

Sound localization in a new-world frugivorous bat, *Artibeus jamaicensis*: Acuity, use of binaural cues, and relationship to vision

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Passive sound-localization acuity and its relationship to vision were determined for the echolocating Jamaican fruit bat (*Artibeus jamaicensis*). A conditioned avoidance procedure was used in which the animals drank fruit juice from a spout in the presence of sounds from their right, but suppressed their behavior, breaking contact with the spout, whenever a sound came from their left, thereby avoiding a mild shock. The mean minimum audible angle for three bats for a 100-ms noise burst was 10°—marginally superior to the 11.6° threshold for Egyptian fruit bats and the 14° threshold for big brown bats. Jamaican fruit bats were also able to localize both low- and high-frequency pure tones, indicating that they can use both binaural phase- and intensity-difference cues to locus. Indeed, their ability to use the binaural phase cue extends up to 6.3 kHz, the highest frequency so far for a mammal. The width of their field of best vision, defined anatomically as the width of the retinal area containing ganglion-cell densities at least 75% of maximum, is 34°. This value is consistent with the previously established relationship between vision and hearing indicating that, even in echolocating bats, the primary function of passive sound localization is to direct the eyes to sound sources.

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I. INTRODUCTION

A major feature of mammalian hearing is the wide, but systematic, variation in the ability of different species to localize sound. Two aspects of sound localization in particular vary in predictable ways: sound-localization acuity and the upper limit of the ability to use the binaural phase-difference cue.

First, sound-localization acuity, as revealed by minimum audible angle, extends over a wide range from the 1–2° acuity of humans and elephants, to the 25° acuity of some rodents and hoofed animals, to the inability of subterranean species to localize brief sounds (H. Heffner and Heffner, 1998). However, this variation is not due to special adaptations on the part of individual species to specific ecological niches, such as whether an animal is a predator or prey, nocturnal or diurnal. Nor is it simply related to the magnitude of the available binaural locus cues, as reflected in an animal's head size. Instead, the variation in sound-localization acuity is related to the width of the field of best vision such that animals with narrow fields of best vision have good localization acuity, whereas those with broader fields of best vision have poorer acuity (R. Heffner and Heffner, 1992b; R. Heffner, Koay, and Heffner, 1999). The explanation for this relationship is that a major function of sound localization is to direct an animal's field of best vision to the source of a sound. The accuracy with which the ears must direct the eyes depends on the width of the visual field being directed. Thus, species with narrow fields of best vision, such as humans, require more accurate information about the locus of a sound source than species with wide visual streaks, such as cattle, and those that do

not use vision (subterranean mammals) do not localize sound at all.

The second feature of sound localization that shows systematic variation is the upper limit of use of the binaural phase cue, a subset of the binaural time cue that involves detecting differences in the phase of a pure tone reaching the two ears. In general, most mammals are able to use both binaural locus cues, the difference in the time of arrival as well as the difference in the intensity of a sound at the two ears, although a few species rely on only one or the other of the cues (R. Heffner and Heffner, 1989, 1992a; Koay *et al.*, 1998b). Among those species that use the binaural time cue, the upper frequency limit for using it can be measured by determining the highest frequency at which the animal can detect differences in the phase of a pure tone reaching the two ears or the highest frequency that can be localized free field using only the binaural phase-difference cue. For example, humans can use the binaural phase cue at frequencies up to 1.3 kHz (Klump and Eady, 1956) and chinchillas up to 2.4 kHz (R. Heffner *et al.*, 1994), whereas the Egyptian fruit bat (*Rousettus aegyptiacus*) can use the binaural phase cue at frequencies as high as 5.6 kHz (R. Heffner, Koay, and Heffner, 1999). This variation in the upper limit of binaural phase is not random, but is inversely related to interaural distance such that small species with close-set ears have a higher upper limit than larger species (e.g., Brown, 1994; R. Heffner *et al.*, 1999). This relationship is based on the fact that the phase cue becomes physically ambiguous at lower frequencies for larger mammals than it does for smaller mammals. However, some interaural distances may be too small to provide useful time differences and an animal may relinquish binaural time analysis altogether, as apparently has happened with some small mammals such as big brown

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bats, hedgehogs, and spiny mice (Koay *et al.*, 1998b; Masterton *et al.*, 1975; Mooney, 1992).

Because an understanding of the variation in sound localization is relevant to the physiological as well as the ecological study of hearing, it is important to extend our observations to additional species. Bats, of which there are more than 950 species, are of particular interest because so many have developed the use of active sonar entailing a variety of auditory specializations. Further, bats are a diverse group ranging from the insectivores familiar in temperate and even cold climates to tropical bats that eat meat, fish, blood, fruit, and nectar—adaptations which impose different demands on sonar for orientation and feeding (Arita and Fenton, 1997). Knowledge of their passive localization abilities would broaden the sample upon which to base an understanding of mammalian sound localization. Moreover, whereas big brown bats have relinquished the use of binaural time cues, Egyptian fruit bats can extract binaural phase cues at higher frequencies than other mammals, which suggests that the study of bats may shed more light on the use of this cue in small mammals.

Accordingly, the purpose of this study was to broaden the sample on which to base a comparative analysis of the hearing of bats by determining the passive sound-localization abilities of the Jamaican fruit bat (*Artibeus jamaicensis*), a microchiropteran bat found in Central and South America. The Jamaican fruit bat is a leaf-nosed bat (*Phyllostomidae*) and, because of its very low-intensity sonar signal, is also known as a whispering bat (Griffin, 1958). Its diet consists of fruit, mainly figs, concealed in leaf clutter high in the canopy, which it locates and identifies using olfaction, although sonar may be used in the final approach to a food item (Bonaccorso and Gush, 1987; Kalko, Herre, and Handley, 1996). Nevertheless, Jamaican fruit bats rely heavily on echolocation for orientation, and their frequency-modulated sonar is comparable to that of insectivorous bats, allowing them to detect and avoid wires of 0.175 mm diameter (Griffin and Novick, 1955). These features are in contrast to those of the old-world fruit bat, *Rousettus aegyptiacus*, that makes limited use of echolocation and relies on olfaction and vision to find fruit (Kwiecinski and Griffiths, 1999). Both of these species differ, in turn, from the insectivorous big brown bat (*Eptesicus fuscus*) that relies on echolocation to identify and capture prey (Arita and Fenton, 1997). At 40–50 g, the Jamaican fruit bat is intermediate in size between the 15-g big brown bat and the 80–150-g Egyptian fruit bat.

This study was a threefold investigation of the passive sound-localization abilities of Jamaican fruit bats to determine how this species compares with other mammals as well as with other bats. First, we determined the animals' left–right sound-localization acuity (minimum audible angle) 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. In addition, sinusoidally amplitude-modulated tones were used to explore the bats' use of envelope-based time cues. Finally, we measured the packing density of their retinal ganglion cells to estimate visual resolution throughout

the retina and evaluate the relation between the width of the field of best vision and sound-localization acuity. The resulting data are compared with those for other mammals.

II. METHODS

The behavioral sound-localization tests used a conditioning procedure in which a hungry animal steadily licked a food spout while sounds were presented from a loudspeaker to its right, but suppressed ongoing eating and broke contact with the spout when sounds were presented from a loudspeaker to its left to avoid a mild shock (H. Heffner and Heffner, 1995). The anatomical procedure involved mapping the ganglion cell densities throughout the retina of a Jamaican fruit bat.

A. Subjects

Three Jamaican fruit bats (*Artibeus jamaicensis*), one female (A) and two males (B and C), were used in the behavioral tests and a fourth bat was used for the anatomical analysis of the retina. The animals were individually housed with free access to water, with vitamin and mineral supplements (Lambert Kay Avimin and Avitron), and received a food reward of fruit juice during the daily test session. The animals typically consumed 18–25 cc of juice in sessions lasting up to 2 h. The natural feeding pattern of these bats is to eat their fill quickly, digest the meal in about 20 min, and then eat at least once more. The long test sessions, accordingly, consisted of periods during which they were not working but instead digesting the food. Additional supplements of fruit juice were given as needed to maintain a healthy body weight.

B. 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 eggcrate foam. The equipment for behavioral control and stimulus generation was located outside the chamber and the animals were monitored via closed-circuit television.

The bats were tested in a cage (37×22×23 cm) constructed of 0.5-in. (1.26-cm) hardware cloth, mounted 93 cm above the floor on an adjustable tripod (see Koay *et al.*, 1998a, for an illustration of the test cage). A food spout (3-mm-diameter brass tube topped with a 7×8-mm ‘lick’ plate) was mounted vertically so that it projected up through the bottom of the cage 6 cm above the cage floor. The spout was attached via an 80-cm-long plastic tube to a 30-cc syringe filled with fruit juice located below the cage. The fruit juice, a mixture of cantaloupe, pear juice, and sugar, finely blended and strained 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 *et al.*, 1990). Both the syringe pump and food reservoir were housed in a high-density polyethylene plastic box (64×212×28 cm) lined with eggcrate foam to eliminate any noise from the pump.

During testing, the bats were placed on a small platform (13×7×7 cm) located directly behind the spout. The top of

the platform was covered with a piece of dampened carpet to facilitate traction and ensure good electrical contact while the bat ate from the spout. The tip of the food spout was placed in front of and at the same height as the platform to minimize obstructions between the animal's ears and the loudspeaker. A contact circuit, connected between the food spout and platform, detected when an animal made contact with the spout and activated the syringe pump to dispense a trickle of juice. 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 platform. The shock was adjusted for each individual to the lowest level that produced a consistent avoidance response (backing away slightly from the spout or lifting its head away from the spout) to a readily detected signal. The bats never developed a fear of the spout, as they readily returned to it after the shock. A 25-W light, 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.

C. Acoustical apparatus

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

1. Broadband noise

The minimum audible angle for Jamaican fruit bats was determined using a standard 100-ms noise burst. Such a signal provides good binaural and monaural locus cues but is brief enough to minimize opportunities for scanning movements. Because echolocation was of no use in determining which speaker had been active, echolocation and scanning movements of the pinnae extinguished early in training. An additional threshold was obtained for Bat A using a train of five 2-ms noise pulses (2 ms on, 18 ms off). The noise bursts were generated by a noise generator (Stanford Research Systems 770, set to produce energy up to 100 kHz). The electrical signal was randomly attenuated over a 3.5-dB range (Coulbourn S85-08 programmable attenuator) from one trial to the next to reduce the possibility of the animals responding on the basis of small intensity differences. The signal was then sent to a rise-fall gate (Coulbourn S84-04; 0.1-ms rise/fall), split into left and right channels, amplified to 68 dB sound-pressure level (Coulbourn S82-24), and routed to one of a pair of loudspeakers. Three matched pairs of Motorola piezoelectric speakers (model KSN1005A) were used. In a single session, the bats were tested at three angles of separation then the speakers were moved to three different angles for a total of six angles in a session. The members of each pair of speakers were switched before each session to reduce the possibility that the animals might respond on the basis of speaker quality. The signal going to the speakers was monitored with an oscilloscope and calibrated at the beginning of

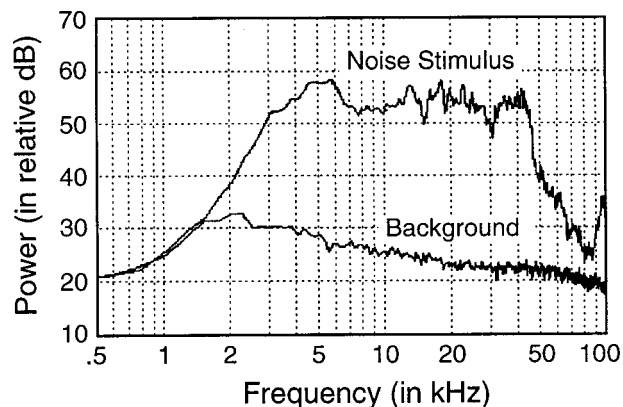


FIG. 1. Spectrum of the broadband noise stimulus used for sound localization (upper line) compared to background noise (lower line). The 100-ms noise burst included frequencies throughout all but the upper half-octave of the hearing range for this species, which at a level of 60 dB SPL extends from 2.8 to 130 kHz (Koay *et al.*, 1999).

each test session (see below). These precautions were adequate to prevent responses to nonlocus cues as attested by each animal's chance performance at small angles of speaker separation.

The spectrum of the noise produced by this acoustic apparatus was monitored using a spectrum analyzer (Zonic 3525) and 1/4-in. (0.64-cm) microphone (Brüel & Kjaer 2619). As illustrated in Fig. 1, the noise spectrum was relatively flat (± 3 dB) between 3 and 45 kHz with energy above background level up to 100 kHz. Thus, the signal included frequencies throughout most of the hearing range of this species (2.8–130 kHz, Koay *et al.*, 1999). A detection threshold for this signal was behaviorally determined for Bat B and found to be -2 dB, so that the signal used for noise localization was approximately 70 dB hearing level. Lower intensities were also used with this animal to assess the effect of intensity on performance.

2. Pure tones

Sine waves were generated by a tone generator (Krohn-Hite 2400 AM/FM Phase Lock Generator) and randomly attenuated over a 3.5-dB range from one trial to the next (Coulbourn S85-08 programmable attenuator). The tones were pulsed (100 ms on and 1000 ms off, for two pulses), shaped by a rise-fall gate (Coulbourn S84-04; 10 ms rise/fall) and bandpass filtered (Krohn-Hite 3550; 1/3 octave above and below the frequency of the tone). Finally, the signal was split into left and right channels, separately amplified (Coulbourn S82-24), and sent to one of two loudspeakers (Motorola piezoelectric KSN1005A). 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 animal's detection threshold. Tones were calibrated at the beginning and end of each test session (see below).

Testing was conducted with the loudspeakers placed 60° apart (30° to the left and right of midline) at the following frequencies: 4, 5.6, 6.3, 8, 12.5, 16, 20, 40, and 56 kHz. Each frequency was presented at 50 dB above the average

absolute threshold for the Jamaican fruit bat (Koay *et al.*, 1999). To assure that motivation and performance had been maintained throughout the session, each session began and ended with a few trials using a stimulus that elicited good performance.

Additional tests used sinusoidal amplitude modulation of an 8-kHz tone (Krohn-Hite 2400 AM/FM Phase Lock Generator) that provided an ongoing binaural time-difference cue in the envelope of the signal. Modulation rates ranging from 50 Hz to 2 kHz at 100% modulation depth were used. A 10-ms rise/decay was retained in order to avoid onset and offset transients.

D. Sound-level measurement

The sound-pressure levels of the stimuli (SPL *re* 20 $\mu\text{N}/\text{m}^2$) were measured and the left and right loudspeakers were equated daily with a 1/4-in. (0.64 cm) microphone (Brüel & Kjaer 4135, protective grid removed), preamplifier (Brüel & Kjaer 2619), measuring amplifier (Brüel & Kjaer 2608), and filter (Krohn-Hite 3202; bandpass range set at 250 Hz–100 kHz) and spectrum analyzer (Zonic 3525) to permit detection of any harmonics that might be present. This 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 towards a loudspeaker (0° incidence).

E. Behavioral procedure

1. Training

The animals were first trained to drink steadily from the spout in the presence of a series of four 400-ms broadband noise bursts (100-ms interburst intervals), presented from a loudspeaker located 90° to the right of the animal. Next, the animals 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 via the spout 2.0 s after left signal onset. Breaking contact with the spout indicated that the animal had detected the new locus of the sound. The light bulb located underneath the cage was turned on while the shock was on to provide feedback for a successful avoidance (since in those cases no shock was actually received by the bat) 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 the basic avoidance procedure, the signals were reduced to one 100-ms noise burst per 2-s trial.

2. Testing

Test sessions consisted of a series of 2-s trials separated by 1.5-s intertrial intervals. Thus, the animals received one signal every 3.5 s and made a decision after each as to whether to break contact or to continue drinking. 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. This avoided using trials in which the animal was grooming or otherwise not engaged in the task.

Each trial had a 22% probability of containing a left signal. The sequence of left–right trials was quasirandom and is described in detail elsewhere (H. Heffner and Heffner, 1995). Both hit- and false-alarm rates were determined for each block of approximately 7–9 left trials and approximately 28–36 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 formula: performance = hit rate - (false-alarm rate \times 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 average false-alarm rate for an session as false-alarm rates may vary within a session depending on the discriminability of the stimulus.

Noise localization thresholds were determined by gradually reducing the angular separation between the left and right loudspeakers. Blocks of trials, usually containing 7–9 left signal trials, were given at each angle until the animal could no longer discriminate reliably (that is, the hit rate no longer differed significantly from the false-alarm rate, binomial distribution, $P > 0.05$). A typical session consisted of approximately 50 to 60 warning trials (plus approximately 200 to 250 associated safe trials) during which six different angles were tested. Daily testing continued until performance no longer improved at any angle, that is, asymptotic performance had been reached (eight sessions for Bats A and C, and nine sessions for Bat B). The mean of the three trial blocks with the highest scores was calculated to represent the best performance for each animal. If none of the trial blocks showed performance above chance, all scores were included in the average. 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°.

Tone localization tests were conducted at a fixed angular separation of 60° (30° to the left and right of the animal's midline), with the animal's performance calculated for blocks of trials containing 7–9 left trials (plus associated right trials). Testing was carried out using a single frequency per session for frequencies that sustained good performance. However, if an animal had difficulty or was unable to localize a particular frequency, as happened at 8 and 12 kHz, broadband noise was presented for several trials to verify that the animal was still sufficiently motivated. Each frequency was tested during at least three sessions for an average of 90–100 warning trials. The top 50% of the trial blocks

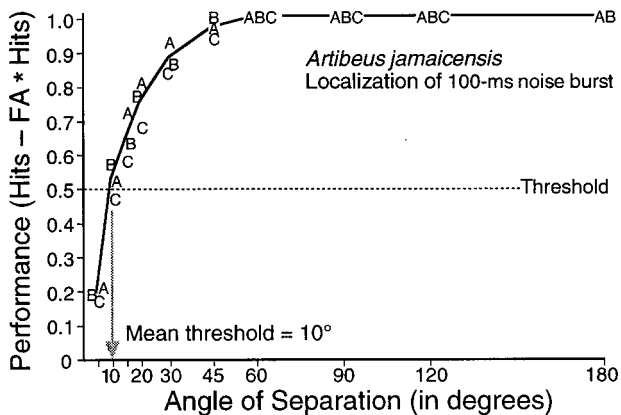


FIG. 2. Sound-localization performance of three Jamaican fruit bats for a single 100-ms burst of broadband noise. Letters indicate individual animals and the dashed line indicates the 0.50-performance level used to define threshold. The arrow indicates the mean threshold of 10°.

were averaged to represent the best overall performance the animals were capable of sustaining.

F. Anatomical procedure

One bat 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 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 heavily gelatinized slides with the ganglion-cell layer uppermost, and stained with thionine (Stone, 1981). The density of the ganglion cells was determined throughout the retina in 0.1-mm steps through the regions of relatively high ganglion-cell density and 0.5-mm steps in the periphery. The number of ganglion-cell nucleoli within a sampling rectangle $33 \times 52 \mu\text{m}$ (0.001716 mm^2) were counted using a 100X oil-immersion objective. To make comparisons between species, the horizontal width of the region encompassing ganglion-cell densities equal to or greater than 75% of maximum density was determined as an indication of the width of the field of best vision. The maximum number of cells/deg² was then 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, and Casagrande, 1980). For additional details of the method, see R. Heffner and Heffner (1992b).

These experiments were carried out with the approval of the University of Toledo Animal Care and Use Committee.

III. RESULTS

A. Behavioral results

1. Noise localization

The ability of the three Jamaican fruit bats to localize 100-ms noise bursts emitted from loudspeakers centered

symmetrically about midline is illustrated in Fig. 2. The animals were capable of near-perfect performance at angles of 45° and larger. Performance began to fall at 30° and no animal performed above chance at 5°. The 50% corrected detection thresholds (to the nearest 0.5°) for animals A, B, and C were 9.5°, 9°, and 11.5°, respectively, for a mean threshold of 10°. Bat A was also tested using a 100-ms burst of five 2-ms noise pulses mimicking the temporal pattern of the echolocation call. Similar excellent performance and the same threshold of 10° were obtained with this stimulus, indicating that there is no unusual sensitivity associated with, or required for, very brief signals.

The extensive training (49 sessions), excellent performance at large and moderate angles, sharp decline in performance as threshold is approached, and close agreement between the animals suggest that the thresholds are representative for this species. As has been found for other mammals, auditory sensory abilities seem to vary little between young, healthy individuals of the same species (R. Heffner and Heffner, 1988, 1991; Koay, Heffner, and Heffner, 1997).

The effect of signal intensity on localizability was also investigated to determine whether it might have had an effect on the bats' performances. This was done by assessing the ability of bat B to localize 100-ms noise bursts of 30–68 dB SPL (32–70 dB above detection threshold) at 60° separation. The resulting performance scores were quite similar at all intensities, ranging from 0.86 to 1.00 and did not differ systematically with intensity. Thus, intensity of the noise burst had no noticeable effect on localizability of these brief broadband signals through a wide range of moderate listening levels, suggesting that any effect of the small variations in intensity used in subsequent tests would be negligible.

2. Pure-tone localization

To determine the ability of Jamaican fruit bats to use the binaural time- and intensity-difference cues for locus, two animals were tested for their ability to localize brief tone pips ranging from 4 to 56 kHz. This test is based on the absence of binaural intensity-difference cues at low frequencies, as low frequencies undergo little or no attenuation as they travel around the head and thus do not present different intensities to the two ears. Low frequencies do, however, permit the comparison of the arrival time of a pure tone at the two ears, referred to as the phase-difference cue. The phase-difference cue becomes ambiguous for pure tones at high frequencies when successive cycles are too close for the nervous system to match the arrival of the same cycle at the two ears. This occurs when more than one-half cycle of the tone occurs during the time it takes for the sound to travel from one ear to the other. Travel time, in turn, is dependent on both the distance between the ears and the distance of the sound source from midline. The calculated frequency at which the phase cue would become physically ambiguous for the Jamaican fruit bat (with a head diameter of 1.78 cm) at an angle of $\pm 30^\circ$ is 12.6 kHz, indicated by the shaded vertical bar in Fig. 3. (For a detailed discussion of phase ambiguity, see Jackson, 1996, or Saberi, Farahbod, and Konishi, 1998; for a formula for calculating the frequency of

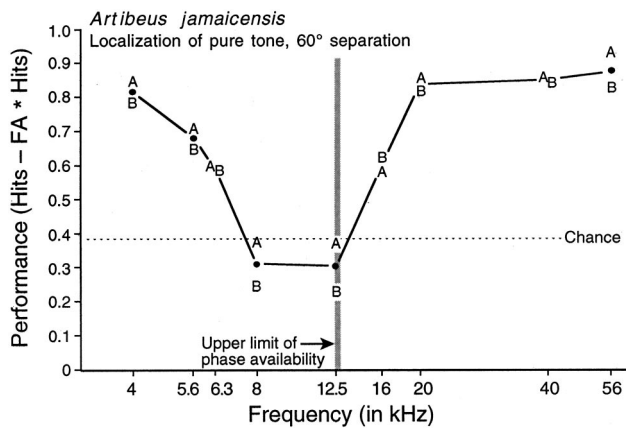


FIG. 3. Sound-localization performance for two Jamaican fruit bats as a function of the frequency of a pure-tone stimulus (two pulses of 100 ms duration, 1-s interpulse interval) at a fixed angle of separation ($\pm 30^\circ$ azimuth). Letters represent individual animals; vertical bar indicates the upper limit of the physical availability of the binaural phase-difference cue at this angle for Jamaican fruit bats (12.6 kHz). Note that the animals perform well at frequencies both above and below the frequency of ambiguity, indicating that they can use both binaural phase- and intensity-difference cues. However, performance falls to chance at 8–12.5 kHz, indicating the absence of adequate locus cues in this frequency range.

ambiguity, see Kuhn, 1977.) Thus, above this “frequency of ambiguity” binaural intensity differences must provide the cue to locus.

Figure 3 illustrates the localization performances of the two Jamaican fruit bats as a function of frequency. The bats showed good agreement in their tone localization and are able to use both binaural locus cues. The bats’ use of binaural phase differences is indicated by their good performance at lower frequencies of 4–6.3 kHz. (Frequencies below 4 kHz were not tested because the hearing of Jamaican fruit bats becomes too insensitive below this frequency to permit undistorted tones at 50 dB above threshold.) Performances were also good at frequencies of 20 kHz and above (ranging between 0.82 and 0.93), frequencies for which only the interaural intensity-difference cue was available. In summary, their good performances at frequencies both above and below the frequency of ambiguity demonstrated that they are capable of using both binaural phase and intensity differences for localization.

However, the performance of both animals fell markedly at intermediate frequencies—at both 8 and 12.5 kHz, Bat A performed above chance on only about half of the trial blocks, and Bat B never performed above chance at all, indicating that neither binaural cue was effective. The upper limit of their use of the binaural phase cue thus appears to be about 6.3 kHz. Wavelengths of 8–12.5 kHz tones are apparently too long for the head and pinnae to shadow and produce an effective binaural intensity difference in a bat of this size at $\pm 30^\circ$, as earlier suggested by acoustic measures on several species of bats (Obrist *et al.*, 1993).

The chance performance at 8–12.5 kHz, at which neither binaural phase nor intensity cues were usable indicates that no other usable cues were available. This finding rules out the possibility that the bats could localize using the transient onset difference, which is the difference in the arrival time of the leading edge of a sound at the two ears. It should

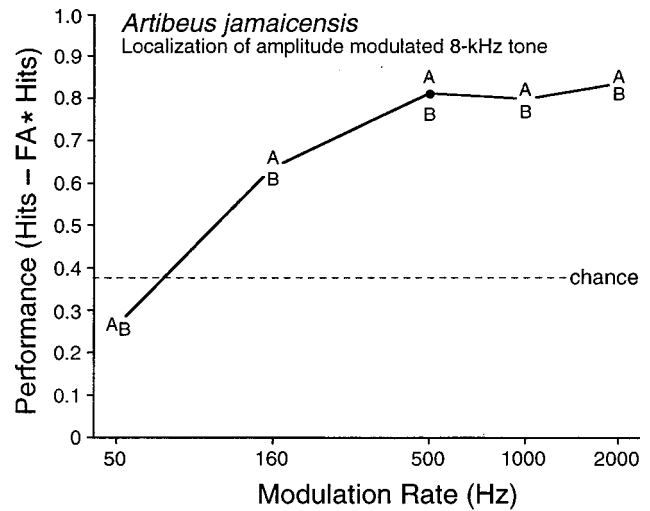


FIG. 4. Sound-localization performance for two Jamaican fruit bats as a function of the modulation rate of an 8-kHz tone at a fixed angle of separation ($\pm 30^\circ$ azimuth). Without modulation, the 8-kHz tone was not localizable (cf. Fig. 3), but modulation rates of 160 Hz or higher permitted good to excellent localization in both bats.

be noted, however, that the magnitude of the onset difference was somewhat reduced by the 10-ms rise/decay time used here to reduce the possibility of onset and offset clicks. Thus, within these limitations, there was no indication that the Jamaican fruit bats used the transient onset difference to localize sound.

3. Sinusoidal amplitude modulation

To further explore the ability of Jamaican fruit bats to use binaural time differences, we modulated the amplitude of the previously unlocalizable 8-kHz tone at rates ranging from 50 to 2000 Hz (sinusoidal modulation, 100% depth). The amplitude modulation presented the bats with an additional time cue, namely the variation in the envelope of the 8-kHz tone. However, it also resulted in the production of sidelobes, i.e., tones of frequencies equal to the 8-kHz tone plus and minus the modulation rate. For example, modulating the 8-kHz tone at 2 kHz produced sidelobes of 6 and 10 kHz. Thus, in analyzing the results, it is necessary to rule out the possibility that any improvement in performance was due to the presence of the sidelobes.

As illustrated in Fig. 4, modulating the tone markedly improved the performance of both bats. Moreover, the improvement was much greater than could be attributed to the presence of sidelobes. For example, the bats’ average performance at a 500-Hz modulation rate was 0.80, whereas the interpolated performance for a sidelobe of 7.5 kHz is less than 0.50 and the 8.5-kHz sidelobe would still be unlocalizable (cf. Fig. 4). Indeed, even at the 2-kHz modulation rate, the animals’ average performance of 0.83 is well above the interpolated performance for a 6-kHz sidelobe, which is approximately 0.60. Thus, it appears that the improvement in performance was due to the ability of the bats to extract a binaural time difference cue from the envelope of the amplitude-modulated signal.

Ganglion Cell Isodensity Contours

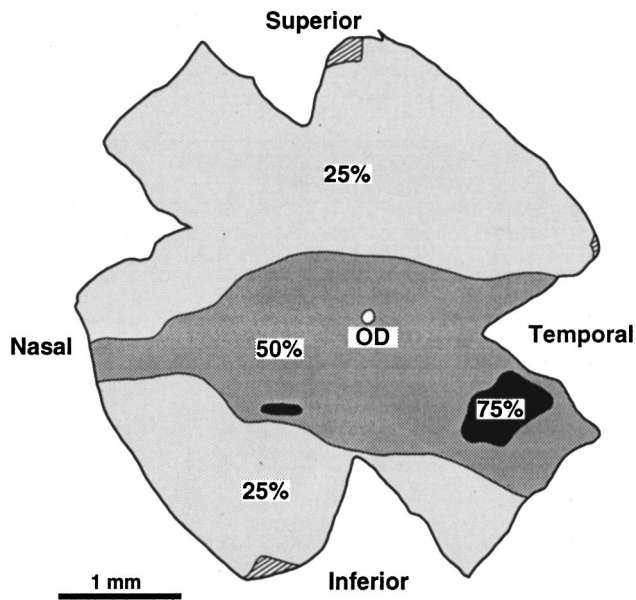


FIG. 5. Retinal ganglion-cell isodensity contours in the retina of a Jamaican fruit bat. Density is expressed as a proportion of the maximum density (9325 cells/mm²). Density gradients are relatively shallow and remain at least 38% of maximum in the inferior retina and at least 30% of maximum in the superior retina. An unpronounced visual streak extending across the entire horizon of the retina can be seen in the region encompassing densities at least 50% of maximum. OD, optic disk; black indicates densities of 75%–100% of maximum; dark gray indicates densities of 50%–75% of maximum; light gray indicates densities of 25%–50% of maximum; hatching indicates areas not counted due to folds in the tissue.

B. Retinal analysis

The flattened retina of the Jamaican fruit bat was approximately 4.4 mm in diameter and subtended approximately 180° of arc. The ganglion-cell layer was well separated from the inner nuclear layer and was unremarkable, with cells ranging from about 4–12 μm diameter. Few small cells having the appearance of glia were observed and were not likely to have contaminated the enumeration of ganglion cells. The isodensity contours of the retina are illustrated in Fig. 5. The ganglion cells reached a relatively high peak density of 9325 cells/mm² that, in an eye of this size, suggests a visual acuity of only 1.1 cycles per degree. This level of acuity is very similar to the 1.35 cycles per degree previously estimated for a closely related species, *Artibeus cinereus* (Pettigrew *et al.*, 1988).

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 gradually toward the periphery. Nowhere does ganglion-cell density fall below 30% of maximum. There is a visual streak across the horizon of the retina in which ganglion cell densities remain above 50% of maximum. The width of the field of best vision for this animal, as defined by the portion of the retina with ganglion-cell densities at least 75% of maximum, is 34° (Fig. 5). This value is much smaller than the 139° in the big brown bat but slightly greater than the 27° in the Egyptian fruit bat, the only other bats for which this measure

is available (R. Heffner, Koay, and Heffner, 1999; Koay *et al.*, 1998b).

IV. DISCUSSION

The 10° threshold of Jamaican fruit bats falls within one standard deviation (2.4°) of the 12° mean threshold for all surface-dwelling mammals (i.e., excluding aquatic and subterranean species). Compared with other mammals, its acuity is most similar to that of Norway rats (9–11°) and sea lions (8.8°) (Kavanagh and Kelly, 1986; Kelly, 1980; H. Heffner and Heffner, 1985; Moore, 1975). Compared with other bats, the Jamaican fruit bat's acuity is slightly superior to the 14° acuity of the big brown bat and even to the 11.6° acuity of Egyptian fruit bats (R. Heffner *et al.*, 1999; Koay *et al.*, 1998b).

Of interest is how well a bat's passive sound-localization ability compares with its active echolocation. Jamaican fruit bats have been reported to reliably avoid wires as small as 0.175 mm using echolocation, although this may be due in part to their relatively slow and cautious manner of flight (Griffin and Novick, 1955). The insectivorous big brown bats, which have a passive localization acuity of 14°, are able to detect and avoid much smaller wires (0.06 mm) using echolocation (Schnitzler and Henson, 1980). In comparison, Egyptian fruit bats, the only old-world fruit bat that echolocates (albeit with tongue clicks rather than phonation) show passive localization acuity (11.6°) comparable to the Jamaican fruit bats, but avoids wires only as small as 0.5 mm using its rudimentary echolocation (Griffin, Novick, and Kornfield, 1958). Thus, among the three species for which data are available, acuities for active and passive localization appear unrelated, suggesting that the two abilities may be served at least in part by independent processes.

A. Sound localization and vision

The Jamaican fruit bats' intermediate localization acuity, coupled with a moderately broad field of best vision, provides support for the hypothesis that sound-localization acuity is driven by the requirements of the visual system. Specifically, sound-localization acuity among mammals appears to be primarily determined by the need to direct the eyes to the source of a sound (R. Heffner and Heffner, 1992b). Indeed, studies of attention support the conclusion that sounds exert a powerful effect on visual attention, but that the relationship is not symmetrical in that vision does not readily direct auditory attention (Spence and Driver, 1997). Thus, it appears that vision is exerting selective pressure on sound-localization acuity rather than the other way around.

Furthermore, 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 upon their fovea, whereas animals with broad fields, such as those with visual streaks, do not require as high a degree of sound-localization acuity to direct their gaze to the source of a sound. The relationship between the

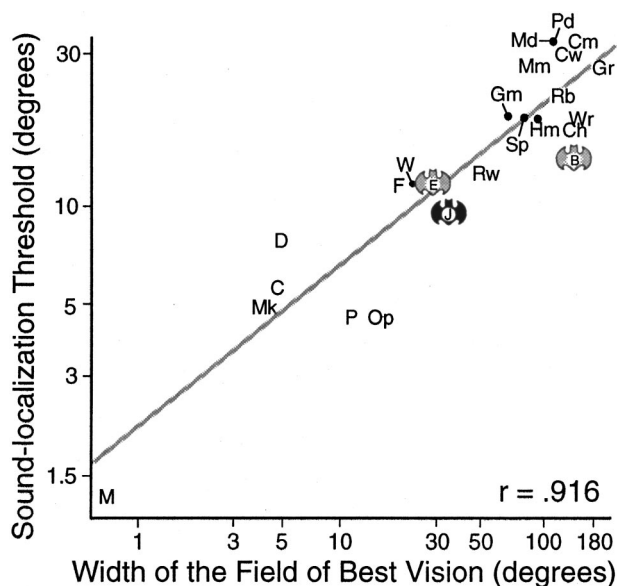


FIG. 6. Relationship between the width of the field of best vision (region of ganglion-cell densities at least 75% of maximum) and sound-localization threshold for 24 species of mammals (note logarithmic scale on both axes). Species with narrow fields of best vision have better localization acuity (smaller thresholds) than species with broad fields of best vision, $r = 0.916$, $P < 0.0001$. **B**, big brown bat (*Eptesicus fuscus*); **C**, domestic cat (*Felis domesticus*); **Ch**, chinchilla (*Chinchilla laniger*); **Cm**, chipmunk (*Tamias striatus*); **Cw**, cow (*Bos taurus*); **D**, dog (*Canis familiaris*); **E**, Egyptian fruit bat (*Rousettus aegyptiacus*); **F**, ferret (*Mustela putorius*); **Gm**, grasshopper mouse (*Onychomys leucogaster*); **Gr**, gerbil (*Meriones unguiculatus*); **Hm**, hamster (*Mesocricetus auritus*); **J**, Jamaican fruit bat (*Artibeus jamaicensis*); **M**, man (*Homo sapiens*); **Md**, domestic mouse (*Mus musculus*); **Mk**, macaque (*Macaca fasciata*); **Mm**, marmot (*Marmota monax*); **Op**, virginia opossum (*Didelphis virginiana*); **P**, pig (*Sus scrofa*); **Pd**, prairie dog (*Cynomys ludovicianus*); **Rb**, domestic rabbit (*Oryctolagus cuniculus*); **Rw**, wild norway rat (*Rattus norvegicus*); **Sp**, spiny mouse (*Acomys cahirinus*); **W**, least weasel (*Mustela nivalis*); **Wr**, wood rat (*Neotoma floridana*); for citations, see Heffner *et al.*, 1994.

width of the field of best vision and passive sound-localization acuity is illustrated in Fig. 6. As can be seen, mammals with narrow fields of best vision are more accurate localizers than mammals with broader fields of best vision, accounting for 84% of the variance ($r = 0.916$). Moreover, mammals that do not rely on vision, such as the subterranean pocket gopher (*Geomys bursarius*), blind mole rat (*Spalax ehrenbergi*), and naked mole rat (*Heterocephalus glaber*), and are adapted to living in dark burrows where visual scrutiny of sound sources is not possible, conform to this relationship by losing virtually all of their ability to localize sound (R. Heffner and Heffner, 1990, 1992c, 1993).

Echolocating bats are another group that one might expect to differ from typical surface-dwelling mammals because of reduced reliance on vision. As can be seen in Fig. 6, however, the three bats in the sample do not deviate from the relationship between width of the field of best vision and sound localization acuity ($P > 0.5$, *t* test). Thus, despite their use of active echolocation for orientation and/or prey capture, tasks accomplished largely by vision in other mammals, the bats examined so far do not appear to be unusual in the relationship between passive hearing and vision.

Although visual acuity itself is not related to sound-localization acuity (R. Heffner and Heffner, 1992b), it is of

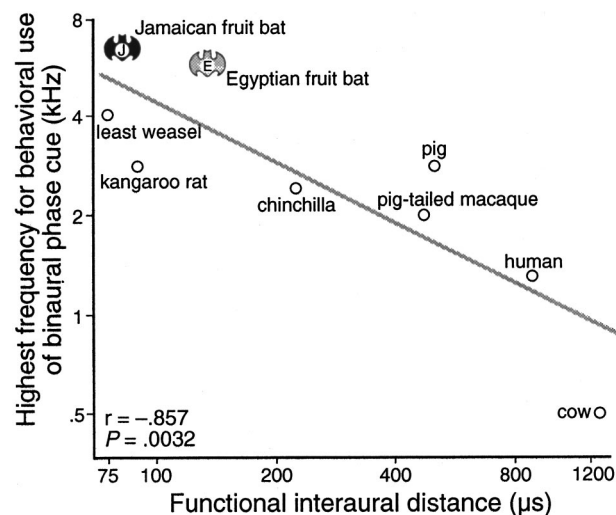


FIG. 7. Relationship between functional interaural distance and the highest frequency at which use of the binaural phase-difference cue has been demonstrated behaviorally (H. Heffner and Masterton, 1980; R. Heffner, 1981; R. Heffner and Heffner, 1987, 1989; R. Heffner *et al.*, 1994; Houben and Gourevitch, 1979; Klump and Eady, 1956). Humans and pig-tailed macaques were tested using dichotic signals; all others were tested using free-field tones.

some interest to compare the visual acuity of the Jamaican fruit bat with that of other bats. The eyes of Jamaican fruit bats are smaller than those of most mammals, but larger than those of most insectivorous bats. Their estimated visual acuity of 1.1 cycles/degree, like that of other new-world fruit bats, is poorer than the visual acuity of old-world fruit bats and many other nocturnal mammals, but superior to that of insectivorous bats (e.g., Bell and Fenton, 1986; Birch and Jacobs, 1979; Pettigrew *et al.*, 1988; Suthers, 1966). They have larger and more distinct nuclei in the central nervous system for interpreting visual information than either big brown bats or the three other phyllostomid species that have been studied (Cotter, 1985; Hope and Bhatnagar, 1979). Thus, Jamaican fruit bats retain intermediate vision, probably as an aid to obstacle avoidance (Kalko *et al.*, 1996), despite their nocturnal habits and use of echolocation. However, multiple regression analysis incorporating information on the visual acuity of Jamaican fruit bats continues to indicate that absolute visual acuity is not a significant factor influencing sound localization ($P > 0.3$).

B. Use of binaural locus cues

The ability of Jamaican fruit bats to localize both low- and high-frequency pure tones indicates that they are able to use both the interaural time cue and the interaural intensity-difference cue. In this respect they are like most other mammals, including Egyptian fruit bats, that also use both binaural locus cues (e.g., R. Heffner and Heffner, 1992a). An interesting feature of the Jamaican fruit bat's ability to use the binaural phase cue, however, is that its 6.3-kHz upper limit is the highest observed so far in a mammal.

The observed upper limit of the use of the binaural phase cue in mammals spans a range greater than 3 octaves: from the 500-Hz upper limit of cattle to the 6.3-kHz upper limit of Jamaican fruit bats. As shown in Fig. 7, this varia-

tion is inversely correlated with interaural distance such that animals with large interaural distances have low upper limits and vice versa ($r = -0.857$, $P = 0.0032$). The explanation for this relationship appears to lie in the physical availability of the phase cue (e.g., Brown, 1994; Jackson, 1996; R. Heffner, Koay, and Heffner, 1999). Briefly, the binaural phase cue requires the nervous system to distinguish one cycle of a waveform from another, match the portion of a cycle reaching one ear with the same portion when it reaches the other ear, and then to determine the difference in the time of arrival. At low frequencies, for which one cycle reaches both ears well before the next cycle reaches the leading ear, the phase cue is unambiguous. However, the cue becomes ambiguous when the wavelength of the tone is short relative to the distance between the ears, specifically when more than one-half cycle of the tone occurs during the time it takes for a sound to reach the two ears, because the individual cycles can no longer be distinguished with certainty. Because the maximum difference in the time of arrival depends on the interaural distance, the phase cue remains physically unambiguous at shorter wavelengths in species with shorter interaural distances. Similarly, the unambiguous wavelengths become shorter when smaller angles are presented because the time delays between the arrival of a sound at the two ears become shorter.

Although the physics of the binaural phase cue suggests that smaller animals should use the phase cue at higher frequencies, eventually an animal may become so small that the time differences available to it provide only approximate indications of locus and it may relinquish the use of binaural time cues entirely. This appears to be the case for big brown bats (*Eptesicus fuscus*), which are unable to localize frequencies below 11.2 kHz, even though its 55- μ s maximum interaural time difference indicates that the binaural phase-difference cue should be unambiguous below 10.5 kHz (given maximally separated sound sources 90° from midline).

The conclusion that big brown bats cannot use binaural time cues in general was supported by the observation that its performance did not improve with amplitude modulated signals (Koay *et al.*, 1998b). Jamaican fruit bats, on the other hand, use the binaural phase cue on both a carrier signal and on an envelope. This suggests that the extraction of binaural time differences from the components of a signal and from the signal's envelope rely on the same neural mechanism. Whether animals with very small interaural distances relinquish the binaural time-difference cue because the time difference itself has become so small as to be of limited use, or because the auditory system cannot phase lock at frequencies high enough to encode phase at usefully small angles, is not known.

The results of the tone-localization tests have implications for phase locking in the mammalian nervous system. First, phase locking is used to encode the pitch of low-frequency sounds as well as to provide the basis for the binaural phase-difference cue. Because the use of phase locking for pitch may be limited to frequencies below about 1 kHz (e.g., Langner, 1997), phase locking at higher frequencies may be solely for the analysis of binaural phase differences

for locus. Thus, the variation in the upper limit of binaural phase suggests that mammals may show similar variation in the upper limit of phase locking (Brown, 1994; Palmer and Russell, 1986). Second, previous studies have found that the ability of an animal to localize pure tones may decline at low frequencies (e.g., R. Heffner and Heffner, 1987). This decline has been attributed to the observation that the phase locking of neurons becomes less precise at low frequencies with multiple discharges sometimes occurring during a single cycle (Rose *et al.*, 1967). Although the performance of the Jamaican fruit bats did not decline when localizing tones (Fig. 3), this may have been because performance does not usually decline until frequency falls below 500 Hz, and the limited low-frequency hearing range of the bats prevented them from being tested below 4 kHz. However, the results of the amplitude modulation test clearly show that the performance of these animals declines for modulation frequencies below 500 Hz and that they are totally unable to extract locus from a 50-Hz modulation rate (Fig. 4). This result suggests that phase locking does indeed become less precise at low rates of modulation just as it does at low frequencies and that the use of an amplitude-modulated signal provides a demonstration of the behavioral effect of this phenomenon on sound localization, as it allows testing to be conducted at lower frequencies than can be done with pure-tone localization.

Finally, it may be noted that there is a potential localization cue that results from the transient onset difference that occurs when the leading edge of a sound reaches one ear before it arrives at the other (e.g., Tobias and Schubert, 1959). However, the Jamaican fruit bat could not localize tones from 8–12.5 kHz, where neither binaural phase or intensity cues were usable, indicating that they could not use any transient onset difference remaining in the envelope of the signal (with its 10-ms rise/decay). Although this does not rule out their ability to use a transient onset delay given more rapid signal onsets, it does suggest that they were relying on the ongoing interaural phase difference to localize the frequencies of 6.3 kHz and below rather than interaural time differences.

ACKNOWLEDGMENT

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