



Sound localization in chinchillas. II. Front/back and vertical localization

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Abstract

The ability of chinchillas to make front/back and vertical locus discriminations was examined behaviorally using a conditioned avoidance procedure. Their minimum audible angle for localizing single broadband noise bursts was 36° for front/back localization and 23° for vertical localization. Sound localization tests using filtered noise demonstrated that the signal must contain high frequencies in order for chinchillas to make front/back and vertical locus judgements and that frequencies in their highest audible octave (i.e., above 16 kHz) contribute to localization. These results support the view that a major selective advantage of high-frequency hearing in mammalian evolution was its utility for monaural as well as binaural sound localization.

Keywords: Pinna; Elevation; Monaural cue; Noise band; Ultrasound; Evolution

1. Introduction

Interaural differences in acoustic spectra and in time are known to be powerful cues for localizing sound in the horizontal plane. However, there are two situations in which these binaural cues are of little use. One is in making front/back discriminations in which sound sources are located symmetrically around the interaural axis (i.e., on the cone of confusion). The other is in making elevation discriminations in the median sagittal plane. In both of these situations binaural difference cues are minimal and the ability to localize is strongly dependent on pinna cues (e.g., Butler, 1975).

The pinna, along with the 3-boned middle ear, is an auditory structure unique to mammals. As such it is tempting to link it to an auditory function also unique to mammals' sensitivity to high frequencies. Indeed, the pinnae may have served as a source of selective pressure for the evolution of the ability of mammals to hear above 10 kHz, or vice versa (Heffner and Heffner, 1992).

The directionality of the pinna is greatest for high frequencies, a fact which has been demonstrated in a variety of mammals (e.g., Calford and Pettigrew, 1984;

Carlile and Pettigrew, 1987; Musicant et al., 1990; Carlile, 1991; Rice et al., 1992). This pinna-generated high-frequency locus information may have provided an early adaptive advantage for high-frequency hearing to animals possessing a pinna. However, most tests of the ability of mammals to localize sound have determined thresholds for left/right discriminations, a task in which binaural cues predominate (for reviews, see Brown and May, 1990; Heffner and Heffner, 1992). As a result, little is known concerning the ability of different species to use pinna cues to localize sound. Thus, given the diversity of size, shape, and mobility of pinnae, as well as the variation in high-frequency hearing among mammals, it would be of interest to explore the variation in the ability to localize sound using only pinna cues.

This report is the second in a series exploring the ability of chinchillas to localize sound. It examines front/back localization acuity, elevation acuity in the median sagittal plane, and the contribution of high frequencies to these discriminations. Thus the focus is on localization tasks in which binaural cues are minimal and the animals must rely chiefly on locus cues produced by the pinnae. These results are then compared to localization performance in left/right discriminations for which binaural cues are available (Heffner et al., 1994). The effect of removing the pinnae on each of these localization tasks is explored in a subsequent report (Heffner et al., 1995).

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2. Methods

Sound-localization acuity was determined using a conditioned avoidance procedure (Heffner and Heffner, 1995). Thresholds were determined in azimuth around the interaural line (i.e., front/back discrimination) and in elevation in the mid-sagittal plane (i.e., vertical discrimination). The effect of progressively filtering out the high-frequency content of a broadband locus signal was determined for both localization tasks. For comparison to a task relying on binaural cues, tests with progressive high-frequency filtering were also carried out for left/right discriminations.

2.1. Subjects

The 11 male chinchillas used in this study were housed individually in glass tanks and given free access to rabbit chow which was supplemented with a daily raisin and occasional vegetables. They received nearly all of their water in the test sessions with supplements given as necessary to maintain adequate body weight. They were weighed daily to monitor their deprivational status; most chinchillas did not require deprivation below 90% of their free-feed weight for good performance. The animals typically consumed 5–15 ml of water during test sessions lasting 30–45 min.

2.2. Behavioral apparatus

The behavioral apparatus has been described previously (Heffner et al., 1994). Its significant features were: a large double-walled acoustic chamber (2.55 × 2.75 × 2.05 m) lined with sound-absorbing foam, a sound-transparent test cage, a small water spout for continuous delivery of water, a syringe pump to control the flow of water (Thompson et al., 1990), and the ability to present a mild electric shock between the spout and the cage floor. The cage contained a wire mesh barrier at shoulder height which required the chinchillas to place their heads in a fixed position in order to make contact with the water spout and receive a water reward (Fig. 1). This procedure was especially important during the front/back tests as it kept the animals from turning their heads toward the sound sources located far to the side and rear. Head position was monitored via closed-circuit television.

2.3. Acoustic apparatus and stimuli

The signal consisted of broadband noise which was equalized (Sentek EQ3) to achieve a relatively flat spectral acoustic signal. The signal was a single 100 or 200-ms noise pulse presented at 66 dB SPL (re 20 μ Pa) measured over the frequency range of 100 Hz to 60 kHz using a 1/4-in. (0.64-cm) microphone (Brüel and Kjaer 4135), sound level meter (Brüel and Kjaer 2608), and filter (Krohn-Hite 3202 set to pass 100 Hz to 60 kHz). The noise

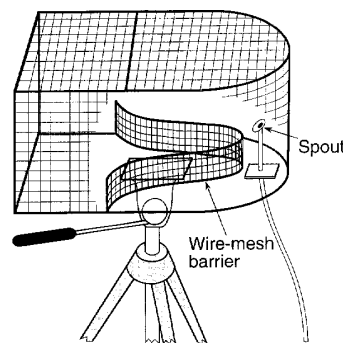


Fig. 1. Test cage illustrating wire-mesh barrier and water spout used to keep the chinchillas' heads oriented straight ahead regardless of the location of the loudspeakers. Water was dispensed from the spout using a syringe pump located outside the test chamber and a sensing switch was connected between the spout and cage floor to detect when an animal was in contact with the spout.

bursts had a fast rise/decay time ($\approx 0.1 \mu$ s) for threshold tests to maximize onset cues, and a slower 50-ms rise/decay time for tests using filtered noise in order to prevent the introduction of high-frequency transients into low-frequency signals. The broadband signals were presented approximately 50 dB above detection threshold. For the azimuthal tests, the speakers were placed on a perimeter bar, 1.03 m in radius, and centered either around the interaural line (on the right side) for the front/back tests or centered around midline for the left/right tests. Another perimeter bar was placed vertically in the median sagittal plane with one speaker placed at 0° elevation and the other at various elevations above the horizon, up to 90° (directly overhead).

The acoustic apparatus was identical to that described previously (Heffner et al., 1994) with two exceptions. First, all of the tests were conducted using loudspeakers which were a combination of a piezoelectric tweeter and a 3-in. (7.6 cm) woofer. Second, the spectrum was not varied in the tests of front/back and vertical localization since these discriminations rely strongly on the spectral difference between sound sources induced by the pinnae. However, the overall intensity of this signal was randomized over a 7-dB range (in 1-dB steps) to reduce the possibility of discriminating subtle differences between the loudspeakers. The pairs of speakers used for testing were closely matched for spectral quality using a Zonic 3525 FFT spectrum analyzer. That these precautions were adequate is attested by the observation that the animals' performances fell to chance at small angles, indicating that the loudspeakers themselves were not easily discriminated.

The effect of progressively removing the high-frequency content of the noise was determined at fixed angles of separation. Because thresholds (and task difficulty) varied among the discriminations in the 3 different planes, the same angle could not be used for all of the tests (for

example a very easy angle in the left/right test could be impossible to discriminate in the elevation test). Instead, the angles were matched for approximate difficulty; for each of the fixed-angle tests, an angle was chosen that was the smallest angle at which the average performance for all animals localizing a broadband signal was approximately 80% and for which performance rarely fell below 70% (note that this sustained performance usually averaged slightly lower than asymptotic performance on which thresholds were based). Thus any reduction in the efficacy of the signal would be likely to result in a decrement in performance. The angles meeting this criterion were: 30° ($\pm 15^\circ$) around the median sagittal plane for left/right tests, 90° ($\pm 45^\circ$) around the interaural line for front/back tests, and 45° above the horizon for elevation tests.

The electrical signal was filtered (Krohn-Hite 3202) using a low-pass filter with a 48 dB/octave roll-off. The low-pass filter settings used were 40, 20, 10, and 5 kHz,

with the 40-kHz setting passing frequencies throughout the high-frequency hearing range for chinchillas (which have a 60 dB SPL high-frequency hearing limit of 33 kHz; Heffner and Heffner, 1991) and the lowest setting (5 kHz) limiting the high-frequency spectrum of the stimulus to frequencies audible to non-mammalian vertebrates such as birds (Dooling, 1980). The resulting spectra are illustrated in Fig. 2a: filtering out high frequencies reduced the overall intensity of the signal so that the 40-kHz band was 66 dB, 20 kHz was 64 dB, and 10 kHz was 61 dB. To maintain similar audibility of the 5-kHz low-pass signal, the intensity was increased to 66 dB. Thus the intensity of the different noise bands were within 5 dB of each other and the intensity of the most restricted noise band was the same as that for the broadest band signal. Furthermore, all signals were approximately 50 dB above the animal's threshold. As the results will show, the differences in performance could not be attributed to simple decrements in intensity.

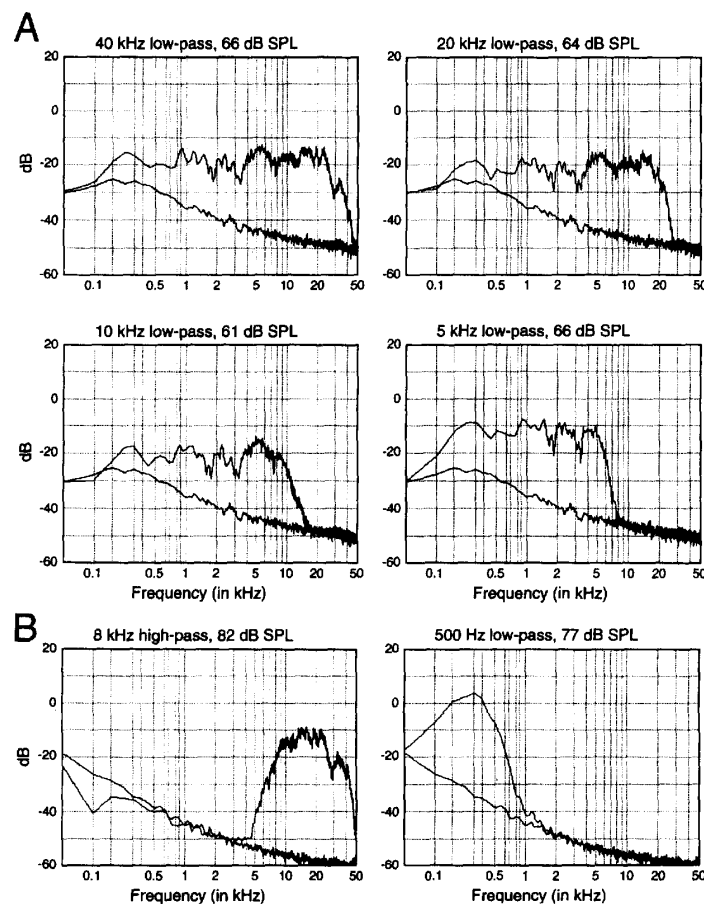


Fig. 2. A: spectra of the noise bands used to test the effects of progressively filtering out the high-frequency content of the locus signal. The background noise level is indicated by the lower spectrum line in each panel. Note that the signal level falls to background within approximately one half octave or less of the filter setting. B: 8-kHz high-pass and 500-Hz low-pass noise used in the front/back threshold tests.

Thresholds for front/back discriminations were also obtained using an 82-dB, 8-kHz high-pass noise and a 77-dB 500-Hz low-pass noise (Fig. 2b) for comparison with previously published left/right thresholds using these stimuli (Heffner et al., 1994).

2.4. Psychophysical procedure

The psychophysical test procedure has been described previously (Heffner et al., 1994; Heffner and Heffner, 1995). Briefly, the animals were tested using a conditioned avoidance procedure in which they were trained to drink steadily from the water spout in the presence of a noise burst emitted from either the right speaker (for left/right discriminations), the rear speaker (for front/back discriminations), or the lower speaker (for elevation discriminations); these constituted the 'safe' signals. They were then trained to break contact with the water spout whenever the noise burst was emitted from the left, front, or upper speaker, respectively ('warning' signals), in order to avoid a mild electric shock delivered through the water spout. A noise burst was presented every 3.3 s (1.8-s trial period plus 1.5-s intertrial interval) with each trial having a 22% probability of being a warning trial.

Calculation of performance scores

Behavioral performance was determined in the following way. Breaking contact with the spout for at least half of the final 150 ms of a warning trial served to indicate that the animal had detected the shift in locus and was considered a 'hit'; similarly breaking contact during the final 150 ms of a safe trial was considered a 'false alarm'. Performance scores for each stimulus condition were calculated based on blocks of 6–10 warning trials. An average performance score was then determined for each stimulus by correcting the observed hit rate for the proportion of false alarms observed under each stimulus condition using the formula:

Corrected Detection

$$= \text{Hit Rate} - (\text{False Alarm Rate} \times \text{Hit Rate})$$

Performance (i.e., corrected detection) could thus range from 100% (100% hits with no false alarms) to 0% (no hits). The level at which the hit rate no longer significantly exceeded the false alarm rate (i.e., the 0.01 level of chance performance) was also calculated; under these test conditions chance performance for the chinchillas ranged from corrected detection scores of approximately 25–40% depending on the individual false-alarm rate (for a detailed discussion of the performance calculation and trial presentation procedure, see Heffner and Heffner, 1988a, 1995, respectively).

Threshold

Thresholds for 2-point acuity were determined by reducing the angular separation between the loudspeakers

within a test session until the hit rate was no longer significantly higher than the false-alarm rate. Asymptotic performance was taken to be the best 3 scores for each angle of separation. Threshold was defined as the angle at which performance was interpolated to be 50%. Testing continued until the animals no longer showed improvement in threshold or suprathreshold performance.

Fixed-angle low-pass filtering tests

Performance scores for each noise band were calculated based on blocks of 8 warning trials and the associated safe trials. During testing, trials with each of the 4 noise bands were interspersed such that no more than 4 warning trials were given consecutively for a particular noise band. Each noise band was thus tested in every session, with each session beginning with a different noise band to avoid potential order effects, until 40 warning trials had been accumulated for each noise band over several sessions.

The care and use of the animals in this study were approved by the University of Toledo Animal Care and Use Committee, which abides by the Helsinki Agreement (NIH DC00179).

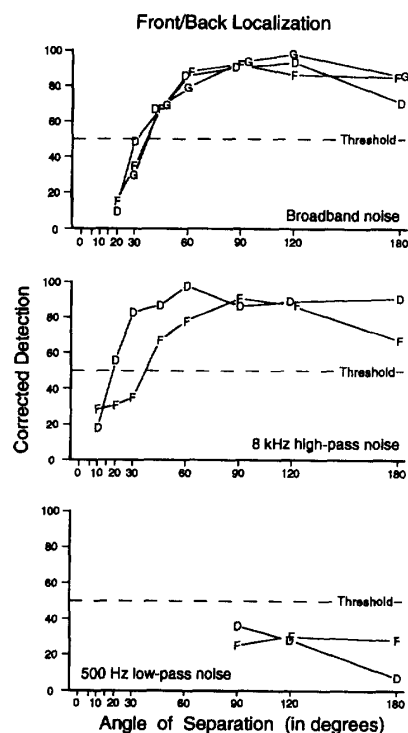


Fig. 3. Front/back thresholds for chinchillas (around the interaural line 90° to their right) for broadband, high-frequency and low-frequency noise. Letters D, F, and G indicate individual animals. Average thresholds were 36° and 28° for broadband and high-frequency noise, respectively. Note that the animals could not localize the 500-Hz low-pass noise.

3. Results

3.1. Front / back discriminations

Thresholds

The ability of chinchillas to discriminate 100-ms noise bursts emanating from loudspeakers located symmetrically in front of and behind their interaural line is illustrated in Fig. 3 for the 3 noise spectra. The 3 animals localizing the broadband noise showed good agreement: each performed well at large angles of separation (i.e., $\pm 60^\circ$), but performance declined rapidly at smaller angles to an average threshold of 36° .

Two of the 3 chinchillas were tested using the 8-kHz high-pass noise stimulus. One animal (D) showed significant improvement over its broadband performance with its threshold improving from 31° to 19° ; the second animal (F) on the other hand, showed no change in performance with its threshold remaining at 37° . The average threshold for this discrimination was thus 28° . Although this is noticeably smaller than the 36° threshold for broadband noise, the fact that it is due entirely to the performance of one animal makes us reluctant to draw any conclusions regarding the comparative ease of localizing high-frequency versus broadband signals.

In sharp contrast to the previous 2 tests, neither animal was able to localize the 500-Hz low-pass signal. As shown in Fig. 3, both animals tested on this task performed at chance even at the maximum separation of 180° . This dramatic and consistent result suggests that chinchillas require high frequencies to perform a front/back locus discrimination.

Effect of low-pass filtering

The role of high frequencies in front/back localization was systematically explored by determining the ability of chinchillas to localize 4 different low-pass noise signals

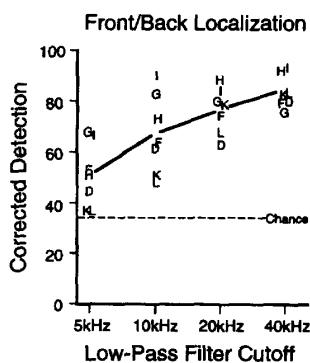


Fig. 4. Performance of 7 chinchillas in a front/back locus discrimination of sound sources separated by 90° as a function of the high-frequency content of the noise signal. Letters indicate individual animals. Note that performance declines with progressive restriction of the high-frequency content.

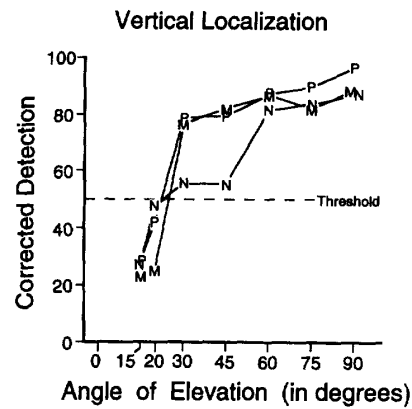


Fig. 5. Thresholds for 3 chinchillas making discriminations between sound sources located at the horizon versus above the horizon in the median sagittal plane. Note that chinchilla M was tested using a 100-ms stimulus while chinchillas N and P were tested using a 200-ms stimulus. Average threshold was 23° .

presented from two speakers located 90° apart (an angle chosen for its moderate difficulty as noted in the Section 2). As shown in Fig. 4, average performance of the 7 animals declined steadily as the upper limit of the noise was progressively reduced from 40 kHz, falling to a performance level of 50% at the 5-kHz low-pass setting. Note that the average performance declined when the low-pass filter setting was reduced from 40 to 20 kHz. Because front-back localization relies primarily on pinna cues, these results demonstrate that the chinchilla's pinna is effective for frequencies above approximately 5 kHz and that the inclusion of frequencies above 20 kHz enhances front-back localization performance, at least at moderately difficult angles of separation (i.e., the 90° angle used here).

3.2. Discrimination of elevation

Of the 3 localization tasks, discrimination in elevation (Fig. 5) appeared to be more difficult for some of the animals; although chinchilla M localized the 100-ms signal without undue difficulty, chinchillas N and P could not discriminate the 100-ms noise bursts and consequently had to be tested using a 200-ms noise burst. It may be noted that human performance also appears to be more variable when discriminating elevation, an effect attributed to differences in pinna morphology (e.g., Butler, 1970; Ivarsson et al., 1980).

Thresholds

Fig. 5 illustrates the ability of the 3 chinchillas to perform a vertical locus discrimination in which one loudspeaker was located at 0° elevation and others at various angles above the animal's horizon. As shown in Fig. 5, all 3 chinchillas were able to achieve good performance at large angles of separation (i.e., $60\text{--}90^\circ$ separation). Perfor-

mance began to decline at 45° for chinchilla N and below 30° for the other 2 animals. However, the thresholds for all 3 animals were quite similar, ranging from 22° to 25° for an average of 23°.

Effect of low-pass filtering

The role of high frequencies in discriminations of elevation was systematically explored by determining the ability of chinchillas to localize the 4 different low-pass signals presented from two speakers located 45° apart, again an angle chosen for its moderate difficulty. As shown in Fig. 6, the performance of the 2 animals declined steadily, reaching the 50% discrimination level at the 10-kHz low-pass setting and falling to chance at the 5-kHz setting.

To determine the effect of increasing the angle of separation on performance, chinchilla P was also tested at an elevation of 75°. As shown in Fig. 6, increasing the angle of separation resulted in only a small increase in overall performance at the 40-kHz setting, but a much larger increase at the lower filter settings. As at the 45° separation, performance declined steadily as the high-frequency content of the signal was reduced, although the degree of the decline was not as great. Thus the importance of high frequencies for vertical localization can be demonstrated at either angle. However, the size of the effect and the low-pass filter setting at which performance falls to chance is dependent on the angle of separation.

3.3. Left/right discriminations around the mid-sagittal plane

Effect of low-pass filtering

For comparison with the results of the two previous tasks, the role of high frequencies was also explored for

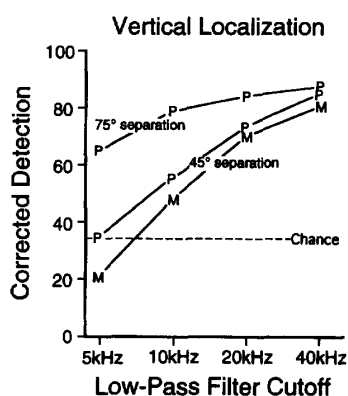


Fig. 6. Overall performance as a function of the high-frequency content of a noise signal for 2 chinchillas discriminating fixed angles of elevation in the median sagittal plane. Note that good performance can be sustained without high frequencies at large angles of separation, but smaller angles of separation require higher frequencies. (Chinchilla P was tested using 200-ms noise bursts and chinchilla M was tested using 100-ms noise bursts.)

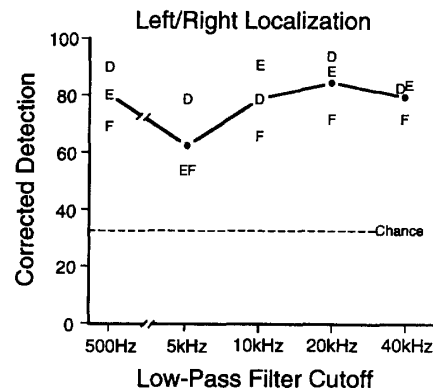


Fig. 7. Overall performance of 3 chinchillas making a discrimination between noise sources placed 15° to the left and right of the midline (30° separation) as a function of the high-frequency content of the noise signal. Note that in this task, in which binaural locus cues were available, performance was not systematically affected as the high-frequency content of the signal was reduced.

left/right localization. Testing was conducted at 30° separation, the smallest angle supporting sustained performance of approximately 80% and was thus of comparable difficulty to the angles used in the tests of front/back and elevation localization.

Fig. 7 shows that there was little difference in the ability of the chinchillas to localize the broadband (i.e., the 40-kHz low-pass signal) and the filtered stimuli. Although performance declined slightly with the 5-kHz low-pass noise, there was no systematic reduction in performance as seen in the two previous tests (cf., Fig. 7 with Figs. 4 and 6). Thus, it appears that chinchillas do not require the presence of high frequencies to perform a left/right sound-localization discrimination, a result which suggests that the binaural time cue is adequate to maintain their level of acuity in this task. This point is discussed in more detail below.

4. Discussion

The purpose of these experiments was to determine the ability of chinchillas to make front/back and vertical locus discriminations—two tasks in which binaural cues are unavailable and the animals must rely on pinna cues. Because pinna cues depend on high frequencies, the high-frequency content of the localization signal was an important variable.

4.1. Front/back localization

Previous research has indicated that for sound localization in the horizontal plane, acuity for front/back discriminations is poorer than for frontally placed sound sources (e.g., Brown et al., 1982; Oldfield and Parker, 1984;

Butler, 1986; Heffner and Heffner, 1988b). For example, humans tested in a 2-point localization discrimination show an increase in thresholds from 1.3° for left/right localization to 9.7° for front/back localization (Heffner and Heffner, 1988b). Similarly, cats show an increase from 4.8° to 9° (Heffner and Heffner, 1988b). The present results demonstrate that front/back thresholds for chinchillas are also poorer than their left/right thresholds. Specifically, whereas the left/right threshold for chinchillas is 17.5° for broadband noise (Heffner et al., 1994), the front/back threshold is 36°. Thus, the present results support the conclusion that localization acuity is greater for left/right than for front/back discriminations.

The observation that the average threshold for the 8-kHz high-pass noise was smaller than for the broadband noise makes it tempting to conclude that high-frequency sounds are easier to localize in a front/back localization test than are broadband sounds. Indeed, it might be argued that the presence of low frequencies degrades the ability to analyze the high-frequency portion of the signal on which pinna cues are based. However, the difference in thresholds is based on only one animal (chinchilla D) and is not statistically reliable (Mann-Whitney U , $P > 0.4$). Moreover, there is also the possibility that the natural variability in thresholds may be greater for front/back than for left/right thresholds. For example, in a study of cats, left/right thresholds were within 1.5° of each other whereas front/back thresholds varied over a range of 6° (Heffner and Heffner, 1988b); similar increased variability has been noted in humans (Flannery and Butler, 1981; Oldfield and Parker, 1986).

4.2. Vertical localization

Research with humans and macaques has indicated that subjects are also less accurate in performing vertical localization than left/right localization (e.g. Brown et al., 1982; Oldfield and Parker, 1984). This conclusion is supported by the present finding of 23° for the chinchillas' vertical threshold compared to 17.5° for their left/right threshold. One study of sound localization in cats, however, did obtain thresholds for vertical localization which were better than those for left/right localization. Using a very long stimulus duration (500-ms noise bursts presented at a rate of 1/s for 8 s) Martin and Webster (1987) found not only unusually good azimuthal acuity for cats of 3.4°, but also found that their vertical acuity was even better — just how much better could not be determined as the loudspeakers could not be placed close enough to get below threshold for most of the animals.

In evaluating this finding, however, it should be noted that animals in vertical (or front/back) localization tests must learn to discriminate small differences in spectra produced by changes in the location of the loudspeakers. This, however, may make them attentive to *any* differences in spectra, including quality differences between

loudspeakers (Brown, 1995), and they can eventually learn to discriminate the members of a pair of loudspeakers, especially if the stimulus is of long duration as it was in that study. As a result, it becomes very important to show that the animals cannot perform the task when locus is no longer a cue —that is, when the sound sources are so close together that they cannot be discriminated on the basis of locus (Heffner and Heffner, 1995). Because the cats studied by Martin and Webster discriminated all of the stimulus angles, a threshold was not actually obtained and the possibility exists that those cats were using differences in loudspeaker quality to perform the discrimination. This possibility is supported by the failure to observe such good vertical acuity for cats in two other laboratories (Heffner and Heffner, unpublished observations; Sutherland et al., 1993). Thus, until strong contrary evidence is forthcoming, it seems that sound localization in the vertical plane is not as acute as left/right localization.

The superior acuity for left/right localization, where binaural cues are available, compared to that for both front/back and vertical localization, where pinna cues predominate, does not necessarily mean that binaural cues are more accurate than pinna cues. This is because there is no information at this time on the ability of chinchillas to perform a left/right discrimination using only pinna cues. For humans, evidence suggests that the binaural cues are slightly better for performing azimuthal localization near the midline than are pinna cues (Butler, 1986). However, spectral pinna cues do contribute to the accuracy of left/right binaural localization (Musicant and Butler, 1984; Oldfield and Parker 1984; Butler and Musicant, 1993) and it is obvious that pinna cues are critical for making front/back and vertical discriminations of locus.

Finally, it may be noted that two of the chinchillas in this study refused to perform the vertical discrimination when a 100-ms noise burst was used and, as a result, had to be tested with a stimulus of 200-ms duration. Although their thresholds were not noticeably different from that of the third animal, which was tested with the 100-ms stimulus, their behavior suggests that in some cases at least the nervous system may require a longer-duration signal for optimal analysis of pinna cues than for binaural cues.

4.3. Role of high frequencies

In order to be effective, pinna cues require the presence of high frequencies in the signal to be localized. In humans, frequencies as high as 15 kHz have been shown to be necessary either for optimal discrimination in the lateral field or in elevation (Hebrank and Wright, 1974; Belendiuk and Butler, 1975). As the 60-dB upper limit of human hearing is at most 20 kHz, this means that the highest octave of the human hearing range is used to derive pinna locus cues.

Like humans, chinchillas require high frequencies to localize sound using pinna cues. The results of both the

front/back and vertical localization tests demonstrate that performance declines as high frequencies are removed from the signal and eventually falls to chance (Figs. 3, 4 and 6). The range of frequencies necessary for pinna cues to be effective depends, of course, on the angle of separation (cf., Fig. 6). In order to perform consistently at 50% or better at the angles of separation used here, vertical localization requires frequencies of 10 kHz or higher whereas front/back localization requires frequencies of 5 kHz or higher (cf., Figs. 4 and 6). It should be noted that performance in both tasks improved as higher frequencies were added to the signal, even for the addition of frequencies above 20 kHz. As the 60-dB upper hearing limit of the chinchilla is 33 kHz (Heffner and Heffner, 1991), this suggests that, like humans, chinchillas use the upper octave of their hearing range for sound localization using pinna cues.

4.4. Implications for the evolution of high-frequency hearing

Among vertebrates, mammals are unique in possessing good high-frequency hearing, i.e., the ability to hear above 10 kHz. Some time ago it was suggested that the selective advantage of mammalian high-frequency hearing is to enable even small mammals to make use of binaural spectral-difference cues to localize sound (Masterton et al., 1969). That is, interaural spectral-difference cues are available to an animal as long as it can hear frequencies with a wavelength short enough to be shadowed by its small head and pinnae. This view is supported by research that has shown that acuity for left/right sound localization in rats and mice is decreased when high frequencies are filtered out (Heffner, 1989; Mooney, 1992; Heffner and Donnal, 1993).

Over time it has become apparent that not all mammals need high frequencies for optimum acuity for left/right localization (Heffner and Heffner, 1992). For example, frontal locus acuity in humans is not adversely affected by the removal of high frequencies from an acoustic signal because the time cues available in the low-frequency portion of the signal provide sufficient locus information (Musicant and Butler, 1984). Similarly, left/right localization acuity in horses is not significantly affected by removal of high frequencies and, indeed, there is evidence that horses have lost the ability to use the binaural spectral difference cue (Heffner and Heffner, 1986, 1988c).

As with humans, the ability of chinchillas to perform a left/right localization discrimination is not affected by the filtering out of high frequencies (Heffner et al., 1994). It should be noted that this finding does not mean that chinchillas do not use the binaural spectral-difference cue. On the contrary, their ability to localize high-frequency tones demonstrates that they readily use binaural intensity-difference cues and, presumably, the spectral-difference cue (Heffner et al., 1994). However, it does

demonstrate that their frontal locus acuity can be sustained by the binaural time cue alone. Thus, for chinchillas, the primary selective advantage of high-frequency hearing may be to enable them to use binaural spectral cues and/or pinna cues to localize sound sources located away from the midline and to make vertical locus judgements. Accordingly, we might conclude that the appearance of pinnae accompanied by an extension of the high-frequency hearing range combined to improve the sound localization ability of mammals within the lateral and vertical auditory fields. Thus it is not surprising that the only bird known to have good acuity throughout auditory space is the barn owl, an animal which has evolved a pinna-like structure and has pushed its upper limit of hearing to just over 12 kHz, higher than that of most birds (Knudsen, 1980; Konishi, 1993).

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