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The effect of an intruded event on peak-interval timing in rats: Isolation of a postcue effect

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Abstract

The present experiment employed the peak-interval (PI) procedure to study the effect of an intruded cue on timing behavior. Rats were trained on a 30-s PI procedure with a tone cue. Subsequently, a 6-s flashing light was paired off-baseline with foot shock (Experiment 1) or presented alone (Experiment 2). Then, in test trials, the light cue was presented 9 s prior to (before) or 3 s after (during) the onset of the timing cue, or the light was omitted (probe). Results showed rightward shifts in peak time occurring on both before and during trials in both experiments. Peak shifts on during trials exceeded the reset prediction in Experiment 1. When PI functions for before and probe trials were normalized in peak rate and peak time, they superimposed better than when functions were adjusted additively along the time axis, suggesting that the light cue may engender a decrease in functional clock rate. The findings suggested that the intruded cue produced both intracue and postcue interference with timing that was enhanced by fear conditioning.

Keywords: Animal timing; Peak-interval procedure; Fear cue; Postcue effect; Clock rate; Rats

1. Introduction

A strategy that has been employed to investigate the mechanisms underlying animal-interval timing is to perturb the timing process by the addition of an intruded event during the timing interval, and to note the effect on timing performance. This strategy has been widely used in the peak-interval (PI) procedure. That procedure is a discrete-trial version of an operant fixed-interval (FI) t s schedule in which the presentation of a timing cue signals the availability of food for the first response to occur t s after the onset of the signal. On baseline test trials that are interspersed with training trials, the signal is presented for a duration of at least twice t, and the reinforcer is omitted. Performance on test trials is characterized by a unimodal momentary response rate function that increases gradually to a maximum value (peak rate) at a time (peak time) that closely approximates t. Thus, peak time is taken as a measure of the subject's estimate of t (e.g., Roberts, 1981). When different values of t are employed, rate-normalized peak-interval functions superimpose when plotted against relative elapsed time, that is elapsed time divided by t or by peak time (e.g., Gallistel and Gibbon, 2000). Such superposition implies a scalar transformation, and is a hallmark of scalar expectancy theory (SET, Gibbon, 1977) of interval timing. The interval clock model of SET, incorporating pacemaker–switch–accumulator, working and reference memory, and comparator modules, provides an account of an impressive number of aspects of timing performance (Church, 1984; Gibbon and Church, 1990).

The earliest reported intruded event in the PI procedure consisted of the insertion of a gap, the temporary termination of the timing cue, during a test trial. For example, Roberts (1981, Experiment 2) trained rats on a 40-s PI procedure with light as the timing cue, and showed that when a 5–10 s gap was introduced at various locations, peak times were 2–4 s longer than those on baseline trials. When response rate functions on gap trials were shifted horizontally so that peaks coincided with that on baseline trials, the functions superimposed, implying that the gap induced an additive shift in the peak time function. Roberts suggested that during the gap the interval clock stopped, and resumed again when the timing cue resumed. A stop mechanism would produce a shift in peak time that is equal to the duration of the gap, whereas a reset mechanism would produce a shift

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by an amount equal to gap duration plus the pre-gap duration of the timing signal. More generally, a cue that is t_1 s in duration presented t_2 s after trial onset would engender a peak shift of t_1 s based on the stop mechanism alone, or a shift of $t_1 + t_2$ s based on the assumption that the cue both stops and resets the clock. Roberts et al. (1989, Experiment 3) reported that gaps of 1, 3 and 9 s produced peak time shifts in pigeons that were closer in general to the reset prediction than the stop prediction. A subsequent parametric study by Cabeza de Vaca et al. (1994) systematically manipulated gap location and duration in separate experiments with pigeons. Their data showed that peak time shift varied positively with both variables in a manner that suggested that the clock stops during the gap, and that memory for pre-gap duration decays non-linearly during the gap, producing the observed shift in peak time. In this account, stop and reset outcomes represent end points on a continuum governed by a single mechanism. A recent elaboration of this model (Buhusi et al., 2006) that takes into account both temporal and non-temporal properties of the gap expands the continuum to include outcomes from run through reset.

Intrusions that consist of added cues instead of gaps may also induce shifts in peak time. One phase of Roberts's (1981) Experiment 2 consisted of test trials in which a 10-s noise was presented as an added cue 10 s after trial onset. There was no effect of the noise cue initially, but an effect gradually emerged so that after 15 sessions, noise occasioned a 17-s shift in peak time, closer to a reset (20 s) than to a stop (10 s) outcome. More recently, Buhusi and Meck (2006) reported that a 5-s noise presented 15 s after the onset of the timing signal produced an immediate shift in peak time that approximated a stop outcome.

Peak shifts anticipated by stop, reset and decay accounts may be characterized as intracue effects, as the mechanisms responsible for the peak shift (stopping or resetting the clock, decay of stored time) operate during the presentation of the intruded event; the maximum shift expected under intracue effects is reset. However, in a recent study using a dual-task in pigeons, Aum et al. (2004) reported that an intruded cue that had been pretrained as a food cue occasioned shifts in peak time that exceeded the reset prediction. Specifically, pigeons were first trained on a PI 30-s schedule with the illumination of a yellow side key serving as the timing cue. Next, in separate sessions, subjects were trained to peck a 6-s red center key on a random interval schedule. Finally, in dual-task test sessions, on some trials, the red center key was illuminated for 6 s at 3, 9 or 15 s after the onset of the timing cue. Results from those trials indicated that, at all three temporal locations of the red key, peak times occurred later than those on baseline test trials by amounts that exceeded the reset prediction, in contrast to previous studies. The stop, reset and decay accounts that have been advanced for results of prior studies, cannot account for Aum et al.'s "over-reset" results, as they posit reset as the maximum expected shift. Thus, these findings demonstrate postcue effects, as the locus of those effects is subsequent to the intruded cue. The authors attributed the over-reset result to a combination of both intracue and postcue mechanisms: a clock reset during the presentation of the intruded cue (intracue), and a delay in the resumption of timing following the presentation of that cue (postcue). As in interpretations of the gap effect, Aum et al.'s account proposes an additive shift in peak time.

The latter study raises at least two questions: is the over-reset result observed by Aum et al. (2004) unique to the preparation/protocol used? Can peak time shifts up to and including reset, such as those obtained in previous studies, mask postcue effects? In the present study, we assess the generality of the over-reset result in a different species with a different intruded cue history, by using rats instead of pigeons, and having the intruded event pretrained as a fear cue in a Pavlovian paradigm, instead of a food cue in an instrumental task. The same temporal parameters as in Aum et al. were used. If the findings of Aum et al. (2004) do not depend upon the valence of the intruded cue, then a fear cue with rats should produce a similar effect as a food cue with pigeons, that is, a rightward shift in the peak-interval function on intruded-cue trials relative to the baseline function, which exceeds the reset prediction.

The second question can be answered only if one can isolate the postcue effect of the added cue. For this purpose, we analyzed the effect of the added cue when it was presented prior to the onset of the timing cue. This type of trial provides a direct assessment of the postcue effect uncontaminated by intracue effects. When the intruded event precedes the timing cue, any effects on timing performance must reflect postcue effects as opposed to intracue effects, such as the stopping or resetting of the clock, or memory decay. Comparisons of trials in which no added cue is presented (probe condition) with trials in which a fear cue is presented either after the start of the trial (during condition) or prior to the start of the trial (before condition) provide data bearing on the intracue and postcue mechanisms induced by the added cue. These comparisons were made when the cue was a fear cue (Experiment 1) or simply a non-conditioned cue (Experiment 2). If part of the shift observed on during trials represents a postcue effect, then a rightward shift should also be expected on trials on which the cue is presented prior to the timing signal, that is, on before trials.

The magnitudes of the shifts depend upon the clock mechanisms involved. For example, under the assumptions that an intruded event both resets a running clock and induces a delay in the initiation of timing, the expected shift in peak time when the event is presented prior to the timing signal should reflect only the postcue delay in the initiation of timing, and thus produce a smaller shift than on intruded-cue trials. However, this ordering of peak times among trial types may also follow from different assumptions. More generally, the peak time shifts occasioned by trials in which the intruded event is presented before or during the trial will depend upon the nature of the intracue (e.g., stop, reset, decay) and postcue (e.g., additive, non-additive) mechanisms. The data of the present study were subjected to analyses intended to distinguish among those mechanisms.

2. Experiment 1

The present study was a systematic replication of Aum et al. (2004), with modification of three factors: species, intruded-cue reinforcer and temporal placement of the intruded stimulus. Rats were initially trained on a discrete-trial PI procedure to