

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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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

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 ran-

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 30° , 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 mm. For *C. perspicillata* with its maximum interaural distance of only 47 mm, the phase cue becomes ambiguous above about 15.6 kHz at 45° speaker separation. (For a detailed discussion of phase ambiguity, see Jackson, 1996, or Saberi, Farahbod, & Kon-

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

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

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 pinnae 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

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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