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Degenerate Hearing and Sound Localization in Naked Mole Rats (*Heterocephalus glaber*), With an Overview of Central Auditory Structures

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ABSTRACT

Behavioral tests of absolute sensitivity and sound localization in African naked mole rats show that, despite their communal social structure and large vocal repertoire, their hearing has degenerated much like that of other subterranean species. First, their ability to detect sound is limited, with their maximum sensitivity being only 35 dB (occurring at 4 kHz). Second, their high-frequency hearing is severely limited, with their hearing range (at 60 dB sound pressure level [SPL]) extending from 65 Hz to only 12.8 kHz. Third, determination of the effect of duration on noise thresholds indicates that, compared with other animals, mole rats require a sound to be present for a much longer duration before reaching asymptotic threshold. Finally, they are unable consistently to localize sounds shorter than 400 ms and cannot accurately localize sounds of longer duration, raising the possibility that they are unable to use binaural locus cues. Thus, it seems that the essentially one-dimensional burrow system of a subterranean habitat produces severe changes in hearing comparable to the changes in vision that result from the absence of light. To explore the relation between vision and sound-localization acuity, retinal ganglion cell densities were determined. The results indicate that naked mole rats have a broad area of best (albeit poor) vision, with maximum acuity estimated at 44 cycles/degree. That mammals with wide fields of best vision have poorer sound-localization acuity than those with narrower fields is consistent with the thesis that a major function of sound localization is to direct the gaze to the source of a sound. However, the fact that subterranean mammals have little use for vision in a lightless environment suggests that they represent an extreme case in this relationship and may explain the fact that, unlike surface-dwelling mammals, they have virtually lost the ability to localize brief sounds. Finally, despite their very limited auditory abilities, the major brainstem auditory nuclei, although relatively small, appear to be present.

Key words: evolution, subterranean, chinchilla, vision, retina, ganglion cells, communication, temporal integration

Subterranean mammals constitute a major ecological group whose auditory abilities are only recently being explored (e.g., Aitkin et al., '82; Bronchti et al., '89; Bruns et al., '88; Heffner and Heffner, '90b; Müller and Burda, '89). The hearing of species adapted exclusively to an underground habitat is of interest because the auditory environment underground differs markedly from that encountered by surface, aerial, or aquatic mammals. Airborne sound propagation is restricted in small tunnels (Heth et al., '86), with the result that auditory stimulation, like visual stimulation, may be more limited than in surface habitats. Similarly, the directionality of both auditory stimuli and the range of possible behavioral responses to those stimuli are usually limited to a single linear dimension, so that there may be little selective advantage in an ability to determine the azimuthal or vertical location of sound sources. Thus subterranean species provide an opportunity to examine the relations between vision and hearing in mammals that have evolved under natural conditions of visual and auditory deprivation.

Because of the limitations of an underground environment for audition, it is perhaps not surprising that degener-

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ate hearing and sound localization have been reported in two subterranean rodents: pocket gophers, a solitary species common in North American (Heffner and Heffner, '90b), and blind mole rats, a solitary species native to the deserts of the eastern Mediterranean (Bronchti et al., '89; Bruns et al., '88; Heffner and Heffner, '92b). Both of these species are unusually insensitive to airborne sound, with maximum sensitivities of only 24 dB and 32 dB SPL, respectively, more than two standard deviations above the mammalian average of 0.4 dB (Heffner and Heffner, '90a). Similarly, both have restricted high-frequency hearing unprecedented in small mammals and comparable to that of much larger species such as humans and elephants (e.g., Betke, '91; Heffner and Heffner, '82). Further, electrophysiological measures suggest that African common mole rats (*Cryptomis hottentotus*) and European moles (*Talpa europaea*) have similarly limited hearing (Aitkin et al., '82; Müller and Burda, '89).

Given these findings, the question arises as to whether a subterranean environment invariably leads to the development of degenerate hearing abilities or whether other factors might exist that could sustain typical mammalian hearing in a subterranean species. One possible factor is the use of vocal signals for intraspecific communication. Although most subterranean species are solitary and have little opportunity to use vocal communications, the naked mole rat is a prominent exception.

Naked mole rats (*Heterocephalus glaber*) are small rodents that live in colonies of as many as 300 individuals. These animals are known to produce at least 17 different vocalizations, each associated with a specific behavioral context (Pepper et al., '91). The fact that these animals possess a relatively extensive repertoire of vocal communications and are in constant communication with other members of their colony raises the question of whether selective pressure for the use of vocal communications might have resulted in the retention of more typical mammalian hearing in that species.

The purpose of this paper is to report the results of tests of absolute sensitivity and sound-localization ability in naked mole rats. As will be seen, this species, like solitary subterranean species, has degenerate hearing. In addition, the results of two anatomical analyses are presented that relate directly to the behavioral results. The first is a preliminary description of the auditory brainstem of naked mole rats that addresses the question of whether their degenerate hearing is reflected in their central auditory anatomy.

The second anatomical result is a description of the density of ganglion cells throughout the retina of a naked mole rat, which is used to explore the relationship among mammals between vision and sound-localization acuity. It has been proposed that a primary function of sound localization is to direct the eyes so that the source of a sound falls within an animal's field of best vision (Heffner and Heffner, '92c). This proposition is supported by the fact that there is a high correlation among mammals between the width of the field of best vision, as determined by retinal ganglion cell density, and sound-localization acuity. That is, animals with narrow fields of best vision require better sound-localization acuity in order to insure that they can visually locate a sound source than do animals with broad fields. Thus, the density gradients of the naked mole rat are presented to provide information regarding the relation between vision and sound-localization acuity in a species for which both vision and hearing may be of limited value.

Abbreviations

Aq	cerebral aqueduct
AVCN	anteroventral cochlear nucleus
Cb	cerebellum
CIC	central nucleus of the inferior colliculus
DC	dorsal cortex of the inferior colliculus
DCN	dorsal cochlear nucleus
DLL	dorsal nucleus of the lateral lemniscus
Hip	hippocampus
IC	inferior colliculus
ILL	intermediate nucleus of the lateral lemniscus
LN	lateral nucleus of the inferior colliculus
LSO	lateral superior olive
MG	medial geniculate body
MSO	medial superior olive
MTB	medial nucleus of the trapezoid body
PVCN	posteroventral cochlear nucleus
SC	superior colliculus
SOC	superior olivary complex
VLL	ventral nucleus of the lateral lemniscus
VTB	ventral nucleus of the trapezoid body
4V	fourth ventricle
7N	seventh nerve

MATERIALS AND METHODS

Four individual naked mole rats were tested with a conditioned avoidance procedure in which a hungry animal was trained to make continuous contact with its mouth on a metal food spout in order to receive a steady trickle of a pureed fruit/vegetable mixture. 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.

Complete audiograms were determined, followed by sound-localization tests with signals of various durations. Because the mole rats had difficulty localizing brief sounds, their ability to detect brief sounds was also examined and compared with that of chinchillas tested in the same apparatus. Finally, descriptions of the auditory brainstem and retina of naked mole rats are presented and related to their auditory abilities.

Subjects

The biology of naked mole rats (*Heterocephalus glaber*) has recently been described in detail (Jarvis and Bennett, '90; Sherman et al., '91). Naked mole rats are the smallest subterranean rodents, weighing approximately 20–40 g, and are relatively long-lived, with lifespans extending well beyond 10 years. They are diurnal despite their exclusive underground existence and their specializations for underground living are extreme: tooth digging, absence of hair, minute eyes, no external pinnae, and poikilothermia (Burda et al., '90; Contreras and McNab, '90; Hildebrand, '85). Unlike most other subterranean species, naked mole rats are not solitary, but live in large colonies with a single breeding queen, a very few breeding males, and as many as 300 nonbreeding workers of both sexes (Alexander et al., '91; Brett, '91; Jarvis, '91). They have an extensive repertoire of vocal communications employing frequencies primarily between 200 Hz and 9 kHz (Pepper et al., '91). Finally, the phyletic affinities of naked mole rats are uncertain, and they have at different times been placed in each of the three suborders of rodents; they are currently linked with the hystricomorpha (Honeycutt et al., '91).

Four laboratory-reared naked mole rat workers approximately 1 year old and weighing 18–28 g were used in this study. They were housed together in four plastic boxes (approximately 14 × 14 × 16 cm high) connected by 1⅞-inch (4.8-cm) glass tubing to simulate tunnels connecting nest chambers, larders, and toilet areas. The ambient temperature was maintained between 30 and 32°C, the temperature of their natural burrows. During testing, the animals received most of their liquids in the test sessions in the form of pureed fruits and vegetables, of which they consumed 2.5–4.5 cc daily. They had free access to commercial rabbit chow and rat chow supplemented with small amounts of fresh fruit or vegetables as needed to maintain their body weights above 80% of their free-feed weights.

Two chinchillas (*Chinchilla laniger*) were used as comparison subjects in a test of absolute sensitivity for broadband noise bursts of different durations. Chinchillas were chosen because their typical temporal integration thresholds are known (e.g., Wall et al., '81) and they could thus serve as a control to insure that our results were not due to any idiosyncracies of our equipment or test procedure. The chinchillas were housed in glass tanks (50 × 26 × 30 cm high) and given free access to rabbit chow supplemented with a daily raisin; they received water in the daily test sessions.

Behavioral apparatus

Testing was conducted in a carpeted double-walled acoustic chamber (Industrial Acoustics Company model 1204; 2.55 × 2.75 × 2.05 m high), the walls and ceiling of which were covered with egg-crate foam to reduce sound reflection. The equipment for behavioral control and stimulus generation was located adjacent to the chamber and the animals were observed over a closed-circuit television. The test room was heated to a temperature approximating that of their natural burrows (30–32°C) to avoid any changes in sensitivity that might occur if their body temperatures were allowed to fall.

The animals were tested in a cage 17.5 cm long × 11.5 cm wide × 13 cm high constructed of ½-inch (1.27-cm) hardware cloth. The cage was mounted on a camera tripod 92 cm above the floor and 8-cm-thick foam rubber pads were placed under the feet of the tripod to reduce the possibility of substrate-borne vibrations. A food spout (8-mm-diameter stainless steel sipper tube) was mounted vertically so that it projected up through the bottom of the cage 2 cm above the floor and 2 cm from the front of the cage. The spout was attached to a 10-cc syringe located below the cage that served as the food reservoir. A food puree consisting of strained fruit or vegetables (commercial baby food: applesauce, pears, peaches, green beans, or mixed vegetables) was dispensed through the spout by using a syringe pump similar to that described elsewhere (Thompson et al., '90). The food delivery rate was adjusted so that the animals obtained 2–4 cc in a test session lasting 15–30 minutes.

A contact circuit connected between the food spout and cage floor served to detect when an animal made contact with the spout and turned on the syringe pump. A constant-current shock generator was connected between the spout and cage floor, and a 25-watt light located 50 cm below the cage was turned on during the shock in order to provide an indication of shock delivery when the animals successfully avoided the shock itself.

Acoustic apparatus

Audiogram. Sine waves were generated by an oscillator (Hewlett-Packard 209A or Krohn-Hite 2400) that was calibrated daily with a frequency counter (Fluke 1900A). The electrical signal was gated on and off with a rise–fall gate (Coulbourn S84-04) to prevent onset transients. The intensity was adjusted with an attenuator (Hewlett-Packard 350D) and the linearity of the attenuator was verified by measuring the acoustic and electrical signals at the various attenuations. The signal was then bandpass filtered (Krohn-Hite 3202) at ⅔ octave centered on the test frequency in order to reduce any noise in the electrical signal, and then connected via either an impedance-matching transformer or an amplifier (Crown D75) to a loudspeaker. The electrical signal was monitored at the loudspeaker for the possibility of distortion or noise with an oscilloscope (BK 1476A).

The loudspeaker was located 0.5 to 1.5 m in front of the cage (the distance being varied as needed to achieve an even sound field of sufficient intensity at each frequency) and oriented toward the position occupied by the animal's head when it was eating from the spout. The loudspeakers used were: a 15-inch (38-cm) woofer for frequencies of 8 Hz to 32 Hz, a subwoofer (Audio Concepts Saturn model, LaCrosse, WI) speaker for frequencies of 32 Hz to 125 Hz, an Infinity RS2000 midrange speaker for frequencies of 125 Hz to 8 kHz, and a Foster ribbon tweeter for frequencies of 4 kHz to 16 kHz. Thresholds for a particular frequency were often obtained by using different loudspeakers in order to eliminate the possibility that some thresholds might be influenced by the peculiarities of a particular speaker.

Testing was carried out with tones in octave steps from 8 Hz to 8,000 Hz with an additional threshold determined at 11,200 Hz. The tones were pulsed, 400 milliseconds on and 100 milliseconds off for five pulses, with rise/decay times of 100 milliseconds for frequencies of 32 Hz and below, 80 milliseconds for 63 Hz, 60 milliseconds for 125 Hz, 40 milliseconds for 250 Hz, 20 milliseconds for 500 Hz, and 10 milliseconds for frequencies of 1 kHz and higher.

The sound pressure level (SPL re 20 μNewtons/m^2) was measured daily with a Brüel & Kjaer (B & K) ¼-inch (0.64-cm) microphone (B & K 4135) or a ½-inch (1.27-cm) microphone (ACO Pacific 7012), preamplifier (B & K 2618), microphone amplifier (B & K 2608), and filter (Krohn-Hite 3202) set to pass one octave above and below the test frequency. The measuring system was calibrated with a pistonphone (B & K 4230). Sound measurements were taken by placing the microphone in the position occupied by an animal's head when it was eating and pointing the microphone directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (±1 dB) in the area occupied by the animal's head and ears. The tones were examined for the presence of overtones or distortion by connecting the output of the microphone amplifier to a spectrum analyzer (Zonic+AND 3525). Analysis indicated that any overtones were more than 10 dB below threshold. As a final precaution, the woofer used to generate the lowest frequencies was placed on 8-cm-thick foam pads to further guard against transmitting vibrations to the animal through the floor.

Temporal summation. In addition to the thresholds for pure tones, the four mole rats were tested for their sensitivity to the broadband noise used in the sound-localization tests, the spectrum of which is shown in Figure 1. The apparatus was the same, with the exception that the signal was produced by a noise generator (Grason Stadler 1285) and the filter was set to pass frequencies between 200 Hz and 12 kHz. A combination speaker consisting of a 3-inch

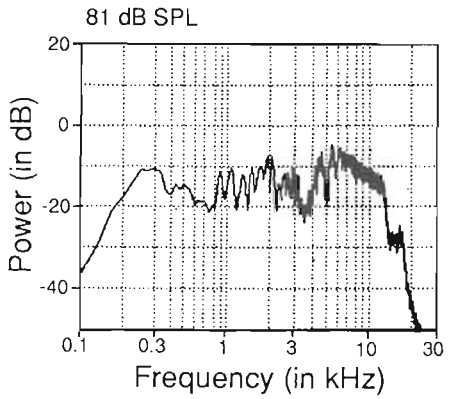


Fig. 1. Spectrum of noise band used for sound localization and for noise-detection thresholds.

(7.62-cm) woofer and a piezoelectric tweeter transduced the signal.

Sound localization. Sound-localization ability was assessed with clicks and noise bursts. The clicks were produced by two 50-μs square wave generators (Coulbourn S78-22), amplified by separate left and right amplifiers (Coulbourn S82-24), and led to two 3-inch (7.62-cm) paper cone loudspeakers. The noise signal was produced by a noise generator (Grason Stadler 1285) set on the 10-kHz energy band to obtain a relatively low-frequency signal. The signal was filtered (Krohn-Hite 3202) to pass frequencies ranging from 200 Hz to 12 kHz in order to concentrate the energy of the signal in the hearing range of the mole rats (the low-frequency cutoff of the noise was determined by the rolloff of the loudspeakers) (Fig. 1). The electrical signal was randomly attenuated by 0–4 dB in 1-dB steps by a programmable attenuator (Coulbourn S85-08) and further varied using a two-channel equalizer (Sentek EQ3), which allowed random switching between two slightly different noise spectra. These small variations in intensity and spectra served to reduce the possibility that the animals could distinguish between the loudspeakers on the basis of some dimension other than locus. The signal was then switched on and off by a rise/fall gate (Coulbourn S84-04, 100 μs rise/decay time), split into left and right lines and led to two amplifiers (Coulbourn S82-24), and finally to two loudspeakers, each consisting of a 3-inch (7.62-cm) woofer and a piezoelectric tweeter mounted directly above the woofer. The loudspeakers were suspended at ear level from a perimeter bar of 1.1 m radius. The intensity of each speaker was set to 81 dB SPL at the beginning of each test session.

The ability to localize brief sounds was examined in three ways. First, two of the mole rats were tested using a 2-second train of clicks presented at the rate of 5 clicks/second. Second, using a fixed angle of 180° separation, the duration of a single noise burst was gradually reduced from 1,000 milliseconds to 100 milliseconds in an effort to train the animals to respond to a single brief sound and to determine the shortest duration that could be localized. Finally, sound-localization thresholds were determined using noise bursts of two different durations. The first was a long-duration stimulus that consisted of three bursts of 700-millisecond noise separated by 100 milliseconds of silence. The second stimulus was a single 400-millisecond noise burst, the shortest duration that all of the animals could localize above chance, as shown below.

Behavioral procedure

Audiogram. An animal that had been deprived of fruit and vegetables for 23.5 hours was placed in the test cage and allowed to consume a steady stream of the fruit/vegetable puree from the food spout. Maintaining contact with the spout served to fix the animal's head in the sound field, thus enabling the sound pressure level in the vicinity of an animal's head to be specified precisely (cf. Heffner and Heffner, '91). It was then trained to stop eating and break contact with the spout momentarily whenever a suprathreshold sound was presented, in order to avoid a mild electric shock from the spout. The shock was adjusted for each individual to the lowest level that would reliably produce an avoidance response. The mildness of the shock was attested by the fact that none of the animals developed a fear of the spout and returned to it without hesitation after the termination of the shock (signaled by the light flash).

Test sessions were divided into 2.5-second trials separated by 1.5-second intertrial intervals. Each trial period contained either a pulsing tone ("warning" signal) or silence ("safe" signal). The contact switch indicated whether an animal was in contact with the spout during the last 150 milliseconds of each trial. If an animal broke contact for more than half of the 150-millisecond response period, a detection response was recorded. The response was classified as a "hit" if the trial contained a pulsing tone, and as a "false alarm" if no tone was presented. Each trial had a 22% probability of containing a tone. Both the hit and false alarm rates were determined for each block of 6–8 warning trials (which also included approximately 30 safe trials) for each stimulus condition. The hit rate was corrected for false alarms to produce a performance measure according to the formula: Performance = Hit rate − (False alarm rate × Hit rate). This measure proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition; the corrected performance measure varies from zero (no hits) to unity (100% hit rate with no false alarms) (cf. Heffner and Heffner, '88).

Auditory thresholds were determined by reducing the intensity of the tone in successive blocks of 6–8 warning trials until the animal no longer responded to the signal above the level expected by chance ($P > .01$). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity in 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold. Threshold was defined as the intensity corresponding to a corrected detection rate of 0.50. 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.

Temporal summation. Sensitivity to noise was determined using the same procedure described for tones. The intensity of the noise was varied in 5-dB steps and thresholds were determined for single bursts of noise of 1,000-millisecond duration, followed by thresholds for 600, 400, and 100 milliseconds. After the thresholds had been determined initially, each was rechecked in at least one session to assure that performance was at asymptote and that there was no further improvement with practice. For purposes of comparison, the thresholds of two chinchillas were also determined for 100-millisecond and 1,000-millisecond noise bursts.

Sound localization. Sound-localization performance was determined by presenting a sound from a loudspeaker

located to the left or right of midline. Sounds coming from the left were arbitrarily designated as warning signals and were followed by shock, whereas sounds from the right were designated as safe signals and were not followed by shock. Thus the animal was trained to respond by breaking contact with the spout whenever a sound came from its left and by maintaining contact when a sound came from the right.

The effect of stimulus duration on sound-localization was determined by testing at a fixed angle of 180° for 12–19 sessions until there was no evidence of further improvement at any stimulus duration. Each session began with long durations; the duration was progressively shortened until performance fell to chance, and the session then ended with testing at a long duration to verify that the animal was still motivated to perform. Asymptotic performance for each stimulus duration was then calculated as the average of the three highest scores from different sessions.

Thresholds were obtained by decreasing the angle of separation between speakers until performance fell to chance. Performance was calculated in the same manner as described for the audiogram, and threshold was defined as the angle at which performance equaled 0.50. Testing continued until performance no longer improved at any angle. The localization stimuli used were a 5 per second click train and noise bursts of various durations.

Histological methods

The brains and eyes of two mole rats that had died of unknown causes were removed and immersed in cold 10% formalin. The brains were embedded in egg yolk and prepared for frozen sectioning by immersion in 25% glycerol for cryoprotection. They were cut in transverse sections 25 μm thick and alternate sections were saved. Sections were mounted on chrome alum/gelatin subbed slides and two series of sections 100 μm apart were stained with either 0.25% thionine or Protargol silver using the method of Joe Adams (personal communication).

The retinae were dissected free from the sclera, mounted on gelatinized slides with the ganglion-cell layer uppermost, and stained with thionine according to the procedure of Stone ('81). The density of the ganglion cells was determined throughout the retina in 0.1-mm steps using a 100× oil-immersion objective and a sampling area of 0.00095 mm^2. The horizontal width of the region encompassing densities equal to or greater than 75% of maximum density was determined as an indication of the width of the field of best vision, as described elsewhere (Heffner and Heffner, '92c). Maximum density was used to calculate the maximum theoretical acuity of mole rats using Shannon's sampling theorem (e.g., DeBruyn et al., '80): $(\sqrt{x})/2$ = maximum theoretical resolvable spatial frequency in cycles/degree, where x = number of ganglion cells per $degree^2$.

RESULTS

All four mole rats readily adapted to the test cage and maintained body weight by eating the fruit/vegetable puree from the food spout. Furthermore, the animals rapidly learned to respond to the tones and were able to avoid the shock by the sixth warning trial of the first training session. Thus the animals appeared to find the basic detection task very easy and their subsequent difficulty in some of the auditory discriminations cannot be ascribed to the test procedure.

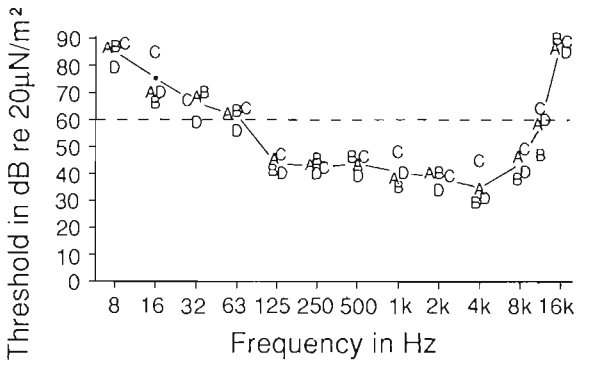


Fig. 2. Audiograms for four naked mole rats. Note the relative lack of sensitivity throughout the audible range and the poor high-frequency hearing. A, B, C, and D represent individual animals; dashed line indicates 60 dB SPL.

Auditory sensitivity

Tones. The audiograms for the four mole rats shown in Figure 2 indicate that there was good agreement between animals. The mole rats responded to frequencies from 8 Hz to 16 kHz with a best frequency at 4 kHz, where their average best sensitivity was only 35 dB. The audiograms are relatively flat in the midrange, with thresholds at these frequencies averaging around 40 dB. This remarkable insensitivity throughout the range of best hearing is a noteworthy feature of their hearing.

Using an arbitrary definition of hearing range as those frequencies audible at a level of 60 dB SPL, the range of naked mole rats extends from 65 Hz to 12.8 kHz; at slightly less than 7.5 octaves, it is one of the more restricted hearing ranges among mammals. Indeed, their very limited high-frequency hearing is a second noteworthy feature; it is shared by other subterranean rodents but has not been observed in surface-dwelling rodents (cf. Aitkin et al., '82; Bronchti et al., '89; Bruns et al., '88; Müller and Burda, '89; Heffner and Heffner, '90b, '92c).

Temporal summation. Because preliminary tests indicated that the mole rats had difficulty localizing short-duration sounds, detection thresholds for noise bursts of 100 to 1,000 milliseconds were determined in order to rule out the possibility that the poor localization performance might be the result of reduced sensitivity to the brief sounds. Although the animals easily responded to the longer duration bursts, they required 15–20 practice sessions before they reached asymptotic performance with the 100-millisecond noise burst. The final results indicated that thresholds varied systematically with duration, with the 1,000-millisecond threshold averaging 8.5 dB lower than the 100-millisecond threshold (Fig. 3). Although the largest improvement in sensitivity occurred between 100 and 400 milliseconds, all animals showed continued improvement between 400 and 600 milliseconds, with three of the four showing further improvement between 600 and 1,000 milliseconds.

These results contrast with the performance of the two chinchillas used for comparison. First, the chinchillas had no difficulty in detecting the 100-millisecond noise burst and reached asymptotic performance with only two practice sessions. Second, as illustrated in Figure 3, the chinchillas were 35–40 dB more sensitive than the naked mole rats at

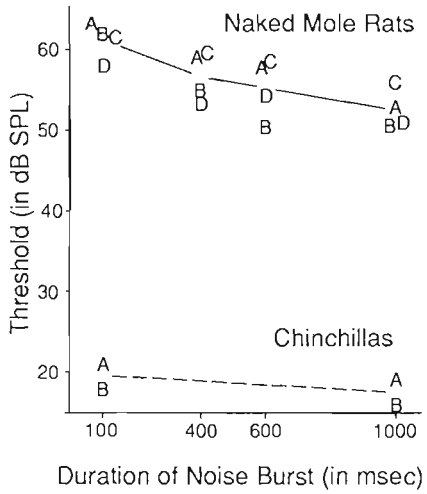


Fig. 3. Detection thresholds for a single burst of noise for four mole rats and two chinchillas. Note the absolute difference in sensitivity between mole rats and chinchillas and the continued improvement in sensitivity of the mole rats for very long durations. Letters represent individual animals.

all durations. Finally, the average improvement in threshold as duration increased from 100 to 1,000 milliseconds was 2 dB—a value consistent with previously published reports of temporal integration in chinchillas (Wall et al., '81), indicating that there was nothing unusual about our procedure that could account for the mole rats' results. Thus it appears that not only are naked mole rats less sensitive to sound than other mammals, but they also require the sound to be present for a longer time before they reach maximum sensitivity.

Sound localization

Effect of signal duration. The ability to localize sound is routinely assessed using a single brief sound such as a click or a 100-millisecond burst of noise in order to prevent an animal from localizing by using scanning movements of the head or pinnae (e.g., Thompson and Masterton, '78). Although mammals vary in their azimuthal thresholds for localizing brief sounds, they generally have little difficulty making a left–right discrimination at large angles of separation (for a review, see Heffner and Heffner, '92a). However, none of the naked mole rats could localize a click-train (5 clicks per second for 2 seconds). Furthermore, even after weeks of practice, only one animal was able to localize a single 100-millisecond noise burst above chance and then only when the sources were separated by 180°. Because further testing indicated that their performance improved as the duration of the noise bursts increased, we investigated the effect of noise duration on their ability to localize 100-millisecond to 1,000-millisecond noise bursts at an angle of 180° separation.

As shown in Figure 4, all of the animals could localize noise bursts of 700 milliseconds or longer with performances exceeding 0.80, indicating that the task itself was not difficult. However, asymptotic performances fell as duration was decreased, with animals A and C unable to localize noise bursts of less than 300 milliseconds. On the other hand, animals B and D were eventually able to localize the 100-millisecond noise burst above chance, although at low performance levels. However, it should be noted that these scores are based on the three best blocks of trials achieved in three to five sessions and, as will be seen, the animals could not consistently localize the 100-millisecond noise burst (cf. Fig. 5). This difficulty localizing brief sounds is a third noteworthy feature of the hearing of naked mole rats—one that is also found in other subterranean rodents (Heffner and Heffner, '90b, '92c).

Effect of signal intensity. Because the mole rats' sensitivity averaged 8.5 dB less for the 100-millisecond noise burst than for the 1,000-millisecond noise burst, the question arose as to whether this difference in detectability might account for the effect of duration on localizability of the two stimuli. To address this possibility, sound-localization ability at 180° separation was retested with the intensity of the 100-millisecond noise burst increased to the same hearing level (HL, i.e., intensity above threshold) as the original 1,000-millisecond noise burst, and the intensity of the 1,000-millisecond noise decreased to the same HL as

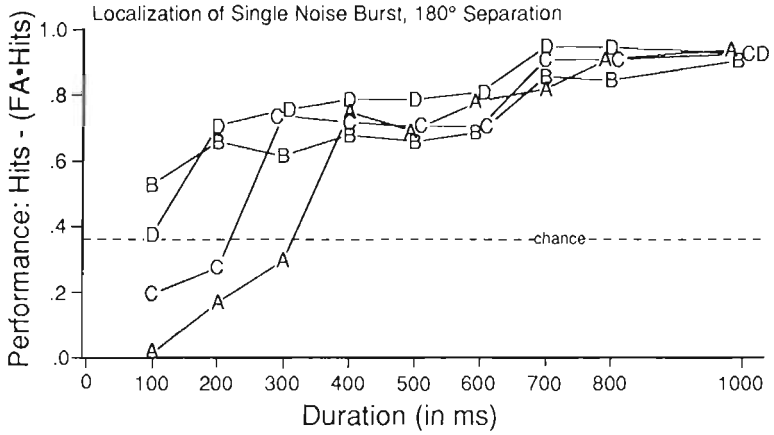


Fig. 4. Sound-localization performance at a fixed angle of 180° separation for four naked mole rats as a function of the duration of a single noise burst. Although very long durations were easily localized, only animals B and D could localize the 100-millisecond burst above chance. Dashed line indicates the .01 level of chance.

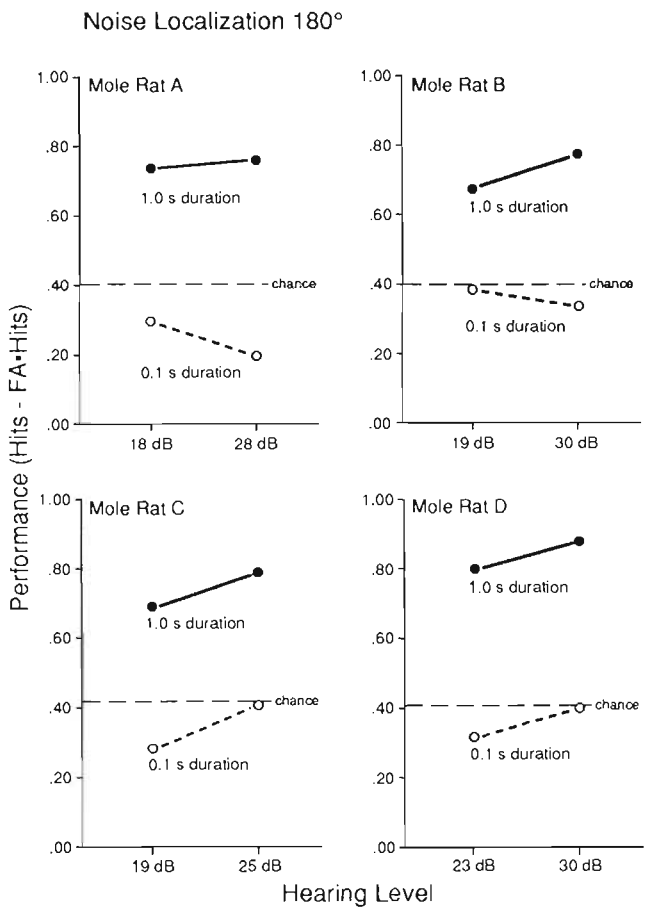


Fig. 5. Sound-localization performance for four mole rats at a fixed angle of 180° separation as a function of the intensity of the noise burst above threshold. Intensity above threshold (i.e., hearing level) varies because of individual differences in sensitivity to the short and long signals. Note that the animals could not localize the 0.1-second noise burst above chance regardless of intensity, whereas performance for the longer 1.0-second noise burst is well above chance for both intensities. Thus, the inability to localize brief noise bursts cannot easily be attributed to reduced sensitivity to brief signals. Dashed line indicates the .01 level of chance, which varies between individuals owing to differences in false alarm rates.

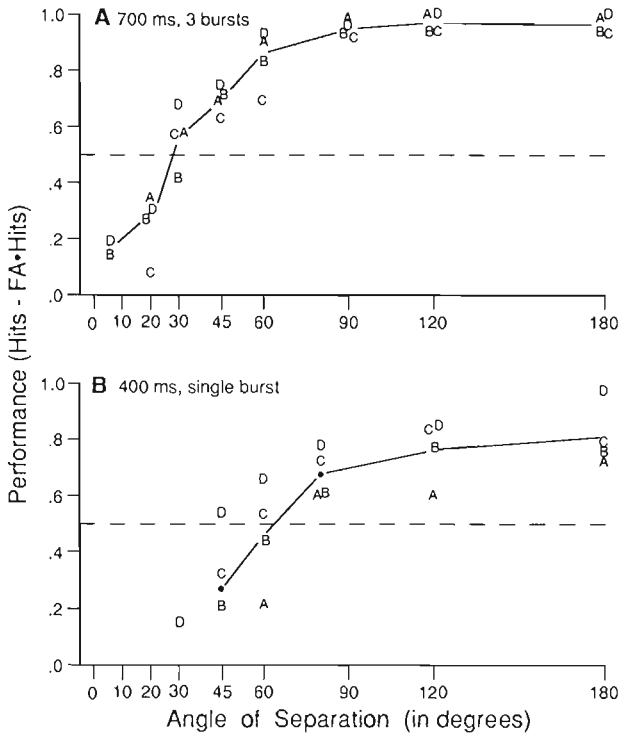


Fig. 6. Sound-localization thresholds for four naked mole rats. Note the difference in thresholds for the long-duration signal in **A** (three bursts of 700 milliseconds each) as opposed to the shorter-duration signal in **B** (a single 400-millisecond burst). Dashed lines indicate threshold level.

the original 100-millisecond noise burst. For example, for mole rat A, the original 1,000-millisecond stimulus was 28 dB HL, whereas the 100-millisecond stimulus was 18 dB HL. Therefore testing was repeated with the 1,000-millisecond stimulus attenuated to 18 dB HL and the 100-millisecond stimulus amplified to 28 dB HL. Testing with the two durations at the two intensities was interspersed throughout each session in different orders each day and continued until six blocks of trials had accumulated for each signal configuration.

As shown in Figure 5, the 1,000-millisecond noise burst was easily localized, even at the lower intensity. On the other hand, the 100-millisecond noise burst was not localizable even when the intensity was increased. Thus, the inability of the mole rats to localize brief sounds cannot be simply attributed to a reduced ability to detect them. The fact that animals B and D were unable to localize the 100-millisecond noise burst above chance when they had previously done so (at least occasionally) illustrates that at best their ability to perform this task was marginal and could not be sustained.

Acuity. Because the mole rats were unable to localize a standard 100-millisecond noise burst consistently, sound-localization thresholds were determined for a train of three 700-millisecond noise bursts and for a single 400-millisecond burst. As shown in Figure 6, the animals showed better performance at large angles when localizing the three long noise bursts than when localizing the single shorter noise burst. Similarly, the average threshold for the train of noise bursts was 28°, whereas that for the single 400-millisecond burst was 63°. As will be seen, these thresholds are similar to those for other subterranean rodents, but much poorer than those for surface-dwelling mammals. Indeed, even the 63° threshold of the mole rats is an overestimate of their ability compared to other mammals, since surface-dwelling mammals are routinely tested with single clicks or 100-millisecond noise bursts, stimuli that the subterranean mammals cannot reliably localize even at 180° separation.

Auditory brainstem

Although a detailed anatomical analysis is beyond the scope of this paper, the fact that the hearing abilities of naked mole rats have degenerated relative to surface-dwelling rodents raises the question of whether their auditory nuclei are correspondingly abnormal. Thus, an overview of the major auditory nuclei may serve as a basis for future studies aimed at understanding the morphological and connectional changes that accompany evolutionary degeneration in auditory capacities.

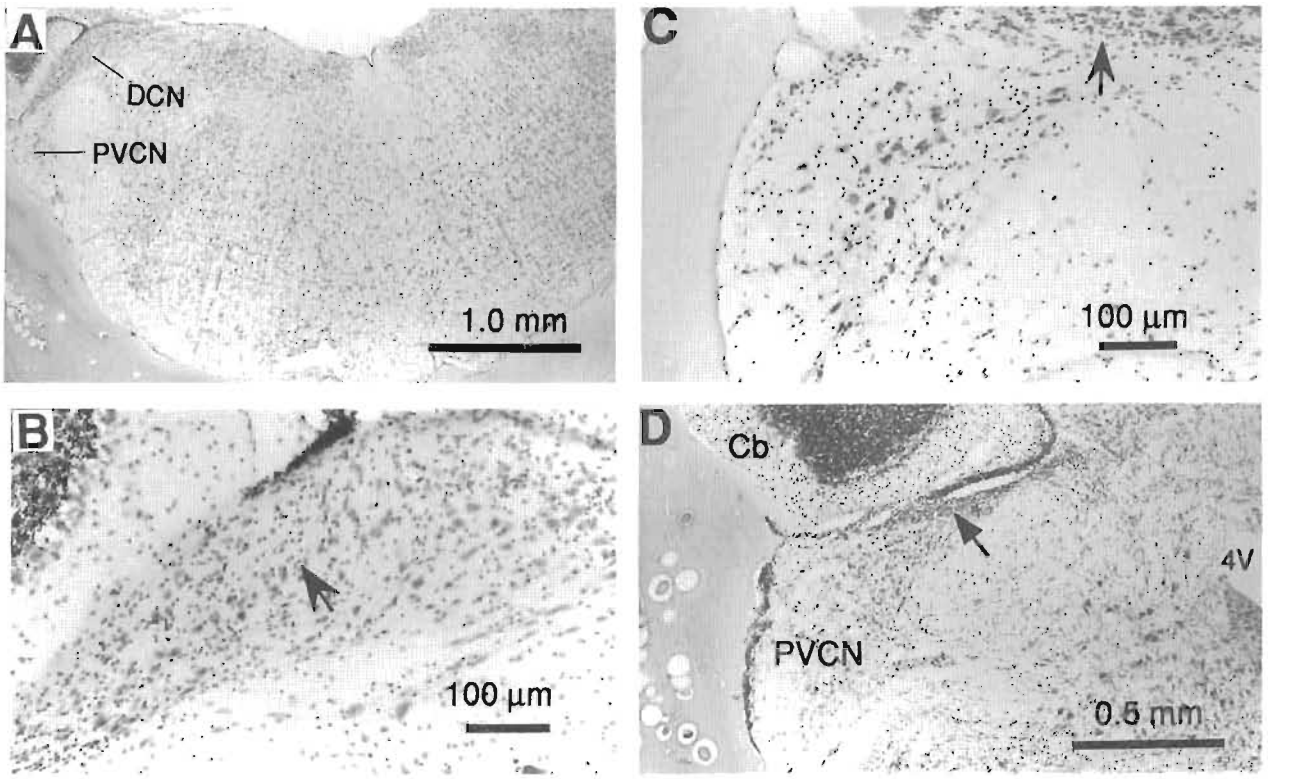


Fig. 7. **A**: Photomicrograph of a transverse section through the brain of a naked mole rat at the level of the PVCN and DCN. **B**: Higher magnification view of DCN showing the fusiform cell layer (arrow). **C**: PVCN showing unclassified large cells and dorsal granule cell cap (arrow). **D**: PVCN 0.5 mm rostral to C and anterior to the DCN, showing an increased cell density and the continuation of the granule cell layer (arrow). A–D thionine stain.

Briefly, all the major auditory nuclei appear to be present and in their normal configuration; none are hypertrophied and none are absent. Yet, as illustrated in the following figures, the nuclei are all relatively small and the structures normally involved in binaural processing for sound localization are exceedingly so.

The brainstem of a mole rat is illustrated at the level of the cochlear nucleus in Figure 7. Figure 7A is a low-magnification view of the brainstem through the posterior portion of the posterior ventral cochlear nucleus (PVCN) at the level of the greatest extent of the dorsal cochlear nucleus (DCN). At higher magnification a distinct fusiform cell layer can be seen in the DCN, but the granule cells, one of the more variable features of cochlear nuclei in different species (e.g., Merzenich et al., '73; Moore, '80), are scattered throughout the DCN. Large multipolar cells are concentrated dorsomedially in the DCN (Fig. 7B). The PVCN contains scattered, primarily large, cells (Fig. 7C) that cannot unequivocally be assigned to specific cell types in the absence of Golgi material. There is a concentration of granule cells in a thin band between the DCN and PVCN that continues anteriorly as a granule cell cap over the ventral cochlear nucleus. Rostrally (0.5 mm) the PVCN contains a greater concentration of cells and its granule cell cap continues anterior to the DCN (Fig. 7D).

Figure 8A illustrates the auditory brainstem of the naked mole rat at the level of the anterior ventral cochlear nucleus (AVCN) and the posterior portion of the superior olivary complex (SOC) (0.9 mm rostral to Fig. 7A). At this low magnification, the continuation of the granule cell cap on the ventral cochlear nucleus with the granule cell layer of the cerebellum is evident. The AVCN (shown at higher magnification in Fig. 8B) typically contains more densely packed cells than the PVCN and a few cells in the medial region appear to be spherical cells, but in no section are large or small spherical cells, which normally provide the major input to the medial superior olive (MSO) and the lateral superior olive (LSO), prominent.

Also visible in Figure 8A are the MSO and medial nucleus of the trapezoid body (MTB); however, the LSO is indistinct, and a band of trapezoid body fibers at the ventral border of the brainstem is not discernible. At this level the SOC, shown at higher magnification in Figure 8C, has achieved its largest size; the MSO, MTB, and ventral nucleus of the trapezoid body (VTB) have a small but ordinary configuration. The MSO consists of a cluster of fusiform cells with their dendrites oriented in a typical medio-lateral direction, and the MTB, although not large, contains relatively large, densely staining cells. At higher magnification the protargol stain (Fig. 8D) reveals that the neurons in the MTB are contacted by numerous punctate endings. These terminals have the appearance of the inhibitory GABAergic terminals illustrated in cats (Adams and Mugnaini, '90), although a histochemical analysis is not available. Calyces, which provide the excitatory input to the MTB that is essential for binaural processing in the LSO (Glendenning et al., '91), were not observed in the MTB of either of the brains we examined. The LSO, as seen at higher power in Figure 8E of a protargol-stained section, is recognizable by its neuropil and by its location medial to the

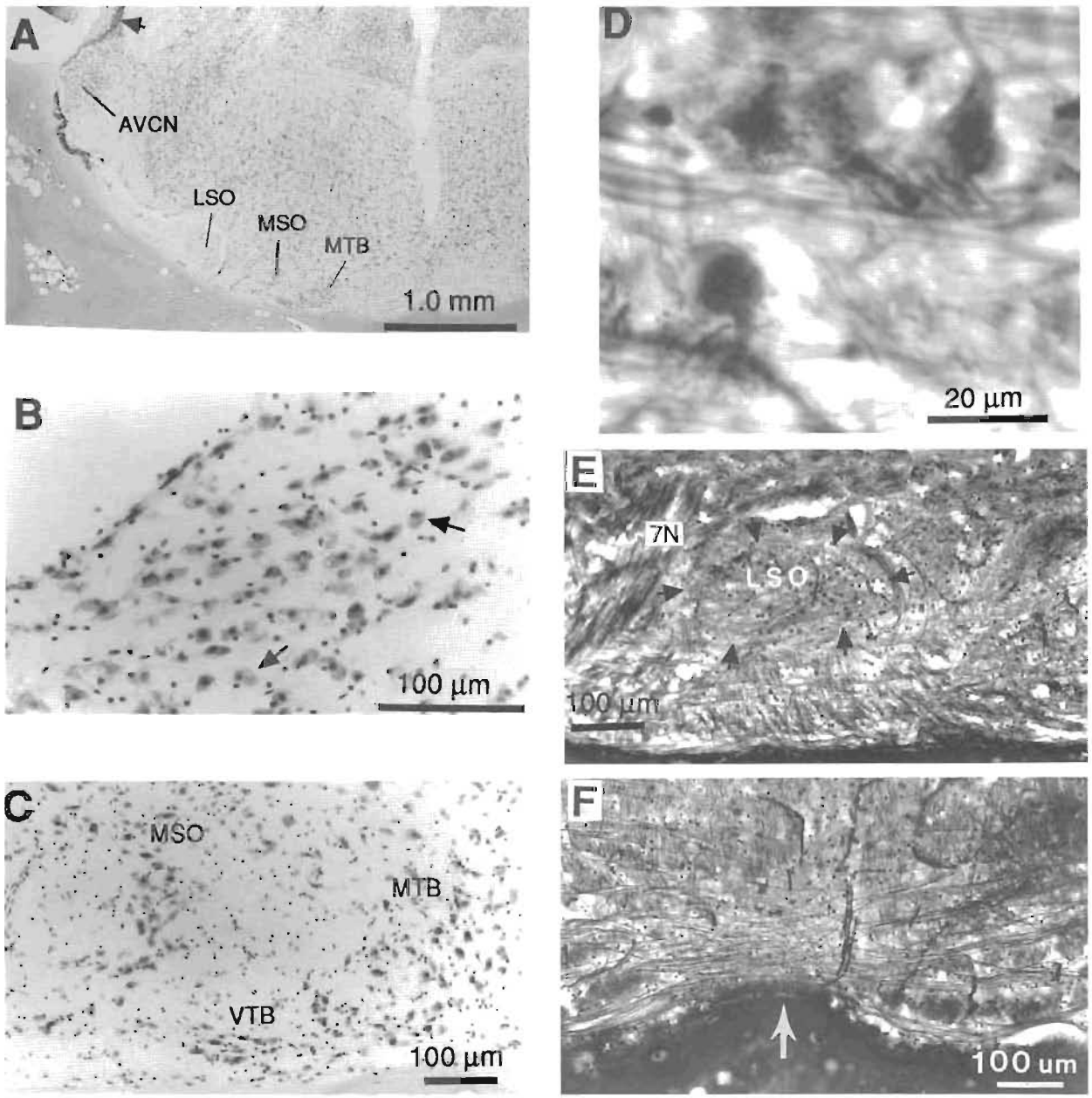


Fig. 8. **A**: Photomicrograph of a transverse section through the left brainstem of a naked mole rat 0.9 mm rostral to Figure 7A, showing the AVCN with the granule cell layer (arrowhead) continuous with the cerebellar granule cell layer, the LSO, MSO, and MTB. **B**: Higher magnification view of the AVCN, revealing only a few spherical cells, two of which are indicated by arrows. **C**: Higher magnification view of the MSO, MTB, and VTB. **D**: Four neurons in the MTB contacted by punctate endings, which appear as small dots seen in sharpest focus over the middle cell in the upper row. **E**: LSO (surrounded by arrows) illustrating its distinctive neuropil and characteristic location medial to the seventh nerve (7N). **F**: Trapezoid body at the base of the brainstem illustrating the sparseness of the decussating auditory fibers; arrow indicates midline. A–C, thionine stain; D-F adjacent section stained with protargol.

exit of the seventh nerve; however, it contains few neurons. Finally, the sparseness of fibers in the trapezoid body (Fig. 8F) suggests that binaural interactions may be minimal in this species compared with most mammals.

Further rostrally in the auditory system, the lateral lemniscus with its embedded nuclei are illustrated in Figure 9A. Figure 9B illustrates the configuration of the posterior inferior colliculus (IC) in an adjacent protargol-stained section, revealing both the central nucleus (CIC) and a prominent dorsal cortex (DC). The caudal thalamus, containing a small but distinct medial geniculate, is illustrated in Figure 9C.

Retinal analysis

The behavioral coordination of the senses and the neural mechanisms of that coordination have long been of interest. Thus the recent indication that, in mammals, sound-localization acuity is related to the width of the best field of vision (Heffner and Heffner, '92c) warrants further scrutiny, particularly in species with unusual auditory or visual

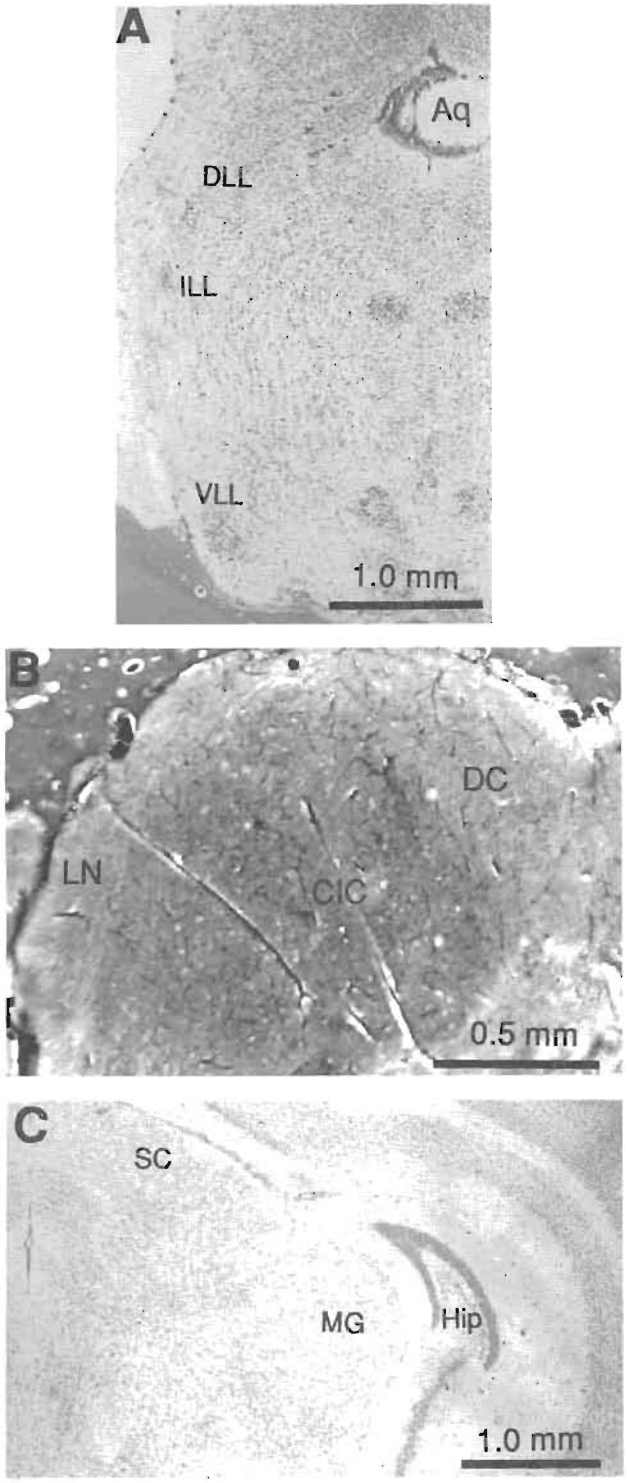


Fig. 9. **A**: Photomicrograph of a transverse thionine-stained section through the left lateral lemniscus 0.8 mm anterior to Figure 8A. There are three groups of cells within the lateral lemniscus that may correspond to the dorsal (DLL), intermediate (ILL), and ventral (VLL) nuclei of the lateral lemniscus (although the latter may instead be a rostral periolivary nucleus). **B**: Adjacent protargol-stained section through the posterior IC illustrating its three major regions as described by Helfert et al. ('91), the central nucleus (CIC), dorsal cortex (DC), and lateral nucleus (LN). **C**: Transverse thionine-stained section through the right caudal thalamus, 1.9 mm anterior to A, illustrating the configuration of the medial geniculate body (MG). Note that cells fill the nucleus all the way to its lateral edge.

adaptations. In order to determine just how the naked mole rat fits this relationship, the density contours of its retinal ganglion cells were determined and estimates made of the width of its field of best vision.

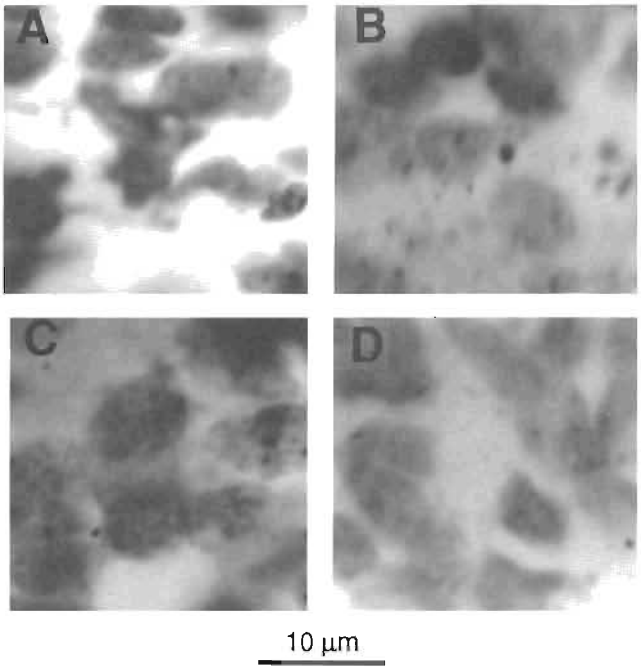
The eye of the naked mole rat is approximately 1.6 mm in outer diameter and contains a retina encompassing approximately 180° and a round lens 0.85–0.9 mm in diameter that nearly fills the remaining space in the eye. The retina of a naked mole rat is a typical avascular retina, possessing a receptor layer, inner nuclear layer, and clearly separated ganglion cell layer. The most unusual aspect of the retina of the naked mole rat is its very small size, which makes it exceedingly difficult to remove from the sclera, flatten, and clean. The small size also imposes greater than usual reservations concerning shrinkage distortion, which occurs at the edges of the retina and along the cuts that are necessary to permit flattening. Normally, density sampling within 0.5 mm of cuts and edges is avoided, but in the case of the naked mole rat, the entire retina lies within 0.5 mm of an edge, precluding this conservative practice. Nevertheless, regions of obvious shrinkage were not sampled, neither were regions obscured by vitreous debris. Despite these limitations, some information concerning the visual capacity of this species and the variation in spatial resolution across the retina can be obtained from this material.

Despite the thickness of the tissue and the shallow depth of field, the ganglion cells illustrated in Figure 10A–D can be seen to be relatively small, approximately 3–8 μm in diameter, and to lack prominent nuclei and nucleoli; there were no large ganglion cells having the appearance of alpha ganglion cells (Peichl, '91). The ganglion cells are densely packed throughout the retina, with a peak density of 21,052 cells/mm^2 (Fig. 10E). The peak density of the ganglion cells in the naked mole rat retina is approximately three times that for the wild Norway rat and even greater than the 15,300 cells/mm^2 in the diurnal gerbil (Heffner and Heffner, '92c). Nevertheless, even this high packing density cannot overcome the disadvantage of the small size of the retina, with the result that the theoretical maximum visual acuity of naked mole rats is only 0.44 cycles per degree.

The density of the ganglion cells falls toward the periphery to approximately half the maximum density. Figure 11 illustrates the isodensity contours of the retinal ganglion cells in the right retina of a naked mole rat. A notable feature is that density does not vary as much as in surface-dwelling mammals. For example, in rats, ganglion cell density declines to approximately 25% of maximum, whereas in cats it declines to 3% of maximum (see Hughes, '77, for these and other examples). Nevertheless, the isodensity contour, encompassing densities at least 75% of maximum, reveals a visual streak dorsal to the optic disk much like that found in other species. This visual streak encompasses approximately 126° of the horizon.

There are two unusual aspects of the visual streak: First, it appears to be broken by a small central region of lower density. Although this may be a true discontinuity, it could easily have resulted from uneven flattening of the retina, imposing artifactual variation in ganglion cell density due to stretching and compression. It could also have resulted from sampling variation imposed by the small area in each sample necessitated by the very small size of the retina itself. For the present analysis, we have treated the visual streak as a single streak in calculating the width of the field of best vision.

The second unusual feature is the small region of high density in the ventral retina; such an additional region of



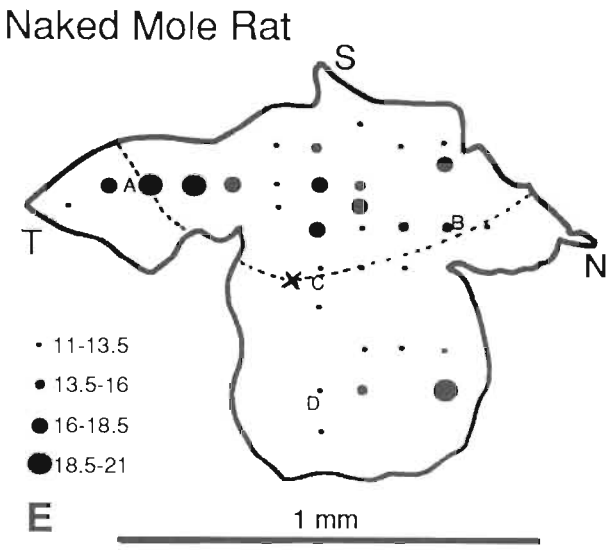


Fig. 10. **A–D**: Photomicrographs of thionine-stained ganglion cells at the locations marked by corresponding letters in E. N, nasal; S, superior; T, temporal; scale bar for A–D = 10 μm. **E**: Ganglion cell density distribution in the retina of a naked mole rat. The filled circles of different sizes indicate the density of ganglion cells at 100-μm intervals in thousands of ganglion cells per mm^2 (gaps in the 100-μm grid are areas where cells could not be counted because of shrinkage or vitreal debris). The × indicates the location of the very small optic disk, and the dashed line indicates the approximate horizon of the retina.

dense ganglion cells is not unprecedented, as it has been reported for wood rats (Heffner and Heffner, '92c) and elephants (Stone and Halasz, '89). In summary, the retina of the naked mole rat resembles that of the pocket gopher, another subterranean species, with respect to the overall configuration of isodensity contours, limited variation in density across the retina, and its relatively poor acuity (Heffner and Heffner, '92c).

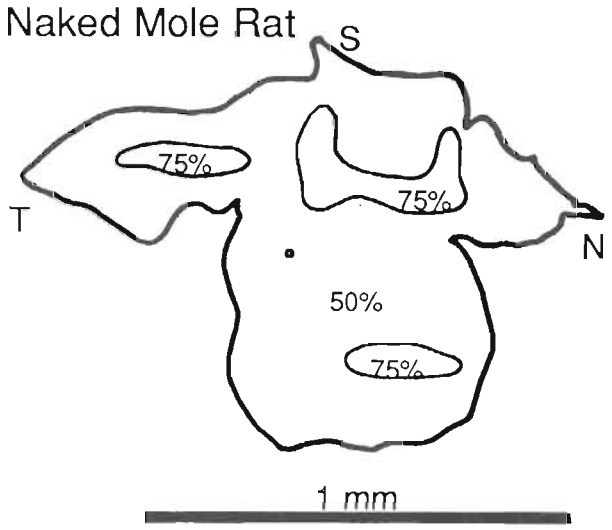


Fig. 11. Retinal ganglion cell isodensity contours in a naked mole rat. Note that density does not fall below 50% of peak density at any location. The horizontal width of the region encompassing ganglion cell densities at least 75% of maximum is 126°. The dot indicates the location of the optic disk. N, S, T, as in Figure 10.

DISCUSSION

The present results reveal several notable features of the hearing abilities of naked mole rats. First, with regard to absolute sensitivity, mole rats are relatively insensitive, require a sound to be present for an unusually long time before reaching maximal sensitivity, and have poor high-frequency hearing. Second, their ability to localize sound is poor in that they lack good acuity and are unable to localize brief sounds. The following discussion examines the abilities of naked mole rats in relation to those of other mammals. Included is an analysis of those aspects of their hearing that are consistent with the common mammalian plan, those aspects that appear degenerate, how their sound-localization abilities are related to their vision, and how their hearing abilities may be reflected in the morphology of their central auditory system.

Absolute sensitivity

Audiogram. The audiogram of the naked mole rats is shown in Figure 12, along with those of other rodents chosen for comparison to illustrate specific aspects of hearing in mole rats. First, the audiograms of the other two species of subterranean rodents for which behavioral audiograms are available, blind mole rats and pocket gophers, are presented to illustrate how the audiograms of naked mole rats compare with those of other subterranean rodents (Heffner and Heffner, '90b, '92b). Second, the range of the audiograms of seven rodents that possess good low-frequency hearing (shaded area in Fig. 12) and the audiogram of a typical rodent with good high-frequency hearing (Norway rat; Kelly and Masterton, '77; Heffner, unpublished) are presented to illustrate how the subterranean rodents compare with surface-dwelling rodents.

Two noteworthy features of the hearing of naked mole rats are their poor sensitivity and restricted high-frequency hearing. As illustrated in Figure 12, naked mole rats are much less sensitive in the middle range of their audiogram than are surface-dwelling rodents. Similarly, naked mole

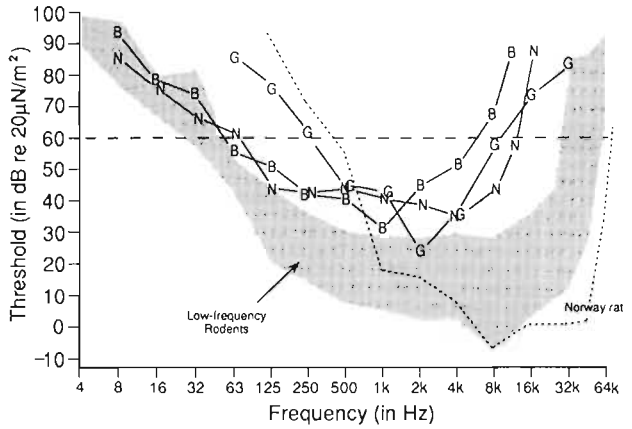


Fig. 12. Audiograms for three subterranean rodents compared to the audiograms for the domestic Norway rat (dotted line, Kelly and Masterton, '77; R. Heffner, unpublished) and seven rodents that hear frequencies below 100 Hz (shaded area): black-tailed prairie dog (*Cynomys ludovicianus*), chinchilla (*Chinchilla laniger*), eastern chipmunk (*Tamias striatus*), gerbil (*Meriones unguiculatus*), groundhog (*Marmota monax*), guinea pig (*Cavia porcellus*), and kangaroo rat (*Dipodomys merriami*) (Heffner and Heffner, '92b). Although all three subterranean species are more sensitive to low frequencies than is the Norway rat, they are less sensitive than many of the low-frequency rodents. B, blind mole rat (*Spalax ehrenbergi*); G, pocket gopher (*Geomys bursarius*); N, naked mole rat (*Heterocephalus glaber*).

rats lack good high-frequency hearing; their high-frequency sensitivity is surpassed even by low-frequency rodents that, as a group, do not hear as high as other rodents such as Norway rats. These two features, poor overall sensitivity and the inability to hear well above 10 kHz, however, appear to be common in subterranean rodents, as indicated by the fact that the audiograms of the subterranean rodents resemble each other more closely than they resemble those of surface-dwelling rodents (Fig. 12). Further, electrophysiological evidence suggests that the hearing of other subterranean rodents may be similarly restricted (Müller and Burda, '89).

The fact that the subterranean rodents studied so far all have poor sensitivity and poor high-frequency hearing is interesting in light of the fact that they are not closely related. Indeed, the three species belong to three different families: Bathyergidae (naked mole rats), Muridae (blind mole rats), and Geomyidae (pocket gophers). Thus their degenerate hearing is not a trait inherited from a common ancestor, but constitutes an example of convergent evolution comparable to the reduction in vision also found in subterranean species.

Turning to their low-frequency sensitivity, the fact that low frequencies propagate in burrows better than do high frequencies (Heth et al., '86) has led to the expectation that subterranean mammals might have evolved exceptional low-frequency hearing. However, although the audiogram of naked mole rats extends well into the low frequencies, these animals are not unusually sensitive. In spite of the fact that they are capable of detecting airborne sounds as low as 8 Hz, their sensitivity to low frequencies is equaled or exceeded by that of seven surface-dwelling rodents—i.e., half of all the rodents that have been tested (Heffner and Heffner, '92b). Thus, it is not possible to argue that subterranean rodents are uniquely specialized for the reception of low-frequency airborne sound, or that their reduced high-frequency hearing was an essential sacrifice to permit exceptional sensitivity to low frequencies. On the other hand, the possibility exists that some subterranean species have extended their low-frequency sensitivity to include substrate-borne vibrations transmitted via bone conduction (cf. Heth et al., '87; Narins et al., '92; Rado et al., '89, '91). However, this possibility has not yet been demonstrated in naked mole rats despite numerous field and laboratory studies of their behavior (cf. Narins et al., '92; Sherman et al., '91).

Temporal integration. Temporal integration, also known as temporal summation, refers to the fact that increasing the duration of a brief sound results in a lower threshold or, in the case of suprathreshold sounds, an increase in perceived loudness. Once a certain duration has been reached, however, further increases in duration have little effect. This duration is called the critical duration and, in humans, is approximately 250 milliseconds (e.g., Algom and Babkoff, '84).

The slope of the relationship between duration and threshold is such that a 10-fold change in duration (e.g., 10–100 milliseconds) generally results in a 10-dB change in threshold. However, the slope can vary with the frequency and complexity of the stimulus, and broadband noise produces a shallower slope (e.g., 7-dB change in threshold per 10-fold change in duration) (Algom and Babkoff, '84; Gerken et al., '90).

Although it was not our original intention to investigate temporal integration in the mole rats, the thresholds obtained to insure that the animals could easily hear the localization stimuli are relevant to this issue. In order to interpret these results, however, it was necessary to obtain similar thresholds in a comparison species. This was necessary not only because temporal integration functions can vary with the stimulus, but also to insure that there was nothing unusual about the test procedure. Because chinchillas are commonly used in auditory experiments and their temporal integration functions for tones have been determined, they were chosen for comparison with the naked mole rats.

As shown in Figure 3, the chinchillas demonstrated little temporal integration between 100 and 1,000 milliseconds, with their average thresholds improving by 2 dB. This result is consistent with that of Wall et al. ('81), which showed that the critical duration for chinchillas for tones is between 100 and 200 milliseconds and that the average change in threshold between 100 and 1,000 milliseconds is about 2 dB. In contrast, the mole rats showed an average improvement of more than 8 dB as duration increased from 100 to 1,000 milliseconds. This difference suggests that in addition to their poor sensitivity and lack of high-frequency hearing, the naked mole rat and, perhaps, other subterranean rodents may differ from other mammals in terms of their temporal integration functions.

In comparing these results, it can be seen that the mole rats were also 35–40 dB less sensitive than the chinchillas. Whether this insensitivity may be related to the fact that the mole rats show greater improvement with duration remains to be determined. However, it has been established that a peripheral hearing loss of cochlear origin results in less improvement in sensitivity as duration increases (e.g., Gerken et al., '90)—the opposite of the effect seen here—which suggests that the mole rats' lack of sensitivity is of central rather than peripheral origin. Indeed, because temporal integration is considered to take place in the

central nervous system (e.g., Gerken et al., '90), these results suggest that there may also be differences in the physiological response properties of the central auditory systems of mole rats and chinchillas.

Auditory sensitivity and vocal communication. Unlike the other subterranean species whose hearing is known, naked mole rats are social and have a large repertoire of vocalizations. Most of the vocalizations emitted by naked mole rats are tonal, consisting of a narrow band of frequency-modulated sound within the range of 1–9 kHz (Pepper et al., '91). The remaining calls consist of broader bands of noise that include transients or harmonics as high as 40 kHz (Pepper et al., '91). Nevertheless, the main energy in the vocalizations of naked mole rats is within their middle and upper hearing range.

The fact that some of the energy in mole rat vocalizations extends beyond their hearing range is a result of the production of harmonics. Indeed, vocalizations often contain abrupt onsets and offsets, generating h igh frequencies that are "nonfunctional" in the sense that the animals do not use them to identify the sounds and that, in fact, may be beyond their hearing range. Examples of such vocalizations are bird calls that extend beyond 10 kHz (Konishi, '69) and rodent vocalizations that extend beyond 100 kHz (Sales and Pye, '74). However, in spite of their large vocal repertoire, frequent vocalizations, and the high-frequency content of some of their vocalizations, naked mole rats are relatively insensitive to sound and are unable to hear high frequencies. Indeed, their hearing ability closely resembles that of solitary subterranean mammals. Thus it appears that the use of a strong vocal communication system has not exerted sufficient selective pressure to sustain high-frequency hearing or auditory sensitivity in naked mole rats.

Sound localization

Sound-localization acuity is typically measured using a brief broadband stimulus, such as a single click or 100-millisecond noise burst (e.g., Heffner and Heffner, '92a). Because such sounds contain both low and high frequencies, they can be localized using either of the binaural cues: the difference in the time of arrival of a sound at the two ears, and the difference in the frequency–intensity spectrum of a sound at the two ears. In addition, animals with external ears have pinna cues available that arise from variation in the high-frequency portion of the spectrum of a sound reaching the eardrum due to the directionality of the pinnae. However, the brevity of the sound prevents an animal from localizing it either by scanning with its head and pinnae or by tracking it.

Naked mole rats, however, are unable to localize reliably sounds as brief as 100 milliseconds and, as can be seen in Figure 4, require a sound to be present for at least 700 milliseconds before reaching asymptotic performance. In this respect they are similar to the pocket gopher and blind mole rat, both of which are unable to localize a 100-millisecond noise burst (Heffner and Heffner, '90b, '92b). Indeed, of these three subterranean animals, the naked mole rat appears to have the best localization ability: Both the pocket gopher and the blind mole rat require durations in excess of 1 second before reaching asymptotic performance, and their thresholds for long-duration sounds are 180°—much poorer than the 63° threshold for naked mole rats.

In contrast to subterranean species, surface-dwelling mammals do not appear to have difficulty localizing brief sounds (Heffner and Heffner, '92a). As a result, most localization tests performed with these species have used only short-duration sounds and it is not generally known whether thresholds might improve if a longer duration were used. However, tests of the ability of domestic cats to perform a left–right locus discrimination found that thresholds improved from 7.2° for a 10-millisecond noise burst to 6° for a sound that remained on until the animals responded (typical length 0.5 seconds) (Heffner and Heffner, '88). Thus, the limited information available suggests that increasing the duration of a sound does not have a large effect on the ability of surface-dwelling mammals to localize sound—at least in a left–right locus discrimination.

The extremely limited ability of subterranean mammals to localize sound gives rise to the possibility that they may lack the ability to use some of the major sound-localization cues. Along this line, the fact that they have virtually no external ear indicates that they probably do not have "pinna" cues available to them beyond the directionality provided by the auditory canal. Further, the observation that they can only localize sounds of relatively long duration gives rise to the possibility that they may not have the ability to use binaural locus cues, but instead rely primarily on scanning movements to localize sound. Although requiring the animals to eat from a food spout greatly restricted their ability to scan the sound field, the animals may have made minor head movements that enabled them to make left–right judgments concerning the approximate location of long-duration sounds. Thus, the possibility exists that the poor localization ability of subterranean rodents is due to the loss of the ability to use binaural locus cues and that their residual ability to localize sounds of relatively long duration is a result of scanning.

Before accepting this conclusion, however, it should be noted that the naked mole rats had difficulty not only in localizing brief sounds but also in detecting them. Although the difficulty in localizing brief sounds could not be attributed to reduced detectability (cf. Fig. 5), the possibility remains that their auditory systems simply have difficulty processing brief sounds. Thus, without further evidence we cannot rule out the possibility that these subterranean animals can perform a binaural analysis on long- but not short-duration sounds.

Sound localization and high-frequency hearing. There is reason to believe that the joint occurrence of an insensitivity to high frequencies and an inability to localize brief sounds is not coincidental. More than 20 years ago it was proposed that mammals evolved the ability to hear above 10 kHz for the purpose of localizing sound (Masterton et al., '69). Specifically, the high-frequency hearing ability of mammals allows most of them to use pinna cues as well as binaural spectral-difference cues to localize sound (for a review, see Heffner and Heffner, '92a). Just how high an animal has to hear in order to make use of these cues depends on the size of its head and pinnae. That is, because the sound-shadowing properties of the head and pinnae depend on their size relative to the wavelength of the sound, small animals need to hear higher frequencies than large animals in order to make use of these cues. Thus, there exists a strong correlation between head size (as defined by interaural distance) and high-frequency hearing, such that small mammals hear higher frequencies than large mammals.

The subterranean mammals, however, constitute an exception to this relationship (for a detailed discussion, see

Heffner and Heffner, '92a). That is, neither the pocket gopher, blind mole rat, nor naked mole rat hear as high as predicted on the basis of their interaural distances. On the other hand, none of these animals can localize brief sounds. Indeed, the fact that animals that lose the ability to localize sound also lose the ability to hear high frequencies supports the contention that high-frequency hearing evolved in mammals primarily to serve sound localization. Thus, without the selective pressure to localize sound, even a social animal such as the naked mole rat that uses vocalizations for intraspecific communication loses the ability to hear high frequencies.

Sound localization and vision. The inability of naked mole rats to localize brief sounds provides support for the recently observed relation between sound-localization acuity and vision (Heffner and Heffner, '92c). It has been suggested that a major factor influencing the variation in sound-localization acuity among mammals is its utility for directing the field of best vision to a sound source for further scrutiny. Thus, species with a narrow field of best vision such as man require very accurate directional information from their auditory system in order to direct their fovea toward a sound source. On the other hand, species with broad fields of best vision can accurately orient visually to a sound source based on only an approximate indication of locus from the auditory system. Naked mole rats have very shallow density gradients in their retinae, similar to the shallow gradients of pocket gophers (Heffner and Heffner, '92c), giving them a relatively broad field of best vision even without a well-defined visual streak. This broad field of best vision encompasses approximately 126° and is associated with very poor sound-localizing acuity.

The relation between width of the field of best vision and sound-localization acuity among mammals is illustrated in Figure 13. This correlation, based on data for 14 species, is high and reliable ($r = .873$, $P < .001$). The species with the narrowest fields of best vision have the best sound-localization acuity, presumably to enable them to direct their narrow visual fields to a sound source. Those with broad fields of best vision have much larger thresholds (i.e., lower sound-localization acuity).

However, Figure 13 suggests that there may be a "ceiling effect" evident among the subterranean species for which both vision and audition are degenerate. Indeed, as plotted, the sound-localization acuity of both underground species (indicated by asterisks) is overestimated and they are more deviant than they appear because their thresholds are based on long-duration sounds, whereas all of the other mammalian thresholds are based on brief sounds, which are not localizable by the pocket gopher and naked mole rat. The result may be that the relation between the two sensory modalities that seems to be strong among species living on the surface ($r = .934$) may be less relevant to subterranean species for whom both hearing and vision are degenerate. That is, living underground in the dark, they have no opportunity to use their ears to guide their eyes and no selective advantage in retaining the ability to do so.

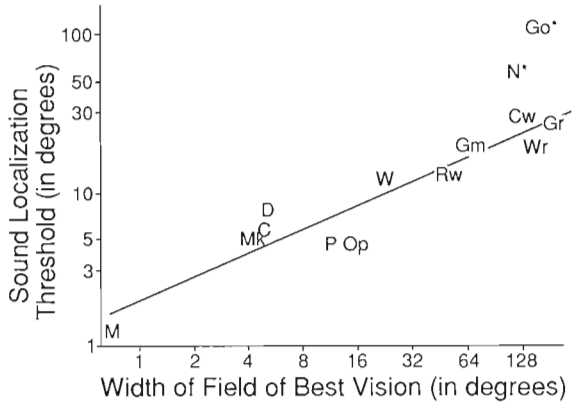


Fig. 13. Relationship between width of the field of best vision (i.e., ganglion cell densities at least 75% of maximum density) and sound-localization threshold for 14 species of mammals. Species with a narrow field of best vision have much better sound-localization acuity than species with broad fields of best vision. With the exception of the pocket gopher and naked mole rat (*), all localization thresholds were obtained using a brief 100-millisecond noise burst or single click. C, cat; Cw, cow; D, dog; Gm, grasshopper mouse; Go*, pocket gopher; Gr, gerbil; M, man; Mk, macaque; N*, naked mole rat; Op, Virginia opossum; P, pig; Rw, wild Norway rat; W, least weasel; Wr, wood rat (Heffner and Heffner, '92c).

Auditory brainstem

The marked reduction of auditory sensitivity and sound-localization ability do not appear to be accompanied by loss of any of the major central auditory structures in naked mole rats. Similarly, blind mole rats and pocket gophers have also retained the major auditory nuclei despite their degenerate hearing (Bronchti et al., '89; Heffner and Heffner, '90b). Thus it seems that auditory functions may be more plastic in their response to changes in habitat than are auditory structures, or, alternatively, that some of the structures in the auditory system have functions in addition to those commonly ascribed to them.

Nevertheless, structures known to process primarily high frequencies or binaural interactions, such as the MSO, LSO, MTB, and trapezoid body (for a recent review, see Helfert et al., '91), are small relative to the width of the brainstem, compared to other species of rodents (Heffner, unpublished observations). This relative smallness is in keeping with the extremely limited overall sensitivity and poor sound localization of naked mole rats and is similar to that reported for other subterranean species, including blind mole rats (Bronchti et al., '89), pocket gophers (Heffner and Heffner, '90b), Japanese moles (Kudo et al., '90), and European moles (Aitkin et al., '82). However, as noted by Kudo et al. ('90), the MSO, a low-frequency nucleus, is well developed in the subterranean species when compared to species that have poor low-frequency hearing, such as mice and rats, and hedgehogs (which have no MSO). Relative to the MSO of rodents such as guinea pigs and kangaroo rats, which do hear low frequencies, the MSO of subterranean species is small (cf. Harrison and Feldman, '70; Schofield and Cant, '91; Webster et al., '68). The continuing presence of structures traditionally considered to be primarily involved in sound localization in species whose sound localization is marginal, if not actually lost, suggests that these structures may also be involved in other functions.

In conclusion, naked mole rats show three degenerate features of their auditory sensitivity that have so far been shared by all of the other subterranean species examined: insensitivity to sounds throughout their hearing range, truncation of high-frequency hearing, and a virtual inability to localize brief sounds. The very poor sound-localization acuity and low ganglion-cell density gradients in the retina support the suggestion that sound localization evolved

to direct the eyes toward objects for further scrutiny. Without the need for sound localization to direct the eyes in the dark one-dimensional world of burrows, there seems to have been little remaining advantage to hearing high frequencies. Although the reduced auditory abilities of naked mole rats do not appear to be accompanied by an obvious loss of major auditory nuclei, the components of the auditory system seem to be reduced in size.

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