Research paper

Laboratory rats (Rattus norvegicus) do not use binaural phase differences to localize sound

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ABSTRACT

The ability of Norway rats to use binaural time- and intensity-difference cues to localize sound was investigated by determining their ability to localize pure tones from 500 Hz to 32 kHz. In addition, their ability to use the binaural time cues present in the envelope of a signal was determined by presenting them with a 1-kHz tone that was amplitude modulated at either 250 or 500 Hz. Although the animals were easily able to localize tones above 2 kHz, indicating that they could use the binaural intensity-difference cue, they were virtually unable to localize the lower-frequency stimuli, indicating that they could not use the binaural phase (time) cue. Although some animals showed a residual ability to localize low-frequency tones, control tests indicated that they were using the transient interaural intensity difference in the onset of a sound that exists after it reaches the near ear but before it reaches the far ear. Thus, in contrast to earlier studies, we conclude that the Norway rat is unable to use the ongoing time cues available in low-frequency tones to localize sound, raising the possibility that the rat may not use interaural time differences to localize sound.

1. Introduction

The ability of mammals to localize sound varies among species not only in acuity, but also in the use of the two binaural locus cues: the difference in the time of arrival of a sound at the two ears and the difference in the frequency-intensity spectra reaching the two ears. Although it appears that most mammals use both binaural cues, some, such as horses and cattle, use only the binaural time-difference cue, whereas others, such as house mice and big brown bats, appear to use only the binaural spectral-difference cue. A few mammals, such as some subterranean rodents, have lost the ability to localize brief sounds altogether and thus do not use either binaural cue (for a review, see Heffner and Heffner, 2003).

The ability of an animal to use the two the binaural cues can be investigated by training it to localize the source of single, brief tone pips (e.g., Masterton et al., 1975), a procedure first used with humans (Mills, 1972; Stevens and Newman, 1936). Specifically, the ability to localize pure tones too low in frequency to generate binaural intensity differences (because they bend around the head with little attenuation) indicates the ability to use the binaural phase cue, which is a binaural time cue (e.g., Zhang and Hartmann, 2006). The ability to localize pure tones too high in frequency to provide a binaural phase cue (because successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears) indicates the ability to use the intensity-difference cue, a special case of the binaural frequency-intensity spectral cue. Among species that use the binaural phase cue, the upper-frequency limit for its use spans more than three octaves, from the 500-Hz upper limit of cattle to the 6.3-kHz upper limit of the Jamaican fruit bat (Heffner and Heffner, 2003). Thus, a comparative study of the upper limit of the use of the binaural phase cue could lead to an understanding of the reasons for this variation, and perhaps of the reasons why some species forego the use of the cue altogether.

In comparing the use of the binaural locus cues by different species, we noted that there was disagreement regarding the highest frequencies at which laboratory rats can use the binaural phase cue. Specifically, Masterton and his colleagues (1975) placed the upper limit for rats between 4 and 8 kHz whereas Kelly and Kavanagh (1986) placed it between 2 and 4 kHz. Because our comparative analysis required a more precise estimate of the upper limit for binaural phase, we decided to test laboratory rats ourselves to determine which estimate was correct. What we found, however, was that we were unable to replicate either upper limit; instead, it appears that laboratory rats are unable to use the binaural phase-difference cue at all. As described in Section 4, this finding is not incompatible with the results of anatomical and physiological studies of sound localization in the rat.

Abbreviations:

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2. Methods

Four rats were trained to localize the source of brief pure tones at a fixed angle of 30° left and right of midline (60° total separation) using a conditioned-suppression avoidance procedure. The ability to localize pure tones below the frequency at which the phase cue becomes ambiguous indicates the use the binaural phase-difference cue whereas the ability to localize pure tones above the frequency of phase ambiguity indicates the ability to use the binaural intensity-difference cue.

2.1. Subjects

Four male hooded rats (Rattus norvegicus, Harlan Sprague–Dawley) were used in this study. Rats A, C, and D were 200 days old at the beginning of testing and 450 days old at the end; Rat B was 90 days old at the beginning and 200 days old at the end. They were housed in standard solid bottom cages with grid covers and pelleted corncob bedding (1/8 in. pellets, Harlan Teklad). The animals were given free access to rodent chow and their body weights were measured daily. Water was available during daily training and testing sessions. Pieces of apple were given as needed to maintain a healthy body weight.

The use of animals in this study was approved by the University of Toledo Animal Care and Use Committee.

2.2. Behavioral apparatus

Testing was conducted in a double-walled sound chamber (IAC model 1204; Industrial Acoustics Co., Bronx, NY, USA; 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were lined with eggcrate foam and the floor carpeted to reduce sound reflections. The equipment used for behavioral control and stimulus generation was located outside the chamber and the rats were monitored over a closed-circuit television. The rats were tested in a cage (28 × 13 × 16 cm) constructed of half-inch (0.127 cm) wire mesh, which was mounted 98 cm above the floor on an adjustable tripod. A water-spout, consisting of 2-mm diameter brass tubing topped with a brass ‘‘lick” plate (2.5 × 1.7 cm), was mounted vertically in the front of the cage. The spout was adjusted to a level that permitted the rats to drink comfortably (4 cm above the floor of the cage). Water was delivered to the reward spout via a flexible plastic tube attached to a 60-cc syringe pump (Yale Apparatus, model YA-12, Wantagh, NY) located outside the sound chamber. The flow rate was adjusted so each animal was able to satisfy its daily water requirements in a animal's right. However, if a rat was not in contact with the spout during the 1-s preceding the trial, data from that trial were not recorded, even though the trial proceeded as usual. This eliminated trials when the rat was grooming or otherwise not engaged in the task. Trial presentation was not resumed until the animal returned to the spout.

a signal is first turned on. This cue occurs even for low-frequency sounds that bend around the head with little or no attenuation and begins when a signal reaches the near ear and lasts until the sound has reached its full intensity at both ears; because the onset cue has been demonstrated in humans to be a short-duration intensity-difference cue (not a time-difference cue), we refer to it here as the transient binaural intensity-difference cue (Elfner and Tomsic, 1968; Perrott, 1969). Thus, the subsequent tests were conducted to determine if the animals could localize low-frequency tones when the possibility of using these alternative cues was reduced.

3.2. Localization of pure tones at 15 dB SL

As previously noted, the ability of some of the animals to localize the 1-kHz tones in the preceding test may have been due to

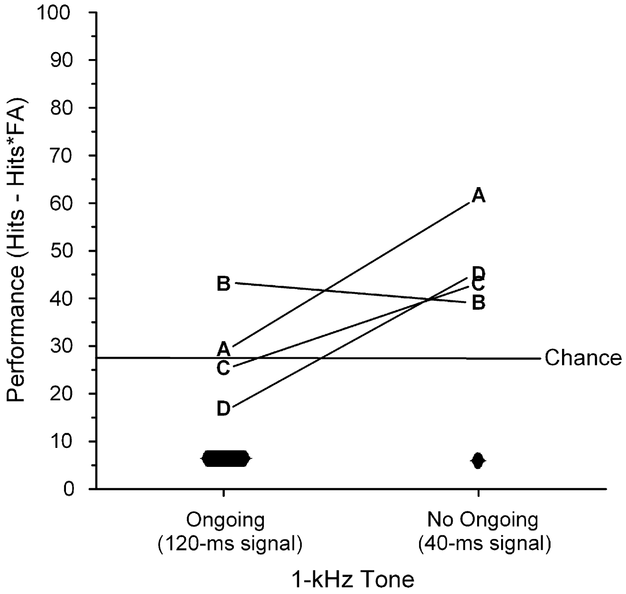

Fig. 4. Tone localization performance of four rats localizing a 1-kHz pure tone at ±30° around midline. Both signals had rise/fall times of 20 ms, but the ongoing signal included 80-ms at full intensity (30 dB above detection threshold). The performance scores for the ongoing signal are those from the initial test. Note that the "No-Ongoing" signal, despite being much briefer, was easier for three of the rats to localize. These results are consistent with the hypothesis that rats localize low-frequency tones using the transient interaural intensity-difference cue.

of the stimuli or increasing the rise/fall time completely abolished the rats' ability to localize the 1-kHz tones (Figs. 2 and 3); in addition, the finding that removing the ongoing portion of a 1-kHz tone either had no effect on or else improved performance further indicated that the rats were localizing the transient portion of the signal (Fig. 4). Finally, measurements of the intensity of sounds at the two ears indicated that the ability of the rats to localize high-frequency tones, and the subsequent decline in performance at lower frequencies, could be explained by the magnitude of the interaural intensity differences (Fig. 5). To be sure, we cannot rule out the possibility that rats use binaural time cues for localizing high frequencies. However, we can think of no reason why rats would retain the ability to use binaural time differences to localize high frequencies for which binaural intensity differences are readily available and relinquish the time cue at low frequencies for which no other localization cue is available. Moreover, a re-examination of the behavioral and physiological literature shows that the evidence supporting the use of binaural time differences by rats is not as convincing as we once believed (see the following sections).

Before proceeding, it is worth noting the evidence for why the transient onset cue is properly viewed as an intensity-difference cue rather than a time-difference cue. In investigating the role of onset in sound localization, Lloyd Elfner and his colleagues pointed out that changing the rise time of a signal has opposite effects on the size of the arrival time difference and the size of the transient interaural intensity difference (Elfner and Tomsic, 1968; Perrott, 1969). Specifically, increasing the rise time of a signal (i.e., turning it on more slowly) increases the difference in the arrival time of a sound at the two ears, but decreases the transient interaural intensity difference. The question of whether the auditory system analyzes the onset cue in terms of time or intensity, then, can be addressed by determining the effect of rise time on sound localization ability. What Elfner and his colleagues found was that increasing the rise time of a signal decreased the ability of subjects to use to the onset cue to either localize or lateralize sound, leading them to conclude that, in humans, signal onset is best viewed as a short-duration binaural intensity-difference cue (Elfner and Tomsic, 1968; Perrott, 1969). As with humans, we found that increasing the rise time of low-frequency tones decreased the ability of rats to localize the tones (Fig. 2), indicating that rats also analyze the onset cue as a transient binaural intensity difference. In short, although one may present an animal with an interaural time difference, the animal's auditory system may process the transient portions of the signal as an intensity difference.

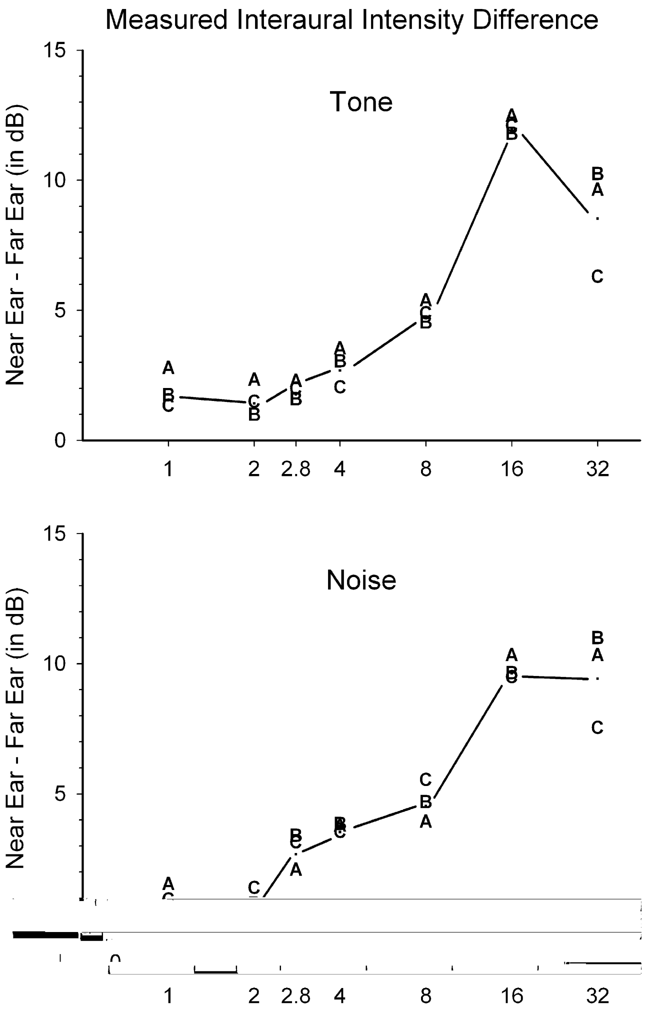

Fig. 5. Interaural intensity difference for pure tones (top) and 1/3-octave noise bands (bottom) for a sound source located 30° from midline. Measurements were conducted on three rats, labeled A, B, and C.

4.1. Comparison with previous behavioral studies

The first tone localization test with laboratory rats was conducted by Masterton and his colleagues in 1975. Using a two-choice procedure in which the animals licked a center water spout to turn on a brief sound (40 dB SL, 40-ms rise/fall, 140 ms total duration) and then walked to the source of the sound (one of two loudspeakers located ±30° around midline), they found that the two rats they tested could localize both low and high frequencies, but not 8 kHz (Fig. 6). Although we cannot explain the inability of their rats to localize 8 kHz, their ability to localize low frequencies is most likely due to the presence of overtones in their signals. This is because at 40 dB above threshold, the sound pressure level of the 1 kHz tone would have been 66 dB, the 500 Hz tone 94 dB, and the 250 Hz tone over 100 dB (Kelly and Masterton, 1977). These levels may well have produced overtones in the 1-kHz tone and would certainly have done so at 500 and 250 Hz.

Thus, the good low-frequency performance of the rats in their study was likely due to overtones that made it possible for them to use the binaural intensity-difference cue to localize.

A later study conducted by Kelly and Kavanagh (1986), used the same two-choice procedure and the same angle of separation and sound level; however, they used a shorter rise/fall time (20 ms) and shorter total duration (65 ms). The average score for their two normal animals is shown in Fig. 6 (they also tested five rats with cortical ablations with similar results). Unlike Masterton and his colleagues, Kelly and Kavanagh found that the rats could easily localize 8 kHz, but had difficulty with 4 kHz, although their performances remained above chance. In comparison to the present study, Kelly and Kavanagh's rats performed well at 2 kHz whereas our animals performed at or near chance. Kelly and Kavanagh checked their sounds with a spectrum analyzer so the presence of overtones in their signal is unlikely. Thus, the only explanation we can offer is that their animals may have been better able to use the transient interaural intensity difference due to the shorter signal duration and rise/fall time.

One issue is whether our failure to replicate either of the previous two studies is due to our using a different behavioral procedure: conditioned suppression as opposed to a two-choice procedure. This appears unlikely for two reasons. First, previous studies have indicated that the two procedures give the similar results on sound localization tests (e.g., Heffner and Heffner, 1988). Second, as can be seen in Fig. 6, rats were able to perform well on some frequencies with both procedures, indicating that they had no difficulty with the requirements of either task. Thus, the difference between the studies is in the frequencies that the animals were able to localize, not in their asymptotic performances.

Finally, rats have been tested on their ability to perceive the locus of clicks presented from two loudspeakers separated by 180° in which the click from one speaker preceded the other by a small time difference (Kelly, 1974); in humans, such a stimulus is usually perceived as a single click coming from the location of the speaker emitting the leading click and that percept is referred to as the "precedence effect" (Wallach et al., 1949). The results of this study showed that, like humans, rats appeared to perceive the paired clicks as coming from the leading speaker. Moreover, they were able to discriminate left-leading from right-leading click pairs for time differences as small as 62 μs. However, before concluding that these results indicate that rats use binaural time differences, it should be noted that the precedence effect can be viewed as an interaural intensity difference (Elfner and Tomsic, 1968). Indeed, this view is supported by the observation that, like the transient
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rats may not have the highly accurate timing of input to the medial superior olive that seems crucial for shaping the interaural time delay functions in the MSO so apparent in species known to use time cues (Grothe, 2003).

4.3. Implications for the role of auditory cortex in sound localization

For a number of years, we have tried to understand why auditory cortex lesions cause a profound sound-localization deficit in some mammals, but not in others. Specifically, it is well established that bilateral auditory cortex lesions abolish the ability to localize sound in cats, dogs, ferrets, macaques, and squirrel monkeys (opossums, hedgehogs, and bushbabies have also been studied, but the results are inconclusive; for a review, see Heffner and Heffner, 1990). However, auditory cortex lesions have little or no effect on sound localization in either the laboratory rat or the wild wood rat (Heffner, 1981; Kelly, 1980; Kelly and Kavanagh, 1986). One possibility is that the role of auditory cortex varies with phylogeny, with carnivores and primates requiring auditory cortex for sound localization, but not rodents. Another possibility, suggested by Kelly and Kavanagh (1986), is that the species difference in the effect of cortical lesions depends on whether or not an animal can localize sound within a hemifield. Unlike primates and carnivores, rats have great difficulty localizing brief sounds within a hemifield. Because one of the main effects of auditory cortex lesions in primates and carnivores is to abolish their ability to localize sound within a hemifield, the negligible effect of cortical lesions in rats may be because they don't possess the ability to localize sound within a hemifield in the first place. As compelling as this explanation appears, it is currently confounded with another species difference in the effect of auditory cortex lesions: in macaques and ferrets, but not in rats, auditory cortex lesions abolish the perception of locus such that the animals have to relearn to associate sounds coming from the left or right with the response of going to the left or right (Heffner and Heffner, 1990; Kavanagh and Kelly, 1987; Kelly, 1980). With the discovery that laboratory rats perhaps

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