

Movement is necessary for landmark-based navigation

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ABSTRACT. The experiments reported here were designed to find out whether mice are capable of homing by visual extra-arena landmarks, when deprived of visual access to such landmarks. Mice were placed in a circular arena, where they could view the experimental room only from a peripheral nest and the centre of the arena, while they could not access the visual cues when moving in-between. This resulted in poor homing in mice. The conclusion drawn is that mice need to view visual cues while moving for their landmark-based navigation.

KEY WORDS : Navigation; Path Integration; Homing.

INTRODUCTION

Previous work showed that mice are incapable of homing from the centre of a circular arena to their nest after viewing a distal landmark array only from a peripheral nest location (ALYAN, 1994). However, rodents are capable of homing successfully after having freely explored the arena (ALYAN & JANDER 1994), and after being passively carried from the nest to the centre of the arena (ETIENNE, 1980; MORRIS, 1981). This supported earlier claims that moving while viewing distal landmarks is necessary for successful landmark-based navigation (STAHL et al., 1987; SUTHERLAND et al., 1987; CHEW et al., 1989; MATTHEWS & BEST, 1997).

Furthermore, ALYAN & JANDER (1997b) found that mice could home by learned landmarks, after having shuttled between the nest and the centre of a circular arena, without any exploratory phase of that arena prior to or during the experiment. This demonstrated that shuttling between only two locations, in full view of the distal landmarks, allows mice to learn distal landmarks and to home by reliance on such cues.

These findings led to one further question that is explored in this study : Can mice learn distal landmark constellations and home by them after viewing them from only two points, but not while shuttling along the path towards either point? A positive finding would indicate that mice, while shuttling, connect the disjoint landmark vistas from the two points via path integration mechanism to form a landmark cognitive representation allowing them to home accurately at a later time, using only landmark constellations.

METHODS

Subjects

Eight lactating female house mice (*Mus musculus* Linnaeus, 1758) with their pups were used. Prior to experimentation they were housed in transparent cages 25 × 50 cm. The floor was covered with wood shavings, and food and water were provided ad libitum all the time. The photoperiod was 12 h light : 12 h dark (dark 7:00 pm to 7:00

am) and all experiments were conducted between 10:00 am and 2:00 pm. The purpose of using mothers with litters was to increase their motivation to go home. Therefore, two strong motivations were exploited in this study : the mothers' motivation to take their pups back to the nest and the mothers' motivation to seek a refuge.

Apparatus

A circular arena, 1.5 m in diameter, was used in all experiments. It rested on ball bearings to allow free rotation in any direction. Four handles were attached to the arena to enable smooth manual rotation. The floor of the arena was painted with a polyurethane-sand mixture for easy cleaning and to provide purchase for the mice during movement. A hole, 3 cm in diameter, was drilled at the periphery of the arena, and led to a tube, which in turn led to a nest box located beneath the arena's floor. The edge of the arena was marked at 5° intervals to record the mice' arrival points at the edge of the arena. In addition, the arena was surrounded up to a height of 40 cm by a Plexiglas sheet that had a one-way screen made of dark-tinted Perspex glued to it. Above the centre of the arena we positioned a 40 W incandescent bulb that reflected all its light downward.

The experimental room was normally lit on one side by natural light through two large windows and from the ceiling by standard fluorescent tubes. Pieces of furniture and wall posters offered additional distal landmarks for the homing mice.

Definitions and data collection

Directions were recorded when the mouse, starting from the centre of the arena, reached the periphery of the arena. Angles were measured clockwise from 0°-360°, with 0° being the nest direction before rotation.

To test for directional tendencies, circular statistics were used (BATSCHELET, 1981; ZAR, 1974). The following parameters were used in evaluating homing performance of mice. A sample analysis yielded a mean vector, m , where m is defined by its polar co-ordinates : θ and r ; where θ is the sample mean direction and r is the length of m . The mean vector length, r , serves as a measure of concentra-

tion as well as dispersion. The larger r is, the less dispersed the directions are around the mean angle.

Procedure

The objectives of this experiment were, first, to find out whether viewing the experimental environment from two locations, with no movement between them, would be sufficient for successful landmark-based navigation from one of these locations to the other and, second, to test whether movement between the two locations, without viewing the external environment while moving, can result in successful landmark-based navigation between the two locations.

Experiment Ia

Each of the eight female mice used in this experiment, with her pups, was taken from her cage and placed in the nest box. A clear Plexiglas cylinder (10 cm in diameter and 15 cm high) surrounded the nest entrance on the surface of the arena. The cylinder had one hole that led to a gray, opaque PVC tube (55 cm long). The other end of the PVC tube led to a hole in an identical Plexiglas cylinder placed in the centre of the arena. Both ends of the PVC tube were blocked with pieces of clear Plexiglas so that the mice could not move between the nest and the centre of the arena. Another identical PVC tube, placed on the opposite side of the central Plexiglas cylinder, led to a third identical Plexiglas cylinder placed at 180° from the one at the nest location. This was to ensure that the mice relied on extra-arena cues and not on certain guiding intra-arena cues, including odor trails, when later tested for spatial navigation. The arena itself was wiped with dilute alcohol solution before testing each mouse, to eliminate odor cues.

Each mouse spent 12 h in the nest box, during which she could go to the surface of the arena enclosed by the Plexiglas cylinder and view the room, which was fully illuminated, from only that location. Thus, mice were capable of viewing distal landmarks from that location. Thereafter, the mouse was placed in a dark box and rotated slowly for 1-2 min, while the experimenter walked around the room. This was done to prevent the mice from associating the nest location with any other point in space by the mechanism of path integration. The mouse was then placed inside the Plexiglas cylinder situated in the centre of the arena. She was left there for 6 h, after which she was taken on another disorientation tour, and ended up in the nest box where she stayed for another 6 h. The mouse was then taken from the nest on a third disorientation tour, during which the surface of the arena was cleaned and had no objects on it and the pups were taken from the nest box. This would eliminate orientation by intra-arena cues, including odor cues. The dark box with the mouse in it was placed in the centre of the arena and the arena, along with the boxed-in mouse, was rotated 6-7 full rotations CW or CCW. The purpose here was to prevent the mice from orienting by relying on path integration mechanism. Therefore, if the mouse navigates towards any point, it would be by means of distal visual cues. One or two pups were dropped inside the box and the box was removed leaving the mother and her pups in the centre of the bare arena. The point at which the mouse arrived at the edge of the arena was recorded for later analysis. Each mouse was tested only once.

Experiment Ib

A similar setup to that of experiment Ia was used here. The difference was that the doors at the end of the tube connecting the Plexiglas cylinders at the nest and the centre were removed. Each of the eight mice now could access the two Plexiglas cylinders through the tube within the 14-18 h they were left there. Again, the room lights were kept on during that time, so that the mice could access distal visual landmarks from their locations. To ensure that the mice would visit the centre, they were induced to retrieve pups from the centre back to the nest 30 times. In addition, a small water cup (3W x 2H cm) was left in the central area as the only source of water. After that, each mouse was placed in the dark box, and taken on a disorientation tour. The surface of the arena was cleared of all objects and the pups were taken from the nest. The mother was then placed in the centre with 1-2 of her pups, and the arena was rotated 6-7 full rotations CW or CCW. The box was then removed and the point at which the mouse arrived at the edge of the arena was recorded for later analysis.

RESULTS

Experiment Ia

The arrival points of the eight females at the periphery of the arena are shown in Fig. 1. The mice took direct paths to the edge of the arena and made no looping or circling. The sample mean angle is 89.28° , while r is 0.06. Therefore, the hypothesis that orientation was random cannot be rejected (V Test; $P > 0.25$).

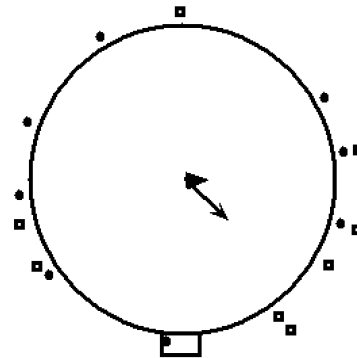


Fig. 1. – The arrival points for the eight mice used in experiment Ia are indicated by the solid arrow and circles. $\bar{\theta} = 89.28^\circ$, $r = 0.06$. Arrival points for the mice that were allowed to shuttle in a dark tube (experiment Ib) are indicated by the open arrow and squares. $\bar{\theta} = 47.5^\circ$, $r = 0.37$ (the rectangle indicates the nest location at 0°).

Experiment Ib

Mice arrival points at the periphery of the arena are shown in Fig. 1. Again, the mice took direct paths to the edge of the arena upon release. The sample mean angle, $\bar{\theta}$, is 47.5° , while r is 0.37. Therefore, the hypothesis that orientation was random cannot be rejected (V Test; $0.05 < P < 0.1$).

DISCUSSION

We can summarize the above findings as follows. First, allowing mice to view the environment from only two different locations results in poor landmark-based orientation. Second, this occurs regardless of whether the mice were, or were not, allowed to shuttle between the two locations, but denied access to visual landmarks while shuttling.

It has previously been shown that viewing distal landmarks from only one location cannot support later navigation to that location from another (ALYAN, 1994). What has been shown here is that viewing the distal landmarks from two locations does not allow successful landmark-based navigation, even though the mice moved between the two locations. In addition, moving between two points per se is not sufficient for successful navigation. This is in contrast to earlier findings that mice navigated successfully when they had access to visual cues while moving (ALYAN & JANDER, 1997a). Thus, the present results support earlier claims that it is necessary to view distal cues while shuttling between locations in order to navigate by such cues, (STAHL et al., 1987; SUTHERLAND et al., 1987; POU CET & BENHAMOU, 1997). Separate vistas of distal cues from different locations, without actual movement between them, do not allow successful navigation by distal landmarks as has been claimed in various theoretical models (WILKIE & PALFREY, 1987; GALLISTEL, 1990; O'KEEFE, 1990; 1991). The present results confirm that rodents require to be fed conjointly with movement and visual information to be able to perform efficient place navigation. Altogether, these reports lend further support to the hypothesis that animals build cognitive representations of their home ranges through motor vector deduction, i.e. based on path integration, and not perceptual vector deduction (ALYAN, 1994; POU CET & BENHAMOU, 1997).

In addition, ZANFORLIN & POLI (1970), and ALYAN & MCNAUGHTON (1999) have shown that normal rats, and rats with hippocampal lesions, were capable of proper homing after shuttling between two points, by making a novel shortcut under a sandy substrate, i.e. no visual cues were accessible since rats were moving underground. The rats could view distal landmarks from the end points only, but not while shuttling. The difference between these two studies and the present results is that path integration was not specifically impaired before homing (ZANFORLIN & POLI, 1970; and ALYAN & MCNAUGHTON, 1999). Thus, both studies indicate that rats form a cognitive representation of their path, which enables them to calculate a novel shortcut by means of path integration when the original route is blocked. This also supports claims that animals could build cognitive representations through path integration.

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