Sound localization acuity in the cat:
Effect of azimuth, signal duration, and test procedure

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The sound localization acuity of cats was determined at $0°$, $30°$, $60°$, and $90°$ from the median sagittal plane for four durations of noise bursts using two behavioral procedures. Similar thresholds were also obtained for humans. The cats' average thresholds for a 40 ms noise burst ranged from $4.8°$ at $0°$ azimuth to $9.0°$ at $90°$ azimuth. Comparable thresholds for humans ranged from $1.3°$ at $0°$ to $9.7°$ at $90°$. The fact that humans and cats had similar thresholds at $90°$ azimuth suggests that the mobile pinnae of the cat are not an advantage in localizing sound in the lateral fields. Varying the duration of the stimulus from 10 ms to 'continuous' had little effect on threshold. No difference was found between the results of the two behavioral procedures.

Introduction

The domestic cat has long been used in the study of the anatomy and physiology of the central auditory system (for a recent review, see Phillips and Brugge, 1985). Information gained from the study of the cat has indicated that sound localization plays an important role in the auditory system. Not only is much of the central auditory system sensitive to the locus of a sound, but a map of auditory space is integrated with visual and somatosensory spatial information in the multimodal regions of the superior colliculus (e.g., Meredith and Stein, 1986; Phillips and Brugge, 1985).

Because of the growing interest in the neurophysiology of sound localization, attention has turned to the fact that the cat possesses mobile pinnae which may significantly affect the physical cues available for localizing sound. Although the pinna seems to have little effect on interaural time

differences (Roth et al., 1980), its directionality results in a strong effect on interaural intensity differences especially at high frequencies (Calford and Pettigrew, 1984; Irvine, 1987; Middlebrooks and Knudsen, 1987; Middlebrooks and Pettigrew, 1981; Phillips et al., 1982). This feature of the cat's pinna has been implicated in the generation of the axial receptive fields in auditory cortex and the inferior colliculus (Middlebrooks and Pettigrew, 1981; Semple et al., 1983). It has even been suggested that the presence of a conical mobile pinnae could enhance the spatial selectivity of central auditory neurons and, by implication, improve localization acuity (e.g., Brown et al., 1982; Gourevitch, 1980; Jeffress, 1975; Phillips and Brugge, 1985). The presence of a map of pinna orientation in register with the sensory spatial maps in the superior colliculus supports the possibility of participation of mobile pinnae in sound localization (Stein and Clamann, 1981).

There is at present no behavioral evidence that the cat's mobile pinnae enhance its ability to localize sound. In the standard test of sound localization acuity, which involves discriminating sound sources located directly in front of the subject, cats have either the same or less acuity

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than animals with nonmobile pinnae such as monkeys and humans (Brown et al., 1982; Martin and Webster, 1987; Mills, 1958). However, binaural locus cues are maximally effective for frontal sound localization and their use may mask a contribution from mobile pinnae. On the other hand, it is not impossible that mobility could actually reduce frontal localization acuity by requiring that the system analyzing interaural differences make additional calculations in the form of direction-dependent adjustments for the effect of the pinnae on the sound reaching the ears, just as the visual system takes into account the position of the eyes in their sockets when interpreting the spatial location of an object imaged on the retina (Matin, 1972).

There are at least two situations in which mobile pinnae might enhance sound localization acuity. The first involves localization of sound in the lateral fields, a situation in which binaural cues are less effective. Research on the human pinna has demonstrated that pinna cues play a significant role in localizing sounds emanating from sources located off to the side (e.g., Musicant and Butler, 1984). Given that even the nonmobile pinnae of humans is important for lateral sound localization, then cats, which presumably can direct their pinnae to optimize the available pinna cues, might be more adept than humans in localizing lateral sound sources.

A second situation in which mobile pinnae might prove advantageous is in the localization of long duration sounds. Because cats rapidly orient their pinnae towards the source of a sound (e.g., Thompson and Masterton, 1978), they may be more accurate in localizing sounds which remain on long enough for them to complete their orienting response as opposed to shorter duration sounds which do not permit scanning.

In order to gain more information on the localization ability of an animal with mobile pinnae, the sound localization acuity of the cat was determined for lateral portions of the frontal quadrant (where binaural cues decrease progressively) and in front/back discriminations (where binaural cues are eliminated) using wide-band noise bursts of various durations. Because there exist no comparable data on localization acuity for a broadband noise at lateral positions for a species with

good localization acuity and non-mobile pinnae, thresholds were also obtained for four human observers for comparison with the cat. Finally, we took this opportunity to compare thresholds obtained with both a two-choice identification procedure and an avoidance detection procedure to determine whether thresholds are influenced by the procedure used to obtain them.

Methods

Subjects

Four cats, two females (cats A and D) and two males (cats B and C), were used in these tests. Complete audiograms for cats A, B, and C and a partial audiogram for cat D had been obtained previously (Heffner and Heffner, 1985, 1987). The animals were housed together in rooms with free access to water. Food was used as a reward and was available only in the test sessions. The animals were weighed daily to monitor their deprivational state.

The external auditory canals of all cats were examined otoscopically and found to be free of any signs of parasites and disease. In addition, their previously determined auditory thresholds indicated normal hearing.

Four humans, three males and one female, ranging in age from 13 to 42 years were also tested. None had a history of auditory or neural disease and all had normal hearing except for a mild loss above 12 kHz in the right ear (subject A) and above 16 kHz in the right ear (subject D).

Behavioral apparatus

Two-choice. Two-choice testing was conducted in a double-walled acoustic chamber (IAC) 2.55 × 2.75 × 2.05 m the walls and ceiling of which were covered with eggcrate foam. An adjacent control room housed the behavioral control and stimulus general equipment and the animals were observed with a closed-circuit television system. The animals were tested in a cage constructed of 1.27-cm hardware cloth (67 × 31 × 41 cm) mounted on 77-cm legs. Three stainless steel response disks (2 × 3 cm) were mounted in a horizontal row 10 cm apart and 21 cm above the floor in the front of the cage. The disks were connected to separate sensing

switches which detected when an animal made contact with them. A small (3-cm diameter) receptacle for the food reward was located on the floor at the front of the cage. This receptacle was connected by plastic tubing to a 100-cc pump reservoir (Davis Scientific Instruments LR132), placed on the floor below the cage, from which small amounts (usually 0.5–1.0 cc) of meat puree were automatically dispensed for correct responses. A 50-watt light illuminated the test chamber and was turned off to signal time-out after errors. A doorbell buzzer was attached to the floor at the rear of the cage and served as an additional error signal.

Conditioned avoidance. Conditioned avoidance testing was conducted in the same apparatus except the three response disks and the food receptacle were replaced by a single food receptacle placed at nose level. The food receptacle also served as a response disk and was in the form of a shallow metal cup shaped to fit over a cat's muzzle. The reward consisted of a meat and vegetable puree dispensed through a tube up to the food receptacle by a worm drive from a 200-cc syringe located on the floor beneath the test cage.

Human testing. The tests with humans were conducted in the same acoustic chamber but the test cage was replaced by a chair and the response disk was replaced by a hand-held button. A subject was seated in a chair with his head centered in the perimeter bar and responded to the warning signals by pressing a hand-held response button.

Acoustic apparatus

Two-choice. Two-choice localization thresholds were determined for single bursts of broad-band noise of four durations: 10 ms, 40 ms, 100 ms and a 'continuous' noise which came on when the animal made an observing response and stayed on until the animal made a side response. The rationales for these particular durations are the following. The shortest practical stimulus was 10 ms. The 40-ms duration was chosen because it is the longest interval before scanning movements of the head and pinnae begin (Thompson and Masterton, 1978) and the 100-ms duration was chosen

because it allowed direct comparison to other species tested with that duration. The continuous stimulus allowed maximum listening time. A 'fast' (10-μs) rise-decay was used throughout. Broadband noise was produced by a noise generator (Grason Stadler 1285) then led through an electronic switch (Grason Stadler 1287), filter (Krohn Hite 3202), attenuator (Hewlett Packard 350D), impedance matching transformer, and finally to a matched pair of dual loudspeakers consisting of a 7.6 cm paper cone speaker mounted in a 500-cc enclosure and a piezoeletric tweeter with a 7.6-cm horn mounted directly above such that the centers of the speakers were 8.9 cm apart. The loudspeakers were mounted on a perimeter bar (102 cm radius) which was centered on the middle of an animal's head when it made an observing response.

This arrangement produced noise with peak intensity in the range of 3–50 kHz and an overall intensity of 69.5 dB SPL (linear scale) at the location of the animal's ears. The spectrum of the noise was measured with a 1/4-in (0.64 cm) Brüel and Kjaer microphone (B&K 4135) with the protective grid removed to obtain linearity, preamplifier (B&K 2618), measuring amplifier (B&K 2608), and band-pass filter (Krohn-Hite 3202). The microphone was placed in the center of the position normally occupied by an animal's head and oriented directly towards the loudspeaker. Measurements were taken at 1/6-octave steps (24 dB/octave attenuation) with the high- and low-pass filter settings at the same frequency (6 dB were added to each measurement to compensate for insertion loss). The resulting spectrum, shown in Fig. 1, shows that the double speaker arrangement produced a broad spectrum with a 30-dB rolloff between 200 Hz and 100 kHz.

For the threshold tests the angular separations used were 0°, 3°, 6°, 10°, 20°, 30°, 45°, and 60°. An azimuthal separation of 0° was achieved by placing the speakers one above the other which resulted in a vertical separation of 3° in the two-choice test and 2° with the smaller speakers in the conditioned avoidance test.

Conditioned avoidance. The conditioned avoidance test used the same noise generator led to a rise-decay gate (Coulbourn S84-08), attenuator
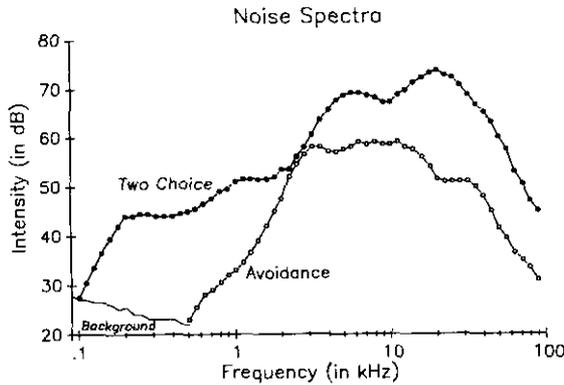
Fig. 1. Spectra of the noise stimuli used in the sound-localization tests and the measurable ambient background noise. (The dual speakers used in the two-choice test were chosen to produce a particularly broad spectrum in order to provide a maximally localizable stimulus in the initial tests. Cats were tested using both stimuli; humans were tested using the conditioned-avoidance stimuli.)

(Hewlett Packard 350D), amplifier (Coulbourn S82-24), mixer panel, and two matched 2.54-cm speakers (Koss P19 mini-stereo headphones). The speakers were mounted on the perimeter bar and produced noise of an overall intensity of 64 dB SPL (linear scale) with peak intensities between 2 and 32 kHz the spectrum of which is illustrated in Fig. 1. The Koss speakers were selected for their small size which facilitated testing at small angles of separation.

Human tests. The signal from the Grason Stadler noise generator (Grason Stadler 1287) was led to a programmable attenuator (Coulbourn S85-08), rise-fall gates (Coulbourn S84-04), a graphic equalizer to equate the spectra of the two loudspeakers (Symmetric Sound Systems, EQ-3), an amplifier (Crown D75), and finally to the same loudspeakers (Koss P-19) used for the conditioned avoidance test with cats. The acoustic signals from the two speakers were equalized (using a B&K 2203 sound level meter, B&K 4131 2.54 cm microphone, and B&K 1613 octave filter) before each test session to reduce the possibility of quality differences between the loudspeakers. The stimulus consisted of a single burst of noise 100 ms in duration and varying over a 7-dB range of attenuation. The unattenuated signal had an overall intensity of 65 dB SPL (A scale) and ranged

from 23 dB SPL at 500 Hz to 52 dB SPL at 20 kHz.

Psychophysical procedures

Two-choice. A hungry animal was trained to initiate a trial by touching the center observing disk with its nose. This 'observing response' served to center the animal's head and to trigger the presentation of a single noise burst from a loudspeaker to the left or right of the animal's midline. The animal was then rewarded by immediate delivery of approximately 0.5 cc of meat puree into the food receptacle if it touched the response disk on the same side as the active speaker. Touching the opposite response disk was followed by a short time out (usually 4 s, during which a doorbell buzzer sounded and the lights in the sound chamber were dimmed) before a new trial could begin. The sequence of left and right trials was determined by a quasi-random schedule (Gellermann, 1933). Side preferences were reduced by using a correction procedure in which the correct side was not changed following an error. These nonrandom correction trials were not used in the computation of performance.

Thresholds were estimated by giving blocks of 40–60 trials at successively smaller speaker separations until the animal could no longer distinguish between the two speakers above chance ($P < 0.01$ binomial distribution). Once threshold had been estimated, blocks of trials were given at angular separations above and below threshold until asymptotic performance was reached. The 50% detection threshold was defined as the angle producing 75% correct performance.

Cats A, B, and C were tested using the two-choice procedure. Thresholds were first determined for speakers centered around 0° azimuth (left/right discrimination) with noise durations of 10, 40, and 100 ms and continuous. Following midline testing, the speakers were moved to a location centered symmetrically around 90° to the animals' right and the animals were trained to make a left response to the leftmost (front) speaker and a right response to the rightmost (rear) speaker. Thresholds were determined for all three cats with stimulus durations of 10, 40, and 100 ms and continuous. Finally, cats B and C were tested
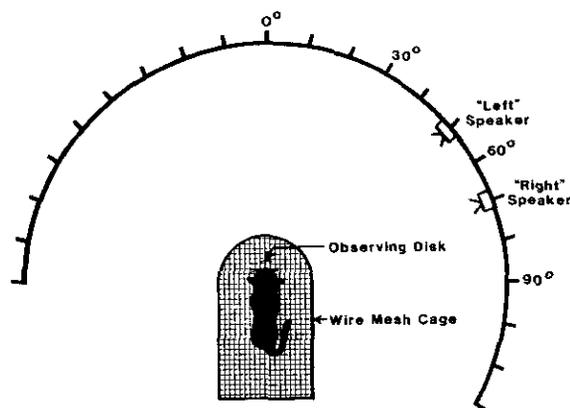
Fig. 2. Diagram of the apparatus for testing sound localization. (A subject in the observing position is centered in the perimeter bar. The four different azimuthal positions around which testing was conducted are indicated. The two speakers illustrate the positions for testing 20 ° separation around 60 °.)

at intermediate positions of 30 ° and 60 ° with a stimulus duration of 40 ms. Fig. 2 provides a diagram of the testing configuration.

Conditioned avoidance. Cats A and D were tested for left/right acuity (around 0 °) using a 100-ms stimulus and the conditioned avoidance procedure. A hungry animal was trained to lick steadily at a metal spout from which the meat-vegetable puree was dispensed at a rate of approximately 4 cc/min as long as the animal maintained contact with the spout. Once an animal had learned to maintain steady contact while a noise burst was emitted every 5 s from a speaker to its right, it was trained to break contact with the spout whenever the noise burst was emitted from a speaker to its left. This was accomplished by following the noise burst with a mild electric shock delivered through the spout. After a few pairings of left noise with shock, the cats learned to avoid the shock by breaking contact with the spout whenever they heard a noise from the left. In this way, breaking contact with the spout could be used as an indication of animal's ability to detect a shift in locus. To provide feedback for successful avoidance, a 50-Watt light in front of the animal was turned on during the shock delivery. To reduce the effect of spurious pauses, the results of a trial were automatically discarded if the animals was not in contact with the spout at any time during the 1 s

immediately preceding a trial, although the trial was presented as usual. Since this criterion was applied equally to safe and warning trials, it did not bias the results.

The test procedure consisted of presenting 2-s trials with a 1-s intertrial interval (i.e., one trial every 3 s). Each trial was either a 'safe' trial during which the noise burst came from the right of midline, or a 'warning' trial in which the noise burst came from the left of midline. Warning trials occurred randomly from 1 to 10 trials after the previous warning trial with the probability of a warning trial occurring being 0.22. No trial was given in the 3 s immediately following a warning trial in order to allow an animal sufficient time to return to the spout.

In order to quantify an animal's performance, the duration of spout contact was measured in 20-ms increments during the final 200 ms of the trial. This measured 'time-in-contact' was averaged separately for the safe trials (S) and the warning trials (W) for each angle of speaker separation tested. A measure of discrimination was then expressed in the form of $S - WS$ for each block of trials at each angle. In trained animals this measure varies from near zero (failure to detect the shift in locus) to 1.00 for perfect performance. In addition the exact probability that the two groups of scores, S and W, belong to the same population was determined for each block of trials at each angle (Mann-Whitney U, exact probability).

Thresholds were determined by reducing the angular separation between the speakers until the cats could no longer distinguish between them above a level expected by chance ($P < 0.01$). Trials were then given in blocks at angular separations above and below threshold until asymptotic performance was reached. The 50% detection threshold was defined as the angle producing a performance score of 0.50 which was determined by interpolation.

Human tests. The tests with humans were conducted using the same stimulus presentation procedure as the conditioned avoidance experiment. The subjects were instructed to listen for the locus of the sounds and to press the button only when they heard a sound from the left-most speaker. A

flash of light signaled the end of a left (warning) trial. A button press was scored as a response and responses during right (safe) trials were compared to responses during left (warning) trials. A performance ratio (S − WS) was computed for every angle of separation at every location and a psychophysical curve generated. Threshold was defined as a performance ratio of 0.50.

Results

Frontal sound localization acuity

Two-choice. Fig. 3 illustrates the ability of three cats to localize noise stimuli of 10 ms, 40 ms, 100 ms, and continuous durations. Overall the animals showed good performances at large angles of separation with performance declining rapidly at angles smaller than 10°.

With the possible exception of the shortest duration (10 ms) the duration of the stimulus had little effect on threshold. The thresholds of the animals at durations of 40 ms, 100 ms, and continuous were similar and ranged from 4° to 7° (Table I). The fact that thresholds for the continuous stimulus were not noticeably better may be due to the fact that the cats did not take the opportunity to scan the sound field, but responded rapidly – usually within 500 ms of stimulus onset. At 10 ms, the shortest duration

TABLE I

THRESHOLD AS A FUNCTION OF STIMULUS DURATION FOR SOUND SOURCES CENTERED AROUND 0°

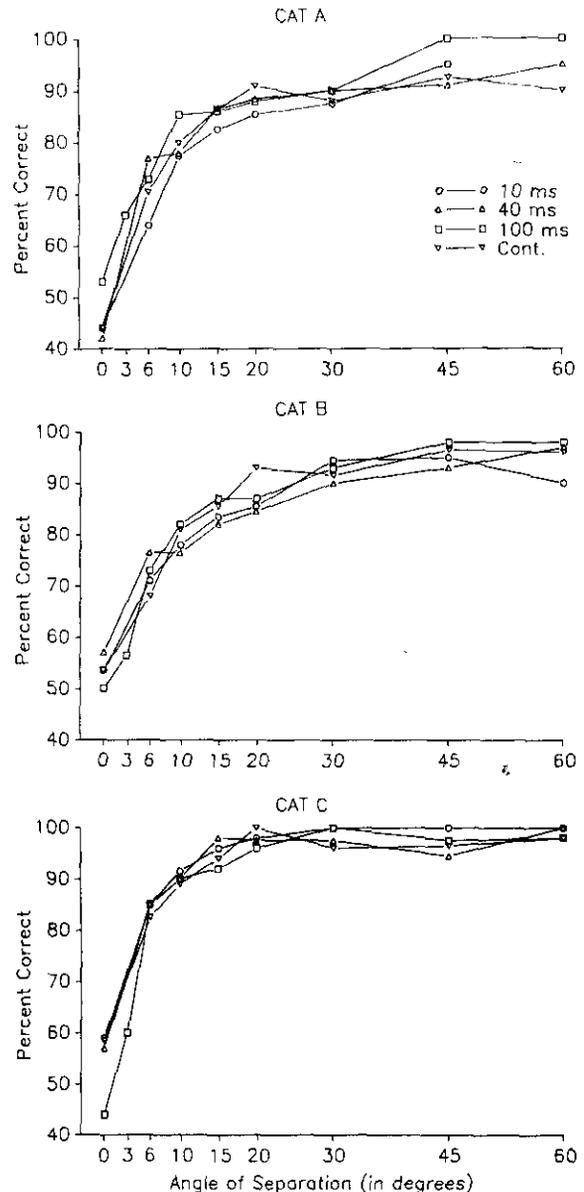|	Stimulus duration			
	10 ms	40 ms	100 ms	continuous
Two-choice:				
Cat A	9°	5.5°	6.5°	7°
B	8.5°	5°	7°	6°
C	4°	4°	4.5°	5°
Mean	7.2°	4.8°	6°	6°
Conditioned avoidance:				
Cat A	–	–	7°	–
D	–	–	4.5°	–
Mean	–	–	5.8°	–

Fig. 3. Sound-localization performance in a two-choice test for three cats discriminating between speakers centered around the midsagittal plane (0° azimuth) using four different stimulus durations.

used, thresholds increased for cats A and B to 9° and 8.5° respectively while cat C's threshold remained 4°. Thus, it appears that cats have little difficulty localizing brief sounds and that increasing the duration of the stimulus beyond 40 ms does not necessarily improve thresholds.
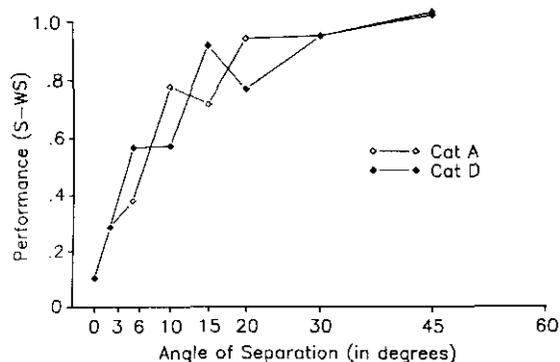
Fig. 4. Sound-localization performance in a conditioned avoidance test for two cats discriminating between speakers centered around the midsagittal plane (100-ms noise burst).

Conditioned avoidance. Approximately two years after the original testing, cat A served as a control animal along with a new cat, D, for comparison to albino cats in a sound localization test using the conditioned avoidance procedure (Heffner and Heffner, 1987). Fig. 4 illustrates their psychophysical curves for localization around 0° using a 100-ms noise burst. As shown in Table I, the conditioned avoidance task yielded thresholds virtually identical to those of the two-choice task.

In summary, there was no difference between the thresholds determined with a two-choice procedure and those determined with a conditioned avoidance procedure. This is despite the fact that two-choice uses only reward and presents equal numbers of left and right trials whereas conditioned avoidance uses both food reward and shock avoidance and presents approximately four times as many right trials as left trials. These results indicate that the thresholds obtained on these two tests are not peculiar to a particular procedure.

Lateral sound localization acuity

After testing was completed on the two-choice left-right discrimination around 0°, cats A, B, and C were shifted to the front-back discrimination in which the loudspeakers were centered around 90° on their right side. When the animals were first presented with this discrimination, they chose the right (as opposed to the left) response disk on every trial regardless of which speaker produced the sound. This pattern of responding 'right' on every trial suggested that in the previous task they

had been responding to the absolute locus of a sound source (i.e., left of midline vs. right of midline) and not to a relative difference in speaker position. Learning to respond differentially to front vs. back required 1 to 4 sessions and was accompanied by a sudden shift within a single session from 50% correct to nearly 100% correct. Following testing at 90°, cats B and C were also tested around 30° and 60°. It should be noted that, in contrast to macaques in a similar test (Brown et al., 1982), the cats never displayed tantrum behavior while being tested at any of these locations suggesting that the task was not unusually difficult for them.

Fig. 5 illustrates the performance and Table II lists the thresholds of cat A at the 0° and 90° positions and cats B and C at all four test positions using the 40-ms stimulus. There was a slight elevation in threshold as testing was conducted at the more lateral positions of 30° and 60° which was more marked in cat B than cat C. At 90° the slope of the psychophysical curves became more gradual and there was greater variability among the three individuals. Thresholds ranged from 6° to 12°, approximately double those for frontal localization for each individual. Thus, even though thresholds increased somewhat as testing was conducted at lateral azimuthal positions, the cats remained relatively accurate.

Cats A, B, and C were also tested using stimulus durations of 10 ms, 40 ms, 100 ms, and 'continuous' at the 90° position using the two-choice task. Performance on all four durations is illustrated in Fig. 6 and thresholds are given in Table III. There was a small effect of duration on the performance of cat A at large angles (Fig. 6a). Increasing the duration of the stimulus had no effect on the performance of either cat B or C.

TABLE II

THRESHOLD AS A FUNCTION OF AZIMUTH, 40-ms NOISE BURST

Azimuth:	0°	30°	60°	90°
Cat A	5.5°	–	–	12°
B	5°	10°	8.5°	9°
C	4°	5°	5°	6°
Mean	4.8°	7.5°	6.8°	9.0°

Similarly, there was no consistent improvement in threshold acuity with increasing stimulus duration as shown in Table III. When localizing around 90° only cat A was affected by stimulus durations shorter than 100 ms, whereas cats B and C showed little change (Table I). Thus, over the range of conditions examined, there was no dramatic or
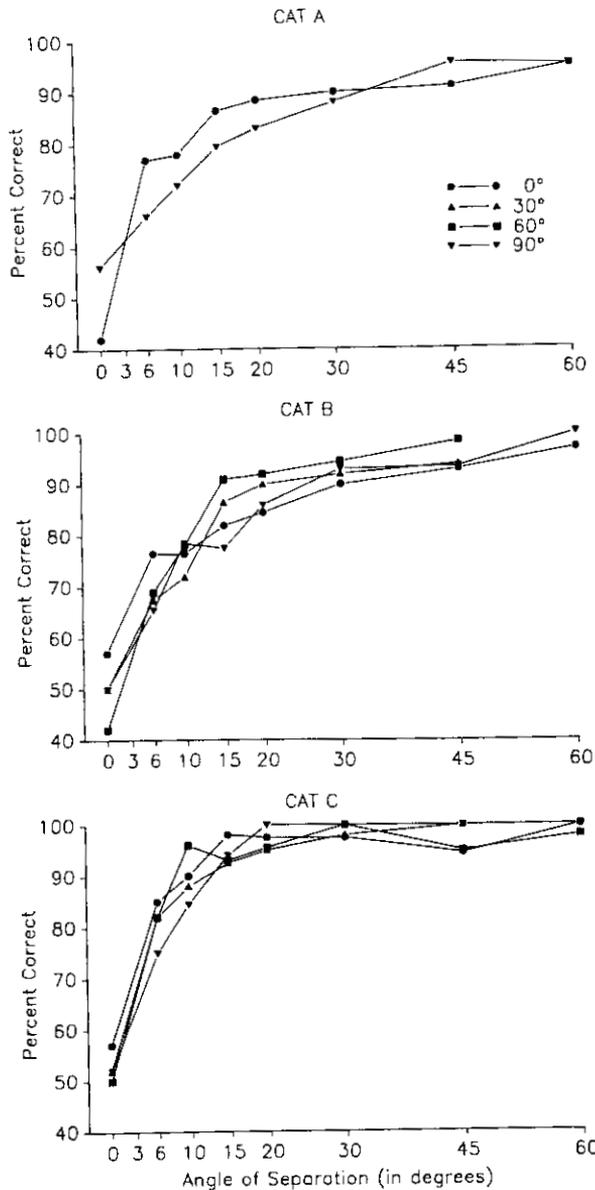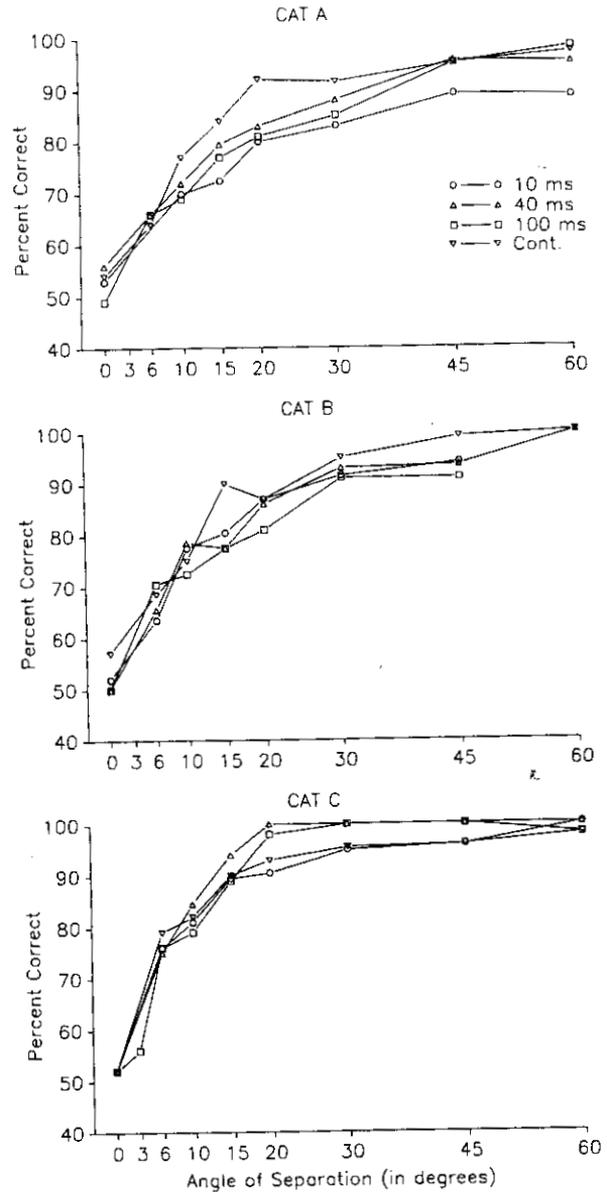

Fig. 6. Sound-localization performance in a two-choice test for three cats discriminating between speakers centered around the interaural line (90°) using four different stimulus durations.

consistent improvement in either performance at large angles or in threshold acuity attributable to increasing the duration of the stimuli.

Pinna movements

The position of the cats' pinnae during testing around 0° and 90° was observed via closed cir-

Fig. 5. Sound-localization performance at lateral azimuthal positions for three cats using a two-choice test (40-ms noise burst).

TABLE III

THRESHOLD AS A FUNCTION OF STIMULUS DURATION FOR SOUND SOURCES CENTERED AROUND 90°

| | Stimulus duration | | | |
	10 ms	40 ms	100 ms	continuous
Cat A	17°	12°	13.5°	9°
B	9°	9°	13°	10°
C	6°	6°	5.5°	5°
Mean	10.7°	9°	10.7°	8°

cuit television and several of the sessions were videotaped. Analysis of these sessions indicated that the animals consistently oriented their right pinna toward the speakers while localizing around 90° to their right. The position of the left pinna varied, sometimes being oriented symmetrically with the right and sometimes being oriented toward the front. This pinna orientation was in contrast to that observed when localizing around 0° in which the pinnae were both oriented frontally. Furthermore, there was very little pinna movement noted within trials. This lack of scanning may have been due to the predictability of the locations of the speakers since there were only two speaker locations used at a time.

Human tests

Table IV lists the sound localization thresholds for four humans at 0°, 30°, 60°, and 90° azimuth using a 100-ms burst of noise. Thresholds increased steadily as testing was conducted at increasing deviations from the mid-sagittal plane and thresholds at the 90° position were approximately 7.5 times as large as those at the 0° position.

TABLE IV

HUMAN THRESHOLD AS A FUNCTION OF AZIMUTH, 100-ms NOISE BURST

Azimuth:	0°	30°	60°	90°
Subject				
A	1.3°	1.8°	3.3°	8.7°
B	0.8°	3.8°	2.0°	9.2°
C	1.0°	2.0°	4.5°	11.2°
D	2.0°	3.5°	7.7°	9.5°
Mean	1.3°	2.8°	4.4°	9.7°

Discussion

Frontal sound localization and a comparison of test methods

As shown in Table I, individual localization thresholds for all but the briefest of stimuli ranged from 4° to 7°. Increasing the duration of the noise burst to permit scanning movements did not result in improved acuity in frontal sound localization in any of the three cats tested. The absence of improvement with increasingly long stimulus durations was unexpected since longer durations permit scanning movements. One explanation is that the use of only two loudspeakers allowed the animals to maintain an optimum pinna orientation and scanning movements would not have improved accuracy. If this is true, then longer durations might prove easier to localize in a situation involving multiple sound sources located around the animal without prior indication as to the direction from which a sound would be presented.

The behavioral procedure used to determine localization acuity also had little effect on the results. Identical thresholds were obtained for Cat A for sounds centered around 0° azimuth in both the two-choice and conditioned avoidance procedures, and the threshold of a previously untested cat, D, fell within the range of thresholds obtained in the two-choice test. Fig. 7 illustrates the close agreement between the average performances of the cats in the two test procedures using the same stimulus duration. Indeed, as shown below, the thresholds reported here with either test procedure agree closely with those reported by previous investigators.

Previous investigations of sound localization acuity in cats have used a two-choice method in which the animals listened to a 500-ms noise sounded five times and then walked to the source of the sound for a food reward (Casseday and Neff, 1973). Despite the use of a long stimulus duration and requiring the animals to move to the actual source (rather than merely indicate its direction or detect a change in direction), the average threshold of 5° agrees with those in this report. Using a similar procedure, Strominger (1969a,b) found thresholds for cats averaging 6.6° and 8.5°. These thresholds are slightly higher and
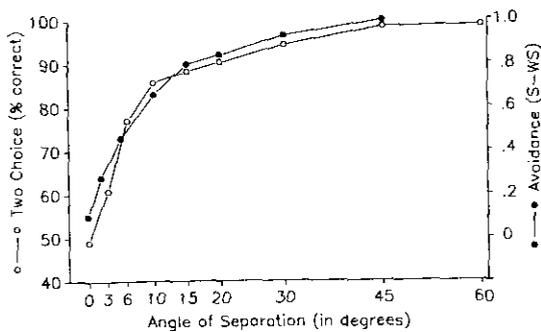
Fig. 7. Comparison of the average sound-localization performance around 0° by cats obtained using two different test procedures. (Signal duration in both tests was 100 ms. Note the close agreement between the two methods for both performance at large angles and for threshold.)

the difference may be due to interpolation error in calculating threshold due to the lack of performance data for angles smaller than 10° for most of the animals. Three of those cats which were tested at an intermediate angle (thereby reducing interpolation error) achieved an average threshold of 4.9° (Strominger, 1969a) which agrees more closely with other thresholds obtained for cats.

A recent study has reported slightly lower thresholds than those found by the present and previous studies (Martin and Webster, 1987). Using a conditioned avoidance procedure Martin and Webster obtained an average threshold of 3.4° for five cats. Although they attributed their lower thresholds to the fact that their task involved the discrimination of two matched sound sources while previous studies used a single sound source, the results of our study, which also used two matched sound sources, make this explanation unlikely.

Because Martin and Webster did not present individual performance curves, it is not possible to determine with certainty why their thresholds were lower than those of other studies. However, it should be noted that they used a tracking procedure and defined threshold as the average of the 'magnitude settings associated with the last six reversals.' In doing so they accepted a score of 0.50 or better on a trial as a correct detection. As a result their thresholds may have been slightly below the 50% detection threshold used by this

and previous studies. That a small change in the definition of threshold could easily account for their results is indicated by the fact that changing the definition of threshold in our study from 50% to 40% detection would result in the same average threshold of 3.4° as that found by Martin and Webster. Similarly, if the false alarm rate rose significantly as threshold was approached, their use of the suppression ratio, $(P - D)/P$, could yield spuriously low thresholds (for a discussion of alternative performance scores see Heffner and Heffner, 1988). Since false alarm rates were not reported it is not possible to determine whether or not this was a factor. Based on the available information, then, it seems reasonable to retain 5° as the 50% sound-localization threshold for this species.

Four conclusions can be drawn from the results of the localization tests around 0°. First, 5° represents a good estimate of the smallest angle that cats are capable of discriminating (at the 50% detection level) around the midsagittal plane. Second, at least in situations where only two loci are being discriminated, the duration of the stimulus has little effect on thresholds in cats. Third, there is no evidence to support the notion that detection methods using shock avoidance result in spuriously low thresholds (c.f. Gourevitch, 1980). Fourth, the similarity of the threshold for this species determined in different laboratories using different test procedures and equipment provides further evidence that different procedures need not lead to different results in the behavioral assessment of auditory capacities.

Sound localization at lateral azimuthal positions

Although it has been suggested that mobile pinnae play a role in sound localization (e.g., Jeffress, 1975; Shaw, 1974), the cat, with its highly mobile pinnae, is not as accurate at localizing frontal sound sources as humans with their immobile pinnae. However, frontal localization involves the use of binaural cues and humans not only have larger heads which generate larger binaural cues (e.g., Heffner and Heffner, 1984), they may also be more sensitive to the cues (Jeffress, 1975; Wakeford and Robinson, 1974). Thus, a more appropriate test of the usefulness of mobile pinnae in sound localization would be the localization of

sounds off to the side where binaural cues are weak or ambiguous.

Initial comparison of the localization ability of cats and humans for laterally placed sound sources, however, does not indicate any superiority of the mobile versus the fixed pinna. As shown in Table IV, humans and cats have virtually the same thresholds when localizing sounds centered on 90° where binaural cues are not available (i.e., the 'cone of confusion'). At all other angles where binaural cues are available, humans are more accurate than cats.

In examining the data for any indication of an advantage of mobile pinnae for sound localization, it can be noted that cats do show less of an increase in threshold at lateral positions than humans. That is, the 90° threshold for cats is only twice their 0° threshold. This result could be interpreted as indicating that mobile pinnae prevent localization acuity from deteriorating significantly as binaural cues become less available. However, a simpler explanation is that the proportionally smaller increase in the lateral localization ability of cats is due to their poorer frontal localization acuity and not to any advantage of their pinnae for lateral localization.

Indeed, it can be argued that mobile pinnae place an animal at a disadvantage for localizing frontal sound sources. Because the position of mobile pinnae can significantly alter the magnitude of the binaural intensity-difference cue (Calford and Pettigrew, 1984; Irvine, 1987; Phillips et al., 1982), it would be necessary for the nervous system to take the position of the pinnae into account in calculating the locus of a sound source. There is some evidence that this does occur (Stein and Clamann, 1981), but the additional calculation could be a source of error and serve to degrade frontal localization acuity.

The importance of pinna position in sound localization has been noted elsewhere (Heffner and Heffner, 1982; Heffner et al., 1982). During tests of frontal sound localization acuity, an Indian elephant was observed to extend its pinnae nearly perpendicular to its head at the beginning of each trial and then return them to the relaxed position against its head following presentation of the sound. This behavior was specific to sound localization since the elephant did not extend its pinnae during tests of absolute or frequency-difference thresholds. Therefore, pinna extension did not seem to be used simply to block out background noise and increase the signal-to-noise ratio. Further, the elephant made more errors on those trials in which it did not extend its pinnae, indicating that pinna extension may be necessary for accurate localization. Although the reason for pinna extension could not be determined with certainty, these observations are compatible with the idea that the auditory system may not be able to fully compensate for variation in pinna position when localizing sound. Thus an animal with mobile pinnae may need to place them in a standard position in order to make precise judgements of sound location.

There remains one reason for suspecting that mobile pinnae may enable the cat to localize lateral sounds more accurately than would be possible with nonmobile pinnae. The large head of humans may serve to enhance not only binaural cues, but monaural cues as well. Although the pinnae of humans and cats are similar in size, the cat lacks the large head of the human and may possibly be at a disadvantage in using monaural cues. Indeed, it can be argued that a more appropriate comparison for the cat would be an animal with nonmobile pinnae and similar head size such as the macaque. Until such a comparison can be made, we cannot rule out the possibility that mobile pinnae confer an advantage in localizing in the lateral fields.

The effect of stimulus duration on front / back localization

The question remains as to whether the contribution of the pinnae depends on scanning or a sort of 'acoustic focusing'. The cats in these experiments oriented their pinna in the direction of the speakers but scanning movements were not observed even when long-duration stimuli were provided. Further, increasing the duration of the stimulus did not significantly improve thresholds beyond those obtained for a 40-ms stimulus (a stimulus too brief to permit pinna movement) (Thompson and Masterton, 1978). These results indicate that scanning is not necessary for the pinnae to contribute to accurate sound localization at far lateral positions. The simple production

of an intensity/spectral difference may be sufficient.

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