No evidence for overshadowing or facilitation of spatial pattern learning by visual cues

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Two experiments were conducted to examine the effects of redundant and relevant visual cues on spatial pattern learning. Rats searched for hidden food items on the tops of poles that formed a square (Experiment 1) or a checkerboard (Experiment 2) pattern. The experimental groups were trained with visual cues that specified the locations of the baited poles. All groups were tested without visual cues so that any overshadowing or facilitation of spatial pattern learning by visual cues could be detected. Spatial choices were controlled by the spatial pattern and by the visual cues in both experiments. However, there was no evidence of overshadowing or facilitation of spatial pattern learning by visual cues in either experiment. The results are consistent with the idea that the representation of the spatial pattern that guides choices is not controlled by the same learning processes as those that produce associations between visual cues and food locations.

An important empirical and theoretical issue in the study of learning is the manner in which one's learning about one cue affects learning about another cue. In most cases, one's learning about one cue competes with learning about other cues (i.e., overshadowing or blocking), and these cue competition effects have inspired and guided some of the most influential ideas about the mechanisms of learning (see, e.g., Rescorla & Wagner, 1972). In other cases, the presence of one cue can facilitate learning about a second cue. For example, taste cues have been found to facilitate learning about odor cues in food aversion learning (e.g., Rusiniak, Palmerino, Rice, Forthman, & Garcia, 1982).

Most studies of interactions among cues (i.e., cue competition or cue facilitation) have been done with the use of stimuli available in conditioning chambers. Recently, however, a number of investigators have expanded the range of stimulus types in studies of cue competition by examining cue interaction in the context of spatial learning paradigms. Rodrigo, Chamizo, McLaren, and Mackintosh (1997) reported that when rats learned about three discrete visual landmarks in the Morris water maze, learning about an additional (fourth) landmark was blocked. In experiments in which the same experimental paradigm has been used (e.g., Sánchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999), evidence has been found that an auditory cue can overshadow a visual landmark cue (and that the landmark overshadows the auditory cue). Blocking among spatial landmarks has also been reported in honeybees (Cheng & Spetch, 2001), and overshadowing has been reported among

spatial cues in a computer-display-based search task in pigeons and humans (Spetch, 1995).

Three studies of cue interactions in spatial learning are particularly relevant to the present experiments. Diez-Chamizo, Sterio, and Mackintosh (1985) examined cue competition effects involving intramaze and extramaze cues in the radial arm maze. They argued that the intramaze cues and extramaze cues corresponded, respectively, to the taxon and locale spatial learning processes distinguished by O'Keefe and Nadel (1978). The importance of this is that, if Diez-Chamizo et al. are correct about the correspondence of the two cue types to these processes (but see Biegler & Morris, 1999), any cue competition found would involve cues used by two distinct learning systems. Evidence for blocking of intramaze cues by extramaze cues, as well as blocking of extramaze cues by intramaze cues, was found. Interestingly, overshadowing occurred asymmetrically: Extramaze cues overshadowed intramaze cues, but not vice versa. Diez-Chamizo et al. noted that this pattern of results is consistent with cue competition effects reported in other (nonspatial) contexts.

Biegler and Morris (1999) argued that the blocking effect is diagnostic with respect to whether spatial learning phenomena can be explained in terms of standard associative processes. They reasoned that blocking among spatial landmarks would not be predicted by cognitive mapping theories (Gallistel, 1990; O'Keefe & Nadel, 1978; Tolman, 1948). By its very nature, a cognitive map would require that multiple, redundant cues be incorporated into the representation that controls spatial behavior. Biegler and Morris pointed out that there are complications involved in the design of cue competition experiments that are particular to spatial paradigms. Nevertheless, they found clear evidence for blocking of spatial landmarks by other spatial landmarks. Although this result would seem to support the view that spatial learning is based on standard as-

sociative processes, Biegler and Morris offered an alternative explanation for their results that appeals to spatially organized representations.

Pearce, Ward-Robinson, Good, Fussel, and Aydin (2001) reported a series of experiments designed to examine cue interactions between the shape of an escape pool (similar to the Morris water maze, but with a shape that allowed locations to be identified on the basis of that shape) and a visual beacon that, in some conditions, also identified the location of the escape platform. Pearce et al. found no evidence that the visual beacon overshadowed environmental shape as a cue to the location of the escape platform. In fact, there was some evidence that the presence of the beacon facilitated control by the shape of the pool. They argued that the lack of cue competition between shape and a visual beacon supports the idea of a separate learning system responsible for learning about locations as defined by the shape of an environment (the *geometric module* described by Cheng, 1986). The failure to find cue competition is important because, following the logic of Biegler and Morris (1999), it suggests that control by the visual beacon and control by the shape of the environment are the result of (at least somewhat) independent learning systems.

In the present experiments, we examined the issue of cue interactions in spatial learning in the context of spatial pattern learning in the pole box paradigm introduced by Brown and Terrinoni (1996). Rats search for food pellets hidden on top of poles in an array of vertical poles. Only some of the poles are baited. In the standard version of this task, there is no information about the identity of the baited poles at the beginning of each trial. However, the baited poles form a consistent spatial pattern in relation to each other. Thus, if rats learn the spatial pattern formed by the baited poles, discovery of one or more baited poles provides information about the location of the remaining baited poles. We have shown that several such spatial patterns can indeed control behavior (Brown, DiGello, Milewski, Wilson, & Kozak, 2000; Brown & Terrinoni, 1996; Brown, Zeiler, & John, 2001; DiGello, Brown, & Affuso, in press; Lebowitz & Brown, 1999).

The spatial pattern learning studied in our laboratory is of interest, in part, because the pattern is not directly perceivable. To learn the pattern, rats must somehow perceive the spatial relations among the baited poles that they have located during trials. These experiences must then come to affect choices made during subsequent trials, contingent on the location of baited poles visited during that particular trial.

In the present experiments, we examined how spatial pattern learning is affected by redundant exposure to visual cues that specify the location of the baited poles. The visual cues were provided on the poles themselves. The critical manipulation was whether, during training, the poles were visually identical (as has been the case in our previous experiments) or the unbaited poles and baited poles differed in color (black vs. striped in Experiment 1, black vs. white in Experiment 2). When baited and unbaited poles are visually distinctive, the location of the baited poles is specified by both the spatial pattern cues and the visual cues. On the basis of the large body of work on cue competition effects, this might be expected to produce overshadowing of spatial pattern learning by the redundant visual cues.

There are also reasons to suspect that cue facilitation, rather than cue competition, might occur in the case of redundant visual and spatial pattern cues. With the visual cues in place, the elements that make up the spatial pattern (i.e., the baited poles) are visually distinct and simultaneously discernable, and the pattern may be visually apparent. It seems possible that rats' ability to discriminate the pattern would thereby be facilitated, resulting in better learning of the pattern when the redundant visual cues are present than when they are not.

However, it is also possible, and this is a particularly interesting possibility, that neither cue competition nor cue facilitation would occur. This would be predicted if spatial learning mechanisms have special properties that do not support cue interaction effects (see Biegler & Morris, 1999), or if visual cues and spatial pattern cues are processed by two different learning systems, in a manner that would be analogous to the view of Pearce et al. (2001) regarding visual cues and environmental shape.

EXPERIMENT 1

The purpose of the present study was to determine the effect of visual cues on learning spatial patterns in rats. More specifically, the study was designed to determine whether the presentation of visual cues would facilitate (*cue facilitation*) or disrupt (*cue competition*) rats' learning of a square spatial pattern of baited poles in a pole box. The primary performance variable in this study was the extent to which the hidden spatial pattern controlled the behavior of rats. To detect the occurrence of cue interaction effects of visual cues on control by spatial patterns, the performance of three groups of rats was compared. The rats in the control group received training similar to the training in the Brown and Terrinoni (1996) study. The experimental groups of rats received identical training except that they were exposed to visual cues that were redundant with the hidden spatial pattern. One experimental group received the same number of training trials as the control group. The second experimental group was to receive an amount of training that resulted in a level of choice accuracy that was similar to that exhibited by the control group. The behavioral control by the hidden pattern in the experimental and control groups was then compared by testing the rats in an environment in which visual cues were absent.

Method

Subjects

The subjects were 39 male Sprague Dawley rats, 2–3 months old when the experiment began. Each subject's weight was determined, and the initial free-feeding weight along with growth curves provided by the supplier (Harlan Sprague Dawley) were used to deter-

mine the expected free-feeding weight of each rat throughout the experiment. Individual diets were adjusted from a starting point of approximately 13 g of Purina Rat Chow daily (immediately after the experimental procedures) in order to maintain each rat's weight between 85% and 90% of the estimated free-feeding weight. The rats were housed in groups of 3 or 4 in a standard colony with a 12:12-h light:dark cycle (although they were sometimes separated during feeding to allow individual diets to be controlled). All experimental procedures were conducted during the dark phase of the cycle.

Apparatus

The experimental apparatus (Figure 1) was a 180 × 76 × 33 cm box, constructed of 1.5-cm-thick plywood and painted flat black. The top of the box was open. A thin layer of bedding was spread on the floor of the apparatus.

Inside the box was a 4 × 4 matrix of poles spaced 13 cm apart (center to center). Each pole was constructed out of a wooden dowel rod, 15.5 cm tall and 1.2 cm in diameter with a 0.5-cm deep well drilled into the top. The well held one pellet, which was replaced weekly. These pellets served as sham bait in order to control for potential olfactory cues. Covering each pole was a polyvinylchoride (PVC) sleeve, 16.5 cm tall, the lower 12.5 cm being 2.1 cm in diameter, and the top portion being 2.7 cm in diameter. The food cup formed by the top portion of each PVC sleeve was 1.0 cm deep and 1.4 cm in diameter. These components were constructed with commonly available PVC plumbing supplies. The food cup had a floor,
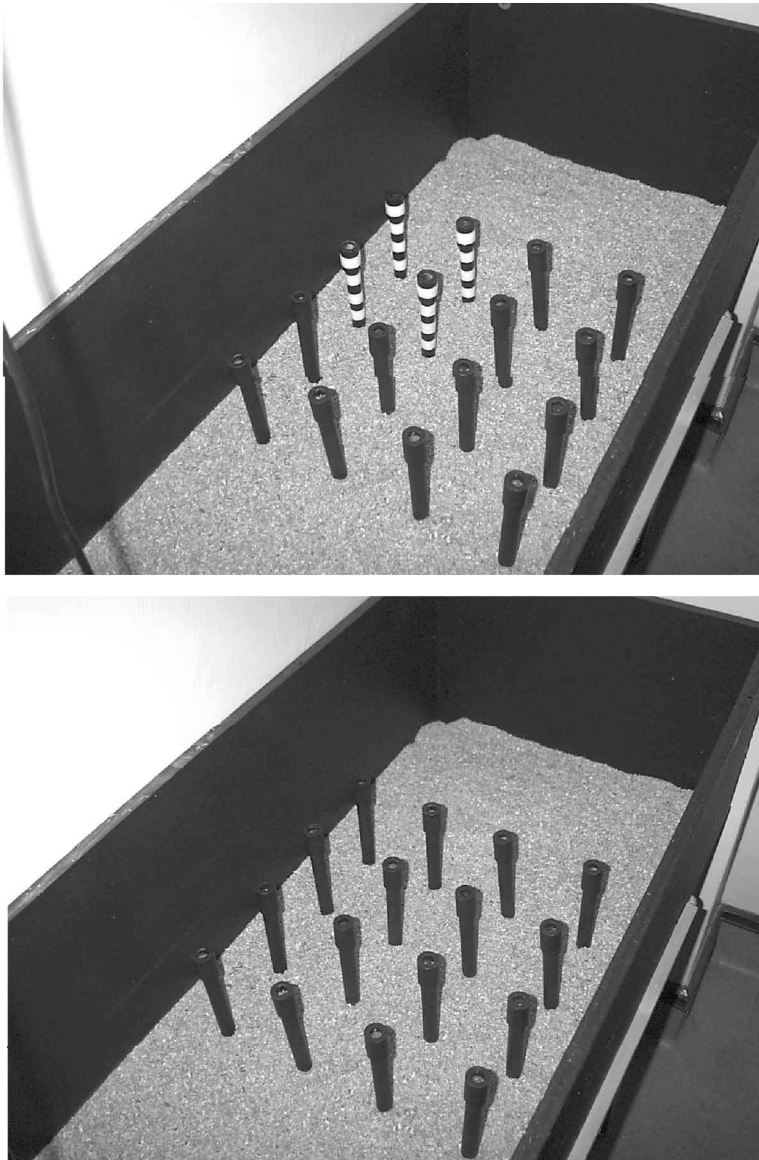
Figure 1. Photographs of the apparatus in Experiment 1. The top panel shows the apparatus with the visual cues marking the locations of baited poles in one of the nine possible exemplars of the square pattern as it appeared during the training phase for the visual cues groups (Groups A and B). The bottom panel shows the apparatus without visual cues as it appeared during the training phase for the no visual cues group and during testing for all groups.

consisting of a layer of nylon mesh material, which separated it from the sham bait pellet on top of the dowel rod. During the training and testing phases, the baited poles had a pellet placed in the food cup on top of this mesh floor. Pole sleeves (including the food cup) were painted black. The visual cues added to poles under some conditions (see the Procedure section below) were white horizontal stripes, 2.0 cm wide and 2.0 cm apart, resulting in the appearance of five black bands separated by four white bands.

In addition to the experimental apparatus, a training apparatus was also used during the pretraining phase. For the control group, the training apparatus was constructed by attaching four poles (with solid black sleeves) of varying heights (2.0, 4.5, 12.5, 15.5 cm) to a thin piece of plywood in a linear fashion, 7.0 cm apart from each other. For the experimental groups, the design of the apparatus was identical, except that the sleeves were striped (as described above).

Procedure

Pretraining. The rats were given 10–20 sucrose pellets (45-mg sucrose pellets, BioServe) for 3 consecutive days in their home cage. Starting on the following day, the training apparatus was placed in one of two open ends of the experimental apparatus. A barrier was placed in the experimental apparatus, separating the training apparatus from the experimental apparatus poles, so that the rats did not have access to the 4 × 4 matrix of poles. Each of the poles on the training apparatus was baited and, for the first trial, extra pellets were scattered around the base of the training apparatus. Pretraining was concluded when a rat had consumed the bait on all four training apparatus poles within 5 min for two consecutive trials.

Training. The rats were randomly divided into three groups. Fourteen rats were assigned to the control group (no visual cues group) and received training similar to that of the rats in the Brown and Terrinoni (1996) experiments. The baited poles were visually identical to the unbaited poles. For each trial, one square (consisting of four adjacent poles that formed a 2 × 2 square) was chosen out of the nine possible exemplars of the square pattern of baited poles (see top panel of Figure 1). A trial began with the rat's being placed in one of two open ends of the apparatus. The open end in which the rat was placed was randomly selected, with the restriction that each

open end was chosen an equal number of times within each block of 10 trials. The identity of the pattern exemplar (baited square) was chosen randomly, with the restriction that each square was baited at least once within a block of 10 trials. The rat was then allowed to choose poles until it chose all four baited poles or until 2 min had elapsed since its last choice. A choice was defined when the rat's snout touched the top of a pole. The control rats were trained for 40 trials.

The other 25 rats were divided into two experimental groups, visual cues Group A and visual cues Group B. The training procedure for these rats was identical to that of the rats in the control group, except that the baited poles were covered with striped sleeves and were therefore visually distinctive. Group A (13 rats) received the same amount of training as the control group (40 trials). The number of training trials received by Group B (12 rats) was determined by their performance relative to the no visual cues group. A performance criterion was calculated on the basis of choice accuracy for the control group during their last trial block (Trials 31–40). During training, the mean choice accuracy of the rats in Group B was calculated for each trial block. When the mean performance of Group B reached or exceeded the performance criterion determined by the no visual cues group, the rats in Group B proceeded to the testing phase. To accommodate this procedure, Group B began the experiment after the other two groups had begun the fourth trial block of training.

Testing. Trials during the testing phase were identical for all groups and were identical to the training phase for the control group. That is, the poles were visually identical for all groups during testing. Three blocks of 15 trials each were conducted.

Results

Training Phase

The number of choices made before choosing all four baited poles during training is shown in the left-hand panel of Figure 2. Group B received the minimum of 10 trials of training because its performance was immediately superior to the terminal (Block 4) performance of the no
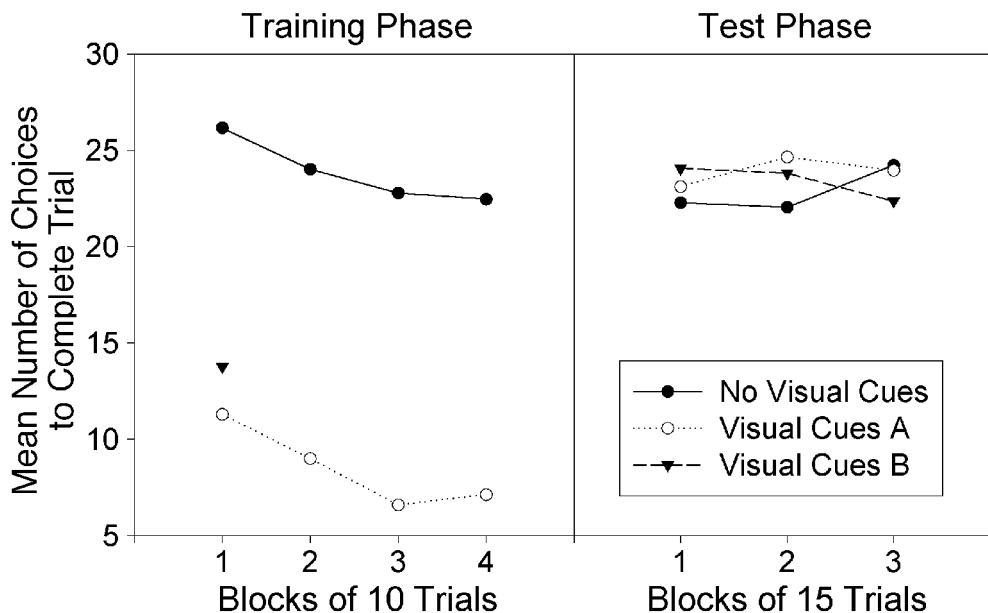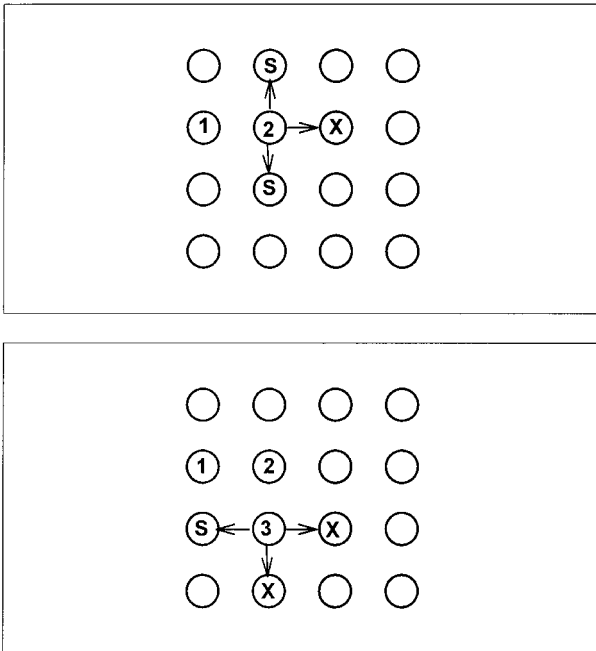

Figure 2. The mean number of choices required to locate the four baited poles during the training and test phases of Experiment 1.

Figure 3. Illustration of the measure of control by a square pattern developed by Brown and Terrinoni (1996). Top panel: Following discovery of the second baited pole (indicated by "2"), there are up to three adjacent, previously unvisited poles to which the rat could move. Up to two of these conform to the square pattern (indicated by "S"), and up to one does not (indicated by "X"). Bottom panel: Following discovery of the third baited pole (indicated by "3"), there are up to three adjacent, previously unvisited poles to which the rat could move. Only one of these conforms to the square pattern and is, in fact, baited (indicated by "S"), and up to two do not conform to the square pattern (indicated by "X"). The measure compares the proportion of moves made to adjacent, previously unvisited poles that are to poles conforming to the pattern (*obtained* proportion in Figure 4) with the proportion expected by chance (the expected proportion is the proportion of poles in the S category, among Ss and Xs). These two proportions are determined for each rat during each trial block.

visual cues group. The performance of the no visual cues group and Group A was compared using a group × block analysis of variance (ANOVA). As seems clear from the figure, the no visual cues group required more choices than did Group A [$F(1,25) = 73.7$]. The number of choices required to locate all four baited poles decreased over blocks [$F(3,75) = 9.2$]. There was no evidence for an interaction between these two factors [$F(3,75) < 1$; all statistical decisions reported in this paper are based on a rejection criterion of $p < .05$].

A set of two analyses was used to determine whether differences in performance of the experimental and control groups were due to (1) differences in the ability to locate the first baited pole, (2) differences in the ability to locate baited poles after discovering the first one, or (3) both. During the last trial block of the training phase, the no visual cues group, Group A, and Group B required means of 3.3, 1.1, and 1.8 choices, respectively, to locate

the first baited pole. The value for the no visual cues group differed from the values for both Group A [$F(1,25) = 137.4$] and Group B [$F(1,24) = 47.4$]. Thus, the visual cues allowed the rats to more efficiently locate the first baited pole.

The measure of choice accuracy following discovery of the first baited pole was chosen in order to allow comparison with the results of Experiment 2 and is very similar to the primary measure in Experiment 2. Choice accuracy is the proportion of choices made, following discovery of the first baited pole but within the first 12 choices, to baited poles. This measure was restricted to the first 12 choices because the visual cues groups seldom made more than 12 choices, and therefore, the restricted measure allows a more direct comparison with the behavior of the no visual cues group. In order to control for any effects related to pole revisits, any choices that were made to poles that had been visited earlier in the trial were not included in this analysis. During the last trial block of the training phase, the mean proportion of the pole choices that were correct for the no visual cues group, Group A, and Group B was .31, .83, and .47, respectively. The value for the no visual cues group differed from the values for Group A [$F(1,24) = 210.4$] and for Group B [$F(1,24) = 40.4$]. The results of these two analyses show that the experimental groups located both the first baited pole and subsequent baited poles more efficiently than did the control group.

Testing Phase

The number of choices made before the rats chose all four baited poles during testing is shown in the right-hand panel of Figure 2. A group × block ANOVA provided no evidence for effects of group [$F(2,36) < 1$] or block [$F(2,72) = 1.2$]. Nor was there a significant interaction between these variables [$F(4,72) = 2.0, p = .10$].

The number of choices made before the rats chose all four baited poles is a measure that includes all of the choices made by the rats in the pole box task. It does not isolate behaviors that specifically relate to control of behavior by the pattern. Brown and Terrinoni (1996) developed a measure that isolates elements of performance that can be attributed to the square pattern (Figure 3). In order to allow a comparison of control by the square pattern in the conditions of this experiment, the Brown and Terrinoni measure was applied to choices made by the rats during the test phase of the experiment.

The top panel of Figure 4 shows the results of the Brown and Terrinoni (1996) measure for choices made immediately following discovery of the second baited pole. For each rat, the number of choices immediately following discovery of the second baited pole that were to adjacent, previously unvisited poles that conformed to the square pattern was divided by the number of choices immediately following discovery of the second baited poles that were to adjacent, previously unvisited poles. The mean of these proportions was compared with the mean proportion that would be expected on the basis of chance. Chance is defined (for each rat) as the mean proportion of
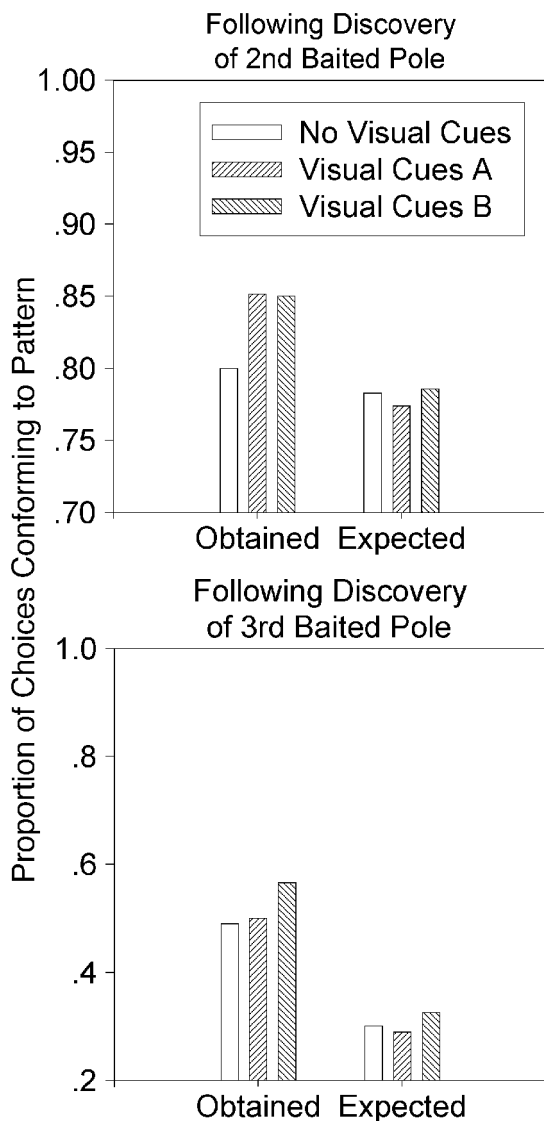
Figure 4. Results of the Brown and Terrinoni (1996) analysis of the results of Experiment 1, which was designed to isolate control of choices by the square pattern. Obtained values are the proportion of choices to previously unvisited poles adjacent to the second (top panel) and third (bottom panel) baited poles discovered, immediately following those discoveries. Expected values are derived from the proportion of previously unvisited, adjacent poles available at the time of those choices that were predicted by the square pattern to be baited.

adjacent, previously unvisited poles (available at the time these choices were made) that conformed to the square pattern (for additional details, see Brown et al., 2000; Brown & Terrinoni, 1996; Lebowitz & Brown, 1999). The bottom panel of Figure 4 shows the corresponding proportions for choices made immediately following the discovery of the third baited pole.

A proportion (expected vs. obtained) × discovery (following second vs. third baited pole) × group ANOVA

(group was the between-subjects factor, and the other two factors were within subjects) confirmed that the empirical proportions of choices conforming to the pattern was greater than the proportion expected on the basis of chance [$F(1,35) = 125.6$]. There was also a significant proportion × discovery interaction [$F(1,35) = 43.9$]. However, there was no evidence that these effects were modulated by (or interacted with) group [group × proportion, $F(2,35) = 1.4$; group × proportion × discovery, $F(1,35) < 1.0$]. To examine the form of the proportion × discovery interaction, two proportion × group ANOVAs were performed, one with the data from each level of discovery. The obtained proportion was greater than the expected proportion in both cases [choices following the second discovery, $F(1,36) = 6.5$; choices following the third discovery, $F(1,35) = 353.8$]. The pattern of results suggests that the interaction was due to greater control by the pattern for choices following the third discovery than for choices following the second discovery.

Discussion

These data provide no evidence for an effect of redundant, relevant visual cues on spatial pattern learning. Clearly, the visual cues came to control behavior, as is shown by the large difference in the choice accuracy of rats in the groups trained with visual cues and the group trained without visual cues. In addition, the square pattern clearly controlled choices during the test phase, albeit to a similar limited degree as has been reported in previous experiments from our laboratory (Brown et al., 2000; Brown & Terrinoni, 1996; Lebowitz & Brown, 1999). Critically, however, there was no evidence that the degree of control by the square pattern differed among the groups.

One possible interpretation of the use of visual cues among the rats in the experimental groups is that the visual cues facilitated location of the general area where the baited poles were but had little effect on the rats' ability to locate baited poles once they were in the general area of the baited square. If this were the case, it might not be surprising that the visual cues had no effect on spatial pattern learning. For example, although most rats usually move from one pole choice to the next by ambulating on all four limbs, some rats occasionally rear up and choose one pole, and then choose a second pole without returning their forelimbs to the floor. In those cases, it is not clear whether the rat has been exposed to the visual cues on the poles when it makes a choice. However, the data clearly show that visual cues increased the efficiency with which the rats located the baited poles, even after the first baited pole was discovered. Thus, the lack of an interaction between visual cue learning and pattern learning occurred even though the visual cues not only guided the rats to the first baited pole, but also facilitated their finding additional baited poles.

As with any set of experimental results in which performance differences are not found (a statistical null result), this pattern of results is relatively difficult to inter-

pret. Therefore, an analogous experiment was conducted in which a very different spatial pattern was used in order to examine the generality and replicability of the result.

EXPERIMENT 2

Experiment 2 was intended to be very similar in design to Experiment 1, with the major exception that the spatial pattern of baited poles was the checkerboard pattern used by Brown et al. (2001). In a 5 × 5 matrix of poles, either the 12 *even-numbered* poles or the complementary set of 13 *odd-numbered* poles were baited on each trial. Both exemplars form a checkerboard pattern, much like the white or black spaces on a chessboard. Brown et al. (2001) found that rats learn to choose poles in conformity with this pattern and that their performance cannot be explained in terms of learning relatively simple response tendencies. Thus, they argued, rats learn at least some of the spatial relations among the poles forming a checkerboard pattern.

In at least some ways, the square pattern used in Experiment 1 and the checkerboard pattern are quite different. There are many exemplars of the square pattern, but only two possible exemplars of the checkerboard pattern. The square pattern is composed of relatively fewer elements. As Brown et al. (2001) pointed out, the checkerboard pattern is potentially unbounded (*iterative*), whereas a square pattern is necessarily limited in spatial scope. Given the many differences between these two patterns, it should be informative to determine whether, as for the square pattern used in Experiment 1, there is an interaction between control by visual cues and control by a checkerboard pattern.

A methodological innovation was introduced in Experiment 2. In our previous experiments involving the pole box, as in most experiments concerned with spatial performance, choices were coded by human observers. We have made earlier (but unsuccessful) attempts to automate the measurement of choices in the pole box in order to increase the efficiency and objectivity of our data collection procedure (Brown et al., 2000). In the present experiment, pole choices were measured by using computer video capture technology.

Method

Subjects

The subjects were 16 experimentally naive rats of the same strain and age as in Experiment 1 and were maintained in the same manner.

Apparatus

The pole box was a rectangular arena measuring 152 × 76 × 34 cm (tall). The arena was painted flat black and was constructed out of 1.5-cm-thick plywood, with the top of the box open. A thin layer of bedding material covered the floor of the apparatus. A 5 × 5 matrix of vertical poles was located in the center of the apparatus, with each end of the arena left open, allowing room for the rat to be placed at the start of each trial (Figure 5). The poles in each row and column were separated by 13 cm.

Each pole was constructed out of a wooden dowel, 15.5 cm tall and 1.2 cm in diameter. PVC sleeves covered each pole. These

sleeves differed from those used in Experiment 1 in that the sleeves were 16.5 cm tall, the lower 12.5 cm being 2.1 cm in diameter, and the top portion being 2.7 cm in diameter. The food cup at the top of each PVC sleeve was 1.0 cm deep and 1.4 cm in diameter. The PVC components were painted flat black. When some or all the poles were white (see the Procedure section below), the lower 12.5 cm of the poles were covered with a thin, white plastic material (normally used to cover shower curtain rods). There was a floor in the well of each PVC sleeve made of nylon mesh material, and pellets were placed in the well. Underneath the nylon mesh floor of the well (in the well drilled in the tops of the wooden dowel rods hidden inside the PVC sleeves), there was a pellet in each of the 25 poles. As in Experiment 1, these "sham baits" were not retrievable by the rats (because they were under the nylon mesh floor). Their purpose was to rule out any possibility that baited and unbaited poles could be discriminated on the basis of smell (see Brown et al., 2000; Brown & Terrinoni, 1996; Lebowitz & Brown, 1999, for further evidence against this possibility). The sham bait pellets were replaced weekly. Additional pellets placed in baited poles were on top of the nylon mesh floor and could be easily retrieved by the rat with its tongue.

During the early part of training, the same training apparatus (with a series of four poles of different heights) as that in Experiment 1 was used. However (unlike in Experiment 1), the poles of the training apparatus had PVC sleeves of increasing height placed over them.

The apparatus was located in a small room with several other objects. Ambient illumination was provided by fluorescent tubes.

A videocamera was mounted directly above the pole box so that its field of view provided an overhead view of the matrix of poles. The image provided by this camera fed into a videocassette 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 drive. The image provided by the camera was processed by a program written in the Microsoft VisualBasic (Version 6) programming language and the CapturePro VisualBasic control (Pegasus Software). This combination of hardware and software allowed the image from the videocamera to be captured at a rate of approximately 20 Hz.

During each video capture cycle, the color values of four pixels corresponding to each pole were determined. These pixels were aligned with the edge of the pole tops so that the points on the pole tops corresponding to the pixels formed a square centered on the center of the pole with sides of 2.0 cm. The program used changes in the color values of these pixels from one sampling cycle to the next in order to detect the white rat's head against the black background of the pole top. Thus, a pole choice was defined by this system as when the rat's snout occluded the top of a pole, corresponding quite well to the definition of a choice in Experiment 1. The program recorded the sequence of pole choices made by each rat.

Procedure

Pretraining. Eight rats were randomly assigned to the cue group, and the remaining were assigned to the no cue group. For the no cue group, the poles of the training apparatus were either all white or all black on each pretraining trial (this alternated over trials). For the cue group, the poles of the training apparatus were the same color as the baited poles during the training phase (see below).

Training. Prior to each trial, either the 13 odd-numbered poles or the 12 even-numbered poles were baited, thereby forming one of the two exemplars of the checkerboard spatial pattern of baited poles. For the rats in the no cue group, the poles were either all black or all white. The rats in the cue group were randomly divided into two subgroups of 4 rats each. For one subgroup, the baited poles were always black and the nonbaited poles were always white. For the second subgroup, the pole color assignments were reversed (see the top panel of Figure 5).

A trial began by placing the rat into one of the two open ends of the pole box, with the end determined randomly for each trial. The
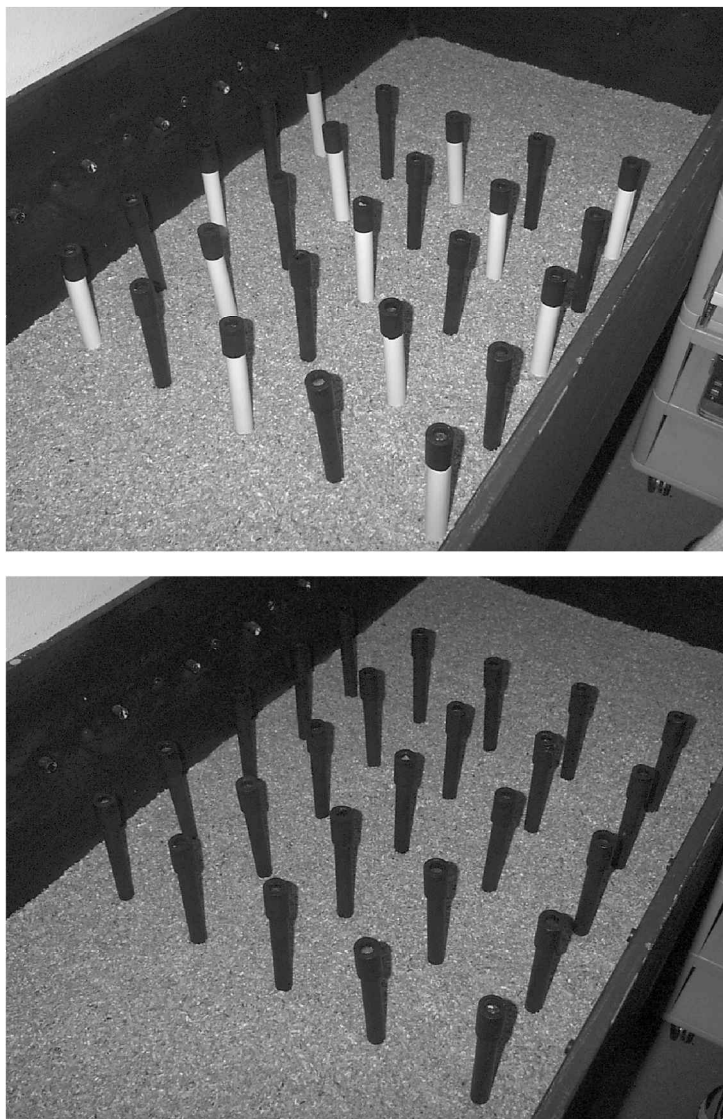
Figure 5. Photographs of the apparatus in Experiment 2. The top panel shows the apparatus with visual cues marking the locations of baited poles in one of the two possible exemplars of the checkerboard pattern as it appeared during the training phase for the visual cues group. The bottom panel shows the apparatus without visual cues, as it appeared during the training phase for the no visual cues group and during testing for both groups.

rats were allowed to explore the pole box and to choose poles until either they had chosen all 12 (or 13) baited poles (as determined by the computer program detecting their choices) or 10 min had elapsed since the trial began.

Training continued for five blocks of eight daily trials. For the cue group, the pattern exemplar on each trial was selected randomly with the constraint that each of the two patterns was in force during four trials of each block. For the no cue group, trials differed in terms of which of the two pattern exemplars was in force, as well as in terms of the pole color (all poles black or all poles white). Each of the resulting four trial types occurred twice within each trial block, randomly ordered.

Testing. During testing, trials and trial blocks were structured identically to the training trials of the no cue group. That is, both groups were tested in trials in which one of the two exemplars of the checkerboard pattern of baited poles was in force, and the poles were either all white or all black. Two blocks of eight trials each were conducted.

Results

The overall measure of choice accuracy used in this experiment was the proportion of initial pole choices that were directed to baited poles, during the first 12 choices made. *Initial* pole choices refers to the first choice of a pole. Thus, revisits were not included in the analysis so that the measure better represented the rats' tendency to choose poles that conformed to the pattern by reducing

Data Coded by Computer Video Analysis
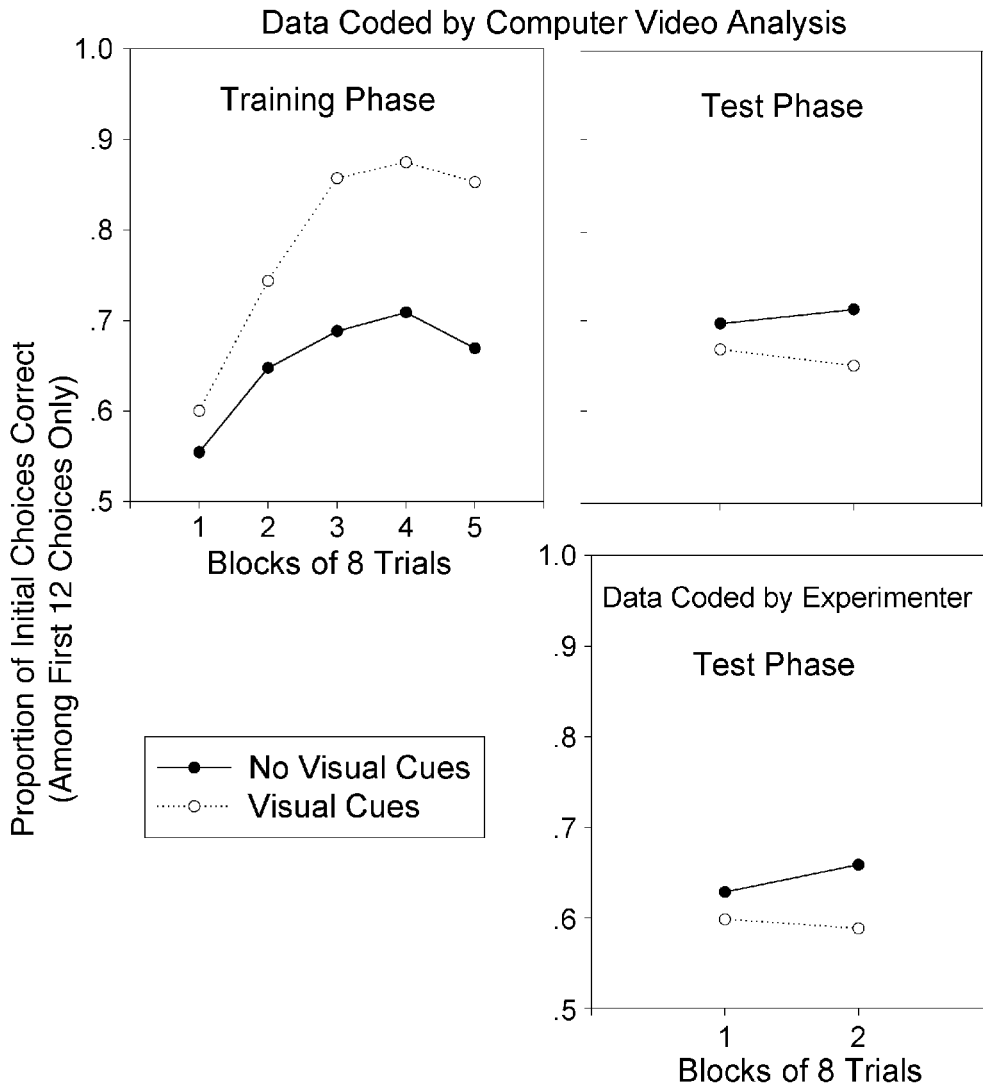
Figure 6. The mean proportion of choices correctly directed to baited poles among the first 12 choices made during the training phase (left-hand panel) and test phase (right-hand panels) of Experiment 2. Choices of poles that had been visited earlier in the trial are not included in the analysis. Data from the test phase are shown as coded by the experimenter (bottom right-hand panel) as well as according to the computer video analysis system (top right-hand panel).

the influence of processes that are involved in any tendency to avoid revisits to poles. Figure 6 shows performance in terms of this measure for the two groups during training and testing. The two top panels of Figure 6 show the data as recorded by the computer video analysis system during the training phase (top left-hand panel) and test phase (top right-hand panel). During training, performance improved over blocks for both groups [confirmed by a group × block ANOVA; effect of block, $F(4,56) = 60.4$] but more so for the cue group than for the no cue group [block × group, $F(4,56) = 6.9$]. The ANOVA also revealed a main effect of group [$F(1,14) = 13.9$]. During testing, no effects of block [$F(1,14) < 1$] or group [$F(1,14) < 1$] and no group × block interaction [$F(1,14) < 1$] were found.

The test phase data provided by the video analysis system were compared with those provided by our standard method of measuring choices by the experimenter (wherein a choice is defined as when the rat touches the top of a pole). There was a fair amount of disagreement between the choices coded by the experimenter and those recorded by the video analysis system. The experimenter recorded 23% more choices than the video system did. However, only 3% of the choices recorded by the video system were not recorded by the experimenter. Thus, the nature of the disagreement is in the form of a more lax criterion for counting a choice on the part of the experimenter. In order to validate the measures provided by the video system against the measure provided by our standard measure, the

data provided by the experimenter were analyzed in the same manner as the choices coded by the computer system. These data are presented in the bottom right-hand panel of Figure 6. The pattern of results was the same: No evidence of an effect of block [$F(1,14) < 1$] or of group [$F(1,14) = 1.04$] and no group $\times$ block interaction [$F(1,14) < 1$] was found.

As in Experiment 1, a second measure, designed to specifically measure the extent to which choices were under control of the spatial pattern, was used. In this case, the measure was the one developed by Brown et al. (2001) for the checkerboard pattern. This measure is the relative

tendency to choose a pole as a function of its spatial relationship to the most recently chosen pole and whether the most recently chosen pole was baited or not. In particular, the tendencies to choose poles that were (1) spatially adjacent to, (2) separated by one pole in a row or column from (referred to as a *skip* choice), or (3) spatially diagonal to the most recently chosen pole were compared. Choices for which the most recently chosen pole had been previously visited were not included in the analysis (because their psychological status as baited vs. unbaited poles is ambiguous). Given the checkerboard pattern, control by the pattern would be revealed if choices to adjacent
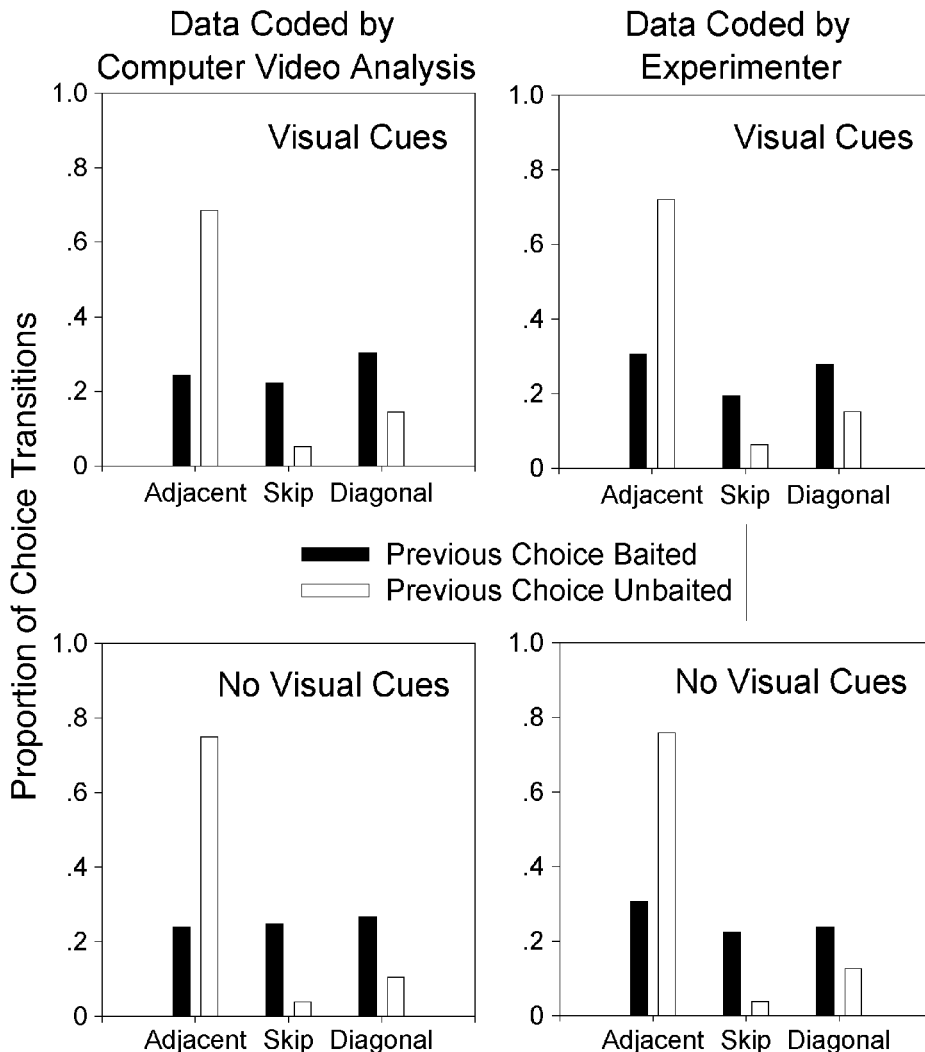

Figure 7. An analysis of control by the checkerboard pattern during the test phase of Experiment 2, modeled after the analysis developed by Brown, Zeiler, and John (2001). Choices are categorized according to the spatial relation between the pole from which the rat moved and the pole to which the rat moved, as well as whether the pole from which the rat moved was baited or unbaited. *Adjacent* moves are to poles immediately adjacent in a row or column, *skip* moves are to poles separated by one intervening pole in a row or column, and *diagonal* moves are to poles separated by one row and one column. Remaining moves do not fit into any of these three categories. Data are shown separately for the group trained with (top panels) and without (bottom panels) the visual cues. Performance was analyzed using both the data produced by the computer video analysis system (left panels) and those coded by the experimenter (right panels).

poles were relatively more likely following choice to an unbaited pole and if skip and diagonal choices are relatively more likely following choice of a baited pole.

Figure 7 shows the results of this analysis for the data from the test phase (data from the two blocks of the test phase are combined). As supported by the checkerboard pattern, adjacent choices appear to be more likely following choice of an unbaited pole, whereas skip and diagonal choices appear to be more likely following choice of a baited pole. The apparent difference in relative tendencies was confirmed by a group × previous choice × choice type × block ANOVA performed on the data coded by the computer video analysis system (left-hand panels of Figure 7). There was an interaction between the effects of choice type and previous choice [$F(2,28) = 284.4$]. However, there was no evidence that this pattern of results differed for the two groups, since there was no evidence for a choice type × previous choice × group interaction [$F(2,28) = 1.4$]. It should also be noted that none of the factors that included block approached significance. The same pattern of results was obtained when the data coded by the experimenter were analyzed [right-hand panels of Figure 7; choice type × previous choice interaction, $F(2,28) = 247.2$; choice type × previous choice × group, $F(2,28) = 1.3$]. No other factors approached significance.

Discussion

The results of this experiment generally parallel those of Experiment 1. As in Experiment 1, there was very clear evidence that the visual cues controlled choices during training in the group that had them available. Also, as in Experiment 1, there was no evidence that control by the spatial pattern during testing was affected by the prior exposure to, and use of, visual cues. Thus, both experiments failed to find either a cue competition effect or a cue facilitation effect of visual cues on spatial pattern learning.

The possibility that prior use of visual cues has no influence on learning of a spatial pattern is strengthened in several ways by this experiment. First, the pattern used in Experiment 2 was very different from that used in Experiment 1. Second, although the different measures preclude direct comparison, the two patterns appear to differ in terms of the degree of behavioral control they exhibited during the test phase of the experiments, with the square pattern apparently showing relatively less control of choices and the checkerboard pattern exhibiting relatively more control. Thus, it is unlikely that the failure to find an effect of visual cue learning on spatial pattern learning was due to a floor effect or ceiling effect.

GENERAL DISCUSSION

The results of the present experiments add to our understanding of spatial pattern learning in three ways. First, the results replicate our previous results for control of spatial choices by square (Brown et al., 2000; Brown & Terrinoni, 1996; Lebowitz & Brown, 1999) and checkerboard (Brown et al., 2001) spatial patterns of baited locations.

Second, we introduced in Experiment 2 a new methodological technique for measuring choices of discrete locations. The use of video analysis for defining pole choices provided a more efficient means of measuring behavior in this paradigm and eliminated the possibility of observer bias in defining choices made by the rats. The pattern of results obtained in Experiment 2 was identical for choices measured by the computer system and those coded by the experimenter, thereby validating the use of measures provided by this technology. However, despite producing the same pattern of results for the behaviors measured in Experiment 2, there was disagreement between the data provided by the standard method and those provided by the new technology. We believe that most of this disagreement was a result of differences in the criteria used to define a choice by this particular experimenter and this particular version of the program. Some of it, however, was due to imperfections in the video analysis system. We are continuing to improve this technology and, as of this writing, we have been obtaining substantially higher levels of agreement between the system and the measures generated by human experimenters.

The primary goal of the present experiments was to examine the effect of redundant visual cues on learning about the spatial pattern of baited locations. The outcome of these experiments predicted by standard views of learning is that the visual cues would have overshadowed other cues controlling spatial performance, as has been found in a number of other experiments (Biegler & Morris, 1999; Rodrigo et al., 1997; Sánchez-Moreno et al., 1999; Spetch, 1995). Although cue facilitation is a less common finding than cue competition, there were reasons to suspect that learning about spatial patterns might be facilitated by visual cues, as was suggested in the introduction. However, no evidence for either of these possible effects of visual cues on spatial pattern learning was found in either experiment.

The basic outcome of these experiments is subject to all of the limitations of any experimental null result. It remains possible that, in fact, spatial pattern learning is either overshadowed by, or facilitated by, visual cues such as the ones used here. However, several considerations appear to reduce the probability that the experiments were not sensitive to such an effect. The two experiments involved very different spatial patterns, somewhat different visual cues, and distinct behavioral measures. In Experiment 1, the number of subjects and observations were relatively large for this type of experimental comparison (in Experiment 2, the number of subjects per comparison group was more common for this type of experiment). Finally, there was clear evidence in both experiments for robust control of choices by the visual cues, showing that this was a relatively strong learning cue. Thus, although the results do not demonstrate that there is no effect of visual cues on spatial pattern learning, they do provide a reasonable opportunity for such an effect to be revealed, and it was not.

The failure to find evidence for overshadowing or cue facilitation is of particular interest, given the suggestions

that cues incorporated into a rich spatial representation (*cognitive map*) would not be expected to show the cue competition effects found in most learning paradigms (Biegler & Morris, 1999; Diez-Chamizo et al., 1985; Pearce et al., 2001). Diez-Chamizo et al. argued that cue competition effects would not be expected when the two cues involved are used by two different learning systems. They tested this idea with the taxon and locale learning systems described by O'Keefe and Nadel (1978) in mind. They found cue competition between intramaze and extramaze cues in a radial arm maze, which they argued would be utilized by the taxon and locale systems, respectively. It is not clear that intramaze and extramaze cues do, in fact, dissociate taxon and locale learning systems (e.g., Brown, 1992; Brown & Drew, 1998; see Biegler & Morris, 1999, for a critical analysis of Diez-Chamizo et al.'s conclusions). However, the basic argument that cues used by two separate learning systems should not show cue competition effects is sound.

Thus, our failure to find an effect of visual cues on spatial pattern learning may be taken as suggestive evidence that spatial pattern learning is based on learning processes or systems that are not closely affiliated with those that directly designate a goal location with a visual cue. This result is consistent with our view that spatial pattern learning, as we have studied it in the pole box apparatus, requires the acquisition of an abstract representation of the geometric properties of the pattern (Brown & Terrinoni, 1996; Brown et al., 2001). In the context of spatial navigation, visual cues are best understood as specifying particular locations as goals, either the location coincident with the landmark itself (*beacon homing*) or a location with a particular spatial relationship to one or more landmarks (*piloting*; see Gallistel, 1990, for a review). In the context of the spatial pattern learning that we have studied in the pole box apparatus, however, the visual cues present in the intra- and extraapparatus environment cannot serve these functions because no visual cue has a consistent spatial relation to goal locations. The only thing that specifies goal locations is previously discovered goal locations—and they were not visually distinctive in the test phases of the present experiments (nor in the standard procedure used in our previous experiments). Thus, spatial pattern learning might involve processes that do not incorporate visual or other exteroceptive cues. This provides an explanation for our finding that the visual cues in the present experiment, despite their strong control of spatial choices, do not affect control by the pattern.

If spatial pattern learning does not involve visual and other extrinsic perceptual information, what is the nature of its mechanism? We have only begun to empirically investigate this question. We suspect that spatial pattern learning involves movement-generated information as the rat travels among the locations (poles) in the apparatus. Information about the spatial relations among visited poles could be generated by the process of *dead reckoning* (or *path integration*; see Biegler, 2000, and Gallistel, 1990, for reviews). Information about the spatial relations

among baited poles (possibly also between baited and unbaited poles; see DiGello et al., in press) could then result in the development of a representation of the spatial pattern.

The present findings complement those recently reported by Pearce et al. (2001), in which a visual beacon failed to overshadow control by the shape of an escape pool. The two sets of experiments involve very different experimental paradigms and measures. In both cases, however, visual cues failed to overshadow control by spatial cues that are thought to be represented in a spatially organized manner—the global shape of the experimental environment in the case of Pearce et al.'s experiments and the spatial pattern in which hidden food items are arranged in the case of the present experiments. These parallel findings provide a strong suggestion that some of the principles of learning about space might differ in important ways from the principles of learning that apply in other domains.

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