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Hearing in the Elephant (*Elephas maximus*): Absolute Sensitivity, Frequency Discrimination, and Sound Localization

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A young Indian elephant was tested to determine its absolute sensitivity, frequency-discrimination thresholds, and sound-localization thresholds. The elephant was found to have an audibility curve similar to that of other mammals but one that is more sensitive to low frequencies and less sensitive to high frequencies than any other mammalian audiogram including human's. The elephant's sensitivity to frequency differences at low frequencies was found to equal that of humans. Finally, the elephant was found to be very accurate at localizing sounds in the azimuthal plane, with thresholds around 1° for broadband noise. The elephant's ability to localize pure tones suggested that it could use both binaural time- and intensity-difference cues to localize sound.

Comparative studies of hearing have shown that the hearing abilities of mammals are not uniform but vary significantly from one species to the next. In particular, the limit of high-frequency hearing in mammals varies from 19 kHz to more than 100 kHz, and the low-frequency hearing limit varies from .03 kHz to 10.3 kHz, a range of more than eight octaves (for a review, see H. Heffner & Masterton, 1980). However, such variation is not limited to absolute sensitivity, as mammalian sound-localization thresholds range from 1° to more than 20° (H. Heffner & Masterton, 1980; Mills, 1958), and frequency difference limens also show significant variation (Fay, 1974; R. Heffner, Heffner, & Masterton, 1971). Thus, mammalian hearing appears to be characterized by a large degree of variation among species in the ability to detect, localize, and discriminate sounds.

In searching for explanations of such variation, it soon becomes apparent that factors related to the size of an animal play an important role in hearing in at least two ways. First, it is generally agreed that the size of the auditory apparatus itself, i.e., the outer, middle, and inner ears, affects the response of the ear to sound. The sizes of the tympanic membrane, auditory ossicles, and bulla have been linked to the frequency response properties of the ear, and the length of the basilar membrane is believed to be a factor in frequency discrimination (e.g., Dallos, 1973; Fleischer, 1978; von Bekesy, 1960). Thus, size is a factor in determining the mechanical response properties of the ear, and variation in the size of the auditory apparatus is undoubtedly linked to the observed variation in hearing ability.

Size has also been observed to be correlated with hearing ability in a second way. Specifically, the ability to hear high-frequency sounds is inversely related to the functional size of an animal's head (where functional head size is defined as the distance between the ears, as measured around the head, divided by the speed of sound; see H. Heffner & Heffner, 1981; H. Heffner & Masterton, 1980; Masterton, Heffner, & Ravizza, 1969). That is to say, mammals with small heads, and therefore close-set ears, appear better able to hear high-frequency sounds than mammals with large heads and wide-set ears. This relation, with its probable basis in the acoustic cues used

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for sound localization, constitutes a second level of explanation—one in which size is relevant to an understanding of the ecological variables involved in the variation in mammalian hearing.

Given the role of size-related factors in hearing, a knowledge of the auditory capacities of mammals ranging in size from the largest to the smallest would seem to be necessary in order to obtain a complete picture of mammalian hearing. However, all animals studied to date have been relatively small, with humans being the largest terrestrial mammals whose auditory capacities are known. This report, then, is the first in a series concerned with the question of hearing in large mammals, i.e., mammals larger than humans. In this report we present the results of auditory tests of absolute sensitivity, frequency-discrimination ability, and sound-localization acuity carried out on an Indian elephant. Though the reason for examining an elephant was to increase our general knowledge of hearing in large mammals, the relation of size to hearing ability in all mammals is specifically addressed for each of these three auditory abilities.

General Method

Subject

The elephant chosen for this study was a 7-yr-old (adolescent) female Indian elephant (*Elephas maximus*) located at the Ralph Mitchell Zoo in Independence, Kansas. The animal's shoulder height was approximately 2.2 m, and the distance between its ears (measured around the upper forehead) was 115 cm. The elephant had no history of serious illness, and its ears were inspected and found to be free of any signs of obstruction or disease.

The elephant was maintained on the regular diet provided by the zoo and was not deprived of food or water for these tests. However, testing was conducted shortly before the animal's morning feeding time, and the elephant could be relied upon to work for the fruit-flavored sugar solution used here as a reward for several hours, especially during the warm months of the year (April to October). Indeed, a typical test session lasted approximately 2 hr during which time the animal completed about 1,000 trials and consumed over 50 l of the sugar solution.

Behavioral Apparatus

The elephant was tested in a cement block room (6.7 × 5.6 × 4.6 m) in which it was normally housed each night. An adjacent area, which was separated from the elephant room by a cement-block wall 1.6 m high topped by a chain-link fence, was used as a control room to house the test equipment.

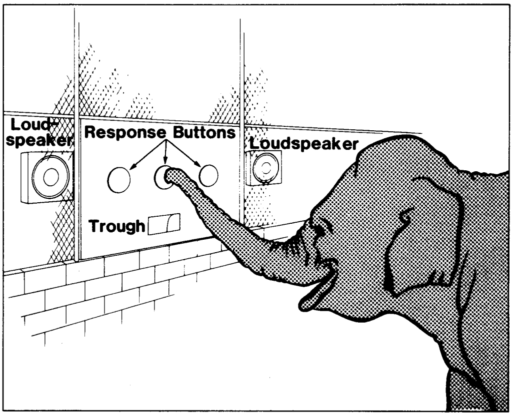

Figure 1. Response panel used to test the elephant. (The elephant was trained to initiate a trial by pressing the center button and then to press the left button or right button, depending on which of two stimuli was presented. Correct responses were rewarded with a fruit-flavored sugar solution delivered into the trough.)

A response panel (70 × 50 cm) was mounted in an opening in the chain-link fence which separated the two rooms (Figure 1). This panel contained three Plexiglas response buttons (13 cm in diameter) in a horizontal row, with a small drinking trough (13 × 15 × 7 cm) at the bottom below the center button. A 25-l reservoir containing water and a 5-l reservoir containing a concentrated fruit-flavored sugar solution (typically strawberry or cherry) were located in the control room and suspended above and to the side of the response panel. These solutions were simultaneously dispensed into the trough in 30–50-ml amounts through two solenoid-operated water valves.

Because of the variety of auditory stimuli employed, the details of the sound generation are described with the appropriate test. In general, tones were produced by one of two oscillators (Hewlett-Packard 200CD and 201CR), noise stimuli, by a noise generator (Lehigh Valley 1524), and clicks, by a square-wave generator (Coulbourn S78-22). The signals were shaped with rise–fall gates (Coulbourn S84-04), amplified with a mixer-amplifier (Coulbourn S82-24), and filtered with a band-pass filter (Krohn-Hite 3202); the intensity was adjusted with attenuators (Hewlett-Packard 350D and/or Coulbourn S85-08). The loudspeakers used consisted of a 15-in. (38-cm) woofer in a .45-m^3 enclosure for very low frequencies, Long L15F dome speakers and enclosed 3-in. (7.6-cm) wide-range speakers for midfrequencies, and Motorola piezoelectric tweeters for high frequencies.

Sound pressure levels (i.e., decibels re 20 $\mu N/m^2$) were measured with a Brüel and Kjaer microphone amplifier (B & K 2203), a 1-in. (2.54-cm) condenser microphone (B & K 4131), and an octave filter (B & K 1613) or a variable band-pass filter (Krohn-Hite 3202 or 3550). A pistonphone (B & K 4220) and a sound level calibrator

Table 1
Effect of Placing the Elephant in the Sound Field on the Measured Intensity of the Sound

Frequency (in Hz)	Change in intensity (in dB)
31.5	−1
63	5
125	4
250	2
500	0
1000	0
2000	2
4000	1
8000	0
16000	3

Note. Measurements were taken at the position of the elephant's left auditory meatus first without and then with the animal in the sound field. The loudspeaker was located 30° to the left of midline.

(B & K 4230) were used to calibrate the sound measuring system. Sound measurements were taken at the position occupied by the elephant's ears both with and without the animal in the sound field. The presence of the elephant increased the sound pressure level by an average of 1.6 dB, with the greatest increase being 5 dB at 63 Hz (Table 1). In order to make the thresholds for the elephant comparable with those published for other species, all thresholds are based on sound pressure measurements taken without the animal in the sound field.

The background noise level was measured at various times under the same conditions in which all testing was conducted—i.e., in the early morning with the ventilating system turned off. Measurements were made with the B & K 2203 microphone amplifier, B & K 4131 microphone, and Krohn-Hite 3550 variable band-pass filter. Background noise measurements were taken at one-sixth octave points from 3.15 Hz to 16 kHz with both the high- and low-pass sections of the filter set to the center frequency. These settings gave a 24 dB/octave slope and an insertion loss of 6 dB, due to overlapping the high- and low-pass filter settings, which was compensated for by adding 6 dB to the resulting measures. Additional measurements taken with a Krohn-Hite 3202 band-pass filter and a B & K 1613 octave filter were in agreement with the initial measurements.

Psychophysical Procedure

The same basic two-choice procedure was used in all of the tests. Briefly, the elephant was tethered 1.2 m in front of the response panel and trained to press the center button with its trunk. This "observing" response positioned the animal's head directly in front of the panel and initiated a trial. A trial consisted of the presentation of one of two stimuli (e.g., tone vs. silence, sound from the left side vs. sound from the right side, tone pips of same frequency vs. tone pips of alternating frequency), with the sequence of trials determined by a quasi-random schedule (Gellermann, 1933). The elephant was required to press the left button when one stimulus was presented and to press the right button when the other stimulus was presented. A correct response was rewarded by dispensing 30–50 ml of fruit-flavored sugar solution into the trough which the animal then sucked into its trunk and blew into its mouth, usually within 2 sec. An error was followed by a short wait (usually 5 sec) before a new trial could be initiated.

Thresholds were determined by reducing the difference between the two stimuli in blocks of 10 to 25 trials until the animal could no longer distinguish the two stimuli. Threshold was statistically defined as the level at which the animal could discriminate between the two stimuli at the .01 one-tailed level of significance (binomial distribution) which was typically the 63% correct level.

Experiment 1: Absolute Sensitivity

Method

Sound production. Sine waves produced by an oscillator were led to a rise–fall gate, attenuator, amplifier, and finally to a loudspeaker. For frequencies below 2 kHz, the 15-in. (38-cm) woofer was used, and for 2 kHz and above a piezoelectric tweeter was used. The speakers were located at ear level 115 cm in front of the animal, 30° to the left or right of midline, and were pointed toward the ear on that side. (Separate audiograms were obtained for the two different speaker locations.) In order to avoid switching transients, a rise–decay time of 20 msec was used for frequencies of 500 Hz and higher. To allow approximately 10 cycles to occur during the rise–decay times of the lower frequencies, we used rise–decay times of 50, 100, 200, 400, and 500 msec for 250, 125, 63, 31.5 and 16 Hz, respectively. All tones were pulsed, with tones of 500 Hz and higher being pulsed at a rate of two per second, i.e., 400 msec on, 100 msec off. At lower frequencies, longer durations were used to compensate for the longer rise–decay times and allow the tone to remain at its full intensity for 380 msec and to be completely off for 80 msec.

Psychophysical procedure. The elephant pressed the center button with its trunk in order to initiate a trial which consisted of either the presence or the absence of a pulsing tone. The elephant was required to wait for four tone pulses to occur (2 sec to 5.8 sec, depending on frequency) and then press the left button if a tone had been presented or to press the right button if a tone had not been presented.

Thresholds were first estimated by the method of descending limits in which the intensity of the tone was reduced in steps of 5 or 10 dB, with blocks of 10–20 trials at each intensity, until the animal could no longer distinguish tone trials from no-tone trials. Once an estimate of threshold had been obtained, a final threshold was determined by using a modified method of constant stimuli. Tones were presented in blocks of 25 trials at intensity levels extending from 10 dB below to 10 dB above the estimated threshold, in 5-dB increments. Testing for a frequency was judged complete when thresholds obtained on different days were within 3 dB of each other. If thresholds differed by more than 3 dB, testing continued until a stable threshold emerged.

Because the elephant was not tested in a sound-treated or anechoic chamber, special precautions were taken to ensure the validity of the results. First, separate threshold testing was conducted first with the speaker located 30° to the left and then 30° to the right of the animal's midline. This procedure ensured that each ear received the sound directly and provided a check on the possible effect of room acoustics. Second, all testing was conducted in the early morning before zoo personnel and visitors arrived, and noise sources such as birds and crickets were cleared from the test room and surrounding area. Finally, the background or ambient noise level of the room was carefully measured on several different occasions.

Results and Discussion

The audiogram of the elephant was determined twice, first with the loudspeakers placed 30° to the left and again with the speakers placed 30° to the right of the animal's midline (see Figure 1). This was done for two reasons. First, directing the speakers toward the animal's ear from the side ensured that the high frequencies would not be shadowed by the animal's head, as might have happened if the speakers were pointed at the forehead. Second, determining the audiogram for these two speaker placements served as a check for the possibility of a differential hearing loss between the two ears or a significant variation in the sound field due to the presence of standing waves and nodes. As can be seen in Figure 2, however, there were no unusually large differences between the left and right audiograms, with the average difference being 3 dB. Since such variation is not uncommon when one ear is compared with the other, or in test–retest comparisons for two ears, the two audiograms suggest that there were no serious anomalies either in the elephant's hearing ability or in the sound field.

Audiogram. Turning now to an analysis of the elephant's hearing, it can be seen that the audiogram exhibits the characteristic shape of mammalian audiograms (cf. H. Heffner & Masterton, 1980). Beginning at the low frequencies, the animal shows a gradual decrease in threshold, to a point of best hearing at 1 kHz. Above 1 kHz, the thresholds begin to increase, with the increase becoming relatively steep as the upper frequency limit of hearing is approached.

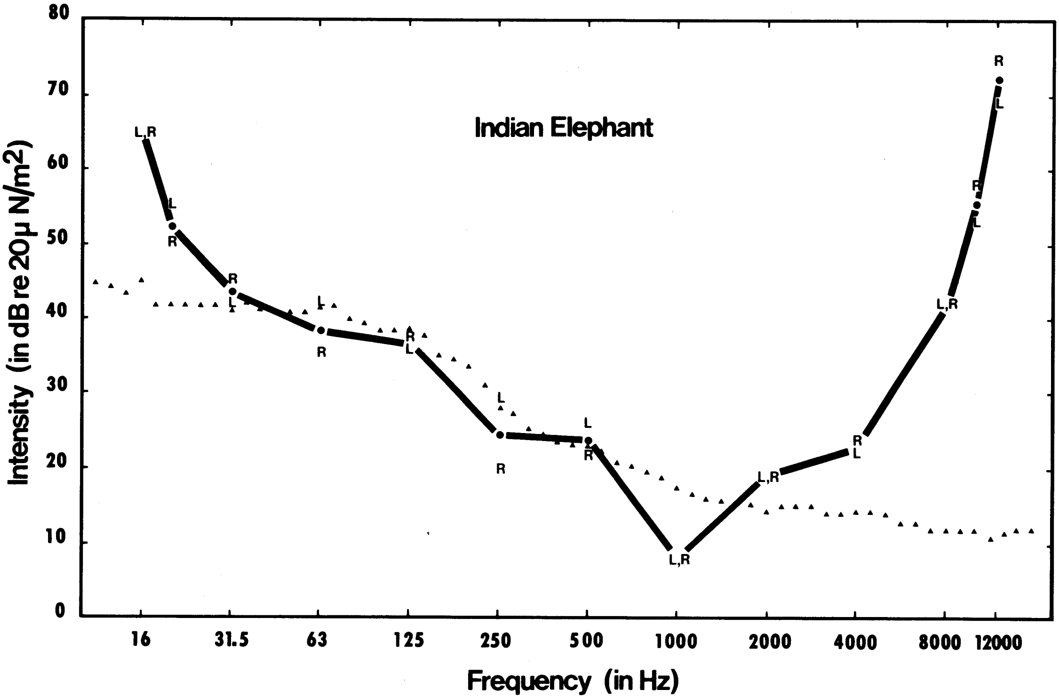

Figure 2. Audiogram of the elephant. (L and R indicate thresholds obtained with the loudspeaker pointed at the left and right ears, respectively; the solid line indicates the average of the two thresholds. Triangles indicate the level of background noise.)

Despite its typical appearance, the audiogram reveals three unique features of elephant hearing. These features concern high-frequency hearing, low-frequency hearing, and best frequency of hearing.

Background noise. Before turning to the details of the audiogram, it is important to consider the possible effects of background noise on the audiogram (see Figure 2). At frequencies below 31.5 kHz, the elephant's thresholds were well above the background noise level, a result suggesting that the noise was not a factor in determining very low frequency thresholds. (It might be noted that below 50 Hz, the background noise in the elephant room was 5–10 dB quieter than most double-wall soundproof chambers we have measured. This is probably due to the fact that all ventilating machinery in the elephant house was turned off during testing.) From 31.5 Hz to 2 kHz, however, the thresholds lie close to the background noise level. Above 2 kHz, the background noise level continued to decrease while thresholds increased, which indicates that background noise was not a factor in high-frequency thresholds.

Because the thresholds from 31.5 Hz to 2 kHz lie close to the background noise level, it appears possible that they may have been affected by the noise. However, just how much these thresholds may have been affected is uncertain—though the masking of tones by carefully filtered noise has been well studied (e.g., Patterson & Green, 1978; Zwislocki, 1978), the spectrum of the natural noise encountered here may have departed significantly from that used in psychophysical studies of masking. As a result, the influence of the ambient noise on thresholds is not easily predicted. Thus, it is not surprising that whereas several of the thresholds are within 3 dB of the background noise level, the 1 kHz threshold is 10 dB below it. In spite of such uncertainty, the close parallel between the background noise level and the thresholds from 31.5 Hz to 2 kHz suggests that the thresholds in this range may represent a minimum estimate of the elephant's sensitivity.

High-frequency hearing. As Figure 2 shows, the thresholds of the elephant increased sharply above 4 kHz as frequency was increased. The elephant was able to hear 12 kHz at a level of 72 dB but was completely unable to hear 14 kHz at 90 dB. Frequencies up to 32 kHz were also tested at levels of 90 dB or greater, but no response to these sounds could be detected. By the 60-dB criterion, then, the highest audible frequency for the elephant at this intensity is 10.5 kHz.

The high-frequency hearing limit of the elephant is the lowest of any mammal yet tested. Whereas the elephant's 60-dB cutoff is 10.5 kHz, the average mammalian cutoff is 55 kHz, and several species, such as bats and porpoises, can hear above 100 kHz (see H. Heffner & Masterton, 1980). Indeed, even the 19-kHz cutoff of humans easily exceeds that of the elephant. However, the elephant's performance was not unexpected, as it has been demonstrated that high-frequency hearing is inversely related to the functional distance between the two ears (H. Heffner & Masterton, 1980; Masterton et al., 1969). Just how the elephant fits this relationship is discussed in a later section.

Low-frequency hearing. A second noteworthy aspect of the elephant audiogram is the low-frequency sensitivity of the animal. The elephant was able to hear 16 Hz at an intensity of 65 dB, and its lowest audible frequency at an intensity of 60 dB is calculated to be 17 Hz.

The elephant's low-frequency sensitivity is superior to that of any mammal yet tested. Whereas humans were previously considered to have the best low-frequency sensitivity of mammals, the 60-dB low-frequency cutoff of humans is nearly one octave higher than the elephant's cutoff. Indeed, the pigeon, which appears to be especially sensitive to infrasound, is the only terrestrial vertebrate known to be more sensitive to low-frequency sounds than the elephant (e.g., Kreithen & Quine, 1979).

It may be noted that while the elephant is more sensitive to low-frequency sounds than other mammals, it is also less sensitive to high-frequency sounds than other mammals. This observation, that the elephant possesses a typical mammalian audiogram, but one that has been shifted toward the lower frequencies, lends support to the idea that the ability to hear high and low frequencies may be related (H. Heffner & Masterton, 1980). This correlation between high- and low-frequency hearing is discussed further in a later section.

Best frequency of hearing. The most sensitive point of the elephant's audiogram is at 1 kHz at which the animal's threshold is 8 dB. One kilohertz is much lower than the average mammalian best frequency of 9.8 kHz, though other species, such as the kangaroo rat, also have a best frequency of 1 kHz (H. Heffner & Masterton, 1980). The 8 dB best sensitivity is within one standard deviation of the average mammalian lowest threshold of −1.5 dB, but this is not particularly sensitive. This apparent lack of sensitivity may be due to the presence of greater background noise levels in the elephant's best range of hearing since most mammals have their most sensitive points at higher frequencies at which background noise levels are generally much lower and thus not a factor. In short, it is not impossible that the elephant may be more sensitive and have a lower frequency of best hearing than the present audiogram shows.

In summary, the elephant possesses good low-frequency hearing coupled with poor high-frequency hearing. Though the animal's best frequency of hearing appears to be near 1 kHz, the animal's true sensitivity in this frequency region may have been masked somewhat by background noise.

Experiment 2: Frequency Difference Limens

The ability to discriminate between sounds on the basis of frequency is believed to depend on the mechanical resolution of frequencies along the basilar membrane. Since this resolution is much sharper in the elephant than in any other animal examined so far (von Békésy, 1960), the elephant may possess unusually good frequency-discrimination ability. Thus, a knowledge of the elephant's frequency-discrimination ability is of interest to the study of cochlear mechanics and frequency analysis in general.

Method

Sound production. Sine waves were produced by two oscillators, one of which was set to a standard frequency while the other was set to a comparison frequency. The sine waves were calibrated with a frequency counter, led to two rise–fall gates, a mixer-amplifier, a programmable attenuator, and, finally, to a loudspeaker.

The auditory stimulus consisted of a train of tone pulses 100 msec in duration, with 100-msec off time and a 20-msec rise–decay time. The tones were presented at a level 50 dB above threshold, but with the intensity of each tone pulse randomly varied ±2.5 dB in half-dB steps in order to reduce the possibility of the elephant's using intensity differences as a cue. The stimulus consisted of a train of tone pulses in which either all the pulses were the same frequency (i.e., $F, F, F, \ldots$) or the pulses alternated in frequency (i.e., $F, F+\Delta F, F, F+\Delta F, \ldots$).

Psychophysical procedure. The elephant was trained to initiate a trial by pressing the center button in order to turn on a train of tone pulses. The animal was then required to wait until at least eight tone pulses had been presented (i.e., 1.5 sec) and then press the left button if the tone pulses were of the same frequency or press the right button if the tones alternated between two frequencies.

Thresholds were determined by reducing the frequency difference (ΔF) until the animal could no longer distinguish between the two types of tone pulse trains. In addition, the frequency of the comparison oscillator was occasionally set to match the frequency of the standard oscillator in order to demonstrate that the animal could not distinguish between the two signals when their frequencies were the same. Trials were given in blocks of 50 for each value of ΔF, and threshold determination was judged complete when testing on at least 3 days yielded a stable threshold. Thresholds were determined for frequencies in octave steps from 250 Hz to 8 kHz, with 2,000–4,000 trials being given for each frequency.

Results and Discussion

Though the elephant learned to perform the frequency discrimination task at a level of 90% correct by the second session, this discrimination proved to be a relatively difficult one. In contrast to the previous task, the elephant could not maintain perfect performance for more than 50 consecutive trials even when large frequency differences were used. Such difficulty is not unusual for mammals—other species also have difficulty with frequency discrimination even when different behavioral procedures are used (e.g., R. Heffner et al., 1971).

The general lower performance of the elephant on frequency discrimination can be seen in the psychophysical functions for the individual frequencies in Figure 3. As can be seen in this figure, the best performance of the animal was 92% correct at 1 kHz, and best performances for the other frequencies ranged between 82% and 89%. Furthermore, rather than exhibiting the typical shape of psychophysical functions (i.e., a high level of performance followed by a steady decline as threshold is neared), performance sometimes fluctuated erratically as the frequency difference was decreased. Such performance makes it misleading to define threshold in terms of the 75% level because performance occasionally fluctuated about this point (cf. 250 Hz, 500 Hz, and 2 kHz in Figure 3). On the other hand, performance near the statistical chance level was much smoother, and threshold judgments by this criterion are relatively straightforward. Therefore, both the 75% correct and the statistical definitions of threshold are considered in the following discussion.

The Weber fractions for the various frequencies are shown in Figure 4 for both definitions of threshold. At the two lowest frequencies, both definitions yield similar thresholds, with values of about .005 for the 75% level and .002 for the statistical threshold level. The Weber fraction increases with frequency in both cases but much more dramatically for the 75% level. Although the statistical level Weber fraction gradually increases to .01 at 8 kHz, the 75% level shows a sharp increase at 1 kHz followed by a slower increase to .048 at 8 kHz. As the psychophysical functions in Figure 3 indicate, this increase is due to the inability of the elephant to perform consistently above 75% correct on frequency differences, which it could still reliably perform above chance level.

Despite the differences at the higher frequencies, both definitions of threshold indicate that the animal was most sensitive at the lower frequencies. This observation

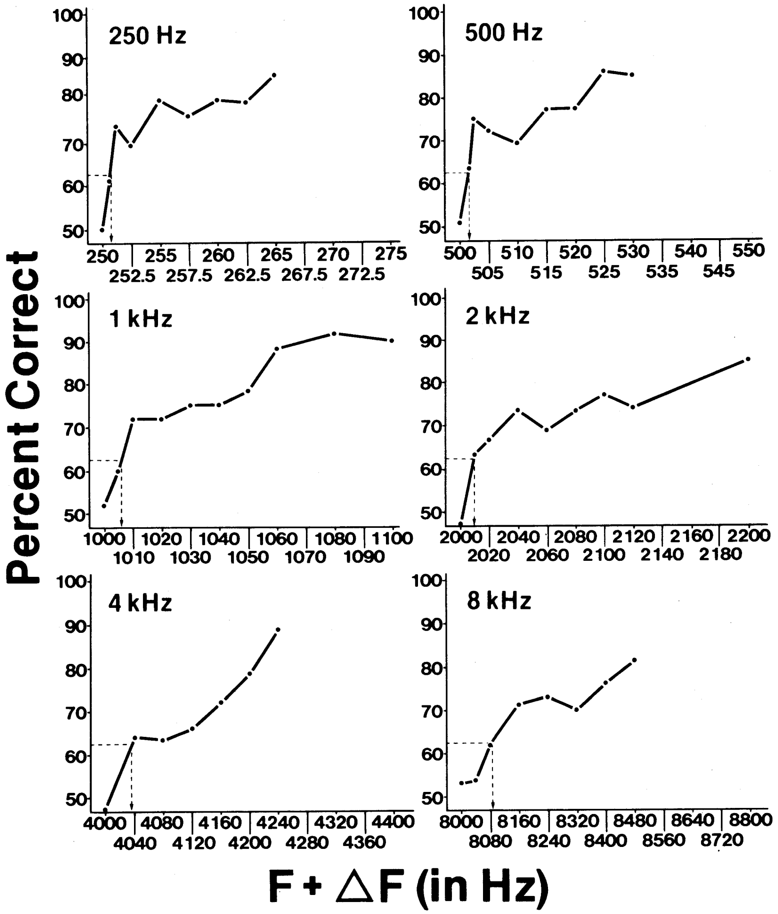

Figure 3. Psychophysical functions obtained in the frequency-discrimination tests. (Dashed lines indicate statistical threshold level.)

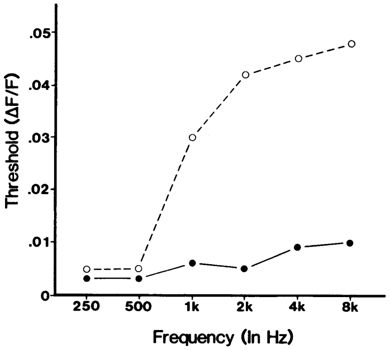

Figure 4. Frequency difference limens as a function of frequency. (Filled circles indicate statistical threshold level; open circles indicate 75% correct threshold.)

is of interest, as a similar increase in sensitivity at lower frequencies in humans has been interpreted as indicating a special low-frequency mechanism for frequency analysis (e.g., Fay, 1974; Wever, 1949). In order to determine whether the elephant's good low-frequency discrimination held for frequencies below 250 Hz, we attempted to obtain thresholds at 32 Hz, 45 Hz, 50 Hz, 63 Hz, 80 Hz, 100 Hz, 125 Hz, 160 Hz, and 200 Hz. However, at these frequencies, the animal's performance proved too variable, occasionally shifting even when the loudspeaker was moved. Therefore, these results were not considered sufficiently reliable to be reported here. In spite of this variation, we found no indication that the difference limens at these frequencies might be any less sensitive than those at 250 Hz and 500 Hz. Therefore, at this time there is reason to believe that the elephant's frequency discrimination is most acute at frequencies below 1 kHz.

In summary, though the elephant had difficulty in performing the frequency-discrimination task, the resulting difference limens suggest that the elephant possesses good frequency resolution, particularly at 250 and 500 Hz, and possibly lower.

Experiment 3: Sound Localization

Since ecological pressures to localize sound appear to be a major factor in the evolution of hearing, knowledge of the localization ability of any mammal is important to our understanding of hearing. However, because of its especially large interaural distance, the elephant's sound-localization ability is of special interest. Specifically, the distance between the ears as measured around the head (interaural distance) is an important factor in sound localization in that it determines the magnitude of the two primary binaural cues for sound localization—the binaural time and intensity-difference cues. For a particular angle, the difference in the time of arrival of a sound at the two ears (Δt) and the difference in the frequency-intensity spectra of a sound reaching the two ears (Δfi) are greater for animals with large interaural distances than for animals with small interaural distances. Thus, it is of interest to know the ability of the elephant—the largest extant terrestrial mammal—to localize sound.

Method

Sound production. Sound-localization thresholds were determined for single clicks, white noise, narrow-band noise centered at octave intervals from 125 Hz to 8 kHz (24 dB/octave roll-off from center frequency), 8 kHz high-pass noise (48 dB/octave roll-off), and pure tones. The white noise, noise band, and pure-tone stimuli consisted of a single burst of sound of 100-msec duration with 50 msec rise–decay (i.e., 50 msec rise, 50 msec on fully, 50 msec decay). In addition, a threshold was determined for a single 5-msec burst of white noise with fast (100-μsec) rise–decay.

In order to produce clicks, .8-msec square waves produced by a square wave generator were led first to a programmable attenuator, then to an amplifier, and, finally, to a dome loudspeaker. White or filtered noises were generated by a noise generator, led to a band-pass filter, a rise–fall gate, programmable attenuator, amplifier, and then to a loudspeaker. Tonal stimuli were produced by an oscillator, led to a rise–fall gate, programmable attenuator, amplifier, and then to a loudspeaker. Two 3-in. (7.6-cm) wide-range loudspeakers were used for filtered noise and tonal stimuli from 125 to 500 Hz. All higher frequency stimuli were transduced with dome tweeters. Tonal stimuli were presented at 40 dB above the animal's threshold as determined in the previous experiment (i.e., at 40 dB sensation level). Click and noise stimuli were presented at a level at least 40 dB above the animal's threshold as estimated by attenuating the stimuli until the animal's localization performance fell to chance or the animal refused to respond. All stimuli were randomly attenuated over a ± 3-dB range from one trial to the next.

A pair of loudspeakers were suspended from a perimeter bar behind the chain fence, 145 cm from the animal and 20 cm above the level of the auditory meatus, with each speaker placed at a specified angle from the animal's midline (e.g., 30° left and 30° right for an angular separation of 60°). The speakers were individually calibrated and were used in matched pairs to prevent the animal from discriminating the speakers on the basis of quality difference instead of locus. In addition, speaker pairs were routinely changed within a session. However, since in no instance was the animal able to discriminate between two speakers when the azimuth of separation was reduced to 0°, it was clear that the elephant was responding to location and not to any difference in spectrum or intensity.

Psychophysical procedure. The elephant pressed the center button in order to initiate a trial, which resulted in the presentation of a brief sound 1 sec later from either the left or the right loudspeaker. The purpose of the 1-sec delay was to ensure that the stimulus was not masked by the sound of the animal's pressing the center button. (Close observation revealed no significant head movements during the delay.) The animal was then rewarded for pressing the button on the side from which the sound came. Threshold was determined by moving the loudspeakers toward the midline until the animal could no longer distinguish left sounds from right sounds. At least 50 trials were given at angles above and below threshold for a particular stimulus in any one session. Threshold determination was judged complete when testing on at least 2 days yielded a stable threshold.

Results and Discussion

Click and white noise. Two types of stimuli were initially used to determine the elephant's ability to localize brief complex sounds: single clicks and single bursts of 100-msec white noise with either a fast (100-μsec) or a slow (50-msec) rise–decay time. Because of the brevity of the stimuli, the animal could not track the sound by moving toward the source, as would be the case with a sound that stayed on until the animal responded left or right. Nor is it likely that the animal could scan the sound field by moving its head, for even a small animal, such as a cat, usually takes at least 100 msec to orient to a sound (Thompson & Masterton, 1978). Therefore, the use of these stimuli constituted a test of the elephant's ability to localize sound without the aid of tracking or scanning movements.

As shown in Figure 5, the elephant was able to localize these stimuli perfectly at angles of 20° or more. Such performance indicates that the sound-localization task was an easy one for the elephant to perform.

As the angle of separation between the loudspeakers was decreased, the animal's performance gradually began to decrease, with performance falling to chance level between .5° and 2°, depending on the stimulus. From Figure 5 it can be seen that below 10° the white noise bursts were more accurately localized than the click and that performance on noise with a fast rise–decay was better than on noise with a slow rise–decay. However, the higher performance on the white noise bursts may be due to the fact that these stimuli were of longer duration and broader frequency spectrum than the

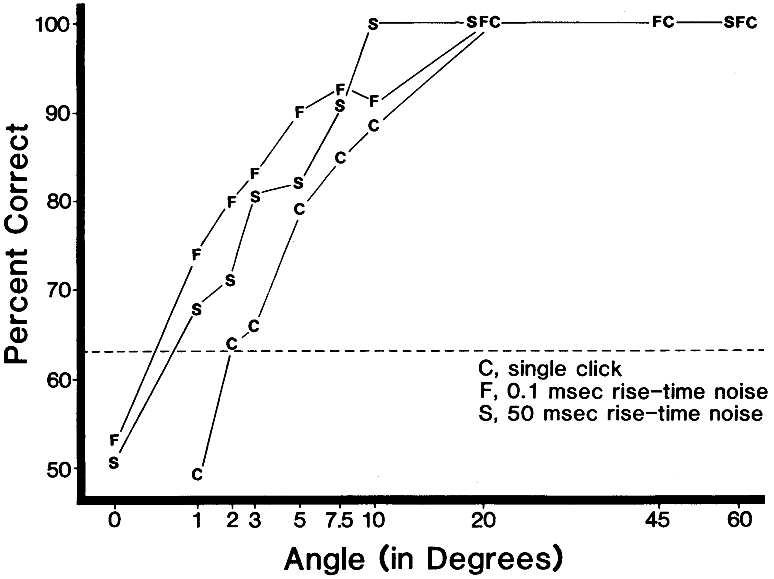

Figure 5. Sound-localization performance for single click and for white noise with .1-msec (fast) and 50-msec (slow) rise times. (Dashed line indicates statistical threshold level.)

click. The higher performance on the fast-onset white noise is also not unusual since sounds with fast onsets are, under certain conditions, more easily localized than those with slower onsets (e.g., Kunov & Abel, 1981).

Pure tones. To explore further the ability of the elephant to discriminate differences in the direction of a sound source, we tested the animal on its ability to localize brief tone pips from 125 Hz to 8 kHz. This test is of physiological significance because the ability to localize low-frequency tones suggests that the animal can use binaural time or phase-difference cues for sound localization whereas the ability to localize high-frequency tones suggests the ability to use binaural spectrum- or intensity-difference cues (e.g., Brown, Beecher, Moody, & Stebbins, 1978; Masterton, Thompson, Bechtold, & RoBards, 1975).

The threshold curves for tone localization are shown in Figure 6. As can be seen in this figure, the performance of the elephant varied not only with angle of separation but with the frequency of the stimulus as well. In addition, the animal's best performance on tones, although reaching 95% correct, was never perfect as it was at large angles for clicks and noise bursts. However, the lower asymptotic performance on tones is not unusual, as most mammals have greater difficulty localizing tones than broadband sounds (cf. Masterton et al., 1975).

Of particular interest is the fact that tone-localization performance appears to separate into three groups on the basis of frequency. Specifically, the elephant's performance on the two lowest frequencies, 125 Hz and 250 Hz, was consistently better, and its thresholds lower, than for any of the higher frequencies. Frequencies in the midrange, 500 Hz, 1 kHz, and 2 kHz, although not localized as well as the lower frequencies, were localized consistently better than higher frequencies. Finally, the two highest frequencies, 4 kHz and 8 kHz, were localized at levels barely above chance even at 60° separation.

The performance of the elephant on the tone-localization test may be interpreted in terms of the animal's ability to make use of the two primary binaural localization cues, time and intensity. According to the duplex theory of sound localization, low-frequency tones are usually localized through use of a phase cue ($\Delta\phi$), a subset of the class of time cues (Δt; for a review, see Woodworth & Schlosberg, 1965). Thus, the azimuth of a low-frequency sound source depends on the difference in the phase of the sound reaching the two ears. But as frequency is increased, the phase cue becomes ambiguous (when the difference in the distance of the two ears from the sound source equals one half of the wavelength of the tone). At this point of phase ambiguity, higher frequencies can be localized accurately only through use of the intensity-difference cue (ΔI). The ΔI cue, however, is of much less use for low frequencies which bend around the head with much less attenuation.

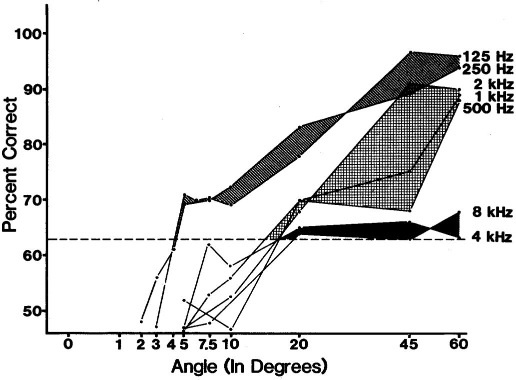

Figure 6. Sound-localization performance for tones. (Note that the elephant's performance appears to fall into three groups as a function of frequency. Dashed line indicates statistical threshold level.)

The ability of the elephant to localize sounds by using both the phase- and intensity-difference cues is illustrated in Figure 7, which shows the animal's performance on tones for a separation of 60°. At 60° separation, the calculated frequency of ambiguity for the phase cue is 310 Hz (indicated by the arrow in Figure 7; see Kuhn, 1977, or Brown et al., 1978, for the formula for calculating the frequency of phase ambiguity). As can be seen in the figure, the elephant was easily able to localize frequencies below 310 Hz at levels above 90% correct, which suggests that it could readily use the phase cue. Above 310 Hz, the elephant could localize 500 Hz to 2 kHz at levels better than 85% correct. Since these frequencies are well above the frequency range in which the phase cue can be used, this result suggests that the elephant can use the intensity-difference cue, though perhaps not so reliably as the phase cue.

Although the ability of the elephant to localize 500 Hz, 1 kHz, and 2 kHz suggests that it could use the intensity-difference cue, it was virtually unable to localize 4 kHz and 8 kHz. Furthermore, this inability was apparent at all angles tested and occurred even when the intensity of the tones was increased or decreased. Thus, it is possible that elephants may be unable to use the intensity-difference cue for frequencies in the upper end of their hearing range. This point is considered further in a later section.

Filtered noise. Although the elephant was unable to accurately localize high-frequency pure tones, these results do not mean that the elephant was incapable of accurately localizing high-frequency sounds in general. As illustrated in Figure 8, the elephant was able to localize filtered noise bands from 125 Hz to 8 kHz with the same accuracy with which it localized broadband stimuli. Indeed, additional testing revealed that the elephant could localize an 8-kHz high-pass noise burst (48 dB/octave roll-off) as easily as the other noise bands, and with a threshold of .7°.

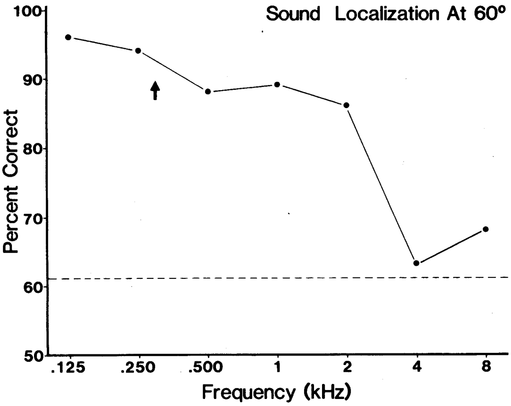

Figure 7. Ability of the elephant to localize tone pips at an angle of 60°. (Arrow indicates frequency above which the phase cue is ambiguous. Note that the elephant can localize tones above and below the point of phase ambiquity, results suggesting that it can use both phase- and intensity-difference cues to localize sound. However, the animal could barely localize 4 kHz and 8 kHz. All tones were presented at 40 dB above absolute threshold. Dashed line indicates statistical threshold level.)

The ability to accurately localize high-frequency noise when the elephant could not accurately localize high-frequency pure tones may be due to the fact that the noise bursts contain an additional sound-localization cue. Specifically, it has been demonstrated that the auditory system can utilize interaural time differences to localize high-frequency sounds that have complex waveforms (e.g., McFadden & Posanen, 1976). This is evidently accomplished by analyzing the interaural time difference present in the fluctuating envelope of the signal, in this case, the noise band. The pure tones used here, however, had no fluctuating envelope, and, presumably, only the intensity-difference cue was available for localizing high-frequency pure tones.

In summary, the elephant was able to accurately localize single clicks and brief bursts of white and filtered noise. Analysis of the animal's ability to localize pure tones suggested that the elephant is capable of using both time and intensity cues to localize sound. However, the poor performance of the animal in localizing high-frequency tones suggests that the elephant relies more heavily on the time cue than on the intensity cue for accurate sound localization.

Role of the pinna in sound localization. Finally, it should be noted that the elephant appeared to make use of its external ears in localizing sound during these tests (R. Heffner, Heffner, & Stichman, 1982). Specifically, the animal extended its pinnae nearly perpendicular to its head just before it pressed the center button. After the center button was pressed and a brief sound had been presented, the animal then moved its trunk to press either the left or the right button, during which time it usually returned its ears to the normal relaxed position against its head. Pinna extension was noted to occur for all stimuli and angles used in these tests. In contrast, the animal had maintained its pinnae in the relaxed position, flat against its head and neck, during the previous absolute thresholds and during the subsequent frequency-discrimination tests. Furthermore, the elephant kept its ears in the relaxed position during a recheck of absolute thresholds for 4 kHz and 8 kHz conducted subsequent to the sound-localization tests. Thus, the elephant was ob-

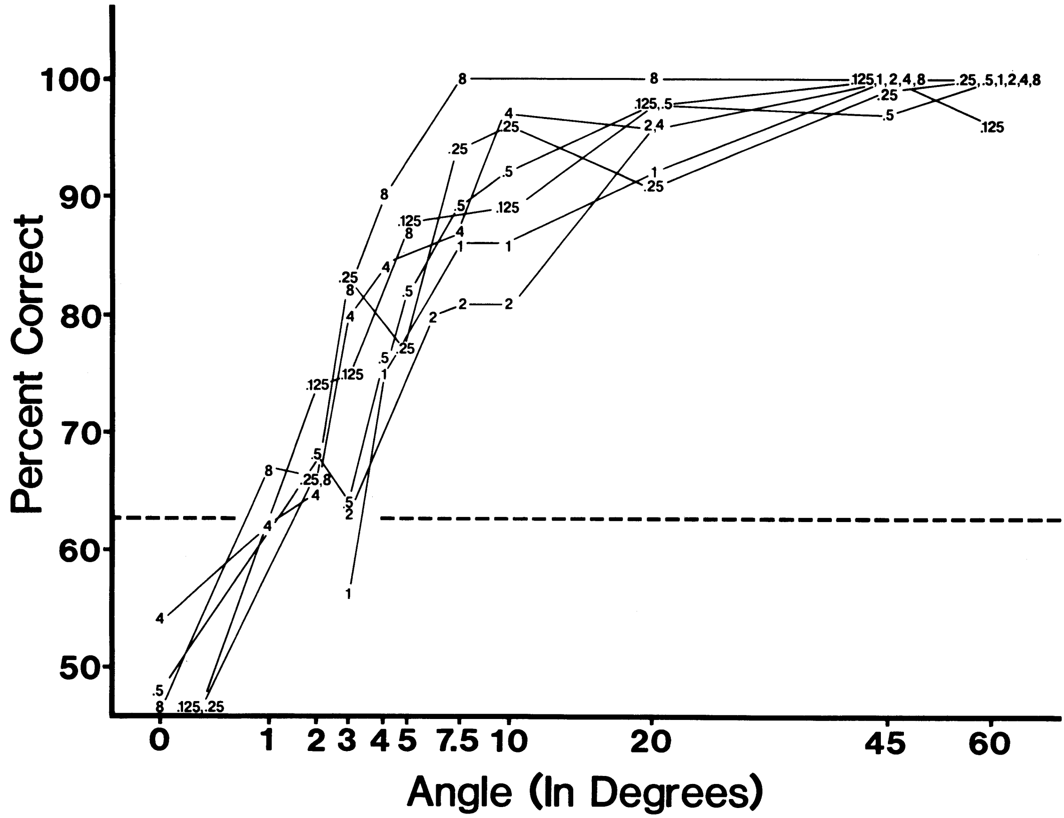

Figure 8. Sound-localization performance for narrow-band noise bursts. (Numbers indicate center frequency of the noise bands. Note that the animal could localize low- and high-frequency noise equally well. Dashed line indicates statistical threshold level.)

served to display pinna extension only during the sound-localization tests. Just what advantage the elephant may have gained from extending its pinnae must await further information concerning the effect of the extended pinnae on the sound reaching the ears.

General Discussion

With the inclusion of the elephant, the sample of mammals whose hearing capacities have been studied now extends from some of the smallest (mice and bats) to the largest of terrestrial mammals. As a result, it is now possible to review some of the parameters of hearing in which size has been implicated as a factor. The following discussion concerns the effect of the results of this study on the previously noted relations concerning high- and low-frequency hearing. In addition, the ability of the elephant to discriminate frequencies and to localize sound is compared with the abilities of smaller mammals.

Audiogram

High-frequency hearing. As was illustrated in Figure 2, the elephant is unable to hear above 12 kHz, replacing humans as the mammal with the lowest high-frequency limit of any mammal yet tested. This result is not unexpected if the inverse relation between high-frequency limit and functional distance between the two ears is accepted (H. Heffner & Masterton, 1980; Masterton et al., 1969). This relation is illustrated in Figure 9 where interaural distance is represented by maximum Δt and high-frequency hearing limit is defined as the highest frequency audible at an intensity of 60 dB (SPL). The correlation between these two parameters is $-.89$ ($p < .001$) and is based on audiograms

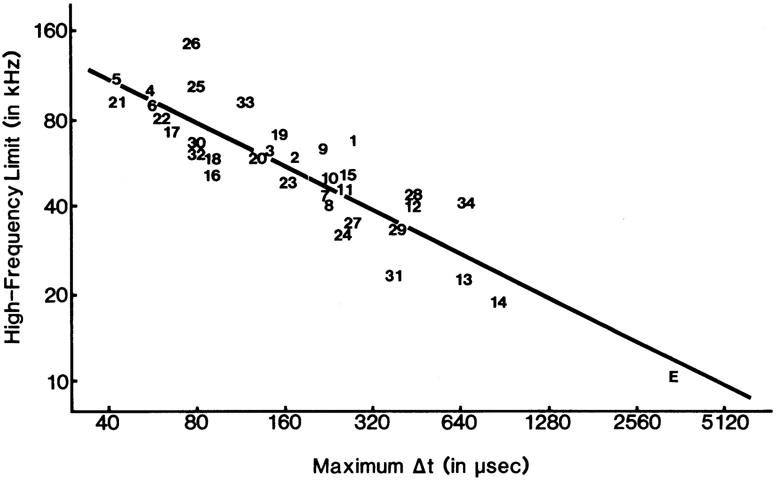

Figure 9. Relation between maximum Δt (maximum interaural distance divided by the speed of sound) and high-frequency hearing limit (highest frequency audible at 60 dB SPL). (All high-frequency limits were determined in air except as noted. E, elephant [*Elephas maximus*]; 1, opossum [*Didelphis virginiana;* Ravizza, Heffner, & Masterton, 1969a]; 2, hedgehog [*Hemiechinus auritus;* Ravizza, Heffner, & Masterton, 1969b]; 3, tree shrew [*Tupaia glis;* H. Heffner, Ravizza, & Masterton, 1969a]; 4, horseshoe bat [*Rhinolophus ferrumequinum;* Long & Schnitzler, 1975]; 5, little brown bat [*Myotis lucifugus;* Dalland, 1965]; 6, big brown bat [*Eptesicus fuscus;* Dalland, 1965]; 7, slow loris [*Nycticebus coucang;* H. Heffner & Masterton, 1970]; 8, potto [*Perodicticus potto;* H. Heffner & Masterton, 1970]; 9, bush baby [*Galago senegalensis;* H. Heffner, Ravizza, & Masterton, 1969b]; 10, owl monkey [*Aotus trivirgatus;* Beecher, 1974a]; 11, squirrel monkey [*Saimiri sciureus;* Beecher, 1974b; Green, 1975]; 12, macaque [*Macaca* sp.; Behar, Cronholm, & Loeb, 1965; Stebbins, Green, & Miller, 1966]; 13, chimpanzee [*Pan troglodytes;* Farrer & Prim, Note 1]; 14, human [*Homo sapiens;* Davis, 1960]; 15, rabbit [*Oryctolagus cuniculus;* H. Heffner & Masterton, 1980]; 16, kangaroo rat [*Dipodomys merriami;* H. Heffner & Masterton, 1980]; 17, cotton rat [*Sigmodon hispidus;* H. Heffner & Masterton, 1980]; 18, gerbil [*Meriones unguiculatis;* Ryan, 1976]; 19, laboratory rat [*Rattus norvegicus;* Kelly & Masterton, 1977]; 20, wood rat [*Neotoma floridana;* H. Heffner, unpublished observations, 1980]; 21, feral house mouse [*Mus musculus;* H. Heffner & Masterton, 1980]; 22, laboratory mouse [*Mus musculus;* H. Heffner & Masterton, 1980]; 23, guinea pig [*Cavia porcellus;* R. Heffner et al., 1971]; 24, chinchilla [*Chinchilla* sp.; Miller, 1970]; 25, dolphin under water [*Inia geoffrensis;* Jacobs & Hall, 1972]; 26, porpoise under water [*Tursiops truncatus;* Johnson, 1967]; 27, killer whale under water [*Orcinas orca;* Hall & Johnson, 1972]; 28, dog [*Canis familiaris;* H. Heffner, 1976]; 29, sea lion in air [*Zalophus californianus;* Schusterman, Balliet, & Nixon, 1972]; 30, harbor seal under water [*Phoca vitulina;* Mohl, 1968]; 31, harbor seal in air [*Phoca vitulina;* Mohl, 1968]; 32, ringed seal under water [*Pusa hispida;* Terhune & Ronald, 1975]; 33, harp seal under water [*Pagophilus groenlandicus;* Terhune & Ronald, 1972]; 34, domestic sheep [*Ovis aries;* Wollack, 1963].)

for 32 genera ranging in size from mouse and bat to elephant and killer whale.

The existence of a strong inverse relation between maximum Δt and high-frequency hearing has been ascribed to selective pressure for accurate sound localization. Briefly, the argument goes as follows: The two binaural cues for sound localization, the difference in time of arrival of a sound at the two ears (Δt) and the difference in frequency-intensity spectra of a sound reaching the two ears (Δfi), depend on the functional distance between the two ears and the sound shadow of the head and pinnae. That is to say, the farther apart the ears, the larger will be the Δt cue for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with wide-set ears both because the sound attenuation is slightly greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which effectively shadow the high-frequency content of sound.

While the two binaural sound-localization cues are readily available to animals with large heads, the effectiveness of either cue is diminished in animals with functionally close-set ears. In the case of Δt, the time differences naturally available may be so small that the nervous system can detect only gross changes in sound direction. However, an animal with a small head always has a Δfi cue available, provided only that it is able to perceive frequencies that are high enough to be effectively shadowed by its head and pinnae. Therefore, given the ecological importance to an animal of localizing sound, animals with functionally close-set ears are subjected to more selective pressure to hear high frequencies than animals with more widely set ears.

The finding that the elephant is unable to hear significantly above 10 kHz has two additional implications for ecological and evolutionary acoustics (H. Heffner & Heffner, 1980; R. Heffner & Heffner, 1980). First, it suggests that when the selective pressure for high-frequency hearing is reduced as a consequence of evolving a large interaural distance, then the upper limit of hearing is reduced to the point at which it does not greatly exceed that of nonmammalian vertebrates such as birds, none of which hear frequencies much higher than 10 kHz. Second, it appears that humans should no longer be considered aberrant among mammals for their lack of ability to hear above 20 kHz. Instead, restricted high-frequency hearing seems to be a consequence of a relatively large interaural distance and not the result of a special adaptation (such as for the reception of speech sounds) as was once widely believed and is still often repeated.

Low-frequency hearing. In previous surveys of mammalian hearing, it has been noted that low-frequency hearing shows a good deal of variation from one species to the next. Humans have a lower limit of about 30 Hz, rats have a limit near 500 Hz, and the little brown bat (*Eptesicus fuscus*) apparently hears no lower than 10 kHz (for a review, see H. Heffner & Masterton, 1980). Thus, the range of low-frequency limits in mammals spans more than nine octaves—dwarfing the four-octave range of high-frequency limits.

In analyzing the variation in low-frequency hearing, it has been noted that in terrestrial mammals, the low-frequency hearing limit usually varies directly with the high-frequency hearing limit, a fact indicating that mammals that have good high-frequency hearing usually have poor low-frequency hearing, and vice versa (H. Heffner & Masterton, 1980). Though this relation appears to be quite strong ($r = .87, p < .01$), there is reason to believe that it does not hold for the extreme lower end of the scales. In particular, humans, who have one of the lowest high-frequency limits of mammals, would be expected to have a low-frequency limit of about 4 Hz—a value several octaves below the actual limit of about 30 Hz. Thus, the question arises as to whether there is a "floor effect" that prevents the hearing of frequencies below some particular low value in mammals.

The effect on this relation of adding the elephant to the sample can be seen in Figure 10. As this figure shows, there is a high correlation between high- and low-frequency hearing for nearly all mammals tested so far. However, in spite of the fact that the elephant has the best low-frequency hearing of any mammal, the 17-Hz limit is well above the .4-Hz limit predicted by the regression equation based on data from other mammals. Thus, the elephant audiogram supports the notion of a floor effect for low-frequency hearing. Just what the significance of this floor effect might be, however, remains to be determined.

Frequency Discrimination

Comparison of the elephant's ability to discriminate frequency with that of other mammals (Figure 11) reveals that above 500 Hz the elephant ranges from good to poor, depending on the definition of threshold used. However, as the elephant had difficulty performing frequency discriminations, there is reason to believe that the 75% thresholds are low because of performance rather than hearing factors and that the statistical threshold is more representative of the animal's ability. Yet regardless of the definition of threshold, the data in Figure 11 show that the elephant is remarkably sensitive at low frequencies even when compared with humans. This observation suggests that the elephant does possess good frequency-discrimination ability, especially at frequencies below 1 kHz, and is not inconsistent with von Békésy's (1960) observa-

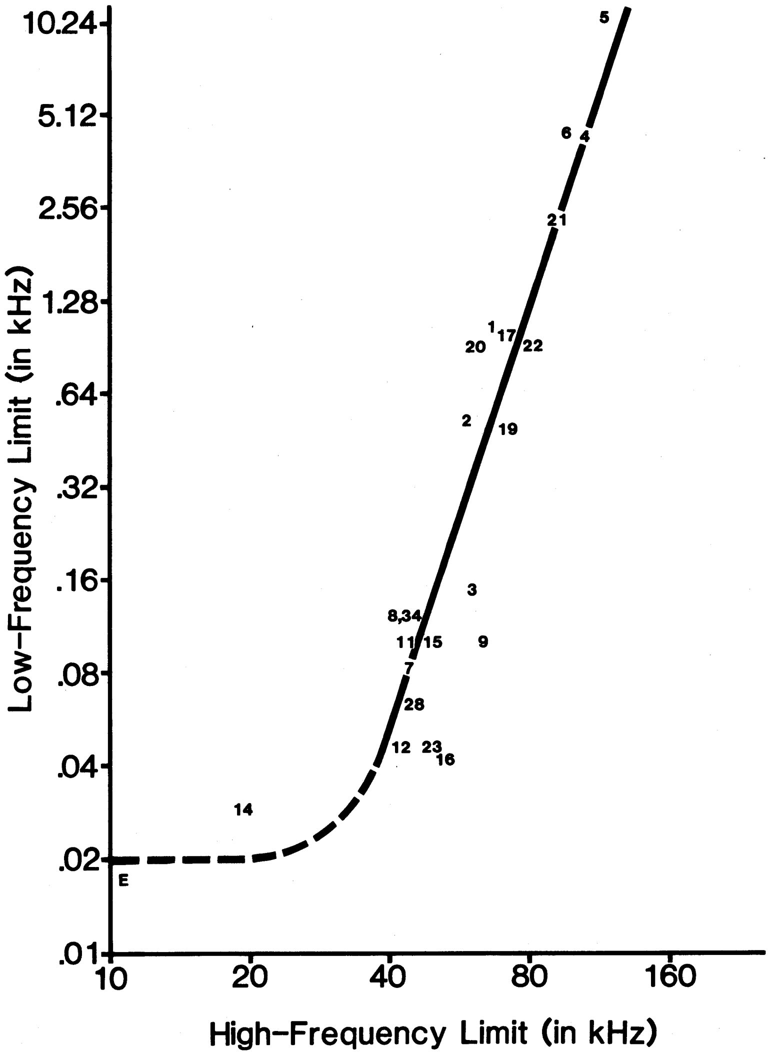

Figure 10. Relation between high- and low-frequency hearing ability in 23 species of terrestrial mammals. (See Figure 9 for key to numbers. E indicates value for elephant.)

tions regarding the mechanical separation of frequencies along its basilar membrane.

Sound Localization

Acuity. The threshold ability of the elephant to localize clicks and noise bursts ranged in the region of 1°. As shown in Table 2, the elephant is more accurate than most other mammals and is equal to humans. Indeed, given the differences in method and the fact that only one elephant has been examined so far, it would not be surprising if, on average, elephants proved to be superior to humans in this ability.

Given the good localization acuity of the elephant, the question arises as to the role of interaural distance in determining localization ability. There are two reasons for suspecting that interaural distance plays a crucial role in determining localization acuity and two additional reasons for caution in accepting such a conclusion. First, a large interaural distance will generate large binaural localization cues in terms of the differences in the time of arrival (Δt) and the intensity of a sound reaching the two ears (ΔI). These larger cues, in turn, should enable the nervous system to more easily localize the source of the sound. Second, perusal of Table 2 suggests that there may be a high correlation between interaural distance and localization acuity, as the smaller animals listed here have poorer acuity than the larger animals.

At the present time, however, we are reluctant to argue that interaural distance plays a determining role in sound-localization acuity for two reasons. First, the animals that have been shown to have poor localization acuity are generally herbivorous or, at most, insectivorous. Since it might be argued that predators, such as carnivores, may be under greater selective pressure to accurately localize sound than are nonpredators, there may exist small carnivores that can accurately localize sound. Second, the number of species whose localization ability is known is small and is not representative of mammals as a whole. In particular, the sample does not include any ungulates—animals that, while relatively large, are generally herbivorous and, therefore, may not need good localization acuity. Thus, the role of interaural distance in determining sound localization acuity must await further information concerning other species of mammals.

Tone localization. The results of the tone-localization test indicated that the elephant is able to use the binaural localization cues of both time (Δt), in the form of phase differences ($\Delta\phi$), and intensity (ΔI). This conclusion is suggested by the fact that the animal could localize frequencies below 300 Hz, where it had to rely on $\Delta\phi$, as well as frequencies from 500 Hz to 2 kHz where ΔI would be the primary binaural cue. How-

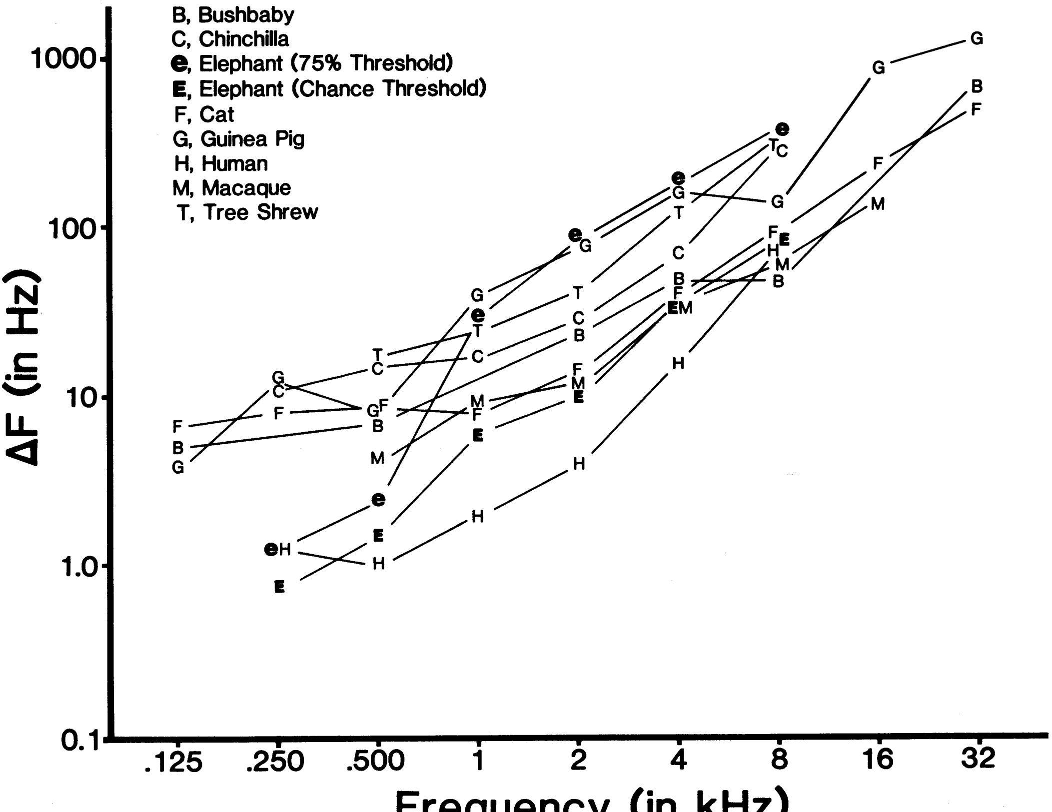

Figure 11. Frequency difference thresholds (ΔF) for eight species of mammals for which low-frequency thresholds are available. (Two curves are shown for the elephant, the 75% definition of threshold, e, and the statistical threshold, E. Note that the elephant is very sensitive to frequency differences at the low end of its hearing range. Data are from, [B] H. Heffner et al., 1969b; [C] Nelson & Kiester, 1978; [F] Elliot, Stein, & Harris, 1960; [G] R. Heffner et al., 1971; [H] Wier, Jesteadt, & Green, 1977; [M] Stebbins, Pearson, & Moody, 1970; [T] H. Heffner et al., 1969a.)

Table 2
Sound-Localization Thresholds for 12 Species of Mammals

Animal	Stimulus	Threshold[a] (in degrees)	Source
Dolphin	click	.9	Renaud & Popper, 1975
Man	tone	1	Mills, 1958
Elephant	noise	1.2	Present article
Seal	click	3.2	Terhune, 1974
Elephant	click	4	Present article
Macaque	noise	4	Brown, Beecher, Moody, & Stebbins, 1980
Opossum	noise	4.6	Ravizza & Masterton, 1972
Cat	noise	5	Casseday & Neff, 1973
Macaque	click	7.5	H. Heffner & Masterton, 1978
Dog	click	8	H. Heffner, unpublished data, 1977
White rat	noise	10	Kelly, 1980
Hedgehog	click	19	Chambers, 1971
Wood rat	noise	19	H. Heffner, unpublished data, 1979
Kangaroo rat	click	24	H. Heffner & Masterton, 1980
White rat	click	29	Kelly & Glazier, 1978

[a] Due to the variety of testing procedures, it is difficult to precisely equate the various thresholds. For the two-choice procedures, threshold is defined as the 75% correct level.

ever, at higher frequencies, i.e., 4 kHz and 8 kHz, the elephant could barely localize above chance levels, even at large angles.

The inability of the elephant to easily localize tones in the upper part of its hearing range may not be unusual for large-headed animals. As has been reported, humans have more difficulty localizing 8 kHz than they do lower frequencies (Mills, 1958). However, few animals have been tested for their ability to localize tones throughout their entire range of hearing. As a result, it is not possible to determine whether such a truncated ability is unusual. Therefore, it is perhaps appropriate to reserve speculation on this point until a time when more information is available.

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