



REVIEW

REVISED **Sonar-guided attention in natural tasks [version 3; peer review: 2 approved]**

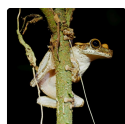
Previous Title 'Spatial attention in natural tasks'

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Little is known about neural dynamics that accompany rapid shifts in spatial attention in freely behaving animals, primarily because reliable, fine scale indicators of attention are lacking in standard model organisms engaged in natural tasks. The echolocating bat can serve to bridge this gap, as it exhibits robust dynamic behavioral indicators of spatial attention while it explores its environment. In particular, the bat actively shifts the aim of its sonar beam to inspect objects in different directions, akin to eye movements and foveation in humans and other visually dominant animals. Further, the bat adjusts the temporal features of sonar calls to attend to objects at different distances, yielding a direct metric of acoustic gaze along the range axis. Thus, an echolocating bat's call features not only convey the information it uses to probe its surroundings, but also reveal its auditory attention to objects in 3D space. These explicit metrics of spatial attention provide a powerful and robust system for analyzing changes in attention at a behavioral level, as well as the underlying neural mechanisms.

Keywords

bats, neuroethology, echolocation, chiroptera, superior colliculus



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We've included the citations suggested by the reviewer.

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Introduction

The auditory world of humans and other animals is noisy, complex, and dynamic. From a barrage of acoustic stimuli, an organism must detect, sort, group, and track biologically relevant signals to communicate with conspecifics, seek food, engage in courtship, avoid predators, and navigate in space (Bee & Micheyl, 2008; Bradbury & Vehrencamp, 2011; Brumm & Slabbekoorn, 2005; Corcoran & Moss, 2017). The success of these natural survival behaviors depends on an animal's attention to stimuli in its sensory environment. Here we focus on overt spatial attention, which we define as an active motor adjustment to focus processing of a selected stimulus to the exclusion of other stimuli (Chun *et al.*, 2011; Lindsay, 2020). How can we monitor rapid shifts in overt spatial attention of animals engaged in natural tasks? Animals such as echolocating bats that produce and modulate sonar calls to probe their environments offer powerful solutions to this central challenge in systems neuroscience. More specifically, the bat's active control over the signals used for sensing its surroundings yields quantifiable metrics of moment-to-moment attention.

Echolocating bats produce sonar signals and process auditory information carried by returning echoes to guide behavioral decisions in a wide range of survival behaviors (Griffin, 1958). There are over 1000 species of bats that use echolocation to forage, find roosts and avoid obstacles; and bats occupy all regions of the earth outside of the arctic zones, from tropical rain forests to savannahs, and from mountains to deserts. Echolocating bat species also show great diversity in diets, including insects, fruit, nectar, blood, and small vertebrates (Denzinger & Schnitzler, 2013; Fenton & Simmons, 2015; Kunz & Racey, 1998). In this review, we focus on adaptive changes in the duration, timing and spectral content of calls produced by insectivorous bats as they localize objects (Busnel & Fish, 1980; Fay & Popper, 1995; Griffin, 1958; Schnitzler & Kalko, 2001; Thomas *et al.*, 2003).

Bats compute the azimuth and elevation of objects from differences in echo intensity, spectrum, and timing at the two ears; they compute an object's distance from the time delay between sonar call emission and echo return (Moss & Schnitzler, 1995; Simmons, 1973; Simmons, 1979). Together, this acoustic information gives rise to a 3D representation of the world through sound (Wohlgemuth *et al.*, 2016). Further, a bat makes active adjustments to its echolocation calls in response to 3D spatial information computed from echo returns (Moss *et al.*, 2011), and therefore, the *features of a bat's calls provides a window into the animal's moment-to-moment attention to objects in the environment.* The echolocating

bat's active sensing system thus presents a powerful opportunity to robustly quantify and analyze sonar-guided attention behaviors and related neural activity patterns.

Spatial attention can be classified in two broad categories: overt and covert. These categories of attention have been studied in humans, mice, owls, and other animals. In visually dominant organisms, saccadic eye movements and fixations to selected stimuli can serve as indicators of overt attention (Hoffman, 1998). By contrast, covert attention requires the subject to attend to a stimulus without directing the sensory organs to inspect it, e.g., foveating a central fixation point and attending to a stimulus in the periphery. Neural recordings in the midbrain (superior colliculus, or SC) of macaques show distinct activity profiles when animals exhibit overt versus covert attention to objects (Krauzlis *et al.*, 2013). Overt attention to an object produces changes in the activity of both sensory and sensorimotor neurons, while covert attention only evokes changes in activity of sensorimotor neurons (Ignashchenkova *et al.*, 2004). Inactivation of the SC demonstrates deficits in covert attention, implicating this structure in a circuit responsible for both overt and covert attention (Lovejoy & Krauzlis, 2010).

The Posner paradigm has been used to probe covert attention by presenting subjects with a cue to the presentation/location of a stimulus and measuring response latency. The cue primes the subject to respond, and intermittent invalid cues yield longer response latencies, presumably due to covert attentional interference (Posner, 1980). In animals, it has been possible to leverage the Posner paradigm to explore the neural mechanisms of covert attention. For example, in mice, it was shown that population responses of neurons in the SC are modulated by covert attention to visual stimuli. Specifically, the data showed that there was enhancement of activity in the area representing the cued spatial location, indicating disinhibition of target space rather than a broad modulation of activity encoding the entire visual field. Based on these findings, the authors propose a neural mechanism for covert attention that biases locations expected to have relevant information (Wang *et al.*, 2022). A modified version of the Posner paradigm has also been used to explore auditory covert attention. In barn owls, for example, it was shown that response latencies to a target sound were reduced when they were presented from a cued location (Johnen *et al.*, 2001). This reduction in response latency appears to be mediated by the optic tectum, the midbrain homologue of the SC in non-mammalian vertebrates. These and other studies suggest that the neural mechanisms of covert and overt attention are broadly conserved across taxa and sensory modalities (Noyce *et al.*, 2023).

Our review focuses on the quantification of spatial attention in insectivorous echolocating bats and subcortical signatures of auditory spatial attention to sonar objects (Kothari *et al.*, 2018). Additionally, we consider published results on auditory cortical responses in passively listening frugivorous bats (Beetz *et al.*, 2017) and speculate on the role of auditory cortex in

sonar-guided attention in freely behaving animals. Both insectivorous and non-insectivorous bats provide valuable insights into the relationship between spatial attention behaviors and the underlying neural mechanisms.

Active sensing signals yield a quantifiable metric of attention

Active sensing falls into two broad categories, *alloactive sensing*, which invokes movement of sensors (eyes, ears, whiskers, etc.) to explore sensory stimuli, and *homeoactive sensing*, which relies on the generation of stimulus energy (sound, electricity) to probe the environment (Zweifel & Hartmann, 2020). Here, we highlight echolocation, a homeoactive sensing system, that offers a quantitative metric of a bat's moment-to-moment attention to objects in its surroundings. Because the bat actively adapts echolocation signal duration, directional aim and frequency content in response to echoes, the features of its sonar calls yield reliable indicators of its spatial attention to objects in its surroundings. In studies of spatial attention in non-human primates the primary indicator of overt spatial attention is eye position (Krauzlis *et al.*, 2013), and while eye position reveals where an animal is directing its attention in azimuth and elevation, its attention along the range axis is often ambiguous (Coubard, 2013). As such, homeoactive sensing, such as echolocation, provides a reliable metric of spatial attention in azimuth, elevation and distance.

Attention to objects along the horizontal axis

The insectivorous bat's echolocation calls are directional, forming a spatial beam pattern, emitted through the mouth or nostrils (Ghose & Moss, 2003; Hartley & Suthers, 1987; Hartley & Suthers, 1989; Jakobsen *et al.*, 2012; Jakobsen *et al.*, 2018; Lee *et al.*, 2017). As such, the bat's sonar beam pattern operates as an "auditory flashlight" to detect, localize and discriminate objects in its surroundings. For example, big brown bats (*Eptesicus fuscus*) aim their sonar beam at selected objects with an accuracy of 3-5 deg, maximizing the signal level of echo returns from prey (Ghose & Moss, 2003) and simplifying sensorimotor transformations for target interception (Ghose & Moss, 2006). When the bat encounters multiple objects, it shows rapid shifts in the direction of acoustic gaze to steer around obstacles and intercept prey (Surlykke *et al.*, 2009). The bat's head aim leads its body in flight maneuvers, and it anticipates a target's future position in a target tracking task, revealing its attention to an object's trajectory for interception planning (Ghose & Moss, 2006; Salles *et al.*, 2020; Salles *et al.*, 2021). Related work shows that Japanese house bats foraging in the field alternate the sonar beam aim between the direction of flight and the anticipated direction of the next prey interception, suggesting that bats shift biosonar attention between objects by alternating acoustic gaze (Fujioka *et al.*, 2014).

Sonar adjustments in call frequency are also indicative of spatial attention to objects in the bat's surroundings. For example, great roundleaf bats (*Hipposideros terasensis*), a species that uses CF-FM echolocation signals, adjust the frequency of their sonar calls to counter the Doppler effect when they fly. These adjustments ensure that echoes return at the frequency to which

the emitter is maximally sensitive and is commonly known as Doppler Shift Compensation (Schnitzler, 1968; Schnitzler & Denzinger, 2011). Interestingly, great round leaf bats not only exhibit Doppler Shift Compensation for targets straight ahead, but also for off-axis objects, indicative of spatial attention to obstacles as well as prey at multiple egocentric locations (Hiryu *et al.*, 2005), revealing a possible behavioral metric for disambiguating overt and covert attention in bats.

Attention to objects along the distance axis

Investigating spatial attention along the distance axis is challenging in visually-guided animals, because the key behavioral metric – eye vergence – is difficult to monitor and may be an ambiguous indicator of attention (Coubard, 2013). By contrast, measurements of call adjustments in echolocating bats provide explicit indicators of their spatial attention along the distance axis. Echolocating bats reduce sonar call duration and the interval between successive emissions as their distance to an object shortens (Griffin, 1958; Griffin *et al.*, 1960; Moss & Surlykke, 2010; Simmons *et al.*, 1979).

What function do range-dependent sonar call adjustments serve, and how can they be used to infer the bat's attention to objects along the distance axis? Sound travels in air at a speed of approximately 344 m/sec in air, and this results in an echo delay time of approximately 6 msec for each meter of target distance (~3 msec to the object, and ~3 msec to return). Bats typically wait for echoes from a selected target to arrive before producing the next call, and the wait time decreases as bats get closer to objects. Thus, the decreasing interval between calls provides an indicator of the bat's attention to objects along the range axis (Surlykke *et al.*, 2009). However, sonar call interval alone does not yield a precise estimate of spatial attention to objects, because bats typically wait a short period of time after the arrival of a target echo to produce the next call.

In complement to changes in call interval, an additional indicator of the bat's attention along the range axis is their control of call duration with changing target distance. FM bats actively avoid overlap between their calls and sonar returns so that they can extract information about targets carried by the features of echoes without interference from the outgoing call (Kalko & Schnitzler, 1993; Surlykke *et al.*, 2009). Evidence that FM bats shift their gaze along the range axis by adjusting the duration of calls comes from a laboratory study in which big brown bats performed a dual task of obstacle avoidance and insect capture (Surlykke *et al.*, 2009). The bat received a food reward for finding its way through the opening of a net to access a compartment containing a tethered insect. As the bat approached the net opening, it shortened the duration of its calls to avoid overlap between sonar vocalizations and net echoes. Once the bat planned its path around the obstacle, but before navigating through the net opening, it increased the duration of its calls as it attended to the more distant prey item. Thus, the bat tolerated overlap of its calls and net echoes as it shifted its acoustic gaze to the food reward behind the net. These active adjustments in call duration provide a direct

metric of the bat's shift in attention to objects along the range axis, and in combination with measures of call interval and beam aim, reveal the object being tracked in 3D location in space.

Under some conditions, the control of sonar call interval is not tightly coupled to call duration. For example, when a bat is tracking an approaching target in the presence of an off-axis clutter object, call rate is adapted to target position, while call duration is adapted to the position of the closest object (target or clutter object) to avoid call-echo overlap (Aytekin *et al.*, 2010). These results show that bats can differentially adjust call duration and rate to track a moving target in the presence of clutter. Similar to the example of round leaf bats discussed earlier, differential control of call rate and duration in a complex acoustic scene may point to an opportunity to disambiguate behaviors for overt and covert attention. Future work should be directed at understanding the relative contributions of overt and covert spatial attention in the analysis of natural sonar scenes.

Tasks that evoke overt sonar-guided attention

When bats perform tasks that require high spatial resolution, they often produce clusters of echolocation calls, embedded in distance-dependent adjustments in repetition rate (Kothari *et al.*, 2014; Moss *et al.*, 2006; Petrites *et al.*, 2009; Sändig *et al.*, 2014). This distinct temporal patterning of sonar calls has been termed, *sonar sound groups* or *sonar strobe groups*, which are characterized by a series of echolocation calls produced at relatively stable and shorter intervals than the surrounding calls. It is worth emphasizing that the intervals between calls within a sonar sound group depend on the bat's distance to objects, and therefore the temporal patterning of calls, not absolute call interval, defines sonar sound groups. Sonar sound groups are produced by bats intercepting targets in clutter (Moss *et al.*, 2006), discriminating target texture (Falk *et al.*, 2011), and avoiding obstacles (Petrites *et al.*, 2009; Sändig *et al.*, 2014). Further, sonar sound groups have been reported in both field and laboratory studies, and the prevalence of sonar call clustering varies reliably with task difficulty. It has therefore been posited that sonar sound group production serves as an indicator of an echolocating bat's attention to objects. These observations motivate the hypothesis that sonar sound group production evokes a sharpened 3D representation of sonar objects [Figure 1](#).

Circuits for attention

The neural underpinnings of spatial attention have been explored in diverse species, at different levels of the central nervous system. fMRI research in humans has suggested that similar cortical networks may be involved in both overt and covert attention, but activity levels are higher for overt attention (Beauchamp *et al.*, 2001). A more recent fMRI study of parietal activity in humans tried to disambiguate signals related to saccade planning from those related to visual attention (Huddleston *et al.*, 2021). Subjects were asked to perform a covert visuospatial attention task with a delayed saccade, providing an opportunity to separate signals for saccade planning

from those involved in spatial attention. In this study, there was much great inter-subject variability in the locus of parietal activation, but different loci for saccade planning versus spatial attention were identified within parietal cortex. Imaging studies lack temporal precision, and therefore extracellular recordings in behaving animals permit assessment of single neuron activity at known locations. Single-cell recordings have been taken in frontal and premotor cortices of macaques performing a covert attention and delayed-saccade task (Messinger & Genovesio, 2022). Pre-motor cortical neuron activity was largely tied to the upcoming saccade event, while frontal cortical neuron activity was tied to the saccade event or spatial attention, but not both. These data suggest that circuits for overt and covert attention share some resources, but also depend on separate spatial attention and saccade planning pathways.

The mammalian SC (non-mammalian optic tectum) has been shown to be differentially active in overt and covert attention tasks (Ignashchenkova *et al.*, 2004), and is therefore a key brain region for studies of attentional mechanisms. Early work demonstrated the role of the mammalian SC in species-specific sensorimotor orienting behaviors (e.g. Goldberg & Wurtz, 1972; Masino & Knudsen, 1992; McIlwain, 1991; Sparks, 1986). The midbrain SC/OT has also been implicated in spatial attention networks (Krauzlis *et al.*, 2013; McPeck & Keller, 2004; Mysore *et al.*, 2011). In echolocating bats, the SC shows specializations that support 3D auditory space representation and acoustic orientation by sonar: A class of neurons in the bat SC responds selectively to the azimuth, elevation, and arrival time of echoes, encoding the direction and distance of sonar targets (Valentine & Moss, 1997; Wohlgenuth & Moss, 2016). Moreover, the bat SC is implicated in the production of sonar orienting behaviors: Microstimulation of the bat SC elicits head/pinna movements and echolocation calls (Valentine *et al.*, 2002), and premotor activity accompanies each sonar vocalization (Kothari *et al.*, 2018; Sinha & Moss, 2007).

The hypothesis that sonar sound groups evoke a sharpened spatial representation leads to the prediction that distance coding of sonar objects by single neurons depends on the bat's sonar call production patterns and corresponding attention to objects in its surroundings. Kothari *et al.* (2018) experimentally tested this hypothesis by recording from neurons in the midbrain superior colliculus (SC) of free-flying big brown bats that actively inspected their environments through echolocation. This study combined neural telemetry, microphone array and high-speed 3D video recordings to quantify single neuron responses to the azimuth, elevation, and arrival time of echoes from physical objects at the ears of the free-flying echolocating bat. They used these data to reconstruct 3D spatial response profiles of auditory neurons to echoes arriving from objects as the bat approached and steered around them. Because the bat reveals its attention to objects through active adjustments in its echolocation behavior, they took the opportunity to sort neural responses to echoes with respect to the animal's sonar-guided attention, indexed by the production of sonar sound groups. They discovered that echoes returning from objects ensounded with sonar sound groups (bat exhibiting overt spatial attention)

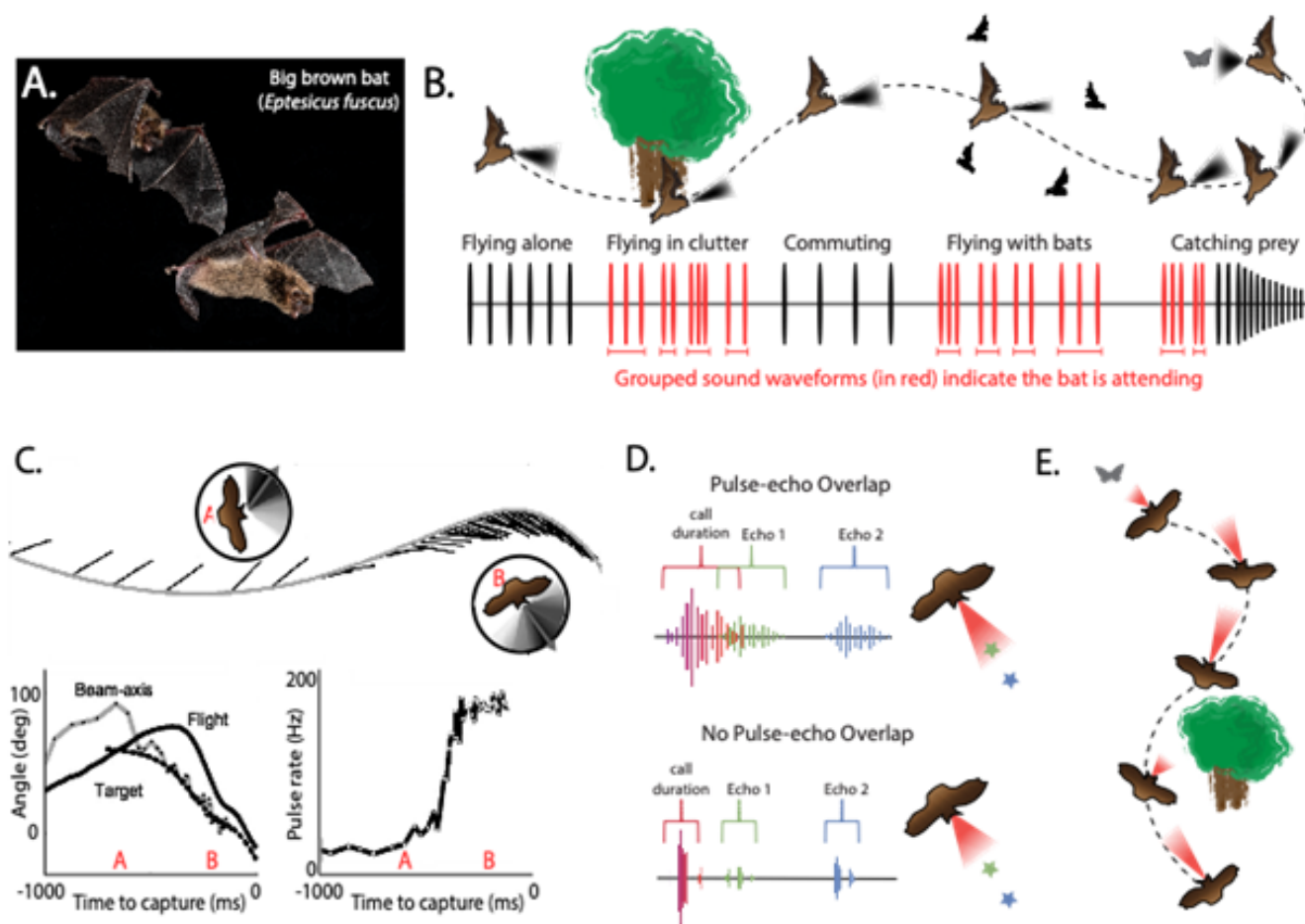


Figure 1. **A.** Photo taken by Dr. Brock Fenton. **B.** Schematic showing a bat flying alone, flying in clutter, commuting, flying with other bats, and chasing prey. The shaded sonar beam pattern illustrates the directional aim of the bat's sound as it inspects objects. The temporal patterning of calls in each scenario is illustrated in the oscillograms below. Bats flying in open space and commuting produce isolated calls at rate of 5–10/second, and they produce calls at high rates, up to 150–200 sounds/sec, during the terminal buzz that precedes prey capture. Bats flying in clutter, with other bats or chasing evasive prey produce clusters of calls, termed sonar sound groups, at rates of 20–80 sounds/sec (in red), which index sonar-guided attention to objects. **C.** The aim of the bat's sonar beam anticipates the direction of flight (A), and once a bat selects its prey, it locks its sonar beam to track it with an accuracy of 3 deg (B). **D.** Bats also adjust call duration to avoid overlap between calls and echoes, and therefore provide a metric of attention to objects along the range axis. **E.** Schematic of call duration adjustments while in flight and attending to clutter or target prey.

evoked sharper echo delay/range tuning than echoes returning from single calls (bat *not* exhibiting overt spatial attention). Importantly, analyses showed that the bat's attention-driven temporal patterning of calls, not absolute call interval, influenced neural spatial response profiles. This study reported that ~50% of SC neurons were influenced by shifts in sonar-guided attention, which may be driven by bottom-up input from brainstem and/or top-down projections from auditory cortex. Further evidence of modulatory effects from outside of the SC comes from an increase in the gamma-band of the local field potential – a signal that represents broad-scale changes in brain state.

A small number of prior publications report on cortical activity of vocalizing bats, but these studies did not investigate the

influence of temporal sound patterning on cortical responses (García-Rosales *et al.*, 2022; Kawasaki *et al.*, 1988). However, neural recordings from auditory cortex of passively listening animals demonstrate the importance of sonar call temporal patterning on the sharpness of cortical responses. Beetz *et al.* (2016) reported that cortical tuning to sounds resembling the natural pattern of sonar call intervals was highly selective. However, they discovered that selectivity was abolished in the same neurons when stimulated with the sounds at artificial and fixed intervals. These findings support the hypothesis that natural temporal patterning of sonar calls evokes a sharpened representation of object location, and that the dynamics of spatial coding are modulated by a behaving animal's attention to objects in its surroundings. Considering observations that the temporal patterning of sonar sounds influences both subcortical

and cortical stimulus responses (Beetz *et al.*, 2016; Beetz *et al.*, 2017; Lopez-Jury *et al.*, 2021), we hypothesize that the effects of spatial attention on neural selectivity are likely mediated through the interplay of bottom-up and top-down circuits. In support of this hypothesis, prior work has demonstrated that inferior colliculus frequency tuning can be altered by cortical perturbations (Jen *et al.*, 1998; Yan & Suga, 1996). These results reveal that top-down cortical inputs can modulate collicular sensory representations, which leads us to posit that bottom-up subcortical activity is integrated with descending cortical inputs to sharpen and shift midbrain responses to echoes with adjustments in sonar-guided attention (Figure 2).

Outlook

The echolocating bat's active adjustments in sonar call features to inspect objects in the environment provide a metric to quantify moment-to-moment overt spatial attention and reveal attention-modulated neural coding dynamics. Recent discoveries of dynamic range tuning evoked by adjustments in the bat's active sensing behaviors demonstrate the power of the echolocating bats to understand the neural underpinnings of spatial attention. And yet, open research questions remain: First, how long are changes in brain activity sustained once an animal directs its attention in space? And second, how do overt and covert attention differentially modulate activity

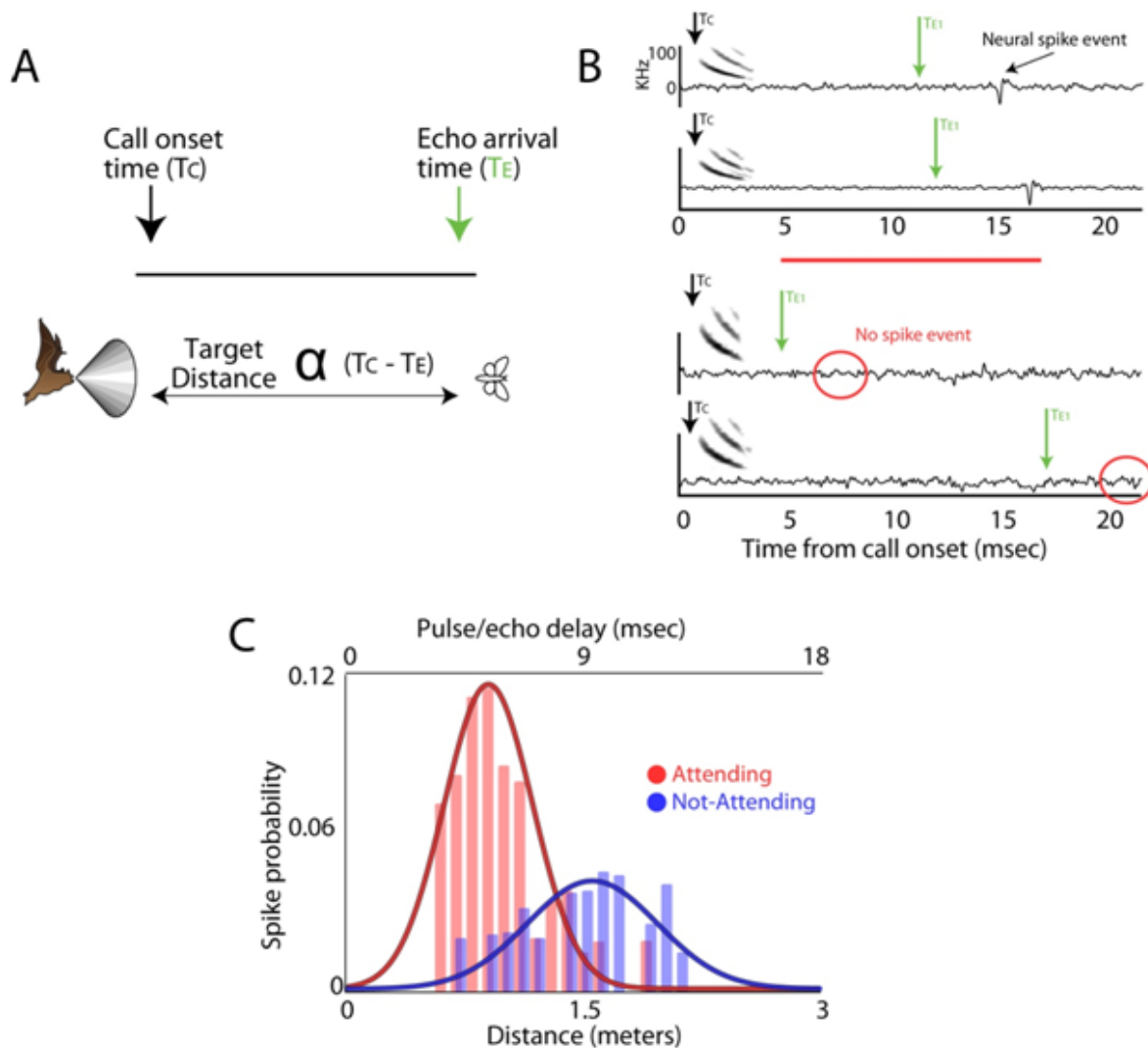


Figure 2. **A.** Schematic depicting target range as calculated from time difference between T_c call onset and T_e echo arrival. **B.** Example of echo evoked 3D responses of SC neurons and their sharpening with sonar guided attention. Neural spike events occur for specific neurons when the target is at a specific range (delayed tuned neurons, top two panels) but not at other delays (lower two panels, first echo returning at a short delay, where the target is too close to evoke a response from this neuron, and second echo returning at a long delay, where the target is too far away to evoke a response from this neuron). **C.** spike probability for a single neuron. For this neuron the preferred echo delay is ~9 ms (1.5 m range) when the bat is not attending to the target but the spike probability increases, sharpens and is shifted to a shorter delay, ~6 ms (1 m), when the bat is attending.

in the brain? Answers to these questions can be addressed by analyzing the punctate and temporally precise features of the bat's calls, which provide discrete timepoints to assess the latency and duration of attentional effects on brain activity. Future research can leverage advances in technology to discover the circuits mediating the neural sharpening that accompanies shifts in spatial attention and delineate the temporal dynamics.

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Data availability

No data are associated with this article.

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Jagmeet Kanwal 

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Most studies on attentional mechanisms so far are restricted to the visual system where eye tracking can be used to gauge attention in animals. Auditory attention is more challenging to study. This is an interesting article, opening the possibility of using bats to advance research and understanding of auditory attention. The authors have addressed my concerns and the writing has considerably improved in its scope and approach.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Version 2

Reviewer Report 14 July 2023

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Julio C. Hechavarria

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I thank the authors for replying to my comments. I find this version much improved and in my

view it can be accepted in its current form. This is a very straight-forward and timely review.

I just have one last comment for the authors.

It is true that there currently aren't any cortical measurements from freely vocalizing bats. Yet, there are neural measurements from spontaneously vocalizing bats and from bats in which vocalizations were evoked using micro-stimulation (Kawasaki *et al.*, 1988¹; Metzner, 1989²; Weineck *et al.*, 2020³; García-Rosales *et al.*, 2022⁴).

I agree that these are not perfect in the sense that the animals are not freely behaving, but they still provide valuable information about the circuits for echolocation/attention. I recognize that studying auditory attention was never mentioned explicitly as a goal in these studies. These are more related to vocal-production circuits, but in the context of the present review vocal production and auditory attention circuits are very related to each other. Many studies on the neural circuits for attention in non-bat models were/are performed in restrained animals under semi-natural conditions. In my personal view, it is valid to consider those results as long as we are aware of the caveats.

One very last note: Some of the citations mentioned above are related to my own work (Hechavarria's group, Frankfurt). I do not like to self-promote my articles, so I leave it to the authors' consideration whether to include the references above in their paper if they consider it relevant.

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Competing Interests: No competing interests were disclosed.

Reviewer Expertise: neurophysiology, bats, behavior, neuroethology, auditory processing, neural oscillations, vocalization

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Version 1

Reviewer Report 21 February 2023

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This is my assesment of the article entitled "Spatial attention in natural tasks", by Wolgemuth et al. This is an interesting and easy-to-follow article. The authors make a strong case for insectivorous bats as a model for attention. I enjoyed reading the paper and the nice summary of the many interesting articles cited in this paper. I do think that some points need clarification, especially for the general reader.

1. Definition of 'attention'. As mentioned, the authors present a strong case for bats as models for attention. Yet, I am lacking a proper definition for this term. What framework can be used to define attention in bats? Is it similar to humas and rodents? Many of the examples described in the text classify as fixed action patterns that require little top-down attention (i.e. frontal to sensory) and are more bottom-up processes controlled by subcortical circuits (at least based on the current consensus). I strongly encourage the authors to provide a definition of attention to make their paper more appealing to the general community.
2. There is little mention of the neocortex. Yet, many of the frameworks that try to explain the neural basis of attention in humans and rodents are cortical ones. A quick note on this would be useful.
3. Many of the examples cited in the text are from insect-eating bats, yet many of these behaviors are found also in fruit-eating bats (carollia, rosettus). Wouldn't these bats also be a good model for attention? Many rodent species also display behaviors that can be used as a marker for attention. What makes insect-eating bats special?
4. From what I gather from this paper, bats display many behaviors that can be used to assess attentional states. Yet, there are not many studies on the neural circuits that enable these processes (e.g. neural recordings in behaving and/or vocalizing bats). Correct? This is a critical point that should be stressed to provide readers with a full accurate picture of the stand of research in bats.

Is the topic of the review discussed comprehensively in the context of the current literature?

Yes

Are all factual statements correct and adequately supported by citations?

Yes

Is the review written in accessible language?

Yes

Are the conclusions drawn appropriate in the context of the current research literature?

Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: neurophysiology, bats, behavior, neuroethology, auditory processing, neural oscillations

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Author Response 02 Jun 2023

Angeles Salles

Reviewer 2: We thank the reviewer for this suggestion, we think this is an important point, and we have added a definition of attention to the manuscript (first paragraph of "Introduction"). We also discuss the roles of subcortical (bottom-up) and cortical (top-down) circuits in driving spatial attention behaviors (last paragraph before "Outlook"). We understand the reviewer's point that our review was limited to the effects of spatial attention on subcortical neurons. One issue is that there are no recordings in the cortex of freely behaving echolocating bats that exhibit shifts in spatial attention. We have now included a discussion of how the temporal patterning of the sounds is an indicator of attention, and that cortical responses are influenced by the temporal arrangement of sounds (last paragraph before "Outlook"). We then link this back to the results found in the midbrain to provide a large-scale view of the bottom-up and top-down interactions we speculate underlie changes in spatial attention. We agree with the reviewer that frugivorous (and other non-insectivorous bats) bats are also good models for spatial attention. We have added text (last paragraph of "Introduction") discussing non-insectivorous bats and the cortical studies performed on these animals, but that the current review is primarily focused on insectivorous bats. This is indeed an important point, and we have added text to the main manuscript (last two paragraphs of the manuscript and in the "Outlook" section) to further motivate this idea.

Competing Interests: No competing interests were disclosed.

Reviewer Report 31 January 2023

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This short review draws attention to a relatively ignored but interesting aspect of echolocation in bats. As the authors state, little is known about fine scale neural dynamics that accompany rapid shifts in spatial attention in freely behaving animals. One reason for this is that attention comprises a constellation of somewhat hypothetical cognitive processes and it is difficult to interrogate animals about their attention. The review proposes that auditory tuning of neurons within the superior colliculus (SC) of bats and a shift in their receptive field represents a component of attention.

Since bats live in the dark, and their visual acuity is low, they rely heavily on acoustic signals for extracting information from their environment. Bats are known to actively shift the aim of their sonar beam to inspect objects in different directions and change their pattern of emission when gleaned information over different distances. Estimating head aim is akin to tracking eye-movements for studying attentional dynamics in humans and nonhuman primates, where a lot of progress has been made on the neural basis of attention. An understanding of the neural mechanisms underlying auditory attention, especially in a non-primate species, however, is lacking. With the development of new machine learning methods for tracking body parts, it should be possible to track head direction and ear pinna movements reliably in bats as they shift their acoustic gaze during an echolocation task. Therefore, echolocating bats provide a unique opportunity to study the neural basis of attentional dynamics in a large taxonomic group of mammals. This effort can translate into providing a deeper insight into the brain mechanisms for attention.

During foraging behavior in bats where insect tracking, pursuit and capture occur, spatial localization is necessary. Accordingly, it is important that the animal be able to sustain attention on its goal to capture an insect. However, in this process, there can be distractions from echoes from non-target objects, including other insects, in the environment. Therefore, a decision has to be made to ignore or not attend to the echo clutter.

Notwithstanding all of the positive aspects of the topic of this review, a clear direction and purpose of writing this focused review remains vague. The review ends abruptly without providing a working model of the attention-related coding dynamics that the authors refer to. Given the large number of studies by the authors and their colleagues, what new information can be gleaned from the already available data vs. additional studies on echo localization in bats? The information presented needs to be incorporated within a basic framework of and mechanisms for possibly sustaining vs. shifting attention during insect capture. Head aim can give us some idea about the overt attention of the animal, but what about covert attention that the animal may be engaged in? Could an animal be periodically and covertly shifting its attention to extract information from non-target echoes? How can the latter be tracked and separated from the ongoing neural activity related to overt attention?

The review can benefit from drawing upon and presenting at least some information about what is known about the neural mechanisms and behavioral paradigms for studying attention in other species - how exactly does studying attention in bats further the overall goal and what is known? What are the attentional networks in the brain involved and how does the SC fit in this scheme?

Are “attentional shifts” in neural tuning triggered by recurrent feedback from egocentric cues related to intention or from the pattern of sound cues? What percent of SC neurons show such shifts?

Elaborating on some of these aspects can significantly improve the impact and contribution of the review to the literature on the mechanisms of attention.

The title needs to represent the primary and almost exclusive focus on bats. A more relevant title can be:

"Attentional dynamics during foraging (or echolocation or target-tracking) in bats".

The last sentence of the abstract, “These explicit metrics of overt spatial attention can be leveraged to uncover general principles of neural coding in the mammalian brain”, is confusing (neural coding of attention? – what aspect?) and unless clarified deviates from the presumed focus of the review. How exactly does it bring us closer to understanding the certain mechanisms of spatial attention?

The sentence, “These discoveries open the door to a wide range of comparative studies of *spatial cognition and neural representation* in animals performing natural tasks.” in the Outlook section, also distracts from the focus of the review. Is the focus on spatial cognition, and neural representation or on attention?

Is the topic of the review discussed comprehensively in the context of the current literature?

Partly

Are all factual statements correct and adequately supported by citations?

Yes

Is the review written in accessible language?

Yes

Are the conclusions drawn appropriate in the context of the current research literature?

Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Neuroethology of echolocation and auditory communication. neural coding, acoustics of social behavior.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have

significant reservations, as outlined above.

Author Response 02 Jun 2023

Angeles Salles

The reviewer raises some important points with respect to overt vs covert attention. We believe that there are some behavioral studies that indirectly imply covert attention in bats by showing that multiple objects can affect vocal-motor adjustments to moving and stationary objects. However, this is quite speculative, and not a definitive example of covert attention. Because covert attention invokes processes that are difficult to observe directly, its study remains a great challenge in animal subjects. We have included a discussion of the behavioral effects of multiple objects on the bat's adaptive sonar (last paragraph in the "Attention to objects along the distance axis" section), and suggest that future work might directly explore covert and overt attention in bats operating in natural sonar scenes. We have also included a new section detailing studies of overt and covert attention in other animals (including humans) in the Introduction (last 2 paragraphs). The section introduces the concept of overt and covert attention, and identifies the challenges to its study. In our view, the most important advantage of bats as a model for spatial attention is that their adaptive behaviors provide quantifiable metrics of attention. In other animals, assessing attention at the behavioral level is much more challenging. We have added text throughout the manuscript to draw distinctions between work in bats and work in other models of spatial attention (second to last paragraph of introduction, sections on attention along the horizontal and distance axes, the section on overt sonar-guided attention). These sections identify the limitations of behavioral paradigms in other species, and how research in echolocating bats would contribute a new and important perspective. The reviewer raises an interesting issue about the source of the attentional shifts in neuronal tuning. At this point, we do not have empirical data that would allow us to specify the source(s) of shifts in neural tuning. However, we speculate that it is the result of interaction of bottom-up and top-down circuitry (last paragraph before "Outlook"). We have also indicated the percentage of SC neurons showing a change in tuning with shifts in sonar-guided attention (second to last paragraph before "Outlook"). We have changed the title to: Sonar-guided attention in natural tasks, to reflect the review's focus on bats, as well as natural foraging and navigation studies. We thank the reviewer for pointing out these issues with the text, and have revised the wording of both sections. In the abstract, we have added more details on the advantages of echolocating bats for both behavioral and neural analyses of spatial attention. In the Outlook, we completely revised the last sentence to instead discuss where future efforts should be directed.

Competing Interests: No competing interests were disclosed.