Three-dimensional auditory localization in the echolocating bat

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Echolocating bats exhibit accurate three-dimensional (3D) auditory localization to avoid obstacles and intercept prey. The bat achieves high spatial resolution through a biological sonar system. Key features of the bat's sonar system are (1) high frequency, directional echolocation signals; (2) high frequency hearing; (3) mobile ears; and (4) measurement of distance from the time delay between sonar emission and echo reception. The bat's sonar receiver is a standard mammalian auditory system that computes azimuth from inter-aural differences and elevation from spectral filtering by the ear [1–3]. Target range is computed from echo arrival time [4,5], and the bat auditory system contains neurons that show echo delay-tuned responses to pulse-echo pairs [6]. Ultimately, information about sound source azimuth, elevation and range converge to create a unified representation of 3D space.

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Introduction

Echolocating bats have evolved a high-resolution 3D acoustic imaging system, which they exploit to forage, avoid obstacles and orient in complete darkness. Bats transmit brief, intense, ultrasound signals and process information contained in the returning echoes to determine the position, size and shape of reflecting objects [7,8]. The acoustic features of sonar signals used to ensonify the surroundings, including the call repetition rate, spectro-temporal profile, and sonar beam aim [9], directly influence the information available to the bat's acoustic imaging system [5] (see inset for terminology). The sonar beam aim is particularly important, because the direction in which the bat transmits its signal ultimately determines the region in space from which the bat receives echo information. Previous research has shown that bats use higher frequency, narrow sonar beams when approaching a target from a distance, and then increase the width of the sonar beam, by decreasing the frequency, as they prepare to intercept a target [10•]. Moreover, because of the directionality of high frequency sounds, bats can use the spectral profile of returning echoes to segregate on-axis from off-axis echoes [11]: on-axis echoes are broader in bandwidth and include the more directional, high frequencies of the sonar vocalizations; whereas off-axis echoes are low-pass filtered. In this way, the directionality of the outgoing sonar beam serves to filter and separate target and clutter echoes. The bat's auditory representation of the environment is then used to guide adaptive motor behaviors, including pinna adjustments, head aim, flight path, and the features of subsequent sonar vocalizations (e.g. [7,12]). Here we review behavioral and neurophysiological data that contribute to our understanding of 3D spatial imaging by echolocation.
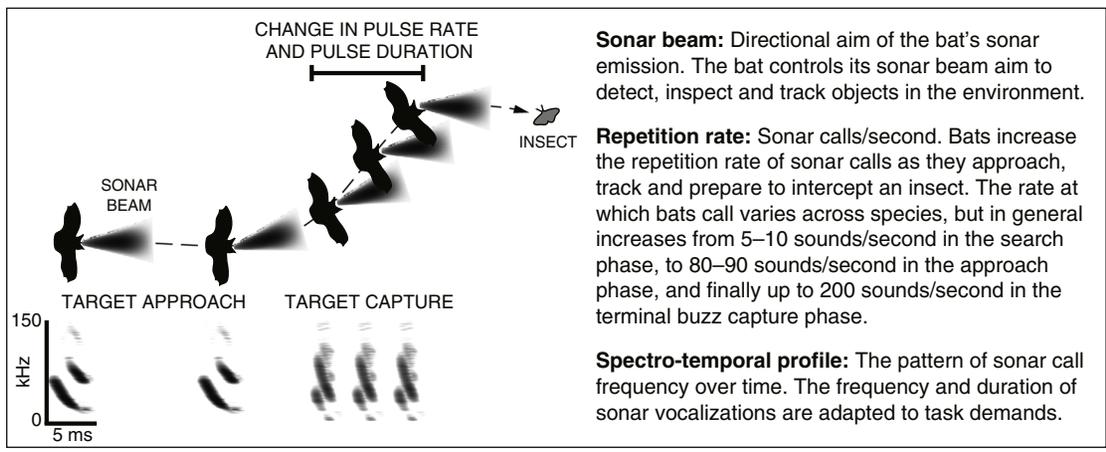

Sonar beam: Directional aim of the bat's sonar emission. The bat controls its sonar beam aim to detect, inspect and track objects in the environment.

Repetition rate: Sonar calls/second. Bats increase the repetition rate of sonar calls as they approach, track and prepare to intercept an insect. The rate at which bats call varies across species, but in general increases from 5–10 sounds/second in the search phase, to 80–90 sounds/second in the approach phase, and finally up to 200 sounds/second in the terminal buzz capture phase.

Spectro-temporal profile: The pattern of sonar call frequency over time. The frequency and duration of sonar vocalizations are adapted to task demands.

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The bat's sonar imaging system is built from a 'standard' mammalian auditory system [13,14] and operates with many of the same cues used by other species to localize sound. Binaural cues for sound localization provide information about the azimuthal position of an acoustic target (Figure 1a) [2]. Monaural cues may contribute to assigning a sound source location in azimuth, and are essential for determining the elevation of a sound source (Figure 1b) [1,15]. Contributing to the head related transfer function (HRTF) is the bat's external ear (pinna-tragus), which modifies the spectrum of echoes that is used by the bat to estimate target elevation [3,16,17]. Interaural spectral cues are thought to provide additional information for determining target angle in the vertical plane [1,18]. Lastly, bats can segregate on-axis from off-axis target echoes (reject clutter) through directional filtering of ultrasound echoes (Figure 1c) [11].

Bats stand out from non-echolocating mammals in their ability to represent 3D auditory space from the arrival time of echoes to determine an object's range (Figures 1d and 2a). Specifically, bats have evolved neural circuitry to estimate target distance from the time delay between sonar emissions and returning echoes [4,19], which, together with binaural (azimuth) and spectral (elevation) cues, renders a 3D representation of auditory source locations. Importantly, the bat's sonar imaging system operates on feedback between orienting behaviors (sonar vocalizations, head and pinna movements) and 3D auditory localization.

Figure 1
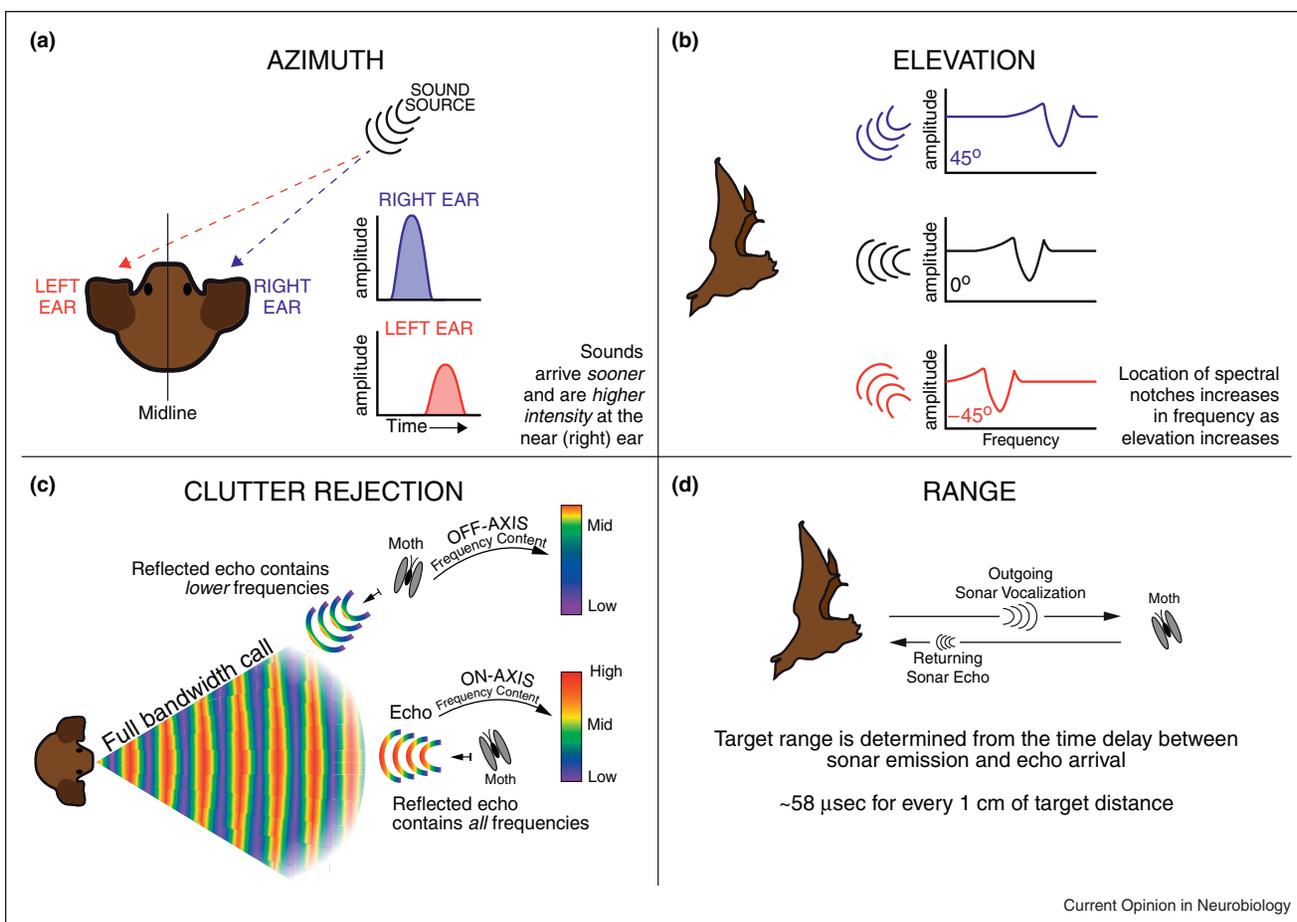
Auditory localization cues for bats. **(a)** Bats use inter-aural differences in sound intensity and arrival time to localize sounds in azimuth. **(b)** Changes in the spectral notch location in the frequency domain are used as cues for localization in the vertical plane [1,17]. **(c)** Bats use the power-frequency structure of returning echoes to determine if echoes are arriving on or off axis. Different frequencies are represented by the color spectrum, with red indicating higher frequencies, and violet representing lower frequencies. Because of the directionality of high frequencies, note how the center of the outgoing sonar beam contains all frequencies (red-violet), but the more peripheral locations of the sonar beam are predominantly lower frequencies (green-violet). On-axis echoes will therefore contain the full frequency bandwidth of the outgoing vocalization (full color spectrum in returning echo), whereas off-axis echoes will be dominated by lower frequencies (greens to blues in returning echo) components [11]. **(d)** Bats use the time delay between outgoing sonar vocalization and arrival time of the returning echo to determine an object's distance, or the pulse/echo delay [4]. Sound travels 1 cm in approximately 29 μs, indicating an average pulse/echo delay of approximately 58 μs for every centimeter of target distance.

Figure 2
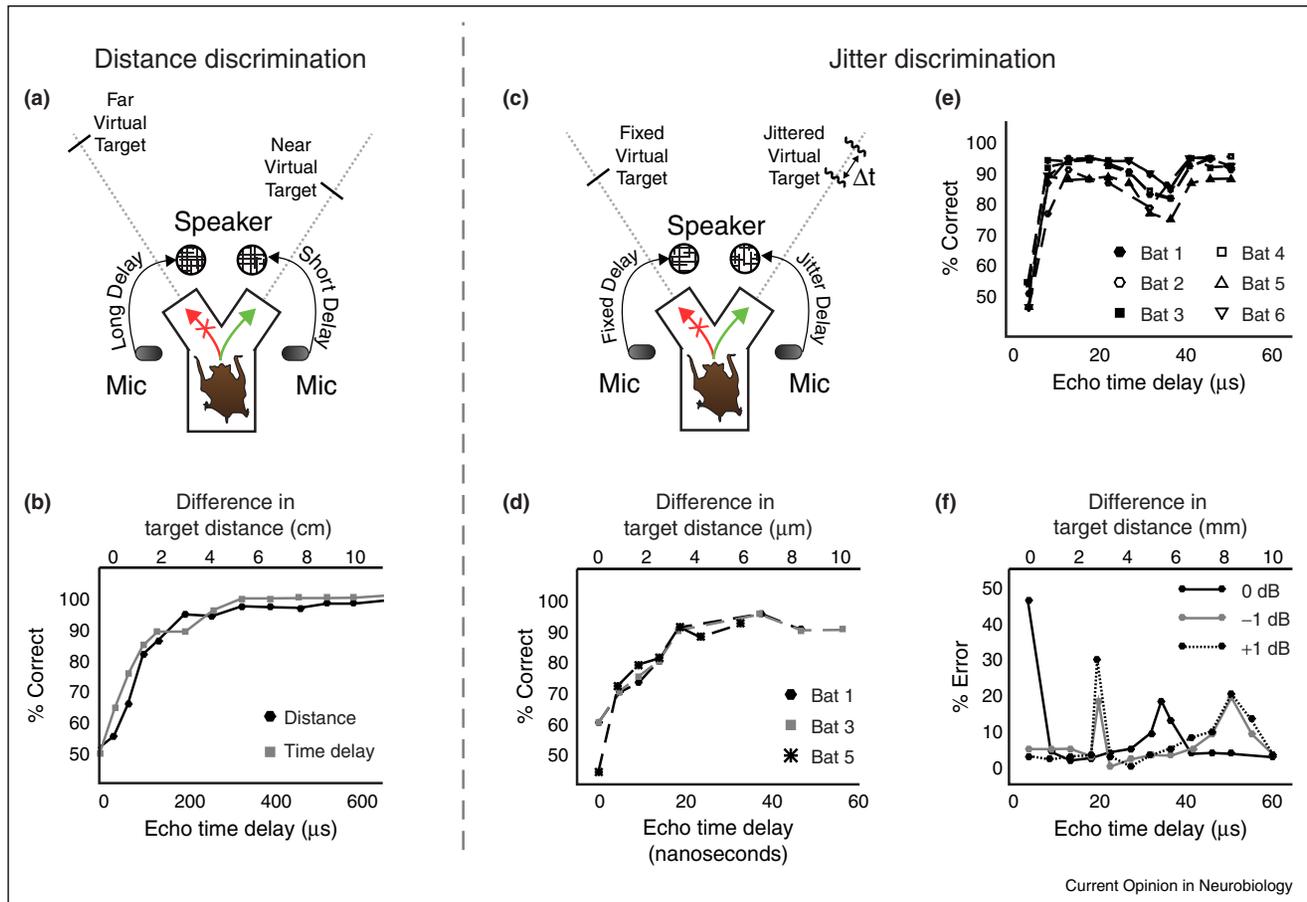
Ranging performance of echolocating bats. **(a)** Behavioral setup for distance discrimination task using two-alternative-forced-choice (2 AFC) paradigm. **(b)** Behavioral performances of big brown bats in the distance discrimination task. Bats show very similar behavioral performances when tested with real objects placed at difference distances and with virtual targets simulating the time-delay differences between the real objects. **(c)** Behavioral setup for jitter discrimination task using 2 AFC paradigm. During both types of behavioral tests **(a, c)**, a bat's sonar vocalizations are recorded by a microphone (m), digitally delayed, and then a modified copy of the sonar vocalization, that is, the simulated echo, is delivered back to the bat from one of the two loudspeakers (s). The pulse-echo delay is controlled precisely by the digital delay. **(d, e, f)** Behavioral performances of big brown bats in the jitter discrimination tasks. Bats are capable of discriminating jittered time-delay not only in the microsecond level **(e)**, but also in the nanosecond level **(d)**. Moreover, the behavioral performances change in a way as would be predicted by the amplitude-latency trading phenomenon when the amplitude of the jittered echo is enhanced or attenuated **(f)**. This figure is re-plotted from [4,27].

The external ear

Animals that specialize in hearing for survival behaviors often show adaptations of the peripheral auditory system for sound localization [20,21]. For many mammals, external ears (pinnae) serve to amplify sound and enhance auditory localization cues [22]. In some mammals, mobile pinnae allow for dynamic sampling of spatial acoustic information [23]. In the bat, movements of the ears can direct reception to a selected region of the acoustic field to improve sonar detection and resolution [24]. In the horseshoe bat (*Rhinolophus*), for instance, the pinnae oscillate front to back out of phase [25], and these movements contribute to vertical localization [3].

Sonar ranging

In contrast to humans and most other mammalian species, echolocating bats exhibit an extraordinary capacity to estimate sound source distance, or a target's range [4,7]. Empirical studies demonstrate that echolocating bats can accurately discriminate between the range of two targets on the order of one centimeter (Figure 2c), which is the accuracy required to intercept small insect prey in flight [4,8,26]. Strikingly, some behavioral studies of the big brown bat's ranging performance demonstrate range jitter discrimination of ≤ 1 microsecond, corresponding to a change in distance of ≤ 0.17 mm (Figure 2e,f). What cues do echolocating bats use to achieve such remarkable accuracy?

The bat's use of pulse-echo delay (P/E delay) to estimate target distance was first demonstrated experimentally by Simmons [4], who reported that the big brown bat's range discrimination performance was comparable for physical targets and virtual targets, simulated by delayed play-backs of the bat's sonar emissions. With virtual targets, visual cues are eliminated, and pulse-echo delays can be precisely adjusted to measure a bat's distance discrimination performance (Figure 2b,d).

Compelling evidence that bats rely on echo delay to estimate target distance comes from a study that exploited *amplitude-latency trading*. In big brown bats, attenuation of sound amplitude delays the neural response latency by 13–18 μs/dB. Notably, in both a range discrimination task (Figure 2a) and range jitter discrimination task (Figure 2c), changes in echo amplitude affect the distance estimation of big brown bats in predictable ways (Figure 2f) [27,28]. Behaviorally, it has been demonstrated that sonar ranging in big brown bats is robust to changes in echo amplitude with changes in target distance through an echo gain control mechanism. At target distances less than 1.5 m, middle ear muscle contractions, combined with a reduction in sonar emission level at short ranges and neural attenuation, serve to offset distance-dependent changes in echo level and thus reduce amplitude influences on perceived target distance [29,30].

Neural mechanisms of 3D auditory localization

Auditory periphery

Spatial localization by sonar requires high frequency hearing to enable detection and localization of sounds with wavelengths short enough to return echoes from small objects. The mechanical properties of the basilar membrane of bats lay the foundation for ultrasonic hearing [31]. For example, the greater horseshoe bat, *Rhinolophus ferrumequinum*, produces a constant frequency (CF) sonar vocalization at around 83 kHz, and this species' basilar membrane reveals an enlarged region that responds to the CF component of its echolocation signal [32,33]. This over representation of biologically relevant sound frequencies in the greater horseshoe bat, as well as in other CF bats, is preserved from the auditory periphery through the ascending auditory pathway [34].

Representation of sound source azimuth and elevation

The cochlear nucleus receives inputs from primary auditory nerve fibers innervating the cochlea and projects to the superior olivary nuclei, which are divided into medial and lateral subdivisions (MSO and LSO, respectively) [14]. The mammalian MSO in most species contains neurons that are selective to inter-aural time differences (ITD), which contribute to azimuthal localization of sound sources [35]. Animals that rely heavily on ITD to estimate sound source azimuth have a comparatively large MSO [36]. It is noteworthy that the morphology and innervation of the MSO varies across bat species, with the mustached bat showing only monaural innervation [37], and the MSO appears to be entirely absent in the rufous horseshoe bat [38]. Research from these two species suggests that the MSO is not always involved in binaural computation of sound source azimuth in bats.

Neurons that respond selectively to inter-aural level differences (ILD's), and contribute to the coding of sound source azimuth, are found throughout the auditory system of mammals, including bats. Studies of the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) have demonstrated ILD processing at several stages of the auditory pathway [39]. ILD sensitive neurons in the LSO, for example, are also sensitive to the overall intensity of the sounds, such that raising the amplitude of sound in both ears results in shorter auditory response latencies in LSO neurons [39]. A population of neurons in the midbrain inferior colliculus (IC) receive input from the LSO, but respond with a nearly constant latency to sounds across a range of sound levels, up to 40 dB [40]. This tolerance allows IC neurons to reliably code for azimuth, irrespective of the amplitude of the sound source. Research on the IC of Mexican free-tailed bats identified a mechanism by which inter-aural sound level differences increase inter-aural timing differences, due to *amplitude-latency trading* [40]. Specifically, each 1 dB change in the sound level shifts the response latency of single IC neurons on average by ∼47 μs. This suggest that sound level differences are converted into timing differences, which then amplify binaural disparities used to localize sound sources [40].

Previous research has also shown that the bat's adaptive orienting behaviors alter auditory representations in the IC, with the spatial tuning profiles of IC neurons influenced by the positions of the pinnae [41]. Responses of IC neurons were initially characterized with the ears at a resting position, and then reassessed at several different positions. Interestingly, not only did the position of the contralateral ear affect the spatial pattern of auditory responses, but the position of the ipsilateral ear also changed auditory responses. These results suggest that the bat can alter responses of spatially selective auditory neurons by adjusting pinna position, and that binaural interactions across the two ears can influence azimuthal coding.

The IC projects to the auditory thalamus, which then projects to auditory cortex (AC). In the AC of the pallid bat, ILD is represented topographically [42]. Data show in this species that an increasing proportion of auditory cortex is activated as the sound source moves from ipsilateral to contralateral locations in auditory space [43], suggesting that sound source azimuth is not encoded by a single locus of activity in AC, but instead by a distributed, population response. This contrasts with

LSO, where ILD is represented focally and influenced by overall sound intensity [39,44], and in IC where a population of neurons involved in space coding show stable latencies across a range of sound amplitudes [39].

Studies of the auditory cortex of the big brown bat report that the frequency, amplitude, and spatial location of a sound source interact to influence cortical responses [45]. Distributed coding strategies such as these are also more resistant to variability in activity at the single neuron level because responses are averaged across many neurons [46]. The echolocating bat is tasked with extracting invariant representations of the acoustic scene using noisy information about the frequency, amplitude, and location of the sound source. By combining signals related to the different acoustic parameters, relevant spatial acoustic information can be extracted from background noise and amplified [45].

Representation of target range

There is no doubt that echolocating bats show remarkable performance in acoustic target ranging, with an acuity of about 1 cm [4]. The question is: what are the neural mechanisms underlying such remarkable sonar ranging? In the auditory system of echolocating bats, there are neurons suitable for coding target range. Early in the auditory pathway in the ventral nucleus of lateral lemniscus (VNLL), and upstream in the inferior colliculus, are neurons whose responses are precisely locked to the onset of sound stimuli and remain stable over a large range of sound frequencies and/or intensities [47,48]. These neurons can code the precise timing of both sonar pulses and echoes, and thus could contribute to the computation of echo delay.

Neurons directly implicated in target ranging show the response property of pulse echo delay-tuning (i.e. P/E delay tuning). P/E delay-tuned neurons have been characterized at multiple levels of the auditory system of echolocating bats, including the inferior colliculus, the superior colliculus, the medial geniculate body, and the auditory cortex [6,49–51]. P/E delay-tuned neurons show facilitated responses to pairs of sounds, separated by a restricted range of delays that mimic the signals the bat would use to estimate the distance to a target (Figure 2). It is noteworthy that the current neurophysiological data indicate that response profiles of single P/E delay-tuned neurons are too broad to support the high resolution ranging accuracy reported in the literature ($\sim$1 cm or 58 μs of echo delay), let alone the submicrosecond time delay discrimination reported from range jitter discrimination tests (<1 mm or <1 μs). As proposed by Suga and colleagues [52], a population of P/E delay-tuned neurons may distinguish delays as small as 2.4–4 μs, but how the brain encodes submicrosecond time delays remains unknown.

Some indications of how neurons in bat AC may code for such small time delays come from recent work examining the influence of behavioral adjustments in sonar vocal amplitude on cortical P/E delay tuning. Research on the mustached bat demonstrated that this bat adjusts the amplitude of the outgoing sonar vocalization in order to keep the amplitude of the returning echo constant (e.g. high amplitude vocalizations for larger target distances) [53•]. Researchers postulate that the bat's call amplitude adjustments align to the response properties of cortical P/E delay tuned neurons. This study, albeit conducted in anesthetized and passively listening bats, suggests how interactions between the bat's adaptive sonar behaviors and cortical representations could enable increased acuity in range coding of targets in the environment. A related neurophysiological study of the AC of the anesthetized and passively listening lesser spear-nosed bat investigated cortical responses to virtual echo flow. When bats were presented with virtual dynamic echo environments, the cortical representation of closer-range targets increased as the passing distance of a virtual target echo decreased [54•]. Another recent study has directly compared the response properties of cortical P/E delay tuned neurons in the Seba's short-tailed bat, *Carollia perspicillata*, stimulated with natural echolocation call sequences and isolated pulse-echo pairs [55••]. This study showed that the cortical P/E delay-tuned neurons are more selective to target distance information when they are stimulated with natural echolocation sequences. These studies demonstrate the importance of simulating natural echo stimuli to investigate auditory localization processes.

A survey of the studies on sonar ranging in bats reveals that the majority of neurophysiological data on echo delay-tuned neurons have been collected from the mustached bat, while the majority of behavioral data on target distance discrimination have been collected from the big brown bat. These two species are not only from two different families, but also contrast greatly in their sonar signal features, raising questions about links between neural and behavioral data. Moreover, except for one study [56], neurophysiological studies of echo delay-tuned neurons in the bat auditory system have been collected from animals that were passively listening to simulated pulse-echo pairs. To bridge this gap, future studies would benefit from neural recording experiments that engage behaving bats in biologically-relevant, dynamically orienting tasks.

Representation of sound source location in three dimensions

Ultimately, the bat interacts with a three-dimensional (3D) world, and as such, auditory localization must involve the combination of cues for azimuth, elevation, and range [5,26]. One structure where 3D representations have been characterized is in the superior colliculus (SC) [50], a layered structure in the mammalian midbrain. The SC integrates visual, auditory, and somatosensory cues about stimulus location to guide species-specific

orienting commands. The bat is an audio-vocal specialist, and as such, 3D auditory representations inform motor commands for spatially-dependent sonar vocalizations, head, and ear movements [57]. Projections from the lower brainstem (e.g. nucleus of the central acoustic tract; [14]),

IC and AC project to the bat SC (IC, [58]; AC, [59]). In the sensory layers of the bat SC, neurons show 3D spatial tuning profiles [50], demonstrating that information about azimuth, elevation, and range is combined. This 3D representation of auditory space is then used to guide

Figure 3
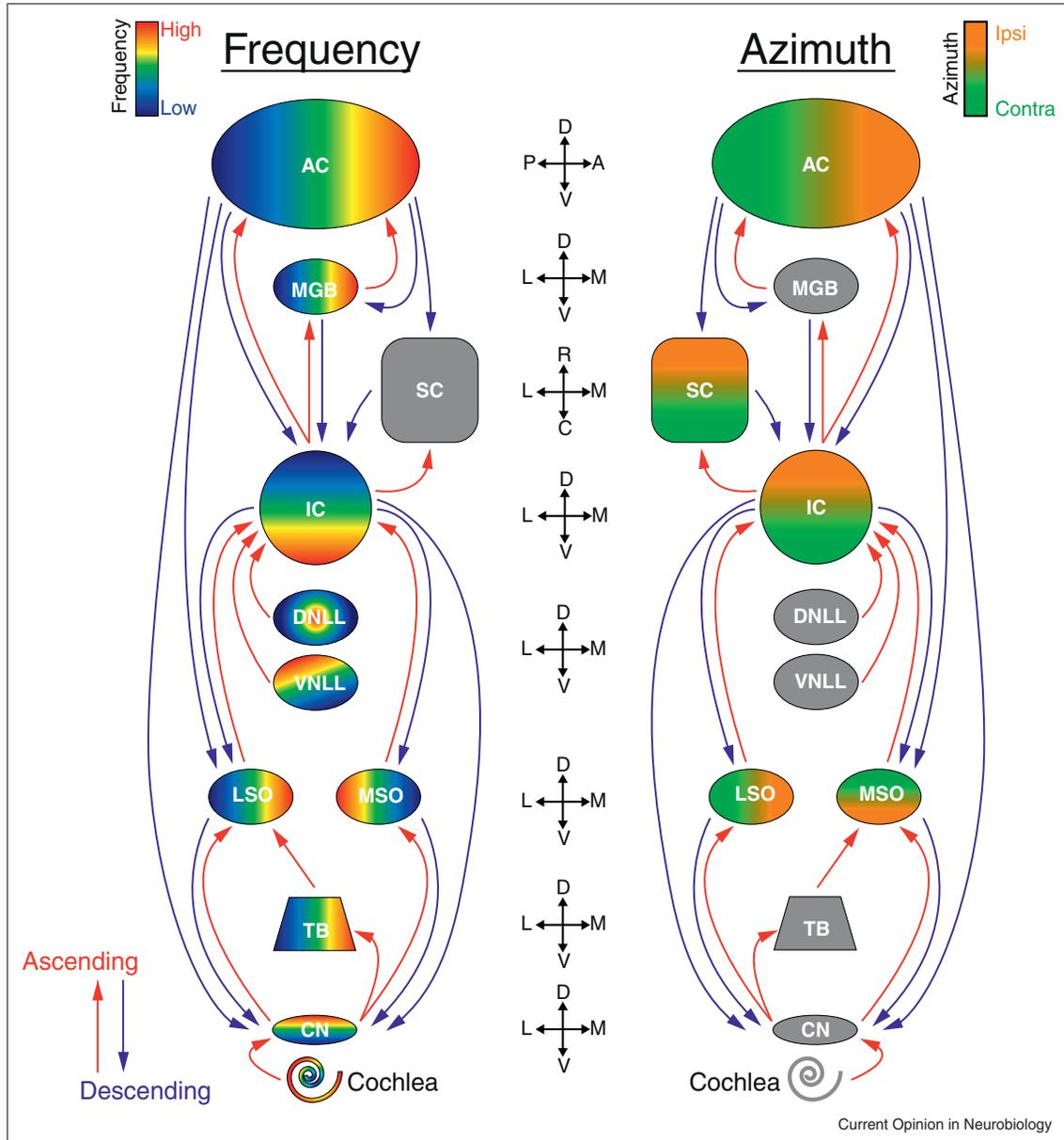
Ascending and descending connections of the bat's auditory system. Left, schematic of the auditory system displaying the tonotopic arrangement of neurons at each stage of the pathway. Blue indicates low frequency tuning, red indicates high frequency tuning (anatomical connections reconstructed from [65]). The topography of tonotopy is shown with respect to anatomical axes indicated in the middle of the figure. Variations in the orientation of topography exist from species to species, and as a result, topography from one species is presented. Right, schematic of the auditory system displaying the spatial topography of neurons in each stage of the pathway. Green indicates contralateral tuning, orange ipsilateral tuning. Anatomical axes for each level are displayed in the middle. Ascending projections are shown in red, descending projection are in blue. Gray indicates no tonotopic or spatial topography for a particular auditory nucleus. AC, auditory cortex (*Pteronotus parnellii*); MGB, medial geniculate body (*Pteronotus parnellii*); SC, superior colliculus (*Eptesicus fuscus*); IC, inferior colliculus (*Eptesicus fuscus*); DNLL/VNLL, dorsal/ventral nucleus of the lateral lemniscus (*Rhinolophus rouxi*); LSO/MSO, lateral/medial superior olivary nucleus (*Rhinolophus rouxi*); TB, trapezoid body (*Rhinolophus rouxi*); CN, cochlear nucleus (*Pteronotus parnellii*).

adaptive motor commands for species-specific orienting behaviors [57,60].

Circuits involved in auditory localization

Auditory localization does not arise through computations in any single brain region, but instead involves flexible circuits throughout the auditory pathway. For example, research on the topographic representation of echo delay in the bat auditory cortex has been shown to be flexible [61••]. This flexibility allows the locus of cortical activation for a particular target distance/echo delay to shift, changing the network properties of the cortex. Previous research has also shown that functional units in the cortex extract a related set of acoustic parameters from an echo stream [62], and by having a flexible topographic representation of target distance/echo delay, different information streams can interact (see Figure 3 for topographic relationship between frequency and location encoding).

Beyond neural circuits within a single brain region, interactions across various levels of the auditory pathway contribute to sound localization processes. And while cortical regions receive their input from brainstem, midbrain and thalamic structures of the ascending auditory pathway, it is important to keep in mind that descending projections also contribute to the processing of acoustic signals (Figure 3; ascending projections in red, descending projections in green). Research by Suga and colleagues has, for example, directly investigated the influence of AC activity on response properties of IC neurons, demonstrating that AC affects both the frequency and spatial tuning of IC neurons [63]. AC was both inactivated and excited, revealing opposing effects upon IC neurons. Pharmacological inactivation of restricted regions of the bat AC resulted in reduced and longer latency responses in IC; whereas, focal electrical activation of bat AC increased neural firing rate and shortened the response latency of IC

Figure 4
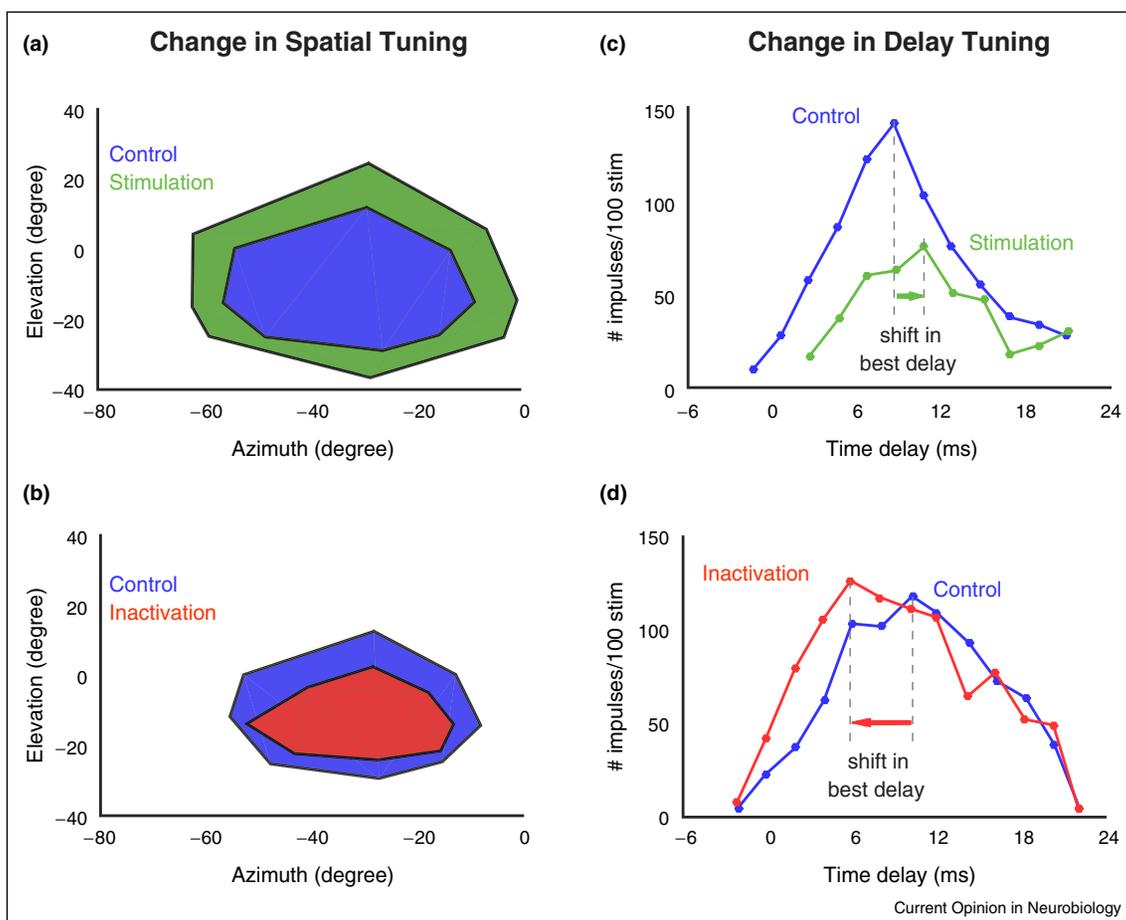
Change in tuning as a result of descending circuit phenomenon. **(a)** Electrical stimulation of AC neurons expands the spatial response area of an IC neuron (stimulation in green, control in blue). **(b)** GABA application to AC neurons narrows the spatial response area of an IC neuron (inactivation in red, control in blue). **(c)** Electrical stimulation of a delay-tuned neuron in the AC shifts the delay tuning curve of a delay tuned neuron in the IC from its best delay of 8.7 to 10.8 ms. The best delay of the stimulated cortical neuron is 6 ms (stimulation in green, control in blue). **(d)** Lidocaine application to a delay tuned neuron in the cortex with the best delay of 6.4 ms shifts the delay tuning curve of a delay tuned neuron in the IC from 10 ms to 6 ms (inactivation in red, control in blue). This figure is re-plotted from [63,64].

neurons. These data are shown in Figure 4, along with complementary data demonstrating cortical influences on IC target range tuning [64]. AC also sends projections to the SC in the bat [59], providing another descending pathway through which the cortex can modulate activity in other midbrain regions. Future studies involving simultaneous neural recordings in more than one of these brain regions would contribute greatly to our understanding of how recurrent feedback contributes to sound localization.

Conclusions

The echolocating bat is an auditory specialist that localizes sonar objects in 3D space. We propose that distributed coding within and across the auditory pathway supports high-resolution sonar imaging in a noisy echo environment. In this review we have highlighted the contributions of neurons in the IC, AC, and SC to the representation of 3D acoustic space, and we propose that future work focused on circuits within and across these brain regions, in freely behaving animals, will shed light on feedback processes that enable echo scene representation. This line of investigation would not only inform our understanding of sonar imaging in bats but natural sound processing in other animals.

Conflict of interest statement
We have no conflicts of interest.

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- •• of outstanding interest

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