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Sound Localization and Use of Binaural Cues by the Gerbil (*Meriones unguiculatus*)

Rickye S. Heffner and Henry E. Heffner
Laboratory of Comparative Hearing, Bureau of Child Research
University of Kansas

Noise-localization thresholds and the ability to localize pure tones at 60° separation were determined for gerbils. The gerbils were trained using a two-choice procedure with observing response in which the gerbils made a left or right response to sounds emanating from their left or right side in order to obtain food. The average 75% correct localization threshold of 7 gerbils for a 100-ms noise burst was 27° with chance performance ($p > .01$) reached at 12°. The ability of 4 gerbils to localize both low- and high-frequency pure tones indicates that gerbils are able to use both phase- and intensity-difference locus cues. The frequency at which tone localization was poorest was 2.8 kHz, well below the theoretical frequency of ambiguity of the phase cue but within the frequency range at which phase locking declines in the mammalian auditory system. The sound localization ability of gerbils is typical of small rodents, and there is no obvious sign that it is affected by the degenerative disorder of the central auditory system which has been recently discovered in gerbils.

The Mongolian gerbil (*Meriones unguiculatus*) has been recognized over the last decade as a useful subject for the study of auditory physiology and neuroanatomy (e.g., Dolan, Mills, & Schmiedt, 1985; Nordeen, Killackey, & Kitzes, 1983; Ryan, Woolf, & Sharp, 1982; Schmiedt, 1982). However, behavioral studies of their auditory capacities have remained limited to the audiogram (Ryan, 1976) and to the development of directional responding (Kelly & Potash, 1986). Because much of the central auditory system of mammals is devoted to an analysis of interaural time and intensity relations important for sound localization, a knowledge of the localization acuity of the gerbil and its use of interaural time and intensity differences would be relevant to electrophysiological and anatomical descriptions of the central auditory system. In addition, an awareness of any differences in auditory function between the gerbil and other common laboratory species, such as the cat and laboratory rat, would aid in interpreting physiological and anatomical differences. Finally, because of the gerbil's specialization for low-frequency hearing, its auditory capacities are of interest for the comparative study of mammalian hearing in general. Accordingly, the present study provides data on the azimuthal sound localization acuity of the gerbil and on its ability to localize pure tones at 60° separation throughout most of its hearing range.

Method

Subjects

Seven gerbils, 4 males and 3 females, were used as subjects in this study. Food was used as a reward and was available only in the test situation. The gerbils were weighed daily to monitor their deprivational status. Their ear canals were examined and found free of signs of disease.

Behavioral Apparatus

The behavioral apparatus was the same as that used to test kangaroo rats (H. Heffner & Masterton, 1980, their Figure 5). The test cage was constructed of ½-in. (1.27-cm) hardware cloth and consisted of one main compartment (20 × 15 × 10 cm) with an "observing" compartment (4 × 6 × 7 cm) mounted on the front and two response compartments (7 × 6 × 7 cm) on the left and right sides. A photocell mounted above and a light mounted below the entrance to each compartment served to detect the entry of an animal into a compartment. Stainless steel cups (30 ml) mounted in the two side compartments served to receive cleaned, hulled millet seeds which were dispensed from modified rat-pellet dispensers. Cue lights mounted on the center observing compartment and on the left and right response compartments provided visual stimuli in the early stages of training. The test apparatus was mounted on a foam covered table 30 cm high and located in a double walled acoustic chamber (IAC, 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were covered with egg crate foam.

Sound Production and Measurement

Sound-localization thresholds for 7 gerbils were determined for a single brief burst of white noise (100-ms duration, 0-ms rise–decay). Noise bursts were produced by a noise generator (Grason Stadler 1285), shaped by a rise–fall gate (Grason Stadler 1287), and amplified (Crown D-75) before being led to a pair of 3-in. (7.6-cm) paper cone speakers mounted in 500-cc enclosures. The speakers were mounted on a semicircular perimeter bar (62 cm radius) centered on the animal's head when it was breaking the beam of the photocell in the observing compartment. The spectrum of the noise (Figure 1) was obtained using a ¼-in. (0.64 cm) Brüel and Kjaer (B&K) microphone (B&K 4135) with the protective grid removed to obtain linearity, preamplifier (B&K 2618), measuring amplifier (B&K 2608) and band-pass filter (Krohn-Hite 3202). Measurements were made by

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Correspondence concerning this article should be addressed to Rickye S. Heffner, who is now at, Department of Psychology, University of Toledo, Toledo, Ohio 43606.

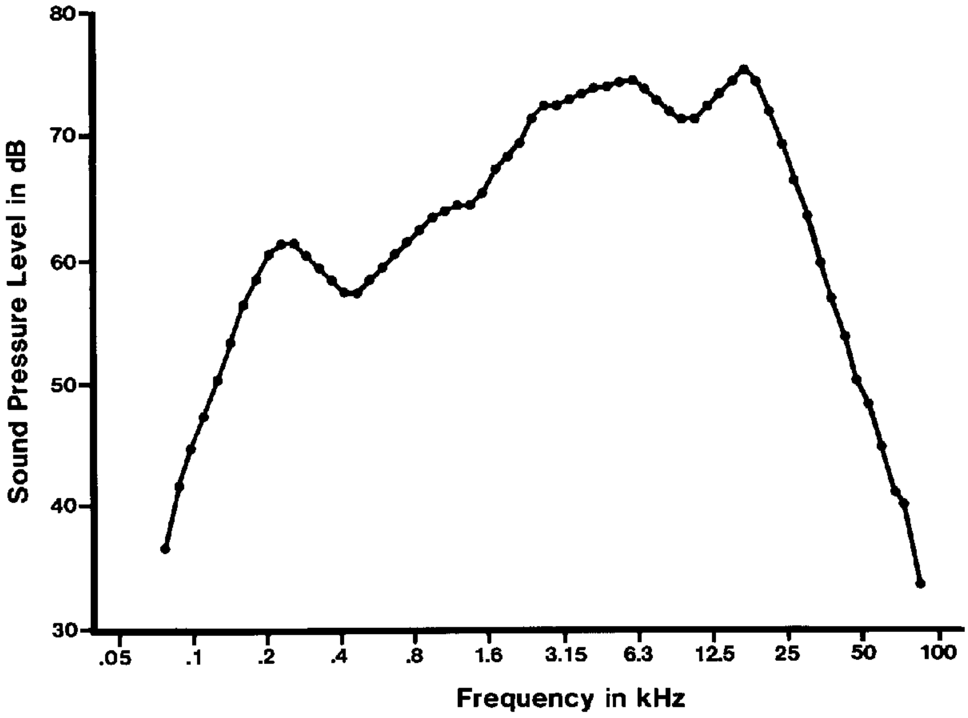

Figure 1. Spectrum of the auditory stimulus used in the noise-localization test.

setting the high- and low-pass sections to the same frequency (e.g., 8 kHz high pass and 8 kHz low pass) and then adding 6 dB (SPL) to the reading to correct for insertion loss.

Four of the gerbils were tested for their ability to localize a single tone pip of 200-ms duration (25-ms rise–fall for all frequencies except 250 Hz for which 50-ms rise–fall was used) at octave intervals between 250 Hz and 32 kHz with the half-octave points of 2.8 and 5.6 kHz also being tested. The tones were produced by an oscillator (Hewlett Packard 209A), shaped by a rise–decay gate (Grason Stadler 1287), filtered (Krohn Hite 3202), amplified (Crown D-75), and finally led to a pair of loudspeakers, which were either 3-in. (7.6-cm) paper cone speakers for frequencies of 250 Hz to 16 kHz or piezoelectric speakers with 3-in. (7.6-cm) horns for 32 kHz. The speakers were placed on the perimeter bar at a fixed angle of 60°, and all tones were presented at 50 dB above the thresholds determined for the gerbil by Ryan (1976). The intensity of the pure tones was measured with a sound level meter (Brüel & Kjaer 2203 or 2608 microphone amplifier, 4131 or 4135 microphone, and 1613 octave filter), and the electrical signal was continuously monitored using a Tektronix 502 oscilloscope.

Psychophysical Procedure

A food-deprived gerbil was placed in the test cage, habituated to the sound of the seed dispensers, and allowed to eat seeds from the food cups. The animal was then shaped to make an observing response and a two-choice discrimination. The observing response consisted of entering the center observing compartment (and breaking the beam of the photocell) which initiated a trial. A trial consisted of the presentation of a single pulse of noise from either the left or right speaker; the animal then responded correctly by entering the response compartment on the same side as the active speaker (breaking the beam of the photocell) and immediately received two millet seeds. If the animal responded incorrectly by entering the response compartment on the side opposite the active speaker, it received no seeds and was given a short "time out" (typically 5 s) during which a trial could not be initiated and the room lights were turned off. (For details of the training procedure see H. Heffner & Masterton, 1980.) The side of the active speaker was determined by a 30-element quasi-random schedule (Gellermann, 1933). To reduce the formation of side preferences, a correction procedure was used in which the correct side was not changed following an error. These correction trials were not used in the calculation of the animal's performance.

Noise-localization thresholds were determined by testing the animal at successively smaller angles until performance dropped to chance. Between two and four different angles were tested in a daily session in approximately 50-trial blocks, with usually 150–250 trials being obtained in each session. A minimum of 200 trials were obtained for each angle. Asymptotic performance at each angle was determined by averaging each animal's two best session scores, with 100–600 trials being included in the final score.

In the tone-localization test, the gerbils were tested at a fixed angle of 60° separation at each frequency for a minimum of 500 trials. Again, 150–250 trials were obtained in a daily session and only one frequency was examined daily. In addition to the total percent correct for each frequency tested during a session, the highest percent correct obtained on a block of 50 consecutive trials was also recorded. This latter score is comparable to those used previously with other species (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1987b; Masterton, Thompson, Bechtold, & RoBards, 1975).

Results

Noise Localization

The average performance of the 7 gerbils localizing a single 100-ms burst of noise is shown in Figure 2. Average performances of 90% correct or better were achieved by each animal for at least one large angle of separation, which indicated that the task was well within their capacity. Performances fell gradually as angles of 60° and smaller were presented. The 75% correct threshold criterion was reached at angles ranging from 19° to 30° for an average of 27°. The animals fell to chance ($p = .01$, binomial distribution) at angles ranging from 8.5° to 14° for an average of 12°.

Tone Localization

The results of the pure-tone localization test are shown in Figure 3. All tones were emitted from speakers separated by 60°, an angle chosen to facilitate direct comparison with other species which have previously been tested using 60° separation. Figure 3a depicts the average performance the gerbils were able to achieve over an entire session of 200–300 consecutive trials and illustrates three points. First, each animal was able to localize low frequencies between 250 Hz and 1 kHz. This ability to localize low-frequency pure tones indicates that gerbils are capable of using binaural phase-difference cues to determine the direction of a sound source (Brown, Beecher, Moody, & Stebbins, 1978; R. Heffner & Heffner, 1987b; Masterton et al., 1975). Second, the animals also performed well at the higher frequencies, particularly at 32 kHz, the highest frequency used, which suggests that they can also use binaural intensity differences to localize. Third, the gerbils show a decrease in performance in their midrange, most marked at 2.8 kHz, which suggests that neither the phase nor the intensity cue is very effective at this frequency. Because the intensities of the tones were equated by setting them at 50 dB (SPL) above threshold, this dip is not due to variations in the effective strength of the acoustic stimulus. However, the dip in performance is not as striking as in some species (cf. R. Heffner & Heffner, 1987b), possibly due to the fact that performance at 60° separation rarely exceeded 80% correct for any frequency. Indeed the gerbils performed at only 87% correct even when localizing broad-band noise at this angle.

Because of the small size of the dip, it seemed appropriate to examine other measures of performance in order to gain confidence in its validity. Accordingly, two additional measures of performance were determined. The first measure is the highest percent correct achieved for a block of 50 consecutive trials and is comparable to the measure used in comparative studies of tone localization in other species (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1987b; Masterton et al., 1975). Again the gerbils show a small but distinct dip in performance at 2.8 kHz. The second measure is a nonparametric index of discriminability, A′, taken from signal detection theory that is relatively unaffected by an animal's response criterion or side bias (Gescheider, 1976; Pollack & Norman, 1964). A′ is calculated according to the

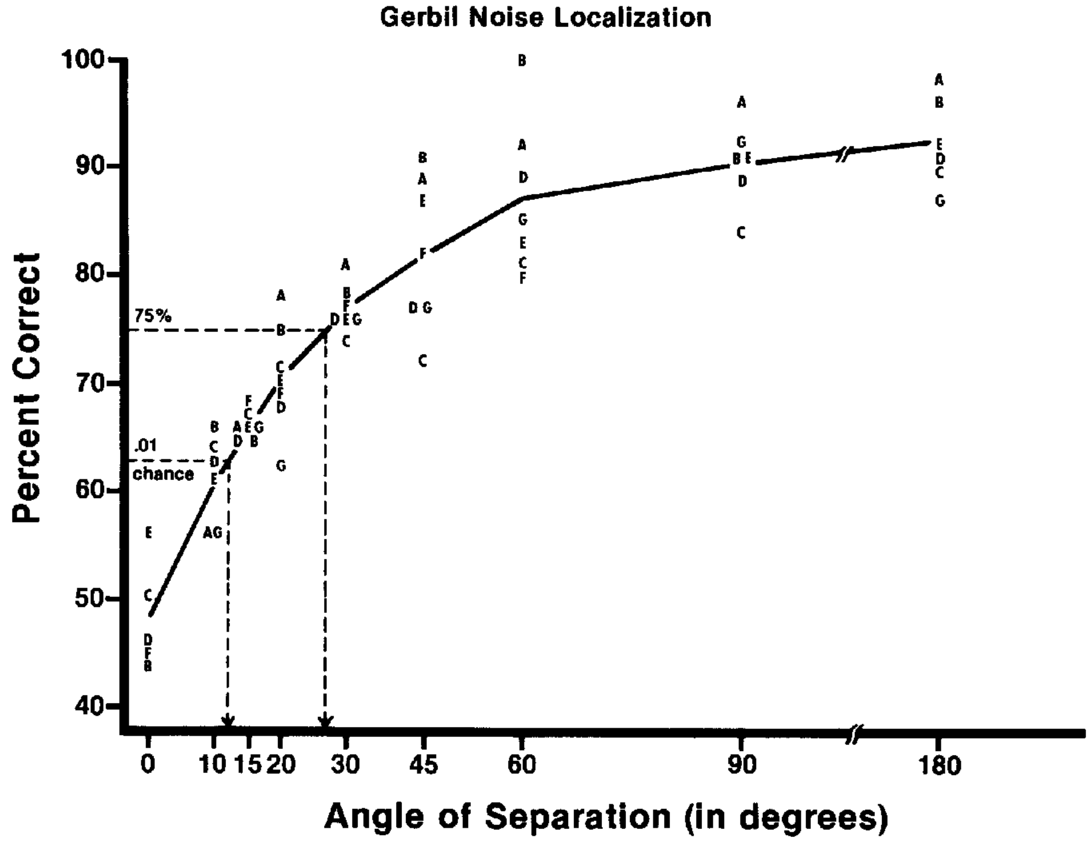

Figure 2. Sound-localization performance of 7 gerbils localizing a 100-ms burst of broad-band noise. (Letters indicate performance of individual animals.)

formula:

$$A' = \tfrac{1}{2} + \left[\frac{(\text{Hits} - FA) \times (1 + \text{Hits} - FA)}{(4 \times \text{Hits}) \times (1 - FA)}\right].$$

As shown in Figures 3b and 3c, both additional measures of performance indicate that the location of the dip in performance is at 2.8 kHz. Thus it seems safe to conclude that the frequency at which both phase and intensity locus cues are least effective for the gerbil is 2.8 kHz.

Discussion

Noise Localization

In making comparisons across species, the localization acuity of the gerbil is very similar to that of the kangaroo rat, which has a 75% correct threshold of 23° for single clicks (H. Heffner & Masterton, 1980). Although localization thresholds for clicks are usually slightly greater than for broadband noise stimuli, owing perhaps to their brevity or narrower spectrum, the kangaroo rat remains the species most like the gerbil among the sample currently available. This similarity is not surprising because the gerbil and kangaroo rat are both adapted to dry sandy deserts and have undergone strong convergent evolution in many aspects of their morphology and physiology, including their inflated bullae and sensitivity to very low frequency sound (H. Heffner & Masterton, 1980; Ryan, 1976), as well as their poor acuity for localizing brief noise bursts.

When compared with other common mammals, it appears that the gerbil is less accurate at localizing brief noise bursts than larger species such as the cat (Casseday & Neff, 1973), dog (H. Heffner, 1976), macaque (Brown, Beecher, Moody, & Stebbins, 1980; H. Heffner & Masterton, 1975), opossum (Ravizza & Masterton, 1972), seal (Terhune, 1974), man (Mills, 1958; Terhune, 1985), and even the Norway rat (H. Heffner & Heffner, 1985a; Kelly, 1980). However, small size (and correspondingly small available interaural time and intensity differences) cannot entirely account for the poor acuity of the gerbil because the least weasel, a species with a slightly smaller interaural distance, has demonstrated greater acuity (R. Heffner & Heffner, 1987b). On the other hand, the gerbil is a prey species and its poor localization acuity may be characteristic of prey (cf. H. Heffner & Heffner, 1984; R. Heffner & Heffner, 1988).

Relation of Acuity to the Degenerative Disease in the Auditory System of the Gerbil

There have recently appeared reports of a degenerative condition in the central auditory system of the gerbil that primarily affects the cochlear nuclei but with age spreads to affect auditory nuclei up to and including the inferior colliculi. The condition consists of a proliferation of microcysts and a loss of neurons. It occurs in wild populations as well as domestic and in at least two species of *Meriones*. The severity of the condition worsens with age and exposure to normal environmental sounds (McGinn & Faddis, 1987; Ostapoff, Morest, Feng, & Kuwada, 1987). The question arises as to whether such abnormality of the central auditory system may contribute to the poor noise-localization thresholds observed

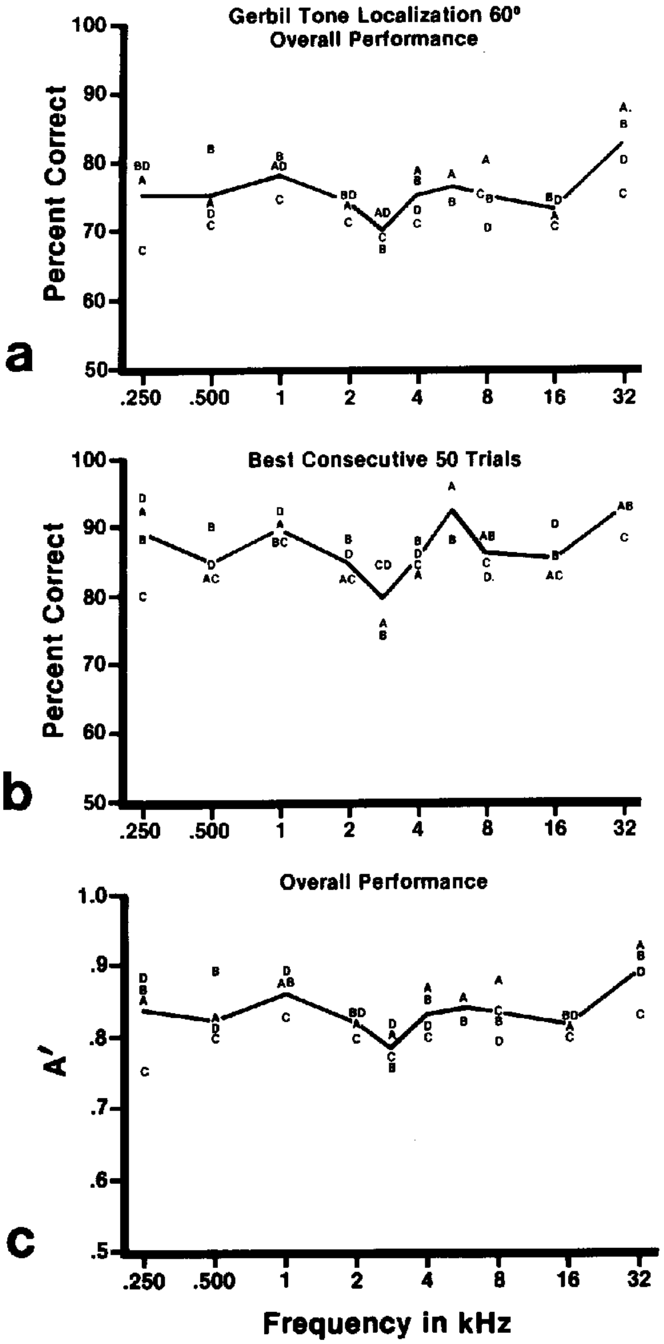

Figure 3. Performance of 4 gerbils localizing 200-ms pure-tone pips separated by 60°. (A: Percent correct during an entire session of 200–300 trials. B: Highest percent correct achieved in a block of 50 trials. C: Nonparametric measure of discriminability [A′] based on scores obtained over entire sessions. Note that all three measures show a decrement in performance at 2.8 kHz. Letters indicate performance of individual animals.)

in the gerbil. This is especially relevant because the cochlear nuclei are the major source of input to the superior olivary complex in which the binaural cues for locus are first analyzed.

Because all gerbils examined so far have been found to have this condition, it is not possible to determine directly its effect on their hearing. However, there are two lines of evidence that suggest that it has little or no effect on sound localization ability. First, as previously noted, the localization acuity of gerbils is not notably different from that of other small rodents. In addition, the variation between individuals, which should be increased by a progressive disorder, does not appear to be greater than that observed in other species (e.g., Brown et al., 1980; H. Heffner & Heffner, 1984; Strominger, 1969). Second, the ability to localize sound is often affected by damage to the auditory system, and the ability to localize tones has been shown to be impaired in albino cats that possess a degenerate medial superior olivary nucleus (R. Heffner & Heffner, 1987a). However, the gerbils had no similar difficulty in localizing tones.

It appears, then, that there are no unusual features in the sound localization ability of gerbils that would suggest that they are subject to a degenerative disorder of the auditory system. Furthermore, the audiogram of the gerbil does not indicate unusual hearing either in terms of absolute sensitivity or frequency range (Ryan, 1976; for a comparative review, see H. Heffner & Heffner, 1985b). Therefore, it appears that the degenerative disorder observed in the cochlear nucleus of the gerbil has no obvious effect on hearing and that any further investigation on this point would require careful testing designed to reveal more subtle effects.

Tone Localization

The ability to localize low-frequency and high-frequency pure tones has been used to demonstrate the duplex theory of sound localization (Stevens & Newman, 1936). Specifically, the ability to localize low frequencies has been attributed to the use of interaural phase differences, and the ability to localize high frequencies has been attributed to the use of interaural intensity differences. The four gerbils tested were able to localize both low- and high-frequency pure tones, demonstrating that they are capable of using both binaural phase and intensity cues to localize sound.

The occurrence of a region of reduced acuity in the midrange has been interpreted as indicating that neither cue is maximally effective in that region (Stevens & Newman, 1936). In some large species that are accurate localizers such as cats, monkeys, and humans, the decrement in tone-localization acuity in the midrange is relatively small (cf. Brown et al., 1978; Casseday & Neff, 1973; Mills, 1972). However, for some other mammals, especially small species and less accurate localizers such as the kangaroo rat, laboratory rat, and least weasel, the decrement can be large (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1987b; Masterton et al., 1975). The decrement observed in the gerbils is intermediate. There is a distinct reduction in performance at 2.8 kHz, but none of the four individuals tested fell to chance at that frequency, thus suggesting some overlap in the availability of the phase- and intensity-difference cues.

The use of the phase-difference cue is based on the ability of the nervous system to determine which ear is receiving the leading signal (i.e., the ear nearest the sound source) and which ear is receiving the trailing signal (i.e., the far ear). The calculated upper limit of the usefulness of the phase cue is dependent on two factors: the distance between the two ears (i.e., interaural distance) and the angle of the loudspeakers from the midline. The formula for calculating the upper limit is

$$F = [6(a/C)\sin\theta]^{-1},$$

where a is the radius of the head, C is the velocity of sound, and θ is the angle of the loudspeaker from the midline (e.g., Brown et al., 1978). Thus the smaller the interaural distance and the smaller the angle, the higher will be the upper limit of usefulness of the phase-difference cue. For the gerbil with an average interaural distance (measured around the head) of 30 mm localizing at an angle of ±30° (the angle used for these tests), the frequency beyond which phase would become ambiguous is 12 kHz—well beyond the 2.8 kHz dip in the gerbil's performance.

There are two possible explanations for the difference between the availability of the phase cue and the actual use of that cue by the gerbil. First, it is possible that gerbils can use phase above 2.8 kHz; although their performance is poorest at 2.8 kHz, it does not fall to chance at this point. By 4 kHz, ½ octave higher, their performance has improved, probably as a result of the availability of the binaural intensity-difference cue, thus making it impossible to determine with a free-field tone-localization test whether they can use phase at 4 kHz. However, free-field tone-localization tests with other animals in which the upper limit of phase is not obscured by the binaural intensity cue (e.g., R. Heffner & Heffner, 1986; R. Heffner & Heffner, 1987b) indicate that there is a steep decline in phase discrimination as frequency increases. Based on these results, it seems likely that the upper limit for the use of phase by the gerbil may be slightly higher than 2.8 kHz but probably below 4 kHz.

The second possibility is that the upper frequency limit of the phase cue is determined by the ability of the auditory system to encode phase information. Although there is as yet no published information on phase coding in the nervous system of the gerbil, that information is available for a few other species.

Synchronization in the auditory nerve of the squirrel monkey begins to decline at frequencies above 1 kHz and is no longer detectable above 5 kHz (Rose, Brugge, Anderson, & Hind, 1967). In the cat, synchronization falls precipitously above 2 kHz and becomes difficult to detect above 4 kHz (Johnson, 1980). Phase locking has been examined in the auditory nerve of two rodents, both with good low-frequency sensitivity; in both the guinea pig and the chinchilla, phase locking begins to decline at 600 Hz and is no longer detectable by 3.5 kHz and 4 kHz, respectively (Palmer & Russell, 1986; Woolf, Ryan, & Bone, 1981). Further, there is evidence that phase locking declines at even lower frequencies within the central nervous system (Rhode & Smith, 1986; Woolf et al., 1981). However, such a limited sample is insufficient to determine the range of abilities in mammals as a whole, and it is well established that the vertebrate auditory system is capable of phase locking up to 10 kHz because it does so in the barn owl (Sullivan & Konishi, 1984). Therefore, it should be noted that although the upper limit for the use of the phase cue may be determined by the phase-locking ability of the gerbil's auditory system, it is possible for a vertebrate to evolve an auditory system capable of phase locking at higher frequencies.

Turning to binaural intensity, it appears that this cue becomes useable by 4 kHz, as demonstrated by the improved performance in most of the gerbils at this frequency. This observation is supported by evidence based on cochlear microphonic recordings, which show that an interaural intensity difference exceeding 6 dB becomes available in gerbils at frequencies above 4 kHz (Plassmann, Kausch, Kuhn, Peetz, & Gottschalk, 1985).

The behavioral results for the gerbil are close to those for the kangaroo rat whose dip occurs ½ octave higher at 4 kHz and whose performance rises again by 5.6 kHz. However, these two species are in contrast to the least weasel (a species of similar interaural distance and auditory sensitivity), for which the usefulness of phase begins to fall at the same point as for the gerbil and kangaroo rat (approximately 2 kHz) but for which the intensity cue does not become useful until 16 kHz is reached, possibly owing to the much smaller pinnae of the least weasel (R. Heffner & Heffner, 1987b).

In summary, the gerbil is a species capable of using both binaural phase- and intensity-difference cues to localize sound but whose acuity is limited in comparison to other species serving as models of a mammalian auditory system in laboratory studies. The possible effect on sound localization of the recently discovered degenerative disorder in the central auditory system of the gerbil is not yet known.

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