Research report

Comparison of the role of somatosensory stimuli in maze learning in a blind subterranean rodent and a sighted surface-dwelling rodent

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Abstract

We compared the role of tactile perception in maze learning in the blind mole rat and in the laboratory rat. Both species were tested in each of two mazes that were identical in complexity but differed in tunnel width and height: the first was only slightly wider than the animal's body width (narrow maze) while the second was about twice the animal's body width (wide maze).

We found that the performances of rats tested in the narrow maze were significantly lower than those tested in the wide maze, as measured by time and number of errors to reach the end of the maze (food reward). The mole rats, in contrast, performed significantly better in the narrow maze than in the wide maze. Further, in contrast to the rats, the mole rats' locomotion in the wide maze was much less continuous than in the narrow maze, reflected in longer and more frequent stops at maze junctions, where they pressed the side of their body tightly against the tunnel walls.

Two main conclusions are derived from this experiment. First, subterranean mammals, such as the blind mole rat, appear to rely more on tactile stimuli while exploring and learning a complex maze than do sighted surface-dwelling rodents, such as rat. The extensive use of this somatosensory channel may compensate for the mole rats' visual deficiency, and thus substantially contribute to their excellent spatial orientation ability, previously demonstrated in field and laboratory conditions. Second, poor performance of surface-dwelling rodents, such as the rats, in spatial-maze learning tasks might not be a consequence of impaired cognitive learning ability, but rather due to testing the animal in a physical situation that does not provide the necessary somatosensory stimuli found in their natural habitat.
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1. Introduction

Subterranean mammals construct sealed underground tunnel systems, comprising networks of shallow feeding tunnels and deeper ones connecting nest, food storage and sanitation chambers, which they inhabit throughout most of their lifetime [26]. Survival and successful reproduction in the underground habitat necessitates a developed directional sense in order to avoid unnecessary, energetically-costly digging [38]. The sensory perception of subterranean mammals seems to be greatly restricted compared to surface-dwelling animals, since vision is excluded and olfactory and airborne sound cues are strongly attenuated by the soil and are effective only over short distances. A limited number of studies both in the field and the laboratory have demonstrated the efficient short and long distance spatial orientation ability

of subterranean mammals (for review, see [7,16]). These animals rely on several specialized non-visual sensory modalities, including the earth's magnetic field directional cues [8,15], and seismic waves to detect prey [23] and possibly also to estimate dimensions of underground obstacles [16,17]. Common to all those sensory channels are their availability for spatial orientation underground, independent of light.

Subterranean mammals excavate burrow systems to the exact diameter of their own body. They are exposed continuously to extensive somatosensory stimuli, which are perceived by their well-developed tactile system [7,26]. Morphological studies have revealed finely-developed sensory vibrissa hairs, mechanoreceptors and somatosensory cortex both in moles [9–11,27] and in the blind mole rat [19,22,25].

Behavioral studies have indicated that various spatial tasks performed by subterranean mammals seem to involve their developed somatosensory channel: e.g. the detection of nearby tunnel blockage, by sensing the propelled air

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rebounding from the obstacle surface while the animal is advancing in the tunnel [16]; finding the shortest path to a goal site using the path integration process [18]; and localizing nearby prey [10]. However, to date, there has been not one single experimental study to test the role of tactile stimuli in spatial orientation for subterranean (fossorial) versus surface-dwelling mammals.

One way of testing the relative significance of somatosensory (tactile) cues for surface-dwelling rodents versus fossorial species is to compare performances in spatial learning task, in mazes designed to provide different somatosensory inputs.

2. Methods

2.1. Animals

We used adult female animals of two species: 24 blind mole rats (*Spalax ehrenbergi*) and 24 laboratory rats (Wistar strain). The mole rats 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 chosen for the experiment had similar dimensions (weight: 130–150 g, body width: 4.5–5.5 cm) and were housed individually (mole rat) or in small groups of three to four individuals (rat) in plastic cages (43 cm × 27 cm × 18 cm) for at least 2 weeks before the beginning of the experiment. The cages contained wood shavings for bedding. The rats were fed with rodent pellets and supplied with water ad lib, while the mole rats received in addition to the pellets carrots and apples (from which they obtained sufficient water). The animals were maintained in the laboratory at a constant temperature (24–26 °C) under a 14:10 h light/dark regime.

2.2. Apparatus

We constructed two mazes from the same components, differing only in their tunnel width and height. The wide maze tunnels were 10 cm × 10 cm, while the narrow maze tunnels were 6 cm × 6 cm. Both mazes (110 cm × 110 cm in size; Fig. 1) consisted of six choice points, with one correct path leading to the end of the maze at the opposite end from the entrance.

The maze floor consisted of vinyl sheeting laid on a plywood board while the walls were constructed from plywood panels with Formica finish on both sides. Each maze was covered with a transparent Perspex lid to enable video filming. The entrance and exit to the mazes were each fitted with a short Perspex tube (6 cm in diameter, 20 cm long) with a movable door that was closed after the animal had passed through it. The tube inserted into the maze exit was attached to a sealed plastic cage that contained a food reward. The experiment took place in a room with no external windows; lighting was provided by two fluorescent lights (40 W) in the ceiling, exactly above the maze and concealed behind a
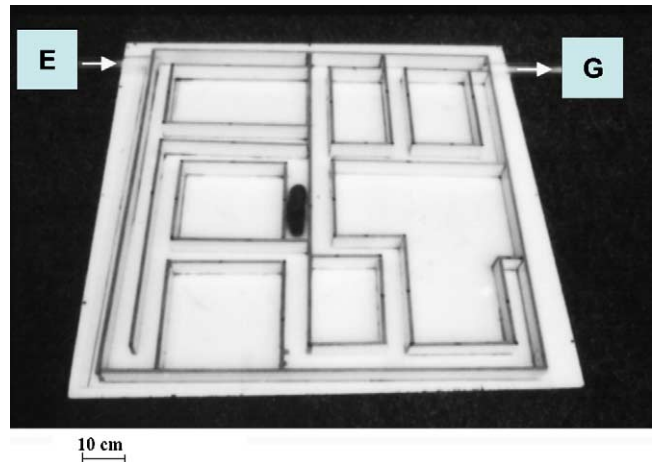

Fig. 1. View from above of the narrow maze used to test both mole rats and rats. E: maze entrance; G: maze exit (goal), where the food reward was placed.

plastic grid diffuser that spread the light evenly across the room, preventing any focal references point. The maze was placed in the center of the room about 1.5 m from the walls. Thus, no visual directional references could be used by the rats (the mole rat is functionally blind).

2.3. Procedure

Two groups (*N* = 12) were formed for each species. Individuals from group 1 were tested in the wide maze while those from group 2 were tested in the narrow maze. All subjects were tested in the same way.

To increase motivation to explore and learn the maze, the animals were deprived of food for 18-h prior to the experiment, and food intake was restricted throughout the 3 days of the experiment in order to maintain each subject at 85% of initial body weight. Two days before testing, each animal was placed in a nest box—a plastic cage (33 cm × 38 cm × 15 cm) connected to a Perspex tube (6.5 cm in diameter, 20 cm long), sealed by an easily removable plastic cap at its distal end. At the beginning of each trial the nest box connection tube was inserted into a slightly wider connection tube attached to the maze entrance, allowing the transfer of the experimental animals to the maze without direct human handling. Each trial began when the movable door at the maze entrance was lifted, allowing the test animal to enter the maze, and terminated either when the animal reached the goal box or after 20 min if it failed to do so. Each animal that entered the goal box was rewarded with a small piece (0.5 cm^3) of apple. At the end of each trial the animal was transferred back to its home cage via the plastic transfer tube. The vinyl sheeting on the maze floor was replaced with new sheeting and all maze parts were washed with alcohol (70%). The experiments took place at the time of day when each species is known to be most active: thus mole-rat tests began at 10:00 h [30] and rat tests began at 18:00 h [2,24].

2.4. Behavioral measurements and statistical analysis

The animals' performance in the mazes was recorded by a remote controlled video camera (Sony, Model No. CCD-TR490E) connected to a monitor (JVC, Model No. VM-14PSN) and analyzed with Statistica software (Statsoft, Inc., Tulsa, OK).

To compare the learning performance of the two species in the narrow and wide mazes we recorded the number of errors made and the time required to reach the end of the maze, during each of the 14 trials of the experiment.

To determine whether there were differences in performances of the animals tested in the wide maze to those tested in the narrow maze in the initial (first and second) trials and the last trials (13 and 14), we used unpaired t tests (for each of the two parameters) comparing group 1 to group 2, for each of the two species separately.

To determine whether there were differences in the learning rate of the animals tested in the two different mazes, we calculated the learning rate of each group as previously described in Kimchi and Terkel [14]. Groups 1 and 2 were compared for each of the two species separately (Mann–Whitney U-test).

In addition, the animals' patterns of movement in the mazes were monitored by counting the number of stops performed while orienting in the maze, and noting their exploration behaviors (e.g. sniffing, whiskers pressing to the walls) and the proximity of their body to the tunnel walls during locomotion. To determine whether there were differences in the numbers of stops performed by the animals tested in the wide maze to those tested in the narrow maze in the initial (first and second) trials, we used unpaired t tests (for each of the two parameters) comparing group 1 to group 2, for each of the two species separately.

3. Results

3.1. Performances in initial two trials

In the two initial trials of the experiment the rats performed significantly better in the wide maze than in the narrow maze, i.e. rats tested in the wide maze required significantly less time (Trial 1: $t(22) = 3.5$; Trial 2: $t(22) = 2.9$, $P < 0.01$) and displayed fewer errors (Trial 1: $t(22) = 4.1$; Trial 2: $t(22) = 3.1$, $P < 0.01$) to reach the end of the maze. The mole rats, in contrast, in the first trial performed significantly better in the narrow maze than in the wide maze, for both parameters (Time: $t(22) = 2.97$; Errors: $t(22) = 3.1$, $P < 0.01$) and in the second trial, only in the number of errors parameter ($t(22) = 2.2$, $P < 0.05$) (Fig. 2).

3.2. Learning rate

The learning curve of the two species in the two mazes was significantly correlated with an exponential growth
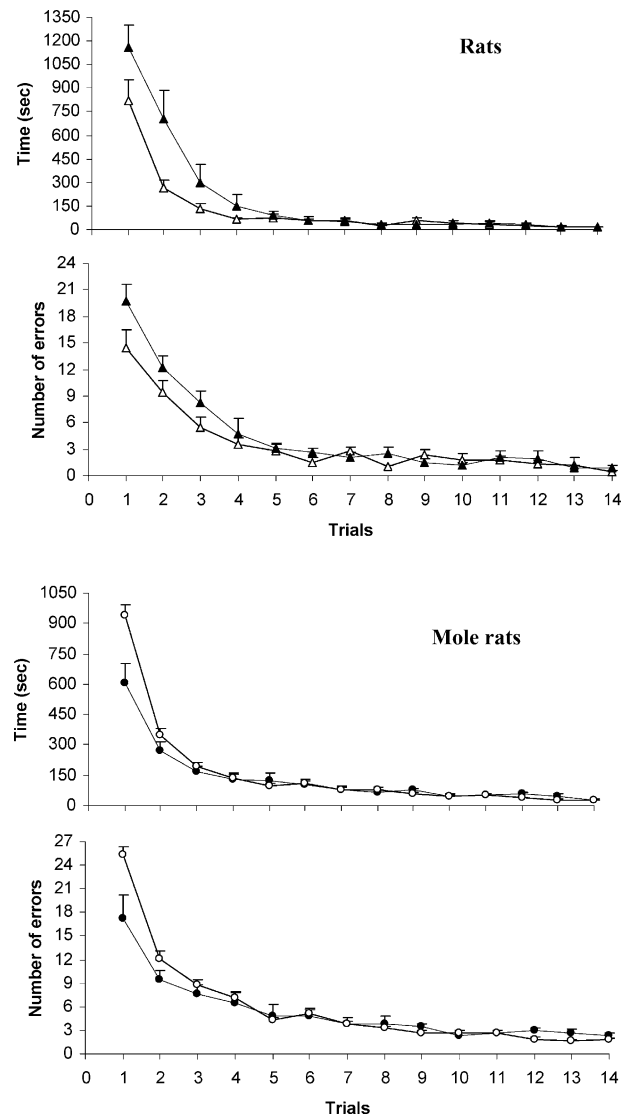

Fig. 2. Time (s) and number of errors of rats (triangle) and mole rats (circle) to reach the food reward in end of the narrow maze (filled symbol) and the wide maze (open symbol), in 14 trials.

regression ($R^2 > 0.9$, $P < 0.01$), expressed by the formula: $Y = a + be^{cx}$. The learning rate of the rats in the wide maze was significantly better than that in the narrow maze for both parameters (Time: $U = 210$; Errors: $U = 230$, $P < 0.01$); whereas the learning rate of the mole rats was significantly better in the narrow maze than in the wide maze in the number of errors parameter ($U = 190$, $P < 0.05$).

3.3. Performance in last two trials

By the last two trials (13 and 14) both rats and mole rats showed similar performances in both parameters with no significant difference between the wide and narrow maze (Fig. 2).
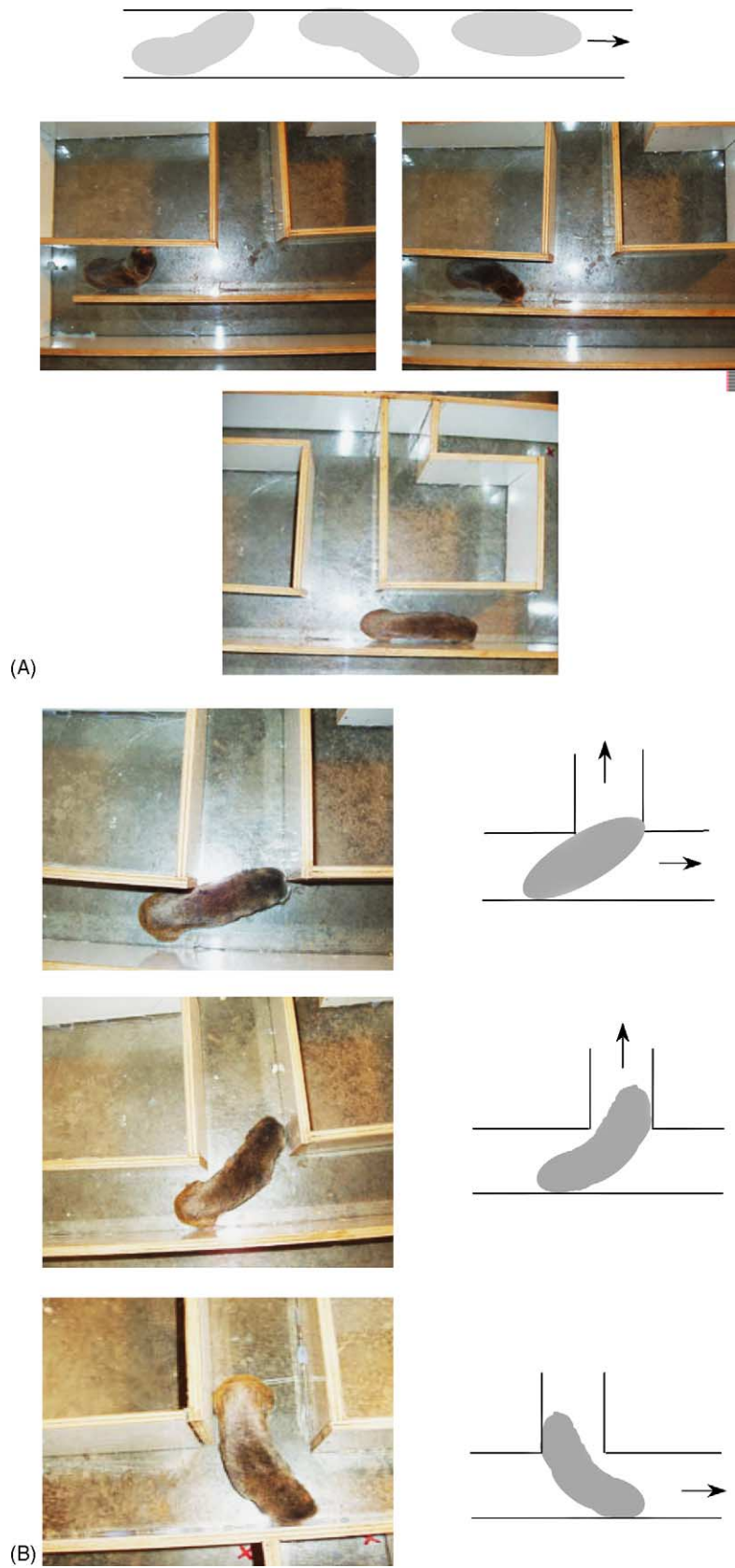
Fig. 3. The unique locomotion pattern of "wall seeking behavior" performed by the mole rats on straight paths (A) and at T-junction (B), mainly in the wide maze.

3.4. Pattern of movement

The locomotion patterns of the two species in the maze substantially differed. In both mazes the mole rats often stopped at the junctions, pressing their lower jaw tightly against a wall ("jaw listening" [28,29]) and also occasionally pressing the vibrissae around their mouth against the wall. Further, in both mazes the mole rats exhibited continual "wall seeking behavior" in which they always moved with the side of the body pressed tightly against one of the walls of the tunnel, often alternating between the two sides (Fig. 3A). Finally, the mole rats exhibited the following unique pattern of movement: when stopping at T-junctions they in most cases maneuvered their body to make contact with several walls simultaneously (i.e. touching with the side of the head, chest and pelvic area). This behavior was more extreme and more frequent in the wide maze than in the narrow maze (Fig. 3B). In contrast, the rats exhibited much less tendency to press their body against the tunnel walls. In the wide maze the rats often moved down the center and only occasionally pressed the side of their body and long vibrissa against the walls. The majority of the rats' stops were also at the tunnel junctions, but unlike the mole-rats, the rats explored their surroundings mainly by sniffing the air above, with almost no body contact with the walls.

In both species the number of stops was the highest during the first trial and gradually decreased until stops became rare in the last three trials (Fig. 4). However, in the first two trials, whereas the rats stopped significantly more frequently in the narrow maze than in the wide maze (Trial 1: $t(22) = 4.0$; Trial 2: $t(22) = 3.3$, $P < 0.01$), the mole rats exhibited the opposite behavior and stopped more frequently in the wide

maze (Trial 1: $t(22) = 2.9$, $P < 0.01$; Trial 2: $t(22) = 2.1$, $P < 0.05$) (Fig. 4).

4. Discussion

The present study was designed to examine the role of somatosensory (tactile) stimulation for exploration and learning of a novel complex tunnel system (maze) in a subterranean (fossorial) rodent, the congenitally blind mole rat, versus sighted surface-dwelling rodent, the laboratory rat.

The results clearly show that experimental change of the available tactile information, by altering the height and the width of the maze tunnel, has a dramatic effect on the spatial learning and behavior patterns of both mole rats and rats.

When the mole rats were tested in a maze with narrow tunnels, thus exposing them to a high level of somatosensory stimulus, their learning performance was better than when tested in a wide tunnel maze; in contrast the rats showed a better learning performance in the wide maze than in the narrow maze. A further difference between the two species was found in the animals' pattern of movement in the two mazes. The mole rats' locomotion in the wide maze was more interrupted than in the narrow maze, with longer and more frequent stops at the maze junctions, where the animals tried to maneuver their body to make simultaneous contact with as many tunnel walls as possible. The rats, in contrast, exhibited fewer stops and less maze section repetition in the wide maze tunnels compared to the narrow maze tunnels.

The above findings appear to reflect the great differences in the nature of the habitats in which these two species live, as well as their evolutionary adaptation to their specific environments.

In nature, mole rats spend most of their time in a narrow tunnel system (in which they carry out all their activities), providing them with a continuous high level of tactile stimuli. If removed from their tunnels and positioned in open space they freeze or move very slowly, searching for the closest wall with which to make body contact (Kimchi and Terkel, unpublished data). Although rats (*Rattus norvegicus*) generally also prefer to move along the walls when exploring novel surroundings, they can also forage effectively for food in open spaces and learn routes to a goal (e.g. food site) without continuously brushing against side walls (for review, see [2,3,24]).

Further, the morphology of the mole rat is substantially more adapted to locomotion in narrow tunnels than that of the rat. Its elongated body shape, reduction of size of all body extremities, including short legs, tail beneath the skin, absence of external ears, and fur that can be combed in both directions, enable it to move easily both forward and backward in the tunnels [26], while its extreme body flexibility enables it to turn on the spot and reverse direction even in a very narrow tunnel only slightly greater than its body diameter.
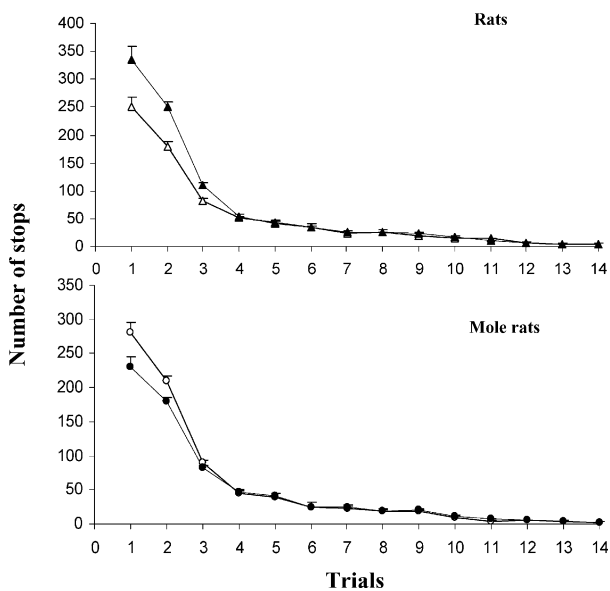

Fig. 4. Number of stops of rats (triangle) and mole rats (circle) to reach the food reward in end in the narrow maze (filled symbol) and the wide maze (open symbol), in 14 trials.

There is also a substantial difference between the environmental sensory information available to the two species for spatial orientation. Unlike the surface habitat of the rats which offers extensive and diverse visual cues, such as landmarks, celestial distance cues, and odor landmarks or trails, etc, the underground habitat of the mole rat is characterized by constant darkness, eliminating use of any visual signals; while auditory (airborne waves) and olfactory cues are substantially attenuated in the soil, and thus can be used only for short distance orientation [7,16]. On the other hand, the mole rat inhabits a tunnel system throughout its entire life and its body is in constant contact with the walls, receiving richer tactile-kinaesthetic information compared to surface-dwelling rodents. A highly developed somatosensory system has been revealed in histological examination of the skin of the mole rat's head and the sensory cortex. Its head skin possesses a large number of mechanoreceptors in the dermal layer and at the base of its hair follicles [19]. Its somatosensory cortex and the somatosensory thalamic nuclei are significantly larger those of the laboratory rat [22,25]. Moreover, other subterranean mammals, such as the star-nosed mole [10,11] and the Eastern mole [11] have also been found to have well-developed somatosensory systems.

Taken all together, two main conclusions can be derived from the present study. First, subterranean mammals, like the blind mole rat, appear to rely more extensively on tactile-kinaesthetic references while learning a multiple maze than do related sighted surface-dwelling species, such as the laboratory rat. The shown repeated tendency of the mole rat to make strong physical contact with the maze walls (Fig. 3A and B) might serve the animal for both short-distance orientation, to sense and avoid obstacles, as well as for its long-distance mechanism of orientation, in order to increase the availability of the self-motion input (e.g. somatosensory, vistibular and kinaesthetic) that is gathers and integrates in the path integration process, enabling it to continuously estimate its relative position in space (path integration has been previously demonstrated in rodents such as rats [21], mice [1], hamsters [13], and mole rats [18]). Further support that body contact with objects may have significant importance for a blind rodent's navigation mechanism (such as in path integration), came from a neurophysiology study that recorded the activity of hippocampal place cells in freely moving rats that were visually deprived shortly after birth [33]. It was found that the blind rats tended to make more frequent exploratory contact with objects set at the periphery of the apparatus, than did sighted rats. Such exploratory contact seems to activate firing of the place cells, and serves to register a tactile-landmark's position in the path integration process, allowing the blind rats to recalibrate their spatial position [33].

A second conclusion that can be derived from the present study is that poor performance of surface-dwelling rodents (e.g. rats, mice, etc.), in spatial-maze learning tasks might not be a consequence of impaired cognitive learning ability, but rather due to lack of experimental provision of the specific factors (e.g. those that optimize somatosensory stimuli) that contribute to their orientation ability in their natural habitat.

These findings can also be viewed in respect to previous studies' findings on deprivation/degeneration of the visual sense in newborn rodents and other mammals. Such experiments have demonstrated that visual deficiency from an early age may result in morphological and physiological changes such as hypertrophy of the facial vibrissae, a corresponding expansion of the somatosensory cortex (rats [35,36], mice and cats [6,31,32]), hippocampal place cells activity similar to that found in sighted individuals [33], behavioral changes reflected in more extensive use of the tactile stimuli in spatial-maze tasks [31,33] and equal and even better performance compared to sighted individuals in different spatial tasks (rats [20,35,36], humans [12,34,37]). One of the common explanations to those findings is that the loss of sight induces a parallel expansion in the morphological, physiological and behavioral somatosensory system, increasing its relative role in the animal's sensory perception and thus successfully compensating for the visual deficit. This explanation may also hold true for animals that lost their sight evolutionarily, as occurred in the blind mole rat and other subterranean mammals.

Moreover, certain studies have emphasized that sensory compensation is more pronounced if the onset of sensory deprivation occurs early in life [4,5]. It is thus reasonable to assume that the blind mole rat, in which about 30 million years of evolution [26] has led to complete loss of vision, should exhibit highly refined sensory compensation changes. We believe that this species, as well as other subterranean mammals, offers a suitable animal model for study of the effects of visual deprivation and other sensory restriction (auditory and olfactory), on sensory system plasticity and substitution.

Acknowledgements

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