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## **Auditory Mechanisms of Echolocation in Bats**

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### **Summary and Keywords**

Echolocating bats have evolved an active sensing system, which supports 3D perception of objects in the surroundings and permits spatial navigation in complete darkness. Echolocating animals produce high frequency sounds and use the arrival time, intensity, and frequency content of echo returns to determine the distance, direction, and features of objects in the environment. Over 1,000 species of bats echolocate with signals produced in their larynges. They use diverse sonar signal designs, operate in habitats ranging from tropical rain forest to desert, and forage for different foods, including insects, fruit, nectar, small vertebrates, and even blood. Specializations of the mammalian auditory system, coupled with high frequency hearing, enable spatial imaging by echolocation in bats. Specifically, populations of neurons in the bat central nervous system respond selectively to the direction and delay of sonar echoes. In addition, premotor neurons in the bat brain are implicated in the production of sonar calls, along with movement of the head and ears. Audio-motor circuits, within and across brain regions, lay the neural foundation for acoustic orientation by echolocation in bats.

Keywords: biosonar, echo scene perception, 3D localization, target ranging, echo-delay tuned neurons

### **Introduction**

Echolocation is an active perceptual system, used by some animals to detect, localize, and classify objects in the environment (Griffin, 1958). The active component of echolocation is the animal's production of sounds that reflect from objects in the environment, and perception is based on information processed from echo returns. Echolocation has been documented in bats, toothed whales, some species of nocturnal birds, some shrews and tenrecs and even from some blind or blindfolded humans (Griffin, 1958; Busnel & Fish, 1980; Nachtigall & Moore, 1988, Thomas, Moss, & Vater, 2004; Fenton & Simmons, 2015). Egyptian fruit bats in the family Pteropodidae, echolocate with tongue clicks rather than vocal signals.

Echolocating bats are nocturnal mammals and navigate by processing information carried by echoes from objects in their surroundings (Griffin, 1958; Neuweiler, 1989). The more than 1,000 species of echolocating bats, and their echolocation signals and behaviors, reflect their diversity in habitat and diet. Many bats eat insects, but some feed on fruit, nectar, blood, or even small vertebrates (Fenton & Simmons, 2015).



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**Figure 1.** Big brown bat, *Eptesicus fuscus* (left) and Egyptian fruit bat, *Rousettus aegyptiacus*, (right), photos taken by Brock Fenton and Ben Falk in a laboratory flight room at Johns Hopkins University.

Consider an echolocating bat hunting insects in the night sky. Light levels are often low, and thus the bat cannot rely on its vision. Obstacles, such as trees, bushes, or manmade buildings are present, but the bat dodges even branches and telephone wires with ease. As the animal flies, it produces vocalizations that are in the ultrasonic range, above 20 kHz, the upper frequency limit of the human hearing. These high frequency signals are well suited to return echoes from small objects, such as insects, because the wavelengths of the signals are short with respect to the reflecting surfaces.

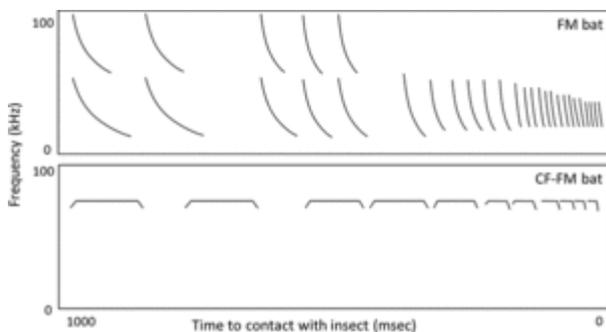
During each attack on a prey item, insectivorous bats rely on changing echo features to guide their movement (Moss, Chiu, & Surlykke, 2011). Imagine that an insect is located off to right of the bat's midline when first detected. The bat computes the horizontal and vertical position of the insect from differences in the perceived onset time, intensity, and spectrum of echoes at its two ears (Simmons et al., 1983; Lawrence & Simmons, 1982; Wotton, Haresign, Ferragamo, & Simmons, 1996). After determining the two-dimensional position of the insect, the bat aims its head at the insect, produces sonar vocalizations, receives new acoustic snapshots of the target, and re-directs its flight path (Ghose & Moss, 2006). Essential to the bat's successful pursuit of prey is the estimation of target distance. The bat determines target distance from the time delay between its sonar vocalizations and the returning echoes (Simmons, 1973). It uses the 3-D information about target location to guide the features of its sonar vocalizations and to position itself to grasp the insect with its wing or tail membrane (Moss & Surlykke, 2010).

As a bat flies toward an insect target, the features of its sonar vocalizations change dynamically. Characteristics of sonar emissions have been used to divide the bat's insect pursuit sequence into different phases: search, approach, and terminal buzz (Griffin, Webster, & Michael, 1960; Webster, 1963A, 1963B). Search phase signals in the big brown bat (*Eptesicus fuscus*), a common northern American species (see Figure 1) are characterized by shallow frequency modulation (FM) at a repetition rate of 5–10 Hz and a relatively long duration of 15–20 msec. Once the bat detects and selects a prey item, it produces approach phase signals at a repetition rate of 20–80 Hz that show steep FM components and are shortened in duration (2–5 msec). In the final phase of capture, the bat emits terminal buzz signals at short durations (0.5–1 msec) and a high repetition rate (up to 150 Hz). In terminal buzz signals, the sound frequency can sometimes drop below 20 kHz (Schnitzler & Kalko, 2001; Surlykke & Moss, 2000). The bat's dynamic sound production pattern is more than a stereotyped sequence of vocalizations; it forms part of a complex set of adaptive behaviors to continuously changing acoustic information (Moss & Surlykke, 2001).

The adaptive echolocation behavior of big brown bats shares features with hundreds of other bats. But across bat species, frequencies dominating the echolocation calls range from <8 kHz to over 200 kHz, and calls can be anywhere from 1 ms to over 100 ms long.

## Echolocation Signal Design

The signal types and sound production mechanisms used by different bat species vary greatly, but all calls produced with the larynx contain some frequency modulated (FM) components (see Figure 2, upper panel), meaning that the frequency varies over the duration of the signal. FM signals are well suited for *target localization*, as they carry information about the 3-D position of small objects, as each frequency in the signal provides a time marker for its arrival time at the bat's ears (Simmons & Stein, 1980; Moss & Schnitzler, 1995). In contrast to FM signals, constant frequency (CF) sounds do not vary the frequency over the duration of the signal, (see Figure 2, lower panel) though most CF signals are combined with FM components. These tonal sounds are well suited to carry information about *target movement* through Doppler shifts in the returning echoes (Schnitzler, 1968, 1973). A Doppler shift is an apparent change in sound frequency that is proportional to the relative velocity of the source (in this case the sonar target) relative to the listener (in this case the bat). If the bat approaches the target, the apparent echo frequency increases, which is noted as a positive Doppler shift. There is evidence that bat species using both FM and CF signals show individual variation in signal structure that may facilitate processing of echo returns from their own vocalizations (Masters, Jacobs, & Simmons, 1991; Suga, Niwa, Taniguchi, & Margoliash, 1987).



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**Figure 2.** Cartoon illustration of a sequence of frequency modulated (FM) echolocation calls (top) and constant frequency (CF) echolocation calls (below). Frequency in kHz is plotted on the Y axis and time in milliseconds on the X axis. Note that the duration and interval between echolocation signals decreases towards time 0, when the bat intercepts its insect prey.

At each phase of insect pursuit, the dynamic sonar sound characteristics used by FM bats reflect adaptive signal designs for different acoustic tasks: target detection, localization, and tracking (Simmons & Stein, 1980). The long, 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 of time; the broadband approach and terminal phase signals are adapted for target localization in three dimensions (Moss & Schnitzler, 1995). The bat actively adjusts the duration and repetition rate of the signals to avoid overlap of sonar emissions (Kalko & Schnitzler, 1993). These phases of insect capture represent distinct modes of action and perception, which guide spatial navigation and prey capture.

Egyptian fruit bats, *Rousettus aegyptiacus*, echolocate with tongue clicks, which are broadband acoustic signals. These clicks are generated in pairs, with beam patterns directed off-axis from the midline. When *R. aegyptiacus* are flying to a landing platform, they direct the maximum slope of the sound beam, not the center, at the target. This strategy maximizes cues for sound localization accuracy (Yovel, Falk, Moss, & Ulanovksy, 2010). By contrast, the insectivorous big brown bat, a laryngeal echolocator that uses FM sonar vocalizations, directs its sound beam straight at the target it is localizing (Ghose & Moss, 2003).

The sonar beam directing behavior of the echolocating bat indicates the animal's attention to objects in space (Ghose & Moss, 2006). This was demonstrated in studies that investigated the big brown bat's echolocation behavior as it performed a dual task: obstacle avoidance and insect capture (Surlykke, Ghose, & Moss, 2009), and a target texture discrimination task (Falk, Williams, Aytekin, & Moss, 2011). The sonar beam pattern of the big brown bat is directional but wide enough to capture echoes 30–60 degrees off axis (Hartley & Suthers, 1989). In both the obstacle avoidance/insect capture and target texture discrimination experiments, the bat directed its sonar

beam axis at objects it was inspecting with an accuracy of  $\sim 5$  degrees, and sequentially shifted its “acoustic gaze” between objects, sometimes with intervals between “glimpses” as short as  $\sim 70$  msec. The bat’s acoustic scanning behavior shares parallels with foveal scanning of objects in animals that rely on vision. In the case of the bat, it is hypothesized that the animal directs its sonar beam axis at objects it is inspecting to take advantage of higher spatial auditory resolution along the midline (Surlykke, Simmons, & Moss, 2016).

## Perception by Echolocation

Detection of objects by echolocation depends on the strength of returning echoes and the hearing sensitivity of the echolocator. Large objects, such as trees, buildings, and the ground reflect strong echoes, and can be detected at distances greater than 10 meters (Stilz & Schnitzler, 2012). Small insect prey can be detected by bats at distances of 3–5 meters (Kick & Simmons, 1984). Laboratory studies of target tracking along the horizontal axis in bats suggest an accuracy of about one degree (Masters, Moffat, & Simmons, 1985; Ghose & Moss, 2003), and accuracy of vertical localization is approximately three degrees (Lawrence & Simmons, 1982). Behavioral studies of distance discrimination in bats using FM echolocation calls report thresholds of about 1 cm, corresponding to a difference in echo arrival time of approximately 60 microseconds (Simmons, 1973). Experiments that require a bat to detect changes in the distance (echo delay) of a jittering target report thresholds of less than 0.1 mm, corresponding to a temporal jitter in echo arrival time of less than one microsecond (Simmons, Ferragamo, Moss, Stevenson, & Altes, 1990).

Several bat species that use CF signals for echolocation adjust the frequency of sonar transmissions to offset Doppler shifts in the returning echoes, the magnitude of which depends on the bat’s flight velocity. These adjustments in the frequency of the CF echolocation calls, referred to as Doppler shift compensation, allow the bat to isolate small amplitude and frequency modulations in sonar echoes that are produced by fluttering insects (Schnitzler, 1968; Neuweiler, Bruns, & Schuller, 1980). Generally, CF signals are long in duration (up to 100 msec) compared to FM sounds (1–20 ms) and are thus ideal to encode echo changes arising from the movement of a fluttering insect over one or more wing-beat cycles. For example, the greater horseshoe bat (*Rhinolophus ferrumequinum*) can discriminate frequency modulations in the returning echo of a fluttering moth of approximately 30 Hz, which is less than 0.5% of the bat’s 83 kHz CF signal component (Schnitzler & Flieger, 1983; von der Emde & Menne, 1989).

Target discrimination and recognition by echolocation has been examined in some bat species. For example, a free flying *Eptesicus fuscus* can effectively discriminate between small objects differing in shape and texture using FM signals (Griffin, Friend, & Webster, 1965; Falk et al., 2011). 3-D target recognition of fluttering insects viewed from novel perspectives has been reported in the greater horseshoe bat, a species that uses a CF echolocation signals (von der Emde & Schnitzler, 1990).

## Neural Substrates of Echo Processing

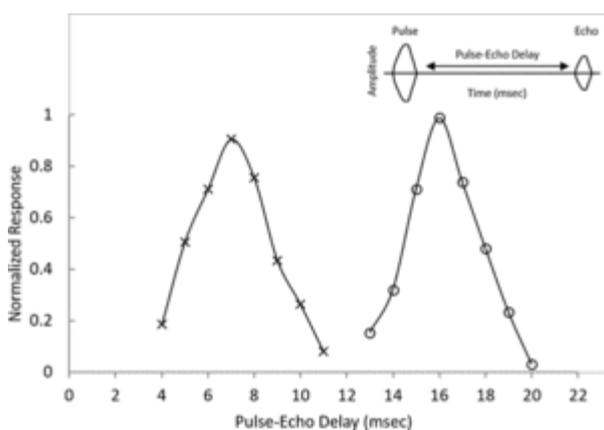
Decades of research have revealed specializations for the processing of sonar echoes in the auditory system of bats. These specializations are built on the fundamental organization of the mammalian auditory system. The bat’s auditory system receives and processes echoes and other sounds in its environment for the task of spatial

perception using acoustic cues (Suga, 1988; Popper & Fay, 1995). Echoes are amplified and filtered by the external ear (pinna), and transmitted via the middle ear from air to the fluid-filled cochlea, and processed by hair cells on the basilar membrane. Sound produces movement of the basilar membrane, which stimulates the hair cells resting on the membrane. The basilar membrane varies in stiffness along its length, and consequently, low frequency sounds produce movement in the apical region and high frequency sounds produce movements at the base. The mechanical properties of the basilar membrane therefore confer a tonotopic representation of sound at the level of the inner ear (Popper & Fay, 1995; Kössl & Vater, 1995). This provides a basis for sound frequency information to be transmitted to brainstem, midbrain, and thalamic nuclei and the primary auditory cortex.

Some bat species using CF echolocation calls show specializations in the peripheral (inner ear) and central auditory (brain) systems for processing echoes in the CF range of their echolocation sounds: For example, the auditory system of the greater horseshoe bat shows a large proportion of neurons devoted to processing this reference frequency, and an expanded representation of 83 kHz can be traced to mechanical specializations of this bat's inner ear (Neuweiler et al., 1980).

An expanded representation of biologically relevant sound frequencies has been reported in other species of bats that use CF signals for echolocation. For example, *Pteronotus parnellii*, the mustached bat, a Neotropical species that produces a multiple-harmonic signal with a dominant second harmonic CF signal at around 60 kHz, shows an expanded representation of this sound frequency from the level of the cochlear nuclei through the midbrain and auditory cortex (Pollak & Casseday, 1989). This expanded representation of 60 kHz is hypothesized to support detection of fluttering insect prey in cluttered environments (Popper & Fay, 1995).

There are other specializations in the bat central auditory system for processing echolocation signals that may play a role in the perception of target distance. In several bat species, researchers have identified neurons in the midbrain, thalamus, and cortex that respond selectively to pairs of FM sounds, separated by a particular delay (Suga & O'Neill, 1979). The pairs of FM sounds simulate a sonar vocalization of the bat followed by an echo, and the time delay separating the two signals corresponds to a particular target distance. Most delay-tuned neurons in the bat auditory system respond in the range of 2–40 milliseconds, corresponding to target distances of approximately 34–590 cm (see Figure 3). These best delays therefore represent a biologically relevant operating range for localizing prey items using echolocation (Suga, 1990).



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**Figure 3.** Cartoon illustration of activity patterns of echo-delay-tuned neurons in the bat central nervous system. An artificial sonar pulse and echo are broadcast (see inset) over changing time delays, and neurons show a maximum

in the midbrain superior colliculus (SC) of the big brown bat, neurons with three dimensional spatial response profiles have been characterized (Valentine & Moss, 1997). Neurons with 3D spatial tuning respond selectively to combinations of sound source azimuth, elevation, and distance. The bat SC also shows premotor specializations to support acoustic orienting by sonar. Specifically, premotor activity occurs with the production of sonar vocalizations and the lead-time of this activity is related to the duration of sonar calls (Sinha & Moss, 2007). In addition, pinna and head movements of the echolocating bat are activated by premotor SC neurons (Valentine, Sinha, & Moss, 2002). Collectively, sensorimotor specializations in the bat SC

response to a particular delay. At shorter and longer delays, the response falls off. The two examples here show best delays of 7 and 16 msec, corresponding to target distances of approximately 1.2 and 2.75 meters.

support spatial orientation by echolocation (Moss & Sinha, 2003; Valentine & Moss, 1997; Valentine et al., 2002).

In some bat species, the frequency and echo-delay tuning of cortical neurons is represented topographically (Pollak & Casseday, 1989; Popper & Fay, 1995). In other words, the best frequency and echo-delay of neighboring neurons shift systematically across the cortical surface. It is noteworthy that topographical organization of delay-tuning has been reported in numerous studies of auditory cortex of the mustached bat, *P. parnellii* (Suga, 1990); however, studies of some FM bat species (big brown bat, *E. fuscus* and little brown bat, *Myotis lucifugus*) have not yet demonstrated a clear topography of target distance representation (Dear, Fritz, Haresign, Ferragamo, & Simmons, 1993; Paschal & Wong, 1994; Shannon-Hartman, Wong, & Maekawa, 1992). In a comparative study of three bat species, *Pteronotus quadridens*, *Pteronotus parnellii* and *Carollia perspicillata*, Hechavarría et al. (2013) report that delay-tuned cortical maps of all three species are blurry, as the response profiles of echo delay-tuned neurons are overlapping, with most showing responses to short echo delays.

Recent studies of echo delay-tuned neurons in the bat auditory cortex show plasticity in response profiles and dependence on stimulus context. For example, Bartenstein, Gerstenberg, Vanderelst, Peremans, and Firzlaff (2014) reported that the representation of target range in auditory cortical neurons of the echolocating bat, *Phyllostomus discolor*, is sensitive to simulated echo flow. Specifically, they show that cortical maps of passively listening bats reveal an expanded representation of short echo delay under acoustic conditions that simulate what a bat would experience when passing a target with decreasing lateral distance. In another study of bat auditory cortical activity, Macías, Mora, Hechavarría, and Kössl (2016) demonstrated that the amplitude of the echolocation pulses and echoes, which bats modulate under naturalistic situations, matches the amplitudes that elicit the maximum responses of cortical delay-tuned neurons. Moreover, neurons tuned to short echo delays respond maximally to low pulse amplitudes, while neurons tuned to long echo delays respond maximally to high pulse amplitudes. Beetz, Hechavarría, and Kössl (2016) compared responses of delay-tuned neurons in the auditory cortex of the bat species, *C. perspicillata*, to sonar broadcasts of natural echolocation call sequences and to isolated pulse-echo pairs extracted from these natural sequences. The authors find that cortical delay-tuned neurons respond broadly to isolated pulse-echo stimuli but to a restricted subset of pulse-echo pairs embedded in natural sequences. These results suggest that response suppression to natural sound sequences serves to sharpen selectivity to pulse-echo delay in cortical neurons.

## Conclusion

Echolocating bats produce high frequency sounds that reflect off objects in their surroundings, and they represent the world by listening to echo returns. The bat's active control over the features of echolocation signals and brain specializations for processing echo returns operate together to allow it to perceive the world through sound.

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