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To take or not to take the shortcut: Flexible spatial behaviour of rats based on cognitive map in a lattice maze

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ABSTRACT

To examine the flexibility of rats' spatial behaviour, we required rats to navigate to one of four boxes on the corners of a lattice maze. The maze consisted of five vertical and five horizontal corridors on a plane parallel to the ground and allowed us to design diverse routes. One box was set as goal and the other three were set as starting points. Both the time to arrive at the goal and the number of errors at the intersections on the route decreased, suggesting that the rats learned the route. As the goal boxes were successively changed, the decrease in the errors and the time to reach the goal became faster. This suggests that the rats learned the spatial layout of the maze, i.e., developed a cognitive map. We then carried out a shortcut test by removing one wall located near the centre of the maze. The rats took the shortcut route when passing through the location around the removed wall made the entire route shorter, but did not pass through the location when passing through the location made the entire route longer. These suggest that rats can flexibly utilize their internal representation of a spatial structure to respond to a change in a learned environment.

1. Introduction

Navigation, moving from the present location to a distant destination, is fundamental behaviour for organisms. In most navigational situations, we have to move to a place that we cannot view from our present location. For navigation in such a large-scale environment, an internal representation of the environment, i.e., a cognitive map, is needed (O'Keefe and Nadel et al., 1978; Tolman, 1948). The existence of cognitive maps has been shown by examining whether one can demonstrate an adaptive reaction to an environmental change, such as taking a shortcut (Gallistel, 1990; O'Keefe and Nadel et al., 1978). We regard one as having cognitive map when one can cope with an environmental change in a learned environment. For example, such a demonstration is achieved by investigating whether one can take a shortcut when a path that has not previously been available becomes possible to pass through.

Some studies have shown that animals can take a shortcut (Chapuis et al., 1987; Gould, 1986; Roberts et al., 2007; Tolman et al., 1992). However, with regard to the results of studies that have experimentally demonstrated animals' ability to take shortcuts, it has been pointed out that a strategy of approaching a familiar landmark close to a food reward at the destination resulted in the shortcut-taking behaviour (Bennett, 1996). Some studies controlled for this point by prohibiting usage of extra-maze cues (Grieves and Dudchenko, 2013; Roberts et al., 2007). However, even in these studies, the experimental environment was relatively simple. Rats inhabit a complex environment in nature. So far, there are few experimental studies that report on animals engaging in any shortcut-taking behaviour after memorizing complex routes in a relatively complex environment.

Rodents prefer novel objects (Berlyne, 1950; Poucet et al., 1986). To prepare a situation in which animals can take a shortcut at a location en route to a destination necessarily leads to some structural changes in the environment. The changes induce animals to frequently visit the changed place because of their preference for novelty. Consequently, the probability of taking the shortcut path is expected to increase. However, if the changed location deviates from the shortest path to the destination, the appropriate behaviour is to avoid passing through the area. In this case, animals have to inhibit their preference for novelty.

Few studies have examined whether animals can demonstrate flexible navigation such that they use a newly available path when it is appropriate but do not use the path when it is inappropriate. The present study has two purposes. The first is to examine whether rats can show flexible navigational behaviour such that they adapt their acquired spatial representation to an environmental change when the spatial structure changes. The other is to examine the usefulness of a lattice maze that we developed, inspired by Okaichi (1996), for a new spatial learning situation in rats.

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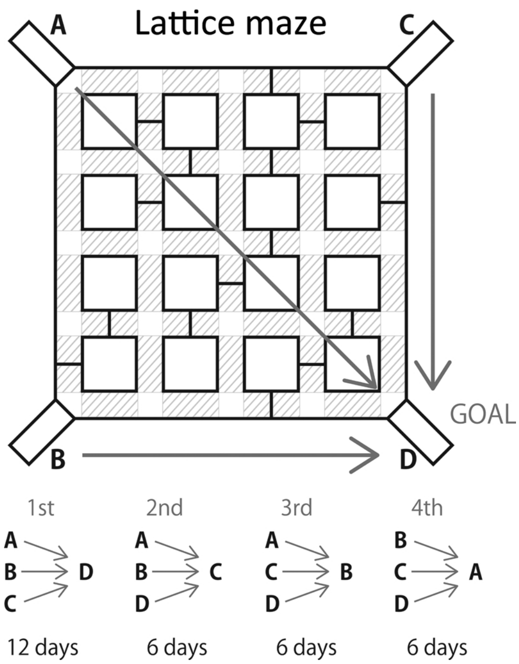

Fig. 1. The lattice maze used in the present study. In this case, rats were required to go to Box D (goal box) from Boxes A–C (starting boxes). The areas with gray diagonal stripes indicate segments for analysis (see the text for details). The bottom schemata show the transition of the goal box.

2. Material and methods

2.1. Subject

We used eight male Long-Evans rats (Japan SLC, Hamamatsu). They were eleven weeks old and weighed 355 ± 14 g (average ± standard deviation) at the beginning of the experiment. They were housed in individual wire home cages (200 × 250 × 187 mm) on a 16/8 h light/dark cycle (lights were on from 8:00 to 24:00) with controlled temperature (23 °C) and humidity (60%). All rats were deprived of food to maintain at 85% of their ad-libitum weights, but were allowed free access to water during all experiments. All experiments in this study were approved by the Animal Experimentation Committee of Kwansei Gakuin University (2012-04).

2.2. Apparatus

All experiments were carried out using a lattice maze made of 5 mm thickness black polyvinylchloride (Fig. 1). The size of the lattice maze was 180 × 180 × 24 cm. On a plane parallel to the ground, the maze had 5 vertical and 5 horizontal corridors that were all 12 cm wide. We could freely set up routes in the maze by inserting and removing internal wall plates. At the four corners of the maze, there were 32 × 13 × 24 cm boxes (Boxes A–D in Fig. 1). In a task trial, one of the boxes was set as a starting box and another was set as a goal box. On the floor of the goal box, a food well (3 cm in diameter and 1.2 cm height) was fixed with Velcro. The maze was set 20 cm above the floor of the experimental room without any partitions. Therefore, rats could see the outside of the maze. Around the maze, there were some experimental items: a shelf close to the first wall, two steel racks close to the second wall, a door on the third wall, and triangle shaped steel posts to attach a web camera on the fourth wall. The rats could use these as extra-maze cues. To record the rats' behaviour, a web camera (BSW20KM, Buffalo, Tokyo) was mounted on the ceiling of the experimental room. After each trial of the experimental task, the maze was wiped with a 0.1% acetic acid solution to clean and deodorize. As a reward for the experimental task, 45 mg food pellets (F2001-J, Bioserv, Flemington, NJ) were used.

2.3. Procedure

All rats were handled for 5 min daily for 12 days. Food deprivation was started from 7 days after the handling began. The weights of the rats were maintained at 85% of the ad libitum weight.

To acclimate to the lattice maze, the rats were allowed to explore the maze for 8 days. On the first two days of the habituation period, all rats explored the inside of the maze without any plate walls. Food pellets were put at all intersections of the maze and inside of the boxes at the 4 corners. The session was ended when the rat collected all pellets or 10 min from the start of the session. After the two days, the rats explored the inside of the maze without any food pellets for 10 min. This daily procedure was carried out for 6 days.

2.3.1. Navigation task

In a daily session, the rat was required to go from one of the 4 boxes to another goal box. The goal box remained in the same location throughout the session and one of the remaining 3 boxes was set as a starting box in each trial. Therefore, there were 3 trials in a daily session and the order of the starting box was at random (Fig. 1). The inner plates were inserted to constitute the layout (Fig. 1). In front of all boxes other than the goal box, plates were also inserted to prevent the rat from entering the box. After the rat was put in the starting box, each trial started with taking away the plate at the starting box. When the root of the rat's tail entered the goal box, it was regarded as arriving at the goal. The rat obtained 6 of the 45-mg pellets as reward. The trial ended after the rat finished the pellets or 10 min after the trial started. In the first 12 sessions, Box D was a goal box. After 12 sessions, the goal box was changed to Box C, and the navigation task was carried out with the remaining 3 boxes as the starting box for 6 sessions. This was followed by the 6 sessions with the Box B as the goal box, and 6 sessions with the Box A as the goal box.

2.3.2. Data analysis

The rats' behaviour was recorded by a web camera. From the recorded movie, the time spent from the start to the goal was measured. For analysis, areas between intersections were set as segments (Fig. 1, diagonal striped areas). The number of passed segments from a start to a goal was counted and from that value, an index for error was determined by subtracting the number of segments for the shortest route between the start and goal.

2.3.3. Shortcut test

After taking away one of the inner wall plates (Fig. 1), the rats were required to reach the goal box from the starting box as in the navigation task. In a daily session, the goal box was fixed and the remaining 3 boxes were set as the starting boxes (3 trials in a day). The order of the starting box was selected at random. The test was carried out for 2 days with the same goal box and on the third day, the goal box changed. All boxes were used as a goal box. The order of the goal box was selected at random for each rat. In total, there were 8 sessions for the shortcut test.

We classified the trials of the shortcut test into 3 types: Shortcut, Equivalent, and Detour trials (Fig. 3a). In Shortcut trials, the route length when the rat passed through the region where the wall plate had been taken away was shorter than that of the original route. In Equivalent trials, the route length did not change from the original route even when the rat passed through the region where the wall plate had been taken away. In Detour trials, the route to the goal became longer than the original route when the rat passed through the region. The number of passages through the region where the wall plate had been taken away was counted for the 3 trial types. The number of the segments after the rat passed through the region where the plate had been removed to reach the goal was also counted.