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BRIEF REPORT

Overshadowing Between Landmarks on the Touchscreen and in ARENA With Pigeons

Kenneth J. Leising
Texas Christian University

Dennis Garlick and Aaron P. Blaisdell
University of California, Los Angeles

The role of generalization decrement in spatial overshadowing was evaluated using a landmark-based spatial search task in both a touchscreen preparation (Experiment 1a) and in an Automated Remote Environmental Navigation Apparatus (ARENA, Experiment 1b). A landmark appeared as a colored circle among a row of eight (touchscreen) or six (ARENA) potential locations. On overshadowing trials, Landmark X was located two positions away from a hidden goal, while another landmark, A, was in the position between X and the goal. On control trials, Landmark Y was positioned two locations away from the goal but without a closer landmark. All subjects were then tested with separate trials of A, X, Y, and BY. Testing revealed poor spatial control by X relative to A and Y, thereby replicating the spatial overshadowing effect. Spatial control by Y was similar when tested in compound with novel landmark (BY) and on trials of Y alone. Thus, overshadowing in a small-scale environment does not appear to be due to a process of generalization decrement between training and testing.

Keywords: navigation, spatial learning, generalization, cue competition, overshadowing

Associative processes may play an important role in spatial learning (Chamizo, 2003; Leising & Blaisdell, 2009). In support, a variety of associative phenomena have been reported in spatial learning experiments, including sensory preconditioning (Blaisdell & Cook, 2005; Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Sawa, Leising, & Blaisdell, 2005) and conditioned inhibition (Sansa, Rodrigo, Santamaría, Manteiga, & Chamizo, 2009), as well as an abundance of experiments involving cue competition. In particular, blocking and overshadowing effects have been demonstrated in a variety of preparations and with many species (Biegler & Morris, 1999; Chamizo, Rodrigo, & Mackintosh, 2006; Cheng & Spetch, 2001; Goodyear & Kamil, 2004; Hamilton & Sutherland, 1999; Rodrigo, Chamizo, McLaren, & Mackintosh, 1997; Sánchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999; Spetch, 1995).

Spatial overshadowing is the reduction in spatial control by a spatial cue (X), also called a landmark, that has been paired with an outcome (e.g., a hidden food goal) in the presence of a more salient landmark (A), compared with a control group in which good spatial control is exhibited by X when trained in the absence of A. The degree of overshadowing in a conventional setting, such as in a conditioning chamber, is typically determined by the relative salience of the cues. Overshadowing between spatial cues, however, is typically determined by their relative proximity to the goal, such that landmarks closer to a goal tend to overshadow landmarks farther away (Chamizo et al., 2006; Cheng, 1989; Cheng, Collett, Pickard, & Wehner, 1987; Goodyear & Kamil, 2004; Lechelt & Spetch, 1997; Spetch, 1995; Spetch & Wilkie, 1994). Overshadowing has become an important effect in evaluating how and what cues come to control spatial behavior (Chamizo, 2003).

Spetch (1995) provided the first conclusive demonstration of overshadowing between similar types of landmarks (e.g., local visual cues). In a touchscreen spatial-search task with pigeons and humans, Spetch compared spatial control by two cues that were positioned at the same absolute distance from a hidden goal location but varied in their relative position to the goal. For the overshadowing condition, Landmark A was located between X and the hidden goal. In the control condition, however, X was the closest landmark to the hidden goal. Despite being equidistant to the goal, X showed stronger spatial control of responding in the control than in the overshadowing condition, thereby indicating spatial overshadowing.

Although prior demonstrations of spatial overshadowing suggest that associative processes play a role in spatial learning, the specific nature of the underlying associative process have yet to be examined. Overshadowing effects in conventional associative paradigms have typically been explained in terms of either an elemental learning process, such as the theoretical accounts by Rescorla and Wagner (1972), Mackintosh (1975), Pearce and Hall

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Kenneth J. Leising, Department of Psychology, Texas Christian University; Dennis Garlick and Aaron P. Blaisdell, Department of Psychology, University of California, Los Angeles.

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Correspondence concerning this article should be addressed to Kenneth J. Leising, Department of Psychology, TX Christian University, 2800 S. University Dr., Box 298920, Fort Worth, TX 76129. E-mail: k.j.leising@tcu.edu

(1980), Wagner (1981), and Miller and colleagues (Denniston, Savastano, & Miller, 2001; Miller & Matzel, 1988), or configural learning processes (e.g., Pearce, 1987, 1994). According to elemental theories, overshadowing is the result of a competitive process between cues A and X during training for behavioral control. According to Pearce's configural theory, however, overshadowing results from a decrement in generalization of the response elicited by the configural-training-cue AX to the elemental-test-cue X. Pearce's (1994) configural theory predicts symmetrical generalization decrements for (a) training on a configural cue AX and testing on element X, and for (b) training on element X and testing on configural cue AX. To test the latter prediction, a control group (configural control) is trained on X and tested on AX. Pearce's configural theory predicts equally poor performance during X in the overshadowing group as during AX in the configural-control groups. Reduced responding in only the overshadowing group and not in the configural-control group, however, would provide evidence against Pearce's account of overshadowing in terms of generalization decrement and strengthen the case that overshadowing is better accounted for by elemental models of associative learning (see discussion by Blaisdell, Denniston, & Miller, 1998; Thorwart & Lachnit, 2010).

Previous demonstrations of overshadowing by a landmark relatively closer to a hidden goal (e.g., Chamizo et al., 2006; Goodyear & Kamil, 2004; Spetch, 1995) have not directly tested for symmetrical generalization decrements as an account of overshadowing. In the present experiments, we used a touchscreen-equipped operant chamber and an Automated Remote Environmental Navigation Apparatus (ARENA; Badelt & Blaisdell, 2008; Leising, Garlick, Parenteau, & Blaisdell, 2009) to investigate whether spatial overshadowing was better explained as an elemental or a configural learning process. Experiments 1a and 1b tested the role of generalization decrement in the touchscreen and ARENA, respectively. Based on previous findings of spatial overshadowing, we predicted that the relative proximity of a stimulus to a hidden goal would determine the degree of behavioral control acquired by that stimulus and the degree of overshadowing. The novel question was whether or not we would observe a decrement in spatial control by a landmark trained as an element but tested in compound with another novel landmark.

General Method

Overview

The stimulus layout for all of the following experiments is shown in Figure 1a. In the touchscreen, a row of disks (units) was displayed across the center of the monitor. In ARENA, a row of plastic modules (units) was arranged on the floor in the center of a small testing room. Each unit served as a location for detecting subject pecking responses and as a location at which a spatial discriminative stimulus (i.e., a landmark) could be presented. On any given trial, one of the units was randomly selected to be the goal. Pecks at the goal activated a food hopper to deliver mixed grain to the subject.

Figure 1b shows the within-subject design of both experiments. Each row depicts the stimulus array presented to the subject on each type of trial. On an overshadowing trial, subjects received compound AX, in which A was positioned at the unit to the left of

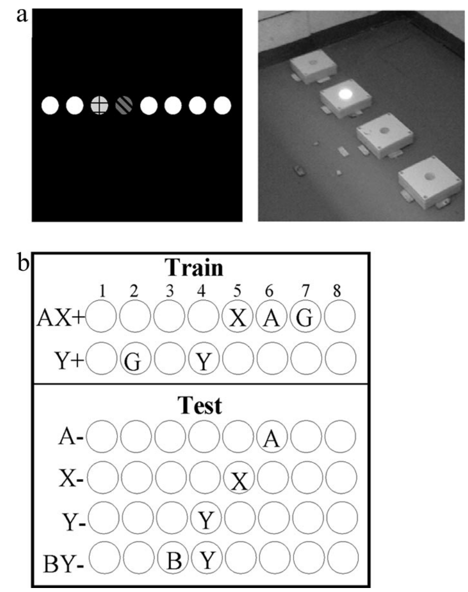

Figure 1. (a) Left-hand panel is an example of the display used for the touchscreen spatial task in Experiment 1a. The eight response units are shown, including two landmarks, one at position three and one at position four. Right-hand panel is a photo of four (of six) ARENA units in the test area. (b) A schematic of the experimental design. The letters A, X, Y, and B denote different colored landmarks and G indicates the location of the hidden goal. The use of "+" indicates the opportunity for reinforcement whereas the use of "–" indicates no opportunity for reinforcement. Numbers along the top denote unit positions along the linear array of eight (Experiment 1a) or six (Experiment 1b) units. Figures are not drawn to scale.

the goal and X was positioned two units to the left of the goal. On control trials, Y was positioned two units to the right of the goal. Thus, X and Y each had the same distance from the goal (but different directions to minimize generalization of responses between these cues). After pigeons had learned to peck at the goal units for food, they were tested separately on A, X, Y, and BY, with B being a novel landmark. We predicted that pigeons would less accurately search at the goal on test trials of X than on test trials with either A or Y, that is, overshadowing of X by A. Moreover, to test whether overshadowing of X by A is better explained by an elemental or a configural-learning associative model, subjects were also tested on trials of Y in compound with novel B. On the test trials, B was placed between Y and the goal (in the same manner as A and X, respectively). A configural associative model predicts poorer spatial control on BY test trials than on Y test trials (Pearce, 1994) as a result of generalization decrement during BY test trials, whereas elemental associative models predict no difference in spatial control between these two types of test trials.

Procedure

All subjects had been previously trained to retrieve mixed grain and pellets from a food hopper. At the beginning of the experiment, pigeons were trained to search for and peck at the goal. On each trial, one unit was randomly selected without replacement to be the goal location. All pecks during the trial and intertrial interval (ITI) were recorded. A trial would terminate with pecks to the goal unit or after 60 s had elapsed. A variable-time (VT) 15-s ITI followed a trial with a correct response (ITI range: 10–20 s), whereas a VT 120-s ITI followed a trial that timed out (ITI range: 60–180 s). Search training progressed in stages during which we manipulated both the schedule of reinforcement and the brightness of the goal unit. A subject that achieved 10 consecutively reinforced (i.e., correct) trials progressed to a new stage, whereas five consecutively nonreinforced (incorrect) trials returned the subject to the previous stage. The schedule of reinforcement increased across stages from continuous (CRF) to a modified fixed-ratio 2 (FR-2) requiring two consecutive pecks to the goal unit and, finally, to an FR-2 followed by a fixed-interval (FI) of 8 s. The FI period was initiated after the second consecutive peck to the goal unit (thereby meeting the FR-2 criterion) and the trial terminated with reinforcement after one additional peck to the goal unit following the 8-s interval. The brightness of the goal was progressively dimmed across training from full brightness to 78%, 61%, and, finally, 35% brightness, at which point it matched the brightness of the rest of the units. The reinforcement schedule and dimming procedures were adapted from Spetch, Cheng, and Mondloch (1992). Sessions lasted for 72 trials or 60 min.

Experiment 1a

This experiment used a spatial-search procedure in a touchscreen operant chamber to study the role of generalization decrement as a source for overshadowing of spatial control by a landmark.

Method

Subjects. One racing homing and three white carneaux pigeons (*Columba livia*; Double T Farm, IA) served as subjects. Subjects had been previously autoshaped in the touchscreen preparation. Pigeons were maintained at 85% of their free-feeding weights. They were individually housed in a colony with a 12-hr light-dark cycle and were provided with free access to water and grit.

Apparatus. Training and testing were conducted in a flat-black Plexiglas chamber (38.0 cm wide × 36.0 cm deep × 38.0 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M), visible through a 23.2 × 30.5 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13.0 cm above the chamber floor. Pecks to the monitor were detected by an infrared touchscreen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V houselight located in the ceiling of the box was illuminated at all times. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the floor. All experimental events were controlled and recorded with a Pentium III-class computer (Dell, Austin, TX). A video card controlled the monitor in the SVGA graphics mode (800 × 600 pixels).

A row of eight 2.0-cm in diameter disks served as stimuli (see Figure 1a). All eight disks were defined by a white border against a black background. The disks were separated by 3.0 cm center to center, and the edges of the row were centered with respect to the monitor. A response area was defined by an invisible border that extended 2.0 mm beyond the visible border of each disk. A 2.0-mm^2 black square was centered within each disk. This black square was not present when a disk served as a landmark. A disk serving as a response unit was filled white to 35% of total possible brightness, or intensity.

Landmark training. During landmark training, all nonlandmark units (except the goal) were lit white to 35% brightness. A unit that served as a landmark location could be filled with one of four colors: brown, pink, yellow, or teal, each to serve as A, B, X, or Y. Color-landmark assignments were counterbalanced across birds. Initially, the goal unit was lit with white light at full brightness. As in search training, the goal was progressively dimmed across training to 78%, 61%, and, finally, 35% brightness. The schedule of reinforcement was also increased from CRF to a modified FR-2 and, finally to an FR-2 + FI 8-s.

Landmark training sessions consisted of 20 compound trials of AX interspersed with 20 trials of Y (see Figure 1b). On compound trials, A was positioned at the unit to the immediate left of the goal and X was positioned adjacent to A (i.e., two units to the left of the goal). On the remaining trials, Y was positioned two units to the right of the goal. Based on the position of landmarks, the selection of the goal position was restricted to units 3 to 8 for AX trials and 1 to 6 for Y trials. The goal location was randomly selected across trials from the range of available units for each trial type. Trials terminated when the peck criterion at the goal was met, after 30 cumulative incorrect (i.e., nongoal) pecks, or after 60 s with no pecks to the screen—whichever came first. Only trials that met the response criterion ended in reinforcement. All trials were followed by a VT 15 s ITI (range: 10–20 s). Each session was terminated after 40 trials or 60 minutes—whichever came first.

Subjects that had not completed landmark training by the 20th session were given a set of separate sessions each of AX or Y in an ABBA design, respectively. After the first set of AX or Y alone sessions, subjects then completed the remainder of the experiment alternating between sessions of AX and Y trials in the same session and sessions of only AX or only Y with a 5 to 1 ratio, respectively. All subjects received at least one set of AX or Y only sessions. Subjects were required to achieve an accuracy of 75% or better on two consecutive sessions in which AX and Y trials were presented in the same session before moving on to testing.

Test. Subjects received a single test session with 3 nonreinforced test trials each of X, A, Y, and BY (for a total of 12 nonreinforced test trials) interspersed among 16 reinforced trials each of AX and Y, as in landmark training (for a total of 32 reinforced trials). On reinforced trials, AX and Y trials were reinforced on an FR-2 schedule. Each test trial was terminated following the FR-2 + FI-8 criterion for pecks at the goal, but no reinforcement was delivered at the termination of the trial (adapted from Spetch, 1995). The goal was always selected to be at location 2 or 3 for test trials with Y and BY, and 6 or 7 for A and X. Test trials on which the criterion was not met were automatically terminated after 60 s or after 30 cumulative incorrect pecks. A VI 15-s ITI followed the termination of each trial.

Results and Discussion

Subjects required an average of 31 (SD = .50) sessions to complete landmark training. All of the subjects met the criterion to advance to testing (i.e., 75% correct across two consecutive sessions of mixed AX and Y trials). Data from the test trials were standardized by concatenating peck data from each trial into an array ranging from −7 to 7, with 0 representing the goal location. The *proportion* of pecks at each location was calculated by dividing the number of pecks at each location in the array by the total number of pecks across all locations. The peak location was that with the highest proportion of pecks. A *t*-test for dependent samples was conducted on the proportion of goal responses on the last day of training with trials of AX and Y. This revealed a difference between landmarks, $t(3) = 10.51$, $p < .01$, such that the mean peak height on trials with AX (M = .78) was greater than on trials with Y (M = .21).

Figure 2a displays the proportion of pecks at each location at test as a function of distance from the goal for test trials of A, X, Y, and BY. The peak place of search was at the goal location for A, BY, and Y, but not for X. Responding on test trials with X showed a bimodal distribution with response peaks at locations −3 and −1, directly to the left and right of X. The bimodal peak during test trials with X indicates weak spatial control relative to Y, thereby demonstrating the overshadowing effect.

The proportion of responses at the goal was also greater on test trials with A or Y than for X. This difference was confirmed by comparing the proportion of pecks at the goal location against chance performance. Chance performance was calculated based on the total number of units minus those occupied by a landmark. All eight units were present on every trial, but locations serving as landmarks were visually distinct (colored) from response locations. Chance performance on tests trials with A, X, and Y was .14, but on test trials of BY was .17. *T*-tests for single means revealed that search at the goal was above chance on test trials of A, $t(3) = 17.23$, $p < .001$, Y, $t(3) = 4.84$, $p < .05$, and BY, $t(3) = 3.34$, $p < .05$, but not on test trials of X, $t(3) = .27$, $p > .10$. No other locations on any trial type were searched above chance, $ts(3) < 1.70$, $ps > .10$. An ANOVA with repeated measures conducted on proportion of goal responses revealed a main effect of landmark, $F(3, 9) = 8.57$, $p < .01$. Planned comparisons revealed that A differed from X, $F(1, 3) = 205.25$, $p < .001$ and Y, $F(1, 3) = 26.01$, $p < .05$, but X also differed from Y, $F(1, 3) = 39.80$, $p < .01$. Most importantly, goal responses did not differ between Y and BY, $F(1, 3) < 1.0$.

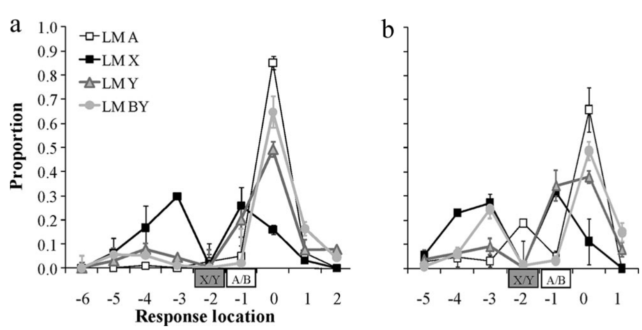

Figure 2. Mean proportion of pecks on test trials in each response location from the touchscreen (a) and ARENA (b). Data from test trials of Y and BY have been reflected around the goal (response location 0) for the purpose of comparison across landmarks. Letters below the *x*-axis indicate test locations of landmarks relative to the goal. Error bars represent standard error of the mean.

The results of Experiment 1a demonstrate the overshadowing effect in spatial search controlled by landmarks in the touchscreen. Spatial search in the presence of A and Y indicated good spatial control, whereas spatial search with X did not. Weak spatial control during trials of X was evident both from the peak of the response distribution and in the proportion of responses made at the goal unit. Furthermore, the equivalent and strong spatial control on test trials with BY and Y after training on Y alone fails to support a generalization-decrement account of overshadowing between landmarks in our touchscreen task.

Experiment 1b

Experiment 1b was conducted to evaluate whether data collected from pigeons searching in an open-field environment would reveal the same pattern of spatial control by landmarks (i.e., the overshadowing effect) as data collected from the touchscreen (Experiment 1a). From the time touchscreens were first used to collect data on spatial-search behavior in pigeons (Spetch et al., 1992), researchers questioned whether the same processes engaged in "real space" tasks would mirror those engaged in the two-dimensional (2-D) touchscreen environment. Though differences have been found in the pattern of spatial control by landmarks in the touchscreen and open field (e.g., Lechelt & Spetch, 1997), most studies have revealed more similarities than differences (e.g., Spetch, Cheng, & MacDonald, 1996). ARENA allows subjects to travel through open space to interact with landmarks and response units, and thus provides a three-dimensional (3D) environment in which to replicate the design of Experiment 1a.

In ARENA, landmarks were colored lights generated by LEDs located within the recessed well of an ARENA module. Six of these modules served as response units. Pigeons received the same overshadowing procedure as those in the touchscreen preparation, except that in ARENA, responses are made at units located on the floor of the test area and food is retrieved from a hopper located in a holding cage adjacent to the test area.

Method

Subjects. Four white carneaux pigeons (*Columba livia*; Double T Farm, IA) served as subjects and were maintained in the same manner as subjects in Experiment 1a. Subjects had previously served in an autoshaping and conditional discrimination procedure in ARENA (Leising et al., 2009).

Apparatus. Experimental manipulations took place in an anechoic room with a 2.3 × 1.5 m test area. The east wall of the room had a full-sized door. A 31.8 × 16.7 cm automated pet door was mounted on the south wall. The bottom of the automated door was 3.8 cm above the floor, 78.0 cm from the west wall, and 112.0 cm from the east wall. Illumination was provided by incandescent lights mounted near the ceiling but oriented upward to provide indirect lighting. A white noise generator provided background noise at 56–63 dB(A). A Sony SSC-DC374 color video camera with wide-angle lens was mounted on the ceiling 2.4 m above the floor of the test area and allowed for viewing and recording of experimental procedures in an adjacent room.

Stimulus presentation and response detection was accomplished by ARENA modules (Badelt & Blaisdell, 2008; see Figure 1a). Each module was a square plastic box measuring 12.9 cm wide and

3.5 cm high. A well measuring 3.0 cm diameter by 3.0 cm was created in the center of the module. A sensor circuit, including sensing and reference electrodes, was enclosed within the module. The sensing field was restricted to the volume within the cup (described in more detail in Badelt & Blaisdell, 2008). The sensor was activated when a pigeon's beak (or any conductive mass) broke the top planar surface and entered the space within the well. The module also housed a transmitter and receiver, which communicated with a PC computer in an adjacent room using radio waves. The network allowed each module to receive command signals, change the status of the LEDs, and send detection events to the computer. Each module was equipped with six LEDs located in the bottom of the response area. Three of the bulbs were positioned horizontally, and the remaining bulbs were positioned vertically facing up toward the opening of the well. The vertical bulbs were used to present colored lights to serve as visual landmarks. The response and stimulus areas of a module were defined by the perimeter of the recessed well.

A hopper like that described in the touchscreen task was mounted on the rear wall of a holding cage located on the other side of the pet door. The walls, floor, and ceiling of the holding cage were made of white acrylic, and the holding cage was illuminated by a 28-V Med Associates houselight.

Six modules served as response units positioned in a single row, and spaced 31.4 cm center to center (Figure 1a shows a photograph of four of the modules). The midpoint of the six units was centered at an imaginary line perpendicular to the food hopper in the holding cage. All units were 100.3 cm from the south wall of the test area and 49.5 cm from the north wall.

Landmark training and testing. Landmark training was conducted as in Experiment 1a. Landmark training sessions consisted of 20 compound trials of AX interspersed with 20 trials of Y (see Figure 1b). On compound trials, A was placed one unit to the left of the goal and X one unit to the left of A (i.e., two units to the left of the goal). On the remaining trials, Y was positioned two units to the right of the goal. Based on the position of landmarks, the selection of the goal location was restricted to units 3 to 6 for AX trials and 1 to 4 for Y trials. On the 20th session, the training procedure was adjusted for two of the four birds to encourage landmark use. During both trial types, the landmark(s) were illuminated 4 s prior to the illumination of the response locations. Subjects rarely pecked before the units serving as response locations were lit. Testing was conducted as in Experiment 1a, with the exception that the goal on test trials was located at units 1 or 2 on trials with Y and BY, and at units 5 or 6 on trials of A and X.

Results and Discussion

Subjects required an average of 21 (SD = 5.24) sessions to complete landmark training. All of the subjects met the criterion to advance to testing (i.e., 75% correct across 2 consecutive days on AX and Y trials). A *t*-test for dependent samples was conducted on the proportion of goal responses on the last day of training with trials of AX and Y. This test revealed that the peak height on trials with AX (M = .75) was greater than with Y (M = .32), $t(3) = 6.04$, $p < .01$.

Figure 2b displays the proportion of pecks at each location at test as a function of distance from the goal for test trials of A, X, Y, and BY. The peak place of search was at the goal location for A, Y, and BY, but not for X, thereby replicating the overshadowing effect found in Experiment 1a. *T*-tests compared the proportion of responses on test trials of A, X, B, and BY at each location against chance (for A, X, and Y chance = .20, and for BY chance = .25). These tests revealed that goal searching was above chance on test trials with A, $t(3) = 3.58$, $p < .05$, Y, $t(3) = 7.33$, $p < .01$, and BY, $t(3) = 6.39$, $p < .01$, but not on trials with X, $t(3) = 1.30$, $p > .10$. No other locations on any test trial were searched above chance, $ts(3) < 2.28$, $ps > .10$. An ANOVA with repeated measures was conducted on the proportion of goal responses and revealed a main effect of landmark, $F(3, 9) = 8.26$, $p < .01$. Planned comparisons confirmed that the proportion of responses at the goal location differed between A and X, $F(1, 3) = 12.88$, $p < .05$, and between X and Y, $F(1, 3) = 11.92$, $p < .05$. No differences were found, however, between A and Y, $F(1, 3) = 3.58$, $p > .10$, and, most importantly, between Y and BY, $F(1, 3) = 3.64$, $p < .10$.

Subjects in Experiment 1b distributed their responses on test trials of X equally to either side of X with few responses falling at the goal location signaled by X during training. On BY test trials, the results indicated good spatial control by Y despite the presence of B, such that the proportion of pecks at the goal location was comparable to trials of Y alone. In light of this, the overshadowing effect observed on test trials with X is better accounted for by an elemental rather than a configural model of associative learning.

Summary and Concluding Discussion

We found evidence for overshadowing between landmarks in both an operant touchscreen task (Experiment 1a) and an operant task in ARENA (Experiment 1b) with pigeons. Spatial control by X, a spatial discriminative cue that was trained in the presence of a more proximal A, was weaker than that exhibited by Y, a spatial cue with the same spatial contiguity with the goal as X but that had been trained in the absence of other landmarks. More importantly, poor spatial control by X at test was not found to be attributable to generalization decrement from training on the AX compound to testing on element X. Test trials of the novel compound BY in which Y, but not B, had been trained as a landmark revealed equally strong spatial control by the BY compound as by Y itself.

These results fail to support a generalization-decrement account (Pearce, 1987, 1994) of overshadowing in either of our operant spatial search procedures. According to Pearce's configural model, overshadowing results from a decrement in generalization of the response conditioned to the AX compound to the X element presented alone at test. Also according to the model, generalization decrement should be equivalent when either training on a compound and testing on one of its elements or with training on an element and testing on a compound containing that element (the other element being novel, see discussion in Blaisdell et al., 1998; Thorwart & Lachnit, 2010). The model therefore predicts equivalent decrements in spatial control to X after training on AX and in testing on BY after training on Y. We found asymmetrical effects in our experiments, however, with no loss of responding to BY at test after training on Y alone. Thus, overshadowing in our procedures appears not to be the product of a configural-encoding process. This is not to say that configural encoding did not take place in our task, or that configural learning sometimes plays an important role in some instances of spatial learning, but that configural-encoding processes were not responsible for the overshadowing deficit observed in our experiments.

Spetch (1995) used a touchscreen procedure similar to ours to produce the first demonstration of spatial overshadowing between landmarks and raised the question of whether touchscreen tasks engage the same processes as "real space" tasks. We found similar overshadowing effects in 2D and 3D environments. Each apparatus differed on a number of dimensions, such as the degree of freedom in movement allotted to the subject; the location of the landmarks and responses (vertical at eye level or horizontal close to the floor); how restricted the subject's vantage point was in the 2D environment of the touchscreen versus the 3D environment of ARENA; delay to, and effort involved in, collecting reward following a correct response; and so forth The similar pattern of results obtained in both of these tasks speaks to the robust nature of the overshadowing effect, suggesting the parsimonious hypothesis that the same learning and memory processes contributed to the effect in both test environments. These findings support the continued use of 2D environments to study associative processes in spatial learning (e.g., Hamilton & Sutherland, 1999; Kelly & Bischof, 2008; Molet, Jozefowiez, & Miller, 2010).

Though the pattern of responding was remarkably similar across test environments, there was one notable exception. The most obvious difference was the greater responding observed to location "−1" on Y test trials and at location "−3" on BY test trials in ARENA. Though not significantly greater than expected by chance, two pigeons tested in ARENA displayed a particularly strong tendency to respond at these locations. No birds showed such tendencies in the touchscreen. The likely explanation for this difference is the greater freedom subjects had in how they approached the display in ARENA than in the more constrained touchscreen environment.

Although our results suggest spatial overshadowing is governed by an elemental learning process, our experiments do not allow us to discern which type of elemental associative model best accounts for overshadowing in the spatial domain. There are many extant models of associative learning that account for a variety of phenomena, acquisition-focused models such as that of Rescorla and Wagner (1972) and Wagner's SOP model (1981), Wagner's replaced elements model (2008), attentional models such as that of Mackintosh (1975) and Pearce and Hall (1980), as well as performance-focused models such as Miller's comparator hypothesis (Denniston et al., 2001; Miller & Matzel, 1988; Stout & Miller, 2007). Future research using the same types of manipulations that distinguish between these models in conventional conditioning paradigms can be focused to dissect the associative processes governing overshadowing and other phenomena of spatial learning.

References

Badelt, S. W., & Blaisdell, A. P. (2008). Capacitive sensors for detecting proximity and response. *Behavior Research Methods, 40,* 613–621.

Biegler, R., & Morris, R. G. (1999). Blocking in the spatial domain with arrays of discrete landmarks. *Journal of Experimental Psychology: Animal Behavior Processes, 25,* 334–351.

Blaisdell, A. P., & Cook, R. G. (2005). Integration of spatial maps in pigeons. *Animal Cognition, 8,* 7–16.

Blaisdell, A. P., Denniston, J. C., & Miller, R. R. (1998). Temporal encoding as a determinant of overshadowing. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 72–83.

Chamizo, V. D. (2003). Acquisition of knowledge about spatial location: Assessing the generality of the mechanism of learning. *Quarterly Journal of Experimental Psychology, 56*B, 102–113.

Chamizo, V. D., Manteiga, R. D., Rodrigo, T., & Mackintosh, N. J. (2006). Competition between landmarks in spatial learning: The role of proximity to the goal. *Behavioural Processes, 71,* 59–65.

Chamizo, V. D., Rodrigo, T., & Mackintosh, N. J. (2006). Spatial integration in rats. *Learning & Behavior, 34,* 348–354.

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes, 15,* 366–375.

Cheng, K., Collett, T. S., Pickard, A., & Wehner, R. (1987). The use of visual landmarks by honeybees: Bees weight landmarks according to their distance from the goal. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology, 161,* 469–475.

Cheng, K., & Spetch, M. L. (2001). Blocking in landmark-based search in honeybees. *Animal Learning & Behavior, 29,* 1–9.

Denniston, J. C., Savastano, H. I., & Miller, R. R. (2001). The extended comparator hypothesis: Learning by contiguity, responding by relative strength. In R. R. Mowrer and S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 65–117). Hillsdale, NJ: Erlbaum.

Goodyear, A. J., & Kamil, A. C. (2004). Clark's nutcrackers (Nucifraga columbiana) and the effects of goal-landmark distance on overshadowing. *Journal of Comparative Psychology, 118,* 258–264.

Hamilton, D. A., & Sutherland, R. J. (1999). Blocking in human place learning: Evidence from virtual navigation. *Psychobiology, 27,* 453–461.

Kelly, D. M., & Bischof, W. F. (2008). Orienting in virtual environments: How are surface features and environmental geometry weighted in an orientation task? *Cognition, 109,* 89–104.

Lechelt, D. P., & Spetch, M. L. (1997). Pigeons' Use of Landmarks for Spatial Search in a Laboratory Arena and in Digitized Images of the Arena. *Learning and Motivation, 28,* 424–445.

Leising, K. J., & Blaisdell, A. P. (2009). Associative basis of landmark learning and integration in vertebrates. *Comparative Cognition & Behavior Reviews, 4,* 80–102.

Leising, K. J., Garlick, D., Parenteau, M., & Blaisdell, A. P. (2009). Behavioral research in pigeons with ARENA: An automated remote environmental navigation apparatus. *Behavioural Processes, 81,* 105–113.

Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review, 82,* 276.

Miller, R. R., & Matzel, L. D. (1988). The comparator hypothesis: A response rule for the expression of associations. In G. H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 22, pp. 51–92). San Diego, CA: Academic Press.

Molet, M., Jozefowiez, J., & Miller, R. R. (2010). Integration of spatial relationships and temporal relationships in humans. *Learning & Behavior, 38,* 27–34.

Pearce, J. M. (1987). A model for stimulus generalization in Pavlovian conditioning. *Psychological Review, 94,* 61–73.

Pearce, J. M. (1994). Similarity and discrimination: A selective review and a connectionist model. *Psychological Review, 101,* 587–607.

Pearce, J. M., & Hall, G. (1980). A model for Pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review, 87,* 532–552.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). New York, NY: Appleton-Century-Crofts.

Rodrigo, T., Chamizo, V. D., McLaren, I. P. L., & Mackintosh, N. J.

(1997). Blocking in the spatial domain. *Journal of Experimental Psychology: Animal Behavior Processes, 23,* 110–118.

Sánchez-Moreno, J., Rodrigo, T., Chamizo, V. D., & Mackintosh, N. J. (1999). Overshadowing in the spatial domain. *Animal Learning & Behaviour, 27,* 391.

Sansa, J., Rodrigo, T., Santamaría, J., Manteiga, R., & Chamizo, V. D. (2009). Conditioned inhibition in the spatial domain. *Journal of Experimental Psychology: Animal Behavior Processes, 35,* 566–577.

Sawa, K., Leising, K. J., & Blaisdell, A. P. (2005). Sensory preconditioning in spatial learning using a touch screen task in pigeons. *Journal of Experimental Psychology*: *Animal Behavior Processes, 31,* 368–375.

Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 166–181.

Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array: I. Touch-screen studies with pigeons and humans. *Journal of Comparative Psychology, 110,* 55–68.

Spetch, M. L., Cheng, K., & Mondloch, M. V. (1992). Landmark use by pigeons in a touch-screen spatial search task. *Animal Learning & Behavior, 20,* 281–292.

Spetch, M. L., & Wilkie, D. M. (1994). Pigeons' use of landmarks presented in digitized images. *Learning and Motivation, 25,* 245–275.

Stout, S. C., & Miller, R. R. (2007). Sometimes-competing retrieval (SOCR): A formalization of the comparator hypothesis, *Psychological Review, 114,* 759–783.

Thorwart, A., & Lachnit, H. (2010). Generalization decrements: Further support for flexibility in stimulus processing. *Learning & Behavior, 38,* 367–373.

Wagner, A. R. (1981). SOP: A model of automatic memory processing in animal behavior. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 5–47). Hillsdale, NJ: Erlbaum.

Wagner, A. R. (2008). Evolution of an elemental theory of Pavlovian conditioning. *Learning & Behavior, 36,* 253–265.

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