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Hearing in Large Mammals: Horses (*Equus caballus*) and Cattle (*Bos taurus*)

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Behavioral audiograms were determined for three horses and two cows. The horses' hearing ranged from 55 Hz to 33.5 kHz, with a region of best sensitivity from 1 kHz to 16 kHz. Cattle hearing ranged from 23 Hz to 35 kHz, with a well-defined point of best sensitivity at 8 kHz. Of the two species, cattle proved to have more acute hearing, with a lowest threshold of −11 dB (re 20 $\mu N/m^2$) compared with the horses' lowest threshold of 7 dB. Comparative analysis of the hearing abilities of these two species with those of other mammals provides further support for the relation between interaural distance and high-frequency hearing and between high- and low-frequency hearing.

Comparative studies of hearing have revealed that variation in the hearing abilities of mammals is closely related to variation in functional interaural distance (i.e., the distance between the ears divided by the speed of sound; Masterton, Heffner, & Ravizza, 1969). In particular, it has been noted that mammals with small interaural distances, such as mice and rats, are better able to hear high-frequency sounds than species with larger interaural distances, such as monkeys, humans, and elephants (for a recent review, see R. Heffner & Heffner, 1982). On the other hand, those species that do not hear high frequencies well are generally better able to hear low-frequency sounds (e.g., H. Heffner & Masterton, 1980). Thus, functional interaural distance, a parameter related directly to high-frequency hearing and indirectly to low-frequency hearing, appears to be a major factor in the evolution of mammalian hearing.

At present, the relation between functional interaural distance and hearing is based primarily on small mammals, as relatively little is known about the hearing abilities of large mammals (i.e., the size of humans and larger). As a result, the generality of conclusions concerning the relation between interaural distance and hearing has had to be limited, especially regarding large mammals. The present report, therefore, is one of a series in which we present information concerning the hearing abilities of two large mammals: domestic horses and cattle (for a previous report, see R. Heffner & Heffner, 1982). The choice of these two species was based primarily on the fact that they have large interaural distances. However, there are three additional reasons why they are of particular interest. First, horses and cattle have functional interaural distances which bracket that of humans, with horses being slightly smaller and cattle somewhat larger. They thereby provide an opportunity to compare the hearing ability of humans with that of animals that have similar interaural distances. Second, horses and cattle represent two orders of mammals, Perissodactyls and Artiodactlys, whose hearing has not been widely studied (Ödberg, 1978). Thus, addition of these two species increases the representativeness of the sample of mammals whose hearing ability is known and allows more general conclusions to be made concerning mammalian hearing. Finally, though not of theoretical importance, a knowledge of the auditory capacities of live-

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stock is considered essential in the prevention of stress in these animals and thus may prove to be of economic significance (Ames, 1974).

Method

The animals were tested with a go–no-go procedure based on the one developed by Stebbins and his colleagues (Moody, Beecher, & Stebbins, 1976; Stebbins, 1970). Briefly, a thirsty animal was trained to maintain contact with an "observing" plate with its head. Tones were presented at random intervals, and the animal was given a water reward for breaking contact with the observing plate and touching a "reporting" plate within 3 sec after tone onset.

Subjects

Initially, three horses and three cattle were used in this experiment. However, during a detailed otologic examination, one of the cattle was found to have ear mites, so its audiogram is not reported here. The animals used here, then, were a quarter horse gelding (Horse A), an Appaloosa mare (Horse B), a Welsh pony × quarter horse gelding (Horse C), and two polled Hereford cows. All animals were between 18 and 20 mo of age (adolescent) at the beginning of testing. The animals were housed in outdoor pens and maintained on mixed grain and hay. Water was used as a reward and was available only in the testing situation. The weight of each animal (450–800 lb.; 202–360 kg) was taken daily and provided an indication of the animal's health and deprivational state.

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 had a ventilating system that could be turned off during testing. These features, combined with the rural location of the station, provided a quiet environment for auditory testing.

Testing was conducted in a large room (7.2 × 5.5 × 2.4 m), the walls and ceiling of which had been lined with fiberglass and sound-absorbing panels (Cellotex) to attenuate outside noise and to reduce sound reflection. A room adjacent to the test room was used to house the test equipment.

During testing, an animal was confined in a rectangular stall (2.4 × 1 × 1.5 m) constructed of 5-cm-diameter pipe mounted on a sawdust-covered wooden floor (Figure 1). Two metal response plates (10 × 8 cm) and a water bowl (1,000-ml capacity) were located at the front of the stall. The plates were mounted vertically in the center of the front of the stall, with the top or "observing" plate 120 cm above the floor and the bottom or "reporting" plate 50 cm below the observing plate. The water bowl was located 10 cm below the reporting plate and was connected to a 50-l water reservoir by an electrically operated water valve. Each of the two response plates was connected to a separate sensing switch which detected when an animal made contact with it.

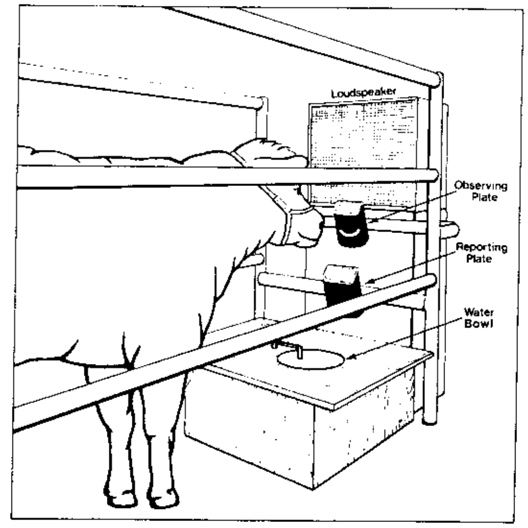

Figure 1. View of the test stall. (An animal was trained to initiate testing by placing its nose or chin on the observing plate. Tones were presented at random intervals, and the animal was given a water reward for breaking contact with the observing plate and touching the reporting plate within 3 sec after tone onset.)

Sound Production and Measurement

The details of the stimulus generation and calibration procedure have been described in detail elsewhere (R. Heffner & Heffner, 1982; R. Heffner, Heffner, & Masterton, 1971). Briefly, sine waves were produced by an oscillator (Hewlett-Packard 200CD) connected to an electronic switch (Coulbourn S84-04), attenuators (Hewlett-Packard 350B and Coulbourn S85-05), amplifier (Coulbourn S82-24), filter (Krohn-Hite 3202), and, by an impedance-matching transformer, to either a 15-in. (38-cm) woofer in a .45-m^3 enclosure (for frequencies of 2 kHz and below) or a piezoelectric tweeter (for frequencies above 2 kHz). This sound system proved capable of delivering relatively undistorted tones from 16 Hz to 50 kHz at an intensity of at least 70 dB (SPL) as measured in the vicinity of the observing plate. The speakers were located at ear level, 115 cm in front of the animals.

In order to avoid switching transients, the electrical signal was electronically keyed with a rise–decay time of 20 msec for frequencies of 125 Hz and above and rise–decay times of 30, 60, and 200 msec for frequencies of 62, 32.5, and 16.7 Hz, respectively. Tones were pulsed at a rate of two per second, 400 msec on and 100 msec off for tones of 62 Hz and higher. Longer on and off times were allowed for lower frequencies to compensate for the longer rise–decay times and permit the sound to remain on at its full intensity for 380 msec and to remain off for at least 50 msec.

The entire sound system was calibrated, and the sound pressure levels (expressed throughout as decibels re .20 $\mu N/m^2$) were measured with either a Brüel and Kjaer (B & K) 1-in. (2.54-cm) microphone, sound level meter (B & K 2203), and octave filter (B & K 1613) or a 1/4-in. microphone (B & K 4135), preamplifier (B & K 2618), microphone amplifier (B & K 2608), and filter (B & K 1613 or Krohn-Hite 3202). Sound pressure measurements were taken by placing the microphone at a site midway between an animal's ears when the animal was making the observing response, and pointing it directly toward the loudspeaker. Special care was taken to ensure that the sound field was homogenous in the vicinity occupied by an animal's ears.

Additional sound pressure level measurements were made in which the lower frequency tones were checked for the presence of significant overtones. This was done to rule out the possibility that an animal might be able to respond to an overtone produced by an otherwise inaudible tone. The check was conducted by measuring the sound pressure level at octave steps above the primary frequency and determining whether the resulting measurement was greater than would be expected if no overtones were present. Measurements for frequencies below 500 Hz revealed no measurable overtones (e.g., a first octave overtone within 30 dB of the primary tone) with the exception of 16.7 Hz. At this frequency, a possible overtone 27 dB less intense than the primary was detected at about 33 Hz. However, as the audiograms show, this overtone was not loud enough to account for the observed thresholds.

The intensity of ambient noise in the test room was also measured from 3.15 Hz to 35.5 kHz in 1/6-octave steps.

Psychophysical Procedure

A water-deprived animal was trained to make a continuous observing response by placing its nose (horses) or chin (cows) on the metal observing plate. This response served to fix the animal's head in the sound field and thus to minimize variations in the sound pressure level at the animal's ears. The animal was then required to report the presence of a tone by breaking contact with the observing plate and touching the reporting plate within 3 sec after tone onset.

A trial consisted of turning on a tone for 3 sec and recording the animal's response. Trials were presented randomly at intervals of 3, 6, 9, 12, 18, 21, 24, 27, or 30 sec. The interval between trials was selected randomly with the restriction that no interval could be used more than three times in a 27-trial sequence. Breaking contact with the observing plate and contacting the reporting plate within 3 sec of tone onset (correct detection) was then rewarded by delivery of 250 ml of water into the bowl. Contact with the reporting plate when a tone had not been presented (a false alarm) was followed by a short wait or timeout (signaled by dimming the room lights) before the session could continue. The false alarm rate was continuously monitored, and the results were discarded if the rate rose above 10%. Failure to report the presence of a tone (a miss) resulted in failure to obtain a reward on that trial.

Thresholds were determined by using a tracking procedure in which the intensity of the tone was increased or decreased as a function of the animal's performance. To be specific, the intensity of a tone was decreased by 4 dB on trials following a correct detection and was increased by 4 dB on trials following a miss. Testing was continued during a session until an intensity was found which the animal failed to detect on four consecutive presentations. Threshold was then defined as the intensity that was detected on 50% of the trials. Testing for a frequency was judged complete when thresholds obtained on three different sessions were within 3 dB of each other. If thresholds differed by more than 3 dB, testing continued until a stable threshold emerged. Finaly, once a complete audiogram had been obtained, each frequency was retested to ensure reliability

Results

Despite their size, neither the horses nor the cattle presented any unusual problems in training. The horses were already accustomed to human handling (i.e., halter broken), but the cattle were unused to human contact and required several sessions before they were acclimated to the testing procedures. Yet in spite of their initial wildness, the cattle proved easier to train—both cows learned to be reliable observers within 3 wk, whereas the horses took 3–7 wk. Overall, the cattle was the easier of the two species to work with both in terms of learning and in temperament.

Horses

The audiograms of the three horses are shown in Figure 2. The behavioral curves are in close agreement with one another for all but the higher frequencies. The audiograms show a gradual increase in sensitivity as frequency is increased to about 500 Hz. At this point the audiogram levels off, with a range of best sensitivity extending from 1 kHz to 16 kHz, with a dip in sensitivity at 4 kHz. Above 16 kHz, sensitivity decreases rapidly until the upper limit of audibility is reached. Overall, at an intensity of 60 dB, the horses' range of hearing extends from 55 Hz to 33.5 kHz.

In low-frequency hearing ability, horses are more sensitive than most other mammals. Indeed, they are easily superior in this regard to a number of rodents and small primates (cf. H. Heffner & Masterton, 1970, 1980). However, horses are not unique in their capacity for low-frequency

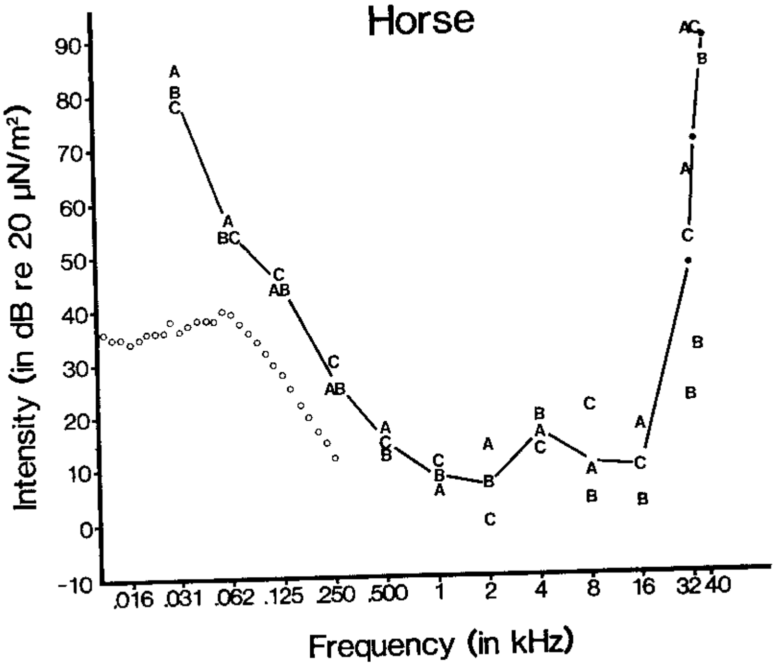

Figure 2. Audiograms of three horses. (Letters indicate individual animals. Open circles indicate the level of background noise.)

hearing. They are equaled or exceeded, for example, by cats, kangaroo rats, elephants, and humans (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1980).

It appears that horses have a broad range of best hearing extending from 1 kHz to 16 kHz, with a dip in sensitivity at 4 kHz. Excluding 4 kHz, the average threshold in this region varies by only ± 2 dB, which makes the selection of one particular best frequency all but impossible. Again, while horses are not the only animal to display such a broad range of best hearing (e.g., rabbits and kangaroo rats; H. Heffner & Masterton, 1980), the lack of a well-defined best frequency is sufficiently unusual to merit notice. Furthermore, the horses' lowest average threshold of 7 dB (at 2 kHz) is somewhat higher than that of most other mammals.

At the upper frequencies, horses exhibit the relatively steep decrease in high-frequency hearing (as compared with the more shallow low-frequency decrease) commonly found in mammals (Masterton et al., 1969). At this point, however, the hearing abilities of the three animals begin to diverge slightly. At an intensity of 60 dB, the highest frequencies audible were 30 kHz, 38 kHz, and 32 kHz for Horses A, B, and C, respectively. These results give the horse an average high-frequency hearing limit of 33.5 kHz, a value lower than that of most other mammals.

In summary, the horse's audiogram ranges from 55 Hz to 33.5 kHz, with a broad band of sensitivity between 1 kHz and 16 kHz. How horses compare with other mammals is described in a later section.

Cattle

The audiograms of the two cows are shown in Figure 3. As can be seen in this figure, the two animals are in close agreement over their entire range of hearing. The audiogram shows a gradual increase in sensitivity as frequency is increased to the point of best hearing at 8 kHz. Above 8 kHz, sensitivity decreases rapidly until the upper limit of audibility is reached. In all, the hearing range of cattle at 60 dB extends from 23 Hz to 35 kHz.

The low-frequency hearing ability of cattle is remarkably good. Not only are cattle more sensitive than horses, they are also

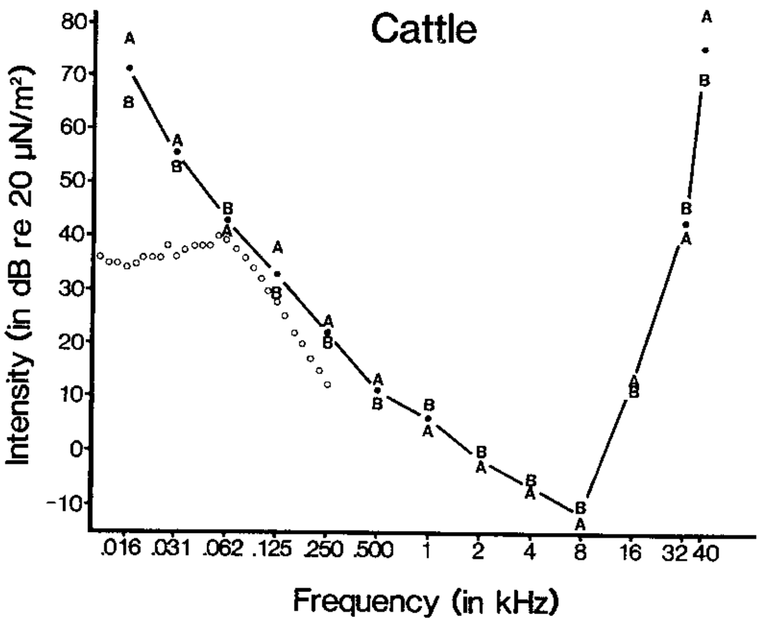

Figure 3. Audiograms of two cattle. (Letters indicate individual animals. Open circles indicate level of background noise.)

slightly more sensitive than humans. Indeed, among mammals, only the elephant is known to possess better low-frequency hearing (R. Heffner & Heffner, 1982).

Turning to the midrange of the cattle audiogram, it can be seen that the animals have a well-defined best frequency at 8 kHz. Indeed, at this frequency the animals are quite sensitive, with a threshold of −11 dB. This makes cattle 18 dB more sensitive than horses and, indeed, more sensitive than most other animals tested, including humans (Sivian & White, 1933). Thus, cattle differ from horses not only in having a well-defined best frequency but in possessing more acute hearing.

Above 8 kHz, the sensitivity of the animals decreases rapidly to an upper limit at 60 dB of 35 kHz. Thus, like horses, cattle do not hear high frequencies as well as most other mammals.

In summary, the cattle audiogram ranges from 23 Hz to 35 kHz, with a well-defined point of best sensitivity at 8 kHz. Just how cattle compare with other mammals is discussed in a later section.

Background Noise Level

The background noise level of the test room was measured in 1/6-octave steps and is indicated by the open circles in Figures 2 and 3. Overall, the test room proved to be relatively quiet due largely to the fact that it was located in a relatively isolated rural building and that the building's ventilating system was shut down during testing. Indeed, the background noise level was below the sensitivity of the sound level meters for all frequencies above 250 Hz.

Comparison of the audiograms with the background noise level shows that background noise was not a factor in determining high- and low-frequency thresholds. At both extremes of the audiograms, the thresholds were much higher than the noise level and therefore were not likely to be significantly affected by it. The potential effect of background noise in the midfrequency range is less easily determined, as the noise level here was too low to be measured. However, the fact that horses and cattle have distinctly different hearing between 500 Hz and 16 kHz indicates that background noise is not responsible for the flattening of the horse audiogram in this region.

Only in the range between 62 Hz and 250 Hz is there any suggestion that the noise level might be affecting the audiogram. This possibility is suggested by the close parallel between the audiograms and the background noise levels in this frequency region. However, although the masking effect of carefully filtered noise has been well studied (e.g., Patterson & Green, 1978; Zwislocki, 1978), it is difficult to predict the effect on the audiograms of the natural noise encountered here. Indeed, pure-tone thresholds have been occasionally noted to be below the measured background noise level (e.g., R. Heffner & Heffner, 1982). Thus, whereas the background noise had little or no effect on most of the frequencies tested, there may have been some influence on frequencies between 62 Hz and 250 Hz.

Discussion

Though hoofed mammals (Perissodactlys and Artiodactlys) comprise about 10% of extant mammalian genera, surveys of mammalian hearing contain only one representative, domestic sheep (Wollack, 1963). With the addition of horses and cattle, the present sample of mammalian audiograms not only includes more large mammals but more adequately represents a mammalian adaptation that was previously underrepresented. The first part of the following discussion compares the hearing abilities of hoofed mammals with those of other mammals. The second part is directed toward the effect of the horse and cattle data on previously proposed explanations of the variation in high-frequency and low-frequency hearing.

Auditory Characteristics of Hoofed Mammals

The audiograms of the horse, cattle, and sheep are shown in Figure 4. In this figure it can be seen that the three species show moderate differences in low-frequency hearing, with cattle being the most sensitive followed by the horse and then sheep. This difference in sensitivity is maintained into the midfrequencies up to about 8 kHz. Unlike the horse, both cattle and sheep show a well-defined point of best hearing in the 8–10 kHz region, with the sensitivity of sheep closely approaching that of cattle. Above 10 kHz, sheep become the most sensitive of the three species and possess an upper limit of approximately 42 kHz—higher than that of horse and cattle.

A comparison of hoofed mammals with other mammals can be made for four fun-

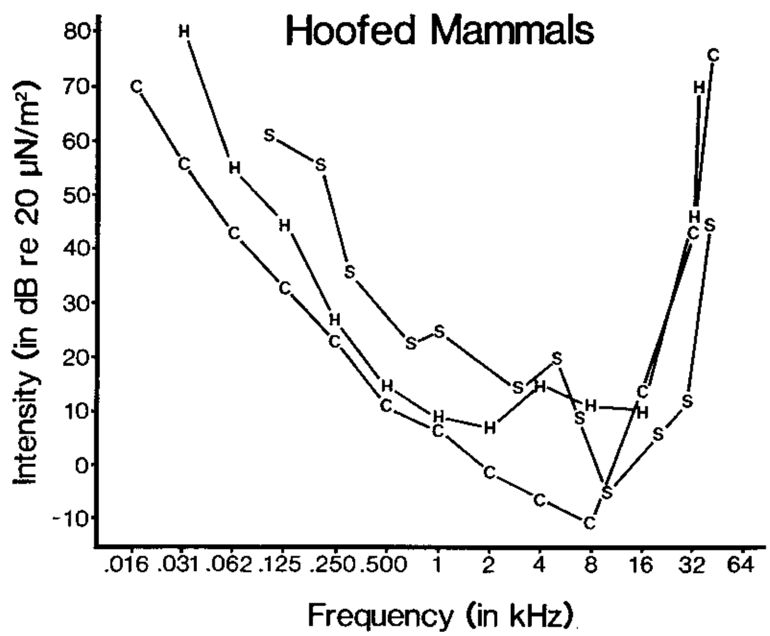

Figure 4. Average audiograms of horse (H), cattle (C), and sheep (S). (Audiogram for sheep from Wollack, 1963.)

damental descriptive parameters of hearing: (a) low-frequency limit—the lowest frequency audible at an intensity of 60 dB; (b) high-frequency limit—the highest frequency audible at 60 dB; (c) best frequency—the frequency with the lowest threshold; and (d) lowest threshold—the sound pressure level of the lowest audible intensity of the audiogram. These four parameters have been discussed elsewhere (H. Heffner & Masterton, 1980) and provide four points of comparison between hoofed mammals and mammals in general (Table 1).

First, it can be seen in Table 1 that whereas the average mammalian low-frequency limit is 196 Hz, all three hoofed mammals hear much lower. Indeed, the 23-Hz lower limit of cattle exceeds the low-frequency hearing ability of humans. Thus, hoofed mammals are better than average in their ability to hear low-frequency sounds.

Second, none of the hoofed mammals tested so far have exceptional high-frequency hearing. Whereas the average mammalian upper limit of hearing is around 51 kHz, the upper limits for hoofed mammals range from 33.5 to 42 kHz. While such high-frequency limits are not unusual, it appears that hoofed mammals are less sensitive to high-frequencies than most other mammals.

Third, though the horse has no single best frequency, the 8 and 10 kHz best frequencies of cattle and sheep closely bracket the 9.1 kHz average best frequency for mammals. This is of interest, for it shows that while both the upper and the lower limits of hearing for these two species are lower than most other mammals', their frequencies of best hearing are very close to the mammalian average.

Finally, comparison of lowest thresholds reveals that while cattle and sheep are more sensitive than average, the horse is less sensitive at its best point than the average mammal. Thus, as with best frequency, the two Artiodactlys more closely resemble each other in this instance than they resemble the horse, a Perissodactyl.

In summary, horses, cattle, and sheep are more sensitive to low frequencies and less sensitive to high frequencies than most other mammals. However, unlike the horse, both cattle and sheep possess well-defined best frequencies at which points they are 13–18 dB more sensitive than the horse. Whether these differences are related to the fact that horses are members of a different mammalian order remains to be determined.

High-Frequency Hearing in Mammals

One of the primary reasons for assessing the hearing abilities of horses and cattle was to determine the relation between interaural distance and high-frequency hearing for large mammals. This relation is illustrated in Figure 5 in which 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. The correlation between these two parameters is $-.89$ ($p < .001$) and is based on audiograms for 34 genera.

The existence of a strong inverse relation between maximum Δt and high-frequency

Table 1
Auditory Characteristics of Hoofed Mammals Compared With the Mammalian Average

Taxon	Low-frequency limit (in Hz)	High-frequency limit (in kHz)	Best frequency (in kHz)	Lowest threshold (in dB)
Perissodactyls				
Horse	55	33.5	1–16	7
Artiodactyls				
Cattle	23	35	8	−11
Sheep	125	42	10	−6
All Mammals				
M	196	51.1	9.1	−1.3
SD[a]	2.5	.8	1.4	9.9

Note. Auditory characteristics of mammals are based on audiograms of more than 30 terrestrial and marine species.
[a] With the exception of that for lowest threshold, *SD* values are expressed in octaves.

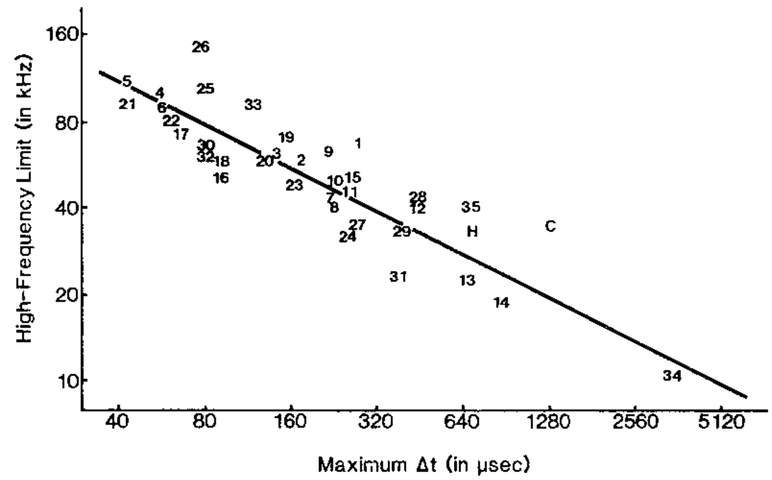

Figure 5. Relation between interaural distance (maximum Δt) and the 60 dB high-frequency hearing limit. (All high-frequency limits were determined in air except as noted. C, cattle; H, horse; **1**, opossum [*Didelphis virginiana*; Ravizza, Heffner, & Masterton, 1969a]; **2**, hedgehog [*Hemiechinus 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 [*Orcinus orca*; Hall & Johnson, 1972]; **28**, dog [*Canis familiaris*; H. Heffner, 1983]; **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**, elephant [*Elephas maximus*; R. Heffner & Heffner, 1980]; **35**, domestic sheep [*Ovis aries*; Wollack, 1963]. The numerical ordering of the individual species follows the taxonomic system of Simpson, 1945.)

hearing has been attributed to selective pressure for the accurate localization of sound (e.g., Masterton et al., 1969; R. Heffner & Heffner, 1980). Briefly, both of 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, respectively. In other words, 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 large interaural distances, both because the attenuation of sound 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 more effectively shadow the high-frequency content of sound.

Although the two binaural sound-localization cues should be available to animals with large heads, the size of either cue is smaller in animals with functionally close-set ears. In the case of Δt, the available time differences may be so small that the nervous system can detect only large changes in sound direction. However, an animal with a small head can use the Δfi cue if it is able to perceive frequencies that are high enough to be effectively attenuated by its head and pinnae. Therefore, assuming that it is important to an animal to localize sound, animals with functionally close-set ears appear to be subjected to more selective pressure to hear high frequencies than animals with more widely set ears.

As was previously noted, both horse and cattle do not hear as high as most mammals, an observation that coincides with their larger than average interaural distance. As can be seen in Figure 5, the 33.5-kHz high-frequency cutoff of the horse is relatively close to its predicted value of 29.3 kHz. On the other hand, cattle, which would be expected to hear only as high as 22.1 kHz, have an actual upper limit of 35 kHz. While the difference between the predicted and observed values for cattle high-frequency cutoff is not great enough to be statistically reliable ($p = .07$), the unexpectedly good high-frequency hearing of cattle is sufficiently unusual to merit special notice. Overall, however, it appears that the high-frequency cutoffs of the horse and cattle are in general agreement with the relation between high-frequency hearing and interaural distance.

Low-Frequency Hearing in Mammals

In surveys of mammalian hearing, it has been noted that low-frequency hearing shows a good deal of variation from one species to the next. In analyzing this variation it has been found that the low-frequency limit of hearing is directly correlated not with interaural distance but with the high-frequency limit of hearing (H. Heffner & Masterton, 1980). This means that animals that have good high-frequency hearing generally have restricted low-frequency hearing, and vice versa. Thus, whereas high-frequency hearing is directly correlated with interaural distance (i.e., maximum Δt), low-frequency hearing is directly correlated with high-frequency hearing.

The relation between high- and low-frequency hearing is illustrated in Figure 6 for terrestrial mammals. As can be seen in this figure, low-frequency hearing improves rapidly as the ability to hear high frequencies declines. Indeed, the trade-off between high- and low-frequency hearing is such that each octave change in high-frequency hearing is associated with a 4.4-octave change in low-frequency hearing.

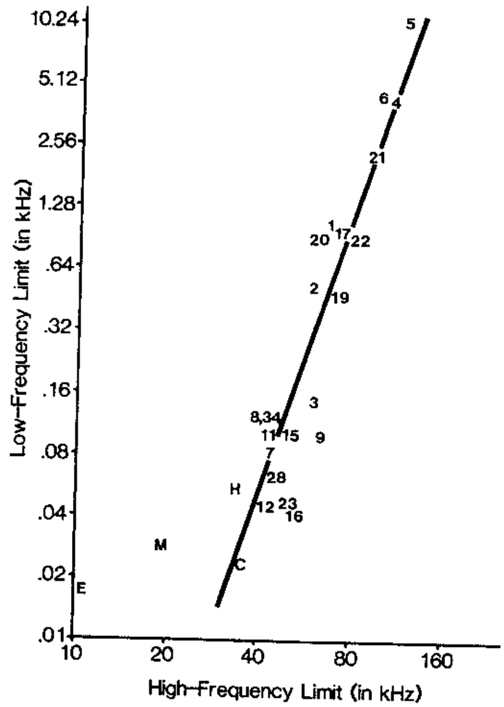

Figure 6. Relation between high-frequency and low-frequency hearing in 25 species of land animals. (C, cattle; E, elephant; H, horse; M, man. See Figure 5 for key to numbers. Values for elephant and man are excluded from calculation of the regression line.)

Though the relation between high- and low-frequency hearing is quite strong, there is reason to believe that it does not apply to all terrestrial mammals. In particular, both man and elephant do not easily fit into the relation since neither of the two hears as low as would be expected from their lack of high-frequency sensitivity. Because man and elephant are two of the best low-frequency hearers, the question arises as to whether the relation does not apply to mammals with exceptionally good low-frequency hearing.

With the addition of horses and cattle, this question can now be at least partially answered. As can be seen in Figure 6, both animals have low-frequency hearing limits quite close to those predicted from their high-frequency limits. Of particular interest, however, are cattle. Not only do cattle have slight better low-frequency hearing than humans, but they also have better high-frequency hearing. This observation suggests that the inability of humans to hear much above 20 kHz is not a concomitant of good low-frequency hearing. As cattle demonstrate, it is possible to possess low-frequency hearing better than that of humans and still hear up to 35 kHz, nearly one octave higher than humans.

The inability of elephants and humans to hear as low as predicted by their high-frequency limits had led to the idea that there might be some sort of "floor effect" that prevents the hearing of frequencies below some particular low value in terrestrial mammals (H. Heffner & Masterton, 1980; R. Heffner & Heffner, 1982). That is to say, an increase in interaural distance may decrease the need to hear very high frequencies and thus enable the audiogram to expand into the lower frequency range. However, once low-frequency hearing has reached a certain point of development, there may be some factor preventing, or else a lack of benefit from, further improvement.

In summary, it appears that the hearing abilities of horses and cattle support the relation between high- and low-frequency hearing. At the present time, this relation, based on 25 species, is quite strong ($r = .84$, $p < .01$; excluding elephants and humans raises the correlation to .91). However, it remains to be determined whether there are other animals that, like elephants and humans, do not closely fit this relation.

Reference Note

1. Farrer, D. N., & Prim, M. M. *A preliminary report on auditory frequency threshold comparisons of human and pre-adolescent chimpanzees* (Report No. 65-66). Holloman Air Force Base, N. Mex.: U.S. Air Force 6571 Aeromedical Research Laboratory, 1965.

References

Ames, D. R. Sound stress and meat animals. Livestock environment proceedings of the livestock symposium (Publication No. SP-0174). *American Society of Agriculture Engineers*, 1974, 324–330.

Beecher, M. D. Hearing in the owl monkey (*Aotus trivirgatus*). *Journal of Comparative and Physiological Psychology*, 1974, *86*, 898–901. (a)

Beecher, M. D. Pure tone thresholds of the squirrel monkey (*Saimiri sciureus*). *Journal of the Acoustical Society of America*, 1974, *55*, 196–198. (b)

Behar, I., Cronholm, J. N., & Loeb, M. Auditory sensitivity of the rhesus monkey. *Journal of Comparative and Physiological Psychology*, 1965, *59*, 426–428.

Dalland, J. I. Hearing sensitivity in bats. *Science*, 1965, *150*, 1185–1186.

Dallos, P. *The auditory periphery*. New York: Academic Press, 1973.

Davis, H. Physics and psychology of hearing. In H. Davis & S. R. Silverman (Eds.), *Hearing and deafness*. New York: Holt, Rinehart & Winston, 1960.

Green, S. Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*). *Journal of the Experimental Analysis of Behavior*, 1975, *23*, 255–264.

Hall, J. D., & Johnson, C. S. Auditory thresholds of a killer whale *Orcinus orca* Linnaeus. *Journal of the Acoustical Society of America*, 1972, *51*, 515–517.

Heffner, H. Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. *Behavioral Neuroscience*, 1983, *97*, 310–318.

Heffner, H., & Masterton, B. Hearing in primitive primates: Slow loris (*Nycticebus coucang*) and potto (*Perodicticus potto*). *Journal of Comparative and Physiological Psychology*, 1970, *71*, 175–182.

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

Heffner, H. E., Ravizza, R. J., & Masterton, B. Hearing in primitive mammals: III. Tree shrew (*Tupaia glis*). *Journal of Auditory Research*, 1969, *9*, 12–18. (a)

Heffner, H. E., Ravizza, R. J., & Masterton, B. Hearing in primitive mammals: IV. Bushbaby (*Galago senegalensis*). *Journal of Auditory Research*, 1969, *9*, 19–23. (b)

Heffner, R., & Heffner, H. Hearing in the elephant (*Elephas maximus*). *Science*, 1980, *208*, 518–520.

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

Heffner, R., Heffner, H., & Masterton, B. Behavioral measurements of absolute and frequency difference thresholds in guinea pig. *Journal of the Acoustical Society of America*, 1971, *49*, 1888–1895.

Jacobs, D. W., & Hall, J. D. Auditory thresholds of a fresh water dolphin, *Inia geofrensis* Blainville. *Journal of the Acoustical Society of America*, 1972, *51*, 530–533.

Johnson, C. S. Sound detection thresholds in marine mammals. In W. N. Tavolga (Ed.), *Marine bioacoustics* (Vol. 2). New York: Pergamon Press, 1967.

Kelly, J. B., & Masterton, B. Auditory sensitivity of the albino rat. *Journal of Comparative and Physiological Psychology*, 1977, *91*, 930–936.

Long, G. R., & Schnitzler, H. U. Behavioral audiograms from the bat *Rhinolophus ferrumequinum*. *Journal of Comparative Physiology*, 1975, *100*, 211–219.

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

Miller, J. D. Audibility curve of the chinchilla. *Journal of the Acoustical Society of America*, 1970, *48*, 513–523.

Mohl, B. Auditory sensitivity of the common seal in air and water. *Journal of Auditory Research*, 1968, *8*, 27–38.

Moody, D. B., Beecher, M. D., & Stebbins, W. C. Behavioral methods in auditory research. In C. A. Smith & J. A. Vernon (Eds.). *Handbook of auditory and vestibular research methods*. Springfield, Ill., Charles C Thomas, 1976.

Ödberg, F. O. A study of the hearing ability of horses. *Equine Veterinary Journal*, 1978, *10*, 82–84.

Patterson, R. D., & Green, D. M. Auditory masking. In E. C. Carterette & M. P. Friedmann (Eds.), *Handbook of perception* (Vol. 4). New York: Academic Press, 1978.

Ravizza, R. J., Heffner, H. E., & Masterton, B. Hearing in primitive mammals: I. Opossum (*Didelphis virginianus*). *Journal of Auditory Research*, 1969, *9*, 1–7. (a)

Ravizza, R. J., Heffner, H. E., & Masterton, B. Hearing in primitive mammals: II. Hedgehog (*Hemiechinus auritus*). *Journal of Auditory Research*, 1969, *9*, 8–11. (b)

Ryan, A. Hearing sensitivity of the mongolian gerbil, *Meriones unguiculatis*. *Journal of the Acoustical Society of America*, 1976, *59*, 1222–1226.

Schusterman, R. J., Balliet, R. F., & Nixon, R. Underwater audiogram of the California sea lion by the conditioned vocalization technique. *Journal of the Experimental Analysis of Behavior*, 1972, *17*, 339–350.

Simpson, G. G. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 1945, *85*, 1–350.

Sivian, L. J., & White, S. D. On minimum audible sound fields. *Journal of the Acoustical Society of America*, 1933, *4*, 288–321.

Stebbins, W. C. Studies of hearing and hearing loss in the monkey. In W. C. Stebbins (Ed.), *Animal psychophysics*. New York: Appleton-Century-Crofts, 1970.

Stebbins, W. C., Green, S., & Miller, F. L. Auditory sensitivity of the monkey. *Science*, 1966, *153*, 1646–1647.

Terhune, J. M., & Ronald, K. The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777): III. The underwater audiogram. *Canadian Journal of Zoology*, 1972, *50*, 565–569.

Terhune, J. M., & Ronald, K. Underwater hearing sensitivity of two ringed seals (*Pusa hispida*). *Canadian Journal of Zoology*, 1975, *53*, 227–231.

Wollack, C. H. The auditory acuity of the sheep (*Ovis aries*). *Journal of Auditory Research*, 1963, *3*, 121–132.

Zwislocki, J. J. Masking: Experimental and theoretical aspects of simultaneous, forward, backward, and central masking. In E. C. Carterette & M. P. Friedmann (Eds.), *Handbook of perception* (Vol 4). New York: Academic Press, 1978.

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