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It's the information!

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ABSTRACT

Learning in conditioning protocols has long been thought to depend on temporal contiguity between the conditioned stimulus and the unconditioned stimulus. This conceptualization has led to a preponderance of associative models of conditioning. We suggest that trial-based associative models that posit contiguity as the primary principle underlying learning are flawed, and provide a brief review of an alternative, information theoretic approach to conditioning. The information that a CS conveys about the timing of the next US can be derived from the temporal parameters of a conditioning protocol. According to this view, a CS will support conditioned responding if, and only if, it reduces uncertainty about the timing of the next US.

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It is widely accepted that animals learn and encode the duration of events in conditioning protocols. Even though timing of events in conditioning protocols has long been demonstrated to have a profound impact on conditioned responding in a variety of paradigms (Blaisdell et al., 1998; Gallistel and Gibbon, 2000; Gibbon and Balsam, 1981; Miller and Barnet, 1993; Savastano and Miller, 1998; see Balsam et al. (2010) for review), the importance of learning and encoding of temporal durations in theoretical treatments of conditioning has most often (with few exceptions) been relegated to the background in favor of conceptual and theoretical accounts which subscribe to the notion that contiguity between a CS and a US is the primary determinant of learning. According to this theoretical position, close temporal contiguity is the basis for the formation of associations between stimuli in a conditioning protocol.

Although the position that contiguity is the basic principle of learning has a long and storied history, empirical data have accumulated that are problematic for this view. A number of experiments demonstrated that repeated temporal contiguity between a candidate conditioned stimulus (CS) and a motivationally important event (US) was insufficient to establish conditioned responding. For example, Kamin (1967, 1969) showed that when rats were first conditioned with one CS, followed by conditioning to a second CS presented in compound with the first CS, conditioning to the new CS did not develop, notwithstanding its close temporal contiguity with the US. In one of the most striking of these experiments, Rescorla (1968) exposed different groups of rats to conditioning protocols which did not differ in the temporal pairing of CS and US, but differed in whether the US presentation was contingent on presentation of the CS. When the contingency between CS and US was made 0 by presenting US's during the intertrial interval (ITI) at the same rate they were presented during the CS, the rats did not develop a conditioned response to the CS. These experiments and the empirical demonstration of similar results (collectively called "cue competition" phenomena), such as overshadowing (Kamin, 1969; Reynolds, 1961) and relative validity (Wagner et al., 1968), indicated that the critical component of the relation between CS and US was not temporal contiguity, but rather the degree to which the US could be predicted given the occurrence of the CS. Put another way, a CS will support conditioned responding to the degree that it provides information about the occurrence of the next US. When Rescorla and Wagner (1972) introduced their canonical associative framework, however, they salvaged the contiguity-dependent view by parsing the continuous stream of stimuli and events experienced by organisms in a conditioning protocol into arbitrarily defined trials of an experimenter-specified length and assuming that the strength of conditioning depended on the prediction error of all cues present during a reinforced trial. The discrepancy between the summed "associative strengths" of all cues present and the asymptote determined the increment in associative value of individual cues. Thus, on a trial-by-trial basis the extent to which one cue has associative value limits the extent to which other cues can gain value. This model allows learning to

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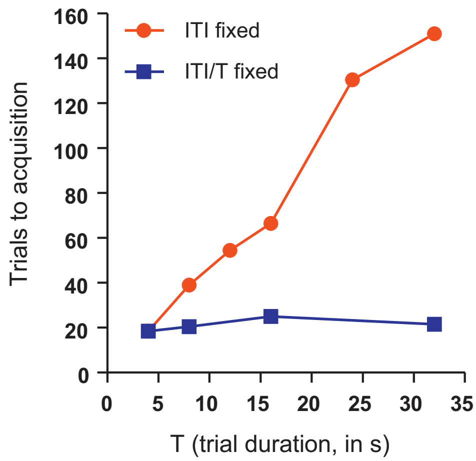

Fig. 1. Acquisition speed as a function of trial CS duration. Different groups of pigeons were exposed to an autoshaping protocol with fixed delays that ranged from 4 s to 32 s. For some groups, the duration of the intertrial interval was kept constant (filled circles). For these groups, the number of trials to acquisition increased with increased CS duration. In other groups (filled squares) the ratio of the intertrial to trial CS duration was kept constant. In these groups, speed of acquisition remained constant regardless of the duration of the trial CS. After Balsam et al. (2010). Original data from Gibbon et al. (1977).

be driven by contiguity but still permits cues to compete with each other for associative value. The general notion of contiguity-based increments and decrements in associative strength has been the conceptual foundation of the study of learning, including the search for the neurobiological basis of learning, for the last 50 years.

There are a growing number of empirical findings that pose problems for traditional associative models of conditioning (see Balsam et al. (2010) for review), but for the purpose of brevity we focus here on one crucial stumbling block. The traditional results cited as evidence of the importance of contiguity in learning are data showing that as the interval between presentation of the CS and US increases, the strength of conditioned responding decreases. This effect has been widely demonstrated in a variety of preparations (e.g., Gibbon et al., 1977; Gormezano and Kehoe, 1981; Ost and Lauer, 1965; Reynolds, 1945; Smith, 1968; Stein et al., 1958; Wickens et al., 1961; Vandercar and Schneiderman, 1967) and cited as evidence for the critical role of contiguity in learning in conditioning protocols. However, it has been repeatedly demonstrated that the effect of increasing the CS–US interval on strength of conditioning depends crucially on the duration of the ITI. The decrement in conditioning that occurs with increasing CS–US interval is eliminated if the ITI is increased in proportion to the CS–US interval (see Gallistel and Gibbon, 2000, for review). Specifically, acquisition speed in conditioning protocols has been shown to be a function of the ratio of cycle time (C; duration between successive US presentations) to trial time (T; duration of conditioned stimulus presentation in delay conditioning; see Gibbon and Balsam, 1981; Gibbon et al., 1977). The number of trials to acquisition is generally similar with similar C/T ratios, regardless of the absolute values of C and T. Fig. 1 shows the results from experiments (Gibbon et al., 1977) where pigeons were exposed to an autoshaping procedure and the effect of increasing CS–US interval on trials to acquisition was assessed. In groups for which the ITI was held constant, the trials to acquisition increased with increasing CS–US interval. However, in groups for which the ITI was increased proportionally to the CS–US interval, the number of trials to acquisition was constant, regardless of the CS–US interval. Thus, what matters in conditioning is not the absolute delay to reinforcement, as asserted by the traditional notion of contiguity, but rather the relative delay to reinforcement. This property of conditioning, which has been demonstrated numerous times in a number of species and preparations, strongly suggests timescale invariance of the conditioning process.

The dire implications of timescale invariance for associative models of conditioning cannot be overstated (see Gallistel and Gibbon (2001) for discussion). Simply put, current associative models have no way of dealing with timescale invariance because they are critically dependent on the notion of a trial of some specified length. Thus, intrinsic features of these models render them exquisitely sensitive to the absolute time scale of the conditioning protocol. As troublesome as timescale invariance is for formal models of associative learning given their trial-based structure, it is perhaps even more damning for the conceptual notion of contiguity as the fundamental principle of learning. If what matters in the learning and emergence of conditioned responding is the relative, not the absolute, delay to reinforcement, then what exactly constitutes a contiguous temporal pairing? What is the critical window of associability? There is no straightforward answer.

For this and other reasons we reject contiguity as the primary principle of learning, and offer an alternative conceptualization of the content and process of learning in conditioning protocols (Balsam and Gallistel, 2009; Balsam et al., 2010). In this paper, we review the primary conceptual and quantitative underpinnings of a model of conditioning based on an information theoretic analysis of the timing of events in conditioning protocols. A more complete treatment is given elsewhere (Balsam and Gallistel, 2009; Balsam et al., 2010).

The conceptual foundation of the information theoretic analysis is that in a conditioning protocol, events or cues (CS presentation) are informative to the extent that they tell the animal something it did not already know about the timing of the next US. The important information to be conveyed is how close (temporally speaking) the animal is to reinforcement. An informative CS is one that tells the animal that the US is relatively near. In other words, informative cues decrease the expected time to the next US. We assume, and extensive evidence has shown, that animals rapidly learn the duration of events in conditioning protocols (Balsam et al., 2002; Drew et al., 2005; Kirkpatrick and Church, 2000a, 2000b; Ohyama and Mauk, 2001). However, according to this view, the durations between events in a conditioning protocol do not determine the extent to which associations will form between the events. Rather, the durations between events *are* the content of learning in conditioning protocols. These learned durations form the basis for the computation of the expected time to reinforcement

Specifically, the underlying logic of the model is that a given cue (CS) will support conditioning to the extent that it reduces uncertainty about the timing of the next US. This is a conceptually intuitive idea, and allows a quantitative formalization made possible by Shannon's (1948) work in information theory. According to Shannon's conceptualization, a signal is informative to the extent that it reduces the receiver's uncertainty about some stochastic aspect of the world. The information conveyed by a given signal can be quantified as the difference in the uncertainty in the presence of the signal and the uncertainty when the signal is ignored or never presented. Applied to conditioning protocols, this means that the information conveyed by a prospective CS is the difference in uncertainty about the timing of the next US in its presence and the uncertainty about the timing of the US in the context. Uncertainty is quantified as the entropies of probability distributions. The entropy measures the uncertainty associated with some random variable, in this case, the variables describe the distributions of CS–US and US–US intervals. Thus, by computing the difference between the US–US entropy and the CS–US entropy, we obtain a measure of the information (reduction in uncertainty) of the timing of the next US conveyed by presentation of the CS. In the basic conditioning protocol, USs are distributed according to a random