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Parallel-arm maze performance of sighted and blind rats: Spatial memory and maze structure

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Abstract

Sighted and peripherally blinded groups of rats learned to obtain a small reward from each arm of an eight-arm parallel maze, and a sighted group was similarly trained on a radial maze. The parallel-sighted and parallel-blind groups were equally slow, and much slower than the radial-sighted group, to attain criterion performance. The three groups shared several response characteristics: selectively avoiding the most recently entered arms, frequently choosing adjacent arms, and an absence of 'spatial generalization' among the arms. The findings support a simple model proposing how subjects identify and choose among the maze-arms.

Rats have an impressive ability to remember places they have visited, an ability which Olton and Samuelson (I976) studied using the eight-arm radial maze. The maze consists of eight identical, equally-spaced arms projecting radially from a central choice area, like the spokes of a wheel. Olton and Samuelson (1976) baited each of the arms with a piece of food and then allowed hungry subjects, placed on the central choice area, to search the maze. They quickly learned to acquire all of the food in only eight or nine choices, obtaining a mean 'choice score' of about 7.5 different arms in their first eight choices on a trial.

Numerous experiments showed that most subjects' arm choices were guided primarily by extramaze cues (those cues available from outside of the maze; Dale and Innis, unpublished manuscript; Olton, Collison and Werz, 1977; Olton and Samuelson, 1976; Suzuki, Augerinos and Black, 1980) and a recent study showed that subjects deprived of access to visual cues by blinding acquired high choice scores very slowly, and were guided by intramaze cues (those cues provided by the apparatus; Dale and Innis, unpubl.).

The following experiment was designed to test a simple model for radial maze performance, the 'tagged-I.D.' hypothesis. This hypothesis proposes that a subject attaches a decaying temporal marker, or 'tag', to an identification code for each arm of the radial maze as it is visited, then selectively enters those arms with the weakest tags. The temporal markers are effective for several hours (Beatty and Shavalia, 1980), although the finding of a 'recency effect' (e.g. Roberts and Smythe, 1979) suggests that the markers become relatively less effective with time: that is, the strength of a tag gradually declines. The identification codes are postulated to be formed on the basis of the spatial relationship, such as position and/or orientation, of each arm with a set of extramaze reference points. Suzuki et al. (1980) provide evidence that for the radial maze the extramaze cues act as a set, or array.

The tagged-I.D. model suggests that, because of the structure of the radial maze, the eight arms each have very different identification codes and performance is limited only by the durability of the temporal markers. Indeed, it is precisely this property that has made the maze so useful for the study of memory processes (e.g., Beatty and Shavalia, 1980; Olton, Becker and Handelrnann, 1980). The following experiment examines the performance of subjects tested on a maze of a different structure, the eight-arm parallel maze. This maze has eight adjacent parallel arms, extending in the same direction from a common platform. The tagged-J.D. hypothesis suggests that subjects should have difficulty developing unambiguous identification codes for these spatially contiguous arms and should, therefore, master the parallel maze more slowly than the radial maze.

Two predictions of the tagged-I.D. hypothesis were tested in the following experiment, using three groups of subjects: sighted groups on each of the radial and parallel mazes, and a peripherally-blinded group on the parallel maze. The first prediction was that sighted subjects would attain accurate performance faster on the radial maze than on the parallel maze. The second prediction concerned the contribution of visual cues to parallel maze performance. Because sighted subjects learn much faster than blind subjects on the radial maze (Dale and Innis, unpubl.), it is natural to expect a similar superiority on the parallel maze (although the parallel maze might be more difficult for all subjects). However, the tagged-I.D. model predicts that the parallel maze should make spatial coding on the basis of extramaze visual cues difficult or impossible so that removing a subject's access to such cues (by blinding) might produce little further deficit. In other words, sighted and blind subjects should be equally slow to acquire the parallel maze task.

Method

Subjects

Twenty-two naive male Long-Evans hooded rats served as subjects. They were 3-5 months of age at the start of the experiment, and were individually housed at 20-22°C under a 12 hr : 12 hr light/dark cycle. The housing room was illuminated dimly (3 lux) by a 40-W lamp directed towards one corner of the room during the 'dark' phase of the cycle, and brightly (180 lux) by fluorescent ceiling lights and the desk lamp during the 'light' phase of the cycle. The subjects were maintained at 80070of their pre-experimental free-feeding weights during the experiment through restricted access to water: they received about 5 min access to water 0-2 h after each daily pre training or test session. Food was freely available in the home cage at all times.

Eight of the subjects were blinded by enucleation, as described below, two weeks before the start of pretraining.

Apparatus

One elevated open field and two elevated straight runways were used in pretraining. A radial maze and a parallel maze were used in the test sessions. All were constructed of 1.2 or 2.4 cm thick plywood.

The open field was 91 cm × 67 cm; it was painted white and had a 4.5 cm high unpainted wooden border. There was a small plastic cup, made from the top of a Kodak 35 mm film container, at the center of the open field. The circular cup had an internal diameter of 3 cm and its sides were 0.5 cm high.

Both straight runways were unpainted, and were about 124 cm long and 9 cm wide. One was enclosed by walls 14.5 cm high and covered by a Plexiglas strip, 0.6 cm thick; the other was enclosed by 19 cm high walls. A small plastic cup was placed 4-5 cm from each end of each runway.

Both the radial maze and the parallel maze were painted grey. The radial maze consisted of eight identical equally-spaced arms, projecting radially from an octagonal platform. The central platform was 31.5 cm in diameter and each of the arms was 80 cm long and 10 cm wide. The central platform and arms were surrounded by walls 16.5 em high. Each arm was covered by a sheet of clear Plexiglas, 76 cm long, 13 cm wide and 0.8 cm thick, which was hinged to the wall at the end of the arm. Thus, the first 4 cm of each arm radiating from the central platform were not covered. A small plastic cup was taped to the surface of the maze about 3.5 cm from the end of each arm.

The parallel maze consisted of eight adjacent parallel arms, separated by wooden walls, projecting in the same direction from a common platform. The common platform was 20 cm x 93 cm and it was not enclosed by walls. Each arm was 80 cm long, 10 cm wide and enclosed by walls 16.5 cm high. The arms were covered by a sheet of clear plastic, 140 cm long, 76 cm wide and 0.2 cm thick. As for the enclosed radial maze, the first 4 cm of each arm were not covered. A small plastic cup was taped to the surface of the maze 3.5 cm from the end of each arm of the maze.

Testing was conducted in a large room (2.1 m × 3.5 m) with white walls, a red brick floor, and a brown and white ceiling with two banks of fluorescent lights. The room contained a variety of objects (e.g., sink and counter, air vent, light switch and timer), and one wall contained two large picture windows, covered with black plywood. The testing room was dimly illuminated by the fluorescent lamps during test sessions, at approximately the same level as the 'dark' phase of the housing room light/dark cycle. Pretraining was conducted in the subjects' home room, which was adjacent to the test room. The home room was smaller than the test room, but of similar construction.

Procedure

Subject assignment. Subjects were randomly assigned to one of 3 groups: parallel-sighted (N = 6 subjects), parallel-blind (N = 8), and radial-sighted (N = 8). One of the eight subjects in the parallel-blind group chose only one or two arms per trial, and did not complete the experiment.

Surgery (enucleation). Eight subjects were blinded under ether anesthesia. One eye was raised from its socket with a pair of forceps and the attached muscle, optic nerve and blood vessels cut with a pair of scissors. A subject was given additional ether, if necessary, before removal of the second eye. Each subject was allowed several minutes to recover before being returned to its home cage, where its condition was monitored for approximately an hour.

Pretraining. All subjects were pre trained and tested during the dark phase of the daily light/dark cycle. Each subject was given five daily 5-min sessions on the open field, always starting in the same corner of the open field. The plastic cup at the center of the open field contained 2.5 ml of tap water at the start of each session. All subjects were then given two daily 5-min sessions on one of the straight runways. Each of the cups at the ends of the runway contained 1.2 ml of tap water at the start of each session. All subjects started at the center of the runway, facing towards one end on the first day and towards the other end on the second day.

Testing. All subjects were given one trial per day. Each of the eight cups on a maze was baited with 0.3 ml of water before each trial. On each trial, a subject was allowed a maximum of 15 min to enter each of the eight arms of the maze and then re-enter one of the arms. The subject was placed on the common (central) platform in front of, and oriented towards, one of the eight arms at the start of each trial. This starting position was varied quasi-randomly across trials, that is, seven arms were represented three times, and one four times, in a sequence of 25 trials.

The subjects in the parallel-sighted and parallel-blind groups were each given 30 daily trials. The subjects in the radial-sighted group were given 12 daily trials. The sequence of arm entries (choices) was recorded manually. A ‘choice’ was recorded whenever all of the animal's body, except the tail, was in the arm. For recording choice sequences, the arms of the radial maze were labelled 1-8 in a clockwise direction (from above); the arms of the parallel maze were also labelled I-S, with the outermost arms being labelled Arm 1 and Arm S.

Results

The acquisition rates for the three groups were compared by considering the numbers of ‘errors,’ i.e., repetitions, and trials required by each subject before attaining a criterion of three out of four ‘errorless’ trials, i.e., three choice scores of 8 in four trials. This was the most stringent (simple) criterion that all subjects reached, and it would be reached very rarely by a subject choosing arms randomly (*P*[three or more choice scores of 8 in four trials] = 5.5×10^{-8}).

As Table 1 shows, the subjects in the radial-sighted group reached criterion much faster than the subjects in the parallel-sighted and parallel-blind groups. The radial- sighted group required' a

Table 1. Total trials and errors required to attain criterion of three out of four consecutive trials without repetition

Subject	Radial-sighted		Parallel-sighted		Parallel-blind	
	Trials	Errors	Trials	Errors	Trials	Errors
1	6	7	14	35	9	34
2	6	11	17	80	13	58
3	6	13	20	59	19	67
4	6	19	20	76	21	49
5	7	11	27	129	27	76
6	8	9	29	95	29	127
7	8	19	—	—	30	83
8	10	23	—	—	—	—
Median	6.5	12	20	78	21	67

median of only 6.5 trials to reach criterion, far fewer than either the parallel-sighted group (median = 20.0; Mann-Whitney $U = 0$, $P < 0.01$) or the parallel-blind group (median = 21; $U = 1$, $P < 0.01$). The difference between the median trials to reach criterion for the parallel-sighted and parallel-blind groups did not approach statistical significance ($U = 20$, $P = 0.47$). Similar results were obtained when the errors-to-criterion measure was considered. The medians were 12, 78 and 67 errors for the radial-sighted, parallel-sighted and parallel-blind groups, respectively.

The choice sequences for each group of subjects were analyzed to determine whether the parallel-maze groups exhibited several response tendencies previously reported for subjects tested on the radial maze (e.g., Olton and Samuelson, 1976). Olton and Samuelson (1976) found that their radial maze subjects selectively avoided repeating the most recently entered arms (the recency effect) and exhibited a slight tendency to choose arms 90° apart (alternate arms), but that the errors which did occur were not in the vicinity of the remaining 'correct,' i.e., unentered, arms; that is, there was no "generalization gradient among the arms" (Olton and Samuelson, 1976, p. 110). It what follows, 'spatial generalization' among the arms of a maze will be measured by the extent to which repetitions occur selectively to arms near to previously unentered arms. Spatial generalization gradients of this type might be expected if arms are identified in terms of their locations, and the similarity of the identification codes for two arms is a function of the distance between them.

The sequential-choice tendencies and recency effects were easy to determine; the spatial generalization score is somewhat more complicated.

The sequential-choice tendency was measured by assigning a transition size to all arm-to-arm transitions within the first eight choices on a trial. On the radial maze, transitions were measured in 45° units, so that adjacent arms are 1 unit apart and Arms 3 and 8 are 3 units apart; the largest transition size possible on the radial maze is 4 units. Adjacent arms are also 1 unit apart on the parallel maze, with transition sizes being assigned proportionally to the other possible transitions so that, for example, Arms 1 and 8 are 7 units apart. Table 2 shows the relative frequencies of the

Table 2. Relative frequency (%) of transition sizes, and mean transition size, for each third of the experiment

Group	Trials	Transition size								
		0	1	2	3	4	5	6	7	x
Radial-sighted	1-4	0	37	32	21	9	—	—	—	2.03
	5-8	0	71	17	8	4	—	—	—	1.45
	9-12	0	78	18	3	1	—	—	—	1.27
Parallel-sighted	1-10	1	38	27	13	7	5	4	5	2.42
	11-20	0	50	18	7	7	6	7	5	2.39
	21-30	0	64	12	7	4	4	3	5	2.00
Parallel-blind	1-10	1	43	20	12	6	7	5	6	2.50
	11-20	0	40	25	15	8	6	4	3	2.39
	21-30	0	49	19	10	9	6	3	4	2.28

various transition sizes, for each group. The data are presented for each third of the experiment, to show the tendency for all groups to make progressively smaller transitions as training progressed. By the end of training, adjacent arm choice was the modal response for all three groups. The mean transition size was consistently higher for the subjects tested on the parallel maze than for those tested on the radial maze (Table 2) but direct comparisons are difficult because the possible transition sizes range from 1 to 4 on the radial maze and, due to its asymmetry, from 1 to 7 on the parallel maze. Moreover, the mean transition size expected from random choice on the parallel maze depends on the particular arm just chosen (see p. 134, Table 4).

The degree of response stereotypy on the parallel maze was too low to account for the high levels of choice accuracy obtained. For example, only 21% of the errorless trials on the parallel maze (sighted group, 29%; blind group, 12%) involved either eight consecutive adjacent arm choices (i.e., 1...8 or 8...1) or adjacent arm choices from a 'middle' arm to one 'end' arm followed by a transition to the other end arm and further adjacent arm choices until the first arm entered was repeated (e.g., 321/87654). These are the only response patterns that could produce errorless performance without the subject's recognizing which arms had been chosen. The degree of response patterning was much higher on the radial maze: eight consecutive adjacent arm choices occurred on 52% of the errorless trials. However, high levels of choice accuracy preceded high levels of response stereotypy. Considering, for example, each subject's first three and last three errorless trials, eight consecutive adjacent arm choices occurred on 29% of the former and 67% of the latter.

The tendency to avoid the most recently entered arms (the recency effect) was measured in terms of the relative probability of repeating an arm on each of the first eight choices following its initial selection on a trial. Given a first entry into one of the arms, two measures were taken: the frequency with which that arm was repeated on each of the next eight choices and the number of opportunities for doing so, e.g., the number of times there actually was a seventh choice, say, after the initial selection of Arm 3. Combining these repetition frequencies, and opportunities, for all eight arms gave the overall repetition frequencies and opportunities. Dividing the overall

Table 3. Relative probability (%) of repeating an arm on each of the next eight choices

Group	Trials	Choice after initial entry of an arm[a]							
		1	2	3	4	5	6	7	8
Radial-sighted	1-4	1	2	4	16	17	16	19	26
	5-8	0	1	2	6	11	15	13	52
	9-12	1	1	0	5	3	4	8	79
Parallel-sighted	1-10	3	9	9	15	15	16	17	15
	11-20	1	5	10	9	20	11	22	22
	21-30	1	6	5	7	10	10	23	39
Parallel-blind	1-10	2	15	12	12	12	14	18	13
	11-20	0	7	10	12	13	14	16	28
	21-30	1	4	8	10	10	12	25	28

[a]The data for all eight arms were combined. See text for details.

repetition frequency by the corresponding overall opportunities for repetition gave the absolute probability of repeating an arm on each of the next eight choices. Table 3 shows, for each third of the experiment, the relative probability of repeating an arm on each of the next eight choices. The relative probabilities were obtained by dividing each of the eight absolute probabilities by the sum of the eight probabilities. All three groups of subjects were more likely to repeat an arm as the number of subsequent choices increased, and the tendency to avoid recently entered arms selectively became stronger as training progressed.

The possibility of spatial generalization among the arms was investigated by testing whether errors (repetitions) tended to occur to arms close to the remaining correct (unchosen) arms. A 'generalization score' was calculated for the first repetition on each trial on the radial maze; the repeated arm was assigned Location 0, and the remaining arms were assigned Locations ± 1 through ± 4, in 45° units, so that adjacent arms were in Locations ± 1 and the arm opposite the repeated arm was in Location 4. With this notation, a subject repeating arms randomly with respect to the remaining correct arms would be expected to obtain a mean genera- lization score of 2.29, and a subject repeating arms close to the remaining correct arms would be expected to obtain a lower generalization score (see Olton and Samuelson, 1976, pp. 108-109). A generalization score was calculated in a similar way for the parallel maze, except that, because of the relative asymmetry of the maze, separate generalization scores had to be calculated for the cases when repetitions occurred to Arms 1 or 8, 2 or 7, 3 or 6, and 4 or 5 (Arms 1 and 8 being the outermost arms). For these calculations, the distance between two arms was simply the difference between their arm numbers, e.g., Arms 7 and 2 are 5 units apart. The expected spatial generalization scores for a subject choosing randomly with respect to the remaining unchosen arms are 4.0, 3.14, 2.57 and 2.29 for repetitions to Arms 1 or 8, 2 or 7, 3 or 6, and 4 or 5, respectively. For example, if Arm 1 was repeated, the remaining correct arms would be located, with equal likelihood, at any of the Locations 2-8, so the average distance between Arm 1 and the remaining correct arm(s) would be $(1 + 2 + \ldots +7) / 7 = 28 / 7 = 4.0$.

Because changes in the degree of spatial generalization might have occurred during acquisition, spatial generalization scores were calculated separately for those trials 'early' and 'late' in

Table 4. Spatial generalization score: mean observed and 'expected' average distance between first arm repeated on a trial and the remaining unchosen arms

The 'expected' average distance is based on random choice.

Group	Arm repeated	Mean distance[a] Expected	Early trial[b] (*N*)[c]	Late trials (*N*)
Radial-sighted	Any	2.29	2.36 (13)	2.29 (17)
Parallel-sighted	1 or 8	4.00	3.06 (16)	4.50 (29)
	2 or 7	3.14	2.80 (5)	2.86 (17)
	3 or 6	2.57	2.54 (15)	3.12 (11)
	4 or 5	2.29	2.38 (12)	2.69 (9)
Parallel-blind	1 or 8	4.00	3.56 (14)	4.73 (34)
	2 or 7	3.14	3.24 (17)	3.55 (27)
	3 or 6	2.57	2.77 (12)	2.33 (14)
	4 or 5	2.29	2.45 (13)	2.25 (12)

[a] 'Distance' is measured in inter-arm units: adjacent arms are one unit apart

[b] 'Early' and 'late' trials are those before and after reaching a criterion of one error or less in the first eight choices of each of three consecutive trials.

[c] *N* = number of observations contributing to mean.

training. For each subject, early and late trials were defined as those before and after reaching a criterion of one error or less in the first eight choices of each of three consecutive trials. This criterion, a choice score of 7 or 8 on each of three consecutive trials, was more lenient than that used to assess acquisition rates (Table 1), *P*[three consecutive trials with choice score of at least 7] = 3.4×10^{-4} (see Olton and Samuelson, 1976, p. 100). However, it distinguished the groups effectively: the subjects in the radial-sighted, parallel-sighted and parallel-blind groups attained this criterion after means of 12.5 errors, 59.7 errors and 55.3 errors, respectively.

The observed mean distances, and those expected with random choice, between the repeated arm and the remaining correct arms are shown in Table 4, together with the number of observations contributing to each mean. Statistical tests (*t*-tests) comparing the observed and expected means produced only two significant differences: the parallel-sighted group exhibited spatial generalization when repeating Arms 1 or 8 early in training, $t(15) = -3.68$, $P < 0.01$, and the parallel-blind group exhibited spatial 'avoidance' when repeating Arms 1 or 8 late in training, $t(6) = 2.29$, $P < 0.05$. The results provide no support for the proposition that subjects make errors (repeat arms) because of confusions concerning the positions of the correct and previously-entered arms.

A final, unexpected, result was that the subjects tested on the parallel maze tended to repeat the outer four arms of the maze (Arms 1, 2, 7 and 8) more often than the inner four arms of the maze (Arms 3, 4, 5 and 6). This pattern of errors occurred whether one considered all repetitions, or just the first repetition on each trial (Table 5). Both the parallel-sighted group and the parallel-blind group repeated the outer four arms of the maze more often than the inner four arms, whether all errors or only the first error on each trial were considered (smallest $x^2(1) = 8.50$, $P <$ 0.01; parallel-sighted group, first error only). In contrast, the subjects in the radial-sighted group

Table 5. Distribution of total errors (and first error on each trial) across arms

Group	Arm repeated 1	2	3	4	5	6	7	8
Radial-sighted	21	24	38	21	36	23	25	20
	(8)	(8)	(18)	(12)	(19)	(9)	(11)	(6)
Parallel-sighted	152	72	68	69	67	82	65	125
	(41)	(17)	(24)	(18)	(10)	(18)	(14)	(37)
Parallel-blind	118	126	68	75	81	88	85	136
	(34)	(45)	(18)	(16)	(18)	(19)	(21)	(37)

tended to repeat Arms 3-6 more often than Arms 1, 2, 7 and 8; the tendency was statistically significant for the total errors measure ($x^2(1) = 6.87$, $P < 0.01$) but not for the first-error-per-trial measure ($x^2 = 3.77$, $0.1 > P > 0.05$).

Discussion

The observed acquisition rates corresponded to the predictions from the tagged-I.D. hypothesis. The parallel-sighted group, hypothetically unable to identify the arms by their spatial relationships with the set of extramaze reference points, exhibited much slower acquisition than the radial-sighted group. The parallel-blind group performed as well as the parallel-sighted group, a result to be expected if the extramaze visual cues had been rendered ineffective by the structure of the parallel maze. Moreover, the presence of a strong recency effect for all three groups is consistent with the suggestion that the subjects selected arms on the basis of the relative recency with which each arm had been entered. In terms of the tagged-I.D. hypothesis, then, the subjects have difficulty specifying distinctive identification codes for the parallel, adjacent arms of the parallel maze. Once such codes have been adequately specified, the subjects are able to avoid repeating arms because the temporal marker, or tag, system is just as effective on the parallel maze as on the radial maze: maze structure affects the formation of the identification codes, not the adequacy of the tagging system. Despite the congruence of the predictions of the 'tagged-I.D.' hypothesis and the experimental results, the presence of strong response tendencies for each of the three groups suggests that 'response strategies' (Olton and Samuelson, 1976), particularly systematically choosing adjacent arms, may have influenced the development of both high choice accuracy and the tendency to selectively avoid the most recently entered arms (the recency effect). In particular, repeatedly choosing adjacent arms (in the same direction) would contribute to the recency effect by reducing a subject's exposure to recently entered arms. The effect would be greater on the radial maze, where subjects would not encounter any 'end' arms. Determining the relative contributions of response tendencies and 'memory factors,' such as those implied in the tagged-I.D. hypothesis, to choice accuracy and the recency effect will require a study in which the experimenter controls the degree of response stereotypy; for example, by using the 'forced-choice' procedure (Zoladek and Roberts, 1978).

The absence of spatial generalization gradients on either maze replicates and extends Olton and Samuelson's (1976) finding, and suggests that repetitions are not primarily due to confusions of arm position. However, spatial generalization may fail to occur for three reasons: very precise spatial discrimination, very imprecise spatial discrimination, or non-spatial discrimination, and different factors may be responsible on the radial and parallel mazes. The arms of the radial maze are apparently identified ‘spatially,’ i.e., in terms of their positions relative to some set of extramaze stimuli (Suzuki et aI., 1980), and the positions and/or orientations of the various arms are sufficiently distinct that their identification codes are virtually never confused. The absence of spatial generalization on the parallel maze, on the other hand, may reflect poor spatial discrimination, i.e., an inability to distinguish among the arms, or non-spatial identification codes, i.e., identification codes based on ‘local,’ intramaze cues rather than on some set of extramaze stimuli.

It is difficult to assess the importance of the blind and sighted subjects' tendencies to repeat the outer four arms of the parallel maze, Arms 1, 2, 7 and 8, more often than the inner four arms, Arms 3, 4, 5 and 6, but the finding has been independently obtained for sighted subjects tested on a 12-arm parallel maze (Buresova, 1980). This bias towards repeating the outer four arms of the parallel maze is surprising, given that the identification codes for the outer arms should be more distinctive than those for the inner arms, making the outer arms less likely to be repeated. One possibility is that this tendency is an artifact of a predisposition among subjects to select arms as far from the experimenter as possible. The experimenter sat nearest Arms 4 and 5 during parallel maze testing and between Arms 1 and 8 during radial maze testing. Other factors may be responsible, however, since such ‘experimenter-avoidance’ has not been detected in other radial maze studies, and such an account may not be possible for Buresova's (1980) results.

The tagged-I.D. hypothesis suggests that subjects have difficulty developing distinctive identification codes for the arms of the parallel maze because the arms all have similar spatial relationships with some set of extramaze cues, but the precise nature of the identification codes has not been specified. There is, however, a considerable body of evidence indicating that inertial (body-movement) cues provided by the vestibular system have a major influence on maze behavior. Spontaneous alternation tests, consisting of two successive trials on a T-maze, show that subjects choose different goal arms on Trials 1 and 2 in about 80% of the tests (e.g. Douglas, 1966a). Douglas (1966a) showed that spontaneous alternation resulted, primarily, from a tendency not to repeat recently-travelled spatial directions, and further studies indicated that subjects with disease of (Douglas, 1966b) or damage to the vestibular system (Potegal, Day and Abraham, 1977) failed to show spontaneous alternation: their Trial 1 and Trial 2 goal-arm choices were the same on about 50% of the tests. A series of studies by Sherrick and Dember convincingly demonstrated that rats are extremely sensitive to the directions of their prior movements (Dember, Sherrick and Harris, 1966; Sherrick, Brunner, Roth and Dember, 1979; Sherrick and Dember, 1966a, 1966b), with the most recent study also demonstrating the absence of directional generalization on the radial maze. Subjects in the Sherrick et al. (1979) study ran along a straight alley and then were placed on the central platform on an 8-arm radial maze in the same room. Given one choice on the radial maze, subjects selectively avoided the arm with the same orientation as the straight alley, choosing each of the remaining seven arms equally often. This result coincides nicely with the absence of spatial generalization of errors observed by

Olton and Samuelson (1976) and in the present experiment. Given these findings, one might expect a failure to obtain spontaneous alternation on a two-arm parallel maze, because there is no way for a subject tested on Trial 2 to avoid the direction moved on Trial 1. This is precisely what occurs: both Douglas, Mitchell and Kentala (1972) and Greenberg (1973) failed to obtain spontaneous alternation on a two-arm parallel maze. There is disagreement on the minimum angle between the goal arms necessary for spontaneous alternation, since Douglas, Mitchell and Del Valle (1974) failed to obtain it when the angle of separation between the goal arms was reduced below 60°, but Jackson (1941) obtained alternation on over 90% of tests with an angle of only 15° between the goal arms.

Taken together, the data on spontaneous alternation are consistent with O'Keefe and Nadel's (1978) ‘cognitive map’ model, which proposes that subjects develop an internal representation of the environment through the integration of movement-related and environmental stimulation. Applied to the tagged-I.D. hypothesis, O'Keefe and Nadel's model suggests that identification codes for the maze-arms may result from an integration of movement-related cues and environmental cues rather than being defined solely in terms of an array of extramaze environmental cues. The involvement of a direction-of-movement component in the identification codes for the arms of the parallel maze could only slow acquisition, since this component of the code would be essentially the same for all arms.

In conclusion, the results of the maze-structure manipulation correspond to the predictions of the tagged-I.D. hypothesis. This hypothesis proposes that, to avoid repeating the arms of a maze, a subject must both distinguish among the arms (the identification codes) and discriminate ‘visited’ from ‘unvisited’ arms (the temporal markers). The tagged-LD. hypothesis may help reconcile the two major theories of hippocampal function cited in connection with radial maze performance: the cognitive map model (O'Keefe and Nadel, 1978) and the ‘working memory’ model (Olton, Becker and Handelmann, 1979). Since the former deals with the identification-code component of the tagged-lD. hypothesis while the latter relates to the temporal-marker component, the cognitive map and working memory models are clearly complements rather than alternatives. Any satisfactory account for maze performance and, more generally, spatial orientation (e.g., Barlow, 1970; Beritoff, 1965) must consider both determinants of behavior.

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