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CHAPTER NINETEEN

AUDITION

Henry E. Heffner and Rickye S. Heffner

Introduction

Fifty years ago, a general review of auditory research could be accomplished in four chapters (Stevens, 1951); today, one review has grown to fourteen volumes with more on the way (Springer Handbook of Auditory Research, R.R. Fay and A.N. Popper, series editors). The growth of auditory research has come about because more areas of neuroscience have been applying their techniques to understanding the neurological basis of hearing. Although a complete understanding requires a multidisciplinary approach, it is often the case that researchers know little about important issues in closely related disciplines—a problem that is becoming widespread in neuroscience (Cahill, McGaugh, & Weinberger, 2001). This problem has been compounded by an emphasis on recent research, giving those new to the field the impression that there is little to be learned from older work (e.g., Moore, Rothholtz, & King, 2001).

One area of auditory research that impinges on all others is the behavioral study of hearing in animals. Because all anatomical and physiological models of auditory processing must eventually be related to behavior, and because virtually all such models are based on animal research, it is obviously necessary to know the hearing abilities of animals. Furthermore, it should be possible to test the validity of such models by studying the effects of central nervous system lesions on hearing, i.e., ablation/behavior experiments.

The purpose of this chapter is to describe two lines of behavioral research: The first is the comparative study of mammalian hearing, that is, the determination of *what* mammals hear and *why* they hear as they do. The second is the study of auditory cortex using the ablation/behavior approach. In doing so, we will highlight issues to be considered when interpreting and applying this research.

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Comparative Study of Mammalian Hearing

The first comparative studies of hearing were conducted in the 19th century by Francis Galton, who used specially constructed whistles to determine the unconditioned responses of animals to high-frequency sounds (Galton, 1883). Galton made several discoveries that have since been supported by modern research, such as that cats have particularly good high frequency hearing and human high-frequency hearing ability declines with age. However, he incorrectly concluded that large dogs could not hear high frequencies, because, unlike small dogs, they showed no reaction to his whistles (H. E. Heffner, 1983). Thus, he was unable to distinguish the inability to hear a sound from the failure to respond to it, although he was well aware of such a possibility. This is the problem with using a simple startle reaction as a test of hearing.

Modern comparative studies of mammalian hearing have focused on the basic auditory abilities of detection, localization, and frequency discrimination. (Interest in the ability to perform more complex auditory discriminations is growing, e.g., Dooling & Hulse, 1989). Before turning to what we know about these basic abilities, it is important to consider how they are measured.

Behavioral measurement of hearing

A number of behavioral procedures for determining the sensory abilities of animals were available by the late 1960's (e.g., Stebbins, 1970). These, along with the use of precision instruments for presenting and measuring sound, made it possible to use conditioning techniques to determine the behavioral hearing abilities not only of mammals, but birds and fish as well (Klump, Dooling, Fay, & Stebbins, 1995). Reptiles, on the other hand, have proven virtually impossible to condition to sound (for an exception, see Patterson, 1966), although they readily learn to make visual discriminations (e.g., Burghardt, 1977). Similarly, no conditioning procedures have been developed for amphibians, although the use of startle reflex modification techniques and the natural tendency of females during mating season to approach the sound of a male have been used to study some aspects of hearing in frogs (e.g., Klump et al., 1995). The fact that amphibians and reptiles do not readily learn to respond to sound suggests that they may lack the neurological mechanisms for doing so.

Some conditioning procedures are better than others. The better ones not only reward an animal for correctly responding to a sound, but they also have good control over responses in the absence of that sound. In the language of signal detection theory, this means that “hits” are sufficiently rewarded and “false positives” are kept under control. A good procedure should also be easy for an animal to learn and should allow their heads to be fixed in the sound field so that the stimulus reaching their ears can be specified with some precision. One procedure that meets these requirements is “conditioned suppression” in which an animal is trained to place its mouth on a spout in order to receive water (or food), and to break contact with that spout whenever a stimulus is presented that signals impending shock (H. E. Heffner & Heffner, 1995a). By carefully

adjusting the reward rate and shock intensity, it is possible to optimize an animal's performance—that is, to maximize its hit rate and minimize its false positive rate. Animals are capable of learning the basic avoidance response within a session or two and the response of placing its mouth on a spout fixes the animal's head within the sound field. Although procedures that use positive reward with a delay or "error time out" as a punisher may work well in some cases, comparisons have shown that shock is a more effective punisher and the combined use of positive reward and shock generally gives better results (e.g., H. E. Heffner & Heffner, 1984).

In a hearing test, sounds are presented to an animal either from a loudspeaker or through headphones. Although headphones make it possible to test each ear separately, problems may arise in calibrating the sound (e.g., Pfingst, Hienz, & Miller, 1975; Zhou & Green, 1995). Moreover, headphones bypass the external ear and thus will not reflect the contribution of the pinae to hearing. Thus, for comparative studies, sounds are best presented from a loudspeaker located in front of the animal in an acoustic environment that minimizes sound reflections, i.e., a free-field (Larsen, 1995).

In measuring an animal's performance, it is necessary to correct its hit rate for false positives (e.g., H. E. Heffner & Heffner, 1985; 1995a). One way to do this is to reduce the hit rate in proportion to the false positive rate using the formula: "Corrected Hit rate = Hit rate ! (Hit rate H False Positive rate);" this formula is sometimes expressed as "Hit rate H (1 ! False Positive Rate)." Another way to correct for false positives is to calculate an animal's percent correct using the formula: "(Hit rate + (1 ! False Positive rate))/2;" note that 1 ! False Positive rate is known as the "correct rejection rate." The threshold for a particular discrimination is then defined as the stimulus that gives a corrected hit rate of .50 or a percent correct of 75%. Experience has shown that thresholds defined in this way remain stable over a range of false positive rates.

Although it has been claimed that performance should be specified using a signal detection measure such as *d'* or *A'* (e.g., Penner, 1995), there are at least two reasons for avoiding such measures when working with animals. First, the values generated by these calculations are non-intuitive and cannot be interpreted without additional information. For example, a corrected hit rate of 50% means that the animal is capable of detecting a signal half of the time and conveys more information than the statement that its *d '* is 2.33 or 1.64 (which are the *d'* values for a 50% hit rate with 1% and 5% false alarm rate, respectively). Second, it is sometimes assumed that one can use such measures to obtain useful information when an animal has a high false positive rate. However, a high false positive rate (e.g., >25%) may indicate that the animal is not carefully attending to the stimulus and is attempting to perform the task by guessing, a situation in which signal detection measures do poorly (Green, 1995).

Detection of sound

The most basic measure of hearing is an animal's *behaviorally-determined* sensitivity to pure tones throughout its hearing range, i.e., its audiogram. Although electrophysiological estimates of absolute sensitivity may be of interest in their own right, they do not accurately reflect behavioral sensitivity. This applies to such

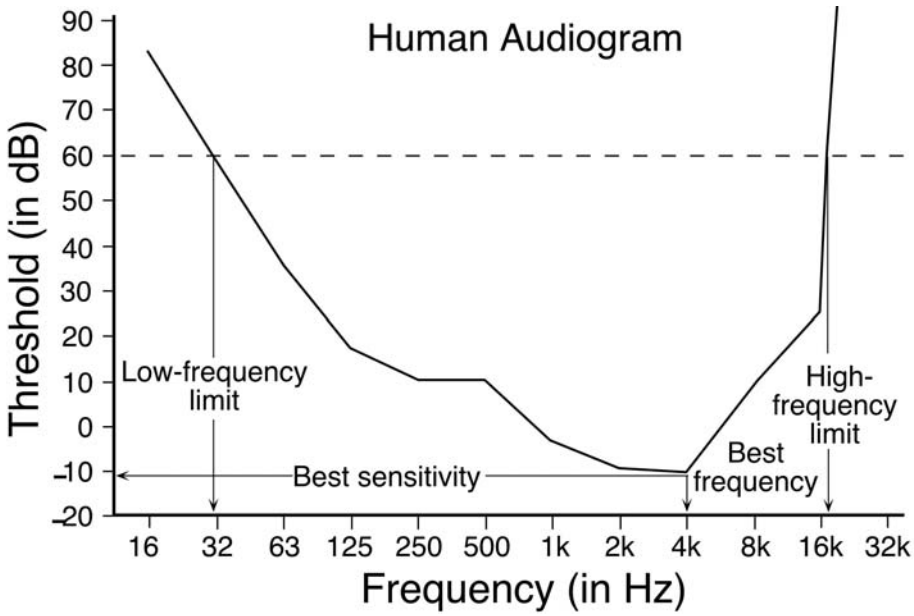

Figure 19.1 Human audiogram illustrating the 60-dB high- and low-frequency hearing limits, best frequency, and best sensitivity. (Adapted from H.E. Heffner & R. S. Heffner, 1992, with permission.)

electrophysiological measures as the cochlear microphonic, thresholds of inferior colliculus neurons, and the auditory brainstem response (see below).

The audiograms of animals are compared on the basis of the following features: high- and low-frequency hearing limits, frequency of best hearing, and best sensitivity (Figure 19.1). Of these measures, the high- and low-frequency hearing limits have proven to be the most interesting. Note that these are defined as the highest and lowest frequencies audible at a particular intensity level.

High-frequency hearing. Mammals differ from other vertebrates in that virtually all of them hear well above 10 kHz, which is the upper limit for birds. Reptiles, amphibians, and fish (with some exceptions) do not hear above 5 kHz (H. E. Heffner & Heffner, 1998). Those few mammals that do not hear above 10 kHz, (i.e., subterranean mammals) are considered to have degenerate hearing (R. S. Heffner & Heffner, 1993).

High-frequency hearing ability varies between different species of mammals—the 60-dB high-frequency hearing limit ranges from 5.9 kHz for the blind mole rat (a subterranean rodent) to over 100 kHz for some bats and porpoises, a range of more than 4.5 octaves (H. E. Heffner & Heffner, 1998). There is substantial evidence that high-frequency hearing evolved in mammals primarily for the purpose of localizing sound; although some species also use high-frequency communication calls, and bats also use their high-frequency hearing for echolocation, these appear to be secondary adaptations.

The existence of variation in the high-frequency hearing of mammals came to the attention of the late R. Bruce Masterton in 1967 when he noticed that smaller mammals generally had better high-frequency hearing than larger ones. Because he was studying

sound localization at the time, he realized that this observation had implications for the use of the two binaural sound-localization cues: the difference in the time of arrival of a sound at the two ears ( ) *t*) and the difference in the frequency-intensity spectra of the sound reaching the two ears (*)fi*). Noting that the magnitude of the *)t* cue decreases with the size of an animal's head, he suggested that the smaller an animal's head, the more dependent it would be on the *)fi* cue (Masterton, Heffner, & Ravizza, 1969). However, for an animal to use the *)fi* cue, it would need to hear frequencies high enough to be effectively shadowed by its head and pinnae because small heads do not block lower frequencies as effectively as large heads. Therefore, the smaller an animal's *maximum ªt* (the time it takes for sound to travel around the head from one ear to the other), the higher it must hear to adequately localize sound.

The relationship between maximum *)t* (sometimes called *functional head size*) and high frequency hearing has proven to be robust *(r* = !0.79, *p* <0.0001) and has been shown to hold for over 60 animals (R. S. Heffner, Koay, & Heffner, 2001a). The only modification to this theory has been the realization of the importance of high-frequency hearing for pinna cues as well as for *)fi*. Over the years, the work of Bob Butler and others has demonstrated that the directionality of the pinna not only provides effective cues for localizing sound in the horizontal plane, but it also provides the primary cues for vertical localization and for preventing front-back confusions (e.g., Butler, 1975; Musicant & Butler, 1984). For pinna cues to be effective in humans, the sounds must contain frequencies above 4 kHz and even sounds as high as 15 kHz have been shown to be necessary for optimal localization performance. Thus, the upper two octaves of human hearing (from 4-16 kHz) appear to be used primarily, if not exclusively, for sound localization as they are not necessary for the perception of speech. As with the *)fi* cue, the smaller the pinnae, the higher an animal must hear in order to extract pinnae cues for sound localization.

The importance of high-frequency hearing for sound localization is also supported by two lines of experimental evidence. First, filtering out high frequencies from a signal has been shown to degrade sound localization performance in monkeys, humans, horses, chinchillas, and mice (Brown, 1994; Butler 1975; H. E. Heffner & Heffner, 1983; R. S. Heffner, Heffner, & Koay, 1995: R. S. Heffner, Koay, & Heffner, 2001b). Thus, mammals require high-frequency hearing to localize sound using either the *)fi* locus cue, pinna cues, or both. Second, it appears that subterranean animals that are adapted to the one-dimensional world of an underground habitat have little use for sound localization and are therefore released from the selective pressure to hear high frequencies. Thus, the pocket gopher, naked mole rat, and blind mole rat do not localize sound and have lost their high-frequency hearing as well as their pinnae (R. S. Heffner & Heffner, 1990; 1992b; 1993). In short, sound localization and high-frequency hearing go hand-in-hand in mammals. Mammals cannot adequately localize sound without high frequencies and those that relinquish the ability to localize sound also give up their high frequency hearing.

Low-frequency hearing. The variation in mammalian low-frequency hearing is even greater than that for high-frequency hearing. Indeed, the 60-dB low-frequency limit for mammals extends from 17 Hz (the Indian elephant) to 10.3 kHz (the little brown bat), a

range of over nine octaves. Analysis of this variation has resulted in two findings. First, mammals appear to fall into two groups: those that hear below 125 Hz and those that do not. Second, low-frequency hearing varies with high-frequency hearing (R. S. Heffner, et al. 2001a).

Figure 19.2 shows the distribution of 60-dB low-frequency hearing limits for mammals (underwater audiograms have been excluded because of the difficulty in equating air and water thresholds). Of the 59 species, 38 have low-frequency hearing limits below 125 Hz while 20 species have low-frequency hearing limits above 500 Hz. Only one species falls within the two-octave gap from 125 to 500 Hz, the subterranean pocket gopher (an animal with degenerate hearing).

We have suggested that the two groups may differ in the mechanisms they use to perceive the pitch of low-frequency sounds (R. S. Heffner et al., 2001a). Briefly, there are two different neural mechanisms that may underlie the perception of pitch (for a recent description, see Moore, 1993). In one, frequency is encoded by temporal mechanisms based on phase locking; this mechanism is limited to low frequencies because phase locking declines as frequency increases. In the second, higher frequencies are encoded by a place mechanism in which tones of different frequencies excite hair cells and fibers at different locations along the basilar membrane. However, the actual frequencies over which either the temporal or the place mechanism is dominant are not agreed upon. Some observations suggest that the upper limit of the temporal mechanism for the perception of pitch is around 4-5 kHz (e.g., Moore, 1993). However, other observations, such as studies of the perception of the pitch of click trains and psychophysical studies of patients with cochlear implants, suggests that temporal coding extends up to only about 300 Hz (Flanagan & Guttman, 1960; Shannon, 1983). Because this latter upper limit corresponds to the 125-500 Hz gap in mammalian low-frequency limits, it suggests that the animals that do not hear below 500 Hz are not using temporal coding for pitch perception. Thus, animals that hear below 125 Hz may be using both temporal and place mechanisms whereas those that do not hear below 500 Hz may be using only the place mechanism.

Various factors, such as body size, phyletic lineage, and lifestyle have been examined in an attempt to explain the variation in low-frequency hearing. So far, the only factor found to be reliably correlated with low-frequency hearing is high-frequency hearing—that is, animals with good high-frequency hearing generally have poor low-frequency hearing (R. S. Heffner et al., 2001a). The degree to which high- and low-frequency hearing are related differs for the two groups of mammals: among those that do not hear below 500 Hz, $r = .691$ ($p = .0015$), whereas for those that hear below 125 Hz, $r = .567$ ($p = .0006$). In either case, high-frequency hearing accounts for considerable variance in low frequency hearing for both groups, suggesting that it may provide a clue for understanding some of the variation in low-frequency hearing.

The existence of such a relationship suggests that good high- and low-frequency hearing are incompatible. One possibility is that there is some anatomical limitation that prevents the mammalian ear from encoding both high and low frequencies. However, there are several species with good high- and low-frequency hearing, including the chipmunk (39 Hz to 52 kHz), least weasel (50 Hz to 60 kHz), bushbaby (92 Hz to 65 kHz), and domestic cat (55 Hz to 79 kHz), suggesting that any anatomical constraints that

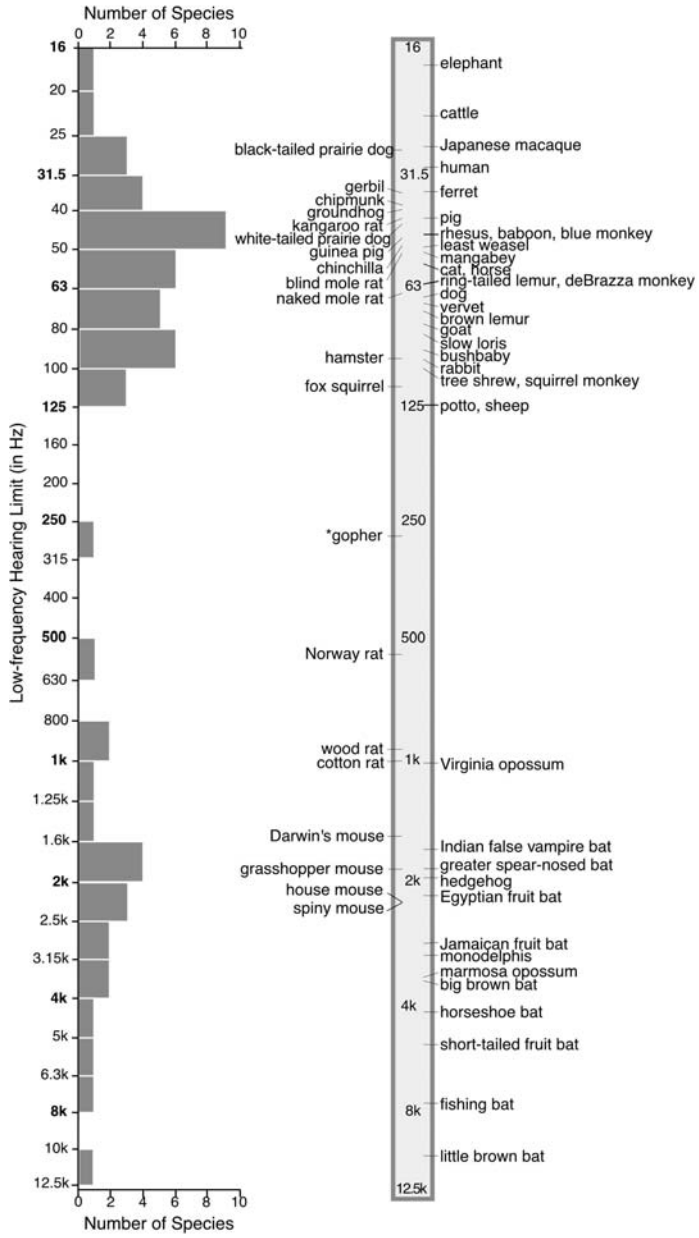

Figure 19.2 Distribution of mammalian low-frequency hearing limits (lowest frequency audible at 60 dB). Note that low-frequency hearing limits fall into two distinct groups with a gap between them at 125 to 500 Hz. Rodents (shown on the left side of the bar) are the only order with members in both groups. (Data from R. S. Heffner et al., 2001a.)
* Note that only the subterranean gopher, which has vestigial high-frequency hearing, falls into the gap between 125 and 500 Hz. Bin width of the histogram is 1/3 octave.

might exist can be overcome. Another possibility is that good low-frequency hearing could be disadvantageous in situations where low-frequency sounds interfere with the analysis of high-frequency sounds. For example, we have noted that animals often localize high-frequency noise slightly more accurately than broadband noise (R. S. Heffner et al., 1995). This suggests that mammals may restrict their low-frequency hearing to prevent the low-frequency component of sounds from interfering with the analysis of the high frequency components needed for sound localization.

Localization of sound

At one time it was believed that all mammals were under selective pressure to localize sound as accurately as possible and that the only factor limiting their accuracy was the availability of the locus cues (as determined by head size). However, it is now clear that animals localize sound only as accurately as is necessary to direct their eyes to the source of a sound. Moreover, an animal may relinquish one or more of the sound localization cues, or even the entire ability to localize sound, if it is not needed for survival.

Measuring sound localization ability. There are two ways to measure sound localization ability. One is to have the subject point in the direction from which a sound appeared to come and measure the *accuracy* of pointing. The other is to have the subject discriminate between two sound sources, bringing the sources closer together until they can no longer be discriminated, a procedure that measures localization *acuity*.

Accuracy of sound localization can be measured by training an animal to orient its head towards the source of a sound. This procedure is commonly used with owls as they have a strong natural orientation response to sound that can be maintained with food reward (e.g., Wagner, 1995). Among mammals, only cats have been successfully trained to orient to the source of a sound (e.g., Populin & Yin, 1998). Most mammals do not reliably point their head to a sound source and there are several reasons why this may be: First, their visual fields may be so broad that they do not need to turn their heads much to see the sound source; second, they may be able to turn their eyes instead of their head; and finally, their natural response to an unexpected sound may be to freeze.

One way to measure localization acuity is to train an animal to discriminate between two sound sources by walking to the source of a sound to receive a reward (e.g., Neff, Diamond, & Casseday, 1975; Thompson, Heffner, & Masterton, 1974). Another common method is to have the animal discriminate between two sound sources by responding when a sound comes from one location but not another (e.g., Brown, 1994; H. E. Heffner & Heffner, 1984). Using the conditioned suppression task, an animal can be trained to maintain contact with a water spout to receive water while a sound is presented from one location and to break contact to avoid a mild electric shock when the sound comes from a different location. In either case, the angle of separation between the two sound sources is then reduced until the animal is no longer able to discriminate between the two sources.

Both accuracy (pointing) and acuity (discrimination) measures give essentially the same results. However, fine-grain comparisons of the two procedures are complicated because accuracy is measured in terms of how much the subject's estimate of location differed from true location whereas acuity is measured in terms of "minimum audible angle," i.e., the smallest angle that can be discriminated (for a recent comparison of the two procedures, see Recanzone, Makhamra, & Guard, 1998). However, minimum audible angle is a better comparative measure of sensory ability because it is not confounded by species differences in the ability to point.

The most common sound-localization measure is the minimum audible angle for a left-right discrimination, in which the animal is trained to discriminate two sound sources located in front of and centered on its midline. The standard stimulus is a 100-ms broadband noise burst, which is too brief to be tracked or scanned, but that contains both high and low frequencies, thus permitting the use of all three sound-localization cues: binaural time difference ( )*t*), binaural frequency-intensity spectral difference ( )*fi*), and pinna cues.

In addition to determining acuity around midline, minimum audible angle can be determined for locations off to the side, including centering the sound sources on the interaural axis (i.e., front-back localization) and for vertically separated sound sources (elevation). Both the front-back and vertical-localization tests measure the ability of an animal to localize in situations where the pinnae provide the primary cues for discriminating locus.

In testing an animal's ability to discriminate two sound sources, it can be difficult to obtain loudspeakers that are perfectly matched for broadband noise. As a result, an animal may shift from discriminating locus to discriminating the quality differences in loudspeakers when the angle of separation is too small to distinguish locus. This problem can be avoided by using several pairs of loudspeakers during a session, by randomizing the intensity of the sound, and by not testing at subthreshold angles for extended periods. However, the crucial test of whether an animal is discriminating sounds on the basis of locus, as opposed to speaker quality, is to demonstrate that there is some small angle at which the animal performs at chance—it is not sufficient to assume that performance would fall to chance if both speakers were placed at 0E.

Variation in sound localization acuity. When early sound-localization studies showed that humans and elephants have better sound-localization acuity than cats and dogs, which in turn have better acuity than rats, it was naturally assumed that the large binaural cues generated by large heads were necessary for good localization. This belief was abandoned when it was subsequently discovered that horses and cattle have poorer acuity than rats (R. S. Heffner & Heffner, 1992a).

Midline sound localization thresholds have been obtained for over 30 different species of mammals, from mice to elephants (H. E. Heffner & Heffner, 1998; R. S. Heffner, Koay, & Heffner 2001b). Thresholds range from about 1E for humans and elephants to more than 20E for horses and cattle, and over 30E for house mice with the subterranean rodents (gopher, blind mole rat and naked mole rat) being unable to localize brief sounds (see Table 19.1)

Table 19.1 Sound localization acuity and use of binaural cues in mammals

Species	Midline Acuity	Binaural Phase Cue	Binaural Intensity Cue
Indian elephant	1.2E	yes	yes*
Human	1.3E	yes	yes
Harbor seal	3.2E	----	----
Domestic pig	4.5E	yes	no
Virginia opossum	4.6E	----	----
Domestic cat	5.2E	yes	yes
Squirrel monkey	5.9E	----	----
Japanese macaque	6.8E	yes	yes
Dog	8.0E	----	----
Sea lion	8.8E**	----	----
Jamaican fruit bat	9.9E	yes	yes
Greater spear-nosed bat	10E	no	yes
Egyptian fruit bat	11.6E	yes	yes
Ferret	11.8E	----	----
Least Weasel	12E	yes	yes
Norway rat	12.2E	no***	yes
Fox squirrel	14E	yes	yes
Big brown bat	14E	no	yes
African pigmy hedgehog	14.3E	no	yes
Short-tailed fruit bat	14.5E	no	yes
Chinchilla	17.5E	yes	yes
Domestic goat	18E	yes	yes*
Hamster	18.8E	----	----
Spiny mouse	18.9E	no	yes
Desert hedgehog	19E	no	yes
Wood rat	19E	----	----
Grasshopper mouse	19.3E	no	yes
Domestic rabbit	22.3E	----	----
Horse	25E	yes	no
Cottontail rabbit	27E	----	----
Gerbil	27E	yes	yes
Merriam's kangaroo rat	27E**	yes	yes
Groundhog	27.8E	yes	yes
Domestic Cattle	30E	yes	no
Black-tailed Prairie dog	32.8E	yes	yes
Eastern chipmunk	33E	yes	yes
House mouse	33E	no	yes

Dashes indicate no data.

*Unable to use binaural intensity cue in the upper octaves of its hearing range.

**Localization tested with clicks. For all other animals, the stimulus was broadband noise.

***Wesolek, C.M. (2004). The inability of the laboratory rat (*Rattus norvegicus*) to use the binaural phase cue to localize sound. Unpublished Masters Thesis. University of Toledo (added after publication).

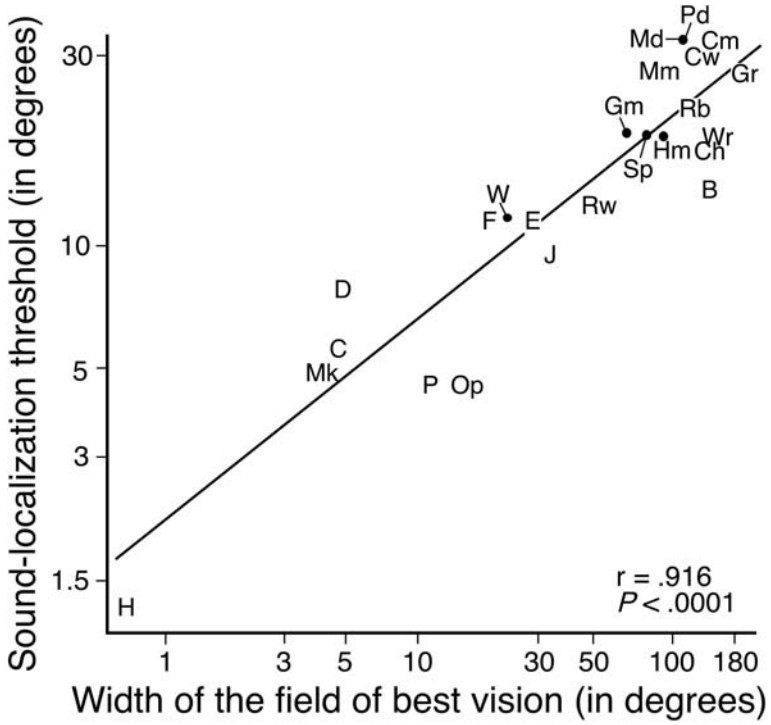

Figure 19.3 Relationship between the width of the field of best vision and sound-localization threshold. The field of best vision is defined anatomically as the area of the retina containing ganglion-cell densities at least 75% of maximum. Species with narrow fields of best vision have better localization acuity (smaller thresholds) than species with broad fields of best vision. **B**, big brown bat; **C**, domestic cat; **Ch**, chinchilla; **Cm** chipmunk; **Cw**, cow; **D**, dog; **E**, Egyptian fruit bat; **F**, ferret; **Gm**, grasshopper mouse; **Gr**, gerbil; **Hm**, hamster; **J**, Jamaican fruit bat; **M**, man; **Md**, domestic mouse; **Mk**, Japanese macaque; **Mm**, marmot; **Op**, Virginia opossum; **P**, domestic pig; **Pd**, prairie dog; **Rb**, domestic rabbit; **Rw**, wild normal rat; **Sp**, spiny mouse; **W**, least weasel; **Wr**, wood rat. (Data from R. S. Heffner et al., 2001c).

The explanation for the variation in mammalian sound localization acuity lies in the fact that the primary function of sound localization is to direct the eyes to the source of a sound (R. S. Heffner & Heffner, 1992c). Just how accurate sound localization must be to direct the eyes depends on the width of an animal's field of best vision. Animals with narrow fields of best vision, such as humans, require good sound-localization acuity to direct their gaze so that the image of the sound source falls upon their field of best vision (e.g., the human fovea), whereas animals with broad fields, such as those with visual streaks, do not require as high a degree of sound-localization acuity to direct their gaze.

The relationship between the width of the field of best vision (estimated from retinal ganglion cell densities) and sound-localization acuity is shown in Figure 19.3. This figure

illustrates that mammals with narrow fields of best vision are more accurate localizers than mammals with broader fields (r = .916). The close relationship between vision and sound localization is further supported by the observation that the subterranean rodents, which are adapted to living in dark burrows where visual scrutiny of sound sources is not possible, have lost virtually all of their ability to localize sound.

Use of binaural locus cues. Mammals vary not only in sound localization acuity, but also in their use of binaural time ($)t$) and binaural spectral ($)fi$) locus cues. Whereas most mammals use both binaural cues, some use only one or the other. Animals that differ in their use of these cues should show corresponding differences in the physiology of their auditory systems.

The ability to use $)t$ and $)fi$ to localize sound can be determined two ways (e.g., R. S. Heffner & Heffner, 1992a). The first is to use headphones to present sounds separately to each ear and varying the relative time of arrival or intensity of the sound at the two ears. However, this test is can only be used with animals that can be fitted with headphones. The second method is to present pure tones from two loudspeakers located in front of the animal at a fixed angle of separation and determine its ability to localize low- and high-frequency pure tones. This test can be used with any animal and is based on the fact that low-frequency pure tones are localized using binaural time-difference cues whereas high frequencies are localized using binaural intensity-difference cues. Briefly, low-frequency pure tones that bend around the head with little or no attenuation can only be localized by comparing the time of arrival of the phase of each cycle of the tone at the two ears, the binaural phase difference cue being a subset of $)t$. However, the phase-difference cue becomes ambiguous for pure tones at high frequencies when successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears. The exact "frequency of ambiguity" depends on an animal's head size and the angle of the sound source relative to its midline—it is higher for smaller heads and sound sources closer midline (e.g., R. S. Heffner et al., 2001c). Pure tones above the frequency of ambiguity, then, must be localized using the binaural intensity-difference cue, a subset of $)fi$. Thus, the ability of an animal to use the two binaural cues can be measured by determining the ability to localize pure tones above and below the frequency of ambiguity.

Most studies of the use of binaural cues have determined an animal's ability to localize pure tones presented from loudspeakers placed 30E to the left and right of its midline. The results of these studies have shown that the majority of mammals are able to localize both low- and high-frequency pure tones, indicating that they can use both binaural phase- and binaural intensity-difference cues. However, some animals can use only one of these cues (Table 19.1). For example, horses and cattle can use binaural time, but not binaural intensity, whereas house mice and big brown bats use binaural intensity, but not binaural time. Finally, a few animals, such as the goat and Indian elephant use both cues, but are unable to use binaural intensity differences for frequencies in the upper octaves of their hearing ranges.

Another aspect of sound localization for which mammals show systematic differences is in the upper frequency limit for use of the binaural phase cue. As shown in

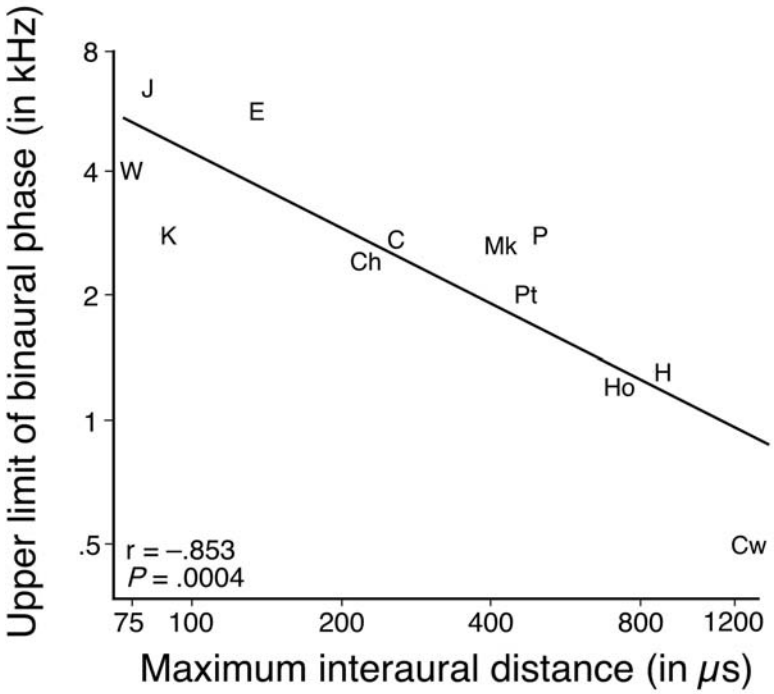

Figure 19.4 Relationship between maximum interaural distance and the highest frequency at which the use of the binaural phase-difference cue has been observed. Although the binaural phase-difference cue is physically available at higher frequencies for animals with smaller heads, the limits shown here represent an animal's behavioral upper limit, not physical availability. **C**, domestic cat; **Ch**, chinchilla; **Cw**, cow; **E**, Egyptian fruit bat; **H**, horse; **J**, Jamaican fruit bat; **K**, kangaroo rat; **M**, man; **Mk**, Japanese macaque; **P**, domestic pig; **Pt**, pig-tailed macaque; **W**, least weasel. (Modified from R. S. Heffner, et al., 2001c).

Figure 19.4, the upper frequency limit for the use of binaural phase spans a range of more than 3 octaves from the 500-Hz upper limit of cattle to the 6.3-kHz upper limit of the Jamaican fruit bat. Specifically, animals with small heads (small interaural distances) are able to use the binaural phase cue at higher frequencies than animals with larger heads. Although this relationship seems obvious because the phase-difference cue is physically available at higher frequencies for animals with smaller heads, it should be noted that the upper limits shown in Figure 19.4 are, in most cases, well below the frequency of ambiguity. Thus, they represent the ability of the animals' auditory systems to extract the binaural phase cue. Because using the binaural phase cue requires that auditory neurons fire in synchrony with the phase of the sine wave (i.e., phase lock), the variation in the upper limit for using binaural phase suggests that there is also variation in the upper limit of phase locking. Interestingly, the Jamaican fruit bat appears capable of phase locking up to at least 6.3 kHz, which is higher than the 5 kHz commonly listed as the upper limit for phase locking in the mammalian auditory system (R. S. Heffner et al., 2001c; Moore, 1997).

Discrimination of frequency

The ability to discriminate frequency has been determined for a small number of species (Fay, 1988). The most common procedure for obtaining frequency discrimination thresholds is to train an animal to discriminate between a standard tone and a comparison tone of higher frequency and then reducing the frequency of the comparison tone until the animal can no longer discriminate the two. Frequency discrimination thresholds are then obtained at frequencies throughout the animal's hearing range.

So far, comparison of the abilities of different species to discriminate frequency has not yielded any theoretical insight (e.g., Fay, 1992). A possible explanation for this may be that the way in which frequency-difference thresholds are obtained does not always yield an accurate estimate of an animal's ability. Some time ago we noticed that some animals appeared to have unusual difficulty performing frequency discriminations, as compared to their performance on detection and localization tasks. Indeed, even an animal as intelligent and as cooperative as the Indian elephant showed poorer asymptotic performance when discriminating frequency (R. S. Heffner & Heffner, 1982). It is possible that the difficulty some animals have in performing a frequency discrimination is due to the way in which the stimuli are presented. That is, it is often easier to train an animal to detect when a tone is changing in frequency than it is to train it to discriminate between discrete tones that differ in frequency. Moreover, there are a number of natural sounds in which the direction of a frequency change is a significant parameter (e.g., communication calls), suggesting that animals may be naturally more experienced in detecting such changes. Thus, a more appropriate test of the ability to discriminate frequency may be determine an animal's ability to detect frequency changes, such as frequency sweeps and frequency-modulated tones.

Final considerations regarding mammalian hearing

It is necessary to emphasize both the importance of knowing what animals hear and that such information must be obtained behaviorally.

General relevance of species differences in hearing. Given the differences in mammalian hearing ranges, sounds that are clearly audible to one species may be completely inaudible to another. An extreme example is the Indian elephant, which hears up to 11.8 kHz, and the little brown bat, which hears down to 10.3 kHz—their hearing ranges show such little overlap that they hear virtually no sounds in common (H. E. Heffner & Heffner, 1998). However, even common laboratory species can have very different hearing abilities, a situation that can lead to problems if not taken into consideration. One such case is a series of studies which concluded that laboratory rats were superior to cebus monkeys in discriminating melodies (D'Amato, 1988). However, inspection of the auditory stimuli reveals that some of the melodies contained frequencies below 500 Hz, which, while clearly audible to monkeys, are beyond the hearing range of rats. As a result, the monkeys had to discriminate between two clearly audible, but different tunes,

whereas the rats had to discriminate between a tune they could hear well and one that contained many inaudible notes. Thus, the results of this study are more likely a demonstration of sensory, rather than cognitive differences between monkeys and rats. Clearly, it is important not to assume that what is audible to one species is equally audible to another.

Acknowledging species differences is also important for the meaningful interpretation of physiological results, especially as it is not uncommon for physiological data from animals to be compared with behavioral data from humans. In such cases, it appears that there is an underlying assumption that auditory neurons in a particular nucleus have the same general properties regardless of the species in which they are found—indeed, a study may even fail to state what species was being studied (e.g., Skottun, 1998). This leads to the construction of auditory models that are composites of different creatures—auditory chimeras—although, since many are half man and half beast, the term "auditory sphinx" might be more appropriate. Such a composite can have interesting results. For example, it has been claimed that single auditory thalamic neurons are able to "distinguish" interaural time differences with the same acuity as human observers (about 10 :s), suggesting that a handful of neurons may account for human localization acuity (Skottun, 1998). However, it turns out that the auditory neurons in question were located in the thalamus of the domestic rabbit, an animal with extremely poor sound localization acuity (~22E vs. the ~1E acuity of humans). Thus, although physiologists can detect neural changes to binaural time differences in the rabbit as small as 10 :s, the rabbit can at best detect differences of about 30 :s, assuming that it is relying solely on the time differences available to it at its threshold with no help from spectral cues, which is by no means certain. In short, physiological results must be compared with behavioral results obtained in the same species in order for the conclusions to be meaningful.

Electrophysiological measures of hearing. Because behavioral tests of hearing are difficult and time consuming, measures of neural responses are often used to estimate what an animal can hear. Some common physiological measures are the cochlear microphonic, thresholds of units in the inferior colliculus, and the auditory brainstem response (ABR). Although such measures cannot help but reflect some aspect of hearing, they are imperfect estimates of actual hearing ability. Moreover, the degree to which they correspond to behavioral thresholds is generally unknown as few studies have attempted to determine the correspondence between behavioral and electrophysiological thresholds (for an exception, see Szymanski, Bain, Kiehl, Pennington, Wong, & Henry, 1999).

An example of the difference between behavioral and electrophysiological results can be seen in the comparison of the behavioral audiogram and ABR thresholds of C57BL/6J x C3HeB/FeJ mice (Koay, Harrington, Heffner, & Heffner, under review). As shown in Figure 19.5, the ABR generally reflects the behavioral audiogram, even to the extent of indicating the animals' best frequency. However, the ABR thresholds overestimate low-frequency hearing while underestimating high-frequency hearing and best sensitivity. Such a discrepancy is not surprising and there are at least two reasons why one would expect the two estimates of hearing to diverge (Szymanski et al., 1999). First, the tones used to generate the ABR are not pure tones because they have rapid

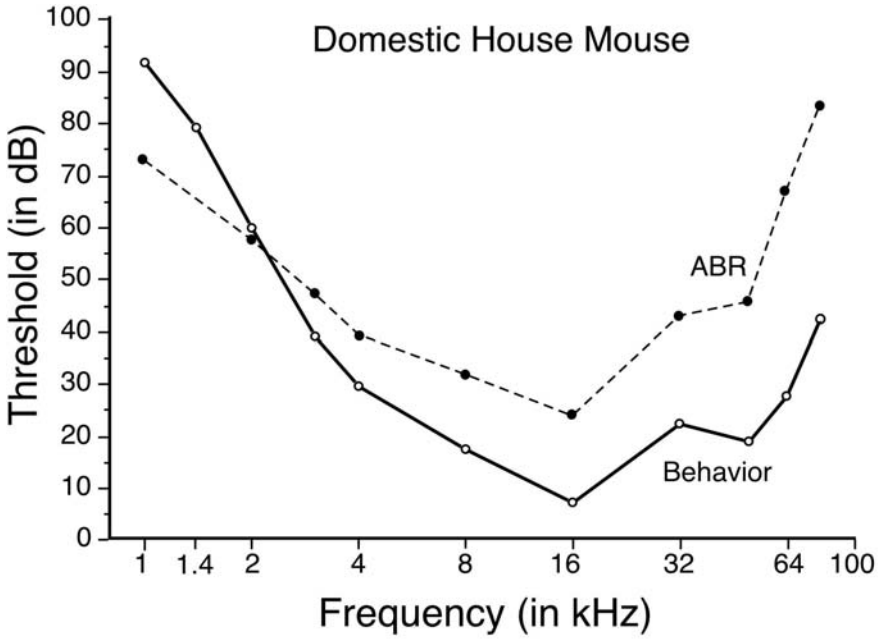

Figure 19.5 Behavioral audiogram and auditory brainstem response (ABR) thresholds of C57BL/6J x C3HeB/FeJ mice. Note that the ABR overestimates low-frequency sensitivity and underestimates high-frequency sensitivity.

onsets which cause "spectral splatter," whereas the tones used in behavioral audiograms have slow onsets to keep the signal pure. Second, the ABR procedure uses very brief tones with effective durations of 2 ms, whereas behavioral audiograms use much longer tone durations of 400 ms or more. However, detection thresholds depend on the duration of a sound, with sensitivity (in humans) improving as the duration of the stimulus increases up to about 200 ms, a process known as temporal integration (e.g., Moore, 1997). Thus, the difference in the purity and duration of the stimuli alone are sufficient to suggest that the ABR will be an imperfect estimate of behavioral sensitivity.

Role of Auditory Cortex in Hearing

The search for the functions of different areas of cortex began during the late part of the 19th century following the discovery of motor cortex in the dog by Fritsch & Hitzig (1870). One of the principal localizationists involved in this search was David Ferrier, a British physician who studied the cortex of various mammals using electrical stimulation and ablation techniques. By observing that stimulation of the temporal lobe of monkeys

resulted in an acoustic startle reaction, Ferrier correctly placed auditory cortex in the upper two thirds of the superior temporal gyrus (Ferrier & Yeo, 1885). His subsequent demonstration that removal of this area abolished all responsiveness to sound was then taken as conclusive evidence that he had successfully identified auditory cortex. However, subsequent ablation studies conducted by other researchers failed to replicate his findings, with the result that William James concluded that Ferrier was most likely wrong (James, 1890). But, as we shall see, Ferrier was essentially correct in both the location of auditory cortex and the effect of its ablation (H. E. Heffner, 1987).

Although it is currently fashionable to infer the function of an auditory center from the response properties of its neurons, historically it has been the results of ablation/behavior studies that have carried the most weight (Neff et al., 1975). Although experimental lesions have been made in all auditory centers, only auditory cortex has been studied extensively. The following sections review the effect of auditory cortex lesions on the detection and localization of sound as well as on the discrimination of frequency, including tone patterns and frequency sweeps. The results are presented by species as the role of auditory cortex can vary greatly from one species to the next.

Making and assessing the effects of cortical lesions

Making cortical lesions. There are two basic methods for making cortical lesions. To date, virtually all experimental lesions of auditory cortex have been permanent lesions made by subpial aspiration. However, it is also possible to make reversible lesions, that is, to temporarily inactivate cortex either by cooling it or by the application of chemicals (Lomber, 1999), a technique that is bound to yield new insights into the role of auditory cortex.

Assessing the effects of cortical lesions. The effects of cortical lesions have been assessed with various behavioral techniques, including the conditioned suppression technique in which an animal is trained to associate a sound with a mild shock. Recently, studies on the neural mechanisms of fear conditioning have suggested that disruption of auditory input to the amygdala could reduce or eliminate the response of an animal to a sound that has been paired with shock (e.g., LeDoux, Sakaguchi, & Reis, 1984). Thus, the question arises as to whether any of the cortical deficits about to be described could be attributed to reduced fear conditioning rather than to a strictly auditory deficit. The answer to the question is, no. Most ablation/behavior studies include control tests to demonstrate that an observed deficit is not due to any attention, motivation, cognitive, or motor disorder. For example, when an animal is unable to discriminate sounds, a routine control test is to use the same procedure to demonstrate that it retains the ability to detect the sounds. Moreover, the loss of the ability to localize sound following cortical lesions can be demonstrated with a pure reward procedure as well as with a shock procedure (e.g., H. E. Heffner & Heffner, 1990b). Thus, except as noted, a reduction in fear conditioning cannot serve as an alternative explanation of the effects of cortical lesions on hearing.

On the other hand, the possibility that the reduced fear response observed following lesions of the amygdala (and other sites) may be due to a hearing loss has never been ruled out. Not only does the possibility exist that such lesions themselves may cause a hearing loss, but the lesions are made stereotaxically and the earbars used to position an animal's head in a stereotaxic device are known to rupture an animal's eardrums. Thus, although a reduction in fear conditioning cannot account for the cortical deficits in hearing, it is not possible to rule out hearing loss as an alternative explanation of the results of fear conditioning studies, especially those using stereotaxically-placed lesions.

Detection of sound

Ablation of auditory cortex has a dramatic effect on absolute sensitivity in monkeys and humans, a small effect in carnivores, and little or no effect in other species that have been tested.

Primates. The effect of both unilateral and bilateral auditory cortex ablation on absolute thresholds has been studied in some detail in macaque monkeys (H. E. Heffner & Heffner, 1986; 1989; 1990a). Unilateral ablation of auditory cortex results in a substantial hearing loss in the ear opposite the lesion (the contralateral ear) with no effect on thresholds in the ear on the same side as the lesion (the ipsilateral ear). The hearing loss is greatest immediately after ablation with pure-tone thresholds improving over a period of a few months to near normal levels. The residual hearing loss is small and best demonstrated by comparing pre- and post-operative thresholds.

Unilateral damage to auditory cortex in humans undoubtedly results in a contralateral hearing loss (e.g., Karp, Belmont, & Birch, 1969). However, because the residual hearing loss is small, especially when part of auditory cortex is spared, and because premorbid audiograms of brain damaged patients are rarely available for comparison, the existence of such a hearing has been controversial.

Bilateral ablation of auditory cortex in Japanese macaques results in a profound hearing loss. Initially, there may be total deafness lasting for a few days to a few months after surgery. Pure-tone thresholds show substantial recovery during the first two months with more gradual recovery thereafter, but the animals continue to show a substantial hearing loss several years after surgery. Thus, Ferrier was correct—lesions of the posterior two-thirds of the superior temporal gyrus in monkeys do result in a profound hearing loss. The failure of his contemporaries to replicate his results was most likely because their lesions did not extend far enough into the depths of the Sylvian fissure and were therefore incomplete (H. E. Heffner, 1987).

Although bilateral damage to auditory cortex in humans is rare, there have been cases showing a hearing loss similar to that observed in macaques. That is, the patient reports a sudden inability to hear any sound followed by gradual, but incomplete recovery (Jerger, Weikers, Sharbrough, & Jerger, 1969; for a review, see H. E. Heffner & Heffner, 1986).

This pattern of the cortical hearing loss—deafness followed by substantial but incomplete recovery—suggests that the detection of sound is primarily mediated by subcortical structures that receive input from auditory cortex. The removal of cortex, then, results in deafness due to the shock of the sudden loss of cortical input (i.e., diaschisis). This is followed by partial recovery as the subcortical areas adjust to the loss of the cortex. There is currently no evidence that the recovery of hearing is mediated by other cortical areas.

Non-primates. The possibility of a cortical hearing loss has been examined in a few other species, none of which have shown the dramatic hearing loss that occurs in primates. Bilateral ablation of all neocortex in the Virginia opossum has no effect on absolute thresholds, whereas bilateral auditory cortex lesions in rats, cats, dogs, and ferrets result in small, but detectable hearing losses (for a review, see H. E. Heffner & Heffner, 1986).

On the other hand, a recent study found that rats were initially unresponsive to sound following temporary inactivation of auditory cortex using muscimol, a GABA-A agonist with an inhibitory effect on neurons (Talwar, Musial, & Gerstein, 2001). However, no control tests were conducted to determine whether the effect was due to a general unresponsiveness to sensory stimuli and no conclusion can be drawn as to whether such inactivation of auditory cortex in rats causes a hearing loss.

Localization of sound

The discovery that auditory cortex ablation in cats results in a sound localization deficit was made over half a century ago by W. D. Neff and his colleagues (Neff & Yela, 1948; Neff, Fisher, Diamond, & Yela, 1956). As with the cortical hearing loss, this deficit is found in some species (primates and carnivores), but not others (rodents).

Primates. Unilateral lesions of auditory cortex result in a complete inability to discriminate the locus of a sound in the hemifield opposite the lesion, an effect that has been demonstrated in both macaques and squirrel monkeys (H. E. Heffner, 1997; Thompson & Cortez, 1983). The animals retain both the normal ability to localize sound in the ipsilateral hemifield and the ability to distinguish sounds arising in the left hemifield from sounds arising in the right hemifield. There is also some residual ability to localize sound in the contralateral hemifield when the source is close to midline (e.g., within 15E of midline), which may be mediated by the intact ipsilateral cortex. In short, unilateral ablation results in a ‘collapse’ of auditory space in the contralateral hemifield.

Bilateral ablation of auditory cortex appears to be the sum of two unilateral lesions—auditory space collapses in both hemifields (H. E. Heffner, 1997; H. E. Heffner & Heffner, 1990b). Although a macaque with a bilateral lesion can be trained to distinguish left *sounds* from right *sounds*, it shows no awareness of the location of the sound *source*. This is demonstrated by the great difficulty the animals have in learning to approach the source of a continuous sound, which they eventually do by using a tracking

strategy (i.e., move to where the sound is loudest). Some operated animals eventually learn to go left or right when the sound is brief, but they appear to be learning to associate a spatial response with an arbitrary sound that has no spatial locus. However, the animals are completely unable to distinguish sounds coming from two locations within the same hemifield. Thus, bilateral auditory cortex lesions appear to result in the total collapse of the left and right auditory hemifields leaving only a residual ability to discriminate between left and right sounds that are devoid of spatial meaning.

The effect of bilateral lesions has also been studied in the bushbaby *(Galago senegalensis*), a prosimian (Ravizza & Diamond, 1974). Although the results suggested that their sound localization ability is only moderately affected by auditory cortex lesions, the results were preliminary and it is not known whether the remaining ability represents a species difference or if the lesions were incomplete.

Most studies indicate that unilateral lesions in humans result in a sound-localization deficit in the hemifield contralateral to the lesion, just as they do in macaques (for reviews, see H. E. Heffner & Heffner, 1990b; Neff et al., 1975). However, the observed deficits do not appear to be as severe as those found in macaques, even for patients in which one hemisphere has been entirely removed (Lessard, Lepore, Poirier, Villemagne, & Lassonde, 2000). One possible explanation is that such patients typically sustained cortical damage early in life, allowing for greater function compensation than occurred in the macaques, all of which were adults at the time of surgery. Surprisingly, a recent study has suggested that sound localization in humans is lateralized such that lesions of right, but not left, auditory cortex result in a sound localization deficit (Zatorre & Penhune, 2001). However, these results rest on the premise that partial lesions of auditory cortex that include primary auditory cortex, AI, are sufficient to produce the classic sound localization deficit—but this may not be true. In macaques, partial lesions of auditory cortex, even if they include substantial portions of primary auditory cortex, do not result in a total collapse of the contralateral auditory field (Harrington & Heffner, 2002). Thus, the results of the study by Zatorre and Penhune should be reevaluated with regard to the location and completeness of the lesions.

The effects of bilateral lesions in humans on sound localization are not clear owing to the rarity of cases with complete bilateral auditory cortex lesions. Indeed, given the severe hearing loss that accompanies such lesions, the patients would be difficult to examine. However, we expect that bilateral lesions in humans, as in macaques, would result in a complete inability to localize sound.

Carnivores. The effect of cortical lesions on sound localization has been studied in cats, dogs, and ferrets (see H. E. Heffner & Heffner, 1990b for a review). All appear to show the same sound-localization deficit as macaques. Specifically, unilateral lesions in cats and ferrets result in a sound-localization deficit in the hemifield contralateral to the lesion and bilateral lesions in cats, dogs, and ferrets result in a deficit in both hemifields. In addition, a study using cats indicated that restricting the lesion to a particular frequency representation in primary auditory cortex affects the ability to localize those specific frequencies (Jenkins & Merzenich, 1984). However, this finding deserves further study in

light of the finding that cats experience a mild hearing loss following cortical lesions and because lesions restricted to primary auditory cortex in monkeys do not appear to result in the classic sound-localization deficit (see above).

Rodents. In contrast to primates and carnivores, bilateral ablation of auditory cortex in the Norway rat, as well as in the wild wood rat (*Neotoma floridana*), does not abolish the ability to localize sound—at most it may result in a slight increase in threshold (e.g., H. E. Heffner & Heffner, 1990b; Kavanagh & Kelly, 1986).

Other species. Two other species that have been examined are the hedgehog, an insectivore, and the Virginia opossum, a marsupial (Ravizza & Diamond, 1974; Ravizza & Masterton, 1972). In both cases, cortical ablation appears to result in increased thresholds for left-right discriminations. However, neither study examined the possibility that, in spite of the animals' ability to perform a left-right discrimination, the lesions may have resulted in a collapse of auditory space within each hemifield. Thus, the complete effect of cortical lesions on sound localization in these species is not known.

The discrimination of frequency

Early electrophysiological studies indicated that frequency was mapped on auditory cortex in an orderly manner (tonotopic maps), giving rise to the idea that cortex is necessary for frequency discrimination (Neff et al., 1975). Once it was discovered that cortical ablation did not totally abolish the ability of the animals to discriminate one frequency from another, testing moved on to the discrimination of tone patterns and frequency sweeps.

Discrimination of discrete frequencies. Studies of the effect of auditory cortex lesions on the ability of macaques to discriminate tones of different frequency have established that auditory cortex lesions result in a small but reliable increase in thresholds (e.g., Massopust, Wolin, & Frost, 1970). For example, the average frequency increment needed to discriminate a 625-Hz tone from higher frequencies was shown to increase from 7.5 Hz to 27.5 Hz (Harrington, Heffner, & Heffner, 2001). Thus, although auditory cortex is not necessary for frequency discrimination per se, its loss does result in an increase in thresholds.

Although an initial study indicated that bilateral auditory cortex lesions in cats abolished the ability to discriminate frequency (Meyer & Woolsey, 1952), a subsequent study failed to find a deficit (Butler, Diamond, & Neff, 1957). However, the two studies used different methods of stimulus presentation giving rise to the idea that although operated animals could detect a *change* in the frequency of an ongoing train of tone pips, they could not discriminate tones of two different frequencies if the presentation of the tones was separated by a long silent interval—that is, they could make a "relative," but not an "absolute" frequency discrimination (Thompson, 1960). However, it has since been demonstrated that cats with auditory cortex lesions retain the ability to make absolute judgements of frequency (Cranford, 1978) and the current view is that such lesions have at most only a small effect on the ability of cats to discriminate frequency.

Although it was established long ago that removal of cortex has no effect on frequency discrimination in the Norway rat (Kelly, 1970), a recent study has suggested that the chemical inactivation by the application of muscimol to auditory cortex results in a temporary inability to do so (Talwar et al., 2001). The implication of this finding is that auditory cortex in rats (and other mammals) is normally involved in the discrimination of frequency. However, no control tests were conducted to rule out alternative explanations of the failure of the rats to respond to a difference in frequency. Thus, we do not at this time know if the results were due to an auditory deficit per se, or to an attentional, cognitive, or motor deficit. Indeed, it is conceivable that the application of muscimol to auditory cortex results in the perception of phantom sound which distracts the animal from external auditory stimuli.

Tone pattern discrimination. Once it was found that cortical lesions did not abolish the ability to discriminate frequency, researchers moved on to determine the role of cortex in discriminating changes in temporal patterns of tones. The tone patterns were typically sequences of three tone pips of a high or low frequency, such as Low-High-Low, High-Low-High, Low-Low-Low, and High-High-High. By using such stimuli, it was hoped to discover how the cortex processed patterns of stimuli that were analogous to the spatial patterns used in visual and somatosensory studies. However, because many of the discriminations proved difficult even for normal animals to learn, the resulting deficits may have been cognitive rather than perceptual in nature. Thus, the significance of this line of research is unclear (for reviews, see Elliott & Trahiotis, 1972; Neff et al., 1975).

Frequency sweeps. The discovery that some auditory cortex neurons are selective for the direction of a frequency change (Whitfield & Evans, 1965) was the motivation for investigating the effect of auditory cortex lesions on the discrimination of frequency sweeps. The results of these studies indicated that bilateral auditory cortex lesions impaired, but did not abolish, the ability to discriminate a rising from a falling frequency sweep (Kelly & Whitfield, 1971).

The motivation for determining the effect of cortical lesions on the discrimination of frequency sweeps by macaques was different. Specifically, Japanese macaques had been shown to lose the ability to discriminate between different forms of their coo call following auditory cortex lesions (H. E. Heffner & Heffner, 1986; 1994; 1995b). Although this result suggested that the animals had an aphasia-like deficit, in that they were no longer able to interpret their vocal communications, the possibility existed that it might be part of a general sensory deficit. Because the coos used in those studies were tonal calls that either rose or fell in frequency, it was necessary to determine whether auditory cortex lesions affected the ability to discriminate frequency sweeps. The results indicated that although the animals could discriminate a rising from a falling frequency sweep, they did so on the basis of absolute frequency differences, e.g., comparing the initial frequency of each sweep, rather than responding to the direction of frequency change. When they were prevented from using that strategy, by randomizing the frequency of the stimuli, their performance fell to chance. Thus, auditory cortex ablation

in macaques abolishes the ability to determine if a sound is *changing* in frequency (Harrington et al., 2001). This result demonstrates that the inability of macaques to discriminate their coo vocalizations is part of a broader sensory deficit. It also raises the question of whether a similar deficit underlies sensory aphasia in humans.

Recent studies have found that cortical lesions impair the performance of gerbils in discriminating rising from falling frequency sweeps (Ohl, Wetzel, Wagner, Rech, & Scheich, 1999; Wetzel, Ohl, Wagner, & Scheich, 1998). However, the group data presented in these studies (no individual data were shown) showed relatively large variance, suggesting that not all of the operated animals were impaired. It has long been the rule that a lesion must consistently result in a deficit before the ablated area can be considered essential for a function (James, 1890). Thus, without knowledge of individual results, no definite conclusion can be reached regarding the role of auditory cortex in gerbils on the discrimination of frequency sweeps.

Final considerations regarding auditory cortex

Auditory cortex has been described on being functionally unilateral with each hemisphere processing sound arising from the contralateral *hemifield* (Glendenning & Masterton, 1983). This view is based on the observation that the majority of neurons in auditory cortex respond best to sounds in the contralateral sound field, that ipsilateral input is usually inhibitory, and that unilateral damage to auditory cortex results in sound-localization deficits confined to the hemifield contralateral to the lesion. Although this view may be valid for sound localization, it does not necessarily apply to other auditory abilities, such as sound detection and discrimination. For these abilities, auditory cortex may be more appropriately characterized as being asymmetrically bilateral with each hemisphere having a greater involvement in processing information from the contralateral *ear* as opposed to the contralateral hemifield.

With regard to the detection of sound, a unilateral auditory cortex lesion in a macaque results in a hearing loss in the ear contralateral to the lesion with thresholds in the other ear completely unaffected. This means that sounds arising from the contralesional hemifield, even if inaudible in the ear on that side because of the unilateral hearing loss, will be detected as long as the sound can reach the other ear (H. E. Heffner & Heffner, 1989). The same applies to the discrimination of frequency change, which is impaired for sounds presented to the contralesional *ear* and not for sounds presented in the contralesional *hemifield* that reach both ears (H. E. Heffner and Heffner, 1994). In neither case, however, is the deficit as severe as that resulting from a bilateral lesion, demonstrating that each hemisphere plays a role in processing sounds from both ears with the opposite hemisphere having a greater role. Thus, although unilateral lesions abolish sound localization in the contralateral hemifield, they affect the detection and discrimination of sounds in the contralateral ear.

It should be noted that the above results are species specific—they apply to macaques, but not necessarily to other mammals, and particularly not to rodents. There is currently no explanation for why some species should show a deficit when others do not. It may be noted that rats have smooth (lissencephalic) brains while carnivores and

primates have highly convoluted (gyrencephalic) brains, or that rats normally have poorer sound localization acuity than primates and carnivores. Whether either factor is related to the observed species differences in cortical function is not known. However, it should be clear that one cannot speak of the function of "auditory cortex" without also stating the species from which the functions have been inferred.

References

Burghardt, G. M. (1977). Learning processes in reptiles. In C. Gans (Ed.), *Biology of the reptilia, Vol. 7: Ecology and behavior A* (pp. 555-681). New York: Academic Press.

Butler, R. A. (1975). The influence of the external and middle ear on auditory discriminations. In: W.D. Keidel & W.D. Neff (Eds.), *Handbook of sensory physiology: auditory system* (Vol. V/2, pp. 247-260). New York: Springer.

Butler, R. A., Diamond, I. T., & Neff, W. D. (1957). Role of auditory cortex in discrimination of changes in frequency. *Journal of Neurophysiology, 20*, 108-120.

Brown, C. H. (1994). Sound localization (pp. 57-96). In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: mammals*. New York: Springer-Verlag.

Cahill, L., McGaugh, J. L., & Weinberger, N. M. (2001). The neurobiology of learning and memory: some reminders to remember. *Trends in Neuroscience, 24*, 578-581.

Cranford, J. L. (1978). Polysensory cortex lesions and auditory frequency discrimination in the cat. *Brain Research, 148*, 499-503.

D'Amato, M. R. (1988). A search for tonal pattern perception in cebus monkeys: why monkeys can't hum a tune. *Music Perception, 5*, 453-480.

Dooling, R. J. & Hulse, S., (Eds.) (1989). *The comparative psychology of audition: perceiving complex sounds*. New York: Lawrence Erlbaum Associates.

Elliott, D. N. & Trahiotis, C. (1972). Cortical lesions and auditory discrimination. *Psychological Bulletin*, 77, 198-222.

Fay, R. R. (1988). *Hearing in vertebrates: a psychophysics databook*. Worcester MA: Heffernan Press.

Fay, R. R. (1992). Structure and function in sound discrimination among vertebrates. In D. B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing*. (pp. 229-263). New York: Springer-Verlag.

Ferrier, D. & Yeo, G. (1885). A record of experiments on the effects of lesion of different regions of the cerebral hemispheres. *Philosophical Transactions of the Royal Society of London, Biology, 175*, 479-564.

Flanagan, J. L. & Guttman, N. (1960). On the pitch of periodic pulses. *Journal of the Acoustical Society of America, 32*, 1308-1319.

Fritsch, G. & Hitzig, E. (1870). Über die elektrische Erregbarkeit des Grosshirns. *Archives für Anatomie Physiologie und Wissenshaftlicke Medicin, 37*, 300-332.

Galton, F. (1883). *Inquires into human faculty and its development*. J.M. Dent & Sons: London.

Glendenning, K. K. & Masterton, R. B. (1983). Acoustic chiasm: efferent projections of the lateral superior olive. *Journal of Neuroscience, 3*, 1521-1537.

Green, D. M. (1995). Maximum-likelihood procedures and the inattentive observer. *Journal of the Acoustical Society of America, 97*, 3749-3760.

Harrington, I. A., Heffner, R. S., & Heffner, H. E. (2001). An investigation of sensory deficits underlying the aphasia-like behavior of macaques with auditory cortex lesions. *Neuroreports, 12*, 1217-1221.

Harrington, I. A. & Heffner, H. E. (2002). A behavioral investigation of "separate processing streams" within macaque auditory cortex. *Abstracts of the 25th Annual Midwinter Research Meeting of the Association for Research in Otolaryngology*, in press.

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

Heffner, H. E. (1987). Ferrier and the study of auditory cortex. *Archives of Neurology, 44*, 218-221.

Heffner, H. E. (1997). The role of macaque auditory cortex in sound localization. *Acta Oto-Laryngologica Supplement, 532*, 22-27.

Heffner, H. E. & Heffner, R. S. (1983). Sound localization and high-frequency hearing in horses. *Journal of the Acoustical Society of America, 93*, S42.

Heffner, H. E. & Heffner, R. S. (1984). Sound localization in large mammals: Localization of complex sounds by horses. *Behavioral Neuroscience, 98*, 541-555.

Heffner, H. E. & Heffner, R. S. (1985). Hearing in two cricetid rodents: wood rat (*Neotoma floridana*) and grasshopper mouse (*Onychomys leucogaster*). *Journal of Comparative Psychology, 99*, 275-288.

Heffner, H. E. & Heffner, R. S. (1986). Effect of unilateral and bilateral auditory cortex lesions on the discrimination of vocalizations by Japanese macaques. *Journal of Neurophysiology, 56*, 683-701.

Heffner, H. E. & Heffner, R. S. (1989). Unilateral auditory cortex ablation in macaques results in a contralateral hearing loss. *Journal of Neurophysiology, 62*, 789-801.

Heffner, H. E. & Heffner, R. S. (1990a). Effect of bilateral auditory cortex lesions on absolute thresholds in Japanese macaques. *Journal of Neurophysiology, 64*, 191-205.

Heffner, H. E. & Heffner, R. S. (1990b). Effect of bilateral auditory cortex lesions on sound localization in Japanese macaques. *Journal of Neurophysiology, 64*, 915-931.

Heffner, H. E. & Heffner, R. S. (1994). Lateralization of the perception of communicative vocalizations in Japanese macaques. In J. R. Anderson, J. J. Roeder, B. Thierry, & N. Herrenschmidt (Eds.), *Current primatology, Vol. III, behavioural neuroscience, physiology and reproduction*. (pp. 1-8). Strasbourg: Universite Louis Pasteur.

Heffner, H. E. & Heffner, R. S. (1995a). Conditioned avoidance. In G. M. Klump, R. J. Dooling, R. R. Fay, & W. C. Stebbins (Eds.), *Methods in comparative psychoacoustics*. (pp. 73-87). Basel: Birkhäuser

Heffner, H. E. & Heffner, R. S. (1995b). Role of auditory cortex in the perception of communicative vocalizations by Japanese macaques. In E. Zimmermann, J. Newman, & U. Juergens (Eds.), *Current topics in primate communication*. (pp. 207-219). Plenum: New York.

Heffner, H. E. & Heffner, R. S. (1998). Hearing. In G. Greenberg & M. M. Haraway (Eds.) *Comparative psychology, a handbook* (pp. 290-303). New York:Garland.

Heffner, R. S. & Heffner, H. E. (1990). Vestigial hearing in a fossorial mammal, the pocket gopher, (*Geomys bursarius*). *Hearing Research, 46*, 239-252.

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

Heffner, R. S. & Heffner, H. E. (1992a). Evolution of sound localization in mammals. In D. B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing*. (pp. 691-715). New York: Springer-Verlag.

Heffner, R. S. & Heffner, H. E. (1992b). Hearing and sound localization in blind mole rats. *Hearing Research, 62*, 206-216.

Heffner, R. S. & Heffner, H. E. (1992c). Visual factors in sound localization in mammals. *Journal of Comparative Neurology, 317*, 219-232.

Heffner, R. S. & Heffner, H. E. (1993). Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. *Journal of Comparative Neurology*, 331, 418-433.

Heffner, R. S., Heffner, H. E., & Koay, G. (1995). Sound localization in chinchillas, II: Front/back and vertical localization. *Hearing Research, 88*, 190-198.

Heffner, R. S., Koay, G., & Heffner, H. E. (2001a). Audiograms of five species of rodents: Implications for the evolution of hearing and the encoding of pitch. *Hearing Research, 157*, 138-152.

Heffner, R. S., Koay, G., & Heffner, H. E. (2001b). Sound-localization acuity changes with age in C57BL/6J mice. In: J. F. Willott (Ed.) *Handbook of mouse auditory research: from behavior to molecular biology*. (pp. 31-35). Boca Raton FL: CRC Press.

Heffner, R. S., Koay, G., & Heffner, H. E. (2001c). Sound localization in a new-world frugivorous bat, *Artibeus jamaicensis*: acuity, use of binaural cues, and its relationship to vision. *Journal of the Acoustical Society of America, 109*, 412-421.

Jackson, L. L., Heffner, R. S., & Heffner, H. E. (1999). Free-field audiogram of the Japanese macaque *(Macaca fuscata*). *Journal of the Acoustical Society of America, 106*, 3017-3023.

James, W. (1890). *Principle of psychology*. New York: Henry Holt & Co.

Jenkins, W. M. & Merzenich, M. M. (1984). Role of cat primary auditory cortex for sound-localization behavior. *Journal of Neurophysiology, 52*, 819-847.

Jerger, J., Weikers, N. J., Sharbrough, F. W. III, & Jerger, S. (1969). Bilateral lesions of the temporal lobe: a case study. *Acta Otol-Laryngologica Supplement, 258*, 1-51.

Karp, E., Belmont, I., & Birch, H. G. (1969). Unilateral hearing loss in hemiplegic patients. *Journal of Nervous and Mental Disorders, 148*, 83-36.

Kavanagh, G. L. & Kelly, J. B. (1986). Midline and lateral field sound localization in the albino rat (*Rattus norvegicus*). *Behavioral Neuroscience, 100*, 200-205.

Kelly, J. B. (1970). The effects of lateral lemniscal and neocortical lesions on auditory absolute thresholds and frequency difference thresholds of the rat. Unpublished Doctoral Dissertation, Vanderbilt University.

Kelly, J. B. & Whitfield, I. C. (1971). Effects of auditory cortical lesions on discriminations of rising and falling frequency-modulated tones. *Journal of Neurophysiology, 34*, 802-816.

Klump, G. M., Dooling, R. J., Fay, R. R., & Stebbins, W. C. (Eds) (1995). *Methods in comparative psychoacoustics.* Basel: Birkhäuser.

Koay, G., Harrington, I. A., Heffner, R., & Heffner, H. (under review). Comparison of behavioral and auditory brainstem response thresholds in C57BL/6J x C3H mice. *Hearing Research*.

Larsen, O. N. (1995). Acoustic equipment and sound field calibration. In G. M. Klump, R. J. Dooling, R. R. Fay, & W. C. Stebbins (Eds.), *Methods in comparative psychoacoustics*. (pp. 31-45). Basel: Birkhäuser

LeDoux, J. E., Sakaguchi, A., & Reis, D. J. (1984). Subcortical efferent projections of the medial geniculate nucleus mediate emotional responses conditioned to acoustic stimuli. *Journal of Neuroscience, 4*, 683-698.

Lessard, N., Lepore, F., Poirier, P., Villemagne, J., & Lassonde, M. (2000). Sound localization in hemispherectomized subjects: the contribution of crossed and uncrossed cortical afferents. *Experimental Brain Research, 134*, 344-352.

Lomber, S. G. (1999). The advantages and limitations of permanent or reversible deactivation techniques in the assessment of neural function. *Journal of Neuroscience Methods, 86*, 109-117.

Massopust, L. C., Jr., Wolin, L. R., & Frost, V. (1970). Increases in auditory middle frequency discrimination threshold after cortical ablations. *Experimental Neurology, 28*, 299-305.

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

Meyer, D. R. & Woolsey, C. N. (1952). Effects of localized cortical destruction on auditory discriminative conditioning in cat. *Journal of Neurophysiology, 16*, 149-162.

Moore, B. C. J. (1993). Frequency analysis and pitch perception. In: W. A. Yost, A. N. Popper, & R. R. Fay, (Eds.), *Human psychophysics* (pp. 56-115). New York: Springer.

Moore, B. C. J. (1997). An introduction to the psychology of hearing, 4th edition. London: Academic Press.

Moore, D. R., Rothholtz, V., & King, A. J. (2001). Hearing: Cortical activation does matter. *Current Biology, 11*, R782-R784.

Musicant, A. D. & Butler, R. A. (1984). The influence of pinnae-based spectral cues on sound localization. *Journal of the Acoustical Society of American, 75*, 1195-2100.

Neff, W. D., Diamond, I. T., & Casseday, J. H. (1975). Behavioral studies of auditory discrimination: central nervous system. In: W. D. Keidel & W. D. Neff (Eds), *Handbook of sensory physiology. Auditory system Vol. V/2* (pp. 307-400). New York: Springer-Verlag.

Neff, W. D., Fisher, J. F., Diamond, I. T., & Yela, M. (1956). Role of auditory cortex in discrimination requiring localization of sound in space. *Journal of Neurophysiology, 19*, 500-512.

Neff, W. D. & Yela, M. (1948). Function of the auditory cortex: the localization of sound in space. *American Psychologists, 3*, 243.

Ohl, F. W., Wetzel, W., Wagner, T., Rech, A., & Scheich, H. (1999). Bilateral ablation of auditory cortex in Mongolian Gerbil affects discrimination of frequency modulated but not of pure tones. *Learning & Memory, 6*, 347-362.

Patterson, W. C. (1966). Hearing in the turtle. *Journal of Auditory Research, 6*, 453-464.

Penner, M. J. (1995). Psychophysical methods. In G. M. Klump, R. J. Dooling, R. R. Fay, & W. C. Stebbins (Eds.), *Methods in comparative psychoacoustics*. (pp. 47-57). Basel: Birkhäuser.

Pfingst, B. E., Hienz, R. & Miller, J. (1975). Reaction-time procedure for measurement of hearing. II. Threshold functions. *Journal of the Acoustical Society of America, 57*, 431-436.

Populin, L. C. & Yin, T. C. T. (1998). Behavioral studies of sound localization in the cat. *Journal of Neuroscience, 18*, 2147-2160.

Ravizza, R. J. & Diamond, I. T. (1974). Role of auditory cortex in sound localization: a comparative ablation study of hedgehog and bushbaby. *Federation Proceedings, 33*, 1917-1919.

Ravizza, R. J. & Masterton, R. B. (1972). Contribution of neocortex to sound localization in the opossum (*Didelphis virginiana*). *Journal of Neurophysiology, 35*, 344-356.

Recanzone, G. H., Makhamra, S. D. D. R., & Guard, D. C. (1998). Comparison of relative and absolute sound localization ability in humans. *Journal of the Acoustical Society of America, 103*, 1085-1097.

Shannon, R. V. (1983). Multichannel electrical stimulation of the auditory nerve in man. I. Basic psychophysics. *Hearing Research, 11*, 157-189.

Skottun, B. C. (1998). Sound localization and neurons. *Nature, 393*, 531.

Stebbins, W.C., Ed. (1970). *Animal psychophysics: the design and conduct of sensory experiments*. New York: Appleton-Century-Crofts.

Stevens, S. S. (1951). *Handbook of experimental psychology*. New York: Wiley.

Suthers, R. A. & Summers, C. A. (1980). Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat*, Rousettus. Journal of Comparative Physiology, 136*, 227-233.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., & Henry K. R. (1999). Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. *Journal of the Acoustical Society of America, 106*, 1134-1141.

Talwar, S. K., Musial, P. G., & Gerstein, G. L. (2001). Role of mammalian auditory cortex in the perception of elementary sound properties. *Journal of Neurophysiology, 85*, 2350-2358.

Thompson, G. C. & Cortez, A. M. (1983). The inability of squirrel monkeys to localize sound after unilateral ablation of auditory cortex. *Behavioral Brain Research, 8*, 211-216.

Thompson, G., Heffner, H., & Masterton, B. (1974). An automated localization chamber. *Behavior Research Methods and Instrumentation, 6*, 550-552.

Thompson, R. F. (1960). Function of auditory cortex of cat in frequency discrimination. *Journal of Neurophysiology, 23*, 321-334.

Wagner, H. (1995). Sound-localization experiments in owls. In G. M. Klump, R. J. Dooling, R. R. Fay, & W. C. Stebbins (Eds.), *Methods in comparative psychoacoustics*. (pp. 183-194). Basel: Birkhäuser.

Wetzel, W., Ohl, F. W., Wagner, T., & Scheich, H. (1998). Right auditory cortex lesion in Mongolian gerbils impairs discrimination of rising and falling frequency-modulated tones. *Neuroscience Letters, 252*, 115-118.

Whitfield, I. C. & Evans, E. F. (1965). Responses of auditory cortical neurones to stimuli of changing frequency. *Journal of Neurophysiology, 28*, 655-672.

Zatorre, R. J. & Penhune, V. B. (2001). Spatial localization after excision of human auditory cortex. *Journal of Neuroscience, 21*, 6321-6328.

Zhou, B. & Green, D. M. (1995). Reliability of pure-tone thresholds at high frequencies. *Journal of the Acoustical Society of America, 98*, 828-836.