Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat

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Behavioral audiograms were determined for four species of Glires: one lagomorph (domestic rabbit, *Oryctolagus cuniculus*) and three feral rodents (cotton rat, *Sigmodon hispidus*; house mouse, *Mus musculus*; and kangaroo rat, *Dipodomys merriami*). Considerable variation in hearing ability was found among the four species with low-frequency hearing limits ranging over 5-1/2 octaves from 50 (kangaroo rat) to 2300 Hz (feral mouse) and high-frequency hearing limits ranging from 49 (rabbit) to 90 kHz (feral mouse). Comparison of the characteristics of each audiogram with the audiograms of other animals of the same Order, Cohort, and Class provide further evidence for the validity of two relationships: (1) interaural distance is strongly and inversely correlated with high-frequency hearing ability, and (2) good high-frequency hearing is apparently incompatible with good low-frequency hearing in most, if not all, land mammals. Furthermore, it is shown that cotton rats and feral mice possess the ability to perform frequency discriminations even at very high frequencies, indicating that there is probably no difference about the way in which they perceive high and low-frequency sounds. Finally, it is shown that kangaroo rats are not unusual in their ability to localize brief sounds, indicating that these animals have not compromised this ability in their acquistion of their unusual low-frequency sensitivity.

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INTRODUCTION

Although audiograms of various animals may be useful for experimental or clinical purposes, a collection of mammalian audiograms, when viewed as a sample of the population of all mammalian audiograms, gives rise to an additional kind of information. Through strict statistical analyses of the between-species variation in hearing in combination with the study of various morphological, ecological, and phylogenic features of the animals involved, it has become possible to identify some of the selective pressures which have played a role in the adaptation and evolution of the ear and auditory system. This information, in turn, has engendered an additional approach to experimentation on the mechanisms of hearing—one emphasizing its adaptive or psychobiological role instead of merely its psychophysics.[1,2] However, the sample of mammals on which past populational analyses of hearing have been based is far from a random or representative one. Among other things, Glires,[3] the cohort containing the orders Lagomorpha and Rodentia, have been underrepresented. As a result, certain conclusions regarding the adaptation and evolution of hearing have had to be weakened or somewhat restricted in their generality.[1]

In recent years, we have had the opportunity to test the hearing of four species of Glires: the domestic rabbit (a lagomorph); and the cotton rat, house mouse, and kangaroo rat (each a feral rodent). Although the purpose of this testing was to balance as well as to enlarge the sample of mammalian audiograms, each of the four species was chosen for reasons intrinsic to itself. Specifically, the domestic rabbit was chosen because it is the most ubiquitous lagomorph; the cotton rat because it is a common New World feral rat; the feral house mouse because it is the most ubiquitous small rodent and because it is conveniently compared with laboratory strains of mice; and finally, the kangaroo rat because its unusually large bullae and central auditory system indicate that it may possess unique hearing abilities. Once the hearing capacities of these animals had been obtained, they were compared with the capacities of previously tested species in order to obtain information relevant to the understanding of the wide variation in two of the most fundamental parameters of hearing: high-frequency and low-frequency hearing limits. Thus, the purpose of this report is to present the results of hearing tests conducted on these four species and thereby expand the available sample of complete mammalian audiograms, to update the sample further by inclusion of the audiograms of other species which have recently become available, and finally, to apply these results to the analysis of the selective pressures involved in the evolution of high-frequency and low-frequency hearing.

I. GENERAL METHOD

The hearing abilities of the four species were determined through use of either of two behavioral techniques: the technique of conditioned suppression or a two-choice positive reward technique. Because the experiments using the conditioned suppression technique have many features in common, a description of this procedure is presented here. For reasons described below, the standard conditioned suppression procedure could not be used with the kangaroo rat. The two-choice procedure which was used instead is described in a later section.

A. Conditioned suppression

The rabbit, cotton rat, and house mouse were tested in cages constructed with thin brass rods. A water

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spout, located at one end of the cage, was connected by rubber tubing to a constant-pressure water reservoir via a solenoid-operated water valve. The two sides of a contact circuit were connected to the spout and to the floor bars of the cage in order to record the number of times the animal licked the spout. A shock-generating apparatus was connected to alternate bars in the walls and floor of the cage. The cage itself was mounted on Fiberglas pads and placed in a burlap-draped double-wall acoustical chamber.

1. Stimulus generation

The details of the stimulus-generation and calibration have been described in detail elsewhere.[4,5] Briefly, sine waves were produced by an oscillator, connected to an electronic switch, then to an attenuator, and finally via an impedence-matching transformer to a wide-range loudspeaker (University, 312). For frequencies above 64 kHz, a power amplifier (McIntosh, MC-30) and an ionic speaker (Ionofane, model 601) were used. In either case, the loudspeaker was located 50 to 75 cm in front of the cage and oriented directly towards the animal's head. 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 wave. Thus, a rise-decay time of 25 ms was used for frequencies of 1 kHz and higher while 50 ms was used for 250 and 500 Hz, 100 ms for 125 Hz, and 250 ms for 63 Hz.

Sound pressure levels (i.e., dB SPL *re* 20 $\mu N/M^2$) were measured with a microphone amplifier (Bruel and Kjaer, 2604), a $\frac{1}{2}$-in. or $\frac{1}{4}$-in. (1.28 or 0.64 cm) condenser microphone (4133 or 4136), and an octave filter (1612). Sound measurements were taken in the position occupied by the animal's head while it was being tested. Great care was taken to ensure that the sound field around the animal's ears was homogeneous.

2. Procedure

In all important respects, the conditioned suppression procedure was the same as that described in previous studies.[4-6] Briefly, the animals were water deprived in their home cage and then trained to lick a spout for a water reward in the test cage. Once steady licking had been established on a variable ratio schedule (10–20%), the animals were given further training in which the offset of a 10-s tone was paired with a brief shock to the feet. After a few tone-shock pairings, the onset of the tone elicited a freezing response incompatible with licking. Thereafter, the cessation or suppression of licking was used as an indication of the animal's ability to hear the tone.

Pure-tone thresholds were first estimated by a method of limits in which the tone intensity was lowered in 5-dB steps until no suppression occurred and then raised until obvious suppression occurred once more. Final threshold values were obtained by the method of constant stimuli in which a series of five intensities 5 dB apart was selected to cover the range from 10 dB above to 10 dB below the animal's estimated threshold. To check for possible artifacts in the sound system to which the animal might be responding, sham trials were administered in which the signal was attenuated at the oscillator to at least 50 dB below the animal's suspected threshold.

Frequency-difference limens were also determined for the cotton rat and house mouse using a similar procedure.[4] For this test the animal was habituated to licking the spout in the presence of a "safe" pulsing tone (0.7 s on, 0.3 s off). A trial consisted of a 10-s "warning" stimulus in which the tone pulses alternated between low and high frequencies (i.e., $F, F+\Delta F, F, F+\Delta F, \ldots$). At the end of the 10-s warning signal, a shock was delivered and the "safe" stimulus was restored (i.e., $F, F, F, \ldots$). After a few pairings with shock, the animal ceased licking whenever there was a large frequency difference in the pulsing tones and this suppression of licking was used as an indication of the animal's ability to discriminate the two frequencies. The tones were presented at an intensity of 30 dB above absolute threshold (i.e., 30 dB SL) as determined in the previous procedure. In addition, sham trials were given in which the alternating tones produced by the two sine wave generators were set to the same frequency, but with the intensities varied by 1–6 dB. No shock was delivered following a sham trial.

For the purpose of quantifying suppression of licking, the number of licks during the 10-s warning period (W), was compared with the number of licks during the 10-s safe period (S) immediately prior to the tone presentation. A measure of suppression could then be expressed in the form of a ratio $(S-W)/S$. In trained animals this measure varies from near zero (no suppression) to unity (perfect suppression). For present purposes, the 0.5 suppression ratio was arbitrarily chosen as the definition of threshold. The use of other definitions of thresholds (e.g., the 0.2 and 0.8 ratios) have no substantial effect on the chief conclusions.

B. Two choice

Because the two-choice procedure was used only with the kangaroo rats, it is described in detail in the section concerning the kangaroo rat.

II. RABBIT *(ORYCTOLAGUS CUNICULUS)*

Despite the large increase in the number of mammalian audiograms in recent years, there exists no representative behavioral audiograms for the order Lagomorpha, an order consisting of two families and ten genera including pikas, rabbits, and hares.[7,8] Of the members comprising this order, the domestic rabbit is probably the most common species: they are a common food source for humans and have been widely used in biological research.[9] For these reasons, domestic rabbits appeared to be a good choice for expanding the sample of mammalian audiograms to include Lagomorphs.

A. Method

1. Subjects

The domestic rabbits chosen for this experiment were New Zealand Whites approximately one year of age.

Each animal received routine otological examination during the course of behavioral testing with special attention given to the possible presence of ear mites. The animals were maintained on a diet of commercial rabbit food supplemented with occasional greens.

2. Apparatus and procedure

The rabbits were tested in an oval cage (91×46×61 cm) with floors and walls constructed of $\frac{3}{16}$-in. (0.48 cm) brass rods and the ceiling constructed of screen mesh. A rat drinking tube was located at one end of the cage.

The conditioned suppression technique was used to assess absolute thresholds (see Sec. I).

B. Results and discussion

Audiograms for two rabbits are shown in Fig. 1. They are in close agreement with each other—the largest difference occurring at 63 Hz, the lowest frequency tested. The audiogram shows a gradual increase in sensitivity as frequency is increased to about 1 kHz. At this point the audiogram levels off with a range of best sensitivity (about 5–10 dB SPL) extending from 1 to 16 kHz which is followed by a rapid decrease in sensitivity until the upper limit of audibility is reached. In all, the domestic rabbit's range of hearing at 60 dB SPL extends from 96 Hz to about 49 kHz.

In low-frequency hearing ability, rabbits are significantly *more sensitive* than most other mammals.[1,4] Indeed, they are far superior in this regard to such animals as bats, but in addition they are also superior to a wide variety of rodents.[6,10-12] However, rabbits are not unique in their capacity for low-frequency hearing. They are equaled or exceeded, for example, by cats, chinchillas, guinea pigs, and humans.[4,13]

It appears that rabbits have a broad range of best frequencies extending from 1 to 16 kHz. Over this range, the average threshold varies by only ±3 dB making the selection of one particular best frequency all but impossible. Again, while rabbits are not the only animal to display such a broad range of best hearing,[13,14] the lack of a well-defined best frequency is sufficiently unusual to merit notice.

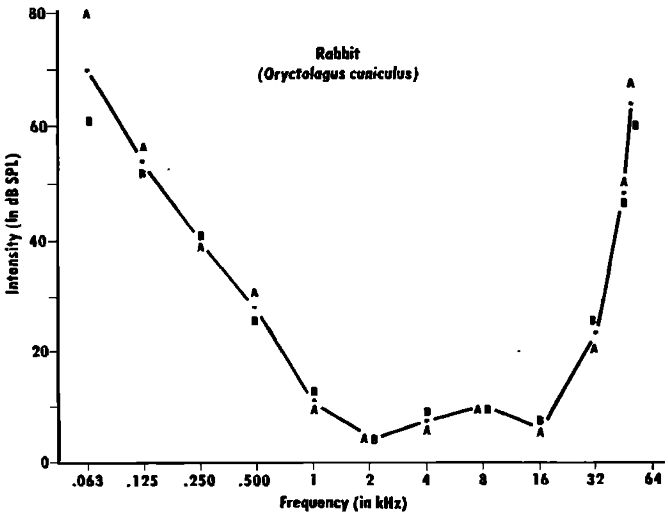

FIG. 1. Audiograms of two domestic rabbits (*Oryctolagus cuniculus*). In this figure and later figures, letters represent thresholds of individual animals. Additional frequencies above 32 kHz are 45 and 50 kHz.

At the upper frequencies, rabbits exhibit the relatively steep decrease in high-frequency sensitivity (as compared to the more shallow low-frequency decrease) commonly found in mammals.[1] With regard to their high-frequency limit, rabbits are about average among mammals with an upper limit less than $\frac{1}{4}$ octave below the average.

In summary, the domestic rabbit is capable of hearing both high and low frequencies and possesses a broad range of best frequencies. How rabbits compare with other Glires is described in Sec. VI.

III. COTTON RAT *(SIGMONDON HISPIDUS)*

Though there exist complete behavioral audiograms for a number of species of rodents,[4,6,12,13,15,16] the available sample of rodent audiograms is far from adequate for population studies. Not only is the number of rodent audiograms quite small when compared to the total number of extant rodent species, but also all of the audiograms have been obtained from domesticated species. Therefore, our knowledge of rodent hearing may also be severely biased.

To study hearing in feral rodents, the cotton rat was chosen as the first subject of study. The choice of the cotton rat was based first on the wide geographical range of this particular species[17] and the fact that it, too, has already been used as a laboratory animal for other purposes.[18,19]

A. Method

1. Subjects

Three feral cotton rats (labeled A, F, and I) were used. Cotton rat A had been obtained from an animal supplier in New Mexico and, therefore, was of unknown age. Cotton rats F and I were the offspring of a female which had been trapped in the Tallahassee, Florida area. Their age was 9 months at the time of testing. The animals were housed individually and maintained on a diet of commercial rat food.

2. Apparatus and procedure

The cotton rats were tested in a rectangular cage (18 ×15×15 cm) constructed out of $\frac{3}{16}$-in. (0.48 cm) brass rods set in a Plexiglas frame. An 18-gauge hypodermic needle with blunted tip was mounted at one end of the cage to serve as a lick spout.

The conditioned suppression technique was used to assess absolute thresholds and frequency-difference limens (see Sec. I).

B. Results and discussion

1. Audiogram

The audiograms of the three cotton rats are shown in Fig. 2. The behavioral curves are in remarkably

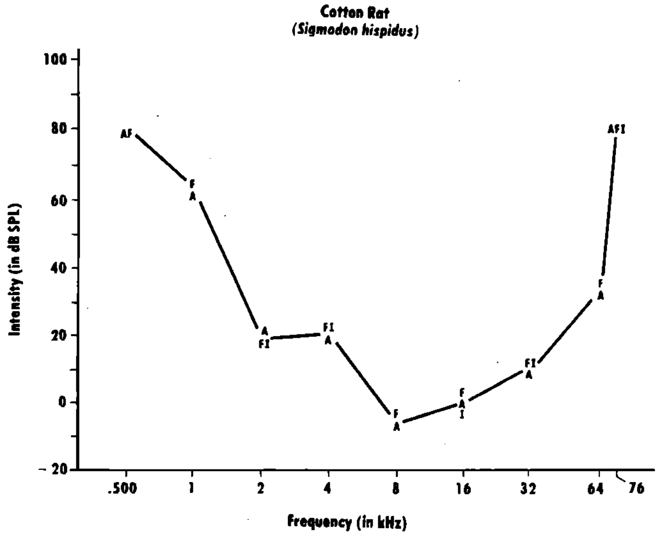

FIG. 2. Audiograms of three cotton rats (*Sigmodon hispidus*).

close agreement with each other with little variation occurring at any of the frequencies tested. The audiogram shows a gradual increase in sensitivity as frequency is increased until the best sensitivity is reached at 8 kHz. Above 8 kHz, the audiogram at first shows a gradual decrease in sensitivity then a sharp decrease above 64 kHz. All three of the cotton rats were able to respond to 76 kHz at 80 dB SPL, but none showed a response to 91 kHz at the same intensity. In all, the cotton rat's range of hearing at 60 dB SPL extends from 1 to 72 kHz.

In low-frequency hearing, the cotton rat is much less sensitive than most other mammals which have been tested. In a comparison with 29 other species of mammals, the cotton rat ranks seventh from the bottom in terms of low-frequency hearing and is surpassed even by the laboratory rat.[6] Indeed, the lack of low-frequency sensitivity in the cotton rat will be seen (in Sec. VI) to serve as an important clue to understanding the interrelationships between several descriptive parameters of hearing.

Turning to the midrange of the cotton rat audiogram, it can be seen that the animals have a relatively well-defined best frequency at 8 kHz. The average sensitivity at this point is −6 dB SPL and though it is possible that the animals might have been more sensitive to some frequency lying between 4 and 16 kHz, the 8-kHz point is the best of those frequencies tested.

The 60-dB high-frequency limit of the cotton rat, at 72 kHz, is considerably higher than that of other mammals and one quite similar to the high-frequency limit of albino rats.[6] We will return to this point in Sec. VI.

2. Frequency limens

It has been suggested that while some animals possess the ability to detect very high frequencies (i.e., in excess of 60 kHz) they may lack the ability to discriminate such high frequencies.[20-22] Alternatively, it has been argued that the usefulness of high-frequency hearing lies in the necessity of using the spectral differences between sounds arriving at the two ears as a cue for sound localization—an ability requiring frequency analysis throughout the frequency range of hearing.[1,23] Therefore, it was of some interest to determine if the cotton rat could indeed discriminate high frequencies as well as merely detect them.

Table I shows the frequency difference thresholds for cotton rat A at 2, 8, 32, and 64 kHz. Note that the animal was able to discriminate frequencies at 64 kHz at a level at least as well (in terms of $\Delta F/F$) as at lower frequencies. Thus, there does not appear to be any discontinuity in mode of transduction or in the ability of the cotton rat to make spectral analyses even at very high frequencies.

In summary, the cotton rat is able to hear high frequencies, but has relatively poor low-frequency hearing. How the cotton rat compares with other Glires is described in Sec. VI.

IV. FERAL HOUSE MOUSE *(MUS MUSCULUS)*

Partly as a result of the current interest in the ultrasonic vocalizations of mice,[24-26] the hearing abilities of house mice have been the subject of numerous studies. Estimates of mouse hearing have been derived from studies which have employed techniques ranging from the pinna (or Preyer) reflex,[27,28] or electrophysiological recording,[29,30] to behavioral conditioning techniques.[7,8,12,31,32]

In reviewing the major behavioral audiograms for mice, two facts soon become apparent. First, there are significant differences between the various published audiograms both in frequency range and in absolute sensitivity. For example, estimates of high-frequency hearing range from 40[31] to 90 kHz[12] while estimates of peak sensitivity differ by more than 20 dB.[12,31,32] Thus, mouse audiograms vary over too broad a range to allow even their average to be used as a reasonable estimate. Second, previous measurements of mouse hearing are based invariably on domesticated varieties. Though most, if not all, of the animals tested seemed to be normal-hearing animals, it is well-known that many laboratory varieties of mice have genetic hearing defects.[29,30] As a result, the audiogram of feral house mice provides a baseline to which the hearing abilities of the domesticated varieties can be compared as well as enlarges the sample of rodent audiograms.

TABLE I. Frequency difference thresholds ($\Delta F/F$).

	Frequency of standard (in kHz)					
Species	2	4	8	16	32	64
Cotton rat	0.015	···	0.020	···	0.019	0.010
Feral mouse	···	0.056	···	0.031	···	0.023

A. Method

1. Subjects

Three feral house mice (labeled A, B, and C) were used. Mice A and B were the offspring of a pregnant female which had been trapped in the Tallahassee, Florida area and were one year of age at the time of testing. Mouse C was also trapped locally and, therefore, its age was unknown. The animals were maintained on a diet of commercial rat food.

2. Apparatus and procedure

The mice were tested in a small rectangular cage (10×8×5 cm). The walls, ceiling, and floor of the cage were constructed of 0.2-cm brass rods. A blunted 21-gauge hypodermic needle was placed at one end and served as the water spout. The cage was placed on a stand 12 cm high and the entire testing apparatus was placed on a burlap-covered surface in the sound chamber.

The conditioned suppression technique was used to assess absolute thresholds as well as frequency-difference limens (see Sec. I).

B. Results and discussion

1. Audiogram

The audiograms of the three feral mice are shown in Fig. 3. The behavioral curves are in close agreement with each other for all but the very lowest frequencies. The audiograms show a gradual increase in sensitivity as frequency is increased to a well-defined best frequency near 16 kHz. Indeed, the mice appear to be quite sensitive at this frequency with an average threshold of −10 dB SPL. Above 16 kHz, the sensitivity of the animals begins to decrease gradually with a steeper decline above 64 kHz. Mice A and B responded to 91 kHz at 58 dB SPL, but failed to respond to 128 kHz at 74 dB SPL. In all, the range of hearing in the feral mouse, at an intensity of 60 dB SPL, extends from 2.3 to 92 kHz.

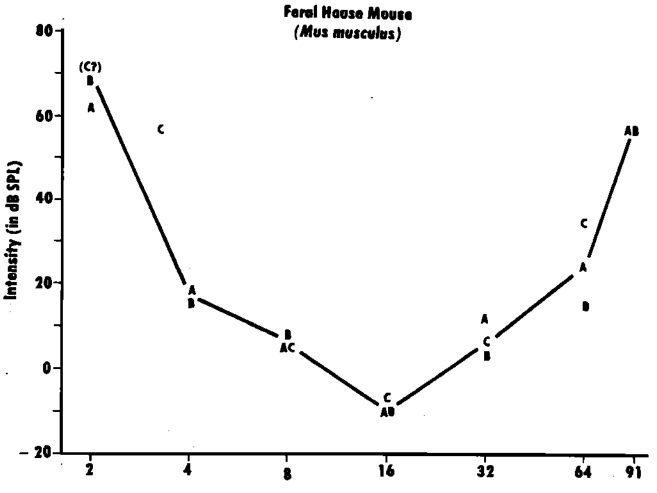

FIG. 3. Audiograms of three feral house mice *(Mus musculus)*. Query indicates incomplete estimation of threshold for mouse C at 2 kHz. Mouse C was also tested at 3.3 kHz.

Returning to the low-frequency end of the audiogram, it can be seen that the animals probably could not hear much below 2 kHz. In spite of repeated attempts it was not possible to obtain a response from any of the animals to frequencies between 1 and 2 kHz (SPL 70–80 dB) in the absence of a marked onset transient. Furthermore, mouse C could barely respond reliably to 2 kHz at a level of 70 dB SPL (higher intensity levels at this frequency produced significant distortion with noticeable overtones). Such a lack of sensitivity to low-frequency sounds is unusual among mammals and, indeed, bats are the only other mammals known to have poorer low-frequency sensitivity.[10,11]

That the poor low-frequency sensitivity of feral mice is not due to a generally lower sensitivity to sounds is demonstrated by their thresholds in the mid-frequency range of their audiograms. With thresholds at 16 kHz ranging from −7 to −11 dB SPL it is clear that the mice can perceive low intensity sounds and, indeed, their best sensitivity exceeds that of the majority of mammals yet tested. Furthermore, the mice are exceptionally sensitive to high-frequency sounds and among terrestrial mammals are exceeded in this capacity only by bats. Indeed, it appears as though the audiograms of the mice have been shifted, with a decrease in low-frequency sensitivity occurring along with an increase in high-frequency sensitivity. This apparent relationship between low-frequency and high-frequency hearing will be returned to in Sec. VI.

2. Frequency limens

Because of the argument surrounding the discrimination of very high frequencies previously mentioned, the frequency discrimination thresholds of two of the mice were also determined (Table I). These results show that the mice were also able to discriminate high frequencies as well as or better than frequencies in the middle or low range of their audiogram. Thus, these data support the conclusion of Ehret[34] that mice are able to discriminate frequencies throughout their range of hearing. Since no discontinuity in absolute or frequency threshold is evident, it can be concluded that there seems to be no great or obvious difference between their perception of high-frequency and low-frequency sounds.

3. Comparison with laboratory house mice

Figure 4 presents the average audiogram of the feral mice along with three behavioral audiograms of laboratory mice which used either the CBA-J strain[31,32] or the NMRI strain.[12] The figure shows that there are notable differences among the laboratory mouse audiograms, especially in high-frequency and low-frequency hearing. Indeed, given the large methodological differences between the studies, it seems premature to make any final conclusions concerning the hearing capacities of the house mouse. However, when all four audiograms are viewed together, three general features can be observed. First, the house mouse appears relative-

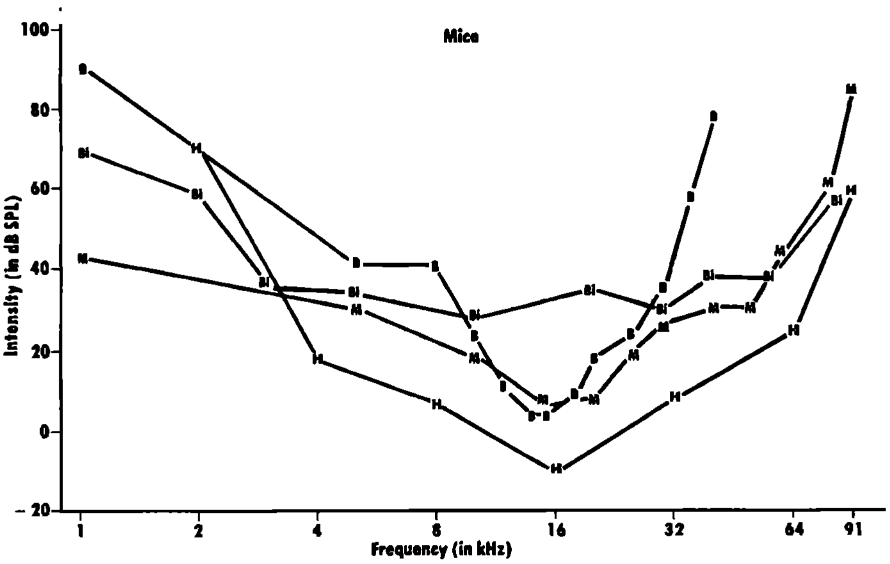

FIG. 4. Average audiograms of feral and laboratory strains of *Mus musculus* from the present and three previous studies. H, present results; B, Berlin[31]; Bi, Birch *et al.*[32]; M, Markl and Ehret.[12]

ly insensitive to low frequencies as most of the audiograms indicate a lack of sensitivity to frequencies below 1 kHz. Second, the house mouse appears to have relatively good high-frequency hearing as all but one of the audiograms indicate that its upper limit of hearing lies beyond 64 kHz. Finally, the best frequency of hearing for this species appears to lie around 16 kHz. Though it may be tempting to conclude that the feral house mouse possesses better absolute sensitivity than the domestic strains, such a conclusion is precluded by the methodological differences and small number of animals involved in each of the studies. Just how house mice compare with other Glires is described in Sec. VI.

V. KANGAROO RAT *(DIPODOMYS MERRIAMI)*

Because the kangaroo rat possesses several unusual morphological features in its auditory system, it has been of special interest in auditory research.[35-37] Of particular interest is the greatly enlarged middle ear cavity, the combined volumes of which exceed that of the brain itself.[16] Recently, it has been demonstrated that the hypertrophied bulla of the kangaroo rat serves to increase the sensitivity of the animal to low-frequency sounds.[16] In addition, kangaroo rats possess a medial superior olive greatly enlarged over that of other mammals of the same size.[37] In sum, kangaroo rats appear to have evolved unusual low-frequency hearing sensitivity not found in most rodents, or for that matter, in most other mammals.[1,16]

The remarkable low-frequency sensitivity of the kangaroo rat raises a number of general issues concerning mammalian hearing. One such issue concerns the inability of most mammals to hear both very low- and very high-frequency sounds. Because low-frequency and high-frequency sensitivity are negatively correlated among mammals,[1] it would seem to follow that the kangaroo rat might have had to sacrifice high-frequency sensitivity in return for its exceptional low-frequency sensitivity. A separate issue concerns the ability of the kangaroo rat to localize sound. Because small animals appear to rely heavily on the perception of high frequencies in order to localize sounds accurately,[1,38] the question arises as to whether the increased low-frequency sensitivity of the kangaroo rat has affected its ability to localize sound or whether the binaural analyzing mechanisms of its brainstem have also adapted to low-frequency hearing.

In previous estimates of the auditory abilities of the kangaroo rat, neither its very high- or very low-frequency hearing abilities, nor its ability for sound localization have been completely determined.[16,39] To answer these questions, a somewhat longer series of auditory tests were carried out. These experiments consisted of the determination of high-frequency and low-frequency hearing thresholds and the determination of threshold and performance curves for the localization of brief sounds.

A. Methods

Because kangaroo rats are adapted to arid habitats (the ones used here were collected in the Sonora desert of Arizona) and normally obtain water only from seeds, they do not find water to be a reward. For this reason our standard procedure could not be used for testing. Given that a different procedure was necessary and wishing to include tests of sound localization, the conditioned suppression technique was replaced by a more compatible two-choice technique using millet seed as a reward. In general, the animals were trained first to enter an observing compartment which faced a loudspeaker (Fig. 5). Having triggered a trial by their entry, the animals were then trained to enter a compartment to the left of the observing compartment if a tone was presented and to enter a compartment to the right if no tone was presented.[40]

1. Subjects

Two feral kangaroo rats were used in this study. The animals had been wild-trapped in the Tucson, Arizona area and their ages were unknown. The animals were maintained on a diet of seeds supplemented with occasional greens.

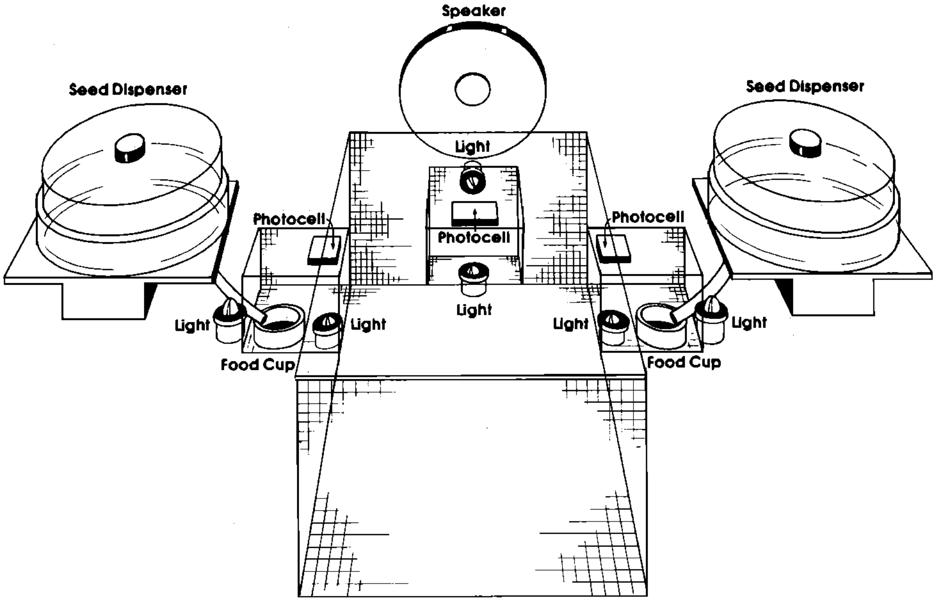

FIG. 5. Test cage used to assess thresholds in kangaroo rats. Note center "observing" compartment and two side "response" compartments. Absolute thresholds were determined with a single speaker mounted as shown. Localization thresholds were determined with two moveable speakers.

2. Details of behavioral apparatus

The kangaroo rats were tested in a 20×15×10-cm cage constructed of $\frac{1}{2}$-in. (1.27-cm) hardware cloth (see Fig. 5). The test cage had three compartments attached to it: an observing compartment (4×6×7 cm) and two side compartments (7×6×7 cm). A photocell mounted above and a light mounted below the entrance of each compartment served to detect the entry of an animal into the compartment. Stainless steel 30-ml measuring cups mounted in the two side compartments served to receive cleaned and hulled millet seeds which were dispensed from modified rat-pellet dispensers. Additional cue lights mounted on the side compartments and in front of the observing compartment were used as visual stimuli in the early stages of training. The entire test apparatus was mounted on a stand 30 cm high and placed on a burlap-covered surface located in a burlap-draped acoustical chamber.

3. Details of stimulus generation

For the pure-tone tests, sine waves were produced, keyed, attenuated, and measured in the usual manner and led to one of two loudspeakers, either a University T202 tweeter (for frequencies from 8 to 64 kHz) or an Acoustic Research 3a speaker system (for frequencies from 50 Hz to 8 kHz). The loudspeakers were placed in front of and slightly above the observing compartment and directed toward it.

For sound-localization tests, the cage was placed in a carpeted room (3×3 m), the walls and ceiling of which were draped with burlap. For click-localization tests, clicks were produced by 0.1-ms square waves, amplified by a power amplifier and led to two 1.5-in. (3.8 cm) dome tweeters (Long Engineering, L15F). These speakers were located 5 ft (1.52 m) in front of the cage on either side of the animal's midline when it entered the "observing" compartment. Testing was conducted at speaker separation angles of 180°, 90°, 60°, 30°, 20°, 15°, 10°, 5°, and 0°.

For tone-pip localization tests, the same sine-wave generating equipment was used except for frequencies below 500 Hz for which 6-in. (15 cm) paper cone speakers were used. The stimuli for this test were purposely set to match as closely as possible those used in the study of Masterton and his colleagues.[38] First, the tone-pips were electronically keyed with rise times of 40 ms, remained at their peak amplitude for 60 ms, and then decayed over 40 ms. Second, the speakers were placed 3.7 ft (1.13 m) from the animal and the intensity of the tone adjusted to 40 dB above the animal's threshold. Finally, the tone-pip testing was done at a constant angle of 60° separation (i.e., 30° left versus 30° right).

4. Training procedure

A food-deprived kangaroo rat was placed in the test cage and accustomed to receiving millet seeds dispensed into the side compartments. After several sessions of acclimatization, the animal was trained to make a two-choice discrimination using visual cues. In this procedure, entry into the center or "observing" compartment initiated a trial which was signaled by turning off the cue light adjacent to the center compartment and by turning on the cue light adjacent to one of the side compartments. Entry into the illuminated side compartment was rewarded by dispensing a millet seed into that compartment while entry into the unilluminated compartment was not rewarded and was followed by a short time-out (signaled by dimming the room lights) before the next trial could be begun. This training served only to accustom the animal to the response requirements of the task.

Once the animal had learned to make the two-choice discrimination using visual cues, auditory training was begun. In this training, entry into the center compartment initiated a trial and turned off the center cue light as before. However, now a pulsed tone (0.2 s on, 0.1 s off) was presented randomly on half of the trials. The animal was required to wait in the observing compartment for at least 1 s before making a response to one or the other side compartments. The end of this observing period was signaled by illuminating *both* of the side compartments. The animal was then rewarded for entry into the left compartment in the presence of a tone or for entry into the right compartment in the absence of a tone. Incorrect responses were followed by a time-out as in the previous visual training. Thus, entry into the left compartment was used as an indication that a tone had been heard while entry into the right compartment was used as an indication that no tone had been heard.

To reduce the possibility of a side preference, a modified correction procedure was used in which the correct side was not changed following an error. These correction trials were not used in the calculation of the animal's performance.

For sound localization tests, the same procedure was used except that now the animal was required to enter the left compartment when a sound emanated from the speaker on the left side and to enter the right compartment when a sound emanated from the speaker on the right side. The procedure of indicating the direction of the sound source by moving left or right (instead of approaching the sound source itself) is the only departure from the localization procedure used by Masterton *et al.*[38]

5. Testing procedure

As in the previous audiogram testing, threshold determination for pure tones 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 the animal could no longer distinguish the tone and no-tone trials. Once an estimate of threshold had been obtained, a second threshold determination was conducted by presenting tones with intensity levels in 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 in terms of the 0.01 one-tailed level of significance (binomial distribution). In addition, each frequency was retested in a subsequent session and testing was judged complete only 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 was determined.

Click-localization thresholds were determined by testing the animal at successively smaller angles until performance dropped to chance levels. A minimum of 200 trials were given at each angle.

In the tone-pip localization tests, no thresholds were determined, but instead, the animal was tested at each frequency to the criterion used by Masterton *et al.*[38] The criterion was a performance level of 90% or better for four successive blocks of 10 trials each. If the animal failed to reach this criterion after 2000 trials, testing was discontinued and the animal's highest score for four successive blocks of 10 trials was used as the final measure of performance. Thus, the scores obtained from this test are a comparative measure of the ability to localize tones of differing frequencies at an angle of 60° and are directly comparable with previous results on other animals.

B. Results and discussion

1. Audiogram

The pure-tone thresholds for two kangaroo rats are shown along with the average of Webster and Webster's results[16] in Fig. 6. Because the results of preliminary testing at the middle frequencies did not differ significantly from the results of the Websters, detailed testing was carried out only at the very high and very low frequencies which they had not tested. Additional de-

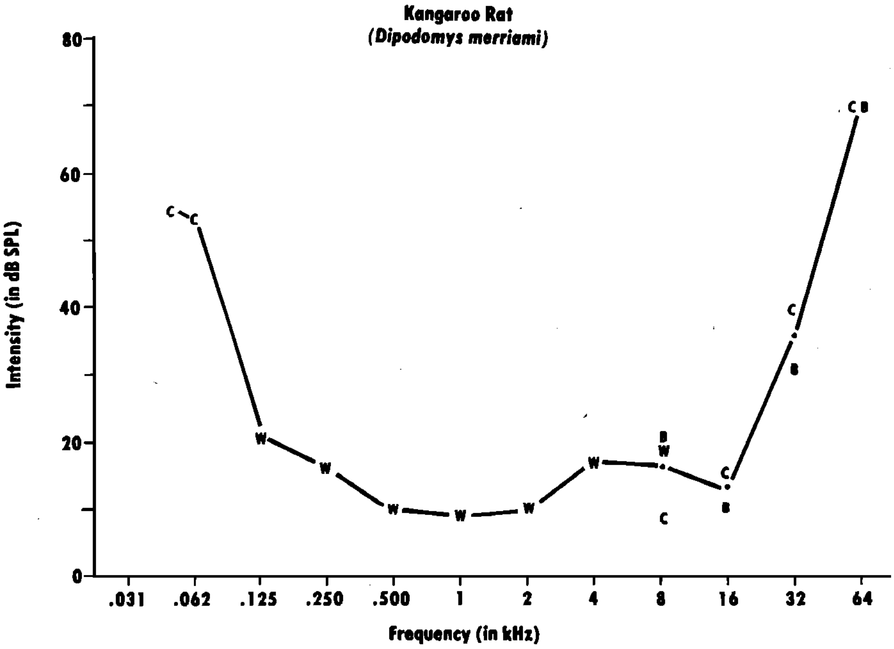

FIG. 6. Composite audiogram of kangaroo rats (*Dipodomys merriami*). Letters B and C represent thresholds of individual animals in present study. *W* indicates thresholds obtained by Webster and Webster.[16]

tailed testing of the two kangaroo rats was, however, conducted at 8 kHz where it was again shown that the results for these animals did not differ significantly from those of the Websters (Fig. 6).

Beginning at the low-frequency end of the audiogram, the present results indicate that the kangaroo rat possesses good low-frequency hearing with a threshold at 50 Hz of 55 dB SPL. Indeed, this unusual ability to hear low-frequency tones made it impossible to determine the lowest frequency which could be perceived at 60 dB, since below 50 Hz,higher intensities produced unavoidable overtones. Thus, this result confirms the earlier finding that kangaroo rats have unusually good low-frequency hearing.[16]

According to the results of the Websters, the kangaroo rat sensitivity gradually increases to a best frequency at about 1 kHz with a small and gradual decline in sensitivity at 4 and 8 kHz. With the addition of the present results for frequencies from 8 to 64 kHz, it can be seen that the sensitivity is relatively flat up to 16 kHz. Above 16 kHz, sensitivity begins to decrease sharply. However, the animals were able to hear 62 kHz at 70 dB SPL and 52 kHz at 60 dB SPL. From these results, then, it appears that the kangaroo rat has the ability to hear high-frequency sounds as well as very low-frequency sounds.

Though the kangaroo rat has retained the ability to hear high frequencies, despite its excellent low-frequency hearing, the question arises whether or not it can hear as high as would be expected on the basis of known relationships between high-frequency sensitivity and other biological characteristics. Specifically, the relationship between high-frequency hearing and the functional distance between the two ears (i.e., the maximum binaural time disparity, Δt) was used to calculate an expected value for the high-frequency limit.[1] The value for the kangaroo rat predicted by this calculation is 74 kHz at 60 dB. This value is more than one standard deviation higher than the obtained value of 52 kHz, although this difference is not large enough to be statistically reliable ($z = 1.38, p > 0.05$). Thus, while it appears that the kangaroo rat may have given up some of its ancestral high-frequency hearing for good low-frequency hearing, it is not unusually deviant in its high-frequency hearing ability. We will return to the possible trade-off between high-frequency and low-frequency hearing in Sec. VI.

2. *Sound localization*

Although the main purpose of studying the kangaroo rat was to determine its audiogram, the unusual audiogram prompted a further question: namely, can the kangaroo rat use its entire frequency range for sound localization or, alternatively, was the extension of its hearing into low frequencies solely for the detection of sound. To obtain a first approximation to the answer of this further question, the most cooperative animal, KR-C, was chosen for testing of its sound localization abilities.

The kangaroo rat was tested first for its ability to localize the source of a 2/s click train and then a single click. In Fig. 7(a) it can be seen that the animal was able to perform at a level between 83% and 93% correct for angles from 30° to 180°. In no case did the animal consistently perform above 95% correct for an entire session of 50 or more trials. Below 30° the animal's performance dropped markedly, falling below chance at about 7°. As determined by an arbitrary 75% correct criterion, localization thresholds were 20° for the click train and 23° for a single click.

The results of the click localization test indicate that the kangaroo rat was clearly able to localize sounds. Indeed, the animal transferred easily from the absolute-threshold task to the sound-localization task and was performing well above change on the first session in which the locus of the sound source was the relevant cue. Therefore, it seems safe to conclude that kangaroo rats can localize brief sounds and are readily able to learn a sound-localization task. However, it must be noted that the kangaroo rat appears to be less able to localize sounds than many other mammals. For example, cats,[41] dogs,[42] monkeys,[43] opossums,[44] seals,[45] and humans,[46] each have localization thresholds ranging from 1 to 6 degrees—far superior to the kangaroo rat thresholds. However, the kangaroo rat is also not unique in its relatively poor localization performance for it appears that the laboratory rat is similarly unable to localize sounds at small angles of separation.[47]

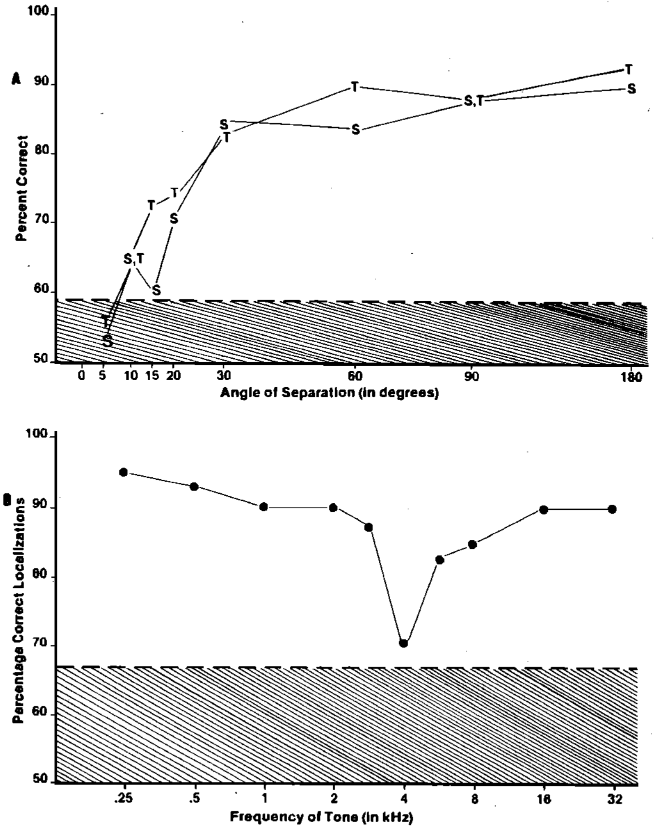

FIG. 7. Sound localization in kangaroo rat. A: Localization of a 2/s click train, *T*, and a single click, *S*, by animal KR-C. B: Localization performance for brief tone pips at 60° separation. Note dip in performance at 4 kHz. Hatched area indicates chance level of performance.

To further explore the ability of the kangaroo rat to discriminate differences in the direction of a sound source, the animal was tested for its ability to localize brief tone-pips of various frequencies. This test is of physiological significance because the ability to localize low frequencies suggests that the animal can use binaural time or phase-difference cues for sound localization, while the ability to localize high frequencies suggests the ability to use binaural spectrum difference cues.[38,48]

The results of this test are shown in Fig. 7(b). The figure illustrates three main points. First, since the kangaroo rat reached a 90% correct criterion on low frequencies ranging from 250 Hz to 2 kHz, it is probably capable of using binaural phase-difference cues to localize the direction of a sound source.[48] Second, since the animal also reached criterion at high frequencies of 16 and 32 kHz, it can also use binaural spectrum difference cues to localize sound. Third, the kangaroo rat showed the same marked decrease in performance in its midrange that many other small-headed animals do.[38] Apparently, near 4 kHz for the kangaroo rat, neither cue is sufficient for the animal to localize at high levels of performance.

The results of the tone localization test demonstrate once more that the kangaroo rat is not unusual in its ability to localize sounds. In its ability to localize tone pips, at least, it appears quite similar to the laboratory rat.[38] Specifically, both animals are able to localize low-frequency and high-frequency tones and both animals show a distinct decrement in performance in the mid-frequency range corresponding to the decrements in the two binaural cues in this frequency range. The only major difference between the two species is that performance is lowest around 4 kHz in the kangaroo rat while the white rat's lowest performance is at 8 kHz. Since the theoretical upper limt of the phase-difference cue for the kangaroo rat under the testing conditions used here is 12 kHz while the white rat's is 8 kHz,[38] (for the formula for calculating the upper limit for the phase cue, see Refs. 48 or 49) this result would seem to mean that the kangaroo rat, unlike the white rat, cannot use the binaural time cue throughout its available range.

In summary, the kangaroo rat does not seem to have sacrificed much of its ability to hear high frequencies in order to hear low-frequency sounds. Nor does the animal lack the ability to localize sounds of either high or low frequencies. However, as Webster and Webster[16] have shown, the kangaroo rat is certainly well-adapted to perceiving low-frequency sounds and it does not appear to be as accurate at sound localization as most other (larger) animals. How the kangaroo rat compares with other animals will be considered further in Sec. VI.

VI. GENERAL DISCUSSION

With the inclusion of the rabbit, cotton rat, feral mouse, and kangaroo rat, the sample of audiograms for the Taxon Glires is increased to the point where comparisons within the cohort may be readily made. The first part of the following discussion compares hearing abilities within Glires and then between Glires and other mammals. The second part is directed to some of the systematic sources of variation in high-frequency and low-frequency hearing throughout mammals, Glires included.

A. Auditory characteristics of Glires and their comparison with other mammals

This discussion is divided into four sections corresponding to four fundamental descriptive parameters of hearing: (1) low-frequency limit—the lowest frequency audible at an intensity level of 60 dB SPL; (2) high-frequency limit—the highest frequency audible at 60 dB SPL; (3) best frequency—the frequency with the lowest threshold; and (4) lowest threshold—the sound pressure level of the lowest audible intensity of the audiogram. These four parameters have been discussed elsewhere[1,5] and differ from previous comparisons only in that 60 dB SPL is used to define the first two parameters instead of 70 dB SPL. Though perhaps not as accurate in defining limits as 70 dB SPL, 60 dB SPL allows the inclusion of the audiograms of several animals for which 70-dB SPL limits are not available.

1. Low-frequency hearing

The low-frequency limit of hearing in nine species of Glires is shown in Fig. 8(a). (Averages and standard deviations are given in Table II.) The low-frequency limits range from 42 in the kangaroo rat to 2300 Hz in the feral mouse with an average value of 198 Hz. This average value is somewhat lower than the mammalian average of 255 Hz (Table II), but with the wide variation in low-frequency limits, this difference is not statistically reliable ($p > 0.05$).

It should be noted, however, that the low-frequency limits shown in Fig. 8(a) appear to fall into two disparate groups. One group contains animals able to hear below 100 Hz; the other group contains animals unable to hear much below 500 Hz. Indeed, in the second group are the cotton rat and feral mouse whose low-frequency limits are in the kilohertz range. It can be noted further that the four Glires with the highest low-frequency limit also are the four species with the highest high-frequency limit [cf. Figs. 8(a) and 8(b)]. Thus, Glires evidence wide variation in low-frequency hearing and this variation appears to be related to the variation in high-frequency limit. (We return to this point below.)

2. High-frequency hearing

High-frequency limits for nine species of Glires are shown in Fig. 8(b). Once more, the distribution of limits covers a wide range, from 33 (chinchilla)[13] to 92 kHz (feral mouse) with an average near 60 kHz. Thus, it appears that Glires as a group are able to hear frequencies far above the 19 kHz upper limit of human hearing—though, on average, they hear only slightly higher than the mammalian average (Table II).

Close inspection of Fig. 8(b), however, reveals that

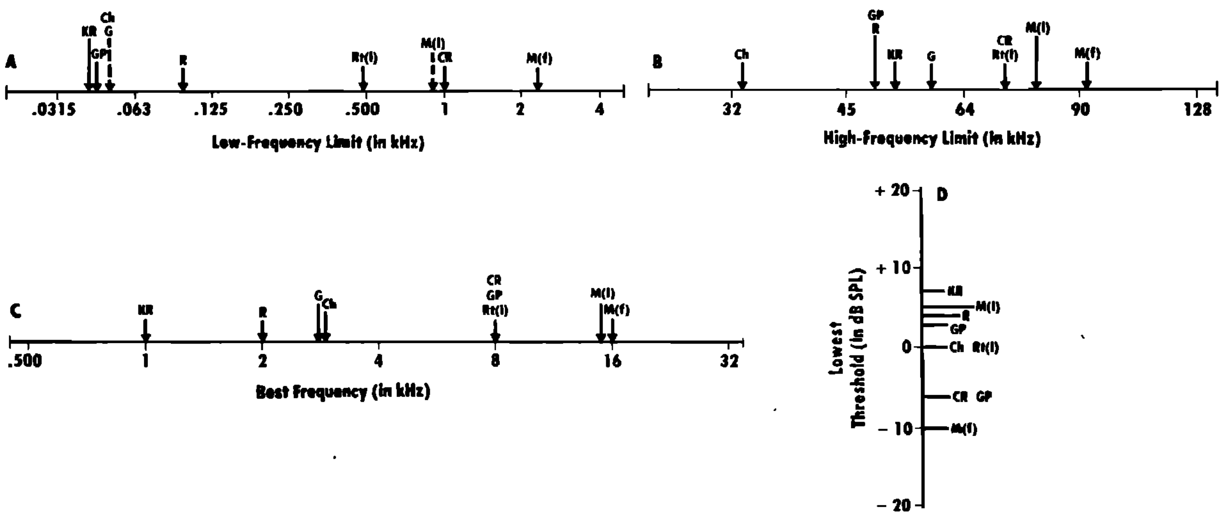

FIG. 8. Auditory characteristics of nine species of Glires. A: Distribution of low-frequency limits (at 60 dB SPL). B: Distribution of high-frequency limits (at 60 dB SPL). C: Distribution of best frequencies. D: Distribution of lowest thresholds. Ch, chinchilla, Miller[13]; M(*f*), feral house mouse, present study; M(*l*), laboratory mouse, averaged from Berlin[31]; Birch *et al.*[32]; and Markl and Ehret[12]; G, gerbil, Ryan[15]; GP, guinea pig, Heffner *et al.*[4]; KR, kangaroo rat, present study; R, rabbit, present study; Rt(*l*), laboratory rat.[6] Dotted lines in A indicate extrapolated values.

not all Glires possess exceptional high-frequency hearing. In particular, the chinchilla with an upper limit of about 33 kHz appears to deviate significantly from the rest of the group ($p < 0.05$). This unusual feature of chinchilla hearing is of significance in the selection of the chinchilla as an experimental animal for auditory research. That is, the chinchilla more closely approximates human high-frequency hearing ability than any other Glires and would seem to be an appropriate choice for auditory research when a correspondence with at least this one feature of human hearing is desired.[50]

3. Best frequency

The best frequencies for the nine species of Glires are shown in Fig. 8(c). These frequencies range from 1 for the kangaroo rat to 16 kHz in the feral mouse with an average of 5 kHz (Table II). Not surprisingly, the distribution of best frequencies parallels the previous two parameters. That is, species which have good high-frequency hearing have higher best frequencies than species with good low-frequency hearing.

Overall, the average best frequency of Glires is *lower* than the average mammalian value ($p < 0.05$). This difference is somewhat surprising in view of the fact that Glires have slightly better than average high-frequency hearing. However, this difference may be due to a sampling bias—the sample of mammals is not a truly random sample, being overweighted with large primates and underweighted with small rodents. For this reason, we are restrained from concluding that Glires might have a lower best frequency than the mammalian average.

4. Lowest threshold

The average lowest threshold for Glires is 0.3 dB SPL, a value similar to the mammalian average (Table II). As Fig. 8(d) shows, lowest threshold varies from +7 dB to −10 dB SPL. Therefore, the Glires do not appear to be unusual among mammals in their lowest threshold.

5. Summary

The hearing characteristics of Glires show marked variation. Some species such as mice, are capable of perceiving very high frequencies while others, such as the chinchilla, lack this ability. On the other hand, chinchillas, kangaroo rats, and gerbils have exception-

TABLE II. Auditory characteristics of glires compared with mammals.

Taxon	Low-frequency limit (in kHz)	High-frequency limit (in kHz)	Best frequency (in kHz)	Lowest threshold (in dB)
Glires: Average	198 Hz	59.3 kHz	5.0 kHz	−0.3 dB
SD	2.4 oct.	0.4 oct.	1.3 oct.	5.5 dB
Mammalia[a]: Average	255 Hz	55.4 kHz	9.8 kHz	−1.5 dB
SD	2.4 oct.	0.7 oct.	1.4 oct.	9.7 dB

[a] The mammalian average and standard deviations are based on samples that are within 5% of the true distribution of mammalian genera per order except for primates (overweighted with ten genera instead of two) and rodentia (underweighted with eight genera instead of twelve).

ally good low-frequency hearing.[13,15] These findings demonstrate that the auditory characteristics of the members of a widely varied taxonomic group cannot be very accurately inferred from the characteristics of other members of the same group. Or, in other terms, habitus is as important a determinant as heritage for the auditory characters of Glires. However, the variations present are not wholly random. It is possible to show relationships between some of the auditory characteristics and other morphological and ecological characteristics. The purpose of the final section is to describe those relationships which appear to account for some of the systematic variation in high-frequency and low-frequency hearing.

B. Systematic variation in the limits of mammalian hearing

1. High-frequency hearing

As previously noted, Glires show wide-spread variation in high-frequency hearing ability with high-frequency limits ranging from 33 to 92 kHz [Fig. 8(b)]. Such variation in high-frequency hearing is not uncommon among mammals and has been ascribed to selective pressure for accurate sound localization.[1,23]

Briefly, the two primary 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 the sound reaching the two ears (Δfi), are closely dependent on the functional distance and the sound shadow of the head and pinna between the two ears. That is, the further apart the ears, the larger will be the Δt for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with wide-set ears both because the sound attenuation is greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which effectively block the high-frequency content of a sound cue (i. e., a head-shadow and pinnae-shadow effect). While these two binaural sound localization cues are readily available to animals with large heads, the effectiveness of either cue is greatly diminished in animals with small heads and small or close-set ears. In the case of Δt, the available time differences may be so small that the nervous system can resolve only gross changes in sound direction or, as is apparently the case in the hedgehog, the nervous system may have lost entirely its mechanism for analyzing the Δt cue.[38]

However, an animal with a small head always has a Δfi cue available, providing only that it is able to perceive frequencies which are high enough to be effectively shadowed by its head and pinnae. Therefore, given the ecological importance for animals to localize brief sounds, animals with functionally close-set ears are subjected to more selective pressure to hear higher frequencies than animals with more widely set ears. This inverse relationship between functional interaural distance and high-frequency hearing has already been

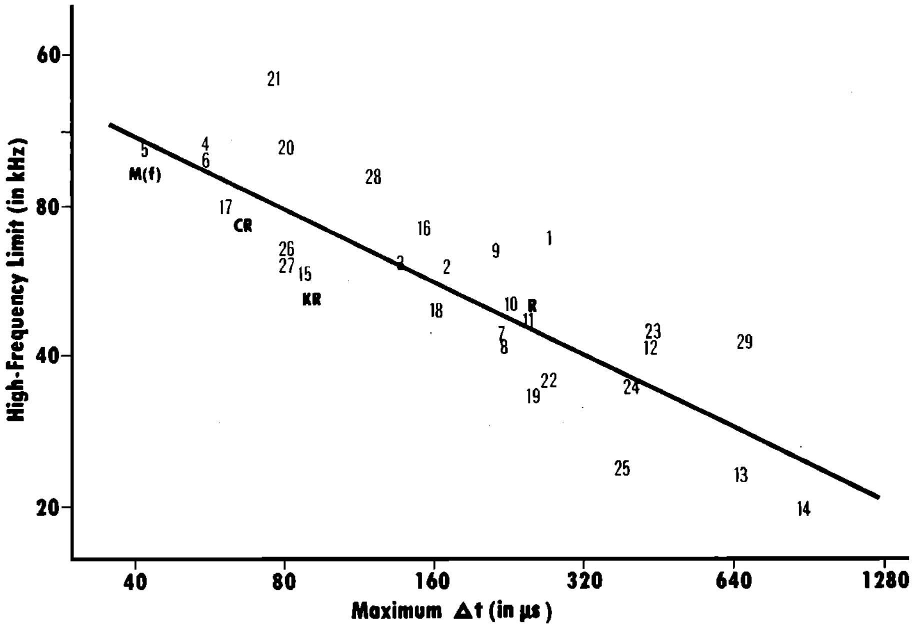

FIG. 9. Relationship between maximum Δt and high-frequency hearing limit. (Numbers indicate values for 28 species and letters indicate values obtained in present study.) CR, cotton rat; KR, Kangaroo rat; M(*f*), Feral house mouse; R, rabbit. 1, Opossum *(Didelphis virginiana)*[51]; 2, Hedgehog *(Hemiechinus auritus)*[52]; 3, Tree shrew *(Tupaia glis)*[53]; 4, Horseshoe bat *(Rhinolophus ferrumequinum)*[11]; 5, Little brown bat *(Myotis lucifugus)*[10]; 6, Big brown bat *(Eptesicus fuscus)*[10]; 7, Slow loris *(Nycticebus coucang)*[5]; 8, Potto *(Perodicticus potto)*[5]; 9, Bushbaby *(Galago senegalensis)*[54]; 10, Owl monkey *(Aotus trivirgatus)*[55]; 11, Squirrel monkey *(Saimiri sciureus)*[56,57]; 12, Macaque *(Macaca sp.)*[58,59]; 13, Chimpanzee *(Pan troglodytes)*[60]; 14, Human[61]; 15, Gerbil *(Meriones unguiculatis)*[15]; 16, Laboratory rat *(Rattus norvegicus)*[6]; 17, Laboratory mouse *(Mus musculus)*, see Fig. 8; 18, Guinea pig *(Cavia porcellus)*[4]; 19, Chinchilla *(Chinchilla sp.)*[13]; 20, Dolphin (underwater) *(Inia geoffrensis)*[62]; 21, Porpoise (underwater) *(Tursiops truncatus)*[63]; 22, Killer whale (underwater) *(Orcinus orca)*[64]; 23, Dog *(Canis familiaris)*[65]; 24, Sealion *(Zalophus californianus)*[66]; 25, Common seal *(Phoca vitulina)*[40]; 26, Common seal (underwater) *(Phoca vitulina)*[40]; 27, Ringed seal (underwater) *(Pusa hispida)*[67]; 28, Harp seal (underwater) *(Pagophilus groenlandicus)*[68]; 29, Sheep *(Ovis aries)*.[69]

demonstrated on a restricted sample of mammals.[1]

The data relevant for this relationship is up-dated to 32 different species of mammals in Fig. 9. In this figure, interaural distance is expressed in terms of the maximum Δt that the animal can experience—that is, the time it takes for sound to travel around the head from one ear to the other; and high-frequency limit is expressed as the highest frequency the animal can detect at an intensity of 60 dB SPL. The correlation between these measures is −0.84, which, with 32 independent points, is highly reliable ($p < 0.01$). Thus, as in previous surveys based on smaller numbers of mammals[1,23] maximum Δt and high-frequency hearing are found to be highly and inversely correlated.

Though maximum Δt and high-frequency limit are correlated in mammals, the same does not appear to hold true for nonmammalian vertebrates. For example, the audiograms of fish,[70] as well as behavioral and electrophysiological data from amphibians and reptiles[71-74] do not reveal any systematic variation in high-frequency hearing which is correlated with maximum Δt. In birds, despite occasional claims to the contrary, there does not appear to be much variation in high-frequency hearing at all and none dependent on head size: small-headed birds, such as canaries, and larger-headed birds such as pigeons and blackbirds, each have nearly the same upper limit of hearing at 8 to 10 kHz.[75] Therefore, the close relationship between high-frequency hearing and maximum Δt appears to be a uniquely mammalian trait as is the ability to hear frequencies above 10 kHz.

2. *Low-frequency hearing in mammals*

In previous surveys of mammalian hearing, it has been noted that low-frequency hearing shows a good deal of variation from one species to another.[1,23] For example, the kangaroo rat and guinea pig have low-frequency limits of less than 0.05 kHz, and the cotton rat and feral house mouse have limits of 1 and 2.3 kHz, respectively [cf., Fig. 8(a)]. Even more extreme comparisons have been noted: humans have a limit of about 0.03 kHz[61] and the bat, *Myotis lucifugus*, has a limit of 10.3 kHz.[10] Thus, the range of low-frequency limits in mammals spans a range of more than 9 octaves—dwarfing the 3-octave range in the distribution of high-frequency limits.

In an attempt to explain this wide variation, a number of parameters have been analyzed. Of these, three have shown particularly persistent correlations with low-frequency limit: high-frequency limit; maximum Δt; and body weight. Table III lists the correlation coefficients between each of these three parameters and low-frequency limit. As can be seen, each of the three parameters is reliably correlated with low-frequency limit: (1) low-frequency limit varies directly with high-frequency limit ($r = 0.87$, $p < 0.01$) indicating that mammals which have a high high-frequency limit also have a high (poor) low-frequency limit; (2) low-frequency limit varies inversely with maximum Δt ($r = -0.77, p < 0.01$) indicating that low-frequency hearing ability increases as interaural distance increases; and (3) low-frequency limit varies inversely with body weight ($r = -0.71, p < 0.05$) indicating that large mammals have better low-frequency hearing than small mammals.

However, while each of the three parameters is reliably correlated with low-frequency limit, analysis using partial correlations shows that each of these three relationships is adequately explained by only one of the three parameters. When the partial correlation between maximum Δt and low-frequency limit or between body weight and low-frequency limit are calculated with high-frequency limit held constant, both correlations drop to insignificance ($r = -0.09, r = 0.11$, respectively). Yet, when either maximum Δt or body weight are held constant, the correlation between high-frequency and low-frequency limits remains reliably high ($r = 0.64$, $0.72, p < 0.05$, see Table III). This analysis suggests that of the three parameters, variation in high-frequency limit has the closest relation to, and may be the key to understanding, the variation in low-frequency limit.

The correlation between high-frequency and low-frequency limits is illustrated in Fig. 10. The slope of the regression line in Fig. 10 shows that each octave change in high-frequency hearing is associated with more than a 3-octave change in low-frequency hearing. Though the relationship shown here appears quite strong, ($r = 0.87, p < 0.01$) there is reason to believe that it does not hold for the extreme lower end of the scales. In particular, humans, who have the lowest high-frequency limit yet known, would be expected to have a low-frequency limit of about 4 Hz—a value several octaves below the actual limit of about 30 Hz (see point labeled H in Fig. 10). Thus, as indicated by the dotted line in Fig. 10, there may be a "floor effect" that prevents the hearing of frequencies below some

TABLE III. Correlations and partial correlations of three parameters with low-frequency limit.

Variable removed	60-dB high-frequency limit	Maximum Δt	Body weight
None	0.87[a]	−0.77[a]	−0.71[a]
60-dB high-frequency limit	···	−0.09	0.11
Maximum Δt	0.64[a]	···	0.11
Body weight	0.72[a]	−0.43	···

[a] $p < 0.05$.

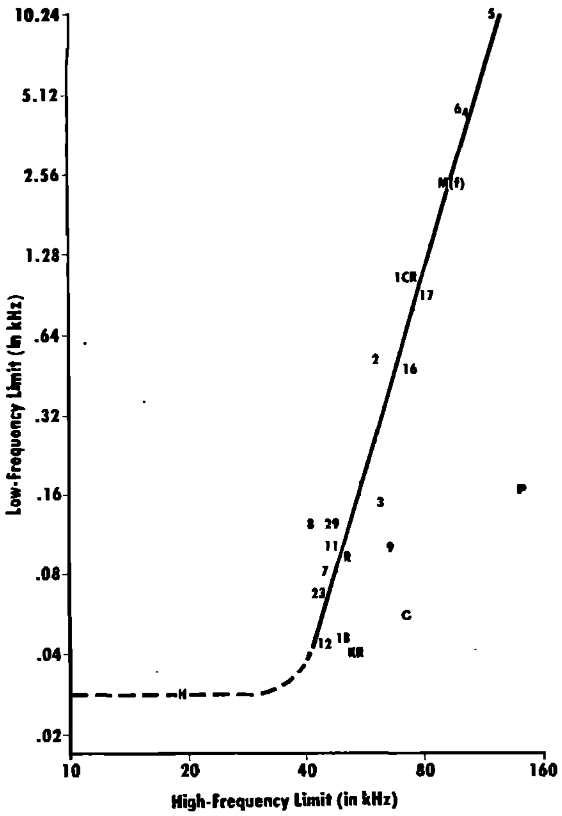

FIG. 10. Relationship between high-frequency and low-frequency limits of hearing in 21 species of land mammals. See Fig. 9 for key to numbers and letters. Value for humans indicated by H. Regression calculated with human value excluded (see text). Excluding humans raises correlation coefficient from 0.87 to 0.93. C indicates estimated values for cat and P indicates values for porpoise (underwater).

particular very low value.

In seeking an explanation of the inverse relationship between high-frequency and low-frequency hearing, one possibility is that the size of the auditory apparatus (e.g., the meatus, ear drum, ossicles, and basilar membrane) may in part determine the frequency response characteristics of the ear. For example, it has been argued that while a small ear may be well-suited for good high-frequency reception, good low-frequency reception may only be possible with a large ear.[76,77] Indeed, the possibility that the size of the middle ear may affect an animal's hearing range is suggested by two additional lines of evidence. First, it has been demonstrated that the enlarged bullae of the kangaroo rat apparently serves to increase low-frequency sensitivity in the sense that experimentally reducing the volume of the bullae results in a decrement in low-frequency hearing.[16] Thus, the enormous middle-ear cavity in kangaroo rats may explain their ability to hear lower than predicted ($p < 0.05$) on the basis of their high-frequency limit (see point labeled KR in Fig. 10). Second, it appears that some marine mammals such as the porpoise (see point P in Fig. 10) have excellent high-frequency *and* excellent low-frequency hearing.[63] Since most animals are transparent to sound in water, with sound directly stimulating their cochleae through their body tissues,[78] this observation suggests that good high- and low-frequency hearing are more easily obtained when the ear drum and middle ear are not a factor.

For these reasons, it is tempting to conclude that good high-frequency hearing is incompatible with good low-frequency hearing as a result of limitations of the middle ear, yet we are reluctant to reach such a conclusion until more species have been tested and the universality of the relationship between high-frequency and low-frequency hearing is more fully determined. Indeed, there is one mammal which seems to strain if not contradict this relationship—namely, the cat. Though the high-frequency and low-frequency limits for the cat have not yet been established, extrapolation of existing data suggests that the cat may possess unusually good high-frequency and good low-frequency hearing (see point C in Fig. 10).[79] Therefore, it may not be impossible for a mammal to evolve an ear capable of transducing both very high and very low frequencies. However, the apparent rarity of these two characters in combination suggests that the selective pressures involved must be both strong and persistent.

ACKNOWLEDGMENTS

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