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Sound localization acuity and its relation to vision in large and small fruit-eating bats: II. Non-echolocating species, *Eidolon helvum* and *Cynopterus brachyotis*

R.S. Heffner *, G. Koay, H.E. Heffner

Department of Psychology, University of Toledo, Toledo, OH 43606, United States

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ABSTRACT

Passive sound-localization acuity for 100-msec noise bursts was determined behaviorally for two species of non-echolocating bats: the Straw-colored fruit bat, *Eidolon helvum*, a large frugivore, and the Dog-faced fruit bat, *Cynopterus brachyotis*, a small frugivore. The mean minimum audible angle for two *E. helvum* was 11.7°, and for two *C. brachyotis* was 10.5°. This places their passive sound-localization acuity near the middle of the range for echolocating bats as well as the middle of the range for other mammals. Sound-localization acuity varies widely among mammals, and the best predictor of this auditory function remains the width of the field of best vision ($r = .89$, $p < .0001$). Among echolocating and non-echolocating bats, as well as among other mammals, the use of hearing to direct the eyes to the source of a sound still appears to serve as an important selective factor for sound localization. Absolute visual acuity and the magnitude of the binaural locus cues available to a species remain unreliable predictors of sound-localization acuity.

1. Introduction

Most bats are specialized for using echolocation, and it is plausible that this specialization may benefit passive localization because the cues used to resolve the location of sound sources are thought to be the same for both reflected and emitted sounds (Fuzessery, 1986; Neuweiler et al., 1980; Pollak et al., 1995; Razak et al., 1999). The auditory nervous systems of echolocating bats are highly derived (although varying greatly among species, e.g., Moss and Sinha, 2003; Casseday et al., 1988; Baron et al., 1996) with specialized mechanisms for capturing insects in flight, obstacle avoidance down to 1 mm or less, and even for detecting fish based on the disturbances on the water's surface (Griffin and Novick, 1955; Grinnell and Griffin, 1958; Schnitzler et al., 1994). Thus it is reasonable to ask if echolocators might use their specializations developed for sonar to enhance their passive localization acuity even though, in passive listening, they do not have control over the nature of the sound being localized.

Other considerations, however, suggests the opposite is also possible—passive localization in echolocating bats may be similar to, or even inferior to, that of non-echolocating mammals. The senses do not evolve in isolation; a perceptual ability must provide a selective advantage in order to be acquired, or to avoid being lost, in evolution. Passive localization among mammals seems to serve to direct vision to sound sources—*if* this is not a very useful function in echolocators, perhaps because their vision is relatively poor, then acute passive localization might not offer a selective advantage (for a review of vision in bats, see Eklof, 2003). To the extent that some bats may have substituted echolocation for vision, the demand for orienting the eyes may no longer exist in those species. Bats also have very small interaural distances that limit the magnitude of interaural locus cues available to them. Although this limitation may be largely compensated in echolocation by their use of extended high-frequencies, naturally occurring sounds may contain much less energy at these high frequencies, thus putting passive localization at a disadvantage. These two considerations—that selective pressure for good passive localization is reduced, and that echolocation derives some of its success from the use of very high frequencies not available in most naturally occurring sounds—suggest the possibility that passive sound localization in at least some bats might even be less acute than in comparable non-echolocating mammals.

We may now be in a position to begin to determine whether the use of echolocation is associated with better or worse passive localization acuity than found in non-echolocators. So far, passive sound localization acuity has been determined for five species of echolocating bats: Big brown bats (*Eptesicus fuscus*, Koay et al., 1998), Jamaican fruit bats (*Artibeus jamaicensis*, Heffner et al., 2001), Short-tailed fruit bats (*Carollia perspicillata*, Heffner et al., 2007), Greater spear-nosed bats (*Phyllostomus hastatus*, Heffner

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* Corresponding author. Tel.: +1 419 530 2684; fax: +1 419 530 2136.
E-mail address: Rickye.Heffner@utoledo.edu (R.S. Heffner).

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et al., 2007), and the click-echolocating, Egyptian fruit bats (*Rousettus aegyptiacus*, Heffner et al., 1999). Although their thresholds are better than those of similar-sized rodents, they are not better than expected based on their vision (Heffner et al., 2007). However, a crucial comparison would be with closely related species that do not echolocate, specifically members of the Pteropodidae. There is fossil evidence of a very early bat capable of powered flight but without cochlear specializations often associated with echolocation (Simmons et al., 2008). Nevertheless, molecular evidence supports the monophyly of bats such that all extant bats are descended from a common ancestor (perhaps a descendant of this early Eocene species) that was capable of flight and echolocation; members of the Pteropodidae subsequently lost echolocation, coming to depend more on vision (e.g., Jones and Holderied, 2007; Springer et al., 2001). We here report the sound-localization acuity of two species of Pteropodidae for comparison to echolocating bats and to other non-echolocating mammals: the Straw-colored fruit bat (*Eidolon helvum*), a large 250 g species native to Africa, and the Dog-faced fruit bat (*Cynopterus brachyotis*), a small 35 g species native to southern Asia.

2. Materials and methods

Sound-localization thresholds were obtained using the same conditioned suppression/avoidance procedure and equipment we have used to test other bats as well as many other mammals (e.g., Koay et al., 1998). Briefly, a bat was trained to break contact with the reward spout if a brief noise burst was presented from its left side, and to continue drinking from the spout if the noise came from its right. Sound localization thresholds were determined by gradually reducing the angular separation between the left and right speakers until the animal could no longer discriminate between them. The anatomical procedure entailed preparing a flat mount of the retina and mapping the ganglion cell densities throughout the retina using a standard procedure (e.g., Koay et al., 1998; Stone, 1981).

2.1. Subjects

Two *E. helvum* (Bat A, female, 266 g and approximately 3 years old, and Bat B, male, 320 g, approximately 9 years old) and two *C. brachyotis* (Bat A male, 38 g, and Bat C, female, 40 g; both approximately 2 years old) were tested. Note that one *E. helvum* (Bat A) and one *C. brachyotis* (Bat A) had been tested previously to determine their behavioral audiograms (Heffner et al., 2006b). The mean maximum functional interaural distance (i.e., the time required for a sound to travel from one auditory meatus to the other, determined by measuring the distance around the head from one auditory meatus to the other and dividing by the speed of sound in air) was 145 μs for *E. helvum* and 86 μs for *C. brachyotis*. A third *E. helvum* was used for the anatomical analysis of the retina. The bats were maintained on a diet of mixed fruit (Barnard, 1995). While on test, they were housed individually in wood and plastic mesh cages (48 × 39 × 95 cm) and allowed to fly daily in the test chamber for exercise. They had free access to water and earned their food in the test sessions, except for occasional supplements to maintain healthy body weights.

All bats were captive born and on loan from the Lubee Bat Conservancy. These experiments were carried out with the approval of the University of Toledo Animal Care and Use Committee.

2.2. Behavioral apparatus

Testing was conducted in a carpeted, double-walled acoustic chamber (IAC model 1204; 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were lined with acoustic foam. The equipment for stimulus generation and behavioral measurement was located outside the chamber and the bats were observed via closed-circuit television.

The bats were tested in custom-built wire mesh cages. So that each species could maneuver easily, the test cage for *E. helvum* measured 50 × 30 × 50 cm and was constructed of 1-in (2.5-cm) mesh, and the cage for *C. brachyotis* was 37 × 22 × 23 cm, constructed of 0.5-in (1.26-cm) mesh. The bats climbed onto a small raised platform in the middle of the test cage to reach a reward spout placed in front of the platform. This configuration minimized acoustic obstructions between the bats and the loudspeakers. The platform was covered with a dampened carpet to provide traction and electrical contact between the bat and reward spout. When the bat licked the reward spout, a steady trickle of fruit juice was dispensed using a syringe pump. The pump was housed in a foam-lined box and placed in the back of the test chamber to eliminate dispenser noise. The fruit juice consisted of a mixture of cantaloupe and pear juice with a multi-vitamin supplement (Lubee Fruit Bat Supplement). Requiring the bat to steadily lick the reward spout for fruit juice served to maintain its head in a fixed position in the sound field. A shock generator was also connected between the reward spout and platform; the shock level was adjusted for each individual to the lowest intensity that produced a reliable avoidance response (breaking electrical contact with the spout). The bats did not develop a fear of the spout, as they readily returned to it after the shock. A 25-W shock-indicator light, placed below the cage, was turned on and off concurrently with the shock to signal a successful avoidance and indicate when it was safe to resume licking the spout. (See Heffner et al., 2006b for detailed descriptions of the two test-cages.)

2.3. Acoustical apparatus and sound measurement

Passive localization thresholds were determined using a 100-ms broadband noise burst, which was of sufficient duration to be localized, but brief enough to minimize scanning. The noise bursts were digitally generated (Zonic A & D 3525, set to produce energy up to its maximum range of 100 kHz) and presented through loudspeakers mounted at ear level on a perimeter bar (102 cm radius) centered on the position occupied by an animal's head while it was licking the spout. The signal was gated on (Coulbourn S84-04; 0.1 ms rise/fall), split into left and right channels, amplified to 66 dB SPL (Coulbourn S82-24), and routed to one of a pair of loudspeakers. During testing, the signal intensity (66 dB SPL) was randomly attenuated up to 3.5-dB on each presentation (Coulbourn S85-08 programmable attenuator) to reduce the possibility of the animals responding on the basis of small intensity differences. The electrical signal going to the speakers was continuously monitored during test sessions with an oscilloscope (Tektronix TDS 210).

The sound pressure levels of the noise bursts (SPL re 20 μNewton/m^2) were measured and equated daily for different speaker pairs with a 1/4-in (0.64 cm) microphone (Brüel & Kjaer 4135), preamplifier (Brüel & Kjaer 2619), measuring amplifier (Brüel & Kjaer 2608), filter (Krohn-Hite 3202; bandpass range set at 250 Hz–100 kHz), and spectrum analyzer (Zonic A & D 3525). The measuring system was calibrated with a pistonphone (Brüel & Kjaer 4230). Sound measurements were taken by placing the microphone in the position occupied by the animal's head and pointing it directly toward a loudspeaker (0° incidence). The noise spectrum was relatively flat (±4 dB) between 3 kHz and 45 kHz with energy above background level up to 100 kHz (for the acoustic spectrum of the signal, see Heffner et al., 2007). Thus the signal contained audible energy throughout the hearing range of both species (Heffner et al., 2006b).

Four pairs of ribbon tweeters (Panasonic EAS-10TH100A) that had been matched for similarity of detail in their noise spectrum were used. Thus, within a single session, the bats could be tested at four different angles of separation before the loudspeakers had to be moved. The loudspeakers within each matched pair were switched before each session to reduce the possibility that the animals might respond on the basis of speaker quality. Further, at least one pair of loudspeakers was placed at an angular separation that was too small to be discriminated by the bats to quickly reveal any artifacts that might arise. These precautions were adequate to prevent responses to non-locus cues, as demonstrated by each animal's inability to discriminate the smaller angles of speaker separation.

2.4. Behavioral procedure

2.4.1. Training

The bats were first trained to steadily lick the spout in the presence of a series of four 100-ms broadband noise bursts (400 ms interpulse interval) presented from a loudspeaker located 90° to their right. Next, they were trained to break contact with the spout (a "detection response" consisting of backing away slightly or lifting the head from the spout) whenever the noise bursts were presented from a loudspeaker located 90° to their left. Breaking contact allowed them to avoid a mild electric shock (0.5 s) delivered via the spout 2.0 s after left signal onset, and indicated that the bat had detected the shift in sound location. A 25-Watt light bulb underneath the cage was turned on concurrently with shock to provide feedback for a successful avoidance (since, in those cases, the bat actually received no shock) and permitted the animals to distinguish between successful avoidance of a shock and false alarms (i.e., breaking contact when the signal was presented from the right side).

2.4.2. Testing

After the animals had been trained in the avoidance procedure, the signals were reduced to a single 100-ms noise burst per 2-s trial for threshold testing. Test sessions consisted of a series of 2-s trials separated by 1.5-s intertrial intervals. Thus the bats received one signal every 3.5 s. The response of an animal on each trial (i.e., whether or not it made a detection response) was defined as the duration of contact with the spout during the last 150 ms of each 2-s trial. If the animal broke contact for more than half of the 150-ms period, a response was recorded. The response was classified as a "hit" if the preceding signal had come from the animal's left side and as a "false alarm" if it had come from the animal's right. If the bat was not in contact with the spout during the 1 s preceding a trial, data from that trial was not recorded even though the trial proceeded as usual. Thus, all trials in which the animal was grooming or otherwise not engaged in the task were automatically discarded.

Each trial had a 22% probability of containing a left signal warning of shock. The sequence of left-right trials was quasi-random and is described in detail elsewhere (Heffner and Heffner, 1995; Heffner et al., 2006a). Hit and false-alarm rates were determined for each block of approximately 7–9 left trials and 28–36 associated right trials given at a particular angle. The hit rate was then corrected for the false alarm rate to produce a performance measure according to the formula: Performance = Hit rate − (False alarm rate × Hit rate). This measure, which can range from 0 (no hits) to 1 (100% hit rate with no false alarms), proportionately reduces the hit rate by the false alarm rate observed for each block of trials at each loudspeaker angular separation, rather than by the average false alarm rate for the entire session. This results in a more precise performance measure for a specific block of trials as false alarm rates vary within a session, depending on the discriminability of the stimulus and the animal's level of motivation.

Noise localization thresholds were determined by gradually reducing the angular separation between the left and right loudspeakers in blocks of trials until a bat could no longer discriminate reliably between them (i.e., the hit rate no longer differed significantly from the false alarm rate, binomial distribution, $p > .05$). This was always followed by testing at a larger angle to verify the bat's motivation and continued good performance before again decreasing the angle of separation. A typical session consisted of approximately 50 to 60 left trials (plus approximately 200 to 250 associated right trials) during which at least four different angles were tested. Daily testing continued until performance no longer improved at any angle, that is, until stable asymptotic performance had been reached. The mean of the three blocks of trials with the highest scores after asymptote had been reached was calculated to represent the best performance for each animal. These means were then plotted as the best performance curve for each individual. Threshold was defined as the angle yielding a performance score of 0.50, which was determined by interpolation. The angles tested were 180°, 120°, 90°, 60°, 45°, 30°, 20°, 15°, 10°, and 5° (*C. brachyotis* was not tested at 20°).

2.5. Anatomical procedure

One *E. helvum* was anesthetized with an overdose of ketamine (80 mg/kg) plus xylazine (4 mg/kg) intramuscularly and perfused with 0.9% saline followed by 10% formalin. The superior sclera of each eye was marked with fine suture before the eye was removed. The retinae were dissected free from the eyes and any vitreous humor removed gently using a fine brush. The retinae were mounted on separate gelatinized microscope slides with the ganglion-cell layer uppermost. They were then stained with thionine (for details of the retinal wholemount procedure, see Stone, 1981).

The density of the ganglion cells was measured throughout the retina in 0.25-mm steps through central regions where ganglion-cell density changed rapidly, and in 0.5 to 1.0-mm steps in the periphery where changes in density were more gradual. The number of ganglion-cell nucleoli within a sampling rectangle 25×38 μm (0.00095 mm^2) were counted under a 100x oil immersion objective. Nucleoli were counted because they are much smaller than whole cells or nuclei and largely avoid the problem of counting elements that lie only partially within the sampling rectangle. To further control for cells only partially within the counting rectangle, all nucleoli touching the upper or left sides of the rectangle were included in the counts, but those touching the lower or right sides of the rectangle were not included. When counted in this manner, it has been repeatedly shown that ganglion-cell densities and distributions vary little within a species, especially in comparison to the differences between species, giving confidence that an estimate based on a single individual reasonably represents the species in cross-species comparisons (Hughes, 1977).

To make comparisons between species, the maximum cell density was determined by detailed sampling with measures taken at intervals as small as 100 microns in the densest regions. This maximum density (in cells/degree^2) was used to determine two values. First, the maximum theoretical resolvable spatial frequency (i.e., acuity—the maximum number of cycles of a square wave grating that can be resolved per degree of visual angle) was calculated using Shannon's sampling theorem (e.g., DeBruyn et al., 1980; Hughes, 1977). The calculation is based on the requirement that for visual features to be distinguished as separate (such as two edges), they must fall on separate neural elements such that acuity in cycles/degree = $[(\text{number of cells/deg}^2)^{1/2}]/2$. Although an estimate based on limiting anatomical factors, this value agrees closely with behavioral measures. For example, for the Big brown bat

(*Eptesicus fuscus*), the values are 0.5 cycles/degree for the behavioral test and 0.7 cycles/degree for the anatomical estimate (Bell and Fenton, 1986). For the domestic cat, behavioral measures of acuity range from about 8.5 to 9.7 cycles/degree and the density of ganglion cells estimates acuity at 8.9 cycles/degree (Belleville and Wilkinson, 1986; Heffner and Heffner, 1992a; Jacobson et al., 1976).

The second determination, which is the width of the field of best vision has been operationally defined (Heffner and Heffner, 1992a) as the horizontal width (in degrees) of the region encompassing ganglion-cell densities equal to or greater than 75% of the maximum density. Although arbitrary, the 75% criterion has proven useful for cross-species comparisons because it is not subject to a floor effect as a low criterion would be because density does not fall much below 50% in some species. Similarly, a higher criterion, such as 90%, becomes subject to minor fluctuations around maximum density, as density can easily fall to 85% then rise again to 95% before falling monotonically (for more detail, see Heffner and Heffner, 1992a).

3. Results

3.1. Noise localization thresholds (minimum audible angles)

The abilities of the two *E. helvum* and the two *C. brachyotis* to localize 100-ms noise bursts are illustrated in Fig. 1. Each individual was capable of performing perfectly (100% hits with no false alarms) at angles of 90° or greater separation. This showed high motivation as well as competence to perform the cognitive and motor requirements of the task. Moreover, individuals within each species showed excellent agreement, providing further confidence in the data. Given strong motivation to perform well (few misses or false alarms), and in the absence of disease, our experience has been that there is very little variation in hearing abilities in mammals and we can have confidence that these individuals are reasonable representatives of their species. Below about 30°, performances declined sharply with the .50 performance threshold averaging 11.7° for *E. helvum* and 10.5° for *C. brachyotis*.

3.2. Retinal analysis

We were able to obtain retinae of one *E. helvum*. The flattened retina was 14.25 mm in diameter and subtended a visual angle of approximately 190°. The retina was typical of Pterodiformes with the receptors arranged not in the usual flat layer, but on what appear to be tiny cones, referred to as papillae, with the peaks pointing toward the vitreal surface of the retina. The function of this arrangement is unknown. The ganglion cells lay above this layer of papillae and are thus relatively easy to view and to count. The ganglion cells reached a peak density of 8421 cells/mm^2, which, in an eye of this size, indicates a potential visual acuity of 3.4 cycles/degree. This is similar to the 1.7–5.5 cycles/degree reported for three other species of *Pteropus* (Neuweiler, 1962; Pettigrew et al., 1988) and the 3.15 cycles/degree reported for *Rousettus aegyptiacus* (Heffner et al., 1999). We should note that the larger of these values, denoting greater acuity, are based on the anatomical limits suggested by the ganglion-cell density and are sometimes slight overestimates when compared to behaviorally tested visual acuity (Muller et al., 2007).

The isodensity contours of the retinal ganglion cells are illustrated in Fig. 2. The region of greatest density is concentrated

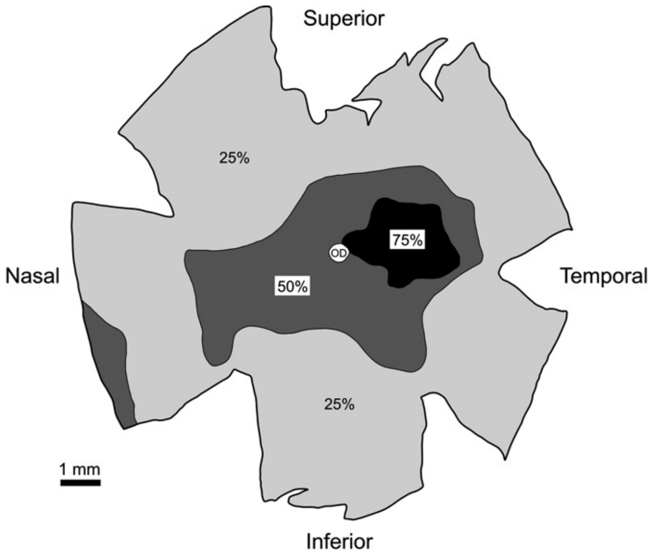


Fig. 2. Isodensity contours of retinal ganglion cells of *Eidolon helvum*. Percentage values and shading indicate the regions encompassed by ganglion cell densities at least 75%, 50%, or 25% of maximum. The region of 75% of maximum (referred to here as the field of best vision) is narrower than found in many rodents, but broader than in primates or carnivores.

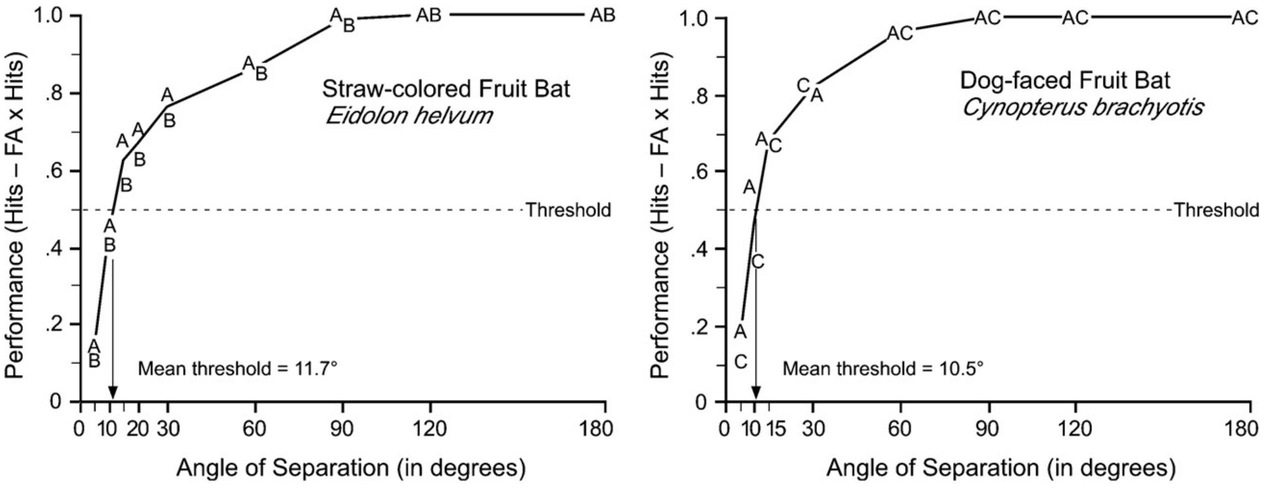


Fig. 1. Sound-localization performance of two *Eidolon helvum* and two *Cynopterus brachyotis*. Note good performance at large angles and sharp declines at angles smaller than 30°. The mean 50% performance thresholds were 11.7° for *E. helvum* and 10.5° for *C. brachyotis*.

temporally to the optic disc, as in most mammals. This is consistent with our measured binocular field of vision of approximately 60°. The density of ganglion cells fall rapidly to 25% of maximum toward the temporal periphery, but more gradually nasally. Note that the density of ganglion cells does not fall below 25% of maximum even at the most peripheral parts of the retina. This density distribution is similar to that of many mammals, but is in contrast to the echolocating bats examined so far in which density of ganglion cells does not usually fall below 50% of maximum, a common character in species with indistinct fields of best vision (c.f., Heffner and Heffner, 1992a; Hughes, 1977). The horizontal width of the field of best vision for *E. helvum* is 45.5° (defined as the region of the retina with ganglion-cell densities of at least 75% of maximum).

Due to agreement obligations with the Lubee Bat Conservancy, we were unable to obtain retinae for analysis from *C. brachyotis*.

4. Discussion

4.1. Echolocators and non-echolocators

As shown in Table 1, the passive localization thresholds for the two non-echolocating species fall within the range of the echolocating bats. As reported previously, passive localization thresholds for bats as a group lie very near the 12° mean for mammals (Heffner et al., 1999, 2001, 2007; Koay et al., 1998). Together these results demonstrate that echolocation does not necessarily entail a sharpening of passive localization acuity and that these may be separate processes despite the apparent use of shared neural components (Razak et al., 1999). Note that the non-echolocating bats are not obviously poorer localizers than the echolocating bats. Rather, both echolocating, non-echolocating, and the unusual tongue-click echolocating bats (*Rousettus*) seem to be similar to each other and to the 'average' mammal. Nevertheless, mammals as a group vary widely in their sound localization acuity, and it is worth examining some potential explanations for this variation and asking if bats are exceptions to these explanations.

4.2. Relation between vision and passive sound localization

4.2.1. Width of the field of best vision

The width of the field of best vision is so far the only reliable predictor of passive sound-localization acuity (Heffner and Heffner, 1992a). Transient sounds alert mammals to potential danger in their environment. Most mammals then direct their visual attention toward the sound source to better identify it so as to take appropriate action—the only exceptions are species that live continuously underground in the dark where vision cannot operate and where action is directionally limited by tunnels. When orienting vision to a sound source, it is the best vision that is directed regardless of its absolute acuity. Thus, species with broad fields of best vision require less precise directional information from hearing than species with narrower fields of best vision to visually capture a sound source (cf., Heffner and Heffner, 1992a). As shown in Fig. 3, the relationship between sound-localization acuity and the width of the field of best vision remains strong with the addition of the non-echolocating *E. helvum* ($r = .889$, $p < .0001$).

Table 1
Passive sound-localization thresholds (minimum audible angles) of bats

Species	Common name	Passive sound-localization threshold in degrees*
Non-echolocators		
Cynopterus brachyotis	Dog-faced fruit bat	10.5
Eidolon helvum	Straw-colored fruit bat	11.7
Atypical echolocator**		
Rousettus aegyptiacus	Egyptian fruit bat	11.6
Echolocators		
Phyllostomus hastatus	Greater spear-nosed bat	9.5
Artibeus jamaicensis	Jamaican fruit bat	9.9
Eptesicus fuscus	Big brown bat	14
Carollia perspicillata	Short-tailed fruit bat	14.7

* Includes only thresholds obtained using procedures that do not permit echolocation to contribute to performance. Accordingly, tests of obstacle avoidance and flying toward a sound-emitting prey are not included.

** This genus of Pteropodidae is believed to have evolved from non-echolocating species and to have secondarily developed echolocation using double tongue clicks for orientation in caves. This is in contrast to the laryngeal calls used by all other echolocating bats (Jones and Holderied, 2007; Waters and Vollrath, 2003). For the purposes of this discussion, this species will be treated as a non-echolocator, although its inclusion among the echolocators does not change the conclusions.

4.2.2. Visual acuity

Absolute visual acuity (i.e., maximum resolvable spatial frequency) does not seem to be a factor in sound localization; it is not reliably correlated with sound-localization acuity even when the aberrant subterranean species are omitted leaving only those species living in a well lit, three-dimensional world ($r = -.33$, $p = .10$). Even when field of best vision is removed as a contributing factor using partial regression analysis, the correlation between visual acuity and sound-localization acuity remains unreliable ($r = -.41$, $p = .063$). On the other hand, if we remove the contribution of visual acuity, the residual correlation between sound-localization and the width of the field of best vision remains robust ($r = .87$, $p < .0001$). Thus, even if the best visual acuity is relatively poor, as it is in most bats (Bell and Fenton, 1986; Pettigrew et al., 1988), it seems that animals still orient their best available vision toward a sound source and this applies to both echolocating and

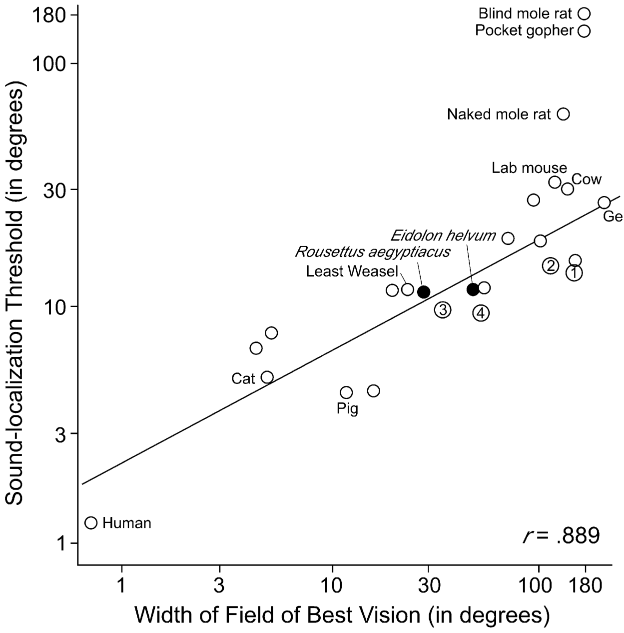


Fig. 3. The relationship between width of the field of best vision and passive sound-localization acuity in mammals. Filled circles indicate two pteropid bats; *E. helvum* (this report) is a non-echolocator and *R. aegyptiacus* (Heffner et al., 1999) echolocates using tongue clicks, primarily for orientation in caves. Echolocating bats are indicated by numerals: 1, *Eptesicus fuscus* (Koay et al., 1998), 2, *Carollia perspicillata* (Heffner et al., 2007), 3, *Artibeus jamaicensis* (Heffner et al., 2001), and 4, *Phyllostomus hastatus* (Heffner et al., 2007). Other cases are shown as open circles with selected species identified for convenience. Note that the blind and naked mole rats are actually poorer localizers than illustrated because they were unable to localize brief sounds at all and were tested using longer-duration signals (Heffner and Heffner, 1992b, 1993). For identification of individual species see Heffner et al., (2007) and for a data table see Heffner and Heffner, (2003).

non-echolocating bats as well as to other mammals. The relationship also applies across both predators and prey, and across nocturnal and diurnal activity cycles. As we have noted previously, the relationship is even supported by underground species whose vision is spread across the retina with little or no region of best acuity. These species, as predicted, also have the most limited sound-localizing ability (Heffner and Heffner, 1990, 1992b, 1993). Thus vision and hearing seem inextricably linked in sound localization.

4.3. Magnitude of binaural locus cues

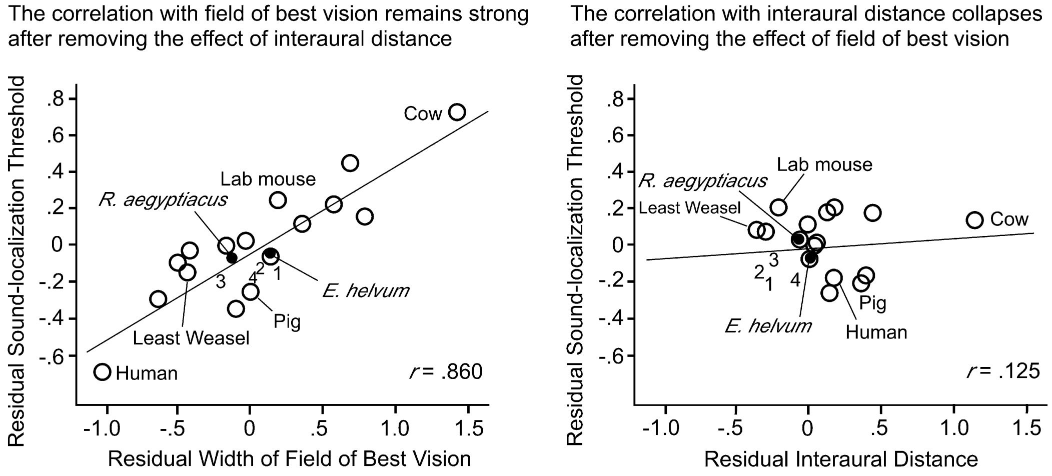
The explanation of the variation in sound-localization acuity described above and elsewhere (e.g., Heffner and Heffner, 1992a) is based on the role that sound localization plays in survival and reproduction—it addresses the question, Why do some mammals localize better than others (Mayr, 1960)? Such an explanation is quite different from one that describes the mechanisms that make sound localization possible or that permit some species to be more acute than others (addressing the question, How?). So far, a mechanistic explanation for the variation in sound localization has not been found. Although we know a great deal about the neural mechanisms underlying sound localization in a few species, we know very little about differences in these mechanisms between species. Indeed, it is likely that there is more than one way to achieve acute passive localization (just as there are different ways to achieve echolocation). Thus it is possible that no *single* anatomical or physiological factor will provide a satisfactory explanation for the variation in passive sound-localization acuity.

One factor that we believe can be ruled out is the magnitude of the binaural locus cues available to a species. If large interaural differences were associated with good passive localization acuity and small interaural differences with poor acuity, then there should be a strong correlation between head size (i.e., functional interaural distance) and sound localization acuity. We would not expect a perfect correlation because both time delays and intensity differences are affected by the shape of the head and pinnae as well as the distance between the ears. The actual correlation among surface-dwelling mammals is $r = -.51$ ($p = .003$). Although reliable, little variability is actually accounted for and there are some dramatically deviant species. Most notably, although some large species including humans, pigs, and elephants have excellent sound-localization acuity, others such as horses and cattle are very poor localizers (cf. Heffner and Heffner, 2003). In addition, larger species tend to have different lifestyles, and even different vision, from smaller species and the moderate correlation owes much of its strength to one of these factors. Multiple regression analysis has revealed that there is one factor that accounts for nearly all of the correspondence between functional interaural distance and passive sound-localization acuity, and that is the width of the field of best vision. As illustrated in Fig. 4, when the width of the field of best vision is held constant so that its influence is removed from both other variables, the correlation between functional interaural distance and sound localization is not significant ($r = .125$, $p = .59$). In contrast, if functional interaural distance is held constant and thus removed as an influence, the correlation between sound localization and the width of the field of best vision is practically unaffected ($r = .86$, $p < .0001$).

Physical cues are necessary for localizing sounds, yet not all large animals make use of the large cues available to them by virtue of the long time delay and the large sound shadow provided by their large heads and pinnae. Although at first surprising, such failure to take advantage of some of the information available in the environment is quite common; for example, ultraviolet radiation is available to all, but many mammals have not evolved the ability to detect it whereas many others do—moreover, they do so using a variety of visual pigments (Jacobs, 1993). On the other hand, some small species such as the bats and least weasels have evolved mechanisms to permit sound localization superior to that of much larger species. Again, just as the visual pigments that permit detection of ultraviolet radiation evolved differently and independently in different lineages (Jacobs et al., 1991), we may find that the mechanisms underlying good localization also vary among mammals.

4.4. Summary

Although we do not yet understand all the mechanisms underlying the variation in mammalian sound localization, an explanation based on selective pressure that was proposed 16 years ago has remained viable (Heffner and Heffner, 1992a). Specifically, passive sound localization allows animals to detect unseen activity in the environment and then direct the eyes for visual scrutiny of the sound source. If the visual analysis that takes place uses only a narrow fovea or area centralis, then the directional information must be relatively precise to avoid the necessity of a visual search.



The correlation with field of best vision remains strong after removing the effect of interaural distance

The correlation with interaural distance collapses after removing the effect of field of best vision

Fig. 4. Left, the residual correlation between the width of the field of best vision and passive sound localization among surface dwelling mammals remains strong even when the contribution of functional interaural distance is removed. Right, in contrast, the residual correlation between functional interaural distance and sound localization becomes unreliable when the contribution of the width of the field of best vision is removed as a factor. [Interaural distance is defined as the time (in microseconds) required for a sound to travel from one auditory meatus to the other; it serves as a proxy for the magnitude of interaural difference cues.]

Alternatively, if an animal has its best vision spread in a broad visual streak, then even an approximate indication of direction to the sound source would be adequate to acquire the visual target within its broad region of best vision. So far, although the sample of bats is still limited, there are no obvious differences between echolocating and non-echolocating bats, or even between echolocating bats and other mammals. Despite a three-fold difference in interaural distance, the passive sound-localization thresholds of the bats we have examined conform to those predicted by their visual characteristics.

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