Control of Choice by the Spatial Configuration of Goals

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Rats gathered pellets from the tops of 15.5-cm-tall poles. In a matrix of poles, bait was located on the tops of poles arranged in either a square (Experiment 1) or linear (Experiment 2) configuration. The specific locations of baited poles varied unpredictably from trial to trial. The data show that the rats' choices were controlled by the spatial configuration of baited locations. This indicates that the rats represented the geometric pattern formed by the locations of food.

Empirical and conceptual work has provided strong evidence that a variety of animals use objects as spatial landmarks. That is, they locate hidden goals according to the spatial relations between them and visible landmarks. The classic example of this is the ability of the digger wasp to locate her nest relative to nearby landmarks (Tinbergen, 1951). More recent work has examined the ability to use landmarks and the mechanisms for doing so in a wide variety of animals (e.g., Cartwright & Collett, 1987; Cheng, 1988, 1989; Collett, Cartwright, & Smith, 1986; Gallistel, 1990; Kamil & Balda, 1985; Suzuki, Augerinos, & Black, 1980).

Apart from the use of perceived landmarks, Cheng and Gallistel (Cheng, 1986; Cheng & Gallistel, 1984; Gallistel, 1990) have also argued that rats use representations of the geometric properties of spaces in locating hidden goals. Cheng (1986) found that rats searching for a hidden goal in a rectangular space were likely to make confusion errors that could be explained in terms of geometrical equivalences. Thus, he argued, rats must represent the space within which they search for food in terms of at least some of its formal geometrical properties.

The performance of rats in the radial-arm maze task has also been used to argue that spatial relations among locations control behavior (e.g., Mazmanian & Roberts, 1983; O'Keefe & Speakman, 1987; Suzuki et al., 1980). However, alternative interpretations of some of the critical data have been offered (Brown, 1992; Leonard & McNaughton, 1990). An experiment by Dallal and Meck (1990, Experiment 3) provides data that are particularly relevant to the present experiment. They used a procedure in which 4 arms of a 12-arm maze were never baited. Thus, to perform accurately, rats had to avoid visiting the never-baited arms as well as avoid revisiting previously visited arms. The critical comparison involved two groups of rats, both of which were trained in one extramaze environment and tested in a second extramaze environment. The geometric pattern of the never-baited arms remained constant for one group but was different in the two environments for the second group. Choice accuracy after the transfer was higher for the first group than for the second group. Thus, the constancy of the geometric pattern of never-baited arms facilitated transfer of performance. This implies that the geometric relations among the never-baited arms were included in the rats' representation of the maze.

We conducted the present experiments to determine whether spatial choices in rats can be controlled by the spatial arrangement of hidden goals. We used an apparatus similar to ones developed by Olton, Walker, Gage, and Johnson (1977); van der Staay, Krechtling, Blokland, and Raaijmakers (1990); and, particularly, Greene and Cook (in press), in that rats were required to locate food hidden on top of vertical poles. The apparatus consisted of a matrix of poles that were just tall enough that the rats had to rear up on their hind limbs to reach the top of a pole. A food pellet could be hidden in a well at the top of each pole. The poles were separated by just enough space that the rats could travel freely among them.

In our experiments, unlike most experiments concerned with spatial choice, we provided no explicit landmarks either inside or outside the apparatus that could control choices. Two details of the procedure ensured this. First, the apparatus was rotated into an unpredictable orientation relative to the extrapparatus environment before each experimental trial. Second, an unpredictable subset of the poles was baited during each trial. Thus, there were no cues predicting the location of goals at the onset of each trial.

However, the baited poles were determined by a geometric pattern. In Experiment 1, four poles were baited and these poles formed a square configuration within the $5 \times 5$ matrix of poles. In Experiment 2, one linear row or column of poles was baited within a $4 \times 5$ matrix of poles. Thus, once one or more baited poles had been located, the geometric rule restricted the locations of other poles that could be baited. Our goal in performing these experiments was to determine whether rats' choices were sensitive to the restrictions imposed by the geometric patterns.
Experiment 1

In Experiment 1, the baited poles were consistently arranged in a square. Thus, once a rat discovered one baited pole, the spatial pattern according to which poles were baited could restrict the search, allowing the rat to find additional bait more efficiently. The primary data analysis was designed to determine whether this was the case. Other than this pattern, no cues as to the locations of the baited poles were available to the rats.

Method

Subjects

The subjects were 15 male Sprague-Dawley rats, approximately 5 months old when the experiment began. They were housed in groups of 3 or 4 in a colony room with a 12:12-hr light:dark cycle. All experimental procedures occurred during the dark phase of the cycle. For 2 weeks before the experiment, we maintained the rats on a mild food deprivation schedule by feeding them 12 g of Purina Rat Chow immediately after the daily experimental treatment.

Apparatus

The apparatus was a 180 cm × 76 cm × 33 cm (tall) box, constructed of 1.5-cm-thick plywood and painted flat black. The top of the box was open. Inside the box was a 5 × 5 matrix of 15.5-cm-tall poles, constructed of unpainted wooden dowel rods (1.2 cm in diameter). The matrix of poles was centered in the box, leaving an open space at each end of the box. The poles in each row or column of the matrix were separated by 13 cm. A 0.5-cm-deep well was drilled into the top of each pole. This depth was intended to allow a single reward pellet to be visually occluded and yet allow a rat to remove the pellet from the well with its tongue. A thin layer of bedding material covered the floor of the box. The apparatus was mounted on a lazy susan, which allowed it to be easily rotated relative to the extraapparatus environment. The apparatus was located in a small room that contained a variety of objects and was illuminated by fluorescent tubes.

A additional training apparatus was placed inside the box during the early phases of training. This apparatus consisted of a series of increasingly tall poles (2.0 cm, 4.5 cm, 12.5 cm, and 15.5 cm), separated by 7 cm and otherwise identical to the poles described earlier. These poles were attached to a cardboard surface that could be placed in the box and hidden under the bedding material.

Procedure

Training. We gave the rats 10–20 of the pellets to be used in the experiment (Bioserve 45-mg sucrose pellets) each day for 3 days. Phase 1 of training began on the following day. We began each trial by placing the rat in one end of the apparatus (chosen randomly) with the training apparatus present in the same end of the box. Each pole of the training apparatus and the experimental apparatus was baited with a single pellet and, during the first one or two training trials only, several pellets were scattered around the base of the training apparatus. In this and all subsequent phases of the experiment, four trials occurred per day, with 10 min separating trials. Throughout the experiment, we chose the orientation of the apparatus (relative to extraapparatus cues) randomly from among eight equally spaced orientations to ensure that spatial cues from the extraapparatus environment did not control performance. Phase 1 of training continued until an individual rat had consumed the pellets on all 4 poles of the training apparatus and at least 10 poles in the experimental apparatus within 3 min during five consecutive trials.

During Phase 2 of training, the training apparatus was not present. Each of the 25 poles was baited before each trial. We placed the rat in one end of the apparatus (randomly chosen) and allowed it to visit poles until it had collected at least 20 of the 25 pellets. If 10 min elapsed without this occurring, we considered the trial to be unsuccessful and terminated it. This training phase continued until a rat had successfully completed 10 trials.

In Phase 3 of training, we introduced the square pattern of baited poles. During the first day of Phase 3 (i.e., the first four trials), we placed a barrier in the apparatus such that only two rows of poles were available to the rat. Within this restricted set of 10 poles, we baited 4 poles, forming a square. We chose this configuration randomly from among the four possibilities in each trial. During the second day of Phase 3, we moved the barrier so that three rows of poles were available. Again, we baited a randomly chosen set of 4 poles forming a square. Likewise, on the third day of Phase 3, four rows of poles were available. We allowed each rat to choose from among the poles until it had retrieved all four pellets or until 5 min had elapsed without a choice.

Testing. After training the rats, we tested them in 120 trials. Before each trial, we baited four poles. These baited poles always formed a square configuration. The top panel of Figure 1 shows an example of the pattern in which poles were baited. We chose the location of this square configuration of four baited poles randomly from among the 16 possibilities. Thus, before any particular trial, the location of the baited poles was unpredictable. Once baited poles were discovered, however, they provided information about the location of additional baited poles. At the beginning of each trial, we placed the rat in one of the two ends of the apparatus (randomly chosen). The rat was allowed to choose poles until it had chosen the four baited poles or 5 min had elapsed without a choice. We defined a choice as the rat’s touching the top of the pole with its snout. We recorded the sequence of chosen poles and videotaped each trial; in cases where the experimenter was unsure about the sequence of choices (because of the speed with which some rats sometimes performed the task), we reviewed the video-tape to determine or confirm the data.

Results and Discussion

Training

One rat consistently failed to retrieve all four pellets during Phase 3 of training and was excluded from the experiment. The remaining rats successfully completed the training.

Testing

We analyzed data from the 120 trials of the experiment in three blocks of 40 trials each, to allow changes in performance to be detected. During Blocks 1–3, the rats ceased making choices for 5 min, and we therefore terminated the trial before discovery of the fourth baited pole, in 18.6%, 12.9%, and 11.0% of the trials, respectively. In completed trials, the rats required means of 26.5, 21.6, and 20.1
Example Pattern in Experiment 1

Example Pattern in Experiment 2

Figure 1. Examples of patterns used to bait the apparatus in Experiment 1 (top panel) and Experiment 2 (bottom panel). B = baited pole. Drawing is not to scale.

choices, respectively, to locate all four baited poles. The values for both measures were reliably different according to repeated measures analyses of variance (ANOVAs), $F(2, 26) = 18.8$ and $F(2, 26) = 21.3$, respectively. (All statistical decisions reported in this article were made using a criterion of $p < .05$.) These differences show that the rats' ability to locate the four baited poles improved over the course of the experiment.

When moving from pole to pole, the rats most often chose poles adjacent to the previously chosen pole in a row or column. Moves to poles diagonally proximal to the previously chosen pole were relatively rare. These facts are illustrated in Figure 2, which shows the mean (over rats) number of moves of these two types per trial in addition to moves to poles that were spatially separated from the previously chosen pole during each block of trials.

Sensitivity to the square pattern in which poles were baited would allow rats to narrow the spatial range of poles they chose after discovering the first baited pole. The top panel of Figure 3 shows the mean number of poles the rats chose between discoveries of baited poles during the three blocks of trials for the four transitions (i.e., from the begin-

Figure 2. The mean number of pole-to-pole moves per trial of the three following types during the three trial blocks of Experiment 1. Adjacent = moves to poles proximal in a row or column to the most recently chosen pole; Diagonal = moves to poles proximal diagonally to the most recently chosen pole; Separated = moves to poles spatially separated by at least one other pole from the most recently chosen pole.

ning of the trial to discovery of the first baited pole, from discovery of the first baited pole to discovery of the second baited pole, etc.). If, after discovering a baited pole, a rat immediately chose another baited pole, the value of this measure was 1. The number of choices made between discoveries differed as a function of both block, $F(2, 26) = 19.5$, and transition, $F(3, 39) = 144.5$. The effects of these variables interacted, $F(6, 78) = 4.15$, apparently because the improvement in performance over blocks did not occur for the first transition (finding the first baited pole), $F(2, 26) = 1.6$, as might be expected, given that no cues specified the location of the baited poles until the first one was discovered. For the other three transitions, there was a reliable reduction in the number of choices between discoveries over blocks, $F(2, 26) = 25.2, 21.4$, and $4.8$ for the transitions from discovery of the first to discovery of the second baited pole, discovery of the second baited pole to discovery of the third baited pole, and discovery of the third baited pole to discovery of the fourth baited pole, respectively.

Perhaps a more precise measure of the rats' ability to efficiently locate another baited pole after discovering a baited pole is the proportion of trials in which the transition was immediate and not separated by any other choices. The mean values of this measure are shown in the bottom panel of Figure 3. As would be expected, the results for this measure were similar to those of the previous measure (in which it is embedded). There were reliable effects of block, $F(2, 26) = 14.8$, and transition, $F(3, 39) = 407.4$, as well as an interaction between the effects of these variables, $F(6, 78) = 4.9$. There was no improvement in performance over blocks for the transition from the beginning of the trial to discovery of the first baited pole, $F(2, 26) = 1.4$, or from discovery of the first baited pole to discovery of the second

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baited pole, $F(2, 26) = 1.4$. However, there was a reliable increase over blocks in the proportion of immediate transitions from discovery of the second baited pole to discovery of the third baited pole, $F(2, 26) = 12.9$, and from discovery of the third baited pole to discovery of the fourth baited pole, $F(2, 26) = 9.0$.

The lack of an improvement in the rats’ ability to locate the first baited pole validates our techniques designed to prevent spatial cues to the location of the baited poles before the first one was discovered. The small number of moves separating discovery of the first baited pole and discovery of the second baited pole is best explained by the rats’ tendency to choose adjacent poles. Given this tendency (shown in Figure 2), it was likely that rats would encounter a second baited pole immediately after discovering the first baited pole. Thus, of most interest in these data are the changes in the last two transitions that occurred over the three blocks. Over the course of the experiment, the rats became more efficient at finding the last two baited poles after discovery of the first two.

The primary data analysis was a set of analytic tools designed to determine whether this ability and the improvement in this ability were produced by sensitivity to the square configuration of baited poles. The analysis involved moves from a baited pole to an adjacent, previously unvisited pole. We examined only moves to adjacent poles in order to simplify the analysis and because of the relative scarcity of other types of moves. We eliminated moves to previously visited poles from the analyses to rule out any effects that previous visits might have (i.e., rats might avoid revisits to poles). Given these restrictions, we could use the choices the rats made immediately after discovering the second baited pole and immediately after discovering the third baited pole to make inferences about control by the square configuration of baited poles.

Figure 4 illustrates the logic of the analysis. The two top panels show the two basic spatial configurations of the first two baited poles discovered. At the time the second baited pole is discovered, the two discovered baited poles either are aligned in a row or column (Panel A) or form the opposite corners of the baited square (Panel B). In either case, there are two poles adjacent to the just-discovered pole (i.e., adjacent to the pole identified as 2 in the figure) that could possibly be baited, according to the rule governing pole baiting. There are also one (Panel A) or two (Panel B) adjacent poles that cannot possibly be baited, according to the rule. Similarly, when the rat has just discovered the third baited pole (Panel C), there is one possibly baited pole and two adjacent poles that are not possibly baited. The purpose of the analysis was to determine whether, under these conditions and restrictions, the rats move from the just-discovered baited pole to possibly baited poles more often than would be expected by chance.

The first step in conducting this analysis was to determine the properties of choices involving moves from the just-discovered second and third baited poles to an adjacent, previously unvisited pole. All of the data reported herein came only from the choices that met these criteria. We analyzed data from moves starting at the newly discovered second baited pole and data from moves starting at the newly discovered third baited pole separately. The expected (on the basis of chance) probability of moving to a possibly baited pole ($E$) was simply the proportion of adjacent, previously unvisited, possibly baited poles ($P_n$, marked P in Figure 4) among the adjacent, previously unvisited poles ($P_n$, marked N or P in Figure 4) at the time the moves included in the analysis occurred: $E = P_n / P_n$.

Note that the phrase “possibly baited pole” means a pole that could be baited according to the rule (that baited poles be in a square configuration), regardless of whether or not the pole is actually baited. Consider moves after discovery of the second baited pole in Panels A and B in Figure 4. Combining the two examples in the figure, the expected proportion of moves to possibly baited poles among moves to adjacent, previously unvisited poles is $4 / 7 = .57$. In the figure we assume that all poles adjacent to the just-discovered baited poles were previously unvisited (aside from previously discovered baited poles). It must be kept in mind that in the actual data analysis, previously visited poles did not enter into the calculation of expected or obtained proportions. For each individual rat during each block of trials, we compared the expected proportion with the obtained proportion ($O$) of moves to adjacent, previ-
A: Two Baited Poles Discovered (aligned)

B: Two Baited Poles Discovered (corners)

C: Three Baited Poles Discovered

Figure 4. Poles and moves included in the primary analysis used in Experiment 1. Numbers indicate the order in which baited poles were previously discovered. P = possibly baited pole; N = not possibly baited pole. Only poles adjacent to the most recently discovered baited pole were included in the analysis, as indicated by the arrows. Although not illustrated, poles that had been previously visited were excluded from the analysis.

Figure 5. The proportion of moves from a baited pole to an adjacent, previously unvisited pole which were to possibly baited poles. The mean proportion obtained (see text for equation) and the mean proportion expected on the basis of chance (see text for equation) are shown over the course of three trial blocks.
poles were designed to prevent this. The lack of an improvement in the rats’ ability to locate the first baited pole over trial blocks (discussed earlier and shown in Figure 3) argues against this explanation. However, we remained concerned that, once rats were in the vicinity of the baited poles, perceptual cues to the location of additional baited poles might have become available. A straightforward test of the possibility that the rats used perceptual cues in making their choices included in the present analyses involved the fact that only some possibly baited poles were actually baited. After discovery of the third baited pole (Panel C in Figure 4) and when the discovered poles were in opposite corners of the square after discovery of the second baited pole (Panel B in Figure 4), all possibly baited poles were also actually baited. However, when the two discovered poles were in the same row or column of the pole matrix (Panel A in Figure 4), possibly baited poles that were actually baited and possibly baited poles that were not actually baited existed. In other words, when the two discovered poles were adjacent, the remaining baited poles could be on either side of the pair.

We conducted two analyses to address any influence of the physical presence of the pellets. The first was intended to determine whether the rats’ choice behavior was influenced by the physical presence of the pellets. For each rat during each trial block, we determined the proportion of moves to possibly baited poles ($M_p$) that were to the actually baited pole ($M_a$): $O = M_p / M_a$. We compared these values with those expected on the basis of chance, which we considered to be the proportion of possibly baited poles that were actually baited at the time the moves were made: $E = P_b / P_s$. As in all of the analyses reported herein, we included only adjacent, previously unvisited poles in the determination of obtained and expected values.

Figure 6 shows the mean values of these proportions. A repeated measures ANOVA failed to reveal a difference between the obtained and expected values, $F(1, 13) = 2.6$. There was no interaction between trial block and data source (obtained vs. expected), $F(2, 26) < 1$. Thus, the data provided no support for the possibility that the rats chose poles on the basis of an ability to perceive the pellets before they made a choice.

Despite the results of this ANOVA, the means shown in Figure 6 may cause concern about an undetected influence of pellet perception on the basic finding. To rule out any such influence, we performed an analysis that was very similar to the one illustrated in the top panel in Figure 5 (comparing the expected and obtained proportions of moves to adjacent, previously unvisited poles that were possibly baited after discovery of the second baited pole). The primary difference was that actually baited poles and moves to actually baited poles were not included in the determination of expected and obtained values, respectively. Thus, the expected proportion was given by the equation $E = (P_a - P_b) / (P_a - P_s)$. The obtained proportion was given by the equation $O = (M_a - M_b) / (M_a - M_s)$. This allowed us to detect any tendency for the rats’ choices to be directed to poles that were possibly but not actually baited. Because of the relatively small number of cases involved, we collapsed the data across trial blocks. The expected proportion of moves to possibly but not actually baited poles among moves to adjacent, unvisited, but not baited poles was .41. The obtained proportion was .62. These values were reliably different, $t(13) = 4.9$.

These data indicate that spatial choice can be affected by the spatial arrangement of previously discovered goals. If goals have consistently been located in a square pattern, choices are made in accordance with that pattern. This phenomenon suggests that the spatial pattern in which locations are baited controls choice. There is, however, an alternative to this explanation of the results of Experiment 1. We tested this alternative in Experiment 2.

**Experiment 2**

Experiment 2 had two purposes. The first was to test the generality of the phenomenon discovered in Experiment 1. Specifically, we wanted to determine whether choice behavior could be controlled by a configuration other than a square.

The second purpose was to test an alternative to control by the geometric pattern as the explanation for the results of Experiment 1. This alternative was that the locations of previously discovered baited poles acquired associative strength and the rats searched for additional poles under the control of spatial generalization from a combination or average of these locations. Consider the situation after discovery of the second or third baited pole (see Figure 4). Not only is (are) the remaining baited pole(s) defined by the geometric rule, but it (they) is (are) also in close proximity to the discovered baited poles. In part because of this, all poles considered in the primary analyses were adjacent to the just-discovered baited pole, ruling out any simple effect.

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*Figure 6.* The proportion of moves from a baited pole to a possibly baited pole which were to an actually baited pole. The mean proportion obtained (see text for equation) and the mean proportion expected on the basis of chance (see text for equation) are shown over the course of three trial blocks.
of spatial proximity among individual poles. However, it remained possible that control by the locations of multiple previously discovered baited poles was combined or averaged to determine search location. In fact, hypothetical mechanisms for combining the influence of spatial landmarks have recently received considerable attention (e.g., Cheng, 1988, 1989; Gallistel, 1990). A process that combines the influences of the locations of previously discovered poles could have directed the rats to the location of possibly baited poles under the conditions of Experiment 1.

The pole(s) closest to the average of the locations of the two (or three) discovered baited poles is (are) the possibly baited pole(s). This fact, rather than representation of the geometric pattern in which poles were baited, could have been responsible for the effect discovered in Experiment 1.

In Experiment 2, poles were always baited in a linear pattern. Under this rule, control of choice by a spatial averaging process would misdirect the rats. Our primary analysis was designed to allow direct comparison with the results of Experiment 1. Moves immediately after discovery of the second baited pole, in cases in which the two discovered poles were adjacent, were included in the analysis. These cases corresponded directly to those illustrated in Panel A of Figure 4, except, of course, that the possibly baited poles and not possibly baited poles had reversed roles in the present experiment relative to Experiment 1. Thus, we hypothesized that if spatial averages or combinations of previously discovered pole locations were responsible for the results of Experiment 1, rats in Experiment 2 would be biased toward choosing poles incorrectly. However, if the rats chose poles under control of the rule according to which poles were baited, the rule would allow them to choose the possibly baited poles in Experiment 2.

**Results and Discussion**

All 6 rats located all four (or five) baited poles during every trial. The 4 rats assigned to have columns baited required a mean of 17.3 choices to locate the four baited poles. The 2 rats assigned to have rows baited required a mean of 17.8 choices to locate the five baited poles. As in Experiment 1, most moves were to poles adjacent in a row or column to the most recently chosen pole. Specifically, means of 10.75, 3.9, and 2.1 pole-to-pole moves per trial were between adjacent, diagonally proximal, and spatially separated poles, respectively.

The mean number of choices made between discoveries of baited poles for the four transitions (from the beginning of the trial to discovery of the first baited pole, from discovery of the first baited pole to discovery of the second baited pole, etc.) are shown in the top panel in Figure 7. The number of choices made differed over the four transitions, $F(3, 15) = 5.0$. The proportions of these transitions that were immediate are shown in the bottom panel in Figure 7. The proportions differed over the four transitions, $F(3, 15) = 8.5$.

The data of primary interest came from an analysis identical to the primary analysis we conducted in Experiment 1. The calculation of expected and obtained proportions of moves to possibly baited poles was the same as in Experiment 1, with the exceptions that (a) we considered only moves made after discovery of a second baited pole that was adjacent to the first discovered baited pole; (b) in the present experiment all possibly baited poles were actually baited; and, most important, (c) the spatial relations of possibly baited poles and not possibly baited poles to the previously discovered baited poles were reversed relative to Experiment 1. Thus, the expected proportion ($E$) of moves to possibly baited poles (i.e., the number of poles that could be baited according to the linear baiting rule, $P_a$) among adjacent, previously unvisited poles ($P_{a_1}$) was given by the equation $E = P_a / P_{a_1}$. The obtained proportion of moves to poles that could be baited according to the linear baiting rule ($M_a$) among moves to adjacent, previously unvisited poles ($M_{a_1}$) was given by the formula $O = M_a / M_{a_1}$.

The mean (over rats) expected proportion of adjacent moves to previously unvisited poles that were possibly baited was .50. The mean obtained proportion was .72. The obtained proportion was reliably greater than the expected proportion, $t(5) = 6.55$.

These results extend those of Experiment 1, in that the rats' choices were controlled by a different spatial configuration of baited poles. The small number of trials used in Experiment 2 relative to Experiment 1 did not allow us to

**Method**

**Subjects**

The subjects were 3 male and 3 female Sprague-Dawley rats, obtained from the same supplier and maintained in the same manner as those used in Experiment 1.

**Apparatus**

The apparatus was similar to that used in Experiment 1. However, it was smaller in size (120 cm × 58 cm × 33 cm tall) and contained fewer poles (a 4 × 5 matrix). The matrix of poles was located at one end of the box, leaving a single open area at the other end of the box. For the initial training phase of the present experiment, we used the same set of shorter training poles we had used in Experiment 1.

**Procedure**

The training procedure was the same as Phases 1 and 2 of the training procedure in Experiment 1. After the rats completed the training session, we randomly assigned them to have either rows or columns of four poles baited on each trial. The bottom panel of Figure 1 shows an example of a pattern of poles for a rat assigned to have rows baited.

We randomly determined the particular row (or column) of poles baited on each trial. In addition, we randomized the orientation of the apparatus relative to extraapparatus cues using the same procedure we had used in Experiment 1. To begin each trial, we placed the rat in the open area at the end of the box. It was then free to choose poles until it had chosen all four or five baited poles or 10 min had elapsed without a choice; we recorded the sequence of poles chosen. There were 5 trials per day, separated by 15 min. We tested each rat in 23–26 trials.
General Discussion

Together, the results of these two experiments indicate that rats can be controlled by, and therefore represent, simple spatial patterns. The location of discovered goals clearly affected rats' subsequent choices in a manner that was consistent with the spatial pattern in which locations were baited. Although the results of Experiment 1 could have been explained in terms of spatial generalization from an average or combination of previously discovered baited locations, the results of Experiment 2 ruled out this possibility. Therefore, the results are best explained in terms of control by a representation of the spatial pattern.

The spatial pattern rapidly acquired control over the rats' performance, and this control was robust. In Experiment 1, control by the square pattern was apparent in the first block of 40 trials. In Experiment 2, control by the linear pattern was apparent even though the experiment was conducted only for approximately 25 trials. In both cases, the rats' tendency to choose a pole in accordance with the pattern was substantially greater than that expected on the basis of chance. This phenomenon and analytic technique thus present a promising avenue to detailed exploration of spatial representations in rats.

The conclusion that the rats represented the spatial patterns used in these experiments complements previous work suggesting that rats represent serial patterns of quantity (e.g., Fountain, 1990; Fountain & Hulse, 1981; Hulse & Dorsky, 1977, 1979) and represent temporal relations among events in an organized, systematic fashion (Honig, 1981).

Of course, the present work is most closely related to research suggesting the existence of representations of spatial relations, or "cognitive maps" (e.g., Brown, Rish, VonCulin, & Edberg, 1993; O'Keefe, 1991; O'Keefe & Nadel, 1979; Roberts, 1984). However, an important difference between the cognitive-map view of radial-arm maze performance and the conclusions following from the present work is that most of the findings suggesting representation of spatial relations in the radial-arm maze have to do with the relations among extramaze cues, which are thought to define the spatial framework guiding the rats' behavior. The present experiments, on the other hand, show that rats can also represent spatial relations among the locations of the hidden goals themselves. The only precedence for this in the radial-maze literature appears to be Dallal and Meck's (1990) study, in which transfer of performance was facilitated if the spatial pattern of never-baited arms was maintained from one extramaze environment to a second (test) environment. Thus, the present results converge on the implication of Dallal and Meck's results that the geometric pattern of the baited (or of the never-baited) locations can control performance. A less closely related precedent for the representation of spatial relations among goals is the work of Menzel (1978), whose results can be interpreted as evidence that chimpanzees represented the spatial relations among locations where food was hidden.

The conclusions following from the present experiments should be distinguished from those having to do with the use of multiple landmarks to locate a single goal. Cheng's

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Figure 7. Two measures of the rats' ability to locate baited poles efficiently in Experiment 2. The top panel shows the mean number of choices the rats made between the beginning of a trial (B) and their discovery of the first baited pole (1), their discovery of the first baited pole and their discovery of the second baited pole (2), and so on. The bottom panel shows the proportion of these transitions in which the rat moved immediately to the next baited pole (i.e., with no other choices intervening).
(1989) vector sum model is the clearest example of this type of model. Cheng provided evidence that the locations of several landmarks, relative to a single hidden goal, were combined to allow the goal to be located. These landmarks were visible, their direction and distance from the subject’s current location were hypothesized to be determined by the system, and stored knowledge regarding their location relative to the goal was used to locate the goal (see also O’Keefe, 1991). The conclusions that follow from the present results are quite different. The present results imply that the spatial relations among multiple hidden goals are part of the stored representation used to locate those hidden goals. In the present experiment, no landmarks were available to assist the rats in using the geometric pattern to locate goals. Although on any particular trial extraapparatus cues or the location within the apparatus itself could serve as a cue to the rat’s location, the rat’s ability to direct its search toward baited poles after discovering baited poles was independent of its location in the apparatus or in the extraapparatus environment. The location of possibly baited poles was defined jointly by the location of previously discovered poles and the spatial relations among baited poles, as experienced by the rat during earlier trials.

Understanding the mechanism(s) rats use to acquire knowledge of spatial relations among hidden goals will require additional experimentation. However, at minimum, it would seem to require that the location of previously discovered poles be stored during each trial in a working memory and that the spatial relation between previously discovered poles and poles discovered subsequently then be encoded in a more permanent memory system that can guide choices during later trials.

References


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