

## Spatial integration during performance in pigeons

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### ABSTRACT

We've shown that pigeons can integrate separately acquired spatial maps into a cognitive map. Integration requires an element shared between maps. In two experiments using a spatial-search task in pigeons, we test spatial combination rules when no shared element was present during training. In all three experiments, pigeons first learned individual landmark-target maps. In subsequent tests involving combinations of landmarks, we found evidence that landmarks collaborate in guiding spatial choice at test (Experiment 1). In Experiment 2, pigeons were trained on two landmarks with different proximities to the target. On tests on a compound of both landmarks, pigeons showed stronger spatial control by the more proximal landmark, a performance overshadowing effect. Extinction of the proximal landmark shifted spatial control to the non-extinguished distal landmark. This reveals that the performance overshadowing effect was associative in nature, and not due to perceptual or spatial biases. This emphasis on spatial control during performance reflects the emphasis on performance processes that were a major focus in Ralph Miller's lab.

For many animals, foraging requires navigating in search of food. While many sensory systems are employed during food seeking, visually-guided foragers can use objects that share a consistent spatial relation to a hidden food item as landmarks to direct search more effectively. The learning of spatial relations between landmarks and food goal have been shown to follow the principles of associative learning (Leising and Blaisdell, 2009; Miller and 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 that serve as landmarks signaling 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 and Cook, 2005; Sawa et al., 2005) to blocking (Stahlman and Blaisdell, 2009; see also Rodrigo et al., 1997), conditioned inhibition (Leising et al., 2012), and overshadowing (Leising et al., 2011; Wong et al., 2016; see also Blaisdell and Cook, 2005; Sánchez-Moreno et al., 1999; Spetch, 1995).

Overshadowing of spatial associations, in particular, has gained wide support from many labs using a variety of procedures—ranging from touchscreen-equipped operant chambers to open field studies—using pigeons as subjects. A common finding is that a landmark more proximal to the target overshadows a more distal landmark (Leising et al., 2011; Spetch, 1995; Wong et al., 2016). Moreover,

spatial overshadowing appears to be governed by competition between the elements of a compound landmark rather than generalization decrement from the training compound to the test element (Leising et al., 2011).

In a more recent study, we report evidence that spatial overshadowing results from a learning deficit at the time of acquisition rather than a performance deficit at the time of test (Wong et al., 2016). Conventional post-training recovery procedures, such as post-training extinction or counterconditioning of the overshadowing landmark, failed to produce a recovery in responding to the overshadowed landmark on a subsequent test.

All of these prior studies address the question of how does information from separate landmarks combine over the course of acquisition. In the current series of experiments, we investigate the question: How do pigeons combine information from separately acquired spatial maps presented together at test? That is, what are the performance rules for spatial map integration? This question is important because in the real world, the learning situation in which an animal learns a landmark-target association often only contains a subset of the relevant features while others are obscured by other objects, terrain, weather conditions, or simply a restricted point of view (e.g., when the animal is sitting in a depression in the terrain on an overcast day). Oftentimes these same landmarks are encountered later in conditions more favorable to having visual access to a more complete set of surrounding landmarks and features. In these situations, the animal must decide

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which landmarks or other cues to utilize when making navigation and foraging decisions.

Two experiments were performed to explore this novel domain. The first asked: How does information from separately-acquired landmarks integrate when presented in compound? The second asked: How do pigeons resolve conflicts between elements within a compound? We test each element of compound of separately trained landmarks whose information about target location is consistent or conflicting. The second experiment also addressed the issues of how spatial proximity to the target and landmark extinction affect spatial control by conflicting landmarks? The motivation for Experiment 2 was the insight that the same principles that govern landmark competition during acquisition may govern landmark competition at the time of test as well, despite each element having demonstrated strong control over spatial search on its own.

## 1. Experiment 1

In this experiment, we explore how multiple, independently trained landmarks guide spatial search when presented in compound. This experiment is analogous to that of Sawa et al. (2005) in which spatial control by a chain of associations was demonstrated after each link of the associative chain had been separately trained. That is, after presenting pigeons with two landmarks A and B with a consistent spatial relationship on the surface of a touchscreen monitor (i.e., an  $A \leftarrow \rightarrow B$  map), and then training pigeons to find a hidden target in the presence of A (i.e., the  $A \rightarrow$  Target map), pigeons made a spatial inference of where to search based on the integrated  $B \rightarrow A \rightarrow$  Target map. In the current experiment, we train four independent landmark Target associations with landmarks A, B, X, and Y. After these relationships have been well learned, we then present pigeons with various compounds consisting of one of the landmarks flanked by two others, such as A flanked by X, or Y flanked by B. These compounds are constructed in such a way that spatial information conveyed by the central landmark should bias the choice of which flanking landmark should exert greatest control on Target search behavior. If pigeons show evidence of such bias, this suggests that landmark information can spontaneously combine and concatenate at test without any prior training. Such ability would seem a useful function for an animal facing novel combinations of informative stimuli in the real world.

### 1.1. Methods

#### 1.1.1. Subjects

Six experimentally-naïve adult White Carneaux pigeons (*Columba livia*) participated in the experiment. Pigeons were individually housed in steel home-cages with metal-wire mesh floors in a vivarium, and a 12-h light-dark cycle was maintained. Testing was conducted 5 days a week during the light cycle. The pigeons were maintained at approximately 85% of their free-feeding weights, and were given free access to grit and water while in their home-cages.

#### 1.1.2. Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide  $\times$  36 cm deep  $\times$  38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550 M) visible through a 23.2  $\times$  30.5 cm viewing window in the middle of the front panel of the chamber. Pecks to the monitor were detected by an infrared touchscreen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V house-light located in the ceiling of the box was used for illumination, except during time outs. Except where otherwise noted, a 5  $\times$  5 grid of empty 12-mm diameter disks with a white border was displayed on the screen during the entirety of each session (see examples in Fig. 1). Four colors, green, red, blue, and yellow, could serve as landmarks (color assignments were counter-balanced across birds). A food hopper (Coulbourn Instruments,

Allentown, PA) was located below the monitor with an access hole situated flush with the floor. When in the raised position, the hopper provided access to pigeon pellets. All experimental events were controlled and data recorded with a Pentium III-class computer (Dell, Austin, TX). A video card controlled the monitor using the SVGA graphics mode (800  $\times$  600 pixels).

### 1.2. Procedure

#### 1.2.1. Pretraining

Pigeons were first trained to peck a white circle that was presented in the center of a blank, dark screen (i.e., the 5  $\times$  5 grid of disks was not present during pretraining). A single peck to the circle resulted in the circle disappearing and the hopper rising for 3 s before lowering again. This was followed by a 60-s intertrial interval (ITI) before the next circle was displayed. Once the pigeon was consistently responding to the circle it progressed to landmark training.

#### 1.2.2. Landmark training Phase 1

Beginning with Phase 1 and continuing throughout the rest of the experiment the 5  $\times$  5 grid was displayed on the screen during the entirety of each session. Phase 1 training consisted of 40 trials with landmark (LM) A and 40 trials with LM B. Trial order was determined randomly and sessions ended after 60 min had elapsed or once all trials were completed, whichever came first. A and B were each assigned a different one of the four colors, counterbalanced across bird (e.g., Bird 1, A = red, B = Green; Bird 2, A = Green, B = Blue, etc.). LM locations were randomly determined across trials from all array locations except those along the outer edges of the array. The disks on either side of the landmark were filled with white (Fig. 1, upper left panel). One of the two white disks was designated the target disk. Pecking the target disk resulted in the hopper being raised for 3 s using a fixed ratio (FR) 1 schedule of reinforcement. For half the birds, the target was to the right of A and to the left of B; and for the other half the target was to the left of A and the right of B. Pecks to the non-target white disk had no effect. Multiple reinforcements were available within a trial, with delivery occurring each time the response criterion was met. Trials terminated after 30 s, after which all disks would appear as white outlines for a 12-s ITI, followed by the next trial. If during a trial a landmark disk was pecked, all disks would appear as white outlines for 5 s, followed by continuation of the current trial. This time-out procedure was implemented to reduce landmark pecks. The trial timer was stopped during the 5-s time-out to ensure a cumulative trial-time of 30 s. To advance to Phase 2 a 75% accuracy for target pecks was required.

#### 1.2.3. Landmark training Phase 2

Training consisted of alternating sessions of A+ and B+ trials as in Phase 1, and of X+ and Y+ training. X+ and Y+ training was similar to A+ and B+ training, except that two different colors were used as LMs X and Y, and the white disks appeared above and below LMs X and Y (Fig. 1, upper right panel). The target was above X and below Y for half the birds, and below X and above Y for the remaining birds. Target pecks were rewarded and time-outs given as in Phase 1. To advance to Phase 3 a 75% accuracy for target pecks was required.

#### 1.2.4. Landmark training Phase 3

The procedure was the same as in Phases 1 and 2, except that 20 trials each of A+, B+, X+, and Y+ trials were interspersed within each session, for a total of 80 trials per session. Also, reinforcement of target pecks was increased to a random ratio (RR) 2 schedule of reinforcement. Once peck rates to all landmarks stabilized, the schedule was increased to an RR5. To advance to the test phase a 75% accuracy for target pecks was required.

#### 1.2.5. Landmark integration tests

Each test session contained 100 trials: 21 trials each of A+, B+, X+

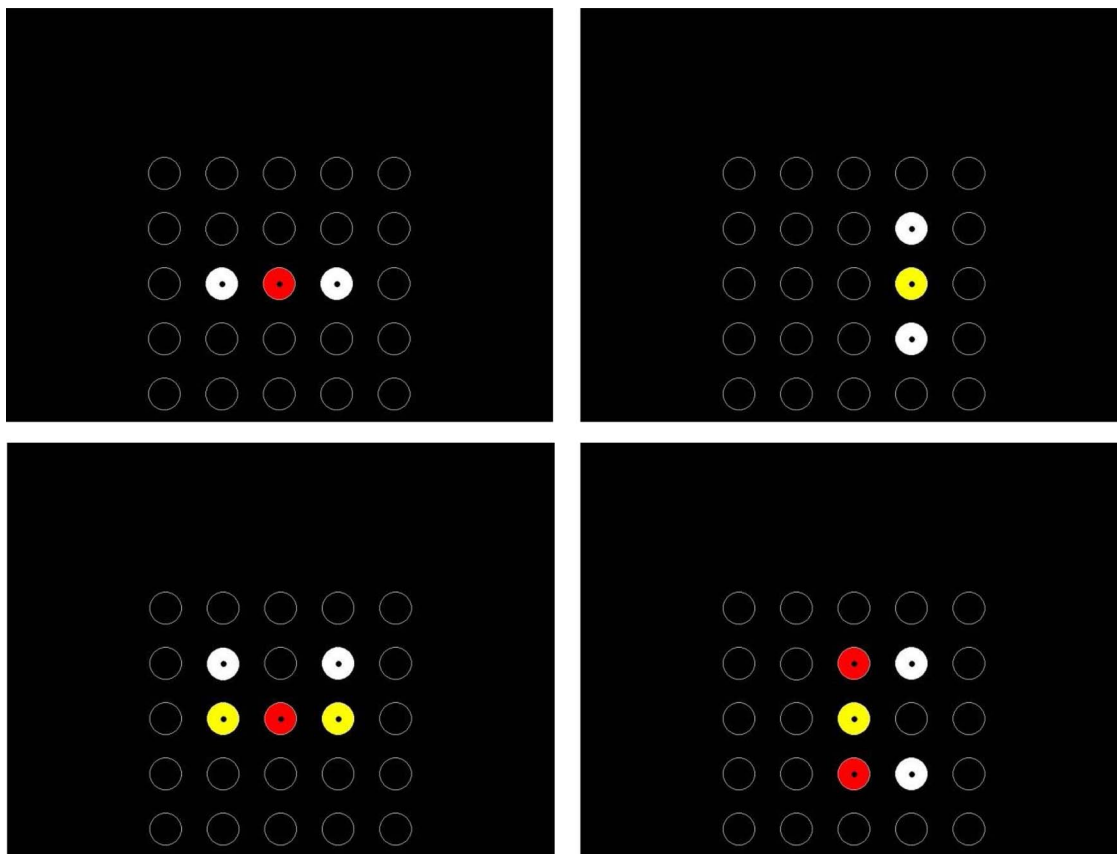


Fig. 1. Screen shots of example trials in Experiment 1. Top Left: A+ training trial. Top Right: X+ training trial. Bottom Left: AX probe trial. Bottom Right, XA probe trial.

and Y+ as in Phase 3, as well as 16 nonreinforced probe trials involving landmark compounds (Fig. 1, lower panels), two trials each of AX-, AY-, BX-, BY-, XA-, XB-, YA-, and YB-. The left-hand letter in the compound trial designation is presented at one location in the array, while the right-hand letter is presented on either side of the first, either left-right (if the left-hand landmark was A or B) or above-below (if the left-hand landmark was X or Y). Thus, an AX- probe trial consists of the presentation of A flanked to the left and right by X (Fig. 1, lower left panel), while an XA- probe trial consists of the presentation of X flanked above and below by A (Fig. 1, lower right panel). Probe trials were presented randomly during the session with a mean of one out of every five trials, and with the constraint that no test trial occurred prior to the 20th trial of the session. On each probe trial, two white disks were also presented each at the correct target location for the redundant landmark (e.g., above each X on AX- trials, and to the right of each A on each XA- trial). Probe trials lasted 30 s and pecks to either white disk had no effect. Time-outs were discontinued during test sessions. Throughout the entire experiment, the x and y screen coordinates of each peck were recorded. For purposes of our hypothesis that the central landmark of each compound probe trial would influence spatial control by the two flanking landmarks, we scored “target” pecks as those to the white disk predicted by chaining the central with flanking landmarks. For example, as shown in the bottom left panel of Fig. 1, LM A should bias the pigeon to peck at the target indicated by the LM X to the right (or left, depending on counterbalancing) of A, rather than to the other white disk.

### 1.3. Results & discussion

Fig. 2 (left panel) shows the mean proportion of target responses on each type of training trial and collapsed across probe trials with A, B, X, and Y as the left-hand member of each compound. Accuracy was

nominally higher to the training elements than to the test compounds. A 2-way repeated-measures Analysis of Variance (ANOVA) with Stimulus Type (element and compound) and Stimulus (A, B, C, D, and combinations thereof) as factors found a main effect of Stimulus Type,  $F(1, 5) = 1604.42$ ,  $p < .001$ ,  $\eta p^2 = 0.997$ , but no effect of Stimulus nor their interaction,  $F_s < 1.0$ . Post-hoc Bonferroni pairwise comparisons revealed that each element differed from each compound test trial, but there were no differences between elemental trials or between compound trials. Single-sample  $t$ -tests comparing performance on each trial type to chance (50%) found that accuracy to be significantly above chance on all trials, all  $t(5) > 3.0$ ,  $p_s < 0.03$ , except those with compound stimulus Y-AB,  $t(5) = 1.12$ ,  $p = .31$ .

Because we found no differences across elements or across compounds, accuracy scores were collapsed across all test trials within each type (elemental and compound; right panel of Fig. 2). A dependent-sample  $t$ -test found significantly lower accuracy on Test compounds compared to Training elements,  $t(6) = 40.06$ ,  $p < .001$ , Cohen's  $d = 3.88$ . Nevertheless, performance was still above chance for both Training elements,  $t(6) = 17.14$ ,  $p < .001$ , and Test compounds,  $t(6) = 5.74$ ,  $p < .01$ .

Pigeons demonstrated strong spatial control by each training element at test, as well as strong spatial control on the compound tests, though significantly less accurate than training performance. The above-chance accuracy on test compounds indicates that pigeons were able to utilize the spatial relationships between the individual elements to guide spatial choice when responding. The spontaneous demonstration of spatial integration on compound trials at the time of test is reminiscent to the cross-phase spatial integration observed across multiple phases of training on a sensory-preconditioning procedure involving spatial associations as reported by Sawa et al. (2005); see also Blaisdell and Cook, (2005). Sawa et al. first trained pigeons on a spatial relationship between landmarks A and B during Phase 1 of sensory

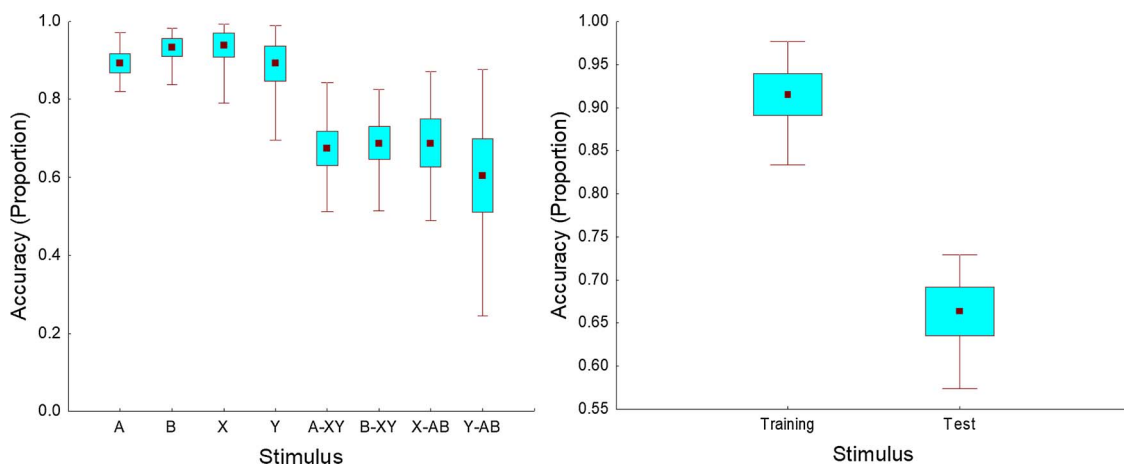


Fig. 2. Results from Experiment 1. Left panel: Proportion of target responses on nonreinforced test trials for each test condition. Right panel: Proportion of responses collapsed across all nonreinforced test trials separately for the training elements (A, B, C, and D) and the test compounds. Black squares indicate the mean, boxes show the SEM, and the whiskers show the entire range (minimum to maximum) of scores.

preconditioning. They then trained pigeons on the spatial relationship between B and a target location on the screen in Phase 2. At test, when presented with LM A which had never been paired with the target, pigeons showed strong spatial control by A, indicating that they had chained the  $A \rightarrow B$  and  $B \rightarrow \text{Target}$  spatial associations, allowing them to make a spatial inference as to the expected screen location of the target based on the  $A \rightarrow B \rightarrow \text{Target}$  integrated spatial map. The critical difference between the study by Sawa et al. and the present study is that our pigeons showed evidence of spontaneously chaining the pair-wise associations between landmarks and targets without explicit training to do so. That is, after learning separately that the target is to the right of A and above X, when tested on compound trials with a central A and with X flanking either side (i.e., XAX), the pigeons were biased to peck at the white disk above the X landmark to the right of A and not to the left of A. On XBX probe trials, on the other hand, the presence of B biased pigeons to peck to the white disk above the X landmark to the left of B, because the target was to the left of B during training.

Thus, in the current experiment, four cues were independently trained with spatial associations to a target. Cues were presented in compound at test such that there were multiple possible cued locations. The overwhelming majority of responses by all subjects was to the target location cued by the spontaneous concatenation of the cues in a systematic way. This suggests a priming-like mechanism operating at the time of test. Thus, spatial integration can occur despite no prior cue-cue associations such as were trained in the study by Sawa et al. (2005).

## 2. Experiment 2

The results of Experiment 1 revealed that pigeons spontaneously use landmark information at test to derive spatial inferences. Like spatial inferences derived from training (e.g., Blaisdell and Cook, 2005; Sawa et al., 2005), spatial inferences derived at test appear to be based on the chaining of spatial associations.

The finding of spatial inferences to compounds of landmarks at test derived from the integration of spatial associations of the separate elements raises the question as to how spatial control would emerge on compound trials when elements signal conflicting information about target location? That is, if two landmarks are presented in compound, but each signals a different white disk as the target, how does the pigeon resolve this apparent conflict? This was the focus of Experiment 2.

We were interested in determining one factor that is likely to be a strong determinant of landmark choice during conflict tests. We and others have previously shown that landmarks that are closer to a target during training exert greater spatial control over more proximal

landmarks, a phenomenon termed spatial overshadowing (Leising et al., 2011; Spetch, 1995; Wong et al., 2016). Our question is whether spatial proximity to the target plays a similar role at the time of performance during the compound test when landmarks signal conflicting target information. We hypothesize that spatial proximity will play a similar role and therefore predict stronger spatial control by a landmark more proximal to its target than by a landmark more distal to its target. Importantly, testing won't be scheduled until the birds have shown equally strong spatial control by each landmark individually during elemental training. This is important as it would rule out different degrees of learning about the landmark as a source of biased choice, and thus, lead to the conclusion that bias can spontaneously emerge as a response factor at the time of testing.

### 2.1. Subjects

Four new experimentally-naïve adult White Carneaux pigeons (*Columba livia*) participated in this experiment. Pigeons were housed and maintained as in Experiment 1.

### 2.2. Apparatus

The same apparatus was used as in Experiment 1, except that the grid was increased to  $8 \times 5$ .

### 2.3. Procedure

#### 2.3.1. Pretraining

Pigeons received pretraining as described for Experiment 1.

#### 2.3.2. Phase 1

Pigeons were presented with 40 A+ (proximal landmark) and 40 B+ (distal landmark) trials in each session. Landmarks were randomly presented in any of the 18 inner locations of the array. Red and green disks served as LMs A and B, counterbalanced across subject. For each training trial two white disks were presented to either side of the landmark (Fig. 3, upper panels). The near left (upper left panel) and far right (upper right panel) white disks (counterbalanced) served as targets for LMs A and B, respectively. Each trial lasted for 30 s, and multiple rewards were available during the trial. Target pecks were initially reinforced on an FR1 schedule, but this was progressively reduced to a RR5 schedule following the procedure of Experiment 1. Pecks to a landmark resulted in a time out as described for Experiment 1. Each trial was separated by a 12-s ITI. An equal number of A+ and B+ trials were presented in randomized order within each session, with the



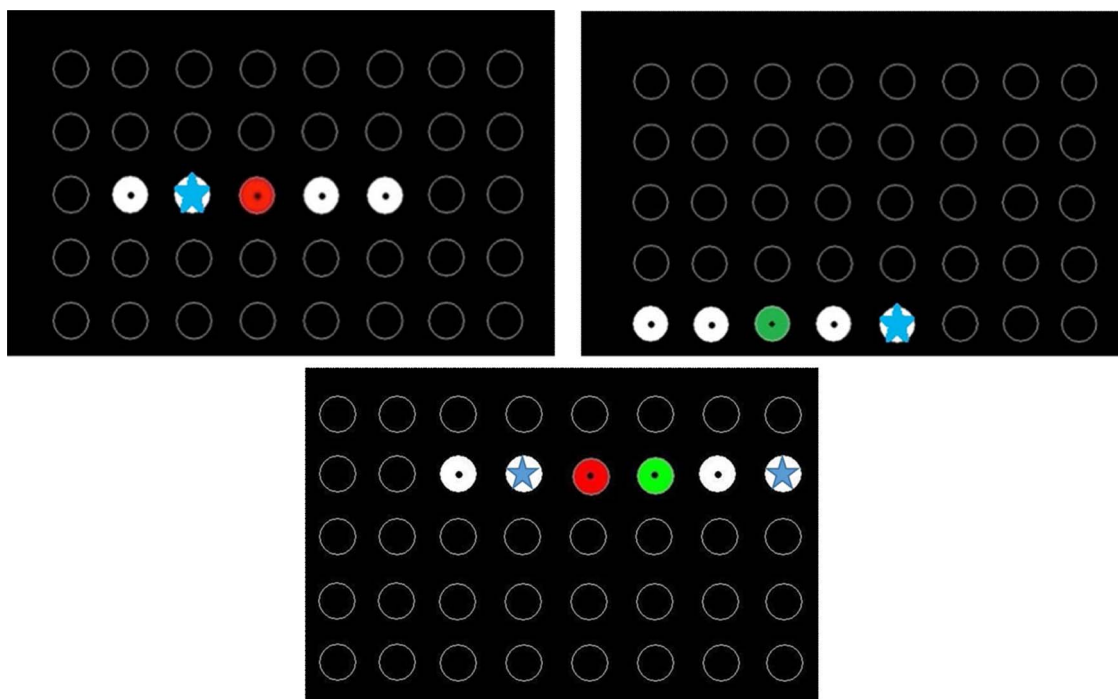


Fig. 3. Screen shots of example element training trials for LM Near (top left) and LM Far (top right), and for compound probe test trials (bottom) in Experiment 2. The 'star' marks which white disks were viable targets as signaled by available landmarks.

constraint that the same trial type could not occur more than twice consecutively. To advance to testing a 75% accuracy for target pecks was required.

### 2.3.3. Phase 2: initial compound tests

During test sessions, pigeons continued to receive A+ and B+ training trials. In addition to these, pigeons also received 15 non-reinforced probe AB- compound trials (Fig. 3, bottom). Probe trials were interspersed among the training trials with the constraints that no two trials in a row could be probe trials, and probe trials were not schedule until after the 10th trial within the test session. During probe trials, both landmarks were presented on same row of the screen at the same time at adjacent disk locations. These trials were not reinforced and lasted 30 s.

### 2.3.4. Phase 3: extinction of the proximal landmark

After the Phase 2 compound tests were concluded, subjects received sessions during which LM B continued to be reinforced, but LM A was extinguished. These sessions were identical to the Phase 1 training except that all trials with LM A were nonreinforced. Once target pecks on A- trials had decreased to at or below 20% of rate of target pecks on B+ trials, subjects were tested again.

### 2.3.5. Phase 4: compound retesting

Birds received another round of compound testing following the exact procedure as in Phase 2, except that LM A continued to be non-reinforced during test sessions.

## 2.4. Results & discussion

### 2.4.1. Initial tests

Accuracy was high to both training elements (A and B) during initial testing (Fig. 4, left panel). On tests of the AB compound, a higher proportion of responses were to A's target than to B's target. This suggests that the landmark with a more proximal target exerted greater behavioral control than did the landmark with a more distal target. A repeated-measures ANOVA on proportion of choices to the target on

elemental trials and choices to A's target on compound AB trials revealed a main effect of trial type,  $F(2, 6) = 6.46, p < .05, \eta p^2 = 0.68$ . Planned comparisons revealed that choices to A's target on AB trials were lower than were target pecks on A alone trials,  $F(1, 3) = 10.29, p < .05$ , Cohen's  $d = 1.63$ , but not on B alone test trials,  $F(1, 3) = 5.38, p = 0.10$ . Target pecks on A versus B trials did not differ.

Single-sample  $t$ -tests revealed above chance (0.25) performance on A alone,  $t(3) = 24.75, p < .001$ , B alone,  $t(3) = 69.94, p < .001$ , and of A's target on AB trials,  $t(3) = 6.81, p < .01$ , but not of B's target on AB trials,  $t < 1.0$ . A dependent-sample  $t$ -test comparing choices of A's target to B's target on AB trials revealed an overwhelming majority of choices were to A's target,  $t(3) = 3.35, p < .05$ , Cohen's  $d = 3.35$ .

### 2.4.2. Post extinction-of-A tests

Extinction of A was shown to be effective in the lower proportion of target responses on test trials of A than of B (Fig. 4, right panel). Furthermore, on AB trials, responding was almost entirely to B's target with almost no responding to A's target. This suggests that extinction of A resulted in an attenuation of A's spatial control. It also suggests that the lower responding to B's target on AB trials prior to extinction-of-A was due not to the failure to detect B but to an increased weighting of A over B by virtue of A being more proximal to the target. This corroborates the same weighting observed in studies of spatial overshadowing (Leising et al., 2011; Spetch, 1995; Wong et al., 2016), except that here the differential weighting of proximal and distal spatial cues occurred at the time of test when both cues were put into conflict, despite similarly high levels of spatial control by each individual cue on its own.

A repeated-measures ANOVA on proportion of target choices on elemental trials and choices to A's target and B's target on compound AB trials revealed a main effect of trial type,  $F(3, 9) = 66.98, p < .001, \eta p^2 = 0.957$ . Planned comparisons revealed that target responses were dramatically lower on A alone than B alone trials,  $F(1, 3) = 34.22, p < 0.01$ , Cohen's  $d = 3.99$ , indicating extinction of A. Likewise, on AB trials, responses to B's target were higher than to A's target,  $F(1, 3) = 571.80, p < .001$ , Cohen's  $d = 19.41$ . Choices of A's target on A alone trials was higher than on AB trials,  $F(1, 3) = 11.51, p < .5$ , Cohen's  $d = 2.38$ . Choices of B's target on B alone trials and on AB trials

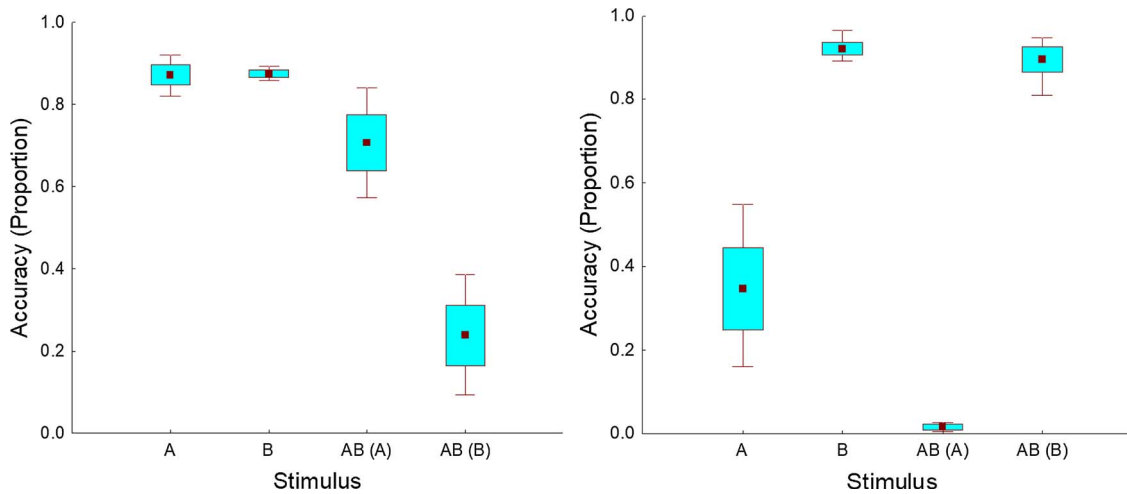


Fig. 4. Results from Experiment 2. Left panel: Proportion of target responses on nonreinforced test trials for each test condition during initial testing. Right panel: Proportion of responses collapsed across all nonreinforced test trials for each test condition following extinction of A. Black squares indicate the mean, boxes show the SEM, and the whiskers show the entire range (minimum to maximum) of scores.

did not differ.

Single-sample *t*-tests revealed above chance (0.25) performance on B alone trials,  $t(3) = 43.73, p < 0.001$ , and of choices to B on AB trials,  $t(3) = 20.54, p < .001$ . Target responses on A alone trials did not differ from chance,  $t < 1.0$ , while on AB trials responses to A's target were significantly below chance,  $t(3) = -37.91, p < .001$ , demonstrating reversed cue competition at the time of performance. Dependent sample *t*-tests revealed lower target responses on A than on B test trials,  $t(3) = 5.85, p < .01$ , Cohen's  $d = 3.99$ , and lower responses to A's target than to B's target on AB test trials,  $t(3) = 23.91, p < .001$ , Cohen's  $d = 19.41$ .

To compare the effects of extinction-of-A on responding at test, we conducted an analysis of test performance prior to versus following extinction-of-A (Fig. 5). A two-way repeated-measures ANOVA conducted on target responses on A-alone and B-alone test trials with Stimulus (A and B) and time (pre and post extinction) as factors revealed a main effect of Stimulus,  $F(1, 3) = 38.35, p < .01, \eta^2 = 0.927$ , a main effect of Time,  $F(1, 3) = 21.45, p < .05, \eta^2 = 0.877$ , and a between factor interaction,  $F(1, 3) = 27.31, p < .05, \eta^2 = 0.901$ . Planned comparisons revealed no difference between A and B prior to extinction but a large difference following extinction,  $F(1, 3) = 34.22, p < .01$ , Cohen's  $d = 19.41$ . Likewise, target responses on A-alone test trials were greater prior to than following extinction,  $F(1, 3) = 25.12, p < .05$ , Cohen's  $d = 3.65$ , whereas target responses on B-alone test

trials were only marginally significantly different prior to versus following extinction of A,  $F(1, 3) = 6.34, p = .09$ , Cohen's  $d = 1.81$ . A similar ANOVA conducted on A-target versus B-target responses on AB test trials revealed no main effect of Time,  $F(1, 3) = 1.07, p = 0.38$ , a marginally significant main effect of Target (A or B),  $F(1, 3) = 7.34, p = 0.07$ , and a significant interaction between factors,  $F(1, 3) = 95.84, p < .01, \eta^2 = 0.969$ . Planned comparisons revealed more responding to A's target than to B's target prior to extinction,  $F(1, 3) = 11.21, p < .05$ , Cohen's  $d = 3.28$ ; but more responding to B's target than to A's target following extinction of A,  $F(1, 3) = 571.80, p < .001$ , Cohen's  $d = 19.41$ . Likewise, responding to A's target was higher prior to than following extinction of A,  $F(1, 3) = 111.87, p < .01$ , Cohen's  $d = 7.31$ , while responding to B's target was higher following extinction of A than prior to it,  $F(1, 3) = 74.99, p < .01$ , Cohen's  $d = 5.81$ .

### 3. General discussion

Our experiments involving the presentation of previously trained elements in compound at test revealed a number of interesting performance processes. In Experiment 1, we found evidence that information from separately trained landmark elements combines in a logical manner to guide spatial control of responding. Specifically, the individual landmarks concatenate by biasing spatial attention in the direction reinforced during training, resulting in a majority of pecks

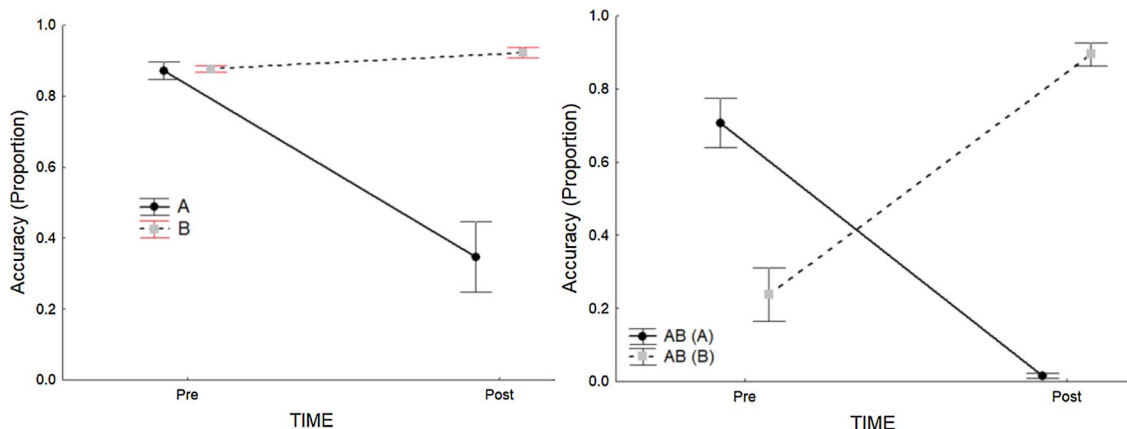


Fig. 5. Results from Experiment 2. Left panel: Proportion of target responses on nonreinforced test trials of A and B prior to and following extinction-of-A. Right panel: Proportion of responses to the A target and B target on nonreinforced test trials of the AB compound prior to and following extinction-of-A. Central symbols indicate the mean, and error bars show the SEM.

directed at the target at the end of the associative chain. This provides an analogous pattern of behavior as found when associative chains are built in piecemeal fashion across consecutive phases of training, such as in a sensory preconditioning procedure (Blaisdell and Cook, 2005; Sawa et al., 2005). Experiment 2 revealed that proximity between landmark and target is a major determinant of spatial control at test, with more proximal landmarks ‘outvoting’ more distal landmarks.

The finding in Experiment 2 mirrors the similar effect observed when landmarks are trained in compound and tested separately, that is, spatial overshadowing. Prior work from our lab (Wong et al., 2016) found that spatial overshadowing may be best accounted for by acquisition-deficit models (e.g., Rescorla and Wagner, 1972) rather than performance-deficit models (e.g., the comparator hypothesis, Miller and Matzel, 1988). The results from Experiment 2 cannot be based on such accounts because each landmark-target association was well learned during acquisition, and presumably no within-compound landmark–landmark associations had been formed prior to test. Such within-compound associations have been shown to be a critical determinant of comparator effects. Similar research has found that humans fail to integrate separately-learned spatial cues when presented in compound at test (Baguley et al., 2006; Du et al., 2017). Instead, like the pigeons in Experiment 2, spatial search in humans on compound tests appears to be guided by each cue independently, with factors like proximity to the target as strong determinants for weighting cue choice.

In conventional procedures used to study associative processes, such as Pavlovian and instrumental conditioning in conditioning chambers, the conditioned response can be measured in only one dimension, typically strength or probability of the response, though temporal characteristics can sometimes be captured as well. As such, the strength of the CR can usually only inform about the strength of the CS-US association. This precludes dissecting and dissociating the many factors that may influence the CR, such as temporal, spatial, and causal information (Blaisdell, 2009). The use of less restrictive apparatus that allow the CR to vary along these other dimensions enable their dissociation. For example, the spatial and temporal attributes of a pigeon’s peck to a touchscreen-monitor can be easily measured and analyzed in relation to stimulus events presented on the screen. This can be especially useful as shown in our experiments when multiple target locations are available and choice behavior can be captured.

The search for general rules of cue integration has been of central concern in experimental psychology, with the use of compound stimuli as a method for identifying and dissecting these rules (Kehoe and Gormezano, 1980). Possible rules that govern stimulus compounds include 1) complete summation (addition), 2) incomplete summation (averaging), and 3) interaction or inhibition (suppressive summation) (Weiss, 1972). Evidence has been found in the literature for each type of combination rule. For example, after separate reinforcement training to run down an alley in the presence of a light on some trials and tone on other trials, rats run faster in the presence of the L + T compound than in the presence of either element alone (Miller and Price, 1971).

In most tests of responses to compounds, there is only a single response for which the degree of responding is all that can be reported. Though rare, there have been a handful of studies where multiple response options are available at test, each associated with one of the elements of the compound. In one such experiment, rats were trained to press a lever in the presence of a tone and pull a loop of wire in the presence of a noise. When tested on the tone + noise compound, rats made more total responses across the two manipulanda than when tested on either element alone (Howard et al., 1976). Notably, whether the two manipulanda were next to each other or on opposite sides of the front panel of the operant chamber had no effect on total responses or percentage of responses to each manipulandum.

Our empirical focus concerns combination rules during performance involving tests of compounds of separately trained visual landmarks. Thus, relevant to this focus is the literature involving tests of novel compounds of previously trained visual elements. Most of these studies

involve pigeons learning instrumental pecking responses to multiple visual instrumental discriminative stimuli as elements, and then tested as elements or in compound. While these studies report conflicting results, Aydin and Pearce (1997) identified a critical factor that appears to explain these conflicts. Compared to element responding, responding during the compound was elevated when the background screen was white, but not when it was dark as it was during the ITI. Thus, as in our experiments where white disks served as response keys, summation effects can be readily observed when the response does not have a necessary spatial component.

Spatial associations have also been shown to play an important role in modulating attentional processes. Associations between visual or auditory contexts or cues, on the one hand, and a target location on the other, can bias spatial attention in humans (Chun and Jiang, 1998; Summerfield et al., 2011; Zimmermann et al., 2017) and pigeons (Wasserman et al., 2014). Our results extend this phenomenon in showing that compounds of separately trained spatial cues can work together or in conflict to bias spatial attention.

Our study involved tests of compound spatial cues. There is a similar literature on tests of compound temporal cues, where each cue signaled a reward at a specific time. For example, rats can be trained to associate a tone and light with two different durations (e.g., 5 s and 20 s, respectively). On subsequent tests of the Tone-Light compound, rats showed a unimodal response distribution centered between the two time intervals signaled by each cue alone (De Corte and Matell, 2016). This indicates that rats are averaging the durations of the two cues on compound trials. Our results involving compounds of spatial cues do not show evidence of spatial averaging, but instead show discrete responses at individual target locations. Similar results have been found for pigeons using landmarks during foraging (e.g., Spetch et al., 1996), and humans in spatial search tasks (Baguley et al., 2006; Du et al., 2017). Why compounds of spatial cues would not produce averaging, but compounds of temporal cues would remain a mystery and is a topic in need of future research.

To conclude, our results add to the growing body of evidence that associative processes play a central role in spatial learning and performance, with the emphasis of this paper on the performance rules involved in spatial cue combination. There are other approaches to cue combination (e.g., Cheng et al., 2013; Xu et al., 2017), but further research is needed to determine which ones apply in the type of small scale navigation a foraging animal faces.

#### Author notes

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