



A subterranean mammal uses the magnetic compass for path integration

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Path integration allows animals to navigate without landmarks by continuously processing signals generated through locomotion. Insects such as bees and ants have evolved an accurate path integration system, assessing and coding rotations with the help of a general directional reference, the sun azimuth. In mammals, by contrast, this process can take place through purely idiothetic (mainly proprioceptive and vestibular) signals. However, without any stable external reference for measuring direction, path integration is highly affected by cumulative errors and thus has been considered so far as valid only for short-distance navigation. Here we show through two path integration experiments (homing and shortcut finding) that the blind mole rat assesses direction both through internal signals and by estimating its heading in relation to the earth's magnetic field. Further, it is shown that the greater the circumvolution and length of the traveled path, the more the animal relies on the geomagnetic field. This path integration system strongly reduces the accumulation of errors due to inaccuracies in the estimation of rotations and thus allows the mole rat to navigate efficiently in darkness, without the help of any landmark, over both short and long distances.

Field and laboratory experiments indicate that, despite their sensory limitations and the scarcity of landmarks in their habitat, subterranean mammals are extremely efficient navigators (1–4) and avoid unnecessary highly costly digging (5). Traveling in the dark using a landmark-independent navigation process, such as path integration (also called dead reckoning; see refs. 6 and 7) may thus play an important role for subterranean species. The blind mole rat (*Spalax ehrenbergi*) uses this navigational strategy to determine the shortest route to a previously visited site in a multiroute maze (8) and also to estimate its position relative to a disconnected tunnel section to link up the separated sections along the shortest bypass (9).

Behavioral studies in crepuscular and diurnally active rodents (10–13), dogs (14), and humans (15) have shown that when tested in darkness and without the availability of nonvisual references, path integration can still occur. In these conditions, this navigational process depends on idiothetic (internal), mainly vestibular signals (6, 16) for estimating rotations, together with proprioceptive feedback from locomotion for assessing translations (6).

However, without the help of a stable external reference direction, path integration is rapidly affected by drift (17–19). This is mainly due to errors in the estimation of rotations that accumulate throughout the journey, leading to a progressive shift in the idiothetic directional reference frame itself. Thus, surface-dwelling rodents are able to travel over limited distances in the dark, using path integration alone, but rely primarily on stable landmarks for piloting (12, 20) and also to reset their path integrator (21).

By contrast, insects such as bees and ants (22–24) are capable of navigating over considerable distances without using landmarks, by relying exclusively on a path integration system that assesses rotations with the help of a celestial directional reference, the sun azimuth. Estimating one's heading with respect to a stable external reference greatly increases the accuracy in the

estimation of (changes in) direction, eliminates cumulative frame shifts, and therefore decreases the accumulation of errors.

For subterranean mammals, visual cues are irrelevant (4). However, directional cues from the geomagnetic field are available underground and have already been shown to act as a light-independent directional reference in mole rats, *Cryptomys* (25, 26) and *Spalax* (27). We therefore investigated whether the congenitally blind mole rat, *S. ehrenbergi*, a subterranean rodent that digs and inhabits an extensively branching tunnel system, uses the geomagnetic field in combination with path integration, i.e., as an external directional reference both for estimating rotations and for coding the orientation of self-generated vectors. There would be a strong evolutionary advantage for the mole rat, as for other subterranean mammals, to possess such a unique light-independent mechanism of orientation. We tested our subjects with natural and altered magnetic fields in two route-finding environments, one with multiple possible routes radiating from a central point (homing test) and one with a multiple-route rectangular maze (shortcut test).

Materials and Methods

Animals. Adult female blind mole rats (*S. ehrenbergi*) were captured in the field in the Tel Aviv area and housed under controlled laboratory conditions [24°C, 14 light:12 dark, regime] for 1–2 months before and during the experiments. All animals were housed individually in similar plastic cages (nest boxes) throughout the entire experimental period.

Setup. The mazes used in both experiments (see below) were made of transparent Perspex tubes (6 cm in diameter), linked by junctions. They were placed between two Helmholtz coils (vertical position), described in a previous paper (27). The horizontal component of the geomagnetic field could thus be shifted by 90° clockwise, whereas its intensity and inclination remained constant, similar to the natural geomagnetic field (Tel Aviv: 32°05'N, 34°48'E; natural magnetic inclination = 47°31'; total natural magnetic field intensity = 44 μT).

The animals' movements in the two mazes were recorded with a video camera attached to the ceiling of the experimental room.

Experiment 1, Homing Test. Apparatus. The wheel-shaped maze was based on the maze used by Chapuis and Scardigli (28). It consisted of eight identical radial tubes inserted into a central round plastic box (Fig. 1A). Peripherally, the radial tubes were interlinked by tubes with cross-shaped junctions (Fig. 1B). The distal arm of each junction was sealed with a plastic cap, which was removed only to provide access to the nest. The three remaining arms had doors that could be locked to control the direction of locomotion.

Procedures. At the start of each trial, the nest box containing one animal was attached to the maze entrance. A trial began when the entrance door opened and terminated when the subject reached the final goal site.

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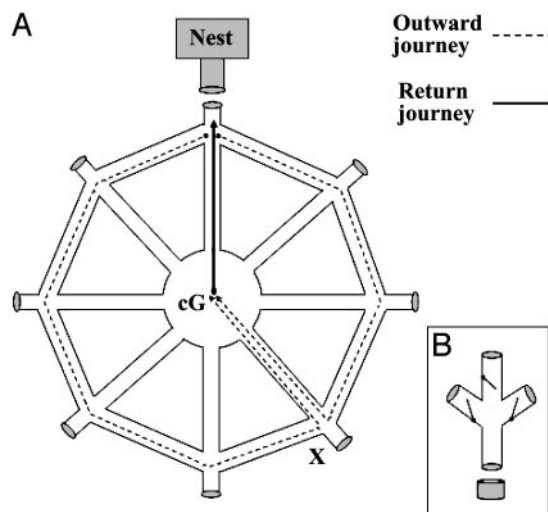


Fig. 1. Apparatus, Experiment 1: wheel-shaped maze used to test homing behavior. (A) The (guided) outward journey leads from the nest to a peripheral junction (X) and then to a central baited goal (cG). There the animal chooses one radial arm to return to the nest. (B) Enlargement of a peripheral junction, which consists of three doors to control the animal's movement and a removable plastic cap to seal the peripheral end of the arm.

Each subject ($n = 6$) underwent five consecutive training trials daily for 8 consecutive days. The animal could run in one direction only along the peripheral route until reaching a junction where the two circumferential doors were locked, whereas the radial door was open and gave access to the central feeding place. From there, the animals were further trained to find the most direct route leading back to the departure site, where they received further food rewards (Fig. 1A). In the test trials, the animals first followed outward journeys of different predefined length and direction (clockwise or counterclockwise) along the maze periphery and eventually reached the central platform (food goal). There, they had to select from among the eight radial tubes, the right tube to return to the point of departure. Each mole rat underwent 9–11 test trials under each of the following six conditions (the sequence of trials was chosen randomly): (i) short length (less than one full round, ≈ 35 –245 cm) outward journey and return route under the geomagnetic field; (ii) as condition i but return route under the altered magnetic field; (iii) medium length (more than one and less than two rounds, ≈ 315 –525 cm) outward journey and return route under the geomagnetic field; (iv) as condition iii but return route under the altered magnetic field; (v) long length (more than three and less than four rounds, ≈ 875 –1,085 cm) outward journey and return route under the geomagnetic field; (vi) as condition v but return route under the altered magnetic field.

In shifted magnetic field trials, the animals were exposed to the magnetic shift for 20–30 sec., i.e., from the moment they reached the central platform to the start of the homing trip after having consumed the food reward.

Elimination of References from the Proximal and Distal Environment. Before every trial, we cleaned the maze tubes with alcohol (70%). Because mole rats are functionally blind, visual cues are irrelevant. We used a sealed room that was well isolated from external sounds (airborne or seismic waves).

To eliminate olfactory cues, the nest box was removed immediately after the subject entered the maze, and the entrance was sealed with a clean plastic cap identical to those that blocked the peripheral ends of all other radial arms (Fig. 1B). Finally, to make it impossible for the animals to base their behavior from

one trial to the next on any external references, the peripheral locations (junction) where (i) the animals started the outward journey and (ii) ended it were changed randomly between trials.

Data Recording and Analysis. The chosen return route was recorded for each trial. On the first-order statistical level, we used the Rayleigh test to determine whether the observed homing directions from particular subjects were significantly orientated (29). On the second-order level, Moore's and Mardia–Watson–Wheeler's nonparametric tests were used to test directionality significance and differences in the orientation of the subjects in two different experimental situations, respectively (29).

Experiment 2, Shortcut Test. Apparatus. A multiroute rectangular maze was used (Fig. 3). In the first phase of the experiment, screw barriers blocked all routes except the path along which the animal was trained. The “short” training path was twice as long and included four times as many turns as the most direct path to the food goal (see Fig. 4, which is published as supporting information on the PNAS web site). The “long” training path was four times as long, with eight times as many turns as the most direct path (Fig. 3A). For the test trials, all barriers were removed.

Procedure. At the start of each trial, the nest box containing one animal was attached to the maze entrance. A trial began when the entrance door opened and terminated when the subject reached the final goal site.

Each subject was trained in 10 consecutive trials on 2 consecutive days to follow either the short (320 cm; 8 turns of 90°) or the long training route (640 cm; 16 turns of 90°) to the feeding box (goal). Next, all routes were opened, and the subjects underwent six additional test trials daily for 2 consecutive days. Four groups of mole rats were tested: (i) those trained in the short route and tested under the geomagnetic field ($n = 7$); (ii) those trained as above and tested under the altered magnetic field ($n = 8$); (iii) those trained in the long route and tested under geomagnetic field ($n = 5$); and (iv) those trained as above and tested under altered magnetic field ($n = 6$).

Elimination of References from the Proximal and Distal Environment. We used the same acoustically isolated room and maze cleaning procedures as in Experiment 1.

To make sure the animals had not used any references (from within or beyond the maze) to find the goal, two control tests were performed: (i) Control for intramaze cues. A naïve group of mole rats ($n = 5$) was trained along a predefined route and then tested in the maze, which had been rotated by 90° , with all routes opened. The location of the nest and feeding box relative to the room, however, remained constant; and (ii) control for room cues. A second naïve group of mole rats ($n = 6$) was trained and then tested in the maze with the same magnetic reference but in a room distant from the training room.

Data Recording and Analysis. The chosen shortcut route was recorded for each trial. We used software for tracking the animal's locomotion and behavior (OBSERVER, Noldus Information Technology, Wageningen, The Netherlands) to analyze the recorded data. The Mann–Whitney U test was used to compare the performances of the two groups that were tested in different magnetic fields during the first experimental trial.

Results and Discussion

In Experiment 1, we tested the animals' ability to return home from the feeding place by the most direct of eight radial routes to the periphery. To determine whether the geomagnetic reference was involved in path integration and whether its influence depended on the sinuosity and length of the outward route, the animals were tested under six different conditions: the outward

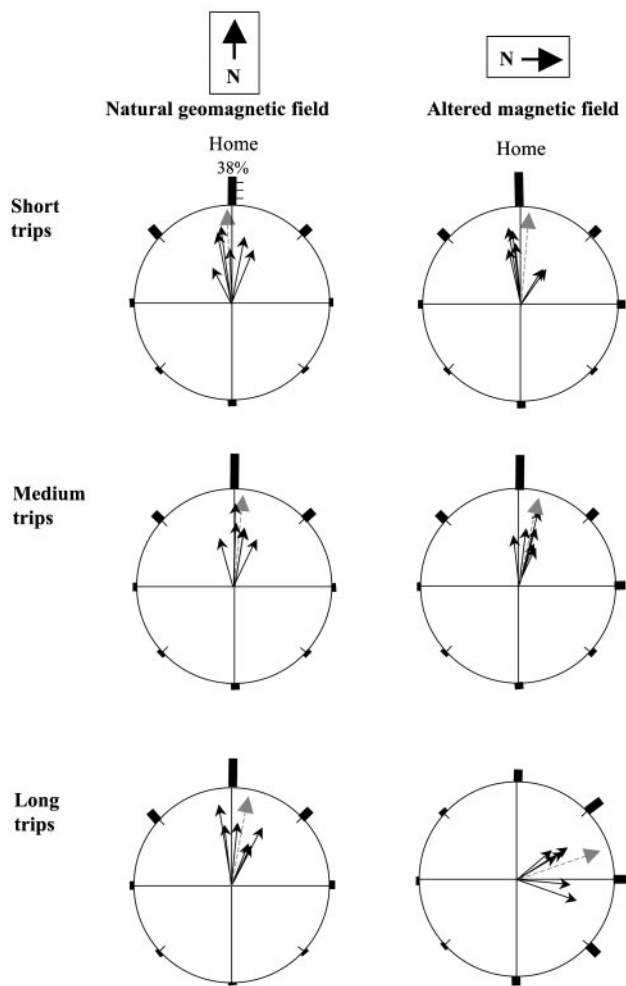


Fig. 2. Experiment 1: homing direction of six subjects, tested under the natural (*Left*) or altered (*Right*) magnetic field and after a short (less than one full round, *Top*) medium (more than one but less than two full rounds, *Middle*) or long (more than three but less than four full rounds, *Bottom*) peripheral outward journey. The histograms around the circles indicate the percentage of trials in which a particular radial arm was chosen by the subjects. Arrows with small arrowheads represent the mean homing direction of each subject; dashed arrows with a large arrowhead represent the mean direction of the whole experimental group. Statistical data are specified in Table 1.

journey, either short, medium, or long, always took place under the earth's magnetic field, whereas the return occurred under either the natural or an altered (90° rotation of the horizontal component) magnetic field.

Under the natural geomagnetic field, the subjects from the three test groups oriented significantly toward the home site departure point, irrespective of the length of the outward journey (i.e., no significant differences were observed either in the vector lengths or in the mean homing direction among the three groups). By contrast, under the altered magnetic conditions, the animals' homing direction followed the shift of the magnetic field but only when the outward journey was long (Fig. 2 and Table 1). In trials with a long outward journey, the mean homing direction was biased by 71° under the altered magnetic field and differed significantly ($P < 0.01$) from the return direction in the natural geomagnetic field (Table 1).

In Experiment 2, we tested whether mole rats also use path integration with the geomagnetic field as a directional reference to return to a previously visited goal via novel shortcuts. Four groups of animals were tested under the following conditions: (i)

trained along a predefined short route and tested under the geomagnetic field; (ii) trained as group *i* and tested under an altered magnetic field; (iii) trained along a predefined long route and tested under the geomagnetic field; and (iv) trained as group *iii* and tested under the altered magnetic field.

We found that the shortcutting performances (route length and number of turns) of the two groups of animals tested under natural geomagnetic field were similar, irrespective of the length of the previously trained route (groups *i* and *iii*). Moreover, the chosen routes were not significantly different from the route length and number of turns of the shortest path to the goal. However, comparing the subjects' performances in test trials under the natural and altered fields revealed that the length and number of turns of the predefined trained path had a significant effect on the animals' behavior. We found no significant difference in the performances between the two groups trained along a short route (Fig. 4). By contrast, in the first trial with all routes open (Fig. 3 *A* and *B*), the animals that had been trained along the long route and then exposed to the shifted magnetic field (group *iv*) exhibited a significantly poorer performance than those tested under the natural geomagnetic field (group *iii*). However, within about three trials, group *iv* adjusted to the new magnetic north and improved its performances, reaching about the level of performance of group *iii* (Fig. 3 *C* and *D*).

In the two control experiments, the animals exhibited similar shortcut ability to the experimental groups, indicating they were not using any intra- or extramaze directional reference to reach the goal.

Taken together, both experiments show that the earth's magnetic field influences the directional component of path integration in mole rats but only if this process has occurred over a relatively long and tortuous path (in our conditions, over ≈ 8 m and three full rotations in the homing task, and over ≈ 6 m and 15 90° turns in the shortcut task). Obviously, the animals orientate at first on the basis of a purely idiothetic assessment of direction but eventually change over to reliance on a path integration system that is assisted by the magnetic compass.

The shift in the animals' behavior can be explained through two different hypotheses (30): (i) The mole rat may perform a single path integration process, on the basis of the two categories of signals indicating direction. At the beginning of a trip, the relative weight of idiothetic directional signals predominates and, with increasing distance, directional information that has been gained with the help of the geomagnetic field becomes more important. (ii) Alternatively, the mole rat may perform two distinct path integration processes, one based on idiothetic signals only and the other on signals indicating the animal's heading with respect to the magnetic north. The switch from using the output of the first integrator to that of the second integrator depends on the sinuosity and length of the path.

The clear change in the animals' orientation during a prolonged outward or training path speaks in favor of the second alternative. A single integrator with mixed inputs would rather have led to an overall estimate of direction and therefore to a less clear-cut change. Note that according to this hypothesis, even if the animal does not use the geomagnetic vector as a reference for path integration during short trips, it must sense and track this vector from the start of a trip to be able to use it subsequently, if necessary (i.e., if the trip will turn out to be a long one).

We still have to consider the functional reasons for using two different types of vector information in relation to the length of a trip and for shifting from one to the other. As already mentioned, purely idiothetic path integration, which is not linked to a stable external reference frame, is highly prone to cumulative errors, with the animals rapidly tending to lose their way as the length and especially the sinuosity of the path increase.

Table 1. Homing direction in six different test conditions of Experiment 1

Subject	Outward journey											
	Short				Medium				Long			
	nEMF		aMF		nEMF		aMF		nEMF		aMF	
	θ_m	r	θ_m	r	θ_m	r	θ_m	r	θ_m	r	θ_m	r
1	349°	0.77**	32°	0.36	26°	0.52*	23°	0.38	25°	0.38	93°	0.51*
2	352	0.81**	354	0.74**	9.7	0.60*	16	0.68**	4	0.69**	51	0.36
3	11	0.64*	350	0.76**	0.7	0.80**	15	0.82**	350	0.88**	58	0.51*
4	22	0.57*	33	0.38	9.7	0.60*	19	0.40	26	0.70**	109	0.70**
5	332	0.35	356	0.60*	2.7	0.63*	8.9	0.67*	352	0.64*	59	0.39
6	358	0.55*	347	0.56*	345	0.46	355	0.51*	21	0.39	57	0.65*
Group means	358	0.96**	5	0.92**	6	0.98**	13	0.96**	10	0.96**	71	0.93**
Mardia–Watson test	B = 0.27, NS				B = 4, NS				B = 14.93, $P < 0.01$			

Rows 1–6 report the mean homing direction (θ_m) and vector length (r) for each subject in 9–11 trials (first-order statistics). The two lower rows report the same parameters for each of the six experimental groups (second-order statistics). Asterisks indicate the degree of significance of the first (test of Rayleigh) and second-order data (test of Moore); *, $P < 0.05$, **, $P < 0.01$. The Mardia–Watson test was used to test the difference between two experimental groups tested with the same outward journey under the natural (nEMF) or altered (aMF) earth’s magnetic field. 0°/360° specifies the home site. NS, not significant.

On the other hand, the geomagnetic field remains a highly reliable directional reference, irrespective of distance. Thus, changing to the use of a path integration system that is assisted by a stable external reference direction decreases the accumulation of errors and endows the mole rat with a highly efficient shortcut and homing ability, irrespective of the outward journey length (the animals exhibited equal homing and shortcut performances in both short and long-distance trips).

Assuming that the geomagnetic reference direction can be used throughout all excursions, irrespective of their length, why does idiothetic path integration control the animals’ behavior in short trips? One possible explanation is that it is easier for the animal to gather and process idiothetic rather than geomagnetic information. For instance, there is extensive evidence that migratory birds and homing pigeons, the species in which the magnetic compass was first discovered, whenever possible use

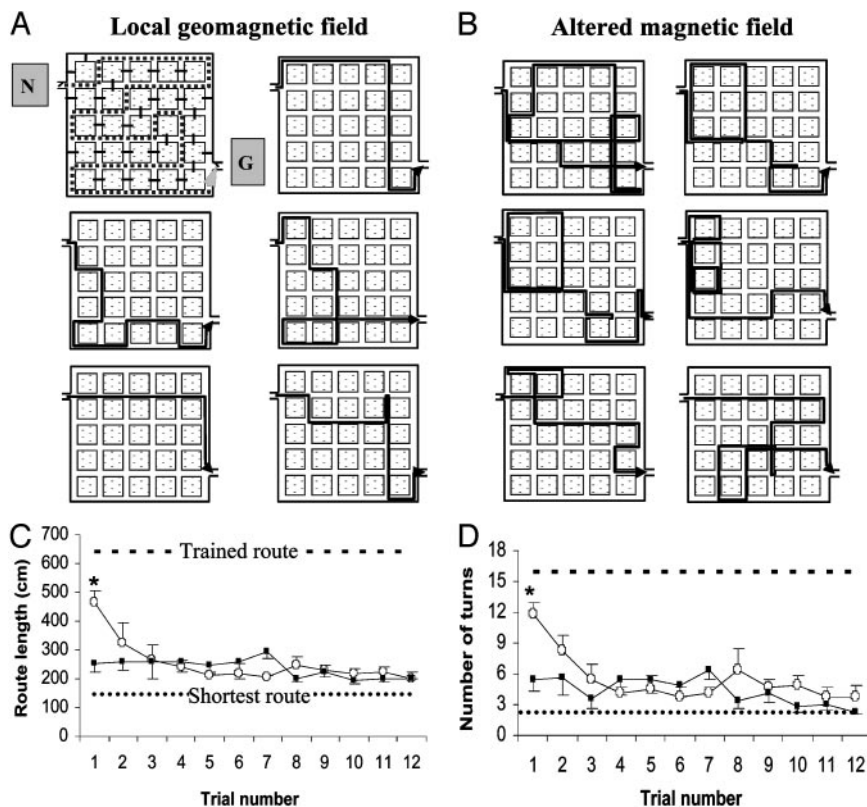


Fig. 3. Experiment 2. (A and B) First shortcut route chosen by each individual trained to follow the long predefined route (dashed line on A) leading from the nest (N) to a feeding goal (G) and tested with all maze routes open. The tests took place either under the natural geomagnetic field (A) or under the altered magnetic field (B). (C and D) Average (\pm SE) route length (C) and number of turns (D) to reach the goal in 12 trials by the group tested under the natural geomagnetic field (filled squares) and the group tested under the altered magnetic field (open circles). The horizontal dashed lines in C and D represent (i) the route length and number of turns of the training path (upper line) and (ii) the route length and number of turns of the theoretical shortest path to the goal (lower line). Asterisks indicate that the results obtained for the natural and the altered magnetic fields differed significantly ($P < 0.01$, Mann–Whitney U test).

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celestial visual references to determine their flight direction and rely on the magnetic compass mainly when visual references are not available (ref. 31; R. Wiltschko, personal communication).

Similar findings were reported for wood mice (*Apodemus sylvaticus*). After a passive unidirectional shift in a sealed chamber and under a reversed magnetic field, these animals changed their homing direction by following, at least partially, the earth's magnetic shift. However, when visual cues were available at the test site, the animals relied on these location-based references for choosing the homing direction and ignored the earth's magnetic reference (32). Note that this experiment showed that the mice used the earth's magnetic field to estimate the direction of the outward journey and then chose the homing direction through compass-assisted route reversal rather than through path integration.

To date, due to its limitations, idiothetic path integration has often been interpreted as a back-up strategy allowing a mammal to explore unfamiliar areas in its immediate vicinity (33) and to navigate over short distances when landmarks are not available. To navigate, mammals rely primarily on visual cues as location-based references that interact and cooperate with path integration but are not used as directional references for the path integration process itself (34). Previous attempts to test the possibility that surface-dwelling rodents use the earth's magnetic field as a stable external reference have failed. Golden hamsters, for instance, do not use the geomagnetic field for assessing the homing direction during hoarding excursions based on path integration (35) and get lost if the outward journey includes more than three to five full rotations (19).

Here we show that a subterranean rodent, the blind mole rat, relies on the geomagnetic field not only for compass orientation (25–27) but also as a directional reference for measuring rotations in the context of path integration. This allows the animal to update its position throughout longer excursions without getting lost through drifting due to random coding of direction. Like the sun azimuth and associated skylight patterns that allow hymenopterans to path integrate over considerable distances with an amazing accuracy (22–24), the geomagnetic field represents a constant general directional reference, which can be used in any habitat with equal efficiency (31). Furthermore, because the geomagnetic field can be perceived irrespective of light (36), it has a crucial evolutionary advantage for species that orient in the dark, as is the case for the *Spalax* mole rat. In light of our current knowledge, we believe that other subterranean species, and possibly also surface-dwelling nocturnal animals, may have evolved the same highly accurate navigation system. This system enables them to assess their relative position in space (3) to compute goal-directed vectors, to avoid unnecessary digging in building and maintaining their tunnel system (9), and possibly to construct a map-like representation of their territory (7, 20), independently of visual cues.

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