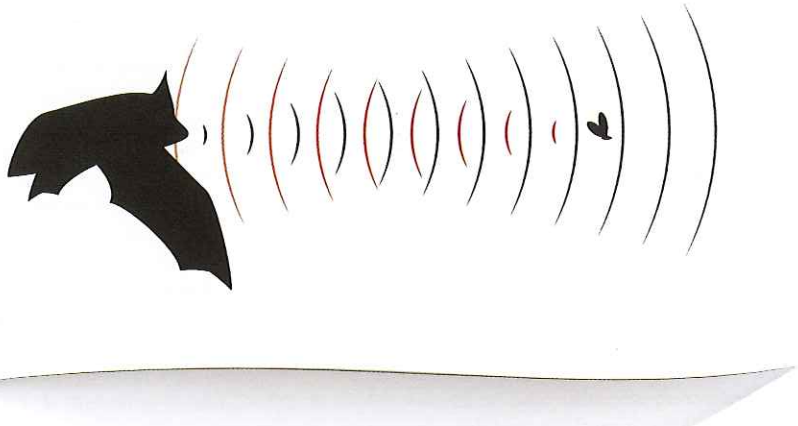
CHAPTER 5

The Biosonar System of Bats



The Neuroethology of Predation and Escape, First Edition. Keith T. Sillar, Laurence D. Picton and William J. Heitler.

The main hurdle to using sound to locate objects is that it only works if the object of interest is making a noise. If animals keep still, they make very little noise and, since keeping still is a prime strategy for both ambush predators and alarmed prey, passive listening has its limitations. Furthermore, a passive listener does not necessarily know in advance what sort of noise an interesting object will make (squeak, rustle, grunt, thump, etc.), so it needs a rather generalised auditory capability to be prepared for a range of possibilities. Then it also faces the challenge that a noise of interest might be masked by background noise which swamps a broadband reception mechanism. The solution evolved by some animals is to use **biosonar**.

In principle, this is very simple – send out a sound wave ('ping') into the environment, and then use the information encoded in the returning echo to locate objects of interest. Because the listener is also the noise-maker, it knows exactly what type of noise to listen for, and can develop specialised mechanisms to separate out that noise from background interference. The general mechanism is called **echolocation**, and how it works is the subject of the present chapter. It turns out that biosonar requires particularly sophisticated computing hardware in the brain, and only a few animals have evolved a proper echolocation capacity. However, two groups of mammals – bats and toothed whales – have done so, perhaps because, as mammals, they already possessed complex brains with an auditory cortex for evolution to act upon. Most of what we know about the neuroethology of echolocation derives from experiments on bats, hopefully for fairly obvious reasons, so the focus of this chapter will be on this group.

5.1 Bat echolocation

Echolocating bats belong to the order Chiroptera, a name deriving from Greek and meaning 'hand wing'. Many bat species emit a series of ultrasonic pulses from their mouths or noses, and then detect the returning echoes to construct an auditory image of their environment. This image is used both for navigation and to detect potential prey. In this way, bats are able to exploit an ecological foraging niche of night-flying insects, in which they encounter little or no competition. Pursuing and capturing prey in flight is known as **aerial hawking**, and bats' nocturnal prowess in this has made them highly successful; indeed, the Chiroptera rank among the most successful and diverse of all mammalian orders[1]. Bats also *glean* – take stationary prey from leaves or the ground, and even *trawl* – catch prey from the surface of water. The acoustic challenges for a bat hunting in an open area high above the ground are very different from those hunting in dense woodland and, as we will see, bats use different echolocating strategies in different habitats.

Despite the often negative public perception of bats, no doubt reinforced by Bram Stoker's tale about Count Dracula, scientists have long noted and marvelled at their agility, manoeuvrability and exceptional skill in capturing insects. Indeed, bats have been the subject of curiosity-driven research from as far back as the late 18th century with the investigations of Italian priest-cum-biologist Lazzaro Spallanzani.

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[1] Bats account for around 20% of all mammals, and there are over 1200 species. Not all bats echolocate – the large Old World 'flying foxes' or fruit bats (often referred to as the Megachiroptera) feed on fruit and nectar, have large eyes, and most do not echolocate. However, the smaller insectivorous bats (often referred to as the Microchiroptera) all use echolocation, although this is often aided by vision and passive hearing.

Spallanzani had diverse interests in biology and physiology; his work on microbes was to pave the way for Louis Pasteur to disprove the theory of spontaneous generation. However, he also had a fascination with bats. He was the first to show that bats deprived of sight could still navigate and avoid obstacles, but that they had great difficulty with this if their ears were plugged. However, it was well over a century later, following the invention of new sound detection devices, that it was discovered that bats emit high-energy, high-frequency sounds when navigating.

In fact, it was just before the USA entered the Second World War that Harvard undergraduate biologist Donald Griffin and colleagues made some seminal discoveries on the ultrasound system of bats (Griffin and Galambos, 1941). They realised, for example, that the sound pulse rate emitted by the bats was not constant but, rather, increased dramatically when the animal approached objects in the environment. The bats were able successfully to avoid very fine 'trip' wires spun across their flight paths, but this ability was impaired when their ears were occluded, as Spallanzani had already shown. The key experiment, however, was that navigation was also adversely affected if the bats' *mouths* were held shut. Thus, when they were prevented either from emitting sounds or from receiving sounds, their navigational system was severely compromised, suggesting that bats send out ultrasonic sound chirps, and then use the returning echoes to 'image' objects in the environment.

5.1.1 Why ultrasound?

The auditory receptors of the human ear are able to detect sound frequencies spanning roughly three orders of magnitude, in the range of 20 Hz to 20 kHz. This is a wide range when compared to, for example, the human visual system (see Chapter 1, Vision), whose receptors detect light with a frequency span of less than one order of magnitude (390–700 nm), but nevertheless is quite poor when compared to the auditory system of other mammals (Figure 5.1). Dogs have an upper frequency limit of about 50 kHz, while cats can hear sounds up to about 80 kHz. However, bats top the scale – some species can

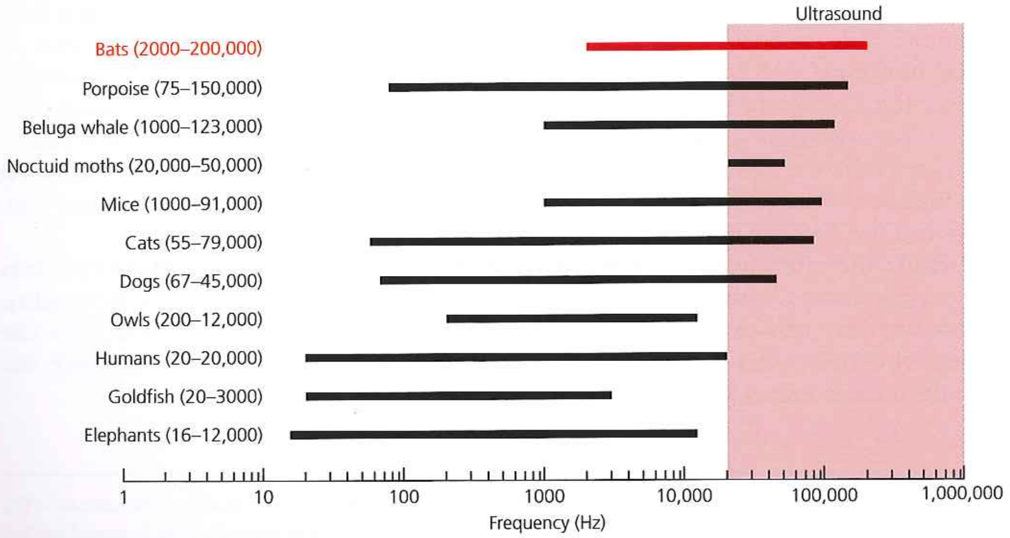

Figure 5.1 A comparison of the acoustic sensitivity range of various predators and prey (note logarithmic scale).

hear up to an amazing 200 kHz in frequency. Sound frequencies which are above the limit of human hearing are called **ultrasound**, and it is within this high frequency range that bat echolocating signals operate.

Why do bats use ultrasound rather than what we regard as more normal sound frequencies? The key advantage is that the higher the frequency of the sound, the smaller the target that can be found by echolocation. To generate an echo, sound must bounce back from an object and, for this to happen, the object must be larger than the wavelength of the sound hitting it, or else the sound just bends around the target by diffraction. A sound of 17 kHz, at the top end of the human hearing range, has a wavelength of about 20 mm, so only objects larger than this will generate echoes when targeted by sound of this pitch. However, if we move into the bat range of 170 kHz, the wavelength drops to just 2 mm, which is short enough to detect the sort of small insect that a bat might be interested in.

5.1.2 Range limits

Airborne echolocation is inherently a short-range process; the maximum range is rarely more than about 25 m. One reason for this is what is known as the **impedance mismatch problem**; bats have to both transmit and receive across an air-water interface (from an acoustic point of view, bats are essentially water), and the difference in inertial properties of these media makes this process inefficient. Marine echolocators, such as dolphins, do not have this problem. Another reason, which is shared with dolphins, is that sound propagates with a spreading wavefront, so intensity drops off with distance following an inverse square law. This is true both for the emitted call and for the returning echo and, consequently, the echo intensity at the location of the emitter decreases with the 4th power relative to range. This rapid attenuation is simply due to geometry, but on top of that there is further attenuation due to absorption. Dry air absorbs ultrasound much more than it does low-frequency sound, and the situation is even worse if the air contains water droplets, since these absorb ultrasound almost completely[2]. Thus, bats – like many aircraft – are grounded by heavy fog.

The overall consequence is that a bat has to 'shout' extremely loudly to have a useful echolocating range. In fact, bats emit signals with an amplitude of up to 140 dB sound pressure level (SPL) at 10 cm (Fenton, 2013), which would be well above the human auditory pain threshold if we could hear it. However, bats also require extremely sensitive ears to detect faint echoes. We will come back to the ways that the bats avoid deafening themselves, and each other, later in the chapter.

5.2 The sound production system

For the most part, mammals generate sounds using the larynx (voice box), and the mechanism relies upon the lungs driving a flow of air over the vocal chords, which vibrate to make the noise. The general pitch of the sound depends on the size of the vocal chords, with long chords producing low sounds and short chords producing high sounds – like a cello compared to a violin. However, within the broad range set by the size, the pitch is determined by the tension in the chords – the higher the tension, the higher the

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[2] It is not the water itself, which completely absorbs the ultrasound – otherwise marine mammals could not use ultrasound – it is the water droplets in air. However, water, like air, does absorb ultrasound more than low-frequency sound.

frequency. In echolocating bats[3], the vocal chords contain two pairs of very thin membranes, which are about 2 mm long, 0.5 mm wide and only 6–8 μm thick. These are stretched as tight as drum skins, and vibrate at ultrasonic frequency as air passes over them. The degree of stretch, and hence the actual frequency, is controlled by the specialised **cricothyroid muscle**, which pulls on the thyroid cartilage to which the folds are attached. This muscle is greatly enlarged in bats compared to other mammals, and wraps around the whole larynx (Suthers and Fattu, 1973).

The sounds emitted by bats usually comprise a **fundamental base frequency**, plus one or more **harmonics** – integer multiples of the base frequency. The fundamental frequency is often about 40 kHz, but the harmonics can reach as high as 200 kHz. The harmonics often contain more energy than the fundamental frequency (i.e. they are the loudest part of the call), and they are crucial in determining certain properties of the insect target.

The echolocation sound is emitted through either the nose or the mouth, depending on the bat species, and anatomical specialisations in the face of the bat can optimise sound propagation. For instance, the nostrils of the nose-emitting horseshoe bat *Rhinolophus hildebrandti*, which broadcasts at a fundamental frequency of 42 kHz, are spaced half a wavelength apart (about 4 mm). This means that lateral sound is cancelled through interference, thus focusing the sound in the forward direction (Pye, 1979). The effect may be enhanced by the complex folds and protuberances of the face (the **noseleaves**), which characterise many bat species and which act as cavity resonators (Zhuang and Müller, 2006). These can shape the direction of the emitted pulse in a frequency-dependent fashion so that, for instance, a low-flying bat could switch between 'looking' ahead for prey and downwards to check the ground position by changing the frequency within a pulse of emitted sound. High-frequency sounds are more focused than low frequency sounds, so this could also, in part, compensate for the increased adsorption at the higher frequency – the bat could maintain sensor range at high sound frequency, but at the expense of 'peripheral vision' available at low frequency (Surlykke *et al.*, 2009).

Bats have to generate their sound for echolocation while simultaneously chasing down agile prey in flight, so the lungs have two functions – to power the sound production, and to provide oxygen for the flight muscles. At first sight, that would seem like double effort but, in fact, it is quite efficient – the bat is breathing fast and heavily due to the cost of flight, and it can produce ultrasound during exhalation almost for free. However, for a perching bat, the energy cost of producing sound pulses is almost as high as it is for flying.

5.2.1 Types of sound: CF and FM pulses

Broadly speaking, there are two main types of echolocating signal found in different bat species (Figure 5.2), although some species can switch between the two, depending on their foraging location. The first type consists of a series of very short sound pulses that each lasts 5 ms or less, and contains a downward sweep of frequencies, typically moving from about 60 kHz down to 20 kHz. These are known as **frequency modulated** (FM) sweeps and, due to the wide range of frequencies within each sweep, this is often referred to as a **broadband** signal. An example of an FM sweep is shown in Figure 5.2A.

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[3] A single genus (*Rousettus*) of Old World fruit bat generates faint and brief echolocating pulses by clicking its tongue rather than passing air through the larynx (Holland *et al.*, 2004). However, these bats are mainly vegetarian, and use echolocation for navigation, not hunting, so we will not deal with them further in this chapter.

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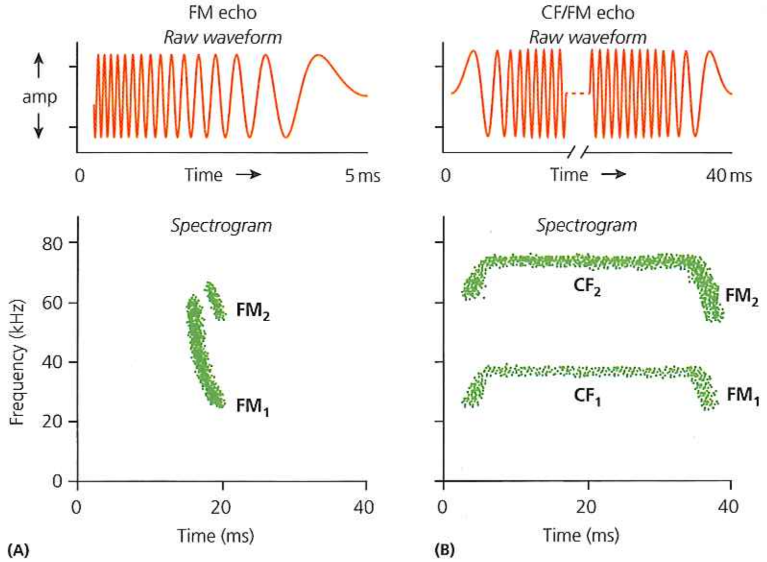

Figure 5.2 Comparison of (**A**) FM and (**B**) CF/FM echolocation pulses. The top panels (orange traces) show highly schematic examples of the raw auditory waveform of the two types, such as one might see if a microphone were connected directly to an oscilloscope. The changes in the horizontal spacing of the oscillations are the changes in sound frequency. The bottom panels (green traces) show real examples of spectrograms. Spectrograms (sometimes called sonograms) show how the frequency (vertical axis) and intensity (colour density) of the call varies with time (horizontal axis). They are calculated from raw waveforms using a digital instrument called a spectrum analyser, and are the normal way of displaying bat calls. Note that both call types in the examples show harmonics in the spectrogram, but these are not included in the waveform schematic. The lower line (FM1, CF1) is the fundamental frequency or first harmonic; the parallel upper line (FM2, CF2) is the second harmonic, with double the frequency of the fundamental. Spectrograms adapted from Neuweiler (2003) with permission from Springer Science + Business Media.

The second type consists primarily of a series of longer-duration **constant frequency** (CF) signals (Figure 5.2B). These bats chirp at a species-specific narrowband frequency, but each chirp usually begins and/or ends with an FM component in which the frequency is rapidly modulated[4]. Many bat species emit pure FM calls, but few, if any, emit pure CF calls; most CF calls have FM components at one or both ends of the signal. Echolocation sounds produced by FM and CF/FM species usually contain two or more harmonics; in the CF/FM call shown in Figure 5.2, for example, the second harmonic of the CF component (CF_2) is the most intense part of the signal, to which the bat's hearing system is specifically tuned.

Why do different bats produce such radically different shapes of sound? This is an obvious and fascinating question, and we will return to it repeatedly in this chapter. To give a sneak preview, though, FM calls are better for computing the prey's range, while CF calls are better for computing the prey's relative velocity. CF calls can also detect prey at greater distances, and give more information about the prey's actual identity. Read on to find out why and how!

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[4] By analogy with human speech, the CF component resembles a vowel in which the sound frequency remains relatively stable for tens to hundreds of milliseconds, while the FM component is more like a consonant in containing rapidly changing frequencies.

5.2.2 Echolocation in predation: a three-phase attack strategy

Hunting by insectivorous bats moves through three predictable phases – **search**, **approach** and **terminal buzz** (Figure 5.3) – with the repetition rate of bat calls markedly accelerating as the sequence progresses from one phase to the next (Griffin *et al.*, 1960; Simmons *et al.*, 1979). For example, let's look at the common pipistrelle bat (*Pipistrellus pipistrellus*), a species that only uses FM signals (Figure 5.3B). During the search phase, the bat's sonar pulses are emitted at a relatively low frequency (5–10 Hz; note that this is the repetition frequency of the *pulses* of sound, not the frequency of the sound *within* each pulse, which is ultrasound), and the beam is aimed in different directions as the bat tries to locate a possible meal (Figure 5.3A). Each pulse is 5–10 ms in duration.

If the bat finds something interesting, it enters an approach phase, where it homes in on the target and tries to find out if it is a suitable prey item. During this phase, the sonar beam fixates on the target, and the frequency at which the bat emits pulses increases to about 80 Hz, while the duration of individual pulses shortens. If the bat likes the sound of what it is hearing, then it initiates the terminal buzz phase and engages in target capture. The pulse repetition rate increases dramatically during this final phase, to as much as 200 Hz, so as to update information as rapidly as possible, and the pulse duration drops to 1 ms or less. The bat actually catches its prey using the membrane between its wings and tail to 'hug' the unfortunate insect and scoop it into its mouth (Webster and Griffin, 1962).

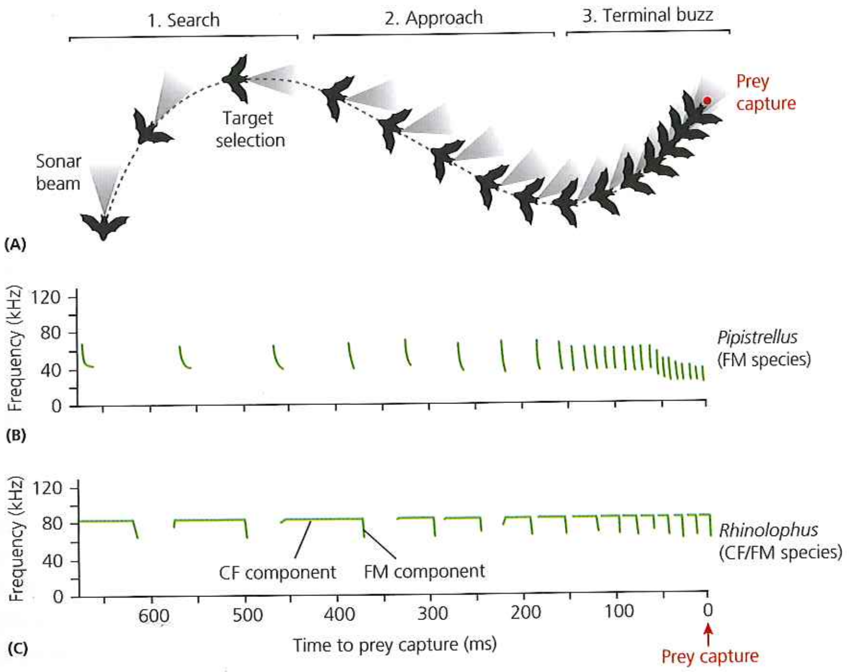

Figure 5.3 Three-phase approach to prey capture. The last 650 ms before capture is shown. **A**: A cartoon showing a bat chasing an insect, illustrating the three phases of prey capture by echolocation. Each silhouette of a bat indicates the time of an emitted call. Adapted from Moss and Surlykke (2010). **B**: FM echolocation calls recorded from a common pipistrelle bat (*Pipistrellus pipistrellus*). **C**: CF/FM echolocation recorded from a horseshoe bat (*Rhinolophus ferrumequinum*). B, C adapted from Schnitzler and Kalko (2001) with permission from Oxford University Press.

Despite the differences between FM and the CF/FM calls, the three phases of the predatory behaviour are present in both types of bat. For example, horseshoe bats use CF/FM calls but, once again, the search phase involves long pulses at low repetition rates which speed up and shorten on approach, with marked acceleration in the terminal buzz phase just before the insect is finally captured (Figure 5.3C). In fact, in the last part of the terminal buzz, the CF component becomes so short that the call waveform becomes quite similar to an FM call.

Superfast muscle

The high-frequency signal emission during prey capture poses an obvious physiological problem, especially for FM bats. Each pulse of an FM call, including those of the terminal buzz, contains a broadband sweep. Sound frequency is controlled by the cricothyroid muscle which, therefore, has to contract during the 4 ms or so between terminal buzz pulses, so as stretch the vocal chords and produce a high pitch at the start of the pulse. It then has to relax within 1 ms or less during the pulse itself, to allow the vocal chords to slacken and the frequency to drop, before having to contract again for the next pulse. Ordinary vertebrate skeletal muscle simply cannot perform contraction/relaxation cycles at rates this high and, in fact, the cricothyroid muscle belongs to a special group known as **superfast muscle**, which has highly specialised excitation-contraction coupling mechanisms (Elemans *et al.*, 2011). Similar muscles have been found in sound-producing organs in reptiles (e.g. the rattlesnake's tail), songbirds and fish, but this is the only superfast muscle known in mammals.

5.2.3 Duty cycle and pulse-echo overlap

There is an important difference between FM and CF calls concerning the **duty cycle** – the proportion of time that a rhythmic signal is active in relation to the interval at which the signal is repeated (the cycle period) (Figure 5.4). For FM bats, the duty cycle is low (Figure 5.4A). Thus, during early approach, the pulses might have 4 ms duration and repeat with a 20 ms interval, giving a duty cycle of 20% while, in the terminal buzz, the repetition interval might be only 5 ms, but the pulse duration can drop to as

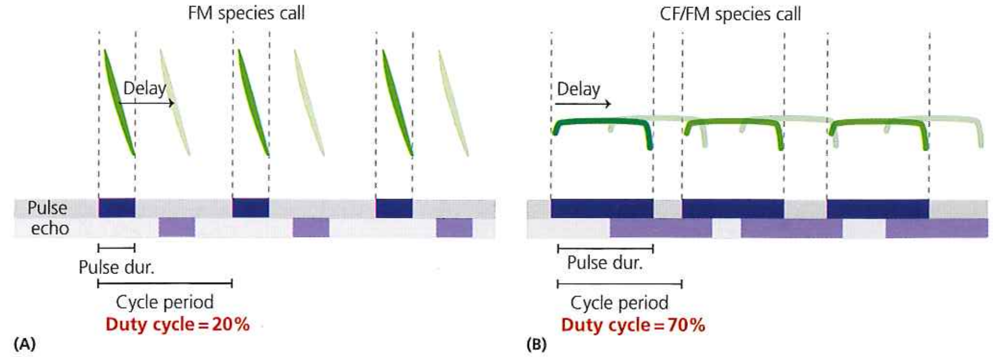

Figure 5.4 Duty cycle and pulse-echo overlap. **A**: FM bats typically have a low duty cycle, where the pulse duration is short compared to the cycle period. This means that, even at short range (where call frequency is high), the delay to the echo is sufficient to ensure that the echo occurs in the silent period between pulses. **B**: CF/FM bats have a high duty cycle and, at the same short range, there may well be considerable overlap between the emitted pulses and the returning echoes. Data are schematic in both sections.

little as 0.5 ms, which gives a duty cycle of 10%. This means that even at quite close range (down to about 10 cm), an FM bat receives the echoes returning from each pulse during the silent intervals between pulses; there is no overlap between the call and the echo.

In contrast, for CF bats, the duty cycle is high (Figure 5.4B) – the calls are long and occupy a greater proportion of each cycle. This means that, as the range shortens, a pulse echo can arrive back at the ear even before the emitting pulse is over, and it may also overlap with the next pulse in the cycle. This raises a problem – how can a CF bat hear the returning echo when it overlaps with the sound it is already producing? It is like trying to talk and listen at the same time, which we all know can be problematical. CF bats mitigate the problem using a phenomenon called the **Doppler shift**. This is described in more detail later, in the section on determining target velocity, but basically it causes the frequency of the returning echo to be slightly different from the frequency of the emitted call. Thus, as long as the bat can find a way of tuning into the echo and not its own call, then it can 'shout' and listen at the same time.

5.3 The sound reception system

5.3.1 Bats have big ears

Given the importance of hearing to bats, it is not surprising that they have big ears. They need them in the search phase to detect weak echoes arriving from distant objects. Large external ears, or pinnae, capture as much sound as possible, and the fact that bat ears are movable means that they can be directed towards faint sound sources. In addition, it has been suggested that the ears may have at least two other structural features that help directionality (Figure 5.5; Kuc, 2009). There are prominent horizontal ridges in many bat ears, which probably provide structural reinforcement to help keep the ears erect, but they

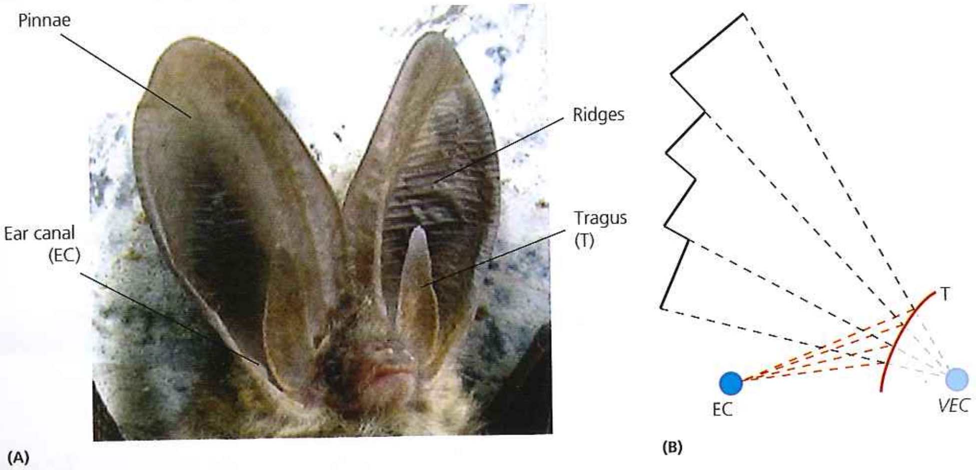

Figure 5.5 Structural features of bat ears help determine the directionality of acoustic signals. **A**: The head and ears of the brown long-eared bat (*Plecotus auritus*). Photograph courtesy of Evelyn Simak (licence CC-BY-2.0). **B**: The ridges in the ear may act as a Fresnel lens, focusing sound to a point which acts as a virtual ear canal (VEC). The tragus (T) intercepts the sound beam and refocuses it to the actual ear canal (EC). Adapted from Kuc (2009) with permission from AIP Publishing LLC.

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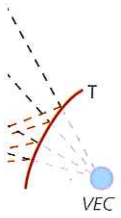

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may well also have an acoustic role. They can act as Fresnel lens[5] elements to focus high-frequency sound down onto the second feature, the tragus, which is the prominent cartilaginous structure sticking up at the front of the ear. The tragus, in turn, can reflect the sound down onto the ear canal itself[6].

5.3.2 Peripheral specialisations: automatic gain control and acoustic fovea

Two important specialisations related to echolocation are found inside bat ears, one of which is particularly important for FM calls and the other for CF calls. Remember that one of the problems that a bat faces is that it is producing a very loud noise right next to its very large ears, but it is listening out for very soft sounds. There is a serious risk of deafening itself during its own call. FM calls have a low duty cycle, in which sound emission is temporally separate from the echo return so, if the bat could shut down its auditory system during the call and re-open it during the gap, the problem would be solved. This is exactly what happens during the search-and-approach phase of FM bats.

The stapes bone, which is one of the auditory ossicles connecting the eardrum to the cochlea, is linked by the stapedius muscle to the surrounding skull. The stapedius muscle is the smallest skeletal muscle in the body for most mammals, but it is massively enlarged in FM bats, and it oscillates in phase with the pulses of the FM call (Henson, 1965). The muscle is activated a few milliseconds before the call, thus stiffening the stapes and attenuating the sound reaching the cochlea during the call, and then relaxes after the call, so that the delayed echo is transmitted at full volume. An apparent problem at short range is that the delay to the echo is very short, so that the muscle does not have time to fully relax between pulses and the echo actually *is* attenuated. However, this is a feature, not a bug! At short range, the echo has much higher intensity than at long range, and the echo attenuation acts like an **automatic gain control**[7] that stabilises the perceived echo intensity (Simmons *et al.*, 1992). The overall effect is to reduce range-dependent changes in intensity, thus enabling the bat to use echo intensity as an indication of target size rather than target range, with the latter parameter being primarily determined from echo delay.

Tensing the stapedius muscle is not an option for bats with CF calls, because there is often overlap between the call and the echo (Figure 5.4B). For these bats, the Doppler shift that we have already mentioned comes into play but, once again, we are going to postpone discussion of this until a later section.

The second specialisation concerns the cochlear basilar membrane and auditory receptors in CF bats (Neuweiler, 2003). In these animals, the membrane does not change

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[5] In a normal lens, light is focused by curvature across the whole surface but, in a Fresnel lens, it is focused by a series of thin surface ridges, each with its sloping side set at a slightly different angle. Consequently, a Fresnel lens can be much thinner than a normal lens.

[6] This is rather like the Cassegrain mirror system of a reflecting telescope. The pinna acts as the primary concave mirror at the back of the telescope that does the light (sound) gathering, while the tragus acts as the secondary convex mirror that focuses light (sound) reflected from the primary mirror onto the eyepiece or detector (the ear canal).

[7] The short-range attenuation in FM bats due to incomplete stapedius muscle relaxation is about 12 dB for each halving of range (Simmons *et al.*, 1992), and this is almost exactly enough to compensate for a 4th power intensity range-dependence due to geometric beam spreading ($2^4 = 16$, $10^{1.2} = 15.8$). Similar 4th power (40 log dB) attenuation is used in the time-varying gain (TVG) feature built into the electronics of top-end research and military marine echo sounders, which operate on the same principles as bat echolocation.

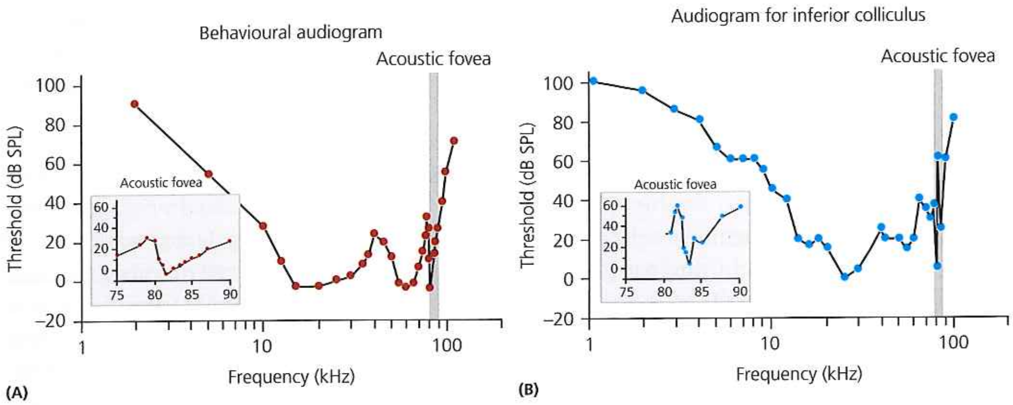

Figure 5.6 The acoustic fovea in the greater horseshoe bat (*Rhinolopus ferrumequinum*) which emits CF/FM calls. **A**: Behavioural audiogram showing how threshold varies with frequency. Note the notch at about 83 kHz, which is the frequency of the second harmonic of the CF component of the call (expanded in the inset). Adapted from Long and Schnitzler (1975) with permission from Springer Science + Business Media. **B**: Neural audiogram of the average of 100 evoked potentials recorded from the inferior colliculus shows a similar notch at the frequency of the second harmonic (expanded in the inset). Adapted from Neuweiler *et al.* (1971) with permission from Springer Science + Business Media.

its vibrational properties uniformly along its length as it does in most other mammals, including FM bats. Instead, it has an expanded region that vibrates close to, but usually slightly above, the frequency containing the main energy in the CF component of the call (usually the second harmonic). This means that there are far more afferent neurons devoted to sensing this narrow band of frequency than there are covering an equivalent range outside the CF frequency, and this makes the bat extremely sensitive to this frequency. Furthermore, the neurons themselves are very finely tuned to this narrow frequency band. This **acoustic fovea** (also called auditory fovea) is species-specific to match the carrier frequency of the CF call. For instance, the greater horseshoe bat (*Rhinolophus ferrumequinum*) emits calls at about 83 kHz when at rest, and its receptors are sharply tuned to have a minimum threshold at 83.3 kHz (Figure 5.6A). This tuning propagates through to neurons in the inferior colliculus concerned with analysing echo signals (Figure 5.6B).

5.4 Eco-physiology: different calls for different situations

Bats are highly efficient foragers; some can capture several hundred insects in a single night, at rates of up to one every six seconds or so. Bats operate in a range of different habitats, from the simple acoustic environment of open sky above a plain field surface, to the complexity of the dense forest canopy. Most bat species have a preferred hunting habitat but can, to a certain extent, move between them, and the types of vocalisation and the modes in which they are employed change in differing habitats (Figure 5.7; Moss and Surlykke, 2010). For many bats, there is a correlation between the complexity of the habitat and the 'FMness' of the call. For instance, the greater mouse-eared bat (*Myotis myotis*) makes narrowband (flattish, CF) calls when hunting in the open, but the calls gets progressively steeper (broadband, FM) as the habitat becomes more cluttered (Figure 5.7, top row). The greater horseshoe bat (*Rhinolophus ferrumequinum*) appears to be an exception to

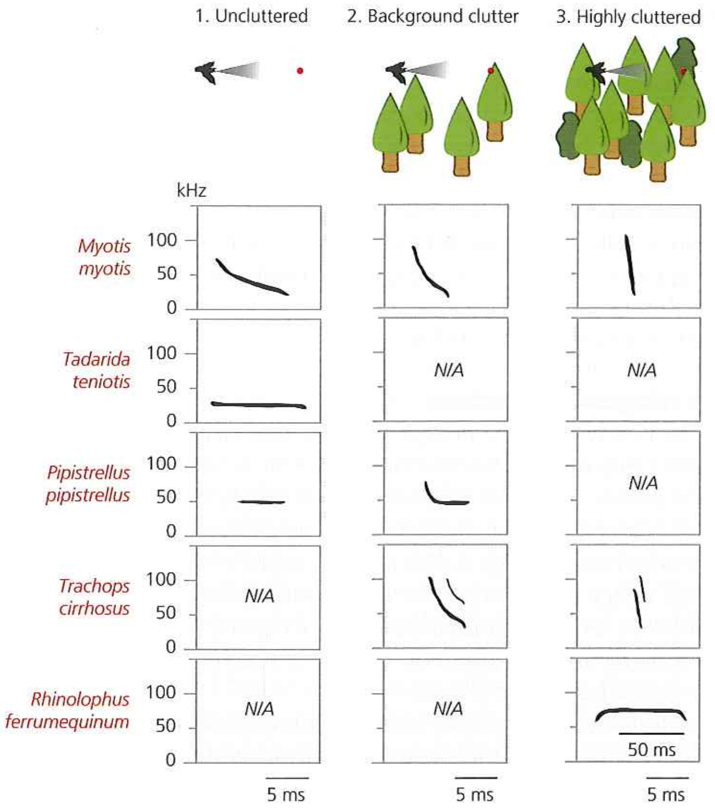

Figure 5.7 Bats employ different search signals in different habitats. For most bats, the more cluttered the environment, the more broadband the call (but note that *Rhinolophus* is an exception and has a different timescale to the others). N/A (not applicable) means that the species does not normally forage in that habitat. Adapted from Schnitzler and Kalko (2001).

this trend, since it makes a CF/FM call with an extended narrow frequency band, even when hunting in a highly cluttered environment (Figure 5.7, bottom row). However, there are good reasons for this, as we will see later.

Why do bats use such different types of calls in different situations? It is all to do with the different jobs that echolocation has to perform, and the different constraints that the environment imposes. The key tasks include determining the actual *existence* of the target, its *range*, its *2D location* and its *velocity* relative to the bat, so that the bat can 'cut the corners' in pursuit. Finally, of course, target *identity* is important; the bat would like to be reasonably sure that it is chasing a tasty insect, not a leaf blowing in the wind!

5.4.1 Target discovery

The first job of the echolocation system is to determine that a potential meal is out there somewhere. As we saw above, long duration, narrowband (CF) pulses, emitted at low repetition rates, are generally favoured when searching for prey in open, uncluttered environments, and this is because this type of call is most effective for detecting prey at long range. Because the target is a far away, there is a long delay between the call and the returning echo, so overlap is not a problem. The long call pulse duration means that the echo is also long duration and, because the signal is relatively narrowband, this allows temporal summation within the receptors tuned to that frequency, thus maximising the detection of weak signals. For instance, during searching, the big brown bat emits pulses at 10–15 Hz, each of 15–20 ms duration, sweeping across a narrow frequency band from only about 26–24 kHz. However, during the approach phase, as the distance between bat and prey shortens, the call repetition rate rises to about 80 Hz, the pulse duration drops to 2–5 ms to reduce overlap, and the frequency sweep increases to broadband with the fundamental covering from 65 to 25 kHz (Moss and Surlykke, 2010).

The situation is different if the bat is hunting in a more cluttered environment with background vegetation. Here, as the danger of collision increases, information has to be updated at a higher rate, and range information becomes more important. As we will see in the next section, FM calls are best for this.

5.4.2 Target range and texture

Target range is relatively easy to compute, at least in principle, because the speed of sound in air is constant. This means that the time interval between an emitted signal and the returned echo is a direct measure of (twice) the distance from bat to target. The CF component of a call is not good for accurate time measurements, because the same set of frequency-dependent receptors gets activated throughout the duration of the narrowband part of the signal, which obscures precise timing information. However, FM calls are ideal, either in isolation or as the terminal part of a CF/FM call. The broadband component bounces off objects in the environment, and then returns to the sender as an echo that spans the same frequency range (Figure 5.8).

Because the slope of the frequency change with time within an FM pulse is very steep, each frequency-dependent auditory neuron is only activated for a brief instant, and so has high timing precision but, since the frequency sweeps across a wide range, many receptors get activated for each pulse. This means that timing information can be extracted from across the whole spectrum, which yields higher accuracy. However, the important information is contained in the *difference* in the activation time between pulse and echo, since the absolute times will be different at different moments during the pulse (high frequencies occur early in the pulse, low frequencies later). As we will see shortly, there are neural circuits in the brain that extract exactly the necessary time differences.

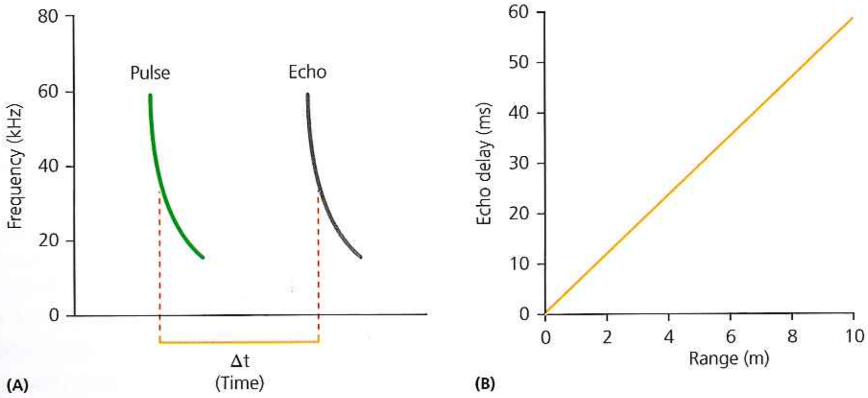

Figure 5.8 Echo delay. **A**: Schematic showing a single-harmonic FM pulse and its echo. The delay is the same at each frequency. **B**: Echo delay increases with target range. The slope of the graph is set by the speed of sound in air, which is about 343 m s^{-1}, and the fact that sound has to travel to and from the target.

The precision with which FM bats calculate target distance is astonishing; the FM-signalling big brown bat, for example, can detect time delays as small as 10 nanoseconds (Simmons *et al.*, 1990) – the equivalent of discriminating a 2 μm difference in range! This level of accuracy is a bit surprising because, from a behavioural point of view, it would seem that an accuracy of 1–2 cm should be sufficient for the bat to capture a flying insect. However, the echoes returning from an insect are used for much more than simple determination of distance. They contain detailed information on target shape and form, which enables the bats to discriminate between different insect species and decide whether the target is sufficiently enticing to be worth the effort of pursuit.

5.4.3 Target location

The location of an object in 3-dimensional space not only requires computation of distance, but also the position of the object in the horizontal and vertical planes. Bats use the same auditory cues as other mammals (described in detail in Chapter 4 on mammalian hearing), namely, binaural time and intensity differences for azimuth position and monaural spectral cues for determining elevation. The elaborate pinna-tragus system in the ear produces particularly enhanced spectral cues. Furthermore, as described earlier, the emitted call can be directional so, if the bat knows which way its head is pointing when it makes the call, it can make a good estimate of the 2D origin of the echo. The directionality is highest at the highest frequency so, for FM bats, the sound is like a searchlight beam that starts with a narrow focus at the high frequency end, but expands as the frequency drops. A wide beam is particularly important in the last stage of the attack, when evasive manoeuvres by the prey can result in large angular changes relative to the bat. Some species can drop their call frequency by about an octave (i.e. halving the frequency) at this stage, which is termed **Buzz II** (Ratcliffe *et al.*, 2013).

5.4.4 Target velocity: the Doppler shift

When a bat is chasing after an insect, both animals are constantly changing flight speed and direction. This is where the CF type of call proves its worth, because a bat emitting these calls can exploit a property of sound called the **Doppler shift** to determine its velocity *relative* to the prey. Imagine that a bat emits a CF pulse at 61 kHz, and that it is gaining on the insect. The insect will be hit by the peaks and troughs of the wave sooner than it would if the range were constant, and so will be ensonified[8] at a slightly higher frequency. This is the Doppler shift. The pulse bounces off the insect, which effectively acts as a second emitter, and travels back to the bat, again undergoing an upward shift in frequency, so that the bat hears an echo at a frequency somewhat above the 61 kHz sound that it generated. Alternatively, if the insect were pulling away from the bat, the bat would hear an echo at a frequency lower than the 61 kHz that it emitted. We are familiar with the general effect from the sound of a car as it passes by at high speed. The sound is high-pitched as the car is approaching, drops as it passes by, and then declines again as it heads off into the distance – the familiar 'nnneeeeeeaaaaaaaaaoooooow' sound!

The key point is that, by measuring the difference in frequency between the call sound that it emits and the echo sound that it receives, the bat can compute its velocity relative to the target (Figure 5.9). If the echo frequency is increased compared to its call, the bat is gaining on the insect but, if it decreases, the bat is losing the race.

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[8] The technical term for when a target is 'illuminated' by a sonar ping. Much dreaded by submariners and, presumably, the prey of bats.

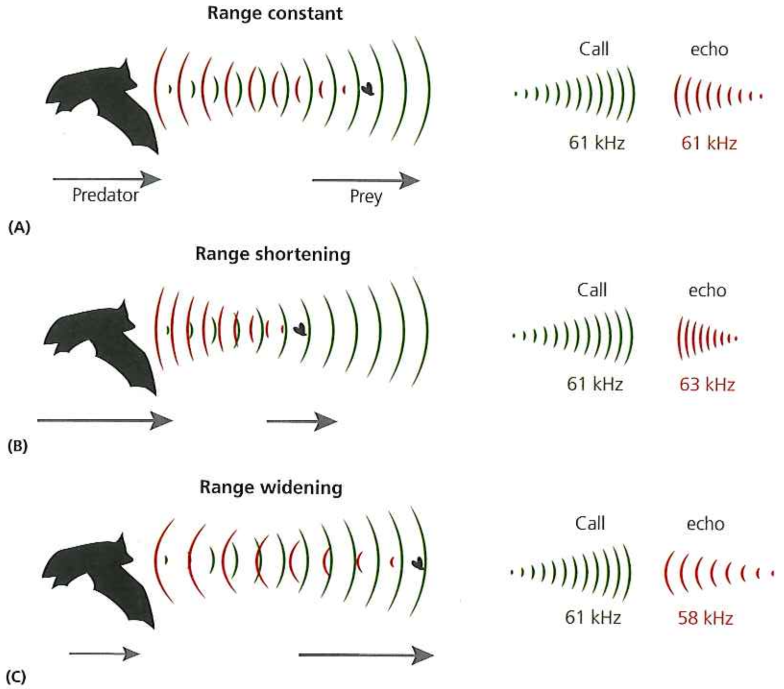

Figure 5.9 Doppler shift can change echo frequency. **A**: The range is constant and there is no Doppler shift; the echo has the same frequency as the call. **B**: The range is shortening and the Doppler shift is upwards; the echo frequency is higher than the call frequency. **C**: The range is widening and the Doppler shift is downwards; the echo frequency is lower than the call frequency. The relative velocity can be calculated from the equation $v = \frac{c\Delta f}{2f}$, where: v = velocity difference, c = speed of sound, f = pulse frequency, Δf = difference between echo and pulse frequency.

At first sight, the Doppler shift would seem to pose a problem, because CF bats have a finely-tuned acoustic fovea and, if the echo frequency changes, then it might move out of the most sensitive region. However, most CF bats can detect an increase in the echo frequency and *reduce* the frequency of their emitted call in response. This **Doppler shift compensation** (DSC) brings the echo back into the preferred foveal frequency. For example, in the case of the horseshoe bat *Rhinolophus ferrumequinum*, the resting CF component of its call is about 83 kHz but, when it is rapidly approaching a target, an uncompensated Doppler shift would cause the echo frequency to increase by several kilohertz, shifting the signal away from the optimum for detection.

In fact, the echo is beautifully maintained at precisely 83 kHz (with a standard deviation of less than 40 Hz) by a gradual and compensatory lowering of the CF component of the call. The shift occurs between rather than within pulses, and it seems that the bat employs a negative feedback control system. The frequency of an echo is compared to the reference frequency of the acoustic fovea and, if it is drifting above the ideal, then the frequency of the next emitted call is adjusted downward to compensate. The downward shift in emitted frequency can be as great as 8 kHz. This all means that the Doppler shift is not a problem, but an opportunity – a triple opportunity, in fact! First, in the process of adjusting its call frequency, the bat can extract precise information about its velocity relative to its target. Second, by shifting the emitted call frequency away from its auditory fovea, the

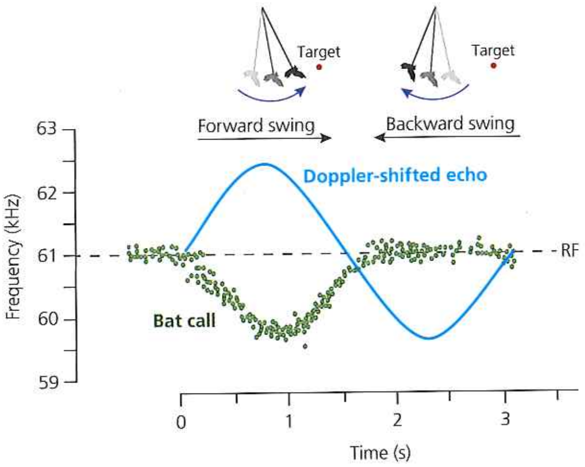

Figure 5.10 Doppler shift compensation. At rest, the moustached bat (*Pteronotus parnellii*) emits a CF call with a resting frequency (RF) of about 61 kHz. As the bat swings towards the target (forward swing phase), the received echo will have an increased frequency, as a result of the Doppler shift (blue line). To compensate for this, the bat lowers the frequency of its emitted calls (green markers), with the result that the echo is received at a constant resting frequency. However, the bat does not compensate for the Doppler shift introduced during on the backwards swing phase. Adapted from Suga (1990a), with permission from Patricia Wynne.

bat reduces the possibility of self-deafening. Finally, with call and echo occurring at different frequencies, the possible confusion caused by any overlap between the two is reduced. Thus, DSC solves three problems with a single adaptation.

An ingenious experiment to illustrate the DSC response was performed on the moustached bat (Figure 5.10). The bat was placed on a swing and then moved to and fro while it was emitting its signature CF/FM call at 61 kHz. At the moment the swing began to move forward, the bat lowered its frequency by over a kilohertz to compensate for the Doppler-mediated change in the returning echoes' frequency by an equivalent amount (Suga, 1990a). However, there was no Doppler shift detectable when the swing moved backward, which would be the equivalent to the insect pulling away from the bat. Presumably, a bat which is losing the race with its intended prey doesn't care to know too much about the fine details of its failure!

5.4.5 Target identity: flutter detection

Arguably the most impressive of all the features of echolocation is the ability it confers on bats using CF calls to detect the fluttering of the wings of their insect prey. They can do this with such exquisite sensitivity that they can even distinguish between different species. Imagine a moth flying across the path of a bat. During each wing beat cycle, the wing will move towards and away from the bat, causing Doppler shifts in echo frequency to occur at the insect's wing beat frequency (Figure 5.11). The changes are small enough that the overall echo frequency stays within the acoustic fovea, where the bat is most sensitive, and this enables very small changes indeed to be detected. For instance, with a target oscillating at 40 Hz, movements as small as 300 μm could be detected by *Rhinolophus* (Schnitzler and Flieger, 1983). The Doppler shifts resulting from these minute oscillations translate into frequency changes of only about 30 Hz from the carrier frequency of 83 000 Hz. The

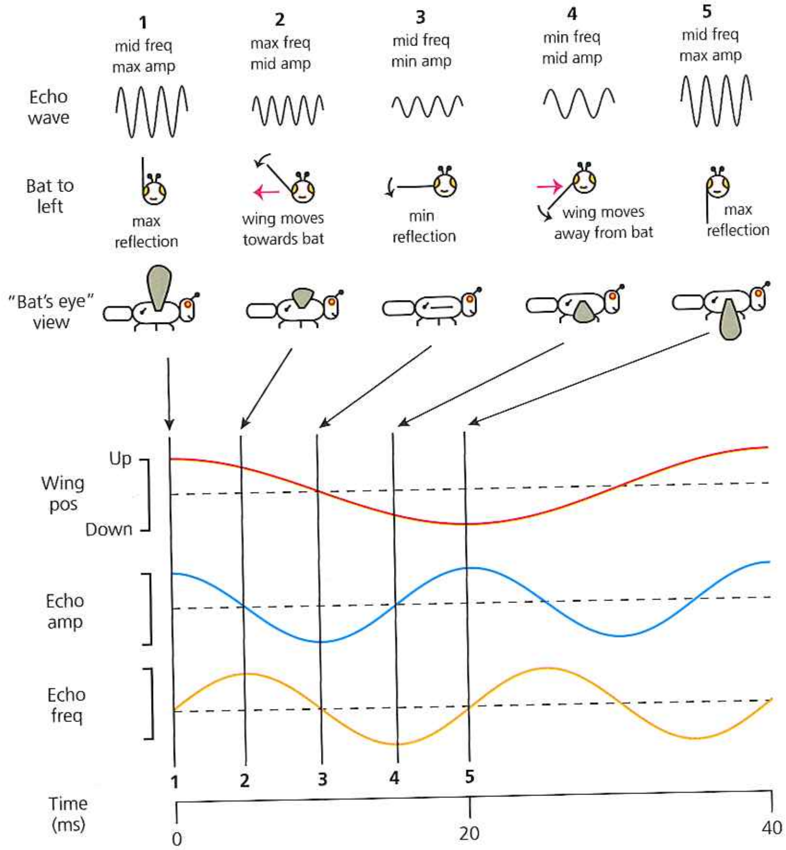

Figure 5.11 Flutter analysis: a schematic showing how the movements of an insect wing produce frequency and amplitude glints in the echo waveform when the insect flies across the path of the bat. The main graphs show how wing position (upper, red), echo amplitude (mid, blue) and echo frequency (lower, orange) vary over a single cycle for an insect beating its wings at 25 Hz. The dashed lines indicate the mid-values for each graph. The cartoons above the graphs show five stages which occur during the downbeat half of the cycle. The insect is viewed head-on (bat to the left) and side-on (bat's eye view), with only one wing shown. For simplicity, the insect is stationary relative to the bat overall. (1) The wing is fully elevated and stationary relative to the bat, so there is maximum reflection and no Doppler shift in the echo. (2) The wing depresses and moves towards the bat, producing an upward Doppler shift, but a reduced reflective profile. (3) The wing is edge-on to the bat and stationary, so there is no Doppler shift and the reflection is minimal. (4) The wing is now moving away from the bat producing a downwards Doppler shift, but the reflective profile is increasing again. (5) At full depression, the wing is again stationary and maximally reflective.

amazing conclusion is that *Rhinolophus* can distinguish sound frequencies with an accuracy of 0.036%.

In addition to frequency modulation, the insect wing movements can also cause amplitude modulation. When the wing is fully elevated, it is 'face on' to the bat, and presents a relatively large reflective surface, so the echo volume will be relatively high. As the wing moves through the horizontal position in the downstroke, it becomes edge-on to the bat, and presents a small reflective surface with a consequent reduction in echo volume. It then becomes face-on again at full depression, before the cycle repeats on the upstroke. This produces two amplitude **glints** per cycle of the insect wings. The precise properties of these glints are species-specific, again helping the bat in identifying the nature of its prey.

The additional information that flutter detection gives a bat is thought to be the main reason that bats like *Rhinolophus* emit long duration CF calls even when hunting in dense vegetation. In this situation, there are numerous background objects that will be reflecting the sound pulse, and many of these are of the same size, and at the same distance, as potential insect prey. The key difference in the sonar signal between a leaf blowing about on the end of a twig and a nearby flying insect is that the latter will be generating give-away regular frequency and amplitude glints. In fact, these bats will not attack non-flying insects and, when they start to home in on an insect that is flying, their pulses show a step increase in duration just before the terminal buzz, which allows them to gather more flutter information at this crucial decision-making stage (Mantani *et al.*, 2012). The superior ability of CF bats using a high duty cycle in detecting these clues gives them a quantifiable advantage over FM bats using a low duty cycle foraging in the same habitat (Lazure and Fenton, 2011).

5.4.6 Jamming avoidance response

What happens if two bats of the same species are trying to hunt (or navigate) within the same area? How does a bat know which sound is an echo to its own call, and which is a call (or echo) belonging to another bat? It turns out that there are a number of different solutions to this problem, but one is surprisingly straightforward. A big brown bat (*Eptisicus fuscus*) flying on its own calls almost continuously but, if two such bats are flying close together and making similar calls, then one or other reduces its call rate dramatically and, in the resulting silent periods, eavesdrops on its neighbour for navigation. The bat needs to make a terminal buzz to actually capture the prey but, up until that moment, freeloading on the neighbour's call is as good a strategy for the bat as making the calls itself (Chiu *et al.*, 2008).

A somewhat more complex response is shown by the Brazilian (also called Mexican) free-tailed bat (*Tadarida brasiliensis*). This species uses FM-type hunting and navigation calls and, if it hears a bat emitting search calls in the same frequency range that it is using itself, it shifts the frequency of its own call by as much as 3 kHz to avoid the competitor. This was demonstrated by two types of experiments (Gillam *et al.*, 2007). In the first, a recording of a bat calling with a particular signature frequency was played repeatedly, and the calls of free-flying bats foraging nearby were recorded. The free-flying bats all avoided calling at the same frequency as that of the recording (Figure 5.12A). The second experiment was more controlled. When a free-flying bat came within range, a recording was suddenly switched on that played at the same frequency as the approaching bat. The free-flying bat almost instantly shifted its own call frequency out of the range of the interruption (Figure 5.12B).

While this so-called **jamming avoidance response** (JAR) can be easily understood at the behavioural level, it is undoubtedly a complex issue at the level of computational neuroscience. The exact mechanisms underlying the shift in frequency are not yet fully understood in the bat. However, much more is known about how weakly electric fish solve a similar signal jamming problem, and we cover this computation in detail in Chapter 6, on electroreception and electric organs.

5.4.7 Food competition and intentional jamming

When a hunting bat closes in on its prey, it emits a terminal buzz to maximise its rate of target information acquisition. However, in so doing, it also broadcasts an unambiguous signal that it has found food, and this is an open invitation to any nearby bats to try to steal

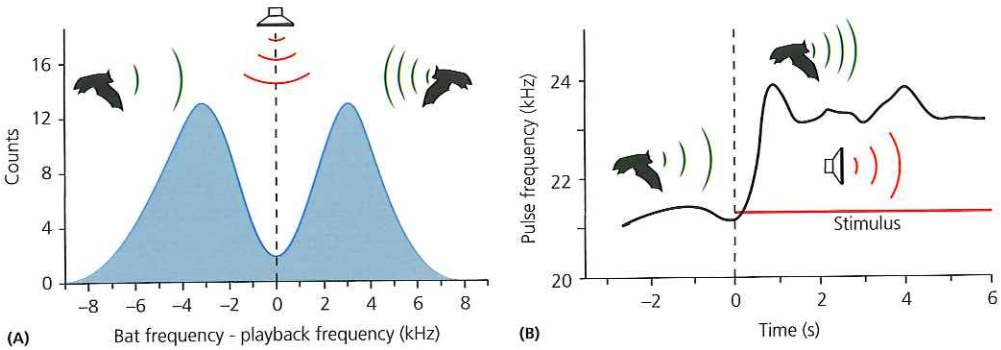

Figure 5.12 The jamming avoidance response (JAR) of Brazilian free-tailed bats. **A**: Free-flying bats avoid the frequency of a bat recording played back on a continuous loop. The histogram shows the count of calls within particular frequency bins relative to the playback frequency (dashed line). **B**: A recording of calls at a particular frequency (red line) is switched on (dashed line) when a free-flying bat calling at the same frequency approaches. The free-flying bat rapidly increases its frequency to avoid that of the playback (the calls are FM calls, and frequency refers to the minimum frequency in the broadband sweep). Data from Gillam *et al.* (2007).

the meal. The terminal buzz is only emitted in the last stages of an attack, so a would-be thief is unlikely to be able to get to the food first, but it has recently been shown that the Brazilian free-tailed bat (the same species that shows jamming avoidance during the search phase, as described above) actively attempts to jam the attack of a conspecific food rival if it hears it emit a terminal buzz (Corcoran and Conner, 2014).

The jamming bat emits a unique **sinusoidal frequency-modulated** (sinFM) call, which starts shortly after the onset of the other bat's terminal buzz. This persists for about 100 ms and repeats throughout the duration of the terminal buzz. As its name suggests, the sinFM call contains rapid oscillations in frequency, and the period of these oscillations is similar to, although not precisely matched to, the pulse period of the terminal buzz itself. Furthermore, the downward phase of the sinFM oscillations (which are actually more saw-tooth than sinusoidal in shape) rather precisely matches the downward FM sweep of the terminal buzz pulses. The result is that the jamming signal mixes in with the returning echoes of the attacking bat, and the attacking bat is completely put off its stroke. Field studies show that the success rate of hunting bats decreases from a capture rate of 30–40% to less than 10% in the presence of a jamming competitor.

If the attacking bat misses its prey due to jamming, then it is likely to swing around and have another go but, in the meantime, the prey is open to attack by the jammer. The tables are now turned, and the loser of the first attack may try to jam the attack of the second bat. This can continue for several cycles, with each bat jamming the attack of the other, and then having a go itself.

5.5 Brain mechanisms of echo detection

As we have seen, bats use their highly specialised echolocating ability to sense the changing details of their environment right down to the beat of an individual insect's wings and, unsurprisingly, the accompanying brain processing is complex. In the earlier chapters on passive hearing in owls and mammals, we discussed brainstem and midbrain

Table 5.1 Three maps within the bat auditory cortex encode different target properties. These maps are discussed in detail in the text.

Area	Signal	Parameter	Output	Activation map
FM-FM	call + echo	time delay	target range (+ size)	caudal – target far rostral – target near
CF-CF	call + echo	frequency	relative target velocity	caudal – constant range rostral – closing in
DSCF	echo only	frequency + amplitude	target flutter	central – high freq. peripheral – low freq. dorsal – high amp. ventral – low amp.

processing mechanisms in some detail. In this chapter, however, we will concentrate on higher processing at the level of the auditory cortex and make only brief mention of earlier stages in the circuit[9]. The cortex mediates the *perception* of the auditory properties necessary for echolocation, but the computation of these properties takes place mainly at sub-cortical levels.

5.5.1 The auditory cortex

The **auditory cortex** in bats is a rather miraculous merger of not one, but at least three, neural maps (Table 5.1), which allow the bat to interpret target range and size, relative velocity and, to some extent, identity (Suga, 1990b). The maps are best known from studies on the Parnell's moustached bat, *Pteronotus parnellii* (Figure 5.13A), and most of the information in this section derives from work on this species – an old, but still highly informative and very readable review is given in Suga (1990a).

The moustached bat broadcasts classic CF/FM signals (Figure 5.13B). The base frequency of the CF component (first harmonic H_1) is about 30.5 kHz in frequency, but is remarkably low in amplitude. In fact, it is so soft that it can probably only be heard by the individual emitting the call, and it does not produce a significant echo. This has interesting and important consequences, as we will see shortly. The second harmonic (H_2) has the highest volume, with the third (H_3) and fourth (H_4) harmonics progressively weaker, but still stronger than the first. The FM component of the signal is a sweep from the CF frequency down to about 25 kHz, but with the same amplitude difference between harmonics as occurs for the CF component.

5.5.2 Range and size analysis: the FM-FM area

As discussed previously, FM-type auditory signals have characteristics which mean that they can be analysed with exquisite timing accuracy and, hence, they are ideal for detecting pulse-to-echo delay and thus target range. There is a half-moon-shaped region in the

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[9] The basic route to the cortex is similar to that of most sensory modalities – auditory information projects through the thalamus, the gateway to the cerebral cortex, and then radiates onto the appropriate cortical area for processing. In the hearing system, the relay stations for auditory information in mammals include the medullary cochlear nucleus and the superior olivary and lateral lemniscus nuclei of the pons (all in the brainstem), the inferior colliculus in the midbrain, and the forebrain medial geniculate nucleus in the thalamus.

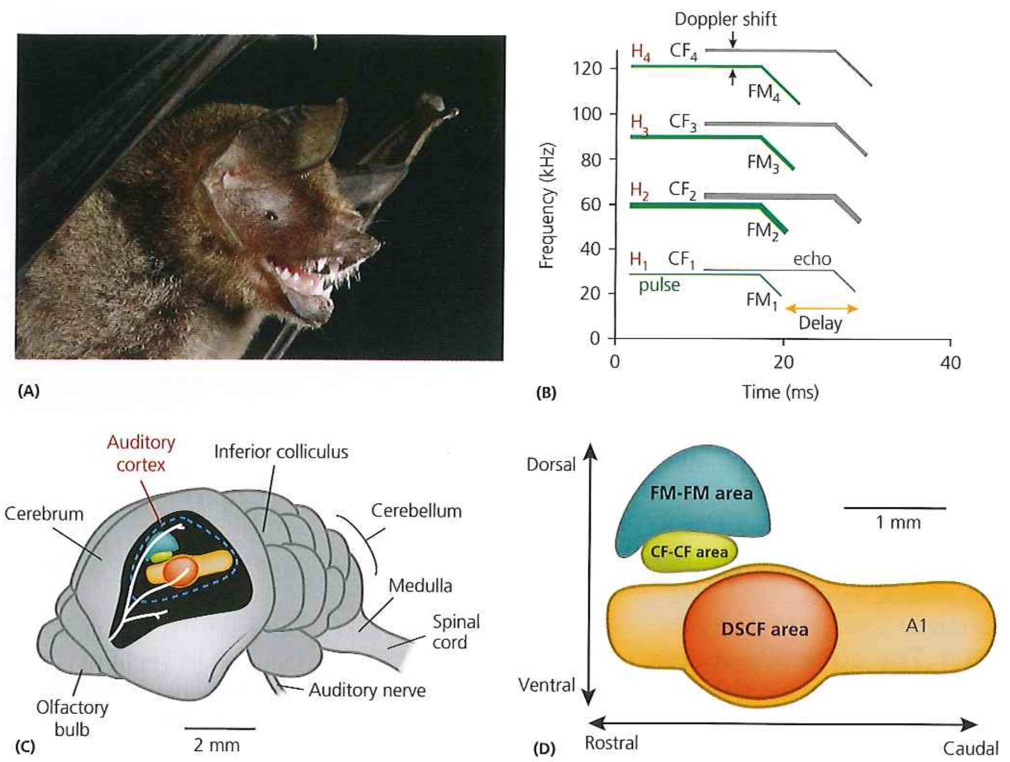

Figure 5.13 Echo processing in Parnell's Moustached Bat (*Pteronotus parnellii*). **A**: The bat. Photograph courtesy of Alex Borisenko, Biodiversity Institute of Ontario. **B**: Schematic of a CF/FM pulse emitted by the bat and the received echo. The pulse component at the fundamental frequency (H1; CF1 + FM1) is much weaker than those of higher harmonics (H2–H4). The echo is delayed in time by about 10 ms, indicating that the target range is currently 1.7 m, and Doppler-shifted slightly upwards in frequency at each harmonic, indicating that the bat making this call is catching up with its target. **C**: The auditory cortex occupies a large part of the cerebrum within the brain. **D**: An expanded view of the auditory cortex, highlighting three areas concerned with processing echo information: FM-FM, CF-CF and DSCF. The DSCF area is an expanded region within the primary auditory cortex (A1). B, C, D adapted from Suga (1990a) with permission of Patricia Wynne.

bat auditory cortex known as the FM-FM area, which is dedicated to this purpose (Figures 5.13D and 5.14). The neurons in this region respond to FM-type auditory input but, in order to get a strong response, the input has to occur as a *pair* of sounds with a short specific interval between them – they are **combination-sensitive neurons**. The neurons spike in response to the echo component of a pulse-echo pair, but different neurons in the region respond to different pulse-echo intervals within the range of about 0–20 ms. In this way, the different neurons code for different target ranges.

There is a further twist to the combination sensitivity story. In the moustached bat, FM-FM neurons only respond well if the *first* sound in the pair is within the range of the fundamental frequency H_1 and the *second* sound in the pair is within the range of one of the higher harmonics (H_2, H_3 or H_4). Now, remember that the H_1 component is so quiet that a bat can only hear its *own* H_1. This means that a bat's FM-FM neurons give a good response only to its *own* call-echo pairs, not to those emitted by other bats. This ingenious mechanism enables these bats to hunt (and navigate in crowded roosts such as caves,

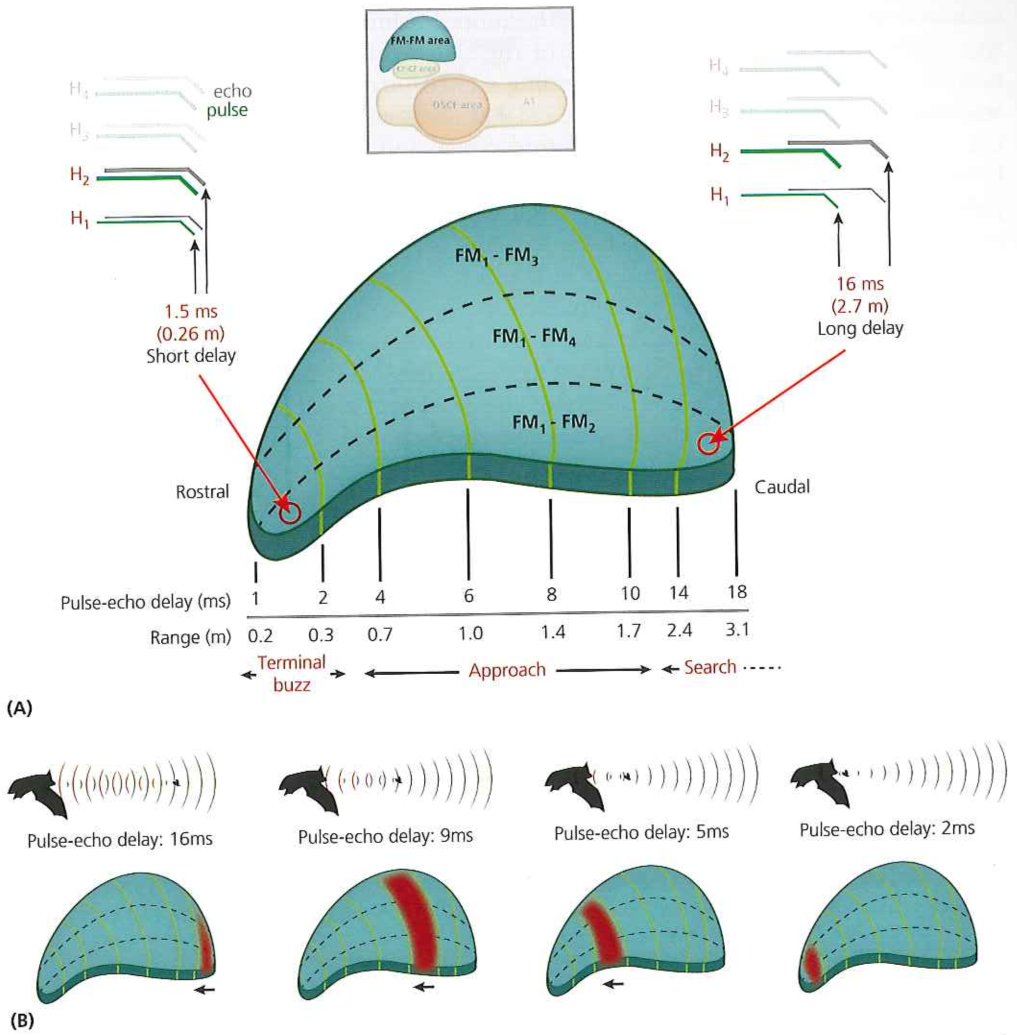

Figure 5.14 The FM-FM area of the bat auditory cortex is specialised for range detection. **A**: The cortex is organised into three slabs containing neurons responding to combinations of the first harmonic pulse with the second, fourth or third harmonic echo, respectively. Neurons within columns shown by the green lines respond to the same pulse-echo delay. Rostral regions contain neurons responding to short pulse-echo delays, indicating a target at short range, while caudal regions contain neurons responding to longer delays, indicating the target is further away. Note the expanded region dedicated to analysing mid-range targets. The pulse-echo diagrams show a slight Doppler shift, indicating that the bat is gaining on its target. Adapted from Suga (1990a) with permission of Patricia Wynne. **B**: As the bat gains on its target, neural activity sweeps from caudal to rostral regions as the range shortens.

or belfries) without being confused by the cacophony of call-echo paired sounds emitted by all of the nearby bats[10].

The delay-sensitive neurons are not randomly located within the FM-FM cortical region, but occur as three adjacent slabs, containing H_1-H_2, H_1-H_4 and H_1-H_3 delay-sensitive

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[10] This is not necessarily the case for all bat species – some respond to the same harmonic in the emitted call and returned echo. We do not know how these bats avoid confusion.

neurons, respectively (Figure 5.14). Furthermore, within each slab, the short-delay sensitive neurons occur at the rostral end of the slab, with longer-delay-sensitive neurons located progressively caudally, thus forming a **chronotopic** map. An approaching object will cause a sweep of activity across the FM-FM area, starting with neurons at the back of the cortex when the target first comes into range, and spreading to the front as contact between the bat and its target becomes imminent. The aim of the game is to reduce the pulse-echo delay to zero, and the bat's brain 'knows' the direction in which activity has to propagate through the cortex to achieve this aim.

Delay specificity is not generated in the cortex itself, since it is already apparent in pre-cortical areas such as the central nucleus of the inferior colliculus (ICC) (Portfors and Wenstrup, 1999). The actual mechanism for its generation is not absolutely certain but, in principle, it is thought to be similar to the Jeffress mechanism described earlier for owls (see Chapter 3). There are many ICC neurons that are frequency-specific, some of which respond to sounds in the H_1 range and others to those in H_2 and higher harmonics. It is likely that the delay-specific ICC neurons act as coincidence detectors that receive input from both H_1- and H_2-specific neurons, but that the H_1 input passes through a delay line. Thus, if the H_1 input produced by a call is delayed by, for instance, 16 ms, then it will sum with the H_2 input produced by the echo from that same call if it is generated by a target 2.7 m away, and the ICC neurons will have an enhanced response to the paired input.

As well as delay processing, there are also sub-sets of neurons within the delay-specific group in the FM-FM area that respond best to different echo *amplitudes*. For a target at a particular range, the amplitude of the echo is determined largely by the size of the target – big targets produce louder echoes from the same call than do small targets. Thus, the location of neurons that are active within the FM-FM region tells the bat not only how far away its potential meal is, but also how big it is.

5.5.3 Velocity analysis: the CF-CF area

Ventral to the FM-FM region lies another auditory map known as the **CF-CF area**, which processes frequency information (Figures 5.13 and 5.15). As its name suggests, this area is dedicated to processing the CF component of the signal, and we have already seen that this is the part of the call that undergoes Doppler shift velocity compensation.

Neurons in the CF-CF area, like those in the FM-FM area, are *combination* sensitive neurons – they respond best if activated by both the fundamental of the emitted pulse and a higher harmonic in the echo. There are two main regions; the dorsal CF_1/CF_2 region responds to the fundamental and second harmonic, while the ventral CF_1/CF_3 region responds to the fundamental and third harmonic.

The layout of the CF-CF region encodes differential velocity (the speed with which the bat is gaining or losing on its target) by using a rather clever **2D tonotopic** (i.e. frequency) map (Figure 5.15). There is a narrowband map of H_1 frequency sensitivity from about 28–31 kHz along the rostro-caudal axis, and a narrowband map of H_2/H_3 frequency sensitivity along an axis at right angles to this. This means that activity in a neuron at a particular *X-Y* coordinate within this map indicates a particular combination of H_1 and H_2/H_3 frequencies.

Imagine a bat emitting a call with H_1 at exactly 30.5 kHz. If the bat is keeping pace with the target and neither gaining nor losing ground, then there will be no Doppler shift, and the returned H_3 echo will be at precisely 91.5 kHz (i.e. three times the fundamental 30.5 kHz). This will activate neurons at the 30.5 × 91.5 kHz intersection

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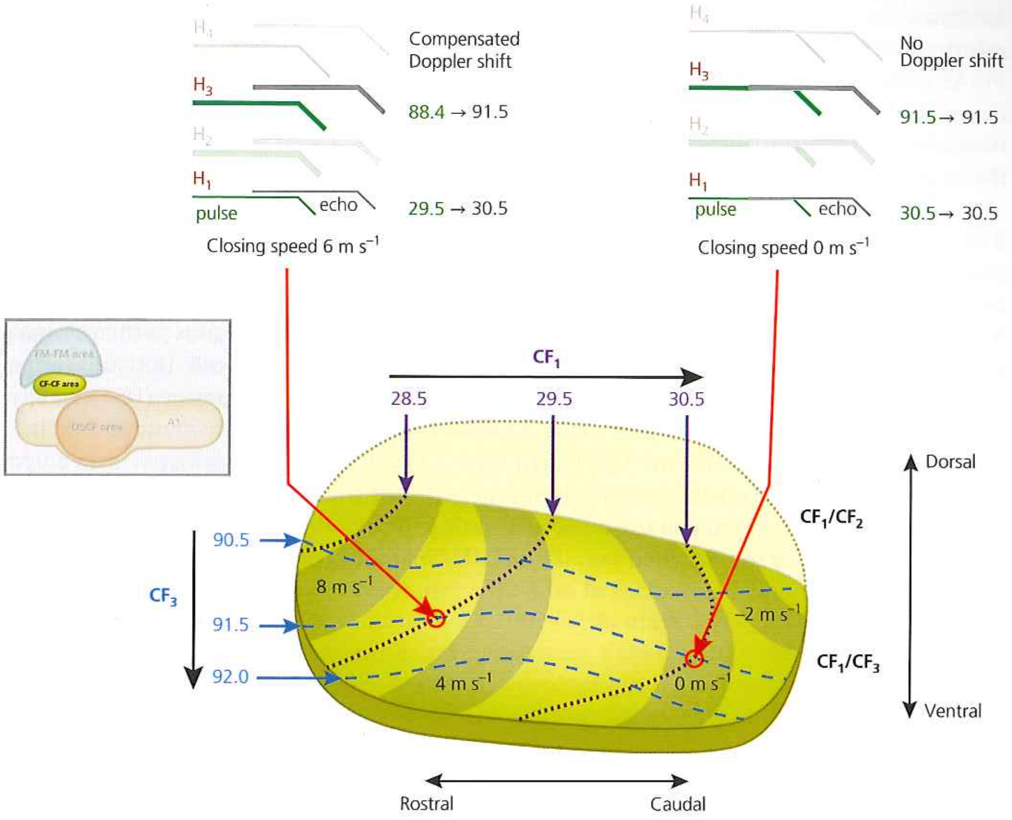

Figure 5.15 Activity in the CF-CF area encodes relative velocity information. There are two regions – CF1/CF2 and CF1/CF3 – but only the latter is shown here in detail. Individual neurons respond to a combination of particular CF1 and CF3 frequencies, depending on their location in the map. Dotted lines (purple, more or less vertical) indicate contours containing neurons responding to particular CF1 frequencies, while dashed lines (blue, more or less horizontal) indicate contours containing neurons responding to particular CF3 frequencies. The grey/yellow bands indicate regions where neurons are all sensitive to the same velocity differential. The pulse-echo diagram at the top right shows constant range (closing speed 0 m s^{-1}) with no Doppler shift, while that on the top left shows closing range with full Doppler shift compensation. With constant range, the pulse and echo have the same frequency but, with closing range, the bat has dropped its emitted pulse frequency in order to maintain the echo within the auditory fovea. Adapted from Suga (1990a) with permission of Patricia Wynne.

(Figure 5.15, right-hand example). However, if the bat is gaining on the target, the echoes will start to Doppler shift upwards in frequency, and the bat will drop its emitting frequency to compensate. For perfect compensation, a bat gaining on its target at a rate of 6 m s^{-1} would need to emit a pulse with H_1 at 29.5 kHz and H_3 at 88.4 kHz. The bat will, of course, hear the emitted H_1 pulse at its actual emission frequency, but the returning H_3 echo will Doppler-shift to 91.5 kHz, thus activating neurons in the CF_1/CF_3 region at the 29.5 × 91.5 kHz intersection (Figure 5.15, left-hand example).

The overall effect is that the 2D tonotopic map generates an implicit velocity map, with activity at the extreme rostral end indicating that the bat is gaining on the target at about 9 m s^{-1}, and activity at the extreme caudal end indicating that the target is pulling away from the bat at about 2 m s^{-1}. In this way, the region of peak activity in the CF-CF map indicates the rate at which the bat is gaining or losing on its prey, which is very useful information for a chase in the dark!

As with the FM-FM region, the actual mechanism for combination sensitivity does not lie in the cortex itself, but earlier in the pathways. It is likely that frequency-specific neurons from the inferior colliculus are integrated within the medial geniculate nucleus, and that may be where the combination sensitivity actually arises.

5.5.4 Fine frequency analysis: the DSCF area

Just ventral to the CF-CF area runs a cortical strip that also contains a tonotopic map, with neurons responding to low frequencies located at the caudal end, and those responding to high frequencies at the rostral end (Figure 5.16). This is thought to be homologous to the **primary auditory cortex** (A1) of other mammals. However, in bats with a CF call, this strip has an expanded central region known as the **Doppler-shifted constant frequency** (DSCF) analysis area. This is the largest sub-region in the auditory cortex, and occupies almost 30% of it.

All of the neurons within the DSCF area have a best frequency response within a very narrow range centred on the second harmonic (CF_2) of the Doppler-compensated echo, irrespective of the frequency of the pulse generating the echo[11]. They are still tonotopically organised but, in the moustached bat, the map is circular rather than linear. The neurons at the centre have best frequencies of 60.6 kHz, but as one moves towards the periphery, the best frequency increases up to 62.3 kHz.

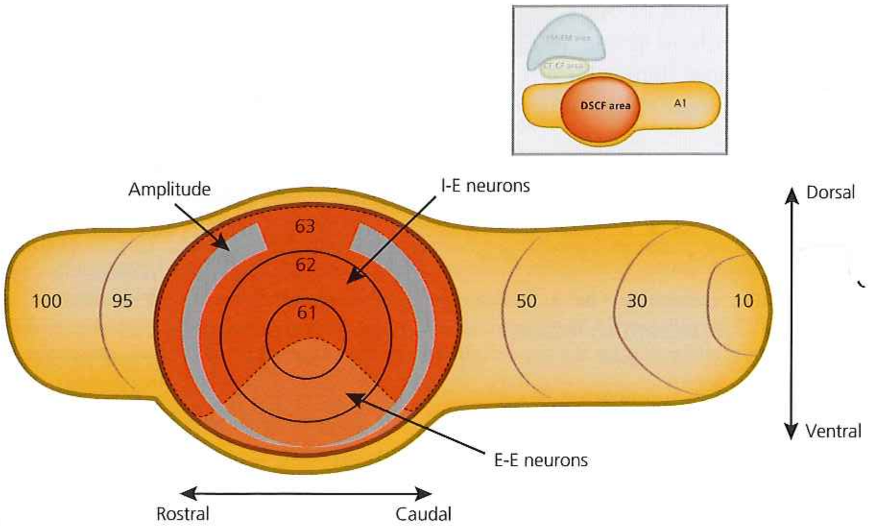

Figure 5.16 The Doppler-shifted constant frequency (DSCF) analysis area. The DSCF area (orange-red) is located within the primary auditory cortex (beige). Within the DSCF, there is a concentric tonotopic map tightly focused on the CF2 frequency, and a radial amplitude map. Neurons in the dorsal region tend to have a fairly high threshold, and are directionally sensitive (I-E), while ventral neurons have very low thresholds, but are not directionally sensitive (E-E). Adapted from Suga (1990a) with permission of Patricia Wynne.

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[11] Some DSCF area neurons do, however, have an enhanced response if they are stimulated with both CF_2 and the first harmonic of the FM portion of the emitted pulse (FM_1), if the delay between the two is within the behaviourally relevant range. However, the facilitation is generated over a broad range of delays, so these neurons are not likely to convey precise range information (Fitzpatrick *et al.*, 1993).

In addition to the frequency map, there is also an amplitude map, with ventral neurons responding best to low-amplitude signals and dorsal neurons responding best to high-amplitude signals. Part of the reason for this difference is that the ventral neurons are excited by the summed input from both ears (E-E neurons), while dorsal neurons are excited by contralateral sound, but inhibited by ipsilateral sound (I-E neurons) (Manabe *et al.*, 1978). The E-E neurons are thus specialised for detection, while the I-E neurons mediate directional selectivity but are less sensitive.

These properties make the DSCF region ideal for detecting the small frequency changes that drive Doppler shift compensation, and also for processing the very small frequency and amplitude changes resulting from target flutter. Flutter parameters are among the most important cues for target identification and that is, indeed, thought to be one of the main analytical functions of the DSCF region. Pharmacological disruption of the DSCF area severely compromises the bat's ability for such detailed frequency analysis, but has no effect on range determination, while disruption of the FM-FM area has the opposite consequences (Riquimaroux *et al.*, 1991).

5.6 Evolutionary considerations

Fifty to sixty million years ago was a busy time for evolution. The dinosaurs had gone, along with about half of all the other animal species, thus leaving a lot of opportunity for the survivors. Flowering plants had recently (geologically speaking) arrived on the scene and were undergoing a massive diversification. Simultaneously, and not coincidentally, insects, too, were speciating and, in particular, the nectar-sucking Lepidoptera made their appearance. While all this was happening, birds were improving their flight capability and challenging insects for daytime dominance in the open sky (Clapham and Karr, 2012), while nocturnal insectivorous mammals were making a meal of insects on the ground. Many insects – especially the moths – then took refuge in night-time flight, which was still, at this time, a relatively safe environment.

Then, about 53 million years ago, the first bats appear in the fossil record (Simmons *et al.*, 2008). Bats are thought to have evolved from shrew-like insectivorous mammals, and these early fossils have claws on all their digits (unlike modern bats), perhaps indicating that they were agile tree climbers. However, the important point is that the earliest fossils show developed wing structures apparently capable of fully-powered flight. Bats were thus able to take to the air and feed off insects at night, if only they could find them.

The question of which came first for bats – flight or echolocation – has long puzzled scientists. However, several lines of evidence are now coming together to indicate that flight came first. Firstly, and most importantly, the earliest known fossil bat had functioning wings, but its cochleae were smaller than those of bats which echolocate. In fact, they were similar in size to modern non-echolocating bats. Secondly, echolocation works best in an open and uncluttered environment, such as the open sky. Of course, some modern bats can operate in dense woodland, but this requires highly sophisticated sonar, and it seems reasonable to suppose that the earliest sonar would have been the simplest. Thirdly, sonar calls are expensive to produce if the bat is stationary, but almost free if it is in flight. One can rather easily imagine that the sound produced by the rhythmic rasping breath of a panting bat chasing a flying insect (perhaps in twilight, at this stage of the story) could have been the starting point for evolution to make use of the returned echo. It is rather harder to imagine that a bat would sit and pant for no reason, and then discover that there were echoes to be exploited.

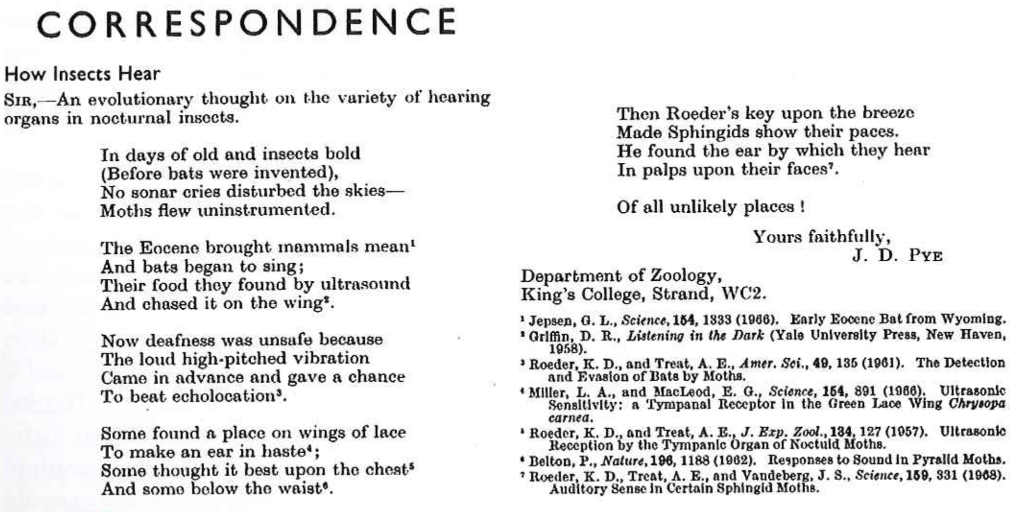
Whatever the exact sequence of echolocation evolution, there is no doubt that the mechanism has undergone massive changes. It is not at all clear whether echolocation evolved once in the ancestral bat, or many times as bats speciated, but it is clear that there have been multiple episodes of divergence, convergence and loss, driven largely by ecological, rather than phylogenetic, influences (Jones and Teeling, 2006). Efforts to reconcile bat phylogeny with the enormous diversity of echolocation modalities have, so far, been largely inconclusive.

5.7 The insects fight back

At this stage, the reader could be forgiven for thinking that the hapless insects are completely defenceless and at the mercy of their aerial predators but, of course, this is not the case. Evolution has given the insects some ingenious ways to fight back, and the interaction between bats and insects is generally regarded as a classic example of a predator-prey arms race (Waters, 2003; Conner and Corcoran, 2012). Moths, crickets, beetles, mantids and other insects have all evolved various adaptations to evade and combat their night-flying predators. So now let us look at some of these anti-bat countermeasures, especially those of the moths which are the main target for many bats.

5.7.1 Moth ears and evasive action

At least 14 families of moths have ears that are tuned to detect the ultrasonic signals emitted by bats, and these have evolved independently in different parts of the body in different groups (Figure 5.17). The most common form is a bilateral pair of thin cuticular plates (tympana), which act as microphone membranes, combined with quite a complicated interior arrangement of tracheal air sacs. However, the neurobiology of bat-detecting ears is usually simple, with only a few sensory neurons attached to each tympanum (in noctuid



CORRESPONDENCE

How Insects Hear

Sir,—An evolutionary thought on the variety of hearing organs in nocturnal insects.

In days of old and insects bold
(Before bats were invented),
No sonar cries disturbed the skies—
Moths flew uninstrumented.

The Eocene brought mammals mean[1]
And bats began to sing;
Their food they found by ultrasound
And chased it on the wing[2].

Now deafness was unsafe because
The loud high-pitched vibration
Came in advance and gave a chance
To beat echolocation[3].

Some found a place on wings of lace
To make an ear in haste[4];
Some thought it best upon the chest[5]
And some below the waist[6].

Then Roeder's key upon the breeze
Made Sphingids show their paces.
He found the ear by which they hear
In palps upon their faces[7].

Of all unlikely places !

Yours faithfully,
J. D. Pye

Department of Zoology,
King's College, Strand, WC2.

[1] Jepsen, G. L., *Science*, **154**, 1333 (1966). Early Eocene Bat from Wyoming.
[2] Griffin, D. R., *Listening in the Dark* (Yale University Press, New Haven, 1958).
[3] Roeder, K. D., and Treat, A. E., *Amer. Sci.*, **49**, 135 (1961). The Detection and Evasion of Bats by Moths.
[4] Miller, L. A., and MacLeod, E. G., *Science*, **154**, 891 (1966). Ultrasonic Sensitivity: a Tympanal Receptor in the Green Lace Wing *Chrysopa carnea*.
[5] Roeder, K. D., and Treat, A. E., *J. Exp. Zool.*, **134**, 127 (1957). Ultrasonic Reception by the Tympanic Organ of Noctuid Moths.
[6] Belton, P., *Nature*, **196**, 1188 (1962). Responses to Sound in Pyralid Moths.
[7] Roeder, K. D., Treat, A. E., and Vandeberg, J. S., *Science*, **159**, 331 (1968). Auditory Sense in Certain Sphingid Moths.

Figure 5.17 How insects hear (Pye, 1968, reproduced with permission from *Nature*).

moths, there are just two). These neurons are not differentially sensitive to frequency, but they do show intensity range fractionation. This means that when a moth hears a bat's ping, it can figure out how far away it is from how many of its sensory neurons are recruited, combined with the spike frequency of the active neurons. The ears are also directionally sensitive, so the moth knows which direction the bat is coming from. Furthermore, and most importantly, the lowest threshold neurons are sufficiently sensitive to hear most bat pings at a range where the returned echo is still too soft for the bat to hear it[12]. This gives the moth a head start in the race for survival.

If a bat call is detected at long range, then a moth usually responds by flying more erratically, which probably makes it harder to detect, because it will not return a stable echo. If the frequency and intensity of the bat call increases dramatically (the terminal buzz), indicating that the bat has locked on and is about to strike, then many moths go into an emergency power dive in a last-ditch attempt to evade capture[13]. The fact that some bats attack their prey by diving below it, and then doing a spectacular, but presumably challenging, 'back flip' to catch it, may be a tactic developed to counter this evasive behaviour of the moth. In fact, this may even be a case where the predictability of an escape response is being exploited by a predator!

Another bat countermeasure to moth ears is simply stealth. The barbastelle bat (*Barbastella barbastellus*) makes a very quiet call, compared to other bats (Goerlitz *et al.*, 2010). The downside for the bat is that it can only detect moths at close range but, within this range, the echo is loud enough for the bat to hear it while the insect is still unaware of the quiet ping – a clear advantage to the bat. In fact, the barbastelle can get almost ten times closer to a moth before it is detected than the more noisy bats with which it competes for the same food. The success of this strategy is indicated by the relatively high proportion of eared-moth remains found in barbastelle faecal pellets, compared with the pellets of noisier bats.

Evasive manoeuvres are not cost-free for a moth, particularly a male moth following the sex-attractant pheromone plume of a conspecific female. He may have travelled a long distance, and thus made a considerable energy investment, in pursuit of a mate, and it would all go to waste if he lost the plume while dodging an unimportant threat. Consequently, male moths carry out a cost-benefit analysis when they hear a bat call. If the odour plume is weak or non-existent, they are risk averse; they take evasive action even to soft, long-range bat calls. However, if the odour concentration is high, then they ignore such calls and only respond to loud calls indicating imminent danger (Skals *et al.*, 2005).

5.7.2 Bad taste

Another moth defence is chemical. Some species, particularly the tiger moths (family Arctiidae – those with the 'woolly bear' caterpillars), can concentrate noxious chemicals in their bodies, such as alkaloids and cardiac glycosides, which they acquire from their plant diet or synthesise *de novo*. These animals are unpalatable to their predators, and many of

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[12] The moth's ears are not nearly as sensitive as the bat's but the echo, of course, has far less energy at the bat's ear than the ping has at the moth's ear.

[13] Jangling keys are a good source of ultrasound, and apparently the moth evasive response was first noticed by one of the pioneers of insect neuroethology, Kenneth Roeder, when he was trying to insert his keys into his front door and noticed he was getting dive-bombed by the moths circling his porch light. This momentous historical event is referenced in Figure 5.17!

them have bright warning colouration to advertise the fact. This **aposematic** strategy works fine in daylight but is, of course, close to useless at night when most bats hunt, so an additional line of defence has evolved.

5.7.3 Shouting back

When a tiger moth detects an inbound bat, it responds by emitting a series of loud ultrasound clicks. These are generated by cuticular plates known as **tymbal organs**, which are pulled and released by a small muscle, so that they click as they buckle back and forth, a bit like pressing the lid of a biscuit tin in and out. This is, evidently, a highly successful countermeasure, since moths whose tymbal organs have been experimentally disabled (by puncturing with a fine pin) are much more likely to get caught by bats than those with intact organs (Corcoran and Conner, 2012).

The main function of such simple clicks is to act as the auditory equivalent of bright colours; they warn a bat that it is not going to enjoy its meal, even if it catches it. The utility of this signal to both participants is evident from the fact that bats often spat out unpalatable moths which they had caught, whose tymbals had been experimentally disabled, and which had therefore not been able to emit the warning clicks. The theory is also supported by the fact that clicking is a less effective defence against naïve bats; the bats have to learn the association between clicks and bad taste. However, the clicks do give some defence even against inexperienced bats, simply by acting as an **acoustic startle stimulus** (**deimatic** display; see Chapter 9, on the mammalian startle reflex), causing momentary alarm and confusion on the part of the bat, which may give the moth just enough time to escape.

The fine detail of the clicks varies between unpalatable tiger moth species but, for many, the overall spectral structure is quite simple (Figure 5.18). This appears to be a case of **Müllerian mimicry**, in which the aposematic signals of different species converge, due to the advantage of sharing the cost of educating the predator (e.g. the dogbane tiger moth and polka-dot wasp moth – Figure 5.18).

Wherever there are animal signals, there are also very likely to be cheats. The milkweed tiger moth is palatable to bats (although it may be unpalatable to other predators) and emits very similar clicks to the dogbane tiger moth, which is definitely unpalatable to bats (Figure 5.18). This is a neat example of **Batesian mimicry**, whereby a harmless species mimics a harmful one as a means of tricking a predator into thinking it poses a threat. If the tymbals are disabled on these imitator moths, the bats will attack and eat them voraciously, indicating that it is, indeed, the clicking that is putting them off.

Sonar jamming

There is, however, at least one group of moths that diverge from this pattern of simple clicks. Moths in the genus *Bertholdia* produce clicks with complex spectral and timing components that scan across a wide range of frequencies, and they produce these clicks only at the last moment before an attack (Figure 5.19). The purpose of the clicks has been the subject of considerable research and debate, but the most likely explanation is that they are a genuine case of **sonar jamming** (Corcoran *et al.*, 2011). As we outlined earlier in the chapter, the neural processing involved in bat echolocation is dependent on crucial timing differences between the calls and their echoes, with single cells in the FM-FM cortical region only responding to specific pulse-echo temporal delays.

Obviously, the moth cannot predict when the bat will call, so crucial to the jamming mechanism is that the moth emits its clicks at high frequency. At least some of these will

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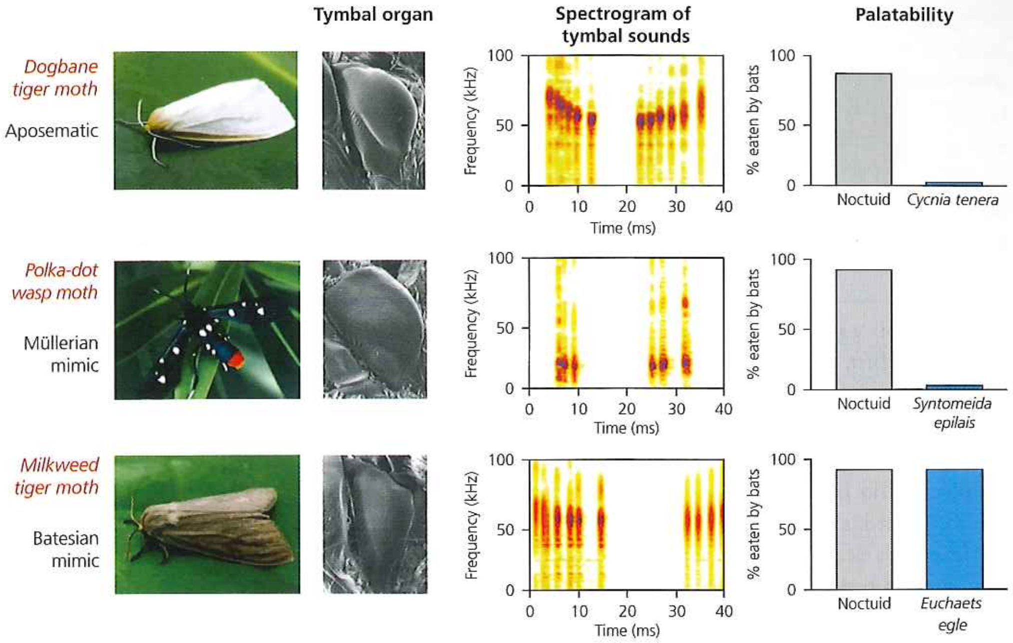

Figure 5.18 Tiger moths emitting tymbal clicks with a simple spectral structure. Each row shows (from left) the common name and defence strategy, a specimen picture, a scanning electron micrograph of the tymbal organ, a sample spectrogram of clicks, the palatability relative to a Noctuid palatable control. Top row: the dogbane tiger moth (*Cycnia tenera*) is highly unpalatable, and its clicks are thought to be a warning (aposematic). Middle row: the polka-dot wasp moth (*Syntomeida epilais*) is unpalatable, and the similarity of its clicks to the dogbane tiger moth (or vice versa!) is thought to result from Müllerian mimicry. Bottom row: the milkweed tiger moth (*Euchaetes egle*) emits similar clicks but is palatable, so it is thought to be a Batesian mimic. Adapted from Conner and Corcoran (2012). Reproduced with permission from Annual Reviews.

occur just before, or just after, the bat's own call echo, and will thus be confused with it. From the bat's point of view, it must be like speaking on a telephone with multiple variable echoes – it evidently finds it extremely difficult to 'speak' at a normal rate, and the terminal buzz becomes distorted or absent. This confuses the bat's range-finding ability at the crucial moment, and the end result is that bats attacking a moth which is producing a jamming response consistently miss their target by 15–20 cm.

5.8 Final thoughts

The story of bat echolocation and the attendant insect response has to be one of the most compelling in the whole of biological science. It is a wonderful exemplar of the endless evolutionary war between predators and their prey, and its study has required a merging of disciplines, including neuroscience, ethology, ecology, morphology and evolutionary biology, all underpinned by the physics of acoustics. It is a classic of neuroethology! There is little commercial or medical motivation behind the research, but the sheer intellectual joy that it has brought to countless biologists, both amateur and professional, is a triumphant vindication of 'blue sky' research (in this case, rather dark-blue sky).

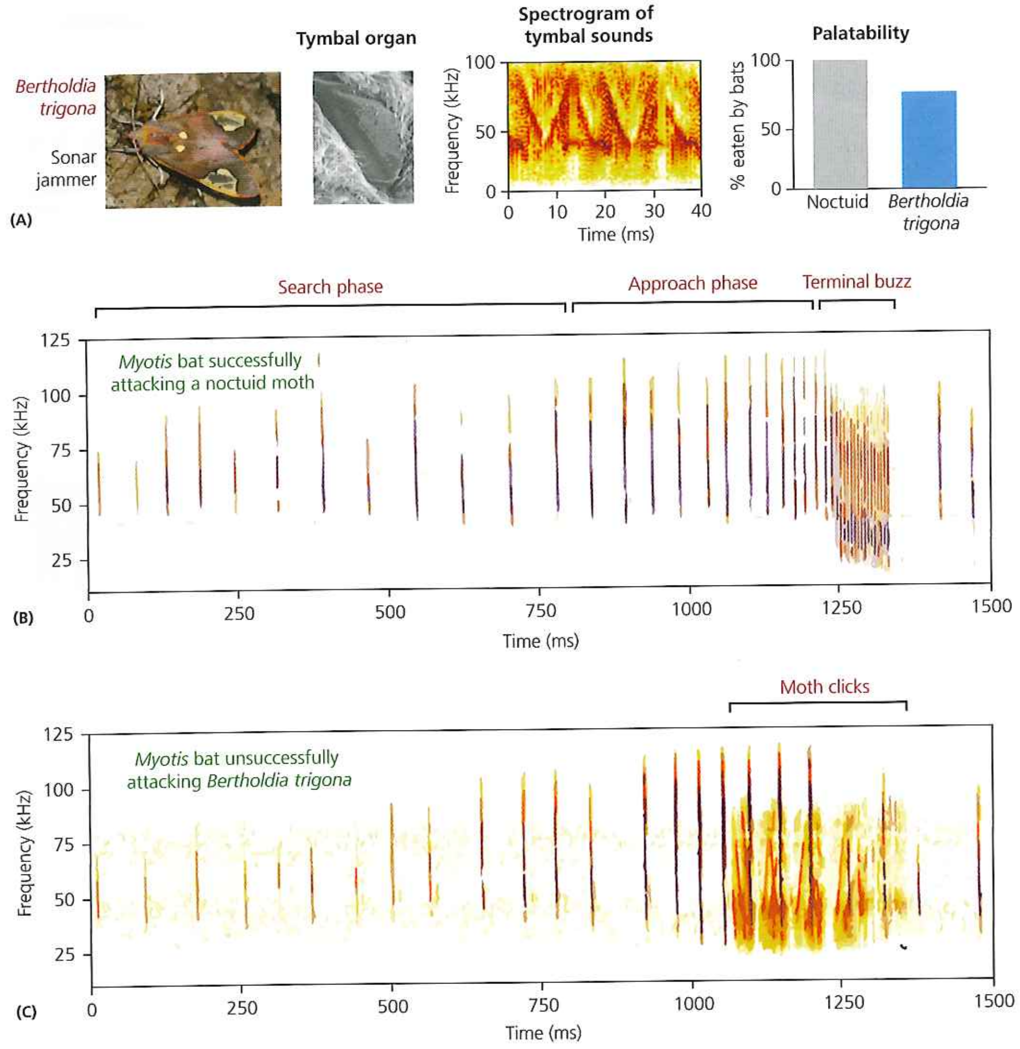

Figure 5.19 Jamming a bat's sonar. **A**: Grote's Bertholdia moth (*Bertholdia trigona*) is palatable to bats, but produces clicks with a complex spectral structure. **B**: Sonogram of calls emitted by a bat successfully attacking a tethered non-clicking, non-Bertholdia moth. Note the clear terminal buzz. **C**: A bat fails in its attack on a tethered sonar-jamming Bertholdia moth, which produces clicks as the bat homes in for its final approach. Note the complete absence of a bat terminal buzz. Adapted from Conner and Corcoran (2012) with permission from Annual Reviews.

5.9 Summary

Bats are one of the few groups of animals that can use their hearing as an active sense to detect prey. Unlike most hunters, they do not just listen for noises made by their quarry but, instead, use their specialised larynx to emit a series of ultrasound chirps, and listen for the returning echoes with highly sensitive ears. They have brain mechanisms that can analyse these echoes in exquisite detail, and determine the range, direction, relative velocity, and even size and species of their potential prey.

FM bats send out short-duration chirps which are modulated across a wide range of frequencies, and these are ideal for accurate range determination of nearby targets. Other bats send out long-duration CF chirps, which have a constant frequency for a large part of their duration, and these are ideal for long-range detection. The CF signal has an added benefit; even at short range, it allows bats to utilise the Doppler shift in the echo to figure out the relative velocity of the prey, so it knows whether to speed up or slow down to avoid overshooting. This mechanism is so sensitive that it can detect the tiny changes in Doppler shift introduced by the movements of the wings of the insect itself, thus enabling the bat to distinguish between different types of prey and non-prey objects.

Biosonar has made bats highly successful night-flying predators, but they do not have it all their own way. Insects have evolved ears that can hear the chirps, and this often gives them sufficient warning to take emergency evasive action. Some insects build up noxious chemicals in their bodies, and these may emit ultrasound chirps of their own to warn the bat that they taste nasty. Others may not actually be noxious, but send out chirps anyway, in the hope of bluffing the bat. Also, some insects send out chirps which seem specifically evolved to jam the bat's sonar so that, even if the bat attacks, it usually misses its target. Furthermore, sonar jamming is not just a defence response of potential prey, it is also used aggressively by some bats in an attempt to steal food from conspecific rivals.

Abbreviations

A1	primary auditory cortex
CF	constant frequency call
DSC	Doppler shift compensation
DSCF	Doppler-shifted constant frequency
FM	frequency modulated call
JAR	jamming avoidance response
sinFM	sinusoidal frequency modulated call

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