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Evolution of Sound Localization in Mammals

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1. Introduction

The ability to locate the source of a sound too brief to be either scanned or tracked using head or pinna movements is of obvious advantage to an animal. Since most brief sounds are made by other animals, the ability to localize such sounds enables an animal to approach or avoid other animals in its immediate environment. Moreover, it can be used to direct the eyes, thus bringing another sense to bear upon the source of the sound. Given the value of sound localization to the survival of an animal, it is not surprising that the need to localize sound has been implicated as a primary source of selective pressure in the evolution of mammalian hearing (Masterton et al. 1969; Masterton 1974).

Because of the obvious survival value of sound localization it might seem logical that all animals are under strong selective pressure to localize sound as accurately as possible. However, in the last decade, it has become apparent that this is not true. Not only are there poor localizers whose limited acuity cannot be attributed to a reduction in the availability of locus cues, but there exists at least one species that lacks entirely the ability to localize brief sounds (R. Heffner and Heffner 1990b). This situation indicates that selective pressure for accurate sound localization must vary between different species of mammals.

The purpose of this chapter is to review the behavioral data on mammalian sound localization in a search for the selective pressures that have played a role in its evolution and also to examine how the need to localize sound has exerted selected pressure on mammalian hearing. In doing so, we will address the following points: What are the basic sound-localization cues and how do mammals vary in the use of these? What is the relationship between the use of the binaural cues and the morphology of the superior olivary complex? How has the need to localize sound influenced the evolution of high-frequency hearing? What accounts for the variation in sound-localization acuity?

2. The Cues for Sound Localization

The locus of a sound can be described in terms of its azimuth, elevation, and distance from the observer. At present, discrimination of elevation has been determined for only a few species and almost nothing is known concerning the comparative ability of mammals to discriminate distance. However, there now exists a large body of information on the ability of mammals to discriminate the azimuth of sound sources and it is this aspect that is the primary focus of this chapter.

In comparing the ability of mammals to localize sound, it is helpful to review the cues that animals use to determine the location of a sound source. These cues can be divided into two general categories. The first are the binaural cues in which the azimuth of a sound source is computed by comparing the input from the two ears. The second are the monaural spectral cues which arise from the variation in the spectrum of a sound due to the directionality of the pinnae and the diffraction of sound by the head and torso.

TABLE 34.1. Effect of head size and azimuth on interaural time difference and the frequency at which binaural phase becomes ambiguous

Animal	Radius of head (in mm)	Interaural time difference (in μsec) Azimuth		Frequency of phase ambiguity (in kHz) Azimuth	
		90°	10°	90°	30°
House mouse	4.5	39	7	12.700	25.400
Dog	47.5	415	72	1.210	2.410
Human	90.0	786	136	0.636	1.270
Elephant	366.0	3,200	555	0.156	0.313

Interaural time difference and frequency of phase ambiguity calculated using the formula from Kuhn (1977).

Although most research has centered on the contribution of the binaural cues, monaural spectral cues, especially those generated by the pinnae, provide the primary information needed to determine elevation and to prevent front-back reversals. As we shall see, the need to use monaural spectral cues appears to have played a greater role than previously recognized in the evolution of mammalian hearing.

2.1 Binaural Locus Cues

The two chief binaural locus cues are the difference in the time of arrival of a sound at the two ears, which can be abbreviated "Δt," and the difference in the frequency-intensity spectra of a sound at the two ears, "Δfi." These two cues play a major role in the localization of sound in the horizontal plane. (For a review of the neural encoding of the binaural locus cues, see Phillips and Brugge 1985).

2.1.1 Binaural Time Cue

The difference in the time of arrival of a sound at the two ears, Δt, for a particular angle depends on the size of an animal's head. Animals with large heads have much larger Δt's available to them than do smaller animals. For example, the Δt cue available to the Indian elephant is approximately 80 times greater than that available to a wild house mouse (Table 34.1). Thus the auditory system of a small mammal would have to achieve much greater resolution of binaural time differences than that of a large mammal in order to attain the same degree of sound localization acuity.

It should be noted that a physically large head does not always result in a large Δt. Animals that hear underwater have a smaller *functional* head size because sound travels faster in water and, in some cases, the sound travels through the head instead of around it (McCormick et al. 1970; Norris and Harvey 1974). Both of these factors act to reduce the difference in the time of arrival of a sound at the two ears.

In order for the auditory system to determine a binaural time difference, it is necessary to compare the time of arrival of a sound at one ear with the arrival of the same portion of the sound at the other ear. In the case of pure tones, this is done by comparing the time of arrival of the same phase of the sine wave at the two ears. This cue is thus referred to as the binaural phase-difference cue or "$\Delta\phi$," a special case of Δt. The existence of a physiological upper limit for the use of the interaural phase-difference cue was suggested by Stevens and Newman (1936), who noted that the auditory nerve is limited in its ability to synchronize with the phase of a stimulus. It has been shown electrophysiologically that phase locking usually begins to decline at about 1 kHz and, in mammals, has not been observed higher than 5 kHz (Rose et al. 1967). Thus, the auditory system is incapable of deriving binaural phase information from high-frequency tones.

Even if the auditory system were capable of phase locking to high frequencies, there is a physical limitation to the upper limit of the usefulness of $\Delta\phi$. Although the auditory system is able to determine the time of arrival of a particular portion of the waveform at the two ears (e.g., the peak of a sine wave) it cannot distinguish a portion of one cycle of a sine wave from the same portion of another cycle. Therefore, in order to use $\Delta\phi$, it is necessary for a particular cycle to reach the far ear before the next cycle reaches the ear nearest the sound source.

The frequency at which the $\Delta\phi$ becomes physically ambiguous can be calculated according to the following formula:

$$F = 1/[6(a/C)\sin\theta]$$

where a is the radius of the head, C is the speed of sound, and θ is the angle of the sound source from the animal's midline.

Basically, $\Delta\phi$ becomes physically ambiguous when the difference in the distance of the two ears from the sound source equals one half of the wavelength of a tone and remains ambiguous for all shorter wavelengths (i.e., higher frequencies). As indicated by this formula, there are two factors which determine the frequency of ambiguity. The first is the size of an animal's head (a): animals with small heads will have a higher frequency of ambiguity than those with large heads due to the smaller time delay between the two ears (Table 34.1). Indeed, $\Delta\phi$ may be physically available to small mammals at such high frequencies that their upper limit for $\Delta\phi$ is determined solely by physiological factors, i.e., their ability to phase lock and to discriminate small binaural time differences. The second factor is the angle of the sound source (θ) from midline: $\Delta\phi$ becomes physically available at progressively higher frequencies as the azimuth of the sound source moves from the side toward the midline owing to the accompanying reduction in effective distance (i.e., time delay) between the two ears (Table 34.1). Thus, the angle of the sound source may determine whether a particular frequency is above or below the frequency of ambiguity.

In contrast to pure tones, mammals are able to extract binaural time information from high-frequency as well as low-frequency complex signals. This is because time information can be obtained from the envelope of high-frequency noise and from its onset, even though the carrier frequency may be above the frequency of ambiguity (e.g., Henning 1974; McFadden and Pasanen 1976). Although the time information extracted from high-frequency signals may not be as reliable as that obtained from low frequencies (e.g., Butler 1986), it nevertheless enables the Δt cue to be used to locate the source of a wide range of sounds.

2.1.2 Binaural Spectral Difference Cue

The heads and pinnae of mammals produce a sound shadow which results in a difference in the fre-
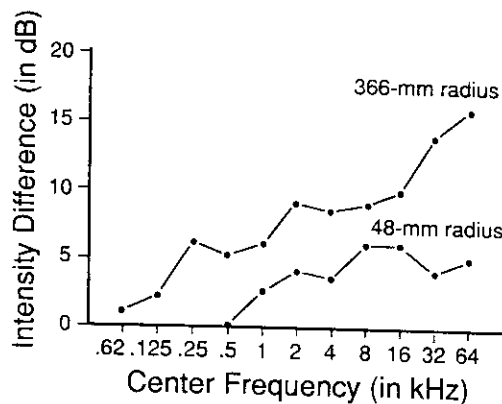

FIGURE 34.1. Sound-shadowing characteristics of two spheres approximating the head size of a dog (48-mm radius) and an elephant (366-mm radius) (cf. Table 34.1). The difference in intensity of a sound at the side nearest and furthest from a loudspeaker was determined for noise bands centered at octave intervals (24 dB/octave rolloff). This comparison supports the idea that small animals must hear higher frequencies than large animals in order for their heads to generate usable binaural intensity differences.

quency–intensity spectra (Δfi) of the sounds at the two ears. The magnitude of the Δfi cue is dependent on the size of the shadowing object so that animals with large heads and pinnae produce a greater sound shadow than small species. This cue is frequency dependent because the attenuation by the head is greater for high frequencies than for low frequencies (Fig. 34.1). The interaction between head size and frequency means that large species not only produce larger overall interaural spectral differences, they also produce differences at lower frequencies than do small species.

The Δfi cue is subject to two limitations. First, low frequencies, whether pure tones or complex sounds, can bend around an animal's head with little or no attenuation. This is a physical limitation in the ability of the head and pinnae to produce a sound shadow. Interestingly, the auditory system is physiologically able to extract spatial information when low-frequency binaural intensity differences are artificially generated by presenting the sounds through headphones even though such intensity differences do not occur in nature (Mills 1972). As illustrated in Figure 34.1, what constitutes a "low" frequency depends upon the size of an animal's head because large heads generate physical

intensity differences at lower frequencies than small heads. Thus, unlike the binaural time cue, the binaural spectral-difference cue cannot be obtained from all complex sounds.

The second limitation is the observation that at very high frequencies a sound may be completely shadowed and not detectable at the far ear (e.g., Butler and Flannery 1980). In this case the Δfi cue can only indicate that a sound occurred in the left or right hemifield and may lead to the erroneous perception that the sound source is located in one ear. In such a case it may be advantageous for the auditory system to ignore intensity differences at very high frequencies as they may add no useful information beyond that available from the lower frequencies and could conflict with the information available from the other locus cues.

The Δfi cue is most reliable for complex sounds that contain high frequencies, particularly broadband noise. As the bandwidth of noise is reduced, localization acuity declines (Brown et al. 1980; Butler 1986). In the case of a pure tone, the interaural spectral cue is reduced to a simple interaural intensity difference (ΔI), a subset of Δfi. However, it has been observed that pure tones do not always provide a reliable interaural intensity difference and are subject to left–right reversals with the result that the intensity of a pure tone may in some cases be greater at the far ear than at the near ear (e.g., Harrison and Downey 1970; Martin and Webster 1989). The results of behavioral studies demonstrate a corresponding difficulty in localizing tonal stimuli in both humans and other mammals (Mills 1972; Brown et al. 1978, 1982; Terhune 1985; Martin and Webster 1987). Indeed, some animals appear to take advantage of the fact that pure tones are difficult to localize. For example, the predator warning calls of animals are often more tonal than other calls, thus making the calling individual more difficult to locate (Marler 1955; for reviews see Erulkar 1972; Brown and May 1990). Nevertheless, most natural sounds are complex sounds containing high frequencies which permit the use of the Δfi cue.

2.2 Monaural Spectral Cues

Monaural cues arise from the differences in the spectrum of a sound reaching an ear from different locations. These differences are due to the directionality of the pinna as well as the diffraction of sound around the head and torso (e.g., Butler 1975; Kuhn 1982; Musicant and Butler 1984b). The primary source of these cues is the pinna and the contribution of pinna cues to localization has been investigated in some detail.

The pinna acts as a funnel that selectively admits into the auditory canal, and in some cases amplifies, high frequencies that emanate from sources located along the pinna's directional axis and slightly above the horizon; high frequencies from other directions are attenuated (e.g., Phillips et al. 1982; Calford and Pettigrew 1984; Butler 1987; Carlile and Pettigrew 1987; Humanski and Butler 1988; Middlebrooks 1990). The spectrum of the sound is also affected by the folds of the pinna and distortion of even the diminutive pinna of humans degrades sound location accuracy (for reviews see Butler 1975; Shaw 1974). Low frequencies, on the other hand, are much less strongly affected by the pinna. Thus pinna cues are dependent on high frequencies and in humans, for example, frequencies above 4 kHz must be present in order for pinna cues to be effective (Belendiuk and Butler 1975; Musicant and Butler 1984b). Indeed, pinna cues can provide highly accurate information providing that the pinna is undistorted and the sound is complex and contains high frequencies (Butler 1986).

Monaural spectral cues are most evident in situations where binaural cues are limited or absent. When localizing sound in the horizontal plane, binaural cues are of limited value in preventing front–back reversals and monaural cues are needed to make front–back judgments with reasonable consistency (Flannery and Butler 1981; Musicant and Butler 1984b). Monaural cues also provide necessary information for localizing sounds off to the side near the interaural line where they are more reliable than binaural cues when low frequencies are absent (Butler 1986). With regard to vertical localization, monaural spectral cues are the main, if not the sole source of locus information as binaural differences are slight or nonexistent (e.g., Butler and Belendiuk 1977; Middlebrooks et al. 1989). Furthermore, the signal must contain high frequencies in order for the elevation of the sound source to be accurately determined (Roffler and Butler 1968a). In short, monaural cues play an important role in horizontal localization and an essential role in vertical localization—and

they require the presence of high frequencies in order to be effective.

3. Variation in the Use of Binaural Locus Cues Among Mammals

The results of comparative studies from several laboratories have revealed that although most mammals are capable of using both binaural time and intensity differences to localize, there are some species that have reduced or lost their ability to use one or the other of these cues.

3.1 Determining the Use of Binaural Locus Cues

The ability of an animal to use binaural locus cues can be determined with either lateralization tests, in which stimuli are presented through headphones, or localization tests in which stimuli are presented through loudspeakers. In a lateralization test of the ability to use binaural time, Δt, an animal is presented with clicks or noise bursts in which the stimulus to one ear precedes that to the other ear and the animal is trained to indicate which ear received the leading sound (e.g., Masterton and Diamond 1964). An animal that uses Δt should be able to discriminate time differences at least as small as the maximum binaural time difference generated by its head and it is inferred that, like humans, the animal perceives a single sound that is lateralized to the ear receiving the leading stimulus. By substituting pure tones, the ability to use the phase cue, $\Delta\phi$, can be measured and the upper frequency limit of the phase cue can be determined (e.g., Wakeford and Robinson 1974).

The lateralization test is used to determine the ability of an animal to use Δfi in the form of ΔI by presenting identical sounds to the two ears which differ only in level and requiring the animal to indicate which ear received the louder signal (e.g., Masterton and Diamond 1964). Again it is assumed that the animal lateralizes the sound to the ear which receives the louder signal. However, an animal can perform such an intensity lateralization test by listening only to the variation in the signal in one ear. As a result it is necessary to randomize the overall level of the signal in order to prevent the animal from performing the task monaurally (e.g., Yost and Dye 1988).

Because of the technical difficulty of placing headphones on animals, many studies have used free-field tone-localization tests to examine the ability of animals to use the $\Delta\phi$ and ΔI cues. This test is based on the fact that low-frequency tones that bend around the head with little or no intensity difference between the two ears can only be localized using the phase cue, $\Delta\phi$. Tones that lie above the frequency of phase ambiguity, on the other hand, can only be localized using the intensity difference cue, ΔI. Thus, the ability of an animal to localize tones below the frequency of phase ambiguity indicates that it possesses the ability to use $\Delta\phi$, and, presumably Δt, whereas the ability the localize high-frequency tones indicates that it can use ΔI and, presumably Δfi.

Although the ability of an animal to localize pure tones can be determined by obtaining thresholds at various frequencies, a standard procedure is to determine localization performance with loudspeakers placed 30° to the left and right of an animal's midline (Masterton et al. 1975). Because the frequency at which phase becomes ambiguous varies with the angle of the sound source, this test has the advantage of keeping the angle of separation, and thus the frequency of ambiguity, constant (cf. Table 34.1 and Section 2.1.1 of this chapter). An additional important feature of this test is that the tones are presented at a constant level above an animal's threshold (e.g., 40-dB sensation level). Thus, an animal's ability to detect the tones is held constant and any variation in performance across frequency reflects an animal's ability to localize.

3.2 Species Using Binaural Phase and Intensity Difference Cues

Most mammals use both binaural locus cues. The use of both time and intensity differences has been demonstrated in 12 species including insectivores, primates, rodents, cetacea, carnivores, and pinnipeds (Table 34.2). Most of these animals were tested for their ability to localize tones above and below the frequency of phase ambiguity. However, lateralization data are available for man (Mills 1972), squirrel monkey (Don and Starr 1972), macaque (Houben and Gourevitch 1979), and the domestic cat (Wakeford and Robinson 1974) which support the results of the tone-localization tests.

TABLE 34.2. Species of mammals grouped by ability to use the main binaural locus cues

| Ability	Species	Source
Use both $\Delta\theta$ and ΔI		
	Tree shrew	Masterton et al. 1975
	Human	Stevens and Newman 1936
	Squirrel monkey	Don and Starr 1972
	Pig-tailed macaque	Brown et al. 1978
	Gerbil	R. Heffner and Heffner 1988c
	Kangaroo rat	Heffner and Masterton 1980
	Norway rat	Masterton et al. 1975
	Bottlenose dolphin	Renaud and Popper 1975
	Red Fox	Isley and Gysel 1975
	Cat	Casseday and Neff 1973
	Least weasel	R. Heffner and Heffner 1987
	Sea lion	Moore and Au 1975
Ability to use $\Delta\theta$ reduced or absent		
	Hedgehog	Masterton et al. 1975
	Spiny mouse	Mooney unpublished Master's thesis
Ability to use ΔI reduced or absent		
	Elephant	R. Heffner and Heffner 1982
	Horse	R. Heffner and Heffner 1986a
	Pig	R. Heffner and Heffner 1989
	Cattle	R. Heffner and Heffner 1986b
	Goat	R. Heffner and Heffner 1986b
Unable to use Δt or Δfi		
	Gopher	R. Heffner and Heffner 1990b
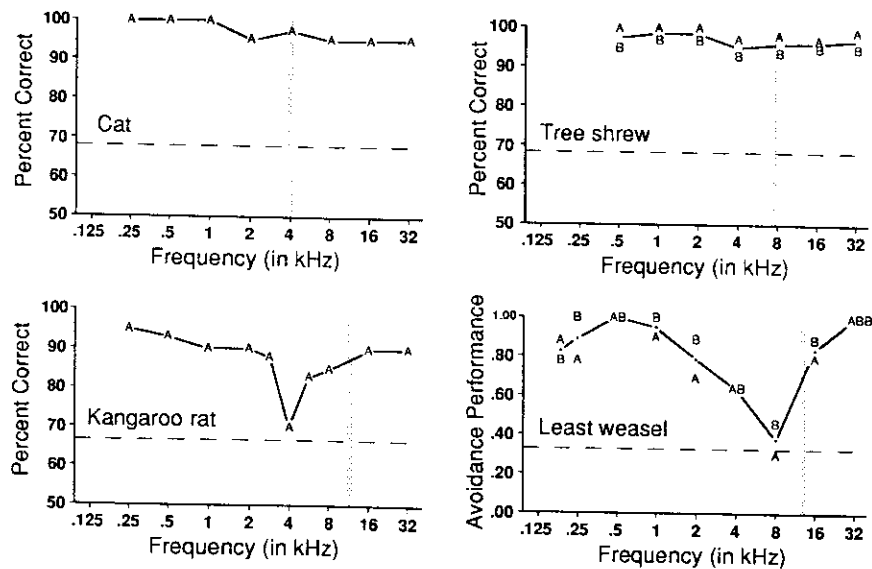
FIGURE 34.2. Sound-localization performance in the horizontal plane as a function of frequency for four species. Tones were presented from two loudspeakers located 30° left and right of midline. Vertical shaded bar indicates the frequency above which binaural phase becomes physically ambiguous. Note that all four species can localize tones above and below the frequency of phase ambiguity indicating that they can use binaural phase and intensity difference cues. Letters indicate individual animals; dashed lines indicate chance level ($p < 0.01$). Note that the tones in this test are presented at a constant level above threshold. (After Masterton et al. 1975; H. Heffner and Masterton 1980; R. Heffner and Heffner 1987.)

Examples of the results of the tone-localization tests are shown in Figure 34.2 for the cat, tree shrew, kangaroo rat, and least weasel. The fact that each of these animals can use both $\Delta\phi$ and ΔI is indicated by their ability to localize tones above and below the frequency at which $\Delta\phi$ becomes physically ambiguous (indicated by the vertical shaded bars).

It can also be seen in Figure 34.2 that some mammals, such as the kangaroo rat and least weasel, show a distinct decrease in performance in the midfrequency range. Such a decrease is usually seen in animals with small heads due to the fact that their ability to use binaural phase declines at frequencies that are too low to generate usable interaural intensity differences. When this occurs, the results can be used to derive an estimate of the upper frequency limit of an animal's ability to use $\Delta\phi$. In using this method, a minimum estimate of an animal's upper limit for $\Delta\phi$ is the frequency just below the point of lowest performance. For the animals in Figure 34.2, this would be 2.8 kHz in the kangaroo rat and 4 kHz in the least weasel. This represents a minimum estimate because it cannot be determined if an animal is using $\Delta\phi$ or ΔI at the point of poorest performance.

However, not all small mammals show a performance decrement in this test. For example, the tree shrew shows no obvious decrement (Fig. 34.2) whereas the Norway rat, which has a head size slightly larger than the tree shrew, has a distinct midfrequency decrement (Masterton et al. 1975; Kelly and Kavanaugh 1986). One interpretation of these results is that the tree shrew's auditory system possesses the ability to use $\Delta\phi$ at higher frequencies than the rat's.

3.3 Species with Limited or Absent Ability to Use Binaural Phase Differences

The idea that all mammals possess the ability to use both binaural cues was first called into question by Masterton and his colleagues (1975). In testing the ability of various mammals to localize pure tones, they discovered that although the hedgehog is able to localize high-frequency tones, it is unable to localize low-frequency tones at frequencies where $\Delta\phi$ is unambiguous (Fig. 34.3).
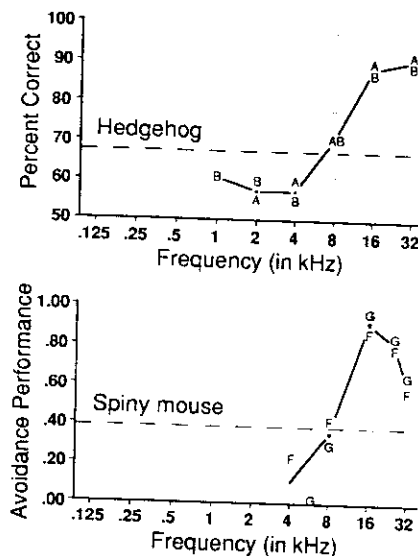

FIGURE 34.3. Sound-localization performance in the horizontal plane as a function of frequency for two species. Tones were presented from two loudspeakers located 30° left and right of midline. Vertical shaded bar indicates the frequency above which binaural phase becomes physically ambiguous. The inability of these two species to localize low-frequency tones suggests that they are unable to use binaural phase cues to localize sound. Letters indicate individual animals; dashed lines indicate chance level ($p < 0.01$). (After Masterton et al. 1975; Mooney unpublished Master's thesis.)

These results indicate that the hedgehog does not use $\Delta\phi$ and, presumably, binaural time (Δt), but is capable of using binaural intensity differences to localize sound.

The possibility exists that other species may also lack the ability to use Δt. In particular, small mammals such as mice which lack good low-frequency hearing may be unable to hear tones low enough for phase locking to occur. One example shown in Figure 34.3 is the spiny mouse whose hearing ranges from 2.2 kHz to 71 kHz (Mooney et al. 1990).

In searching for a reason as to why an animal would relinquish the use of a major binaural locus cue, it might be argued that an animal with a small head and close-set ears may lose the time cue because the available time differences are too small for its nervous system to resolve. However, it should be noted that other small mammals, such as the tree shrew, Norway rat, gerbil, kangaroo rat,
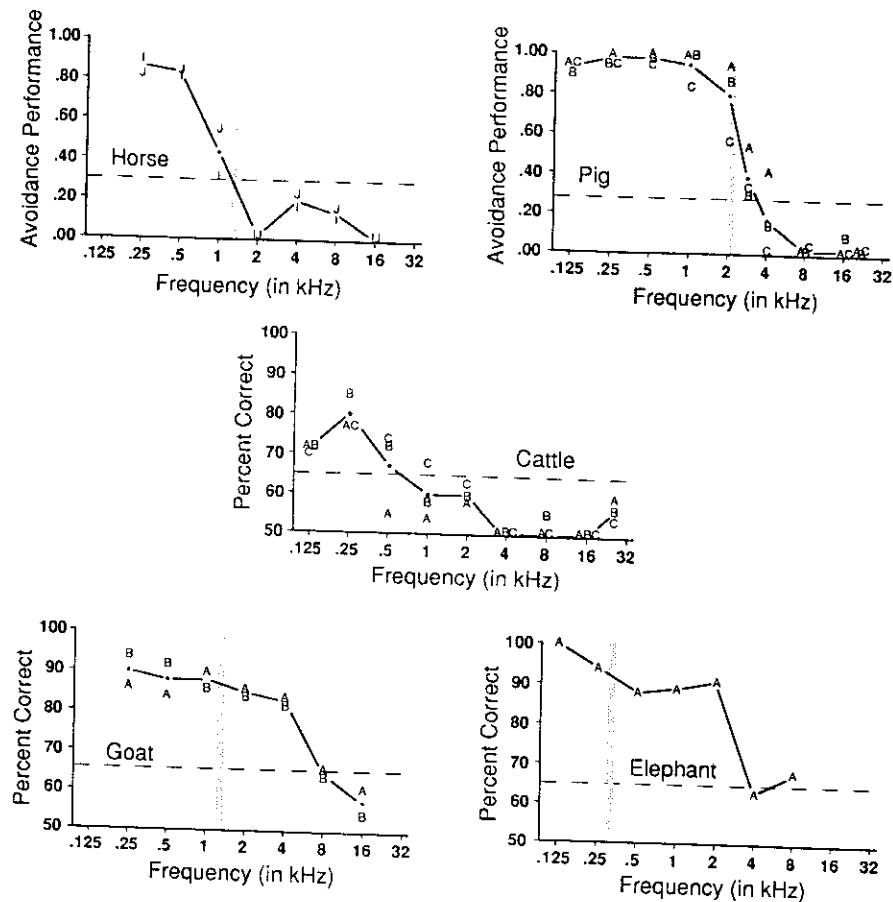
FIGURE 34.4. Sound-localization performance in the horizontal plane as a function of frequency for five species. Tones were presented from two loudspeakers located 30° left and right of midline. Vertical shaded bar indicates the frequency above which binaural phase becomes physically ambiguous. These animals have either partly or completely lost the ability to use binaural intensity cues as indicated by their inability to localize some or all of the tones above the frequency at which binaural phase becomes ambiguous. Letters indicate individual animals; dashed lines indicate chance level ($p < 0.01$). (After R. Heffner and Heffner 1982, 1986a, 1989.)

and least weasel, all have interaural distances smaller than the hedgehog's, and yet are able to use $\Delta\phi$. Thus there is currently no good explanation as to why some animals have relinquished use of $\Delta\phi$.

3.4 Species with Reduced or Absent Ability to Use Binaural Intensity Differences

As a wider variety of species have been examined, it has become apparent that not all mammals use the binaural intensity-difference cue. So far five species of mammals (horse, pig, cattle, goat, and elephant) appear to have lost part or all of the ability to localize pure tones above the frequency of phase ambiguity (Fig. 34.4) (R. Heffner and Heffner 1982, 1986a 1986b, 1989).

Some species, such as goats and elephants, have only partially lost the ability to use ΔI. That is, they are unable to localize pure tones in the upper 2 to 3 octaves of their hearing range, but retain the ability to use ΔI at lower frequencies. Horses, however, are completely unable to localize tones above the frequency of phase ambiguity, suggesting that the inability of this species to use ΔI is total. The results of tests on pigs and cattle suggest that they might retain some residual ability to use ΔI because some individuals were able to localize

tones slightly above the frequency of phase ambiguity (R. Heffner and Heffner 1986b, 1989). However, the frequency of phase ambiguity is calculated based on a sphere of the same diameter as the head of an average animal and does not take the actual shape of the head into account. It is thus possible that individual variation in frequency of phase ambiguity may account for the performance of some individuals and that pigs and cattle, like horses, completely lack the ability to use binaural intensity differences.

The ability of horses to perform binaural phase and intensity discriminations was further examined using headphones (R. Heffner and Heffner 1988a). The results of these lateralization tests demonstrated that horses can discriminate binaural phase differences from 250 Hz to 1.2 kHz, but fall to chance at frequencies of 1.3 kHz and above. This determination of the upper frequency limit of binaural phase discrimination is in keeping with the results of the tone localization test (cf. Fig. 34.4). More important, however, was the finding that the animals were unable to discriminate stimuli based on interaural intensity differences when the overall level of the signal was randomized to prevent them from making the discrimination monaurally. Thus, the results of both localization and lateralization tests indicate that horses are unable to use the binaural intensity difference cue, ΔI, and, presumably, Δfi.

In searching for an explanation as to why animals would relinquish ΔI, the possibility arises that it could result from reduced selective pressure to localize sound, perhaps owing to the reduced demands of domestication. However, although some of these species, particularly horses and cattle, are not accurate localizers, others are very accurate. In particular, the 4.5° threshold of the pig makes it more accurate than cats or macaques, while the 1.2° threshold of the elephant makes it as accurate as humans and dolphins. Furthermore, the fact that elephants have not been selectively bred makes it unlikely that the reduction or loss of ΔI is the result of domestication.

Nor have these animals given up the use of ΔI because the cue is unavailable to them. One feature common to these animals is that they are all large mammals. As a result they have relatively large heads and pinnae which generate large binaural intensity differences. Measurements of

the physical cues available to horses, for example, reveal the presence of binaural intensity differences of more than 20 dB (H. Heffner and Heffner 1984). Indeed, we suggest that the reason these animals have reduced or eliminated their use of binaural intensity differences is because the available intensity differences are *too* large.

Given the large heads and pinnae of these animals the situation can arise in which a sound, or the high-frequency component of a sound, is audible in the ear nearest the sound source and *inaudible* in the far ear. As previously noted, the spectral difference cue will indicate only the hemifield in which the sound arose and could possibly degrade the locus information derived from the binaural time cue. Thus, if the high-frequency portion of a sound is not audible in both ears, the resulting Δfi cue will add little useful locus information beyond that provided by the other cues.

One way to reduce the occurrence of an unusable Δfi cue is to reduce the ability to hear high frequencies. However, if an animal is under pressure to hear high frequencies for other purposes, such as to prevent front–back reversals, then it might be advantageous for their auditory systems to reduce or eliminate the binaural intensity difference at high frequencies from the computation of locus.

3.5 Species Using Neither Binaural Time Nor Intensity

We now know that there exists at least one species that is incapable of localizing any brief sound — high- or low-frequency, pure tones or complex noise — indicating that it cannot use any of the major locus cues. This animal is the pocket gopher (*Geomys bursarius*), an animal that is specialized for living underground in an essentially one-dimensional world where azimuthal locus may have little significance (R. Heffner and Heffner 1990b). Because gophers can only discriminate the loci of long-duration sounds (i.e., greater than 0.5 sec) and then only at angles greater than 90° separation, they demonstrate little sound localization ability beyond homing or scanning. Although other fossorial species have not been tested systematically, it has been suggested that they also have little response to locus (Burda et al. 1990).
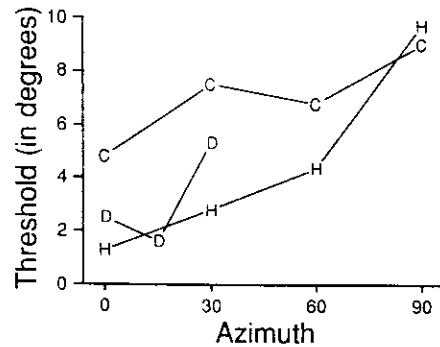
FIGURE 34.5. Sound localization acuity as a function of azimuth for cat (C), human (H), and dolphin (D). Note that cats are as accurate as humans in localizing sound sources centered around 90° azimuth, a front-back discrimination in which monaural spectral cues play a major role. (Data from Renaud and Popper 1975; R. Heffner and Heffner 1988a.)

4. Use of Monaural Spectral Cues

The contributions of monaural spectral cues to sound localization are most evident in preventing front-back reversals and in localizing in the vertical plane—two situations in which binaural cues are relatively ineffective.

4.1 Sound Localization in the Horizontal Plane

Most of what we know about the role of monaural spectral cues in horizontal localization comes from the studies of human sound localization, particularly those of Butler and his colleagues. Monaural locus cues arise primarily from the directionality of the pinna with the diffraction of sound by the head and torso also contributing information (Butler 1975; Kuhn 1982; Musicant and Butler 1984b). Pinna cues require the presence of high frequencies and, in man, frequencies above 4 kHz are necessary in order for the pinna to play an effective role in localization (Belendiuk and Butler 1975; Musicant and Butler 1984b). Furthermore, monaural localization improves as the bandwidth of the stimulus increases (Butler 1986). Thus, the ability to use monaural spectral cues is best demonstrated by tests employing broadband noise containing high frequencies (cf. Brown et al. 1980).

Pinna cues result from the selective amplification and attenuation of different frequencies by the pinna depending on the location of the sound source. This can be demonstrated by measuring the effect of the head and pinna on the sound reaching the auditory meatus (e.g., Shaw 1974). Indeed, the importance of the effect of the pinna on the sound spectrum is demonstrated by the fact that the apparent location of a sound source can be shifted simply by changing the spectral content of the sound with the new perceived location corresponding to the position predicted by the transfer function of the pinna (Butler and Flannery 1980; Flannery and Butler 1981; Musicant and Butler 1984a, 1985; Butler 1987). Furthermore, distorting or filling the convolutions of the pinna dramatically reduce the ability to use monaural localization cues (e.g., Butler 1975).

Although binaural cues play a dominant role in localizing sound near the midline, both in front and in back, monaural spectral cues become increasingly important as the sound source moves off to the side (Musicant and Butler 1984b, 1985; Butler 1986). Furthermore, monaural spectral cues are the primary means for preventing front-back reversals (e.g., Musicant and Butler 1984b; cf. Boring 1942). However, the reliance on monaural spectral cues may be more widespread than is generally realized. As Butler and Flannery (1980) have noted, monaural cues provide the only means of localizing sounds that are inaudible in the ear furthest from the source, a common occurrence with high-frequency transient sounds.

The fact that sound-localization acuity decreases as the sound source is located progressively farther from the midline indicates that monaural cues are generally not as effective as the binaural cues. This decrease in acuity with azimuth has been demonstrated in cats and dolphins, as well as in humans, using complex sounds (Fig. 34.5) and in monkeys using tones (Renaud and Popper 1975; Brown et al. 1982; R. Heffner and Heffner 1988b). However, it is of interest to note that the increase in thresholds in the cat is proportionally less than that for humans. This suggests that the cat's relatively large and mobile pinnae may enhance its ability to use monaural locus cues. Thus, the difference in acuity between monaural and binaural localization in animals with large and mobile pinnae may be significantly less than that found in humans.
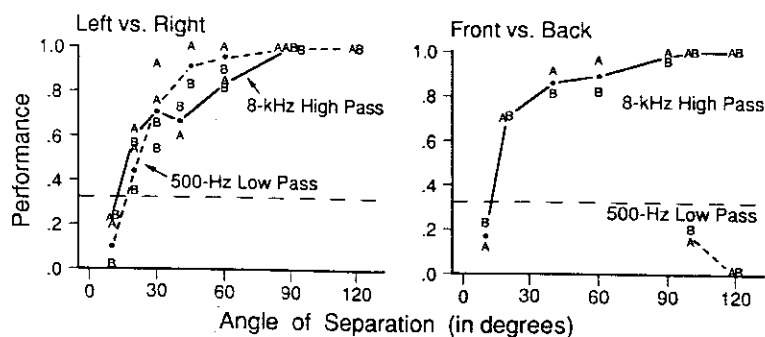
FIGURE 34.6. Localization of continuous (3-sec duration) high- and low-pass noise in the horizontal plane by horses. Either high- or low-pass noise could be localized in the left-right discrimination where the sound sources were centered on midline. However, only the high-pass noise could be localized in the front-back discrimination where the sound sources were centered on 90° azimuth. Horizontal dashed line indicates chance level. (Data from R. Heffner and Heffner 1983.)

A number of studies have examined the directional properties of the pinnae of other mammals. Measurements of the filtering characteristics of the pinnae have been examined in cats (Phillips et al. 1982; Calford and Pettigrew 1984; Irvine 1987), guinea pigs (Carlile and Pettigrew 1987), and bats (Fuzessery and Pollak 1985). These studies have demonstrated that all of these pinnae, despite their different sizes and configurations, act as directional filters in much the same way as the human pinna.

As with humans, other mammals also require the presence of high frequencies in order to make use of monaural spectral cues. This has been demonstrated in the case of the horse (an animal that hears well above 10 kHz and yet does not make use of binaural spectral cues) by assessing sound localization ability for 500-Hz low-pass and 8-kHz high-pass noise. As shown in Figure 34.6, two horses were able to localize either high- or low-frequency noise when the sound sources were centered on the midline (a left-right discrimination) and binaural time cues were available. However, only the 8-kHz high-pass noise could be localized when the sound sources were centered 90° from midline (a front-back discrimination) and monaural spectral differences were the primary cue. This finding demonstrates that horses, which do not use interaural intensity differences, nevertheless require the presence of high frequencies in order to use monaural spectral cues. This in turn suggests that the need to use monaural spectral cues may by itself exert strong selective pressure for good

high-frequency hearing. We will return to this point in Section 6.1.

4.2 Sound Localization in the Vertical Plane

Monaural spectral cues play a primary role in localizing sound in the vertical plane — a situation in which binaural cues are relatively ineffective. As in azimuthal localization, the pinnae selectively amplify and filter different frequencies depending on the elevation of the source (for a review, see Fuzessery 1986). Studies of human localization have demonstrated that vertical localization depends on the same variables as monaural localization in the horizontal plane. Specifically, maximum accuracy is obtained with broad-band complex sound which includes frequencies above 7 kHz and the pinna must be intact (Roffler and Butler 1968a; Butler and Planert 1976). Indeed, all the information necessary for vertical localization in humans appears to be contained in the frequencies above 4 kHz (Butler and Helwig 1983). Furthermore, both ears participate in vertical localization with the ear nearest the sound source playing the major role (Humanski and Butler 1988). Finally, the apparent elevation of a sound varies as a function of frequency (Roffler and Butler 1968b; Butler and Helwig 1983).

In addition to humans, behavioral measures of the role of frequency in vertical localization have been obtained for the cat, macaque, opossum, and

porpoise. Most of these animals appear to be highly accurate with thresholds of 4° for the cat (Martin and Webster 1987), 3° for the macaque (Brown et al. 1982), and 1° for the bottlenose dolphin (Renaud and Popper 1975). The opossum, on the other hand, was found to have a threshold of 14° (Ravizza and Masterton 1972). However, this may be an underestimation of the animal's ability because the spectrum of the noise used to test the opossum probably lacked high frequencies as the transducers were hearing-aid receivers which normally roll off at 8 kHz. Indeed, the importance of high frequencies, particularly those above 8 kHz, for accurate vertical localization has been demonstrated in macaques as well as in man (Brown et al. 1982).

4.3 Mobile Pinnae

The fact that most mammals possess mobile pinnae suggests that this character must be of some value. The degree of pinna mobility ranges from the 180° mobility of horse pinnae to the unmoving pinnae of humans. The fact that human pinnae are immobile leaves us unable to conceptualize the advantage of such movement through introspection.

It has often been speculated that pinna mobility confers an advantage in localizing sound (e.g., Jeffress 1975) and to a certain extent this appears to be true. As noted in Section 4.1 of this chapter there is evidence that the mobile pinnae of cats enhance their ability to localize sound in the lateral fields where binaural cues are less effective and it has been shown in the cat that preventing pinna movements by denervating the external ear muscles reduces localization acuity (Siegmund and Santibañez-H 1981). Moreover, some bats appear to require normally mobile pinnae in order to make discriminations in the vertical plane (Mogdans et al. 1988). Thus, pinna mobility may be an effective way of enhancing monaural spectral cues. However, mobile pinnae could potentially interfere with the use of the binaural spectral differences because the magnitude of the cue would depend on the orientation of the pinnae. As a result it would be necessary for the nervous system to take pinna position into account in calculating locus. Although there is some evidence that this does occur in the cat (Stein and Clamann 1981), it would nevertheless be a potential source of error.

It should also be noted that mobile pinnae are not uniquely associated with good sound localization acuity. The best example is the horse, an animal with extremely mobile pinnae and poor sound localization acuity (see Section 7 in this chapter). Although the horse has a large head and correspondingly large binaural cues available to it, it has a midline localization threshold of 22° for noise (H. Heffner and Heffner 1984). Nor is its acuity for localizing off to the side where monaural spectral cues predominate much better even when presented with long-duration sounds that permit scanning (cf. Fig. 34.6). These results suggest that pinna mobility must serve another purpose, at least in the horse. One possibility is that they serve as mobile directional filters, amplifying sounds originating from in front of the opening while attenuating sounds from behind. As such they would enhance an animal's ability to pick out signals embedded in a noisy world without having to move its head.

5. Variation in the Superior Olivary Complex

Numerous studies of the response properties of neurons in the medial and lateral superior olivary nuclei (MSO and LSO, respectively) have been carried out since the early investigations of Galambos and his colleagues (1959) and of Boudreau and Tsuchitani (1968). These have been reviewed in detail elsewhere (e.g., Aitkin et al. 1984; Phillips and Brugge 1985; Irvine 1986) and will not be described here. In general the superior olivary complex has been shown to be the major brainstem structure for neural interaction between input from the two ears. Neurons in the LSO have been shown to be sensitive to intensity differences at the high frequencies to which they are tuned. On the other hand, neurons in the MSO are sensitive to frequencies in the lower portion of an animal's audiogram and have been shown to respond as a function of the interaural time differences. Because mammals differ in their use of binaural time and intensity cues, it is reasonable to expect these differences to be reflected in the morphology of the MSO and LSO.

This may be true for the MSO as it has been demonstrated that the size of this nucleus is directly related to the ability of a species to use the binaural phase cue, $\Delta\phi$ (Masterton et al. 1975). That is, the

smaller the MSO, the less an animal is able to use $\Delta\phi$; and an animal that lacks an MSO, i.e., the hedgehog, is completely unable to use this cue. This finding has received recent support from the observation that the spiny mouse, which has almost no MSO, does not appear to use $\Delta\phi$. Thus, there is some truth to the statement by Irving and Harrison (1967) that the MSO is not essential for sound localization per se. However, the presence of an MSO does seem to be necessary for the use of binaural time cues.

For the LSO, however, there does not seem to be any simple correspondence between morphology and ability to use binaural intensity differences. Animals with a well-developed LSO may possess the ability to use ΔI, as in the case of the cat (Masterton et al. 1975), or they may entirely lack the ability to use ΔI as in the case of the pig (R. Heffner and Heffner 1989). Similarly, one can find an undistinguished LSO in animals which possess the ability to use ΔI, such as man (e.g., Mills 1972; Moore 1987), as well as in animals that lack the ability to use ΔI such as horses and cattle (R. Heffner and Heffner 1986a). Therefore, at this time it does not appear that the gross morphology of the LSO simply reflects the degree to which an animal uses the binaural spectral difference cue. (For additional discussions of the relationship between the superior olivary complex and hearing ability see R. Heffner and Heffner 1987, 1990b; R. Heffner and Masterton 1990.)

Apparently the LSO has functions beyond sound localization and these functions may be differentially represented in different species. What these functions might be remains largely unknown, yet at least one can be suggested and others may soon be recognized. In rodents and most bats the LSO has the distinction of being a major source of small olivocochlear efferents (Altschuler et al. 1983; White and Warr 1983; Aschoff and Ostwald 1987). Therefore, it is possible to conceive of a species which retains a nucleus recognizable as an LSO even if that nucleus plays no role in sound localization because its component cells perform other important functions.

6. Evolution of High-Frequency Hearing

The ability of mammals to hear high frequencies is unique among vertebrates as neither fish, amphibians, reptiles, nor birds are able to hear above 10

kHz. However, the ability of mammals to hear high frequencies is not uniform, but varies over a range of nearly 4 octaves from around 10 kHz in elephants and gophers to over 100 kHz in some bats and underwater species (Jacobs and Hall 1972; R. Heffner and Heffner 1982, 1990b; Wenstrup 1984).

There are three commonly suggested explanations for the variation in high-frequency hearing among mammals. Two of these address the question of "why" species differ in their ability to hear high frequencies: One involves the use of high frequencies for sound localization, and the other involves their use in communication. The other explanation addresses the question of "how" animals hear sound; it involves the size of the physical apparatus for transducing sound. Thus, these theories encompass both the functional and the structural levels of biological explanation (see Mayr 1961).

6.1 High-Frequency Hearing and Sound Localization

Over 20 years ago it was proposed that mammals evolved high-frequency hearing for the purpose of localizing sound (Masterton et al. 1969). The basis for this proposal was the observation that the ability of mammals to hear high-frequency sounds is correlated with the size of the head or, more precisely, with 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. Thus, 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. Indeed, over the years the correlation between functional interaural distance and high-frequency hearing has remained strong (Fig. 34.7).

At the time, the existence of this relationship was explained in terms of the binaural locus cues. Briefly, the availability of the binaural cues, Δt and Δfi, depend on the functional distance between the two ears and the sound shadow of the head and pinnae. That is, the farther apart the ears, the larger will be the Δt cue for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with wide-set ears both because the sound attenuation is greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which effectively shadow the high-frequency
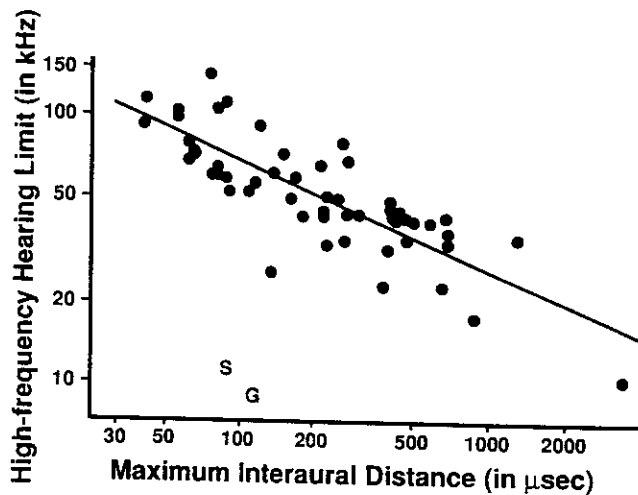
FIGURE 34.7. Relation between maximum interaural distance and the highest frequency that a species can hear at 60 dB SPL ($r = -0.84$, $n = 55$, $p < 0.001$). This relationship is explained by the fact that mammals with small heads need to hear higher frequencies than larger mammals in order to use monaural and binaural spectral cues for sound localization. Not included in the correlation coefficient are two fossorial mammals, the blind mole rat, *Spalax ehrenbergi*, (S) and the pocket gopher, *Geomys bursarius*, (G) —evidence indicates that these animals have lost their high-frequency hearing and their ability to localize sound as part of their adaptation to a subterranean habitat (cf. R. Heffner and Heffner 1990b). (See H. Heffner and Heffner 1985a; R. Heffner and Heffner 1990b,c, for individual points.)

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

In recent years evidence has appeared that shows that although this explanation is not incorrect, it is incomplete. The primary source of this evidence comes from the observation that large mammals have reduced, and in some cases abandoned, the use of binaural intensity cues and yet have retained their high-frequency hearing. For example, humans, which hear an octave higher than any nonmammalian vertebrate, rely much more on binaural time than on binaural intensity differ-

ences. Indeed, binaural intensity differences can be eliminated with little effect on localization performance so long as binaural time cues remain (Belendiuk and Butler 1978). A more extreme case is the horse which has completely abandoned the use of binaural intensity differences and yet can hear up to 33.5 kHz. However, both humans and horses require the presence of high frequencies for preventing front–back reversals and for vertical localization.

The above observations suggest that high-frequency hearing evolved in mammals to enable the use of monaural as well as binaural spectral cues for sound localization. Accordingly, the observed correlation between functional head size and high-frequency hearing reflects the need for mammals to hear high frequencies in order to use both types of cues—because the directionality of the pinnae is dependent on the wavelength of sound, animals with small heads and pinnae will need to hear higher frequencies than larger animals in order to obtain usable monaural as well as binaural spectral cues. Indeed, the variation in high-frequency hearing is probably best explained by a combination of factors involving both head and pinna size.
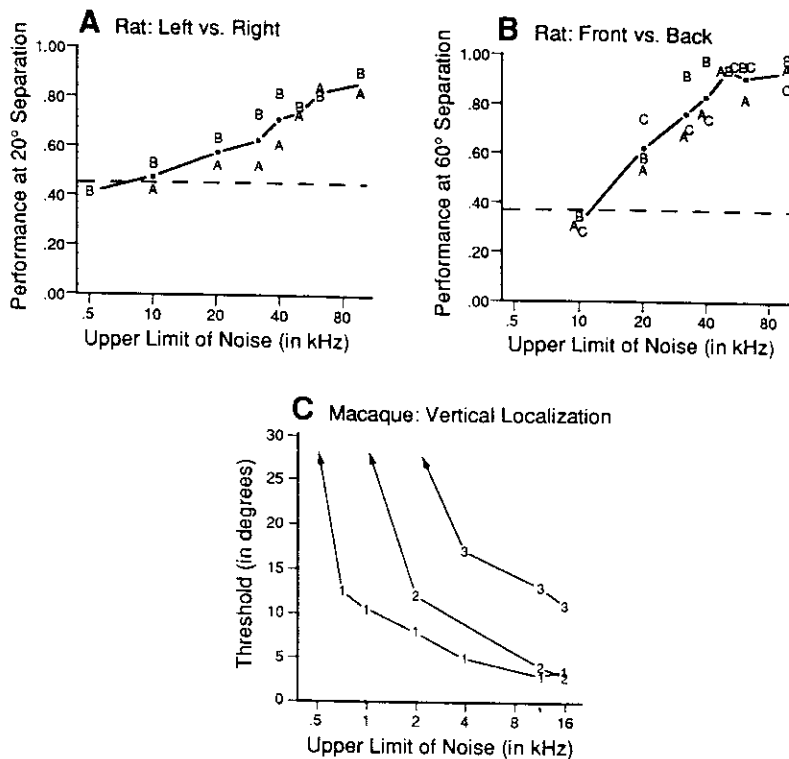
FIGURE 34.8. Effect of removing high frequencies on sound localization. Letters and numbers represent individual animals. Norway rats (A and B) were tested with a train of 100-msec noise bursts; macaques (C) were tested with 300-msec noise bursts. (Data from Brown et al. 1982 and R. Heffner and Heffner 1990a).

The idea that the ability to hear high frequencies provides mammals with monaural and binaural spectral cues is supported by the results of localization experiments in which high frequencies were progressively removed. As shown in Figure 34.8, localization performance declines when high frequencies are removed from broad-band noise signals. This decrease in performance can be seen in a left–right localization task in which Norway rats were required to discriminate two loudspeakers located 20° apart and centered on midline (Fig. 34.8A), a task in which both binaural and monaural cues are available. This result indicates that unlike large mammals, small mammals require the presence of high frequencies for left–right localization (cf. Fig. 34.6). A decrease in performance can also be seen in rats in a front–back localization task in which the loudspeakers were located 60° apart and centered 90° from midline (Fig. 34.8B), a task in which monaural cues predominate. Finally, as Brown and his colleagues have demonstrated,

vertical sound-localization thresholds in monkeys show a progressive increase as high frequencies are removed (Brown et al. 1982; Fig. 34.8C). Thus, it appears that high frequencies are necessary for the optimal performance of small mammals in situations where binaural cues are available and for all mammals in situations requiring the use of monaural spectral cues.

Finally, if high-frequency hearing evolved primarily to support sound localization, then it would be expected that any species which could not localize sound would lose its ability to hear high frequencies. This appears to have happened in fossorial mammals. As previously noted, the pocket gopher has lost virtually all ability to localize sound and there is reason to suspect that the blind mole rat may have done the same (Burda et al. 1990; R. Heffner and Heffner 1990b; see also Section 3.5 of this chapter). As previously shown in Figure 34.7, these two species also have much poorer high-frequency hearing than expected

based on their head size. It is also of interest to note that these animals lack significant pinnae which would enhance monaural spectral cues. Thus, while one might speculate on other reasons why fossorial mammals might lose the ability to hear higher than nonmammalian vertebrates, it should be noted that their inability to hear high frequencies is consistent with their relinquishing the ability to localize sound.

6.2 Alternative Explanations of High-Frequency Hearing

6.2.1 Ultrasonic Communication

There has been much interest in the fact that some species of mammals vocalize at ultrasonic frequencies (i.e., frequencies beyond the range of human hearing). In addition to bats, which are known to use ultrasonic vocalizations for echolocation, it has been demonstrated that ultrasonic vocalizations are used for communication by some small rodents and may also be used by other mammals such as insectivores (e.g., Sales and Pye 1974; Geyer and Barfield 1979). Thus, one possibility is that mammals evolved high-frequency hearing in order to use high frequencies in vocal communication.

If mammals evolved high-frequency hearing primarily for communication, then one might expect that those with good high-frequency hearing would either emit high-frequency vocalizations or else use their high-frequency hearing to detect the communications of other species, i.e., to "eavesdrop." Furthermore, the variation in high-frequency hearing should be related to the spectrum of the vocalizations—that is, animals with good high-frequency hearing should vocalize at higher frequencies than those with poorer high-frequency hearing.

Relating the spectrum of the vocalizations to hearing range is not simple. Vocalizations often contain abrupt onsets and offsets generating high frequencies that are "nonfunctional" in the sense that the animals do not use them to identify the sounds and which, in fact, may be beyond their hearing range. Examples of such vocalizations are bird calls which extend beyond 10 kHz (Konishi 1969) and rodent vocalizations which extend beyond 100 kHz (Sales and Pye 1974). However, even if the high-frequency portion of a vocalization

is within an animal's hearing range it may contain no significant information. For example, although human speech contains measurable energy up to 7 kHz, the portion above 3 kHz may be filtered out with no effect on intelligibility (Green 1976). However, functional analyses of animal vocalizations are usually not available.

The main evidence suggesting that high-frequency communication has played a role in the evolution of high-frequency hearing is the observation that some small rodent species emit high-frequency vocalizations (for a review, see Sales and Pye 1974). These vocalizations, which have been observed in approximately twenty species of mice and rats, usually lie in the frequency range above 30 kHz and vocalizations around 50 kHz are not uncommon. Furthermore, behavioral observations indicate that such vocal communications play an important role in reproduction. Thus, it is clear that many small rodents, and perhaps other small mammals as well, use high frequencies for communication.

However, there are other animals with good high-frequency hearing that do not appear to send or receive ultrasonic vocalizations. One example is the tree shrew which is able to hear above 60 kHz (H. Heffner et al. 1969), but which emits vocalizations only within the range from 400 Hz to 15 kHz (Binz and Zimmermann 1989). Other examples of animals whose hearing extends well above the frequency range of their vocalizations are dogs, macaques, pigs, and goats, all of which hear above 40 kHz, as well as horses and cattle which hear above 30 kHz (cf. Kiley 1972; Green 1975; Fox and Cohen 1977; Walser et al. 1981; for hearing ranges, see R. Heffner and Heffner 1990c).

In summary, a comparison of the high-frequency hearing abilities of mammals with the spectra of their vocalizations indicates that many mammals, including humans, hear higher than necessary for perceiving their vocalizations. This suggests that although some mammals use high frequencies for communication, the main source of selective pressure for the development of mammalian high-frequency hearing lies elsewhere.

6.2.2 Size of Auditory Apparatus

Crucial to an understanding of the high-frequency hearing ability of mammals is the analysis of the response properties of the mammalian ear and how
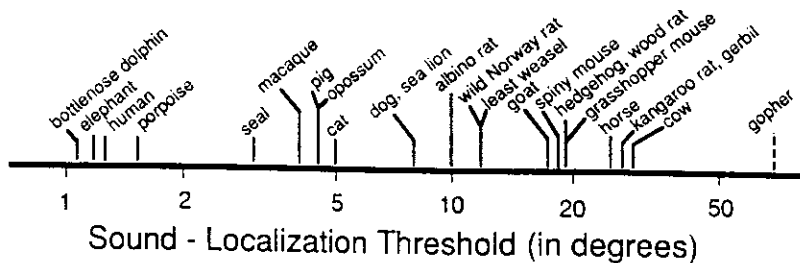
FIGURE 34.9. Variation in acuity for sound localization in the horizontal plane. (The threshold for the Gopher is indicated with a dashed line because it could not be tested using brief stimuli as were all other species.)

these vary between species. One factor believed to be important in the transduction of high-frequency sounds is the size of the various components of the ear. For example, the mass of the middle ear bones, their lever ratios, the volume of the bulla, the area of the tympanic membrane, the length of the basilar membrane, and the number of turns in the cochlea could all selectively enhance or inhibit the reception or transduction of sounds of different frequencies (e.g., Webster 1966; Ehret 1977; Fleischer 1978; Plassmann and Brandle, Chapter 31; Webster and Webster 1984; West 1985). Unlike the previous two factors which ask why mammals hear high frequencies, analysis of the relation between size and frequency response attempts to determine how mammals hear sound.

Because mammals vary in their ability to hear high frequencies, it follows that there must be some anatomical correlates of this functional variation. Because size is an important factor in determining frequency response, it would be expected to be correlated with high-frequency hearing. Furthermore, it is possible that the size of an animal's head may indeed restrict the size of the auditory apparatus thus limiting its hearing range.

However, there are several reasons for believing that the high-frequency hearing of mammals is not simply a function of allometric scaling. First, large animals can always evolve small ears and small animals can, within limits, increase the size of their ears—witness kangaroo rats and gerbils with bullae that can equal the volume of the braincase (e.g., Webster and Webster 1984; Webster and Plassman, Chapter 31). Second, despite the range in size of birds, from small finches to large owls, their high-frequency hearing ability does not vary with the size of the animal (cf. Dooling 1980).

Finally, it seems unlikely that a major sensory attribute such as hearing range is under little or no selective pressure from the environment, but simply varies passively as a function of the physical size of the peripheral auditory apparatus. Instead, it seems more likely that such variation is the result of differences in selective pressure for high-frequency hearing.

7. Evolution of Horizontal Sound-Localization Acuity

Over the years a number of studies have determined the ability of mammals to localize sound. The results of these studies have demonstrated that the sound-localization acuity of mammals as measured by the ability to discriminate sound sources located around the midline in the horizontal plane is far from uniform. As shown in Figure 34.9, midline sound-localization acuity varies from about 1° in humans, elephants, and porpoises to more than 20° in horses and gerbils with at least one species, the pocket gopher, unable to localize brief sounds.

In attempting to account for this variation, a number of ecological and morphological factors have been examined. 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, none of these have proven particularly satisfying; some, such as predator vs prey, are difficult to quantify and all appear to have major exceptions.

Of the many possible explanations, two deserve closer scrutiny. The first is the role of the availability of locus cues in determining sound-local-

ization acuity. The sound is the relation of hearing to vision.

7.1 Availability of Binaural Cues

At one time it was generally believed that all mammals were under strong selective pressure to localize sound as accurately as possible (e.g., Masterton and Diamond 1973). Were this true, then, the main source of variation in sound-localization acuity would be the size of the physical cues available to each animal. Because the magnitude of the binaural locus cues is largely determined by interaural distance, it was expected that any variation in localization acuity would be correlated with interaural distance. Indeed, given the limited data available as recently as 1980, this appeared to be the case: Humans with their large interaural distances were the most accurate localizers, monkeys and cats with intermediate interaural distances were somewhat less accurate, and rats with the smallest interaural distances were least accurate (Fig. 34.10A). The fact that the dolphin with its small functional interaural distance (as a result of underwater hearing and the transmission of sound though its jaw) was also accurate could be attributed to auditory specializations resulting from its use of sonar.

As more species were tested it became apparent that a large interaural distance did not automatically result in good localization acuity. This was particularly true in the case of horses and cattle which, despite their large heads, have poorer acuity than many small rodents (H. Heffner and Heffner 1984; R. Heffner and Heffner 1986b). Furthermore, although a small interaural distance may be a limiting factor in acuity, some small species possess relatively good acuity when compared to many other species with equal or larger interaural distances (e.g., the least weasel and the grasshopper mouse; R. Heffner and Heffner 1987, 1988d).

The relation between head size (functional interaural distance) and sound-localization threshold among all mammals tested to date is illustrated in Figure 34.10B. The correlation coefficient (excluding the echolocating dolphin) is currently -0.57 which, although statistically reliable ($p < 0.01$), accounts for only 32% of the variance. As a result we can no longer accept the notion that all species are under equal selective pressure to localize accurately and that the variation in sound-localization acuity simply reflects the availability of locus cues.

7.2 The Relation to Vision

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 toward a sound source (Pumphrey 1950). Indeed, this reflex is faster and more accurate than the visual orienting reflex to a brief flash of light (Whittington et al. 1981). Furthermore, there appears to be some correspondence between brainstem nuclei involved in sound localization and those responsible for eye movement (Irving and Harrison 1967). Given the existence of this close relationship between sound localization and vision, the possibility arises that the degree of sound-localization acuity might be related to some aspect of vision (R. Heffner and Heffner 1985).

In searching for a relation between vision and sound-localization acuity, we have considered several possibilities. Among them are visual acuity and the size of the binocular and panoramic visual fields. However, the one visual parameter that seems to correlate best with sound-localization acuity is the size of the field of best vision.

When visually orienting to a sound, it is not simply the head or the eyes that are directed to the source of the sound, but the part of the visual field with the best visual acuity, that is, the "area centralis." In species such as humans, the area of best vision, i.e., the fovea, subtends an angle of only 1 to 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. 34.11; for a review of retinal variation, see Hughes 1977). Species with progressively larger fields of best vision, therefore, should require correspondingly less precision in order to orient so that the sound-producing object is placed within their field of best vision. Thus, if the major source of selective pressure for sound localization in mammals is the need to visually locate the source of a sound, then we
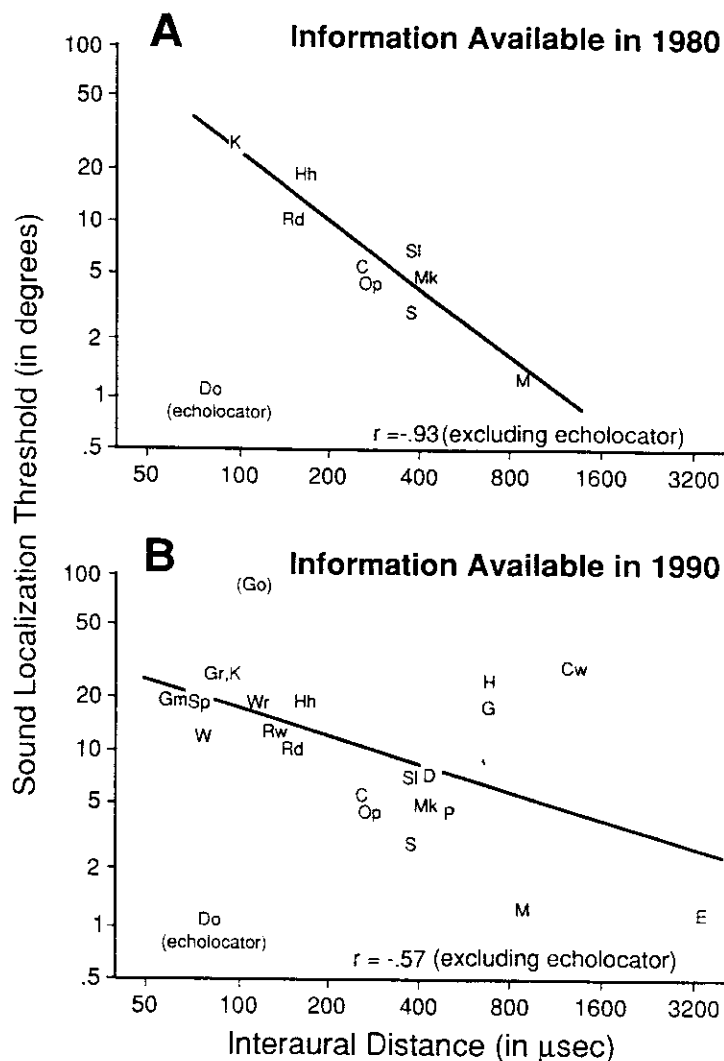
FIGURE 34.10. (A) Relation between functional inter-aural distance and sound-localization acuity among the eight species of mammals for which behavioral thresholds had been published in 1980; note the strong relationship with the exception of the echolocating dolphin. (B) The relationship as it stands with the information available in 1990; with the addition of 12 new species, interaural distance no longer seems to be a useful explanatory factor. C-domestic cat (*Felis catus*) (R. Heffner and Heffner 1988a), Cw-domestic cow (*Bos taurus*) (R. Heffner and Heffner 1986b), D-domestic dog (*Canis familiaris*) (H. Heffner and Heffner 1984), Do-dolphin in water (*Tursiops truncatus*) (Renaud and Popper 1975), E-elephant (*Elephas maximus*) (R. Heffner and Heffner 1982), G-domestic goat (*Capra hircus*) (R. Heffner and Heffner 1986b), Gm-grasshopper mouse (*Onychomys leucogaster*) (R. Heffner and Heffner 1988d), Go-gopher (*Geomys bursarius*) (R. Heffner and Heffner 1990b), Gr-gerbil (*Meriones unguiculatus*) (R. Heffner and Heffner 1988c), H-domestic horse (*Equus caballas*) (H. Heffner and Heffner 1984), Hh-hedgehog (*Paraechinus hypomelas*) (H. Heffner and Heffner 1984), K-kangaroo rat (*Dipodomys meriami*) (H. Heffner and Masterton 1980), M-man (R. Heffner and Heffner 1988a), Mk-macaque (*Macaca nemestrina* and *M. mulatta*) (Brown et al. 1980), Op-opossum (*Didelphis virginiana*) (Ravizza and Masterton 1972), P-domestic pig (*Sus scrofa*) (R. Heffner and Heffner 1989), Rd-domestic rat (*Rattus norvegicus*) (Kelly and Glazier 1978), Rw-wild rat (*Rattus norvegicus*) (H. Heffner and Heffner 1985b), S-harbor seal in air (*Phoca vitulina*) (Terhune 1974), Sl-sea lion (*Zalophus californianus* (Moore 1975), Sp-spiny mouse (*Acomys cahirinus*) (Mooney, unpublished Master's thesis), W-least weasel (*Mustela nivalis*) (R. Heffner and Heffner 1987), Wr-wood rat (*Neotoma floridana*) (H. Heffner and Heffner 1984). The threshold for the pocket gopher (Go) is for a 1.5-sec noise burst as this animal, unlike the other mammals in this figure, is unable to localize brief sounds.
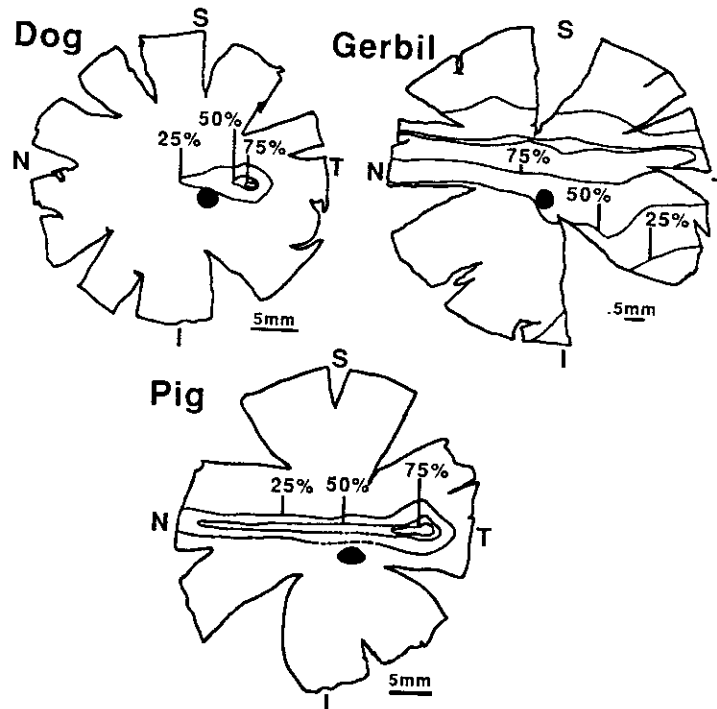
FIGURE 34.11. Ganglion cell density contours in three mammals showing the contour lines encompassing densities 25%, 50%, and 75% of the maximum density for each species. "Area centralis" is operationally defined as the part of the retina containing ganglion cells with packing densities equal to or greater than 75% of maximum. The dog has a small area centralis whereas the gerbil, with its visual streak, has a broad area centralis. 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 1988e.)

would expect sound-localization acuity to be closely correlated with the size of the area centralis.

In order to determine the correlation between sound-localization acuity and size of the field of best vision, we have begun to obtain anatomical measures of the area centralis in animals for which sound-localization thresholds are available. Because the density of retinal ganglion cells is known to correspond to behavioral measures of visual acuity (e.g., Rolls and Cowey 1970), measuring the density of ganglion cells in retinal wholemounts (cf. Stone 1981) 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 area centralis.

Using an arbitrary definition of the area centralis 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 measured the size of the area centralis in 12 species. These measurements have shown that the size of the area centralis varies from approximately 1.5° in man to more than 180° in some species such as gerbils and cattle (cf. fig. 34.11). The relation between the width of the area centralis and sound-localization thresholds is shown in Figure 34.12. As indicated in this figure, the width of the area centralis is positively correlated with sound-localization threshold ($r = 0.91, p < 0.0001$). That is, animals with narrow fields of best vision, such as cat and man, have smaller thresholds (better sound-localization acuity) than those with broader fields of best vision, such as the cow and gerbil.

Although the present sample is small, it includes a broad range of species from five orders of mammals encompassing surface and underground dwellers, nocturnal 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 a small area centralis. 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.

8. Summary: Evolution of Mammalian Sound Localization

The evolution of mammals was accompanied by two events of particular relevance to sound localization. The first was the development of the three-ossicle middle ear which proved able to transduce frequencies beyond the 10-kHz range of nonmammalian vertebrates. The second was the appearance of the pinna which functions as the major source of monaural spectral cues for sound localization—cues that play a crucial role in preventing front–back reversals and in localizing in the vertical plane. The combination of these two anatomical events was fortunate as the pinna can provide reliable monaural spectral cues only if the ear is able to transduce high frequencies. Expanded high-frequency hearing also increased the magnitude of the binaural spectral-difference cue, especially for small mammals. Thus, we suggest that the use of monaural and binaural spectral cues served as major sources of selective pressure for the reception of frequencies above 10 kHz.

Primitive mammals thus had three basic locus cues – binaural time differences, binaural spectral differences, and monaural spectral differences, which they could use to their advantage as they expanded into new niches. In the case of echolocating bats, this expansion was spectacular as their hearing ability allowed them to move into the niche of nocturnal flying predators in which they are unchallenged.

In spite of the obvious survival value of sound localization, not all mammals are able to localize sound accurately. This variation in localization acuity is primarily due *not* to differences in the availability of the physical locus cues, but rather to variation in selective pressure for good acuity. One
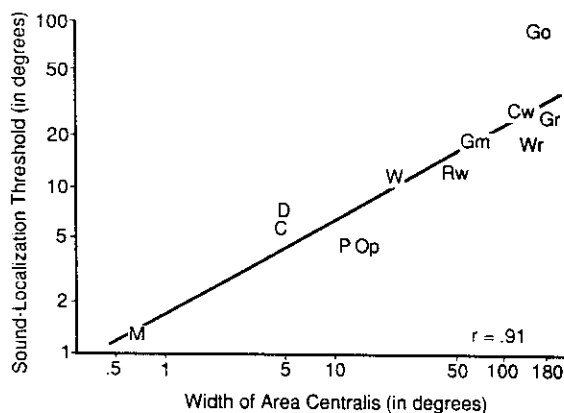

FIGURE 34.12. Relation between the horizontal width of the area centralis (i.e., the field of best vision) and sound localization acuity. Mammals with narrow fields of best vision, such as man, have small localization thresholds, whereas species with wide fields of best vision, such as some rodents and ungulates, have much larger localization thresholds. Letters represent different species (see Fig. 34.10 for key).

of the major uses of sound localization is to enable an animal to direct its gaze to the source of a sound for further scrutiny. Because animals with narrow fields of best vision require more accurate localization to direct their gaze than do animals with broad fields of best vision, sound-localization acuity varies with the size of the field of best vision or area centralis. Apparently it is the *function* of sound localization, i.e., directing the attention of other senses toward the sound-producing object, and not simply the physical cues available to the auditory system, which underlies the variation in mammalian sound-localization acuity.

Moreover, not all mammals have retained full use of the sound-localization cues. There are species that have partially or completely relinquished one or more of the major cues. The ability to use binaural time cues has been lost by some small mammals for reasons that are not yet fully understood. Reliance on the binaural spectral-difference cue has also been reduced or eliminated by some large animals – this may have occurred because the high-frequency components of sounds may not be audible in the ear furthest from the source (with the result that no "difference" cue is available), coupled with the fact that the large binaural time

differences available to them provide for sufficient localization acuity. Finally, monaural spectral cues may have been relinquished by aquatic mammals that have lost their pinnae as they adapted to a marine environment. However, all of the locus cues appear to have been relinquished by at least some of the fossorial mammals that have adapted to the one-dimensional world of an underground environment where sound-localization ability may be of little value.

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