Hearing and sound localization in blind mole rats (*Spalax ehrenbergi*)

Rickye S. Heffner and Henry E. Heffner

Department of Psychology, University of Toledo, Toledo, Ohio, USA

(Received 18 March 1992; Revision received 21 May 1992; Accepted 24 May 1992)

Two blind mole rats were tested for their ability to detect and localize sound. The results indicate that blind mole rats have severely limited, and probably degenerate, auditory abilities. Although their 60-dB low-frequency hearing limit of 54 Hz is within the range for other rodents, the highest frequency they can hear at a level of 60 dB SPL is only 5.9 kHz, giving them the poorest high-frequency sensitivity yet observed in any mammal. In addition they have poor sensitivity as indicated by the fact that their lowest threshold is only 32 dB SPL (at 1 kHz). Finally, they are unable to localize brief sounds but retain a rudimentary ability to localize sounds of 0.5 s or longer. These results, combined with those of previous studies of subterranean species (i.e., blind mole rats, naked mole rats, and pocket gophers), suggest that poor auditory sensitivity, the loss of high-frequency hearing, and an inability to localize brief sounds is a degenerate state which may be characteristic of subterranean mammals. Thus it appears that an exclusive adaptation to a subterranean lifestyle (where airborne sound propagates poorly and where directional responses are limited by the tunnels) can result in vestigial auditory abilities just as the absence of light results in vestigial vision.

Evolution; Subterranean; Audiogram; Vision; Comparative; Rodent

Introduction

Among the major types of habitats available to mammals—surface, aerial, aquatic, and subterranean—exclusively subterranean habitats are of interest because the auditory environment underground differs markedly from that encountered in other environments. Airborne sound propagation is restricted in small tunnels (Heth et al., 1986) and auditory stimulation, like visual stimulation, may thus be more limited than in other habitats. In addition, the directional information from sound sources as well as the range of directional responses available to the animals is reduced to a single linear dimension such that there may be little, if any, selective advantage in an ability to determine the location of sound sources (R. Heffner and Heffner, 1990a, 1991b).

Recent research has indicated that the auditory abilities of subterranean mammals may indeed be limited. So far, three species (pocket gopher, naked mole rat, and blind mole rat) have been shown to have unusually poor high-frequency hearing with the highest frequencies audible at a level of 60 dB SPL ranging from 8.7 kHz to approximately 11 kHz (Bronchti et al., 1989; R. Heffner and Heffner, 1990a, 1991b). Further, these animals have proved to be remarkably insensitive

to sound with their lowest thresholds 20-35 dB poorer than the mammalian average (R. Heffner and Heffner, 1990b; cf. Fay, 1988). Finally, both the pocket gopher and naked mole rat have been shown to be totally unable to localize brief sounds (e.g., 100 ms noise bursts) and have poor localization acuity even when localizing long-duration sounds (R. Heffner and Heffner, 1990a, 1991b). Thus, there is good reason to believe that a subterranean habitat is associated with a dramatic reduction in hearing abilities.

In extending our studies of mammalian hearing, we have recently had the opportunity to examine the hearing of blind mole rats. These animals are of particular interest because they have vestigial eyes which are covered by skin and fur and are believed to lack pattern vision because the retinogeniculate projection degenerates during the neonatal period (Bronchti et al., 1991; Sanyal et al., 1990). As a result, they provide a test of the hypothesis that the primary purpose of the ability to localize sound is to direct the eyes to the source of the sound (R. Heffner and Heffner, 1992b). In addition, it has been proposed that blind mole rats possess exceptional low-frequency hearing (Bronchti et al., 1989) suggesting that at least one aspect of their hearing may actually have undergone significant improvement relative to other mammals. Thus, the purpose of this study was to determine both the sound localization ability of blind mole rats and to replicate their audiogram to further our understanding of the effect of a subterranean habitat on hearing.

Correspondence to: Rickye S. Heffner, Department of Psychology, University of Toledo, Toledo, OH 43606, USA.

Materials and Methods

Two blind 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 reward spout in order to receive a steady flow of pureed food. 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 signal. This procedure was then used to determine complete audiograms and sound-localization acuity for noise bursts of various durations.

Subjects

Blind mole rats (*Spalax ehrenbergi*) are medium sized rodents (130–350 g) native to the deserts of the eastern Mediterranean. Owing to their extreme specializations, their taxonomic status is controversial and they are assigned to their own family, Spalacidae (Nevo, 1979), currently considered to be a branch of the Muroidea that diverged in the Lower Miocene (Savic and Nevo, 1990). They are tooth diggers using their heads as shovels to push loose dirt; they have no external pinnae; their 1-mm diameter eyes are completely covered by fur and skin; finally, they are diurnal despite spending their entire lives underground (Bronchti et al., 1991; de Jong et al., 1990; Nevo, 1990). It seems that the atrophied eye of blind mole rats is capable of sensing photoperiod information even though it is unlikely to permit pattern vision (Bronchti et al., 1991; Sanyal, et al., 1990). Blind mole rats are asocial, making contact with other individuals only for mating (Nevo, 1961) and at least some of their communications are thought to be seismic (Heth et al., 1987; Rado, et al., 1987; Rado et al., 1991).

Two animals, one male and one female, weighing 140 g were used in this study. They were housed individually in covered glass tanks (50 cm × 26 cm × 30 cm high) containing a 22-cm length of plastic pipe (10.2 cm diameter) which served as a nest box. They had free access to dry rat chow and obtained water in the test sessions from applesauce mixed with peanut butter. In addition, their diet was supplemented with apple, carrot, potato, sweet potato, lettuce, and seeds given as needed to maintain health.

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 the chamber were covered with eggcrate 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 system.

The animals were tested in a cage 17.5 cm long × 11.5 cm wide × 13 cm high constructed of 2-mm welded wire mesh (2.54-cm mesh size). 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 below the cage so that it projected up into the cage 3 cm above the floor and 2 cm from the front of the cage. The spout was attached to a 25 cc syringe located below the cage which served as the food reservoir. A 50:1 mixture of applesauce and peanut butter was dispensed using a syringe pump similar to that described by Thompson et al., (1990). The rate of food delivery was adjusted so that the animals could obtain 10-15 cc in a 20–30 min test session. A contact circuit connected between the food spout and cage floor served to detect when an animal made contact with the spout. In addition, a constant current shock generator was connected between the spout and cage floor and a 25-watt light was mounted 0.5 m below the cage to indicate when the shock was turned on. [It is not known whether the animals actually used this signal since their vision is vestigial; although they do have the ability to detect diurnal light cycles, it is not clear whether this ability is served by non-visual photoreceptors or the retina (Pevet et al., 1984; Sanyal et al., 1990).]

Acoustic apparatus

Audiogram. Sine waves were generated by a tone generator (Krohn-Hite 2400 AM/FM Phase Lock Generator) which was calibrated daily with a frequency counter (Fluke 1900A). The electrical signal was switched on and off by an electronic switch (Coulbourn S84-04) and the intensity adjusted with an attenuator (Hewlett-Packard 350D). The signal was then band-pass filtered (Krohn-Hite 3202; 1/3 octave above and below the test frequency) to reduce any noise in the electrical signal. Finally the signal was sent via either an impedance-matching transformer or an amplifier (Crown D75) to a loudspeaker. The electrical signal going to the loudspeaker was monitored using an oscilloscope (BK 1476A) for distortion and noise. The loudspeaker was placed approximately 1 m in front of the cage (with the distance varying by as much as 0.5 m 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 the animal contacted the spout. The loudspeakers used were: a 15-in (38-cm) woofer for frequencies of 8 Hz to 4 kHz, an Infinity RS2000 6-in (15.2-cm) midrange speaker for frequencies from 125 hz to 500 Hz, a dome tweeter for frequencies of 2 kHz and 4 kHz, and a

Foster ribbon tweeter for frequencies from 4 kHz to 11.2 kHz. (The same frequency was often tested using different loudspeakers in order to check for the possibility that a threshold might be influenced by the peculiarities of a particular speaker, however no differences were found.) The tones were pulsed, 400 ms on and 100 ms off for 5 pulses, with rise decay times of 60 ms for frequencies of 125 Hz and below, 40 ms for 250 Hz, 20 ms for 500 Hz, and 10 ms for frequencies of 1 kHz and higher.

The sound pressure level was measured daily with a 1/2-in (1.27-cm) microphone (ACO Pacific 7012), preamplifier (Brüel and Kjaer 2618), microphone amplifier (Brüel and Kjaer 2608), and filter (Krohn-Hite 3202 set to pass 1 octave above and below the test frequency). The measuring system was calibrated with a pistonphone (Bruel and Kjaer 4230). Sound measurements were taken by placing the microphone in the position occupied by an animal's head and pointing it directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (within a 2-dB range) in the area occupied by the animal's head and ears while the animal contacted the spout.

Additional precautions were followed to avoid erroneously low thresholds: Low-frequency tones were examined for the presence of overtones or distortion using a spectrum analyzer (Zonic 3525). Analysis indicated that any overtones present were below threshold. The 15-in woofer used to transduce the lowest frequencies rested on 8-cm of foam as a further precaution against transmission of vibrations to the animals through the floor. Finally, the linearity of the attenuator was verified over the range of attenuation used in threshold determinations by measuring its output voltage.

Sound localization. Broadband noise with energy concentrated below 10 kHz was used in order to accommodate the signal to the hearing range of the animals. The signal was produced by a noise generator (Grason Stadler 1285) set on a 10-kHz bandwidth, filtered (Krohn-Hite 3202) to pass frequencies below 20 kHz, and led to a programmable attenuator (Coulbourn 585–08) which randomly attenuated the signal by 0–7 dB in 1-dB steps in order to reduce the possibility that the animals could distinguish between the loudspeakers on the basis of small intensity differences. The electrical signal was switched by a rise/decay gate (Coulbourn S84-04) set at 0 ms rise/decay time to provide abrupt onsets. Finally the signal was split into left and right lines, connected to two amplifiers (Coulbourn S82-24) and delivered to one of two loudspeakers, each consisting of a 3-in (7.62-cm) woofer and a piezo-electric tweeter. Because of the limitations of the small woofer, these speakers had a steep roll-off below 200 Hz (Fig. 1A).
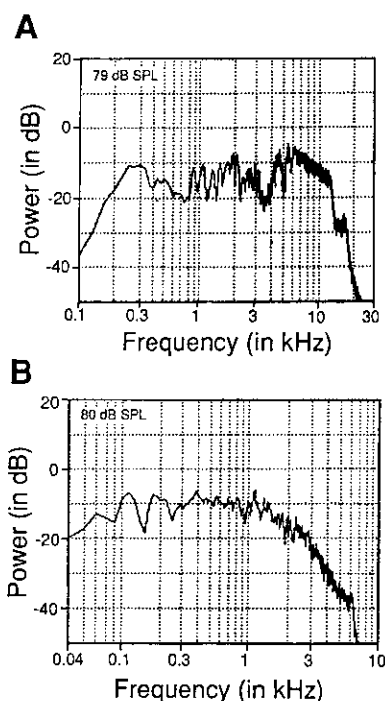

Fig. 1. Spectra of the two noise stimuli used in the sound localization tests. (A) noise used for detailed testing. (B) low-frequency noise used in additional tests. Note the different scales for frequency.

Because of the possibility that the animals might perform better with increased energy in the low-frequency range, additional tests were performed with larger (5.5-in, 14-cm) woofers (Infinity RS2000) which produced measurable energy from below 40 Hz to 6 kHz (Fig 1B).

Three pairs of speakers were centered around an animal's midline (i.e., the midsagittal plane) and suspended at ear level from a perimeter bar of 1.1 m radius. The three pairs were separated by different angles to allow rapid switching between angles within a session. Exploratory tests were also conducted with the speakers placed on the perimeter bar at various locations in front of and behind the animals. Each pair of speakers had been matched by human observers to reduce the possibility that the animal could discriminate between them on the basis of slight spectral differences; subsequent testing indicated that the animals could not distinguish between the speakers when the angle of separation was below threshold.

The intensity of the loudspeakers was equated at 79 dB SPL at the beginning of each daily test session using the sound-measuring equipment described above with the measuring filter set to pass between 63 Hz and 50 kHz. The duration of single noise bursts varied from 100 ms to 2.5 s in order to examine the effect of duration on localization performance at 180° separation. Localization thresholds were determined for three 700-ms bursts of noise separated by 100 ms as well as for single 400-ms bursts of noise.

Behavioral procedure

Audiogram. The mole rats were tested using a conditioned avoidance procedure in which a hungry animal was placed in the test cage and allowed to consume a steady stream of the apple sauce/peanut butter mixture from the food spout (approximately 0.5 cc/min). Maintaining contact with the spout served to fix the head of an animal in the sound field thus enabling the sound pressure level in the vicinity of the animal's head to be precisely specified. They were then trained to stop eating and break contact with the spout momentarily (detection response) whenever a warning signal in the form of a loud sound was presented. Breaking contact with the spout within 2.6 s enabled the animals to avoid the shock from the spout and served as an indication that they had heard the sound. The shock was adjusted for each individual to the lowest level that reliably produced an avoidance response. The mildness of the shock was attested by the fact that neither of the animals developed a fear of the spout and both returned to it without hesitation after the termination of the shock and light flash.

Test sessions were divided into 2.6-s trials, separated by 1.5-s intertrial intervals. Each trial period contained either a pulsing tone ('warning' signal) or silence ('safe' signal). A contact circuit detected whether an animal was in contact with the spout during the last 150 ms of each trial. If an animal broke contact for more than half of the response period, a detection response was recorded. This response was classified as a 'hit' if the preceding signal had been a warning signal, or as a 'false alarm' if the preceding signal had been a safe signal. Each trial had a 22% probability of containing a warning signal. Both the hit rate and false alarm rate were determined for blocks of 6–8 warning trials (which were accompanied by approximately 30 safe trials) for each stimulus condition. The hit rate was corrected for false alarm rate to produce a performance measure of corrected detection 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 (rather than the false alarm rate averaged for the session as a whole) and varies from zero (no hits) to unity (100% hit rate with no false alarms).

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 warning signal above the level expected by chance ($P < 0.01$). Once a preliminary threshold had been obtained for a frequency, final threshold determination was conducted by presenting tones varying in intensity by 5-dB increments extending from 10 dB below the estimated threshold to 10 dB above. Threshold was defined as the intensity at which a corrected detection performance of 0.50 was achieved. Thresholds for a frequency were repeated on successive days until asymptotic values were obtained. Testing was carried out at octave steps from 8 Hz to 8 kHz and at 11.2 kHz. Once testing had been completed throughout the hearing range, each frequency was retested to ensure reliability.

Sound localization. Two sound-localization tests were administered. First, the effect of signal duration on localization performance was determined at a fixed angle of 180° separation for noise bursts varying from 100 ms to 2.5 s. Second, two-point localization acuity for left-right sound sources was determined using noise bursts of two different durations: a single 400-ms noise burst, which was the briefest signal which the animals could localize at 180°, and three 700-ms bursts separated by 100 ms which seemed to elicit asymptotic acuity. Both durations have previously been used with other subterranean species (R. Heffner and Heffner, 1990a, under review).

In both tests, signals in the right hemifield were arbitrarily designated as safe signals, and those from the left hemifield were designated warning signals–the animal's task was to respond by breaking contact with the spout whenever a sound came from its left. Blocks of trials containing 6–10 warning signals were presented at decreasing angles of separation until the performance scores fell below 0.25 and the hit rate was no longer significantly greater than the false alarm rate ($P > 0.01$). Threshold was defined as the angle at which the corrected detection performance equaled 0.50. Daily testing continued until performance no longer improved at any angle.

For the tests examining the effect of stimulus duration on sound-localization performance, testing continued for 13–15 sessions until there was no evidence of further improvement with practice. Asymptotic performance for each stimulus duration was then calculated as the average of the best three sessions.

Results

Audiogram

The animals required 25 sessions of training to learn to make the avoidance response and to become reliable observers of low-intensity sounds; testing was completed in an additional 51 sessions. Fig. 2 illustrates the audiograms for the two mole rats. The animals show good agreement throughout their hearing range suggesting that they are probably representative of their species. Both individuals responded to sounds from 8 Hz to 11.2 kHz with a distinct point of most sensitive hearing at 1 kHz. Nevertheless they were remarkably insensitive throughout their hearing range and even at their frequency of best hearing (1 kHz) they could hear only as low as 32 dB SPL. Using an
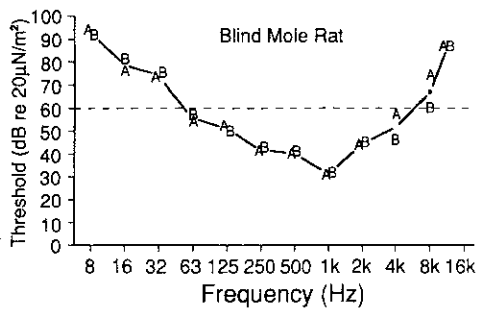
Fig. 2. Audiograms for two blind mole rats (animals A and B). Note the relative lack of sensitivity throughout the audible range and the poor high-frequency hearing.
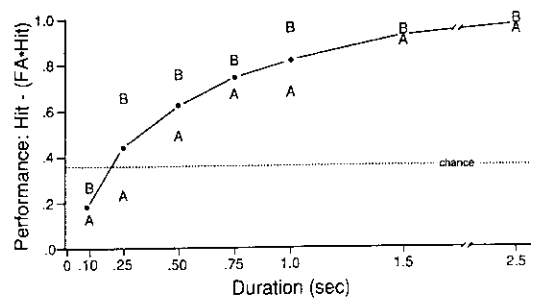

Fig. 3. Sound-localization performance at a fixed angle of 180° for two blind mole rats (animals A and B) as a function of the duration of a single noise burst (Fig. 1A). Although very long durations were easily localized, neither animal could localize a single 100-ms noise burst above chance. Dotted line indicates the 0.01 level of chance.

arbitrary standard of the highest and lowest frequencies audible at an intensity of 60 dB SPL (cf. Masterton et al., 1969), the hearing range of the blind mole rats extended from 54 Hz to only 5.9 kHz giving them a comparatively narrow hearing range of less than seven octaves and the most restricted high-frequency hearing yet observed among mammals.

Sound localization

Effect of signal duration. The ability to localize sound is routinely assessed using a single brief complex signal such as a click or a 100-ms burst of broadband noise. Such stimuli provide both interaural time and spectral cues but minimize the possibility of homing and scanning movements (Thompson and Masterton, 1978). However, the mole rats were unable to localize a single 100-ms noise burst at a separation of 180° despite weeks of training using a range of speaker separations and front-back as well as left-right locations.

Because the animals could not localize a standard 100-ms noise burst, their ability to localize longer noise bursts from 100 ms to 2.5 s at a constant angle of 180° (90° to their left and right) was measured in order to determine the shortest noise burst at which testing could reasonably be carried out. Fig. 3 illustrates the performance of the two animals in this task. At durations of 1.5 s or longer, both animals showed good performance indicating that the basic discrimination and reporting task was well within their capability. However, performance decreased at shorter durations with animal A falling to chance at 250 ms and B at 100 ms.

Acuity. Because the acuity of the animals could not be determined using a standard 100-ms stimulus, acuity tests were carried out with two different stimuli which had previously been used in tests with other subterranean species (R. Heffner and Heffner, 1990a, under review): (1) a train of three noise bursts, each 700 ms in duration and separated by 100 ms, which provided a long-duration signal with additional abrupt onsets and offsets to maximize the cues available to the mole rats, and (2) a single noise burst of 400 ms duration, the

briefest signal both animals could localize above chance at 180°, which also permitted comparison with other subterranean species. Fig. 4 illustrates the performance of the two mole rats for both the long and shorter durations.

When localizing a train of three 700-ms noise bursts (Fig. 4), the mole rats achieved thresholds of 29°. However, because of the difference in stimulus duration, this threshold is not comparable to those achieved by surface rodents localizing much briefer stimuli. Somewhat more comparable are the thresholds illustrated in Fig. 4 using a 400-ms noise stimulus. Although this stimulus is also of relatively long duration, the mole rats were able consistently to discriminate between only the most widely separated loci; their average threshold was 180° and neither could discriminate 90° separation above a level expected by chance.

It should be noted that during a trial the animals either maintained contact with the food spout or else broke contact for the duration of the trial; they did not break contact at the beginning of each trial to scan the sound field. To be sure, we cannot rule out the possibility that minor head movements made while they were in contact with the spout might account for the better performance for long-duration signals. However,
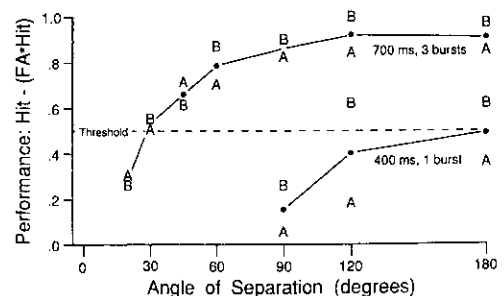

Fig. 4. Sound-localization thresholds for two blind mole rats (animals A and B) for the noise stimulus shown in Fig. 1A. Note the difference in threshold for the long-duration signal (three bursts of 700 ms each) as opposed to the shorter-duration signal (a single 400-ms burst). Dashed line indicates 50% detection threshold.

the possibility exists that the better performance was because their auditory systems require a comparatively long time to process the signals.

Effect of spectrum

Because the hearing range of mole rats is restricted to relatively low frequencies, we investigated the possibility that they might localize low-frequency noise better than broad-band noise. This was done by determining their ability to localize long- and short-duration signals at wide and narrow angles using the lower-frequency noise stimulus illustrated in Fig. 1B. However, there was no difference in their performance in localizing this stimulus compared to the broad-band stimulus illustrated in Fig. 1A. Thus, the poor localization performance of the mole rats is not readily attributable to an absence of critical frequencies in the stimulus.

Discussion

Absolute sensitivity

Audiogram of blind mole rats. The audiogram as determined in the present study is shown in Fig. 5 along with the behavioral audiogram for the same species determined by Bronchti and colleagues (1989) using a double grill box procedure. Despite some differences, there is general agreement between the two audiograms regarding the major aspects of hearing in blind mole rats. Both depict an animal with extremely limited high-frequency hearing, good low-frequency hearing, and generally poor overall sensitivity. Moreover, both audiograms indicate that the best hearing occurs around 1 kHz.

Above 250 Hz the present audiograms diverge from the results obtained by Bronchti and colleagues suggesting better sensitivity in the grill box than the conditioned avoidance procedure. Such a difference is not
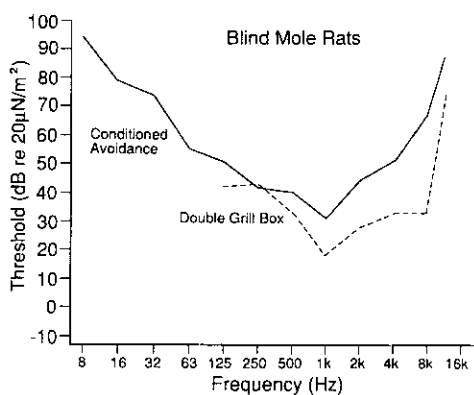

Fig. 5. Audiograms for blind mole rats obtained by two different behavioral methods. Solid line, present report; dashed line, results obtained using a double grill box (Bronchti et al., 1989).

unexpected. In the double grill box procedure the sound intensity is determined by averaging several measurements made within the relatively large area of the grill box and the animals have the opportunity to seek out regions of intensity higher than the average. It has long been suspected and recently demonstrated that methods which permit an animal to move about in a varying sound field can result in spuriously lower thresholds than those which restrict the animal to a small, homogeneous sound field–a result of the ability of animals to seek out regions of greater intensity (R. Heffner and Heffner, 1991a). This observation, coupled with the use of a performance measure that does not correct the detection rate for false alarms, suggests that the double grill box procedure probably overestimated the sensitivity of blind mole rats.

Turning to the low-frequency end of the audiogram, we found that the low-frequency sensitivity of the blind mole rats is comparable to that of other rodents and mammals–a point discussed in detail below. However, although the animals were able to hear as low as 8 Hz at a level of 93 dB SPL, we were unable to find evidence of any unusual low-frequency sensitivity which Bronchti and his colleagues (1989) suggested might exist between 20 and 125 Hz (cf. Fig. 5). In considering this point, we explored the possibility that our animals' thresholds might have been partially masked by the sound generated by ingesting the food. However, the food purée was a thin liquid and did not require mastication; further, the fact that the stimulus duration was 2.6 s meant that momentary swallowing noises would not be long enough to mask the entire signal. Finally, comparison of audiograms for cats obtained in a double grill box with those obtained while the animals continuously ate a food paste showed little difference at low frequencies (although they diverged at higher frequencies where the possible presence of standing waves in the double grill box would have made it difficult to specify precisely the intensity of the sound) (R. Heffner and Heffner, 1985). Thus it seems likely that the present audiogram is an accurate estimation of the animals' sensitivity.

How blind mole rats compare with other mammals. For comparative purposes it is useful to describe the audiogram of a species using four quantitative measures (Masterton et al., 1969): 'high-frequency limit', defined as the highest frequency audible at 60 dB SPL; 'best frequency', the frequency to which an animal is most sensitive; 'best intensity', the lowest intensity to which an animal can respond; and 'low-frequency limit', the lowest frequency audible at 60 dB SPL. The values of these parameters for 17 species of rodents (all for which data are available) are listed in Table I. For graphic comparison, we have chosen two groups of rodents of particular interest: rodents known to have good low-frequency hearing and two subterranean ro-

TABLE I

Auditory parameters for rodents

Animal	Low-frequency limit (kHz)	High-frequency limit (kHz)	Best frequency (kHz)	Lowest threshold (dB)
Low-frequency rodents				
Prairie dog [1]	0.029	26.0	4	20
Gerbil [2]	0.036	58.0	2.9	3
Chipmunk [1]	0.039	52.0	1.0	17
Groundhog [3]	0.040	27.5	4.0	21
Kangaroo rat [4]	0.042	52.0	1.0	9
Guinea pig [5]	0.047	49.0	8.0	−6
Chinchilla [6]	0.050	33.0	1.0	1
Subterranean rodents				
Blind mole rat [7]	0.054	5.9	1.0	32
Naked mole rat [8]	0.065	11.5	4.0	35
Pocket gopher [9]	0.270	8.7	2.0	24
High-frequency rodents				
Norway rat [10]	0.520	72.0	8.0	0
Woodrat [11]	0.940	56.0	8.0	−3
Cotton rat [4]	1.00	72.0	8.0	−6
Darwin's mouse [12]	1.55	73.5	11.0	−3
Grasshopper mouse [11]	1.85	68	8.0	9
Spiny mouse [12]	2.30	71.0	8.0	14
House mouse (wild) [4]	2.30	92.0	16.0	−10

Animals listed in descending order of ability to hear low-frequencies. [1] R. Heffner and Contos, 1989; [2] Ryan, 1976; [3] Conesa, Heffner and Heffner, 1991; [4] H. Heffner and Masterton, 1980; [5] R. Heffner, Heffner and Masterton, 1971; [6] R. Heffner and Heffner, 1991a; [7] present report; [8] R. Heffner and Heffner, 1991b; [9] R. Heffner and Heffner, 1990a; [10] Kelly and Masterton, 1977, R. Heffner, unpublished; [11] H. Heffner and Heffner, 1985; [12] Mooney, Heffner and Heffner, 1990.

dents for which behavioral audiograms are available, pocket gophers, and naked mole rats (Fig. 6).

High-frequency hearing. Perhaps the most striking feature of the hearing ability of the blind mole rats and the other two subterranean rodents is their extremely restricted high-frequency hearing range. As shown in Table I and Fig. 6, the 60-dB upper limit ranges from 5.9 kHz for blind mole rats to 8.7 kHz for pocket gophers, and 11.5 kHz for naked mole rats. In one respect, however, pocket gophers differ from the other two species, as well as from other mammals–their sensitivity declines gradually at high frequencies. As a result, they are capable of hearing up to 32 kHz provided the sound is of sufficient intensity.The inability of the subterranean mammals to hear high frequencies stands in marked contrast to other mammals. A characteristic feature of mammals is their ability to hear frequencies well beyond the 10-kHz upper limit of non-mammalian vertebrates–an ability probably made possible by the evolution of the mammalian middle ear which is more efficient in transmitting high frequencies to the cochlea than are the middle ears of non-mammals (e.g., Saunders and Rosowski, 1979). Indeed,

the average upper limit for mammals is 48 kHz and most rodents hear much higher (cf. Table I). Thus, the high-frequency hearing of the subterranean rodents is deviant when compared with other rodents or with terrestrial mammals in general ($P < 0.005$ and $P < 0.002$, respectively, Mann-Whitney U).The poor high-frequency hearing of the three subterranean rodents suggests that the ability to perceive high frequencies is of little use to animals living underground. Whereas some mammals use their high-frequency hearing for a number of purposes, such as echolocation and ultrasonic communication, the most common use is for sound localization. Specifically, high-frequency hearing plays a role in two aspects of sound localization. First, high frequencies are needed to provide pinna cues for reducing front-back confusions as well as for localizing in the vertical plane (e.g., R. Heffner and Heffner, 1992a; R. Heffner et al., 1992; Musicant and Butler, 1984; Roffler and Butler, 1968). Because the directionality of the pinna is dependent on the wavelength of a sound relative to the size of the pinna, the smaller the pinna, the higher an animal must be able to hear in order to use locus cues produced by the pinna. Thus, Norway rats with a small pinna require sounds containing frequencies up to 40 kHz in order to reach asymptotic performance on a front-back discrimination (R. Heffner and Heffner, 1992a) whereas chinchillas with a larger pinna typically reach asymptote with sounds containing frequencies only up to 20 kHz (R. Heffner, Koay, and Heffner, 1992).

Second, high frequencies also play a role in azimuthal sound localization using binaural spectral differences. Because low frequencies can bend around an animal's head with little or no attenuation, the spectral-difference cue is dependent on the wavelength of the sound. For spectral cues to be effective the sound
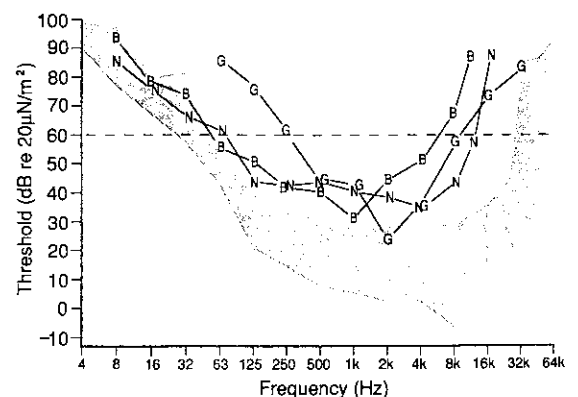

Fig. 6. Audiograms for three subterranean rodents compared to the audiograms for the seven surface-dwelling rodents which hear low frequencies. (B = blind mole rat, G = pocket gopher, N = naked mole rat (R. Heffner and Heffner, 1990a, 1991b)). Shaded area encompasses the audiograms for seven low-frequency rodents (cf. Table I). Note that blind and naked mole rats fall among the low-frequency rodents at very low frequencies.

must contain frequencies high enough to be effectively shadowed by an animal's head and pinnae so that there will be a difference in the spectra of the sounds reaching the two ears. Thus, the smaller an animal's head and pinnae, the higher it must hear in order to obtain a useable spectral-difference cue.

The need for small animals to hear high frequencies in order to use binaural spectral differences has long been used to explain the observation that mammals with small heads generally have better high-frequency hearing than mammals with larger heads (Masterton et al., 1969). However, it should be noted that the size of the pinnae is undoubtedly correlated with head size and thus a correlation between head size and high-frequency hearing may also reflect the fact that small animals require high-frequencies in order to use pinna cues. Indeed, it has been noted that some animals, such as horses, do not use binaural spectral-difference cues, but nevertheless retain good high-frequency hearing which they use to make front-back discriminations using pinna cues (R. Heffner and Heffner, 1992a). Thus, the evolution of the pinna as well as the need to use binaural spectral cues may have served as a major source of selective pressure for the reception of frequencies above 10 kHz.

The relationship between head size and high-frequency hearing shown in Fig. 7 illustrates the degree to which the three subterranean rodents are deviant. As can be seen, other mammals with similar head sizes have high-frequency hearing limits higher than 50 kHz. Within this context, it is significant to note that the subterranean rodents are unable to localize brief sounds and, lacking pinnae, cannot use pinna locus cues. The fact that animals which are virtually incapable of localizing sound also cannot hear high frequencies supports the contention that the ability of
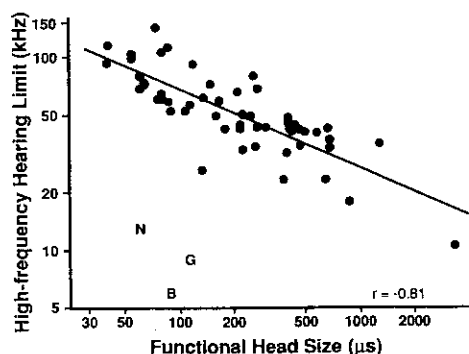

Fig. 7. High-frequency hearing limit (highest frequency audible at 60 dB SPL) as a function of head size (measured as the number of μs required for a sound to travel from one auditory meatus to the other) for 64 species of mammals. In general, mammals with small heads hear higher frequencies than those with larger heads. The three subterranean species are marked exceptions to this relationship.
B = blind mole rat, G = pocket gopher, N = naked mole rat.

mammals to hear above 10 kHz probably evolved primarily to serve sound localization.

Best frequency. The frequency at which the subterranean rodents are most sensitive ranges from 1 kHz for the blind mole rat to 4 kHz for the naked mole rat (Table I). Although these best frequencies are lower than the mammalian average of 6.8 kHz, they are not significantly different from the 2.3-kHz average for the group of seven low-frequency rodents illustrated in Fig. 6 ($P > 0.5$, Mann-Whitney U). Thus, in terms of best frequency, the subterranean rodents closely resemble other rodents with good low-frequency hearing.

Best intensity. A common feature of the hearing of the three subterranean species is their pervasive lack of sensitivity. Whereas the average best intensity of mammals is 0.4 dB (R. Heffner and Heffner, 1990b), the best intensity of the subterranean rodents ranges from 24 dB to 31.5 dB. Although the 9.3-dB average best intensity of the seven low-frequency rodents places them in the least sensitive half of the mammalian range, these rodents are still significantly more sensitive than the subterranean rodents ($P = 0.008$, Mann-Whitney U). Thus, it appears that subterranean rodents have lost the sensitivity which other rodents and other mammals possess and hence the sensitivity their ancestors probably once possessed.

Low-frequency hearing. Low-frequency sounds propagate better than high frequencies within the underground tunnels inhabited by subterranean mammals (Heth et al., 1986). Hence, it is widely accepted that mole rats are specially adapted to hear low-frequency sounds (e.g., Bronchti et al., 1989; Burda et al., 1990). For this reason, it is of special interest to compare the low-frequency hearing of these rodents with that of other rodents and other mammals.

At present, audiograms are available for 14 species of rodents in addition to the three subterranean species (Table I). The 60-dB low-frequency hearing limits for these 14 species range from 29 Hz to 2.3 kHz with a mean low-frequency limit of 230 Hz (median 161 Hz). However, as can be seen in Table I, these 14 rodents can be divided into two groups on the basis of their low-frequency hearing: seven species with a low-frequency limit of 50 Hz and below, and seven with low-frequency limits above 500 Hz.

Of the two groups of rodents, blind and naked mole rats more closely resemble the low-frequency rodents listed in Table I. Although their 60-dB low-frequency limits are slightly poorer than those of the seven low-frequency rodents, this discrepancy may be owing to their overall poor sensitivity; at very low frequencies (and high intensities) they are just as sensitive as some of the other low-frequency rodents (cf. Fig. 6). The pocket gopher, on the other hand, is intermediate between the two groups of rodents.

From this comparison, it can be concluded that

although subterranean rodents have good low-frequency hearing, their low-frequency hearing is not exceptional among rodents. Similarly, it is not exceptional among mammals in general since good low-frequency hearing is common among other mammals as well. For example, other mammals with 60-dB low-frequency limits below 50 Hz include primates (humans, baboons, macaques), carnivores (ferrets and least weasels), artiodactyls (pigs and cattle), and proboscidea (Indian elephants) (cf. Fay, 1988).

Although blind mole rats do not have exceptional low-frequency hearing, it nevertheless remains the only aspect of their audiogram that is not degenerate. That is, in spite of the fact that these animals probably have lost the ability to hear high-frequencies and have lost a good deal of their overall sensitivity to sound, they have retained the ability to hear low-frequencies. This suggests that there is some selective advantage for the blind mole rats to hear low frequencies despite reduced selective pressures for most aspects of hearing.

It has been suggested that subterranean rodents rely on low-frequency sounds for communication (e.g., Heth et al., 1986). In the case of blind mole rats, low-frequency communication is of two types: 1)–airborne vocalizations below 8 kHz with the main energy concentrated between 500 and 600 Hz (Capranica et al., 1973; Heth et al., 1988; Nevo, Heth, Beiles, and Frankenberg, 1987), and 2)–substrate-borne vibrations with the main energy between 100 Hz and 300 Hz which they produce by tapping their heads on the roofs of their tunnels (e.g., Heth et al., 1987; Rado et al., 1987). At present it appears that they may detect substrate-borne vibrations via bone conduction by contacting the substrate with their jaws (Rado et al., 1989) although their somatosensory systems may also play a role (Nevo et al., 1991). Thus blind mole rats may use their low-frequency hearing for communication.

Sound localization

Blind mole rats together with pocket gophers and naked mole rats share an inability to localize brief sounds (i.e., a 100-ms burst of broad band noise) (R. Heffner and Heffner, 1990a, under review). Only when permitted to listen to much longer-duration sounds (e.g., three bursts of noise each 700 ms long) do they display an acuity near 30°–an acuity equalled or exceeded by surface dwelling rodents localizing a 100-ms noise burst (for a review, see R. Heffner and Heffner, 1992a). This remarkable absence of an ability once thought to be a mammalian characteristic may be an example of convergent evolution. That is, despite their distant phylogenetic relationship, the subterranean rodents display a similar adaptation to a habitat in which both the direction of airborne sound propagation and the directional responses to sound are limited by the burrow system.

The inability of blind mole rats to localize brief sounds provides support for the recently observed relation between sound-localization acuity and vision (for a detailed discussion of this relationship, see R. Heffner and Heffner, 1992b). Briefly, it has been suggested that a major factor influencing the variation in sound-localization acuity among mammals is the need to direct the field of best vision toward a sound source for further scrutiny. Just how accurate sound localization must be depends upon the width of an animal's field of best vision. Animals with narrow fields of best vision, such as humans, require good sound localization acuity in order to direct their gaze so that the visual image of the sound source falls upon their fovea. Animals with broad fields of best vision (such as visual streaks), on the other hand, do not require such acuity.

Blind mole rats, with their minute eyes buried beneath fur and skin, present an extreme case in which an absence of both pattern vision and visual fields is accompanied by a virtual inability to localize brief sounds. Thus they support the suggestion that the ears are under selective pressure to provide locus information accurate enough to direct the eyes, and in the complete absence of this pressure from the visual system, sound-localization degenerates. In addition, developmental evidence from both owls and guinea pigs suggests that, in ontogeny as well as in evolution, the eyes serve to calibrate sound localization (Knudsen and Knudsen, 1989; Withington-Wray, et al., 1990). Since blind mole rats have no pattern vision to coordinate with auditory space, they need not localize at all.

Although the need to direct the gaze appears to be a major factor influencing localization among mammals, it should be noted that this relationship applies to the use of 'passive' sound localization–that is, the localization of sounds produced by the action of other animals in the environment. Some species such as bats and porpoises that no longer rely on vision for scrutinizing their environment use echolocation instead for that purpose. In such cases, the question arises as to whether these animals use their passive localization ability to direct their sonar to objects of interest for further scrutiny. If so, then we might expect that their passive localization acuity would be determined by the effective beamwidth of their echolocation pulses.

Relation of hearing to other characteristics of blind mole rats

The overall insensitivity to sound with a region of residual sensitivity to airborne vibrations between approximately 125 Hz and 4 kHz and the inability to perform all but the most rudimentary localization tasks have implications for our understanding of other characteristics of blind mole rats. First, is the division of the cochlea into apical and basal subsystems. Although the basal subsystem appears typically mammalian, the

apical subsystem is similar to the basilar papilla of reptiles (Bruns et al., 1988; Raphael et al., 1991). The functional significance of this unusual anatomical arrangement is not yet known, however the suggestion that it might serve enhanced sensitivity to low-frequency airborne vibration is not borne out by the present results.

Second, the auditory sensitivity of blind mole rats corresponds to the spectrum of their communication calls. These vocalizations contain energy primarily between 500 Hz and 4.5 kHz with the major components near 500 Hz (Capranica, 1973; Heth et al., 1988). These are approximately the frequencies which have been shown to propagate best in their underground burrows (that is, 440 Hz; Heth et al., 1986). Thus, it appears that the underground acoustic environment has played a role in shaping the auditory sensitivity and the spectrum of vocalizations of these animals.

Finally, despite their limited auditory abilities, the auditory brainstem of blind mole rats corresponds to the typical mammalian pattern (Bronchti et al., 1989). Like the other subterranean rodents with limited hearing (pocket gophers and naked mole rats), there has been no marked degeneration in central auditory structures with the possible exception of the lateral superior olive. Typically a high-frequency nucleus, the lateral superior olive of blind mole rats is 'poorly differentiated' (Bronchti et al., 1989) as might be expected from the very limited high-frequency input available to it (cf. R. Heffner and Masterton, 1990). Indeed, the auditory system remains developmentally vigorous enough to invade visual structures, such as the lateral geniculate nucleus in the thalamus, which no longer receives input from the vestigial eyes (Bronchti et al., 1989).

References

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.

Bronchti, G., Rado, R., Terkel, J. and Wollberg, Z. (1991) Retinal projections in the blind mole rat: A WGA-HRP tracing study of a natural degeneration. Dev. Brain Res. 58, 159–170.

Bruns, B., 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.

Burda, H., Bruns, V. and Müller, M. (1990) Sensory adaptations in subterranean mammals. In: E. Nevo and O.A. Reig (Eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels, Wiley-Liss, New York pp. 269–293.

Capranica, R.R., Nevo, E. and Moffat, A.J.M. (1973) Vocal repertoire of a subterranean rodent (Spalax). J. Acoust. Soc. Am. 54, S121.

Conesa, J., Heffner, R.S., and Heffner, H.E. (1991) Hearing in large rodents: Groundhogs Marmota monax. Abstr. Assoc. Res. Otolaryngol. 14, 24.

de Jong, W., Hendriks, W., Sanyal, S., and Nevo, E. (1990) The eye of the blind mole rat (Spalax ehrenbergi): Regressive evolution at the molecular level. In: E. Nevo and O.A. Reig (Eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels, Wiley-Liss, New York. pp. 383–395.

Fay, R. (1988) Hearing in Vertebrates: A Psychophysics Databook. Hill-Fay Associates, Winnetka, IL.

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

Heffner, H. 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. and Contos, C.A. (1989) Hearing in two ground-dwelling squirrels: Eastern chipmunk and black-tailed prairie dog. Abstr. Assoc. Res. Otolaryngol. 12, 233–234.

Heffner, R.S. and Heffner, H.E. (1985) Hearing range of the domestic cat. Hear. Res. 19, 85–88.

Heffner, R.S. and Heffner, H.E. (1990a) Vestigial hearing in a fossorial mammal, the pocket gopher (Geomys bursarius). Hear. Res. 46, 239–252.

Heffner, R.S. and Heffner, H.E. (1990b) Hearing in domestic pigs (Sus scrofa) and goats (Capra hircus). Hear. Res. 48, 231–240.

Heffner, R.S. and Heffner, H.E. (1991a) Behavioral hearing range of the chinchilla. Hear. Res. 55, 109–116.

Heffner, R.S. and Heffner, H.E. (1991b) Hearing in subterranean mammals: Naked mole rats Heterocephalus glaber. Abstr. Assoc. Res. Otolaryngol. 14, 24.

Heffner, R.S. and Heffner, H.E. (1992a) Evolution of sound localization in mammals. In: A.N. Popper, R.R. Fay and D.B. Webster (Eds.), The Evolutionary Biology of Hearing, Springer-Verlag, New York, pp. 691–716.

Heffner, R.S. and Heffner, H.E. (1992b) Visual factors in sound localization in mammals. J. Comp. Neurol. 317, 219–232.

Heffner, R.S. and Heffner, H.E. (under review) Vestigial hearing and sound localization in subterranean naked mole rats: Heterocephalus glaber.

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

Heffner, R.S., Koay, G. and Heffner, H.E. (1992) Importance of high frequencies and the contribution of the pinnae to sound localization in chinchillas. Abstr. Assoc. Res. Otolaryngol. 15, 50.

Heffner, R.S. and Masterton, R.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.

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.

Heth, G., Frankenberg, E. and Nevo, E. (1988) "Courtship" call of subterranean mole rats (Spalax ehrenbergi): Physical analysis. J. Mammal. 69, 121–125.

Heth, G., Frankenberg, E., Raz, A. and Nevo, E. (1987) Vibrational communication in subterranean mole rats (Spalax ehrenbergi). Behav. Ecol. Sociobiol. 21, 31–33.

Kelly, J.B. and Masterton, R.B. (1977) Auditory sensitivity of the albino rat. J. Comp. Physiol. Psychol. 91, 930–936.

Knudsen, E.I. and Knudsen, P.F. (1989) Vision calibrates sound localization in developing barn owls. J. Neurosci. 9, 3306–3313.

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

Mooney, S.E., Heffner, H.E. and Heffner, R.S. (1990) Hearing in two species of rodents: Darwin's leaf-eared mouse (*Phyllotis darwini*) and the spiny mouse (*Acomys cahirinus*). Abstr. Assoc. Res. Otolaryngol. 13, 176.

Musicant, A.D. and Butler, R.A. (1984) The influence of pinna-based spectral cues on sound localization. J. Acoust. Soc. Am. 75, 1195–1200.

Nevo, E. (1961) Observation on Israeli populations of the mole rat. Mammalia 25, 127–144.

Nevo, E. (1979) Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. 10, 269–308.

Nevo, E. (1990) Evolution of nonvisual communication and photoperiodic perception in speciation and adaptation of blind subterranean mole rats. Behaviour 114, 249–276.

Nevo, E., Heth, G., Beiles, A. and Frankenberg, E. (1987) Geographic dialects in blind mole rats: Role of vocal communication in active speciation. Proc. Natl. Acad. Sci. USA 84, 3312–3315.

Nevo, E., Heth, G. and Pratt, H. (1991) Seismic communication in a blind subterranean mammal: A major somatosensory mechanism in adaptive evolution underground. Proc. Natl. Acad. Sci. USA 88, 1256–1260.

Pevet, P., Heth, G., Haim, A. and Nevo, E. (1984) Photoperiod perception in the blind mole rat (*Spalax ehrenbergi*, Nehring): Involvement of the Harderian gland, atrophied eyes and melatonin. J. Exp. Zool. 232, 41–50.

Rado, R., Himelfarb, M., Arensburg, R., Terkel, J. and Wollberg, Z. (1989) Are seismic communication signals transmitted by bone conduction in the blind mole rat? Hear. Res. 41, 23–30.

Rado, R., Levi, N., Hauser, H., Witcher, J., Adler, N., Intrator, N., Wollberg, Z. and Terkel, J. (1987) Seismic signalling as a means of communication in a subterranean mammal. Animal Behav. 35, 1249–1266.

Rado, R., Wollberg, Z. and Terkel, J. (1991) The ontogeny of seismic communication during dispersal in the blind mole rat. Animal Behav. 42, 15–21.

Raphael, Y., Lenoir, M., Wroblewski, R. and Pujol. R. (1991) The sensory epithelium and its innervation in the mole rat cochlea. J. Comp. Neurol. 314, 367–382.

Roffler, S.K. and Butler, R.A. (1968) Factors that influence the localization of sound in the vertical plane. J. Acoust. Soc. Am. 43, 1255–1259.

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

Sanyal, S., Jansen, H.G., de Grip, W.J., Nevo, E. and de Jong, W.W. (1990) The eye of the blind mole rat, *Spalax ehrenbergi*; Rudiment with hidden function? Inves. Ophthalamol. Vis. Sci. 31, 1398–1404.

Saunders, J.C. and Rosowski, J.J. (1979) Assessment of hearing in animals. In: W.F. Rinetelmann (Ed.), University Park Press, Baltimore, MD pp. 487–529.

Savic, I.R. and Nevo, E. (1990) The spalacidae: Evolutionary history, speciation and population biology. In: E. Nevo and O.A. Reig (Eds.), Evolution of subterranean mammals at the organismal and molecular levels. Wiley-Liss, New York, pp. 120–153.

Thompson, G. and Masterton, R.B. (1978) Brain stem auditory pathways involved in reflexive head orientation to sound. J. Neurophysiol. 41, 1183–1202.

Thompson, M., Porter, B., O'Bryan, J., Heffner, H.E. and Heffner, R.S (1990) A syringe-pump food-paste dispenser. Behav. Res. Methods Instru., Comp. 22, 449–450.

Withington-Wray, D.J., Binns, K.E. and Keating, M.J. (1990) The maturation of the superior collicular map of auditory space in the guinea pig is disrupted by developmental visual deprivation. Eu. J. Neurosci. 2, 682–692.