

Adaptive echolocation behavior of bats and toothed whales in dynamic soundscapes

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ABSTRACT

Journal of Experimental Biology has a long history of reporting research discoveries on animal echolocation, the subject of this Centenary Review. Echolocating animals emit intense sound pulses and process echoes to localize objects in dynamic soundscapes. More than 1100 species of bats and 70 species of toothed whales rely on echolocation to operate in aerial and aquatic environments, respectively. The need to mitigate acoustic clutter and ambient noise is common to both aerial and aquatic echolocating animals, resulting in convergence of many echolocation features, such as directional sound emission and hearing, and decreased pulse intervals and sound intensity during target approach. The physics of sound transmission in air and underwater constrains the production, detection and localization of sonar signals, resulting in differences in response times to initiate prey interception by aerial and aquatic echolocating animals. Anti-predator behavioral responses of prey pursued by echolocating animals affect behavioral foraging strategies in air and underwater. For example, many insect prey can detect and react to bat echolocation sounds, whereas most fish and squid are unresponsive to toothed whale signals, but can instead sense water movements generated by an approaching predator. These differences have implications for how bats and toothed whales hunt using echolocation. Here, we consider the behaviors used by echolocating mammals to (1) track and intercept moving prey equipped with predator detectors, (2) interrogate dynamic sonar scenes and (3) exploit visual and passive acoustic stimuli. Similarities and differences in animal sonar behaviors underwater and in air point to open research questions that are ripe for exploration.

KEY WORDS: Active sensing, Ultrasound production, Transmission and reception, Hearing, Auditory perception, Scene analysis, Predator–prey interactions

Introduction

Echolocation (see Glossary) is a major sensory modality in two diverse and highly successful orders of mammals: bats and toothed whales. These animals produce ultrasonic signals (see Glossary) and process information carried by echo returns as they move through their surroundings. Echolocation makes it possible to orient and forage in complete darkness, and to exploit food niches not available to animals that rely primarily on vision. For example, echolocation is used by bats to feed at night while avoiding diurnal

predators. Similarly, echolocating toothed whales can pursue their prey in environments with limited visual cues, and can therefore successfully feed in turbulent waters and in the deep sea, where visually dominant animals cannot efficiently forage. Echolocating bats and toothed whales represent nearly 20% of all mammalian species, and they have a significant impact on terrestrial as well as marine ecosystems (Bowen, 1997; Ramirez-Francel et al., 2021).

Over many decades, Journal of Experimental Biology has published work on animal echolocation, which provides a rich literature for our Centenary Review. The term ‘echolocation’ was coined by Donald Griffin following his seminal discoveries on bat navigation and foraging (Griffin, 1944). After Pierce and Griffin (1938) established that bats produce ultrasonic pulses, Griffin and Galambos (1941) showed through a series of elegant experiments that bats use these signals to detect prey and avoid obstacles by listening to returning echoes. Much of Griffin’s earlier work was summarized in his classic book, *Listening in the Dark* (Griffin, 1958). Initial studies of echolocation in dolphins were carried out by Kellogg (1961) and Norris et al. (1962), starting a new branch of experimental investigations of echolocators in aquatic environments. Here, we attempt to bridge these lines of research, by comparing and contrasting the production, transmission and reception of echolocation signals of bats and toothed whales as they operate in dynamic soundscapes (see Glossary).

Both echolocating bats and toothed whales broadcast sounds and use information contained in the returning echoes to determine the position, size and other features of objects (Au, 1993; Moss and Schnitzler, 1995; Thomas et al., 2004; Wisniewska et al., 2012). Echolocation exploits general functions of the mammalian auditory system that support sound detection over a wide range of frequencies and intensities, fine spectro-temporal discrimination and noise rejection. Humans also demonstrate the ability to use echoes for navigation, and can sense reverberation in rooms of different sizes and outdoors (Supa et al., 1944; Kellogg, 1962; Thaler et al., 2019). However, the resolution of human echolocation is poor, because we only hear up to 20 kHz, far below the ultrasonic auditory range of echolocating animals (Fay and Popper, 1994).

In this Review, we provide a comparison of echolocation in bats and toothed whales. In recent decades, new technologies have enabled major advances in the study of echolocating animals both in the laboratory and in their natural environments, deepening our understanding of their active-sensing systems. Differences in physical challenges imposed by the two media as well as by the size differences between bats and dolphins have been reviewed recently (Madsen and Surlykke, 2013; Brinkløv et al., 2022). Here, we consider challenges that animals encounter when using echolocation to navigate complex 3D environments and to intercept moving, evasive prey. We also discuss the use of passive acoustic listening and vision by bats and toothed whales; these sensory channels complement echolocation, allowing the animals to

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Glossary

Acoustic gaze

Directional aim of sonar transmission and reception to maximize detection and discrimination of echoes.

Acoustic glint

Spectral broadening and amplitude peak in sonar echoes produced by the moving wings of fluttering prey; sometimes also used to refer to a single sonar reflector.

Acoustic scatter

The return of sound from objects in the form of echoes; can broadly refer to the reflection, diffraction or refraction of sound.

Biosonar

Animal echolocation.

Biotope

The habitat or environment where animals live.

Constant absolute target direction interception strategy

The pursuer adjusts both its direction of motion and its speed to maintain a constant absolute direction to an erratically moving target. Unlike constant bearing, this approach minimizes the time it takes for a pursuer to intercept an unpredictably moving target. In missile guidance, this is referred to as proportional navigation.

Constant bearing interception strategy

The pursuer maintains a constant angle between its heading (velocity vector) and the target over the closing range.

Constant frequency (CF)

Stable tonal component of sound.

Doppler shift compensation

Adjustment in sonar call frequency to offset frequency shifts introduced by the relative velocity of an echolocating animal.

Duty cycle

Percentage of time that sound is present relative to silence.

Echolocation

The process by which sound energy is produced in order to return echoes for the purpose of localizing and discriminating objects in the environment.

Frequency modulated (FM)

Sound that changes in frequency over time.

On-axis beam

Directional aim of maximum sound energy towards an object.

Sonar field of view (FOV)

Region of space sampled by echolocation signals.

Sonar scene analysis

Parsing and integrating echo snapshots from stationary and moving sonar objects in the environment.

Soundscapes

Multiple sound sources in the environment.

Spherical spreading

Sound pressure halving for each doubling of distance.

Stereopsis

Visual depth perception arising from retinal disparity of binocular images.

Ultrasonic signals

Signals making use of sound frequencies above the upper limit of human hearing of ~20 kHz.

targets, such as insects and fish. Still, the returning echoes are very weak: for insects, fish and squid, about 0.001–0.1% (or –50 to –30 dB) of the signal energy, measured at 1 m range, returns to the bat or the dolphin (Norman and Jones, 1980; Surlykke et al., 1999; Au et al., 2010a; Madsen et al., 2007). To obtain audible echoes, echolocating bats and toothed whales emit signals that are more intense than any other animal sounds (Wahlberg and Surlykke, 2014). Below, we present an overview of the characteristics of bat and toothed whale echolocation signals and the acoustic cues these animals use to localize objects in their surroundings.

The intensity and frequency composition of returning echoes depend on sound production characteristics, features of the target and the acoustic properties of the medium (see Box 1). There are many similarities in biosonar signal adjustments among bats and toothed whales navigating 3D space, and yet their sonar differs in several important ways (Madsen and Surlykke, 2013). Bat echolocation calls are much longer in duration (0.5–100 ms) than the ones produced by toothed whales (<0.1 to ~10 ms). There is much less diversity in the acoustic features of toothed whale biosonar signals compared with bat echolocation calls (Fenton et al., 2014). When approaching prey, both bats and toothed whales decrease the intensity and intervals between sound emissions. Bats also modify the bandwidth and duration of their echolocation emissions, but in toothed whales such changes are only pronounced in some species (Fenton et al., 2014).

Another noteworthy difference between bat and toothed whale sonar is the directionality of emitted sound pulses. Emitting directional echolocation signals is advantageous, as this decreases the reception of clutter echoes and gives the echolocator salient localization cues for tracking and intercepting targets of interest. Bat echolocation operates with a much broader sonar field of view

Box 1. Echolocation in air and underwater – the effects of transmission media

Acoustic signals propagating through air and water differ in many respects. For example, the speed of sound in water is 4.4 times higher than that in air, resulting in the wavelength of a given frequency being 4.4 times longer in water than in air (Fig. 1). Sound production intensity and directionality depend on the ratio between emitter size and wavelength (Michelsen, 1992); therefore, aquatic animals must increase the frequency of their sound emissions and/or the physical size of the emitter to maintain high directionality and efficient sound production. The reflectivity of targets is also dependent on the size-to-wavelength ratio; thus, the frequency content of the sonar signals affects the acoustic scatter (see Glossary) returning to the echolocator (Wahlberg and Larsen, 2017).

Acoustic signals travelling through a biotope (see Glossary) are weakened and distorted by different processes. At short distances from the source, spherical spreading (see Glossary) affects sound intensity at the receiver. The cross-sectional area of the sound beam increases approximately with the square of the range, such that the sound intensity is reduced by the inverse square of the distance to the source (Larsen and Wahlberg, 2017). In addition to geometric spreading losses, signal energy is absorbed as a result of interactions between the acoustic wave and the surrounding medium. High-frequency signals are more rapidly attenuated than lower frequency ones (Lawrence and Simmons, 1982; Wahlberg and Larsen, 2017). In air, bat echolocation signals can rarely be recorded at ranges larger than a few tens of meters (Surlykke and Kalko, 2008). In water, absorption is much less, and low-frequency blue whale communication signals at 20–80 Hz can be picked up at distances of hundreds of kilometers (Sirovic et al., 2007), whereas high-frequency echolocation clicks emitted by harbor porpoises at 130 kHz can be detected up to a range of about 100 m (Nuutila et al., 2018).

solve natural tasks. Finally, we outline major research problems for the future and propose questions for new lines of research.

Echolocation signal characteristics and processing in bats and toothed whales

Echolocation builds upon the interplay between an animal's sound production and reception systems, as well as its ability to rapidly process and react to incoming streams of echoes in a dynamic soundscape. Bat and toothed whale biosonar signals (see Glossary) contain sound frequencies generally above 20 kHz, in some cases up to 200 kHz (Thomas et al., 2004; Fenton et al., 2014). Ultrasound is needed as ultrasonic frequencies efficiently reflect off small

(FOV; see Glossary) than that of toothed whales, dictated by the smaller size of their emitters (mouth or nostrils). In toothed whales, there is a gradient of decreased beam widths from the smallest species (harbor porpoise) to the largest one (sperm whale; Au, 1993; Möhl et al., 2003; Koblitz et al., 2012; Jensen et al., 2018). But even the widest transmission beam in toothed whales is only about 10 deg, as compared with ~40–60 deg in some bats at dominant call frequencies (Hartley and Suthers, 1989; Ghose and Moss, 2003; Jakobsen and Surlykke, 2010).

Apart from the effects of physical size on sonar transmission directionality, there may be functional advantages of wider sonar beam widths produced by bats in comparison with those of toothed whales. As the bat echolocation detection range of insect prey is of the order of meters, it may be difficult to track prey using a very narrow beam, especially if the prey tries to escape the approaching predator. In toothed whales, it is advantageous to operate with a very narrow beam, both to minimize returning clutter echoes and to increase the sound intensity of the on-axis beam (see Glossary) to optimize target detection and tracking. Most aquatic prey do not detect ultrasound, so the risk of prey ‘steering away’ from the sound beam is much less than for terrestrial prey. It is noteworthy that both toothed whales and some echolocating bats increase their transmission beam width in the final capture phase, potentially to monitor background and permit motor adjustments to intercept prey (Jakobsen and Surlykke, 2010; Wisniewska et al., 2015).

The auditory system of echolocating animals shows the standard organization of other mammals, while it is also specialized to receive and process echoes to represent the location and movement of objects (Suga, 1988; Covey and Casseday, 1995; Supin et al., 2001; Mooney et al., 2012). Many of the same cues used by other species to localize sound and to process complex patterns of acoustic information are exploited by echolocating animals for orientation and perception (Moss and Carr, 2012). These cues include comparisons of the intensity and arrival time of sounds at the two ears to localize sound source direction (Blauert, 1996). Where bats and toothed whales stand out from other mammals is in their ability to estimate target range from the time delay between the outgoing sonar signal and returning echo (Hartridge, 1945; Simmons, 1973; Au, 1993), and they show extraordinary spatial resolution along the range axis (Moss and Schnitzler, 1989; Simmons et al., 1990; Murchinson, 1980; Finneran et al., 2019). Below, we discuss the ways in which echolocation signals are produced and processed by bats and toothed whales in more detail.

Bat production and reception of echolocation signals

Echolocating bat species have varied diets, which include insects, fruit, nectar and small vertebrates; here, we focus mainly on echolocation calls of insectivorous species. In bats, sounds are produced either in the larynx with superfast muscles (Elemans et al., 2011) or, in some frugivorous species, by tongue clicks (Yovel et al., 2010; Lee et al., 2017). Most bat echolocation calls are in the ultrasonic range, but there are some exceptions, e.g. *Eumops floridanus*, the Florida bonneted bat, produces echolocation calls in the human-audible range (Vannatta et al., 2021). Fig. 1 illustrates that bat echolocation sounds are transmitted through the mouth or the nostrils (Hartley and Suthers, 1987, 1989). Echolocation sound intensities have been reported above 140 dB re. 20 μ Pa, measured 10 cm from the bat (Surlykke and Kalko, 2008) but are typically in the range 100–120 dB (Thomas et al., 2004).

Across bat species, there is great variation in the time and frequency structure of sonar signals, which is illustrated in Fig. 2. Many species emit frequency-modulated (FM; see Glossary)

sweeps, initially lasting as long as 10–20 ms, during the search phase of insect pursuit. As bats approach prey, they shorten their low-duty cycle (see Glossary) signals at higher repetition rates (Fenton et al., 2014). Some species, such as horseshoe bats, emit longer, high-duty cycle calls (up to 100 ms) with constant-frequency (CF; see Glossary) components preceded and followed by FM sweeps, which they also shorten as they close in on prey (Denzinger and Schnitzler, 2013).

Echolocating bats are equipped with sensitive hearing that extends well into the ultrasound range (Moss and Schnitzler, 1995), which enables the detection of sonar returns from small insect prey. Some bat species that produce long-duration, high-duty cycle CF–FM signals show mechanical specializations of the basilar membrane in the inner ear and an expanded representation of the CF component of their calls at each stage of auditory processing in the brain, from the cochlear nucleus to the auditory cortex (Neuweiler et al., 1980). Many CF–FM bats exhibit Doppler shift compensation (see Glossary) in flight to stabilize echo frequencies in the region of their maximum hearing sensitivity and frequency selectivity (Schnitzler, 1968; Long and Schnitzler, 1975), which allows them to detect and discriminate acoustic glints (see Glossary) that are produced by fluttering insect prey (Trappe and Schnitzler, 1982; Schnitzler and Flieger, 1983; von der Emde and Schnitzler, 1990). The use of Doppler shift compensation in sonar scene analysis (see Glossary) is discussed below.

Bats must not only detect objects but also localize them with high accuracy. Bats that use FM sonar calls can discriminate microsecond differences in echo arrival time, corresponding to range differences in the millimeter range (Simmons, 1973, 1979; Simmons et al., 1990; Moss and Schnitzler, 1995; Wohlgemuth et al., 2016b). Further, FM bat hearing sensitivity, call intensity and perceived loudness of echoes are adjusted with target distance (Kick, 1982; Simmons et al., 1992; Hartley, 1992a,b), which collectively serves to stabilize the level of echo sensation, thereby minimizing jitter in auditory response latencies and facilitating high-ranging accuracy (Kick and Simmons, 1984).

Directional localization discrimination by echolocating bats is ~1 deg in the horizontal plane (Simmons et al., 1983) and 3 deg in the vertical plane (Lawrence and Simmons, 1982; Wotton et al., 1995). The bat's pinna–tragus system (Fig. 1) produces changes in the spectrum of incoming echoes, creating patterns of interference that are used by the bat to estimate target elevation (Lawrence and Simmons, 1982; Wotton et al., 1995; Simmons et al., 2002). Interaural spectral cues may provide additional information for determining target angle in the vertical plane (Grinnell and Grinnell, 1965; Aytekin et al., 2004), and movable pinnae also serve to boost sonar localization cues (Grinnell and Schnitzler, 1977; Mogdans et al., 1988; Wohlgemuth et al., 2016a,b; Yin and Müller, 2019; Aytekin et al., 2004).

Toothed whale production and reception of echolocation signals

In toothed whales, sounds are generated in the nasal passages right beneath the blowhole and emitted through the melon, a fatty container resting on the telescoped mouth (Fig. 1; Au et al., 2010b; Cranford et al., 2011). Sound emissions are often extremely intense when measured at close range, in some cases back-calculated to beyond 220 dB re. 1 μ Pa, 1 m from the animal (reviewed by Wahlberg and Surlykke, 2014). Echolocation signals from toothed whales can be grouped into four major categories, all consisting of transient clicks (duration 10–80 μ s; Fig. 2), except for the longer-duration frequency upsweeps made by deep-diving beaked whales (duration of a few 100 μ s; Fenton et al., 2014). Available data

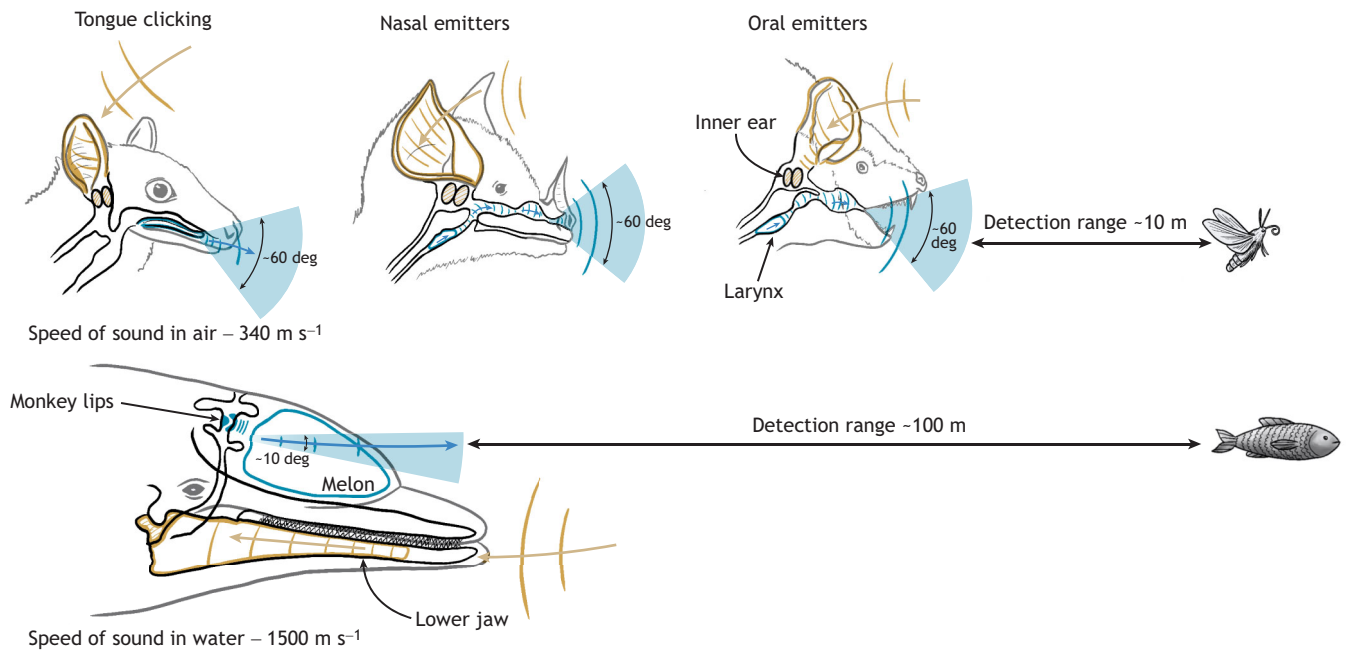


Fig. 1. Sound production and reception mechanisms in bats and toothed whales. Note that the speed of sound in water is approximately 4.4 times faster than that in air. Bats display different production and emission mechanisms (lingual and laryngeal, nasal and oral). The sonar emission patterns produced by bats are much broader than those of toothed whales. Bats receive echoes with their ears, whereas toothed whales receive sound through their lower jaw. Sonar signals produced by animals are shown in blue, and echoes received are shown in yellow.

suggest that the majority of echolocating species of toothed whales include higher frequencies in their signal emissions than do bats (Wahlberg and Surlykke, 2014), which boosts echo reflectivity from small objects. The bandwidth of many delphinid clicks ranges from a few tens of kilohertz to over 100 kHz, whereas, for porpoises, it ranges from about 110 to 150 kHz (Møhl and Andersen, 1973). The high-frequency content of toothed whale echolocation signals helps to reduce the sonar beam width compared with that of bats. Beaked whales and sperm whales use clicks of lower frequency and rely on their large size to obtain a directional sonar beam.

Similar to bats, the hearing sensitivity of echolocating delphinids changes with target distance, showing higher thresholds for echoes at short delays. This serves to stabilize the received echo within a suitable dynamic range for central auditory processing (Nachtigall and Supin, 2008; Linnenschmidt et al., 2012; Supin and Nachtigall, 2012). Toothed whales lack pinnae, and sounds enter the head directly through the fatty tissues in the lower jaw and other facial areas (Fig. 1; Møhl et al., 1999). Their directional localization accuracy is nonetheless similar to that of bats (Branstetter et al., 2022), and it appears to benefit from the detachment of their inner ears from the skull and surrounding air sacs (Mooney et al., 2012; Cozzi et al., 2016). They exhibit high sensitivity in the ultrasonic frequency range where they emit sonar clicks. Because of the higher speed of sound in water than in air (Box 1), the Doppler shift experienced by toothed whales is much smaller than that experienced by bats for a given velocity, making it unlikely to serve any function in toothed whale biosonar. Like echolocating bats, toothed whales can discriminate small differences in target range/echo delay (Murchinson, 1980; Au, 1993; Finneran et al., 2019).

Predation by echolocating mammals

Differences between the speed of sound and transmission loss in air and underwater (Box 1) affect the range and time scales over which echolocating bats and toothed whales pursue prey. Bat sonar is

restricted by the transmission loss of ultrasonic signals in air, and bats can typically only detect insect prey within a few meters (Siemers et al., 2005; Finger et al., 2022), whereas toothed whales can detect fish and squid at ranges up to hundreds of meters (Waters et al., 1995; Au et al., 2004). The large difference in sonar detection distances leads to differences in the time periods over which bats and toothed whales chase their prey. For bats, the time interval from prey detection to interception is less than 1 s (Griffin et al., 1960; Kalko and Schnitzler, 1993), whereas in toothed whales, the pursuit of prey can last many seconds (Johnson et al., 2004; Wisniewska et al., 2015).

Echolocation signals of bats and toothed whales show similar temporal patterning as they forage, from the time of prey detection to interception (Fig. 2). Both aerial and aquatic echolocators adjust the inter-signal emissions so that the echo from a target of interest is received before the next signal is produced (Griffin, 1958; Griffin et al., 1960; Schnitzler and Kalko, 2001; Madsen and Surlykke, 2013; Wisniewska et al., 2014); this simplifies the task of computing target range from the delay between isolated pulses and echoes (Simmons, 1973; Au, 1993; Surlykke and Moss, 2000). As the echolocator approaches its prey, each echo is received at progressively shorter delays, which means that the bat or toothed whale waits less time to receive target echoes.

As sound emissions are directional, the echolocator not only estimates the range to prey but also computes its direction in azimuth and elevation. Echolocators also control the direction of the emitted signals to 'sweep past' targets of interest, presumably to localize and detect movement of prey (Ghose and Moss, 2003, 2006; Wisniewska et al., 2012). In the capture phase, echolocating mammals broaden the sonar beam, which yields a larger acoustic FOV when preparing to intercept prey (Jakobsen and Surlykke, 2010; Jakobsen et al., 2012, 2013; Wisniewska et al., 2015). Both bats and toothed whales hear over a broader spatial region than the beam width of their transmitted sonar signals; therefore, all echoes

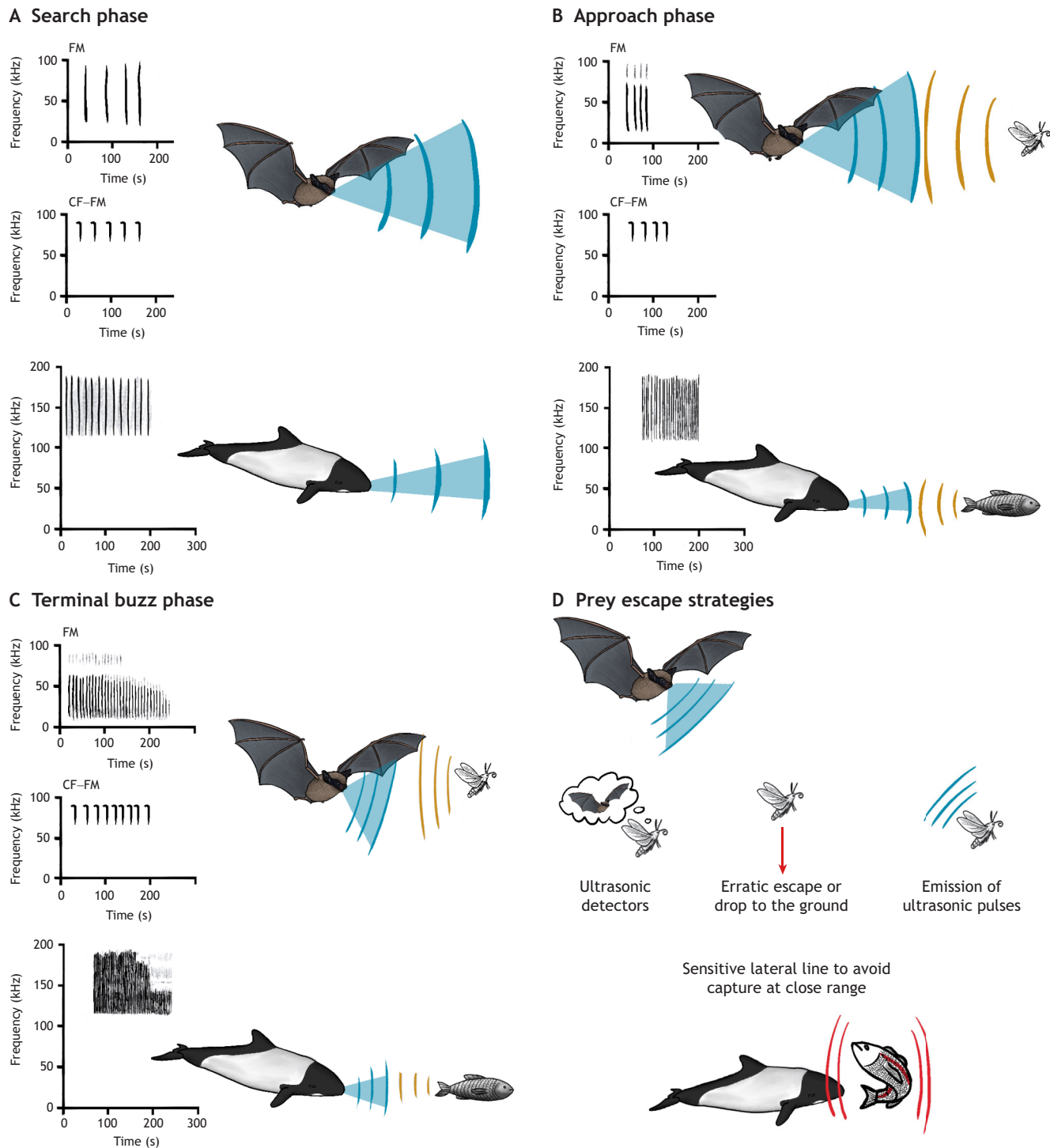


Fig. 2. Echolocating foraging signals and prey escape responses. The illustrations show the echolocation signals for frequency modulated (FM) and constant frequency (CF)–FM foraging bats and toothed whales and the sensory-guided evasion strategies of their prey. Spectrograms of the echolocation signals are also shown. Sonar signals produced by animals are shown in blue, and echoes received are shown in yellow. (A) Search phase signals, which are adapted for target detection. (B) Approach phase signals, produced by the bat or toothed whale after detection and selection of a prey item. (C) The terminal buzz phase, which is produced prior to prey capture. (D) Sensory mechanisms used by prey to detect bats and toothed whales and avoid capture at different distances from their predators.

from objects in the path of the sonar beam return to the animals' ears. In the future, combined measurements of both directional sonar emissions and hearing in diverse bat and toothed whale species will contribute to a deeper understanding of prey tracking by echolocation.

Echolocating animals reduce the intensity of their sonar emissions so that echoes are received at levels that fall within a suitable dynamic range for processing (Hartley, 1992a,b; Schnitzler and Kalko, 2001; Au and Benoit-Bird, 2003; Supin and Nachtigall, 2012; Stidsholt et al., 2021). In bats, the amplitude of received

echoes is further modulated by contractions of middle ear muscles that accompany each sonar vocalization (Suga and Jen, 1975). In toothed whales, there is a similar reduction in hearing sensitivity right after the production of echolocation clicks (Supin and Nachtigall, 2012), and one study reported that the middle ear muscles are not involved (Schröder et al., 2017). Further experimentation is needed to understand the role of middle ear muscles in toothed whale sonar, and to explain any alternative mechanism of hearing sensitivity reduction during click production.

How do bats use echolocation to localize and intercept moving prey?

As a bat flies toward an insect target, the features of its sonar vocalizations change. Characteristics of sonar emissions have been used to divide the bat's insect pursuit sequence into phases: search, approach and terminal buzz (Fig. 2; Griffin et al., 1960; Kalko and Schnitzler, 1993; Schnitzler and Kalko, 2001). Search phase signals in the big brown bat (*Eptesicus fuscus*) are characterized by shallow frequency modulation at a repetition rate of 5–10 Hz and duration of 15–20 ms. Once the bat detects and selects a prey item, it produces approach phase signals at a repetition rate of 20–80 Hz; these signals show steep frequency modulation and shorten in duration (2–5 ms). In the final phase of capture, terminal buzz signals shorten further (0.5–1 ms); they are produced at very high repetition rates (as high as 150–200 Hz) and show a drop in sound frequency below 20 kHz (Surlykke and Moss, 2000). This dynamic sound production pattern is characteristic of most insectivorous bat species (Schnitzler and Kalko, 2001). Further, bats show flexibility in echolocation pursuit sequences, revealing that bats can adapt to changing acoustic information (Moss and Surlykke, 2010).

At each phase of insect pursuit, the sonar sound characteristics used by FM bats reflect adaptive signal designs for different acoustic tasks: target detection, localization and tracking (Simmons and Stein, 1980). The long-duration, shallow FM signals produced during the search phase are adapted for target detection, as sound energy is concentrated in a narrow frequency band over an extended period; the broadband and short-duration approach and terminal phase echolocation signals are adapted for target localization in 3D space (Moss and Schnitzler, 1995). Adjustments in the duration of FM sonar calls are illustrated in Fig. 3A and discussed further below in the context of sonar scene analysis.

As described above, CF–FM bats adjust the frequency of sonar emissions as they forage on the wing to compensate for Doppler shifts in echoes, which then allows them to detect the fluttering movements of their prey (Schnitzler, 1968). Adjustments in sonar call frequencies of high duty cycle CF–FM signals also ensure that calls and echoes are processed in separate frequency channels in the bat's auditory system (Neuweiler et al., 1980). This is illustrated in Fig. 3B and discussed below.

The textbook literature on bat echolocation behavior reports a continuous and regular decrease in sonar call interval with a reduction in target range (e.g. Nachtigall and Moore, 1988). However, subsequent studies have revealed fine temporal patterning of the production of echolocation signals layered on the overall changes in call interval with target distance. Specifically, both FM and CF–FM bats produce clusters of echolocation signals, referred to as sonar sound groups, particularly when they encounter challenging sonar tasks, such as navigating tight spaces, tracking moving prey or discriminating the features of objects (Moss et al., 2006; Petrites et al., 2009; Sändig et al., 2014; Ding et al., 2022). The function of sonar sound groups in biosonar imaging has yet to be fully delineated.

Fundamental to computations for target tracking is the relationship between the region of the environment sensed by the animal (acoustic gaze; see Glossary) and the animal's intended movements. Ghose and Moss (2006) reported an adjustable linkage between acoustic gaze and motor output in a flying echolocating bat, which serves to simplify the transformation of sensory acoustic information to flight motor commands. This finding has been extended to consider the bat's strategies to intercept erratically flying prey. Studies of target pursuit in animals, ranging from dragonflies to fish, and dogs to humans (McBeath et al., 1995; Olberg et al., 2000; Fajen and Warren, 2004), have suggested that they all use a constant bearing interception strategy (see Glossary) to pursue moving targets. However, Ghose et al. (2006) demonstrated that bats use a constant absolute target direction interception strategy (see Glossary) during pursuit. Unlike constant bearing, this approach minimizes the time it takes for a pursuer to intercept an unpredictably moving target.

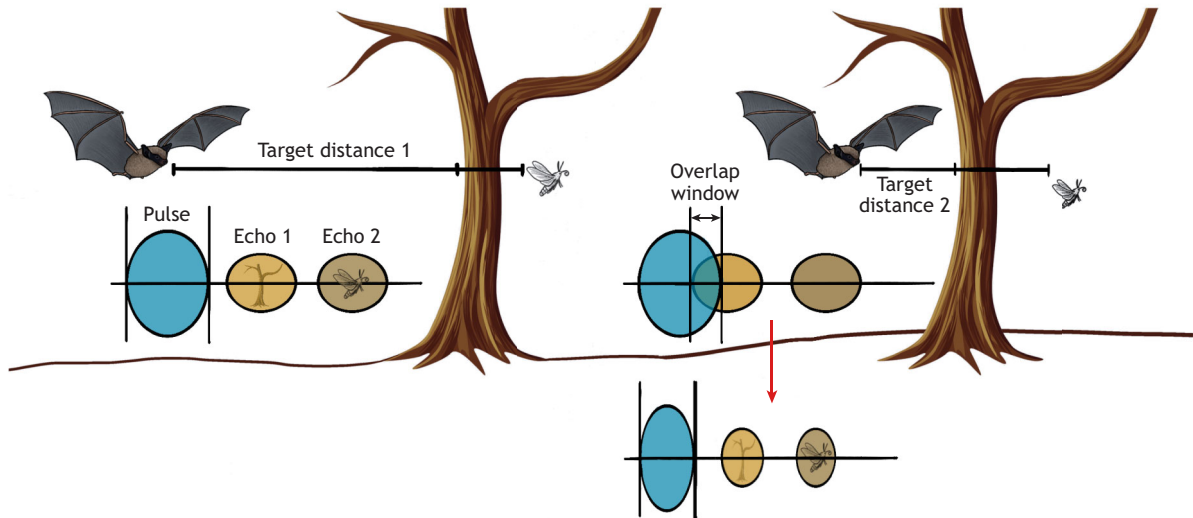
These findings suggest that echolocating bats predict the future position of a moving target, but they do not empirically demonstrate the implementation of internal prediction models in these animals (Fig. 3C). Salles et al. (2020) provided the first direct evidence that bats rely on internal models of target motion to predict the future position of a moving target. They trained bats to rest on a perch and track a tethered target that sometimes disappeared behind an occluder. High-speed video and audio recordings captured the bat's head aim and echolocation behavior. These recordings showed that the echolocating bat estimated a target's velocity from a series of echo snapshots and used this estimate to predict when a moving target would reappear from behind an occluder. Predictive tracking of moving targets by other echolocating animals under natural foraging conditions is ripe for study (Salles et al., 2021).

How do toothed whales use echolocation to localize and intercept moving prey?

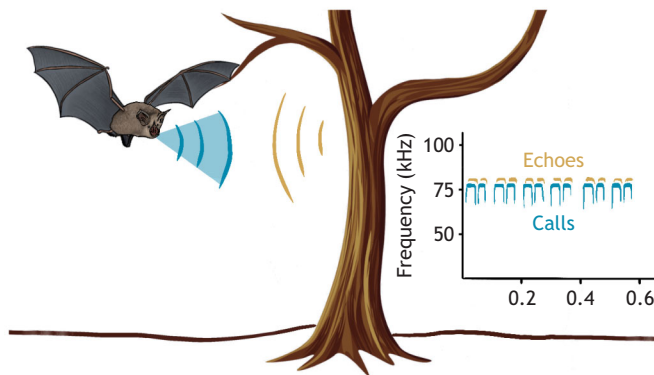
Just like bats, toothed whales adjust their echolocation signals with distance to a selected target (Fig. 2). In the search phase, they emit regular patterns of relatively long inter-click intervals. As discussed above, when a target of interest is recognized, the inter-click interval is adjusted to always be larger than the two-way travel time from the emitter to the target and back (Au, 1993). At close range to the target, the echolocator enters the buzz phase, when it emits clicks at a very high rate, although at this stage the inter-click intervals are still longer than the two-way travel time (Wisniewska et al., 2012). In the buzz phase, the source level of clicks is reduced to yield echoes from nearby prey within the dynamic processing range of the receiver, and the transmission beam width broadens (Wisniewska et al., 2015). The difference between search and buzz phase clicks is not as large as in bats, except in the case of beaked whales, which emit search signals consisting of upsweeps of relatively long duration and broadband transients in the buzz phase (Johnson et al., 2004). In other toothed whales, beam broadening does not seem to be accomplished by a drop in sound frequency, as seen in many bat species, but may be caused by changes in emitter aperture through melon adjustments (Wisniewska et al., 2015). Toothed whales direct their acoustic gaze at the target of interest when approaching both stationary prey (Wisniewska et al., 2012) and freely moving ones (Vance et al., 2021). It seems likely that toothed whales can predict the motion of prey targets just like bats can (Salles et al., 2020), but further experimentation is needed to confirm this.

Finally, 'pulse packets', where echolocation clicks are emitted in bouts with pauses in between, produced by echolocating toothed whales (Turl and Penner, 1989; Ivanov, 2004; Finneran, 2013;

A FM bats control pulse duration



B CF-FM bats separate calls and echoes into different frequency channels



C Bats predict their prey's route

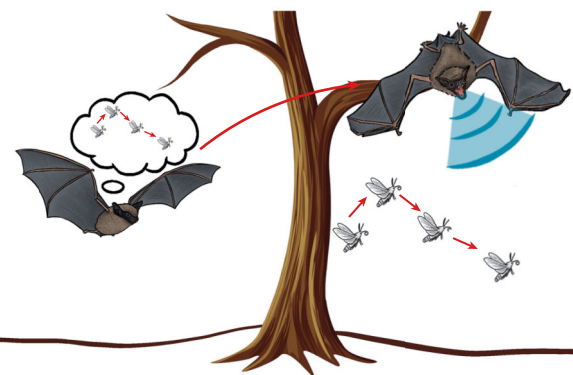


Fig. 3. Sonar call adjustments and tracking of prey. (A) FM bats shorten echolocation calls to avoid overlap between emission and target echoes. (B) CF-FM bats exhibit Doppler shift compensation as they fly, which effectively separates calls and echoes into different frequency channels. (C) Illustrates the echolocating bat's internal model of a moving target's trajectory, which enables predictive tracking and interception of prey.

Ladegaard et al., 2019) share characteristics of the clustered sound groups produced by echolocating bats (Moss et al., 2006; Petrites et al., 2009; Sändig et al., 2014; Ding et al., 2022), but their functional role remains to be fully understood. Pulse packets make several echoes available for the echolocator, potentially increasing the probability of detecting faint echoes from remote objects. They could also aid in tracking targets if the echolocator can extract information about target movement from a packet of sonar emissions (Finneran et al., 2014).

The evolutionary arms race between echolocating predators and their prey

The prey species of bats and toothed whales have evolved a variety of strategies to evade detection and capture. Some prey minimize detection by the echolocator by shaping their body or evolving physical characteristics to reduce acoustic reflectivity (Shen et al., 2018; Au et al., 2019). Some prey have evolved ultrasound hearing to detect their echolocating predators (Surlykke, 1988; Mann et al., 1997). Once detected and pursued by the echolocator, prey initiate erratic trajectories or other behaviors to avoid capture (Roeder, 1962; Webb, 1978; Yager and Spangler, 1997; Triplehorn and Yager, 2005; Domenici and Blake, 1997; Tytell and Lauder, 2008;

Wilson et al., 2011). The evasive behavior of prey challenges the echolocating predator to rapidly adjust its own behavioral strategies for prey interception (Box 2). The effects of acoustic signals generated by insects and conspecifics on bat prey capture are the topics of other recent reviews (Corcoran and Moss, 2017; Jones et al., 2021).

The interaction between the echolocator and its prey appears to be a driving force in the evolution of echolocation behavior and performance. Based on theoretical calculations using the sonar equation, Surlykke (1988) proposed that bats may reduce their call source levels when approaching insects to increase the probability of detecting their prey before insects are alerted to an impending attack. The extent to which toothed whales also adjust signal amplitude to delay their detection by ultrasound-hearing fish prey remains to be investigated.

Sonar scene analysis

As an animal seeks food, tracks targets and steers around obstacles, its distance and direction to objects continuously change. Such natural behaviors invoke dynamic feedback between 3D scene representation and action selection for spatially guided behaviors. Parsing, integrating and organizing complex acoustic stimuli to

Box 2. Predator–prey interactions

Aerial prey of echolocating bats

Once detected, aerial prey species are in trouble, as they have limited time to escape. There is little evidence that insects use mechanosensors to detect bats (Triblehorn and Yager, 2005), but many insects have evolved ultrasound hearing to detect the signals of echolocating predators (Roeder, 1962; Yager, 1999). Ultrasound triggers a variety of counter-predator responses in insects equipped with bat detectors, including erratic escape maneuvers, drops to the ground or the production of clicks that serve to startle, warn and/or 'jam' the echolocating predator (Miller and Surlykke, 2001; Corcoran and Connor, 2012). Other strategies could include avoiding areas frequented by foraging bats (Lewis et al., 1993), flying close to vegetation (Rydell, 1998) or water (Svensson et al., 2002), and the evolution of body shapes that may mitigate bat attacks (Barber et al., 2015). See Fig. 2, upper panels.

Aquatic prey of echolocating marine mammals

Toothed whales can detect prey hundreds of meters away using echolocation (Madsen and Surlykke, 2013). Because of their longer pursuit times, toothed whales appear to be more likely than bats to adjust their biosonar tracking over long time scales to their prey (Vance et al., 2021). In stark contrast to the aerial prey of echolocating bats, very few of the 30,000+ species of fish can hear underwater echolocators (Popper and Fay, 2011). Only shad have been shown to hear ultrasound (Mann et al., 1997); these fish respond to ultrasonic clicks by swimming away from a transducer, and their response is greater at higher click rates (Wilson et al., 2011). Shad are relatively uncommon in the stomach contents of delphinids, suggesting that ultrasonic hearing reduces predation of these species. However, recent findings suggest that at least some harbor porpoises have overcome acoustic-driven escape responses in shad (Elliser et al., 2020). It is unclear whether harbor porpoises have evolved adaptations to their sonar emissions that undermine detection of these signals by their prey, such as reducing the source level of their signals (as suggested for bats; Surlykke, 1988). The fact that ultrasonic detectors are uncommon among fish and squid suggests that the evolutionary pressure to develop such defense mechanisms is small compared with that of aerial prey. Because underwater prey species have exquisitely sensitive lateral line organs tied to rapid escape circuitry (Eaton et al., 2001), most have not evolved acoustic sensors to detect predators at long distances, but instead operate with a short safety zone created by the viscous properties of the medium and the limited maneuverability of toothed whales in relation to that of their prey. See Fig. 2, lower panels.

support such behaviors are tasks of 'auditory scene analysis' (Bregman, 1990), which is coordinated with motor behaviors to enable successful navigation in the environment. For the echolocating animal, the analysis of auditory scenes builds upon its active production of sounds that reflect from objects in the environment.

It is important to consider that echolocating animals operate in noisy environments. Not only do biotic and abiotic sound sources interfere with target echo processing but also the animal's own sonar signals return cascades of echoes from clutter objects in the environment. The animal must therefore sort and track sound sources from targets of interest in the presence of distractor sounds, many of which occur close together in time. This challenge is partially solved by the directionality of echolocation signals, which can serve to filter out echoes from off-axis objects. It is likely that other adjustments in sonar signal features and trajectory path selection also contribute to the echolocating animal's ability to negotiate complex echo soundscapes (Moss et al., 2011, 2014). The contribution of active sonar adjustments to the analysis of sonar scenes by echolocating animals is discussed below.

Echolocating bats adjust the direction and range of their acoustic gaze

Echolocating bats adaptively adjust the features of sonar vocalizations in response to information obtained from echo returns. Therefore, the bat's behavioral control of its sonar calls provides a window into its perceptual world. Importantly, the bat adjusts the direction and duration of its calls to probe information from different locations in space, and this vocal-motor control, coupled with head and pinna movements, yields a measure of the animal's acoustic gaze and analysis of echoes from objects in its surroundings.

Direction of acoustic gaze

The sonar beam of a bat can be likened to an auditory flashlight, sampling a limited region of acoustic space at a given point in time. The bat's aim of the beam directly influences the echo information it samples from the environment, and the bat can control the region of space it inspects by moving its head and/or noseleaf (Hartley and Suthers, 1987; Ghose and Moss, 2003; Linnenschmidt and Wiegerebe, 2016). Laboratory studies of sonar emission patterns of the big brown bat show that the sonar beam is broad enough to collect echo information from objects within a ~60 deg cone (Ghose and Moss, 2003), which would enable simultaneous inspection of objects in the frontal plane. However, the bat's behavior demonstrates that it does not inspect objects simultaneously. Instead, the bat shifts the direction of its sonar beam by moving its head to accurately and sequentially point the axis in the direction of closely spaced objects (Surlykke et al., 2009). Field studies reveal that foraging Japanese house bats, *Pipistrellus abramus*, shift their sonar beam aim between the direction of flight and the anticipated direction of the next prey interception (Fujioka et al., 2017).

Range of acoustic gaze

Bat sonar operates in 3D space, and the bat adjusts the intensity and duration of calls to sample echoes from targets at different distances (Fig. 3). FM bats avoid overlap between their outgoing sound and returning echoes, and vocal-motor adjustments in call duration therefore provide an indirect measure of where the bat is attending along the distance axis. For example, the big brown bat can shift its sonar gaze from a close obstacle to distant prey, by changing the duration of its calls (Surlykke et al., 2009). Big brown bats show similar dynamic adjustments in the direction and distance of acoustic gaze in a target discrimination task (Falk et al., 2011).

Sonar scene analysis in echolocating toothed whales

While pursuing prey, toothed whales show similar adjustments in biosonar signals to those of bats (Madsen and Surlykke, 2013). They swim in 3D murky waters and are active at night-time. So, just like bats, the sonar system is not only used for detecting and pursuing prey but also for navigating 3D space. While searching for prey, toothed whales scan for targets of interest (Verfuss et al., 2005). When they detect a target, the inter-click intervals may decrease to allow the animal to collect information about prey location, before they enter the buzz phase, where hundreds of clicks are emitted every second (Au and Benoit-Bird, 2003; Wisniewska et al., 2012), avoiding overlap between outgoing signals and returning echoes, as discussed above (Au, 1993; Wisniewska et al., 2012). Toothed whale scanning behavior continues throughout approach and capture of prey (Verfuss et al., 2009) or during approach of an artificial target (Wisniewska et al., 2012). Research has yet to detail how sonar signal adjustments contribute to the toothed whale's analysis of underwater sonar scenes, but

preliminary work has revealed processes that show similarities to those of bats (Moss et al., 2014).

Vision and passive listening in echolocating animals

Echolocating animals can operate in complete darkness, but other sensory cues offer complementary information that guides navigation and foraging. Here, we present examples from both bat and dolphin studies that illustrate potential benefits of using vision and passive listening to localize objects in their surroundings.

Echolocating bats' use of vision and passive listening

Echolocating bat species differ in their visual sensitivity and acuity (Suthers, 1966; Eklöf, 2003; Eklöf et al., 2014), but even species that show low acuity can benefit from the combined use of vision and echolocation to steer around obstacles, discriminate objects and capture insect prey (Williams et al., 1966). Insectivorous big brown bats, for example, show superior obstacle avoidance performance when visual and acoustic cues are available, compared with either cue alone (Jones and Moss, 2021). By contrast, there are also reports in the literature that vision can interfere with obstacle avoidance in echolocating bats (McGuire and Fenton, 2010); however, this observation is likely due to high light levels affecting the animals' behavior (Bradbury and Nottebohm, 1966).

Insectivorous bats that forage on summer nights can benefit from environmental light to detect prey using vision (Eklöf and Jones, 2003). Interestingly, insectivorous bats that are active before dusk or under a full moon show reduced echolocation call rates relative to those operating in greater darkness, suggesting that bats use both vision and echolocation when light is available (McGowan and Kloepper, 2020). Similarly, echolocating Egyptian fruit bats, *Rousettus aegyptiacus*, reduce their sonar click rate as a function of light level in a navigation task (Danilovich et al., 2015), and they appear to differentially weight their use of visual and echoic information according to the task and environmental conditions (Danilovich et al., 2015; Danilovich and Yovel, 2019).

Some echolocating bats rely heavily on passive hearing to find prey. Examples are found in the frog-eating fringe-lipped bat, *Trachops cirrhosus*, which uses the mating calls produced by its prey to find an evening meal (Tuttle and Ryan, 1981; Page and Ryan, 2008), and the pallid bat, *Antrozous pallidus*, which listens to sounds generated by the movement of terrestrial scorpions, beetles and crickets to localize prey (Fuzessery et al., 1993).

The role of vision in echolocating toothed whales

The eyes of toothed whales have many distinct features, suggesting that vision may play a larger part in their lives than previously recognized. The eyes are placed on the side of the head directed somewhat forward, giving animals a wide visual field, with binocular overlap in a 20–30 deg region in front and slightly below their body axis (Dral, 1977; Dawson, 1980). It is unknown but possible that toothed whales show stereopsis (see Glossary). Interestingly, each dolphin retina has two foveae (Mass and Supin, 1995): one fovea projects forward, whereas the other projects to the side and slightly backwards (Mass and Supin, 1995). It seems that the visual 'Umwelt' (von Uexküll, 1934) of dolphins is unique among mammals, with a field of binocular overlap in front, and two foveae to each side of the animal. Their visual acuity underwater is comparable to that of humans in air, whereas their visual acuity in air is lower (Herman, 1975).

Whales and dolphins are regularly observed 'spy hopping', poking their heads vertically out of the water, seemingly to obtain a visual overview of the area around them. Trained dolphins can

perform complicated visual tasks (Herman and Tavalga, 1980), and during public performances they can execute behavioral tasks requiring visual planning, such as jumping up through a hoop placed a few meters above the water surface. This all indicates that the role of vision is important for toothed whales, in addition to their well-developed echolocation. Psychophysical studies of echolocation in trained animals further indicate a large difference in the animal's acoustic and swimming behavior and performance when they are blindfolded (Atem et al., 2009; de Ruiter et al., 2009; Bakkeren et al., 2023), suggesting the importance of vision in the sensory biology of toothed whales. However, further studies are needed to fully understand how vision complements and modifies echolocation behavior.

Echolocation and social communication

There is growing evidence that echolocation signals can serve a communicative function. For example, foraging animals may alert nearby conspecifics to the presence of abundant prey by producing feeding buzzes. The extent to which echolocating animals emit feeding buzzes to alert conspecifics to feeding sites (as gulls are known to do; Frings et al., 1955) or simply as a byproduct of their foraging behaviors remains unknown. Echolocating animals appear to make use of passive cues generated by foraging conspecifics, and future research should expand our knowledge on such communicative behaviors (Fig. 4).

Social calls and eavesdropping in echolocating bats

Early research on the calls produced by echolocating bats focused on sonar localization (Griffin, 1958), which was followed decades later by intensive research on their social communication calls (see Salles et al., 2020; Jones et al., 2021). Typically, bat echolocation and social calls are assigned to distinct categories, although some early researchers in the field raised the possibility that functions of the two call types can overlap (Möhres, 1967).

Bat social calls are typically longer in duration and lower in sound frequency than echolocation calls (Fenton, 2003; Bohn et al., 2006; Salles et al., 2019). There is emerging knowledge of the functional role of certain call types in some species (e.g. Prat et al., 2016; Fernandez et al., 2021a,b; Hörmann et al., 2021) and how social calls change over development (Fernandez et al., 2021a,b). For example, big brown bats produce FM bouts when competing for prey, and these social calls have been characterized as food-claiming calls (Wright et al., 2011, 2014; Fig. 4). However, further research is needed to deepen our understanding of social communication signals in echolocating bats.

Jones and Siemers (2011) highlight the communicative potential of bat echolocation calls, which has received growing research attention in recent years. Echolocation calls can carry social information about individual identity (Masters et al., 1995; Kohles et al., 2020) and sex (Kazial and Masters, 2004). Bat social calls are sometimes interjected during echolocation-based foraging and may carry information about social hierarchy for food claiming (Wright et al., 2014). It is noteworthy that several studies report that echolocating bats eavesdrop on the feeding buzzes of conspecifics to identify foraging sites (Fig. 4; Gillam, 2007; Dechmann et al., 2009; Cvikel et al., 2015). Although it can be useful to classify calls as having echolocation or social functions, research advances will benefit from the recognition that they can serve both purposes.

Social calls and eavesdropping in echolocating toothed whales

Toothed whales may make use of passive listening to a larger extent than previously assumed to monitor activities of conspecifics

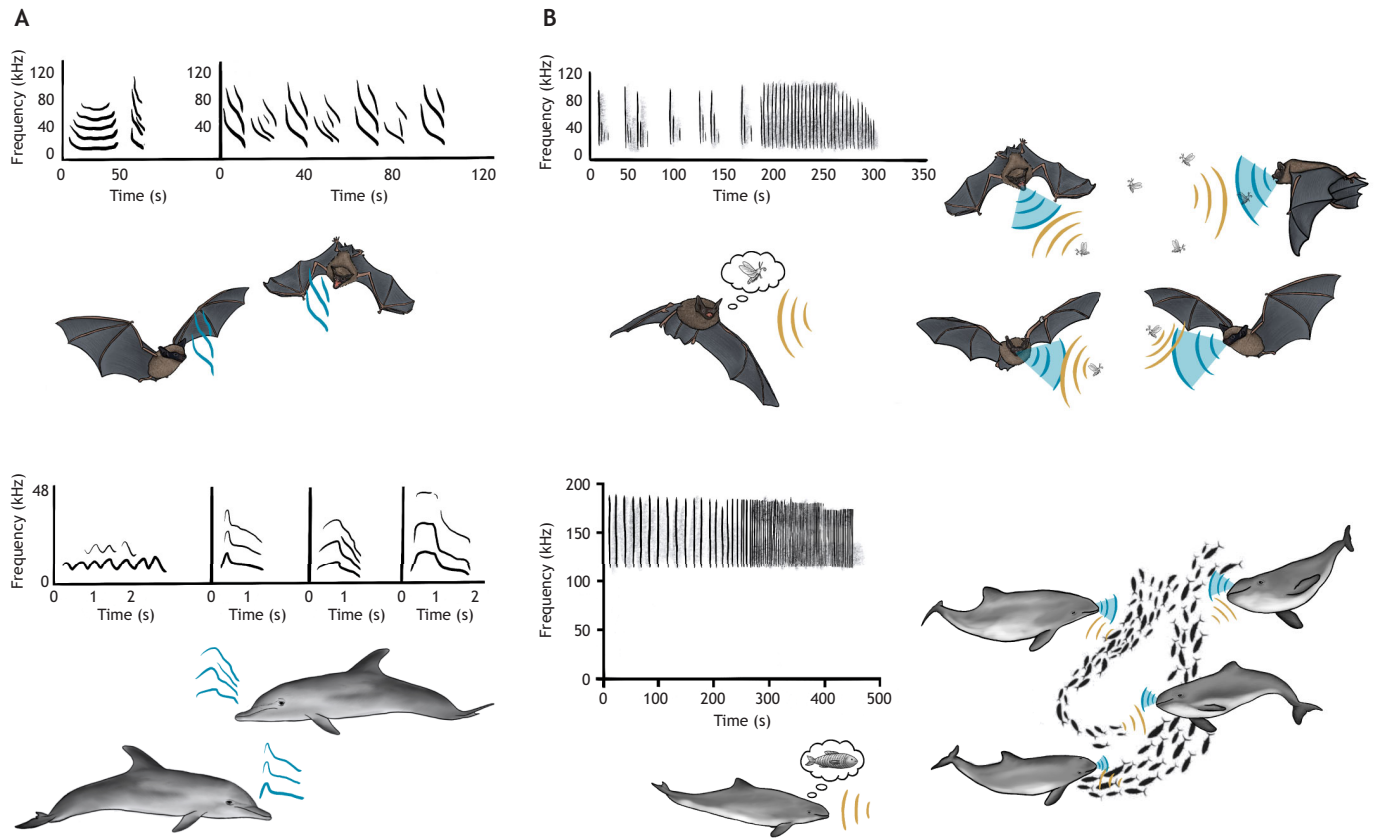


Fig. 4. Communication and eavesdropping in bats and toothed whales. (A) Spectrograms illustrate lower-frequency and/or longer-duration communication signals in bats (top) and toothed whales (bottom). (B) Echolocating animals can eavesdrop on the feeding buzzes (spectrograms) produced by conspecifics to identify foraging sites.

(Alcázar-Treviño et al., 2021). While foraging in groups, animals often emit social calls (Fig. 4) amidst echolocation sequences (Similä and Ugarte, 1993; Jensen et al., 2011). Foraging toothed whales sometimes reveal their presence and activity to attract conspecifics to the feast (Fig. 4; Barret-Lennard et al., 1996; Götz et al., 2005). Trained dolphins emit ‘victory squeals’ as the final part of their buzzes when catching fish (Ridgway et al., 2014), and wild dolphins sometimes produce ‘feeding bray calls’ while foraging (Janik, 2000), which corroborates the notion that they intentionally try to attract conspecifics to a food source. It is also possible that dolphins eavesdrop on the echolocation sequences of conspecifics to gain extra information about prey (Xitco and Roitblat, 1996). By contrast, some solitary foragers, such as beaked whales, are quiet except when emitting biosonar signals, probably to minimize exposing themselves to conspecifics and potential predators such as orcas (Johnson et al., 2004). Synchronized audio and video recordings of social interactions of toothed whales in the field can shed light on the richness of their social behaviors.

Challenges and opportunities

Since the discovery of echolocation in bats and toothed whales, scientists have made great strides in understanding the behavioral and neural mechanisms that enable this mode of sensing. When *Journal of Experimental Biology* first published research on animal echolocation, commercial audio and video recording devices were not capable of capturing the high-frequency sounds and agile behaviors of echolocating animals operating under natural conditions. The acoustic behaviors of bats intercepting insects in

the dark and dolphins tracking fish underwater were outside the operating range of standard instrumentation. Initially using custom devices, researchers characterized the sonar signals of diverse species, measured animal performance in sonar target localization and discrimination tasks, and quantified the adaptive sonar behaviors of animals carrying out natural behaviors.

With recent advances in technology and a growing interest in the cognitive processes that support natural behaviors, there are exciting opportunities to unlock new knowledge of animal sonar systems, both in the laboratory and in the field. For example, miniaturized high-speed audio and video recording devices, along with on-animal data tags (Johnson et al., 2004; Prat and Yovel, 2020), make it possible to explore the fine-scale dynamics of bat and toothed whale interactions with their surroundings (Johnson et al., 2004; Corcoran and Connor, 2012, 2014; Fujioka et al., 2014; Wisniewska et al., 2016; Stidsholt et al., 2021). New animal tracking technology can also shed light on biosonar interrogation of natural environments and behavioral strategies that enable foraging in complex environments. Further, detailed recordings of echolocating animals performing natural tasks can reveal the precursors of mode switching between sonar localization and acoustic communication with conspecifics. Collectively, work in these areas will inform a deeper understanding of natural scene analysis by echolocation in air and underwater.

Comparative studies of echolocating bats and toothed whales are fundamental to understanding both specializations and general principles of animal sensing systems. Specific to biosonar, there are many open scientific questions to explore. How do echolocating

animals represent natural scenes as they move through the environment? Does echolocation signal production give rise to perception that differs from passive acoustic monitoring of the surroundings? Do bats and toothed whales integrate echo snapshots to perceive a stable and continuous representation of their surroundings? When echolocating animals operate in groups, can they eavesdrop on the calls and echoes of conspecifics to localize prey and obstacles? The answers to these questions will provide key scientific breakthroughs in the next 100 years.

Conclusion

In this Review, we have considered how the physics of sound transmission in air and underwater constrains sonar signal production and echo reception, resulting in differences in echolocation signal design, operating ranges and response times of aerial and aquatic echolocating animals. In addition, prey behaviors may further influence the ways in which bats and toothed whales have evolved to use echolocation as they forage. Despite some differences, there are commonalities between the sonar discrimination performance and communication behaviors of bats and toothed whales: future work will deepen our knowledge of the similarities and differences between aerial and aquatic echolocation as animals negotiate natural sonar scenes.

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