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Internal clock and memory processes in animal timing

Cabeza de Vaca, Soledad, Ph.D.

City University of New York, 1993

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INTERNAL CLOCK AND MEMORY PROCESSES IN ANIMAL TIMING

by

SOLEDAD CABEZA DE VACA

A dissertation submitted to the Graduate Faculty in Psychology
in partial fulfillment of the requirements for the degree
of Doctor of Philosophy, The City University of New York.

1993

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

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Abstract

INTERNAL CLOCK AND MEMORY PROCESSES IN ANIMAL TIMING

by

Soledad Cabeza de Vaca

Adviser: Professor Bruce L. Brown

Temporal control of behavior under a signalled fixed-interval (FI) schedule was investigated within the framework of a three-processes internal clock model.

Six pigeons were exposed to a peak procedure, in which signalled FI 30 s trials were mixed with extended unreinforced (baseline) trials. On test sessions, the signal on some of the unreinforced trials was interrupted (break) for a period of time after trial onset. Inferences about clock operation were based on comparisons between the peak time (time of maximum rate) obtained on baseline and on break trials.

Results of previous studies have been interpreted as indicating that animals may adopt different timing strategies--stop-retain or reset--when confronted with within-trial stimulus change. According to the stop-retain prediction, breaks of the same duration should produce identical peak times independently of their location in the trial.

According to the reset prediction, breaks of different durations with identical offset times should produce similar peak times.

In Experiment 1, three breaks differing in duration and/or location were used to evaluate the adequacy of this interpretation. The results indicated that each type of break produced a different magnitude of shift in peak times. The obtained shifts were longer than those predicted by the stop-retain hypothesis but shorter than those predicted by the reset hypothesis. In contrast to the stop-retain and reset models, the pattern of results suggested that both duration and location of the break influenced the shift on peak time.

These results may be understood in terms of an alternative model based on memory processes, according to which the clock stops at break onset, and time accumulated in working memory is partially lost during the break. To assess the possibility of such a decay process, Experiment 2 used three manipulations in which the duration and/or location of the breaks were systematically varied.

The parametric manipulations produced peak time shifts that were nonlinear functions of break duration, and that varied linearly with break location for a given duration. The obtained peak times were more

consistent with a continuous memory decay model than with those predicted by either the stop-retain or the reset hypotheses.

Alternative interpretations to the memory decay model are considered. In addition, the present findings are discussed in relation to the implications for the internal clock model.

To my late grandfather Luis Nieto Antúnez. He always hoped that his "saltimbanqui" (little tumbler) would reach higher and she finally did.

To the memory of George F. Gahles, my "american father", with love and gratitude.

And, to my husband Luis Galindo, whose love, encouragement, patience, and support made it possible.

Acknowledgements

I would not be writing this today without the help of Bruce Brown and Nancy Hemmes. Throughout the years they have been excellent teachers and advisors not only at a professional level, but also at a personal level. Thank you both for everything that you have done for me.

My special thanks to Robert Lanson, who encourage me to start in the Learning Processes Subprogram and whose support had never faltered.

I also want to thank several students who being involved in the working of the lab participated in conducting the experiment: Townsend Harris High School at Queens College students Karin Hsieh, Helen Palmos, and Rondolf Taylor; Learning Processes graduate students James Jakubow, Chris Kladopoulos, Sue Vener, and Wei Yang; and, Queens College undergraduate student Paul Gunther. Although not directly involved with the running of the study, Angela Carotenuto (Learning Processes) and Karen Goodman (Queens College) also deserve to be thanked for their help with my lab work while I was writing.

I thankfully acknowledge the Staff and Faculty of the Queens College Psychology Department for their support and assistance.

Finally, a different kind of thanks to my parents for being who they are, and to family and friends, both here in the USA and in Spain. All of them have contributed in some way to the present work.

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GENERAL INTRODUCTION

The body of empirical data showing that animals can adapt their behavior to time has been growing since Pavlov's finding of the conditioned reflex and Thorndike's formulation of the law of effect. Although there are countless experiments dealing with temporal parameters such as the interval between conditioned and unconditioned stimuli, delay to reinforcement, interresponse time, and postreinforcement pause, the nature of temporal stimuli and mediating mechanisms are still not well understood (Church, 1989). One potential mechanism, a pacemaker-counter or internal clock system, has been proposed in several current explanations of animal timing (Church, 1978; Killeen & Fetterman, 1988; Treisman, 1963). The clock model proposed by Gibbon and Church (e.g., Church, 1984; Gibbon & Church, 1984; Gibbon, Church, & Meck, 1984) assumes that subjective time (time accumulated in the internal clock) changes systematically with real time. This model involves three processes. The clock process consists of a pacemaker which is the source of pulses, a switch that gates pulses from the pacemaker, and an accumulator that records the number of pulses. The memory process includes a working memory that stores information about the current trial, and a reference memory that stores the time value recorded in working memory at the end of a reinforced trial. Behavior is controlled by a comparator process that compares current time (working memory) with previously stored times (reference memory). A response occurs on the basis of some criterion of similarity between these two values.

Some of the properties of this clock model have been explored using a procedure first developed by Catania (1970), later refined by S. Roberts (1981), and since then used by many others (e.g., Cheng & W. Roberts, 1989; Church, Miller, Meck, & Gibbon, 1991; Meck & Church, 1984; W. Roberts, Cheng, & Cohen, 1989). In this peak procedure, signalled fixed-interval (FI) trials are mixed with unreinforced trials. On unreinforced trials, the signal remains on for a much longer duration than the FI value, and no response is reinforced. Rate of responding on unreinforced trials is found to increase as a function of time with a maximum near the time of reinforcement, and then to decrease.

According to the internal clock model, the onset of the signal on a discrete FI trial closes the switch that gates pulses to the 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 occasions retrieval of a value from reference memory. As trial time elapses and the difference between the current accumulated value and the reference memory value decreases, the probability of responding increases. However, with additional time beyond the expected time of reinforcement, the difference grows, and hence, 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.

In the peak procedure, inferences about clock operating mode are based on comparisons between the peak times obtained on two types of trials: uninterrupted baseline trials and break trials in which the signal is interrupted for a few seconds. S. Roberts' (1981) study represents the first systematic application of this procedure to the study of the internal clock. In his Experiment 2, rats were exposed to a mix of FI 40 s and baseline (80 s) trials signalled by the houselight and separated by dark, variable 60 s intertrial intervals (ITI). On test sessions, half of the baseline trials were changed to break trials and different break parameters were studied on successive blocks of sessions. The houselight was turned off for 10 s starting at second 10, in the first condition (10 sessions); for 5 s starting at second 5, in the second condition (5 sessions); and for 5 s starting at second 15, in the third condition (5 sessions). During the next 10 sessions, the houselight remained on but a sound was turned on for 10 s starting at second 10. In all break (light off) trials, the peak time increased by an amount that was similar to the duration of the break in comparison to baseline trials. These results suggested that the clock stopped accumulating time during the break, and that postbreak time was added to the accumulated prebreak time. However, the addition of the sound produced a decrease in peak rate and a gradual increase in peak time that eventually became greater than the increase produced by the 10 s blackout. S. Roberts suggested that since trials with sound were never reinforced, the sound may have become a signal for the absence of food and, that as such, it began to reset the clock.

In a partial replication of S. Roberts' study, W. Roberts et al. (1989) exposed pigeons to differentially signalled (houselight and tone) FI 15 s and FI 30 s trials mixed with 90 s unreinforced trials with each signal, and dark ITIs (10-40 s). Baseline and break trials were presented on alternating test sessions. In three successive blocks of 16 sessions, the signal on break trials was turned off for 9, 3, and 1 s respectively, always starting at second 9. All break trials produced decreases in peak rate and increases in peak time that were similar to the duration of the break plus the time elapsed before the break, suggesting 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-trial 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 as mutually exclusive timing strategies resulting from differential operation of a single mechanism. Instead, they may be regarded as the two outcomes of a dichotomous process reflecting the combined effects of two different components of the internal clock model--switch and working memory.

The present study used double dissociation tests in an attempt to clearly distinguish between outcomes and explanations involving switch and/or working memory operation.

If the switch opens at break onset and closes at break offset, and if accumulated time is retained during the break, then peak time on break trials will only depend on the duration of the break. This will be referred as the "stop-retain" hypothesis. It predicts that breaks of the same duration will yield similar peak times, and 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 only depend on the location of the break. This is 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. If, on the other hand, reset occurs at break offset, then breaks identical in offset 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 differ in duration and/or location. Although the 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 may have been due to either differential switch latency for opening and closing, or partial resetting.

An alternative explanation of these results, based on a memory decay model, was evaluated in Experiment 2 of the present study. According to the memory decay view, the switch opens at break onset; that is, 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 produced 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 phenomenon found in many delayed-matching-to-sample (DMTS) experiments, the trace-decay hypothesis advanced by

W. 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, three breaks differing in duration and/or location were used to evaluate the adequacy of the dichotomous--stop-retain and reset--model. According to the stop-retain prediction, 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 produce similar peak times if reset occurs at break onset and the switch remains closed during the break. However, if reset occurs at break offset or if the switch does not close until signal resumption, breaks differing in duration ending at the same time should produce similar peak times. Thus, 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 Carnaux 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-h light:dark cycle.

Experimental sessions were conducted five 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 at the same time.

Apparatus

Sessions were conducted in three standard size (36.8 cm x 50.8 cm x 34.3 cm) pigeon chambers with white sides and rear walls (BRS/LVE, model 132-02) containing three-key aluminum intelligence panels. Three 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 intelligence panel. 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. Birds were trained to eat from a lighted hopper until their eating latencies were less than 2 s. In successive steps, access to food was gradually reduced from 20 to 1 s while variable interfood intervals were increased from a mean of 15 s to a mean of 30 s. Following magazine training, pigeons were exposed to autoshaping trials consisting of presentation of a 5 s white key conditioned stimulus (*CS*) followed by 3 s access to food (*US*), separated by 60 s intertrial intervals (*ITI*). The first keypeck after CS onset turned the keylight off and was immediately followed by 3 s access to food. After four consecutive trials with a peck, the keylight remained on continuously and every keypeck produced access to food. The session ended when the pigeon had made 50 responses. During this and all other pretraining sessions, the houselight was on. All pigeons met the keypeck acquisition criterion within the first 2 sessions. During the next session, a 15 s random-interval ($t = 1$, $p = .067$) reinforcement schedule was in effect until 60 reinforcers had been obtained. For the next 8 sessions, the schedule was changed to random interval 30 s ($t=1$, $p=.033$), with sessions ending after 42 reinforcers. During the last 3 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. Trials were signalled by the onset of the houselight. On reinforced trials (FI trials), the first response after 30 s turned the houselight off and produced 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 geometrically distributed duration with a mean of 30 s ($t=1$, $p=.033$; Fleshler & Hoffman, 1962). Forty-two FI trials and 18 Baseline trials were randomly mixed, with intertrial intervals geometrically distributed with minimum 15 s and mean 60 s ($t=1$, $p=.022$). This procedure was in effect for 60 sessions. 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.

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: 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 (see Figure 1 for schematic description). 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 three 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 block randomized in pairs, that is, if the first unreinforced trial was a Break trial, the next was a Baseline trial.

Data analysis

Sessions always started with five FI trials for which no data were taken. For the next 60 trials, keypecks were recorded in 1-s bins. On Baseline and Break trials, keypecks were recorded over the interval 0-90 s, and on FI trials over the interval 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 cancelled and the trial was extended like 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.

Peak time was defined as the "median" of the response rate function over the interval 0-90 s. The calculation of peak time involved an iterative procedure (S. Roberts, 1981; W. Roberts et al., 1989). First, the median over 0-90 s was found. Second, a new median was computed over the interval of which the first median was the center. This process was repeated until a median was found that was within .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.

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 3-Breaks condition, only data from the last 6 sessions (55-60) were considered. Figure 2 shows mean response rate functions for the FI and Baseline trials over the last 6 baseline sessions. During baseline sessions, all pigeons acquired a temporal discrimination, that is, the response rate rose to a maximum and then declined, with elapsed trial time. The superposition of the rising limb of the Baseline function on the FI function indicates no discrimination between reinforced and unreinforced trials. Although there were individual differences in peak times, the group mean peak time (28.9 ± 1.3 s, SEM) was not reliably different from 30 s (t-test, $p > .05$). (See Appendices A and B for individual and group peak times and peak rates obtained from this and all subsequent manipulations).

Figure 3 presents group mean response rate functions for each type of break, for the first 2 and the last 12 sessions of the 3-Breaks condition. As in Figure 2, Baseline and FI functions show tight superposition. In addition, Baseline and Break functions look very similar except that the Break trial functions are shifted to the right. However, the shift seems more pronounced for sessions following the first 2, at least for the Late break. A repeated measures analysis of variance of peak times yielded a significant interaction among trial type (Baseline, Break), break type (Early, Late, Long), and sessions (1-14) [$F(26,130) = 2.18$, $p<.0023$]. Additional tests for each break type showed a reliable increase in peak time across sessions for the Late break trials [$F(13,65) = 4.64$, $p<.0001$], but no change across sessions for the Early and Long break trials [$p>.70$]. Since the triple interaction was not present when the analysis was limited to the first 2 or the last 12 sessions, separate analyses were conducted for sessions 1-2 and 3-14 for all break trial types.

Figures 4-9 present individual bird's mean response rate functions across the last 12 sessions for each type of break. The left side panels on each Figure show keypeck rate as a function of trial time. As the group data showed (Figure 3), Baseline and Break functions have similar shapes that preserve the individual response patterns of each subject. This similarity is more evident on the right side panels of the Figures in which the functions have been superposed in terms of their peak times.

The Break functions were shifted horizontally to the left by an amount equal to the difference between the peak times (peak time shift).

Visual inspection of daily peak times suggested that Baseline and Break peak times were correlated; that is, on sessions in which the Baseline peak time was later the Break peak time was also later, independently of the type of break. The mean Pearson correlation coefficients 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, that is, on differences between Baseline and Break peak times obtained on a given session.

Figure 10 presents peak time shift as a function of sessions for each type of break. For the first 2 sessions, Early and Late breaks yielded similar peak time shifts (8.5 ± 1.2 s and 7.7 ± 2.3 s) that were shorter than the shift produced by the Long breaks (20.9 ± .9 s); Scheffe test, $\underline{p} < .05$). While both Early and Late shifts were not reliably different from the shift expected from the stop-retain prediction (dotted lines), Long shifts were not reliably different from the reset prediction (dashed lines) ($\underline{t}$-tests, $\underline{p} > .05$).

In contrast, during later sessions (3-14), all three break types produced peak time shifts that were reliably different from each other

(Scheffe test, $p < .05$). For the Early, Late, and Long breaks the shifts were : Early 8.1 ± .8 s, Late 13.8 ± .8 s, and Long 20.2 ± .2 s. Furthermore, the obtained shifts were reliably different from the shifts expected from both the stop-retain and the reset predictions [Early: $t(5) = 2.6$ and 4.7; Late: $t(5) = 10.1$ and 9.4; Long: $t(5) = 27.7$ and 4.1, respectively, $p < .05$].

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 the predictions of the dichotomous model. Stop-retain would predict 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. In later sessions, the results are closer to the reset prediction (Figure 4), but not entirely consistent with it. That reset did not occur at break onset is evident from the differences between the peak time shifts obtained with Early and with Long breaks. Moreover, if working memory had reset at break offset the two breaks with identical offsets--Late and Long--should have yielded identical peak time shifts, and they did not.

The apparent change in the operation of the clock with amount of training is reminiscent of data reported by Brown, Hemmes, and Cabeza de Vaca (1992). In their study, trials started with a cue associated with an FI 30 s which was abruptly changed to a cue associated with an FI 60 s (shift trials). As in the present study, pigeons initially responded in a manner that was consistent with the stop-retain prediction, with subsequent sessions producing behavior that suggested resetting. Other studies have also shown stop-retain-like behavior in acquisition (Gibbon & Balsam, 1981, split trials), or early in training followed by a change in performance with additional sessions (S. Roberts, 1981, Experiment 2, sound; S. Roberts & Church, 1978, FI trials with breaks). However, W. Roberts et al. (1989) and Cheng and W. Roberts (1989, peak procedure with multimodal trials) found reset-like performance at the outset of training. Although these studies comprise a wide variety of procedures that could account for the differential outcomes, they all included some form of within-trial stimulus change which represents a common feature with the present study. Some of these results suggest a change in the operation of the clock with amount of training, but it remains unclear how this parameter modifies the way the clock operates. One possibility is that amount of training influences clock processes other than working memory, such as the speed of switch opening and closure. The observed peak time changes with training may be attributable to a decrease in latency to open the switch at break onset, an increase in latency to close the switch at break offset, or both. However, this mechanism does not account for the differential changes found for the different types of break.

Unlike W. Roberts et al. (1989, Experiment 3) who found shifts that were consistent with those predicted by the reset hypothesis, the peak time shifts in the present study were consistently longer than expected from the nominal stop-retain prediction but not so long as those expected from the nominal reset prediction. In addition, while S. Roberts (1981, Experiment 2) found that the two breaks of equal duration but differing in location produced equivalent peak time shifts, in the present study, Early and Late break trials produced reliably different shifts, following the second session. However, as in the present 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 of partial resetting.

The results of the present study may be understood in terms of a variation of the partial reset hypothesis, according to which the clock stops at break onset (i.e., the switch opens), and time accumulated in working memory is partially lost during the break. In this view, the partial loss is not the result of resetting as such but the result 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 might 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, Experiment 2 implemented a parametric manipulation by systematically changing the duration and/or location of the breaks.

EXPERIMENT 2

The results of Experiment 1 suggest that during the break the accumulator contents are subject to a decay process. The notion that temporal information might 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 what is it exactly 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. Roberts & Grant, 1976; Roitblat, 1984; Staddon, 1984). An example of a decay-like process is the <u>subjective shortening process</u> 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 (<u>RI</u>) 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, & W. 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 RI durations (Church, 1980; Spetch & Wilkie, 1983); ITI and RI values used during training relative to those in testing (Spetch & Wilkie, 1983; Spetch & Rusak, 1992); 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 decay-like process, in which temporal information is gradually lost in working memory. In this view and in the context of the present study, the break during the FI signal might be understood as a retention interval for the amount of subjective time elapsed prior to break onset. However, if the value in working memory (prebreak accumulated time) decays during the break then, at the end of the break, the retained value will be less than the corresponding value in a nonbreak trial. Thus, more time will be needed to reach the responding criterion; consequently, the peak time on a break trial will be delayed by the duration of the break plus 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 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 ($\log \underline{d}$), 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:

$$\log \underline{d}_t = \log \underline{d}_0 * \exp(-\underline{bt})$$

where $\log \underline{d}_t$ represents discriminability at delay $\underline{t}$, $\log \underline{d}_0$ is discriminability at zero delay, and $\underline{b}$ is a time constant representing the rate of decrement in discriminability (McCarthy & White, 1987).

Experiment 2 explored the posited memory decay process by using three parametric manipulations in which the duration and/or location of breaks were systematically varied.

Based on the assumption that subjective time is a linear function of real time (Gibbon, 1977; Gibbon & Church, 1981), a mathematical model of peak time was developed, in which the location of the peak time represents the additive result of the reinforced duration, the break duration, and the time lost during the break (see Figure 11). That is,

$$PT = t^* + t_b + [t_p - f(t)] \qquad (1)$$

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 prebreak time retained at time t, where t is elapsed time during the break. Nominally, $t^* = 30$ s, but may differ from that value as a result of performance bias. When there is no break (i.e., Baseline trials), PT will be equal to t^*, since $t_b = 0$ and $t_p = f(t)$. 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). In 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). Since the amount of prebreak time retained depends on the decay occurring during the break, peak time predictions were evaluated by allowing $f(t)$ to take different forms: exponential, power, logarithmic, and linear (Wixted & Ebbesen, 1991).

In an attempt to determine the effects that the break parameters have on the rate of decay, Experiment 2 implemented three different manipulations. In the first, the onset of the break was fixed while break duration, and thereby break offset, varied. In the second, the duration of the break was fixed while break onset and offset changed. And finally, the offset of the break was fixed while 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, each block consisting of 14 FI, 1 Baseline, 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 3-Breaks condition of Experiment 1 was reintroduced.

In the first manipulation, Duration-Fixed-Onset, breaks always started 6 s after trial onset but they lasted for different durations: 3-, 6-, 9-, 12-, or 15-s (Figure 12, 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 (Figure 12, center panel).

In the last manipulation, Duration-Fixed-Offset, breaks started at different times, but always ended 21 s after trial onset. The break durations were the same as those used in the Duration-Fixed-Onset manipulation (Figure 12, bottom panel).

Results and Discussion

Peak times obtained in the successive replications of the 3-Breaks condition were used to assess stability of performance across manipulations. Repeated measures analyses of variance of peak times within and between replications showed no change across sessions (in all comparisons minimum $p > .17$). As in the last sessions of Experiment 1, Early (9.2 ± .25 s), Late (14.2 ± .52 s), and Long (20.4 ± .20 s) break trials produced reliably different peak time shifts (Scheffe test, $p < .05$). In addition, the peak time shifts were reliably different from both the stop-retain and the reset predictions [Early: $t(5) = 12.8$ and 11.2; Late: $t(5) = 15.8$ and 13.1; Long: $t(5) = 27.0$ and 3.0, respectively, $p < .05$]. These results indicate no apparent change in peak time shift resulting from intervening manipulations. Therefore, subsequent analysis focussed on the effects of the three parametric manipulations.

Stop-retain and Reset versus a Decay Process

Figure 13 shows peak time shift as a function of break duration, with the discontinuous lines representing the nominal shifts predicted by stop-retain (dotted line) and reset (dashed line). As shown in this figure, the Duration-Fixed-Onset manipulation produced a peak time shift function that was inconsistent with the linear changes predicted by either the stop-retain or the reset hypotheses. The nonlinearity of the function was confirmed by a trend analysis yielding reliable linear and quadratic components [$F(1,20) = 1165.46$, $p<.0001$ and 4.89, $p<.039$, respectively].

The peak time shifts obtained during the Location manipulation, as shown in Figure 14, are again clearly 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 [$F(1,20) = 305.79$, $p<.0001$]. To evaluate the extent to which the obtained function differed from the predicted functions, the slopes of the individual peak time functions were calculated through linear regression analyses. The group mean slope (0.56 s/s) was reliably different from both the stop-retain (0 s/s) and the reset (1 s/s) slopes [$t(5) = 11.46$ and 9.0, $p>.01$, respectively]. For individual birds the slopes ranged from 0.32 to 0.64 s/s with percentage of explained variance accounted for (r^2*100) ranging from 92.9 to 98.5%.

The adequacy of the decay model was further investigated in the Duration-Fixed Offset manipulation. When the onset of the break is fixed, the difference between the stop-retain and the reset predictions is constant for all durations; thus the two parallel discontinuous lines on Figure 13. However, when breaks of different durations have identical offset times, differences between the two predictions are maximized, providing a clearer picture of the relationship predicted by a nonlinear continuous model. The results of the Duration-Fixed-Offset manipulation are presented in Figure 15. The trend analysis of the peak time shift function showed again the presence of both a linear and a quadratic component [$F(1,20) = 156.12$ and 28.33, $p<.0001$], inconsistent with the linear changes expected from both the stop-retain and the reset predictions.

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 a nonlinear function of break duration, and the Location manipulation yielded a shift function with a slope that differed from the predicted slopes. In all three manipulations standard errors of the mean (see Figures 13, 14, and 15) provided evidence that the obtained functions departed from predictions based on a dichotomous model. The obtained results are more consistent with an interpretation 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 contrasted against 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 during the break. Since 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 during the break would only depend 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 only a function of 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 are 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 within a given duration. In an attempt to differentiate between these two models, exponential and power functions were fitted to the peak times obtained in the two Duration 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 (proportion of data variance accounted for). Both functions were reasonably accurate (see Figure 16). For five of the six birds, the percentage of explained variance was higher for the exponential fit than for the power fit. However, the differences were not large and with only five data points to evaluate the fits the probability of detecting a reliable difference, even if one existed, was considered too low to pursue 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.

The results presented in Figure 10 may be compatible with this interpretation. Since the peak time shifts for the Late break trials are about halfway between the two predictions (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 of Early and Long trial outcomes, it may not be that evident since the difference between the stop-retain and the reset predictions is smaller than for the Late break trials.

To evaluate the stochastic interpretation of the present results, data from all the 3-Breaks condition were examined 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 (1990) 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, and 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 the present data. The results obtained from an analysis based on Gibbon's (personal communication,

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 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 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 3-Breaks condition manipulations.

Figures 17, 18, and 19 present individual bird's frequency distributions of stop points in Baseline and Break trials for each type of break--Early, Late and Long. 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. However, examination of the distributions revealed no indication of bimodality. A quantitative analysis was undertaken to determine the extent to which Break trials distributions differed in variability from Baseline trials distributions. For each distribution, the mean of the absolute deviations from the median of the distribution was calculated (see Table 2). Repeated measures analyses of variance of the mean deviations yielded no reliable differences in variability for the Baseline distributions across break types ($p > .34$), but a reliable difference for the Break distributions [$F(2,10) = 13.66$, $p < .0014$]. Variability in the frequency distributions for Late breaks was reliably larger than for Early or Long breaks (Scheffe test, $p < .05$), 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 since 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 outcomes for Late breaks (15 s) is 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, prediction that is 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 since 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 the present results.

The failure to find increased variability in all break distributions is somewhat surprising. If the switch opens at break onset and closes at break offset, 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 failure to find an increase in variability from Baseline to Early break distributions, as well as, the decrease in variability found in the Long break distributions. The variability in retained time at the end of an Early break would be small and could be compensated by the decrease in switch latency; hence, the total variability may not be reliably different from the variability on a Baseline trial. In contrast, at the end of a Long break trial, the combination of decreased variability in switch latency and retained times close to zero would result in reduced total variability as compared to a Baseline trial. Further experimental manipulations would be required to determine the adequacy of this account.

GENERAL DISCUSSION

The main finding of the present study 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 the dichotomous model since the obtained peak times were longer than predicted by the stop-retain hypothesis, but shorter than those predicted by the reset hypothesis. The present 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 end points 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., $\underline{t} = \underline{t} + 1$) 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 since 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 the present study favor an exponential model over a power model, both models account for a large proportion of the data variance, and the present data do not clearly distinguish between them.

Determinants of Clock Reset

The results of the present study 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 may 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 the present study suggest another mechanism to clear the clock contents--a decay process operating in working memory. Other studies have also suggested that reset may be the result of a gradual decay process. For example, S. Roberts (1981, Experiment 3) 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 is not completely reset when a reinforced trial begins, the subjective time when food is delivered on that trial would be greater than if the clock had been completely reset. This longer reinforced duration 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, using 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. In 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 2 s ITI, suggesting that the clock could be reset rapidly. However, the results also indicated 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 the present study is the similarity between the duration of the longest break and the duration of the minimum ITI. Throughout the present study, the ITI values used were geometrically distributed and, with a minimum of 15 s, the distribution contained a substantial number of interval values close to 15 s. 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 after signal offset, 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 may have determined a rate of reset that did not permit working memory to clear totally after only 5 s. Similarly, the results of Church et al. (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. Roberts et al., 1989, Experiment 3, with pigeons) could be attributable to procedural variations, since the studies differ in the implementation of the experimental manipulations and the specific parameters used.

The apparent discrepancy between the results of the present study and those of S. Roberts' rests on the outcomes obtained with breaks of equal durations. While in S. Roberts' 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 the present study, 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 may have produced peak time increases with a difference that, even though in the right direction, was too small to be reliable.

The peak time increases on break trials obtained by both S. Roberts and the present study indicate at least partial retention of prebreak time. In contrast, W. Roberts et al. (1989) found peak time increases that indicated complete reset. In addition, while in the first two studies there was no systematic difference between baseline and break peak rates, in the W. Roberts et al. study the peak rates on break trials were lower than on baseline trials. However, the W. Roberts et al. study included a procedural feature that differentiates it from the former two. While W. Roberts et al. presented unreinforced baseline and break trials in different sessions, in S. Roberts' and the present study they were presented in the same sessions. It is plausible that the presentation of break trials in different sessions may have increased the discriminability of the break as a signal for the absence of food. This interpretation is consistent with S. Roberts' 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.

Relative-Duration Interpretation

An alternative interpretation of the present results is based on an extension of Spetch and Wilkie's (1983) subjective shortening notion. Spetch and Rusak (1989) proposed that 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 to the duration of the temporal context comprised of both ITI and RI periods. Introducing increases in ITI and/or RI 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 RIs, 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. 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, while the shifts obtained in S. Roberts (1981) and in the present study both using longer ITI values (60 s) were more consistent with smaller decreases.

However, this perceptual interpretation does not accommodate the results obtained in the Location manipulation. Since 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 showed that peak time shift increased with increasing onset time.

Although the relative-duration hypothesis does not account for all the present 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 since 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 the present study. Future research could attempt to determine the extent to which temporal discrimination results from a combination of perceptual and memorial processes.

Appendix A

Individual and Group Peak Times in all experimental conditions

	#3853		#3285		#3862		#3267		#3273		#3283		Group	
	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK
Baseline sessions	27.4		30.4		31.6		24.8		31.6		26.1		28.7	
3-BREAKS CONDITION														
Early breaks														
Exp1: ses. 1-2	27.3	40.5	29.3	39.6	30.2	38.1	27.7	32.3	28.5	36.9	24.1	31.2	27.9	36.4
ses. 3-14	27.9	36.0	30.5	40.0	29.4	38.3	27.9	36.0	32.9	42.8	25.0	33.8	28.9	37.8
Exp2: rep 1	28.3	36.8	30.7	40.9	27.6	38.1	27.2	36.6	33.6	42.9	24.8	34.5	28.7	38.3
rep 2	24.4	33.3	32.9	43.8	27.9	37.6	31.2	39.6	31.5	39.6	26.1	35.8	29.0	38.3
rep 3	26.4	36.2	31.6	41.9	28.4	38.6	27.9	37.5	33.1	41.4	26.4	36.5	29.0	38.7
Late breaks														
Exp1: ses. 1-2	25.0	35.6	31.2	46.4	30.2	42.2	26.0	30.5	32.3	32.4	26.4	30.3	28.5	36.2
ses. 3-14	27.4	39.5	30.3	47.4	28.8	43.6	28.2	40.6	31.9	44.9	24.4	37.5	28.5	42.3
Exp2: rep 1	27.5	38.5	31.2	48.3	29.8	41.4	29.4	43.5	32.9	46.6	24.9	40.0	29.3	43.1
rep 2	25.6	36.6	32.3	48.4	29.3	42.4	30.3	45.7	31.1	44.3	26.2	41.4	29.1	43.1
rep 3	27.7	38.9	31.4	48.7	28.5	43.5	28.7	44.2	32.9	45.2	26.4	44.1	29.3	44.1
Long breaks														
Exp1: ses. 1-2	25.9	48.5	28.2	49.3	30.3	50.3	28.2	46.5	28.6	52.9	26.9	45.7	28.0	48.9
ses. 3-14	27.5	47.9	31.2	52.3	28.6	48.5	27.5	47.4	32.3	52.4	24.5	44.5	28.6	48.8
Exp2: rep 1	25.9	46.5	31.3	51.9	28.6	49.9	30.2	48.2	33.0	52.2	25.5	45.5	29.1	49.0
rep 2	25.2	45.8	31.6	52.7	29.6	49.3	29.4	49.9	30.9	51.3	26.3	47.3	28.8	49.4
rep 3	26.3	47.7	31.8	52.9	28.8	49.3	28.5	49.1	33.1	52.4	27.2	48.0	29.3	49.9
EXPERIMENT 2														
Duration-Fixed Onset														
3 sec	28.5	33.7	31.2	36.6	29.1	34.9	29.1	31.8	33.2	39.3	24.4	29.6	29.3	34.3
6 sec		37.0		43.9		39.9		36.9		42.5		34.3		39.1
9 sec		40.7		46.2		42.8		41.9		47.1		37.2		42.7
12 sec		43.0		50.2		47.7		46.4		51.1		41.1		46.6
15 sec		47.9		52.3		49.9		48.8		54.4		44.9		49.7
Location														
at 3	25.4	34.1	31.8	40.8	30.3	37.1	28.9	37.1	31.6	38.4	24.7	32.8	28.8	36.7
at 6		35.0		42.0		39.2		39.1		39.3		34.3		38.2
at 9		35.4		45.1		39.1		40.3		41.6		35.6		39.5
at 12		36.9		47.1		42.7		41.9		44.1		38.2		41.8
at 15		38.0		47.9		44.3		44.9		45.3		39.4		43.3
Duration-Fixed Offset														
3 sec	28.5	35.6	31.5	39.9	27.7	35.7	29.5	39.9	32.5	40.5	26.1	33.3	29.3	37.5
6 sec		39.4		47.6		41.4		44.8		44.8		45.5		43.9
9 sec		48.4		50.6		46.6		47.0		48.9		46.5		48.0
12 sec		50.6		50.0		48.4		47.3		49.9		46.9		48.9
15 sec		50.1		50.4		48.1		48.7		52.5		47.6		49.6

BL = Baseline trials; BK = Break trials; Exp = Experiment 1 or 2; ses. = sessions; rep = replication of 3-Breaks condition in Experiment 2

Appendix B

Individual and Group Peak Rates in all experimental conditions

	#3853		#3285		#3862		#3267		#3273		#3283		Group	
	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK	BL	BK
Baseline sessions	0.99		1.88		2.17		1.13		0.62		2.60		1.56	
3-BREAKS CONDITION														
Early breaks														
Exp1: ses. 1-2	1.07	1.03	2.05	1.88	1.96	1.93	1.45	1.31	0.61	0.37	2.94	3.05	1.68	1.60
ses. 3-14	0.93	1.00	2.24	2.05	2.18	2.08	1.46	1.46	0.74	0.86	2.57	2.67	1.69	1.69
Exp2: rep 1	1.25	1.14	2.06	1.88	2.08	2.07	1.84	1.92	1.07	0.95	2.15	2.26	1.74	1.70
rep 2	1.14	1.07	2.04	2.03	2.53	2.10	1.52	1.64	1.11	1.07	2.23	2.29	1.76	1.70
rep 3	1.23	1.42	2.31	2.27	2.10	2.09	1.69	1.75	0.95	0.58	2.96	2.81	1.87	1.82
Late breaks														
Exp1: ses. 1-2	1.21	1.14	2.11	1.48	1.95	1.88	1.33	1.22	0.88	1.01	3.03	3.02	1.75	1.63
ses. 3-14	1.01	1.08	2.09	1.81	2.06	1.71	1.38	1.40	0.67	0.72	2.65	2.55	1.64	1.55
Exp2: rep 1	1.21	1.40	1.76	1.68	2.37	1.90	1.73	1.78	1.11	1.18	2.26	2.07	1.74	1.67
rep 2	1.22	1.14	2.07	2.06	2.24	2.02	1.70	1.48	0.95	0.86	2.29	1.73	1.75	1.55
rep 3	1.23	1.20	2.31	2.05	2.06	1.86	1.71	1.59	1.06	0.44	2.48	1.92	1.81	1.51
Long breaks														
Exp1: ses. 1-2	1.23	1.03	2.02	2.20	1.73	2.12	1.28	1.45	0.80	0.81	2.85	2.89	1.65	1.75
ses. 3-14	1.10	1.00	2.19	2.33	2.11	2.02	1.33	1.54	0.86	0.84	2.58	2.60	1.70	1.72
Exp2: rep 1	1.07	1.18	2.06	1.77	2.01	2.00	1.64	1.79	0.98	0.87	2.32	2.33	1.68	1.66
rep 2	1.09	1.13	2.09	2.03	2.18	2.21	1.65	1.57	0.96	0.98	2.33	2.17	1.72	1.68
rep 3	1.35	1.32	2.30	2.16	2.21	2.20	1.75	1.94	1.09	0.88	2.25	2.43	1.83	1.82
EXPERIMENT 2														
Duration-Fixed Onset														
3 sec	1.27	1.28	2.24	2.13	2.26	2.17	1.67	1.69	0.71	1.03	2.36	2.39	1.75	1.78
6 sec		1.31		2.10		2.09		1.56		0.65		2.48		1.70
9 sec		1.27		2.14		2.26		1.60		0.91		2.37		1.76
12 sec		1.28		2.26		2.09		1.43		0.64		2.30		1.67
15 sec		1.25		2.22		2.11		1.48		0.69		2.40		1.69
Location														
at 3	1.11	1.03	2.10	2.23	2.53	2.27	1.60	1.59	1.14	1.13	2.18	2.26	1.78	1.75
at 6		1.08		1.86		2.37		1.42		0.97		2.32		1.67
at 9		1.15		1.92		2.18		1.59		0.98		2.13		1.66
at 12		0.98		1.93		2.19		1.64		0.77		2.08		1.60
at 15		0.89		1.82		1.94		1.66		0.86		1.70		1.48
Duration-Fixed Offset														
3 sec	1.10	0.99	2.14	1.78	2.44	1.87	1.69	1.33	0.91	0.79	2.26	1.44	1.76	1.37
6 sec		0.96		2.09		2.10		1.52		0.77		1.94		1.56
9 sec		1.04		2.10		2.17		1.80		0.82		2.26		1.70
12 sec		0.90		2.28		2.26		1.62		0.80		1.90		1.63
15 sec		1.11		2.24		2.26		1.68		0.99		2.28		1.76

BL=Baseline trials; BK=Break trials; Exp=Experiment 1 or 2; ses.=sessions; rep=replication of 3-Breaks condition in Experiment 2

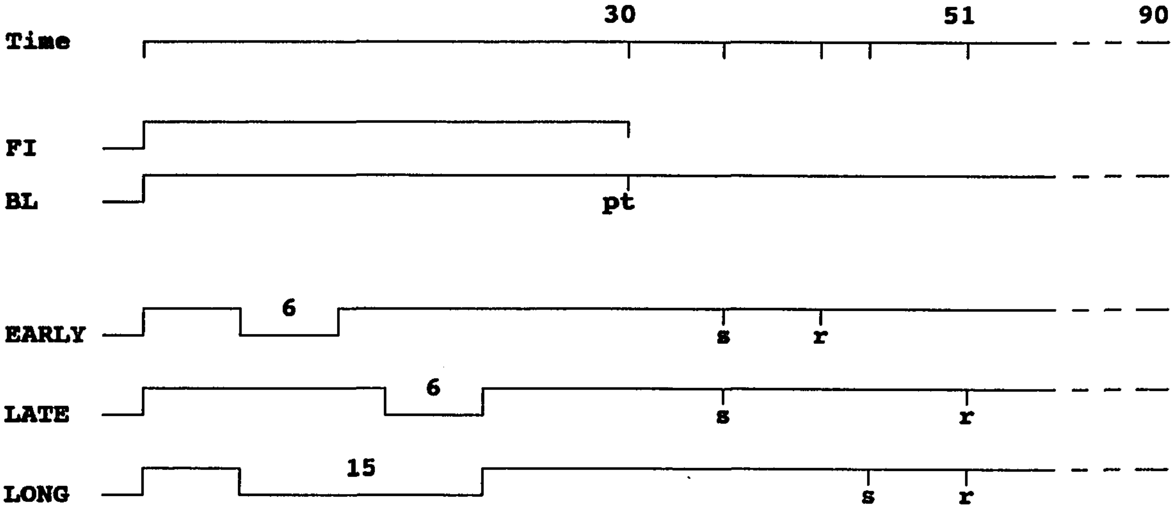


FIGURE 1. Procedure diagram for the 3-Break Condition. pt represents the expected location of the peak time on Baseline trials; s (stop-retain) and r (reset) the expected location of the peak times on Break trials.

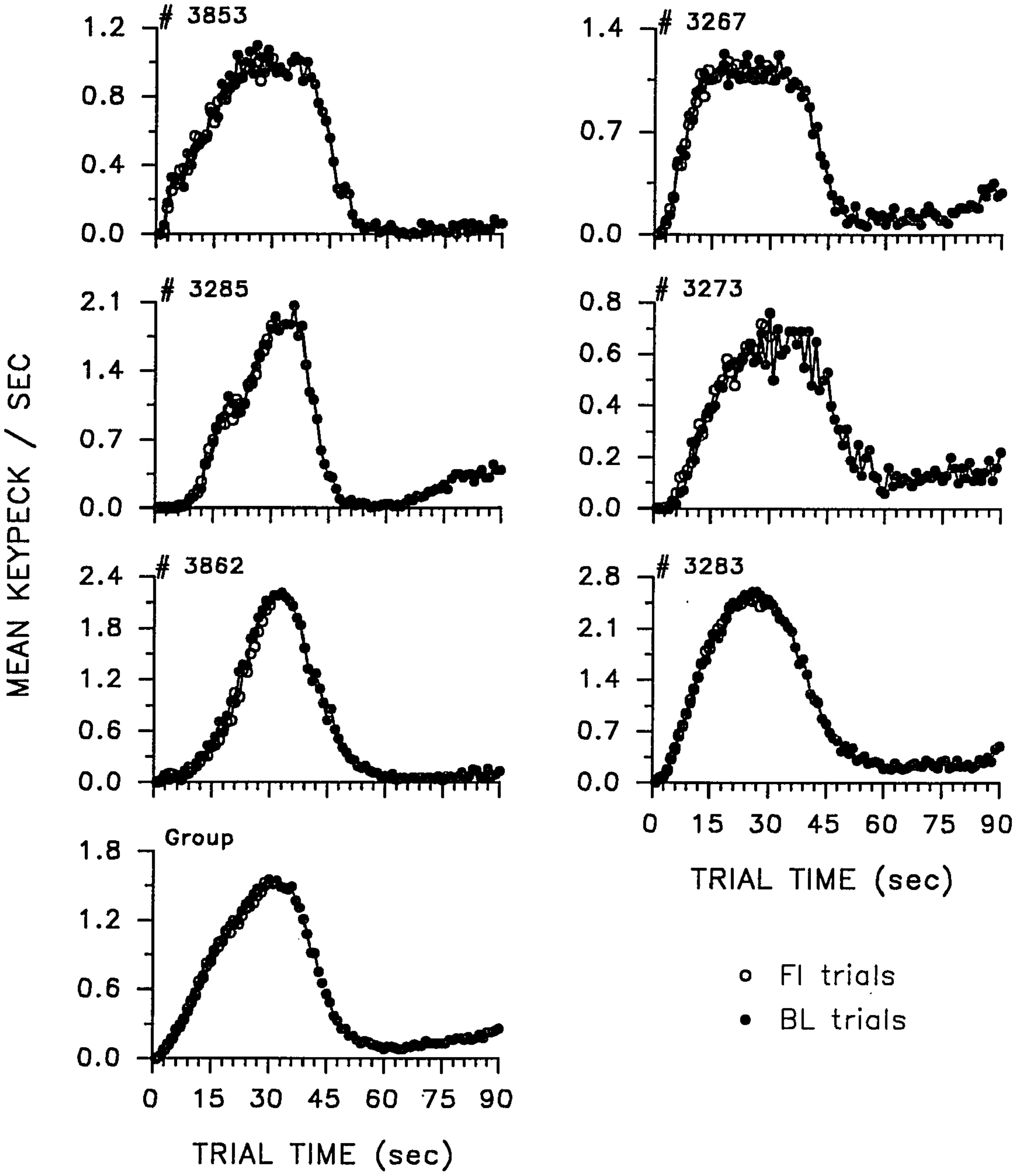


FIGURE 2. Individual and group mean keypeck rate as a function of elapsed trial time during the last 6 baseline sessions (55-60). Rate per sec is plotted separately for FI and Baseline trials.

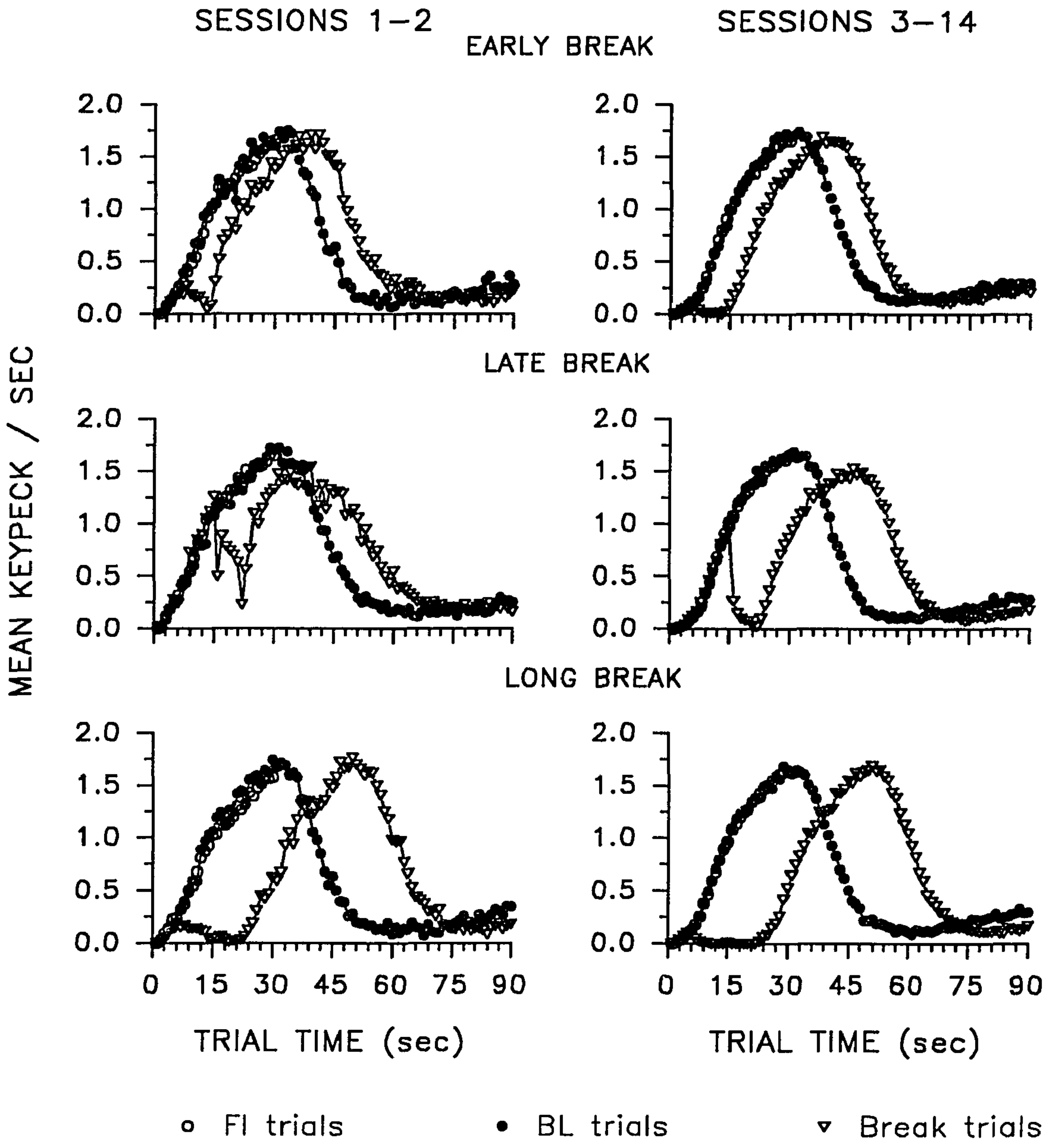


FIGURE 3. Group mean keypeck rate as a function of elapsed trial time during the first 2 and the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

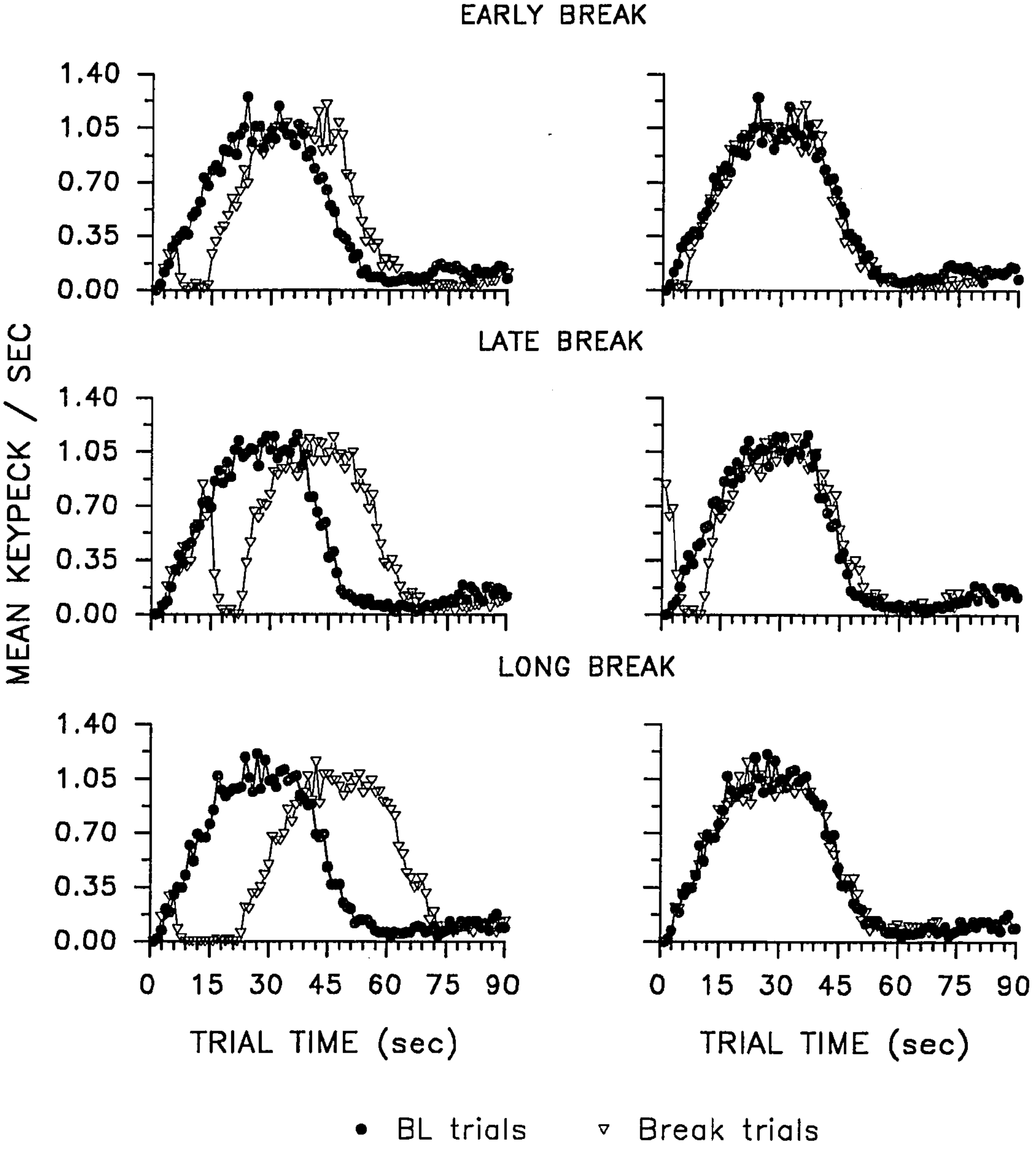


FIGURE 4. Pigeon #3853 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

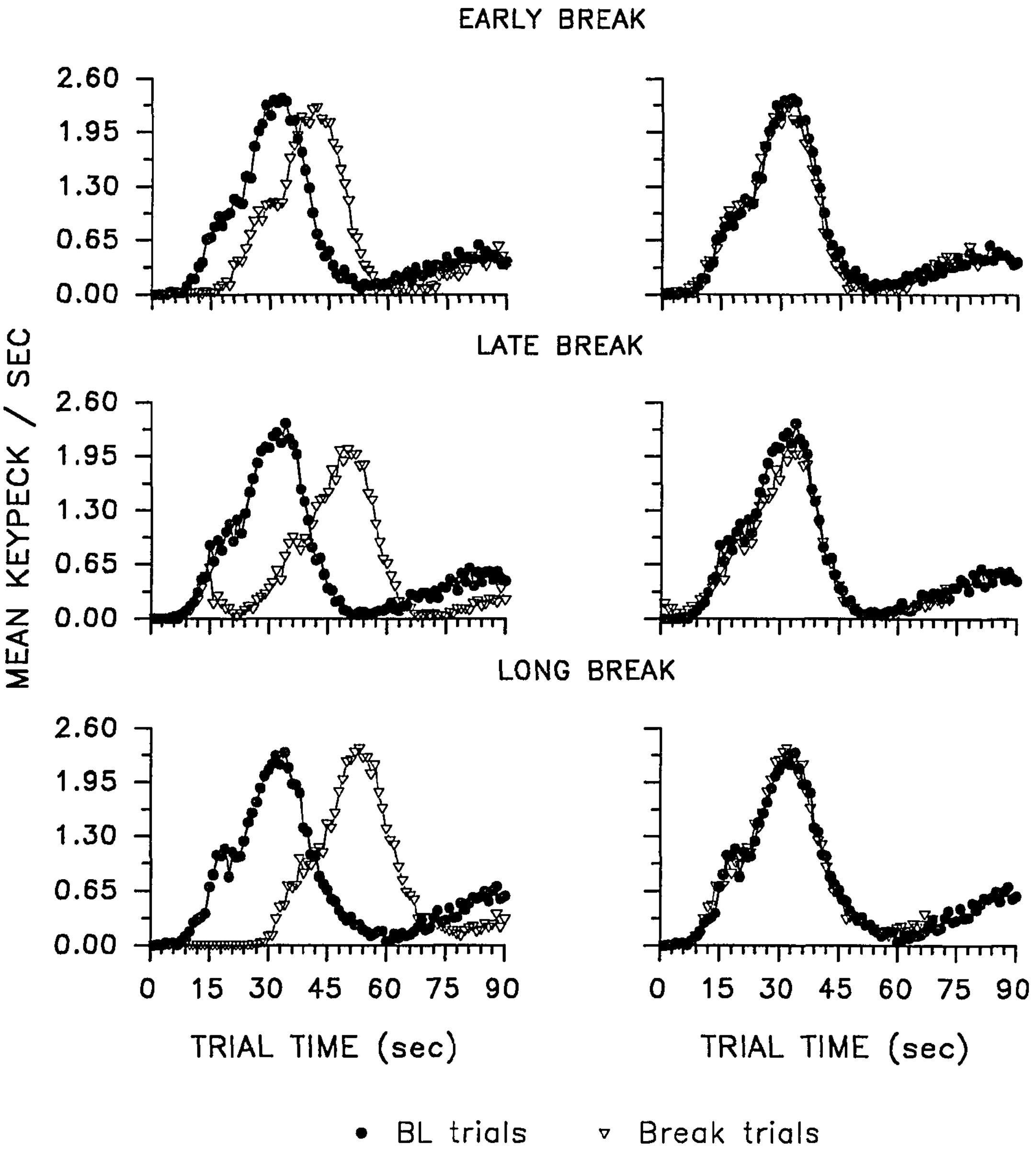
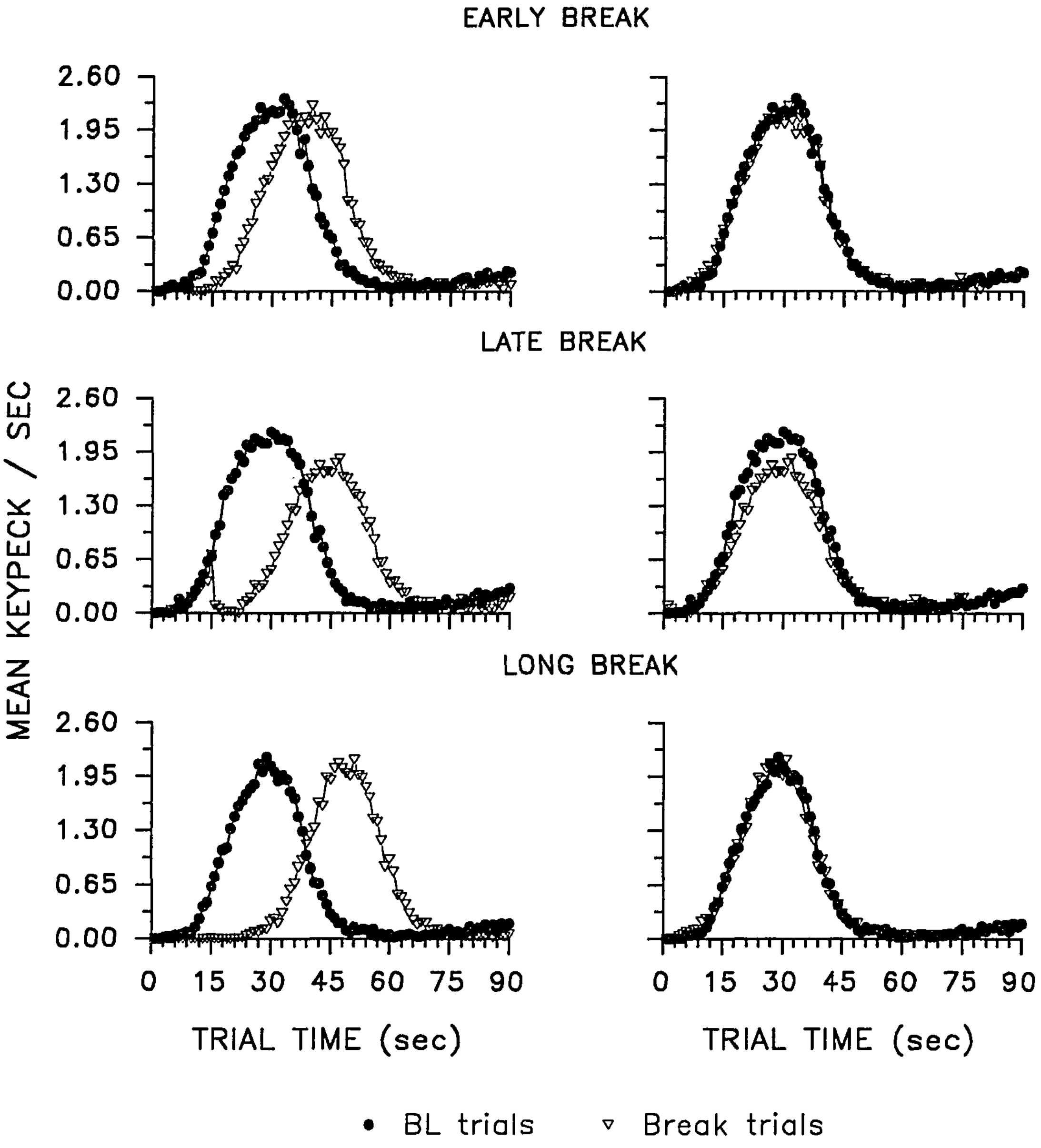


FIGURE 5. Pigeon #3285 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.



EARLY BREAK

LATE BREAK

LONG BREAK

FIGURE 6. Pigeon #3862 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

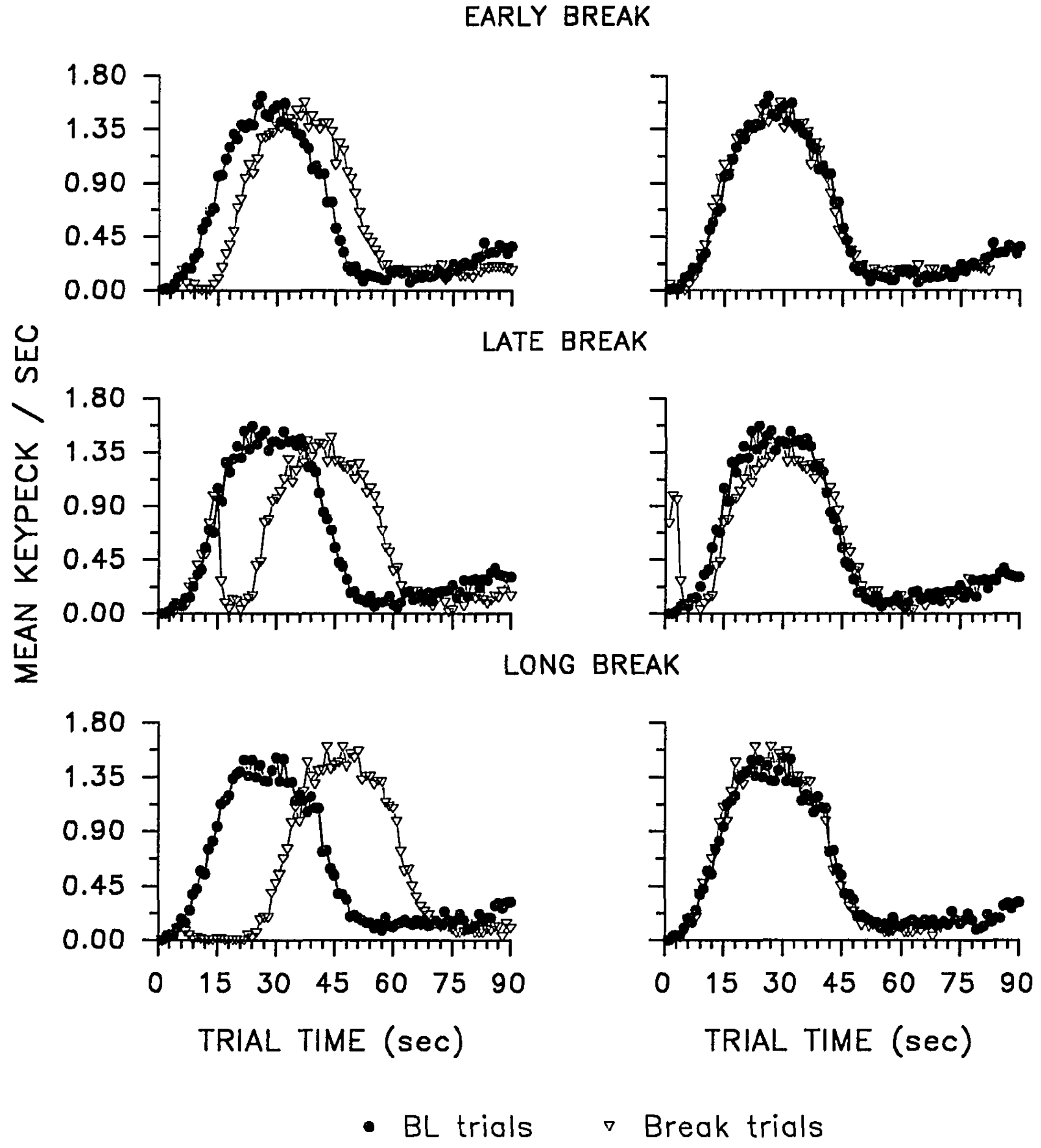


FIGURE 7. Pigeon #3267 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

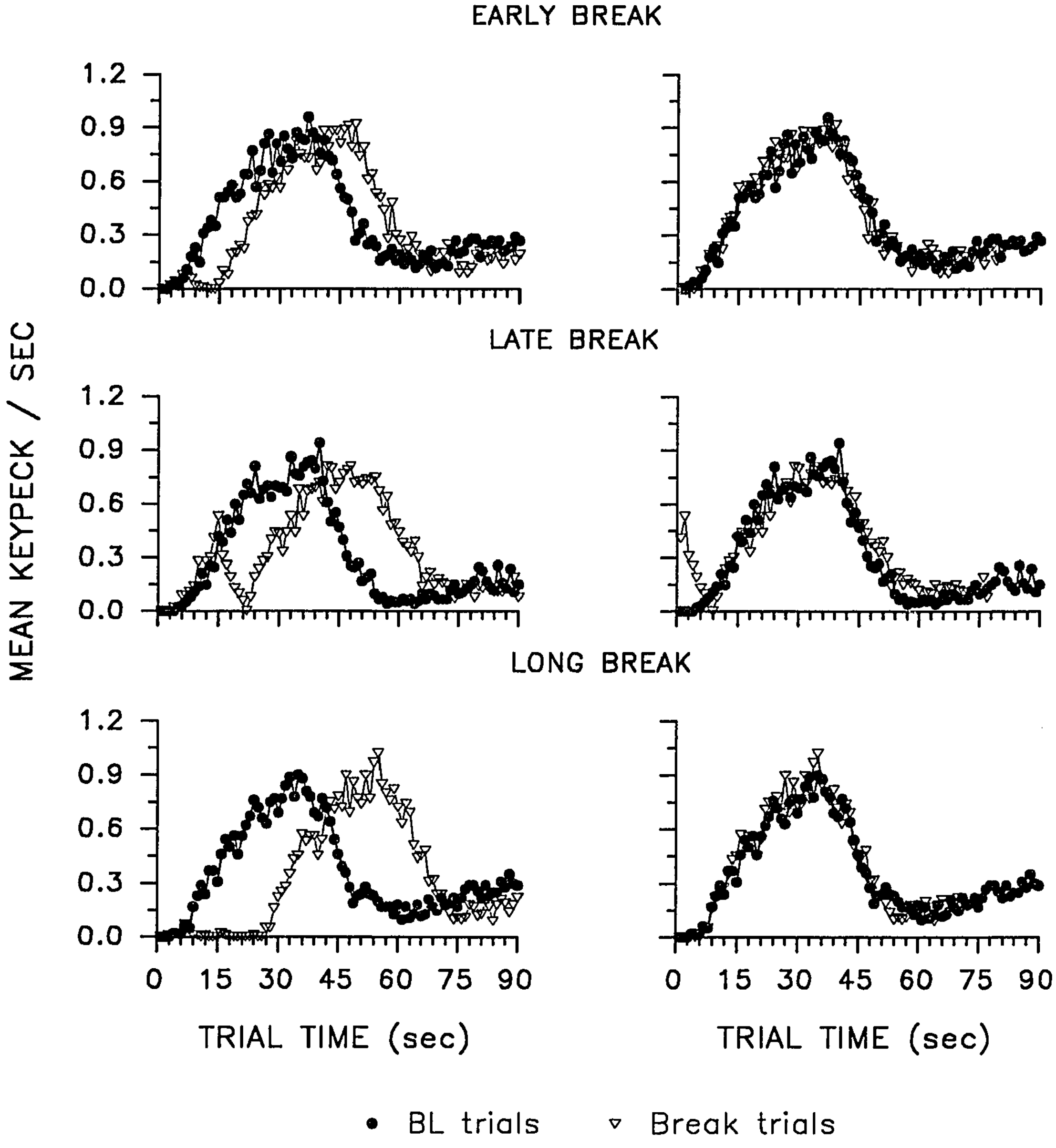


FIGURE 8. Pigeon #3273 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

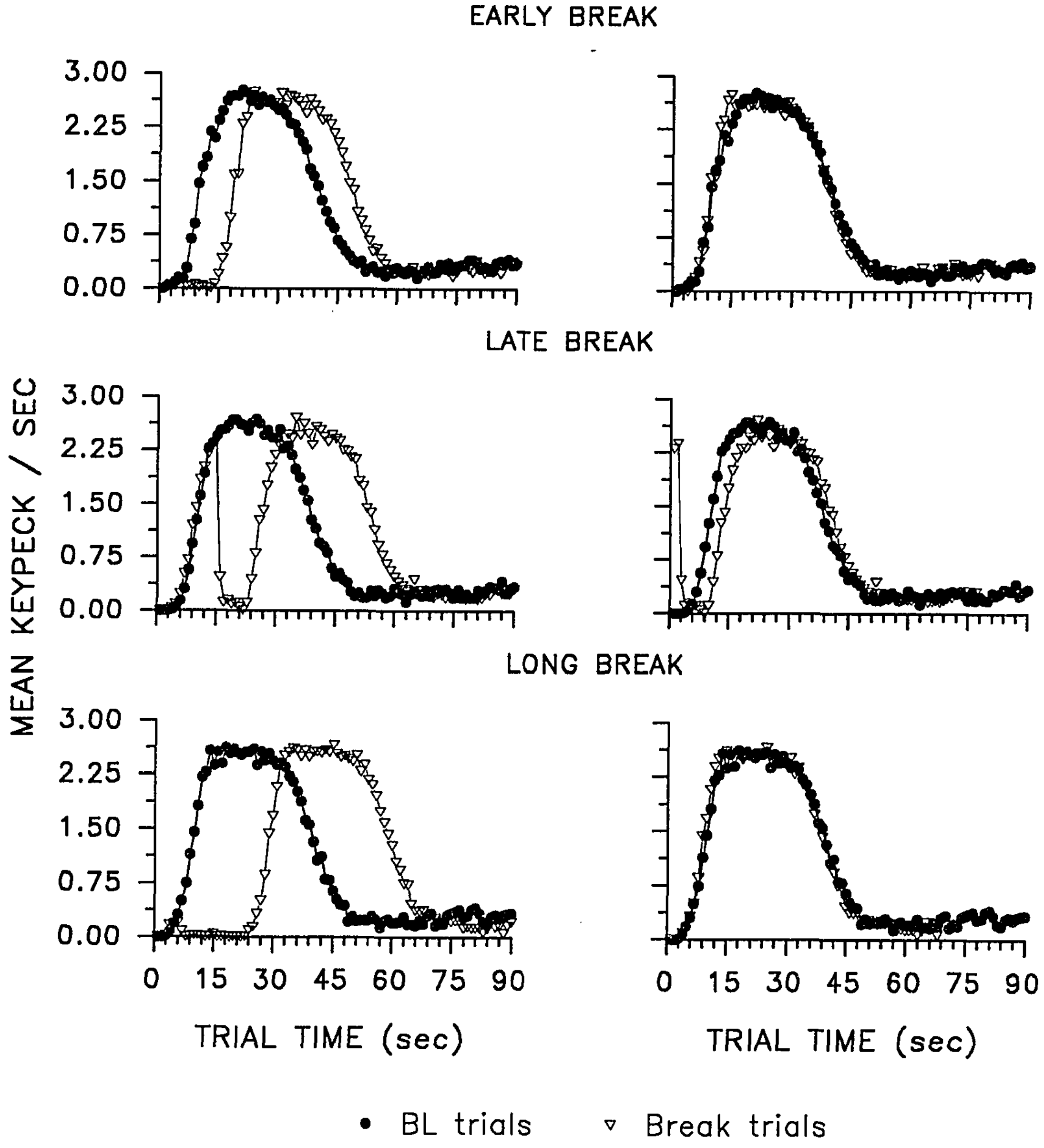


FIGURE 9. Pigeon #3283 mean keypeck rate as a function of trial time during the last 12 sessions with breaks. On the right side panels, Baseline and Break functions are superposed in terms of their peak times.

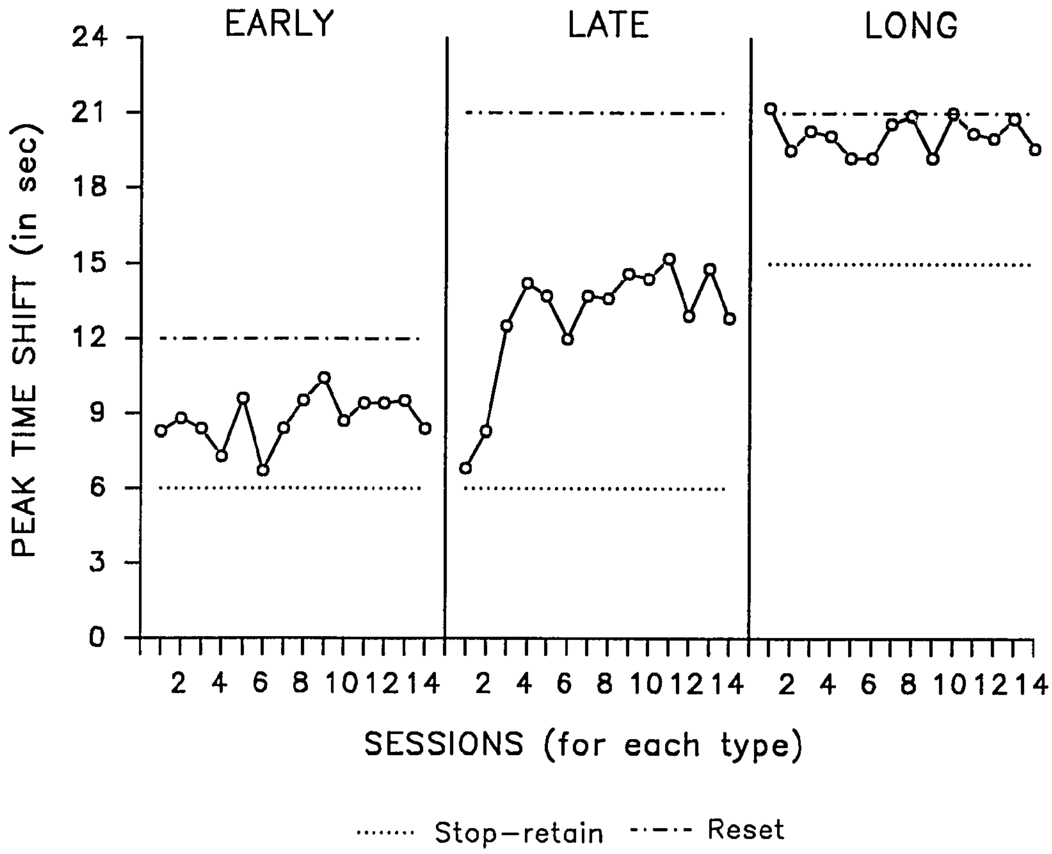


FIGURE 10. Group mean peak time shift as a function of sessions in the 3-Breaks condition. Vertical panels refer to each type of Break; on each panel, the horizontal lines represent the nominal shift predicted by the stop-retain and reset hypotheses.

$$PT = t^{*} + t_b + [t_p - f(t)]$$

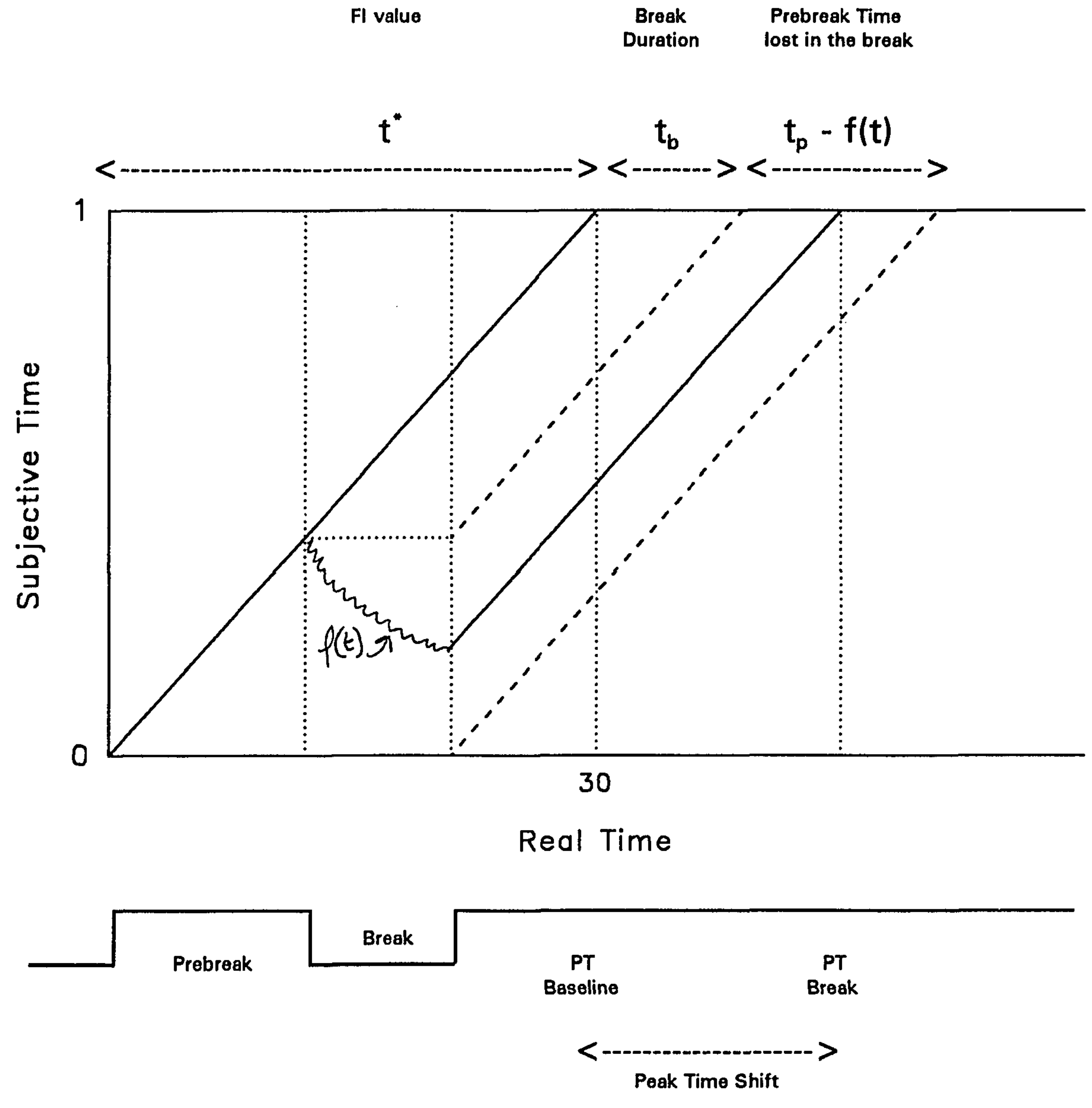
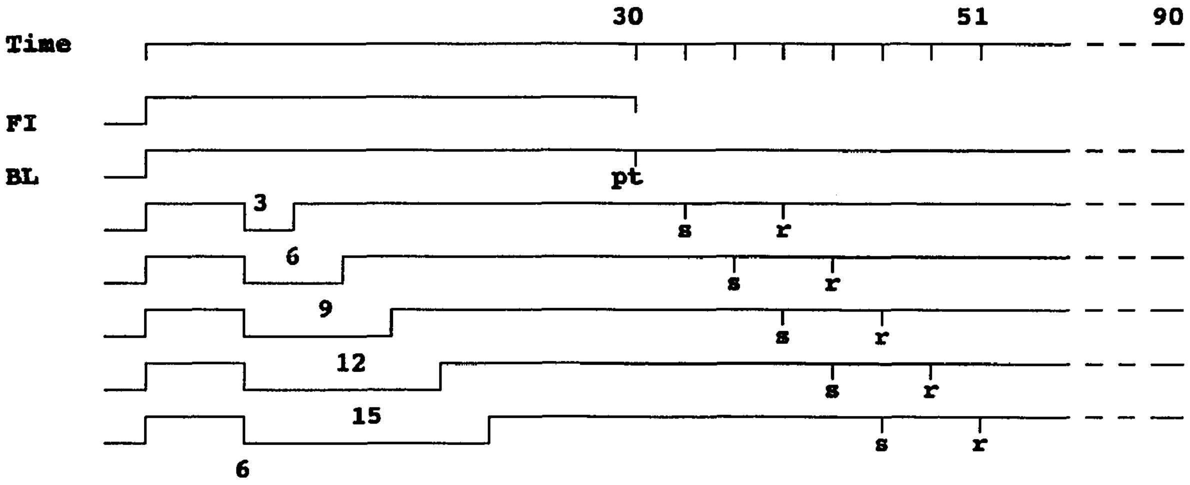


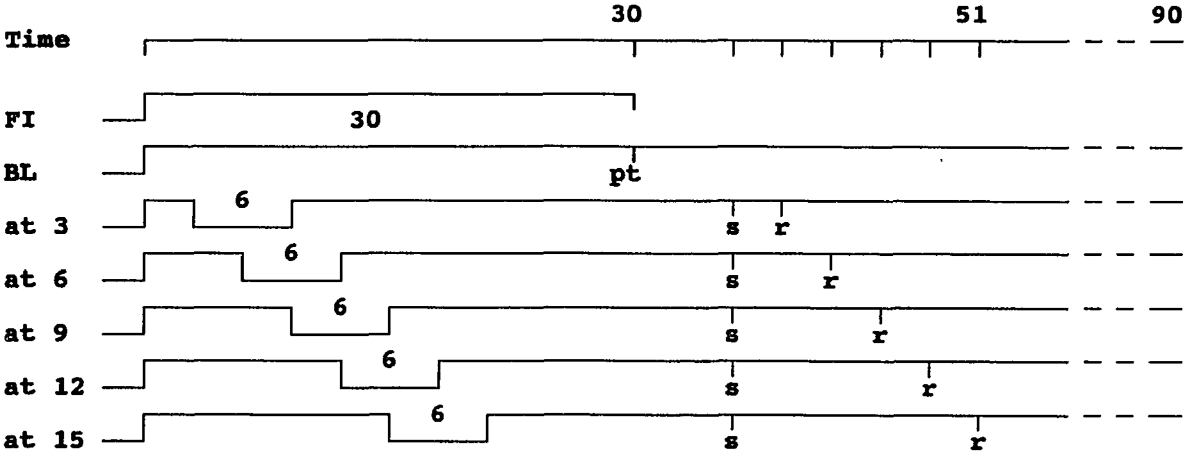
FIGURE 11. Subjective time as a function of real time.

FIGURE 12. Procedure diagrams for the three parametric manipulations. pt represents the expected location of the peak time on Baseline trials; s (stop-retain) and r (reset) the expected location of the peak times on Break trials.

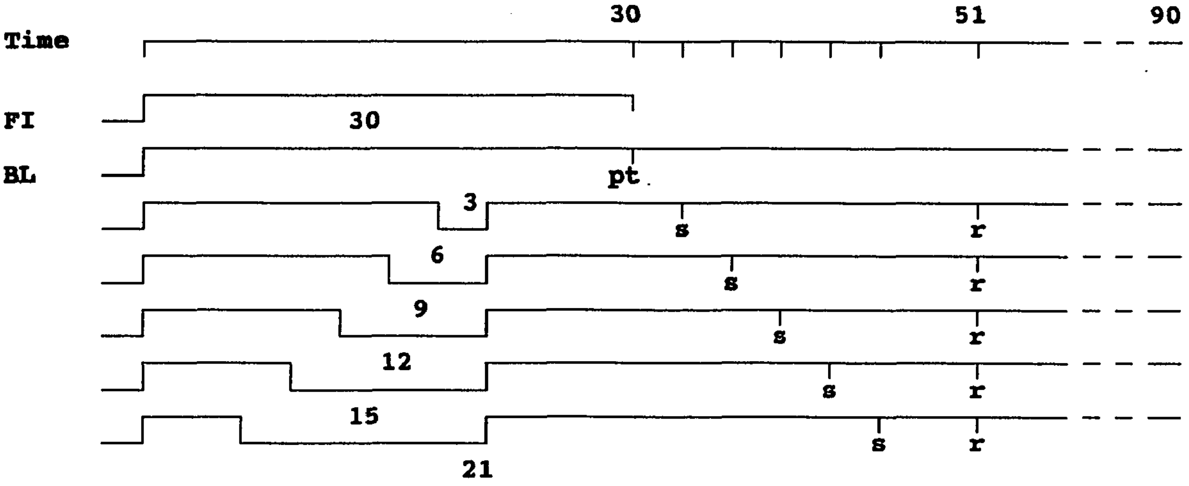
Duration-Fixed-Onset



Location



Duration-Fixed-Offset



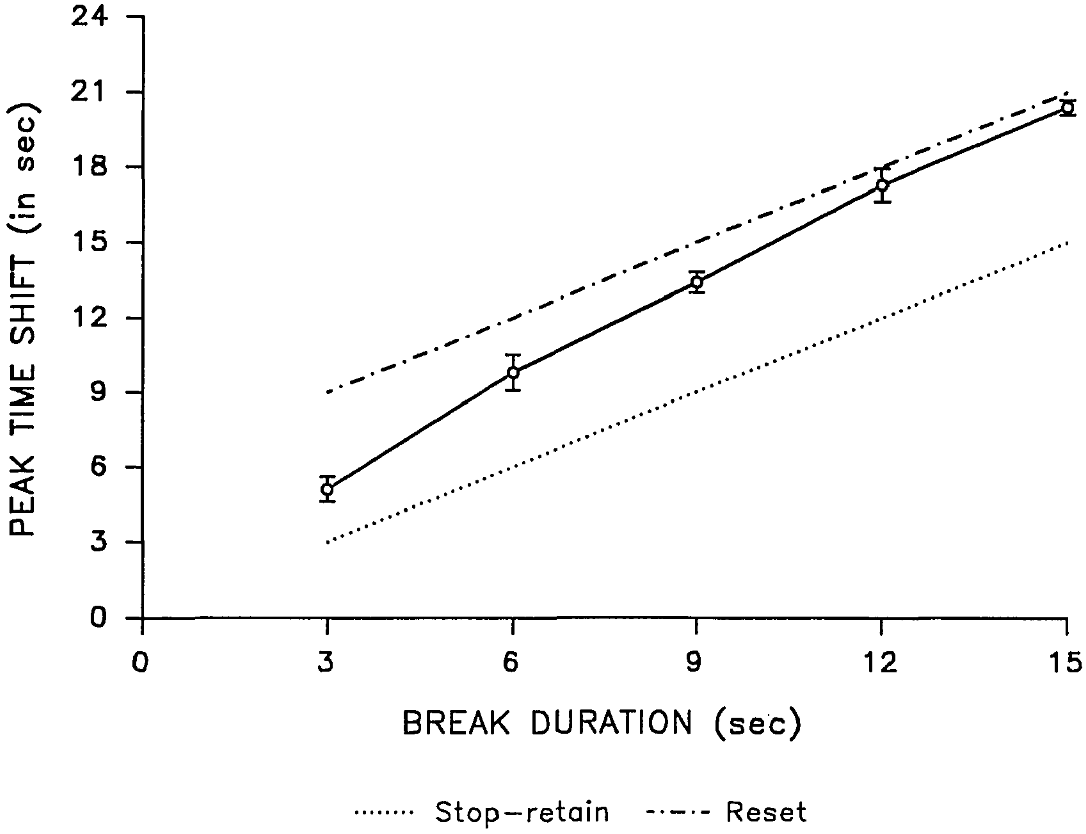


FIGURE 13. Duration-Fixed-Onset manipulation: Group mean peak time shift as a function of break duration. The discontinuous lines represent the nominal shifts predicted by stop-retain and reset. Error bars = SEM (Standard Error of the Mean).

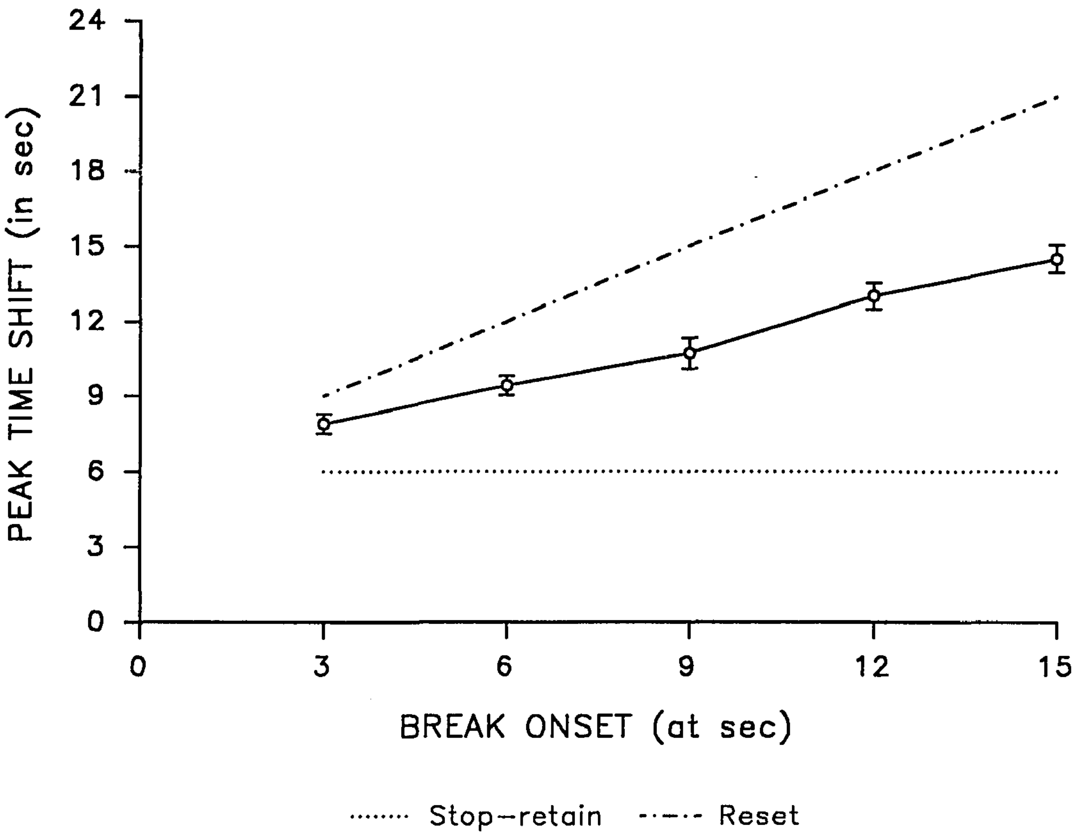


FIGURE 14. Location manipulation: Group mean peak time shift as a function of break onset. The discontinuous lines represent the nominal shifts predicted by stop-retain and reset. Error bars = SEM

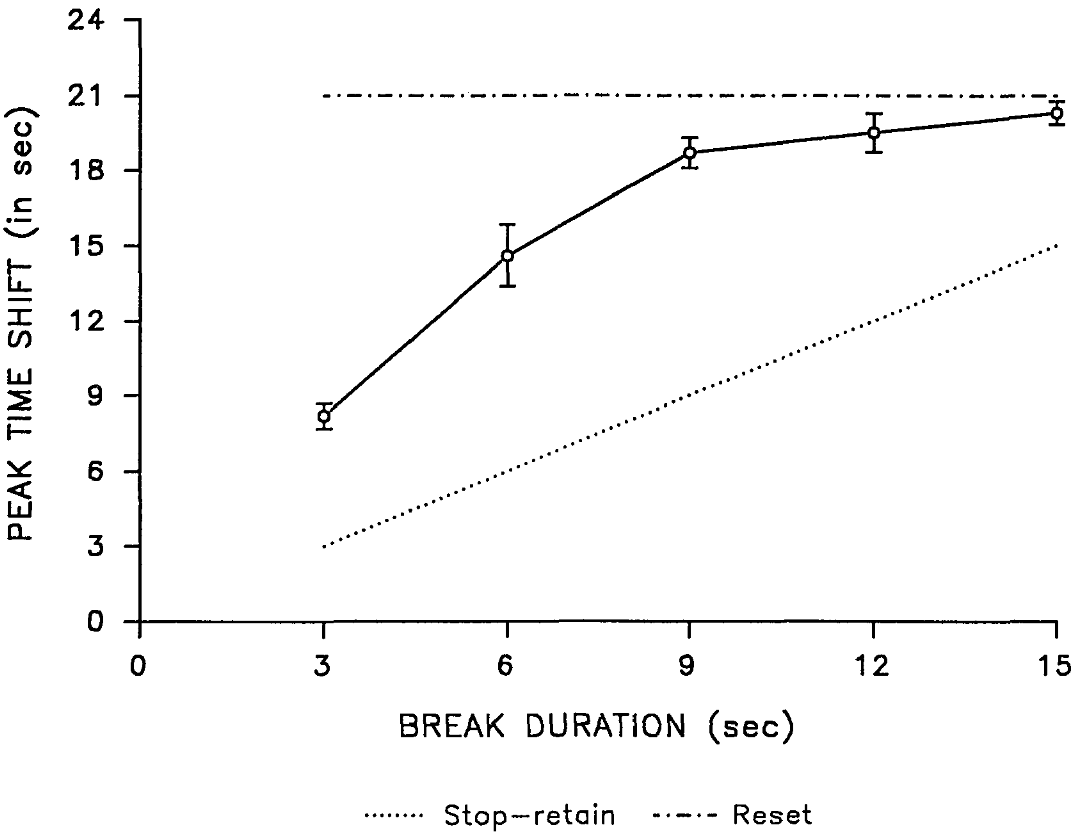


FIGURE 15. Duration-Fixed-Offset manipulation: Group mean peak time shift as a function of break duration. The discontinuous lines represent the nominal shifts predicted by stop-retain and reset. Error bars = SEM

TABLE 1. Prebreak retained time and predicted peak time for different forms of decay.

Function	Retained Time	Predicted Peak Time
		$PT = t^* + t_b + [t_p - f(t)]$[1]
linear	$f(t) = t_p - at$	$PT = t^* + t_b + at_b$
log	$f(t) = t_p - a\log(t)$	$PT = t^* + t_b + a\log(t_b)$
power	$f(t) = t_p\, t^{-a}$	$PT = t^* + t_b + t_p(1 - t_b^{-a})$
exponential	$f(t) = t_p \exp(-at)$	$PT = t^* + t_b + t_p(1 - \exp(-at_b))$

(1) t^* = subjective estimate of the time to reinforcement

t_b = break duration

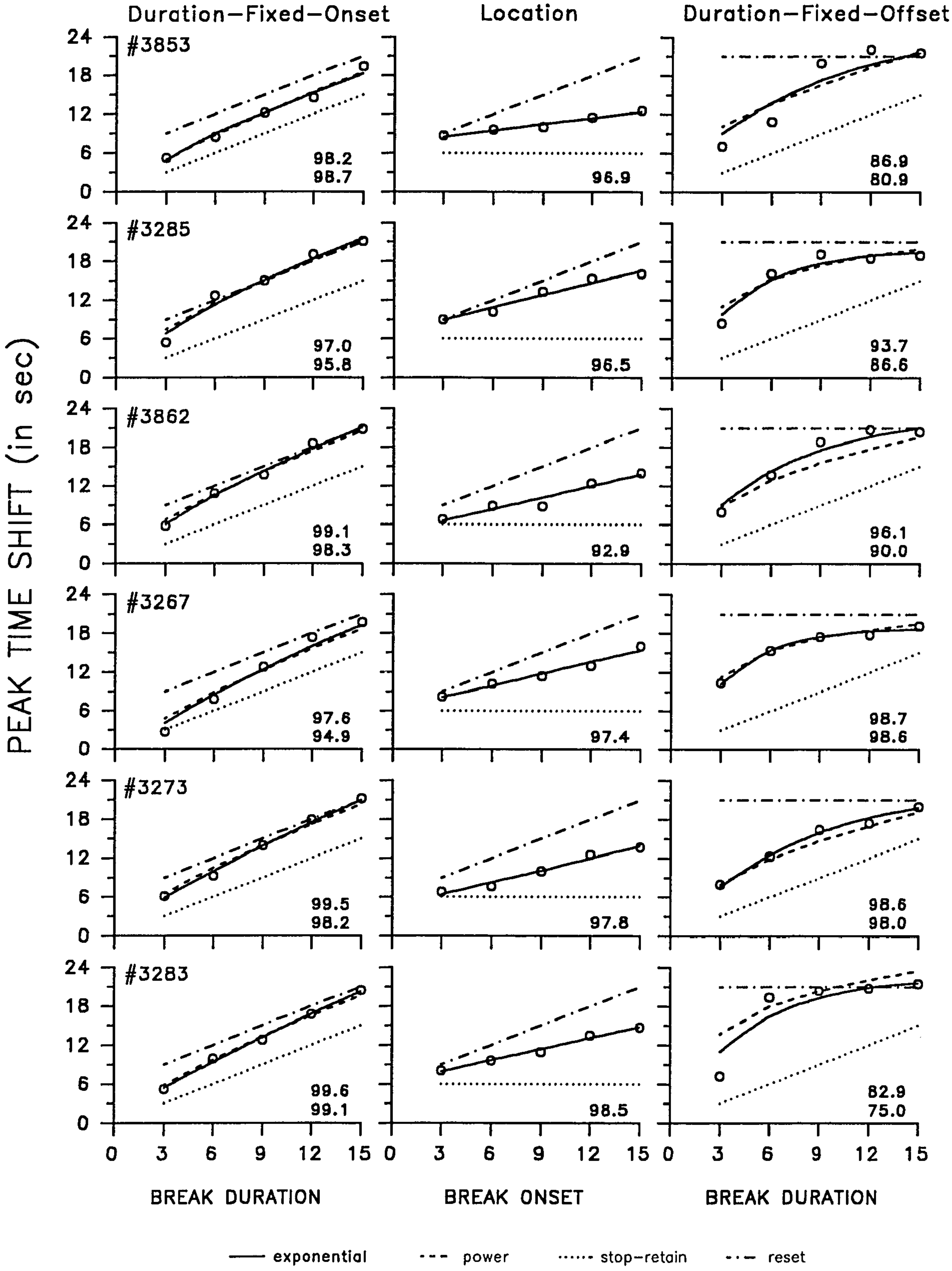
$[t_p - f(t)]$ = time lost during the break, where:

t_p = time elapsed before break onset

$f(t)$ = amount of prebreak time retained at time t, where:

t = elapsed time during the break.

FIGURE 16. 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.


Duration–Fixed–Onset
Location
Duration–Fixed–Offset
PEAK TIME SHIFT (in sec)
#3853
98.2
98.7
96.9
86.9
80.9
#3285
97.0
95.8
96.5
93.7
86.6
#3862
99.1
98.3
92.9
96.1
90.0
#3267
97.6
94.9
97.4
98.7
98.6
#3273
99.5
98.2
97.8
98.6
98.0
#3283
99.6
99.1
98.5
82.9
75.0
0
6
12
18
24
0
3
6
9
12
15
BREAK DURATION
BREAK ONSET
BREAK DURATION
exponential
power
stop–retain
reset

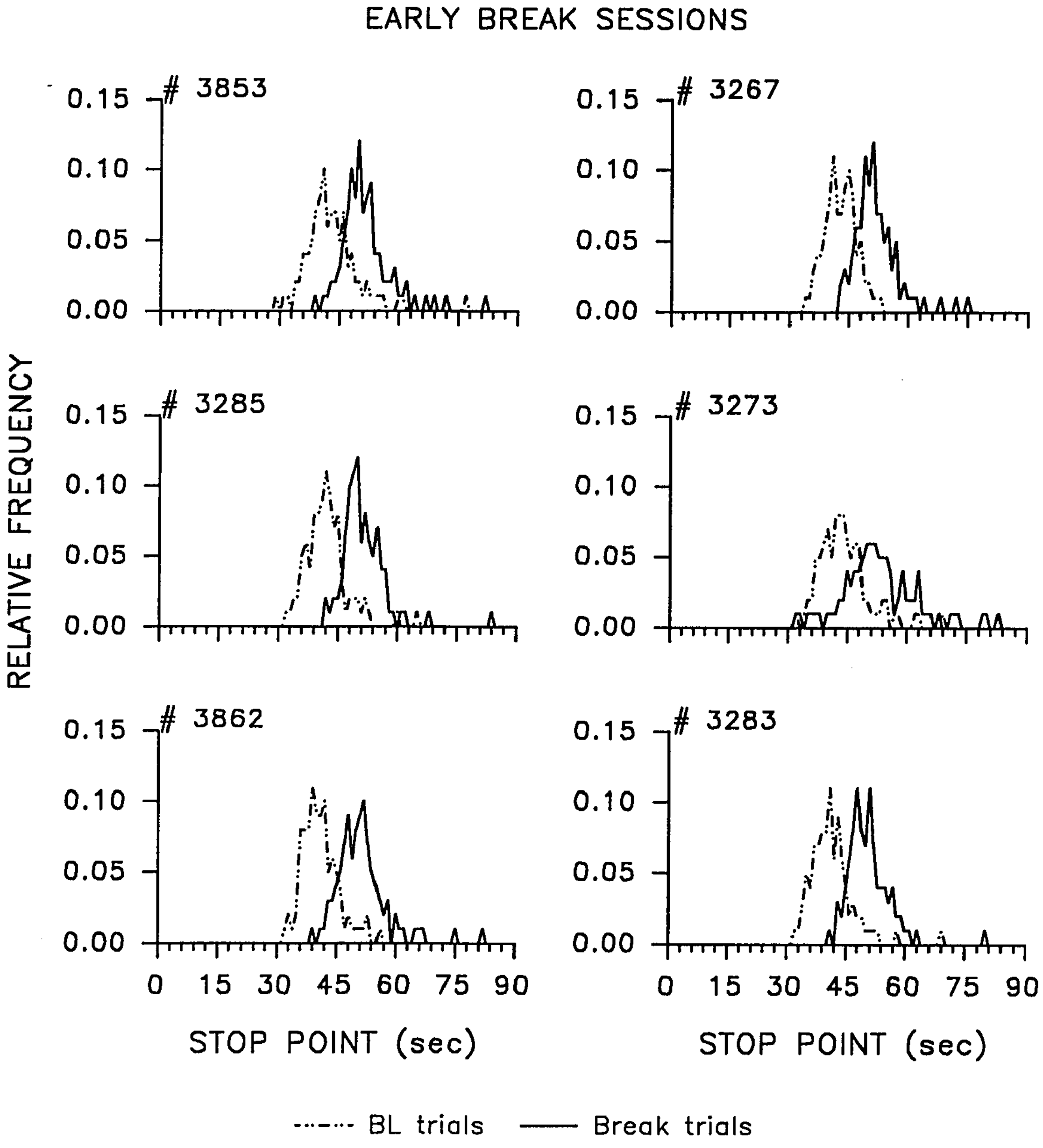


FIGURE 17. Frequency distributions of stop points on Baseline and Early Break trials.

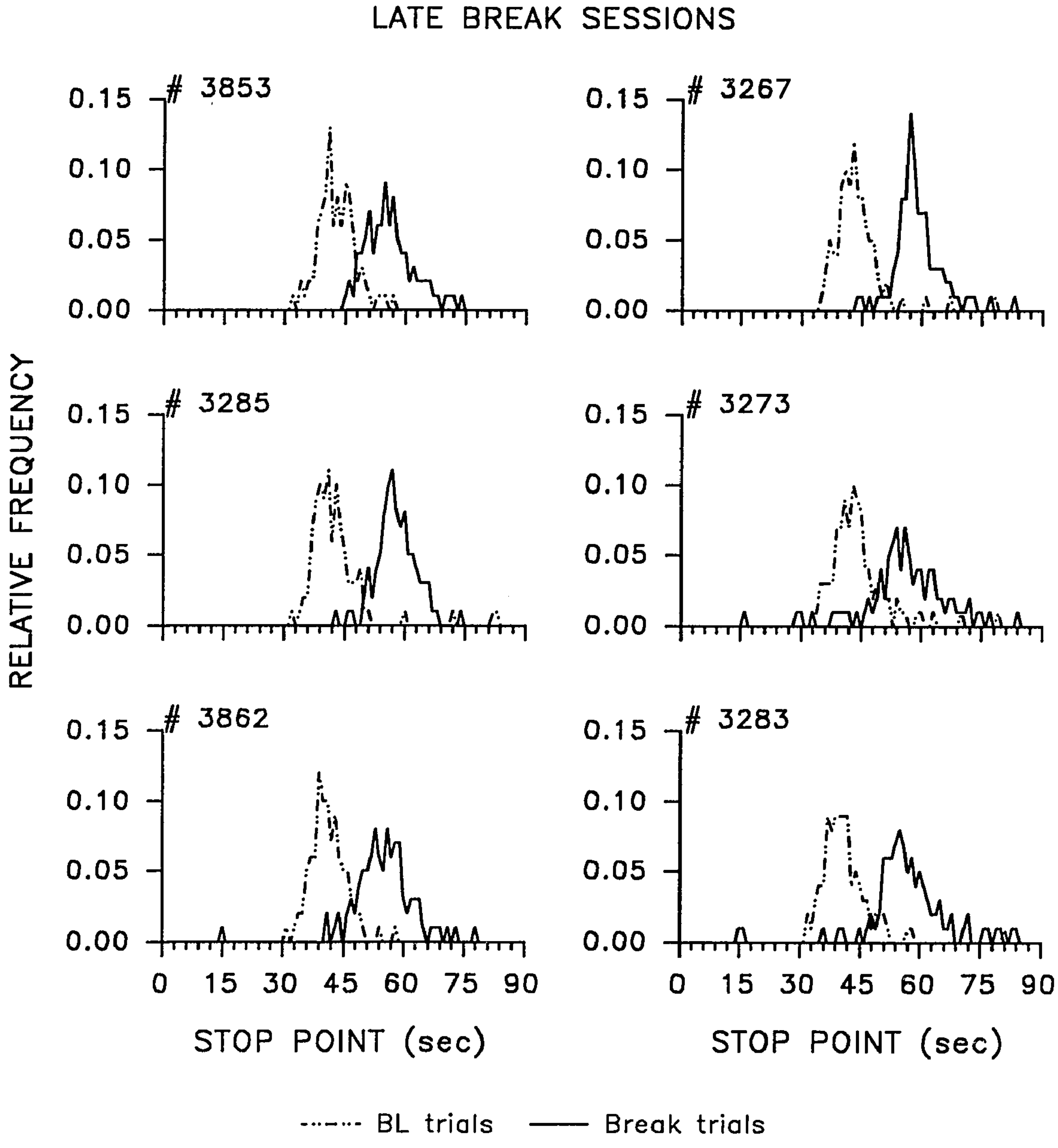


FIGURE 18. Frequency distributions of stop points on Baseline and Late Break trials.

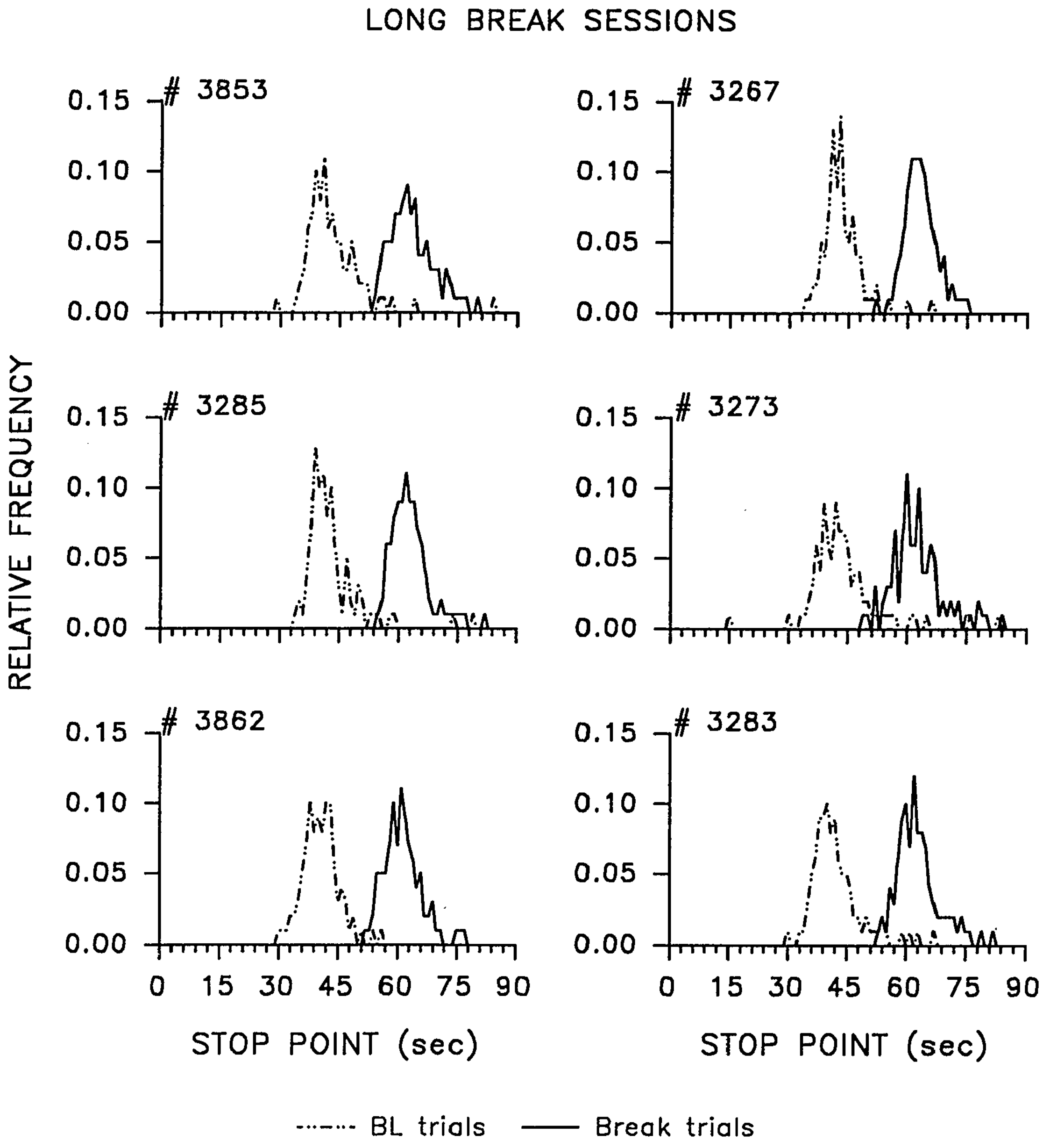


FIGURE 19. Frequency distributions of stop points on Baseline and Long Break trials.

TABLE 2. Group mean values (sec) of median and mean deviation from the median for the distribution of stop points. Values for Baseline and Break distributions are presented separately for each type of break.

	Median		Mean Deviation		
	BL	BK	BL	BK	Diff
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

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