

## Exploration and navigation in the blind mole rat (*Spalax ehrenbergi*): global calibration as a primer of spatial representation

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### SUMMARY

The aim of this study was to uncover the process of initial spatial mapping of the environment. For this, blind mole rats (*Spalax ehrenbergi*), were tested in an unfamiliar square arena, in order to reveal how they construct a spatial representation. The mole rats first displayed a build-up phase, in which they gradually formed a path along the perimeter while travelling slowly, frequently pausing and repeating previously travelled segments of the path. This behaviour was followed by a free-travel phase, in which the mole rats appeared to locomote smoothly along the perimeter and through the centre of the arena while travelling faster with fewer stops or repetitions of path segments. Familiarity with the environment was reflected in local shortcuts at the arena corners and global shortcuts (crosscuts) through the arena centre. We suggest that scanning the perimeter throughout the build-up phase constitute a process of calibration, i.e. forming an initial representation of the size and perhaps the shape of the environment – a sort of basic global map. We further suggest that this calibration is later used for navigation, as indicated by the emergence of global crosscuts in the subsequent phase. Further investigation of the build-up phase, e.g. by manipulating environment size, might provide additional insight into the course of establishment of global environment representation (mapping).

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/211/17/2817/DC1>

Key words: open field, cognitive map, subterranean rodent, locale system.

### INTRODUCTION

The ability to navigate efficiently is crucial for an animal, allowing it to access food, encounter a mate, or migrate over extreme distances. In order to navigate, an animal may use a taxon system, which is a set of landmarks along specific routes, or a locale system, which is a spatial representation of the environment, a cognitive map (O'Keefe and Nadel, 1978). Forming a cognitive map is generally ascribed to the process of exploration: 'The hippocampal locale system is assumed to form the substrate for maps of environments an animal has experienced; these maps are established in the hippocampus during exploration, a species-specific behaviour pattern concerned with the gathering of information...' (O'Keefe and Nadel, 1978). It has been further suggested that exploration is necessary in order to form a metric representation of the available working space or to identify the relationships between the animal's movement and external cues (Whishaw and Brooks, 1999). Gallistel (Gallistel, 1990) suggested that the cognitive map is formed by combining an egocentric geometric representation with a geocentric measurement by means of path integration of the available space. Jacobs and Schenk (Jacobs and Schenk, 2003), however, suggested that two phylogenetically, and neurally-remote mechanisms, positional ('bearing') and directional ('sketch') maps, are integrated in forming the cognitive map. It was also suggested that map construction during exploration involves a shift from sequential information processing, which is based on piloting from one landmark to the next (Zadicario et al., 2005), to orienting, in which piloting also involves a calculation of compass direction to one specific location and, ultimately, a shift to map navigation (Avni et al., 2006). Even so, the actual existence or nature of a cognitive

map has not as yet been established, with some claiming that a cognitive map either does not exist or that its existence cannot be proven and it is thus irrelevant (e.g. Bennett, 1996). Moreover, it has not yet been empirically demonstrated how this spatial representation is produced through exploration.

In the present study, we assumed that possession of any sort of global spatial representation can be considered as having a cognitive map, as in the general definition of a 'cognitive map' used by Gallistel (Gallistel, 1990), and unlike the stricter definition coined by O'Keefe and Nadel (O'Keefe and Nadel, 1978). We posed the question of what is the very basic or primordial form of an initial global representation. An initial ('draft') map could be formed, for example, by first acquiring representation of the geometry of the environment and, later on, adding featural cues to this draft (Cheng, 1986; Gallistel, 1990). Another basic form could be that of a representation of the environment by its principle or symmetry axes (Cheng and Gallistel, 2005; Gallistel, 1990) (for a review, see Cheng, 2005). In any case, each of these primitive forms of global environmental representation is acquired and constructed *via* exploration of the environment. Accordingly, in the present study we introduced our model animal, the blind mole rat (*Spalax ehrenbergi*), into an unfamiliar environment and tracked its behaviour in order to uncover the construction of spatial representation.

The blind mole rat is a subterranean rodent that digs a borrow system in which it stays most of its life (Rado et al., 1992). As indicated by its name, the blind mole rat is a completely blind species (Cooper et al., 1993); nevertheless, its circadian clock is influenced by external light (Oster et al., 2002). Although mole rats' eyes had undergone degeneration during the course of their evolution, the

mole rats have evolved effective compensatory means to efficiently navigate and find their way. Indeed, mole rats were found to have strong tactile (Kimchi and Terkel, 2004; Klauer et al., 1997) and magnetic sensory abilities (Kimchi et al., 2004; Kimchi and Terkel, 2001a), and produce and utilize seismic vibrations (Kimchi et al., 2005; Nevo et al., 1991), all of which could facilitate the mapping of an unfamiliar environment. Most importantly, the mole rat seems to have developed a spatial representation capacity that is comparable with that of sighted rodents, and in some cases may even exceed them; e.g. mole rats were more efficient in learning and solving a labyrinth than rats and voles (Kimchi and Terkel, 2001b). A mole rat in the wild spends most of its life in a closed tunnel system that may span over 40 m in length. It repeatedly patrols and monitors this territory for changes. For example, when the tunnel is breached to the outside, the mole rat quickly identifies the location and runs there to seal it (Rado et al., 1992; Zuri and Terkel, 1996). Evidence that mole rats possess a sort of 'mental' or imaginary map of their tunnel system comes from their striking ability to dig bypasses to reconnect a tunnel bisected by an obstacle. Moreover, they are able to identify and exploit the shortest available detour of the obstacle when provided with short and long detour choices (Kimchi and Terkel, 2003). Such efficiency in bypassing an obstacle to reconnect to the tunnel system would be impossible without some sort of global representation of the environment. In light of these abilities, we examined the mole rats' behaviour in the present study when exploring an unfamiliar walled arena. Specifically, we posed the question of whether a mapping process could be identified in the structure of exploration of the mole rat and whether some evidence of the animal's use of such representation might be revealed.

## MATERIALS AND METHODS

### Study animals

Six female and six male adult mole rats (*Spalax ehrenbergi* Nehring 1898) were obtained from a colony maintained at Tel-Aviv University, Israel. The mole rat is a blind fossorial rodent that in nature inhabits tunnels which it digs to its own body width (Rado et al., 1992). Excavating their burrow system using their sharp incisors, the mole rats' activity is entirely subterranean, and they can be found above ground only when forced to be there in the brief period of dispersal of the young, or when driven out of their burrow by another mole rat (Rado et al., 1992; Zuri and Terkel, 1996). Along with their vestigial eyes and lack of external ears, mole rats have an elongated trunk, relatively short legs and no tail, thereby being well adapted to travel both forward and backward in their borrows (Eilam and Shefer, 1992); they are also well adapted to the low O<sub>2</sub> and high CO<sub>2</sub> levels found in underground tunnels (Mendelssohn and Yom-Tov, 1999; Nevo, 1999). Our study animals were housed individually in small cages (35 cm × 25 cm × 20 cm) under a 14h:10h L:D photoperiod. Food (carrots, apples and standard rodent chow) was provided *ad libitum*.

### Apparatus

Testing was carried out in a square open field (2 m × 2 m) enclosed with a 0.5 m-high opaque Plexiglas walls and a blue PVC floor, placed in an air-conditioned room (22°C). During testing, the room was illuminated by three 300 W light bulbs directed to the white ceiling, providing diffused illumination of the arena. A video camera (Ikegami B/W ICD-47E, Tokyo, Japan) was placed 2.5 m above the centre of the arena, providing a top view that was recorded onto a computer by means of a video grabber (VideoHome GrabBeeX) as a MPEG1 digital file.

### Procedure

At the beginning of each test session, an individual mole rat was placed at the bottom right corner of the open field, facing the corner and in contact with the arena wall. The experimenter quietly left the room and the behaviour of the mole rat was then video-recorded for 30 min, after which the animal was returned to its cage. The arena was sprayed with detergent, wiped with a cloth and dried before the next animal was introduced. Testing took place between 08:00–14:00 h, which is within the activity hours of mole rats in the wild (Zuri and Terkel, 1996).

### Data acquisition and analysis

The video files were analyzed using 'Ethovision' (Noldus Information Technologies, Wageningen, NL), which tracks the progression in the arena, providing the time and location of the study animal five times per second. For analysis, the arena was divided into a perimeter zone, which was defined as a 0.15 m strip along the arena walls, and a centre zone, which was a 1.7 m × 1.7 m square, in order to differentiate between travelling at the perimeter and through the centre. Additionally, corner zones were defined as a 0.15 m × 0.15 m square at each arena corner. Another division of the arena into 36 identical 0.33 m × 0.33 m sectors was applied in order to depict the time that mole rats spent at various locations in the arena. The mole rats greatly varied in behaviour over the course of the 30 min of observation. Some individuals rapidly expanded their exploration whereas others were slower to encompass the entire arena space; some quickly entered the centre, others never did so within the observation period. To overcome this variability, behaviour was compared in terms of the temporal order of occurrence rather than in strict time frames. The temporal unit for comparison was a lap; a path that encompassed the entire perimeter, starting and ending at the corner in which the mole rat had been placed at the beginning of the observation. From 'Ethovision' we extracted the total distance that the mole rats travelled in the course of observation, the time spent and the number of visits (entries) to each of the 36 arena zones, the average travel speed, and the speed when entering a corner zone. We further extracted or scored manually from the video files the following parameters: (1) total number of laps; (2) lap length – the distance (in metres) that a mole rat travelled in a lap; (3) lap duration – the time elapsed (in seconds) from departure until return to the start location of the lap; (4) number of stops in a lap – a stop was defined as the absence of forward progression for at least 1 s; (5) interstop distance – the distance (in metres) between each two consecutive stops; (6) retreating – incidence of backward walking that occurred when a mole rat stopped along a wall and then rapidly moved backwards as if retreating along the path it had just travelled; (7) retracing – the incidence of reversal of direction of progress that occurred when a mole rat performed a U-turn to progress in the opposite direction, thus retracing part of the path it had just travelled; (8) facing the centre – incidence of a behaviour that occurred when a mole rat stopped along the arena walls with its trunk in contact with the wall and turned its head about 45° to face the arena centre; (9) corner shortcuts – when a mole rat progressed along a wall toward a corner but instead of reaching the corner it diverted in an arc toward the near half of the perpendicular wall (see Fig. 5B); (10) crosscuts through the centre – when a mole rat left the perimeter zone and returned to it by either travelling to the opposite wall or to a distant half of a perpendicular wall (see Fig. 5B); (11) behaviour at the end of crosscuts – for each crosscut, behaviour when approaching the wall was classified as: (i) bumping into the wall; (ii) approaching the wall in the same direction as the preceding part of the crosscut;

(iii) intermittent travel (switching between progressing and pausing), which may also include head turns; (iv) slowing down; or (v) curving the path to parallel the wall. See Movie 1 in the supplementary material for representative examples of these behaviours.

### Statistics

Unless noted otherwise, data were compared by repeated-measures ANOVA, in which the between-group factor was gender (female or male) and the within-group factor were the successive temporal intervals (laps). When data deviated significantly from normal distribution (Kolmogorov–Smirnov test for normality), we carried

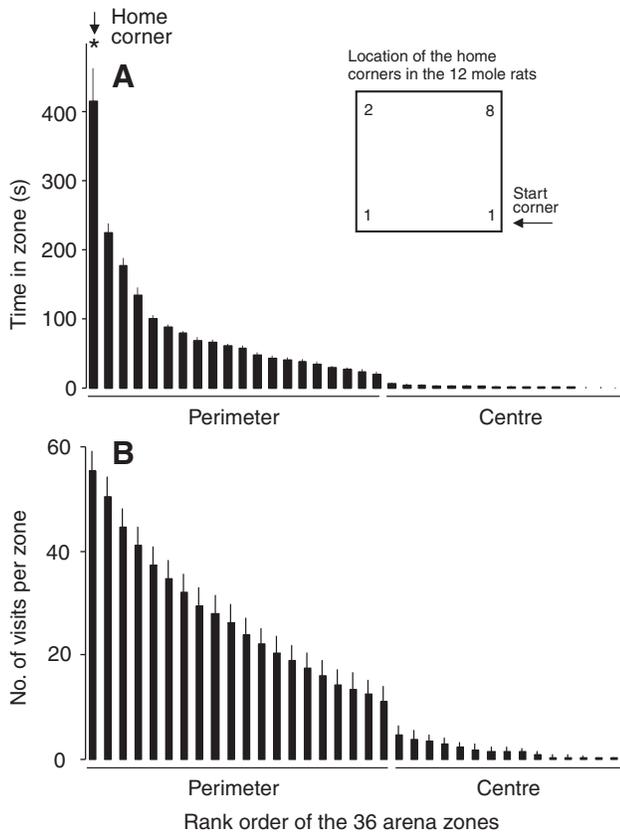


Fig. 1. (A) Distribution of time (s) spent in the 36 arena zones. For each mole rat, the time spent in each zone was measured and ranked from high to low. Each rank was then averaged for the 12 mole rats and values are given  $\pm$ s.e.m. As shown, there was one zone in which the mole rats spent significantly greater time compared with the next rank. To quantify the change across ranks, the difference between each two successive ranks was calculated (i.e. the difference between ranks 1 and 2, between ranks 2 and 3, 3 and 4, and so on). A one-way repeated measures ANOVA was then carried out on the differences between ranks, revealing a significant difference between differences of consecutive ranks ( $F_{34, 374}=13.7$ ;  $P<0.00001$ ). Tukey HSD *post-hoc* test revealed that the difference between the first two ranks was different from all other differences ( $*P<0.0001$ ). Inset: number in each corner indicates the number of mole rats that spent the highest amount of time in that corner. Arrow represents the start corner, where the mole rats were introduced into the arena. As shown, eight mole rats favoured the top right corner, and only one favoured the start (bottom right) corner. (B) Distribution of visits in the arena zones. For each mole rat, the number of visits (entries) into each of the 36 arena zones was counted and ranked from high to low. Each rank was then averaged for the 12 mole rats and values are given  $\pm$ s.e.m. As shown, there was no one zone to which the mole rats paid significantly more visits, as opposed to the distribution of time spent in zone (A).

out the ANOVA on arcsine- or square-root-transformed raw data. The alpha level was set to 0.05.

## RESULTS

### Spatial distribution of activity

Of the 36 arena zones, there was one corner zone in which the mole rats spent significantly more time than in any other zone (Fig. 1A). In other rodents, such a prominent zone has been termed the home base (Eilam and Golani, 1989). Only for one mole rat was this the start corner, i.e. the position at which the mole rats were introduced into the arena at the beginning of the observation; whereas eight mole rats spent the extended cumulative time at the top right corner of the arena (Fig. 1A, inset). In contrast to the time spent at the various zones, there was no one zone that the mole rats visited significantly more than any other zone (Fig. 1B). Furthermore, for only one mole rat was there a match between the zone where the greatest cumulative amount of time was spent and the most visited zone.

### Build-up of paths along the arena walls (laps)

When a mole rat was introduced into the arena at the beginning of the observation, it initially performed a phase of building-up a path that gradually covered the entire arena perimeter, whereas entering the centre of the arena typically occurred only at a later phase of the observation. The gradual build-up of the perimeter path is shown for one mole rat in Fig. 2. As shown, the path was first extended from the starting corner to an adjacent corner. By gradually retracing and/or retreating along past paths and progressing to new sectors along the perimeter, the path was then extended from one corner to the next, until it had covered the entire perimeter. We defined such a roundtrip that encompassed the entire perimeter as a lap, and subsequently used laps as the structural units in the temporal organization of exploration in mole rats. Accordingly, the following results are shown first for the build-up of activity along the arena perimeter during successive laps and then for crossing the centre. The mole rats greatly varied in their activity, as reflected in the overall distance they travelled and in the number of laps. As shown in Table 1, males were more active, traversed greater distances and performed more laps compared with females.

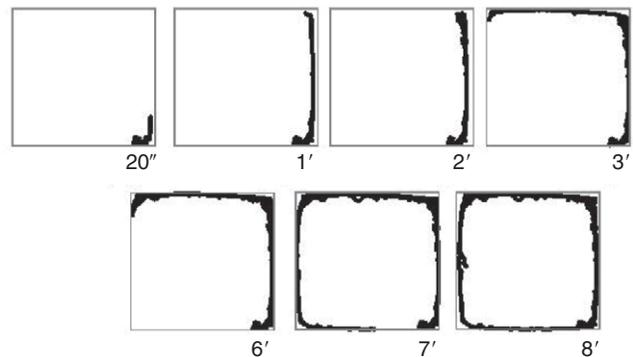


Fig. 2. The gradual build-up of the first lap of one representative mole rat. The lap is shown in cumulative path segments, with the duration of each depicted below as seconds (") or minutes (') from start of the trial. As shown, by 1' the mole rat had extended the path from the start corner (where it was introduced into the arena) to the next corner. By 3' it had reached the furthest corner, and for the next 3 min it retraced the previous path, until 7', when it progressed to the fourth corner and then completed the perimeter path (8').

Table 1. Occurrence of laps, crosscuts and corner shortcuts

	Males						Females						Gender effect ( $t_{10}$ ; $P$ ) 0.82; 0.43
	202	245	350	142	246	347	195	220	184	369	170	170	
Total distance (m)													
Total number of laps	12	15	32	5	16	29	5	9	5	16	6	4	<b>2.32; 0.043</b>
<i>Crosscuts through the centre</i>													
First lap with a crosscut	0	4	2	3	1	7	0	0	2	3	0	0	
Total number of crosscuts	0	9	3	5	12	37	0	0	2	10	0	0	
Number of crosscuts per lap*	–	0.75	0.09	1.7	0.75	1.6	–	–	0.5	0.71	–	–	
<i>Corner shortcuts: the number of visits to a corner until a shortcut first occurred</i>													
Start corner	–	5	6	5	4	4	10	7	5	5	–	2	
Second corner	6	2	5	6	2	7	4	14	–	5	9	17	
Third corner	2	15	30	4	4	3	14	6	–	18	19	5	
Fourth corner	3	4	11	6	5	2	5	–	–	4	10	9	

On average, a corner shortcut occurred at the eighth visit to that corner.

Significant differences are shown in bold.

\*Number of crosscuts per lap was calculated by dividing the number of crosscuts by the number of laps taken once the first crosscut was performed.

Therefore, the data below are given separately for females and males.

#### Behavioural changes across successive laps

An observer could easily notice that the first lap substantially differed from subsequent laps in that it took a long time to complete it. The first lap also comprised slow progression, numerous backtrackings, frequent stops, and many head turnings to face the centre. Backtrackings took the form of either retreating (a fast backward withdrawal along the arena wall), or retracing (a 180° U-turn followed by forward locomotion along the arena wall; see Movie 1 in supplementary material). In order to highlight the difference between the first lap and subsequent laps, we compared the first four laps performed by each mole rat (Table 2A). We limited the comparison to only the first four laps since this was the minimal

number of laps undertaken by all mole rats (Table 1). The results of a two-way ANOVA are summarized as gender effect (between females and males) and over the first four consecutive laps (within-group effect). Except for the distance travelled, there was a significant change over the first four laps in all parameters, as detailed in Table 2A. A Tukey HSD test revealed a significant difference only between the first lap and the three following laps (Table 2A). The difference between the first lap and the following laps is demonstrated in the change in travelling speed between laps (Fig. 3A). Moreover, even for the distance travelled in a lap there was a considerable, albeit non-significant, decline over successive laps (Fig. 3B). Despite the significant differences between males and females for all parameters shown in Table 2A, none of the interactions (laps  $\times$  gender) were significant, implying that the same trend of change across laps occurred in both females and males.

Table 2. Comparison of parameters of behaviour between laps

A							
Behaviour	Group	1st lap	2nd lap	3rd lap	4th lap	Gender effect ( $F_{1,10}$ ; $P$ )	Lap effect ( $F_{1,10}$ ; $P$ )
Distance travelled in a lap (m)	Males	21.2 $\pm$ 5.7	15.6 $\pm$ 3.1	15.2 $\pm$ 4.4	9.6 $\pm$ 1.2	37.8; <b>&lt;0.0001</b>	1.9; 0.14
	Females	49.8 $\pm$ 13.1	27.8 $\pm$ 5.4	29.4 $\pm$ 9.5	29.6 $\pm$ 8.9		
Lap duration (min)	Males	4.4 $\pm$ 1.4	1.9 $\pm$ 0.5	1.9 $\pm$ 0.8	1.2 $\pm$ 0.4	8.7; <b>0.014</b>	3.2; <b>0.036</b>
	Females	6.7 $\pm$ 1.3	3.7 $\pm$ 0.9	3.9 $\pm$ 1.4	4.6 $\pm$ 1.9		
Speed of travelling in a lap (cm s <sup>-1</sup> ) <sup>2,3,4</sup>	Males	9.7 $\pm$ 1.7	14.8 $\pm$ 1.7	17.2 $\pm$ 3.0	16.8 $\pm$ 3.5	0.2; 0.697	5.5; <b>0.004</b>
	Females	12.1 $\pm$ 1.6	14.5 $\pm$ 2.2	14.7 $\pm$ 2.2	13.1 $\pm$ 2.1		
Inter-stop distance (m) <sup>3</sup>	Males	0.8 $\pm$ 0.3	1.1 $\pm$ 0.3	1.8 $\pm$ 0.6	1.5 $\pm$ 0.5	0.7; 0.225	3.7; <b>0.022</b>
	Females	0.7 $\pm$ 0.1	0.9 $\pm$ 0.2	1.0 $\pm$ 0.2	0.9 $\pm$ 0.2		
Number of stops in a lap <sup>3,4</sup>	Males	42.5 $\pm$ 13.8	19.3 $\pm$ 6.2	18.2 $\pm$ 9.7	11.3 $\pm$ 5.1	5.9; <b>0.035</b>	4.4; <b>0.011</b>
	Females	77.0 $\pm$ 25.6	37.7 $\pm$ 8.6	35.5 $\pm$ 12.3	41.2 $\pm$ 15.2		
Backward walks (retreats) in a lap	Males	12.8 $\pm$ 5.2	2.5 $\pm$ 1.1	4.0 $\pm$ 2.7	1.8 $\pm$ 1.1	2.2; 0.167	4.12; <b>0.0146</b>
	Females	12.3 $\pm$ 4.9	8.0 $\pm$ 3.5	7.3 $\pm$ 3.5	8.0 $\pm$ 3.0		
Reversals of progress direction (retraces) in a lap <sup>3</sup>	Males	3.0 $\pm$ 0.9	0.8 $\pm$ 0.6	1.0 $\pm$ 0.7	0.7 $\pm$ 0.4	29.5; <b>0.0003</b>	4.8; <b>0.0078</b>
	Females	11.5 $\pm$ 3.4	5.2 $\pm$ 1.5	3.7 $\pm$ 1.1	5.3 $\pm$ 2.6		
Incidence of facing the centre in a lap <sup>3,4</sup>	Males	21.0 $\pm$ 7.7	11.7 $\pm$ 5.3	7.7 $\pm$ 4.1	4.8 $\pm$ 1.8	1.7; 0.219	6.5; <b>0.0016</b>
	Females	31.2 $\pm$ 12.6	12.7 $\pm$ 3.7	11.3 $\pm$ 4.4	14.8 $\pm$ 5.6		
B							
Behaviour	Group	1st visit	2nd visit	3rd visit	4th visit	Gender effect ( $F_{1,10}$ ; $P$ )	Lap effect ( $F_{1,10}$ ; $P$ )
Speed within the corner zone (cm s <sup>-1</sup> )	Males	17.5 $\pm$ 3.2	21.7 $\pm$ 2.3	26.1 $\pm$ 2.8	23.7 $\pm$ 3.0	1.9; 0.199	6.9; <b>0.001</b>
	Females	20.1 $\pm$ 2.6	27.4 $\pm$ 2.3	28.1 $\pm$ 3.7	29.7 $\pm$ 3.9		

Significant differences are shown in bold.

None of the interactions (lap  $\times$  gender) were significant (data not shown).

There was no significant difference between laps 2, 3 and 4 (Tukey HSD test). Superscript numbers in the 'Behaviour' column indicate the number of the lap from which the first lap significantly differed (Tukey HSD test).

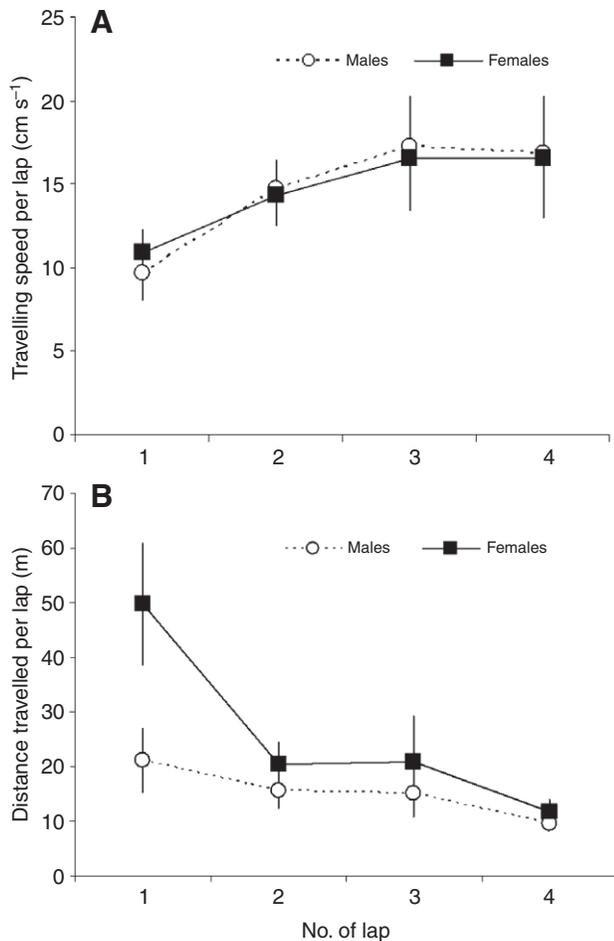


Fig. 3. (A) Travelling speed in the first four laps ( $\text{cm s}^{-1}$ ). Results are shown for males (open circles) and females (filled squares). There was a significant increase in travelling speed between laps (two-way repeated measures ANOVA,  $F_{3, 30}=5.5$ ;  $P<0.004$ ), with a Tukey HSD *post-hoc* test revealing that the first lap differed from all other laps ( $P<0.05$ ). No significant difference between males and females was found ( $F_{1, 10}=0.16$ ;  $P=0.69$ ). Lap  $\times$  gender interaction was not significantly different ( $F_{3, 30}=2.03$ ;  $P=0.13$ ). (B) Travelled distance in the first four laps (m). Results are shown for males (open circles) and females (filled squares). There was a considerable decrease in travelled distance between lap, however, this difference was not significant (two-way repeated measures ANOVA,  $F_{3, 30}=1.94$ ;  $P=0.14$ ). There was a significant difference between males and females ( $F_{1, 10}=37.8$ ;  $P<0.0002$ ), indicating that in each lap females travelled greater distance than males. Lap  $\times$  gender interaction was not significantly different ( $F_{3, 30}=0.49$ ;  $P=0.69$ ).

Of the eight parameters shown in Table 2A, five decreased across the four first laps, reflecting that the mole rats first travelled slowly, so that lap duration was long, and also retreated frequently by backward walk or made frequent U-turns to retrace their former path. They also made frequent stops so that interstop distance was short in the first lap. In some of the stops during the first lap, the animals' trunk was aligned in contact with the arena wall while their head was turned laterally to face the arena centre. These behaviours declined over subsequent laps, in which the mole rats travelled faster, stopped less frequently and at greater inter-stop distances, and rarely retreated or retraced their paths (Fig. 4A).

### Local shortcuts at the arena corners

During the build-up of trajectories along the arena walls another notable change occurred, when the blind mole rats started to 'cut' the arena corners. That is, in early arrivals at a corner they travelled all the way in, sometimes even bumping into the corner. Later on, they started to take 'local' shortcuts at corners by moving in an arched path without entering the corner. Fig. 5A illustrates such behaviour of a mole rat at one corner. Shortcuts occurred differentially at the various arena corners, as detailed in Table 1, bottom. For example, after shortcutting a specific corner, the mole rat could bump into other corners, and each corner took a different number of visits before a shortcut occurred (Table 1). Indeed, shortcuts never occurred in the first visit to a corner, and on average they occurred only at the eighth visit. Another indication that the mole rats learnt the location of the corners was that when entering a corner zone they moved even faster toward that corner (see travel speed at the corner zone shown in Table 2B compared to the general speed shown in Table 2A).

### 'Global' crosscuts through the arena centre

After the build-up of trajectories that encompassed the entire perimeter, another notable change occurred, when the mole rats started to take crosscuts through the centre of the arena. Individual mole rats greatly varied in their tendency to enter the centre, with five of the males and two females doing so frequently whereas the remainder never crossed the centre (Table 1). Of those animals that did cross the centre, six did so from the second lap onward, and one took a crosscut during the first lap (Table 1). This latter exceptional mole rat differed from the others in abandoning the arena walls at the beginning of the experiment. In all, as illustrated in Fig. 4A, crosscuts through the centre occurred at a relatively late stage, typically after the completion of two laps. Once a crosscut had occurred, it was then performed, by most mole rats, at least every other lap (Table 1).

As seen in Fig. 4A, crosscuts did not converge to a specific corner (compare with Fig. 4B showing crosscuts through the centre in home base behaviour of other rodents). Moreover, arena crosscuts did not involve a departure or return to a specific zone. To highlight this aspect, we calculated an average number of crosscuts per zone for departure zones and for return zones. This was performed, for example for departures, by summing for each mole rat the total number of crosscuts and dividing this by the number of zones from which a crosscut had started. We found that in the 12 mole rats, the average ratio ( $\pm$  s.e.m.) was  $1.21 \pm 0.12$  crosscuts per zone for departures, with a maximum ratio of 1.8 crosscuts. A similar calculation for the zones at which crosscuts terminated, revealed an average ratio of  $1.23 \pm 0.07$  crosscuts per zone, with a maximum of 1.6 crosscuts. These ratios indicate that there was no specific zone at which crosscuts were repeatedly originated or terminated. Therefore, crosscuts through the arena centre did not converge or depart from one place but rather diverged over various perimeter zones.

Travelling through the centre was faster compared with the first lap [average  $\pm$  s.e.m. ( $\text{cm s}^{-1}$ ): crosscuts  $26.14 \pm 2.32$ ; first lap  $11.25 \pm 1.98$ ; these were calculated only for mole rats that crossed the centre]. In crosscuts, mole rats typically moved continuously from wall to wall without stopping. Only 11% of all crosscuts included stops, with an average of  $1.22 \pm 0.16$  stops per crosscut (calculated for only crosscuts with stops). Interstop distance during crosscuts was higher compared with the first lap [average  $\pm$  s.e.m. (m):  $1.7 \pm 0.23$ ; compared with the shorter interstop distance shown in Table 2A]. Because of these differences in behaviour, crosscuts do

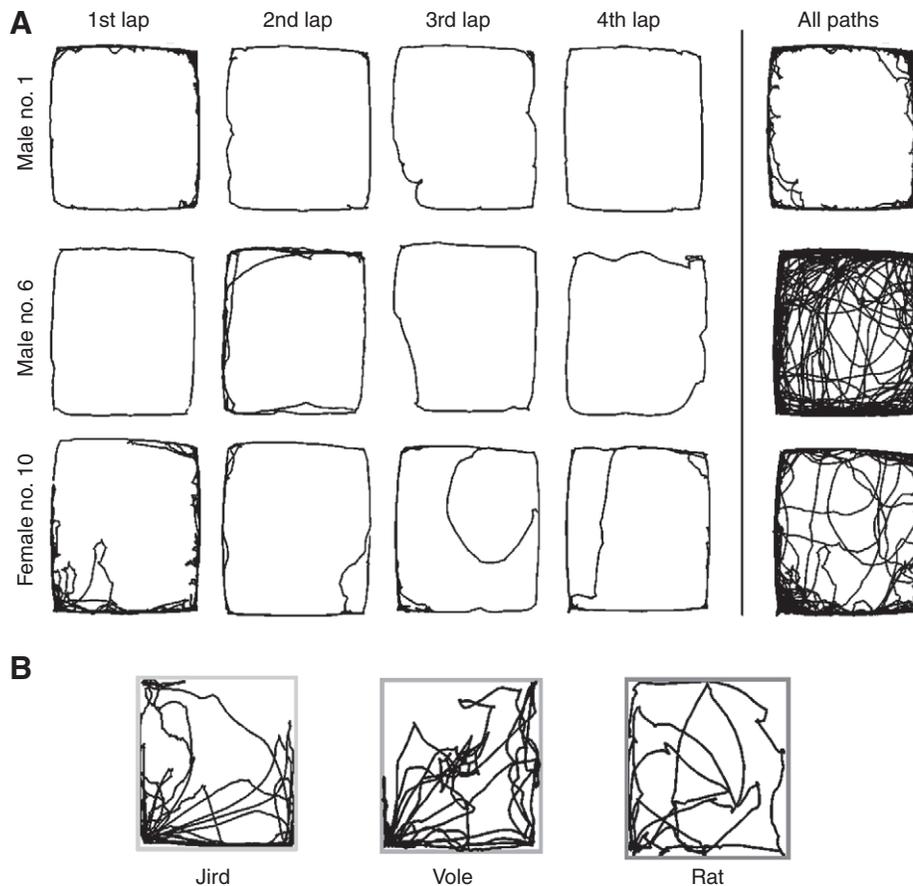


Fig. 4. (A) Exemplary travel paths of three representative mole rats. The first four laps for each mole rat are depicted from left to right. The right column shows the cumulative path for the entire test. In the first lap, the mole rats travelled along the perimeter while retracing travelled segments, with very short detachments from the arena wall. In the following laps, few retracing are seen and the mole rats start to perform corner shortcuts and crosscuts through the centre. As shown in the cumulative path of the entire test, crosscuts did not converge to a specific location. (B) Representative paths of home base behaviour of three other rodent species: a jird (*Meriones tristrami*), a vole (*Microtus socialis*) and a laboratory Long-Evans hooded rat, tested in a 1.8 m × 1.8 m (jird), or 2 m × 2 m (vole and rat) illuminated arena similar to that used in the present study. Paths were taken after the period of home base establishment. As illustrated in these exemplary paths, crosscuts through the centre converge to the home base (the bottom left corner in each rodent path schema), in contrast to the crosscuts of the mole rats (Fig. 3A), which did not regularly converge to a specific sector of the arena. [Image of travel path of a jird was modified from Zadicario et al. (Zadicario et al., 2005).]

not seem to represent exploration of an unfamiliar environment as does the first lap.

Approaching the wall at the end of crosscuts could take a variety of forms. As shown in Table 3, in nearly half of the crosscuts, the mole rats curved their travel path to parallel the wall. Alternatively, mole rats switched to intermittent travel or slowed down toward the wall. These three forms of behaviour, which altogether characterized 70% of the crosscuts, may indicate that the mole rats adjusted their path when approaching the wall. In about 30% of the crosscuts, the animals maintained the same travelling mode from the start to the end of the crosscut, and in only one crosscut, a bump into the wall was noted (Table 3).

As indicated above, crosscuts through the arena centre and corner shortcuts did not characterize the period of build-up (first lap) but were prevalent thereafter in those mole rats that had taken crosscuts and shortcuts. This is shown in Fig. 5B, where the number of corner

shortcuts and centre crosscuts was very low in the first 5 min, when build-up occurred (as seen in the duration of the first lap in Table 2). After 5 min, the number of shortcuts and crosscuts increased and stabilized at a relatively higher rate (Fig. 5B).

## DISCUSSION

In this study, we tested the spatial behaviour of the blind mole rat, a congenitally blind subterranean rodent, exploring an unfamiliar arena. When introduced into a corner of the arena, the mole rat first progressed with frequent stops, retraces and retreats, to gradually build-up a path along the perimeter. Subsequent laps were faster with fewer stops and the mole rats soon started taking shortcuts at arena corners and crosscuts through the arena centre. In the following discussion, we suggest that the gradual build-up of the first lap is a process of spatial calibration in which mole rats obtain a sense of the area available for exploration. In light of the observed change in the mode of exploration after the build-up phase, we suggest that calibration is a primeval form of a cognitive map (global space representation).

### Build-up of activity and patrolling the perimeter

Two phases of exploration were apparent: a build-up phase and a free-locomotion phase. During build-up, mole rats travelled slowly along the perimeter with frequent pauses to turn their head toward the open area, or to retrace/retreat along previously travelled perimeter sectors, until their path encompassed the entire perimeter. The gradual completion of the first lap took a longer time in females, which also displayed more retracing and pausing compared with males. This is in line with the finding that compared with females, male mole rats are quicker to leave the start location and to enter

Table 3. Behaviours displayed by the mole rats when approaching the wall at the end of a crosscut

Behaviour	Frequency	Percentage out of total behaviours
Bumping into the wall	1	1.3
Approaching the wall	22	28.2
Intermittent travel, may include head turns	15	19.2
Slowing down	3	3.8
Curving the path to parallel the wall	37	47.4
Total	78	100.0

Data presented were pooled for all mole rats.

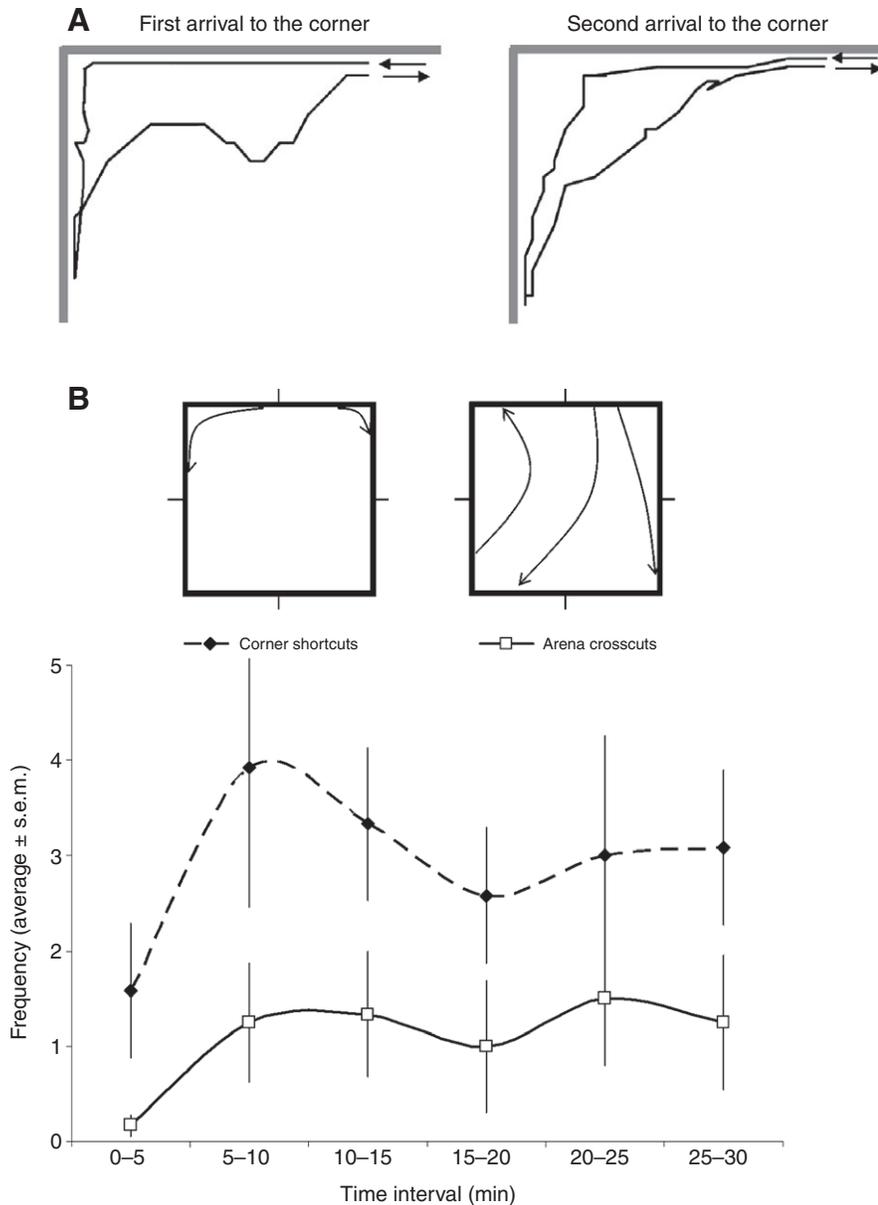


Fig. 5. (A) Shortcuts taken at a corner. In the first visit to the corner (left), the mole rat travelled into the corner. In the second visit (right) it did not reach the corner, but rather travelled in an arc to form a shortcut. Arrows indicate the direction of travel. (B) Number (average  $\pm$  s.e.m.) of corner shortcuts (filled diamonds) and crosscuts through the centre (open squares) throughout the duration of the test, shown for 5 min intervals. Definition of corner shortcuts and crosscuts are depicted at the top part of the figure. In the first 5 min interval the number of corner shortcuts and crosscuts was very low, but in subsequent 5 min intervals they increased and stabilized. A paired *t*-test comparing the first (0–5 min) and second (5–10 min) interval revealed significant differences in both the number of corner shortcuts ( $t_{11}=-2.75$ ,  $P<0.019$ ) and the number of crosscuts ( $t_{11}=-2.5$ ,  $P<0.029$ ).

new areas, due to their active search for females (Heth et al., 1987). Indeed, Heth et al. (Heth et al., 1987) noted that male mole rats had larger territories than females, and that during the breeding season, it is the male that digs its way to the female's burrow. This explanation is similar to the polygyny-range size theory, predicting that polygynous males that actively search for mates, will be better in navigation-related tasks compared with females (Saucier et al., 2008). This theory is considered strongest among those explaining sex differences in spatial ability (Jones et al., 2003). It is therefore possible that the quicker and less 'hesitant' completion of the first lap by males is a result of their presumed adaptation to a larger territory and to their need to search for females. After building-up the first lap, the 'mode' of travel changed, as the mole rats travelled faster, covering greater interstop distances and making fewer stops, head turns, retraces and retreats (see Movie 1 in supplementary material). This change resulted in shorter lap duration and travel distance compared with the first lap, and an appearance of smooth and continuous travel along the perimeter. A reminiscent change in the mode of travel was found in mole rats and rats over successive

exploration trials in a maze (Kimchi and Terkel, 2004), probably indicating an increased familiarity with the environment. A process of build-up of activity was also noted in other animals. For example, in Lorenz's description (Lorenz, 1952) of water shrews, which have relatively poor vision and rely more on their olfactory sense: "In a territory unknown to it, the water-shrew will never run fast... it moves, in strange surroundings, only step by step, whiskering right and left all the time... gradually the little laps of the course which have been 'learned by heart' and which can be covered quickly begin to increase in length as well as in number until they fuse and the whole course can be completed in a fast, unbroken rush."

Spatial behaviour of the studied mole rats was organized as a set of laps that did not converge to a specific area. This is unlike sighted rodent species that, when placed in illuminated environments, organize their locomotion in relation to a focal location or home base, where they spend the greatest cumulative duration of time and perform specific behaviours, e.g. rats (Eilam and Golani, 1989; Hines and Whishaw, 2005); mice (Clark et al., 2006; Drai et al., 2001); spiny mice (Eilam, 2004); voles (Eilam et al., 2003) and jirds

(Zadicario et al., 2005); (see also Fig. 4). When tested in dark environments, some rodent species form a home base (Eilam, 2004; Gorny et al., 2002; Hines and Whishaw, 2005; Nemati and Whishaw, 2007) whereas others first use looping behaviour, travelling in entwined paths that cross to form loops in varying locations, and only then establish a home base (Avni et al., 2006). As opposed to mole rats, the structural unit of home base behaviour is the round trip, which starts at the home base and typically ends in direct dashing back to it (Eilam and Golani, 1989; Whishaw et al., 2001). In the present experiment, although there was one zone where the mole rats spent a significantly greater amount of time, their visits were scattered over the various zones and no direct high-speed travel toward one specific zone was observed. Indeed, a lack of home base behaviour was previously described in the mole rat (Erez, 2005). The organization of exploration as a set of laps is reminiscent of the 'perimeter patrolling' behaviour, which was suggested as a mechanism of gathering information before establishing trails and home base (Avni and Eilam, 2008). However, travelling along the walls by the mole rat may simply be due to its subterranean lifestyle of living in tunnels in its exact body width (Rado et al., 1992; Zuri and Terkel, 1996), and thereby relying on the tactile sensation recorded by the numerous tactile skin sensory structures (Klauer et al., 1997). Indeed, mole rats were shown to be more efficient in navigating in a maze with alleys the width of their body compared with navigating in a wider-alley maze (Kimchi and Terkel, 2004). In other words, the mole rats were able to increase the amount of information gathered during exploration when contiguous with the walls of the arena and thereby stimulating their tactile sensors. In addition to their different spatial organization, sighted rodents tested in dark conditions spend considerably more time in the open areas of the environment than when tested in light conditions (Brillhart and Kaufman, 1991; Eilam, 2004; Price et al., 1984; Zadicario et al., 2005), whereas the mole rats in the present test spent on average 98% of the time in the perimeter (data not shown). Mole rats also differ from sighted rodents in their activity level. As shown in Table 4, activity of mole rats falls near the average of sighted rodent species tested in dark. However, mole rats activity is higher when compared with sighted nocturnal rodents tested in light, but not when compared with a sighted diurnal rodent (the fat sand rat) tested in light. This is in accordance with the diurnal mode of activity in mole rats (Zuri and Terkel, 1996). In all, the results of the present test indicate that mole rats' spatial behaviour differs from that of sighted rodents in a way that calls attention to a possible mechanism of acquiring global spatial representation, as detailed below.

#### Local and global shortcuts (crosscuts)

The ability to perform shortcuts is considered as an indication that the navigator possesses some sort of representation of the environment (Bennett, 1996; O'Keefe and Nadel, 1978; Tolman, 1948). See also Foo et al. (Foo et al., 2007), who demonstrated the use of a beacon located at a target in order to perform a shortcut. The mole rats displayed two types of shortcuts. In repeated visits to the corners of the arena, travel speed when entering the corner zone increased, and the mole rats occasionally took local shortcuts across the corner, without travelling all the way into it. This suggests that they had some way of sensing that they were approaching the corner. They also took global shortcuts, for example between opposite arena walls, but only after completion of the build-up lap.

The ability to take global shortcuts has been described in a variety of rodent species, usually through homing experiments [but see Etienne et al. (Etienne et al., 1998)], for example, rats, mice, gerbils and hamsters are able to take a homing shortcut after reaching a goal (Alyan, 1996; Etienne et al., 2000; Mittelstaedt and Mittelstaedt, 1982; Whishaw et al., 2001). Although shortcuts can be performed by using visual or other external cues, when these are unavailable (e.g. in darkness), animals employ path integration (Maaswinkel and Whishaw, 1999; Shettleworth and Sutton, 2005), the process of computing one's location in relation to its starts point of travelling (Etienne and Jeffery, 2004; Etienne et al., 1996). Indeed, when tested in two maze types, mole rats employed path integration in order to shortcut back to the start location, with the direction of path integration affected by a magnetic compass in some conditions (Kimchi et al., 2004). As opposed to the above mentioned experiments, in the present study there was no target destination for shortcuts. Instead, mole rat crossed the centre to another wall, a behaviour that we termed 'crosscut'. Global crosscuts were not directed to a specific location; rather, they were scattered over all the perimeter zones, reaching an average of  $1.23 \pm 0.07$  crosscuts per zone, with the low standard error indicating that there was no one zone in which many crosscuts terminated. This implies that crosscut ability probably did not depend on visual cues (as the mole rat is blind) or on beacons located at a target terminal for shortcuts. The use of beacons for crosscuts is unlikely since this requires a beacon in each of the zones to which crosscuts were taken (Shettleworth and Sutton, 2005), for example, this would require 23 beacons for the mole rat that took a total of 37 crosscuts to 23 different zones. It should be noted that while mole rats are blind, they possess other capacities such as magnetic field sensation (Kimchi et al., 2004) and seismic vibration sensation (Kimchi et al., 2005; Rado et al., 1998) which could be used for

Table 4. Open field activity of wild and laboratory rodents

Species	Travelled distance (m)		Speed (m min <sup>-1</sup> )		Difference	Duration (min)	Open field	Source
	Lights on	Lights off	Lights on	Lights off				
<b>Mole rat</b>	<b>237±23</b>		<b>8±1</b>			<b>30</b>	<b>2 m×2 m</b>	<b>Present study</b>
Jird ( <i>Meriones tristrami</i> )	172±69	523±91	3±1	10±2	Significant	50	2 m×2 m	Avni et al., 2006
Fat sand rat ( <i>Psammomys obesus</i> )	115±12	122±10	11±0	12±0	n.s.	10	2 m×2 m	Avni and Eilam, 2008
Vole ( <i>Microtus socialis</i> )	181±25	203±34	6±1	7±1	n.s.	30	2 m×2 m	Unpublished data
Spiny mouse ( <i>Acomys cahirinus</i> )	61±9	110 ±12	6±1	11±1	n.a.	10	2 m×2 m	Eilam, 2004
Laboratory rats (Long Evans)	187±13	206±6	6±0	7±0	n.s.	30	22 m×2 m with 1 object	Yaski and Eilam, 2007
Laboratory mice (C57)	93±9	131±13	3±0	4±0	Significant	30	1.55 m diameter	Clark et al., 2006 (Exp 1)

n.a., not available; n.s., non significant.

crosscut guidance. Nevertheless, such capacities polarize the environment, providing directional rather than the positional information provided by beacons (Jacobs and Schenk, 2003).

Global crosscuts involved higher travel speed and greater interstop distance compared with the first lap, indicating that they involve only little, if any, exploration. The fast and uninterrupted travel through the centre also does not seem to be an 'escape' of stressed animals since the mole rats could avoid the centre by remaining at the relatively safe perimeter. Furthermore, before reaching the wall, in most crosscuts, mole rats displayed a change in behaviour compared with the preceding part of the crosscut, smoothly curving their path to parallel the wall (as in corner shortcuts), travelling intermittently up to the wall, or slowing down. Implicit in these behaviours is that the mole rats could estimate their proximity to the wall and adjust their path to preclude bumping (the latter occurred in only one crosscut; see Table 3; Fig. 4; Movie 1 in supplementary material). Indeed, mole rats were previously shown to be able to estimate distances. When trained to traverse a tunnel toward a food reward located in a fixed distance from the start point of the tunnel and then probed without food, mole rats were found to stop and make a U-turn after traversing the distance to the location of the food reward (Marom, 2005). We therefore suggest that the global crosscuts from wall to wall can be interpreted as if the mole rats possessed a representation of the size and perhaps the shape of the environment, which allowed them to compute crosscuts during laps. In other words, the animals might have used a global representation of the arena, perhaps in combination with path integration and/or directional cues such as magnetic compass or seismic vibration, in order to estimate the travelling distance and direction, i.e. the vector needed for a crosscut to another wall.

#### A primitive global map?

Thus far, we have introduced two phases of exploring an unfamiliar environment by the blind mole rat: (a) a gradual build-up of activity; and (b) a subsequent phase of free locomotion along the perimeter combined with crosscuts through the centre. These structural phases raise the question of their function or their underlying mechanisms. Here we suggest that the build-up and free-locomotion phases reflect a gradual establishment of local and then global spatial representation, a sort of primordial 'cognitive map'. A model on the establishment of spatial representation suggests that spatial learning and navigation are based on three phases of information processing (Avni et al., 2006). First is a sequential information processing (piloting) phase, in which animals travel from one landmark to the next. The second travel mechanism is that of parallel information processing (orienting), in which the traveller pilots from landmark to landmark and in parallel maintains a compass direction to a specific location (e.g. home base location). The third phase is that of map-based navigation, or continuous information processing (navigating), which relies on a detailed spatial representation containing 'sets of connected places' and providing 'a large choice of possible paths between any two points in the environment' (O'Keefe and Nadel, 1978). While piloting and orienting have been demonstrated in open field behaviour of rodents (Avni et al., 2006), map-based navigation in the open field has not yet been shown. Nevertheless, we suggest that mole rat behaviour after the first lap seems to reflect a basic form of navigating: the animals appear to travel freely and continuously along the arena walls, taking crosscuts from wall to wall and rounding their paths at the arena corners.

Specifically, we suggest that, upon being introduced into the arena, mole rats first establish an estimate of the size of the available

space and in the subsequent phase they navigate along and within the represented arena. In these hierarchical phases, the build-up of the perimeter path in the first lap seems to be a stage of spatial calibration, in which the mole rats form some representation of the environment in terms of size, and perhaps also of shape (geometry). Whishaw and Brooks (Whishaw and Brooks, 1999) suggested that animals explore their environment in order to calibrate their 'working space'. Indeed, in the build-up phase, the animals travelled slowly with frequent stops and retreats, thus allowing thorough exploration and scanning of the perimeter (Kramer and McLaughlin, 2001; Loewen et al., 2005) while gaining the opportunity to gather the information needed for mapping. Moreover, only after the build-up phase did the mole rats start to take global crosscuts through the centre, which may indicate that they had acquired a basic representation of the arena (O'Keefe and Nadel, 1978; Tolman, 1948) that was probably sufficient to allow an estimation of travel distance to the other wall. Indeed, an observer could notice the change in the behaviour of the mole rats after the build-up phase, when in addition to crosscuts they started to progress faster, in longer bouts, and with less stops and less retreating or retracing. Further support for the notion that mole rats take crosscuts only after gaining a certain estimation of the area size comes from the single mole rat that took a crosscut through the centre in the first build-up lap. This crosscut was tangled compared with the other crosscuts taken by this or other mole rats, indicating that it was not a planned crosscut but rather a search path (Muller and Wehner, 1994; Zadicario et al., 2005). Further research using manipulation of environment size is required for a further understanding of how the build-up phase and the suggested process of calibration act in the process of establishing a spatial representation (map).

In summary, we suggest that the product of the slow and gradual build-up of a perimeter path is a process of spatial calibration – a sort of primeval representation ('map') of the space available for travelling. Exploration in the subsequent phase serves to validate and extend this 'draft' map. We also suggest that this process is probably limited by species-specific perceptual or calibration abilities, and that if the available space is greater than can be estimated by that species' ability, the navigator must ignore, at least initially, some of the available space and focus on exploring only a limited part of the environment. The suggested process may offer a first characterization of the mechanism of build-up that leads to primitive map navigation in the open field. Studying the build-up process may assist in further understanding the process of establishing spatial representation.

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#### REFERENCES

- Alyan, S. H. (1996). Evidence for resetting the directional component of path integration in the house mouse (*Mus musculus*). *Ethology* **102**, 629-638.
- Avni, R. and Eilam, D. (2008). On the border: perimeter patrolling as a transitional exploratory phase in a diurnal rodent, the fat sand rat (*Psammomys obesus*). *Anim. Cogn.* **11**, 311-318.
- Avni, R., Zadicario, P. and Eilam, D. (2006). Exploration in a dark open field: A shift from directional to positional progression and a proposed model of acquiring spatial information. *Behav. Brain Res.* **171**, 313-323.
- Bennett, A. T. D. (1996). Do animals have cognitive maps? *J. Exp. Biol.* **199**, 219-224.
- Brillhart, D. B. and Kaufman, D. W. (1991). Influence of illumination and surface structure on space use by prairie deer mice (*Peromyscus maniculatus bairdii*). *J. Mammal.* **72**, 764-768.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition* **23**, 149-178.
- Cheng, K. (2005). Reflections on geometry and navigation. *Connec. Sci.* **17**, 5-21.

- Cheng, K. and Gallistel, C.** (2005). Shape parameters explain data from spatial transformations: comment on Pearce et al. (2004) and Tommasi and Polli (2004). *J. Exp. Psychol. Anim. Behav. Process.* **31**, 254-259.
- Clark, B. J., Hamilton, D. A. and Whishaw, I. Q.** (2006). Motor activity (exploration) and formation of home bases in mice (C57BL/6) influenced by visual and tactile cues: modification of movement distribution, distance, location, and speed. *Physiol. Behav.* **87**, 805-816.
- Cooper, H. M., Herbin, M. and Nevo, E.** (1993). Visual system of a naturally microphthalmic mammal: the blind mole rat, *Spalax ehrenbergi*. *J. Comp. Neurol.* **328**, 313-350.
- Drai, D., Kafkafi, N., Benjamini, Y., Elmer, G. and Golani, I.** (2001). Rats and mice share common ethologically relevant parameters of exploratory behavior. *Behav. Brain Res.* **125**, 133-140.
- Eilam, D.** (2004). Locomotor activity in common spiny mice (*Acomys cahirinuse*): the effect of light and environmental complexity. *BMC Ecol.* **4**, 16.
- Eilam, D. and Golani, I.** (1989). Home base behavior of rats (*Rattus norvegicus*) exploring a novel environment. *Behav. Brain Res.* **34**, 199-211.
- Eilam, D. and Shefer, G.** (1992). Reversal of interleg coupling in backward locomotion implies a prime role of the direction of locomotion. *J. Exp. Biol.* **173**, 155-163.
- Eilam, D., Dank, M. and Maurer, R.** (2003). Vole scale locomotion to the size of the open-field by adjusting the distance between stops: a possible link to path integration. *Behav. Brain Res.* **141**, 73-81.
- Erez, A.** (2005). Behavioral and morphological aspects in the blind mole-rat *Spalax ehrenbergi*. MSc Thesis, Tel Aviv University, Israel.
- Etienne, A. S. and Jeffery, K. J.** (2004). Path integration in mammals. *Hippocampus* **14**, 180-192.
- Etienne, A. S., Maurer, R. and Seguinot, V.** (1996). Path integration and its interaction with visual landmarks. *J. Exp. Biol.* **199**, 201-209.
- Etienne, A. S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J. and Seguinot, V.** (1998). Navigation through vector addition. *Nature* **396**, 161-164.
- Etienne, A. S., Boulens, V., Maurer, R., Rowe, T. and Siegrist, C.** (2000). A brief view of known landmarks reorients path integration in hamsters. *Naturwissenschaften* **87**, 494-498.
- Foo, P., Duchon, A., Warren, W. Jr and Tarr, M.** (2007). Humans do not switch between path knowledge and landmarks when learning a new environment. *Psychol. Res.* **71**, 240-251.
- Gallistel, C. R.** (1990). *The Organization of Learning*. Cambridge: Bradford/MIT Press.
- Gorny, J. H., Gorny, B., Wallace, D. G. and Whishaw, I. Q.** (2002). Fimbria-fornix lesions disrupt the dead reckoning (homing) component of exploratory behavior in mice. *Learn. Mem.* **9**, 387-394.
- Heth, G., Nevo, E. and Beiles, A.** (1987). Adaptive exploratory-behavior-differential patterns in species and sexes of subterranean mole rats. *Mammalia* **51**, 27-37.
- Hines, D. J. and Whishaw, I. Q.** (2005). Home bases formed to visual cues but not to self-movement (dead reckoning) cues in exploring hippocampectomized rats. *Eur. J. Neurosci.* **22**, 2363-2375.
- Jacobs, L. F. and Schenk, F.** (2003). Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychol. Rev.* **110**, 285-315.
- Jones, C., Braithwaite, V. and Healy, S.** (2003). The evolution of sex differences in spatial ability. *Behav. Neurosci.* **117**, 403-411.
- Kimchi, T. and Terkel, J.** (2001a). Magnetic compass orientation in the blind mole rat *Spalax ehrenbergi*. *J. Exp. Biol.* **204**, 751-758.
- Kimchi, T. and Terkel, J.** (2001b). Spatial learning and memory in the blind mole-rat in comparison with the laboratory rat and Levant vole. *Anim. Behav.* **61**, 171-180.
- Kimchi, T. and Terkel, J.** (2003). Detours by the blind mole-rat follow assessment of location and physical properties of underground obstacles. *Anim. Behav.* **66**, 885-891.
- Kimchi, T. and Terkel, J.** (2004). Comparison of the role of somatosensory stimuli in maze learning in a blind subterranean rodent and a sighted surface-dwelling rodent. *Behav. Brain Res.* **153**, 389-395.
- Kimchi, T., Etienne, A. and Terkel, J.** (2004). A subterranean mammal uses the magnetic compass for path integration. *Proc. Natl. Acad. Sci. USA* **101**, 1105-1109.
- Kimchi, T., Reshef, M. and Terkel, J.** (2005). Evidence for the use of reflected self-generated seismic waves for spatial orientation in a blind subterranean mammal. *J. Exp. Biol.* **208**, 647-659.
- Klauer, G., Burda, H. and Nevo, E.** (1997). Adaptive differentiations of the skin of the head in a subterranean rodent, *Spalax ehrenbergi*. *J. Morphol.* **233**, 53-66.
- Kramer, D. L. and McLaughlin, R. L.** (2001). The behavioral ecology of intermittent locomotion. *Am. Zool.* **41**, 137-153.
- Loewen, I., Wallace, D. G. and Whishaw, I. Q.** (2005). The development of spatial capacity in piloting and dead reckoning by infant rats: use of the huddle as a home base for spatial navigation. *Dev. Psychobiol.* **46**, 350-361.
- Lorenz, K.** (1952). *King Solomon's Ring: New Light on Animals Ways*. New York: Meridian Books.
- Maaswinkel, H. and Whishaw, I. Q.** (1999). Homing with locale, taxon, and dead reckoning strategies by foraging rats: sensory hierarchy in spatial navigation. *Behav. Brain Res.* **99**, 143-152.
- Marom, Y.** (2005). Path integration as a navigation tool in the blind mole rat (*Spalax ehrenbergi*). Msc Thesis, Tel Aviv University, Israel.
- Mendelsohn, H. and Yom-Tov, Y.** (1999). *Fauna palaestina: Mammalia of Israel*. Jerusalem: Keterpress Enterprises.
- Mittelstaedt, H. and Mittelstaedt, M. L.** (1982). Homing by path integration. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 290-297. Berlin: Springer Verlag.
- Muller, M. and Wehner, R.** (1994). The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **175**, 525-530.
- Nemati, F. and Whishaw, I. Q.** (2007). The point of entry contributes to the organization of exploratory behavior of rats on an open field: an example of spontaneous episodic memory. *Behav. Brain Res.* **182**, 119-128.
- Nevo, E.** (1999). *Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Global Convergence*. Oxford: Oxford University Press.
- 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.
- O'Keefe, J. and Nadel, L.** (1978). *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.
- Oster, H., Avivi, A., Joel, A., Albrecht, U. and Nevo, E.** (2002). A switch from diurnal to nocturnal activity in *S. ehrenbergi* is accompanied by an uncoupling of light input and the circadian clock. *Curr. Biol.* **12**, 1919-1922.
- Price, M. V., Waser, N. M. and Bass, T. A.** (1984). Effects of moonlight on microhabitat use by desert rodents. *J. Mammal.* **65**, 353-356.
- Rado, R., Wollberg, Z. and Terkel, J.** (1992). Dispersal of young mole rats (*Spalax ehrenbergi*) from the natal burrow. *J. Mammal.* **73**, 885-890.
- 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.* **183**, 503-511.
- Saucier, D., Shultz, S., Keller, A., Cook, C. and Binsted, G.** (2008). Sex differences in object location memory and spatial navigation in Long-Evans rats. *Anim. Cogn.* **11**, 129-137.
- Shettleworth, S. J. and Sutton, J. E.** (2005). Multiple systems for spatial learning: dead reckoning and beacon homing in rats. *J. Exp. Psychol.* **31**, 125-141.
- Tolman, E.** (1948). Cognitive maps in rats and men. *Psychol. Rev.* **55**, 89-208.
- Whishaw, I. Q. and Brooks, B. L.** (1999). Calibrating space: exploration is important for allothetic and idiothetic navigation. *Hippocampus* **9**, 659-667.
- Whishaw, I. Q., Hines, D. J. and Wallace, D. G.** (2001). Dead reckoning (path integration) requires the hippocampal formation: evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) test. *Behav. Brain Res.* **127**, 49-69.
- Yaski, O. and Eilam, D.** (2007). The impact of landmark properties in shaping exploration and navigation. *Anim. Cogn.* **10**, 415-428.
- Zadicario, P., Avni, R., Zadicario, E. and Eilam, D.** (2005). 'Looping'- an exploration mechanism in a dark open field. *Behav. Brain Res.* **159**, 27-36.
- Zuri, I. and Terkel, J.** (1996). Locomotor patterns, territory, and tunnel utilization in the mole-rat *Spalax ehrenbergi*. *J. Zool.* **240**, 123-140.