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Forum

Neural coding of 3D spatial location, orientation, and action selection in echolocating bats

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Echolocating bats are among the only mammals capable of powered flight, and they rely on active sensing to find food and steer around obstacles in 3D environments. These natural behaviors depend on neural circuits that support 3D auditory localization, audio-motor integration, navigation, and flight control, which are modulated by spatial attention and action selection.

Echolocation in bats

Echolocating bats produce intense high-frequency sounds and process information carried by echo returns to locate and discriminate objects in their surroundings. With over 1000 species of echolocating bats, there is great diversity in sonar signal structure and production. Most bats exploit specialized vocal production mechanisms to generate frequency-modulated (FM) calls, which some species combine with constant frequency (CF) components. Less common are sonar clicks produced by the tongue [1]. Echolocation operates through audiovocal feedback, whereby the bat adjusts the features of its sonar emissions in response to the information extracted from echo returns. Bats compute the 3D location and movement of objects from the arrival time, spectral content, and interaural differences in echoes at the two ears, and they direct their sonar beam at objects they are actively inspecting, analogous to foveal fixation in visual animals [2]. Bats rely on echo arrival time to estimate object distance and decrease the duration of calls as echo arrival time shortens. Many bat species that use CF sonar signals exhibit Doppler shift compensation: they adjust call frequency to compensate for velocity-induced Doppler shifts as they fly, which serves to stabilize echo returns in the spectral region of maximum hearing sensitivity [3]. Because echolocation invokes active listening, the bat's sonar signal adjustments provide explicit moment-to-moment metrics of action selection and sonar-guided attention to objects in its surroundings (Figure 1).

Auditory processing of natural sounds

To negotiate their natural environments, echolocating bats must parse and track a cacophony of sounds reaching their ears. These sounds include streams of echoes from their own sonar calls, as well as calls, echoes, and social communication signals from nearby conspecifics. This auditory scene analysis problem is comparable to the cocktail party phenomenon described in humans and other species. In bats, the problem is solved by three elements: (i) the combined effects of directional sonar emissions, echoes, and hearing; (ii) active control of the sonar beam aim and spectro-temporal call patterning, and (iii) neural circuits that enable selective processing of biologically salient signals. Mechanisms differ between bats that use CF–FM calls and those that use FM signals alone, and we therefore discuss them separately in the following paragraphs.

Many bat species that use CF–FM signals show specializations in sound frequency processing. In particular, many CF–FM bats operate with an 'acoustic fovea', an expanded frequency representation throughout the auditory pathway and exceptionally sharp tuning at the CF sound frequencies used for echolocation. These auditory specializations have been traced to mechanical specializations of the basilar membrane. A noteworthy champion of sound frequency analysis is the greater horseshoe bat, *Rhinolophus ferrumequinum*, which lowers the frequency of its CF calls proportional to its flight velocity, receiving echo returns at around 83 kHz, the region of its 'acoustic fovea'. This refined audiovocal behavior, commonly known as Doppler shift compensation, exploits auditory specializations for sound frequency analysis, which CF–FM bat species use to detect and recognize insect prey, whose wingbeats carry signatures in echo returns [3].

Bat species that use broadband FM echolocation signals show specializations in auditory temporal processing that enable fine target range (echo delay) discrimination. Many species show echo delay discrimination thresholds in the microsecond range [4]. The posited neural substrate of sonar ranging is a class of echo delay-tuned neurons that shows facilitated responses to call-echo pairs over a restricted range of delays. Echo delay-tuned neurons have been characterized in the midbrain, thalamus, and auditory cortex of bats. Although exquisitely detailed cortical echo delay/range maps in the mustached bat have been featured in the literature, this highly ordered topography is the exception, rather than the rule in bats [5]. In contrast to visual and somatosensory maps that directly reflect the layout of the sensory epithelium, auditory spatial coding emerges from central neural computations, which do not require topographic organization.

In bat species that use CF–FM and FM signals, response selectivity to acoustic communication signals has been described in the same midbrain and cortical areas that also show selectivity to echolocation call

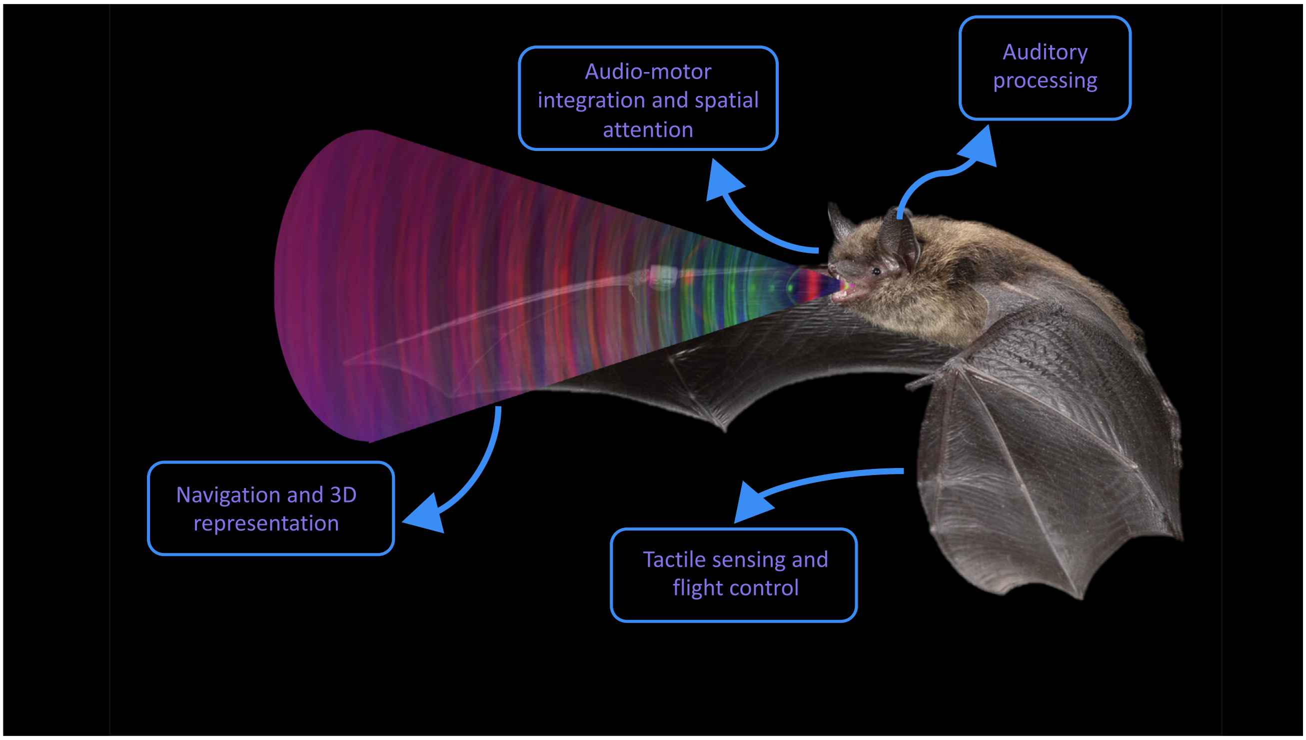

Figure 1. Neural specializations support natural behaviors of echolocating bats. Schematic depicting auditory processing of natural sounds, audio-motor integration, navigation, and flight control, which are modulated by spatial attention and action selection in echolocating bats. Bat photo courtesy of Charles Francis.

features [6]. It has been posited that auditory attention and action selection dynamically modulate neural circuits to decode context-dependent sound meaning.

Audio-motor integration, spatial orientation, and attention

Echolocation operates through an audio-vocal feedback system, which invokes fine vocal-motor adjustments in response to information acquired from echoes. The superior colliculus (SC), a sensorimotor hub of the mammalian brain, reveals audio-motor specializations in echolocating bats that support acoustic orienting by sonar. Auditory neurons in the bat SC show 3D spatial tuning to sonar objects and premotor bouts of activity before the production of sonar calls. Microstimulation of the bat SC evokes head and pinna movements, along with the production of echolocation calls [7]. Neural telemetry recordings from the SC of free-flying echolocating bats revealed spatially selective responses to echoes from physical objects in the environment and showed that the bat's sonar-guided attention in this natural task modulates neural coding of object distance [8]. These findings highlight the dynamics of spatial coding that depend on an animal's motor decisions and attention to objects in its surroundings.

Navigation and 3D spatial representation

Echolocating bats navigate 3D space, and concordantly, bat hippocampal place cells exhibit 3D fields. Unlike rodents, however, theta rhythm in bats is not continuous, which has called into question the generality and role of theta in the formation of place cells [9]. Evidence of nonoscillatory phase coding in the bat hippocampus offers an alternative mechanism for place field formation [10]. Recently reported hippocampal recordings show dynamic remapping from allocentric to egocentric coordinates when flying bats encounter conspecifics along a flyway, suggesting that action selection and spatial attention modulates hippocampal coding [11].

Tactile sensing supports flight control

Echolocating bats exhibit great agility as they maneuver in dense forests and intercept erratically moving prey. A series of experiments demonstrated that somatosensory specializations support bat flight control [12]. A very thin and flexible membrane stretches across the five bones of the bat hand-wing, and embedded in this membrane are microscopic mechanosensory hairs. Displacement of the wing hairs activates lanceolate endings and Merkel cells at the base, which transmit signals through the dorsal root ganglia to the central somatosensory pathway. Removal of bat wing hairs with a depilatory cream affects flight control: after hair removal, bats fly faster and make wider turns as they steer around obstacles. Cortical recordings from S1 show directionally selective responses to airflow stimulation, with a majority of neurons responding most vigorously to reverse airflow, that is, from the trailing to the leading edge of the wing, which signals impending stall [12]. These somatosensory specializations highlight the strong evolutionary pressures that shape animal nervous systems.

Concluding remarks

In this overview, we offer a snapshot of some of foundational discoveries uncovered by neuroethological experiments on echolocating bats. Studies of the bat midbrain, neocortex, and hippocampal formation collectively demonstrate that neural coding is modulated by an animal's behavioral state and its action planning in a variety of natural contexts, from foraging and steering around obstacles to communicating with conspecifics and navigating over different spatial scales. Among the goals for future work is delineating the mechanisms underlying switches in neural coding that accompany selective attention and motor decisions. More broadly, findings and experimental paradigms from research in bats may be leveraged to study other model organisms. Comparative, interspecies approaches would be imperative for separating specializations from general principles and for advancing current knowledge of the neural underpinnings of natural, species-specific behaviors.

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Declaration of interests

The authors declare no competing interests in relation to this work.

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