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MAGNETIC COMPASS ORIENTATION IN THE BLIND MOLE RAT *SPALAX EHRENBERGI*

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Summary

The blind mole rat *Spalax ehrenbergi* is a solitary, subterranean rodent that digs and inhabits a system of branching tunnels, with no above-ground exits, which it never leaves unless forced to. To survive, the mole rat must be able to orient efficiently in its tunnel system. The sensory channels available for spatial orientation in the subterranean environment are restricted in comparison with those existing above ground. This study examined the possibility that the mole rat is able to perceive and use the earth's magnetic field to orient in space. Experiments were performed using a device constructed from a pair of electromagnetic 'Helmholtz coils', which create a magnetic field whose direction and strength can be altered. In the first experiment, we tested a group of mole rats (*N*=33) in an eight-armed maze under the earth's natural magnetic field to determine whether they have directional preferences for the location of their sleeping nest, food chamber and toilet site. A second group of mole rats (*N*=30) was tested for their directional preference after the earth's magnetic field had been experimentally shifted by 180°. We found that the first group exhibited a significant preference (*P*<0.001) to build both their sleeping nest and their food store in the southern sector of the maze, whereas the second group shifted the location of their nests (*P*<0.01) and food store (*P*<0.05), to the northern sector of the maze, corresponding to the shift in the magnetic field. In the second experiment, we tested whether the magnetic compass orientation found in the first experiment depends on a light stimulus by testing a group of mole rats in the eight-armed maze under total darkness. No significant difference in directional preference between light and dark test conditions was observed. It can be concluded, therefore, that, in contrast to some amphibians and birds, magnetic compass orientation in the mole rat is independent of light stimulation.

In the third experiment, we examined whether mole rats (*N*=24) use the earth's magnetic field as a compass cue to orient in a labyrinth. In the first stage (trials 1–13), the animals were trained to reach a goal box at the end of a complex labyrinth until all individuals had learned the task. In the second stage (trial 14), half the trained mole rats underwent another labyrinth trial under the earth's natural magnetic field, while the other half were tested under a magnetic field shifted by 180°. We found a significant decrease (*P*<0.001) in performance of the mole rats tested under the shifted magnetic field compared with the group tested under the natural magnetic field.

The findings from these experiments prove that the mole rat is able to perceive and use the earth's magnetic field to orient in space.

Key words: navigation, magnetic compass, orientation, directional preference, mole rat, *Spalax ehrenbergi*, subterranean mammal.

Introduction

Survival and reproduction are dependent on accurate spatial orientation and localization of food patches, mates and escape routes, as well as awareness of the locations of neighbours.

Surface-dwelling animals live in a complex environment providing a multitude of orientation cues including such visual cues as the sun, the stars or familiar landmarks. Mammals in a subterranean environment, in contrast, in which the number and variety of sensory stimuli are extremely restricted, have consequently needed to evolve special sensory adaptations for survival. Of all the subterranean rodents, the blind mole rat (*Spalax ehrenbergi*) shows the most extreme adaptations to life underground (MacDonald, 1985). It is a solitary, subterranean rodent that digs and inhabits its own tunnel system, which it never leaves unless forced to. The tunnel system is closed, with no above-ground exits, and with links between food storage chambers, toilet chambers, a sleeping nest and foraging areas. The vestigial eye of the mole rat responds only to light and dark and lacks pattern vision (Rado et al., 1991). It is therefore unlikely that the mole rat uses the visual system for spatial orientation in its complex tunnel system. Like other subterranean mammals, the mole rat also demonstrates poor auditory sensitivity, loss of high-frequency hearing and an inability to localize brief sounds (Heffner and Heffner, 1992). In addition, both the directional information from sound sources and the available range of directional responses are reduced to a single linear dimension, limiting any selective advantage in ability to determine the location of sound sources (Heffner and Heffner, 1990; Heffner and Heffner, 1991). Although olfactory cues are used by the mole rat for marking intraspecific territory boundaries (Zuri et al., 1997), olfactory signalling for differential marking of paths in the tunnel system is problematic since, when the animal moves, its fur brushes the tunnel walls and therefore spreads olfactory cues in a non-selective manner.

In an earlier study, we found that, despite these sensory limitations, the mole rat has excellent spatial orientation ability both in captivity (Kimchi and Terkel, 2001) and in nature (T. Kimchi and J. Terkel, unpublished data). It seems, therefore, that the mole rat has evolved an unknown mechanism for underground orientation, enabling it to survive in the harsh conditions of the subterranean niche.

In this study, we tested the hypothesis that the blind mole rat can perceive and use the signals of the earth's magnetic field for spatial orientation.

Materials and methods

Animals

Adult blind mole rats (*Spalax ehrenbergi* Nehring 1898) of both sexes, belonging to the chromosomal species 2N=58 (Nevo, 1985), were trapped in the Tel-Aviv area and maintained in an animal laboratory at Tel Aviv University, Tel Aviv, Israel (32°05′N, 34°48′E, natural magnetic inclination 47°31′, total natural magnetic field intensity 44 μT) in individual plastic cages (33 cm×38 cm×14 cm). The cages contained wood shavings for bedding, and the animals were fed with rodent pellets, carrots and apples. They were maintained in the laboratory at constant room temperature (24–26 °C) under a 14 h:10 h light:dark regime for 3 months before testing.

Experiments I and II

Helmholtz coils

To test our hypothesis that mole rats are able to perceive the earth's magnetic field and use it for spatial orientation, we built an apparatus, based on the Helmholtz coils system built by Wiltschko and Wiltschko (Wiltschko and Wiltschko, 1975), designed to establish experimentally a new local south–north magnetic field. The system consisted of a pair of round coils (2 m diameter) each wrapped with 200 turns of copper wire. The coils were positioned vertically and parallel, 1 m apart, inducing a horizontal magnetic field. A round wooden table centred between the two coils functioned as a stand for the eight-armed maze and the complex labyrinth (see below). The 'Helmholtz coils' were positioned in the middle of a room with no external windows and lit evenly with two fluorescent ceiling lights (40 W). The coils were attached to a power supply with voltage regulator (variace) and control box that enabled us to set the direction and intensity of the electric current, which in turn determined the intensity of the induced magnetic field. The horizontal axis of the pair of coils was placed parallel to the north–south axis of the earth's magnetic field while inducing a magnetic field twice the intensity of the natural magnetic field but in the opposite polar direction. We were therefore able to shift the polarity of the earth's natural magnetic field by 180 ° without changing its intensity or inclination. The uniformity of intensity of the magnetic field induced by this system in the region between the two coils was found to correspond to the magnetic field uniformity calculations (Kirschvink, 1992) for circular Helmholtz coils.

The intensity of the magnetic field between the pair of coils was measured using a Gauss meter (model 404, F.W. Bell Co.) throughout each experiment. Magnetic field component direction was measured using an inclination/declination meter and a direction (polarity) compass.

Eight-armed maze

In nature, the mole rat inhabits a sealed branching tunnel system excavated according to the width of its body diameter and linking the food storage chambers, toilet chambers and sleeping nest. To test the ability of the animal to detect the magnetic field, an eight-armed maze was built to resemble the tunnel system of the mole rat in the field: the maze consisted of eight identical Perspex tubes (30 cm long, 6 cm in diameter), which matched the mole rat body's width. All eight proximal ends of the tubes were inserted like spokes into one central round plastic box (30 cm in diameter), while each distal end was connected to a separate sealed plastic box (31 cm×20 cm×13 cm; Fig. 1). The mole rat could choose

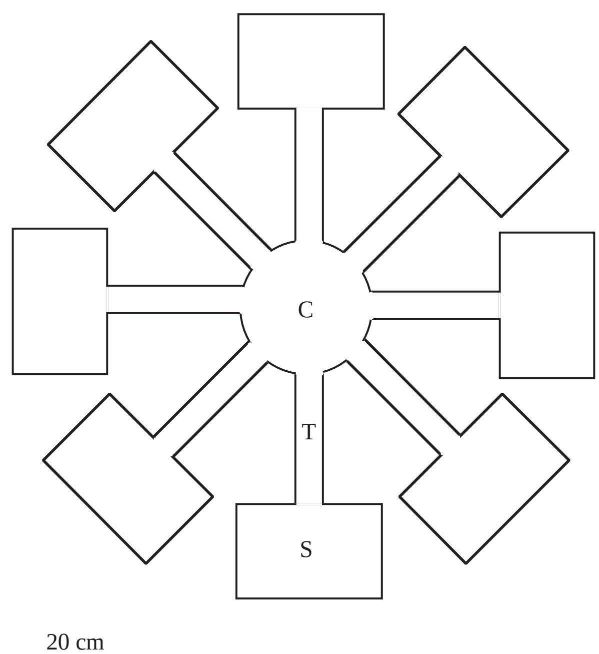

Fig. 1. Diagram of the eight-arm maze, which consisted of eight plastic tubes (T) inserted into a central round plastic box (C), with each distal end connected to a sealed plastic box (S). All mole rats tested were allowed to move freely among the eight boxes and to choose where to locate their sleeping nest, food and toilet chambers.

among the eight sealed boxes to serve as food storage chambers, toilet or sleeping nest.

Procedures

Adult mole rats were placed individually in the centre chamber of the eight-armed maze, together with nesting materials (paper strips) and food (carrots and rat pellets). During the 2-day test period, each mole rat wandered freely in the maze, exploring the boxes and eventually choosing sites for sleeping nest, food storage and toilet. At the end of each test period, the locations of the chosen sites were recorded and the system was thoroughly cleaned.

Experiment I. One group of 33 mole rats was tested under the earth's natural magnetic field. The tests were replicated in three identical eight-armed mazes placed in three separate rooms to eliminate the possibility that the directional preference of the animals might be influenced by local interference in a specific room (e.g. outside noise, air currents, activity of other tested mole rats). Each experimental animal was tested in the maze once only.

To determine whether the directional preference exhibited by the first group of mole rats was dependent on the polarity of the earth's magnetic field, we tested a second group (N=30) in the same way, after shifting the horizontal (directional) component of the earth's magnetic field surrounding the tested animals by 180° using the Helmholtz coils, leaving intensity and inclination unchanged.

Finally, a third group of mole rats (N=15), tested 2 months previously under the earth's natural magnetic field, was tested again under the altered magnetic field.

Experiment II. After the first experiment had confirmed that the mole rat possesses magnetic compass orientation ability, we examined whether this ability is dependent on the availability of light, as found for certain animals (for a review, see Deutschlander et al., 1999). The mole rats (N=44) were kept in total darkness for 4 days prior to the experiment and then tested in the same eight-armed maze under total darkness. Half the animals were tested under the earth's natural magnetic field and the other half under the earth's magnetic field shifted by 180°.

Statistical analyses

We used two χ^2-tests. The first compared the number of mole rats choosing to build their sleeping nest, food chamber and toilet site in the northern (northwest, north, northeast) compared with the southern (southwest, south, southeast) sector of the eight-armed maze; and the second compared the number of mole rats choosing to build each of the three sites in the eastern (northeast, east, southeast) compared with the western (northwest, west, southwest) sector of the maze.

We also performed χ^2-tests to compare the directional preference of the mole rats tested in the maze under dark compared with light conditions.

Experiment III

Helmholtz coils

We used the Helmholtz coils in the same way as described for experiments I and II (see above) to alter the polarity of the earth's magnetic field without changing its intensity or inclination.

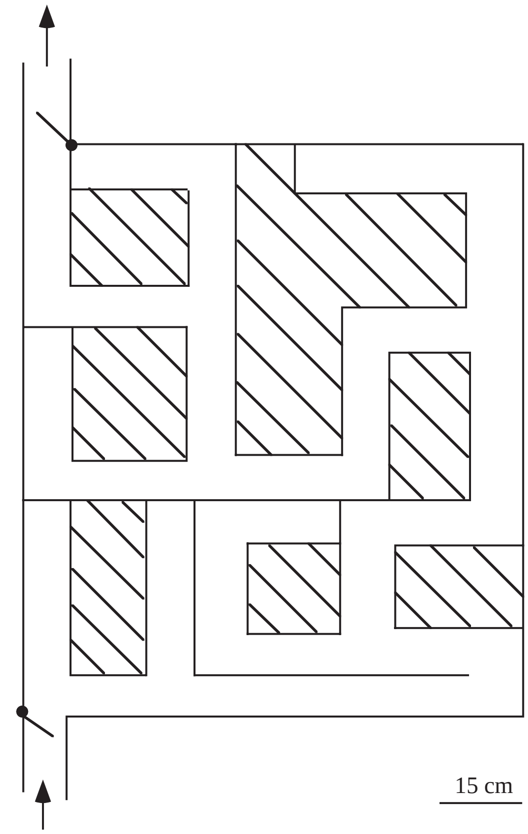

Fig. 2. Diagram of the complex labyrinth, which consisted of six dead-end paths and one correct path with 10 turns leading to the end of the labyrinth. Movable doors were fitted to both the entrance and exit.

Complex labyrinth

The complex labyrinth (110 cm×110 cm×9 cm) consisted of three elements (Fig. 2). The floor was a piece of vinyl sheeting laid on a plywood board. The labyrinth itself was constructed from plywood panels with a Formica finish on both sides. The panels were 9 cm high, 10 mm thick and spaced 8 cm apart to form a path 8 cm wide. The pathways consisted of six dead-end paths and one correct path with 10 turns leading to the end of the labyrinth at the opposite end from the entrance. The labyrinth was placed on the vinyl sheet and covered with a transparent Perspex lid (110 cm×110 cm). The movable entrance door was fitted with an opening (6 cm in diameter) into which one end of a Perspex tube (30 cm long and 6 cm diameter) was inserted while the other end was attached to the plastic cage containing the test animal. Thus, the animals could be transferred to the labyrinth without handling. A plastic tube inserted into a similar door at the exit was attached to another sealed plastic cage that contained a food reward (see below).

At the end of each trial, the labyrinth was cleaned by replacing the plastic sheeting on the floor with clean new sheeting and washing the Formica walls with alcohol (70 %). The experiments were recorded by a remote-controlled video camera (Sony, model no. CCD-TR490E) connected to a monitor (JVC, model no. VM-14PSN).

Procedures

The first two experiments demonstrated that mole rats are able to perceive and use the earth's magnetic field when choosing a site for nest and food chambers.

In this experiment, we tested whether they are capable of using the earth's magnetic field to orient towards a goal at the end of a complex labyrinth. In the experimental procedure, each of 24 animals underwent five consecutive trials daily in the complex labyrinth for three consecutive days. A trial began when the entrance door was lifted. The animal entered the labyrinth and was allowed 20 min to reach the goal box. At the end of each trial, the animal was returned to its home cage using the plastic transfer tube.

To increase motivation to explore and learn the labyrinth, the animals were kept at 85–90 % of their initial body mass throughout the 3 days of the experiment. Each animal that reached the goal box within the time period was rewarded with a small piece of apple (0.5 cm^3) placed in the goal box.

The experiment had three stages. In the first stage (trials 1–13), all the experimental animals were trained to reach a goal box until they showed no further significant improvement in performance for three consecutive trials. In the second stage (trial 14), half the trained mole rats were tested once under the earth's natural magnetic field, while the other half were tested once under a magnetic field altered by 180 °. In the third stage (trial 15), both groups were tested once more under the natural magnetic field.

For all 15 trials, two variables were recorded: (i) the time required to reach the end of the labyrinth; and (ii) number of errors before reaching the end of the labyrinth.

Statistical analyses

We used *t*-tests for independent samples to compare the performance (time and number of errors) of the mole rats in the experimental and control groups for each of the three stages of the experiment.

Table 1. *The number of mole rats choosing to locate their sleeping nest, food chamber and toilet chamber in the north or south sector of the eight-armed maze (experiment I)*

		Number of mole rats		
Type of site	Direction	Group 1 (N=33) Natural mf	Group 2 (N=30) Altered mf	Group 3 (N=15) Altered mf
Sleeping nest	North	3	21**	12*
	South	23***	6	3
Food chamber	North	5	18*	12*
	South	23***	7	3
Toilet chamber	North	13	11	6
	South	13	9	5

χ^2-tests (north *versus* south): *P<0.05, **P<0.01, ***P<0.001.

Group 1 was tested under the earth's natural magnetic field (mf); group 2 was tested under a magnetic field shifted by 180 °; group 3 was tested under a magnetic field shifted by 180 ° after having been tested once previously under the earth's natural magnetic field (taken from group 1).

Results

Experiment I

No significant differences were found in directional preference among the animals tested in the three different rooms, so all the data were pooled.

We found that, under the earth's natural magnetic field, the first group of mole rats exhibited a significant preference to build both their sleeping nest and their food store in the southern sector of the eight-armed maze (χ^2=15.38, P<0.001, for the nest; χ^2=11.5, P<0.001, for the food store) (Fig. 3A,B; Table 1). When we experimentally shifted the direction of the earth's magnetic field in the maze by 180 °, the second group of mole rats shifted the location of their nests and food stores to the northern sector of the eight-armed maze (χ^2=8.33, P<0.01, for the nest; χ^2=6.0, P<0.05, for the food store) (Fig. 3A,B; Table 1). No significant directional preference was observed in the location of the toilet chamber either under the earth's natural magnetic field or under the altered magnetic field (χ^2=0, not significant, for the earth's natural magnetic field; χ^2=2.0, not significant, for the altered magnetic field) (Fig. 3C; Table 1).

The third group of mole rats (taken from group 1) had shown a significant preference for the southern sector of the maze for their nest and food store when tested 2 months earlier under the earth's natural magnetic field (see Results for group 1). When re-tested under a magnetic field shifted by 180 °, they shifted the location of their nests and food store to the northern sector of the maze (χ^2=5.4, P<0.05, for the nest; χ^2=5.4, P<0.05, for the food store) (Table 1).

No significant difference was observed between group 2 (tested once in the maze) and group 3 (tested twice in the maze) in the directional preference for nest, food chamber or toilet chamber.

Experiment II

We found that the mole rats tested under the earth's natural magnetic field in total darkness showed a significant directional preference to build both their sleeping nest and food store in the southern sector of the eight-armed maze (χ^2=4.57, P<0.05, for the nest; χ^2=4.0, P<0.05, for the foodstore) (Table 2). When we shifted the direction of the earth's magnetic field experimentally by 180 °, while keeping the animals in total darkness, they shifted the location of their nest and food reservoir accordingly and significantly preferred to build both sleeping nest and food store in the northern sector of the eight-armed maze (χ^2=6.3, P<0.05, for the nest; χ^2=5.4, P<0.05, for

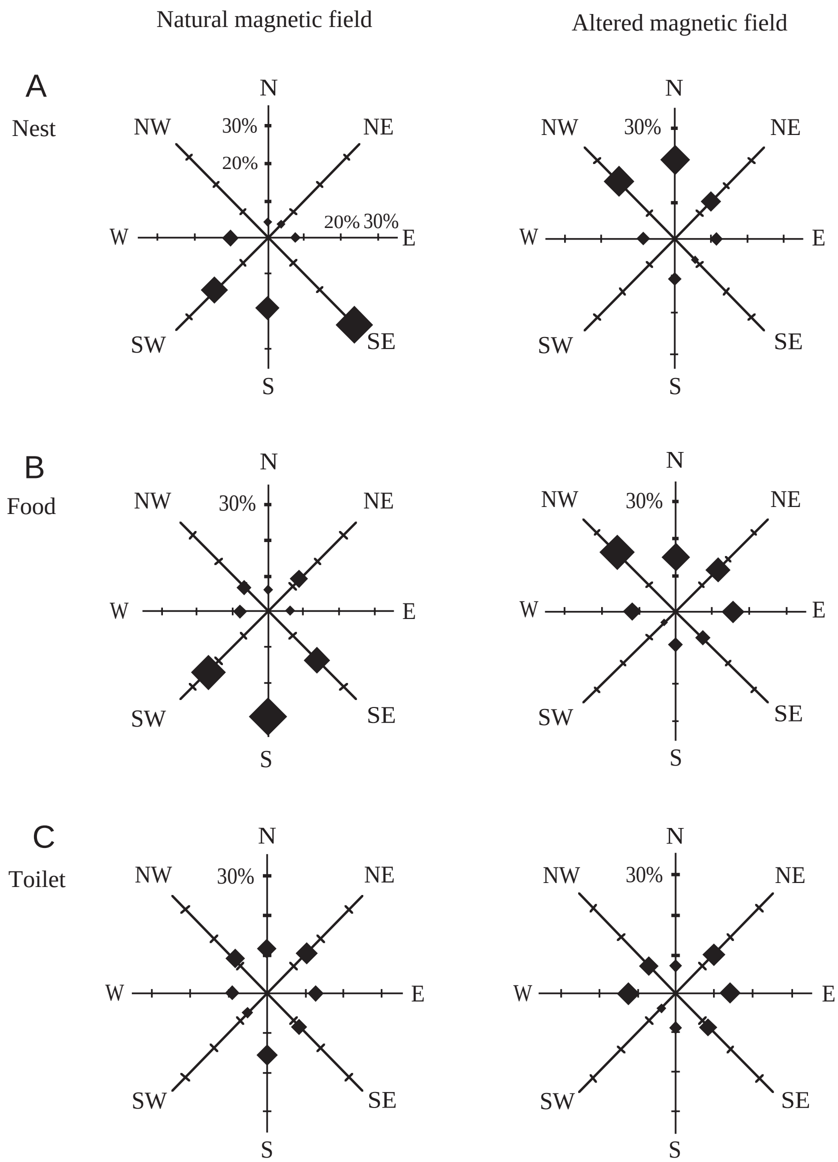

Fig. 3. The percentage of mole rats choosing to locate their sleeping nest (A), food chamber (B) and toilet chamber (C) in each of the eight plastic boxes under the earth's natural magnetic field (left-hand column, N=33) and when the earth's magnetic field had been shifted by 180° (right-hand column, N=30). The size of the black square is proportional to number of mole rats selecting a particular sector.

the foodstore) (Table 2). No significant directional preference was observed for the toilet chamber site in the animals tested in the dark under either the earth's natural magnetic field or the altered magnetic field (Table 2).

Experiment III

In the first stage, when both groups were tested under the earth's natural magnetic field, we found no significant differences in the animals' performance (time and number of errors) between the two groups in all trials (1–13). In the second stage (trial 14), when the control group was tested under the earth's natural magnetic field and the experimental group was tested under an altered magnetic field, significant differences were found between the performances of the two groups. The mole rats tested under an altered magnetic field required significantly more time (t=6.25, P<0.001) and made more errors (t=3.86, P<0.001) in reaching the goal box compared with the control group (Fig. 4). In the third stage

Table 2. *The number of mole rats choosing to locate their sleeping nest, food chamber and toilet chamber in the north or south sector of the eight-armed maze when tested under conditions of darkness (experiment II)*

		Number of mole rats	
Type of site	Direction	Group 1 (N=22) Natural mf	Group 2 (N=22) Altered mf
Sleeping nest	North	3	12*
	South	11*	4
Food chamber	North	4	12*
	South	12*	3
Toilet chamber	North	8	6
	South	5	5

χ^2-tests (north *versus* south): *P<0.05.

Group 1 was tested under the earth's natural magnetic field (mf); group 2 was tested under a magnetic field shifted by 180°.

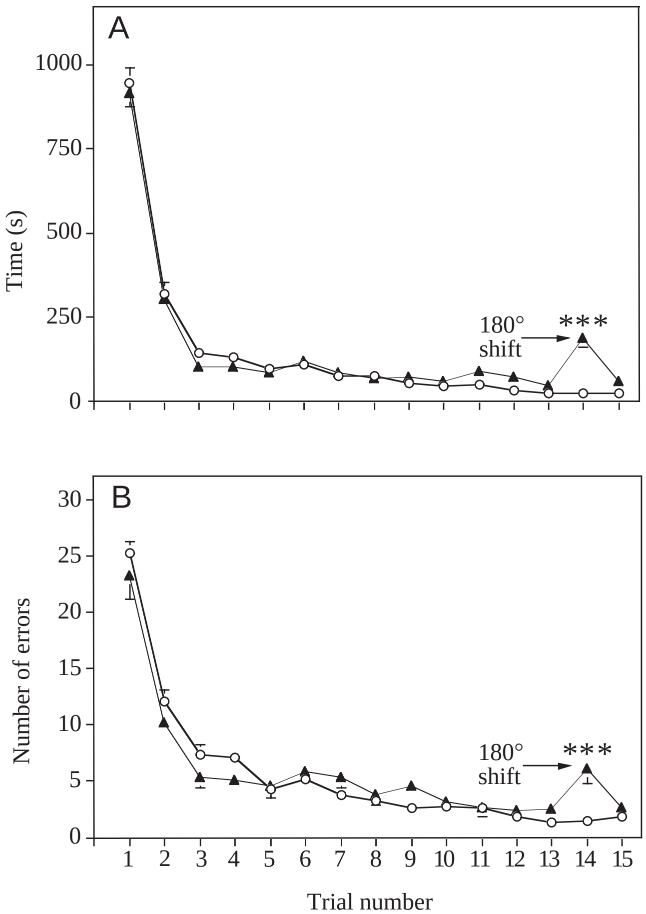

Fig. 4. The time required (A) and the number of errors made (B) by the mole rats in reaching the end of the labyrinth in the control (open circles) and experimental (filled triangles) groups. Values are means ± s.e.m., N=12. In trial number 14, the mole rats were tested under a magnetic field rotated by 180°: t-test for independent samples, ***P<0.001.

(trial 15), when both groups were re-tested under the natural magnetic field, no significant difference was found in the animals' performance (time and number of errors) between the two groups.

Discussion

The present study was designed to determine whether the blind mole rat possesses the ability to use the earth's magnetic field for spatial orientation. The study was divided into two parts. In the first part, we tested whether the blind mole rat uses magnetic compass cues to select the sites for the main functional chambers (sleeping nest, food and toilet chambers) in its habitat. In the second part, we examined whether the mole rat is capable of using the earth's magnetic field to orient towards a goal.

Testing for magnetic compass orientation is possible only when the test animals show reliable suitable orientation in control tests, which provide the reference for the response to the experimentally altered magnetic field (Wiltschko and Wiltschko, 1995). Most studies on magnetic compass orientation have used a circular arena to show that altering the earth's magnetic field around the tested animals results in a concomitant deflection of the animal's directional preference (reptiles, Lohmann and Lohmann, 1993; amphibians, Phillips, 1986; rodents, Marhold and Wiltschko, 1997; Mather and Baker, 1981). However, it is essential to adapt the test apparatus to the specific characteristics of the experimental animal, especially in a species specialized to a specific niche, such as a subterranean sealed and branching tunnel system (dug to the precise width of the animal's body). In the present study, we used an eight-armed maze designed to resemble the mole rat's underground tunnel system (see Materials and methods).

We found that, under the earth's natural magnetic field, mole rats showed a strong directional preference to locate their sleeping nest and food caches in the southern sector of the maze. When the polarity of the earth's magnetic field was shifted by 180°, the mole rats shifted their nest and food store locations to the northern sector of the maze. The sleeping nest and food store constitute the most central part of the territory in the field. The mole rat uses only one sleeping nest, which also serves as a hiding place from which it can escape when threatened (Zuri and Terkel, 1996). The food cache contains all the food that the animal stores for times of need in the dry season. It is crucial, therefore, for the mole rat to retain an awareness of the location of both nest and food chambers from any place within its territory.

With regard to the toilet site, the mole rats did not show any magnetic compass orientation preference under either natural or altered magnetic fields. Careful examination of the pattern of urine and faeces placement revealed several sites containing mainly urine and one larger site containing both urine and faeces. These findings may suggest that toilet sites function not only to concentrate mole rat waste matter but also for scent marking. Many mammals, such as wolves (Peters and Mech, 1975; Sillero-Zubri and MacDonald, 1998), hyenas (Gorman and Mills, 1984), rats (Gregory and Cameron, 1989) and moles (Gorman and Stone, 1990), scent-mark their territory to deter strangers from entering. In our laboratory, Zuri et al. (Zuri et al, 1997) found that mole rats deposit their urine and faeces at their territorial borders. By observing the behaviour of neighbouring mole rats, they demonstrated that the function of such deposits is to delay the entry of conspecifics into the territory. The authors suggested that, in nature, this channel of communication might inhibit potential intruders from entering the territory. In the present study, the plastic boxes were placed at the edges of the apparatus, and the mole rats appeared to use several of them as scent-marking stations, facing different directions, perhaps to deter potential intruders.

In contrast to the results of the present study, Marhold et al. (Marhold et al., 2000), in their study of directional preference in the blind mole rat under the earth's natural magnetic field, carried out in a circular arena, found a significant directional preference for building the nest at 72° and food caches at 37°, but only when pooling all their results (including repetition when testing the same animals several times). However, when they analyzed the results for each animal separately, the authors noted: 'The mean position of nests, caches or latrines estimated for each animal was, apart from a few exceptions, not significantly different from random distribution, partly due to small sample sizes.' Finally, the investigators concluded that 'compared to the directional preferences exhibited by Zambian mole rats, *Cryptomys anselli* (cf. Burda et al., 1990; Marhold and Wiltschko, 1997), the present findings on *Spalax* were less uniform and more difficult to interpret' since 'the employed experimental design was not as optimal for *Spalax* as for *Cryptomys* and it should be modified in future designs' (Marhold et al., 2000). We believe that the failure of these authors to reveal a strong directional tendency, in contrast with our own findings in the present study, was mainly the result of the apparatus they used (a circular arena), which was more suitable for testing species that naturally inhabit and explore open field areas than for species, such as the blind mole rat, that almost never explore an open field area.

A second problem in the study of Marhold et al. (Marhold et al., 2000) is that the experimental period for each animal was only 4 h, which is insufficient time for habituation to a test apparatus. Consequently, most of their tested animals failed entirely to construct nests (51 %), food caches (84 %) or latrines (91 %). In a preliminary experiment, we observed that the mole rats required between 12–48 h to build a sleeping nest, food and toilet chambers in the eight-armed maze. In the present study, therefore, each animal tested was given an acclimation period of 48 h to move freely about the maze, which resulted in all the tested mole rats constructing nests, food caches and a toilet site.

In some animals, the ability to use the earth's magnetic field for spatial orientation has been shown to be light-dependent (e.g. in birds, Wiltschko and Wiltschko, 1982; Wiltschko et al., 1993; in amphibians, Phillips and Borland, 1992). In contrast, other groups of animals, including arthropods (Arendse, 1978; Lohmann et al., 1995; Schmitt and Esch, 1993) and marine turtles (Lohmann, 1991; Lohmann and Lohmann, 1993) are able to orient with respect to the magnetic field in the absence of light (for a review, see Deutschlander et al., 1999). Mole rats are exposed to flashes of light when pushing excess soil into above-ground mounds. Although this light acts as a Zeitgeber to entrain the mole rats' circadian rhythm (Rado et al., 1991; Rado et al., 1992), we have shown here that light does not play a role in the mole rats' ability to use the earth's magnetic field for spatial orientation, corresponding well with the finding in the Zambian mole rat (Marhold and Wiltschko, 1997).

In the second part of the present study, we showed that mole rats are capable of using the earth's magnetic field to orient towards a goal. The mole rats that had learned the correct path in a complex labyrinth to the goal box under the earth's natural magnetic field were disoriented following alteration of the earth's magnetic field. Disorientation was expressed in the significant increase in time (sevenfold) and number of errors (fourfold) required to reach the goal box compared with the control group. These results show, for the first time, that the mole rat not only uses the earth's magnetic field to determine the location of nest and food chambers in its territory but is also capable of using this magnetic field to navigate towards a nearby (several metres away) goal.

The fact that alteration of the magnetic field significantly interfered with the mole rats' ability to reach the goal, but did not disorient the animals entirely, indicates as we have previously suggested (Kimchi and Terkel, 2000) that mole rats probably also use other means of orientation, such as motor sequence learning, a cognitive map and other light-independent mechanisms, in addition to the earth's magnetic field.

Since the use of familiar auditory and olfactory sensory cues in the underground tunnel system is limited, and visual cues such as the sun, stars and landmarks are totally unavailable, the mole rat would benefit greatly from the selective evolution of a unique sensory system enabling it to perceive and exploit the earth's magnetic field for spatial orientation.

Such an orientation mechanism is capable of facilitating the mole rats' performance of a variety of activities in its extensive and complicated tunnel system, such as shuttling between food patches and food chambers (Galil, 1960) and defensive patrolling of territory borders (Zuri and Terkel, 1996), as well as for long-distance orientation, as when orienting towards reproduction sites (Rado et al., 1992).

To summarize, we believe that the ability to exploit the earth's magnetic field for spatial orientation in a habitat where other sensory cues are lacking may be vital for the survival of a solitary animal living below the ground under extremely harsh conditions. Such conditions demand enormous energy expenditure (Vleck, 1979), with a concomitant high risk of overheating (Rado et al., 1993), when digging new tunnels. We believe that for the blind mole rat, as for other subterranean mammals, magnetic compass orientation has evolved as one of the primary mechanisms of both short- and long-distance orientation.

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