

# Evidence for the use of reflected self-generated seismic waves for spatial orientation in a blind subterranean mammal

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## Summary

Subterranean mammals like the blind mole-rat (Rodentia: *Spalax ehrenbergi*) are functionally blind and possess poor auditory sensitivity, limited to low-frequency sounds. Nevertheless, the mole-rat demonstrates extremely efficient ability to orient spatially. A previous field study has revealed that the mole-rat can assess the location, size and density of an underground obstacle, and accordingly excavates the most efficient bypass tunnel to detour around the obstacles. In the present study we used a multidisciplinary approach to examine the possibility that the mole-rat estimates the location and physical properties of underground obstacles using reflected self-generated seismic waves (seismic ‘echolocation’).

Our field observations revealed that all the monitored mole-rats produced low-frequency seismic waves (250–300 Hz) at intervals of  $8 \pm 5$  s (range: 1–13 s) between head drums while digging a bypass to detour an obstacle. Using a computerized simulation model we demonstrated that it is possible for the mole-rat to determine its distance from an obstacle boundary (open ditch or stone) by evaluating the amplitude (intensity) of the seismic wave reflected back to it from the obstacle interface. By evaluating the polarity of the reflected wave the mole-rat could distinguish between air space and solid obstacles.

Further, the model showed that the diffracted waves from the obstacle’s corners could give the mole-rat precise information on the obstacle size and its relative spatial position.

In a behavioural experiment using a special T-maze set-up, we tested whether the mole-rat can perceive seismic waves through the somatosensory system and localize the source. The results revealed that the mole-rat is able to detect low frequency seismic waves using only its paws, and in most cases the mole-rats determined accurately the direction of the vibratory source. In a histological examination of the glabrous skin of the mole-rat’s paws we identified lamellate corpuscle mechanoreceptors that might be used to detect low frequency seismic waves.

The combined findings from these different approaches lead us to suggest that a specialized seismic ‘echolocation’ system could be used by subterranean mammals to determine the most energy-conserving strategy with which to bypass an obstacle, as well as to estimate their distance from the surface, keeping their tunnels at the optimal depth.

Key words: spatial orientation, obstacle, echolocation, seismic signal, *Spalax ehrenbergi*, mole-rat, subterranean mammal.

## Introduction

The blind mole-rat is a solitary subterranean rodent that digs and inhabits its own branching tunnel system, which it does not leave unless forced to (e.g. if water floods its tunnels). In nature the mole-rat encounters different types of obstacles that block and disconnect sections of its tunnel. In a recent field study using various open ditches and wood or stone obstacles we found that mole-rats are able to detect the presence of obstacles blocking their tunnel path and burrow a highly efficient detour to accurately rejoin the two disconnected parts of the tunnel. The mole-rats used two different bypass strategies, depending on the size of the ditch encountered: a bypass *around* short ditches, or a bypass *under* long (over 300 cm length) ditches (Kimchi and Terkel, 2003a). The

physical properties of the encountered obstacles affected the burrowing distance from the obstacle edge: (a) for open ditches, a side bypass 10–20 cm from the obstacle boundaries; or (b) for wood or stone obstacles, a side bypass 3–8 cm from the obstacle boundaries. When the obstacle was placed asymmetrically across the tunnel, the mole-rats always burrowed their bypass around the shorter side, while they showed no preference for a particular side in symmetrically placed ditches (Kimchi and Terkel, 2003b). These findings demonstrated the mole-rat’s ability to estimate the size and shape of the obstacle, its own exact position relative to the obstacle boundaries and even the obstacle’s density, through the soil medium.

How can one explain this remarkable spatial orientation ability? Whenever possible, surface-dwelling mammals use vision to localize and assess obstacles in their path (Schone, 1984). Under dark conditions, when obstacles cannot be detected visually, animals shift to an alternative, light-independent mechanism such as touch (using the somatosensory system), if the obstacle is in close contact with their body (Carvell and Simons, 1990). In order to localize and assess more distant obstacles in the dark, a specialized mechanism of orientation known as echolocation has been shown to be used by a limited group of mammals (e.g. bats, Schnitzler et al., 2003; whales and dolphins, Purves and Pilleri, 1983). These animals emit ultrasonic (high frequency) sounds to locate and estimate the size, distance and type of object ahead by detecting the reflected sound waves from the object's interface (see Busnel and Fish, 1980; Griffin, 1974; Nachtigall and Moore, 1988). However, none of the above-mentioned mechanisms of orientation explain how a blind mammal such as the mole-rat, with a hearing range limited to low frequency sounds (Heffner and Heffner, 1992), detects and assesses distant buried obstacles, and also accurately estimates and maintains its own optimum digging depth.

The mole-rat is adapted behaviourally, anatomically and physiologically to transmitting and perceiving low frequency seismic signals (Rado et al., 1987, 1998; Heth et al., 1987, 1991). From a geophysical perspective, soil in general is a good conductor for such low frequency seismic waves and for propagating them for a long distance with relatively little attenuation (depending on the physical properties of the soil; Liu et al., 1979; Steeples et al., 1997; Bachrach et al., 1998; Bachrach and Nur, 1998).

Insects, frogs, snakes and lizards, and even some species of mammals, use seismic signals for communication, food detection and to avoid hazards (reviewed in Narins, 2001; Mason and Narins, 2001; Hill, 2001; Randall, 2001). Previous studies have shown that the mole-rat produces vibrational signals for long-distance communication by rapidly striking the flattened anterodorsal surface of its head against the tunnel roof. It was also shown that the mole-rat can perceive and respond both behaviourally and neurologically to neighbouring mole-rats' 'head drumming' (Heth et al., 1987, 1991; Rado et al., 1987, 1998).

Consequently, we hypothesized that one of the mechanisms employed by the mole-rat to orient in its underground habitat might be the use of low frequency seismic waves reflected back to it, in a type of echolocation system. We applied a multidisciplinary approach to test whether such a mechanism could be used by the mole-rat to assess the relative distance, dimensions and density of underground obstacles. In a field study we examined whether the mole-rat indeed generates seismic waves while burrowing a bypass tunnel to detour an obstacle. We then used a computer simulation to determine the physical characteristics of seismic waves reflected by subterranean obstacles in order to determine the feasibility of their perception by the mole-rat. Finally, we used both behavioural tests and histology to determine whether the mole-

rat can perceive seismic waves through its feet using the somatosensory system.

## Materials and methods

### *Field study: the characteristics of seismic waves generated during construction of a bypass tunnel*

#### *Study site*

The field study took place in an uncultivated field with dominant vegetation of grasses and geophytes around Tel-Aviv. The field was populated by blind mole-rats (*Spalax ehrenbergi* L.) belonging to the chromosomal species  $2n=58$  (Nevo, 1991). The study was carried out during the wet season (October to April) in 2001 and 2002.

#### *Procedure*

Two conditions were examined. In the first condition, in seven separate mole-rat territories (at least 50 m apart), identified above ground through the mounds of excavated soil forming a straight line, we dug a small rectangular ditch (50 cm×60 cm) across a tunnel, bisecting it into two disconnected parts, as previously described (Kimchi and Terkel 2003a,b). For each ditch, six vertical geophones (Geo space GSC-20D, Houston, TX, USA; vibration detection above 20 Hz) were inserted in the ground at 30–40 cm intervals, at a distance of 15–20 cm from the boundaries of the ditch (Fig. 1A), and connected to a multi-channel tape-recorder (6 channels analog tape, TASCAM, Montebello, CA, USA) (Fig. 1A). Using this geophone array we recorded the seismic waves generated by each mole-rat in its respective territory throughout the entire process of burrowing the bypass tunnel to detour the obstacle and reconnect the two disconnected tunnel parts.

In the second condition, in five separate mole-rat territories with no obstacle obstructing the mole-rat's path, using the same equipment as for the first condition, we recorded the seismic waves that the animal generated while digging a tunnel of about 200 cm length (estimated by observing the above-ground mounds of earth excavated by the mole-rat).

The seismic waves recorded in the field were transferred to a computer, viewed with Sound Forge software (Sonic Foundry, Inc., Madison, WI, USA), and analyzed by standard seismic data processing software (ProMAX, Englewood, CO, USA).

#### *Computer seismic simulator modeling: general considerations*

The computer simulations were used to determine the physical characteristics of seismic waves being reflected by different types of underground obstacles in order to determine the feasibility that those reflected waves can be used by the mole rat to assess the location, size and density of the obstacle.

Our simulated model was carried out under the assumption that the seismic energy travels as acoustic waves (P waves) in the subsurface, where the mole-rat dwells (Zuri and Terkel, 1996; Heth, 1989). In all simulations, the mole-rat was replaced by a basic seismic recording system in which the

source and the receiver were located in the same spatial position.

In a purely acoustic medium, where both source and receiver are located in the same place, the shape and strength of the reflected signal are governed by two variables: distance from the source to reflecting object; and the reflection coefficient at the reflection point. The acoustic reflection coefficient ( $C$ ) at the boundary separating two materials (1 and 2) is defined by:

$$C = \frac{V_2\rho_2 - V_1\rho_1}{V_2\rho_2 + V_1\rho_1}, \quad (1)$$

where  $V$  is the acoustic velocity (P-wave velocity) and  $\rho$  is the density of the material. The material characteristic  $V\rho$  is known as the acoustic impedance (Sheriff, 2002). In the case where the second material is air, for which the density is practically zero, the reflection coefficient is equal to  $-1$ .

The wavelength  $\lambda$  is determined by:

$$\lambda = \frac{V}{f}, \quad (2)$$

where  $V$  is the velocity and  $f$  is the dominant frequency.

To simulate the seismic source generated by the mole-rat's head drumming, using seismic data-processing software we built a synthetic zero-phase wavelet pulse with a dominant frequency of 300 Hz that matched the amplitude spectrum of a typical seismic wave generated by a mole-rat detouring an obstacle (see Fig. 1B,C; recorded head-drum *vs* synthesized pulse). To simulate the mole-rat's underground habitat (non-packed soil; density of about  $1.1 \text{ g cm}^{-3}$ ) we used a velocity of  $85 \text{ m s}^{-1}$  (based on the field records of Rado, 1993) and a velocity of  $330 \text{ m s}^{-1}$  with zero density for air space. The software used for the computer simulation was a standard finite-difference modeling of the acoustic wave equation (Kelly et al., 1976). This software allows for a variety of source functions, generation of synthetic seismograms and snapshots of wave propagation at specified times.

#### Laboratory studies: perception of seismic waves

For intraspecific long-distance communication it has been demonstrated that the mole-rat is able to perceive low frequency seismic signals *via* bone conduction, by pressing its lower jaw against the tunnel wall (Rado et al., 1989, 1998).

In spatial orientation based on an echolocation mechanism, in contrast to intraspecific communication, the transmitter and receiver source are the same individual. As such, a mole-rat which produces seismic waves by head-drumming on the tunnel roof, is unlikely could change its head position and press its lower jaw against the tunnel wall within less than the 10 ms required to perceive the reflected signal from close by obstacles (about 50 cm away). This led us to hypothesize that for spatial orientation the mole-rat might perceive the seismic waves through those other body parts that are always tightly pressing the tunnel floor, such as its paws.

The aim of the following experiment was to test whether the mole-rat can both perceive and locate the source of seismic

waves (similar to those generated by the mole-rat in nature) only through its paws.

#### (a) Behavioural experiment

##### Animals

Adult mole-rats of both sexes were trapped in the Tel Aviv area and maintained in individual plastic cages ( $33 \text{ cm} \times 38 \text{ cm} \times 14 \text{ cm}$ ) with wood shavings for bedding, at Tel Aviv University, for 1–2 months before the beginning of the experiment. The animals were kept under a constant light regime (14 h:10 h L:D) and room temperature ( $24\text{--}26^\circ\text{C}$ ), and received rodent chow, carrots and apples *ad libitum*, from which they obtained sufficient water.

##### Apparatus

The set-up described below was specially designed to ensure that the seismic signals would be transferred only to the mole-rats' paws, *via* the maze floor, and could not be perceived through the animal's lower jaw, which has been previously found to be used for long-distance intraspecific communication (referred to as 'jaw-listening'; Rado et al., 1989, 1998).

##### Set-up

The experimental set-up was as follows (see Fig. 2A,B): a wooden board ( $140 \text{ cm} \times 80 \text{ cm} \times 2 \text{ cm}$ ) was placed on a layer of sponge (4 cm thick) on a table in the centre of the room. Two transparent Perspex tubes (6 cm in diameter) were joined to form a T-maze comprising a 60 cm long entrance tube (with two movable doors, one near the entrance and the second half way along) intersecting another perpendicular tube (50 cm) in the middle. A 3.5 cm width slit was cut out along the entire length of both tubes. The entire T-maze was then suspended 1 cm above the wooden board with the slit facing downwards (Fig. 2B). It was supported by three clip clamps connected by arms to two peripheral tables placed about 30 cm from the wooden board (Fig. 2A). This design enabled the experimental animals to locomote in the suspended tubes with only their feet protruding from the slit and in contact with the board surface (Fig. 2B). There was no contact between the tubes and the wooden floor, and any vibratory signals produced on the board could thus be perceived only through the animal's paws.

##### Vibratory source

Two sources of vibratory signals were used.

(1) Head-drumming by a stimulus mole-rat. The stimulus mole-rat was placed in one of two additional and identical Perspex tubes, either to the left or to the right of the experimental animal. Each tube (6 cm in diameter, 30 cm long) was sealed at one end and fitted with a movable door at the other end to ensure that the stimulus mole-rat could not exit from the tube. The two tubes were tightly attached one on each side of the wooden board, with their sealed ends each facing the opening of one end of the perpendicular tube at a distance of 15 cm from it. The seismic signals generated by the stimulus mole-rat when it head-drummed against the upper part of the

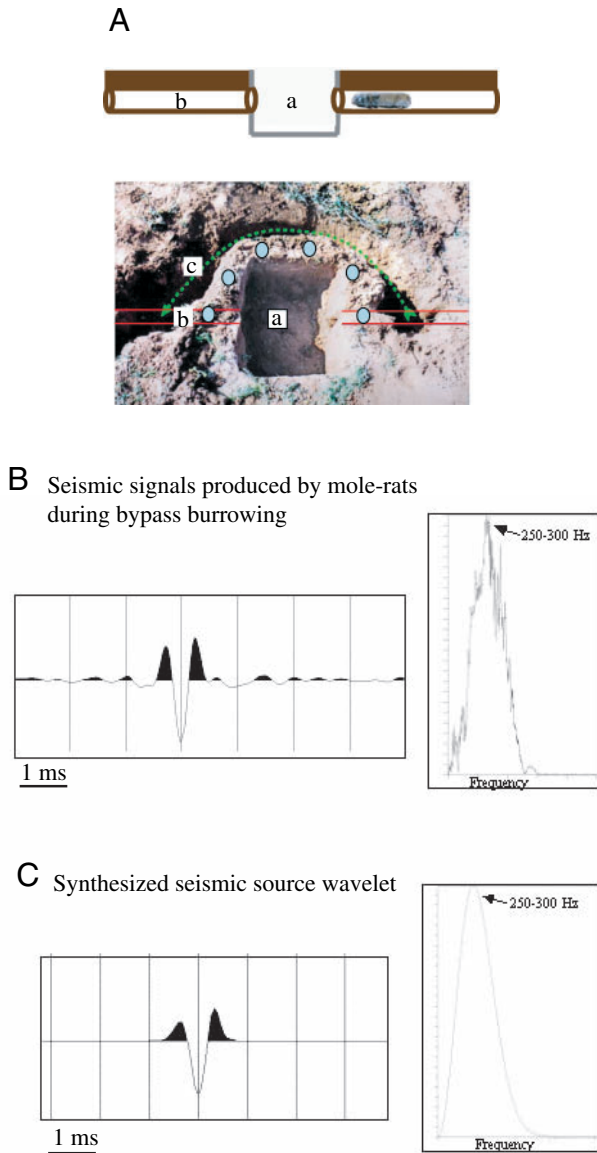


Fig. 1. (A) Schematic side view drawing of the obstacle (ditch) created across the mole-rat tunnel (upper part), and an overhead photo of a bypass burrowed by a mole-rat around a ditch (lower part). The location of the recording geophones used to record the seismic waves produced by the mole-rat while it dug the bypass tunnel are marked schematically (filled circles): a, small ditch; b, location of the original tunnel; c, bypass tunnel around the ditch. (B) Typical seismic signal and amplitude spectrum generated by the mole-rat during bypass burrowing recorded by the geophones in the field. (C) Synthesized wavelet pulse that matched the amplitude spectrum of a typical mole-rat's seismic signal recorded in the field, used in the computer simulations.

tube rat were transmitted along the wooden board and reached the experimental mole-rat's paws (Fig. 2B).

(2) Mechanical vibration (mini-shaker). The second source of vibrations was transmitted to the wooden board using a mini-shaker (Bruel and Kjaer model 4810, Naerum, Denmark) placed at a distance of 15 cm from one of the two perpendicular tube's openings (as in the mole-rat stimulus). The shaker was

connected to a pulse generator (Wavetek LTD, San Diego, CA, USA) and a power amplifier that controlled the spectral characteristics of the produced vibrations. The shaker was set to produce a series of three seismic waves at 1–2 s intervals each, consisting of a single tap whose spectral characteristics (intensity and frequency) were similar to typical seismic waves generated by mole-rats while head-drumming.

To monitor and adjust the mechanical shaker so that the characteristics of the vibratory signals generated would resemble those produced by a mole-rat, we attached one geophone firmly to the wooden board and another one to the maze tubes. The vibrations detected by the geophones were recorded and viewed using Sound Forge software. Spectral analysis was used to ensure that the frequency content and phase of the mechanical signal were similar to those generated by the mole-rat in the field, and that indeed no vibrations produced by the vibratory source (on the wooden floor) were transmitted to the maze tubes.

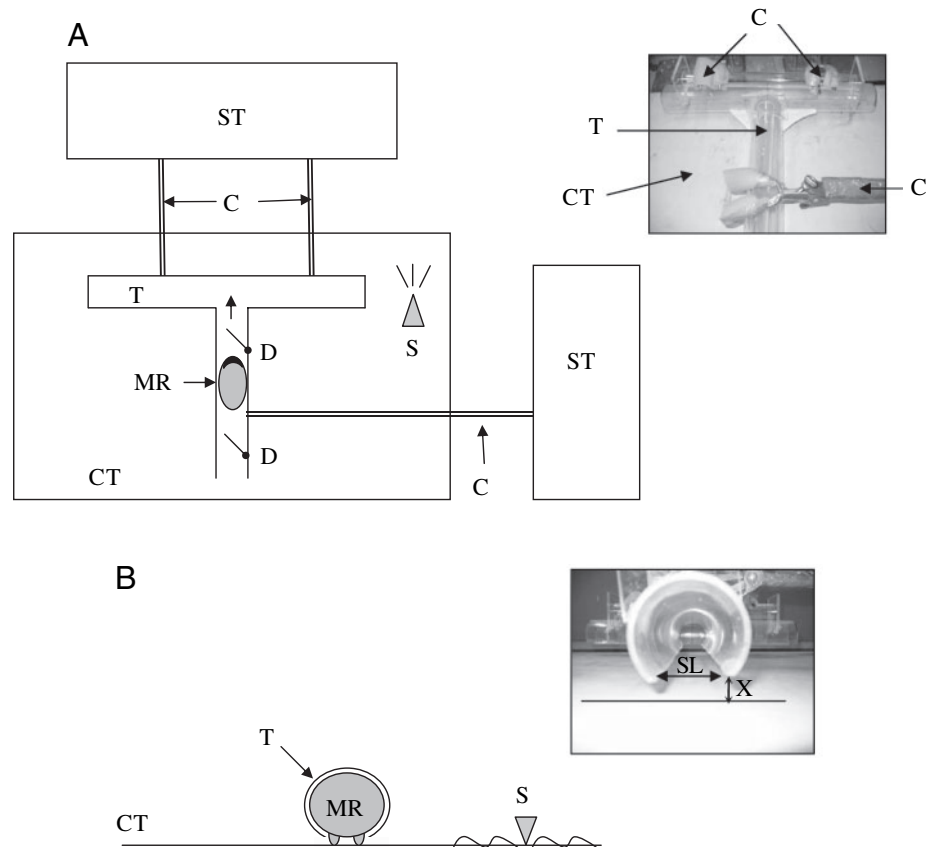
#### Procedure

*Pre-testing (acclimation).* In order to acclimatize the animals ( $N=14$ ) to the apparatus, they were allowed to move freely in the maze for 4 days, 15 min a day each. For three additional days (10 trials a day) the animals were trained to move from the maze arm entrance to the T-junction, passing the two doors that were opened by the researcher. At the T-junction each animal was given the choice to turn either right or left, into one of the two maze arms. To increase the animals' motivation to explore the apparatus, we placed a food reward (small piece of apple) at the far end of both maze arms. Animals that reached the far end of the maze arm received the food reward. After consuming the reward the animal was removed from the maze tube and returned to its nest box, using a Perspex transfer tube.

*Experimental tests.* Mole-rats are solitary and highly aggressive territorial animals. Two mole-rats being introduced into the same tube quickly move toward each other and generate frequent head-drumming against the tunnel roof, which elicits extreme mutual aggression (Shanas and Terkel, 1997; Rado et al., 1987). This natural spontaneous aggressive behaviour was exploited in the design of the present experiment. We tested the mole-rats' ability to locate the direction of the seismic (vibratory) source and to turn in that direction. The 14 trained animals were divided randomly into two equal groups. One group was exposed to seismic stimuli produced by a stimulus mole-rat, and the second group to those produced by a mechanical mini-shaker.

(1) Mole-rat stimulus. First, the experimental mole-rat was transferred from its nest box into the entrance tube using a connecting tube. The first door was then closed behind the mole-rat and the nest box was removed. The mole-rat now faced the T-junction with the doors in front and behind it closed. At this stage the stimulus mole-rat was inserted using a connecting tube into one of the two Perspex tubes (either right or left) attached to the wooden board. Within a few seconds the stimulus animal started to head-drum, generating

Fig. 2. Schematic drawings and photos (insets) of the set-up used to test whether the mole-rat can perceive and localize seismic waves only through the paws. (A) Top view: ST, supporting table anchoring the suspended maze; T, suspended T-maze; CT, central table; D, doors controlling access to the entrance maze tube; C, clamp arms suspending T maze 1 cm above the central table; S, vibratory stimulus (mechanical shaker or stimulus mole-rat) source producing seismic waves on the central table; MR, mole-rat. (B) Back view of the entrance tube: SL, slit (3.5 cm width) in maze tube, enabling the experimental animal to move in the tubes with only its feet in contact with the board surface; X, gap of 1 cm between the suspended maze tube and the board surface; other letters are as in A.



intense seismic waves that were transferred to the wooden board. If such behavior did not occur spontaneously we triggered the stimulus animal to start drumming by gently touching its fur with a small brush. After a few seconds of head-drumming we opened the door adjoining the T-junction, allowing the experimental animal to freely select right or left turn.

The animals were tested individually for two days, 20 trials per day. For each trial the laterality of the vibratory source was selected using a random table.

(2) Mechanical shaker stimulus. The experimental mole-rats in this group were tested individually for their ability to identify the direction of the seismic stimulus produced by the mechanical shaker. The test procedure was the same as in the previous (mole-rat stimulus) group.

#### Control tests

In order to verify that the mole-rats were relying on seismic waves and not on airborne sound or olfactory cues to determine the position of the vibratory source, we performed the following control test using the same animals and procedure of the experimental tests but with the vibratory source (the stimulus mole-rat or the mechanical shaker) positioned on a narrow wooden board to the right or left of the perpendicular tube ends, at a distance of 10 cm from the edges of the central table. In this way airborne sound waves and possibly olfactory cues could pass to the experimental mole-rats, but seismic waves could not.

#### Data recording and analysis

The performances of the two groups of animals (one exposed to vibratory stimuli produced by a stimulus mole-rat and the second to a mechanical mini-shaker) were recorded in the same way. We recorded the directional choice as correct when the

mole-rat turned into the maze arm leading to the vibratory source, from a total of 20 trials a day, on the two test days.

We initially used Wilcoxon matched pairs tests for each of the animal groups separately, in order to compare between the mole-rats' performances on days 1 and 2. Since we found no significant difference between the performances over the two days we pooled the data for each group. We then used the pooled data to compare between the performances of the two separate animal groups using Mann-Whitney *U*-test. Further, for each of the two groups we used Wilcoxon matched pairs test to compare between the animals' performance in the experimental *vs* control; and between the experimental *vs* random directional choice (50%). A Bonferroni correction was applied to set alpha level to 0.025 due to the multiple comparisons.

#### (b) Histological examination

##### Animals

Two adult mole-rats and two adult Levant voles (*Microtus guentheri* L.), all trapped in the Tel Aviv area, were used. We chose the vole to serve as a comparison to the mole-rat for the following reasons: (1) it is a rodent systematically close to the mole-rat; (2) it inhabits niches similar to those inhabited by the mole-rat; (3) it spends a substantial amount of time in an underground tunnel system; and (4) as far as we know, there has not been a single report that this species, in contrast to the mole-rat, produces and/or uses seismic vibrations for communication, spatial orientation or any other task.

### Procedure

All animals were sacrificed with an overdose (80 mg/100 g) of a combination of Ketamine (Ketalar; Parke-Davis, Ann Arbor, MI, USA) and Xylazine (Rompun; Bayer, Leverkusen, Germany). The toes and toe-pads from both forefeet and hindfeet were removed, kept in 10% formaldehyde solution for 3 days, decalcified with EDTA, dehydrated, embedded in paraffin and sectioned at 5–7  $\mu\text{m}$  either perpendicular or parallel to the skin surface. The serial sections were mounted on gelatin-coated microscope slides and stained with Hemotoxylin and Eosin. The slides were examined using a light microscope for the presence and number of rapidly adapting mechanoreceptors (e.g. Pacinian corpuscles receptors) in each foot.

### Results

#### Field experiment: the characteristics of seismic waves generated by the mole-rat during construction of a tunnel bypass

Seismic waves produced by the animals were monitored throughout the entire process of digging the bypass (mean

length of dug bypass:  $182 \pm 10$  cm), which lasted on average  $230 \pm 25$  min (mean  $\pm$  S.E.M.).

Clear seismic waves were recorded from all seven monitored mole-rats throughout the process of burrowing a tunnel to bypass an obstacle. The seismic waves consisted of a sharp single head drum with frequency band between 250–300 Hz (Fig. 1B), with maximum energy concentrated around 300 Hz. The mean ( $\pm$  S.E.M.) amplitude of the waves was  $49.5 \pm 12.0$  dB (range: 36–70 dB). The mole-rats generated on average  $198 \pm 15$  seismic waves per meter of bypass tunnel burrowed. We observed no significant difference in this variable between the different stages of the bypass construction or between animals. Analysis of 40 sequential vibrations produced by a mole-rat during the bypass tunneling revealed that the average time interval between the head-drums was  $8 \pm 5$  s (range: 1–13 s).

The control ( $N=5$ ) mole-rats, digging a tunnel with no obstacle in front, burrowed 1 m of tunnel at the same speed as the mole-rats burrowing a bypass tunnel ( $128 \pm 12$  vs  $126 \pm 10$  min  $\text{m}^{-1}$ , accordingly). The low frequency seismic waves (around 300 Hz) produced while burrowing were similar for both sets of mole-rats. However, the control animals produced significantly fewer seismic waves/meter than those burrowing a bypass tunnel ( $95 \pm 12$  taps  $\text{min}^{-1}$  vs  $198 \pm 15$  taps  $\text{min}^{-1}$ , accordingly;  $t$ -test for independent samples,  $t_{10}=5.1$ ,  $P<0.001$ ).

#### Computer simulator model

In the first simulation we attempted to evaluate the mole-rat's ability to estimate its distance from a reflected air–soil interface while burrowing a new tunnel. The simulation model consisted of a single-source/single-receiver (the mole-rat's body) located at 30 or 50 cm from the soil–air interface. The simulation demonstrated that the amplitude of the reflected seismic signal is inversely proportional to the distance of the mole-rat from the reflecting interface, i.e. the greater the distance, the weaker the reflection that reaches the mole-rat (Fig. 3). The arrival time of the reflected energy is also proportional to the distance from the interface: each 10 cm from the obstacle boundary results in a time delay of about 2.5 ms.

In the second simulation we evaluated the mole-rat's ability to

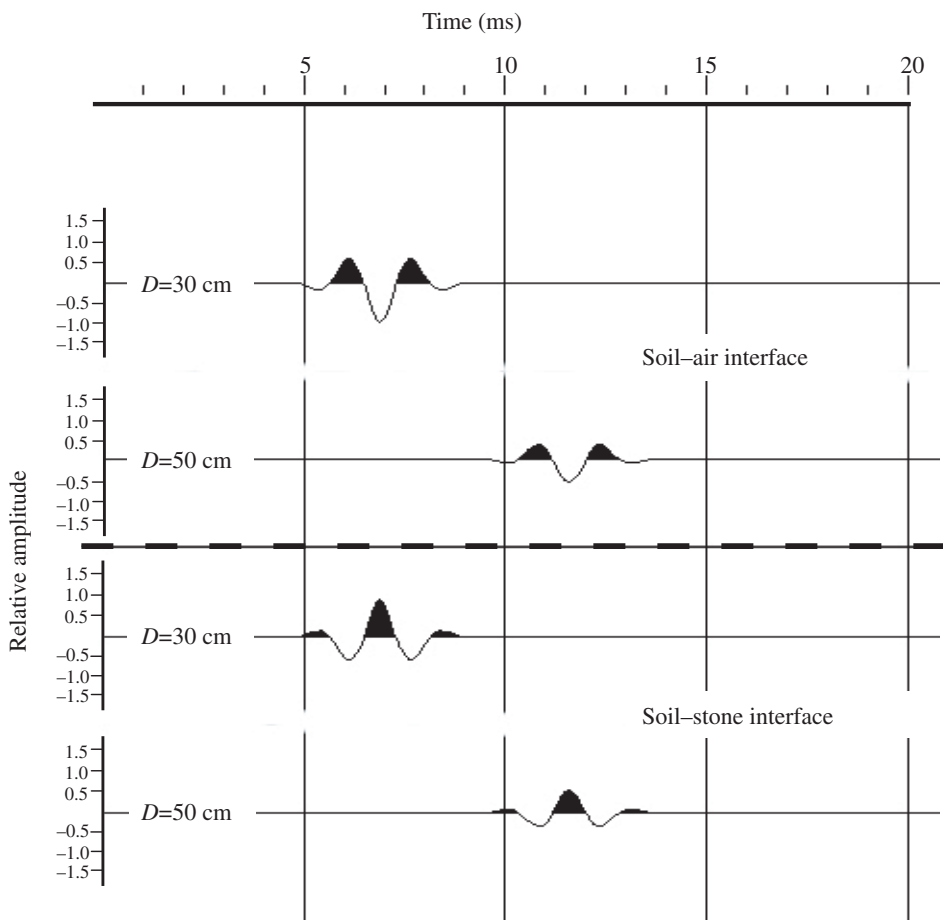


Fig. 3. A simulation model, consisting of a single-source/single-receiver (the mole-rat's body) located at 30 or 50 cm distance  $D$  from two different reflecting interfaces (upper part: soil–air interface; lower part: soil–stone interface). The scheme presents the polarity, amplitude and relative time delay of the reflected wave returning to the mole-rat (the source location) from the two interfaces.

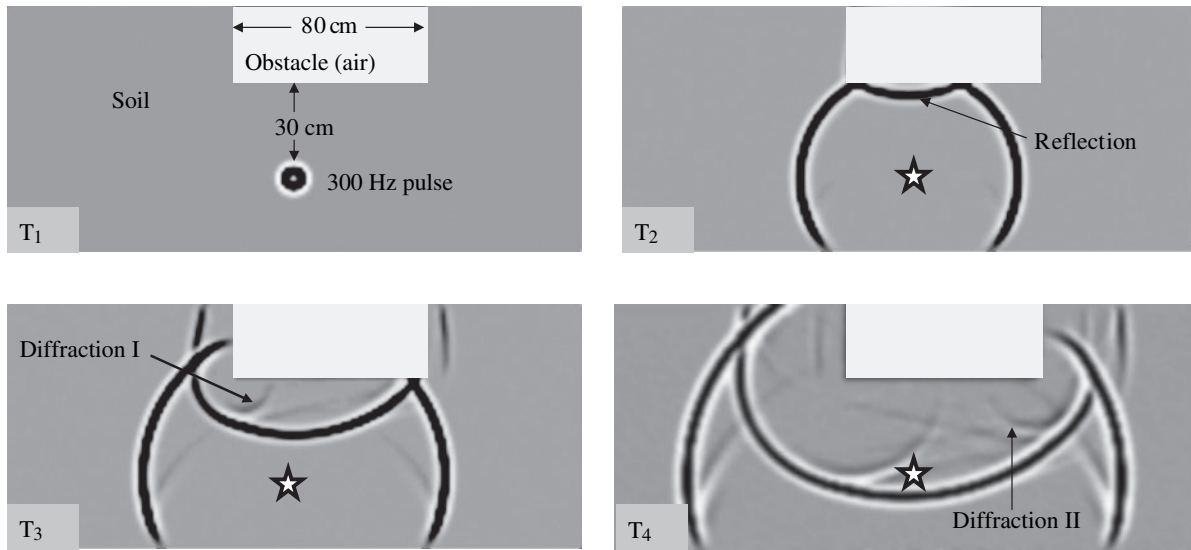


Fig. 4. A series of four photos from a simulation of seismic waves:  $T_1$  (the time that the seismic pulse was generated): the source is located 30 cm from an asymmetrically aligned open ditch, where the left corner of the ditch is closer to source than the right corner.  $T_2$  (4 ms after the pulse was generated): a seismic wave reflected from the nearest obstacle wall.  $T_3$  (5.5 ms after time the pulse was generated): a seismic wave diffracted from the obstacle's closest corner.  $T_4$  (8 ms after the pulse was generated): a seismic wave diffracted from the obstacle's more distant corner. Stars indicate the location of the source and receiver (individual mole-rat).

distinguish between reflected interfaces of air-soil and soil-solid material (an open ditch compared to a solid obstacle). As in the previous simulation, this model consisted of a single-source/single-receiver located at 30 or 50 cm from the reflected interface with the same geometry, except that we replaced the air with a solid material (typical stone), which has an acoustic velocity of  $2000 \text{ m s}^{-1}$  and a density of  $1.8 \text{ g cm}^{-3}$ . The simulation demonstrated that both amplitude and time delay of the reflected wave decrease as a function of the distance from the reflected interface, as in the previous example. However, since solid materials (stone, wood, etc) are denser (i.e. their velocity is greater) than non-packed soil, the reflected energy from the soil–solid material interface has a smaller reflection coefficient and therefore smaller amplitude than that reflected from the soil–air interface. Further, the polarity of the reflected pulse is now positive in contrast to the negative polarity of the reflection from the soil–air interface (Fig. 3).

The third simulation evaluated the mole-rat's ability to estimate the size and position of obstacles using reflected seismic waves. In the field the mole-rat has been shown to distinguish between a small and a large ditch and its relative position from the obstacle in the case of an asymmetrical ditch. To simulate this situation a two-dimensional model was digitized (Fig. 4). The rectangular obstacle was an open ditch (soil–air interface) and the source/receiver (the mole-rat) was located inside the simulated soil (acoustic velocity of  $85 \text{ m s}^{-1}$ ). A zero-phase wavelet with a dominant frequency of 300 Hz was used as the source function. The wave-front simulation was calculated by solving the two-dimensional acoustic wave equation using a finite-difference scheme to determine the spatial and temporal numerical derivations (Kelly et al., 1976). The simulation revealed that three major

reflected waves eventually reached the source location (Fig. 4). The first and strongest one was the reflection wave from the soil–air boundary. Next were two weaker waves, constituting the secondary diffractions from the ditch corners (see Fig. 4,  $T_3$  and  $T_4$ ). Since the source is located closer to the left corner, the diffraction from this corner reaches the source first (see diffraction wave I).

This simple simulation shows that the 'information' about the location of the obstacle corners is contained in the diffracted energy. If the diffractions can be perceived by the mole-rat, then the question remains as to how it identifies them as diffractions (and not reflections) and how it determines their laterality.

In the third simulation we assumed that the mole-rat can detect reflected/diffracted energy through at least two of its paws (we used left forepaw and left hindpaw). We also assumed that the mole-rat generates at least two single head-taps at different distances from the obstacle's closest boundary (in this simulation at 30 and 35 cm) (Fig. 5A). If the animal is able to assess the difference between the return time of the reflection and diffraction waves detected by the forepaw and hindpaw (whether left or right), there would be no difference between the first and second tap reflected wave, while for the diffraction wave there would be a substantial difference between the two taps (Fig. 5B). This would enable the mole-rat to differentiate between the reflected waves and the diffracted waves. Following identification of the diffraction wave, its laterality must be determined. From the mole-rat's perspective, the closer diffracting corner will be the side from which the first diffraction wave reaches its paws (in this simulation from the left corner). Further, similar to the reflection waves, the amplitude and time delay of the

diffraction waves are proportional to the distance of the mole-rat from the obstacle corners, and this information could be used by the mole-rat to estimate the size of the obstacle.

### Perception of seismic waves

#### Behavioural experiment

Experiment test: All mole-rats (from both groups) succeeded in locating and selecting the correct maze arm leading toward the stimulus mole-rat or mechanical shaker vibratory source in most of the trials (>80%; Table 1).

No significant difference was found in the performance between the first and the second day of the experiment for both types of (animal groups) vibratory source (mechanical shaker:  $Z=1.2$ ,  $P=0.2$ ; stimulus mole-rat:  $Z=0.3$ ,  $P=0.7$ ; Table 1).

The performance of the animals exposed to vibration generated by the stimulus mole-rat was significantly better than that of those exposed to vibration generated by the mechanical shaker ( $U=3.5$ ,  $P<0.01$ ).

Control test: The animals failed to correctly localize the side of the vibratory stimulus when the vibratory waves could not reach their feet (only air-borne waves and possibly some olfactory cues were available). The performance of all animals in the control test was significantly lower than that in the experimental test (mechanical shaker:  $Z=2.4$ ,  $P<0.025$ ; stimulus mole-rat:  $Z=2.4$ ,  $P<0.025$ ); and not different from

random directional choice (mechanical shaker:  $Z=0.9$ ,  $P=0.3$ ; stimulus mole-rat:  $Z=0.8$ ,  $P=0.4$ ) (Table 1; Fig. 6).

#### Histological examination

Defined lamellate corpuscle mechanoreceptors resembling Pacinian corpuscle receptor morphology were found in both the forepaws and hindpaws of the mole-rats but not of the voles. These structures were usually oval or elliptic in shape, with a diameter of 30–60  $\mu\text{m}$  and in clusters of up to three corpuscles (Fig. 7). The corpuscular structures were distributed mainly in the dermis and subcutaneous tissue of the glabrous skin. Most (~80%) of them were found in the toe region and the remainder in the distal part of the paws. There were 15–20 corpuscles per foot, with no substantial difference in shape, size or number between the forefeet and hindfeet.

### Discussion

In two recent field studies we showed that when a mole-rat tunnel is experimentally blocked, the animal is able to assess the obstacle's dimensions, density and relative distance, and accordingly select the best-fit digging strategy in order to bypass the obstacle and rejoin the two disconnected tunnel sections (Kimchi and Terkel, 2003a,b).

As far as we know, none of the sensory channels that are used to detect and assess obstacles in short-distance orientation by surface-dwelling mammals are accessible for subterranean mammals like the mole-rat (Kimchi and Terkel, 2002). Nonetheless, the mole-rat demonstrates an amazing ability for efficient spatial orientation (see Introduction). We thus hypothesized that it might be using a light-independent sensory mechanism adapted to the unique conditions of its underground habitat: a type of echolocation mechanism based on seismic waves.

A number of terrestrial invertebrate and vertebrate species are known to use seismic waves (vibration) for intraspecific communication (e.g. white-lipped frog, Lewis and Narins, 1985; Narins, 1990; kangaroo rats, Randall and Lewis, 1997;

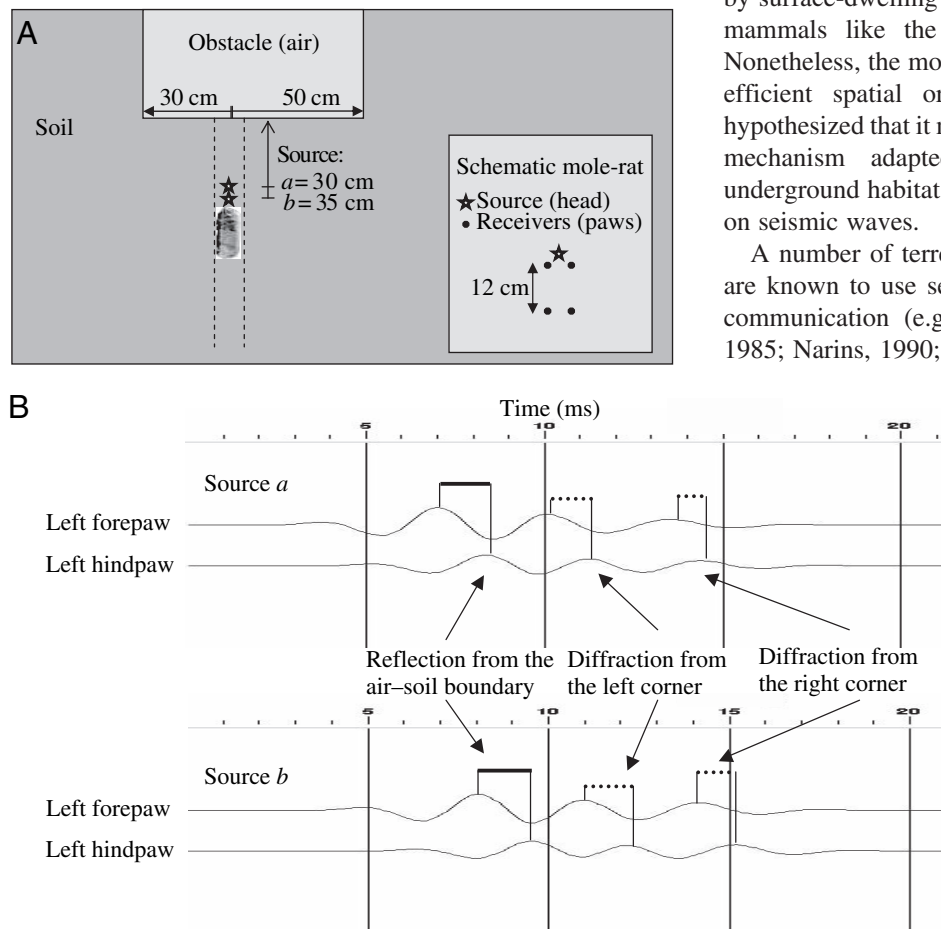


Fig. 5. Illustration of the computer simulation demonstrating how the mole-rat might detect the diffraction waves from the obstacle corners. In this simulation the mole-rat generates at least two seismic waves (the source was at a distance  $a=30$  cm and  $b=35$  cm from the obstacle boundary) and perceives the reflection and diffractions waves using receptors in the forepaws and hindpaws. (A) The mole-rat's position relative to the obstacle boundary while it generates the two seismic waves. (B) The relative time delay of the reflected and diffracted waves as they should reach the mole-rat's left forepaws and left hindpaws from each of the two sources.

Table 1. The success (%) of each subject in selecting the correct maze arm leading to the vibratory source

Subject	Vibratory source					
	Mechanical shaker			Stimulus mole-rat		
	Experiment		Control	Experiment		Control
Day 1	Day 2	Day 1		Day 2		
1	80	90	50	100	100	50
2	90	90	45	90	100	55
3	85	90	40	95	95	55
4	85	85	40	95	95	50
5	80	100	55	100	95	40
6	90	90	55	85	90	55
7	85	80	50	95	90	60
Mean $\pm$ S.E.M.	85.0 $\pm$ 1.5	89.3 $\pm$ 2.3	47.9 $\pm$ 2.4	94.3 $\pm$ 2.0	95.0 $\pm$ 1.5	52.1 $\pm$ 2.4

Values are % success of each subject ( $N=14$ ) during 20 trials/day test, when the generated vibratory signals could reach only the mole-rats' feet (Experiment) or could not reach any of the mole-rats' body parts (Control).

blind mole-rat, Rado et al., 1987; Heth et al., 1987; Cape mole-rat, Bennet and Jarvis, 1988; Narins et al., 1992). Some predators use the seismic waves produced by their prey for directional localization (e.g. sand scorpions, Brownell and Farley, 1979; Brownell and Hemman, 2001; sandfish lizard, Hetherington, 1989; Namib desert golden mole, Narins et al., 1997; for more detail, see Narins, 2001; Hill, 2001).

Common to all the above processes in which information is obtained seismically is that the source of the signal is one individual while the recipient is another. In contrast, we present here evidence supporting a novel application of seismic waves by a subterranean animal: the use of self-generated seismic waves reflected from an obstacle interface in order to estimate the obstacle's size, shape, density and distance; and the use of self-generated seismic waves reflected from the surface interface to estimate the tunnel digging depth.

#### Seismic waves generated by the mole-rat

The characteristics of the seismic waves produced during excavation of a detour tunnel in this study differed markedly

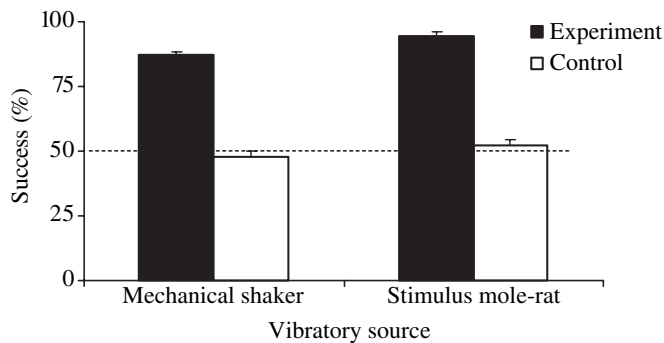


Fig. 6. Success (%) in selecting the correct maze arm leading to the vibratory source when the generated vibratory waves could only reach the mole-rat's feet (Experiment) or did not reach any part of the mole-rat's body (Control). Values are means  $\pm$  S.E.M. ( $N=7$  subjects in each of two stimulus sources). Broken line represents random choice (50%) of maze arm.

from those waves shown previously to be used in social intraspecific long-distance communication. The latter seismic waves produced by a series of rapid head drums (average 4 taps  $s^{-1}$  at a frequency range of 150–250 Hz; Rado et al., 1987; Heth et al., 1987). In contrast, during bypass tunnel excavation the mole-rats produced single low-frequency seismic waves with an average time interval between waves of  $8 \pm 5$  s (range 1–13 s interval) at a frequency range of 250–300 Hz.

The finding that mole-rats burrowing a bypass tunnel around an obstacle produce significantly more seismic waves per meter of tunnel digging than those digging a straight tunnel with no obstructions, provides additional support for the possibility that the mole-rat uses seismic waves for spatial orientation. It further implies that during performance of a more complex spatial orientation task, such as estimating the type and position of underground obstacles, production of

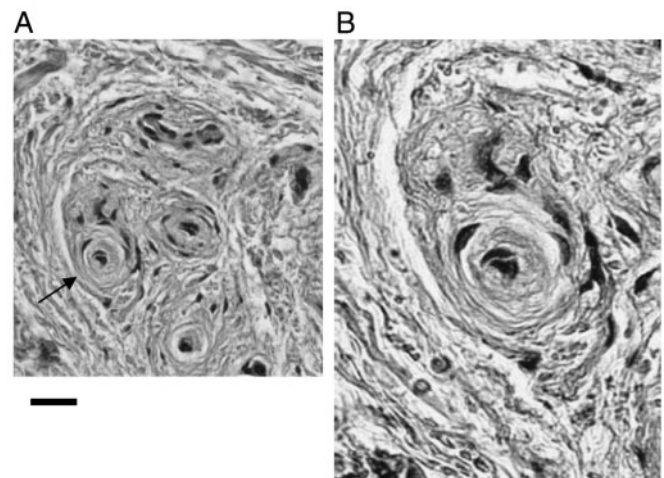


Fig. 7. Lamellate corpuscle mechanoreceptors found in both the forepaws and hindpaws of the mole-rat, possibly used to detect seismic waves. (A) Cluster of three corpuscle structures. Scale bar, 10  $\mu$ m. (B) Close-up of the corpuscle marked with arrow in A.

frequent seismic waves (per burrowing length) assists in better spatial discrimination.

Together, these two findings suggest the use of seismic waves as a type of 'echolocation' mechanism during burrowing, differing in quality and function from the seismic waves (head-drum) produced in social communication.

#### *Computer modeling*

Using computational modeling, we examined the reflection wave characteristics of seismic waves such as those generated by the mole-rat and reflected from the obstacle boundaries. The resulting data indicated the feasibility of using seismic echoes for short-distance spatial orientation.

The computer simulation reveals that the seismic waves generated by a mole-rat can be reflected back to the animal from both the soil-air interface and the soil-solid material interface. We suggest that these reflected seismic waves may be used by the mole-rat to assess the size, shape and density of an obstacle and possibly also to assess its digging depth, in the following way. Differentiation between obstacle densities (i.e. reflected interfaces of soil-air vs reflected interfaces of soil-solid material) can be performed by analyzing the polarity of the reflected signal. Solid obstacles (stone, wood, etc.) reflect seismic waves with the same polarity as the transmitted waves, whereas an open ditch reflects waves with the opposite polarity. The relative distance from the obstacle boundary can be estimated both from the amplitude and the time delay of the reflected signal.

The simulation also showed that generation of a single seismic signal and perception of the reflected wave by a single detector might be sufficient for the mole-rat to maintain a constant distance from a reflected interface (obstacle boundary and ground surface). However, the animal's ability to determine the closest corner of an asymmetrical obstacle, by detecting the diffraction waves from the obstacle's corners, can be explained only if the mole-rat has generated at least two seismic waves and that the reflected waves are perceived by at least two detectors on its body (e.g. on two different paws). This is necessary because in this task the mole-rat must first identify the diffraction waves and then distinguish them from the reflection waves.

Although these acoustic modeling tests allow a theoretical explanation for the field observation (Kimchi and Terkel, 2003a,b), we would like to emphasize that some practical difficulties remain unsolved in this study.

In standard seismic work it is commonly assumed that the maximum observable resolution in the recorded data is  $\lambda/4$  (Sheriff, 2002). Thus, if we assume that the mole-rat produces seismic waves with a dominant frequency of 300 Hz (present study) and that the soil velocity is  $85 \text{ m s}^{-1}$  in the subsurface (Rado, 1993), the mole-rat can possibly detect and distinguish between objects with a minimal spatial resolution of 7 cm (i.e. the mole-rat probably cannot detect items smaller than about 7 cm). Relative to the size of the mole-rat (length 15–20 cm) and its surrounding habitat, this is a very low resolution for spatial orientation (in comparison, in some insectivorous bats

echolocation resolution can reach less than 0.5 mm using ultrasound waves of up to 120 kHz; Nachtigall and Moore, 1988; Schnitzler et al., 2003). This limited frequency band, which initially appears to be disadvantageous, may have been adopted by the mole-rat to serve as a filter to screen out irrelevant seismic waves. The reflections from small objects (e.g. stones and roots) and/or any other type of irrelevant high frequency noise in the mole-rat's underground surrounding can thereby be avoided.

Finally, we would like to emphasize that the computational modeling presented in this study only provides a theoretical model for the lab/field observations. However, although the simulations were based on very simplistic models compared to the variables faced by the mole-rat in its natural habitat (i.e. obstacles with rough surfaces, non-homogeneous soil and obstacle composition), the concept remains the same. It is most likely that in nature the main reflected waves are masked by stronger noise (secondary seismic waves) and thus the mole-rat's sensory system must perform in a poor signal-to-noise ratio. This would require the mole-rat to possess an effective amplifying capability as well as some kind of frequency filter.

#### *Perception and localization of seismic waves through the animals' paws*

We suspect that the mole-rat uses more than one sensory channel for perception of seismic waves. In intraspecific long-distance communication it was demonstrated both behaviourally and electrophysiologically that the mole-rat is able to perceive low frequency seismic waves *via* bone conduction, by pressing its lower jaw against the tunnel wall. The vibrations are thought to be processed mainly by the auditory system (Rado et al., 1998). Nevertheless, the authors do not rule out partial involvement of the somatosensory system in this process (Rado et al., 1998). Indeed, other studies have implicated somatosensory system perception through body mechanoreceptors of the animals (Nevo et al., 1991; Heth et al., 1991).

In contrast to intraspecific communication, where the transmitter and receiver are separate entities, in detection and estimation of underground obstacles the transmitter and receiver are the same (the individual mole-rat). The physical properties of seismic echoes would require the mole-rat to perceive the reflecting echo within about 7 ms if the obstacle is 30 cm away. Since it would not be possible to move from head-drumming to jaw-listening within such a short time, somatosensory detection of the reflected seismic waves through the animal's feet, which are in constant contact with the ground, might be a more feasible solution.

The laboratory behavioural experiment supports this idea, having shown that the mole-rat can efficiently perceive seismic waves through its paws and accurately localize the position of the vibratory source (mole-rat head-drumming or seismic waves generated by a mechanical shaker).

In a complementary histological study we found that the glabrous skin (mainly in the dermis and subcutaneous tissue) in the paws of both the forefeet and hindfeet of the mole-

rat contain (lamellate corpuscle) mechanoreceptors that morphologically resemble Pacinian corpuscles. These alike structures, found to be concentrated in the toe region and the distal part of the paws of various mammals (cats, macropod marsupials and primates), are known to be very sensitive to vibrations, in particular at frequencies ranging from 10 to 400 Hz, with maximum sensitivity between 100 and 300 Hz (reviewed in McIntyre, 1980). Thus, it is highly possible that these somatosensory receptors found in the mole-rat paws are responsible, at least in part, for the detection of seismic waves, and thus constitute part of the animal's spatial orientation mechanism. Such a possibility was also suggested for another subterranean mammal. Catania and Kaas (1995, 1996) found that the large forepaws of the star-mole, *Condylura cristata*, have a huge representation in the somatosensory cortex, suggesting that the forepaws provide an important sensory surface, possibly used in detecting ground vibrations.

We suggest that the rationale for the mole-rat possibly using two signal-detection systems (i.e. jaw and feet) might be related to differences in the amplitudes of the seismic waves perceived and analyzed by the animals in the two tasks (i.e. social communication vs spatial orientation).

In spatial orientation (seismic 'echolocation'), as presented in this study, the waves travel in the soil for short distances (tens of centimetres), while in social seismic communication (Rado et al., 1987; Randall et al., 1997; Heth et al., 1987; Narins et al., 1992) the waves travel a distance of several to tens of meters, suggesting that different amplification systems might be required for the different tasks.

To examine this suggestion we first determined whether there is a substantial difference between the amplitude of the seismic waves generated for communication and those possibly generated for seismic echolocation. We found no significant difference between the strength (amplitude) of seismic waves generated by the mole-rat while burrowing a bypass (present study:  $49.5 \pm 12.0$  dB) to that produced for social communication (Rado, 1993). We also found that the overall variations in the strength of the waves were no more than a factor of two. This is not surprising if we consider that it is the restrictions imposed on the animal by its habitat (narrow tunnels), its manner of generating vibration (head-drumming), and its small body dimensions, that impose this acoustic limitation (the frequency and amplitude of the seismic waves produced by the mole-rat).

A detailed field study of the amplitude decay of the seismic signal generated by the mole-rat, as a function of the distance, was demonstrated by Rado (1993). Rado found that the mole-rats' seismic vibrations decay exponentially (expressed by the formula  $y = 3847.6 \times 10^{(-0.65537x)}$ , where  $y$  = acceleration,  $x$  = distance). Using Rado's decay formula to compare the strength of vibrations traveling a distance of 0.6–1.0 m (typical seismic wave travel distance in echolocation), to their strength after traveling a distance of a few (3–4) meters (typical travel distance used in communication), revealed that in communication the waves will reach the mole-rat 30–90-fold weaker than in echolocation. If we double the travel distance

of the waves used for communication the difference can even reach 3–4 orders of magnitude.

Thus it seems that although the amplitude of the seismic waves produced by the mole-rat for social communication and spatial orientation (seismic 'echolocation') are probably alike in both frequency content and amplitude, the amplitude of the waves perceived by the mole-rat should be substantially different in the two tasks, due to the difference in the travel distance of the waves.

It is thus theoretically possible that the two detection systems are optimized for different amplitude ranges of seismic waves and thus for different functions. Confirmation of this hypothesis requires further comprehensive field observations and computer simulations.

#### *Conclusions and evolutionary aspects*

Any spatial orientation using self-generated substrate-borne reflecting vibrations (seismic 'echolocation') must incorporate the following requirements: (1) the animal must have the morphological structures and behavioural repertoire to generate a seismic signal with suitable geophysical transmission properties (e.g. wave amplitude and frequency); (2) the medium in which the animal dwells must be able to conduct such seismic waves; (3) the animal must possess sensory structures capable of detecting reflection and diffraction waves from the ground, and a neural network that transmits the signal to the appropriate brain regions; and (4) the animal must have a neural system capable of extracting the reverberating waves from the ambient noise, and of quantifying them, in order to respond with the appropriate behaviour.

The means of generating seismic signals used by the blind mole-rat was first discovered by Rado et al. (1987) and Heth et al. (1987). The two research groups found that the mole-rat produces low frequency (150–250 Hz) seismic signals by rapidly striking the flattened anterodorsal surface of its head against the tunnel roof. It was further found that the mole-rat responds both behaviourally and neurologically to such low-frequency seismic signals (Heth et al., 1987, 1991; Rado et al., 1987, 1998).

To date, the use of seismic signals by the blind mole-rat has only been demonstrated with relation to long-distance intraspecific communication (Heth et al., 1987; Rado et al., 1987). Other fossorial mammals also seem to be able to use the seismic channel for communication as well as for prey detection (reviewed by Mason and Narins, 2001; Narins, 2001; Randall, 2001).

The present study is the first to demonstrate that fossorial mammals might also use seismic signals in some kind of seismic 'echolocation' mechanism, when orienting underground.

We have shown that low frequency seismic waves generated by the blind mole-rat while digging its burrow can be reflected back to the animal from the surface of underground obstacles and are probably perceived through the specialized lamellate corpuscle mechanoreceptors in its paws. The computer

modeling also demonstrated that those reflected seismic waves could carry with them information on the spatial position, size and density of underground obstacles.

This type of low frequency seismic waves could thus serve the mole-rat as a reliable spatial orientation tool to accurately dig the optimum energy-conserving bypass tunnel while detouring an obstacle, as shown recently (Kimchi and Terkel, 2003a,b). Further, it is possible that such a mechanism might also be used by the animal to determine and continuously monitor its digging depth, ensuring that its tunnel will be dug parallel to the surface at a depth of 15–20 cm, which is correlated with the depth of its underground food sources (geophytes) and the optimal abiotic conditions (e.g. temperature, atmospheric conditions) (Heth, 1989; Zuri and Terkel, 1996).

We suggest that the unique characteristics of the underground habitat, which impose extreme sensory restrictions and survival costs (e.g. extremely energy-costly digging, exposure to high CO<sub>2</sub> and low O<sub>2</sub> pressure), exerted strong evolutionary pressure on subterranean mammals, such as the blind mole-rat, to develop and utilize such a complex specialized short-distance mechanism of orientation. This would enable them to avoid unnecessary, energy-costly digging, as well as reducing other risks to survival (e.g. exposure to the surface and consequent high predation risk).

Future studies combining neuroethological and physiological approaches will also contribute to clarifying the mechanism of this specialized spatial orientation system. Particularly interesting problems are how the mole-rat manages to extract the reflected waves from the ambient noise and to quantify and rapidly process this information, in order to respond with the appropriate behaviour.

Finally, further research is needed to examine whether this mechanism is also used by other subterranean mammals that have convergently evolved in this fascinating underground habitat.

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## References

- Bachrach, R. and Nur, A.** (1998). Ultra shallow reflection in unconsolidated sediments: Rock physics base for data acquisition. *SEG extended abstracts*, **1**, 866-869.
- Bachrach, R., Dvorkin, J. and Nur, A.** (1998). High resolution shallow-seismic experiments in sand, Part II: Velocities in shallow unconsolidated sand. *Geophysics* **63**, 1234-1240.
- Bennet, N. C. and Jarvis, J. U. M.** (1988). The reproductive biology of the Cape mole-rat, *Georchus capensis* (Rodentia, Bathyergidae). *J. Zool. Lond.* **214**, 95-106.
- Brownell, P. H. and Farley, R. D.** (1979). Orientation to vibrations in sand by the nocturnal scorpion *Paruroctonus mesaensis*: Mechanism of target localization. *J. Comp. Physiol. A* **131**, 31-38.
- Brownell, P. H. and Hemman, L. V.** (2001). Vibration sensitivity and a computational theory for prey-localizing behavior in sand scorpions. *Amer. Zool.* **41**, 1229-1240.
- Busnel, R. G. and Fish, J. F.** (1980). *Animal Sonar System*. NATO ASI Series. New York: Plenum Press.
- Carvell, G. E. and Simons, D. J.** (1990). Biometric analysis of vibrissal tactile discrimination in the rat. *J. Neurosci.* **10**, 2638-2648.
- Catania, K. C. and Kaas, J. H.** (1995). Organization of the somatosensory cortex of the star-nosed mole. *J. Comp. Neurol.* **351**, 549-567.
- Catania, K. C. and Kaas, J. H.** (1996). The unusual nose and brain of the star-nosed mole. *Bioscience* **46**, 578-586.
- Griffin, D. R.** (1974). *Listening In The Dark*. 2nd edition. New York: Yale University Press.
- Heffner, R. S. and Heffner, H. E.** (1992). Hearing and sound localization in blind mole-rats (*Spalax ehrenbergi*). *Hear. Res.* **62**, 206-216.
- Heth, G.** (1989). Burrow pattern of the mole-rat *Spalax ehrenbergi* in two soil types (terra-rossa and rendzina) in Mount Carmel, Israel. *J. Zool. Lond.* **217**, 39-56.
- Heth, G., Frankenburg, E. and Nevo, E.** (1987). Vibrational communication in subterranean mole-rats (*Spalax ehrenbergi*). *Behav. Ecol. Sociobiol.* **21**, 31-33.
- Heth, G., Frankenburg, E., Pratt, H. and Nevo, E.** (1991). Seismic communication in the blind subterranean mole-rat: patterns of head thumping and of their detection in the *Spalax ehrenbergi* superspecies in Israel. *J. Zool. Lond.* **224**, 633-638.
- Hetherington, T. E.** (1989). Use of vibratory cues for detection of insect prey by the sand swimming lizard *Scincus scincus*. *Anim. Behav.* **37**, 290-297.
- Hill, P. S. M.** (2001). Vibration and animal communication: A review. *Amer. Zool.* **41**, 1135-1142.
- Kelly, K. R., Ward, R. W., Treitel, S. and Alford, R. M.** (1976). Synthetic seismograms: A finite difference approach. *Geophysics* **41**, 2-27.
- Kimchi, T. and Terkel, J.** (2002). Seeing and not seeing. *Curr. Opin. Neurobiol.* **12**, 728-734.
- Kimchi, T. and Terkel, J.** (2003a). Mole-rats (*Spalax ehrenbergi*) select bypass burrowing strategies in accordance with obstacle size. *Naturwissenschaften* **90**, 36-39.
- Kimchi, T. and Terkel, J.** (2003b). Detours by the blind mole-rat follow assessment of location and physical properties of underground obstacles. *Anim. Behav.* **66**, 885-891.
- Lewis, E. R. and Narins, P. M.** (1985). Do frogs communicate with seismic signals? *Science* **227**, 187-189.
- Liu, H. P., Anderson, D. L. and Kanamori, H.** (1979). Velocity dispersion due to inelasticity: implication for seismology and mantle composition. *Geophys. J. R. Astronom. Soc.* **47**, 41-58.
- Mason, M. J. and Narins, P. M.** (2001). Seismic signal by fossorial mammals. *Amer. Zool.* **41**, 1171-1184.
- McIntyre, A. K.** (1980). Biological seismography. *Trend. Neurosci.* **3**, 202-205.
- Nachtigall, P. E. and Moore, P. W. B.** (1988). *Animal Sonar: Processes and Performance*. NATO ASI series, New York: Plenum Press.
- Narins, P. M.** (1990). Seismic communication in anuran amphibians. *Bioscience* **40**, 268-274.
- Narins, P. M.** (2001). Vibration communication in vertebrates. In *Ecology of Sensing* (ed. F. G. Barth and A. Schmid), pp. 127-148. Berlin, Heidelberg, New York: Springer-Verlag.
- Narins, P. M., Reichman, O. J., Jarvis, J. U. M. and Lewis, E. R.** (1992). Seismic signal transmission between burrows of the Cape mole-rat, *Georchus capensis*. *J. Comp. Physiol. A* **170**, 13-21.
- Narins, P. M., Lewis, E. R., Jarvis, J. U. M. and O'Riain, J.** (1997). The use of seismic signals by fossorial southern African mammals: A neuroethological gold mine. *Brain Res. Bull.* **44**, 641-646.
- Nevo, E.** (1991). Evolutionary theory and process of active speciation and adaptive radiation in subterranean mole-rats, *Spalax ehrenbergi* superspecies in Israel. *Evol. Biol.* **25**, 1-125.
- 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.
- Purves, P. E. and Pilleri, G. E.** (1983). *Echolocation in Whales and Dolphins*. New York: Academic Press.
- Rado, R.** (1993). Seismic communication in mole-rats. PhD thesis, Tel-Aviv University, Israel.
- Rado, R., Levi, N., Hauser, H., Witcher, J., Adler, N., Intrator, N., Wollberg, Z. and Terkel, J.** (1987). Short communication. Seismic

- signalling as a means of communication in subterranean mammal. *Anim. Behav.* **35**, 1249-1266.
- Rado, R., Himelfarb, M., 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., Terkel, J. and Wollberg, Z.** (1998). Seismic communication signals in the blind mole-rat (*Spalax ehrenbergi*): electrophysiological and behavioral evidence for their processing by the auditory system. *J. Comp. Physiol. A* **183**, 503-511.
- Randall, J. A.** (2001). Evolution and function of drumming as communication in mammals. *Amer. Zool.* **41**, 1143-1156.
- Randall, J. A. and Lewis, E. R.** (1997). Seismic communication between the burrows of kangaroo rats, *Dipodomys spectabilis*. *J. Comp. Physiol. A* **181**, 525-531.
- Schnitzler, H. U., Moss, C. F. and Denzinger, A.** (2003). From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386-394.
- Schone, H.** (1984). *Spatial Orientation. The Spatial Control of Behavior in Animals and Man* (ed. R. B. Capanica, P. Marler and N. T. Adler). New Jersey: Princeton University Press.
- Shanas, U. and Terkel, J.** (1997). Mole-rat harderian gland secretions inhibit aggression. *Anim. Behav.* **54**, 1255-1263.
- Sheriff, E. S.** (2002). *Encyclopedic Dictionary of Applied Geophysics*, fourth edition. Tulsa: SEG publication.
- Steeple, D. W., Green, A. G., McEvilly, T. V., Miller, R. D., Doll, W. E. and Rector, J. W.** (1997). A workshop examination of shallow seismic reflection surveying. *The Leading Edge* **16**, 1641-1647.
- Zuri, I. and Terkel, J.** (1996). Locomotor patterns, territory, and tunnel utilization in the mole-rat *Spalax ehrenbergi*. *J. Zool. Lond.* **240**, 123-140.