

Hearing in Large Mammals: Sound-Localization Acuity in Cattle (*Bos taurus*) and Goats (*Capra hircus*)

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Sound localization acuity of 3 cattle (*Bos taurus*) and 2 goats (*Capra hircus*) was determined for brief complex sounds in a two-choice procedure. Thresholds around the median sagittal plane averaged 30° and 18°, respectively. For comparison, thresholds were obtained in the same test apparatus for humans (0.8°) and a dog (8°). Although the relatively poor acuity of cattle and goats compared with most mammals comes as some surprise, given their large interaural distances and the large binaural locus cues available to them, it is not unexpected when other factors are considered. Like other poor localizers (both domesticated and nondomesticated), cattle and goats are prey species with their best vision directed throughout nearly the entire horizon. In contrast to mammals with very narrow foveal fields, they may not need very accurate locus information from their auditory systems to direct their gaze to a sound source.

The results of recent sound-localization tests in an increasingly broad sample of mammalian species have revealed that localization acuity varies over an unexpectedly wide range (for a review, see R. S. Heffner & Heffner, 1992a). Because the ability to localize sound in the horizontal plane is largely dependent on the availability of binaural locus cues (i.e., the difference in the time of arrival and the frequency-intensity spectra at the two ears), one may expect that animals with large heads, which generate correspondingly large binaural cues, ought to have better localization acuity than smaller animals. However, the variation in localization acuity cannot be explained simply in terms of the available binaural cues. Although many of the more accurate localizers are indeed large (e.g., humans, elephants, and pigs), others have smaller interaural distances (e.g., cats, macaques, seals, and opossums; Brown, Beecher, Moody, & Stebbins, 1980; H. E. Heffner & Heffner, 1990; R. S. Heffner & Heffner, 1982, 1988a, 1989; Mills, 1958; Ravizza & Masterton, 1972; Terhune, 1974).

Even stronger contradictory evidence comes from the demonstration that there exists at least one large mammal that has remarkably poor sound-localization acuity. Specifically, it has been demonstrated that horses, which have an interaural distance similar to that of humans, are nevertheless worse localizers than small rats. Horses, therefore, provide an important exception to the observation that large mammals are accurate localizers (H. E. Heffner & Heffner, 1984, 1985). Thus, even though a large head results in correspondingly large binaural locus cues, it is not necessary nor, at least for horses, sufficient to guarantee good acuity.

Because horses are the only large mammal currently known to have poor localization acuity, it is of theoretical importance to determine whether or not they are unique in this trait. Extending localization tests to other large species will not only

indicate whether poor localization acuity is widespread among large species but will also contribute to the effort to determine the factors that account for differences in sound-localization acuity. Accordingly, we have extended our investigation to two additional species of large mammals, domestic cattle and goats. Like horses, cattle and goats are large herbivores and primarily prey species. However, as members of the order Artiodactyla, they have a long evolutionary history separate from horses and the Perissodactyla.

Method

Sound-localization thresholds in the azimuthal plane were determined for 3 cows and 2 goats in a two-choice test procedure with brief bursts of broad-band noise. For comparison, localization thresholds were also obtained for 3 humans in the same apparatus used for testing the cattle, and a dog was tested in the apparatus used for the goats.

Subjects

Three yearling cows (*Bos taurus*), two Herefords and one Simmental, and 2 female goats (*Capra hircus*) of a mixed breed Swiss type with erect pointed ears were used in this study. All were approximately 8 months old at the beginning of testing. The cattle weighed 300–450 kg and the goats weighed 24–28 kg at the beginning of testing, and all continued to grow and gain weight. The cattle were housed in an outdoor pen and maintained on a standard diet of mixed grain and hay. The goats were housed together in an indoor room and given free access to prairie hay supplemented by small amounts of mixed grain. Water was used as a reward, and the animals received most of their water in the test sessions. The animals were weighed daily and were given additional water as needed to maintain health.

One mongrel bitch, which weighed 20 kg, was also tested. It was housed in a room with other dogs and given free access to dry dog food. Like the cows and goats, it also received most of its water in the test sessions with additional water provided as needed to maintain health.

The 3 human subjects, 2 men and 1 woman, were 23–36 years old.

The ears of all subjects were inspected before testing and were found to be free of damage or disease. The audiograms of the cattle

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and the goats have been published elsewhere (R. S. Heffner & Heffner, 1983, 1990a).

Behavioral Apparatus

The cattle were tested in a large converted dairy barn located on the grounds of the Kansas State Agriculture Experiment Station in Mound Valley, Kansas (see H. E. Heffner & Heffner, 1984). The barn had been lined with fiberglass insulation and sound absorbing panels (Sound Stop, Sunberry, Pennsylvania) to attenuate outside noise and reduce sound reflection. The test equipment was housed in an adjacent room, and the animals were observed on closed-circuit television.

For testing, the cattle were led into a stall (1.0 m wide \times 1.5 m high \times 2.4 m deep). Three metal response plates (10 \times 7 cm) and a water bowl (25 cm in diameter) were located at the front of the stall within easy reach of the cows. The water bowl, located below the center response plate, was connected with tubing to a 50-liter water reservoir. An electrically operated water valve inserted in the water line controlled the flow of water to the bowl. Each of the response plates was connected to a separate sensing switch that detected when the animal made contact with it. (For an illustration of the test apparatus, see H. E. Heffner & Heffner, 1984). In the tests on humans, the subjects placed their heads in the location normally occupied by the cows' heads and touched the response plates with their hands.

The goats and dog were tested in a stall (93 \times 47 \times 108 cm) constructed of welded wire attached to a wooden frame and located in a large double-walled acoustic chamber. The stall was designed so that an animal's head and shoulders stood above the wooden frame (R. S. Heffner & Heffner, 1990a). The animals placed their heads through an opening in the front of the cage in order to reach the response plates so that there were no obstructions between their ears and the sound sources. Two small metal response plates (5 \times 3 cm) were placed 75° to the left and right of the animal's head just within reach of its nose; these were connected to sensing switches that detected the animal's contact. A metal strip down the center of a large plastic spoon (7 \times 4 cm) was connected to a third sensing switch that served to detect observing responses. Correct responses were rewarded by dispensing water from an 800-ml water reservoir via an electrically operated water valve into the observing spoon.

Acoustic Apparatus

The cattle were trained to localize broadband noise and clicks. Broadband noise was generated with a duration of 100 ms and a 0.1-ms rise-decay by a noise generator (Model 1524, Lehigh Valley Electronics, Fogelsville, PA) and then fed to a programmable attenuator (Model S85-08, Coulbourn, Lehigh Valley, PA), then to a rise-fall gate (Model S84-04, Coulbourn), an amplifier (Model S82-24, Coulbourn), and finally to one of five pairs of loudspeakers (7.6-cm diameter paper cone loudspeakers mounted in 500-cc enclosures). To produce the clicks, 1.0-ms square waves were generated by a square-wave generator (Coulbourn S78-22), led to a programmable attenuator, then to the amplifier, and finally to one of five pairs of loudspeakers (3.5-cm dome, Model L15F, Long). The matched pairs of loudspeakers were placed on a perimeter bar of 1.5-m radius centered around an animal's head when it was touching the center response plate. Testing was conducted with one pair of speakers for a block of 25-50 trials, and then testing was switched to a different pair of speakers at a different angle of separation.

The same noise-generating equipment was used for goats except that only one pair of loudspeakers (a 7.6-cm diameter paper cone speaker in a 500-cc enclosure mounted directly below a 5-cm piezoelectric tweeter) was used. (See R. S. Heffner & Heffner, 1988a, for

the spectrum of the noise produced by the speakers.) The speakers were placed on movable stands 1 m from the center of an animal's head when it was making an observing response.

In order to reduce the possibility that the animals could distinguish the loudspeakers on the basis of cues other than locus, the loudspeakers were matched in intensity with a sound-level meter (Model 2203 microphone amplifier, Brüel and Kjaer, Naerum, Denmark, and Model 4131 microphone on the linear scale). That this procedure was sufficient to prevent the animals from using nonlocus cues was directly demonstrated in the behavioral results: No animal distinguished between the loudspeakers when the azimuth of separation was reduced to 5° or when the speakers were placed one above the other for 0° azimuthal separation.

A wide variety of stimuli were used in training and threshold estimation in an effort to elicit the animals' best performance. These stimuli included broadband noise, bandpass noise at octave intervals, and 2-kHz high-pass and low-pass filtered noise. In addition, cattle were also presented with a variety of click stimuli, including clicks generated by 0.1-ms and 1.0-ms square waves, single clicks, and click trains from 2 to 20 per second. As broadband noise was localized most accurately, it was used for detailed threshold determinations.

All stimuli used in threshold determinations were presented at an intensity at least 40 dB above the animal's thresholds (64-68 dB SPL) as estimated by attenuating the stimuli until their performance fell to chance.

Psychophysical Procedure

A thirsty animal was trained to initiate a trial by placing its nose on the center observing plate (or spoon, in the case of the goats and dog). This observing response served to center the animal's head within the array of loudspeakers and triggered the presentation of a sound from a loudspeaker in their left or right hemifield. The animal was then rewarded with water (35 ml for cattle and 3 ml for goats and the dog) if it touched the response plate on the same side as the active loudspeaker. Touching the opposite response plate was followed by a short wait (3-15 s, signaled by a dimming of the lights in the test room) before a new trial was initiated. A typical session lasted 60 min, during which the cattle ran 200-600 trials and consumed 7-20 L of water and the goats and dog ran 100-350 trials and consumed 300-1,000 ml of water.

The sequence of left-right trials was determined by a quasi-random schedule (Gellermann, 1933). In order to reduce side preferences, a correction procedure was used in which the correct side was not changed after an error. These correction trials were not used in computing performance.

Localization thresholds were determined by reducing the angular separation between two loudspeakers until an animal could no longer distinguish left from right stimuli. Psychophysical functions were then constructed by averaging each animal's scores from its 3 best sessions (asymptotic performance) with a minimum of 100 trials per angle. Threshold is defined as the smallest separation that yields a 75%-correct performance. The .01 level of chance (binomial distribution) was 63% correct.

Results

Cattle

The ability of the cattle to localize single 100-ms bursts of broadband noise is shown in Figure 1. Each point represents an animal's asymptotic performance at a particular angle. As can be seen, the cattle easily performed this task at large angles

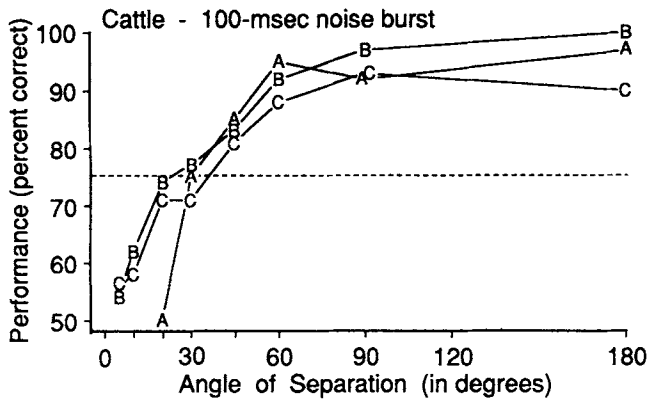


Figure 1. Sound-localization performance of 3 cows in localizing a single 100-ms noise burst. (A, B, and C represent the 3 animals. Dashed line indicates the 75%-correct threshold.)

and consistently achieved 90% correct or better at angles greater than 60° of separation. At smaller angles the animals showed good agreement with decreasing performance until chance performance was reached at 20° of separation for Cow A and 10° for Cows B and C. The 75%-correct threshold criterion was interpolated to be 30°, 23°, and 37° for Cow A, B, and C, respectively, with an average threshold of 30°.

The performance of the cattle for localizing either single clicks or click trains (5 clicks per second) was poorer than their performance with broadband noise, and the thresholds for clicks were larger, 44° for single clicks and 39° for click trains. Slightly poorer acuity for clicks than for broadband noise has been noted in other species (e.g., H. E. Heffner & Heffner, 1984; R. S. Heffner & Heffner, 1982).

Humans

In order to rule out room acoustics or some other unsuspected defect of the listening situation, 3 humans were tested with clicks in the same apparatus under the same two-choice procedure. The humans' thresholds averaged 0.8°, which suggests that there was nothing inherent in the test situation or room acoustics that prevented accurate sound localization.

Goats

Figure 2 illustrates the ability of two goats to localize single 100-ms noise bursts. Both goats performed at 90% correct or better at angles of 60° and larger, which indicates that they had no difficulty with the behavioral task. Performance declined as the angle of separation was reduced until chance performance was reached at 10° and 5° for Goats A and B, respectively. The 75% thresholds were 20° for Goat A and 16° for Goat B, and the average threshold was 18°.

Dog

Figure 3 illustrates the performance of 1 dog tested in the same apparatus and with the same procedure and stimuli as

for the goats. The dog performed better than either goat at every angle tested and its performance did not fall to chance until the speakers were placed at 0° azimuthal separation. The 75% localization threshold was 8°, which is similar to previously reported thresholds for dogs (H. E. Heffner, 1976) and indicates that there was nothing unusual about the room acoustics, test procedure, or stimuli that would prevent accurate sound localization.

Discussion

Sound Localization in Hoofed Mammals

The sound-localization thresholds for cattle and goats are presented in Table 1 along with those of the other two species of hoofed mammals for which data are available, horses and pigs. A comparison of these animals indicates that, with the exception of pigs, hoofed mammals are poor localizers. Thus not only are horses not unique among hoofed mammals in their rather limited ability to localize sound, but three of the four species tested possess localization thresholds well above the 11.2° mean for other surface-dwelling mammals (R. S. Heffner & Heffner, 1992a). Not all hoofed mammals have poor localization acuity, however. Indeed, the 4.6° threshold of pigs places it among the most accurate localizers, exceeded only by seals, elephants, humans, and dolphins (Figures 4 and 5). Given such variation, even among a restricted group of mammals, the question arises as to why sound localization varies so widely. Accordingly, the rest of this discussion examines four factors that may contribute to the variation of sound-localization acuity among mammals: interaural distance, domestication, status as predator or prey, and width of the field of best vision.

Interaural Distance

As previously noted, the sizes of an animal's head and pinnae determine the size of the available binaural locus cues. As a result, one may expect that head size measured as the

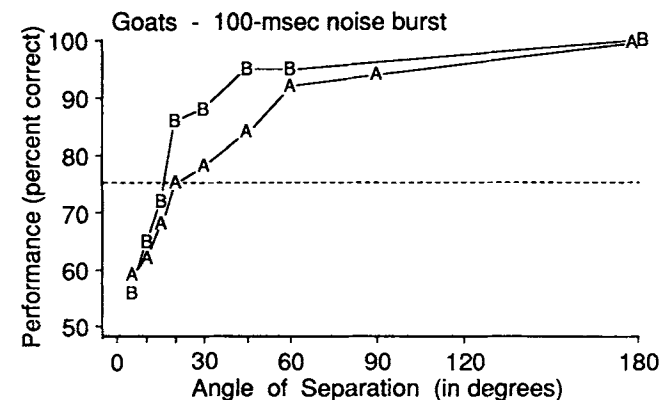


Figure 2. Sound-localization performance of 2 goats in localizing a single 100-ms noise burst. (A and B represent the 2 animals. Dashed line indicates the 75%-correct threshold.)

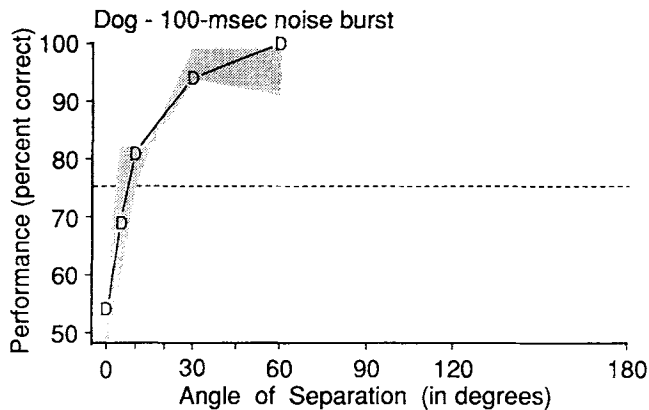


Figure 3. Sound-localization performance for 1 dog in localizing a single 100-ms noise burst. (Dashed line indicates the 75%-correct threshold. Shading indicates range of performances for three dogs tested previously; see H. E. Heffner, 1976).

distance between the two ears would explain some of the variation in sound-localization acuity. Figure 4 illustrates the relation between interaural distance and sound localization threshold among 24 mammals. The correlation coefficient is reliable ($r = -.404, p < .05$) but reveals that interaural distance accounts for only 16% of the variation in localization acuity. Indeed, if the animals are arranged according to the magnitude of interaural distance and the larger one third is compared with the smaller one third, their sound-localization thresholds do not differ (Mann-Whitney $U, p > .05$).

Because the actual magnitude of the interaural differences in time and intensity depends on the shape of the head and its topographic features, the estimated magnitudes, which assume that the head is a smooth sphere, are almost certainly not exact. It is possible that the large species with poor acuity may actually have only small interaural differences available to them because of some aspect of the shape of their heads. This possibility was examined in a previous study in which the interaural intensity differences and time differences between the two auditory meatus of horses was measured (H. E. Heffner & Heffner, 1984). The interaural time difference of horses was found to exceed that for both cats and humans at angles of 30° or smaller, and the interaural intensity differ-

ence between the two ears exceeded 5 dB at angles of 20° or larger for frequencies of 4 kHz and higher. Thus the interaural-difference cues available to horses are as large or larger than the cues available to species with far better localization acuity.

In conclusion, it seems that among hoofed mammals, as among mammals in general, there is no simple correspondence between interaural distance and sound-localization acuity (R. S. Heffner & Heffner, 1992b). Indeed, as seen in Table 1, the most accurate hoofed mammal is also the smallest. Horses, cattle, and goats are poorer localizers than one would predict from their interaural distances, and these species serve to reduce considerably the correlation depicted in Figure 4. Nevertheless, these animals represent a large and successful mammalian adaptation, and a convincing theory of the evolution of sound localization must account for their abilities as well as those of others.

Domestication

Because horses, goats, and cattle are domesticated animals, the question arises as to whether their poor localization acuity may be owing to the protection from danger or the selective breeding that characterizes domestication. If so, then it seems reasonable to expect a more general auditory deterioration, rather than a specific reduction of a single aspect of hearing. Indeed, it has been noted that the pocket gopher, a species that apparently lost the ability to localize sound because of reduced selective pressures, has also undergone a reduction in overall sensitivity, including a loss of high-frequency sensitivity (R. S. Heffner & Heffner, 1990b). Thus, if domestication results in a reduction in localization acuity, then one may expect a reduction in other auditory capacities as well.

However, this does not seem to be the case: Although cattle and goats are poor localizers, they, along with domestic cats and domestic sheep, are the most sensitive of all land mammals in their ability to detect sounds of low intensity (R. S. Heffner & Heffner, 1983, 1985, 1990a; Wollack, 1963). Such acute sensitivity suggests that they are still under selective pressure for good hearing. Thus, in arguing that domestication has led to a reduction in localization acuity, it is necessary to account for the excellent absolute sensitivity that these animals possess and, indeed, to address the possibility that their enhanced sensitivity may also have resulted from domestication.

Nevertheless, to examine the question of whether domestic species in general are less accurate localizers, we divided the sample of 24 species with published localization thresholds into 13 wild species, 8 domesticated species that have been both protected from predation and subject to selective breeding, and 3 arguably domesticated species that have been protected from predation but not subject to selective breeding. All 24 species are shown in Figure 5 with the three questionable species indicated in parentheses and placed among the wild species.

Eleven species are encompassed by a broad definition of domestication, that is, protection from predation without selective breeding. With this definition the sound-localization abilities of both domestic and wild mammals span the range from very accurate to very inaccurate. A statistical compari-

Table 1
Sound Localization in Hoofed Mammals

Species	Interaural distance (in μ s)	Threshold (in degrees)
Perisodactyl		
Horse ^a	684	25.0
Artiodactyl		
Pig ^b	498	4.6
Cattle	1,281	30.0
Goat	680	18.0

Note. Interaural distance is the maximum time required for a sound to travel around the head from one ear to the other. Note that the species with the smallest interaural distance, pigs, is the most accurate localizer, whereas the largest species, cattle, is the least accurate.

^a From H. E. Heffner & Heffner (1984). ^b From R. S. Heffner & Heffner (1990a).

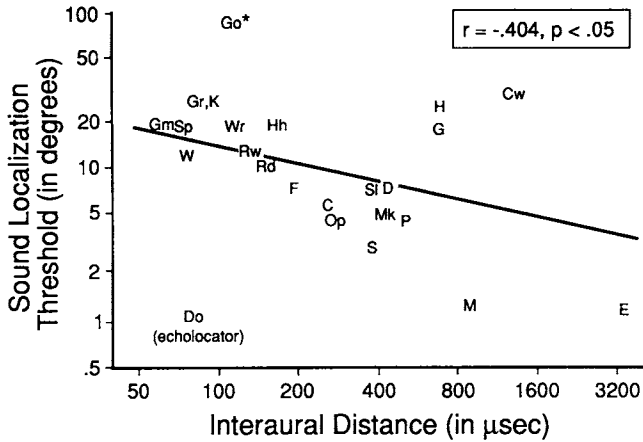


Figure 4. Relation between sound-localization thresholds and interaural distance as measured by the number of microseconds required for a sound to travel from one auditory meatus to the other. (Although larger species with greater interaural distances tend to have smaller thresholds than smaller species, there are prominent exceptions, particularly among the large species. If the echolocating dolphin is excluded from the calculation, the correlation rises to $-.57, p < .01$, but the outliers remain. Note that the localization threshold of the pocket gopher is actually greater than plotted because it could not localize brief sounds at all and its threshold was obtained with continuous pulses of noise. C = cat [R. S. Heffner & Heffner, 1988a]; Cw = cow [this study]; D = dog [this study]; Do = dolphin [Renaud & Popper, 1975]; E = elephant [R. S. Heffner & Heffner, 1982]; F = ferret [Kavanagh & Kelly, 1987]; G = goat [this study]; Gm = grasshopper mouse [R. S. Heffner & Heffner, 1988c]; Go* = gopher [continuous noise bursts; R. S. Heffner & Heffner, 1990b]; Gr = gerbil [R. S. Heffner & Heffner, 1988b]; H = horse [H. E. Heffner & Heffner, 1984]; Hh = hedgehog [Chambers, 1971]; K = kangaroo rat [H. E. Heffner & Masterton, 1980]; M = mankind [this study]; Mk = macaque [Brown, Beecher, Moody, & Stebbins, 1980; H. E. Heffner & Heffner, 1990]; Op = opossum [Ravizza & Masterton, 1972]; P = pig [R. S. Heffner & Heffner, 1989]; Rd = Norway rat domestic [Kavanagh & Kelly, 1986]; Rw = Norway rat wild [H. E. Heffner & Heffner, 1985]; S = seal [Terhune, 1974]; SI = sea lion [Moore, 1975]; Sp = spiny mouse [Mooney, 1992]; W = weasel [R. S. Heffner & Heffner, 1987]; and Wr = wood rat [R. S. Heffner & Heffner, 1988c].)

son between the most broadly defined domestic animals and the remaining wild animals reveals no difference between the two groups (Mann-Whitney $U, p > .05$).

However, it can easily be argued that the broad definition of domestication is inappropriate because it includes elephants, humans, and gerbils (indicated by parentheses in Figure 5). If we include as domesticated only the species which have been subject to selective breeding (Ratner & Boice, 1975), we eliminate humans and Indian elephants from the group because they are not selectively bred and thus not domesticated by this more restrictive definition. Similarly, gerbils (in parentheses in Figure 5) were only recently imported and bred from a small stock for use as pets and research animals, and the minimal selective breeding (and even protection from predation) may have had insufficient time to effect change. Accordingly, every combination of inclusion and exclusion of these three questionable species among the domesticated and wild species was examined. Each led to the same result: In the current sample, domesticated animals are not less accurate localizers than wild animals (Mann-Whitney $U, p > .05$).

A final indication of the lack of effect of domestication on localization acuity can be found in a comparison between wild Norway rats and inbred laboratory strains of albino Norway rats. Sound-localization thresholds are 12.8° for the wild rats and 11.1° for domestic albino rats, an insignificant difference (H. E. Heffner & Heffner, 1985; Kavanagh & Kelly, 1986; Kelly, 1980). Indeed, not only are laboratory rats just as accurate as wild rats, they are the most accurate localizers of all rodents tested.

Although it is impossible to rule out domestication as a contributing factor in some species, domestication does not invariably, or even frequently, result in poor sound-localization acuity. Factors that account for the variation among both large and small domesticated and nondomesticated mammals must be sought elsewhere.

Predators Versus Prey

A further examination of Figure 5 reveals that the more accurate localizers tend to be predatory in their habits and

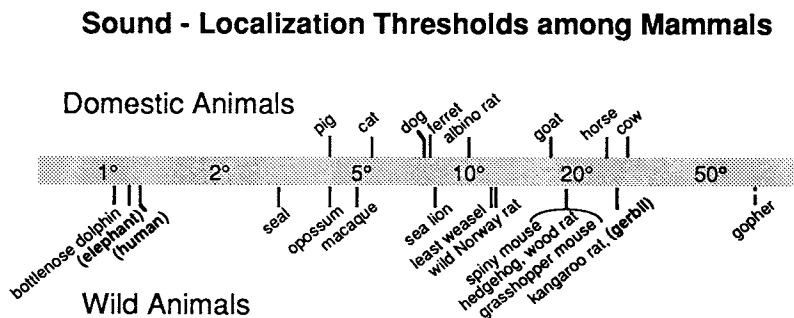


Figure 5. Sound localization among domestic and wild mammals. (Parentheses indicate species that are protected from predation but are not selectively bred [human and elephant] or have been selectively bred for only a few generations [gerbil]. Note the log scale for thresholds. For sources of the published thresholds, see caption to Figure 4.)

the less accurate localizers tend to be prey species. This tendency holds true among the entire sample of 24 mammals ($r = .606$, $p < .002$; R. S. Heffner & Heffner, 1992b). This correlation accounts for only 37% of the variation in localization acuity, however, and is confounded by other sensory differences between predators and prey that may themselves be important for understanding auditory differences. The most promising difference in this regard is the width of the most acute visual field.

Width of the Field of Best Vision

There is one visual characteristic that seems to be common among the less accurate localizers regardless of whether they are large or small, domesticated or not, predators or prey: Poor localizers tend to have their most acute vision (as indicated by the density of their retinal ganglion cells) concentrated in a broad horizontal streak so that their best vision encompasses a wide angle, sometimes including nearly the entire horizon. Both cattle and goats possess visual streaks, especially marked in cattle, and thus conform to this trend (Hebel & Holländer, 1979; Hughes & Whitteridge, 1973).

The relation between the width of the most acute visual field and sound-localization acuity (Figure 6) is reliable ($r = .911$, $p < .001$) and remains strong even when the contributions of such other factors as interaural distance, status as predator or prey, visual acuity, or nocturnal versus diurnal habits are removed mathematically (R. S. Heffner & Heffner, 1988d, 1992b). It is suggested that this relation is not fortuitous but rather provides insight into the role of sound localization in adapting to various lifestyles. Prey species, such as cattle and goats, benefit from the ability to see predators approaching from any location on the horizon, and their laterally placed eyes with their best vision spread across the horizon of the retina permit them to see well in nearly all directions. As a consequence, however, any noise source, such as a predator's stepping on a twig or rustling grass, is already in the animal's field of good vision; there is no need for the auditory system to provide precise locus information to direct

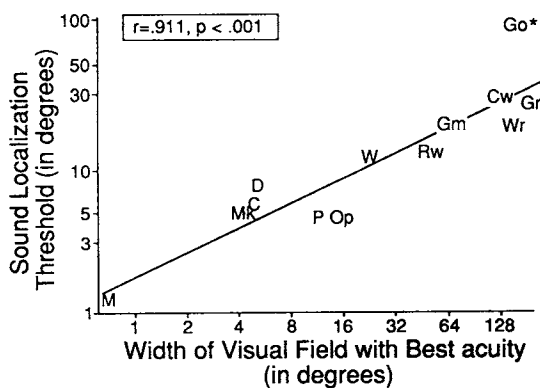


Figure 6. Relation between sound-localization acuity and the width of the visual field with best acuity. (For a description of the methods for estimating acuity across the retina, see R. S. Heffner & Heffner, 1992b. See Figure 4 for abbreviations and citations.)

the eyes toward the sound source for further scrutiny and identification. In contrast, more predatory species, such as cats and dogs, and species that manipulate small objects, such as humans and elephants, seem to benefit from large binocular visual fields for improved depth perception and from concentrating their best visual acuity in the center of that binocular field (Hughes, 1977; Stone & Halasz, 1989). These species have narrow fields of good vision that are oriented frontally, and they may conceivably derive much benefit from auditory information that accurately directs their fovea or area centralis toward a sound source for visual examination. It follows that the factors that contribute most to the observed variation in sound localization are not input factors, such as the magnitude of the physical cues for locus (although cues of very small magnitude must surely impose limits on acuity). Rather the strongest factors are output factors—factors that involve the use to which the auditory information is put, that is, directing the animal's eyes (see Hafter & DeMaio, 1975; Pumphrey, 1950).

In summary, both cattle and goats are relatively inaccurate localizers of sound, especially when their large interaural distances are considered. However, they share important characteristics with other poor localizers both domesticated and wild. Both cattle and goats are prey species with their best vision directed throughout nearly the entire horizon. In contrast to species with a very narrow area centralis, their ears do not need to provide very accurate locus information to direct their visual attention to a sound source. Although this relation is based on available, complete information for only 13 of the 24 species tested, it includes species of varying and extreme lifestyles as well as more familiar species, which suggests that it may apply to mammals as a whole (R. S. Heffner & Heffner, 1992b).

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