REVIEW

Sensing in a noisy world: lessons from auditory specialists, echolocating bats

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ABSTRACT

All animals face the essential task of extracting biologically meaningful sensory information from the ‘noisy’ backdrop of their environments. Here, we examine mechanisms used by echolocating bats to localize objects, track small prey and communicate in complex and noisy acoustic environments. Bats actively control and coordinate both the emission and reception of sound stimuli through integrated sensory and motor mechanisms that have evolved together over tens of millions of years. We discuss how bats behave in different ecological scenarios, including detecting and discriminating target echoes from background objects, minimizing acoustic interference from competing conspecifics and overcoming insect noise. Bats tackle these problems by deploying a remarkable array of auditory behaviors, sometimes in combination with the use of other senses. Behavioral strategies such as ceasing sonar call production and active jamming of the signals of competitors provide further insight into the capabilities and limitations of echolocation. We relate these findings to the broader topic of how animals extract relevant sensory information in noisy environments. While bats have highly refined abilities for operating under noisy conditions, they face the same challenges encountered by many other species. We propose that the specialized sensory mechanisms identified in bats are likely to occur in analogous systems across the animal kingdom.

KEY WORDS: Active sensing, Acoustic interference, Animal communication, Jamming, Noise

Introduction

To find mates and food sources or evade predators, animals must use one or more of their senses to detect, localize and discriminate stimuli from the noisy backdrop of their natural habitats (Stevens, 2013; Bradbury and Vehrencamp, 2011). Sensory systems have evolved to detect and discriminate stimuli that are important to the organism’s survival and reproduction (Capranica and Moffat, 1983; Wehner, 1987). However, animals routinely encounter situations where there is an abundance of stimuli (abiotic or biotic) that have the capacity to interfere with biologically relevant signals. These stimuli are commonly referred to as noise (see Glossary). Natural environments are composed of numerous competing stimuli, which have the potential to serve as signal or noise, depending on an animal’s current behavioral goal (Fig. 1).

Animals have evolved a variety of mechanisms for sensing in noisy environments. Signalers are well known for making behavioral adjustments to compensate for noise, such as shifting their calling frequencies to avoid spectral overlap with competing background signals (Shannon et al., 2016). However, receivers also make behavioral adjustments in noise; for example, moving to a more favorable location or increasing active scanning of the environment (Brumm and Slabbekoorn, 2005). Animals also tend to rely more on multi-modal sensing (see Glossary) in noisy environments, processing congruent stimuli acquired through complementary senses and/or placing greater weight on modalities that are less subject to interference (Munoz and Blumstein, 2012). For instance, animals may rely on visual and acoustic stimuli from a common source (Taylor and Ryan, 2013) or depend more on hearing in darkness (Danilovich et al., 2015).

Echolocation and electrolocation are considered ‘active’ sensory modalities, because they operate through the animal’s production of signals (sound and electricity, respectively) into the environment to generate sensory information, which then guides behaviors (Nelson and MacIver, 2006). Active sensing (see Glossary) also refers to an organism’s movements that influence sensory signal reception (Schroeder et al., 2010), and the contribution of movement to perception is widespread throughout the animal kingdom. Primates, for example, are well known for using rapid eye movements, or saccades, to sequentially direct their foveae at objects in a scene (Land, 2006). Active gaze control (i.e. head or eye movements that control sampling of visual information) is important to animals as diverse as jumping spiders, stalk-eyed flies and zebra finches (Tarsitano and Andrew, 1999; Ribak et al., 2009; Eckmeier et al., 2008). Many animals actively control sniffing to improve olfactory sampling (e.g. Catania, 2006), explore objects through touch by whisking (Ganguly and Kleinfeld, 2004; Towal and Hartmann, 2006) and localize sound sources by moving the head and ears (pinnae) (Populin and Yin, 1998). Active control of sensing results in influxes of sensory information, which are used to inform further actions (Schroeder and Lakatos, 2009). This leads to action–perception feedback loops, where available sensory information drives the acquisition of future information. Under noisy conditions, active sensing improves stimulus detection and discrimination in support of diverse survival tasks.

In this review, we consider echolocating bats as model organisms to gain a broader view of the mechanisms by which animals cope with noisy sensory environments. To use echolocation or biological sonar, an animal produces acoustic signals and then compares their temporal and spectral features with those of returning echoes (Griffin, 1958; Surlkyke et al., 2014). This process allows echolocating animals to reconstruct acoustic scenes. Biological sonar can also be considered a form of ‘auto-communication’—that is, a system in which signaler and receiver are the same individual. Many of the factors that improve communication under conditions of noise (Brumm and Slabbekoorn, 2005) are well developed in bats for auto-communication under low light levels.
Echolocation itself is inherently subject to noise interference: target echoes are often several orders of magnitude weaker than echolocation signals, and sonar calls and echoes are separated by tens of milliseconds or less (Moss and Surlykke, 2010). Target echoes can easily be masked by the bat’s own emission, or by ‘clutter’ echoes (see Glossary) returning from other objects in the environment (Fig. 1). Bats also must contend with the rustling of wind and noise from flowing water, conspecific calls and chorusing insects that produce sounds in the ultrasound range. Despite these challenges, bats perform natural echolocation behaviors with apparent ease. For example, bats exit cave roosts, sometimes amongst thousands of echolocating conspecifics (Gillam et al., 2010), capture evasive insects in a fraction of a second (Kalko, 1995), and navigate in darkness through dense foliage, while flying at high speed (Kong et al., 2016). Tight coordination and adaptive control of both signal emission and echo reception are central to the success of bats. By studying these sensory specialists, we hope to gain broader and deeper insight into how animals in general cope with noisy sensory environments.

We begin this review by briefly summarizing the mechanisms bats use to localize target echoes and separate them from background clutter echoes (see also Moss and Surykyyke, 2010). Next, we consider how bats adapt to ecological scenarios involving noise, including interactions with conspecifics and prey. We also highlight the importance of multi-modal sensing to the success of bats. We finish by relating these findings to common sensory problems faced by a variety of animals.

**Fundamentals of echolocation: common problems and solutions**

More than 1100 bat species use echolocation for a wide variety of tasks, and in diverse habitats (Denzinger and Schnitzler, 2013; Fenton and Simmons, 2015). Bat auditory systems are composed of the same basic neural architecture and pathways as those of other mammals (Popper and Fay, 1995). Like other animals, bats compare the amplitude and arrival time of sounds at their two ears to determine the azimuth of sound sources (Wotton et al., 1995). Bats can use elevation-dependent spectral cues to determine the vertical range of frequencies. Depending on the focal animal’s current behavioral goals.

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**Glossary**

**Active sensing**
Use of active processes to influence the influx of sensory information.

**Attention**
Selectively processing stimuli that are relevant to the current behavioral task.

**Call direction**
The bat call’s aim, as indicated by the axis of greatest acoustic energy.

**Call directionality**
A measure of the width of the sonar beam.

**Clutter**
Echoes returning from objects that are not the focus of an echolocating animal’s attention.

**Frequency modulated**
A call that changes in frequency over time.

**Masking**
A situation where one sensory stimulus influences the perception of a second stimulus.

**Low-pass filter**
Changing a sound so that lower frequencies are enhanced relative to higher frequencies.

**Multi-modal sensing**
The use of multiple sensory modalities for sensory perception.

**Noise**
Environmental stimuli that have the potential to interfere with the sensation of biologically meaningful stimuli.

**Narrowband**
A call whose acoustic energy is concentrated within a relatively short range of frequencies.

**Ranging**
Determining the distance to a target object.

**Receptive field**
The specific range of stimuli that elicit a response from a sensory neuron.

**sinFM**
Sinusoidally frequency-modulated calls: specialized signals used by Mexican free-tailed bats to jam the echolocation of conspecifics.

**SNR**
Signal to noise ratio: a measure of the ratio between the strength of the signal that is being attended to and the competing background noise.

**Spatial release**
The process of using binaural hearing cues to reduce acoustic masking of sounds that are coming from different directions.

**SPL**
Sound pressure level: a measure of the amplitude of an acoustic signal.

**Tymbal organ**
A sound-producing structure found in some insects, including tiger moths (Family Noctuidae, subfamily Arctiinae).

**Waggle**
Rapid head movements that change the orientation of the ears and are proposed to amplify auditory cues used for target localization.

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**Fig. 1. Cartoon illustration of a noisy acoustic environment of a bat.** A focal bat (left) emits an echolocation signal (black). Echoes (gray) return simultaneously from a potential prey item and a tree obstacle. A second insect emits an acoustic signal (red), and a conspecific echolocates nearby (green). Note that each of these acoustic stimuli could serve as signal or as noise, depending on the focal animal’s current behavioral goals.
Most bats produce short (<20 ms) frequency-modulated (FM; see Glossary) calls that are followed by long silent intervals, during which time bats listen for echo returns from objects (Griffin, 1958; Schnitzler and Henson, 1980; Moss and Schnitzler, 1995). FM calls have a low duty cycle, i.e. a low proportion of time filled with sound. Approximately 200 bat species produce calls that start or end with FM components, but also include a constant frequency (CF) component (approximately 8–100 ms). Long CF calls (>50 ms) have a high duty cycle, i.e. a large percentage of the time is filled with sound. High duty cycle bats can hear echoes at the same time that they are producing much more intense calls. This is possible because the relative motion of the flying bat with respect to its target introduces Doppler shifts in sonar returns, which separates the sound frequencies of calls and echoes into different listening channels. High duty cycle bats have highly specialized auditory systems (Neuweiler et al., 1980) that enable fine frequency discrimination (e.g. Long and Schnitzler, 1975). Greater horseshoe bats, species that use long CF signals for echolocation, can discriminate and recognize fluttering insect prey by listening to spectral and amplitude modulations in echoes (von der Emde and Menne, 1989; von der Emde and Schnitzler, 1990). This specialized form of echolocation also serves to reject noise outside a narrow frequency band used for target echo detection and discrimination, which for the greater horseshoe bat is about 83 kHz. Unless otherwise noted, the discussion that follows applies to FM, or low duty cycle, bats, which rely heavily on the timing of calls and echoes to extract spatial information from the environment (Moss and Schnitzler, 1995). For further discussion of bats that use high duty cycle calls, we refer the reader to recent reviews (Fenton et al., 2012; Schnitzler and Denzinger, 2011).

Assignment of calls and echoes through dynamic control of signal duration, timing and frequency

To accurately localize and sort object echoes in the environment, a bat must solve several problems: target echo detection, localization, recognition and tracking, in the midst of acoustic noise. This is achieved in large part by the echolocating bat’s dynamic and adaptive control of biosonar emissions: bats modulate the duration, intensity, frequency, directionality (see Glossary), direction of the sonar beam (see Glossary) and timing of emissions to optimize echo reception from targets, while minimizing acoustic interference (Griffin and Schnitzler, 2010). Bats adapt the features of echolocation calls they use to localize and track insect prey (Fig. 2), which can be categorized into three phases (Griffin et al., 1960). The ‘search phase’, insectivorous FM bats produce sonar calls at a rate of 3–20 Hz, depending on the species (Holderied and von Helversen, 2003). After detecting a target echo, the bat enters the ‘approach phase’, in which call rate steadily increases and call duration decreases. The sweep of the FM sonar signals also becomes progressively steeper (Fig. 2A). In the ‘terminal buzz phase’, the pulse rate approaches its maximum of 150–200 Hz and intensity decreases (Jakobsen et al., 2013). Bats have specialized ‘superfast’ muscles in the larynx that allow such extraordinary call rates (Elemans et al., 2011).

By re-aligning the echolocation sequence so that the time from the beginning of each echolocation call until the end of the next call is stacked in a sequence (to illustrate a ‘sonar stream’; Fig. 1B), certain features of the echolocation sequence stand out. Fig. 2A shows an acoustic recording of a Mexican free-tailed bat (Tadarida brasiliensis) hunting prey under natural field conditions. Call emissions are shown in black. Simulated target echoes have been added to the figure (in red), based on the physics of sound propagation in air and measured 3D positions of the bat and prey. Assumptions about echo arrival times have been verified in several studies, where echoes were recorded from microphones placed directly behind the bat (e.g. Hiryu et al., 2007). Fig. 2B shows that bats progressively shorten both pulse duration and pulse interval (time between successive pulses) such that the echo returns after the end of the outgoing pulse but before the beginning of the next pulse. By shortening pulse duration, bats avoid temporal overlap between pulses and echoes that could lead to masking (see Glossary) or interference of echo detection from the sonar call emission (Kalko and Schnitzler, 1993). Pulse structure also changes over the sequence. The bat uses relatively long and narrowband calls (see Glossary) in the search phase (pulse 4 in bottom row of Fig. 2A). These calls concentrate acoustic energy within limited frequency bands, which facilitates echo detection (Griffin et al., 1960; Surylkke and Moss, 2000). Short, broadband calls used late in the attack (e.g. pulse 28 in Fig. 2A) allow the bat to integrate ranging information across many auditory neurons tuned to different frequencies (Simmons and Kick, 1984), and therefore they are well suited for distance measurement (Simmons and Stein, 1980; Surylkke, 1992). This allows precise distance measurement for the final prey interception maneuver.

The echo stream in Fig. 2B also illustrates that, despite the dramatic reduction in pulse intervals late in the sequence, bats typically allow sufficient time for target echoes to return prior to the next emission. This allows bats to avoid ambiguity in assigning echoes to the correct pulse, a requirement for accurate range estimation. Another strategy for ensuring correct assignment of pulses and echoes is to produce two or more calls in groups (i.e. ‘sound groups’), flanked by sonar signals at longer intervals (Kothari et al., 2014), which serves to link calls and echoes through distinct temporal patterning. Bats may integrate echo information within sound groups to increase sonar resolution (Moss et al., 2006). Pulses within a group may also have distinct time–frequency profiles (Jung et al., 2007; Ratcliffe et al., 2011; Hiryu et al., 2010), which could aid further in call–echo assignment. Fig. 2D shows the call Cercartetus brevirostris producing triplets of calls that increase in sound frequency. This may allow the bat to match calls and echoes not only by their temporal patterning but also by their frequency. A similar strategy has been reported in the big brown bat operating in a highly cluttered environment (Hiryu et al., 2010). This suggests that bats can simultaneously store multiple time–frequency call profiles, against which echo returns are compared.

Echo feature recognition

Echolocating bats face the fundamental task of recognizing echoes from their own sonar emissions and distinguishing them from other sounds in the environment. Psychophysical experiments have been conducted that measure the echolocating bat’s ranging performance in playback experiments that electronically delay the arrival of simulated sonar echoes. These experiments support the idea that bats compare the time–frequency structure of the outgoing call with the echo return. Bats that use FM signals suffer reduced ranging ability when listening to echoes that are manipulated in time–frequency structure, i.e. sweeping from low to high frequencies (Masters and Jacobs, 1989), when natural FM signals are replaced by noise bursts (Surylkke, 1992), altered sweep shape (Masters and Raver, 2000) or have the time–frequency structure from another individual bat (Masters and Raver, 1996). Bats can also learn to differentiate calls from different individuals based on subtle
differences in the distribution of energy across frequencies (Yovel et al., 2009). If given sufficient training, a bat can learn to discriminate with high accuracy the delay between its own call and echoes having a different time–frequency structure (Masters and Raver, 1996). In one study, bat sonar ranging performance was disrupted by broadband insect clicks that arrived within a short time window of echoes (Miller, 1991). Collectively, these studies show that bats utilize the distinct time–frequency structure of their own echoes to detect and discriminate their signals from other noises, and that bats can learn to recognize novel call and echo patterns when given sufficient time.

Adaptive control of sonar beam aim, directionality and intensity
In noisy environments, echoes can return simultaneously from many objects. How do bats perceptually segregate object echoes in cluttered environments? One solution is to sequentially aim the sonar beam axis (i.e. to control call direction; see Glossary) to inspect targets of interest (Fig. 3A; Sarylkke et al., 2009; Falk et al., 2011; Seibert et al., 2013). Bat sonar emissions and hearing are both directional, and increasingly so at higher frequencies (Fig. 2B; Aytekin et al., 2004; Jakobsen et al., 2013). Echoes returning from objects off-axis from the bat’s beam aim are both weaker and low-pass filtered (see Glossary; right inset in Fig. 3C). The bat’s auditory system can separate off-axis low-pass-filtered clutter echoes from on-axis target echoes, which prevents clutter echoes from masking target echoes (Bates et al., 2011). This observation is based on the following. Echoes are detected by populations of neurons that respond to different frequency components of the bat’s FM sonar signals (Simmons et al., 1990). The latency of neural firing, which registers echo arrival time, depends on echo intensity, with neurons firing at shorter latencies for higher amplitude echoes (Simmons and Kick, 1984; Simmons, 1989). Because of the directionality of sonar signal production and reception, echoes returning from targets along the bat’s midline are more intense than echoes returning from the bat’s periphery, and this intensity difference is registered by the bat’s auditory system as differences in arrival time of echoes from objects along the midline and off to the bat’s side. Importantly, directional differences in echo intensity are greater for high-
frequency components of sonar signals than for low-frequency components. In other words, at the bat’s periphery, high-frequency components of echo returns are weaker and therefore registered at longer neural response latencies than low frequencies, and this creates a temporal misalignment of the low- and high-frequency components of echo returns from objects off to the bat’s side. This misalignment has the effect of ‘defocusing’ objects in the bat’s periphery (Bates et al., 2011). Thus, a combination of the physics of sound transmission in the environment and the effect of sound intensity on neural response latency differentially affects sonar processing of low- and high-frequency target echoes arriving from off-axis objects. Bates et al. (2011) hypothesize that the sonar defocusing of off-axis clutter echoes prevents these signals from masking target echoes in the bat’s central ‘field of view’, determined by its beam aim. In this context, it is noteworthy that bats show spatial release (see Glossary) from masking at small angular separations of target and clutter. For example, one study reports that bats achieve complete spatial release from masking when sound sources are separated by only 23 deg (Sümer et al., 2009), far better performance than is achieved by animals that do not echolocate.

By adjusting call frequency or mouth aperture, bats can dynamically control the directionality of their sonar emissions (Jakobsen et al., 2013). One recent study found that bats alter the size of their mouth gape to adjust the width of their sonar beam as they move through habitats that differ in spatial structure (Kounitsky et al., 2015). This appears to be another strategy that allows bats to adaptively avoid acoustic interference from off-axis objects in different environments.

Bats also alter their beam directionality during the last moments of an attack on an insect. Specifically, late in attacks on prey, bats typically decrease their calling frequency, which broadens the sonar beam (Jakobsen and Sørlbye, 2010). This may be an adaptive response to ensure that the prey stays in the ensonified volume through to the end of the attack, when prey might otherwise maneuver outside the sonar beam (Corcoran and Conner, 2016).

Active control of sound reception
Complementing active control of sonar emissions, bats also control the shape, separation and orientation of their pinnae. Pinna movements were first studied in high duty cycle CF bats (Griffin et al., 1962) and more recently in a low duty cycle FM bat, Eptesicus fuscus (Wohlgemuth et al., 2016b). Wohlgemuth et al. (2016b) trained *E. fuscus* to rest on a platform and track prey items that were moved along different trajectories using a motorized pulley system. This allowed the investigators to monitor sonar vocalizations and ear movements with high precision as bats tracked moving prey. *Eptesicus fuscus* employ two types of pinna movement; the first type is associated with rapid head rotations or ‘waggles’ (see Glossary) that alternate the vertical orientation of the two pinnae relative to echo returns, and the second, which has been observed in both *E. fuscus* and high duty cycle bats, involves changes in the erectness and separation between the pinnae.

Regarding the first type, bats produced waggles more often when targets moved along complex trajectories. Wohlgemuth et al. (2016b) hypothesized that these ear movements amplify interaural-level cues and spectral cues in a manner that is analogous to visual motion parallax, where head movements are used to aid depth perception.

For the second type of pinna movement, erect pinnae focus the ears towards echoes in front of the bat; lateral ear deformations increase the distance between the tips of the pinnae and change their shape, which amplifies sounds coming from more-peripheral regions (Gao et al., 2011). In a target-tracking study, *E. fuscus* increased inter-pinna separation as targets approached it on a platform, broadening the bat’s acoustic field of view when it faced the challenge of intercepting a fast-moving target (Wohlgemuth et al., 2016b). Bats also made rapid changes to inter-pinna separation as they tracked moving prey, a behavior that might enhance cues for sonar localization accuracy.

These studies show that bats exhibit fine control over their acoustic field of view, which they change through head and ear movements, under different contexts (such as distance to a target).
and over millisecond time scales in coordination with sonar vocalizations. These mechanisms should enhance the bat’s ability to extract acoustic information under noisy sensory conditions.

**Neural basis of echolocation**

To understand mechanisms that allow bats to operate in acoustically noisy and dynamic environments, it is important to consider how the bat’s brain processes echoes and compares them with outgoing emissions. Here, we consider aspects of the bat’s neural machinery that are relevant to echo processing under dynamic and noisy conditions. We also direct the reader to reviews of other aspects of neural signal processing in the bat’s sonar receiver (Suga, 1990; Simmons, 2012; Wohlgemuth et al., 2016a).

The bat’s brain is specialized for extracting sonar signal features that are important for echolocation. Specific neurons have been characterized that respond selectively to a restricted range of pulse–echo delays (Suga and O’neill, 1979), signal durations (Casseday et al., 1994), frequency modulation rates (Razak and Fuzessery, 2008) and sound source directions (Valentine and Moss, 1997). The features encoded by these neurons (i.e. their receptive fields, see Glossary) tend to cover those that the bat processes as it echolocates in the natural environment. For example, individual delay-tuned neurons show strongest responses to delays from 1 to 36 ms (up to roughly 6 m of target distance), which corresponds to the bat’s operating range for small objects, such as insect prey (Dear et al., 1993).

Neurophysiological studies have revealed specializations in the processing of biologically natural sound sequences in passively listening bats. For instance, research has shown that midbrain neurons are more selective to broadcasts of natural sonar emissions than simple, computer-generated FM sweeps or noise (Wohlgemuth and Moss, 2016) and are selective to the temporal dynamics of sound stimulation (Sanderson and Simmons, 2005), providing evidence that bat neural pathways are selective to acoustic features of their own calls. More research is needed to determine the neural basis of this selectivity, and how it changes over time.

Studies have also begun to change our understanding of how the bat’s brain processes streams of echoes (Bartenstein et al., 2014; Beetz et al., 2016). It is increasingly clear that bat neural pathways process not only individual pulse–echo pairs but also streams of pulses and echoes across a sequence. For example, the auditory cortex of many bat species shows topographic organization, with systematic shifts in echo delay tuning of neurons located along the rostrocaudal axis (e.g. Suga, 1990; Kössl et al., 2014). It was long assumed that this map was static, but a recent study demonstrated that the map changes rapidly and dynamically when a sequence of pulses and echoes is presented to a passively listening, anesthetized bat (Bartenstein et al., 2014). When pulses and echoes were presented at progressively shorter delays, such as occurs when approaching a target (see Fig. 2B), the map shifted towards a higher representation of short delays. The degree and direction of the shift depended on the sequence of pulses and echoes that were presented. This, and other recent neurophysiological (Beetz et al., 2016) and behavioral studies (Kugler et al., 2016; Warnecke et al., 2016), shows that bats are specialized for integrating the flow of echoes as they return from multiple sonar pulses.

Mechanisms have been proposed to explain how the bat nervous system might compute the spatial location of objects in an echo scene (Simmons, 1973, 2012; Simmons et al., 1990; Valentine and Moss, 1997). These discussions remain speculative, because almost all neurophysiological studies of the bat auditory system have been conducted with artificial sonar stimuli that simulate the bat’s sonar emissions and echo returns, rather than echo returns from the bat’s own sonar vocalizations. Moreover, studies of the bat nervous system have been largely conducted in passively listening, and often anesthetized, bats in the laboratory. We are therefore left with the question of how neural responses to artificial stimuli in passively listening bats informs us of activity patterns that are evoked by echoes of the bat’s sonar vocalizations. No doubt, the representation of noisy sonar scenes arises from the activity of populations of neurons (Simmons, 2012). Recent studies of the dynamics of echo-evoked activity in the bat sonar receiver of the free-flying actively echolocating animal indeed demonstrate remapping and shifts in 3D spatial tuning of midbrain auditory neurons with the bat’s sonar inspection of objects (Kothari et al., 2016). These findings can serve to motivate a broad and intense investigation of neural activity patterns in animals that freely explore noisy sensory environments.

**Acoustically noisy ecological scenarios**

Here, we examine in detail three ecological scenarios where bats are faced with noisy environmental conditions. These scenarios highlight the flexibility that is afforded to bats by using multiple mechanisms for overcoming challenging sensory conditions.

**Scenario 1: echolocating conspecifics**

Bat echolocation calls are among the most intense acoustic signals in nature, sometimes exceeding 140 dB sound pressure level (SPL) (see Glossary) at 0.1 m (Holderied et al., 2003; Sürlykke and Kalko, 2008). Bats routinely encounter conspecifics when departing from a shared roost, commuting or foraging. A potential challenge arises when a bat must filter high-intensity conspecific calls to detect and discriminate echo streams that are at a much lower sound level. This problem has received considerable attention in the literature over the past 15 years (e.g. Ulanovsky et al., 2004; Gillam et al., 2007; Cvikel et al., 2015a). Much of the discussion in the literature has focused on the hypothesis that, like electric fish (Heiligenberg, 1991), bats alter the frequency of their emissions to avoid spectral overlap with conspecific calls, a behavior known as the jamming avoidance response (JAR).

Early evidence for JAR in bats came from studies of bats calling alone or in pairs in the wild (Habersetzer, 1981; Ulanovsky et al., 2004; Ratcliffe et al., 2004). Pairs of bats flying together frequently adjusted their peak calling frequency to maintain a 3–4 kHz separation. Field (Gillam et al., 2007) and laboratory (Bates et al., 2008; Takahashi et al., 2014) playback experiments later confirmed this finding: bats rapidly (in one study <200 ms) adjust their calling frequency to avoid spectral overlap between playbacks and the most shallowly FM components of their calls. Another study examined the call structure of bats flying alone or in pairs in a laboratory (Chiu et al., 2009). Bats adjusted their call structure when flying near conspecifics to a degree that was dependent on the baseline similarity between the two bats’ calls when flying alone. That is, pairs of bats that had similar calls when flying alone made larger changes to their calls when flying together. These studies conclusively demonstrate that at least some bats use the JAR to avoid acoustic interference from conspecifics.

Recent studies have led to an alternative hypothesis for observed frequency changes in groups of echolocating bats (Cvikel et al., 2015a; Götze et al., 2016). Namely, the authors hypothesize, and have found strong evidence, that some bats alter call frequency as a reaction to the physical presence of other bats, not their acoustic presence. These studies show that not all bats use JAR, and that frequency shifts alone are not sufficient for demonstrating JAR in bats. This alternative hypothesis does not explain the data from...
some previous studies that controlled for the physical presence of bats either by using playback experiments (Gillam et al., 2007; Takahashi et al., 2014) or by carefully measuring the positions and orientations of the bats that were present (Chiu et al., 2010). Thus, it appears that some, but not all, bats use JAR.

Regardless of whether they employ JAR, bats are likely to use multiple mechanisms to correctly sort conspecific calls from their own echoes (see discussions in Ulanovsky and Moss, 2008; Bates et al., 2008). A bat’s own echoes are likely to form predictable streams (Fig. 2B) and have a time–frequency structure and directional cues that will differ from calls of conspecifics (Yovel et al., 2009). One recent study found that Pipistrellus kuhlii solved the problem of extreme acoustic interference from conspecifics not by adjusting call frequency but by increasing call duration, intensity and pulse rate (Amichai et al., 2015). These adjustments all improve the signal-to-noise ratio (SNR; see Glossary) of calls over background noise, a finding that indicates the problem posed by conspecific calls (at least when numerous conspecifics are present) is acoustic masking, not differentiating one’s own calls from those of conspecifics.

There are conflicting data on how bats adjust their calling rate in response to conspecifics. Some studies indicate that bats decrease their calling rate when calls of one conspecific are present (Jarvis et al., 2010, 2013; Adams et al., 2017), but others have found that bats increase their calling rate, particularly when faced with calls of numerous bats (Amichai et al., 2015; Lin et al., 2016). Suppressed calling rates have been interpreted as evidence for group cooperation (Adams et al., 2017), but alternatively this could indicate that bats are devoting more of their attention (see Glossary) to passively listening to conspecific calls (Barber et al., 2003).

Collectively, these studies demonstrate that bats use numerous mechanisms for separating signals and noise, and their reliance on these mechanisms can shift depending on the prevailing conditions.

**Scenario 2: competing with conspecifics for food**

Group foraging involves a fundamental tradeoff: bats can improve searcher efficiency by eavesdropping on the feeding calls of conspecifics (Gillam et al., 2007; Dechmann et al., 2009), but this can increase competition for food. A high density of foraging bats also increases the complexity of the acoustic and physical environment, taking the bat’s attention away from foraging (Cvikel et al., 2015b). Bats may be under selective pressure to fend off competitors, even though they themselves benefit from eavesdropping on others. Recent research has revealed multiple acoustic strategies that bats use during competition for food.

One such strategy is the use of food-claiming calls. A recent laboratory study showed that big brown bats make specific communication calls called FM bouts (FMBs) when competing with other bats for a prey item (Wright et al., 2014). FMB calls contain individual-specific signatures, and, when produced, they caused an increase in the spatial separation between the bats. Bats that produced more FMBs were more likely to capture food items (Fig. 4A). Field studies have shown that pipistrelle bats (Pipistrellus spp.) produce social calls that might have a similar function (Barlow and Jones, 1997). Pipistrelles produce these calls more often when food density is low, and playbacks of the social calls had a deterrent effect on conspecifics. Bats at foraging sites are frequently observed chasing conspecifics while emitting social calls (e.g. Miller and Degn, 1981). Dominant bats could be aggressively chasing away competitors and advertising their presence with specialized, individual-specific calls. This would not only reduce competition for food but also simplify the acoustic and physical environment so that the bat can focus attention on finding prey (Cvikel et al., 2015b).

Another strategy observed in pairs of big brown bats competing for food is ‘silent behavior’ (Chiu et al., 2008). Specifically, when flying within 1 m of conspecifics, paired bats routinely (approximately 40% of the time) ceased echolocating for periods of 0.2–2.55 s (Fig. 4B). These behaviors were almost never observed in bats flying alone. Silence was more common when pairs of bats had echolocation calls with similar design. This could be interpreted in one of two ways: (1) bats could use silence as a mechanism for avoiding jamming from conspecifics that produce similar calls to their own, or (2) the similarity in call design between the two bats could make it easier for the bat engaging in silent behavior to use the conspecific’s calls and echoes for its own sonar system. This could, in turn, enable a bat’s stealth attack on the prey item. At present, these hypotheses remain untested.

Finally, Mexican free-tailed bats use sinusoidally frequency-modulated (sinFM; see Glossary) calls to jam the echolocation of competing bats attempting to capture prey (Corcoran and Conner, 2014). Bats produce sinFM calls only when a competing bat is in the approach and terminal buzz phase of prey capture (Fig. 4C, Fig. 5B). When conspecifics produced sinFM calls that overlapped their feeding buzz, bats captured prey during only 6% of attacks, compared with 35% when no sinFM calls were present. Playback experiments showed that the timing and time–frequency structure of sinFM calls are important for interfering with the competitor’s attack. 3D reconstructions of bat flight trajectories showed bats engaged in extended bouts of food competition where they took turns jamming one another while the other bat attempted to capture prey (Fig. 4C).

Studies of food competition strategies give insight into how bats cope with acoustic interference. First, these data provide further evidence that bats are a potential source of acoustic interference, either because of the calls that they make or because of their physical presence as a sound-reflecting object. Second, silent behavior indicates that bats are capable of orienting by eavesdropping on the calls (and perhaps echoes) of conspecifics. Third, specialized sonar-jamming calls demonstrate that, despite the extraordinary adaptations observed in echolocating bats, they are not impervious to acoustic interference, particularly when trying to capture prey. Jamming signals provide insight into fundamental constraints on echolocation, a topic we discuss further below.

**Scenario 3: insect noise**

Aside from bats, chorusing insects such as katydids are one of the most common sources of ultrasound in the environment (Robinson and Hall, 2002). Playback experiments provide evidence that insect noise is a potential source of acoustic interference for bat echolocation. Gillam and McCracken (2007) recorded T. brasiliensis echolocation calls in the field in the presence of silence or playbacks of insect noise that varied in peak frequency from 16.5 to 29 kHz. Bats shifted their calling frequency upward depending on the frequency of the playback, always maintaining a 2–4 kHz separation between their calling frequency and that of the insect noise. This finding indicates that bats exhibit a JAR not only in response to conspecifics but also to a variety of interfering signals.

Several insects, including several families of moths (Blést et al., 1963; Barber and Kawahara, 2013; Corcoran and Hristov, 2014) and tiger beetles (Yager and Spangler, 1997), produce bursts of ultrasonic clicks in response to the attack cries of bats. Clicks produced at relatively low rates have the primary function of warning bats that the insect is toxic (Hristov and Conner, 2005; Ratcliffe and Fullard, 2005); some palatable moths also mimic these sounds to deceive bats (Barber and Conner, 2007).
Of particular interest here are some species of tiger moths and hawkmoths that produce clicks at high rates to jam bat echolocation (Corcoran et al., 2009; Kawahara and Barber, 2015). Like the jamming sinFM calls of bats, these clicks are produced during the bat’s approach and buzz phases of echolocation. Psychophysical (Miller, 1991) and neurophysiological (Tougaard et al., 1998) experiments show that clicks disrupt the target ranging ability of bats by multiple orders of magnitude, but, to do so, clicks must occur within 1–2 ms of echo returns. Moths cannot anticipate when this window will occur, so their solution is to click at extremely high rates (as high as 4000 clicks s \(^{-1}\)) that ensure some clicks will co-occur with each set of echo returns. Experiments pitting bats against jamming moths found that bats often continued prey pursuit through the barrage of noise, but missed the prey by a distance similar to the errors observed in psychophysical and neurophysiological experiments (Corcoran et al., 2011).

How do the jamming signals described above interfere with bat echolocation? The specialized jamming signals of bats and moths might provide insight into how bats process and segregate echoes from noise. Because these signals appear to have evolved specifically to jam bat sonar, they might contain elements that either infiltrate or disrupt the bat’s neural pathways. Currently, this discussion is speculative because no studies have examined how the structure of jamming signals affects their disruptive capacity.

Moth clicks and bat sinFM calls have dramatically different acoustic structures, but they also have some common features (Fig. 5). Both signals occupy a high proportion of time during the bat’s terminal buzz, overlap spectrally with the bat’s calls, and have frequency components that change rapidly over time. Tiger moths produce bursts of 20–30 clicks at a time through the sequential buckling and elastic recoil of their tymbal organ (see Glossary) (Blest et al., 1963). Clicks are very short (0.24 ms) and broadband. The peak frequency of clicks in a series decreases and then increases with the sequential buckling and elastic recoil of striations on the surface of the tymbal. In comparison, sinFM calls consist of one to five relatively long (mean 65 ms) syllables that are produced as long as a competing bat continues its buzz. These calls oscillate up and down over the frequency band of conspecific buzz calls (Fig. 5B).
SinFM calls oscillate at a rate of 166 Hz, which is similar to the bat’s calling rate of 154 Hz during the feeding buzz (Corcoran and Conner, 2014). This suggests that the rhythmic sinFM oscillations might have evolved specifically to elicit responses from neurons that fire in response to feeding buzz calls.

The acoustic structure of bat and moth jamming signals hints at the possibility that they have specific features that infiltrate the bat sonar receiver. It is unlikely that bats perceive jamming signals as actual echoes, because bats have highly refined echo discrimination abilities (Masters and Raver, 1996; Corcoran et al., 2010). A more likely possibility is that the acoustic structure of jamming signals actively disrupts echo processing in the bat’s neural pathways. Further behavioral and neurophysiological experiments are required to test these hypotheses.

Multi-modal sensing as a mechanism for coping with noise

A common solution to sensing in noisy environments is to use multiple sensory modalities (Munoz and Blumstein, 2012). Bats provide numerous examples of this phenomenon, both as short-term behavioral responses and as evolutionary adaptations to specific foraging niches (Schnitzler and Kalko, 1998). Echolocation is poorly suited for detecting objects resting on vegetation or the ground because target and background echoes return nearly simultaneously. Bats that acquire stationary food items from surfaces (including insects, fruit and nectar) show increased reliance on passive listening (reviewed by Jones et al., 2016), olfaction (Korine and Kalko, 2005) and vision (Bell, 1985; Eklöf and Jones, 2003). Bats that forage close to vegetation tend to have larger eyes and better visual acuity than bats that forage in open spaces (table 2 in Eklöf, 2003). These examples show an increased reliance on multi-modal sensing for bats that forage in cluttered habitats.

There is increasing evidence that bats routinely integrate echo-acoustic and visual information to perceive their surroundings (Horowitz et al., 2004; Orbach and Fenton, 2010; Boonman et al., 2013). A recent study showed that Egyptian fruit bats (Rousettus aegyptiacus) alter their echolocation signaling rate depending on light levels (Danilovich et al., 2015). Despite having excellent vision, these bats never ceased echolocating entirely. This could be because echolocation and vision provide complementary sensory information. Echolocation allows detection of small targets under low light levels, and provides better ranging ability, whereas vision is effective over longer distances and provides better spatial resolution along the dimensions of azimuth and elevation (Boonman et al., 2013). We propose that multimodal sensing may be widespread in naturally behaving animals, and is not only a means for coping with uncertainty in preferred sensory modalities (Munoz and Blumstein, 2012).

An open question is to what extent bats rely on vision for obstacle detection and avoidance. If a bat is subject to severe acoustic interference, such as when flying amongst hundreds of calling conspecifics, could it utilize vision to avoid flying into vegetation or other bats (Kong et al., 2016)? Some studies have modified either light levels (Horowitz et al., 2004) or the visual conspicuousness of obstacles (Orbach and Fenton, 2010) to show that bats can use vision for obstacle avoidance. However, further experiments are needed that independently control for both the visual and echo-acoustic cues of obstacles.

Discussion

Bats exhibit numerous adaptations to successfully operate in noisy sensory environments. Central to the bat’s success is the ability to dynamically coordinate signal emission and reception over fine time scales (Moss and Surykke, 2010; Wohlgemuth et al., 2016b). These adjustments optimize information acquisition and minimize the effects of interference arising from background objects, such as the signals produced by conspecifics and insects. The bat sonar

Fig. 5. Sonar jamming signals of moths and bats. (A) Clicks produced by the tiger moth Bertholdia trigona to jam the sonar of the big brown bat, Eptesicus fuscus (Corcoran et al., 2009). (B) Intraspecific sonar jamming signals (sinFM) of the Mexican free-tailed bat, Tadarida brasiliensis (Corcoran and Conner, 2014). Oscillograms and spectrograms are shown of the jamming signals alone (top), and spectrograms are shown of jamming signals made during a bat attack sequence (bottom). Note the distinctive time–frequency structures of the jamming signals, and that they are both produced to overlap in time and frequency with the attacking bat’s feeding buzz.
system can be considered a highly refined form of animal communication, where the signaler and receiver are one and operate through shared neural processes that have evolved over tens of millions of years. Here, we relate studies of bat echolocation in noisy environments to sensory challenges encountered by a wide range of animals.

**Dynamic representations of echo scenes**
The bat’s auditory system is specialized to process features of sonar pulses and echoes. The neural basis of acoustic imaging by sonar is still an area of active investigation, but both behavioral (Chiut et al., 2009; Yovel et al., 2009) and neurophysiological studies (Wohlgenuth and Moss, 2016; Kothari et al., 2016) indicate that bat auditory systems have evolved to detect and discriminate features of their own calls from other sounds. An exciting recent discovery is that the receptive fields of bat auditory neurons change rapidly in ways that appear to facilitate the transformation of echo streams into perceptual representations of auditory objects (Bartenstein et al., 2014; Beetz et al., 2016). It has also been reported that 3D spatial response profiles of midbrain neurons remap to represent shorter distances with higher resolution when freely echolocating big brown bats adjust their echolocation behavior to inspect sonar objects (Kothari et al., 2016). These findings, illustrated in Fig. 6, indicate that the bat’s auditory receiver changes dynamically on a very rapid time scale. What remains to be investigated are the ways in which acoustic clutter or noise contribute to dynamic neural representations. We hypothesize that neurons tracking targets in the presence of acoustic clutter sharpen their response areas, and this can be tested through systematic empirical studies.

Dynamic sensory processing is important to the lives of many, if not all, animals. For example, in the presence of masking noise, birds and other animals adjust the frequency of their courtship signals to improve the SNR (Shannon et al., 2016). It has been proposed that a tradeoff exists between optimizing signal transmission and saliency of the signal to the receiver (Patricelli and Blickley, 2006). A bird that shifts its calling frequency in noise could improve the SNR at the receiver, but the female receiver might be less responsive to this altered signal. It therefore benefits receivers to have flexible feature detection and recognition systems, especially under noisy conditions. Future research on sensory representation in dynamic environments may reveal the extent to which animals other than bats encode dynamic natural stimuli.

**Signal interference**
A downside of selective feature recognition may be that it puts animals at increased risk to specific types of interference, which can be exploited by other animals. This appears to occur in the jamming signals of bats and moths (Fig. 5). Active sensory interference also appears to occur in other communication systems. For example, male oyster toadfish (Opsanus tau) produce precisely timed ‘grunts’ that interfere with communication between competing males and females (Mensinger, 2014). These grunts might reduce the perceived frequency of advertisement calls made by competitors, and thereby reduce their attractiveness to females. Thus, interference signals provide distinct opportunities for probing the inner workings of animal communication receivers.

**Coordination between sender and receiver**
Sensing requires animals to first detect and discriminate signals from noise and then extract meaningful information from those signals. Animals must have in place mechanisms for achieving each of these sensory tasks. Bats have solved this problem elegantly, again because they actively control signal emission and reception with respect to behavioral state and informational need. As discussed above, bats shift rapidly from producing signals that are optimized for detection to signals that are optimized for localization and feature extraction. This is possible because bat echolocation operates through an action-perception loop to adjust signal parameters dynamically with informational needs. Because sender and receiver are the same individual in bat echolocation systems, there is rapid and tight coordination between call production and echo processing. It follows that the level of coordination between sender and receiver in other animal communication systems should impact both the timing and reliability of signal transmission and reception. This proposal can be tested directly through comparative analyses of communication behaviors throughout the animal kingdom.

**Comparative studies of active sensing in noisy environments**
While bats and other echolocating animals actively control the timing and features of biosonar signals used to probe the environment, active sensing operates in species throughout the animal kingdom (Schroeder et al., 2010). Active sensing refers to the movements animals make to modify sensory input, which in turn guides future behaviors. Eye movements, for example, allow an animal to scan the

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**Fig. 6. Cartoon representation of dynamic echo delay response profiles of three idealized neurons, shown separately in red, blue and green, in the bat auditory system.** Along the lower x-axis are spectrograms of echolocation calls produced by an FM bat through the search, approach and capture phases of insect pursuit. Solid horizontal lines below calls at each insect pursuit phase represent signal duration, and dotted lines represent the interval between successive calls. Note that call duration and interval decrease progressively from search to approach to capture phases. The y-axis shows relative echo delays (target distances) over which the neurons respond. The upper x-axis plots the relative response of the neurons to echo delays at each of these insect capture phases. Neurons 1, 2 and 3 respond to the search and approach phases of insect pursuit, but at different echo delays: neuron 1 responds to the longest echo delays, neuron 2 to intermediate echo delays, and neuron 3 to short echo delays. At the capture phase, only neuron 3 responds to a subset of echoes from the calls produced at a high repetition rate (short intervals). Note that neurons 1 and 2 show shifts in responses to shorter echo delay as the bat adapts its echolocation behavior and approaches the prey. At the end of the approach phase, the echo delay response areas of the three neurons are close to overlapping. All three neurons show a sharpening of echo delay tuning with increasing call repetition rate. This cartoon is based on a synthesis of data reported in Suga and O’Neill (1979); Sullivan (1982); Wong et al. (1992); Bartenstein et al. (2014); Beetz et al. (2016); Kothari et al. (2016).
environment and represent objects across a broad panorama. The visual stimuli acquired through eye movements are also used to inform decisions for subsequent behaviors (Land, 2006). Similarly, head and ear movements introduce changes in acoustic signals received at the two ears to enhance cues for auditory localization and influence perception of an auditory scene (Populin and Yin, 1998; Wohlgenuth et al., 2016b). Along related lines, sniffing and whisking serve to modulate sensory signals that can be used to build up information over time (Ganguly and Kleinfeld, 2004; Catania, 2006; Towl and Hartmann, 2006). We propose that quantitative analyses of the echolocating bat’s adaptive behaviors in noisy environments will provide the motivation for new lines of investigation on active sensing in a wide range of species across the animal kingdom. Ultimately, such comparative studies of active sensing will serve to differentiate between species-specific specializations and general solutions animals employ to perform natural behavioral tasks in noisy sensory environments.

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