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Sound Localization in Large Mammals: Localization of Complex Sounds by Horses

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The idea that large mammals localize sounds more accurately than small mammals has been noted frequently and is usually explained by reference to their large interaural distance and the correspondingly broad binaural time (Δt) and spectral (Δfi) differences between their two ears. Sound-localization thresholds for single clicks and 100-ms noise bursts were determined for horses, and the magnitude of the binaural time (Δt) and spectral (Δfi) cues for sound direction were measured on a horse. Although horses have relatively large interaural distances and physically broad binaural-localization cues available to them, their sound direction thresholds were markedly poorer than those of other large mammals—averaging 22° for noise and 30° for clicks. It appears that sound-localization acuity is not determined simply by the physical availability of binaural cues.

In recent years it has become apparent that the ability of mammals to localize sound varies from one species to the next (for a review, see R. Heffner & Heffner, 1982). Although some animals, such as humans and elephants, are able to resolve the locus of the source of a brief sound to about 1°, other mammals are not nearly so accurate. Monkeys and cats have thresholds of 4°–5°, and some rodents are unable to resolve angles smaller than 20° (Brown, Beecher, Moody, & Stebbins, 1980; Casseday & Neff, 1973; H. Heffner & Masterton, 1980; Kelly, 1980).

In seeking an explanation of this wide variation, it is usually suggested that an animal's interaural distance plays the determining role (e.g., R. Heffner & Heffner, 1982; cf. Iversen, 1978); that is, a large interaural distance generates large binaural localization cues both in the time of arrival (Δt) and the frequency-intensity spectrum (Δfi) of a sound reaching the two ears. These physically larger cues, in turn, enable the nervous system to analyze the azimuth of the sound source more accurately. Indeed, comparing the localization acuities of the few species for which data have been available has suggested that there is a strong positive relation between interaural distance and localization acuity (R. Heffner & Heffner, 1982).

Because of this close relation between interaural distance and localization acuity, it might be expected that all animals with a relatively large interaural distance would be accurate localizers of sound. As a test of this hypothesis, in the present experiments we measured the ability of horses to localize clicks and brief noise bursts and also the magnitude of the binaural Δt and Δfi cues available to them. As seen later, the results indicate that the availability of large binaural localization cues does not in itself guarantee good localization acuity.

General Method

The following experiments are divided into three sections. The first two sections concern the two behavioral tests used to determine sound localization acuity. The third concerns the measurement of the Δt and Δfi cues available at a horse's ears.

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First, the localization ability of three horses was determined by a two-choice procedure with water as a reward (cf. H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1982). Briefly, an animal was trained to touch its nose to an "observing" plate in order to position its head in front of an array of loudspeakers and trigger a sound. Upon presentation of the sound, the animal touched either a left or a right "response" plate, depending on whether the sound came from the left or right of midline.

Second, to establish that the localization acuity determined with the previous procedure was no mistake, the localization ability of two additional horses was determined by a shock avoidance procedure (cf. H. Heffner & Whitfield, 1976; Ravizza & Masterton, 1972). In these tests, the animal was trained to maintain contact with a water bowl in order to receive a continuous trickle of water. A brief sound was then presented once every 5 s from one of the two loudspeakers located to the left and right of the animal's midline. Sounds coming from the left side were followed within 4 s by a mild electric shock delivered through the water bowl. Sounds from the right had no contingency whatever attached. The animals rapidly learned that they could avoid shock by breaking contact with the bowl whenever a sound was emitted from the left side. This breaking of contact was then used to indicate that the animal had detected the locus of the sound source.

Finally, the magnitude of the Δt and Δfi cues were determined for a horse. The Δt was calculated by placing a ¼-in. (0.64-cm) microphone at the entrance of first one ear and then the other and determining the difference in the arrival time of a sound from various loudspeaker locations. Similar measurements were also made on a cat and a human for comparison. The magnitude of the Δfi cue was estimated from measurements made with the microphone placed just outside the left auditory meatus (inside the pinna). In this instance, a loudspeaker emitting the same noise stimulus used in the behavioral tests was moved around the head, and its intensity was systematically determined for the different speaker locations in octave steps.

Experiment 1:
Two-Choice Localization Test

Method

Subjects. Three horses between 21 and 23 months old (adolescent) were used in this test: a 340-kg quarterhorse gelding (Horse A), a 350-kg Appaloosa mare (Horse B), and a 260-kg Welsh pony × quarterhorse gelding (Horse C). They were housed in outdoor pens and maintained on a standard diet of mixed grain and hay. Water, used as a reward, was available only during test sessions, and the animals were weighed daily to monitor their deprivational state.

At the beginning of testing, each animal was sedated with xylazine (0.8 mg/kg), and each external auditory meatus was carefully inspected. Each meatus was found to be free of obstruction or disease. In addition, behavioral audiograms of the same animals gave no indication of abnormality (R. Heffner & Heffner, 1983a).

Behavioral apparatus. Testing was conducted on the grounds of the Kansas State Agriculture Experiment Station in Mound Valley, Kansas. The building in which the tests were conducted was relatively isolated from the rest of the Station, and its ventilating system was turned off during testing. These features, combined with the rural location, provided a quiet environment for auditory testing.

In order to attenuate outside noise and to reduce sound reflection, testing was conducted in a large room (7.2 × 5.5 × 2.4 m), which had the walls and ceiling lined with fiberglass and sound-absorbing panels (Cellotex). A room adjacent to the test room was used to house the test equipment and to observe the horses on closed-circuit television.

During testing, the animal was confined to a rectangular stall (2.4 × 1 × 1.5 m) mounted on a sawdust-covered wooden floor (Figure 1). Three metal response plates and a water bowl were located at the front of the stall within each reach of the horse. The water bowl, located below the response plates, was connected with tubing to a 50-liter water reservoir. An electrically operated water valve inserted in the water line controlled the flow of water to the bowl. The water valve was mounted on the water bowl, and the click that it emitted when it was operated served as a signal that water was being delivered. Each of the response plates was connected to a separate sensing switch which detected when the animal made contact with it.

Acoustical apparatus. Two types of stimuli were used: clicks and broad-band noise. To produce the clicks, square waves were generated by a square wave generator (Coulbourn S78-22), led to a programmable attenuator (Coulbourn S85-08), then to an amplifier (Coulbourn S82-24), and finally to one of 10 loudspeakers (Long L15F, 3.5-cm dome loudspeaker). Broad-band noise was generated by a noise generator (Lehigh Valley 1524), led to the programmable attenuator, then to a rise-fall gate (Coulbourn S84-04), then to the amplifier, and finally to one of the 10 loudspeakers (7.6-cm paper cone loudspeakers mounted in 500-cc enclosures).

The loudspeakers were mounted on a perimeter bar (1.5-m radius) which was centered on the position occupied by the intersection of the animal's interaural line and midline when it was touching the center response plate. In order to reduce the possibility that the animals could distinguish the loudspeakers on the basis of quality or intensity, the five pairs of loudspeakers were matched for clicks and noise by human observers. The intensities of loudspeakers were then equated by measuring the intensity at the center plate with a sound level meter (Brüel & Kjaer 2203 microphone amplifier and 4131 microphone using the linear scale) and adjusting for differences with the programmable attenuator. That such procedures were sufficient to prevent the animals from using nonlocus cues was directly demonstrated in the behavioral results: No animal could distinguish between the loudspeakers when the azimuth of separation was reduced to 0°.

A wide variety of stimuli were used in training and threshold estimation. These stimuli included clicks generated by 0.1-ms and 1.0-ms square waves, single

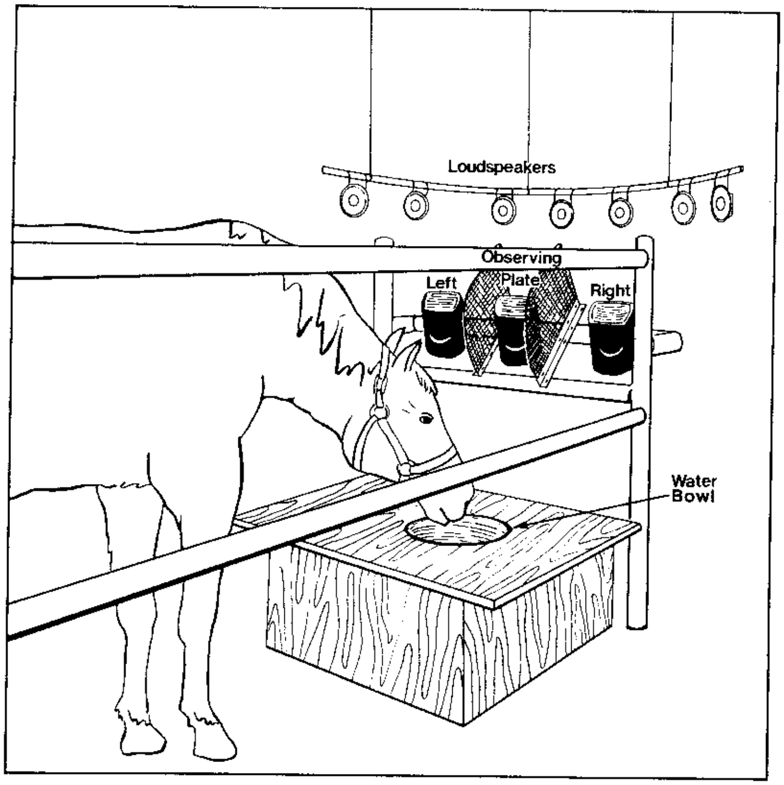

Figure 1. Test stall used in two-choice test of sound localization. (A horse initiated a trial by touching the observing plate with its nose. It then touched either the left or the right response plate to indicate whether a sound had come from a loudspeaker on its left or right side, respectively. Correct responses were rewarded by delivering water into the water bowl. The hardware-cloth panels separating the response plates served to prevent an animal from responding to the side plates too rapidly.)

clicks and click trains ranging from 2 to 20/s, broad-band noise, and filtered noise. Of the two types of clicks, the animals localized the 1.0-ms (lower pitch) click more accurately than the shorter duration (higher pitch) click, and broad-band noise was generally localized more accurately than either high-frequency or low-frequency filtered noise. Therefore, to illustrate the horses' optimal performance on these two classes of stimuli, the results presented here are based on their localization of single 1.0-ms clicks and single 100-ms bursts of broad-band noise (.1-ms rise-decay).

Finally, all stimuli used in localization determinations were presented at an intensity level at least 40 dB above the animals' thresholds as estimated by attenuating the stimuli until their performance fell to chance.

Psychophysical procedure. A water-deprived animal was trained to initiate a trial by placing its nose on the center plate. This observing response served to center the animal's head within the array of loudspeakers and immediately triggered the presentation of a sound from a loudspeaker to the left or the right of the animal's midline. The animal was then rewarded with 35 ml of water if it touched the response plate on the same side as the active loudspeaker. Touching the opposite response plate was followed by a short wait of 3–15 s (signaled by dimming the lights in the test room) before a new trial could be initiated. A typical session lasted 60 min during which an animal received 200–600 trials and consumed 6–20 liters of water.

The sequence of left-right trials was determined by a quasi-random schedule (Gellermann, 1933). In order to reduce side preferences, a correction procedure was used in which the correct side was not changed following an error. Side preferences were further prevented from affecting the results by discarding the data on the few occasions when an animal's performance suggested the occurrence of a response bias.

Localization thresholds were determined by reducing the angular separation between two loudspeakers until the animal could no longer distinguish left from right stimuli. Psychophysical functions were then constructed by averaging each animal's scores from its three best sessions (asymptotic performance) with a minimum of 100 trials per angle. Threshold is defined two ways: (a) as the smallest separation yielding a 75% correct performance and (b) as the smallest separation at which the animal could discriminate between the two stimuli at the .01 one-tailed level of significance (binomial distribution), which was generally 63% correct.

Results and Discussion

Broad-band noise localization. Sound-localization thresholds were determined by using single 100-ms bursts of white noise. The results of this test are shown in Figure 2A. Each point represents an animal's asymptotic performance at a particular angle. As can be seen, none of the horses had difficulty with this task at large angles, and at 180° (speakers 90° to the left and right) their scores ranged from 93% to 100% correct. At smaller angles, the animals showed more individual variation, especially Horse C, whose performance declined at smaller angles to 75% correct at 58°. However, the

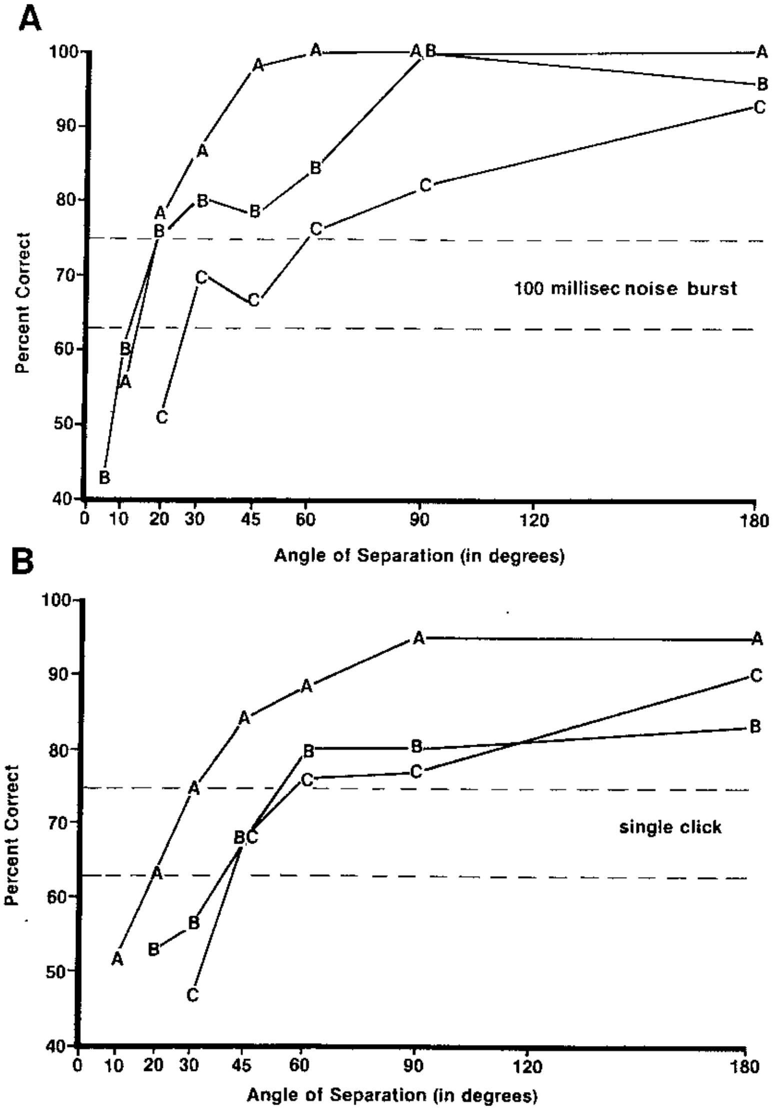

Figure 2. Sound-localization performance on the two-choice tasks for a single 100-ms noise burst (panel A) and a single click (panel B). (A, B, and C within the panels represent the 3 animals used in this test. Dashed lines indicate the 75% correct threshold and the 63% correct level which, in this task, represents the .01 statistical threshold.)

other two animals were able to maintain a higher level of performance (especially Horse A, whose performance remained at 100% at angles as small as 60°), and these animals showed close agreement at threshold. Considering the performance of these two best animals, however, the resulting 75% threshold of 19° is much poorer than the noise thresholds of other large mammals. Indeed, as discussed below, mammals with much smaller interaural distances can localize broad-band noise as accurately as 5° under the same behavioral and psychophysical conditions. Thus, these results were our first indication that horses might lack good sound-localization acuity.

Single click localization. The ability of horses to localize single clicks generated by 1.0-ms square waves is shown in Figure 2B. As expected, the overall performance of the animals with this stimulus was measurably poorer than it was with broad-band noise (e.g., R. Heffner & Heffner, 1982). Only Horse A was able to maintain performance above 90% and then only for the two largest angles. With 75% correct as threshold once more, Horse A had a threshold of 31°, and Horses B and C had thresholds of 38° and 41°, respectively.

It is of interest that two humans tested in the same apparatus, using the same two-choice procedure, yielded a 75% click-localization threshold of 0.8°. Thus, the results of this test again suggested that horses might lack good sound-localization acuity.

Experiment 2: Conditioned Avoidance Localization Test

Though the results of the two-choice tests just described suggest that horses may not localize sound as accurately as other mammals their size, we were reluctant to accept this conclusion without verification from an entirely different procedure.

A shock-avoidance procedure was chosen for this test because it requires very little learning and very little motor prowess on the part of the animal. To perform the task, an animal need only drink water from a bowl and then momentarily withdraw when a warning signal indicates impending shock—a response not unlike the natural reaction of an animal at a water hole to signs of danger. Indeed, this more classic task has been used successfully many times to assess hearing in severely brain-damaged animals and in otherwise intractable animals (e.g., Masterton, Heffner, & Ravizza, 1969; Ravizza & Masterton, 1972).

Method

Subjects. Two new 3-yr-old horses (Shetland ponies), a male (104 kg) and a female (100 kg), were used in this second test. The animals were housed in indoor pens and maintained on mixed grain and hay. Water was used as a reward and was available only in the testing situation. As before, the ears of both animals were carefully inspected and found to be free of any signs of obstruction or disease.

Behavioral apparatus. In order to minimize ambient noise, testing was conducted in a laboratory room 3.2 × 2.5 × 2.4 m. In order to reduce sound reflections the walls of the room were lined with acoustic foam, the floor was covered with carpeting, and burlap was loosely draped from the ceiling. A nearby room was used to house the test equipment, and the animals were continuously observed by closed-circuit television.

During testing, the horse was confined to a rectangular stall (145 × 60 × 80 cm) specially constructed so as to reduce possible interference with the sound field around the animal's head (Figure 3). The water bowl was located in a position that allowed the horse to drink comfortably while centering its head in front of the perimeter bar from which loudspeakers were suspended. To prevent the noise emitted by the water valve from being audible to the animals, we packed the valve in fiberglass and located it with the water reservoir in an adjacent room. A touch-sensing switch, connected at one end to the water bowl and at the other end to the flank of an animal with an electroencephalographic electrode, served to detect when the animal made contact with the bowl. Mild electric shock was provided by a shock generator connected to the water bowl and the flank electrode.

Acoustical apparatus. The click and noise stimuli were generated and presented in the same manner and with the same equipment used in the previous two-choice tests. Training stimuli consisted of 5/s noise bursts and 5/s click trains. The test stimuli were single clicks produced by a 1.0-ms square wave and single 100-ms bursts of white noice (.1-ms rise-decay).

Psychophysical procedure. The avoidance procedure was similar to that described elsewhere (H. Heffner & Whitfield, 1976). Briefly, a thirsty animal was trained to make steady contact with the water bowl with its mouth. This was accomplished by providing a steady trickle of water (140 ml/min through a pulsing water valve) as long as the horse maintained steady contact with the bowl.

The animals were initially trained to drink steadily from the bowl while a 4-s train of broad-band noise bursts (100 ms in duration, 5/s) was presented once every 5 s from a loudspeaker located 90° to the right

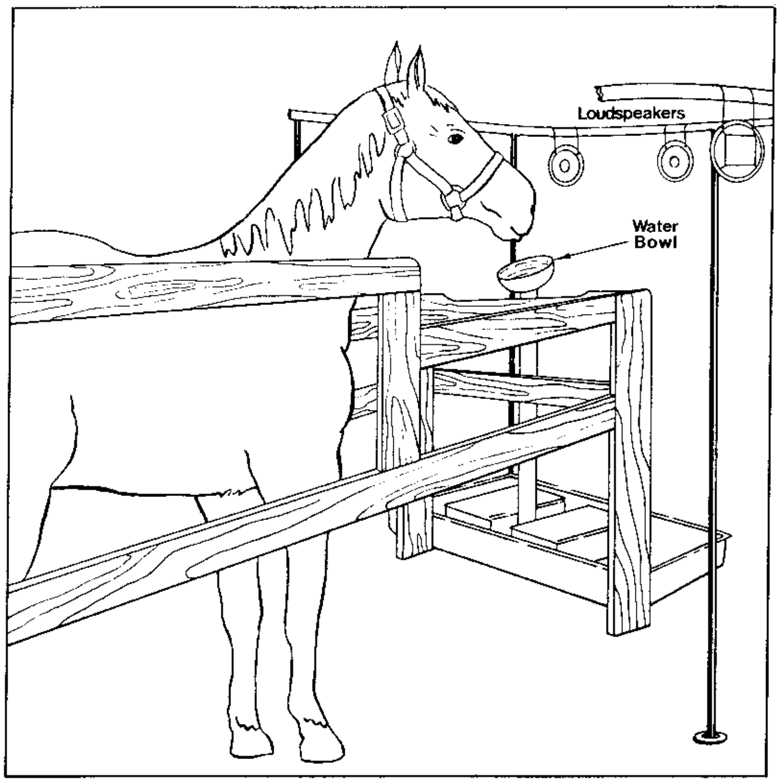

Figure 3. Test stall used in the conditioned-avoidance test of localization. (An animal was trained to maintain steady contact with the water bowl in order to obtain a slow but steady trickle of water. The animal was then trained to cease drinking when a sound was emitted from a loudspeaker located on its left side in order to avoid a mild electric shock. Sounds emitted from speakers on the right side were not followed by shock, and the animal soon learned to continue drinking when they were presented.)

of the animal, the stimulus side that was never paired with shock. By the eighth session, the animals had learned to maintain steady contact for an hour or more. Further training consisted of occasionally switching the auditory stimulus to a loudspeaker 90° to the animal's left side and following its offset 4 s later with a mild electric shock delivered between the water bowl and the electrode on the animal's flank. After only a few pairings of the left sound with shock, the animal learned to avoid the shock by breaking contact with the bowl whenever the noise burst was presented from the left side. In order to provide feedback for successful avoidance, the lights in the test room were momentarily turned off each time shock was delivered. Thus, the lights served to indicate that a warning trial was over and that the animal could return to the water bowl. In the following tests, cessation of contact was used as an indication of an animal's ability to perceive a shift in locus.

The presentation of right (safe) and left (warning) trials was randomized, with a warning trial likely to occur anywhere from 1 to 10 trials after the previous warning trial. Longer intervals between warning trials were occasionally inserted to prevent an animal from using the time since the last warning trial as a cue. No trial was given in the 5 s immediately following a warning trial in order to allow an animal sufficient time to return to the water bowl.

For the purpose of quantifying an animal's response, the duration of bowl contact was measured in 0.1-s increments beginning 0.5 s after stimulus onset until 3.5 s later—at the end of the trial. This measured "time in contact" was then averaged separately for the right or safe (S) trials and the left or warning (W) trials for each angle of separation. A measure of discrimination could then be expressed in the form of a ratio (S−W)/S for each angle. In trained animals this measure varies from near zero (failure to discriminate) to unity (perfect discrimination). In order to reduce the effects of spurious pauses, the results of a trial were automatically discarded if the animal was not in contact with the bowl at any time during the 1 s immediately preceding the trial, though the trial and shock were presented as usual. Because this criterion was applied equally to safe and warning trials, it did not bias the results.

Sound-localization thresholds were determined by reducing the duration of the stimulus to a single click or noise burst and then reducing the angular separation between the left and right loudspeakers until the animal could no longer distinguish the two stimuli. Once a preliminary threshold had been obtained, threshold testing was continued while the shock level and the animal's deprivation level were varied. Psychophysical functions were then plotted by taking the average of the scores from each animal's best three sessions (asymptotic performance) with a minimum of 25 warning trials per angle. Threshold was arbitrarily defined in either of two ways: (a) as the smallest angle yielding a suppression ratio of .5 (i.e., 50% detection) and (b) as the smallest angle at which the animal could discriminate between the two stimuli at the .01 one-tailed level of statistical reliability (Mann-Whitney *U* test; Siegal, 1956), which in this case was usually a suppression ratio of .25.

A typical session lasted 60–90 min during which an animal received 275–375 trials (18% of which were warning trials) and consumed 6–9 liters of water.

Results and Discussion

Training. The animals were initially trained to localize a 4-s train of noise bursts (5/s) coming from 90° to their right (safe) or left (warning) side. This proved to be an easy task, and both animals reached asymptotic performance $[(S-W)/S > .95]$ by the end of the first session in which the warning stimulus was presented. The animals were then given 4 additional weeks of practice which were spent perfecting their performances at smaller angles and reducing the noise stimulus either to a single 100-ms burst or to a single click.

Broad-band noise localization. Sound-localization thresholds were determined for the two horses by using single 100-ms bursts (0.1 ms rise-decay) of noise. The results of this test are shown in Figure 4A in which each point represents an animal's asymptotic performance at a particular angle. At large angles the animals had no difficulty performing the discrimination, which illustrates the fact that the task itself was a simple one for them to perform. As the angle of separation was reduced below 90°, their performances began gradually to drop, reaching the .50 performance level at about 25° and the chance level at about 17°. Overall, the two animals showed close agreement.

Click localization. The performance of the two animals on the click-localization test was also quite good at large angles (Figure 4B). In this test, the animals maintained asymptotic performance down to 60° separation. Below this angle their performance fell off somewhat more sharply than in the noise-localization test. The average .50 performance threshold for single clicks was 30°, while the statistical threshold was about 22°. Again, the animals showed no major individual differences in their performance.

Comparison of two-choice and conditioned avoidance results. In comparing the results of the two-choice and conditioned avoidance tests, one noticeable difference is the degree of variation shown by the two techniques. Though only two animals were used in the avoidance procedure, these animals show better agreement with each other on both tests than any combination of two animals in the two-choice procedure. This result may be attributable to the procedure used. However, we suspect that it is more likely due to the selection of more mature animals for the avoidance task.

Because the two procedures utilize different means of calculating performance, it is somewhat difficult to make a detailed comparison between the two sets of results. However, it can be argued that a 75% correct performance on the two-choice test, which is midway between a perfect score of 100% and a chance score of 50%, is analogous to a score of .50 on the avoidance task, which is also midway between a perfect score of 1.00 and a chance score of 0. In addition, both performances can be compared at the point at which both drop below the .01 one-tailed level of statistical significance.

The two threshold levels for the two tests are compared in Table 1. In this table, the thresholds for the two-choice tests are based on the best animal or, because of the close agreement of Horses A and B in the white noise test, on the best two animals. For the avoidance thresholds, however, both animals' scores are averaged together, because the two animals showed no significant variation. When compared on their ability to localize noise, it can be seen that the two best two-choice animals are 4° to 6° better than the two avoidance animals, depending on the definition of threshold. On click localization, however, the threshold of the best two-choice animal is vir-

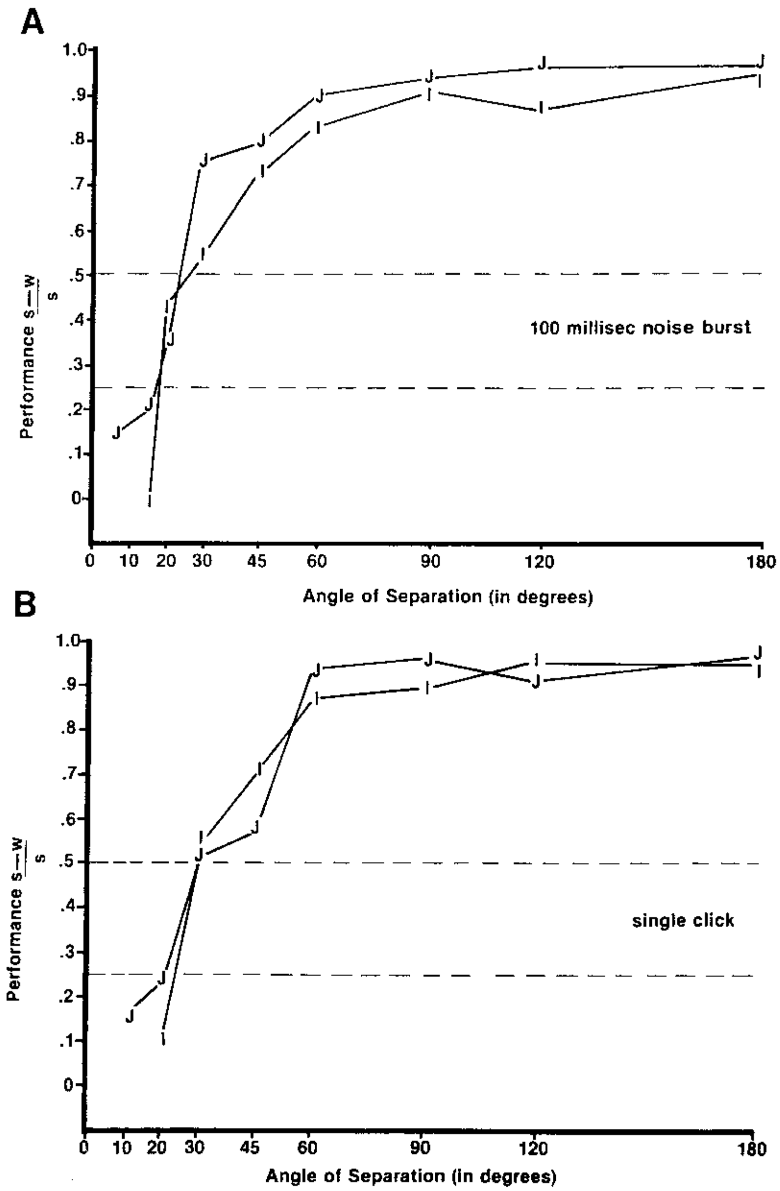

Figure 4. Sound-localization performance on the conditioned-avoidance task for a single 100-ms noise burst (A) and single click (B). (I and J represent the 2 animals used in this test. Dashed lines indicate the .50 suppression threshold and the .25 suppression level which, in this task, represents the .01 statistical threshold.)

tually identical to those of the avoidance animals. In short, though the animals tested in the avoidance task showed less intersubject variability, the results of both tests yield similar thresholds, and both support the conclusion that horses cannot localize sound accurately.

Experiment 3: Measurement of Available Δt and Δfi Cues

Given the results of the two previous experiments, the question arises as to why horses are unable to localize sound accurately. Throughout this article, it has been

Table 1
Sound-Localization Thresholds

Task	Threshold	
	50% discrimination[a]	Statistical threshold[b]
Noise		
Two choice[c]	19°	13°
Avoidance	25°	17°
Click		
Two choice[d]	31°	20°
Avoidance	30°	22°

[a] 75% correct for the two-choice task, and .50 level of performance for the avoidance task. [b] .01 chance discrimination. [c] Average of Horses A and B. [d] Horse A only.

assumed that a horse's head, because of its relatively large size, generates binaural locus cues that should be large enough to permit accurate sound localization. However, the inability of horses to localize sound accurately leads to the question of how large these cues really are.

The relative magnitude of the binaural sound-localization cues available to mammals can be estimated from the interaural distance. By measuring the maximum distance that a sound must travel around the head from the opening of one auditory canal to the opening of the other, it should be possible to estimate the relative availability of the time (Δt) and spectral (Δfi) localization cues. The interaural distances of the 5 horses tested here ranged from 16.8 cm (Horse J) to 24.5 cm (Horse C), with an average of about 21 cm. In comparison, a typical value for cats is 7 cm (Roth, Kochhor, & Hind, 1980), and for humans it is about 30 cm (Woodworth & Schlosberg, 1965). Thus, horses would be expected to have significantly larger binaural cues available to them than cats, but not as large as those for humans.

Although interaural distance is inextricably related to the magnitude of binaural cues, it is probably not a perfect predictor. Species with similar interaural distances, but differently shaped heads and pinnae, almost certainly differ in the magnitude of the cues they receive. Therefore, it seemed worthwhile to investigate further the magnitude of the horse's binaural cues.

Method

The purpose of this experiment was to determine the magnitude of the Δt and Δfi cues for the horse at angles from 0° to 90°. This was done by measuring the arrival time and intensity of sounds at the ears with a microphone. For comparison, measurements of the Δt cue were taken under the same conditions for a human and a cat.

Materials. The horse used to obtain binaural Δt and Δfi measurements was one that had been euthanized and then donated to our laboratory. The animal weighed 120 kg and had a maximum interaural distance of 18.2 cm (as measured around the top of the head). The pinnae were fixed, with the openings pointing at an angle of about 65° from midline.

Measurements of binaural Δt were also made on a 52-kg human female (28.6-cm interaural distance measured around the front of the head) and a 5.5-kg cat (12.2-cm interaural distance measured around the top front of the head).

Sound production. Clicks and broad-band noise were generated as previously described in Experiments 1 and 2. In order to facilitate measurements of interaural time differences, the clicks were generated with a 10-μs square wave instead of the 1-ms duration used in the behavioral tests. All measurements were conducted in the test chamber described in Experiment 2.

Sound measurement. Sound measurements were made using a ¼-in. (0.64-cm) Brüel and Kjaer (B&K) microphone (B&K 4135) with windscreen (B&K UA0385), preamplifier (B&K 2618), and measuring amplifier (B&K 2608). For Δt measures, the output of the measuring amplifier was fed into a Tektronix 502 oscilloscope, the time calibration of which was verified with a Fluke 1910A multicounter, and the difference in the time of arrival of the sound at the two ears was determined. For Δfi measures, a Krohn-Hite 3202 filter was connected to the measuring amplifier and was set to bandpass mode (24 dB/octave attenuation).

Procedure. The horse's head was positioned in the test stall, with the center of the head located at the center of the perimeter bar. This placed the head in the same position as that occupied by a behavioral animal during testing. Human Δt measurements were made with the subject seated, with her head placed on a chin rest that centered it within the perimeter bar. Measurements of the cat Δt were made with an anesthetized cat (ketamine 20 mg/kg) whose head was also centered within the perimeter bar.

Δt. The microphone was oriented vertically at the base of the opening of a pinna. The loudspeaker was mounted on the perimeter bar directly in front of the head (i.e., 0°), and the microphone was placed first at one ear and then at the other. By noting that the position of the peak of the acoustic signal on the oscilloscope was the same for each ear, it was possible to verify that the head was precisely centered within the perimeter bar. Once the head had been centered, the speaker was moved from 0° to 5°, 10°, 15°, 20°, 30°, 45°, 60°, 75°, and 90°. The interaural time difference was calculated for each angle by noting the difference in the arrival time of the click at the two ears.

Δfi. An incision just large enough to accommodate the microphone was made in the base of the left pinna of the horse. The microphone was then inserted so that it was directly in front of the opening of the auditory meatus. The loudspeaker was placed on the perimeter bar at 0°, and sound level measurements were made of the broad-band noise at eight different band-pass settings from 125 Hz to 16 kHz in octave steps. At each setting, both the high- and low-pass filters were set to the same frequency (e.g., 125 Hz high pass and 125 Hz low pass) in order to obtain a narrow-band pass. These measures were repeated at angles of 5°, 10°, 15°, 20°, 30°, 45°, 60°, 75°, and 90° left and right of midline. The Δfi for a particular frequency band was calculated by subtracting the measured sound level for a particular angle to the left of midline from the sound level measured at the corresponding angle to the right of midline (e.g., the reading at 5° left minus the reading at 5° right).

Results and Discussion

Δt. The measured interaural time differences for horse, human, and cat are shown in Figure 5. When the loudspeaker was located 90° from midline, the human Δt was 635 μs, and the cat Δt was 361 μs. Both of these measurements are in good agreement with the human and cat values published elsewhere (Roth et al., 1980; Woodworth & Schlosberg, 1965). As expected from head-size measurements, the horse Δt of 501 μs at 90° was intermediate to the human and cat values.

Close inspection of Figure 5, however, reveals an interesting reversal in the relative sizes of the horse and human Δts. Whereas the human Δt exceeds the horse Δt at large angles, the horse actually has the larger Δt at angles below 35°. This result appears to be due to the fact that the horse head is much less spherical than the human head. Specifically, a horse's head is cylindrical in shape, with the ears located somewhat dorsally at the back of the head. As a result, the sound path for sound-source locations near the midline is around the front of the head. However, as the loudspeaker is moved off to one side, the shortest sound path to the ear on the opposite side is over the top of the horse's head. Because the horse's head is relatively narrow, the end result is that the Δt cue does not increase at larger angles as rapidly as it would for a more spherically shaped head.

In spite of the shape of its head, there is no reason to believe that the horse's localization acuity is limited by the availability of the Δt cue. Not only is the horse's Δt cue

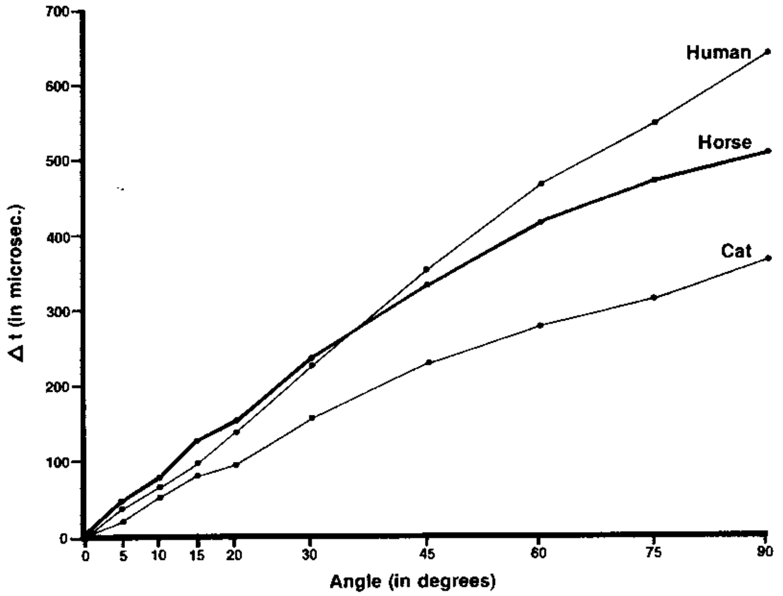

Figure 5. Measured interaural time difference (Δt) for horse, human, and cat. (Note that below 35° the horse experiences a larger Δt locus cue than the human subject.)

consistently larger than a cat's, but it is even larger than that of many humans at small angles of separation. Furthermore, the largest horse used in the behavioral tests had a head size one third larger than the horse head used for these measurements and thus would have been expected to have had available a somewhat larger Δt cue. Thus, the inability of horses to localize as accurately as humans and cats cannot be attributed to the lack of a sufficient binaural time cue.

Δfi. Interaural intensity differences were measured for the horse with the same noise stimulus as used in the behavioral experiments. The results of these measurements, shown in Figure 6, illustrate two important points. First, as is well known, low-frequency sounds bend around the head with little or no attenuation and thus do not provide a reliable intensity-difference cue (e.g., Harrison & Downey, 1970; Kuhn, 1977; Mills, 1958). As Figure 6 shows, sounds 2 kHz and lower provide only a small intensity difference, particularly at small angles. However, above 2 kHz, there is a distinct intensity difference between the two ears which begins at small angles of separation around midline and increases steadily at larger angles. Because the horse has an upper hearing limit of about 33 kHz (R. Heffner & Heffner, 1983a), it apparently receives reliable interaural intensity differences over the upper four octaves of its hearing range.

Given the Δfi cue available to the horse, the question arises as to whether it is sufficient to enable an animal to localize sound accurately. Although we do not as yet know the interaural intensity-difference thresholds of the horse, we do know what they are for other mammals that do accurately localize sound. In particular, the rhesus monkey, which has a 75% correct sound-localization threshold of 4°, has an interaural Δfi for complex sounds (i.e., binaural clicks) of about 3 dB (H. Heffner & Masterton, 1978). Referring to the intensity differences from 4 kHz to 16 kHz in Figure 6, it can be seen that a Δfi threshold of 3

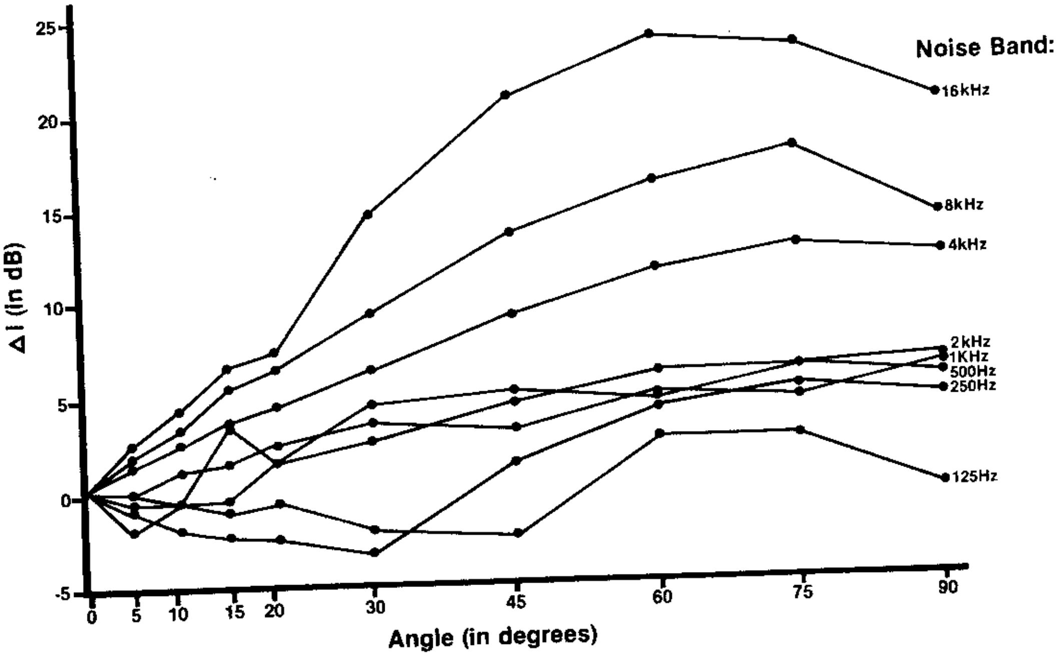

Figure 6. Measured binaural intensity difference for a horse. (Noise stimulus was the same noise used in the behavioral experiments. The noise band analysis was accomplished by filtering the noise at the sound level meter.)

dB would lead to a predicted free-field localization threshold of 5°–10°. However, these values are significantly lower than the 19°–25° noise-localization thresholds found in the behavioral experiments. Thus, the horse receives a Δfi cue that is sufficiently large to permit accurate sound localization, at least in monkeys.

The second point to be considered is the directionality of the horse's pinna. As can be seen in Figure 6, the maximum intensity differences occur at 60°–75°, depending on frequency. These results correspond to the orientation of the pinnae toward approximately 65° from midline. Such directionality of the pinnae is common in mammals and has been studied in detail in the cat (e.g., Phillips, Calford, Pettigrew, Aitkin, & Semple, 1982). Further, the pinnae of the horse are also highly movable—from pointing directly forward to almost directly backward. This mobility of the pinnae leads to the possibility that a horse might localize sound by orienting its pinnae in such a way as to maximize the binaural Δfi cue.

Though pinnae movements might be expected to be most helpful with longer duration sounds that would allow active scanning, one might also expect them to be of benefit in localizing brief sounds in our test situation in which only one angle of separation was tested at a time. That is to say, with experience, a horse should learn that a sound was to come from either of only two locations and position its ears to maximize its performance. However, the persistence of poor localization thresholds over thousands of trials suggests that either such a tactic is not particularly helpful or else horses simply do not use their pinnae as an aid for localizing a brief sound.

Availability of binaural locus cues. The analysis of the binaural locus cues indicates that the horse has a comparatively large Δt cue available to it. In addition, the available Δfi cue appears large enough to support accurate localization in other mammals. Thus, the poor localization acuity of the horse cannot be due to an insufficiency of binaural cues. Instead, it follows that the horse has not developed the neural capacity to take advantage of the binaural cues available to it.

General Discussion

Although the sound-localization ability of horses is of interest in itself, a comparison of the localization abilities of horses with other mammals is of special interest as it may shed some light on the selective pressures involved in the evolution of hearing. The first part of this discussion, therefore, concerns the comparison of the localization ability of horses with that of other mammals. The second part is directed to some potential correlates of sound-localization acuity and the selective pressures that may be involved in the evolution of such acuity.

Horses Versus Other Mammals

The sound-localization abilities of 13 species of mammals are compared in Table 2. In comparing the different animals, it is important first to note the stimulus used to ascertain the threshold. As can be seen, noise bursts yield a lower threshold than do clicks (cf. elephant, white rat, and horse). Further, it can be seen that localization thresholds (for clicks and noise) range from less than 1° to 30°. For the most part, those animals with good localization tend to be animals with large interaural distances, such as dogs, cats, humans, and elephants. The animals with less acute localization are mainly animals with small interaural distances, such as rodents. Because interaural distance determines to a large extent the size of the binaural localization cues, it is this observation that suggested in the past that sound-localization ability was largely determined by interaural distance.

With the addition of data on the horse, however, it is now apparent that localization acuity is not simply determined by interaural distance or by the availability of large binaural cues. With an interaural distance of 21 cm (as measured around the head from the opening of one auditory meatus to the opening of the other), the horse has the benefit of a significantly larger distance than cats, dogs, and monkeys and only slightly smaller than humans. Furthermore, as demonstrated in Experiment

Table 2
Sound-Localization Thresholds for 13 Species of Mammals

Animal	Stimulus	Threshold[a]	Source
Human	click	0.8°	Present article (Experiment 1)
Dolphin	click	0.9°	Renaud & Popper, 1975
Elephant	noise	1.2°	R. Heffner & Heffner, 1982
Seal	click	3.2°	Terhune, 1974
Elephant	click	4°	R. Heffner & Heffner, 1982
Macaque	noise	4°	Brown, Beecher, Moody, & Stebbins, 1980
Opossum	noise	4.6°	Ravizza & Masterton, 1972
Cat	noise	5°	Casseday & Neff, 1973
Dog	click	8°	H. Heffner, unpublished, 1977
White rat	noise	10°	Kelly, 1980
Hedgehog	click	19°	Chambers, 1971
Wood rat	noise	19°	H. Heffner, unpublished, 1978
Horse	noise	22°	Present article
Kangaroo rat	click	24°	H. Heffner & Masterton, 1980
White rat	click	29°	Kelly & Glazier, 1978
Horse	click	30°	Present article

[a] Threshold is defined as the 75% correct level for two-choice procedures and the .50 performance level for conditioned suppression and avoidance procedures.

3, the Δt cue available to horses is larger than that available to cats and, in the case of small angles, also larger than that experienced by humans. Thus, on the basis of available binaural cues alone, one would expect the horse to have a localization acuity better than that of cats and only slightly less than that of humans. The fact that the horse can localize no more accurately than a rat demonstrates that the availability of binaural cues for sound localization is *not* the determining factor in localization acuity.

Potential Correlates of Sound-Localization Acuity

Because the correlation between interaural distance and sound localization acuity no longer appears to be reliable, it follows that the observed differences in sound-localization acuity are the result of variation in the degree of selective pressure for accurate localization. Thus, the question arises as to what the sources of these pressures may be. At the present time, there are several factors that have been or might be proposed as playing a role in the evolution of accurate sound localization, and there is as yet little evidence for choosing between them. Of these, four are worth mentioning here. They are (a) whether an animal is usually a predator or prey (i.e., its trophic level), (b) the type of habitat occupied by an animal, (c) whether an animal is primarily nocturnal or diurnal, and (d) an animal's visual capacities.

Whether an animal is primarily a predator or prey may influence the degree of selective advantage conferred by accurate sound localization. To be successful, a predator may need to know exactly where its prey is, whereas the prey, in order to escape, may need only an approximate idea of where the predator is. The good localization acuity of cats and dogs and the poor acuity of rodents and horses support this hypothesis. However, it should be noted that there are likely to be other reasons for an animal to localize sound accurately, and at least one nonpredatory species, the elephant, is an accurate localizer. Nevertheless, the predator/prey distinction seems to correspond to much of the data.

The type of habitat preferred by a species may also influence the usefulness of accurate sound localization. Animals living in dense jungle or brush, where vision is obstructed (such as many primates) might have to rely more heavily on sound to locate nearby animals than those living on open plains (such as horses). Though it is not always possible to assign an animal to a particular type of habitat, this factor also seems to account for some of the variation in localization ability.

A third factor is the circadian cycle of a species (nocturnal vs. diurnal). Animals that are active at night when vision is less useful (especially on moonless or overcast nights) might find accurate sound localization more advantageous than those active during daylight. Animals that are polyphasic, such as the large herbivores (e.g., elephants and horses), would be expected to be well adapted to both light and dark environments (as they are visually; see Walls, 1942) and should also be good localizers. Contrary to that expectation, among the animals whose sound-localization ability is known, the most accurate localizers are diurnal (man and macaque), with only one polyphasic animal (elephant) showing good acuity. The other polyphasic animal (horse) is an exceptionally poor localizer. On the other hand, among primarily nocturnal animals, both good localizers (cat and opossum) and poor localizers (three species of rats and hedgehog) can be found. Thus the circadian cycle, after the accumulation of more data, may be a less influential factor for sound localization than it initially might appear.

Finally, the possibility exists that the variation in mammalian sound-localization ability may be related to the relative contributions of other sensory modalities in localizing the position of an object in space (Gourevitch, 1980). In particular, it has been argued that a principal function of sound localization is to direct the eyes toward the source of a sound so that the sound source can be located and identified visually (Hafter & DeMaio, 1975; Pumphrey, 1950). Along this line, it has been noted that there is a positive correlation between the size of the binocular visual field and sound-localization acuity (R. Heffner & Heffner, 1983b). Mammals with frontally placed eyes and, therefore, large binocular visual fields are better able to localize frontally placed sound sources than are animals with narrow binocular fields (and wide panoramic vision). Because the size of the binocular field indicates the degree to which the eyes are directed frontally, this correlation may indicate that the greater the degree of frontal vision, the more precision is called for in using sound localization to direct the eyes to an object located in the binocular field. However, the final appraisal of this relation probably should await further information, particularly the establishment of the visual acuity of the same animals.

In conclusion, as the number of species for whom sound-localization thresholds are available has increased, it is no longer possible to argue that variations in hearing and sound localization are simply the result of using different psychophysical procedures (see Iversen, 1978) or that differences in localization acuity are due to the size of the available cues (cf. Masterton & Diamond, 1973; Masterton et al., 1969). Instead, the ability of mammals to localize frontally placed sound sources varies significantly from one species to the next, evidently in response to variation in other sources of selective pressure for accurate sound localization. The exact sources of this selective pressure, however, remain to be determined.

References

Brown, C. H., Beecher, M. D., Moody, D. B., & Stebbins, W. C. (1980). Localization of noise bands by Old World monkeys. *Journal of the Acoustical Society of America, 68,* 127–132.

Casseday, J. H., & Neff, W. D. (1973). Localization of pure tones. *Journal of the Acoustical Society of America, 54,* 365–372.

Chambers, R. E. (1971). *Sound localization in the hedgehog* (Paraechinus hypomelas). Unpublished master's thesis, Florida State University.

Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *Journal of Genetic Psychology, 42,* 206–208.

Gourevitch, G. (1980). Directional hearing in terrestrial mammals. In A. N. Popper & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 357–373). New York: Springer Verlag.

Hafter, E. R., & DeMaio, J. (1975). Difference thresholds for interaural delay. *Journal of the Acoustical Society of America, 57,* 181–187.

Harrison, J. M., & Downey, P. (1970). Intensity changes at the ear as a function of the azimuth of a tone source: A comparative study. *Journal of the Acoustical Society of America, 47,* 1509–1518.

Heffner, H., & Masterton, B. (1978). Contribution of auditory cortex to hearing in the monkey (*Macaca mulatta*). In D. J. Chivers & J. Herbert (Eds.), *Recent advances in primatology: Vol. 1. Behaviour* (pp. 735–754). New York: Academic Press.

Heffner, H., & Masterton, R. B. (1980). Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *Journal of the Acoustical Society of America, 68,* 1584–1599.

Heffner, H., & Whitfield, I. C. (1976). Perception of the missing fundamental by cats. *Journal of the Acoustical Society of America, 59,* 915–919.

Heffner, R., & Heffner, H. (1982). Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *Journal of Comparative and Physiological Psychology, 96,* 926–944.

Heffner, R., & Heffner, H. (1983a). Hearing in large mammals: Horses (*Equus caballus*) and cattle (*Bos taurus*). *Behavioral Neuroscience, 97,* 299–309.

Heffner, R., & Heffner, H. (1983b). Sound localization acuity in mammals and its relation to visual fields [Abstract]. *Journal of the Acoustical Society of America, 73,* S42.

Iversen, S. D. (1978). Hearing and acoustic communication in primates: Concluding discussion. In D. J. Chivers & J. Herbert (Eds.), *Recent advances in primatology* (Vol. 1, pp. 849–852). New York: Academic Press.

Kelly, J. B. (1980). Effects of auditory cortical lesions on sound localization of the rat. *Journal of Neurophysiology, 44,* 1161–1174.

Kelly, J. B., & Glazier, S. J. (1978). Auditory cortex lesions and discrimination of spatial location by the rat. *Brain Research, 145,* 315–321.

Kuhn, G. F. (1977). Model for the interaural time differences in the aximuthal plane. *Journal of the Acoustical Society of America, 62,* 157–167.

Masterton, B., & Diamond, I. T. (1973). Hearing: Central neural mechanisms. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception* (Vol. 3, pp. 407–448). New York: Academic Press.

Masterton, B., Heffner, H., & Ravizza, R. (1969). The evolution of human hearing. *Journal of the Acoustical Society of America, 45,* 966–985.

Mills, A. M. (1958). On the minimum audible angle. *Journal of the Acoustical Society of America, 30,* 237–246.

Phillips, D. P., Calford, M. B., Pettigrew, J. D., Aitkin, L. M., & Semple, M. N. (1982). Directionality of sound pressure transformation at the cat's pinna. *Hearing Research, 8,* 13–28.

Pumphrey, R. J. (1950). Hearing. *Symposium of the Society for Experimental Biology, 4,* 1–18.

Ravizza, R. J., & Masterton, B. (1972). Contribution of neocortex to sound localization in opossum (*Didelphis virginiana*). *Journal of Neurophysiology, 35,* 344–356.

Renaud, D. L., & Popper, A. N. (1975). Sound localization by the bottlenose porpoise *Tursiops truncatus. Journal of Experimental Biology, 63,* 569–585.

Roth, G. L., Kochhor, R. K., & Hind, J. E. (1980). Interaural time differences: Implications regarding the neurophysiology of sound localization. *Journal of the Acoustical Society of America, 68,* 1643–1651.

Siegel, S. (1956). *Nonparametric statistics for the behavioral sciences.* New York: McGraw-Hill.

Terhune, J. M. (1974). Directional hearing of a harbor seal in air and water. *Journal of the Acoustical Society of America, 56,* 1862–1865.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation.* New York: Hafner.

Woodworth, R. S., & Schlosberg, H. (1965). *Experimental psychology.* New York: Holt, Rinehart & Winston.

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