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Vestigial hearing in a fossorial mammal, the pocket gopher (*Geomys bursarius*)

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Behavioral tests of hearing and sound localization in the North American pocket gopher (*Geomys bursarius*) show that it is unique among mammals. It has a severely attenuated range of hearing and only rudimentary ability to localize sound. In these respects, the hearing of gophers can be properly termed 'vestigial' and suggests that life underground can produce as severe a change in hearing as a light-less world produces in vision or an odorless world produces in olfaction.

Audiogram; Sound localization; Evolution; Comparative

Introduction

Animals living in environments in which one or another sensory stimulus is limited or absent have been known to lose the ability to perceive that stimulus. The best known examples are the reduction or loss of vision in cave-dwelling species and in underground (fossorial) mammals such as moles and mole rats and the reduction in olfaction in cetacea (e.g., Darwin, 1859; Nowak and Paradiso, 1983). Given such changes in vision and olfaction in environments deprived of appropriate stimuli, the question arises as to whether an environment exists in which sound transmission is so limited as to result in a similar reduction or loss of hearing ability.

Although sound propagates freely in air and water, it is severely restricted in small underground burrows. There, airborne sound of both low and high frequencies rapidly attenuates with distance (Heth et al., 1986). Further, the essentially one-dimensional space of a burrow limits the directionality of airborne sound and would seem to reduce the usefulness of the ability to localize sound, a factor which has proved to be an important source of selective pressure shaping mammalian hearing (Heffner and Masterton, 1990; Masterton et al., 1969).

Recently, several studies have indicated that a fossorial lifestyle may indeed be accompanied by changes in hearing ability. Specifically, the ability of two species of mole rats (*Spalax ehrenbergi* and *Cryptomys hottentotus*) to hear high-frequency sounds appears to be limited to about 10 kHz (Bruns et al, 1988; Müller and Burda, 1989; Bronchti et al, 1989). Although such a restricted upper limit is not unknown among mammals (Heffner and Heffner, 1982), it is sufficiently unusual to suggest that fossorial mammals have undergone a reduction in their hearing capacities as a result of their adaptation to an underground environment.

The North American rodent most specialized for underground living is the pocket gopher, *Geomys bursarius*. This small mammal inhabits burrows up to 1 m below the surface and ventures above ground only on rare occasions to disperse over short distances. It forages on underground stems and tubers, and, unlike the many burrowing rodents that forage on the surface, it has little need for vigilance against surface predators. In

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this report we present evidence that not only do gophers have restricted hearing, but their ability to localize sound is vestigial. Because the hearing of this species seems so deviant from the mammalian norm, it also seemed appropriate to examine the normal brainstem structures subserving audition, particularly the binaural nuclei in the superior olivary complex, for signs of degeneration or abnormal development.

Methods

Subjects

Wild trapped animals from Hutchinson, Kansas, U.S.A, were housed individually and maintained on a variety of fruit, roots, alfalfa, seeds, and rabbit pellets. Altogether, six female gophers, designated A through F, were used in this study. The ears of these animals were examined at post mortem and found to be free of parasites and disease. During testing the amount of fruit and wet vegetables which the animals received was reduced and water was available only during the test session. Sessions were conducted daily during which the gophers consumed 2.5–5 ml of water during a 20–30-min period. Each animal was weighed before each session to monitor its health and deprivational state.

The gophers were tested with a conditioned avoidance procedure in which a thirsty animal was trained to make continuous contact with its mouth on a water spout in order to receive a steady trickle of water. Warning signals were then presented at random intervals and followed at their offset by a mild electric shock delivered through the spout. By breaking contact with the spout, an animal both avoided the shock and indicated that it had detected the warning signal.

Behavioral apparatus

All testing was conducted in a carpeted double-walled acoustic chamber (Industrial Acoustics Company model 1204; $2.55 \times 2.75 \times 2.05$ m) the walls and ceiling of which were covered with eggcrate foam to reduce sound reflection. An adjacent control room housed the behavioral control and stimulus generation equipment and the animals were observed with a closed-circuit television system. Although the television camera emitted an acoustic signal around 10 kHz, the camera was far enough from the animal that it did not mask the test signal — a point which was verified by replicating thresholds at 8 and 16 kHz with the camera turned off.

The animals were tested in a cage ($38 \times 21 \times 23$ cm) constructed of half-inch (1.27 cm) hardware cloth attached to a brass-rod (0.24 cm diameter) frame. To reduce sound shadows and reflections, the brass rod was used to form the frame of only the floor, ceiling, and back of the cage — no vertical supports were used on the front or sides of the test cage. In addition, the front of the cage was rounded to eliminate corners (for a drawing of the shape of such a cage, see Heffner and Heffner, 1988c). The cage was mounted on a camera tripod 1 m high, and 5-cm thick foam rubber pads were placed under the feet of the tripod to reduce the possibility of substrate-borne vibration.

Because the gophers were unable to maintain steady contact with a standard water spout, a modified water spout was used. Water was dispensed though a hole in the center of a stainless steel disk (2×2.5 cm diameter) which was mounted atop a vertical stainless steel tube located in the front of the cage 4 cm above the cage floor. 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 the adjacent control room. A contact switch 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 cage floor and a 15-watt light mounted 0.5 m below the cage was turned on when shock was being delivered.

Acoustical apparatus

Audiogram. Sine waves were generated by an oscillator (Hewlett-Packard 209A), switched on and off by an electronic switch (Coulbourn S84–04), attenuated with a manually-operated attenuator (Hewlett-Packard 350D), filtered with a band-pass filter (Krohn-Hite 3202) which was set at 1/3-octave points above and below the test frequency, and then connected via either an impedance-matching transformer or an amplifier (Coulbourn S82–24) to a loudspeaker. The electri-

cal signal going to the loudspeaker was monitored with an oscilloscope (BK 1476A) for the possibility of distortion or noise. The loudspeaker was located approximately 1 m in front of the cage (with the distance varied as needed to achieve an even sound field of sufficient intensity for each frequency) and oriented toward the position occupied by the animal's head when it was drinking from the spout. The loudspeakers used were a 38-cm (15-in) woofer (for 32 Hz–8 kHz), a 30.5-cm (12-in) woofer (for 63 Hz–2 kHz), a 12.7-cm (5-in) midrange (for 250 Hz–2 kHz), and a ribbon tweeter (Foster E110T02; for 4 kHz–45 kHz). The tones were pulsed, 400 ms on and 200 ms off, with rise decay times of 160 ms (32–63 Hz), 80 ms (125 Hz), 25 ms (250 Hz), 20 ms (500 Hz–2 kHz), and 10 ms (4 kHz–45 kHz).

The sound pressure level (SPL re 20 $\mu N/m^2$) was measured daily with either a Brüel and Kjaer (B & K) 1-inch (2.54-cm) microphone (B & K 4131), sound level meter (B & K 2203), and octave filter (B & K 1613), or a 1/4-inch (0.64-cm) microphone (B & K 4135), preamplifier (B & K 2618), microphone amplifier (B & K 2608), and filter (B & K 1613 or Krohn-Hite 3202). The measuring systems were calibrated with a pistonphone (B & K 4220). Sound measurements were taken by placing the microphone in the position normally occupied by an animal's head when the animal was drinking and pointing the microphone directly toward the loudspeaker (0° incidence). Care was taken to ensure that the sound field was homogeneous in the area occupied by the animal's head and ears. Low-frequency tones were examined for the presence of overtones or distortion by measuring the sound pressure level at octave steps above the primary frequency and determining whether the resulting measurement was greater than would be expected if no overtones were present. Additional controls included monitoring the electrical signal on the oscilloscope and carefully listening to the sound. When distortion was suspected, the sound system was modified by reducing the amplitude of the signal, narrowing the bandwidth of the bandpass filter, or changing loudspeakers. Finally, the linearity of the attenuator was verified with the sound level meter over the range of attenuation used in threshold determination.

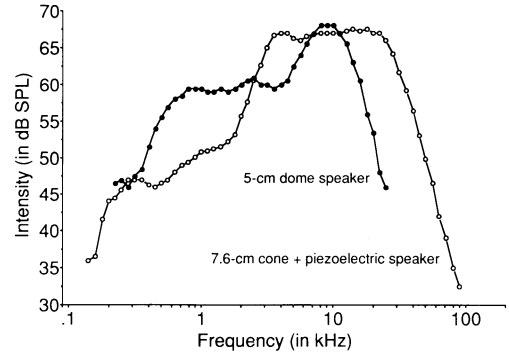


Fig. 1. Spectra of two of the noise bands used to test sound localization.

The ambient noise level in the test chamber was measured from 3.15 Hz to 100 kHz in 1/6 octave steps.

Sound localization. A broad-band noise signal was produced by a noise generator (Coulbourn S81–02), connected to a filter (Krohn-Hite 3202), and to a programmable attenuator (Coulbourn S85–08). The electrical signal was then split into left and right lines and connected to two electronic switches which were set to 0 rise-fall (Coulbourn S84–04), a two-channel equalizer (Sentrek SHQ 1205B), two amplifiers (Coulbourn S82–24), and, finally, to two loudspeakers. For detailed testing, a pair of 5-cm dome loudspeakers (Long L15F) which had been matched by human listeners were used (see Fig. 1 for the spectrum of the signal). To prevent the animals from discriminating between the loudspeakers on the basis of sound quality rather than locus, the noise spectra of the two loudspeakers were analyzed daily with the sound measuring system described above and matched by adjusting the equalizer. The intensity of the noise was 46 dB above the gophers' detection threshold and was varied randomly over a 7-dB range in 1-dB increments in order to prevent the gophers from using any slight speaker imbalance as a cue. The loudspeakers were suspended at ear level from a perimeter bar of 1.1 m radius.

Supplementary tests were performed using additional loudspeakers including 1.27-cm and 2.54-cm headphone transducers, 7.62-cm cone loudspeakers, and a combined 7.62-cm cone and

piezoelectric speaker system (the spectrum of which is also illustrated in Fig. 1).

Behavioral procedure

Audiogram .

Audiograms were determined behaviorally using a conventional conditioned avoidance procedure in which the detection of a pure tone was indicated by momentarily ceasing to drink from a water spout (Heffner and Heffner, 1988a). The gophers were partially deprived of wet food and water and trained to maintain steady contact with the water spout for 20 min in order to receive a continuous trickle of water. They were then trained to stop drinking and break contact with the spout (detection response) whenever a loud sound was presented in order to avoid a mild electric shock. The level of shock was adjusted for each individual to the lowest level that would reliably produce an avoidance response. The mildness of the shock was empirically verified by observing that none of the animals developed a fear of the water spout in that they returned to it without hesitation. The presentation of the shock was accompanied by turning on the light mounted below the cage; turning the light off signaled to the animal that it could return to the water spout, which it did readily. Drinking from the spout served to fix the animals' heads in relation to the sound source thus enabling the sound pressure level in the vicinity of the animal's head to be precisely specified ($\pm$ 1 dB).

The test procedure consisted of presenting 2.5-s trials with a 1.5-s intertrial trial interval (i.e., one trial every 4 s). Each trial was either a 'safe' trial during which no tone was presented or a 'warning' trial which consisted of a 2.5-s train of tone pulses. Warning trials occurred from 1 to 7 trials after the previous warning trial with each trial having a 0.22 probability of being a warning trial.

The trials were scored by determining whether an animal was in contact with the spout during the last 150 ms of each trial. (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 during the 1 s immediately preceding the trial, although the trial was presented as usual.) For each stimulus intensity the hit rate (percentage of responses during warning trials) was determined and was then corrected for false alarm rate (percentage of responses during safe trials) according to the following formula: Performance = hit rate $-$ (false alarm rate $\times$ hit rate) (Heffner and Heffner, 1988a). This measure varies from zero (no detections) to unity (100% hit rate with no false alarms).

Auditory thresholds were determined by reducing the intensity of the tone in successive blocks of five to ten warning trials until the animal no longer responded to the warning signal above the level expected by chance ($p > 0.01$). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity by 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold. Threshold was defined as the intensity at which a detection performance of 0.50 was achieved. Thresholds were repeated on successive days until asymptotic values were obtained. Once testing had been completed throughout the hearing range, each frequency was rechecked to ensure reliability.

Sound localization. Sound localization was examined similarly by training the gophers to maintain contact with the water spout when noise bursts were emitted from a loudspeaker to their right (safe trials) and to cease drinking whenever noise bursts were emitted from a loudspeaker to their left (warning trial). Localization acuity was determined by reducing the angle between the speakers until the gopher's performance fell to chance. Threshold was defined as the angle which yielded a score of 0.50.

Anatomical methods

Two pocket gophers were euthanized and then perfused through the heart with 0.9% saline followed by 10% formalin. The brains were prepared for frozen sectioning by immersion in a cryoprotectant (25% glycerine) and cut in coronal sections 25 μm thick. Alternate series of sections were stained with either thionine or Protargol. The auditory brainstem was compared with similarly prepared and stained sections from a wide variety of rodents and other mammals. Cat and rat were chosen for illustration because they best illustrate

the relation of gophers to species whose auditory nuclei and auditory abilities have been thoroughly described.

Results

Auditory sensitivity

Complete audiograms were obtained for two gophers (A and B) with additional points obtained for two other animals (C and D). The audiograms show comparatively good agreement between animals indicating that they are probably representative of their species (Fig. 2). The hearing of the gopher extends from 45 Hz to 32 kHz with the most sensitive point at 2 kHz. Neither animal A nor B could hear 32 Hz at 88 dB or 45 kHz at 89 dB.

The hearing of the gopher is unique in that the animals are unusually insensitive. At their best frequency of 2 kHz their average threshold is only 24 dB, making them the least sensitive of any mammal yet tested. This lack of sensitivity contributes to the fact that their hearing range (measured by the conventional criteria of the lowest and highest frequencies audible at an intensity of 60 dB) extends from only 350 Hz to 8.7 kHz — the most restricted of any mammal yet tested.

The gopher audiogram is also unique in that the high-frequency portion departs from the characteristic shape of mammalian audiograms. Mammalian audiograms are typically asymmetrical with a rapid decrease in sensitivity as the upper limit is approached. For most mammals, increasing the intensity of the test tones above 60 dB SPL does not significantly increase the ability to detect higher frequencies (e.g., Heffner and Heffner, 1982, 1985a). However, the gopher is an exception in that its high-frequency sensitivity decreases gradually so that increasing the intensity from 60 to 84 dB SPL extends its upper limit by almost two octaves. This result is significant because it indicates that the gopher still possesses the neural mechanisms necessary for the detection of frequencies up to 32 kHz, but that the transmission of high frequencies may be restricted by more peripheral non-neural mechanisms. For example, gophers have extremely narrow external auditory canals (0.6 mm diameter) which may contribute to their reduced sensitivity.

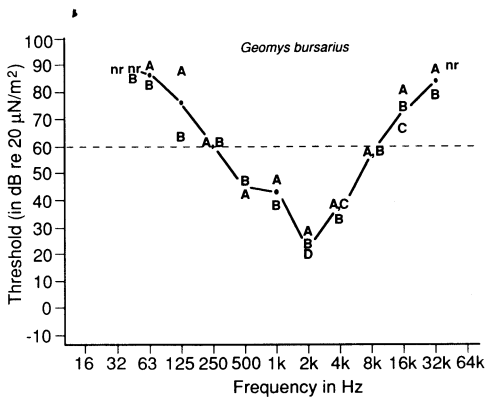


Fig. 2. Audiogram of the pocket gopher. Note restricted sensitivity and narrow hearing range of gophers. A, B, C and D represent individual gophers, 'nr' indicates no response.

Sound localization

The ability to localize sound is typically assessed using a brief sound, such as a 100-ms noise burst, in order to prevent an animal from localizing by using scanning movements of the head or pinnae. Although mammals vary in the accuracy with which they can localize brief sounds, they generally have little difficulty making a left-right discrimination at large angles of separation (e.g., Heffner and Heffner, 1984, 1988a).

Within in a few weeks, however, it became apparent that the gophers could localize neither a 100-ms noise burst, nor a continuous train of 100-ms noise bursts, regardless of the angle of separation. Because this inability was so remarkable, we began a series of tests to assure ourselves that this result was not peculiar to the stimulus or to the two animals initially chosen for this test.

Effect of varying the stimuli. Although it was soon established that the gophers could discriminate loudspeakers located 90° left and right of midline when a 2.5-s burst of broad-band noise was used, the possibility that other stimulus configurations might yield good performance was systematically investigated. The first step was to insure that the noise burst was easily audible to the animals. Once detection thresholds had been established for the noise burst, the intensity was varied over a range of 20–46 dB above threshold.

However, changing the intensity did not result in a noticeable change in performance.

The next step was to vary the spectrum of the signal on the possibility that the auditory system of the gopher might be specialized to process only a restricted frequency range that might have special (but unsuspected) relevance to an underground existence. This was done by using low-frequency filtered noise (1 kHz low pass, 48 dB/octave), high-frequency noise (1 kHz high pass, 48 dB/octave), as well as broad-band (unfiltered) noise. The use of the various loudspeakers listed in the Methods section varied both the spectrum and the size (from 1.25 cm to 7.62 cm) of the sound source. In addition, the distance of the loudspeakers from the animal was varied from 7.5 cm to 100 cm on the possibility that the narrow spaces of the gopher's natural environment might make them less attentive to sounds from a distance. The purpose of all of these manipulations was to discover a stimulus configuration that would reveal the best performance of which these animals are capable. However, none of these attempts resulted in improvement in their performances.

The angle of separation between the loudspeakers was varied from large (180°) to small (30°). Reasoning that front-back discriminations might be useful in tunnels, front-back and even a combination of left-front (30° left) versus right-back (150° right) locations were tried.

Of the various parameters, only the duration of the stimulus proved to have any effect on performance. That is, the gophers were able to localize long-duration noise bursts at large angles of separation, a point described in detail below. However, no animal was able to discriminate the locus of a sound which was less than 0.5 s in duration.

Generality across individuals. Altogether four gophers were tested on their ability to localize sound. None of the animals was able to localize the source of a 100-ms noise burst at angles of separation up to 180° despite thousands of training trials.

This is not to say that the animals were incapable of performing auditory discriminations. As will be described below, the animals were able to localize long-duration noise bursts. Furthermore,

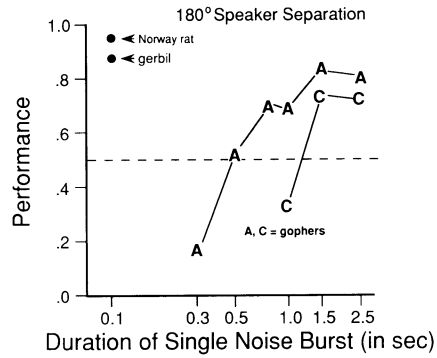


Fig. 3. The ability of two gophers (A and C) to discriminate between sound sources separated by 180° is dependent on the duration of the noise burst. Unlike other species which reliably localize 100-ms noise bursts (rat and gerbil are illustrated as examples), gophers can discriminate the locus only of long-duration sounds (Norway rat and gerbil data from Heffner and Heffner, 1985b, 1988b).

the gophers were able to discriminate noise bursts which differed in loudness or spectrum. Indeed, their sensitivity to monaural spectral differences made it necessary to give particular care to matching the output of the speakers with the equalizer before every test session.

Effect of stimulus duration. The effect of stimulus duration on localization performance was studied in detail in the two best animals (A and C). As shown in Fig. 3, asymptotic performance in discriminating between two loudspeakers located 90° to the left and right of the animal (for 180° total separation) was reached at a duration of 1.5 s. However, even at a 2.5-s duration, the animals were not able to perform the discrimination perfectly, indicating that this was a comparatively difficult task for them. Performance declined rapidly at shorter durations with performance scores of 0.50 falling at 0.5 s for gopher A and at about 1.25 s for gopher C.

Although not studied as systematically, there appeared to be no reliable difference in the ability of the animals to localize a single long noise burst and a series of shorter bursts as long as each burst exceeded 400 ms. For example, animal C could not localize a train of five 100-ms noise bursts with 450 ms between individual bursts.

The inability of gophers to localize brief sounds is in sharp contrast to the ability of other rodents.

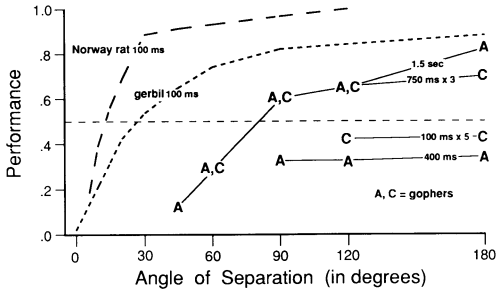


Fig. 4. Asymptotic performance of two gophers (A and C) localizing long-duration noise bursts in the azimuthal plane. Gopher A was tested using a single noise burst of 1.5 s or 400 ms; Gopher C was tested using three noise bursts of 750 ms or five bursts of 100 ms. Their 50% threshold with the longer durations was approximately 80°. Performance with the briefer signals never exceeded 50% detection. In contrast, Norway rats and gerbils localizing a single noise burst of 100 ms achieve thresholds of 12° and 27°, respectively (Heffner and Heffner, 1985b; Heffner and Heffner, 1988b).

As illustrated in Fig. 3, both gerbils, one of the least accurate rodents, and Norway rats, the most accurate rodent, are easily able to localize a 100-ms noise burst at 180° (Heffner and Heffner, 1985b, 1988b). Indeed, the performance of the gophers is so poor that it raises the question of whether they are qualitatively, as well as quantitatively, different from other mammals. That is, although the performance of the animals on long duration sounds may indicate the existence of a residual ability to localize sound, it is also possible that gophers have totally lost the ability to localize sound. That is, the animals may have been performing the discrimination on the basis of the monaural cues generated by differences in locus (e.g., intensity gradient) without extracting locus information.

Sound localization threshold. Sound localization thresholds were obtained for animals A and C using long-duration sounds. Fig. 4 illustrates that regardless of whether a single long burst (1.5 s) or multiple bursts (three 750-ms pulses) were used, the gophers could achieve a localization threshold of only 80°. When the duration was shortened to a single pulse of 400 ms or to five pulses totalling 500 ms, discrimination never rose above chance. Again, the markedly better performance of Norway rats and gerbils localizing a brief noise burst is illustrated for comparison (Heffner and Heffner, 1985b, 1988b). Despite this rudimentary ability to distinguish between long-duration sounds at large angles of separation, it must be emphasized that by conventional criteria using a single brief noise burst, gophers are unable to localize sound.

Auditory brainstem morphology

Despite the unusual behavioral results, the auditory nuclei in the brainstem of the pocket gopher do not deviate qualitatively from the mammalian pattern. The dorsal and ventral cochlear nuclei are present and contain all the expected types of cells. Similarly, the three major nuclei of the superior olivary complex (SOC) are clearly delineated and the inferior colliculus and medial geniculate are unremarkable.

Figure 5 illustrates the configuration and relative size of the dorsal (DCN), anteroventral

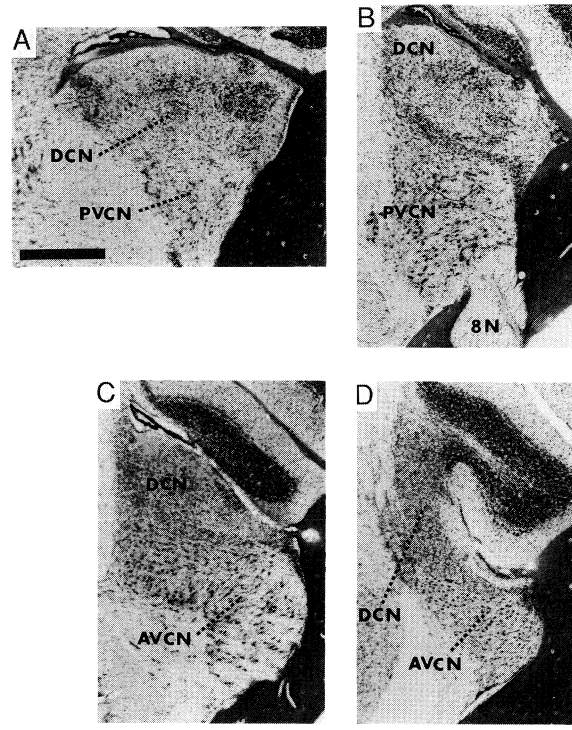
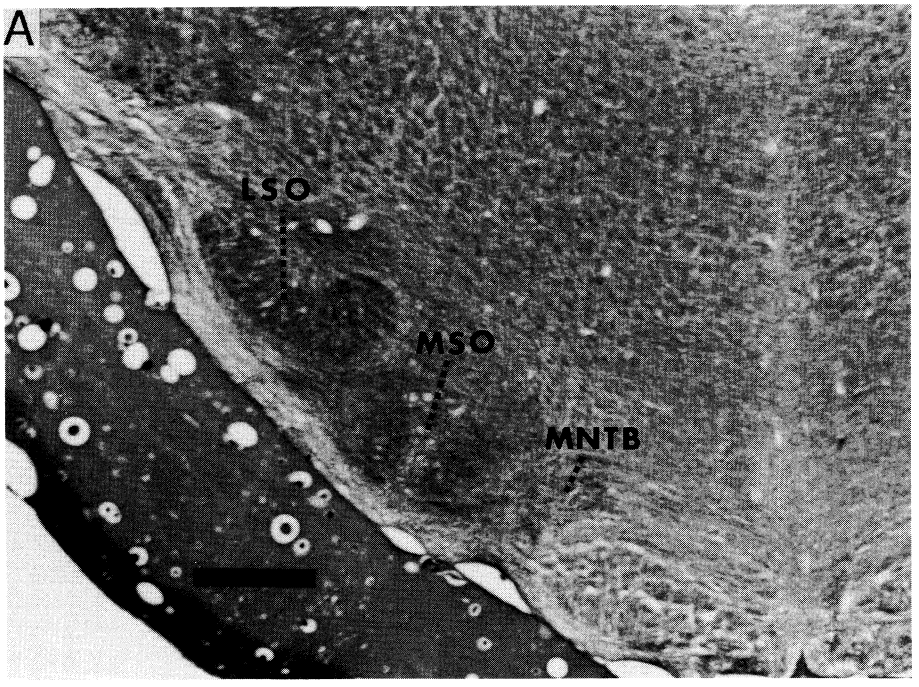
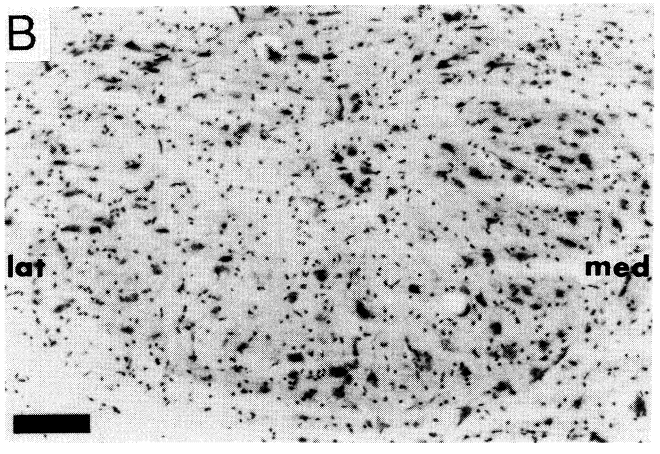


Fig. 5. The right cochlear nucleus of the pocket gopher arranged from caudal (A) to rostral (D). Sections A–C 300 μm apart, sections C and D 150 μm apart; thionine stain; AVCN = anteroventral cochlear nu., DCN = dorsoventral cochlear nu., PVCN = posteroventral cochlear nu., 8N = auditory nerve; scale bar = 0.5 mm.





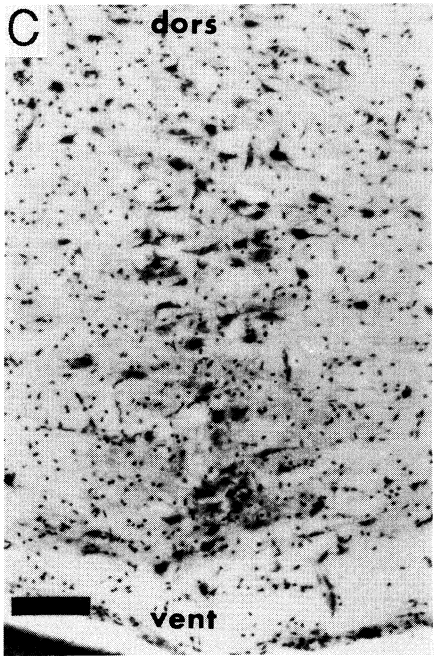


Fig. 6. The left superior olivary complex of the pocket gopher. (A) protargol stain showing the U-shaped neuropil of the LSO and the pale column of cells flanked by dense neuropil of the MSO; scale bar equals 0.5 mm. (B) higher magnification of the LSO in an adjacent section stained with thionine to reveal the near absence of neurons in the lateral portion of the nucleus; scale bar equals 0.1 mm. (C) higher magnification of the MSO in an adjacent section stained with thionine to reveal the column of fusiform cells; scale bar equals 0.1 mm. LSO = lateral superior olive, MNTB = medial nu. of the trapezoid body, MSO = medial superior olive.

(AVCN), and posteroventral (PVCN) cochlear nuclei. The DCN (Fig. 5a–d) extends throughout the entire rostro-caudal length of the cochlear nucleus and may be somewhat larger than usual in small rodents. It has a clearly delineated granular/fusiform layer and its granule cells fuse with a layer of cerebellar granule cells rostrally (Fig. 5d). The PVCN (Fig. 5a–b) contains a variety of large and small cells which appear to include octopus cells and multipolar cells but few globular cells. The AVCN (Fig. 5c–d) is small relative to the rest of the cochlear nucleus and spherical cells, especially small spherical cells, seem to be few in number.

The SOC is illustrated in Fig. 6. The medial superior olive (MSO), lateral superior olive (LSO), and medial nucleus of the trapezoid body (MNTB) are well defined by their neuropil as revealed by a Protargol stain (Fig. 6a). The MSO (Fig. 6c) is in the typical form of a column of fusiform cells, many with medially and laterally oriented dendrites which can be followed for some distance from the cell body. The LSO (Fig. 6b) is in the shape of a shallow 'U'. It also contains fusiform cells with dendrites oriented perpendicularly to the borders of the nucleus — again a typical mammalian configuration. The presence of typical neurons in both the MSO and LSO suggests that in the gopher, as in other more thoroughly studied species, the nuclei of the SOC receive input from both the contralateral and ipsilateral cochlear nuclei and are suited to compare the auditory input at the two ears.

On the other hand, the LSO is unusual in the low density of its cells (Fig. 6b). The low cell density is especially marked in the lateral portion of the nucleus where we would expect lower frequencies to be represented. The MNTB is smaller than in most rodents and the principle cells themselves seem small but otherwise typical — round, densely staining, and contacted by calyx-type endings. The ventral acoustic stria and the trapezoid body, consisting of the axons that make binaural interaction possible, are small. The small ventral acoustic stria is not unexpected in view of the small size of the AVCN from which these axons originate.

In Fig. 7, the configuration of the SOC at the level of the greatest extent of the LSO is illustrated for the pocket gopher, cat, and Norway rat. Examination of serial sections from several individuals of each species indicates that the MNTB of the gopher is the smallest of the three, and that its MSO is intermediate, being larger than the MSO of the rat, but smaller than that of

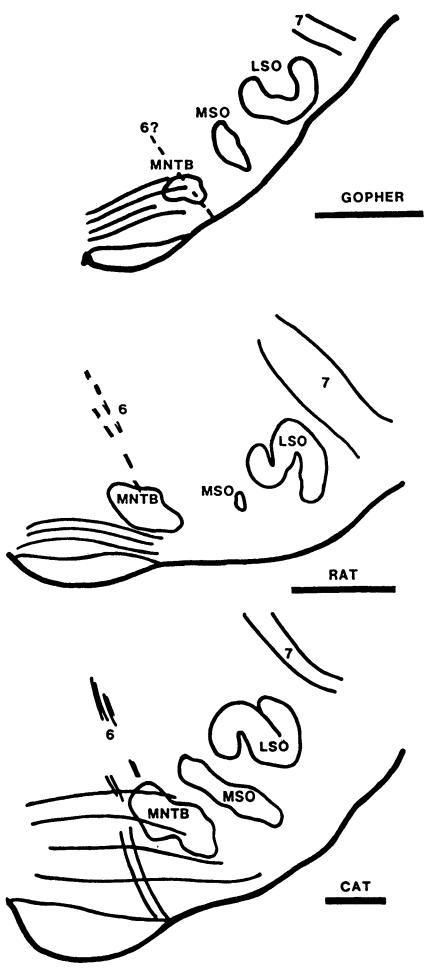


Fig. 7. Outline of the right brainstem and the three major nuclei of the superior olivary complex through the level of the greatest extent of the LSO for pocket gopher, domestic cat and Norway rat. In the gopher, as in the cat, the three nuclei are approximately equal in size, but unlike the cat, they do not fill the area between the sixth and seventh nerves and are not densely packed with neurons. The MNTB is smallest in the gopher and the MSO is intermediate in size. The LSO differs from both the rat and cat in that it consists of only two limbs rather than three, only one of which is filled with neurons. LSO = lateral superior olive, MNTB = medial nu. of the trapezoid body, MSO = medial superior olive, 6 = sixth nerve; 7 = seventh nerve; scale bar equals 1 mm.

the cat. The LSO appears to be similar in size in all three but the size of the LSO of the gopher may be misleading since its lateral limb contains so few cells.

Based on the limited analysis presented here, there is no obvious feature in the morphology of the auditory system which corresponds to the restricted auditory abilities of the gopher. Nevertheless, quantitative comparisons among a variety of species of the volume of the auditory nuclei and the number of cells they contain may reveal peculiarities in the pocket gopher that are not obvious in the simple morphology of the nuclei.

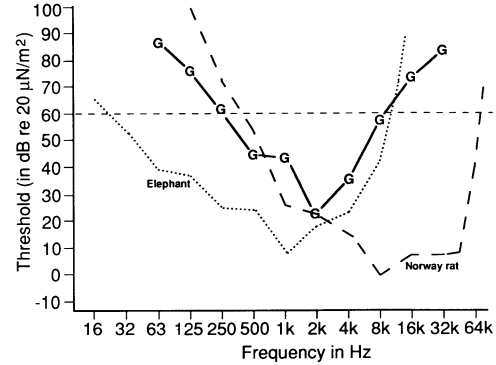


Fig. 8. Audiogram of the pocket gopher with Norway rat and elephant for comparison (Heffner and Heffner, 1982; Kelly and Masterton, 1977). Note the restricted sensitivity and narrow hearing range of gophers.

Discussion

The gopher is unique both in terms of its restricted hearing and its inability to localize sound. The following discussion describes why we believe that these two features are related.

Audiogram

Compared to other mammals, the hearing of the gopher is unusual in at least two ways: First, the gopher has relatively poor overall sensitivity with a best sensitivity of only 24 dB (at 2 kHz). This makes it the least sensitive of any of the more than 60 species of mammals which have been tested.

The second unusual feature is the gopher's restricted high-frequency hearing. With a 60-dB upper hearing limit of 8.7 kHz the gopher has the poorest high-frequency hearing of any mammal (Heffner and Heffner, 1985a).

Comparing the gopher with the Norway rat, a rodent of comparable body weight and interaural distance, reveals the uniqueness of its hearing. As shown in Fig. 8, the low-frequency hearing of both rodents is similar up to 2 kHz at which point the gopher's hearing begins to decline while the rat's continues to improve (Kelly and Masterton, 1977).

In other mammals, restricted high-frequency hearing is accompanied by a compensating extension of low-frequency hearing (e.g., Heffner and Heffner, 1985a). For example, the elephant (Heffner and Heffner, 1980, 1982) has a high-frequency hearing limit of 10.5 kHz which is accompanied by a low-frequency limit of 17 Hz, the lowest of any mammal yet tested (Fig. 8). However, the gopher, even though it has similarly restricted high-frequency hearing, does not have extended low-frequency hearing. This is especially notable since good low-frequency hearing is not uncommon among other small rodents such as gerbils, kangaroo rats, and chipmunks (Heffner and Contos, 1989; Heffner and Heffner, 1988b; Heffner and Masterton, 1980; Ryan, 1976).

Overall, the gopher audiogram has the appearance of a rat audiogram which has been truncated above 2 kHz. As previously noted the gopher has a very small auditory meatus. Because decreasing the diameter of a tube through which sound travels decreases the high frequency content of the output, it is conceivable that the small diameter of the gopher's meatus accounts for its truncated audiogram. Indeed, the fact that gophers can hear up to 32 kHz if the amplitude of the signal is increased above 60 dB SPL suggests that their poor high-frequency hearing is due to a peripheral restriction rather than to any changes in their sensorineural ability to process high-frequency sounds.

The general idea that fossorial mammals lack the ability to hear high frequencies has been proposed previously (Heffner et al., 1987) and also demonstrated by Bruns and his colleagues based on electrophysiological responses to sound in the blind mole rat (*Spalax ehrenbergi*) (Bruns et al., 1988). Using both cochlear microphonic and evoked response data, they suggested that this species is also unable to hear much above 10 kHz,

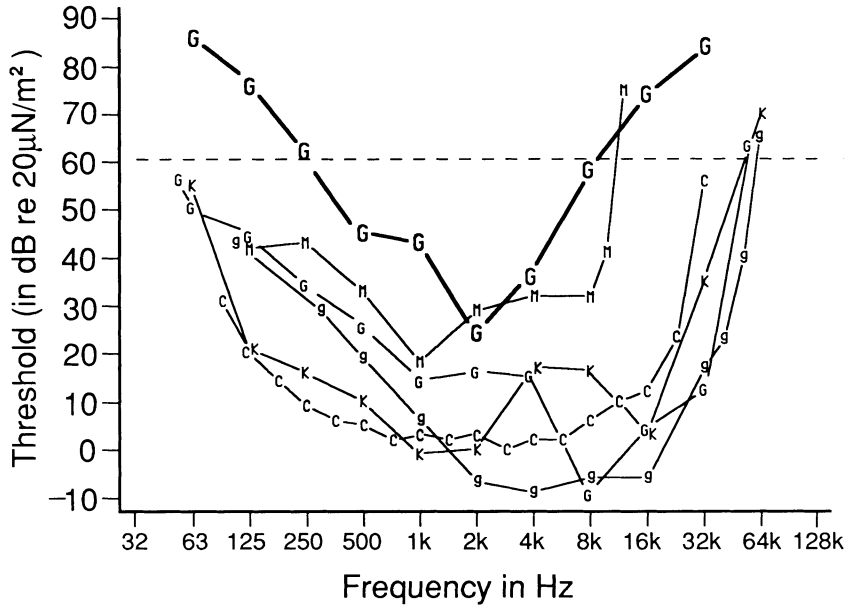


Fig. 9. Comparison of the gopher audiogram with those of selected rodents. C, chinchilla (Miller, 1970); g, gerbil (Ryan, 1976); G, guinea pig (Heffner et al., 1971); boldface G, gopher (present study); K, kangaroo rat (Heffner and Masterton, 1980); M, blind mole rat (Bronchti et al., 1989).

a finding which has subsequently been supported by the results of a behavioral study in which the animals were tested in a shuttle box (Bronchti et al., 1989). They further noted that the blind mole rat appeared to be relatively insensitive compared to other rodents. That a restricted upper limit of hearing may be common among fossorial mammals is supported by the evoked response audiogram of the African common mole-rat (*Cryptomys hottentotus*) (Müller and Burda, 1989).

A comparison of the behavioral audiograms of the gopher and blind mole rat with those of four low-frequency rodents (chinchilla, gerbil, guinea pig, and kangaroo rat) illustrates several points (Fig. 9). To begin with, the audiograms of the gopher and mole rat are quite similar — both species have restricted high-frequency hearing, neither is particularly sensitive at their best frequency, and their low-frequency hearing is not as sensitive as the other low-frequency rodents.

Although there are small differences between the gopher and mole rat audiograms, it is difficult to determine their significance. This is because the shuttle box method used to test the mole rats suffers from the limitation that the intensity of the sound at the animals' ears cannot be determined accurately because the animals are permitted to move freely about in the box. Thus, the intensity of the sound at an animal's ears depends on which part of the sound field it is in as well as whether it is facing the sound source. Just how much the sound field may vary depends upon such factors as the size of the box, its acoustic reflectiveness, and its location in the sound field. However, in spite of these difficulties, the audiograms of the gopher and mole rat clearly resemble each other more than they do those of other rodents, supporting the idea that adaptation to an extremely fossorial lifestyle results in systematic changes in the audiogram.

The question arises as to whether fossorial mammals are specialized for low-frequency hearing as a result of their adaptation to an underground environment which favors the transmission of low frequencies over high frequencies. However, as Fig. 9 shows, the gopher and mole rat are actually *less* sensitive to low frequencies than many other rodents. Although it has been suggested that the mole rat is sensitive to very low frequencies (Bronchti et al., 1989), the possibility

that the animals were responding to overtones or to substrate vibration has not been ruled out. This is especially important since difficulty was encountered with sound measurement at low frequencies and the electrophysiological evidence does not confirm exceptional low-frequency hearing (Bruns et al., 1988). Thus, it currently appears that fossorial rodents have relatively poor low-frequency hearing typical of many rodents (see Heffner and Heffner, 1985a, for a review), and have also lost their high-frequency sensitivity. Just why this loss might have occurred is addressed in the next section.

Sound localization

The restricted high-frequency hearing of the gopher poses a marked exception to the close relationship between interaural distance and high-frequency hearing (e.g., Heffner and Heffner, 1985a; Heffner and Masterton, 1990; Masterton et al., 1969). Among mammals, high-frequency hearing is inversely related to functional interaural distance — that is the distance around the head from ear to ear divided by the speed of sound (interaural time difference). This relation is illustrated for 53 mammals in Fig. 10 which shows that animals with small interaural time differences such as bats, mice, or dolphins hear higher frequencies than animals with larger interaural time differences such as horses, humans, and elephants.

The existence of this relationship has been attributed to selective pressure for small species to hear frequencies high enough to be shadowed by their head and pinnae thereby enabling them to use the interaural spectral-difference cue and the monaural pinna cues for localizing sound (Heffner, 1989; Heffner and Heffner, 1982, 1983, 1985a; Masterton et al., 1969). The gopher has a small interaural distance of 110 μs which, according to the regression line in Fig. 10, suggests that its 60-dB high-frequency hearing limit should be approximately 65 kHz — nearly 3 octaves higher than actually observed. This marked deviation from the mammalian pattern suggests that the gopher is under little selective pressure to localize sound — a suggestion supported by the present results.

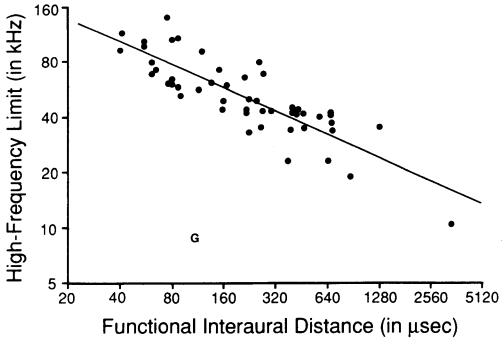


Fig. 10. Relation between interaural distance and highest frequency audible at 60 dB SPL among mammals ($r = -0.84$). The gopher (G) differs markedly from other mammals. For individual data points, see Heffner and Heffner, 1985a.

The sound localization threshold of gophers is far worse than that of any other mammal yet tested (Heffner and Heffner, 1987, 1988a,b; Heffner and Masterton, 1990). Fig. 4 illustrates their unique inability by comparison with Norway rats and gerbils, the most and least accurate localizers respectively among rodents, (Heffner and Heffner, 1985b, 1988b). Not only are gophers completely unable to localize brief sounds, they also have only a rudimentary ability to localize the source of long-duration sounds leading us to question whether they can extract spatial information from sound at all.

In summary, the pocket gopher has the poorest absolute sensitivity and sound localization acuity yet encountered among mammals. In addition, it lacks the ability to hear the high frequencies which other small mammals use to localize sound (Heffner, 1989). It is these limited hearing abilities, in comparison with the far superior acuity of other mammals, which suggest that the gopher's hearing might properly be considered vestigial. Although unusual, such a discovery is not surprising in a species whose responses to the attenuated sounds which reach it in its burrow are largely limited to moving forwards or backwards in a one-dimensional world.

The auditory brainstem

It is a reasonable and widely held belief that the morphology of the superior olivary complex is related to the ability of an animal to use the binaural cues for locus (cf., Masterton et al., 1975). Thus it is surprising but not unprecedented to find that the SOC in the pocket gopher consists of the

expected nuclei in their expected configuration (cf. Heffner and Heffner, 1989; Heffner and Masterton, 1990). The only suggestion of aberration in the auditory brainstem lies in the small AVCN, small ventral acoustic stria, and scarcity of cells in the lateral LSO. These characteristics, however, seem unimpressive in comparison with the vestigial auditory abilities of gophers. As for the binaural nuclei of the SOC, it is likely that functions in addition to sound localization are subserved there in rodents, at least one of which, the olivocochlear system, is well known (Campbell and Henson, 1988; Helfert et al., 1988; White and Warr, 1983; Winter et al., 1989). Until quantitative comparisons become available among a wide sample of species whose behavioral abilities are known, the significance of these variations in the size of auditory nuclei in the pocket gopher cannot be evaluated. In our search for poorly developed auditory nuclei, we were surprised to note that one structure, the DCN, may actually be larger than in most small rodents. The auditory functions of this structure remain a mystery (e.g., Masterton and Granger, 1988) and its strong development in a species with vestigial hearing lends plausibility to the notion that it may be involved in other systems as well (Itoh et al., 1987; Mugnaini, 1989; Saadé et al., 1989a,b; Weinberg and Rustioni, 1987).

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References

Aitkin, L.M., Horseman, B.G. and Bush, B.M.H. (1982) Some aspects of the auditory pathway and audition in the European mole, *Talpa europaea*. Brain Behav. Evol. 21, 49–59.

Bronchti, G., Heil, P., Scheich, H. and Wollberg, Z. (1989) Auditory pathway and auditory activation of primary visual targets in the blind mole rat (*Spalax ehrenbergi*): I. 2-deoxyglucose study of subcortical centers. J. Comp. Neurol. 284, 253–274.

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

Campbell, J.P. and Henson, M.M. (1988) Olivocochlear neurons in the brainstem of the mouse. Hear. Res. 35, 271–274.

Darwin, C. (1859) The Origin of Species by Means of Natural Selection. Reprinted by Random House, Toronto, p. 102–112.

Heffner, H.E. and Heffner, R.S. (1983) Sound localization and high-frequency hearing in horses. J. Acoust. Soc. Am. 73, S42.

Heffner, H.E. and Heffner, R.S. (1984) Sound localization in large mammals: localization of complex sounds by horses. Behav. Neurosci. 98, 541–555.

Heffner, H.E. and Heffner, R.S. (1985a) Hearing in two cricetid rodents: Wood rat (*Neotoma floridana*) and grasshopper mouse (*Onychomys leucogaster*). J. Comp. Psychol. 99, 275–288.

Heffner, H.E. and Heffner, R.S. (1985b) Sound localization in wild Norway rats (*Rattus norvegicus*). Hear. Res. 19, 151–155.

Heffner, H.E. and Masterton, R.B. (1980) Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse and kangaroo rat. J. Acoust Soc Am. 68, 1584–1599.

Heffner, R.S. (1989) The evolution of mammalian high-frequency hearing. Abstr. Assoc. Res. Otolaryngol. 166–167.

Heffner, R.S. and Contos, C.A. (1989) Hearing in two ground-dwelling squirrels: Eastern chipmunk and black-tailed prairie dog. Abstr. Assoc. Res. Otolaryngol. 233.

Heffner, R.S. and Heffner, H.E. (1980) Hearing in the elephant (*Elephas maximas*). Science 208, 518–520.

Heffner, R.S. and Heffner, H.E. (1982) Hearing in the elephant: Absolute thresholds, frequency discrimination and sound localization. J. Comp. Physiol. Psychol. 96, 926–944.

Heffner, R.S. and Heffner, H.E. (1987) Localization of noise, use of binaural cues and a description of the superior olivary complex in the smallest carnivore, the least weasel (*Mustela nivalis*). Behav. Neurosci. 101, 701–708, 744–745.

Heffner, R.S. and Heffner, H.E. (1988a) Sound localization in a predatory rodent, the northern grasshopper mouse (*Onychomys leucogaster*). J. Comp. Psychol. 102, 66–71.

Heffner, R.S. and Heffner, H.E. (1988b) Sound localization and use of binaural cues by the gerbil (*Meriones unguiculatus*). Behav. Neurosci. 102, 422–428.

Heffner, R.S. and Heffner, H.E. (1988c) Sound localization acuity in the cat: Effect of azimuth, signal duration and test procedure. Hear. Res. 36, 221–232.

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

Heffner, R., Heffner, H. and Masterton, B. (1971) Behavioral measurements of absolute and frequency difference thresholds in guinea pig. J. Acoust. Soc. Am. 49, 1888–1895.

Heffner, R.S. and Masterton, B. (1990) Sound localization: Brainstem mechanisms. In: M. Berkley and W.C. Stebbins (Eds.) Comparative Perception, Vol.1: Discrimination, Wiley and Sons, New York, pp. 285–314.

Heffner, R.S., Richard, M.M. and Heffner, H.E. (1987) Hear-

ing and the auditory brainstem in a fossorial mammal, the pocket gopher. Neurosci. Abstr. 13, 546.

Helfert, R.H., Schwartz, I.R. and Ryan, A.F. (1988) Ultrastructural characterization of gerbil olivocochlear neurons based on differential uptake of 3H-D aspartic acid and a wheatgerm agglutinin-horseradish peroxidase conjugate from the cochlea. J. Neurosci. 8, 3111–3123.

Heth, G., Frankenberg, E. and Nevo, E. (1986) Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (*Spalax ehrenbergi*). Experientia 42, 1287–1289.

Itoh, K., Kamiya, H., Mitani, A., Yasui, Y., Takada, M. and Mizuno N. (1987) Direct projections from the dorsal column nuclei and the spinal trigeminal nuclei to the cochlear nuclei in the cat. Brain Res. 400, 145–150.

Kelly, J.B. and Masterton, R.B. (1977) Auditory sensitivity of the albino rat. J. Comp. Physiol. Psychol. 9. 930–936.

Masterton, R.B. and Granger, E.M. (1988) Role of the acoustic striae in hearing: Contribution of dorsal and intermediate striae to detection of noises and tones. J. Neurophysiol. 60, 1841–1860.

Masterton, B., Heffner, H. and Ravizza, R. (1969) Evolution of Human hearing. J. Acoust. Soc. Am. 45, 966–985.

Masterton, B., Thompson, G.C., Bechtold, J.K. and RoBards, M. (1975) Neuroanatomical basis of binaural phase-difference analysis for sound localization: A comparative study. J. Comp. Physiol. Psychol. 89, 379–386.

Miller, J.D. (1970) Audibility curve of the chinchilla. J. Acoust. Soc. Am. 48, 513–523.

Mugnaini, E. (1989) Architecture, neuronal typology and efferent connections of the dorsal cochlear nucleus (DCN). Abstr. Assoc. Res. Otolaryngol. 3.

Müller, M. and Burda, H. (1989) Restricted hearing range in a subterranean rodent *Cryptomys hottentotus*. Naturwissenschaft. 76, 134–135.

Ryan, A. (1976) Hearing sensitivity of the Mongolian gerbil (*Meriones unguiculatis*). J. Acoust. Soc. Am. 59, 1222–1226.

Saadé, N.E., Frangieh, A.S., Atweh, S.F. and Jabbur, S.J. (1989a) Dorsal column input to cochlear neurons in decerebrate-decerebellate cats. Brain Res. 486, 399–402.

Saadé, N.E., Bassim, Y.R., Atweh, S.F. and Jabbur, S.J. (1989b) Auditory influences via cochlear nucleus on cuneate neurons in decerebrate-decerebellate cats. Brain Res. 486, 403–406.

Weinberg, R.J. and Rustioni, A. (1987) A cuneocochlear pathway in the rat. Neurosci. 20, 209–219.

White, J.S. and Warr, W.B. (1983) The dual origins of the olivocochlear bundle in the albino rat. J. Comp. Neurol. 219, 203–214.

Winter, I.M., Robertson, D. and Cole, K.S. (1989) Descending projections from auditory brainstem nuclei to the cochlea and cochlear nucleus of the guinea pig. J. Comp. Neurol. 280, 143–157.