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Interactions between response stereotypy and memory strategies on the eight-arm radial maze

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Abstract

Three groups of water-deprived rats collected water from the ends of the 8 arms of an 8-arm radial maze. Sighted subjects, and subjects blinded either with or without pre-enucleation experience on the radial maze, all retrieved the water efficiently. Most of the subjects exhibited the same response stereotypy, regularly choosing 8 adjacent arms of the maze, then stopping in the center of the maze. The strategies underlying this performance were analyzed by interrupting trials and rotating the maze 180° after the subject had made 3 choices. Sighted subjects depended on extramaze stimuli, naive-blind subjects depended on intramaze stimuli and experienced-blind subjects ignored their initial 3 choices after the trial was interrupted. Choice accuracy was equally good whether the subject was returned to the position from which it had been removed, or returned to the opposite side of the central platform. All 3 groups of subjects maintained their stereotyped adjacent-arm responding only as long as such responding was consistent with high choice accuracy. Response stereotypy was prevalent on the radial maze, but response strategies were secondary to memory strategies.

Introduction

The eight-arm radial maze is a maze with 8 identical arms projecting radially outward from a central platform, like the spokes of a wheel²⁹. It has been used extensively in studies of spatial memory in animals^{14,26,27,37}, including studies of the physiological^{2,9,10,12,15,17,19,21,30,44,46}, pharmacological^{11,12,31,48}, and developmental^{8,13,47} components of spatial memory. Radial maze performance has been examined for a variety of species^{1,3,6,32,39,40,49} and under a variety of test procedures^{5,18,20,38,45,50,51}. Response stereotypy, that is, subjects repeatedly choosing arms a fixed distance apart—particularly adjacent arms—has been so prominent on the radial maze^{1,6,8,13,19,30,31,38,45,48,50,51} that at least two computer simulation programs have been developed to account for the effects of response patterns on radial maze performance^{7,42}.

The prevalence of response stereotypy raises the possibility, but does not prove, that response algorithms (response strategies) may play a major role in radial maze performance. Although numerous experiments have shown that subjects can solve the radial maze problem using memory for sets of extramaze stimuli^{18,23,28,45,51}, there are situations in which response patterns appear to be important for the accurate choice of arms on the maze^{32,38,45,48,50}. Showing that

accurate radial maze performance can be maintained after response stereotypy has been eliminated^{30,51} is, clearly, different than showing that response stereotypy plays no role in choice accuracy when it is permitted to occur. The following experiment examines how subjects exhibiting a high degree of response stereotypy adjust to a test procedure under which response stereotypy and high choice accuracy (that is, obtaining the water efficiently) are incompatible.

Materials and Methods

Subjects

The subjects were 14 male Long-Evans hooded rats aged about 5 months at the start of the experiment. Four sighted subjects (sighted group) had received about 20 trials on the radial maze before the experiment began. The blind groups had been peripherally blinded by enucleation under deep ether anesthesia as part of another experiment⁴. The 6 subjects in the naive-blind group had received about 30 trials on the radial maze after enucleation, whereas the 4 subjects in the experienced-blind group had received 12 trials on the radial maze before enucleation and about 10 trials on the maze after enucleation. The subjects were individually housed at a temperature of ca. 22°C under a 12 h : 12 h light/dark cycle. The housing room was brightly illuminated by ceiling lights during the 'light' phase of the cycle, and dimly illuminated by a 60-W lamp during the 'dark' phase of the cycle. The subjects had free access to food throughout the experiment, but were maintained at 80-90% of their free-feeding weights by providing only 3-5 minutes' daily access to water.

Apparatus

The octagonal central platform of the (enclosed) radial maze was 31.5 cm in diameter and each of the arms extending radially outwards was 80 cm long and 10 cm wide. The arms were equally spaced, 45° apart. The central platform and arms were surrounded by walls 16.5 cm high. The maze was painted gray. Each arm was covered by a piece of clear Plexiglas, 0.8 cm thick, hinged to the wall at the end of the arm. A small plastic cup was taped to the surface of the maze about 3.5 cm from the outer end of each arm. A small wooden holding box (22 cm × 15 cm × 13 cm) was used to detain the subjects when trials were interrupted. The experimental room was 2.1 m × 3.5 m, with a sink, counter, boarded windows, fan vent, door and fluorescent ceiling lights providing a large number of visual and auditory cues. The experimenter wore a laboratory coat and always sat in the same location. A Rustrak event recorder (Gulston Industries) was used to record the time spent on the center platform between choices in the free-choice phase.

Procedure

The experiment was conducted in two phases: the free-choice phase and the interruption phase. For the sighted and the experienced blind subjects, the interruption phase was immediately after the free-choice phase. For the naive-blind subjects, the free-choice phase occurred about 6 weeks after the end of the interruption phase.

Free choice phase. During this phase of the experiment subjects were tested once daily. Each subject was placed in the center of the maze and allowed to obtain 0.3 ml of tap water from each

of the 8 cups on the maze. The subjects were free to choose the arms of the maze in any order. The sighted group and the experienced-blind group were permitted to make 9 choices on each trial; the subjects in the naive-blind group were permitted to make 10 choices per trial. On each trial, the sequence of arm choices was recorded manually and the time spent in the center of the maze between choices (choice time) was recorded using the Rustrak event recorder. The criterion for entering the center of the maze was that a subject's nose crossed the vertical plane dividing an arm from the center platform; the criterion for leaving the center platform was that the root of the subject's tail crossed the same plane. Data were collected from consecutive sessions, until data were obtained from 5 trials on which 8 different arms were selected before any were repeated.

Interruption phase. Each subject was given two trials daily for 22 days. The intertrial interval was about one hour, which each subject spent in its cage in the housing room. Each of the plastic cups on the maze contained 0.3 ml of tap water at the start of each trial. The starting orientations of the subjects were varied across trials. Five types of trials were administered: one control (free-choice) trial and 4 types of test trials. On the control trial, the subject was placed on the center platform and remained in the maze until it had entered each of the 8 arms. On test trials the subject was removed from the maze after 3 choices and detained for 60 s in a wooden holding box in an adjacent room. The subject was picked up as it left the third arm, and returned to the maze about 90 s later. On half of the test trials, the maze was rotated 180° while the subject was in the holding box (rotate-maze trials); on the other half of the trials it was not rotated (remove-subject trials). On half of the test trials, the subject was returned to the center platform oriented in the same direction it had faced when it was picked up, that is, it was placed as if it had just left the third arm chosen at the start of the trial (replace trials). On the other half of the test trials, the subject was displaced 180° from its initial orientation, that is, it was placed on the maze as if it had just left the arm directly opposite the one from which it had been picked up (displace trials). The 4 types of test trials were thus remove subject/replace, remove subject/displace, rotate maze/replace, and rotate maze/displace trials. Rotating the maze changed the relationship between the available intramaze and extramaze stimuli, while simply removing the subject for 90 s did not. After being returned to the maze, each subject was allowed to continue choosing arms until it had entered all 8 arms of the maze.

The subjects were given two control trials on each of the first two days in this phase of the experiment. Over the next 8 sessions each of the 4 types of test trial was given twice, once as the first trial on a day and once as the second trial. The remaining 8 trials, one on each day, were control trials. Since the subjects were performing accurately on the maze, 12 more daily sessions were given without any control trials. There were 3 blocks of 4 sessions, with each of the 4 test trials being presented twice in each block, once as the first trial on a day and once as the second.

Results

Free-choice phase

The 3 groups of subjects made very few errors (arm repetitions) before entering all 8 arms on a trial, so that very few trials had to be discarded before obtaining 5 trials on which each subject started by choosing 8 different arms (errorless trials). No trials were discarded for the sighted group, a total of 3 trials were discarded for subjects in the experienced-blind group and 8 trials were discarded for subjects in the naive-blind group. Overall, 11 trials were discarded before data from 70 errorless trials were obtained: 4 trials were discarded because a subject repeated one arm during its first 8 choices on the trial, 3 trials were discarded because a subject that had made 8 different choices did not make a ninth choice in under 4 minutes, and 4 trials were discarded because the recorder failed.

Response stereotypy on the free-choice trials was measured by the relative frequency (%) with which subjects made adjacent-arm transitions during the first 8 choices (7 transitions). Response stereotypy was very high for all 3 groups: 81%, 78%, and 98% for the sighted, experienced-blind and naive blind groups, respectively. Two subjects in the sighted group, 3 in the experienced-blind group, and 5 in the naive-blind group began every trial by choosing 8 consecutive adjacent arms. It may be surprising, given the high degree of response stereotypy shown by all of the groups, that most of the subjects stopped in the center of the maze as soon as they had entered all of the arms. Table 1 shows, for each subject in the experiment, the median time spent in the center of the maze before each choice during a trial. Table 1 also shows the percentage of adjacent-arm transitions occurring during the first 8 choices on a trial. Only two subjects did not choose adjacent arms a majority of the time (Table 1). Subject 3 in the sighted group chose alternate arms of the maze (90° turns) on 31% of its choices. Subject 4 in the experienced-blind group chose alternate arms on 80% of its choices.

Separate analyses of variance were conducted on the center times for each group of subjects. Before analysis, the center times were transformed to reduce the differences in variance across choices, $y = \log_{10}(x + 1)$ (ref. 16). All 3 groups exhibited a significant change in center times during the trial: sighted group, $F_{7,21} = 13.49$, $P < 0.01$; experienced-blind group, $F_{7,21} = 7.83$, $P < 0.01$; naive-blind group, $F_{7,35} = 15.94$, $P < 0.01$. Post-hoc analyses (Newman-Keuls, $P < 0.01$) indicated that, for each group, the center time before the ninth choice was longer than any of the preceding center times. There were no differences among the center times before choices 2-8. Table 1 shows that 12 out of 14 paused after their eighth choice on a trial. The ‘task completion pause’ exhibited by these 12 subjects suggests that these subjects could recognize that they had entered all of the arms without having to repeat one. Only two subjects, Subject 3 in the experienced-blind group and Subject 6 in the naive-blind group, exhibited the distribution of center times to be expected of an animal relying on a response algorithm to select arms. Both of these subjects always chose 8 adjacent arms, then re-entered one without pausing in the center of the maze.

Table 1. Median center time (s) before choices, and proportion of adjacent-arm transitions in a subject’s first eight choices

Group	Subject	Adjacent-arm transitions (%)	Choice								
			2	3	4	5	6	7	8	9	
Sighted	1	100	1	0	1	1	1	1	1	1	19
	2	86	3	6	4	3	1	6	16	160	
	3	40	3	2	2	2	2	2	3	71	
	4	100	1	1	1	1	1	1	1	5	
Experienced-blind	1	100	1	1	1	2	1	2	1	50	
	2	100	1	1	1	1	1	1	3	22	
	3	100	1	1	0	0	1	0	1	1	
	4	14	1	1	1	2	3	4	5	155	
Naive-blind	1	91	18	9	11	17	7	15	15	74	
	2	100	1	1	1	1	1	1	1	16	
	3	100	1	1	1	1	1	1	1	14	
	4	100	1	1	1	1	1	1	1	66	
	5	100	2	1	2	2	1	1	2	25	
	6	100	1	1	1	1	1	1	1	1	

Interruption phase

Choice accuracy. The 3 groups of subjects selected arms accurately during the 4 preliminary control (free-choice) trials. The mean number of different arms selected in the first 8 choices on a trial was 7.88 for the sighted subjects, 7.94 for the experienced-blind group, and 7.62 for the naive-blind group.

Over the next 20 days each subject received each of the 5 trial types 8 times. No subject ever repeated an arm during the first 3 choices on a trial. Therefore the accuracy of arm selection was assessed by calculating the ‘accuracy score,’ the number of arms entered for the first time during Choices 4-8. After the maze was rotated 180°, there were two possible coordinate systems (sets of reference points) according to which the subjects might have chosen arms: a maze-based coordinate system (control by intramaze cues) and a room-based coordinate system (control by extramaze cues). Subjects could obtain high accuracy scores according to the maze-based coordinate system by not repeating particular arms of the maze and high room-based choice accuracy scores by not repeating particular locations in the room (regardless of the specific arms in those locations). Both maze-based and room-based accuracy scores were calculated for the trials on which the maze was rotated. The two coordinate systems were coincident on the other trials. The mean accuracy scores for each group are shown in Table 2.

Statistical analyses were conducted to determine whether choice accuracy was influenced by (a) the orientation with which a subject was returned to the maze on test trials, and (b) the discrepancy between the intramaze and extramaze cues produced by rotating the maze 180° after the third choice on a trial. Choice accuracy was the same for all groups, whether the subject was returned to the maze in its pre-removal orientation or in a new orientation. Analyses of variance

Table 2. Mean accuracy scores as a function of group, coordinate system, and type of trial.

Trial-type	Coordinates	Group Sighted	Blind	
			Experienced	Naive
Control (free choice)	room/maze	4.94	4.88	4.79
Remove subject/replace	room/maze	4.31	4.38	4.21
Remove subject/displace	room/maze	4.38	4.31	4.44
Rotate maze/replace	room	4.06	3.06	2.58
	maze	2.66	3.41	3.79
Rotate maze/displace	room	3.72	3.25	2.60
	maze	2.94	3.25	3.87

Mean accuracy score: mean number of room locations (room coordinate system) or arms of the maze (maze coordinate system) entered for the first time during Choices 4-8 on a trial.

(Group \times Trial-type) compared the mean accuracy scores of the 3 groups on the remove-subject/displace trials and the remove subject/replace trials, and on the rotate maze/replace and the rotate maze/displace trials (in the latter case, using both the room-based and maze-based accuracy scores). The trial-type main effects were not significant for any of the analyses: Remove-subject trials, displace vs replace, $F_{1,11} = 1.56$, $P > 0.1$; Rotate-maze trials, displace vs replace (maze-based), $F_{1,11} = 0.48$, $P > 0.1$; Rotate-maze trials, displace vs replace (room-based), $F_{1,11} = 0.12$, $P > 0.1$. Consequently, the effects of maze rotation were analyzed after combining the choice accuracy data from the replace and displace trials, so that the remaining analyses were performed over the ‘remove subject’ and ‘rotate maze’ trials, without regard to the subject's orientation on being returned to the maze. The results for each group were analyzed separately, since the important issue was whether each group depended upon extramaze or intramaze stimuli, not how the accuracy scores of the 3 groups compared.

Each group's accuracy scores on the rotate-maze trials were compared with the mean accuracy score expected for a group making Choices 4-8 randomly, after choosing 3 different arms during Choices 1-3. It is easily calculated that such a group would obtain a mean accuracy score of 2.44 (out of 5). The sighted group's room-based accuracy score of 3.89 was significantly different from the random-choice score, $t_3 = 12.96$, $P < 0.01$, but its maze-based mean accuracy score of 2.80 was not, $t_3 = 1.67$, $P > 0.1$. The naive-blind group's maze-based mean accuracy score of 3.83 was significantly different from the random-choice score, $t_5 = 10.69$, $P < 0.01$, but its room-based accuracy score of 2.59 was not, $t_5 = 1.31$, $P > 0.1$. Thus the sighted subjects selectively avoided locations in the room while the naive-blind group selectively avoided particular arms of the maze.

On the rotate-maze trials, the experienced-blind group obtained a room-based mean accuracy score of 3.16 and a maze-based mean accuracy score of 3.33. Both of these scores were significantly different from the mean accuracy score expected from random choice, $t_3 = 5.71$, $P < 0.05$ and $t_3 = 5.72$, $P < 0.05$, respectively. The experienced-blind group's accuracy was also compared with the mean accuracy score expected for a subject choosing 3 arms on Choices 1-3 and 5 arms on Choices 4-8, but making the two sets of choices independently. A mean accuracy

score of 3.125 (that is, $5 \times 5/8$) would be expected from such ‘independent choice.’ Since the experienced-blind group chose an average of 3.0 different arms during Choices 1-3 and an average of 4.91 different arms during Choices 4-8 on the rotate-maze trials, it approximated the choice-accuracy assumptions for the independent-choice comparison. Neither the experienced-blind group's room-based mean accuracy score, 3.16, nor its maze-based mean accuracy score, 3.33, was significantly different from the mean accuracy score of 3.125 expected from independent choice, $t_3 = 0.25, P > 0.1$ and $t_3 = 1.30, P > 0.1$, respectively. Thus, the experienced-blind subjects were not selecting arms randomly after the intramaze and extramaze stimuli were opposed. They appear to have chosen arms accurately before and after maze rotation, but to have made the two sets of choices independently.

Response stereotypy. The degree of response stereotypy was measured by calculating the proportion of adjacent-arm transitions during Choices 4-8 on a trial. Choices 4-8 were used to allow the data from control and test trials to be compared directly. The percentages of adjacent-arm choices on the control (test) trials were 86% (74%), 70% (66%) and 78% (76%) for the sighted, experienced-blind and naive-blind groups, respectively.

The relationship between response stereotypy and choice accuracy was examined by considering only those remove-subject trials on which a subject started by choosing 3 adjacent arms. This occurred on 77% (172/224) of the remove-subject trials. The rotate maze trials were not considered because the room-based and maze-based coordinate systems were contradictory on such trials, resulting in a pair of accuracy scores for each trial. The Choice 4-8 response sequences were divided into two categories, based on their relation to the Choice 1-3 response pattern. Choices 4-8 were classified as ‘continued stereotypy’ when both Choices 1-3 and Choices 4-8 involved successive adjacent-arm choices in the same direction, for example, 123-45678 or 123-12345. All other response sequences were classified as ‘discontinued stereotypy.’

Two mean accuracy scores were calculated for each category of trial: the observed mean accuracy score and the mean accuracy score which would have been obtained had the subject continued to exhibit its Choice 1-3 response stereotypy after Choice 4, that is, the ‘expected’ mean accuracy score (see Table 3). Note that the expected mean accuracy score was determined by the particular arm chosen following the interruption as well as by the pre-interruption response pattern. For example, compare the choice sequences 123-45678 and 123-78123.

The observed, and expected, mean accuracy score was 4.29 on the continued-stereotypy trials. However, a mean accuracy score of 4.37 was observed on the discontinued-stereotypy trials. This compared favorably to a mean accuracy score of 2.83 which would have occurred had the subjects continued their Choice 1-3 response patterns after their fourth choice. It is notable that on 24 out of the 116 trials on which subjects discontinued their Choice 1-3 response stereotypy during Choices 4-8, they in fact chose a series of 5 adjacent arms, but reversed the direction in which they moved around the maze (for example, 123-87654). Response stereotypy thus continued on the interrupted trials when it was consistent with high choice accuracy. Table 3

Table 3. Mean accuracy scores on remove-subject trials, as a function of response pattern relative to Choice 1-3 response stereotypy.

Group	Response stereotypy relative to Choice 1-3 stereotypy		
	Continued Observed	Discontinued Observed	Expected
Sighted	4.29 (14)	4.26 (34)	2.76
Experienced-blind	4.17 (12)	4.41 (34)	2.91
Naive-blind	4.33 (30)	4.42 (48)	2.81
All subjects	4.29 (56)	4.37 (116)	2.83

Number of trials with specified response pattern in parentheses;^a ‘expected’ mean accuracy score is that obtained by continuing the response stereotypy exhibited on Choices 1-3 during Choices 4-8.

shows that all 3 groups exhibited the same relationship between response stereotypy and choice accuracy. In fact, 12 of the 13 subjects which discontinued their Choice 1-3 response stereotypy scored higher than they would have by continuing their Choice 1-3 response stereotypy (*t*-tests, $\alpha = 0.05$).

Discussion

The main result of this experiment was that rats exhibiting stereotypic response patterns on the radial maze were, nevertheless, not relying on response algorithms, or rules. The sighted subjects relied on extramaze, probably visual, cues^{23,45,51} and the naive-blind subjects relied on intramaze cues. The intramaze cues may have been odor trials, tactile stimuli, or movement-generated vestibular, kinesthetic or proprioceptive stimuli^{26,33,51}. Varying the orientation in which the subject was returned to the maze on interrupted trials would have influenced the choice accuracy of subjects relying on a response rule, but it had no effect on our subjects. Moreover, the task-completion pause immediately after choosing the last baited arm on free-choice trials suggests that the animals were relying on other cues concurrently with the exhibited response stereotypy. These results imply that not only can rats select from several search strategies when tested on a particular spatial problem^{34,44,45}, they can use several strategies simultaneously. The response stereotypy exhibited by our subjects appeared to represent a secondary response strategy superimposed upon a primary dependence on environmental or movement-generated cues. The subjects’ response stereotypy was ‘flexible’^{27,44} in that ongoing response patterns were interrupted when they were incompatible with efficient reward collection, but not otherwise⁵⁰.

It was surprising that the naive-blind and the experienced-blind subjects responded differently to the interruption procedure. The naive-blind group relied on intramaze cues whether or not the maze was rotated during a trial. The experienced-blind subjects, with prior sighted experience on the radial maze, chose arms accurately on the remove-subject trials but not on the rotate-maze trials. It seemed as though the animals disregarded their initial 3 choices after the maze was rotated in the middle of a trial. An obvious possibility is that these subjects were sensitive to both intramaze and extramaze stimuli. When the relationship between the two sets of stimuli, and therefore the experimental context, was changed, the subjects simply ‘started fresh.’ There is

considerable evidence that rats segregate their memories of places according to the environmental context^{22,24,35-37} and that a change of context may cause a subject to ‘reset’ its spatial memory^{26,43,45}. We did not identify the particular extramaze cues to which the experienced-blind subjects responded, but extramaze auditory cues were available, and both sighted and blind rats can navigate using distant auditory cues⁴⁴.

Our data suggest that the task-completion pause may provide a measure for determining whether response patterning in individual subjects reflects reliance on a response algorithm: subjects relying on a response algorithm should not stop until they encounter an empty reward cup, while subjects relying on environmental cues should stop as soon as they have collected the last reward. Most of our subjects (12/14) did the latter, pausing as soon as all 8 arms had been entered. Consequently, the inference that response stereotypy reflects dependence on an underlying response strategy must be made cautiously^{30,32,48}.

The question remains as to why response patterns would be so prevalent on the radial maze when subjects could perform so well without them (for example, on the remove-subject trials). There are two possible answers, both implying that response stereotypy reflects a secondary strategy for finding water on the radial maze. On the one hand, subjects may exhibit response stereotypy because they are foraging efficiently, obtaining all of the water after travelling the least possible distance or in the least possible time⁵⁰. According to this point of view, response stereotypy should develop only after a subject has learned to solve the radial maze problem by other means. On the other hand, response patterns may have occurred on the free-choice trials because subjects were using movement-generated stimuli to guide their choices on such trials³³. Rats are sensitive to the directions they have travelled on a maze⁴¹ and vestibular cues can be important to spatial orientation³³. From this perspective, response stereotypy would simplify a subject’s movement-based record of where it had recently been. This movement-produced record would supplement a ‘spatial memory’ based on environmental cues^{25,26,37}. Both of these suggestions are consistent with the finding that choice accuracy declined on the remove-subject trials relative to the control (free-choice) trials during the interrupt phase of the experiment. While our results show that rats are not relying on ‘ballistic’ response programs (algorithms) to solve the radial maze problem, they do not eliminate the possibility that response stereotypy reflects one of the two processes just mentioned.

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