Occasion Setting During a Spatial-Search Task With Pigeons

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A spatial task was used to investigate if a stimulus could set the occasion for responding to a landmark. Pigeons were trained with a positive occasion setter (OS; a colored background display) signaling the contingency between a landmark (LM; visual patterned stimulus) and the location of a rewarded response. The two most common tests of an OS (transfer tests and post-training extinction of the OS) were then conducted. In Experiment 1, two occasion setting pairs were trained \((++-\text{XA}/\text{YB}++/\text{A}-/\text{B}-)\) with unique spatial relationships to a reinforced goal location. Transfer tests (XB− and YA−) revealed more responding to a landmark when paired with the same OS from training (e.g., XA) than on transfer tests, which was greater still than landmark-only trials (A−). Three pigeons demonstrated good spatial control of responding by the LM on transfer tests. In Experiment 2, the contingency and spatial relationship (e.g., left or right) between LM A and the goal were signaled by the OS \((+++\text{XA}/\text{YA}++++/+++\text{ZB}/\text{IC}++/+++\text{A}-/\text{B}-)\). LM C was trained without an OS to assess the role of training history during transfer. Transfer tests again indicated an OS could facilitate responding and the LM controlled the location of responding. Training history affected spatial control, but not facilitation, by LM C. Lastly, post-training extinction of X had no effect on facilitation or spatial control during subsequent XA trials. These experiments are the first to evaluate conditional control of spatial information by landmarks using both of the standard tests for occasion setting.

Keywords: occasion setting, spatial learning, landmarks, conditional discrimination, pigeons

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In nature, whether or not a response leads to an outcome (e.g., courtship behavior and copulation, respectively) is often influenced by the presence or absence of a discriminative stimulus (DS; e.g., a receptive female) in the environment. Furthermore, several DSs may be structured in a hierarchical fashion. For example, in an operant serial feature-positive procedure, reinforcement is delivered when a response occurs in the presence of a DS (A; e.g., a tone), but only if DS A was preceded by another stimulus, X (e.g., a light). Within an associative learning framework, the second stimulus, X, can be described as setting the occasion for a reinforced response in the presence of the DS (i.e., occasion setting). Hierarchical accounts of occasion setting assume that stimuli are represented individually and hierarchically. More specifically, these accounts state that the DS and occasion setter (OS) are encoded by the subject as individual elements, and the OS modulates the information value of the DS. Herein we refer to the modulator element as an OS, and the element that is the target of the modulation as the DS, or landmark, if it provides stable spatial information (e.g., distance and direction) regarding the location of a reinforced response. Procedures in which the outcome is delivered when A is paired with X (XA+), but not in its absence (A−), are referred to as occasion-setting training, though we discuss other methods of solving this discrimination.

In an operant serial feature-positive procedure, the task can be solved by modulation of A by X, such as using an if–then rule to respond to DS (A) only if it is preceded by the OS (X→A). However, a feature-positive discrimination can also be solved without modulation. For example, X could come to control responding as a DS itself by forming a direct connection to the reinforced response during XA trials or by entering into a unique configuration with A (e.g., \(p = \) a unique configuration of X and A; Pearce, 1987). Previous research has identified two training parameters critical to observing modulation: the onset of the OS should precede that of the DS, and the DS should be more salient than the OS. After successful acquisition of occasion setting, an OS exhibits several unique properties, including (a) modulation of responding to a DS by an OS transfers to other DSs to the degree that the transfer DS has a history of partial reinforcement (e.g., Rescorla, 1986b), and (b) trials of the OS unpaired with the DS or outcome (i.e., extinction) should not disrupt subsequent modulation of responding to the DS in the presence of the extinguished OS (e.g., Rescorla, 1986a).

Holland (1995) investigated both characteristics of an OS within an operant serial feature-positive procedure. During training, rats received two occasion-setting pairs (X→A+/A−→Y/B+/B−), as well as exposure to a third DS (C+) trained without an OS. Holland (Experiment 1) tested whether modulation by an OS (X)
would transfer to a DS (B) trained in a separate occasion-setting relationship (Y→B) and to a DS (C) with no previous pairings with an OS, as well as whether control by the OS would survive extinction treatment (X→C). Transfer tests showed good transfer of X to B, weak transfer to C, and no disruption of control by X following extinction. Close inspection of these data indicate that although transfer of control by X to B did occur, it was incomplete relative to responding to the originally trained OS–DS pair (X→A). Incomplete transfer is a common finding in the literature (see Bonardi, 1996, for a review).

In occasion setting, the OS can modulate if a subject responds in the presence of a conditional stimulus (CS) or DS, but another interesting question is whether the OS can modulate when and where a subject responds. The effectiveness of X in facilitating responding to A is determined both by its contingency and its temporal contiguity with A (Bonardi & Jennings, 2007; Holland, 1986, 1998; Holland, Hamlin, & Parsons, 1997; Miller & Oberling, 1998; Nakajima, 2009). Furthermore, by plotting the temporal distribution of responding (Roberts, 1981), research on occasion setting has demonstrated that the expected time of an unconditioned stimulus (US; e.g., food) delivery can be modulated (Bonardi & Jennings, 2007; Nakajima, 2009) by an OS. Bonardi and Jennings (2007) reported evidence that rats learned to predict that food was delivered 6 s after A when it was preceded by X, but 30 s after A when it was preceded by Y. Additional tests revealed modulation by X and Y, and not direct X-food and Y-food temporal control by the OS. Occasion setting of temporal relations has also been reported in an operant task with pigeons (Nakajima, 2009). Much less research has investigated whether an OS can control where a subject responds.

Previous research has demonstrated a role for spatial context (i.e., where) in setting the occasion for a visuomotor association in rats (Eacott, Easton, & Zinkivskay, 2005), bees (T. S. Collett, Fauria, Dale, & Baron, 1997; see Zhang, Si, & Pahl, 2012, for a review), ants (Wehner & Srinivasan, 1981), and humans (Mole, Gambet, Bugallo, & Miller, 2012). Few studies have investigated how a context or stimulus can set the occasion for the correct spatial response relative to a landmark. T. S. Collett and Kelber (1988) trained honeybees to search for sucrose relative to the same two yellow and blue cylinders (landmarks) in identical huts (Contexts X and Y) positioned at different locations in the environment. In Context X, the location of sucrose was between the two yellow cylinders, whereas in Context Y, the sucrose was at a different position to the east of the two blue triangles. On test trials without sucrose, the bees searched more often in the expected location of sucrose appropriate for that context. This result demonstrates that contextual stimuli (trees, buildings, etc.) can set the occasion for a spatial response to landmarks.

Though parallels have been found between occasion setting by contexts (combinations of cues present throughout a session) and discrete cues (distinct cues with clear onsets and terminations during a session; e.g., Hall & Mondragón, 1998), the vast majority of research investigating occasion setting has used discrete cues for both the OSs and the DS or CS. Additionally, nearly all previous experiments on contextual control of visual or spatial discriminations report acquisition data, but do not include the types of postacquisition tests (e.g., extinction of the OS and transfer to DSs with different training histories) needed to thoroughly investigate occasion setting of spatial information. Lastly, to our knowl-
the location of the goal) was greater for the landmark because of its asymmetry with respect to the goal (i.e., the background could not signal the goal to its left or right because it covered the entire search space). If the influence of each cue on spatial behavior in our task was based solely on its proximity and stability to the goal, spatial learning models would predict that responding would always be strongly biased in the direction of the landmark indicated by the most proximal and stable cue, the landmark. However, in our task, the reliability of the spatial information provided by the landmarks was dependent on the presence of an OS. In Experiment 2, the spatial proximity of the landmark to the goal was maintained, but the stability of a landmark was manipulated across trials. Spatial learning models are equipped to predict spatial accuracy in the presence of a landmark (e.g., Battaglia, Jacobs, & Aslin, 2003; Biegler & Morris, 1993; Byrne & Crawford, 2010; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Miller & Shettleworth, 2007; Ratliff & Newcombe, 2008), whereas hierarchical theories from the associative literature are best poised to code the identity of a landmark in an occasion-setting task or does the OS provide the critical information regarding where to respond (e.g., T. S. Collett & Kelber, 1988)? Second, if critical information is encoded by the subject as part of a landmark–outcome association, will an OS’s modulation transfer to other landmarks with similar or different training histories? These questions mirror those that have been asked in traditional occasion-setting paradigms: Does the OS act directly on a specific CS, on the response evoked by the CS, on a specific CS–outcome association, or on the threshold for activation of the outcome representation (Bonardi et al., 2012; Swartzentruber, 1995)? Importantly, the inclusion of a spatial component allows us to investigate the nature of stimulus control by the OS and landmark using two measures (amount of responding and spatial control).

**Experiment 1**

During operant occasion setting, a stimulus (the OS) signals the contingency between a discriminative stimulus (e.g., landmark) and a reinforced response (e.g., goal). In Experiment 1, two occasion-setting pairs (e.g., XA+/A−/YB+/B−) were trained with unique spatial relationships to a reinforced goal location (e.g., +−XA/YB−−; see Figure 1). The experimental design for Experiment 1 is described in Table 1. The procedure used in Experiment 1 (and Experiment 2) was selected to encourage hierarchical learning. In occasion setting, many of the conditions that support hierarchical learning are contradictory to the conditions that support configural learning (Miller & Oberling, 1998). Two of these conditions are temporal priority of the OS and enhanced salience of the landmark. In our procedure, the OS preceded the onset of the landmark, and the landmark was expected to be perceived as more salient than the OS via its stable spatial relationship and more proximal spatiotemporal relationship to the location of the hidden goal. Following training, nonreinforced transfer trials (XB−− and YA−−) were presented.

Transfer tests (e.g., XB−−) were used to evaluate whether an OS would continue to facilitate responding when paired with a different landmark, and whether the spatial information provided by the LM or OS during training determined the spatial distribution of responding. We predicted more responding on a trial when a landmark was paired with a different OS from training than on landmark-only trials, but less responding than on trials of the LM paired with the same OS from training. Regarding spatial control of behavior, on a transfer trial like XB, there are at least three possible results. The first is that OS X signals the B−goal spatial relationship based on previous training of X with A (e.g., +−XA, +−XB), henceforth referred to as OS control. Second, the landmark present on the trial (e.g., B) with OS X signals the location of the goal based on the B−goal spatial relationship encountered during training (e.g., YB−−, XB−−), henceforth referred to as landmark control. Lastly, the OS and LM both signal the goal location, and the result of direct competition would be similar levels of responding at both sides of the landmark (i.e., the goals signaled by the OS and B). Spatial learning models predict that the stable landmark should control the location of responding during transfer tests more than the unstable OS, and hierarchical accounts of occasion setting predict that the OS should control whether or not responding occurs in the presence of the landmark. Furthermore, hierarchical theories predict that transfer of modulation by the OS would be specific to the LM–goal association encountered during training (e.g., +−XA), and consequently limited to the generalization that occurs between the two landmarks, A and B.

**Method**

**Subjects.** Six White Carneaux pigeons (*Columba livia; Double T Farm, Glenwood, IA), between 18 and 24 months old at the
time of testing, served as subjects. Pigeons were maintained at 80% to 85% of their free-feeding weights. They were individually housed in a colony with a 12-hr light–dark cycle and had free access to water and grit. Experimental procedures occurred during the light portion of the cycle. Subjects previously participated in three operant studies investigating timing behavior, reward sensitivity, and working memory, but the pigeons were naïve to the stimuli and procedures used in this study.

**Apparatus.** Training and testing were conducted in a flat-black Plexiglas chamber (45 cm wide × 41 cm deep × 46 cm high). All stimuli were presented by computer on a color LCD monitor (L1750; Hewlett-Packard, Palo Alto, CA) visible through a 40 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 12 cm above the chamber floor. Pecks to the monitor were detected by an infrared touch screen (EZ-170-WAVE; eScreen, Houston, TX) mounted on the front panel. A 28-V houselight located in the ceiling of the box was illuminated at all times. A food hopper mounted on the front panel. A 28-V houselight located in the ceiling of the box was illuminated at all times. A food hopper located in the center of the front panel, its access hole flush with the floor. All experimental events were controlled and recorded with a computer. A video card controlled the monitor in the SVGA graphics mode (800 × 600 pixels). All experimental events were orchestrated via Microsoft Visual Basic 6.0 software.

**Stimulus displays.** There were three types of visual stimuli: response locations, OSs (X and Y), and landmarks (A and B). Response locations were a series of eight squares that were 2 cm². OS X and Y were red- or blue-colored backgrounds that filled the entire display except for the predesignated response locations (see Figure 1). In the absence of an OS, the background appeared black.

If a response location was selected to be a landmark, it was replaced with an image of a 2-cm² green box with thin vertical white stripes or a yellow box with thick white horizontal stripes. Assignment of OS color (red or blue) to landmark color (green or yellow) was counterbalanced across birds.

**Procedure.**

**Training.** The subjects were initially trained via a mixed Pavlovian-instrumental procedure to peck a white circle displayed in the center of the monitor. After pecking was reliable, eight squares were arranged in a row in the center of the monitor. On each trial, one of the eight squares was selected as the goal and marked by being filled white to full brightness, whereas the remaining squares were filled to 35% brightness. Within and across sessions, the brightness of the goal location was reduced to 50% brightness, and responses at the goal were reinforced on a continuous reinforcement (CRF), Random Ratio (RR) 2, and then RR4, schedule (cf. Leising, Sawa, & Blaisdell, 2012). Subjects advanced to a new reinforcement schedule and a dimmer goal marker with 10 consecutive correct trials, or regressed with five consecutive incorrect trials.

OS training consisted of four types of trials: +−→X; YB→+; A−; and B− (see Table 1 and Figure 1). A square that served as a landmark (A) was replaced with one of the two color-line patterns described previously. On A-only and B-only trials, the landmark was presented for 30 s, with no opportunity for reinforcement. On XA trials, the color of the entire display (X) changed for a fixed-time 40-s interval. The onset of A was delayed according to a variable-time 10-s schedule (ranging from 5 s to 15 s in increments of 5 s), but always coterminated with X. Thus, A was presented for a mean duration of 30 s during XA trials. The goal was always one location to the left of A, and pecks during A were reinforced until offset. YB trials were conducted in a similar

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**Table 1**

**Experimental Design and Predictions**

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Test trials</th>
</tr>
</thead>
<tbody>
<tr>
<td>Train +−→X A−/ YB→+ /B−</td>
<td>Previouly trained</td>
</tr>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
</tr>
<tr>
<td>Test predictions</td>
<td>A</td>
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<tr>
<td>OS</td>
<td>←−</td>
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<tr>
<td>Landmark</td>
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<tr>
<td>Spatial control</td>
<td>←−</td>
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</table>

**Experiment 2**

<table>
<thead>
<tr>
<th>Test trials</th>
</tr>
</thead>
<tbody>
<tr>
<td>Train +−→X A−/ YB→+ /B−/ +−→C</td>
</tr>
<tr>
<td></td>
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<tr>
<td>OS</td>
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<tr>
<td>Landmark</td>
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<tr>
<td>Spatial control</td>
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**Note.** The columns indicate separate trial types that were tested following successful acquisition of OS training. Extinction of C and X occurred after Test 3 in the 2 days immediately prior to Test 4. The arrows indicate the spatial relationship of each stimulus to the hidden goal (based on the landmark): “←−” = the goal was located left of the landmark; “→−” = the goal was located to the right of the landmark; “?” = the direction indicated by the landmark is not clearly known; empty cells indicate no predicted relation. The predicted amount of pecking is the sum of responses across all of the response locations.

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manner, with the exception that the goal was one location to the right of B. The placement of a landmark within the response squares varied from one trial to the next. Goal locations were selected randomly without replacement from Locations 3 through 6. Thus, there was an unstable relationship between the location of a landmark and the OS, the OS and hidden goal, and between the landmark and the context; the spatial relationship between the landmark and goal, however, remained stable across all trials. We did not expect the black background on landmark-only trials to serve as a negative OS because of the presence of the black background without a landmark during the intertrial interval and at the beginning of each session (see Figure 1). At the start of OS training, the location of the goal was marked with a white square at 50% brightness, whereas the remaining locations were filled to 35% brightness. Within and across sessions, the brightness of the goal marker was reduced to 35% brightness, and responses at the goal were reinforced on a CRF, RR2, and then RR4, schedule. Subjects advanced to a new reinforcement schedule and a dimmer goal marker with 10 consecutive correct trials, or regressed with five consecutive incorrect trials. Sessions initially consisted of 48 trials with 12 trials of each type. Once subjects reached the RR4 schedule of reinforcement, the number of trials per session was increased to 64, with an equal number of the four trial types.

After the brightness of the goal was reduced to 35%, it was indistinguishable from the remaining response locations; thus, subjects were required to search for the hidden goal location based solely on its spatial relationship to the landmark. All of the pigeons were simultaneously advanced to novel-combo testing only after all six subjects completed two sessions with (a) the goal unmarked, (b) responses reinforced on an RR4 schedule, (c) the correct response on 80% of occasion-setting trials, and (d) the discrimination ratio (pecks at the correct location divided by all responses) greater than or equal to .60. The video in the online supplemental materials shows one full trial with a pigeon on an RR4 schedule and the goal indistinguishable from the other locations.

**Novel-combo test.** The order of test trials each day was counterbalanced across all subjects. On Sessions 73 to 78, subjects received one nonreinforced test trial of A, B, YA, XB, and YA per session for six sessions. A test session began with 48 training trials, followed by a block of test trials and an additional 16 training trials. A test session consisted of (a) an equal number of reinforced (XA+ and YB+) and nonreinforced trials (A− and B−), as in training; and (b) a block of six consecutive nonreinforced test trials. On occasion-setting test trials, the landmark always appeared 10 s after the OS, and landmark-only trials were always 30 s in duration.

**Measures.** The amount of responding was the sum of pecks to all response locations. This measure indicates the overall excitatory strength of the stimuli, irrespective of spatial accuracy. Regarding spatial control, the test data were collected such that the direction of the “goal” during a trial was always designated relative to the landmark and consistent with the landmark–goal relationship encountered during training. On novel-combo trials, the OS and landmark predicted the goal in different directions (i.e., on different sides of the landmark). We first calculated the proportion of pecks at each location by dividing the pecks at that location by the sum of pecks at all locations. Spatial control was calculated as the proportion of pecks to the goal location predicted by the landmark (based on training), minus the proportion of pecks to the response location to the immediate other side of the landmark, which was the goal location signaled by the OS (based on training). This measure differentiates between spatial control by a cue as a landmark or as a beacon (e.g., Mackintosh, 2002). The difference from 0 indicates the strength of spatial control (i.e., larger values indicating greater spatial control), and the sign of the value indicates the direction of control (i.e., positive values indicate more landmark control).

**Statistical analysis.** We report the results of repeated measures analysis of variance (ANOVA) tests conducted on either the amount of responding or spatial control of responding, with Trial Type as the repeated measure. Tukey’s honestly significant difference (HSD) post hoc tests were then conducted to isolate differences within a main effect of trial type. Single-sample t tests comparing the spatial difference score (i.e., spatial control) with zero were used to evaluate OS versus landmark control at test. Positive difference scores that are greater than zero indicate more landmark control, scores less than zero indicate more OS control, and no statistical difference from zero indicates equal control by the OS and landmark. Effect sizes and confidence intervals for ANOVAs, t tests, and post hoc tests were computed using SPSS (IBM, New York, NY) code published by Smithson (2001). Confidence intervals for Tukey post hoc tests were computed using the t value and degrees of freedom from the equivalent paired t test (Rosenthal, 1991). Effect sizes and confidence intervals are reported for every F test or t test comparison at the level of p < .10.

**Results**

During testing, the onset of the landmark on occasion-setting trials was fixed at 10 s after the OS. To equate the duration of occasion-setting trials with landmark-only trials (30 s), only responses occurring during the last 30 s of occasion-setting trials (when the landmark was present) were included in the analysis. The two trial types in each condition were functionally equivalent (trained, XA and YB; novel-combo, XB and YA; landmark-only, A and B), but differed in the direction of the goal relative to the landmark. Before collapsing, we tested separately for any directional biases in the amount of responding (the sum of pecks to all eight response locations) or spatial control (pecks to the goal location divided by pecks made to all eight locations). Trial Type (trained, XA and YB; novel-combo, XB and YA; landmark-only, A and B) and Direction (Left vs. Right) were included as repeated measures in an ANOVA conducted on amount of responding or spatial control, which revealed main effects of Trial Type for both, Fs(2,10) > 105.30, ps < .001 (η² > .95, 95% CIs [.81 ≤ η² ≤ .97]), but no main effects of Direction, Fs(1,5) < 2.84, ps > .10 (η² > .36, 95% CIs [.00 ≤ η² ≤ .68]), and no interaction for either, Fs(2,10) < 1.43, ps > .10. The subsequent analyses collapsed across similar trial types and we refer to them as trained, novel-combo, and landmark-only.

Figure 2 displays the mean total responses (i.e., to any location in the array) across days of testing for the two types of test trials. Across test days, we expected more extinction during novel-combo trials than the previously trained trials because none of the novel-combo trials were ever reinforced, whereas the majority of the previously trained trials were reinforced during each test session. To determine if and when a significant drop occurred in responding during novel-combo transfer trials, we compared the mean
during Day 1 with subsequent days using paired-samples $t$ tests (see Figure 2). No difference was found between Days 1 and 2, $t(6) = .10, p = .92$, but the amount of responding was significantly less on Day 3 compared with Day 1, $t(5) = 2.59, p = .05$ ($d = .60, 95\%$ CI [.13, 1.06]). Consequently, all of the remaining analyses were performed with Days 1 and 2 of testing.

**OS training.** All birds advanced to testing after 72 sessions (including pretraining).

**Novel-combo test.**

**Amount of responding.** Figure 3 displays the amount of responding for each trial type. Responding during the transfer trials was lower than the training trials, but greater than landmark-only trials. This observation was confirmed by a repeated measures ANOVA conducted on amount of responding, with Trial Type (trained, novel-combo, landmark-only) as the repeated measure, which revealed a significant main effect of Trial Type, $F(2, 10) = 52.75, p < .0001$ ($\eta^2 = .91, 95\%$ CI [.66, .95]). Tukey’s HSD post hoc tests revealed that trained test trials differed from all other trial types, $p < .001$ ($d > 1.79, 95\%$ CIs [.58 $\leq d \leq$ 12.57]); additionally, responding on novel-combo test trials was greater than landmark-only test trials, $p = .01$ ($d = 1.53, 95\%$ CI [.42, 2.85]).

**Spatial control.** One pigeon emitted a mean of one peck (i.e., to any location) across both days of testing during both novel-combo trials (YA and XB), which was much less than the group mean of 21 ($SD = 13.16$) and much less than even the bird with the next fewest pecks (13.25). With so few responses, this subject’s proportion data were unreliable, and consequently, the following analysis contains only the remaining subjects ($n = 5$).

**Discussion**

The aim of Experiment 1 was to evaluate spatial control by an OS and LM during transfer tests following training in an operant feature-
positive spatial task. The novel-combo transfer tests indicated that the OS facilitated responding to the landmark above that of responding to the landmark-only test, but to a lesser degree than on test trials of the OS with the same landmark from training. This is consistent with much of the literature on occasion setting (see Schmajuk & Holland, 1998, for a review). A similar pattern of results was also found when evaluating the spatial distribution of responding.

These results partially address the questions raised earlier. First, the amount of responding on novel-combo transfer trials (in which a previously trained landmark was paired with a different OS from training) was below that of trials of the landmarks paired with the same OS from previous training, indicating that amount of responding was not simply the summation of OS–outcome and landmark–outcome associations. Rather, as predicted, the amount of responding was largely controlled by the OS facilitating responding to specific landmark–goal associations. Second, evaluation of the spatial distribution of responding on the trained OS-landmark and novel-combo test trials indicated that, as predicted, spatial search was primarily controlled by the landmark. On novel-combo trials, the spatial information provided by the OS and landmark were incongruent. If responding were controlled solely by the OS, then we would have expected responding to have been to the side of the landmark away from the goal in Figure 4b. If the landmark and OS shared control equally, or if the landmark simply served as a beacon for where to respond, then the proportion of responding should have been the same to the left and right of the landmark (see the “Other” group in Figure 4b). Lastly, if the landmark primarily controlled search, then most of the responding should have been to the right of the landmark in Figure 4b (at the goal). Data from three pigeons indicated some degree of spatial control by the OS or landmark. These pigeons responded predominantly to the right of the landmark at the location of the goal signaled by the landmark. Two pigeons responded indiscriminately to the left and right of the landmark, which could be indicative of control by both the OS and LM. In sum, these data indicate that for all birds, the excitatory strength of responding to an OS–LM pair was reduced during the novel-combo transfer tests. For three birds, responding during novel-combo transfer tests reflected their learning of specific landmark–goal associations encountered during training.

In previous research with honeybees, specific landmark–goal associations also determined search behavior in a spatial task. T. S. Collett and Kelber (1988, Experiment 2) trained honeybees to search for the location of sucrose relative to two yellow cylinders present in Context X, and at a different location signaled by two blue triangles (the yellow cylinders were not present) present in Context Y. After training, novel-combo transfer tests with the landmarks switched to the other context (e.g., blue triangles in Context X) indicated that bees searched at the position defined by the landmarks, not the context. Furthermore, the switch caused no noticeable deficit in spatial accuracy. Similar to honeybees, but in contrast to pigeons, humans tested in a comparable design also displayed good spatial control by the landmark (i.e., no deficit in spatial accuracy) during novel-combo transfer tests (Ruprecht et al., 2014). This difference may reflect differences in experience with hierarchical relations and landmarks, or an innate propensity for learning about specific items (pigeons) versus the relationship between items (humans; e.g., Wright, 1997; see Shanks, 2010, for a review).

The results of Experiment 1 indicate that the stability of the landmark was weighted heavier than the reliability of the colored background with respect to control of spatial search. The specific landmark–goal associations from training best matched spatial responding during transfer tests of the landmark paired with a different OS from training. The aims of Experiment 2 were to use a more complex occasion-setting task to reduce the stability of LM.
A, and to further investigate the nature of the deficit during incongruent trials in Experiment 1.

**Experiment 2**

The preponderance of evidence in Experiment 1 indicated that more spatial control was exerted by the landmark–goal association learned during training than the direct OS–goal association. This is consistent with much of the occasion-setting research, which has reported modulation by an OS of a specific CS–outcome association (Holland, 1983). In occasion setting of timing behavior, it was similarly found that the CS–outcome association (i.e., not the OS–outcome) controlled the timing of the response (Bonardi & Jennings, 2007; see also Nakajima, 2009, for an operant procedure). However, Experiment 1 and previous research have not investigated whether training that encourages modulation of spatial or temporal information by the OS (e.g., \(+\leftrightarrow XA+/YA\leftrightarrow+/A−\) ) will result in transfer of OS control to another DS (e.g., Bonardi & Jennings, 2007; T. S. Collett & Kelber, 1988; Nakajima, 2009). In Experiment 1, the information value of the OS was minimal. Each distinct landmark (A and B) was associated with a unique spatial relationship to the goal (left or right of the landmark), and thus the OS was simply needed to determine whether or not a response in the presence of a landmark would lead to reward. There are many manipulations to reduce the value of the landmark, including those applicable outside (e.g., lowering the brightness of the LM) and within the domain of spatial learning (e.g., increasing proximity or lowering stability). In Experiment 2, the spatial proximity of the landmark to the goal was maintained, but the stability of a landmark was manipulated across trials. Consequently, a high reliability but low stability and proximity OS was paired with a landmark that was low in reliability and stability but high in proximity. We expected this manipulation to increase control of spatial behavior by the LM–goal spatial relationship signaled by the OS.

In Experiment 2, the same landmark (A) was trained with two OSs, such that the spatial relationship of the landmark to the hidden goal was ambiguous without exposure to the preceding OS (\(+\leftrightarrow XA+/YA\leftrightarrow+/A−\) ). This type of training should encourage reliance on X and Y to disambiguate the direction in which to respond to LM A. We also included training trials with another OS–landmark pair (\(+\leftrightarrow ZB/B−\) ), as well as a DS/LM (C \(\leftrightarrow+\) ) that did not rely on an OS to signal the contingency or direction of the goal. After training, various transfer tests were used to determine the influence of each cue on the amount of responding and spatial control. A key procedural difference between this study and most previous studies was that we did not extinguish C prior to transfer testing (see Swartzentuber, 1995, for a review). We were interested in whether the amount of responding and spatial control by C would be affected if the OS and landmark were both at full excitatory strength during novel pairings (cf., Bonardi, 1996).

The first set of transfer tests (novel incongruent, YB−) in Experiment 2 was similar to the novel-combo test (YA−) in Experiment 1, but with the addition of a transfer test with a landmark not previously trained with an OS (XC−). During training, specific LM–goal associations were expected to control spatial accuracy in the presence of LMs B and C. Additionally, some degree of stimulus equivalence was expected between LMs A and B because of their common training history (i.e., being paired with an OS during training), which LM C did not share. Consequently, OS Y should be better able to facilitate responding to B (instead of A) than OS X to C (instead of A). Any decrement that occurred during novel-incongruent tests could be the result of external inhibition, generalization decrement, or spatial incongruence. On the second set of transfer tests, the OS and landmark provided congruent spatial information regarding the direction of the goal relative to the landmark. On these tests, no difference was expected between an OS paired with a landmark with or without previous occasion-setting training. However, the match in spatial information provided by each cue may increase the amount of responding and spatial control relative to the novel-incongruent test. Bonardi et al. (2012) manipulated the outcome associated with a CS in two occasion-setting pairings (X \(\rightarrow A\rightarrow\) sucrose, and Y \(\rightarrow B\rightarrow\) oil). Transfer of performance (responses per minute, or amount of responding) was better to other CSs (C and D) when the outcome paired with the transfer CS matched that paired with the OS during occasion-setting training. In our experiment, the outcome was the same, but the direction of the goal relative to the landmark differed. We predicted that X and Y would facilitate more responding when paired with landmarks that shared a common spatial relationship (e.g., \(+\leftrightarrow XA+\leftrightarrow ZB\) ) during training.

Following transfer testing, we extinguished OS X and LM C. The goal of extinction of X was to determine whether X would continue to facilitate responding to A after weakening any direct connection between X and the rewarded goal. If X was acting to facilitate responding via a direct connection, then responding to A should be diminished. However, if X was acting independent of any direct connection, responding to A should be unchanged following extinction of X. Additionally, previous research has found some evidence for enhanced transfer of modulation by an OS following extinction of the OS (Holland, 1989).

**Method**

**Subjects.** Six White Carneaux pigeons (Columba livia; Double T Farm, Glenwood, IA) served as subjects. Pigeons were between 18 and 24 months at the time of testing. Pigeons were maintained and housed as in Experiment 1. All birds were experimentally naive prior to the start of the experiment.

**Apparatus.** Training and testing were conducted in an apparatus identical to Experiment 1.

**Stimulus displays.** Stimuli were identical to that of Experiment 1, with the exception of an additional colored background (cyan).

**Procedure.**

**Training.** Pretraining was identical to that of Experiment 1. The experimental design for Experiment 2 is described in Table 1. Occasion-setting sessions consisted of six trial types: \(+\leftrightarrow XA+\rightarrow\) YA--; \(\rightarrow+\leftrightarrow ZB\rightarrow\) C--; \(\rightarrow A\rightarrow\) ; and B−. On YA and ZB trials, the hidden goal was one response location to the left of the landmark. On YA and C trials, the hidden goal was one response location to the right of the landmark. Trials were presented in the same manner as in Experiment 1, with the exception of C trials. On C trials, the background remained black throughout the trial and responses at the hidden goal were reinforced in a manner identical to A on YA trials. Sessions initially consisted of 48 trials, with eight trials of each type. Once subjects reached the RR4 schedule
of reinforcement, the number of trials per session was increased to 64, with an equal number of the six trial types.

In contrast to Experiment 1, birds were independently advanced to testing based on their performance. After each subject completed two sessions in which the correct response was made on 80% of all occasion-setting trials, and the discrimination ratio (pecks at the correct location divided by all responses) was greater than or equal to .60, the subject was advanced to the next test condition. A minimum of 30 retraining sessions were required in between each test.

Novel-incongruent test. Novel-incongruent testing occurred for 2 days. The order of test trials each day was counterbalanced across all subjects in each testing condition. All subjects received one nonreinforced trial of XA, ZB, YA, YB, XC, C, A, and B per session for two sessions. A test session began with 48 training trials, followed by a block of test trials, and an additional 24 training trials. A test session consisted of (a) an equal number of reinforced (XA, YA, ZB, and C) and nonreinforced trials (A and B), as in training; and (b) a block of eight consecutive nonreinforced test trials. On occasion-setting test trials, the landmark always appeared 10 s after the OS, and landmark-only trials were always 30 s in duration.

Novel-congruent test. All subjects received one nonreinforced trial of XA, YA, ZB, A, B, C, and XB per session for two sessions. Trials were presented in the first transfer test session.

Novel-ambiguous test. All subjects received one nonreinforced trial of XA, YA, ZB, XB, XC, ZC per session for two sessions. The direction of the goal relative to the landmark on ZA trials was ambiguous, as A had been paired with X (goal to left of A) and Y (goal to right of A) during training. The direction of the goal relative to the OS (X) was incongruent with that predicted by the landmark on XC, YB, and ZC trials.

Postextinction test. During two extinction sessions, pigeons received pseudorandom presentations of X and C without the opportunity for reinforcement. Each session consisted of 16 trials of X and C, with the constraint that neither trial type could occur more than 3 times in a row. Following extinction, test sessions of only nonreinforced test trials of XA, YA, ZB, YC, XB, A, B, and C were given.

Measures and statistical analysis. The measures and statistical analyses were identical to those used in Experiment 1.

Results

A program error led to a shortened duration of nonreinforced test trials of C (15 s) relative to the other landmark-only test trials (30 s). This undoubtedly influenced the overall amount of responding on test trials with C, but should not have greatly influenced spatial control by C. (And the statistical analysis of spatial control by C supports this.) Consequently, the amount of responding on C trials was not analyzed. The spatial distribution of responding during each test can be found in the online supplemental material.

Training. Subjects achieved the necessary response criterion to advance to testing during OS training with a mean of 41 (SD = 4) sessions. One subject’s training was discontinued after failing to meet the criterion to advance to testing after 60 sessions of training (n = 5).

Novel-incongruent test.

Amount of responding. Novel-incongruent transfer tests evaluated the number of pecks during two transfer trials, XC and YB. The direction of the goal relative to the OS and landmark was incongruent in each combination of OS and landmark, such that during training the OS and landmark signaled the goal in opposite directions. Figure 5 displays the amount of responding, in the same manner as Experiment 1. Landmarks A and B elicited no responses for any bird and thus could not be included in the statistical analysis. A repeated measures ANOVA conducted on mean responses across all eight response locations, with Trial Type (XA, ZB, YA, XC, and YB) as the repeated factor, revealed a significant main effect of Trial Type, F(4, 16) = 15.23, p < .0001 (η² = .79, 95% CI [.44, .85]). Post hoc analysis (Tukey’s HSD) revealed that XA, ZB, and YA differed from XC and YB, ps < .001 (ds > 1.33, 95% CIs [.06 ≤ d ≤ 2.85]), but did not differ from each other, ps > .62. Responding on XC did not differ from YB, p = .60.

Spatial control. Figure 5 shows the spatial difference score of responses during Trial Types XA, ZB, YA, C, XC, and YB. A high percentage of pecks occurred at the goal predicted by the landmark on the previously trained OS pairings (XA, YA, and ZB), a moderate level was observed during the novel-incongruent YB transfer tests, and spatial control by the landmark was lowest during XC transfer tests. These observations were supported by a repeated measures ANOVA conducted on mean percentage of pecks to the goal with Trial Type (XA, ZB, YA, XC, and YB), which revealed a significant main effect of Trial Type, F(5, 20) = 5.77, p = .002 (η² = .59, 95% CI [.15, .69]). Post hoc analysis revealed that spatial control by the landmark during XA, YA, ZB, and C differed from XC, ps < .05 (ds > .132, 95% CIs [.05 ≤ ds ≤ 2.84]), but not YB, ps > .27. However, XC and YB did not statistically differ from one another, p = .23.

![Figure 5](image-url)
We compared the spatial control by the landmark during each trial type with zero. Separate single-sample t tests revealed control by the landmark during training trials XA, YA, YA, and novel-incongruent trial YB, \( t(4) > 3.60, p < .05 \) (\( ds > .161, 95\% \text{ CIs [.22 ≤ ds ≤ 3.31]} \)), all differed significantly from zero, whereas control during XC was not significantly different from zero, \( t(4) = .49, p = .65 \).

**Novel-congruent test.** Subjects were advanced to novel congruent testing following a mean of 32 additional training sessions (\( SD = 3.1 \); i.e., Session 73). A paired-samples \( t \) test comparing the amount of responding during the two novel-congruent configuration transfer tests across Test Session 1 and Test Session 2 revealed a significant reduction in responding across sessions, \( t(4) = 3.56, p = .02 \) (\( d = .159, 95\% \text{ CI [.21, 3.28]} \)), which was not found during the previous novel-incongruent transfer test, \( t(4) = .35, p = .75 \). As previously mentioned, we are most interested in evaluating responding before significant extinction occurs. Consequently, all subsequent analyses include data only from Test Session 1.

**Amount of responding.** The amount of responding and spatial distribution of pecks were recorded during two novel-congruent transfer trials, XB and YC, and during the previously trained OS pairs. On novel-congruent trials, the direction of the goal relative to the OS and landmark was congruent in each novel configuration of a landmark with a different OS from training. Figure 6 displays the amount of responding across all locations during each test trial. Landmarks A and B elicited no responses for any bird, and thus could not be included in the statistical analysis. A repeated measures ANOVA conducted on mean responses across all eight response locations, with Trial Type (XA, XB, YA, XB, YC) as the repeated factor, revealed a significant main effect of Trial Type, \( F(4, 16) = 7.47, p < .01 \) (\( \eta^2 = .65, 95\% \text{ CI [.19, .75]} \)). Post hoc analysis revealed that ZB and YA differed from XA and YC, \( p < .05 \) (\( ds > .1.13, 95\% \text{ CIs [−.07 ≤ ds ≤ 2.52]} \)), but not from each other \( p = .98 \). Similarly, more responding was observed on XA than XB and YC, but was only marginally nonsignificant, \( p > .06 \) (\( ds > .1.08, 95\% \text{ CIs [−.10 ≤ ds ≤ 2.43]} \)), but did not differ significantly from ZB and YA, \( p > .80 \). Responding during novel-configuration XB and YC trials did not differ from one another, \( p = .99 \).

**Spatial control.** Spatial control was analyzed as in the previous tests. Figure 6 also shows spatial control by the landmark during test trials XA, YA, ZB, C, XB, and YC. Spatial control by LMs B and C on transfer test trials is similar to that of the landmarks on the other test trials. A repeated measures ANOVA conducted on the difference score with Trial Type (XA, ZB, YA, C, XB, and YC) revealed weak evidence for a main effect of landmark, \( F(5, 20) = 2.68, p = .05 \) (\( \eta^2 = .40, 95\% \text{ CI [.00, .53]} \)). Post hoc analysis (Tukey’s HSD) revealed weak evidence for more spatial control by XA, ZB, and YC than XB, \( p > .07 \) (\( ds > .65, 95\% \text{ CIs [−.23 ≤ ds ≤ 1.76]} \)), but all other comparisons revealed nonsignificant differences, \( p > .12 \).

We also compared spatial control during each trial type to zero. Separate single-sample \( t \) tests revealed all trial types significantly differed from zero, \( t(4) > 3.65, p < .05 \) (\( ds > .1.63, 95\% \text{ CIs [.23 ≤ ds ≤ 182.47]} \)).

**Novel-ambiguous test.** Subjects were advanced to testing following a mean of 38 additional training sessions (\( SD = 1.8 \); i.e., Session 111). No responses were recorded to any location on XC trials. The analysis below includes only the critical tests with ZA and ZC compared with ZB.

**Amount of responding.** Figure 7 displays the amount of responding during tests of the original training trials, as well as two novel-configuration transfer trials, ZA and ZC. The direction of the goal relative to A on novel pairings of Z and A was ambiguous, whereas during the other test trial, Z and C signaled conflicting spatial information regarding the goal location. A repeated measures ANOVA conducted on mean responses to all eight response locations, with Trial Type (ZB, ZA, and ZC) as the repeated factor, revealed a significant main effect of Trial Type, \( F(2, 8) = 7.33, p = .02 \) (\( \eta^2 = .65, 95\% \text{ CI [.03, .79]} \)). Post hoc analysis revealed that ZB differed from ZC, \( p = .02 \) (\( d = 1.59, 95\% \text{ CI [.21, 3.28]} \)), but not from ZA, \( p = .48 \). The difference between ZA and ZC was nonsignificant, \( p = .08 \) (\( d = 1.59, 95\% \text{ CI [.21, 3.28]} \)).

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**Figure 6.** Mean sum of pecks at all eight locations and spatial control during Test 2 of Experiment 2. Test trials include those presented during training (XA, YA, and ZB) and novel-congruent (XB and YC) transfer trials. All test trials were nonreinforced. Error bars represent the standard error of the mean.

**Figure 7.** Mean sum of pecks at all eight locations and spatial control during Test 3 of Experiment 2. Test trials include those presented during training (XA, YA, and ZB), and novel-incongruent (XC, YB, and ZC) and novel-ambiguous (ZA) transfer trials. All test trials were nonreinforced. Error bars represent the standard error of the mean.
Spatial control. Figure 7 also shows spatial control during each test trial. There were no responses to the goal during trials of ZC, and only two responses across all birds to any location, which prevented any meaningful comparisons. Given the direction of the goal relative to A was ambiguous on ZA trials, we specified the direction of the goal based on training trials of ZB (i.e., to the left of A, as the goal occurred to the left of B during ZB training trials). A paired-samples t test compared spatial control on trials of ZB and ZA trials and found no reliable difference, t(4) = 1.18, p = .30.

We also compared the difference score from each trial type to zero. Separate single-sample t tests revealed good spatial control during trials of ZB, t(4) = 38.12, 95% CI [14.82, 71.15], and ZA, t(4) = 3.95, p = .02 (d = 1.77, 95% CI [0.30, 3.58]).

Postextinction test. Extinction of C and X. Subjects were advanced to extinction training following a mean of 43.2 additional training sessions (SD = 0.5; i.e., Session 154). Figure 8 shows responding across sessions of extinction trials with X and C.

Amount of responding. There were no responses recorded on B or XB trials during testing, and only two birds responded to YC, thus preventing any meaningful comparisons. LM A elicited responses from only one bird and thus could not be included in the statistical analysis. Responding during trials of an OS with the same landmark from training remained reliable. Figure 9 displays data from the remaining test trials. A repeated measures ANOVA conducted on mean responses across all eight response locations during test trials of the training stimuli (XA, YA, and ZB) revealed no statistical difference between the trial types, F(2, 8) = .01, p = .91. Critically, XA (M = 25.20, SEM = 12.40) did not differ from YA (M = 29.20, SEM = 20.75), t(4) = .44, p = .68.

Spatial control. Too few pigeons responded to the goal on YC or XB trials to make meaningful comparisons. Figure 9 displays spatial control during the remaining test trials. Paired-samples t tests were used to compare spatial control during XA and YA, which found no reliable difference, t(4) = .84, p = .45, or between ZB and XA, t(4) = 1.32, p = .26. We also compared the difference score during tests of these trial types to zero. Single-sample t tests revealed the difference score significantly differed from zero during training trials XA, t(4) = 54.66, p < .0001 (d = 24.44, 95% CI [9.48, 45.64]), ZB, t(4) = 3.82, p = .02 (d = 1.71, 95% CI [0.27, 3.48]), and YA, t(4) = 4.00, p = .02 (d = 1.79, 95% CI [0.31, 3.62]), whereas C did not, t(4) = 1.00, p = .37.

Discussion

In Experiment 2, the spatial relationship of a landmark (A) to a hidden goal was determined by the OS (X or Y) that preceded it. Pigeons learned the task quickly and to a high degree of accuracy (M = 87.14% pecks at goal, SD = 4.64, across all four types of training trials during Test 1). During novel-incongruent tests, we replicated the effect found in Experiment 1 (novel-combo test with YA), such that the amount of responding during the novel-incongruent transfer test with YB was found to be greater than B alone, but also lower than trials of the previously trained OS-landmark pairing (YA). Unlike Experiment 1, the spatial distribution of responding on YB trials indicated spatial control by B to the same degree as the previously trained YA (exactly like the humans behaved in Experiment 1 of Ruprecht et al., 2014). On the other novel-incongruent trial XC, responding to C during XC trials was weak and indicated poor spatial control (see Figure 5). On novel-congruent trials, spatial control during XB was unchanged.
whereas control by C improved when it was paired with OS Y (which signaled congruent spatial information regarding the direction of the hidden goal). On novel-ambiguous test trials, A was paired with Z and the location of responding relative to A was controlled by OS Z. Lastly, extinction of OS X did not disrupt subsequent modulation of A by X.

**Congruence and training history.** Training history did not have a noticeable effect on the amount of responding observed during novel pairings of X and Y with B or C during the novel-incongruent or congruent tests. During the novel-incongruent test, more responding was observed during previously trained OS–landmark pairs (XA, YA, and ZB) than novel-configuration transfer tests (XC and YB), but no statistical differences were found between trial types within each category. The same pattern of responding was observed during the novel-congruent (XB and YC) test. Thus, the training history of B and C did not influence the amount of responding on transfer trials. The effect of congruence on amount of responding should be most apparent when comparing novel-incongruent to novel-congruent transfer tests, but no statistical difference was found. This suggests that reduced responding on the novel-incongruent transfer trials in Experiment 2 (and likely on novel-combo trials in Experiment 1) was the result of changes in the stimulus conditions (e.g., generalization decrement or external inhibition) at test, and not competition between OS and LM control.

Spatial control by LM B, which was paired with an OS during training, was insensitive to changes in stimulus conditions and spatial interference during transfer tests (XB and YB). Spatial control during transfer tests of LM B paired with a different OS from training was similar to control during tests of the previously trained OS–landmark pairs (e.g., ZB), which indicates an insensitivity to changes in the stimulus conditions (i.e., novel configurations). Insensitivity of OS modulation to spatial interference was supported by the absence of a reliable difference in spatial control during novel-incongruent versus congruent transfer tests. The influence of training history on OS modulation can be evaluated by comparing performance during transfer tests of B with performance during transfer tests of a landmark without prior occasion-setting training (XC and YC). Spatial control by C during YC novel-congruent trials, but not XC (incongruent), was comparable with that of the previously trained OS–landmark pairs (see Figures 6 and 7). This contrasts with that observed on transfer tests with LM B, which suggests training history influenced transfer performance. Regarding spatial interference, there was a large difference in spatial control by C when paired with X (incongruent) and Y (congruent). Because the overall change in the stimulus conditions (e.g., generalization decrement) was identical on XC and YC trials, the difference in performance between trials is best explained by conflicting spatial information (i.e., spatial interference) regarding the location of the goal signaled by the OS and the landmark. Spatial control during a transfer test with C was disrupted by spatial interference (e.g., XC), but not by changes in the stimulus conditions of C at test (e.g., YC).

This result is consistent with previous research reported by Bonardi (1996) on the role of generalization decrement during transfer testing. Pigeons were trained with two Pavlovian occasion-setting pairs (XA+/A−/YB+/B−) and two pseudo occasion-setting pairs (XC+/C−/YD+/D+). Transfer tests with novel pairings of CSs and OSs from training revealed incomplete transfer on XB trials but complete transfer on XD trials. This result demonstrates that incomplete transfer when an OS is paired with a different CS (or DS) from training may be caused by factors other than the novelty of the pairing (e.g., generalization decrement).

In Experiment 2, spatial interference reduced spatial control only when an OS was paired with a landmark that did not previously participate in occasion setting. Training history played a role in determining how well an OS facilitated where, but not how much, subjects responded to a landmark (see Ruprecht et al., 2014, for a comparison with performance by humans in the same task).

**Spatial control by an OS.** In Experiment 2, we reduced the stability of LM A and expected that this manipulation would result in greater spatial control of responding by the OS when paired with a different LM during transfer testing. As reported earlier, good spatial control on YB transfer tests was observed; however, the location of responding was again consistent with the LM–goal association from training, and inconsistent with the LM–goal association signaled by the OS. One strategy for interpreting these effects involves retrieval of the LM–goal memories from training at the time of testing (e.g., T. S. Collett & Kelber, 1988; Holland, 1989). According to the retrieved-memory interpretation, on YB tests, Y should have retrieved a memory for responding to the left of A, which was weighted less than the memory retrieved by B (i.e., respond to the right). On XC, X should have retrieved a memory of responding to the right of A, which competed equally with the memory retrieved by C (i.e., respond to the left). Both trials types were disrupted (i.e., fewer mean pecks than previously trained OS pairs), but B continued to control spatial behavior, whereas C did not. This difference can be attributed to the training histories of B and C, but these data do not allow us to dissociate between the various explanations of why training history mattered.

One intriguing possibility relates to Rescorla’s (1985) suggestion that the OS lowers the threshold for activation of the US representation in the presence of a DS previously trained with an OS. In this manner, OS Y lowered the threshold for activation of the LM B–goal, but not C–goal, association despite never being paired with B or C during training. In sum, despite the increased weight expected to OSs X and Y, the landmark continued to control the location of responding during novel-incongruent transfer tests. During novel-ambiguous tests, Z was paired with A and C on separate trials. The direction of the goal relative to A was ambiguous without a previously trained OS (X or Y). If the landmark was again given more weight than the OS, then on ZA trials, the LM A–goal associations from training would result in equal responding to left and right of A at test. Alternatively, if the OS was weighted higher than LM A, then the LM B–goal association signaled by OS Z would result in responding to the side of A consistent with the direction signaled by Z during training trials of ZB. On ZC trials, OS Z (goal to the left) and LM C (goal to the right) signaled conflicting spatial information regarding the location of the hidden goal. Test data revealed that pigeons responded to the side of A on ZA trials consistent with the B–goal association during training with ZB. Indeed, there was no difference in the amount of responding or spatial control of responding between ZB (previously trained) and ZA (ambiguous), though ZB did differ from ZC (incongruent) in both measures. Once again, responding to C, a landmark with no prior OS-landmark training, was disrupted when there was spatial incongruence between the goal signaled by the OS (Z) and the landmark (C).
Based on the retrieved-memory interpretation, during the ZA test, Z should have retrieved a memory for responding to the right of B, which was not incongruent with the memory retrieved by A (to the left or right). However, on ZC trials, Z should have retrieved a memory of responding to the right of B, which was incongruent with the memory retrieved by C (to the left). Responding on ZA trials was the only case in which both the amount of responding and spatial control did not differ from the previously trained trials. Why so much responding during ZA? Was it that the identity of A was completely ignored and mistaken for B? The results of ZC trials eliminate this possibility. If the identity of Landmarks C and A were not detected following Z, then the amount of responding and spatial control on ZA and ZC trials would have been similar. Another possibility, consistent with a hierarchical account, is that prior training of A and B increased generalization between them. However, that does not explain why ZA elicited more responding than XB trials. In previous cases (YB and XB), two unambiguous memories regarding the location of the goal were always retrieved (e.g., memory based on Y and B), but on ZA, only one unambiguous memory based on OS Z would have been retrieved. Enhanced performance may be the result of a combination of the lack of spatial interference between retrieved memories of the OS and LM, and acquired equivalence between A and B. Lastly, the ZC test also rule out an alternative interpretation to the role of spatial interference with LM C during XC and YC in Tests 1 and 2, respectively. It is possible that improved performance on YC trials in Test 2 may have been related to attenuated generalization decrement following exposure to XC in the first set of transfer tests. However, ZC represents a third exposure in which generalization decrement should be further reduced, but spatial incongruence should still be present. Weak performance during ZC trials suggests spatial incongruence was the cause of disrupted control by C on XC and ZC trials.

Posttraining extinction. A hallmark of an OS is that modulation of a DS (or CS) is resistant to extinction of the OS. X was extinguished across two sessions (see Figure 8). Following extinction of X, performance on a test with XA showed no disruption in control by C on XC and ZC trials. The second is that the OS would facilitate responding to specific landmark goals (e.g., a discriminative stimulus) and a reinforced response location (i.e., goal). There were at least two distinct possibilities regarding the role of the OS in a landmark task. The first is that an OS–goal association would control the amount of responding and location of behavior. In Experiment 1, the OS was a perfect predictor of the landmark–goal contingency and spatial relationship; thus, the landmark could be largely ignored minus a role for anchoring the response (e.g., see Experiment 3 in T. S. Collett & Kelber, 1988). The second is that the OS would facilitate responding to specific landmark goals. In this scenario, the identity of the landmark would be critical as the pigeons learned to respond to the left or right of specific landmarks. Figure 10 displays the mean difference score (i.e., spatial control) for the proportion of responses at the goal signaled by the LM, minus the proportion of responses at the goal signaled by the OS across each testing condition and experiment. Experiment 1 demonstrated that if control by either the LM or OS was observed, it was the landmark-retrieved memory, not the OS, that controlled search for the location of the hidden goal. This is consistent with findings from the temporal domain suggesting that subjects encode specific CS–outcome intervals when trained in occasion-setting tasks (Bonardi & Jennings, 2007; Nakajima, 2009). Experiment 2 further explored conditional control by manipulating the stability of the spatial relationship of a landmark (A) to the goal. Pigeons learned the task, and transfer tests indicated that congruent spatial information from the OS- and LM-retrieved memories mattered only when the OS was paired with a landmark that had not been previously trained with an OS (see Figure 10). Lastly, posttraining extinction of X did not disrupt modulation of A by X during subsequent testing. Taken together, these results suggest that spatial control of responding is similar to that of temporal control, and provided by the landmark), the OS can signal the location of an expected goal (e.g., on novel-ambiguous ZA trials).

Our results are inconsistent with Bonardi et al. (2012), who reported that transfer of performance (responses per minute) was better to other CSs (C and D) when the outcome paired with the transfer CS matched the outcome paired with the OS during occasion-setting training. One critical difference is that we manipulated the spatial location of an outcome signaled by a cue (i.e., goal to the left vs. right), whereas Bonardi et al. manipulated the quality of the outcome (i.e., oil vs. sucrose). Transfer performance (amount of responding and spatial accuracy) in our task was not facilitated by a match in the expected location of the outcome based on the OS and landmark. The quality of an outcome is likely more biologically significant to rats than the direction of the outcome relative to a landmark for pigeons, which may explain why congruence did not affect performance in our task. For humans completing a task and transfer tests nearly identical to Experiment 2, however, spatial congruence did increase the amount of responding at the goal signaled by the landmark relative to the novel-incongruent test (Rupecht et al., 2014).

**General Discussion**

A spatial-search task was used to explore how conditional control of behavior could be extended to the spatial domain. During occasion-setting training, a colored background stimulus (the OS) signaled the contingency between a landmark (e.g., a discriminative stimulus) and a reinforced response location (i.e., goal). There were at least two distinct possibilities regarding the role of the OS in a landmark task. The first is that an OS–goal association would control the amount of responding and location of behavior. In Experiment 1, the OS was a perfect predictor of the landmark–goal contingency and spatial relationship; thus, the landmark could be largely ignored minus a role for anchoring the response (e.g., see Experiment 3 in T. S. Collett & Kelber, 1988). The second is that the OS would facilitate responding to specific landmark goals. In this scenario, the identity of the landmark would be critical as the pigeons learned to respond to the left or right of specific landmarks. Figure 10 displays the mean difference score (i.e., spatial control) for the proportion of responses at the goal signaled by the LM, minus the proportion of responses at the goal signaled by the OS across each testing condition and experiment. Experiment 1 demonstrated that if control by either the LM or OS was observed, it was the landmark-retrieved memory, not the OS, that controlled search for the location of the hidden goal. This is consistent with findings from the temporal domain suggesting that subjects encode specific CS–outcome intervals when trained in occasion-setting tasks (Bonardi & Jennings, 2007; Nakajima, 2009). Experiment 2 further explored conditional control by manipulating the stability of the spatial relationship of a landmark (A) to the goal. Pigeons learned the task, and transfer tests indicated that congruent spatial information from the OS- and LM-retrieved memories mattered only when the OS was paired with a landmark that had not been previously trained with an OS (see Figure 10). Lastly, posttraining extinction of X did not disrupt modulation of A by X during subsequent testing.Taken together, these results suggest that spatial control of responding is similar to that of temporal control, and
furthermore, modulation by an OS in a spatial task is similar to that observed in more conventional occasion-setting tasks.

Cheng et al. (2007) applied Bayesian principles to model how multiple landmarks compete for spatial control of behavior in tasks similar to Experiments 1 and 2. Bayes’s (1763) theorem suggests that a cue’s contribution to the control of behavior, including spatial behavior, should be weighted inverse to its variance. For example, Cheng et al. described spatial overshadowing, in which the presence of a more proximal landmark reduced spatial control by a distal landmark (Leising, Garlick, & Blaisdell, 2011; Spetch, Cheng, & Mondloch, 1992), as the result of the distal landmark given less weight because of the increased variance inherent in the relatively longer distance of the distal than proximal landmark to the goal. Thus, different weightings are assigned to cues according to Bayesian principles. In another example, T. S. Collett and Kelber (1988) found that proximal landmarks were weighted more than distal landmarks on transfer tests when the search space was enclosed, but when the bees searched on an open platform, the more proximal landmarks were weighted less than the distal landmarks. In this case, the higher variance of spatial information provided by distal cues must have been weighted less than (or counteracted by) the reduced variance provided by the high salience of the distal cues from the open platform. In the current experiments, we have cues that differed in proximity, stability, and reliability. When the stability of the LM was reduced in Experiment 2, our results indicate that more weight was given to the LM—goal memory retrieved by the OS. Bayesian models may be able to model our data, but more experiments that vary each dimension are critical to determining how weights are assigned, as well as how weights from different dimensions are combined to determine overall variance.

Configural theory (Pearce, 1987, 1994) also makes predictions regarding how cues come to control behavior. Our results are inconsistent with traditional configural theory, which predicts that the configuration of X and A present on XA trials would be represented in memory as a unique configuration (e.g., X = X, A = A, \( p = X + A \)). The configurations formed by novel combinations of the OSs and landmarks (e.g., \( q = X + B \)) would bear little resemblance to the original XA configuration. After training on XA and YB (Experiment 1), the novel test configuration of XB should elicit little responding, according to a configural account, but reliable responding was observed. Responding on XB trials could be explained by a configural account by appealing to generalization between configurations. But three pieces of evidence argue against this account of the results of Experiments 1 and 2. First, in both experiments, the LM and OS (colored background) were not paired in the same spatial arrangement with each other across trials. Within each trial type (e.g., XA), the LM and goal appeared in four different positions across trials, which would require four different configurations of the background and LM for accurate responding to the goal for one trial type and 16 configurations for all trial types in Experiment 2. With 16 configurations, and four for each trial type, explanations based on generalization between configurations become less plausible. Second, from a configural perspective, there is no explanation for more accurate responding on YB than XC trials, or why accuracy would improve from XC to YC trials. In both cases, the pairings were equally novel and should have resulted in the same amount of generalization decrement. Third, in previous studies with honeybees, the OS was contextual information located outside of the search space (e.g., a hut). T. S. Collett and Kelber (1988) trained honeybees to enter separate huts to search for sucrose at different locations relative to the same four landmarks. The bees searched near the landmarks inside each hut (OS), so they could not form a configuration of the hut and landmarks together. These data are similar to the findings we report in Experiment 2, which suggests that at the very least, the configural account is not necessary to explain our results.

Newer conceptions of configural learning (e.g., Honev & Watt, 1998; Kutlu & Schmajuk, 2012; Brandon, Vogel, & Wagner, 2000) are more relevant to Experiment 2 because they include a role for both elements and configurations through connections to a hidden unit. At present, hierarchical and neo-configural theories make so many of the same predictions that there is little room for empirical evidence to distinguish between them (e.g., Bonardi et al., 2012). Additionally, there is no reason to assume these learning mechanisms are mutually exclusive. In other tasks, it has been found that different learning mechanisms can occur simultaneously during training and that the conditions (e.g., stimuli) at test may result in the expression of one over the other (Packard & McGaugh, 1996). Furthermore, we suggest there is no reason to assume that the various mechanisms for occasion setting, including CS-specific, US-specific, and CS-US specific (see Swartzentruber, 1995, for a review) are mutually exclusive. It is likely that under most conditions, each mechanism contributes to OS performance, and under certain conditions, one mechanism will predominate. The inclusion of spatial or temporal information in occasion-

Figure 10. Spatial control across experiments. The mean difference score (see text for details) for data collected in Experiments 1 and 2. The data from Experiment 2 are displayed separately for each novel-configuration transfer test and the postextinction test of XA. “Incon.” refers to the test trials in which the location of the goal signaled by the OS and landmark were incongruent, compared with trials in which both cues provided congruent spatial information, or “Cong.” “Ambig.” refers to the test trial in which the direction of the goal relative to A was ambiguous, and “Post.” refers to test trials conducted after the extinction of OS X. Error bars represent the standard error of the mean.
setting tasks may prove fruitful for researchers try to determine the conditions that engage each mechanism.

Research conducted from an associative learning perspective on the amount of behavior elicited during occasion-setting procedures has identified many of the factors that distinguish the hierarchical account from configurual and other accounts (e.g., Bonardi et al., 2012; Schmajuk & Holland, 1998; Swartzentruber, 1995). However, analyzing data only in one dimension (amount of responding) neglects much of the richness of behavior (it occurs in space and time). One aim of these experiments was to introduce a procedure that connects previous research on amount of responding with nonspatial cues to spatial control by landmarks, to encourage more research on occasion setting by those working from within associative and spatial frameworks. In particular, future work can examine the role of conditional if–then relationships between landmarks, meaning both OS and landmark will need to have a clear spatial role (unlike the current experiments). The use of a touchscreen procedure enables work with rats, pigeons, monkeys, and apes to be conducted with the same apparatus. The results reported here highlight the need for additional research modeling spatial behavior in occasion-setting tasks, manipulating the variance of factors influencing spatial control, and on the comparative analysis of occasion setting in spatial tasks.

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