

TIMING IN RESPONSE-INITIATED FIXED INTERVALS

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Different events can serve as time markers that initiate intervals in schedules of reinforcement. Pigeons were exposed to fixed-interval (FI) schedules in which the onset of the interval was signaled by the illumination of a key light or initiated by a peck to a lighted key. Food was delivered following the first response after the interval elapsed. In Experiment 1, three pigeons were exposed to a multiple schedule. One component was a standard FI schedule: Key light illumination signaled the onset of the interval. The other component was a response-initiated fixed-interval (RIFI) schedule: The first key-peck response determined the onset of the interval. In Experiment 2, three pigeons were exposed to a multiple FI–RIFI schedule of reinforcement and on occasional trials food was not delivered (i.e. “no-food” or “peak trials”). A yoking procedure equated reinforcement rates between the schedule types in both experiments. Absolute response rates early in the intervals were higher in the RIFI schedules of both experiments. Normalized response-rate gradients, ogive fits of normalized response gradients, and breakpoints were not systematically different for the schedule types in Experiment 1, indicating similar patterns of responding between interval onset and food delivery. However, during peak trials in Experiment 2 the duration of responding at a high rate was longer for RIFI schedules than FI schedules. This suggests that timing precision was reduced in the RIFI schedules and that relative “distinctiveness” of a time marker may determine its efficacy.

Key words: response-initiated fixed interval, temporal discrimination, timing, time markers, key peck, pigeons

Events that predict when other events will occur in the future are time markers. Reacting efficiently and effectively to time markers is essential for learning any three-term contingency in which antecedents and consequences are distributed in time. Sometimes those time markers are exteroceptive stimuli (e.g., a traffic light turns yellow) and sometimes they are behavior associated with no exteroceptive

stimulus change (e.g., pressing a cross-walk button). In spite of the extensive work in animal learning investigating temporal and stimulus control, current conceptualizations of timing do not address whether different types of time markers may differentially affect future behavior that relies on them. It is possible that responses and exteroceptive stimuli influence future behavior differently. For example, a response may be a more salient time marker (i.e., result in more accurate and precise temporal control of behavior) than an exteroceptive stimulus change because it requires action from the subject. The overarching objective of the two experiments presented below was a quantitative comparison of key pecking in fixed-interval schedules when responses and exteroceptive stimuli served as time markers. Understanding whether differences in these two types of time markers affect temporal discrimination is important for developing treatments for many psychoneurological impairments. Inabilities to accurately anticipate when predictable events will occur in the environment are associated with, for

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This research was completed as part of the first author's dissertation in psychology at West Virginia University and was supported by the Eberly College of Arts and Sciences and the Department of Psychology. Portions of these data were presented at the Society for the Quantitative Analyses of Behavior Conference in 2013. The authors thank Karen Anderson, Jim Belanger, Mike Perone, and Miranda Reed for helpful comments and discussion on an earlier version of the manuscript

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doi: 10.1002/jeab.120

example, schizophrenia (see Ward et al., 2012), Parkinson's disease (e.g., Rammseyer & Classen, 1997), and autism spectrum disorder (e.g., Allman et al., 2011).

Temporal discrimination—discriminating the duration of some interval—is most often evaluated behaviorally using fixed-interval (FI) schedules of reinforcement (see Guilhardi & Church, 2004). In FI schedules, a reinforcer (e.g., food) is delivered contingent on the first response after some fixed interval has elapsed (Skinner, 1938). The onset of the interval to food availability is most often marked in time or signaled to the organism via an exteroceptive stimulus change such as the illumination of a light (e.g., Nevin, 1971; Dews, 1978), delivery of a reinforcer (e.g., Catania & Reynolds, 1968; Lejeune & Wearden, 1991), or the onset of an auditory stimulus (e.g., Roberts & Church, 1978; Guilhardi & Church, 2005). These stimuli have likely been chosen because they are controlled procedurally by the experimenter and there is an underlying assumption that they function equivalently to other, less controlled options, such as a response (see Buhusi & Meck, 2000).

Timing has been evaluated extensively in FI schedules using response-rate gradients—response rate as a function of time to food (e.g., Dews, 1978; Gentry, Weiss, & Laties, 1983; Lejeune & Wearden, 1991). When responding is aggregated across multiple trials, response rate increases as time to food decreases in an ogive pattern. Relatively little research has directly compared responding during intervals initiated via the onset of an exteroceptive stimulus and intervals initiated via a response.

Response-initiated fixed-interval (RIFI) schedules are procedurally similar to FI schedules except the interval to food availability does not start timing until the first response on a trial. In comparison to temporal discrimination research using FI schedules, research using schedules in which a response is required to initiate the interval has been much less widespread. Research using RIFI schedules, which are also referred to as tandem FR 1-FI schedules (e.g., Shull, 1970) and, in experimental behavioral ecology, self-initiated fixed-interval schedules (e.g., Vasconcelos & Urcuioli, 2008), has found behavior to be somewhat similar to that observed under FI schedules (see also Weaver & Branch, 2008). Although absolute response rates tend to be higher early in RIFI than FI

schedules of the same duration, response rates in RIFI schedules increase as time to food decreases in a similar ogival pattern when responding is aggregated across multiple trials (Fox and Kyonka, 2013).

To date, two experiments have directly compared temporal discrimination between intervals initiated by an exteroceptive stimulus change and intervals initiated by a response. Caetano and Church (2009) found a nose-poke response and a .5-s presentation of a house light functioned similarly as time markers to control responding during intervals to food for rats. Although the between-groups design they used resulted in a large disparity in overall response rates between groups, relative response rates across the interval (i.e., response patterning) were similar in the two groups.

In both FI (Schneider, 1969) and RIFI schedules (Mechner, Guevrekian, & Mechner, 1963; Shull, 1970), responding on individual trials tends to be characterized by a “low-high” pattern. The “low-high” pattern is a period of disengagement with few or no target responses at the beginning of a trial, followed by a period of engagement toward the end of the trial as time to food decreases. The mean duration of these low periods, or the point of transition from the low period to the high period on individual trials, is not systematically different in FI and RIFI schedules (Fox and Kyonka, 2013).

Fox and Kyonka (2013) used a within-subject design to compare timing in FI and RIFI schedules. The time marker that signaled the start of an interval was a key-light onset in FI schedules and the first key peck after light onset in RIFI schedules. Fox and Kyonka evaluated the temporal distribution of responses in both schedules as a function of time since the time marker event. Response rates were higher early in the RIFI schedules, and interfood intervals (IFIs) were longer and more variable in the RIFI schedules. However, response patterning assessed from normalized response-rate gradients, breakpoints, and ogive fits was similar in the two schedule types, suggesting equivalent temporal discrimination. The overall aim of the two experiments that follow was to investigate how responses and key light illuminations might function differently as time markers. Experiment 1 is an extension of Fox and Kyonka (2013) designed to rule out temporal control by IFI as an alternative explanation for the results of that experiment. In Experiment 2,

we sought to determine the efficacy of responses as time markers in a peak procedure.

Experiment 1

It stands to reason that the most reliable time marker is not necessarily the most salient event or the event that exerts the greatest control over the temporal distribution of responses. As such, it is possible that in Fox and Kyonka's (2013) experiment, pecking was not controlled by key-light onset or the first peck, but by some other recurring event such as food delivery. Because one of their goals was to compare obtained rates of reinforcement in the two schedule types, Fox and Kyonka allowed the rate of reinforcement to vary depending on response latency in the RIFI schedules. As a result, reinforcement rates were lower and IFIs were longer and more variable in the RIFI schedules.

To the extent that time between food deliveries determined responding, the longer, more variable IFIs in RIFI schedules might have produced response gradients that were more variable than they would have been if IFIs had been as consistent as in FI schedules. Fox and Kyonka (2013) concluded key-light illumination and key pecks engendered equivalent temporal discrimination in their procedure. However, if food delivery also controlled behavior, two alternative explanations for the comparable normalized response gradients exist. 1) Apparently comparable responding in the two schedule types resulted from the combination of differences in time-marker efficacy for pecks versus light onset, and of differences in IFI distributions. For this explanation to be consistent with previous results (Fox & Kyonka, 2013), key pecks would have to result in more precise timing than key light onset in interval schedules, but the greater variation in IFIs contributed enough noise that the difference in time marker efficacy was not detectable. 2) Food delivery overshadowed other time markers, specifically key lights or pecks. This would only produce the equivalent temporal control Fox and Kyonka previously reported for FI and RIFI schedules if the obtained differences in IFI distributions for the two types of schedules were too small to affect response gradients.

Previous research suggests that reinforcer delivery may be a more salient time marker than the onset of other stimuli (e.g., Freestone & Church, 2010), and that IFIs control temporal

discrimination (e.g., Higa, Wynne, & Staddon, 1991; Wynne & Staddon, 1988) and response latency (Rutter, 1990). In FI schedules, the IFI is roughly constant, whereas in RIFI schedules it is more variable (Fox & Kyonka, 2013). To more accurately compare key-light illuminations and key pecks as time markers, it is necessary to degrade temporal control exerted by food delivery, and make food delivery an equally efficacious time marker in both schedule types. One way to do this is to equate the FI and RIFI IFIs, such that reinforcement rates in the two schedule types are approximately equal. The objective of Experiment 1 was to compare FI and RIFI performance under such circumstances. If FI and RIFI response gradients remain the same when rates of reinforcement are equated, the previously obtained similarities cannot be an artifact of different IFI distributions.

Method

Subjects. Three White Carneau pigeons, numbered 301, 302 and 303 were maintained at 85% of their free-feeding weight plus or minus 15g through appropriate postsession feedings. Pigeons were housed individually in a vivarium with a 12-hr light/12-hr dark cycle and had continuous access to water. All pigeons had varied experimental histories, including previous exposure to FI schedules immediately prior to Experiment 1.

Apparatus. Standard operant chambers (25.5 cm deep x 32 cm wide x 33.5 cm high) enclosed in sound-attenuating boxes equipped with ventilation fans were used. Each chamber contained three response keys arranged 6 cm apart and 24 cm above the floor of the chamber. Response keys could be illuminated red, green or white. A grain hopper (5.5 cm high x 6 cm wide) was located below the middle response key and 5.5 cm from the floor. A house light was located at the top of the chamber on the wall opposite the response keys. The grain hopper aperture was illuminated during reinforcer presentation, and the hopper contained Purina Nutrigrain pigeon pellets. A force of approximately 0.15 N was required to register a response on any key. All experimental events were controlled through a computer and MED-PC[®] interface located in an adjacent room.

Procedure. Each condition lasted 20 sessions and data from the final 6 sessions of each condition were used in analyses. During

food-hopper presentation all key lights and the house light were extinguished and the hopper light was illuminated. During intertrial intervals (ITIs) the house light was illuminated, and during all trials it was extinguished.

A multiple-schedule arrangement was used in Experiment 1. Each session was divided into two components. An FI schedule operated in one component and an RIFI schedule operated in the other. Each component lasted 30 min or 20 trials, whichever came first. Only Pigeon 303 reached the maximum component duration, 12 times in total, in the RIFI 30-s schedule; of these only one occurred in the last six sessions used for analysis. The FI and RIFI components were differentiated by the color of the illuminated key (either red or green). The FI and RIFI components were presented in pseudorandom order in each session, determined with the constraints that a component could not be presented first on more than two consecutive days and each component was presented first an equal number of times.

During the RIFI component, key pecks produced access to food on an RIFI schedule. On each trial, the center key was illuminated either red or green. The first peck to the center key started the fixed interval timing down to food availability and the first response after the interval elapsed resulted in 5-s access to food. Food delivery was followed by a variable time (VT) 5-s ITI and the presentation of the next trial. Pigeons 301 and 303 were exposed to 15-s schedules first, followed by 30-s schedules. The order was reversed for Pigeon 302.

During the FI component, responding produced access to food on an FI schedule. In each condition, the duration of the FI was the same as that of the RIFI (15 or 30 s). However, to ensure that rates of reinforcement were equivalent in the two components, the ITI between food delivery and the illumination of the key light to initiate the subsequent FI on each trial was yoked to response latencies in the RIFI component from the previous day. Response latencies are the times from key light illumination to the first response on individual trials. In RIFI schedules, this response initiated the interval to food. The first response had no programmed consequence in FI schedules unless it occurred after the interval elapsed, in which case it resulted in food delivery. During RIFI trials, the time from the end of food delivery to

the first response on the subsequent trial was recorded for all trials (i.e., VT 5-s ITI + first-response latency). These times then became the ITIs for the FI schedule component the following day. Each new FI trial began after the yoked ITI elapsed. For example, if the response latency from the first RIFI trial on a Tuesday was 8 s after a 3-s ITI, then the ITI for the first FI trial on the following Wednesday was 11 s. During Session 1 for each condition, because there were no data from a previous RIFI component to yoke, VT 5-s ITIs were used in the FI component.

After the yoked ITI elapsed in FI components, the center key was illuminated either red or green, initiating the interval. For each pigeon, a single key color was always associated with one of the two schedule types. The first response after the interval elapsed resulted in 5-s access to food. The two components were separated by a 30-s blackout during which all lights were extinguished. The second component immediately followed the blackout.

Results

Reinforcement rates were calculated by dividing the total number of reinforcers obtained per component by the total time spent in the component including ITIs and food-hopper presentations. Reinforcement rates for the last six components of a condition were calculated separately and then averaged. The three pigeons obtained a mean 1.70 ($SEM=0.40$) and 1.74 ($SEM=0.30$) food deliveries per min in the FI and RIFI 15-s schedules, respectively. The mean number of reinforcers obtained per min in the FI and RIFI 30-s schedules were 1.17 ($SEM=0.14$) and 1.16 ($SEM=0.15$), respectively. Group means were representative of individual pigeon reinforcement rates in the two schedule types. For each pigeon and at both 15- and 30-s intervals, 95% confidence intervals for reinforcement rates in FI and RIFI schedules overlapped by at least 32.6% and up to 89.3%, indicating that yoking successfully equated reinforcement rates.

Figure 1 shows responses per min as a function of time (s) since stimulus onset (FI) or first response (RIFI) for each pigeon in each condition. To generate the response-rate gradients, intervals were divided into bins equal to 10% of the corresponding interval and responses per min were calculated for

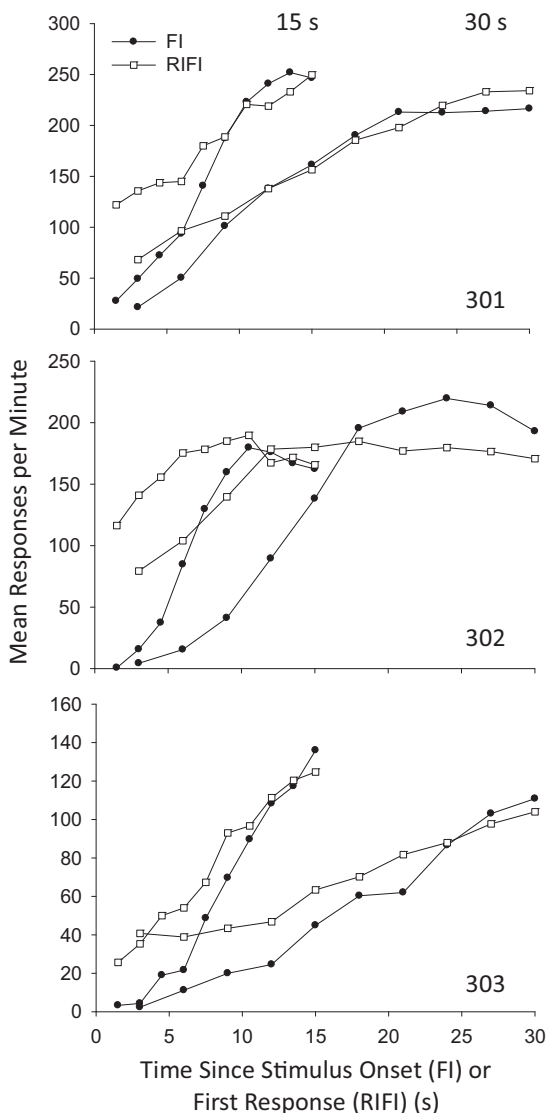


Fig. 1. Mean responses per min as a function of time in bins equal to 10% of the corresponding interval for each pigeon in each condition of Experiment 1. Note different y-axis scales for each pigeon.

each bin. Response rates increased as time to food decreased in both schedule types. The primary difference in the response-rate gradients for the two schedule types was that response rates early in the interval were higher in the RIFI schedules than the corresponding FI schedules across pigeons and conditions. Aggregated across pigeons and interval durations, absolute response rates during the first half of RIFI schedules were 199.06% of rates

during the first half of FI schedules. During the second half of the FI and RIFI schedules response rates were nearly equivalent—response rates in the FI schedules were 102% of rates in the RIFI schedules.

Although absolute response rates at the start of intervals were higher in RIFI than FI schedules (Fig. 1), response patterning in both schedule types could be characterized as low-high in nature: a relatively low rate of responding early in the interval, followed by a relatively high rate of responding until food was delivered. Breakpoints are quantitative estimates of the point in each interval when response rate switched from low to high. We calculated breakpoints (Guilhardi & Church, 2005) by running an exhaustive search for the time of the response (t_1) in each trial that maximized the index $t_1(r - r_1) + t_2(r_2 - r)$, where t_1 is the duration from interval onset to breakpoint, t_2 is the duration from breakpoint to food delivery, r_1 is the response rate during t_1 , r_2 is the response rate during t_2 , and r is the mean response rate in the trial.

Figure 2 shows mean breakpoints from each schedule for each pigeon. Trials in which three or fewer responses occurred or the response rate before the breakpoint was higher than the response rate after the breakpoint were excluded from the analysis. Across pigeons and interval durations, a mean of 3.67 ($SD = 7.61$) more trials were excluded in RIFI than FI schedules. Breakpoints were later in the FI than RIFI schedules for Pigeons 302 and 303, but earlier in the FI schedules for Pigeon 301. Across subjects and schedule types, mean breakpoints were 6.86s ($SD = 1.46$) later in 30-s schedules than in 15-s schedules. Across subjects and interval durations, mean breakpoints were 0.06s ($SD = 1.03$) later in FI schedules than in RIFI schedules. There was no systematic difference in breakpoints between the FI and RIFI schedules.

The functional relation between response rate and time since interval onset (Fig. 1) may reveal differences not detected by comparing single-trial measures such as first-response latency and breakpoint. However, to compare changes in response rates as time to food decreased (i.e., response patterns), it is necessary to control for differences in absolute response rates obtained in the two schedule types. Normalizing the gradients from Figure 1 is one way to accomplish

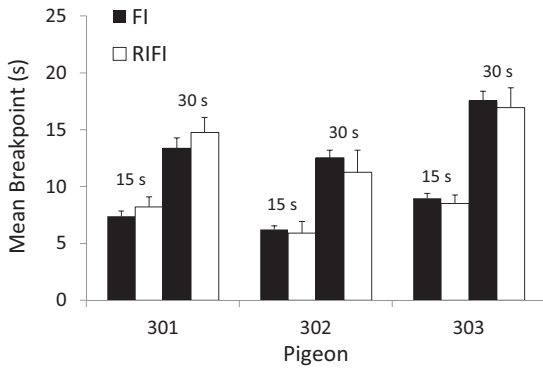


Fig. 2. Mean breakpoint for each pigeon in each condition of Experiment 1. Error bars represent 95% confidence intervals.

this. To calculate normalized response rates, each interval was divided into 10 bins equivalent to 10% of the corresponding interval. The minimum response rate observed across the 10 bins in the interval was then subtracted from the response rate in each bin. The remaining value in each bin was then divided by the remaining maximum response rate observed across bins in the interval. This adjustment ensured that the normalized response rate curves for all the gradients in both schedules ranged from 0 (the normalized minimum response rate) to 1 (the normalized maximum response rate). By normalizing the response-rate gradients the general pattern of changes in response rate across the intervals in the two schedule types can be compared while controlling for the differences in absolute response rate that were observed. Figure 3 shows normalized response rate as a function of normalized time from the relevant time marker (i.e., the onset of the key light in FI schedules and the first peck in RIFI schedules) for each pigeon in each condition.

For a quantitative characterization of the functional relation between response rate and time since the start of the interval, an ogive function (Guilhardi & Church, 2005) was fitted to the normalized response-rate gradients using Equation 1:

$$y(t) = \frac{1}{1 + e^{-(t-a)/b}} \quad (1)$$

The a parameter determines the center of the function (the time in which the response rate reached half of its maximum), and the b parameter determines the slope of the function

at time $t = a$. Smaller values of b indicate steeper slopes and therefore more abrupt changes in the response gradients. More abrupt changes occur when the range of obtained breakpoints from individual trials is smaller.

For each pigeon and condition, parameters a and b of Equation 1 were fitted to individual-pigeon normalized response-rate gradients to maximize variance accounted for (VAC) using a nonlinear optimization algorithm (Microsoft Excel Solver). Higher values of parameter a and lower values of parameter b are typically indicative of better temporal control. The best fitting line from the model is shown as solid (FI) and dashed (RIFI) lines on the normalized response-rate gradients in Figure 3.

For 11 out of 12 of the ogive fits, VAC was .97 or greater. The exception was the fit for Pigeon 302 in the RIFI 15-s condition (VAC=.66). Parameter estimates from Equation 1 are listed in Table 1. Across pigeons, the mean a parameter was 0.49 ($SD=0.1$) and 0.46 ($SD=0.14$) and the mean b parameter was 0.12 ($SD=0.03$) and 0.12 ($SD=0.04$) for FI and RIFI schedules, respectively. Across pigeons there were no systematic differences between FI and RIFI conditions based on the centers and slopes of the ogive fits.

Discussion

In Experiment 1, three pigeons were exposed to FI and RIFI 15- and 30-s schedules of reinforcement in a multiple-schedule arrangement. Reinforcement rates in the two schedule types were equated by yoking the ITIs in the FI schedule to the first-response latencies from the previous day's RIFI schedule. Equation 1 fitted the normalized response gradients well; VAC was generally greater than .97. Therefore, ogive parameters can be compared directly for the two schedule types. Breakpoints, ogive model fits to normalized response-rate gradients, and visual inspection of the normalized response-rate gradients indicated no systematic difference in response patterns between the two schedule types. The additional response requirement to initiate the interval in RIFI conditions—the response time marker—did not have a consistent effect on response patterning across pigeons. This was true despite higher absolute response rates early in the RIFI schedules and equivalent rates of reinforcement in the FI and RIFI schedules.

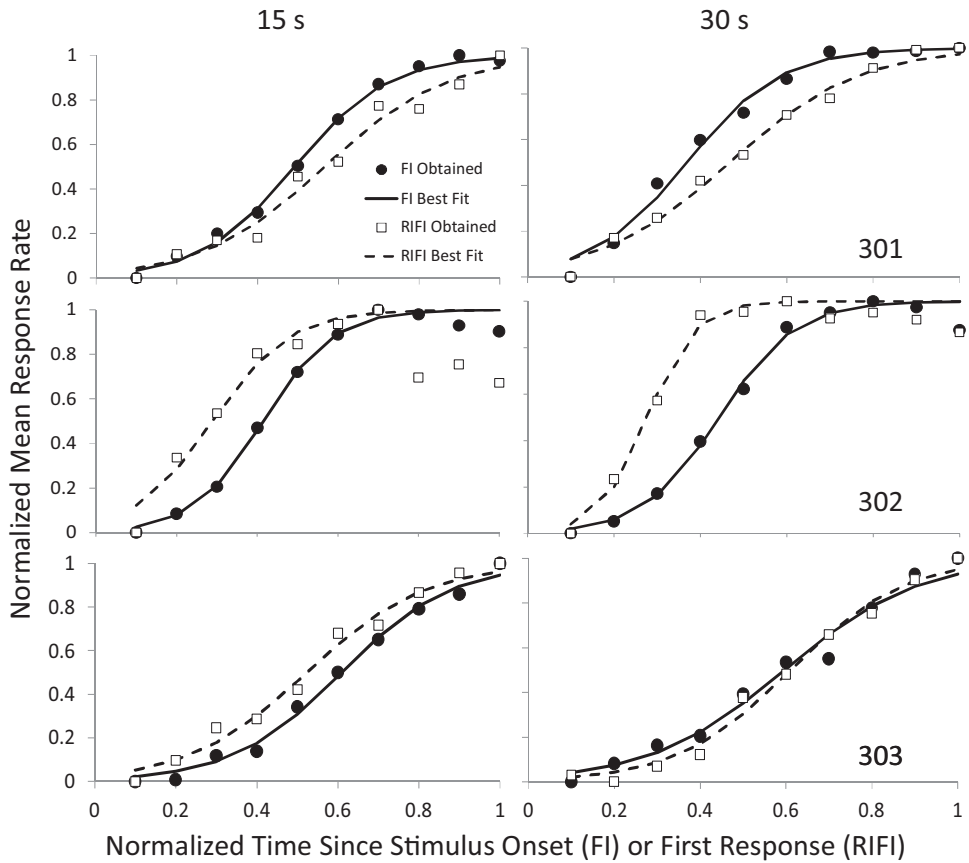


Fig. 3. Normalized mean response-rate gradients as a function of normalized time for each pigeon in each condition of Experiment 1. The solid lines represent the best-fitting ogive function for the FI schedules and the dashed lines represent the best-fitting ogive function for the RIFI schedules.

Table 1
Ogive model parameter estimates (Equation 1) for Pigeons 301–303 in Experiment 1

Subject	Parameter	Schedule(type/length (s))			
		FI 15	RIFI 15	FI 30	RIFI 30
301	<i>a</i>	0.49	0.57	0.37	0.47
	<i>b</i>	0.12	0.15	0.11	0.15
	VAC	0.99	0.98	0.99	0.99
302	<i>a</i>	0.41	0.29	0.44	0.28
	<i>b</i>	0.09	0.10	0.09	0.06
	VAC	0.99	0.66	0.99	0.97
303	<i>a</i>	0.61	0.52	0.60	0.61
	<i>b</i>	0.14	0.15	0.16	0.13
	VAC	0.99	0.99	0.98	0.99

Note. FI = Fixed Interval; RIFI = Response-Initiated Fixed Interval; VAC = Variance Accounted For.

Characterizations of FI and RIFI schedules in Experiment 1 were consistent with previous research employing one or both schedule types. Response-rate gradients aggregated from the last six sessions of each condition in Experiment 1 were ogival in FI (Branch & Gollub, 1974) and RIFI (Fox & Kyonka, 2013) schedules; and responding on individual trials could be characterized as taking a “low-high” pattern in FI (Schneider, 1969) and RIFI (Fox & Kyonka, 2013) schedules. The results of Experiment 1 indicate that the equivalence of responses and exteroceptive stimuli as time markers obtained in previous research (Caetano & Church, 2009; Fox & Kyonka, 2013) was not a result of procedural idiosyncrasies or differences in the distribution of IFIs across schedule types.

Fox and Kyonka (2013) reported similar response patterns in FI and RIFI schedules, but they did not control reinforcement rates. Experiment 1 confirms that normalized response gradients and breakpoints are similar in FI and RIFI schedules regardless of whether IFIs are free to vary (Fox & Kyonka, 2013) or if they are equated. Together, the results of both experiments suggest key-light illuminations and key pecks are equally efficacious as time markers and, furthermore, that when schedules always end in food, temporal discrimination is similar. Moreover, response rates were higher early in the RIFI schedules than corresponding FI schedules in Fox and Kyonka’s previous study and in Experiment 1. These findings suggest that the differences in absolute response rates between the two schedule types observed by Fox and Kyonka were not an artifact of longer, more variable IFIs in the RIFI schedule, but of the response-initiation requirement in the RIFI schedules.

Experiment 2

One prevailing issue across all three previous experiments (Caetano & Church, 2009; Fox & Kyonka, 2013; Experiment 1) evaluating responses and exteroceptive stimuli as time markers is that responding was always interrupted by food delivery. It can be difficult to evaluate how behavior is temporally controlled in these experimental arrangements because the animal may simply start responding on a trial and continue to respond until food is delivered. The increase in response rate as time to food decreases observed in these experiments suggests anticipation of food delivery;

however, it does not necessarily depend on the animal having learned the time of food delivery. In order to evaluate the time in which the animal has learned to expect food delivery, the animal must be tested in the absence of food delivery. One way to conduct such a test is to employ a peak procedure.

Peak procedures are modified FI schedules in which occasional trials are no-food trials or “peak” trials (Catania, 1970; Roberts, 1981). No-food trials last longer than food trials (standard FIs) and they end without reinforcement. On no-food trials it is possible to obtain additional measures of temporal discrimination, including a response-rate gradient after the usual time of reinforcer delivery and start and stop times for responding on individual trials (Church, Meck, & Gibbon, 1994). Start times are the point before food delivery when the animal starts responding (analogous to breakpoints), and stop times are the point after typical food delivery when the animal stops responding. Experiment 2 included FI and RIFI no-food trials in a multiple schedule arrangement similar to that used in Experiment 1.

Responding on no-food trials provides opportunities to obtain additional measures of temporal discrimination and may provide a clearer picture of potential differences in temporal discrimination when an interval is initiated with a stimulus (FI) or a response (RIFI). In some cases, stop times and the descending response gradients obtained after typical food delivery may be more sensitive measures of temporal discrimination than breakpoints and ascending response gradients obtained before typical food delivery (Kyonka & Grace, 2010). If accuracy is affected by the time marker in FI and RIFI schedules, response-rate gradients, the time of peak response rate, and start and stop times will be shifted to the left (earlier) or right (later), relative to the other schedule type. If timing precision is affected by the time markers in FI and RIFI schedules, start and stop times will be different and peak curves will have different widths, but the time of peak response rate will be similar.

Method

Subjects and Apparatus. As in Experiment 1.

Procedure. Conditions lasted 40 sessions and data from the final 12 sessions of each condition were used in analyses. A multiple-schedule

arrangement was used in Experiment 2, similar to the one used in Experiment 1. Each session was divided into two components—an FI and an RIFI component—and each lasted 45 min or 25 trials, whichever came first. No components were terminated as a result of the 45 min limit. Each component was associated with either a red or green key light, and the order in which the components were presented on a daily basis was pseudorandom with the constraints that a component could not be presented first on more than two consecutive days and each component was presented first an equal number of times. Pigeons 301 and 303 were exposed to 30-s schedules first, followed by 15-s schedules, and the order was reversed for Pigeon 302.

Regular FI and RIFI trials were the same as in Experiment 1. No-food trials started the same as regular FI and RIFI trials; that is, the only discriminative cue distinguishing no-food trials from food trials occurred after the interval elapsed (i.e., the passage of time). Each no-food trial lasted three times as long as the scheduled interval. Responses in no-food trials had no programmed consequence, except for the first response in RIFI no-food trials, which started the no-food interval timing. After the no-food trial timer elapsed, the key light extinguished and the ITI and subsequent trial followed.

One of every five trials was a no-food trial. The order of food and no-food trials within blocks of five intervals was determined randomly with the constraint that no more than two no-food trials could occur consecutively during any session. In each component, 20 trials were food trials and 5 trials were no-food trials, for a total of 40 food trials and 10 no-food trials per session.

Reinforcement rates in the FI and RIFI components were yoked as in Experiment 1: ITIs in the FI component were yoked to the VT 5-s ITI plus the first-response latency in each trial from the previous day's RIFI component.

Results

Reinforcement rates were obtained by dividing the total number of reinforcers obtained per component by the total time spent in the component including ITIs and food-hopper presentations. Reinforcement rates for the last six components of a condition were calculated separately and then averaged. The mean number of reinforcers obtained per min by

the three pigeons in the FI and RIFI 15-s schedules were 1.28 ($SEM=0.09$) and 1.28 ($SEM=0.12$), respectively. The mean number of reinforcers obtained per minute in the FI and RIFI 30-s schedules were 0.74 ($SEM=0.10$) and 0.74 ($SEM=0.09$), respectively. Group means were representative of individual pigeon reinforcement rates in the two schedule types. For each pigeon, 95% confidence intervals for reinforcement rate in FI and RIFI schedules overlapped by at least 55.2% and up to 90.2% in both the 15- and 30-s intervals. As in Experiment 1, the yoking procedure was successful in equalizing reinforcement rates in the FI and RIFI schedules across pigeons and conditions.

All results related to Experiment 2 reported from this point forward are based on analyses of responding that occurred during no-food trials. Figure 4 shows the proportion of first-response latencies that occurred in bins equal to 10% of the corresponding interval. There was a consistently greater (with one exception) proportion of relatively long first-response latencies in the RIFI schedule across pigeons and conditions. In the 15-s interval conditions, 72%, 93%, and 53% of first-response latencies in the RIFI schedule exceeded the median first-response latency in the FI schedule for Pigeons 301, 302, and 303, respectively. In the 30-s interval conditions, 45%, 95%, and 73% of first-response latencies in the RIFI schedule exceeded the median first-response latency in the FI schedule for Pigeons 301, 302, and 303, respectively.

If response gradients were scalar invariant, the relative frequency distributions for 15- and 30-s intervals in Figure 4 should superimpose. To quantify deviations from scalar invariance, we calculated the portion of nonoverlapping data in first-response latency relative frequencies for distributions from 15-s and 30-s intervals for each schedule type and pigeon. For any two relative frequency distributions with the same number of bins, the nonoverlapping portion (NOP) equals the sum of the absolute value of the difference in relative frequency in each bin, divided by two. For the distributions in Figure 4:

$$NOP = \frac{\sum_{t=1}^{20} |y(t)_A - y(t)_B|}{2}. \quad (2)$$

In Equation 2, $y(t)_A$ is the relative frequency of first-response latencies in bin t of the frequency

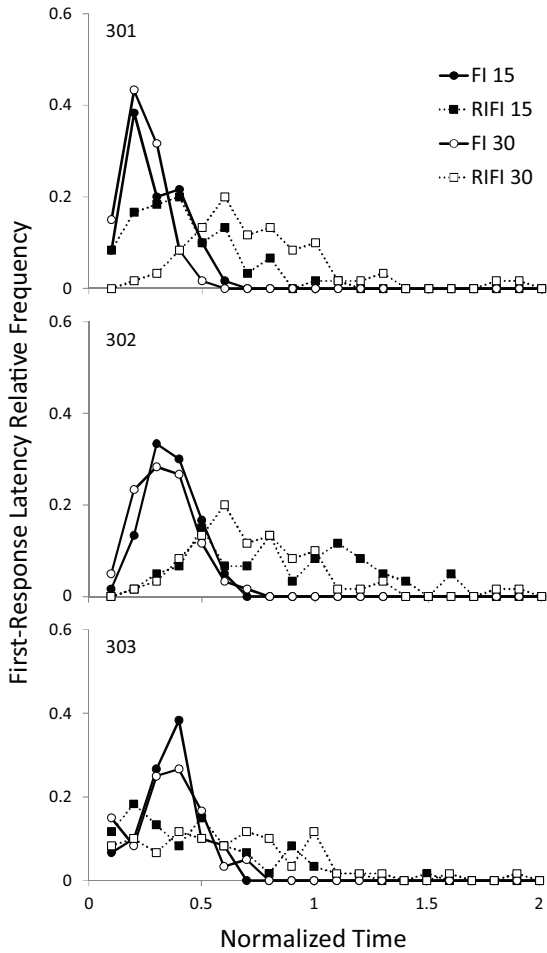


Fig. 4. Relative frequency distributions of first-response latencies for each pigeon in each condition of Experiment 2. Each graph shows the proportion of first-response latencies in each schedule that occurred as a function of time in bins equal to 10% of the corresponding interval.

distribution for one schedule and $y(t)_B$ is the frequency of first-response latencies in bin t of the frequency distribution for the other schedule. An NOP of zero indicates total superimposition of distributions and an NOP of one indicates that distributions did not overlap at all. The NOPs of FI 15-s and FI 30-s frequency distributions were 0.23, 0.15, and 0.20 for Pigeons 301, 302 and 303, respectively. For RIFI 15- and 30-s distributions, NOPs were 0.37, 0.30, and 0.30 for Pigeons 301, 302 and 303, respectively. We also calculated NOPs for FI and RIFI schedules with the same schedule values. The NOPs of FI and RIFI 15-s frequency distributions were 0.25, 0.67, and 0.24, and

NOPs for FI and RIFI 30-s distributions were 0.18, 0.70, and 0.46 for pigeons 301, 302 and 303, respectively. Although first-latency frequency distributions were not completely scalar invariant, distributions with different schedule values but the same schedule type were more alike than distributions with the same schedule value and different schedule types, indicating that schedule type influenced frequency distributions more than schedule value did.

Figure 5 shows responses per min as a function of time (s) since stimulus onset (FI) or first response (RIFI) for each pigeon in each condition. These gradients show how responding changed as the time of typical food delivery came and went. To calculate the response-rate gradients, no-food intervals were divided into bins equal to 10% of the corresponding interval and responses per min were calculated for each

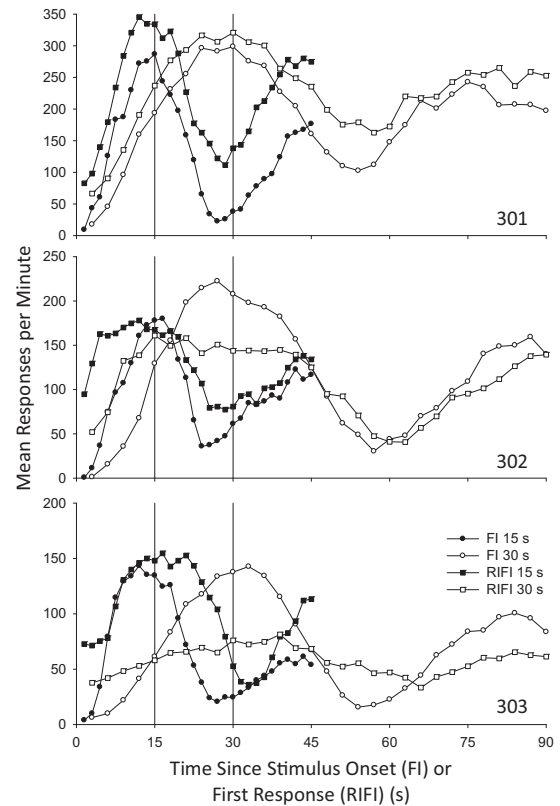


Fig. 5. Mean responses per min as a function of time in bins equal to 10% of the corresponding interval for each pigeon in each condition of Experiment 2. Solid vertical lines represent the time of programmed food availability on food trials (15 and 30 s). Note different y-axis scales for each subject.

bin. In both schedule types, response rates in the 15- and 30-s intervals increased as time to typical food delivery decreased, peaked near the time of typical food delivery, and then decreased. Consistent with the “ramped”-Gaussian function reported previously on peak trials (see Kirkpatrick, Miller, Betti, & Wasserman, 1996; Monteiro & Machado, 2009), responding began to increase toward the end of both the 15- and 30-s no-food intervals. Consistent with previous research, response rates were higher at the start of the RIFI schedules. Aggregated across pigeons and interval durations, absolute response rates during the first half of RIFI schedules (between 0–7.5 s and 0–15 s for 15 and 30-s schedules, respectively) were 188.24% of rates during the first half of FI schedules.

As in Experiment 1, response-rate gradients were normalized to permit comparisons of changes in response rate (i.e., response pattern) in the two schedule types. Figure 6 shows normalized response rate as a function of normalized time (in bins equal to 10% of the corresponding interval) for each pigeon in FI

conditions (top graph) and RIFI conditions (bottom graph). In the top graph of Figure 6, the FI normalized response-rate gradients are similar across pigeons and are approximately scalar invariant across interval durations. In the bottom graph of Figure 6, there is more variability in the RIFI normalized response-rate gradients. While all the normalized RIFI functions could be described as “ramped” Gaussian functions with peaks at the approximate time of food delivery on food trials, the peaks were wider than in the FI schedules and the functions for 15- and 30-s intervals do not superimpose as consistently as in the FI schedules.

To quantify potential differences in the FI and RIFI normalized response-rate gradients, the following Gaussian function was fitted to the data up to time $2t$, where t is the scheduled interval duration, for each pigeon to maximize variance accounted for (VAC) using a nonlinear optimization algorithm (Microsoft Excel Solver):

$$y(t) = e^{-(t-b)^2/2c^2}, \tag{3}$$

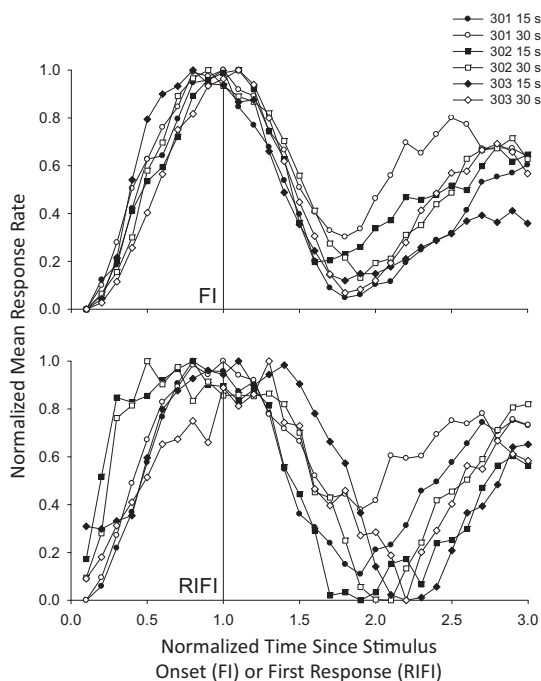


Fig. 6. Normalized mean response-rate gradients as a function of normalized time for each pigeon in FI (top) and RIFI (bottom) schedules in Experiment 2. Solid vertical lines represent the time of programmed food availability on food trials.

where b is the normalized time of the peak (peak location; timing accuracy), and c is the standard deviation (width of the peak; timing precision). Parameter estimates from Equation 3 are shown in Table 2. The model provided a good fit for the data with a mean VAC of 0.91 ($SD=0.05$) across pigeons. The standard deviation (c) parameter estimate was larger in the RIFI than FI schedule for all pigeons at both interval durations. There was no systematic difference between the schedule types for the peak time (b) parameter estimates.

Figure 7 shows group mean normalized response gradients combined across interval duration with the mean best fitting Gaussian functions overlaid. These normalized gradients and Gaussian fits were consistent with the fits to gradients for individual pigeons. As with the individual-pigeon fits to Equation 3 displayed in Table 2, group mean normalized FI and RIFI gradients had similar peak locations (b parameter) but the RIFI gradient had a wider peak (c parameter).

To examine responding in the FI and RIFI no-food trials with a finer grain of analysis, start, stop, and middle times were calculated for individual no-food trials. Showing only local response rates that were aggregated across trials

Table 2
Gaussian model parameter estimates (Eq. 3) for Pigeons 301–303 in Experiment 2

Pigeon	Parameter	Schedule (type/length (s))			
		FI 15	RIFI 15	FI 30	RIFI 30
301	<i>b</i>	0.94	0.96	1.00	1.04
	<i>c</i>	0.38	0.41	0.48	0.53
	VAC	0.98	0.95	0.86	0.87
302	<i>b</i>	1.00	0.80	1.01	0.90
	<i>c</i>	0.41	0.51	0.43	0.56
	VAC	0.91	0.91	0.95	0.83
303	<i>b</i>	0.91	1.11	1.02	1.10
	<i>c</i>	0.41	0.59	0.38	0.55
	VAC	0.93	0.99	0.92	0.84
Means	<i>b</i>	0.95	0.96	1.01	1.01
	<i>c</i>	0.40	0.50	0.43	0.55
	VAC	0.94	0.95	0.91	0.85

Note. FI = Fixed Interval; RIFI = Response-Initiated Fixed Interval; VAC = Variance Accounted For.

as described above may give the impression that response rates increased and decreased gradually as the time of food delivery came and went. However, visual inspection of raster plots and extant literature (e.g., Cheng & Westwood, 1993; Church, Meck, & Gibbon, 1994) suggest that the ramped Gaussian in Figure 6 is an inaccurate depiction of behavior in individual trials. Responding on individual trials is better characterized by a “low-high-low” pattern. That is, on any given no-food trial in FI and RIFI schedules, responding typically started at low rate, increased at some breakpoint to a high

rate of responding (the “start” time), remained in this “high-rate state” until a second breakpoint (the “stop” time), at which time responding decreased to a second low rate.

To identify these high-rate periods, a low-high-low analysis was conducted on each no-food trial up to time $2t$, where t is the scheduled interval duration (Church et al., 1994). This involved an exhaustive search for the best fitting model that maximized the index $t_{L1}(r - r_{L1}) + t_H(r_H - r) + t_{L2}(r - r_{L2})$, where r was the overall mean response rate on a no-food trial, r_{L1} , r_H , and r_{L2} were the response rates in the first low, the high, and the second low states, respectively, and t_{L1} , t_H , and t_{L2} were the durations of those respective states. The sum of the start time and half of the high-rate state duration defined the middle time—the midpoint of the start and stop time. The middle time is a single-trial alternative measure to the time of peak response rate from the aggregated response-rate gradients.

Low-high-low analysis was used to calculate the start and stop times that maximized the difference between the first and second low-rate states and the high-rate state between them. Start and stop times are individual-trial measures of temporal discrimination that take into account all the responses recorded during a trial. Trials in which the start time occurred after the programmed interval duration or the stop time occurred before programmed interval duration were excluded from the analysis. Across

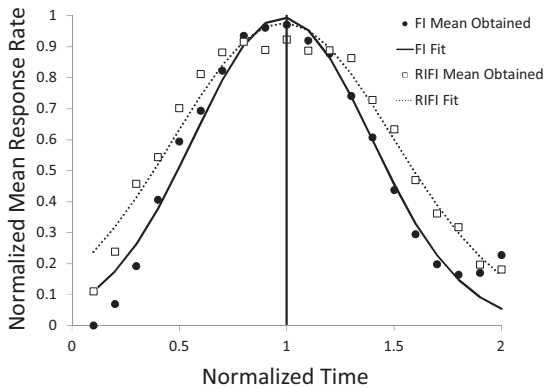


Fig. 7. Normalized group mean response gradients combined across interval durations for the FI (solid circles) and RIFI schedules (open squares). Solid (FI) and dotted (RIFI) indicate mean best fitting Gaussian. Solid vertical line indicates scheduled interval duration on food trials.

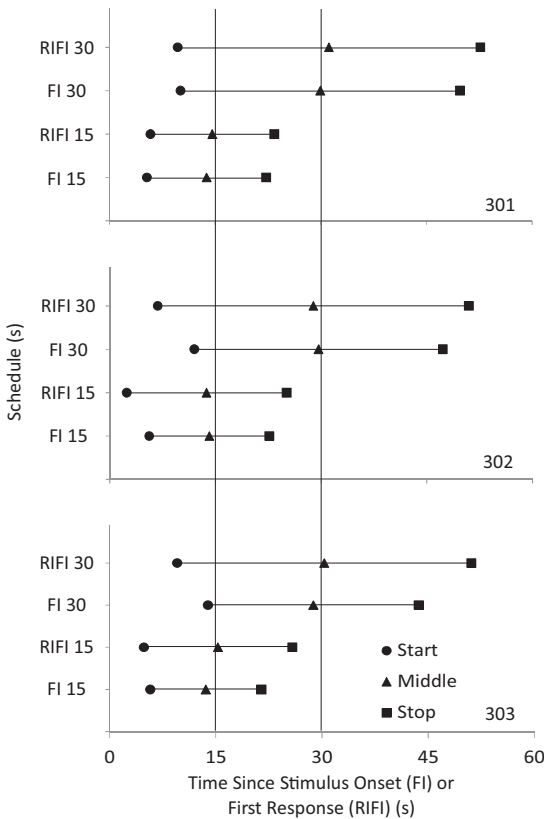


Fig. 8. Mean start, middle, and stop times for each pigeon in each condition of Experiment 2. The solid vertical lines represent the time of programmed food availability on food trials (15 and 30 s).

pigeons a total of two and five trials were excluded from the FI and RIFI schedules, respectively.

Figure 8 shows mean start, middle, and stop times obtained using low-high-low analysis for the FI and RIFI 15- and 30-s schedules. For all pigeons and all conditions, the middle time was located near the time of typical food delivery. RIFI mean middle times were later in four of six comparisons (three pigeons x two interval durations). In six of six comparisons, the RIFI mean high-rate state duration was longer than the corresponding FI high-rate state duration. For Pigeons 301, 302, and 303 the RIFI 15-s high-rate state duration was 0.64 s, 5.64 s, and 5.24 s longer, respectively, than the FI 15-s high-rate state duration. Similarly, for Pigeons 301, 302, 303 the RIFI 30-s high-rate state duration was 3.32 s, 8.91 s, and 11.78 s longer, respectively, than the FI 30-s high-rate state duration.

Start times were earlier in RIFI schedules in five of six comparisons. Stop times were later in RIFI schedules in six of six comparisons.

In RIFI schedules, unlike FI schedules, the onset of the key light was not a time marker: it did not signal the interval had begun and was not predictive of time to food. However, it is possible pigeons reacted to the stimulus change as if it were a time marker. To assess the role of key light onset as a potential time marker in RIFI schedules, we compared bivariate correlations between first-response latencies and start times in both schedule types for each pigeon. If key-light onset marked the beginning of the timed interval, first-response latency and start time should be positively correlated. This was the case in FI schedules, $r = .73, p < .001$, but not RIFI schedules, $r = .07, p = .21$, indicating key-light onset functioned as a time marker in FI, but not RIFI schedules.

Table 3 shows correlations between first-response latency and measures of temporal control obtained from responding on peak trials in Experiment 2 pooled across pigeons and interval durations. For both schedule types, first-response latency was positively correlated with start and stop times calculated from the beginning of the interval (i.e., key light onset in FI and the first response in RIFI). It was also correlated

Table 3

Correlations between timing parameters derived from peak trials in Experiment 2, pooled across pigeons and conditions. The z-score reported in the last column compares correlation coefficients for FI and RIFI schedules (two-tailed). Z-scores are shown instead of dependent-samples t scores because there were >300 in all comparisons.

Parameters	r		z
	FI	RIFI	
Latency & Start	.73	.07	11.41***
Latency & Stop	.48	.29	2.98**
Latency & Middle	.59	.25	5.61***
Latency & HSD	.24	.30	-0.86
Start & Stop	.63	.49	2.73*
Start & HSD	.30	.10	2.78*
Start & Middle	.80	.71	2.81*
Stop & HSD	.93	.92	0.92
Stop & Middle	.97	.96	1.95
HSD & Middle	.82	.77	1.81

Note. FI = Fixed Interval; RIFI = Response-Initiated Fixed Interval; HSD = high-rate state duration; * $p < .05$, ** $p < .01$, *** $p < .001$.

with middle times, the midpoint of start and stop times, and high-rate state durations (HSDs; stop time–start time). Correlations between latency and HSD were not different in FI and RIFI schedules. Correlations between latency and all other timing parameters were greater in FI schedules than RIFI schedules. These positive correlations are additional evidence that the stimulus change was a more effective time marker in FI than RIFI schedules. All correlations between timing parameters were positive for both schedule types. With the exception of the correlation between latency and HSD, if first-response latency or start time was one of the variables included in the correlation, the correlation for FI schedules was greater than the correlation for RIFI schedules.

Discussion

In Experiment 2, three pigeons were exposed to FI and RIFI 15- and 30-s schedules of reinforcement in a multiple-schedule arrangement. No-food trials were included during both FI and RIFI components to assess timing in the absence of food delivery. In order to equate reinforcement rates in the two schedule types, the ITIs in the FI schedule were yoked to the response latencies from the previous day's RIFI schedule. With this yoking procedure in place, interfood intervals were equated for the two schedule types. In addition, one food delivery did not predict time to the next in either schedule type, therefore, food could not function as an effective time marker.

Normalized response-rate gradients on no-food trials indicated more between-subject variability and a generally wider peak in the RIFI schedules, though the gradients in both schedule types peaked at the approximate time of typical food delivery. Gaussian fits (Table 2 and Fig. 7) indicated no difference in peak location, but wider normalized peaks in RIFI than FI schedules for all pigeons at both interval durations. Similarly, the low-high-low analysis of responding on individual trials indicated similar middle times in the two schedule types, but longer high-rate state durations in the RIFI schedules for six of six comparisons. Together, these results suggest that while timing accuracy was unaffected by the type of time marker employed, timing precision was reduced in the RIFI schedules when a response initiated the interval to food.

It is interesting that there were more relatively long first-response latencies in RIFI schedules. These findings are consistent with previous research (e.g., Shull, 1970; Rutter, 1990; Fox & Kyonka, 2013; Wynne & Staddon, 1988), but are a bit paradoxical because longer first-response latencies in RIFI schedules result in lower rates of reinforcement. In RIFI schedules, initiating the interval as early as possible after stimulus onset is necessary to maximize rate of reinforcement, yet behavior does not appear sensitive to this contingency. One explanation is that in interval schedules “linear waiting [first-response latencies increase linearly with increases in IFIs] is an obligatory process in pigeons” (Wynne & Staddon, 1988 p. 209). In other words, pigeon first-response latencies may be controlled by time between food deliveries and not necessarily by reinforcement density or response effort. Wynne & Staddon provide evidence that this “obligatory linear waiting” (p. 209) is quite robust. It also suggests that although they are used as measures of temporal control in other schedules, the responses that initiate intervals in RIFI schedules do not reflect discrimination of interval duration.

Consistent with previous research (Fox & Kyonka, 2013) and Experiment 1, response rates early in the RIFI schedules were higher than in the corresponding FI schedules in Experiment 2. Response rates from Experiment 2 provide additional evidence that the higher absolute response rates observed early in RIFI schedules relative to FI schedules are not an artifact of the longer IFIs and lower reinforcement rates observed by Fox and Kyonka, 2013 but of the response-initiating requirement in the RIFI schedule.

Accuracy and precision of timing behavior have been shown to be affected by a variety of variables. For example, reducing motivation by reducing food deprivation (Balci, Ludvig, & Brunner, 2010; Plowright, Church, Behnke, & Silverman, 2000), by manipulating reinforcer magnitude (Galtress & Kirpatrick, 2009; Ward & Odum, 2006, 2007), or by manipulating dopamine levels (Balci, Ludvig, Abner et al., 2010; Ward et al., 2009) can result in altered timing accuracy and precision. A reduction in attention via some disruptor can also result in altered timing accuracy and precision (e.g., Buhusi & Meck 2006a, 2006b; Ward & Odum, 2007). Exposing humans to an aversive event

results in estimating intervals as relatively longer in duration (e.g., Langer, Wapner, & Werner, 1961; Droit-volet & Meck, 2007; Watts & Sharrock, 1984). The administration of dopamine agonists leads to an overestimation of time and the administration of dopamine antagonists leads to an underestimation of time (e.g., Body et al., 2013; Cheung et al., 2007; Matell, Bateson, & Meck, 2006; Matell, King, & Meck, 2004).

By contrast, very little research has evaluated how interval timing is affected by differences in time-marker dimension (Caetano & Church, 2009; Fox & Kyonka, 2013). Stop times and high-rate state durations in Experiment 2 are the first positive evidence that interval timing precision may be reduced when a response marks the start of an interval compared to the onset of a light. However, it is not the first experiment to show that manipulating the physical dimensions of time markers can produce differences in timing performance. Studies have shown that auditory stimuli are consistently estimated as longer than visual stimuli of the same duration (e.g., Goldstone & Lhamon, 1974; Penny, Gibbon, & Meck, 2000); bright lights are estimated as longer in duration than dim lights of the same duration (Kraemer, Brown, & Randall, 1995); and filled intervals (constant tone) are estimated as longer in duration than empty intervals (start and end of intervals demarcated by a brief tone) of the same duration (Santi, Miki, & Hornyak, 2005).

It is possible that stimulus onset functioned as a time marker and exerted control over behavior in both FI and RIFI schedules. Temporal control of behavior may have been less precise in the RIFI schedules because the delay from stimulus onset to food delivery was variable. While possible, we think this is very unlikely. Fox and Kyonka (2013) provide substantial evidence that interval onset, not stimulus onset, controls behavior in RIFI schedules. In addition, there was no systematic correlation between first-response latencies and start times in RIFI schedules across pigeons in Experiment 2.

Comparisons of correlations between timing parameters suggested that responding in FI schedules was less variable and more controlled by stimulus onset than responding in RIFI schedules. Consistent with previous work by Church, Meck, and Gibbon (1994) comparing the pattern of correlations, start times were positively correlated with stop times and HSDs

were positively correlated with middle times for both FI and RIFI schedules in Experiment 2. Church, Meck, and Gibbon reported negative correlations between start time and HSD, but in Experiment 2, start time and HSD were slightly positively correlated in both schedule types.

It is perhaps surprising that when the time marker was a response, timing was less precise than when the time marker was an exteroceptive stimulus because timing accuracy and precision are at least in part affected by variables related to attention. Therefore, it may be predicted that timing precision would be higher in RIFI schedules than FI schedules because attending to the start of the interval is required in RIFI but not FI schedules. In FI schedules, attending to the onset of the interval seems less likely to occur on every trial—the pigeon may be engaged in grooming behavior, be turned away from the stimulus light, or be engaged in another activity that blocks attending to stimulus onset in the FI schedule—although, the likelihood of this occurring was reduced in Experiments 1 and 2 by pairing the offset of the house light with key-light onset. Following this rationale, some experimental preparations require an organism to gaze at a specific location (monkeys; e.g., Lau & Glimcher, 2005) or peck a key (pigeons; e.g., Vasconcelos & Urcuioli, 2008 but cf. Fox & Kyonka, 2014) in order to initiate a trial. The results of Experiment 2 suggest this may be at the very least a false assumption—a diffuse and salient exteroceptive stimulus is at least as, and possibly more, efficacious as a time marker than a response.

General Discussion

The results of Experiment 1 suggest that interval onset (key light in FI and first response in RIFI), not food delivery, was the salient time marker controlling behavior in both FI and RIFI schedules presented here. The results of Experiment 2 confirmed this and further, they indicated that timing precision was reduced in RIFI schedules.

Associative conditioning theories of selective attention suggest a potential explanation for the reduced temporal precision observed in RIFI schedules in Experiment 2. Mackintosh (1975) posited stimulus-specific learning rate parameters determined the magnitude of the change in

response strength attributable to each discriminative stimulus in the subject's environment. Each learning rate was determined by the amount of information conveyed by the stimulus. It may be that the "surprisingness" or the relative "distinctiveness" of an event or the response-reinforcer relation itself is what determines its utility as a time marker, and thus its control over the temporal pattern of responding.

Imagine an average "informativeness" score with a scale 0–1 is calculated for each event that predicts time to reinforcement, on the basis of all events of the same type regardless when they occurred in the interval. In RIFI 15-s schedules, the first response of the trial and the first response after the interval elapses are informative: They respectively signal that food will be available in 15 s and that food will be delivered immediately, so they are assigned a score of 1. All other responses are assigned a score of 0 because they provide no information about when food will be available. If a pigeon pecked an average 10 times per interval in RIFI 15 s, pecking was 0.2 informative—noninformative key pecks in the interval reduced the relative "distinctiveness" of the more informative ones. In FI schedules, only the last peck provides any information about food. If the same pigeon pecked 7 times per interval, informativeness of pecks would be 0.14 in the FI 15 s. However, the key-light illumination that signaled the onset of the interval always indicated that food would be available in 15 s. It was never uninformative and never redundant, so its score was 1 and its relative "distinctiveness" was not degraded by other similar stimuli. In this hypothetical example, even though pecks were less informative in FI than RIFI schedules, key-light illumination was always highly informative (even if information at a delay is assumed to decay over time), and completely distinct because there were no other key-light illuminations with scores of zero to degrade it. A highly informative and distinct cue was present in FI schedules but absent in RIFI schedules of the experiments presented here, which could account for the greater precision observed in FI schedules.

Caetano and Church (2009) controlled for such "attentional factors" (p. 299) by yoking the stimulus onset that marked the beginning of intervals in an FI 20-s schedule to responses in a differential reinforcement of low rate (DRL) schedule. Unlike RIFI schedules, DRL schedules

do not provide measures of temporal discrimination precision that can be compared directly to temporal discrimination precision in FI schedules. However, subsequent responses could not interfere with time marker efficacy in DRL schedules, because they effectively cancelled the interval. For FI and DRL schedules, respectively, stimulus onset and nose pokes occurred equally often and were equally informative and distinct. Consistent with predictions of associative conditioning theories of selective attention, temporal discrimination was equivalent in the two schedules. Taken with the differences in temporal discrimination obtained in Experiment 2, these results collectively suggest that the relative informativeness and distinctiveness of a time marker may determine its efficacy in the temporal control of behavior.

References

- Allman, M. J., DeLeon, I. G., & Wearden, J. H. (2011). Psychophysical assessment of timing in individuals with autism. *American Journal on Intellectual and Developmental Disabilities, 116*, 165–178.
- Balci, F., Ludvig, E. A., Abner, R., Zhuang, X., Poon, P., & Brunner, B. D. (2010). Motivational effects on interval timing in dopamine transporter (DAT) knockdown mice. *Brain Research, 1325*, 89–99.
- Balci, F., Ludvig, E. A., & Brunner, D. (2010). Within-session modulation of timed anticipatory responding: When to start responding. *Behavioural Processes, 85*, 204–206.
- Body, S., Cheung, T. H. C., Valencia-Torres, L., Olarte-Sanchez, C. M., Fone, K. D. F., Bradshaw, C. M., & Szabadi, E. (2013). Pharmacological studies on performance on the free-operant psychophysical procedure. *Behavioural Processes, 95*, 71–89.
- Branch, M. N., & Gollub, L. R. (1974). A detailed analysis of the effects of d-amphetamine on behavior under fixed-interval schedules. *Journal of the Experimental Analysis of Behavior, 21*, 519–539.
- Buhusi, C. V., & Meck, W. H. (2000). Timing for the absence of a stimulus: The gap paradigm reversed. *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 305–322.
- Buhusi, C. V., & Meck, W. H. (2006a). Interval timing with gaps and distractors: evaluation of the ambiguity, switch, and time-sharing hypotheses. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 329–338.
- Buhusi, C. V., & Meck, W. H. (2006b). Time sharing in rats: A peak-interval procedure with gaps and distractors. *Behavioural Processes, 71*, 107–115.
- Caetano, M. S., & Church, R. M. (2009). A comparison of responses and stimuli as time markers. *Behavioural Processes, 81*, 298–302.
- Catania, A. C. (1970). Reinforcement schedules and psycho-physical judgments: A study of some temporal properties of behavior. In W.N. Schoenfeld (Ed.), *The theory of reinforcement schedules*. New York: Appleton-Century-Croft.

- Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, 28, 155–161.
- Cheng, K., & Westwood, R. (1993). Analysis of single trials in pigeons' timing performance. *Journal of Experimental Psychology: Animal Behavior Processes* 19, 56–67.
- Cheung, T. H. C., Bezzina, G., Hampson, C. L., Body, S., Fone, K. C. F., Bradshaw, C. M., & Szabadi, E. (2007). Evidence for the sensitivity of operant timing behaviour to stimulation of D1 dopamine receptors. *Psychopharmacology*, 195, 213–222.
- Church, R. M., Meck, W. H., & Gibbon, J. (1994). Application of scalar timing theory to individual trials. *Journal of Experimental Psychology: Animal Behavior Processes*, 20, 135–155.
- Dews, P. B. (1978). Studies on responding under fixed-interval schedules of reinforcement: II. The scalloped pattern of the cumulative record. *Journal of the Experimental Analysis of Behavior*, 29, 67–75.
- Droit-Volet, S., & Meck, W. H. (2007). How emotions colour our perception of time. *Trends in Cognitive Sciences*, 11, 504–513.
- Fox, A. E., & Kyonka, E. G. E. (2013). Pigeon responding on fixed-interval and response-initiated fixed-interval schedules. *Journal of the Experimental Analysis of Behavior*, 100, 187–197.
- Fox, A. E., & Kyonka, E. G. E. (2014). Choice and timing in pigeons under differing food deprivation states. *Behavioural Processes*, 106, 82–90.
- Freestone, D. M., & Church, R. M. (2010). The importance of the reinforcer as a time marker. *Behavioural Processes*, 84, 500–505.
- Galtress, T., & Kirkpatrick, K. (2009). Reward value effects on timing in the peak procedure. *Learning and Motivation*, 40, 109–131.
- Gentry, G. D., Weiss, B., & Laties, V. G. (1983). The microanalysis of fixed-interval responding. *Journal of the Experimental Analysis of Behavior*, 39, 327–343.
- Goldstone, S., & Lhamon, W. T. (1974). Studies of auditory-visual differences in human time judgment: Sounds are judged longer than lights. *Perceptual and Motor Skills*, 39, 63–82.
- Guilhardi, P., & Church, R. M. (2004). Measures of temporal discrimination in fixed-interval performance: A case study in archiving data. *Behavior Research Methods, Instruments, & Computers*, 36, 661–669.
- Guilhardi, P., & Church, R. M. (2005). Dynamics of temporal discrimination. *Learning and Behavior*, 33, 399–416.
- Higa, J. J., Wynne, C. D. L., & Staddon, J. E. R. (1991). Dynamics of time discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, 17, 281–291.
- Kirkpatrick, K., Miller, S. S., Betti, C. A., & Wasserman, E. A. (1996). Cyclic responding by pigeons on the peak timing procedure. *Journal of Experimental Psychology: Animal Behavior Processes*, 22, 447–460.
- Kraemer, P. J., Brown, R. W., & Randall, C. K. (1995). Signal intensity and duration estimation in rats. *Behavioural Processes*, 34, 265–268.
- Kyonka, E. G. E., & Grace, R. C. (2010). Rapid acquisition of choice and timing and the provenance of the terminal-link effect. *Journal of the Experimental Analysis of Behavior*, 94, 209–225.
- Langer, J., Wapner, S., & Werner, H. (1961). The effect of danger upon the experience of time. *American Journal of Psychology*, 74, 94–97.
- Lau, B., & Glimcher, P. W. (2005). Dynamic response-by-response models of matching behavior in rhesus monkeys. *Journal of the Experimental Analysis of Behavior*, 84, 555–579.
- Lejeune, H., & Wearden, J. H. (1991). The comparative psychology of fixed-interval responding: Some quantitative analyses. *Learning and Motivation*, 22, 84–111.
- Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review*, 82, 276–298.
- Matell, M. S., Bateson, M., & Meck, W. H. (2006). Single-trials analyses demonstrate that increases in clock speed contribute to the methamphetamine-induced horizontal shifts in peak-interval timing functions. *Psychopharmacology*, 188, 201–212.
- Matell, M. S., King, G. R., & Meck, W. H. (2004). Differential modulation of clock speed by the administration of intermittent versus continuous cocaine. *Behavioral Neuroscience*, 118, 150–156.
- Mechner, F., Guevrekian, L., & Mechner, V. (1963). A fixed interval schedule in which the interval is initiated by a response. *Journal of the Experimental Analysis of Behavior*, 6, 323–330.
- Monteiro, T., & Machado, A. (2009). Oscillations following periodic reinforcement. *Behavioural Processes*, 81, 170–188.
- Nevin, J. A. (1971). Rates and patterns of responding with concurrent fixed-interval and variable-interval reinforcement. *Journal of the Experimental Analysis of Behavior*, 16, 241–247.
- Penny, T. B., Gibbon, J., & Meck, W. H. (2000). Differential effects of auditory and visual signals on clock speed and temporal memory. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 1770–1787.
- Plowright, C. M. S., Church, D., Behnke, P., & Silverman, A. (2000). Time estimation by pigeons on a fixed interval: the effect of pre-feeding. *Behavioural Processes*, 52, 43–48.
- Rammsayer, T., & Classen, W. (1997). Impaired temporal discrimination in Parkinson's disease: Temporal processing of brief durations as an indicator of degeneration of dopaminergic neurons in the basal ganglia. *International Journal of Neuroscience*, 91, 45–55.
- Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 242–268.
- Roberts, S., & Church, R. M. (1978). Control of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 4, 318–337.
- Rutter, S. (1990). Responding initiated by pecks on a start key. *Behavioural Processes*, 21, 59–67.
- Santi, A., Miki, A., & Hornyak, S. (2005). The perception of empty and filled time intervals by rats. *Behavioural Processes*, 71, 144–156.
- Schneider, B. A. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior*, 12, 677–687.
- Shull, R. (1970). A response-initiated fixed-interval schedule of reinforcement. *Journal of the Experimental Analysis of Behavior*, 13, 13–15.
- Skinner, B. F. (1938). *The behavior of organisms*. New York: Appleton-Century-Crofts.

- Vasconcelos, M., & Urciuoli, P. J. (2008). Deprivation level and choice in pigeons: A test of within-trial contrast. *Learning & Behavior, 36*, 12–18.
- Ward, R. D., & Odum, A. L. (2006). Effects of prefeeding, intercomponent-interval food, and extinction on temporal discrimination and pacemaker rate. *Behavioural Processes, 71*, 297–306.
- Ward, R. D., & Odum, A. L. (2007). Disruption of temporal discrimination and the choose-short effect. *Learning & Behavior, 35*, 60–70.
- Ward, R. D., Kellendonk, C., Simpson, E. H., Lipatova, O., Drew, M. R., Fairhurst, S., & Balsam, P. D. (2009). Impaired timing precision produced by striatal D2 receptor overexpression is mediated by cognitive and motivational deficits. *Behavioral Neuroscience, 123*, 720–730.
- Ward, R. D., Kellendonk, C., Kandel, E. R., & Balsam, P. D. (2012). Timing as a window on cognition in schizophrenia. *Neuropharmacology, 62*, 1175–1181.
- Watts, F. N., & Sharrock, R. (1984). Fear and time estimation. *Perceptual and Motor Skills, 59*, 597–598.
- Weaver, M. T., & Branch, M. N. (2008). Tolerance to effects of cocaine on behavior under a response-initiated fixed-interval schedule. *Journal of the Experimental Analysis of Behavior, 90*, 207–218.
- Wynne, C. D. L., & Staddon, J. E. R. (1988). Typical delay determines waiting time on periodic-food schedules: Static and dynamic tests. *Journal of the Experimental Analysis of Behavior, 50*, 197–210.

Received: April 13, 2014

Final Acceptance: November 10, 2014