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Bats: Vision or echolocation, why not both?

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Abstract

Echolocation allows bats to navigate in complete darkness. Yet, some bats also have keen eyesight. A new study shows that bats integrate these sensory modalities, even when light abundance would make it possible for them to rely solely on vision.

Most species of bat navigate in darkness by emitting ultrasonic pulses and listening to the returning echoes that reflect from objects in the environment. In this way, bats build an acoustic image of their surroundings, but, contrary to popular belief, bats are not blind. Some bat species have a keen sense of sight that would allow them to navigate in daytime without the aid of echolocation. In particular, Egyptian fruit bats *(Rousettus aegyptiacus*; Figure 1) are cave dwellers that have prominent eyes which allow them to see even in low light conditions[1,2]. Additionally, these bats are lingual echolocators, that is, they use tongue clicks as a form of echolocation to aid their navigation[3,4]. Furthermore, these bats have been shown to have excellent spatial memory and navigation skills that, with the aid of landmarks, enable them to visit distant food sources over repeated instances[5]. In urban settings, such as Tel-Aviv, Egyptian fruit bats have been found to forage for fruit during daytime. With such keen eyesight and spatial memory, the question remained to what extent these bats need to aid their daytime navigation with echolocation. In a paper in this issue of *Current Biology*, Ofri Eitan, Yossi Yovel and colleagues[6] show that even in broad daylight Egyptian fruit bats continue to use echolocation to aid obstacle avoidance while flying.

Eitan and colleagues[6] observed and recorded wild bats while they engaged in daytime foraging and drinking. Given the impressive visual ability of Egyptian fruit bats, the investigators predicted that echolocation would not be used much during daytime. Nevertheless, their observations revealed not only that these bats echolocate when flying during the day, but also that they modulate their echolocation in a similar way as when they are flying in the dark. Bats can dynamically modulate the parameters of their echolocation based on the information obtained from the returning echoes[7]. Generally, as echolocating bats approach obstacles, targets and landing platforms, they increase the rate at which they produce the sonar pulses. This increase in pulse rate enables the bat to improve the accuracy of the information regarding the location and other features of the ensonified

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object. Thus, when these changes in emission rate occur, it can be considered that the bat is making use of the information in the returning echoes and thus it can be characterized as functional echolocation. Eitan and colleagues[6] recorded wild bats during the day as they navigated around trees in search of food and perching sites, as well as while they approached a pool to drink water. They measured modulation in the rate of echolocation of the Egyptian fruit bats as they take off and land on the trees, approach food and water sources, and navigate around obstacles. The pool they recorded the bats getting water from has a decorative wall and as the bats ascended from drinking water they had to avoid the wall. The bats increased their click rate as they approached the water and reduced it as they ascend. Yet, when subsequently faced with this wall obstacle, the bats increase the click rate, a strong indication that they are aiding their visual navigation with acoustic information. Furthermore, the authors found no difference in the echolocating behavior of the bats when compared to night-time flights in the same area.

The new work of Eitan and colleagues[6] shows that bats in the wild are using echolocation to guide their flight maneuvers around obstacles and for landing and foraging, even when the abundance of light would make it possible for them to rely solely on visual information. In this way, their research suggests that bats use both sensory modalities, especially as task complexity increases. Bats present a unique opportunity to understand how the brain integrates multisensory information for spatial navigation. This research sets the groundwork to investigate how spatial representations can be made and modulated by different sensory modalities.

While previous work from the same group has shown that Egyptian fruit bats regulate the use of echolocation depending on the light availability, this new study[6] shows that bats continue to use echolocation in broad daylight; this is a strong continuation of this research focus. Until now, it had been shown that bats continued to echolocate in dim light (up to 35 lux)[8], much lower than the bright daylight in which bats were reported echolocating in this current work (>10,000 lux). In that previous report, where the strongest light conditions tested were 35 lux, bats decreased the intensity and rate of their clicks as light conditions increased; and this was evidenced both in wild bats foraging outside and in bats in the laboratory flying in a tunnel. This is different from the new study of Eitan and colleagues[6] that found no difference in the echolocation parameters between day and night. In a later study, this same group probed the extent to which bats integrate information from both sensory modalities, audition and vision[9]: Bats were trained to discriminate different objects either using both echolocation and vision, or each modality on its own; and under these circumstances, the trained bats showed a strong reliance on vision for object discrimination. Furthermore, it was tested whether bats could transfer acoustic information to a visual task. For this they trained bats in the dark to discriminate two objects, one flat and one with holes. Then the objects were placed in acrylic glass boxes to prevent differential acoustic cues and the room was illuminated. Afterwards, bats were tested for whether they could continue discriminating the objects. Some of the bats were able to translate the acoustic information to solve the visual task, suggesting that bats are in principle able to solve cross-modal tasks. Finally, they tested the relative weight that bats placed on each modality and found that for navigation, the bats tend to rely mostly on visual cues but upon approaching an object, bats relied more on echolocation. This ties in well with the results from the recent report where the bats increased the echolocation rate when negotiating around the wall on the water pool as they ascended even though they had no constraints on visual information.

These questions have also been studied in other bat species, which unlike Egyptian fruit bats are laryngeal echolocators – that is, they use their larynges to produce the sonar signals used for navigation. For these bats, vision is to a greater extent considered a secondary sensory modality. Regardless of this, studies have found that also for these bats integrating visual and auditory information can be beneficial. For example, work from this same group studied visual detection ranges and found that echolocation was preferred when detecting small target prey while vision aided monitoring of distal landmarks[10]. Other groups have added evidence to the importance of sensory integration in laryngeal echolocators by demonstrating that the availability of auditory and visual cues enhanced the ability of bats to navigate around an obstacle[11] and while navigating through tunnels[12]. While flying, bats also collide less with more optically reflective objects, further supporting the idea that bats can make use of visual cues for navigation[13]. Unsurprisingly, the usefulness of light strongly depends on the stimuli: Wild laryngeal echolocating bats, like deer in headlights, show increase collisions when transitioning suddenly from dark to a well-lit area[13]. These studies in laryngeal and lingual echolocating bats suggest that, with the right light conditions, bats can benefit from the availability of both sensory modalities to build an accurate representation of their environment.

Building on these strong foundations for the behavioral aspects of multisensory integration for spatial representation in bats, the question arises: What are the neural correlates of the auditory modulation of visual information, and *vice versa*? For example, one could hypothesize that the availability of visual cues could sharpen neural responses to echo-returns in the auditory cortex of freely flying bats. Additionally, it would be interesting to study spatial representations in hippocampal place and grid cells while the animals navigate under varying conditions of light and as they modulate their echolocation. What more can we learn from these multisensory specialists?

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Figure 1. Egyptian fruit bat.

Rousettus aegyptiacus in flight at the Toronto Zoo. Note the prominent eyes and the raising of the lip that enables the emission of the tongue clicks used for echolocation. (Photo: Brock Fenton.)