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Seismic communication signals in the blind mole-rat (*Spalax ehrenbergi*): electrophysiological and behavioral evidence for their processing by the auditory system

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Abstract Based on morphological and behavioral findings we suggest that the seismic vibratory signals that blind mole-rats (*Spalax ehrenbergi*) use for intraspecific communication are picked up from the substrate by bone conduction and processed by the auditory system. An alternative hypothesis, raised by others, suggest that these signals are processed by the somatosensory system. We show here that brain stem and middle latency responses evoked by vibrations are similar to those evoked by high-intensity airborne clicks but are larger in their amplitudes, especially when the lower jaw is in close contact with the vibrating substrate. Bilateral deafening of the mole-rat or high-intensity masking noise almost completely eliminated these responses. Deafening also gradually reduced head-drumming behavior until its complete elimination about 4–6 weeks after surgery. Successive vibrations, at a rate of 0.5 vibrations/s, elicited prominent responses. At rates higher than 2 vibrations/s the amplitude of the brain stem response did not change, yet the middle latency response disappeared almost completely. It is concluded that the seismic signals that mole rats use for long distance communication are indeed processed primarily by the auditory system.

Key words Mole-rat · Seismic signals · Auditory system

Abbreviations *ABER* auditory brain-stem-evoked response · *MLR* middle latency response

Introduction

The blind mole-rat, *Spalax ehrenbergi*, is a subterranean rodent that shows striking behavioral, morphological and physiological adaptations to fossorial life (Nevo 1979, 1982). It is a highly solitary species that digs its tunnel system to its own size, and which it never leaves unless forced to (Nevo 1961). Encounters between individuals are very rare and are limited to the mating season, to contacts between mother and pups, and to incidental intrusion of an individual to a foreign tunnel system.

We and others have shown that for long-distance communication this subterranean rodent uses vibratory (seismic) signals that are produced by rapidly tapping its head on the roof of the tunnel (Heth et al. 1987; Rado et al. 1987). These vibrations consist of low-frequency components (Rado et al. 1987) that match both the hearing capacity of the mole-rat (Bronchti et al. 1989; Bruns et al. 1988; Burda et al. 1989, 1990; Heffner and Heffner 1992) and the transmission properties of the underground habitat (Liu et al. 1976). Based on behavioral and morphological observations we suggested that these seismic signals are perceived by the mole-rats by pressing the lower jaw against the tunnel wall and transmitted thereafter to the inner ear mainly by bone conduction (Rado et al. 1989). This enables minimal loss of energy, thereby compensating for the low efficiency of the middle ear in transferring airborne sounds to the inner ear (Rado et al. 1989). This assumption has been challenged by an alternative hypothesis (Nevo et al. 1991), suggesting that the seismic signals are processed by the somato-sensory system.

In this study we present electrophysiological and behavioral evidence corroborating our assumption that the seismic signals used by the blind mole-rat for long-distance communication are indeed perceived and processed primarily by the auditory system. Preliminary results have been previously published in a symposium proceedings.

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Materials and methods

Animals

In this study we used a total of 30 adult mole-rats of both sexes, weighing between 150 and 250 g, with no hearing deficiencies. We trapped the animals in the Tel Aviv area and the northern parts of the Israeli Negev desert, and housed them individually in the laboratory in plastic cages (33 cm × 38 cm × 14 cm) under a 14/10 h light-dark regime, and a constant temperature of 22 ± 2 °C. We supplied rodent chow *ad libitum* and twice a week sufficient fresh vegetables and fruit to eliminate the need for drinking water.

Electrophysiological experimental set up

We conducted all the electrophysiological experiments in a double-wall sound attenuation chamber (IAC type 1203 A). The experimental set up comprised two cylindrical Plexiglas tubes 80 cm and 30 cm long with a diameter of 7 cm, placed on separate tables with their openings facing each other at a distance of 2 cm so as to avoid vibrational cross-talk between the two tubes. We determined the position of the animal within this experimental setup according to the purpose of each experiment. Airborne sounds were delivered by a calibrated speaker placed facing the opening of one end of the 80-cm-long tube but not touching it, so as to minimize its vibration by the sounds. Vibratory signals were produced by a Brüel and Kjaer (type 4810) mechanical mini shaker placed under the long tube at a distance of 60 cm from the animal's head.

Stimulation procedures

Auditory signals consisted of clicks, lasting 0.2 ms, generated by a square-pulse generator (Digitimer 4030), and broad-band (0.02–20 kHz) masking noise generated by a Brüel and Kjaer white-noise generator (type 1405). Amplitude control was achieved with a Hewlett Packard attenuator (type 350D) and a custom-made power amplifier. The sounds were delivered through the above mentioned speaker and monitored for pressure levels (expressed in dB SPL re 20 µPa) by a calibrated condenser microphone (type 4134) connected to a 1/3-octave filter (type 1616) and a sound level meter (type 2209) from the same company.

Vibratory signals were produced by 0.2-ms square pulses which activated the above-mentioned mini shaker. We covered the tip of the mini shaker with rubber to soften the tap and adjusted it to barely maintain contact with the Plexiglas tube. Acceleration was monitored and measured by a Brüel and Kjaer accelerometer (type 4371) connected to the sound-level meter, operating on a vibration measurements mode. All values are given in 'peak acceleration'. The acceleration of the standard vibratory stimulus used in our experiments was 7.8 ms^{-2} (unless otherwise stated). The basis for selecting this acceleration value was two fold: Firstly, under laboratory conditions (within a Plexiglas tube), the peak acceleration produced by a mole-rat, measured at a distance of 20 cm, is about 21 ms^{-2} ; Secondly, in nature the distances that mole-rats communicate by vibrations are far greater than 20 cm. These acceleration values are well within the range of vibration signal intensities for biological signals (Markl 1983). The spectral content of these vibrations and the vibrations produced by mole-rats in the field and under laboratory conditions were comparable.

Recording procedures

We recorded event-related responses elicited by airborne sounds or vibratory stimuli differentially from the scalp of anesthetized animals (a mixture of 27 mg kg^{-1} Ketalar and 0.6 mg kg^{-1} xylazine) by means of two stainless-steel needle electrodes inserted subcutaneously, one at the vertex and the other one over the temporal cortex. A grounding electrode was inserted into the animal's back. Potentials [short latency, 0–10 ms, auditory brain-stem-evoked

responses (ABER) and middle latency, 20–30 ms responses (MLR)] were AC amplified, band-pass filtered (0.02–5.0 kHz; Digitimer LN Neurolog System), monitored on the face of a CRT, digitized (sampling rate: 10.0 kHz), averaged (256–512 repetitions, RC electronics hard/software) and stored on a PC for off-line analyses. Response amplitudes are expressed in mean peak to peak values \pm standard deviations (SD).

Results

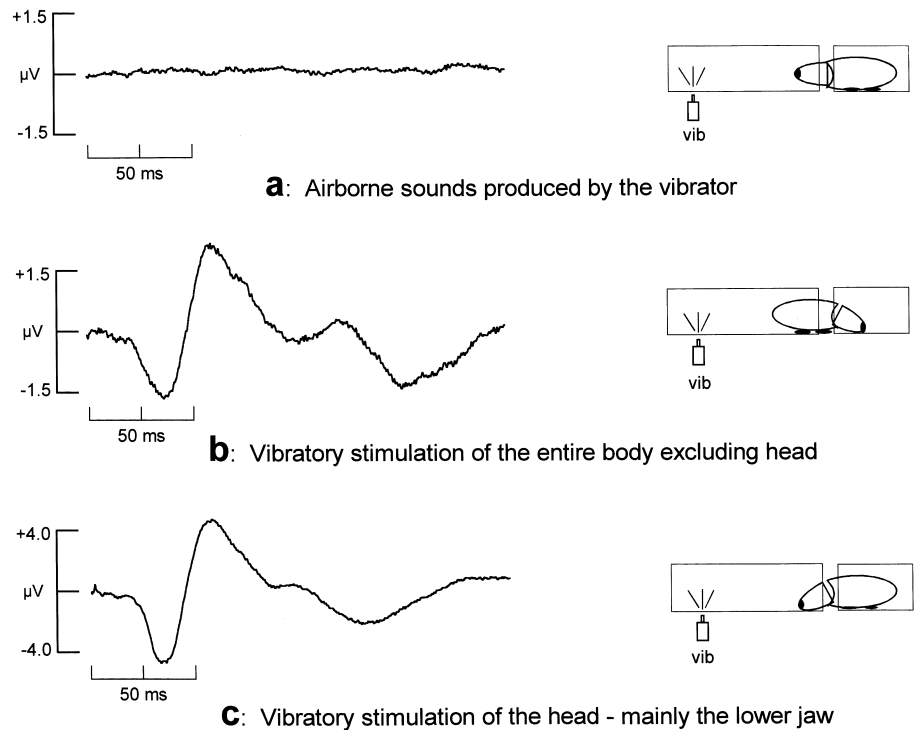
We conducted two main series of electrophysiological experiments and a set of behavioral experiments in this study. In the first series we determined whether the responses measured from the mole-rat's brain were indeed elicited by the vibrations per se, or rather by the airborne sounds produced by the mini-shaker. The second series of experiments, which constitutes a major part of this study, was designed to disclose the sensory modality by which the seismic vibrations are perceived and processed. The behavioral experiments were intended to corroborate the results of the electrophysiological experiments.

Airborne sounds or vibrations?

To answer this question we exposed three mole-rats to vibratory stimulation under three different experimental settings. 1) An anesthetized animal was placed inside the short Plexiglas tube with its head facing, but not touching, the long tube (Fig. 1a). It was thus able to hear the air borne sounds produced by the vibrator tapping the long tube but was not exposed to the vibrations. 2) The animal's body was situated inside the long tube with its head inside the short tube (Fig. 1b). Under these conditions the mole-rat was able to hear the airborne sounds that the mini-shaker produced, while its body, except for the head, was also in physical contact with the vibrating substrate. 3) The animal's body was situated inside the short tube while its head was inside the long tube with the lower jaw touching the Plexiglas floor of this tube. In this position the animal was able to hear the air-borne sounds produced by the vibrator and its lower jaw was in physical contact with the vibrating substrate (Fig. 1c). The acceleration of the vibrating substrate and the sound pressure produced by the mini-shaker, measured at the distal end of the long tube, were 7.8 m s^{-2} and 77 dB SPL, respectively. Stimulation rate in all these experiments was 0.5 stimuli/s.

The results of these experiments are depicted in Fig. 1. It can be seen that the airborne sound produced by the mini-shaker did not elicit any detectable response (Fig. 1a), while the same stimulus causing vibration of the substrate in contact with either the body of the mole-rat (Fig. 1b) or only its head (Fig. 1c), elicited marked responses. Evidently, when only the head was exposed to the vibrations, the MLR was significantly stronger than when the entire body except the head was stimulated ($7.6 \pm 1.5 \text{ } \mu\text{V}$ and $2.0 \pm 1.7 \text{ } \mu\text{V}$ peak to peak ampli-

Fig. 1a–c Vibratory stimuli versus airborne sounds – a schematic drawing of the experimental set-up and concrete data demonstrating the difference in a middle latency response (MLR). **a** The animal is exposed to the air-borne sounds (70 dB SPL, peak intensity) but not to the vibrations (7.8 m s^{-2}) produced by the mini-shaker (*vib*) as it vibrates the longer tube. **b** The animal is exposed to the sound produced by the vibrator and its body is also in contact with the vibrating substrate. **c** The animal's head, especially its lower jaw, rests on the floor of the vibrating tube. Note that no response was elicited in **a**, whereas in **b** and **c** marked responses were evoked. A maximum response was elicited in **c**



tudes, respectively; $n = 3$ animals, $P < 0.005$; paired *t*-test).

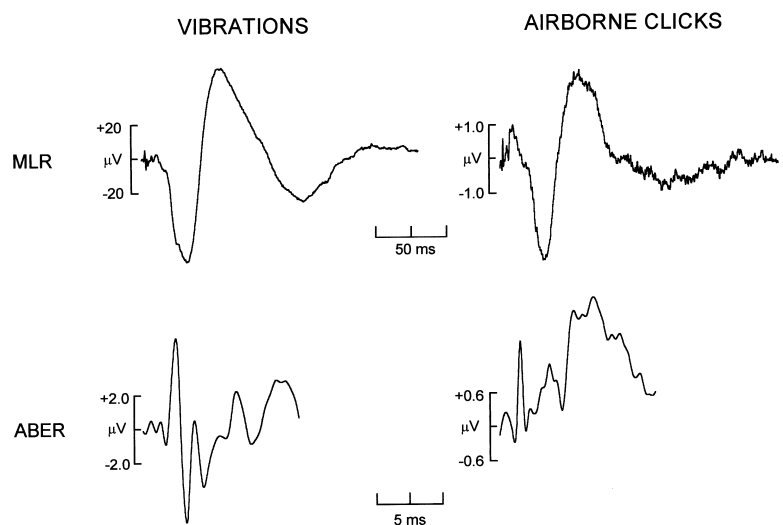
The response pattern elicited by the vibratory stimulus was very much like the one evoked by a high-intensity (120 dB SPL peak intensity) airborne click (Fig. 2). Both consisted of several components starting with a typical ABER within the first 10 ms followed by a MLR with a peak latency of about 30 ms and some additional late components.

During these experiments we observed that the waveform and amplitudes of the responses to the vibratory stimuli were highly dependent on the exact position of the mole-rat's lower jaw with respect to the vibrating floor of the tube. When the lower jaw was

barely touching the vibrating substrate, the response was complex and relatively weak (Fig. 3a). When the lower jaw was lying on the vibrating substrate the amplitude of the response was $5.9 \pm 2.1 \mu\text{V}$ ($n = 7$; Fig. 3b). The response was significantly higher when the lower jaw was gently pressed against the tube wall by means of a rubber-coated screw that pushed the head in a dorso-ventral direction ($33.2 \pm 26.0 \mu\text{V}$; $n = 5$; $P < 0.05$; unpaired *t*-test; Fig. 3c).

It is evident from these results that under these experimental conditions, the vibrations per se rather than the airborne sound (produced by the vibrator), elicited a response. It is also apparent that these vibrations are picked-up primarily by the lower jaw.

Fig. 2 Averaged MLR (*upper row*) and averaged brain stem response (ABER, *lower row*) evoked by repetitive vibratory stimulation (left, 7.8 m s^{-2}) and by high-intensity (120 dB SPL peak intensity) airborne clicks (*right*). Stimulation rate in both cases: 0.5 stimuli/s. During exposure to the vibratory stimulus, the mole-rat's head was pressed against the bottom surface of the Plexiglas tube. Note the similarity in shape and time course of the MLRs in both cases but the marked difference in amplitudes



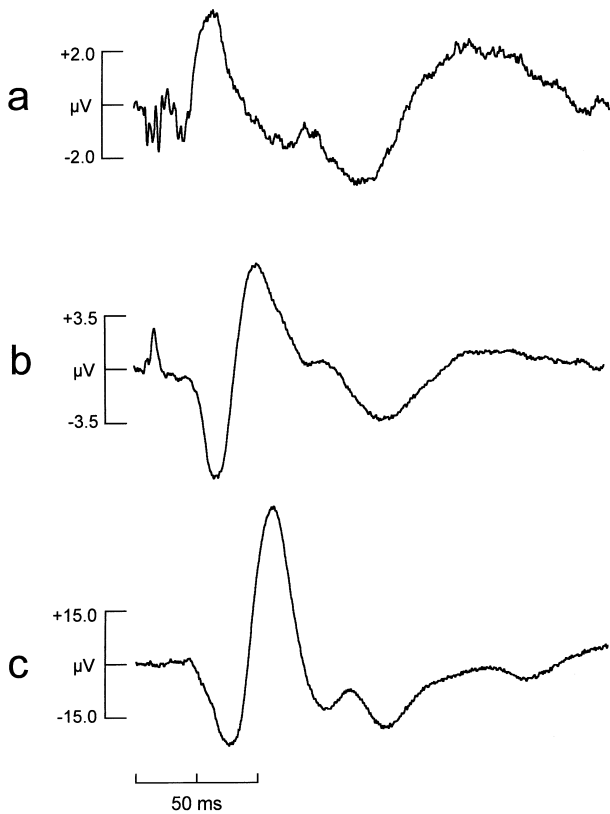


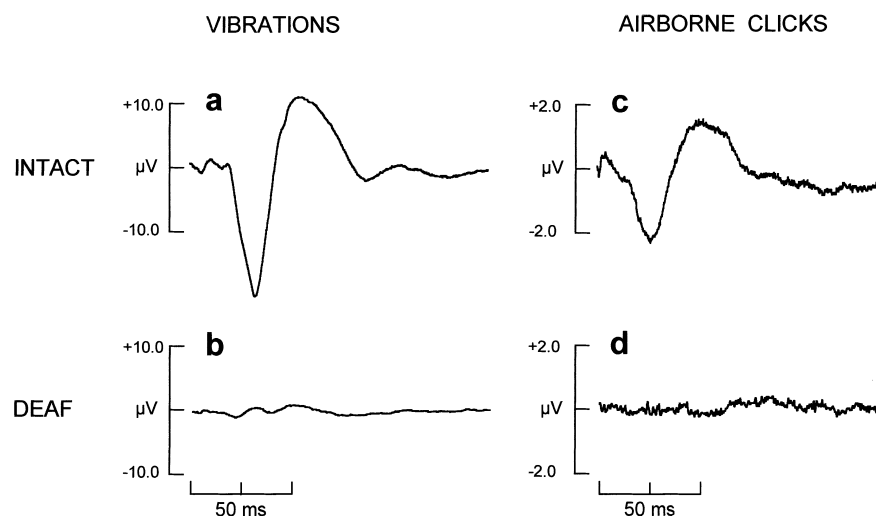
Fig. 3a–c Effect of lower jaw position with respect to the vibrating substrate on the middle latency response. **a** The lower jaw is barely touching the bottom surface of the vibrating tube. **b** The lower jaw is lying on the vibrating substrate. **c** The lower jaw is firmly pressed against the bottom surface of the vibrating tube

Somatosensory or auditory system?

Are the seismic vibrations processed by the somatosensory or auditory system? To answer this question we tested the responses elicited by auditory and vibratory stimuli in binaurally deafened mole-rats and compared them with those elicited in intact animals under exactly

the same conditions. In addition we checked the responses elicited by vibratory stimuli in intact animals that were exposed to high-intensity background white masking noise. Binaural deafness was achieved by bilateral mechanical destruction of the middle and inner ears. All animals were checked for normal hearing before going through the deafening procedure. Under deep ether anesthesia the tympanic membranes of the mole-rats were slit and the middle and inner ears were gently crushed with the aid of a narrow spatula, penetrating through the external ear canal. After this surgical procedure the animals were treated for 1 week with Durabiotic (0.1 mg/100 g BW i.m., TEVA). Six animals showing complete behavioral recovery from vestibular impairment were used in these experiments. The experimental protocol consisted of recording brain responses to high-intensity airborne clicks (120 dB SPL peak intensity), and to vibrations (7.8 m s^{-2}), while the animal was housed in the Plexiglas tube with either its lower jaw pressed optimally to the vibrating substrate or when just lying on it. All the stimuli were presented at a rate of 0.5 stimuli/s. We tested each animal, under these conditions, immediately after behavioral recovery (2 weeks after surgery, for most animals) and 3 weeks later. Following behavioral tests (see below) the animals were sacrificed and checked for the destruction of the middle and inner ears. It is apparent (Fig. 4a) that the substrate vibrations elicited a very prominent MLR in intact animals ($33.3 \pm 26.0 \mu\text{V}$; $n = 5$), while in the deafened animals (Fig. 4b) the average amplitude was significantly smaller ($2.4 \pm 1.2 \mu\text{V}$; $n = 5$; $P < 0.01$, unpaired t -test). The amplitude of this residual response in the deaf animals was essentially the same ($P = 0.75$; paired t -test) whether the lower jaw was pressed against the vibrating substrate ($2.4 \pm 1.2 \mu\text{V}$; $n = 5$) or just touching it ($3.1 \pm 2.3 \mu\text{V}$; $n = 5$). The high-intensity airborne clicks evoked a distinct MLR pattern in the intact animals that was very similar to the one elicited by the vibrations, albeit weaker (Fig. 4c). However, in deaf animals airborne sounds failed to elicit either an ABER or an apparent MLR (Fig. 4d).

Fig. 4a–d Effect of bilateral deafening of the mole-rat on the averaged MLR evoked by a vibratory stimulus (7.8 m s^{-2}) (**a** and **b**) and by a high-intensity airborne click (120 dB SPL peak intensity) (**c** and **d**). Exposure to vibrations was performed with the animal's lower jaw pressed firmly against the vibrating substrate. Note, in the deaf animal, the residual response to vibration and lack of response to the airborne click



To further assess the association between seismic communication and hearing capacity we also examined whether deafening the animals has any effect on the animal's head-drumming behavior. This was evaluated by introducing pairs of mole-rats, a test animal and a naive one (taken from our colony), into a Plexiglas tube (100 cm long, 7 cm in diameter) with a barrier made of crossed spokes at the midpoint, separating the two. Two parameters served as the criteria for estimation: 1) the number of test animals that performed head-drumming after introduction to a partner; and 2) the number of head-drumming bursts produced by the tested animal within the first 5 min after introducing the two animals into the tube. Since mole-rats occasionally perform spontaneous head-drumming, we took into account only mole-rats that performed at least three head-drumming bursts within the 5-min test (which is beyond chance).

We tested seven control (intact) and eight deafened animals (six of which had been tested in the electrophysiological experiments) with the same partner before deafening as well as 2 weeks, 4 weeks and 8–10 weeks post-surgery. Body weight and general health of the mole-rats were examined before each test. Figure 5 summarizes the results of these experiments. It is evident (Fig. 5a) that the number of deafened mole-rats that had previously drummed with their control partners gradually declined with time until complete cessation 8–10 weeks after deafening. Furthermore, the number of head-drumming bursts that deaf animals performed within the 5-min test period declined significantly, as compared to the control animals, from about 36 bursts before deafening to 6.5, 3 and zero, 2 weeks, 1 month and 2 months after deafening, respectively (Fig. 5b). The slight and gradual decrement in the number of head-drumming bursts that control animals performed during the test period reflected, apparently, behavioral habituation.

These electrophysiological and behavioral experiments suggested that the vibratory stimuli are picked-up and processed primarily by the auditory system. Since deafening did not completely eliminate the response to the vibratory stimulus, a negligible contribution of the somatosensory system could not be excluded. To substantiate these assumptions we tested the responses to vibrations at four different accelerations, ranging between 7.8 m s^{-2} and 0.3 m s^{-2} , with and without a stationary high-intensity background masking noise. We used four intact mole-rats whose lower jaws were pressed against the vibrating substrate. It can be seen (Fig. 6) that while an acceleration of 7.8 m s^{-2} with no background noise elicited a very prominent response ($35.6 \pm 32 \mu\text{V}$), the same acceleration in the presence of the masking noise evoked a significantly weaker response ($21.6 \pm 25.8 \mu\text{V}$; $P < 0.05$; paired *t*-test). Moreover, while weaker accelerations (1.3 and 0.9 m s^{-2}) with no masking noise still elicited remarkable responses ($6.9 \pm 5.4 \mu\text{V}$ and $5.8 \pm 5.0 \mu\text{V}$, respectively), these accelerations in the presence of the masking noise did not evoke essentially any response.

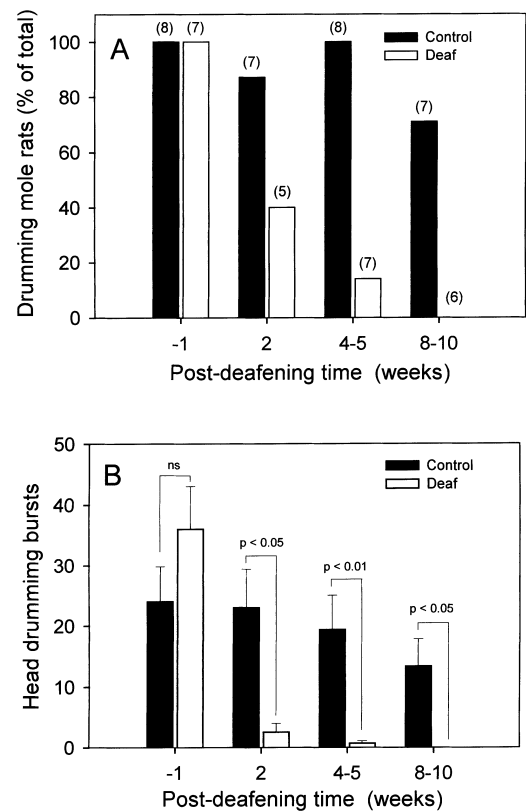


Fig. 5A, B Effect of bilateral deafening of the mole-rat on head-drumming behavior when confronted with an intact animal. The test animal (*deaf* or *control*) and a naive one were introduced into a Plexiglas tube with a barrier of crossed spokes at the midpoint, separating between the two. Effect on the number of drumming animals **A** and on the number of head-drumming bursts produced by the deaf animal **B** as a function of time after deafening. Number of bursts were counted within the first 5 min after introducing the two animals into the tube. Values represent means \pm SE. *Figures above bars* in **A** represent number of tested animals for **A** and **B**. Note that while there was only a moderate decrease with time in the number of bursts produced by the control animals, this behavior dropped significantly in the deaf animals (one sided *t*-test)

Effect of vibratory rate

Typically, an individual mole-rat dialoguing with another specimen produces several sequential series of head-drumming bursts. The mean (\pm SD) number of bursts in each series is 8.6 ± 8.2 ; each burst lasts $0.31 \pm 0.06 \text{ ms}$ and consists of 4.1 ± 0.9 head drums (Heth et al. 1987, 1991; Rado et al. 1987). The time interval between consecutive bursts, within a single series, ranges between 0.4 and 2.0 s (R. Rado et al., unpublished observations). This rate is very high considering the fact that in animal models, the amplitude of auditory MLR, evoked by a click, is markedly reduced at click rates faster than 1 s (e.g. Buchwald et al. 1981). Thus, we checked the recovery cycle of the MLR by using repetitive vibrations and airborne clicks at different rates. Accelerations (7.8 m s^{-2}) and sound pressure levels of the airborne clicks (peak: 120 dB SPL) were kept constant. In four animals that were held in the tube

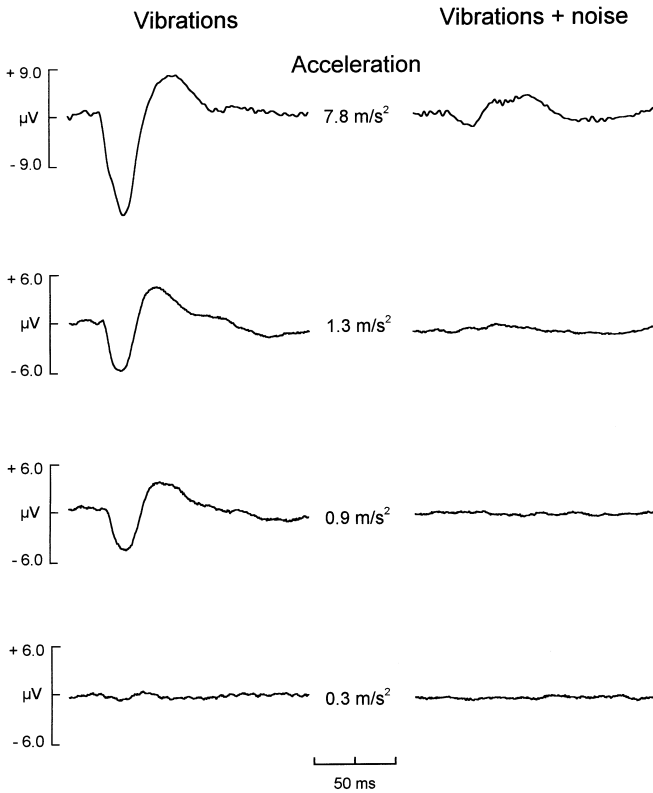
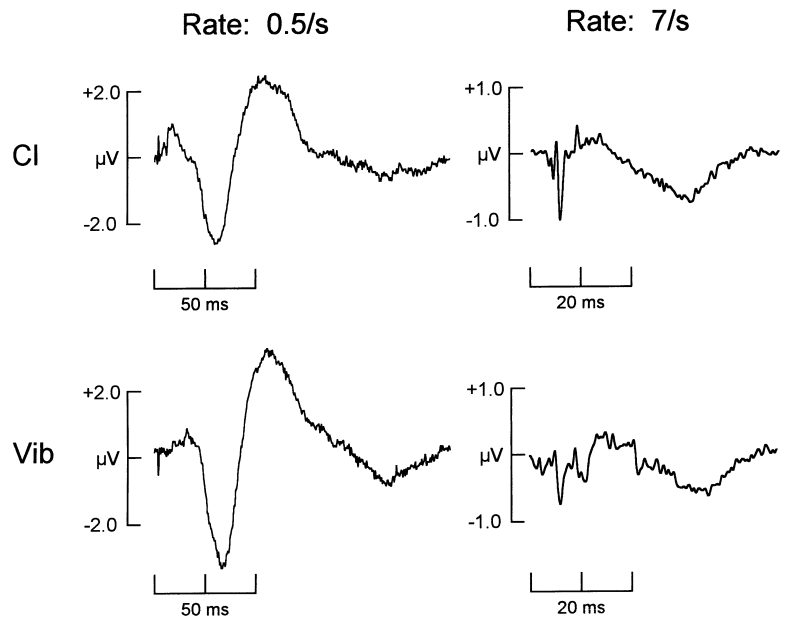


Fig. 6 An illustration of the effect of vibrations at different accelerations on the MLR with and without concurrent exposure to high-intensity masking noise. Note that in the absence of masking noise an acceleration as low as 0.3 m s^{-2} was still effective in eliciting a small response, while in its presence only residual responses were detected and only at the relatively high accelerations. All the measurements were taken with the animal's lower jaw pressed firmly against the vibrating substrate

with their lower jaw in contact with the Plexiglas floor, responses to both vibrations and airborne clicks were

Fig. 7 Effect of stimulation rate on the MLR. *Upper row (Cl)*: responses to high-intensity airborne clicks. *Lower row (Vib)* responses to vibrations. The animal's lower jaw in this experiment was lying on the vibrating substrate. Note that at a rate of 0.5 stimuli/s both the clicks and the vibrations elicit marked responses while at a rate of 7 stimuli/s there is a clear ABER but only a residual MLR. Note also that at the lower rate the responses evoked by the clicks and by the vibrations are essentially the same



tested at two different rates: 0.5 and 7 stimuli/s. The results (Fig. 7) show that at a rate of 0.5 stimuli/s both airborne clicks and vibrations elicited remarkable responses ($3.9 \pm 0.3 \text{ } \mu\text{V}$ and $4.9 \pm 0.8 \text{ } \mu\text{V}$, respectively; $n = 4$) while at a rate of 7 stimuli/s the amplitude of the main MLR component was selectively eliminated, leaving an ABER and a relatively small MLR with a latency markedly shorter than that of the main MLR component. In fact, in one animal tested with three different rates, 0.5, 1.8 and 4 vibrations/s, there was a marked attenuation of the response already at a rate of 1.8 vibrations/s and at a rate of 4 vibrations/s no visible response was apparent.

The fact that the main component of the MLR could not follow vibration rates higher than 2/s raised the question of how mole-rats perceive the natural bursts of vibrations that they use for communication. To resolve this problem we recorded averaged MLRs in mole-rats exposed to sequential bursts of vibrations, each consisting of 4 or 10 vibrations at a rate of about 7 vibrations/s with 2-s interbursts intervals. As seen in Fig. 8, a maximum response was evoked only by the first vibration in each burst. The amplitudes of all other successive responses decreased abruptly. This phenomenon was more pronounced when each burst consisted of 10 vibrations.

The solution to the apparent problem is thus simple. Averaging many successive trials, at a relatively high rate, also eliminated almost completely the responses that were evoked by the first few stimuli. This phenomenon was avoided in the second experimental paradigm in which the time interval between successive bursts was long enough, as in nature. The amplitudes of residual MLRs that remained under the first experimental paradigm were negligible as compared to the amplitudes of the components that were eliminated. These relatively small responses may indeed be somato-

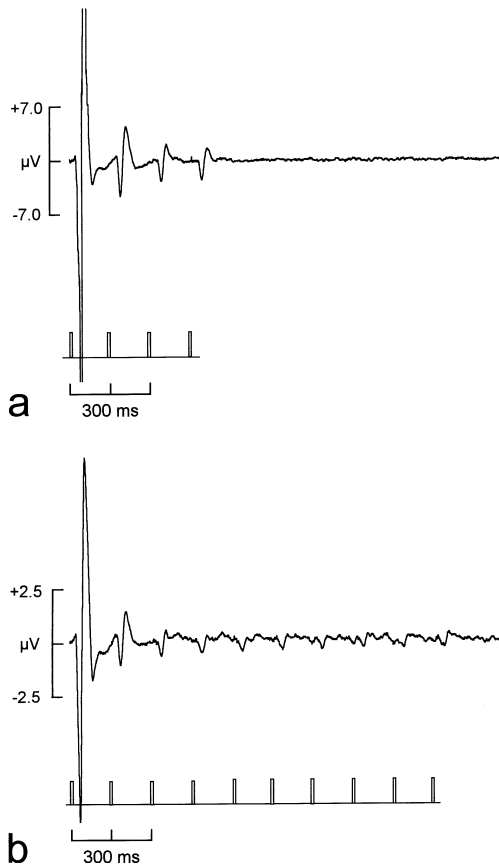


Fig. 8a, b Averaged MLRs evoked by sequential bursts of vibrations, each consisting of 4 **a** and 10 **b** consecutive vibrations at a rate of 7 vibrations/s. Interburst interval in both cases was 2 s. Note that a maximum response was elicited only by the first vibration in each burst. The amplitudes of all other successive responses declined quite abruptly. This phenomenon was more prominent in the longer burst case

sensory components that are embedded in the overall response.

Discussion

The isolation imposed on the blind mole-rat by the subterranean environment exerted on this rodent an evolutionary pressure that yielded two parallel communication systems: one, based on airborne vocalizations (Capranica et al. 1974; Heth et al. 1986, 1988; Nevo et al. 1987); and the other, on bursts of substrate-borne (seismic) vibrations (Heth et al. 1987; Rado et al. 1987). Due to their physical properties, seismic signals are very suitable as means for long-distance communication between solitary subterranean animals inhabiting separate tunnel systems. It is possible that such signals exchanged between isolated individuals may convey information regarding territorial boundaries, sexual attraction and individual recognition. Indeed, seismic vibration as a means for intraspecific communication is not unique to the blind mole-rat. It is evident that at least one other

subterranean mole-rat, the Cape mole-rat (*Georychus capensis*), uses vibrations produced by drumming the hind legs on the burrow floor for that purpose (Narins et al. 1992). Indications for a possible use of seismic communication have also been described for other rodents (e.g., Bennett and Jarvis 1988; Bridelance and Paillette 1985; Jarvis and Bennett 1991; Kenagy 1976; Narins et al. 1992; Randall 1984, 1993, 1994).

Based on morphological features and behavioral observations we suggest that the substrate-borne vibrations used by the blind mole-rat are picked up directly from the tunnel by the lower jaw and transmitted, by means of bone conduction, to the auditory system for further processing. A special incudo-periotic joint, an extension of the glenoid fossa underneath the bulla tympanum and a unique articulation between the lower jaw and the skull (Rado et al. 1989) creates a solid continuity between the lower jaw and the ossicles of the middle ear whenever the jaw is not active in mastication (Topachevski 1976). Such physical contact occurs, for instance, during the pressing of the lower jaw against the tunnel wall. As a result, whenever the lower jaw vibrates, under such conditions, the vibrations are transmitted directly to the incus, stapes and oval window, skipping over the eardrum and the malleus. This 'jaw hearing apparatus' enables transmission of the seismic signals to the cochlea with minimal loss of energy, thereby compensating for the low efficiency of the middle ear in transferring airborne sounds to the inner ear (Rado et al. 1989). The poor sensitivity of the blind mole-rat to airborne sounds, which is also reflected behaviorally (Bronchti et al. 1989; Heffner and Heffner 1992), is therefore not a real limitation on establishing long-distance communication between individuals inhabiting separate and relatively remote tunnel systems (Heth et al. 1987; Rado et al. 1987). Since airborne sounds are effective only for relatively short distances, they are typically used by the blind mole-rat for communication between individuals temporarily in the same tunnel (Heth et al. 1986, 1988; Nevo et al. 1986, 1987), e.g., between adults incidentally encountering each other, between females and males during the mating season and between mother and pups. Thus, in this respect too the relatively high threshold to airborne sounds is not a major limitation, especially if the stethoscopic effect within the tunnel system is also taken into account.

Hypothetically, the vibratory seismic signals can be perceived and processed by either the somatosensory or auditory system or by both. In our first series of experiments (Fig. 1) we proved that the prominent MLRs evoked by the vibrations were mediated mainly by the lower jaw. However, we could not distinguish precisely which of these two sensory systems, the auditory or somatosensory, picks up and processes these signals. The high resemblance in latency, shape and duration of the responses evoked by the vibratory stimuli and by the high-intensity airborne clicks; the similar ABER evoked by the two kinds of stimuli; the precise position and firm physical contact between the lower jaw and the vibrating

substrate essential to evoke an optimal response; and the almost complete elimination of the MLR by masking noise or by deafening the animal – all provided firm evidence supporting the primary role of the auditory system in the processing of the vibratory signals. The behavioral experiments provided further support for this possibility.

Processing of seismic signals by the auditory system is not without antecedents. The use of such signals for intraspecific communication has also been demonstrated in other vertebrates (Brill et al. 1988; McCormick et al. 1970; Narins and Lewis 1984; Narins 1990). Thus, it is not unexpected that in the blind mole-rat processing of the seismic signals is also accomplished by the auditory system. It is also pertinent to mention that the temporal pattern of airborne sounds used by many vertebrates for intraspecific communication, greatly resembles that of the bursts of seismic signals produced by the mole-rat.

Head drumming as a means of producing communicative signals and pressing the lower jaw against the tunnel wall for receiving or “listening” apparently represent innate behavior in the blind mole-rat. Indeed, even isolated mole-rats occasionally perform spontaneous head drumming and quite frequent “jaw listening”, apparently to explore the environment and maintain communication with their conspecifics (Zuri and Terkel 1996). Thus, it is not too surprising that deaf animals still show intensive ‘jaw listening’ and ‘head-drumming’ behavior after their deafening, although with time this behavior declines. Head drumming drops essentially to zero after about 2 months, whereas ‘jaw listening’ is reduced significantly after three months, most likely reflecting the animal’s “frustration” at its inability to perceive the vibrations (this issue will be dealt with in more detail in a separate article).

Based on some electrophysiological experiments, similar in some respect to ours, Nevo et al. (1991) suggested that the seismic signals that the blind mole-rat uses for intraspecific communication are perceived and processed by the somatosensory system rather than by the auditory system. These authors claimed that: 1) by tapping on the roof of a Perspex tunnel in which an anesthetized mole-rat was housed they evoked a mid latency response which was not eliminated by high-intensity white-noise masking; 2) by tapping on an identical Perspex tunnel placed on a separate table from the one housing the mole-rat (in order to avoid vibrations), they evoked, in some individuals, low-amplitude auditory components that were eliminated by the same masking noise; 3) deafening mole-rats did not eliminate the response induced by such tapping and that 3 weeks post-deafening these animals responded, by head-drumming to finger tapping of the experimenter. This last finding is only briefly described with no documented illustration, followed by a comment that a detailed report will be published elsewhere. Unfortunately, to date we have not been able to trace such a report. A close look at the methodology and data raised some

concern regarding the interpretation of the results. From the illustrations and data provided it is evident that the latency of the response that they recorded (either to its onset or to its peak) was about 30–40% shorter than the latency of the MLR we recorded; its duration was, at best, eight times shorter and its highest amplitude was much smaller. This is also manifested by the signal to background activity ratio which was much better in our recordings than in theirs in spite of the fact that we averaged at the most 512 (usually only 256) sweeps, whereas they averaged 1024 sweeps. Curiously, judging by their illustrations, there was no evidence for an ABER as a result of tapping on the same tunnel where the mole-rat was housed. Yet, the same tapping while exposing the animal to a high-intensity white-noise masking did evoke a complex waveform that appeared as an ABER.

It is very hard to evaluate from their illustrations the properties of the low-amplitude auditory response that they observed in some individuals. Indeed, due to the low sensitivity of the mole-rat to airborne sounds (Bronchti et al. 1989; Bruns et al. 1988; Burda et al. 1989, 1990; Heffner and Heffner 1992) we were also unable to evoke a noticeable response under similar conditions. However, as we have shown, by increasing the intensity of this stimulus we evoked a prominent response, similar in shape, latency and duration to the one evoked by the vibratory stimulus.

How can this discrepancy in the main response be reconciled in spite of the similarity in the methodology? In our study we demonstrate a significant dependence between the rate of vibratory stimuli and response amplitude, due to habituation and the averaging procedure, up to a complete abolishment of response at rates higher than 2 vibrations/s. Unfortunately, in their article, Nevo et al. (1991) did not mention the rate at which their stimuli were presented and this issue was not raised at all. If they used higher rates than 2 stimuli/s, as we suspect, they may have greatly attenuated or completely abolished the auditory response. This possibility is supported by the fact that in our experiments residual MLRs were observed even when stimulating rates were higher than 2/s. Low-amplitude responses to vibrations also remained in the deafened animals. In both cases these were negligible as compared with the response components that disappeared as a result of the high rate of stimulation or of the deafening. These residual responses may indeed be somatosensory components that are embedded in the overall response but are obscured by the much higher amplitude auditory components. When the latter are abolished they then become discernible.

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