each foreleg of a cricket. The posterior tympanum is usually the responding structure. Sound pressure at its external surface is compared to that delivered by a tracheal tube to the inside surface. This internal pressure includes inputs from a pair of spiracles on each side of the thorax, and from the tympana of the opposite foreleg. Katydids have a similar system, except that the two tracheal tubes do not meet, and thus pressures from spiracles or tympana on one side of the body cannot be compared to those to the opposite side.

turning to the spiracle. The membrane separating the two tracheal tubes at this point is transparent to lower frequency sounds. In principle, a cricket tympanum could thus receive samples of ambient sound pressures from four locations: (1) just outside the tympanum; (2) just outside the spiracle on the same side of the body; (3) just outside the spiracle on the opposite side of the body, and (4) just outside the tympana on the opposite foreleg. In practice, the input from the

FIGURE 3.32 Tympanal ears of water boatman (Corixidae, Hemiptera) (A) A submerged water boatman with a trapped air bubble around its body (arrows) for breathing. The air bubble acts as a resonant impedance matching device that converts waterborne sounds into airborne sounds. Normal modes of bubble range from 1.4 kHz when the bubble is fresh to 3.4 kHz as the bubble shrinks due to the water boatman's breathing. (B) External view of one of the paired tympanal ears on the thorax of the boatman. The external surface of the ear is always covered by the air bubble. A clubbed structure sits on top of the tympanum. (C) Section through one tympanal ear, showing shape of club and air space inside the animal under the tympanum. Sounds captured by the air bubble cause the tympanum to vibrate. This vibration in turn induces the club arm to rock and feed back on the tympanum to create strong resonant behavior. The right and left ears have normal modes at slightly different frequencies, presumably to provide sensitive hearing over the full range defined by the changing resonances of the air bubble. (B,C after [290].)

opposite tympana is negligible, but the other three sources contribute jointly to tympanum movement and direction [246]. Cockroaches do not have tympana, but may use tracheal tubes to convey airborne sounds to sensory organs inside their legs [324, 325]).

FAR-FIELD SOUNDS IN WATER Particle velocities in an aquatic far field are usually too small to be detected directly by motion sensors. Receivers thus turn to large surfaces that can concentrate the sound pressure variations and convert them into localized tissue motion. The usual solution is to use an air bubble to capture waterborne sounds and convert their high pressure/low displacement motion into low pressure/high displacement motion that can be detected. Aquatic insects called water boatmen use air bubbles trapped around their bodies both for respiration and as sound-capturing mechanisms (Figure 3.32) [290, 291]. The more common strategy is to use an air bubble inside the animal. Because air is more compressible than water, sounds propagating through the wet tissues of the animal cause the bubble to compress and expand in synchrony with the rise and fall of pressure [133]. If a thin membrane around the bubble is connected to motion sensors in the ear, the aquatic animal will be able to hear far-field sounds. Since the far field for high frequencies begins much closer to a sound source than that for low frequencies, the linking of ears to air bubbles effectively increases the maximum frequency detectable by an aquatic receiver far from the sound source.

We have already discussed how bony fish use gas-filled swim bladders to maintain buoyancy and, in some species, produce communication sounds. Given the reciprocity principle for sound, it should not be surprising that some fish utilize the system in reverse by converting far-field pressure variation into synchronized expansions and compressions of the swim bladder. If this motion of the swim bladder membrane is coupled to the existing auditory organs, the differential motion induced in the hair cells and otoliths will generate electrical signals in the sensory cells as with near-field sounds.

A number of fish taxa have evolved linkages between their swim bladder and their ears (Figure 3.33). The effectiveness of these linkages can be measured by comparing acoustic sensitivity before and after deflation of the swim bladder or removal of the linkages [181, 385]. In some cod (Gadidae), squirrelfish (Holocentridae), and croakers (Sciaenidae), the swim bladder has a pair of tubular extensions that terminate very close to the saccule on each side of the head [182, 270, 283, 296]. In each of these fish, the linkages provide enhanced sensitivity to high-frequency and far-field sounds. Many members of the herring family (Clupeidae) exhibit similar extensions, but each of these terminates in one or a pair of air-filled bullae that abut the utricle in each ear. These structures provide sensitivity to very-high-frequency far-field sounds such as the echolocation pulses of foraging dolphins and porpoises [144, 214, 287]. Otophysans (including goldfish, minnows, zebrafish, piranhas, characins, neotropical electric fish, and catfish) have a chain of four small bones (called **Weberian ossicles**) on each side of the body that

FIGURE 3.33 Role of swim bladder and other air bubbles in fish far-field hearing (A) Fish such as toadfish and sunfish lack any direct linkages between the swim bladder and the ears except intervening tissues. They are largely limited to near-field sounds. (B) Cod, squirrelfish, croakers, and drums have air-filled extensions of the swim bladder that terminate near the saccule in each ear. They can hear far-field sounds and much higher frequencies than toadfish. (C) Some herring and shad have swim bladder extensions similar to those in (B), but each of these terminates in one or more air-filled bullae that are linked to the nearby utricle. This combination makes them highly sensitive to the ultrasonic echolocation pulses of hunting dolphins. (D) Swim bladder of typical otophysan fish (goldfish, minnows, catfish) is connected to two parallel chains of 1–4 Weberian ossicles (blue). These chain ossicles use leverage off the backbone (grey) to transmit swim bladder vibrations to a perilymphatic sac (red). Latter in turn conveys vibrations to single endolymphatic sac whose fluids connect directly to each saccule. (E) African electric fish (Mormyridae) lack any special links to swim bladder, but each ear contains an air-filled sac just adjacent to the saccule. (F) Anabantoid fish such as gouramis also lack any links between their swim bladder and their ears. However, they are air-breathing and have special chambers for holding air bubbles for respiration laterally to each inner ear. The saccule is separated from the underlying air bubble by at most a thin epithelium or sheet of bone

links the swim bladder to the ear on the same side [283, 378]. This mechanism has resulted in some of the most sensitive and widest bandwidth auditory systems known in fish [200]. Eels lack both Weberian ossicles and extensions of the swim bladder, but some species still possess very sensitive far-field hearing. It has been suggested that the backbone may serve as the critical linkage in this group [320].

Other fish taxa use air bubbles that are separate from their swim bladders. Gouramis (Anabantoidei) are air-breathing fish that carry a small bubble of air in a suprabranchial cavity

FIGURE 3.34 Section through ear of toothed (Odontocete) whale Intermediate- and high-frequency sounds are captured by a thin "pan bone" section on each side of the lower jaw and conducted through special oil channels to the joints between the jaw and the skull. Sounds delivered by this route then propagate a short distance through soft tissues to the nearby ear. The ear consists of two loosely connected clam-shell like bones, the periotic bone on top and the tympanic bone below. These are suspended by ligaments in an air-filled cavity. Incident sounds cause a thin portion of the tympanic bone called the tympanic plate to vibrate near its junction with the periotic bone. A chain of middle-ear ossicles then modifies this movement and transfers it to the inner ear located in the periotic bone. Baleen (mysticete) whales have a generally similar structure except that the jaw does not appear to conduct sounds and the periotic-tympanic complex is less acoustically isolated from the skull. It is thought that the low-frequency sounds used by mysticetes are captured by the skeleton and conducted directly to the ears. (After [162, 265].)

lateral to each ear. The vibrations induced in this bubble by ambient sound pressures are communicated through a very thin skeletal wall and into the saccule [178, 316]. African electric fish (Mormyridae) have a small air-filled bladder adjacent to the saccule of each ear [81, 111]. These air bubbles increase the sensitivity of the ear by 30 dB over the unaided range of these fishes' hearing (200–1200 Hz).

Among the fishes that produce sound signals, many, such as toadfish, damselfish, gobies, sculpins, and cichlids, lack elaborated coupling structures [180, 182]. Similarly, there are many fish with sensitive hearing that do not produce sound signals [179, 180, 182]. One explanation for the poor correlation between sound communication and hearing ability in fishes is that species with minimal adaptations do not need to communicate over long distances and thus can exchange sound signals with simpler ears. Elaborate ears in species with minimal sound communication may arise where hearing is important for finding prey or avoiding predators. In addition, several authors have noted that fish with the most sensitive ears tend to be found in acoustically quiet environments [5]. Thus the levels of ambient noise may be a better predictor of ear structure in fish than a reliance on acoustic communication.

The ears of whales (Cetacea) also require air spaces to mediate reception of underwater far-field sounds (**Figure 3.34**). Toothed whales and porpoises (Odontocetes) utilize high-frequency sound to echolocate their prey (see Chapter 14). Sounds focused and emitted through the head melon return as echoes and are captured by wide and very thin portions on each side of the lower jaw called "pan bones" [10, 262]. Sounds are then transferred between each pan bone and the corresponding ear by special fat- and wax-filled channels in the lower jaw [141, 171, 249, 262] The channels function as wave guides. One group of odontocetes, the beaked whales (Ziphiidae) may use both the jaw and a mass of fatty tissue in the throat to conduct sound to the ears [79, 80]. The odontocete ear is a clam-like structure, with a periotic bone on top and a tympanic bone below. It lies in a skull cavity at the base of the lower jaw, surrounded by air-filled foam. The ear is not in direct bone contact with the skull, but is suspended from it by ligaments [162, 163]. This configuration prevents sound from entering the ear by bone conduction through the skull. The inner ear with its sensory cells is lodged in the periotic bone. The cup-shaped tympanic bone is loosely linked to the periotic bone on its top side, thick and dense on its bottom and internal sides, and very thin on the side opposite the end of the lower jaw. This thin portion of the tympanic bone is called the tympanic plate. Three articulated bones inside the air-filled tympanic cavity link the upper edge of the tympanic plate to the inner ear. They are positioned so that they rotate back and forth in a small arc around their center of gravity when the top of the tympanic plate moves in and out. Sound waves propagating from the jaw channels into nearby wet tissues exert oscillating pressures on the thin tympanic plate. Because the tympanic cavity is filled with air, it is compressible, and the top of the tympanic plate vibrates in synchrony with the varying sound pressures. The bottom of the thin wall is fixed to the heavy parts of the tympanic bone and acts as a hinge. These vibrations of the tympanic plate are then transferred to the inner ear by the chain of middle ear ossicles [138, 139, 265, 266].

Baleen whales (mysticetes) include the largest animals on the planet and are well known for their production of extremely low-frequency communication sounds [64, 97,

236, 350, 351, 366]. Coupling of ambient sounds to their ears is poorly understood. One suggestion is that parts of the skeleton are sufficiently similar to water in acoustic impedance that some incident sound energy is absorbed by the skeleton and conducted through the bones to the ears. Most mammals minimize bone conduction of absorbed or body-generated sounds (e.g., chewing) to their ears. One way to do this is to ensure that the primary point of articulation between the middle ear bones linking the tympanum to the inner ear is also the center of gravity of those bones [18]. Any vibrations conducted to the ear by the skeleton would then move all parts in synchrony and there could be no stimulation of the inner ear. Mysticete whales, true seals (Phocidae), burrowing mammals, and elephants all have very heavy middle-ear bones in which the articulation point is not the center of gravity [137, 140, 162, 163, 223, 264, 299]. The inner-ear capsule and the middle-ear bones might then move differentially in these animals, which allows the marine mammals to receive bone-conducted low-frequency vibrations from the water and the terrestrial animals to receive them from seismic vibrations.

SURFACE PROPAGATED SOUNDS A variety of animals detect sounds by monitoring vibrations at the surface between two media. Insects and spiders living on plants are very sensitive to oscillations in the plant surface caused by internal bending waves [20, 68, 69, 71]. Many animals that live on or burrow in the ground can detect Rayleigh waves propagating on the surface of the substrate [46, 257, 258]. Water striders and spiders attend to ripples on the surface of the water, and orb spiders monitor both longitudinal and transverse vibrations of the strands in their webs [20, 29, 228, 368].

These species sense the motion of the surface and not the pressure variations inside either of the media. Waves on the water's surface attenuate rapidly and become distorted due to dispersion of the component frequencies. This limits the range of useful detection and characterization of water surface signals to under one meter [19, 368, 369]. Bending waves in plants are also dispersive, but attenuation is a bit less, and both spiders and insects living on the surface may be able to detect signals from up to several meters from the source [20, 164, 242]. Elephants appear able to detect very low-frequency Rayleigh waves on the Earth's surface at distances of kilometers [7]. In all of these contexts, low frequencies attenuate less rapidly than high frequencies, and most animals communicating at surfaces favor the lowest frequencies that their bodies can detect. Although sound speeds in water and solids are much higher than those in air, those on the surface of water or the ground are generally less than those in air [112]. For example, signal propagation on the water's surface is usually less than 1 m/sec, and Rayleigh waves in soil and bending waves in plants both propagate at speeds of 50–200 m/sec [46, 112, 242, 258]. As a result, signal propagation is slower on surfaces than within large volumes of air or water.

A receiver of surface signals must first couple the particle movements of the boundary into its body. Most species use their legs as the coupling devices [19, 68, 71], although whirligig beetles use their antennae [170], and some fossorial rodents lay their heads against the substrate or even bury them in the ground [256]. Legs have the advantage that they are jointed and held in position by adjustable muscle tension. This tensioned flexibility of the legs and the mass of the attached body make the entire animal a resonant device that can amplify the small particle movements of the boundary over successive cycles [112]. Spiders, fiddler crabs, and treehoppers can fine-tune the normal modes of this resonance by adjusting their posture and muscle tension [2, 3, 19, 66].

Once coupled into the body, two or more parts of the body must respond to these vibrations by moving out of phase so that auditory sensors can be stimulated (Figure 3.35). Spiders, scorpions, and their relatives have large numbers of **slit organs** embedded in their exoskeletons [20, 21]. These slits are V-shaped in cross section and particularly abundant near leg joints. Compression of the legs due to induced vibrations causes the openings of the slits to close, and this triggers motion sensitive cells located at the base of each slit. Spiders also have hairs that span leg joints and monitor leg flexure. Many insects have pit-like **campaniform sensilla** on their exoskeletons that function similarly to the slit sensors of spiders [302, 352]. In addition, internal **chordotonal organs** monitor the flexing of insect leg joints, and **subgenual organs** monitor differential rates of acceleration of the exoskeleton and the fluid hemolymph inside each leg [382]. All of these organs have been implicated in the detection of substrate vibrations [71, 90, 361]. In frogs, substrate vibrations absorbed by the body pass through the pectoral girdle and along a muscle that connects to the **operculum**—a moveable window—on the wall of the inner ear. Like fish, frogs have a saccule, and the vibrations transferred to it by the opercular movements allow the frog to monitor seismic sounds [258]. Like insects, most terrestrial mammals can detect some substrate vibration using existing flexure and touch receptors. Elephants and fossorial moles and rodents have evolved middle-ear bones that are much more massive than expected, given their body sizes. As noted earlier, these species appear to rely on differential inertia of the middle-ear bones and the rest of the body to stimulate the inner ear with vibrations absorbed from water or solid substrates and conducted by the skeleton to the ears [223, 225, 227, 263, 264, 299].

Modification of captured sound signals

The primary modification tasks undertaken by animal ears are amplification, filtering, and impedance matching. Note that these are similar to the same tasks required for sound radiation (see Chapter 2). Since these three processes are invariably linked, we outline below some of the known designs and discuss how they affect each of these tasks.

A number of terrestrial animals gather sound waves in the large open end of a horn and deliver it in an amplified form to one side of a tympanum. Horns also facilitate tympanic responses to incident sounds by providing a more gradual

FIGURE 3.35 Substrate vibration receptors of arthropods (A) Lyriform organ consisting of multiple slit organs on the leg of a spider (*Cupiennius salei*). (B) Campaniform organ on antenna of silk moth (*Antheraea polyphemus*). (C) Diagram labeling segments of typical insect leg. (D) Section through lower femur of stink bug (*Nezara virdula*) showing femoral chordotonal organ. The organ includes two ligaments: one attached to the tip of the tibia at one end and the side of femur at the other, and the second to a muscle that flexes the tibia relative to the femur. The first ligament contains several sensory cells along its length and at its base on the femur wall. The second ligament has sensory cells only at its base. Both ligaments are stretched and relaxed as the tibial segment of the leg moves relative to the femur. (E) Section through the upper tibia of a green lacewing (*Chrysoperla carnea*), showing the subgenual organ. The membranous velum spread across the tibial cavity detects inertial movements of fluid hemolymph relative to the exoskeleton of the tibia. Sensory cells attached at their base to the tibial wall and by long dendritic filaments to the velum are stretched or relaxed as the velum moves differentially from the tibial wall. (D after [238]; E after [382].)

match between the low acoustic impedance of the open air and the higher impedance of the tympanum. The tracheal tubes used by katydids and crickets to sample sound fields act as horns with the large opening at the thoracic spiracle and the small opening just behind the tympana in each foreleg [241]. At the high frequencies typically used for conspecific communication, the trumpet-shaped tracheae of katydids can amplify the sound pressures delivered to the tympanum by nearly tenfold [246]. A V-shaped entry slit along the ventral midline of praying mantids provides a 1.8-fold amplification of incident sounds for the two tympana lining its walls [384]. While frogs and toads have tympana on the outsides of their heads, reptiles, birds, and mammals all have their tympana at the end of a tapering canal inside their heads. This canal acts as a horn and can produce surprisingly significant amplification. Mammals extend the large opening of each canal with a horn-shaped **pinna** [312], and some birds achieve a similar effect by positioning special feathers around their canal opening [74, 176]. Note that all horns are resonant structures with a limited bandwidth: low cutoff frequencies are determined by the diameter of the large opening, and high cutoff frequencies depend on the length and shape of the horn [112]. The relative size, shape, mobility, and placement of the pinnae vary widely among mammals and can significantly affect their acoustic properties (**Figure 3.36**).

The ancestors of terrestrial vertebrates retained the fluid-filled inner ear of fish when they moved onto land. This created a major mismatch of acoustic impedances: how could the high displacement and low pressure movements of a tympanum exposed to airborne sounds be transformed into low displacement and high pressure fluid movements inside the inner ear? Early terrestrial vertebrates acquired several mechanisms that solved this problem [319]. A first step was the addition of two small membranous "windows" in the bony inner ear capsule. Pushing in on the **oval window** caused fluids to move in the cavity and bulge the **round window**

FIGURE 3.36 Alternative types of pinna design in terrestrial mammals (A) Simple ovate pinnae: brown greater galago (*Otolemur crassicaudatus*). (B) Triangular-shaped pinnae completely fixed at base, as found in canids and felids: red fox (*Vulpes vulpes*). (C) Immobile semicircular pinnae fixed to the side of the head, as found in monkeys and apes, mongooses, and some rodents: chimpanzee (*Pan troglodytes*). (D) Pinnae with tubular base allowing independent rotation, as found in many herbivores: black rhinoceros (*Diceros bicornis*). (E) Pinnae with the outer and upper quadrant deleted or notched, as found in some rodents and bats: Patagonian mara (*Dolichotis patagonum*). (F) Highly elongated pinnae, as found in aardvarks, rabbits, and some bats and marsupials: black-tailed jackrabbit (*Lepus californicus*).

outwards; pulling out on the oval window caused the fluids to move in the opposite direction and bend the round window inward. Another step was the evolution of a mechanical lever system connecting the tympanum to the oval window. This lever converted the large displacements of low pressure at the tympanum into small displacements of high pressure at the oval window. Finally, with the enlargement of the tympanum to a size much larger than the oval window, a large amount of sound energy could be captured by the tympanum and concentrated on the much smaller area of the oval window.

Web Topic 3.4 ***Levers and ears***

Different types of lever systems provide mechanical advantages and match acoustic impedances for improved hearing in animals. Here we outline the general classes of levers and indicate which are used in the middle ears of amphibians, reptiles, birds, and mammals.

The physics of terrestrial (and secondarily aquatic) vertebrate middle ears has been studied in some detail [1, 59, 73, 135, 137, 148, 203, 208, 223, 226, 264, 266, 268, 312, 319]. As a rule, the relative size of tympanum and oval window is the dominant factor matching airborne to inner ear impedances. Tympana are reported to be 20–50 times as large as the corresponding oval windows for frogs, 10–13 times as large in lizards, 11–40 times as large in birds, and 10–32 times as large in mammals. Although amphibians, birds and reptiles, and mammals have evolved ossicular linkages independently [118, 211] and use somewhat different lever mechanisms (see Web Topic 3.4), the amount of pressure and velocity transformation achieved is fairly similar among the taxa. Typical

FIGURE 3.37 Insect scolopidial mechanoreceptors In each example shown here, one to several sensory cells extend long ciliary dendrites into a sheath formed by scolopale cells. These contain stiff rods of actin and perhaps other motile proteins. Flexure of the dendrite stimulates the sensory cells which then send nerve impulses down their axons. Details of the structure of scolopidia vary with taxon and function. (A) Scolopidum from sensory organ in ear of a locust. (B) Scolopidum from femoral chordotonal organ of a lacewing. (C) Scolopidum sense organ on mouthparts of a beetle larva. (After [382].)

values for each mechanism show 10- to 50-fold changes in pressure and velocity. Since the effects of concurrent impedance matching mechanisms are multiplicative, acoustic impedances at the oval window can be increased several hundred times over that at the tympanum, and this can significantly improve the transfer of airborne sound waves into the fluids of the inner ear. Note however, that transforming oval window impedances beyond a good match for the inner ear fluids can be as ineffective as no transformation. There is an intermediate level of transformation that is optimal, and this may explain the relatively convergent values seen in the different vertebrate taxa.

Like a horn, the middle-ear complex of higher vertebrates has its own resonances and can be inefficient at frequencies significantly different from its normal modes [137, 264]. Many species have their middle-ear resonances matched to the sound frequencies of greatest importance. Elephants, mysticete whales, true seals, and burrowing rodents and insectivores that respond to low-frequency signals all have larger and denser ossicles than might be expected for their body sizes. Echolocating bats have their ears tuned to ultrasonic frequencies. Parallel adjustments must, of course, be made in the inner ear, and it is not always clear whether the middle ear or the inner ear plays the final role in limiting auditory bandwidths [314]. Other constraints, such as isolation of the inner ear from bone-conducted sound in most mammals [18] or the use of the eardrum as a sound radiator in bullfrogs [292], may compromise the degree to which middle-ear resonances can be matched to behaviorally salient sound frequencies.

Detection and analysis of received sound signals

DETECTION Once sound energy is extracted from the propagating medium and modified as necessary, stimuli are ready for detection. The sensory cells used for vibration detection are remarkably uniform within each of two major sound-signaling taxa (arthropods and vertebrates). Arthropods use bipolar neurons whose long ciliary dendrite is usually surrounded by a sheath of accessory cells [161]. The ciliary component contains nine pairs of parallel tubules arranged in a circle, but lacks the central pair of tubules of traditional cilia and flagella. In insects, several sensory cells may be clustered into a **scolopidium** (Figure 3.37). Scolopidial cells containing stiff scolopale rods form a sheath that encloses the sensory cell dendrites and bathes them in a specialized ionic fluid. The stiffness of the rods is adjustable by the scolopale cells

FIGURE 3.38 Vertebrate auditory hair cells Four sensory hair cells that are stimulated when either fluid movements, otoliths, or overlying membranes bend stereocilia toward the kinocilium. Both types of cilia are supported in each cell by a dense cuticular plate. Note that the two hair cells on left are oriented (polarized) differently from the two on the right. By having different hair cells oriented in different directions, the ensemble as a whole can monitor fluid, otolith, or membrane movements in any direction. Hair cells synapse with the dendrites of afferent nerves, which, unlike a typical neuron, are myelinated for rapid propagation like axons. Some hair cells may also receive input from efferent nerves that modulate their behavior and sensitivity. Supporting cells and a basal membrane provide a firm matrix in which the hair cells are distributed.

[382]. Scolopidia are the most common sensory structures within insect hearing organs.

The dendritic sheaths of arthropod mechanoreceptors may be attached to the base of a pivoting sensory hair (all arthropods), inserted into the hollow base of a sensory slit (spiders) or campaniform pit (insects), grouped under statoliths inside a statocyst (crustaceans), or clustered with similar cells into scolopidia to form chordotonal or subgenual organs [20, 382]. The majority of spider and insect receptors are stimulated by bending or compression; crustacean receptors tend to be stimulated by stretching. Arthropod mechanoreceptors can be extremely sensitive: at optimal frequencies, responses to displacements of 1 nm (10^{-7} cm) are common, and the hairs on cricket cerci may trigger at displacements of only 0.05 nm [20, 326, 353]. As a point of reference, the diameters of single atoms range between 0.03 and 0.3 nm!

Vertebrates also use ciliated sensory cells for sound detection, but lacking their own axons, these **hair cells** must synapse with other neurons [70]. Each hair cell hosts a single **kinocilium**, (showing the expected circular ring of nine pairs of tubules around a single pair), and an adjacent bundle of 20–100 **stereocilia** (more appropriately called **microvilli**), each containing thin filaments of the protein actin (Figure 3.38). The stereocilia are usually arranged according to height, with the taller ones closest to the marginally positioned kinocilium. The tips of the stereocilia are linked to each other such that motions induced by nearby fluid or tissue vibrations bend the entire bundle cohesively [175]. Bending the bundle toward the kinocilium depolarizes the hair cell, and bending it away hyperpolarizes the cell. Bending the bundle at other angles stimulates the cell in proportion to the fraction of the movement which parallels the kinocilium-midpoint axis. Vertebrate hair cells are thus inherently directional. Electrical changes in the hair cell modulate the impulse rates of the synapsed nerve cells. In many mammals and some birds, the kinocilium disappears in adults, but the directional polarization of the stereocilia responses remains fixed. The inner ears of most vertebrates contain two or more types of hair cell that differ in size, shape, and the number of nerves with which they have synapses. The functions of these different cell types differ in the different vertebrate taxa and will be taken up in the next sections. Vertebrate hair cells are as sensitive as those in arthropods; threshold displacements under 1 nm are common. Goldfish respond down to 0.1 nm, and squirrel monkey hair cells are reported to detect 0.01 nm displacements [283, 306].

FREQUENCY RANGE AND RESOLUTION The bandwidths of auditory receptors can be maximized by adjusting their size, electrical and mechanical properties, and the ways in which they are linked to the medium or auxiliary structures. The orientation of directional hair cells in vertebrates relative to the passage of sound waves near a receptor organ, and the number and linkages between adjacent stereocilia can also be adjusted to diversify a cell's normal modes. Despite all these options, no single sensory cell is likely to have enough bandwidth to cover the frequency ranges provided by the coupling and modification organs. The solution is to have many cells, each tuned to a different normal mode (called its **characteristic frequency** in hearing organs), which collectively span the range of frequencies needed.

This solution solves another problem. Many animals must identify the frequencies in ambient sounds in order to

discriminate between species-specific signals and noise, characterize the pattern in a signal, or use the differential propagation of different frequencies to estimate the location of a signal source. A single sensory cell may be able to depolarize and hyperpolarize in synchrony with the oscillating motion of the sound waves. The impulse rate of the attached nerve will then be equal to (or at least proportional to) the frequency of the sound (a phenomenon called **phase-locking**). If the brain can measure these impulse rates, it will have a reasonable estimate of the sound frequency. However, this only works up to the maximal rate at which nerves can fire (several kHz). In addition, a sensory cell can only track the peaks and valleys of the entire waveform. The variation in the amplitude of a complex sound containing many frequencies may correspond to only one or a few of those components (e.g., harmonics), or it may not correspond to any (e.g., beats). If multiple sensory cells are used, each tuned to a different normal mode, then each component frequency stimulating the sensory cells can be identified. Frequency resolution can be improved by adjusting the mechanical and electrical properties of the sensory cells to reduce their bandwidths. This may require more cells to cover the full frequency range needed, but it will provide improved frequency resolution.

Animal ears that decompose complex signals into frequency components are essentially performing a Fourier analysis of the sound. Like the spectrograms used by researchers, the ear provides the brain with the relative amplitude of each band of frequencies that it is able to extract. Also like spectrograms, ears tend to ignore relative phase information except when component frequencies are so similar that the ear cannot separate them. Then their relative phases may affect the apparent amplitude assigned to that band of components.

In some animals, the frequency spectrum of a sound is estimated by a single organ; in others, it is assembled in the brain using the inputs of many different organs. For example, each hair and bristle sensor, slit organ, or campaniform pit organ on the exoskeleton of an arthropod usually contains only one (insects) or up to four (spiders) sensory cells and thus has a limited frequency resolution for each sensor. However, by varying the physical properties of the attached hair, slit, or pit, the collective input from many sensors provides an animal with a wide frequency range and reasonable discrimination between different frequency components [20, 37, 53, 112, 347, 349]. For sensory hairs and bristles, length is a major property that can be adjusted in this way. In part, this is due to **boundary layers** of medium adjacent to the exoskeleton that are kept from moving in the sound near field due to friction against the exoskeleton surface (Figure 3.39). This inert boundary layer is thicker for low frequencies than it is for high ones, and is thicker in air than it is in water for a given frequency. In all media, a shorter hair may respond only to high frequencies, whereas a longer hair that sticks out past the large boundary layer may be the only sensor to detect low frequencies. Evolutionary fine-tuning can be achieved by varying the stiffness of the hair and its base attachment, how far it can rotate, (often set by placing its base inside a walled socket of limited diameter), and the mechanical and electrical tuning of the attached sensory cells. In air, the cross-sectional area of the hair can also affect its normal modes. While such fine-tuning works well for frequencies below 1 kHz, it is difficult to move any hair or bristle at the velocities required for even higher frequencies. Sensory hairs, like slit and pit organs, are largely limited to low frequency sounds and near field conditions.

Insects use chordotonal organs to monitor flexing, stretching, and other proprioceptive tasks, and subgenual organs to detect movements of hemolymph inside their exoskeletons [108, 234, 382]. Again, multiple organs or organ regions can provide frequency discrimination by assigning separate zones of the overall frequency range to different organs. For example, Hemipteran insects that exchange substrate signals in plants use chordotonal organs in their legs to monitor low frequencies (50–100 Hz), and two subpopulations of subgenual organ scolopidia to separately monitor intermediate (200 Hz) and higher (700–1000 Hz) frequencies [71]. The subgenual scolopidia can detect differential bending of their dendrites as small at 0.1 nm at higher frequencies and are thus very sensitive.

Most terrestrial insects use tympana as the coupling organs for far-field hearing [147, 382, 383]. These may be located on any part of the body, including the thorax (tachinid flies and praying mantis), abdomen (cicadas and locusts), wings (lacewings), air-filled mouthparts (sphingid moths), or forelegs (crickets and katydids). In the majority of species, sensory scolopidia are directly attached to the inner surfaces of the tympana. This is true of grasshoppers, mole crickets, mantids, lacewings, tiger and scarabid beetles, tachinid and sarcophagid flies, moths, and some butterflies. In crickets and katydids, however, the scolopidia are attached along one side to the leg wall and along the other to the surface of the tracheal tube that forms part of their pressure differential ear system. Because this tube acts as a horn, the sound sample that it delivers to the ear is usually much greater than that received at the tympanum. Both the tympanum and the tracheal wall move relative to the leg wall, stimulating the scolopidia.

The number of scolopidia per tympanum in insects varies from 1–2 in noctuid moths up to several thousand in cicadas. The majority of species make do with 30–80 scolopidia. Frequency ranges and resolution seem better correlated with ear function than with numbers of scolopidia. Many insects such as moths, mantids, beetles, and lacewings use their ears to detect and avoid echolocating bats. Their hearing is typically limited to high frequencies (30–60 kHz). Conversely, female trachinid and sarcophagid flies that parasitize male crickets, katydids, or cicadas use their ears to find suitable victims. Their 100-scolopidia ears are mostly tuned to a narrow band of frequencies matching the male calling signals of their hosts, although ears of either sex may also detect bat echolocation sounds [147, 183, 297, 343].

Frequency resolution, but not necessarily frequency range, seems to be a priority for those insects that solicit

FIGURE 3.39 Sensory hairs and boundary layers A single mechanoreceptor hair is shown extending into the adjacent medium during passage of a near field sound. Molecular velocities (shown using size of arrows) vary with horizontal location (due to wave action) and height above the animal's body surface (due to friction close to that surface). The boundary layer, in which there is little near-field flow, is thicker for low frequencies than for high frequencies. Long hairs extend past the boundary level for all but the lowest frequencies, whereas short hairs are exposed to near-field motion only for high frequencies. Different hairs can thus be made frequency-specific simply by adjusting their length. Finer tuning can be accomplished by varying hair thickness, stiffness, socket attachment design, etc. (After [348, 20].)

mates with acoustic advertisement or acoustic duetting. Strategies for achieving frequency resolution vary with the taxon (Figure 3.40). The tympana of grasshoppers and locusts are divided into regions of different thickness and acoustic properties. As a result, the normal modes of this surface are quite complex, with different regions being set into maximal vibration by different frequencies. The cluster of 60–80 scolopidia in each ear (called a **Muller's organ**) is connected to the tympanum by three legs of a tripod. Each leg contacts a different region of the tympanum, and thus different parts of the vibrating membrane stimulate different scolopidia in the Muller's organ. Complex sounds are thus broken down into component bands of 3.5–4.1 kHz, 5.5–6.5 kHz, and 16–19 kHz [36, 239, 342, 374]. A similar mechanism may operate in cicadas [345].

The acoustic scolopidia in katydid and cricket ears are arranged in linear rows along the axis of the tracheal tube to which they are attached [222, 244, 245, 341, 382, 383]. The scolopidia differ in shape, size, and electrical properties so that they form a graded series with units responding best to low frequencies at the proximal (close to the body) end, and those responding best to high frequencies at the distal (furthest from the body) end. Whereas some katydids show a fairly even progression of characteristic frequency along the main axis of their acoustic organs, other katydids and most crickets show uneven progressions. Crickets, for example, have large numbers of scolopidia with characteristic frequencies close to the dominant harmonic of the male calling song. A second and more distal cluster favors the higher frequencies used for other types of calls in the male repertoire. In many species, the organ on its distal end terminates with a third broadly tuned cluster devoted to bat echolocation frequencies.

A sequential ordering of auditory units according to characteristic frequency within a hearing organ is called **tonotopy**. There are several reasons why tonotopy might be favored over more random dispersions of differently tuned sensory cells. Where characteristic frequencies are largely determined by mechanical properties of the sensory cells, adjacent cells with very different resonances may interfere with each other. When cells with similar resonance modes are clustered, this source of interference is reduced [211]. In fact, when adjacent cells have similar characteristic frequencies, there is often increased linkage between them, so that stimulation of one can trigger stimulation in similar cells nearby. In many tonotopic organs, a **tectorial membrane**

FIGURE 3.40 Frequency resolution devices in locusts and katydids (A) Side view of locust or grasshopper showing location of one of its two tympana just below the wing and on the first abdominal segment. (B) Expanded view from inside locust ear showing Mueller's organ and associated nerve attached to inside of tympanum. The approximate locations within this organ of the four key clusters of scolopidia are shown. (C) Plots of minimal stimulus intensity required to elicit a response versus stimulus frequency for single cells (*not* multiple cell averages) from each of the four key clusters of Mueller's organ scolopidia. The frequency with the lowest threshold intensity is the characteristic frequency of that unit. (D) Side view of katydid showing location of one of its two ears on the tibia of a foreleg. (E) Diagram of the inside of the tibia showing the linear array of auditory scolopidia (called the crista acustica) between the trachea and the membrane lining the space behind a tympanum. A subgenual organ located just above the crista is not shown here. (F) Sample threshold curves for three sensory cells in a katydid crista showing monotonic ordering of characteristic frequency according to location along the array. (B, C,E,F after [243].)

overlays the dendrites or stereocilia of the sensory cells. Because a membrane (unlike a solid statocyst) bends differently in different locations, local clusters of cells with similar frequencies can share stimulation. This makes the cluster of cells more sensitive to low-amplitude signals and allows for entrainment of all adjacent cells to a narrow frequency band [12]. Sound-induced oscillations of bare stereocilia or scolopidia would damp away quickly if exposed only to the ambient fluids [112]. A tectorial membrane provides a larger mass that "rings" long enough to trigger the relevant nerves. An even more effective mechanism for ensuring the sharing of local stimulation in tonotopic ears is overt movement by a sensory cell when stimulated by its characteristic frequencies. Mammalian outer hair cells do this by physically changing shape when stimulated, whereas those in other terrestrial vertebrates and the sensory cells in the Johnston's organs of mosquitoes and *Drosophila* wave their stereocilia or dendrites when excited [107, 123-126, 149, 211, 212]. This physical motion is then communicated to adjacent cells through direct contact or indirectly through a tectorial or other membrane. Such **auditory amplification** requires the expenditure of energy, and because it functions as a nonlinear feedback

mechanism, can lead to dysfunctional behaviors such as the spontaneous production of sound by hearing organs. (This is one cause of human tinnitus, or "ringing in the ears" after loud sounds or head injuries). Despite some dysfunctional aspects, auditory amplification is apparently common in both arthropods and vertebrates, and provides a very effective means for improved detection of low-amplitude sounds and more refined frequency resolution.

Web Topic 3.5 ***Auditory amplification***
Both arthropods and vertebrates use active motion of auditory receptors to amplify responses to low level sound stimuli. Here we examine some of the data demonstrating this mechanism in insects, mammals, and lizards.

All vertebrates use tuned hair cells for frequency resolution and amalgamations of many cells to insure broad frequency ranges. Most species use phase locking to measure lower sound frequencies. Depending on the species, fish detect and analyze acoustic signals in the saccule, utricle, lagena, and, if present, the macula neglecta. The saccules of most fish have two classes of hair cells with different electrical responses to sound stimulation and in some cases with different shapes and sizes [104, 283]. Each class favors a different portion of the species' frequency range even in toadfish, in which hearing is limited to frequencies less than 300 Hz, and goldfish, in which hearing can range from 50–5000 Hz. Most fish cannot detect sounds above 5 kHz, although as noted earlier, some herring and shad probably use special swim bladder coupling devices and their utricle to detect the ultrasonic (80–120 kHz) echolocation pulses of porpoises [144]. Frequency discrimination in fish without swim bladders or air bubble devices requires frequency differences of 10% or more, whereas in fish with such devices, only 3–5% differences are required. Although the goldfish shows some degree of tonotopic structure in its saccule, most fish do not exhibit tonotopic organizations in any of their hearing organs.

Amphibians retain the saccule, lagena, and utricle of their fish ancestors, and the saccule and lagena retain their auditory functions [195]. The saccule is the main receptor organ for low-frequency (<100 Hz) seismic signals transmitted from the pectoral girdle and through the operculum into the inner ear. In addition, frogs and toads have developed two other patches of hair cells in the inner ear: the **amphibian papilla** and the **basilar papilla**. Each of these patches is located inside its own tubular recess adjacent to the saccule, and each has an overlying tectorial membrane attached to the hair cells. The amphibian papilla is elongate and twisted in shape, with a tonotopic organization. It responds to moderate-frequency (80–1000 Hz) airborne sounds from a wide variety of sources. The basilar papilla is generally tuned to the higher-frequency components in the display calls of the males, and usually lacks tonotopic structure. Amphibian inner ears can function up to the frequency limits set by the mass and efficiency of their middle-ear structures (3–6 kHz), and can discriminate between frequencies as long as they differ by more than 10–30% [104].

Lizards, birds, and mammals lack an amphibian papilla, but the basilar papilla of their amphibian ancestors has been elongated to accommodate a greater range of frequencies and, in some cases, to provide better frequency resolution. Whereas lizard papillae tend to be straight, those of birds must be curved or twisted to fit in the head, and those in mammals are so long that they are coiled like a seashell, and thus called a **cochlea**. In all three taxa, the papilla/cochlea contains three fluid-filled tubes (Figure 3.41). The central tube, the **scala media** is sandwiched between the other two and bathes the stereocilia of the hair cells. One outer tube, the **scala vestibuli**, connects to the fluid-filled cavity just inside the oval window, and the other, the **scala tympani**, connects to a cavity just inside the round window. Although the two tubes are linked at their opposite ends by a small duct called the **helicotrema**, fluid only passes between them during very slow pressure variations. The hair cells rest on a **basilar membrane** adjacent to the scala tympani, and extend their stereocilia into a tectorial membrane inside the scala media cavity. When sound waves are introduced through the oval window, fluid pressures rise and fall inside the scala vestibuli faster than fluid can move through the helicotrema. This causes the scala vestibuli to swell and contract. As it does so, it bends the scala media and its associated structures into and out of the scala tympani, causing the round window to move in and out to alleviate the resulting changes in scala tympani pressures. Because the basilar and tectorial membranes move differentially during this bending, the stereocilia are stimulated.

Web Topic 3.6 ***Animations of vertebrate ears***
One movie can be worth a thousand still images. Here we provide links to a number of websites that provide free animations of middle and inner ears in operation.

Reptiles, birds, and mammals all have tonotopic ears. In birds and mammals, the hair cells tuned for the highest frequencies occur at the oval window end of the papilla and cochlea, respectively, and those responding to the lowest frequencies are found at the opposite end [121, 298]. In lizards, the low-frequency region may be at either end of their papilla; often, it is found in the middle between two regions of high-frequency hair cells [210, 213]. Lizards tend to have shorter papillae and fewer hair cells for their body size than birds and mammals, and their upper frequency limit is about 8 kHz. Birds have more refined middle-ear designs and longer papillae and can hear up to 10–12 kHz. The articulated middle ear ossicles and very long cochleae of mammals allow upper frequency limits of 150 kHz or higher.

Frequency resolution in reptiles, birds, and mammals is achieved through a combination of mechanisms. All of these taxa employ low-frequency phase locking, structural and electrical tuning of hair cells, and linking of adjacent cells through tectorial membranes. They also use local

FIGURE 3.41 Structure of typical mammalian inner ear (A) Inner ear showing semicircular canals (on left), oval and round windows at base of cochlea, and coiled cochlea (right). (B) Cross section through cochlea at point indicated in (A). Sound enters the cochlea at the oval window and propagates down the scala vestibuli. This propagation causes the partition between the scala vestibuli and the scala tympani to bulge into and out of the latter. This in turn stimulates the hair cells in the partition. (C) Detail of mammalian hair cell distribution in partition. Hair cells are sandwiched between a tectorial membrane that lies on top of the hair-cell stereocilia and a basilar membrane the overlays the scala tympani. Bending of this sandwich causes the tectorial membrane to move differentially from the basilar membrane and produce a shearing force on the stereocilia. In most mammals, inner hair cells (which constitute at most 20–25% of the total hair cells in the cochlea) are arrayed in a single row parallel to the cochlear axis. These are the only hair cells that send auditory information to the brain. The more numerous outer hair cells are arranged in 3–5 parallel rows and respond to auditory stimulation by changing shape and amplifying the movements of the tectorial membrane. Bird papillae have a similar configuration except that the papilla is curved and not coiled. A cross section shows a continuous and graded series of hair cell types instead of two discrete classes, and the hair cells are distributed in a mosaic instead of in linear rows. A higher percentage (65–80%) of the hair cells in bird papillae send auditory information to the brain. Amplification is achieved by the movement of stereocilia of a subset of the hair cells rather than by the hair cells changing shape.

amplification by active hair-cell or stereocilia motion, at least for high-frequency resolution. In fact, each of the three taxa has independently evolved multiple hair cell types to divide up the tasks of detection and amplification [107, 121, 211, 212, 306]. Finally, birds and mammals taper their basilar membranes so that the high-frequency end is narrow, thick, and stiff, and the low frequency end is wide, thin, and flexible. When propagating sound waves, this heterogeneous membrane interacts with the fluids of the scala vestibuli and the scala tympani in complex ways [112]. Wave propagation along the papilla/cochlea is dispersive, and velocities vary with location and frequency. The result is the generation of stationary modes along the basilar membrane as a function of sound frequency: maximal bending occurs near the oval window end for high frequencies, and at successively greater distances along the membrane for lower frequencies. This is often called the **place principle** of bird and mammal hearing. The width and stiffness gradient of the basilar membrane is typically adjusted so that the location of maximal bending for a given frequency matches the characteristic frequencies of the nearest hair cells. The place principle thus augments the existing tonotopy of the organ. Because mammals have a much longer basilar membrane than birds, the place principle plays a much larger role in the fine-tuning of the cochlea than in the papilla (Figure 3.42).

Behavioral tests on various birds and mammals show minimally detectable differences in frequency of 2–4% for chickens and doves; 0.5–1% for owls, parrots and songbirds; 5–7% for chinchillas and gerbils; 1–5% for monkeys and elephants; and 0.1–0.5% for humans and echolocating bats [92, 196]. Behavioral responses are difficult to obtain on lizards, but neurobiological measures suggest that several species differ from most birds and mammals by not following Weber's Law (see Chapter 8) [12, 172]. Instead of showing a constant minimal percentage difference in discriminated frequencies, (the Weber's Law prediction), these lizards discriminate

FIGURE 3.42 Body size and vertebrate tonotopic inner ear design (A) Animals with larger body sizes usually have a larger inner ear (here measured by the length of their basilar membrane). However, mammals (black), which curl their cochlea, have longer basilar membranes than birds (red) or lizards (blue) of the same body size, and among the lizards, hearing specialists (4–6) have longer basilar membranes than nonspecialists (1–3). (B) Longer basilar membranes can host more hair cells, and this could be used to extend the frequency range of hearing (here measured as number of octaves (doublings) between the lowest and highest detectable frequencies). Although mammals tend to have larger frequency ranges than birds (with the exception of high-frequency specialists (14 and 15)), and birds larger ranges than lizards, within each taxon there is little evidence that frequency range depends upon basilar membrane length. (C) An alternative use of the additional hair cells is that they increase frequency resolution by spreading each subset of the overall frequency range over a longer basilar membrane. This graph shows that mammals have the longest segments of membrane/octave, birds and hearing-specialist lizards show the next-longest segments, and lizard nonspecialists show the least. This pattern fits known levels of frequency resolution in these taxa. Note that the barn owl (10), an avian hearing specialist, has a segment length/octave value similar to that of mammals of the same weight. (D) Ranges of variation in numbers of hair cells/mm of basilar membrane in representative lizards, birds, and mammals. Birds and mammals of similar body size have similar total numbers of hair cells. Although birds tend to have shorter basilar membranes than mammals, they also have wider ones, allowing for more hair cells across that greater width. More hair cells across the membrane allow for refined temporal and amplitude resolution within a given frequency band. Species key: (1) European wall lizard (*Podarcis muralis*); (2) granite spiny lizard (*Sceloporus orcutti*); (3) alligator lizard (*Elgaria multicarinatus*); (4) tokay gekko (*Gekko gecko*): (5) bobtail skink (*Tiliqua rugosa*); (6) savannah monitor lizard (*Varanus exanthematicus*); (7) canary (*Serinus canaria*); (8) budgerigar (*Melopsittacus undulatus*); (9) starling (*Sturnus vulgaris*); (10) barn owl (*Tyto alba*); (11) pigeon (*Columba livia*); (12) chicken (*Gallus gallus*), (13) emu (*Dromaius novaehollandiae*); (14) mouse (*Mus musculus*); (15) horseshoe bat (*Rhinolophus ferrum-equinum*); (16) kangaroo rat (*Dipodomys merriami*); (17) gerbil (*Meriones unguiculatis*); (18) mole rat (*Spalax ehrenbergi*); (19) Norway rat (*Rattus norvegicus*), (20) chinchilla (*Chinchilla langer*), (21) rabbit (*Oryctolagus cuniculus*), (22) cat (*Felis catus*), (23) human (*Homo sapiens*), (24) bottlenose dolphin (*Tursiops truncatus*), (25) cow (*Bos taurus*), and (26) Asian elephant (*Elephas maximus*). (After [91, 96, 121, 172, 173, 177, 209-211, 311].)

between two frequencies only if they differ by a fixed absolute difference in frequencies. Weber's Law is also partially violated for certain birds (such as parrots and owls) and mammals (echolocating bats) that can discriminate smaller than expected frequency differences for specific regions of their overall frequency ranges.

Web Topic 3.7 ***Measuring auditory resolution***
Many different measures have been developed to compute and compare the frequency, amplitude, and temporal resolutions of animal ears. Here we define a number of these measures and outline their differences and similarities.

DYNAMIC RANGE AND AMPLITUDE RESOLUTION Single mechanoreceptors respond linearly to increasing signal amplitude only over a limited range. Each receptor has a minimum threshold amplitude that is required for it to respond at all, and at high enough amplitudes, its response saturates. As with frequency range, **dynamic range** is best extended by combining multiple sensory units with different thresholds and saturation points. The simplest example occurs in noctuid moths, whose tympanal ears contain only two scolopidia: both are tuned to the same characteristic frequency, but one is 20 dB more sensitive than the other. Bladder grasshoppers have a pair of auditory organs in each of six adjacent abdominal segments, each less sensitive than the one before it in the progression toward the posterior end [358]. Spiders often cluster up to 30 sensory slits into a compound **lyriform organ** [20]. Each slit in the cluster has a slightly different threshold and saturation level but covers an amplitude range of about 10 dB. By overlapping the ranges of different slits, the entire organ can provide nearly uniform coverage over a 40 dB dynamic range. Most animals with complex ears use a similar strategy of pooling the outputs of sensory cells or organs with different ranges. The overall dynamic range is usually limited by the lowest achievable threshold. Active amplification mechanisms and refined coupling and modification devices are most often used to extend the dynamic range to low levels.

Among other functions, amplitude resolution allows animals to compare reception of the same sound at two or more hearing organs and compute the angular position of the sound source, compare observed to expected amplitudes to estimate the distance to a sound source, compare display amplitudes of alternative mates, and use signal amplitude as a measure of aggressiveness during a contest. For a single mechanoreceptor, frequency and amplitude resolution will often be confounded: a low amplitude sound at the receptor's characteristic frequency and a high amplitude sound at some other frequency may produce exactly the same response in the receptor. One solution is to have multiple cells with the same characteristic frequency but different amplitude ranges (as in the noctuid moth ear). However, this creates another problem: small animals are limited in the number of sensory cells they can accommodate in their ears, and each cell added to improve amplitude resolution is a cell that cannot be used to improve range or resolution of temporal, frequency, or location information. An alternative is to host dedicated brain cells that compare relative responses of each class of receptors to known tuning curves, identify likely confounds, and compute a corrected amplitude estimate. However achieved, wax moths and katydids achieve amplitude resolutions as low as 1–2 dB [15, 153], and typical mammals and birds show minimal resolutions of 0.8–4 dB [92, 329].

TEMPORAL RANGE AND RESOLUTION A major constraint on both temporal range and resolution in animal ears is that some interval must elapse between two sounds or sound components in order for the receptor (or brain) to considers them as separate events. How long an interval is necessary? All acoustic instruments including ears must deal with a trade-off between temporal and frequency resolution: improving one invariably undermines the other (see Web Topic 2.4). Increasing the resonance of auditory receptors, whether electrically, mechanically, or through active amplifiers, will tune the receptors to increasingly narrow bands. The temporal cost is that it will also reduce damping, making the receptors "ring" when stimulated. The longer they ring, the less likely they are to discriminate between two closely successive events.

To a larger degree than for frequency or amplitude resolution, temporal resolution depends on processes that occur not in the ear, but in the brain of the receiver. There are thus many different measures of temporal resolution depending on what stage in the process is being tested. Responses at the coupling stage can be extremely fast: successive events need be separated by only 150–200 μsec to be discriminated as separate by noctuid moth tympana [244]. However, behaviorally determined temporal resolution tends to be significantly slower: minimal perceived gaps for test stimuli input to a single ear are 4–8 msec in insects and 1–4 msec in vertebrates [92, 119, 196]. Exceptions include the superior ability of some birds to discriminate between very fine temporal patterns in complex sounds [92, 93]; and, as we shall see in Chapter 14, echolocating bats and dolphins have evolved very special skills for measuring short time delays between successive acoustic events.

DIRECTIONALITY Directionality refers to the ability of a receiver to determine the distance (range), horizontal angle (**azimuth**), and vertical angle (**altitude**) of a sound source. We briefly discussed amplitude and spectral contrast mechanisms that animals might use for ranging at the beginning of this chapter. How might animals determine the azimuth and altitude of a sound source?

Hearing organs that rely on near-field sounds in fluids can exploit the fact that the axis of molecular oscillation in the medium is significantly affected by the location of the sound source. The axis of movement points directly back toward a monopole source. Vibrational axes may not point

FIGURE 3.43 Polarization patterns of hair cells in fish ears All vertebrate hair cells are polarized: maximal stimulation requires that the cell's stereocilia be bent along an optimal axis. The separate hearing organs inside the inner ears of fish are usually subdivided into regions within which all hair cells have the same polarity. Pooled input from different regions enables the fish's brain to compute the location of a sound source. In each polarity map in this figure, the fish's head is to the left; upward is dorsal for the lagena and saccule maps, and toward the middle of the fish's side for the utricle maps. Arrows indicate the direction of bending that maximally stimulates hair cells in that region. The lagena and utricle usually have two distinct regions with opposing polarities. Polarization maps in the saccule vary among species. Hearing generalists (e.g., toadfish) divide the saccule into 4 regions with hair cell axes pointing in each of four perpendicular or opposite directions. Otophysans, which use ossicles to connect the swim bladder to the ear, have only two regions which are polarized vertically in opposite directions. A variety of other patterns are also shown. (After [282].)

at the source when a receiver is sufficiently close to dipole or quadrupole vibrators, but there are still patterns in the near field which can be sampled and computations used to estimate source locations [157, 281]. Because each sensory hair on an arthropod's exoskeleton usually has its own preferred axis of movement, a receiver can identify or compute the direction of medium motion by sensing which hairs are most bent in the sound field [53]. The antennae and Johnston's organs of mosquitoes and *Drosophila* can also compare near-field fluid movements with their preferred axes of vibration [240, 305]. We have seen that vertebrate hair cells are maximally stimulated when their stereocilia are bent toward and away from the kinocilium. The saccules, utricles, and lagenas of fish are organized so that hair cells in each of several subregions are oriented in the same direction, but those in different subregions are oriented in different directions (Figure 3.43). Pooling the output from all these regions allows their brains to estimate the likely azimuth and altitude of near-field sound sources [283]. Fish hair cells are sufficiently sensitive that they may be able to use this mechanism at distances even beyond the usually defined transition between near and far fields [105].

Animals attending to far-field sounds, sounds propagated at boundaries, or sounds inside solid substrates estimate source azimuth and altitude by comparing a sound's times of arrival, amplitudes, and phases at 2–8 different hearing organs. Participating sensors include pairs of ears in crickets, katydids, grasshoppers, cicadas, lacewings, moths, and terrestrial vertebrates, and the subgenual, chordotonal, and touch/stretch receptors in the legs of elephants, hemipteran insects, and spiders. For an animal with a pair of ears, a sound will arrive simultaneously at the two ears only when it is located in the plane equidistant from them and perpendicular to the line joining them. The maximal delay in arrival at the two ears occurs when the sound source is located along an extension of the line joining the two ears. An animal can identify a source azimuth by rotating around the center of the line joining its ears until the sound arrives at both ears simultaneously. The source will then either be in front of it or directly behind it. Alternatively, the times of arrival could be forwarded to the brain, which then computes the azimuth of the source without the head or body being turned. Note that if the line joining the two ears is parallel with the Earth's surface, there is no way this animal can detect the altitude of the sound source without invoking other mechanisms. If the line joining the ears is not parallel with the Earth's surface, the animal will have to rotate its body in both the vertical and horizontal planes before the sound will arrive simultaneously at the two ears. Such a movement could be used to estimate both azimuth and altitude. Alternatively, it could use other mechanisms to determine the sound azimuth, and forward the delay times to the brain to compute the altitude. Many

owls have one ear set slightly lower on their heads than the other, and both cats and humans have asymmetries in the shape of their external ears that permit altitude estimation using time delays [41, 169]. Both azimuth and altitude can also be computed by a brain if the animal has more than two hearing organs and these are not all set at the same height in the body.

An animal's ability to estimate azimuth or altitude using interaural time delays is limited by its body size and the speed of propagation of the relevant sound. Body size is important because it limits the maximum distance that can exist between two or more auditory organs and thus the maximum delay between arrival times of a sound. Animals with sensors in their legs may have a certain advantage in this respect, because they can stretch out their legs to increase the interaural distance. Even so, the delay in a sound's arrival at multiple ears will be very small in small animals: in air, the maximum delay for a 1 cm insect would be only 30 μsec. In a human, the maximal delay averages 656 μsec, and in elephants, it can be over 3 msec. Medium also affects minimal resolution. The situation in water is more challenging than that in air: higher sound propagation speeds produce only a 7 μsec delay for a 1 cm snapping shrimp. On the other hand, bending waves in plants have significantly lower propagation speeds than sound in air: a 1 cm insect might experience up to a 100–200 μsec delay. This might make use of interaural time delays quite feasible for small plant-dwelling insects and spiders [20, 66, 71]. In addition to body size and sound speed, sound source resolution depends upon the minimal time delays that can be measured in the receiver's brain. Threshold values for measuring interaural time delays can be much smaller than those observed for discrimination of successive events at a single ear. Short delays can be measured by summing the outputs of the ears onto single cells in the brain. Different brain cells are preset to delay input from one ear relative to the other by fixed amounts. The brain cell that delays the input from the ear nearer the source by just the amount of delay in arrival times will show the strongest summed response. Knowing which cell responds then indicates which delay is present. In humans, this technique allows the detection of interaural delays down to 10 μsec.

Instead of comparing relative arrival times, an animal might compare the relative amplitudes of a sound at multiple ears. As with time delays, it could identify azimuth by rotating its head or body until both ears experience the same amplitude, or it could send differential amplitude information to the brain, where the azimuth could be computed. Most ears are too close together to exploit the slightly lower amplitude of a low frequency at a far ear due to greater spreading loss. However, if the wavelengths in the incident sound are smaller than the size of the animal's head or body separating the ears, diffraction and shadowing of the far ear can generate significant amplitude differences. Animals can make this work in ingenious ways. For instance, the ear-containing forelegs of katydid females are too small to produce diffraction even at ultrasonic wavelengths, yet the males emit ultrasonic courtship calls. Females can still localize males because their bodies are large enough to produce significant diffraction differences at their spiracle openings. These differences are then conveyed to the tympana through the tracheal tubes [246].

As we saw in Chapter 2, diffraction when wavelengths are similar to the intervening object can be quite complicated. The amplitude of a diffracted sound at an animal's ear will depend on the sound wavelength, the size and shape of the animal, and the azimuth and angle of the sound source relative to the animal's body axis. Because different frequencies will be diffracted differently depending on the location of the sound source, an animal can use the perceived frequency spectrum of a known sound to estimate its location. The spectrum can provide both azimuth and altitude information [134]. Amplitude differences between ears can be magnified further using pinnae or other directional horns as auditory coupling organs. Pinnae are also very useful for resolving whether a sound source is in front or behind an animal, and many mammals can rotate their pinnae to provide single ear estimates of source azimuth. Some mammals have elaborate ridges and crenulations on their pinnae that alter the frequency spectrum of complex sounds at the ear in response to the altitude of the sound source. This is another way in which a single ear can provide elevation information. Note that all of these mechanisms require that pinnae and their elaborations be as large or larger than the relevant sound wavelengths. The small pinnae on small animals are effective only if their ears can detect and process sufficiently high frequencies [135].

What if animals are so small that they do not diffract sounds of interest and they cannot resolve the necessarily short arrival delays at multiple ears? The most common solution is to use a pressure differential coupling device [61, 169, 188, 195, 244, 246]. Grasshoppers, cicadas, frogs, lizards, and birds create a pressure differential system by linking the inner sides of their two tympana with air spaces or air-filled membranous sacs. Each tympanum then samples sound amplitudes at two locations. For example, cricket and katydid tympana compare the amplitude just outside their surface with that at openings of tracheal tubes on the animal's thorax. If the samples arrive on the opposite sides of the tympanum at the same amplitude and in phase, the tympanum will not move; any other set of relationships will cause the tympanal and tracheal membranes to vibrate in concert with the sound. For wavelengths larger than the distance between the two sample points, the samples on the two sides of the tympanum will be in phase when the sound source is located in the plane equidistant from the two sample points and perpendicular to the line joining them. At all other locations, the two samples will be out of phase and the tympanum will vibrate. Other factors being equal, the maximal amplitude of vibration will occur when the sound source is located along the extended line joining the two sample points. Although one pressure differential ear can thus provide some azimuth information, computations based on data from two or more ears provide

even more accurate localization. Note that this system can break down when wavelengths are smaller than the distance between the sample points: if one sample is exactly one cycle behind the other, the tympanum will not move even though the two samples are no longer equidistant from the source. As sound frequency increases, the number of situations in which this ambiguity arises increases. At high enough frequencies, diffraction may finally be possible and the ears can then act as pressure detectors. Note that pressure differential ears become ineffective at very low wavelengths where the difference in phase between the two samples is small. Crickets manage to respond to lower frequencies than similarly sized insects by slowing down the delivery of the tracheal sample and thereby increasing the apparent phase differences [246].

Tachinid flies present another ingenious solution to the small animal problem [303, 305]. Their two tympana are located next to each other on the midline of the thorax. Each end of a semiflexible lever arm is connected to one of the tympana. The normal mode of this linked system is tuned to the dominant frequency in the calling songs of the male crickets that are parasitized by female flies. Oscillations of the tympanum nearest a calling cricket are transmitted to the more distant tympanum by the lever arm, suppressing the amplitude of the latter's oscillations due to the sound and delaying its response. This generates both an amplitude difference and a time delay between the two tympana that is large enough for the fly brain to use to estimate azimuth. A slightly different version of this solution is used by sarcophagid flies which locate and parasitize calling cicadas.

Most animals use some combination of mechanisms to achieve overall directionality, but different taxa use different combinations. How do the different combinations compare? Fish such as cod (Gadidae) use their heterogeneously polarized hearing organs to estimate azimuth and altitude of sound sources with accuracies within 12–20° [104]. Small terrestrial insects such as crickets and katydids, with pressure differential ears and higher frequency diffraction, manage similar azimuth resolutions of 15–20° but much less accurate altitude estimates (45° in crickets) [16, 119, 380]. Tachinid flies, with their unusual lever system, can achieve 1–3° azimuth accuracy [221]. Frogs, relying on pressure differentials, diffraction, and interaural time delays also manage a 15–30° azimuth accuracy and 23–45° altitude resolution [119]. Small birds, like frogs, rely on a combination of pressure differential, diffraction, and interaural delay mechanisms, and similarly achieve 20–30° azimuth accuracy [169]. Predatory birds, (in part because they are larger), rely more heavily than small birds on interaural time delays and achieve azimuth resolutions of 2–12° (hawks) and 1–7° (owls). Owls achieve similar resolutions for altitude angles and, like mammals, do so using frequency spectrum differences generated by complex feather structures around the ear opening. Mammals, with their extraordinarily high-frequency hearing and elaborate pinnae, tend to rely on diffraction and delay times for azimuth estimation, and frequency spectrum contrasts for sound source altitude [41, 42, 135]. Azimuth accuracy ranges from 1–5° for dolphins, elephants, primates (including humans), cats, and many echolocating bats to 10–30° for most other nonfossorial mammals. Altitude resolution is usually more difficult than azimuth resolution in any given species; values range from 2–3° for dolphins and humans to 20–30° for other mammals.

Body Size and Sound

One of the more robust generalizations we can make about animal sound communication is that small animals usually communicate with high-frequency sounds and that larger animals tend to use low-frequency sounds. This pattern persists despite the large number of contributing factors and differences among taxa and habitats in the relative weighting of these factors. Several common threads, however, stand out as acting in concert to produce this pattern.

On the signal production side, we saw in Chapter 2 that it is difficult for an animal to produce an intense sound with a wavelength more than twice its body dimensions [24, 25]. Many animals *can* produce sounds with wavelengths longer than their bodies, but the cost is an increasingly rapid drop in the efficiency of sound radiation, and thus in sound intensity, with increasing wavelength. For animals communicating over a distance, that cost might be compensated for by the lower heat and scattering losses of slightly longer wavelengths. However, radiation efficiency drops off faster with increasing wavelength than propagation efficiency does. For wavelengths more than 2–3 times the size of the signaler, radiation losses will outstrip any propagation benefits. These effects are nicely exhibited in Figure 3.44A, which shows the dominant frequencies in the male display calls of insects. These are compared to the minimal frequencies (maximal wavelengths) that would still allow each insect to emit maximally intense sounds. As predicted, the frequencies favored by each species decrease with increasing body size. However, all observed frequencies fall below those predicted for maximal intensity radiation. With the exception of displaying male fruit flies, differences between observed and expected frequencies are small, or at most, moderate, in magnitude. This is likely due to a tradeoff between lower radiation intensity and better propagation. Whereas all of these insects rely on far-field sounds to attract mates, fruit fly males perform their displays at close range, and females are within the near field of the male's sounds. Thus the flies can use much longer-wave sounds and still achieve the requisite active space. Such observations support the notions that there is a minimal frequency that an animal can use for long-distance communication, and that this limit is inversely correlated with the signaler's body size.

On the signal reception side, we get a similar effect, but for a different set of reasons. We saw in this chapter that the ability to identify the location of a sound source requires the presence of sufficiently high-frequency components in the propagated sound. For larger animals that have pressure detector ears, sufficient phase and intensity differences between ears used for localization exist only for wavelengths

FIGURE 3.44 Three explanations for inverse correlations between favored sound frequencies and body size (A) Relationship between male advertising call frequency and body size in a sampling of terrestrial insects. Also shown are minimal frequencies for monopole (solid line) and dipole (dashed line) sources at each size that ensure maximal radiation efficiency and thus signal intensity at the source. Monopole sources: waxmoths (red), cicadas (green), mole cricket burrows (orange). Dipole sources: crickets and katydids (black) and fruit flies (blue). (B) Relationship between highest audible sound frequency and inter-aural distances for various mammals. Echolocating bats (red), burrowing rodents (blue), cats (green), humans (orange), and elephants (yellow). Others (black) are primates and rodents. Line is best fit to points excluding the burrowing rodents which use low frequency seismic signals.) (C) Fletcher model predicting optimal frequencies for sound communication after combining effects of sound production, propagation, and reception constraints (solid line) versus actual frequencies used by different birds and mammals (ellipses). Optimal frequency is here predicted to be proportional to body mass raised to the –0.4 power. Birds (red), cats (green), dogs (grey), monkeys (black), gorillas (purple), humans (orange), horses (blue), and elephants (yellow). (A after [25]; B after [135]; C after [114].)

smaller than the size of the receiver's head (including its pinnae) [134, 135]. Smaller animals that have pressure differential ears also require a sufficiently small wavelength before the phase or intensity differences at the two openings for an ear are detectable [246]. In both cases, localization requires the ability to hear sounds of sufficiently small wavelength and thus sufficiently high frequencies. The minimum frequency required for localization should thus decrease as the distance between the ears (pressure detector species) or sampling points (pressure differential species) increases. Note that there is no penalty to localization if an animal can hear even higher frequencies than this limit, but in most species, higher frequencies suffer sufficiently higher propagation losses that it may not be worth attending to them. Thus we might expect the highest audible frequency that an animal can hear to decrease with increasing interaural distance. This is in fact what one finds for a wide sampling of mammals (Figure 3.44B). Again, there are exceptions to this correlation when sound communication is largely short-range or when the medium propagates only certain wavelengths: obvious examples include marine fish, burrowing rodents, and arthropods communicating on plant stems.

Ideally, one would like to combine all factors to see whether the negative correlation between body size and communication frequency for some individual factors is preserved. Fletcher [113, 114] has provided a general model for this correlation that integrates sound production, propagation, and reception components. He concludes that in general, the optimal frequencies for sound communication will always be inversely correlated with body size. He specifically predicts that the optimal frequency for a species will, on average, be proportional to its body mass raised to the –0.4 power (Figure 3.44C). Although available data appear to fit this prediction, there are still insufficient samples to exclude the possibility that optimal frequency is instead simply proportional to body length or width, and (since body mass is usually proportional to an animal's linear measure cubed), to body mass raised to the –0.33 power. Whatever the actual scaling, Fletcher's model and existing data support the idea that an animal's size seriously curtails the frequencies that it can use for sound communication. At times, this can be a handicap to the sender, the receiver, or both, but at other times it can be exploited in interesting ways. We shall return to this point in later chapters.

SUMMARY

1. Sound signals typically degrade during propagation to the receiver. Some species have developed acoustic adaptations that minimize degradation and maximize the **active space** of their signals. **Ranging** is the assessment of degradation in a signal; it allows a receiver or eavesdropper to estimate the distance to the sender.
2. The amplitudes of all frequencies in a sound signal decrease equally with distance from the sender due to spreading losses. Where the medium is stratified with respect to flow, temperature, or pressure, refraction may decrease sound amplitudes faster or slower than expected given spreading losses alone. Spreading losses are reduced by refraction when terrestrial senders call at dawn, are upwind, or call between the understory and the canopy in a dense forest; they are more severe on hot days, when the sender is downwind, or when the caller is above the forest canopy.
3. The frequency spectrum of a sound often changes as it propagates between sender and receiver. A plot of the change in amplitude for each possible frequency component is called the **frequency response** of that medium and situation. In most environments, amplitudes of propagating high-frequency sounds attenuate faster than those of low-frequency ones because of heat losses and scattering by objects in the sound path between sender and receiver. Heat losses and scatter are generally more severe in terrestrial environments than in aquatic ones.
4. A boundary between media can also alter the frequency response along the path between sender and receiver. It does so by reflecting waves toward the receiver. These waves can then interfere (positively or negatively) with the waves that have traveled directly between the two parties. In many cases, the reflected waves suffer a phase shift at the boundary, causing negative interference and cancellation of low frequencies. For sound in air propagating over soft earth, a **ground wave** can restore some of the lowest frequencies, at least over moderate distances. As a result, the frequency response graph for sound propagation in air but near the ground often has a **notch** in which intermediate frequencies are severely attenuated, but very low and high frequencies continue to propagate well. Boundary interference also results in high attenuation of low-frequency sounds propagating just under the surface in water. There are no restorative effects in water to minimize this filtering.
5. When sender and receiver are both located between the same two or more reflective boundaries, the medium for sound propagation becomes a **waveguide**. The complex reflections from the multiple surfaces result in certain frequencies (normal modes) being favored over others during propagation. Typically, there is a **cutoff frequency** below which propagation is negligible. Waveguides can seriously distort signal patterns over long distances.
6. A third type of boundary effect occurs when the sound propagates in one medium but the receiver is located in another adjacent medium. The receiver must then rely on whatever version of the sound is detectable on its side of the boundary. This is the case for insects exchanging signals on the water's surface, insects and spiders communicating through bending waves inside plants, and elephants and burrowing mammals communicating with seismic signals. All of these situations attenuate high frequencies faster than low frequencies, and the resulting sound waves, like waveguides, may have complex resonances and favored modes.
7. Temporal patterns in propagating sounds are most often altered by **reverberations** (echoes). Airborne sound signals propagating in forests acquire more reverberations than do similar sounds in open country. Echoes from fish swim bladders create reverberations under water. If the original signal has elaborate modulations, these will be degraded by added reverberations; if the signal consists of a long single frequency, it may be enhanced by becoming longer and louder to receivers. Most forest birds avoid modulations in their songs and calls. In open country, on the other hand, slow-amplitude modulations may be added to signals as they pass through wind vortices or heat bubbles. Open country birds thus favor rapid amplitude modulations for long distance signals, or rely more heavily on frequency modulation for pattern.
8. Sounds propagating on a water or solid substrate boundary, inside plants, or in air or water waveguides will suffer **dispersion**, in which different frequencies propagate at different speeds. This can create major distortions in the temporal and frequency patterns by the time a signal reaches a receiver.
9. Noise is a ubiquitous problem for animals communicating with sound signals. In most habitats, noise is more likely to mask low frequencies (due to wind in air and waves in water), and high frequencies (due to insects in air and snapping shrimp in water). Bending waves inside plants can be masked by rustling of the leaves and branches. Human-caused (anthropogenic) noise is increasingly a problem for sound-communicating animals in the wild. When faced with significant noise, animals may focus more on intermediate frequencies, limit signaling to periods of relative quiet, or increase signal amplitude to ensure effective long-distance communication.
10. All animal ears use differential motion between special mechanoreceptors and the rest of their body to detect sounds. As with sound radiation, coupling of ambient sounds into an ear is hindered if the wavelengths are significantly larger than the animal, and the acoustic impedance of the medium and the ear are sufficiently different. Animals have evolved special adaptations to enhance coupling, modification of captured sounds, and detection.

11. Small hairs on the exoskeleton and plumose antennae of arthropods move more easily in a near field than does the rest of the body. This differential movement provides the necessary coupling for near-field sounds. In other species, the internal sensory hairs are covered by heavy objects (**statoliths** in crustaceans and **otoliths** in fish). These masses accelerate more slowly in near fields than do the hairs and other soft tissues; and this differential movement bends the hairs and stimulates the sensory cells.
12. Terrestrial animals have thin membranes called **tympana** to couple far-field sounds in air into their ears. In mammals and moths, the tympana are stretched over closed cavities. The resulting **pressure detectors** compare external sound pressures to the reference pressure in the closed cavity. The tympana of grasshoppers, cicadas, crickets, katydids, frogs, lizards, and birds compare sounds sampled at two different locations in the far field and thus serve as **pressure differential detectors**. All use the exterior of a tympanum as one sample point. Crickets and katydids use tracheal tubes to convey a second sample taken outside their thorax to the other side of the tympanum. In grasshoppers, cicadas, and all terrestrial vertebrates except mammals, the insides of the two tympana are connected by an airspace or air-filled sacs. The second sample is thus taken outside the tympanum of the opposite ear.
13. In water, a number of fish use swim bladders or accessory air sacs the way terrestrial animals use tympana—to capture far-field sounds and convert them into oscillations of the cavity wall. Swim bladder movements are conveyed to the ears by small bones or intervening tissues. Toothed whales use fat-filled jawbones to convey far-field sounds to a thin bone in the ear that converts the pressure variations into vibrational motion. Baleen whales and true seals appear to capture sounds in various parts of their skeletons and convey them to ears that respond to bone-conducted sounds.
14. Boundary-propagated sounds are usually coupled into receiver bodies through their legs. Tension and posture can be varied to improve resonance of the body relative to frequencies of interest. Spiders use slits and insects use pits in the exoskeleton that are then compressed and expanded as a result of the coupled vibrations. These arthropods also use stretch receptors and blood movement detectors to monitor leg and body vibrations. Frogs absorb seismic signals through their bodies and convey them through a specialized muscle to their ears.
15. Terrestrial animals use horns, articulated chains of bones, or successive membranes of decreasing size to modify captured sounds and reduce impedance mismatches between the ambient medium and their bodies. While these devices can increase the sound energy delivered to inner ears, they usually have their own resonant properties that may constrain the animal's auditory range and resolution.
16. Arthropod and vertebrate auditory mechanoreceptors all have dendrites with a ciliary component. Vertebrate receptors accompany this **kinocilium** with multiple **stereocilia**. Bending, compressing, or stretching these mechanoreceptors constitutes the primary transduction step for hearing. Both types of sensors can be extremely sensitive: threshold movements as small as or smaller than the diameters of single atoms are common in both groups.
17. Many insects use their ears largely to detect and avoid echolocating bats. They tend to have simple ears tuned to ultrasonic frequencies and few adaptations for frequency resolution. Taxa that use their ears for intraspecific communication usually have more sophisticated mechanisms for breaking complex sounds down into separate frequency bands and assessing the relative amplitude of each band. They thus perform some level of Fourier analysis. Broad frequency ranges and good frequency resolution can be achieved simultaneously by the presence of many sensory cells, each tuned to a different subset of the overall frequency range. In tonotopic ears, the sensory cells are arrayed in order of their resonant **characteristic frequencies**. Tonotopy reduces interference between stimulated cells with very different characteristic frequencies. In many tonotopic ears, the sensory cells are covered with a **tectorial membrane** that insures that all cells in a given band are stimulated simultaneously. In both arthropods and vertebrates, some sensory cells physically vibrate when stimulated; this can stimulate adjacent cells with similar characteristic frequencies leadung to **auditory amplification**. Frequency resolution can be further refined for lower frequencies through **phase locking**, in which nerve impulses being sent to the brain by the sensory neurons are synchronized with peaks in the waveform of the relevant sound frequency.
18. **Dynamic range** is largely set by the lowest amplitude signals that can be detected. Although arthropod and vertebrate mechanoreceptors are so sensitive that the potential dynamic range for animals should be enormous, ambient noise is often sufficiently high that it sets the floor for the effective dynamic range. Amplitude resolution, like frequency resolution, is largely limited by the number of sensory cells that are tuned to the same frequency but at different amplitude thresholds. In insects, amplitudes must differ by 1–2 dB at favored frequencies to be discriminated; equivalent thresholds for birds and mammals are 0.8–4 dB.
19. There is a trade-off in most auditory systems between frequency and temporal resolutions. Sensory cells that are narrowly tuned (large Q) will have worse temporal resolution than more broadly tuned and rapidly damped cells. In many cases, brain processes (e.g., phase-locking) can be invoked to improve temporal resolution. In practice, separate acoustic events will be discriminated by insects if they are separated by at least 4–8 msec; birds and mammals require intervening intervals of only 1–4 msec.
20. Animals can use any of four different kinds of information to identify the azimuth and altitude of a sound source. In near fields, hearing organs can often use the direction of molecular motion in the medium to estimate both azimuth and altitude. Time delays in the arrival of a far field sound at two or more hearing organs are often used either behaviorally (by rotating until the delay is zero) or computationally (by the brain) to identify the source azimuth. This cue

becomes decreasingly useful as receiver size gets smaller. Amplitude differences provide a third type of far-field cue, and azimuth can again be identified using turning or brain computation. Animals larger than relevant wavelengths rely on diffraction to create amplitude differences at two or more hearing organs; animals smaller than relevant wavelengths use one or more pressure differential organs that are inherently directional. The fourth cue, changes in far-field frequency spectra at the ear as a function of source angle, is used by many mammals and by some birds to estimate the altitude of a sound source.

21. Both sender constraints and receiver constraints contribute to the widely found inverse relationship between an animal's body size and the sound frequencies it uses for communication.

Further Reading

General reviews of environmental modification of propagating airborne sounds can be found in Wiley and Richards [371], Forrest [117], and Slabbekoorn [335]. Embleton [102] and Attenborough [8] provide more technical accounts of the relevant physics, and Brum and Slabbekoorn [49] discuss the sources and consequences of terrestrial noise. Substrate and boundary sound propagation is lucidly described by Markl [217]. Introductions to sound propagation in marine environments include Rogers and Cox [307] and Tyack [357]. Advanced marine treatments include Caruthers [56] and Tolstoy and Clay [354].

Fletcher [112] discusses the underlying physics of sound reception in both arthropod and vertebrate taxa. Michelsen and Larsen [244], Michelsen [246], and Greenfield [127] provide highly readable but more detailed reviews of sound propagation and hearing in insects. Other good reviews of arthropod hearing include Popper et al. [284] on crustaceans; Barth [20] on spiders; Wilcox [368] on water-surface dwellers; Čokl and Doberlet [71], Virant-Doberlet and Čokl [361], and Cocroft and Rodriquez [68] on insects communicating through plants; and McIver [234], Hoy and Robert [147], Keil [161], Robert and Hoy [303], Field and Matheson [108], Yager [383], Yack [382], and Robert [305] on the structure and function of insect mechanoreceptors in general and ears in particular.

Good reviews of vertebrate hearing strategies include Popper and Fay [283] on fishes; Lewis and Narins [195] on amphibians; Manley [210, 213] on lizards; Dooling et al. [92] and Dooling [93] on birds; Heffner and Heffner [134], Rosowski [312], Heffner [135], and Brown and May [42] on terrestrial mammals; and Ketten [163] and Hemilä et al. [138,141] on marine mammals. The evolutionary modifications required when the early terrestrial ancestors of whales and dolphins moved to the water are summarized by Nummela et al. [267, 269]. Recent discoveries about active amplification in hearing organs are described for insects by Göpfert and Robert [123, 124], and for vertebrates by Robles and Ruggero [306] and Fettiplace [107].

COMPANION WEBSITE
sites.sinauer.com/animalcommunication2e

Go to the companion website for Chapter Outlines, Chapter Summaries, and References for all works cited in the textbook. In addition, the following resources are available for this chapter:

Web Topic 3.1 ***Transfer functions***
Here we discuss methods for measuring transfer functions of black boxes in general, and blocks of propagation medium specifically. What assumptions have to be met to make these measurements, and what happens if they are not met?

Web Topic 3.2 ***Dispersive sound propagation***
Sound propagation with dispersion can result in major changes in a signal's waveform and in the speed with which the signal propagates as a whole. Here we provide more details on dispersive sound propagation for each of the contexts in which communicating animals are likely to encounter it.

Web Topic 3.3 ***Animal communication and anthropogenic noise***
To what degree does noise generated by human activities interfere with sound communication in animals? Recent studies in both terrestrial and marine environments suggest that there are increasing problems, but animals can sometimes adapt.

Web Topic 3.4 ***Levers and ears***
Different types of lever systems provide mechanical advantages and match acoustic impedances for improved hearing in animals. Here we outline the general classes of levers and indicate which are used in the middle ears of amphibians, reptiles, birds, and mammals.

Web Topic 3.5 ***Auditory amplification***
Both arthropods and vertebrates use active motion of auditory receptors to amplify responses to low level sound stimuli. Here we examine some of the data demonstrating this mechanism in insects, mammals, and lizards.

Web Topic 3.6 ***Animations of vertebrate ears***
One movie can be worth a thousand still images. Here we provide links to a number of websites that provide free animations of middle and inner ears in operation.

Web Topic 3.7 ***Measuring auditory resolution***
Many different measures have been developed to compute and compare the frequency, amplitude, and temporal resolutions of animal ears. Here we define a number of these measures and outline their differences and similarities.