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Timing in a variable interval procedure: Evidence for a memory singularity



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ABSTRACT

Rats were trained in either a 30 s peak-interval procedure, or a 15–45 s variable interval peak procedure with a uniform distribution (Exp 1) or a ramping probability distribution (Exp 2). Rats in all groups showed peak shaped response functions centered around 30 s, with the uniform group having an earlier and broader peak response function and rats in the ramping group having a later peak function as compared to the single duration group. The changes in these mean functions, as well as the statistics from single trial analyses, can be better captured by a model of timing in which memory is represented by a single, average, delay to reinforcement compared to one in which all durations are stored as a distribution, such as the complete memory model of Scalar Expectancy Theory or a simple associative model. This article is part of a Special Issue entitled: Associative and Temporal Learning

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1. Introduction

There has recently been considerable interest in examining the link between the temporal control of behavior and associative learning processes. Gallistel and Gibbon (2000) proposed that a number of behavioral phenomena, typically understood by reference to associative processes, can be alternatively understood as resulting from decisions based upon a perception of time. Broadly, they argue that the decision to respond is based upon an estimate of rates of return. Specifically, they argued that the cumulative time until reward during a conditioned stimulus is compared to the cumulative time until reward when the conditioned stimulus is absent, and a decision of whether to respond depends on this ratio passing a response threshold. This proposal has resulted in a number of studies examining this relationship, with some reports supporting the theory (Balsam et al., 2006; Gottlieb, 2008; Harris et al., 2012), and others finding discrepancies (Delamater and Holland, 2008; Golkar et al., 2013; Gottlieb and Rescorla, 2010). Irrespective of whether this model proves to be an accurate predictor of associative learning, it has been eminently successful in highlighting the lack of temporal specification of most associative accounts, which have focused on whether, rather than when, responding should occur.

One issue that is critical to any attempt to bridge these two approaches to understanding behavior is to identify the form and content of the memory that is used to guide the temporal control of behavior. For example, in an operant timing task such as the peak-interval procedure, a subject is given a food reward for the first desired response after a criterion time has elapsed. After training, the average rate of responding ramps up as a function of time until the criterion duration, and declines thereafter, leading to maximal levels of responding around the time that the reward has been programmed to be available. What is the content and form of the memory that is in play here? One possibility that follows from a simple associative perspective is that the strength of responding at each moment in time is modified by excitation (and inhibition) resulting from reinforcement (and the lack thereof), and variability in "perceived" time results in a broad array of response strengths. Models such as the Behavioral Theory of Timing (Killeen and Fetterman, 1988), the Learning to Time Theory (Machado, 1997), and the Spectral Timing model (Grossberg and Schmajuk, 1989) are varied instantiations of this general idea. Thus, in such a model, no explicit expectancy of the time of reward is generated. Alternatively, Scalar Expectancy Theory (SET) proposes that the animal learns the time (in terms of an internal clock count) at which reward was obtained (Gibbon, 1977; Gibbon et al., 1984). Specifically, SET proposes that elapsed time is represented by the linear accumulation of pulses released from a pacemaker. When reinforcement is provided, the accumulated count, which is directly proportional to elapsed time, is stored in reference memory. However, due to variability in the speed of the pacemaker across trials, the subjective time at which reward occurs will vary across trials. As a result, a distribution of reward time memories will be created which reflect every time at which reinforcement was obtained. In addition, SET proposes that there is variability in the memory encoding process, which would also lead to a memory distribution.

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Responding is generated following a comparison of the elapsed pulse count in the accumulator with a random sample from the memory distribution. Specifically, high rate responding is proposed to occur throughout the interval during which the relative discrepancy (|memory sample-accumulator count|/memory sample) is smaller than a threshold level of similarity. This similarity threshold is also proposed to exhibit normal variability across trials. Together then, SET proposes four primary sources of variability between trials: variability in the clock rate, variability in the memory encoding process, variability in the memory sampling process and variability in the similarity threshold used in the decision process. In contrast to the associative account, in this framework, an explicit expectation of reward exists for every time at which reward has been obtained, and responding is based on a sample of this knowledge. While these models obviously differ in the content of memory, in both frameworks, the form of memory is a distribution (of response strengths or reward times).

An alternative possibility, suggested by recent work from our lab, is that temporal memory is composed of an average of past reinforcement times. Specifically, we showed that rats trained in a mixed-interval peak procedure in which two different modality cues predicted two different delays to reward availability (e.g., tone = 10 s, light = 20 s) will respond maximally at a time between the trained criterion durations (e.g., 16 s) when presented with the compound cue (tone + light) in extinction (Swanton et al., 2009). Importantly, the breadth of responding to the compound cue was scalar (i.e., it had the same relative width as the response functions from the component cues). Similar results have been seen using a range of durations, duration ratios, and cues (Kurti et al., 2013; Matell and Kurti, 2013a; Matell et al., 2011; Swanton and Matell, 2011).

We interpreted these data as indicating that the onset of the two cues led to the simultaneous retrieval of the two component temporal memories, which due to their discrepancy, were then integrated or averaged, and the resulting expectation timed in an otherwise normal manner. Intriguingly, such scalar behavior to the compound cue constrains the possible ways in which temporal memories can be represented. For example, if temporal control is instantiated by the sequential activation of a distribution of response strengths following an associative model, then the compound response function would presumably result from the combined activation of the temporal generators activated by each cue. However, simulations of this scenario in which the two component response functions are pooled (with all possible combinations of weights) does not produce a scalar response form at an intermediate time (it is always wider than scalar), and frequently produces a multi-modal response function (depending on the component response rates and weights). Similarly, if the compound stimulus led to a (weighted) average of the each cue's temporal memory distribution, the average distribution would be relatively wider than the component distributions and would potentially have multiple modes (again depending on the component memory spreads and weights). Thus, in scenarios in which response strength or entire memory distributions are pooled or averaged, compound responding should be broader than scalar.

In contrast, if the organism randomly sampled memories for each duration as proposed by SET (i.e., one from the short memory distribution and one from the long memory distribution), and then timed the average of these samples, the compound response function would be narrower than scalar. Such a result emerges because a random sample from one of the tails of the short distribution is highly likely to be offset by a less extreme sample or one biased in the other direction from the long distribution, thereby creating less variability in the average than that seen in the component distributions. More broadly speaking, this narrowing of the average expectation follows from the central limit theorem, in that the variability of a sample mean is always smaller than the variability of the sample distribution.

In summary, models of timing in which temporal memories are represented as a distribution (of either explicit expectations or response strengths) are generally unable to account for the scalar form seen in stimulus compounding situations. Instead, these results suggest that the mnemonic representation of time is composed of a single expectancy. Specifically, the average of two discrepant singular expectations will itself be a singular value. As such, responding will reflect the same sources and levels of variability as that of the component durations, and the response form will therefore be scalar. In information processing terms, this would imply that there is variability in the clock and decision stages, but not in the memory stage (i.e., there is either no memory distribution and only an average expectation, or the value sampled from the distribution is a single measure of central tendency, such as the mean).

While these compounding data suggest that the memory for a fixed interval schedule of reinforcement may be represented by a singular expectation, it is also important to investigate whether such integration processes may be at work when a single cue is associated with multiple, different times of reward, such as under mixed fixed-interval schedules or variable-interval schedules. Previous work using mixed fixed-interval schedules associated with a single cue typically demonstrated multi-modal response functions, unless the ratio of the two durations was small (Leak and Gibbon, 1995; Whitaker et al., 2003), or the probability of reinforcement at the earlier duration was very low (Whitaker et al., 2008). These multi-modal response patterns are obviously not consistent with the two (or more) different durations being integrated into a single expectation (note, however, that these data do not preclude each fixed-interval being represented by a singular expectation). Instead, the form of responding in these tasks was well accounted for by the simple summation of two independent peak functions, each centered near the respective fixed intervals (Whitaker et al., 2003, 2008).

Why should the single interval schedules be represented by a single average expectancy when the mixed-interval schedules generate multiple, potentially distinct, expectations? The obvious answer to this question is that in the mixed-interval schedule the animal experiences multiple durations to reinforcement, whereas there is only a single delay to reinforcement under a single fixedinterval schedule. However, a bit of reflection suggests that this is not a sufficient answer. An assumption made by all models of timing is that there is variability in the rate of the processes composing the clock. As a result, the subjective delay to reinforcement under a single fixed-interval schedule will vary across trials, and therefore, in both cases the organism experiences multiple delays to reinforcement. The difference then appears to be how much variation there is for the experienced durations. When there is a small amount of relative variability, the organism may conclude that this variation is a result of sensory error and form a single expectation, whereas when the relative variability is large, the organism may attribute the variation to the environment, and form multiple expectations. One simple way in which this could be implemented without forming a distribution is just computing the ratio between the expected and obtained reinforcement time. A similar suggestion was made by Jones and Wearden (2003) in their perturbation model in which reference memory is updated only when the proportional difference between currently experienced reinforcement time and the expected time passes a threshold level of dissimilarity (e.g., 20% difference).

In keeping with this idea, an examination of the pattern of responding to constrained variable intervals may be informative. In contrast to the multi-modal response functions seen with mixed FI schedules, work using a uniformly distributed 30–60 s variable

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