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Spatial learning and memory in the blind mole-rat in comparison with the laboratory rat and Levant vole

TALI KIMCHI & JOSEPH TERKEL
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel-Aviv University

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Studies dealing with spatial orientation in mammals have mostly dealt with surface-dwelling species. We studied the ability of a subterranean rodent to orient in space and compared it with two species of rodents that spend most of their lives above ground. The solitary blind mole-rat, *Spalax ehrenbergi*, inhabits an extensive, branching tunnel system that it digs itself and in which it spends its entire life. We examined its ability to learn and remember a winding path towards a goal in a multiple labyrinth and compared it with Levant voles, *Microtus guentheri*, and laboratory rats, *Rattus norvegicus*. The mole-rats learned significantly faster than the rats and voles. Furthermore, their ability to remember the maze was significantly better than that of the rats after 2, 7, 30 and 60 days from the end of the learning experiment and significantly better than the voles after 120 days. The mole-rats still retained ca. 45% of their optimal performance at the end of the learning experiment after 4 months compared with 20% for the voles after 4 months and less than 20% for the rats after 2 months. Despite having lost its vision, the mole-rat was thus more able to orient in a complex maze than the surface-dwelling vole and laboratory rat. We suggest that the mole-rat compensates for the sensory limitations imposed by the subterranean niche and for its loss of vision by relying on the Earth's magnetic field and internal cues to steer its course efficiently. We discuss the possible mechanisms of orientation.

Successful foraging, reproduction, predator avoidance and territorial defence all depend on accurate spatial orientation or spatial localization of food patches, mates, escape routes and neighbours (Able 1980). Almost all the research to date relating to spatial orientation has been carried out on animals that live above ground (for review see Schmidt-Koening & Keeton 1978; Able 1980; Healy 1998), while little has been done on subterranean mammals, mainly because of the inherent difficulties in observing and studying them both in the laboratory and in the field (Burda et al. 1990). The existing evidence comes primarily from field studies that have focused either on homing behaviour in *Geomys* (Howard & Childs 1959) and *Scapanus* (Giger 1973), or on the ability to avoid obstacles by digging bypass tunnels in *Cryptomys* (Eloff 1951), *Tachyoryctes* (Jarvis & Sale 1971), *Heterocephalus* (Brett 1991), *Geomys* (Reichman & Smith 1990) and *Talpa* (Armstrong & Quilliam 1961). These studies support the notion that subterranean mammals possess a highly developed spatial orientation ability.

Of all the subterranean rodents, the blind mole-rat, *Spalax ehrenbergi*, seems to show the most extreme adaptations to life underground (MacDonald 1985). It is a solitary fossorial rodent that excavates and inhabits a sealed system of branching underground tunnels with no external above-ground exits. The tunnels, which the mole-rat digs to its own body width, link food storage areas, toilet chambers and a sleeping nest. The mole-rat spends its entire life in this tunnel system and never leaves it unless forced to. Spatial orientation within this underground environment must be based on a restricted sensory input, as auditory and visual cues are limited. A highly developed directional sense (Hildebrand 1985) and the ability to learn a tunnel system would seem to be essential for navigation of the mole-rat's complex tunnel system. There would also be a strong evolutionary advantage to precise orientation to avoid unnecessary digging in the soil, which incurs energetic costs (Vleck 1979) and risk of overheating (Rado et al. 1993).

We examined the ability of mole-rats to learn and remember a complex maze, compared with voles, *Microtus guentheri*, and laboratory rats, *Rattus norvegicus*. We hypothesized that the ability of the mole-rat to orient in, learn and remember a maze, as a result of the evolutionary pressures of living in a closed tunnel system, would be superior to that of voles and rats, which use underground

Correspondence: T. Kimchi, Department of Zoology, George S. Wise Faculty of Life Sciences, Tel-Aviv University, Tel-Aviv, 69978, Israel (email: kimhita@post.tau.ac.il).

tunnel systems but spend much of their life above ground.

For an animal to possess an efficient spatial orientation ability it must also possess spatial memory, that is, of the location in space of places that are vital to survival, such as food sources, home base, potential predator or conspecific sites, and to keep track of those locations (Olton 1979; Roberts 1992). Therefore, we first examined the capacity of the three species of rodents to learn a complex maze, and then their ability to remember it for up to 4 months.

METHODS

Study Animals

We used three species of adult animals of both sexes: 48 blind mole-rats, 40 Levant voles and 45 laboratory rats. The mole-rats and the voles were captured in the field in the Tel-Aviv area and the laboratory rats were purchased from the Biology and Medicine Research Colony at Tel-Aviv University, Israel. All animals were housed in plastic cages (38 × 33 cm and 15 cm high) in small groups (four or five individuals from the same species and sex in a cage), except for the mole-rats, which were housed individually in plastic cages (43 × 27 and 18 cm high). The cages contained wood shavings for bedding, and the animals were fed rat pellets, carrots and apples ad libitum; water was available for the rats and the voles ad libitum while the mole-rats obtained sufficient water from their food. The animals were maintained in the laboratory at a constant temperature (24–26°C) under a 14:10 h light:dark regime (corresponding to the local light:dark regime at that time in the field).

Apparatus

The complex maze (110 × 110 cm and 9 cm high: Fig. 1) was constructed of three elements. The floor was a piece of vinyl sheeting on a plywood board. The maze itself was constructed from plywood panels with Formica finish on both sides. The panels were 9 cm high, 10 mm thick and spaced 8 cm apart to form a tunnel 8 cm wide. The maze pathway consisted of six choice points and one correct path leading to the end of the maze at the opposite end from the entrance. The maze was placed on the vinyl sheet and covered with a transparent Perspex lid 110 × 110 cm. The maze entrance and exit were each fitted with a Perspex tube (30 cm long and 6 cm in diameter) with a movable door that closed after the animal had gone through. The tube inserted into the maze exit was attached to a sealed plastic cage which contained a food reward (see Procedure).

At the end of each trial we cleaned the maze by replacing the vinyl sheeting on the maze floor with clean new sheeting, and by washing the walls with alcohol (70%). The experiment took place in a room without any external windows. Lighting was provided by two fluorescent lights (40 W) attached to the ceiling. The maze was placed in the centre of the room about 1.5 m from the walls. The experiments were recorded by a remote-controlled video camera (Sony, Model no. CCD-TR490E) connected to a monitor (JVC, Model no. VM-14PSN).

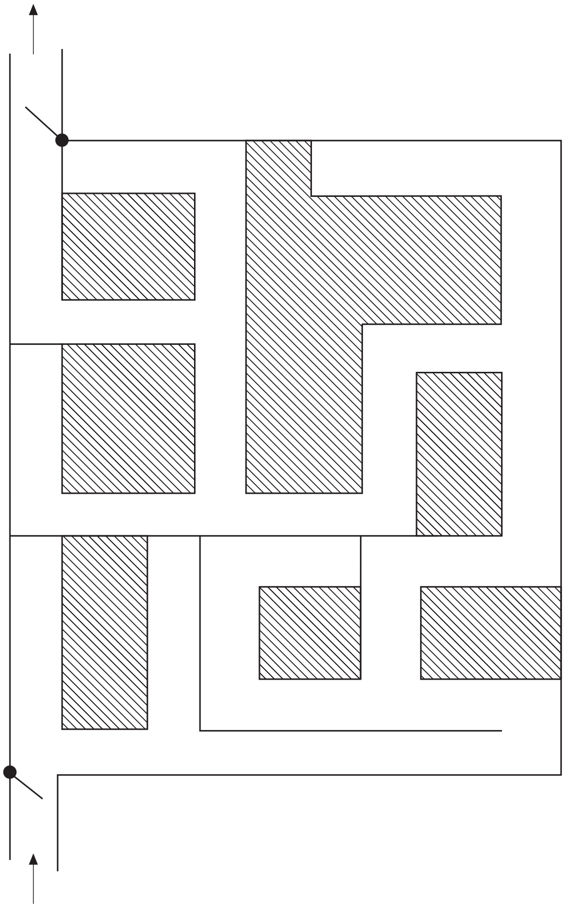

Figure 1. Complex maze used to test spatial learning and memory in the mole-rat, laboratory rat and Levant vole.

Procedure

For all three species the test procedure was the same unless otherwise indicated. To increase motivation to explore and learn the maze we deprived the animals of food for a fixed time interval prior to testing (for further details see Ethical note).

Two days before each test, we placed each animal in a plastic cage connected to a Perspex tube (20 cm long, 7 cm in diameter), the distal end of which was sealed by a plastic cap that could be removed easily. At the beginning of the trial the tube attached to the cage was fitted to the Perspex tube attached to the maze entrance. Thus we could transfer the animals to the maze without handling them. A trial began when the movable door in the entrance was lifted, allowing the test animal to enter the maze, and terminated either when it reached the goal box or after 20 min if it failed to do so. Each animal that reached the exit plastic cage obtained the reward of a small piece (0.5 cm^3) of apple. At the end of each trial we returned the animal to its home cage in the plastic transfer tube. The experiments took place at the time of day when each species is known to be most active. Mole-rat tests began at 1000 hours (according to the activity time observed by Rado et al. 1993), vole tests began at 1400 hours (Cohn-Shlagman 1981; Benjamini 1989) and rat tests at 1900 hours (Barnett 1963; Hart 1982). We recorded three parameters: (1) time required to reach the end of the maze; (2) number of errors made; and (3) total distance travelled during each trial.

Learning (acquisition) experiment

Each animal underwent five consecutive trials daily for 3 consecutive days. The animals were tested in eight groups (five or six individuals/group). All members of each group completed a trial before the group proceeded to the next trial. At the end of each learning day the animals were returned to their cages and provided with water and sufficient food to maintain their body weight at 80–85% of full weight during the 3 days of the experiment (see Ethical note).

Memory (retention) experiment

To determine whether the three species differ in their retention of maze learning, all the animals took part in a retention test. The animals in each species were divided into five random groups (8–10 individuals/group). Each animal was tested only once at only one of the five time intervals: 2, 7, 30, 60 or 120 days from the end of the learning experiment. Each group of animals was food deprived for a fixed time interval prior to the test period (see Ethical note). At the end of the single-day memory experiment the animals received food and water ad libitum.

Ethical Note

In a pilot study we found that when the animals were satiated they were not motivated to reach the end of the complex maze. Although the use of a simpler maze might have overcome this problem, such a solution would have missed the purpose of the experiment, since our goal was to test the three species in a situation closely resembling the complex tunnel systems that they occupy in their natural habitat. Therefore, to increase the motivation of these animals to explore the test apparatus, we limited their food consumption, but to an extent that did not cause physical, behavioural or health problems. We ran a preliminary test in which the rats and voles were food deprived (water remained available ad libitum) for 24–26 h prior to being placed in the maze. During this period the animals never reached less than 85% of their initial body weight. The mole-rats were food deprived for 22–24 h, at which time they reached 80–85% of their initial body weight. In all three species, animals that were food deprived for a shorter period failed to complete the maze, and were unable to learn it. The same procedure was followed in the actual learning experiment. All of the deprived animals returned to their initial body weight within 4 days of the 3-day learning experiment. Just prior to the memory experiment the animals were again food deprived, and a day later were provided with food ad libitum. The mole-rats and voles were then released at their site of capture in good physical condition.

As we are aware that in nature rats, voles and mole-rats might not experience such a long period of food deprivation, our future studies on spatial orientation will seek other ways of motivating the animals to complete the tasks.

Statistical Analysis

We performed all statistical tests with Statistica software for Windows (Statsoft, Inc. Tulsa, OK, U.S.A.). To determine whether there were sex differences in the three species tested, we used a two-way repeated measures ANOVA in the learning experiments (trial × sex) and memory experiments (retention groups × sex) for the three parameters recorded for each species.

Learning experiment

To determine whether there were differences between the performances of the three species in the initial trial of the learning experiment we first used one-way ANOVA for each of the three parameters tested (time, number of errors or path length). This was followed by two-tailed unpaired *t* tests to examine differences between the species (mole-rats × rats; mole-rats × voles).

In comparative learning studies learning rate can be very informative when the starting points of the learning curves are the same. Since the starting points of our three species did not meet the above criterion (see Results) we compared their learning rates following Dukas & Real (1991) for stage 1 and Sokal & Rohlf (1981) for stages 2 and 3.

(1) Stage 1. To estimate the best learning curve fit for each species, we used User-Specified Nonlinear Regression analysis with Statistica software. The best learning curve was established by calculating the coefficient of determination (R^2) for each learning curve.

(2) Stage 2. To linearize ($Y=a+bX$) the relationship between the dependent (time, number of errors or path length) and independent (trials) variables for each species we used reciprocal transformations. This enabled us to calculate the slope (b) of each learning curve that indicated the species' learning rate.

(3) Stage 3. We used Tukey tests to examine differences between the learning rates of the three species by comparing the slopes of the linear regression lines (b) of all three.

To examine day to day differences in retention performance between the three species during acquisition (medium-term memory, see McFarland 1981), we used the two-tailed *t* test for dependent samples, comparing the performance of the last trial of each day to the first trial on the following day, that is, trial 5 to trial 6, and trial 10 to trial 11 for each species.

Table 1. Two-way ANOVAs of maze performance (time, number of errors and path length) of male versus female mole-rats, rats and voles in the learning and memory experiment

	Mole-rats		Rats		Voles	
	F	*P*	*F*	*P*	*F*	*P*
Learning experiment						
Time	0.08	NS	0.16	NS	0.67	NS
Number of errors	0.08	NS	0.31	NS	0.55	NS
Path length	0.15	NS	0.69	NS	0.13	NS
Memory experiment						
Time	0.36	NS	0.86	NS	1.56	NS
Number of errors	0.34	NS	0.42	NS	0.55	NS
Path length	0.52	NS	0.56	NS	0.32	NS

ANOVAs were sex × trial in the learning experiment and sex × retention group in the memory experiment. The degrees of freedom in the learning experiment are 1 (two sexes) and 690, 645, 570 ((five trials × number of subjects)−(15 trials × two sexes)) for mole-rats, rats and voles, respectively. The degrees of freedom in the memory experiment are 1 and 46, 43 and 38 (total number of subject—two sexes) for mole-rats, rats and voles, respectively. See Appendix for raw data.

Memory experiment

To examine differences between the performances of the three species in long-term memory (McFarland 1981) we used the following procedure.

(1) We calculated the success rate of each individual in retaining the performance it had at the end of the learning experiment, after each time interval (2, 7, 30, 60 or 120 days), using the following formula: $(a-b)/(a-c)$, where a=performance in trial 1 in the learning experiment, b=performance in the memory experiment, c=performance in trial 15 (last trial) in the learning experiment. The success rate values are from 0 to 1 (or 0–100%); a success rate of 1 could be attained only if the performance of the animal in the memory experiment was equal to that at the last trial in the learning experiment.

(2) To determine whether there were differences in the performance of the three species in long-term memory we compared the success rate of the three species at each time interval using Kruskal–Wallis and Tukey tests to compare each two species.

RESULTS

Sex Differences

No significant sex differences were found in the time, number of errors and path length required by the voles, rats or mole-rats to reach the end of the maze in the learning or memory experiment (Table 1, Appendix).

Learning Experiment

The performance of the three species differed significantly in the first trial (one-way ANOVA: time: $F_{2,127}=61$, $P<0.0001$; errors: $F_{2,127}=111$, $P<0.0001$; path length: $F_{2,127}=95$, $P<0.001$; Fig. 2).

The learning curve of the three species was highly correlated with an exponential growth regression ($R^2>0.9$), expressed by the formula: $Y=a+b\mathrm{e}^{cx}$ (Fig. 3). After linearizing the exponential learning curve we compared the learning rate (curve slopes) of the three species. The learning rate of the mole-rats was significantly higher than that of the voles (Tukey test: $P<0.001$) in all three parameters, and higher than that of the rats (Tukey test: $P<0.05$) for time and path length (Table 2). The voles had the lowest learning rate among the three species in all three parameters (Table 2).

Medium-term memory

Since all the animals were exposed to the maze for 3 consecutive days we could examine their medium-term memory by comparing the first trial of a given day to the last trial of the previous day. Although the rats' performance in the first trial of the second and third day was significantly lower than in the last trial of the previous day (paired t test: trial 5 versus trial 6: time: $t_{44}=7.95$, $P<0.001$; errors: $t_{44}=7.24$, $P<0.001$; path: $t_{44}=7.5$, $P<0.001$; and for trial 10 versus trial 11: time: $t_{44}=8.8$, $P<0.001$; errors: $t_{44}=9.4$, $P<0.001$; path: $t_{44}=9.5$, $P<0.001$), no change in performance was shown by the mole-rats (paired t test: trial 5 versus trial 6: time: $t_{47}=1.2$,

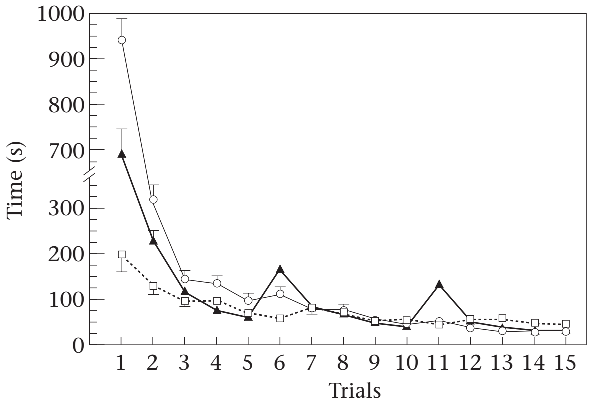

Figure 2. Time (s) ±SE required by the mole-rats (○), rats (▲) and voles (□) to reach the end of the complex maze in 15 trials.

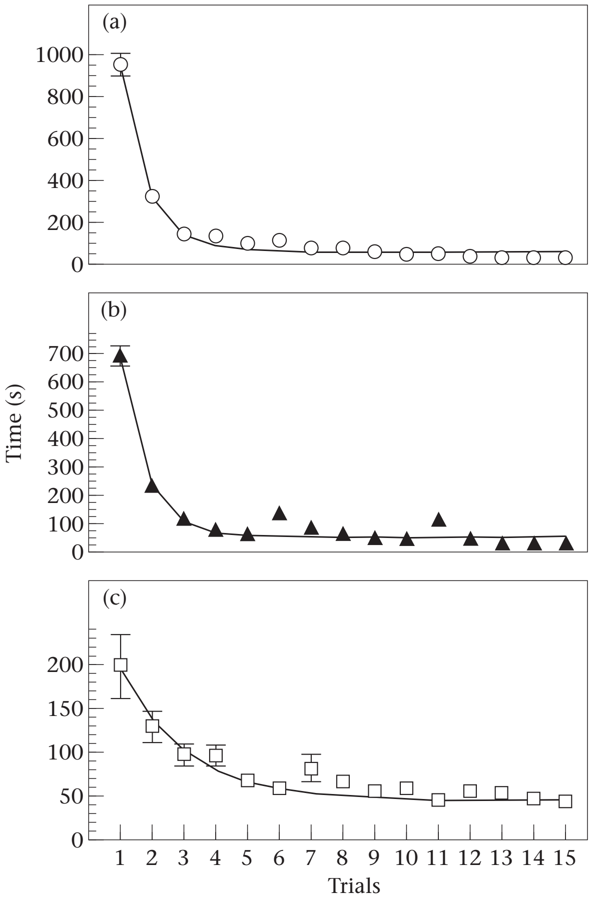

Figure 3. Best learning curves calculated for (a) mole-rats, (b) rats and (c) voles with mean time+SE as the parameter. (a) $Y=62.1+2796e^{-1.16X}$, $R^2=0.987$; (b) $Y=51.9+2203e^{-1.23X}$, $R^2=0.993$; (c) $Y=45+2390e^{-0.48X}$, $R^2=0.974$. Note that the scales of the Y axis differ in the three plots.

NS; errors: $t_{47}=1.3$, NS; path: $t_{47}=7.5$, NS; and for trial 10 versus trial 11: time: $t_{47}=1.6$, NS; errors: $t_{47}=0.1$, NS; path: $t_{47}=0.3$, NS) or by the voles (paired t test: trial 5 versus trial 6: time: $t_{39}=1.41$, NS; errors: $t_{39}=1.26$, NS; path: $t_{39}=0.1$, NS; and for trial 10 versus trial 11: time: $t_{39}=1.8$, NS; errors: $t_{39}=1.0$, NS; path: $t_{39}=0.6$, NS; Fig. 4).

Long-term memory

We tested long-term memory by measuring the performance of the experimental animals 2, 7, 30, 60 and 120 days after the learning experiment. However, since the rat performed poorly on the 60-days memory test, they were not tested at 120 days. Kruskal–Wallis tests revealed significant differences in the performances of the three species in all three parameters recorded in all five groups: 2-days retention (time: $H_{2,31}=15.4$, $P<0.0005$; errors: $H_{2,31}=14.1$, $P<0.001$; path: $H_{2,31}=8.9$, $P<0.01$), 7-days retention (time: $H_{2,29}=12.9$, $P<0.005$; errors: $H_{2,29}=6.04$, $P<0.05$; path: $H_{2,29}=10.8$, $P<0.005$), 30-days retention (time: $H_{2,29}=8.6$, $P<0.05$; errors: $H_{2,29}=6.3$, $P<0.05$; path: $H_{2,29}=6.05$, $P<0.05$) and 60-days retention (time: $H_{2,30}=9.4$, $P<0.01$; errors: $H_{2,30}=13.7$, $P<0.001$; path: $H_{2,30}=16.4$, $P<0.01$).

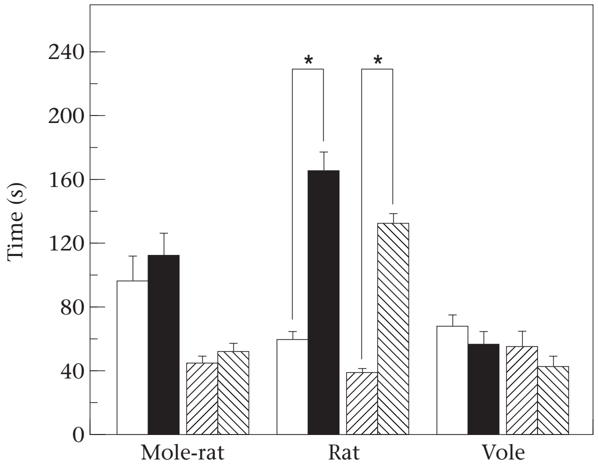

Figure 4. Mean time+SE required to reach the end of the maze in trial 5 (□) and trial 10 (▨) compared to trial 6 (■) and trial 11 (▧), respectively. Both trial 6 and trial 11 were performed 20 h after the previous trial. *$P<0.001$, t test for dependent samples.

The mole-rats' memory of the maze 7, 30 and 60 days after the learning experiment was significantly better than that of the rats for all three parameters and significantly better than that of the voles after 120 days for time and number of errors (Fig. 5). The voles performed significantly better than the rats in the 30- and 60-days memory tests for number of errors and path length, whereas in the 7-days memory retention test the voles performed better than the rats only with regard to path length (Fig. 5).

DISCUSSION

Sex Differences

We did not find any sex differences in either the ability to learn and navigate in a complex maze or in long-term

Table 2. Learning rates ±SE of mole-rats, rats and voles in the parameters time, number of errors and path length

Parameter	Mole-rats (N=48)	Rats (N=45)	Voles (N=40)
Time	0.0033±0.0002	0.0025±0.0002	0.0019±0.0003
Number of errors	0.039±0.002	0.036±0.003	0.029±0.001
Path length	0.0131±0.0026	0.0068±0.0004	0.0050±0.0007

Values of the learning rates represent mean calculated slope (b) of the linearized (using reciprocal transformation) learning curves (see Methods for further details).

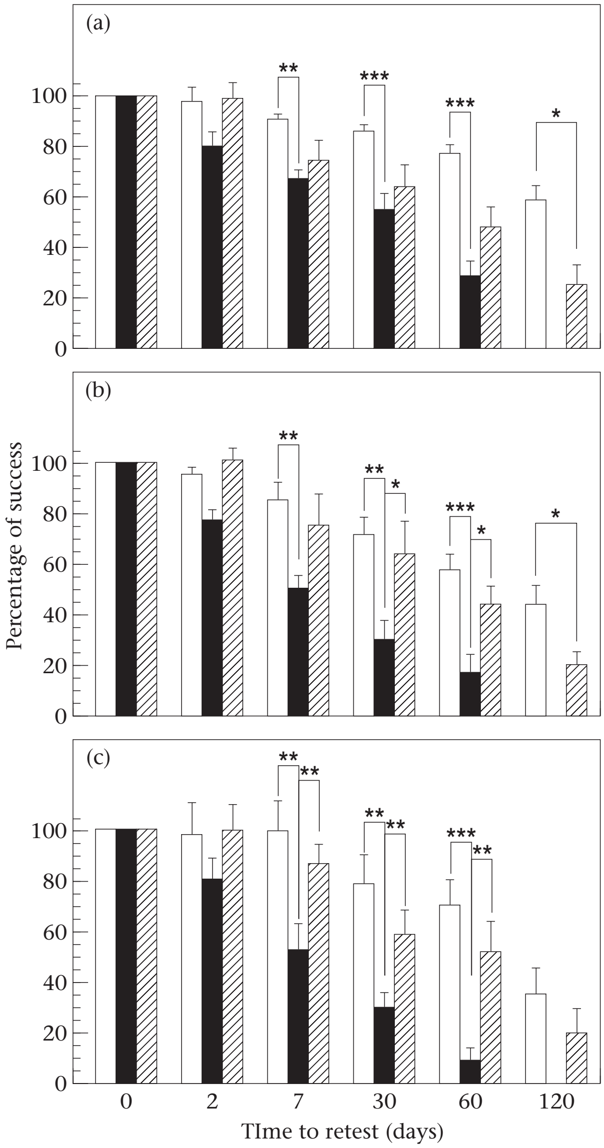

Figure 5. Long-term memory in mole-rats (☐), rats (■) and voles (▨). Mean+SE retention of performance (2, 7, 30, 60 or 120 days after learning experiment) for (a) time, (b) number of errors and (c) path length. The retention rate for each species was calculated as: $(a-b)/(a-c)$, where a=performance in trial 1 in the learning experiment, b=performance in the memory experiment, c=performance in trial 15 (last trial) in the learning experiment. $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$, Tukey test.

spatial memory in mole-rats, Levant voles and laboratory rats. Previous studies have reported conflicting results regarding sex differences in maze learning in a variety of rodent species, using several types of spatial tasks (see reviews by Harris 1978; Halpern 1986; Gaulin & Hoffman 1988). Males have been reported to perform better than females in meadow voles, *Microtus pennsylvanicus*, tested in a water maze (Kavaliers et al. 1998), in symmetrical mazes (Gaulin & FitzGerald 1989) and in a radial maze (Gaulin & FitzGerald 1986); laboratory rats tested in an open maze (Barrett & Ray 1970), in a T maze (Means & Dent 1991) and in a radial maze (Dawson 1972); and inbred mice, *Mus musculus*, tested in a radial maze (Mishima et al. 1986). In contrast**,** no sex differences were found in the performance of prairie voles, *Microtus ochrogaster*, tested in a symmetrical maze (Gaulin & FitzGerald 1989) and in a water maze (Sawrey et al. 1994); montane voles, *Microtus montanus*, tested in a water maze (Sawrey et al. 1994); laboratory rats tested in a radial maze (van Haaren et al. 1987); and inbred strains of mice tested in a radial maze (Lambertty & Gower 1988) and in a water maze (Berger-Sweeney et al. 1995).

Sex differences in spatial orientation tasks of rodents have often been related to male–female differences in home range size. Gaulin & FitzGerald (1986, 1989) noted that the male advantage in maze tasks is limited to those species in which males have naturally larger home ranges than females. In species in which male home range increases during the breeding season, for example, in deer mice, *Peromyscus maniculatus* (Wolff 1989) and meadow voles (Madison and McShea 1987), males perform better than females in spatial orientation tasks only during the breeding season (Gaulin & FitzGerald 1989; Galea et al. 1996). However, in both pine voles, *Microtus pinetorum*, and prairie voles, where home range sizes are sexually isometric, spatial performance of the two sexes is the same (Gaulin & FitzGerald 1989; Sawrey et al. 1994).

Field studies on mole-rats (Zuri & Terkel 1996), wild rats (Barnett 1963) and Levant voles (Bodenheimer 1949; Cohn-Shlagman et al. 1984) revealed no differences in average size of male and female home ranges throughout the year, supporting our results of no statistically significant sex differences in spatial learning or memory in all three species.

Other investigators have interpreted the conflicting results regarding sex differences in maze performance as a consequence of sex differences in exploration levels, activity levels, motivation or other factors (Joseph 1979; Joseph & Gallagher 1980; van Haaren et al. 1987).

Spatial Learning and Memory

As with other fossorial animals, direct field observation of the mole-rat is impossible. Consequently, knowledge of their natural history is limited (Burda et al. 1990) and no comparative data are available on the ability of fossorial mammals such as the mole-rat to learn and remember spatial tasks. Our initial working hypothesis was that the mole-rat has evolved a highly developed ability to learn and remember a complex tunnel system, as one of many adaptations to its underground habitat. We compared its spatial learning and memory with those of two surface-dwelling rodents (vole and rat) in identical testing conditions in a complex maze.

In the first trial the mole-rats performed poorly compared with the other two species, because they ran back and forth on the same dead-end paths (primarily at the starting point of the maze). This stereotyped behaviour which appears in unfamiliar surroundings seems to form the basis of their natural exploratory behaviour (Eilam et al. 1995) and is part of a cluster of adaptations to tunnel life. After the initial trial, as the mole-rats became familiar with the maze, the initial repetitive stereotyped running declined and their performance improved markedly, reaching a similar performance to the rats and the voles by trial 3. Overall, the mole-rats showed a better spatial learning rate than the voles and rats.

The better spatial learning of the mole-rat may be related to the species' differences in home range size and complexity: in contrast to the rats and voles, which inhabit simple tunnel systems with several surface exits (Cohen-Shlagman 1981; Hart 1982), the mole-rats inhabit an extensive and winding subterranean tunnel system that can reach 70 m in total length (Zuri & Terkel 1996) extending over an average area of 340 m^2 (Nevo 1961). During a 24-h period they travel about 17 times the total length of their territory in a stereotyped patrol pattern (Zuri & Terkel 1996). In contrast, most of the wild rats' activity is on the surface on fixed paths at short distances (<30 m) from their burrows (Barnett 1963; Hart 1982). Like the wild rats, the activity of voles in Israel is concentrated on fixed surface paths (<10 m) around the tunnel system exits (Cohen-Shlagman 1981; Cohen-Shlagman et al. 1984).

In a previous study, a correlation was observed between home range size and spatial orientation ability: two species of gerbils (*Meriones crassus* and *Meriones lybicus*), occupying an arid niche with sparse resources requiring long-distance travel for food, were better at spatial orientation than *Meriones shavu*, which occupies a semiarid niche with more abundant food resources (Komerovsky 1993). In addition, meadow voles, which have a home range of 400 m^2, 10 times larger than that of pine voles, were better at spatial orientation in a radial maze (Gaulin & FitzGerald 1986).

Our results also show that the spatial memory of mole-rats is better than that of voles and rats. Good spatial memory is vital to the survival of the mole-rat. (1) During the wet season mole-rats collect and store food in special chambers, exploiting the resource several months later during the dry season when the soil is hard and food is scarce (Galil 1960). Returning to the storage site depends on good spatial memory. (2) During the dry season mole-rats excavate along a moisture gradient from drier towards moist soil, where digging requires less energy and food is more abundant (Zuri & Terkel 1997). Since mole-rats start to dig towards more moist soils before a moisture gradient is detectable (Zuri 1993), they may remember the locations of the moist soils from previous seasons. (3) At the beginning of the breeding season (October–December), many female mole-rats return to the breeding mound that they used the previous year (R. Rado & J. Terkel, unpublished data). At the same time, the males begin to dig long straight tunnels leading towards the females (Rado et al. 1992). Such orientation ability supports the idea of excellent spatial memory.

We suggest that the high spatial learning ability of the mole-rat has allowed it to survive in the harsh conditions of its subterranean environment, by enabling it to avoid unnecessary energy expenditure in digging (Vleck 1979), as well as the risks of hypoxic-hypercapnic atmospheric pressure in the tunnel system (Arieli 1990) and overheating (Rado et al. 1993). The complex maze we used was specially designed to resemble the complex tunnel system that the mole-rat inhabits in the field. Testing the mole-rat and the other two rodents in other spatial tasks, such as an open field test, may yield somewhat different results.

Mechanisms of Navigation

The restricted number and variety of sensory stimuli in the subterranean environment in comparison with those above ground have led to the evolution and specialization of specific sensory channels in the mole-rat. The eyes are vestigial organs that respond only to light and dark (Rado et al. 1991), thereby eliminating the use of visual orientation mechanisms. The mole-rat, like other subterranean mammals, has poor auditory sensitivity, particularly to high frequencies, so it cannot localize brief sounds (Heffner & Heffner 1992). Olfactory cues, used by mole-rats for marking intraspecific territory boundaries (Zuri et al. 1997), are not effective for steering a course to a new area (Burda et al. 1990). Furthermore, the mole-rat's fur brushes the tunnel walls as it moves, thereby transferring any olfactory cues along the path.

In spite of its sensory limitations, the mole-rat is able to orient efficiently within its complex tunnel system. We suggest that a possible mechanism for learning a specific route involves memorizing a fixed sequence of body rotations within its space (i.e. turn left at the first junction, turn right at the third junction and so on). In addition, the mole-rat may acquire some general knowledge of the compass direction of the goal from various points in the maze. This general knowledge of direction can probably be achieved by using certain mechanisms of orientation. Recently, we found that the mole-rat is able to use the Earth's magnetic field to select the location of the nest and food chamber in an eight-arm maze. Furthermore, mole-rats that had learned to orient in a complex maze under the Earth's natural magnetic field became disoriented after its alteration. Thus the mole-rat may orient towards a specific goal by using the Earth's magnetic field (Kimchi & Terkel 1999).

A second mechanism of orientation the mole-rat might use is based on internal cues or path integration to create a cognitive map of the surroundings, previously suggested for *Cryptomys* (Eloff 1951) and *Talpa* (Quilliam 1966). Later studies showed that, in the absence of visual cues, rodents such as hamsters, *Mesocricetus auratus* (Etienne et al. 1986), gerbils, *Meriones unguiculatus* (Mittelstaedt & Mittelstaedt 1980, 1982) and rats, *Rattus norvegicus* (Benhamou 1997), are able to use vestibular and kinaesthetic information to construct a mental map of their surroundings (also known as path integration). The main advantage of the cognitive map mechanism over motor sequence learning is that it is highly flexible, and if one path leading to a specific goal is blocked another can be easily substituted (O'Keefe & Nadel 1978). Evidence that subterranean mammals might possess such a mechanism has been found for example, in the European mole, *Talpa europea* (Armstrong & Quilliam 1961), pocket gopher, *Thomomys bottae* (Reichman & Smith 1990), African mole-rat, *Cryptomys bgalkei* (Eloff 1951) and recently in the blind mole-rat (unpublished data). These species are able to deviate from their set course to avoid local obstacles created by flooding or other mechanical damage by digging a bypass tunnel, and then resume their previous direction. This behaviour can be effective only if these animals possess a mental map of the subterranean tunnel system and are thus able to perceive their position in space relative to segments of the other tunnel system.

In summary, although the mole-rat may also use olfactory and auditory cues for short-distance spatial orientation, we believe that it mainly uses three mechanisms to orient in the absence of landmarks: (1) learning and memorization of specific routes (series of turns) using motor sequence orientation; (2) internally generated cues that enable it to built a mental map of its subterranean tunnel system; and (3) magnetic compass orientation for short- and long-distance orientation. Further field and laboratory study is required to clarify the mechanisms of orientation used by the mole-rat.

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Appendix A1. Maze performance (mean time, number of errors and path length ±SE) of male and female mole-rats, rats and voles in the learning experiment

	Mole-rat		Rat		Vole	
Trial	Male	Female	Male	Female	Male	Female
Time (s)						
1	982.3±72.2	910.3±62.0	643.1±51.2	741.3±91.3	186.3±57.2	222.7±36.4
2	307.6±53.0	328.0±42.5	220.0±25.7	236.0±37.8	122.8±29.3	128.7±36.1
3	170.4±33.3	126.7±16.2	129.0±18.7	105.2±12.5	79.4±11.8	106.8±23.8
4	145.8±32.1	125.1±17.4	80.2±7.2	73.4±6.4	101.1±6.9	90.3±17.3
5	78.2±14.0	111.7±25.9	60.2±5.8	59.7±7.2	59.0±7.5	55.4±9.0
6	103.3±18.7	118.5±21.7	173.8±17.4	156.0±15.8	44.4±6.5	48.3±11.5
7	59.0±7.9	89.1±16.4	83.9±12.4	82.3±10.7	75.0±11.0	109.0±33.6
8	65.3±8.6	80.5±22.6	71.2±11.0	58.5±8.9	58.9±7.1	76.8±18.2
9	44.9±8.4	65.9±9.9	40.5±3.3	52.8±5.8	51.8±5.3	54.8±10.2
10	38.9±7.0	50.1±5.7	37.5±3.1	40.2±4.3	50.2±9.7	64.6±12.7
11	50.4±6.3	54.8±6.8	116.9±14.0	146.0±14.9	43.1±9.6	42.4±4.4
12	30.5±4.7	39.3±7.0	52.5±6.8	44.7±4.2	49.1±6.9	58.9±9.1
13	30.9±4.6	22.8±1.5	34.4±3.5	36.9±3.2	41.4±6.2	64.0±14.9
14	25.6±2.9	24.2±3.5	29.9±2.6	31.2±2.8	40.6±4.9	48.1±6.9
15	23.4±3.2	24.5±2.3	26.0±2.0	30.2±1.7	44.6±4.6	45.3±4.3

Appendix A1. *Continued*

	Mole-rat		Rat		Vole	
Trial	Male	Female	Male	Female	Male	Female
No. of errors						
1	25.6±1.4	24.9±1.4	12.5±0.8	13.0±0.8	6.1±1.3	8.4±0.8
2	11.8±1.7	12.3±1.2	5.9±0.7	5.5±0.7	5.2±0.7	5.7±0.7
3	8.0±1.1	6.8±1.1	4.6±0.5	3.6±0.3	2.5±0.3	2.8±0.3
4	7.3±1.1	6.9±1.0	2.9±0.3	2.8±0.3	4.1±0.8	2.8±0.5
5	3.8±0.7	4.5±0.4	2.1±0.2	2.6±0.3	2.5±0.4	2.2±0.3
6	5.0±0.7	5.3±0.8	6.1±0.4	5.3±0.4	1.7±0.2	2.6±0.5
7	2.9±0.4	4.3±0.7	2.6±0.4	2.9±0.4	2.8±0.3	3.0±0.4
8	2.5±0.4	3.7±0.4	2.1±0.2	2.6±0.3	2.0±0.2	2.3±0.3
9	2.3±0.3	2.8±0.4	1.2±0.2	1.9±0.2	1.4±0.2	1.7±0.2
10	2.3±0.4	2.9±0.4	1.1±0.1	1.3±0.2	1.6±0.4	1.8±0.3
11	3.1±0.2	2.3±0.3	4.0±0.5	4.5±0.4	1.2±0.3	1.4±0.2
12	1.8±0.3	1.8±0.3	1.8±0.3	1.4±0.2	1.7±0.2	2.0±0.3
13	1.3±0.2	1.4±0.2	1.3±0.2	1.1±0.2	1.5±0.2	1.7±0.3
14	1.5±0.3	1.5±0.2	1.2±0.2	1.1±0.2	1.4±0.2	1.5±0.2
15	1.6±0.2	1.5±0.3	1.2±0.2	1.0±0.1	1.0±0.2	1.8±0.2
Path length (cm)						
1	31.7±3.1	30.1±1.3	17.0±1.3	14.6±1.3	8.6±1.6	7.4±1.1
2	18.0±2.3	19.5±1.0	6.7±0.5	8.2±1.0	6.9±1.0	5.7±0.6
3	13.6±2.1	11.5±0.6	6.9±0.7	5.4±0.6	4.8±0.5	4.4±0.6
4	13.0±1.8	13.0±0.5	5.3±0.5	4.6±0.5	5.9±0.9	4.3±0.6
5	6.6±1.0	4.6±0.6	4.8±0.4	4.4±0.6	4.2±0.5	4.6±0.7
6	8.3±0.9	6.7±0.9	10.0±0.8	8.7±0.9	4.3±0.5	4.2±0.6
7	5.6±0.5	5.6±0.7	7.1±0.8	5.6±0.7	4.5±0.4	4.7±0.4
8	5.7±0.7	4.8±0.5	5.6±0.5	4.8±0.5	3.7±0.2	3.2±0.3
9	5.6±0.5	4.3±0.4	4.0±0.2	4.3±0.4	3.5±0.2	2.9±0.2
10	5.3±0.6	5.0±0.6	2.8±0.2	5.0±0.6	3.5±0.3	3.0±0.2
11	5.7±0.4	6.9±0.7	6.1±0.8	6.9±0.7	3.4±0.3	3.1±0.3
12	4.6±0.6	3.8±0.2	5.2±0.9	3.8±0.2	3.7±0.3	3.4±0.4
13	4.0±0.3	3.4±0.2	3.6±0.4	3.4±0.2	3.7±0.3	3.1±0.3
14	3.2±0.4	2.3±0.3	3.3±0.3	2.3±0.3	3.8±0.4	3.5±0.4
15	2.6±0.2	2.8±0.4	3.1±0.3	2.7±0.3	3.6±0.3	3.3±0.3

Appendix A2. Maze performance (mean percentage of success for time, number of errors and path length ±SE) of male and female mole-rats, rats and voles in the memory experiment

	Mole-rat		Rat		Vole	
Memory group (days)	Male	Female	Male	Female	Male	Female
Time						
2	97.1±1.0	96.6±1.4	85.3±2.3	76.0±5.3	97.8±7.1	100±3.4
7	89.3±2.7	91.5±3.2	71.8±4.5	61.7±4.5	86.4±11.3	72.3±12.2
30	89.1±2.6	83.1±3.5	51.7±11.8	57.3±8.1	71.4±8.5	65.83±13.1
60	78.8±5.8	75.2±4.5	29.6±8.2	36.6±6.6	54.4±11.2	52.4±6.4
120	58.4±5.8	59.3±6.6			20.9±7	22.3±8.1
No. of errors						
2	100±1.8	90.4±5.7	82.5±4.6	72.0±5.6	100±5.3	100±6.3
7	72.5±8.5	87.3±10.5	46.5±7.3	54.3±8.3	71.3±8.4	79.5±12.2
30	65.0±10.5	73.1±9.4	16.9±11.6	40.8±12.1	60.0±12.2	68.6±10.2
60	58.0±7.5	59.9±9.9	14.0±9.7	23.9±10.6	41.6±10.3	52.38±12.0
120	38.2±9.6	45.4±11.2			15.4±5.3	25.8±10.6
Path length						
2	95.6±9.0	94.9±2.8	78.6±5.7	85.1±12.3	100±11.4	98.3±3.2
7	97.1±8.3	94.4±5.5	47.5±13.0	60.0±9.4	92.8±6.3	85.6±5.2
30	80.3±7.1	82.8±13.3	15.8±10.7	35.2±5.2	56±5.5	60.8±6.5
60	73.1±13.4	71.2±3.5	9.7±7.6	7.5±8.2	48±10.2	46.3±8.5
120	32.5±12.1	35.6±7.2			19±3.5	22±4.2