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Echolocation in Bats

Bats have a bad reputation. The mere mention of bats usually conjures up an image either of darting furry missiles streaking about in attics or caves, or of vintage vampire movies in which an intruding bat sooner or later is transformed into Bela Lugosi. This tawdry reputation is unfortunate, since it might prevent all but the most committed students from learning about the sophisticated navigational tricks these remarkable animals use as they relentlessly track down their prey on the wing in total darkness.

Along with rodents, bats are the most numerous order of mammals and are the most diversified of any order of animals on Earth. This evolutionary success comes as no surprise when one appreciates the advantage bats have over virtually all other insect-eating vertebrates: They are powerful fliers and they can echolocate. Bats achieve this latter advantage by emitting a series of brief ultrasonic sounds from their mouths or noses and then perceiving objects in their immediate environment from the echoes of these sound pulses that return to their ears. The ability to use ultrasonic echoes to “light up” an invisible world and interrogate it with an acoustic flashlight gives an echolocating bat the ability to exploit the plentiful resources of night-flying insects with little or no competition from other insect-eating predators pursuing the same food source.

Bats are of the order Chiroptera, of which there are two suborders: **Megachiroptera** are large bats with big eyes and simple ears. There are about 150 species of these bats, which are generally vegetarian and usually have no echolocating ability. The other suborder, **Microchiroptera**, is much larger in number, having approximately 800 species. These are small bats (usually with thumb-sized bodies and about a 14-inch wingspan) with small eyes and complex ears. Most of the Microchiroptera are insectivorous, and all of them echolocate. Bats are found almost everywhere in the world, except for the chilly climates of the Arctic and Antarctic continents. All bats can see to varying degrees, and non-echolocating species have more prominent eyes.

The diets of bats vary considerably and are often determined by what is available from season to season or even from one night to the next. Bats in temperate climates eat mainly insects, whereas bats from other environments eat frogs, mice, birds, fish, and scorpions, in addition to fruit, nectar, and pollen. The insect eaters are usually the most skillful fliers; most of these bats are on the wing continuously while hunting their prey. In a typical evening an insectivorous bat will eat about 500 mosquito-sized insects; that's a lot of bugs. A small number of species regularly eat fish; these bats soar over the water and use echolocation to detect ripples created by the fins or heads of fish at the surface of the water; some catch their aquatic prey with weblike specializations of their feet. Finally, yes, a few species of bats do feed on blood, usually of birds, domestic cattle, or the occasional other handy mammal. However, these species are quite rare—only about three in number—and are found only in Central or South America.

Bat roosts are often found in caves, rock crevices, and trees, as well as available attics or barns, and of course, a belfry now and then. Like the barn owls that we will discuss in Chapter 3, bats spend most of their daylight hours in their roosts, venturing out only at night in search of an evening meal. Also like barn owls, bats rely on a keen sense of hearing to track their prey. However, a major difference between barn owls and bats is that bats reflect their own emitted sounds off environmental objects, essentially inducing their prey to reveal themselves, while owls rely on their prey to make a noise in order to detect them. It is this remarkable ability of bats to use echolocation as a device for the detection, tracking, identification, and capture of prey that is the focus of this chapter.

The Behavioral Repertoire of Bats

Although the agility and quickness of bats in avoiding stationary objects and capturing insects had been appreciated for centuries, not until the pioneering studies of the Italian biologist Lazzaro Spallanzani beginning in 1794 were the first critical clues revealed as to the mechanism underlying the bat's ability to negotiate its environment. Spallanzani found that bats that were deprived of sight could still navigate normally, avoiding obstacles in a room as usual, but

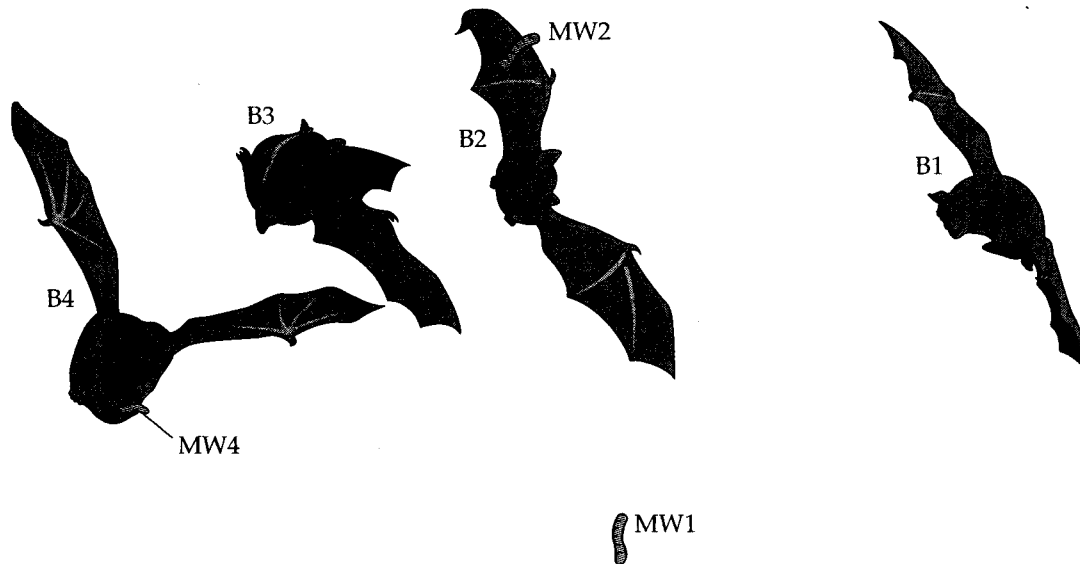
bats whose ears were plugged were dramatically impaired, often colliding with obstacles that were easily avoided by normal bats. Thus he made the critical discovery that bats somehow use their hearing to detect objects and movement in the environment. Not until more than a century later, however, did a young neurobiologist, Donald Griffin, begin a landmark series of studies that solved the mystery of echolocation.

In 1938, Griffin, with a colleague, G. W. Pierce, used a newly invented device that could detect very high frequencies (well beyond those that could be heard by the human ear) and discovered that bats emit high-energy ultrasonic pulses when flying in a room. Griffin correctly reasoned that, because ultrasound is attenuated rapidly in the atmosphere, it would be useful only for tracking prey or avoiding objects that were relatively nearby. Consistent with this idea, Griffin and his colleagues made a critical observation: Flying bats normally emitted pulses at a rate of about 10 to 30 per second, but when bats flew near an object, they increased their pulse rate dramatically, from 50 to 250 per second. Using this increase in pulse rate as a measure of the bat's acuity, Griffin found that the bat could detect and avoid thin strands of wire less than 1 mm in diameter. He went on to show (as Spallanzani had shown earlier) that plugging the bat's ears severely impaired its ability to avoid objects. Equally importantly, he found that preventing the bat from emitting a cry by taping its mouth closed also dramatically impaired object avoidance by the bat. Thus Griffin's experiments showed that the sounds the bats were hearing during flight had to be the echoes of their own emitted ultrasonic pulses, which were reflected off the wires in their flight paths. On the basis of this insight, Griffin coined the term **echolocation** to describe the process by which bats navigate within their environment.

Subsequent behavioral experiments have revealed the incredible precision of object detection and recognition by echolocating bats. For example, in a now classic experiment by Griffin and colleagues, flying bats were found quite able to discriminate between mealworms tossed in the air (which the bats readily captured and devoured; Figure 2.1) and similar-sized plastic discs that, when tossed in the air, would reflect echoes similar to those of the mealworms. The bats quickly learned to ignore the plastic discs.

Cues That Bats Use to Decode Their Acoustic Environment

As we shall see in this section, bats are capable of detecting extremely small details of objects in their environment. What features of the echo might allow the bat to make such fine discriminations while on the wing? To address this question it is first important to appreciate that bats can emit two kinds of ultrasonic signals. One kind is a short pulse (less than 5 ms long) that sweeps across a wide range of frequencies, from about 100 Hz to 25 kHz. This is called a frequency-modulated pulse, or an **FM sweep**.



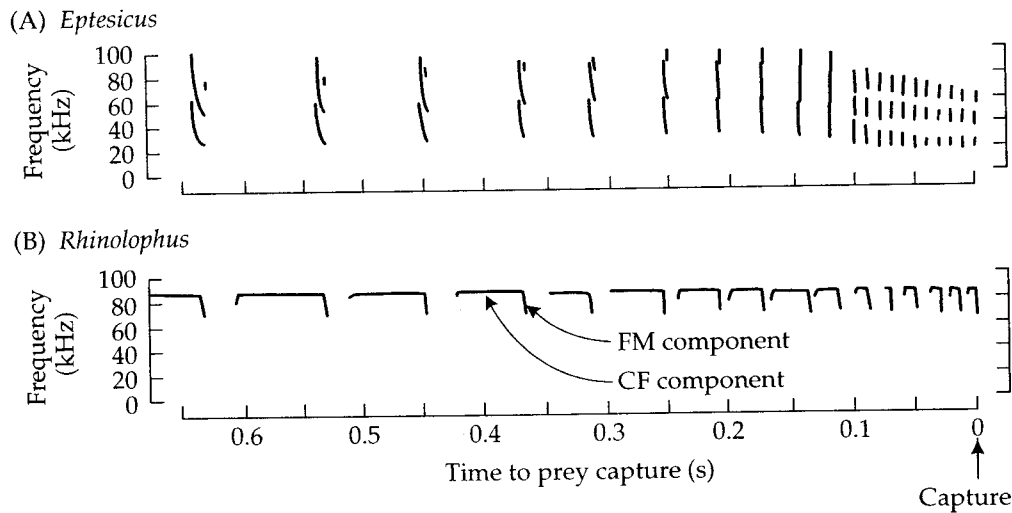
2.1 A bat capturing its prey

Drawings made from photographs of a bat capturing a mealworm tossed into the air. "B1" through "B4" and "MW1" through "MW4" reflect the relative positions of predator (bat) and prey (mealworm), respectively, throughout the sequence. (MW3 does not appear because the mealworm has been scooped up in the bat's tail at B3.) After Webster and Griffin 1962.

A typical example of this type of pulse being emitted by the big brown bat, *Eptesicus fuscus*, is shown in the sonogram in Figure 2.2A. Because an FM sweep covers a wide range of frequencies, it is also called a **broadband signal**. The second kind of ultrasonic signal used by bats consists of a **constant frequency (CF)** and is typically much longer in duration (5–30 ms) than an FM pulse. A CF pulse is illustrated by the cry of the horseshoe bat, *Rhinolophus ferrumequinum*, in Figure 2.2B. Many bat species use combinations of both types of pulses, giving rise to three basic categories of bats: CF bats, FM bats, and combined CF-FM bats (actually the horseshoe bat whose ultrasonic signals are illustrated in Figure 2.2B is a CF-FM bat; notice the brief FM sweep at the end of each CF pulse).

Two other important features of bat cries can be seen in Figure 2.2A. First, notice that for the FM sweeps, in addition to the **fundamental frequency** there are first and second **harmonics** (harmonics are simple multiples of a fundamental frequency). As we shall see later in this chapter, these harmonics are extremely important for bats in their detection and pursuit of prey. The second important feature of the sonograms in Figure 2.2 is that the bats, as they approach their prey (in both cases insects), increase the repetition rate and decrease the duration of their cries. This is a highly typical pattern that we will discuss shortly.

Using the kinds of sound pulses (and their resultant echoes) that we have described here, what kinds of information do bats use to detect various attributes of both moving and stationary objects in their acoustic environment? Each target has multiple features, each with its own acoustic signature. We discuss



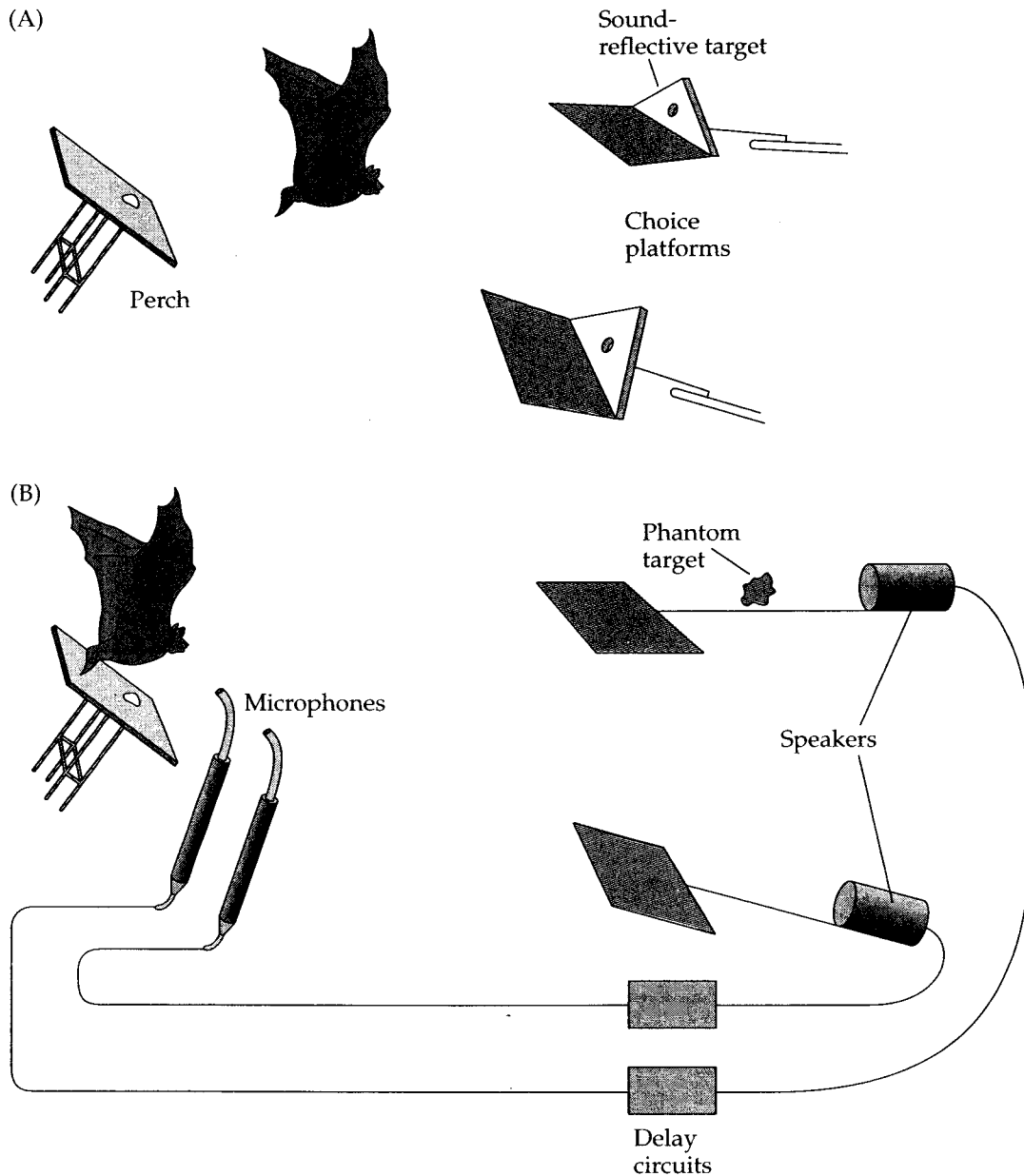
2.2 Bats emit ultrasonic signals

The ultrasonic signals that bats emit can be recorded and plotted as shown. Here bat cries were measured as bats approached and captured their prey. (A) Some bats, like *Eptesicus*, use primarily FM signals. (B) Other bats, like *Rhinolophus*, use a combination of FM and CF signals. Note how the rate of the cry goes up dramatically as the bats near their prey. After Camhi 1984; data from Simmons, Fenton, and O'Farrell 1979.

each of these features—distance, subtended angle, absolute size, azimuth, elevation, and velocity—in the sections that follow.

Distance. Bats measure distance by comparing the time between an emitted sound pulse and its returning echo. Rapid FM sweeps are especially well suited for determining target distance (also called target range) because both the emitted pulse and the returning echo sweep very quickly through a wide range of sound frequencies (as we shall see, sweeping across a wide frequency range also gives useful information for target identification). Thus each frequency within the FM sweep provides a single, very brief frequency point at which the bat can make a pulse–echo time determination.

A creative behavioral experiment by James Simmons illustrates clearly that the pulse–echo delay provides distance information to the bat. FM bats (*Eptesicus*) were trained to obtain a food reward by flying to one of a pair of platforms to which sound reflective triangular “targets” had been affixed. The platforms were at different distances from the bat’s home perch, and only one of the platforms, the more distant one, was the reward site (Figure 2.3A). The near and far platforms were randomly alternated left and right so that the bat could not use these position cues to find the reward. The bats were very accurate in their distance perception; they could learn to discriminate platforms that were separated along a distance axis by only about 5 cm. Then Simmons played a clever trick on the bat. He removed the targets from the platforms and mounted microphones on the bat’s perch that recorded the cries it emitted when choosing platforms. Simmons passed



2.3 Bats determine distance by evaluating the pulse–echo delay

(A) A bat can be trained to choose the closer of two platforms to obtain a food reward. (B) Speakers adjoining each platform can play back “phantom” echoes following a bat’s cry. In this way it can be shown that bats use the delay between a pulse and an echo to determine distance. After Camhi 1984; data from Simmons 1973.

the recorded cries through a variable delay circuit that allowed him to present these pulses at any time he wanted following the bat’s own cry; thus he created synthetic, or phantom, echoes (Figure 2.3B). When the bat was then tested with echoes whose delays corresponded to two “phantom” platforms at different distances, it correctly chose the pulse–echo delay corresponding to the more distant platform; thus this delay was clearly an important signal for target distance to the bat.

Finally, Simmons reduced the delay times systematically and found that bats could discriminate pulse–echo delays of only 60 μ s, corresponding to distances of only 10 to 15 mm. Thus these behavioral experiments showed that bats are extremely accurate in using pulse–echo delay for ranging information. But, as we shall see shortly, the best is yet to come from Simmons’s behavioral experiments.

Subtended angle. This parameter (also called the angular size) is determined by the loudness of the echo. However, loudness alone is insufficient to determine the true size of an object, since objects of identical angular size (loudness) can be either small and very close, or big but far away.

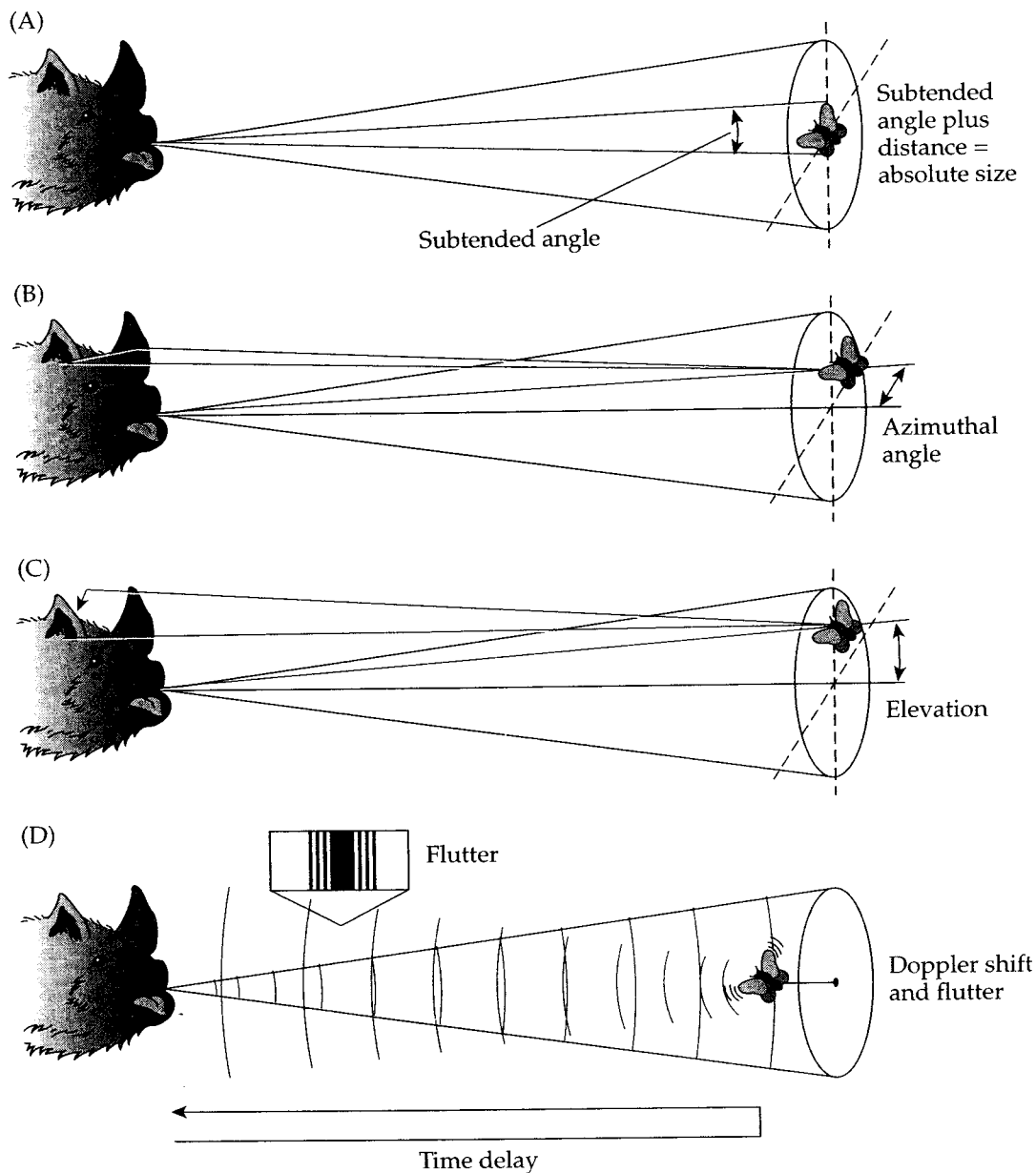
Absolute size. Bats compute the absolute size of an object by combining distance information (delay) and angular size information (amplitude) (Figure 2.4A). Thus if the bat hears an echo that is very small in amplitude but has a very short delay, it knows that a tiny object (e.g., a moth) is nearby; an echo with the same amplitude but a very long delay might indicate that a large object (e.g., a bird) is some distance downrange.

Azimuth. Like barn owls (see Chapter 3), bats are thought to use predominantly binaural cues for determining where an object is on the horizon (Figure 2.4B). However, recent cellular evidence indicates that bats can also obtain some azimuthal information from only one ear.

Elevation. Bats use two basic strategies to determine elevation. Since they can move their ears, many bats compare echo amplitudes with their ears in various positions. In addition, some bats have specialized flaplike structures within their pinnae to provide additional elevation information (Figure 2.4C).

Velocity. For animals that hunt on the wing and whose prey are also in flight, it is critical to be able to accurately estimate not only absolute velocity, but also the relative velocity of the predator with respect to the prey. Bats compute both their absolute and relative velocities by analyzing the **Doppler shift** of their echoes’ frequencies. We have all experienced the Doppler shift of a sound. Imagine standing on a platform and hearing a train go whizzing by, all the while sounding its bell. As the train approaches the sound appears higher, and as it withdraws the sound appears lower. However, the actual frequency of the bell is unchanged (as it would be heard, for example, by the train’s engineer, who remains at a fixed distance from the sound source).

The Doppler shift of the perceived frequency of the train’s bell is due to the fact that, in addition to the bell’s constant frequency, the train’s movement (e.g., toward the listener) brings the bell’s sound to the listener’s ear at a *higher* frequency than that of the bell alone. Now, for our bat on the wing chasing a flying insect, an echo that returns at a slightly higher frequency than that of the bat’s emitted call tells the bat that it is gaining on its target; conversely, a returning echo frequency that is lower than the call indicates that the target is outdistancing the bat (Figure 2.4D).

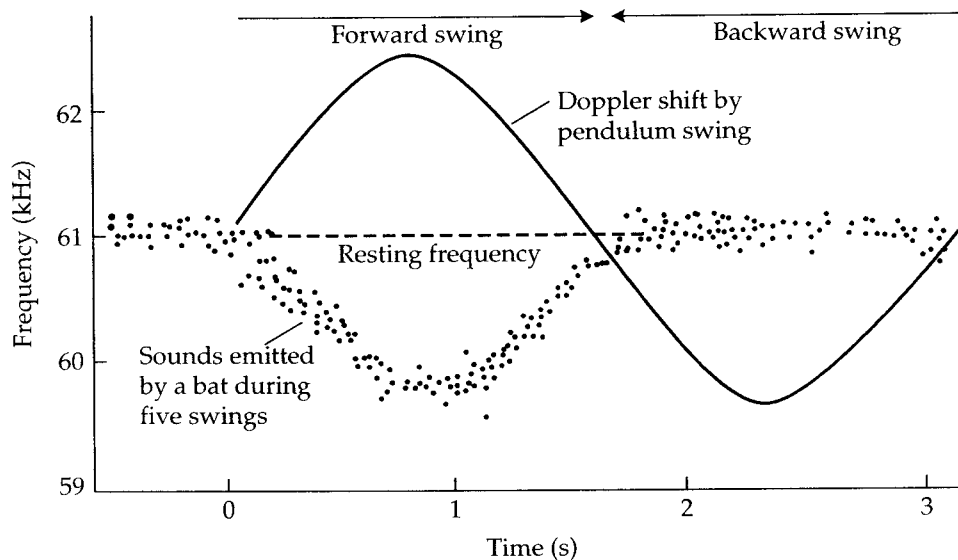


2.4 Features of a bat's cry that help locate and identify a target

Different aspects of a bat's cry provide important information for target location and identification. (A) The subtended angle provides loudness information. Together with the pulse-echo delay (which encodes distance), this parameter can inform the bat of the size of an object. (B) The azimuthal angle tells the bat where the object is in the horizontal plane. (C) Elevation is determined by the angle of the sound, which the bat determines by moving its ears up and down. (D) Doppler shift is used to determine the relative velocity of a target, as well as the flutter of the target (which aids in target identification). After Suga 1990.

Earlier we saw that FM signals are well suited for range analysis. Now we come to the value of CF signals: They are extremely well suited for Doppler shift analysis because the long CF pulses (typically 10–100 ms long) emitted by bats permit an ongoing, very sensitive analysis of small shifts in that sin-

gle (narrowband) frequency, which is the essence of a Doppler shift analysis. In addition, long CF pulses significantly increase the range at which targets can be located because they greatly add to the total energy of the bat's call. Bats that use Doppler shift analysis are extremely sensitive to a very narrow range of frequencies immediately around the CF component of their emitted pulses. This increase in sensitivity to a selective narrow range of frequency is sometimes called the **acoustic fovea** of the bat (by analogy to the high sensitivity of the fovea of the retina in the visual system). As we shall see later in this chapter, the acoustic fovea is due to a disproportionate representation of this CF frequency within the auditory system all the way from cochlea to cortex. One of the best-studied examples of Doppler shift analysis has been in the horseshoe bat *Rhinolophus*, whose hearing is extremely sensitive to 83 kHz, the frequency of its CF pulse (see Figure 2.2B). This bat (as well as all other CF bats) encounters an interesting problem while flying because the CF component of its echo has a frequency not of 83 kHz, to which the bat is most sensitive, but rather a higher, Doppler-shifted frequency somewhere between 83 and 87 kHz. To solve this problem the bat lowers the frequency of its call to prevent the echoes from returning at a frequency outside the bat's acoustic fovea (83 kHz). Thus while flying, the bat constantly adjusts its CF call frequency just enough to have the echo always return at 83 kHz, so as to keep the echo in the bat's most sensitive hearing range. This adjustment is called **Doppler shift compensation**. An example of Doppler shift compensation for another bat, the mustached bat, is shown in Figure 2.5.



2.5 Doppler shift compensation

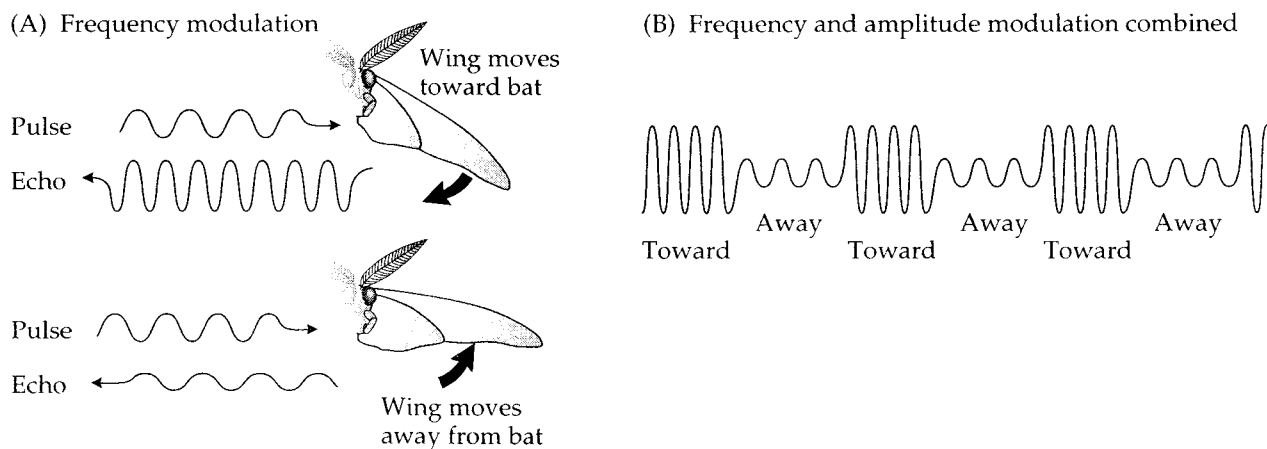
In this experiment a bat was placed on a swing. At rest the bat emitted a cry at about 61 kHz (each cry is indicated by a single dot). Once the swing started forward, the bat lowered the frequency of its cry to keep the returning echo in its acoustic fovea. The frequency returned to normal as the swing slowed down before swinging back the other way. No Doppler shift compensation occurred when the swing was going backward. After Suga 1990.

In addition to keeping the echo in the bat's most sensitive range, Doppler shift compensation has the advantage of keeping the bat's emitted sound pulse (which is very loud) outside the bat's most sensitive range, while keeping the softer echo, which is the critical information, inside that range. In this sense Doppler shift compensation greatly improves the signal-to-noise ratio for this critical frequency-based analysis.

In addition to the value that Doppler shift analysis has for velocity determination, it has another great value to the bat: It is very useful in sensing the **flutter** of a target (Figure 2.6). This feature is of obvious significance to the bat, since many of its prey are insects whose wingbeats produce fluttering echoes. Doppler analysis is good for flutter detection because the CF signal produces a strong echo (called an **acoustic glint**) when it strikes the beating wing at right angles but a weaker echo when it strikes the wing at lesser angles (as would occur during repeated wingbeat cycles). The result is a subtle frequency and amplitude modulation of the returning Doppler-shifted echo.

Just how subtle is quite amazing. Using a variant of the two-choice procedure shown in Figure 2.3A, experiments showed that horseshoe bats can discriminate simulated wingbeat oscillations of 35 cycles/s. The Doppler shifts caused by these minute oscillations would modulate an 83,000 cycle/s echo by only about 30 cycles/s! Thus the bat can discriminate minuscule fluctuations in sound frequencies with incredible accuracy.

An observation by Gerhard Neuweiler illustrates the value of flutter detection in the natural environment. Some horseshoe bats forage for insects in



2.6 Using Doppler shift to determine flutter

Doppler shift provides a mechanism for determining the amount of flutter an object exhibits. (A) Part of flutter determination is derived from frequency modulation of the cry: As the wing of prey such as a moth moves toward the bat, the echo increases in frequency; the opposite is true as the wing moves away from the bat. (B) Flutter can also be determined by amplitude modulation of the echo: As the wing moves toward the bat, the echo will be slightly louder than as the wing moves away from the bat. Amplitude and frequency modulation are combined in flutter analysis.

forests by hanging upside down from tree limbs while constantly acoustically scanning the environment for flying insects. The bats take off in pursuit only after detecting an insect. Neuweiler and colleagues observed that during the stationary scanning phase of prey detection, the bats emitted only long CF calls with no FM component, showing that they detect fluttering insects by the CF signal alone. The bats then included an FM component in their call when distance determination (echo delay) was important for tracking and capturing the insect.

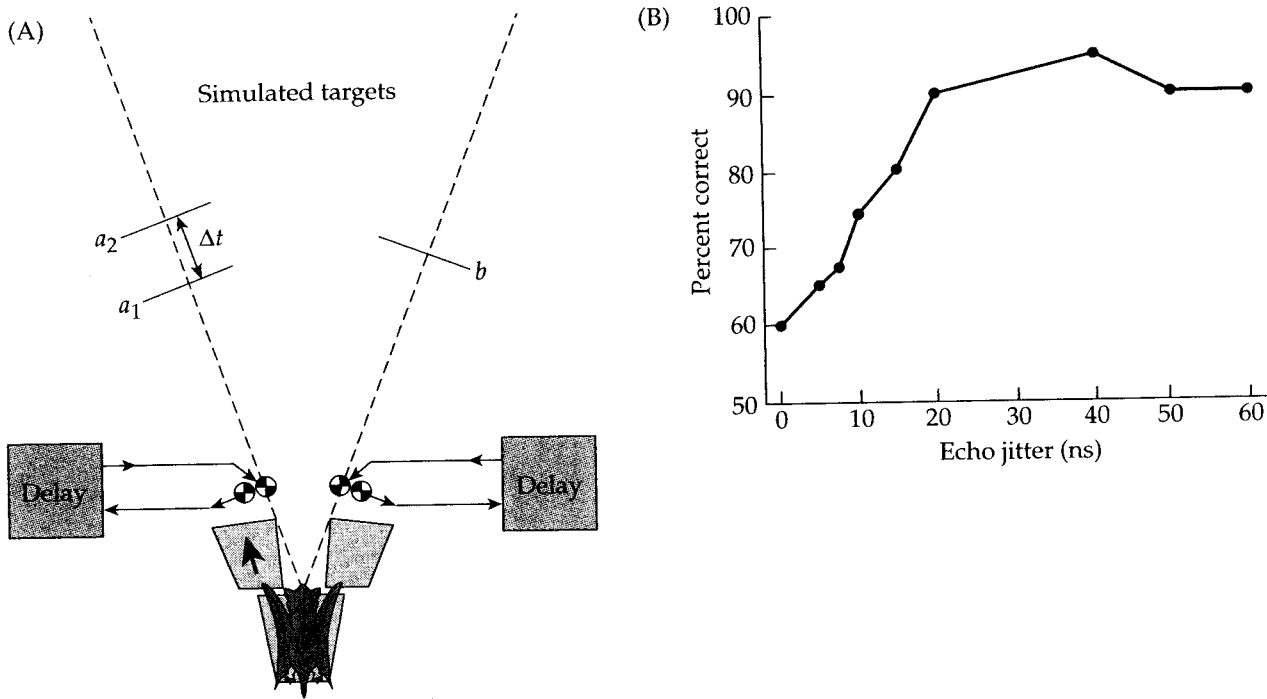
Thus far we have seen that bats use CF and FM components of their calls to different advantages for different aspects of prey location. But before we leave the behavioral side of the story, another observation warrants mention. Recall that Simmons showed that bats can discriminate temporal differences in pulse–echo delays of about 60 μ s (see Figure 2.3). Simmons later developed a variation on his two-speaker paradigm (Figure 2.7A) and trained the big brown bat, *Eptesicus*, to detect a target that “jitters” (rapidly switches) in range between two distances. By systematically reducing the time interval between jitters, Simmons could measure the bat’s threshold for perceiving the jitter.

In a variety of experiments, Simmons and his colleagues found that these bats could perceive echo-delay changes as small as 10 to 12 ns (i.e., a few millionths of a second!) in the jitter task (Figure 2.7B). These delays would correspond to distance changes in target range of only about 2 μ m (i.e., 2 millionths of a meter). It is hardly likely that the bat needs to resolve such minute differences in target distances to obtain simple distance information. Simmons has suggested the creative idea that bats use this incredible resolving power in echo-delay changes to scan and recognize the “acoustic texture” of objects, perceived in terms of a fine-grained range profile. Thus the bat can use its high temporal resolution to determine the actual physical attributes of an object in its environment, in essence acoustically “feeling” the object to determine its shape and texture.

The hunting bat

Now we know how bats can use their sonar capabilities to detect objects in their nocturnal environment, but how are these skills coordinated in the bat’s primary passion in life: capturing prey? An example of the pattern of echolocation during a typical bout of prey catching is shown in Figure 2.8: Shelley Kick and Simmons took a series of stroboscopic photographs of a bat tracking an insect, while simultaneously recording the bat’s calls. This example illustrates the three basic stages of pursuit and capture.

The first stage is the **search stage**, during which the bat emits species-typical pulses at a steady, low repetition rate of about 10 per second. The habitat within which the bat forages plays a major role in the type of signal employed in this stage: Bats that hunt in dense forests or in vegetation close to the ground typically have calls with a strong FM component, or they may have only an FM sweep. These characteristics are consistent with the bat’s need to gain considerable distance information about the nature of its target among background



2.7 Using jitter to reveal the bat's sensitivity to pulse-echo delays

A variant of the task shown in Figure 2.3 allows precise behavioral measurements of the bat's sensitivity to pulse-echo delays. (A) The bat must discriminate between an acoustically "jittering" target (a_1 - a_2 , which simulates a target rapidly moving slightly closer and farther away; Δt = change in distance between the two phantom targets, which constitutes the size of the jitter interval), and a fixed target (b). The bat is extremely sensitive to very small differences in the range of a target. (B) The bat performs well above chance, with delays in the range of only 30 ns. After Simmons 1989.

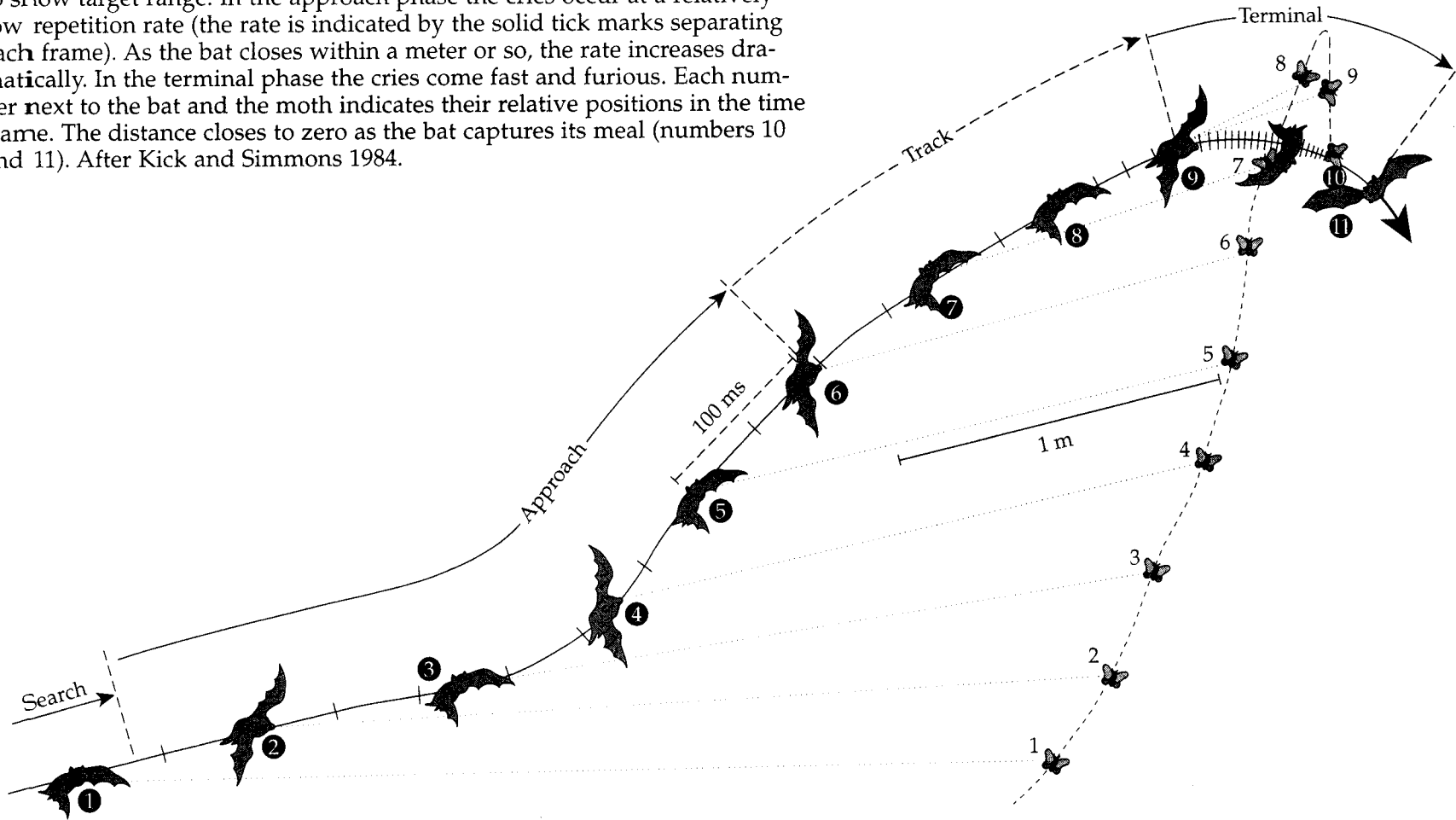
clutter. Bats that hunt in more open spaces are more likely to emit long CF pulses, which are better suited for long-range detection. In the search phase, bats can detect objects up to about 5 m away.

The second phase is the **approach stage**, typically signaled by the bat's turning its head and ears toward the target and increasing the repetition rate of its call to about 50 pulses per second. Usually in this stage the pulse length decreases in CF bats and the FM sweep steepens and increases in bandwidth in virtually all bats, presumably to increase range and directional information as the bat closes in on its target.

The final stage is the **terminal stage**, which is characterized by a sudden increase in pulse repetition rate of up to 200 per second in FM bats and 100 per second in CF-FM bats. This final adjustment occurs because when the distance between bat and prey is very close, the range and angular position of the bat change very quickly and need to be constantly updated by the rapid emission of signals to ensure accurate tracking. Once the bat is upon its prey, it scoops it up in its wing or tail (see Figure 2.1) and consumes it on the spot, soon turning its attention to the next insect at hand.

2.8 Stages of prey pursuit and capture

Images are based on stroboscopic photographs taken at 100 ms intervals. The thin dotted line connects corresponding images of the bat and the insect to show target range. In the approach phase the cries occur at a relatively low repetition rate (the rate is indicated by the solid tick marks separating each frame). As the bat closes within a meter or so, the rate increases dramatically. In the terminal phase the cries come fast and furious. Each number next to the bat and the moth indicates their relative positions in the time frame. The distance closes to zero as the bat captures its meal (numbers 10 and 11). After Kick and Simmons 1984.



Neural Mechanisms of Echolocation

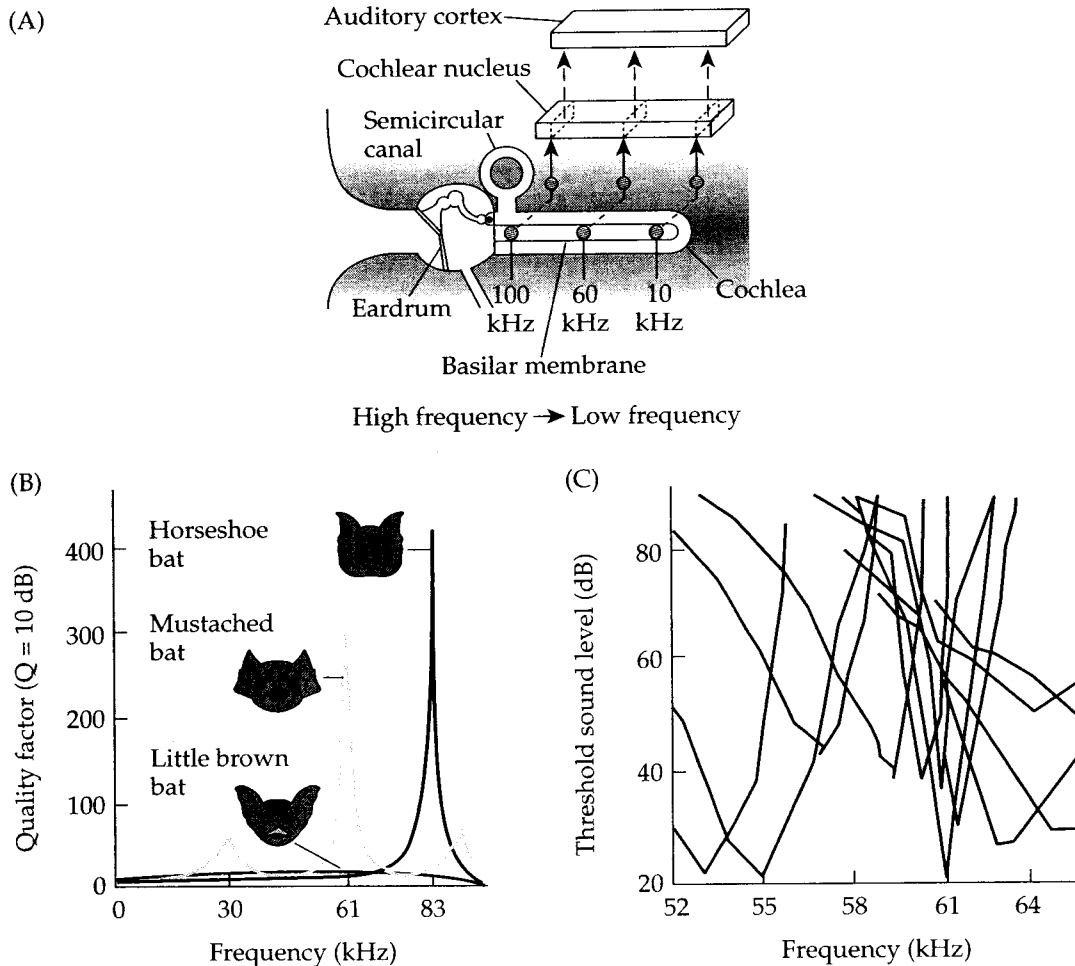
Many regions in the central nervous system of the bat are sites for the processing of auditory signals. As one ascends to higher levels, the processing becomes more specialized and complex, but important specializations relevant to echolocation exist right at the beginning of the auditory system in the structure responsible for transducing sound, the cochlea, located in the inner ear.

The basilar membrane and primary sensory neurons

The cochlea houses the **basilar membrane**, the thin elongated membrane that vibrates in response to sound hitting the eardrum (Figure 2.9A). Vibration of the basilar membrane stimulates small hair cells, which in turn excite primary auditory neurons in the spiral ganglion; the auditory message is then transmitted to the central nervous system. Excursions of the basilar membrane must encode all aspects of sound reaching the bat's ear. For example, loudness is coded by the rate of discharge of the hair cells, and the duration and temporal features of the sound are coded by the patterns of hair cell discharge. The frequency of the sound signal is encoded by the *place* on the basilar membrane that is maximally vibrated by the sound (Figure 2.9A): High frequencies vibrate nearest the eardrum (the base), low frequencies farther out on the membrane (the apex). In bats that use long CF pulses (e.g., for Doppler shift analysis), a striking specialization (an abrupt thickening and lengthening) of the basilar membrane is located at exactly the place where the frequency of the CF component of their echoes will be cast in response to Doppler shift compensation. The exact place of this specialization on the basilar membrane depends on the species-typical frequency of the CF component. The important point is that even at the first stage of neural processing in the basilar membrane, the bat's auditory system is specialized for echo analysis. As mentioned earlier, by analogy to the retina of the visual system, the specialized region on the basilar membrane is sometimes referred to as the acoustic fovea.

An additional specialization exists in the primary auditory neurons of the bat, which are extremely sharply tuned to the frequency of the CF component of the call. That is, the frequency at which some of these neurons respond best is narrowly focused around the CF component (Figure 2.9C). Moreover, because of the disproportionate length of the acoustic fovea on the basilar membrane, many more sensory neurons encode information from this region. Thus, from the basilar membrane at each stage to higher brain regions, a disproportionate number of neurons are dedicated to processing sounds in this critical frequency range.

A final specialization that begins at the ear and is recapitulated at higher neural levels as well, addresses a potentially critical problem for the bat: Its emitted call is very loud (between 90 and 110 dB at about 10 cm from the mouth), and the returning echo is much fainter, but it is the echo that the bat must perceive. How does the bat avoid swamping its very sensitive auditory system by the emission of its own call? Why are the bat's ears not still ringing



2.9 The bat's sensitivity to frequency

(A) The frequency of a sound is first processed on the basilar membrane of the cochlea. It is then further processed at higher stages in the auditory system. (B) Different species of bats are most sensitive to different frequencies. For example, the mustached bat is most sensitive to 61 kHz, while the horseshoe bat's most sensitive frequency is 83 kHz. (C) The primary auditory neurons of the bat are tuned to species-specific preferred frequencies. This example shows the response thresholds for 12 neurons of a mustached bat. For each neuron the threshold drops precipitously at a specific frequency. The plunge is especially steep for neurons that respond to frequencies near 61 kHz (the CF_2 harmonic). After Suga 1990.

from its own call when the echo of that call returns and must be detected? The bat's solution to this problem is quite clever: It dramatically (and very briefly) reduces its auditory sensitivity *just during* the emission of a call.

FM bats and CF bats achieve this trick somewhat differently. FM bats, which emit very short signals, use two strategies: (1) They briefly (for about 5–10 ms) contract their middle ear muscles during a call, thereby attenuating the actual loudness of the signal, and (2) at an upstream auditory center (the nucleus of the lateral limniscus) the call-induced auditory signal is further attenuat-

ed. Thus the bat actively reduces its auditory processing so as to be less sensitive to its own call and thereby more responsive to the echo of that call.

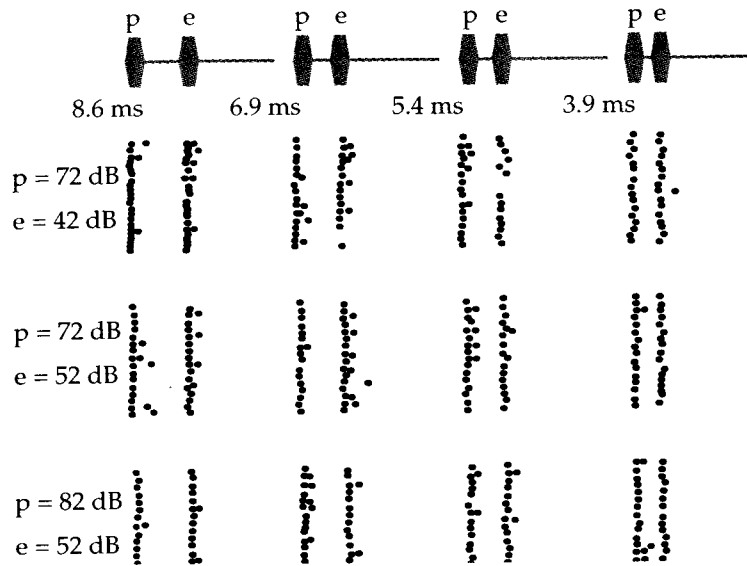
CF bats have a related but different problem: Since their calls overlap with the returning echo (which is optimal for Doppler shift analysis), they cannot afford to shut down auditory processing during a call because they would also miss important features of the echo. The way CF bats solve the problem is in some ways more straightforward than the approach of FM bats. CF bats simply are relatively deaf to the frequency of their emitted calls, which are typically a few kilohertz lower than the frequency to which they want to be very sensitive, the Doppler shift-compensated echo (recall that the bat keeps this echo in its acoustic fovea by lowering the frequency of its emitted call). Thus CF bats, in large measure as a result of the structure of their basilar membranes, are strongly stimulated by their echoes but weakly stimulated by their own calls. Of course, many species of bats (like the horseshoe bat, whose ultrasonic signals are shown in Figure 2.2B) use a combination of CF and FM calls; these bats employ a combination of the strategies we have described here to ensure that they reduce their own sensitivity during the emission of a sound pulse.

The inferior colliculus

Another critical feature of auditory processing of echo information is the encoding of the time interval between an outgoing call and the returning echo. It appears that interneurons in a midbrain auditory structure, the inferior colliculus, are well suited for this task. George Pollak and his colleagues have extensively examined neurons in the inferior colliculus and found that they are exquisitely sensitive to small temporal differences in incoming auditory signals, responding to pairs of FM pulses with remarkable fidelity. This is exactly the feature one would want in an interneuron that acts as an accurate time marker for the delay between a call and an echo.

As shown in Figure 2.10, inferior colliculus neurons have a very fixed response time (their response latency) both to the first of two FM pulses (simulating a call) and to the second pulse (simulating an echo). Each response typically consists of only one or at most two action potentials; such a phasic response is important for encoding brief signals that occur in succession.

Two other features of the response profiles shown in Figure 2.10 warrant mention: First, as the pulse-echo delay is increased, the neurons faithfully reflect the increase across a broad range of biologically realistic delays. Second, as the intensity of either the pulse or the echo is increased, the response latency remains remarkably constant. This is a highly important and specialized feature of these collicular neurons, since most neurons in sensory systems respond with a progressively shorter latency to stronger stimuli. This typical response would create a problem for delay-coding neurons of the inferior colliculus because it would introduce a huge source of error if loud calls had shorter latencies than their much weaker returning echoes. Pollak and his colleagues have shown that these specialized features of inferior colliculus neurons are due to two facts: (1) they are very sharply tuned to only one particu-



2.10 Sensitivity of neurons in the inferior colliculus to pulse-echo delays

Neurons in the inferior colliculus are very sensitive to pulse-echo delays. At the top, four different simulated pulse-echo delays are presented to the bat. Each pair of dots reflects the occurrence of one or more action potentials of a neuron in the inferior colliculus in response first to the pulse, then to the returning echo. The three sets of traces (from top to bottom) reflect different levels of loudness for the pulse (p) or the echo (e). In all cases the action potentials remain accurately time locked to the occurrence of the pulses and echoes. After Pollock et al. 1977.

lar frequency within an FM sweep, and (2) they have a very low threshold for firing an action potential. Thus within a full FM sweep of a call there is a family of responding collicular neurons, each responding to only a small frequency segment of the sweep, and each of these neurons also responds to the identical frequency of the returning echo. This ability to lock on to a specific frequency of both call and echo with such fidelity makes these collicular neurons excellent encoders of pulse-echo delays and hence critical for determining distance information.

Finally, as alluded to earlier, a highly disproportionate number of collicular neurons are sharply tuned to the CF component of a bat's call. Thus the acoustic fovea, which we saw was initiated in the basilar membrane, is maintained and even further expanded (in terms of the proportion of auditory neurons responsive in this narrow frequency range) at the level of the inferior colliculus. That these neurons are indeed involved in the processing of target information occurring in nature was shown by an elegant experiment by Pollak and colleagues, who tape-recorded the echoes from the wings of flying moths and showed that when they delivered this stimulus to a bat, its inferior colliculus neurons faithfully encoded the wingbeat frequency of the moth.

The auditory cortex

Once the auditory signals resulting from calls and returning echoes have been analyzed at lower auditory processing centers, they are sent to the auditory cortex, where the signals are combined in separate regions of cortex to encode individual parameters important for echolocation. Over the last two decades, Nubuo Suga and his colleagues have carried out a series of seminal studies in the analysis of cortical processing of echolocation, especially in one species, the mustached bat, *Pteronotus*. They found that different processing tasks are parceled

out among several anatomically distinct areas of the bat's cortex. In the sections that follow we will consider three such areas and the special auditory information they encode.

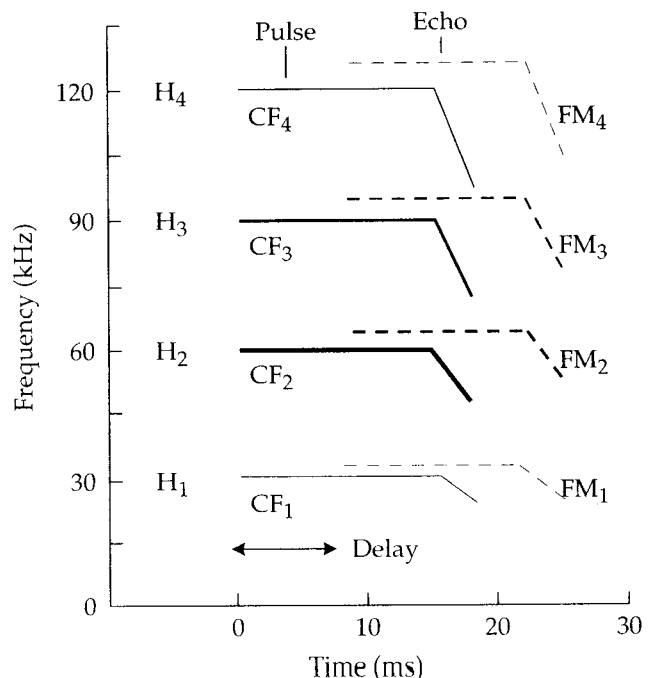
DISTANCE CODING IN THE FM-FM AREA. The call of the mustached bat consists of a long CF component followed by a short FM component (Figure 2.11). Each sound pulse contains four harmonics that differ in their relative amplitude: the second harmonic, H_2 , is the strongest, followed in decreasing order of amplitude by H_3 , H_4 , and H_1 (the fundamental frequency). Each component of this complex call structure encodes different aspects of the auditory world, which in turn are mapped onto different cortical areas. We will consider the brief FM component of the call first.

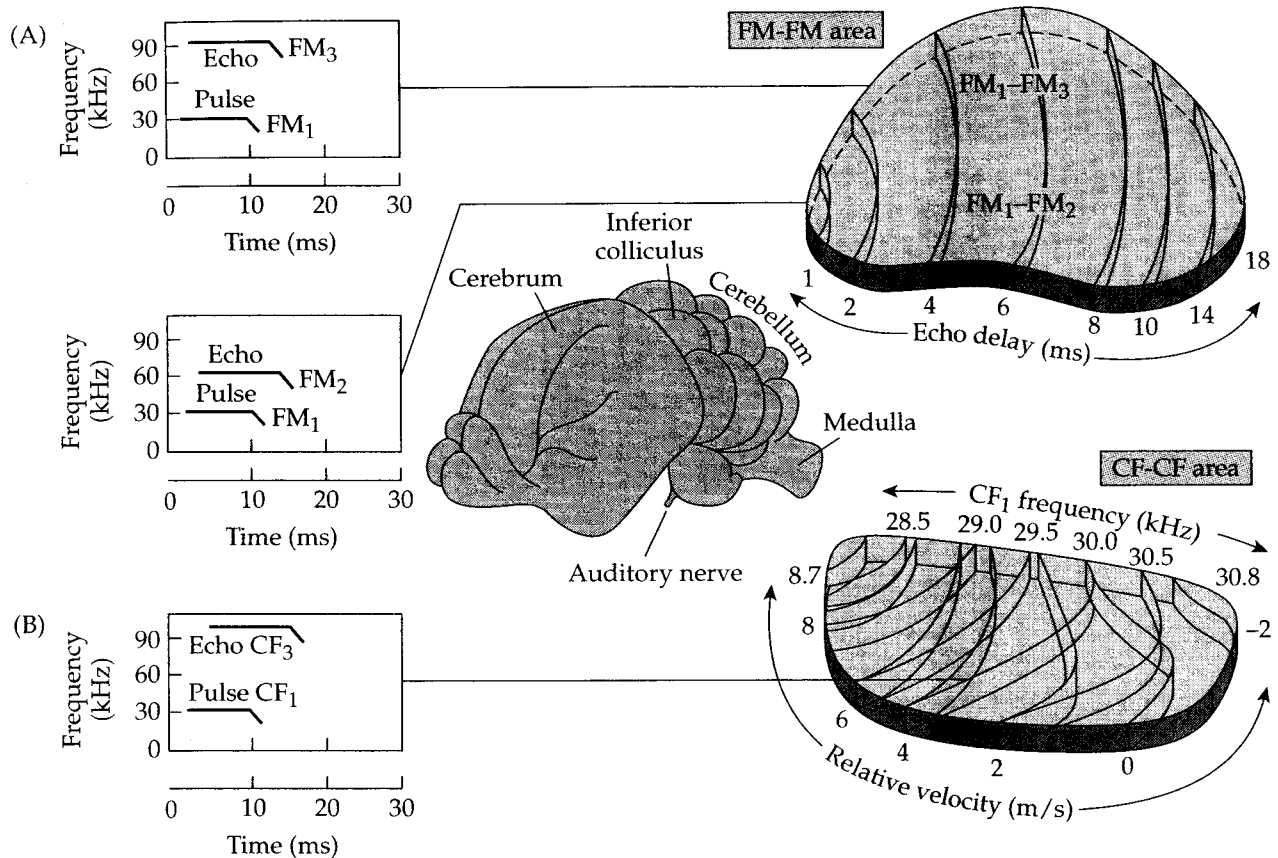
Recall that the FM signal provides the primary cue for measuring the time interval between a call and its echo, which is used to measure distance to a target. Suga and colleagues found that a family of echo delays are represented systematically in the region of auditory cortex that they call the **FM-FM area** (Figure 2.12A). In this region neurons respond poorly to a call alone, to an echo alone, or to either a CF or an FM tone alone. However, they respond extremely well to the FM component of a call followed by its FM echo, with each neuron having a particular delay it responds to best (these are called FM-FM neurons).

FM-FM neurons compare the fundamental of the emitted call FM_1 with the higher harmonics of the delayed echo FM_2 , FM_3 , or FM_4 . Each of the three types of delay-sensitive neurons occupies its own territory within the FM-FM area (see Figure 2.12A). Furthermore, each neuron is tuned not only to a par-

2.11 Components of the mustached bat's call

The cries of bats contain several harmonics (H_1 – H_4). In this case the call of the mustached bat is illustrated. Each call (solid line) and returning echo (dashed line) begin with a long CF component and end with a short FM component. The thickness of each line indicates the relative loudness at each harmonic. The second harmonic (at about 60 kHz) is loudest, and the first harmonic (the fundamental) is softest. After Suga 1988.





2.12 Auditory cortex areas specialized for echolocation

The auditory cortex of the mustached bat is specialized to detect specific combinations of pulses and echoes. (A) The FM-FM area contains neurons that respond to unique combinations of the FM components of the pulse and echo. These cells are specialized to encode distance information. They are arranged in an orderly fashion on the cortex (shown at right) so that progressive distances are represented by neighboring cells. (B) The CF-CF area encodes velocity information. These neurons are most sensitive to unique combinations of the CF component of the pulse and echo. As with the FM-FM area, the CF-CF area is arranged in orderly fashion such that neighboring cells encode progressively greater velocities (shown at right). The inset illustrates the overall anatomy of the bat brain. After Suga 1990.

particular delay but to a particular amplitude, suggesting that these neurons can code for a target that is of a particular size and at a particular distance. Finally, the FM-FM area neurons are organized in columns perpendicular to the surface of the cortex, with the neurons within a particular column responding to a particular delay, and with different columns (and thus different preferred delays) increasing along a single axis of orientation (see Figure 2.12A).

Suga and coworkers found that the source of the call-echo delay signal to FM-FM cortical neurons is different groups of neurons in the inferior colliculus—one group tuned to the call FM₁, the other tuned to the higher harmonics of the FM echo. These groups then project to the cortex via a relay, the medi-

al geniculate nucleus. The mechanism for delay coding in the medial geniculate appears to be similar to that involved in interaural time-delay computation by the barn owl (as we will discuss in Chapter 3); that is, the neural response to the FM₁ pulse is delayed as it travels to the nucleus, but the response to the echo is not delayed. Thus neurons in the medial geniculate act as “coincidence detectors” that respond best to a particular pulse–echo delay. A range of different delay lines thus form an array of geniculate neurons that respond to a range of echo delays, which in turn are transmitted to the FM-FM area of cortex.

VELOCITY CODING IN THE CF-CF AREA. We now turn to the CF component of the call (see Figure 2.11). Recall that this component is used for Doppler shift analysis, which the bat uses for computing the relative velocity of a target. To accomplish this task, neurons must analyze the frequency relationship between the call and the echo. Suga and colleagues found such neurons in a region of the auditory cortex they call the **CF-CF area** (Figure 2.12B). They distinguished two types of CF-CF neurons: CF₁-CF₂ and CF₁-CF₃, each of which occupies a distinct subterritory of the CF-CF area. These neurons responded extremely well to the *combination* of a 30 kHz tone (CF₁; see Figure 2.11) with tones of about 61 kHz (CF₂) or 92 kHz (CF₃), which are the second and third harmonics, corresponding to a returning Doppler-shifted echo. As in the FM-FM area, these neurons did not respond to a call alone, to an echo alone, or to a CF or an FM pulse alone. They required the combination of two CF signals—the pulse plus the echo—to fire optimally.

Suga and colleagues suggested that CF-CF neurons are devoted primarily to encoding velocity information. They, too, are arranged in columns, each neuron within a column coding for a particular combination of frequencies (see Figure 2.12B). These columns are arranged regularly along the surface of the cortex in a fascinating way: The preferred CF₁ frequency increases along one axis, and the CF₂ and CF₃ frequencies increase along another axis at right angles to the CF₁ axis. Thus the CF-CF region is organized by a dual frequency coordinate system in which a specific location represents a particular relative target velocity. Within both the CF₁-CF₂ regions and the CF₁-CF₃ regions there is an axis of velocities between –2 and +9 m/s (see Figure 2.12B), with a disproportionate number of neurons representing velocities from 0 to 4 m/s, which are speeds that indeed arise in nature during critical activities for the bat, such as capturing prey.

The source of the CF-CF signals to cortex appears to be much the same as that of the FM-FM signals. Specialized neurons in the inferior colliculus are tuned to specific single frequencies: CF₁, CF₂, or CF₃. These cells send their signals to medial geniculate neurons, which in turn integrate them and send them to the relevant CF-CF subarea.

DOPPLER SHIFT CODING IN THE DSCF AREA. A final cortical region discovered in the mustached bat by Suga and colleagues, and by far the largest (occupying about 30% of the entire primary auditory cortex), contains neurons that code for

only certain frequencies and amplitudes of echoes, specifically Doppler-shifted CF_2 signals. This region, which they call the **DSCF area**, contains neurons that respond best only in an extremely narrow frequency range, between 60.6 and 62.2 kHz (when the bat's resting CF_2 is 61 kHz). The exact frequencies represented in the DSCF area vary among individual bats according to their own resting CF_2 frequencies; thus Suga and his colleagues suggested that each bat's auditory system is personalized.

Neurons in the DSCF are sharply tuned both to a particular frequency and to a particular amplitude. In effect they are the cortical counterpart of the acoustic fovea. Interestingly, these cells respond purely to the amplitude and frequency of the *echo* CF_2 regardless of the frequency of the call that gave rise to that echo. Like other areas, the DSCF area is arranged in columnar fashion, each neuron within a column preferring a particular combination of CF_2 and amplitude, and the columns arranged radially in a systematic fashion according to best frequency. Suga suggested that neurons in the DSCF area contribute to the great acuity of frequency and amplitude discrimination that the bat exhibits, especially in its acoustic fovea.

A creative experiment by Suga and coworkers supports the view that specific aspects of bisonar signals are processed in highly regionalized areas of auditory cortex. These workers found that selective inactivation of different critical regions had very different consequences for auditory processing: Pharmacological inactivation of the DSCF area severely disrupted frequency discrimination in the bat but did not affect delay discrimination. Conversely, inactivation of the FM-FM area (see Figure 2.12A) disrupted discrimination of delay but not of frequency. Taken collectively, Suga's work shows that the bat's auditory cortex contains a family of highly organized maps, each coding a different aspect of pulse-echo interaction; this collection of maps provides an extraordinary "atlas" that endows the bat with its remarkable ability to process complex auditory information.

A final question remains to be addressed: Why do mustached bats emit so many harmonics in their calls when a single frequency could, in principle, do the job? Suga suggested a fascinating reason. He pointed out that bats not only have to deal with prey in a one-on-one contest; they also have to deal with hundreds of other bats back home in the colony, where they must use their echolocation to navigate around their careening colleagues. To help cope with this air-traffic controller's nightmare, bats make use of their **first harmonic**, which is the weakest component of their emitted call (see Figure 2.11). In fact, it is so weak that other bats can hardly hear it; they hear mainly the much louder higher harmonics of their roostmates. Recall, however, that the higher harmonics alone cannot excite FM-FM or CF-CF cortical neurons; these neurons require the combination of the first harmonic with a higher harmonic.

When a bat emits its own call, it can hear its own first harmonic, which, in combination with the higher harmonics of its echoes (that are Doppler-shifted or delayed), can stimulate its own FM-FM or CF-CF neurons. Every bat's cortical neurons thus need a dual password for activation: the first harmonic, heard only by the bat itself, and one of several higher harmonics. Even though the

lower processing centers of other bats can respond to the higher harmonics, the cortical neurons of the other bats are “deaf” to them because these sounds arrive at their cortex unaccompanied by the all-important first harmonic.

Why Are Any Moths Left?

Given the incredible prey-tracking and prey-catching abilities of bats described in this chapter, the following question arises: How can the humble moth (or other nocturnal insects such as lacewings) hope to evade this awesome predator? Must they simply be resigned to the role of hapless victim? Inspection of any street lamp or porch light on a summer’s evening tells us no, there are still plenty of moths around. How can this be so?

It turns out that, through coevolution, moths have developed the ability to hear the ultrasonic calls used by bats and have developed several clever countermeasures to avoid becoming a bat meal. For example, if a moth hears a bat in the search phase of its hunt (see Figure 2.8), which the moth can detect because of the low repetition rate of the bat’s call, the moth simply flies the other way. Since the bat’s outgoing call is louder to the moth than the returning echoes are to the bat, the moth can usually hear the bat before the bat detects the moth, and therefore it can effectively move out of harm’s way. If the moth hears a bat that has already detected it and is in the approach or (even worse) the terminal phase, which the moth can tell because the calls are progressively louder and because they are coming at a very high repetition rate (see Figure 2.8), the moth takes more dramatic evasive action. It either folds its wings and power-dives directly for the ground, seeking protective foliage, or it flies and tumbles erratically in the air, making its flight path quite unpredictable. This latter strategy could confound the bat’s flutter analysis, which requires regular AM and FM modulation of the echo (see Figure 2.6). Thus the bat might mistake the tumbling moth for a falling leaf.

Finally, some moths have developed the ability to confuse the bat by emitting their *own* ultrasonic sounds (which are roughly matched in frequency to a bat’s). They do this only when the bat is in the terminal stage of pursuit and thus the bat calls are coming in fast and furious. The net result is that the bats often, remarkably, sharply veer away as if avoiding an obstacle, apparently indicating that the triumphant moth has effectively jammed the bat’s sonar system. Thus the bat-moth story is an excellent illustration of the relative stability that coevolution can bestow upon diverse species locked into the point and counterpoint of predator-prey interactions.

Summary

We have seen that bats use echolocation to locate, identify, track, and capture their prey, which is usually a nocturnal flying insect. Bats use two basic kinds

of signals: FM sweeps (broadband signals) of short duration (less than 5 ms), and CF pulses (narrowband signals), which are long in duration (5–100 ms). Bats perform a series of complex analyses comparing the timing and frequency of their emitted calls and the returning echoes to determine important aspects of a target: (1) *Distance* is measured by the pulse–echo delay (FM sweeps are especially good for this determination). (2) *Angular size* is measured by echo amplitude. (3) *Absolute size* is measured by combining distance and angular size measurements; (4) *Spatial localization* is measured by binaural comparisons for azimuth, and by echo amplitude at different ear positions for elevation. (5) *Relative velocity* is measured by Doppler shift analysis (CF signals are especially good for this; Doppler shift analysis also aids in detecting the flutter of an insect's wings). The frequency of the CF component of the call used for Doppler shift analysis is overrepresented throughout the auditory nervous system; this increase in sensitivity to a selective narrow range of frequency is called the *acoustic fovea*. Bats use Doppler shift compensation of their calls to ensure that returning echoes will remain in their acoustic foveas.

There are three basic stages to a hunt, during which bats use different call repetition frequencies: (1) the *search stage* (10 Hz), (2) the *approach stage* (50 Hz), and (3) the *terminal stage* (100–200 Hz). The higher repetition frequencies greatly aid in moment-to-moment range determination necessary for tracking pursuit and capture.

The auditory nervous system of the bat is highly specialized for echolocation. In the cochlea, the *basilar membrane* is specialized to be especially sensitive to the frequency of the Doppler-shifted echo. This sensory structure forms the initial substrate for the acoustic fovea. In addition, primary sensory neurons are very sharply tuned to the frequency of the Doppler-shifted echo. Farther upstream, neurons in the *inferior colliculus* are highly specialized to faithfully respond to the timing differences between calls and echoes. Finally, in the cortex, different tasks are parceled out across anatomically distinct regions of cortical real estate. In one region, the *FM-FM area*, neurons encode distance information, with different columns of neurons responding best to different pulse–echo delays. In another region, the *CF-CF area*, neurons encode velocity information, with specific columns of neurons responding best to different frequency differences between a call and an echo. Finally, in a third region, the *DSCF area*, neurons are highly responsive to the Doppler-shifted echo frequency and amplitude, making them well suited for Doppler shift analysis.

Moths have coevolved with bats and thus can hear and respond to a bat's calls. If a moth hears a bat in the search stage, which is characterized by a low repetition rate of its call, the moth simply flies the other way. If the bat is in the approach or terminal stage, each of which is characterized by much higher repetition rates, the moth will either power-dive to the ground or randomly tumble, making its flight path unpredictable. Finally, some clever moths emit their own ultrasonic pulses to jam the sonic signals of the tracking bat. The interlocking behaviors of the bat and moth provide a beautiful example of relative species stability achieved through coevolution of a predator–prey relationship.

Recommended Reading

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