

Correspondence

Bats regulate biosonar based on the availability of visual information

Sasha Danilovich^{1,*}, Anand Krishnan²,
Wu-Jung Lee², Ivailo Borrisov³,
Ofri Eitan³, Gabor Kosa⁴,
Cynthia F. Moss^{2,5}, and Yossi Yovel^{1,3,*}

The study of inter-sensory integration has focused largely on how different sensory modalities are weighted and combined in perception [1–3]. However, the extent to which information acquired through one sensory modality is modulated by another is yet unknown. We studied this problem in the Egyptian fruit bat (*Rousettus aegyptiacus*), an animal equipped with two modalities supporting high resolution distal sensing: biosonar and vision [4,5]. Egyptian fruit bats emit ultra-short, broad-band lingual echolocation clicks that enable accurate spatial orientation and landing [5]. They also rely heavily on vision, exhibiting high absolute sensitivity [4]. Here, we examine how visual information, regulated by altering ambient light level, influences biosonar sampling by Egyptian fruit bats. We tracked bats in the field and demonstrated that they routinely echolocate outdoors under a wide range of light levels. In the laboratory, under biologically relevant light levels, bats increased both echolocation click rate and intensity at lower light levels, where visual information was limited. These findings demonstrate how sensory information from one modality (vision) may influence sensory sampling of another (biosonar). Additionally, the bats adjusted biosonar sampling in a task-dependent manner, increasing click rate prior to landing. They did not cease echolocating under light conditions, which leads us to hypothesize that Egyptian fruit bats use echolocation to complement vision for accurate estimation of distance.

In order to quantify the light levels under which Egyptian fruit bats naturally forage, we tracked and recorded five wild fruit bats with on-board miniature GPS and microphone devices (Supplemental experimental procedures). Bats foraged under a wide range of light

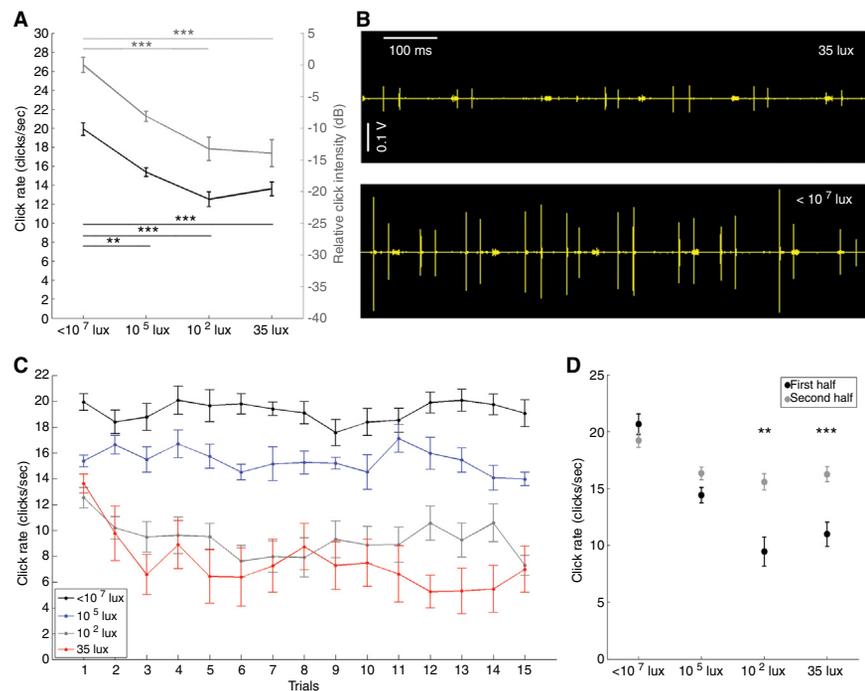


Figure 1. Bats regulate biosonar sampling based on the availability of vision.

(A) Naïve bats' click rate (left Y-axis, mean \pm s.e., black line) and click intensity (right Y-axis, mean \pm s.e., gray line). The averages were calculated across all individuals for each of the light levels (B) On-board audio recordings of echolocation in the laboratory under different light levels. X and Y scale bars are the same for both recordings. Note how both the rate and intensity of clicks increase in the dark. (C) Echolocation rate as a function of experience in 4 light levels (mean \pm s.e.). (D) Click rate at the first and the second half time of the flight (mean \pm s.e.) through the corridor. The symbols are defined as following: * $p < 0.05$, ** $p < 10^{-2}$, *** $p < 10^{-3}$. The number of bats participating in each condition is specified in the Supplemental experimental procedures. Data were collected at Tel-Aviv University and Johns Hopkins University. Also see Figures S1 and S2.

levels (10^{-3} –50 lux; Table S1). Importantly, all bats produced echolocation clicks outdoors, demonstrating that the Egyptian fruit bat relies on echolocation not only in dark caves, as previously speculated [4], but also during orientation and foraging in diverse light environments. As this range of natural outdoor light levels should allow use of vision in this species [6], we next examined if and how Egyptian fruit bats alter their sensory sampling through biosonar at different light levels.

In the laboratory, naïve Egyptian fruit bats flew through a flight corridor ($1.8 \times 3 \times 1.8 \text{ m}^3$) and landed on the far end under four different light levels (<math><10^{-7}</math>, 10^{-5} , 10^{-2} and 35 lux; Supplemental experimental procedures). These light levels span the range of light levels they experience when foraging in the wild (Table S1). We tested a minimum of nine bats in each condition. The lowest light level we tested (<math><10^{-7}</math> lux, or 'complete darkness') is equivalent to the light level

within the cave roosts of these bats and is below their visual detection threshold [6]. The highest tested light level (35 lux, or 'fully lit') is equivalent to the illumination at a typical foraging site in an urban environment. The bats increased echolocation sampling by more than 50% (from 13 ± 3 clicks per second in the fully lit condition to 20 ± 3 clicks per second in complete darkness, mean \pm s.e., Figure 1a; Kruskal-Wallis test: $H = 38.86$, $df = 3$, $p < 0.0001$). Post-hoc analysis of all possible comparisons revealed significant differences between the complete darkness condition and all other light levels ($p < 0.01$ for 10^{-5} , 10^{-2} and 35 lux). The bats did not stop echolocating even in the fully lit condition. Note that Egyptian fruit bats emit clicks in pairs [5] (Figure 1B). The increase in click rate with the decrease in light level results from a decrease in interval between click pairs, not the interval between clicks within a pair, which remains relatively stable (Figure S1).

The bats also significantly increased click intensity under low light level conditions, by up to 14 dB in complete darkness (Figure 1A,B; Figure S2; Kruskal-Wallis test: $H = 24.16$, $df = 3$, $p < 0.0001$). A *post-hoc* analysis of all comparisons revealed significant differences between the intensity of clicks produced in the complete darkness condition and the two highest light levels ($p < 0.001$ for 10^{-2} and 35 lux).

To test whether the novelty of the environment or of the captive situation influenced the findings above, we compared the bats' click rates when they flew in the same flight corridor over 15 consecutive trials under the same light condition. The echolocation rate decreased over successive trials at a light level of 35 lux, but this decrease was not statistically significant (Figure 1C; Friedman's test with a Bonferroni correction for the different light levels: $\chi^2 = 26.7$, $df = 14$, $p = 0.08$). Under the other light levels, bats showed no change in echolocation behavior over trials ($\chi^2 < 24.8$, $df = 14$, $p > 0.14$ for all light levels).

We also sought to assess whether Egyptian fruit bats adjust their echolocation rate according to the immediate task they were performing. While laryngeal echolocating bats have been shown to adjust echolocation sampling in a task-dependent manner (e.g. increasing call rate before landing) [7], adaptive echolocation sample rate has not previously been described in fruit bats of the Pteropodidae family. We compared the click rate during the first half of the flight time, after the bat took off, and the second half, when the bat was preparing for landing. The bats increased echolocation rate significantly when preparing to land under the two highest light level conditions (Figure 1D; Wilcoxon signed-rank test with a Bonferroni correction for the different light levels: $z > 3.43$, $p < 0.01$ for both light levels). However, there was no change in click rate under the two lowest light conditions ($z < 2.1$, $p > 0.14$ for both light levels), presumably because the bats were operating at their maximal physiological click rate (ca. 20 Hz), potentially constrained by the tongue muscles. This is in contrast to laryngeal echolocating bats whose call repetition rate can reach up to 200 Hz [7]. These findings suggest that information acquired by echolocation (e.g., range) is important for landing, even when vision is available.

Our results demonstrate that Egyptian fruit bats adjust biosonar sampling based on the availability of visual information and according to the task they are performing. Previous research on multisensory integration has focused on perception, showing that information gathered with one sensory modality can influence the perception through another [3], and that sensory information from different modalities is weighted to achieve an estimate with maximum reliability [1,2]. However, to the best of our knowledge, no study has investigated the influence of multisensory information on sensory acquisition.

Importantly, in our lab experiments, bats never ceased echolocating completely, even when ambient light provided adequate visual information to orient, suggesting that the bats benefit from the multisensory input through vision and echolocation. The bats increased biosonar click rate in the dark by more than 50% relative to the fully lit condition (Figure 1A). They also increased the click rate by up to 65% when they prepared to land in the light conditions relative to take off (Figure 1D). In both situations, additional echo information is beneficial, either because vision is limited, or because landing requires more frequent sensory updates and accurate distance information to guide fine maneuvering [7]. We hypothesize that Egyptian fruit bats consistently use echolocation to estimate the range of nearby objects, even when light levels are high, such as when landing on a tree in a lit urban environment. While vision allows accurate angular localization and is superior to biosonar in long distance navigation and orientation [8], echolocation enables accurate range estimation of nearby objects (up to ca. 20 m) [9] with finer resolution than vision. For example, laryngeal echolocating bats have been shown to measure target range with an accuracy of about 1 cm (and even < 1 mm in some tasks) [8]. Range estimation by vision is far poorer. Even humans, highly visual animals with acuity that far exceeds that of bats, make range estimation errors that are at least an order of magnitude larger (i.e., 24 cm at 0.8 m) than bat sonar ranging [10].

In summary, Egyptian fruit bats regulate their use of biosonar based on available visual information and task demands. When flying near objects, they rely on both vision and biosonar for complementary sensory information. These bats therefore

are an excellent model for further research on sensory sampling and multisensory integration.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, two figures and one table can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.11.003>.

ACKNOWLEDGMENTS

This work was supported by the Human Frontier Science Program (HFSP grant no. RGP0040/2013) the National Science Foundation, NSF (IOS-1010193), the Air Force Office of Sponsored Research (FA9550-14-1-0398) and the Office of Naval Research (N00014-12-1-0339). In addition, we would like to thank L. Harten, A. Goldshtein, M. Warnecke, N. Yanagisawa, A. Vadaparty, S. Sharda and W. Xian for their help.

REFERENCES

- Burr, D., and Alais, D. (2006). Combining visual and auditory information. *Prog. Brain Res.* 155, 243–258.
- Raposo, D., Sheppard, J.P., Schrater, P.R., and Churchland, A.K. (2012). Multisensory decision-making in rats and humans. *J. Neurosci.* 32, 3726–3735.
- Shams, L., Kamitani, Y., and Shimojo, S. (2000). What you see is what you hear. *Nature* 408, 788.
- Neuweiler, G. (2000). *The biology of bats* (Oxford University Press, NY).
- Yovel, Y., Falk, B., Moss, C.F., and Ulanovsky, N. (2010). Optimal localization by pointing off axis. *Science* 327, 701–704.
- Boonman, A., Bumrungsri, S., and Yovel, Y. (2014). Nonecholocating fruit bats produce biosonar clicks with their wings. *Curr. Biol.* 24, 2962–2967.
- Tian, B., and Schnitzler, H.U. (1997). Echolocation signals of the Greater Horseshoe bat (*Rhinolophus ferrumequinum*) in transfer flight and during landing. *J. Acoust. Soc. Am.* 101, 2347–2364.
- Geva-Sagiv, M., Las, L., Yovel, Y., and Ulanovsky, N. (2015). Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nat. Rev. Neurosci.* 16, 94–108.
- Boonman, A., Bar-On, Y., Cvikel, N., and Yovel, Y. (2013). It's not black or white on the range of vision and echolocation in echolocating bats. *Front. Physiol.* 4, 248.
- Viguier, A., Clément, G., and Trotter, Y. (2001). Distance perception within near visual space. *Perception* 30, 115–124.

¹Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 6997801, Israel. ²Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD 21218, USA. ³Department of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel. ⁴School of Mechanical Engineering, Faculty of Engineering, Tel Aviv University, Tel Aviv 6997801, Israel. ⁵Department of Neuroscience, Johns Hopkins University, Baltimore, MD 21218, USA.
*E-mail: danielovi@mail.tau.ac.il (S.D.); yossiyovel@hotmail.com (Y.Y.)