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Timing: An attribute of associative learning

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ABSTRACT

The evidence reviewed in this paper suggests that when two events occur in spatiotemporal proximity to one another, an association between the two events is formed which encodes the timing of the events in relation to one another (including duration, order, and interval). The primary evidence supporting the view that temporal relationships are encoded is that subsequent presentation of one event ordinarily elicits behavior indicative of an expectation of the other event at a specific time. Thus, temporal relationships appear to be one of several attributes encoded at acquisition.

Contents

1. Introduction

The simplest form of associative learning is Pavlovian (i.e., classical) conditioning. In Pavlovian conditioning, an association is formed between an initially neutral stimulus and an unconditioned stimulus (US) such that subsequent presentation of the now-conditioned stimulus (CS) presumably activates an anticipatory representation of the US. Anticipation of the US causes the animal to emit a conditioned response (CR) appropriate for the specific US.

Pavlov (1927) and many subsequent researchers have identified numerous behavioral phenomena that arise within Pavlovian conditioning. Here we cannot convey the richness of the empirical corpus, but we will review briefly some of those key phenomena such as acquisition, cue competition (e.g., overshadowing), conditioned inhibition, and associative interference (e.g., retroactive interference) in which temporal relationships appear to be critical. The first goal of this review is to highlight the fact that temporal relationships are encoded as a part of any association by showing that they strongly influence these key Pavlovian behavioral phenomena. The behavioral phenomena to be described will be analyzed within the framework of the temporal coding hypothesis (TCH, e.g., Savastano and Miller, 1998), which is a set of hypotheses concerning how temporal information is used within any associative model. The tenets of the TCH can be summarized as follows:

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(a) close contiguity between events is both necessary and sufficient for the formation of an association; (b) the temporal relationship between the associated events is encoded as part of the association (also see Honig, 1981); (c) this temporal information plays a critical role in determining the topology, magnitude, and timing of the response elicited when one of the associates is subsequently presented; and (d) subjects can superimpose temporal relationships when they share a common element, even when the relationships were independently acquired, thereby allowing for the expression of temporal relationships between cues that were never actually paired together (i.e., temporal integration). The second goal of this review is to present recent refinements of the TCH concerning (a) the time at which temporal integration occurs, (b) the associative structure of temporal integration, and (c) the directional nature of the temporal coding.

2. Acquisition with different temporal arrangements

Pavlov (1927) was the first to investigate the effects of the CS–US interval on CR. He used four different temporal arrangements between the CS and the US. In forward delay conditioning, the CS is presented before the US and stays on until the US is presented. In forward trace conditioning, the CS is presented, and then the US occurs at some time after the termination of the CS. In simultaneous conditioning, the CS and US are presented at the same time. In backward [trace] conditioning, the US occurs such that it terminates prior to the onset of the CS. Pavlov found that simultaneous and backward conditioning do not produce appreciable CRs; that with trace conditioning, longer intervals between the CS and US produce weaker CRs; and that in forward delay conditioning the CR grows weaker as the interval from CS onset to US onset is increased. These results have been repeatedly confirmed in subsequent experiments (e.g., Cooper, 1990; Mackintosh, 1983; Matzel et al., 1988; Rescorla, 1988).

The contiguity principle, to which Pavlov (1927) subscribed, assumes that good contiguity is merely a catalyst for forming associations, and differences in responding to CSs trained with different temporal arrangements are the result of differences in the strength of the resultant associations. The closer the two stimuli are in time, the greater the strength of the association will be, and consequently the more robust the CR to that CS. It is noteworthy that this principle seems well suited for most temporal arrangements in simple excitatory Pavlovian conditioning. However, it is challenged by the weak conditioned responding observed following simultaneous conditioning, which according to the contiguity principle should yield maximal responding because simultaneity is synonymous with perfect contiguity (i.e., the CS and US could not be closer in time). Similarly, according to the contiguity principle, backward trace and forward trace conditioning with identical intervals between the CS and US should produce equally strong associations and hence result in equally strong conditioned responding. However, forward conditioning consistently results in more robust responding than backward conditioning. Thus, the contiguity principle provides an incomplete account regarding the role of contiguity in conditioning.

The TCH better accounts for the behavior observed with simultaneous and backward conditioning. According to the TCH, an association is formed between the CS and the US with each of the four different temporal arrangements, and the specific temporal relationship is encoded as part of the resultant association. In both simultaneous and backward conditioning, the specific temporal relationships between the CS and US do not give the CS any predictive value; hence, the CS fails to elicit anticipatory responding in either case. Miller et al. demonstrated the validity of this view by showing that rats can encode interval relationships in simultaneous conditioning (e.g., Barnet et al., 1991) and backward conditioning (e.g., Arcediano et al., 2003; Molet et al., 2012) as well as trace conditioning with relatively long interstimulus intervals (e.g., Cole et al., 1995). These researchers used sensory preconditioning (i.e., S2–S1 trials followed by S1–US trials, resulting in conditioned responding to S2) and second-order conditioning (i.e., S1–US trials followed by S2–S1 trials, resulting in responding to S2) procedures modified to reveal these three elusive varieties of conditioning (see Fig. 1). Basically, the TCH posits that the so called simultaneous and backward conditioning deficits are not deficits in forming associations; the associations are formed but do not support anticipatory responding, which is what is assessed in most laboratory conditioning preparations. Alternatively stated, the so called simultaneous and backward conditioning deficits are not associative deficits, but performance deficits. Presented below are a few experiments supporting these conclusions.

For the sake of clarity, we will describe only the critical experimental group for each demonstration, all of which used different versions of second-order conditioning to reveal learning that would often have been latent if we had assessed only responding to the first-order CS (i.e., S1; see the left side of Fig. 1). Cole et al. (1995; see Fig. 1A) gave first-order S1–US pairings with a 5-s gap (i.e., trace interval), followed in Phase 2 by S1–S2 pairings in a backward fashion (i.e., S1 just before S2). Counterintuitively, they observed a stronger CR to the second-order stimulus (S2) than the first-order stimulus (S1). Barnet et al. (1991; see Fig. 1B) exposed rats to simultaneous presentations of S1–US (5-s duration); in Phase 2 they were exposed to 5-s presentations of S2, each of which terminated with the onset of a 5-s presentation of S1. At test, strong responding to S2 was observed. Molet et al. (2012; see Fig. 1C), adapting the procedure of Arcediano et al. (2003) to rats, administered S1-footshock US pairings in a backward relationship (i.e., US–S1) with a 4-s gap (i.e., trace interval) between termination of the US and onset of S1 in Phase 1, followed by S2–S1 pairings in a forward relationship with a 5-s gap between termination of S2 and onset of S1 in Phase 2. When tested on S2, rats exhibited a robust CR. The right side of Fig. 1 depicts the hypothetical integrated temporal maps following each experimental situation.

According to the TCH, the rats had encoded the temporal relationships between S1 and the US and between S1 and S2, thereby forming two independent temporal maps, which included the order and interval between the paired events. These temporal maps presumably were integrated by superimposing the representation of the common element from the two phases of training (i.e., S1), thereby allowing S2 to predict an impending US when rats were tested, a relationship that is conducive to conditioned responding to S2.

Taken together, these findings support the view that the temporal relationships among events during training are encoded as attributes of the association. Additionally, this series of experiments showed that when subjects independently acquire two associations with a common element (e.g., S1–US and S2–S1), each with its own temporal relationship, they behave as if the two unique cues have a known temporal relationship despite their never having been paired. Seemingly, they have integrated the two associations to create a third association with its own temporal relationship (S2–US). This tenet is what makes the TCH unique in comparison to real-time models (e.g., Church and Broadbent, 1990; Machado, 1997; Staddon and Higa, 1999; Sutton and Barto, 1990; Vogel et al., 2003; Wagner, 1981). This is particularly evident in the case of temporal integration involving a backward association (e.g., Arcediano et al., 2003; Molet et al., 2012). Indeed, it is hypothesized that subjects encoded the specific intervals from the US to S1 and from S2 to S1, and that they were able to retrieve the backward temporal location of the US with respect to S1 when S2 was presented at test. This challenges the view adopted by most