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SOUND LOCALIZATION IN MAMMALS: BRAIN-STEM MECHANISMS

Rickye S. Heffner

Department of Psychology, University of Toledo, Toledo, Ohio

R. Bruce Masterton

Department of Psychology, Florida State University, Tallahassee, Florida

Due to technological advances in animal psychophysics and to a persistent interest in the evolution of hearing and its physiological substrates, the hearing abilities of a widening array of animals are becoming better known. There are now good behavioral audiograms on more than 45 species of mammals, representing at least 10 orders and 2 subclasses (e.g., see R. S. Heffner & Heffner, 1983a, 1985a). There are also sound-azimuth thresholds for at least 19 species in 9 orders of mammals (R. S. Heffner & Heffner, 1988a; Table 2 below). Although these totals are large and growing, they remain a very small fraction of the entire population of extant mammals (which contains more than 900 genera in 18 orders and 3 subclasses). And regardless of their numerical size, the two samples remain far from random. In both samples there are too many Primates and too few Rodents, Marsupials (pouched mammals), Chiroptera (bats), Insectivora (shrews, moles, hedgehogs, etc.), and Artiodactyla (deer, antelope, cattle, etc.). Nevertheless, the range of hearing and sound localization abilities, and the morphological specializations accompanying a few unusual ecologies can now be glimpsed.

The increase in the available sample of species now permits a tentative comparative analysis of sound localization—an analysis that often allows a kind of insight into a sensory system's contribution that is not possible

through physiological experimentation alone. To be sure, physiological experimentation cannot be replaced as the ultimate test for a specific structure–function hypothesis. However, the hypotheses themselves are often best generated by the wider vista provided by comparative methods. The present review is directed toward that general goal.

Broad and detailed reviews of the psychophysics and the anatomical or physiological mechanisms for sound localization can be found elsewhere and only inescapable references to this broad literature will be made here (e.g., Aitkin, 1986; Irvine, 1986; Masterton & Imig, 1984; Phillips & Brugge, 1985). Instead, this review focuses on some of the comparative data surrounding sound localization and the neural mechanisms subserving it in the hope that it can suggest directions for further research both into structure–function relations and into the evolution and adaptation of the auditory system. Because little is yet known about the anatomy, physiology, or psychophysics of the sound-localization dimensions of elevation or distance, the following remarks are confined to azimuth and azimuthal localization.

Any discussion of the evolution of hearing abilities of mammals and the brainstem mechanisms on which they depend is based on a foundation of psychophysical data that allows us to compare the abilities of a wide variety of mammals. Therefore, it is appropriate to devote at least a small amount of space to a discussion of how those data are obtained and how the methods of comparative psychophysics have themselves evolved to a point where comparisons can be made between species that differ greatly in their life-styles and their motor and intellectual capacities.

ANIMAL PSYCHOACOUSTICS

All modern psychophysical methods designed for animal testing have in common the ability to control motivation and to provide quick and reliable consequences not only for "hits" and "correct rejections" (both correct responses), but also to provide clear negative consequences for errors in the form of "misses" and "false alarms." Thus, it is now possible to reduce errors and maximize correct responses to obtain very reliable discriminations. With the use of a microcomputer both types of errors and correct responses can be routinely detected and measured by any of a variety of electronic devices. Raw data are easily recorded, statistics calculated, and both the stimuli and consequences modified during the testing session. For example, a hungry animal licking pureed food extruded from a small tube can be quickly trained to indicate a change in its sound field if the change is followed by an avoidable shock. In this case, the cessation of licking (sensed by an electronic contact circuit connected between the lick tube

and the cage floor) serves as an indicator of detection (R. S. Heffner & Heffner, in press). The microcomputer continuously records and calculates false alarm rate, hits, and misses, and changes the stimulus parameters. If desired, it can even track the animal's threshold by incrementing the stimulus after each miss and decrementing it after each hit (R. S. Heffner & Heffner, 1983a; Stebbins, 1970). The availability of this exquisitely detailed information on the behavior of the subject allows the use of strict statistical definitions of threshold including signal-detection analyses of performance (e.g., R. S. Heffner & Heffner, 1988a).

Another important feature of modern psychoacoustic methods is that they allow the animal to maintain its head and ears in a fixed location relative to the sound source. As a result, a uniform sound field can be maintained around the ears and the direction of sound sources relative to the animal's head and ears can be determined precisely. Most conditioned-suppression and avoidance methods and several "go/no-go" techniques accomplish head and ear stabilization by requiring the animal to place its mouth on a water spout or lick plate where it can be detected by a contact circuit (e.g., R. S. Heffner & Heffner, 1983b, 1987; Ravizza, Heffner, & Masterton, 1969). The two-choice procedures can accomplish this same degree of head stabilization by requiring an orienting or stabilizing response for the acoustic stimulus (and a chance for reward) to be presented (e.g., H. Heffner & Masterton, 1980; R. S. Heffner & Heffner, 1982, 1988c, in press).

These new procedures, depending largely on electronic circuitry and the slavish dependability of the microcomputer, stand in sharp contrast to previously available techniques which required constant vigilance from the experimenter to observe and judge responses, resolve ambiguities, and record and calculate performance throughout a session while the animal moved about within a relatively large and heterogenous sound field. However, it is the ability to control precisely the location of the subjects' ears relative to a sound source that has probably contributed more than any other factor to the reliability of animal psychoacoustical data.

The results obtained by the modern methods have led to a high degree of agreement in results between different methods within a laboratory and between different laboratories. For example, Fig. 1 shows the close agreement both in asymptomatic performance and in sound-localization thresholds of cats using two different behavioral methods. These thresholds also agree with those obtained for cats in other laboratories (R. S. Heffner & Heffner, 1988e). Such empirical support for both the precision and the validity of animal psychoacoustical measures suggests that most modern data provide an acceptable foundation for the study of the natural variation in hearing and sound localization and their relation to ecology on one hand and to neurological and otological structures on the other.

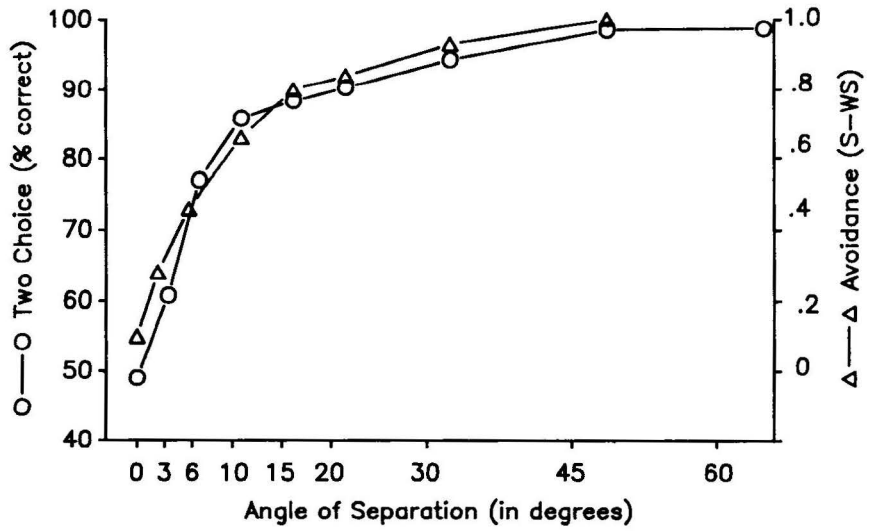


FIGURE 1. Sound-localization performance of 2 groups of domestic cats measured by two different behavioral methods approximately 2 years apart. In the two-choice method the cat touches a center "orienting" switch to hear a sound, then touches a left or right touch switch (corresponding to left or right sound source) with its nose to receive reward. In the avoidance method a thirsty cat indicates a shift in sound source location by cessation of drinking in order to avoid a mild electric shock. The close similarity of the results suggests that both methods are probably valid indicators of the cat's ability. From R. S. Heffner & Heffner (1988e).

COMPARATIVE ANATOMY OF SOUND-LOCALIZATION MECHANISMS

Although an interesting array of relations are present between behavioral performance on one hand, and gross morphological or ecological variables on the other hand, the comparative investigation of sound-localization ability has now gone far beyond these to include neuroanatomical, neurophysiological, and neurochemical correlates as well. To make sense of this large variety of data, it is necessary first to review briefly what is known about the neural mechanisms of sound localization.

The second-order anatomical projection known to subserve the fundamental elements of hearing and azimuthal sound localization consists of the ventral acoustic stria and trapezoid body of the medulla. Figure 2 shows the second-order auditory fibers from cochlear nucleus reaching the right superior olivary complex. Figure 2 also shows that there is a major intrinsic pathway within the superior olivary complex itself, one arising from the cells of the medial nucleus of the trapezoid body (MTB) and ending in the lateral superior olive (LSO). The presence of this pathway, together with the extrinsic pathways, brings two major binaural nuclei, the LSO and MSO, into relatively immediate neural contact with both cochlear

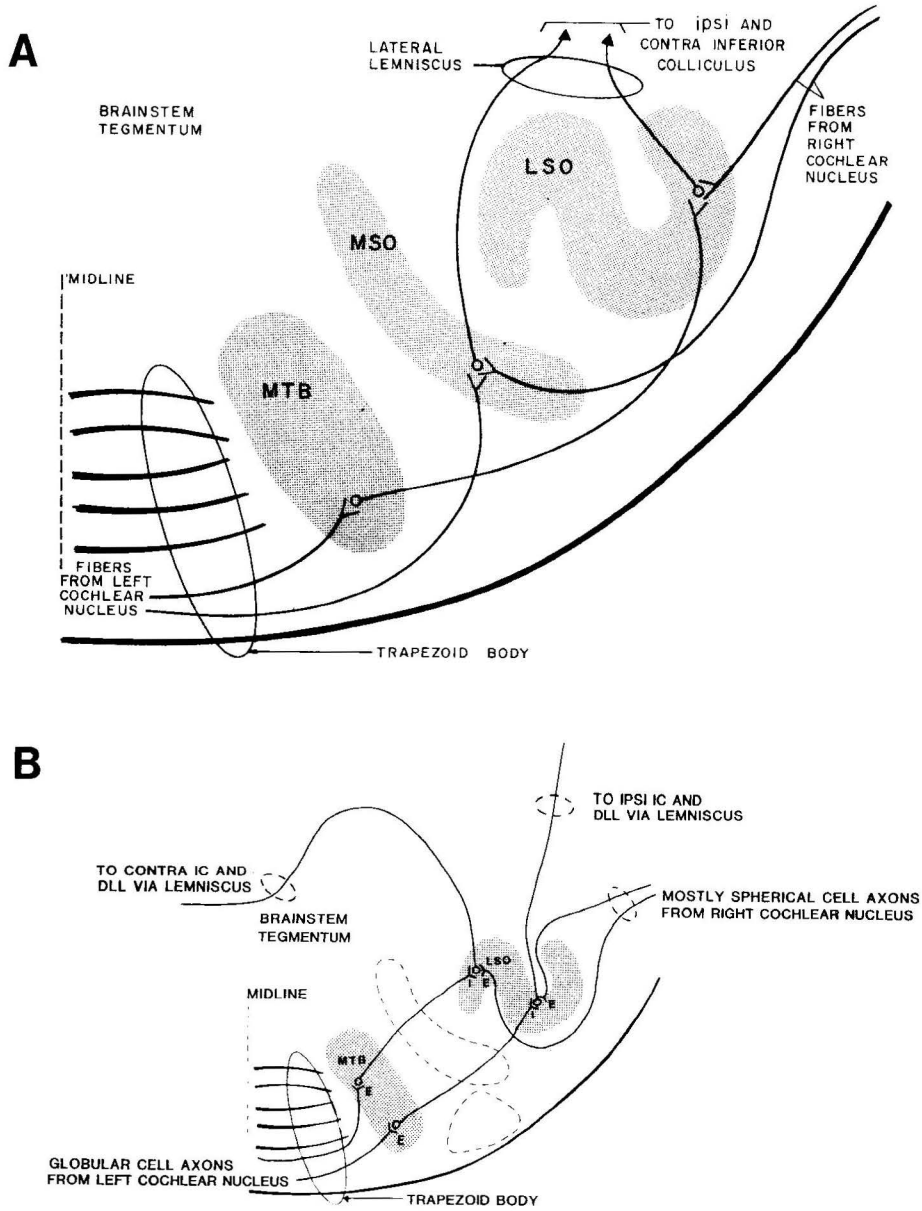


FIGURE 2. (*A*) Major sound-localization nuclei in superior olivary complex of cat. Nine periolivary nuclei are not shown. Note intrinsic pathway from MTB to LSO. (*B*) LSO–MTB system for analyzing binaural spectrum differences. E, Excitatory synapse; I, inhibitory synapse.

nuclei and, therfore, with both ears. it should be noted that there are direct connections by which convergence of binaural input can occur in the cochlear nuclei (Cant & Gaston, 1982). However, the time delays over this pathway are too long (>1 msec in cat) for neural interaction to occur during most forms of sound localization (Mast, 1970), leaving the second-order projection target as the primary locus of binaural interaction. Discovered by Stotler (1953) and by Rasmussen (1946) more than 35 years ago, these systems have proven to be the neuroanatomical substrate serving azimuthal sound localization in the sense that damage anywhere along their route results in severe and unrecoverable deficits in azimuthal sound-localization ability (e.g., Casseday & Smoak, 1981; Jenkins & Masterton, 1982; Masterton, Glendenning, & Nudo, 1981; Masterton, Jane, & Diamond, 1967).

The pathways shown in Fig. 2 are well suited to their task of analyzing binaural locus cues. They are very fast and reliable; the synapses of the ventral cochlear nucleus and MTB are perhaps the shortest-latency synapses found anywhere in the nervous system (e.g., Guinan, Guinan, & Norris, 1972; Guinan, Norris, & Guinan, 1972; Li & Guinan, 1971). At both the ventral cochlear nucleus and the MTB, the incoming fibers encapsulate the postsynaptic cells in a way that virtually guarantees a minimum time delay in synaptic action (e.g., Morest, 1968; Tolbert, Morest, & Yurgelun-Todd, 1982). Therefore, the difference in the two pathways terminating in the superior olives is small enough (<1 msec in cat) for the impulses evoked by stimulation of one ear to reach the MSO and LSO in time to interact neurophysiologically with the impulses evoked at the other ear (e.g., Rosenzweig & Amon, 1955). This neuroanatomical convergence and neurophysiological interaction is the reason that students of sound localization have focused many of their physiological and comparative investigatioans on the superior olivary complex or on the inferior colliculus which receives most of the efferent projections from the superior olivary complex (Fig. 2).

A second, perhaps more satisfying line of evidence, which leads to the conclusion that it is the superior olivary complex that is the key to azimuthal sound localization, is shown in Fig. 3. The figure summarizes a number of ablation–behavior experiments in which sound-localization ability was tested before and after section of one or another of the pathways shown in Fig. 2 (Jenkins & Masterton, 1982; Thompson & Masterton, 1978). Figure 3 shows that there is a sharp difference in the behavioral deficits resulting from monaural deafness (M in Fig. 3) or section of the trapezoid body (T in Fig. 3), which contains the input to the superior olives, as opposed to section of one lateral lemniscus (L in Fig. 3), which contains the output from the superior olives. Damage to the input results in a broad sound-localization deficit encompassing both left and right auditory hemifields. In sharp contrast, damage to one lateral lemniscus results in a virtually total loss of sound-localization ability in the

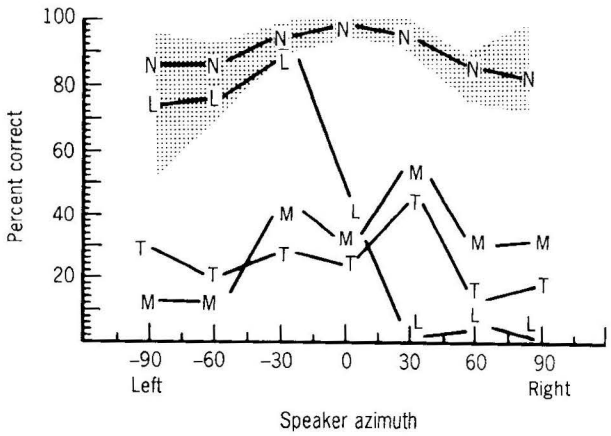


FIGURE 3. Behavioral performance of normal (N) and monaural (M) cats and cats with section of either the trapezoid body (T) or left lateral lemniscus (L). Gray area represents range of 10 normal cats. Damage of pathway to the superior olives (M or T) results in poor performance throughout auditory field. However, unilateral section of output of superior olives results in sharp deficit confined to contralateral hemifield. Adapted from Jenkins & Masterton (1982). Analogy with the effects of section before or after optic chiasm gives rise to the notion of an acoustic chiasm, a process localizable to the superior olives.

hemifield of auditory space contralateral to the damage, while the same ability in the ipsilateral hemifield seems to remain normal. Because the lateral lemniscus provides the output of LSO and MSO while the trapezoid body provides their input (Fig. 2), it follows that the difference between the two deficits is the result of the integrative and distributive activity taking place in the superior olivary complex itself.

It should also be noted that the differences in the deficits resulting from section of the trapezoid body (T in Fig. 3) as opposed to section of one lateral lemniscus (L in Fig. 3) is analogous to the difference in deficits seen in the visual system with sections before and after the optic chiasm. It is this similarity in deficits (auditory nerve, ventral acoustic stria, or trapezoid body section equivalent to optic nerve section; lateral lemniscus section equivalent to optic tract section) that has given rise to the notion that the superior olivary complex serves mammals as an acoustic chiasm (Glendenning, Hutson, Nudo, & Masterton, 1985; Glendenning & Masterton, 1983).

The analogy between the *function* of the acoustic, optic, and even the somatosensory chiasms does not hold for their *anatomy*. In the optic or somatosensory systems the sensory fields are represented point for point on the receptor surface. Therefore, the chiasmatic function of their respective decussations contralateralizes the neural activity representing one sensory hemifield merely by sorting and distributing the ascending fibers to the appropriate side of the brain—no subtle interactions or reinte-

grations are necessary. In the auditory system, however, the auditory hemifield is *not* represented in the chochlea. Therefore, a mere sorting and redistribution of the ascending fibers cannot accomplish the same task. It follows that while the optic or somatosensory chiasms are structures, the acoustic chiasm must be a process. Nevertheless, it is a process that performs the same function and it is localizable to the superior olivary complex. The following discussion turns on variations in the SOC among mammals and the associated variations in auditory abilities.

VARIATIONS OF THE SUPERIOR OLIVARY COMPLEX

The superior olivary complex in the cat (stripped of its 9 periolivary nuclei) is shown in Fig. 2. Although often accepted as the standard configuration for mammals, the same set of structures in other mammals takes on markedly different forms. This variation has stimulated several analyses of the relation of the form of the SOC to phyletic lineage, to other morphological variables, and to auditory abilities. An example of a phyletic analysis is given in Fig. 4 which shows the form of the superior olivary complex in seven mammals with sequential kinship to humans. Both the absolute and relative size of the constituent structures varies markedly. On one hand, MSO varies from large in macaque and human to very small in the opossum and none at all in the hedgehog. Although the MSO clearly increased in size in the human lineage, this change is not unique in the human line. It can be found in any set of species ordered according to increasing size. Of particular relevance to audition, there seems to be an even stronger relation between size of the MSO and low-frequency auditory sensitivity since even very small species with good low-frequency hearing, such as gerbils, kangaroo rats, and least weasels, have a well-developed MSO (for a review, see R. S. Heffner & Heffner, 1985a). In this instance, comparative psychophysics has supported conclusions derived from electrophysiological and anatomical studies that the MSO is primarily concerned with localization of sound sources emitting low frequencies.

Table 1 shows the number of neurons in the MSO in 25 animals. The data reveal that MSO is larger in large land mammals and smaller or nonexistent in either small or marine mammals: In general, the size of the medial superior olive is loosely related to the size of the animal. However, statistical analysis shows that it is not body size itself, or even head size, that is the closest correlate of the number of cells in the MSO (note dolphin in Table 1). Instead, the closest correlate ($r = 0.79$) is the functional distance between the ears (that is, interaural distance divided by the speed of sound; Masterton, Heffner, & Ravizza, 1969). In land mammals with large interaural distances, MSO is large; in most mammals with small interaural distances or in marine mammals even with large absolute but small functional interaural distances, MSO is either small or nonexistent

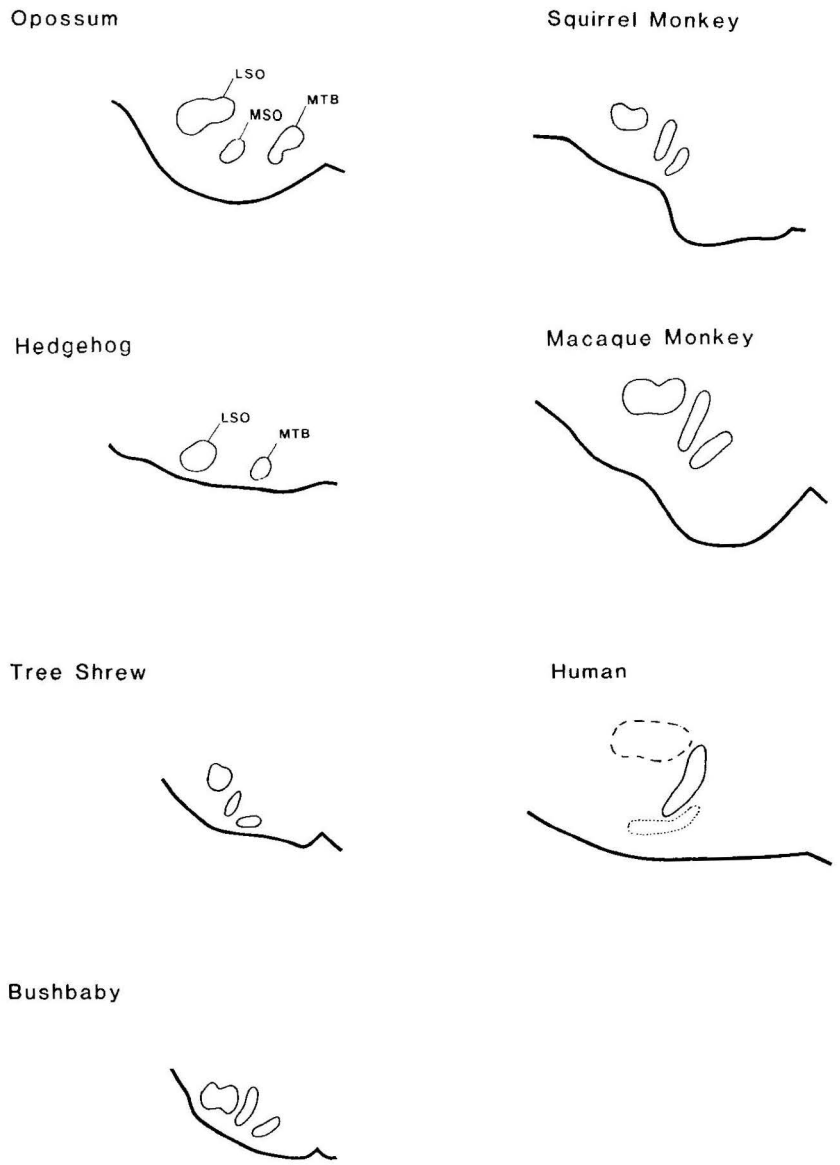


FIGURE 4. Outlines of sound-localization nuclei in the left half of the brainstem in 7 mammals with increasing kinship with humans, not drawn to scale. Note variation in relative size of MSO (and its absence in hedgehog) and in the size and shape of LSO. The broken lines representing the MTB and LSO in humans indicates that these nuclei are only marginally present.

TABLE 1. Number of Neurons in the Medial Superior Olivary Nucleus in 25 Mammals

Animal	Number of Cells in MSO	Source[a]
Hedgehog	0	2
Bat, *Carollia*	0	2
Bat, *Phyllostomus*	0	2
	100	1
Bat, *Myotis*	0	1,2
Tree shrew	1269	3
Loris	2723	3
Galago	2781	3
Marmoset	2423	3
Squirrel monkey	3279	2
Owl monkey	4263	3
Spider monkey	2570	1
	4270	3
Vervet monkey	5480	3
Macaque monkey	3420	1
	5253	2
	5285	3
Human	4260	2
Rat	690	1
	616	2
Mouse	210	1
	128	2
Gerbil	1100	1
Hamster	300	1
Guinea pig	2360	1
	2547	2
Chinchilla	3090	1
	3157	2
Squirrel	1426	2
Ground squirrel		
Citellus tridecemlineatus	1240	1
Citellus beechii	1010	1
Cat	4200	1
	5895	2
	5795	3
Dolphin	0	2

[a] 1, Harrison and Feldman (1970); 2, Harrison and Irving (1966); 3, Moore and Moore (1971).

(Table 1). However, this sample is heavily weighted with primates, which tend to be large animals with good low-frequency sensitivity, and does not include MSO cell counts for some very small species with large MSOs and good low-frequency sensitivity, such as kangaroo rats and least weasels. Therefore, it is still possible, as discussed below, that the number of cells in the MSO is a function of the low-frequency hearing ability of the species and the correlation with interaural distance will decrease as the sample becomes more representative of mammals.

Similarly, the LSO varies in size and shape within the human lineage and to an even greater degree when other species are included. In some mammals, such as cats and rats, the LSO has a characteristic horizontal S shape, but its orientation varies and it even appears inverted in rats relative to cats. In other mammals, the LSO is U, M, or W shaped, or an irregular oval. Figure 5 shows the form of LSO in a variety of mammals together with their high- and low-frequency hearing limits. Also illustrated is a hypothetical composite, or "prototype" LSO. The modifications of the prototype LSO indicated by shading in Fig. 5 give rise to each of the forms of LSO presently known. It can be concluded that the form of LSO has been established by the addition or subtraction of similar elements or modules which have been added or lost medially as high-frequency hearing increased or decreased in the evolution of a species. Because the LSO is primarily a high-frequency nucleus that rarely contains cells with characteristic frequencies near an animal's low-frequency hearing limit, it is not surprising that there are not similar additions to the lateral limb of the LSO as low-frequency hearing extends below approximately 0.1 kHz.

In summary, because of their separate relations to high- and low-frequency hearing, the variation in size and differentiation of LSO is almost inverse to that of MSO (cf. Fig. 5 and Table 1). LSO reaches its most complex form in animals with the smallest functional interaural distance, the same animals whose hearing extends into the highest frequency range (such as bats and dolphins) whereas LSO is smallest and least well-differentiated in animals with a large functional interaural distance and poorest high-frequency hearing (such as humans and elephants).

Therefore, it has been concluded that in the absence of relatively large interaural time-difference cues, small animals have exploited the second interaural cue for sound localization, the intensity-difference or, more precisely, the spectrum-difference cue. Since it is high-frequency sounds that are best shadowed by head and pinna and therefore produce the greatest interaural spectrum differences, these same animals have an extended high-frequency hearing range. This inverse relation between functional interaural distance and high-frequency hearing limit was first noted nearly 20 years ago (Masterton et al., 1969) and has remained strong despite a doubling of the sample of species—including animals such as mouse and elephant which were chosen specifically to test the application of the relation to the extremes of small and large species. Figure 6

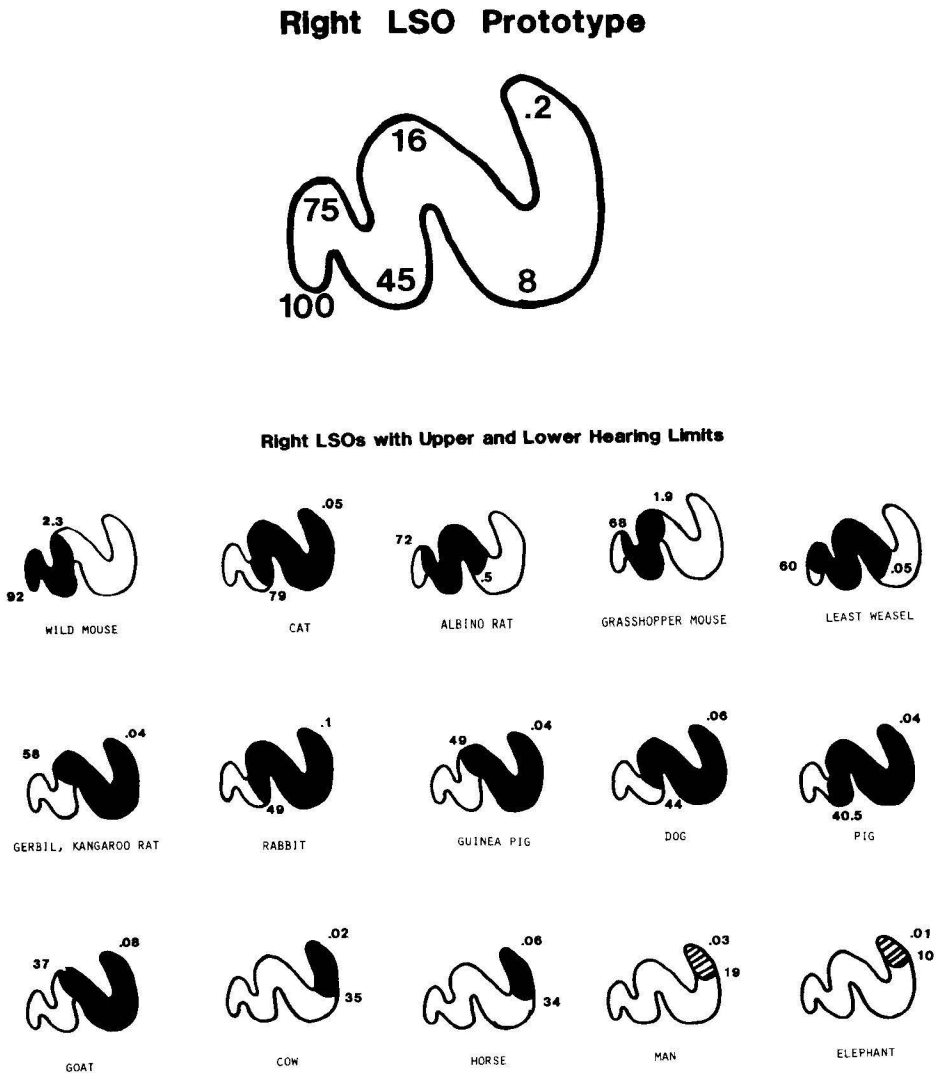


FIGURE 5. Outlines of (right) lateral superior olive and upper and lower limits of hearing in 15 mammals together with imaginary composite or prototype above. Outlines are drawn from coronal sections through largest part of each LSO and are not to the same scale. Shaded area indicates shape actually found in each species. Because LSO is strictly tonotopic, its form whether S, M, U, or W shaped roughly indicates the animal's frequency range of hearing. Thus, horizontal S-shaped LSOs in rat and cat are not really inversions of each other but instead are left–right transpositions along a sequential tonotopic map reflecting their differences in range of hearing.

illustrates this relation as it now stands with 45 species. All subgroups of mammals contribute to the correlation of −0.85 ($p < 0.001$, solid line in Fig. 6). The correlations for rodents alone (dashed line in Fig. 6) and primates alone (dotted line in Fig. 6) are −0.83 and −0.81, respectively.

Figure 6 also notes the existence of a dramatic exception to the relation in the form of the pocket gopher represented in Fig. 6 by G (R. S. Heffner, Richard, & Heffner, 1987). In these animals azimuthal sound-localization ability is vestigial possibly as a result of their extreme fossorial habits (see Table 2). The absence of high-frequency sensitivity in a small species with vestigial sound localization is further evidence for the belief that the chief selective pressure for high-frequency hearing derives from pressures for accurate sound localization.

In contrast to the LSO–MTB system that is well developed in mammals with high-frequency hearing, the MSO is best developed in large animals with large functional interaural distances which maximize the range of interaural time differences. Animals with large MSOs tend to have extended low-frequency hearing ranges (see H. E. Heffner & Heffner, 1984; R. S. Heffner & Heffner, 1982, 1983a, 1985a; Masterton et al., 1969). It should be noted that these two systems are not incompatible and that some

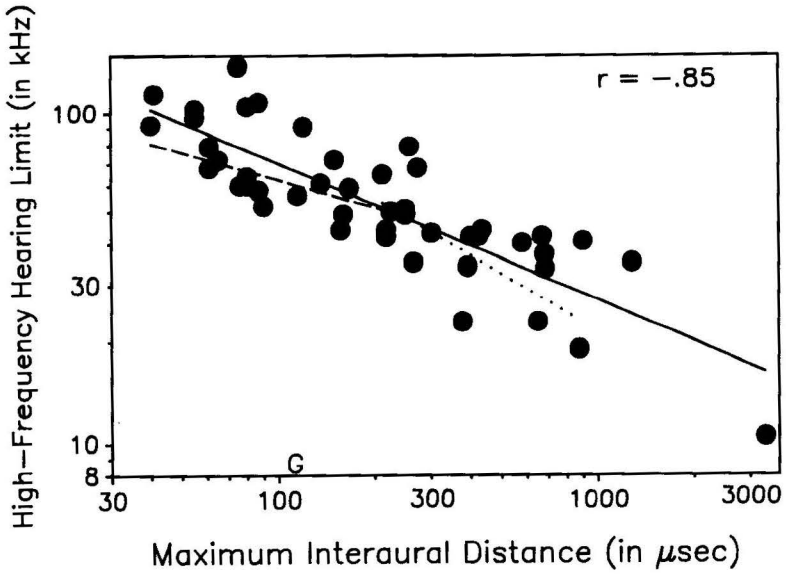


FIGURE 6. Relation between maximum functional interaural distance (interaural distance/speed of sound) and the highest audible frequency (at 60 db SPL) for the more than 40 mammals with complete behavioral audiograms. The correlation of −0.85 (—) does not vary with order as shown by the dashed line for Rodents and the dotted line for Primates. Nor does it vary with most ecologies, whether marine or echolocation. Only the highly fossorial pocket gopher, G, is exceptional.

TABLE 2. Azimuth Thresholds for 19 Species of Mammals

Animal	Stimulus	Threshold[a] (deg)	Source
Human	Click	0.8	H. E. Heffner & Heffner (1984)
Dolphin	Click	0.9	Renaud & Popper (1975)
Elephant	Noise	1.2	R. S. Heffner & Heffner (1982)
Seal	Click	3.2	Terhune (1974)
Macaque	Noise	4	Brown, Beecher, Moody, & Stebbins (1980)
Pig	Noise	4.5	R. S. Heffner & Heffner (1989)
Opossum	Noise	4.6	Ravizza & Masterton (1972)
Cat	Noise	5	R. S. Heffner & Heffner (1988e)
Dog	Click	8	H. Heffner (unpublished)
Albino rat	Noise	10	Kelly (1980)
Least weasel	Noise	12	R. S. Heffner & Heffner (1987)
Norway rat, wild	Noise	12.8	H. E. Heffner & Heffner (1985)
Hedgehog	Click	19	Chambers (1971)
Wood rat	Noise	19	R. S. Heffner & Heffner (1988a)
Grasshopper mouse	Noise	19.3	R. S. Heffner & Heffner (1988a)
Horse	Noise	22	H. E. Heffner & Heffner (1984)
	Click	30	H. E. Heffner & Heffner (1984)
Kangaroo rat	Click	27	H. Heffner & Masterton (1980)
Gerbil	Noise	27	R. S. Heffner & Heffner (1988c)
Pocket gopher	Noise	>60	R. S. Heffner, Richard, & Heffner (1987)

[a] Threshold is 75% correct for two-choice procedures and 0.50 performance level for conditioned suppression and avoidance procedures.

species have developed both to a high degree of refinement. The best examples of this are found in the Carnivora, particularly the domestic cat and least weasel, which possess large and well-developed MSOs and LSOs and have hearing ranges that extend far into both the low and high frequencies.

The presence of two binaural cues for azimuthal localization, two types of adaptation of hearing range to these cues, and two sets of anatomical structures for analyzing these cues suggests that the discussion might profitably turn to each alone.

THE HIGH-FREQUENCY, LSO–MTB SYSTEM

Through electrophysiological experimentation, the LSO–MTB system has been shown to be an interaural spectrum-difference analyzer (Boudreau & Tsuchitani, 1968, 1970). Figure 7 shows that a sound reaching the far ear of an animal has a different spectrum from that reaching the near ear due to the unequal attenuation of high frequencies over the somewhat longer

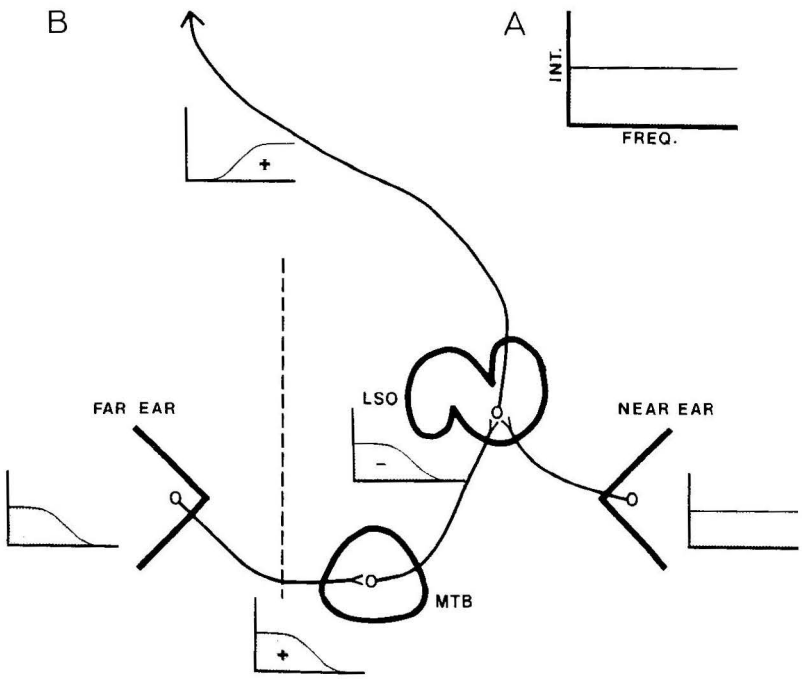
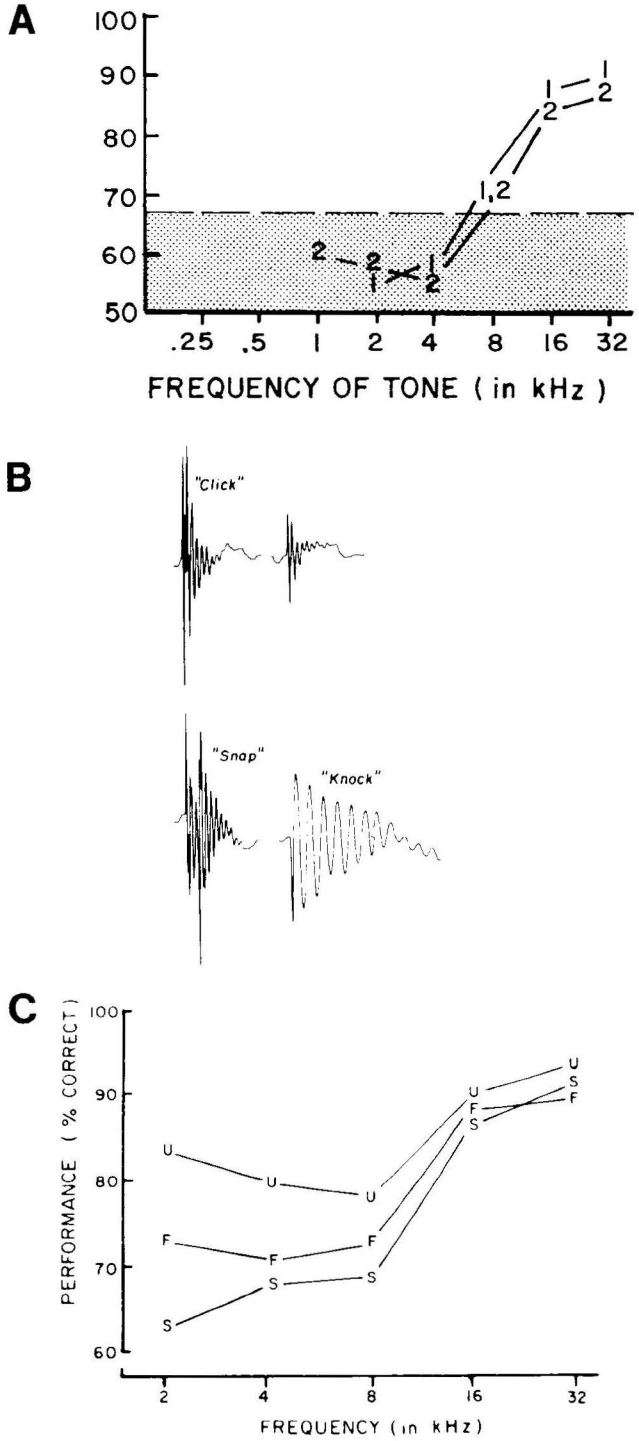


FIGURE 7. Binaural spectrum subtraction performed by LSO–MTB system for a white-noise sound source to the right of midline (---). (*A*) Graph of sound spectrum (frequency-by-intensity) used in (*B*) to show spectral differences present at the ears and represented at each nucleus in LSO–MTB system; + and − indicate excitatory and inhibitory synaptic activity, respectively. Spectral subtraction at LSO depends on change in transmitter substance from excitatory to inhibitory only in contralateral pathway. Spectrum represented in output of LSO is spectrum at right ear minus spectrum at left ear.

distance traveled and the sound shadow provided by the head and pinnae. After the two different spectra are faithfully encoded by each cochlea, they are relayed via the cochlear nuclei to the lateral superior olives. However, as the neural activity representing the contralateral spectrum is transmitted to the LSO, the MTB changes it from excitatory to inhibitory in its effect, so that when it reaches the LSO the neural activity evoked by the spectrum from the far ear is subtracted from the neural activity evoked by the spectrum of the near ear (Fig. 7).

This simple neurochemical trick of changing the transmitter substance from excitatory to inhibitory along the contralateral pathway but not along the ipsilateral pathway means that the output of LSO represents the interaural spectrum difference, frequency by frequency, exactly as might be expected from psychophysical experiments into interaural intensity-difference phenomena (Boudreau & Tsuchitani, 1970; Hutson, Glendenning, & Masterton, 1987).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2 4 8 16 32
FREQUENCY (in kHz)

In animals that have only an LSO–MTB system and little or no MSO system, this apparatus serves well enough for sound localization, certainly for sounds whose content includes high frequencies. However, as the frequency of a single pure tone is lowered, the sound shadows provided by head and pinnae become less effective and such animals have more and more difficulty localizing the source of the sound. Figure 8*A* shows the poor low-frequency sound-localization ability of hedgehogs, which have an MTB–LSO system but no MSO system at all (see Fig. 4 and Table 1). It can be seen that a hedgehog is a relatively accurate localizer of high-frequency tones while it cannot localize low-frequency tones at all, despite the fact that it can hear and respond to such tones in other ways (Masterton, Thompson, Brunso-Behtold, & RoBards, 1975). Fortunately for the hedgehog and similar mammals, however, most natural environmental sounds as well as all brief or transient sounds have sharp onsets which always contain high frequencies (Fig. 8*B*). Therefore, even animals with a pure MTB–LSO system, such as hedgehogs, dolphins, and most bats, have no difficulty localizing natural sounds despite their difficulty with low-frequency tones (Fig. 8*C*).

In general, sound-localization mechanisms depending only on MTB–LSO processing provide a reasonably good system for most small animals. Certainly it permits easy localization of a sound to at least one quadrant of space and to within plus or minus 15° or less with 50% accuracy (Table 2).

However, evidence of the limitations of this interaural spectrum-difference system is now obvious—small species tend to be among the least accurate localizers (Table 2). Several reasons for this limitation can be noted. For example, interaural intensity differences for pure-tone stimuli are unreliable and even occasionally reversed at some frequencies (Aitkin, 1986; Harrison & Downey, 1970; Irvine, 1986). Yet natural sounds usually contain a range of frequencies permitting a more reliable interaural spectral analysis (Δf_i) as opposed to a simple interaural intensity comparison for only one frequency (ΔI). For very large animals with large head and pinna shadows, another disadvantage arises. The interaural intensity difference can become so great that many sounds are entirely inaudible in the far ear, thus stimulating only the near ear and indicating only the hemifield of its source (R. S. Heffner & Heffner, 1982). It now appears that some very large mammals (e.g., horses, pigs, and elephants) have given up the ability to

FIGURE 8. (*A*) Hedgehog sound-localization performance for pure tones at 60° speaker separation. The hedgehog's pure LSO–MTB system provides only interaural intensity-difference cue and this cue begins to disappear below 10 kHz. (*B*) Waveforms of three natural sounds. Note rapid, nonsinusoidal onset in addition to fundamental resonance sinusoid. (*C*) Same as (*A*) except tone onsets were either unkeyed (U), fast-keyed (F), or slow-keyed (S). Note improvement in performance at low-frequencies when onset time of tone is shortened and transient high frequencies intrude. From Masterton, Thompson, Brunso-Bechtold, & RoBards, (1975).

use interaural intensity differences to localize sound over some or all of their high-frequency hearing range just as the hedgehog has given up the use of interaural phase over its low-frequency range (Fig. 9). Instead, these animals have turned to an MSO system which takes advantage of the large interaural time differences produced by their large heads (R. S. Heffner & Heffner, 1982, 1986a, 1986b, 1988b). Monaural pinna cues may also contribute to sound localization in these species as a supplement to or substitute for the binaural cues. Indeed, the horse, which lacks the ability to use interaural intensity differences, requires high frequencies to localize sound in the lateral fields using monaural pinna cues and cannot locate sounds on the cone of confusion if the sound does not contain high frequencies (R. S. Heffner & Heffner, 1983b).

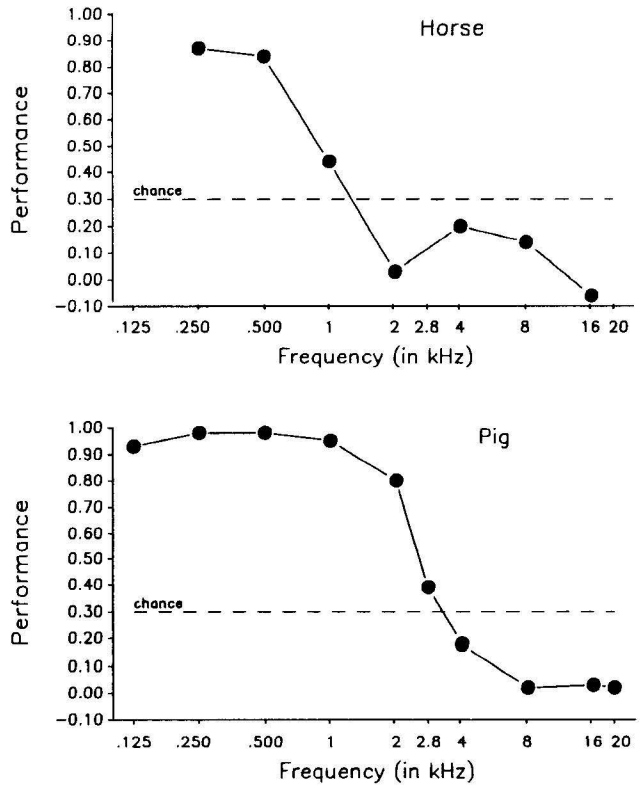

FIGURE 9. Average sound-localization performance for pure tones at 60° speaker separation for two horses and three pigs. Performance is good for low-frequency pure tones which provide an interaural phase-difference cue, but falls to chance at high frequencies which provide only an interaural intensity-difference cue. This pattern of performance suggests a pure MSO, or non-LSO, system which may be the case for the horse. However, it is not the case for the pig which has a prominent LSO as well as MSO. After R. S. Heffner & Heffner, 1986a, 1986b, 1988b, 1989.

Before leaving the discussion of the LSO–MTB system, we should note that there is no simple relation between the size and complexity of the LSO and the ability to use the interaural spectrum difference cue to localize sound (R. S. Heffner & Heffner, 1986b). Most species have a well-developed LSO and good ability to use the cue (e.g., R. S. Heffner & Heffner, 1987, 1988c; Masterton et al., 1975). But species exist in which the size of the LSO is seemingly unrelated to the ability to localize using the interaural intensity cue. For example, humans have an undistinguished LSO but retain accurate intensity-difference analysis (Mills, 1958; Moore, 1987). Conversely, the pig has lost nearly all ability to use the cue yet retains a well-developed LSO (R. S. Heffner & Heffner, 1989). Therefore, it can be concluded that the LSO has functions beyond sound localization and these functions may also be differentially represented in different species. In rodents, for example, LSO has the additional property of being a major source of olivocochlear efferents (Altschuler, Parakkal, & Fex, 1983; White & Warr, 1983). Therefore, even in the absence of participation in sound localization, rodents would probably retain an LSO. Therefore, the presence of a large or well-differentiated LSO is neither a necessary nor sufficient condition to predict capability for interaural spectrum-difference analysis. A clearer understanding of the range of functions of the LSO must await additional comparative behavioral and electrophysiological data on species that differ in their use of the binaural locus cues and in their central auditory anatomy.

With the several limitations on the use of interaural spectrum differences, it is not surprising that animals large enough to carry a large head with widely spaced ears (and therefore an interaural distance that provides large time differences between the two ears) invariably add a second system to their LSO–MTB system. As noted, this time-analysis system seems to be a major function of the MSO.

THE LOW-FREQUENCY MSO SYSTEM

The possibility that the medial superior olive might be analyzing interaural time differences was first suggested by the neuroanatomical work of Stotler (1953) and then demonstrated with a neurophysiological recording by Galambos, Schwartzkopff, and Rupert (1959). As already noted, Stotler described the convergence of second-order neurons on MSO as shown in Fig. 2. He then pointed out that the synapses on the dendrites of the MSO cells might be exactly what was needed to explain the psychophysics of azimuthal localization based on interaural time differences (Stotler, 1953).

Galambos and his colleagues managed to record the responses of a single MSO neuron in 1959. They showed that the cell's probability of response was a reliable function of the interaural time difference. Although they managed to record from only one cell, their discovery encouraged

others to investigate the phenomenon and more cells with the same property were soon found despite the technical difficulty involved (e.g., Chan & Yin, 1984; Goldberg & Brown, 1968; Guinan, Norris, & Guinan, 1972; Hall, 1965). The MSO units that change their response over the physiological range for sound localization have a characteristic delay, that is, a particular interaural time difference to which each is most sensitive (Rose, Gross, Geisler, & Hind, 1966). If one envisions a population of such cells, each cell with a different characteristic delay, the response of the entire population could serve as a high-resolution time-difference encoder. Since there are about 5000 neurons available in each MSO of a cat (although not all are sensitive to interaural time differences), such a mechanism is not improbable.

Figure 10 shows the way that the MSO is thought to analyze binaural time differences. In general, the idea is that the time delay of the sound reaching the far ear is made up for by time delays in conduction and transmission over the neural pathways from each ear to the MSO contralateral to the sound source. In reality this system can accommodate an even larger range of interaural time delays than might be expected from the schematic in Fig. 10. That is, because of intensity–latency trades in the cochlea itself and at each synapse of the pathway, the near ear is favored and the far ear disfavored beyond that due to the difference in neural conduction distances alone (Masterton et al., 1967). Therefore, it can be expected that a population of near-coincidence detecting units in MSO, something like those envisioned by von Bekesy (1930) and Jeffress (1958) on psychophysical grounds alone, may be very close to the way MSO actually functions (Chan & Yin, 1984; Yin & Kuwada, 1983).

Although there are cells in MSO that do not seem concerned with interaural time differences and there are cells in other structures that might be time-sensitive, it now seems relatively safe to conclude that high resolution of interaural time differences depends on the MSO system. However, there is one further detail to the MSO interaural time-difference hypothesis provided by comparative data.

The MSO time-sensitive cells can be used for analyzing interaural *phase* differences at frequencies low enough for first- and second-order neurons to phase-lock to the waves of the tone. However, interaural phase differences cannot be analyzed for azimuth if the interaural distance is greater than one-half the wavelength of the stimulating tone. This physical limit is present because at higher frequencies (or at longer interaural distances) the MSO cannot tell which ear is leading and which ear is lagging in phase. Further, there is a neurophysiological upper limit to the frequency that can be followed by phase-locking in order for the two monaural phases to be faithfully represented in the neural activity reaching the MSO. In the mammals studied so far, phase-locking cannot be detected much above 2 or 3 kHz (R. S. Heffner & Heffner, 1987; Johnson, 1980). Therefore, it was a surprise when it was discovered that some bats with

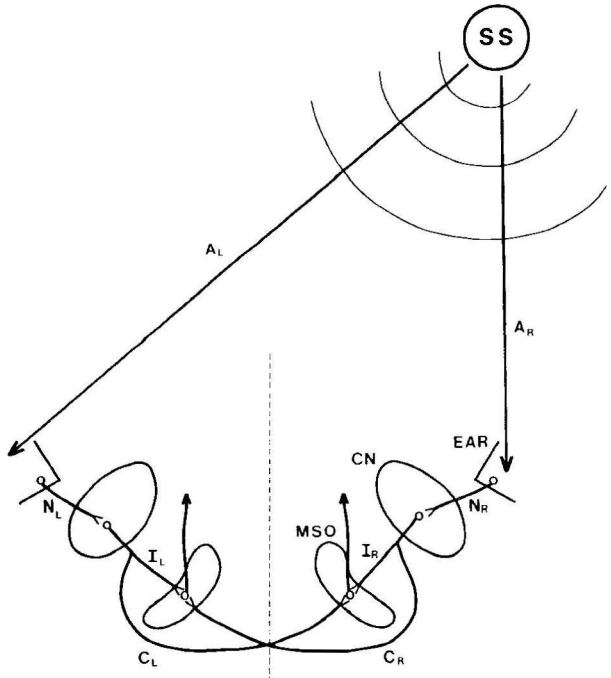

FIGURE 10. Schematic of still hypothetical mechanism of MSO system for analyzing interaural time-differences. Difference in lengths of neural pathways (e.g., IL versus CR) presumably offset the difference in length of the sound path to the two ears (AR versus AL). For a sound source to the right, neural activity from both ears would reach the left MSO at (nearly) the same time. Neurons in MSO are known to be sensitive to small time-of-arrival differences.

interaural distances too large to analyze the phase differences of the very high frequencies in their own echo-locating chirp (not to mention the unlikelihood that their neurons could phase-lock at such high frequencies) nevertheless possessed an MSO (see Zook & Casseday, 1982). However, this apparent contradiction to the general rule seems to be resolved since it has been shown that even in humans, the interaural time delay in the *envelope* of a complex sound (as opposed to the phase difference of the frequencies constituting the sound itself) can also be used for sound-localization purposes (McFadden & Posanen, 1976). That is, even though a bat cannot analyze the interaural phase differences within its own chirp, the envelope of the chirp's echo provides a time-of-arrival and phase differences at the two ears and these differences are related to the azimuth of the echo source. Apparently, some bats make use of this cue with an MSO system in addition to the usual MTB–LSO system for analyzing spectrum difference cues.

SELECTIVE PRESSURES AFFECTING SOUND LOCALIZATION

Despite much progress toward understanding the neural mechanisms of sound localization, there is still no generally accepted explanation as to why sound localization thresholds vary as widely as they do among the species shown in Table 2. In other words, we do not yet understand the selective pressures acting on sound-localization acuity and the relative reliance on the binaural locus cues. Even less is known about the contribution of monaural localization and the advantage or disadvantage conferred by a mobile pinna.

From the foregoing discussion concerning the brainstem nuclei involved in sound localization, it would seem that a mechanistic explanation for the range of acuity might be evident. Although such an explanation would tell us how some species are capable of more accurate localization than others and not why, interest in such explanations is high and they merit a brief examination. By perusing the data in Table 1 (number of cells in MSOs), Fig. 5 (configuration of LSOs), and Table 2 (localization acuities of mammals), one can see that possession of a large LSO or MSO is no guarantee of good localization acuity. For examples, horses have a large MSO but are poor localizers; gerbils and kangaroo rats have large MSOs and LSOs but are poor localizers. On the other hand, species that are good localizers tend to have at least one of the olivary nuclei well developed (the MSO in humans, monkeys, and elephants; the LSO in dolphins); sometimes both are well developed (seal, pig, cat). Thus, it is possible that among mammals good development of at least one of the main olivary nuclei may be necessary to support accurate sound localization.

A second kind of explanation for the variation in sound-localization acuity is based on interaural distance. For many years it seemed reasonable to accept that all mammals are under strong and equal selective pressure to localize as accurately as possible and that the source of variation in acuity is the difference in the magnitude of the physical cues available to them. Since the magnitude of the locus cues are, in turn, mostly determined by interaural distance, this idea remained uncontradicted by the limited data available at the time: 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 their small interaural distances were least accurate of all (Table 2). As more species were examined, however, it became apparent that a large interaural distance does not automatically result in good localization acuity—as exemplified by the poor acuity of some large mammals such as horses and cattle (H. E. Heffner & Heffner, 1984; R. S. Heffner & Heffner, 1986b). Nor is a very small interaural distance always accompanied by poor localization acuity, as demonstrated by the ability of the least weasel and grasshopper mouse to localize more accurately than many other species with the same or larger interaural distances (R. S. Heffner & Heffner, 1987, 1988a).

The relation between interaural distance and sound-localization acuity for the 18 species already tested is illustrated in Fig. 11. The correlation is statistically reliable ($r = -0.59$). However, it accounts for only 35% of the variance in acuity and the presence of markedly deviant animals suggests the presence of at least one other factor. The search for other plausible factors has taken the form of two related questions: First, are particular life-styles associated with particular localization abilities (e.g., predators versus prey, underground versus above-ground habitat)? Second, can the overall variation in sound localization be related to a single unifying factor which might in turn lead to an explanation of the role of localization acuity in the life of all mammals? Limited evidence has begun to accumulate that bears on each of these questions.

It has been noted that intermediate-sized predators (cats and dogs) seem to localize sound more accurately than prey species whether large or small (e.g., hoofed mammals, rats). This observation suggests that trophic level, that is the degree to which an animal is a predator or prey, might be an important factor in acuity. To determine the generality of this observation, several species were selected for testing. First, the only family of the Artiodactyla containing predatory species, Suidae, was examined. The domestic pig was found to be a very accurate localizer compared to mammals in general and particularly when compared to the prey species of

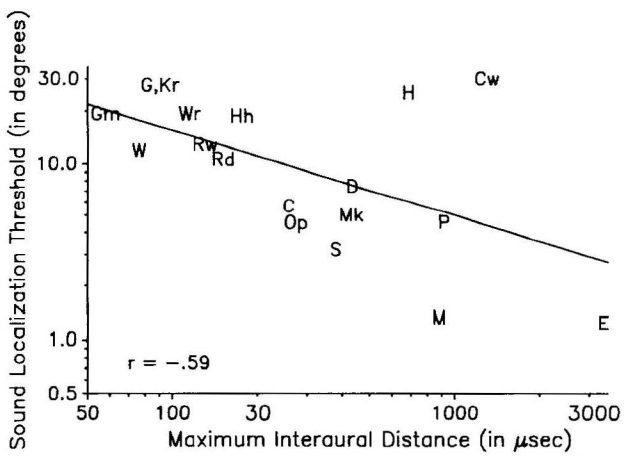

FIGURE 11. Relation between interaural distance and sound-localization threshold among 18 species of mammals. Although the correlation is reliable ($p < 0.01$), the presence of deviant species, specifically the large prey animals and the small predatory animals, suggests that additional factors have influence. (C, cat; Cw, cow; D, dog; E, elephant; G, gerbil; Gm, grasshopper mouse; H, horse; Hh, hedgehog; Kr, kangaroo rat; M, man; Mk, rhesus monkey; Op, opossum; P, pig; Rd, domestic Norway rat; Rw, wild Norway rat; S, seal; W, least weasel; Wr, wood rat.

that order (R. S. Heffner & Heffner, 1989). Second, two small predatory species were selected to determine whether a predatory life-style might overcome some of the disadvantage resulting from a small interaural distance. The species were the least weasel, a carnivore but the smallest member of that order, and the grasshopper mouse, again the only predatory member of an order comprising prey species. The mouse-sized carnivore (the least weasel) although not as accurate as much larger carnivores nevertheless was found to localize more accurately than any prey (R. S. Heffner & Heffner, 1987). The grasshopper mouse, which is even smaller, localizes more accurately than other rodents of similar size (R. S. Heffner & Heffner, 1988a). Thus, interaural distance may be a factor that limits the localization acuity of very small mammals, but a predatory life-style does appear to be associated with increased sound-localization acuity, and prey seem to be capable of less acuity than their interaural distances can support.

Despite the interest that this hypothesis holds, it is limited in that trophic level is not easily quantified. Many mammalian species occupy intermediate trophic levels (some primates and rodents), others are scavengers (opossum), and others are neither predator nor prey (elephant). Thus, even if, after additional species are examined, strong predators remain more accurate localizers than exclusively prey species, a more general explanatory factor that would apply readily to all species would remain desirable.

The second group of mammals that may be under different selective pressure for localization are those living in a one-dimensional space (in tunnels below the ground) as opposed to those living in two- or three-dimensional space (on the ground or in the air). This factor is plausible because both sound propagation and the directional responses available to animals are greatly restricted in tunnels. Several of the species listed in Table 2 live underground but still forage on the surface (least weasel, grasshopper mouse, kangaroo rat, and gerbil), thus remaining subject to the selective pressures common to other species that live exclusively on the surface. However, the pocket gopher (*Geomys bursarius*), the most specialized North American rodent for underground living, and the Old World mole rats rarely if ever venture above ground. Recently completed auditory tests with the pocket gopher reveal that they have the most restricted frequency range and least sensitive hearing of any mammals yet tested. In addition, the pocket gopher is also unable to localize single brief (100 msec or less) noise bursts emitted from loudspeakers 180° apart (R. S. Heffner, et al., 1987). Thus the pocket gopher has very unusual auditory characteristics which may be attributable to its underground habitat. Only one other strongly fossorial mammal has been examined, the mole rat, *Spalax*, and electrophysiological recordings from its auditory system indicate that it may also have a very restricted hearing range (Bruns, Muller, Hofer, Heth, & Nevo, 1988). Thus, it seems likely that hearing is affected

by unusual environmental adaptations including underground hearing and it will be useful to examine this idea in additional species that vary in their degree of fossorial specialization.

Although it seems clear that factors such as interaural distance, life-style, and habitat have contributed to the differences in sound-localization acuity among different mammalian species, the question remains as to whether there is some more fundamental factor that alone accounts for the variation. The possibility exists that there may be a common factor that explains why very different species should possess similar localization acuity, such as humans and elephants, or horses and gerbils. In searching for such a factor we have noted, as have others, that localizing a sound source is closely tied to localizing it visually (e.g., Pumphrey, 1950). That is, a principal function of sound localization seems to be to direct the eyes toward the source of a sound so that it can be identified visually. It is this functional relation that may be the basis for the heretofore puzzling correlation between the number of neurons in the MSO and the number of neurons in the abducens nucleus (Harrison & Irving, 1966). Although anatomical studies since that time have revealed no direct neural connection between the MSO and the abducens nerve nucleus (or other nuclei in the eye-position system), the abducens nucleus is an "eye-azimuth" motor nucleus and is involved in visually locating objects in space just as the MSO is involved in locating them acoustically. These observations led to a search for a visual parameter that might be a unifying factor explaining the differences in sound-localization acuity among all mammals.

In searching for visual correlates of sound-localization acuity, it can be noted that animals with large overlapping, or binocular, visual fields (mostly primates and carnivores and perhaps predatory species in general) tend to have good sound-localization acuity, whereas those with less overlapping, or small binocular, fields (usually hoofed animals and rodents and perhaps prey species in general) have poorer acuity (R. S. Heffner & Heffner, 1985b). Because the size of the visual fields is quantifiable, a correlation coefficient can be computed. At a statistically reliable value of $r = 0.70$, this factor accounts for almost 50% of the variation in sound-localization acuity, but it lacks intuitive explanatory value and contains several deviant points (i.e., species) which suggest other related visual parameters should be examined.

One such parameter that seems promising is a measure of the horizontal width of the subfield of most acute vision. That is, a very narrow field of best vision, such as the foveal field in humans, may place demands on sound-localization accuracy in order to place the narrow fovea directly on the sound source. Animals with their most acute vision located in a broad horizontal streak (horses, cattle, and some rodents) may, however, have less demands on accurate eye direction. Since retinal ganglion-cell density maps can be used to derive a measure of the width of the area of best vision that can be applied to all species, this measure of vision is quantifiable and

allows comparison with sound-localization acuity. Among eight species the correlation between sound-localization threshold and the width of the area of best vision is strikingly high and reliable ($r = 0.96$, $p < 0.01$; R. S. Heffner & Heffner, 1988d). If this relation remains strong with a larger number and variety of species, it will reinforce the notion that a primary function of the azimuthal sound-localization system is to allow an animal to direct its visual system for scrutinizing an object or event more closely. That this function might have been the single most influential factor in the evolution of sound localization among mammals has some intuitive appeal (Pumphrey, 1950).

REFERENCES

Aitkin, L. (1986). *The auditory midbrain.* Contemporary neuroscience. Clifton,NJ: Humana Press.

Altschuler, R. A., Parakkal, M. H., & Fex, J. (1983). Localization of enkephalin-like immunoreactivity in acetylcholinesterase-positive cells in the guinea-pig lateral superior olivary complex that project to the cochlea. *Neuroscience,* **9,** 621–630.

Boudreau, J. C., & Tsuchitani, C. (1968). Binaural interaction in the cat superior olive S-segment. *Journal of Neurophysiology,* **31,** 442–454.

Boudreau, J. C., & Tsuchitani, C. (1970). Superior olive S-segment cell discharge to tonal stimulation. In W. D. Neff (Ed.), *Contributions to Sensory Physiology* (Vol. 4, pp. 144–213). New York: Academic Press.

Brown, C. H., Beecher, M. D., Moody, D. B., & Stebbins, W. C. (1980). Localization of noise bands of Old World monkeys. *Journal of the Acoustical Society of America,* **68,** 127–132.

Bruns, V., Muller, M., Hofer, W., Heth, G., & Nevo, E. (1988). Inner ear structure and electrophysiological audiograms of the subterranean mole rat, *Spalax ehrenbergi. Hearing Research,* **33,** 1–10.

Cant, N. B., & Gaston, K. C. (1982). Pathways connecting the right and left cochlear nuclei. *Journal of Comparative Neurology,* **212,** 313–326.

Casseday, J. H., & Neff, W. D. (1973). Localization of puretones. *Journal of the Acoustical Society of America,* **54,** 365–372.

Casseday, J. H., & Smoak, H. A. (1981). Effects of unilateral ablation of anteroventral cochlear nucleus on localization of sound in space. In J. Syka & L. Aitkin (Eds.), *Symposium on neuronal mechanisms of hearing* (pp. 277–282). New York: Plenum Press.

Chambers, R. E. (1971). *Sound localization in the hedgehog (Paraechinus hypomelas).* Unpublished master's thesis, Florida State University, Tallahassee.

Chan, J. C. K., & Yin, T. C. T. (1984). Interaural time sensitivity in the medial superior olive of the cat: Comparison with the inferior colliculus. *Neuroscience Abstracts,* **10,** 844.

Galambos, R., Schwartzkopff, J., & Rupert, A. (1959). Microelectrode studies of superior olivary nuclei. *American Journal of Physiology,* **197,** 527–536.

Glendenning, K. K., Hutson, K. A., Nudo, R. J., & Masterton, R. B. (1985).

Acoustic chiasm, II. Anatomical basis of binaurality in lateral superior olive of cat. *Journal of Comparative Neurology*, **232**, 261–285.

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

Goldberg, J. M., & Brown, P. B. (1968). Functional organization of dog superior olivary complex: An anatomical and electrophysiological study. *Journal of Neurophysiology*, **31**, 639–656.

Guinan, J. J., Jr., Guinan, S. S., & Norris, B. E. (1972). Single auditory units in the superior olivary complex. I. Responses to sounds and classification based on physiological properties. *International Journal of Neuroscience*, **4**, 101–120.

Guinan, J. J., Jr., Norris, B. E., & Guinan, S. S. (1972). Single auditory units in the superior olivary complex. II. Locations of unit categories and tonotopic organization. *International Journal of Neuroscience*, **4**, 147–166.

Hall, J. L. (1965). Binaural interaction in the accessory superior olivary nucleus of the cat. *Journal of the Acoustical Society of America*, **37**, 814–823.

Harrison, J. M., & Downey, P. (1970). Intensity changes at the ear as a function of the azimuth of a tone source: A comparative study. *Journal of the Acoustical Society of America*, **47**, 1509–1518.

Harrison, J. M., & Feldman, M. L. (1970). Anatomical aspects of the cochlear nucleus and superior olivary complex. In W. D. Neff (Ed.), *Contributions to Sensory Physiology* (Vol. 4, pp. 95–142). New York: Academic Press.

Harrison, J. M., & Irving R. (1966). Visual and nonvisual auditory systems in mammals. *Science*, **154**, 738–743.

Heffner, H., & Masterton, R. B. (1980). Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *Journal of the Acoustical Society of America*, **68**, 1584–1599.

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). Sound localization in wild Norway rats (*Rattus norvegicus*). *Hearing Research*, **19**, 151–555.

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

Heffner, R. S., & Heffner, H. E. (1983a). Hearing in large mammals: Horses (*Equus caballus*) and cattle (*Bos taurus*). *Behavioral Neuroscience*, **97**, 299–309.

Heffner, R. S., & Heffner, H. E. (1983b). Sound localization and high-frequency hearing in horses. *Journal of the Acoustical Society of America*, **73**, S42.

Heffner, R. S., & Heffner, H. E. (1985a). Hearing in mammals: The least weasel. *Journal of Mammalogy*, **66**, 745–755.

Heffner, R. S., & Heffner, H. E. (1985b). Auditory localization and visual fields in mammals. *Neuroscience Abstracts*, **11**, 547.

Heffner, R. S., & Heffner, H. E. (1986a). Localization of tones by horses: Use of binaural cues and the role of the superior olivary complex. *Behavioral Neuroscience*, **100**, 93–103.

Heffner, R. S., & Heffner, H. E. (1986b). *Variation in the use of binaural localization cues among mammals*. Abstracts of the ninth midwinter research meeting of the Association for Research in Otolaryngology, p. 108.

Heffner, R. S., & Heffner, H. E. (1987). Localization of noise, use of binaural cues, and a description of the superior olivary complex in the smallest carnivore, the least weasel (*Mustela nivalis*). *Behavioral Neuroscience,* **101,** 701–708.

Heffner, R. S., & Heffner, H. E. (1988a). Sound localization in a predatory rodent, the northern grasshopper mouse (*Onychomys leucogaster*). *Journal of Comparative Psychology,* **102,** 66–71.

Heffner, R. S., & Heffner, H. E. (1988b). *Interaural phase and intensity discrimination in the horse using dichotically presented stimuli.* Abstracts of the eleventh midwinter research meeting of the Association for Research in Otolaryngology, p. 233.

Heffner, R. S., & Heffner, H. E. (1988c). Sound localization and use of binaural cues by the gerbil (*Meriones unguiculatus*). *Behavioral Neuroscience,* **102,** 422–428.

Heffner, R. S., & Heffner, H. E. (1988d). The relation between vision and sound localization acuity in mammals. *Society for Neuroscience Abstracts,* **14.**

Heffner, R. S., & Heffner, H. E. (1988e). Sound localization acuity in the cat: Effect of azimuth, signal duration, and test procedure. *Hearing Research,* **36,** 221–232.

Heffner, R. S., & Heffner, H. E. (1989). Sound localization, use of binaural cues, and the superior olivary complex in pigs. *Brain, Behaviour and Evolution,* **33,** 248–258.

Heffner, R. S., Richard, M. M., & Heffner, H. E. (1987). Hearing and the auditory brainstem in a fossorial mammal, the pocket gopher. *Society for Neuroscience Abstracts,* **13,** 546.

Hutson, K. A., Glendenning, K. K., & Masterton, R. B. (1987). Biochemical basis for the acoustic chiasm? *Society for Neuroscience Abstracts,* **13,** 548.

Irvine, D. R. F. (1986). The auditory midbrain. *Progress in Sensory Physiology,* **7,** pp. 1–279.

Jeffress, L. A. (1958). Medial geniculate body: A disavowal. *Journal of the Acoustical Society of America,* **30,** 802–803.

Jenkins, W. M., & Masterton, R. B. (1982). Sound localization: The effects of unilateral lesions in the central auditory system. *Journal of Neurophysiology,* **47,** 987–1016.

Johnson, D. H. (1980). The relationship between spike rate and synchrony in responses of auditory-nerve fibers to single tones. *Journal of the Acoustical Society of America,* **68,** 1115–1122.

Kelly, J. B. (1980). Effects of auditory cortical lesions on sound localizations of the rat. *Journal of Neurophysiology,* **44,** 1161–1174.

Li, R. Y.-S., & Guinan, J. J. (1971). Antidromic and orthodromic stimulation of neurons receiving calyces of Held. *M.I.T. Quarterly Progress Report,* No. 100, pp. 227–234.

Mast, T. E. (1970). Binaural interaction and contralateral inhibition in the dorsal cochlear nucleus of the chinchilla. *Journal of Neurophysiology,* **33,** 108–115.

Masterton, R. B., Glendenning, K. K., & Nudo, R. J. (1981). Anatomical-behavioral analyses of hindbrain sound localization mechanisms. In J. Syka & L. Aitkin (Eds.), *Symposium on neuronal mechanisms of hearing* (pp. 263–275). New York: Plenum Press.

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

Masterton, R. B., & Imig, T. (1984). Neural mechanisms for sound localization. *Annual Review of Physiology,* **46,** 275–287.

Masterton, R. B., Jane, J. A., and Diamond, I. T. (1967). The role of brainstem auditory structures in sound localization. I. Trapezoid body, superior olive and lateral lemniscus. *Journal of Neurophysiology,* **30,** 341–359.

Masterton, R. B., Thompson, G. C., Brunso-Bechtold, J. K., & RoBards, M. J. (1975). Neuroanatomical basis of binaural phase-difference analysis for sound localization: A comparative study. *Journal of Comparative and Physiological Psychology,* **89,** 379–386.

McFadden, D., & Posanen, E. G. (1976). Lateralization at high frequencies based on interaural time differences. *Journal of the Acoustical Society of America,* **59,** 634–639.

Mills, A. W. (1958). On the minimum audible angle. *Journal of the Acoustical Society of America,* **30,** 237–246.

Moore, J. K. (1987). The human auditory brain stem: A comparative view. *Hearing Research,* **29,** 1–32.

Moore, J. K., & Moore, R. Y. (1971). A comparative study of the superior olivary complex in the primate brain. *Folia Primatologica,* **16,** 35–51.

Morest, D. K. (1968). The collateral system of the medial nucleus of the trapezoid body of the cat, its neuronal architecture and relation to the olivocochlear bundle. *Brain Research,* **9,** 288–311.

Phillips, D. P., & Brugge, J. F. (1985). Progress in neurophysiology of sound localization. *Annual Review of Psychology,* **36,** 245–274.

Pumphrey, R. J. (1950). Hearing. *Symposium of the Society for Experimental Biology,* **4,** 1–18.

Rasmussen, G. L. (1946). The olivary peduncle and other fiber projections of the superior olivary complex. *Journal of Comparative Neurology,* **84,** 141–219.

Ravizza, R. J., Heffner, H., & Masterton, R. B. (1969). Hearing in primitive mammals. I. Opossum (*Didelphis virginiana*). *Journal of Auditory Research,* **9,** 1–7.

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

Renaud, D. L., & Popper, A. N. (1975). Sound localization by the bottlenose porpoise *Tursiops truncatus. Journal of Experimental Biology,* **63,** 569–585.

Rose, J. E., Gross, N. B., Geisler, C. D., & Hind, J. E. (1966). Some neural mechanisms in the inferior colliculus of the cat which may be relevant to localization of a sound source. *Journal of Neurophysiology,* **29,** 288–314.

Rosenzweig, M. R., & Amon, A. H. (1955). Binaural interaction in the medulla of the cat. *Experientia,* **11,** 498–500.

Stebbins, W. C. (1970). Studies of hearing and hearing loss in the monkey. In W. C. Stebbins (Ed.), *Animal psychophysics* (pp. 41–66). New York: Appleton-Century-Crofts.

Stotler, W. W. (1953). An experimental study of the cells and connections of the superior olivary complex of the cat. *Journal of Comparative Neurology,* **98,** 401–432.

Terhune, J. M. (1974). Directional hearing of the harbor seal in air and water. *Journal of the Acoustical Society of America*, **56,** 1862–1865.

Thompson, G. C., & Masterton, R. B. (1978). Brain stem auditory pathways involved in reflexive head orientation to sound. *Journal of Neurophysiology*, **41,** 1183–1202.

Tolbert, L. P., Morest, D. K., & Yurgelun-Todd, D. A. (1982). The neuronal architecture of the anteroventral cochlear nucleus of the cat in the region of the cochlear nerve root: Horseradish peroxidase labelling of identified cell types. *Neuroscience*, **7,** 3031–3052.

von Bekesy, G. (1930). Ueber das Richtunghoren bei einer Zeitdifferenz oder Lautstarkenungleichheit der beiderseitigen Schalleinwerkungen. *Physikalische Zeitschrift*, **31,** 857–868.

White, J. S., & Warr, W. B. (1983). The dual origins of the olivocochlear bundle in the albino rat. *Journal of Comparative Neurology*, **219,** 203–214.

Yin, T. C. T., & Kuwada, S. (1983). Binaural interaction in low-frequency neurons in inferior colliculus of the cat. III. Effects of changing frequency. *Journal of Neurophysiology*, **50,** 1020–1042.

Zook, J. M., & Casseday, J. H. (1982). Cytoarchitecture of auditory system in lower brainstem of the mustache bat, *Pteronotus parnellii*. *Journal of Comparative Neurology*, **207,** 1–13.