SENSORY TRAPS

Acoustic mirrors as sensory traps for bats

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Sensory traps pose a considerable and often fatal risk for animals, leading them to misinterpret their environment. Bats predominantly rely on their echolocation system to forage, orientate, and navigate. We found that bats can mistake smooth, vertical surfaces as clear flight paths, repeatedly colliding with them, likely as a result of their acoustic mirror properties. The probability of collision is influenced by the number of echolocation calls and by the amount of time spent in front of the surface. The echolocation call analysis corroborates that bats perceive smooth, vertical surfaces as open flyways. Reporting on occurrences with different species in the wild, we argue that it is necessary to more closely monitor potentially dangerous locations with acoustic mirror properties (such as glass fronts) to assess the true frequency of fatalities around these sensory traps.

Anthropogenic changes to the environment, such as habitat alteration or interference with food resources, are often evidently detrimental to wild animals. Furthermore, ecologically novel cues are capable of misleading animals into responding maladaptively to formerly reliable environmental cues (*1*–*4*). Well-known examples are artificial light sources attracting insects and birds at night (*5*) or smooth human-made surfaces that aquatic insects mistake for bodies of water because of similar light polarization patterns (*6*). To find, evaluate, and mitigate such sensory traps requires consideration of the sensory ecology of a particular animal (*7*, *8*). The primary sensory modality for most bats is their echolocation system (*9*, *10*). Bats use the returning echoes of emitted calls to detect, classify, and localize objects in their environment (*11*–*13*).

In a previous study, we showed that bats perceive any extended, smooth, horizontal surface as a water body, resulting in drinking attempts. This is attributable to the acoustic mirror properties of smooth surfaces, which reflect calls away from the bat except for a strong perpendicular echo from below (*9*) (Fig. 1A). Several observations of bats colliding with smooth vertical surfaces (such as glass windows) suggest that bats have problems recognizing them (*14*–*16*). This raises concerns about the millions of artificial vertical smooth surfaces introduced in bat habitats and their hazard potential for injuries. We predicted that these collisions are based on the acoustic mirror paradigm and investigated the underlying sensory mechanism and possible occurrence in natural settings.

For our flight room experiments, we flew greater mouse-eared bats (*Myotis myotis*) in a continuous, rectangular flight tunnel (height 2.3 m, width 1.2 m) in the dark. A smooth metal plate (1.2 m × 2.0 m) was placed 1.2 m away from a corner of the felt-covered tunnel, either horizontally on the ground or vertically on the wall. The bats' flight behavior was recorded with two high-speed cameras (100 fps) and their echolocation calls with an ultrasound microphone (Fig. 1B) (*17*). Eleven bats were presented with the horizontal plate on the first night and the vertical plate on the second night. The order was reversed for 10 other bats. A trial lasted between 5 and 15 min with, on average, 20 passes by the plate. We counted drinking attempts as well as collisions with the plate, the ground, and the normal wall. Of 21 individuals, 19 collided with the vertical plate at least once (on average 22.8% of passes) but never with the horizontal plate (Wilcoxon matched-pair test, $P < 0.001$) nor any other parts of the wall. Thirteen individuals made at least one drinking attempt from the horizontal plate (on average 13.0% of passes), but none from the vertical plate (Wilcoxon matched-pair test, $P = 0.002$) (Fig. 2). After the experiments, all bats were carefully examined and no injuries were found.

To understand the sensory basis of those collisions with the vertical plate, we conducted analysis of the flight and echolocation behavior in the space immediately in front of the plate ("plate zone," limited by the plate's perpendicular projection; Fig. 1B) for 25 bats when flying toward the vertical plate. On the basis of our high-speed recordings, we categorized the approach events into three groups: (i) "near collision," where bats approached to within 25 cm of the plate (body-to-plate distance) but did not touch it; (ii) "collision with maneuver," where bats collided with the plate despite clear evasive maneuvers at the last moment; and (iii) "collision without maneuver," where bats collided without any noticeable evasive action. We measured the time and counted echolocation calls from entering the plate zone until reaching the closest point to the plate (either collision or turning point). We further calculated the bat's flight speed, the three-dimensional angle between its flight trajectory and the plate, and its distance to the plate when it entered the plate zone. The 78 events of approaching the plate (3.1 ± 1.8 events per individual, mean ± SD) consisted of 25 "near collision" events, 13 "collision with maneuver" events, and 40 "collision without maneuver" events (movie S1). We found that for "collision without maneuver" approaches, bats produced fewer calls, spent less time in front

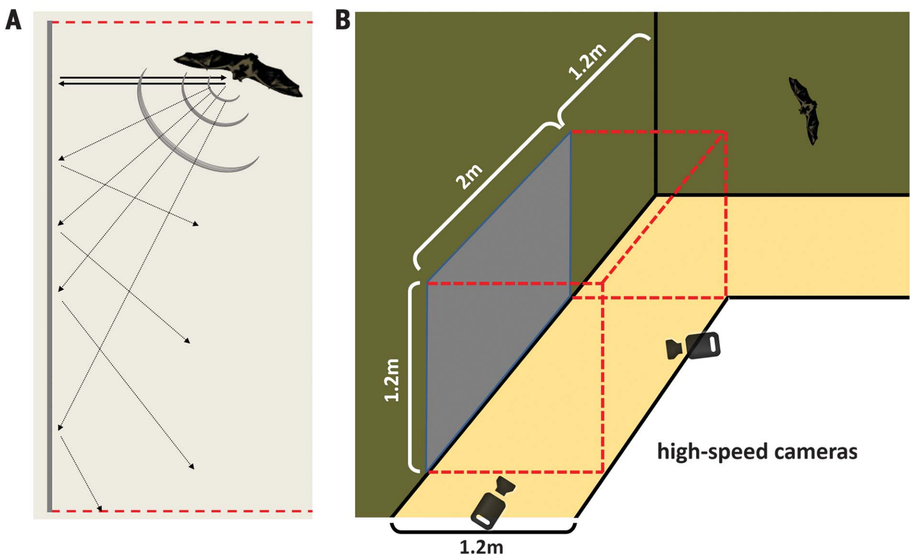

Fig. 1. Experimental setup. (**A**) Schematic of sound propagation at a smooth, vertical surface (top view). For a bat within the red-dashed "plate zone," sound impinging at an oblique angle is reflected away while only the perpendicularly impinging sound is reflected back. (**B**) Flight tunnel setup depicting the vertical situation. The smooth metal plate is shown in gray on the wall; the dashed lines represent the plate zone. In the horizontal situation, the smooth plate was lying on the floor of the plate zone (fig. S1).

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of the plate, approached the plate at a more acute angle, entered the plate zone closer to the plate, and had higher flight speeds relative to the "near collision" situation (Fig. 3 and table S1). Values of the "collision with maneuver" approaches ranged between those of the other two categories and were generally closer to those of "collision without maneuver."

Bats adapt their echolocation system to varying situations, thus revealing their perception of the environment. We compared the echolocation calls of colliding bats (32 sequences of 19 individuals) with a control situation of flying past a normal wall (15 sequences of 10 individuals) (*17*). We found that during approach to the plate, the bats emitted significantly shorter calls, decreased their pulse interval, and lowered their end frequency (Fig. 4 and table S2).

To investigate our findings' generality, we studied the effect of smooth, vertical surfaces on the flight behavior of different bat species in the field, conducting experiments near three bat colonies for one night each (*17*). After all individuals had left the colony, we placed one or two smooth, black, flexible plastic plates (2 m × 1 m, or 2 m × 2 m combined) vertically 1 to 3 m from the colony entrance (either perpendicular or parallel to the roost, but never in the actual flight path). We observed returning bats for 4 hours with an infrared camera while presenting the plate uncovered (i.e., smooth) or covered with a rough, ribbed plastic mat or branches (alternated in 15-min intervals). We counted 12, 1, and 10 collisions, respectively, at the three colonies when presenting the smooth plate, but none with the covered plate (movie S2).

Our results demonstrate that bats repeatedly collide with smooth, vertical surfaces both in the laboratory and in natural habitats. This is likely attributable to the acoustic mirror properties of smooth surfaces, where echolocation calls are being reflected away from the bat and no echoes return from the position of the plate while the bat is still outside the plate zone (*9*). Rough surfaces, on the other hand, produce clear echoes, which is why bats collided only with the smooth surface.

However, bats can exhibit a behavioral avoidance reaction when on a collision course. This can be explained by the second acoustic characteristic of a smooth surface: As soon as a bat enters the plate zone, any part of the calls reaching the plate perpendicularly will be reflected back to the bat more strongly than before (Fig. 1A and movie S3), whereas the perpendicular echo should disappear if there were a real open space. Our interpretation is further supported by an increased collision avoidance when bats approached the vertical plate at greater angles. The approach angle influences the echo strength: At smaller, more acute angles, the perpendicular echo strength is likely decreased as a result of the directionality of the bat's echolocation beam. Here, most of the call energy is aimed to the front of the bat and rapidly drops toward the side (*18*, *19*). But most important, the behavioral analyses showed that bats were more likely to avoid collisions when emitting higher numbers of calls. This complies with a bat's strategy to increase call rate when in need of more information (*12*, *13*). Also, slower flight speed and a greater entrance distance to the plate increased time in the plate zone and thus the chance to detect and avoid the plate.

The bats' echolocation behavior suggests that they did not approach the vertical smooth surface to land on or catch an object (*12*, *20*). In that

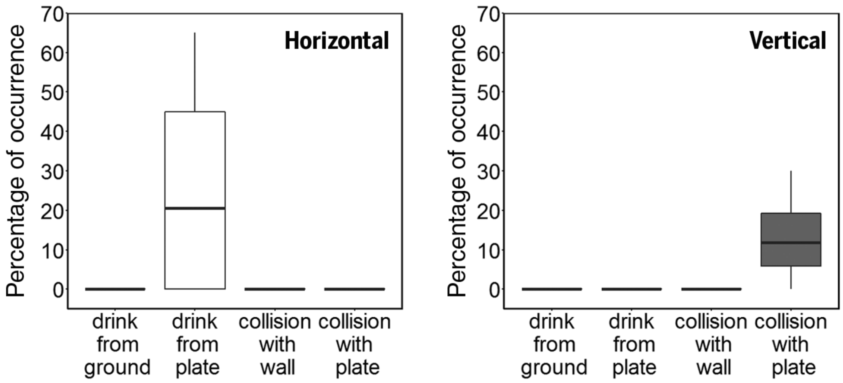

Fig. 2. Percentage of drinking attempts and collision events. Values were calculated per individual relative to its total number of passes in the horizontal versus vertical setup (median, interquartiles, and range; N = 21 bats).

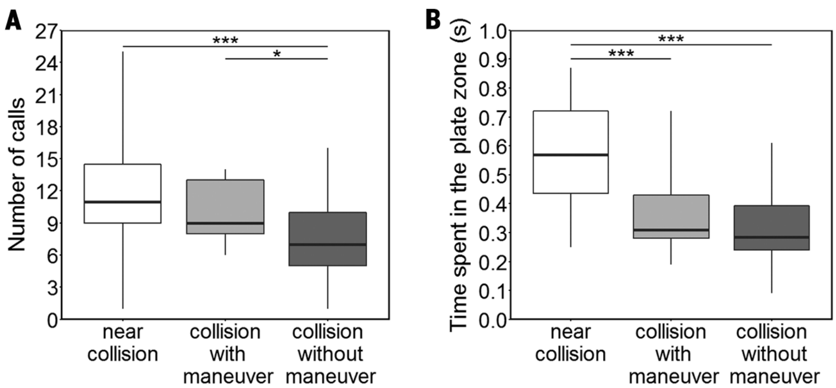

Fig. 3. Number of calls and time spent in the plate zone for the three approach categories. (**A**) Number of calls; (**B**) time spent in plate zone. Events are categorized as "near collision" (white, N = 25), "collision with maneuver" (light gray, N = 13), and "collision without maneuver" (dark gray, N = 40) (median, interquartiles, and range; N = number of events). *P < 0.05, ***P < 0.001.

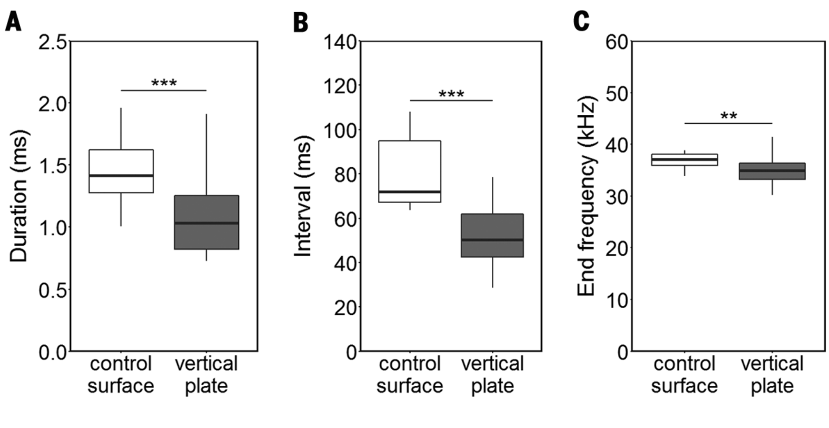

Fig. 4. Echolocation call parameters when approaching the vertical plate and a control surface. (**A** to **C**) Comparison for call duration (A), pulse interval (B), and call end frequency (C) (median, interquartiles, and range). **P < 0.01, ***P < 0.001.

case, they would decrease their pulse interval and lower their end frequency even more than we saw in our bats (see table S2). Because the plate does not reflect any echoes toward the bat until the bat is next to it, we suggest that they considered it to be an opening in the wall and intended to escape the room through this apparent, constrained flyway (*21*, *22*).

In the horizontal setup, bats never collided with but carefully approached the surface to drink. Thus, they demonstrate an orientation-dependent interpretation of their ensonified environment as the direction of the same cue (the lack of echo from an area ahead) elicits a different behavior. The change in amplitude of the perpendicular echo from a rough to a smooth surface might further give bats an orientational cue (movie S3). If the perpendicular echo is perceived from below in combination with otherwise missing echoes, bats interpret this as a water surface and can use it as a height estimator (*9*, *23*). Coming from the side, it warns them of an approaching obstacle in what they have until now construed as a clear flight path, if they have had enough time to process it. Bats have been found to fly against smooth surfaces in the lab and the field (*14*–*16*), but these observations were interpreted with a focus on visual influence and failed to explain the underlying sensory mechanism [however, see (*16*), pp. 51–52]. Furthermore, bats have been found dead and injured next to human-made structures such as the glass facades of a convention center or towers (*17*, *24*–*26*).

We now understand that smooth, vertical surfaces demonstrate a possible acoustic sensory trap for bats. Although none of our bats was hurt, an often higher flight speed in natural settings might lead to serious injuries such as concussions, broken wings, or broken jaws. Injured bats are often only accounted for as a by-product of investigations on avian mortality and furthermore might crawl away or fall prey to predators (*27*), thus concealing and underestimating the actual numbers of fatalities. For a better understanding of the actual impact on bats, increased monitoring and systematic recording of collisions at vertical mirror situations (such as big glass surfaces) are required. Moreover, smooth, vertical surfaces should be avoided at crucial sites such as "migratory highways," key foraging habitats, or bat colonies. And finally, mitigation efforts such as ultrasonic bat deterrents could be tested around selected human structures. Only if we identify and evaluate the real extent of collisions with acoustic mirrors can we avoid or mitigate potential detrimental effects on bat populations.

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SUPPLEMENTARY MATERIALS

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Building-blind bats

Human-generated structures now dominate much of the planet, but they have existed for but a blink of an eye from an evolutionary perspective. Animal sensory systems evolved to navigate natural environments and so may not always be reliable in anthropogenic ones. Greif *et al.* show that echolocating bats appear to perceive smooth vertical surfaces as open areas, a mistake that often leads to collisions (see the Perspective by Stilz). With millions upon millions of smooth vertical surfaces in our world today, such misperceptions could have considerable negative impacts on bat survival.

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