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Sound Localization Acuity and its Relation to Vision in Large and Small Fruit-eating Bats: I. Echolocating Species, *Phyllostomus hastatus* and *Carollia perspicillata*

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

Dept. of Psychology, University of Toledo, Toledo, OH 43606

Abstract

Passive sound-localization acuity for 100-msec noise bursts was determined behaviorally for two species of bats: *Phyllostomus hastatus*, a large bat that eats fruit and vertebrates, and *Carollia perspicillata*, a small species that eats fruit and nectar. The mean minimum audible angle for two *P. hastatus* was 9°, and that for two *C. perspicillata* was 14.8°. This places their passive sound-localization acuity near the middle of the range for mammals. Sound localization varies widely among mammals and the best predictor of a species' acuity remains the width of the field of best vision ($r = .89, p < .0001$). The five echolocating bats that have been tested do not deviate from this relationship suggesting that despite their specialization for echolocation, the use of hearing to direct the eyes to the source of a sound still serves as an important selective factor for sound localization.

Keywords

sound localization; vision; echolocation

1. Introduction

The ability of mammals to localize sound varies widely from one species to the next (H. Heffner and Heffner, 2003). Two-point acuity for localizing brief sounds around the midline varies from the 1–2° threshold of humans and elephants to 30° or more for house mice and cattle, with subterranean rodents (gopher, blind mole-rat, and naked mole-rat) being unable to localize brief sounds at all. As previously noted, this variation does not appear to be due to special ecological adaptations, such as whether an animal is a predator or prey, diurnal or nocturnal; nor is it related to the magnitude of the available binaural locus cues, as indicated by an animal's head size (R. Heffner and Heffner, 1992; R. Heffner et al., 2001). Instead, the variation in sound-localization acuity is related to the width of the field of best vision such that animals with narrow visual fields have good sound-localization acuity, whereas those with broader visual fields have poorer acuity. The explanation for this relationship is that the acuity of sound localization is affected by its use in directing an animal's visual orienting to the source of a sound. The visual orienting response is one of the most consistent behaviors to result upon hearing a sound (Haftner and DeMaio, 1975; Pumphrey, 1950)—indeed, it is more rapid than the visual orienting response to a flash of light (Whittington et al., 1981). The accuracy with which the ears must orient vision (by moving the head and/or the eyes) depends on the width

Corresponding author: Rickye Heffner, Dept. of Psychology MS #948, University of Toledo, 2801 W. Bancroft St., Toledo, Ohio 43606, Phone: 419-530-2684, Fax: 419-825-1659, Email: Rickye.Heffner@utoledo.edu.

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of an animal's field of best vision, with the result that species with narrow fields, such as humans, require greater sound localization acuity than species with wide visual streaks, such as cattle; those that do not use vision (subterranean mammals) do not localize brief sounds at all.

Because the majority of bats use echolocation in place of vision for obstacle avoidance and foraging, the need to direct the eyes to the source of a sound might be reduced or even eliminated. So far, however, this does not appear to be the case. At present, passive sound localization acuity has been determined in three species of echolocating bats: the big brown bat, *Eptesicus fuscus*, a species that catches insects in open spaces, the Jamaican fruit bat, *Artibeus jamaicensis*, a frugivore that forages among clutter, and the Egyptian fruit bat, *Rousettus aegyptiacus*, a megachiropteran frugivore that uses simple tongue clicks for echolocation. Despite their specialization for echolocation, these three species have thresholds that are consistent with the relationship between passive sound localization and vision that has been seen in other mammals (R. Heffner, Koay, and Heffner, 2001). It seems that passive sound localization remains useful in guiding visual orienting, even in echolocators. However, bats are a diverse order, and before we can conclude that there are no differences between echolocating bats and other mammals in the factors that influence passive sound localization, thresholds from a larger sample of bats must be included.

As part of a continuing survey of hearing in bats, we report here the sound-localizing abilities of two echolocating bats from the Phyllostomidae, a diverse family of New-world bats. *Phyllostomus hastatus*, the greater spear-nosed bat, is the second largest New-world bat and an omnivore that often preys on small vertebrates; *Carollia perspicillata*, the short-tailed fruit bat, is a small species that eats fruit, nectar, and pollen. They represent different lifestyles that complement those of the three bats described above for which thresholds are already known. Often called whispering bats, phyllostomids echolocate using short, frequency-modulated (FM) pulses of very low intensity. Within Phyllostomidae, the species that eat fruit, nectar, or even other vertebrates usually rely more on smell, vision, or passive listening during foraging. Echolocation is then used primarily for orientation and flying in clutter (e.g., Holler and Schmidt, 1996).

2. Materials and methods

Sound-localization thresholds were obtained using the same conditioned suppression/avoidance procedure and equipment we have used to test many other mammals, including other bats (e.g., Koay et al., 1998). Briefly, a bat was trained to avoid a mild electric shock by ceasing to drink fruit juice from a spout whenever a 100-ms noise burst was presented from its left side while continuing to drink when the noise burst came from its right side. 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).

2.1. Subjects

Two female *Phyllostomus hastatus* (Bat B, at 70 g and Bat C, at 66 g; both approximately 5 years old) and two male *Carollia perspicillata* (Bat A and Bat C, at 17 g and approximately 1 year old) were tested. Note that one *P. hastatus* (Bat B) and one *C. perspicillata* (Bat A) had been tested previously to determine their behavioral audiograms (Koay et al., 2002; Koay et al., 2003). The mean maximum functional interaural distance (i.e., the time required for a sound to travel from one auditory meatus to the other) was 108 μ s for *P. hastatus* and 47 μ s for *C. perspicillata*. A third individual of each species 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 $\times$ 39 $\times$ 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.

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; $2.55 \times 2.75 \times 2.05$ 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. Two 50W incandescent lights provided illumination within the sound chamber.

The bats were tested in custom-built wire mesh cages. So that each species could maneuver easily, the test cage for *P. hastatus* measured $50 \times 30 \times 50$ cm and was constructed of 2.5-cm mesh, and the cage for *C. perspicillata* was $37 \times 22 \times 23$ cm constructed of 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 vitamin 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 (backing away slightly or lifting its head from the spout). The bats did not develop a fear of the spout, as they readily returned to it after the shock. A 25W 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 Koay et al., 2002 and 2003 for detailed descriptions of the test-cages.)

2.3. Acoustical apparatus and sound measurement

Passive localization thresholds were determined using a 100-ms broadband noise burst (Fig. 1), 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 $20 \mu\text{Newton/m}^2$) 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). Noise 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). As illustrated in Fig. 1, the noise spectrum was relatively flat (± 4 dB) between 3 kHz and 45 kHz with energy above background level up to 100 kHz. Thus the signal contained audible energy up to at least 80 kHz for both species, which encompassed most of their hearing range (except for approximately 0.5 octave at the upper end of the hearing range for *C. perspicillata*; Koay et al., 2002,2003).

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 artifact that might arise and to rule out echolocation of the active speaker. 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.

2.5. Behavioral procedure

2.5.1 Training—The bats were first trained to steadily lick the spout in the presence of a series of four 100-ms broadband noise bursts presented from a loudspeaker located 90° to their right. Next, they were trained to break contact with the spout (a “detection response”) whenever the noise bursts were presented from a loudspeaker located 90° to their left. Breaking contact with the spout allowed the bat to avoid a mild electric shock (0.5 s) delivered via the spout 2.0 s after left signal onset and indicated that the animal had detected the shift in sound location. The 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). After the animals were trained in this basic avoidance procedure, the signals were reduced to one 100-ms noise burst per 2-s trial.

2.5.2. 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 and decided whether to break contact or to continue drinking after each noise pulse. 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 discarded.

Each trial had a 22% probability of containing a left signal. The sequence of left-right trials was quasi-random and is described in detail elsewhere (H. Heffner and Heffner, 1995; H. Heffner et al., 2006). 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 $\times$ 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. (For discussions of why d' may not be an appropriate measure of performance for psychophysical studies of animals, see Green, 1995 and H. Heffner and Heffner, 2003.)

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 motivation and continued good performance before again decreasing the angle of separation. A typical session consisted of approximately 50 to 60 warning trials (plus approximately 200 to 250 associated safe trials) during which at least four different angles were tested. Daily testing continued until performance no longer improved at any angle, that is, until asymptotic performance had been reached. The mean of the three blocks of trials with the highest scores at asymptote 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. perspicillata* was not tested at 45°).

2.6. Anatomical procedure

One individual of each species 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 0.1-mm steps through central regions where ganglion-cell density changed more rapidly, and in 0.5-mm steps in the periphery where changes in density were more gradual. The number of ganglion-cell nucleoli within a sampling rectangle $33 \times 52 \mu\text{m}$ (0.001716 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 lying 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, thus providing 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 being taken at 100 micron intervals in the denser regions. This maximum density (in cells/degree²) 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, Wise, and Casagrande, 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 = [(the number of cells/deg²)^{1/2}]/2. Although an estimate, this value agrees closely with behavioral measures. For example, for the big brown bat, the values are 0.7 and

0.5 cycles/degree, respectively (Bell and Fenton, 1986), and for the domestic cat, behavioral measures of acuity range from about 8.5 to 9.7 cycles/degree and the ganglion cell density estimates acuity as 8.9 cycles/degree (Belleville and Wilkinson, 1986; R. Heffner and Heffner, 1992a; Jacobson et al., 1976).

The width of the field of best vision has been operationally defined (R. 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 R. Heffner and Heffner, 1992a).

3. Results

3.1. Noise localization thresholds (minimum audible angles)

The ability of the two greater spear-nosed bats (*P. hastatus*) to localize single 100-ms noise bursts emitted from loudspeakers centered symmetrically about midline is illustrated in Fig. 2. The bats were capable of performing perfectly (100% hits with no false alarms) at angles equal to or greater than 60° separation. Such performance at large angles indicates high motivation and good ability to perform the behavioral task. Performance began to fall sharply at angles smaller than 30° and neither animal performed above chance at 5°. Difficulty in discriminating small angles is also reflected in the bats' false alarm rates, which ranged from 0 – 3% at angles larger than 60°, to 10 – 15% at angles of separation smaller than 15°. Chance performance at a small angle is evidence that there were no acoustic or other artifacts that might have provided spurious cues as to which loudspeaker was active. Bat B's 50% threshold (corrected for false alarms) was 9.5° and Bat A's threshold was 8.5°, resulting in a mean threshold of 9°. The sharp decline toward threshold and good agreement between the two individual bats provide further confidence in these results.

The localization ability of the two short-tailed fruit bats (*C. perspicillata*) is illustrated in Fig. 3. Again, the bats were capable of perfect performance at large angles and performance fell sharply to chance at angles of 5 – 10°. As expected, the false alarm rates for *C. perspicillata* increased with increasing difficulty of the discrimination ranging from approximately 4% at 100° to 21% at 5° (at which angle performance was not above chance). There is good agreement between the two individuals tested, with bat A's threshold at 15° and bat C's at 14.5°, for a mean localization threshold of 14.8°.

3.2. Retinal analysis

The flattened retina of *P. hastatus* was 4.6 mm in diameter and subtended approximately 180° of arc. The ganglion cells were typically small, about 7 µm in diameter, with a distinguishable nucleus and nucleolus. The smaller, darkly staining glia and the faint cells without an obvious nucleolus that were located below the main layer of ganglion cells were not included in the enumeration of ganglion cells. The ganglion cells reached a peak density of 7868 cells/mm²; this high density was achieved because the ganglion cells were actually packed in a layer two cells thick in the densest region. In such a small eye, even this high density indicates a visual acuity of only 1.2 cycles/°. This is comparable to the 1.1 cycles/° in another phyllostomid, the Jamaican fruit bat (*Artibeus jamaicensis*; R. Heffner, Koay, and Heffner, 2001a). The isodensity contours of the retinal ganglion cells are illustrated in Fig. 4. The region of greatest density (and thus best visual acuity) is concentrated, as in most mammals, in the temporal region. This is consistent with a binocular visual field of approximately 40°. The density of

ganglion cells falls gradually across the horizon of the eye. Temporally, the density falls below 50% of maximum, but nowhere does the density fall below 25% of maximum. In the nasal retina, the density remains relatively high, not falling below 50% of maximum. Such a relatively flat density distribution across the retina is seen in other species with relatively poor vision and stands in contrast to the majority of mammals in which density falls below 25% of maximum throughout at least the periphery of the retina (c.f., R. Heffner and Heffner, 1992a; Hughes, 1977). The width of the field of best vision for this species, as defined by the portion of the retina with ganglion-cell densities at least 75% of maximum, is 51° .

The retina of *C. perspicillata* is also illustrated in Fig. 4. Its flattened retina was smaller, approximately 2.6 mm in diameter. The ganglion cells were readily discernible and in a distinct layer. There were patchy areas of shrinkage in the peripheral edges of the retina and these areas were not included in the density measures. In addition, the superior edge of the retina was lost in processing, but this damage did not interfere with the delimitation of the field of best vision. The highest concentration of cells was $18,358 \text{ cells/mm}^2$ —a relatively high value compared to many mammals, but, because the eye is so small, the visual acuity is calculated to be $0.94 \text{ cycles/}^\circ$. This is very similar to the $0.71 \text{ cycles/}^\circ$ estimated using a behavioral measure, the optomotor response (Suthers, 1966). The region with the 75% densest concentration of ganglion cells is spread more broadly across the superior retina in a region 110° wide. Outside this densest area, density of the ganglion cells falls gradually below 50% of maximum toward both the nasal and temporal edges of the retina, but, as in *P. hastatus*, nowhere does it fall below 25% of maximum.

4. Discussion

4.1. Bats compared to other mammals

The addition of thresholds for the greater spear-nosed bat and the short-tailed fruit bat not only increases the number of species available for statistical analysis, but also broadens the range of passive sound-localization thresholds known for bats so that it now extends from 9° to nearly 15° (Fig. 5). Nevertheless, this range remains relatively narrow when compared to the range for mammals as a whole, or even when compared with other orders such as rodents, as can be seen in Fig. 5. The thresholds for bats lie in the middle of the distribution for mammals, which is an approximately normal distribution with a mean of 12° . Despite their small size, bats are better localizers than some larger mammals including most rodents and hoofed mammals. This relatively good passive localization in such small mammals supports the assertion that head size, and the resulting magnitude of interaural locus cues, does not determine localization acuity. The following discussion explores some of the factors thought to influence passive localization acuity among mammals.

4.2. The relation between vision and passive sound localization

As previously noted, the width of the field of best vision is the only reliable predictor of passive sound-localization acuity so far proposed ($r = .890$, $p < .0001$; R. Heffner and Heffner, 1992a). Mammals can use sound as an alerting signal that something important is happening in the environment. They may then direct their visual attention toward a sound source to examine and evaluate it—the only exceptions being species that live underground in the dark. The results reported here for bats are consistent with this relationship. Note that the relationship between size of the visual field and sound localization acuity remains strong regardless of absolute visual acuity (R. Heffner and Heffner, 1992). 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 vision toward a sound source.

The relationship between the width of the field of best vision and passive sound localization acuity for airborne sounds is illustrated in Fig. 6. Species whose best vision is concentrated within a relatively narrow field (e.g., the human fovea) have relatively accurate auditory locus information allowing them to foveate a target accurately. Species whose best vision is spread more broadly across the retina can acquire visual targets within those broad fields with less accurate direction from the auditory system. The addition of the two species of bats in this report brings the number of bat species available for analysis to five, and all are consistent with the relationship established by other mammals. Although this may at first seem surprising, it is important to recognize that bats do use their vision for orientation to the environment and, in some cases, for identifying foods (Bell and Fenton, 1986; Buchler and Childs, 1982; Eklöf, 2003; Hessel and Schmidt, 1994; Williams and Williams, 1970). By examining the species for which information is available (Fig. 6), we can see that the relationship between sound localization and field of best vision applies across a wide range of mammals, including species with good and poor visual acuity, nocturnal and diurnal activity cycles, and both predators and prey. The only deviant species are those that are strongly adapted to a subterranean lifestyle and virtually never venture above ground. In those cases, vision is degenerate (loss of external eyes in the blind mole rat is the most extreme) and there is no value in directing vision when there is no light (R. Heffner and Heffner, 1993).

Visual acuity (two-point resolution in cycles/degree) remains an *unreliable* predictor of sound-localization acuity ($r = -.330, p = .107$). Its weak correlation with sound localization is due to the mutual correlation of each of these factors with the width of the field of best vision. Multiple regression analysis supports this suggestion, revealing that visual acuity remains unreliably correlated with sound-localization acuity even when the influence of the width of the field of best vision is removed statistically ($r = .453, p = .068$). On the other hand, when visual acuity is removed, the contribution of the width of the field of best vision to sound-localization acuity remains strong and reliable ($r = .824, p < .0001$). Thus among the mammals currently available for analysis, the width of the field of best vision best predicts how well a species will localize sound. Bats are not an exception to this relationship.

4.2.1. Magnitude of binaural locus cues—Although the magnitude of the physical cues to locus would seem to set limits on achievable localization acuity, it has not been a robust predictor of the differences in acuity between species. Head size (specifically the time required for a sound to travel from one auditory meatus to the other) is a major factor in determining the magnitude of both the interaural time difference and the interaural intensity/spectral difference available to an animal. Thus it serves as a proxy for these cues. Although head size, expressed as maximum interaural distance, is correlated with passive sound-localization thresholds ($r = -.521, p = .004$), this relationship falls to chance when the influence of the width of the field of best vision is removed statistically ($r = -.311, p = .225$). Therefore, the apparent contribution of interaural distance to the variation in sound-localization acuity can be largely accounted for by the common variance each of these factors shares with the width of the fields of best vision.

Similarly, high-frequency hearing, which enables use of interaural spectral-difference cues and pinna cues (R. Heffner, Koay, and Heffner, 2001b), is moderately correlated with sound-localization acuity ($r = .426, p = .024$). But again, this relationship is due to the common correlation of both factors with the width of the field of best vision. When the contribution of the width of the field of best vision is removed statistically, the correlation between sound localization and high-frequency hearing falls to chance ($r = .105, p = .69$).

In summary, although the magnitude of the binaural cues, and in particular the availability of the high-frequency cues, are important *mechanisms* in sound localization, they do not appear to be determinants of the wide species differences observed in sound-localization ability.

Instead, mammals seem to hear as high as needed to support a passive localization acuity that is adequate to direct their fields of best vision. The fact that the primary source of selective pressure for high-frequency hearing in mammals is the need to passively localize sound is further supported by the observations that filtering out high frequencies from a sound degrades localization acuity and that subterranean mammals that have lost the ability to localize brief sounds have also lost the ability to hear high frequency sounds (H. Heffner and Heffner, 2003). The five species of bats examined so far are consistent with this relationship. Their fields of best vision are neither very wide nor very narrow and their sound-localization acuity is near the mean for mammals.

It should be noted that the sample of bats is still too small to speculate with confidence on whether echolocation has resulted in passive sound-localization acuity that is better or worse than seen in other mammals with similar fields of best vision. However, with the exception of the Egyptian fruit bat (*Rousettus aegyptiacus*), a Pteropid species that echolocates with simple tongue clicks rather than laryngeal pulses, all of the bats tested so far have slightly better sound-localization acuity than predicted by the width of their fields of best vision. It remains to be seen whether laryngeal echolocation is associated with slightly enhanced passive localization of sound. Of particular interest in this regard will be comparisons to sound localization thresholds for non-echolocating bats.

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Fig. 1. Acoustic spectrum of the broadband noise localized by the greater spear-nosed bats (*P. hastatus*) and the short-tailed fruit bats (*C. perspicillata*). Background noise is indicated by the lower line. The noise spectra for each speaker were used to match the speaker pairs used for testing.

Fig. 2. Sound-localization performance of two greater spear-nosed bats (*P. hastatus*) for a single 100-ms noise burst. Letters indicate individual animals and the dashed line indicates the 0.50 performance level (corrected for false-alarm rate) that defines threshold. The arrow indicates the mean threshold of 9°.

Fig. 3. Sound-localization performance of two short-tailed fruit bats (*C. perspicillata*) for a single 100-ms noise burst. Letters indicate individual animals and the dashed line indicates the 0.50 performance level (corrected for false-alarm rate) that defines threshold. The arrow indicates the mean threshold of 14.8°.

Greater spear-nosed bat
Phyllostomus hastatus

Short-tail fruit bat
Carollia perspicillata

Fig. 4.

Retinal ganglion cell isodensity contours for the greater spear-nosed bat (*P. hastatus*) and the short-tailed fruit bat (*C. perspicillata*). Percentage values and density of 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 as the field of best vision) is broader in *C. perspicillata* than in *P. hastatus*. OD denotes optic disc. (For examples of isodensity contours in other species of mammals, see R. Heffner and Heffner, 1992, and Hughes, 1977).

Sound-Localization Thresholds of Mammals

Fig. 5.

Sound-localization thresholds of the greater spear-nosed bat (*P. hastatus*) and the short-tailed fruit bat (*C. perspicillata*) compared to the behavioral thresholds for all other mammals that were obtained using brief sounds. (*The naked mole rat, pocket gopher, and blind mole rat were tested with longer-duration signals because they could not localize brief sounds; aquatic mammals tested underwater are not included in this analysis.) Note that threshold is displayed on a log scale that expands the representation of smaller angles to better illustrate the large number of species with thresholds smaller than 20°.

Fig. 6.

Relation between the width of the field of best vision and sound-localization threshold. Species with narrow fields of best vision have better sound-localization acuity than species with broad fields of best vision. The five species of bats appear consistent with the relationship established by other mammals despite their adaptation for echolocation. Note that the three subterranean species (8*, pocket gopher, 9*, naked mole rat and 10*, blind mole rat) deviate from the pattern of surface-dwelling mammals; because they had to be tested using longer-duration signals, their localization ability is actually worse than indicated here and their deviation is, in reality, more pronounced. Because their hearing and vision are both reduced, the subterranean species have been omitted from the statistical analyses. **Cp**, **Short-tailed Fruit Bat** (*C. perspicillata*, current report); **Ph**, **Greater Spear-nosed Bat** (*P. hastatus*, current report); 1, Virginia Opossum (*Didelphis virginiana*, Ravizza and Masterton, 1972); 2, **Egyptian Fruit Bat** (*Rousettus aegyptiacus*, R. Heffner et al., 1999); 3, **Big Brown Bat** (*Eptesicus fuscus*, Koay et al., 1998); 4, **Jamaican Fruit Bat** (*Artibeus jamaicensis*, R. Heffner et al., 2001a); 5, Japanese Macaque (*Macaca fuscata*, H. Heffner and Heffner, 1990); 6, Human (Mills, 1958); 7, Groundhog (*Marmota monax*, Conesa et al., 1992); 8*, Pocket Gopher (*Geomys bursarius*, R. Heffner and Heffner, 1990); 9*, Naked Mole Rat (*Heterocephalus glaber*, R. Heffner and Heffner, 1993); 10*, Blind Mole Rat (*Spalax ehrenbergi*, the retina is highly degenerate and the animal's eyes are buried below skin and muscle; R. Heffner and Heffner, 1992b); 11, Grasshopper Mouse (*Onychomys leucogaster*, R. Heffner and Heffner, 1988b); 12, Gerbil (*Meriones unguiculatus*, R. Heffner and Heffner, 1988a); 13, Wild Norway Rat (*Rattus norvegicus*, H. Heffner and Heffner, 1985); 14, Laboratory Mouse (*Mus musculus*, R. Heffner et al., 2001b); 15, Hamster (*Mesocricetus auratus*, Izraeli et al., 2002); 16, Chinchilla (*Chinchilla laniger*, R. Heffner et al., 1994); 17, Domestic Dog (*Canis familiaris*, H. Heffner, 1978); 18, Domestic Cat (*Felis domesticus*, R. Heffner and Heffner, 1988c); 19, Least Weasel (*Mustela nivalis*, R. Heffner and Heffner, 1987); 20, Ferret (*Mustela putorius*, Kavanagh and

Kelly, 1992); 21, Domestic Pig (*Sus scrofa*, R. Heffner and Heffner, 1989); 22, Domestic Cattle (*Bos taurus*, R. Heffner and Heffner, 1992c).