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Functional daylight echolocation in highly visual bats

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Bats rely on echolocation for operating in dim light or dark conditions. Accordingly, most research on echolocation is performed under dark conditions with a few exceptions. Bat species that emerge to forage before sunset have been shown to use echolocation even in relatively high light levels[1–3]. It has been argued that for insectivorous bats, as light levels decrease, echolocation rapidly becomes advantageous over vision for detecting tiny insects during dusk or dawn[2] and that information from the two sensory modalities is integrated[4,5]. Functional use of echolocation in broad daylight in insectivorous bats has been scarcely reported[6,7]. Here, we report functional use of echolocation in broad daylight in highly visual fruit bats.

In recent years, there have been numerous observations of diurnal activity of a typically nocturnal species, the Egyptian fruit bat (*Rousettus aegyptiacus*), in Israel. Most activity has been observed in urban environments, mainly in Tel Aviv, with daily reports of bats active in the middle of the day when light levels are more than 10,000 lux. Fruit bats (family Pteropodidae) have excellent vision. Most fruit bats — except species in the genus *Rousettus* — do not rely on echolocation. Despite their visual abilities, Egyptian fruit bats use lingual echolocation clicks, which probably evolved independently of laryngeal echolocation[8]. Until recently, it has been widely accepted that Egyptian fruit bats only use echolocation to maneuver in dark caves, but recently they were shown to echolocate when foraging outdoors at night[8]. The discovery of diurnal activity in Egyptian fruit bats offers the opportunity to examine the use and functionality of echolocation under conditions that favor vision. We hypothesized that fruit bats would rarely use echolocation in broad daylight.

We will refer to bats that are active during daytime as ‘diurnal bats’. We conducted video and acoustic recordings of bats while they emerged from their colony, foraged at fruit trees and drank from an artificial pool. Contrary to our prediction, bats regularly used echolocation as they emerged from their colony and when flying near fruit trees. The bats increased their click rate while

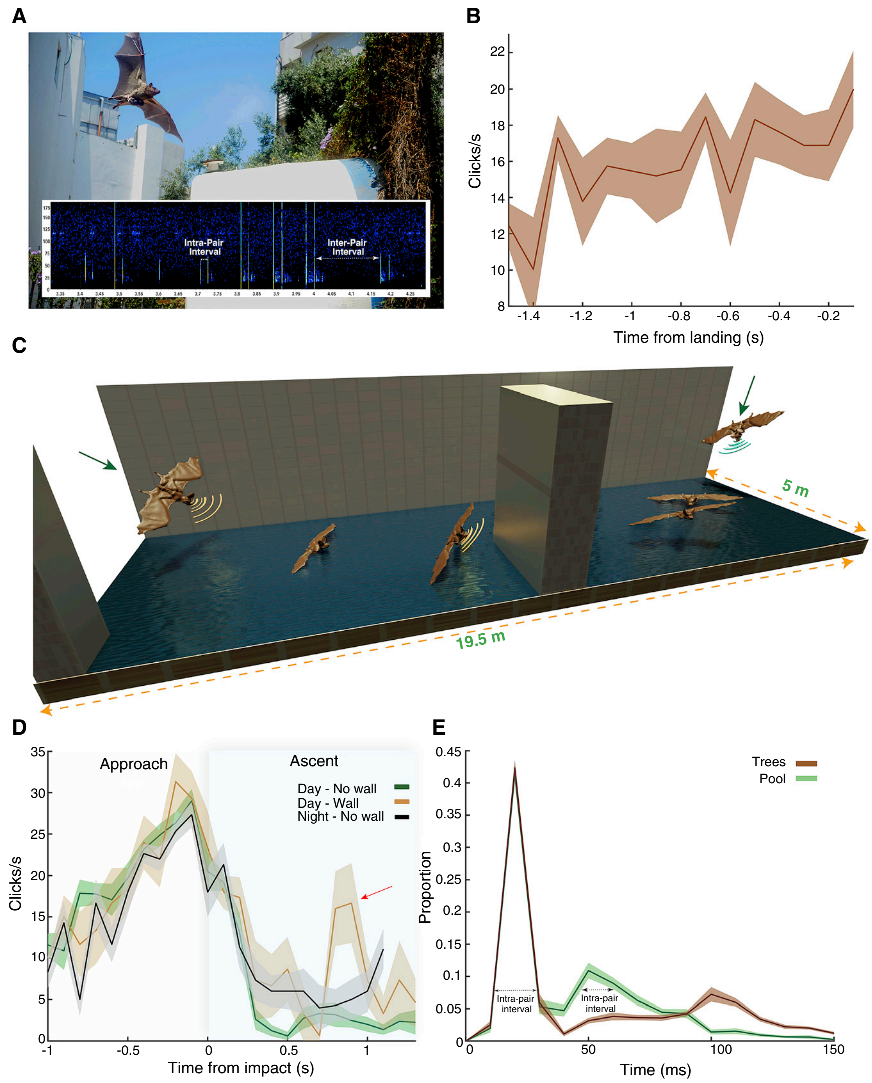

Figure 1. Functional echolocation use in diurnal fruit bats.
(A) Top trace: A female carrying a pup emerges from the colony during daytime (at 11:45 am). Bottom trace: The bat’s echolocation sequence is shown (as a spectrogram). Double headed arrows depict the intra- and inter-pair intervals. (B) The bats increased their click rate prior to landing on the tree; time ‘0’ depicts the landing time, n = 10 ± SE. (C) A schematic of the artificial pool where the bats were drinking during daytime. The pool was 19.5 x 5m^2 partially divided into two halves by a wall. The bats approached the pool from both sides. The right trace illustrates a typical drinking event; the bat echolocates with high click rate (in green) when it approaches the water but decreases the rate after ascending from the water. The left trace illustrates a flight path where the bat increases its click rate during the approach, decreases it after the water impact but increases its rate (in light brown) when it ascends in front of the wall. Arrows depict the flight direction of the bats. (D) Echolocation during drinking events in three conditions (day without a wall in green, n = 17 ± SE; night in black, n = 15 ± SE; and day with a wall, n = 5 ± SE, in light brown). The sequence is divided into two phases: approach and ascent, ‘0’ is the water impact. The red arrow depicts the bats’ echolocation rate in front of the wall. (E) The bats increased their click rate in the pool compared with the trees. A bimodal distribution of the clicks’ intra- and inter-pair intervals in the pool (in green, n = 22 ± SE); and foraging during the daytime (in brown, n = 21 ± SE). The average intra-pair interval is 20 ms for all conditions. The average inter-pair interval in the trees is ca 100 ms, doubled the average inter-pair interval in the pool, which is ca 50 ms.

landing on trees and descending to drink from the pool, and they reduced it when ascending from the pool, showing that echolocation is functional even in broad daylight.

We first recorded Egyptian fruit bats as they emerged from their colony in central Tel Aviv (Figure 1A and Video S1A). We recorded a total of 500 emerging bats, 72% of which (n = 360) used echolocation when outside. We recorded the bats during 70 days at different times of the day between 9:30 and 15:30. The proportion of bats using echolocation did not significantly depend on the time of the day (mixed effect Generalized Linear Model (GLM) , with a logit link function, with the proportion of echolocating bats per hour set as the explained variable and the time of day as fixed effect, P = 0.93, df = 498).

We next examined whether bats use echolocation while foraging, landing and flying near fruit trees. We recorded 21 different individuals (Supplemental information) as they flew between and occasionally landed on *Ficus* trees. All of the bats echolocated while flying near the trees, when landing on the branches, and when taking off (Video S1B). Bats even echolocated while they had large pieces of fruit in their mouths (Video S1C).

We next examined whether the diurnal fruit bats changed their click rate before landing, as regularly observed in free-moving laryngeal bats[9], and as demonstrated in the lab for fruit bats[8]. Fruit bats significantly increased their click rate from 12.4 ± 1.2 (mean ± SE from here on) clicks/s when flying in open air to 19.9 ± 2.1 clicks/s prior to landing on a branch (Figure 1B; GLM with click rate as the explained parameter, time from landing as fixed effect and individual bats as a random effect, $P < 0.05$, df = 339). To further test the functionality of diurnal fruit bat echolocation, we video- and audio-recorded the bats while they were approaching an artificial pool to drink (Figure 1C and Video S1D). All bats (n = 22) echolocated while approaching the water surface, increasing their click rate during the approach to a peak rate of 31.3 ± 3.4 clicks/s (Figure 1D). As far as we know, this is the fastest echolocation rate ever reported for Egyptian fruit bats. Conversely, when the bats ascended from the water, they decreased their echolocation rate to 0.6 ± 0.4 clicks/s (Figure 1D). In some cases, when the bats ascended in front of a large obstacle (a large wall, see schematic Figure 1C) they ceased clicking for 0.4 ± 0.1s but started again while approaching the wall.

In addition, to examine whether the diurnal echolocation rate during drinking differed from that in low light levels, we recorded the bats approaching the water at the same pool at night (~1 lux). There was no significant difference in bats' echolocation under day and night conditions. The diurnal condition (day/night) and the interaction between diurnal condition and time from/to touching the water did not affect the echolocation rate in both the approach and ascent phases (GLM with click rate set as the explained parameter, time from the water impact, condition — day /night — and the interaction between time and condition as fixed effects, and individual bats as a random effect; Supplemental information).

It has been previously shown that Egyptian fruit bats increase click rate by decreasing their click inter-pair intervals and not the intra-pair intervals. Here too, the average intra-pair interval was the same (~20 ms) in all conditions, but the average inter-pair interval was significantly lower when approaching and ascending from the water than when foraging (57.7 ± 3.4 vs. 98.5 ± 11 ms, respectively, P = 0.000006, Wilcoxon rank sum test; Figure 1E and Statistics in Supplemental information).

Integrating sensory information across different modalities can often be advantageous over relying on one sensory system. Integration of visual and echolocation information has been suggested to occur under dim light conditions in Egyptian fruit bats[8] and other bat species[5]. Here, we show functional use of echolocation even in broad daylight by a highly visual bat. We suggest that echolocation provides better distance estimation accuracy than vision and is thus advantageous when flying near obstacles such as trees or when descending to drink[8]. Supporting this suggestion, the maximal click rate we measured was not different when performing the same task (drinking) during day or night time, suggesting that complementary information is acquired by echolocation. Further supporting this suggestion, recordings from on-board audio tags of free-flying fruit bats collected for a previous study[8] revealed that when commuting high above the ground, where echo-reflecting objects are not in range, these bats hardly echolocate, showing that they can turn their echolocation off when it is not useful. Moreover, unlike laryngeal echolocators, lingual echolocators do not minimize the costs of echolocation by coupling sound emission to the wingbeat. Lingual echolocation has probably evolved independently in Egyptian fruit bats after the loss of laryngeal echolocation by their common ancestor. This study shows how echolocation could be useful in parallel to vision.

SUPPLEMENTAL INFORMATION

Supplemental information includes experimental procedures, one figure and one video and can be found with this article online at https://doi.org/10.1016/j.cub.2022.02.075.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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