RUNNING HEAD: DISSOCIATING TIMING AND MOTIVATION

Interval Timing and Motivation are Dissociable when Interval-Initiating Responses are
Discriminable from Target Responses

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Abstract

Data have accumulated suggesting that motivation and timing are correlated processes, yet few studies have tested whether motivation and timing are procedurally dissociable. This may be attributed to the fact that the most common framework in which to study timing, the pacemaker-accumulator model, does not readily suggest a route by which to dissociate motivation and timing. In contrast, the behavioral systems framework suggests that motivation and timing could be dissociated if subjects were trained in response-initiated (RI) interval-timing procedures rather than in common externally-initiated (EI) procedures. RI procedures were predicted to enhance temporal control and yield timing performance robust to fluctuations in motivation. Experiment 1 tested this hypothesis by training rats to either initiate switch-timing trials with a single press on the lever associated with the shorter FI schedule (SL-RI), or wait for switch-timing trials to be initiated (EI). Motivation was varied through pre-feeding. SL-RI and EI rats showed similar levels of temporal control and sensitivity to pre-feeding in their switch-timing performance. Experiment 2 tested a revised RI hypothesis, the discriminative-RI hypothesis, which predicts that as the trial-initiating response becomes progressively different from target responses, motivation and timing are increasingly dissociated. This experiment replicated Experiment 1 and added a trial-initiating condition in which a nose-poke into a nose port (NP-RI) initiated trials. As predicted, the sensitivity of switching-timing performance to pre-feeding scaled such that EI > SL-RI > NP-RI. These data suggest that it is possible to dissociate timing and motivation, challenging the notion that these processes are correlated.

Keywords: Interval Timing, Motivation, Behavioral Systems, Response Initiation, Pre-feeding

Interval Timing and Motivation are Dissociable when Interval-Initiating Responses are Discriminable from Target Responses

Introduction

Interval timing is the entrainment of behavior to periodicities of biologically significant events in the scale of seconds-to-minutes, signaled by a *time-marker* (Buhusi & Meck, 2005; Gibbon, 1977, Sanabria & Killeen, 2007). Such entrainment is not just a feature of behavior, it is a critical ability leveraged in various contexts (Marshall & Kirkpatrick, 2015; McMillan, Spetch, Sturdy, & Roberts, 2017), including learning (Gallistel & Gibbon, 2000; Holland, Hamlin, & Parsons, 1997) and decision making (Gruart, Meck, & Doyere, 2012; Wittmann & Paulus, 2008). Although the predominant theory of timing—scalar expectancy theory (SET; Buhusi, Oprisan, & Buhusi, 2018; Gibbon, 1977)—suggests that fluctuations in motivation should *not* affect timing, extant data suggest that timing and motivation interact. Indeed, timing (a) requires the synchronous action of neural circuits involved in both timing and motivation (Bailey, Simpson, & Balsam, 2016; Berridge & Kringelbach, 2013; Coull, Hwang, Leyton & Dagher, 2012; Galtress, Marshall, & Kirkpatrick, 2012; Kirkpatrick, 2014); and (b) is sensitive to fluctuations in motivation induced by, for example, pre-feeding and satiation (e.g., Daniels & Sanabria, 2017; Daniels, Overby, & Sanabria, 2018; Eskin & Bitterman, 1960; Galtress & Kirkpatrick, 2009), changes in reward magnitude (e.g., Avlar et al., 2015; Cambraia, Vasconcelos, Jozefowicz, & Machado, 2019; Balci, Wiener, Çavdaroglu, & Coslett, 2013; Daniels et al., 2015a, b; Ludvig, Balci, & Spetch, 2011; McSweeney, Hinson, & Cannon, 1996), and alterations in dopamine signaling (e.g., Avlar et al., 2015; Balci et al., 2013; Balci, 2014; Drew, et al., 2007; Meck, Cheng, MacDonald, Gainetdinov, Caron, & Çevik, 2012; Taylor, Horvitz, & Balsam, 2007). Such observations have led to the conclusion that motivation and timing are correlated, if not inseparable processes (Avlar et al., 2015; Galtress, Marshall, & Kirkpatrick, 2012; Balci, 2014):

changes in motivation for an incentive necessarily affect the timing of that incentive, and vice versa. Although more recent work suggests that it is possible to computationally dissociate timing and non-timing processes (Balci, Freestone, & Gallistel, 2009; Daniels et al., 2015a, b; Laude, Daniels, & Zentall, 2016; Sanabria & Killeen, 2008), including motivation (Daniels & Sanabria, 2017a; Daniels, Overby, & Sanabria, 2018; Watterson, Mazur, & Sanabria, 2015), to our knowledge no study has *directly* tested whether it is possible to *procedurally* dissociate motivation and timing. In the present paper, we report two experiments that assess whether such a dissociation is possible.

Figure 1A-B shows two common procedures for assessing timing performance. In the fixed-interval (FI) schedule of reinforcement (Figure 1A), reinforcement (signified by a “candy” symbol) is contingent upon the first response after some interval since time-marker presentation (signified by a “lightbulb” symbol) has elapsed. Following time-marker presentation, well-trained subjects typically start responding at a relatively low-rate and then transition abruptly to a high-rate (Schneider, 1969; cf. Daniels & Sanabria, 2017; Gentry, Weiss, & Laties, 1983). In the switch-timing procedure (Figure 1B), a variant of the FI schedule, subjects are trained to search for food contingent upon the first response at the end of a Short FI at one location or a Long FI at another location (Balci, Papachristos, Gallistel, Brunner, Gibson, & Shumyatsky, 2008; Daniels et al., 2015a; Stubbs & Pliskoff, 1969). Importantly, the active FI is not differentially signaled. Following time-marker presentation, well-trained subjects start responding on the Short FI, and if reinforcement is not forthcoming, switch over to the Long FI. In Long FI trials, there are at least two potential indices of timing: the time to the last response on the Short-FI (latency-to-depart; LTD) and the time to the first response on the Long-FI lever (latency-to-switch; LTS). Typically, researchers analyze LTDs (e.g., Balci, Freestone, & Gallistel, 2009) or LTSs (e.g., Daniels et al.,

2015a; cf. Fox, Prue, & Kyonka, 2016); here we analyze both as suggested by Gupta, Daniels, Ortiz, Stephens, Overby, Romero, Conrad, & Sanabria (2019).

Figure 1C shows a schematic of the predominant theoretical framework for studying timing performance (Buhusi et al., 2018; Gibbon, 1977; Treisman, 1963): the pacemaker-accumulator (PA) family of computational timing models (of which SET is the most common instantiation). Briefly, PA models generally assume that, following time-marker presentation, a pacemaker emits pulses at some rate ($1/c$, where c = average inter-pulse interval), which are counted by an accumulator (A). When adapted for switch-timing procedures, it is assumed that the pulse count in A is continuously compared to a pulse count sampled from memory (m) such that, when the pulse count in A becomes sufficiently similar to the pulse count sampled from m , responding switches from the Short FI to the Long FI. However, PA models implicitly assume that *all* target responses are the output of a timing process and thus *all* performance indices characterize that timing process. Thus, if fluctuations in motivation alter timing performance, such alterations must be attributed to a motivation-induced change in PA parameters (Bacli, 2014; Galtress et al., 2012; Kirkpatrick, 2014). PA models, therefore, do not readily suggest a route by which to procedurally dissociate motivation and timing.

An alternative framework for interpreting timing performance is the behavioral systems framework (Freestone & Balci, 2019; Sanabria, Daniels, Gupta & dos Santos, 2019; Timberlake, 1984, 1993, 1994, 2000; Timberlake & Lucas, 1989; Timberlake & Washburne, 1989; see also Barnett, 1975; Collier, 1981; Domjan, 1994; Fanselow, 1994; Tinbergen, 1951). According to this framework, behavioral procedures (e.g., FI and switch-timing) entrain and constrain specific behavioral subsystems. Figure 2A shows an ethogram-like schematic of the rats' predatory behavior subsystem, which has been studied in various contexts, including FI schedules of

reinforcement (e.g., Silva & Timberlake, 1998a, b, 1999, 2005). This predatory behavioral subsystem, or any other behavioral subsystem, may be decomposed into constituent latent behavioral modes (signified by “circles containing underlined text”) and modules (signified by “bolded text”), and observable actions (signified by “italicized text”) which interface modes and modules with the environment (signified by the “FI schedule”). These behavioral modes, modules, and actions are hierarchically organized and sequentially but probabilistically linked.

An important implication of the behavioral systems approach is that transitions between behavioral modes may be inferred from the timing of mode-specific actions (see Killeen et al., 2002 and Sanabria, et al., 2019). Insofar as different actions occur at the beginning, middle, and end of a FI trial (e.g., Staddon & Simmelhag, 1971), so do different behavioral modes (Lucas, Timberlake, Gawley, 1988; Timberlake, 1994). Whereas grooming and post-food focal search occurs at the beginning third of a FI, just after reinforcement (Timberlake & Gawley, 1989; Timberlake & Lucas, 1989; Timberlake, 2000; Staddon & Simmelhag, 1971; Staddon & Ayres, 1975), lever pressing and general and pre-food focal search occurs in the latter two-thirds of a FI trial (Killeen & Pellon, 2013; Timberlake & Gawley, 1989; Silva & Timberlake, 2005). General search is largely characterized by investigative behaviors such as sniffing and sub-threshold responses at the lever and reinforcement receptacle (Lucas, Timberlake, & Gawley, 1988; Timberlake, 1994; Timberlake & Lucas, 1989). Timberlake and colleagues have argued forcefully that what animals learn in interval timing procedures is to time transitions between general search and pre-food focal search (Silva & Timberlake, 1998a, b, 1999, 2005).

Figure 2B shows a potential mapping of the rats’ predatory behavioral subsystem to switch-timing performance. Consistent with single FI schedules, switch-timing may be conceived of as entraining the same behavioral modes (signified by “circles containing

underlined text”), but with a slight modification: after failing to find food at the Short-FI in Long-FI trials, subjects transition back to general search before returning to pre-food focal search (signified by the “bidirectional arrow connecting pre-food focal search on the Short FI with general search on the Long FI”). This configuration is supported by the observation that there is typically a 2-s or longer difference between LTDs and LTSs, indicating that subjects are pausing (see Gupta et al. 2019; Maggi et al. 2014, Tosun, Gür, & Balci, 2016). Such a pause may be indicative of subjects transitioning back to general search before returning to pre-food focal search at the Long-FI (Killeen, Hall, Reilly, & Kettle 2002; Sanabria et al. 2019), rather than a continuation and spatial relocation of pre-food focal search, which would predict shorter transitions¹. This suggests that, whereas the last target response on the Short FI (LTDs) demarcate transitions from pre-food focal search to general search, the first target response on the Long FI (LTSs) demarcates transitions from general search back to pre-food focal search.

Although the differential sensitivity of behavioral modes to time is well documented (i.e., general search and pre-food focal search but not post-food focal search is sensitive to time), there is scant data on the sensitivity of behavioral systems to changes in motivation. Instead, it is assumed that the activated subsystem depends on the motivational state of the subject (Sanabria et al. 2019); whereas a hungry animal will be engaged in the predatory subsystem (Timberlake & Silva, 1995), a fearful animal will be engaged in the defensive subsystem (Fanselow, Hoffman, & Zhuravka, 2019) and a sexually aroused animal will be engaged in the mating subsystem (Domjan & Gutiérrez, 2019). Nonetheless, Timberlake (2000) suggested that post-food focal

¹ The alternative configuration, a continuation but spatial relocation of pre-food focal search, predicts that the difference between LTDs and LTSs should only be affected the distance between the manipulanda on which the Short FI and Long FI are programmed. Previous work (see Figures 3H and 4H in Daniels & Sanabria, 2017b) suggests that the time it takes to traverse the typical space between two levers flanking a reinforcer receptacle is less than 1 s.

search is sensitive to the magnitude of reward. Similarly, Killeen (1994, 1995) has suggested that changes in arousal precipitated by changes in motivation are largely reflected in the pauses prior to initiation of responding (also see Killeen et al., 2002). These considerations suggest that the time spent in post-food focal search is inversely related to motivation: as motivation increases, time spent in post-food focal search decreases; as motivation decreases, time spent in post-food focal search increases.

Given this working hypothesis, the behavioral systems framework suggests a potential route by which to dissociate motivation and timing: train subjects to emit a response that demarcates post-food focal search and general search. In typical implementations of interval timing procedures, trials are externally initiated (EI) after a pre-defined inter-trial interval, such that subjects may be in post-food focal search or general search at the beginning of the trial. If a subject is still in post-food focal search at trial initiation, the transition from general search to pre-food focal search would happen later in the interval, because a transition between post-food focal search and general search would have to happen first. Thus, variability in timing performance would reflect the variability of both post-food focal search and general search durations; that is, it would reflect variability in motivation and timing, not just in timing. As such, pre-feeding would be expected to exacerbate the likelihood that subjects are in post-food focal search following trial initiation, delaying and increasing the variability of transitions from general search to pre-food focal search.

To avoid confounding motivational and timing effects, subjects may be trained to self-pace trials in response-initiated (RI) interval timing procedures (e.g., Fox & Kyonka, 2013, 2015, 2016; Mechner & Guevrekian, 1962; Mechner, Guevrekian, & Mechner, 1963; Mechner, 1994; Shull, 1970). In these procedures, trial initiation is contingent upon a specific action, ensuring

that subjects are in general search and not post-food focal search at the beginning of the trial. Despite this theoretical advantage of RI procedures, no study has explicitly determined whether timing performance in RI and EI interval timing procedures are differentially sensitive to fluctuations in motivation. We hypothesized that RI interval timing procedures dissociate motivation and timing, thereby (a) facilitating temporal control of target responses and (b) yielding target responses that are robust to fluctuations in motivation. That is, RI procedures are expected to circumscribe the effect of fluctuations in motivation to the time it takes to emit a trial-initiating response—the latency-to-initiate (LTI)—while yielding robust timing performance indices. We refer to this implication of Timberlake’s behavioral systems framework as the *RI hypothesis*.

Experiment 1: Response-Initiated Discrete-Trials Switch-Timing

We tested the RI hypothesis by comparing, under two levels of motivation, the performance of rats trained in a RI discrete-trials switch-timing task to performance of rats trained in an EI discrete-trials switch-timing task. Specifically, hungry rats initiated switch-timing trials for themselves and for other hungry rats by pressing the Short-FI lever. Following acquisition of stable performance, rats were exposed to a single 1-h pre-feeding probe. Rats that initiated trials, compared to those who did not, were expected to produce more consistent LTSs and LTDs that are also more robust to pre-feeding. Pre-feeding was expected to selectively lengthen the LTIs of rats that initiated trials.

Methods

Subjects

Twenty-four male Wistar rats (Charles River Laboratories, Hollister, CA) served as subjects. Rats arrived on postnatal day 60 and were triple-housed immediately upon arrival. Rats

were housed on a 12:12 h light cycle, with dawn at 1900 h; all behavioral training was conducted during the dark phase of the light cycle, starting at approximately 0800 h and ending at approximately 1000 h. Following four days of acclimation to the colony room, food access was reduced daily from 24 to 18, 12, and finally 1 h/day. Food was placed on home-cages 30 min after the end of each experimental session and taken away 1 h later. This ensured that at the beginning of the next session weights were, on average, 85% of *ad libitum* weights, as estimated from growth charts provided by the breeder. Water was always available in home-cages. All animal handling procedures used during this study followed National Institutes for Health Guidelines and were approved by the Arizona State University Institutional Animal Care and Use Committee.

Apparatus

Experiments were conducted in 12 MED associates (ST. Albans, VT, USA) modular test chambers (8 chambers measured 305 mm long, 241 mm wide, and 210 mm high; 4 chambers measured 305 mm long, 241 mm wide, and 292 mm high), each enclosed in a sound- and light-attenuating box equipped with a ventilation fan that provided masking noise of approximately 60 dB. The front and back walls and the ceiling of test chambers were made of Plexiglas; the front wall was hinged and served as a door to the chamber. One of the two aluminum side panels served as a test panel. The floor consisted of thin metal bars positioned above a catch pan. The reinforcer receptacle was a square opening (51-mm sides) located 15 mm above the floor and centered on the test panel. The receptacle provided access to a dipper (MED Associates, ENV-202M-S) fitted with a cup (MED Associates, ENV-202C) that could hold 0.01 cc of a liquid reinforcer (~33% sweetened condensed milk diluted in tap water; Kroger, Cincinnati, OH). The receptacle was furnished with a head-entry detector (ENV-254-CB). A multiple-tone generator

(MED associates, ENV-223) was used to produce a 15-kHz tone at approximately 75 dB through a speaker (MED Associates, ENV-224 AM) centered on the top of the wall opposite the test panel and 240 mm above the floor of the chamber. Two retractable levers (ENV-112CM) flanked the reinforcer receptacle. Lever presses were recorded when a force of approximately 0.2 N was applied to the end of the lever. Three-color light stimuli (ENV-222 M) were mounted above each lever; they could be illuminated yellow, green, and red (only yellow was used in the present experiment). A house light located behind the wall opposite to the test panel could dimly illuminate the test chambers. Experimental events were arranged via a MED PC® interface connected to a PC controlled by MED-PC IV® software.

Procedure

Training sessions occurred 7 days/week. Each session began with a 3-min warmup period during which the houselight was illuminated.

Lever shaping. Immediately following the warmup period, the houselight was turned off and the first trial began with the delivery of 5 s of access to reinforcement, which was counted from the detection of a head-entry into the reinforcement receptacle. Further reinforcement was scheduled on a variable time 45-s inter-trial interval (ITI). Both the left and right levers were extended for 8 s prior to the delivery of reinforcement. If either lever was pressed during the 8-s presentation, the levers were immediately retracted, and reinforcement delivered. This phase continued until rats were reliably obtaining reinforcement from the reinforcement receptacle and pressing at least one of the levers. The houselight remained lit throughout the entire session.

Yoked-Trials Training. Rats were randomly assigned to groups Short FI-lever response-initiated (SL-RI; $n = 12$) and externally-initiated (EI; $n = 12$). Trials in groups SL-RI and EI were

mutually yoked: for each yoked pair of SL-RI and EI rats, the SL-RI rat initiated every trial for both rats but could not initiate trials until both the SL-RI and the EI rat had completed the preceding trial and ITI. Trial availability was signaled to SL-RI rats by turning off the houselight and extending both levers. One lever was designated the initiation lever (left for half of the SL-RI rats, right for the other half); pressing it while the houselight was off initiated a trial. Trial-initiating responses (a) illuminated the yellow light above both levers for the SL-RI and yoked EI rat, (b) turned off the houselight and extended both levers for the yoked EI rat, and (c) activated a fixed-interval (FI) 2-s schedule of reinforcement on either the left or right lever (selected by sampling without replacement from a 6-item list) for both rats; extinction was programmed in the other lever. Completion of the schedule turned off the yellow lights, retracted the levers, and activated the dipper. The dipper was deactivated 2.5 s after a head-entry was detected. Following reinforcement, a house-light lit ITI commenced that was at least 2-s long but continued until both rats completed the preceding trial. SL-RI rats then initiated the next trial as described above. The ITI for EI rats was thus equal to the time it took SL-RI rats to initiate trials plus the latency-to-initiate (LTI). This phase continued until SL-RI rats were reliably initiating trials and all rats in both groups were reliably lever pressing.

FI 8-s FI 16-s Baseline Training. Rats were trained on a dependent concurrent FI 8-s FI 16-s schedule of reinforcement. Trials were organized as described in *Yoked-Trials Training*, except that the FI 2-s FI 2-s schedule was replaced with a FI 8-s FI 16-s schedule. For SL-RI rats, FI 8-s was programmed on the initiation lever; for half of the EI rats, FI 8-s was programmed on the left lever; for the other half, FI 8-s was programmed on the right lever. This training continued for a minimum of 20 sessions and until the median, interquartile range (IQR = difference between third and first quartile, or $Q3 - Q1$), and coefficient of quartile variance [$CQV = IQR /$

($Q3 + Q1$)] of latencies to switch (LTSs; time to first response on the FI 16-s; Figure 1B) were deemed stable. Stability was defined as a non-significant ($p > .05$) regression over the last 5 days for LTS medians, IQRs, and CQVs.

Prefeeding Probe. In a single session immediately following detection of stability, rats were provided access to food for an hour prior to, instead of after, the session.

Data Analysis

The distribution of LTDs and LTSs in *FI 8-s FI 16-s Baseline Training* stabilized after 29 training sessions. The last five days of training were used to characterize baseline performance and the single session pre-feeding probe characterized the effect of pre-feeding. For each feeding regimen (baseline, pre-feeding), the dependent measures listed in Table 1 were directly tagged or calculated from the distribution of responses across the Short-FI and Long-FI levers in Long-FI trials; Short-FI trials were not included because LTSs are not typically observed in Short-FI trials. Specifically, the median, inter-quartile range (IQR: 3rd quartile – 1st quartile), and coefficient of quartile variation [$CQV = IQR / (3^{rd} \text{ quartile} + 1^{st} \text{ quartile})$] of LTDs and LTSs were analyzed because such metrics are robust to outliers and proportional to the mean, standard deviation (SD), and coefficient of variation (CV) when data are approximately normally distributed (Huber, 1972). Whereas LTDs and LTSs assessed timing performance, median LTIs assessed pre-feeding induced fluctuations in motivation. Additionally, to assess overall schedule control from temporal control we analyzed start and persistence ratios. The start ratio was defined as the proportion of trials in which the first response on the Short FI occurred before the first response on the Long FI; the persistence ratio was defined as the proportion of trials in which the last response on the Short FI was followed by rather than preceded by the first response on the Long FI.

All dependent measures listed in Table 1 were log or log-odds transformed and then analyzed via Bayesian variants of traditional null-hypothesis significance tests (ANOVA and *t*-tests) in JASP (Love et al. 2016). Bayesian analyses were conducted because they reduce the impact of outliers, missing data, and allow for evidential support to be quantified for both the alternative and null hypotheses (for in-depth descriptions of these tests, see Kruschke, 2014; Rouder, Morey, Speckman, & Province, 2012; Rouder, Morey, Verhagen, Swagman, & Wagenmakers, 2016). Briefly, in Bayesian analyses, posterior distributions of parameters of a likelihood function are generated through the convolution of a likelihood function (e.g., the equations and distributions specified by ANOVA and *t*-tests) and prior distributions characterizing prior knowledge about the parameters of those likelihood functions. Although JASP allows for some level of control over the prior distribution in these tests, default settings of JASP were retained. The default settings assume diffuse priors reflecting little knowledge of potential effects, thereby letting the data determine the outcome of analyses.

A model-selection approach was implemented wherein information from the Bayesian analyses are used to calculate Bayes Factors (BF)—a model selection metric that characterizes the strength of evidence for a given alternative model (*i*) relative to the null model (0). More formally, a BF is the ratio of the probability of a model given the data over the probability of a competing alternative model, such as the null hypothesis, given the same data (Kass & Raftery, 1995). Importantly, each potential effect contained within an analysis can be recast as a model embodying that effect. For example, in a dependent samples *t*-test assessing the effect of feeding regimen (baseline, pre-feeding) there is a null-hypothesis model that assumes no effect of feeding regimen, and an alternative hypothesis model that assumes an effect of feeding regimen. Similarly, in a 2 (initiation type: EI, SL-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) repeated

measures Bayesian ANOVA there are five potential models: a null-hypothesis model, an initiation-type model, a feeding-regimen model, an initiation-type + feeding-regimen model, and an initiation-type $\times$ feeding-regimen model.

Typically, a $BF \geq 3$ is taken as an indication of substantial evidence for a specific model (Kass & Raftery, 1995). BFs were natural-log transformed such that models with a natural-log BF ($\ln BF_{i0}$, nomenclature adopted from Jarosz & Wiley, 2014) $\geq +1.098$ were considered as having substantial evidential support and models with a $\ln BF_{i0} \leq -1.098$ were considered as indicating substantial evidential support for the null model. Any $\ln BF_{i0}$ s between $+1.098$ and -1.098 were considered as not providing enough evidential support to make any strong claim, although the direction may indicate a tendency toward supporting the alternative or null hypothesis.

In each analysis, each i th model was compared to the null (0) model; models with a $\ln BF_{i0} \geq 1.098$ were considered candidate models. If there was more than one candidate, the $\ln BF_{i0}$ s were compared among candidate models, with the candidate model with fewest free parameters² serving as a reference. For a more complex model to be chosen, the $\ln BF_{i0}$ of the more complex model had to be at least 1.098 units larger than the $\ln BF_{i0}$ of the simpler model. This process continued until the model with the largest $\ln BF_{i0}$ and the fewest number of free parameters was selected.

Note that wherever there existed *a priori* predictions in baseline, models were selected in two stages. In the first stage, models were selected from an omnibus ANOVA or *t*-tests

² Whereas a model containing only a feeding regimen parameter has 1 free parameter, a model containing an initiation type $\times$ feeding regimen parameter has 3 free parameters. This is because of the hierarchical nature of ANOVA, a model with an interaction parameter must also contain parameters for the main effects.

describing performance with parameters only available in baseline (e.g., initiation type). In the second stage, models were selected from an omnibus ANOVA describing performance with parameters available in both feeding regimens (e.g., initiation type and feeding regimen). However, the null model of this analysis included all the parameters from the baseline analysis such that what was estimated was whether adding feeding regimen to or having feeding regimen interact with parameters of the previous model improved the overall fit. Otherwise, tests were conducted in a manner consistent with experimental design and available data.

Results

Is switch-timing performance differentially sensitive to feeding regimen as a function of initiation type?

Figure 3A-F shows the baseline median, IQR, and CQV of LTDs and LTSs of each rat as a function of initiation type (EI, SL-RI). SL-RI was predicted to enhance temporal control of LTDs and LTSs. However, Bayesian independent *t*-tests provided little evidence for an initiation-type model describing LTD and LTS variability (i.e., IQRs and CQVs; largest $\ln BF_{10} = -0.845$), suggesting that SL-RI and EI rats produced similarly variable LTDs and LTSs. Likewise, there was little evidence for an initiation-type model describing LTD and LTS medians (largest $\ln BF_{10} = -0.338$).

Figure 3G-L shows the difference between Pre-feeding (PF) and Baseline (B) for the median, IQR, and CQV of LTDs and LTSs of each rat as a function of initiation type (EI, SL-RI). SL-RI, but not EI, was predicted to result in LTDs and LTSs robust to changes in motivation. Bayesian 2 (initiation type: SL-RI, EI) $\times$ 2 (feeding regimen: baseline, pre-feeding) mixed model ANOVAs revealed that LTD medians ($\ln BF_{10} = -1.038$) but not LTS medians

($\ln BF_{10} = 2.184$) were robust to pre-feeding regardless of initiation type. Interestingly, both LTS and LTD variability (i.e., IQRs and CQVs) were insensitive to pre-feeding (largest $\ln BF_{10} = 0.566$). These results suggest that the sensitivity of LTDs and LTSs to changes in motivation does not depend on initiation type.

Are LTIs, start ratios, and persistence ratios affected by initiation type or feeding regimen?

Figure 4A, C, and E shows the baseline median latency-to-initiate (LTI), start ratio, and persistence ratio of each rat as a function of initiation type (EI, SL-RI); Figure 4B, D, and F shows the difference between Pre-feeding (PF) and Baseline (B) for the LTI, start ratio, and persistence ratio of each rat as a function of initiation type (EI, SL-RI). LTIs were predicted to increase with pre-feeding. However, Bayesian dependent t -tests revealed substantial evidence for the null model ($\ln BF_{10} = -1.246$), indicating that LTIs were in fact robust to pre-feeding. Bayesian 2 (initiation type: EI, SL-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) mixed model ANOVAs revealed little evidence for any effect of initiation type or feeding regimen on start and persistence ratios (largest $\ln BF_{10} = 0.076$). This indicates that despite pre-feeding elongating LTSs, SL-RI and EI rats started on the Short FI and remained on the Long FI after a switch equally as often.

Discussion

Experiment 1 revealed little evidence supporting the RI hypothesis, indicating that the SL-RI discrete-trials switch-timing procedure does not dissociate motivation and timing. Relative to those of EI rats, LTDs and LTSs of SL-RI rats were neither under greater temporal control nor were they more robust to pre-feeding. Additionally, LTIs of SL-RI rats were not sensitive to pre-feeding. These data may suggest that neither the pre-feeding manipulation nor the initiation-type manipulation were effectively implemented. Nonetheless, LTSs but not LTDs

were sensitive to pre-feeding, regardless of initiation type. This effect suggests that pre-feeding was sufficient to affect performance, albeit in an unexpected way. It cannot be ruled out, on the other hand, that the initiation-type manipulation (trial onset contingent on pressing Short FI lever vs. passage of variable time) was too weak to reveal initiation-type effects.

The observed insensitivity of trial-initiating responses to changes in motivation is incongruent with extant data (Fox & Kyonka, 2014; Mechner & Guevrekian, 1962; Mazur et al., 2014; Watterson et al., 2015). However, there is a critical difference between the present implementation of SL-RI switch-timing and the RI procedures implemented in previous studies. In the present study, reinforcement followed half of the lever insertions 8 s later. Associating lever insertion with imminent reinforcement is known to promote the attribution of incentive value to levers (Beckmann & Chow, 2015; Davey & Cleland, 1982; Holland, 1977), which in turn promotes interaction with the levers and facilitation of habit development (Everitt & Robbins, 2005; Vandaele, Pribut, & Janak, 2017); habits are insensitive to manipulation by disruptors such as pre-feeding (Dickinson 1985; Vandaele, Pribut, & Janak, 2017). Given that habit development is also facilitated by extended training (Dickinson 1985; Yin & Knowlton, 2006), it is likely that trial-initiating responses were insensitive to pre-feeding because (a) in the SL-RI switch-timing procedure lever insertion was a reliable cue for both trial initiation and imminent reinforcement, and (b) the trial-initiating response was extensively trained prior to pre-feeding, and was trained for longer than switch-timing. Importantly, these hypotheses suggest that a free-operant design, in which discriminative stimuli other than levers signal trial availability and imminent reinforcement, would restore the sensitivity of trial-initiating responses, and thus SL-RI LTIs, to pre-feeding.

Although the discrete-trial design of SL-RI switch-timing may explain the insensitivity of the trial-initiating response to pre-feeding, it does not necessarily explain the failure of SL-RI to enhance temporal control. It is possible that the failure to enhance interval timing was due to some generalization between trial-initiating responses and target responses. Trial-initiating responses differed from Long-FI target responses in time (trial-initiating responses happened earlier in the interval) and location; they had, however, similar topographies. This similarity may have promoted response generalization, such that initiating responses were sometimes associated with reinforcement later in the interval, and target responses were sometimes associated with trial initiation. As such, generalization between initiating responses and target responses could have precluded the enhancement of temporal control.

Discriminability of initiating responses and target responses is likely a positive function of the number of dimensions on which initiating responses and target responses differ. We thus hypothesized that as initiating responses become progressively different from target responses, RI is expected to more accurately signal the transition from post-food focal search to general search, and thus to better enhance temporal control and dissociate motivation and timing. We refer to this revised RI hypothesis as the *discriminative RI hypothesis*.

Experiment 2: Response-Initiated Free-Operant Switch-Timing

Experiment 2 tested the discriminative RI hypothesis, and thus whether motivation and interval timing are dissociable. Rats were trained in a multiple RI EI switch timing procedure in which manipulanda were always available, and active manipulanda were signaled by discriminative stimuli. Initiating responses were discriminable from target responses as a function of either two or three dimensions. Rats were trained with EI, SL-RI, and nose-poke RI (NP-RI), where SL-RI is discriminable from target responses as a function of time and location

(as in Experiment 1), and NP-RI is discriminable from target responses as a function of time, location, and form. Motivation was manipulated via 1 h and 24 h pre-feeding probes; the different pre-feeding durations were included in case the 1 h pre-feeding probe from Experiment 1 was ineffective. Extinction probes were also included to determine whether RI selectively dissociates motivation and timing, or more generally dissociates timing and non-timing processes.

Compared to EI, NP-RI was predicted to improve temporal control of LTDs and LTSs and protect LTDs and LTSs from pre-feeding. Because NP-RI is more discriminable from target responses than SL-RI, SL-RI was predicted to have the same effects, but to a lesser degree. NP-RI and SL-RI LTIs were predicted to be sensitive to pre-feeding and extinction, but LTIs in NP-RI were predicted to be more sensitive to pre-feeding and extinction than SL-RI. Additionally, it was predicted that if RI generally dissociates non-timing and timing processes rather than selectively dissociating motivation and timing, then NP-RI should protect LTDs and LTSs from extinction, and so should SL-RI, but to a lesser degree.

Methods

Subjects

Eight naïve male Sprague Dawley rats (Charles River Laboratories, Hollister, CA) served as subjects. Subjects arrived on post-natal day (PND) 61 and were immediately pair-housed in a vivarium on a reverse 12:12 h light cycle, with lights on at 1900 h. All behavioral training was conducted during the dark phase of the cycle, starting at approximately 1130 h and ending approximately at 1330 h. Following four days of acclimation to the colony room, food access was reduced daily from 24 to 18, 12, and finally 1 hour per day. Food was placed on home-cages

30 min after the end of each experimental session and taken away 1 hour later. This ensured that at the beginning of the next session weights were, on average, 85% of *ad libitum* weights, as estimated from growth charts provided by the breeder. Water was always available in home-cages. All animal handling procedures used during this study followed National Institutes for Health Guidelines and were approved by the Arizona State University institutional Animal Care and Use Committee.

Apparatus

Experiments were conducted in 8 of the 12 MED Associates (St. Albans, VT, USA) modular test chambers detailed in Experiment 1 (Chapter 2; 2 chambers were 305 mm long, 241 mm wide, and 210 mm high; 4 chambers were 305 mm long, 241 mm wide, and 292 mm high). Chambers were modified to include a nose-poke device (ENV-114M) at the bottom of the panel opposite the response panel containing the levers and reinforcement receptacle, flush with the floor. This device could be internally illuminated with green, yellow, and/or red LEDs.

Procedure

All experimental sessions were 2 h long and began with a 3-min warm-up. During this warm-up period, no stimuli were activated.

Reinforcer Shaping. Rats were initially acclimated to the operant chambers and trained to obtain reinforcement. After the 3-min warm-up, a single reinforcer was delivered by raising the liquid dipper. A single head-entry into the reinforcement receptacle broke an infrared beam, 10 s later the liquid dipper was lowered and a fixed-time 90-s inter-trial interval (ITI) commenced.

Manipulandum Shaping. After a single day of *Reinforcer Shaping*, rats were shaped to press levers and nose poke the nose-poke device using a Pavlovian conditioned approach procedure.

After the 3-min warm-up, a 1-kHz tone was activated, and a single reinforcer was delivered. A single head-entry into the reinforcement receptacle broke an infrared beam; 5 s later the liquid dipper was lowered, the 1-kHz tone deactivated, and a variable-time 45-s ITI commenced. At the end of each ITI, a single manipulandum (i.e., left lever extended, right lever extended, or all lights in the nose-poke device) was pseudo-randomly selected from a list, such that no manipulandum could be selected in more than six consecutive trials; the selected manipulandum was activated. If 8 s elapsed after manipulandum activation, the manipulandum was deactivated (i.e., left lever retracted, right lever retracted, lights in the nose-poke device turned off), the 1-kHz tone was turned on, and a single reinforcer delivered. Alternatively, if a response was made on the active manipulandum before 8-s elapsed (i.e., a lever press on the activated lever, or a nose poke on the nose-poke device) the manipulandum was deactivated, the 1-kHz tone was turned on, and a single reinforcer delivered.

Lever Press and Nose Poke Training. After four days of *Manipulandum Shaping*, rats were trained to press the left and right lever and nose poke the nose-poke device for reinforcement. After the 3-min warmup, a single manipulandum was pseudo-randomly selected and activated, as described in *Manipulandum Shaping*. Following a single response on the active manipulandum, the manipulandum was deactivated, the 1-kHz tone was activated, and a single reinforcer delivered. A head-entry into the reinforcement receptacle deactivated the 1-kHz tone and lowered the liquid dipper 2.5 s later. After the liquid dipper was lowered, a fixed-time 5-s ITI commenced.

Response-Initiated Switch-Timing Shaping: Response-Initiation. After four days of *Lever Press and Nose Poke Training*, rats were trained to initiate switch-timing trials. After the 3-min warmup, both levers and the nose-poke device were activated. Initiation types were signaled by

activating one of three tones (3-kHz, 8-kHz, or 15-kHz), pseudo-randomly sampled from a list such that no initiation type could occur in more than six consecutive trials. Each tone indicated whether the trial was initiated by nose poking the nose-poke device (NP-RI), pressing the Short-FI lever (SL-RI; see *Switch Timing* below), or waiting for the experimenter to initiate the trial (EI). EI trials were initiated after 2.5 s since tone onset, and until rats had ceased to press the levers and nose poke the nose-poke device for 0.25 s. The initiation type signaled by each tone was counterbalanced across all rats such that no tone served as the signal for a specific initiation type in more than 2-3 rats.

Switch-Timing. Following trial initiation, the active tone was deactivated, the houselight illuminated for either a fixed-interval (FI) 1-s (Short FI) or a FI 4-s (Long FI), pseudo-randomly sampled from a list such that neither FI occurred in more than four consecutive trials within an initiation type, and in no more than 12 consecutive trials across initiation types. For some rats, the left lever delivered reinforcement according to the Short FI and the right lever delivered reinforcement according to the Long FI, and vice versa for the other rats. This assignment was also counterbalanced across tone-initiation assignment, such that within each pattern of tone-initiation assignment there was at least one rat for which the Short FI was programmed on the left lever and one rat for which the Long FI was programmed on the left lever. The first press on the active FI lever after the active FI elapsed turned off the houselight and delivered a single reinforcer. A head-entry into the reinforcer receptacle broke an infrared beam and then deactivated the dipper 2.5 s later. This was immediately followed by a tone signaling the next initiation type. The ITI was thus equal to the time it took rats to initiate trials in NP-RI and SL-RI, and equal to the time it took rats to quit lever pressing or nose poking in EI, with a minimum ITI of 2.5 s. Collectively, these are referred to as latencies-to-initiate (LTI).

Punishment. Prescribed performance in the switch-timing procedure involves responding first on the Short FI and eventually switching over to the Long FI. To encourage this sequence, trials were terminated without reinforcement if (a) the first response after trial initiation was on the Long FI, (b) if the Short FI was active and a response was made on the Long FI at any point during the trial, or (c) if the Long FI was active and a response was made on the Short FI after a response on the Long FI.

Training Order. Rats were trained such that reinforcement was initially contingent upon FI 1-s FI 4-s only in EI; NP-RI and SL-RI were terminated with reinforcement following initiating responses. Reinforcement contingent upon FI 1-s FI 4-s in NP-RI and SL-RI was slowly introduced as rats learned to correctly respond in the presence of the tone and engage in switch-timing FI 1-s FI 4-s in the presence of the houselight. This was assessed by inspecting the number of obtained reinforcers in the previous two sessions; if rats earned more than 600 reinforcers, FI 1-s FI 4-s was introduced following SL-RI and then following NP-RI.

Switch-Timing Training. Once rats were trained on FI 1-s FI 4-s in all initiation types, they were trained up to the timing conditions of interest in the following order: FI 4-s FI 12-s A, FI 6-s FI 18-s, and FI 4-s FI 12-s B. All rats experienced the same order of conditions; the two FI 4-s FI 12-s conditions allowed for assessment of potential order effects. Punishment continued as described in *Response-Initiation and Switch-Timing Shaping*, until subjects had experienced a minimum of 5 sessions of training with punishment in each condition and until performance was deemed stable. Punishment was then removed, and subjects were trained for a minimum of 7 sessions and until performance was again deemed stable. Stability was assessed visually and confirmed via a non-significant regression of the critical dependent measures as described in Experiment 1.

Single-Initiation Type Testing: Pre-feeding. Following confirmation of stable performance in the FI 4-s FI 12-s A and the FI 6-s FI 18-s timing conditions, 5 sessions were conducted using a single initiation type (EI, SL-RI, or NP-RI), then 5 more sessions were conducted using only another initiation type, and 5 more sessions were conducted using only the third initiation type. The order in which initiation types were implemented was counterbalanced. In each block of five sessions, the first and second sessions served as baselines and the third and fourth sessions served as 1-h and 24-h pre-feeding probes, respectively. In the 1-h PF, rats were given continual access to food at their home-cages 1 h immediately prior to testing. In 24-h PF, rats were given continual access to food at their home-cages 24 h prior to testing. To return to baseline performance on the fifth session, rats were not given 1 h of post-experimental feeding after the 24 h pre-feeding probe. The fifth session was not used in data analysis. At the end of testing, rats were returned to *Switch-Timing Training*.

Yoked-ITI Pre-feeding. Following confirmation of stable performance in the FI4-s FI 12-s B schedule, rats were tested as described in *Pre-feeding*. However, EI ITIs for each rat were changed from 2.5 s to a list containing the 1st, 2nd (median), and 3rd quartiles of the same rats' NP-RI LTIs during pre-feeding portion of *Pre-feeding* in the FI 4-s FI 12-s A (first determination) condition.

Extinction. Immediately following *Yoked-ITI Pre-feeding*, rats started another round of 15 *Single-Initiation Type Testing* sessions; EI LTIs were returned to their original length of 2.5 s. Pre-feeding probes were substituted with extinction sessions, wherein the liquid dipper normally containing sweetened condensed milk was empty.

Data Analysis and Results

Single-Initiation Type Testing began on session 51 for FI 4-s FI 12-s A, session 104 for FI 6-s FI 18, and session 136 for FI4-s FI 12-s B. Dependent measures were analyzed and calculated as described in Experiment 1 in addition to a new dependent measure: the discrimination ratio (DR), which was defined for each initiation types as the number of trials in which the first response was the correct initiating-response divided by the total number of trials; see Table 1. Additionally, due to equipment malfunction, Rat 5 had only 1 baseline session prior to pre-feeding in the SL-RI FI 6-s FI 18-s condition and Rat 4 had only 1 baseline session prior to pre-feeding in the SL-RI FI 4-s FI 12-s B condition.

The number of completed trials under 1-h and 24-h pre-feeding was substantially less than baseline, on average a 2- to 3-fold decrease. To determine whether 1-h and 24-h pre-feeding sessions could be collapsed into a single pre-feeding factor for analysis, the effect of feeding duration on LTDs, LTSs, and LTIs was assessed via Bayesian dependent *t*-tests within each switch-timing condition and initiation type. There was little evidence for a feeding duration model describing LTD and LTS dependent measures, or LTIs ($-1.090 \leq \ln BF_{10} \leq 0.946$), suggesting that switch-timing performance was similar across pre-feeding durations. Thus, the 1-h and 24-h pre-feeding sessions were collapsed into a single factor of pre-feeding for all dependent measures. Data were analyzed as described in Experiment 1.

Is switch-timing performance differentially sensitive to feeding regimen as a function of initiation type?

Figure 5A-F shows the baseline median, IQR, and CQV of LTDs, and LTSs for each rat as a function of the Long FI in each timing condition (FI 12-s A, FI 18-s) and initiation type (EI, SL-RI, NP-RI). NP-RI was predicted to enhance temporal control of LTDs and LTSs relative to SL-RI and EI, SL-RI was predicted to enhance temporal control of LTDs and LTSs relative to EI. To asses this prediction, LTS and LTD dependent measures were submitted to a 3 (initiation

type: EI, SL-RI, NP-RI) $\times$ 2 (timing: FI 4-s FI 12-s A, FI 6-s FI 18-s) Bayesian repeated measures ANOVAs. These revealed substantial evidence for a timing model describing LTD medians ($\ln BF_{10} = 7.292$) and IQRs ($\ln BF_{10} = 3.225$) and LTS medians ($\ln BF_{10} = 43.275$) and IQRs ($\ln BF_{10} = 7.508$), indicating that LTD and LTS medians and IQRs scaled with the timing condition. Correspondingly, there was no substantial evidence for a timing, initiation type, timing + initiation type, or a timing $\times$ initiation type model describing LTD CQVs (largest $\ln BF_{10} = 0.951$) or LTS CQVs (largest $\ln BF_{10} = -0.055$), suggesting that CQVs were relatively invariant to both initiation type and timing conditions.

Figure 5G-L shows the pre-feeding – baseline median, IQR, and CQV of LTDs and LTSs for each rat as a function of the Long FI in each timing condition (FI 12-s A, FI 18-s), and each initiation type (EI, SL-RI, NP-RI). NP-RI was predicted to protect LTDs and LTSs from changes in motivation more than SL-RI, and SL-RI was predicted to protect LTDs and LTSs from changes in motivation more than EI. To assess these predictions, LTD and LTS dependent measures were submitted to 3 (initiation type: EI, SL-RI, NP-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) $\times$ 2 (timing: FI 12-s A, FI 18-s) Bayesian repeated measures ANOVAs. These analyses revealed substantial evidence for adding a feeding regimen parameter to the model describing LTD medians ($\ln BF_{10} = 10.776$), IQRs ($\ln BF_{10} = 18.439$), and CQVs ($\ln BF_{10} = 5.329$), indicating that LTDs increased with pre-feeding. These analyses also revealed substantial evidence for adding an initiation type $\times$ feeding regimen parameter to the model describing LTS medians ($\ln BF_{10} = 16.681$), indicating that whether LTSs were affected by pre-feeding depended on initiation type. Dependent *t*-tests probing this interaction revealed substantial evidence for adding a feeding regimen parameter to the model describing LTS medians in EI ($\ln BF_{10} = 7.960$) and SL-RI ($\ln BF_{10} = 2.677$) but not NP-RI ($\ln BF_{10} = 0.259$), indicating that pre-feeding increased

the median LTSs in EI, less so in SL-RI, and substantially less so in NP-RI. There was also substantial evidence for adding a feeding regimen parameter to the model describing LTS IQRs ($\ln BF_{10} = 24.870$) and CQVs ($\ln BF_{10} = 20.528$), indicating that pre-feeding resulted in more variable LTSs in all initiation types.

Taken together, these data suggest that LTDs and LTSs scaled as expected from FI 4-s FI 12-s A to FI 6-s FI 18-s. Although LTDs and LTSs in SL-RI and NP-RI were not under greater temporal control relative to LTSs in EI, LTS medians in NP-RI but not SL-RI or EI were robust to pre-feeding. LTS medians in SL-RI were less robust to pre-feeding than LTS medians in NP-RI but more robust to pre-feeding than LTS medians in EI. Interestingly, LTS variability increased with pre-feeding in all three initiation types. Additionally, Short FI performance was affected by pre-feeding: LTD medians, IQRs, and CQVs were all elevated with pre-feeding.

Are latencies-to-initiate, discrimination ratios, start ratios, and persistence ratios affected by initiation type, feeding regimen, or timing condition?

Figure 6A-H shows baseline individual median LTIs, discrimination ratios, start ratios, and persistence ratios, and their change with pre-feeding, as a function of timing condition (FI 12-s A, FI 18-s), and initiation type (EI, SL-RI, NP-RI). LTIs were predicted to be sensitive to pre-feeding, but NP-RI LTIs were expected to be more sensitive to pre-feeding than SL-RI LTIs. To assess this prediction, LTIs were submitted to a 2 (initiation type: SL-RI, NP-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) $\times$ 2 (timing: FI 12-s, FI 18-s) Bayesian repeated measures ANOVA. This analysis revealed substantial evidence for an initiation type + feeding regimen + timing model describing LTIs ($\ln BF_{10} = 24.676$), indicating that NP-RI LTIs were longer than SL-RI LTIs and that both NP-RI LTIs and SL-RI LTIs increased with pre-feeding and timing conditions. It is worth noting that when inspected individually, LTIs are more sensitive to pre-feeding regimen ($\ln BF_{10} = 9.885$) than timing ($\ln BF_{10} = 1.781$) or initiation type ($\ln BF_{10} = 4.753$).

Discrimination ratios were well above 0.33 for all rats in all initiation types. This indicates that rats adequately learned to discriminate tone-initiation type associations. To determine whether discrimination of these tone-initiation type associations was affected by initiation type, feeding regimen, or timing condition, discrimination ratios were submitted to 3 (initiation type: EI, SL-RI, NP-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) $\times$ 2 (timing: FI 12-s, FI 18-s) Bayesian repeated measures ANOVAs. These analyses revealed substantial evidence for an initiation type $\times$ timing + initiation type $\times$ feeding regimen model describing discrimination ratios ($\ln BF_{10} = 15.791$). Probes of the initiation type $\times$ timing interaction comparing timing conditions within each initiation type via dependent samples *t*-tests revealed substantial evidence for a timing model describing EI ($\ln BF_{10} = 1.386$) but not SL-RI ($\ln BF_{10} = 0.423$) or NP-RI ($\ln BF_{10} = -1.085$) discrimination ratios, indicating that EI discrimination ratios increased between timing conditions. That is, with extended training the ability of rats to withhold responding for 2.5 s increased. Probes of the initiation type $\times$ feeding regimen model comparing feeding regimen within each initiation type via dependent samples *t*-tests revealed substantial evidence for a feeding regimen model describing EI ($\ln BF_{10} = 5.273$) and NP-RI ($\ln BF_{10} = 2.357$) but not SL-RI ($\ln BF_{10} = -0.091$) discrimination ratios, indicating that EI discrimination ratios increased with pre-feeding and NP-RI discrimination ratios decreased with pre-feeding. Thus, whereas pre-fed rats were more likely to wait the full 2.5 s, pre-fed rats lever pressed more when the initiation tone signaled a nose-poke initiating responses.

It is possible that the selection of models containing parameters for initiation type and/or feeding regimen describing LTDs and LTSs was due to differences in start and/or persistence ratios. To assess whether any of these ratios were sensitive to initiation type, feeding regimen, or timing condition the start and persistence ratios were submitted to 3 (initiation type: EI, SL-RI,

NP-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) $\times$ 2 (timing: FI 12-s, FI 18-s) Bayesian repeated measures ANOVAs. There was substantial evidence for an initiation type + feeding model describing start ($\ln BF_{10} = 6.544$) and persistence ratios ($\ln BF_{10} = 15.096$), indicating that both start and persistence ratios were sensitive to initiation type and reduced by pre-feeding. Post-hoc tests revealed that start ratios were well described by an initiation type model when comparing NP-RI and EI ($\ln BF_{10} = 1.781$), NP-RI and SL-RI ($\ln BF_{10} = 3.318$), but not EI and SL-RI ($\ln BF_{10} = 0.724$), indicating that start ratios were higher in NP-RI than EI or SL-RI. Post-hoc tests also revealed that persistence ratios were well described by an initiation type model when comparing EI and SL-RI ($\ln BF_{10} = 2.805$), NP-RI and SL-RI ($\ln BF_{10} = 7.601$), and NP-RI and EI ($\ln BF_{10} = 2.102$), indicating that persistence ratios were highest in NP-RI, lowest in SL-RI, and intermediate in EI.

Taken together, these data suggest that subjects readily learn to discriminate the tone-initiation type associations; and that interestingly, pre-feeding affects discrimination ratios such that when pre-fed, rats were more likely to wait the full 2.5 s in EI trials, less likely to nose-poke in NP-RI trials, and continued to press the Short FI lever in SL-RI trials. NP-RI appears to enhance but does not yield robust schedule control. Indeed, although pre-feeding increased the latency to initiate RI trials, it also reduced the probability subjects started on the Short FI and the probability subjects persisted on the Long FI after a switch. This suggest that it is possible that some of the effects of initiation type and pre-feeding on LTDs and LTSs are a produce of changes in schedule rather than temporal control.

Are LTS medians robust to pre-feeding when EI ITIs are yoked to pre-feeding-induced longer LTIs?

The previous analysis indicates that LTS medians, but not IQRs and CQVs, were robust to pre-feeding in NP-RI; LTD medians, IQRs, and CQVs were sensitive to pre-feeding

regardless of how trials were initiated. This suggests that RI protects LTS medians from changes in motivation as initiating responses become progressively different from target responses. However, it is also possible that such protection was merely due to a pre-feeding-induced increase of NP-RI LTIs in *Pre-feeding*. To assess this possibility, rats were trained in a second determination of FI 4-s FI 12-s (FI 4-s FI 12-s B) and were then tested in *Yoked-ITI Pre-feeding*, wherein EI ITIs in pre-feeding probes were yoked to NP-RI LTIs in pre-feeding probes from *Pre-feeding* FI 4-s FI 12-s A.

Figure 7A-B shows the median LTI and pre-feeding – baseline median LTS as a function of FI 4-s FI 12-s determination (A, B), within each initiation type (EI, SL-RI, NP-RI). Visual investigation of this figure suggests that the yoking procedure adequately yoked EI LTIs to pre-feeding lengthened NP-RI LTIs from *Pre-feeding*. To determine whether LTSs in EI were robust to pre-feeding when EI LTIs were yoked to NP-RI LTIs, LTS medians were analyzed via 3 (initiation type: EI, SL-RI, NP-RI) $\times$ 2 (feeding regimen: baseline, pre-feeding) $\times$ 2 (determination: FI 4-s FI 12-s A, FI 4-s FI 12-s B) Bayesian repeated measures ANOVAs. Because the previous analyses indicated substantial evidence for an initiation type $\times$ feeding regimen model, the null model of this analysis contained all the parameters of a 2 (feeding regimen: baseline, pre-feeding) $\times$ 3 (initiation type: EI, SL-RI, NP-RI) repeated measures ANOVA to determine the extent to which adding a determination or determination interaction parameter improved model fit. These analyses revealed substantial evidence for adding a determination parameter ($\ln BF_{10} = 2.429$), but not determination $\times$ feeding ($\ln BF_{10} = 1.381$) or determination $\times$ feeding $\times$ initiation type ($\ln BF_{10} = -1.838$) parameter, to the initiation type $\times$ feeding regimen model describing LTSs. The inclusion of a determination parameter indicates that LTSs increased by 0.5 s between FI 4-s FI 12-s determinations, but the effect of pre-feeding

within each initiation type was independent of FI 4-s FI 12-s determination. Thus, the robustness of LTS medians in NP-RI to pre-feeding is attributable to response initiation *per se* rather than to longer and more variable NP-RI LTIs.

Are LTIs, LTDs, and LTSs differentially sensitive to extinction as a function of initiation type?

If initiating responses generally dissociate timing and non-timing processes rather than selectively dissociate timing and motivation, NP-RI should yield LTS medians robust to extinction more than SL-RI and EI. Likewise, SL-RI should yield LTSs robust to extinction more than EI. Additionally, NP-RI LTIs were expected to be more sensitive to extinction than SL-RI LTIs; although nose-pokes and lever-presses delay trial onset following EI, EI LTIs were not expected to be sensitive to extinction. These predictions were assessed visually because inspection of performance under extinction revealed idiosyncratic changes in LTIs and LTSs.

Figure 8A-I shows the mean median LTI, LTD, and LTS as a function of trial under both baseline and extinction sessions in all three initiation types. Whereas NP-RI LTIs and SL-RI LTIs lengthened with extinction, EI LTIs did not. EI LTIs were initially longer than the programmed 2.5 s under baseline and extinction sessions, indicating that at the beginning of each session subjects responded on the levers and nose-poke device when EI was signaled. NP-RI LTIs were initially 7-s and then stepped up to about 35-s. SL-RI LTIs were initially 1.5-s but did not lengthen in a systematic manner, oscillating between very short and very long LTIs. Both NP-RI and SL-RI LTIs returned to 7-s and 1.5-s, respectively, at the beginning of the second extinction session, suggesting the spontaneous recovery of LTIs between consecutive extinction sessions. LTIs do not appear to show evidence of extinction bursts, which would be indicated by a transient shortening of LTIs at the beginning of extinction. Taken together, these data suggest

that both NP-RI LTIs and SL-RI LTIs are sensitive to extinction; NP-RI LTIs may be more sensitive to extinction than SL-RI LTIs.

LTDs and LTSs in all three initiation types lengthened with extinction. Whereas LTDs were initially 6 s and LTSs 8 s, both then increased to about 50 s by the end of each extinction session. Both LTDs and LTSs return to their initial lengths at the beginning of the second extinction session, suggesting spontaneous recovery of both LTDs and LTSs. Thus, these data indicate that neither NP-RI or SL-RI yield LTDs or LTSs robust to extinction.

Discussion

Experiment 2 revealed some evidence supporting the discriminative RI hypothesis. Although overall schedule control was improved in NP-RI compared to SL-RI and EI (Figure 6E and 6G), temporal control of LTDs and LTSs was similar across initiation types (Figure 5E and 5F). Interestingly, the sensitivity of LTSs, but not of LTDs, to pre-feeding scaled with the discriminability of initiating responses from target responses, such that $EI > SL-RI > NP-RI$ (Figure 5H); LTDs were sensitive to pre-feeding under all initiation types (Figure 5G). Both NP-RI and SL-RI LTIs were similarly sensitivity to pre-feeding (Figure 6B). Pre-feeding also reduced schedule control (Figure 6F and G), suggesting that some of the observed effects of pre-feeding on timing may be attributable to reductions in schedule control rather than temporal control. Importantly, the dissociation of motivation and interval timing observed in NP-RI performance is attributable to response initiation *per se*, rather than to longer LTIs (Figure 7). This dissociation was selective, as LTDs and LTSs were sensitive to extinction regardless of the initiating-response (Figure 8). Taken together, these data suggest that, as initiating responses become progressively discriminable from target responses, initiating responses increasingly and

selectively dissociate motivation and timing. Thus, Experiment 2 provides some evidence for the discriminative RI hypothesis.

General Discussion

The purpose of the reported experiments was to test whether motivation and timing are procedurally dissociable. The behavioral systems approach to learning, cognition, and motivation suggests that, whereas general search and pre-food focal search are sensitive to the periodicity of reinforcement, post-food focal search is sensitive to other factors, including fluctuations in motivation. This indicates that if rats are trained to pace their own trials in response-initiated (RI) interval timing procedures, rather than pacing their trials for them in externally-initiated (EI) interval procedures, motivation and timing would be dissociated. This is referred to as the RI hypothesis. According to the RI hypothesis, performance in RI procedures relative to performance in EI procedures should be under greater temporal control and should be robust to fluctuations in motivation, with the effects of the latter circumscribed to the latency-to-initiate in RI procedures. Experiment 1 tested the RI hypothesis.

In Experiment 1, some rats (SL-RI) were trained to initiate their trials and those of other rats (EI) in a switch-timing task. In this task (Fox, Prue, & Kyonka, 2016), there are two potential target responses: the latency-to-switch (LTS) to the later source of food (Long-FI; Daniels et al., 2015b), and the latency-to-depart (LTD) from the earlier source of food (e.g., Balci et al., 2008). After performance stabilized, rats were challenged with a 1-h pre-feeding probe. Surprisingly, SL-RI and EI rats had equally variable LTDs and LTSs (Figure 3C-F) that were also equally sensitive to pre-feeding (Figure 3I-L). However, when taken in the context of previous work, these data indicate that the Short-FI initiating-response may have been too similar to target responses, thus promoting generalization between initiating responses and target

responses. Indeed, although the Short FI initiating-response differs from target responses as a function of time and location, all these responses are lever presses. This consideration led to a revision of the RI hypothesis, the *discriminative* RI hypothesis. According to the discriminative RI hypothesis, as initiating responses become progressively different from target responses, motivation gains selective control over initiating responses and time gains selective control over target responses. Experiment 2 tested the discriminative RI hypothesis.

Experiment 2 added a third interval-initiation condition to those in Experiment 1: initiation via nose-poke response (NP-RI). Whereas SL-RI differed from target responses as a function of only time and location, NP-RI differed from target responses as a function of time, location, and form. The temporal variability of target responses was similar across trial types regardless of motivational state (Figure 5C-F and Figure 5I-L), but—consistent with the discriminative RI hypothesis—the median of NP-RI LTSs was substantially less sensitive to pre-feeding than SL-RI and EI LTSs (Figure 5H). The latency-to-initiate RI trials (LTIs) were more sensitive to changes in motivation than to changes in the time to reinforcement ($\ln BF_{\text{Feeding0}} = 9.885$; $\ln BF_{\text{Timing0}} = 1.781$; cf. Figure 6A with figure 6B); LTSs showed the opposite pattern of sensitivity, greater sensitivity changes in the time to reinforcement than changes in motivation ($\ln BF_{\text{Timing0}} = 76.268$; $\ln BF_{\text{Feeding0}} = 0.486$; cf. Figure 5B and 5D with Figure 5H and 5J); LTDs show the opposite pattern as well, but to a lesser extent than LTSs ($\ln BF_{\text{Timing0}} = 13.513$; $\ln BF_{\text{Feeding0}} = 6.280$; cf. Figure 5A and C with Figure 5G and 5I). LTDs and LTSs, even those in NP-RI trials, lengthened with the removal of reinforcement (Figure 8). Experiment 2 thus provides some evidence for the discriminative RI hypothesis, thereby supporting the notion that motivation and timing are procedurally dissociable.

Importantly, the results of Experiment 2 clarify the results of Experiment 1. Although the sensitivity of SL-RI LTIs to motivational state depends on whether the switch-timing procedure is programmed as a discrete-trials (Experiment 1) or free-operant procedure (Experiment 2), the sensitivity of LTSs to pre-feeding in SL-RI does not (cf. Figure 6B with Figure 4B). Pre-feeding lengthened SL-RI LTIs in Experiment 2 but lengthened LTSs in SL-RI in both Experiments 1 and 2. Short-FI initiating responses in Experiment 1 likely became habitual because of an interaction between prolonged training (Dickinson, 1985) and the levers acting as time-markers (Vandaele et al., 2017), both of which have been documented to promote habitual like behavior (Vandaele, Mahajan, Ottenheimer, Richard, Mysore, & Janak, 2019; Morrison, Bamkole, & Nicola, 2015). This suggests that for LTIs to be sensitive to motivation, the interval must be initiated on manipulanda that do not also serve as time-markers. In contrast, LTSs in SL-RI are likely sensitive to pre-feeding because Short FI initiating responses and target responses are identical in form (both are lever presses), thus likely promoting generalization between Short FI initiating responses and target responses. This suggests that initiating responses need to be highly discriminable and uniquely associated with trial initiation to dissociate motivation and timing; initiating responses should not be confounded with target or other (e.g., consummatory) responses.

The similar levels of temporal control achieved across initiation types in both experiments is inconsistent with the discriminative RI hypothesis but consistent with previous work on RI-FI and RI-peak (Fox & Kyonka, 2013, 2015, 2016). It is worth noting, however, that NP-RI enhanced overall schedule control: start ratios and persistence ratios were higher in NP-RI compared to EI and SL-RI (Figure 6E and 6G). This suggests that even if NP-RI does not enhance temporal control, it at least promotes starting on the Short-FI, switching, and then

persisting on the Long-FI compared to EI and to a lesser extent SL-RI. Such an enhancement cannot be dismissed; although this outcome may be interpreted as consistent with the discriminative RI hypothesis, it was not a formal prediction.

The insensitivity of temporal control to initiating responses may be due to the level of temporal control engendered by the switch-timing task; if temporal control was already at a ceiling, initiating responses would not be expected to further enhance temporal control.

Temporal control was just slightly greater in LTSs than in LTDs (cf. Figures 3E and 5E with Figures 3F and 5F; for Figure 3, focus on the subpopulation with CQVs < 0.2 in LTSs). Previous research has found similar differences in the variability of starts and stops in responding on the peak procedure (e.g., Cheng, Westwood, & Crystal, 1993; Gallistel, King, & McDonald, 2004; Gibbon & Church, 1992), with such differential variability further modulated by alternative sources of reinforcement (Matell & Portugal, 2007; Sanabria, Thraillkill, & Killeen, 2009).

Sanabria, et al. (2009) observed that as alternative sources of reinforcement become richer, starts and stops become less variable; and as the alternative sources of reinforcement becomes leaner, starts and stops become more variable. Such effects appear to be larger for starts than stops. The rich alternative source of reinforcement presumably specifies and controls alternative behaviors that would otherwise interfere with peak timing. By analogy, insofar as the Short-FI is an alternative source of reinforcement when subjects time the Long-FI, it likely specified and controlled alternative behaviors that would have otherwise interfered with the expression of Long-FI performance, thereby enhancing temporal control of switching (LTDs and LTSs) to the Long FI, potentially to a ceiling. Whereas substantial heterogeneity in estimates of temporal control was observed in Experiment 1, a subset of subjects had CQVs < 0.2 ; and almost all subjects displayed high temporal control in Experiment 2 (cf. Figures 3E and F with Figures 5E

and F). This difference is likely a product of the rather stringent reinforcement contingencies implemented during training. Whereas in Experiment 1 subjects could allocate their behavior across the Short FI and Long FI in any pattern, in Experiment 2, only the prescribed behavioral sequence of starting on the Short FI and then switching to the Long FI was reinforced.

The similar sensitivity of LTS variability to motivational state across trial types is also inconsistent with the behavior systems framework. This framework suggests that time spent in post-food focal search is an inverse function of motivation, predicting that response initiation increases the robustness of both timing accuracy and precision, not just accuracy, to fluctuations in motivation. It thus appears that the sensitivity to fluctuations in motivation is not circumscribed to post-food focal search, but may be present also, perhaps to a lesser extent, in subsequent behavioral modes, affecting both dwelling times in each mode and the probability of transitioning between modes. This graded effect appears to be reflected in the stronger pre-feeding effect on LTDs over LTSs (cf. squares in Figure 5G with 5H), and in the stronger effect on NP-RI LTIs over NP-RI LTDs (cf. triangles in Figure 6B with 5G). This revised prediction also suggests a general loss of schedule control consistent with the pre-feeding induced reduction in both start and persistence ratios (Figure 6F and 6H). However, this adjustment of the behavior systems prediction requires a direct test, such as observing how the dynamics of the predatory subsystem respond to fluctuations in motivation.

Nonetheless, further support for the behavioral systems framework comes from an interesting parallel between the present data and those obtained from subjects trained in tandem and chained schedules of reinforcement. Killeen (1994, 1995) argued that motivational effects were likely reflected in pauses between the initiation of responding; and Killeen et al. (2002) argued that such pauses may be indicative of subjects returning to general search and/or post-

food focal search. Although such pauses emerge naturally from the microstructure of responding in interval schedules of reinforcement (Daniels & Sanabria, 2017a; Brackney, Cheung, Neisewander, & Sanabria, 2011; Shull, 2004), these motivation-sensitive pauses are more clearly revealed in chain and tandem schedules, as time spent in an initial link (e.g., Daniels & Sanabria, 2017b; Fischer & Fantino, 1968; Malott 1966; Nevin, Mandel, & Yarensky, 1981). In well trained animals, EI switch-timing may function essentially as a heterogeneous two-link tandem schedule, in which the Short FI serves as the initial link that is “completed” (the actual completion of the FI is not required) before switching to the Long-FI terminal link. This conceptualization suggests that RI switch-timing may function as a three-link schedule in which the initial link must be completed (initiating-response). It is possible that the effect of pre-feeding decays across links, thus yielding the same scaling of pre-feeding sensitivity as suggested in the revision of the behavioral systems prediction. This suggestion predicts that pre-feeding effects should be larger in single schedules of reinforcement than in chain or tandem schedules. Between-experiment comparisons suggests pre-feeding effects are indeed of a greater magnitude in single FI schedules and the peak-procedure (~20 % increase in latencies and peak-times; Daniels & Sanabria, 2017a; Plowright et al. 2000) than switch-timing (~12-15% increase in LTSs); future experiments should aim to replicate and expand upon this finding. Moreover, this implies that motivational effects are modulated by the number of discriminable links in the schedule rather than by the discriminability of initiating responses per se.

The sensitivity of interval timing performance to extinction regardless of initiation type is consistent with the interpretation of EI and RI switch-timing as functionally similar to performance in a chained or tandem schedule in well trained subjects. In the present study, extinction resulted in a lengthening of LTIs, LTDs, and LTSs regardless of initiation type. In

chain schedules, extinction appears to affect performance in both initial and terminal links, and to a greater degree than pre-feeding (e.g. Mansfield & Rachlin, 1970; Nevin et al., 1981). More recently, Thrailkill & Bouton (2015) showed that extinction of either an entire chain or just the initial link is sufficient to reduce responding in terminal links. Additionally, extinction of just the terminal link reduces performance in the initial link (Thrailkill & Bouton, 2016a). Such effects appear to require response emission during extinction, as exposure to just discriminative stimuli in extinction without the opportunity to perform the operant response does not alter performance (Thrailkill & Bouton, 2015, 2016a; Steinfeld, Alcalá, Thrailkill, & Bouton, 2019; for a review see Thrailkill & Bouton, 2016b). Taken together, these data suggest that tandem and chained schedules, such as RI, dissociate motivation and interval timing but not extinction and interval timing (see Killeen, Hall, & Bizo, 1999).

Additionally, the conceptualization of switch-timing as operating as a 3-link tandem schedule of reinforcement in well trained animals may explain one of the interesting discrepancies between Experiments 1 and 2: LTDs were sensitive to pre-feeding in Experiment 2 but not in Experiment 1. In Experiment 1, because of the loose reinforcement contingencies, some animals were well trained, and some animals were not. The spread of start and persistence ratios is much larger in Experiment 1 than in 2, with some animals in Experiment 1 frequently starting at the Long FI rather than at the Short FI schedule, or switching back-and-forth between the Short FI and Long FI schedules in more than half of the trials (cf. Figures 4C and E with Figures 6E and G, respectively). The bimodal distribution of schedule control in Experiment 1 likely reduced the degree to which the switch-timing procedure operated over behavior like 3-link tandem schedule of reinforcement. Such a reduction would reduce the sensitivity of Short-FI responses (and LTDs) to pre-feeding because they were not adequately discriminated from Long-

FI responses. However, this does not mean that better training alone would have facilitated a dissociation of timing and motivation. Indeed, better SL-RI training (Experiment 2) still failed to dissociate timing and motivation³.

Although the behavioral systems account of the present data needs further theoretical formalism and empirical testing, it is worth noting that just as PA models could not suggest a route by which to dissociate interval timing and motivation, PA models cannot easily reconcile the present data. Assuming that performance is governed by a single clock, the obtained pre-feeding effects across LTDs and LTSs in EI and RI switch-timing would force the conclusion that pre-feeding reduces the speed of the clock in proportion to the discriminability of initiating responses or links. Though not unreasonable, an implication of this conclusion is that the magnitude of clock-speed effects should be the same across all measures of interval timing within a specific initiating-type. This is in contrast with the differential pre-feeding effects in LTDs and LTSs in all three initiating-types. Alternatively, it might be assumed, following precedent, that the decision to start responding is relatively independent of the decision to stop responding, and that the decision to start responding is more sensitive to fluctuations in motivation than the decision to stop responding (Balci 2014; Balci, Ludvig, & Brunner, 2010; Balci, Gallistel, Allen, Frank, Gibson, & Brunner, 2009; MacDonald, Cheng, & Meck, 2012; Taylor et al., 2007). This predicts that insofar as LTSs denote when subjects start responding on the Long FI, LTSs should be more sensitive to fluctuations in motivation than LTDs; this was observed in Experiment 1 but not Experiment 2. Additionally, PA models cannot account for

³ Switch-timing training appears to be critical for determining whether inferences about interval timing may be drawn from the distribution of LTDs. Indeed, similar difficulties in interpreting effects on LTDs have been observed elsewhere (e.g., Gupta et al., 2019). In contrast, the sensitivity of LTSs to various manipulations appears to depend less on training (LTS effects in Experiments 1 and 2 were replicated). This suggests that LTSs are a more reliable expression of interval timing. Consistent with this conclusion, and as mentioned elsewhere in the discussion, LTSs are more sensitive to timing than feeding regimen compared to LTDs.

some of the reduced schedule control without assuming non-specific effects of pre-feeding on parameters of PA models. Indeed, without introducing assumptions that cause PA models to perform differently as the interval elapses (such as pre-feeding effects on clock-speeds or response-thresholds decaying as a function of time in the session), thus resembling the behavioral systems framework, PA models cannot account for the present data. Moreover, whereas an expanded PA model would only account for the relationship between timing and motivation, the behavioral systems framework can more generally account for the relationship between motivation and instrumental responding.

There are a few potential limitations of the present study. First, it is possible some of the effects are an artifact of the concomitant pre-feeding-induced reduction in the number of completed trials. Rats completed fewer trials in 1 h than in 24 h pre-feeding, and the number of trials completed scaled such that $EI > SL\text{-}RI > NP\text{-}RI$ in both baseline and pre-feeding. However, there was little evidence that LTS variability differed between the 1 h and 24 h pre-feeding manipulations, and LTS variability in NP-RI was similar to LTS variability in SL-RI and EI. Additionally, in other RI procedures, the variability but not the mean of timing performance is sensitive to pre-feeding even when the number of obtained reinforcers was held constant (e.g., Watterson et al., 2015). Second, motivation was only manipulated via pre-feeding, neglecting other routes by which to alter motivation, such as changes in the magnitude of reinforcement (e.g., Cambraia, et al., 2019; Daniels et al., 2015b). It is thus unclear whether RI schedules dissociate all aspects of motivation from interval timing (for a review see Bailey et al., 2016), or just pre-feeding effects from interval timing. Third, the present experiments only focused on maintenance of interval timing. As such, there is at least one untested prediction of the

discriminative RI hypothesis: as initiating responses become progressively different from target responses, acquisition of target responses should be increasingly facilitated.

Overall, the present study provides some evidence in support of the discriminative RI hypothesis and thus the behavioral systems framework of learning, cognition, and motivation, which inspired the RI hypothesis and can be modified to account for the present data. Specifically, timing accuracy, but not precision, is robust to a motivational challenge if the to-be-timed interval is initiated with a discriminable response. Those interested in studying or isolating motivation as it pertains to timing, or cognition more generally, should consider procedurally dissociating motivation and cognition by training subjects in response-initiated procedures. At a minimum, these procedures should be programmed with unique initiating responses that differ in time, location, and form from target, if not all other, responses (e.g., reinforcer receipt). Additional consideration should be given to the exact training protocol; attending to details such as strictness of reinforcement contingencies, provenance of alternative reinforcement, and whether to program the procedure as discrete-trials or free-operant. Under the right conditions, it is possible to procedurally dissociate timing and motivation.

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Table 1*Switch-timing performance dependent measures*

Dependent Measure	Definition
Latency-to-initiate (LTI)	Time to initiate a trial following onset of initiation stimulus
Latency-to-Depart (LTD)	Time to last response on the Short FI after trial initiation
Latency-to-Switch (LTS)	Time to first response on the Long FI after trial initiation
Start Ratio	Proportion of trials in subjects start on the Short FI; that is, proportion of trials in which the first response on the Short FI occurred before the first response on the Long FI
Persistence Ratio	Proportion of trials in which subjects remain on Long FI after a switch; that is, the proportion of trials in which the last response on the Short FI was followed rather than preceded by the first response on the Long FI
Discrimination Ratio*	Proportion of trials in which the first attempt to initiate the trial was the correct initiating-response

Note. Bolded dependent measures explicitly address *a priori* predictions. *Discrimination ratios are not reported in Experiment 1 because rats were trained and tested with only one initiation type. Discrimination ratios were calculated as follows for each trial type; EI DR = Number of Trials where LTI = 2.5 s / Total Number of EI Trials; SL-RI DR = Number of SL-RI Trials wherein the first initiating response was a Short FI lever press / Total Number of SL-RI Trials; NP-RI DR = Number of NP-RI Trials wherein the first initiating response was a nose-poke / Total Number of NP-RI Trials.

Table 2*Experiment 2 Order of Single-Initiation Type Testing*

Single-Initiation Type Testing Condition	Testing Session	Rat							
		1	2	3	4	5	6	7	8
FI 4-s FI 12-s A: Pre-feeding	1-5	NP-RI	SL-RI	EI	NP-RI	SL-RI	EI	EI	NP-RI
	6-10	SL-RI	NP-RI	NP-RI	EI	EI	SL-RI	NP-RI	EI
	11-15	EI	EI	SL-RI	SL-RI	NP-RI	NP-RI	SL-RI	SL-RI
FI 6-s FI 18-s: Pre-feeding	1-5	EI	EI	SL-RI	SL-RI	NP-RI	NP-RI	SL-RI	SL-RI
	6-10	NP-RI	SL-RI	EI	NP-RI	SL-RI	EI	EI	NP-RI
	11-15	SL-RI	NP-RI	NP-RI	EI	EI	SL-RI	NP-RI	EI
FI 4-s FI 12-s B: Yoked-ITI Pre-feeding	1-5	SL-RI	NP-RI	NP-RI	EI	EI	SL-RI	NP-RI	EI
	6-10	EI	EI	SL-RI	SL-RI	NP-RI	NP-RI	SL-RI	SL-RI
	11-15	NP-RI	SL-RI	EI	NP-RI	SL-RI	EI	EI	NP-RI
FI 4-s FI 12-s B: Extinction	1-5	NP-RI	EI	EI	SL-RI	NP-RI	SL-RI	NP-RI	SL-RI
	6-10	EI	NP-RI	SL-RI	NP-RI	SL-RI	EI	SL-RI	EI
	11-15	SL-RI	SL-RI	NP-RI	EI	EI	NP-RI	EI	NP-RI

Note. The third and fourth sessions in each Single-Initiation Type Testing condition (i.e., sessions 3, 4, 8, 9, 13, and 14) were preceded by 1 h and 24 h pre-feeding, respectively.

Figure 1. Schematic of two common interval timing procedures and the pacemaker-accumulator (PA) family of computational models. Schematics of simple fixed-interval (FI; Panel A) and switch-timing (Panel B) schedules of reinforcement are based on most common implementations. PA model schematic (Panel C) adapted from Figure 1 of Daniels, Fox, Konyka, & Sanabria (2015a).

Figure 2. An ethogram-like schematic of the rat's predatory subsystem. Conceptualized under FI schedules of reinforcement (Panel A) and Switch-Timing tasks (Panel B). Adapted from Figure 1 of Sanabria et al. (2019) and Figure 1 of Timberlake (2000).

Figure 3. Experiment 1: Externally- and Short-Lever Response-Initiated (EI, SL-RI) Switch-timing Performance Under Baseline and Pre-feeding Conditions. Latency-to-depart (LTD; Panels A, C, E, G, I, K) and latency-to-switch (LTS; Panels B, D, F, H, J, L) medians (Panels A, B, G, H), IQRs (Panels C, D, I, J), and CQVs (Panels E, F, K, L) as a function of initiation type (EI = white squares; SL-RI = grey circles), overlaid with the median and inter-quartile range of each initiation group. The first two columns (Panels A-F) show baseline performance; the last two columns (Panels G-L) show the difference between pre-feeding (PF) and baseline (B) performance. In Panels G-L, dotted lines indicate zero difference. ^Indicates substantial evidence (i.e., $\ln BF_{10} \geq 1.098$) for a feeding regimen model describing the difference between pre-feeding and baseline; when ^ appears for both EI and SL-RI it indicates the effect of pre-feeding occurs when data are pooled across those groups.

Figure 4. Experiment 1: Externally- and Short-Lever Response-Initiated Switch-Timing Schedule Control Under Baseline and Pre-Feeding Conditions. Median latencies-to-initiate (Panels A and B), start ratios (Panels C and D), and persistence ratios (Panels E and F), overlaid with the median and inter-quartile range of each initiation group. The first column (Panels A, C, and E) shows baseline performance; the second column (Panels B, D, and F) shows the difference between pre-feeding and baseline performance. In Panels B, D, and F, dotted lines indicate zero differences.

Figure 5. Experiment 2: Externally-, Short-Lever Response-Initiated, and Nose-Poke Response-Initiated (EI, SL-RI, NP-RI) Switch-timing Performance Under Baseline and Pre-feeding Conditions. Latency-to-depart (LTD; Panels A, C, E, G, I, K) and latency-to-switch (LTS; Panels B, D, F, H, J, L) medians (Panels A, B, G, H), IQRs (Panels C, D, I, J), and COVs (Panels E, F, K, L) as a function of the timing condition (Long FI = 12-s A, 18-s) in each timing condition within each initiation type (EI = white squares; SL-RI = grey circles; NP-RI = black triangles). The first two columns (Panels A-F) show baseline performance and the last two columns (Panels G-L) show the difference between pre-feeding (PF) and baseline (B) performance. In Panels G-L, dotted lines indicate zero differences. **Indicates substantial evidence (i.e., $\ln BF_{10} \geq 1.098$) for a timing condition model. ^Indicates substantial evidence for a feeding regimen model describing the difference between pre-feeding and baseline. When ** or ^ appears for EI, SL-RI, and NP-RI it indicates that the effect of interest occurs when data are pooled across those conditions.

Figure 6. Experiment 2: Externally-, Short-Lever Response-Initiated, and Nose-Poke Response-Initiated (EI, SL-RI, NP-RI) Switch-timing Schedule Control Under Baseline and Pre-feeding Conditions. Median baseline and pre-feeding – baseline (PF – B) median latency-to-initiate (Panel A & B), and baseline and PF – B discrimination (Panel C & D), start (Panel E & F), and persistence ratio (Panel G & H) for each rat as a function of timing condition (Long FI = 12-s A, 18-s) within each initiation type (EI = white squares; SL-RI = grey circles; NP-RI = black triangles). Note that the dotted line in Panels B, D, F, and H indicate zero differences. *Indicates substantial evidence (i.e., $\ln BF_{10} \geq 1.098$) for an initiation type model. **Indicates substantial evidence for a timing condition model. ^Indicates substantial evidence for a feeding regimen model describing the difference between pre-feeding and baseline. Note that when ^ appears for SL-RI and NP-RI in Panel B and for EI, SL-RI, and NP-RI in Panel H, it indicates that the effect of pre-feeding is observed when data are pooled across those conditions.

Figure 7. Experiment 2: Externally-, Short-Lever Response-Initiated, and Nose-Poke Response-Initiated (EI, SL-RI, NP-RI) LTIs and LTSs Under FI 4-s FI 12-s Determinations. Median latency-to-initiate (LTI; Panel A) and pre-feeding (PF) – baseline (B) median latency-to-switch (LTS; Panel B) as a function of FI 4-s FI 12-s determination (A, B) within each initiation type (EI = white squares; SL-RI = grey circles; NP-RI = black triangles). Whereas Panel A shows the successful yoking of EI LTIs to NP-RI LTIs, Panel B shows whether pre-feeding effects on median LTSs depended on such yoking. ^Indicates substantial evidence (i.e., $\ln BF_{10} \geq 1.098$) for a feeding regimen model describing the difference between pre-feeding and baseline.

Figure 8. Experiment 2: Externally-, Short-Lever Response-Initiated, and Nose-Poke Response-Initiated (EI, SL-RI, NP-RI) Switch-timing Performance Under Extinction. Mean median LTI (Panels A-C), LTD (Panels D-F), and LTS (Panels G-I) back transformed from the log scale as a function of trial in FI 4-s FI 12-s Baseline (filled circles, solid line) and Extinction sessions 1 (white squares, dashed line) and 2 (white triangles, dashed line) within EI (Panels A, D, and G), SL-RI (Panels B, E, and H), and NP-RI (Panels C, F, and I) conditions. Baseline data are averaged over the two sessions preceding extinction. Note that the data was truncated at the median number of trials completed within each initiation type, and thus the data for the last trial shown is the mean of four rats.