How to turn the corner: Discrimination of path shapes in rats

Nobuya Sato[1] · Ayaka Sato[1]

Abstract

The internal representation of a path shape is an element that constructs an internal representation of an entire route or environment. In the present study, we examined the ability of rats to discriminate path shapes. The rats learned to discriminate between an oval-shaped runway and a square-shaped one and to respond to one of two response boxes on the two sides of the runways. After the learning sessions, we tested which of the inner and outer walls the rats used as cues for discrimination using different wall shapes. The results suggest that the rats used the shape of the inner walls for the discrimination. Subsequently, the learning sessions, in which different shapes of the inner and outer walls were used, continued. There was a tendency for the rats to show better performance when the shape of the inner walls was congruent with the rule in the original learning, suggesting again that the rats used the shape of the inner wall for the discrimination. In addition, similar results were obtained when the task was conducted in the dark, suggesting that rats can discriminate path shapes using non-visual information.

Keywords Navigation · Route recognition · Looped runway · Geometric cue · Wall structure

Introduction

When we navigate in an environment, identification of the current location, which is principally accomplished via two systems, is crucial. One is through dead reckoning or path integration, which is calculation of the current location accomplished by accumulating a series of pieces of self-movement information about distances and directions from a starting point (Etienne & Jeffery, 2004; McNaughton et al., 2006). This can be seen as using idiothetic information.

The other is by identifying the current location through recognition of the scene spreading out before your eyes. This includes recognizing not only a scene itself, but also landmarks (Poucet & Benhamou, 1997). In a closed environment, we can use geometric cues to identify a place or a direction, especially in a disoriented situation (Cheng, 1986; Cheng et al., 2013). This is supposed to be accomplished through computation of geometric structures (Cheng, 1986) or through matching currently obtained visual information with that in the targeted location (Stürzl et al., 2008). In any case, it is achieved by utilizing visual information. Thus, in most organisms, visual information and idiothetic information primarily act as cues for navigation, especially for identifying a current location.

For effective navigation in a large-scale environment in which information about a destination cannot be obtained from the current location, an internal representation of the environment that encodes allocentric relationships between places is required. Such an internal representation is known as a *cognitive map* (O'Keefe & Nadel, 1978; Tolman, 1948). A path that connects places is thought to be one important element for constructing a cognitive map (Lynch, 1960), and multiple paths compose a route that is also one of the spatial representations indispensable to navigation in a large-scale environment. Thus, the shape of a path is also considered to be an important component for the construction of a cognitive map. In the context of path integration in animals, however, the shape of a path has seldom been thought to matter. In cases of path integration, only the relative spatial relationship between two points is focused on, although there are infinite possible paths between two points. In addition, it has been known that the representation of a path tends to be distorted; the angle of an intersection tends to be regularized into a right angle even though it is more or less than 90°, and a curved path is often recalled as a straighter one (Byrne, 1979; Milgram & Jodelet, 1976; Moar & Bower, 1983; Sadalla & Montello, 1989; Tversky & Schiano, 1989). Even in the same path connecting two points, one including a turn is different from one consisting of a curve. Turning a corner comprises a

✉ Nobuya Sato
    nsato@kwansei.ac.jp

[1] Department of Psychological Sciences, Kwansei Gakuin University,
    1-1-155, Uegahara, Nishinomiya, Hyogo 662-8501, Japan

local abrupt change in the direction in which one is heading, whereas a curve comprises a gradual change. Thus, the representation of a path is a critical issue; examining the discriminability of path shapes can be a basis for revealing the nature of the cognitive map.

Rodents have been widely used in neuroscientific (Eichenbaum et al., 1999; Moser et al., 2008; O'Keefe & Nadel, 1978) as well as behavioral (Gallistel, 1990; Poucet, 1993; Tolman, 1948) studies of navigation. Many studies in rats have demonstrated the involvement of sensitivity to geometric cues (Cheng et al., 2013) and of path integration (McNaughton et al., 2006) in navigation. Meanwhile, the recognition of path shapes in rats, that is, whether they can discriminate them, has rarely been examined. In the present study, we examined whether rats can discriminate the shapes of looped runways. In addition, the present study aimed to manifest how visual and idiothetic cues are involved in the discrimination of path shapes. Rats can solve spatial problems without visual cues (Maaswinkel & Whishaw, 1999; Wallace et al., 2002), suggesting that they do not necessarily rely on visual information for spatial processing. Although idiothetic cues are useful to recognize a current location relative to a reference location as in path integration, their usefulness in recognition of path shapes is not evident. The difference in path shapes is expected to provide visually different information, like the geometric difference in corners of a rectangular box (Cheng, 1986). In the present study, we examined the importance of visual cues for the discrimination of path shapes by limiting visual information. We also examined which of the structures of the inner or outer walls are critical for the discrimination of path shapes. Relatively speaking, the outer walls may provide more visual information than the inner walls, whereas the inner walls may provide more idiothetic information than the outer walls if rats run along the inner walls in a looped runway. We aimed to compare the relative importance of visual and idiothetic cues in the discrimination of path shapes by examining the relative effectiveness of the inner and outer walls as a discriminative cue.

Methods

Subjects

Twenty-four male 11-week-old Long-Evans rats (Japan SLC, Hamamatsu) were used as subjects. At the beginning of the experiments, their average weight was 308 g. They were individually housed in a stainless-steel wire cage (200 x 250 x 187 mm) in a 12/12-h light/dark cycle (the lights were on from 9:00 to 21:00) with controlled temperature (23 °C) and humidity (60%). All rats were deprived of food to maintain 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 (2017-04, 2018-04, 2019-07).

Apparatus

We used four types of runways, which were made of 5-mm thick gray polyvinyl chloride boards (Fig. 1). All runways were formed as a circuit track, that is, the path started from a starting point and was connected back to that starting point. The size of the runways was 100 x 50 x 20 cm, and the width of the path was 12 cm. The Rectangle runway consisted of four right-angle corners (Fig. 1a) and the Oval runway consisted of four round-shaped corners (Fig. 1b). The Rectangle and Oval runways had the same structure for their respective inner and outer walls. The Rectangle-oval(R-o) and Oval-rectangle(O-r) runways consisted of two different structures for the inner and outer walls. The R-o runway had four right-angled outer walls and four round-shaped inner walls (Fig. 1c), and the O-r runway had four round-shaped outer walls and four right-angled inner walls (Fig .1d). The runways used in the experiments were placed on a table 70 cm above a floor and surrounded by black curtains. During the experiments, white noise (70 dB) was presented.

On the inner and outer side walls along the middle of a longer straight path, there were two food boxes. A rat could insert its nose into a box through a 5 x 5 cm square hole in the wall. We defined the area around the food boxes as a choice point. The rats ran toward a choice point from a starting point and chose one of the food boxes. Behind and in front of the starting point, wall plates could be inserted to hold the rats at the starting or choice points. If the rats made a correct response, they could obtain chocolate-flavored (F07256, Bioserv) or banana-flavored (F07257, Bioserv) pellets delivered to the food box by food dispensers (ENV-203, Med associates).

Procedure

The present experiments consisted of four phases (Fig. 1e). With 16 rats, all experiments were carried out under the light condition, and with the remaining eight rats, they were carried out in the dark condition. All of the experiments were carried out by a female experimenter.

Habituation and shaping All of the rats were familiarized with the Rectangle and Oval runways. The rats freely explored one of the runways for 10 min per day. They explored each runway twice, 4 days in total. During the habituation, plastic plates were placed over the response boxes; hence, the rats were not able to make nose-poke responses. Subsequently, we placed a rat in an area (39.5 cm x 12 cm) segmented by two plates, and shaped the rat's nose-poke responses to the boxes.
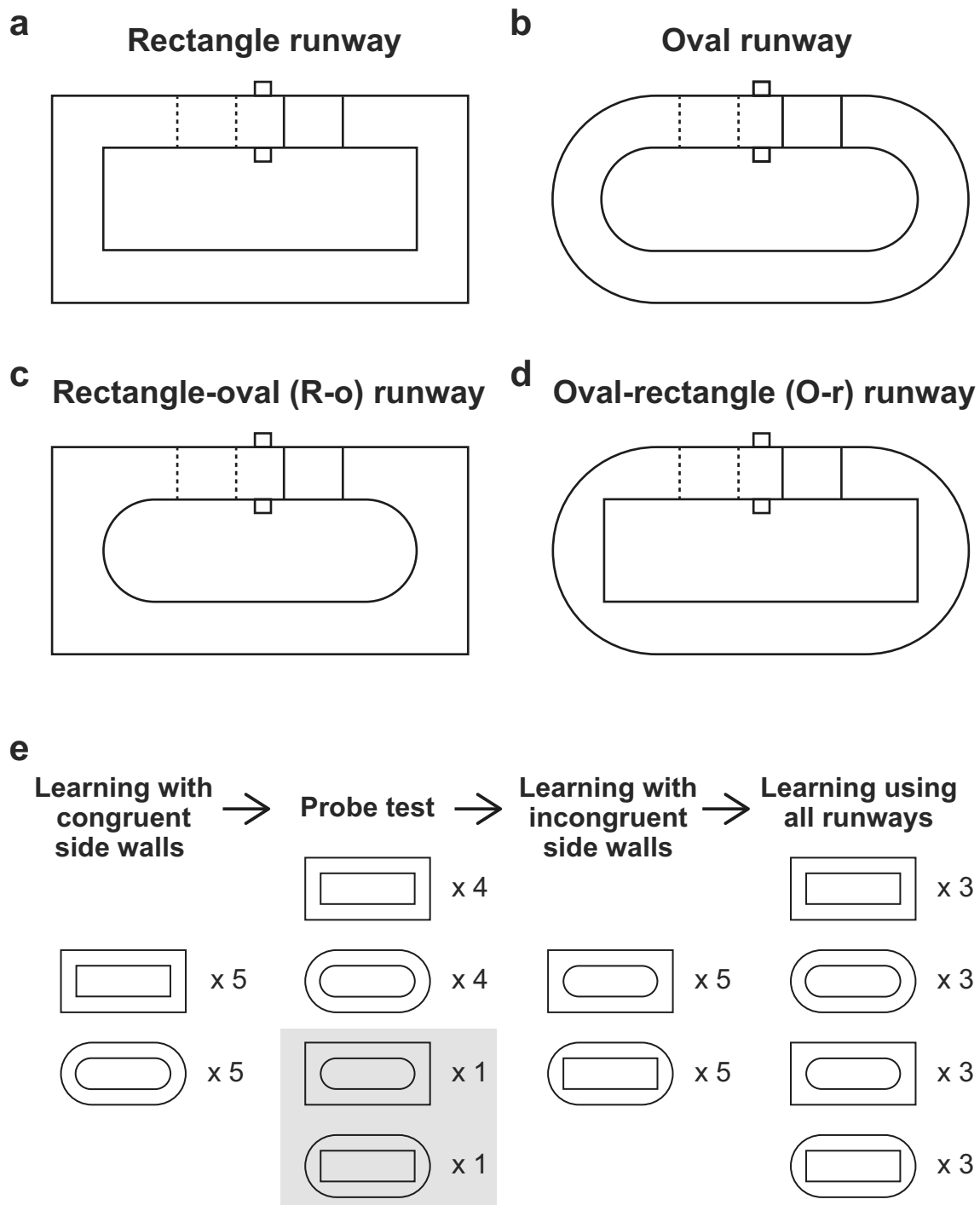
Fig. 1 Runways used in the experiment (**a–d**) and the experimental procedure (**e**). The small boxes in the upper portion of each drawing indicate the response boxes. The areas between the solid and dashed lines in the runways indicate the start area when the rats run clockwise and counterclockwise, respectively. There were four experimental phases: learning with congruent side walls, probe test, learning with incongruent walls, and learning using all walls (**e**). The numbers in (**e**) indicate the number of trials in which the runway was used in a session of each procedure. The shaded runways were presented in the probe trials

After 2 days of shaping, 10 min per day, the rats came to respond well to the box of both sides.

Runway shape discrimination task After the shaping of the nose-poke response to the food box, the learning of a discrimination task was started using the Rectangle (Fig. 1a) and Oval (Fig. 1b) runways. In the task, the rats were required to choose one of the two food boxes depending on the shape of the runway. We set up a starting area (14.5 x 12 cm) at the left or right side of the choice point using two

plates (Fig. 1). A trial of the task was started by opening the plate that was on the far side from the choice point after the rat was put in the starting area. The rats were required to run down the runway and choose one of two food boxes corresponding to the shape of the runway. Half of the rats ran clockwise and the other half ran counterclockwise. The direction of the runs was constant for each rat. Half of the rats were required to choose the box on the inner wall when the runway was square-shaped and that on the outer wall when the runway was round-shaped. The remaining rats were required to make the converse correspondence. If the rats chose the correct box at the choice point, they could get five flavored pellets. Expecting the differential outcome effect (Trapold, 1970), different flavored pellets were used for rewards. The chocolate- and banana-flavored pellets were delivered to the inner and outer food boxes, respectively. If the rats made an error, they continued the trial without getting out of the runway and had to run more until they could choose the correct box. After every trial, the runway was cleaned with a 20% ethanol solution. There were five Rectangle trials and five Oval trials, in total ten trials in a daily session. The order of the trials in a session was in accordance with the Gellermann sequence (Gellermann, 1933). The learning of the ten trials in a daily session was continued until the rats met a learning criterion, which was set at 80% correct responses in two consecutive sessions. This is above the chance level (50%), which was confirmed by a binomial test, p = 0.01182, 95% CI [0.56 0.94]. After reaching the criterion, the rats were put through the discrimination task with extinction trials. In two randomly selected trials of the ten trials, no food pellet was granted even when the rats made correct responses. This was continued until the rats met another criterion, which was set at 80% correct responses in three consecutive sessions. When a rat responded to the box on the one side in all trials in three consecutive sessions, the rat was put through a correction procedure. In the correction procedure, the runway in which the rat made the wrong response was presented in all ten trials of a daily session, and this continued until the rat made correct responses in eight out of ten trials. Rats that did not meet the criteria within 50 sessions were excluded.

Probe test session After reaching the criteria, we tested what cue the rats used to discriminate the runway shapes. In the test sessions, two non-consecutive probe trials were randomly inserted in ten trials of a session (Fig. 1e). In the remaining eight trials, four Rectangle and four Oval runways were randomly used, and the procedure was the same as in the learning phase. In a probe trial, the R-o or O-r runway was presented, and no reward was presented. After a test session, the same learning session as in the learning phase was carried out. We carried out eight test sessions.

Learning session using the R-o and O-r runways After the test sessions, we retrained the rats to discriminate the shape of the runway using the R-o and O-r runways (Fig. 1e). The order of presentation of the runways was in accordance with the Gellermann sequence (Gellermann, 1933). To examine which of the inner and outer walls were effective as a cue for discrimination, we divided the rats into halves and randomly assigned them to inner and outer groups. For the rats in the inner group, a response to the box corresponding to the shape of the inner wall was regarded as a correct response applying the correspondence between the path shapes and response boxes in the original discrimination task (using the Rectangle and Oval runways). For the rats in the outer group, a response to the box corresponding to the shape of the outer wall was regarded as a correct response. For example, when a response to the inner box for the Rectangle runway was correct in the original discrimination task, a response to the inner box for the O-r runway (oval outer and rectangle inner walls) was correct for the inner group in this task, and a response to the outer box was correct for the outer group. For a correct response, five pellets were granted. The correspondence between the flavor of pellets and the box was the same as in the original discrimination task. There were ten sessions in this procedure.

Learning session using all runways After the learning sessions with the R-o and O-r runways, five sessions of the discrimination task with all four of the runways was carried out (Fig. 1e). Each of the four runways was randomly presented three times; there were 12 trials in total in a session. The same rule for correct responses as in the original discrimination task was applied.

Results

In the light condition, the rats learned to discriminate the shapes of the runways. Five of the 16 rats needed the correction procedure. Two rats did not reach the criteria and were excluded from the following procedures. The remaining rats reached the criterion in the first phase (the sessions in which all of the trials were rewarded) in 18.2 ± 11.3 sessions (mean ± SD) and in the second phase (the sessions with partial reinforcement) in 7.1 ± 3.5 additional sessions. Although most rats ran along the inner walls (Online Supplemental video), there was no bias of responding to the inner or outer response boxes in the first learning phase; the average percentage of responding to the inner box was 49.2 ± 18% (mean ± SD). This is not statistically different from chance level (50%), $t(15) = 0.19$, $p = .86$, Cohen's $d = .05$.

In the dark condition, the rats also learned to discriminate the shape of the runway. Three of the eight rats needed the correction procedure. All of the rats satisfied the learning

criteria. They reached the criterion in the first phase in 23.6 ± 10.6 sessions (mean ± SD) and in the second phase in 8.4 ± 5.1 additional sessions. The average percentage of responding to the inner box was 48.1 ± 17%. Again, there was no bias of responding to the inner or outer boxes, $t(7) = 0.32$, $p = .76$, Cohen's $d = .11$.

Probe test

After that, we carried out a test to examine which of the inner and outer walls the rats used as the cue for discriminating the shape of the runway using the corners with the different shapes of the inner and outer walls (the R-o and O-r runways, Figs. 1c, d). The test was carried out as probe trials that were inserted into the standard discrimination task using the rectangle and oval runways. The test results showed that most rats chose the box that corresponded to the shape of the inner wall of the original learning phase in the probe trials (Fig. 2a). The mean proportion of the responses to the box that corresponded to the inner wall in the probe trials was 0.66 ± 0.04 (mean ± SD), and this was significantly higher than chance level, $t(13) = 3.65$, $p < .005$, Cohen's $d = .97$. We also analyzed the data using a generalized linear mixed model (GLMM) with a binomial link function on the response side data (to the inner or outer boxes). The model included the runway shape, the learning rule (in the rectangle and oval runways, the inner and outer response boxes were required, respectively, and vice versa),

and their interaction as fixed effects and the subject's identity as a random effect. This revealed a significant interaction, $\beta = -3.19$, $p < .0001$, 95% CI [-4.19, -1.89], suggesting that in the probe trials, the rats chose the box that corresponded to the shape of the inner wall of the original learning phase. Main effects of the runway shape, $\beta = 0.73$, $p < .05$, 95% CI [0.08, 1.38], and the learning rule, $\beta = -1.16$, $p < .0005$, 95% CI [-1.81, -0.51], were significant. The intercept was also significant, $\beta = 0.58$, $p < .0005$, 95% CI [0.26, 0.91], suggesting biased responses of the rats to the inner response box.

The result was similar in the dark condition; the rats chose the box that corresponded to the shape of the inner wall in the original learning phase (Fig. 2b). The mean proportion of the choice of the box that corresponded to the inner walls was 0.74 ± 0.15, and it was significantly higher than chance level, $t(7) = 4.43$, $p < .005$, Cohen's $d = 1.57$. Although the percentages of the responses to the box that corresponded to the inner wall looks higher in the rats tested in the dark condition than those tested in the light condition (Fig. 2), they were not statistically different, $t(20) = 1.22$, $p = .23$, Cohen's $d = .55$. Similar analysis using a GLMM revealed significant main effects of the runway shape, $\beta = 1.14$, $p < .05$, 95% CI [0.26, 2.02] and the interaction, $\beta = -4.79$, $p < .0001$, 95% CI [-6.59, -2.99]. This also suggests that the rats chose the box corresponding to the shape of the inner wall in the probe trials.
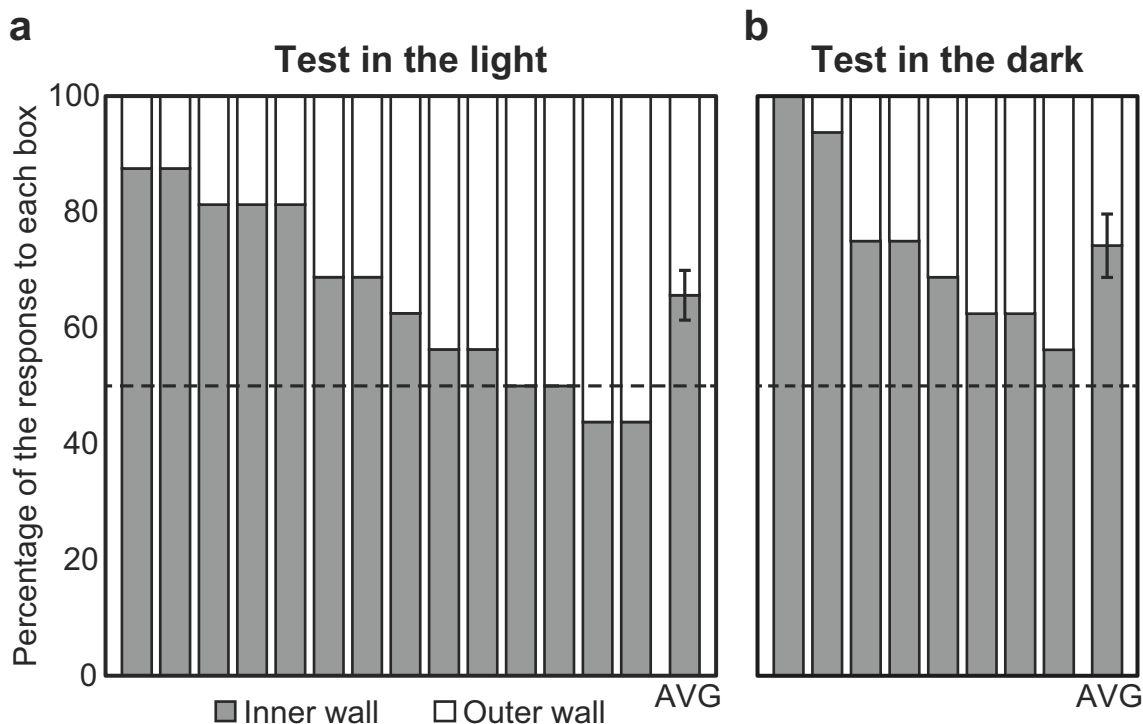

Fig. 2 Results of the probe test in the light (**a**) and dark (**b**) conditions. The shaded and open bars indicate the percentage of the responses to the box that corresponded to the shape of the inner and outer walls, respectively. The bars in each panel indicate the response of each rat except for the rightmost one, which indicates the average. The error bar indicates the standard error of means

Learning with the incongruent shapes of side walls

After the test sessions, the rats learned to discriminate the shape of the runway using the R-o and O-r runways. In the light condition, the rats in the inner group (n = 7) demonstrated stable high performance, whereas those in the outer group (n = 7) demonstrated fewer correct responses (Fig. 3a). In the dark condition (n = 4 for both groups), the results were similar except that the group difference disappeared in the latter half of the sessions (Fig. 3b). A three-way mixed design analysis of variance (ANOVA) with a between-subjects factor of the light condition (light, dark) and group (inner, outer) and a within-subject factor of session (10) revealed a significant effect of session, $F(9, 162) = 5.24$, $p < .0001$, $\eta_p^2 = .23$, but neither significant main effects of condition, $F(1, 18) = 2.48$, $p = .13$, $\eta_p^2 = .12$, nor group, $F(1, 18) = 0.52$, $p = .48$, $\eta_p^2 = .03$. There was a significant group x session interaction, $F(9, 162) = 2.05$, $p = .04$, $\eta_p^2 = .10$. No other interactions were statistically significant, Fs < 1. The analysis of simple effects revealed that the performance of the inner group was higher than that of the outer group from session 1 to session 5. This suggests that the rats in the inner group learned to discriminate faster than those in the outer group. The analysis using a GLMM on the correct responses with group (inner, outer) and session as fixed effects and subject's identity as a random effect revealed similar results. It revealed main effects of

group, $\beta = -1.48$, $p < .05$, 95% CI [-2.65, -0.32], and session, $\beta = 0.14$, $p < .0001$, 95% CI [0.10, 0.17], and an interaction, $\beta = 0.10$, $p < .05$, 95% CI [0.02, 0.17]. Because the models that added the lighting condition or the side of the response box as the fixed effects resulted in higher Akaike Information Criterion (AIC) values, we rejected them.

Learning using all runways

To examine the effect of learning to attend to the shape of the inner or outer walls on the original learning, the discrimination task was carried out using all four of the types of runways. Two of the four runways had congruent walls, that is, inner and outer walls of the same shape (the Rectangle and Oval runways) and the other two had incongruent walls (the R-o and O-r runways). Figure 4 shows the proportion of correct responses. For the light condition, a three-way ANOVA with a between-subjects factor of group (inner, outer) and within-subject factor of wall congruency (congruent or incongruent shapes of the inner and outer walls) and session (5) revealed a tendency of a main effect of group, $F(1, 12) = 3.57$, $p = .08$, $\eta_p^2 = .23$. A tendency of group x wall congruency x session was also revealed, $F(4, 48) = 2.31$, $p = .07$, $\eta_p^2 = .16$. This suggests that the rats in the outer group tended to show poorer performance in the trials with the congruently shaped corner walls (the Rectangle and Oval runways), especially in the
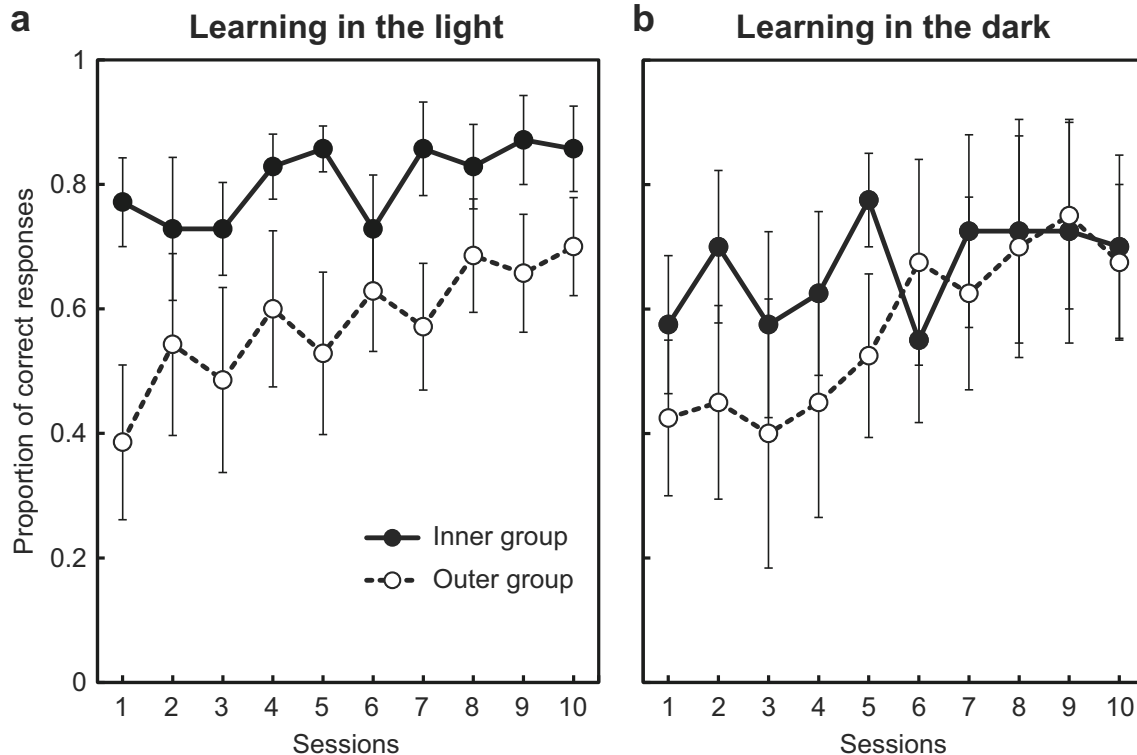

Fig. 3 Results of the learning with incongruent side walls in the light (**a**) and dark (**b**) conditions. The solid lines with filled markers indicate the proportion of correct responses in the inner group and the dashed lines with open markers indicate those in the outer group. The error bars indicate the standard error of means
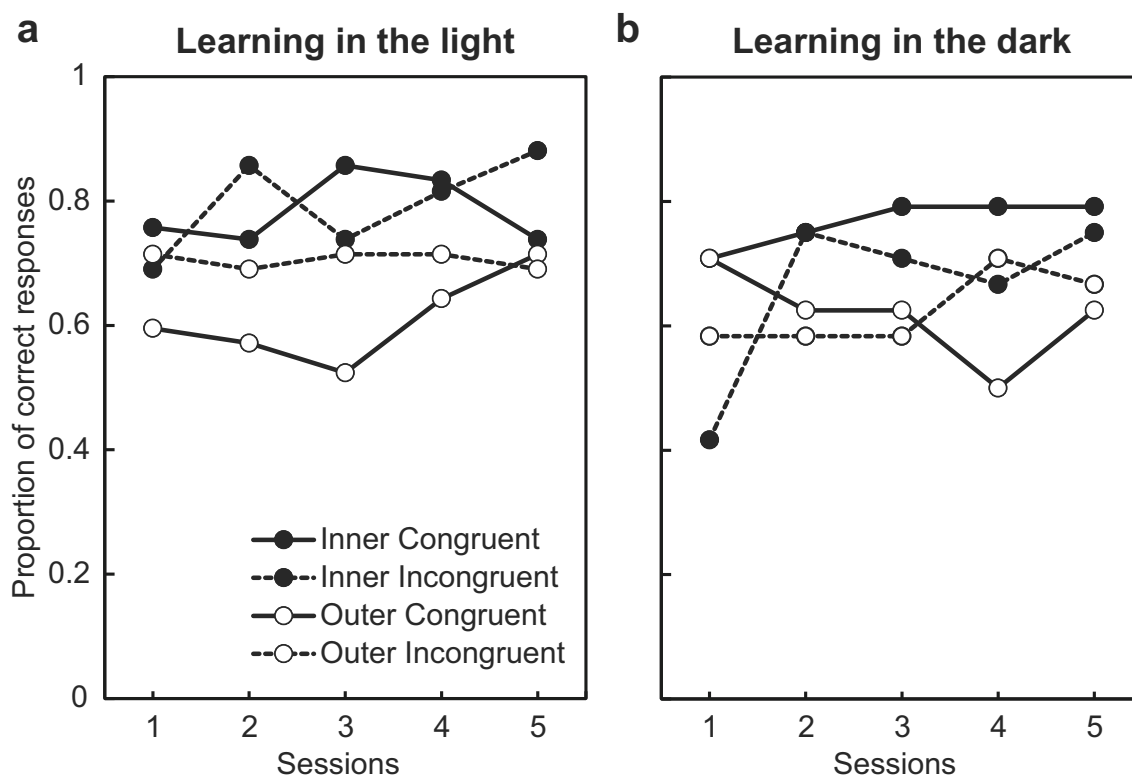
Fig. 4 Results of the learning using all runways in the light (**a**) and dark (**b**) conditions. The filled and open markers indicate the proportion of correct responses in the inner and outer groups, respectively, and the solid and dashed lines indicate those in the trials with the congruent and incongruent side walls, respectively

early sessions of this learning (Fig. 4a). For the learning in the dark condition, a similar ANOVA revealed no significant effects, $Fs < 2.01$, $ps > .12$, $\eta_p^2 < .26$. The analysis using a GLMM on the correct responses with the group, the runway shapes, and the side of the response box as fixed effects and subject's identity as a random effect revealed a main effect of group, $\beta = -1.55$, $p < .0005$, 95% CI [-2.42, -0.68], and an interaction of group x runway shapes, $\beta = 0.42$, $p < .0005$, 95% CI [0.19, 0.65]. No other effects reached significance. The models that included the lighting condition or session as the fixed effects resulted in higher AIC values.

Discussion

In the present study, we examined whether rats can discriminate the path shape of looped runways. The rats learned to choose one of two response boxes and make a nose-poke response depending on the shape of the corners of the runway. The fact that the rats learned to discriminate the path shapes of the runways suggests that the path shapes act as a discriminative stimulus; that is, the path shapes work as a cue and can control behavior other than passing through the path. Several previous studies also showed that the shape of a surrounding environment influenced behavior in rats. The shape of an

experimental room can work as a sufficiently effective cue to retrieve a learned location even when the landmark information that was effective in the learning phase is removed in the test phase (Ramos, 2000). There is also a report that the shape of an arena influenced the travel path of rats in the arena (Yaski et al., 2011): the travel path became a circular shape in a round arena while it became straight in a square arena.

Although most of the rats in the present study learned to discriminate the path shapes, two rats did not satisfy the learning criterion. In the course of learning, some rats showed biased responses to one side of the boxes and needed the correction procedure. The choice of response between the two side boxes after running a runway might be relatively difficult for rats. We used different reward pellets to reinforce the response to each box, expecting a differential outcome effect (Trapold, 1970). Before the present study, we carried out a preliminary experiment using only standard food pellets for reinforcement. In that experiment, the rats seemed to have difficulty discriminating between the two boxes. A differential outcome effect was observed in most rats, whereas for some rats, it might have been not enough to establish the discrimination. In addition, the rats were required to differentially respond to the inner and outer boxes on the longer straight path in the runways depending on the contingency of the shape of the corners. This can be seen as a symbolic

matching-to-sample procedure, in a sense. In addition, since there is a time lag between the presentation of the cue of the path shapes corresponding to a sample stimulus and the presentation of the response boxes corresponding to comparison stimuli, it can be seen as a delayed matching-to-sample procedure. This might be responsible for the difficulty of the task.

In the present study, we also aimed to examine how the visual (allothetic) and idiothetic cues are involved in the discrimination of path shapes. In the dark condition, the rats could discriminate the path shape without visual information, suggesting that they can use idiothetic information to discriminate the path shapes. We also examined which of the inner or outer wall shapes are critical for the discrimination using probe tests. The results of the tests suggest that the rats utilized the shape of the inner wall as a cue for the discrimination. This tendency was the same in the dark condition. In the probe trials, responses that were congruent to the shape of the inner wall were as frequent in the dark condition as in the light condition, or they were rather more frequent. This also suggests that the discrimination of the shape of the corners depends on non-visual information.

The discrimination might be accomplished by utilization of self-movement or proprioceptive information that is also involved in the path integration process. Several studies suggest the importance of vestibular information in the processing of path integration (Cohen, 2000; Wallace et al., 2002). A conceivable possibility is that the rats might have used somatosensory information from their vibrissae to discriminate the path shapes. Rodents obtain different types of information through their vibrissae (Diamond et al., 2008; Kleinfeld et al., 2006). It is likely that the rats obtained the structural information about the inner wall through their vibrissae.

In the probe trials, the rats tended to biasedly respond to the inner box. This might have been caused by the fact that the rats ran along the inner wall. Although this behavior seems to reflect thigmotaxis in rats (Barnett, 1963; Grossen & Kelley, 1972), the outer walls are not so different from the inner walls in that sense. In fact, such biased responses were not observed in the first learning phase. In addition, in the GLMM analyses of the data of the incongruent learning and four runway-learning phases, the models including the factor of the side of the boxes (inner/outer) resulted in worse evaluation, suggesting that in those phases, the side of the response boxes was not less relevant to the rats' responses. The biased responses to the inner box might be a tendency that appeared in an ambiguous situation like in the probe trial.

The results of the extra learning using the runways with incongruent wall shapes indicated that the inner wall group learned the discrimination faster than the outer wall group. This also suggests that the rats tended to use the inner wall to discriminate the shapes of the corners. The better performance of the inner wall group compared with the outer wall group was the same between the light and

dark conditions, suggesting that the shape information of the inner wall was used through sensory modalities other than visual. Meanwhile, the performance in the dark condition was worse in general as compared to that in the light condition (Fig. 3). This might suggest that visual information is also important for discriminating the shapes of corners.

In the learning using all four of the runways, the rats in the outer group demonstrated poorer performance in the trials in which the shapes of the inner and outer walls were congruent, that is, the Rectangle or Oval runway was presented. In the preceding procedure, the rats learned to discriminate only the shape of the R-o and O-r runways. The rats assigned to the outer group could use the same strategy as in the first learning phase if they used the shape of the outer walls as the discriminative cue. However, they might also have persisted in using the shape of the inner wall as the discriminative cue in the phase using the incongruent wall shapes. In that case, they had to reverse their responses to the inner and outer boxes. The reversal response learning possibly made the performance in the trials with the congruent shapes of the corner walls worse.

The present results indicate that path shapes work as discriminative stimuli, and that the representation of path shapes has an ability to control behavior. It also implies that rats can construct internal representations of path shapes. The representation of path shapes likely becomes an element of cognitive maps that provide a foundation for navigation. In other words, the system used for path recognition might be involved in the formation of cognitive maps. Several studies have indicated that rats can take a shortcut (Grieves & Dudchenko, 2013; Roberts et al., 2007; Sato et al., 2018). This might be achieved through an inference from or operation of the representation of path shapes. It is suggested that replay of hippocampal place cells demonstrates activity mentally simulating the path that is not actually taken in the trial (Gupta et al., 2010). Further studies including this neural mechanism are expected to manifest the functional details of the internal representation of path shapes.

Supplemental video Example video recordings that show rats' behavior in runways in the first learning phase.

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