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Sound localization in common vampire bats: Acuity and use of the binaural time cue by a small mammal

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Passive sound-localization acuity and the ability to use binaural time and intensity cues were determined for the common vampire bat (*D m t*). The bats were tested using a conditioned suppression/avoidance procedure in which they drank defibrinated blood from a spout in the presence of sounds from their right, but stopped drinking (i.e., broke 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 13.1°—within the range of thresholds for other bats and near the mean for mammals. Common vampire bats readily localized pure tones of 20 kHz and higher, indicating they could use interaural intensity-differences. They could also localize pure tones of 5 kHz and lower, thereby demonstrating the use of interaural time-differences, despite their very small maximum interaural distance of 60 μs. A comparison of the use of locus cues among mammals suggests several implications for the evolution of sound localization and its underlying anatomical and physiological mechanisms.

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I. INTRODUCTION

The ability of mammals to localize sound is not uniform, but varies between species in two important ways. First, sound-localization acuity as measured by the minimum audible angle for brief sound ranges from about 1° for humans and elephants to more than 25° in mice, rabbits, and cattle, with subterranean rodents being virtually unable to localize brief sounds at all (Heffner and Heffner, 2003). This variation can be accounted for by the relationship between auditory localization and vision in which species with narrow fields of best vision appear to require more acute locus information to direct their gaze to the source of a sound than do species with broad visual fields or visual streaks (Heffner and Heffner, 1992c).

The second way in which the sound-localization ability of mammals varies is in the use of the binaural time and intensity cues for locus, which are demonstrated by the ability of an animal to localize low- and high-frequency pure tones (e.g., Heffner and Heffner, 2003). Specifically, low-frequency pure tones that bend around the head with little or no attenuation are localized by comparing the time of arrival of the phase of each cycle of the tone at the two ears and this is thus often referred to as the binaural phase-difference cue. The phase-difference cue becomes ambiguous for pure tones at higher frequencies when successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears. The exact "frequency of ambiguity" depends on an animal's head size and the angle of the sound source relative to its midline—it is higher for smaller heads and sound sources closer to midline. Pure tones above the frequency of ambiguity, then, must be localized using interaural intensity differences if they are available.

Using the ability to localize low- and high-frequency pure tones as an indication of the ability to use the binaural time and intensity cues, it has been found that although most mammals use both binaural cues, many do not. For example, it is now known that hedgehogs, rats, and some bats do not use binaural time cues, whereas pigs, horses, cattle, and alpacas do not use binaural intensity cues (Heffner and Heffner, 1986, 1989; Heffner and Heffner, 2003; Heffner *et al.*, 2014). Subterranean rodents appear to use neither binaural cue, as they are virtually incapable of localizing brief sounds (Heffner and Heffner, 1990, 1992b, 1993). Moreover, the highest-frequency pure tone that can be localized using the interaural phase-difference cue also varies considerably, from 250 Hz for the Indian elephant to 6.3 kHz for the Jamaican fruit bat (Heffner and Heffner, 1982; Heffner *et al.*, 2001c). Why some animals fail to use one or the other binaural locus cue and why the upper frequency limit for the binaural phase cue varies is not currently known.

To further explore this variation in mammalian sound localization, the ability of the common vampire bat (*D m t*) to localize sound was determined. Common vampire bats are best known for their highly specialized digestive physiology and behavior that enables them to live on blood, primarily of large bovids. However, their hearing abilities are also of interest because they are more sensitive to low frequencies than any of the bats tested so far (Heffner *et al.*, 2013). With such relatively good low-frequency sensitivity for a small bat, their performance on a task requiring the use of the low-frequency-based binaural phase cue, despite the small magnitude of the available time difference, was of special interest.

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II. METHODS

Sound-localization thresholds (i.e., minimum audible angles) were obtained using the conditioned suppression/avoidance procedure in which a bat was trained to break contact with a reward spout if a brief noise burst was presented from its left side, and to continue feeding from the spout if the noise came from its right. The ability to localize pure tones at an angle of 60° separation was used to determine the ability to use the binaural locus cues.

A. Subjects

Three male *D[illegible]n t* (referred to as A, B, and C) were approximately 3–3.5 years old at testing and weighed 23–29 g. They were individually housed in wood and plastic mesh cages (48 × 39 × 95 cm). They had free access to water and received their meals of defibrinated attenuated by the head and pinnae, therefore the binaural intensity-difference cue is not available and localization must rely on time cues (Mills, 1972 no longer discriminate reliably between left and right sounds (i.e., the hit rate no longer differed significantly from the false alarm rate, binomial distribution, > 0.05). This was always followed by testing at a larger angle to verify the bat's motivation and continued good performance before again decreasing the angle of separation. Daily testing continued until performance no longer improved at any angle. Asymptotic performance was calculated by averaging the three blocks of trials with the highest scores; these were taken from at least two, and usually three, different sessions. These means were then plotted as the asymptotic performance curve for each bat. Threshold was defined as the angle yielding a performance score of 0.50, which was determined by interpolation. The angles tested were 180

lateral superior olivary nucleus, with dendrites extending medially and laterally, receiving bilateral input from the anteroventral cochlear nuclei, and sending output to the ipsilateral inferior colliculus (e.g., Grothe, 2000; Schwartz, 1992). The important physiological characteristics of an MSO are sensitivity to interaural time differences, responses limited primarily to low frequencies, excitatory responses to input from each ear, and a more recent recognition of the importance of bilateral inhibition (Brand *et al.*, 2002; Grothe, 2003). However, there appear to be many likely exceptions to this typical configuration. For example, we know that some MSO cells in some species respond to higher frequencies and in "atypical" fashion, and the MSOs of some small mammals are "non-classic" in that they do not possess all these standard features, leading some to suggest that those MSOs are not involved in the analysis of interaural time differences for sound localization (e.g., Grothe, 2000; Grothe and Park, 2000; Grothe *et al.*, 2010). Although the auditory brainstems of many species have been studied (e.g., Baron *et al.*, 1996; Grothe, 2000; Schwartz, 1992), not all of the anatomical and physiological characteristics are known for each species. For example, the presence of an MSO is often based on the location and appearance of a cell group, with little information on its anatomical connections or the binaural response properties of its neurons. Nevertheless, based on the limited information now available for bats, we can search does not preclude the use of the binaural phase-difference cue and this raises questions about the limits of neural phase locking on which the phase cue is thought to depend.

4. Upper limit of phase locking in the auditory system

If an animal is to use the binaural phase cue, then it must hear frequencies low enough to permit synchronous firing (neural phase locking) to support a binaural phase comparison. Similarly, the highest frequency at which the cue can be used would seem to be affected by the ability of the nervous system to phase lock at high frequencies. In other words, a species should be able to use the phase cue at frequencies as high as the highest frequency at which its auditory system can phase lock, as long as the cue is physically unambiguous. It has been shown that the upper limit of strong phase locking in mammals is about 3 kHz, with synchrony statistically detectable up to about 5 kHz (e.g.,

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