

# Spatial patterns and memory for locations

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Rats obtained food from the tops of vertical poles in a  $5 \times 5$  matrix of locations. On each trial, the baited locations formed one of the two possible exemplars of a checkerboard spatial pattern. During training, locations that had been visited earlier in the trial were indicated by a visual cue. Following training, performance with and without the visual cues was compared. Spatial choices were controlled by the checkerboard spatial pattern. The visual cues enhanced the ability of rats to avoid revisits of locations. However, the visual cues did not enhance control by the spatial pattern, as would be expected if the same spatial memories were involved in avoidance of revisits and coding the location of baited locations.

A series of experiments in our laboratory has shown that spatial choices in rats can be controlled by the spatial relations among discrete locations containing hidden food items (Brown, DiGello, Milewski, Wilson, & Kozak, 2000; Brown & Terrinoni, 1996; Brown, Yang, & DiGian, 2002; Brown, Zeiler, & John, 2001; DiGello, Brown, & Affuso, 2002; Lebowitz & Brown, 1999). In these experiments, rats search for single food pellets hidden on top of vertical poles in a matrix of poles. No visual or other perceptual cues are available to indicate the location of the poles that are baited on a particular trial, and the location of the baited poles changes unpredictably over trials. However, there are consistent spatial relations among the baited poles, and the critical finding is that such spatial patterns come to control the choices made by the rats, thereby increasing the efficiency with which they locate the baited poles. We have found evidence for control by square (e.g., Brown & Terrinoni, 1996), linear (e.g., DiGello et al., 2002), and checkerboard (Brown et al., 2001) patterns of baited poles. Dallal and Meck (1990) reported evidence for similar control of choices by the spatial configuration of baited arms in the radial maze (but see Olthof, Sutton, Slumskie, D'Addetta, & Roberts, 1999).

Much of the spatial learning and memory literature concerns the mechanisms involved in using perceptual cues as beacons or landmarks to guide behavior to a goal location. In contrast, a critical feature of the spatial pattern learning that has been investigated using the pole box paradigm is that the content of the learned spatial pattern cannot be in terms of, or anchored to, perceptual cues, because the placement of the baited locations with respect to such cues changes unpredictably from trial to trial. Thus, for the spatial pattern to control choices, it

must be abstracted from the visual or other perceptual cues that specify the location of particular poles.

Our previous investigations have focused on the conditions that produce behavioral control by spatial patterns. That work was motivated by the hypothesis that exposure to consistent spatial relations among the baited poles results in an abstract representation of those spatial relations. However, a different set of questions involves the means by which rats use the learned spatial pattern to locate baited locations. Once a representation of the spatial pattern has been acquired, it must affect performance by guiding choices to poles that are relatively more likely to be baited. This analysis indicates that two distinct sets of processes are involved in the control of choices by spatial patterns: First, acquisition of a representation of the pattern occurs over trials. The resulting representation is independent of perceptual cues and the location of particular poles. Second, within each trial the rat must keep track of visited locations and use information about their locations and bait statuses, combined with the acquired representation of the abstracted spatial pattern, to guide choices to the remaining baited poles. Consider the case of a  $2 \times 2$  square pattern of baited poles within a  $5 \times 5$  matrix, for example. Choosing 1, 2, or 3 of the 4 baited poles can allow the rat to determine the location of the square within the larger matrix (i.e., to determine which of the 16 possible exemplars of the square pattern is present on that particular trial), but only if the location of those baited poles is coded in memory.

So far, we know little about the processes that allow rats to use the acquired representation of the spatial pattern to increase choice accuracy. Some information about the ways in which a learned pattern affects spatial choice performance was provided by DiGello et al. (2002). In their experiment, the rats exposed to a row pattern (one of five rows of poles was baited on each trial) were more likely to choose poles in the same row following choice of a baited pole and more likely to choose poles in a different row following choice of an unbaited pole. This finding indicates that the representation of the row pat-

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tern can guide choices away from unbaited rows as well as encourage choices to remain in the baited row once it is located.

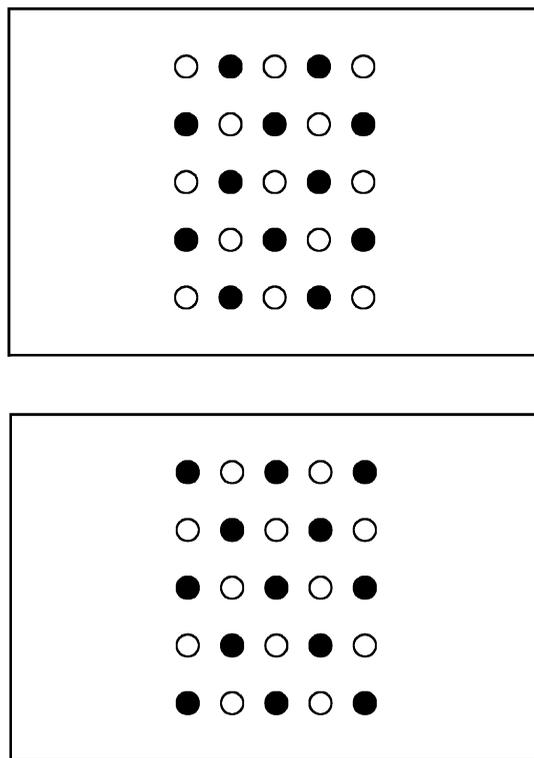
Using a learned spatial pattern to increase choice accuracy requires discrimination of the location of poles that have been visited during the current trial and their status as baited or unbaited. In the case of a square pattern, for example, Brown and Terrinoni (1996) showed that a rat that had located the two baited poles forming one side of the square was then more likely to choose a pole indicated by the square pattern than a pole not indicated by the pattern. This is possible only if the locations of the two baited poles discovered earlier in the trial are coded and remembered. It is well-known that rats discriminate previously visited locations from those not yet visited in multiple-location spatial tasks. In the radial-arm maze, for example, rats avoid revisits to previously visited arms of the maze with a high degree of accuracy (Olton & Samuelson, 1976). Although the tendency to avoid revisits in the pole box task does not appear to be as strong, it is clear that rats have a corresponding ability to avoid revisiting locations in this task as well (e.g., Lebowitz & Brown, 1999).

The present experiment examines the relationship between control of choices by a spatial pattern and the ability/tendency of the rat to avoid revisits to poles. Accurate choice in the pole box task requires that the rat discriminate and remember the locations of previously visited poles for two reasons. First, avoiding revisits to those locations would increase choice accuracy directly. Second, the location of previously visited poles, in combination with information about whether those poles were baited, seems necessary for the represented pattern to guide choices to additional baited poles. But are these two functions of remembering the locations of baited poles based on the same spatial memories?

We have recently argued that pattern learning is independent of visual cue learning (Brown et al., 2002) based on the lack of overshadowing of control by a square pattern when redundant, relevant visual cues are available. We have also argued that spatial pattern learning and serial pattern learning have at least some important processes in common, based on the facilitation of spatial pattern learning by a coincident serial pattern (Brown, DiGian, Fabian, & Smith, 2003). In both cases, the presence or lack of an interaction between control by a spatial pattern and another factor that might control spatial choices was taken to indicate commonality or independence of psychological mechanism, respectively. Analogous logic underlies the present experiment. We manipulated a variable that was expected to (and did, in fact) affect the ability of rats to avoid revisits to poles. If the same memories for the locations of previously visited poles are involved in the use of spatial pattern information, then control by spatial patterns should also be modulated by that variable.

In the present experiment, rats were exposed to a checkerboard pattern in a  $5 \times 5$  pole box. As illustrated

in Figure 1, the checkerboard pattern of baited poles has two exemplars. The checkerboard pattern exemplar in force on each trial was unpredictable. Thus, it was not possible to learn to choose particular poles on the basis of visual landmarks. Control by the checkerboard pattern was assayed using measures developed by Brown et al. (2001). In the pole box apparatus, rats have a fairly strong tendency to choose poles that are spatially adjacent to the pole most recently chosen. With a checkerboard pattern in force, such choices are reinforced only following choice of an unbaited pole. Brown et al. (2001) showed that choices of poles adjacent to the last pole chosen become less likely when the most recently chosen pole was baited, whereas different kinds of choices (that are reinforced following choice of a baited pole) became more likely. These results provide evidence that choices are controlled by the checkerboard pattern. There are at least two different possible mechanisms of such control. Brown et al. argued that at least in part, this control must be based on an abstracted representation of the spatial relations among the baited poles rather than on learned response tendencies that correspond to the pattern. The evidence came from transfer of control following training in which only some poles in the matrix were accessible. In such transfer tests, rats demonstrated response tendencies that were consistent with the checkerboard



**Figure 1.** Filled symbols represent baited poles in a  $5 \times 5$  pole box baited in a checkerboard pattern. The pattern exemplar on each trial is chosen randomly from the two possibilities.

pattern, even though they had not had an opportunity to learn those response tendencies. For purposes of the present experiment, on the basis of Brown et al.'s (2001) evidence, we assume that control by the checkerboard pattern is based on a representation of the spatial relations of which the pattern is composed.

It was expected that evidence for control of choices by the checkerboard pattern would be obtained. The focus was on the need to remember the location of previously chosen poles during each trial in order to utilize knowledge of the checkerboard pattern. The first choice on each trial cannot be more accurate than expected by chance (50%). However, knowledge of the checkerboard pattern combined with memory of the location of the first pole chosen and its bait status (baited vs. unbaited) would provide sufficient information to allow subsequent choices to be directed to baited poles.

During training, a visual cue was provided that distinguished poles previously visited during the trial from poles not yet visited. During the test phase of the experiment, this cue was available only during half of the trials. It was expected that the presence of the visual cues would increase the ability of the rats to avoid revisits to poles. The central question was whether control by the spatial pattern would be facilitated by these cues. If the same spatial memory for pole locations is involved in the ability of rats to avoid revisits to poles and to remember the location(s) of previously visited pole(s) that specify which of the two exemplars of the checkerboard pattern is in force, then cues identifying those locations should facilitate both of these abilities.

## METHOD

### Subjects

Twelve male Sprague Dawley rats (Harlan Sprague Dawley, Indianapolis, IN) began the experiment. They were housed on a 12:12-h reverse light:dark cycle and were tested during the dark phase of the cycle. Starting 2 weeks prior to the experiment, food (Lab Diet 5012; PMI Nutrition, Brentwood, MO) intake was restricted so that each rat was maintained at 85%–95% of normal body mass. Ad-lib access to water continued. Food restriction began with 12 g of food per day, and diets were adjusted to maintain the target body mass. Changes in normal body mass with age were calculated and accounted for using growth curves provided by the vendor. The rats were approximately 4 months old when training began.

### Apparatus

The pole box apparatus used in this experiment (Figure 2) was similar to that used by Brown and Terroni (1996). The pole box apparatus was a 1.17-m square arena surrounded by a wall 37 cm tall. The bottom 14 cm of the wall was constructed of 2.0-cm thick plywood and painted flat black (as was the floor of the arena). The top 23 cm of the wall was constructed of Plexiglas. One wall of the pole box was attached to a wall of the laboratory room in which the apparatus was housed. The top of the box was open. A 19 cm × 15 cm start box was attached to the outside of the arena, opposite the laboratory wall. A metal guillotine door could be operated remotely (via a string and pulley system) to allow the rat to enter the apparatus from the start box.

There was a 5 × 5 matrix of 16.5-cm tall poles centered in the arena. The base of each pole was a translucent funnel turned upside

down, such that the 8.5-cm diameter funnel was centered over an 8.0-cm diameter hole in the floor of the arena. A combination of polyvinylchloride (PVC) and foam components formed the top of each pole, which was attached to the funnel base by an inner core of wooden dowel. The top of each pole was a 5.3-cm diameter white PVC connector ("Duraplex" D2464, Consolidated Plumbing Industries). The PVC connector surrounded a 0.8-cm thick foam ring, which surrounded a 0.6-cm thick inner PVC ring. The PVC ring formed the wall of a 1.0-cm deep, 1.2-cm diameter well. The top edge of this well was flush with the other components of the pole top. The floor of the well was formed by nylon mesh, under which there was a single reinforcement pellet, from the same source as those used to bait the poles (Noyes 45-mg black sucrose pellets, Product F05480). This "sham" pellet was not accessible to the rat and was included as a control for odor cues. It was changed weekly. The poles in each row or column of the matrix were separated by 21.0 cm (center to center).

An additional training apparatus was placed inside the box during the early phases of training. This apparatus consisted of a single row of increasingly tall poles (2.0 cm, 4.5 cm, 12.5 cm, and 15.5 cm), separated by 7 cm.

A video camera was mounted directly above the pole box such that its field of view provided an overhead view of the matrix of poles. The image provided by this camera fed into a video cassette recorder, allowing a video record of each trial to be obtained. The image also fed into a computer, via an Intel PC Camera Pro and its corresponding software driver. The image provided by the camera was processed by a program written using the Microsoft Visual Basic (version 6) programming language and the CapturePro control (Pegasus Software). This combination of hardware and software allowed the image from the video camera to be captured at a rate of approximately 20 Hz.

Choices were defined by an experimenter who monitored the image provided by this system. A choice was defined when any part of the rat (although this was, in fact, always the rat's snout) impinged on the perimeter of a pole top formed by the PVC connector. The experimenter designated each choice by placing the computer mouse cursor on the image of that pole and clicking. Under some conditions (as described below), this procedure resulted in a visual stimulus corresponding to that pole. A computer data (LCD) projector (Sony Model XG-E1100U) projected an image via a mirror onto the bottom of the apparatus. The image could include white circles projected onto the holes underneath any of the poles. Because of the translucent material of the funnels (of which the base of each pole was constructed), the poles could be individually illuminated. This process is illustrated in the inset of Figure 2. Thus, as the rat made choices, poles at particular locations could be illuminated or not illuminated in accordance with the behavior of the rat. Poles would either change from being illuminated to nonilluminated ("turn off") or vice versa ("turn on") when the rat chose that particular pole. The program also recorded the sequence of choices and the latency of each choice.

### Pretraining Phase

The pretraining phase began with the provision of 10–20 pellets (Noyes 45-mg black sucrose pellets, Product F05480) to each rat for 3 days in its home cage. This procedure ensured that the rats were familiar with the reward. Starting on the following day, each rat was placed in the pole box with access only to the training apparatus and two rows of poles. The other three rows of poles were not present, and were replaced with a false floor. The training apparatus was placed in the center of the arena. Each of the four poles of the training apparatus was baited with a single pellet, as were the poles in the two remaining rows. On the first day of exposure to the pole box, pellets were also scattered on the floor of the arena near the poles. The rats were allowed to explore the apparatus for 10 min or until the pellets in the training apparatus had all been consumed. This phase continued for three daily trials.



**Figure 2.** The pole box apparatus used in the present experiments. The inset shows poles illuminated and nonilluminated.

### Training Phase

For each trial, one of the two exemplars of the checkerboard pattern (i.e., either the 13 “odd numbered” poles or the 12 “even numbered” poles) was randomly chosen, and the corresponding poles were each baited with a single pellet. For half of the rats, all of the poles were illuminated at the beginning of every trial, and for the remaining half, the poles were dark at the beginning of every trial.

Each rat was first placed in the start box and, after approximately 5 sec, the start box door was opened remotely by the experimenter, allowing the rat to enter the arena. The experimenter observed the image of the pole box provided to the computer by the camera mounted directly above the box. When the rat impinged on the outer boundary of a pole (which could only happen when the rat reared up to investigate the contents), the experimenter indicated a choice of that pole using the computer mouse. In addition to providing a record of the location of the pole chosen by the rat, this mouse click resulted in a change in the illumination status of the pole: For the rats starting with all poles illuminated, choice of the pole removed the illumination, whereas for the other rats, choice of the pole resulted in its being illuminated.

The rat was allowed to choose poles until all (12 or 13) baited poles had been chosen or 10 min had elapsed since the beginning of the trial. Each rat experienced 48 daily trials.

### Test Phase

Ten daily trials were conducted during the test phase of the experiment. Five of those trials (randomly chosen for each rat) were just like the training trials. During the remaining half of the trials, there was no change in illumination status when the rat chose a pole; instead, the illumination status of poles remained as it was at the beginning of the trial.

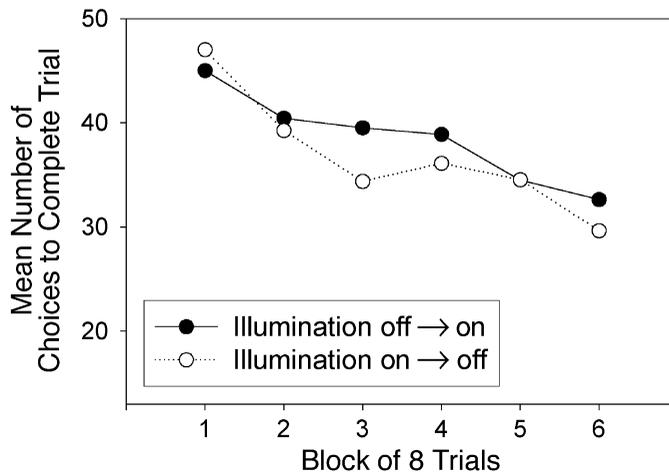
## RESULTS

### Training Phase

The first analysis determined that improvement in performance took place over the course of the training phase of the experiment. Figure 3 shows the mean number of choices taken to choose all 12 (or 13) baited poles

over the course of six blocks of eight trials each. Data are shown separately for the 6 rats for which choices produced pole illumination and for the 6 others for which choices removed illumination. It should be noted that only trials in which the rat chose all of the baited poles within 10 min are included. That result occurred during means of 2.9, 7.8, 7.6, 7.7, 7.9, and 7.9 of the eight trials during Blocks 1–6, respectively. A group  $\times$  block analysis of variance (ANOVA; mixed design) provided evidence of a difference in the number of choices required to locate the baited poles over the trial blocks [ $F(5,40) = 9.5$ ; the decision criterion for all analyses in this article was  $p < .05$ ]. There was no evidence for a difference depending on the illumination change condition [ $F(1,8) = 1.16$ ] and no interaction between the effects of these variables [ $F(5,40) < 1$ ]. Because the nature of the pole illumination change did not have an effect on performance, this variable was not included in subsequent data analyses.

Evidence for acquisition of control by the checkerboard pattern was obtained using the logic and measure developed by Brown et al. (2001). The measure is based on the spatial relations among poles that are the targets of consecutive choices. As the rats make choices in the pole box task, they most commonly choose a pole that is spatially adjacent to the most recently chosen pole. Rats also commonly move from a pole to another that is separated by one intervening pole (in a row or column) from the most recent choice or move to a pole that has a “diagonal” relation to the most recently chosen pole. These three choice transitions are illustrated in Figure 4, and are referred to as “adjacent,” “skip,” and “diagonal” moves, respectively. With a checkerboard pattern in force, it is advantageous for the rat to make relatively more adjacent moves following choice of an unbaited pole, and rela-



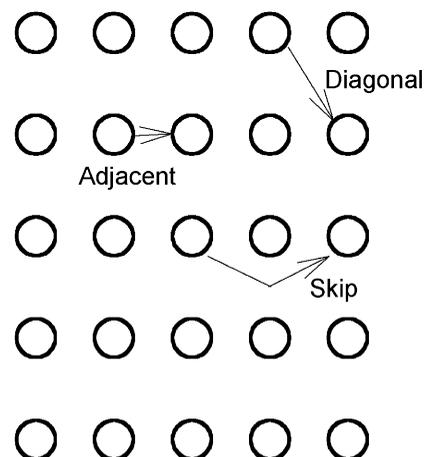
**Figure 3.** The mean number of choices taken to complete trials over the course of the training phase of the experiment. Data are shown separately for the conditions in which the pole base was illuminated and in which illumination was removed when a pole was chosen.

tively more skip and diagonal moves following choice of a baited pole. An increase in these tendencies with exposure to the pattern is taken as evidence for behavioral control by the pattern.

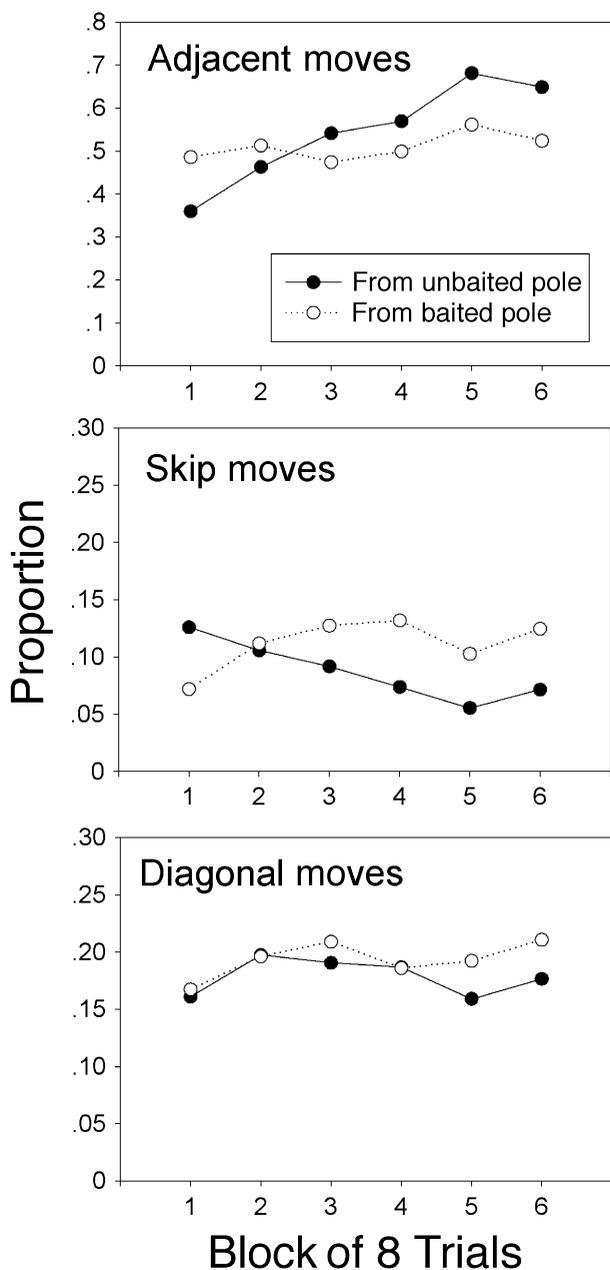
Figure 5 shows the proportion of choice transitions (“moves”) for each of the three types of interest. It is important to note that these choices are only those that followed the first choice of a particular pole. Moves that followed a revisit of a pole are not included in this analysis, because of the ambiguous status of a revisited pole that had been baited at the beginning of the trial. The proportions are shown separately for choices immediately following choice of an unbaited versus a baited pole. A block  $\times$  move type  $\times$  bait status ANOVA revealed a three-way interaction among the effects of these variables [ $F(10,110) = 8.4$ ]. Interpretation of interactions among effects that include move type must be tempered because, given that most choices made involved moves of these three types, values for the three move types are not independent. Thus, values for the three move types were analyzed separately. For adjacent moves, there was an interaction between the effects of block and bait status [ $F(5,55) = 12.2$ ]. This interaction can be attributed, at least in part, to an increase in the probability of adjacent moves following choice of an unbaited pole [ $F(5,55) = 17.6$ ]. There was no evidence for a change in the probability of adjacent moves following choice of a baited pole [ $F(5,55) = 1.9$ ]. For skip moves, there was also an interaction between the effects of block and bait status [ $F(5,55) = 6.67$ ], which can be attributed to both a decrease in the probability of skip moves following choice of an unbaited pole [ $F(5,55) = 4.5$ ] and an increase in the probability of skip moves following choice of a baited pole [ $F(5,55) = 2.53$ ]. For diagonal moves, there was no evidence for an interaction between the effects of block and bait status [ $F(5,55) < 1.0$ ]. Thus,

the probability of move types changed over blocks in a manner predicted if the checkerboard pattern acquired control of choices, at least for adjacent and skip moves.

The ability of the rats to avoid revisits to poles already chosen, and the acquisition of that ability, was examined in terms of the number of choices per trial of poles that had been chosen earlier. Because such revisits were quite rare early in the trial, this measure was calculated separately for the first 12 choices of each trial and for subsequent choices (12 being the minimum number of choices required to complete a trial). Values for the first block



**Figure 4.** A schematic illustration of three spatial relationships between consecutive choices and the corresponding “move types” used in measuring behavioral control by the checkerboard spatial pattern. Given the checkerboard pattern, adjacent moves following choice of an unbaited pole and skip or diagonal moves following choice of a baited pole are consistent with the pattern in which poles are baited.



**Figure 5.** The mean probabilities of adjacent (top panel), skip (middle panel), and diagonal (bottom panel) moves over the eight trial blocks of the training phase following choice of an unbaited or a baited pole.

were unusually low and not comparable to values for the later blocks, due to the fact that the rats often failed to complete trials during the first block (see above). Thus, data from Block 1 were not included in the analyses of the results. The mean (over rats) values of this measure are shown in Figure 6. The figure shows the mean number of choices per trial as a function of whether poles were baited or unbaited at the beginning of the trial and whether they were novel (not previously visited during

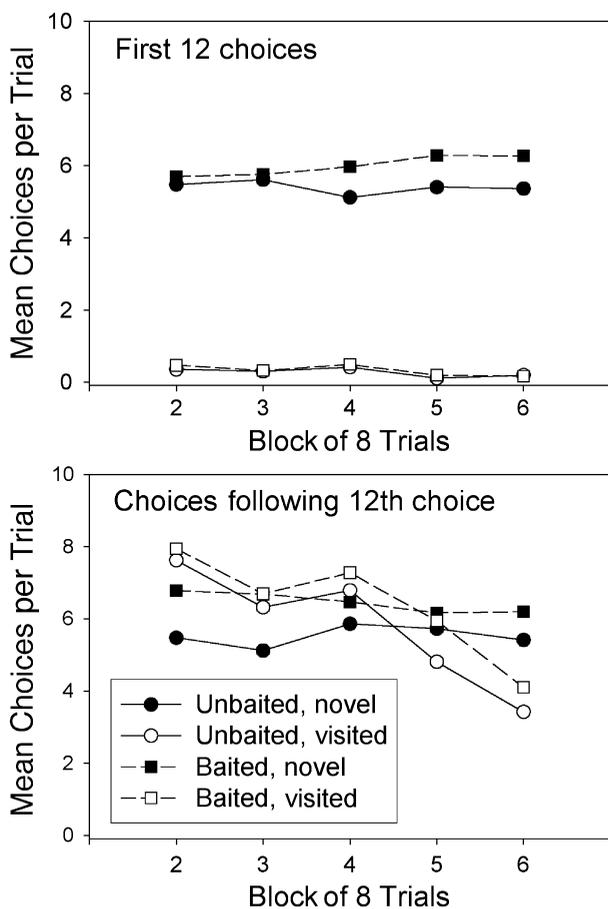
the trial) or previously visited. Note that only choices to novel, baited poles are “correct” in the sense of resulting in pellet reinforcement. Revisits were very rare during the first 12 choices, as would be expected even if the rats chose poles randomly. Thus, statistical analysis of these data was restricted to determining that among the choices of novel poles, there were more choices of correct (baited) than of incorrect poles [ $F(1,11) = 24.7$ ] and that this difference increased over the course of blocks as shown by a bait status  $\times$  blocks interaction [ $F(4,44) = 7.6$ ]. Analysis of choices following the 12th choice (bottom panel of Figure 6) allowed the rats’ abilities to choose correct poles and to avoid revisits to be independently evaluated. A blocks (2–6)  $\times$  previous visit status  $\times$  original bait status ANOVA demonstrated an effect of blocks [ $F(4,44) = 11.8$ ] that was due to a decrease in the total number of choices made over the course of Blocks 2 through 6 [linear contrast:  $F(1,11) = 63.1$ ]. Poles baited at the beginning of a trial received more visits than those that were not baited [ $F(1,11) = 122.5$ ], and there was no main effect of visit status [ $F(1,11) < 1$ ]. However, there was an interaction between visit status and block [ $F(4,44) = 14.9$ ]. No other interaction terms were significant.

To understand the interactions among the effects of the variables, a block  $\times$  bait status ANOVA was performed at each level of visit status. In the case of poles that had not been previously visited, there was a significant effect of block [ $F(4,44) = 2.7, p = .04$ ]. However, linear contrasts did not identify a linear trend as responsible for this effect [ $F(1,11) = 3.7$ ]. Baited poles were visited more often than unbaited ones [ $F(1,11) = 59.9$ ]. An interaction between the effects of bait status and block [ $F(4,44) = 4.6$ ] appeared to be due to a diminished effect of bait status as training progressed. In the case of poles that had been visited earlier in the trial, there was an effect of block [ $F(4,44) = 13.4$ ] due to a decrease in the number of revisits over blocks [linear contrast:  $F(1,11) = 78.0$ ]. Poles that had been baited at the beginning of the trial (but were no longer baited due to having previously been visited) were visited more often than poles that had not been baited at the beginning of the trial [ $F(1,11) = 14.1$ ]. There was no evidence for an interaction between the effects of bait status and block [ $F(4,44) < 1$ ].

### Test Phase

On the first choice of each trial, the rats chose a baited pole during a mean of 47.5% of the trials (50% would be expected by chance). This result confirms that there were no perceptual cues indicating which of the poles were baited.

Control by the checkerboard pattern was assessed in the test phase using an analysis of adjacent, skip, and diagonal moves analogous to that described above for the training phase. The mean values are shown in Figure 7 for trials with the light cues present and absent; mean values were evaluated using a cue condition  $\times$  move type  $\times$  bait status ANOVA. Critically, there was no effect of



**Figure 6.** The mean number of initial choices and revisits made to poles that were baited and unbaited at the beginning of the trial during the training phase of the experiment. Data are shown separately for the first 12 choices of trials (top panel) and choices following the 12th choice (bottom panel). Data from Block 1 are not included because the rats failed to complete most trials during that trial block.

cue condition nor any interactions between cue condition and other factors (all  $F$ s < 1). The signature of control by the checkerboard pattern—the interaction between the effects of move type and bait status—was significant [ $F(2,24) = 75.8$ ]. This interaction was probed using bait status  $\times$  cue condition ANOVAs for each of the three move types. Adjacent moves were more likely following choice of an unbaited rather than a baited pole [ $F(1,12) = 162.1$ ]. Skip moves and diagonal moves were more likely following choice of a baited rather than an unbaited pole [ $F(1,12) = 61.8$  and  $F(1,12) = 7.8$ , respectively].

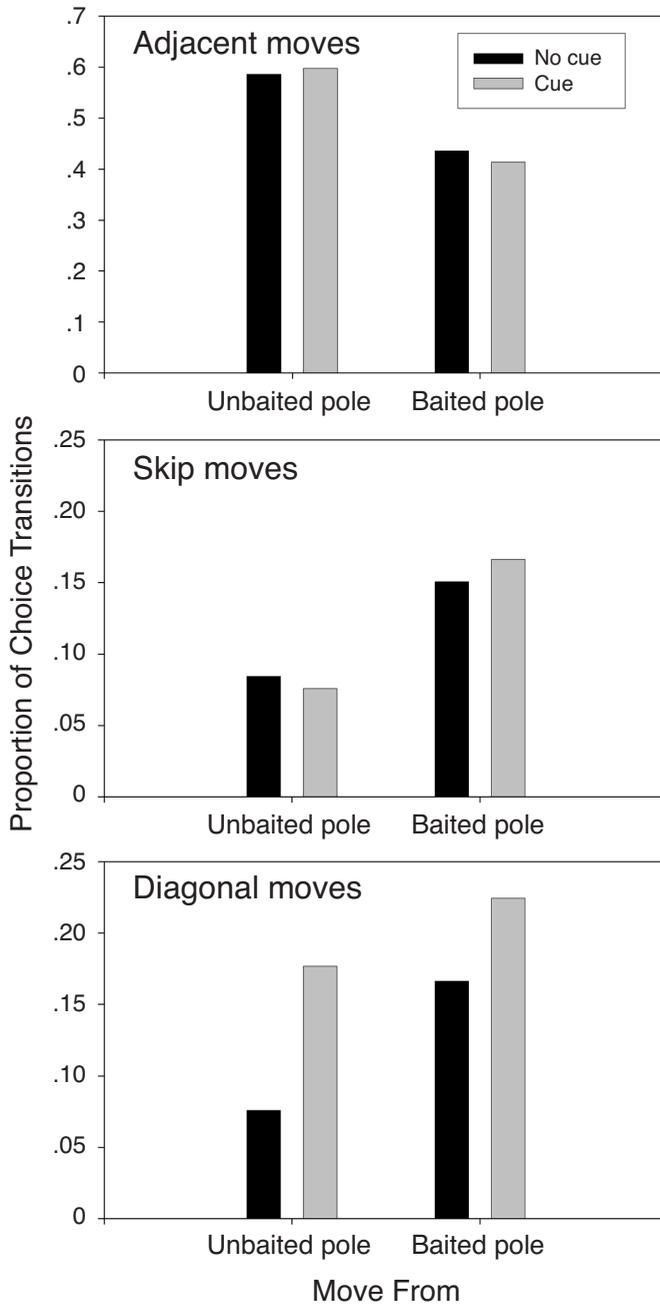
As in the training phase, the ability of the rats to avoid revisits to poles already chosen during the test phase was examined in terms of the number of choices per trial of poles that had or had not been chosen earlier in the trial. The mean (over rats) numbers of choices made on trials with or without cues present are shown in Figure 8. Choices of poles that were initially baited or unbaited are

reported separately for initial choices and for revisits of poles already chosen during a trial. Mean values are shown separately for the first 12 choices (top panels) and choices following the 12th choice (bottom panels). As in the training phase, revisits to poles were quite rare early in the trial, so the focus of analysis was on choices made following the 12th choice. A trial type (light cues present vs. absent)  $\times$  bait status  $\times$  visit status (initial visit to a pole vs. revisit) ANOVA was used to evaluate the relative numbers of choices made following the 12th choice. This analysis revealed higher numbers of choices in the cue absent than in the cue present trials [ $F(1,11) = 83.0$ ], more choices of poles that were baited at the beginning of the trial than of those initially not baited [ $F(1,11) = 123.7$ ], and more choices of poles not previously visited than of revisits [ $F(1,11) = 42.7$ ]. No evidence emerged of a three-way interaction among the effects of these variables [ $F(1,11) < 1$ ], of an interaction between trial type and bait status [ $F(1,11) < 1$ ], nor of an interaction between bait status and visit status [ $F(1,11) = 4.6$ ,  $p = .06$ ]. There was, however, an interaction between the effects of trial type and visit status [ $F(1,11) = 78.0$ ]. We probed this interaction using two bait status  $\times$  visit status ANOVAs. In the case of trials with no light cues, the poles baited at the beginning of a trial received more visits than did those not baited [ $F(1,11) = 52.9$ ]. However, there was no evidence of a difference in the number of visits to novel poles and revisits [ $F(1,11) = 2.0$ ] or of an interaction between the effects of these variables [ $F(1,11) = 1.6$ ]. In the case of trials with light cues, the poles baited at the beginning of a trial received more visits than those not baited [ $F(1,11) = 49.2$ ], and there were more visits to novel poles than revisits [ $F(1,11) = 200.5$ ]. There was no evidence of an interaction between the effects of these variables [ $F(1,11) = 3.2$ ].

## DISCUSSION

The rats' performance in this experiment improved substantially over the course of training, although it never approached perfection, which would require approximately 13 choices to complete each trial (the first choice is expected to be an unbaited pole on half of the trials and, in principle, the remaining choices should be all remaining baited poles). The level of choice accuracy found in this experiment is consistent with that found in our previous work using spatial patterns of baited poles in the pole box task. Control of choices by the checkerboard pattern is clearly shown by the different distributions of adjacent, skip, and diagonal moves following choice of baited and unbaited poles during both the training and testing phases of the experiment. This tendency for rats to choose poles that are consistent with the checkerboard pattern replicates the earlier findings of Brown et al. (2001).

It is also clear that the rats were controlled by the visual cues distinguishing previously visited and unvisited poles. In the test phase of the experiment, rats made

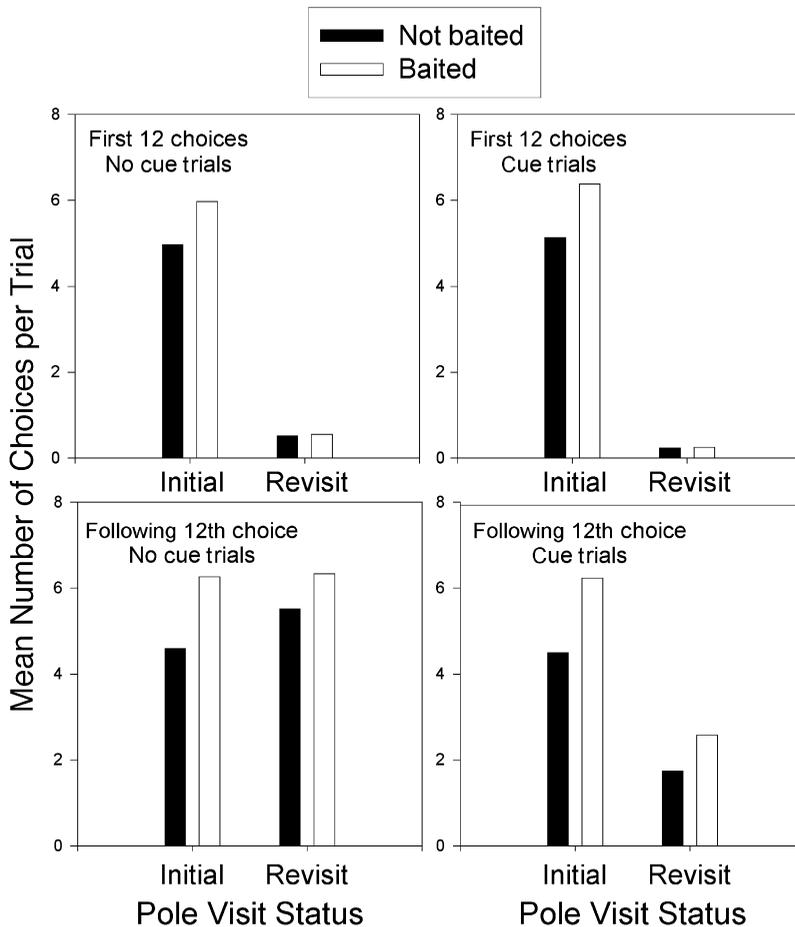


**Figure 7.** The mean probability of adjacent (top panel), skip (middle panel), and diagonal (bottom panel) moves during the test phase following choice of an unbaited or of a baited pole during trials with the light cues absent or present.

more than twice as many pole revisits during trials without visual cues as during trials with cues. It is important to emphasize that the visual cues were not reliable predictors of the presence or absence of food on the poles, as only half of the poles were baited at the beginning of each trial. The cues instead distinguished the poles that had been visited earlier during the trial from those that had not. Thus, the diminished ability of the rats to avoid re-

visits of poles during the test phase of the experiment when cues were not present indicates that the cues were functioning as an indication of the location of previous visits.

Of primary interest is the relationship between the improved ability to avoid revisits that the cues allowed and control of choices by the checkerboard pattern. According to the view of spatial pattern learning outlined in the introduction, the checkerboard pattern results in an ab-



**Figure 8.** The mean number of initial choices and revisits made to poles that were baited or unbaited at the beginning of the trial during the test phase of the experiment. Data are shown separately for the first 12 choices of trials (top panels) and choices thereafter (bottom panels) and for choices during light-cue absent trials (left panels) and light-cue present trials (right panels).

stract representation that is not anchored to specific locations. During each trial, the pattern exemplar in force must be determined as the rat visits specific poles and determines whether they are baited. Working memory for these locations, in combination with the learned spatial pattern, allows choices to be directed to remaining baited poles. This view predicts that if information about the original status of a pole as baited or unbaited and information about previous visits to poles are both coded in the same memory, then the facilitation provided by the visual cues corresponding to visited poles should allow the pattern to better guide choices to baited poles, because rats can better remember the location of the pattern elements (baited poles) found earlier in the trial.

Simply stated, there is no evidence for any such relationship. In particular, we found no evidence that the distributions of move types following choice of baited versus unbaited poles were modulated by the presence of the cues. This finding provides evidence that control of choices by the checkerboard pattern and by the location of previously visited poles are based on two independent processes.

Additional evidence for the independence of control by the checkerboard spatial pattern and by previous visits to particular poles comes from the fact that the tendency to visit poles that were elements of the pattern exemplar more often than poles that were not was not modulated by previous visits to the poles. Rather, this tendency remained stable as the tendency to avoid revisits to poles developed (Figure 6), and it was not modulated by the presence or absence of cues during the test phase of the experiment. Thus, although the rats demonstrated an ability to avoid revisits, the ability to choose poles that conformed to the checkerboard pattern was not affected by previous pole visits. The additive relationship between the effects of these factors in determining the choices made by the rats indicates that the factors were based on independent processes.

Why would memories for pole locations that allow rats to avoid revisits be independent from memories that allow rats to track the status of those locations as spatial pattern elements? We propose that a common set of spatial working memories that served both of these func-

tions would be problematic, because the content of such memories would involve an intrinsic conflict. Avoidance of revisits of spatial locations has been explained in terms of the location being coded as an item in working memory (Olton, 1978) or in terms of a tag on a more comprehensive representation of the experimental environment (i.e., a “cognitive map”; Gallistel, 1990). Regardless of their structure, such memories reduce the likelihood of revisiting locations later during a trial by means of a response alternation tendency (e.g., Gaffan & Davies, 1982). Although the mechanism by which such spatial working memories reduce the likelihood of revisits is not known, one clear possibility is that they code the fact that food is no longer available at that location. The memories of pole visits required for spatial patterns to control choices, on the other hand, must identify the location of poles that were found to be baited earlier in the trial. Thus, the content required for these two spatial working memory functions conflicts. In terms of avoiding revisits to poles, the fact that visited poles are depleted of any food should control behavior; in terms of using the spatial pattern to increase search efficiency, the fact that some visited poles *were* baited should control behavior. Roberts (2002) has recently argued that a difference between human and animal cognition is that animals are unable to discriminate the temporal features of events (i.e., *when* an event occurred). This theory suggests an inability to code both the present and original bait status of a location in the same memory. The present data suggest that for locations originally baited but currently depleted, this conflict requires the use of two independent spatial working memory systems: One system allows the rat to avoid revisits, the other allows determination of the current spatial pattern exemplar.

## REFERENCES

- BROWN, M. F., DIGELLO, E., MILEWSKI, M., WILSON, M., & KOZAK, M. (2000). Spatial pattern learning in rats: Conditional control by two patterns. *Animal Learning & Behavior*, **28**, 278-287.
- BROWN, M. F., DIGIAN, K. A., FABIAN, S. A., & SMITH, W. (2003). *Spatial and serial pattern learning*. Unpublished manuscript.
- BROWN, M. F., & TERRINONI, M. (1996). Control of choice by the spatial configuration of goals. *Journal of Experimental Psychology: Animal Behavior Processes*, **22**, 438-446.
- BROWN, M. F., YANG, S. Y., & DIGIAN, K. A. (2002). No evidence for overshadowing or facilitation of spatial pattern learning by visual cues. *Animal Learning & Behavior*, **30**, 363-375.
- BROWN, M. F., ZEILER, C., & JOHN, A. (2001). Spatial pattern learning in rats: Control by an iterative pattern. *Journal of Experimental Psychology: Animal Behavior Processes*, **27**, 407-416.
- DALLAL, N. L., & MECK, W. H. (1990). Hierarchical structures: Chunking by food type facilitates spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, **16**, 69-84.
- DIGELLO, E., BROWN, M. F., & AFFUSO, J. (2002). Negative information: Both presence and absence of spatial pattern elements guide rats' spatial choices. *Psychonomic Bulletin & Review*, **9**, 706-713.
- GAFFAN, E. A., & DAVIES, J. (1982). Reward, novelty, and spontaneous alternation. *Quarterly Journal of Experimental Psychology*, **34B**, 31-47.
- GALLISTEL, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- LEBOWITZ, B. K., & BROWN, M. F. (1999). Sex differences in spatial search and pattern learning in the rat. *Psychobiology*, **27**, 364-371.
- OLTHOF, A., SUTTON, J. E., SLUMSKIE, S. V., D'ADDETTA, J., & ROBERTS, W. A. (1999). In search of the cognitive map: Can rats learn an abstract pattern of rewarded arms on the radial maze? *Journal of Experimental Psychology: Animal Behavior Processes*, **25**, 352-362.
- OLTON, D. S. (1978). Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 341-374). Hillsdale, NJ: Erlbaum.
- OLTON, D. S., & SAMUELSON, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, **2**, 97-116.
- ROBERTS, W. A. (2002). Are animals stuck in time? *Psychological Bulletin*, **128**, 473-489.

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