

Hearing in Large and Small Dogs: Absolute Thresholds and Size of the Tympanic Membrane

Henry E. Heffner

Laboratory of Comparative Hearing, Bureau of Child Research
University of Kansas

Comparative studies of hearing have shown that the ability of different species of mammals to hear high-frequency sounds is inversely related to the distance between their ears (i.e., functional interaural distance). In order to determine whether this relation applies to within-species as well as to between-species variation in interaural distance, the audiograms of dogs ranging in size from a Chihuahua to a Saint Bernard were determined. The results indicated that there is no significant relation between interaural distance and the high-frequency hearing ability of individual dogs. Further analysis, which included measurements of the tympanic membrane, indicated that neither interaural distance nor area of the tympanic membrane is related to variation in high-frequency hearing, low-frequency hearing, or absolute sensitivity among dogs.

Comparative studies of hearing have revealed that the ability of mammals to hear high-frequency sounds is far from uniform, varying widely from one species to the next. Humans are generally capable of hearing 19 kHz; elephants hear only as high as 10 kHz; monkeys, 42 kHz; rats, 72 kHz; and bats, 115 kHz (for a recent review, see R. Heffner & Heffner, 1980). Thus, high-frequency hearing in mammals varies over a range of at least three octaves.

In searching for an explanation of this variation, it has become apparent that the size of the animal plays some role. In particular, the high-frequency limit of hearing is correlated with the functional distance between the two ears where functional distance (Δt) is defined as the distance between the ears divided by the speed of sound in the ecological medium they occupy (H. Heffner & Masterton, 1980; Masterton, Heffner, & Ravizza, 1969). That is to say, land mammals with small heads and close-set ears (or marine mammals even with wide-set ears) are better able to hear high-

frequency sounds than land mammals with large heads and wide-set ears. To be more precise, high frequency hearing varies inversely with interaural distance and ultimately with the interaural time and intensity difference cues used for sound localization. Thus, the variation in mammalian high-frequency hearing is not random nor particularly related to echo-locating or marine habitats but, instead, appears to vary predictably with functional interaural distance.

Because the relation between functional interaural distance and high-frequency hearing that has been established for comparisons *among* species is so strong (i.e., $r = -.89$), the question arises: Is it also present among individuals of the same species; that is, do individuals with close-set ears have higher limits of hearing regardless of their species? Indeed, since the frequency response of the ear seems closely related to the physical size of the ear, such that small ears are better able to transduce high frequencies than large ears (e.g., Fleischer, 1978), it is conceivable that individuals with small heads and therefore smaller ears might be better able to hear high frequencies than do larger individuals.

One way to test this extension of the relation is to determine the variation in high-frequency limit among individuals of a species that varies widely in interaural distance. Dogs are one such species. Because dogs vary greatly in size and inter-

This research was supported by National Institutes of Health Grants NS 12992 and HD 02528 to the Bureau of Child Research, University of Kansas, and by Biomedical Sciences Support Grant RR 07037 to the University of Kansas.

Requests for reprints should be sent to Henry Heffner, Laboratory of Comparative Hearing, Bureau of Child Research, University of Kansas, P.O. Box 738, Parsons, Kansas 67357.

aural distance, a determination of high-frequency limits in large and small dogs offers the opportunity to determine whether high-frequency hearing varies with interaural distance within a species. Indeed, that such variation might occur in dogs was suggested by Galton in 1883 when he observed that small dogs readily responded to his high-frequency whistle whereas large dogs did not.

The primary purpose of this investigation, then, was to establish whether high-frequency hearing varies among dogs of greatly differing interaural distance. Once this investigation began, however, it became apparent that the results might have a bearing on the effect of body size and interaural distance on other hearing parameters as well (such as low-frequency hearing and maximum sensitivity) and that each of these results might be of further relevance if some measure of the size of the animal's ears, such as the tympanum, could also be obtained. Therefore, this report presents a comparison of several parameters of hearing in large and small dogs as well as an analysis of the variation in tympanic size, body size, and interaural distance.

Method

The experimental procedures used here can be conveniently divided into two parts, one behavioral and the other anatomical. The behavioral procedure consisted of determining the hearing abilities of dogs by use of a two-choice psychophysical technique. The animal indicated the presence or absence of a tone by making one response when a tone was perceived and a different response when it was not perceived. The anatomical procedure consisted of dissecting the ears of 15 dogs of varying size and interaural distance, including the largest and smallest animals used in the behavioral study, and measuring the area of their tympanic membranes.

Subjects

Four dogs (chosen on the basis of their interaural distances) were used in the complete hearing tests. The animals were a 2-yr-old female Chihuahua, a 4-yr-old male Dachshund, a 2-yr-old male Poodle, and a 2-yr-old male Saint Bernard. In addition, the upper limit of hearing was determined for a fifth dog, a 1-yr-old male Pointer, and is included in this report. Anatomical measurements of the tympanic membrane were made on the ears of 15 dogs, including the Chihuahua and Saint Bernard used in the behavioral study.

Behavioral Apparatus

The three smaller dogs and the Pointer were tested in a cage constructed of $\frac{1}{2}$ -in. (1.27-cm) hardware cloth attached to a wooden frame (90 × 65 × 65 cm). Four water spouts and associated cue lights were mounted on the front of the cage as shown in Figure 1. Three of the spouts were mounted in a horizontal row 40 cm apart, with the center or "observing" spout recessed so that an animal had to place its head through an opening in the cage in order to reach it. The two side spouts projected into the cage as did the fourth (reward) spout, which was located 30 cm below the level of the observing spout. A constant-pressure water reservoir was connected to the bottom or "reward" spout by an electrically operated water valve. Each of the four water spouts was connected to a separate sensing switch, which detected when an animal made contact with it. A loudspeaker was located 50 to 100 cm in front of the cage and oriented toward the position occupied by the animal's head when it was licking the observing spout. The test cage was mounted on 65-cm legs and placed in a burlap-draped acoustical chamber.

The front of the cage was adjustable in that it could be raised or lowered to accommodate the different-sized dogs. In order that there would be no obstruction between the dog's ears and the loudspeaker when the animal was licking the observing spout, the position

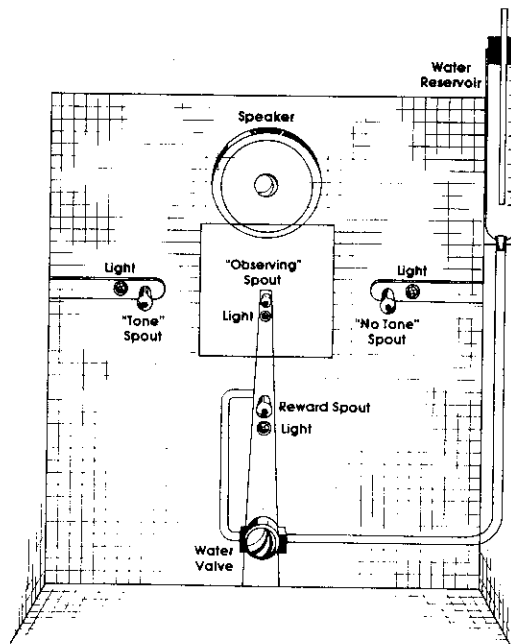


Figure 1. Inside view of the front panel of the test cage. (A dog initiated a trial by placing its head through the opening and licking the observing spout. It then licked either the tone spout to indicate the presence of a tone or the no-tone spout to indicate the absence of any tone. Correct responses were rewarded with water at the reward spout. The cue lights adjacent to the spouts were primarily of use in training.)

of the observing spout could be varied forward or backward so that each dog had to place its entire head (and ears) through the center opening in order to reach it.

The Saint Bernard was tested in a cage similar to the one described above except that a water bowl replaced the reward spout and the dimensions of the cage were scaled up to accommodate its larger size.

Acoustical Apparatus

Details of stimulus-generation and calibration have been described elsewhere (R. Heffner, Heffner, & Masterton, 1971). Briefly, sine waves were produced by an oscillator connected to an electronic switch, then to an attenuator, and finally by an impedance-matching transformer to a wide-range loudspeaker (Acoustic Research 3a or University T202 tweeter). In order to avoid switching transients, the onset and offset of the tone were slowed to allow at least 10 full cycles of the stimulus to occur during rise and fall of the tone with a minimum rise-decay of 25 msec.

The entire apparatus was carefully calibrated at each frequency for each cage configuration. Actual sound pressure levels (i.e., decibels re $20 \mu\text{N}/\text{m}^2$) were measured with a microphone amplifier (Brüel & Kjaer [B & K] 2604), $\frac{1}{4}$ -in. (.64-cm) microphone (B & K 4135), and an octave filter (B & K 1612). The sound measurements were taken with the microphone in the position occupied by the animal's head when it contacted the observing spout. Slight adjustments of the speaker and cage were made to ensure that the sound field around the animal's ears was homogeneous and that the sound was always louder at the observing spout than elsewhere in the cage.

Psychophysical Procedure

Training. Initially, the dogs were trained to perform the two-choice procedure by using visual cues as follows: A water-deprived animal was placed in the cage and trained to lick the observing spout in order to receive water, which was delivered through the reward spout. Once the dog had learned to lick the observing spout, it was trained to follow this response by licking one of the two side spouts in order to receive water. At this stage of training, a visual cue was introduced in which the light adjacent to the observing spout would come on to signal that a trial could be begun. When the dog licked the observing spout, the observing light was turned off, and the light adjacent to one of the side spouts was turned on. A response to the illuminated side spout was followed by turning off the side light and turning on the light adjacent to the reward spout. Thus, at this stage of training, the dog needed only to contact in sequence the spouts adjacent to the lights in order to obtain a reward. When the dog licked the reward spout, a water reward was delivered, and the reward light was then turned off. If the animal licked the incorrect side spout, its light was turned off, no reward was given, and the room lights were momentarily dimmed. The animal was then permitted to initiate another trial after a short delay (usually 3-5 sec).

Once a dog had learned the two-choice procedure by tracking the visual cues (usually one to three sessions), auditory training was begun. This stage consisted of turning on a train of tone pulses (.2 sec on, .1 sec off) on those trials in which a left response was correct. Initially, an animal would have both the visual and the auditory cue (i.e., left light and tone vs. right light and silence), with the visual cue being gradually eliminated by turning on both of the side lights when the observing response was made. The dogs generally required two to four sessions to learn to perform on the basis of the auditory cue alone.

Testing. For audiometric testing, then, the dog placed its head through the opening in the cage to contact the observing spout with its mouth. This response fixed the dog's head in relation to the sound field and initiated a trial. Tones were presented randomly on half of the trials and were turned on as soon as the animal made the observing response. The animal was required to maintain continuous contact with the observing spout (and, presumably, listen) for 1 sec before making a side response. At the end of this listening period, the observing light was turned off, both side lights were turned on, and the animal's first response to either side spout was registered. Of course, the animal was rewarded only for responding to the left spout in the presence of a tone (regardless of whether the tone eventually proved to be subliminal) and to the right spout if no tone was presented. Errors were not rewarded but were followed, instead, by an error-time-out before the next trial could be begun. In order to reduce the possibility of an animal developing a response bias, a correction procedure was used in which the stimulus condition (and response requirement) was not changed following an error. This procedure forced the animal to respond eventually to the other side before it could receive a reward. Because the animal could respond correctly on such trials without using the auditory cue, these trials were not used in the calculation of an animal's performance.

Threshold determination was conducted in two ways: First, the threshold for a particular frequency was estimated by reducing the intensity of the tone in steps of 5 or 10 dB, with blocks of 10 or 20 trials given at each intensity, until an animal could no longer distinguish the tone and no-tone trials. Once an estimate of threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity by 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold. At least 50 trials were given at intensities just above and below threshold, with threshold defined statistically as the lowest intensity at which an animal could distinguish tone trials from no-tone trials at the .01 two-tailed level of significance (binomial distribution), which is 35 correct in 50 trials. Each frequency was then retested in the same manner in a subsequent session, and testing was judged complete if the two thresholds were within 3 dB of each other. If the thresholds differed by more than 3 dB, testing was continued until a stable threshold value emerged.

Thresholds were determined first for tones in the midfrequency range (4, 8, and 16 kHz) following which the low and then the high frequencies were tested. Once thresholds had been obtained for all frequencies,

each threshold was briefly retested to ensure that it had not changed.

Anatomical Procedure

The average body weight and interaural distance for each behavioral animal and 13 others were recorded.

The bullae of each of 15 dogs were removed and dissected to expose the tympanic membrane. The image of the membrane was then projected with an opaque projector, and its outline was traced. The area of the tympanic membrane was measured with a planimeter, with each membrane being measured four times to ensure reliability. The measurements for an animal's two ears were then averaged to arrive at a value for that particular animal.

Results

Anatomy

The areas of the tympanic membranes of 15 dogs are shown in Figure 2. The areas ranged from 30 mm² to 55.2 mm² for animals ranging in body weight from 4.3 kg to 45.5 kg. It is of interest to note that the dogs with the largest and smallest tympanic membranes were the Saint Bernard and the Chihuahua used in the behavioral study. Furthermore, although the ears of the other three behavioral animals were not measured, the high correlation between body size and area of the tympanic membrane ($r = .83$, $p < .01$) suggests that the tympanic membranes of these animals were inter-

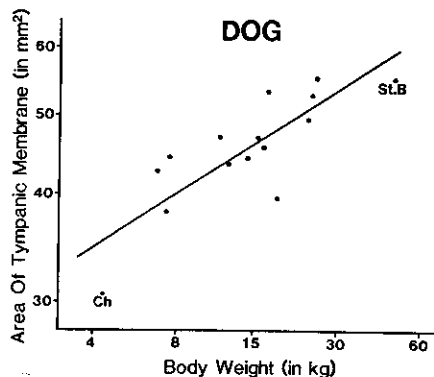


Figure 2. Relation between body weight and area of the tympanic membrane (Ch, the Chihuahua, and St.B, the Saint Bernard, used in the behavioral section). (Note the positive relation between body size and area, $r = .83$).

mediate in size to the other two animals'. Thus, it appears that the tympanic membranes of dogs show significant variation in size, with those of the largest dog used in the behavioral study nearly twice the area of those of the smallest dog. Just how this variation in tympanic size is related to hearing ability can be seen in the following sections.

Behavior

Complete audiograms obtained for four of the dogs are shown in Figure 3. Beginning at the low-frequency end, the audiograms show a gradual increase in sensitivity as frequency is increased until the point of best sensitivity is reached at about 8 kHz. Above 8 kHz the audiograms decrease in sensitivity, with the decrease becoming relatively steep above 32 kHz. Thus, at a level of 60 dB (SPL) the audiograms range from 67 Hz to 45 kHz.

High-frequency hearing. Comparison of the audiograms in Figure 3 shows that there is little variation in high-frequency hearing. This finding is more clearly shown in Table 1, which lists the 60-dB high-frequency cutoffs (i.e., highest frequency audible at 60 dB) for the four dogs and for an additional animal (the Pointer) whose high-frequency hearing alone was measured. As shown in the table, the high-frequency cutoffs range only from 41 kHz to 47 kHz. Indeed, four of the five cutoffs were within 2 kHz of each other. On the basis of the differences in their interaural distances, one would have predicted a difference of more than 10 kHz in the cutoffs of the largest and smallest dogs. Yet, the largest and smallest dogs had identical cutoffs. Therefore, there is no clear or reliable relation between high-frequency hearing and interaural distance among these animals.

In considering the similarities and differences among the audiograms of the dogs, the possibility arose that the type of pinna of each dog may have affected its threshold. Of the dogs used here, the Chihuahua had erect pinnae, and the others had hanging or pendant pinnae. As can be seen in Table 1, however, there does not appear to be any difference between the Chihuahua's upper

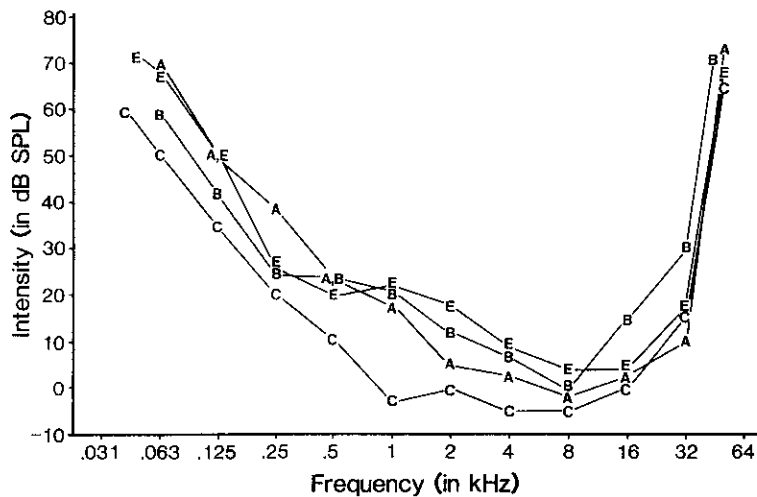


Figure 3. Audiograms of four dogs. (A, Chihuahua; B, Dachshund; C, Poodle; E, Saint Bernard.)

limit and the limits of the other dogs. In order to further explore for a possible pinna effect, however, the Dachshund was retested with its pinnae taped over its head to expose the auditory canal. A comparison of these thresholds with those taken with the pinnae in their normal position revealed no differences at 8 kHz and below and, perhaps surprising, only minor differences (less than 3 dB) at the higher frequencies. Thus, the type and position of the pinnae do not appear to have any large effect on the audiogram, although what effect they do have is at the highest frequencies.

From these results, it appears that the high-frequency hearing ability of individual dogs is relatively uniform and does not vary either with interaural distance or, for that matter, with the size of the tympanic mem-

brane. Whereas differences in high-frequency cutoffs of greater than 10 kHz would have been expected if the *interspecies* relation between interaural distance and high-frequency hearing applied, the actual *intraspecies* variation was only 6 kHz and unrelated to interaural distance. Therefore, the correlation between interaural distance and high-frequency hearing does not appear to apply to variation within a species. However, these same results support the relation for between-species variation, as a later section shows.

Additional hearing parameters. Though high-frequency hearing does not vary much among individual dogs, the question arises as to whether other hearing parameters might vary with the size of the animal. Specifically, it has been noted that large animals have better low-frequency hearing

Table 1
Descriptions of the Five Dogs, With Actual and Predicted High-Frequency Hearing Cutoffs

Dog	Breed	Age (in yr)	Maximum Δt (in μsec) ^a	High-frequency cutoff (in kHz) ^b	
				Predicted ^c	Actual
A	Chihuahua	2	320	40	47
B	Dachshund	4	370	38	41
C	Poodle	2	400	36	46
D	Pointer	1	510	33	45
E	St. Bernard	1	650	29	47

^a Maximum interaural distance measured around the head divided by the speed of sound in air.

^b Highest frequency audible at 60 dB (SPL).

^c Predicted from the relation between interaural distance and high-frequency hearing.

and tend to be more absolutely sensitive to sound than small animals (e.g., H. Heffner & Masterton, 1980; Khanna & Tonndorf, 1978; von Bekesy, 1960). However, a perusal of the dogs' audiograms (Figure 3) again reveals no obvious link between these two parameters and the size of the animal. Indeed, the animal with the best sensitivity and best low-frequency hearing was the Poodle, a dog of only average size. Thus, there does not seem to be any particular relation between body size and either low-frequency hearing or maximum sensitivity among individual dogs.

Discussion

The primary conclusion of this study is that there is little variation in the audiograms of individual dogs and what variation does exist is not reliably related to the size of the animal, its interaural distance, or the area of its tympanum. This relative invariance of hearing within a species, if it holds for other species, has at least two immediate implications: one concerning the relation between interaural distance and high-frequency hearing, the other concerning the effect of tympanic area on hearing.

Interaural Distance and High-Frequency Hearing

Within species. Though the relation between interaural distance and high-frequency hearing is well established for comparisons between different mammalian species, the results of this investigation strongly suggest that a similar relation does not occur among individual dogs. Thus, in view of the lack of evidence to the contrary, it appears that high-frequency hearing is not related to *individual* variations in interaural distance or, for that matter, to its direct correlates, head size and body size. It can be concluded that the high-frequency limit of hearing is a species character, not an individual character, and therefore, short of environmental extremes, it is more a product of "heritage than of habitus."

Between species. Though not an individual character, high-frequency hearing is a species character, and one that is closely

related to interaural distance. This relation is illustrated in Figure 4 in which interaural distance is represented by maximum Δt and high-frequency hearing limit is defined as the highest frequency audible at an intensity of 60 dB. The correlation between these two parameters is -0.89 ($p < .001$) and is based on audiograms for 32 genera of mammals ranging in size from mouse and bat to elephant and killer whale, with the dogs in the present experiment clustered about the mammalian midrange. It should be noted that this relation accounts for almost 80% of the known variation among mammalian upper limits of hearing regardless of their ecological medium, sonar or echo-location abilities, or, for that matter, any other adaptation strategy.

The existence of a strong inverse relation between maximum Δt and high-frequency hearing has been ascribed to selective pressure for accurate sound localization (e.g., Masterton et al., 1969; R. Heffner & Heffner, 1980). Briefly, the argument goes thus: The two binaural cues for sound localization, the difference in time of arrival of a sound at the two ears (Δt) and the difference in frequency-intensity spectra of a sound reaching the two ears (Δfi), depend on the functional distance between the two ears and the sound shadow of the head and pinnae. That is to say, the farther apart the ears, the larger will be the Δt cue for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with wide-set ears, both because the sound attenuation is slightly greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which effectively shadow the high-frequency content of sound.

Although the two binaural sound-localization cues are readily available to animals with large heads, the magnitude of either cue is diminished in animals with functionally close-set ears. In the case of Δt , the time differences naturally available may be so small that the nervous system can detect only large changes in sound direction. However, an animal with a small head always has a Δfi cue available, providing only that it is able to perceive frequencies that are high enough to be effectively shadowed by its head and pinnae. Therefore, given the ecological importance to an animal of lo-

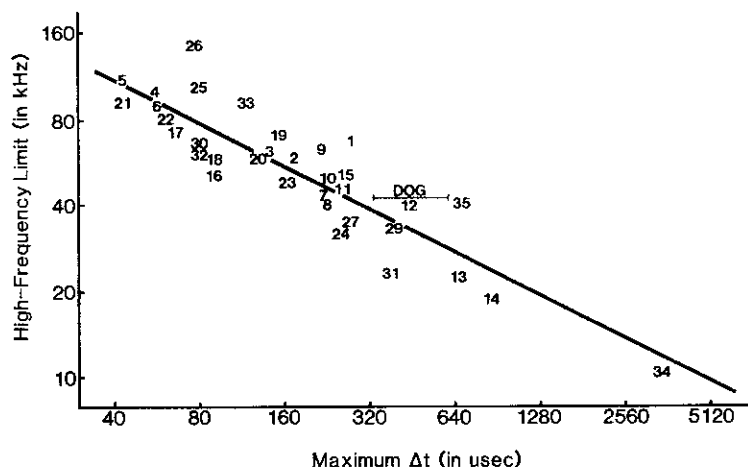


Figure 4. Relation between interaural distance (maximum Δt) and the 60-dB high-frequency hearing limit. (Horizontal line indicates range of interaural distances for dogs. The high-frequency limits were obtained from published behavioral audiograms, which were determined in air except as noted. Values for maximum Δt were derived from measurements made by the author. 1, opossum [*Didelphis virginiana*; Ravizza, Heffner, & Masterton, 1969a]; 2, hedgehog [*Hemiechinus auritus*; Ravizza, Heffner, & Masterton, 1969b]; 3, tree shrew [*Tupaia glis*; H. Heffner, Ravizza, & Masterton, 1969a]; 4, horseshoe bat [*Rhinolophus ferrumequinum*; Long & Schnitzler, 1975]; 5, little brown bat [*Myotis lucifugus*; Dalland, 1965]; 6, big brown bat [*Eptesicus fuscus*; Dalland, 1965]; 7, slow loris [*Nycticebus coucang*; H. Heffner & Masterton, 1970]; 8, potto [*Perodicticus potto*; H. Heffner & Masterton, 1970]; 9, bush baby [*Galago senegalensis*; H. Heffner, Ravizza, & Masterton, 1969b]; 10, owl monkey [*Aotus trivirgatus*; Beecher, 1974a]; 11, squirrel monkey [*Saimiri sciureus*; Beecher, 1974b; Green, 1975]; 12, macaque [*Macaca* sp.; Behar, Cronholm, & Loeb, 1965; Stebbins, Green, & Miller, 1966]; 13, chimpanzee [*Pan troglodytes*; Farrer & Prim, Note 1]; 14, human [*Homo sapiens*; Davis, 1960]; 15, rabbit [*Oryctolagus cuniculus*; H. Heffner & Masterton, 1980]; 16, kangaroo rat [*Dipodomys merriami*; H. Heffner & Masterton, 1980]; 17, cotton rat [*Sigmodon hispidus*; H. Heffner & Masterton, 1980]; 18, gerbil [*Meriones unguiculatus*; Ryan, 1976]; 19, laboratory rat [*Rattus norvegicus*; Kelly & Masterton, 1977]; 20, wood rat [*Neotoma floridana*; H. Heffner, unpublished observations, 1980]; 21, feral house mouse [*Mus musculus*; H. Heffner & Masterton, 1980]; 22, laboratory mouse [*Mus musculus*; H. Heffner & Masterton, 1980]; 23, guinea pig [*Cavia porcellus*; R. Heffner et al., 1971]; 24, chinchilla [*Chinchilla* sp.; Miller, 1970]; 25, dolphin underwater [*Inia geoffrensis*; Jacobs & Hall, 1972]; 26, porpoise under water [*Tursiops truncatus*; Johnson, 1967]; 27, killer whale under water [*Orcinus orca*; Hall & Johnson, 1972]; 29, sea lion in air [*Zalophus californianus*; Schusterman, Balliet, & Nixon, 1972]; 30, harbor seal under water [*Phoca vitulina*; Mohl, 1968]; 31, harbor seal in air [*Phoca vitulina*; Mohl, 1968]; 32, ringed seal under water [*Pusa hispida*; Terhune & Ronald, 1975]; 33, harp seal under water [*Pagophilus groenlandicus*; Terhune & Ronald, 1972]; 34, elephant [*Elephas maximus*; R. Heffner & Heffner, 1980]; 35, domestic sheep [*Ovis aries*; Wollack, 1963]. The numerical ordering of the individual species follows the taxonomic system of Simpson, 1945.)

calizing a sound source, animals with functionally close-set ears are subjected to more selective pressure to hear high frequencies than animals with more widely set ears.

Just how do dogs fit into the overall relation between interaural distance and high-frequency hearing? It can be seen in Figure 4 that the upper limit of hearing of dogs is fairly close to the value predicted from the interaural distance of the smallest dog but that it becomes increasingly more divergent for the larger dogs. Indeed, the Saint Bernard heard frequencies higher than would be expected on the basis of its

interaural distance ($p < .05$). What this means, biologically, is that high-frequency hearing ability apparently cannot change rapidly enough to follow the variation in interaural distance among individuals or even varieties within a species.

Size of the Tympanic Membrane

Because the size of the tympanic membrane, like the size of other parts of the ear (e.g., auditory canal, bulla, middle ear bones), is considered to be a factor in determining the response properties of the

ear (e.g., Dallos, 1973; Khanna & Tonndorf, 1969; von Bekesy, 1960), it seemed appropriate to determine the degree of its variation in dogs. As was previously noted, the area of the tympanic membranes of dogs varies widely. Indeed, the Saint Bernard used in this study possessed a tympanic membrane with nearly twice the area of the Chihuahua's. What is interesting is that a similar degree of variation seems to exist among humans, whose tympanic membranes have been reported to vary from 50 mm² to 90 mm² (von Bekesy & Rosenblith, 1951). Thus, while the tympanic membranes of dogs differ in size, such variation within a species may not be rare or even unusual.

Correlational analysis shows, not unexpectedly, that the variation in the area of the tympanic membrane is positively correlated with body weight ($r = .83, p < .01$) and somewhat less well correlated with interaural distance ($r = .70, p < .01$). Further analysis with partial correlations, however, reveals that when body weight is statistically held constant, the correlation of tympanic area with interaural distance is no longer statistically reliable ($r = -.22, p > .05$). When interaural distance is statistically held constant, however, the correlation between body weight and area of the tympanic membrane remains relatively high ($r = .63, p < .05$). It appears, then, that the area of the tympanic membrane and, presumably, the overall size of the hearing apparatus are directly related to body weight and only indirectly related to interaural distance. Thus, while tympanic area varies in size with body weight, high-frequency hearing varies with functional interaural distance.

The apparent lack of correlation between tympanic area and hearing ability among dogs, however, does not mean that it is not an important determinate of hearing. Indeed, the physics of the relation between size and sound reception are well known, and, as the now classic case of the kangaroo rat illustrates, an animal that is under selective pressure to extend its hearing range must often change the size of its auditory apparatus to do so (e.g., Webster & Webster, 1972, 1975). Furthermore, it is possible that by using headphones and measuring the sound pressure level at the tympanic

membrane, some difference in sensitivity related to size might have been observed. However, a distinction may be made between the sensitivity of the *ear* (defined as all structures from the tympanic membrane on in to the central nervous system) and the sensitivity of the *animal* (which consists of the contributions of the auditory canal and pinna and includes the effect of the animal's head and body on the sound field). From the present results, it appears that in the latter sense of the term, there is no obvious correlation among dogs between the size of a dog or the size of its tympanum and its auditory sensitivity.

Reference Note

1. Farrer, D. N., & Prim, M. M. *A preliminary report on auditory frequency threshold comparisons of human and pre-adolescent chimpanzees* (Report No. 65-66). Holloman Air Force Base, N. Mex.: U.S. Air Force 6571 Aeromedical Research Laboratory, 1965.

References

- Beecher, M. D. Hearing in the owl monkey (*Aotus trivirgatus*). *Journal of Comparative and Physiological Psychology*, 1974, 86, 898-901. (a)
- Beecher, M. D. Pure tone thresholds of the squirrel monkey (*Saimiri sciureus*). *Journal of the Acoustical Society of America*, 1974, 55, 196-198. (b)
- Behar, I., Cronholm, J. N., & Loeb, M. Auditory sensitivity of the rhesus monkey. *Journal of Comparative and Physiological Psychology*, 1965, 59, 426-428.
- Dalland, J. I. Hearing sensitivity in bats. *Science*, 1965, 150, 1185-1186.
- Dallos, P. *The auditory periphery*. New York: Academic Press, 1973.
- Davis, H. Physics and psychology of hearing. In H. Davis & S. R. Silverman (Eds.), *Hearing and deafness*. New York: Holt, Rinehart & Winston, 1960.
- Fleischer, G. Evolutionary principles of the mammalian middle ear. *Advances in Anatomy, Embryology and Cell Biology*, 1978, 55, Pt. 5, 1-70.
- Galton, F. *Inquiries into human faculty and its development*. London: J. M. Dent & Sons, 1883.
- Green, S. Auditory sensitivity and equal loudness in the squirrel monkey (*Saimiri sciureus*). *Journal of the Experimental Analysis of Behavior*, 1975, 23, 255-264.
- Hall, J. D., & Johnson, C. S. Auditory thresholds of a killer whale *Orcinus orca* Linnaeus. *Journal of the Acoustical Society of America*, 1972, 51, 515-517.
- Heffner, H., & Masterton, B. Hearing in primitive primates: Slow loris (*Nycticebus coucang*) and potto (*Perodicticus potto*). *Journal of Comparative and Physiological Psychology*, 1970, 71, 175-182.
- Heffner, H., & Masterton, R. B. Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *Journal of the Acoustical Society of America*, 1980, 68, 1584-1599.

- Heffner, H. E., Ravizza, R. J., & Masterton, B. Hearing in primitive mammals: III. Tree shrew (*Tupaia glis*). *Journal of Auditory Research*, 1969, 9, 12-18. (a)
- Heffner, H. E., Ravizza, R. J., & Masterton, B. Hearing in primitive mammals: IV. Bushbaby (*Galago senegalensis*). *Journal of Auditory Research*, 1969, 9, 19-23. (b)
- Heffner, R., & Heffner, H. Hearing in the elephant (*Elephas maximus*). *Science*, 1980, 208, 518-520.
- Heffner, R., Heffner, H., & Masterton, B. Behavioral measurements of absolute and frequency difference thresholds in guinea pig. *Journal of the Acoustical Society of America*, 1971, 49, 1888-1895.
- Jacobs, D. W., & Hall, J. D. Auditory thresholds of a fresh water dolphin, *Inia geoffrensis* Blainville. *Journal of the Acoustical Society of America*, 1972, 51, 530-533.
- Johnson, C. S. Sound detection thresholds in marine mammals. In W. N. Tavolga (Ed.), *Marine bioacoustics* (Vol. 2). New York: Pergamon Press, 1967.
- Kelly, J. B., & Masterton, B. Auditory sensitivity of the albino rat. *Journal of Comparative and Physiological Psychology*, 1977, 91, 930-936.
- Khanna, S. M., & Tonndorf, J. Middle ear power transfer. *Archiv für Klinische und Experimentelle Ohren-, Nasen- und Kehlkopfheilkunde*, 1969, 193, 78-88.
- Khanna, S. M., & Tonndorf, J. Physical and physiological principles controlling auditory sensitivity in primates. In C. R. Noback (Ed.), *Sensory systems of primates*. New York: Plenum Press, 1978.
- Long, G. R., & Schnitzler, H. U. Behavioral audiograms from the bat *Rhinolophus ferrumequinum*. *Journal of Comparative Physiology*, 1975, 100, 211-219.
- Masterton, B., Heffner, H., & Ravizza, R. The evolution of human hearing. *Journal of the Acoustical Society of America*, 1969, 45, 966-985.
- Miller, J. D. Audibility curve of the chinchilla. *Journal of the Acoustical Society of America*, 1970, 48, 513-523.
- Mohl, B. Auditory sensitivity of the common seal in air and water. *Journal of Auditory Research*, 1968, 8, 27-38.
- Ravizza, R. J., Heffner, H. E., & Masterton, B. Hearing in primitive mammals: I. Opossum (*Didelphis virginianus*). *Journal of Auditory Research*, 1969, 9, 1-7. (a)
- Ravizza, R. J., Heffner, H. E., & Masterton, B. Hearing in primitive mammals: II. Hedgehog (*Hemiechinus auritus*). *Journal of Auditory Research*, 1969, 9, 8-11. (b)
- Ryan, A. Hearing sensitivity of the mongolian gerbil, *Meriones unguiculatus*. *Journal of the Acoustical Society of America*, 1976, 59, 1222-1226.
- Schusterman, R. J., Balliet, R. F., & Nixon, R. Underwater audiogram of the California sea lion by the conditioned vocalization technique. *Journal of the Experimental Analysis of Behavior*, 1972, 17, 339-350.
- Simpson, G. G. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 1945, 85, 1-350.
- Stebbins, W. C., Green, S., & Miller, F. L. Auditory sensitivity of the monkey. *Science*, 1966, 153, 1646-1647.
- Terhune, J. M., & Ronald, K. The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777): III. The underwater audiogram. *Canadian Journal of Zoology*, 1972, 50, 565-569.
- Terhune, J. M., & Ronald, K. Underwater hearing sensitivity of two ringed seals (*Pusa hispida*). *Canadian Journal of Zoology*, 1975, 53, 227-231.
- von Bekesy, G. *Experiments in hearing*. New York: McGraw-Hill, 1960.
- von Bekesy, G., & Rosenblith, W. A. The mechanical properties of the ear. In S. S. Stevens (Ed.), *Handbook of experimental psychology*. New York: Wiley, 1951.
- Webster, D. B., & Webster, M. Kangaroo rat auditory thresholds before and after middle ear reduction. *Brain, Behavior and Evolution*, 1972, 5, 41-53.
- Webster, D. B., & Webster, M. Auditory systems of Heteromyidae: Functional morphology and evolution of the middle ear. *Journal of Morphology*, 1975, 146, 343-376.
- Wollack, C. H. The auditory acuity of the sheep (*Ovis aries*). *Journal of Auditory Research*, 1963, 3, 121-132.

Received January 11, 1982

Revision received May 24, 1982 ■