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Hearing in domestic pigs (*Sus scrofa*) and goats (*Capra hircus*)

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Behavioral audiograms were determined for three pigs and two goats. The hearing of the pigs ranged from 42 Hz to 40.5 kHz with a region of best sensitivity from 250 Hz to 16 kHz. Hearing in goats ranged from 78 Hz to 37 kHz with a well-defined point of best sensitivity at 2 kHz. Because these animals are unable to localize high-frequency tones, it seems unlikely that selective pressure to use the interaural spectral-difference cue for sound localization is behind their high-frequency hearing. Instead, we suggest that these and other hoofed mammals evolved high-frequency hearing in order to use monaural locus cues which prevent front/back locus reversals.

Audiogram; Psychophysics; Ungulates; Ultrasonic; Sound localization; Evolution

Introduction

We have been engaged in a comparative study of the auditory capacities of mammals in the hope of identifying the selective pressures involved in hearing (e.g., Heffner and Heffner, 1985a,b). Because the ability of mammals to hear high-frequency sounds is known to be related to the functional distance between the two ears (Masterton et al., 1969), we have obtained the audiograms of mammals ranging in size from mice to elephants (Heffner and Masterton, 1980; Heffner and Heffner, 1982). However, the sample of mammalian audiograms remains heavily weighted with relatively small species for the practical reason that large animals are not easily accommodated in the laboratory.

The purpose of this study was to increase our sample of larger mammals by determining the audiograms of the domestic pig (*Sus scrofa*) and goat (*Capra hircus*). The pig is a member of the Artiodactyla, a large and successful Order consisting primarily of large herbivorous animals. In particular, the pig is a member of the most primitive Infraorder in the Artiodactyla; it is omnivorous and even predatory, eating most small animals that it comes across, and has the least specialized stomach and foot anatomy among the Suborders of Artiodactyla (Nowak and Paradiso, 1983). Although domesticated, pigs quickly return to the wild state and feral pigs are common. The goat is a member of a more recently derived family of the Artiodactyla, the Bovidae. It is strictly herbivorous, eating rough forage and browsing on leaves and bark, and it possesses a specialized digestive tract that enables it to survive on such a diet.

Methods

Both species were tested with a conditioned avoidance procedure in which a thirsty animal was trained to make continuous contact with its mouth on a water spout in order to receive a steady trickle of water. Tones were then presented at random intervals and followed at their offset by a mild electric shock delivered through the spout. By breaking contact with the spout during tone presentations, an animal both avoided the shock and indicated that it had heard the tone.

Subjects

Three four-month-old female pigs (referred to as A, B, and C) of three different breeds (Duroc,

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Hampshire, and Yorkshire, respectively) and two six-month-old female goats (A and B) of mixed breed were used in this experiment. The animals were housed in rooms and had free access to food. Water was used as a reward and was available only during the test sessions. The animals were weighed daily to monitor their deprivational state. The pigs weighed 19–26 kg at the beginning of the experiment and 36–43 kg two months later at the end testing. The goats weighed 20–25 kg throughout testing.

Behavioral apparatus

Both species were tested in a rectangular cage ($93 \times 47 \times 108$ cm) constructed of welded wire (5×10 cm mesh) mounted on a wooden frame with a wire door in the rear. In order to eliminate obstructions between the sound source and an animal's ears, the cage was designed so that an animal's head and shoulders stood above the wooden frame. In addition, the animal placed its head through an opening in the front of the cage during testing in order to reach a water spout. Water was delivered to the pigs through a spout made from 1/4-in (0.64-cm) copper tubing mounted on a 68-cm high stand in front of the test cage. Because goats did not readily drink from the tubing, water was delivered to them in a 7-cm oval spoon connected to the water reservoir via plastic tubing.

Testing was conducted in a double-walled sound chamber ($2.55 \times 2.75 \times 2.05$ m) the walls and ceiling of which were lined with eggcrate foam to reduce sound reflection. The water spout was connected by plastic tubing to an electrically operated water valve and a 1-liter water reservoir, both of which were located outside the chamber in an adjacent control room. A contact circuit connected between the water spout and cage floor served to detect when an animal made contact with the spout, and a constant-current shock generator was connected between the spout and the cage floor. A loudspeaker was located 1 m in front of the cage at the level of an animal's ears when it was drinking.

Acoustical apparatus

Sine waves were generated by an oscillator (Hewlett-Packard 209A), switched on and off by an electronic switch (Grason Stadler 1287), attenuated with an attenuator (Hewlett-Packard 350D), filtered with a band-pass filter (Krohn-Hite 3202) which was set at 1/3-octave points above and below the test frequency, and then led via either an impedance-matching transformer or an amplifier (Crown D75) to a loudspeaker (a ribbon tweeter or piezoelectric tweeter for frequencies above 4 kHz, and a 12-in (30.5-cm) or 15-in. (38-cm) woofer for lower frequencies). Test frequencies ranged from 32 Hz to 64 kHz in octave steps with 45 kHz used as an additional frequency.

Frequencies of 500 Hz and above were pulsed with a 400 ms on-time and 100 ms off-time using a 20 ms rise-decay time. Rise-decay times of 40, 80, 150, and 300 ms were used for 250 Hz, 125 Hz, 63 Hz, and 32 Hz, respectively with longer on and off times to compensate for the longer rise-decay times.

The sound pressure level (re 20 μNewtons/meter^2) was measured with either a Brüel and Kjaer (B and K) 1-in. (2.54-cm) microphone (B and K 4131), sound level meter (B and K 2203), and octave filter (B and K 1613), or a 1/4-in. (0.64-cm) microphone (B and K 4135), preamplifier (B and K 2608), and filter (B and K 1613 or Krohn-Hite 3202). The microphones were calibrated with a pistonphone (B and K 4220). Sound measurements were taken by placing the microphone in the position normally occupied by an animal's ears when the animal was drinking and pointing the microphone directly toward the loudspeaker (0° incidence). Care was taken to ensure that the sound field was homogeneous in the area occupied by the animal's head.

The intensity of the ambient noise in the test chamber was measured in 1/6-octave steps from 3.15 Hz to 100 kHz. Measurable background noise (greater than 10 dB SPL) was present in the test chamber only at frequencies below 125 Hz and never exceeded 18 dB. At frequencies where it was measurable, the background noise remained 10–30 dB below the thresholds of the animals.

Psychophysical procedure

A thirsty animal was trained to make steady contact with its mouth on the water spout in order to receive a steady trickle of water (20–30 ml/min) which was delivered as long as the animal main-

tained contact with the spout. This served to center the animal's head in the sound field. Once an animal had learned to drink steadily, it was trained to break contact with the spout whenever a tone was presented. This was accomplished by presenting a 2-s train of tone pulses followed by a mild electric shock delivered through the spout. The level of shock was individually adjusted for each animal to the lowest level that would reliably produce an avoidance response. The mildness of the shock was empirically verified by observing that none of the animals ever developed fear of the water spout and returned to it without hesitation after receiving a shock. After a few pairings of tone with shock, the animals learned to avoid the shock by breaking contact with the spout whenever they heard a tone. In this way, breaking contact with the spout could be used as an indication of an animal's ability to detect a tone. In order to provide feedback for successful avoidance, a light in the test chamber was momentarily flashed on each time a shock was delivered. This light served to indicate to the animal that the shock had been delivered and that it was safe to return to the spout.

The test procedure was similar to that used previously (e.g., Heffner and Heffner, 1985a) in which trials consisting of a train of tone pulses (400 ms on, 100 ms off) was presented for 2.0 s at random intervals 5.5 s to 55 s after the previous trial. The onset of the tone was restricted to time periods at 5.5-s intervals (i.e., 5.5 s, 11.0 s, 16.5 s, ... 55 s) so that there was a maximum of 10 time periods during which a tone might occur. The number of times in which a tone occurred in a particular time period was adjusted so that each of the 10 periods had the same probability (0.23) of containing a warning signal. This resulted in some sequences in which no tone occurred so that the probability of the tenth time period containing a tone was also 0.23. Thus, a trial began 5.5 s after the previous trial and ended either after presentation of a tone or 60.5 s later (if no tone was presented).

The response of an animal on each trial was determined and a measure of performance was calculated separately for each intensity at each frequency using the formula: Corrected Hit Rate = (Hit Rate − False Alarm Rate)/(1 − False Alarm Rate) (cf. Heffner and Heffner, 1985a). In trained animals, this measure varies from about 0 (failure to detect a tone) to 1.0 (perfect detection without false alarms).

Auditory thresholds were determined for each frequency by reducing the intensity of the tone in 5-dB steps until the animal could no longer distinguish tone trials from silent trials. Threshold was defined as the lowest intensity which resulted in a corrected hit rate of 0.50.

Results

Pigs

The audiograms of the three pigs are shown in Fig. 1. The animals were easily trained and the results show good agreement between animals. Average false alarm rates for the three pigs remained below 5% for pig A and 6% and 7% for pigs B and C respectively.

Beginning at 32 Hz the animals showed steady improvement in sensitivity as frequency was increased to about 250 Hz. There followed a broad range of good sensitivity extending from 250 Hz to 16 kHz. Sensitivity declined rapidly above 32 kHz with pig C unable to hear 45 kHz at a level of 84 dB. None of the animals was able to hear 64 kHz at 74 dB. Overall, at an intensity of 60 dB, the average range of hearing for pigs extends from 42 Hz to 40.5 kHz with a best sensitivity of 9 dB at 8 kHz.

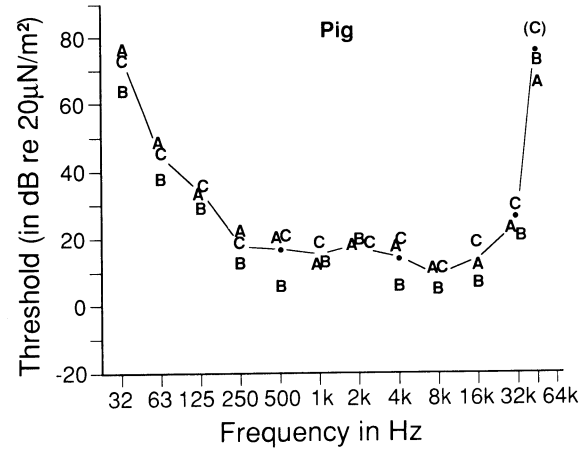

Fig. 1. Audiograms of three pigs. (Letters indicate individual animals; parentheses indicate no response at that intensity.)

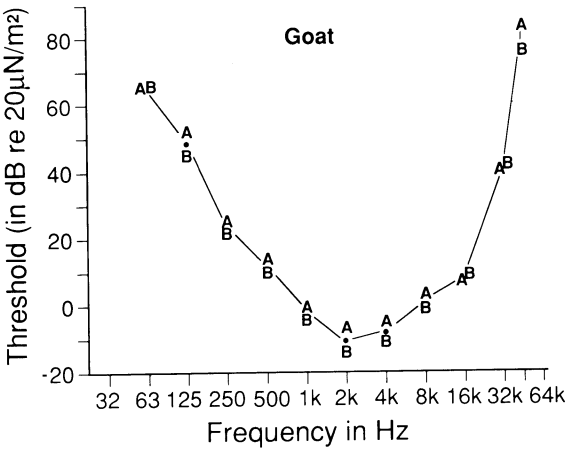

Fig. 2. Audiograms of two goats. (Letters indicate individual animals.)

Goats

The audiograms for the two goats are shown in Fig. 2. The two goats also show good agreement in their thresholds and their false alarm rates were also low — below 3%.

Beginning at 63 Hz, the animals showed steady improvement to a well-defined point of best sensitivity of −11 dB at 2 kHz. This was followed by a gradual decline in sensitivity up to 16 kHz and then a more rapid decline above 16 kHz. At an intensity of 60 dB, the average range of audibility for goats extends from 78 Hz to 37 kHz.

Both pigs and goats have good high-frequency sensitivity which extends approximately 1 octave above the 18-kHz upper limit (at 60 dB) of man. Similarly both have good low-frequency hearing compared to most mammals, but pigs hear approximately 1 octave lower than goats (42 Hz vs. 78 Hz respectively). Both pigs and goats have a broad range of good sensitivity between 250 Hz and 16 kHz within which they can detect sounds of 20 dB or less. However, goats displayed a well-defined point of best sensitivity within that range where they attained a sensitivity 20 dB greater than that of pigs.

Discussion

With the addition of pigs and goats to the previously tested horses, cattle, and sheep, there are now five hoofed mammals whose hearing has been behaviorally determined. In the first part of the discussion we describe the hearing abilities of this group. In the second part, we compare the hearing of hoofed mammals with that of mammals in general in a discussion of the selective pressures

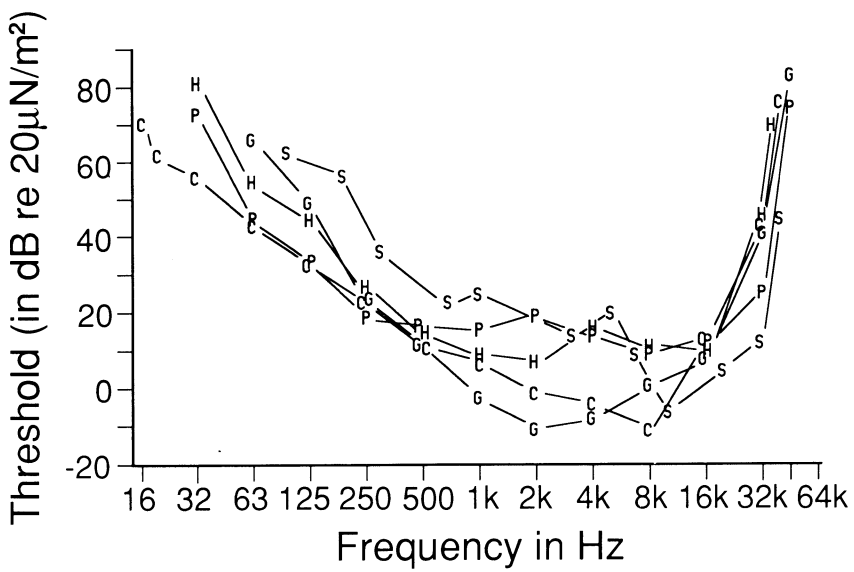

Fig. 3. Average audiograms of hoofed mammals. (C = cattle, G = goat, H = horse, P = pig, S = sheep. Heffner and Heffner, 1983a; Wollack, 1963.)

which may have influenced the evolution of high- and low-frequency hearing.

Auditory characteristics of hoofed mammals

The audiograms of five species of hoofed mammals are shown if Fig. 3. In this figure, it can be seen that their ability to hear high frequencies varies by less than 1/3 octave; at an intensity of 60 dB, their upper limits range from 33.5 kHz in horses to 42 kHz in sheep with an average of 37.5 kHz (Table I). Overall, the high-frequency hearing ability of hoofed mammals is below the mammalian average of 48 kHz ($P < 0.05$). This relative lack of good high-frequency hearing is a characteristic of large mammals and, as discussed in detail below, is related to the cues for sound localization.

Turning to low-frequency sensitivity, it can be seen that hoofed mammals show considerable variation; at an intensity of 60 dB, their lower limits range from 23 Hz in cattle to 125 Hz in sheep, a span of 2.5 octaves. Overall, their average low-frequency hearing limit of 55 Hz is significantly lower than the 180 Hz average for all terrestrial mammals (Table I, $P < 0.05$) Indeed, the low-frequency hearing ability of hoofed mammals is lower than that of any other order of mammals, including primates (which have an average low-frequency limit of 64 Hz). Again, good low-frequency hearing is usually, although not exclusively, a characteristic of large mammals.

Finally, all of the hoofed mammals examined so far have a relatively broad range of good sensitivity to sound. Their average frequency of best sensitivity of 4.8 kHz is within one-sixth octave of the mammalian mean of 6.86 kHz (Table I). In addition, their average best sensitivity is −2.4 dB, well within one standard deviation of the mammalian mean of 0.4 dB. Thus even though the hearing range of hoofed mammals seems to be shifted toward the low frequencies, their best hearing remains typical of mammals as a whole.

High-frequency hearing in mammals

One of the unique features of mammals is their ability to hear high-frequency sounds. Whereas non-mammalian vertebrates do not hear significantly above 10 kHz, and most do not even hear that high, the high-frequency hearing limit of mammals ranges from about 10 kHz to over 100 kHz (e.g., Heffner and Heffner, 1985b; Kermack, 1989; Masterton et al., 1969). This difference between the hearing abilities of mammals and non-mammals has led to the search for the selective pressures which led to the development of this ability, that is, why mammals hear high frequencies.

TABLE I

AUDITORY CHARACTERISTICS OF HOOFED MAMMALS COMPARED WITH THE MAMMALIAN AVERAGE

	Low-frequency limit (in Hz)	High-frequency limit (in kHz)	Best frequency (in kHz)	Lowest threshold (in dB)
Perissodactyla				
Horse	55	33.5	1	7.0
Artiodactyla				
Pig	42	40.5	8	9.0
Cattle	23	35.0	8	−11.0
Goat	78	37.0	2	−11.0
Sheep	125	42.0	10	−6.0
Mean	55 *	37.5 *	4.8	−2.4
Terrestrial mammals				
Mean	180	48	6.8	0.4
SD	0.77 octave	0.2 octave	0.48 octave	7.6 dB

Auditory characteristics of mammals based on audiograms of more than 40 species of terrestrial mammals; * Indicates that the mean for hoofed mammals is lower than the mean for terrestrial mammals ($P < 0.05$).

Over twenty years ago it was proposed that mammals evolved the ability to hear high frequencies in order to localize sound accurately (Masterton et al., 1969). This proposal was based on the observation that mammals with small heads, and therefore close-set ears, are better able to hear high-frequency sounds than those with large heads and wide-set ears. At present the correlation between head size (specifically, maximum interaural distance)and high-frequency hearing is -0.84 ($P < 0.00001$) and is based on data from 52 species. As shown in Fig. 4, this relationship also applies to pigs and goats.

The significance of this correlation for sound localization was originally believed to lie in the fact that the magnitude of the binaural spectral cues is dependent on an animal's functional head size. That is, the farther apart the ears, the larger the difference in the time of arrival of a sound at the two ears. Similarly, the difference in the frequency-intensity spectra of a sound reaching the two ears is greater for animals with large heads and pinnae. However, the magnitude of the spectral cue is also dependent on frequency and an animal with a small head can make use of the spectral cue if it is able to perceive frequencies that are high enough to be effectively shadowed by its head and pinnae. Thus, it has been argued that animals with functionally small heads are under greater selective pressure to hear high frequencies than larger animals in order to make use of the binaural spectral-difference cue.

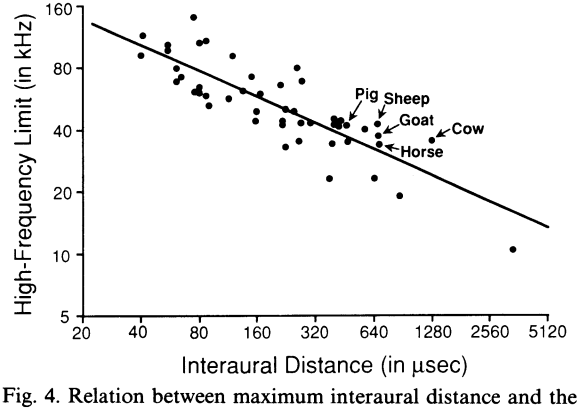

Fig. 4. Relation between maximum interaural distance and the highest frequency audible at 60 dB SPL for both terrestrial and underwater mammals. (The correlation among the 52 species represented is -0.84, $P < 0.0001$.)

The idea that mammals need to hear high frequencies in order to use the binaural spectral-difference cue has recently been supported by sound localization experiments which show that the ability of rats and cats to perform a left-right locus discrimination decreases when the high frequencies are removed from the signal (Heffner, 1989). However, in spite of this evidence, it is becoming increasingly apparent that the need to use the binaural spectral cue cannot account for the high-frequency hearing ability of all mammals. This is because there exist animals which, despite their good high-frequency hearing, have partially or completely lost the ability to use the binaural intensity-difference cue.

The results of localization tests using pure-tone stimuli have indicated that all of the hoofed mammals examined so far have partially or completely lost the ability to localize high-frequency pure tones. Of the four species tested, horses, cattle, and pigs are unable to localize tones higher than 1 kHz to 2 kHz. Since this is the frequency range in which the phase difference cue becomes ambiguous for these animals, this result suggests that they are unable to use the binaural intensity difference cue and, presumably, the spectral-difference (Heffner and Heffner, 1989a,b; 1989). In the case of horses, the inability to use binaural intensity-difference cues was further supported by dichotic experiments (Heffner and Heffner, 1988). Goats, on the other hand, are able to localize pure tones up to 4 kHz —at least one octave above the limit for binaural phase — demonstrating that they do possess at least minimal ability to use the binaural intensity-difference cue (Heffner and Heffner, 1986b). However, they are unable to localize pure tones at higher frequencies, a finding which suggests that they do not use high-frequency hearing to maximize the spectral cue.

One explanation is that high-frequency hearing in these animals is vestigial and has no function. One possibility is that the process of domestication has increased the head size of these species while their high-frequency hearing has remained constant (cf. Heffner, 1983). However, analysis of the data represented in Fig. 4 reveals that hoofed mammals do not hear significantly higher than expected based on their interaural distances. Another possibility is that domestication has

selected against sound localization so that these animals have lost the ability to use high frequencies for localization as a first step in losing sound localization altogether. However it seems unlikely that the loss of the frequency-intensity spectral cue is the result of reduced selective pressure for accurate sound localization since pigs, which have lost the use of this cue can localize as accurately as cats and monkeys (Heffner and Heffner, 1989). Further, we now know that a reduction in selective pressure for sound localization is associated with a loss in the ability to hear high frequencies. Specifically, pocket gophers which are strongly adapted to an underground environment (in which airborne sound follows one-dimensional tunnels) have lost both the ability to localize sound and the ability to hear frequencies above 10 kHz (Heffner and Heffner, 1990). Thus, the fact that hoofed mammals hear well above 10 kHz indicates that high frequencies continue to provide useful information. We suggest that the information provided forms the basis for using monaural cues for sound localization.

Monaural localization and high-frequency hearing

The spectrum of a sound reaching an ear is dependent on the location of the sound source relative to the head and ear. Different locations generate different spectra due in part to the directionally-dependent filtering properties of the pinna as well as to other factors such as the configuration of the head and shoulder and the angle of the sound source to the auditory canal. Over the years it has become apparent that these monaural cues play an important role in human sound localization both in the vertical and horizontal planes and that they are dependent on high frequencies. In the case of vertical localization, which is dependent entirely on monaural cues, Roffler and Butler (1968) demonstrated that accurate localization depends on the presence of frequencies above 7 kHz.

With regard to localization in the horizontal plane, the importance of binaural cues has long overshadowed the contribution of monaural cues. However, although binaural cues can give accurate information, they cannot be used to distinguish between front and back locations. Thus, as Butler and his colleagues have demonstrated, monaural cues are needed to determine whether a sound is located in the front or back hemifield (Belendiuk and Butler, 1975; Musicant and Butler, 1984). In addition, they have shown that in humans monaural localization in the horizontal plane relies on frequencies above 4 kHz (Musicant and Butler, 1984).

Although it might be argued that some mammals do not have to localize in the vertical plane, the importance of avoiding front-back reversals is obvious. Even though binaural time differences available from the low-frequency portion of a sound may provide sufficient information as to the left-right location of a sound source, monaural cues are necessary to determine whether the sound source is located in the front or rear quadrant. Thus, we suggest that a major function of high-frequency hearing in mammals is to permit the use of monaural cues and prevent front-back reversals.

Recent studies of the ability of mammals to localize sound in the lateral fields demonstrate that high-frequency hearing is important in distinguishing between front and rear sound sources. For example, front-back discrimination in laboratory rats, which hear up to 76 kHz (at 70 dB), begins to decline when frequencies above 40 kHz are removed from the signal. Similarly, performance in cats, which hear up to 85 kHz (at 70 dB), also declines when frequencies above 40 kHz are removed (Heffner, 1989).

Like rats and cats, hoofed mammals require high frequencies in order to perform a front-back discrimination. Both horses and pigs are unable to perform a front-back discrimination using 500-Hz low-pass noise although they can perform a left-right discrimination with the same stimulus with only a slight increase in threshold (Heffner and Heffner, 1983b; Heffner, unpublished observations). On the other hand, with an 8-kHz high-pass signal, neither animal has any difficulty performing a front-back discrimination (using pinna cues) or a left-right discrimination (since binaural time information is available in the envelope of the signal) (McFadden and Pasanen, 1976). Thus, there is reason to believe that, like other mammals, hoofed mammals require high frequencies in order to use monaural locus cues for front-back discriminations even if they cannot perform a binau-

ral intensity-difference analysis using the same frequencies.

In conclusion, mammals appear to have evolved high-frequency hearing in order to localize sound. Although most mammals use their high-frequency hearing to maximize binaural spectral differences, some mammals do not. However, we suggest that all mammals use their high-frequency hearing to enhance their ability to make front-back distinctions using monaural cues. The one exception to this rule is the gopher, a mammal which has lost its high-frequency hearing and is unable to make locus judgments of front-back or left-right (Heffner and Heffner, 1990). Thus, we argue that high-frequency hearing evolved for the purpose of using monaural locus cues alone or in combination with binaural spectral difference cues.

Low-frequency hearing in mammals

It has long been noted that low-frequency hearing varies widely among mammals (Heffner and Masterton, 1980; Masterton et al., 1969). For example, the 60-dB low-frequency hearing limit of the elephant is 17 Hz whereas the little brown bat has a lower limit of 10.3 kHz (Dalland, 1965; Heffner and Heffner, 1982). Thus, the low-frequency hearing limits of mammals span a range of more than 9 1/2 octaves. In comparison, high-frequency hearing limits range from 8.7 kHz, in the gopher, to 140 kHz in the porpoise, a range of 5 octaves (Heffner and Heffner, 1990; Johnson, 1967).

In searching for possible explanations of the variation in low-frequency hearing, previous analyses have examined three factors: body weight, interaural distance, and high-frequency hearing limit (Masterton et al., 1969; Heffner and Masterton, 1980; Heffner and Heffner, 1985b). The results of multiple regression analysis have indicated that, of these three factors, only high-frequency hearing is significantly correlated with low-frequency hearing ($r = 0.78$, $P < 0.01$). That is, there appears to be a trade-off such that animals with good high-frequency hearing generally have poor low-frequency hearing and vice versa. The apparent relation of both interaural distance and body size to low-frequency hearing is due entirely to the correlation of each with high-frequency hearing.

Although the relationship between high- and low-frequency hearing continues to hold for the majority of mammals, over the years a number of exceptions have appeared. These exceptions are of particular interest in that they may indicate the presence of unusual abilities brought on by adaptation to unusual environments.

The first obvious exception has been the underwater hearing of marine mammals. Animals such as the porpoise and beluga whale have extremely good high-frequency hearing and are able to hear well above 100 kHz (Johnson, 1967; Johnson et al., 1989; White et al., 1977). Yet these animals have also retained good low-frequency hearing thus giving them unusually broad hearing ranges. This unusual ability may be due to the fact that the transmission of sound can bypass the middle ear in underwater species (McCormick et al., 1970), an observation which suggests that the middle ear may be a limiting factor in high- and low-frequency hearing.

A second exception appears to be underground mammals. This is exemplified by the gopher and the blind mole rat. The gopher and mole rat are fossorial rodents which cannot hear well above 10 kHz, yet have unexceptional low-frequency hearing (Bronchti et al., 1989; Bruns et al., 1988; Heffner and Heffner, 1990; Muller and Burda, 1989). The gopher appears to have given up high-frequency hearing in its adaptation to a fossorial habitat due to the fact that it does not localize sound (a superfluous ability in the one-dimensional world of tunnels). Without sound localization there is little selective pressure to hear the high frequencies normally important for sound localization in small mammals. That this loss has not been accompanied by improved low-frequency hearing suggests that the hearing range does not automatically shift to include low frequencies simply because a species does not hear high, but rather that selective pressure for low-frequency sensitivity must be present.

Given that there are important exceptions to the general relationship between high- and low-frequency hearing, the question arises as to whether hoofed mammals fit the general pattern. Examining this relation among terrestrial surface dwellers reveals that there remain seven species which deviate significantly from the regression

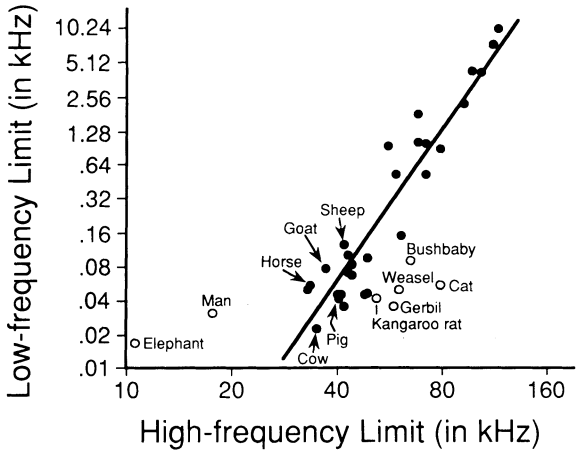

Fig. 5. Relation between the highest and lowest frequencies audible at 60 dB SPL for 37 species of terrestrial mammals. (The regression line as plotted does not include the seven species, represented by open circles, that differ markedly from the remaining 30 species (i.e., human and elephant which do not hear as low as predicted and kangaroo rat, least weasel, gerbil, bushbaby and domestic cat which hear much lower than predicted). The relation is such that for every octave increase in high-frequency hearing, there is a loss of 4.6 octaves of low-frequency hearing. $r = 0.95$, $P < 0.0001$. Inclusion of the seven deviant species lowers the correlation to $r = 0.78$, $P < 0.0001$.)

line ($P < 0.01$, indicated by the open circles in Fig. 5). Removal of these seven species from the analysis raises the correlation coefficient from 0.78 to 0.95. Removal of additional species does not raise the correlation any further whereas removal of any other combination of seven species actually lowers it. Thus, the 30 remaining species show a high correlation between high-and low frequency hearing ($r = 0.95$, $P < 0.001$).

Fig. 5 reveals that both pigs and goats, and indeed, all of the hoofed mammals, are not deviant but rather conform closely to this relationship — their good low-frequency hearing is accompanied by modest high-frequency hearing. This finding suggests that hoofed mammals are typical mammals and are not unusual in their sensitivity to low frequencies.

Examination of the seven deviant species shows that they fall into two groups. First, there are two species, those with the best low-frequency hearing, that nevertheless do not hear as low as expected on the basis of their very limited high-frequency hearing. Man and elephants, despite their 60-dB low-frequency hearing limits of 31 Hz and 17 Hz respectively, do not hear nearly as low as the approximately 2 Hz and 0.2 Hz currently predicted by their limited high-frequency hearing (Fig. 5). For this reason, we have previously suggested the possibility of a 'floor effect' limiting the low-frequency hearing of mammals (Heffner and Heffner, 1982; Heffner and Masterton, 1980). Whether this floor effect is due to physiological limitations of the auditory apparatus in responding to very low frequencies or to the absence of useful information at those frequencies remains unresolved.

In contrast, there are five species whose low-frequency hearing extends beyond that predicted by their high-frequency hearing resulting in a broad hearing range (open circles to the right of the regression line in Fig. 5). Thus some terrestrial species have developed an ear capable of transducing sound over a very broad range. Cats provide the most extreme example of this ability in their 60-dB hearing range of 55 Hz to 79 kHz. Cats, along with gerbils, least weasels, kangaroo rats, and bushbabies illustrate that good high-frequency hearing is not physically or physiologically incompatible with good low-frequency hearing even for airborne sound.

In summary, the observation that most terrestrial mammals show a strong inverse correlation between high- and low-frequency hearing suggests that there may be physical and/or physiological constraints which make it difficult for a mammal to have both good high- and low-frequency hearing. However, the fact that some have developed a broad range of hearing indicates that it is possible to overcome these constraints given sufficient selective pressure. The nature of those selective pressures must await the discovery of additional species with similarly broad hearing since gerbils, kangaroo rats, least weasels, bushbabies and cats have no obvious unique features of lineage, habit, or habitat in common. It is also of theoretical interest to determine the morphological features which these animals have evolved which permit them to hear both high and low frequencies. In the case of gerbils and kangaroo rats, it has been argued that their hypertrophied bullae enable them to extend their hearing into the lower frequencies in an adaptation to their desert environment and the predators found

there (Fleischer, 1978; Lay, 1972; Webster and Webster, 1984). However the least weasel, a mouse-sized carnivore, is able to hear high and low frequencies as well as these desert rodents yet it lacks hypertrophied bullae and does not inhabit deserts (Heffner and Heffner, 1985b). Thus, there seems to be more than one mechanism to permit mammals to hear over a broad range of frequencies and more than one reason for doing so.

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