Principles of
ANIMAL COMMUNICATION
Second Edition

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Chapter 3

Sound Signal Propagation and Reception

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.

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.

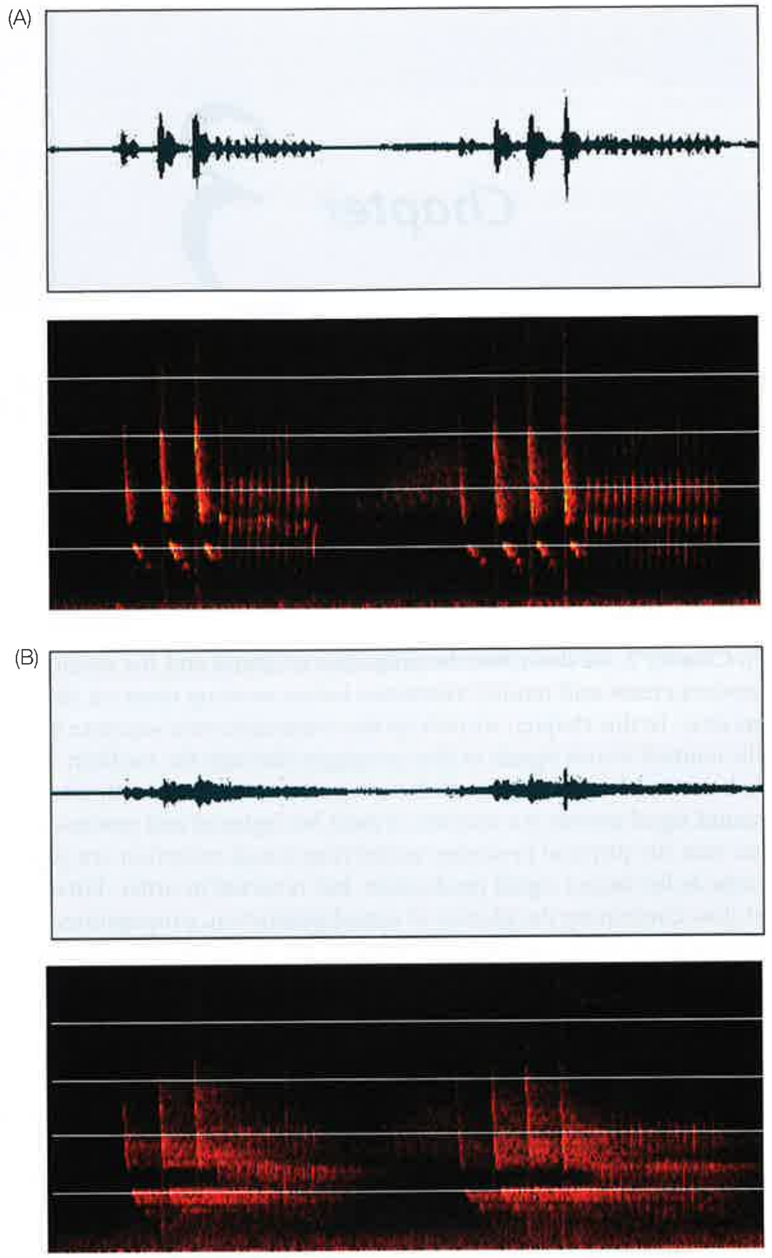


FIGURE 3.1 **Degradation in song of male cardinal (*Cardinalis cardinalis*) due to long-distance propagation** (A) Waveform (top) and spectrogram (bottom) of male song recorded close to bird. (B) Waveform and spectrogram of the same song recorded several hundred meters away in the forest. White lines 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).

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 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

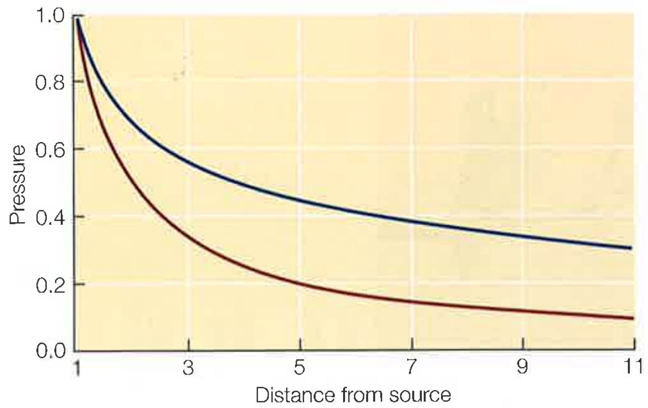


FIGURE 3.2 **Spreading losses during sound propagation** Red line shows drop in sound pressure with increasing distance from the sound source in a free field with spherical (3-dimensional) spreading. Pressure decreases by 6 dB for every doubling of distance. Blue line shows slower drop for cylindrical 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.

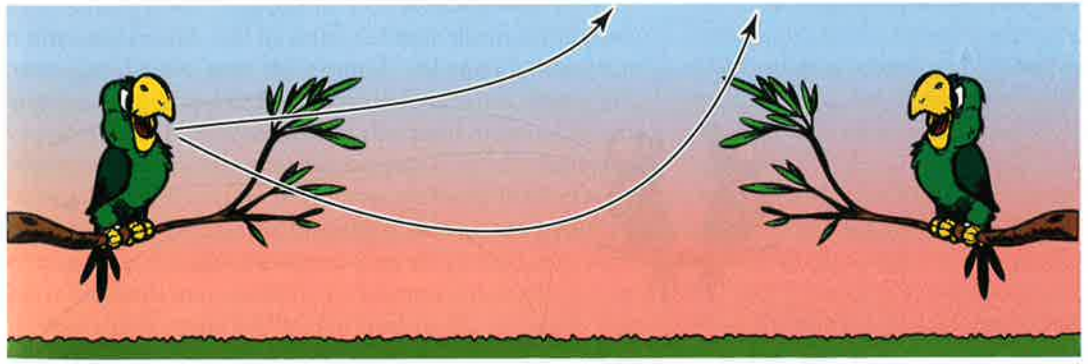


FIGURE 3.3 **Refraction of sound waves for a receiver close to the ground on a hot day** The warm ground heats the immediately adjacent layer of air, and this generates a gradient of decreasing air temperatures, (and thus sound speeds), with increasing height above the ground. Sound traveling parallel 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.

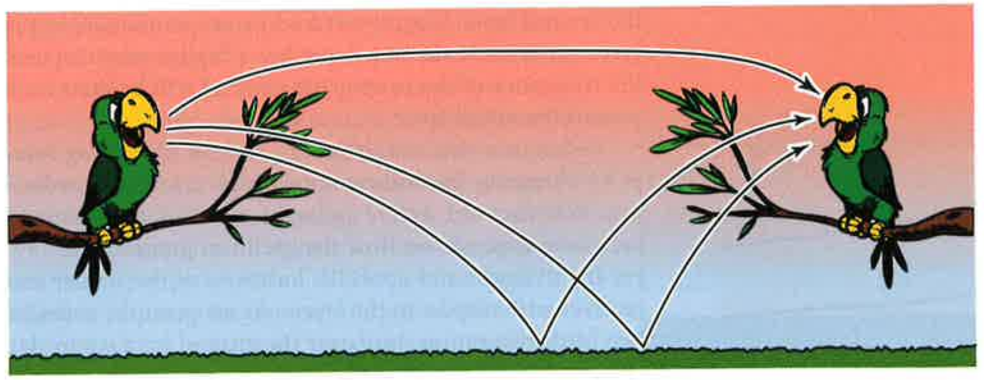


FIGURE 3.4 **Refraction of sound waves for a receiver close to the ground on a clear night or at dawn** The earth radiates its heat back into the sky on a clear night, generating a gradient of increasing temperatures, (and thus sound speeds), with increasing height above the ground. Sound that would 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.

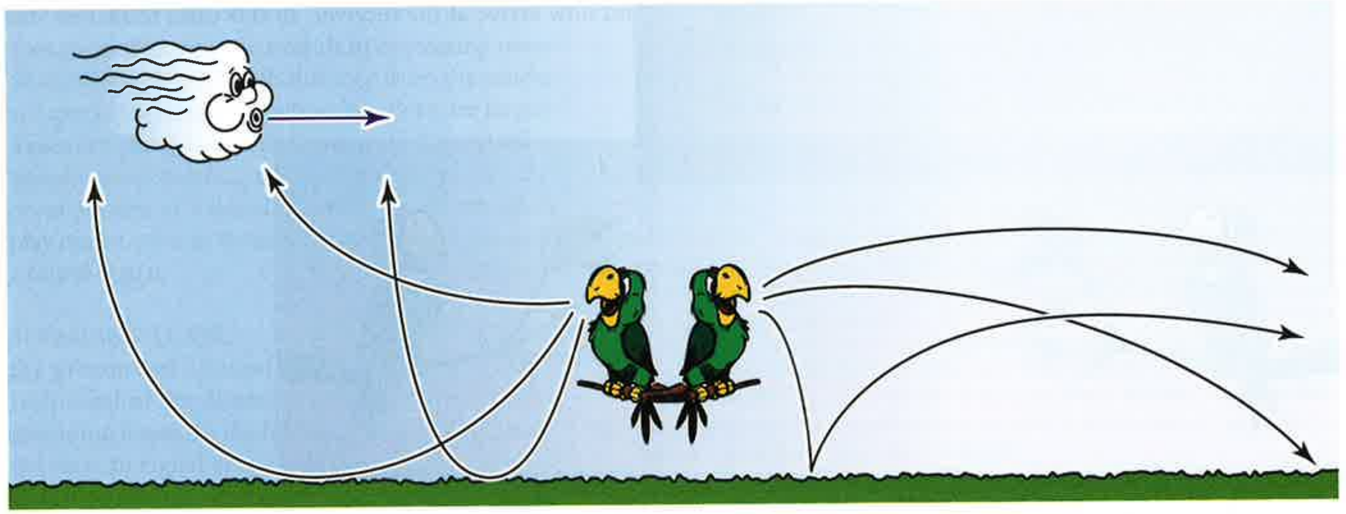


FIGURE 3.5 **Refraction of sound waves near the ground due to wind** In this figure, wind is blowing from left to right. When a receiver is upwind from the sender, wind slows down the propagation speed. Because wind speed is least near the ground and increases with increasing height above the ground, 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.

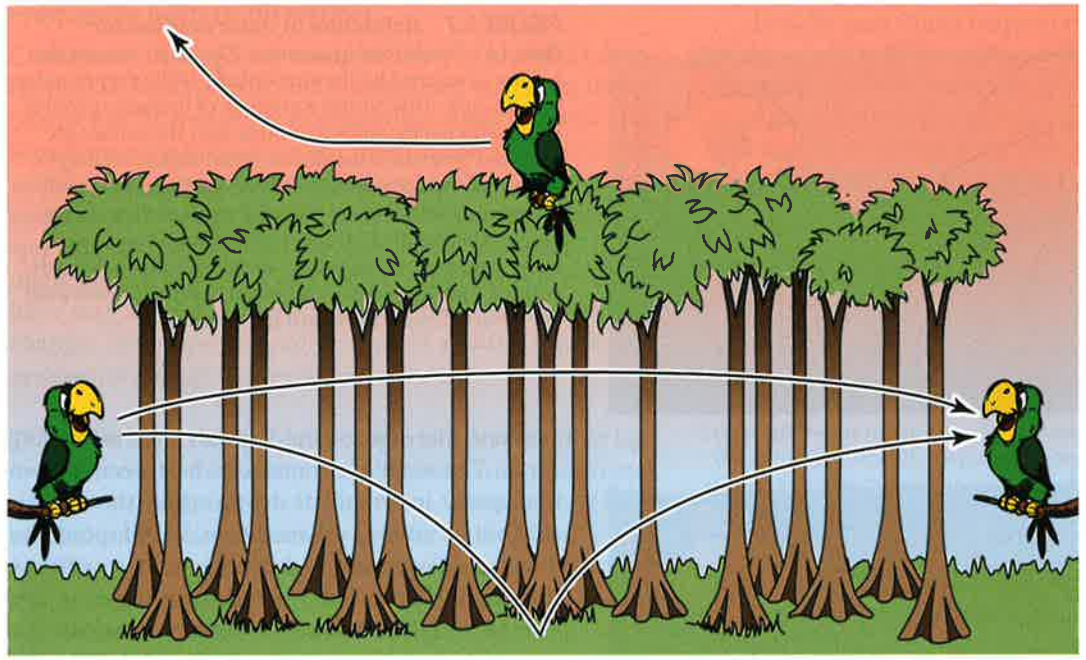


FIGURE 3.6 **Refraction of sound waves inside a forest** The canopy traps incident sunlight and heats up, whereas shade and evaporation leave the ground and understory cool. Air temperatures and thus sound speeds increase along a gradient between the ground and the underside of the canopy. Bird sounds 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.

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 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.

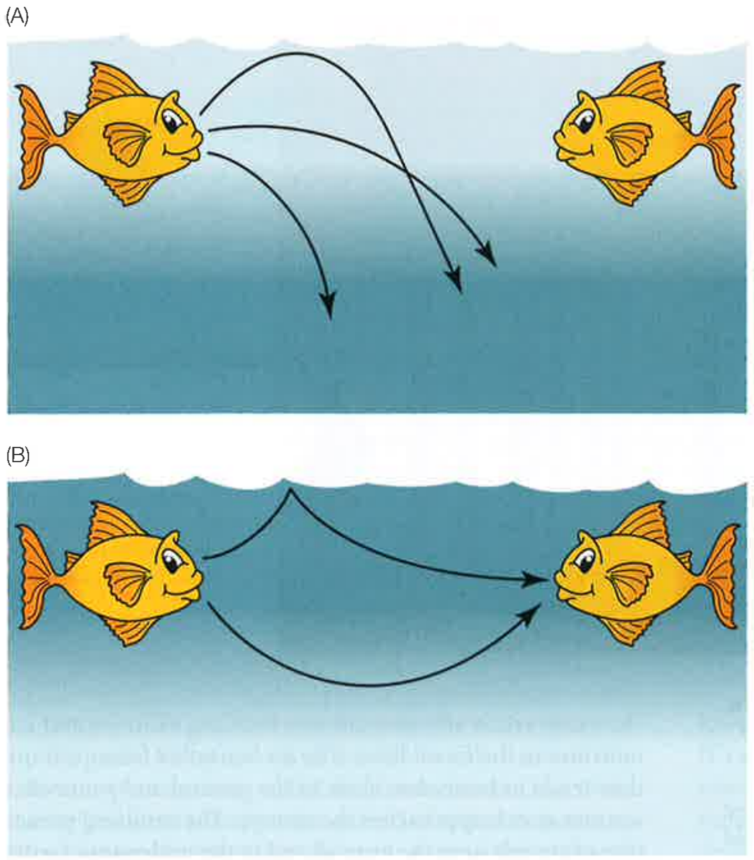


FIGURE 3.7 Refraction in water near the surface (A) Conditions in summer. The water nearest the surface is warmed by the atmosphere, while deeper waters remain cold. This creates a gradient of decreasing sound speed with depth. Sounds emitted near the surface are refracted down into the slower-speed 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 (*S*ound *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].

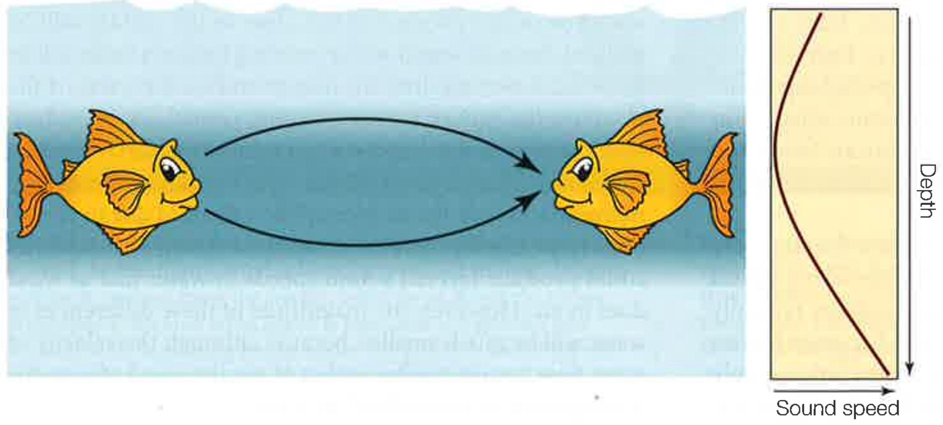


FIGURE 3.8 Refraction in deep ocean SOFAR channel in summer Graph on right shows typical deep ocean sound speed profile with increasing depth. Sound speed depends on water temperature (which is highest near surface and decreases to minimum value with depth) and water pressure (which is least at the surface, 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.

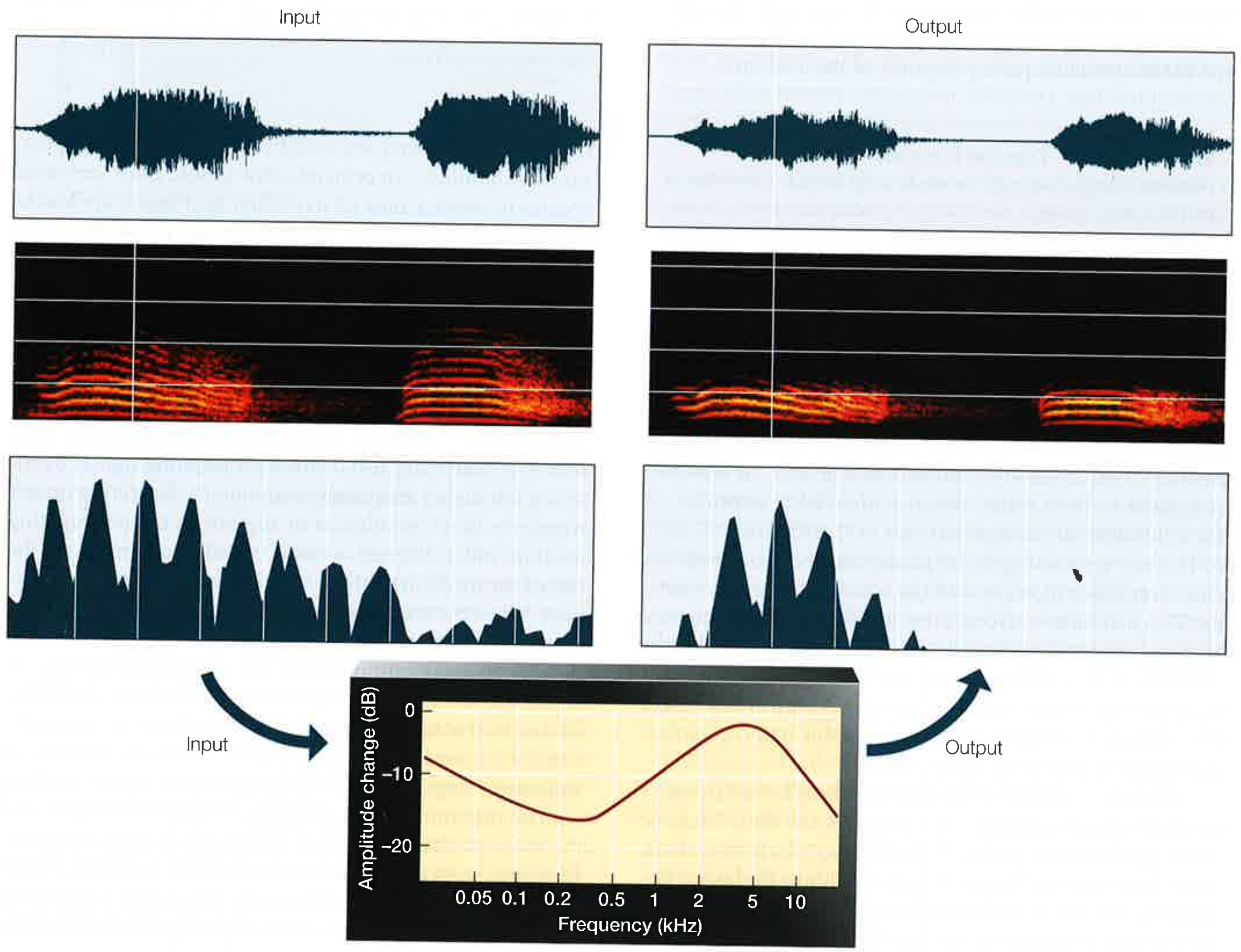
Frequency pattern distortion

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.

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?

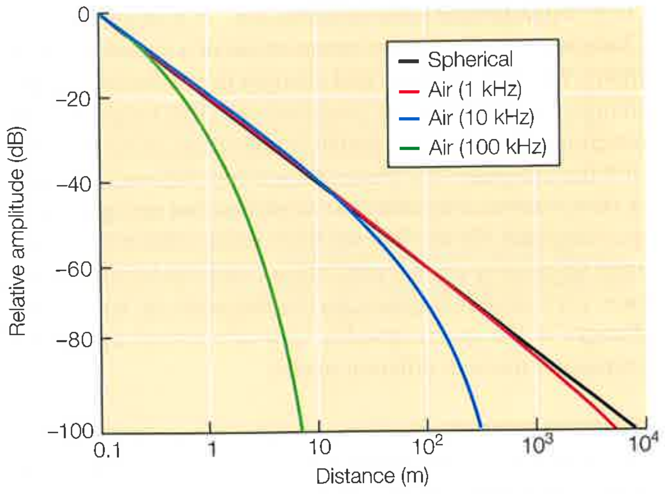


FIGURE 3.10 Frequency- and distance-dependent heat losses during sound propagation Black line shows decrease in dB of the amplitude of a sound due to spherical spreading alone during propagation over different distances. Red line shows expected decrease in amplitude due to spreading combined with heat 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].)

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

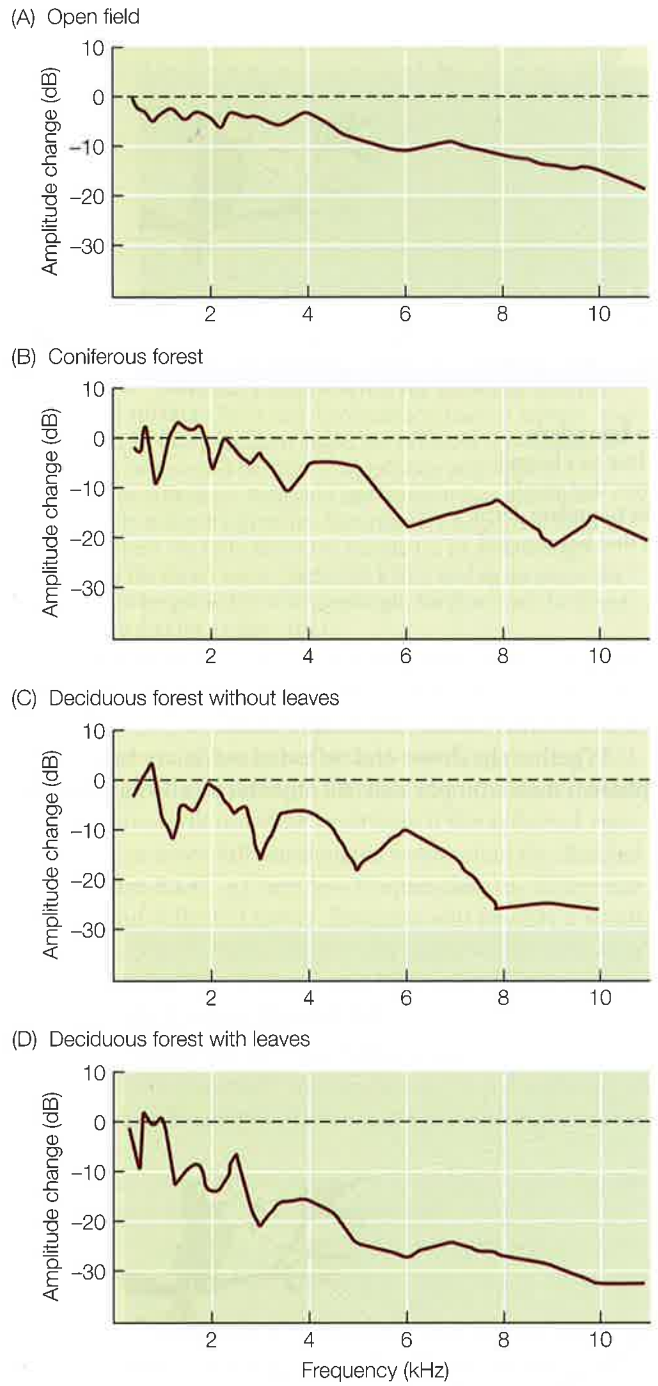


FIGURE 3.11 Scattering and heat losses in temperate terrestrial habitats Frequency response graphs for sound propagation in air across a distance of 100 m (A) over an open field, (B) in a coniferous forest, (C) in a deciduous forest without leaves, and (D) in a deciduous forest with leaves. All samples 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].)

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

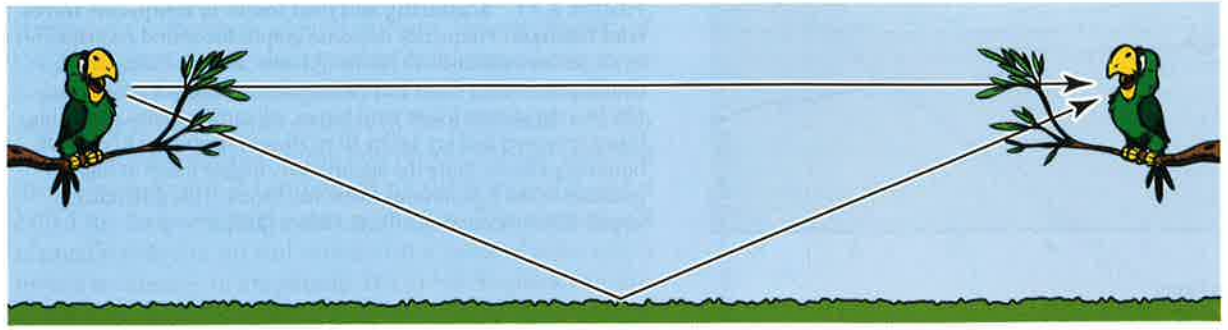


FIGURE 3.12 Interference between direct and reflected waves near a boundary When sender or receiver are located in one medium, but one or both are close to a boundary with another medium of quite different acoustic impedance, sound waves that would otherwise have missed the receiver can now reach it 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 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.

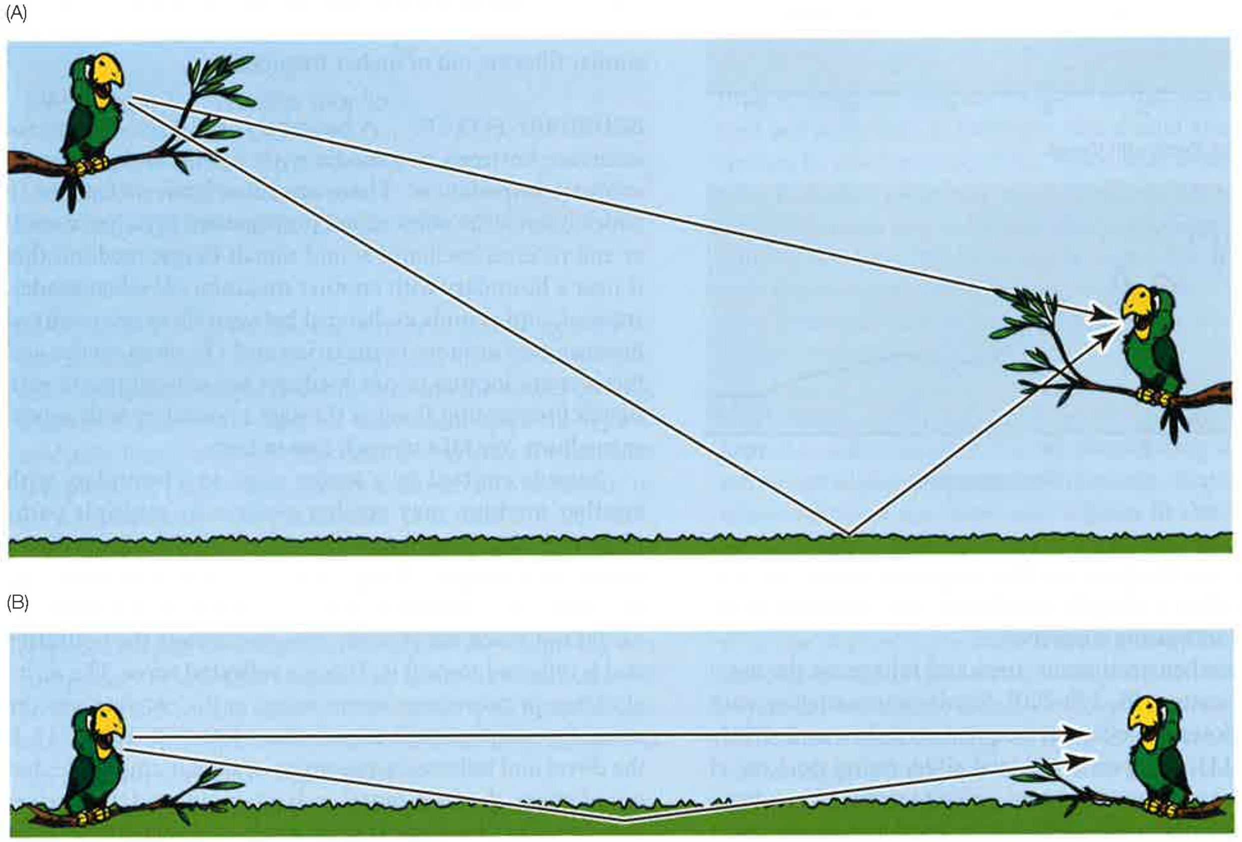


FIGURE 3.13 Effects of sender and receiver height on boundary interference If one or both parties are high above a nearby boundary (A), the path taken by the direct wave will be significantly shorter than that taken by the reflected wave. As a result, the amplitude of the reflected wave will be much 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.

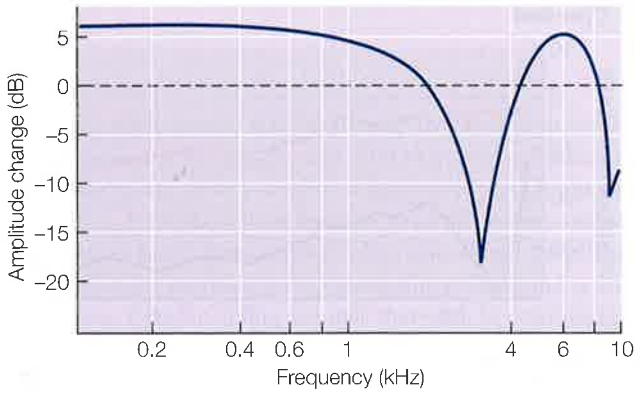


FIGURE 3.14 Boundary interference for airborne sounds over a hard surface For a very hard surface, such as asphalt, and any biologically likely incident angle, the reflected wave from the nearby hard surface will be large in amplitude and without any phase shifts at reflection. Reflected and direct waves 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].)

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

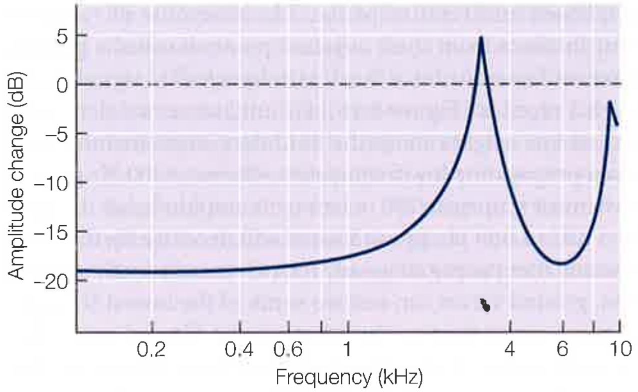


FIGURE 3.15 Boundary interference for airborne sounds at low incident angles The boundary surface is here assumed to be hard enough to produce a reflected wave of large amplitude, soft enough that the critical angle is larger than the incident angle defined by the proximities of sender and receiver to 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].)

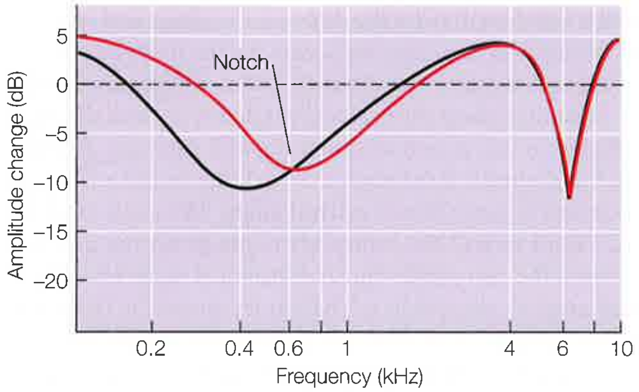


FIGURE 3.16 Boundary interference for airborne sounds at low incident angles and over soft substrates Frequency responses for propagation over ground covered with fresh snow (black) and soft earth inside a woodland (red). As in Figure 3.15 direct and reflected waves interfere negatively for low frequencies 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.

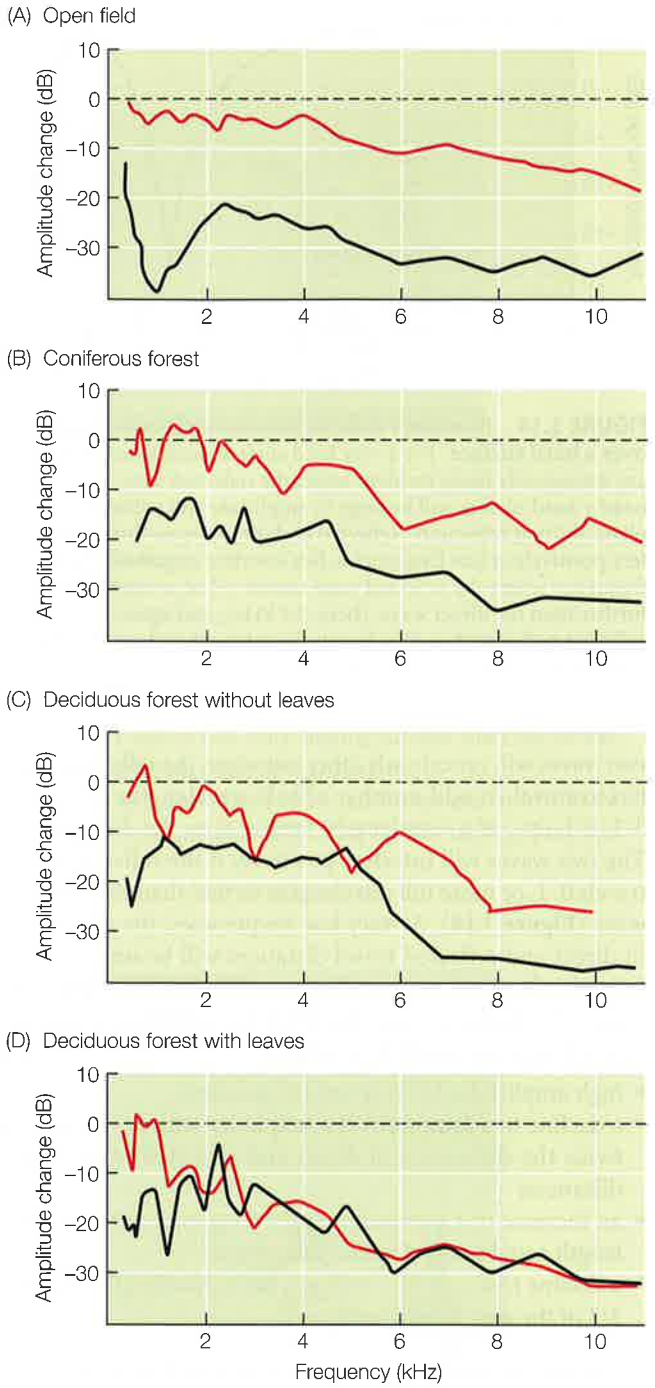


FIGURE 3.17 Measured frequency response curves near ground in temperate terrestrial habitats These graphs show the same four contexts of Figure 3.11. The frequency response for each habitat with both sender and receiver 10 m above the ground (red) is compared to response when both are at ground level (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

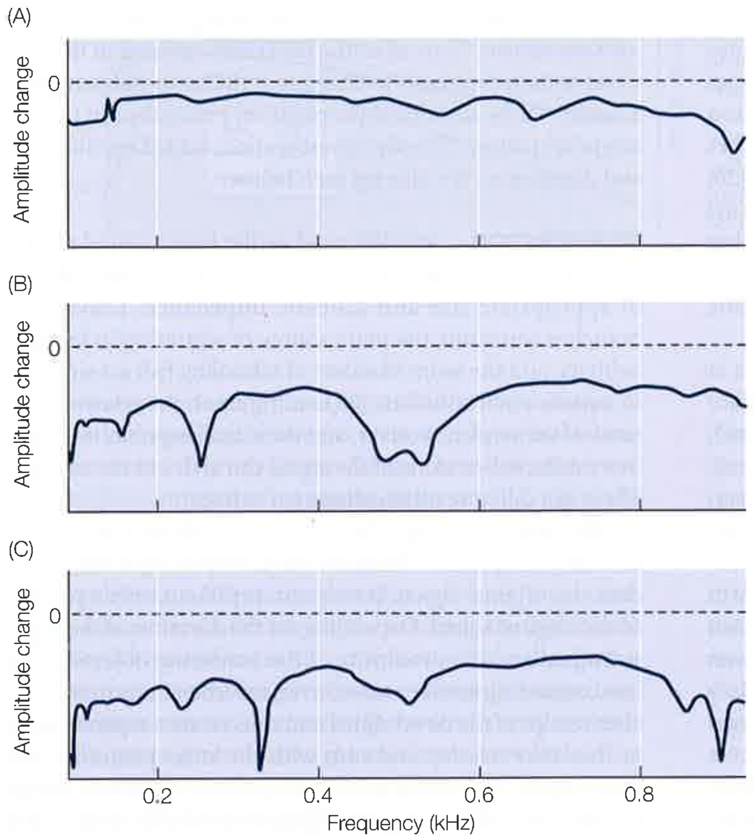


FIGURE 3.18 Predicted frequency response in a marine waveguide Low-frequency sounds propagating in a waveguide created by the ocean surface and bottom. The examples assume 60 m total water depth and positioning of the sender and receiver (e.g., humpbacked whales) at 15 m depth. Dashed lines indicate 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].)

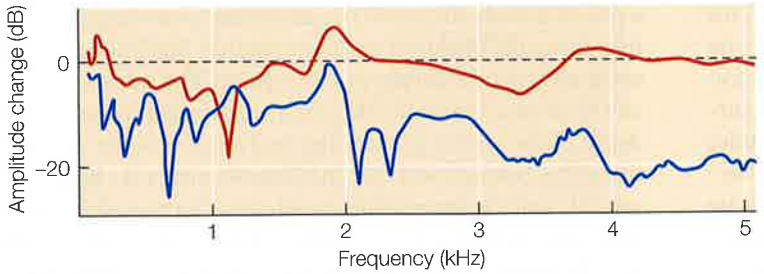


FIGURE 3.19 Frequency response of sound propagating plant stems Plots show frequency dependence of sound propagation over a 3 cm distance (red) and a 17 cm distance (blue) within the stems of the plant *Thesium bavarum*, a common host for substrate-signaling shield bugs (Cydnidae, Hemiptera). Interference 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 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].

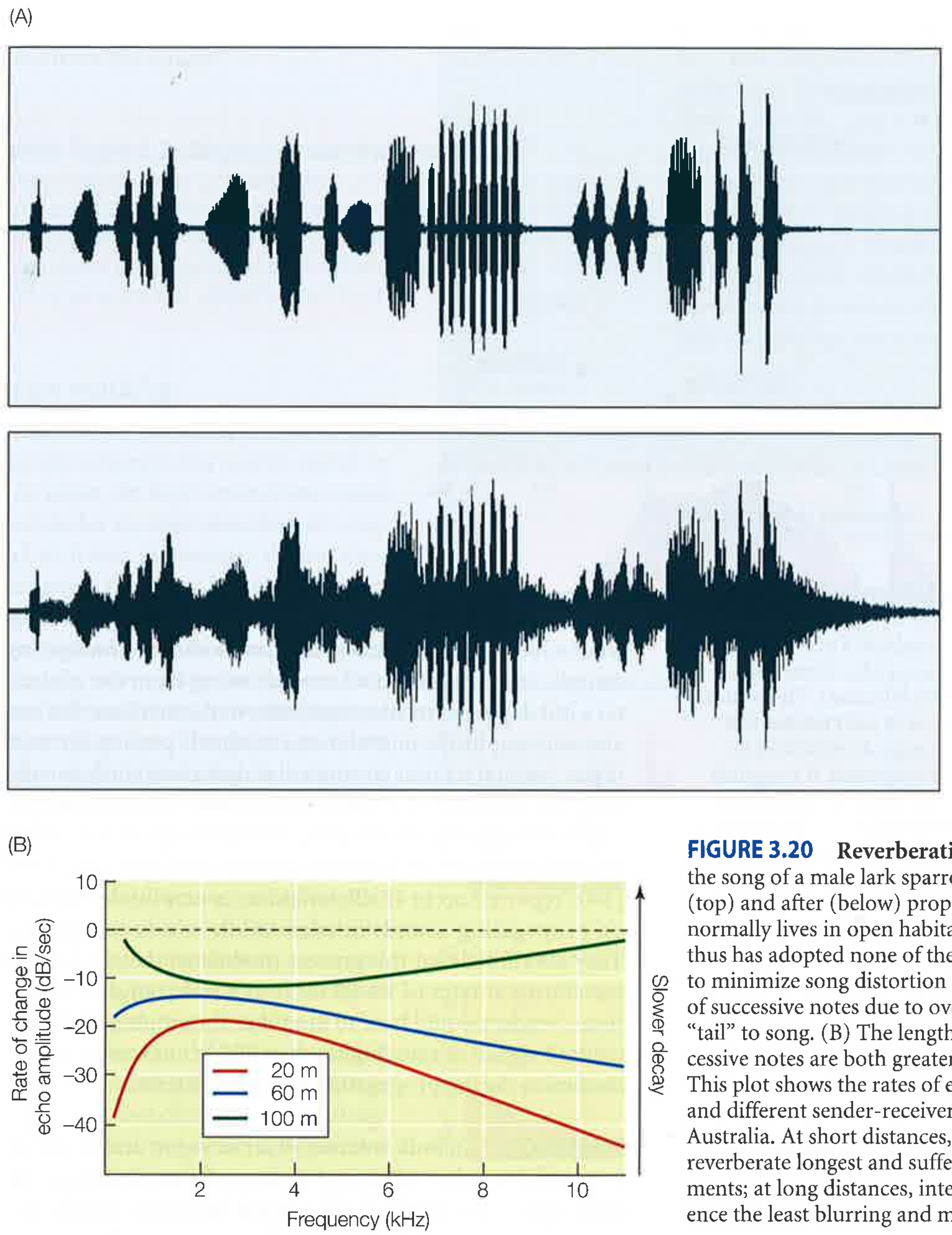


FIGURE 3.20 Reverberations in forests (A) Waveform of the song of a male lark sparrow (*Chondestes grammacus*) before (top) and after (below) propagation in a thick forest. This species normally lives in open habitats where reverberations are rare and thus has adopted none of the specializations used 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].)

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.

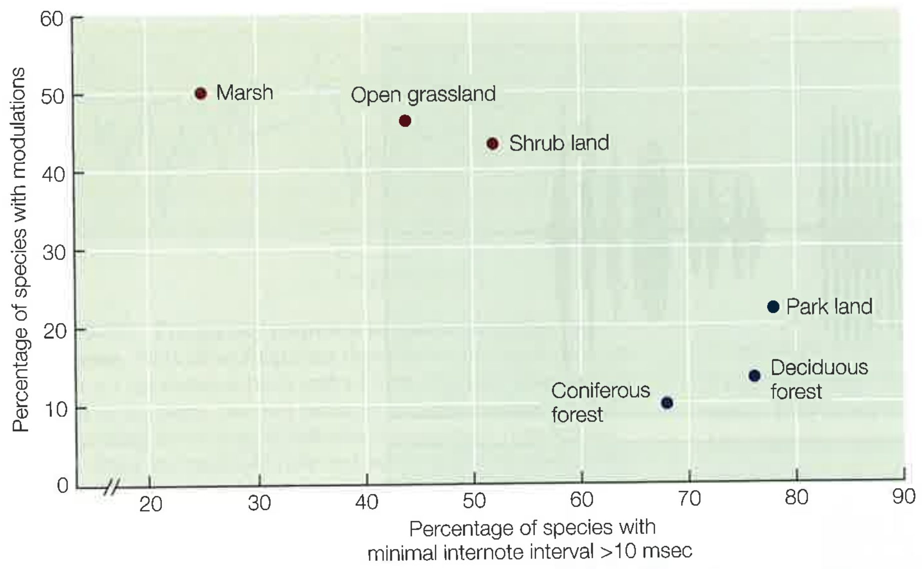


FIGURE 3.21 Correlations between habitat and temporal patterns in birdsong The horizontal axis in this graph indicates the percentage of 120 North American songbird (Oscine) species in each of 6 habitat types that space successive elements in their songs at intervals of 10 msec or more (abscissa). The 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

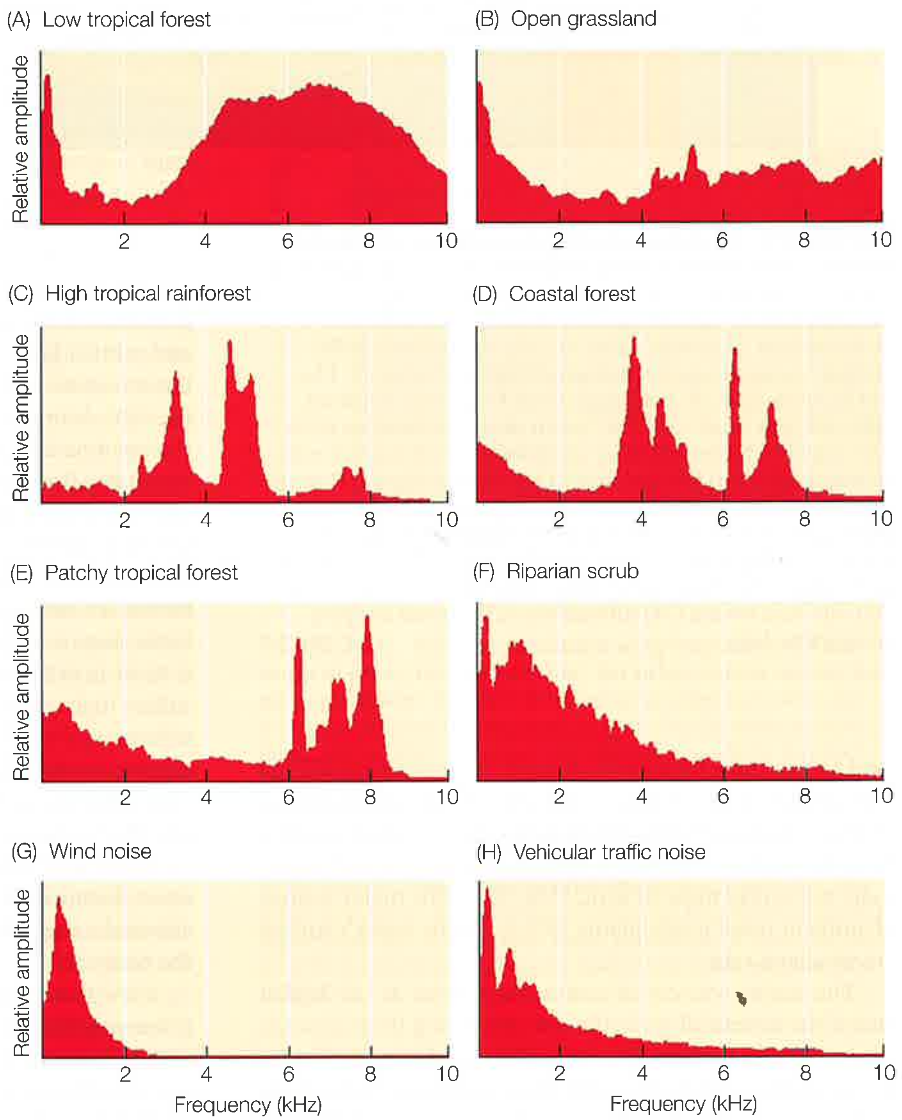


FIGURE 3.22 Frequency dependence of ambient noise in terrestrial habitats (A) Low tropical forest: low-frequency band due to wind; high-frequency band due to forest insects and birds. (B) Open grassland: high wind noise similar to (A) but reduced animal noise. (C) High tropical rainforest: very low wind 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].)

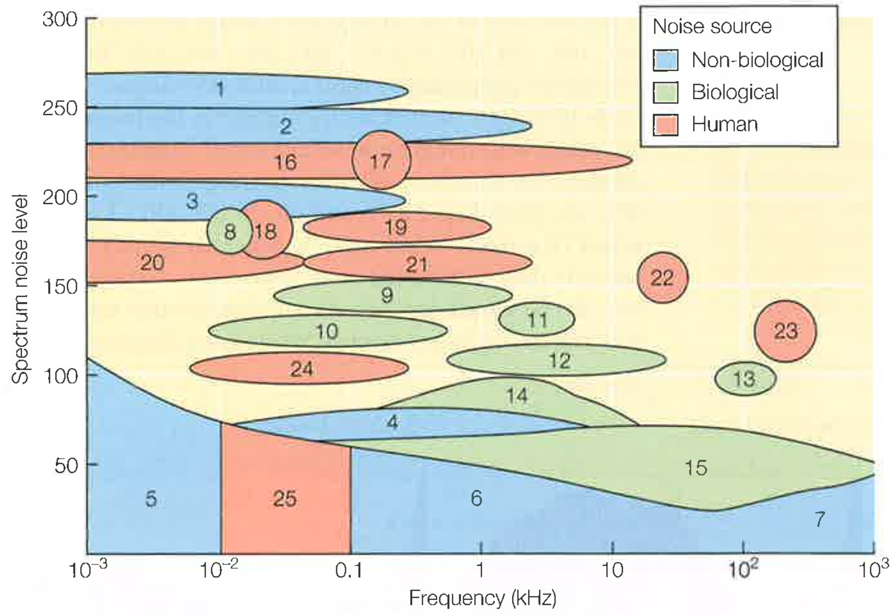


FIGURE 3.23 **Frequency dependence, relative amplitude, and sources of ambient noise in the ocean** Natural nonbiological sources of noise: (1) undersea earthquakes; (2) sea floor volcanic eruptions; (3) lightning strikes; (4) heavy rain and storm winds on sea surface; (5) seismic noise; (6) calm surface 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.

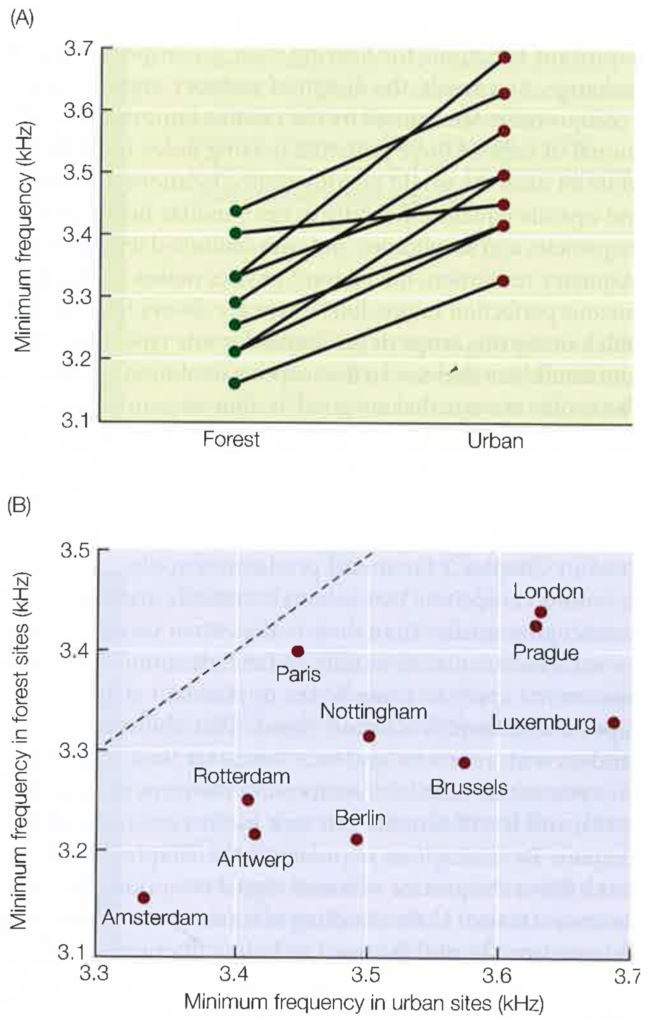


FIGURE 3.24 **Shifts in minimum song frequencies in the songs of great tits (*Parus major*) for urban versus nearby forest populations** For each of 10 European cities and towns, an average of 30 great tit songs were recorded in the urban environment, and another 30 songs were collected in a nearby forested 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**).

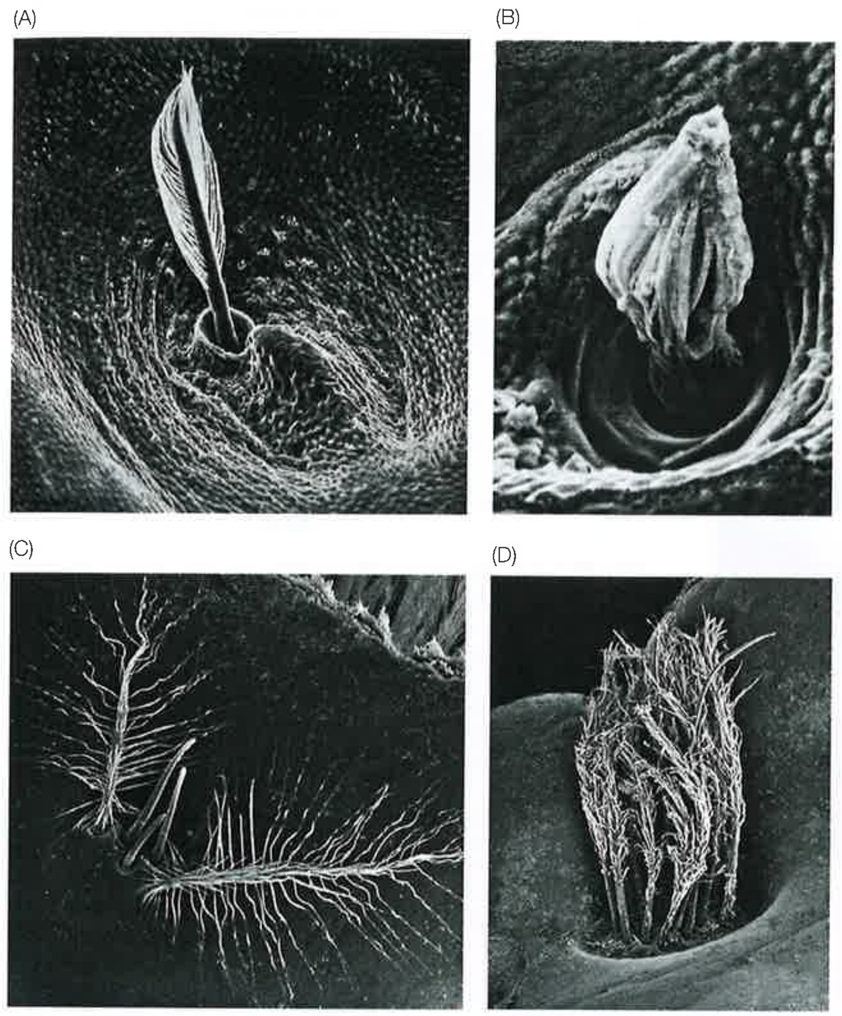


FIGURE 3.25 Sensory hairs on exoskeletons of aquatic crustaceans (A) Filiform hairs on carapace of rock lobster (*Palinurus vulgaris*). (B) Hair-fan receptor on carapace of European lobster (*Homarus gammarus*). (C) Hair-pit organs on claws of young crayfish (*Cherax destructor*), and (D) similar organs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

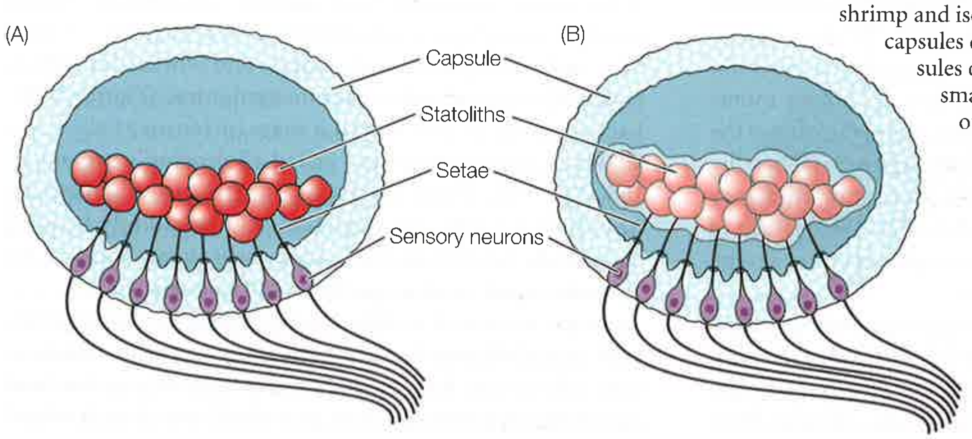


FIGURE 3.26 Crustacean statocysts These organs can be located at the base of the antennules (in crabs, lobsters, and crayfish), on the head (in amphipods), or on the tail (in mysid shrimp and isopods). They consist of open or closed capsules embedded in the exoskeleton. The capsules of crayfish and lobsters 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.

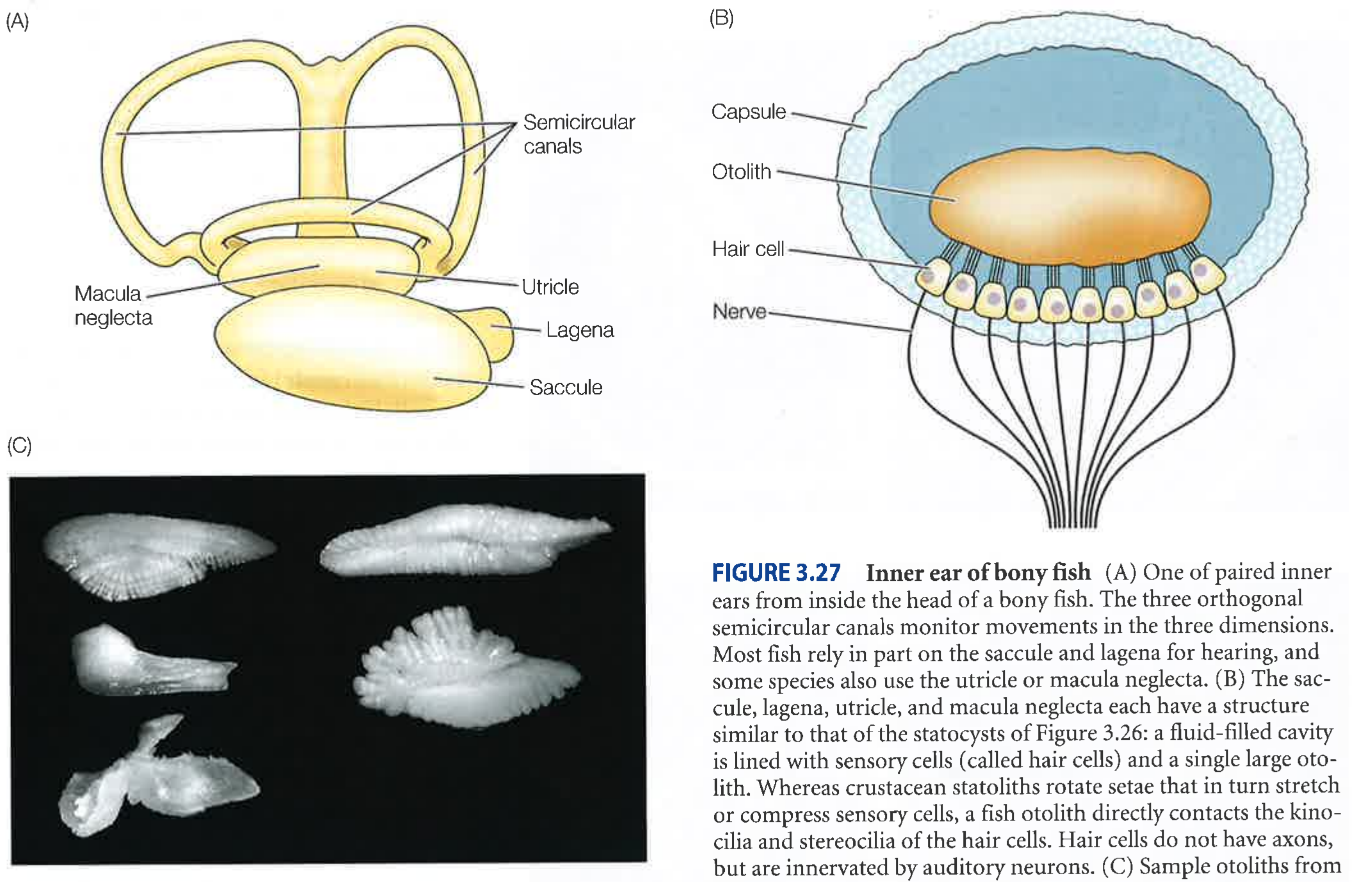


FIGURE 3.27 Inner ear of bony fish (A) One of paired inner ears from inside the head of a bony fish. The three orthogonal semicircular canals monitor movements in the three dimensions. Most fish rely in part on the saccule and lagena for hearing, and some species also use the utricle or macula neglecta. (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'

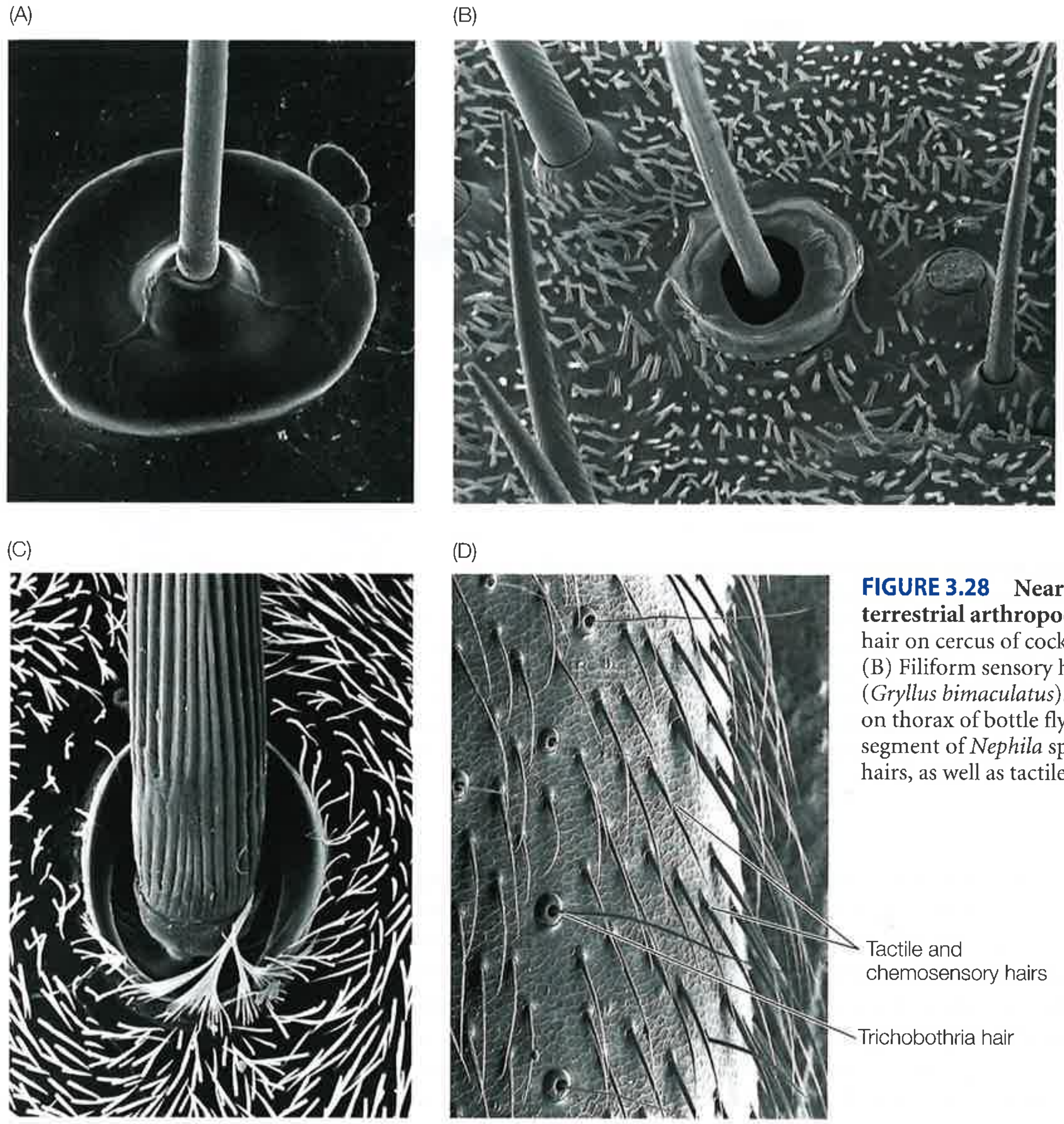


FIGURE 3.28 Near-field sensory hairs of terrestrial arthropods (A) Filiform sensory hair on cercus of cockroach (*Periplaneta* spp.). (B) Filiform sensory hair on cercus of cricket (*Gryllus bimaculatus*). (C) Grooved sensory hair on thorax of bottle fly (*Calliphora* spp.). (D) Leg segment of *Nephila*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

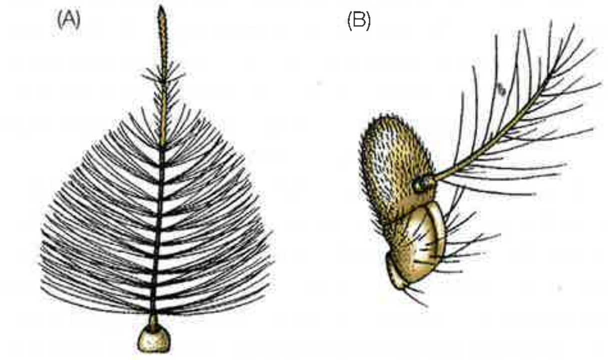


FIGURE 3.29 Near-field antennae of insects (A) Plumose antenna of male mosquito used to detect wingbeats of nearby female. (B) Antennal arista of female fruit fly used to detect near-field song created by courting male's wings.

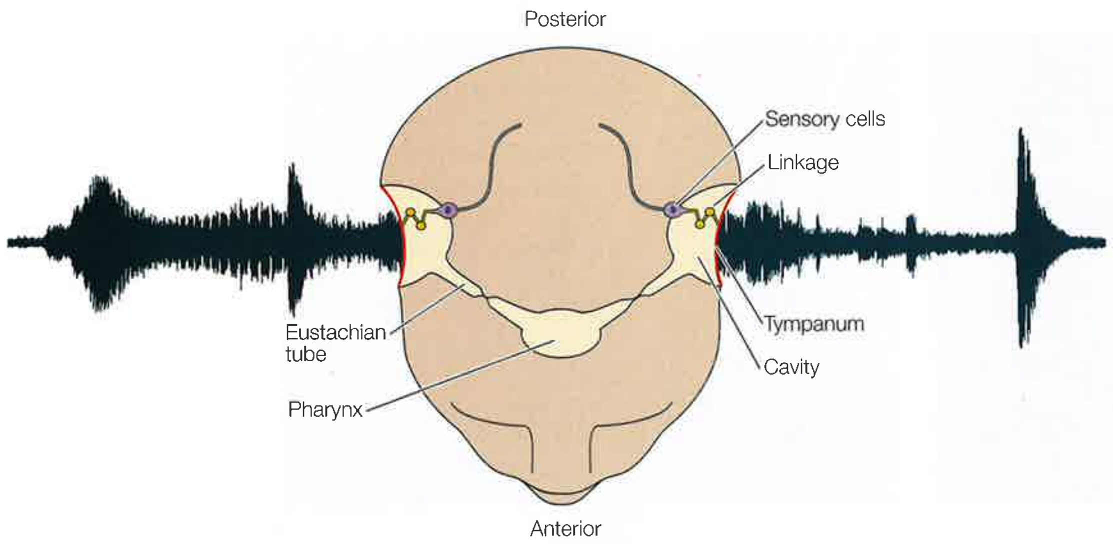


FIGURE 3.30 **Pressure detector ears** Diagrammatic cross section through head of a typical mammal with a pressure detector ear on each side of the head. Each ear is structurally and dynamically independent of the other. A thin tympanic membrane is stretched over a closed cavity in head. This membrane 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].

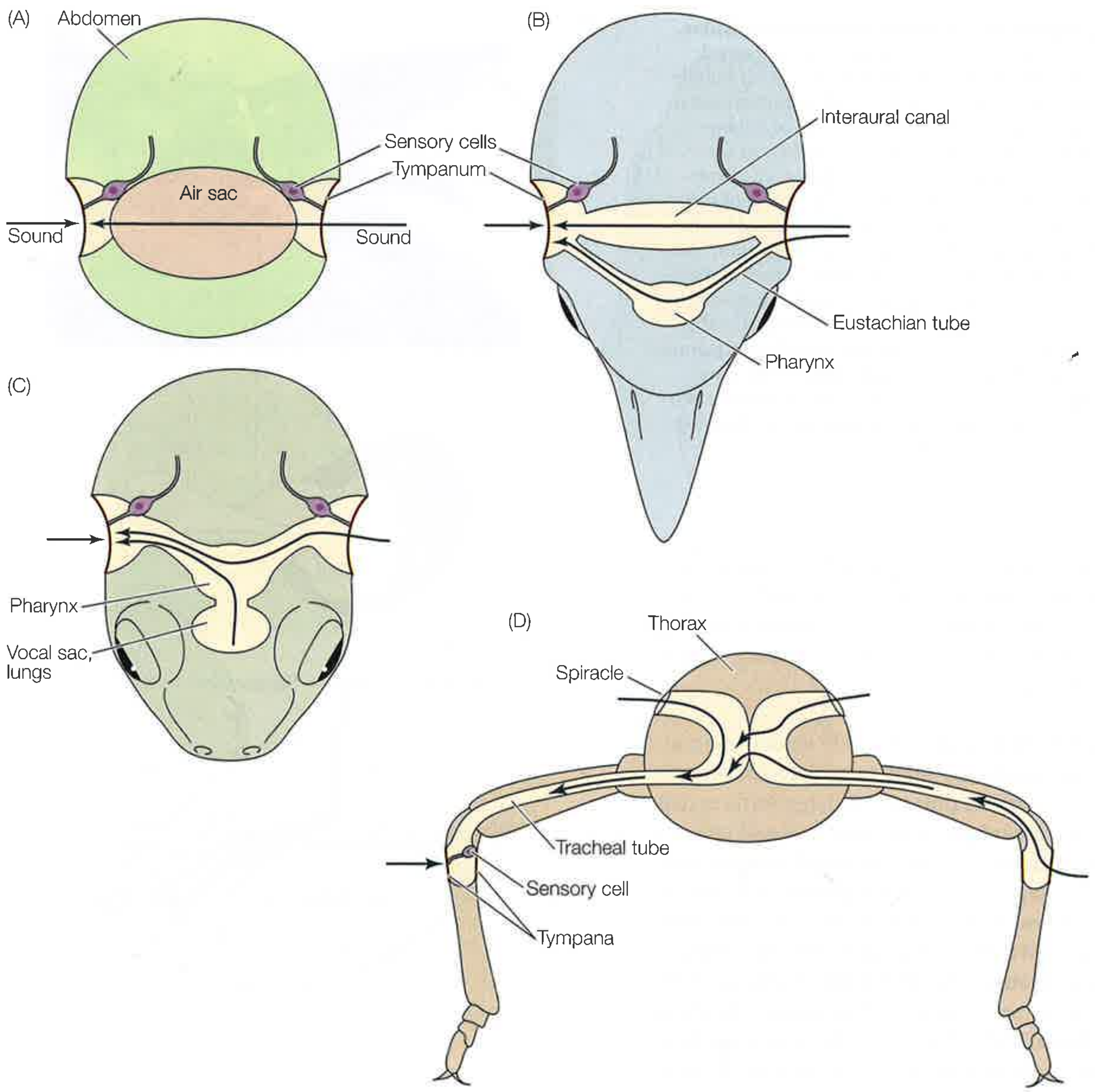
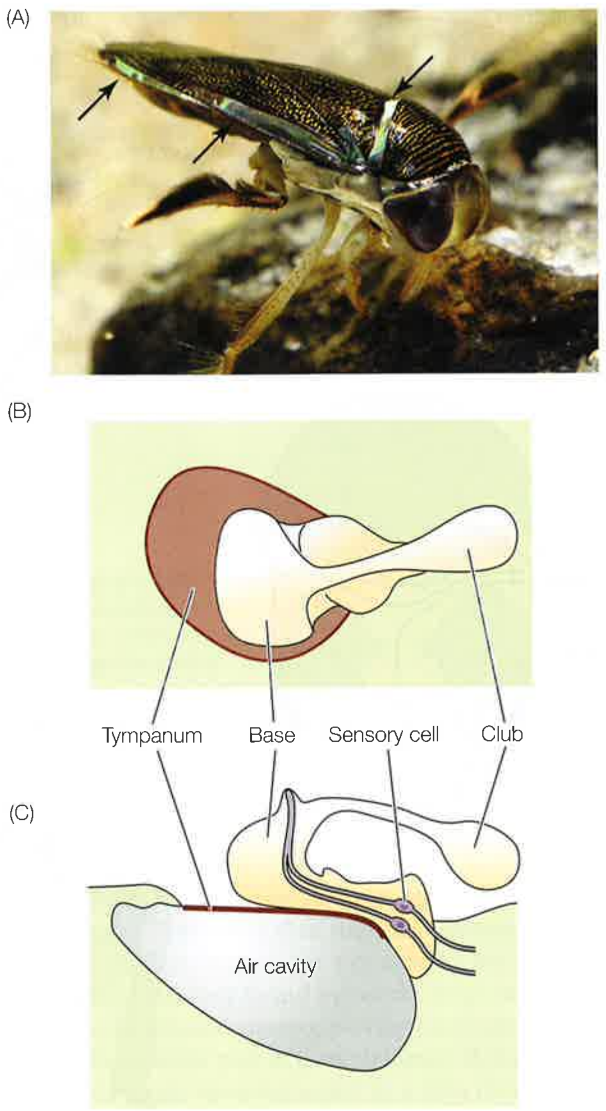


FIGURE 3.31 **Pressure differential ears** (A) Tympanic ears on opposite sides of body joined by one or more air sacs in center (grasshoppers, cicadas). Arrows show paths delivering sound to each side of left-hand tympanum. The same pattern occurs at the other ear. The tympanum moves when the pressures 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.

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 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 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].

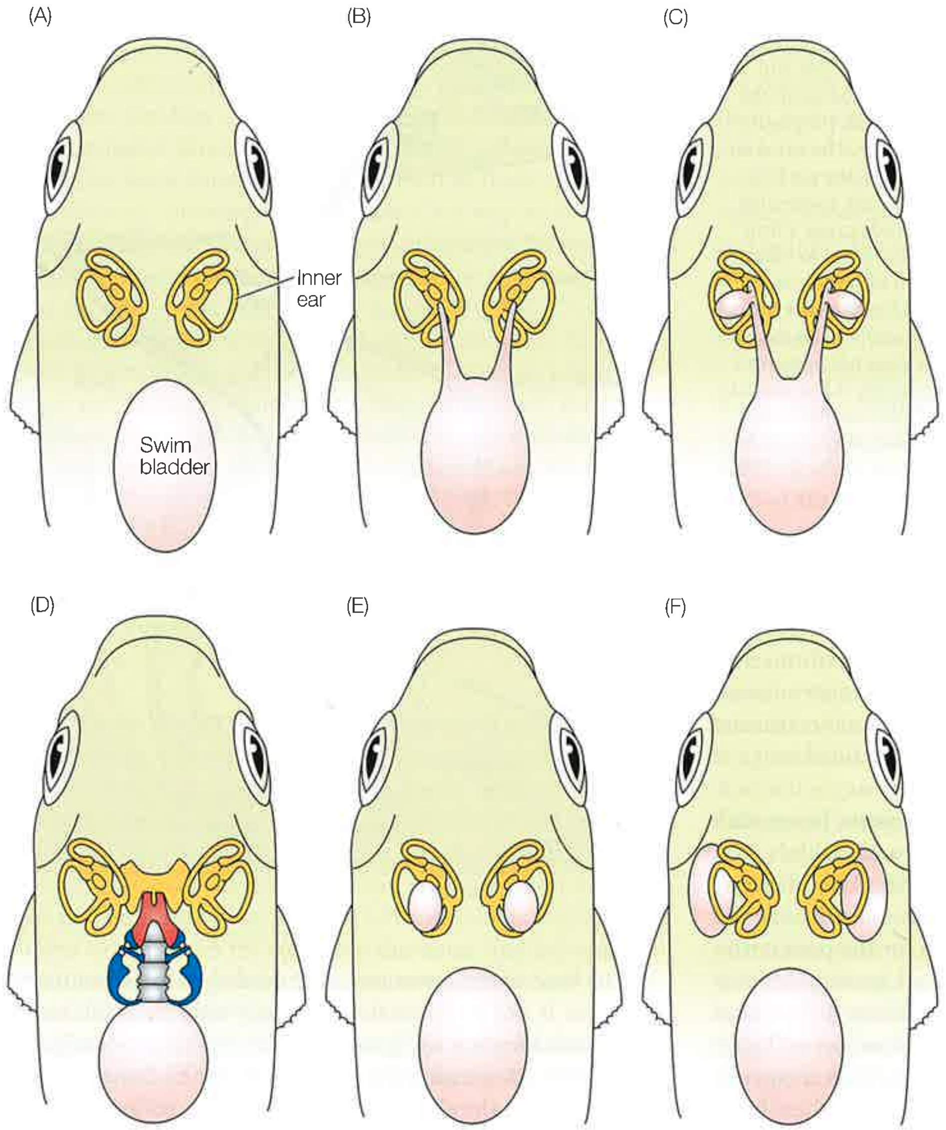


FIGURE 3.33 Role of swim bladder and other air bubbles in fish far-field hearing (A) Fish such as toadfish and sunfish lack any direct linkages between the swim bladder and the ears except intervening tissues. They are largely limited to near-field sounds. (B) Cod, squirrelfish, croakers, and drums have 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

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

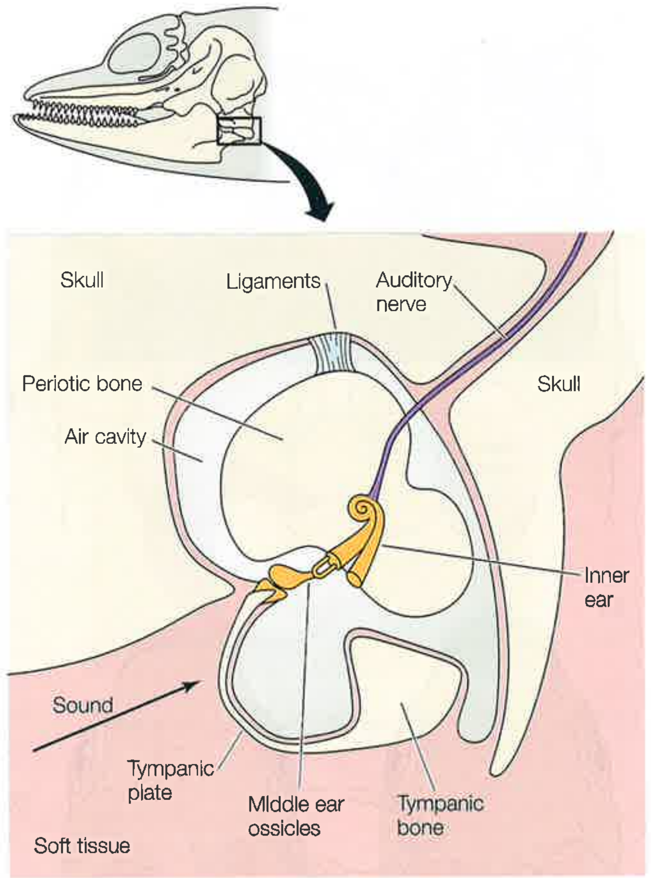


FIGURE 3.34 Section through ear of toothed (Odontocete) whale Intermediate- and high-frequency sounds are captured by a thin "pan bone" section on each side of the lower jaw and conducted through special oil channels to the joints between the jaw and the skull. Sounds delivered by this route then propagate 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

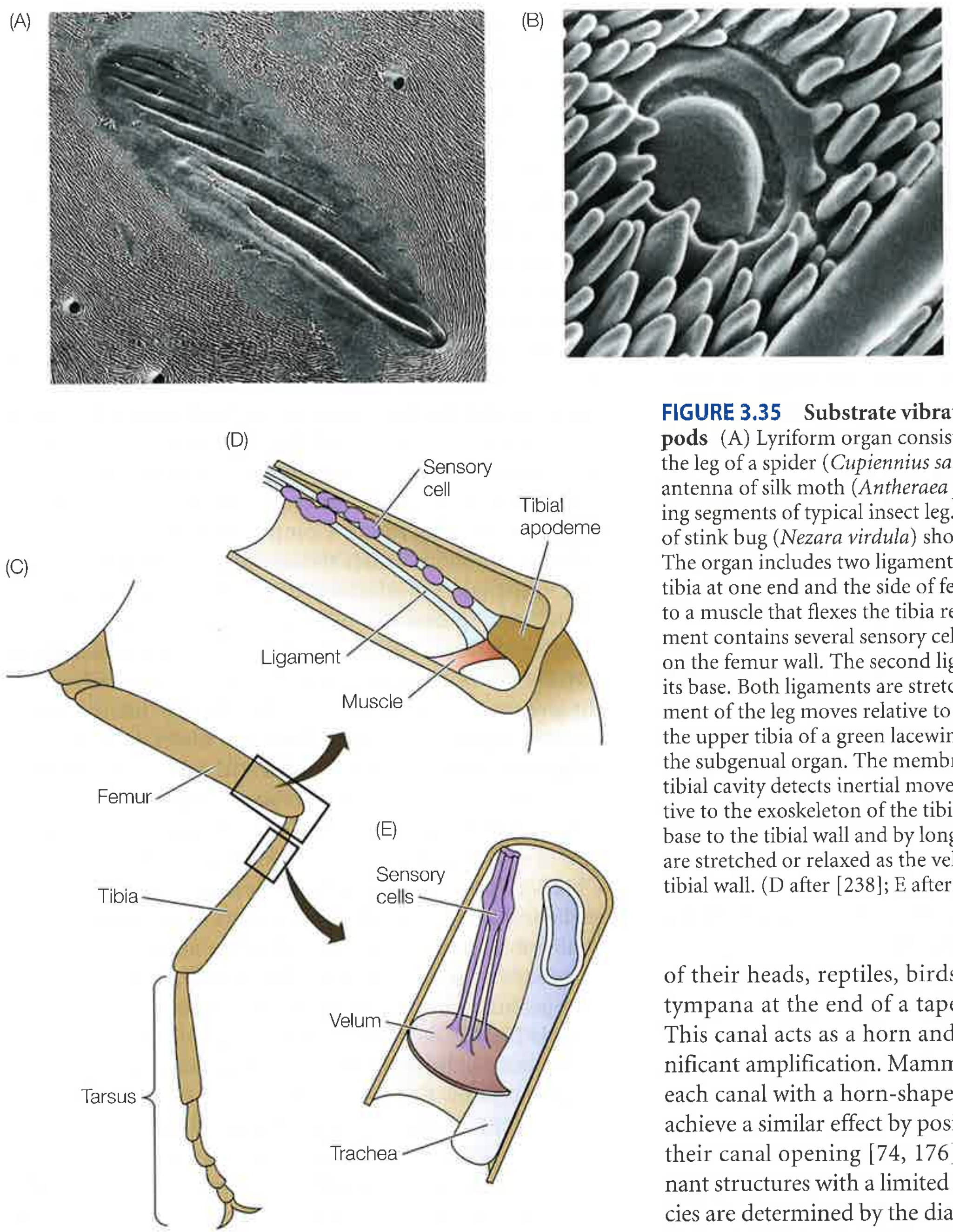


FIGURE 3.35 Substrate vibration receptors of arthropods (A) Lyriform organ consisting of multiple slit organs on the leg of a spider (*Cupiennius salei*). (B) Campaniform organ on antenna of silk moth (*Antheraea polyphemus*). (C) Diagram labeling segments of typical insect leg. (D) Section through lower 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** 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.

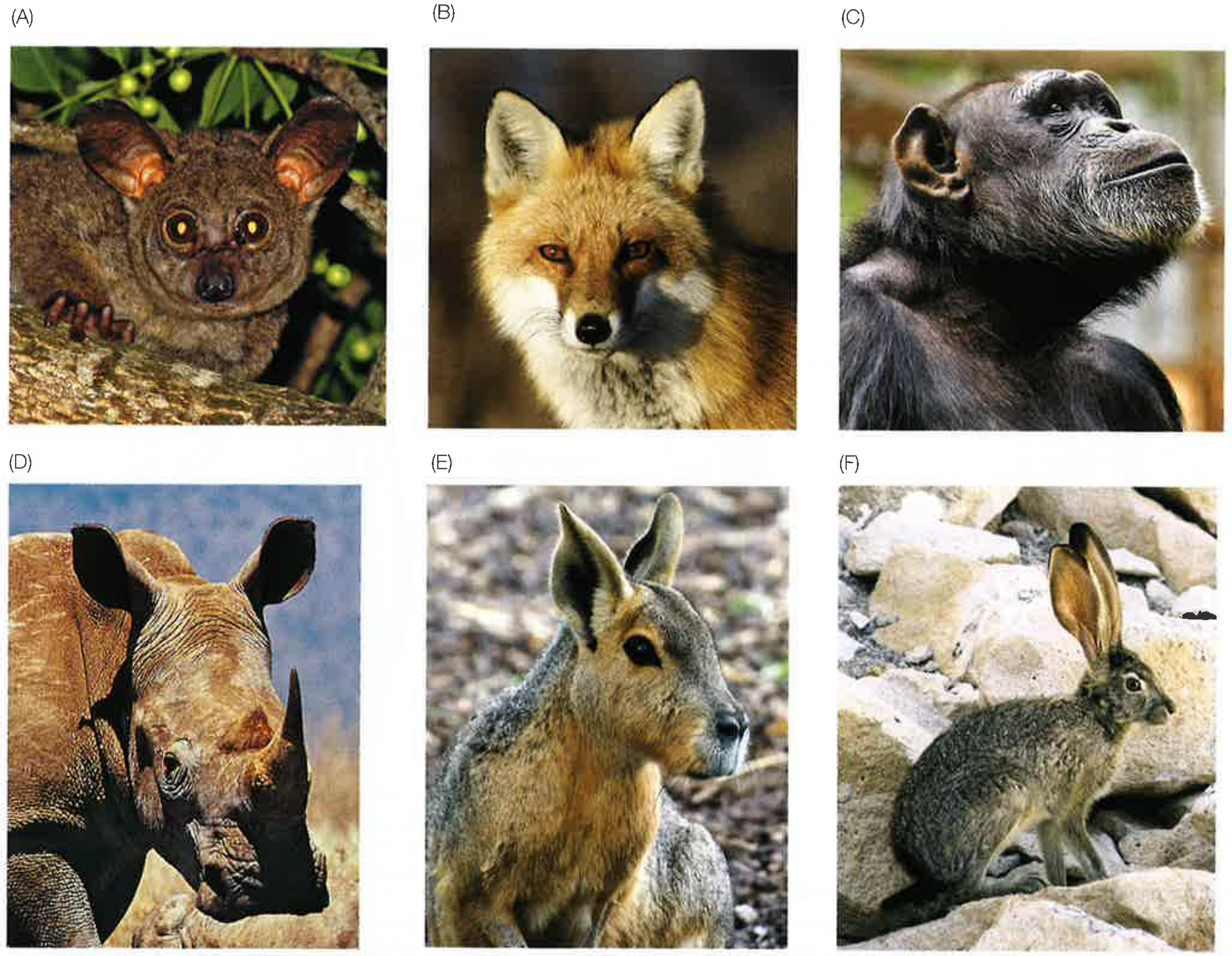


FIGURE 3.36 Alternative types of pinna design in terrestrial mammals (A) Simple ovate pinnae: brown greater galago (*Otolemur crassicaudatus*). (B) Triangular-shaped pinnae completely fixed at base, as found in canids and felids: red fox (*Vulpes vulpes*). (C) Immobile semicircular pinnae fixed to the 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*).

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

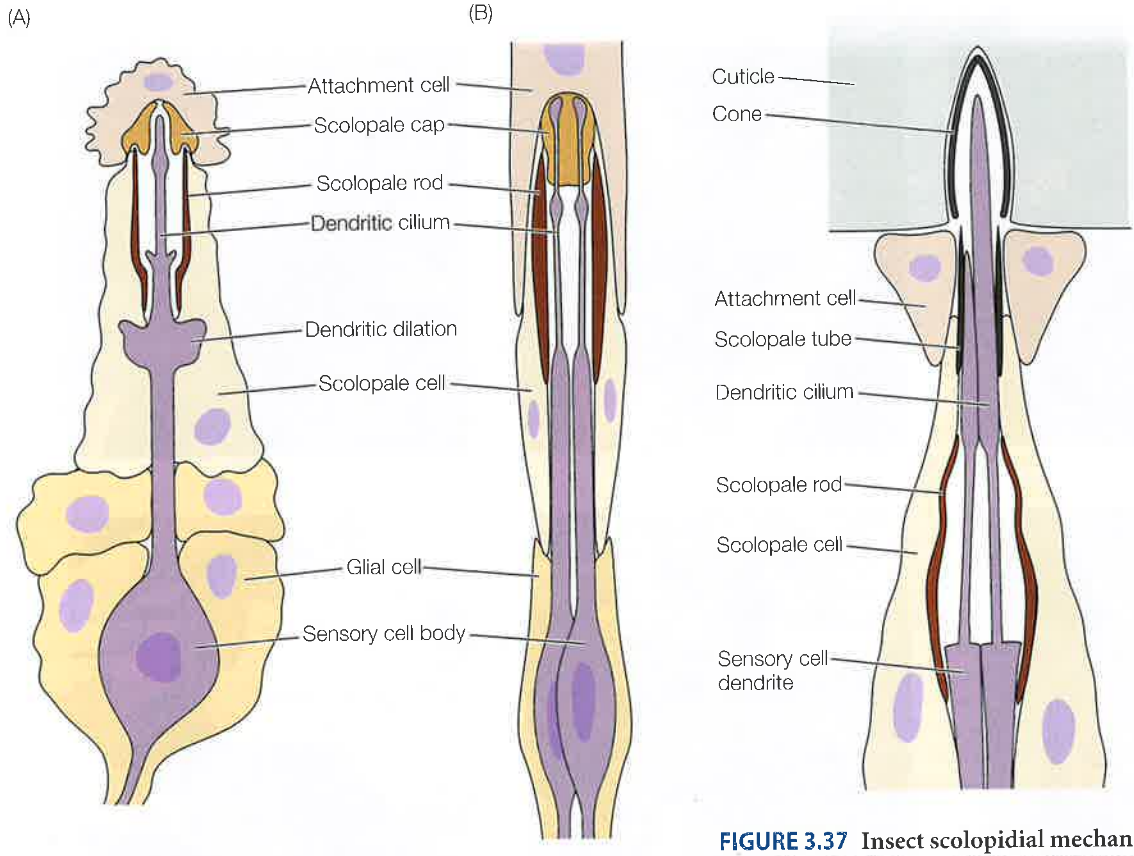


FIGURE 3.37 Insect scolopidial mechanoreceptors In each example shown here, one to several sensory cells extend long ciliary dendrites into a sheath formed by scolopale cells. These contain stiff rods of actin and perhaps other motile proteins. Flexure of the dendrite stimulates the sensory cells which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

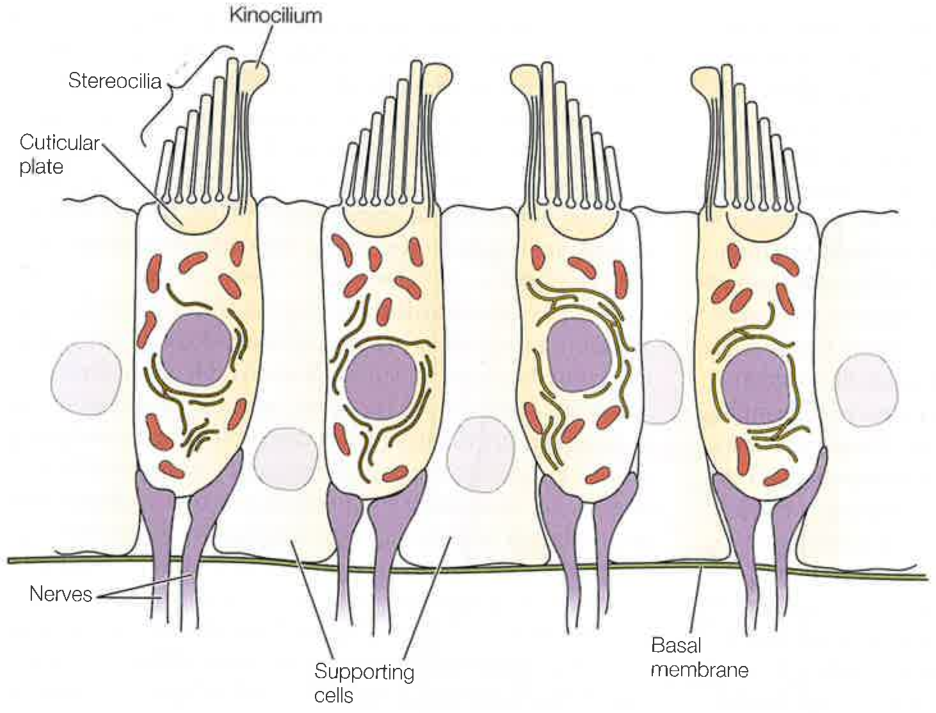


FIGURE 3.38 Vertebrate auditory hair cells Four sensory hair cells that are stimulated when either fluid movements, otoliths, or overlying membranes bend stereocilia toward the kinocilium. Both types of cilia are supported in each cell by a dense cuticular plate. Note that the two hair cells on left 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.

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 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].

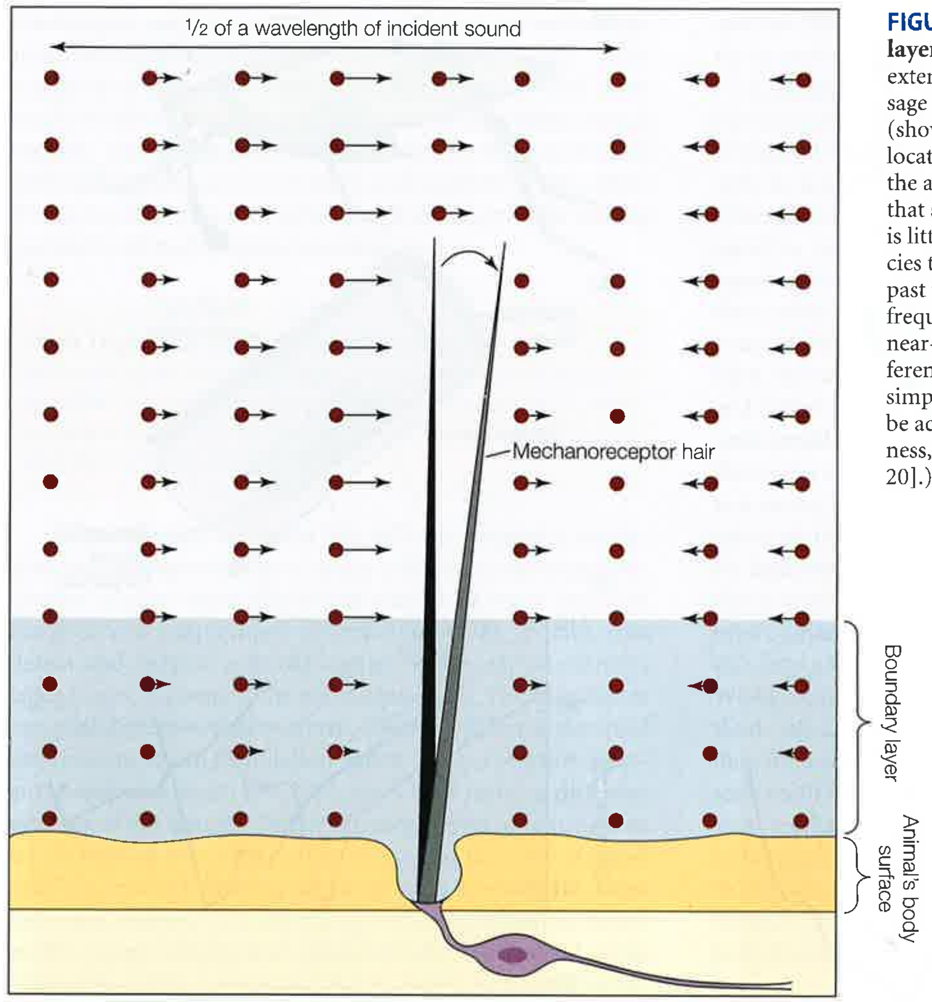


FIGURE 3.39 Sensory hairs and boundary layers A single mechanoreceptor hair is shown extending into the adjacent medium during passage of a near field sound. Molecular velocities (shown using size of arrows) vary with horizontal location (due to wave action) and height above the animal's body surface (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].)

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**

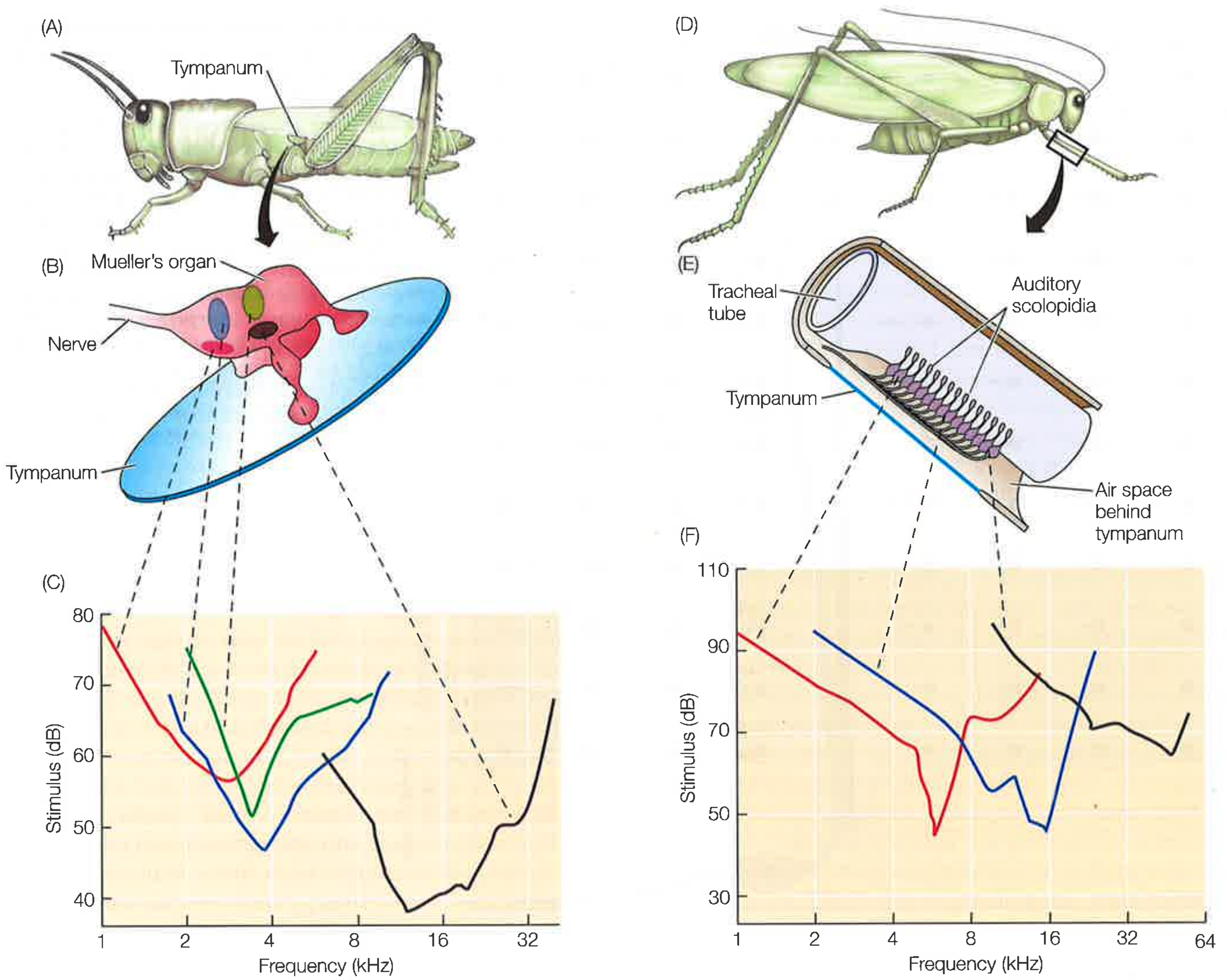


FIGURE 3.40 Frequency resolution devices in locusts and katydids (A) Side view of locust or grasshopper showing location of one of its two tympana just below the wing and on the first abdominal segment. (B) Expanded view from inside locust ear showing Mueller's organ and associated nerve attached to 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

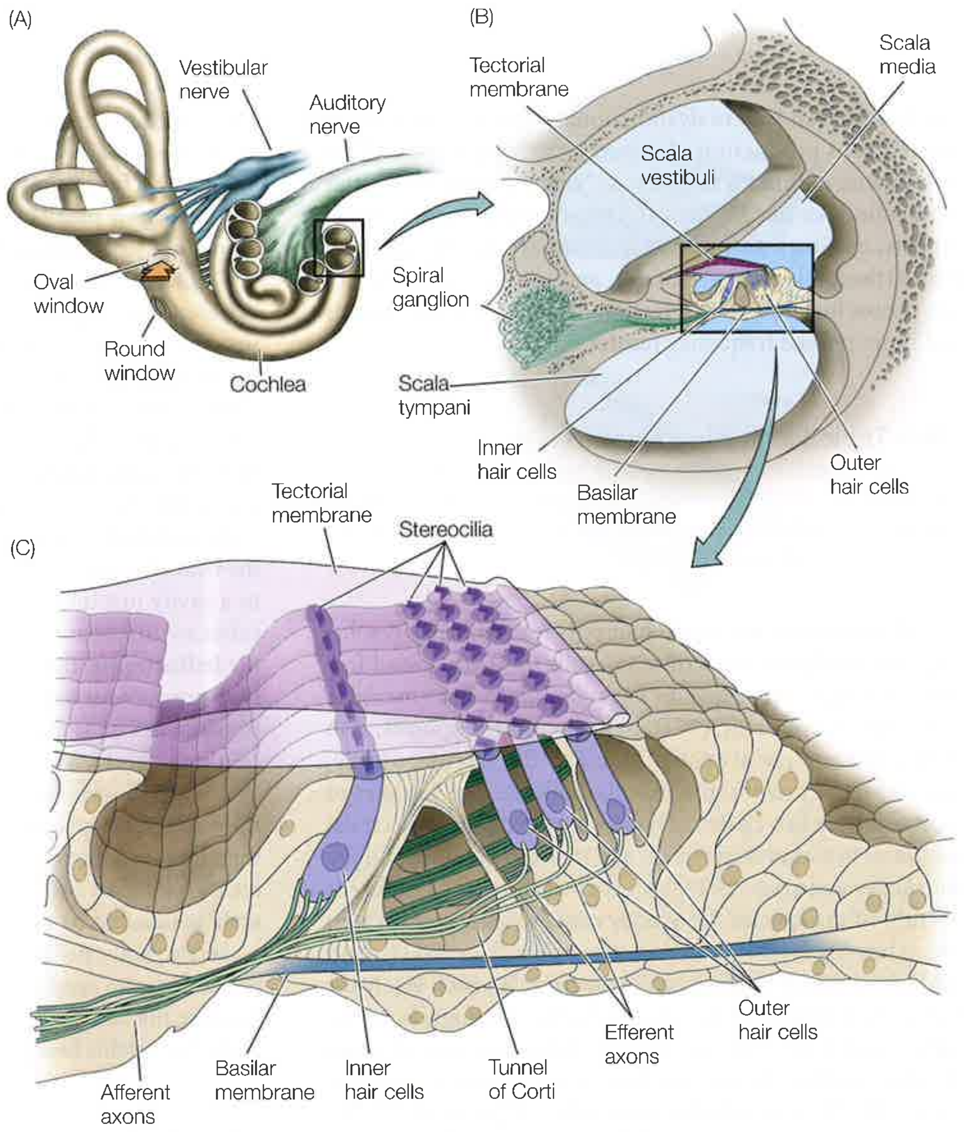


FIGURE 3.41 Structure of typical mammalian inner ear (A) Inner ear showing semicircular canals (on left), oval and round windows at base of cochlea, and coiled cochlea (right). (B) Cross section through cochlea at point indicated in (A). Sound enters the cochlea at the oval window and propagates down 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

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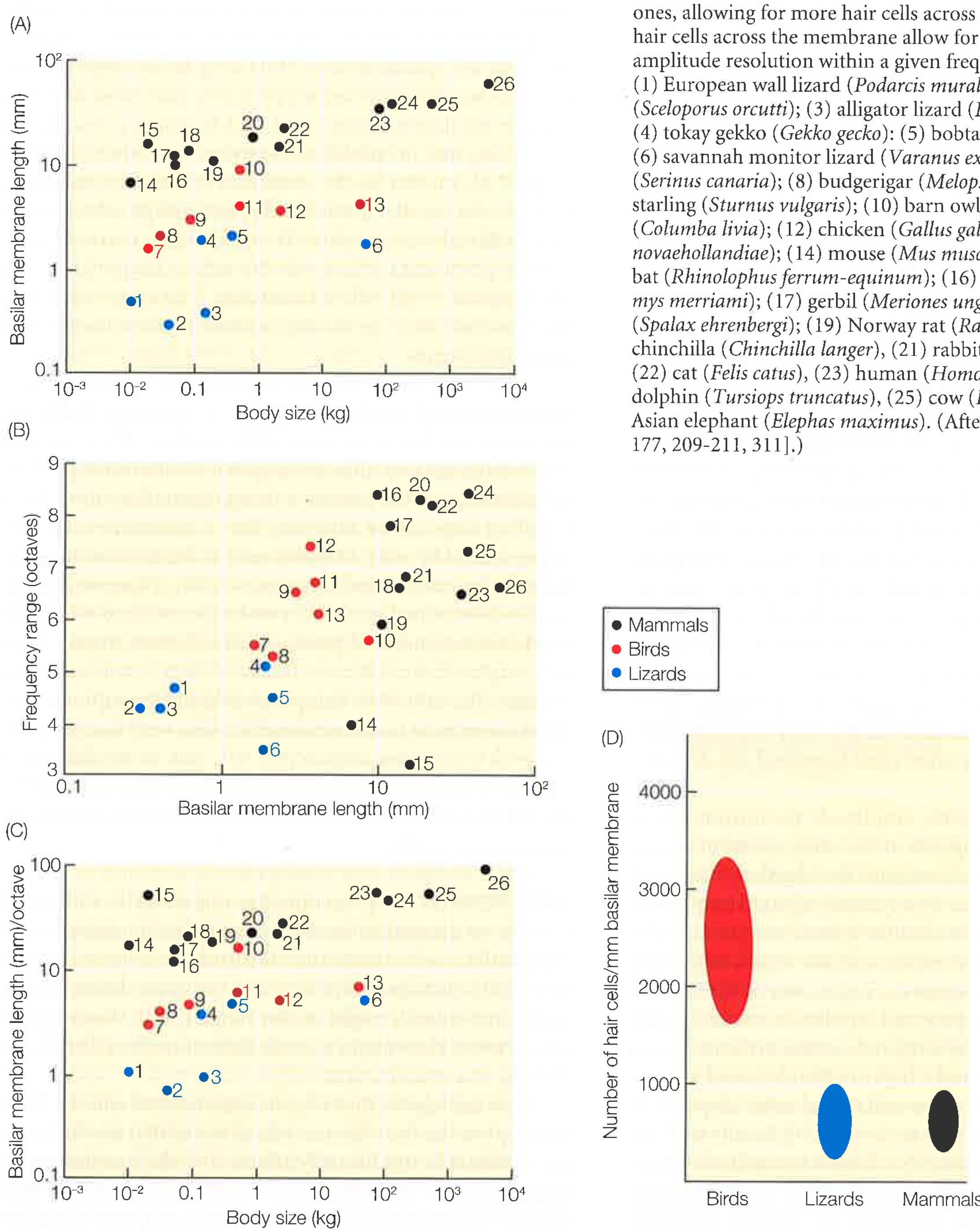
FIGURE 3.42 Body size and vertebrate tonotopic inner ear design (A) Animals with larger body sizes usually have a larger inner ear (here measured by the length of their basilar membrane). However, mammals (black), which curl their cochlea, have longer basilar membranes than birds (red) or lizards (blue) 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].

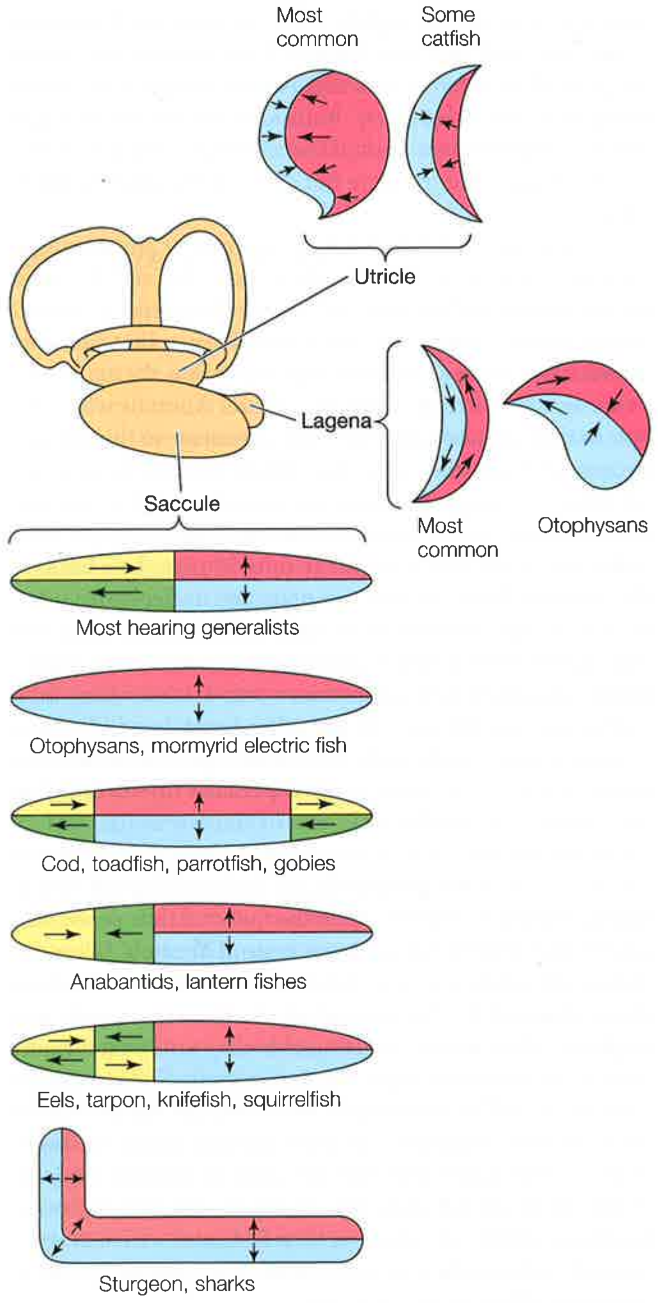
TEMPORAL RANGE AND RESOLUTION A major constraint on both temporal range and resolution in animal ears is that some interval must elapse between two sounds or sound components in order for the receptor (or brain) to consider them as separate events. How long an interval is necessary? All acoustic instruments 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 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].

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].)



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

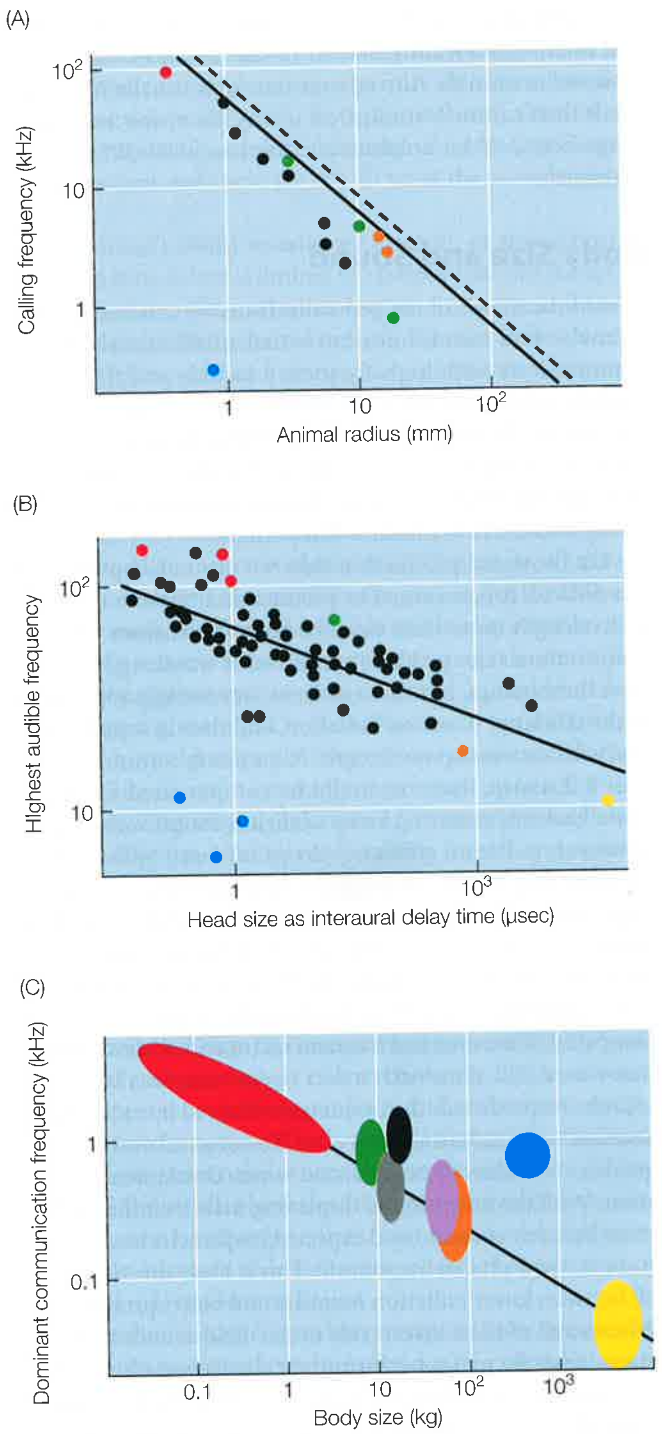


FIGURE 3.44 Three explanations for inverse correlations between favored sound frequencies and body size (A) Relationship between male advertising call frequency and body size in a sampling of terrestrial insects. Also shown are minimal frequencies for monopole (solid line) and dipole (dashed line) sources 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 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
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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.