



Adaptation of timing behavior to a regular change in criterion



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ABSTRACT

This study examined how operant behavior adapted to an abrupt but regular change in the timing of reinforcement. Pigeons were trained on a fixed interval (FI) 15-s schedule of reinforcement during half of each experimental session, and on an FI 45-s (Experiment 1), FI 60-s (Experiment 2), or extinction schedule (Experiment 3) during the other half. FI performance was well characterized by a mixture of two gamma-shaped distributions of responses. When a longer FI schedule was in effect in the first half of the session (Experiment 1), a constant interference by the shorter FI was observed. When a shorter FI schedule was in effect in the first half of the session (Experiments 1, 2, and 3), the transition between schedules involved a decline in responding and a progressive rightward shift in the mode of the response distribution initially centered around the short FI. These findings are discussed in terms of the constraints they impose to quantitative models of timing, and in relation to the implications for information-based models of associative learning.

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1. Introduction

The Darwinian fitness of animals involves the adjustment of their behavior to environmental regularities, such as the correlation between biologically significant stimuli (associative learning) and the timing of those stimuli. Whereas associative learning dynamics have been extensively studied for 40 years (Rescorla and Wagner, 1972; Pearce and Bouton, 2001; Killeen et al., 2009), research on timing has been primarily focused on steady-state performance (Church, 2006; Grondin, 2010; Machado et al., 2009). Few studies have examined how behavior adjusts to changes in the periodicity of biologically significant stimuli and, consequently, our understanding of timing dynamics is incipient. The purpose of the present study is to describe and account for trial-by-trial changes in operant performance when the timing of reinforcement changes abruptly but regularly.

Studies on timing dynamics rely primarily on laboratory rats and pigeons as experimental subjects (but see Rivière et al., 2000), and on the fixed-interval (FI) schedule of reinforcement (e.g. Guilhardi et al., 2006), or some variation of this schedule, to assess the temporal control of behavior. In the FI schedule, the first response following a *criterion* (a fixed time since the onset of the trial)

is reinforced. Two typical variations of the FI schedule are the response-initiated-delay (RID) schedule, in which reinforcement is delivered at the criterion if a response is produced before the criterion elapses (e.g. Wynne and Kalish, 1999), and the peak interval (PI) procedure, in which a portion of FI trials are substituted by longer non-reinforced trials (e.g. Roberts, 1981; Rodríguez-Gironés and Kacelnik, 1999).

FI and RID studies use the post-reinforcement pause (PRP), the interval between trial onset and the first response, as the primary measure of temporal control. These studies have shown that an unpredictable disruption of periodic reinforcement by a series of trials with short criteria yields a rapid reduction in PRP in the trials following each short-criterion trial; after the disruption, PRP recover at a rate that is inversely proportional to the length of the disruption (Higa, 1996a; Higa et al., 2002). If periodic reinforcement is disrupted by long-criteria trials, however, changes in PRP are negligible (Higa, 1997; Ludvig and Staddon, 2004) or so weak as to require very long disruptions (Higa and Tillou, 2001). When changes in PRP are observed during a long-criterion disruption, recovery of shorter PRPs following the disruption is very rapid (Higa and Tillou, 2001). Changes in PRP following long-criterion disruptions are made more visible in *single-transition paradigms*, in which the disruption is maintained for the remainder of the session (Higa, 1996b; Higa et al., 1993). Even in single-transition paradigms, however, downshifts in PRP in response to downshifts in the criterion are faster than upshifts in PRP in response to upshifts in the criterion (Higa et al., 1993; Higa, 1996b).

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The use of PRPs allows for a trial-by-trial analysis of changes in the temporal control of behavior, but neglects evidence of temporal control that is visible in the responses that follow the first response in FI and RID. These latter responses are examined in the PI procedure. This procedure uses measures of central tendency of the distribution of responses in non-reinforced trials to establish the *peak time*, which typically coincides with the criterion and serves as an estimate of the time when the subject expects reinforcement (Roberts, 1981). Studies on timing dynamics based on peak time estimates have yielded disparate results. Using rats, Meck et al. (1984) found that, when the criterion in the PI schedule was either increased or reduced permanently across sessions, the peak time was fixed for several sessions at an intermediate time before settling at the new criterion. In contrast, Rodríguez-Gironés and Kacelnik (1999) found that it took several intermediate steps for European starlings to complete a downward transition between PI schedules. Moreover, whereas the change in peak time in response to a criterial upshift in Meck et al. (1984) was symmetrical to the change in response to a criterial downshift, Lejeune et al. (1997) observed abrupt changes in peak time when rats transitioned from a short to a long criterion, but more progressive changes when transitioning from a long to a short criterion. Both Meck et al.'s (1984) and Lejeune et al.'s (1997) findings stand in contrast to the slower changes in PRPs in criterial upshifts relative to downshifts.

Despite their limited scope, the results obtained from PRP-based studies are sufficiently consistent to support informative quantitative models of timing dynamics (Luzardo et al., 2013; Staddon et al., 2002a,b). In contrast, research focused on peak times provides a more comprehensive view of temporally controlled behavior, but the exiguous data it has provided support seemingly inconsistent findings. To develop a model of timing dynamics comparable to those of associative learning dynamics, it may be beneficial to implement the simpler behavioral paradigms that have shown consistent results in PRP-based studies, and apply to those results a comprehensive analytic approach akin to that of peak-time-based research. To that end, the present study examined changes in response rate within individual FI trials using a single-transition paradigm similar to that used by Higa (1997). Unlike Higa's (1997) study, however, the present study implemented the transition regularly in the middle of each session. This modification allowed us to examine whether our experimental subjects anticipated the regular transition between schedules. Also, our analysis was not restricted to changes in PRP, but considered changes to the distribution of responses over time within each trial.

The present study involved the analysis of response-rate functions in trials around a regular transition between two FI schedules (Experiments 1 and 2) and between and FI schedule and the discontinuation of reinforcement (Experiment 3). This analysis was focused on answering two questions: (1) Is the change in reinforcement time anticipated? (2) Following the change in reinforcement time, how does control from the previous reinforcement time wane?

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Four experienced male pigeons (*Columba livia*) served as experimental subjects; they were housed individually in a room with a 12 h:12 h day:night cycle, with dawn at 0600 h. Each bird had free access to water and grit in their home cages. Experiments were conducted during the day. Running weights were monitored daily and were kept at about 80% of free-feeding weights. Each pigeon was weighed immediately prior to an experimental session and was excluded from a session if its weight exceeded 8% of its

running weight (i.e. 86.4% of free-feeding weight). When required, a supplementary feeding of ACE-HI pigeon pellets (Star Milling Co.) was given at the end of each day, at least 12 h before experimental sessions were conducted.

2.1.2. Apparatus

Experimental sessions were conducted in four MED Associates modular test chambers. The test panel contained a plastic transparent response key (25 mm in diameter: MED Associates, ENV-123AM), centered horizontally 70 mm from the ceiling. The key could be illuminated by white light from two diodes. Activation of the key generated a 100-ms period in which no further activations were registered. A rectangular opening (52 mm wide, 57 mm high) located 20 mm above the floor and centered on the test panel provided access to milo when a grain hopper was activated (Coulbourn Instruments, H14-10R). A houselight (MED Associates, ENV-215M) was mounted 12 mm from the ceiling on the sidewall opposite the test panel. The houselight dimly illuminated the chamber throughout each experimental session.

2.1.3. Procedure

2.1.3.1. Fixed-interval 15-s pretraining. Pigeons were first introduced to a fixed-interval (FI) 15-s schedule of reinforcement. In this schedule, the onset of a trial was signaled by the illumination of the center key with white light. The first keypeck after 15 s from trial onset turned off the center key and activated the hopper for 2.5 s, which served as reinforcer. The next trial started immediately after turning off the hopper. Each session finished after 60 trials or 90 min, whichever happened first. Each pigeon was pretrained for three sessions.

2.1.3.2. Experimental training. Experimental sessions were similar to FI 15-s pretraining sessions, with a few exceptions. First, in each session, trials were divided into two halves of 30 trials each. Each bird experienced two different schedules of reinforcement during each session, one schedule in each half. One schedule was always FI 15-s; the other was either FI 45-s or variable interval (VI) 45-s. Sessions containing a VI 45-s schedule were conducted for purposes unrelated to this experiment and are not analyzed here. Each bird experienced 23–27 consecutive sessions with each schedule permutation: FI 15-s then FI 45-s (*Short-First*); FI 45-s then FI 15-s (*Long-First*); FI 15-s then VI 45-s; VI 45-s then FI 15-s (the latter two permutations were not analyzed). The order of presentation of each schedule permutation was counterbalanced across birds.

2.1.4. Data analysis

The last 10 sessions of Short-First and Long-First sessions were analyzed. Key pecks within each trial in these sessions were averaged within 1-s bins. Only the first 15 and 45 bins were analyzed in FI 15-s and FI 45-s trials, respectively. Data were first averaged within each bin across blocks of 5 consecutive trials. This level of aggregation revealed the 5-trial blocks around the middle of the session where the transition in FI performance took place. We called these blocks of trials the *transition period*.

A simple model of transition between FI schedules assumes that the FI requirement in the first half of the session interferes with FI performance in the first few trials of the second half of the session. This interference is likely to be expressed as responding under the control of the first FI schedule while the second FI schedule is in effect (Catania and Reynolds, 1968). The joint control of behavior by multiple timing requirements is well characterized by models that assume parallel processes controlling responding around each of the two requirements (Leak and Gibbon, 1995). Such parallel processes yield a bimodal distribution of responses over time (Whitaker et al., 2003, 2008). Thus, a bimodal distribution

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