Sound Localization in an Old-World Fruit Bat (*Rousettus aegyptiacus*): Acuity, Use of Binaural Cues, and Relationship to Vision

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The passive sound-localization acuity of Egyptian fruit bats (*Rousettus aegyptiacus*) was determined using a conditioned-avoidance procedure. The mean minimum audible angle for left–right discrimination for 3 bats was 11.6°—very near the mean for terrestrial mammals. The bats also were able to localize low- and high-frequency pure tones, indicating that they can use both binaural phase-difference and binaural intensity-difference cues to localize sound. Moreover, they were able to use the binaural phase-difference cue up to at least 5.6 kHz, which is higher than other mammals yet tested. The width of the Egyptian fruit bats' field of best vision was 27°. This value is consistent with the hypothesis that the role of passive sound localization is to direct the eyes for visual scrutiny of sound sources. Thus, the passive localization abilities of these echolocating megachiropteran fruit bats do not deviate from the patterns established for nonecholocating mammals.

Bats, with more than 950 species, constitute one of the most widespread and numerous orders of mammals, second only to rodents. Moreover, they are unique in that they are the only mammals to have evolved true flight. Yet, until recently, bats were considered to be the least known of mammalian orders (Walker, 1968), and it is only in the past 30 years that they have come to be heavily studied.

One aspect of bats that has been studied extensively is their hearing ability because many species use echolocation to orient themselves in their environment as well as to locate prey. Despite this interest, little is known about the passive sound-localization acuity of bats, even though some of them rely on passive localization to locate prey (Arita & Fenton, 1997; Barclay, Fenton, Tuttle, & Ryan, 1981; Fuzessery, Buttenhoff, Andrews, & Kennedy, 1993; Ryan & Tuttle, 1987). Indeed, out of nearly 1,000 species, the passive sound-localization acuity of only 2 bats has been determined (Fuzessery et al., 1993; Koay, Kearns, Heffner, & Heffner, 1998). However, such a sample is far too small to establish either the passive sound-localization acuity of bats or the cues that they use to localize, especially given the large variation in these abilities that is known to occur in mammals (R. S. Heffner & Heffner, 1992a).

The purpose of this study was to increase knowledge of the hearing of bats by determining the passive sound-localization abilities of Egyptian fruit bats (*Rousettus aegyptiacus*), megachiropteran bats found in Africa and the Middle East. Unlike the more numerous microchiropteran bats that use echolocation to orient themselves and to detect

and locate prey, the approximately 150 species of megachiropteran bats, also referred to as Old-World fruit bats, rely instead on vision and olfaction to orient themselves and to find food; most do not use echolocation at all (Neuweiler, 1989; Nowak, 1991). Only one genus, the cave-roosting *Rousettus*, contains species (including *Rousettus aegyptiacus*) capable of echolocation. This species uses a rudimentary echolocation system based on tongue clicks rather than laryngeal phonation, as do all other echolocating bats (Griffin, Novick, & Kornfield, 1958). Although their echolocation is adequate for orienting in caves, their vision is better for detecting obstacles smaller than 1 mm (Griffin et al., 1958). Being fruit eaters, they do not require echolocation to hunt prey as do insectivorous or most carnivorous bats (see Arita & Fenton, 1997, for a discussion of the variety of echolocation in bats). Because of its more limited use of echolocation and the simple form of its signal (clicks rather than phonation that changes in frequency over time), this genus may be of interest for comparisons with both echolocating microchiropteran bats and nonecholocating mammals.

This study was a threefold investigation of the passive sound-localization abilities of Egyptian fruit bats to determine how this species compares with other mammals. First, we determined the bats' left–right sound-localization acuity by using a standard 100-ms broadband noise burst. We then examined their ability to use binaural time- and intensity-difference cues for sound localization by determining their ability to localize pure tones at a fixed angle of 60° horizontal separation. Finally, we measured the packing density of their retinal ganglion cells to estimate visual resolution throughout the retina to evaluate the relationship between the width of the field of best vision and sound-localization acuity. The resulting data were compared with those of other mammals.

Method

The behavioral sound-localization tests used a conditioned-avoidance procedure in which a hungry bat steadily licked a food

spout while sounds were presented from a loudspeaker to its right but ceased eating and broke contact with the spout when sounds were presented from a loudspeaker to its left to avoid a mild shock (H. E. Heffner & Heffner, 1995). The anatomical procedure involved mapping the ganglion-cell densities throughout the retina of an Egyptian fruit bat.

Subjects

Three Egyptian fruit bats (Rousettus aegyptiacus), 1 male (labeled B) and 2 females (labeled A and C), were used in the behavioral tests, and a 4th bat was used for the anatomical analysis of the retina. The bats were individually housed with free access to water (supplemented with vitamins and minerals) and received fruit juice during the daily test session. They typically consumed 40–50 mL of fruit juice in sessions lasting 60–80 min. Additional supplements of fruit were given as needed to maintain body weight comparable to that of wild bats.

Behavioral Apparatus

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

The bats were tested in a cage (50 × 30 × 40 cm) constructed of 1-in. (2.54-cm) hardware cloth, mounted 93 cm above the floor on four thin legs attached to its frame (see Koay, Heffner, & Heffner, 1998, for an illustration of the test cage). A food spout (3-mm-diameter brass tube topped with a 10 × 15-mm lick plate) was mounted vertically so that it projected up through the bottom of the cage 7.5 cm above the cage floor. The spout was attached by an 80-cm-long flexible tube to a 50-mL syringe located below the cage that served as the food reservoir. A fruit puree consisting of a mixture of melon, banana, applesauce, peanut butter, dry milk powder, and vitamin supplement, finely blended and sieved through a tea strainer (0.5 × 1.0-mm openings), was dispensed through the spout by a syringe pump similar to that described elsewhere (Thompson, Porter, O'Bryan, Heffner, & Heffner, 1990). Both the syringe pump and the food reservoir were housed in a high-density polyethylene plastic box (64 × 212 × 28 cm) lined with egg-crate foam to eliminate the noise of pump activation.

During testing, a bat was placed on a small platform (31 × 14 × 8 cm) located directly behind the spout. The top of the platform was covered with a piece of dampened carpet to facilitate traction and to ensure good electrical contact as the bat ate from the spout. The tip of the food spout was placed in front of and approximately 5 mm below the front of the platform to minimize obstructions between the bat's ears and the loudspeaker. The bat positioned itself above and slightly behind the spout while eating such that the lick plate was entirely covered by its jaw and could not interfere with the sound field. A contact circuit, connected between the food spout and the platform, served to detect when the bat made contact with the spout and activated the syringe pump. Requiring the bat to maintain mouth contact with the spout served to fix its head within the sound field.

Finally, a mild shock was delivered by a shock generator connected between the food spout and the platform. The shock was adjusted for each bat to the lowest level that produced a consistent avoidance response to a readily detected signal. The bats never developed a fear of the spout because they readily returned to it after having received the shock. A 15-W lightbulb, mounted 0.5 m

below the cage, was turned on and off with the shock to signal successful avoidance and to indicate when it was safe to return to the food spout.

Acoustical Apparatus

Sound-localization ability was assessed using both broadband noise bursts and pure tones. The sounds were presented through loudspeakers mounted at the bat's ear level on a perimeter bar (102-cm radius and 101-cm height) and centered on the position occupied by the bat's head while it was eating from the food spout.

Broadband noise. The minimum audible angle for these Egyptian fruit bats was determined using a broadband noise whose spectrum contained frequencies throughout most of the hearing range of this species. A complex signal was chosen because it provides good binaural and monaural locus cues that are readily localized by most mammals, but the 100-ms duration was brief enough to minimize opportunities for scanning movements. This is also the stimulus that has been used most frequently to determine the localization acuity of other species, thereby facilitating comparisons.

Broadband noise bursts, 100 ms in duration, were generated by a noise generator (set to produce energy up to 100 kHz; Grason-Stadler 1285, Grason-Stadler Co., West Concord, MA). The electrical signal was randomly attenuated over a 3-dB range (Coulbourn S85–08 programmable attenuator, Coulbourn, Lehigh Valley, PA) from one trial to the next to reduce the possibility of the bats responding on the basis of small intensity differences. The signal was then sent to a rise–fall gate (0.1-ms rise–fall; Coulbourn S84–04), split into left and right channels, amplified to a 68-dB sound pressure level (SPL; Crown D-75, Crown International, Inc., Elkart, IN), and routed to four matched pairs of piezoelectric speakers (Motorola KSN1005A, Motorola, Chicago, IL). The signal going to the speakers was monitored by the experimenter on an oscilloscope (B & K Precision 1476 A, Dynascan, Tokyo, Japan). Threshold testing was conducted using single 100-ms noise bursts.

The spectrum of the noise produced by this acoustic apparatus was monitored using a spectrum analyzer (Zonic 3525, Zonic Corp., Tokyo, Japan) and a 0.25-in. (0.635-cm) microphone (Brüel & Kjaer 2619, Brüel & Kjaer, Naerum, Denmark). As illustrated in Figure 1, the noise spectrum was relatively flat, between 3 and 45
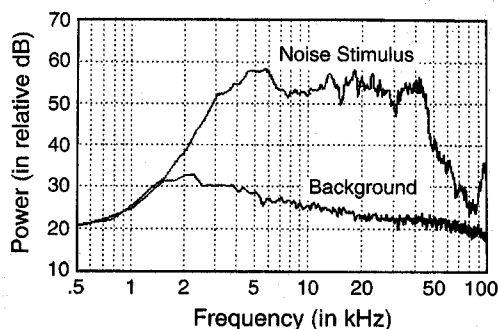

Figure 1. Spectrum of the broadband noise stimulus used for sound localization (upper line) compared with background noise (lower line). The 100-ms noise burst was presented at a 68-dB sound pressure level (SPL) and included frequencies throughout most of the hearing range for Egyptian fruit bats, which at a level of 60-dB SPL extends from 2.25 to 64 kHz (Koay, Heffner, & Heffner, 1998).

kHz, with energy up to 100 kHz. Thus, the signal included frequencies throughout the hearing range of this species except for less than 0.5 octaves at the upper and lower ends of its audible spectrum.

Pure tones. Sine waves were generated by a tone generator (Krohn-Hite 2400 AM/FM Phase Lock Generator, Krohn-Hite, Avon, MA) and were randomly attenuated over a 3-dB range from one trial to the next (Coulbourn S85–08 programmable attenuator). The tones were pulsed (100-ms on and 900-ms off, for two pulses), shaped by a rise–fall gate (10-ms rise–fall; Coulbourn S84–04), and band-pass filtered (0.33 octaves above and below the frequency of the tone; Krohn-Hite 3550). Finally, the signal was split into left and right channels, separately amplified (Crown D-75), and sent to two loudspeakers (Panasonic ribbon supertweeter EAS-H400/6, Matsushita Electric, Osaka, Japan). The acoustic signal at the location of a listening bat was analyzed for overtones using a spectrum analyzer (Zonic 3525), and any harmonics in the acoustic signal were at least 40 dB below the fundamental frequency and below the bat's detection threshold.

Testing was conducted in half-octave steps from 4 to 50 kHz with the loudspeakers 60° apart (30° to the left and 30° to the right of midline). In addition, Bat C was tested at two intermediate frequencies of 4.5 and 5.0 kHz. Each frequency was presented at 50 dB above the average absolute threshold for Egyptian fruit bats (see Koay, Heffner, & Heffner, 1998).

Sound-Level Measurement

The sound pressure levels of the stimuli (SPL re $20\mu N/m^2$) were measured, and the left and right loudspeakers were equated daily with a 0.25-in. (0.635-cm) microphone (Brüel & Kjaer 4135), preamplifier (Brüel & Kjaer 2619), measuring amplifier (Brüel & Kjaer 2608), and filter (band-pass, 250 Hz–100 kHz; Krohn-Hite 3202). 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 bat's head and pointing it directly toward a loudspeaker (0° incidence).

Behavioral Procedure

The bats were first trained to eat steadily from the food spout in the presence of a series of four 100-ms broadband noise bursts (400-ms interburst intervals) presented from a loudspeaker located 90° to the right of the bats. Next, the bats 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 to avoid a mild electric shock (0.5 s) delivered through the spout (2.0 s after left signal onset). Breaking contact with the spout usually lasted for the entire trial and indicated that a bat had detected the shift in locus. The lightbulb located underneath the cage was turned on while the shock was present at the spout. The light provided feedback for successful avoidance (because in those cases no shock was actually received by the bats) and permitted the bats 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 bats were trained in the basic avoidance procedure, the signals were reduced to one noise burst per 2-s trial.

Test sessions consisted of a series of 2-s trials that began with the onset of a stimulus. To present the trials at a slower pace, the 2-s trial intervals were separated by 1.5-s intertrial intervals during which no signals were presented. Thus, the bats received one signal every 3.5 s and made a decision after each as to whether to break contact or to continue eating. The response of a bat on each trial (i.e., whether it made a detection response) was operationally

defined as the duration of contact with the spout during the last 150 ms of each trial. Recording only the response at the end of the 2-s trial period gave the bat sufficient time to react to the signal. If the bat broke contact for more than half of this final 150-ms period, a detection response was recorded. The response was classified as a "hit" if the preceding signal had come from the bat's left side and as a "false alarm" if it had come from the bat's right side. Breaking contact during the intertrial interval had no effect on the presentation of trials. However, if the bat was not in contact with the spout during the 1 s preceding a trial, data from that trial were not recorded even though the trial proceeded as usual. This permitted us to avoid using trials when the bat was grooming or was otherwise not engaged in the task.

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. E. Heffner & Heffner, 1995). Both hit and false-alarm rates were determined for each block of 8–10 left trials and 32–40 associated right trials for each stimulus type and angle. The hit rate was then corrected for the false-alarm rate to produce a performance measure according to the following formula: Performance = Hit Rate – (False-Alarm Rate × Hit Rate). This measure varies from 0 (no hits) to 1 (100% hit rate with no false alarms). Note that the calculation proportionately reduces the hit rate by the false-alarm rate observed for each block of trials in each stimulus condition rather than by the false-alarm rate averaged for the session as a whole.

Noise-localization thresholds were determined for a single 100-ms broadband noise burst. The angular separation between the left and right loudspeakers was gradually reduced symmetrically around the midline, with blocks of trials containing 8–10 left signal trials given at each angle until the bat could no longer perform the discrimination (i.e., the hit rate no longer differed significantly from the false-alarm rate; binomial distribution, $p > .05$). Sessions typically consisted of approximately 45–60 left trials (plus approximately 160–240 associated right trials) and usually tested four different angles, ranging from angles that were readily discriminated to those that were difficult or impossible to discriminate. Daily testing continued until performance no longer improved at any angle (18 sessions for Bat A and 13 sessions for Bats B and C), and the mean of the 25% of trial blocks with the highest scores was calculated. This mean was then plotted as the asymptotic performance curve for each bat. Threshold was defined as the angle yielding a performance score of .50, which was usually determined by interpolation. The actual angles tested were 180°, 120°, 90°, 60°, 45°, 30°, 20°, 15°, 10°, and 5°.

Tone-localization tests were conducted at a fixed angular separation of 60° (30° to the left and 30° to the right of the bat's midline), with the bat's performance calculated for blocks of trials containing 8–10 left trials. Testing was carried out using a single frequency per session for frequencies that sustained good performance. However, if a bat had difficulty or was unable to localize a particular frequency, as occurred at 8 kHz, tones of a localizable frequency were presented for several trials to verify that the bat was sufficiently motivated. Each frequency was tested over several nonconsecutive sessions for an average of 90 left trials. The top 25% of the trial blocks were averaged to represent the best performance of which the bats were capable.

Anatomical Procedure

One bat was anesthetized with an overdose of ketamine (80 mg/kg) plus xylazine (4 mg/kg) administered intramuscularly and perfused with 0.9% saline, followed by 10% formalin. The superior

surface of the eyes was marked with fine suture, and the eyes were removed and the retinas dissected free from the sclera. The retinas were then mounted on gelatinized slides with the ganglion-cell layer uppermost and stained with thionine (Stone, 1981). The density of the ganglion cells was determined throughout each retina in 0.2-mm steps through the regions of relatively high ganglion-cell density and 1.0-mm steps in the periphery. The number of ganglion-cell nucleoli within a sampling rectangle of $35 \times 53\mu m$ (0.001855 mm^2) was counted using a $100 \times$ oil-immersion objective. To make comparisons between species, the horizontal width of the region encompassing ganglion-cell densities greater than or equal to 75% of maximum density was determined as an indication of the width of the field of best vision. The maximum number of cells per square degree was used to calculate the maximum theoretical resolvable spatial frequency in cycles per degree (i.e., the maximum number of cycles of a square wave grating—alternating black and white bars—that can be resolved per degree of visual angle) using Shannon's sampling theorem (e.g., DeBruyn, Wise, & Casagrande, 1980). For additional details of the method, see R. S. Heffner and Heffner (1992c).

## Results

Behavioral Results

Noise localization. The ability of the 3 Egyptian fruit bats to discriminate standard 100-ms noise bursts emitted from loudspeakers centered symmetrically about midline is illustrated in Figure 2. The bats performed well at angles of 30° or larger, achieving asymptotic performances well above .80 corrected detection. Performance rapidly declined as the angle of separation fell below 20°. The thresholds for Bats A, B, and C were 12°, 11°, and 12°, respectively, for an overall average of 11.6°. The close agreement between the 3

subjects suggests that the thresholds obtained are representative of this species.

Pure-tone localization. The ability to use binaural locus cues was assessed using free-field presentation of pure tones of both low and high frequencies. This test is based on the absence of binaural intensity differences at low frequencies, because low frequencies undergo little or no attenuation as they travel around the head. However, low frequencies do permit the comparison of the temporal relationship of the signals at the two ears in the form of a phase-difference cue. This phase-difference cue becomes ambiguous for pure tones at high frequencies when more than one-half cycle of the sine wave occurs while the sound travels from one ear to the other. Tones above this "frequency of ambiguity" cannot be localized using the binaural phase cue because it is not possible to distinguish one cycle of the waveform from the next, with the result that binaural intensity differences provide the main locus cue (for a detailed discussion of phase ambiguity, see Jackson, 1996, or Saberi, Farahbod, & Konishi, 1998; for the formula for calculating the frequency of ambiguity, see Kuhn, 1977).

The calculated frequency at which the phase cue would become physically ambiguous for Egyptian fruit bats (with a head diameter of 3 cm) at an angle of ±30° is 7.6 kHz, indicated by the vertical bar in Figure 3. Thus, the ability to localize pure tones below 7.6 kHz suggests that Egyptian fruit bats can use the binaural phase-difference cue, and the ability to localize higher frequency pure tones suggests that this species can use the binaural intensity-difference cue.

As indicated by the asymptotic performances illustrated in Figure 3, the 3 Egyptian fruit bats showed good agree-
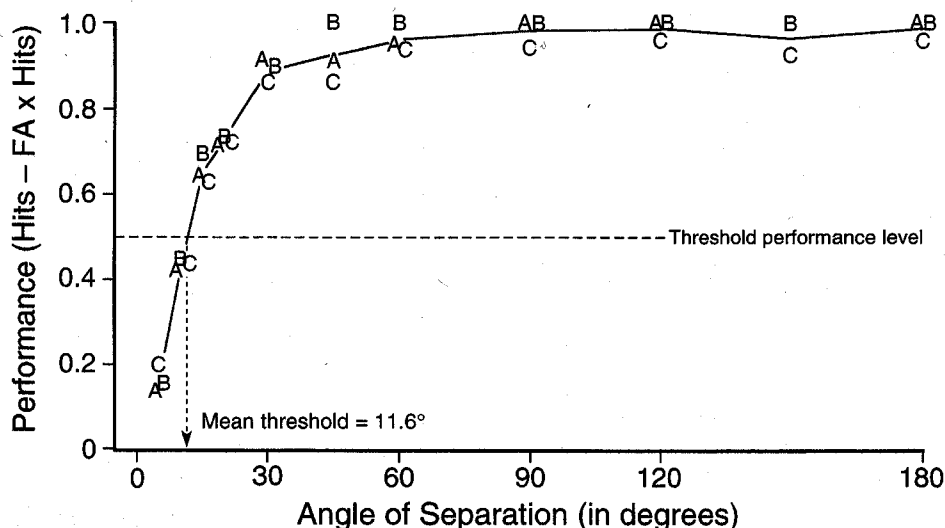
Figure 2. Sound-localization performance of 3 Egyptian fruit bats for single 100-ms bursts of broadband noise. A, B, and C indicate the 3 individual bats, and the dashed line indicates the 0.50 asymptotic performance level used to define threshold (arrow). Each point in the psychophysical curves for each bat represents testing over at least three sessions; the scores for each bat at each of the angles most crucial for determining threshold (10°–30°) are based on at least 40, to as many as 54, left trials (defining hit rate) and approximately four times as many right trials (defining false-alarm [FA] rate).
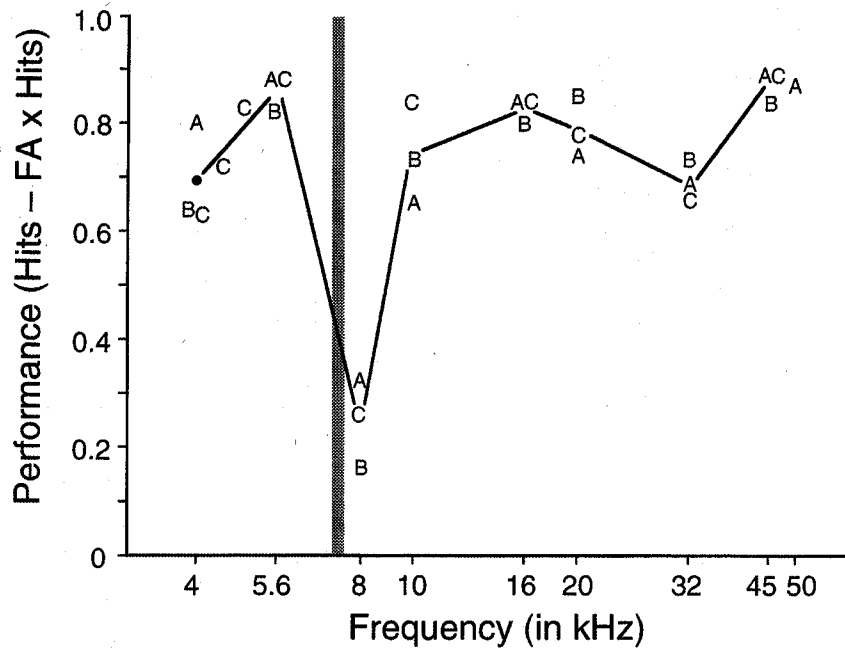
Figure 3. Sound-localization performance of 3 Egyptian fruit bats as a function of frequency of a pure-tone stimulus at a fixed angle of separation (±30° azimuth). A, B, and C represent the 3 individual bats; the vertical shaded bar indicates the upper limit (7.6 kHz) of the physical availability of the binaural phase-difference cue for Egyptian fruit bats estimated using the spherical head model. Note that the bats performed well at frequencies both above and below the frequency of ambiguity, indicating that they can use both binaural time- and intensity-difference cues. However, performance decreased to chance level at 8 kHz, a frequency for which the phase-difference cue is physically ambiguous but which does not produce a usable binaural intensity difference. The performance of each bat at each frequency is based on a minimum of 32 left trials (up to as many as 152 left trials), with approximately four times as many right trials. FA = false alarms.

ment in their tone-localization ability and good use of both binaural locus cues. Their use of binaural phase differences is indicated by their good performance at lower frequencies of 4–5.6 kHz. (Frequencies below 4 kHz were not tested because the hearing of Egyptian fruit bats does not extend much below 4 kHz and testing at these lower frequencies would have required sound levels in excess of 90-dB SPL to achieve constant intensities of 50 dB above hearing threshold.) Performances were also good (ranging between .66 and .89) at frequencies between 10 and 50 kHz, for which the phase cue was unavailable, thus forcing reliance on the intensity cue. By their good performances at both low and high frequencies, the bats demonstrated that they are capable of using both binaural phase-difference and binaural intensity-difference cues for localization.

It should be noted that not all frequencies were localized with equal ease. All 3 bats performed at chance levels (scores of approximately .30 or less) at 8 kHz, suggesting that neither binaural cue was effective. As shown by others (Obrist, Fenton, Eger, & Schlegel, 1993), 8 kHz is too low a frequency for the head and the pinnae to form an effective sound shadow to produce useful binaural intensity differences at ±30°; as predicted, it is also too high to produce an unambiguous binaural phase cue.

Retinal Analysis

The flattened retina of the Egyptian fruit bat was approximately 11.5 mm in diameter and subtended approximately 180° of arc. Although the ganglion-cell layer was unremarkable, the receptor-cell layer was highly unusual, arranged in a honeycomb of peaks and valleys, as has been reported for other Megachiroptera (e.g., Murphy, Howland, Kwiencinski, Kern, & Kallen, 1983). The isodensity contours of the retina are illustrated in Figure 4. The ganglion cells reached a relatively high peak density of 9,704 cells/mm², which, in an eye of this size, suggests a visual acuity of 3.15 cycles/degree. This level of acuity is essentially identical to that previously estimated for *Rousettus* (2.7–3.03 cycles/degree; Marks, 1980).

The region of greatest ganglion-cell density, and thus of best vision, is concentrated in the temporal retina. From this region, the density of the ganglion cells decreases relatively smoothly, but not steeply, toward the periphery, with most of the retina containing densities greater than 25% of maximum. The field of best vision incorporating the portion of the retina with ganglion-cell densities at least 75% of maximum was 27° in horizontal width, as illustrated in Figure 4. This value is less than the 139° for big brown bats,
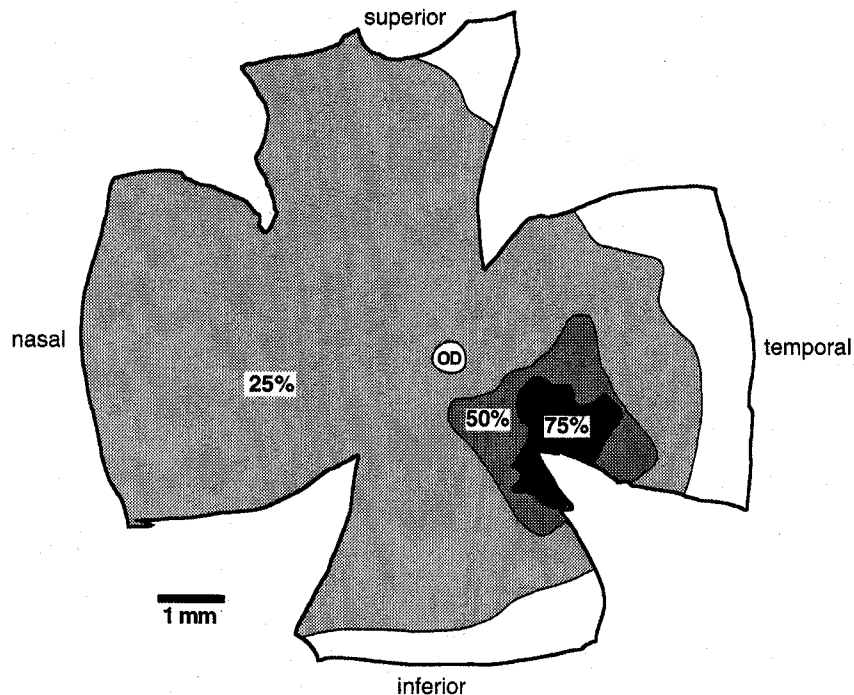
Figure 4. Retinal ganglion-cell isodensity contours in the retina of an Egyptian fruit bat. Density is expressed as a proportion of the maximum density (9,704 cells/mm²), and density gradients of 25%, 50%, and 75% are indicated by deepening shades of gray. Density gradients were relatively shallow, and density fell below 25% of maximum only in the temporal rim of the retina. OD = optic disk.

the only other bats for which this measure is available (Koay, Kearns, et al., 1998).

Discussion

Passive Localization Acuity of Egyptian Fruit Bats and Comparison With Other Mammals

Figure 5 illustrates the minimum audible angles for all mammals for which data are available. Compared with other mammals, the 11.6° threshold of Egyptian fruit bats is about average—the mean threshold for all surface-dwelling mammals (i.e., excluding aquatic and subterranean species) being 11.3°. The acuity of Egyptian fruit bats is most similar to that of Norway rats (12.8°), least weasels (12.0°), and ferrets (11.8°; H. E. Heffner & Heffner, 1985; R. S. Heffner & Heffner, 1987; Kavanagh & Kelly, 1987).

Passive sound-localization acuity has been determined in only two other species of bats: big brown bats (*Eptesicus fuscus*) and pallid bats (*Antrozous pallidus*). The big brown bats were tested with the same conditioned-avoidance procedure and free-field psychophysical methods used here with Egyptian fruit bats, and they achieved an average minimum audible angle of 14° (Koay, Kearns, et al., 1998). That threshold is only slightly larger than the 11.6° of the Egyptian fruit bats, and it, too, falls well within one standard deviation of the mean for terrestrial mammals. It should be noted that thresholds for big brown bats did not change significantly when six pulses of their 1.5-ms echo call were presented as the stimulus to be localized (Koay, Kearns, et al., 1998).

In contrast, the pallid bats were tested using a procedure in which they flew from a fixed perch to the sound of an anesthetized cricket tossed onto the floor (Fuzessery et al., 1993). Landing errors produced an estimate of the pallid bats' threshold of ±1°, making pallid bats one of the most accurate mammals known (cf. Figure 5). Recently, however, it has been suggested that gleaning bats may use low-intensity echolocation signals to supplement passive hearing during prey capture (Schmidt, Hanke, & Pillat, 1998). If so, then the 1° acuity of pallid bats may represent a combination of active and passive localization.

Active Versus Passive Localization in Egyptian Fruit Bats

Although the use of echolocation has not been extensively examined in Egyptian fruit bats, some information is available for comparison with their passive localization threshold of 11.6°. Egyptian fruit bats have been reported to reliably avoid obstacles as small as 1 mm by using echolocation (Griffin et al., 1958). This suggests that these bats not only can detect such obstacles but also can localize the returning echo well enough to avoid bumping into the obstacles with their relatively large bodies and broad wingspan. How such performance is achieved with their simple echolocation and whether it requires good spatial resolution are unknown. It is also noteworthy that, although Egyptian fruit bats and big brown bats have similar passive
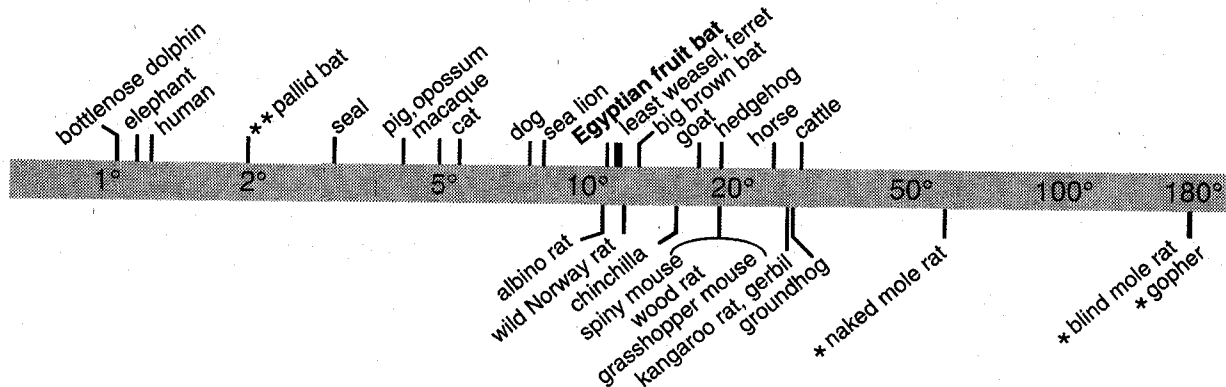
Sound-Localization Thresholds Among Mammals

Figure 5. Range of sound-localization thresholds among mammals. All thresholds are minimum audible angles for brief signals obtained with standard psychophysical techniques except as noted. *Subterranean species were tested using a series of brief noise bursts because they were unable to localize a single 100-ms noise burst above threshold level. **Pallid bats' threshold is based on landing error for bats flying to the sound of a cricket on a noisy substrate. Note the log scale.

localization acuity, microchiropteran bats are able to detect and avoid obstacles as small as 0.06 mm (Griffin et al., 1958; Schnitzler & Henson, 1980). These differences between active and passive localization suggest that the two abilities are not reflections of identical mechanisms.

Sound Localization and Vision

Egyptian fruit bats have relatively large eyes, and their estimated visual acuity of 3.15 cycles/degree is similar to the 3.0–5.5 cycles/degree of other megachiropteran bats (for reviews, see Pettigrew, Dreher, Hopkins, McCall, & Brown, 1988; Suthers, 1966). They search for food at dusk and at night using vision and olfaction, reserving echolocation for obstacle avoidance in dark cave roosts. Thus, Egyptian fruit bats are under much the same selective pressures to use vision as are other nocturnal mammals, and it is not surprising that their visual acuity is comparable with that of nocturnal rodents (cf. Birch & Jacobs, 1979; R. S. Heffner & Heffner, 1992c). As expected, their vision is superior to that of most Microchiroptera, whose very small eyes are rarely able to resolve more than 2 cycles/degree and sometimes far less, such as *Eptesicus fuscus* (0.75 cycles/degree; Koay, Kearns, et al., 1998) or *Rhinolophus rouxi* (0.35 cycles/degree; Pettigrew et al., 1988).

We have previously noted (R. S. Heffner & Heffner, 1992c) that the variation in sound-localization acuity among mammals appears to result from the need to direct the field of best vision to the source of a sound. Just how accurate sound localization must be to direct the eyes seems to depend on the width of an animal's field of best vision: Animals with narrow fields of best vision, such as humans, require good sound-localization acuity to direct their gaze so that the visual image of the sound source falls on their fovea, whereas animals with broad fields of best vision, such as

those with visual streaks, do not require as high a degree of sound-localization acuity to direct their gaze.

The relationship between the width of the field of best vision and passive sound-localization acuity is illustrated in Figure 6. As can be seen, mammals with narrow fields of best vision are more accurate localizers than mammals with broader fields of best vision. However, mammals that do not rely on vision would not be expected to conform to this relationship. Indeed, subterranean rodents, such as pocket gophers (*Geomys bursarius*) and naked mole rats (*Heterocephalus glaber*), which are adapted to living in dark burrows where visual scrutiny of sound sources is not possible, deviate significantly from this relationship ($p <$ .01, *t* test; Figure 6). Moreover, a third subterranean species, blind mole rats, with their vestigial eyes, is virtually unable to localize sound at all (R. S. Heffner & Heffner, 1990, 1992b, 1993). The question of whether bats, particularly those that have developed echolocation, have decreased their reliance on vision to the point that the relationship between vision and sound localization no longer applies to them remains to be addressed.

As can be seen in Figure 6, however, both Egyptian fruit bats and big brown bats conform to the relationship between width of the field of best vision and sound-localization acuity ($p >$ .5, *t* test). Thus, despite their use of echolocation for orientation or prey detection, both of which are tasks accomplished by vision in other mammals, the bats examined so far are like most other mammals in that the selective pressure for passive sound-localization acuity is determined by the need to direct the gaze to the source of a sound.

Use of Binaural Locus Cues

The ability of Egyptian fruit bats to localize both low- and high-frequency pure tones indicates that they are able to use
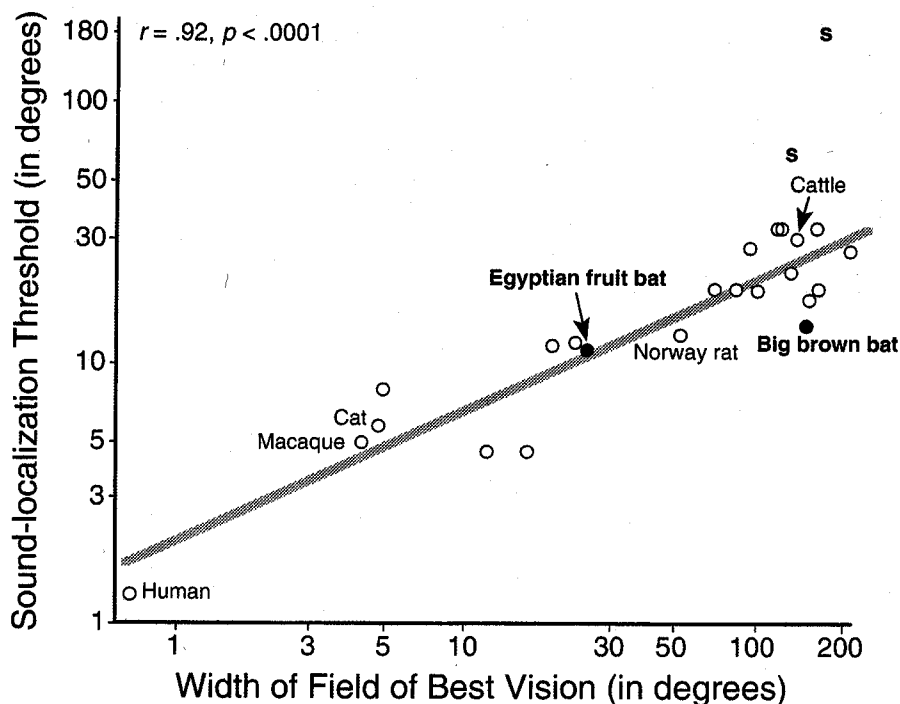
Figure 6. Relationship between the width of the field of best vision (region of ganglion-cell densities at least 75% of maximum) and sound-localization threshold for 23 species of mammals. Species with narrow fields of best vision have better localization acuity (smaller thresholds) than species with broad fields of best vision. Some familiar species are identified for convenience. (Two additional subterranean species, indicated by S, deviated significantly from the relationship, and their inclusion lowered the correlation coefficient to .86.)

both binaural locus cues (i.e., the difference in the time of arrival of a sound at the two ears and the difference in the intensity of a sound at the two ears, respectively). In this respect, they are like many other mammals, because most of those that have been tested are also able to use both binaural locus cues (e.g., R. S. Heffner & Heffner, 1992a). However, Egyptian fruit bats differ from big brown bats (microchiropterans and the only other bats tested for this ability), which are unable to localize low-frequency tones and, presumably, are unable to use the binaural time-difference cue.

Before concluding that the difference in the use of binaural cues may signal a difference between Megachiroptera and Microchiroptera, it should be noted that some other small mammals also have relinquished the ability to use the binaural time-difference cue, specifically, spiny mice (*Acomys cahirinus*) and hedgehogs (*Paraechinus hypomelas*; R. S. Heffner & Heffner 1992a; Masterson, Thompson, Bechtold, & RoBards, 1975). This suggests that the heads of some mammals may be too small to generate useful binaural time differences, causing them to relinquish the use of this cue (for a discussion of this issue, see Koay, Kearns, et al., 1998). Thus, we suspect that larger members of the microchiroptera may be able to use the binaural time-difference cue, and, indeed, there exists electrophysiological evidence suggesting that at least some of them do (e.g., Fuzessery, 1997; Grothe & Park, 1998).

When pure tones are localized using the binaural time cue,

it is referred to as the binaural phase cue. This is because time information is processed by auditory neurons firing in synchrony with the tone (i.e., phase locking), and it is the difference in the phase of the signal reaching the two ears that constitutes the binaural phase cue. However, the binaural phase cue is limited to relatively low frequencies because it is not possible to distinguish one cycle of a waveform from another at higher frequencies. As a result, the phase cue is physically available only if the difference in the time of arrival of the sound at the two ears is less than one-half cycle—otherwise it is not possible for the nervous system (or any system) to determine which ear is receiving the sound first (R. S. Heffner & Heffner, 1992a; Masterson et al., 1975). The difference in the time of arrival, or interaural delay, is determined by the size of an animal's head as well as by the angle of the sound source from the midline. As a result, the binaural phase cue is physically available at higher frequencies for mammals with smaller heads or, more specifically, smaller interaural distances. Thus, one might expect the upper limit of the ability to use the binaural phase cue to vary among mammals as a function of interaural distance.

The variation in the upper limit for binaural phase discrimination is illustrated in Figure 7 for eight species of mammals capable of using this cue. Two were tested by presenting dichotic phase differences using headphones, whereas the others were tested using free-field pure tones.
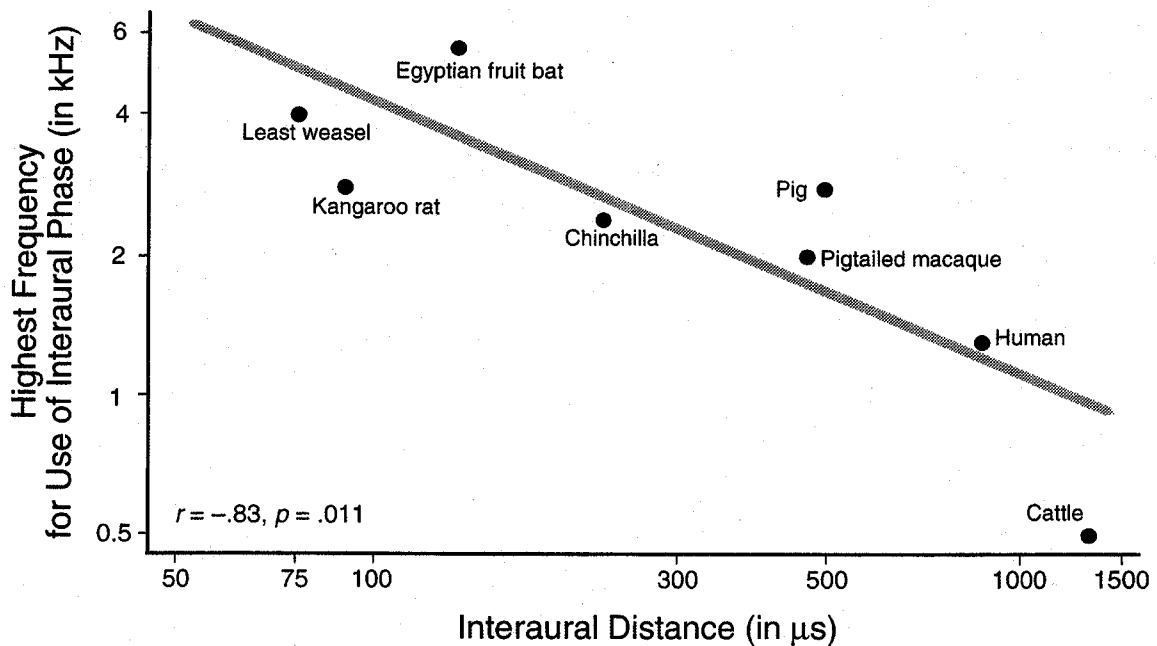
Figure 7. Relationship between functional interaural distance and the upper frequency limit at which the ability to use the binaural phase-difference cue has been demonstrated (H. E. Heffner & Masterton, 1980; R. S. Heffner, 1981; R. S. Heffner & Heffner, 1987, 1989; R. S. Heffner, Heffner, Kearns, Vogel, & Koay, 1994; Houben & Gourevitch, 1979; Klump & Eady, 1956). Humans and pigtailed macaques were tested using dichotic signals; all others were tested using free-field tones.

The main difference between the two procedures is that the dichotic studies usually result in a more precise estimate of the upper limit because frequencies are usually tested in steps of 100 Hz, whereas the free-field test is usually conducted in octave or half-octave steps. As a result, the data from the free-field tests may slightly underestimate the upper limit of use of the binaural phase cue. It is important to note that these upper limits reflect not the physical availability of the phase cue but the physiological limits of the species, because, in each case, the animals lost the ability to use the binaural phase cue before the cue became physically unavailable.

As shown in Figure 7, the variation in the upper limit of the use of the binaural phase cue spans a range of more than 3 octaves: from the 500-Hz upper limit of cows to the 5.6-kHz upper limit of Egyptian fruit bats. As expected, this variation is closely related to interaural distance ($r = .83$, $p = .011$). Although this relationship is not surprising, it has implications regarding phase locking in the auditory system, on which the binaural phase cue depends. Specifically, it has been observed that the upper limit of phase locking in the auditory nerve varies between species (Palmer & Russell, 1986). Should this upper limit also prove to be significantly correlated with interaural distance, then it would appear that the main source of selective pressure on phase locking is the need to use the binaural phase cue. Alternatively, failure to find a significant correlation between the upper limit of phase locking and interaural distance would support the idea that phase locking in the auditory system plays an important

role in the analysis of periodic sounds such as those found in communication signals (Langner, 1992).

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