

Spatial Pavlovian Conditioning

by

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ABSTRACT

Three experiments used a spatial serial conditioning paradigm to assess the effectiveness of spatially informative conditioned stimuli in eliciting tracking behavior in pigeons. The experimental paradigm consisted of the simultaneous presentation of 2 key lights (CS2 and CTRL), followed by another key light (CS1), followed by food (the unconditioned stimulus or US). CS2 and CTRL were presented in 2 of 3 possible locations, randomly assigned; CS1 was always presented in the same location as CS2. CS2 was designed to signal the spatial, but not the temporal locus of CS1; CS1 signaled the temporal locus of the US. In Experiment 1, differential pecking on CS2 was observed even when CS2 was present throughout the interval between CS1s, but only in a minority of pigeons. A control condition verified that pecking on CS2 was not due to temporal proximity between CS2 and US. Experiment 2 demonstrated the reversibility of spatial conditioning between CS2 and CTRL. Asymptotic performance never involved tracking CTRL more than CS2 for any of 16 pigeons. It is inferred that pigeons learned the spatial association between CS2 and CS1, and that temporal contingency facilitated its expression as tracking behavior. In a third experiment, with pigeons responding to a touchscreen monitor, differential responding to CS2 was observed only when CS2 disambiguated the location of a random CS1. When the presentation location of CS1 was held constant, no differences in responding to CS2 or CTRL were observed.

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In Pavlovian conditioning, a conditioned response (CR) is elicited by a conditioned stimulus (CS) by virtue of its pairing with an unconditioned stimulus (US). A long tradition of research on Pavlovian conditioning (Bitterman, 2006; Rescorla, 1988) has shown that the circumstances under which conditioning is effective closely parallel those that support causal attribution (Cabrera et al, 2009; Wasserman et al, 1996): an effective CS precedes the US (e.g., Kamin, 1963), is temporally and spatially contiguous with the US (e.g., Christie, 1996; Kaplan, 1984), and is temporally correlated with the US (Gibbon, 1977; Rescorla, 1967).

Whereas temporal relations are a prevalent concern in the study of Pavlovian conditioning (e.g., Gallistel and Gibbon, 2000), spatial relations have been mostly neglected. Research has largely focused on the process of learning *when* something happens, not *where* it happens (Bowe, 1984). The only spatial relation that has received some attention is contiguity, typically in the context of high temporal correlation and contiguity. Silva, Silva and Pear (1992), Christie (1996) and Cabrera et al. (2009) demonstrated that a CS that is temporally correlated with a US is more effective when presented nearer the US. Chamizo and Rodrigo (2004) demonstrated that landmarks (CS) more effectively facilitate finding a hidden platform (US) in a Morris maze the closer they are to the platform (for a review of spatial conditioning in the Morris maze, see Chamizo, 2003). Spatial contiguity of CS and US appears to facilitate attribution of US causality to the CS by preschoolers (Kushnir and Gopnik, 2007). In the

present study we aimed at establishing whether spatial contiguity and correlation can engender Pavlovian conditioning, under temporal conditions that would not otherwise maintain conditioned responding.

Prior studies using serial conditioning (Wasserman et al., 1978) and second-order conditioning (Rescorla and Cunningham, 1979) of autoshaped keypecking have demonstrated that pigeons respond to a second-order stimulus (CS2) that signals the location of an upcoming first-order stimulus (CS1) that is paired with food (US). The design based on two stimuli, CS2 and CS1, is primarily a pragmatic solution to the limitations of the standard operant chamber, which typically holds a single food dispenser. The location of a CS cannot be correlated with a fixed US location, and varying US-location is not always practical and may introduce unwanted confounds (e.g., US location and its distance from the animal may be confounded). The solution implemented by Wasserman and colleagues and Rescorla and Cunningham was to fix the location of the US, precede its presentation by the CS1, and precede the presentation of the CS1 by a CS2 that signaled the location of the CS1. We adopted this tactic in our research design.

Figure 1 depicts the stimulus arrangement within each training cycle in Wasserman et al.'s (1978) Experiment 1. In each cycle, the CS2 was presented for 10 s, along with a control (CTRL) stimulus located where the CS1 would *not* be presented. The CS2 was immediately followed by a 10-s CS1; the CS1 was immediately followed by the US.

Each US and subsequent CS2 presentation were separated by a 60-s inter-trial interval (ITI). Pigeons pecked substantially more on CS1 than on CTRL. Although the spatial relation between CS2 and CS1 might have engendered differential responsiveness to the CS2 relative to CTRL, alternative explanations were not ruled out. In particular, the CS2 signaled not only where the CS1 would appear, but also when the CS1 and the US would appear. Short CS durations relative to an extended ITI (small CS/ITI ratio) have been demonstrated to enhance conditioning (Gibbon et al, 1977; Terrace et al, 1975; Tomie et al, 1989). In the case of Wasserman et al. (1978), the CS2 was an excellent temporal predictor of the CS1—on every trial there were exactly 10 s ($1/6^{\text{th}}$ of the ITI) of separation between CS2 onset and CS1 onset. However, because the CTRL was presented at the same time as the CS2, the CTRL was also temporally correlated with the CS1 and with the US, so temporal correlation between stimuli, by itself, cannot explain the differential responsiveness to the CS2 over CTRL. Nonetheless, it is still unclear whether the spatial relation between CS2 and CS1 was sufficient for differential CS2 conditioning. It is possible that, without its close temporal correlation with CS1 and US, CS2 might have been ineffective.

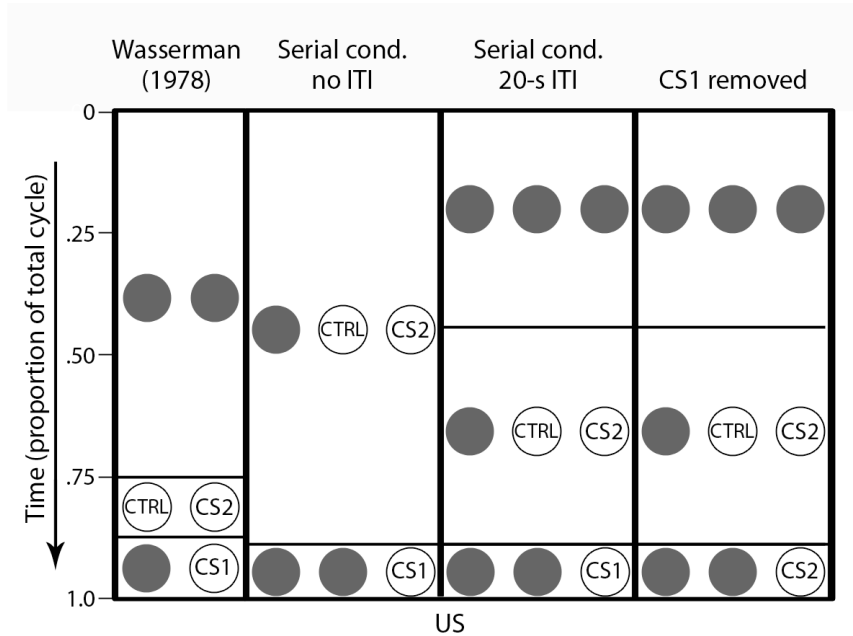


Figure 1. Sketch of Wasserman et al.'s (1978, Experiment 1) procedure and the procedures used in Experiment 1 in the present study. Procedures are indicated by the labels on the top, and separated from each other by thick vertical lines. Events are temporally organized, starting from the top and progressing downward; they are scaled to cycle duration (excluding US). Each circle signifies a response key; their horizontal arrangement indicates the location of stimuli. This arrangement was randomly permuted between cycles (locations shown here are illustrative). See text for further details.

Rescorla and Cunningham (1979) addressed one of the limitations in the study by Wasserman et al. (1978). Pigeons were first trained to respond reliably to a CS1 paired with food. Following training, they

implemented a second-order conditioning design, in which every 60 s a 5-s CS2 was paired with a 5-s CS1. Unlike Wasserman et al. (1978), the CS2 was never presented in temporal proximity of the US. One group was exposed to a CS2-CS1 pairing that was spatially contiguous to the CS1 (i.e., on the same key), and the second group was presented with a CS2 that was always on the key opposite from the CS1. Acquisition was significantly enhanced in the contiguous group, but terminal response rates were the same for both groups. Their study demonstrated that the temporal relation between CS2 and US could not explain the results obtained by Wasserman and colleagues, but did not rule out the possibility that the temporal relation between CS1 and CS2 was necessary for CS2 effectiveness.

In the present study we modified Wasserman and colleagues' (1978) design to minimize the likelihood that the temporal correlation between CS2, CS1, and US influenced spatial CS2-CS1 conditioning. In Experiment 1, the CS2 preceded the presentation of the CS1 (i.e., they were temporally contiguous), but the CS2 duration was at least half of the variable interval between CS1 presentations (Figure 1, *Serial cond.*). That is, when the CS2 duration was half of the ITI (CS/ITI ratio = $\frac{1}{2}$), the onset of the CS1 could occur between 5.5 and 61.6 s after the onset of the CS2. Thus, the temporal correlation between CS2 and CS1 was very weak. To demonstrate the importance of the spatial relation between CS2 and CS1 in eliciting pecking to the CS2, a control condition was implemented in

which CS1 was eliminated and CS2 was extended until the onset of the US. By removing CS1, CS2 became a standard automaintained stimulus, with its offset followed immediately by the US (Figure 1, *CS1 removed*). We anticipated that, even though the CS2 was now temporally contiguous to the US, it would not elicit differential key pecking relative to a concurrent CTRL. Additionally, an overall decline in responding to CS2 would suggest that second-order responding in previous phases was not maintained solely by the temporal proximity of the second-order cues to the US. Experiment 2 was aimed at demonstrating that the discriminative control exerted by the CS2 relative to the CTRL could be reversed.

EXPERIMENT 1

Method

Subjects

Eight experienced adult pigeons (*Columba livia*) were housed individually in a room with a 12:12-hr day:night cycle, with dawn at 0600 hr. They had free access to water and grit in their home cages. The pigeons' running weights were based on 80% of their free-feeding weights. Each pigeon was weighed immediately prior to an experimental session and was excluded from a session if its weight exceeded 8% of its running weight. When required, a supplementary feeding of *ACE-HI* pigeon pellets (Star Milling Co.) was given at the end of each day, at least 12 hr before experimental sessions were conducted. Supplementary feeding amounts

were equal to 50% of the average amount fed over the last day, plus 50% of the deviation in weight from the last day, plus 50% of the current deviation from target running weight.

Apparatus

Experimental sessions were conducted in 8 modular test chambers (305 mm long, 241 mm wide, and 292 mm high), each enclosed in a sound- and light-attenuating box equipped with a ventilating fan. The floor consisted of thin metal bars positioned above a catch pan. The front and rear walls and the ceiling of the experimental chambers were made of clear plastic, and the front wall was hinged and functioned as a door to the chamber. One of the two aluminum side panels served as a test panel. The test panel contained three plastic translucent response keys (25 mm in diameter) aligned horizontally, 70 mm from the ceiling. The keys could be illuminated by white, green and red light emitted from two diodes located behind the keys. A rectangular opening (52 mm wide, 57 mm high) located 20 mm above the floor and centered on the test panel could provide access to milo (grain sorghum) when a grain hopper behind the panel was activated. A house light was mounted 12 mm from the ceiling on the sidewall opposite the test panel. The ventilation fan mounted on the rear wall of the sound-attenuating chamber provided masking noise of approximately 60 dB. Experimental events were arranged via a Med-PC® interface connected to a PC controlled by Med-PC IV® software.

Procedure

Autoshaping. The experiment proper was preceded by autoshaping of pecking on a green-lit key. Each daily experimental session started with the illumination of the house light, which remained continually illuminated during the session. Each session consisted of 80 cycles. Each cycle began with a variable inter-trial interval (ITI) of mean 40 s (each ITI was selected randomly without replacement from a 12-item Fleshler-Hoffman list; Fleschler and Hoffman, 1962), after which one of three response keys was randomly selected with equal probability and illuminated green for 5 s (the primary conditioned stimulus, or CS1). Immediately following the offset of the CS1, the food hopper was activated for 2.5 seconds (the unconditioned stimulus, or US), which terminated the cycle. There were no programmed consequences for pecking any key at any time, but pecks on the green light (which constituted the conditioned response, or CR) were recorded with a temporal resolution of 100 ms. After 6 sessions, all pigeons were pecking reliably to the CS1, and serial conditioning began.

Serial conditioning, no ITI. Figure 1 depicts the stimulus arrangement in this phase. The arrangement was similar to autoshaping, with one exception. Each cycle initiated with 2 of the 3 response keys randomly selected and illuminated—one red, one white—during the interval that served as the ITI in autoshaping (mean duration = 40 s). The

simultaneous offset of both keys was followed by the onset of the CS1, followed by the US.

One of the 2 colors, red or white, was presented always on the same key as the subsequent CS1, thus indicating its location and serving as a (spatial) CS2. The other color always appeared on 1 of the 2 remaining keys where the CS1 would *not* be presented during that trial, constituting an explicitly spatially unpaired control stimulus (CTRL). The assignments of red and white were counterbalanced such that, for half of the birds, red served as the CS2 and white as CTRL, and vice versa for the other half. These assignments aimed at equalizing mean response rate during autoshaping training across CS2-color groups. Fifteen sessions were conducted.

Color counter-biasing. Even though serial conditioning was effective in 2 of the 8 birds in the previous phase, it was of some concern that both of these birds were in the group with a red CS2. Because these birds had previously been exposed to an experiment in which a red key was paired with food, it was possible that their experimental history was enhancing responding to the red key. Before initiating the next phase of the experiment, all pigeons were exposed to a color counter-biasing condition to attenuate potential effects of prior experience.

Color counter-biasing sessions consisted of a multiple schedule with 2 components, a concurrent independent variable-interval 20 s variable-interval 20 s (VI 20 s VI 20 s) component on the red and white

keys, alternated with a fixed 20-s extinction component on the green key. The VI durations were constructed by randomly sampling without replacement from 2 12-item Fleshler-Hoffman lists, one for each VI. The locations of red and white colors were randomized; the remaining location was assigned to the green color in the subsequent trial. In this way, the locations of the red and white keys were never the same as the location of the green key in the subsequent trial. When responding stabilized, the proportion of VI pecks on the red key was calculated for the last 5 sessions. The 4 birds with the highest proportion had the red color assigned as CTRL and white assigned to CS2. The reverse assignment was applied to the other 4 birds.

Serial conditioning, 20-s ITI. Figure 1 depicts the stimulus arrangement in this phase. The arrangement was similar to the initial serial conditioning phase, except that a variable 20-s ITI was introduced, after which 2 of the 3 response keys—the CS2 and the CTRL—were randomly selected and illuminated—one red, one white—for a variable 20 s interval, with a minimum 5 s duration. The duration of the ITI and of the CS2 and CTRL were sampled from 2 separate 12-item Fleshler-Hoffman lists. The offset of both keys was followed by the CS1, which was followed by the US. Note that the cycle duration (40 s, excluding the US) was the same as in the previous serial conditioning phase. Forty-nine sessions were conducted.

CS1 Removed. In previous conditions, CS2 and CTRL were designed to be imprecise temporal predictors of the upcoming CS1 and US. However, the onset of CS2 and CTRL signaled, on the average, the middle of the cycle; the possibility remained that responding to CS2 could be maintained by the small degree of temporal prediction it provided. That is to say, responses to CS2 could be an artifact of the birds anticipating *when* the US would be presented, instead of *where* the CS1 would be presented. To test this possibility, we held all conditions constant from the previous phase, except that the 5-s presentation of CS1 was replaced by the color representing CS2. Thus the CS2 was illuminated for a variable 20-s interval *plus* the adjacent fixed 5-s interval that was previously taken up by the CS1 (Figure 1). If responding to CS2 was due to its temporal proximity to the US, this should be reflected in an increase in responding to a CS2 that was now also temporally contiguous to the US. A decline in responding in this phase during the original CS2 period would indicate that responding was not due to temporal proximity to the US, supporting the hypothesis that it was due to the spatial relation between CS2 and CS1. Sixty-five sessions were conducted.

Data analysis

Each cycle where at least one keypeck was made on a stimulus constituted a response to that stimulus; subsequent keypecks on the same stimulus within the same cycle were not considered for analysis. For

the *CS1 Removed* phase, a response to CS2 was counted only if it occurred during the period in which CS2 was presented in previous phases, between CS2 onset and 5 s before US.

At the end of each serial-conditioning phase, responding was pooled over the last 5 sessions, for each subject. Acquisition of second-order responding in a conditioning phase was defined, for each subject, as emitting more than 20 responses to either CS2 or CTRL over the last 5 sessions (i.e., 5% of cycles) of that phase. A binomial test was conducted for each bird that met the second-order responding criterion. In this test, responses to CS2 and responses to CTRL counted as observations (cycles with both a CS2 and a CTRL response counted twice); responses to CS2 counted as successes. The test indicated the probability of the observed number of successes given the null hypothesis that successes and failures were equally probable. CS2 proportions that were less probable than a significance threshold of $\alpha = .001$ indicated that CS2 was reliably tracked more than CTRL. The proportion of responding to CS2 over CTRL was calculated for each conditioning phase as the ratio of successes to observations, pooled over the last 5 sessions of the phase. Average proportions of CS2 responses were based on data pooled over multiple birds.

Results

Autoshaping to CS1 was demonstrated in all birds by the first training session. By the sixth and final training session, 7 of 8 pigeons pecked the CS1 at least once in 90% of trials. P64, the pigeon that pecked the CS1 the least, did so in 70% of cycles.

In the *No ITI* phase, responding to the CS1 was maintained in at least 90% of trials for 5 of 8 birds. Among the other 3, P64, the lowest responder during autoshaping, pecked the CS1 in 27% of cycles, whereas P62 and P69 pecked the CS1 in 36% and 48% of cycles, respectively. Only 2 birds (P68 and P69) acquired second-order responding; both of them demonstrated differential responding on CS2 over CTRL [pooled CS2 proportion = .97; $p < .001$ for these 2 pigeons]. No subjects were found to respond differentially on CTRL over CS2.

The color counter-biasing procedure generated high rates of responding on the red and white keys, and eliminated responding to the green key (the CS1 color). Calculating the proportion of responses as described in the data analysis section, the mean proportion of responses on the color that would represent CS2 in subsequent phases was .48; the proportion of cycles with a response on the green key (CS1) was .04.

When the 20-s ITI was introduced and the CS2 duration was shortened to 20 s, 7 of 8 birds satisfied the criterion for acquisition of the second-order response. Six of these 7 birds responded differentially to CS2 over CTRL [pooled CS2 proportion = .78; $p < .001$ for all 6 pigeons].

The bird that did not respond differentially to CS2, P66, still responded more to CS2 than to CTRL [CS2 proportion = .64; $p = .03$]. The left half of each panel in Figure 2 depicts responding during the 20-s ITI phase.

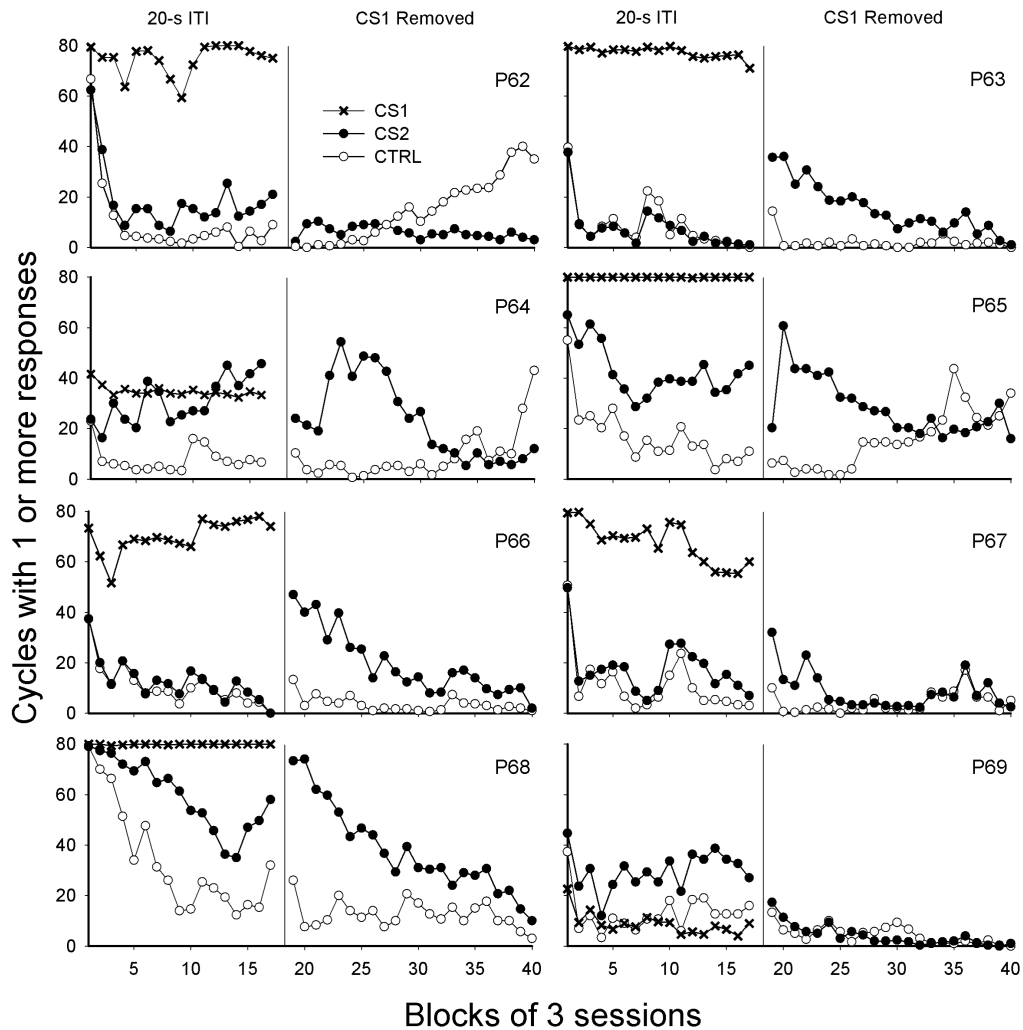


Figure 2. Cycles with at least one peck to CS1 (X symbols), CS2 (closed circles), and CTRL (open circles) across the 20-s ITI and CS1 Removed phases (left and right half of each panel, respectively) of Experiment 1. Cycles were averaged over sessions in blocks of 3;

each session had 80 cycles. In the *20-s ITI* phase, all birds except P64 and P69 pecked steadily on CS1; all birds except P63 pecked on at least 5% of the cycles on CS2 or CTRL, but mostly on CS2, in the last 5 sessions of this phase. The removal of CS1 generally reduced CS2 pecking; it reduced and even reversed the differential pecking on CS2 relative to CTRL.

Removal of the CS1, such that CS2 remained illuminated until the hopper was activated, led to a decline in responding to CS2 for all 6 pigeons that responded differentially to CS2 in the previous phase (Figure 2, right half of each panel). Of those 6 birds, 4 still maintained second-order responding, but their pooled proportion of responses to CS2 relative to CTRL was only .36. The apparent reversal in CS2 vs. CTRL responding appears to be driven mainly by P62, P64, and, to a lesser extent, P65.

Discussion

In Experiment 1, a stimulus (CS1) that was paired with food (US) elicited tracking behavior. A stimulus of variable duration (CS2) that was informative of the location of CS1 was more effective in eliciting tracking responses than a similar but spatially uninformative stimulus (CTRL). This effect was observed even when CS2 and CTRL took over the whole interval between US and subsequent CS1 presentations, but only in 2 of 8 birds. When CS2 and CTRL durations were halved, the effect was

noticeable in 6 birds. The enhancement of the effect suggests that temporal proximity of CS2 to the CS1 and US facilitated conditioning of CS2. When CS1 was replaced by a prolonged CS2, however, responding during the original CS2 interval declined in absolute terms and relative to CTRL. The latter result suggests that it was the temporal proximity of CS2 to CS1 that was critical for the enhancement of CS2 conditioning. But the duration of CS2 relative to ITI was probably too short to maintain responding by itself (see Gibbon, 1977), and the temporal proximity of CS2 to CS1 was the same as that of CTRL to CS1. Thus, it appears that the temporal proximity of CS2 to CS1 potentiated CS2 conditioning that was driven by the spatial relation between CS2 and CS1.

EXPERIMENT 2

The instrumental training provided by the color counter-biasing procedure in Experiment 1 might have facilitated the maintenance of CS2 responding in the subsequent ITI 20-s condition. In Experiment 2 we sought to replicate the effects observed in that training phase without resorting to preliminary instrumental training. We also sought to demonstrate a reversal of discriminative control by interchanging the colors representing CS2 and CTRL. If the pigeons reversed preference when the colors were switched, it would show that the effect is preserved independent of any potential color preferences. We also examined the effect of manipulating the duration of ITI and CS2 on spatial conditioning

while holding the cycle length constant. Decreasing the CS2 duration and lengthening the ITI should facilitate responding to CS2 in pigeons that otherwise would not demonstrate second-order responding, as shown in Experiment 1. We anticipated that even these pigeons would demonstrate differential responding to CS2 relative to CTRL when the CS2/ITI ratio was short enough.

Method

Subjects

Eight experienced pigeons, different from those in Experiment 1, served as subjects. Housing and feeding conditions were as in Experiment

Apparatus

The apparatus described in Experiment 1 was used.

Procedure

Autoshaping. Pecking to the CS1 was autoshaped using the procedure previously described in Experiment 1. Birds were ranked by probability of responding in any given cycle; ranking was counterbalanced across CS2-color (red or white) assignments.

Serial conditioning, 20-s ITI. This was a replication of the corresponding phase in Experiment 1; procedural details can be found therein. Unlike in Experiment 1, however, this phase was not preceded by a color counter-biasing procedure. Thirty-four sessions were conducted.

Serial conditioning, 30-s ITI. Experimental conditions were similar to those in the preceding phase, but cycles began with a variable 30-s ITI,

and CS2 duration was shortened to a variable 10 s, with a minimum 5-s duration. CS2 color assignment and the rate of CS1 and US presentation remained unchanged. As in the preceding phase, the cycle (excluding US) was 40 s long. Forty sessions were conducted.

Reversal of CS2. Experimental conditions were similar to those in the previous phase, but color assignments of red and white to the CS2 and CTRL were reversed. Sixty-one sessions were conducted.

Data Analysis

Data were analyzed as described in Experiment 1.

Results

Autoshaping to CS1 was demonstrated in all birds by the first training session. By the end of the autoshaping phase, all pigeons made at least one peck to the CS1 on 90% of trials.

Responding during serial conditioning is depicted in Figure 3. With a 20-s ITI (left panels), 4 of 8 pigeons met the criterion for acquisition of second-order responding and their data were further analyzed. Although P22 met this criterion and responded slightly more to CS2 than CTRL by the end this phase, it was excluded from analysis because of the strong negative trend in CS1 responding. The other 3 excluded birds (P18, P40, and P45) responded almost exclusively to CS1. Every bird that acquired

second-order responding differentially allocated most of those responses to CS2 [pooled CS2 proportion = .97; $p < .001$ for all 4 pigeons].

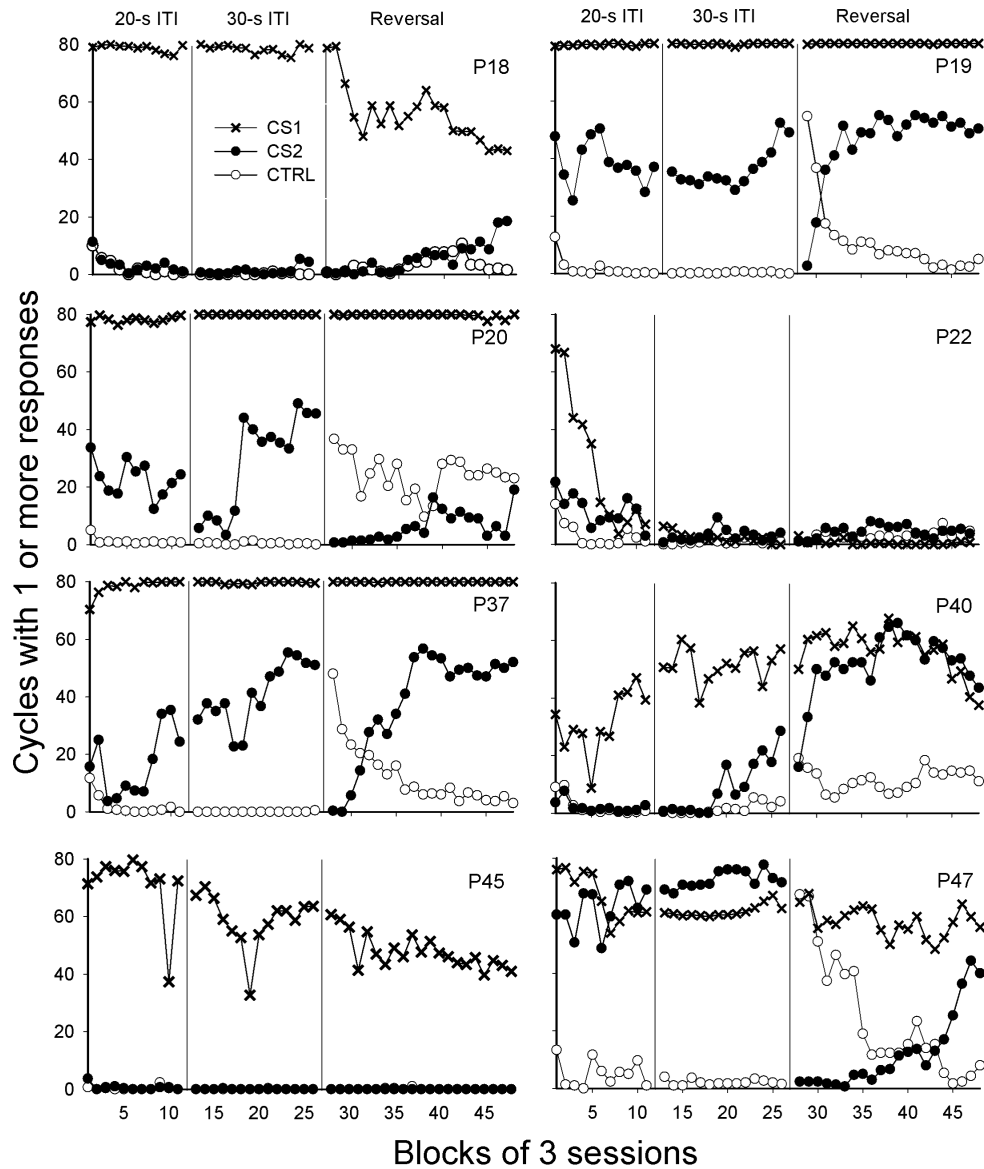


Figure 3. Cycles with at least one peck to CS1, CS2, and CTRL across the 20-s ITI, 30-s ITI, and CS2 Reversal phases (left, center, and right third of each panel, respectively) of Experiment 2. Cycles were

averaged over sessions in blocks of 3; each session had 80 cycles. In the 20-s *ITI* phase, all birds except P22 and P40 pecked steadily on CS1; 4 birds (P19, P20, P37 and P47) pecked on at least 5% of the cycles on CS2 or CTRL, but mostly on CS2, at the end of this phase. The lengthening of ITI and compensating shortening of CS2 increased the differential pecking to CS2 of 3 birds (P20, P37, and P40). Four of the 5 birds that demonstrated conditioning to CS2 in the 30-s *ITI* phase tracked the new CS2 when CS2 and CTRL assignments were reversed; P20 was the exception.

During the 30-s ITI phase (Figure 3, center panels), responding on CS2 increased for each of the 4 birds that acquired second-order responding in the previous phase (P19, P20, P37, and P47). For these birds, the average increase in the percentage of cycles with a CS2 response from the last 5 sessions of the 20-s ITI phase, to last 5 sessions of the 30-s ITI phase was 34%, with a range from 7% to 54%. The proportion of CS2 responses remained above .97 across both phases. P40, which was previously responding almost exclusively to CS1, came to peck CS2 around session 54 of the 30-s ITI phase. By the last 5 sessions of the 30-s ITI phase, P40 responded on CS2 on 28% of the cycles; the proportion of CS2 responses relative to CTRL was .98. P40 maintained responding on CS2 even after CS2 color changed in the following experimental phase.

When the colors representing CS2 and CTRL were reversed (Figure 3, right panels), responding reliably shifted toward the new CS2 for 4 of the 5 birds that pecked differentially to CS2 in the previous phase [$p < .001$ for all 4 pigeons]. The proportion of CS2 responses pooled across all 5 birds, including the subject that failed to show a reversal in preference (P20), was .76.

Discussion

Experiment 2 replicated the effects observed in Experiment 1. As expected, when the CS2 was shortened and the ITI was lengthened, responding to CS2 increased in absolute terms and relative to CTRL for all birds that demonstrated second-order conditioning with a longer CS2 and shorter ITI. Only 1 bird, however, acquired CS2 conditioning when the CS2 was shortened. These results confirm that temporal proximity between CS2 and CS1 facilitates CS2 conditioning, although the parameters used in the current experiment may not have been adequate for observing CS2 conditioning for every bird. Experiment 2 also demonstrated that responding to CS2 was not due to color assignment, and that differential responding was mostly reversed when spatial contingencies were reversed.

EXPERIMENT 3

In the previous experiments, it was demonstrated that pigeons may track a second-order stimulus (CS2) that is *spatially* correlated with a first-order stimulus (CS1), despite the CS2 bearing only a weak *temporal* correlation to the CS1 and US. The focus of our question was to determine the role of spatial correlation in Pavlovian conditioning. Our manipulation, however, was subject to the limitations of a standard 3-key, 3-color operant chamber. Such an arrangement severely restricts the spatial variability with which the stimuli may be presented, and offers only 3 possible choices (colors) for stimuli.

Using touchscreen technology, varying stimulus presentation location is limited only by the number of pixels on the screen, of which there are thousands. Similarly, the potential for stimulus variability is enhanced in the dimensions of color, shape, and size. While manipulations involving touchscreens may be less prevalent than those employing a standard “Skinner box,” the technology has been around for some time. Touchscreen chambers have been implemented to demonstrate spatial components in learning phenomena such as overshadowing (Leising et al., 2011) and sensory preconditioning (Garlick et al., 2005). In addition, there is evidence to suggest that the processes engaged in a two-dimensional touchscreen task are similar to those engaged in a three-dimensional open field task, (Spetch et al., 1996,

1997; Sawa et al., 2005; Blaisdell & Cook, 2005; Leising et al., 2011).

These findings add generality and “real-world” application to the touchscreen chamber, beyond that of a standard Skinner box.

The purpose of the present experiment was two-fold. First, we set out to replicate findings from the previous study in a novel medium, the touchscreen-equipped operant chamber. Our manipulation was similar to that of the original study, except that stimuli were presented in 1 of 40 possible locations on screen, a marked increase from the previous 3 locations. Second, we aimed at determining if responding to the CS2 was maintained simply by spatial contiguity between stimuli (CS2-CS1), or if it was enhanced by the spatial prediction of a variable CS1 location afforded by the CS2. It was hypothesized that when the CS1 location is held constant (and thus also the CS2 location is constant), pigeons respond less to the CS2 than when their locations are variable, because under constant-location conditions the CS2 is less informative of the location of the upcoming CS1.

Method

Subjects

Eight adult pigeons (*Columba livia*) were housed individually in a room with a 12:12-hr day:night cycle, with dawn at 0600 hr. They had previous experience with the operant chambers described in Experiment 1, but were naïve to a touchscreen-equipped chamber. They had free

access to water and grit in their home cages. The pigeons' running weights were based on 80% of their free-feeding weights. Each pigeon was weighed immediately prior to an experimental session and was excluded from a session if its weight exceeded 8% of its running weight. When required, a supplementary feeding of *ACE-HI* pigeon pellets (Star Milling Co.) was given at the end of each day, at least 12 hr before experimental sessions were conducted. Supplementary feeding amounts were equal 50% of the deviation in weight from the last day, plus 50% of the current deviation from target running weight, plus a proportion of feeding amounts over the previous three days.

Apparatus

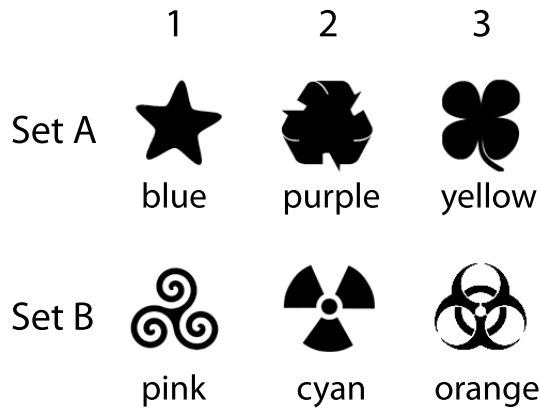
Experiments were conducted in an operant chamber (370 mm x 400 mm x 390 mm), furnished with a 304 x 228 mm Acoustic Pulse Recognition (APR) LCD screen (1024 x 768 resolution; Elo Touchsystems 1515L, Rochester, NY) mounted in the front wall of the chamber and a house light mounted in the back. A 550 mm x 650 mm aperture, centered just below the screen, allowed access to a food hopper when it was activated. All stimuli presented on the screen and the measurement of contacts with the screen were controlled with software written in Microsoft Visual Basic 6[®]. The house light and food hopper were controlled by the computer via optically isolated relay switches, and were powered by a 28-

volt power supply. The experimental chamber was mounted inside a sound-attenuating cubicle.

Procedure

Random-location autoshaping. The experiment proper was preceded by autoshaping of pecking on a 32 mm x 32 mm conditioned stimulus (CS1), presented on the touchscreen monitor. For each pigeon, the CS1 was selected from one of two 3-stimulus set (Figure 4, top), minimizing repeats across pigeons. CS1 assignment was fixed across random-location phases. For half of the pigeons the CS1 was selected from Set A and for the other half from Set B. Each daily experimental session started with the illumination of the house light, which remained continually illuminated during the session. Each session consisted of 40 cycles. Each cycle began with a variable inter-trial interval (ITI) of mean 40 s (each ITI was selected randomly without replacement from a 10-item Fleshler-Hoffman distribution; Fleshler and Hoffman, 1962), after which the CS1 was presented for 5 s. Stimulus locations for each daily session were determined at the session start by selecting randomly without replacement from a list of 40 locations. The coordinates of all 40 locations were arranged in a 8 x 5 rectangular grid such that stimuli were always at least 61 mm from the top of the screen, and at least 23 mm from the left, right, and bottom. Immediately following the offset of the CS1, the food hopper was activated for 3 s (the unconditioned stimulus, or US), which

Stimulus Assignment by Condition



Stimulus assignment	CS1	A-1	A-1	B-1	B-1	A-1	B-1
	CS2	---	A-2	---	B-2	A-3	B-3
	CTRL	---	A-3	---	B-3	A-2	B-2
		<i>Rnd-AS</i>	<i>Rnd-Serial</i>	<i>Fixed-AS</i>	<i>Fixed-serial</i>	<i>Rnd-reversal</i>	<i>Fixed-reversal</i>
		Condition					

Figure 4. (Top panel) Depiction of stimulus sets used in Experiment 3.

One set was used for “random-location” phases, and the other for “fixed-location” phases. Assignment of stimulus set to condition was counterbalanced across birds. (Bottom panel) Example of potential stimulus assignments for 1 subject. Each column represents a different experimental phase. Note that only one possible

combination is presented here, and assignments of CS1, CS2, and CTRL were counterbalanced across birds.

terminated the cycle. There were no programmed consequences for pecking the screen at any time, but pecks on the CS1 (the conditioned response, or CR) were recorded. After 15 sessions, all pigeons were pecking reliably to the CS1, and serial conditioning began.

Random-location serial conditioning. The arrangement was similar to autoshaping, except that the mean ITI duration was reduced from 40 to 20-s. Once the ITI elapsed, 2 different stimuli were presented simultaneously, each in a separate random location, for a variable 20-s interval and at least for 5 s. The simultaneous offset of both stimuli was followed by the onset of the CS1 for 5 s, followed by the US. Note that the total duration of the cycle, 48 s, remained unchanged from autoshaping.

One of the 2 simultaneous stimuli was presented *always* in the same location as the subsequent CS1, thus indicating its location and serving as a (spatial) CS2. The other stimulus always appeared at a location on the grid where the CS1 would *not* be presented during that trial, constituting an explicitly spatially unpaired control stimulus (CTRL). For each bird, the stimuli that served as CS2 and CTRL were selected from the same stimulus set used in autoshaping, but excluding the stimulus that already served as CS1. The assignment of the 3 stimuli to

the role of CS1, CS2, or CTRL was counterbalanced across the 8 birds. Thirty sessions were conducted.

Fixed-location autoshaping. For each bird, the stimulus set from which CS1, CS2, and CTRL were selected alternated between random- and fixed-location phases (see Figure 4). For instance, if Set A was used for random-location phases in one bird, Set B was used for fixed-location phases in the same bird.

Autoshaping during this condition was similar to the previous autoshaping phase, except that the location of CS1 remained constant throughout. Prior to the start of the condition, stimulus locations were chosen randomly for each bird, such that every bird received the CS1 in a different location, but the selected location remained constant across 15 conditioning sessions.

Fixed-location serial conditioning. This phase was similar to the random-location serial conditioning phase, except that the locations of CS2 and CS1 were held constant for the entirety of this phase. The location of the CS1 remained the same from the immediately prior autoshaping condition; CS2 was always presented in that location as well. In contrast, the location for CTRL varied from trial to trial and across sessions, just as in the random-location serial conditioning phase. Fifteen sessions were conducted.

Reversal of random-location CS2 and CTRL. Experimental conditions were similar to those in the random-location serial conditioning phase, including the set from which stimuli were selected. The only exception was that the stimulus assignments of CS2 and CTRL were reversed. Thirty sessions were conducted.

Reversal of fixed-location CS2 and CTRL. Experimental conditions were similar to those in the fixed-location serial conditioning phase. The only exception was that the stimulus assignments of CS2 and CTRL were reversed. Thirty sessions were conducted.

Data analysis.

Each cycle where at least one peck was made on a stimulus constituted a response to that stimulus; subsequent keypecks on the same stimulus within the same cycle were not considered for analysis. All dependent measures were based on the separate count of responses to CS1, CS2, and CTRL, for each subject, over the last 5 sessions of each serial-conditioning phase. Prior sessions were not analyzed. R_{CS2} and R_{CTRL} were computed by summing the responses on each stimulus, CS2 and CTRL, within the same location manipulation, *random* and *fixed*, across reversals. For instance, random-location R_{CS2} is the sum of

responses to CS2 during *Random-location serial conditioning* and during *Reversal of random-location CS2 and CTRL*.

The primary dependent measure, obtained from individual pigeons, was the log (base 2) odds of responses to CS2: $\log_2(R_{CS2} / R_{CTRL})$. This measure was obtained separately for the random- and fixed-location phases. It indicates how many more responses were made to CS2 than to CTRL; high log-odds are indicative of conditioning. Ninety-five percent confidence intervals (CI) around mean log-odds established the robustness of conditioning. Conditioning was assumed only for positive mean log-odds with CI not enveloping zero.

Log-odds that the *first* response in each trial occurred on CS2, $\log_2(First_{CS2} / First_{CTRL})$, were evaluated post-hoc. Individual session data (see Figure 5), revealed that it was common for a single cycle to consist of responses to both CS2 and CTRL. However, our operational definition of a response treats any cycle with responding to both CS2 and CTRL as equivalent responding to both stimuli, regardless of which stimulus elicited the first response, and independent of the total number of responses to either stimulus. Initial keypeck on any given trial should also be a reliable indicator of conditioning, and that a log odds ratio of the first response should return results consistent with our primary measure. Conditioning was established as above.

Bias toward one stimulus image, of the 2 that served as CS2 and CTRL, was measured as the log-odds of responses to the preferred image. Within each location manipulation, an image was preferred when the sum of responses to that stimulus, across reversals, was higher than the sum of responses to the other stimulus. For instance, if for a particular pigeon images A1 and A2 served as CS1 and CTRL in the random-location phases, and the sum of responses over both random-location serial-conditioning phases was 125 for A1 and 195 for A2, then A2 is said to be preferred over A1, and the random-location bias for this pigeon was $\log_2(195 / 125) = 0.64$. Note that bias is always positive. Differences in bias between random- and fixed-location phases were evaluated using a 2-tail paired-sample t-test.

Combined overall responding was computed for each pigeon and location manipulation, by summing all the responses made to CS2 and CTRL across serial-conditioning phases. Differences in overall responding between random- and fixed-location phases were evaluated using 2-tail paired-sample t-tests.

Results

Over the last 5 sessions of random-location autoshaping, all pigeons responded on CS1 during at least 91% of cycles. Individual subject data during each condition (CS1 autoshaping training excluded) is depicted in Figure 5. Figure 6 (left) shows the mean log-odds of

responses to CS2 in random- and fixed-location phases. The mean log-odds was significantly positive for the random-location phases, which means that CS2 was chosen substantially more often than would have been predicted by chance. This result supports the assumption of spatial conditioning of CS2 pecking when the CS1 location was variable. In contrast, the mean log-odds was not significantly different from zero in the fixed-location phases. This result does not support the assumption of conditioning when the CS1 location was constant. Taken together, these results suggest that the variability in the location of CS1 is necessary for spatial conditioning to take place.

The secondary measure of preference, log-odds that the first response in each trial occurred on CS2 $\log_2(\text{First}_{\text{CS2}}/\text{First}_{\text{CTRL}})$, was in agreement with our primary measure. The average $\log_2(\text{First}_{\text{CS2}}/\text{First}_{\text{CTRL}})$ was 0.97, 95% CI [0.26, 1.67] during the random location phases, and -0.05, 95% CI [-1.96, 1.86] during the fixed location phases. Similar to mean $\log_2(B_{\text{CS2}}/B_{\text{CTRL}})$, mean $\log_2(\text{First}_{\text{CS2}}/\text{First}_{\text{CTRL}})$ reached significance only during random location phases.

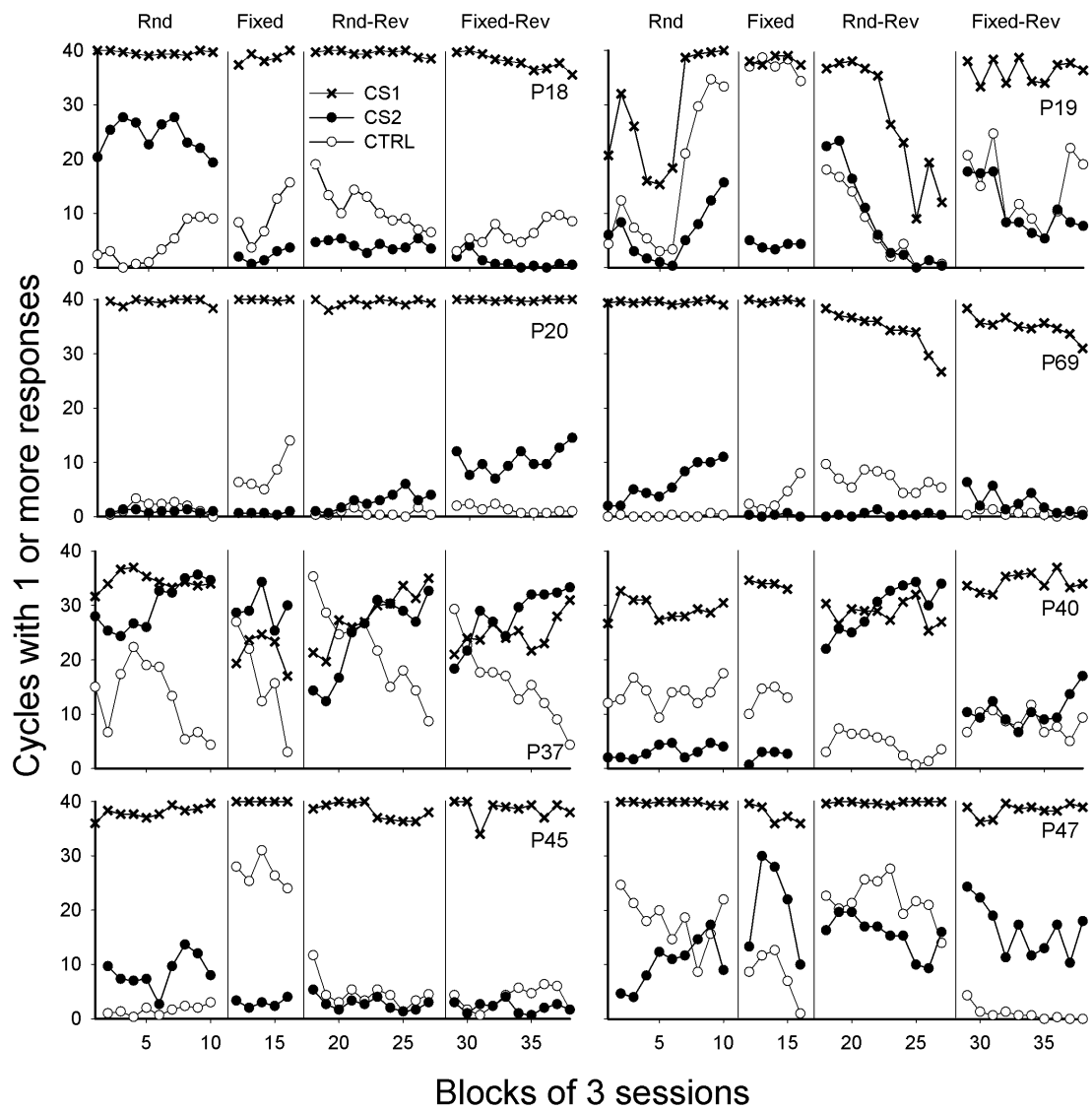


Figure 5. Cycles with at least one peck to CS1, CS2, and CTRL across the *Random-location*, *Fixed-location*, and reversal phases of Experiment 3. Cycles were averaged over sessions in blocks of 3; each session had 40 cycles.

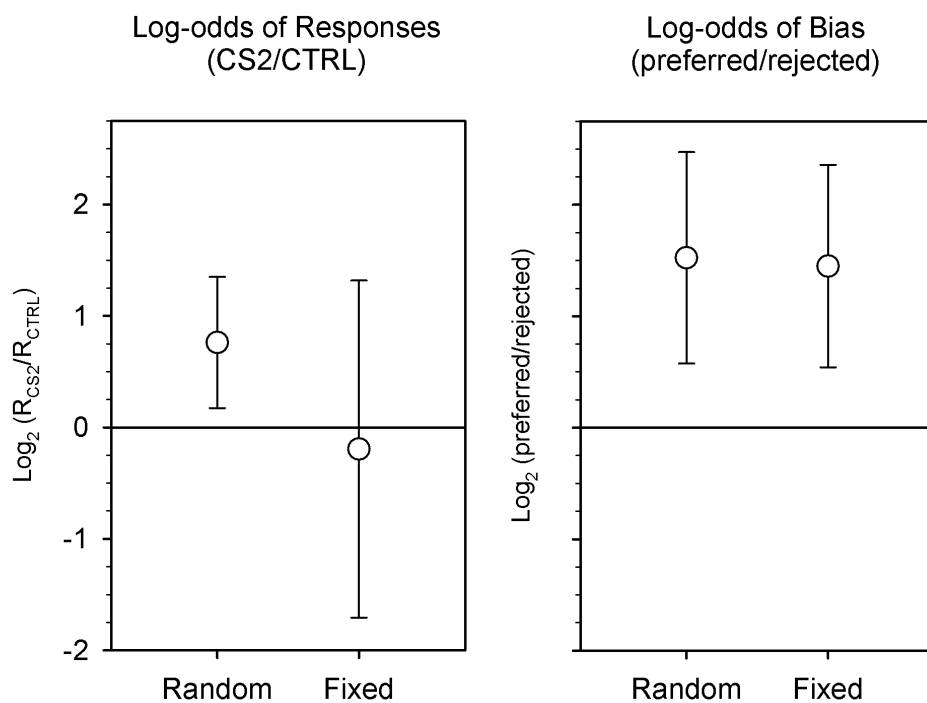


Figure 6. (Left) Log-odds of responding to CS2 over CTRL during the last 5 sessions of the random and fixed location phases. Positive log-odds indicate conditioning, and vertical bars represent 95% confidence intervals. (Right) Log-odds of responding to “preferred” stimulus over the non-preferred alternative, during the last 5 sessions of the random and fixed location phases. Vertical bars represent 95% confidence intervals.

Figure 6 (right) depicts measures of stimulus bias. Analyses of bias indicated that certain images elicited substantially more responding than others, independent of phase or condition type, as shown by the positive CI. On average, the preferred image engendered $2^{1.52} = 2.87$ (random-location) and $2^{1.45} = 2.73$ (fixed-location) more responses than the non-preferred image. There was no significant difference in bias across random- and fixed-location phases [$t(7) = .15, p = .88$].

Figure 7 shows the mean combined responses to CS and CTRL in random- and fixed-location phases. With 40 possible trials to respond on either stimulus, the maximum possible combined trials with a response was 80. On the average, pigeons responded to about 1 stimulus per trial in both random- and fixed-location phases. Combined responses did not differ significantly between random- and fixed-location phases [$t(15) = 0.36, p = .72$].

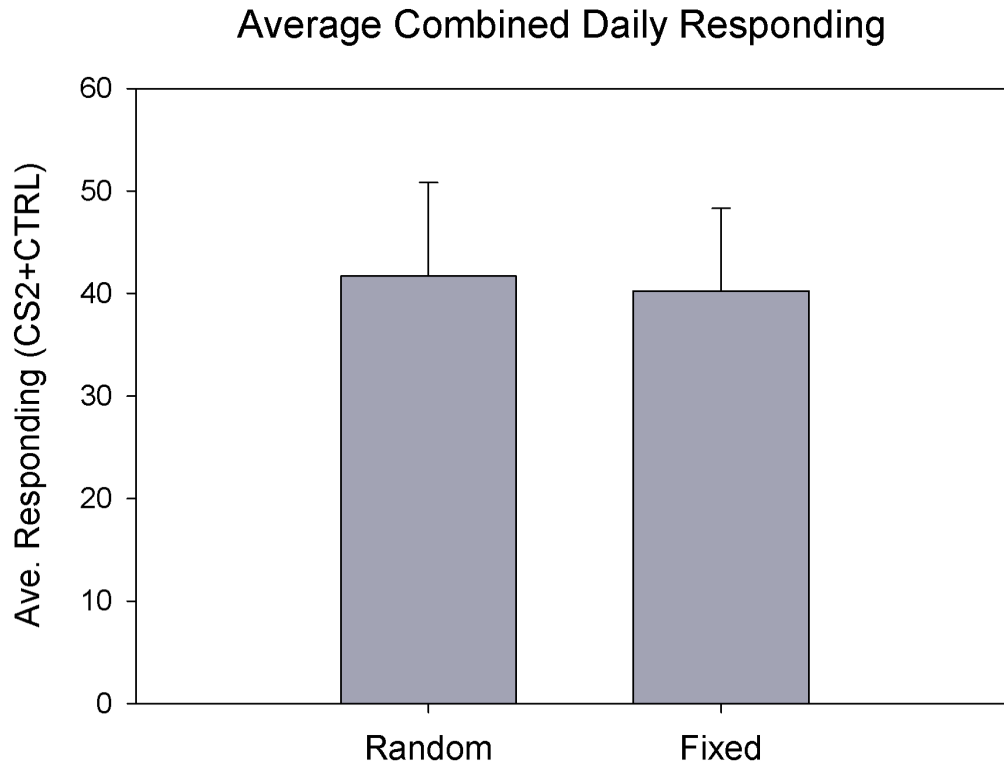


Figure 7. Average combined daily responding during the last 5 sessions of the random-location and fixed-location phases. High levels of responding and no significant difference in combined responding during either phase type demonstrates that obtained log-odds ratios were not influenced by a general lack of responding during either phase.

Discussion

Behavior during the random-location phases corroborates findings from the previous study. Pigeons pecking on a touchscreen monitor differentially tracked a second-order stimulus (CS2) that was *spatially* correlated with a first-order stimulus (CS1), despite the CS2 only bearing a *weak temporal* correlation to the CS1 and US. During the fixed-location

phases, when the presentation location of CS1 (and thus CS2) remained constant across trials and sessions (but CTRL location varied), pigeons did not track CS2 more than CTRL.

These findings suggest that conditioned pecking on CS2 depended on its capacity to disambiguate the location of CS1. When CS1 location was variable, CS2 was pecked significantly more often than CTRL. If pigeons were responsive to the predictability of CS1 location afforded by the spatial correlation between CS1 and CS2, then it is reasonable to expect more conditioned responding when the location of CS1 was variable. When CS1 location was constant across trials and sessions, CS2 provided information about the location of the forthcoming CS1 that was redundant with information provided by the location of previous CS1 presentations.

Several implications arise these results. As with the previous two experiments, findings from Wasserman et al. (1978) and Rescorla and Cunningham (1978) were replicated in that spatial contiguity facilitated second-order conditioning. However, results from the fixed-location experiments suggest that spatial contiguity alone was not sufficient to engender more responding to CS2 than CTRL. Conditioned responding to CS2 was dependent on a variable CS1 presentation location. Only when CS1 presentation locations were variable was conditioning to CS2 observed.

A comparison of responding to each cue while it served as either CS2 or CTRL was essential to determine conditioning independent of bias. The distinct and idiosyncratic biases toward particular stimuli led to high variability in the data among pigeons, compared to the previous study. Nonetheless, no significant differences in bias were observed between random- and fixed-location phases. It is important to note that during the fixed-location phases, the location of CTRL varied, while only CS2 and CS1 location was held constant. It is possible that the variability in the location of the stimulus may be sufficient to elicit pecking, and that the diminished log-odds ratios observed in the fixed-location phases were a product of increased pecking to CTRL elicited by the relative variability of its location, not decreased conditioned responding to CS2. Further research is needed to elucidate this matter. Specifically, an arrangement in which the location of CS2 and CTRL were fixed, thereby eliminating location variability for both stimuli, would aid in determining why responding to CTRL increased during fixed location phases.

Another potential issue confounding our interpretation of the results is that CS1 and CS2 locations in the fixed-location phase remained constant throughout all sessions for each bird, but varied among birds. Chosen at random for each bird from the original set of 40? presentation locations, the fixed stimulus location varied in distance from the hopper among birds. It has been shown that a CS is more effective the closer it is to the US (Cabrera et al., 2009). This variability in CS effectiveness may

have resulted in differences in responding to CS2 or CTRL, relative to their proximity to the hopper.

GENERAL DISCUSSION

Three experiments demonstrated that pigeons may track a second-order stimulus (CS2) that is *spatially* correlated with a first-order stimulus (CS1), despite the CS2 bearing only a weak *temporal* correlation to the CS1 and US. These results extend the findings of Wasserman et al. (1978) and Rescorla and Cunningham (1979) to conditions in which the timing of a spatially informative stimulus, CS2, is only weakly correlated to the timing of CS1 and US.

The *No ITI* phase of Experiment 1 demonstrated that CS2 could elicit differential tracking even when it takes the entire interval between CS1 presentations. This effect was observed only in a minority of birds, but the effect on these birds was unlikely to be observed by chance, and no bird responded more to the spatially uninformative CTRL key than to CS2. This is a sign that, although the CS2-CS1 spatial correlation might have been learned in the absence of a temporal correlation, at least a weak temporal correlation may be necessary to reliably observe the tracking response. Results from the *20-s* and *30-s ITI* phases in both experiments are consistent with this hypothesis. At least half of the birds acquired responding to CS2 or CTRL when the ITI was 20 s or longer, and those birds responded substantially more to CS2 than to CTRL.

A few arguments may be advanced against our interpretation of the data. It may be argued that in the *20-s ITI* condition, where the onset of the CS2 marked, on the average, the middle of the interval between CS1 presentations, such temporal information might have been enough to elicit conditioned responding to the CS2, and that the spatial information provided by CS2 played no role in conditioning. Such an argument, however, would not explain why responding was directed to CS2 and not to CTRL, both of which were equally informative of the time of onset of CS1 and US. Also, we know of no autoshaping study in which responding to a CS of equal duration of the ITI was maintained (see Gibbon, 1977). It may also be argued that, in a larger context of the whole-day cycle, the CS2 was temporally informative of the CS1 and US because all 3 happened only in the sub-context of the experiment. It is well known, however, that such coincidence is not sufficient to maintain tracking behavior, as any random control test would easily demonstrate (see Rescorla, 1967). Finally, it may be argued that the CS2 and CS1 functionally constituted a single compound stimulus that was temporally contiguous to the US, and thus what we interpret as spatial conditioning is simply responding that fell on the CS2 element of a larger, “temporally” conditioned stimulus. The *CS1 Removed* phase of Experiment 1 was intended to evaluate this hypothesis. According to the compound-stimulus hypothesis, if CS1 was eliminated and CS2 was extended until the onset of the US, responding to the CS2—during the period in which it was

originally shown—should not decline and may even increase. The evidence shown in Experiment 1 (Figure 2, right half of each panel) did not support this prediction.

We thus conclude that most pigeons learned the spatial association between CS2 and CS1, and that a minimum temporal correlation between these stimuli was mostly—but not always—necessary for the spatial association to be expressed as tracking behavior. Such minimum temporal correlation, by itself, does not support tracking behavior, but may be a determinant of the topography of the response that spatial conditioning elicits (Timberlake et al, 1982). It is possible that conditioned responses not recorded in the experiments reported here, such as approach to CS2 without pecking, are more effectively elicited by spatial contingencies. It is remarkable, nonetheless, that tracking elicited by spatial conditioning updates quickly to the reversal of spatial contingencies, as shown in the *Reversal* phase of Experiment 2.

After demonstrating that spatial conditioning is not simply subsidiary to “temporal” conditioning, Experiments 1 and 2 left one question open: are spatial contiguity and correlation both necessary for spatial conditioning? Rescorla (1968) demonstrated that a tone CS did not elicit conditioned suppression if its presence and absence had the same probability of being followed by a shock US, despite the temporal contiguity of CS to US when CS was present. Van Hest et al. (1986) found that pigeons in a long box (60 cm) would only track a distant CS when the

time between food presentations was unpredictable. When food was delivered on a fixed interval, pigeons would not approach the CS and engaged in goal-tracking (hopper approach) behavior. Effective CSs typically signal an increased probability of the US, i.e., they disambiguate the timing of the next US. In the present study, CS2 disambiguated the location of the next CS1. In Experiment 3, a “fixed-location” condition was conducted in which CS2 did not provide such disambiguation. If spatial disambiguation were critical for spatial conditioning, it would be expected that fixing the location of CS1 would preclude spatial conditioning, and responding to CS2 would decrease. This is precisely what we observed in Experiment 3.

The finding that spatial correlation can elicit second-order serial conditioning, even under conditions where CS2-US temporal correlation is minimal, was upheld across three experiments. While we recognize potential limitations to our interpretation of the data from the fixed-location touchscreen phases, we maintain the view that a second-order stimulus engenders more conditioned responding when that stimulus disambiguates the variable location of an upcoming first-order stimulus.

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