INTRODUCTION

Psychophysical studies have shown that localization of a sound source is accomplished using two types of cues, binaural difference cues and spectral cues. Sounds located off the midline will arrive at the near ear in advance of the far ear, creating an interaural time difference cue (ITD). Additionally, for high frequencies, the head creates an acoustic shadow, causing the sound at the far ear to be attenuated with respect to that arriving at the near ear. This provides the interaural level difference (ILD) cue to sound source location. The salience of these binaural cues is dependent on the frequency content of the sound and its source location. ITDs are largest for locations along the interaural axis and decrease as the source sound moves away from there. The “cone of confusion” phenomenon arises because all of the positions subtending the same angle with respect to the interaural axis will give rise to the same ITD. At the lowest sound frequencies where they are present, ILD cues follow much the same spatial pattern as ITD cues. At higher frequencies, however, the spectral filtering properties of the external ears differentially boost or attenuate the signal depending on its location in space (Carlile 1990; Carlile and King 1994; Middlebrooks et al. 1989; Musicant et al. 1990; Rice et al. 1992; Shaw 1974), creating a complex but spatially unambiguous pattern of interaural spectrum differences. The spectral filtering properties of the pinna and concha of the external ear also provide monaural cues for sound location.

Psychophysical studies in humans have emphasized the importance of pinna-based spectral cues in resolving ambiguous binaural cues, both in the midsagittal plane (Blauert 1969; Gardner and Gardner 1973; Hebrank and Wright 1974; Oldfield and Parker 1984a; Roffler and Butler 1968), and in the horizontal plane (front-back errors) (Musicant and Butler 1984; Oldfield and Parker 1984a). Other reports have suggested that spectral cues influence sound localization even when binaural cues are not ambiguous (Butler and Musicant 1993; Musicant and Butler 1984). Psychophysical studies in animals have investigated the contribution of pinna-based spectral cues to sound localization by selectively filtering the sound source spectrum (e.g., Huang and May 1996a), or physically, by surgically altering the characteristics of the external ear (Heffner et al. 1996).

Studies using animals have also emphasized the role of pinna-based spectral cues in neural mechanisms of sound localization at the level of both the midbrain and the cortex (see Brainard 1994 for review). For example, neuronal sensitivity to a combination of monaural spectral cues and ILDs appears to form the basis for the map of auditory space in the mammalian superior colliculus (SC) (Carlile and King 1994; King et al. 1994; Middlebrooks 1987; Palmer and King 1985; Wise and Irvine 1985). Moreover, in juvenile ferrets, removal of the pinna and concha, either unilaterally or bilaterally, disrupts the emergence of topographic order in this representation, emphasizing the importance of spectral cues provided by the external ear in the development of auditory spatial tuning in the SC (Schnupp et al. 1998).

Effects on auditory localization behavior of early unilateral
hearing losses have been examined in humans (Slattery and Middlebrooks 1994; Wilmington et al. 1994), ferrets (Parsons et al. 1999), and barn owls (Knudsen et al. 1984a,b). No attempts have been made, however, to investigate the behavioral consequences of altering spectral localization cues during development. Because early pinna and concha removal disrupts the development of the auditory space map in the SC to an extent not observed with other manipulations of auditory localization cues and most likely also affects spatial processing at other levels of the auditory pathway, we have investigated the impact of this procedure on the sound localization abilities of adult ferrets.

A preliminary account of some of these findings has been published (Parsons et al. 1998).

METHODS

Animals

Pigmented male and female ferrets were used in these experiments. Five animals had their pinna and concha removed bilaterally on postnatal day \( (P) 27 \), just before the typical age at which auditory brain stem responses can first be evoked in this species (Moore and Hine 1992). The surgical procedure has previously been described by Schnupp et al. (1998). Briefly, the ferrets were anesthetized with alphaxalone/alphadolone acetate (SAFFAN, 4 ml/kg ip) and the pinna and concha of each ear removed, leaving sufficient cartilage to ensure that the ear canal remained patent. For brevity, we will refer to the group of ferrets that had their pinna and concha bilaterally removed in infancy as the pinnae-removed group.

Six normal adult ferrets were used to measure relative localization in the horizontal plane, and four animals were tested in the midsagittal plane. One of the normal animals tested in the midsagittal plane was also tested in the horizontal plane. Three different normal animals were used in the absolute localization task.

The ferrets were housed individually in rack-mounted cages, with free access to water and a high-protein carnivore diet. One day before testing, and throughout the testing period, the animals were deprived of water in their home cages. Instead, they received vitamin-supplemented water during the twice-daily testing sessions.

Apparatus

Training and testing were performed in sound-attenuated chambers. Two chambers were used. The floor plans of these are shown schematically in Fig. 1. One chamber was used exclusively for measuring spatial acuity in the horizontal plane; the other chamber was used to test the absolute localization ability of ferrets in the horizontal plane and acuity in the midsagittal plane. The floors were constructed of Formica-covered particleboard, with a radius of 75 cm. Near the center of each arena was a raised platform (37 cm \( \times \) 12 cm, 3 cm high), which was covered with perforated stainless steel plates over a dampened sponge to form a conductive surface. Each ferret was trained to stand on the platform and lick a water spout, which, in most cases, required the animal to place its head through a hole in a vertical grid. This ensured that, as the spout was licked, the head was consistently positioned at the center of the testing arena. Licking the center spout from the platform completed an electrical circuit and initiated the presentation of a noise burst from a randomly chosen speaker at the periphery of the chamber. In response to the noise burst, the ferrets were required to approach and lick the appropriate response spout. The number and exact location of the response spouts varied according to the experiment, but typically these were positioned close to the target speakers. Stainless steel plates were fixed to the floor of the arena near the periphery so that the ferrets had to stand on these to lick a response spout. This action completed an electrical circuit and notified the computer of the response of the ferret. Each spout was connected to a water reservoir. Solenoid valves (Flo-control, Valaeder Pneumatics, Cambridge, UK) controlled the water flow.

Both testing arenas were enclosed by 25 mm\(^2\) wire mesh. In the case of the relative localization arena, the lid of the sound-attenuating chamber served as its ceiling, whereas, for the absolute localization arena, the metal grid enclosure was dome-shaped. In both chambers,
the speakers were mounted on a rail outside the grid, and the response spouts protruded through the grid.

The walls and ceiling of the relative localization chamber comprised a 36-mm layer of rock wool sandwiched between two sheets of galvanized iron, which were lined with 75-mm Class 0 acoustic foam. The absolute localization testing arena was housed in a double-walled sound-attenuating chamber. Each wall was constructed of 15-mm-thick medium density fiber board, separated by a 4-cm gap. The walls and ceiling of the chamber were lined with 50-mm thick MELATECH sound-absorbing foam (The Noise Control Center, Leicestershire, UK).

Psychophysical methods

AZIMUTH ACUITY PROCEDURE. The discrimination task that we used to test the localization acuity of the ferrets was a 2-source-1-interval (2S1I) task. After licking the central start spout, the ferrets were presented with a single noise burst. They were required to respond to a left-located spout or a right-located spout, depending on whether the sound presented from the left or the right speaker. A correct response was rewarded with water drops. Incorrect responses were not rewarded. After an incorrect response, the stimulus was again presented from the same location as a correction trial. Correct responses were rewarded in correction trials, but these trials did not count toward the score of the animal. In ~12% of the trials, the ferrets received a drop of water from the center spout before stimulus presentation. These center reward trials were disregarded when the score of the animal was calculated and when the total number of trials was calculated. The ferrets were required to complete 100 trials per session, and 2 sessions were run per day. Each session started with 10 practice trials and, at the conclusion of the 100 trials from which performance was calculated, included sufficient extra trials to satiate the animal.

We tested the ferrets for their ability to discriminate between two speakers placed symmetrically about the anterior midline position (0°), and symmetrically about either 45° to the left or the right of the midline (lateral condition). During the acquisition phase of this task, the speakers were placed at their maximum separation of 90° around the anterior midline position. The ferrets were initially trained to approach a continuous broadband sound source coming from one of the speakers, and to lick the associated response spout. Once they had learned this response, the stimulus duration was reduced to 2,000 ms, then to 1,000 ms. These long stimulus durations were maintained until the ferrets had attained a consistently high level of performance (≥90% correct in 4 consecutive sessions).

We obtained psychometric functions using noise bursts of three different durations (500, 100, and 40 ms). Beginning with a speaker separation of 90° in the midline condition or 80° in the lateral condition, the angle was reduced once a ferret scored ≥90% correct in two consecutive sessions. We reduced the angle of separation about the center position in two series. In the first series, the speaker separation was reduced by 10° every session until performance for 100 trials was not significantly different from that expected by chance according to the binomial distribution (<63%, 0.01 level of significance). When performance dropped to the chance level, we increased the speaker separation by 20° and started the second series. In the second series, the speaker separation was reduced provided that scores from two consecutive sessions were matched (P > 0.10, binomial distribution). In this manner, we reduced the speaker separation in 10° increments until the mean performance over the two matched sessions fell below 56.5% correct, the critical value for above chance performance in 200 trials at the 0.05 level of significance, or until the ferrets had matched scores at the smallest angular separation (6°). Angular reductions were always made by moving each speaker toward the other by half of the intended distance, thus keeping them symmetrical about the original center position. In some cases, a speaker separation of 0° was also used, by placing one speaker directly above the other.

Psychometric functions were constructed by combining data from the first series with data from the matched scores of the second series. Logistic curves were fitted to the psychometric functions, and the angular separation that resulted in 75% performance (P75) was estimated from the parameters of these functions. The P75 values were used to compare the performance of the pinnae-removed ferrets with that of the normal ferrets.

ELEVATION ACUITY PROCEDURE. As in the relative localization task in the horizontal plane, we used a 2S1I procedure for measuring the minimum angle of speaker separation that ferrets could discriminate in the midsagittal plane. The speakers were placed symmetrically about a position 45° in elevation. Ferrets were trained to respond to their left when the sound was presented from the upper speaker and to their right when the sound was presented from the lower speaker. During the initial training period, the speakers were separated by 80°, and a looped noise burst, providing a continuous stimulus, was presented from one or other speaker. Once near perfect performance was attained, the duration of the stimulus was reduced to 1,000 ms and then to 500 ms, where the first of the psychometric functions was measured. Further psychometric functions were measured using 200- and 40-ms noise bursts.

The ferrets were required to complete 100 trials in a session. At the start of a testing block, the speakers were placed 80° apart (i.e., at 85° and at 5° above the horizon). The speaker separation was reduced from 80° once the ferrets had achieved two consecutive sessions with scores over 90%. Alternatively, if they did not reach this level of performance after four sessions at 80°, we reduced the angle if the scores from two subsequent consecutive sessions were statistically matched. Further angular reductions in speaker separation were made in 10° steps if the scores in two consecutive sessions at each angle matched. This procedure continued until the average performance from two matched sessions fell below 56.5%, or until the ferret completed two consecutive matching sessions at the minimum speaker separation of 10°. In all cases we compared performance between sessions using probabilities based on binomial distributions (P > 0.10). Logistic curves were fitted to the psychometric functions, and P75 values were calculated from the fitted functions.

ABSOlUTE LOCALIZATION PROCEDURE. Twelve speakers were spaced at 30° fixed intervals around the perimeter of the testing arena. These were hidden from view by a muslin sheet. The ferrets were tested twice a day, completing ~100 trials in each session. We began with 2,000 ms noise bursts and then progressively reduced the stimulus duration so that ~300 trials were performed at each of the following: 1,000, 500, 200, 100, and 40 ms. The duration of the stimulus was kept constant within a session and reduced at the start of the next session. Using this paradigm, we normally collected at least 25 trials at each location for each stimulus duration. After completion of the testing block, which lasted for 12–14 days, the ferrets were allowed free access to water and wet food in their home cage for at least 4–5 days, whereupon they were tested again. Data were collected in this manner from a total of four testing blocks. They were regularly weighed during the testing procedure to ensure that adequate body weight was maintained.

A personal computer running our own software directed the signal generation, recorded the responses of the ferrets, and controlled the delivery of rewards. In the first two blocks, a ferret initiated a trial by standing on the center platform, placing its head through a hole in the head-positioning grid and licking the center spout, whereupon the stimulus was immediately presented. On the third and fourth blocks the start procedure was varied slightly in the following manner. The animals were required to maintain contact with the spout for a variable length of time (0.5–2.0 s) before the stimulus was presented, to ensure that they waited for and attended to the sound before moving off the platform. The head-positioning grid was removed because it interfered with a separate experiment that measured the head orientation of these animals during the localization task. During the delay period, the ferrets were required to maintain contact with the center spout until
the stimulus was presented. If they broke contact, no stimulus was delivered, and the animal had to lick the center spout again until the stimulus was presented. In the absence of the head-positioning grid, correct head and body position was maintained by removing the front portion of the conductive base-plate. This meant that the ferrets had to assume a straight body position with their back legs on the rear of the platform while licking the center spout. In 5% of the trials, the ferrets received a reward from the center spout. Center reward trials were excluded from the analysis.

On presentation of a stimulus, the ferrets were required to approach the hidden, active loudspeaker location and lick the adjacent response spout. A correct response was rewarded with a measured amount of water. Incorrect responses were not rewarded and were followed by correction trials. A limit of three correction trials was set, after which a continuous noise stimulus was presented from the same location. Correction trials ensured that an equal number of rewards were obtained from each speaker location and were designed to prevent response biases from occurring.

Signal generation

RELATIVE LOCALIZATION CHAMBER. Tucker Davis Technology (TDT, Gainesville, FL) system I hardware controlled by Auditory Laboratory Digital Investigation Sound System (ALDISS) (Carlile and Hollingshead 1992) was used to produce the broadband (10-ns rise-fall, 800–24,000 Hz) noise stimuli used to measure spatial acuity in the horizontal plane. Because finite impulse response (FIR) filtering was not available to generate the stimuli on-line, the impulse responses of the speakers were measured before the behavioral study started. The fast Fourier transform (FFT) of the response was calculated and the amplitude spectra inverted and phase spectra randomized so that we could match the outputs of the two speakers. For each of the three stimulus durations and each speaker, 20 presynthesized files were generated. These were stored to disk and were randomly selected throughout a testing session. Digital to analogue (D/A) conversion was performed using the TDT hardware, and the stimuli were delivered via a programmable attenuator (TDT PA3) and QUAD 240 amplifier at a single sound level of 70 dB SPL. The sound level was measured at the center spout using a Bruel & Kjaer type 1618 microphone where the center of the ferret’s head would be during the presentation of a stimulus. The FFT was calculated for each speaker at its position in the chamber, and FIR filters were computed from the inverted Fourier spectra. FIR filters were used to flatten the output of the speakers. The sound pressure level from each speaker was measured at the position occupied by the ferret’s head, and adjusted to 70 dB SPL. After the second block of trials, we randomly varied the sound pressure level across trials (8 dB in 2-dB increments). This was done to reduce the possibility of the ferrets being able to identify the speakers on the basis of loudness cues alone.

Statistical analysis

The specific statistical tests used are indicated in the appropriate results section. Where statistically significant variations in the results were observed, pairwise group comparisons were performed using the Bonferroni correction for multiple comparisons. The convention to be used in describing the results of the analyses of variance is to report significant main effects and interactions, then to report mean differences between the groups bounded by these interactions.

In the absolute localization task we assessed the performance of the ferrets using two main measures: the mean unsigned error magnitude (which is inversely proportional to the accuracy of the responses) and the percentage of correct responses. In calculating the error magnitude, we did not include front-back errors but reported their occurrence separately.

Acoustics

We assessed the acoustical consequences of pinna removal in infancy by recording spectral transfer functions (STFs) bilaterally in three of the ferrets that had been used in the behavioral study. The animals were anesthetized with domitor (250 μg/kg) and ketamine (60 mg/kg ip), and additional doses were provided intravenously as necessary. Body temperature was monitored and held constant at 39°C. A small midline scalp incision was made so that a metal bar could be attached to the skull. This bar was then clamped to a supporting post behind the animal’s body. The posterior aspect of the external auditory meatus was exposed on each side by making an incision behind the remaining external ear. The microphone assemblies consisted of Sennheiser cartridges (KE 4–211-2) attached to a 12-mm polythene tube (1 mm ID, 1.5 mm OD). Each one was positioned alongside the body, and the probe tube extension was inserted into the external auditory meatus and glued in place with cyanoacrylate, so that it protruded <1 mm into the ear canal. The animal was then placed on a small table in an anechoic chamber. Acoustic signals consisted of digitally constructed 32768-point Golay codes (Zhou et al. 1992), played and recorded at 100 kHz, using TDT System II equipment, and delivered through a Kef T27 loudspeaker that was mounted on a vertical hoop with a radius of 0.65 m. Movement of the speaker along the hoop allowed the vertical angle of the stimulus to be varied, whereas rotation of the hoop around the animal changed the azimuthal angle. The signal recorded by the probe microphone was passed through an anti-aliasing filter (7-pole elliptic filter, Fc, 30 kHz) and digitized. Measurements were made at 10° intervals in azimuth (with the exception of a 30° wide region directly behind the animal, which our robotic hoop could not reach) and elevation. Azimuths ipsilateral to the ear in which the microphone was implanted were denoted by negative numbers. The stimulus-recording system was calibrated at the end of each experiment by measuring the transfer function of the probe microphone assembly alone, which was left in place in the anechoic chamber after removal of the animal. The plastic extension of the probe microphone was embedded in plasticine to reduce cross-talk across its walls.

The acoustical recordings made from the animal’s ears were analyzed as described by Zhou et al. (1992) and amplitude spectra of the transfer function were obtained for each position. The contributions of the speaker and microphone to the measured STFs were removed by subtracting the amplitude spectra measured during calibration recordings (made without the animal present). In the case of interaural plots, the right ear functions were then subtracted from the left ear functions. The plots were then smoothed with a linear Gaussian filter (SD ~250 Hz). Finally, directionality transfer functions (DTFs) were calculated by subtracting the mean STF from each of the individual functions.
This procedure removes the location-independent components of the STF, which will vary with the precise location of the recording microphone within the ear canal, and illustrates how the filtering of the outer ear varies with sound source location (see Schnupp et al. 1998, for more details).

RESULTS

Spectral localization cues

Overall, compared with the normal ferrets, the acoustical recordings in the pinnae-removed ferrets showed, as expected, fewer location-dependent spectral features. This is illustrated in Fig. 2, which shows the DTFs recorded from the left ear of one normal and two of the pinnae-removed ferrets at four different azimuths and at 0° elevation. For the normal ferret (bold solid line), a broad gain in transmission was present for anterior sound directions (Fig. 2, A and B), which had largely disappeared at the interaural axis (Fig. 2C), before being replaced by a negative gain at lower frequencies in the posterior hemifield (Fig. 2D). The DTF recorded at 0° azimuth also provides clear evidence for a spectral notch centered at ~24 kHz (Fig. 2A). In contrast, none of these features were apparent in the head-related transfer functions (HRTFs) of either pinna-removed ferret. The monaural spectral cues recorded in these animals are very similar to those previously reported from this laboratory for adult ferrets in which the pinna and concha were removed either acutely, just before the measurements were made (Carlile and King 1994), or in infancy (Schnupp et al. 1998).

Monaural recordings in the azimuthal plane in a normal animal revealed notable front-back differences (Fig. 3A). From 10–20 kHz there was a significant drop in transmission for ~150° and a positive gain at ~30°. Moreover, as in previous reports (Carlile and King 1994; Schnupp et al. 1998), we observed a spectral notch in the anterior field, which varied from 22 kHz for positions straight ahead to ~27 kHz for positions near ~60°. The interaural azimuth DTF was similarly quite asymmetric about the interaural axis (Fig. 3B). The acoustical measurements in the pinnae-removed animals still showed some spectral features (Fig. 3, C–F), notably a notch at ~20 kHz (Fig. 3, C and D) in one case, but these tended to vary much less with speaker position. The clearest difference between the normal and pinna-removed ferrets is that the degree of front-back asymmetry in the horizon spectral cues was much reduced; this is particularly evident in the monaural DTF plots (Fig. 3, C and E).

Recordings in the midsagittal plane showed that there are fewer spectral features than in the horizontal plane for both normal and pinna-removed ferrets (Fig. 4), although, in comparing Figs. 3 and 4, it is important to note that fewer spatial locations were sampled in the midsagittal plane. The monaural DTF in the normal animal did, however, show a general trend for higher gain at lower elevations, with the exception of a notch at 23 kHz for near-horizontal (Fig. 4A). This trend was reversed in the pinna-removed ferrets, indicating that the spatial pattern of spectral cues is altered but not abolished in these animals (Fig. 4, C and E). More importantly, the interaural DTF for the normal animal contained notable deviations from 0 dB, implying that the ears were not symmetrical (Fig. 4B).

The interaural spectral differences in the pinna-removed ani-

![Fig. 2. Directionality transfer functions (DTFs) from one normal (thick line) and 2 pinnae-removed (thin and dotted line) ferrets at the 4 different azimuthal locations indicated. These plots show how the transmission gain produced by the external ear varies with both stimulus frequency and location. The direction-dependent features present in the normal DTFs, which most likely form the basis for resolving front-back confusions, are missing in both pinna-removed ferrets.]
mals contained fewer features (Fig. 4, D and F), especially for F9670 in which these measurements were mostly noise (Fig. 4F). It is interesting to note that this animal performed less well when tested for its ability to localize in the midsagittal plane than the other pinnae-removed ferret, F9669.

Minimum audible angles in the horizontal plane

Logistic curves were fitted to the psychometric function data obtained from each animal. Representative examples of the raw data and the fitted functions are shown in Fig. 5. In each case, the logistic curve provided a very good fit to the psychometric data, as indicated by the $R^2$ values of 0.90 for F9724 (left panel) and 0.80 for F9669 (right panel).

The logistic curves obtained from the pinnae-removed ferrets at the midline and in the lateral sound field are presented in Figs. 6 and 7, respectively. These curves are superimposed over a shaded region, which represents the range of psychometric functions obtained from the normal ferrets. At the larger speaker separations, the animals were able to perform the task well, as reflected by their high percent correct scores. However, as the speaker separation was reduced, the task became more difficult, and the performance of all the animals declined. The performance of the pinnae-removed ferrets was comparable with that of the normal ferrets, both at the midline and in the lateral field. We calculated minimum audible angles (MAAs) from the
parameters of these fitted logistic functions, using a 75% correct performance criterion (P75).

Mean group MAAs and their standard deviations are presented in Table 1. A repeated measures ANOVA was used to determine whether significant differences occurred between the pinnae-removed and control groups. A separate analysis was performed for the midline and lateral data because there was an unequal number of within-subject data points between the two speaker placement conditions.

**MIDLINE CONDITION.** The main effect of group was not significant \(F(1, 8) = 0.085, P = 0.779\), but we did find a significant main effect of duration \(F(2, 7) = 6.380, P = 0.026\). As stimulus duration was reduced, the performance of the ferrets declined, as reflected in the P75 values (see Table 1). There was no interaction between the factors group and duration \(F(2, 7) = 1.270, P = 0.338\).

**LATERAL CONDITION.** As with the midline data, the main effect of group was not significant \(F(1, 6) = 0.599, P = 0.468\), whereas the main effect of duration was significant \(F(2, 5) = 29.276, P = 0.002\). There was no significant interaction between the factors duration and group \(F(2, 5) = 4.503, P = 0.082\), indicating that, as for the midline condition, the pinnae-removed ferrets performed as well as the normal animals.

**Vertical localization: midsagittal plane minimum audible angles**

Logistic curves were fitted to the psychometric functions obtained from ferrets tested in the midsagittal plane. These curves were used to estimate the minimum audible angles (MAAs) at different frequencies and elevations. The MAAs were derived from the fitted logistic functions and were used to evaluate the performance of the ferrets in the midsagittal plane.
FIG. 5. Psychometric function data (●) and logistic curves for a normal ferret (left) and a pinnae-removed ferret (right) obtained in the lateral sound field for the horizontal relative localization task. Logistic curves such as these were fitted to the data from each ferret and were used to estimate minimum audible angles.

FIG. 6. Midline psychometric functions from the relative localization task. Lines represent logistic curves that were fitted to the psychometric function data of the pinnae-removed ferrets following testing in the relative localization task about the anterior midline. Shaded regions represent the areas bounded by the psychometric functions of the normal ferrets. The ferrets were tested using 3 stimulus durations. The performance of the pinnae-removed ferrets overlapped that of the normal ferrets.

FIG. 7. Lateral sound-field psychometric functions. Logistic curves were fitted to the psychometric function data of the pinnae-removed ferrets following testing in the relative localization task in the lateral sound field. In this condition, the speakers were placed symmetrically about a position 45° to the left or 45° to the right of 0°. Shaded regions represent the areas bounded by the psychometric functions of the normal ferrets. As with the midline condition, the pinnae-removed ferrets performed within or very close to the normal range.
curves are presented in Fig. 8. In this condition it was not possible to site the response spouts in close proximity to the target speakers. The ferrets were, nevertheless, able to make the association between the stimulus source and the appropriate response spout. This is shown by their performance at wide angles of speaker separation, especially when localizing the 500-ms stimulus. Under these conditions, most ferrets scored around 90% correct. As the angular separation of the speakers was reduced, the performance declined, and MAAs (P75) were calculated from the parameters of the fitted functions.

Because only two pinnae-removed ferrets were tested, we did not make a formal comparison between these animals and the normal ferrets. We were able to estimate MAAs from all animals when a 500-ms noise burst was used as the test stimulus. The MAAs obtained from the pinnae-removed ferrets tended to be marginally larger than those of the normal ferrets. This difference was accentuated at the two shorter stimulus durations. In fact, one of the pinnae-removed ferrets (F9670) failed to perform above chance when tested with 200-ms noise bursts at the maximum speaker separation of 80°. We were able to obtain psychometric functions from the other pinnae-removed ferret, F9669, at 200 and 40 ms. However, this ferret had P75 values that were close to the maximum speaker separation at both of these stimulus durations.

Absolute localization in the horizontal plane

We tested three normal ferrets and three pinnae-removed ferrets on the absolute localization task. Given the similarity in the spectral localization cues measured from normal ferrets (Carlile 1990; Carlile and King 1994; Schnupp et al. 1998) and the very consistent effects of pinna and concha removal on those cues observed both in this (Figs. 2 and 3) and earlier studies (Carlile and King 1994; Schnupp et al. 1998), we have combined the behavioral data from each group. Overall, the pinnae-removed animals showed significant deficits compared with the normal animals. They achieved a score of 60% (averaged across all testing sessions), compared with 70% correct responses by the normal animals \( [F(1, 48) = 22.049, P < 0.001] \). They also were less accurate (mean unsigned errors of 15° for the pinnae-removed ferrets and 11° for the normal animals; F(1, 48) = 22.033, P < 0.001), and made significantly more front-back errors (F(1, 40) = 35.674, P < 0.001).

Further examination of these results revealed that the differences in performance were not uniformly distributed across all testing conditions. In some conditions, the pinnae-removed animals per-

### TABLE 1. Horizontal plane minimum audible angles of normal and pinnae-removed ferrets

<table>
<thead>
<tr>
<th>Stimulus Duration</th>
<th>Normal Values</th>
<th>Pinnae-Removed</th>
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<tbody>
<tr>
<td></td>
<td>Midline MAA</td>
<td>Lateral MAA</td>
</tr>
<tr>
<td>500 ms</td>
<td>10 ± 5 (6)</td>
<td>18 ± 10 (6)</td>
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<tr>
<td>100 ms</td>
<td>10 ± 4 (6)</td>
<td>24 ± 15 (6)</td>
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<tr>
<td>40 ms</td>
<td>16 ± 8 (5)</td>
<td>34 ± 29 (5)</td>
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Values are means ± SD with number of subjects in parentheses. Minimum audible angles (MAA; expressed in deg) were defined as the angle corresponding to a score of 75% correct and were derived from the logistic curves fitted to each psychometric function.

![FIG. 8. Logistic curves fitted to psychometric functions that were obtained from ferrets tested in the midsagittal plane. Four normal ferrets (top panels) and 2 pinnae-removed ferrets (bottom panels) were tested on this task. The ferrets were tested with 3 different stimulus durations (500, 200, and 40 ms). Dashed line in the top right panel represents the logistic function that fitted the data (shown by the crosses) obtained from 1 of the 4 normals. This animal was tested 3 times and produced a very similar psychometric function on each occasion. Only when tested with a 500-ms stimulus were the pinnae-removed ferrets able to perform as well as the normal ferrets. At the 2 shortest stimulus durations, psychometric functions could be obtained from only 1 of the pinnae-removed ferrets (F9669, solid line). The other pinnae-removed ferret (F9670) is represented by the dotted line in the 500-ms panel and by the open circles in the 200-ms panel; these circles indicate the score obtained on 5 separate tests at the maximum speaker separation of 80°. Because F9670 did not perform above chance with 200-ms noise bursts, this ferret was not tested at 40 ms.](http://jn.physiology.org/DownloadedFrom)
formed as well as the normals, whereas in others the differences were dependent on a number of factors such as speaker location, stimulus duration, or experience.

Effect of stimulus duration on performance in the absolute localization task

Stimulus duration was a significant factor in the performance of both groups of ferrets. Performance declined as the duration of the stimulus was reduced. Figure 9A presents the percent correct responses at stimulus durations of 1,000, 500, 200, 100, and 40 ms for the normal group and pinnae-removed group, pooled across all speaker locations for the first of the four blocks of trials. Clearly, both groups had little difficulty in accurately localizing the source of stimuli that were either 1,000 or 500 ms in duration, although the performance declined at shorter durations. Figure 9B-F shows the percent correct responses for the pinnae-removed group and the normal group at each of the 12 speaker locations. Each radial plot presents results from tests using a different stimulus duration.

A repeated measures ANOVA (group × position, within subject factor duration) was used to analyze these data. The main effect of duration was highly significant \[ F(4, 45) = 178, P < 0.001 \]. Bonferroni comparisons of the mean percent scores showed that every decrease in stimulus duration, except between 100 and 40 ms, resulted in a significant degradation in performance (\( P < 0.001 \)).

The interaction between duration and group was not significant \[ F(4, 45) = 1.846, P = 0.137 \], but the interaction between stimulus duration and location was significant \[ F(11, 48) = 4.356, P < 0.001 \]. When ferrets were tested with a 1,000- or a 500-ms stimulus, there was no difference in performance due to the location of the sound source. However, variations in performance at the different spatial locations began to emerge at the three shortest stimulus durations and were most pronounced at 100 and 40 ms. There was also a significant interaction between the factors duration, group, and location \[ F(11, 48) = 2.297, P = 0.024 \]; at the three shortest durations, location-dependent differences between the groups emerged.

It is clear from these results that the duration of the stimulus is an important factor in determining performance in this sound localization task. Further discussion of the differences between the normal and pinnae-removed ferrets will be made in the context of the improvement in localization performance that was observed over the course of testing.

Contribution of head movements to auditory localization

Because stimulus duration had a marked effect on the performance of both groups of ferrets, we measured the latency from stimulus onset to the initiation of target-directed head movements. A video frame contrast detection device sampling at a rate of 50 Hz (VP 2000, HVS Image, UK) was used to...
make these measurements. We found that the mean ± SD latency was 186 ± 76 ms (170 trials) for normals and 205 ± 64 ms (180 trials) for pinnae-removed animals. Head motion cues therefore cannot assist the ferrets in localizing brief sounds of 40 or 100 ms in duration and probably contribute little, if anything, to the performance of the animals at 200 ms. These cues could, however, influence the localization of stimuli longer than 200 ms in duration. Moreover, our measurements suggest that localization of stimuli of 1,000 ms in duration might benefit from the ferret actually leaving the platform and following the sound source through an intensity gradient.

**Improvement in performance with further testing**

Our data were collected from four blocks of testing trials. Within each block, ~300 trials at each of the five durations were collected. Over the course of the experiment, both groups of ferrets showed a noticeable improvement in performance, particularly at the shortest stimulus durations. To eliminate any confounding effects of head movements, we have concentrated here on how the performance of both groups of ferrets changed over the four testing blocks for the tests using a 40-ms stimulus. We performed separate repeated measures analyses of variance for each of our three localization indices. The between-subjects factors were group and speaker location and the within-subjects factors were stimulus duration and testing block.

**CORRECT RESPONSES.** The improvement in correct responses is shown in Fig. 10. Pooling the data shows that, overall, the proportion of correct responses increased over the four blocks [\(F(3, 46) = 18.710, P < 0.001\)]. Most of the improvement that was observed occurred between the second and third blocks. The interaction between block and speaker location was significant [\(F(11, 48) = 4.028, P < 0.001\)] and was due to an improvement in performance in the most anterior and posterior regions. No significant improvement in performance was found at the lateral locations.

The higher order interactions show that the improvement in performance was dependent on speaker location and stimulus duration. Although there was no significant interaction between the factors block, group, and location [\(F(11, 48) = 1.951, P = 0.056\)], the overall interaction between the factors block, group, location, and duration was significant [\(F(12, 47) = 5.039, P < 0.001\)]. Only at the shorter stimulus durations were significant variations observed, and these differences will be described for the 40-ms data.

The normal group showed an improvement in performance at 0°, 30°, and 60°. At 0° and 30°, the improvement in performance was manifest between the first and second blocks, whereas, at 60°, the performance improved after the second block of trials. The pinnae-removed ferrets also showed an improvement in the frontal sound field, although this appeared to occur more gradually. At 0° the improvement was shown between the second and third blocks of trials, whereas, at 30°, it was apparent only between the first and fourth block of trials. At 60° and 330°, the performance in the first and second blocks differed from that in the fourth, but not the third block.

Although both groups exhibited an improvement at several locations, there is some evidence that they did so at a different rate. This effect is clearer when one compares the performance of the groups in each block. At 0°, there was no difference between the groups in the first block of trials, but by the second block of trials the normal ferrets had improved and performed significantly better than the pinnae-removed group. However, the pinnae-removed group subsequently improved and scored equally as well as the normal group in the third and fourth blocks. At 180°, both groups showed a similar improvement in performance, particularly between the first and second blocks of trials, and at no stage did we observe a group difference in their scores. Nevertheless, throughout the course of the experiment, the normal ferrets tended to make more correct responses at most speaker locations than the pinnae-removed ferrets. Indeed, significant differences between the groups were noted at two of the speaker locations in three of the four testing blocks, as indicated in Fig. 10.

![Fig. 10. Improvement in percent correct responses with training.](https://example.com/fig10.png)
ACCURACY OF RESPONSES IN THE ABSOLUTE LOCALIZATION TASK. As with the percent scores, the pinna-removed ferrets initially made significantly larger localization errors than the normals at several speaker locations. These group differences occurred with stimulus durations of ≤500 ms, although the stimulus locations at which significant differences were found varied with the duration of the stimulus.

Overall, the accuracy with which both groups of ferrets responded improved over the course of the experiment [F(3, 46) = 25.927, P < 0.001]. The variation in error magnitude with stimulus location is shown for 40-ms noise bursts and for each of the four testing blocks in Fig. 11. In both groups, there was a tendency for the size of the errors to decrease with practice, and paired comparisons indicated that most of the improvement in performance occurred between the second and third blocks. The interaction between the factors block and location was significant [F(11, 48) = 2.959, P = 0.005] and reflected the fact that performance at the frontal and rear locations significantly improved, whereas no change was observed at the lateral positions.

The overall interaction between the factors block, group and location was significant [F(11, 48) = 2.545, P = 0.013], indicating that the improvement shown by the groups differed as a function of both speaker location and testing block. Error magnitude declined in both groups, although a more marked improvement was shown by the pinna-removed group. In fact, the normals showed a significant improvement at 0° only, whereas the pinnae-removed group made significantly smaller errors at all anterior locations except 30 and 60°, and also showed a significant improvement at 180 and 210°. Significant intergroup differences were present at several anterior and posterior speaker locations for the first and second testing blocks. However, the improvement shown by the pinnae-removed group was such that by the fourth block, aside from one location on the right side, their performance could not be distinguished statistically from that of the normal group.

FRONT-BACK ERRORS. As expected from their more symmetrical pattern of spectral localization cues, the pinnae-removed ferrets made significantly more front-back errors than the normal ferrets. In keeping with other localization studies, these errors were defined as responses made when stimuli originating in the anterior sound field were mislocalized into the ipsilateral posterior sound field and vice versa. For these measurements, stimuli presented at or responses made to either 90 or 270°, which lie on the interaural axis, were ignored. Few front-back errors were made by either group of ferrets with stimulus durations of 1,000 or 500 ms. However, both normal and pinnae-removed ferrets made increasingly more front-back errors as the duration of the stimulus was reduced. As we have done with the other measures of performance, we will describe these data for the 40-ms stimulus duration only.

Figure 12 shows the proportion of front-back errors made by the two groups at each speaker location for each of the four testing blocks. In the first block of trials there were no locations at which the pinnae-removed ferrets made significantly more front-back errors compared with the normal ferrets. Differences between the two groups began to emerge in the second block of trials, with the pinnae-removed ferrets making significantly more front-back errors than the normal ferrets at 0 and 150°. These differences arose as a result of an increase in the incidence of front-back errors made by the pinnae-removed ferrets, relative to their performance in the first block of trials, rather than an improvement by the normal group. With subsequent testing, the performance of the normals did improve, particularly in the posterior hemifield, and, in the third and fourth testing blocks, these animals made very few front-back errors at any location. The pinnae-removed ferrets also showed some improvement in front-to-back errors, but continued to make a high proportion of back-to-front errors. Indeed, these animals made significantly more front-back errors than the normals at several posterior speaker locations in both the third and fourth testing blocks (Bonferroni tests, P < 0.05).

Thus in keeping with the improvement observed with the other measures of localization performance, both groups made fewer front-back errors with practice. A much greater improvement was shown, however, by the normal animals. This suggests that the
normal animals are able to resolve front-back confusions arising from binaural cues, probably through the use of pinna-based cues, and that they become better at making this discrimination compared with the pinnae-removed animals.

**Influence of Testing Procedure.** Our testing procedure was changed slightly after the second testing block, with the introduction of a variable delay at the center spout and the removal of the head-positioning grid. However, subsequent testing suggested that the improvement in the performance of the ferrets could not be attributed to these changes. After completion of the fourth testing block, two pinnae-removed ferrets were each tested using the two methods at stimulus durations of 200, 100, and 40 ms. The ferrets were tested over 4 100-trial sessions at each of these durations, and we alternated the testing method. There was no evidence to suggest that the method of testing the animals affected their performance. In comparing the two methods, we found that the percent scores at each of the speaker locations were significantly correlated (Spearman’s rho correlation coefficients; 200 ms, \( r = 0.7217, P = 0.007 \); 100 ms, \( r = 0.825, P = 0.001 \); 40 ms, \( r = 0.720, P = 0.008 \)). Further, there was no significant difference between the mean scores using the two testing methods \( F(1, 4) = 2.951, P = 0.161 \). It should also be pointed out that both groups of ferrets were tested in exactly the same manner. Any improvement shown by one group due to the altered procedure should also have been seen in the other group.

**Discussion**

This study examined the behavioral consequences of bilaterally removing the pinna and concha of the external ear in infancy. When these animals were trained and tested in adulthood, we observed deficits in their ability to localize broadband sounds, both in the horizontal plane, where spectral localization cues have traditionally been thought to play a minimal role, and in the midsagittal plane, where spectral cues are thought to play a major role in sound source localization.

Acoustical measurements were taken from several of the pinnae-removed ferrets after the behavioral study. These measurements confirmed that bilateral pinna and concha removal severely disrupts spectral cues. Compared to the HRTFs of normal ferrets (Carlile 1990; Carlile and King 1994), the HRTFs of the pinnae-removed ferrets showed fewer directional features. Thus, the behavioral results produced by the pinnae-removed ferrets can be interpreted in terms of impoverished spectral localization cues. Indeed, the extent of the deficit seen in the midsagittal plane appeared to be correlated with the extent to which their spectral cues were degraded. In terms of the accuracy of responses on the absolute localization task, the differences between the two groups were most apparent during the initial stages of testing, suggesting that, with practice, the pinnae-removed ferrets can learn to utilize the remaining localization cues more effectively.

**Localization in the horizontal plane**

The HRTFs of normal ferrets show several location-dependent features, which are altered or removed by pinna removal (Carlile and King 1994; Schnupp et al. 1998). A prominent feature of the ferret’s HRTF is the asymmetric gain in signal transmission with respect to the interaural axis. Mid- to high-frequency sounds originating from ipsilateral locations in front of the interaural axis are associated with positive gains of up to \( \sim 12 \) dB and a location-dependent notch, where the transmission gain is reduced over a narrow frequency band. In contrast, midfrequency sounds located well behind the interaural axis have a negative gain. Carlile and King (1994) speculated that this azimuthal asymmetry probably aids in resolving front-back ambiguities in binaural localization cues. Indeed, our results clearly show that pinnae-removed animals make significantly more front-back errors compared with normal animals. This is presumably due to the relative absence of asymmetric features about the interaural axis in both the monaural and binaural spectral cues available to these animals.

As shown in other studies (e.g., May and Huang 1996; Mills 1958; Oldfield and Parker 1984b; Rauschecker and Kniepert
we found that the localization performance of the normal ferrets was best in the frontal sound field and declined at more lateral locations. It has been suggested that the dependence of performance on sound source location may reflect either the availability of certain spectral features, such as the midfrequency notches seen in the cat’s HRTFs for anterior sound locations (Huang and May 1996a; May and Huang 1996), or the rate at which these features change as a function of sound source location (Carlile 1990). Thus accurate head-orienting responses by cats to sound sources in the frontal sound field are observed only when the stimulus bandwidth includes frequencies between 5 and 18 kHz, the region containing the spectral notches (Huang and May 1996a).

Compared with those measured in the cat, ferret HRTFs include a less prominent spectral notch that increases in center frequency as the sound source is moved away from the anterior midline. This feature is eliminated by removal of the pinna and concha (Figs. 2 and 3) (see also Carlile and King 1994; Schnupp et al. 1998). Our present data show that, at least during the early stages of our absolute localization experiment, pinnae-removed ferrets localize broadband sounds significantly less well than normal animals in this region of space, lending support to the hypothesis that location-dependent spectral features are an important aid to the localization of frontal sound sources (Huang and May 1996a; Rice et al. 1992). The contribution of spectral cues is not, however, restricted to regions of space in which the HRTFs contain notches. We found that normal ferrets were also better able than the pinnae-removed animals to localize sounds in the posterior hemifield. This suggests that other spectral features, such as the negative transmission gain centered on 15–16 kHz, which is also eliminated by pinna removal, may play a significant role in the localization of sound sources behind the animal. Further support for the existence of salient spectral localization cues throughout the horizontal plane is provided by the presence at near-threshold sound levels of normal maps of sound azimuth in the SC of monaural guinea pigs (Palmer and King 1985) and ferrets (King et al. 1994). Given the recent finding that the perception of an externalized sound source resulting from the presentation of virtual auditory space stimuli over ear phones to human listeners becomes degraded only after considerable smoothing of the HRTFs (Kulkarni and Colburn 1998), it seems likely that the most prominent peaks and valleys rather than the fine structure of the spectral cues contribute to auditory localization.

In estimating localization accuracy in the horizontal plane, we excluded front-back errors because we thought it more informative to describe their occurrence separately. However, apparent front-back errors made close to the interaural axis may actually have been a component of normal error variance (Wightman and Kistler 1997). Thus, in removing front-back errors, we may have masked the difference between the groups. This aside, it is notable that even without the contribution of front-back localization errors, the pinnae-removed group performed significantly less well, particularly during the early stages of the experiment, than the normal group in making absolute localization judgments in the horizontal plane.

The finding that pinna-based cues provide an important contribution to azimuthal localization that goes beyond the resolution of front-back confusions is also seen in humans. Occluding the convolutions of the external ears (Musicant and Butler 1984) or filtering particular frequency components on the basis of the HRTFs (Butler and Musicant 1993) degrades localization performance in the horizontal plane, even though ITD and ILD cues are still available.

Our results for relative localization, in which the ferrets were required to discriminate between two sound-source locations, showed that pinnae-removed ferrets were not deficient in this task compared with normal ferrets. Thus residual binaural cues appear to be sufficient for this spatial acuity task, which is not surprising given that symmetrical discriminations about the interaural axis were not required. It is also likely that the absolute localization task was more demanding in that the ferrets had a number of different response choices to make (Perrett and Noble 1995), whereas for the midline MAA task, the required decision was simply to respond to the left or the right. By examining the effects of varying the frequency composition of noise stimuli on sound localization, Huang and May (1996a,b) also concluded that spectral cues provided by the external ears are more important for tasks that require cats to identify the absolute location of sound sources than for their ability to detect small differences in stimulus location within the horizontal plane.

Localization in the midsagittal plane

Although most studies of mammalian auditory localization have assumed that the ears are relatively symmetrical, there are reports of small asymmetries in humans (Carlile and Pralong 1994; Middlebrooks et al. 1989; Searl et al. 1975) and guinea pigs (Hartung and Sterbing 1997). Consequently, both monaural and binaural spectral cues may be available for localizing sound sources in the midsagittal plane. The HRTFs recorded in this study from an animal with intact pinnae suggest that this may be the case in ferrets as well. We found that, when a 500-ms stimulus was used, the pinnae-removed ferrets performed nearly as well as the normal ferrets in the midsagittal plane task, but performed comparatively poorly at shorter stimulus durations. In fact, one of these animals failed to achieve scores that were above chance level at the maximum speaker separation used when tested with 200-ms noise bursts. The other pinnae-removed ferret performed slightly better, but still only attained P75 values that were close to the largest of the speaker separations. Both pinnae-removed ferrets exhibited fewer location-dependent features than the normals in their midsagittal plane spectral cues and particularly in the spatial pattern of interaural spectral differences. Indeed, no clear features were apparent in the interaural spectral differences for the ferret that was unable to localize shorter duration stimuli in the midsagittal plane, suggesting that the performance of these animals might be correlated with the degree to which the pinna-based localization cues had been altered.

Adaptation to altered localization cues

Other studies that have altered normal localization cues during development have shown behaviorally and physiologically that some degree of adaptation to abnormal localization cues can occur. For example, barn owls (Knudsen 1984a) and ferrets (Parsons et al. 1999) reared with one ear plugged can...
develop near normal localization ability. Similarly, in these species, the auditory space map in the optic tectum of the barn owl (Knudsen 1985) and the SC of the ferret (King et al. 1988) is able to align reasonably closely with the map of visual space, even when these animals are reared with abnormal binaural cues produced by an ear plug. In contrast, if spectral localization cues are altered in infancy by pinna and concha removal, normal topographic order in the representation of auditory space in the ferret SC fails to develop (Schnupp et al. 1998). The present study suggests that, unless they are given adequate training, ferrets also have a limited capacity to adapt behaviorally to impoverished spectral localization cues during development.

Another study that investigated the effects of altering spectral localization cues was performed on adult chinchillas. Heffner et al. (1996) compared the sound localization ability of adult chinchillas before and after bilateral or unilateral pinna removal. Their study did not address possible compensations in localization mechanisms. The greatest deficits shown by the pinnae-removed chinchillas were found in their ability to make front-back discriminations and to make discriminations in the midsagittal plane. Heffner et al. (1996) found no effect on the ability of the chinchillas to make left/right discriminations in the anterior horizontal plane, but did report a small decrement in performance in another test using a fixed angle of speaker separation. Overall, their results are very similar to ours and support the notion that little adaptation to the altered spectral localization cues has taken place in ferrets in which the pinna and concha were removed bilaterally in infancy.

Adaptation to altered spectral localization cues has, however, recently been shown to occur in adult humans (Shinn-Cunningham et al. 1998; Hofman et al. 1998). Shinn-Cunningham et al. (1998) presented altered HRTFs over headphones, which accentuated cue differences for locations in front of the subject and degraded those from peripheral locations. Initially, localization performance was superior at frontal locations and poorer at peripheral locations, although these listeners were able to adapt rapidly, to some extent, to the new localization cues. Hofman et al. (1998) fitted ear molds in the external ears of adult listeners and measured free-field localization. As expected, immediate disruptions in vertical localization were measured, whereas horizontal localization within the oculomotor range was unimpaired. After several weeks of wearing the ear molds, elevation performance returned to near normal levels, suggesting that these individuals had adapted to the new cues.

A partial neurophysiological adaptation to the altered spatial cues produced by modifying the external ear structures has been observed in barn owls. Removal of the facial ruff and preaural flap changes the spatial locations corresponding to particular ILD and ITD values. This procedure is followed, both in juvenile and adult birds, by an adaptive change in the representation of these cues in the optic tectum, which tends to reestablish a correspondence between the auditory and visual representations in this nucleus (Knudsen et al. 1994).

These studies clearly demonstrate that plasticity in the neural representation of spectral localization cues is present in both the developing and mature auditory system. Nevertheless, there is likely to be a limit on the capacity of the auditory system to accommodate changes in these cues (King 1999). In the experiments by Shinn-Cunningham et al. (1998) and by Hofman et al. (1998), subjects were required to form new spatial associations with a different set of spectral cues to regain localization proficiency. Our experiments were, however, based on a much greater range of azimuthal sound locations and examined the consequences of a more severe disruption of spectral localization cues. For example, by making these cues spatially ambiguous about the interaural axis, we appear to have limited any acoustical basis by which the ferrets could resolve front-back confusions.

**Improvement in performance in the absolute localization task**

Overall, the pinnae-removed ferrets performed poorly on the absolute localization task compared with the normal ferrets. Over the course of the experiment, both groups showed a significant improvement in their performance. This can clearly be seen when comparing the results of the first block of testing trials with the last block of testing trials (Figs. 10–12). In the first block of trials, localization accuracy (Fig. 11) was poorer in the pinnae-removed animals, whereas, in the last block, intergroup differences were less evident. Thus the degree of improvement in localization performance and the rate at which it occurred appeared to differ for the two groups.

Performance in a variety of sensory discrimination tasks has been reported to improve with practice (Gilbert 1998). Because both groups of ferrets received a comparable period of training and were tested in exactly the same manner, it is unlikely that the relatively greater improvement in localization accuracy exhibited by the pinnae-removed ferrets can be attributed to a difference in the way they learned the acoustical characteristics of the testing chamber. Moreover, as the improvement was observed with 40-ms noise bursts, the pinnae-removed ferrets could not have benefited more from head movements, which in ferrets have a latency of >100 ms following stimulus onset. Although a comparable improvement in performance by the normal ferrets was found at all speaker positions, the pinnae-removed ferrets showed a greater improvement in the anterior sound field than for other regions of space. The pinnae-removed ferrets even showed some reduction in front-back errors within the anterior hemifield, although they continued to mislocalize anterior source sounds to the posterior hemifield slightly more than the normals. These animals did develop a response bias toward anterior locations in the last two blocks of trials, although it is unlikely that this fully accounts for their reduction in front-to-back errors because we observed no corresponding increase in back-to-front errors.

Despite the impoverished spectral cues available to the pinnae-removed ferrets, which appear to account for the overall difference in performance between the two groups, these animals may have learned to utilize subtle spectral cues, including those produced from reflections off the body or parts of the testing apparatus, or to make relatively greater use of residual binaural cues. Given that the improvement in performance was observed with repeated testing, our results appear to highlight the importance of training in promoting an adaptation to altered localization cues.

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REFERENCES

BLAUERT, J. Sound localization in the median plane. Acustica 22: 205–213,
1969.

BRAINARD, M. S. Neural substrates of sound localization. Curr. Opin. Neuro-

BUTLER, R. A. AND MUSICANT, A. D. Binaural localization: influence of
stimulus frequency and the linkage to covert peak areas. Hear. Res. 67:

CARLILE, S. The auditory periphery of the ferret. II. The spectral transfor-

KNUDSEN, E. I., ESTERLY, S. D., AND KNUDSEN, P. F. Monaural occlusion alters
sound localization during a sensitive period in the barn owl. J. Neurosci.

Knudsen, E. I. Experience alters the spatial tuning of auditory units in the optic
tectum during a sensitive period in the barn owl. J. Neurosci. 5: 3094–3109,
1985.

Knudsen, E. I., Esterly, S. D., AND Knudsen, P. F. Monaural occlusion alters
sound localization during a sensitive period in the barn owl. J. Neurosci.

Knudsen, E. I., Esterly, S. D., AND Olsen, J. F. Adaptive plasticity of the audi-

Knudsen, E. I., Esterly, S. D., AND Olsen, J. F. Adaptive plasticity of the audi-

Knudsen, E. I., Knudsen, P. F., AND Esterly, S. D. A critical period for the recov-

Kulkarni, A. AND COBURN, H. S. Role of spectral detail in sound-source

May, B. J. AND HUANG, A. Y. Sound orientation behavior in cats. I. Local-

MIDDLEBROOKS, J. C. Binaural mechanisms of spatial tuning in the cat’s

MIDDLEBROOKS, J. C., MAKOUS, J. C., AND GREEN, D. M. Directional sensitivity
of sound-pressure levels in the human ear canal. J. Acoust. Soc. Am. 86:

1938.

MOORE, D. R. AND HINE, J. E. Rapid development of the auditory brainstem

MUSICANT, A. D. AND BUTLER, R. A. The influence of pinnae-based spectral

MUSICANT, A. D., CHAN, J. C. K., AND HIND, J. E. Direction-dependent spectral

OLDFIELD, S. R. AND PARKER, S. P. A. Acuity of sound localization: a topogra-
phy of auditory space. II. Pinna cues absent. Perception 13: 600–617,
1984a.

OLDFIELD, S. R. AND PARKER, S. P. A. Acuity of sound localization: a topogra-
600, 1984b.

PALMER, A. R. AND KING, A. J. A monaural space map in the guinea-pig

infancy on sound localization in ferrets. Assoc. Res. Otolar. Abstr. 21:

localization in the ferret: adaptation to chronic monaural occlusion during

PERRETT, S. AND NOBLE, W. Available response choices affect localization of

RAUSCHECKER, J. P. AND KNIEPERT, U. Auditory localization behaviour in


ROFFLER, S. K. AND BUTLER, R. A. Factors that influence the localization of

cues disrupt the development of the auditory space map in the superior

SEARLE, C. L., BRAIDA, L. D., CUDDEY, D. R., AND DAIVIS, M. F. Binaural pinna
455, 1975.

SHAW, E. A. G. Transformation of sound pressure level from the free field to the

SHINN-CUMMINGS, B. G., DURLACH, N. I., AND HELD, R. M. Adapting to

SLATTERY, W. H., III, AND MIDDLEBROOKS, J. C. Monaural sound localization:
supernormal versus chronic unilateral impairment. Hear. Res. 75: 38–46,
1994.

WIGHTMAN, F. L. AND KISTLER, D. J. Monaural sound localization revisited. J.

WILMINGTON, D., GARY, L., AND JAHRSDOERFER, R. Binaural processing after
corrected congenital unilateral conductive hearing loss. Hear. Res. 74:

WISE, L. Z. AND IRVINE, D. R. F. Topographic organization of interaural inten-
dity differences sensitivity in deep layers of cat superior colliculus: impli-
cations for auditory spatial representation. J. Neurophysiol. 54: 185–211,
1985.

ZHOU, B., GREEN, D. M., AND MIDDLEBROOKS, J. C. Characterization of
external ear impulse responses using Goly codes. J. Acoust. Soc. Am. 92: