

9 Auditory Perception

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Summary

There have been three main sources of selective pressure on the ability of animals to perceive sound (Masterton and Diamond, 1973). The first has been the need to *detect* a sound, an ability that enables an animal to determine the presence of sound-producing objects in its environment, which in most cases are other animals. The second has been the need to *localize* the source of a sound so that an animal can either approach or avoid the sound source. Finally, an animal must be able to *identify* the biological meaning or relevance of the sound so that it may respond appropriately to the sound source.

Over the last decade our knowledge of the auditory abilities of animals in general and farm animals in particular has increased markedly. In the case of mammals, farm animals have been the object of study because it was necessary to determine the hearing abilities of large mammals in order to answer certain questions concerning the evolution of human hearing (e.g. R. Heffner and Heffner, 1983b). Because farm animals are relatively easy to handle, they made convenient subjects for experiments designed to answer questions which could not be addressed with standard laboratory animals.

The purpose of this chapter is to review what is known about the ability of farm animals to detect and localize sound in light of our knowledge concerning hearing in birds and mammals. In doing so, we have taken a broad definition of farm animals and, where information is available, have included pets, predators, and pests often encountered on farms. Also included in this chapter is a brief description of how to test the hearing ability of farm animals. Because little is currently known concerning the ability of animals to identify sounds, this topic is not covered.

Detection of Sound

Measuring absolute sensitivity

The basic test of hearing consists of determining the ability of an animal to hear pure tones at intervals throughout its hearing range. This is done by training the animal

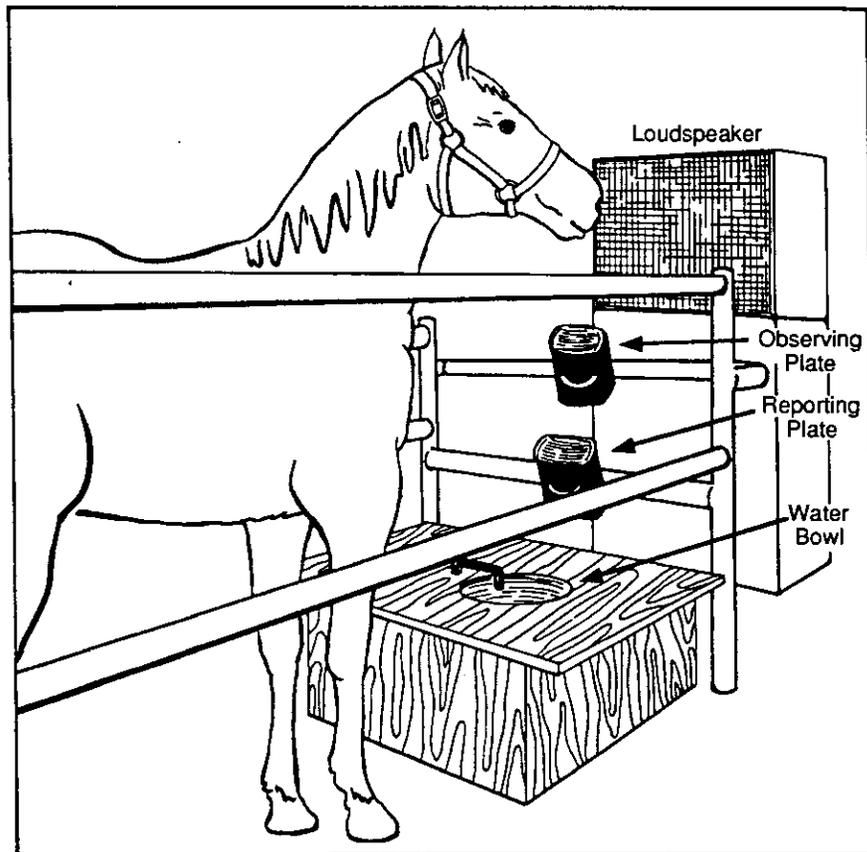


Fig. 9.1. Apparatus used to test hearing in horses and cattle. The animal was trained to place its nose on the observing plate and listen for a tone. Tones were presented at random intervals and the animal was given a water reward for touching the reporting plate within three seconds after onset of the tone (modified from H. Heffner and Heffner, 1983).

to respond to a tone and then reducing the intensity of the tone until the animal fails to respond. There are a number of behavioural procedures which can be used to train an animal to respond to sound. One procedure which has been used with farm animals is a 'go/no go' procedure in which an animal is trained to make a specific response whenever it hears a sound (e.g. R. Heffner and Heffner, 1983b).

In the go/no go procedure, a thirsty animal is led into a test stall and trained to place its nose on an 'observing' plate located in front of a loudspeaker (Fig. 9.1). Tones are then presented at random intervals and the animal is trained to break contact with the observing plate and touch a 'reporting' plate whenever it hears a tone. A response made in the presence of a tone is rewarded by delivering water into a bowl located below the reporting plate. However, if the animal responds when no tone is present, it is given a short wait or 'time out' of 5–15 s during which testing is halted. Testing is continued until the animal has received sufficient water which generally takes about 1 h each day.

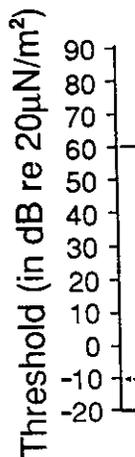


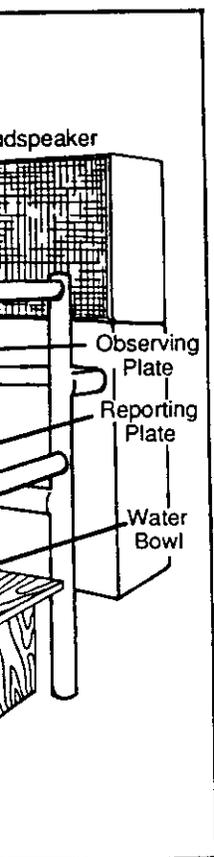
Fig. 9.2. Average hearing thresholds for horses and cattle compared to those of a group of human subjects.

Once an animal is trained for testing is begun. The animal's nose is placed on the animal's threshold. The tone is then presented at the tone half the intensity of the previous tones of various intensities. These thresholds are obtained and the animal is given water. This process takes eight to ten minutes.

The audiogram

The pure-tone hearing thresholds are shown in Fig. 9.2. The hearing thresholds of a particular frequency are indicated by small values. The hearing thresholds at low frequencies are small values. The hearing thresholds at high frequencies are large values. The hearing thresholds at low frequencies are small values. The hearing thresholds at high frequencies are large values.

The human hearing thresholds of most normal human beings are that auditory range is a range of 0 to 20 dB. The hearing thresholds decrease in intensity as the frequency is approached.



Animal was trained to place
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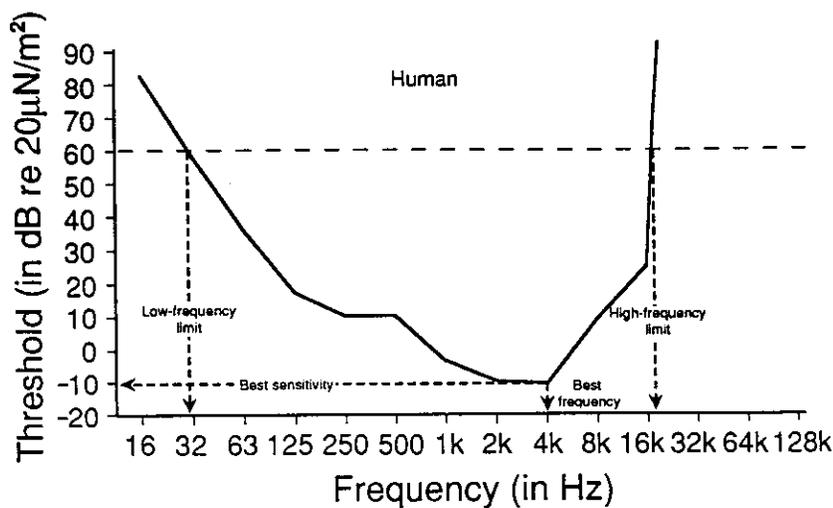


Fig. 9.2. Average audiogram for seven human subjects. To make the results comparable to those of animal studies, tones were presented from a loudspeaker placed in front of the subjects instead of using headphones (Heffner and Heffner, unpublished).

Once an animal has learnt to report reliably the presence of a tone, threshold testing is begun. This consists of gradually reducing the intensity of the tone until the animal no longer responds, implying that it can no longer hear the tone. The animal's threshold for that tone is then defined as the intensity at which it can detect the tone half of the time (i.e. 50% detection). Thresholds are then determined for tones of various frequencies taken in octave steps across the animal's hearing range. These thresholds are then used to construct an audiogram. It should be noted that obtaining and verifying a complete audiogram can be a lengthy procedure which takes eight to ten weeks of daily testing.

The audiogram

The pure-tone thresholds of an animal are used to construct an audiogram in which thresholds are plotted for tones of different frequency, an example of which is shown in Fig. 9.2. In this figure, each point represents the lowest intensity at which a particular frequency could be detected 50% of the time. Thus, large decibel (dB) values indicate that a tone had to be fairly intense before it could be detected while small values indicate that a less intense tone could be heard. Because sound, like temperature, is typically measured with a scale which has no absolute zero, negative values indicate only that the intensity of a sound is less than the 0 dB reference level.

The human audiogram shown in Fig. 9.2 demonstrates the characteristic shape of most normal audiograms. Beginning at the low frequencies, the audiogram shows that auditory sensitivity improves gradually as frequency is increased. Often, there is a range of best sensitivity in the middle of the audiogram followed by a gradual decrease in sensitivity which becomes a rapid decrease as the upper limit of hearing is approached.

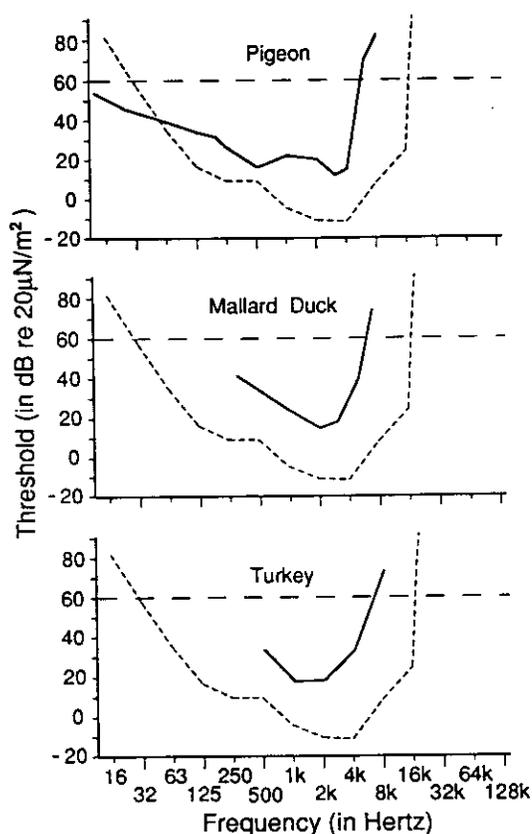


Fig. 9.3. Audiograms for the pigeon, mallard duck and turkey (solid lines). Human audiogram from Fig. 9.2 (dashed lines) is shown for comparison.

For comparative purposes, the audiogram can be described with four parameters (Masterton *et al.*, 1969). These are: (i) 'high-frequency limit' – arbitrarily defined as the highest frequency which an animal can hear at a sound pressure level (SPL) of 60 dB; (ii) 'low-frequency limit' – arbitrarily defined as the lowest frequency which can be heard at 60 dB; (iii) 'best frequency' – the frequency to which the animal is most sensitive; and (iv) 'best intensity' – the lowest intensity to which an animal can respond. As shown in Fig. 9.2, the corresponding values for humans are 17.6 kHz for our high-frequency limit and 31 Hz for our low-frequency limit with a best frequency of hearing around 4 kHz at which point our best sensitivity is -10 dB.

Hearing in birds

The audiograms of the mallard duck (*Anas platyrhynchos*), pigeon (*Columba livia*) and turkey (*Melegris gallopavo*) are shown in Fig. 9.3 (Trainer, 1947; Maiorana and Schleidt, 1972; Hienz *et al.*, 1977; Kreithen and Quine, 1979). Compared with humans (dashed line in each figure), it can be seen that the high-frequency hearing

of birds is notably poor and, indeed, no bird is able to hear much above 10 kHz (cf. Fay, 1988). Although their best frequency of hearing is in the same range as that of humans, these three species are not as sensitive as humans. Less is known about the low-frequency limit of birds as few species have been tested at low frequencies. However, there is evidence that pigeons have excellent low-frequency hearing which they may use for navigation (Kreithen and Quine, 1979).

The audiograms of four additional species of birds which are commonly found around farms are provided for comparison – starling (*Sturnus vulgaris*), red-winged blackbird (*Agelaius phoeniceus*), eastern sparrow hawk (*Falco sparverius*), and barn owl (*Tyto alba*) (Fig. 9.4) (Trainer, 1947; Konishi, 1973; Hienz *et al.*, 1977; Dooling *et al.*, 1986). The hearing abilities of these species are similar to those of the previous birds with one exception: the barn owl possesses greater sensitivity than the other birds, an adaptation which may be explained by the fact that it is a nocturnal predator which uses its hearing to locate prey.

In summary, the high-frequency sensitivity of birds is notable in that they do not hear significantly above 10 kHz. In most birds, both low-frequency sensitivity and best sensitivity are unremarkable with the exceptions of the pigeon, which appears to have exceptionally good low-frequency hearing, and the barn owl, which has excellent sensitivity at its best frequency of hearing.

Hearing in mammals

The hearing sensitivity of mammals differs from that of birds in several ways. First, most mammals possess the ability to hear frequencies above 10 kHz with the high-frequency limit of some mammals, such as bats and porpoises, extending beyond 100 kHz (cf. Fay, 1988). Second, whereas the auditory sensitivity of birds is relatively uniform, the hearing ability of mammals, particularly their ability to hear high and low frequencies, varies widely from one species to the next.

Hoofed mammals

The audiograms for horses (*Equus caballus*), sheep (*Ovis aries*), goats (*Capra hircus*), pigs (*Sus scrofa*) and cattle (*Bos taurus*), are shown in Fig. 9.5 (Wollack, 1963; R. Heffner and Heffner, 1983b, 1990a). As illustrated in this figure, the high-frequency hearing of hoofed mammals not only surpasses that of birds, but it also exceeds the high-frequency hearing of humans (dashed lines in each figure). The upper frequency limit of these animals ranges from 33.5 kHz in horses to 42 kHz in sheep. These animals also have relatively good low-frequency hearing with low-frequency limits ranging from 23 Hz for cattle (surpassing human low-frequency hearing) to 125 Hz for sheep. The best frequency of hearing varies from 2 kHz for horses and goats to 10 kHz for sheep. Best sensitivity varies from -11 dB for cattle and goats, making them as sensitive as humans, to 9 dB for pigs. Overall, the hearing sensitivity of hoofed mammals is similar to that of humans with the most significant difference being the ability of these animals to hear frequencies above the human upper limit of hearing, i.e. ultrasonic sounds.

The audiograms shown in Fig. 9.5 were obtained with animals whose ears were free of any signs of damage or disease – pathological conditions, such as the presence

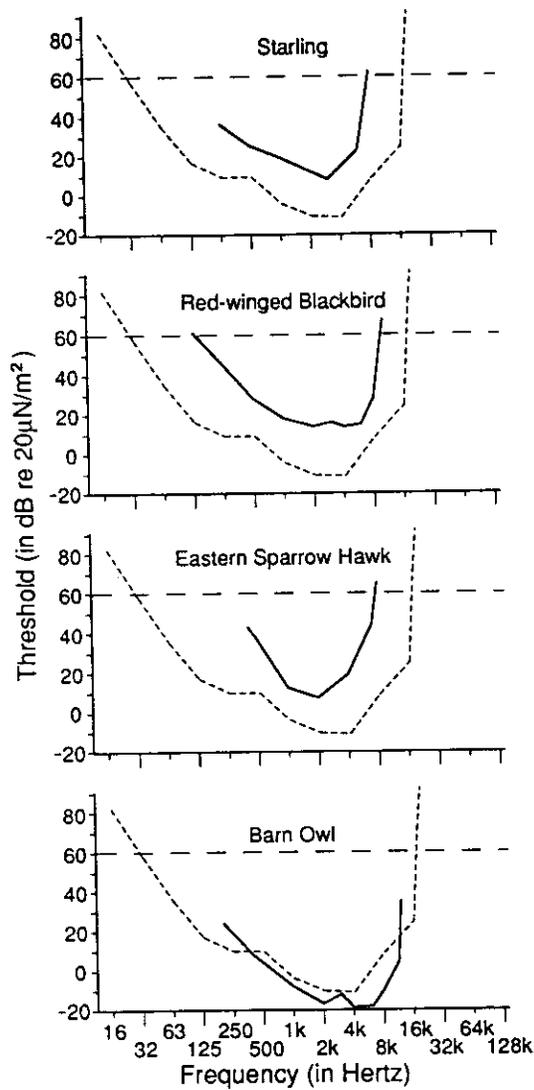


Fig. 9.4. Audiograms for the starling, red-winged blackbird, eastern sparrow hawk and barn owl (solid lines). Human audiogram is shown by dashed lines. Note the good sensitivity of the owl.

of ear mites, can substantially affect an animal's hearing. In particular, ear mites, which are often found in cattle and goats, have been shown to have a dramatic effect on an animal's ability to hear sound.

In the case of cattle, ear mites, *Raillietia auris*, are associated with redness, ulceration, and bleeding of the tissue lining the auditory canal as well as blockage of the canal by a thick plug of pus which may extend for 3 cm or more (R. Heffner and Heffner, 1983c). The pus, acting as an ear plug, attenuates middle frequencies

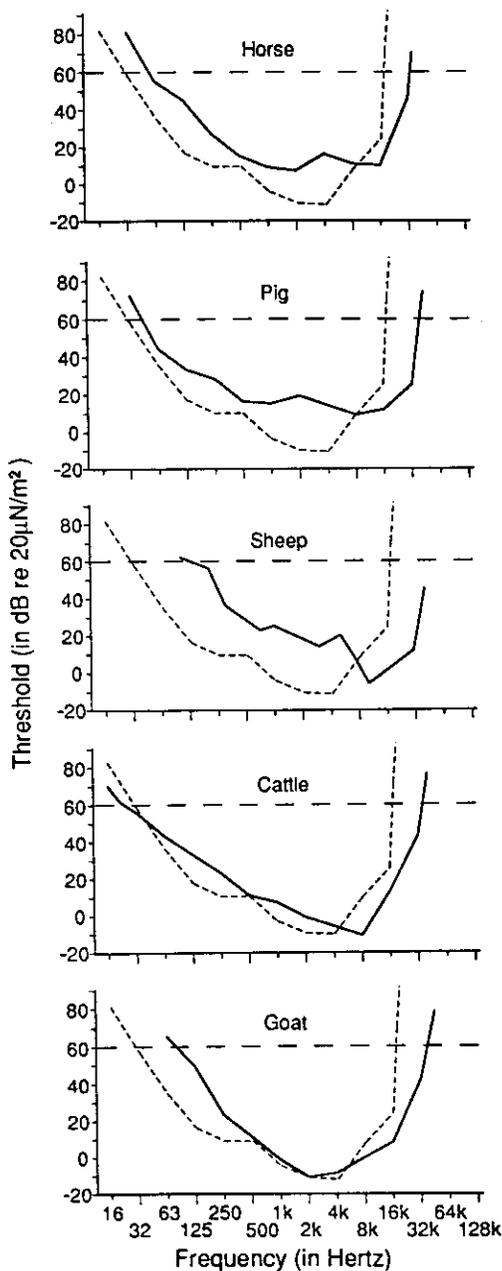


Fig. 9.5. Audiograms for the horse, pig, sheep, cattle and goat (solid lines). Human audiogram is shown by dashed lines.

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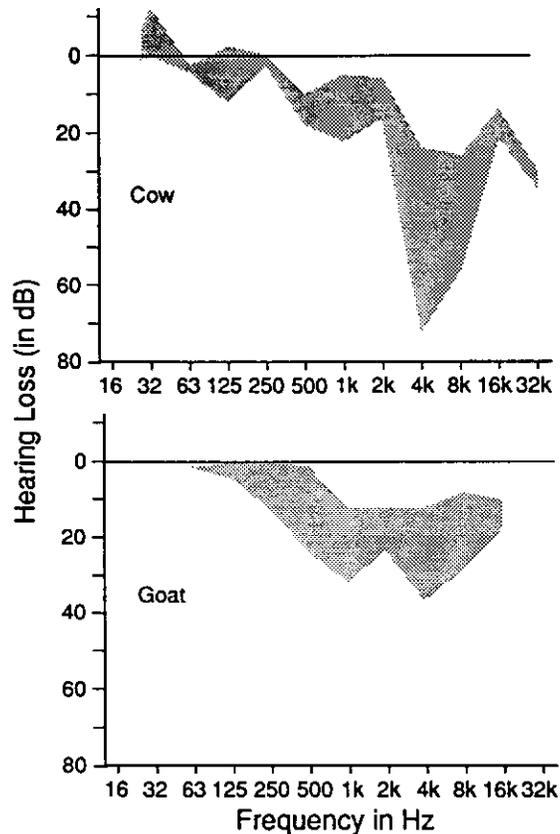


Fig. 9.6. Effect of ear mite infestation on the hearing of a cow (top) and a goat (bottom). Shaded areas indicate range of the hearing losses which varied markedly from day to day (R. Heffner and Heffner, 1983a and unpublished).

more effectively than low and high frequencies (R. Heffner and Heffner, 1983a). In cattle, this results in a hearing loss which is most severe around 4 and 8 kHz while frequencies below 500 Hz are unaffected (Fig. 9.6). This should not be considered an unusual condition as a survey of eight separate herds in southeastern Kansas found that 66% of the animals examined were infested with ear mites (R. Heffner and Heffner, 1983c). Ear mites are also found in goats and, although the effects are not as severe as in cattle, their presence does result in a definite hearing loss (Fig. 9.6; R. Heffner and Heffner, unpublished).

Carnivores

The audiograms of the domestic cat (*Felis domesticus*), dog (*Canis familiaris*) and ferret (*Mustela putorius*) show that these animals hear higher frequencies than hoofed mammals with their upper limits of hearing ranging from 42 kHz for the ferret to 79 kHz for the cat (Fig. 9.7) (Heffner, 1983; Kelly *et al.*, 1986; R. Heffner and Heffner,

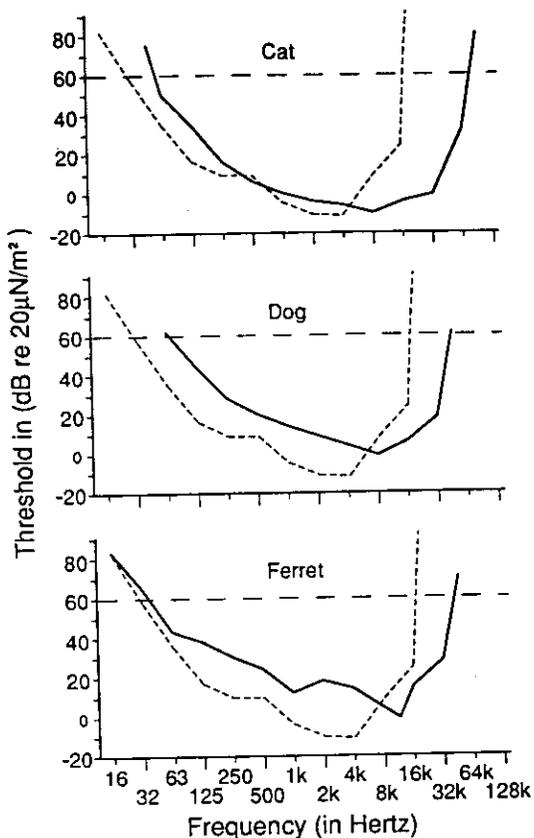


Fig. 9.7. Audiograms for the domestic cat, dog and ferret (solid lines). Human audiogram is shown by dashed lines.

1985b). Low-frequency limits for these three carnivores are very similar and range from 36 Hz for the ferret to 67 Hz for the dog. In terms of sensitivity, the ferret and dog are very similar while the cat is the most sensitive. Indeed, cats share with humans, cattle, and goats the distinction of being the most sensitive of all mammals tested so far.

Glires

Glires is a cohort containing the orders Lagomorpha and Rodentia. Audiograms for the domestic rabbit (*Oryctolagus cuniculus*), domestic Norway rat (*Rattus norvegicus*), and wild house mouse (*Mus musculus*), shown in Fig. 9.8, indicate that, as a group, these animals possess better high-frequency hearing than any of the previous groups (Kelly and Masterton, 1977; H. Heffner and Masterton, 1980). The high-frequency hearing limits range from 49 kHz for the rabbit to 92 kHz for the wild house mouse. On the other hand, the low-frequency limits of these animals are not as low as the other mammals and range from 96 Hz for the rabbit to 2.3 kHz for the house

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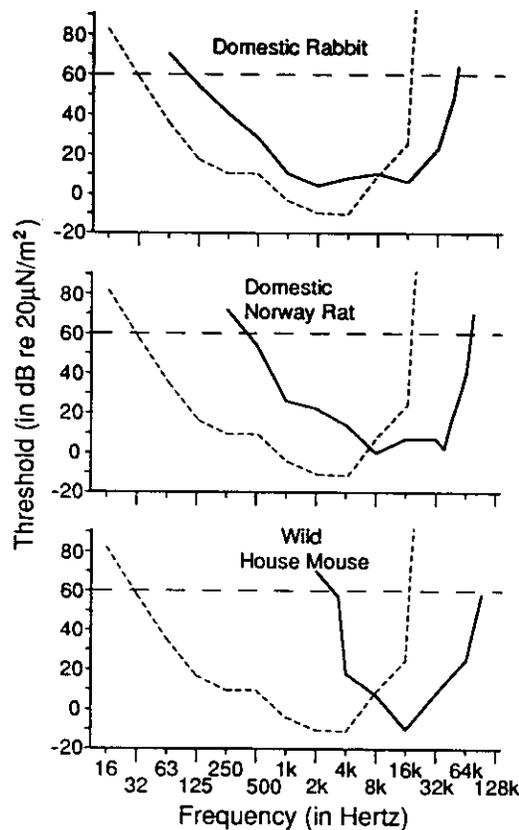


Fig. 9.8. Audiograms for the domestic rabbit, domestic Norway rat and wild house mouse (solid lines). Human audiogram is shown by dashed lines.

mouse. Indeed, the audiograms of the rat and mouse illustrate the phenomenon that animals with good high-frequency hearing often lack good low-frequency hearing.

Perception of ultrasound by mammals

Before continuing, it is of interest to note that there are currently a number of devices on the market which emit sounds above the human hearing range (i.e. ultrasound) for the purpose of repelling other animals. Claims have been made that high-frequency sound from 16 kHz to around 40 kHz can be used to repel deer, dogs, mice, rats, fleas, cockroaches and flies, and the list continues to grow despite the lack of evidence that these devices are effective.

Although such devices are usually advertised as being audible only to pests, all farm mammals are capable of hearing ultrasound (cf. Figs 9.5, 9.7 and 9.8) and one must consider whether ultrasonic repellents might stress these animals. In the case of ultrasonic flea collars, the question arises as to whether the ultrasound might cause

a hearing loss in the animal wearing it. However, it may be that ultrasonic repellents cause no more stress in farm animals than in the animals they are supposed to repel.

Evolution of high-frequency hearing

The most striking difference between the hearing of birds and mammals is the ability of mammals to hear frequencies well beyond the range of birds (and other non-mammalian vertebrates as well; cf. Fay, 1988). Whereas birds are unable to hear much above 10 kHz, and amphibians and reptiles do not even hear this high, the average upper limit for mammals is 48 kHz with some species able to hear above 100 kHz. Such a significant difference in abilities leads to the question of *how* mammals are able to hear so high and *why* they do so.

How mammals hear high frequencies

It is generally accepted that one of the main factors accounting for the ability of mammals to hear high frequencies is the unique three-boned middle ear of mammals which transmits sound from the ear drum to the cochlea. Unlike non-mammalian vertebrates which possess a single middle ear bone, the mammalian middle ear contains an articulated chain of three auditory ossicles. Studies of the frequency response or transfer function of the middle ear of various vertebrates have demonstrated that the mammalian ear is far more efficient in transmitting high frequencies to the cochlea than are the middle ears of non-mammalian vertebrates (e.g. Saunders and Rosowski, 1979). Thus, mammals are able to hear higher frequencies than non-mammalian vertebrates because their middle ear permits them to transduce frequencies above 10 kHz.

Why mammals hear high frequencies

The second question is why mammals hear high frequencies, that is, what advantage does this ability confer upon them? Recent research has indicated that mammals use their high-frequency hearing primarily to localize the source of a sound. Specifically, high-frequency hearing enables mammals to use both pinna cues and binaural spectral-difference cues to localize sound.

In addition to the three-boned middle ear, mammals evolved another unique auditory structure: the external ear or pinna. One of the primary features of the pinna is that it acts as a directional filter, amplifying sounds originating from in front of the ear while attenuating sounds from behind. As such they enhance an animal's ability to pick out signals embedded in a noisy world. However, the possession of a pinna has another important consequence: by making the opening of the ear canal asymmetric, the pinnae enable an animal to determine whether a sound is coming from the front or back. In other words, the pinnae provide the primary, if not the only, means for avoiding front-back confusions. This is demonstrated by the fact that front-back localization is all but impossible when the pinnae are distorted or absent (Musicant and Butler, 1984; R. Heffner *et al.*, 1992).

In order to make front-back discriminations, however, it is necessary that the sound contain high frequencies. This is because the pinnae are not directional for low

frequencies which can bend around the pinnae with little or no attenuation. Exactly how high the sound must be in order for the pinnae to play an effective role in sound localization depends on the size of the pinnae. In the Norway rat, front-back localization requires frequencies above 10 kHz and maximum performance is not attained unless frequencies up to at least 40 kHz are present (R. Heffner and Heffner, 1992a). Thus, the ability to hear high frequencies enables the pinnae to play an essential role in mammalian sound localization.

High-frequency hearing also plays a role in one of the two binaural locus cues in which the sound reaching the two ears is compared in order to determine the location of the sound source. Briefly, there are two primary binaural local cues: the difference in the time of arrival of a sound reaching the two ears and the difference in the frequency-intensity spectrum of the sound at the two ears. In both cases, the magnitude of the cues depends on the size of an animal's head. That is, the further apart the ears, the larger will be the difference in the time of arrival of the sound at the two ears. Similarly, the difference in the spectra of a sound reaching the two ears is greater for animals with wide-set ears. This is because the sound attenuation is greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which shadow the high-frequency portion of a sound. As a result the sound reaching the ear nearest the sound source is of greater intensity and contains more high-frequency sound than the sound reaching the far ear.

Although the two binaural locus cues are readily available to animals with large heads, the effectiveness of either cue is diminished in animals with close-set ears. In the case of the time cue, the available difference may be so small that the auditory system can detect only gross changes in sound direction. Similarly, a small head is less effective than a large head in blocking sounds with the result that it produces a smaller spectral difference. However, an animal with a small head can increase the size of the spectral difference cue available to it if it is able to hear frequencies that are high enough to be effectively shadowed by its head and pinnae. Thus, the smaller an animal's head the higher it must hear in order to obtain a usable spectral-difference cue.

The correspondence between head size and high-frequency hearing in mammals is illustrated in Fig. 9.9. In this figure, head size is defined as the 'functional' distance between the two ears, where functional distance is defined as the time it takes for sound to travel from one ear to the other. As can be seen, mammals with small heads and close-set ears are better able to hear high-frequency sounds than species with large heads and wide-set ears. That the high-frequency hearing ability of mammals enhances the ability of small mammals to use the binaural spectral-difference cue is indicated by the fact that removing frequencies above 10 kHz degrades the ability of the Norway rat to make left-right judgements regarding the location of a sound source (R. Heffner and Heffner, 1992a).

It can also be seen in Fig. 9.9 that there are three known species which do not hear as high as would be expected from their head size. These are the pocket gopher (*Geomys bursarius*, R. Heffner and Heffner, 1990b), blind mole rat (*Spalax ehrenbergi*, Bronchti *et al.*, 1989), and naked mole rat (*Heterocephalus glaber*, R. Heffner and Heffner, 1991), rodents which spend almost their entire lives underground. However, not only have these animals lost the ability to hear high frequencies, they have also lost virtually all ability to localize sound (R. Heffner and Heffner, 1990b).

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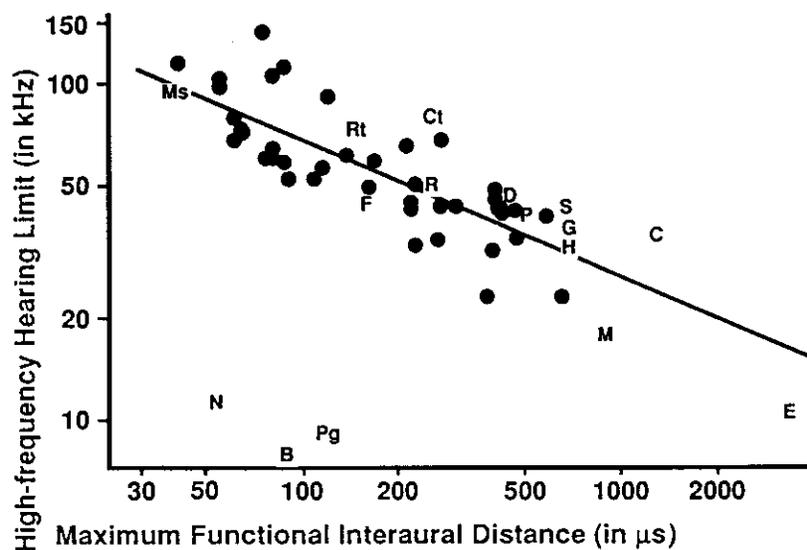


Fig. 9.9. Relationship between maximum functional interaural distance and the 60 dB high-frequency hearing limit in mammals. B, blind mole rat; C, cattle, Ct, cat; D, dog; E, elephant; F, ferret; G, goat; H, horse; M, man; Ms, house mouse; N, naked mole rat; P, pig; Pg, pocket gopher; R, rabbit; Rt, Norway rat; S, sheep. For species represented by filled circles, see R. Heffner and Heffner, 1985a.

and unpublished). Evidently, animals which have adapted to the one-dimensional world of an underground habitat have little use for sound localization. Thus, rather than attenuating the link between high-frequency hearing and sound localization in mammals, these animals make the point that mammals which lose their ability to localize sound also lose their high-frequency hearing.

Of the two roles of high-frequency hearing in sound localization, it appears that the use of high frequencies for pinna cues may be more fundamental than their use in the binaural spectral difference cue. The evidence for this conclusion comes from research on the ability of farm animals to localize sound. Specifically, it has been discovered that some large mammals, such as horses, pigs, and cattle, do not use the binaural spectral cue, but, instead, rely on the binaural time difference cue for making left-right locus decisions (R. Heffner and Heffner, 1986, 1989, 1992a). However, these animals do hear high frequencies and they do require their high-frequency hearing to use pinna cues to make front-back discriminations. Therefore, of the two functions, it appears that the necessity of high-frequency hearing in order to use pinnae cues is the more ubiquitous and may have played the greater role in the evolution of mammalian high-frequency hearing.

Finally, it should be noted that some small rodents and insectivores vocalize in the ultrasonic range thereby giving rise to the possibility that mammals evolved high-frequency hearing in order to use high frequencies for communication (e.g. Sales and Pye, 1974; Geyer and Barfield, 1979). Indeed, a number of species of mice

and rats emit vocalizations in the frequency range above 30 kHz and vocalizations above 50 kHz are not uncommon. However, many if not most mammals which possess ultrasonic hearing do not appear to send or receive ultrasonic communications. In particular, dogs, pigs, sheep and goats, all of which hear above 40 kHz, as well as horses and cattle, which hear above 30 kHz, do not use ultrasonic sounds for communication (cf. Kiley, 1972; Fox and Cohen, 1977; Walser *et al.*, 1981; R. Heffner and Heffner, 1990a). Thus, the fact that high-frequency hearing is not closely linked with the use of ultrasonic communication suggests that those species which do vocalize in the ultrasonic range are making use of an ability which initially served another function.

Variation in low-frequency hearing

It has long been noted that low-frequency hearing varies widely among mammals (Masterton *et al.*, 1969). Whereas the elephant has a low-frequency hearing limit of 17 Hz, the little brown bat hears only as low as 10.3 kHz (see R. Heffner and Heffner, 1982). Thus, the low-frequency limits of mammals span a range of more than nine octaves. In comparison, high-frequency hearing limits vary over a range of only four octaves.

In searching for possible explanations of this variation, several factors have been examined: body weight, head size and high-frequency hearing (R. Heffner and Heffner, 1990a). 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.

However, there are exceptions to this relationship which suggest that adaptation to unusual environments may result in atypical abilities (R. Heffner and Heffner, 1990a). The first exception are marine mammals that hear under water, such as the porpoise and beluga whale, which possess good high-frequency and good low-frequency hearing. Because sound transmission in these animals can bypass the middle ear, this finding suggests that the middle ear may limit the frequency range of an animal. The second exception are underground mammals, such as pocket gophers and mole rats, which cannot hear well above 10 kHz, yet have unexceptional low-frequency hearing. These animals have given up high-frequency hearing, apparently because they do not use sound localization in their underground environment, and their hearing has not extended into the lower frequency range, apparently because there has been no selective pressure to hear low frequencies.

Given that there are important exceptions to the relationship between high- and low-frequency hearing, the question arises as to how farm animals fit the general pattern. Examining this relationship among the remaining mammals (i.e. disregarding underground and underwater animals) reveals that there are still seven species which deviate significantly from the regression line. The deviant species are indicated by open circles in Fig. 9.10 and their removal from the analysis raises the correlation coefficient from 0.78 to 0.95. However, as shown in Fig. 9.10, all of the hoofed mammals conform closely to this relationship - their good low-frequency hearing is accompanied by modest high-frequency hearing. Similarly, the mouse, rat and rabbit also fit the relationship.

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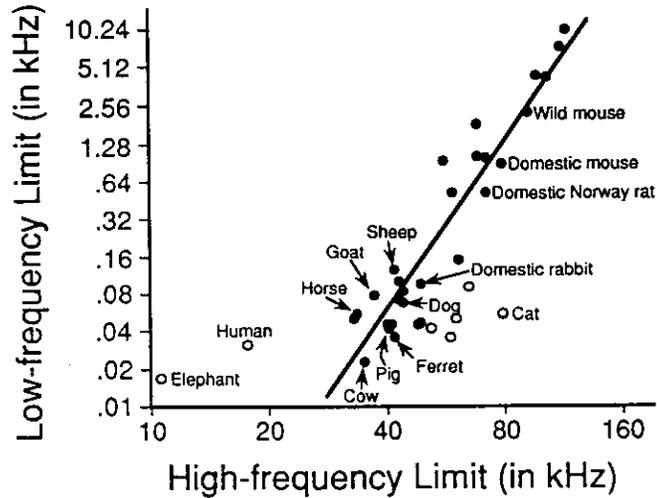


Fig. 9.10. Relationship between 60 dB high-frequency and 60 dB low-frequency hearing limits. Open circles represent animals which deviate significantly from the relationship. For species represented by unlabelled circles, see R. Heffner and Heffner, 1985a.

Of the seven species which deviate significantly from this relationship, the domestic cat is one of five whose low-frequency hearing extends beyond that predicted by its high-frequency hearing (open circles to the right of the regression line in Fig. 9.10). This indicates that these animals have a broader range of hearing than most other mammals. Indeed, cats with their hearing range extending from 55 Hz to 79 kHz have the broadest range of hearing of any terrestrial surface dweller (cf. Fig. 10.7). Thus, cats, along with gerbils, least weasels, kangaroo rats and bushbabies, demonstrate that it is possible for an animal to achieve good high- and good low-frequency hearing.

Localization of Sound

Determining sound localization ability is more complex than determining absolute thresholds because localization ability varies depending on the relative location of the sound source and the type of sound being localized. First, animals are more accurate in localizing in the horizontal plane than in the vertical plane. Second, localization acuity is best for sound sources located directly in front with acuity steadily decreasing for locations off to the side (e.g. R. Heffner and Heffner, 1988). Finally, spectral composition is a factor in that broad-band noise with an abrupt onset is generally easier to localize than narrow-band noise, and pure tones are the most difficult of all. Indeed, this latter fact appears to be exploited by some animals whose tonal calls make it more difficult for predators to localize them (Marler, 1955; Brown and May, 1990).

Most studies have measured sound localization acuity in the horizontal plane for

sound sources located in front of the animal. Generally, this has involved having an animal perform a left-right discrimination. Thus, unless otherwise noted, it can be assumed that an animal's sound localization acuity refers to its ability to perform a left-right discrimination using a brief complex sound, such as a noise burst or click.

Sound localization cues

As previously described, there are two sets of sound localization cues. The first set of cues are the binaural locus cues which consist of the difference in the time of arrival of a sound at the two ears and the difference in the frequency-intensity spectra of a sound at the two ears. These two cues are effective for localizing sound in the horizontal plane with their effectiveness decreasing as the location of the source moves from the front to the side.

The second set of cues are monaural cues which arise from the differences in the spectrum of a sound reaching a single ear from different locations. These differences are due to the fact that high frequency (short wavelength) sounds cannot readily bend around the head and pinna. As a result, the high frequency portion of a sound reaching an ear depends on the location of the sound source relative to that ear (e.g. Musicant and Butler, 1984). Because the primary source of these cues is the pinna, they are usually referred to as pinna cues. Pinna cues play an important role in horizontal localization by improving acuity for laterally placed sound sources (as opposed to sound sources located near midline) and by reducing front-back reversals. In addition, they provide the main cues for vertical localization.

Because birds lack an external ear and are unable to hear frequencies much above 10 kHz, it seems unlikely that they can use monaural spectral cues to localize sound. This conclusion is supported by the observation that, unlike mammals, birds are unable to localize sound in the horizontal plane with only one ear (Park and Dooling, 1991). Indeed, although some owls have evolved a facial ruff analogous to the mammalian pinna, they appear to use the binaural spectral cues which the ruff generates to perform vertical localization (Knudsen, 1980).

Although birds lack pinnae, they have another anatomical feature which mammals lack and which some birds may use for sound localization. Specifically, the middle ear cavities on each side are connected to each other by two air passages: an interaural canal lying ventral to the brain case; and eustachian tubes which fuse together before joining the nasopharynx (Knudsen, 1980). It has been proposed that this arrangement may enhance sound localization by allowing sound reaching one ear to travel through the head to partially cancel out the sound reaching the other ear thereby producing an intensity difference between the two ears (Lewis and Coles, 1980). However, it should be noted that the degree to which birds rely on these interaural passages for sound localization has not been established and the transmission of sound between the two ears in the barn owl appears to be too insignificant to play a role in sound localization (Moiseff and Konishi, 1981).

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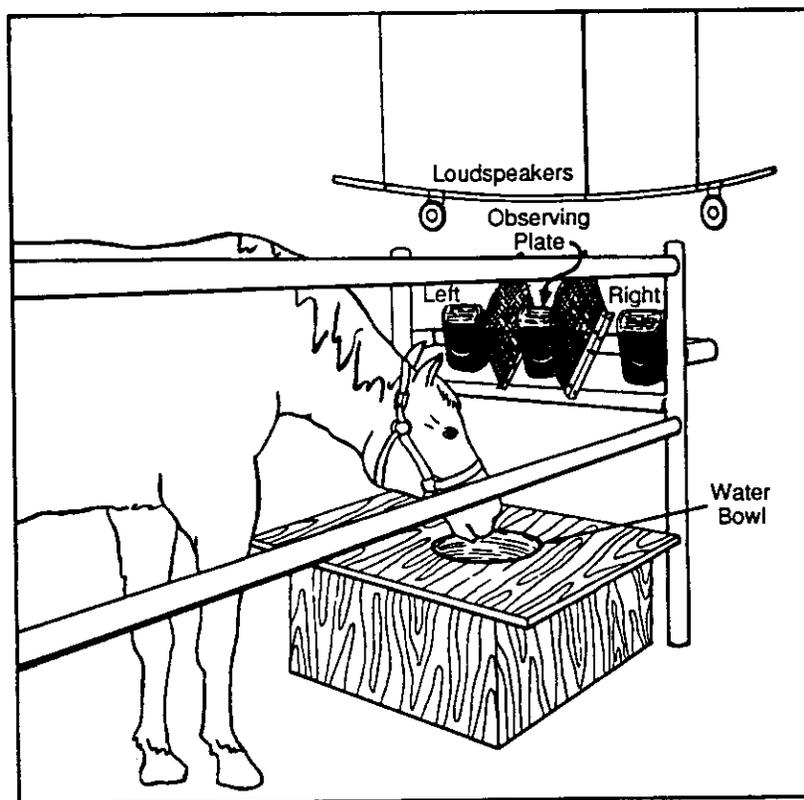


Fig. 9.11. Apparatus used to test sound localization in horses and cattle. An animal initiated a trial by touching the observing plate with its nose. It then touched either the left or right response plate to indicate whether a sound had come from a loudspeaker on its left or right side, respectively. Correct responses were rewarded by delivering water into the water bowl. The hardware-cloth panels separating the response plates served to prevent an animal from responding to the side plates too rapidly (modified from H. Heffner and Heffner, 1984).

Measuring sound localization acuity

There are two basic procedures for determining sound localization ability. The most common is to measure an animal's 'two-point sensitivity' by training it to discriminate between the same sound presented from one of two loudspeakers and then reducing the angular separation between the two speakers until the animal is no longer able to perform the discrimination. The second procedure exploits an animal's natural tendency to orient to the source of a sound and determines sound localization acuity by measuring the accuracy (i.e. the amount of error) with which an animal orients its head to a sound.

An animal's two-point locus acuity can be determined using a two-choice procedure. In this procedure a thirsty animal is led into a test stall and trained to place its nose on an observing plate located in front of an array of loudspeakers (Fig. 9.11).

A sound is presented from a loudspeaker located to the left or right of the animal and the animal is trained to touch one of two response plates located to its left or right. A response to the plate located on the same side as the sound source is rewarded by delivering water into a bowl located below the observing plate while an incorrect response is followed by a 5–15 s wait before the animal can try again. Thresholds are typically defined as the smallest angle which yields a performance of 75% correct (i.e. half way between perfect and random performance).

The orienting response is used to measure localization accuracy by measuring the accuracy of an animal's head orientation to a sound. Although this procedure has occasionally been used with mammals (e.g. Thompson and Masterton, 1978), its greatest success has been in measuring the sound localization ability in owls (Knudsen *et al.*, 1979). By using a search coil technique to measure head orientation, Knudsen and his colleagues have been able to measure the accuracy with which the barn owl (*Tyto alba*) localizes sound. Furthermore, by rewarding correct orientations with food, they have been able to maintain an animal's orientation response for long periods.

Birds

Although a number of studies have measured the ability of birds to localize sound in the horizontal plane, it is difficult to compare the results from birds because of the existence of important procedural differences between studies. In particular, various studies have used different localization stimuli, such as noise, tones, and bird calls, all with good reason, but with the result that the thresholds are not comparable. Comparisons are further complicated by the fact that several different definitions of thresholds have been used. However, one procedural difference that does not appear to affect thresholds is the use of different behavioural methods such as whether the animal is trained using positive reward or punishment, or whether it is required to locate the source of the sound or simply report a change in the location of the sound source (cf. R. Heffner and Heffner, 1988). However, the proficiency with which a test is administered can and does affect its outcome.

Most studies of bird sound localization have examined songbirds and the general procedure has been to train the animal using a two-choice left–right discrimination. The results of these studies have indicated that thresholds for songbirds for noise stimuli commonly range from 20° to 30° separation (for reviews, see Knudsen, 1980; Park and Dooling, 1991).

Turning to farm animals, sound localization behaviour has been studied in chickens (*Gallus domesticus*) by exploiting the natural behaviour of setting hens to search for chicks when they emit a distress call. By placing a chick behind one of two cardboard screens and observing the ability of a hen to locate it, Engelmann estimated the localization acuity of the hens to be about 4° (Engelmann, 1928). However, before concluding that hens are better able to localize than songbirds, it should be noted that the same study, using similar techniques, significantly overestimated the localization acuity of cats and dogs. Thus, this result needs to be confirmed with modern techniques before it can be accepted.

Sound localization thresholds have been determined for the pigeon (*Columba livia*) using a heart-rate conditioning procedure (Lewald, 1987). In this procedure, an

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animal is habituated to a sound presented from one location while the occasional presentation of the sound from a different location is paired with electric shock. This results in a change in the animal's heart rate whenever it detects a change in location. By measuring heart rate for different angles of separation, it has been shown that pigeons can detect angles as small as 4° (Lewald, 1987). However, it should be noted that threshold was defined as the smallest angle eliciting a statistically significant change in heart rate (i.e. $P = 0.025$, one-tailed distribution). In contrast, most other studies define threshold as the smallest angle at which an animal scores 75% correct which is usually well above the statistical threshold. Thus, while the pigeon probably localizes sound more accurately than songbirds, the 75% correct definition of threshold would place their threshold at a somewhat larger angle than 4°.

Finally, the sound localization ability of the barn owl (*Tyto alba*) has been carefully studied by measuring their orientation to sound (Knudsen *et al.*, 1979). These results have shown that the barn owl can orientate to a frontally placed sound source with an average error of about 2°, an accuracy which is comparable to a two-choice 75% threshold of 3.5°. Thus, the barn owl, a nocturnal predator which uses its hearing to locate prey, has the best sound localization acuity of any bird yet tested.

Mammals

The ability of mammals to localize sound has been determined for over 20 species representing nine different orders of mammals from marsupials and insectivores to proboscidea and artiodactyls (cf. R. Heffner and Heffner, 1992a). Furthermore, tests performed on several species by different laboratories using different methods have yielded comparable results (cf. R. Heffner and Heffner, 1988). Thus, not only does there exist information on the localization abilities of a variety of mammals, but there is reason for confidence in the validity of the data.

Because a knowledge of the exact location of a sound source would appear to be of obvious importance, it seems reasonable to assume that all animals are under strong selective pressure to localize sound as accurately as possible. Yet the results of studies to date have indicated that not all mammals do so. Indeed, the ability of mammals to localize sound has been shown to range from around 1° (e.g. elephants and humans) to more than 25° (e.g. gerbils and cattle) with some species (i.e. the pocket gopher) completely unable to localize brief sounds (R. Heffner and Heffner, 1992a, c).

Hoofed mammals

The sound localization thresholds of the four species tested so far span a wide range (Fig. 9.12). Three of the species, goats, horses and cattle, have thresholds of 18°, 25° and 30°, respectively, which place them well below the median acuity for mammals of 12°. On the other hand, pigs, with a threshold of 4.6°, are among the most accurate localizers.

Carnivores

Not surprisingly, carnivores tend to be among the more accurate localizers. As shown in Fig. 9.12, thresholds for the cat, dog and ferret are 5.7°, 8° and 8.5°, respectively.

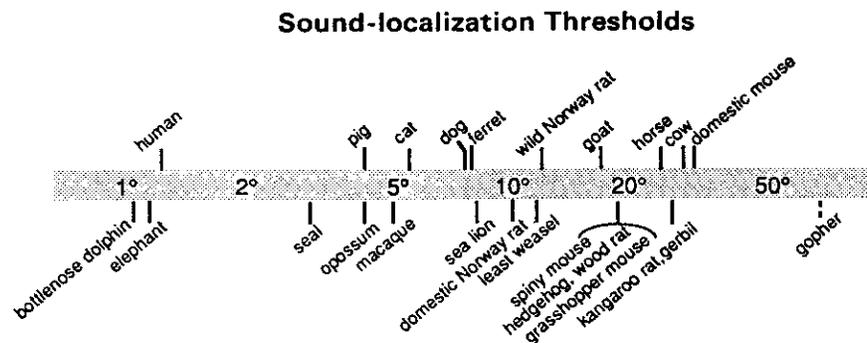


Fig. 9.12. Sound localization acuity in the horizontal plane for 25 mammals. With the exception of the gopher (dashed line) all animals were tested using brief broad-band stimuli. (Note log scale.)

Rodents

Although rodents tend to be among the less accurate mammals, the 12.8° threshold of the wild Norway rat places it close to the median for mammals (H. Heffner and Heffner, 1985). Although data are not available for the wild house mouse, a recent study shows domestic mice to have a threshold of 33° (R. Heffner, unpublished).

Variation in mammalian sound localization acuity

Until recently it was believed that all mammals were under strong selective pressure to localize sound as accurately as possible. The fact that some animals are unable to localize as accurately as others was explained in terms of the variation in the magnitude of the locus cues available to each animal. That is, because the magnitude of the binaural locus cues is largely determined by the size of the head and pinnae, it was expected that any variation in localization acuity was due to species differences in head and pinna size. Indeed, the observation that humans were more accurate than cats which, in turn, were more accurate than rats appeared to support this idea.

As more species were tested it became apparent that a large head did not automatically result in good localization acuity. Indeed, this theory became untenable when it was discovered that horses and cattle, despite their large heads, have poorer acuity than many small rodents (H. Heffner and Heffner, 1984; R. Heffner and Heffner, 1992b). Furthermore, although a small interaural distance may be a limiting factor in acuity, it was found that some small species possess relatively good acuity when compared to other species of equal or larger head sizes (cf. the least weasel and grasshopper mouse, Fig. 9.12).

In searching for the source of the variation in acuity, a number of factors have been considered. Among these are the possibility that various lifestyles, such as predator vs. prey, nocturnal vs. diurnal, or surface dwelling vs. underground, might be associated with variation in localization acuity. However, all of these possibilities have major exceptions and none has remained satisfactory when subjected to statistical analysis (R. Heffner and Heffner, 1992c).

There is, however, one factor which does seem to account for the variation in

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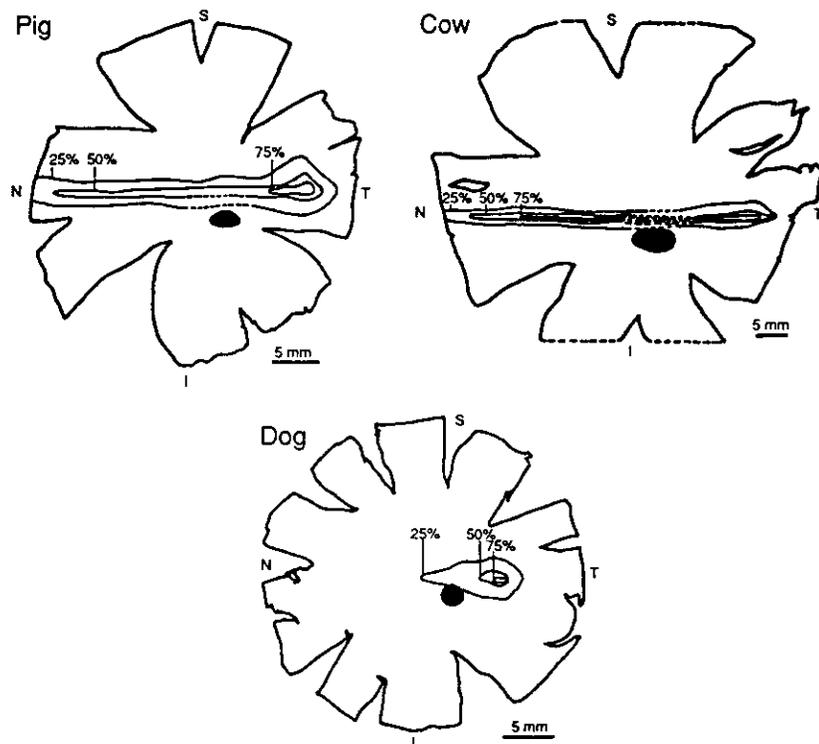


Fig. 9.13. Drawings of the retinæ of a pig, cow and dog, illustrating the variation in the width of the field of best vision as estimated from the density of retinal ganglion cells. The contour lines encompass densities 25%, 50% and 75% of the maximum density for each species. The field of best vision is operationally defined as the part of the retina containing ganglion cells with packing densities equal to or greater than 75% of maximum. The dog has a narrow field of best vision whereas the cow, with its visual streak, has a very broad field. The pig has a visual streak combined with a small area of increased density located temporally. I, inferior; N, nasal; S, superior; T, temporal (data from R. Heffner and Heffner, 1992c).

locus acuity. In examining the utility of sound localization, it has been observed that one of the most consistent responses to an unexpected sound is the orienting reflex in which the head and eyes are turned towards a sound source (Pumphrey, 1950). When visually orienting to a sound, however, it is not simply the head or the eyes that are directed to the sound source, but the part of the visual field with the best visual acuity. In species such as humans, the area of best vision, i.e. the fovea, subtends an angle of only 1–2°. As a result, auditory localization has to be very precise in order to direct the fovea to the sound source. However, most mammals have a broader area of best vision which in some cases covers nearly the entire horizon of the eye and is referred to as a visual streak (Fig. 9.13; cf. Hughes, 1977). Species with progressively broader fields of best vision, therefore, should require correspondingly less precise auditory information in order to place a sound source within their field of best vision.

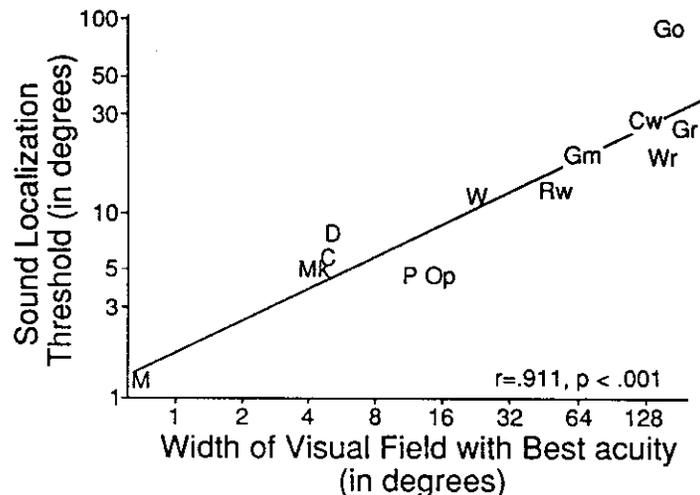
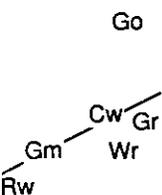


Fig. 9.14. Relationship between width of the field of best vision and sound localization threshold for 13 species of mammals (note log scales). Species with a narrow field of best vision have much smaller sound localization thresholds (greater acuity) than species with a broad field. C, cat; Cw, cow; D, dog; Gm, grasshopper mouse; Go, gopher; Gr, gerbil; M, man; Mk, macaque; Op, opossum; P, pig; R, wild Norway rat; W, least weasel; Wr, wood rat (modified from R. Heffner and Heffner, 1992c).

In order to determine the correlation between sound localization acuity and the size of the field of best vision, we have obtained anatomical measures of the visual acuity in animals for which sound localization thresholds are available. Because the density of ganglion cells in the retina is known to correspond to behavioural measures of visual acuity (e.g. Rolls and Cowey, 1970), measuring the density of ganglion cells in retinal wholemounts can provide an anatomical estimate of the relative acuity of the different parts of the retina. Given a picture of the variation in the density of ganglion cells, it is possible to arrive at a measure of the size of the field of best vision.

Using an arbitrary definition of field of best vision as the horizontal width (in degrees) of the region of the retina containing ganglion cell densities equal to or greater than 75% of the maximum density, we have determined the size of the field of best vision in 13 species (R. Heffner and Heffner, 1992c). These measurements have shown that the size of this field varies from approximately 1.5° in humans to around 180° in some species such as cattle (cf. Fig. 9.13). The relation between the width of the field of best vision and sound localization thresholds is shown in Fig. 9.14. As indicated in this figure, the width of the field of best vision is positively correlated with sound localization threshold ($r = 0.91$, $P < 0.001$). That is, animals with narrow fields of best vision, such as cats and humans, have lower thresholds (better sound localization acuity) than those with broader fields of best vision, such as cattle.

Although the sample is as yet small, it includes a broad range of species from five orders of mammals encompassing surface and underground dwellers, nocturnal

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and diurnal activity patterns, predators and prey, and body sizes ranging through more than five orders of magnitude. Furthermore, included in this sample are animals with good sound localization acuity as well as those with poor acuity and animals with large as well as those with small areas of best vision. Thus, although we are continuing to increase our sample, there is no reason to believe that the high correlation between sound localization acuity and width of the area centralis is the result of a restricted or unrepresentative sample.

Effect of Domestication on Hearing

When discussing the sensory abilities of domesticated animals, the question often arises as to whether their abilities have been reduced owing to protection from danger or selective breeding which characterize domestication. From the information we have available, it appears unlikely that the hearing abilities of farm animals have been reduced as a result of domestication (e.g. R. Heffner and Heffner, 1992b). With regard to auditory sensitivity, the high-frequency sensitivity of domesticated mammals is well within the range of that expected for animals of their size (cf. Fig. 9.9). Similarly, low-frequency sensitivity is not unique with the exception of the domestic cat which has unexpectedly good low-frequency hearing (cf. Fig. 9.10). Finally, in terms of best sensitivity, domestic mammals appear to have either average or exceptionally good hearing as cats, cattle and goats are among the most sensitive vertebrates.

Turning to sound localization, it might be speculated that the poor acuity of horses, goats and cattle may have arisen through domestication. However, there are several reasons why this is unlikely (for a detailed discussion, see R. Heffner and Heffner, 1992b). First, there are domestic species which possess good acuity. For example, domestic pigs are among the most accurate mammals and the domestic Norway rat is slightly more accurate than the wild Norway rat (Kavanagh and Kelly, 1986; R. Heffner and Heffner, 1989). Second, when mammals have lost the ability to localize sound (e.g. the pocket gopher), this loss has been accompanied by a general reduction in overall sensitivity including a loss of high frequency hearing (R. Heffner and Heffner, 1990b). However, the fact that domesticated animals have good high-frequency hearing and that cattle and goats have excellent sensitivity indicates that they do not fit the profile of an animal whose sound localization has degenerated. Finally, as was previously noted, the poor localization ability of horses, goats and cattle is predicted by the correspondence in mammals between the width of the field of best vision and localization acuity. In short, they appear to localize as accurately as necessary in order to direct their gaze to the source of a sound. Thus, there is no reason to believe that the hearing of domestic animals has undergone any reduction as the result of domestication.

Acknowledgement

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