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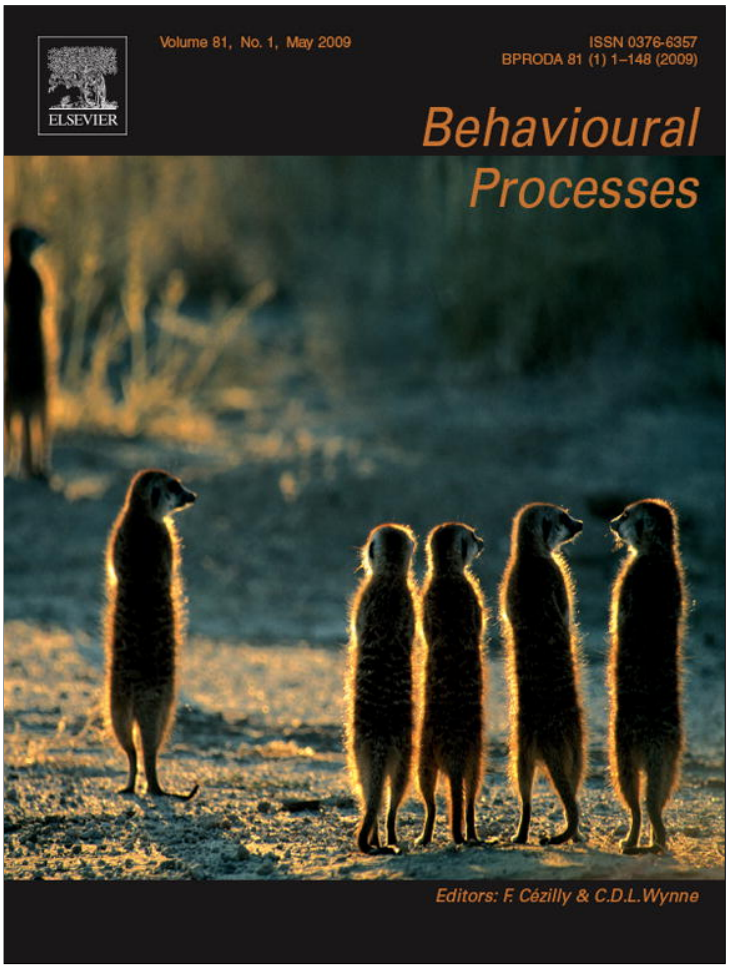

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Blocking of spatial control by landmarks in rats

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ABSTRACT

We investigated spatial blocking among landmarks in an open-field foraging task in rats. In Phase 1, rats were presented with A+ trials during which landmark (LM) A signaled the location of hidden food. In Phase 2, rats were given AX+ trials in which LM X served as a redundant spatial cue to the location of food. Additionally, BY+ trials were given as a within-subjects overshadowing-control procedure. At test, rats received nonreinforced presentations of LM X and LM Y on separate trials. Rats took longer to find the training goal location in the presence of LM X than of LM Y, thereby demonstrating that spatial control by LM X was blocked by prior learning with LM A. This constitutes the first evidence in rats for spatial blocking of one proximal landmark by another—approximating a conventional blocking design.

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1. Introduction

Blocking is a paradigmatic example of a cue-competition effect in Pavlovian conditioning. Blocking is defined as the poor behavioral control by a conditioned stimulus (CS) that had been paired with the unconditioned stimulus (US) in the presence of a previously established CS. For example, if a rat has learned that the presentation of a flashing light reliably predicts the delivery of sucrose, subsequent simultaneous pairings of a tone with the light followed by sucrose will produce weak responding to the tone alone. In this case, the flashing light is said to have blocked conditioning of the tone (Kamin, 1969; see also Moore and Schmajuk, 2008).

Kamin (1969) initially discovered blocking in a conditioned emotional response preparation; however, blocking effects have been found in other Pavlovian conditioning paradigms, as well as among discriminative stimuli (Balleine and Dickinson, 2006; Rescorla, 1999). In addition to blocking the magnitude of a conditioned response, blocking of information contained in an association has been found as well. For example, Barnet et al. (1993) found stronger blocking of CS X by CS A in a conditioned lick suppression procedure in rats when both CSs had the same temporal relationship to the US, such as both forward or both simultaneous, than when each CS had a different temporal relationship to the US, such as one forward and the other simultaneous or vice versa. Thus, the temporal information encoded as part of the association was blocked. Blocking of information has been more thoroughly investigated in spatial behavior. Most of these investigations, however, have focused on blocking across separate spatial domains, such as between intra-maze and extra-maze cues (Diez-Chamizo et al., 1985; March et al., 1992; Redhead et al., 1997).

Few studies have examined the blocking effect within a single spatial domain. Cheng and Spetch (2001) obtained the blocking effect in the spatial domain with honeybees using a conventional design; they found that pretraining a landmark to indicate the spatial location of sugar blocked subsequent conditioning to other cues when added to the experimental array. This is the only study to date, however, that has demonstrated blocking within a single spatial domain using a conventional design. No comparable studies exist for vertebrates. This is perhaps due to the difficulty of obtaining adequate performance from experimental subjects using a traditional blocking design (e.g., A+ training, followed by AX+ training). Rodrigo et al. (1997) found evidence for blocking of one landmark by a previously trained array of cues in rats in a water maze. Biegler and Morris (1999) found spatial blocking in a similar open-field procedure in rats. Interestingly, in each case, the authors cited a need to pretrain a configuration of multiple landmarks to block a new landmark added during Phase 2 (see also Biegler and Morris, 1996). Both Rodrigo et al. (1997) and Biegler and Morris (1999) found that rats' overall performance suffered when only a single landmark had been pretrained. Biegler and Morris (1996) speculated that their initial procedure provided insufficient polarizing cues for the rats to sufficiently encode their location relative to the goal.

We report an experiment where we examined spatial blocking in rats using a conventional design involving only one pretrained landmark. We utilized a procedure that we thought would reduce the problems associated with single-landmark training in rats' spatial

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performance. We trained rats to search for hidden food at a specific location on an open field based upon the placement of a landmark (i.e., A+). Following this treatment, we added a second landmark to the array (i.e., AX+). We found evidence for blocking of X by initial training of A+, relative to an overshadowing (i.e., BY+) control condition. This result has implications for our understanding of the content of spatial cognition, and particularly for classic spatial mapping theories. This is the first experiment demonstrating the blocking effect utilizing a traditional design in rats.

2. Method

2.1. Subjects

Ten female Long–Evans rats (*Rattus norvegicus*) obtained from Harlan Laboratories (Indianapolis, IN) served as subjects. Subjects were pair-housed in translucent plastic tubs with a substrate of wood shavings in a vivarium maintained on a 12-h dark/12-h light cycle. All experimental manipulations were conducted during the dark portion of the cycle. Rats were maintained at 85% of their free-feeding weights with daily feedings of 15 g of standard rat chow, but with free access to water at all times while in their home cages. All rats had prior experience in unrelated appetitive conditioning experiments in conventional operant conditioning chambers.

2.2. Apparatus

The experimental apparatus consisted of a flat panel of wood (1.52 m × 1.52 m), painted white and placed on a table 94 cm above the floor. Sixteen Tupperware cups were arranged in a 4 × 4 grid. The cups measured 6.35 cm in height and 7.62 cm in diameter. Adjacent cups were spaced 31.75 cm apart (center to center). Velcro strips were located equidistant between each cup (approximately 15.9 cm from the center of the adjacent cups). The cups were sunk into the floor of the arena, with the top lip of each cup extending 2 cm above the arena surface. The cups were filled halfway with cedar wood shavings. Froot Loops could be placed in the cups either on top of or buried underneath the wood shavings (see Section 2.3).

Procedures were conducted in an undergraduate classroom, with multiple polarizing extra-maze cues available to the rats. Doors were located directly north and northwest of the open field. The open field was flanked on the east and west walls by lab benches with various laboratory equipment (e.g., beakers, operant chambers, paper towels, etc.). A large dry-erase board hung on the south wall of the room. Desks were arranged mostly to the south of the apparatus. The room was dimly lit by fluorescent bulbs on the east side and a small incandescent lamp in the southwest corner of the room. The open field was located in the center of the room.

Four distinctly shaped and colored blocks of wood served as landmarks. An orange-and-blue arch and a green C-shape served as LMs A and B, counterbalanced; a red rectangle and an orange triangle served as LMs X and Y, counterbalanced. All experimental landmarks were approximately 10.16 cm × 5.08 cm × 2.54 cm.

2.3. Procedure

2.3.1. Pretraining

During all phases of the experiment, each rat was individually placed on the center of the north edge of the arena. During pretraining, rats were allowed to explore the open-field arena and search for food in the absence of intra-maze landmarks. The first session had one trial and all subsequent sessions in the experiment had two trials. During the first six sessions, two Froot Loops were placed in a randomly selected (without replacement) cup, hereafter called the goal cup, with two cereal pieces placed immediately outside the cup. The next five sessions consisted of two cereal pieces partially buried in wood shavings in the goal cup so that about half of each piece was visible. A trial ended if the rat found and ate all the available food, or if 3 min had elapsed from the beginning of the trial. A cup choice was defined as the placement of the nose to the shavings of the cup. This behavior was very clear and readily scored; when searching a cup, the rats would clearly pause in navigating the open field and thrust their noses downward to the shavings. The termination of a choice occurred when the subject had moved approximately 10 cm away from the most recently chosen cup. If a rat searched in a cup, for example, then moved further than 10 cm from the cup, and returned to the same cup to search again, this was scored as two consecutive choices to the same cup. It should be noted that this rarely happened in any phase, but it was important to define this choice criteria in the event of such occurrences. The trial ended when the rat had found the goal cup and consumed the food or 3 min had elapsed, whichever came first. On all trials throughout the experiment, an experimenter scored behavior, always standing approximately 2 m to the immediate south of the open field. Multiple people scored behavior, and while no formal measure of inter-rater reliability was made, all experimenters received equivalent training with feedback on the scoring procedure. Throughout the experiment, we recorded all cup choices made during each trial and the latency to find the goal. There were eleven sessions in the pretraining stage.

2.3.2. Phase 1

2.3.2.1. A+ training. As in pretraining, only one of the 16 cups (the goal) contained food on each trial in Phase 1. The goal cup was randomly selected without replacement, assuring that each cup served as the goal once in every block of 16 trials. LM A was present on each trial in Phase 1. For half of the rats ($n = 5$), LM A was placed to the immediate west of the goal cup; for the remaining rats LM A was placed to the immediate east of the goal cup, measuring 15.9 cm from center to center (top panel of Fig. 1). In the first five sessions of Phase 1 subjects were allowed to search for two Froot Loops, one partially buried and the other completely buried under the wood shavings in the cup. In the next seven sessions of Phase 1, only one Froot Loop was available and was completely buried beneath the wood shavings.

2.3.3. Phase 2

2.3.3.1. AX+/BY+ training. Following Phase 1 of blocking treatment, rats received Phase 2 of blocking treatment (AX+) as well as overshadowing-control treatment (BY+). Each session consisted of one AX+ trial and one BY+ trial, with the order of presentation counterbalanced across subjects within session and across sessions within subject. The reward was partially buried (as in Phase 1) during the first two sessions of Phase 2 and was completely buried for the remaining six sessions of Phase 2. On AX+ trials, LM A was in the same place relative to the goal as it was in Phase 1. LM X was placed 15.9 cm (center to center) from the goal on the opposite side of the goal relative to LM A. For example, if LM A was to the west of the goal for a particular rat, then LM X was placed to the east of the goal. For each subject, LMs B and Y had the same spatial relationship to the goal as did LMs A and X, respectively (middle panels of Fig. 1). The location of the goal cup was randomly selected in the same manner as in Phase 1

2.3.4. Test phase

2.3.4.1. X–/Y–. At test, rats received six sessions of nonreinforced test trials of LMs X and Y, separately. Each session contained one X– trial and one Y– trial. Trial order was counterbalanced across subjects within session and across sessions within subject. Although no food was present on any trial, the "goal" cup was defined as the cup that would have contained food according to the Phase 2 procedure. A trial terminated after the rat searched in the unbaited goal

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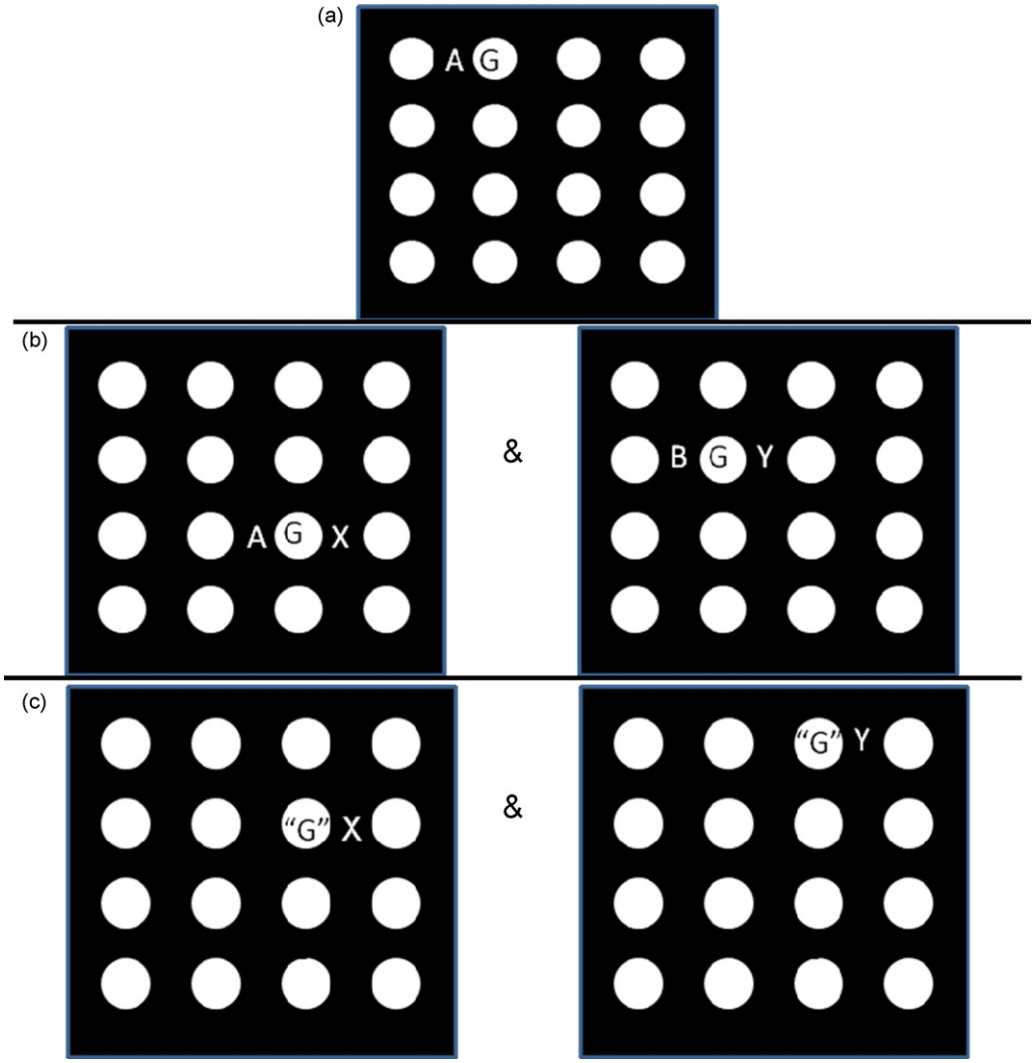

Fig. 1. Schematic of the experimental design. Panel (a) denotes Phase 1 training. Panel (b) denotes Phase 2 (i.e., blocking) training. Test trials are represented by panel (c). The location of food is marked by (G). The training goal location at test (i.e., without food) is denoted by "G". Landmarks are denoted by (A, X, B and Y). Unfilled white circles represent unbaited cups.

cup or after 3 min, whichever came first. The location of the goal cup was randomized in the same manner as Phases 1 and 2.

3. Results

3.1. Pretraining

All rats readily learned to search for the hidden food in the arena as indicated by an increase in the number of cups searched by the rats across sessions; the mean number of cups searched during the first three sessions was 2.55 (SD = 0.32), while the mean number of cups searched across the final three sessions of pretraining was 5.26 (SD = 1.06).

3.1.1. Phase 1

Spatial control of search by LM A was rapidly acquired in Phase 1 (see Fig. 2, Panel A). Rats acquired the A-Goal spatial association over twelve sessions in Phase 1 training, as indicated by multiple behavioral measures, including a decrease in the number of overall searches before food was discovered and a substantial decrease in latency to find the goal. A repeated-measures ANOVA revealed a main effect of session on mean total choices to find food, $F(23, 184) = 4.83$, $p < 0.001$. The mean latency to find food across the first three trials of Phase 1 was 91.9 s (SD = 52.0); the mean latency for the rats to find food across the final three trials of Phase 1 was 19.4 s (SD = 8.24). A dependent samples t-test found a significant difference between latencies at the beginning and end of training, $t(27) = 5.10$, $p < 0.001$

3.1.2. Phase 2

Rats made a mean of 1.54 choices (SD = 0.72) to find the goal on AX trials and a mean of 1.34 choices (SD = 0.41) choices to find the goal on BY trials (see Fig. 2, Panel B). This difference was not significant, $t = 0.77$, $p > 0.05$, and indicates that there were no differences in the number of errors made between AX+ and BY+ trials.

3.1.3. Test

Rats made a mean of 2.6 choices (SD = 0.92) to find the goal cup on X– probe test trials but a mean of only 1.8 choices (SD = 0.51) to find the goal cup on Y– probe test trials (Fig. 3). A dependent samples t-test found the number of choices on Y– trials to be significantly lower than on X– trials, $t(9) = 2.37$, $p < 0.05$, evidencing significant blocking of spatial control by LM X due to prior training of LM A.

A reviewer had suggested the possibility that differences in the rats' search efficiency during Phase 2 trials might have accounted

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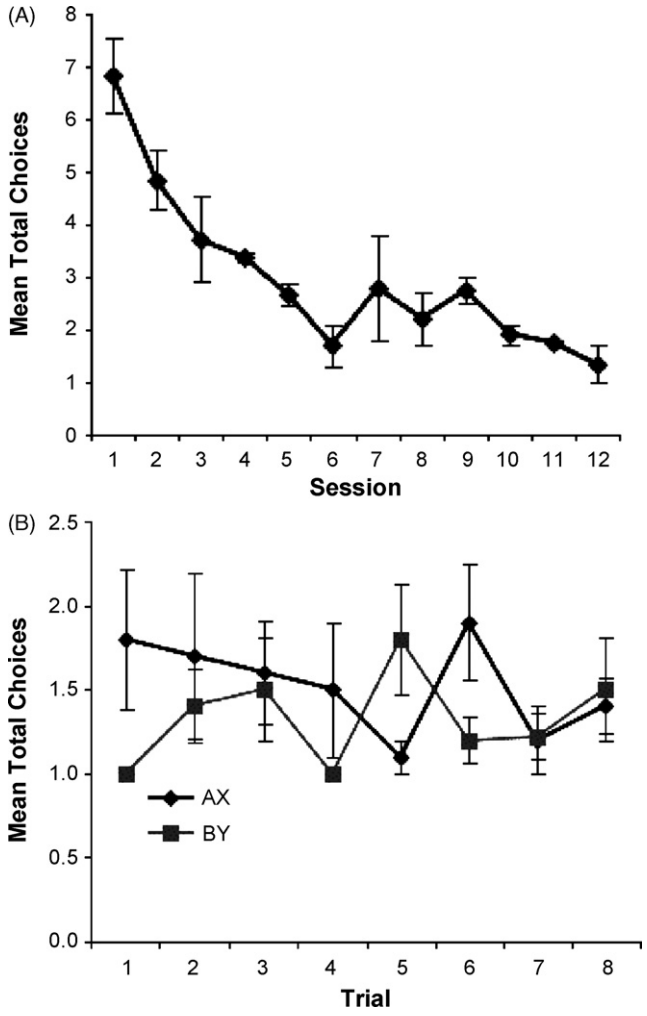

Fig. 2. (Panel A) Mean total choices to find the food goal across sessions in Phase 1. (Panel B) Mean total choices to find the food goal on Phase 2 trials with landmark arrays AX and BY. Error bars signify the standard errors of the mean.

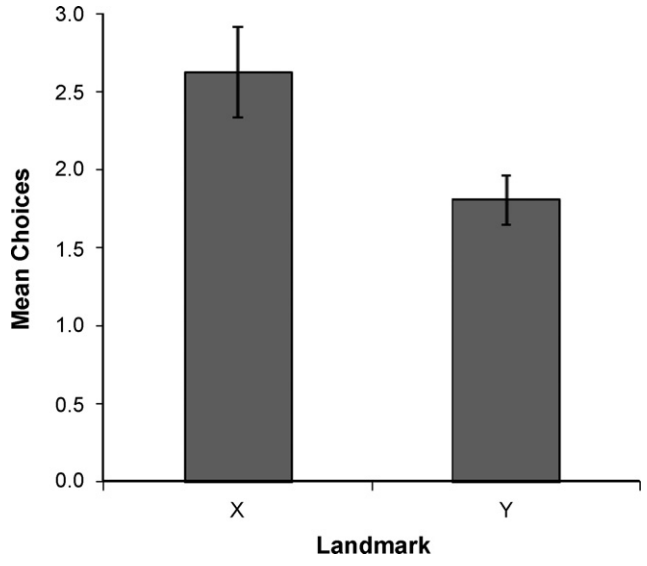

Fig. 3. Mean total choices at test on X– and Y– trials, collapsed across six test sessions. Error bars signify standard errors of the mean.

for the significant blocking effect obtained at test. If rats had found the goal location more frequently during BY+ trials than during AX+ trials, we might expect this pattern to continue when testing Y– and X– at test. Rats only failed, however, to find the hidden food on two trials (out of 160) during Phase 2 training, and both of those trials were BY+ trials. Additionally, there was no significant difference between the latency to trial termination between the two trial types. These observations argue against unrelated artifacts of Phase 2 training as the source of the blocking effect demonstrated at test.

We considered the possibility that the rats had learned to use the cues as beacons rather than as landmarks to find the hidden food. As beacons, the subjects could have simply approached Cue A in Phase 1, or compound Cue AX and BY in Phase 2, and then searched randomly in the cups proximal to the cue(s) (Mackintosh, 2002). O'Keefe and Nadel (1978) would refer to this not as spatial learning, but as guidance learning, and predict that blocking would occur in this situation. If rats were beacon homing, then our results would not evidence blocking of spatial information, but rather a more conventional associative blocking like that previously shown in Pavlovian conditioning paradigms.

We tested the hypothesis that the rats were beacon homing in Phase 1 by examining the relative proportion of landmark-adjacent (i.e., west or east of the LM) searches on hidden-food trials that occurred to the goal cup. On the one hand, if the rats were using LM A as a beacon rather than as a landmark, we should expect that they would search indiscriminately between the two cups. If, on the other hand, they had learned the spatial relationship (both distance and direction) between the LM A and the goal, we should see a disproportionately higher percentage of searches occur to the goal cup, and relatively little of the reflective error (i.e., searches to the cup on the side of the LM in the opposite direction from the goal). Out of a total of 140 Phase 1 trials, rats searched in a LM-adjacent cup on 131 trials. Of these trials, the rats searched in the goal cup first (relative to the reflective error) on 121 trials or 92.4%; the rats only made the reflective error on 10 trials during this phase. A sign test demonstrated that this difference is highly significant, $p < 0.001$. Looking to the individual rats' data, nine out of 10 rats searched the goal cup at greater than chance levels relative to the reflective error, all $ps < 0.01$. The single rat that did not reach significance chose the goal cup first on five out of six trials; the reason it did not reach significance was due to its failure to make a LM-adjacent search on eight trials during Phase 1.

We also examined the proportion of trials at test on which a rat's first LM-adjacent search was to the goal cup. Again, we only considered trials in which a LM-adjacent search was made. On X– trials, the rats' first LM-adjacent cup search was to the goal cup on 16 of 29 searches. A sign test indicated that this proportion is not above chance, $p = 0.36$. On Y– trials, the rats' first LM-adjacent cup search was to the goal cup on 20 of 30 searches. A sign test indicated that this proportion was significantly above chance level performance, $p < 0.05$. This provides further evidence for the spatial blocking effect. Additionally, these tests provide ample evidence that the rats used cue Y as a landmark, and not as a beacon. In other words, the rats were not searching randomly around cue Y, but had learned the spatial relationship (distance and direction) between the cue and hidden food.

4. Discussion

These results constitute the first unambiguous evidence for spatial blocking of a single landmark by another in rats. Contrary to previous results from Biegler and Morris (1996), we did not have difficulty obtaining strong performance during training using a conventional blocking design consisting of a single blocking landmark. The most notable experiment that has demonstrated similar

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findings (Cheng and Spetch, 2001) was performed in a between-subjects design with honeybees. Our study adds to the literature on spatial blocking by extending this effect to a vertebrate species and in a completely within-subjects design.

Our findings have important implications for the role of associative processes in spatial behavior (see also Blaisdell, in press; Blaisdell and Cook, 2005; Sawa et al., 2005). O'Keefe and Nadel's (1978) cognitive mapping theory indicates that blocking should not generally occur in the spatial domain; they postulated that environmental changes should provoke curiosity-driven exploration by the subject. Exploration serves to incorporate new spatial and contextual components into the cognitive map through a remapping process. According to O'Keefe and Nadel, spatial information is not stored in a traditional associative framework, where individual cue-outcome links are encoded separately as mere associative strengths. They postulate that blocking in the spatial domain should only occur within a limited scope of learning rules (e.g., beacon homing or route learning) or when curiosity-driven exploration is somehow prevented. Our results indicate a departure from the predictions made by O'Keefe and Nadel's theory. We observed blocking in the spatial domain using a conventional design despite the fact that we did not restrict the rats' exploratory behavior. Additionally, examination of the test data indicates that the animals were able to utilize cues as landmarks indicating the specific location of a goal. Of the two cups that were immediately adjacent to the landmark, the rats searched in the goal cup at a disproportionately high rate. This is inconsistent with a beacon homing strategy (e.g., Mackintosh, 2002) and suggests the contribution of associative processes to spatial learning beyond merely route-formation. Rather, associative processes appear to contribute to spatial cognition as well.

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