

Internal Clock and Memory Processes in Animal Timing

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Temporal control of behavior was investigated within the framework of an internal clock model. Pigeons were exposed to signaled fixed-interval 30-s trials mixed with extended unreinforced (baseline) trials. On unreinforced break trials, the signal was interrupted for a period of time after trial onset. In Experiment 1, comparisons between the peak time obtained on baseline and on break trials produced peak time shifts that were longer than those expected if the clock had stopped during the break but shorter than if the clock had reset. In Experiment 2, systematic manipulations of duration and location of breaks produced peak time shifts that were nonlinear functions of break duration and that varied linearly with break location. The obtained peak times were more consistent with a continuous memory decay model than with the stop–retain or the reset hypotheses.

Current research on animal timing has been guided by a model known as the “internal clock” (Church, 1978; Treisman, 1963). According to the clock model proposed by Gibbon and Church (e.g., Church, 1984; Gibbon & Church, 1984; Gibbon, Church, & Meck, 1984), the onset of the signal on a discrete fixed-interval (FI) trial closes a switch that gates pulses to an accumulator. At the time of reinforcement, the accumulated pulses are stored in reference memory, establishing a distribution of values related to the reinforced duration. On subsequent trials the signal causes retrieval of a value from reference memory. Responding is based on a discrepancy rule and a decision threshold. The difference between the current accumulated time (working memory) and the reference memory value is constantly updated. Responding occurs when the ratio of that difference to the reference memory value falls below the decision threshold. As trial time elapses, the relative difference decreases and the probability of responding increases. However, if reinforcement is omitted and the trial signal remains on beyond the expected time of reinforcement, the relative discrepancy grows and responding decreases again. This account suggests that the temporal locus of maximum rate (peak time) should be close to the reinforced duration and that peak time may

be taken as the subject’s estimate of the programmed FI value.

This research was concerned with performance of the clock when the FI signal was briefly interrupted (break) during the trial. Previous research with this paradigm has produced mixed results: S. Roberts (1981, Experiment 2) reported data suggesting that the clock stopped accumulating time during the break and that postbreak time was added to the accumulated prebreak time. By contrast, W. A. Roberts, Cheng, and Cohen (1989) concluded that the clock reset during the break.

The results of these and of other studies using different procedures (e.g., Church, 1978, 1980; S. Roberts & Church, 1978) have raised the possibility that animals may adopt one of two different timing strategies—stopping or resetting—when confronted with within-trials stimulus change. However, outcomes that have been taken as indicating that the clock stops (the switch opens during the break) also imply retention of the accumulated time in working memory during the break. Furthermore, outcomes suggesting resetting indicate only that the time value in working memory at the end of the break was zero, with no direct implication for switch operating mode. Therefore, stopping and resetting cannot be considered to be mutually exclusive timing strategies resulting from differential operation of a single mechanism. Instead, they may be regarded as dichotomous outcomes that reflect the combined effects of two different components of the internal clock model: switch and working memory.

In Experiment 1 we used double dissociation tests in an attempt to clearly distinguish between outcomes and explanations involving switch operation, working memory operation, or both. Timing was studied using a peak procedure (Catania, 1970; S. Roberts, 1981), under which signaled FI trials are mixed with unreinforced test trials. On test trials, the signal remains on much longer than the FI value. The mean rate of responding on these trials increases as a function of time with a maximum (peak) near the FI value and then decreases. Location of the peak is taken as an index of the expected time of reinforcement (i.e., the reference memory value retrieved for that trial).

On test break trials, the signal is interrupted for a few seconds. If the switch opens at break onset and closes at the

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end of the break, and if accumulated time is retained during the break, then peak time on break trials will depend only on the duration of the break. We refer to this as the *stop-retain hypothesis*. It predicts that breaks of the same duration will yield similar peak times and that breaks of different durations will produce different peak times independently of the location of the breaks.

If breaks reset the working memory value, then peak time will depend only on the location of the break. We call this the *reset hypothesis*. If working memory resets at break onset, and if the switch remains closed, then breaks identical in onset times should yield similar peak times independently of break duration. On the other hand, if reset occurs at the end of the break, then breaks with identical ending times should yield similar peak times independently of the duration of the breaks.

Applying a similar logic, S. Roberts (1981, Experiment 2) used breaks that differed in duration, location, or both. Although two breaks of the same duration (5 s) yielded similar peak times independently of location (10 and 15 s after trial onset), and different from the peak time produced by a longer break (10 s), the peak times for all break types were delayed more than would have been expected if duration of the break were the only controlling factor. S. Roberts proposed that this unpredicted finding might have been attributable to either differential switch latency for opening and closing or partial resetting.

We evaluated an alternative explanation of these results, one that was based on a memory decay model, in Experiment 2. According to the memory decay view, the switch opens at break onset (i.e., the clock stops accumulating time). However, the time accumulated before the break is gradually lost during the break, thereby producing more delayed peak times than those predicted by the stop-retain hypothesis but less delayed than those predicted by the reset hypothesis. In addition, if a break is long enough, it may produce a peak time increase that would be indistinguishable from that predicted by the reset hypothesis.

This description is compatible with the subjective shortening process proposed by Spetch and Wilkie (1983) to account for the *choose-short effect* found in many delayed matching-to-sample (DMTS) experiments, the trace decay hypothesis advanced by W. A. Roberts and Grant (1976), or the reduction of event saliency invoked by Staddon (1984). It is also consonant with mathematical formulations of memory decay found in the animal and human literature (McCarthy & White, 1987; Watson & Blampied, 1989; White, 1985; Wickelgren, 1977; Wixted & Ebbesen, 1991).

Experiment 1

Following the double dissociation rationale, we used three breaks differing in duration, location, or both to evaluate the adequacy of the stop-retain model versus reset model. According to the stop-retain prediction, breaks of different durations should yield different peak times, and breaks of the same duration should produce identical peak times independently of location. According to the reset predictions, breaks differing in duration with identical onset times should pro-

duce similar peak times if reset occurs at break onset and the switch remains closed during the break. However, if reset occurs at the end of the break or if the switch does not close until signal resumption, breaks differing in duration ending at the same time should produce similar peak times. The temporal parameters (duration and placement) that defined the break types (early, late, and long) were chosen to distinguish between these predictions.

Method

Subjects

Six experimentally naive, adult male White Carneaux pigeons were maintained at 80% of their free-feeding weights. They were housed individually in stainless steel cages with water and grit continuously available in a room maintained on a 12:12 light-dark cycle. Experimental sessions were conducted 5 days a week during the first half of the light portion of the cycle. The 6 pigeons were randomly assigned to two squads and within each squad to one of the three experimental chambers. All 3 birds in a squad were run simultaneously.

Apparatus

Sessions were conducted in three standard size (36.8 cm × 50.8 cm × 34.3 cm) pigeon chambers with white sides and rear walls (BRS/LVE, Model 132-02) containing three-key aluminum front panels. Three Industrial Electronic Engineers, Inc. (IEE) stimulus projectors (BRS/LVE, Pattern IC-900-696) were used to transilluminate the clear lucite center keys with white light. The side keys remained dark throughout the session. Masking noise was provided by ventilation fans and white noise delivered through speakers mounted behind the front panels. All experimental contingencies and response recording were controlled by an IBM AT microcomputer connected to an Opto 22 interface, both located in an adjacent room. The three experimental chambers were run at the same time but independently of each other using programs written with the CONMAN control language (Spyder Systems) running at a resolution of 10 inputs per second. For all birds, a standard size chamber with stainless steel side and rear walls and a three-key aluminum front panel was used during magazine training.

Procedure

Pretraining. Following magazine training, pigeons were exposed to autoshaping trials consisting of presentation of a 5-s white key conditioned stimulus (CS) followed by a 3-s access to food (unconditioned stimulus [US]), separated by 60-s intertrial intervals (ITIs). After 4 consecutive trials with a peck, the keylight remained on continuously and every keypeck produced access to food for 50 additional responses. In the next session, reinforcement was programmed according to a random-interval (RI) 15-s schedule with uncollected reinforcers remaining available beyond a single cycle. For the next 8 sessions, the schedule was changed to an RI 30-s schedule with sessions ending after 42 reinforcers. RIs were generated by CONMAN with cycle time set at 1 s and probabilities set at .067 and .033 for the 15-s and the 30-s schedules, respectively. During the last three pretraining sessions, food access was reduced to 2 s.

Baseline sessions. After pretraining, pigeons were exposed to the peak procedure. The center keylight remained on throughout the session, and trials were signaled by the onset of the houselight. On

reinforced trials (FI trials), the first response after 30 s turned the houselight off and produced a 2-s access to food. On unreinforced trials (baseline trials), no food was given, the houselight remained on, and the trial ended independently of responding. Baseline trials lasted for 90 s plus a variable extension with a mean of 30 s. ITIs lasted for a minimum of 15 s plus a variable extension with a mean of 45 s. The distributions of extended intervals were generated using Fleshler and Hoffman's (1962) algorithm with $N = 18$ for the unreinforced trials and $N = 60$ for the ITIs. Each session consisted of 47 reinforced trials and 18 unreinforced trials. Sessions always started with 5 of the 47 FI trials. For the remaining 60 trials, the order of trial presentation was completely randomized on the basis of previous pilot data that showed that constraints in the order of presentation could influence performance in both reinforced and unreinforced trials. This procedure was in effect for 60 sessions.

Three-breaks condition. Over the next 42 sessions, half of the unreinforced trials included breaks. Break trials were the same as baseline trials except that the houselight was turned off for a period of time after trial onset. There were three types of break trials (see Figure 1): (a) an early break, the houselight was turned off for 6 s starting at Second 6; (b) a late break, the houselight was turned off for 6 s starting at Second 15; and (c) a long break, the houselight was turned off for 15 s starting at Second 6.

For each pigeon, only one type of break was run during the session. Break trial type was assigned to pigeons and sessions using Latin squares balancing in blocks of 3 sessions. Therefore, each bird was exposed to a total of 14 sessions with each type of break. As in baseline sessions, reinforced and unreinforced trials were randomly mixed. However, presentation of baseline and break trials was randomized in 2-trial blocks (i.e., if the first unreinforced trial was a break trial, the next unreinforced trial, when presented, was a baseline trial and vice versa).

Data Analysis

Except for the 5 warm-up FI trials for which no data were taken, keypecks were recorded in 1-s bins. On baseline and break trials, keypecks were recorded over 0–90 s and on FI trials over 0–30 s. In addition, after food was set up on FI trials, the latency of the keypeck that produced the food was also recorded. If no keypeck

was made 55 s after food was set up, reinforcement delivery was canceled and the trial was extended as in a baseline trial, ending independently of responding. Throughout the study, the proportion of FI trials that were cancelled for any subject was always less than 1% of those presented on any given manipulation.

The calculation of peak time was similar to the procedure described by S. Roberts (1981) and used by W. A. Roberts et al. (1989). For all manipulations, the procedure involved the location of a median time that was based on the response rate function over 0–90 s. First, a median over the 0- to 90-s range was found. Then, successive iterations located the medians of shrinking intervals. On each iteration, the range was determined by the location of the previous median, so that the limits of the new interval were equidistant from that median. When the median was less than 45 s, the lower limit of the new range was 0 s and the upper limit was twice the value of the median. When the median was greater than 45 s, the upper limit of the range was set at 90 s, whereas the lower limit was a value equal to twice the difference between the median and 45 s. This process was repeated until a median was found that was within 0.05 s of the previous median. Peak rate was defined as the response rate at the peak time, computed by linear interpolation between the centers of the two nearest bins.

Peak times and peak rates were calculated for each bird on each session. For individual birds, mean peak times were based on the mean response rate functions across sessions. Group mean peak times represent the average of the individual birds' mean peak times. For all statistical analyses in both experiments, we adopted a rejection criterion of .05.

Results

Visual inspection of the daily response rate functions showed that performance became stable for all birds after Session 40. However, to maintain equality in the number of baseline trials resulting from the three-breaks condition, we used only data from the last 6 sessions (55–60). Although there were individual differences in peak times (Cabeza de Vaca, 1993), the group mean peak time ($SE_M = 28.9 \pm 1.3$ s) was not reliably different from 30 s (t test, ns).

THREE-BREAKS PROCEDURE DIAGRAM

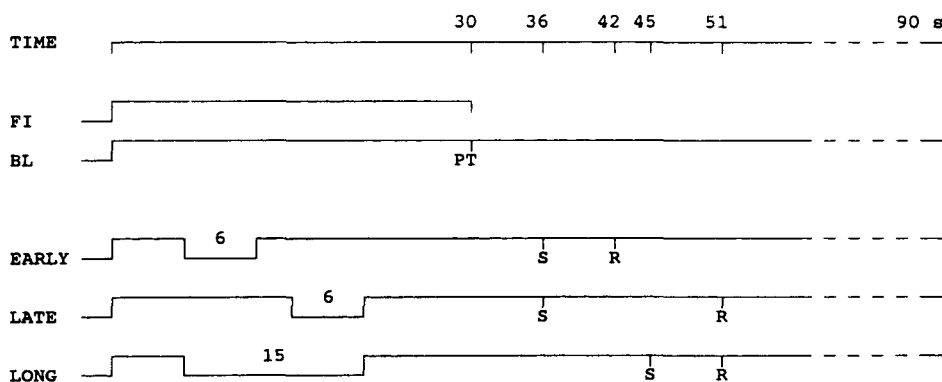


Figure 1. Procedure diagram for the three-breaks condition showing a fixed-interval (FI) trial, a baseline trial (BL), and the three types of break trials (early, late, and long). *PT* represents the nominal location of peak time on baseline trials; *S* (stop-retain) and *R* (reset at the end of break) represent the expected location of the peak times on break trials.

Figure 2 shows group mean response rate functions for each type of break for the last 12 sessions of the three-breaks condition. The superposition of the rising limb of the baseline function on the FI function indicated no discrimination between reinforced and unreinforced trials. In addition, baseline and break functions looked highly similar except that the break trial functions were shifted to the right.

Visual inspection of daily peak times suggested that baseline and break peak times were correlated (i.e., on sessions in which the baseline peak time was later, the break peak time

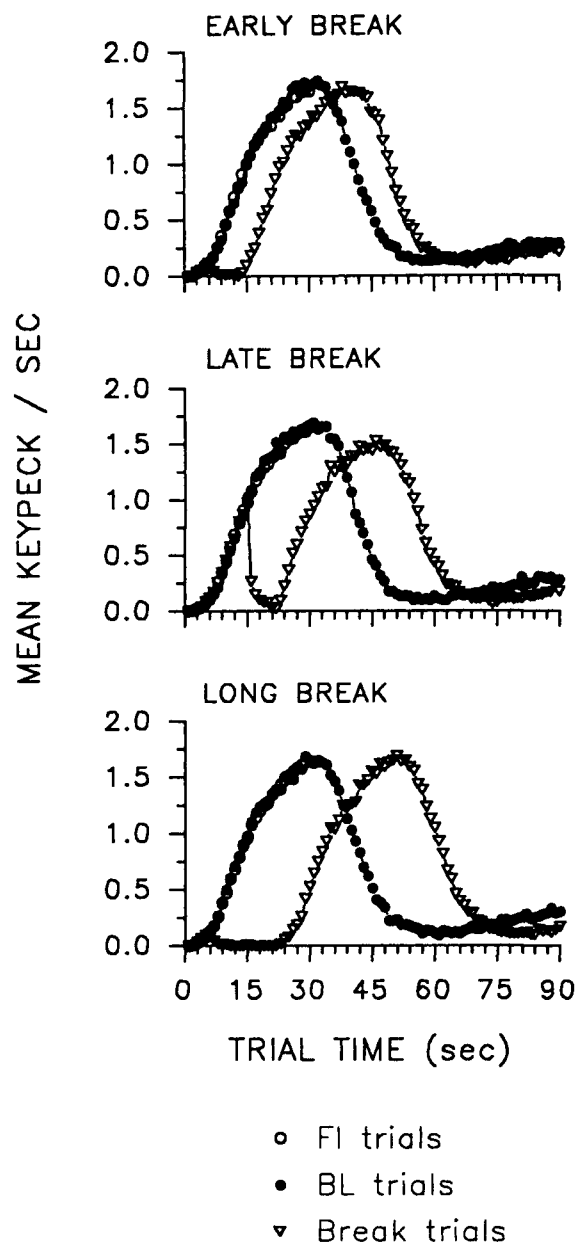


Figure 2. Group mean keypeck rate as a function of elapsed trial time during the last 12 sessions with breaks. For each type of break, rate per second is plotted separately for fixed interval (FI), baseline (BL), and break trials.

was also later, independent of the type of break). The mean Pearson product-moment correlation coefficients between the baseline and break peak times for the sessions run with early, late, and long break trials were .57, .36, and .70, respectively. Therefore, subsequent analyses were based on daily peak time shifts (i.e., on differences between baseline and break peak times obtained on a given session).

Figure 3 shows peak time shift as a function of sessions for each type of break. Repeated measures analyses of variance (ANOVAs) of peak time shifts showed that for each type of break, the data were stable after the first 2 sessions. The mean peak time shifts (Sessions 3-14) for the early (8.1 ± 0.8 s), the late (13.8 ± 0.8 s), and the long (20.2 ± 0.2 s) break trials were reliably different from each other (Scheffé test). Furthermore, the obtained shifts were reliably longer than the shift expected from the stop-retain prediction (see Figure 3, dotted lines) and reliably shorter than the reset prediction (dashed lines): early, $t_s(5) = 2.6$ and 4.7; late, $t_s(5) = 10.1$ and 9.4; and long, $t_s(5) = 27.7$ and 4.1, respectively.

Discussion

The presentation of different types of breaks during the trial produced different magnitudes of shift in peak times, but the shifts were not consistent with either a stop-retain or a reset model of clock performance. The stop-retain model predicts identical shifts for breaks of equal duration placed at different locations. Thus, early and late breaks should produce identical peak time shifts, which should be shorter than the shift produced by the long break. This was the case for the first 2 sessions but not in later sessions. This transient effect is reminiscent of data reported in other studies showing stop-retain-like behavior in acquisition (Gibbon & Balsam, 1981) or early in training followed by a change in performance with additional sessions (Brown, Hemmes, & Cabeza de Vaca, 1992; S. Roberts, 1981, Experiment 2; S. Roberts & Church, 1978). These results suggest an apparent change in the operation of the clock with amount of training, but it remains unclear how this parameter modifies the way the clock operates.

Following Session 2, our data were highly stable and exhibited a different pattern. The peak time shifts seemed to change in the direction of the reset prediction (see Figure 3) but were not entirely consistent with it. That reset did not occur at break onset was evident from the differences between the peak time shifts obtained with early and long breaks. Moreover, if working memory had reset at the end of the break, the two breaks with identical ending times—late and long—should have yielded identical peak time shifts, but they did not.

Unlike W. A. Roberts et al. (1989, Experiment 3), who found shifts that were consistent with those predicted by the reset hypothesis, the peak time shifts in our study were consistently longer than expected from the nominal stop-retain prediction, but not as long as those expected from the nominal reset prediction. In addition, although S. Roberts (1981, Experiment 2) found that the two breaks of equal duration but differing in location produced equivalent peak time shifts, in

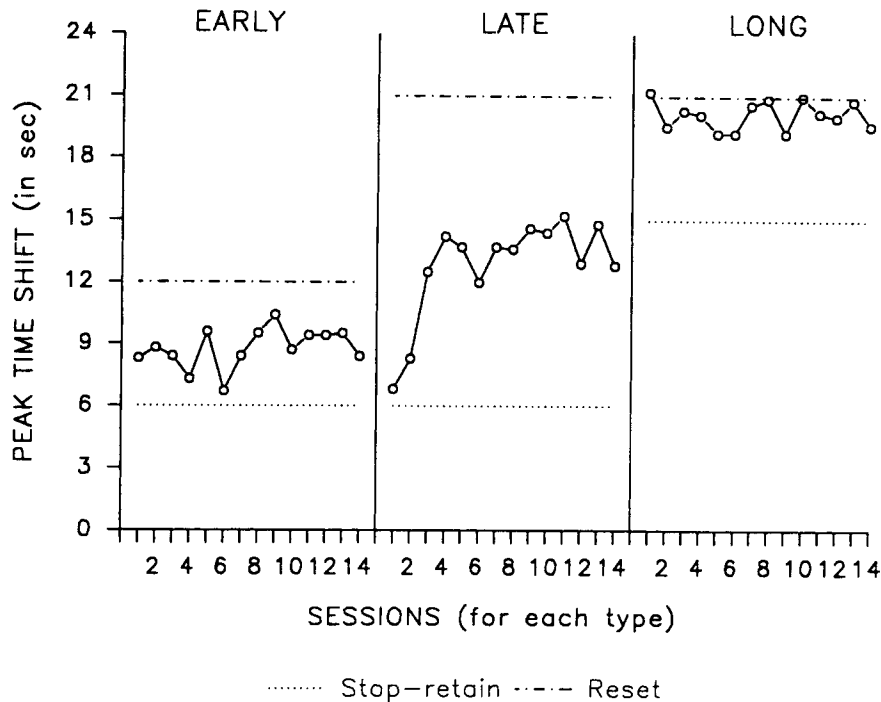


Figure 3. Group mean peak time shift as a function of sessions in the three-breaks condition. Vertical panels represent each type of break; on each panel, the horizontal lines represent the nominal shift predicted by the stop-retain and reset at the end of break hypotheses.

this study, early and late break trials produced reliably different shifts. However, as in this study, the shifts obtained by S. Roberts were also longer than expected from the nominal stop-retain prediction. S. Roberts indicated that the results were consistent with the stop-retain hypothesis and that the difference between obtained and predicted peak times could have been the result of differential switch latency or partial resetting.

A variation of the partial reset hypothesis is consistent with the results of our study. Partial resetting implies that the clock stops at break onset (i.e., the switch opens) and that time accumulated in working memory is partially lost during the break. In the version proposed here, the partial loss is not the result of resetting as such but of a continuous decay process. The differential losses observed in the early, late, and long break trials may reflect the influence of duration and location of the break on the decay process.

Wilkie (1988) proposed a similar interpretation for the results obtained with pigeons in a duration discrimination (symbolic matching-to-sample) procedure, in which he found that with 2-s ITIs, classification of a 6-s sample as short or long depended on the sample duration of the preceding trial (2 s or 10 s). Wilkie suggested that such proactive interference was unlikely if complete reset occurred immediately after every trial, and he proposed that it may be more useful to abandon the working memory resetting notion in favor of exploring the variables controlling a passive decay process. To assess the possibility of such a decay process, in Experiment 2 we implemented a parametric manipulation by

systematically changing the duration of the breaks, location of the breaks, or both.

Experiment 2

The results of Experiment 1 suggest that during the break the working memory contents are subject to a decay process. The notion that temporal information may be gradually lost with the passage of time is encountered in many different forms throughout the literature related to the study of memory. Although there is no agreement as to exactly what it is that decays during a delay, most models for temporal discrimination concur in that performance accuracy depends on both the duration of the event to be judged and the time elapsed since presentation of the event (Church, 1980; Honig, 1978, 1981; Maki, 1984; W. A. Roberts & Grant, 1976; Roitblat, 1984; Staddon, 1984). An example of a decaylike process is the *subjective shortening process* proposed by Spetch and Wilkie (1983) to account for the choose-short effect encountered in their DMTS research. Spetch and Wilkie found that increasing the retention interval produced an increase in the proportion of short as opposed to long responses under different experimental manipulations. According to their model, the duration of the sample in working memory shortens during the retention interval. As the working memory of the long sample shortens, it becomes more like the reference memory of the short sample, hence increasing the tendency to respond as if the longer samples

were short. The reliability of the choose–short effect has been confirmed by the results of many different studies (Fetterman & MacEwen, 1989; Kraemer, Mazmanian, & Roberts, 1985; Spetch, 1987; Spetch & Rusak, 1989; Wilkie, 1988). However, it has also been shown that the effect is greatly influenced by procedural variables, such as ITI and retention-interval durations (Church, 1980; Spetch & Wilkie, 1983); ITI and retention-interval values used during training relative to those in testing (Spetch & Rusak, 1992; Spetch & Wilkie, 1983); and the specific type of DMTS procedure used (i.e., duration discrimination with simultaneous choice, successive choice, or many-to-one sample to comparison; Grant & Spetch, 1991, 1993).

Although Spetch and Wilkie (1983) did not specify the mechanism responsible for the foreshortening process, it could be the result of a decaylike process in which temporal information is gradually lost in working memory. In this view and in the context of this study, the break during the FI signal may be understood as a retention interval for the amount of subjective time elapsed prior to break onset. If the value in working memory (prebreak accumulated time) decays during the break, then the retained value will be less than the corresponding value in a nonbreak trial at the end of the break. Thus, more time will be needed to reach the criterion for responding, thereby delaying the peak time. This delay will depend on the duration of the break and an amount of time that would be a function of the rate of decay.

In accord with available data, most memory decay models have posited nonlinear decay functions (Wixted & Ebbesen, 1991). For example, White (1985) proposed an exponential model of memory decay in DMTS that was based on Davison and Tustin's (1978) formulation of signal-detection performance. According to White's model, the decrease in accuracy observed with increasing retention intervals is the result of the loss of sample discriminability ($\log d$), measured in terms of the logarithms of ratios of choice responses to the comparison stimuli. The reduction of discriminability of a sample with increasing time since its presentation was well-described by a negative exponential function of the form: $\log d_t = \log d_0 \times \exp(-bt)$, where $\log d_t$ represents discriminability at delay t , $\log d_0$ is discriminability at zero delay, and b is a time constant representing the rate of decrement in discriminability (McCarthy & White, 1987).

In an extension of the foregoing logic and based on the assumption that subjective time is a linear function of real time (Gibbon, 1977; Gibbon & Church, 1981), we developed a mathematical model of peak time in which the location of the peak time could be represented as the additive result of the reinforced duration, the break duration, and the time lost during the break (see Figure 4).

That is,

$$PT = T^* + T_b + [T_p - f(t)], \quad (1)$$

where PT is predicted peak time, T^* reflects the subjective estimate of the time to reinforcement, T_b is break duration, T_p is time elapsed before break onset, and $f(t)$ represents the amount of subjective prebreak time retained at time t , where t is elapsed time during the break and ranges from 0 to T_b .

Nominally, $T^* = 30$ s, but it may differ from that value as a result of performance bias. When there is no break (i.e., baseline trials, Outcome a in Figure 4), PT will be equal to T^* because $T_b = 0$ and $f(t) = T_p$. If there is a break but there is no decay during the break, then $f(t)$ will be equal to T_p , and PT will be delayed by the duration of the break (i.e., stop–retain, Outcome b in Figure 4). By contrast, if the decay during the break is complete, then $f(t)$ will be zero, and PT will be delayed by the duration of the break plus the time elapsed before break onset (i.e., reset, Outcome d in Figure 4). Alternatively, partial decay may occur during the break, producing intermediate peak times (see Figure 4, Outcome c). Subjective prebreak time may decay during the break in different ways affecting the location of the peak time. Differential predictions of peak time location may be evaluated by allowing $f(t)$ to take different forms: exponential, power, logarithmic, and linear (Wixted & Ebbesen, 1991).

The adequacy of the preceding formulation was evaluated in Experiment 2 by implementing three parametric manipulations. In the first, the onset of the break was fixed and break duration, and thereby break end, varied. In the second, the duration of the break was fixed and the onset and the end of break changed. Finally, the end of the break was fixed and the duration and onset varied. The results of the three manipulations were used to evaluate predictions made on the basis of a dichotomous model (stop–retain and reset) and a continuous memory decay model.

Method

Procedure

The subjects, apparatus, and general procedure were the same as those used in Experiment 1. However, all break trial types were presented within each session rather than on different sessions. Reinforced and unreinforced trials were randomly presented in three blocks of 20 trials, with each block consisting of 14 FI trials, 1 baseline trial, and 5 break trials. Each of three different manipulations lasted for 12 sessions and was preceded and followed by at least 12 sessions in which the three-breaks condition of Experiment 1 was reintroduced.

In the first manipulation—duration with fixed onset—breaks always started 6 s after trial onset, but they lasted for different durations: 3, 6, 9, 12, or 15 s (see Figure 5, top panel). During the location manipulation, breaks were always 6 s long, but they started at different times: 3, 6, 9, 12, or 15 s after trial onset (see Figure 5, center panel). In the last manipulation—duration with fixed end—breaks started at different times but always ended 21 s after trial onset. The break durations were the same as those used in the first duration manipulation (see Figure 5, bottom panel).

Results and Discussion

Peak times obtained in the successive replications of the three-breaks condition were used to assess stability of performance across manipulations. Repeated measures ANOVAs of peak times within and between replications showed no change across sessions (minimum obtained $p > .17$). As in the last sessions of Experiment 1, early (9.2 ± 0.25 s), late (14.2 ± 0.52 s), and long (20.4 ± 0.20 s) break trials produced reliably different peak time shifts (Scheffé test). In

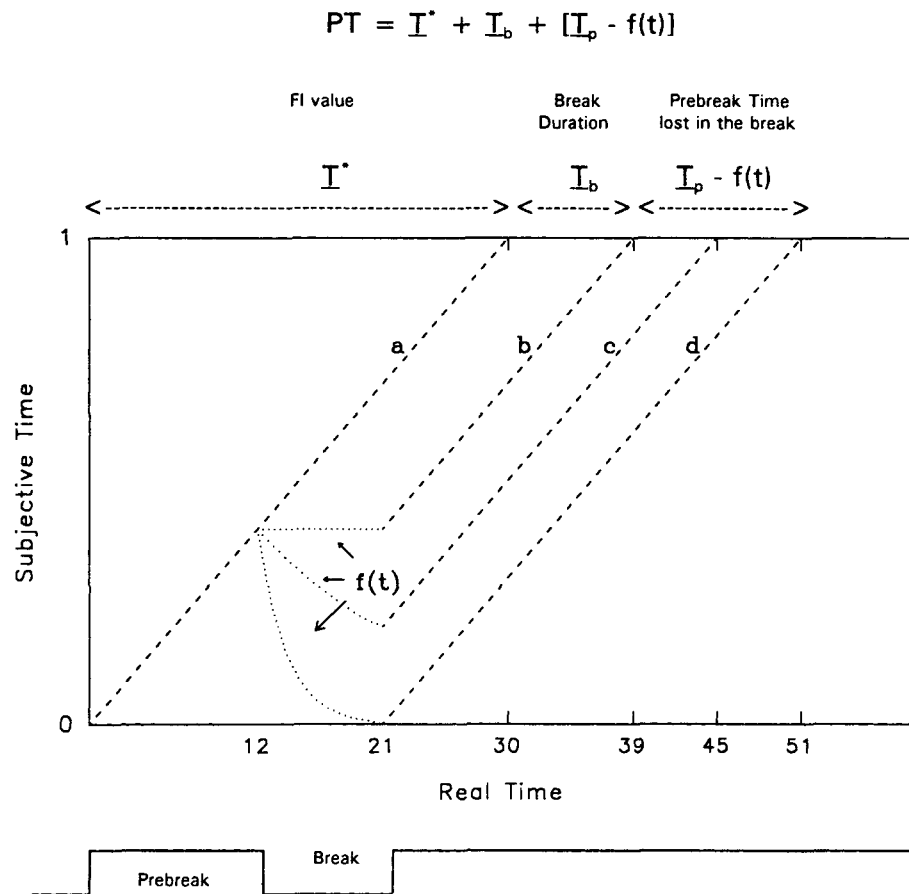


Figure 4. Subjective time as a function of real time (dashed lines) on trials without a break (Outcome a) and trials with a 9-s break starting 12-s after trial onset (Outcomes b–d). Dotted lines represent possible decay [$f(t)$] occurring during the break. Peak times for Outcomes a–d are represented on the abscissa. PT = predicted time peak; T^* = the subjective estimate of the time to reinforcement; T_b = the break duration; T_p = the time elapsed before break onset; $f(t)$ = the amount of subjective prebreak time retained at time t ; t = the elapsed time during the break; FI = fixed interval.

addition, the peak time shifts were reliably different from both the stop–retain and the reset predictions: early, $rs(5) = 12.8$ and 11.2 ; late, $rs(5) = 15.8$ and 13.1 ; and long, $rs(5) = 27.0$ and 3.0 , respectively. These results indicate no apparent change in peak time shift resulting from intervening manipulations. Therefore, subsequent analysis focused on the effects of the three parametric manipulations.

Stop–Retain and Reset Versus a Decay Process

Figure 6 displays the peak time shift functions obtained in each manipulation. The top panel of this figure shows that the function relating peak time shift to break duration, when break onset was fixed, was inconsistent with the linear changes predicted by either the stop–retain or the reset hypotheses, as indicated by the standard errors at each data point. The nonlinearity of the function was substantiated by a trend analysis yielding reliable linear and quadratic components, $Fs(1, 20) = 1,165.46$ and 4.89 , respectively.

The peak time shifts obtained during the location manipulation (see Figure 6, center panel) were again different from the shifts predicted by both the stop–retain and the reset hypotheses. The trend analysis of the obtained shift function yielded only a significant linear component, $F(1, 20) = 305.79$. To evaluate the extent to which the obtained function differed from the predicted functions, we calculated the slopes of the individual peak time functions through linear regression analyses. The group mean slope (0.56 seconds per second [s/s]) was reliably different from both the stop–retain (0 s/s) and the reset (1 s/s) slopes, $rs(5) = 11.46$ and 9.0 , respectively. For individual birds, the slopes ranged from 0.32 to 0.64 s/s, with the percentage of explained variance accounted for ($R^2 \times 100$) ranging from 92.9% to 98.5%.

The adequacy of the decay model was further investigated in the second duration manipulation, which maximized the differences in the predicted outcomes. When the end of the break was fixed, the nonlinearity of the relationship between

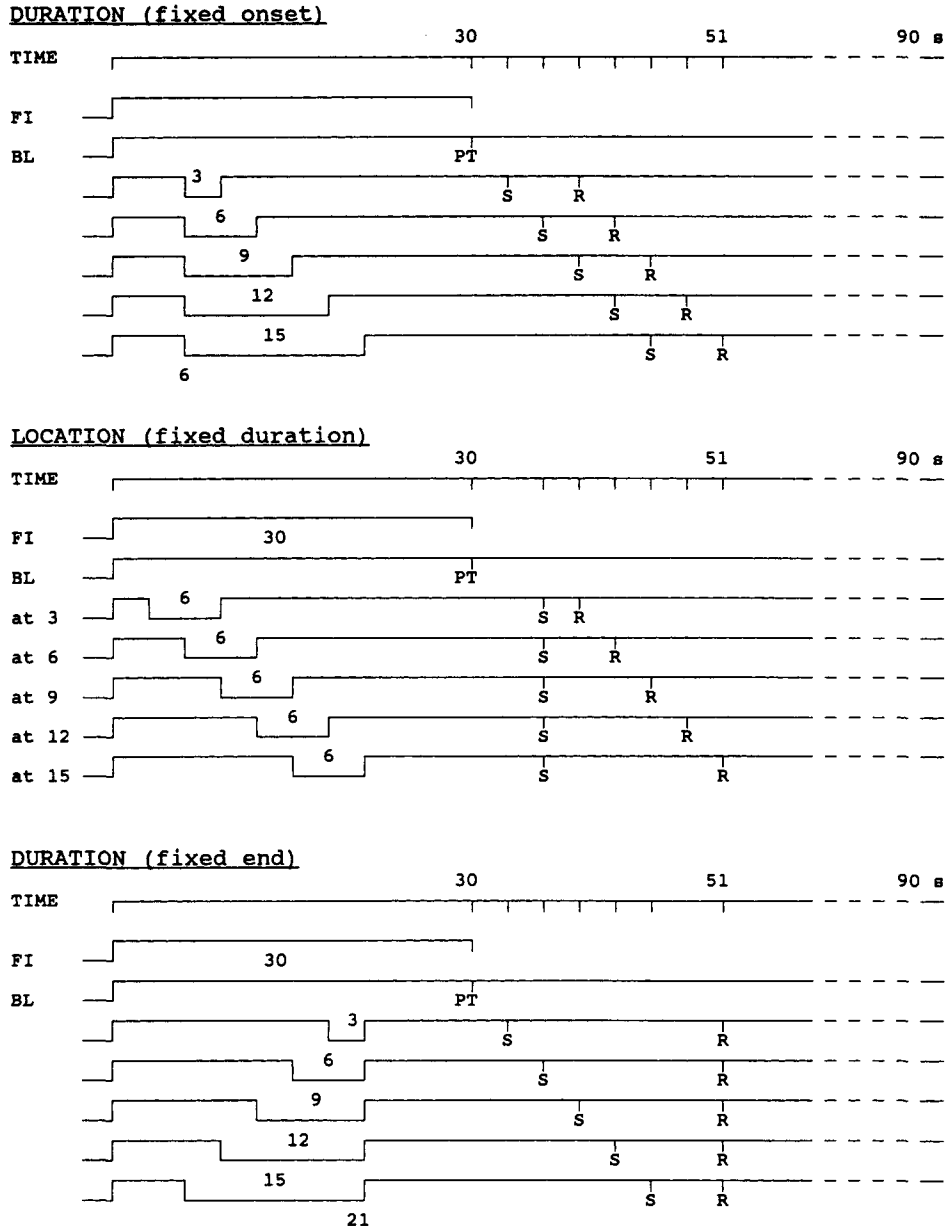


Figure 5. Procedure diagrams for the three parametric manipulations showing a fixed-interval (FI) trial, a baseline (BL) trial, and the different types of break trials on each manipulation. *PT* represents the expected location of the peak time on baseline trials; S (stop-retain) and R (reset) represent the expected location of the peak times on break trials.

peak time shift and break duration was more evident, as can be seen in the bottom panel of Figure 6. The deviation of the function from the linear predictions was confirmed by the presence of both a linear and a quadratic component, $F_s(1, 20) = 156.12$ and 28.33 , respectively.

In conclusion, the results of the parametric manipulations are not compatible with those predicted by either the stop-retain or the reset hypotheses. The two duration manipulations produced peak time shifts that were nonlinear functions of break duration, and the location manipulation yielded a shift function with a slope that differed from the predicted

slopes. The obtained results are more consistent with an interpretation that is based on a continuous decay process.

Evaluation of the Decay Models

To explore the form of the decay process, the peak times obtained during the parametric manipulations were compared with peak time predictions resulting from different forms of decay. In the mathematical model developed to predict peak time (see Equation 1), $f(t)$ represents the amount of prebreak time retained at time t , where t is time elapsed

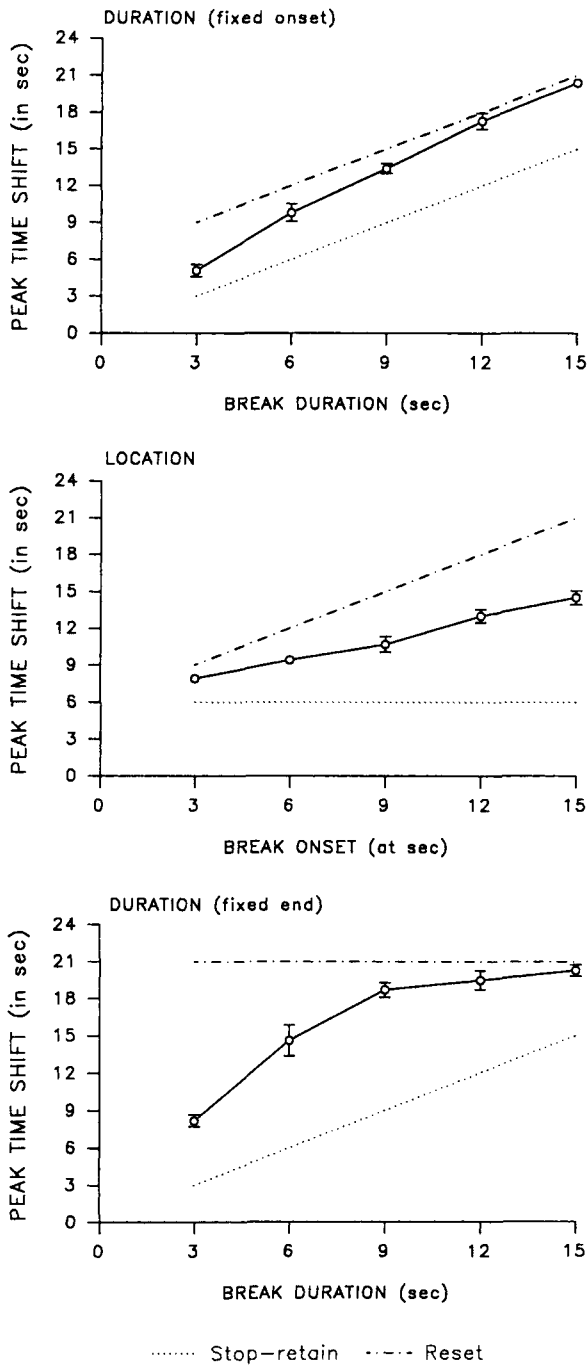


Figure 6. Group mean peak time shift functions obtained on each parametric manipulation. On each panel, the discontinuous lines represent the nominal shifts predicted by stop-retain and reset. Error bars indicate the standard error of the mean.

during the break. Because the amount of time retained at the end of the break depends on the decay occurring during the break, different forms of decay would result in different peak time predictions (see Table 1).

If decay were a linear function of duration, the decay rate would be constant and the amount of prebreak time lost dur-

ing the break would depend only on the duration of the break. If decay were a logarithmic function of duration, the rate of decay would not be constant, but the time lost during the break would still be a function of only the duration of the break. Therefore, for a given duration, both linear and logarithmic models of decay predict constant peak times with different break locations, predictions that were not supported by the results of the location manipulation. Thus, neither linear nor logarithmic models account for the observed decay.

The obtained peak times were more consistent with those predicted by power or exponential models of decay. In both, peak times are a nonlinear function of break duration and vary linearly with break location. In an attempt to differentiate between these two models, we fit exponential and power functions to the peak times obtained in the three parametric manipulations, using a nonlinear least squares regression analysis program (iterative Marquardt-Levenberg fitting algorithm, PeakFit, Jandel Scientific), and the quality of the fit was evaluated by the coefficient of determination (the proportion of data variance accounted for). Both models provided reasonably accurate fits (see Figure 7). When break duration was fixed, (location manipulation), a linear change was predicted by both models and accounted for at least 93% of the variance. In the two duration manipulations, the percentage of explained variance was higher for the exponential fit than for the power fit for 5 of the 6 birds. However, the differences were not large, and, with only 5 data points to evaluate the fits, the probability of detecting a reliable difference, even if one existed, was considered too low to justify further analysis.

Stochastic Process Versus a Continuous Decay Process

An alternative interpretation of these results considers stop-retain and reset as two mutually exclusive outcomes of a stochastic process, with the transition from one to the other occurring on a probabilistic basis during the break within a trial. That is, the outcome on each trial is either stop-retain or reset. If the momentary probability of a transition is stationary, then the transition points should be geometrically distributed in the break interval. The longer the break, the higher is the probability of a reset outcome. A general feature of this model is that peak times across trials should be bimodally distributed, with the relative likelihood of each modal peak time depending on break duration. However, averaging across trials would result in an aggregate peak time that would seem to vary continuously with break duration. Moreover, within a given break duration, the aggregate peak time shift would appear between those predicted by stop-retain and reset.

In Figure 3 the peak time shifts for the late break trials are about halfway between the two predictions (6 vs. 21 s, dashed lines). The stochastic interpretation would imply that reset occurred in half of the trials and that a frequency distribution of trial outcomes would show bimodality. Although this bimodality would also be present in the frequency distributions

Table 1
Prebreak Retained Time and Predicted Peak Time for Different Forms of Decay

Function	Retained time	Predicted peak time
Linear	$f(t) = T_p - at$	$PT = T^* + T_b + aT_b$
Logarithmic	$f(t) = T_p - a \log(t)$	$PT = T^* + T_b + a \log(T_b)$
Power	$f(t) = T_p t^{-a}$	$PT = T^* + T_b + T_p(1 - T_b^{-a})$
Exponential	$f(t) = T_p \exp(-at)$	$PT = T^* + T_b + T_p[1 - \exp(-aT_b)]$

Note. $PT = T^* + T_b + [T_p - f(t)]$, where T^* = subjective estimate of the time to reinforcement; T_b = break duration; T_p = time elapsed before break onset; $f(t)$ = amount of prebreak time retained at time t ; and t = elapsed time during the break (0 to T_b). In each function, a is a constant governing rate of decay.

of early (6 vs. 12 s) and long trial (15 vs. 21 s) outcomes, it may not be evident, because the difference between the stop-retain and the reset predictions was smaller than for the late break trials.

To evaluate the stochastic interpretation of these results, we examined data from all sessions under the three-breaks condition following Gibbon and Church's (1990) model of trial-by-trial data analysis. In an extension of Schneider's (1969) "break-run" analysis of FI performance, Gibbon and Church proposed a "break-run-break" analysis of data obtained on baseline trials in the peak procedure. In the break-run-break analysis, performance on each trial is characterized by two abrupt changes in response rate—a change from a low to a high rate (break-run, or "start" point) and a change from a high to a low rate (run-break, or "stop" point). In an extensive analysis of data from uninterrupted trials, Gibbon and Church found that the start and stop points were positively correlated and that they bracketed the target reinforced time. An implication of this analysis is that both start and stop points reflect subjective estimates of time to reinforcement; therefore, either could be used to explore the properties of the clock on a trial-by-trial basis.

The presentation of a break during the trial introduces artifactual problems in the determination of the start point but should not affect the determination of the stop point. Therefore, it seemed appropriate to rely only on stop points for the analysis of our data. The results obtained from an analysis that was based on Gibbon's (personal communication, May 1992) least squares regression analysis program, developed to determine start and stop points, were compared with those obtained from a modified version (stop points only) using all of the baseline trials from the last 20 baseline sessions of Experiment 1. Inspection of the frequency distributions of stop points calculated both ways showed no systematic differences, suggesting that the modified analysis did not introduce a bias on the determination. In addition, correlations between session peak times and session mean stop times were calculated to further validate the use of stop points as an alternative dependent measure. For individual subjects, the Pearson product-moment correlation coefficients across the 20 baseline sessions were .89, .76, .90, .78, .91, and .84. Therefore, the stop-only method was used to determine the stop points in baseline and break trials for all data from the three-breaks condition manipulations.

According to the stochastic model, the distribution of stop points on break trials should be bimodal and therefore more

variable than the distribution of stop points on baseline trials. Figure 8 shows the frequency distributions of stop points in baseline and late break trials. No indication of bimodality in the break trials distributions was evident at the 15-s nominal separation of outcomes predicted by the stochastic model. A quantitative analysis was undertaken to compare variability of distributions across conditions.

For each distribution, we calculated the mean of the absolute deviations from the median of the distribution (see Table 2). Repeated measures ANOVAs of the mean deviations yielded no reliable differences in variability for the baseline distributions across break types ($p > .34$), but there was a reliable difference for the break distributions, $F(2, 10) = 13.66$. Variability in the frequency distributions for late breaks was reliably larger than for early or long breaks (Scheffé test), which did not differ from each other. Further analyses of the change in mean deviation scores from baseline to break distributions for each type of break showed a reliable increase in variability for the late breaks, $t(5) = 3.14$, a reliable decrease for the long breaks, $t(5) = 3.15$, and no difference for the early breaks.

The results of the quantitative analysis lend some support to the stochastic interpretation because the model predicts larger variability in the frequency distribution from late break trials than in the distributions from early and long break trials. However, because the nominal difference between the stop-retain and the reset predictions of stop time for late breaks (15 s) was large, in contrast to the difference for the early or long breaks (6 s), the model would also predict that the late break distributions would show some evidence of bimodality, a prediction that was not supported by the data.

The results of the trial-by-trial analysis are not incompatible with the memory decay interpretation. An exponential model of decay can also account for the larger variability found on the late distributions. If rate of decay is not constant from trial to trial, it would introduce some variability in retained time at the end of the break. This variability would be greater in late break trials because retained time is a function of both prebreak time and decay, and prebreak accumulated time is larger in late than in early and long trials (see Table 1). This account, together with the absence of bimodality in the frequency distributions of stop times, leaves the decay model as a viable interpretation of these results.

The failure to find increased variability in all break distributions is somewhat surprising. If the switch opens at

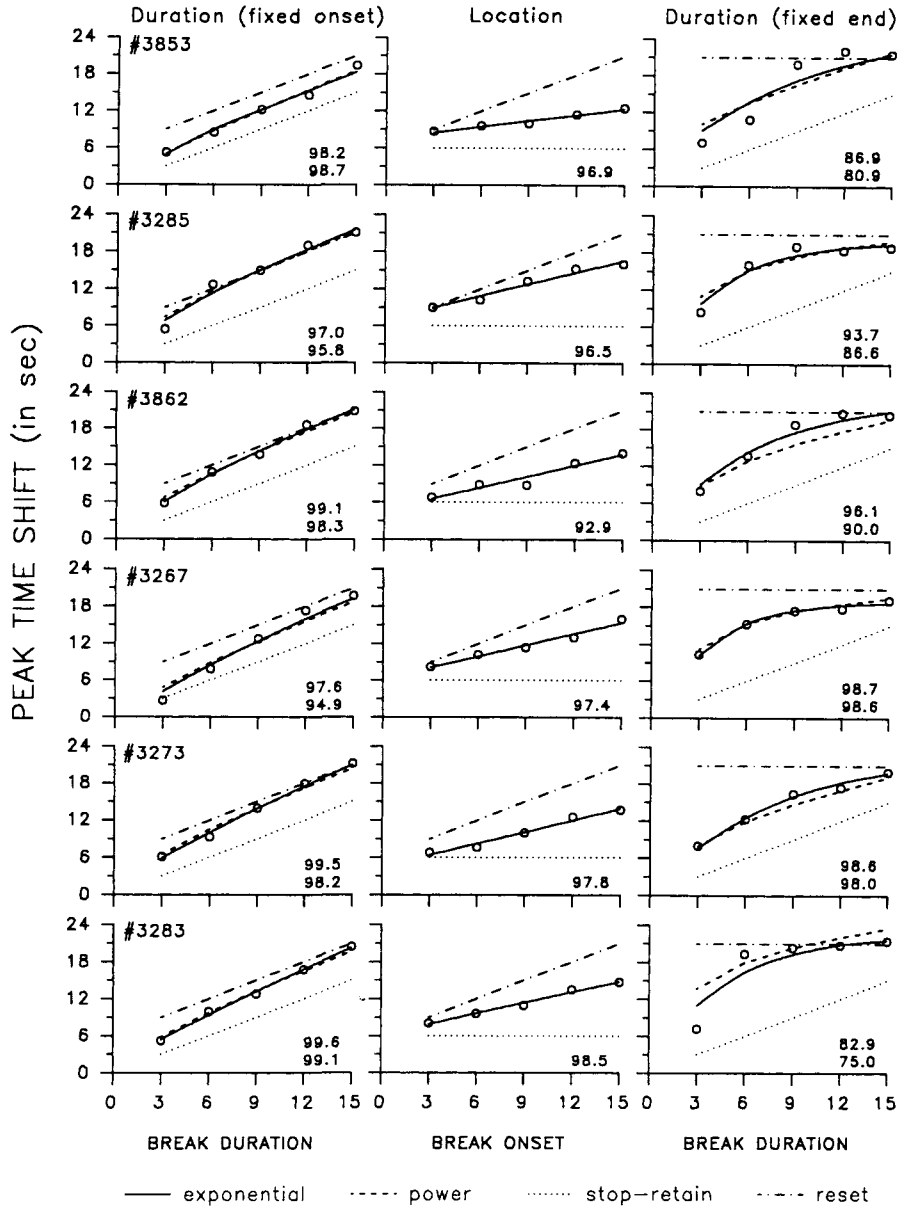


Figure 7. Fit of exponential and power functions to obtained peak time shifts for the three parametric manipulations. The numbers on each graph represent the percentage of data variance accounted for by the exponential (top) and power (bottom) fits.

break onset and closes at the end of the break, break trials contain a source of variance not present on baseline trials, a source that would be expected to add to the total variability on each trial (Gibbon & Church, 1984). However, it is possible that a separate mechanism overrides the expected increase. For example, attentional factors have been shown to influence the latency to operate the switch (Meck, 1984). The onset of the signal on a baseline trial follows longer intervals between signal presentations (i.e., ITI) than do postbreak signal presentations. Greater attention to signal onset following a break could decrease variability in switch closure

latency, thereby compensating for the additional operation of the switch.

The decrease in switch latency variability jointly with the exponential model of decay provides a tentative interpretation of the stop time results on early and long break trials. The variability in retained time at the end of an early break would be small, whereas variability owing to switch latency would be less than that on baseline trials. Hence, the total variability may not be reliably different from the variability on a baseline trial. By contrast, at the end of a long break trial, the combination of decreased variability in switch

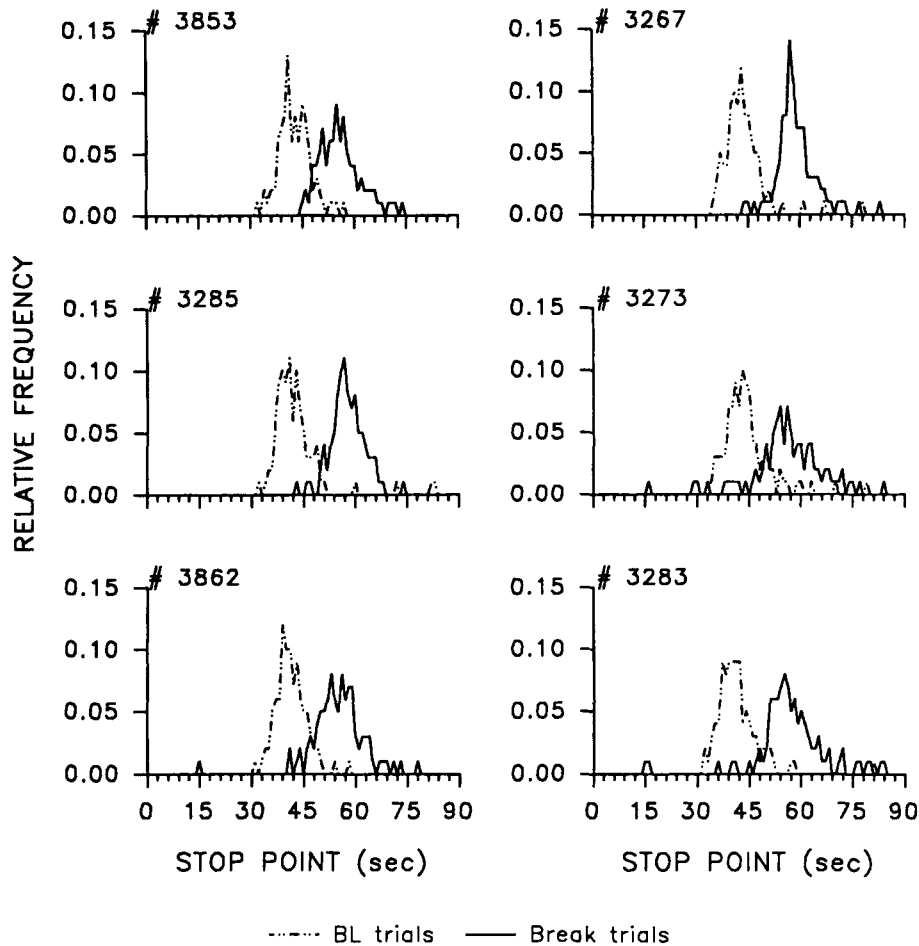


Figure 8. Frequency distribution of stop points in baseline (BL) and break trials from sessions run with late breaks in the three-breaks condition.

latency and retained times close to zero would result in reduced total variability as compared with a baseline trial. Further experimental manipulations would be required to determine the adequacy of this account.

General Discussion

The main finding of this research was that introducing a break during the trial produced differential changes in peak

time that depended on the duration and the location of the break. The results do not support a dichotomous model, because the obtained peak times were longer than those predicted by the stop-retain hypothesis but shorter than those predicted by the reset hypothesis. These results are more consistent with a model in which the clock switch opens at break onset and time accumulated before the break is gradually lost during the break. In this decay model, outcomes indicating stop-retain and reset may represent the two endpoints of a continuous memory decay process and need not be taken as reflecting two different timing strategies.

Consistent with the results of other studies of memory decay processes, the results of Experiment 2 suggest that memory decay is a nonlinear function of time (e.g., Wixted & Ebbesen, 1991). When the decay process was allowed to take different forms (linear, log, power, and exponential), the exponential function was found to give the best description of the decay process: The obtained peak times were a nonlinear function of break duration but varied linearly with break location. A power function also provided a reasonable fit to the data; however, that function is undefined for break durations equal to zero and requires a modification (e.g., $t =$

Table 2
Group Mean Values (in Seconds) of Median and Mean Deviation From the Median for the Distribution of Stop Points

Stop point	Median		Mean deviation		
	BL	BK	BL	BK	Difference
Early	41.5	50.4	4.6	4.9	0.3
Late	41.4	55.7	4.4	6.0	1.6
Long	41.2	61.6	4.7	4.1	-0.6

Note. Values for baseline (BL) and break (BK) distributions are presented separately for each type of break.

$t + 1$) to accommodate baseline trials. The latter is also true for a logarithmic function. Both log and linear functions were considered poor descriptors of decay rate because both predicted peak times that varied with break duration but not with break location, predictions that were incompatible with the results obtained from the early and late break trials and the location manipulation.

The results of Experiment 2 are consistent with those of White (1985) and Watson and Blampied (1989), who also found that a simple exponential function provided a good fit to the data obtained in animal DMTS studies. However, McCarthy and White (1987) found that a rectangular-hyperbolic model gave a slightly better fit to the animal data and was necessary to account for human data from studies using retention intervals longer than 10 s. The adequacy of both the exponential and hyperbolic models has been recently challenged by Wixted and Ebbesen (1991), who proposed that a power function provided a better description of the data obtained from different animal and human studies. Although the results of this research favor an exponential model over a power model, both models account for a large proportion of the data variance, and our data do not clearly distinguish between them.

Determinants of Clock Reset

The results of this research have implications for a feature of the internal clock model that has received little attention in the timing literature. An implicit assumption of the clock model is that the contents of the clock must be cleared periodically. Most procedures used to study the properties of the clock present a mix of reinforced and unreinforced trials, and in all cases there is evidence of temporal control. This implies that reset of clock contents must occur after both reinforced and unreinforced trials.

It has been proposed that delivery of reinforcement resets the clock, at least partially (S. Roberts, 1981). When food was omitted at the end of an FI trial, S. Roberts (1981, Experiment 3) found a decrease in peak time on the subsequent trial, suggesting that the clock might not have been reset and that delivery of food may be necessary to reset the clock. This result is consistent with the response enhancement found following reinforcement omission in maze learning and operant FI schedules (e.g., Amsel & Roussel, 1952; Staddon & Innis, 1969) and suggests that clock reset may be a factor in such effects (see Staddon, 1974, for a different interpretation).

However, little has been said about how resetting occurs in the absence of reinforcement. If the decay observed during the break represents a phenomenon similar to what occurs at the end of a trial, the results of this research suggest another mechanism to clear the clock contents—a decay process operating in working memory. The results of other studies have also suggested that reset may be the result of a gradual decay process. For example, S. Roberts (1981, Experiment 4) found an increase in peak time following a decrease in the ITI from a variable 60-s to a fixed 5-s duration. If the clock does not completely reset during the short ITI, the subjective time when food is delivered on the subsequent trial would be

greater than if the clock had been completely reset. This longer reinforced duration would be stored in reference memory and would increase the peak time on subsequent baseline trials. These results are consistent with Wilkie's (1988) finding that in a symbolic matching-to-sample task with a fixed 2-s ITI, the classification of a 6-s sample as short or long was influenced by the duration of the sample (2 s or 10 s) on the preceding trial. By contrast, Church (1980), in a series of experiments using time estimation tasks with signal durations ranging from 2 to 8 s, found above-chance accuracy with a 2-s ITI, suggesting that the clock could be reset rapidly. However, the results also indicate that accuracy increased with increasing ITI values (2–32 s). The discrepancies among these studies suggest that the speed of reset may be a property of the clock that could be influenced by procedural parameters.

An interesting feature of this research is the similarity between the duration of the longest break and the duration of the minimum ITI. Throughout this research the set of ITI values contained a substantial number of intervals close to 15 s, the minimum ITI value. The fact that the peak times obtained with the longest break (15 s) were consistently closer to the reset prediction than those obtained with shorter breaks raises a question regarding the role of the ITI as another parameter of the experimental procedure that could influence the decay process. It is plausible that the ITI values used during initial training may determine the speed with which the clock resets when the signal is turned off and that given the same stimulus configuration (break), the same reset rate would apply. Previously mentioned results lend some support to this notion. For example, the fact that the peak time after a reinforced trial was later when the ITI was changed from 60 s to 5 s (S. Roberts, 1981) suggests that exposure to the 60-s ITI might have determined a rate of reset that did not permit working memory to clear totally after only 5 s. Similarly, the results of Church, Miller, Meck, and Gibbon (1991), who found that changing the ITI from 2 s to 120 s did not influence peak time, suggest that a fast decay rate established by the shorter ITI transferred to the longer ITI condition.

Some of the observed differences between the results of Experiment 1 and those obtained by other investigators using the peak procedure (S. Roberts, 1981, Experiment 2, with rats; W. A. Roberts et al., 1989, Experiment 3, with pigeons) could be attributable to procedural variations because the studies differ in the implementation of the experimental manipulations and the specific parameters used.

The apparent discrepancy between the results of this research and those of S. Roberts rests on the outcomes obtained with breaks of equal durations. Although in S. Roberts's (1981) study the two breaks of the same duration (5 s) located at different times (10 and 15 s after trial onset) produced peak time increases that were not reliably different (7.2 s and 9.2 s, respectively), in our research early and late breaks yielded different peak times (8.1 s and 13.8 s, respectively). It is plausible that the combination of a shorter break duration and a smaller difference in break location used by S. Roberts might have produced peak time increases with a difference

that, even though in the same direction, was too small to be reliable.

The peak time increases on break trials obtained by both S. Roberts (1981) and us indicate at least partial retention of prebreak time. By contrast, W. A. Roberts et al. (1989) found peak time increases that indicated complete reset. In addition, in the first two studies there was no systematic difference between baseline and break peak rates, whereas in the W. A. Roberts et al. study the peak rates on break trials were lower than on baseline trials. However, W. A. Roberts et al. included a procedural feature that differentiated it from the former two. Although W. A. Roberts et al. presented unreinforced baseline and break trials in different sessions, in S. Roberts's and our research they were presented in the same sessions. It is plausible that the presentation of break trials in different sessions might have increased the discriminability of the break as a signal for the absence of food. This interpretation is consistent with S. Roberts's finding that when breaks consisted of the addition of a sound instead of the interruption of the trial signal, the peak rates were also lowered. These results suggest that conditions that foster discrimination of break trials as unreinforced trials would result in abrupt reset.

The speed of reset is likely to be mediated by neural mechanisms involved in memory processes. In investigations of hippocampal function, rats with fimbria-fornix lesions produced peak times that suggested that the clock had completely reset after breaks ranging from as short as 0.5 s to 5 s (e.g., Meck, Church, & Olton, 1984; Olton, Meck, & Church, 1987). The same lesions also interfered with spatial working memory (Meck et al., 1984). Because lesions of avian hippocampus also produce deficits in spatial working memory (Sherry, 1990), that structure may also mediate temporal working memory in pigeons.

Relative-Duration Interpretation

An alternative interpretation of our results is based on an extension of Spetch and Wilkie's (1983) subjective shortening notion. Spetch and Rusak (1989) proposed that the duration of a sample, in DMTS preparations, is judged not in terms of its absolute value but relative to a background value. In this view, the duration of a sample is compared with the duration of the temporal context comprised of both ITI and retention-interval periods. Introducing increases in the duration of the ITI, the retention interval, or both, should increase the background time leading to a decrease in the perceived duration of the sample. According to this *relative-duration hypothesis*, and assuming that breaks in the peak procedure could function as retention intervals, the introduction of breaks produces an increase in background time that could lead to decreases in the perceived duration of the prebreak interval. The increases in peak time produced by the breaks could then be understood on the basis of a decrease in the perceived prebreak duration: smaller shifts representing small decreases (i.e., more like stop-retain) and larger shifts reflecting large decreases (i.e., more like reset). The peak time shifts obtained during the two duration manipulations are consistent with this interpretation.

The relative-duration hypothesis also predicts that the introduction of breaks after training with short ITI values should increase the background time and decrease prebreak perceived duration relatively more than if training had been conducted with longer ITI values. W. A. Roberts et al. (1989), using relatively short ITI values (10–40 s), found peak time shifts that were consistent with large decreases in the perceived prebreak duration, whereas the shifts obtained by S. Roberts (1981) and us, both using longer mean ITI values (60 s), were more consistent with smaller decreases.

However, this perceptual interpretation does not accommodate the results obtained in the location manipulation. Because the duration of the break was fixed, the background time remained constant; therefore, delaying the onset of the break should have resulted in smaller decreases in prebreak time and thus in smaller peak time shifts. The obtained results show that peak time shift increased with increasing onset time.

Although the relative-duration hypothesis does not account for all of our data, some aspects of this interpretation may be worth pursuing. Even though the emphasis of this interpretation is on perceptual processes, it does not preclude the operation of memorial processes because one of its main assumptions is that both sample and background times are subject to a foreshortening process not unlike the memory decay observed in this research. Future research could attempt to determine the extent to which temporal discrimination results from a combination of perceptual and memorial processes.

In summary, the results of our research demonstrate that the shift in peak time obtained by introducing a break in the trial signal is a nonlinear function of the break duration and that it varies linearly with the break location. The obtained peak time shifts are considered to be the result of a decay process operating in working memory.

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