



Echolocating bats detect but misperceive a multidimensional incongruent acoustic stimulus

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Coherent perception relies on integrating multiple dimensions of a sensory modality, for example, color and shape in vision. We reveal how different acoustic dimensions, specifically echo intensity and sonar aperture (or width), are important for correct perception by echolocating bats. We flew bats down a corridor blocked by objects with different intensity–aperture combinations. To our surprise, bats crashed straight into large (aperture) walls with weak echo intensity as if they did not exist. The echolocation behavior of the bats indicated that they did detect the wall, suggesting that crashing was not a result of limited sensory sensitivity, but of a perceptual deficit. We systematically manipulated intensity and aperture by changing the materials and width of different reflectors, and we conclude that a coherent echo-based percept is created only when these two acoustic dimensions have certain relations which are typical for objects in nature (e.g., large and intense or small and weak reflectors). Nevertheless, we show that these preferred relations are not innate. We show that young pups are not constrained to these relations and that new intensity–aperture associations can also be learned by adult bats.

perception | sensory integration | bats | echolocation

Is an apple red more than round or round more than red? We usually perceive a red sphere-like object roughly the size of our fist as an apple, but when this same object is observed from a distance (without proper reference), it might seem to be a cherry, and when it is colored black, it might be perceived as a plum (Fig. 1A). Size, color, and shape are all dimensions, or features, of the visual modality. Objects typically carry sensory information in different dimensions within the same sensory modality. The brain combines these different dimensions to create a coherent percept, but there is limited knowledge on how it does so. While many have studied how information acquired from different sensory modalities complement each other (1–5), there is much less understanding of how different dimensions of the same sensory modality are integrated and weighed (6). Studies on multidimensional visual-based perception found that face perception is dependent on the accurate combination of a few critical facial features (7). Furthermore, some face-selective cells in the brain of macaque monkeys were found to respond best to a correct combination of face geometry and contrast: a match between the values of different dimensions elicited a stronger neural response (8). In the auditory domain, in humans, recognition of music stored in long-term memory was better when both melody and rhythm were available compared to when each dimension was available alone (9).

In this project, we studied intrasensory multidimensional perception in the auditory domain. Echolocating bats are masters of acoustic perception. Through echolocation, they can compute an object's 3D location and also generate some perception of its shape, texture, and size (10–14). To do this, bats extract different acoustic dimensions (e.g., spectrum and intensity) from the echoes reflected back from the object.

This study resulted from a surprising preliminary observation: we found that naïve echolocating bats crash straight into a large foam wall as if it was not there, even though they should have no

difficulty to detect it; we have trained dozens of bats in rooms covered with foam walls and never observed such collisions. We hypothesized that the bats crashed into the wall because of its incoherent acoustic characteristics, namely, it reflected echoes from a wide aperture, but the overall echo was very weak. We hypothesized that we were witnessing a perception error and we thus set to examine how bats integrate different acoustic dimensions to create coherent perception. Whenever possible, we tested naïve bats to avoid usage of spatial memory over sensory information (15).

When flying toward an object, four main acoustic dimensions play a role in shaping echo-based perception: the echo's spectrum, intensity, temporal structure, and sonar aperture. The aperture is the spread of angles of incidence from which echoes are reflected. It can be assessed using binaural hearing or monaural hearing according to the temporal spread of the echoes. Perception of an object might be ambiguous because these dimensions cannot be translated into physical dimensions in a one-to-one manner. Spectrum is mostly influenced by texture (12, 16), but it also reflects size and shape and varies with point of view (17–19); temporal cues convey texture and depth (20, 21); intensity reflects size (22), but also material (23), and might also convey information on texture (10); while sonar aperture is mostly determined by size (24–26).

To study how bats weigh different acoustic dimensions, we designed an experiment that allowed us to independently vary the sonar aperture and intensity of an object while controlling for its spectrum and temporal cues. We flew bats down a corridor blocked midway with different objects and tested their behavior,

Significance

How do we build a perception from incoming sensory information? To accurately perceive the environment, the brain has to integrate information across different sensory modalities and to analyze multiple sensory dimensions within a sensory modality. We studied this integration in echolocating bats, the masters of active acoustic sensing. By presenting them with targets whose acoustic dimensions were incoherent, we managed to induce misperception, which caused the bats to repeatedly try to fly through a wall even though they detected it with their echolocation. We demonstrate that certain relations between the dimensions must hold to allow accurate perception. Nevertheless, adult bats can learn new relations rapidly. Notably, no misperception was observed in pups, confirming that these relations are not innate.

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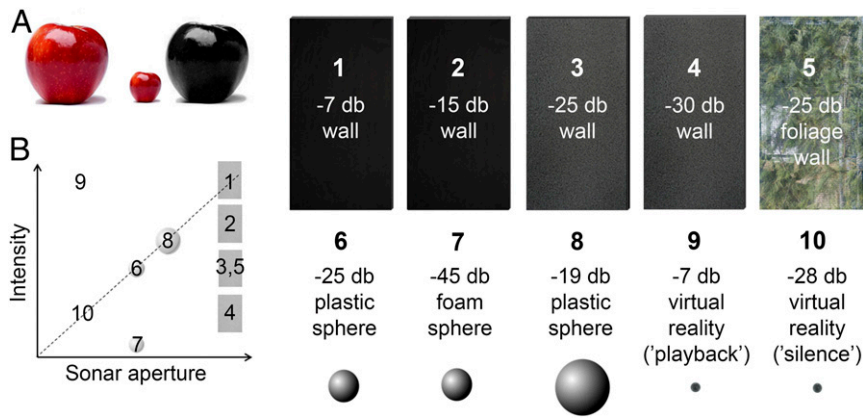


Fig. 1. Multidimensional perception of echolocation. (A) In the visual system, size and color should match for correct perception. The left red apple illustrates the correct relations of these dimensions. On the right, one of the dimensions is altered, and the apple might be perceived as a cherry (when size is altered) or a plum (when color is altered). (B) The schematic illustrates the possible relations between the two acoustic dimensions, sonar aperture and intensity, and the targets used in this experiment. The dashed line depicts the relation between these two dimensions for most natural objects. Targets 1 to 4 were used in the reflective walls experiment. Target 5 was used in the foliage experiment. Targets 6 to 8 were used in the spheres experiment. Targets 9 and 10 were used in the virtual reality experiment.

i.e., whether they turned back, tried to land, or tried to fly through. We examined objects with several aperture–intensity combinations (Fig. 1B). Natural targets typically exhibit a positive correlation between intensity and sonar aperture. Thus, we predicted that the bats would correctly perceive targets with this correlation, like targets 1, 6, 8, and 10 in our study (Fig. 1B). In contrast, we hypothesized that bats might misperceive objects whose acoustic dimensions relate in an untypical manner (e.g., large aperture with low intensity) like targets 3 and 4 in our study (Fig. 1B).

We tested *Pipistrellus kuhlii* bats (Kuhl’s pipistrelles), which are prime echolocators and generalist foragers (27–29). They employ frequency-modulated (FM) laryngeal echolocation calls and are considered to rely almost exclusively on echolocation: their eyes are tiny and provide poor acuity [as was found for a closely related species (30)]. We also tested a bat species with different echolocation signals and prime vision. *Rousettus aegyptiacus* (Egyptian fruit bats) uses ultrashort and broad-banded lingual echolocation clicks (31, 32), but, unlike Kuhl’s pipistrelles, Egyptian fruit bats have big eyes with good visual acuity and good sensitivity (33–35). Although we abolished vision in the experiments by flying the bats in complete darkness, we hypothesized that the different reliance on echolocation in the everyday life of these two species and their different echolocation design might affect their object perception via echolocation.

We found that a match between the intensity and aperture of an object is essential for coherent perception. Altering the natural relations of these dimensions caused misperception that resulted in collision with a target even though the bats detected it. Nevertheless, learning of the new relations between these dimensions was rapid. We also found that the integration weights of aperture and intensity are likely species-specific.

Results

Sonar Aperture Is Not Sufficient for Perception. First, we tested the role of echo intensity in perception by keeping the aperture constant and varying reflectivity (“reflective walls” experiment). An object’s reflectivity defines how much of the energy impinging on an object is reflected back, so controlling reflectivity allows manipulating echo intensity [reflectivity values along the paper are always reported as the target strength (36) at a distance of 1 m; *Materials and Methods*]. We flew 130 naïve Kuhl’s pipistrelles down a 3-m-long, 0.9-m-wide, and 1.9-m-high corridor made of tarpaulin that was blocked midway with a wall made

of materials with different acoustic reflectivity (the same corridor was used in all experiments below except for the “virtual reality” experiment and one of the conditions in the “spheres” experiment; *SI Appendix, Fig. S1*). The wall covered the entire cross-section of the corridor, and its target strength varied between –7 dB (plastic wall; target 1 in Fig. 1B) to –30 dB (foam wall; target 4 in Fig. 1B). Hence, the loudest wall (–7 dB) had positively correlated intensity and aperture (it was large and highly reflective), in accordance with most natural objects, while the –30-dB wall had negatively correlated physical dimensions (large aperture and weak intensity), thus representing an object rarely encountered in nature. Naïve bats flew one-by-one down the corridor in complete darkness to abolish vision. Each bat flew down the corridor one time without any accommodation to it. At least 27 naïve individuals were flown in each reflectivity condition (Table 1). Bats readily detected the high-reflectivity walls and either tried to land or turned around before reaching them, flying back to the release point. In contrast, and to our surprise, the great majority of the bats collided with large quiet (low-reflectivity) walls as if they did not exist. This difference was highly significant, with all bats (100%) colliding with the –30-dB foam wall, while only 6% of them collided with the –7-dB plastic wall ($\chi^2 = 72.03$, $df = 3$, $P < 10^{-5}$; χ^2 test for independence; Fig. 2A).

Table 1. Number of bats that participated in each experiment

Species/experiment	–30 dB	–25 dB	–15 dB	–7 dB
<i>Pipistrellus kuhlii</i>				
Reflective walls	30	40	27	33
Learning	—	12*	—	—
Foliage			23	
Spheres	25 (8 in –25 dB, 9 in –19 dB, 8 in –45 dB)			
Virtual reality		18 (corridor) + 6* (landing)		
<i>Rousettus aegyptiacus</i>				
Reflective walls	34	32	31	33
Pups	—	—	—	37

All groups were of mixed sex. 10 Kuhl’s pipistrelles and 13 Egyptian fruit bats (additional to the numbers in the table) were omitted from the study due to video malfunction or because no echolocation was recorded (see *Video and Audio Analysis* in *Materials and Methods*).

*Bats marked with an asterisk were drawn from the bats in the ‘Reflective Walls’ experiment. All other bats participated in one experiment only.

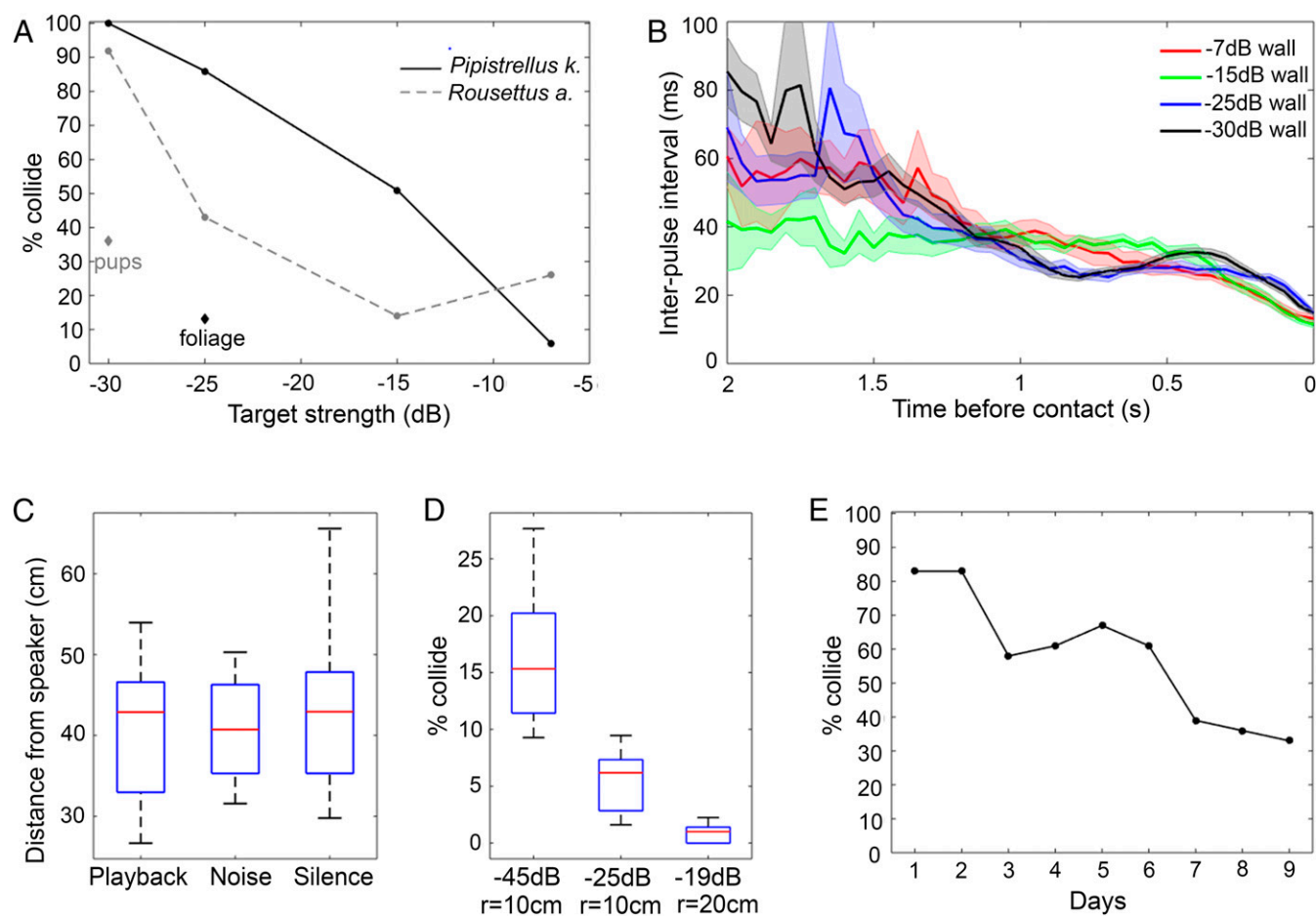


Fig. 2. The role of aperture and intensity in echolocation perception. (A) Collision rates for naïve Kuhl's pipistrelles flying toward a wall with different reflectivity (reflective walls experiment, depicted by black line). Each point depicts the percent of naïve bats that collided in one specific condition (hence, there are no SD bars). Black diamond depicts performance of Kuhl's pipistrelles that were tested with a foliage wall (-25 dB). Data of Egyptian fruit bats are shown in gray. Gray diamond depicts Egyptian fruit bats pups tested with foam wall (-30 dB). (B) Interpulse intervals (IPIs) under different reflectivity conditions in reflective walls experiment. Time 0 is the moment of contact with the wall (landing or crashing). (C) The distance at which bats passed a virtual reality speaker placed in the corridor when it played back the amplified bats' own echolocation calls ("playback"), a constant synthesized sound ("noise"), or nothing ("silence"; virtual reality experiment). The distance was averaged per bat over repeating trials. The box plot depicts the median distance of all bats. (D) Collision rate with two 10-cm-radius spheres with different reflectivity and one 20-cm-radius sphere (spheres experiment). Collision rate was calculated per bat over repeating trials. The box plot depicts the median proportion of collisions of all bats. (E) Collision rate of a group of bats tested with a -25 -dB large wall over consecutive days (learning experiment). All results presented in panels B–E are for *Pipistrellus kuhlii*.

The bats did not attempt to maneuver around the large quiet walls; they continued flying into the wall in a straight trajectory. Importantly, many of the bats collided with the wall repeatedly within seconds; they collided once and then seemingly tried to go through the wall again and again (as many as five times), suggesting that collision was driven by a perception deficit (Movie S1). Of the bats that avoided collision with the -7 -dB wall, 48% attempted to land on the wall and the rest turned back and flew in the opposite direction. The bats showed a gradual increase in collision rate with the decrease in reflectivity ($P < 0.04$ for all pairwise comparisons, Fisher's exact test with an FDR correction; Fig. 2A).

To exclude the possibility that bats collided with weakly reflecting walls because they perceived them as a sparse diffusive reflector (such as a foliage hedge) they could fly through, we flew 23 naïve Kuhl's pipistrelles with a "wall" made of foliage that had the same target strength as the weak wall, blocking the same corridor (target strength was -25 dB; "foliage" experiment; Materials and Methods; target 5 in Fig. 1B and SI Appendix, Fig. S2). Only 13% of the bats collided with the foliage wall compared to 86% of the bats that collided with the -25 -dB foam wall

($\chi^2 = 31.19$, $df = 1$, $P < 10^{-4}$, χ^2 test for independence; Fig. 2A). The remaining 87% of the bats landed on the leaves or turned back when closing in on the foliage, clearly demonstrating that they did not perceive the foliage and the foam wall in the same way. Differences in echo spectra could not explain the different collision rates between the different walls or between the walls and the foliage wall (SI Appendix, Fig. S3). We hypothesize that the -25 -dB foliage wall was perceived differently from the -25 dB wall due to its temporal structure (Discussion).

Could it be that the bats did not detect the weakly reflecting walls? This is highly unlikely when taking into account that Kuhl's pipistrelles are known to forage on midges whose reflectivity is far lower than any of the walls (-60 dB target strength at 1 m) (36). Moreover, the echolocation of the bats revealed that they clearly detected even the weakest reflecting wall. Echolocating bats increase their emission rate in a stereotypical manner when approaching an object (27, 28, 37). Indeed, when flying down the corridor, the bats increased their pulse repetition rate in all conditions (Fig. 2B). The interpulse intervals (IPIs) started decreasing at the same location relative to the wall and reached the same intervals just before contact,

regardless of wall reflectivity. Therefore, collisions with the low-reflectivity walls were not due to a sensory difficulty in detecting the targets, and probably resulted from a perceptual deficit. The fact that 70% of bats repeatedly collided with the -30 -dB wall sequentially (within 1 to 2 s) strengthens this conclusion.

Echo Intensity Alone Cannot Increase the Perceived Size of an Object.

We showed that a large object can be misperceived if its echo intensity is too weak, but can intensity also work in the opposite direction, i.e., making an object seem larger because it is louder? To test this, we examined how bats perceive an object with intensity as high as a wall but with a small sonar aperture. This test could not be achieved with a physical object because small targets will never be as loud as a reflective wall (or even close to it). We thus flew Kuhl's pipistrelles down a corridor with a virtual-reality playback system that recorded the bats' echolocation signals and played back controllable echoes in real time (with a $1\text{-}\mu\text{s}$ delay; "virtual reality" experiment; *SI Appendix, Fig. S1*). A 6.5-cm -diameter speaker was positioned in the center of the corridor, facing the release point, playing one of three treatments: 1) "playback," where the bats' own calls were recorded and amplified and played back, mimicking an object with a small sonar aperture (6.5-cm diameter) but reflecting very loud echoes, as would be reflected from a large wall (-7 dB reflectivity; target 9 in Fig. 1*B* and *SI Appendix, Fig. S4*); 2) "noise," where a synthesized signal was played back to the bats in response to their calls. The synthesized signal was a time-reversed Kuhl's pipistrelle-like signal, and it had a fixed intensity (99 dB SPL at 1 m, similar to the intensity of the -7 -dB wall at 1 m), independent of the signal emitted by the bat. We chose an unnatural signal because this condition aimed to validate that the bats were not just responding to any sound produced by the system. In the third treatment 3), "silence," nothing was played back to the bat (i.e., the bat only received echoes from the setup itself; target 10 in Fig. 1*B*). The same 18 bats were flown in all conditions in a randomized order (*Materials and Methods*).

Since the target (i.e., the speaker) was very small, we could no longer measure the collision rate to test whether bats perceive it or not (no bats collided with it). Instead, we tested how the bats perceived its size. To this end, we measured the distance of the bats from the speaker at the moment they passed it when flying down the corridor (we averaged the distance of 10 flights per bat). The bats' radial distance from the speaker was, on average, 40 to 43 cm, and there was no difference between the three treatments ($\chi^2 = 0.11$, $df = 2$, $P = 0.9$, Friedman test; width and length of the corridor in this experiment were changed to 1.5 m and 4 m, respectively; Fig. 2*C*). This suggests that the bats did not perceive the speaker as larger than it actually was even when it was emitting sound mimicking echoes as loud as the echoes of a large wall. Similar to the reflective walls experiment, if the bats perceived the speaker as larger than it was because of its intensity, more bats were expected to turn around and not fly down the corridor in the playback compared to the silence condition. However, there was no difference in the proportion of bats that passed the speaker in the three treatments (50% , 44% , and 56% of the bats passed the speaker in the first trial in the playback, noise, and silence treatments, respectively; $\chi^2 = 0.66$, $df = 2$, $P = 0.71$, Cochran's Q test). Our results thus suggest that echo intensity is important for perception (as shown in the reflective walls experiment), but is probably not sufficient on its own, without an equivalent aperture, to shape size perception. More specifically, echo intensity is probably not enough for generating a percept of a larger object when the aperture is small and the two dimensions must be aligned for correct perception.

Several previous studies have suggested that bats perceive virtual echoes as representing real objects ($38\text{--}40$). To test this

with our setup, we ran a separate control study in which we trained Kuhl's pipistrelles to detect and land on a cubic target in a flight room, and we then tested the bats by replacing the real object with our playback system embedded in foam. We found that bats readily landed on the playback system when it was playing back the bat's own calls (*Materials and Methods*). However, we would like to point that one never knows exactly how bats perceive virtual echoes. For example, the bats might have simply ignored our playback. Nevertheless, both the wall experiments (above) and the sphere experiments (below) suggest that certain relations are required between the acoustic dimensions of an object to allow proper perception.

So far, we have either examined very large or very small objects varying in their aperture-intensity relations. To further examine how bats perceived objects with different relations, we replaced the wall with one of three different spheres with different aperture-intensity relations, thus tiling the aperture-intensity ratio space (targets 6 to 8 in Fig. 1*B*, spheres experiment). For each sphere, we flew eight or nine Kuhl's pipistrelles down the corridor with a sphere hanging midway at different heights (*SI Appendix, Fig. S1*). Each bat flew multiple times, and its collisions were quantified (*Materials and Methods* and *Movies S2* and *S3*). As expected, there was a difference in bats' collision rate when varying the size (and intensity) of the spheres ($H = 20.1346$, $df = 2$, $P < 10^{-4}$, Kruskal-Wallis test for a comparison of all three groups; $Z < -3$, $P < 10^{-2}$ for all post hoc pairwise comparisons, Mann-Whitney U test with FDR correction; Fig. 2*D*). Like with the walls, an analysis of the echolocation revealed that the bats detected the spheres, even the weakly reflecting foam sphere (*SI Appendix, Fig. S5*), implying that sensory limitations only played a partial role in collision.

After we tiled the intensity-aperture space, we could use a generalized linear mixed-effects model to quantify the importance of intensity and aperture in perception. We used a GLM to model the perception of the object as an obstacle under different intensity-aperture combinations (using data from all three experiments together: reflective walls, spheres, and virtual reality). As a proxy of perception, we used the proportion of behavioral responses that suggest perceiving the object as an obstacle, including turning around or attempting to land. This analysis revealed a significant effect of the interaction between intensity and aperture ($B = 0.15$, $df = 280$, $P = 0.03$), implying that the relation between them is essential for perception. No effect was found for intensity or aperture separately ($B = 0.09$, $df = 280$, $P = 0.14$; $B = -0.66$, $df = 280$, $P = 0.8$; respectively).

The spheres experiment also directly strengthened the importance of the combination of both echo intensity and echo aperture for perception. The spheres and walls experiments cannot be directly compared because, in the case of the spheres, the bats were not always flying down the corridor straight toward them (as in the case of the walls). We thus first have to determine how many of the bats flew toward the sphere. If we take the -45 -dB sphere's collision rate (i.e., $\sim 15\%$) as an estimate of the bats that flew straight toward the sphere, then approximately three times less bats collided with a same-size -25 -dB sphere ($\sim 5\%$). This suggests that, if 100% of the bats flew straight toward the sphere (as was the case for the walls), then only $\sim 33\%$ would collide with it: much less than with the -25 -dB foam wall. Altogether, this analysis suggests that less bats collided with a small -25 -dB sphere than with a large -25 -dB wall, pointing to the importance of both aperture and intensity in perception. Note that $\sim 15\%$ is an underestimate, and the real rate was probably higher because some bats avoided the -45 -dB sphere. Accordingly, the collision rate with the -25 -dB sphere was probably even lower relative to the -25 -dB wall.

Bats Can Learn New Associations between Perceptual Dimensions.

Our results suggest that echo intensity and aperture must have a coherent relation between them for correct perception (e.g., a large aperture and high intensity). At last, we examined whether this perceptual relation is fixed or whether new associations between perceptual dimensions can be acquired through learning. Specifically, we tested whether bats can learn to perceive an object with a large sonar aperture but a weak intensity (e.g., a foam wall) as a large barrier. We flew 12 Kuhl's pipistrelles with a -25 -dB wall blocking the same corridor, allowing them to experience the object once every day. Within 9 d, the collision rate was reduced from 83% to 33%. This indicates that the bats learned to associate the stimulus with an obstacle and that it is relatively rapid (there was a significant negative correlation between the day of the trial and the collision rate: $r = -0.92$, $P = 0.0004$, Pearson's correlation; there was also a significant difference in the collision rate between the first and last day: $P = 0.041$, exact McNemar's test; Fig. 2E).

A Comparison with a Lingual Echolocator Bat Species with Prime Vision. To examine interspecies differences in acoustic-based perception, we tested Egyptian fruit bats in the reflective walls experiment with the same walls as reported above for Kuhl's pipistrelles. At least 31 naïve bats were tested in each condition. The overall behavior was similar, with a great majority of the bats colliding with the weak-intensity nonreflective walls, and only a small minority colliding with the loud reflective walls, suggesting that, also for Egyptian fruit bats, intensity plays an important role in object perception (Movie S4). There was a significant difference in collision rate between the walls of different reflectivity ($\chi^2 = 46.59$, $df = 3$, $P < 10^{-5}$; χ^2 test for independence; Fig. 2A). Post hoc tests showed that Egyptian fruit bats collided with a -30 -dB wall significantly more than with any other wall, and with a -25 -dB wall more than with a -15 -dB wall, while collision rate did not differ between the other walls ($P < 10^{-3}$ for all pairwise comparisons of -30 -dB wall, $P = 0.018$ for the comparison between -25 -dB and -15 -dB walls, and $P > 0.2$ for all other pairwise comparisons, Fisher's exact test with FDR correction). All of the bats that avoided collision with the -7 -dB wall did so by attempting to land on the wall and not by turning around (as half of the Kuhl's pipistrelles did), probably because of the reduced maneuverability of this species in comparison to Kuhl's pipistrelles.

The collision with the foam wall was probably not a result of a detection problem, as previous studies found that Egyptian fruit bats can detect wires with a diameter <6 mm (41) [in some studies, even <0.46 mm (42, 43)], which reflect much weaker echoes than a -30 -dB wall. However, despite the overall similarity in the behavior, Egyptian fruit bats collided significantly less than Kuhl's pipistrelles with the -30 -dB, -25 -dB, and -15 -dB walls (-30 dB, $\chi^2 = 11.19$, $df = 1$, $P < 0.01$; -25 dB, $\chi^2 = 14.55$, $df = 1$, $P < 10^{-3}$; -15 dB, $\chi^2 = 10.28$, $df = 1$, $P < 0.01$, χ^2 test for independence with FDR correction) and significantly more with the -7 -dB wall ($\chi^2 = 6.34$, $df = 1$, $P = 0.012$).

Note that both species should be able to assess the echo intensity and aperture of the walls. Both are able to detect much weaker echoes than our low-intensity walls (36, 41–43), and both of them have wide echolocation beams and similar hearing directionality. The 6-dB horizontal beam width of Kuhl's pipistrelles at 40 kHz is $\sim 90^\circ$ (SI Appendix, Fig. S6), and Egyptian fruit bats' beam is only slightly narrower (see figure 3a in Yovel et al. [44]). This means that, when either species is released into the flight corridor, its beam covers a circle with a diameter of 3 m at the distance of the wall, thus covering the entire wall, which was only 90 cm wide. The hearing directionality of the two species is also rather similar, and both of them should be able to

hear the entire reflecting wall. The echolocation wavelength to ear width ratio, which dictates hearing directionality, is similar in both species (*Materials and Methods*), and this is also supported by previous directionality measurement on very close species (45).

Finally, we tested whether the preference for certain dimension combinations is innate. We flew 37 young Egyptian fruit bat pups with a -30 -dB wall blocking their corridor and found that only 36% of the pups collided with the wall, significantly less than the 92% of the adults that collided with the same wall ($\chi^2 = 23.61$, $df = 1$, $P < 10^{-4}$, χ^2 test for independence; Fig. 2A). Together with the finding that new relations between the dimensions can be learned by adult bats, we suggest that the relations between the dimensions are not innate but rather the result of learning by young bats. We could not repeat this experiment with Kuhl's pipistrelles because no pups were available.

Discussion

To our great surprise, echolocating bats from two species with very different sensory strategies collided with foam walls and tried to fly through them as if they did not exist. Because the bats had no sensory difficulty to detect the walls, we suggest that this behavioral deficit was a result of a sensory perceptual mismatch, i.e., a sensory illusion. Specifically, when faced with a large object that reflects weak echoes that are much too weak for its size, bats did not perceive it as an obstacle. This misperception was so severe that almost 100% of the bats collided with the foam wall and 70% of the Kuhl's pipistrelles (which heavily rely on echolocation) did not give up and repeatedly tried to fly through the foam wall three times in a row or more (Movie S1). There are numerous examples of sensory illusions that trick our perception, some of which result from a mismatch of dimensions (46–49). We humans are mostly used to visual sensory biases, while this study shows an acoustic illusion in echolocating bats. We cannot be sure how the bats perceived the mismatch we created. They might have erroneously perceived the walls as much smaller than they really were, or perhaps they did not perceive them as an object at all. In the vision literature, there are many examples of visual mismatches that result in wrong size perception (50–53).

Our findings imply that echo intensity and aperture together play a role in perception. Namely, a loud echo will probably not be perceived as representing a large object unless it is accompanied by a large sonar aperture. Goerlitz et al. (24) also found that intensity is not sufficient for generating a perception of large objects. They placed virtual-reality objects emitting very loud echoes in flyways of bats exiting a cave, but found no evasive response, suggesting that the bats did not perceive the objects as larger than they really were (they did not test the effect of changing the aperture). Heinrich et al. (25) argued that the sonar aperture is more important than intensity for size perception. They exposed bats to virtual acoustic targets produced by an array of speakers. They controlled the sonar aperture by altering the number of active speakers in the array and manipulated the intensity by altering the intensity of the speakers. They found that the bats' performance in estimating the width of the target could be explained by the changes in the sonar aperture alone (regardless of the intensity of playback). The finding that performance is similar when relying on aperture only, or when intensity and aperture are both available, does not prove that bats do not use intensity. It could be, for example, that, under the conditions in that experiment, the aperture alone was sufficient in allowing maximum performance, so no performance change was detected when intensity cues were added. We found that intensity is clearly important for perception and specifically for size perception. Moreover, bats in that study were trained, while our bats were naïve. Training may result in relying on a single

sensory cue to perform the task while ignoring the other, a phenomena known as overshadowing (54). Our results suggest that the combination of intensity and aperture is vital for perception, as was also indicated by the generalized linear model that we used to analyze the data. Our results are coherent with the Gestalt idea, according to which the whole is different from the sum of its parts.

Two previous studies suggest that the integration of coherent acoustic dimensions (other than the ones we tested) is essential for size-invariant perception in echolocating bats (17, 19). For example, Firzlaiff et al. (19) found that echo duration (implying object depth) and echo intensity (implying its size) must covary in a meaningful way for *Phyllostomus discolor* to associate scaled virtual objects with the target object. Moreover, they found a population of neurons in the auditory cortex of the bats that responded preferentially to the size-invariant objects and not to other incoherent combinations of these dimensions.

Intensity and aperture are not the only acoustic dimensions defining object perception. Bats collided much more with a foam wall than with a foliage wall, demonstrating that they perceived them differently, even though these two objects were identically loud (−25 dB) and had a similar sonar aperture and spectrum (Figs. 1B and 2A and *SI Appendix*, Fig. S3). One option is that the bats relied on the different temporal depth of the echoes of the two objects. While the on-axis echo of a wall is typically a mirror of the emitted signal (often termed a “glint”), the echo from a foliage wall is diffusive and composed of many reflections returning with slight time differences between them (*SI Appendix*, Fig. S7) (21). Bats could also rely on the spectral variability of consecutive echoes, which is typically larger in the foliage wall than in the smooth wall (*SI Appendix*, Fig. S3 D and E). Apart from the foliage wall, the other walls should have not differed in their temporal cues (*SI Appendix*, Fig. S7). Unlike the visual system, where distance is inferred (55), echolocating bats can accurately and directly compute the distance of an object according to the delay between their echolocation emission and echo reception (56), making time an important cue. Moreover, an object’s aperture can also be encoded in the time domain, with the echoes of larger objects spreading more than those of smaller objects in time when observed from an angle (*SI Appendix*, Fig. S8). Temporal information could thus also be used to assess aperture.

The two bat species exhibited a different perceptual threshold for sensing the wall as a wall, implying that they integrate differently the two acoustic dimensions (i.e., intensity and aperture). Ironically, even though Kuhl’s pipistrelles are experts in detecting very weak targets such as mosquitos, the threshold of Kuhl’s pipistrelles for perceiving the wall was ~10 dB higher than for Egyptian fruit bats (Fig. 2A; we defined the detection threshold as the reflectivity at which 50% of the bats collided). In other words, Kuhl’s pipistrelles had more trouble perceiving the weakly reflecting walls. Kuhl’s pipistrelles rely almost solely on echolocation (27, 28, 36) in comparison to the extensive reliance of Egyptian fruit bats on vision (33–35) [Egyptian fruit bats mainly use echolocation to detect cave walls and tree branches (43).] Even though our experiments were conducted in complete darkness, and thus with no vision, we speculate that this difference in their everyday strategy makes Kuhl’s pipistrelles rely more on echolocation and thus become more “surprised” when acoustic dimensions are not coherent. An alternative explanation might be that Egyptian fruit bats are exposed to objects with more combinations of acoustic dimensions and thus were not deceived by the mismatch we created. Naturally, the different echolocation designs of the two species could also play a role in the differences we see in behavior, with Kuhl’s pipistrelles employing frequency-modulated (FM) laryngeal echolocation

calls (27–29) and Egyptian fruit bats employing ultrashort broadband lingual echolocation clicks (31, 32), but it is important to note that both species should have had no problem to assess the echo intensity and aperture of the wall, as we explained above (*Results*).

Note that, since Egyptian fruit bats are much larger, they are less maneuverable than Kuhl’s pipistrelles. Nevertheless, it likely did not affect the differences in collision rate but rather altered the avoidance behavior of the bats when approaching the wall. While 48% of the Kuhl’s pipistrelles avoided collision with the high-intensity wall by turning back when approaching it, none of the Egyptian fruit bats attempted to do so. Instead, Egyptian fruit bats attempted to land on the wall. Therefore, differences in maneuverability were reflected in the way they avoided collision.

The perceptual preference for specific intensity–aperture relations raises the immediate question whether bats are born with these preferences or acquire them as a result of sensory experience. An examination of young pups suggests that the latter is true. Pups collided significantly less with a −30-dB wall compared to adults, suggesting that adult sensory perception is shaped by experience (Fig. 2A). Our results show that perception remains plastic in this task, as adult bats of both species were able to associate new dimension combinations (e.g., a large-aperture/low-intensity object). This plasticity is probably the reason why bat researchers do not observe bats colliding with foam walls in anechoic rooms (we have never observed this until testing naïve bats).

In two recent studies, Greif et al. showed that bats will collide with highly reflective smooth vertical walls when they approach them from an angle (57) and that they will try to drink from smooth horizontal surfaces (58). These are also examples of perception illusions, but we argue that they demonstrate a fundamentally different aspect of acoustic perception than the one we show here. In both of these examples, the echo reflected from the artificial object accurately mimics the echo of a natural object: a hole in the case of a smooth vertical surface and water in the case of a horizontal smooth surface. Accordingly, in Greif et al. (57), the bats collided with a vertical wall only when approaching it from an angle in which no echo was reflected (the “mirror effect”) because they perceived it as a hole. In our setup, the bats collided with the foam wall from all directions (even when flying straight toward it) because a dimension mismatch hindered them from perceiving it as a wall. In these previous studies, the bats were “tricked” to perceive the wrong scene by mimicking its sensory characteristics. The visual equivalent would be a human walking into a transparent glass door due to mistaking it for an opening. Our study demonstrates a different type of sensory illusion, in which the stimulus does not mimic an alternative scene but exhibits incoherence between two acoustic dimensions. To our knowledge, such an acoustic mismatch illusion has not yet been described in echolocation.

Materials and Methods

Animals. A total of 196 *P. kuhlii* (Kuhl’s pipistrelles) and 167 *R. aegyptiacus* (Egyptian fruit bats) performed the experiments. The bats were caught at roosts housing several thousands of bats in central Israel. They were brought to Tel Aviv University in groups of 16 to 30, tested within a few days, and then released at their roost. Most Kuhl’s pipistrelles were ringed for future identification. In all other bats (all Egyptian fruit bats and some Kuhl’s pipistrelles that were not ringed), the fur was slightly cut so that we could avoid reusing the same individuals during that season. During their stay in the laboratory, the bats were housed on a natural day/night cycle and were provided with water and food ad libitum.

All experiments were performed with permission of the Israeli National Park Authority and the Tel-Aviv University IACUC (permit number L15-007). All bats were tested (see below) within 1 to 4 d from capture except bats that participated in the learning experiment, which were released within 11 d.

The number of bats that took part in each experiment is specified in Table 1.

Experimental Setup and Procedure. The experiments took place in an acoustic room in the zoological garden in Tel Aviv University ($2.5 \times 4 \times 2.5 \text{ m}^3$). A corridor ($0.9 \times 3 \times 1.9 \text{ m}^3$) was set up in the middle of the room (*SI Appendix, Fig. S1*). The corridor's walls and ceiling were made of white reflective tarpaulin and did not allow the bats to land on them. Different obstacles, varying in their acoustic reflectivity and sonar aperture, were placed in the middle of the corridor, and the bats' reaction to them was tested (colliding or not colliding; *Video and Audio Analysis*). A high-speed infrared camera (125 fps, OptiTrack; NaturalPoint) was situated near the target (0.3 m above ground) facing upward to document the bats' interaction with the obstacle. An ultrasonic microphone (UltraSoundGate CM16/CMPA; Avisoft) was placed near the camera pointing 45° upward, facing the release point of the bats. The microphone was connected to an A/D converter (Hm116; Avisoft) and recorded audio at a sampling rate of 250 kHz for Egyptian fruit bats and 375 kHz for Kuhl's pipistrelles. The A/D converter was connected to a desktop located in a control room outside the experimental room (*SI Appendix, Fig. S1*).

All experiments were conducted in light level of $<10^{-7}$ lux. (All lights from electronic devices were abolished by covering them with black felt.) Light levels were measured inside the corridor with a light detector (SPM068 with ILT1700; International Light Technologies) with a resolution of 10^{-7} lux. Therefore, the light level in the corridor was below the threshold of the device and below the visual threshold of Egyptian fruit bats (59). Kuhl's pipistrelles have much smaller eyes, providing low visual sensitivity and acuity (60); therefore, it is safe to assume that they could not see in this light level either. We thus refer to this light level as complete darkness. Night-vision goggles were used by the experimenter throughout the experiments.

The bats were kept in a dark carrying cage for 15 min before the experiment to allow their eyes to adapt to the dark. Then, they were released one at a time at 1.5 m above ground by an experimenter seated on a chair at the corridor entry. Each bat was tested in a single trial without any training or accommodation (except for in the learning, spheres, and virtual reality experiments; see below). The microphone and camera were triggered by another experimenter sitting in the control room.

Experimental Treatments.

Reflective walls. In this experiment, the obstacle completely blocked the corridor (*SI Appendix, Fig. S1*). The obstacle was an identical-area wall with different acoustic reflectivity hung from the ceiling. The different target strengths of the targets were -30 dB (3 cm foam), -25 dB (3 cm foam with 2-mm plastic board), -15 dB (2-mm plastic board covered with felt), -7 dB (2-mm plastic board; see *Acoustic Measurements*). Both Kuhl's pipistrelles and Egyptian fruit bats were tested in this experiment.

Foliage. To test whether a low-reflectivity wall might be perceived by the bats as something they can pass through, we tested Kuhl's pipistrelles with a plastic mesh (3-mm diameter, 10-mm opening) covered with Tamarix branches and leaves (*SI Appendix, Fig. S2*). This "wall" was hung from the ceiling in the same way as the reflective walls. The wall's target strength was measured to be -25 dB, the same as one of our least reflective walls.

Learning. A subset of Kuhl's pipistrelles first used for the reflective walls experiment was then flown daily, one trial every day, with a low-reflectivity wall (-25 dB), to document their learning.

Spheres. To tile the intensity-aperture space, we flew Kuhl's pipistrelles with three targets with smaller aperture: a 20-cm-diameter plastic sphere with -25 dB reflectivity, a 20-cm-diameter foam sphere with -45 dB reflectivity, and a 40-cm-diameter plastic sphere with -19 dB reflectivity. Each bat was tested in many trials, and the percentage of collisions was calculated per bat (the chances of colliding on a single trial were very low because of the small object size, so hundreds of naïve bats would be required if we did not reuse the same individuals).

The two 20-cm-diameter spheres were tested in the same corridor as the wall. The 40-cm-diameter sphere was tested in a slightly bigger corridor ($1.5 \times 3.5 \times 2.1 \text{ m}$), the same corridor used for the virtual reality experiment (see below).

The sphere was placed at the center of the corridor (hanging on a 0.4-mm fishing wire; *SI Appendix, Fig. S1*) at four different heights in a random order. At each height, the bat was released from the same position as noted above, and its number of collisions in ~ 10 flights past the sphere (back or forth in the corridor) was estimated. Each bat performed three rounds of these four heights (12 rounds in total). The height of the spheres was changed while the bats were in a fabric bag.

In this experiment, a second high-speed infrared camera was used. It was placed behind the take-off location facing the sphere to allow a better estimate of collisions (along with the camera below the sphere, which was present in all experiments).

Virtual reality. Kuhl's pipistrelles were flown with a playback system that allowed recording the bat's echolocation signals and playing them back (while controlling their intensity) in real time. The delay of the system was $1 \mu\text{s}$, thus placing the virtual object at the same distance from the bat as the physical speaker emitting it (i.e., there was virtually no delay between the real echo from the speaker and the played echo). The system included a condenser ultrasound microphone (CM16/CMPA40-5V; Avisoft) and an ultrasonic speaker (Vifa) connected to an amplifier. It was controlled by a NUCLEO-F446RE processor (STMicroelectronics). The program controlling the system was written in an Mbed compiler workspace. We accounted for the frequency response of the system by high-pass filtering the output according to the inverse response of the system's frequency response. Note that it is very hard to get a "flat" frequency response, but, as we were comparing three playback conditions among each other (see below) and they all used the same system, this should have been a fair comparison for our purpose.

In these experiments, the corridor was replaced with a slightly bigger corridor ($1.5 \times 3.5 \times 2.1 \text{ m}$) to avoid resonances caused by echoes reflected from the walls and picked up by the playback system. The tarpaulin wall at the rear end of the corridor was replaced with fine mesh to enable bats to land after crossing the corridor. Since the speaker of the system is directional, we wanted the bats to fly as little as possible in the wrong direction. The playback speaker (6.5 cm) was placed on a pole in the center of the corridor at 1.60 m height, facing the release point. The playback microphone was attached 0.25 m below the speaker, tilted upward $\sim 25^\circ$ (*SI Appendix, Fig. S1*). The target strength of the entire system (microphone and speaker) was -28 dB (at 1 m), thus representing a small, weakly reflecting object. All other parts of the system were situated on the floor of the corridor and covered with black felt. Two cameras were used; one was placed on a small tripod at 0.3 m height below the playback system facing upward and another on a tripod behind the release point at 1.5 m height facing the corridor. Two ultrasonic microphones were used (in addition to the playback's microphone): one situated on the camera behind the releasing point facing the corridor (to record the playback emission) and the other at the same height on the other end of the corridor behind the mesh wall (to record the bat). These microphones were used to ensure the playback system was working during the experiments.

The virtual reality experiment had three conditions. 1) In the playback condition, the bat's own calls were recorded, amplified, and played back, imitating real echoes but returning from a highly loud object. The intensity of the playback system was calibrated to emit echoes with a target strength of a -7 -dB wall from 1 m, and it behaved like a real target: echoes were weaker when the bat was far from the playback system and stronger when it was closer. Since the playback was of the bat's own calls, if the bat changed its signal (e.g., shortening it), the playback changed as well. 2) In the noise condition, a time-reversed synthesized Kuhl's pipistrelles signal was played back to the bats in response to every echolocation call. This signal always had the same intensity (target strength of -7 dB at 1 m), regardless of the distance of the bat, and it was fixed (i.e., always the same synthesized signal with the same spectrotemporal characteristics). This condition allowed us to examine whether an observed response was merely a reaction to the sound produced by the system. 3) In the silence condition, the system was turned off to test the bats' response to the natural echoes coming back from the playback system.

All bats flew in all conditions. The bats were assigned to three groups, each performing the conditions in a different order. The different conditions were counterbalanced throughout the day. To get an accurate measurement, each bat was flown for many trials and the distance was averaged across trials. The bats were flown until they performed at least 10 flights in which they passed the playback system in a direct flight. There was no statistical difference between naïve bats performing the condition for the first time and bats performing their second or third condition in any of the parameters tested (2D distance from playback system, $U > 18$, $P > 0.05$ for all conditions, Mann-Whitney test; crossing rate at the first trial, $P > 0.15$ for all conditions, Fisher's exact test; see *Video and Audio Analysis*). This was true for all three conditions, and we therefore pooled all of the data for each condition from all bats together.

A subset of animals from the reflective walls experiment was also trained and tested in a landing task with the playback system. Experiments took place in a large acoustic room in the zoological garden ($5.6 \times 4.5 \times 2.5 \text{ m}^3$) in a light level of 9×10^{-3} lux. This light level was the minimal limit of the tracking system used (see below), but since Kuhl's pipistrelles have small eyes and low

acuties even in high light levels [for comparison, closely related species from the *Pipistrellus* genus were found to have acuties of 0.9 in $>3,000$ lx, while humans have acuity of 1.3 in 5×10^{-4} lux (30)] and rely extensively on echolocation, it is safe to assume that vision was not used. The bats were trained two or three times a week for 4 wk to land on the wooden cubic target ($15 \times 15 \times 15$ cm³) placed on a pole to receive a food reward. We tested whether and how long it will take bats to land on a playback target with the same reflectivity as the wooden target. We compared landing time between three conditions: 1) a wooden target (−7 dB), 2) a foam cubic target of the same size (−26 dB; will be referred to as “foam target”), and 3) a foam cubic target that amplified its echoes using the playback system (−7 dB; will be referred to as “playback target”). Both the foam target and the playback target had a speaker implemented inside the foam and a microphone attached to the pole 0.3 m below, but only in the playback target was the speaker playing. Note that reflectivity was much higher with the speaker playing. The location of the target (wood, foam, or playback) was randomly moved in the room after every trial. The target was placed with the speaker and microphone directed toward the direction from which the bat approached.

A tracking system with 16 Raptor 1,280*1,024-pixel cameras and 4 Raptor-12 4,096*3,072-pixel cameras (Motion-Analysis) was used to track the bats' flight. The system operated at 200 frames per second. Center of mass of the bat was tracked by gluing three spherical reflective facial markers (3x3 Designs) to the bat's back with mounting tape. Each bat performed 15 trials per day, 5 in each condition in a random order, for 2 consecutive days. We found that the bats landed on all targets (they readily landed on the virtual target) and that there were no differences in the time it took them to find and land on each of the targets from the moment of release, suggesting that they perceived the playback target as a real one ($P = 0.22$, $df = 2$, Friedman test).

Pups. Egyptian fruit bat pups (6 to 7 wk old) that were born in the laboratory were also tested in the reflective walls experiment with a −30-dB wall. These bats had not experienced foam walls before being tested.

Acoustic Measurements. We ensonified the different objects to estimate their target strength. All ensonifications were conducted in a quiet anechoic room. A speaker (Vifa) connected to an UltraSoundGate player 116 device (Avisoft) was placed on a tripod at 1.3 m height. It played a 3-ms-long, 40-kHz sine and kuhlii-like synthesized signal 90 to 30 kHz down-sweep with a peak intensity at 40 kHz with a sampling rate of 500 kHz. Recordings were performed using a 46DD-FV 1/8-inch CCP-calibrated microphone (GRAS) placed on top of the speaker and digitized using an UltraSoundGate 116Hm device (Avisoft). Sampling rate of recording was 375 kHz.

For target strength measurements, the different targets were placed in front of the speaker and microphone at 1-m distance, and the relative echo sound pressure reflecting from them was recorded. Then, the microphone was removed and placed instead of the targets to measure the relative incident sound pressure. We then calculated the target strength by dividing the peak intensities of the incident and echo sound pressure for each target. The measurements for the −19-dB sphere were conducted the same way but from a 1.5-m distance. The calculation was corrected for 1 m. To ease the reading by a nonexpert, we will refer to target strength as reflectivity. Both signals (sine and kuhlii-like signal) gave similar results. The measurements from multiple ensonifications were averaged per target.

Although the target strength throughout the paper is the target strength calculated as described above, for peak frequency of 40 kHz, we also ensonified the four wall targets with a 25- to 45-kHz down-sweep to calculate their target strength at 30 kHz (the peak intensity of Egyptian fruit bats' echolocation call). The results were only slightly different (40-kHz signal, −7 dB, −15 dB, −25 dB, and −30 dB; 30 kHz, −5 dB, −19 dB, −25 dB, and −27 dB).

For power spectra and impulse response measurements, we used the same setup and played a 2-ms-long linear chirp that sweeps from 90 to 30 kHz. All targets were measured at 1 m distance except for the two low-reflectivity walls (−25 dB and −30 dB) that were very weak and therefore measured at 0.4 m distance in order to better represent the higher and weaker frequencies. For each target, 24 recordings were averaged and normalized by the peak intensity, thus making any differences caused by the different distances of the targets negligible.

Hearing Directionality Measurements. Ear width was measured on three Kuhl's pipistrelles and three Egyptian fruit bats with a caliper. Ear width was 12 and 6 mm in Egyptian fruit bats and Kuhl's pipistrelles, respectively. We estimated the ear width to echolocation signal wavelength (the main factor

influencing the horizontal hearing directionality) close to the frequency with the most energy in each species (25 kHz and 40 kHz in Egyptian fruit bats and Kuhl's pipistrelles, respectively).

Video and Audio Analysis. Each trial of the experiments (except for virtual reality trials) was behaviorally classified as a collision or noncollision trial based on the video recording. In case of the walls, noncollision trials included attempting to land on the target or turning back when near it. Bats whose videos did not enable us to see the moment of contact with the wall were omitted from the study (13 Egyptian fruit bats and 10 Kuhl's pipistrelles). Three independent observers classified each video. The scores of the observers (i.e., proportion of colliding) were then averaged.

In case of the first two spheres (−25-dB plastic sphere and −45-dB foam sphere; targets 6 and 7 in Fig. 1B), noncollision trials included avoiding the target (flying through the tunnel without touching the sphere), attempting to land on the sphere, or turning back when near it. In this experiment, touching the target is considered as a collision (i.e., everything from a full body collision to touching it with the tip of the wing, apart from landing attempts). Two independent observers classified each video. For each bat, the number of collisions was divided by the number of times the bat flew in the tunnel. These proportions were then averaged across bats. For the third larger sphere (−19-dB plastic sphere; target 8 in Fig. 1B), we scored collisions during the experiment itself with one observer viewing the sphere from below and one from the side, both noting collisions. Because collisions were extremely rare, there was no point in watching all of the videos again.

For the virtual reality experiment, one observer classified the videos as crossing the playback speaker or not crossing, which included turning back or attempting to land on the walls or on the playback speaker. For trials in which the bat passed the playback system, the 2D position of the bat in relation to the playback speaker at the moment of passing it was manually marked on the movie frame (using an in-house Matlab software; MathWorks). We then calculated the Euclidean distance between the passing points and the playback speaker and compared the different conditions.

For audio analysis, all recordings of Egyptian fruit bats were manually examined using Saslab (Avisoft) to ensure that the bats echolocated (unlike Kuhl's pipistrelles, Egyptian fruit bats can stop echolocating entirely).

We analyzed the echolocation behavior of a subset of Kuhl's pipistrelles tested in the reflective walls experiment (30, 21, 8, and 9 bats for −30-dB, −25-dB, −15-dB and −7-dB walls, respectively; half of the bats turned back when approaching a −7-dB wall and their audio files could not be used). Audio and video files were first synchronized using a synchronized event visible in both the audio and video recordings (a finger snap). We then detected and analyzed the echolocation signals emitted by the bats along the approach, aiming to examine changes in repetition rate (interpulse intervals) using in-house Matlab software. The interpulse intervals were binned into 150-ms bins with 100 ms overlap between bins to see how they change over time as the bat was approaching the target. This analysis was not conducted on Egyptian fruit bats because, in complete darkness, they operate at their maximal echolocation rate and thus cannot increase it when approaching the target (61).

The same analysis was conducted on Kuhl's pipistrelles approaching −25-dB and −45-dB spheres (for seven of the eight bats in each condition). Since, in these conditions, the bats flew multiple times and the sphere was placed at four different heights throughout each bat's session, we analyzed the first collision for each height (hence, four recordings per bat when possible). The interpulse intervals were first averaged per bat and then between bats.

Statistical Analysis. In the reflective walls experiment, we compared collision rate between walls of different reflectivity using χ^2 for independence. Post hoc analysis included testing all possible comparisons with an FDR correction. When the assumptions of χ^2 were not met, Fisher's exact test was used instead. The same tests were used for comparing collision rate between foliage and −25-dB wall (foliage experiment) and to compare pups and adults that were flown with a −30-dB wall (pups experiment). In the spheres experiment, each bat was flown for multiple trials, and collision rate was calculated for all these trials. We then compared collision rates between bats that were flown with different spheres using Kruskal-Wallis test due to the small sample size ($n = 8$ or 9 per group). Post hoc analysis included testing all possible comparisons between spheres with a Mann-Whitney test with an FDR correction. In the playback experiment, we averaged the distance at which the bat passed the playback speaker in 10 flights. Since all bats participated in all conditions, the average distance was compared between conditions with a Friedman's test. We also tested whether the rate of bats crossing vs. not crossing the playback speaker on their first flight differed

between conditions with Cochran's Q test for related samples. In the learning experiment, we tested the correlation between the day of trial and collision rate with Pearson's correlation.

We used a generalized linear mixed-effects model with a logit link to explain perception across all aperture–intensity experiments (reflective walls, spheres, and virtual reality). We used the proportion of behavioral responses that suggest perceiving the object as an obstacle (e.g., turning around and landing) as a proxy for perception (we will term these two behaviors as “perception” in the following discussion). Therefore, the behavioral response (i.e., perception) was the dependent variable, while reflectivity and sonar aperture were used as independent fixed factors and bat ID as a random factor. Sonar aperture was calculated as the percentage of the cross section that the object covered out of the entire cross section of the corridor (with the walls being 1).

Because the spheres and playback speaker covered only a small section of the corridor, the probability of encountering (i.e., flying directly toward them) by chance was much lower than with the wall, and we thus had to normalize the bats' performance in these conditions. We used the response rate to the –25-dB plastic sphere as a reference for the same-sized –45-dB foam sphere, and the playback speaker was used as reference for the silent-speaker condition. Even if this assumption is partially wrong, it alters the

results in a direction that strengthens our conclusions because it underestimates the number of random encounters, so it is a fair assumption. For example, the bats perceived the foam sphere in 7% of the trials and the plastic sphere in 12%. The normalized perception rate for the plastic sphere was thus $7/12 \times 100\%$. Overall, we used the behavior in the following conditions in the model: –30-dB wall, –25-dB wall, –15-dB wall, –7-dB wall, silent speaker, and foam sphere.

In the playback condition, we used only the first flight of each bat in the corridor. Bats that turned back before reaching the speaker or landed on the walls before the speaker were considered as “perceiving.” Normalization was performed as for the spheres. The perception rate for the playing-back speaker was taken as the encounter rate, and the perception rate with the silent speaker was normalized accordingly.

Data Availability. The data, methods, and code are available in the main text and *SI Appendix*.

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1. M. H. Giard, F. Peronnet, Auditory-visual integration during multimodal object recognition in humans: A behavioral and electrophysiological study. *J. Cogn. Neurosci.* **11**, 473–490 (1999).
2. D. Raposo, J. P. Sheppard, P. R. Schrater, A. K. Churchland, Multisensory decision-making in rats and humans. *J. Neurosci.* **32**, 3726–3735 (2012).
3. M. O. Ernst, M. S. Banks, Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* **415**, 429–433 (2002).
4. D. Alais, D. Burr, The ventriloquist effect results from near-optimal bimodal integration. *Curr. Biol.* **14**, 257–262 (2004).
5. C. R. Fetsch, A. H. Turner, G. C. DeAngelis, D. E. Angelaki, Dynamic reweighting of visual and vestibular cues during self-motion perception. *J. Neurosci.* **29**, 15601–15612 (2009).
6. A. Tversky, Features of similarity. *Psychol. Rev.* **84**, 327–352 (1977).
7. N. Abudarham, G. Yovel, Reverse engineering the face space: Discovering the critical features for face identification. *J. Vis.* **16**, 40 (2016).
8. S. Ohayon, W. A. Freiwald, D. Y. Tsao, What makes a cell face selective? The importance of contrast. *Neuron* **74**, 567–581 (2012).
9. S. Hébert, I. Peretz, Recognition of music in long-term memory: Are melodic and temporal patterns equal partners? *Mem. Cognit.* **25**, 518–533 (1997).
10. Y. Yovel, M. O. Franz, P. Stilz, H.-U. Schnitzler, Complex echo classification by echolocating bats: A review. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **197**, 475–490 (2011).
11. N. Ulanovsky, C. F. Moss, What the bat's voice tells the bat's brain. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 8491–8498 (2008).
12. S. Schmidt, Evidence for a spectral basis of texture perception in bat sonar. *Nature* **331**, 617–619 (1988).
13. J.-E. Grunwald, S. Schörrich, L. Wiegube, Classification of natural textures in echolocation. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 5670–5674 (2004).
14. J. A. Simmons *et al.*, Target structure and echo spectral discrimination by echolocating bats. *Science* **186**, 1130–1132 (1974).
15. G. Neuweiler, F. P. Möhres, “The role of spacial memory in the orientation” in *Animal Sonar Systems Biology and Bionics*, R. G. Busnel, Ed. (Laboratoire de Physiologie Acoustique, 1966), pp. 129–140.
16. B. Falk, T. Williams, M. Aytekin, C. F. Moss, Adaptive behavior for texture discrimination by the free-flying big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol.* **197**, 491–503 (2011).
17. D. von Helversen, Object classification by echolocation in nectar feeding bats: Size-independent generalization of shape. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **190**, 515–521 (2004).
18. R. Simon, M. W. Holderied, C. U. Koch, O. Von Helversen, Floral acoustics: conspicuous echoes of a dish-shaped leaf attract bat pollinators. *Science* **333**, 631–633 (2011).
19. U. Firzlauff, M. Schuchmann, J. E. Grunwald, G. Schuller, L. Wiegube, Object-oriented echo perception and cortical representation in echolocating bats. *PLoS Biol.* **5**, e100 (2007).
20. C. F. Moss, H.-U. Schnitzler, Accuracy of target ranging in echolocating bats: Acoustic information processing. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **165**, 383–393 (1989).
21. Y. Yovel, P. Stilz, M. O. Franz, A. Boonman, H.-U. Schnitzler, What a plant sounds like: The statistics of vegetation echoes as received by echolocating bats. *PLoS Comput. Biol.* **5**, e1000429 (2009).
22. J. A. Simmons, J. A. Vernon, Echolocation: Discrimination of targets by the bat, *Eptesicus fuscus*. *J. Exp. Zool.* **176**, 315–328 (1971).
23. H. S. Seddeq, Factors influencing acoustic performance of sound absorptive materials. *Aust. J. Basic Appl. Sci.* **3**, 4610–4617 (2009).
24. H. R. Goerlitz, D. Genzel, L. Wiegube, Bats' avoidance of real and virtual objects: Implications for the sonar coding of object size. *Behav. Processes* **89**, 61–67 (2012).
25. M. Heinrich, A. Warmbold, S. Hoffmann, U. Firzlauff, L. Wiegube, The sonar aperture and its neural representation in bats. *J. Neurosci.* **31**, 15618–15627 (2011).
26. M. Heinrich, L. Wiegube, Size constancy in bat biosonar? Perceptual interaction of object aperture and distance. *PLoS One* **8**, e61577 (2013).
27. K. V. Kalko, Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Anim. Behav.* **50**, 861–880 (1995).
28. H. U. Schnitzler, E. Kalko, L. Miller, A. Surlykke, The echolocation and hunting behavior of the bat, *Pipistrellus kuhlii*. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **161**, 267–274 (1987).
29. U. Goiti, P. Vecin, I. Garin, M. Saloña, J. R. Aihartza, Diet and prey selection in Kuhl's pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in south-western Europe. *Acta Theriol.* **48**, 457–468 (2003).
30. J. Eklöf, “Vision in echolocating bats,” PhD thesis, Göteborg University, Göteborg, Sweden (2003).
31. R. A. Holland, D. A. Waters, J. M. V. Rayner, Echolocation signal structure in the Megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810. *J. Exp. Biol.* **207**, 4361–4369 (2004).
32. Y. Yovel, M. Geva-Sagiv, N. Ulanovsky, Click-based echolocation in bats: Not so primitive after all. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **197**, 515–530 (2011).
33. G. Neuweiler, Bau und leistung des flughundauges (*Pteropus giganteus*). *Zeitschrift für vergleichende Physiologie* **46**, 13–56 (1962).
34. G. Neuweiler, *The Biology of Bats* (Oxford University Press, NY, 2000).
35. R. S. Heffner, G. Koay, H. E. Heffner, Sound localization in an old-world fruit bat (*Rousettus aegyptiacus*): Acuity, use of binaural cues, and relationship to vision. *J. Comp. Psychol.* **113**, 297–306 (1999).
36. A. Boonman, Y. Bar-On, N. Cvikel, Y. Yovel, It's not black or white-on the range of vision and echolocation in echolocating bats. *Front. Physiol.* **4**, 248 (2013).
37. E. K. V. Kalko, H. Schnitzler, Plasticity in echolocation signals of European pipistrelle bats in search flight: Implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**, 415–428 (1993).
38. H. R. Goerlitz, M. Hübner, L. Wiegube, Comparing passive and active hearing: Spectral analysis of transient sounds in bats. *J. Exp. Biol.* **211**, 1850–1858 (2008).
39. D. Genzel, L. Wiegube, Size does not matter: Size-invariant echo-acoustic object classification. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **199**, 159–168 (2013).
40. J. A. Simmons, C. F. Moss, M. Ferragamo, Convergence of temporal and spectral information into acoustic images of complex sonar targets perceived by the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **166**, 449–470 (1990).
41. D. A. Waters, C. Vollrath, Echolocation performance and call structure in the Megachiropteran fruit-bat *Rousettus aegyptiacus*. *Acta Chiropt.* **5**, 209–219 (2003).
42. C. A. Summers, “Acoustic orientation in the Megachiropteran bat *Rousettus*,” PhD thesis, Indiana University, Bloomington, IN (1983).
43. D. R. Griffin, A. Novick, M. Kornfield, The sensitivity of echolocation in the fruit bat, *Rousettus*. *Biol. Bull.* **115**, 107–113 (1958).
44. Y. Yovel, B. Falk, C. F. Moss, N. Ulanovsky, Optimal localization by pointing off axis. *Science* **327**, 701–704 (2010).
45. M. K. Obrist, M. B. Fenton, J. L. Eger, P. A. Schlegel, What ears do for bats: A comparative study of pinna sound pressure transformation in chiroptera. *J. Exp. Biol.* **180**, 119–152 (1993).

46. A. W. Roe, H. D. Lu, C. P. Hung, Cortical processing of a brightness illusion. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 3869–3874 (2005).
47. M. Shadlen, T. Carney, Mechanisms of human motion perception revealed by a new cyclopean illusion. *Science* **232**, 95–97 (1986).
48. L. Kaufman, J. H. Kaufman, Explaining the moon illusion. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 500–505 (2000).
49. C. Chubb, G. Sperling, J. A. Solomon, Texture interactions determine perceived contrast. *Proc. Natl. Acad. Sci. U.S.A.* **86**, 9631–9635 (1989).
50. G. Buckingham, M. A. Goodale, Lifting without seeing: The role of vision in perceiving and acting upon the size weight illusion. *PLOS Comput. Biol.* **5**, e9709 (2010).
51. E. Brenner, W. J. van Damme, Perceived distance, shape and size. *Vision Res.* **39**, 975–986 (1999).
52. R. L. Gregory, Distortion of visual space as inappropriate constancy scaling. *Nature* **199**, 678–680 (1963).
53. A. H. Holway, E. G. Boring, Determinants of apparent visual size with distance variant. *Am. J. Psychol.* **54**, 21 (1941).
54. C. Rowe, Multisensory learning: From experimental psychology to animal training. *Anthrozoos* **18**, 222–235 (2005).
55. S. O. Murray, H. Boyaci, D. Kersten, The representation of perceived angular size in human primary visual cortex. *Nat. Neurosci.* **9**, 429–434 (2006).
56. J. A. Simmons, The resolution of target range by echolocating bats. *J. Acoust. Soc. Am.* **54**, 157–173 (1973).
57. S. Greif, S. Zsebok, D. Schmieder, B. M. Siemers, Acoustic mirrors as sensory traps for bats. *Science* **357**, 1045–1047 (2017).
58. S. Greif, B. M. Siemers, Innate recognition of water bodies in echolocating bats. *Nat. Commun.* **1**, 107 (2010).
59. A. Boonman, S. Bumrungsri, Y. Yovel, Nonecholocating fruit bats produce biosonar clicks with their wings. *Curr. Biol.* **24**, 2962–2967 (2014).
60. J. Eklöf, G. Jones, Use of vision in prey detection by brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* **66**, 949–953 (2003).
61. S. Danilovich *et al.*, Bats regulate biosonar based on the availability of visual information. *Curr. Biol.* **25**, R1124–R1125 (2015).