Sound localization in chinchillas
III: Effect of pinna removal

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Abstract

The ability of chinchillas to make left/right, front/back, and vertical locus discriminations was determined before and after surgical removal of the pinnae. The animals were tested behaviorally using a conditioned avoidance procedure. In the left/right localization tests, removal of both pinnae had no effect on localization acuity for broadband noise but did result in a small decrement in performance when localizing low-pass filtered noise. In the front/back localization tests, removal of a single pinna resulted in a small but consistent decrement in performance when the sound sources were located in the hemifield on the same side as the intact pinna, and a greater decrement when the sound sources were located in the hemifield on the side of the missing pinna; removal of both pinnae resulted in the largest decrement in performance. Finally, vertical localization acuity and performance when localizing low-pass filtered noise were greatly impaired following removal of both pinnae. These results demonstrate the importance of the pinnae in performing front/back and vertical localization tasks in which binaural cues are not available.

Keywords: Binaural; Monaural; Spectrum; Lateral field; Elevation

1. Introduction

The mammalian pinna modifies the spectra of high-frequency sounds reaching the middle ear as a function of the locus of the sound source, thereby contributing cues to source location throughout an animal's acoustic space (Butler, 1975). In humans, normal pinnae are essential for making vertical locus discriminations and discriminations in the far lateral sound fields (e.g., front/back discriminations), situations in which binaural locus cues are minimal or absent (e.g., Roffler and Butler, 1968; Blauert, 1969/1970; Musicant and Butler, 1984). Distortions of the pinnae in humans that compromise or eliminate pinna cues greatly reduce azimuthal localization accuracy in the lateral sound field and elevation discriminations at every azimuth (e.g., Musicant and Butler, 1984; Oldfield and Parker, 1984; Humanski and Butler, 1988).

Although much is known concerning the role of the pinnae in humans, there have been no comparable investigations in other species. Moreover, humans may not be an ideal species from which to generalize to other mammals

for two reasons. First, human pinnae do not extend very far from the head and are incapable of movement whereas the pinnae of most mammals are larger relative to their head size and are also usually mobile. Such pinna movements serve to aim their directional filtering capacities and have been shown to play a role in echolocation in bats (Lawrence and Simmons, 1982; Mogdans et al., 1988). Second, pinna cues are dependent on high frequencies (Fuzessery, 1986; Carlile, 1990; Rice et al., 1992) and the upper limit of hearing of most mammals is significantly higher than that of humans (e.g., Heffner and Heffner, 1992). Although 'high-frequency' is a relative term (in this case the wavelength of a sound relative to some dimension of the pinna), the question nonetheless arises as to whether other mammals require the upper portion of their hearing range for optimal use of pinna locus cues.

Accordingly, a better understanding of the auditory functions of the pinna and the degree to which these functions rely on high frequencies in different species would broaden our understanding of sound localization in mammals as well as our appreciation of the selective pressures acting on the evolution of high-frequency hearing in mammals. In an effort to develop a basis for a comparative analysis of the role of the pinnae in hearing, we have examined the sound-localization ability of chin-

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chillas, a species with relatively large and mobile pinnae and whose high-frequency hearing limit is approximately 1 octave higher than that of humans (Heffner and Heffner, 1991).

This report is the third in a series exploring the ability of chinchillas to localize sound (Heffner et al., 1994, 1995). It examines the role of the pinnae in sound localization by determining the effect of pinna removal on the ability of chinchillas to make left/right, front/back, and elevation locus discriminations. The localization stimulus in these tests consisted of a broadband noise in which the high-frequency content of the signal was progressively reduced by low-pass filtering.

2. Methods

A conditioned avoidance procedure was used to assess sound-localization ability before and after removal of one or both pinnae. Two types of abilities were assessed: (1) sound-localization acuity for left/right and vertical discriminations using broad-band noise, and (2) the ability to localize sound in three planes (left/right, front/back, and vertical) under conditions of progressive low-pass filtering of the noise stimulus.

2.1. Subjects

Eleven chinchillas were used in these tests (with some individuals used in more than one test): five in the left/right test, six in the front/back test, and two in the elevation test. They received nearly all of their water in the test sessions with supplements given as necessary to maintain adequate body weight. The animals were weighed daily to monitor their deprivational status and typically consumed 5-15 ml of water during test sessions lasting 30-45 min.

2.2. Behavioral apparatus

The behavioral apparatus was identical to that described previously (Heffner et al., 1994). Its significant features were: a large double-walled acoustic chamber 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 a shock generator connected between the spout and the cage floor. The cage contained a wire mesh barrier at shoulder height which further constrained an animal's head position while it was making contact with the water spout (Heffner et al., 1995). 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 and the animals' contact with the water spout was measured electronically.

2.3. Acoustic apparatus and stimuli

The acoustic apparatus and sound-measuring equipment were identical to those used for similar tests with normal chinchillas (Heffner et al., 1995). The signal consisted of broadband noise which was equalized (Sentek EQ3) to achieve a relatively flat spectral acoustic signal containing audible energy at the high-frequency end of the chinchilla's hearing range as well as audible energy at frequencies as low as 200 Hz (for spectra see Heffner et al., 1995). The signal was a single 100- or 200-ms noise pulse presented at 66 dB SPL (re 20 μPa) measured over the frequency range of 100 Hz to 60 kHz using a 1/4" (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 bursts had a fast rise/decay time (≈ 0.1 μs) 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. For vertical localization tests, a perimeter bar was placed vertically in the median sagittal plane with one speaker placed at 0° elevation (on the horizon) and the other at various elevations above the horizon, up to a maximum possible of 90° (directly overhead).

All of the tests were conducted using loudspeakers that were a combination of a piezoelectric tweeter and a 3" (7.6 cm) woofer. The pairs of speakers used for testing were closely matched for spectral quality using a Zonic 3525 FFT spectrum analyzer. The spectrum was not varied in the tests of front/back and vertical localization since these discriminations rely 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 the animals discriminating between the loudspeakers on the basis of non-locus cues. That these precautions were adequate is attested by the observation that the animals' performances fell to chance when discriminating the smallest angles or when localizing the most restricted noise band, 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 in each plane. Because the minimum audible angle differed in the three 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 (see Heffner et al., 1995). Instead, the angles were matched for approximate diffi-

culty; that is, the angle chosen was the smallest which resulted in an average performance of 80% for animals localizing a broadband signal 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). By using such a moderately difficult stimulus angle, any reduction in the effectiveness of the signal would be likely to result in a decrement in performance. The angles meeting this criterion were: 30° (± 15°) around the median sagittal plane for left/right tests, 90° (±45°) around the interaural line for front/back tests, and 45° for vertical localization. However, chinchillas without pinnae were unable to localize the 45° vertical separation; hence the effect of low-pass filtering was assessed using a 75° vertical separation and compared to normal performance at that angle.

The electrical signal was generated by a noise generator (Grason-Stadler GS1285) and filtered (Krohn-Hite 3202) using a low-pass filter with a 48-dB per 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). Filtering out high frequencies reduced the overall intensity of the signal so that the 40-kHz low-pass signal was 66 dB, 20-kHz low-pass was 64 dB, and 10-kHz low-pass 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 differed by no more than 5 dB 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 animals' thresholds.

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 a 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 a 'warning' signal was presented (a noise burst emitted from the left, front, or upper speaker, respectively) 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.

2.4.1. 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:

CorrectedDetection = HitRate

$$- (FalseAlarmRate \times HitRate)$$

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, 1988, 1995, respectively).

2.4.2. Threshold

Thresholds for two-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 three 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.

2.4.3. Fixed-angle low-pass filtering tests

Performance scores for each noise band were calculated based on blocks of eight warning trials and the associated safe trials. During testing, trials with each of the four noise bands were interspersed such that no more than four 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.

2.5. Surgical procedure

Pinna removals were performed under aseptic conditions. The animals were anesthetized using 0.5 mg/kg

Acepromazine followed by 40 mg/kg Ketamine. The fur was clipped around the pinna to be removed, the area cleaned with surgical soap and alcohol, and the animal was covered with sterile drapes. Blood vessels were cauterized around the circumference of the pinna approximately 1 cm above the scalp and the skin and cartilage were cut with scissors. The outer skin was then pulled over the exposed edge of the cartilage, sutured with 000 silk suture, and antibiotic ointment (Panalog) was applied. The pinnae were removed bilaterally in a single surgery in chinchillas D, E, J, M, and P; they were removed in two unilateral surgeries in F, G, H, I, K, and L, so that the role of the near versus the far pinna in front/back discriminations could be determined. Recovery in each case was uneventful. The total area of the pinna that was removed was determined by flattening the pinna on paper, tracing its border, and calculating the area using a digitizing tablet and computerized planimetry.

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

3. Results

3.1. Surgical results

The actual area of the pinna removed ranged from 18.0 to 32.5 cm^2. Because the pinna was removed approximately 1 cm above the level of the scalp in each case, most of this variation resulted from natural variation in pinna size and shape. There were no differences in the size of the area of the pinnae removed bilaterally between the groups of chinchillas used in each of the localization tests (Mann-Whitney U, $P > 0.05$). Similarly, there was no difference

in the removed areas of the left and right pinnae in the animals tested after unilateral pinna amputation ($P > 0.05$).

3.2. Left / right localization

3.2.1. Acuity

Sound-localization thresholds for a 100-ms broadband noise burst were determined before and after removal of both pinnae for two chinchillas. Prior to surgery, the thresholds for chinchillas D and E were 16° and 18°, respectively. As can be seen in Fig. 1, there was no change in their thresholds, indicating that pinna removal has no effect on left/right localization acuity for broadband stimuli. Similarly, performance at angles above threshold was not reliably affected. Only performance at 30°, the angle at which performance begins to decline for normal chinchillas, showed any indication of a slight decrement.

Because only two animals were tested on this task, the possibility remains that bilateral pinna removal may result in a small increase in threshold which would be detected if additional animals were tested. This possibility is suggested by the low-pass filtering test (see below) that indicated that not all chinchillas could perform as well as animals D and E in another left/right localization test following pinna removal. However, if bilateral pinna removal does result in a threshold increase, it is not a large effect.

3.2.2. Low-pass filtering

Fig. 2 illustrates the effect of bilateral pinna removal on the ability of five chinchillas to localize low-pass noise bursts at a 30° angle of separation (15° left and right of midline). As can be seen, bilateral pinna removal results in a small, but consistent decrement in performance. At each filter setting the average performance of the operated

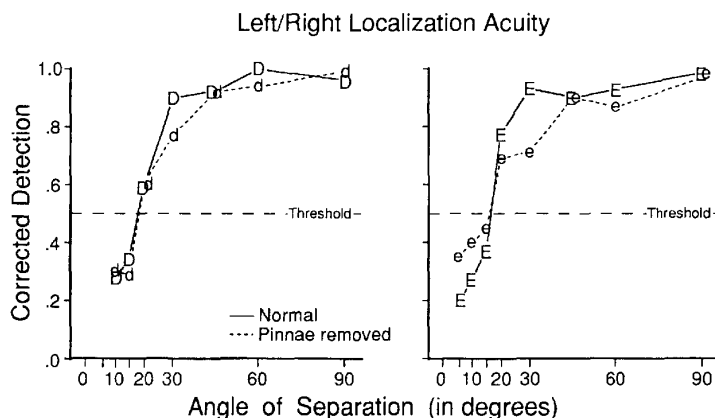Left/Right Localization Acuity

Fig. 1. Left/right localization acuity of two chinchillas (animals D and E) localizing a single 100-ms noise burst before and after bilateral pinna removal. Pre-operative performance indicated by upper case letters and solid lines, post-operative performance indicated by lower case letters and dashed lines. Horizontal dashed line indicates the 0.50 threshold level. Note that bilateral pinna removal had no noticeable effect on asymptotic performance or threshold.
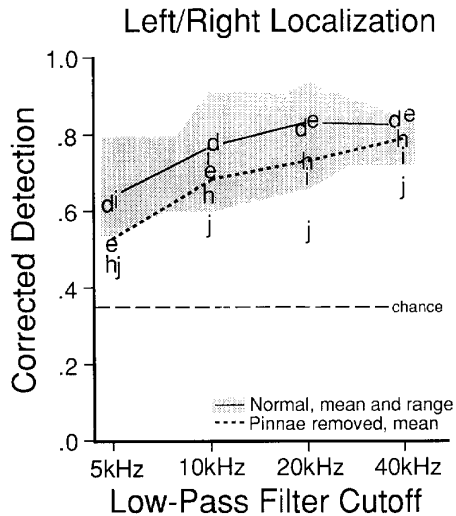
Left/Right Localization

Fig. 2. Left/right localization performance of five chinchillas (indicated by individual letters) following bilateral pinna removal. The signal was a low-pass filtered noise burst from loudspeakers centered on the midline and separated by 30°. The mean and range of performance of four normal chinchillas are indicated by the solid line and shading. The mean of the five chinchillas without pinnae is indicated by the dashed line. The horizontal dashed line indicates the 0.01 chance level. Note the small, but consistent effect of bilateral pinna removal. Because 33 kHz is the highest frequency chinchillas hear at a level of 60 dB SPL (Heffner and Heffner, 1991), the 40-kHz low-pass noise includes their highest audible frequencies.

chinchillas for the broadband (40 kHz) stimulus was 0.46 —well below the normal score of 0.85. Performance declined as high frequencies were filtered out, with the average performance falling to chance for the 5-, 10-, and 20-kHz low-pass noise bands indicating that the remaining parts of the outer ear did not produce a useable spectral cue at these lower frequencies. The remaining ability of the animals to localize the 40-kHz low-pass signals is probably due to the directional properties of the auditory canal and the small remaining stumps of the pinnae.

The effect of removing one pinna and leaving the other intact depended on whether the testing was conducted in the hemifield on the same side as the intact pinna. The average performance of the three animals tested with the loudspeakers located in the hemifield of the intact ear (the 'near' pinna group in Fig. 3) showed a small but consistent decrement. On the other hand, the three animals in which the loudspeakers were located in the hemifield of the ablated pinna (with only the 'far' pinna intact) showed a much larger effect. Specifically, these animals showed a substantial decrease in performance even when high frequencies were available (20- and 40-kHz low-pass filter settings) and were unable to localize the 5- and 10-kHz cutoffs above chance; indeed, at these lower filter settings their performances were no better than those of animals without any pinnae (Fig. 3).

animals is slightly below that of the intact animals, although the average for the operated animals remains within the normal range for all but the 5-kHz filter setting. However, whether this decrease in performance is due to a reduction in the availability of binaural spectral differences cues, a reduction in monaural pinna cues, or both cannot be determined from these data. Regardless, there appears to be only a modest contribution of the pinnae to left/right localization in chinchillas.

3.3. Front / back localization

The effect of unilateral and bilateral pinna removal on the ability to perform front/back discriminations was determined using broadband and low-pass noise with loudspeakers located 45° in front of and behind the interaural line (a 90° separation). The contribution of the pinnae to front/back localization, shown in Fig. 3, can be described as follows. With both pinnae intact, the six chinchillas were able to localize all of the noise bands but their performances declined gradually as the high frequencies were filtered out. However, even with the 5-kHz filter cutoff, the animals were able to perform above chance levels (see Heffner et al., 1995 for a detailed discussion of normal performance). Removal of both pinnae dramatically reduced the ability of the animals to perform the task. As shown in Fig. 3, the average performance of the
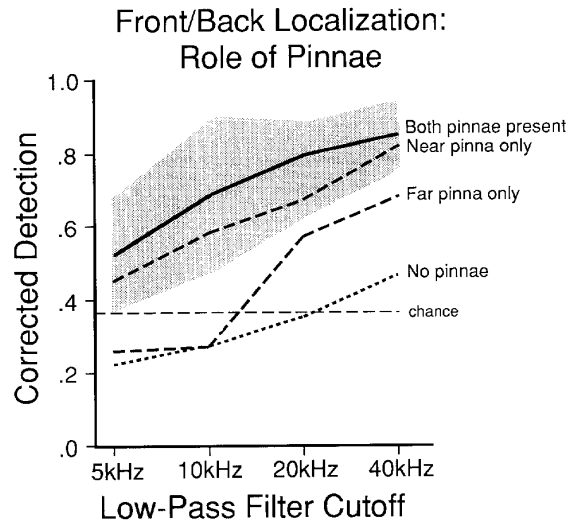
Front/Back Localization: Role of Pinnae

Fig. 3. Effect of unilateral and bilateral pinna removal on front/back localization. Loudspeakers were 45° in front of and behind the interaural axis (90° separation). Solid line and shading indicate the mean and range of performance for six animals before surgery. The two dashed lines each indicate the average performance of three animals following unilateral pinna removal. The dotted line indicates the average performance of all six animals following bilateral pinna removal. The horizontal dashed line indicates the 0.01 chance level. Note that while removal of both pinnae has a severe effect on performance, the effect of removing a single pinna depends on whether testing is conducted in the hemifield ipsilateral or contralateral to the remaining pinna.
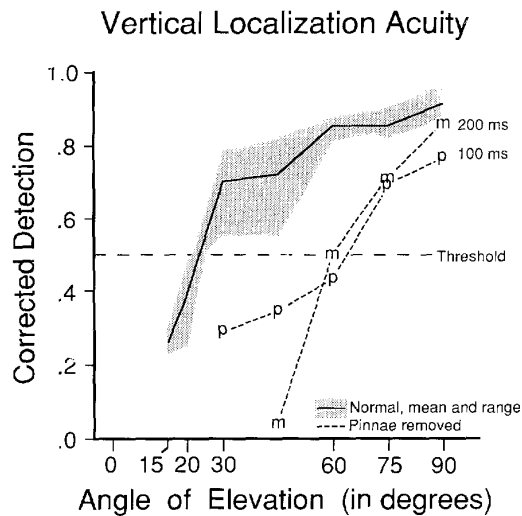
Vertical Localization Acuity

Fig. 4. Effect of bilateral pinna removal on the vertical localization acuity of two chinchillas (indicated by letters) which were tested with either a 200-ms (animal P) or 100-ms (animal M) noise burst. The mean and range of three normal animals are indicated by the solid line and shading. Note the effect of bilateral pinna removal on both threshold and asymptotic performance. Horizontal dashed line indicates the 0.50 threshold level.

In summary, the performance of the chinchillas following bilateral removal of their pinnae demonstrates that they rely heavily on the use of pinna cues to distinguish between front and rear sound sources. In addition, the differential effect of the near versus the far pinna demonstrates that whereas most of the cues are derived from the near pinna, the far pinna can contribute to sound localization when the signal contains frequencies above 10 kHz.

3.4. Vertical localization

3.4.1. Acuity

As has previously been noted the discrimination of elevation is more difficult than the discrimination of azimuth and results in greater variation in performance between animals (Heffner et al., 1995). Thus, while chinchilla M was tested pre- and post-operatively with a 100-ms duration signal, chinchilla P had to be tested with a 200-ms signal in order to enable the animal to work reliably. A third chinchilla, N, had such great difficulty even with the 200-ms signal that it could not be tested postoperatively.

The effect of bilateral pinnae removal is shown in Fig. 4 where the results of the two operated animals are shown in relation to the mean and range of their own and a third chinchilla's normal performances. As can be seen, the performances of the two operated animals are below normal at all angles tested and their thresholds of 60° and 64° are well above the normal average of 23°. This result

demonstrates that the pinnae are essential for all but the grossest discriminations of vertical locus in chinchillas.

3.4.2. Effect of low-pass filtering

The effect of low-pass filtering on vertical sound localization has previously been assessed in chinchillas by testing them at a fixed angle of 45° (Heffner et al., 1995). However, because bilateral removal of the pinnae resulted in a substantial increase in threshold, it was necessary to use a larger angle, hence a separation of 75° was chosen. The ability of chinchillas M and P to localize broadband (40-kHz low-pass) and low-pass filtered noise following bilateral pinna removal is shown in Fig. 5; the preoperative ability of chinchilla P, the only animal tested at the 75° separation, is shown for comparison.

As can be seen in Fig. 5, bilateral pinna removal markedly depressed performance for the broadband (40 kHz low-pass) signal even at this large angle. Moreover, performance declined sharply as the high frequencies were removed. Neither animal was able to localize the 5-kHz low-pass signal above chance. The performance of these two animals is in marked contrast to the preoperative performance of animal P, which could easily localize even the 5-kHz low-pass signal at the 75° angle of separation used here—indeed, its performance on the 5-kHz low-pass noise easily exceeds that of the operated animals' performances on the broadband (40-kHz low-pass) signal. These
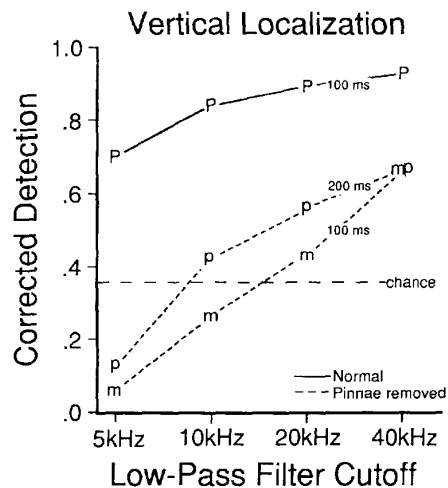
Vertical Localization

Fig. 5. Effect of bilateral pinna removal on the performance of two chinchillas (indicated by lower case letters) localizing low-pass filtered noise bursts with the loudspeakers separated by 75° in elevation. The normal performance of animal P is indicated by the upper case letter (P) and solid line. Note that following pinnae removal, animal P had to be tested with a 200-ms duration signal. Bilateral pinna removal had a severe effect on the animals' performance thereby demonstrating the importance of the pinnae for vertical localization. Horizontal dashed line indicates the 0.01 chance level.

results demonstrate the importance of the pinnae for vertical sound localization.

4. Discussion

The purpose of these experiments was to examine the effect of removing the pinnae on sound localization involving left/right, front/back, and vertical discriminations. The following discussion describes the role of the pinnae in situations in which binaural cues are the primary cues (left/right discriminations) as well as in situations in which pinna cues are the primary cues (front/back and vertical discriminations). Also discussed are the increase in variability in performance when binaural cues are not available, the role of the near and far pinnae, and the relation between pinna cues and high-frequency hearing in mammals.

4.1. Localizing sound where binaural cues are available

Studies of sound localization have demonstrated that humans rely primarily on binaural locus cues for localization in the frontal quadrant with little noticeable contribution from pinna cues (e.g., Musicant and Butler, 1984). The present results indicate that the same is true for chinchillas. Specifically, removal of both pinnae had no effect on the left/right localization acuity for the two chinchillas that were tested (see Fig. 1). Examination of the animals' suprathreshold performances also revealed no effect of pinna removal with the possible exception of their performance at 30°, the angle of separation at which performance normally begins to decline as threshold is approached.

However, the low-pass noise test, conducted at 30°, did reveal a small, but consistent decrement in performance (see Fig. 2). Specifically, the average performance of the five animals without pinnae was consistently lower than that of normal chinchillas for all filter settings. The decrement was most marked for the 5-kHz low-pass noise where the performance of three of the five animals was below the normal range. It should be noted that pinna removal did not entirely abolish the ability to use spectral cues. This conclusion is indicated by improved performances when higher frequencies were available, most likely the result of spectral cues produced by the head shadow, the stumps of the pinnae, or the auditory canal. The demonstration of an effect in the low-pass noise tests, but not in the acuity test, may be due to individual differences between the animals. As can be seen in Fig. 2, the two animals used in the acuity test (chinchillas D and E) out-performed the other three animals in localizing the 40-kHz low-pass noise when it was used in the filtering test. Thus it is possible that a small decrement in acuity might have been detected had all of the chinchillas been tested for acuity following pinna removal.

Although it is possible that the decrease in performance in the low-pass noise test resulted from the loss of pinna cues that normally supplement binaural cues, it is conceivable that pinnae removal may have affected the animals' ability to use the binaural locus cues themselves — that is, the difference in the time of arrival of a sound at the two ears and the difference in the frequency-intensity spectrum reaching the two ears. First, pinna removal affects the frequency-intensity spectrum reaching the ear because the pinnae are major contributors to the change in the spectrum of a sound that occurs as its location changes relative to an animal's head (e.g., Phillips et al., 1982; Jen and Sun, 1984; Carlile and Pettigrew, 1987; Musicant et al., 1990; Rice et al., 1992; Carlile and King, 1994; Chen et al., 1995). Second, it is possible that pinna removal may change the difference in the time of arrival of a sound at the two ears since the base of the pinna increases an animal's effective head size and, correspondingly, the magnitude of the binaural time cue for any given angle.

In summary, the possibility exists that the left/right locus discrimination, for which binaural cues are readily available, is affected by bilateral pinna removal, but the effect is both small and variable, especially in comparison to the marked effect on localization in situations in which binaural cues are absent. However, it is not possible at this time to determine whether this effect is due to a disruption of the pinna cues, the binaural cues, or both. The finding that the contribution of the chinchilla pinnae to azimuthal localization in the frontal quadrant is at best minimal is consistent with studies of the contribution of pinna cues to human sound localization (e.g., Musicant and Butler, 1984).

4.2. Localizing sound when binaural cues are not available

The importance of the pinnae to sound localization is most clearly shown in the locus discriminations in which binaural cues are not available. In the front/back test, binaural cues were virtually eliminated by centering the loudspeakers on the interaural axis, i.e., on the 'cone of confusion' (e.g., Mills, 1972). Similarly, binaural cues are not available in the elevation test because the time of arrival of a sound at the two ears does not change with elevation and the change in the spectrum of a sound should be the same for a sound source located on the midline, except for small differences induced by asymmetries of the pinnae themselves. As expected, pinna removal had a large effect on the ability to perform both of these discriminations.

With regard to front/back localization, bilateral pinna removal almost completely eliminated the ability of the chinchillas to localize a single noise burst at an angular separation of 90° (see Fig. 3). Similarly, the effect on vertical localization was to raise thresholds by almost 3-fold. That removal of both pinnae did not entirely eliminate the ability to make front/back or vertical discrimina-

tions is most likely due to the directional properties of the auditory canals and the small remaining stumps of the pinnae.

4.2.1. Variability of performance using pinna cues

Individuals differ substantially in their ability to localize using pinna cues. Among both normal and operated animals there was more variability between animals in the front/back and elevation tests than in the left/right test. This variation was most evident in the elevation tests. As a normal, chinchilla M readily localized 100-ms noise bursts at angles as small as 30°, whereas the remaining two animals required training with longer durations and were not able to approach that level of discrimination with signals less than 200 ms in duration (Heffner et al., 1995). After pinna removal, chinchilla M continued to localize 100-ms noise bursts, but chinchilla P had increased difficulty and chinchilla N could not be tested with any stimuli approaching comparability to the normal animals. Similar marked differences in the ability of humans to use pinna cues have also been noted (Flannery and Butler, 1981; Oldfield and Parker, 1986), especially for discriminations of elevation (Butler, 1970; Butler and Belendiuk, 1977; Oldfield and Parker, 1984; Noble, 1987). This variability in behavioral capacity may be attributable to the variability in the pinnae themselves (Flannery and Butler, 1981) and to differences in their filtering characteristics from one individual to another (Irvine, 1987; Carlile, 1990; Musicant et al., 1990; Rice et al., 1992).

4.2.2. Near pinna versus far pinna

Although the largest effect on front/back localization resulted from removal of both pinnae, removal of only one pinna also had a noticeable effect. Indeed, a decrement in performance was observed regardless of the side on which the animal was tested, demonstrating that both the near and far pinnae play a role in localization off to the side. Thus, although the pinna nearest the sound source provides the most effective cues, the far pinna also contributes to localization. However, as can be seen in Fig. 3, the contribution of the far pinna depends on the presence of frequencies above 10 kHz — if the sound contains only frequencies of 10 kHz and lower, then performance is identical to that when both pinnae are removed.

The effectiveness of a single pinna in humans has been investigated by filling the contours of one pinna leaving only a smooth opening to the auditory canal (Blauert, 1969/1970; Musicant and Butler, 1984; Humanski and Butler, 1988) or by plugging the ear canal (Oldfield and Parker, 1986). The results of these studies have demonstrated that for localization off to the side, the near pinna of humans contributes much more than the far pinna; indeed in humans the far pinna alone seem unable to localize sounds on the cone of confusion, although its presence may enhance performance over that of the near pinna alone (e.g., Musicant and Butler, 1984; Butler, 1986;

Oldfield and Parker, 1986). Thus, the far pinna of chinchillas seems to contribute more to localization than the far pinna of humans.

The observation that, in chinchillas, the far pinna approaches the effectiveness of the near pinna when high frequencies are present may be due to the extension of the pinnae of chinchillas above the head well into the direct path of the sound. In contrast, the pinnae of humans lie low on the side of the head and the far pinna is in the head's sound shadow where it receives relatively less of the high frequencies in a broadband sound (e.g., Dirks and Gilman, 1979). Thus, in chinchillas, the far pinna is able to receive and make use of frequencies above 10 kHz in discriminating the locus of sounds. The small, but consistent decrement in localization in chinchillas following removal of the far pinna demonstrates that the far pinna normally contributes to localization even on the cone of confusion.

4.2.3. High frequencies and pinna directionality

There are no published measures of the pinna transform functions for chinchillas, but data are available for cats, guinea pigs, mice, bats, and ferrets that give some information regarding the frequencies for which the pinnae are directional. Measures of the directionality of the pinna in cats indicate that it is directional for frequencies as low as 4–5 kHz (Calford and Pettigrew, 1984; Rice et al., 1992). The smaller pinnae of ferrets, on the other hand, rapidly lose their directionality below 8 kHz (Carlile, 1991) and those of mice lose directionality below about 20 kHz (Chen et al., 1995).

With regard to chinchillas, the results shown in Fig. 3 give an indication of the frequencies used by the pinnae to generate locus cues. Specifically, the localization of 40-kHz low-pass noise by chinchillas with both pinnae removed is not significantly different from that of normal animals localizing the 5-kHz low-pass noise (Mann-Whitney U, $P = 0.40$). In other words, filtering out frequencies above 5 kHz in normal animals is tantamount to removing the pinnae — in order to make use of pinna locus cues, it is necessary for chinchillas to hear at least above 5 kHz, and their performance improves as higher frequencies are added (cf., Fig. 3). That is, in order to use their pinnae effectively for sound localization, they must hear frequencies above the upper limit of nonmammalian vertebrates. This observation is consistent with the thesis that an important source of selective pressure for the evolution of high-frequency hearing in mammals is the advantage conferred upon them of being able to localize sound sources using pinna cues to supplement binaural locus cues (Heffner and Heffner, 1992; Heffner et al., 1995).

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