Spatial serial conditioning maintained with minimal temporal contingency

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A R T I C L E   I N F O

A B S T R A C T

Two 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 consecutive presentations of CS1, but only in a minority of pigeons; prevalence of differential pecking was enhanced when CS2 duration was halved. 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.

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1. Introduction

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 et al., 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 et al. (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. CS location cannot be correlated with a US location that is fixed, 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 et al. (1978, 1996) and Rescorla and Cunningham (1979) 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.

Fig. 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) stim-

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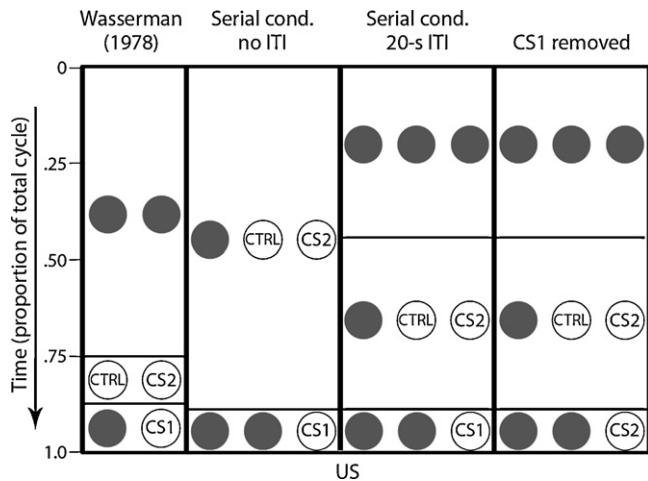E-mail address: Federico.Sanabria@asu.edu (F. Sanabria).

Fig. 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 permutated between cycles (locations shown here are illustrative). See text for further details.

ulus located where the CS1 would not be presented.[1] 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 (1/6th 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.

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 et al. (1978), 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 et al.'s (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 (Fig. 1, *Serial cond.*). That is, when the CS2 duration was half of the ITI (CS/ITI ratio = 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 (Gamzu and Williams, 1973), with its offset followed immediately by the US (Fig. 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.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Eight experienced adult pigeons (*Columba livia*) were housed individually in a room with a 12:12-h day:night cycle, with dawn at 06.00 h. 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 h 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.

2.1.2. 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

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[1] Wasserman et al. (1978) refer to these 2 stimuli as "compound CS2". Because only one element of the compound stimulus was in the location of the CS1, we refer to that element as the CS2. Because the other element served as non-associative control, we refer to it as the "control stimulus" or CTRL.