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Spatial and temporal response patterns on the eight-arm radial maze

Robert H. I. Dale

Six maze-experienced hooded rats were timed during five trials on which they collected water from all arms of an eight-arm radial maze, then made five more choices. All subjects frequently exhibited a "task-completion pause:" The subjects rarely spent more than 1 sec in the center of the maze between choices until they had entered all eight arms, then stopped in the center of the maze. In contrast, the time spent in each arm gradually increased until all of the water had been obtained, then decreased slightly. Four subjects began every trial by choosing eight consecutive adjacent arms. The task-completion pause indicates that these subjects recognized when all of the arms had been entered, without having to repeat one. Therefore, even extreme degrees of response stereotypy do not imply a fundamental dependence on response strategies.

Spatial memory in rats has been studied by measuring the efficiency with which they obtain food from all of the arms of an eight-arm radial maze [13]. During studies of the sensory basis of radial maze performance [4], subjects frequently stopped in the center of the maze after choosing all eight arms, but before repeating any of them. This "task-completion pause" suggests that subjects often recognize when all of the available reward locations have been visited, without having to return to one. Several reports have mentioned observing the same phenomenon [3, 24], without providing any supporting evidence. The following experiment concerns several characteristics of the task-completion pause.

For subjects selecting each arm of a maze on the basis of its location relative to a set of extramaze stimuli [13, 22], the task-completion pause is not surprising: in fact, two simple models of spatial memory predict it [11, 20]. On the other hand, subjects depending solely on response algorithms, such as "choose adjacent arms in a clockwise direction" [13], would not be expected to pause after choosing the eighth arm. They would be expected to pause, if at all, only after encountering an unbaited arm. The task-completion pause thus provides one way of determining whether subjects exhibiting a high degree of response stereotypy are relying solely on response strategies to solve the radial maze problem. A pause indicates that additional processes are involved.

High degrees of response stereotypy commonly occur when rats are tested on the radial maze: in particular, subjects choose sequences of adjacent arms [5, 7, 10, 15, 17, 22, 24, 26]. Similar response patterning has been observed in *Betta splendens* [19], pigeons [2, 18], mice [6, 16], gerbils [25], and children [1]. Given the prevalence of response patterning in radial maze experiments, it is important to demonstrate that the presence of response stereotypy, by itself, does not imply the exclusive use of a response algorithm.

Method

Subjects
Six male hooded rats served as subjects. They were about 5 months old, and had had 25 trials of radial maze experience at the start of the experiment. They were allowed free access to food in their home cages, but were maintained at 80% of their free-feeding weights by providing only 5 min daily access to water. They were individually housed at 20-22°C under a 12 hr:12 hr light/dark cycle. The housing room was dimly illuminated during the "dark" phase of the cycle and brightly lit during the "light" phase of the cycle.

Apparatus
The radial maze consisted of eight equally-spaced arms projecting radially outwards from a central, octagonal platform, with adjacent arms being separated by 45°. The central platform was 31 cm wide and each of the arms was 76 cm long and 7.5 cm wide. The maze was painted grey. There was a small plastic cup 2.5 cm from the outer end of each arm. The test room was 2.0 m by 3.5 m, with a sink, counter, boarded windows, fan vent, door and fluorescent ceiling lights providing a variety of potential visual and auditory cues. The experimenter wore a lab coat throughout testing and always sat in the same location in the room. The test room was dimly illuminated by a bank of fluorescent ceiling lamps. Response rates were recorded using a Rustrak event recorder (Gulton Industries).

Procedure
All subjects were tested once a day, for 11 days, during the dark phase of their light cycle. A subject was placed in the central platform of the radial maze, and allowed to collect 0.3 ml of water from each of the eight cups on the maze. Each subject was permitted to make five choices after all of the water had been obtained during a trial, making a total of at least 13 choices per trial. The sequence in which the arms were chosen was recorded manually. A Rustrak recorder was used to measure the time spent on the central platform between choices (center time) and the time spent in an arm after choosing it (arm time). These response measures were recorded for all except the last choice on each trial. 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 entering an arm was that the root of the subject's tail crossed the same plane.

Results

The mean center times and arm times during each subject's last five trials are presented in Table 1. The mean center times and mean arm times are shown for the last seven choices before all of the water was obtained on a trial (Choices -7 to -1) and for the next 4 choices (Choices +1 to +4). For example, the center time for Choice -5 represents the time spent in the center of the maze when five choices remained before all of the water was collected, and the arm time for Choice -5 represents the time spent in the arm selected five choices before all of the water had been obtained. This somewhat cumbersome terminology was necessary because one subject (No.2) made one error (repetition) before obtaining all of the water on each of three trials. For the other

Table 1. Mean center times and arm times during a trial

Subject		Choice‡									
	-7	-6	-5	-4	-3	-2	-1	+1	+2	+3	+4
1	1	1	1	1	3	1	3	10	4	4	10
2 Center	1	1	1	1	2	2	3	11	29	11	7
3 Time*	1	1	1	1	1	1	1	30	12	14	4
4 (sec)	1	1	1	1	1	1	1	30	26	19	23
5	1	1	1	1	1	1	1	32	12	7	1
6	1	1	1	1	1	1	1	57	14	10	10
Group mean	1	1	1	1	2	1	2	28	16	11	9
1	12	12	13	15	17	19	21	14	8	19	13
2 Arm	10	9	12	12	14	16	27	24	33	37	29
3 Time†	13	17	20	18	13	27	36	22	28	18	12
4 (sec)	10	11	12	12	16	23	24	49	30	27	39
5	11	12	11	13	13	13	21	16	10	21	20
6	10	12	12	12	15	18	23	23	13	11	9
Group mean	11	12	13	14	16	19	25	25	20	22	20

* Time before each choice
† Time in arm after choice
‡ Choices -7 to -1 are the last seven choices before all water was collected from the arms of the maze. Choices +1 to +4 are the first four choices after all of the water had been collected.

five subjects, who always chose eight different arms with their first eight choices, Choices -7 to -1 correspond to the second through eighth choices during a trial, respectively.

The mean center times for all subjects followed the same pattern. Individual subjects crossed the center of the maze in 1-2 sec until all of the water had been obtained, then paused in the center of the maze for means of between 10 sec and 57 sec. The mean center times decreased across subsequent choices. While only 3 out of 210 choices (1.4%) before the water was depleted involved a center time of 5 sec or more, 23 out of 30 choices (76.7%) made immediately after the water was depleted (Choice 1) had a center time of at least 5 sec. An analysis of variance was conducted to compare the mean center times across choices within a trial, after the center times had been transformed to reduce the unequal variances across choices ($y = \log_{10}(x + 1)$) [8]. The mean center times changed significantly across choices, $F(10, 50) = 31.27$, $p < 0.01$. A post-hoc analysis (Newman-Keuls, $p < 0.01$) indicated that there were no differences among the center times for Choices -7 to - 1, but that the center time for Choice +1 was significantly longer than any of the preceding center times.

The mean arm times presented a different pattern across choices within a trial. The mean arm times gradually increased from about 10-12 sec early in a trial to about 20-25 sec when the last cup of water was obtained. In contrast to the center-time data, there was no increase in arm times after all of the water had been obtained. An analysis of variance conducted across choices, with transformed arm times ($y = \log_{10}(x + 1)$) [8], indicated that the arm times changed significantly across choices, $F(10, 50) = 4.69$, $p < 0.01$. A post-hoc analysis (Newman-Keuls, $p < 0.01$) found no significant differences among Choices -5 to +4. While the subjects spent a relatively long

time in each arm, much of that time was spent drinking. According to samples taken on earlier trials (75 observations per subject), the subjects required about 10 sec to consume the water in each arm of the maze, and there was no increase in drinking time across choices during a trial.

Response stereotypy was measured by the number of adjacent-arm transitions made before and after all of the water had been collected from the arms of the maze. Five subjects emptied the eight water cups in the minimum of eight choices on every trial, while the remaining subject (No. 2) required eight choices on two trials and nine choices on three trials. All subjects made five choices after all of the water had been obtained on a trial. The percentages of adjacent-arm choices before (and after) obtaining all of the water were 14 (36), 24 (12), 100 (64), 100 (64), 100 (80) and 100 (36) for Subjects 1 through 6, respectively. In other words, four subjects always chose adjacent arms while collecting the water from the maze, while two subjects did not. It is notable that the mean task-completion pause (choice time before Choice +1) for the four "adjacent-arm" subjects, 37.3 sec, was much longer than the task-completion pause for the two subjects which did not exhibit such response stereotypy, 10.5 sec. This is not what one would expect if subjects exhibiting response stereotypy were relying on response algorithms, whereas subjects not showing response stereotypy were relying on memory for environmental cues.

Discussion

The data clearly show that experienced, normal rats tested on the radial maze pause in the center of the maze as soon as they have obtained all of the rewards from the arms of the maze, and before re-entering any of the arms. This task-completion pause indicates that subjects recognize that they have entered all of the arms as soon as they have done so. The task-completion pause was evident even when subjects exhibited strong response stereotypy during the trial, and it is difficult to see why an animal choosing arms entirely on the basis of a response algorithm should stop as soon as the last reward has been obtained. Therefore, for intact rats, even dramatic response stereotypy does not allow us to infer that the animals are relying on a response algorithm. Other evidence is required before such a conclusion may be drawn [12, 27]. The subjects in this experiment apparently engaged in stereotyped responding in addition to selecting arms on the basis of another strategy, rather than relying on a response algorithm instead of some other strategy.

The relationship between response strategies and observed response patterns is important because response patterns are quite prevalent in radial maze studies, and because of the possibility that response strategies, even when they are used, are simply a convenience for the sake of foraging more efficiently [26]. Determining the relationship between response stereotypy and response algorithms may be particularly important for subjects given brain lesions [9, 14, 23] or treated with drugs [15, 21, 24] for the express purpose of disrupting memory systems. Such manipulations may selectively eliminate one of several strategies available to an intact, untreated animal. For these subjects, any inference that the manipulation has caused a strange in strategy must be made cautiously [9, 14, 21]. Several procedures [12, 27] allow one to determine whether subjects perform effectively after the use of response algorithms has been eliminated. The task-

completion pause measure will allow one to determine, without a change in procedure, whether subjects currently exhibiting response stereotypy are depending solely on response algorithms.

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