Problem solving in the rat: Piecemeal acquisition of cognitive maps

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The purpose of this experiment was to compare the problem-solving performance of rats allowed to explore either one or two tables of Maier's three-table-problem apparatus on successive days. The feeding experience and test trial were administered on the day after all tables and runways had been explored in this piecemeal fashion. No rat that explored only one table and runway per day was able to solve the problem, whereas 60% of the rats that explored two tables and their interconnecting runways did solve the problem. All rats that explored the entire apparatus on each exploratory day were able to solve the problem. These data support the notion that animals can conceptually link objects experienced successively into cognitive representations which specify the constant relationships existing between those objects. The existence of such an absolute spatial mechanism makes it unnecessary for an organism to depend upon relative spatial mechanisms such as routes or cues.

In recent years the concept of a cognitive map has become a major theoretical construct in theories of spatial cognition. Although first introduced by Tolman (1948), the cognitive map concept received its most sophisticated treatment by O'Keefe and Nadel (1978), inasmuch as they elaborated a number of major properties of cognitive maps. Specifically, cognitive maps were differentiated from systems that relied on extant cues and orientations in the guidance of behavior. For example, a cognitive map allows an animal to react to stimuli that are not immediately present (i.e., act at a distance). Additionally, it is an information structure in which the distance and direction between various environmental objects are specified. Another property of a cognitive map is that it allows organisms "to link together conceptually parts of an environment which have never been experienced at the same time" (O'Keefe & Nadel, 1978, p. 2). It is to this latter property of a cognitive map that this paper is addressed.

Inasmuch as organisms acquire information about a region by virtue of exploratory activity (O'Keefe & Nadel, 1978) and inasmuch as this process involves a series of successive experiences, such information must be transformed into a cognitive structure in which the distance and direction between the various successively experienced objects are indicated before it can be used in the solving of problems such as the taking of the shortest route to food, etc. Spatial information results when various objects in a cognitive representation exist as a simultaneous pattern rather than merely as a series of temporally ordered experiences (Ellen & Anschel, 1981). If objects are part of a simultaneous pattern, then an organism "knows" that the objects are related to each other spatially in a reciprocal manner (i.e., if A is to the left of B, then B is to the right of A). In contrast, if objects are related only as a successive pattern of events, then an organism "knows" only the temporal order in which the objects were experienced (i.e., if the animal approached A then B, it "knows" that A comes before B, but it does not have a cognitive structure in which the two objects are spatially, or reciprocally, related).

The three-table problem (Maier, 1932a) is prototypical of tasks that can assess the existence of such spatial representations or cognitive maps. The threetable problem is a two-phase problem followed by a test trial. In the first phase, the animal is allowed to explore the entire apparatus. During the second phase, it is fed on one of the tables. During the test trial, it is placed on one of the remaining tables and required to return to the table on which it was just fed. Each day the food table and start table are varied in a quasi-randomized manner so that the animal does not learn a specific orientation (turn strategy) or location of the food. A correct choice is thus a novel response resulting from the integration of the feeding experience and the previously acquired cognitive representation of the problem space (i.e., the spatial relations existing among the tables).

A number of studies have shown that animals not allowed to explore the entire apparatus prior to the feeding phase and test trial fail to go to the baited table on the test trial regardless of repeated daily test-

A version of this paper was presented at the Seventy-Fifth Annual Meeting of the Southern Society for Philosophy and Psychology, Atlanta, GA, March 31-April 2, 1983, and at the Sixtieth Annual Meeting of the Georgia Academy of Science, April 22-23, 1983. The patience of Martha Turner and Majella Hardie in the typing of various versions of this manuscript is appreciated. The authors' mailing address is: Department of Psychology, Georgia State University, University Plaza, Atlanta, GA 30303.

ing. The failure to solve the problem by animals not receiving the prior exploratory experience has been attributed to a lack of opportunity for the animals to acquire a cognitive representation into which the feeding experience can be integrated (Herrmann. Bahr, Bremner, & Ellen, 1982; Stahl & Ellen, 1974). Over a period of several days, however, the animals do locomote over the entire apparatus. On each daily test trial the animals run between two different tables via an interconnecting runway. It might then be expected that such a cumulative, piecemeal locomotor experience would allow for the gradual acquisition of a cognitive map accompanied by a gradually improving ability to solve the problem. In no experiment, however, has such an improvement been observed. This failure of animals to profit from the piecemeal locomotor experience that is afforded by the test trial is troublesome in light of the fact that a major property attributed to a cognitive representation, such as a map, is its property of conceptually integrating parts of an environment that have been separately and/or individually experienced.

The failure of animals to perform above chance levels without an exploratory phase might result from their failure to learn the spatial relationship existing between the particular pair of tables visited during the test trial. Alternatively, it is possible that although the spatial relationships between individual pairs of tables are acquired they do not combine to form a cognitive representation of the entire problem environment. Some support for the former possibility comes from Maier (1932b), who noted that two locations in an environment do not become related spatially unless an animal has been engaged in bidirectional locomotion between the two locations. Over a series of test trials on the three-table task, the animals do, indeed, run back and forth between pairs of tables, but unfortunately, the return trip for any given pair of tables may come several days later, on another test trial.

Inasmuch as both possibilities are present in threetable-task experiments in which animals are not given the prior exploratory experience, it was our intent in the present study to ensure that the spatial relationships between the various pairs were acquired by giving the animals a daily exploratory experience over separate pairs of tables. This procedure ensured that the animals engaged in bidirectional locomotion between various pairs of tables within a restricted time frame. By virtue of this procedure, a failure to solve the problem on the test trial could not then be attributed to a failure to acquire the necessary spatial relationships between individual pairs of tables; to the extent that the animals were able to solve the problem under these conditions, we would have evidence that the individually and separately acquired spatial relationships could be integrated into a unified cognitive representation of the problem space.

METHOD

The experiment was conducted in two parts, separated by approximately 6 months. The time of day for testing and the experimenter were the same for both parts.

Subjects

Fifteen male, naive Long-Evans hooded rats, obtained from Charles River Breeding Laboratories and maintained on a 23-h deprivation schedule, were assigned randomly to the three groups of Part 1. The animals were 90 days old at the beginning of the experimental period and were housed in individual cages in a colony room maintained at 20°C on a 16-h-on(0700-2300)/8-hoff(2300-0700) light-dark cycle.

Another 15 naive Long-Evans hooded rats, provided by the laboratory breeding program, were used in Part 2. There were nine males and six females ranging in age from 65 to 90 days at the beginning of the experimental period. Housing conditions and deprivation schedule were as in Part 1 of the experiment.

The weights of the animals in Part 1 were not taken. For Part 2, the average body weights of the animals ranged from 86% to 90% of their ad-lib weight.

As in Part 1, the animals of Part 2 were assigned randomly to their respective experimental conditions. The random assignment of the animals in Part 2 resulted in the following distribution of sexes among the three experimental groups (described in procedure): 1-TAB, one male and four females; 2-TAB, three males and two females; 3-TAB, five males.

Apparatus

A version of the Maier three-table apparatus, consisting of three runways (each 154 cm long) radiating from a common center point with each terminating at the entrance to a separate table, was used. In Part 1, the three runways were joined at the center by a Yshaped insert that was placed into a position flush with the runways. This ensured that the angles between the runways remained constant. Each table was approximately 81×46 cm. They were faced with a wooden screen that hindered the observation of one table from another. The entrance to each table had an 8×10 cm opening in the wooden screen. The entire apparatus, including the centerpiece, was painted a flat black and elevated 66.5 cm above the floor. The apparatus was housed in a 651×322 cm room. One side of the room consisted of partially covered windows; the other sides contained empty bookshelves, stacked tables, and a large laboratory sink.

The apparatus and testing room were the same in Part 2 and Part 1; however, the center part of the apparatus was changed for Part 2. The Y insert used in Part 1 was replaced by a circular insert with a diameter of 20.5 cm. This center point was used so that the animals would have a larger area on which to turn around.

Procedure

Prior to the beginning of each part of the experiment, each animal was handled 10 min daily for 5 days. For the next 5 days, they were trained to run on runways that were similar to those of the apparatus. The deprivation schedule for the animals began on the day prior to the start of board training. During board training, a board was placed between two chairs. A dish of wet mash, made from Purina Rat Chow pellets, was placed on each chair. During pretraining, each animal was first placed in the middle of the board. If an animal did not spontaneously move along the board, it was gently and briefly nudged. If the nudge did not prompt the animal to move along the board, the animal was gently pushed to one of the chairs. Care was taken to push an animal back onto the board if the animal started to fall.

In both parts of the experiment, three groups of animals were formed—a one-table (1-TAB) group, a two-table (2-TAB) group, and a three-table (3-TAB) group. The groups differed in terms of the nature of the exploratory opportunity given during the exploratory phase. Animals in the 1-TAB groups were allowed to explore only one table and its runway to the center on a given day. On subsequent days, they explored different tables and their runways to the center so that by the end of 3 days all tables and their runways to the center point had been individually and separately explored. Animals in the 2-TAB groups explored two tables and their interconnecting runways, with the result that by the end of 3 days they had covered all combinations of the runways and tables. It should be noted that for this group there was always a common table and runway in each succeeding day's exploration.

The 3-TAB groups constituted the control condition. Animals in the 3-TAB groups explored all three tables and their interconnecting runways on each exploratory day. The animals in all groups were placed individually onto the apparatus at the center point until the entire group had been placed onto the apparatus. The daily exploratory phase lasted 15 min for all animals.

After 3 days of exploration, each of the groups was given a test trial on the 4th day. On this 4th day, no exploratory experience was given to any of the groups. Instead, the rats in each group were merely placed on the table designated as the food table for that day's test trial and were given access to approximately 50 g of wet mash for 2 min. The food dish was sufficiently large so that all animals had easy access to the dish at the same time. After the 2min feeding phase, the animals were removed as a group from the baited table and placed in the carrying cage. The animals remained in the carrying cage until they were returned to their home cage. Care was taken to ensure that food was left on the table when the animals were removed (Herrman et al., 1982). The animals were then individually tested by being placed one at a time on one of the unbaited tables, which was designated as the start table for that test trial. A dish of wet mash covered with a wire screen was placed on the remaining table as an olfactory control. The guillotine door on the start table was then raised and the test trial was begun. The animals were allowed 3 min to leave the start table and 1 min to reach the food table. A correct response was scored only if an animal went directly from the start table to the food table. If the animal chose the food table, it was allowed to eat for the amount of time that it took the experimenter to lower the door of the start table, record the animal's choice, and walk to the food table (approximately 30 sec).

On each test trial, the schedule of start and food tables was quasi-randomized to keep the animals from learning a particular place or turn strategy. In Part 1, the only constraints on the schedule were that the same table not be used for more than two consecutive test trials and that the route to the food table not involve the same turn on more than two consecutive test trials. In Part 2, the schedule of start and food tables was arranged so that each table served as the food table an equal number of times. The correct choice involved an equal number of right and left turns over the 18 trials. Moreover, the schedule was arranged so that for the 2-TAB group a particular test route and a particular exploration route were separated by 1, 2, or 3 days an equal number of times.

The order of testing for the animals within a group varied daily. The animals were assigned to a test position of 1 to 5. The animal that was tested first on one day was moved to position 5 on the next day, and all other animals advanced one position. Over five test trials, an animal was tested in all positions.

Finally, it should be emphasized that, inasmuch as each test trial day was separated by 3 days of exploration, the entire procedure required 72 days. Pretraining and test trials were carried out 7 days a week with minor exceptions. If there was a break in the procedure, it came after a test trial and before the next exploratory cycle.

RESULTS

To ensure that the 15-min exploration period did indeed provide an opportunity for the animals to engage in bidirectional locomotion over the various parts of the apparatus available to them, the sector entry behavior for each animal over the course of the 54 exploratory days was analyzed. For the 2-TAB and 3-TAB groups, a sector entry was defined as the rat's leaving one runway and placing all four paws onto another runway. In the case of the animals in the 1-TAB group, a sector entry was counted when the animal went from the runway to the table or vice versa.

Animals in the 1-TAB group made an average of 10 sector entries per day (range = 4 to 16). Animals in the 2-TAB group averaged 9 sector entries per day (range = 4 to 16). The animals in the 3-TAB group were on Sectors A, B, and C an average of 3, 3, and 4 times, respectively, per day. It is clear from these results that the animals in all groups locomoted back and forth between the parts of the apparatus that were available to them. Furthermore, animals of the 3-TAB group tended to distribute their activity equally among the three tables.

Figure 1 (A and B) shows the percent correct for each animal in each of the three groups in both parts of the experiment. The dotted line in the figure represents the score (72%) that would be expected to occur by chance 5% of the time or less according to expansion of the binomial equation. It is apparent from Figure 1 that all animals in both 3-TAB control groups achieved this level of performance. In con-



Figure 1. Individual performance (% correct) of rats exploring varying numbers of tables. The dotted line represents the performance level that could occur by chance 5% of the time or less. The solid line represents group means.

trast, no animal in the 1-TAB group in either part of the experiment met this level of performance. Three animals in each of the 2-TAB groups were able to score above this level.

The percent correct scores for each group in both parts of the experiment were compared using a twoway ANOVA with Parts 1 and 2 as Factor 1 and number of tables explored as Factor 2. Since there was no significant Factor 1 effect [F(1,24) = .00,p = .971 or interaction between Factors 1 and 2 [F(2,24) = .81, p = .45], the percent correct scores for the two parts of the experiments were then pooled into the respective exploratory groups. When this was done, the resulting pooled 1-TAB group was correct 49% of the time. The pooled 2-TAB group was correct 72% of the time, and the pooled 3-table group was correct 87% of the time. An ANOVA of the pooled data revealed a significant effect of number of tables explored [F(2.27) = 22.02, p < .0001]. Post hoc tests showed that the scores of the 2-TAB and 3-TAB groups were no different (Tukey's HSD p > .01), whereas the scores of the 1-TAB group were significantly lower than either the 2-TAB or 3-TAB groups (Tukey's HSD p < .01).

Finally, a chi-square analysis indicated that the number of animals in each group scoring 72% correct or better increased as the number of tables explored on a day increased $[\chi^2(2) = 20.357, p < .001]$. Fisher's exact probability test indicated that significantly more animals in the 3-TAB group than in the 2-TAB group solved the problem (p = .05). Thus, the difficulty of the problem was increased when the animals were given access to only one or two tables on each exploratory day.

This latter point is further substantiated in the results of Table 1, which shows the number of animals reaching the .05 criterion level at the various stages of the testing period. When four or fewer trials have been given, the animal's performance is impossible to interpret, since a score of 100% correct has a high likelihood of occurrence according to an expansion of the binomial equation. In contrast, a score of five correct out of five trials could have occurred by chance only 3% of the time. Accordingly,

 Table 1

 Number of Animals Performing at Criterion Levels

 During Various Stages of Testing

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	Trials	% Correct to be at Criterion	1-TAB	2-TAB	3-TAB	
	5	100	0	2	8	
	6	100	0	2	8	
	9	89	0	3	10	
	12	83	0	2	10	
	15	80	0	4	10	
	18	72	0	6	10	

Note-The criterion score is that score which would occur, given that particular number of trials, by chance 5% of the time or less. to determine if improvement occurred over the course of testing, we began our examination from the fifth trial onward. As can be seen in Table 1, 8 of the 10 animals of the 3-TAB group reached or passed the .05 level of performance within the first five trials; the remaining 2 animals reached criterion by the ninth test trial. In the 2-TAB group, however, the animals required considerably more testing, with the concomitant increase in exploration opportunities, in order to reach criterion. In fact, it was only after 12 trials that the majority of the animals in the 2-TAB group reached criterion.

It is clear that none of the 1-TAB animals reached the criterion level within 18 test trials. Furthermore, examination of the performance of individual animals in that group revealed no consistent pattern of improvement over the course of testing, with the performance levels for 8 of the 10 animals of the 1-TAB group remaining at or below 50% correct over the last 10 trials. The remaining 2 animals performed at 65% to 67% correct—a value still below the .05 criterion level for that number of test trials.

Finally, as can be seen from Table 2. the performance of those animals in the 2-TAB group that scored 72% or more correct did not depend on whether a given test pair of tables corresponded to the pair explored on the 1st, 2nd, or 3rd day of the exploratory cycle. These animals were just as likely to be correct when the test path corresponded to that explored on the 1st day of the exploratory cycle as they were on the 3rd day of the cycle. In contrast. animals that failed to score 72% or better tended to be correct more frequently when the test pair of tables corresponded to those explored on either the 3rd or 2nd day of the cycle. The poorest performance occurred when the pair of tables corresponded to the pair explored on the 1st day of the cycle (i.e., 3 days before the test trial). A repeated measures ANOVA with performance level as the between-groups factor and day in the exploratory cycle as the repeated confirmed measures factor this impression [F(2, 14) = 4.44, p = .032]. Post hoc analysis (Tukey's HSD, all ps > .01) indicated that for the group whose performance was above 72% correct there was no difference in performance when the test pair corresponded to the pair explored on the 1st, 2nd, or 3rd day of the exploratory cycle. For those animals whose performance was below 72% correct, post hoc tests showed that the poorest performance occurred when the test pair of tables corresponded to the pair explored on the 1st day of the cycle. When the test pair of tables corresponded to that explored on the 2nd or 3rd day of the cycle, performance was facilitated as compared with what it was when the test pair matched the pair explored on the 1st day of the cycle.

This difference between the animals that scored above and those that scored below 72% correct was the only apparent difference between these animals.

Table 2 Correct Performance as a Function of When the Test Route was Explored During the Exploratory Cycle									
		% Correct When Test Tables Matched							
Group	Total % Correct	1st Pair Explored	2nd Pair Explored	3rd Pair Explored					
Animals scoring above 72% N = 6	81.1	83.2	76.2	83.8					
Animals scoring below 72% N = 3*	58.7	38.7	64.3	73.0					

*One animal which showed a turn tendency (15/18 turns to the same side) was omitted from this analysis.

Animals that met the criterion level entered an average of 7.7 sectors per exploratory day, regardless of which pair of tables and runways were available, whereas those that did not meet criterion entered 9.8 sectors per day. A three-factor ANOVA with passing versus failing as the between-groups factor and exploratory cycle (1-18) and pair of tables explored (AB, AC, BC) as the within-groups factors revealed neither significant between-group differences [F(1,8) = .91, p=.37] nor significant interactions involving the group factor [group × exploratory cycle, F(17,136) = .24, p=1.0; group × pair, F(2,16) = .20, p=.82; group × exploratory cycle × pair, F(34,272) = .95, p=.55].

DISCUSSION

The results of this experiment provide clear evidence that animals can learn the spatial relations existing among the three tables of the three-table task by merely exploring pairs of tables and their interconnecting runways on successive days. Sixty percent of animals given this type of exploratory experience were correct on 72% or more of the test trials. Also, this piecemeal two-table exploration constituted a more difficult type of spatial learning task than did exploration of the entire three-table apparatus at one time. Although 60% of the animals in the 2-TAB group were correct, all of the animals in the 3-TAB group solved the problem at that level or better.

It is of interest to note that the animals in the 2-TAB group that solved at the 72% criterion performed equally well regardless of whether a particular pair of tables corresponded to the pair explored on the 1st, 2nd, or 3rd day of the exploratory cycle. This fact suggests that although the pairs of tables and their interconnections were sequentially experienced over several days, nontheless, these successive experiences became a unitary representation on the day of the test trial when the animals were merely given the feeding experience prior to testing. This finding most closely illustrates the property that a cognitive map allows organisms "to link together conceptually parts of an environment which have never been experienced at the same time" (O'Keefe & Nadel, 1978, p. 2). In contrast, the animals of the 2-TAB group which failed to solve the problem performed at criterion levels only when a particular pair of tables corresponded to the pair explored on the 3rd day of the exploratory cycle. It would appear that, for these animals, the sequentially experienced routes between the two tables remained merely a temporally ordered pattern, with the most recently experienced route in the exploratory cycle being the most salient.

The differences between the animals that did well and those that failed in the 2-TAB group provide clear examples of each of two current hypotheses of spatial information processing. According to one model (Olton, 1978), a place is converted into an element in working memory independently of its spatial context. Spatial information is transformed into a list of discrete nonspatial items, with the item most recently entered into the list being the best remembered. This model contrasts sharply with the cognitive map theory of Tolman (1948) and O'Keefe and Nadel (1978). The latter theorists assert that spatial information is not treated in a sequential fashion, but rather in a simultaneous manner in which stimuli in space are located relative to each other and to the total environment.

It is apparent from our results that both types of spatial processing are possible, but to the extent that the spatial representation is of the list variety, it is less effective than that of the map variety when a problem requires the integration of information that is not experienced at the same time. It is also evident that, although a piecemeal exploratory experience can lead to learning of the spatial relationships among the tables, there is some minimum number of elements in the problem space that must be experienced for this spatial learning to occur. We have previously shown that exploration of either tables only or runways only did not allow the animals to learn the spatial relations among the tables (Ellen, Parko, Wages, Herrmann, & Doherty, 1982). In the present experiment, running back and forth along the runway to a table on one day and along another runway to another table on succeeding days was not sufficient to allow the three tables to become spatially related in the rat's cognitive representation of the problem space.

A possible explanation for the poor performance of the animals in the 1-TAB group is that they were not exposed to each part of the apparatus as often as the animals in the 2-TAB and 3-TAB groups. For example, the 3-TAB animals were given access to each table on 54 different days, and the animals in the 2-TAB groups saw each table and runway 36 times on 36 different days. In contrast, the animals of the 1TAB group were exposed to each table and runway on only 18 separate occasions. It will be recalled from Table 2 that although 8 of 10 animals in the 3-TAB group were at criterion levels or better by the completion of five test trials, the animals in the 2-TAB group showed a different pattern. As testing progressed, with its concomitant increase in daily exposure to each pair of tables, the number of animals reaching criterion levels of performance increased. Thus, while two animals were at criterion levels by the end of five test trials (18 exploration days), two additional animals did not reach the criterion level until 13-15 days of testing (39-45 exploration days). and the final two animals to reach criterion levels required 16-18 test trials (48-54 exploration days). Clearly, while exploration of all of the apparatus at once is a more efficient procedure, a piecemeal exploration is sufficient to allow animals to acquire a unitary cognitive representation provided that a sufficient number of exploration days are given. Whether the 1-TAB group could have incorporated the individual sectors into a cognitive map with more days of exploration remains a problem for future investigation.

Finally, it is important to take note of the fact that animals in both the 2-TAB and 3-TAB exploratory groups were able to solve the problem despite the fact that on the day of the test trial they were given a feeding experience only prior to the test trial. As long as there is a cognitive representation of the spatial relations existing among the tables, it is not necessary for the animals to explore the apparatus immediately prior to a test trial. It is equally clear that this cognitive representation can be retrieved or reactivated by the feeding experience and can be integrated with the feeding experience in order to enable the animal to solve the problem on the test trial. It would thus appear that once an animal has a cognitive representation of a problem space, such a representation may be reactivated by exposure to a location that is represented in that problem space.

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(Manuscript received October 17, 1983; revision accepted for publication February 25, 1984.)