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Adaptive Vocal Behavior Drives Perception by Echolocation in Bats

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Abstract

Echolocation operates through adaptive sensorimotor systems that collectively enable the bat to localize and track sonar objects as it flies. The features of sonar signals used by a bat to probe its surroundings determine the information available to its acoustic imaging system. In turn, the bat's perception of a complex scene guides its active adjustments in the features of subsequent sonar vocalizations. Here, we propose that the bat's active vocal-motor behaviors play directly into its representation of a dynamic auditory scene.

Introduction

Bat echolocation is an active and adaptive system: Its success depends upon tight coupling between the animal's action (sonar signal production, head aim and flight path control) and perception that is derived from auditory processing of the information carried by echoes. The audiomotor behaviors that contribute to echolocation in bats collectively support distal sensing for spatial navigation, orientation and target acquisition in environments as diverse as tropical rainforests, arid deserts and urban environments [1, 2].

Over 1000 bat species echolocate by producing constant frequency (CF) or frequency modulated (FM) sonar pulses via the larynx. Specialized fast muscles support rapid (up to 200 per second), intense (up to 140 dB at 10 cm), short (down to 0.5 ms) ultrasonic vocalizations (up to 200 kHz) [3-5]. Pteropodidae (flying foxes) do not echolocate, except the genus *Rousettus*, which produces brief (50-100 μ s) sonar tongue clicks [6].

Echolocating bats adjust the time-frequency structure of their sonar calls as they approach targets (Figure 1a). For example, in a typical aerial insectivore, the big brown bat, *Eptesicus fuscus*, **search phase signals** are characterized by shallow frequency modulation (FM) at a repetition rate of 5-10 Hz and 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 with steep FM and reduced duration (2-5 msec). In the final phase of capture, **terminal buzz phase signals** shorten further (0.5-1 msec) and are produced at a very high repetition rate (up to 200 Hz; [7]). The bat's adaptive changes in sonar signal time-frequency structure as it detects, approaches and intercepts food support task-specific perceptual requirements [8].

Only bat species that track and intercept moving prey produce terminal buzz phase signals. Some bat species trawl for fish or insects over water, and prior to prey capture, trawling bats show the same pattern of sonar signal change as aerial insectivores, including high

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repetition, short duration calls characteristic of terminal buzz sequences. In contrast, when bats glean for prey sitting on surfaces, they do so without producing terminal buzz sequences [9, 10]. Frugivorous bats also feed on stationary food items, using a combination of echolocation and other sensory modalities and like insect-gleaning bats, they do not produce terminal buzzes when approaching food. The ubiquitous occurrence of sonar buzzes in trawling and aerial captures points to their importance in rapid sampling of moving prey position, and serves to illustrate the bat's adaptive control over acoustic information flow.

Bats extract information about the environment from the features of echoes. They listen to echo interaural spectrum, amplitude and timing to estimate the direction and distance of sonar targets [11, 12]. Bats that produce narrow band echolocation signals can use Doppler shifts in returning echoes to detect fluttering insect prey and its own relative velocity with respect to objects in the environment [13-16].

The bat's active control over echolocation signal design and directional aim are coordinated with aerial locomotion, and these adaptive sonar behaviors directly impact the flow of acoustic information used to sense the environment. The information extracted from sonar echoes, in turn, guides subsequent echolocation call design (Figure 1b). This intimate linkage between audition and action is fundamental to perception by echolocation, and here we review recent literature that uncovers new discoveries on adaptive sonar behaviors. We organize our review around feedback control over timing, direction and frequency of sonar echo returns.

Adaptive control over sonar signal timing and duration

To successfully negotiate a complex environment, an animal must control the timing of motor behaviors in coordination with dynamic sensory information (Figure 2). It is noteworthy that the pulse interval (PI), the time interval between the onset of one call and the next, does not always change continuously with decreasing target distance; rather it can remain relatively stable for fixed intervals, interrupted by longer gaps, over extended periods. The periods of stable sound repetition rate (sonar "strobe groups") occur when the bat is selecting a target, changing the direction of its flight path, and in proximity to obstacles (Figure 2a). The hypothesis is that stable signal repetition rates sharpen the bat's representation of space and are used in planning a flight trajectory that requires detailed object localization and tracking [17, 18].

FM-bats generally avoid overlap between outgoing sounds and returning echoes by adjusting pulse interval (PI) as well as call duration. Call duration decreases as the bat approaches an object, but at all distances, the bat typically waits until the object echo has been received before producing the next call, hence "placing" the echo in a window between the end of one pulse and the beginning of the next. Vocal-motor adjustments in call temporal parameters provide an indirect measure of where the bat is attending along the distance axis (Figure 2b).

In a task that required the big brown bat to negotiate its way through a small net opening to gain access to a tethered insect, the animal made adjustments in call duration as it approached the net, shortening its calls to avoid pulse-net echo overlap. Once the bat had planned its path through the opening it increased the duration of its calls to find the tethered prey before actually flying through the opening, tolerating pulse-net echo overlap [19] (Fig. 3a). These results suggest that the bat first inspected the net opening and then shifted its gaze to the more distant insect, offering a clear example of vocal adjustments to sequentially sample objects along the range axis.

Aytekin et al. [20] monitored the echolocating bat's adaptive sonar tracking behavior under controlled conditions. Big brown bats were trained to track an approaching tethered target from a stationary platform in the presence of a distracter, which was introduced at different distances and angular offsets from the approaching target. The results showed that the bat adjusted its call duration to the closest of objects: When the target was behind the distracter, the bat adapted its call duration to avoid overlap between its pulses and distracter echoes, and when the target moved in front of the distracter, the bat made further reductions in call duration to avoid overlap between its calls and target echoes (Figure 2c). The magnitude of this effect was greatest when the angular offset between the target and distracter was smallest (5-10 deg). Surprisingly, however, the average PI was not influenced by the presence of the distracter, showing that the bat's dynamic changes in PI and duration can be decoupled during target approach in the presence of an obstacle.

Adaptive control of sonar signal direction

The bat's sonar beam can be likened to an auditory flashlight, sampling a limited region of acoustic space at a given point in time. Some bat species emit echolocation calls through the open mouth and others through the nostrils. In species that emit calls through the open mouth, the size of mouth opening can alter directional characteristics of sonar signals [21]; in species that emit calls through the nostrils, a nose leaf shapes the directional characteristics of sonar signals [22]. 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, or in nasal echolocators, also by moving the nose leaf. Laboratory studies of sonar emission patterns of the big brown bat, *E. fuscus*, show that the beam is broad enough to collect echo information about objects within a 60-90 deg cone, which could support simultaneous inspection of objects within a wide angle in the frontal plane [23]. However, data from obstacle avoidance, insect capture (Figure 3a) and target discrimination (Figure 3b) studies demonstrate that the bat does not direct the beam to inspect objects simultaneously but, instead, shifts the direction of its sonar beam aim to accurately (± 3 deg) point the axis in the direction of closely spaced objects *sequentially*, corroborating what the temporal vocalization data show when a bat encounters a complex environment [19, 24]. Auditory localization accuracy is highest along the midline [25, 26], and the sequential inspection of objects in these tasks is hypothesized to enable high spatial resolution of objects and motor planning for flight control [27]. In addition, recent psychophysical data suggest that FM bats may experience acoustic blur from off-axis echoes, which could minimize clutter interference in the natural environment [28].

The tongue clicking Egyptian fruit bats (*Rousettus aegyptiacus*) have another beam-aiming strategy for localization. Instead of pointing their beam directly at the target as laryngeal echolocators, each sonar signal in a pair is directed to either side of a landing platform, such that the maximum slope, not the peak, is aimed at the location where the bat prepares to land [6] (Figure 3c). These reported differences may be attributed to the species (big brown bat vs. Egyptian fruit bat), mechanisms of echolocation (laryngeal vs. lingual) and/or the echolocation tasks (obstacle avoidance/prey capture vs. landing). To distinguish between these possibilities requires further study.

Bats can actively control the directionality of the sonar beam in flight. Field data from a mouth emitting trawling species, *Myotis daubentonii*, show that in the field increased call intensity is coupled to an increase of directivity, such that the more intense sonar calls are also narrower. *M. daubentonii* may achieve both an increase in intensity and directionality by opening the mouth wider [21]. It is likely that other mouth emitting aerial and trawling bats also show the same coupling of increased intensity and directionality. Laboratory data also shows a dramatic broadening of the sonar beam just before capture in *M. daubentonii*

and *E. serotinus*, due to an octave decrease in frequency [29] (Figure 3d). Since a similar frequency drop in the terminal phase is typical for many trawling and aerial hawking bats, it is likely that many species broaden the beam width in the field right before prey capture to collect echo information from a wide field of view including prey and background.

Phyllostomid bats, nasal echolocators, achieve high directionality of their sonar beam by emitting signals through nostrils surrounded by a nose leaf. Measurements taken from *Carollia perspicillata* flying in a large room show that the beam half amplitude angle is only 18° [22]. Phyllostomids are generally frugivorous and find food in cluttered habitats. Their narrow sonar beam reduces off axis echoes and may make it easier to negotiate clutter.

Adaptive control over sonar signal frequency

Active control over sonar signal frequency also helps bats to solve a variety of echolocation tasks, including clutter rejection, sorting echoes from multiple objects in a complex environment, and separating their own signals and echoes from those of conspecifics (Figure 4).

Sorting echoes in a complex, cluttered environment

Detection of insect prey in dense vegetation presents an acoustic challenge to echolocating bats, and adaptive sonar behavior enables the separation of target echoes from background clutter. For example, bats that produce long CF signals exhibit a behavior referred to as Doppler shift compensation, which aids in the detection of fluttering insect prey. These bats compensate for Doppler shifts introduced by their own flight velocity by reducing the frequency of their CF emissions so as to receive echo returns at the frequency to which their auditory systems are maximally tuned. Doppler shift compensation behavior allows bats to hear rapid frequency and amplitude modulations in echoes returning from fluttering insects. These modulations stand out from overlapping background echoes from nearby stationary objects, such as leaves and branches [14, 15].

A series of experiments have been conducted in hipposiderid CF bats to investigate their Doppler-shift compensation [13, 30, 31] as they orient in a restricted environment. Results show that bats constantly adjust both their call frequency and amplitude in flight in order to stabilize frequency and amplitude of returning echoes from objects at different directions and distances. Importantly, the adaptive shifts in call frequency suggest that the bat alters its attention to objects at different directions and distances in the environment (Figure 4a).

FM bats have a different strategy to deal with clutter. In general the more cluttered the habitat, the shorter the bat's echolocation search sounds, the higher the call frequency and the broader the bandwidth [32] and the lower the emitted intensity [5, 33]. Some bats show other adjustments of call frequency to habitat. For example, in open space, the ghost bat (*Diclidurus albus*) emits orientation/search calls with stable frequency from call to call, but when diving down to hunt in the understory it produces calls with the peak frequency alternating from call to call [34]. Frequency alternation, or even emitting three tones, is the signature of the calls of many emballonurid bats hunting for insects on the wing in semi-open habitats in the Neotropics. Thus, the data indicates that adaptive frequency alternation help the bats disentangle echoes and perhaps calls of sympatric bats in complex environments [35].

A study of the FM big brown bat showed that this species also adjusts the frequency of its calls to separate echoes from objects in a complex environment. Bats were trained to fly through a maze extending over 6 m, consisting of chains hanging from the ceiling in rows. Each FM sonar vocalization produced by the bat resulted in a cascade of echoes from the

chains located at different distances and directions from the animal. Typically, FM bats adjust the interval between successive vocalizations to receive and process echo returns before producing a subsequent call, allowing the bat to accurately measure echo delay from each sonar cry. Thus, the interval between calls changes with the bat's distance to objects (Figure 1a). Echo returns from the chain maze, however, occurred over an extended period of time, creating overlap with the next sound and echoes. Thus the animal might confuse the association between a given vocalization and returning echoes, which could compromise its estimate of distance to the chains. Instead, as the bat negotiated the chain maze, it produced sonar "strobe groups" with large differences in the terminal frequency between sonar signals within the group. The adjustment in terminal call frequency occurred only when the bat was oriented towards the chain array, suggesting that this adaptive vocal behavior allowed the bat to avoid ambiguous assignment of echo delays and correctly assign echoes from objects returning at different delays [36] (Figure 4b).

Jamming avoidance

Bats often encounter other vocalizing bats as they forage in the field. When a bat encounters an individual of the same species foraging in its vicinity, it faces the challenge of sorting its own vocalizations and echo returns from those of conspecifics.

Field studies show that FM bats adjust the spectral and/or temporal features of echolocation calls when foraging in groups in order to avoid signal jamming [37-39] (Figure 4c). Modification in call design, which occurs in echolocating bats when flying with conspecifics, can be regarded as a strategy to separate and selectively process echoes from self-generated calls.

When paired bats compete for prey in a large flight room, they make frequency adjustments in their sonar calls to minimize interference from the signals of conspecifics. The magnitude of call adjustments depended on the baseline similarity of calls when bats flew alone [40] (Figure 4 d). Another study of big brown bats in the laboratory confirmed that the animal shifts its call frequency when a sound of similar frequency is broadcast in close proximity [41].

A series of laboratory studies of free-flying big brown bats have uncovered another adaptive behavior in response to conspecifics. In addition to frequency adjustments, big brown bats competing for prey sometimes go silent. The prevalence of silent behavior depended on the spatial separation of the bats as they flew together and on the baseline similarity of their calls when they flew alone, suggesting that silence is also a jamming avoidance response. Typically the trailing bat tended to go silent, raising the possibility that it used the vocalizations and echoes from the leading bat to orient [42].

Summary and Conclusions

The timing, duration, directional aim, intensity, and frequency content of sonar signals used by a bat to "illuminate" the environment have a direct impact on the information available to its acoustic imaging system. In turn, the bat's perception of the echo scene guides its control over the features of subsequent sonar vocalizations. Thus, the bat's adaptive sonar behavior is integral to its perception of auditory objects, analogous to the linkage between eye/head movements and visual perception [43, 44]. The bat's adjustments in sonar call features reveal how its motor behaviors can contribute directly to solving the perceptual problem of sorting/tracking sounds arriving from different directions and distances. They also suggest that adjustments in call features provide reliable indicators of the bat's attention to objects at different locations.

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References

1. Griffin, DR. Listening in the dark. 2.ed. Yale Univ. Press; Cornell University; New York: 1986. 1958
2. Thomas, JA.; Moss, CF.; Vater, M., editors. Echolocation in bat and dolphins. The Chicago University Press; Chicago, IL: 2004.
3. Schnitzler H-U, Moss CF, Denzinger A. From spatial orientation to food acquisition in echolocating bats. *TREE*. 2003; 18:386–394.
4. Schuller, G.; Moss, CF. Vocal control and acoustically guided behavior in bats. In: Thomas, JA.; Moss, CF.; Vater, M., editors. Echolocation in bats and dolphins. University of Chicago Press; Chicago: 2004. p. 3-16.
5. Surlykke A, Kalko EKV. Echolocating bats cry out loud to detect their prey. *PLoS ONE*. 2008; 3(4):e2036(1)–e2036(10). [PubMed: 18446226]
6. Yovel Y, Falk B, Moss CF, Ulanovsky N. Optimal Localization by Pointing Off Axis. *Science*. 2010;701–704. [PubMed: 20133574] * This study reports that the echolocating Egyptian fruit bat produces pairs of tongue clicks that are aimed such that the maximum slope, not the peak, is directed at a landing platform.
7. Surlykke A, Moss CF. Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J.Acoust.Soc.Am*. 2000; 108:2419–2429. [PubMed: 11108382]
8. Moss C, Surlykke A. Probing the natural scene by echolocation in bats. *Frontiers in Behavioral Neuroscience*. 2010; 4:1–16. [PubMed: 20126432]
9. Ratcliffe JM, Dawson JW. Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. *Anim.Behav*. 2003; 66:847–856.
10. Jones G, Webb PI, Sedgeley JA, O'Donnell CFJ. Mysterious Mystacina: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *J.Exp.Biol*. 2003; 206:4209–4216. [PubMed: 14581591]
11. Moss, CF.; Schnitzler, H-U. Behavioral studies of auditory information processing. In: Popper, AN.; Fay, RR., editors. Hearing by bats. Springer; 1995. p. 87-145.
12. Simmons JA. The resolution of target range by echolocating bats. *J.Acoust.Soc.Am*. 1973; 54:157–173. [PubMed: 4738624]
13. Hiryu S, Katsura K, Lin L-K, Riquimaroux H, Watanabe Y. Doppler-shift compensation in the Taiwanese leaf-nosed bat (*Hipposideros terasensis*) recorded with a telemetry microphone system during flight. *J.Acoust.Soc.Am*. 2005; 118:3927–3933. [PubMed: 16419835]
14. Neuweiler G, Bruns V, Schuller G. Ears adapted for the detection of motion, or how echolocating bats have exploited the capacities of the mammalian auditory system. *J.Acoust.Soc.Am*. 1980; 68:741–753.
15. Schnitzler H-U. Die Ultraschall-Ortungslaute der Hufeisen-Fledermäuse (Chiroptera-Rhinolophidae) in verschiedenen Orientierungssituationen. *Z.vergl.Physiol*. 1968; 57:376–408.
16. Schnitzler H-U, Kalko EKV. Echolocation by insect-eating bats. *BioScience*. 2001; 51:557–569.
17. Moss CF, Surlykke A. Auditory scene analysis by echolocation in bats. *J.Acoust.Soc.Am*. 2001; 110:2207–2226. [PubMed: 11681397]
18. Moss CF, Bohn K, Gilkenson H, Surlykke A. Active Listening for Spatial Orientation in a Complex Auditory Scene. *PLoS Biology*. 2006; 4:615–626.
19. Surlykke A, Ghose K, Moss CF. Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*. *J.Exp.Biol*. 2009; 212:1011–1020. [PubMed: 19282498] * This study provides the first empirical demonstration that echolocating FM-bats sequentially inspect closely spaced objects by adjusting the directional aim of the sonar beam.

20. Aytekin M, Mao B, Moss CF. Spatial perception and adaptive sonar behavior. *J.Acoust.Soc.Am.* 2011; 128:3788–3798. [PubMed: 21218910]
21. Surlykke A, Pedersen SB, Jakobsen L. Echolocating bats emit a highly directional sonar sound beam in the field. *Proc.R.Soc.B.* 2009; 276:853–860.
22. Brinkløv S, Jakobsen L, Ratcliffe JM, Kalko EKV, Surlykke A. Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (Phyllostomidae). *J.Acoust.Soc.Am.* 2011; 129
23. Ghose K, Moss CF. The sonar beam pattern of a flying bat as it tracks tethered insects. *J.Acoust.Soc.Am.* 2003; 114:1120–1131. [PubMed: 12942989]
24. Falk B, Williams T, Aytekin M, Moss CF. Adaptive behavior for texture discrimination by the free-flying big brown bat, *Eptesicus fuscus*. *J.Comp.Physiol.A.* 2011 In press.
25. Middlebrooks JC, Green DM. Sound localization by human listeners. *Annu. Rev. Psychol.* 1991; 42:135–159. [PubMed: 2018391]
26. Langendijk EHA, Kistler DJ, Wightman FL. Sound localization in the presence of one of two distracters. *J.Acoust.Soc.Am.* 2001; 109:2123–2134. [PubMed: 11386564]
27. Ghose K, Moss CF. Steering by hearing: A bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law. *J. Neurosci.* 2006; 26:1704–1710. [PubMed: 16467518]
28. Bates ME, Simmons JA, Zorikov TV. Clutter rejection in bat sonar is achieved by image defocusing from harmonic beamforming. *Science.* 2011 in press. * The authors of this study report that temporal misalignment of FM harmonics serves to smear echo delay (target distance) perception in bats, and they propose that this effect would cause perceptual blurring of objects from off-axis echoes.
29. Jakobsen L, Surlykke A. Vespertilionid bats control the width of their biosonar sound beam dynamically during prey pursuit. *Proc.Natl.Acad.Sci.USA.* 2010; 107:13930–13935. [PubMed: 20643943] * This paper reports that FM-bats broaden the width of the sonar beam just prior to prey capture, which could help the bat track prey, even if it makes evasive maneuvers.
30. Hiryu S, Katsura K, Lin L-K, Riquimaroux H, Watanabe Y. Radiation pattern of echolocation pulse in Taiwanese leaf-nosed bat, *Hipposideros terasensis*. *Acoust.Sci.& Tech.* 2006; 27:108–110.
31. Hiryu S, Shiori Y, Hosokawa T, Riquimaroux H, Watanabe Y. On-board telemetry of emitted sounds from free-flying bats: compensation for velocity and distance stabilizes echo frequency and amplitude. *J.Comp.Physiol.A.* 2008; 194:841–851.
32. Neuweiler G. Auditory adaptations for prey capture in echolocating bats. *Physiol.Rev.* 1990; 70:615–641. [PubMed: 2194220]
33. Brinkløv S, Kalko EKV, Surlykke A. Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav.Ecol.Sociobiol.* 2010; 64:1867–1874.
34. Jung K, Kalko EKV, Helversen Ov. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J.Zool.* 2007; 272:125–137.
35. Ratcliffe JM, Jakobsen L, Kalko EKV, Surlykke A. Frequency alternation and an offbeat rhythm indicate foraging behavior in the echolocating bat, *Saccopteryx bilineata*. *J.Comp.Physiol.A.* 2011; 197:413–423.
36. Hiryu S, Bates ME, Simmons JA, Riquimaroux H. FM echolocating bats shift frequencies to avoid broadcast–echo ambiguity in clutter. *Proc.Natl.Acad.Sci.USA.* 2010; 107:7048–7053. [PubMed: 20351291] * Vocalization data in this study show that bats flying in a spatially complex environment adjust the frequency of successive sonar calls to avoid ambiguity in assigning echoes from objects at different distances.
37. Obrist MK. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav.Ecol.Sociobiol.* 1995; 36:207–219.
38. Ratcliffe JM, ter Hofstede HM, Avila-Flores R, Fenton MB, McCracken GF, Biscardi S, Blasko J, Gillam E, Orprecio J, Spanjer G. Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*. *Can.J.Zool.* 2004; 85:966–971.
39. Ulanovsky N, Fenton MB, Tsoar A, Korine C. Dynamics of jamming avoidance in echolocating bats. *Proc.R.Soc.Lond.B.* 2004; 271:1467–1475.

40. Chiu C, Xian W, Moss CF. Adaptive echolocation behavior in bats for the analysis of auditory scenes. *J.Exp.Biol.* 2009; 212:1392–1404. [PubMed: 19376960] • This paper provides evidence that FM bats flying in close proximity adjust the frequency of echolocation calls to avoid sonar jamming. The magnitude of the adjustment depends on the baseline similarity of the bats' vocalizations when they fly alone.
41. Bates ME, Stamper SA, Simmons JA. Jamming avoidance response of big brown bats in target detection. *J.Exp.Biol.* 2008; 211:106–113. [PubMed: 18083738]
42. Chiu C, Xian W, Moss CF. Flying in silence: Echolocating bats cease vocalizing to avoid sonar jamming. *Proc.Natl.Acad.Sci.USA.* 2008; 105:13115–13120.
43. Hafed ZM, Krauzlis RJ. Ongoing eye movements constrain visual perception. *Nature Neuroscience.* 2006; 9:1449–1457.
44. Kowler E. The role of visual and cognitive processes in the control of eye movement. *Rev. Oculomot. Res.* 1990; 4:1–70. [PubMed: 7492527]

Highlights

Bats adjust the duration and interval of vocalizations to control the temporal flow of information.

Echolocating bats control the directional aim of the sonar beam to inspect closely spaced objects.

Bats adjust the frequency of sonar cries to sort echoes from multiple objects and avoid jamming.

Figure 1.

Adaptive vocal behavior drives perception by echolocation in bats. **(a)** Echolocation calls made by different bat species when approaching a food item. The top panel shows calls generated by *Artibeus jamaicensis*, a fruit-eating bat. The bat does not have terminal phase calls when approaching fruits. The middle one is a series of calls made by *Myotis daubentonii* when approaching an insect prey. This bat produced frequency-modulated calls and shortened pulse intervals when flying close to the target. The bottom panel shows echolocation calls produced by *Rhinolophus capensis*, a bat species that used constant frequency calls, when chasing prey. This bat also uses shorter pulse intervals when the target is close. **(b)** The bat generates high frequency calls and listens to echoes from obstacles and food items. The bat's auditory system processes the information it receives from the environment and extracts features of calls and echoes in order to probe its surroundings. The bat adjusts temporal features, direction and frequency of its calls in order to adapt to different conditions.

Temporal Control **Figure 2.**

Adaptive control over sonar signal temporal characteristics. **(a)** Left: Top view of the big brown bat's flight path as it attempts to capture an insect (blue circle) positioned near a plant (green asterisks). The arrow represents the flight direction. The red segment on the flight path, displays the bat's position when it produced "strobe groups," sonar signals produced in clusters with stable pulse interval (5% tolerance). Right: The pulse interval of the sonar signals produced by the bat flying along the path shown on the left. The red circles denote the strobe groups (Adapted from [18]). **(b)** The bat actively controls pulse duration in order to avoid overlap between outgoing pulses and incoming echoes. The top panel shows a long duration call, which overlaps with the first returning but not the second one. The bottom panel illustrates how the bat's decrease in call duration prevents overlap from echoes arriving at a short delay. Call duration can serve as an indicator of the bat's attention to objects along the range axis (Adapted from [8]). **(c)** Call duration changes as a function of distance to target. The dots connected by a gray line show changes in call duration with target distance in baseline trials in an open room. The asterisks connected by black lines show call duration with changing target distance, but in the presence of a stationary distracter pole at 70 cm. In the plot, the distracter is indicated by a vertical line at 70 cm. Note that call duration is shorter than in baseline trials when the target is behind the distracter, suggesting that the bat is avoiding overlap between its calls and echoes from the distracter.

Figure 3.

Adaptive control over sonar signal direction. The closed circles around the room represent the microphone array in (a)-(c). **(a)** Plan view of a big brown bat's flight path through the opening of a net to gain access to a tethered insect on the other side. The bat continuously changes the directional aim of its sonar beam axis to scan the obstacles and the target. Sonar beam axes marked in green indicate are directed towards the left side of hole A, sonar beam axes marked in light blue are directed toward the right side of hole A, and sonar beam axes marked in red are directed toward the tethered insect (Adapted from [19]). **(b)** Plan view of the flight path and sonar beam axis of successive sonar calls produced by the big brown bat as it performs a target discrimination task. S+ is a smooth bead, and S- is a textured bead. The bat is rewarded for tapping S+ in flight. As the bat approaches the two beads, it initially directs its beam toward S- (vocalization numbered 1, magenta). The subsequent increase in call duration before the bat flies past S- indicates that its gaze has shifted beyond the bead (vocalization numbered 2, green). After the bat turns, it aims its beam at S+ (vocalization numbered 3, yellow; adapted from [24]). **(c)** Plan view of sonar beam axes produced by the Egyptian fruit bat trained to land on a platform. This bat species produces pairs of tongue clicks to lock onto the target and land on it. Each click in a pair points toward either side of the landing spot, with the maximum slope, not the peak, of the sonar beam directed at the platform. The vector average of a pair of clicks points toward the landing spot (Adapted from [6]). **(d)** Horizontal directionality measured for sonar calls of *Eptesicus serotinus* during the approach (blue) and terminal phase (red) of insect pursuit. The bat widens its sonar beam in the terminal phase of insect pursuit by lowering the frequency from 35 to 18 kHz (Adapted from [29]).

Frequency Control **Figure 4.**

Adaptive control over sonar signal frequency. **(a)** The Taiwanese leave-nosed bat (*Hipposideros terasensis*) changes the frequency of its calls to compensate for Doppler shifts in echoes during landing. The dashed line is the estimated compensated frequencies of the pulses, assuming the echoes coming from the wall in front of the bat. The solid line is the estimated compensated frequencies of the pulse, assuming the echoes coming from walls at different angles. The actual frequency adjustments made by the bat fits well in between these two estimated lines, suggesting that the bat alternated its attention directed at the front and side walls of the room (Adapted from [31]). **(b)** Echolocation calls of the big brown bat produced as it negotiated a chain maze. The bat's calls are recorded by a wireless microphone placed on top of its head and echoes are recorded with an ultrasonic microphone on the floor. HF indicates the highest call frequency, LF represents the lowest call frequency and ΔF means the difference between a pair of sounds' frequency. The frequency difference within a sonar strobe group suggests that the bat shifts the frequency from call to call to avoid confusion associating vocalizations and echoes returning at different delays (Adapted from [36]). **(c)** Two *Tadarida teniotis* calls recorded in the field. The top panel is the zoom in of the bottom panel. Red and blue dots represent the minimum frequency of different bats' vocalizations (Adapted from [39]). **(d)** Measures of call frequency produced by two individual big brown bats competing for a single prey item in a large laboratory room. The top panel shows the inter-bat distance as a function of time and the bottom panel shows the call frequency of both bats as a function of time. Vocalizations generated by different bats are displayed in different colors (red and blue). The difference between paired bats' call frequencies increases as they fly close to each other (Adapted from [40]).