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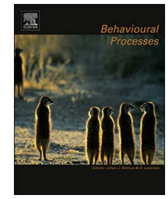

Temporal map formation in appetitive second-order conditioning in rats

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A B S T R A C T

Three experiments examined whether second-order conditioning resulted in the formation of a fully-featured temporal map, as proposed by the temporal coding hypothesis. Experiments 1 and 2 examined second-order conditioning with different first- and second-order relationships. Measures of the strength of second-order conditioning were mostly consistent with the temporal coding hypothesis; second-order conditioning was best with arrangements in which CS2 occurred prior to the time that the US normally occurred during CS1-US presentations. However, there was no evidence of anticipatory timing during CS2 during second-order conditioning. A third experiment directly examined whether a fully-featured temporal map was formed during second-order conditioning by examining the acquisition of anticipatory timing in subsequent reinforced second-order trials. The results of Experiment 3 suggested that the effects obtained in Experiments 1 and 2 were due to learning of the temporal order and coincidence of events that resulted in the formation of an ordinal temporal map, but that precise durations were not encoded.

1. Introduction

During a standard Pavlovian conditioning task, a neutral event (the conditioned stimulus, CS) is paired with an outcome (the unconditioned stimulus, US). After several such pairings, the CS comes to elicit anticipatory conditioned responses (CRs) indicating that the subject has learned to associate the two events. Second-order conditioning (SOC) involves presentations of a conditioned stimulus followed by an unconditioned stimulus such as food or shock in a standard conditioning arrangement. In the key second phase, the original CS (CS1) is now paired with a novel CS (CS2) in the absence of the US. Second-order conditioning is apparent if responding is observed to CS2, even though this stimulus was never directly presented with the US (Rescorla, 1980).

Second-order conditioning is a specific instance of a set of conditioning paradigms that are thought to necessitate integration of information across phases (see, for example, Ward-Robinson, 2004). In the case of SOC, the activation of a previously learned CS1 → US relationship during the CS2 → CS1 pairing phase may allow for determination of the CS2 → US relationship. While there is evidence that temporal integration may occur (e.g., Barnet et al., 1997; Cole et al., 1995), whether precise temporal information is transferred between phases in SOC is unknown. Answering this more challenging question requires comparison of different temporal arrangements of CS1 and CS2, an issue that has been largely overlooked in the literature. Rats do learn to time the duration of the CS, such that the distribution of the CR peaks at about US delivery (e.g., Kirkpatrick and Church, 2000), suggesting that specific temporal information is available for transfer. Any effect of order and/or timing of events may support the notion that temporal information was transferred, and critically the nature of these effects could indicate the degree of specificity of information that is integrated across phases. A common approach to the study of order and timing effects has been to alter the CS1-CS2 relationship during the second-order phase. Various manipulations with simultaneous CS1/CS2 (e.g., Stout et al., 2004; Rescorla, 1982), backward CS1 → CS2 (e.g., Mowrer et al., 1988; Williams and Hurlburt, 2000), and forward CS2 → CS1 (e.g., Kehoe et al., 1981; Stout et al., 2004; Rescorla, 1982; Kim et al., 1996; Williams and Hurlburt, 2000) presentations have shown at least some evidence for SOC, with successful conditioning most often observed with forward presentations.

The most systematic approach to this question has been that of Miller and colleagues (e.g., Cole et al., 1995; Barnet et al., 1997; Stout et al., 2004; Barnet et al., 1991), which led to the development of the temporal coding hypothesis (Savastano and Miller, 1998; Arcediano and Miller, 2002). The temporal coding hypothesis proposes that second-order conditioning is promoted by the formation of a temporal map that encodes the CS1 → US interval and CS2 → CS1 interval. Through the process of temporal integration in memory, the CS2 → US interval is determined. If the CS2 → US interval is an arrangement that would normally result in the expression of CRs in first-order conditioning, then CRs will be observed in SOC. For example, Cole et al.

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(1995) initially trained rats with a delay conditioning (5-s CS1 → shock US) or trace conditioning (5-s CS1 → 5-s trace → shock US) arrangement. SOC involved CS1 → CS2 presentations in the absence of shock. Critically, the trace conditioning group displayed better SOC even though this group exhibited poorer first-order conditioning. Cole et al. (1995) argued that the trace group would have formed a CS1-CS2-US map in which CS2 was in a forward relationship with the US. On the other hand, the delay group would have formed a CS1-US-CS2 map in which CS2 was in a backward arrangement with the US, which would not result in very robust conditioning. One key factor in this experiment is that there was a built-in control for generalization (although there may have been differences in contextual conditioning): the trace group should have exhibited weaker generalization because of their weaker first-order conditioning, so generalization alone cannot account for the pattern of results.

An important feature of the temporal coding hypothesis is the notion that SOC is promoted by temporal integration. However, it is not clear whether temporal integration necessitates precise timing information. Kirkpatrick and Balsam (2016) described two alternative conceptual frameworks within which temporal maps may reside. One possibility is that temporal maps rely on detection of coincidence and order of events, but that the timing of events would rely on a separate delay processing module. Alternatively, temporal maps may contain fully-integrated, feature-rich encoding of coincidence, order, and timing information. The present series of experiments sought to determine whether second-order conditioning involves the generation of a fully-featured temporal map. Such a map should reveal itself not only in the effectiveness of SOC as a function of the order in which the stimuli are presented, but also in the temporal gradients (timing) of responding during CS2. If rich temporal information is acquired in SOC, one would expect to see a temporal gradient during CS2 that peaks near the expected time of US delivery. To investigate whether a fully featured temporal map is indeed acquired, we delivered SOC under different arrangements and examined both the strength (conditioning) and timing (distribution) of CRs.

2. Experiment 1

Experiment 1 examined SOC in an appetitive conditioning paradigm with rats. All the rats received first-order conditioning (FOC) with a 10-s CS1 followed by food. SOC involved nonreinforced presentations of a 10-s CS2 together with the 10-s CS1. Four different arrangements were employed: forward CS2→CS1, backward CS1→CS2, simultaneous CS1 + CS2, and unpaired CS1 ~ CS2. These temporal arrangements were chosen because they have been commonly employed arrangements in prior investigations because they provide controls for non-associative effects such as habituation, but only rarely have they been directly compared.

Based on the temporal coding hypothesis, we predict that only the forward and simultaneous arrangements should result in SOC, because these arrangements result in predictive information (e.g., CS → US) that is effective for FOC (e.g., Barnet et al., 1997). The unpaired group provides a control for generalization against which to assess the other three groups. Experiment 1 also examined timing during CS2-only peak trials to determine whether the rats express learning of the CS2 onset-***US***[1] interval. This interval is 20 s in the forward arrangement and 10 s in the simultaneous arrangement. Thus, one would expect to observe peaks in responding during CS2 around these times.

[1] Here and throughout a stimulus that appears in bold-italics denotes an expected event that does not occur. In the context of the temporal coding hypothesis, the ***US*** expectation develops through the process of temporal integration.

2.1. Method

2.1.1. Animals

The subjects were 24 experimentally-naïve male Sprague-Dawley rats (Harlan UK). On arrival, the rats weighed 120–140 g; they were housed in pairs based on initial weight. The rats were given ad libitum food access for one week, after which they each received 15 g of food per day. Water was freely available in the home cages and experimental chambers. All rats received handling each day beginning three days after arrival to the colony room.

2.1.2. Apparatus

The experimental procedures were conducted in twelve identical chambers (25 × 30 × 30 cm), each of which was situated within a ventilated, noise-attenuating box (74 × 38 × 60 cm). The chambers were in two rooms with six chambers per room. Each chamber was equipped with a speaker for delivering auditory stimuli, a houselight, a food cup, and a water bottle. The speaker was located on the right side of the back wall of the chamber, on the opposite wall from the food cup. The houselight was situated on the top-center of the wall above the food cup. A magazine pellet dispenser (Model ENV-203) delivered 45-mg Noyes (Improved Formula A) pellets into the food cup. Each head entry into the food cup was transduced by an LED-photocell. The water bottle was mounted outside the chamber; water was available through a tube that protruded through a hole in the lower-center of the back wall of the chamber. Med-PC for Windows (Tatham and Zurn, 1989), running on two Pentium III 800-mHz computers (one for each set of six chambers), controlled experimental events, and recorded the time at which events occurred with 2-ms resolution.

2.1.3. Procedure

Each animal was randomly assigned to one of four groups ($n = 6$) – Simultaneous, Backward, Forward, or Unpaired. The timing and order of CS and US presentations during first- and second-order conditioning is displayed in Fig. 1. The arrows below each procedural diagram indicate the intervals that could be learned directly in FOC (solid lines) and indirectly through temporal integration in SOC (dashed lines).

2.1.3.1. First-order conditioning (Sessions 1–8). All rats received 8 sessions of first-order conditioning (FOC) that comprised 32 trials with a fixed duration 10-s houselight stimulus, immediately followed by the delivery of a 45-mg Noyes pellet (see Fig. 1). The time from stimulus termination (or food delivery) to the next stimulus onset, the intertrial interval (ITI), was an exponentially distributed random interval with a mean of 200 s and a minimum of 100 s.

2.1.3.2. Second-order conditioning (Sessions 9–18). The procedure for SOC was adapted from Hatfield et al. (1996). SOC followed the last session of FOC and consisted of 10 sessions of 16 trials, each with the same ITI as in FOC. A 10-s, 70-db white noise that served as CS2 was introduced during this phase (see Fig. 1). In Group Simultaneous, the light and noise were presented simultaneously. In Group Backward, the onset of the noise stimulus followed immediately after the houselight switched off (CS1 → CS2). In Group Forward, the opposite stimulus arrangement was presented. Group Unpaired received unpaired presentations of the noise and light stimuli; the two stimuli were separated by an exponentially-distributed random interval with a mean of 100 s and a minimum of 50 s, with a pseudo-random determination of which stimulus would occur during the specified time, with the constraint that the total number of CS1 and CS2 occurrences had to be equal. Testing of SOC was achieved by recording both the magnitude and pattern of responding during 30-s peak trials, which consisted of non-reinforced noise only presentations.

The first three sessions of SOC (9–11) began with two reinforced FOC trials to maintain responding. During the remainder of the session, there were three different trial types that were randomly intermixed: