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Authors

Wong, Jared
Leising, Kenneth J.
Blaisdell, Aaron P

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Spatial Overshadowing in Pigeons: Evidence for an Acquisition Deficit

Jared Wong¹, Kenneth J. Leising², & Aaron P. Blaisdell¹

¹University of California, Los Angeles

²Texas Christian University

We investigated theoretical accounts of spatial overshadowing using a landmark-based spatial-search task in a touchscreen preparation with pigeons. Pigeons first learned to find a hidden target on a screen using a compound of two visual cues as landmarks. Landmark A was proximal to the target while landmark X was distal to the target. Experiment 1 replicated our prior spatial overshadowing effect whereby landmark A overshadowed the development of spatial control by X. Spatial control by X was also poorer than by landmark Y which had been paired with the target alone but with the same absolute distance to the target as X had. Thus, the poor spatial control by X was not merely due to the greater X-target distance (relative to the A-target distance). Experiments 2a and 2b failed to find recovery from spatial overshadowing of X through either post-training extinction or counterconditioning of overshadowing landmark A, respectively. We interpret our results as being consistent with acquisition-focused models of elementary associative learning, but not with performance-focused models.

Spatial learning and memory are important psychological processes for animals that move around their world. A number of distinct learning mechanisms have been identified that may play a role in spatial learning, such as configural processes (Cheng, 1989; Pearce, 1987; 1994) and associative learning processes (Miller & Shettleworth, 2007, 2008; Leising & Blaisdell, 2009), as well as more specialized forms of spatial cognition, such as vector addition (e.g., Cheng, 1989; Collett, Cartwright, & Smith, 1986) and cognitive mapping (O'Keefe & Nadel, 1978). While there is evidence for the contributions of each of these processes in certain domains of spatial learning, associative processes are a likely primary candidate for learning allocentric relations between objects in space. Allocentric spatial relations involve the external, metric spatial relationships between objects or places in Euclidean space independent of the subject's position within the spatial framework. Allocentric information can be used to navigate between and among sets of landmarks and goal locations that are the target of spatially-localized responses, such as returning to a home base, locating a hidden food source, and navigating escape routes. Given the widespread and central role of associative processes in generating goal-directed behavior (Blaisdell, 2008), we believe they are likely the primary mechanism for allocentric spatial learning (Leising & Blaisdell, 2009; see also Miller & Shettleworth, 2007). A spatial association encodes both the strength and the spatial relationship between the paired events.

Recently, our lab has reported evidence supporting the notion that associative processes underlie spatial learning in a wide range of foraging tasks, through experiments involving discriminative visual spatial cues (a.k.a. landmarks) that signal hidden target locations that were instrumentally associated with food. These tasks range from the acquisition of spatial control by landmarks (Blaisdell, 2009) and sensory preconditioning (Blaisdell & Cook, 2005; Sawa, Leising, & Blaisdell, 2005) to blocking (Stahlman & Blaisdell, 2009; see also Rodrigo, Chamizo, McLaren, & Mackintosh, 1997), conditioned inhibition (Leising, Sawa, & Blaisdell, 2012) and overshadowing (Leising, Garlick, & Blaisdell, 2011; see also Sánchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999; Spetch 1995). In most of these tasks, the accuracy of responding was used to measure

learning and revealed effects similar to those previously found using rate or magnitude of behavior. This suggests accuracy is a useful measure capable of revealing the same underlying associative processes within studies of spatial learning.

Research into associative learning processes, however, has uncovered numerous phenomena which has necessitated the development of a wide variety of theories to account for them. An example is the phenomenon of overshadowing. Overshadowing occurs when the presence of a more salient cue competes with the establishment of a conditioned response to a less salient cue when both are presented in compound and followed by the US during training (Pavlov, 1928). While overshadowing has been typically interpreted as a function of competition between two discrete elements (e.g., Miller & Matzel, 1988; Rescorla & Wagner, 1972), it has also been interpreted as the result of generalization decrement after configural learning, where testing on the less salient cue after training on a compound of two cues results in the test cue being quite dissimilar from the training compound (e.g., Pearce, 1987). Tests using conventional Pavlovian conditioning have yielded support for both elemental (e.g., Blaisdell, Denniston, & Miller, 1998) and configural (reviewed in Pearce, 1987) accounts of overshadowing. If spatial learning is governed at least in part by associative processes, then it becomes important to investigate the types of associative theories that best account for spatial learning.

We recently found evidence supporting an elemental over a configural account of spatial overshadowing (Leising et al., 2011). Pigeons were trained in an operant spatial-search procedure in which they were reinforced for pecks to a target circle located among a linear array of eight circles presented on a computer monitor. On some trials, two adjacent circles in the array could each be filled in with a different solid color (e.g., red, green, blue, etc.). A white circle to one or the other side of the two colored circles served as the target, and pecks at the target would activate the food hopper located below the touchscreen. Thus, the two colored circles served as visual spatial discriminative stimuli (i.e., landmarks) by which to locate the target from among the remaining set of white circles (AX+). Of the two landmarks, landmark A was proximal to the target while landmark X was more distal. On nonreinforced probe tests with only landmark A or X (i.e., A- and X-, respectively), we found good spatial control by proximal landmark A, but poor spatial control by distal landmark X. Notably, the poor spatial control by X was not due to its absolute distance to the target during training. On control trials, the pigeons had also learned to find the target with only a single landmark Y that was the same distance from the target as was X, but with no additional landmarks present during training (i.e., Y+). Thus, more proximal landmarks overshadow spatial control by more distal ones (see also Spetch, 1995). To test Pearce's (1987) configural-processing account of spatial overshadowing, after training on Y alone, we presented Y on nonreinforced test trials (i.e., Y-) with a more proximal, but previously untrained landmark B located between Y and the target. Pearce's model predicts equivalent generalization decrement when subjects are tested on a compound after elemental training as when subjects are tested on an element from a training compound (Blaisdell et al., 1998; Pearce, 1987). Leising et al. (2011), however, found a decrement in spatial control on X- test trials, but not on BY- test trials. This asymmetry suggested that the decrement in spatial control by X was not due to generalization decrement, as predicted by Pearce's configural theory, but to an elemental process whereby A and X competed for behavioral control of spatial search.

Although these results do not fit a configural account of the spatial overshadowing reported by Leising et al. (2011), there remains a large set of theoretical accounts for overshadowing that are based on elemental processes. Most contemporary theories of overshadowing (and other cue-competition phenomena such as blocking and stimulus relative validity; and cue-interaction phenomena such as conditioned inhibition) explain the effect in terms of an acquisition or a performance process (Blaisdell, 2003). Acquisition-focused accounts explain the overshadowing effect as being due to the acquisition of a weak or no association between the overshadowed CS and the US (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981). Performance-focused accounts, on the other hand, explain overshadowing as being due not to a

failure to learn a sufficiently-strong overshadowing CS-US association, but due to the failure of the association to influence responding to the overshadowed CS at test (e.g., Miller & Matzel, 1988; Stout & Miller, 2007). Evidence for a performance-deficit account of overshadowing comes from manipulations that occur following overshadowing training and before testing on the overshadowed stimulus. Post-training manipulations that have been found effective in reducing the overshadowing deficit include extinction of the more salient overshadowing CS A (Kaufman & Bolles, 1981; Matzel, Schachtman, & Miller, 1985), placement of a long retention interval between overshadowing training and test (i.e., spontaneous recovery; Kraemer, Lariviere, & Spear, 1988), and presenting a US reminder prior to testing (Kasprow, Cacheiro, Balaz, & Miller, 1982). While such findings are not universal to all experimental paradigms (e.g., Holland, 1999), they are sufficiently widespread to have spurred theoretical developments to account for cue competition in terms of expression deficits (e.g., Miller & Matzel, 1988), though some acquisition-deficit theories have been proposed that can also handle these so-called retrospective-revaluation effects (e.g., Dickinson & Burke, 1996; Van Hamme & Wasserman, 1994). Recovery from overshadowing and other cue-competition effects, therefore, have served as an important test bed for comparing acquisition-focused versus performance-focused theories of associative learning.

In this paper, we report a series of experiments investigating the effect of post-training manipulations that target the effectiveness of a more proximal overshadowing landmark A in its ability to overshadow spatial control by a more distal landmark X. Although we borrowed from the design and procedure of Leising et al. (2011), some of the stimulus parameters have been changed. Thus, Experiment 1 served as a replication of Leising et al. (2011) to demonstrate that both a more distal (to the target) landmark Y and a more proximal landmark A are both capable of exerting good spatial control over responding, while A is able to overshadow spatial control by more distal landmark X. In Experiment 2a, we used an extinction procedure to extinguish spatial control by the overshadowing landmark A and assessed its effects on subsequent spatial control by the overshadowed landmark X (cf. Kaufman & Bolles, 1981; Matzel et al., 1985). On the one hand, if spatial overshadowing reflects an acquisition deficit, as characterized by some models of acquisition (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972), then no recovery of spatial control by the overshadowed landmark should be observed (cf. Holland, 1999). On the other hand, if spatial overshadowing reflects a performance deficit (e.g., Miller & Matzel, 1988) or the operations of a revised acquisition-deficit model (e.g., Dickinson & Burke, 1996; Van Hamme & Wasserman, 1994), then extinction of the overshadowing landmark should improve spatial control by the overshadowed landmark. Experiment 2b pursued this same question using a counterconditioning procedure in which the overshadowed landmark was subsequently retrained to a target at a new spatial location after overshadowing treatment (cf. Blaisdell et al., 1998 for a similar manipulation of temporal retraining on overshadowing in a conditioned suppression procedure in rats).

Experiment 1

Experiment 1 served as a replication of the spatial-overshadowing effect reported by Leising et al. (2011). The purpose was to determine if a non-overshadowed landmark, Y, that was distal to the target location would be capable of developing comparable spatial control to that of an overshadowing landmark, A, that was separately paired with the target in the presence of a distal overshadowed landmark, X; see Table 1). At test, if Y-alone probe trials reveal spatial control that is comparable to that of A-alone probe trials, while if X-alone probe trials result in poor spatial control, then it would demonstrate that the poorer spatial control by X than by A was due to the overshadowing treatment rather than to X having a greater distance to the target relative to A.

Table 1*Experimental design for Experiment 1.*

Landmark Training	Testing (spatial control)		
	X	Y	A
AX+ / Y+ / T1+ / T2+	Low	High	High

Note. Landmark A was the overshadowing landmark, X was the overshadowed landmark, and Y was the non-overshadowed landmark that was one response location from the target (i.e., equidistant from the target as X). T1 and T2 were the training landmarks. A '+' indicates reinforcement. The slash (/) separates events that are interspersed. 'Low' and 'High' indicate predicted spatial control by the landmark at test.

Method

Subjects

Four White Carneaux pigeons (*Columba livia*; Double T Farm, Iowa) that had previously served as subjects in spatial learning tasks on the touchscreen were used. Subjects were individually housed in steel home cages with metal wire mesh floors in a vivarium. Experiments occurred at approximately the midpoint of the light portion of the 12-hr light-dark cycle. All subjects were under a food-restriction schedule and were maintained at 85% of free-feeding weight, but were allowed free-access to water and grit while in their home cages.

Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide x 36 cm deep x 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 x 30.5 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13 cm above the chamber floor. Pecks to the monitor were detected by an infrared touch screen (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, except when an incorrect choice was made. 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 x 600 pixels).

For stimulus displays, a linear array of eight 2 cm x 2 cm squares placed on a black background served as stimulus locations (Figure 1). The left edge of the leftmost square was located 3.5 cm from the left-side border of the touchscreen viewing window and the right edge of the rightmost square was located 3.5 cm from the right-side border of the touchscreen viewing window. The squares were 10.6 cm from the top edge of the touchscreen viewing window and 10.5 cm from the bottom. The squares were separated by 3.0 cm center to center. Between trials, when not serving as possible response locations, all eight squares were black with a white border against a black background (Figure 1a). A response area was defined by an invisible border that extended 2.0 mm beyond the visible border of each square. A 2.0-mm diameter white dot was centered within each square. This white dot was not present when a square served as a landmark. A square serving as a possible response location was filled white to 35% of full brightness.

Procedure

Pretraining. Subjects had been previously trained to retrieve mixed grain and pellets from a food hopper, and had been autoshaped to peck a lit square chosen randomly from among the eight locations.

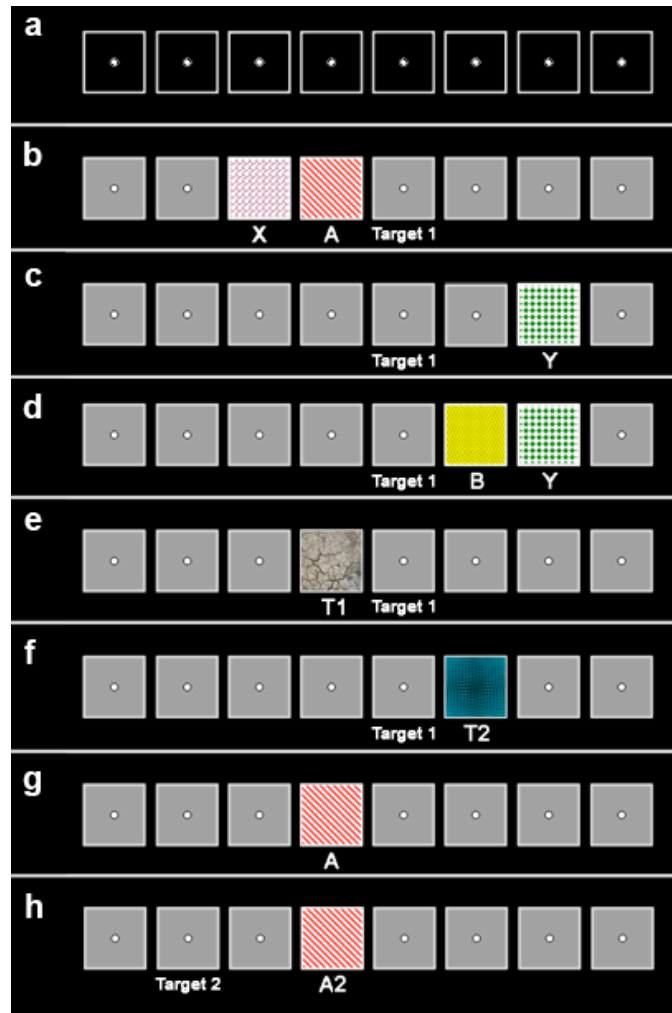


Figure 1. Stimuli display for Experiments 1 (Panels a-c), 2a (Panels a-b, d-g), and 2b (Panels a-b, d-f, h), not drawn to scale. Panel a depicts the touchscreen display during intertrial intervals when no stimuli are presented. Panels b, c, d, e, and f depict landmarks A, X, B, Y, T1, and T2 relative to the unmarked Target (indicated as Target 1, which would correspond to Location 0 in Figures 2-5). These are examples of trials, with actual location of the landmarks and target in the array varying across trials as described in the text. All non-landmark squares were lit white to 35% brightness. Panel g depicts Phase 2 (Extinction) of Experiment 2a, where non-reinforced A trials were presented alone (along with T1 and T2 trials). Panel h depicts the retrained landmark (A) and its Target location (indicated as Target 2) during Phase 2 (Retraining) of Experiment 2b, along with T1 and T2 trials. Other than T1 and T2, all images used as landmarks were counterbalanced across birds, as were their positions relative to the unmarked Target location (i.e., left or right).

Search Training. At the beginning of the experiment, pigeons were trained to search for and peck at the target following the procedure of Leising et al. (2011; originally adapted from Spetch, 1995). On each trial, one square was randomly selected with replacement to be the target location. All pecks during the trial and ITI were recorded. A trial would terminate with pecks to the target (see details below) or after 60 s had elapsed. A variable-time (VT) 15-s intertrial interval (ITI) followed a trial with a correct response, whereas a VT60-s ITI followed a trial that timed out. Search training progressed in stages during which both the schedule of reinforcement and the brightness of the target square were manipulated. A subject that achieved ten consecutively reinforced (i.e., correct) trials progressed to the next scheduled stage, whereas five consecutively non-reinforced (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 (FR2) requiring two consecutive pecks to the target area, and finally to an FR2 followed by a fixed-interval (FI) of 8 s. The FI period was

initiated after the second consecutive peck to the target marker (thereby meeting the FR2 criterion) and the trial terminated with reinforcement after one additional peck to the target marker following the 8-s interval. As performance improved, the brightness of the target location was dimmed from full brightness to 80%, to 50%, and finally 35%. This dimming occurred within sessions, as well as across sessions, depending on each subject's performance. The reinforcement and dimming procedures were adapted from Spetch, Cheng, and Mondloch (1992) and was also used by Leising et al. (2011). Sessions lasted for 72 trials or 60 min, whichever came first.

Landmark Training. Once pigeons were reliably pecking the target square, lit to 35% brightness, landmark training began. During landmark training, all non-landmark squares (except the target) were lit white to 35% brightness. A square that served as a landmark location was one of four visually distinct stimuli in terms of texture and color. These stimuli were counterbalanced across birds in their assignments as landmarks A, B, and Y. Initially, the target square was colored white at full brightness. The target square was again dimmed across and within session to 78%, 61%, and finally 35% brightness. The schedule of reinforcement increased from CRF, to a modified FR2, and finally to an FR2 + FI 8-s.

Landmark training sessions consisted of 20 compound trials of AX+ (Figure 1b) interspersed with 20 trials of Y+ (Figure 1c). To promote responding to the task during sessions containing non-reinforced trials, subjects also received training on two training landmarks, T1 and T2 (20 trials of each, interspersed throughout each session; Figures 1e and 1f, respectively). This amounted to a total of 80 trials per session. The training landmarks were also visually distinct from each of the aforementioned landmarks in terms of both color and texture. The purpose of having two training landmarks with opposing spatial relations to the target was to reduce any side biases relative to the landmarks. For half the subjects, on the compound trials, A was positioned at the location to the immediate left of the target, and X was positioned to the immediate left of A (i.e., two locations to the left of the target). On the remaining trials, Y was positioned two locations to the right of the target. The directions of all landmarks (including T1 and T2) relative to the target location were counterbalanced for the remaining half of the subjects. The position of the target was restricted (counting up from the left most square in the array) to locations one to four for AX trials and five to eight for Y trials; and on the training landmark trials, the position of the target was restricted to locations two to eight for T1 trials, and one to seven for T2 trials (again, the directions of the landmarks relative to the target was counterbalanced). The placement of the target was quasi-randomly selected from one trial to the next, such that subjects received an equal number of trials with the target at each possible target location within each session. Trials terminated when the peck criterion at the target was met, after 20 cumulative incorrect (i.e., non-target) pecks, or after 60 s with no square pecks, whichever came first. All trials were followed by a VT 15-s ITI. Each session was terminated after 80 trials or 60 min, whichever came first. Following the procedures of Leising et al. (2011), subjects that had not completed landmark training after the 20th session were given separate sessions each of AX-only or Y-only sessions (both still interspersed with T1 and T2 trials) in an ABBA design, respectively. After the first set of AX-only or Y-only sessions, subjects alternated between sessions of AX and Y trials in the same session and AX-only or Y-only trials with a 5 to 1 ratio, respectively. Subjects advanced to the Test phase after completing two consecutive sessions in which the FR2 + FI8-s reinforcement criterion was met on 80% of trials (i.e., percent correct), as well as discrimination ratios (DR; pecks at the previously-reinforced target location divided by all responses) above .5 for all AX, Y, T1, and T2 trials.

Test. All subjects received a single test session with four non-reinforced test trials each of landmarks A, X, and Y (for a total of 12 non-reinforced probe trials), and 20 reinforced trials each of T1 and T2 as in training (for a total of 40 reinforced training landmark trials), leading to a total of 52 trials in each test session. Test trials were intermixed among the reinforced trials, with the restriction that the first five trials could not be test trials. Additionally, all test landmarks (i.e., X, Y, and A) could not occupy the two leftmost and two rightmost squares. The locations for the two training landmarks were randomized as during training. Each test trial was terminated following the FR2 + FI8-s criterion for pecks at the target, but no reinforcement was delivered at the termination of the trial (adapted from Spetch, 1995; Leising et al., 2011). Training landmark trials on which the criterion was not met were automatically terminated after 60 s or after 20 cumulative incorrect pecks (i.e., as during training). Trial order and target position were counterbalanced across subjects. A variable 15-s ITI followed the termination of each trial. The session was terminated after 52 trials or 60 min, whichever came first.

Results & Discussion

Subjects required an average of 88.00 ($SD = 13.67$) sessions to complete landmark training. 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 target location. The percentage 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 result of which was then multiplied by 100. The peak location was that with the highest percentage of pecks. Figure 2

(Top panel) shows the average percent of pecks at each response location at test as a function of distance from the target (0) for A and X test trials, while the bottom panel shows the same data for Y trials. The peak search location was at the target for A and Y trials, but not X trials, where the peak search was at location -1, indicating good spatial control for landmarks A and Y, but not X. The percent of responses at the target for test trials with A and Y was also greater than to test trials with X. This difference was confirmed via a one-sample *t*-test against chance performance, which was calculated based on the total number of response locations that were not occupied by a landmark (i.e., landmark pecks were excluded from analysis). Chance performance was thus calculated by dividing one by the number of non-landmark locations (i.e., $1/7 = .14$). Search at the target was above chance on test trials of A, $t(3) = 7.03, p < .01, d = 3.51, 95\% \text{ CI } [.71, 6.35]$ and Y, $t(3) = 6.91, p < .01, d = 3.46, 95\% \text{ CI } [.69, 6.25]$, but not of X, $t(3) = -2.63, p = .08$, which instead showed search above chance at location -1, $t(3) = 4.09, p = .03, d = 2.05, 95\% \text{ CI } [.19, 3.85]$. No other response locations were searched above chance on any trial type, $t(3) < 1.00$.

A one-way ANOVA with repeated measures conducted on the percentage of responses to the target location revealed a significant difference among trial types A, X, and Y, $F(2, 9) = 32.46, p < .01, \eta^2 = .87, 95\% \text{ CI } [.52, .92]$. Planned comparisons revealed that X differed from A, $t(3) = 6.19, p < .01, d = 5.32, 95\% \text{ CI } [5.19, 5.44]$, as well as Y, $t(3) = 5.97, p < .01, d = 5.21, 95\% \text{ CI } [5.08, 5.33]$. More importantly, target responses did not differ between A and Y, $t(3) = .31, p = .77$, suggesting similar spatial control. Because this study was too underpowered for any conventional equivalence test results to be meaningful, we will not report those results (this applies to the rest of the experiments described in this article as well).

The results of Experiment 1 demonstrate the spatial overshadowing effect in a landmark-based search task, as well as the ability of a landmark (Y) not immediately proximal to the target location to acquire good spatial control. Search in the presence of A produced good spatial control reflecting the A-target spatial relationship, whereas search in the presence of X did not (i.e., no behavioral evidence for control by the training X-target spatial relationship), as can be seen in both the percent of pecks to the target location, as well as the distribution of pecks. Furthermore, the fact that the highest peak in X trials occurred at the -1 position suggests generalization to landmark X from A (cf. Sawa et al., 2005).

The similarity in performance, both with respect to percent of pecks to the target location and the distribution of pecks across the response array between trials with landmarks A and Y indicates that poor spatial control in the presence of landmark X was due to overshadowing, and not its distance from the target, as landmarks X and Y were equidistant from the target location (though in opposite directions). Moreover, the ability of Y to acquire good spatial control also shows that subjects had no difficulty perceiving landmarks that were two locations away from the target. Thus, it is unlikely that poor spatial control by the overshadowed stimulus (X) was due to a perceptual failure.

Experiment 2a

Experiment 2a investigated the theoretical account for overshadowing between landmarks. As discussed in the Introduction, there are many theoretical accounts of overshadowing that posit elemental associative processes. These theoretical approaches can be categorized into those that fail to account for extinction-mediated recovery from overshadowing (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981), and those that do (Dickinson & Burke, 1996; Miller & Matzel, 1988; Van Hamme & Wasserman, 1994).

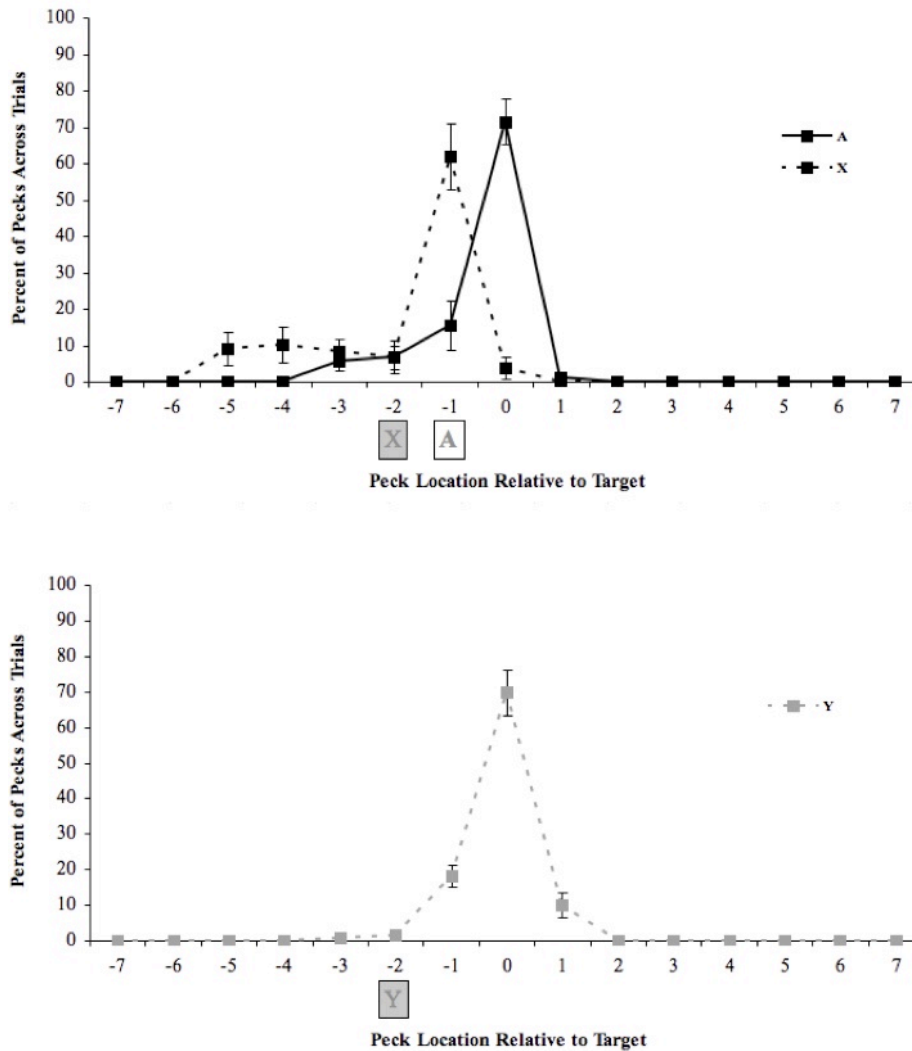


Figure 2. Percent of pecks as a function of peck location for Experiment 1. The data were standardized via concatenation of the peck data into an array ranging from -7 to 7, with 0 representing the unmarked Target location. The locations for landmarks A, X, and Y are indicated below the x-axes for reference; the data for subjects in which these actual landmark locations were counterbalanced were consolidated and standardized for analysis such that landmark A (the overshadowing landmark) is displayed in the -1 location while landmark X (the overshadowed landmark) and landmark Y (the non-overshadowed landmark) are displayed in the -2 locations. Error bars represent ± 1 SEM.

Following overshadowing training as described in Experiment 1, we administered post-training extinction of overshadowing landmark A and observed its effects on spatial control by overshadowed landmark X (see Table 2; cf. Leising et al., 2015). After training with compound landmark AX+ in Phase 1, subjects received conventional extinction treatment in which A was presented without reinforcement in Phase 2. If spatial control by X is best explained as a performance decrement, we should observe an increase in spatial control by X after extinction of A. We compared within-subject spatial control by X to spatial control by another landmark Y, that during overshadowing training had been paired with the target in the presence of a

more proximal landmark B (BY+). Because B was not extinguished in Phase 2, Y should continue to show poor spatial control indicative of an overshadowing effect.

Table 2
Experimental design for Experiment 2a.

Phase I	Phase II	Testing (spatial control)			
		X	Y	A	B
AX+ / BY+ / T1+ / T2+	A- / T1+ / T2+	?	Low	Low	High

Note. Landmarks A and B were the overshadowing landmarks, while X and Y were the overshadowed landmarks. T1 and T2 were the training landmarks. A '+' indicates reinforcement, while a '-' indicates nonreinforcement. The slash (/) separates events that are interspersed. 'Low' and 'High' indicate predicted spatial control by the landmark at test.

Method

Subjects

As in Experiment 1, six pigeons that had previously served as subjects in spatial learning tasks on the touchscreen were used. Subjects received the same care as described previously, and were naïve with respect to the visual stimuli used in this experiment.

Apparatus

The same apparatus and stimuli were used as in Experiment 1.

Procedure

Pretraining and Search Training were as in Experiment 1.

Phase 1 (Landmark training). As in Experiment 1, except that landmark training sessions consisted of 20 reinforced compound trials of AX+ (Figure 1b) interspersed with 20 reinforced compound trials of BY+ (Figure 1d), along with reinforced training trials with landmarks T1+ and T2+ (20 trials of each, interspersed throughout each session; Figure 1e & 1f). This amounted to a total of 80 trials per session. For half the subjects, on the compound trials, A was positioned at the location to the immediate left of the target, and X was positioned to the immediate left of A (i.e., two locations to the left of the target). On the remaining trials, B and Y were positioned one and two locations, respectively, to the right of the target. The directions of all landmarks (including T1 and T2) relative to the target location were counterbalanced for the remaining half of the subjects. The position of the target was restricted (counting up from the left most square in the array) to locations one to four for AX trials and five to eight for BY trials. The position of the target on T1 and T2 trials were restricted as in Experiment 1.

Phase 2 (Extinction). All subjects received 40 non-reinforced (i.e., extinction) trials of A- per session (Figure 1g), interspersed with 20 reinforced trials each of T1 and T2, resulting in a total of 80 trials per session. As such, responses to the square located to the immediate right of A were not reinforced, nor were pecks to other squares on trials with A. T1 and T2 trials remained identical as in the previous phase to ensure that subjects continued responding during each session. Placement of a landmark on the touchscreen varied across trials as in Phase 1. During this phase, the target location, as well as all the other non-landmark locations, were lit to 35% brightness (i.e., indistinguishable from one another). To prevent extinction of A from affecting responding to T1 and T2, the schedule of reinforcement during this phase started from CRF, to a modified FR2, and finally to an FR2 + FI 8-s as in the previous phase. All subjects received a minimum of seven sessions before moving on to testing. As soon as a pigeon had two consecutive sessions in which the DR for A trials was less than .5, and the percent correct for T1 and T2 trials remained above 80%, it progressed to the Test phase. Each session was terminated after 80 trials or 60 min, whichever came first.

Test. All subjects received a single test session with four non-reinforced test trials each of landmarks X, Y, A, and B (for a total of 16 non-reinforced probe trials), and 20 reinforced trials each of T1 and T2 as in Phases 1 and 2 (for a total of 40 reinforced training landmark trials), leading to a total of 56 trials in the session. Test trials were intermixed among the reinforced trials, with the restriction that the first five trials could not be test trials. Additionally, all test landmarks (i.e., X, Y, A, and B) could not occupy the two leftmost and two rightmost squares. The locations for the two training landmarks were randomized as during training. Each test trial was terminated following the FR2 + FI8-s criterion for pecks at the target, but no reinforcement was delivered at the termination of the trial. Training landmark trials on which the criterion was not met were automatically terminated after 60 s or after 20 cumulative incorrect pecks (i.e., as during training). Trial order and target position were counterbalanced across subjects. A variable 15-s ITI followed the termination of each trial. The session was terminated after 56 trials or 60 min, whichever came first.

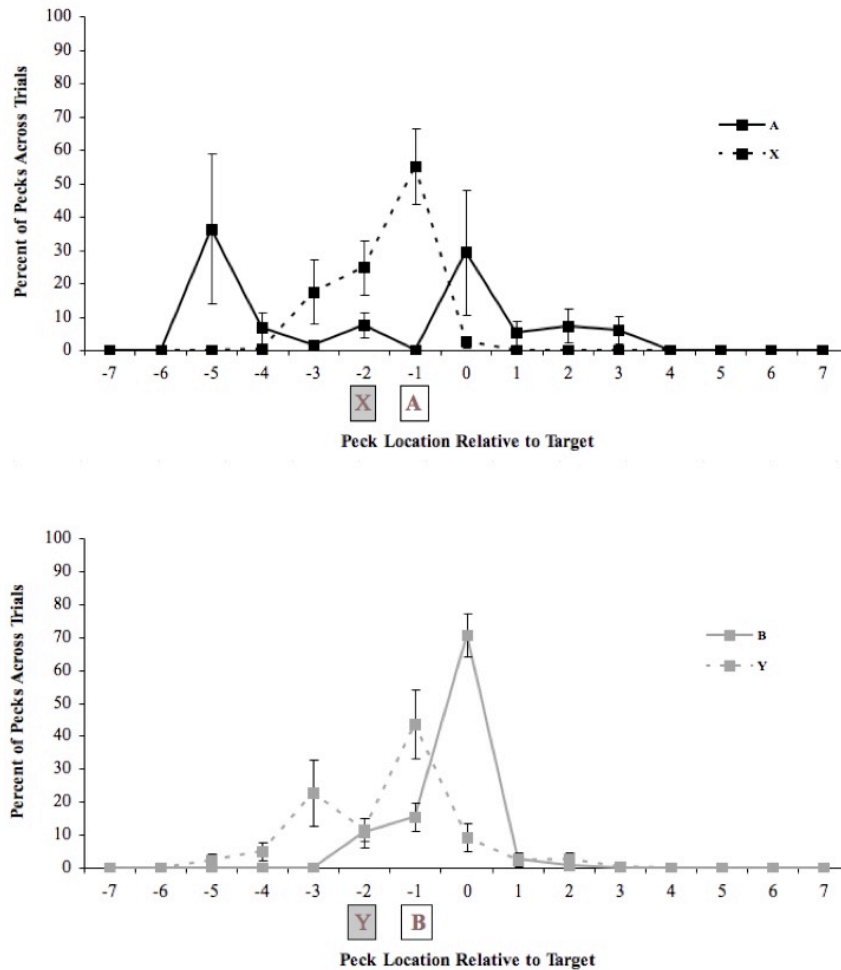


Figure 3. Percent of pecks as a function of peck location for Experiment 2a, displayed as in Experiment 1 (Figure 2). The locations for landmarks A, X, B, and Y are indicated below the x-axes for reference; the data for subjects in which these actual landmark locations were counterbalanced were consolidated and standardized for analysis such that overshadowing (A and B) and overshadowed landmarks (X and Y) are displayed in the -1 and -2 locations, respectively. Error bars represent ± 1 SEM.

Results & Discussion

Subjects required an average of 19.5 ($SD = 10.7$) sessions to complete landmark training (Phase 1) and an average of 18.8 ($SD = 10.5$) sessions to complete extinction training (Phase 2). If there were no pecks to any

response location during any trial, which would happen frequently during test trials of the extinguished landmark A, the data were omitted.

Figure 3 (Top panel) shows the average percent of pecks at each response location at test as a function of distance from the target (0) for A and X test trials, while the bottom panel shows the same data for B and Y test trials. The peak search location was at the target for B trials, but not any of the other trials. The search locations for X and Y showed a similar distribution with response peaks at -1, replicating the overshadowing effect as demonstrated by Leising et al. (2011) and in Experiment 1. The bimodal response peaks on test trials with A (at locations 0 and -5) cannot be meaningfully interpreted given the very small absolute number of responses at these locations from the three birds that did respond on test trials with A (Table 3).

Table 3

Total number of pecks across all test trial types in Experiment 2a.

Bird Name	Trial Type			
	A	X	B	Y
Cosmo	11	41	137	83
Gambit	0	22	47	52
Orwell	1	59	58	79
Storm	0	7	165	24
Wolverine	40	85	263	73
Xavier	0	2	119	344
<i>M</i>	8.67	36.00	131.50	57.33

Note. Landmarks A and B were the overshadowing landmarks, while X and Y were the overshadowed landmarks. Landmark A was extinguished in Phase 2.

The percent of responses at the target for test trials with B was greater relative to trials with all other landmarks. Single-sample *t*-tests conducted against chance performance (.14 as in Experiment 1) revealed that search at the target was above chance for test trials of B, $t(5) = 7.32, p < .01, d = 2.99, 95\% \text{ CI} [1.02, 4.94]$, but not for that of A, $t(2) = .58$, X, $t(5) = -6.31$, or Y test trials, $t(5) = -1.01, ps > .10$. No other response locations were searched above chance on any trial type, $ts(5) < 1.94, ps > .10$.

As mentioned previously, the distribution of responses was very similar between X and Y trials, which exhibited their highest peaks at location -1. Paired samples *t*-tests on proportion of responses during testing at locations 0 (i.e., target), -1, -2, and -3 between X and Y trials revealed no significant differences, $ts(5) < 1.75$. This suggests that response distributions between these two overshadowed landmark trials were similar to each other. Also, while the peak responses for X and Y were no different from each other (at location -1), a paired-samples *t*-test revealed that these peaks were significantly lower in magnitude than that for B, $ts(5) < 4.19, ps < .04, ds = .59$ and 1.08 respectively, $95\% \text{ CIs} [.38, .80]$ and $[.88, 1.28]$ respectively.

A one-way repeated-measures ANOVA conducted on mean percent of responses at the target (i.e., location 0) revealed a significant difference between X, B, and Y trials, $F(2, 15) = 47.58, p < .01, \eta^2 = .86, 95\% \text{ CI} [.64, .91]$. (Data from A trials could not be included in the analysis because there were no responses from half the subjects in such trials due to extinction training.) Planned comparisons indicated that responses

during B trials were significantly higher than that during both X and Y trials ($ps < .01$). Additionally, the two overshadowed landmarks X and Y did not differ significantly in proportion of target responses.

The results of Experiment 2a demonstrate the overshadowing effect in a landmark-based spatial search task. Search in the presence of B produced good spatial control, whereas search in the presence of X and Y did not. The weak spatial control in X and Y were reflected in both the percent of pecks to the target location, as well as the distribution of pecks, which were no different than each other. Additionally, the fact that the highest peak in X and Y trials occurred at the -1 position (similar to what was observed in test trials with X in Experiment 1) again suggests a generalization to landmark Y from B, and to X from the pre-extinguished A. Search in the presence of A showed the poorest spatial control indicated by the lack of responses during probe trials by half the subjects, and a high degree of variance between the remaining half, reflecting strong extinction learning. The results also indicate an absence of recovery of spatial control by X after A had been extinguished, as the response profile to X was neither qualitatively nor quantitatively different than that to Y. This suggests that it is unlikely that a latent X-target association had developed during spatial overshadowing in this procedure.

Furthermore, it has been demonstrated that the discriminability and proximity between individual elements within a compound stimulus determine whether retrospective revaluation effects (if the elements are discriminable and sufficiently far apart) or mediated generalization effects (if the elements are similar and proximal to one another) are obtained (e.g., Liljeholm & Balleine, 2009). Since the visual stimuli used as landmarks in the current experiment could be construed as being similar and close to one another, it might be tempting at first glance to attribute the generalization to landmark Y from B (and to X from the pre-extinguished A) to mediated generalization, and it was this that impeded the emergence of any retrospective revaluation effects, as opposed to a deficit in the acquisition of X-target and Y-target associations. However, our data do not support this notion, because we would have also observed extinction of spatial control by X (similar to the extinguished A) if mediated generalization were the case.

Experiment 2b

In Experiment 2a, we tested whether post-training extinction of an overshadowing landmark resulted in the recovery of spatial control by an overshadowed landmark. No recovery was observed. Experiment 2b was similar to Experiment 2a, except that instead of post-training extinction of the overshadowing landmark, we retrained overshadowing landmark A to a new target location. Would retraining of A result in the recovery of spatial control by overshadowed X (see Table 4)? Blaisdell et al. (1998) reported that the degree of overshadowing to an aversive CS depended on the similarity between the X-US and A-US temporal relationships. Overshadowing was only observed when the A-US and X-US temporal relationships matched. In a follow-up set of experiments in which A and X initially shared the same temporal relationship to the US, Blaisdell, Denniston, and Miller (1999) showed that overshadowing could be abolished by retraining A with a different temporal relationship to the US. This outcome is consistent with an expression-focused, rather than acquisition-focused account of the overshadowing effect. Experiment 2b explores this effect in the spatial domain: Does poor spatial control by X result from an acquisition deficit or a performance deficit? We tested this by retraining A to a new target location following successful overshadowing training. If spatial overshadowing is mediated by a strong A-target association that competes with the X-target association when the two landmarks signal the same target, then a post-training shift in the A-target location should recover spatial control by landmark X at test.

Table 4
Experimental design for Experiment 2b.

Phase I	Phase II	Testing (spatial control)			
		X	Y	A	B
AX+ / BY+ / T1+ / T2+	A2+ / T1+ / T2+	?	Low	High	High

Note. Landmarks A and B were the overshadowing landmarks, while X and Y were the overshadowed landmarks. Here, A2+ indicates retraining A to a new target (i.e., ‘Target 2’ in Figure 1, Panel h). A ‘+’ indicates reinforcement. A slash (/) separates events that are interspersed. ‘Low’ and ‘High’ indicate predicted spatial control by the landmark at test.

Method

Subjects

As in Experiment 2a, but with experimentally-naïve pigeons. It is worthwhile to note that all subjects, but one, were newly acquired pigeons, and thus had substantially less experience with experiments in operant chambers compared to subjects in Experiment 2a, which may have contributed to the increased amount of training needed to reach criterion performance in Phase 1.

Apparatus

The same apparatus and stimuli were used as in Experiments 1 and 2a.

Procedure

Pretraining, Search training, and Phase 1 (Landmark training) were as in Experiment 2a.

Phase 2 (Retraining of A). All subjects received 40 retraining trials of landmark A with its new target location (i.e., A-target 2) per session, interspersed with 20 reinforced trials each of T1 and T2, resulting in a total of 80 trials per session. The target for A was now located two locations to the opposite direction of the original target (Figure 1h). T1 and T2 trials remained identical as in the previous phase to ensure that subjects continued responding during each session. The placement of a landmark on the touchscreen varied across trials. During this phase, the target location, as well as all the other non-landmark locations, were lit to 35% brightness (i.e., indistinguishable from one another). As in Phase 1, the schedule of reinforcement during this phase started from CRF, to a modified FR2, and finally to an FR2 + FI8-s. All subjects were given at least seven sessions in this phase. After completing the seventh session, and from that point on, subjects that had two consecutive sessions in which the DR for all trials was above .5, as well as having a percent correct for T1 and T2 trials above 80%, progressed to the Test phase. Each session was terminated after 80 trials or 60 min, whichever came first.

Test. As in Experiment 2a.

Results & Discussion

One subject failed to show evidence during testing of having acquired spatial control by Landmark B. Its data were removed from all subsequent analyses.

The remaining five subjects required a mean of 50.2 ($SD = 21.4$) sessions to complete landmark training (Phase 1) and a mean of 102.8 ($SD = 45.6$) sessions to complete retraining (Phase 2). Figure 4 (Top panel) shows the mean percent of pecks at each response location at test as a function of distance from the target location for A and X test trials, while the bottom panel shows these data for B and Y test trials. The peak search location was at target 1 (location 0) for B and target 2 (location -3; indicated by T₂ in Figure 4) for A

trials, but not any of the other trials. The search locations for X and Y were consistent with those in Experiment 2a, again demonstrating the overshadowing effect.

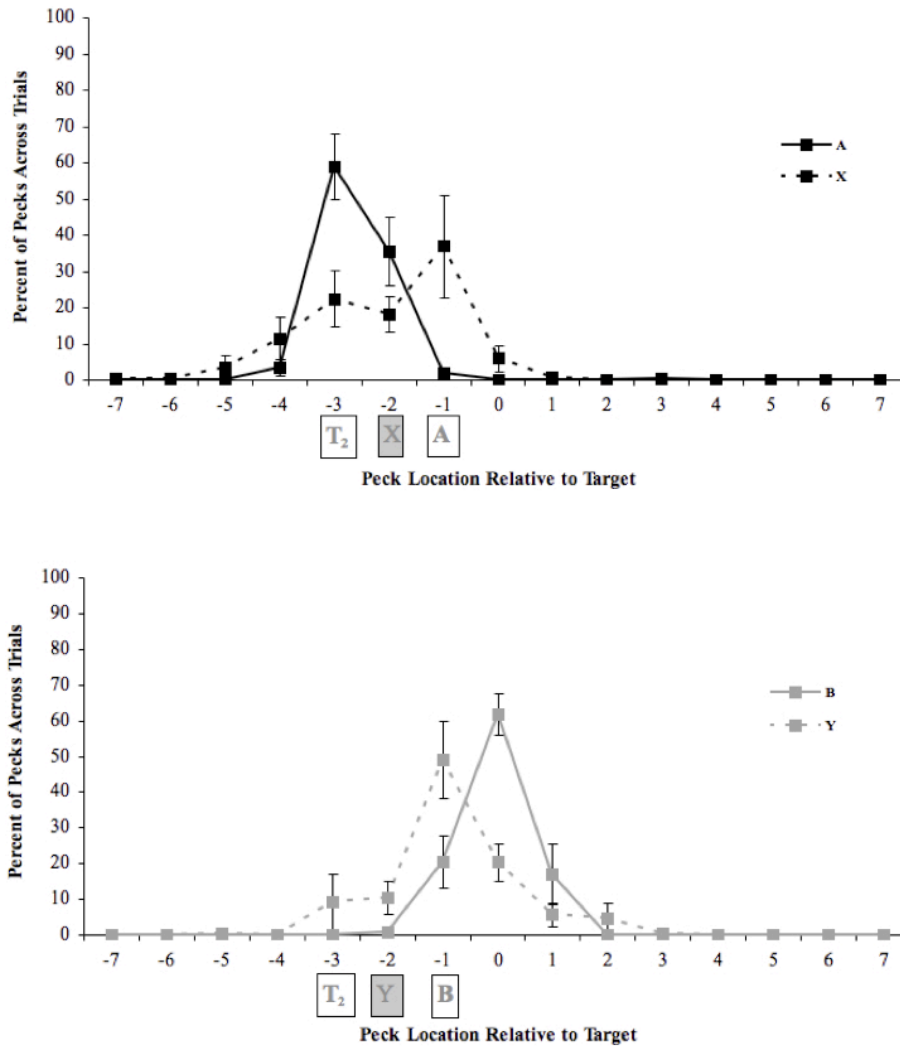


Figure 4. Percent of pecks as a function of peck location for Experiment 2b, displayed as in Experiment 2a (Figure 3). The locations for landmarks A, X, B, and Y are indicated below the x-axes for reference; the data for subjects in which these actual landmark locations were counterbalanced were consolidated and standardized for analysis such that overshadowing (A and B) and overshadowed landmarks (X and Y) are displayed in the -1 and -2 locations, respectively. ‘T₂’ indicates the Phase 2 Target location for A. Error bars represent ± 1 SEM.

Single sample *t*-tests conducted against chance performance (.14 as in Experiments 1 and 2a) revealed that search at target 1 (location 0) was above chance for test trials of B, $t(4) = 8.20$, $p < .01$, $d = 3.67$, 95% CI [1.09, 6.25], but not for X, $t(4) = -2.30$, or Y test trials, $t(4) = 1.22$, $ps > .08$. A similar test for A could not be conducted because no subjects made any responses at this location during these trials. A *t*-test at the retrained (target 2) location for A (i.e., location ‘-3’) revealed that search was above chance for test trials of A, $t(4) = 4.45$, $p < .01$, $d = 1.99$, 95% CI [.38, 3.55], but not for X, $t(4) = 1.07$, or Y test trials, $t(4) = -.61$, $ps > .34$. A similar test for B could not be conducted because no subjects made any responses at this location during these trials. Beyond these, except for responses at location -1 on Y test trials and -2 on A test trials, no other response locations were searched above chance on any trial type, $ts(4) < 1.01$, $ps > .10$.

For the aforementioned Y test trials at location -1, responses were found to be above chance performance, $t(4) = 3.27, p = .02, d = 1.46, 95\% \text{ CI } [.12, 2.74]$. Nonetheless, the fact that this did not occur at location 0 indicates poor spatial control and thus a strong overshadowing effect. Interestingly, it was also revealed that the percent of responses were found to be above chance performance for A trials at location -2 (i.e., one location to the right of the A target location), $t(4) = 2.29, p = .04$. This likely reflects a broader generalization gradient around A's new target 2 which is farther from A than was the original target 1.

As in Experiment 2a, we found that the highest peaks of responding on trials of X were at location -1. There appears to be a discernable peak only at location -1 for Y trials. Nevertheless, a paired-samples *t*-test at both locations -1 and -3 revealed that responses were not different than each other, $t_s(4) = -1.01$ and 2.19 , for X and Y respectively, $p_s > .09$. A paired-samples *t*-test was also conducted for responses for A and B test trials at their respective target locations (i.e., locations -3 and 0, respectively), revealing no significant difference in the magnitudes of those peaks, $t(4) = -.24, p = .82$. This indicated that responding to these two target locations were no different from each other both in terms of magnitude and relative spatial control.

A repeated-measures ANOVA conducted on the average percent of responses for trials A, X, B, and Y at target 1 (location '0') and target 2 (location '-3') revealed a significant main effect of response location, $F(3, 12) = 7.20, p < .01, \eta_p^2 = .31, 95\% \text{ CI } [.03, .47]$, and a significant trial type X response location interaction, $F(3, 12) = 27.42, p < .01, \eta_p^2 = .78, 95\% \text{ CI } [.59, .84]$. Planned comparisons involving responses to B trials at target 2 and A trials at target 1 cannot be conducted because subjects did not respond at all at these locations during their respective trials. However, a qualitative appraisal of Figure 4 indicates that this interaction is largely driven by high responding during B trials and low responding during A trials at target 1, and vice-versa at target 2.

Further examination of the data from individual subjects revealed two response profiles for spatial control by X (see Figure 5), something that was not observed in Experiment 2a. Three subjects (Subgroup X1) appeared to show a spatial response profile characteristic of spatial overshadowing in our procedure (i.e., a peak at location -1), while two of the subjects (Subgroup X2) appeared to show spatial sensory preconditioning in which integration of an X-A spatial map with an A-target 2 spatial map resulted in an X-target 2 spatial inference (cf. Blaisdell & Cook, 2005; Sawa et al., 2005), as evidenced by peak spatial control at location -3. The percent of pecks at location -3 between these two groups of subjects was revealed to be significantly higher for subgroup X2 than for subgroup X1, $t(3) = 3.48, p < .04, d = 3.56, 95\% \text{ CI } [3.45, 3.65]$. A similar test was conducted for location -1, which revealed the percent of pecks to be marginally higher for the subgroup X1 than subgroup X2, $t(3) = 2.79, p = .07$ (bearing in mind that there were only three subjects in the former subgroup and two subjects in the latter subgroup). For subgroup X1, responding at the peak location (i.e., position -1) was greater than chance, $t(2) = 3.21, p = .04, d = 1.85, 95\% \text{ CI } [-.19, 3.84]$; as was the case for subgroup X2, where responding at the peak location (i.e., location -3) was significantly higher than chance, $t(1) = 9.53, p = .03, d = 6.74, 95\% \text{ CI } [-.15, 15.19]$. The peak magnitude of these two subgroups at their respective peak locations were not found to be different from each other, $t(3) = 1.00, p = .39$.

Like the results of Experiment 2a, the results of Experiment 2b effectively demonstrated the overshadowing effect in a landmark-controlled spatial-search task, wherein responding in the presence of B produced good spatial control, whereas search in the presence of X and Y did not. We again observed a generalization to landmark Y from B. It remains unclear why 2 types of response profiles to X were observed, as further research with greater statistical power will be needed to shed more light on these speculative findings. Nevertheless, in both cases, we again did not obtain evidence of post-training-facilitated recovery of spatial control by the overshadowed landmark X. As such, we did not produce a spatial equivalent of the

recovery effect obtained by Blaisdell et al. (1999), again failing to find evidence for the acquisition of a latent X-target spatial association during overshadowing training.

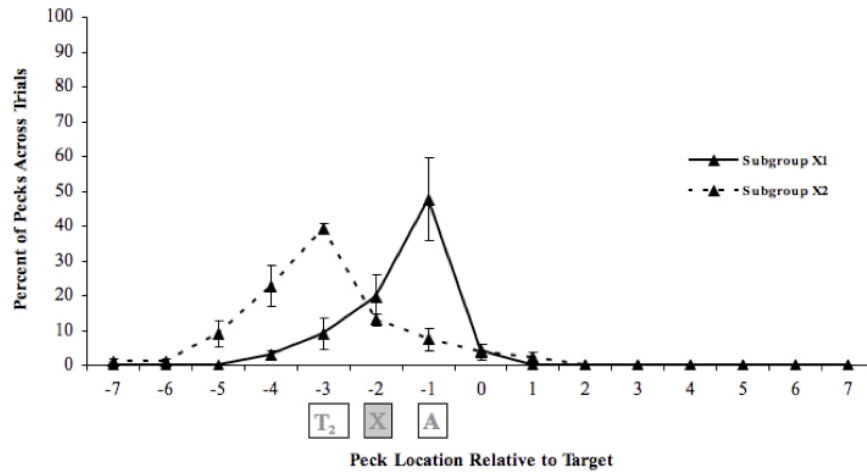


Figure 5. Percent of pecks on X trials as a function of peck location for Experiment 2b, separated by subjects in Subgroup X1 (subjects that showed the characteristic spatial overshadowing response profile) and Subgroup X2 (subjects that generalized X from the Phase 2 A-target spatial relationship) subgroups. ‘T₂’ indicates the new target location for A in Experiment 2b. Error bars represent ± 1 SEM.

General Discussion

In Experiment 1, we compared spatial control by non-overshadowed-landmark Y and overshadowed-landmark X that were both distal and equidistant to the target. Poor spatial control by X relative to Y therefore suggests overshadowing by more proximal landmark A that accompanied X during training. We then examined whether extinction (Experiment 2a) or retraining (Experiment 2b) of spatial control by overshadowing landmark A would affect subsequent spatial control by overshadowed landmark X. Contrary to what has been found in aversive Pavlovian conditioning and human causal learning paradigms (e.g., Blaisdell et al., 1999; Beckers, Vandorpe, Debeys, & De Houwer, 2009; Dickinson & Burke, 1996; Kaufman & Bolles, 1981; Matzel et al., 1985; Wasserman & Berglan, 1998), but consistent with appetitive Pavlovian conditioning (Holland, 1999), we found no evidence of post-training recovery from overshadowing to X. Our data support the contention that overshadowing in the spatial domain reflects a deficit in learning, as opposed to a deficit in performance.

One notable observation is that responses to X in all three experiments were not randomly distributed across all response locations, but were instead clearly localized. This might appear to support a generalization decrement account of overshadowing consistent with Pearce’s (1994) configural theory, rather than elemental accounts that attribute overshadowing to cue competition. However, prior studies wherein X was tested in compound (i.e., AX) after being trained alone showed better spatial control, compared to a condition where compound training occurred before testing X itself (as described in the Introduction; Leising et al. 2011), contradict this notion – Pearce’s generalization decrement account would predict no such difference. As such, our results still support the position that spatial overshadowing is probably controlled by elemental learning processes that are consistent with the associative accounts by Rescorla and Wagner (1972), Mackintosh (1975), Pearce and Hall (1980), or Wagner (1981). It also supports the notion that this failure to observe recovery from spatial overshadowing may be that spatial overshadowing simply reflects an acquisition deficit.

This alternative received strong support, especially when again considering the nature of the response to the overshadowed landmark. Rather than a lack of responding to the overshadowed landmark, responding showed a degree of spatial control, though not as sharp as did the overshadowing landmark. The location of spatial control suggested generalization from the overshadowing landmark. Generalization of spatial control has been reported by others in both overshadowing (Chamizo, Rodrigo, & Mackintosh, 2006; Leising et al., 2011) and sensory preconditioning (Sawa et al., 2005).

If it is the case that associative processes govern spatial learning, then why did we fail to observe recovery from overshadowing? One possibility is that compound AX+ training might have simultaneously caused competition and positive mediation between A and X. Timberlake, Sinning, and Leffel (2007) reported evidence for the simultaneous occurrence of both competition between A and X for spatial control, and mediation of spatial control of X by A in a Morris water maze swim-escape task. Thus, while A might overshadow spatial control by X due to compound conditioning, post-training extinction (Experiment 2a) or counterconditioning (Experiment 2b) of A might mediate a similar change in behavioral control by X as well, thereby mitigating recovery from overshadowing. Indeed, we found evidence in two of five subjects of Experiment 2b for sensory preconditioning, a form of mediated conditioning.

A second possibility might be our use of a within-subject design in which both the experimental (AX) and control (BY) conditions are assessed within subjects. To our knowledge, all prior examples of recovery from overshadowing in nonhuman animals come from experiments utilizing between-subjects designs. Thus, our design was somewhat novel, and it is possible that a within-subject design (involving the use of a greater number of cues, thus necessitating greater discrimination learning between sets of cues) is less than optimal for expression of retrospective revaluation effects.

A third reason for why recovery from overshadowing was not observed following post-training manipulations of A include the use of an appetitive reinforcer, to which Holland (1999) also attributed as a possible reason for his failure to observe recovery from extinction-mediated overshadowing. Perhaps if we had used an escape/avoidance procedure by which the pigeons were required to make an instrumental response at the target to avoid an aversive stimulus, such as an electric shock, we might have observed recover of spatial control by X after extinction or counterconditioning of A.

Finally, an uninteresting possibility is that the birds simply failed to detect the presence of X during training, and thus did not receive sufficient training to learn about the X-goal association. This is unlikely for several reasons. One, the goal is randomly determined on each trial, so the pigeons view the landmarks from multiple viewpoints. In addition, pigeons learned to avoid pecking at the location of LM X during training, which indicates it was detected. Third, performance on Y in Experiment 1 suggests that a landmark positioned two locations from the goal provides useful information regarding the location of the goal.

Taken together, our data do not support revised-acquisition and performance-focused accounts of overshadowing. One commonality shared between these models is their use of within-compound associations, and it could be that there is something about spatial learning paradigms that hinders the use of within-compound associations that have otherwise been demonstrated in conventional Pavlovian conditioning procedures. Furthermore, it could also be the case that such within-compound associations extinguish more rapidly during post-training manipulations of A, thereby attenuating retrospective recovery of spatial control by X. Further work employing systematic exploration of parameters in spatial and non-spatial learning paradigms would be needed to shed light on this possibility.

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