Sound Localization in a Predatory Rodent, the Northern Grasshopper Mouse (*Onychomys leucogaster*)

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A comparison of the ability of mammals to localize sound revealed that among the animals examined to date, none of the rodents have been able to localize as accurately as the carnivores. Because all of these rodents are prey animals, the question arises as to whether their poor localization acuity is a phyletic trait of Rodentia or whether it is a trait common to prey species that may be under less selective pressure than predators to localize sound accurately. To answer this question, sound localization acuity was determined in a species that is both predatory and a rodent, the northern grasshopper mouse. Localization thresholds for a single 100-ms noise burst were determined for three grasshopper mice using a conditioned avoidance procedure. Their 50% discrimination threshold of 19° is larger than that of any of the previously tested carnivores and well within the range of other rodents. However, calculations of the binaural sound localization cues available to rodents (based on their head size) suggest that the grasshopper mouse may make more efficient use of the available locus cues than other rodents. Thus, although the grasshopper mouse cannot localize as accurately as carnivores, it appears to be more accurate than predicted for a nonpredatory rodent of its size.

The ability of mammals to localize a brief sound is not uniform but varies widely among species. Specifically, sound localization acuity varies from less than 1° to more than 20°, with elephants and humans being the most accurate, horses, gerbils, and kangaroo rats being the least accurate, and species such as cats and monkeys being intermediate (for a review, see H. Heffner & Heffner, 1984).

Explanations for this variation can be sought at two complementary levels, "how" and "why." We can examine physical and physiological mechanisms that underlie sound localization, and ask questions such as how different pinna shapes affect acuity or how binaural locus cues are encoded. At another level, we can examine why localization acuity varies and ask whether some taxonomic groups or species with a particular lifestyle are more accurate than others and why this is so. These approaches are complementary in biology; the investigation reported here is of the latter type.

In seeking an explanation as to why sound localization varies, we have noted that acuity seems to vary between phyletic taxa. For example, the four rodents so far examined are less accurate localizers than the three carnivores (R. Heffner & Heffner, 1987). Although the sample is small, seven families are represented, suggesting that the difference is not restricted to one or two select subgroups. Further, the inability of the rodents to localize as accurately as the carnivores cannot be due entirely to the small magnitude of the binaural locus

cues resulting from their smaller head size, because the smallest carnivore is able to localize sound more accurately than rodents with larger heads (R. Heffner & Heffner, 1987). Thus the question arises as to whether the rodents are poor localizers as a result of a conservative character in their phyletic lineage or whether some other factor might account for their performance, opening the possibility that some species of rodents might be accurate localizers.

One factor that may influence sound-localization acuity is the trophic level of the species—that is, the degree to which it is a predator or prey. Predatory species such as cats, dogs, and some primates are more accurate localizers than rodents and even large prey species such as horses (H. Heffner & Heffner, 1984; R. Heffner & Heffner, 1987). Thus it is possible that the poor localization acuity of the rodents examined so far is not a result of their small size or phyletic heritage but rather because prey species derive less advantage than predators from accurate localization. That is, to be successful, a predator may need to know precisely where its prey is, but its prey may need only an approximate indication of where the predator is in order to avoid capture.

One test of the possibility that rodents are poor localizers because they are prey would be to examine localization acuity in a species that is both a rodent and a predator. The grasshopper mouse (*Onychomys leucogaster*) is such a rodent. The grasshopper mouse is a member of the genus *Onychomys*, which first diverged from *Peromyscus* in the late Miocene and only appeared in its present form in the middle Pliocene (McCarty, 1978). It is a small, nocturnal, burrowing rodent that inhabits short grass prairies and deserts. Its range overlaps that of the kangaroo rat, a rodent of similar size and poor localization acuity (H. Heffner & Masterton, 1980). The grasshopper mouse is rarely preyed upon but is itself a predator relying on animal material (mostly insects but including other rodents) for its diet (Hansen, 1975). Its specialization

for predation is reflected in its relatively large home range, and it has undergone marked specialization in both its digestive physiology and in its adrenal hormones for an aggressive predatory way of life (Horner, Taylor, Padykula, 1965; for a species account, see McCarty, 1978). These carnivorelike adaptations, along with the fact that it has been shown to rely predominantly on audition for locating active prey (Langley, 1983), suggest the grasshopper mouse as a candidate for studying the role of trophic level in the evolution of sound localization.

In this article we describe the sound localization acuity of the grasshopper mouse in the azimuthal plane as determined by a conditioned avoidance procedure.

Method

Subjects

Three grasshopper mice (*Onychomys leucogaster*) from different litters, 1 female and 2 males, 4–12-months old and weighing 40–58 g were used. The animals were reared in the laboratory from mice that had been trapped in western Kansas. Their audiograms had been determined previously and showed no signs of abnormality (H. Heffner & Heffner, 1985a); their ear canals were examined and found free of signs of disease. Because auditory thresholds generally show little variation among healthy individuals of the same species and because abnormalities due to disease are usually apparent (e.g., R. Heffner & Heffner, 1983, 1988), testing three individuals is sufficient to gain a reliable estimate of acuity.

The mice were maintained in the laboratory on insects, seeds, and a powdered vitamin supplement. Water was used as a reward and was available only in the test sessions. The mice were weighed daily to monitor their health and deprivational status. Because grasshopper mice are such small animals and because they are adapted to semi-arid conditions, they consumed only 1.5–2.5 ml of water in a typical session lasting 15–20 min.

Behavioral Apparatus

The behavioral apparatus was the same as that used to assess the audiograms (H. Heffner & Heffner, 1985a). The test cage was mounted on a table covered with acoustic foam and located in a double-walled sound chamber (Industrial Acoustics; 2.55 × 2.75 × 2.05 m). A blunted 22-ga. hypodermic needle, which served as a water spout, was mounted so that it protruded just inside the front of the cage. The spout was connected by plastic tubing to an electrically operated water valve and a 25-ml water reservoir, both of which were located in an adjacent control room. A contact circuit connected between the water spout and cage floor served to detect when an animal made contact with the spout. A constant current shock generator was connected between the spout and the cage floor.

Sound Production and Measurement

Sound-localization thresholds were determined for a single brief burst of white noise (100 ms duration, 0.01 ms rise–decay). Broadband noise was generated by a noise generator (Grason Stadler 1285), gated by a rise–fall gate (Grason Stadler 1287), and led through an impedance matching transformer to a pair of matched wide-range speakers consisting of a 7.6-cm paper cone speaker mounted in a 500-cc enclosure and a piezoelectric tweeter with a 7.6-cm horn mounted directly above such that the centers of the speakers were 8.9 cm apart. The loudspeakers were mounted on a perimeter bar (102 cm radius), which was centered on the middle of an animal's head when it was drinking. This arrangement produced noise with peak intensity in the range of 3 to 50 kHz and an overall intensity of 69.5 dB SPL (linear scale) at the location of the animal's ears. (For the spectrum of the noise, see H. Heffner & Heffner, 1985b.)

Psychophysical Procedure

Training. The avoidance procedure used here is similar to that described elsewhere (H. Heffner & Heffner, 1985b). A thirsty animal was trained to place its mouth on the water spout by providing a steady trickle of water (0.15 ml/min) as long as it maintained steady contact. This response also served to center the animal's head in the sound field. The mice were initially trained to drink steadily while a series of broadband noise bursts (five 100-ms bursts with 100-ms interburst intervals) was presented once every 5 s from a loudspeaker located 90° to the right of the animal. These trials in which the signal emanated from a speaker to the right of the animal's midline were the safe trials (S). After the animals had learned to maintain steady contact for 15 min or more, occasional warning trials (W) were introduced in which the auditory stimulus was switched to a loudspeaker 90° to the animal's left side, and its offset was followed by a mild electric shock delivered between the water spout and the cage floor. After only a few pairings of the left sound with shock, the animals learned to avoid the shock by breaking contact with the spout whenever the noise burst was presented from the left side. In order to provide feedback for successful avoidance, a light in the darkened test room was momentarily flashed on each time shock was delivered. Thus the light served to indicate that a warning trial was over and that the animal could return to the water spout. Cessation of spout contact was used as an indication of an animal's ability to perceive a shift in locus.

The presentation of right (S) and left (W) trials was randomized, with a warning trial likely to occur from 1 to 10 trials after the previous warning trial. Occasionally, 10 consecutive safe trials were presented in which locus did not shift and no shock was delivered in order to prevent an animal from using either the time or the number of safe trials since the last warning trial as a cue. No trial was given in the 5 s immediately following a warning trial in order to allow an animal sufficient time to return to the spout. In order to reduce the effects of spurious pauses, the results of a trial were automatically discarded if the animal was not in contact with the spout at some time during the 1 s preceding the trial, although the trial and shock were presented as usual. Because this criterion was automatically applied to both safe and warning trials, it did not bias the results.

Testing. For the final testing the duration of the stimulus was reduced to a single 100-ms noise burst in order to prevent the animals from using scanning movements of the head and pinnae. Sound-localization thresholds were first estimated by gradually reducing the angular separation between the left and right loudspeakers until the animal could no longer distinguish the two stimuli. Threshold testing was then conducted with trials given in blocks at angles both above and below threshold. Psychophysical functions were then plotted by taking the average of the performance scores from each animal's best three sessions (asymptotic performance), with a minimum of 20 warning trials per angle. During each session, a mouse received between 50 and 100 trials, 18% of which were warning trials.

For the purpose of quantifying an animal's response, the duration of spout contact was measured during the last 200 ms of the trial in 20-ms increments. This measured "time in contact" was averaged separately for the right (S) trials and the left (W) trials for each angle of separation. A measure of discrimination performance could then be expressed in the form of the ratio $(S - W)/S$ for each angle. This ratio, which has long been used in animal psychophysics (e.g., Hen-

dricks, 1966; Ravizza, Heffner, & Masterton, 1969) incorporates a correction for guessing by adjusting the observed *hit rate* according to the observed *false alarm* rate (see Green & Swets, 1966, Equation 5.2). This ratio was used to illustrate each animal's performance and to determine its 50% discrimination threshold. The statistical significance of each score was also determined by comparing the occurrence of responses during safe and warning trials using the binomial distribution (Hays, 1963). However, because of the high false alarm rate of one of the animals, these customary measures were in disagreement, and it became necessary to devise a new performance score ($S - WS$) more sensitive to false alarms than the old performance ratio. A comparison of this new performance score with the old ratio, false alarm and hit rates, statistical chance, and A', a nonparametric measure of discrimination (Pollack & Norman, 1964), is presented in the Results.

Results

The ability of the three grasshopper mice to localize 100-ms noise bursts is illustrated in Figure 1 using the standard suppression ratio $(S - W)/S$. Although the animals were able to perform relatively well at angles of 30° and larger, it was apparent that this was not an easy task for them. Not only was it difficult for them to perform perfectly at large angles (i.e., score 1.0), but it was often necessary to begin a session by presenting trials with a 2-s train of noise bursts as practice trials before testing with a single burst per trial. Nevertheless, the mice maintained asymptotic performance down to about 30° below which their performances dropped sharply falling to chance at 17°–18°.

For the purpose of comparison, sensory thresholds are usually reported in terms of the stimulus producing 50% discrimination, which in this case is the angle at which $(S - W)/S = 0.50$ (Figure 1). This definition of threshold results in interpolated thresholds of 18.5°, 15.5°, and 18.5° for Mice A, B, and C, respectively. However, this result leads to an anomaly in the case of Mouse B in that its threshold, unlike

that of the other two mice (as well as comparable thresholds of other species), is not above chance ($p > .05$). To understand how this occurred, it is necessary to examine the hit and false alarm rates of the three mice individually (Figure 2).
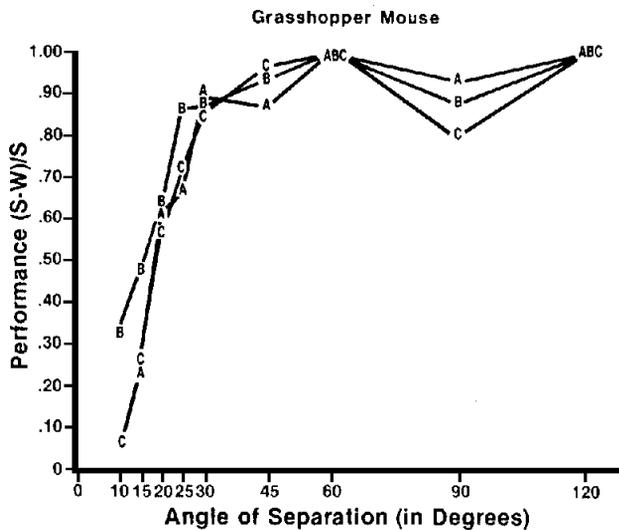

Figure 1. Sound localization performance in the azimuthal plane, calculated by the formula (S–W)/S, for three grasshopper mice. (A, B, and C represent individual animals.)
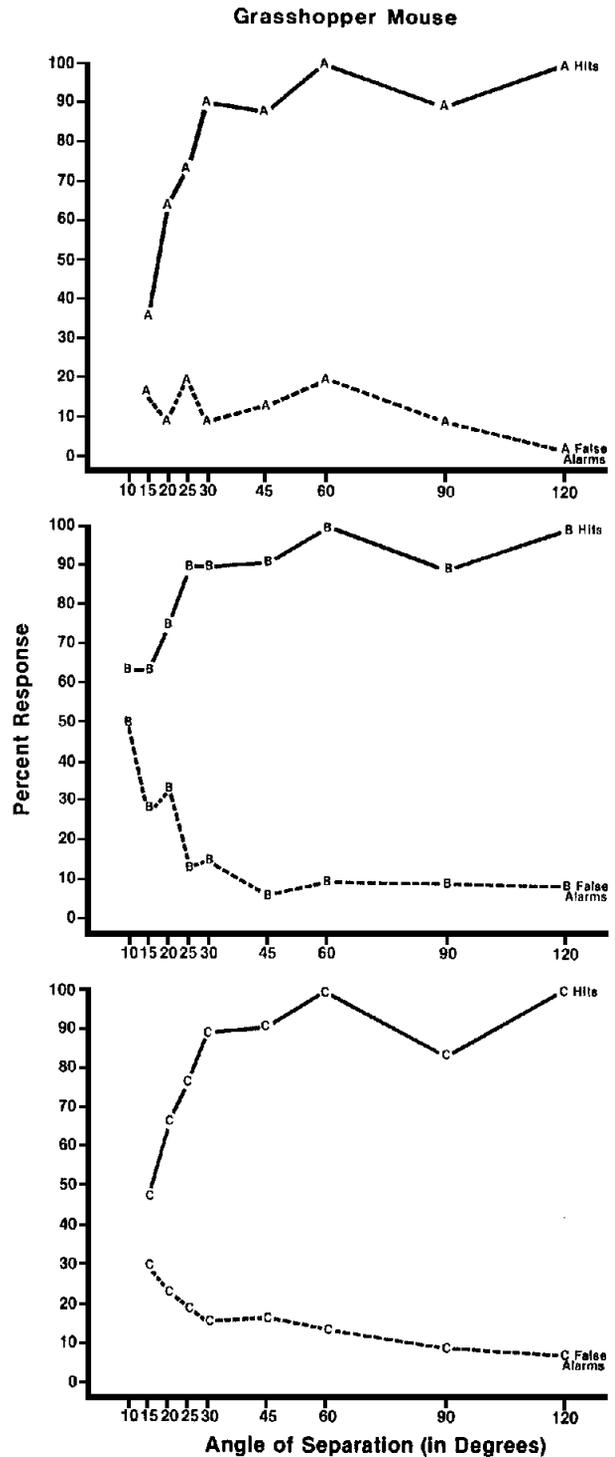

Figure 2. Percentages of hits (correct detections) and false alarms for the three grasshopper mice. (Note different false alarm rates of the three mice as threshold was approached. A, B, and C represent individual animals.)

All three mice had hit rates of around 90% or greater and had false alarm rates that remained below 20% for large angles of separation. As the angle decreases and the stimuli become less discriminable, hit rates typically begin to fall rapidly while false alarm rates increase only slightly, a pattern observed in Mice A and C. However, Mouse B displayed a different pattern in which hit rates fell slightly while false alarm rates rose markedly. Thus Mouse B was able to maintain a high hit rate by increasing its false alarm rate to as high as 50%.

Unfortunately, the suppression ratio, $(S - W)/S$, can give misleading results when high hit rates are accompanied by high false alarm rates. This is illustrated in an extreme example in which a hit rate of 100% (i.e., $W = 0$) will yield a perfect performance ratio (1.0) for any false alarm rate less than 100% (i.e., $S > 0$). In this situation, safe scores of both 1.0 (no false alarms) and 0.01 (99% false alarms) result in a performance ratio of 1.0, implying perfect detection for both, even though a safe score of 0.01 and a warning score of 0 are not significantly different from each other and indicate chance performance.

To better correct for the effect of a high false alarm rate, we applied a second calculation in which the hit rate is proportionately reduced by the false alarm rate: Corrected Hit Rate = Observed Hit Rate − (Observed Hit Rate × False Alarm Rate). This can be computed by the formula $S - WS$, where S is the average safe score and W is the average warning score. This calculation yields scores from 0 (*failure to discriminate*) to 1.0 (*perfect discrimination*). Unlike the suppression ratio, a score of 1.0 can result only from a hit rate of 100% and a false alarm rate of 0%.

Figure 3 shows a plot of the animals' performances using $S - WS$. These curves are similar to those in Figure 1, with the most obvious difference being that the animals never score 1.0 due to the fact that they always have some false alarms. The effect of this calculation on the 50% discrimination threshold is shown in Table 1. Note that the change in

Grasshopper Mouse

Figure 3. Sound localization performance in the azimuthal plane, calculated by the formula $S - WS$, for three grasshopper mice. (A, B, and C represent individual animals.)

Table 1
Comparison of Four Measures of Performance

Animal	50% discrimination (S-W)/S	50% discrimination S-WS	A' = 0.80	Statistical chance (p = .01)
A	18.5	18.5	18.0	17.0
B	15.5	20.0	20.0	18.0
C	18.5	19.5	19.5	17.5
M	17.5	19.3	19.2	17.5

threshold from $(S - W)/S$ to $S - WS$ varies with the false alarm rate, with the result that thresholds for Mice A and C changed little. In contrast, the threshold for Mouse B with its high false alarm rate at small angles increased by 4.5°, which brought its threshold much closer to those of the other two mice.

Although the $S - WS$ calculation resulted in more reasonable threshold values in that the 0.50 performance score for Mouse B was not likely to be due to chance ($p < .01$), it also seemed useful to compare this measure to a "bias-free" measure of performance taken from signal detection analysis before accepting them as final. A nonparametric measure of sensitivity, A' (Gescheider, 1976; Pollack & Norman, 1964), was calculated according to the formula:

$$A' = 1/2 + \left[\frac{(\text{Hits} - \text{FA}) \times (1 + \text{Hits} - \text{FA})}{(4 \times \text{Hits}) \times (1 - \text{FA})}\right],$$

where hits equals the hit rate and FA equals the false alarm rate. A' varies from 1.00 for perfect performance to 0.50 when hit and false alarm rates are equal.

Although the application of signal detection theory does not provide a threshold, the angle at which a particular value of A' is reached may be useful for comparisons. A value of 0.80 was chosen because calculations using data from other species indicated that it usually resulted in an angle near the 50% detection threshold (H. Heffner & Heffner, 1985b; R. Heffner & Heffner, 1987). The angle yielding an A' of 0.80 was determined for each grasshopper mouse and compared with the other definitions of threshold in Table 1. It can be seen that A', $S - WS$, and statistical chance are in agreement in the rank ordering of the three animals. In particular, unlike $(S - W)/S$, all three measures show Mouse B to have a slightly higher threshold than the other two mice. Because of this agreement, we are accepting the $S - WS$ calculation as a better indication of the 50% threshold than the suppression ratio.

Discussion

Sound-localization thresholds of five species of rodents and three species of carnivores are shown in Table 2. The threshold of the grasshopper mouse is more like that of other rodents than it is like that of carnivores. The 19° threshold of the grasshopper mouse is larger than that of any of the carnivores, including the least weasel with its similarly small interaural distance. Among rodents, the 19° threshold of the grasshopper mouse appears to be about average.
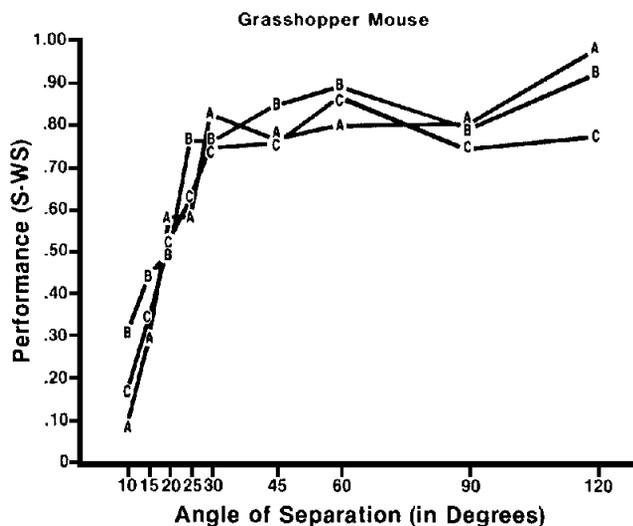
Table 2
Sound-Localization Thresholds for Rodents and Carnivores

Species	n	Maximum interaural distance in μs[a]	50% detection threshold in degrees (M ± SD)	Binaural time disparity at threshold in μs	Source
Carnivores					
Cat	5	258	5 ± 1.2	14	Casseday & Neff, 1973
Dog[b]	4	435	8 ± 2.1	39	H. Heffner, 1976
Least weasel	2	76	12 ± 1.0	10	R. Heffner & Heffner, 1987
Rodents					
Norway rat, wild	3	130	13 ± 0.4	19	H. Heffner & Heffner, 1985b
Grasshopper mouse	3	61	19 ± 0.7	13	This report
Wood rat	4	115	19 ± 4.1	24	H. Heffner, 1978
Kangaroo rat[b]	1	90	27	27	H. Heffner & Masterton, 1980
Gerbil	7	87	27 ± 4.0	27	R. Heffner & Heffner, in press

[a] Time required for a sound to travel around the head from one auditory meatus to the other.

[b] These species were tested using a single click as the stimulus rather than a single brief burst of noise with the result that their thresholds may appear slightly greater than they would had noise been used (cf. H. Heffner & Heffner, 1985b; R. Heffner & Heffner, 1982).

However, it should be noted that the grasshopper mouse has the smallest interaural distance of the rodents in Table 2, and, as has been noted elsewhere, interaural distance may be a limiting factor in sound-localization acuity (R. Heffner & Heffner, 1987). This is due to the fact that the size of the binaural locus cues (i.e., the time and intensity differences between the two ears) for a given angle is determined largely by the size of the head and the resulting distance between the ears. Although sound-localization acuity may be improved by increasing the precision with which binaural time differences are analyzed and by expanding high-frequency hearing in order to provide larger binaural intensity differences, a very small animal may still be unable to overcome the disadvantages of a small interaural distance to localize as accurately as a larger animal.

Although the grasshopper mouse has a moderately large threshold, it appears to make much more effective use of the available locus cues than the other rodents. As illustrated in Figure 4, the localization acuity of the four nonpredatory rodents is positively correlated with the availability of binaural locus cues as determined by interaural distance ($r = .98$, $p < .05$). However, the grasshopper mouse clearly does not fit this relation, because its 19° threshold is far better than the 53° threshold predicted by the regression line.

The exceptional ability of the grasshopper mouse can also be illustrated by estimating the size of the interaural time difference available at threshold for it and the species to which it is being compared (Table 2). (Calculations assume a spherical head and a distant sound source, as described in detail by Kuhn, 1977.) It can be seen that the available binaural time cue is probably smaller for the grasshopper mouse at its threshold than it is for any of the other rodents. Of all the species listed, only the least weasel has a smaller time difference available at its threshold. These values approach the approximately 8 μs calculated to be available to man at his threshold of 1° (Mills, 1958). It is likely that interaural intensity differences are similarly limited in such a small species (cf. Harrison & Downey, 1970). Thus, although the localization threshold of the grasshopper mouse is not outstanding

among rodents, the grasshopper mouse is more accurate than would be expected based on its interaural distance, suggesting that like the least weasel, it is under strong selective pressure to localize sound as accurately as possible within the limits imposed by the cues available to it.

In conclusion, the carnivorous grasshopper mouse is more accurate in localizing sound than would be predicted for nonpredatory rodents with similarly small interaural distances. In spite of this fact, it does not localize as accurately as carnivores and large rats. Whether this is because it is simply not possible for such a small animal to localize any more accurately or because sound localization acuity is a conservative phyletic trait that changes more slowly than some other physiological or morphological features (e.g., digestive or adrenal physiology) is not yet certain.
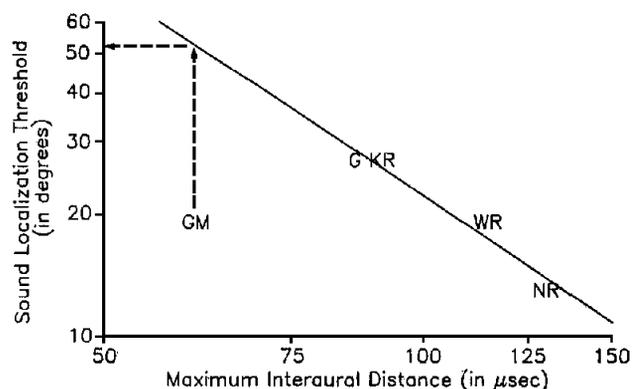

Figure 4. Relation between head size (maximum interaural distance) and sound localization threshold among rodents. (The correlation based on herbivorous [nonpredatory] rodents is 0.98 ($p < .05$]. This relation results in a predicted threshold for the grasshopper mouse of 53°—far greater than its actual threshold of 19°—suggesting that predatory rodents are under more selective pressure to localize sound accurately. G, gerbil; GM, grasshopper mouse; KR, kangaroo rat; NR, Norway rat; WR, wood rat. See Table 2 for references.)

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Kintsch Appointed Editor of *Psychological Review*, 1989–1994

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