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Formation of a Simple Cognitive Map by Rats

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Cognitive mapping implies the development of an internal representation of the spatial relationships among objects in the environment. One can assess the development of a cognitive map by demonstrating that an animal can select, when appropriate, a novel path to reach a goal in the absence of landmarks and when path integration does not provide an adequate account. Rats were trained to find reinforcement in two of three goal boxes in a three-arm maze. In test, the rats were given a choice between two novel paths, one that led to the goal box that had been baited during training, the other that led to the goal box that had been unbaited during training. When they were trained in the absence of distinctive intramaze cues (Experiment 1), no preference was found; however, when distinctive intramaze alley cues were present during training but were unavailable as directional cues during testing (Experiment 2), the rats demonstrated a significant preference for the correct novel path. These results suggest that under appropriate conditions rats are able to form simple cognitive maps of their environment.

For most animals, effective foraging, and thus survival, requires the ability to navigate. Animals may navigate by using objects, or landmarks, as cues by which to orient themselves (Cartwright & Collett, 1983). They can also use information about direction and distance traveled to return home from a foraging episode in the absence of external cues, a process known as path integration. In the absence of landmarks, ants have been shown to rely on path integration to return to their nest after foraging excursions (Müller & Wehner, 1988; Wehner & Srinivasan, 1981). Similar results have been found with golden hamsters (Etienne, Maurer & Saucy, 1988).

However, path integration is only reliable on relatively short journeys because in the absence of landmarks, distance and direction errors often accumulate as an animal updates its position, leading the animal to miss its intended goal. To compensate for these limitations, many animals also rely on landmarks, when available, to guide their navigation.

It has also been suggested that animals may be able to navigate by using an internal representation of the spatial relationships among objects in their environment, or a cognitive map (Tolman, 1948). Unlike landmark use, the development of a cognitive map implies that locations are represented in a common coordinate system and that goal-directed behavior among them is possible even when familiar pathways are not available. Landmarks may be the organizing features of a cognitive map, but they do not need to be present for an animal to locate a goal.

The navigational process that an animal uses may depend on the particular context in which the animal finds itself. If landmarks are present, it may use them. In the absence of landmarks, it may use path integration. However, the ability to use a cognitive map could provide the animal with a flexible and adaptive strategy should the environment change. O'Keefe and Nadel (1978) proposed a formal theory of how cognitive maps develop. They suggested that an animal uses a combination of sensory and motor information to establish its location in space. Then,

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the animal uses the relationship of landmarks to locate its position on a cognitive map relative to the location of the goal.

Similarly, Jacobs and Schenk (2003) proposed parallel map theory, suggesting the use of two distinct mapping systems. The first mapping system creates a *bearing map* and is based on directional and proprioceptive cues. Animals create maps of their environment based on how far, at what speed, and in which direction they have traveled. This map is created with the same information that animals use when navigating via path integration. The second system creates a *sketch map* that is composed of local landmarks involving a small area of an environment. The integrated map emerges when bearing and sketch map information are combined. The advantage of a cognitive map is that the animal does not merely learn to make an explicit response in the presence of a specific landmark (or configuration of landmarks), but it also can use the map defined by the landmarks to make a novel response (see also Gallistel, 1990).

To show evidence of cognitive mapping in animals, several criteria must be met. First, an animal should have the ability to take a novel path to reach a goal (Tolman, Richie, & Kalish, 1946). Second, if a familiar route is blocked, an animal should be able to use an alternative route in an efficient manner (i.e., rather than learning by trial and error; Tolman & Honzik, 1930). Third, the alternative process of path integration must not independently be able to account for the results. Lastly, choice of path and execution must occur in the absence of external cues, such as directly accessible landmarks that would allow for other means of reaching the goal (Bennett, 1996).

In one study of detour use, Tolman and Honzik (1930) trained rats to run to a single goal box by way of three separate paths that differed in their distance to the goal. After rats had experience with all three paths and the shortest path was blocked, rats chose the second shortest path. However, when the shortest path was blocked beyond the point in the maze where the second shortest path rejoined the first path, the rats went directly to the third path, the only path that still allowed access to the goal (see also Tolman, Richie, & Kalish, 1946). The rats' ability to choose a novel path that led to the goal box was not tested, however.

A more recent experiment with dogs provides better support for cognitive mapping in animals (Chapuis & Varlet, 1987). In an open field, dogs were led from a starting point to a location where food was hidden. The dogs were shown the food and were walked back to the starting point. Then the dogs were led to a second hidden food location, somewhat farther away and at an angle of about 30 degrees from the original starting point. They were shown the food there and were then led back to the starting point. The dogs were let off their lead and allowed to find the hidden food in both locations. The dogs first ran to the closest food location and then ran directly to the second hidden food location, without going back to the starting point. This ability to take a novel shortcut showed that the dogs had some representation of the environment and where the second food location was relative to the first. The fact that the dogs were trained in an open field without distinctive local cues suggests that they were not using landmarks. However, in such a natural setting, it is impossible to eliminate distal, or even subtle, proximal landmarks that might be used as cues to indicate the direction of the second goal.

Previous studies of cognitive mapping ability in animals failed to eliminate landmark use as a possible explanation of successful navigation. In Experiment 1, we asked whether rats have the ability to form a cognitive map in the absence of distinctive intramaze or extramaze cues.

Experiment 1

Method

Subjects. Ten experimentally naïve male Long-Evans hooded rats (*Rattus norvegicus*), approximately 240 days old, served as subjects. The rats were acquired from Harlan Laboratories (Indianapolis, IN). The rats were individually housed and maintained at 80% of their free-feeding body weights, about 410 grams, for the duration of the experiment. They had free access to water in their home cage and they were maintained under a 12-hour/12-hour light/dark cycle. The rats' care was in accordance with University of Kentucky institutional guidelines.

Apparatus. The apparatus used was a three-arm maze (see Figure 1). Each arm extended 67.5 cm from the central platform to the goal box. The inside of each arm was 9.1 cm wide. The goal box at the end of each arm was 9.1 cm wide by 9.1 cm long. Between the central goal box and each side goal box was an alley 32.0 cm long and 9.1 cm wide. All alleys and goal boxes in the maze had walls that extended 14.2 cm high. The central platform was in the shape of a trapezoid. The maze was made of wood and painted black.

During training, sliding doors in the side walls of the goal boxes blocked the alleys (shown in black in Figure 1) connecting the goal boxes. The entire apparatus was covered with four sheets of translucent plastic 0.4 mm thick. This material transmitted diffuse light and allowed the experimenter to see the outline of the rat in the maze but prevented the use of extramaze cues by the rat while it was moving through the apparatus. To further eliminate the potential use of extra-maze cues, the maze was rotated 90 degrees prior to each session. The apparatus was elevated 75.2 cm above the floor and was placed in the center of the experimental room. Diffuse fluorescent lights which extended diagonally across the ceiling of the room provided general illumination.

The reinforcers used were 1/4 pieces of Froot Loops®. Each food cup had a false mesh bottom. A piece of Froot Loop was placed below the false bottom in each side arm to provide similar olfactory cues in the side goal boxes.

Procedure

Training. Rats were trained to eat from the food cups located in the goal boxes at the end of each of the three arms. The rats were then trained to obtain food from two of the three goal boxes. For each rat, the same two arms were consistently baited, either the center and left arms or the center and right arms (counterbalanced over rats). Errors during training were defined as entries into the nonbaited arm prior to entry into both baited arms, as well as reentry into a baited arm prior to retrieval of the second food reward.

Rats were run in squads of five, one trial per rat, four times a day with about 7 min between trials. The running order within a squad was reversed on alternating days so that the rats did not always follow the same rat in training. The entire maze was cleaned with a mild detergent after each trial to further prevent the possible use of differential odor cues. Rats were trained to a criterion of 18 out of 20 consecutive trials correct.

Testing. Rats participated in two trials per day during testing. The first trial was an additional training trial. The second trial was a test trial during which doors blocked entry to both side arms from the central platform and the sliding doors in the goal boxes were raised to reveal the alleys that connected the center goal box to the side goal boxes (the two side walls on the center goal box and the interior walls on the side goal boxes). Once at the center goal box, the rat could consume the ¼ Froot Loop and was permitted to choose between the two novel paths (one that led to the arm that had always been baited in training, the other that led to the arm that was never baited in training). On test trials both side goal boxes were baited with a piece of Froot Loop. Once the choice was made, entry into the other novel path was blocked by lowering the sliding door closest to that alternative path. The rat was permitted to consume the piece of Froot Loop, and the trial ended. Each rat received one test trial per day for nine days.

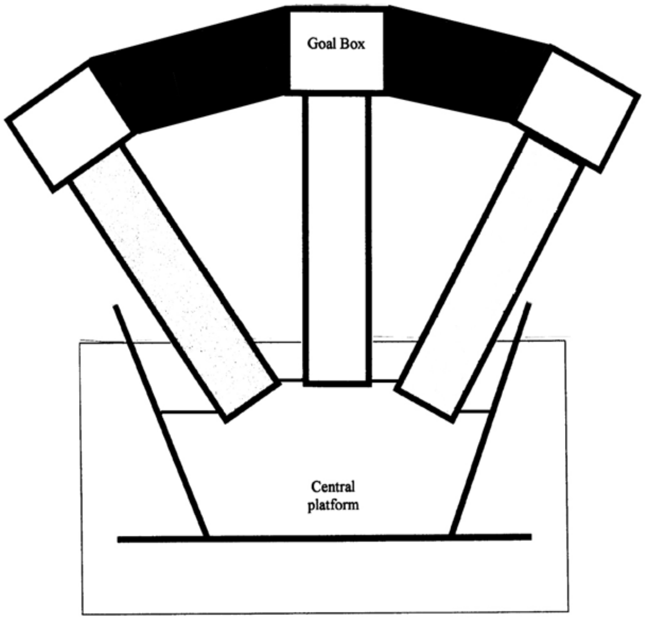

Figure 1. Schematic drawing of the three-arm maze used in Experiment 1. Side arms were accessible from the central platform and doors that led from the center goal box to both side arms were blocked in training. Black areas show the path from the center goal box to the side arm goal boxes that were available on test trials. Entrance to the side arms via the central platform was blocked on test trials.

Results

Rats reached the acquisition criterion in an average of 17 sessions (M = 67.4 trials). On test trials, rats chose the correct novel shortcut that led to the arm that had been consistently baited in training on only 49.0% of the trials. Thus, the rats failed to choose the correct path at levels significantly better than chance, $t(9) < 1$. Choice of the correct path was not different for the two counterbalancing groups. Both groups chose the correct novel shortcut 49.0% of the time. There was no significant correlation between the number of trials to reach criterion and overall performance, $r = .07$, $p > .05$. That is, rats that learned the task more quickly did not perform differently on test trials from rats that learned the task more slowly.

Discussion

After training rats to find food in one side goal box but not the other and blocking the familiar paths to the two side goal boxes, rats failed to choose the path leading to the goal box that had been baited in training more than the path leading to the goal box that had not been baited in training.

Although the rats did not appear to form a cognitive map in this experiment, it may be that landmarks, that may be necessary for the formation of a cognitive map, were absent. The present apparatus may not have provided the rats with sufficient cues during the acquisition phase for them to organize the spatial information provided. Specifically, the similarity of the arms meant that the only cues to arm choice during training were present at the time of the initial choice (at the center platform), and they were not available at the time of reinforcement. If animals build a cognitive map through exploration, as proposed by Poucet (1996), landmarks may play a crucial role in organizing the spatial information needed to form a cognitive map.

Experiment 2

Several investigators have failed to find evidence for the formation of cognitive maps in rats (e.g., Benhamou, 1996; Olthof, Sutton, Slumskie, D'Addetta, & Roberts, 1999; Prados, Chamizo, Mackintosh, 1999); however, the conditions under which the rats were tested (e.g., insufficient cues in training) may not have been optimal for their formation. Similarly, in Experiment 1, the conditions under which rats were trained (i.e., the absence of distinctive cues) may have precluded the formation of a cognition map. Thus, the purpose of Experiment 2 was to determine whether rats could use prominent landmarks to form a simple cognitive map and then take a novel path to reach a goal without the use of directional landmarks to guide choice behavior.

Method

Subjects. Twenty experimentally naïve, male, Long-Evans hooded rats (*Rattus norvegicus*) 56 days of age (Harlan Laboratories, Indianapolis, IN) served as subjects. The rats were individually housed and were maintained at 90% of their free-feeding body weights for the duration of the experiment.

Apparatus. The apparatus used was the modified three-arm maze from Experiment 1 (see Figure 2). The maze was painted white, except for the center goal box which was black to distinguish it from the other two goal boxes. A door in each side arm could be lowered to confine the rat in the incorrect arm following an error during training.

An insert lined the left arm and walls with aluminum sheet metal. Another insert lined the right arm and walls with hardware cloth (0.5 cm spaced wire mesh). Both inserts extended the 67.5 cm length of the side arm, from the entrance of the arm at the central platform to just before the goal box. Thus, on test trials, when the side goal boxes were visible from the center goal box, the side-arm liners were not visible from the center goal box. The center arm had no insert.

The reinforcers used in the experiment were mini chocolate chips (Kroger brand) and quarter pieces of Honey Nut Cheerios ® (chocolate was always used in the center goal box, a piece of Cheerio in the side goal box). A piece of Honey Nut Cheerio was placed below the false bottom in each side arm to provide similar olfactory cues in the side goal boxes.

Procedure

Training. Rats were trained as in Experiment 1 to retrieve food rewards from two of the three goal boxes. However, if a rat made an error, a door was lowered, blocking the rat's exit from the incorrect arm for 30 sec. Rats were run to a criterion of 18 out of 20 consecutive trials correct (90%) followed by 30 overtraining trials. Overtraining trials were introduced to ensure sufficient experience with the arm cues and their associated consequences.

Testing. Rats experienced four trials per day during testing. The first, second, and fourth trials were additional training trials. The third trial of the day was a test trial. Each rat received one test trial per day for nine days. Testing procedures were identical to those from Experiment 1.

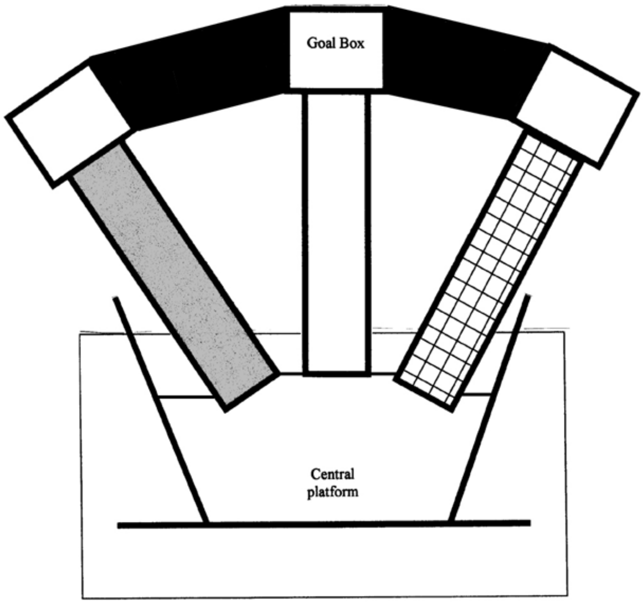

Figure 2. Schematic drawing of the three-arm maze used in Experiment 2. Shading depicts the different textured arm inserts used as intramaze cues. Side arms were accessible from the central platform and doors that lead from the center goal box to both side arms were blocked in training. Black areas show the path from the center goal box to the side arm goal boxes that were available on test trials. Entrance to the side arms via the central platform was blocked on test trials.

Results

Rats reached the acquisition criterion in an average of 13 sessions (M = 53.45 trials). On the first day of testing, 15 out of the 20 rats (75%) chose the correct novel path (the path leading to the goal box that had been consistently baited during training). A binomial test indicated that this was significantly different from chance (50%), $p = .037$. Over the 9 test trials, rats chose the correct novel path on 62.4% of the trials. A one-sample t-test indicated that this level was significantly above chance, $t(19) = 3.65$, $p = .002$. The rats were rewarded regardless of the path they chose. Therefore, it was expected that performance would decrease because all choices were reinforced. In fact, performance did decrease over test trials, from 75% correct on the first test trial to 62.4% correct when performance was pooled over the test trials.

There was a marginally significant correlation between number of trials to criterion in training and overall performance on test trials, $r = .433$, $p = .056$. This result suggests that rats that took longer to reach criterion performed better on test trials than those that learned quickly.

There was also a positive correlation between the number of errors made in training and the number of choices of the correct novel path; however, this correlation too did not quite reach statistical significance, $r = .417$, $p = .07$. Finally, there was a significant positive correlation between the number of errors made during overtraining and test performance, $r = .491$, $p = .028$. Rats that made more errors during the overtraining phase chose the correct novel path more than rats that made fewer errors during overtraining.

Discussion

Rats showed a significant tendency to choose the correct novel path during test trials and, importantly, they did soon the first test trial. Furthermore, it is unlikely that the animals learned which shortcut to take during the multiple test trials because both side goal boxes were baited and performance did not improve over the test trials. These results suggest that the rats had formed an internal representation of the spatial relationship between the center goal box and baited side goal box. When given a choice between two novel pathways, rats generally chose the novel path that led to the arm that had been baited in training.

There was also a significant correlation between the number of errors made in overtraining and overall test performance, suggesting that the aversiveness of being confined in the unbaited goal box may have helped motivate the rats to overcome their natural exploratory tendency. It is also possible that animals that made more errors learned not only where the food was located, but also which places to avoid.

General Discussion

Rats in Experiment 1 failed to demonstrate cognitive mapping ability, but rats in Experiment 2 were successful. The results of Experiment 2 cannot easily be accounted for by either landmark use or path integration. Although distinctive arm cues were available during training, the testing procedure prevented their use on novel test trials. If animals were navigating based on the presence of distinct arm cues, then they would have been unable to choose the novel path that led to the arm that had been baited in training because those cues were unavailable at the time of test.

The typical view of path integration is that it provides a vector and distance from home, allowing an animal to return directly after foraging. Such path integration could not be used in these experiments because the rats had to navigate between intermediate points, rather than from a goal back to a start location. A more recent view of path integration is that it can also be used to navigate from home to a familiar goal by way of a novel path or even among familiar goals (Collette & Graham, 2004; Etienne, Maurer, & Séguinot, 1996). Such a theory of path integration goes well beyond the original use of the term. To adopt this view requires that the animal integrate experiences between acquisition and test trials and how such a process would occur is not specified.

Furthermore, an important distinction between the use of a cognitive map and even this expanded view of path integration is in the role of landmarks. In the formation of a cognitive map, it is assumed that relations among the landmarks allow the cognitive map to be ‘stitched together.’ If a cognitive map has formed, on test trials, it should be sufficient for a landmark to serve as a cue that identifies the animal’s location on the map. If, however, an animal were using path integration alone, it should be able to take the appropriate novel path in the absence of landmarks. In Experiment 1, the rats had few distinctive landmarks available during training and under these conditions, on test trials, the rats performed at chance. Thus, it appears that path integration cannot account for the performance of rats in the two experiments together.

Although the role played by brief confinement in the unbaited goal box during acquisition following an error is not clear, this procedure should not have affected the presence or absence of path integration. However, it may have made the path to the incorrect goal box more distinctive, thus providing an additional salient cue during acquisition that may have helped the rats to form a cognitive map.

The notion of cognitive mapping in animals is not novel; however, previous studies of cognitive maps in animals have either failed to demonstrate such an ability (e.g., Benhamou, 1996; Olthof, Sutton, Slumskie, D'Addetta, & Roberts, 1999; Prados, Chamizo, Mackintosh, 1999) or have failed to eliminate all possible use of landmarks at the time of test (Chapuis & Varlet, 1987; Tolman, 1948). The results from the present experiments demonstrate that rats are able to take novel shortcuts to goal locations by forming a spatial representation of their environment, under conditions that do not allow for the use of landmarks and cannot be explained by the use of path integration.

References

Benhamou, S. (1996). No evidence for cognitive mapping in rats. *Animal Behaviour,* **52**, 201-212.

Bennett, A. (1996). Do animals have cognitive maps? *The Journal of Experimental Biology,* **199**, 219-224.

Cartwright, B. A., & Collett, T. S. (1983). Landmark learning in bees. *Journal of Comparative Physiology A,* **151**, 521-543.

Chapuis, N., & Varlet, C. (1987). Short cuts by dogs in natural surroundings. *The Quarterly Journal of Experimental Psychology,* **39**, 49-64.

Collette, T. S., & Graham, P. (2004). Animal navigation: Path integration, visual landmarks and cognitive maps. *Current Biology,* **14**, 475-477.

Etienne, A. S., Maurer, R., & Saucy, F. (1988). Limitations in the assessment of path dependent information. *Behavior,* **106**, 81-111.

Etienne, A. S., Maurer, R., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *The Journal of Experimental Biology,* **199**, 201-209.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review,* **110**, 285-315.

Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis. Proceedings of the National Academy of Science,* **85**, 5287-5290.

O'Keefe, J. & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, U.K.: Oxford University Press.

Olthof, A., Sutton, J. E., Slumskie, S. V., D'Addetta, J., & Roberts, W. (1999). *Journal of Experimental Psychology: Animal Behavior Processes,* **25**, 352-362.

Poucet, B. (1993). Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychological Review,* **100**, 163-182.

Prados, J., Chamizo, V. D., & Mackintosh, N. J. (1999). Latent inhibition and perceptual learning in a swimming-pool navigation task. *Journal of Experimental Psychology: Animal Behavior Processes,* **25**, 37-44.

Tolman, E. C. (1948). Cognitive maps in rats and man. *Psychological Review,* **55**, 189-208.

Tolman, E. C., & Honzik, C.H. (1930a). Insight in rats. *University of California Publications in Psychology,* **4**, 215-232.

Tolman, E. C., Richie, B. F., & Kalish, D. (1946). Studies in spatial learning. I. Orientation and short-cut. *Journal of Experimental Psychology,* **36**, 429-434.

Wehner, R., & Srinivasan, M. V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Psychology A,* **142**, 315-338.