

Use of Binaural Cues for Sound Localization in Two Species of Phyllostomidae: The Greater Spear-Nosed Bat (*Phyllostomus hastatus*) and the Short-Tailed Fruit Bat (*Carollia perspicillata*)

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Unlike humans, not all mammals use both of the binaural cues for sound localization. Whether an animal uses these cues can be determined by testing its ability to localize pure tones; specifically, low frequencies are localized using time-difference cues, and high frequencies are localized using intensity-difference cues. We determined the ability to use binaural cues in 2 New World bats, *Phyllostomus hastatus*, large omnivores, and *Carollia perspicillata*, small frugivores, by testing their tone-localization ability using a conditioned avoidance procedure. Both species easily localized high-frequency tones, indicating that they could use the interaural intensity-difference cue. However, neither species was able to use the phase-difference cue to localize either low-frequency pure tones or amplitude-modulated tones (which provided an envelope for additional time analysis). We now know of 3 bat species that cannot use binaural time cues and 2 that can. Further exploration of localization in bats may provide insight into the neural analysis of time cues in species that do not hear low frequencies.

Keywords: Chiroptera, evolution of hearing, interaural time difference, interaural intensity difference

Mammalian sound-localization abilities differ greatly in both acuity and the ability to use the physical cues for locus (H. E. Heffner & Heffner, 2003). We have a much better understanding of some of these differences than of others. For example, variation in acuity is related to the width of the field of best vision such that species like humans with narrow foveal fields have good sound-localization acuity, whereas those with broad visual fields (visual streaks) such as cattle have poor localization acuity. 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, mammals with narrow fields of best vision require more accurate information about the locus of sound sources than those with wide visual streaks. This relationship was initially observed in nonecho-locating mammals, but applies as well to bats and other specialized mammals. Moreover, those species that do not use vision, such as strictly subterranean mammals, do not localize sound at all (R. S. Heffner & Heffner, 1992b, 1993; R. S. Heffner, Koay, & Heffner, 2008).

Species differences in the cues used for sound localization are less well understood. There are two binaural cues to locus in the azimuthal plane, one based on intensity and the other on time.

High frequencies are effectively blocked by the head, resulting in a difference in intensity at the two ears; the higher the frequency, the more effectively it is blocked such that a simple intensity difference becomes a spectral difference if multiple frequencies are present, as they are in nature. Low frequencies can be localized using the time-difference cue in which the arrival of a sound at the two ears is compared. In the case of a pure tone, the time of arrival of each sine wave is compared at the two ears (interaural phase-difference cue). If the signals are complex, fluctuations in the envelope at the two ears can also be compared, and if signal onsets are abrupt, a transient intensity difference and onset delay provide yet another source of locus information.

Most mammals examined so far use both binaural cues, but there are a few species known to rely on only one cue or the other (H. E. Heffner & Heffner, 2003). In particular, several species of rodents and bats as well as hedgehogs are unable to use the binaural time cues (R. S. Heffner & Heffner, 1992a; Koay, Kearns, Heffner, & Heffner, 1998; Masterton, Thompson, Bechtold, & RoBards, 1975; Wesolek, Koay, & Heffner, 2007). Although these species are all relatively small, giving rise to the possibility that some interaural distances may be just too small to provide useful time differences, some equally small mammals, including Jamaican fruit bats (*Artibeus jamaicensis*) and Egyptian fruit bats (*Rousettus aegyptiacus*), retain the ability to localize sound sources using the interaural time-difference cue despite their small size (R. S. Heffner, Koay, & Heffner, 1999, 2001b). Thus, there is yet no clear factor that distinguishes between those small species that do and those that do not use time cues.

To further explore the use of the binaural locus cues in small mammals, we have examined the ability to use the interaural phase- and intensity-difference cues to localize sound in two species of the family Phyllostomidae: the Greater spear-nosed bat,

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Phyllostomus hastatus, a large (70 g) omnivorous species that preys on insects and small vertebrates, and the Short-tailed fruit bat, *Carollia perspicillata*, a small (15 g) species that eats fruit, nectar, and pollen. Like others in this family, both use low-intensity sonar, at least for flying in clutter, and usually rely more on smell, vision, and passive hearing for foraging (Holler & Schmidt, 1996). Despite their small heads and the consequent small magnitude of locus cues, their passive sound-localization acuity is near the mean for mammals (approximately 12°), with *P. hastatus* being somewhat more acute with a threshold of 9° and the small *C. perspicillata* less acute with a threshold of 15° (R. S. Heffner, Koay, & Heffner, 2007).

Method

To determine the ability of bats to use the binaural time- and intensity-difference cues for locus, we tested two individuals of each species for their ability to localize brief pure-tone pips ranging from 2 kHz to 64 kHz (*P. hastatus*) or from 8 kHz to 71 kHz (*C. perspicillata*). This test is based on the absence of binaural intensity-difference cues at low frequencies given that frequencies of wavelengths greater than the head diameter undergo little or no attenuation as they travel around the head and thus do not present different intensities at the two ears (e.g., Plack, 2005, p. 46). Low frequencies do, however, permit comparison of the arrival time of corresponding parts of a sine wave at the two ears, that is, the phase-difference cue. Similarly, a carrier tone that is otherwise not localizable can be amplitude-modulated at a low rate to produce an envelope on which to base a binaural phase comparison. 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 angle of the sound source from the midline according to the following formula:

$$\text{Frequency of ambiguity} = 1/[6(a/C)\sin \Theta],$$

where a is the radius of the head in millimeters, C is the speed of sound (.3434 mm/μs in air), and Θ is the angle of the sound source from the bat's midline (based on Woodworth & Schlosberg, 1954). In summary, above the frequency of phase ambiguity, binaural intensity differences, if they are present, are the only binaural cues available for localization in azimuth, whereas below this frequency, binaural phase-difference cues are available.

Tone-localization performance was assessed throughout as much of the hearing range as possible, within the constraints of producing an easily audible pure tone, at least 40–50 dB above absolute threshold for each species (Koay, Bitter, Heffner, & Heffner, 2002; Koay, Heffner, Bitter, & Heffner, 2003). Moreover, to test lower frequencies usually localized well by most species, a pure tone that was easily heard but that was not localizable was sinusoidally amplitude modulated at rates as low as 500 Hz to determine whether the bats could extract a binaural time-difference cue from the envelope of the signal.

We used the same conditioned suppression/avoidance procedure and equipment used to test many other mammals, including other bats (e.g., Koay, Kearns, et al., 1998). Briefly, a bat was trained to

avoid a mild electric shock by breaking contact with the reward spout whenever a tone burst was presented from its left side while continuing to drink from the spout when the tone came from its right side.

Subjects

Two female *Phyllostomus hastatus* (Bat B at 70 g and Bat C at 66 g; both approximately 5 years old) and two male *Carollia perspicillata* (Bat A and Bat C, both at 17 g and approximately 1 year old) were tested. Note that these bats had been tested previously to determine their noise-localization acuity (R. S. Heffner et al., 2007) and behavioral audiograms (Koay et al., 2002, 2003). The mean maximum functional interaural distance (i.e., the time required for a sound to travel from one auditory meatus to the other) was 108 μs for *P. hastatus* and 47 μs for *C. perspicillata*. The bat colonies were maintained on a diet of mixed fruit (Barnard, 1995) and a dietary supplement (Lubee Fruit Bat Supplement, HMS Zoo Diets, Bluffton, IN). In addition, the *P. hastatus* were provided finely chopped meat for extra protein. While on test, the bats were housed individually in wood and plastic mesh cages (48 × 39 × 95 cm) and allowed to fly daily in the test chamber for exercise. They had free access to water and earned their food in the test sessions, except for occasional supplements to maintain healthy body weights.

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

Behavioral Apparatus

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

Sounds were presented through loudspeakers at ear level, mounted on a perimeter bar (102 cm radius, 101 cm height) and centered on the position occupied by a bat's head while it was drinking from the spout. The bats were tested in custom-built wire mesh cages. So that each species could maneuver easily, the test cage for *P. hastatus* measured 50 × 30 × 50 cm and was constructed of 2.5-cm mesh, and the cage for *C. perspicillata* was 37 × 22 × 23 cm constructed of 1.26-cm mesh. The bats climbed onto a small raised platform in the middle of the test cage to reach a reward spout placed in front of the platform. This configuration minimized acoustic obstructions between the bats and the loudspeakers. The platform was covered with a dampened carpet to provide traction and electrical contact between the bat and reward spout. When the bat licked the reward spout, a steady trickle of fruit juice was dispensed using a syringe pump. The pump was housed in a foam-lined box and placed in the back of the test chamber to eliminate dispenser noise. The fruit juice consisted of a sieved mixture of cantaloupe, pear juice, and the Lubee Fruit Bat Supplement. Requiring the bat to steadily lick the reward spout for juice served to maintain its head in a fixed position in the sound field. A shock generator was connected between the reward spout and platform. The shock level was adjusted individually to the lowest intensity that produced reliable avoidance (backing away

slightly or lifting its head from the spout). The bats did not develop a fear of the spout, as they readily returned to it after the shock. A 25-W shock-indicator light below the cage was turned on and off concurrently with the shock to signal successful avoidance and indicate when it was safe to resume licking the spout. (See Koay et al., 2002, 2003, for details of the test cages.)

Acoustical Apparatus and Sound Measurement

Pure tones were generated using a digital tone generator (Zonic A & D 3525, Zonic Corp., Tokyo, Japan). The tones were randomly attenuated over a 3.5-dB range from trial to trial (Coulbourn S85-08 programmable attenuator, Coulbourn Instruments, Lehigh Valley, PA) to thwart responses based on any slight intensity imbalance between the speakers. Because tone localization is difficult for most species, the tones were pulsed (100 ms on and 900 ms off) for two pulses. The tones were shaped by a rise–fall gate (Coulbourn S84-04; 10 ms rise/fall) and bandpass filtered (Krohn-Hite 3550, Krohn-Hite Corp., Avon, MA), set to 1/3 octave above and below the tone frequency. Finally, the signal was split into left and right channels, separately amplified (Crown D75, Crown International Inc., Elkhart, IN) and sent to one of two loudspeakers (Panasonic EAS-10TH400C, Panasonic Electronic Devices Co., Ltd., Osaka, Japan). The acoustic signal at the location of a listening bat was analyzed for overtones using a spectrum analyzer (Zonic A & D 3525); any harmonics in the acoustic signal were at least 40 dB below the fundamental frequency and below the bat'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) for *P. hastatus* at the following frequencies: 2, 4, 5.6, 8, 12.5, 16, 32, and 64 kHz. Because the two *C. perspicillata* had difficulty maintaining reliable performance at 60°, they were tested with loudspeakers at 90° separation (45° left and right of midline). Frequencies tested were 8, 12, 16, 25, 32, 50, and 71 kHz. A 20-ms rise–decay was used with the 2-kHz tone, with higher frequencies shaped using a 10-ms rise–decay to avoid onset and offset transients.

Additional tests used a 4-kHz or 8-kHz carrier tone, sinusoidally amplitude modulated at .5, 1, or 2 kHz (Krohn-Hite 2400 AM/FM Phase Lock Generator, 100% modulation depth) to provide an ongoing binaural time-difference cue in the envelope of the signal. Amplitude-modulated tones have previously been used to demonstrate the use of time cues when they enable a species to localize a frequency at which neither the phase cue nor intensity cue is available and that is not localizable without the modulation (R. S. Heffner et al., 1999, 2001b).

Sound Level Measurement

The sound pressure levels (SPLs) of the stimuli (SPL re 20 μ Newton/m²) were measured and the left and right loudspeakers were equated daily with a 1/4-in. (0.64 cm) microphone (Brüel & Kjaer 4135; Brüel & Kjaer, Naerum, Denmark), with correction for protection grid, preamplifier (Brüel & Kjaer 2619), measuring amplifier (Brüel & Kjaer 2608), and spectrum analyzer (Zonic A & D 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 bat's head and pointing it directly toward a loudspeaker (0° incidence).

Behavioral Procedure

Training. All four bats had previously been tested to determine their noise-localization thresholds and generalized to the tone-localization task without difficulty. In this task, the bats were trained to steadily lick the reward spout in the presence of two 100-ms tone bursts (900-ms interpulse interval), presented from a loudspeaker located to their right (30° for *P. hastatus* and 45° for *C. perspicillata*). Next, they were trained to break contact with the spout (a “detection response”) whenever the tone bursts came from a loudspeaker to their left; breaking contact allowed the bats to avoid a mild electric shock (0.5 s), delivered from the spout 2.0 s after left signal onset. More important, this avoidance response indicated that the bat had perceived the shift in sound location. The light bulb underneath the cage was turned on concurrently with shock to provide feedback for a successful avoidance (because, in those cases, the bat actually received no shock) 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).

Testing. Test sessions consisted of a series of 2-s trials (100 ms on and 900 ms off, for two pulses) separated by 1.5-s intertrial intervals. Thus, every 3.5 s, the bats received two brief tone pulses and decided whether to break contact or continue drinking after the tone burst. The response on each trial was defined as the duration of contact with the spout during the last 150 ms of the 2-s trial. If the bat 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 bat's left side and as a “false alarm” if it had come from the bat's right. If the bat was not in contact with the spout during the 1 s preceding a trial, data from that trial were not recorded, although the trial proceeded as usual. Thus, any trials in which the bat was grooming or otherwise not engaged in the task were discarded.

Each trial had a 22% probability of containing a left signal. The sequence of left–right trials was quasirandom and is described in detail elsewhere (H. E. Heffner & Heffner, 1995). Hit and false alarm rates were determined for each block of approximately 7–9 left trials and 28–36 associated right trials. 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 ranges from 0 (no hits) to 1 (100% hit rate with no false alarms), and proportionately reduces the hit rate by the false alarm rate observed for each block of trials rather than by the average false alarm rate for the entire session. This results in a more precise performance measure for a specific block of trials as false alarm rates often vary within a session (depending on the discriminability of the stimulus and the bat's level of motivation).

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, broadband noise was presented for several trials to verify that the bat remained sufficiently motivated. Each frequency was tested in at least three sessions for an average of 90–100 left trials. The top

50% of the trial blocks were then averaged to represent the best overall performance the bats were capable of sustaining.

Results

Pure-Tone Localization

Figures 1 and 2 illustrate the tone-localization performance of *P. hastatus* and *C. perspicillata*, respectively, relative to the theoretical availability of the binaural cues for localization (indicated by arrows). At an angle of $\pm 30^\circ$, the phase cue is calculated to become physically ambiguous at frequencies higher than 9.6 kHz for *P. hastatus*, which has a maximum interaural distance of 108 μ s. For *C. perspicillata*, with its maximum interaural distance of only 47 μ s, the phase cue becomes ambiguous above about 15.6 kHz at $\pm 45^\circ$ speaker separation. (For a detailed discussion of phase ambiguity, see Jackson, 1996, or Saberi, Farahbod, & Konishi, 1998.) At frequencies below the frequency of phase ambiguity, binaural phase differences are available to provide a potential locus cue, whereas at higher frequencies, only interaural intensity differences are available.

Interaural intensity differences are present at wavelengths short enough to be deflected by the head and pinnae, that is, wavelengths shorter than the head diameter (for a detailed discussion, see Christensen-Dalsgaard, 2005). For *P. hastatus* with a head diameter of approximately 2.4 cm, intensity differences at the two ears should be strongest above 14.5 kHz, and for *C. perspicillata* with a head diameter of 1.03 cm, intensity differences should be stron-

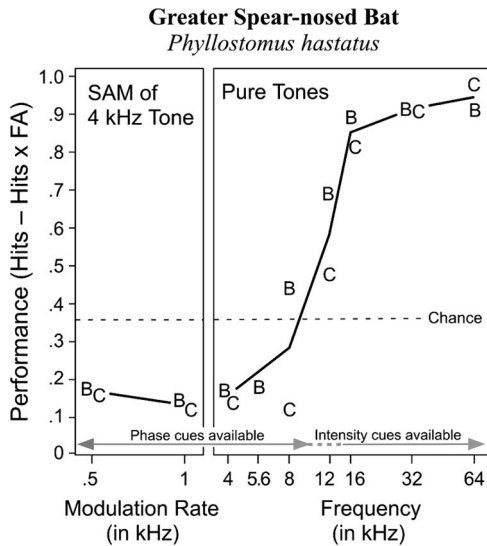


Figure 1. Sound-localization performance for two Greater spear-nosed bats (*Phyllostomus hastatus*) as a function of the frequency of a pure-tone stimulus (two pulses of 100-ms duration, 1-s interpulse interval) at 60° separation. Letters represent individual bats. Note that the bats perform well only at high frequencies for which the interaural intensity-difference cue is available, and below that frequency performance falls sharply, reaching chance performance at 10 kHz. The left panel depicts performance using an unlocalizable 4-kHz tone that was amplitude modulated at 500 Hz or 1 kHz to produce an envelope, providing a further basis for a binaural phase analysis. Note that the frequency scale is not continuous across the two panels.

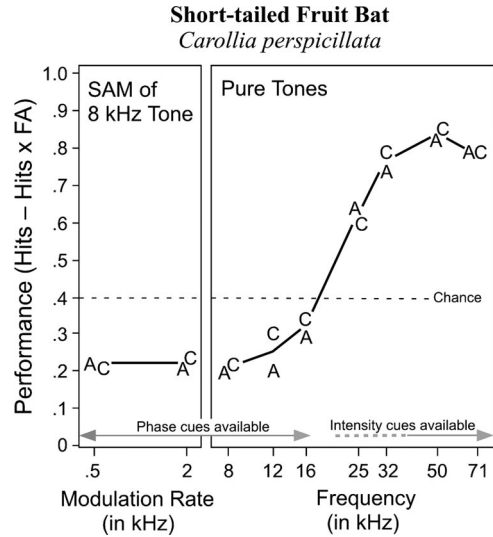


Figure 2. Sound-localization performance for two Short-tailed fruit bats (*Carollia perspicillata*) as a function of the frequency of a pure-tone stimulus (two pulses of 100-ms duration, 1-s interpulse interval) at 90° separation. Letters represent individual bats. Note that this species also performs well only at high frequencies for which the interaural intensity-difference cue is available; below that frequency performance falls sharply, reaching chance performance at 14.5 kHz. The left panel depicts performance using an unlocalizable 8-kHz tone that was amplitude modulated at 500 Hz or 2 kHz to produce an envelope, thereby providing a further basis for a binaural phase analysis. Note that the frequency scale is not continuous across the two panels.

gest above 33.4 kHz. However, detectable head shadowing can occur even 2 octaves lower (where wavelengths are 4 times as long as the head diameter), perhaps accounting for the residual but poor performance at frequencies just below those indicated.

As shown in Figure 1, the two *P. hastatus* agreed closely, with good performance at frequencies of 16 kHz and higher indicating good use of interaural intensity differences for localization. Although Bat B occasionally performed above chance at 8 kHz, performance at all other frequencies below 16 kHz was consistently at chance for both bats. By failing to localize low frequencies, while at the same time showing good motivation and performance at high frequencies, the bats demonstrated that they are unable to use interaural phase differences to localize pure tones.

Figure 2 illustrates the tone localization performance of *C. perspicillata*. Again, the two individuals agreed and performed well at high frequencies, indicating good ability to localize using interaural intensity differences. At frequencies below 32 kHz, performance declined sharply, falling to chance at 16 kHz and below. Because good performance returned rapidly within a test session when high frequencies were presented, the poor performance at low frequencies indicates an inability to use the interaural phase-difference cue for localization.

Besides showing that neither of these species can localize using the interaural phase-difference cue, the chance performance at low frequencies also indicates that neither species showed evidence of localizing using the available transient onset delay. This brief cue is the difference in the arrival time of the leading edge of a sound at the two ears and is usually considered a type of time cue, but it

can also be thought of as a transient intensity difference. Regardless of how it is viewed, it is usually considered a weak cue (e.g., Krahe, Larsen, & Ronacher, 2000; Perrott, 1968) and did not support sound localization in either of these species. It should be noted, however, that the magnitude of the transient intensity difference was somewhat reduced by the 10-ms rise–decay time used to avoid onset and offset clicks in the acoustic signal. Thus, within these limitations, there was no indication that *P. hastatus* or *C. perspicillata* used the transient onset delay to localize sound.

Sinusoidal Amplitude Modulation

To further explore the ability of *P. hastatus* and *C. perspicillata* to use binaural time differences, we sinusoidally modulated the amplitude of a pure tone that the bats could not localize. For *P. hastatus*, we used a 4-kHz carrier tone modulated at 500 Hz and 1 kHz (see Figure 1); for *C. perspicillata*, we used an 8-kHz carrier tone modulated at 500 Hz and 2 kHz (see Figure 2). The amplitude modulation presented the bats with an additional time cue in the delay of the components of the envelope at the two ears. However, modulation also results in side lobes, that is, tones of frequencies equal to the carrier frequency plus and minus the modulation rate. For example, modulating the 4-kHz tone at 1 kHz for *P. hastatus* produced side lobes of 3 and 5 kHz. Modulating the 8-kHz tone at 2 kHz for *C. perspicillata* produced side lobes at 6 and 10 kHz. It is important to note that modulation rates were chosen so that the higher frequency side lobes remained too low to be localized using an intensity difference. As shown in Figures 1 and 2, the modulation of the envelope and the presence of side lobes did not improve localizability for either species as both continued to perform at chance. Thus, neither species was able to localize using interaural time differences in either the carrier wave, envelope, or onset of the sound.

Discussion

Use of Binaural Locus Cues by Bats

As expected, both species of bats were able to localize high-frequency pure tones. Indeed, they performed as well with these tones as they had with broadband noise at this test angle (R. S. Heffner et al., 2007). We interpret this to mean that both bats can use the interaural intensity-difference cue for localization.

The good localization of high frequencies contrasted sharply with the failure to localize lower frequencies that require comparing the phase of either a pure tone or envelope at the two ears. For wavelengths longer than the head diameter—below approximately 14.5 kHz for *P. hastatus* and 33.4 kHz for *C. perspicillata*—the head becomes a less effective sound obstacle, and intensity differences between the two ears diminish. Within less than an octave below these frequencies, the bats' performances fell sharply to chance and did not recover. Taken together, these results suggest that the collapse of performance as the midrange of frequencies is approached is due to the reduced magnitude and unreliability of the interaural intensity-difference cue at these frequencies, coupled with the inability of these bats to take advantage of the interaural phase difference that is present at lower frequencies.

Three other bats have been tested for the use of locus cues. Like the two species reported here, Big brown bats (*Eptesicus fuscus*)

could not use the binaural time cue to localize pure tones. Moreover, performance did not improve when the envelope, as well as the carrier signal, provided an ongoing time difference (Koay, Kearns, et al., 1998). Because none of these three species could localize signals from which the intensity cue was absent, we also conclude that they could not use the transient onset delay in the envelope of the signal (with its 10-ms rise–decay). Although this does not rule out their ability to use the onset delay given sharper signal onsets, it does suggest that this transient time cue was also not usable by any of the bats that could not use the ongoing time cues. In contrast, Jamaican fruit bats (*Artibeus jamaicensis*) and Egyptian fruit bats (*Rousettus aegyptiacus*) are able to use binaural time cues, as demonstrated by their ability to localize low-frequency pure tones and amplitude-modulated envelopes of unlocalizable carrier tones (R. S. Heffner et al., 1999, 2001b).

Use of Time Cues by Small Mammals

For many years, it was assumed that all mammals use both the binaural time- and intensity-difference locus cues, just as humans do (Stevens & Newman, 1936). This changed in 1975 when it was reported that the Long-eared hedgehog (*Hemiechinus auritus*) was unable to localize using binaural time cues (Masterton et al., 1975). At first, it was conceivable that such an inability might be an oddity, restricted perhaps to specialized insectivores. Since then, several rodents and bats have been discovered to be unable to use binaural time cues such that we now know of six species that lack this ability. (During this time, the discovery was also made that some mammals do not use the binaural intensity-difference cue; H. E. Heffner & Heffner, 2003). The question, then, is why an animal would relinquish the use of binaural time cues. We can think of at least three possibilities: Their heads may be too small to generate useful time delays, they do not need to localize sound accurately, or they do not hear the low frequencies that must be localized using time delays.

First, those mammals that are unable to use binaural time cues are relatively small species with small heads. Thus, it is possible that their ears are too close together to generate useful binaural time differences. If so, we might expect that animals with head sizes below some minimum would not use the binaural time cue. To see whether this was the case, we compared the maximum time it would take sound to travel around the head from the opening of one auditory meatus to the other in the six species unable to use the binaural time cue with the seven smallest species that do use that cue. Figure 3 shows the considerable overlap between the two groups; five species that *do* use time cues have functionally smaller heads than the hedgehog and Norway rat (*Rattus norvegicus*) that *do not* use them. Thus, small head size does not seem to be an insurmountable barrier that forces small species to forego the use of binaural time cues for localization. Nevertheless, it is still possible that below some functional head size, such as 75 μ s, no mammal uses time cues.

Second, some small mammals may not need to localize sound accurately and thus give up use of one of the locus cues. If so, then one might expect those animals that do not use the binaural time cue to be among those with poorer sound localization acuity. However, as Figure 4 shows, there is almost complete overlap in localization acuity of those animals that do and those that do not use binaural time cues. Moreover, it is not difficult to find animals

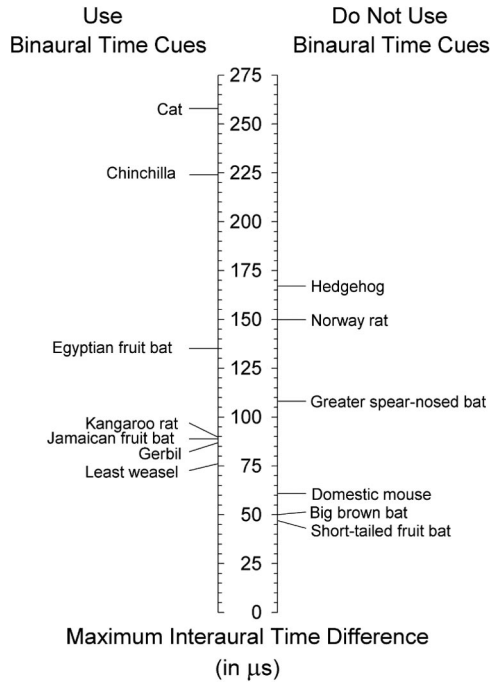


Figure 3. Distribution of interaural distances among species that do use binaural time cue for localization and those that do not. Although all the species that do not use the time cues are small, there are several similarly small species that do use the cue. Data taken from Casseday & Neff, 1973; H. Heffner & Masterton, 1980; R. S. Heffner & Heffner, 1987, 1988; R. S. Heffner, Heffner, Kearns, Vogel, & Koay, 1994; R. S. Heffner et al., 1999, 2001b; Koay, Kearns, et al., 1998; Masterton et al., 1975; Wesolek et al., 2010.

that, in spite of not using time cues, are nevertheless more accurate at localizing sound than some larger animals that do use time cues: For example, compare Norway rats and three bats that do not use time cues with larger, but less accurate, chinchillas (*Chinchilla laniger*) that do use the cues (see Figures 3 and 4). Thus, loss of time cues does not necessarily compromise acuity, and the argument that animals give up one of the locus cues because they have less need to localize sound accurately is not supported.

Finally, we have noted that mammals fall into two groups based on their low-frequency hearing (R. S. Heffner, Koay, & Heffner, 2001a). Most mammals for which audiograms are available are able to hear frequencies below about 125 Hz at a level of 60 dB SPL, but about one third of the species do not hear below about 500 Hz. To investigate the possibility that the use of the binaural time cue might be related to the ability to hear low frequencies, we compared low-frequency hearing in our two groups of small mammals. As shown in Figure 5, all the mammals with good low-frequency hearing use binaural time cues, but so do two of the species that do not hear low frequencies. The remaining species with poor low-frequency hearing do not use the binaural time cues.

Use of time cues by species with good low-frequency hearing is not surprising because the binaural time cue is the only locus cue usable at low frequencies where interaural intensity differences and pinna cues are not available. If a species hears low frequencies, then it would be forced to use the time cue to localize the source of low-frequency sounds. (Only the subterranean rodents

that do not localize sound, presumably using neither binaural cue effectively, are exceptions as they use low frequencies for purposes other than directional information; H. E. Heffner & Heffner, 2003.) Yet, having poor low-frequency hearing does not necessarily mean that an animal does not use binaural time cues; of the eight species in this group, the Jamaican fruit bat and the Egyptian fruit bat do use the binaural time cue despite their inability to hear significantly below 2 kHz (R. S. Heffner et al., 1999, 2001b, 2003; Koay, Heffner, & Heffner, 1998). They use the time cue, although it is physically available and unambiguous only for frequencies in the lowest 2 octaves of their hearing ranges. This, however, reminds us that the time cue is also available over at least part of the audible range of the other six species that do not use the cue. Most notable in this regard is the Norway rat for which the time cue is available over approximately 3.5 octaves of its hearing range (Wesolek et al., 2010). Thus, although the use of the binaural time cue accompanies good low-frequency hearing, some mammals that have poor low-frequency hearing nevertheless still use the binaural time cue.

Physiological Implications

The ability to use interaural time differences for localization should be reflected in the response properties of an animal’s auditory system. Specifically, in species that use time cues, we would expect to find neurons that respond to interaural delays within the range naturally available to an animal with its head size. Although responses to interaural delays have been reported in small mammals, the delays that elicit these responses are often an

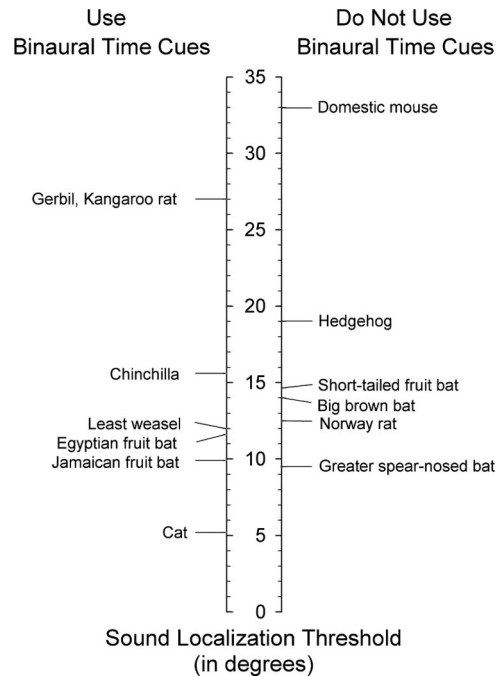


Figure 4. Distribution of sound-localization thresholds among small species that do use the binaural time cue for localization and those that do not. Inability to use the time cue is not associated with poorer sound-localization acuity. For sources of data, see Figure 3 and H. E. Heffner & Heffner, 1985; R. S. Heffner et al., 2007.

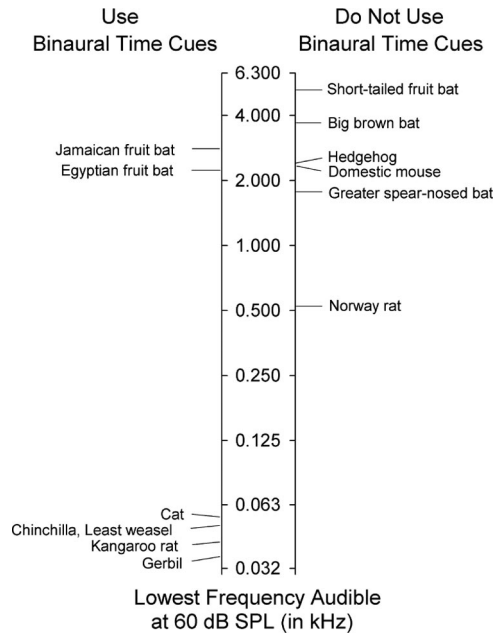


Figure 5. Distribution of low-frequency hearing limits among small mammals that do use the binaural time cue for localization and those that do not. Most of the species with poor low-frequency hearing do not use the binaural time cue, but the Jamaican fruit bat and the Egyptian fruit bat do use the cue. These cases are important because they demonstrate that even very small species do not have to hear very low frequencies to localize sound using the binaural time cue. They force us to ask why six species with similar low-frequency hearing, similar magnitude of time delays, and similar sound-localization abilities are unable to use the time cue. For sources of data, see Figure 3 and R. S. Heffner et al., 2001a, 2003; Koay, Heffner, & Heffner, 1998.

order of magnitude longer than those possible based on their interaural distances (e.g., Fuzessery, 1997; Kelly & Phillips, 1991). The significance of such an absence of responses to biologically meaningful delays in small mammals, particularly bats, has recently been addressed (Grothe, 2000; Grothe & Park, 2000). Focusing on physiological responses and neural connections in the superior olivary complexes of small mammals, these authors concluded that species with interaural distances smaller than a “few tens of microseconds” are not likely to use binaural time cues for sound localization. Our behavioral studies with bats and small rodents show that many species are consistent with this conclusion. However, there are enough small species that do use time cues for localization (see Figure 3) to demonstrate that any difficulties attributable to small head size or neural timing capacities have been circumvented in several mammalian lineages. The clearest instance of overcoming limitations that a small interaural distance might entail is the use of time cues in two bats. The Jamaican fruit bat is particularly small, and neither species hears low frequencies typically associated with time delay analysis in the brainstem. However, the brainstem auditory nuclei are some of the most variable in the mammalian brain, and the remarkable variation of these nuclei in bats has been emphasized repeatedly (e.g., Covey, 2005; Grothe, 2000). Such variation suggests that an examination of the neural responses to time delays in very small species that use time cues might

reveal that the mammalian nervous system is capable of discriminating smaller time differences than have so far been recognized.

The use of interaural phase differences for localization requires neural synchrony with the sounds that are localized, that is, phase locking. Accordingly, we should observe phase locking in synchrony with signals that are localized using the time cues—either carrier signals or the envelopes of amplitude-modulated sounds. This implies that phase locking should be observable at relatively high frequencies in small species that use the phase-difference cue for sound localization. However, the limited evidence available so far comes from studies of larger mammals and indicates that phase locking begins to weaken above 600–1000 Hz (depending on species), and phase locking above 5 kHz has been virtually undetectable in the few species examined (cat [*Felis catus*], Johnson, 1980; guinea pig [*Cavia porcellus*], Palmer & Russell, 1986; squirrel monkey [*Saimiri sciureus*], Rose, Brugge, Anderson, & Hind, 1967; chinchilla, Woolf, Ryan, & Bone, 1981). Indeed, some believe that neurons in the central nervous system only phase lock below 2 kHz (Grothe, 2000). So far, phase locking to pure tones has not been found at all in the three species of bats examined (*Pteronotus parnellii* and *Tadarida brasiliensis*, Grothe & Park, 2000; *Antrozous pallidus*, Lohuis & Fuzessery, 2000). Here again, our recent behavioral results indicate greater variation in mammals than has yet been demonstrated. Specifically, we should be able to record phase locking at frequencies above 5 kHz in the two bats that use the binaural phase-difference cue at high frequencies (R. S. Heffner et al., 1999, 2001b). Bats may provide an excellent opportunity to explore the limits of mammalian phase locking by comparing physiological responses in auditory neurons in closely related species that differ in their ability to use the interaural time-difference cue. The tremendous morphological variation in the auditory brainstems of bats, as well as in their auditory abilities, has barely been explored, despite the potential to reveal the extremes of capabilities of the mammalian nervous system.

It is interesting that neural phase locking to the envelope of a signal has been recorded in bats that do not show phase locking to pure tones (*Antrozous pallidus*, Fuzessery, 1997; Lohuis & Fuzessery, 2000; *Tadarida brasiliensis*, Grothe & Park, 1998). However, it has been argued that synchronous firing to the envelope of signals in very small species does not serve passive localization (Grothe & Neuweiler, 2000). We are inclined to agree as it so far appears that every species unable to use the binaural time cue in pure tones is also unable to use the time cue in amplitude-modulated tones (e.g., current report; Koay, Kearns, et al., 1998). Conversely, the bats that can localize amplitude-modulated tones can also localize pure tones using the phase-difference cue. These observations support the idea that the extraction of binaural time differences for sound localization, whether from the components of a signal or from its envelope, is a single function and probably relies on a single neural mechanism.

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