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Effects of Increasing the Time to Reinforcement on Interval Timing in Rats*

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The experiment examined interval timing in rats during a momentary, unsigned, increase in the time to reinforcement. A session began with intervals programmed according to a fixed interval (FI) 60 s reinforcement schedule, changed to either an FI 90 s, FI 120 s, or FI 180 s schedule at an unpredictable point, and then returned to an FI 60 s schedule after 1, 8, or 24 successive long intervals had elapsed. Overall, postreinforcement wait time duration increased with increases in the scheduled time to reinforcement. The amount by which wait time increased did not depend on the duration of longer intervals, but did depend on the number of longer intervals intercalated into a session. The results indicate that rats are sensitive to moment-by-moment changes in the time to reinforcement and support other studies showing an asymmetry between timing upward and downward shifts in the criterion for reinforcement of an FI schedule.

When exposed to periodic reinforcement, most animals adapt to the time when reinforcers are available by showing a distinctive change in the organization of their behavior during the interval time between reinforcers – that is, animals appear to “time” the interval. One example comes from fixed interval (FI) reinforcement schedules. During an FI schedule, a reinforcer is available after a fixed amount of time has elapsed since delivery of the preceding reinforcer. Most animals and humans readily learn about the regularity of the criterion interval between reinforcers, so that they pause or *wait* after reinforcement before they start responding. Following the post-reinforcement *wait time* there is either a gradual acceleration in responding (e.g., Ferster & Skinner, 1957) or an abrupt change from a low to high rate of responding called a “break-and-run” (Schneider, 1969) as the end of the interval nears. The entire process is termed *interval timing*.

A characteristic of interval timing is *proportional timing* (e.g., Gibbon, 1977; Richelle & Lejeune, 1980). This is a result in which dependent measures such as wait time duration and the location of a break-point in an interval are proportional to the time between reinforcers (e.g., Dews, 1970). The break point in an interval, when responding shifts from a low to high rate, is about two-thirds the FI requirement (e.g., Schneider, 1969). Wait time is generally a smaller fraction of the

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interval requirement, ranging from one-fourth to one-half the interval duration depending on the species and range of intervals studied (e.g., Lowe & Harzem, 1977; Shull, 1970; Wynne & Staddon, 1988).

The problem of how organisms time is usually approached from the view of psychophysics (e.g., Gibbon & Allan, 1984), where the focus is on generating steady-state levels of performance and testing the limits or capacity of the system (e.g., Stebbins, 1970). For example, most studies focus on performance measured after extensive training and hundreds of trials of exposure to a single interval (e.g., Cheng & Westwood, 1993; Innis, 1981; Meck & Church, 1984; Schneider, 1969). In contrast, other methods measure timing under changing, dynamic situations.

Studies on temporal dynamics show that rats and pigeons readily detect within (e.g., Church & Lacourse, 1998; Higa & Staddon, 1997; Wynne & Staddon, 1988) and across session (e.g., Lejeune, Ferrara, Simons, & Wearden, 1997; Wynne & Staddon, 1992) changes in the prevailing time to reinforcement, often after a single trial. For example, Higa, Wynne, and Staddon (1991) presented pigeons a sequence of intervals consisting of 99 15-s intervals and a single 5-s interval. The location of the short interval was randomized across sessions and its occurrence was not signaled. For the majority of birds, a short interval decreased wait time in the next interval. In other words, wait time “*tracked*” the change in the interval requirement for reinforcement. Furthermore, a short interval changed wait time only in the next interval: After an initial decrease, wait time quickly returned to levels seen in intervals before the short interval (called a “one-back” effect). Lejeune et al. (1997) reported similar rapid-timing effects with a peak-procedure. They varied, across sessions, the criterion for reinforcement (i.e., the FI requirement) and found that rats readily tracked changes in the criterion, measured as the peak time of responding during probe trials. These results indicate that part of the timing mechanism is fast acting and is sensitive to within and across session changes in the properties of individual intervals.

What happens when long intervals are intercalated into a series of shorter intervals or when there is a transition to longer intervals? Experimental results show that the adjustment in wait time to longer intervals is gradual, in comparison to timing a decrease in the interval requirement. For example, Wynne and Staddon (1992) showed that pigeons’ wait times adjusted almost immediately to a decrease in the interval duration and more slowly in response to an increase in the interval under conditions in which the intervals change across sessions. Higa, Thaw, and Staddon (1993) also reported similar effects (with pigeons) when changes in the interval requirement occur within a session. They exposed pigeons to a series of intervals that either decreased (Step-Down) or increased (Step-Up) in duration. During the Step-Down condition, wait time decreased after the first short interval and remained short in subsequent intervals. However, during the Step-Up condition, wait time increased after the first long interval and continued to increase (gradually) across several intervals. Rats show similar timing dynamics during a single upward and downward shift in the criterion for reinforcement (e.g., Higa, 1997a).

These results suggest that rats and pigeons track both increases and decreases in the interval duration, although the overall pattern of adaptation differs. However, Higa (1997b) reports a different set of results, using a variation of the Step-Down and Step-Up procedure. Rats were exposed to two schedules: During a short square wave (SSW) schedule, the intervals changed twice per session from 120 to 30 to 120 s; during a long square wave (LSW) schedule, the intervals changed from 120 to 480 to 120 s. The rats tracked the SSW condition, but failed to track a brief transition to longer intervals in the LSW condition. Wait time was approximately the same in all intervals. Pigeons, too, do not track increases in the interval requirement during repetitive (cyclic) transitions, under chronic conditions (e.g., Innis & Staddon, 1970; Staddon, 1967).

Why do animals track a single transition to longer intervals (e.g., Step-Up), but fail to track long intervals when the intervals are intercalated into a series of shorter intervals (e.g., LSW)? At least four factors may explain these results. First, from an empirical point of view, the number of transitions in a sequence of intervals and experience with these transitions may account for tracking and failures to track. If so, then animals should track a LSW sequence early in training. The first transition to longer intervals in a LSW series is identical to a Step-Up series, which animals are able to track albeit tracking is gradual. Unfortunately, previous studies (e.g., Higa, 1997b; Innis & Staddon, 1970) have not reported whether tracking occurs early during training and deteriorates over time. Second, the failure to track may depend on the relatively long interval durations used (8 min in the rat study, 3 and 6 min in the pigeon studies). Third, performance may depend on the number of long intervals intercalated into the short-interval series. If adaptation of wait time to an increase in the interval duration is gradual (as indicated by the Step-Up results), then increasing the number of long intervals within a series will provide an opportunity to observe an increase in wait time duration. Fourth, failure to track may also depend on the magnitude of change in the interval requirement. As far as we can determine, no study has yet systematically examined the effect of varying the magnitude of change on temporal tracking.

In the present study, we address these issues by systematically varying the number and duration of long intervals intercalated into a series of relatively shorter intervals. We examined magnitude effects by varying the difference between the duration of long and shorter interval durations, so that the intervals changed from 60 s to either 90, 120, or 180 s, and then returned to 60 s.

Method

Subjects

Five adult male Sprague Dawley rats, at the start of the study, served as subjects. The rats were already trained to lever press and had limited experience with a continuous reinforcement schedule, but they were naïve with respect to the timing procedure used in this study. They were tested five to six days a week and given supplementary food at the end of each day to maintain them at approximately 80% of their free-feeding body weight. Rats had free-access to water in their home cage and were housed singly in a colony with a 12:12-h light:dark cycle (light on at 07:00 h). The experiment took place during the light part of the cycle.

Apparatus

We conducted the experiment in five standard operant chambers. Each chamber was approximately 20 cm high, 27 cm wide, and 31 cm deep. Mounted on the front panel of each chamber was a flat lever, 5 cm x 2 cm, located 3.5 cm above the floor and 8 cm from the right wall to the center of the lever. Mounted directly above the lever was a lamp approximately 3 cm in diameter. The chamber provided access to liquid reinforcers (diluted condensed milk) through an aperture 3 cm by 3 cm and 5 cm to the left of the lever, center to center. A light located on the back wall illuminated the chamber. A sound attenuating apparatus enclosed each chamber and a ventilation fan masked extraneous noise. An IBM-compatible computer (located in an adjacent room) and a program written in BASIC for windows controlled the experimental events and recorded all lever presses emitted by each subject.

Procedure

For all conditions, a session began with the delivery of a reinforcer (marking the start of a session and the first interval) followed by 50 intervals programmed according to an FI schedule. The houselight remained on throughout a session; the light above the lever was always on except when a reinforcer was being delivered. Reinforcement consisted of a 3-s access to a 0.10 ml dipper holding a 2:1 mixture of water and condensed milk.

The experiment consisted of three phases. During Phase 1, we exposed rats to a baseline condition in which all intervals delivered reinforcers according to an FI 60 s schedule. During the experimental conditions (following this baseline phase), we intercalated 1, 8, or 24 FI 180 s intervals into the series of FI 60 s intervals, holding constant the number of intervals in a session (to 50). The FI 180 s intervals always occurred in succession, and we randomized their location in a session with one constraint: At least 10 FI 60 s intervals had to occur before the first and after the last FI 180 s interval. We varied the number of FI 180 s intervals across sessions such that each condition (1, 8 or 24 intervals) occurred once in a block of 3 sessions, for five blocks. Phases 2 and 3 were similar to Phase 1, except the longer intervals were FI 120 s and FI 90 s, respectively. We conducted a baseline condition before each phase and after the final phase of the study. All rats received the same conditions and number of sessions per condition, with the exception of rat 15 (Phase 1) and rat 14 (Phase 3). The number of sessions of exposure to each condition remained the same for these subjects, however, because of human error, they received a different sequence of 1, 8, and 24 long-intervals.

Results

Figures 1, 2, and 3 present mean wait time duration for all subjects and the group from Phase 1, 2, and 3, respectively. Figure 4 presents mean wait time from the final baseline condition (conducted after Phase 3 of the study). For all baseline conditions, we present mean wait time in all intervals. For the experimental conditions, varying the location of a transition to, and number of, longer FI intervals meant that a variable number of short FIs preceded and followed the long-FI set. Therefore, to determine the effect of a transition on responding we extracted, from each session, wait time from the long-FI set and the 10 FI 60 s intervals preceding and following the long-FI set, for a total of 21, 28, and 44 intervals out of 50 for the 1, 8, and 24 conditions, respectively. For all conditions, baseline and experimental, we based mean wait times on all sessions of training, 10 total for baseline conditions and five for the experimental conditions.

Baseline Conditions

Overall, wait time appears to increase slightly within a session. For exam-

ple, in Figure 1, the average wait time during the first five intervals is approximately 27 s and increases to roughly 36 s in the last five intervals. A two-way

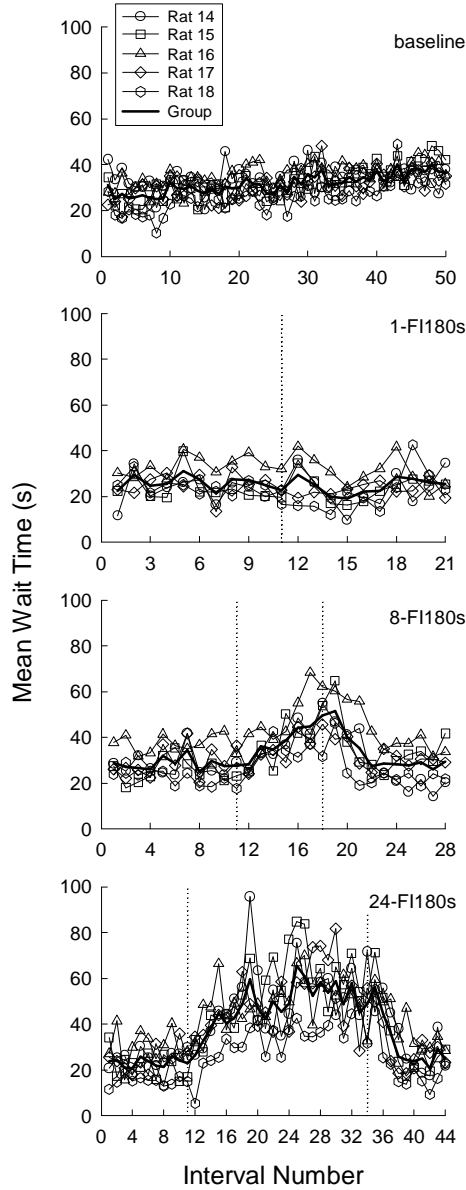


Figure 1. Results from Phase 1 of the study. The top panel shows mean wait time in each of the intervals of the baseline condition, for all rats and the group. The other panels show mean wait time from conditions in which the number of long FI 180 s intervals varied, specifically, wait time during the long interval(s) and the 10 FI 60 s intervals preceding and following a set of long intervals. The dashed vertical lines mark the occurrence of the first and last FI 180 s intervals. In the 1-FI 180 s case, only one dashed line is given. See text of details about which intervals were extracted from each session.

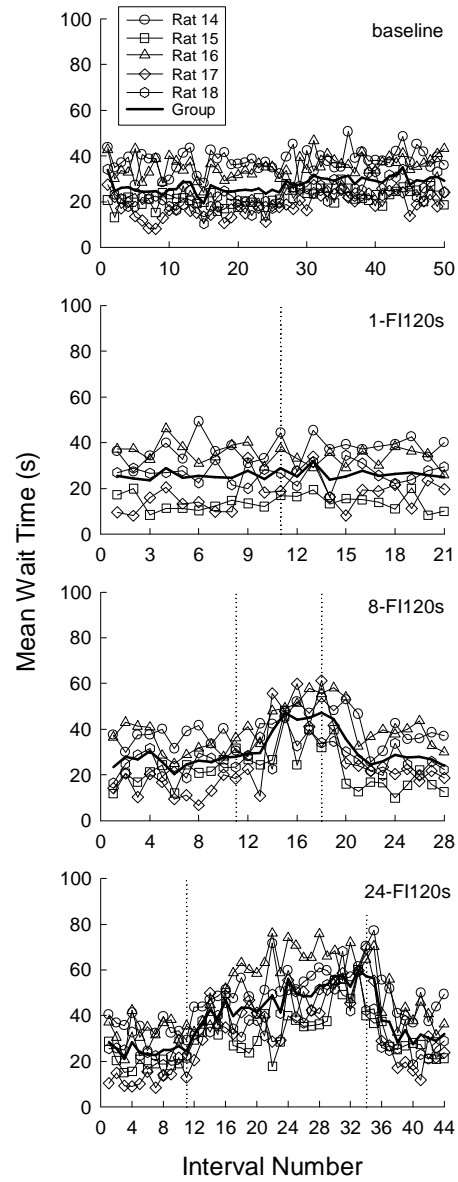


Figure 2. Results from Phase 2 of the study. The top panel shows mean wait time in each of the intervals of the baseline condition, for all rats and the group. The other panels show mean wait time from conditions in which the number of long FI 120 s intervals varied, specifically, wait time during the long interval(s) and the 10 FI 60 s intervals preceding and following a set of long intervals. The dashed vertical lines mark the occurrence of the first and last FI 120 s intervals. In the 1-FI 120 s case, only one dashed line is given. See text of details about which intervals were extracted from each session.

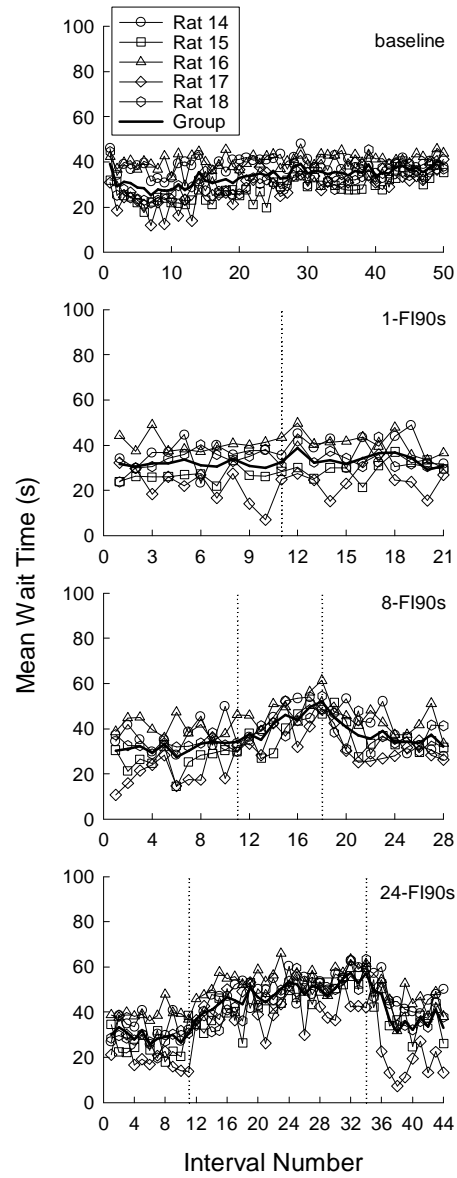


Figure 3. Results from Phase 3 of the study. The top panel shows mean wait time in each of the intervals of the baseline condition, for all rats and the group. The other panels show mean wait time from conditions in which the number of long FI 90 s intervals varied, specifically, wait time during the long interval(s) and the 10 FI 60 s intervals preceding and following a set of long intervals. The dashed vertical lines mark the occurrence of the first and last FI 90 s intervals. In the 1-FI 90 s case, only one dashed line is given. See text of details about which intervals were extracted from each session.

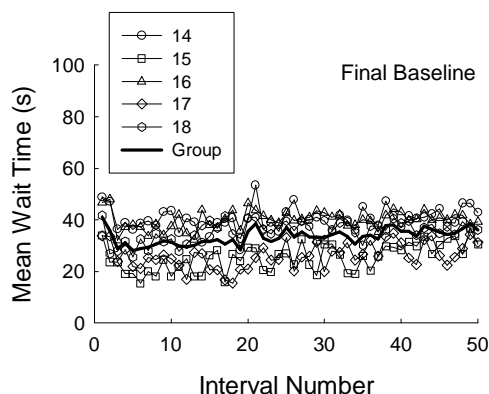


Figure 4. Mean wait time in each of the intervals from the last baseline condition of the study, for all rats and the group.

repeated-measure analysis of variance (ANOVA) conducted on interval number (within a session) and baseline number revealed a significant difference (alpha level set at 0.05 for all the analyses) in overall wait time duration across the four baseline conditions, $F(3,588) = 3.717$. Wait time also changed across the intervals within a session, $F(49,588) = 7.969$. Finally, there was a significant interaction between baseline and interval number, $F(147,588) = 1.384$.

Effect of the Number of Long Intervals

A single long interval intercalated into a series of FI 60 s intervals did not produce systematic changes in wait time, regardless of the duration of the long interval. Wait time in the interval following a single long interval (interval number 11 in the figures) appears slightly longer than that in the preceding intervals. For example, in Figure 3, wait time in intervals 11 and 12 increase from about 33 to 39 s, respectively. However, the effect was not statistically significant. In comparison, wait times did change systematically in the 8- and 24-long interval conditions. For example, during the 8-FI 180 s condition (Figure 1), overall wait time increased from 30 s (during the FI 60 s preceding a transition) to about 50 s (during the FI 180 s intervals). Similarly, during Phase 3 (Figure 3), wait time increased from approximately 30 s in the FI 60 s intervals to about 57 s in the 24 FI 90 s intervals.

To determine whether the changes seen in the 8- and 24-long interval conditions were significant, we conducted a two-way repeated measures ANOVA on wait time before, during and after a set of long intervals. Specifically, we compared mean wait time from the 10 intervals preceding the first long FI-interval (intervals 1–10 in the figures), the long FI-intervals (intervals 11–18 for the 8 long interval conditions and intervals 11–34 for the 24 long interval conditions), and the 10 intervals following the last long FI-interval (intervals 19–28 for the 8 long interval conditions and intervals 35–44 for the 24 long interval conditions).

The analysis revealed a significant interaction effect between changes in wait time during the different intervals in a session (i.e., before, during, or after a long-set of intervals) that depended on the number of long intervals a session, for the FI 180 s conditions, $F(2,8) = 17.820$, and FI 120 s conditions, $F(2,8) = 8.761$. Pairwise multiple comparisons using a Tukey Test indicate that wait time was longer during 24 FI 180 s intervals than 8 FI 180 s intervals, $q = 5.810$. Wait times were also significantly longer during 24 FI 120 s intervals than 8 FI 120 s intervals, $q = 7.484$, conditions. Another set of pairwise comparisons conducted on wait times from the 10 intervals *following* a long-set (i.e., during FI 60 s intervals) revealed no significant differences between the 24-FI 180 s or 8-FI 180 s conditions, $q = 0.815$. However, wait times were significantly longer during FI 60 s intervals when those intervals were preceded by 24 FI 120 s intervals than when they were preceded by only 8 FI 120 s intervals, $q = 4.678$.

Effect of the Duration of the Long Intervals

The data presented in the figures suggest that wait time was shorter, overall, in Phase 3. However, a two-way repeated measures ANOVA on wait time, with duration of longer intervals (FI 180 s, FI 120 s, or FI 90 s) and changes in interval duration within a session as the factors, was not significant for the 8, $F(2,16) = 2.534$, and 24, $F(2,16) = 0.850$, long interval conditions.

Discussion

Previous studies indicate that the adjustment of wait time to a single within-session increase in the interval requirement is gradual in comparison to timing a decrease in the duration of the interval. For example, when intervals change from 15 to 5 s within a session, pigeon wait times decrease after the 5-s interval and remained the same (i.e., short) in subsequent intervals. In contrast, when the interval requirement changes from 15 to 45 s, wait time increases after the first 45-s interval and continues to increase gradually across several intervals (Higa, et al., 1993). Rats show similar timing dynamics during single upward and downward shifts in the criterion for reinforcement (e.g., Higa, 1997a). However, rats and pigeons are sometimes unable to track a series with more than one transition in the interval requirement, as is found during cyclic and non-cyclic square-wave interval series. Wait times do not change according to the changes in the interval duration; instead, wait times are approximately the same duration in all intervals (Higa, 1997b; Innis & Staddon, 1970; Staddon, 1967).

To understand these results, the present study focused on how rats time a temporary transition to longer intervals, and how temporal performance depends on the number and duration of long intervals intercalated into a series of shorter intervals. First, we found that rats do not track a single long interval. This differs from previous studies that show animals readily track a single shorter interval among longer intervals. For example, Higa et al. (1991) report results from a study with pigeons in which a single 5-s interval was intercalated in a series of 99, 15-s intervals: The pigeons decreased their wait time in the interval immediately following the

5-s interval. Second, in contrast to previous studies (e.g., Higa, 1997b) our rats tracked a temporary transition to 8 and 24 long-intervals. Wait time was significantly longer during the FI 120 s and FI 180 s intervals in a series, and changed gradually over several of the longer intervals. The gradual increase is similar to that found when the time to reinforcement increases once in a session (e.g., Step-Up condition, Higa et al., 1993, 1997a).

Third, overall performance during a set of long intervals depended on the number of long intervals appearing in the series. Specifically, wait time was longer during 24 than eight FI 180 s and FI 120 s intervals. We did not observe differences between wait time from the 24 and eight FI 90 s intervals. Given the gradual adaptation of wait time to longer intervals, it is probably not surprising that increasing the number of long intervals produced longer wait times: More intervals provided an opportunity for wait times to continue to increase in duration with each successive long-interval.

Fourth, a hallmark of interval timing is proportional timing (e.g., Richelle & Lejeune, 1980; Schneider, 1969), which is when a temporal dependent measure of timing (e.g., postreinforcement wait time) is proportional to variations in an independent variable (e.g., the interval requirement of an FI schedule). In the present study, we expected to find evidence of proportional timing. Wait time should have increased with increases in the FI requirement, from FI 60 (baseline) to FI 90, FI 120, and FI 180 s. Instead, when looking at performance from just the long intervals, we found that wait time was generally longer during 8 and 24 long-intervals in a session (i.e., animals tracked the within-session increase in the FI requirement), but the amount by which wait times increased did not depend on the prevailing FI duration.

Together, these results point to several key processes in understanding the conditions under which animals track, and fail to track, unsignaled changes in the prevailing interval duration. For one, a reliable finding is an *asymmetry* in timing increases and decreases in the time to reinforcement: rapid during a decrease in the interval duration and gradual during an increase. As in previous studies (e.g., Higa et al., 1993), our rats' wait times adapted gradually to an increase in the interval duration. The pattern of responding during long intervals may be explained as a form of hysteresis: Effects from short intervals in a rat's recent experience can have a persistent effect on behavior, causing an animal to respond "short" during longer intervals (e.g., Higa, 1996; Wynne & Staddon 1992). For example, suppose we exposed a rat to a series of intervals consisting of more long (say 75%) than short intervals (25%). One could assume that the rat's memory for long intervals is stronger, and as a result, will have a stronger tendency to emit a long wait time. However, because short wait times (i.e., latencies) necessarily occur before longer wait times, the tendency to respond short, even though it may be weak, necessarily preempts a tendency to respond long during long intervals (e.g., Staddon & Higa, 1991). In our experiment, a "preemption" effect from short intervals may explain the gradual increase in wait times during a transition to longer intervals.

Next, previous studies with pigeons show that the effect of a short interval is not always localized to wait time in the next interval (i.e., a one-back effect). Instead, the frequency of the occurrence of an interval can change wait times in future,

upcoming, intervals. For instance, wait times following eight shorter intervals were shorter overall than that after one or two short intervals (e.g., Higa, 1996). Our results support this general effect, but with transitions to longer intervals, in two ways. First, overall wait time duration was longer during 24 in contrast to 8 long-intervals. Second, wait times *after* a set of long intervals were generally longer after 24 FI 120 s intervals than after just eight FI 120 s intervals.

It is important to note that the pattern of wait times we obtained may be related to a *within-session* effect (e.g., McSweeney, Hatfield, & Allen, 1990). Several studies show systematic changes in responding as a function of time in a session. A typical pattern is an increase then decrease in response rate as a session progresses (e.g., McSweeney & Hinson, 1992). In our study, baseline levels of responding – an initial decrease followed by an increase in wait time duration – may have been part of a similar process. However, given that the location of a set of long intervals varied across sessions, it is unlikely that the pattern of responding during an experimental condition is the exclusive result of a process that occurs irrespective of changes in the programmed time to reinforcement.

Finally, while we observed one-back tracking during the 8- and 24-long interval conditions, increasing with increases in the programmed interval duration, overall wait time was approximately the same during these longer intervals. Given that chronic exposure to a periodic reinforcement schedule usually produces proportional timing (e.g., Dews, 1970; Gibbon, 1977; Richelle & Lejeune, 1980; Schneider, 1969; Staddon, 1965), we expected to find an increase in wait time with increases in the magnitude of the FI value. It might be argued that wait times did not differ during the long FI intervals because of a ceiling effect on wait time duration or that rats are unable to discriminate intervals larger than 90 s. However, previous studies report temporal control (with wait time as a dependent measure) with longer FI values in a large range (e.g., FI 15 s to FI 480 s, Lowe, Harzem, & Spencer, 1979). On the other hand, failures to find changes in wait time may be related to the persistent effect from the short (FI 60 s) intervals preceding a transition to longer intervals. Many long (FI 180, FI 120, FI 90 s) intervals may be needed to “overcome” the effect of the preceding FI 60 s intervals. As we stated earlier, the tendency to respond “short” may preempt a tendency to respond “long.” Indeed, our data show that wait times sometimes continued to increase across the long FI-intervals.

It is not clear to what extent our results depend on the order of conditions. Our results (specifically failure to find proportional timing) may depend on exposure to the longest FI schedule in the first condition. However, there is little evidence from previous studies that timing dynamics depends on the order of conditions (e.g., Wynne & Staddon, 1988). Nevertheless, proportional timing is usually observed after chronic and “massed” exposure to an interval duration. In the present study, the number of long intervals (1, 8, or 24) varied across sessions. Moreover, we exposed our rats to each condition for only five sessions at a time. It may be that chronic exposure is necessary for observing proportional timing.

To conclude, the present study shows that interval timing is sensitive to an un signaled increase in the interval requirement of an FI reinforcement schedule. Rats adapt to an upward transition by gradually increasing their wait time across

several intervals. When the interval requirement returns to a baseline level, wait times also gradually decrease. The overall pattern depended on the number but not the duration of longer intervals in a session. However, wait times during the long intervals did result in proportional timing. A test for future experimental and theoretical work is to understand how timing depends on interactions among individual intervals, by determining how temporal performance depends on the number of intervals preceding a transition and the effect of “massed” exposure to a condition.

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