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Spatial memory in pigeons on a four-arm radial maze

Robert H. I. Dale

Abstract

Pigeon spatial memory was examined using a four-arm radial maze. The maze had four arms, spaced at 90° intervals, extending radially from a central choice area. Subjects were forced into three arms, then permitted two choices to enter the remaining ann. Five subjects chose accurately (90% correct) with delays of 5 min or less, their choices depended on extramaze cues, and the food in the target arm provided no essential cues. After an incorrect first choice, subjects' second choices were more accurate than chance. These data suggest that, while spatial memory has many similar characteristics in rats and pigeons, pigeon spatial memory appears less durable.

The demonstration that rats exhibit an accurate and durable spatial memory on the radial maze (Beatty & Shavalia, 1980; Olton & Samuelson, 1976) has stimulated studies on a variety of species, including pigeons (Bond, Cook, & Lamb, 1981; Olson & Maki, 1983; Roberts & Van Veldhuizen, 1985; Spetch & Edwards, 1986). Earlier experimenters experienced considerable difficulty using radial mazes to examine spatial memory in pigeons. Bond et al. and Olson and Maki concluded that pigeons exhibited little or no spatial memory on the eight-arm radial maze once response patterning had been accounted for, and Roberts and Van Veldhuizen obtained accurate performance only after elaborate and extended training in an enclosed (opaque walls) radial maze. In contrast, Spetch and Edwards reported rapid acquisition of accurate performance using an open-field feeding environment with eight feeding sites arranged in a circle around the perimeter of a room. They argued that the open-field arrangement facilitated the demonstration of spatial memory because it did not artificially restrict the subject's path between feeding sites.

The study reported below examined spatial memory in pigeons, using a four-arm radial maze constructed of chicken wire. This apparatus may be considered intermediate between those used by Roberts and Van Veldhuizen (1985) and Spetch and Edwards (1986). Like Roberts and Van Veldhuizen's maze, it restricted the subject's routes between food sites; like Spetch and Edwards's open-field arrangement, it permitted subjects an unobstructed view of the environment.

The present experiment used a forced-choice procedure, which prevented high choice accuracy based on response patterning (see Roberts & Van Veldhuizen, 1985). It focused on three aspects of the subjects' performance. First, previous data (Olson & Maki, 1983; Roberts & Van Veldhuizen, 1986) suggest that choice accuracy after brief retention intervals may be related to the number of arms in the retention set. If so, the pigeons in the present experiment should sustain asymptotic choice accuracy over retention intervals intermediate between the 8-16 minutes over which pigeons sustained accuracy on a T-maze delayed-alternation task (Olton & Maki, 1983) and the 3 minutes over which asymptotic choice accuracy was sustained on the eight-arm radial maze (Roberts & Van Veldhuizen, 1985). Second, the experiment is the first to use maze rotation to compare the relative importance of extramaze and intramaze cues in pigeon radial maze performance, although this procedure has been productive with rats (Dale & Innis, 1986) and intramaze cues have been selectively altered in research with pigeons (Roberts & Van Veldhuizen, 1985; Spetch & Edwards, 1986). Finally, measuring the accuracy of a second choice, after an initial error, determines whether the second choice is simply a guess or whether it involves "a second examination of working memory" (Roitblat & Scopatz, 1983, p. 218).

Method

Subjects

Six White Carneaux pigeons were maintained at approximately 80% of their initial free-feeding weights (range 78-86%) by restricting their access to food. They were individually housed under 24-hour lighting conditions, with continuous access to water in their home cages. They had received extensive experience (30-70 trials) on an eight-arm radial maze, under both free-choice (all arms accessible) and forced-choice (access to one arm at a time for the first three choices) test procedures. They had exhibited high choice accuracy and considerable response stereotypy during the free-choice phase, but responding was erratic, with low choice accuracy, under the forced-choice procedure. Two of the six subjects stopped responding entirely, and another two often failed to complete eight choices within 10 minutes. The procedure used on the four-arm maze was developed with the two subjects that had stopped responding on the eight-arm maze. Thus the present experiment, like Roberts and Van Veld- huizeri's (1985) experiments, involved subjects with extensive training.

Apparatus

The four-arm radial maze consisted of four equally spaced arms, 90° apart, extending radially from a central choice area, in the shape of a "+" -maze. It was constructed of 1.3 cm plywood, 4 cm by 4 cm pine rods, and 2.5 cm chicken wire. It had an octagonal central choice area with a diameter of 1.1 m. The central choice area was surrounded by chicken-wire sides, supported by eight 0.4-m high pine rods. Four equally spaced holes, 36 cm high by 21 cm wide, in the chicken wire permitted access to the arms of the maze. The central choice area was covered by a removable lid, made of chicken wire on a plywood frame. Each arm of the maze was made of chicken wire on a pine rod frame, and was 47 cm long, 30 cm wide, and 36 cm high. A 140-ml plastic cup, with its bottom half covered with black electrical tape, was inserted into a plywood strip at the outer end of each arm. Access to the arms was controlled by wooden doors, 24 cm wide and 42 cm high, which the experimenter could raise by means of a pulley system. The floor of each arm was covered with cardboard.

The testing room was large (4.2 m × 5.5 m) and contained a variety of office equipment and experimental apparatus. It was lighted by two windows and several banks of fluorescent lights. The experimenter sat in a corner of the room, about 2 m from the maze, concealed by a fiberboard screen with a plastic one-way window.

Procedure

Baseline Training
Subjects were given between 40 and 48 trials, with one or two trials each day. After each cup was baited with 5 Canadian peas (about 1.0 g), a subject was placed in the central choice area and forced to choose three arms of the maze, in a predetermined order. One door was opened at a time. When a subject left one arm, the door to the next arm was opened and the door to the arm it had just left was closed. The particular three arms chosen and their order were counterbalanced across blocks of trials. After choosing the third arm, the subject was confined in the centre of the maze for 5 s, then all four doors were opened at once. The subject was permitted two choices, with all of the arms available, to enter the fourth (target) arm of the maze. The subject was removed from the maze after two choices, or after a correct fourth choice followed by a pause of 3 min in the centre of the maze.

Delay Phase I
The delay between the first three choices and the next two was varied during this phase of the experiment. Subjects were tested 6-7 days a week. Subjects were given two trials each day, at least 1 hour apart. Each subject received 10 trials with delays of 5 s, 5 min, and 30 min. Trial order and the particular arm used as the target were counterbalanced across conditions. The experimenter left the room during the 30-min delay, returning about 1 min before the end of the delay.

No-Food Control Phase I
Each subject was given four trials on which the target (fourth) arm was baited and four trials with the target arm unbaited. Two trials were given each day, at least 1 hour apart, with trial order counterbalanced across conditions. The delay was 5 s.

Delay Phase II
Each subject was given 10 trials with each of four delays. The delays were 5 s, 30 s, 10 min, and 20 min. Subjects were tested 5-7 days a week, with 2-4 trials each day, and at least 1 hour between consecutive trials. Counterbalancing was the same as in Delay Phase I. The experimenter left the room during the 10-min and 20-min delays, returning about 1 min before the end of the delay.

No-Food Control Phase II
This phase was identical to No-Food Control Phase I.

Delay Phase III
This phase was conducted to determine whether the experimenter's leaving the test room during the 10-30 min delays might have disrupted performance. Subjects were tested 6-7 days a week, with four trials each day, and at least 1 hour between trials. Ten trials were administered under each of four conditions. Two conditions involved delays of 15 sand 20 s, while the other two conditions involved an 8-min delay. On half of the 8-min trials (experimenter leave), the

experimenter left the room during the delay and returned 30 s before the end of the interval. On the other half of the 8-min trials (experimenter stay), the experimenter remained behind the screen throughout the delay. Counterbalancing was the same as in Delay Phase 1.

Maze Rotation

Each subject was given 12 trials with a 40-s delay between the three forced-choices and the two test choices. Between 3-5 trials were given each day, for 3 days, with at least 1 hour between consecutive trials. Six of the 12 trials were control trials on which the maze was touched, but not rotated, during the delay. The remaining six trials were experimental trials on which the maze was rotated 90°. The rotation was clockwise on three experimental trials and counterclockwise on the other three trials.

Results

Baseline Training

Choice accuracy was measured by the proportion of trials on which a subject selected the target arm with its two test choices. Chance performance levels were calculated by considering a subject that chose arms randomly, without replacement. This assumption of choosing without replacement is appropriate since the subjects in this experiment repeated a correct first choice on only 2 out of 454 opportunities. A subject choosing randomly without replacement would select the target arm with a probability of .25 on its first choice and, if the first choice were incorrect ($p = .75$), choose the target arm with a probability of .33 on the second choice. The overall probability of randomly choosing the target arm during Choices 1 and 2 would be $.50 = (.25 + (.75 \times .33))$.

Subjects 1-6 had mean choice accuracies of 0.95 (38 correct choices/40 trials), 1.00 (45/45), 1.00 (48/48), 0.90 (43/48), 1.00 (45/45), and 0.63 (30/48), respectively, during pretraining. Subjects 1-5 chose arms with above-chance accuracy (z-score approximation of Binomial distribution, $p = .01$), whereas Subject 6 did not, $z = 1.59$, $p > .05$. No further data are presented for Subject 6, which failed to acquire the task.

Delay Phases

The choice accuracy data from the three delay phases are shown in Table 1. Table 1 indicates the probability of choosing the target arm on the first test choice (Choice 1), the probability of choosing the target arm on the second choice after an incorrect first choice (Choice 2), and the overall probability of choosing the target arm during the two test choices (Choices 1 & 2). Analyses of variance were conducted for both the overall choice accuracy and the accuracy on Choice 1. There were significant effects of delay on both Choice 1 accuracy, $F(10, 40) = 6.33$, $p < .01$, and overall choice accuracy, $F(10, 40) = 5.59$, $p < .01$. Both measures indicated that choice accuracy declined as the delay before testing increased.

The mean overall choice accuracy was compared, at each delay, with the choice accuracy expected for a subject choosing randomly (0.50). The mean overall accuracy scores were significantly above chance with all delays between 5 s and 8 min, and at the 30-min delay (*t*-test, $p < .01$, one-tailed, $MS_e = 2.076$, $df = 40$). The subjects' mean Choice 1 accuracy was also compared, at each delay, with the choice accuracy expected for a subject choosing randomly (0.25). Their mean Choice 1 accuracy was significantly above chance with all delays from 5 s to 5 min, and for the 30-min delay (*t*-test, $p < .01$, one-tailed, $MS_e = 2.944$, $df = 40$).

The subjects were very accurate on Choice 2, after the first choice was incorrect. Because of the small numbers of observations at each delay (due to few incorrect first choices), the Choice 2 data were combined across delays of 5 s to 5 min, and delays of 8 min to 30 min. The group mean Choice 2 accuracy (0.80) for the 5-s to 5-min delays exceeded chance (0.33), $t(4) = 9.51$, $p < .01$, as did the group mean Choice 2 accuracy (0.48) for the 8-min to 30-min delays, $t(4) = 6.23$, $p < .01$.

Overall choice accuracy was the same whether or not the experimenter left the room during the 8-min delay (experimenter stay = 0.76; experimenter leave = 0.68), $t(4) = 1.00$, $p > .1$. Thus the experimenter's departure during the long delays did not influence choice accuracy.

No-Food Control Phases

The data from the eight no-food control trials (Phases I and II combined) show that the food provided no essential cues. The subjects chose correctly on every trial, $p(\text{correct}) = 1.00$, whether or not food was present in the target arm.

Maze Rotation

The subjects received six control trials without maze rotation and six experimental trials with a 90° maze rotation. Following maze rotation, choice accuracy was assessed both with regard to room coordinates (whether a previously baited location in the room was visited) and maze coordinates (whether a particular arm of the maze was entered). Choice accuracy was above chance on the control trials (0.80), $t(4) = 3.09$, $p < .05$, as was the room-based choice accuracy on the experimental trials (0.77), $t(4) = 6.53$, $p < .01$. The maze-based choice accuracy (0.43) was not significantly different from chance (0.50), $t(4) = -0.49$, $p < .1$. Thus the subjects selected the target arm on the basis of extramaze, room-based cues rather than intramaze cues.

Discussion

This experiment extended the results of earlier studies (Olson & Maki, 1983; Roberts & Van Veldhuizen, 1985; Spetch & Edwards, 1986) comparing spatial memory in pigeons and rats. The subjects chose the target arm accurately, relied primarily on extramaze cues, and obtained no crucial cues from the food in the target arm. In each of these respects, their performance resembled that of rats (Dale & Innis, 1986). The major difference was that the pigeons' choice accuracy declined with delays longer than 5 min, whereas rats maintain high choice accuracy with retention intervals of at least 4 hours (Beatty & Shavalia, 1980).

The high choice accuracy with delays of 5 min of the four-arm maze is consistent with the asymptotic choice accuracy obtained with 3-min delays on the eight-arm maze (Roberts & Van Veldhuizen, 1985), and 16-min delays on a T-maze (Olson & Maki, 1983). These three studies provide indirect evidence that the retention interval over which pigeons can maintain accurate spatial memory declines as the number of arms in the memory set increases (see Roberts & Van Veldhuizen, 1985). Future studies must directly demonstrate the nature of the relationship.

Finally, since their second choices were accurate following first-choice errors (cf. Roitblat & Scopatz, 1983), the pigeons were able to reexamine spatial memory and select the correct arm of the maze after an initial error. Thus models of spatial memory will need to include a mechanism for reassessing memory representations when the first assessment is incorrect.

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