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The Effects of a Gap and Positive and Negative Concurrent Task Events on Peak Time in the Peak-Interval Procedure

by

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

2005

UMI Number: 3169890

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

April 29, 2005

Date

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Abstract

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by

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The effect of reinforcement history of a concurrent task cue on pigeons' timing behavior was evaluated using a peak interval procedure. Pigeons were trained to peck a side key on a peak interval procedure. Then separate discrimination training established one center-key light cue as an S+ and another as S-. During the test phase, the S+, S-, and gap (brief termination of the timing side-key light) events were presented at three different temporal locations within sessions, and the effect of each cue on responding to the side key on probe trials was assessed. Peak times under the S+ condition exceeded those under the S- and gap conditions in all three locations and peak times under the gap condition occurred later than those under the S- condition. Peak times under the S+ condition exceeded values predicted by stop and reset clock mechanisms; peak times under the gap condition fell between stop and reset predictions; peak times under the S- condition tended to be lower than values predicted by the stop mode. In a subsequent phase, the extinction of the S+ cue resulted in shortened peak times. In a final phase, the reinforcement of the S+ cue again produced substantially later peak times for that cue. The results suggest that the history of reinforcement is a critical determinant of the effect of a concurrent task cue on timing performance. A combination of delay in resumption of timing following the S+ cue presentation, and clock reset at the end of the task cue is suggested as mediating peak shift observed on concurrent task trials.

Acknowledgments

I greatly acknowledge my mentor, Dr. Bruce L. Brown for his guidance and encouraging support during the time period of this dissertation research. He showed a role model as a teacher and researcher. I am grateful to Dr. Nancy S. Hemmes and Dr. Robert N. Lanson for their suggestions and comments on this research. I thank my wife, Youngboon Kim. She has been always with me during all phases of this project. I also thank my baby son, Francisco JiHyuk Aum, who filled my hearts with joy, love, and happiness. I dedicate this dissertation to my parents, Jungsook Kim and Sukyoul Eum for their giving me a talent to pursue this difficult project and an opportunity to study in the United States.

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The Effects of a Gap and Positive and Negative Concurrent Task Events on Peak Time in the Peak-Interval Procedure

Animal timing behavior has been studied under several different procedures (e.g., temporal generalization, bisection, peak interval). In the peak interval (PI) procedure, reinforced fixed-interval (FI) trials (food trials) are randomly intermixed with nonreinforced trials (empty trials). On food trials, the first response to occur after a fixed time from signal onset is reinforced, and the trial ends. On empty trials, the trial signal duration lasts longer than on food trial, and reinforcement is omitted. An inter-trial interval (ITI) follows each trial. Under the PI procedure, the function representing response rate plotted against time on empty trials is nearly symmetric in real time about the peak time (PT), the temporal locus at which the highest response rate occurs. The PTs are typically close to the FI values, indicating animal's timing of the reinforcer delivery time (Cheng & Roberts, 1991; Meck & Church, 1983; Roberts, 1981).

To investigate the mechanisms underlying timing behavior in the PI procedure, researchers have measured the effect of stimulus changes during the presentation of the timing stimulus.. One type of stimulus change is the brief termination of the timing stimulus during the trial, called "gap."

The Effect of a Gap on Animal and Human Timing

When a timing stimulus is briefly interrupted by a gap, several studies (e.g., Roberts, 1981; Roberts, Cheng, & Cohen, 1989) have shown that timing ceases during the gap period. In addition, it has been reported that the time accumulated before the gap is either retained (Roberts & Church, 1978), partially retained (Cabeza de Vaca, Brown, & Hemmes, 1994; Roberts, 1981), or not retained (Roberts et al., 1989) after the gap. For example, in the study by Roberts (1981, Experiment 2), rats were pretrained to press a lever for food reinforcers in the presence of a houselight, and were then exposed to a PI procedure composed of food and empty trials. On food trials, the first response to occur 40 s after houselight onset produced food. On empty trials, the trial lasted 80 s plus a geometrically distributed duration, without reinforcement. In a subsequent phase, on some empty trials, the houselight was turned off (gap) for 5 s or 10 s on different sessions, starting at 10 s from trial onset. Compared to PT on empty trials without the gap (baseline trials), PT on 5- and 10-s gap trials occurred about 8 s or 13 s later, respectively, supporting the inference that animals are not timing during the interruption of an ongoing timing signal (gap), and that the accumulated time before the gap is partially retained after the gap.

The effect of a gap on timing performance has been explained using a temporal information processing model (Church, 1984; Gibbon, 1977; Gibbon, Church, & Meck, 1984) which was developed to describe animals' timing behavior controlled by relative time (the scalar property of timing behavior). The model incorporates an internal clock which includes clock, comparator, and memory storage processes . In the model, as applied to the PI procedure, pulses are generated by a pacemaker with the onset of a timed stimulus, and are gated to an accumulator via a switch (clock process). The number of pulses in the accumulator on the current trial is compared with a remembered number of pulses associated with reinforcement (comparison process). If the two numbers are close enough, responding is initiated. If the response is reinforced, the number of pulses in the accumulator is transferred to a more permanent reference memory and stored for later retrieval (memory storage process) (Gibbon, 1991). The gap event has been considered to affect the operation of the clock, that is, during the gap the clock may stop or reset (e.g., Roberts, 1981; Roberts & Church, 1978). Depending on the retention of the accumulated number of pulses in the accumulator during the gap, timing behavior conforms to either a stop (retention), partial reset (partial retention), or reset (no retention) prediction (Roberts, 1981; Roberts et al., 1989).

As an alternative to the stop-reset hypothesis, Cabeza de Vaca et al. (1994) proposed a continuous decay process in memory for the currently timed interval during the gap. In their Experiment 1, pigeons were pretrained to peck a constantly illuminated white center key and were subsequently exposed to a PI procedure. Each trial was signaled by the onset of the houselight (HL). On empty trials, the HL lasted for 90 s plus a variable extension. Three different types of gaps were programmed on empty trials. On early gap trials, the houselight (HL) (timing signal) was turned off for 6 s starting 6 s after trial onset; for late gap trials, the HL was turned off for 6 s starting at 15 s; for long gap trials, the HL was turned off for 15 s starting at 6 s. Accordingly, the effect of the location and duration of the gap on timing could be studied. If timing stops during the gap while time accumulated before the gap is retained, gaps of the same duration (i.e., early and late gap trials) would produce identical PTs regardless of the location of the gap (stop-retain prediction). If timing stops during the gap and the clock resets to zero at the end of the gap , gaps ending at the same time (i.e., late and long gap trials) would produce identical PTs regardless of the duration of the gap (reset prediction). The data, however, did not support either prediction. That is, compared to PTs on early gap trials, PTs on late gap trials occurred later, indicating that the location of the gap was important in determining PTs. Compared to PTs on late gap trials, PTs on long gap trials occurred later, indicating that the duration of the gap was important in determining PTs. In addition, the amount of the shifts in PTs (PT shifts) on early, late, and long gap trials compared to PTs on baseline trials was greater than the shift expected from the stop-retain prediction and shorter than the shift expected from the reset prediction.

To explain the results, Cabeza de Vaca et al. proposed a continuous memory decay process operating in animal's working memory. That is, the internal clock stops at the onset of the gap, and the time accumulated before the gap is gradually lost during the gap. In particular, based on the fit between the predicted and the obtained PTs, they suggested that the decay function is a power or exponential function of the time elapsed before the gap, which predicts both the duration and location effects of the gap. Compared to the stopwatch metaphor in which the internal clock can be stopped or reset during a gap, the memory decay process provides an alternative account of both the stop and reset interpretations of the gap effect. That is, a short and early gap allows for little decay of the accumulated time during the gap, whereas a long and late gap allows for more complete decay.

Similar to animals, a disruptive effect of a gap on timing has also been shown in human observers. However, a different explanation has been given. In a study by Fortin and Masse (2000, Experiment 1), human participants were trained to produce a 2000-ms interval of tone with two successive key presses in practice sessions. In experimental sessions, the interval was interrupted by a 3, 4, 5, or 6-s gap that occurred 500 ms or 1500 ms after the beginning of the trial. Participants were instructed to produce the same target interval, 2000 ms, as in the training sessions, without including the duration of the gap. Mean produced intervals, not including the gap, were longer than 2000 ms across all durations and locations of the gap. Mean produced intervals did not differ as a function of the duration of the gap, but they were longer when the gap occurred later (1500 vs 500 ms). The increased temporal production as a function of temporal location of the gap was explained in terms of attentional competition between time estimation and expectation of the occurrence of the gap. That is, attentional shifts between time estimation and expectation of the gap transiently blocked pulse accumulation during the time estimation and led to underestimation of time. The expectancy account was further supported when trials without gaps were included in Experiment 3. In that experiment participants were told that no gap would occur on some trials. Compared to mean produced intervals in gap trials, mean produced intervals in no-gap trials were the longest. Furthermore, to decrease the expectation of the gap, some no-gap trials were signaled by a verbal cue ("No interruption in this trial") in Experiment 4. Mean produced intervals in those signaled no-gap trials were shorter compared to the unsignaled no-gap trials, indicating that the expectation of the gap played a major role in the lengthened produced intervals in the unsignaled no-gap trials.

In addition to the brief interruption of a timing stimulus using a gap procedure, another type of stimulus change during the presentation of the timing stimulus has been to present a discrete or continuous concurrent task cue while animals are timing. In contrast to the very recent appearance of animal studies in this area (e.g., Lejeune, Macar, & Zakay, 1999), a substantial amount of human research has been conducted on the interference effect of the concurrent task on timing under dual task situations.

The Effect of a Concurrent Task on Human and Animal Timing

It is a general finding that a disruption in timing occurs when human participants are asked to keep track of time while performing some demanding nontemporal task during the interval. The disruption is represented by shortened perceived time and more variable time judgments compared to the control condition in which no distracting nontemporal task is given (Brown, 1997). Moreover, when the difficulty of the concurrent nontemporal task increases, greater disruption in timing has been observed (e.g., Brown, 1985, 1997; Fortin & Rousseau, 1987; Hicks, Miller, Gaes, & Bierman, 1977; Zakay, Nitzan, & Glicksohn, 1983). Many different types of tasks which require different kinds of information processing have been shown to disrupt timing, including perceptual (e.g., pursuit rotor tracking, mirror drawing), verbal (e.g., providing synonyms, classifications of presented words according to their meanings), and cognitive tasks (e.g., memory task, mental arithmetic task).

For example, in Zakay et al. (1983), participants were informed in advance that they would be required to reproduce the duration of an interval during which they performed a verbal task. There were three different levels of difficulty in the verbal task. In the easy level, the task was to read words presented in cards; in intermediate level, it was to name words for pictures of various objects; in difficult level, the task was to provide synonyms for given words. Compared to reproduced intervals in the timing task alone condition, reproduced intervals in concurrent verbal task conditions were shorter. In addition, among the concurrent verbal task conditions, the reproduced intervals were longest under the easy level task and shortest under the difficult level task. That is, as the concurrent verbal-task difficulty increased, subjective time estimation decreased.

In Brown's study (1997, Experiment 3), participants were asked to produce a 2- or 5-s interval repeatedly depending on the condition by pressing a response key (i.e., a computer mouse button). At the same time, participants were presented with a series of subtraction problems and asked to detect wrong answers. For easy math problems, the minuend and subtrahend consisted of a single random value. For difficult math problems, the minuend consisted of a random two-digit value and the subtrahend consisted of a single random value. Compared to mean temporal productions in the control condition in which no math task was given, mean temporal productions were longer in the presence of the math task, indicating shortened perceived time. In addition, mean temporal productions were longer in the difficult math-task condition than in the easy math-task condition. Variability measure also showed disrupted timing under the concurrent task condition. Compared to the control condition, SDs of the produced intervals in the two math-task conditions were greater. In addition, in the 5-s timing task, SDs of the produced intervals were greater in the difficult math-task condition than in the easy math-task condition.

The disruption in humans' timing under the concurrent task has been generally explained in terms of the attentional model of time perception (Brown, 1985, 1997; Hicks, Miller, & Kinsbourne, 1976; Macar, Grondin, & Casini, 1994; Thomas & Weaver, 1975; Zakay, 1989; Zakay et al., 1983). In that model, a cognitive timer is assumed to accumulate subjective time units or pulses emitted by a pacemaker in the accumulator of an internal clock. Subjective duration is directly related to the number of pulses stored in the accumulator at the end of the to-be-estimated period. The timer demands attentional resources for its operation. Accordingly, subjective duration is considered to be a direct function of the amount of attention allocated to the timer (Zakay,1989). As nontemporal information processing demands increase under dual task situations, lower attentional resources are available for the timer. Accordingly, the perceived duration becomes decreased (Brown, 1985, 1997). More specifically, each time attention is diverted from the timer by concurrent task processing (attentional shift), a certain number of pulses are lost resulting in underestimation of elapsed time (Macar et al., 1994). In addition, many pulses not fully processed or missed under a difficult concurrent task lead to unreliable and variable time judgment (Brown,1997). Zakay and Block (1996, 1997) proposed that the effect of attention to the concurrent nontemporal task is mediated within the internal clock by an attentional gate located between the pacemaker and the switch. The gate, which is seen as being under attentional control, operates when an organism's attention is allocated to time and allows for the transfer of pulses to the accumulator via the switch within the internal clock. The gate is open less widely and less frequently when a subject attends to a nontemporal task while timing. As a result fewer pulses emitted by pacemaker pass through to the accumulator and fewer pulses are stored in the accumulator, producing a shortened perceived duration.

In most of the work on the effect of concurrent task on timing, the task cue is coextensive with the timing task cue from the beginning of the interval. In a few studies (Casini & Macar, 1997; Macar et al., 1994), a discrete concurrent task cue (e.g., a brief light intensity increment) was used. Casini and Macar argued that disruption in humans' timing under dual task situations can occur not only during the presentation of the concurrent task cue but also prior to the presentation of the task cue, as in the gap study by Fortin and Masse (2000). In their Experiment 1, a transient increment (weak or strong) in the luminous intensity of a timed stimulus, a green diode, occurred at early, middle, or late thirds of the interval. The duration of the green diode was either 2.5 s or 3.5 s. Participants were asked to identify both the duration (short or long) and the intensity increment (weak or strong) of the timed stimulus by pressing the appropriate keys (two response keys for each hand) at the end of each trial. The results indicated an increase in percentage of "short" responses when the intensity increment occurred later in the trial. The authors argued that the location effect of the concurrent task was produced by participants' expectation of the occurrence of the intensity increment. That is, the expectancy produced attentional shifts from the timing task to the intensity task, and more attentional shifts occurred when the intensity increment occurred late in the interval, resulting in lower amount of attention allocated to the timing task.

To test the expectancy hypothesis further, trials in which no intensity increment occurred were added in their Experiment 2, and participants were told that the increment would take place in most of trials. In that experiment, the percentage of "short" responses on no-increment trials was higher than that when the increment occurred early in the interval, even though it was lower than that when the increment occurred late in the interval, indicating joint effects of expectancy and of processing of the concurrent task information.

In contrast to humans' underestimated timing (or shortened perceived time) in the presence of a concurrent nontemporal task, no disruption in timing has been reported in a number of animal studies (Crystal & Miller, 2002; Leak & Gibbon, 1995; Meck & Church, 1984; Olton, Wenk, Church, & Meck, 1988). For example, Meck and Church (1984) showed that rats are able to time two intervals simultaneously and independently without interference. In their study, rats were initially trained under an FI 50-s reinforcement schedule signaled by a houselight. Then, they were exposed to a PI procedure in which the houselight remained on until 130 s on unsegmented empty trials. Then, on half of both food and empty trials, a 1-s white noise cue was presented after 0, 10, 20, 30, 40, 60, 70, 80, 90, 100, 110, and 120 s following trial onset, which was signaled by the illumination of a houselight (segmented food and empty trials). The response rate function was fairly symmetrical on unsegmented empty trials with a median PT at around 50 s. On segmented empty trials, response rate decreased briefly whenever the white noise was presented, then the rate gradually increased as time elapsed until the next white noise presentation. A scalloped pattern of responding was observed between noise bursts. In spite of the abruptly decreased response rate during the white noise presentation, indicating detection of that event, PTs on those segmented empty trials still occurred at around 50 s. That is, an overall scalloped pattern of responding was also observed for the longer interval. In addition, temporal discrimination indexes which were calculated by dividing the highest response rate during any second of the interval by mean overall response rate were similar in the unsegmented and segmented empty trials. Moreover, response rate decreased during 51 s and 52 s even though no segment signal was presented during the time interval, indicating animals' timing of 10 s segment intervals. Based on the results, the authors argued that the segment signals, which led to response decrements, did not affect temporal discrimination of the overall interval, and that rats timed the overall 50 s and the segment 10 s intervals simultaneously and independently without interference. A mitigating consideration is that in that study, the reinforcer was still available after 50 s on segmented food trials. Therefore, PTs on the segmented empty trials are considered to have resulted from the effect of reinforcement. That is, the presentation of the reinforcer at 50 s on both segmented and unsegmented food trials might have led subjects to store different reinforcer delivery times in their reference memory for segmented and unsegmented houselight trials (a shorter reinforcer delivery time for segmented trials than that for unsegmented trials). Accordingly, the animals might have shown the same PT on both segmented and unsegmented empty trials based on the different reinforcer delivery times stored even though their timing of the houselight duration stopped during the presentation of the white noise.

In addition to simultaneous temporal processing, research with rats has also shown simultaneous temporal and spatial processing (Crystal & Miller, 2002). In an open-field box, which had a food trough on each wall, rat's entries into the food trough were detected by photobeam interruption. During pretraining sessions, the rat's approach to the food trough on each wall was reinforced according to FI 1-s schedule. During training sessions, the reinforcer-available active location of the food trough changed in a clockwise direction among the four locations after each reinforcer was presented, and approaches to the active location were reinforced according to FI 60-s or FI 30-s schedule depending on the location. For a penalty group, the amount of food reward in the active location decreased (range: 1-8 pellets) as the number of approaches to the inactive location increased; for a no-penalty group the amount of food reward in the active location was always one pellet. For both penalty and no penalty groups, the highest rate of approaching always occurred at the active location, indicating rats' processing the reinforcer-related spatial information. In addition, the number of rat's approaches to the active location increased throughout the FI at each active location, indicating rats' processing the reinforcer-related temporal information at each location of the food trough. That is, the rats processed both the reinforcer-related spatial and temporal information simultaneously in each trial. However, when relative response rate (proportion of the maximum response rate) at active locations was plotted against relative time (proportion of the rewarded interval) for FI 30 s and FI 60 s, the two distributions failed to superimpose, indicating that the rats did not time the two intervals in a scalar manner. The failure of superposition was not due to a visit to an inactive location. When the data in the low-interference trials, in which few or no responses occurred at inactive locations, were analyzed, the relative response rate functions were still not superposed. Accordingly, the authors concluded that simultaneous temporal and spatial information processing produced a failure of scalar timing.

In contrast to simultaneous timing of two intervals and simultaneous temporal and spatial information processing, other researchers have found a disruptive effect of a concurrent nontemporal task on animals' timing performance. That is, performance in the presence of a concurrent task was consistent with subjective shortening. In the study by Lejeune et al. (1999, Experiment 1), a discrete concurrent task cue was presented during the timed stimulus in an animal analogue of human dual task procedures. Pigeons were trained in a matching-to-sample task to discriminate between 10 s and 40 s of white noise signals by pecking on a left or a right green comparison key (choice response) depending on the duration of the sample noise stimulus. The comparison stimuli (left and right green keys) were presented immediately after the termination of the sample white noise. In addition, pigeons were trained to peck on a blue center key under a variable ratio (VR) schedule. During testing, various durations (i.e., 10, 20, 25, and 40 s) of the white noise were presented and 5-s blue center key was presented 3 s after the white noise onset on half the trials. Compared to the baseline trials in which the blue center key was not presented during the white noise, the percentage of "long" choice for each test duration was lower on the dual task trials, indicating underestimation of the sample duration. In Experiment 2, the 5-s blue center key was presented later and ended 3 s before the termination of the white noise. The percentages of "long" choices were much lower than those in Experiment 1 on dual task trials, replicating the location effect of a discrete concurrent task cue in human timing literature (Casini & Macar, 1997; Macar et al., 1994). According to the stop-retain hypothesis, timing is suspended during the VR cue (the blue center key) and time accumulated prior to the VR cue is retained. This hypothesis predicts the same percentage of "long" choices between Experiment 1 and 2. Therefore, much lower percentages of "long" choices in Experiment 2 than those in Experiment 1 on dual task trials were inconsistent with the stop-retain hypothesis. According to the reset hypothesis, the VR cue occasions reset of the clock and initiation of timing when the VR cue terminates. This hypothesis predicts that the same percentage of "long" responses would be obtained for all sample stimulus (white noise) durations in Experiment 2 because the remaining duration of the white noise after the end of the VR cue presentation was identical. The percentage of "long" choices, however, increased as the duration of the white noise signal increased in Experiment 2, inconsistent with the reset hypothesis. According to the expectancy hypothesis, timing prior to the VR cue should be disrupted owing to the expectancy of the VR cue. That is, after they were trained in Experiment 1, the pigeons expect the occurrence of the VR cue from the beginning of the sample stimulus presentation in Experiment 2. Each attention shift due to expectancy of the VR cue blocks pulse accumulation by opening the switch of the internal clock, thereby producing underestimation. This hypothesis predicts greater underestimation with later presentation of the VR cue in Experiment 2 compared to the early location of the VR cue in Experiment 1. The lower percentages of "long" choices at 20, 25, and 40 s of the sample white noise stimulus on dual task trials in Experiment 2 than those in Experiment 1 were consistent with the prediction based on the expectancy hypothesis. The difference in the percentage of "long" choices on dual task trials between Experiment 1 and 2, however, could also be attributed to the difference in the amount of training because the same birds were used in both experiments. While the authors favor the expectancy account, the findings are also consistent with the decay hypotheses.

Sutton and Roberts (2002) also showed disruption of timing in a concurrent nontemporal task procedure in which the task cue was coextensive with the timing task cue, in line with most human studies of dual task effects. In their Experiment 1, pigeons were pretrained under two different types of matching-to-sample tasks. In a duration matching-to-sample task a vertical or horizontal sample presented for 2 or 10-s on the center key was followed by red and green comparisons on the side keys. Correct choice responding was related to the duration of the sample. In a pattern matching-to-sample task, the 10th peck during the vertical or horizontal sample on the center key was followed by blue and yellow comparisons on the side keys. Correct choice responding was related to the pattern of the sample. Subsequently, Time Only sessions were alternated with Divided Attention sessions. Only the duration matching task was presented during Time Only sessions. Duration and pattern matching tasks were randomly presented during Divided Attention sessions in which the type of matching task was unpredictable until the comparisons were presented. After birds reached a 90 % accuracy criterion on both Time Only and Divided Attention sessions, Time Only and Divided Attention test sessions were given in which sample durations of 2, 3, 4.5, 6.7, and 10 s were presented without reinforcement on probe trials. Compared to Time Only test sessions, the percentage of "long" responses was lower on duration judgment trials in Divided Attention sessions for all test sample durations except for 2 s. That is, birds tended to underestimate the sample durations on dual task trials. In Experiment 2, the concurrent nontemporal task was a spatial location discrimination. In a duration matching-to-sample task, a white sample (keylight) presented for 2 or 10 s on either the left or the right side key was followed by red and green comparisons. Correct choice responding was related to the duration of the sample. In a spatial location matching-to-sample task, the 10th peck to the left or the right side key during the white sample was followed by blue and yellow comparisons on the side keys. Correct choice responding was related to the location of the sample. Time Only sessions were alternated with Divided Attention sessions as in Experiment 1. Then, test sessions were given in which on probe trials intermediate durations of the sample (2, 3, 4.5, 6.7, and 10 s) were presented without reinforcement as in Experiment 1. The percentage of "long" responses on duration judgment trials in Divided Attention test sessions was greater at the short test durations (2, 3, 4.5 s) and lower at the long test durations (6.7, 10 s) compared to that in Time Only test sessions. Contrary to previous human studies, divided attention task did not produce consistent underestimation at all durations. Rather, it produced errors of both overestimation and underestimation in time judgment for the training durations (that is, choose the "long" response for the short training duration and choose the "short" response for the long training duration) in both Experiment 1 and 2. In addition, the slope of the regression lines fitted to the function was greater for the Time Only function than for the Divided Attention function. A higher frequency of errors in the duration matching task in Divided Attention sessions compared to in Time Only sessions was explained in terms of divided attention. That is, divided attention between temporal and nontemporal information processing results in accuracy decrement.

Compared to the matching-to-sample task, the PI procedure provides more information regarding timing in that it yields a direct measure of estimated duration. Aum, Brown, and Hemmes (2004) used the PI procedure to investigate the effect of a concurrent task cue on timing. In their study, pigeons were trained to peck the left side key on an FI 30-s schedule under the PI procedure, and in separate sessions to peck a 6-s center key on a random interval (RI) 24-s schedule. During test sessions, the RI cue (task cue) was presented at one of three different temporal loci after trial onset during some probe trials: 3, 9, and 15 s (early, middle, and late, respectively). In subsequent sessions, instead of the 6-s presentation of the task cue, the FI cue (the left side key) was darkened for 6 s (gap) during some probe trials, and no reinforcement was available during the gap. If the concurrent task cue interferes with timing of the FI cue, PT would be expected to increase in comparison to baseline probe trials in which no concurrent task cue was presented. According to the internal clock model, any one of three different sizes of PT shift was anticipated on task trials. If timing ceases during the task cue, the PT shift would be equal to the duration of the task cue regardless of its temporal location (stop mode). If the clock resets at the end of the task cue, then the PT shift would be equal to the duration of the task cue plus the time accumulated by the clock prior to the task cue (reset mode). If subjective accumulated time decays in memory (Cabeza de Vaca et al., 1994) during the intruded event, then the PT shift would be intermediate to those predicted by the stop and reset alternatives. Finally, a somewhat similar prediction of an intermediate effect would follow if the expectation of the task cue prior to its occurrence blocked pulse accumulation during the timed interval (Lejeune et al., 1999). The limiting case for memory decay and expectancy is the reset prediction. The results showed that PT shifts on gap trials increased as a function of the temporal location, but fell between stop and reset predictions, replicating the results in a previous study (Cabeza de Vaca et al.). Surprisingly, the rightward shift in PI function occasioned by the presentation of the task cue exceeded the predictions of both stop and reset modes at all locations. Accordingly, neither memory decay nor expectancy mechanism could account for those results. The over-reset PT shift on the concurrent task cue trials was explained by the authors in terms of the suspension of timing based on off-task behavior occasioned by the task cue, in addition to temporal mechanisms mediated by clock processes. That is, the presentation of the task cue produced off-task behavior, with respect to the schedule maintained on the FI key, that outlasted the task cue, and timing behavior appropriate to the interval schedule on the FI key resumed when off-task behavior ceased after some interval had passed (Aum et al., 2004).

Purposes of the Present Study

The difference in PT shifts between task and gap conditions in Aum et al. (2004) is attributable to any of several differences between the two types of intruded events. First, the concurrent task cue was higher in stimulus intensity than the gap stimulus (see

Buhusi & Meck, 2000, and Buhusi, Sasaki, & Meck, 2002, for the effect of the attributes of the gap on interval timing in animals). Second, the FI cue was illuminated during the presentation of concurrent task cue, whereas the FI cue was not illuminated during the presentation of the gap. Third, in the concurrent task condition, the interrupting event (presentation of the center-key light) was dissimilar to the ITI condition, whereas the event (termination of the timing side-key light) in the gap condition was the same as the ITI condition (see Kaiser, Zentall, & Neiman, 2002, and Hinton & Meck, 1997, for the effect of the similarity between gap and ITI on interval timing in animals). Fourth, overall reinforcer rate was higher in the concurrent task condition than in the gap condition. Fifth, the concurrent task cue was associated with a high probability of reinforcement, whereas the gap was associated with extinction. Finally, the concurrent task cue, but not the gap, occasioned relatively high response rates to the intruded cue.

The first three differences between conditions noted above are related to differences in stimulus properties between the concurrent task cue and gap. The last three differences are related to differences in reinforcement history between the concurrent task cue and gap. In relation to the differences in reinforcement history, the concurrent task cue served as a potential positive discriminative stimulus (S+) for center-key pecking, whereas the gap served as a negative discriminative stimulus (S-) because no reinforcement could be earned in the presence of the gap. In Pavlovian terms, the concurrent task cue might have functioned as an excitatory conditioned stimulus (CS+); whereas the gap might have functioned as an inhibitory conditioned stimulus (CS-).

The major purpose of the present study was to investigate the variables controlling the difference in PTs between concurrent task and gap conditions. Because the role of reinforcement history has not been addressed in studies of concurrent task effects, reinforcement history was manipulated for two stimuli (red and green center keylights) while the stimulus properties of the two stimuli were controlled in the present study.

Separate discrimination training first established one cue as an S+ and another as an S-. The effect of each cue on responding to the side key (timing key) on probe trials in the PI procedure was assessed subsequently in test sessions. In addition, to further evaluate the effect of history of reinforcement, the S+ cue was extinguished in the next phase, and PT on the extinguished S+ trials was compared to PT on S- and gap trials. To do that, the cues (center keylight colors) associated with S+ and S- were balanced across birds. This procedure effectively controls for the first three stimulus factors, while manipulating history of reinforcement between cues. Moreover, in contrast to Aum et al. (2004), in which the overall reinforcer rate differed between task cue and gap sessions, the overall reinforcer rate was held constant by presenting the concurrent task cue and gap events in the same sessions. As a technical modification, the trial duration and mean ITI were increased to 120 s and 45 s, respectively, in order to facilitate measurement of PT.

Depending on the variables controlling the difference in PTs between concurrent task and gap events, different results were predicted. If the difference in PT between the concurrent task and gap conditions in Aum et al. (2004) was due only to differences in stimulus properties, peak shifts under both S+ and S- conditions would exceed those under a gap condition in which the intruded event was the cessation of the FI signal; however, the shift should be similar for S+ and S- conditions. In addition, the extinction of the S+ cue in the second experimental phase should have no effect on PT. Alternatively, if the difference in PTs between the concurrent task cue and gap conditions in Aum et al. was due only to differences in histories of reinforcement, peak shifts under the S+ condition should exceed those under S- and gap conditions. In addition, the extinction of the S+ cue in the later phase should produce a decrease in PT.

Method

Subjects

Ten adult white king pigeons that were experimentally naïve were maintained at 80 % of their free-feeding weights. They were housed individually in home cages with water and grit continuously available. A 12:12 hr light-dark cycle was maintained in the home cage room. Experimental sessions were conducted 5 days a week during the light period of the cycle.

Apparatus

The apparatus was the same as that used in Aum et al. (2004). Sessions were conducted in five identical standard size chambers (37 cm H x 31 cm W x 34 cm D) constructed of aluminum interior walls, and a stainless steel mesh floor (BRS/LVE, Inc, Laurel, MD, USA, Model SEC-002). Ventilation fans and white noise delivered through speakers mounted behind the panels provided masking noise. The front panel was equipped with a houselight, three response keys, and a grain hopper. The houselight lamp (Sylvania, No. 1829, 28VDC, .07 amp) was located 1.5 cm from the top and 17 cm from the right side of the panel. The three response key apertures (2.5 cm) were centered 8.25 cm apart horizontally and 8 cm from the top of the panel. Stimulus projectors (BRS/LVE, TQL-015, and IC-901, pattern 696) mounted behind the keys could illuminate the center and left side clear Lucite keys (BRS/LVE, PPK-001) with red, green, or yellow light. The right side key was always dark. A hopper aperture (5.5 cm W x 5 cm H) was centered 6 cm below the center key and a grain feeder (BRS/LVE, GFM-001) was mounted behind the hopper aperture. Pigeons' hopper entries were detected by a photocell assembly mounted inside the feeder. All experimental contingencies and response recording were programmed with MED-PC software in a computer located in an adjacent room.

Procedure

Pretraining. Pigeons were trained to eat food from the food hopper through magazine training. Then, pigeons were trained to peck the left key through a discrete-trial autoshaping schedule of grain reinforcement in which presentation of the 10-s left yellow key was followed by 1.5 s access to food. A keypeck during the trial produced a reinforcer and terminated the trial. The ITI was 60 s. Each session ended after 60 trials. When at least 80 % of available reinforcers were earned in a session, autoshaping training terminated. In the next two sessions, discrete trials were presented in which the keylight was illuminated until a reinforcer was earned. In the first session, reinforcement was contingent upon a single response (fixed ratio 1, FR1). In the second session, the reinforcement schedule on each trial was FR2. Trials were separated by an ITI drawn from a set of four equally spaced, rectangularly distributed values (mean: 30 s, range: 15-45 s). Each session ended when 40 reinforcers were earned. On these and all subsequent sessions, the houselight was illuminated throughout the session, and the reinforcer was 1.5-s access to mixed grain timed from the insertion of the bird's head into the hopper aperture.

Fixed-interval training (5 sessions). After pretraining, pigeons were exposed to a discrete FI 30-s reinforcement schedule. Sessions consisted of 77 discrete FI trials signaled by illumination of the left yellow keylight. The first left-key peck response after 30 s terminated the left keylight and produced a reinforcer. The ITI was drawn from a set of four equally spaced, rectangularly distributed values (mean: 45 s, range: 30-60 s).

Peak interval training (51 sessions). After FI training, pigeons were exposed to the PI procedure. Each session was composed of 77 reinforced FI trials and 33 nonreinforced empty trials. Each trial began with the onset of the left yellow keylight following an ITI that had the same values as during FI training sessions. On reinforced trials (FI trials), an FI 30-s reinforcement schedule was operative for the left yellow keylight; on nonreinforced trials (baseline probe trials), the left yellow keylight remained illuminated for 120 s. The order of trials was determined randomly within blocks containing 7 FI and 3 baseline probe trials.

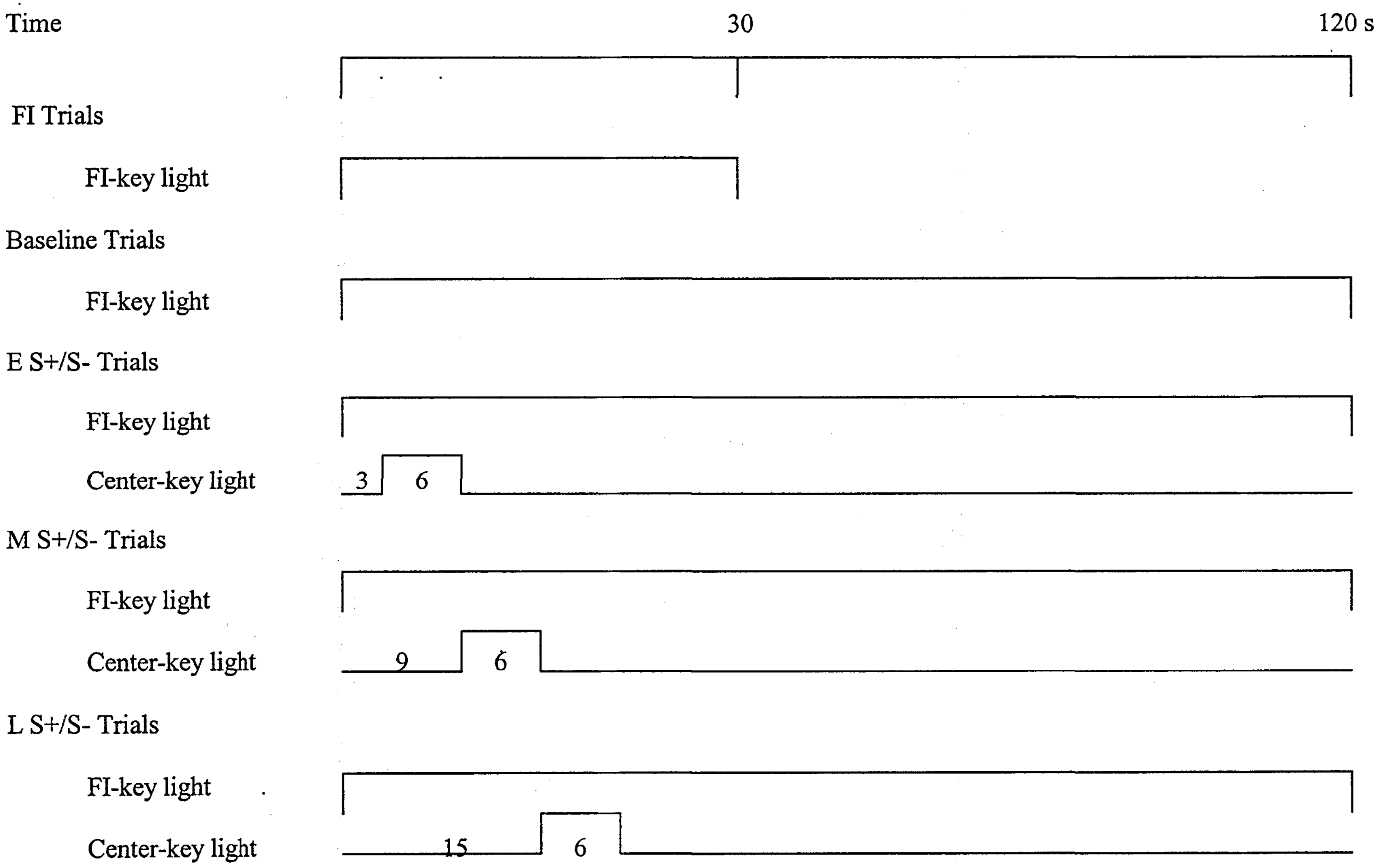
Random-interval (RI) training. After PI training was completed, pigeons were trained to peck the center key when illuminated by a red or green keylight which was presented for 6 s on each trial. For birds 1, 2, 5, 8, and 9 the keylight was red; for birds 3, 4, 6, 7, and 10 the keylight was green. In the first session, a discrete-trial autoshaping procedure was in effect with the red or green keylight for 70 trials. The ITI was 60 s. The criterion for autoshaping was a minimum of one peck on at least 90 % of the trials in a session. On subsequent sessions, a modified random-interval (RI) schedule (mean ITI: 12 s; range: 6-18 s) was implemented for the red or green keylight in which the first response in each successive second (bin size, *t*) of the 6-s trial period produced a reinforcer with probability *p*. Once a reinforcer was programmed in a bin, it remained available on successive bins within a trial until earned. Across sessions, p was decreased from 1.0, to .5, .0833, and .0416, which corresponded to RI 1 s, 2 s, 12 s, and 24 s, respectively. For each bird, the criterion for a change in p value across RI sessions was a minimum of one response on at least 90 % of the trials in a session. Each session was composed of 70 trials.

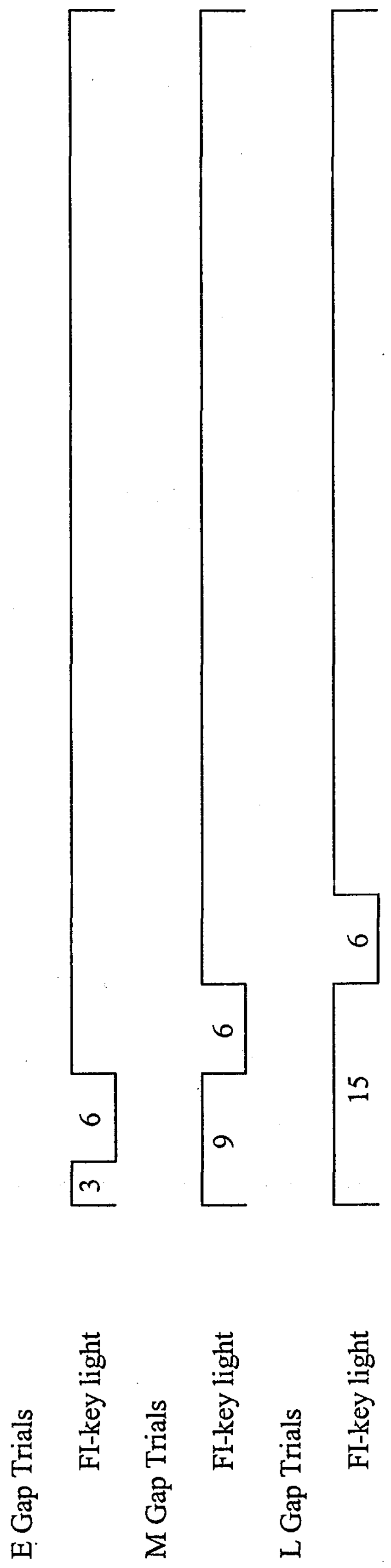
Discrimination training (3-4 sessions). Center red and green keylights were established as a positive discriminative stimulus (S+) and a negative discriminative stimulus (S-) through discrimination training. The colors of the center keylights used as S+ and S- were balanced across birds. For birds 1, 2, 5, 8, and 9 the red keylight was S+ and the green keylight was S-; for birds 3, 4, 6, 7, and 10 the green keylight was S+ and the red keylight was S-. S+ cue was associated with a RI 24-s schedule, whereas S- cue was associated with extinction. The discrete RI and extinction trials were 6 s in duration presented in a random order. Each trial began with the onset of S+ or S- following an ITI with a mean of 12 s (range 6-18 s). Each session consisted of 140 S+ and 140 S- trials and lasted about 1.17 hrs. The criterion for discrimination learning was a discrimination ratio (DR) of at least 0.8 in three successive sessions. The DR was calculated by dividing the mean response rate under S+ by the sum of the mean response rate under both S+ and S-. Birds were continuously run in this phase until performance reached the discrimination criterion.

Alternated PI and discrimination training phase 1 (29 PI and 28 discrimination training sessions). Pigeons were exposed to the PI and discrimination training sessions that were in effect during the preceding two phases in daily alternation.

Concurrent task and gap phase 1 (task/gap phase 1) (25 sessions). The two squads of 5 pigeons were run consecutively within days in test sessions consisting of 110 trials and lasting about 3.19 hrs. During this phase, sessions were structured similarly to those in the PI training phase, but there were different types of probe trials. The temporal arrangement of stimulus events during the probe trials is shown in Figure 1. Probe trials consisted of the following types of nonreinforced empty trials: baseline, S+, S-, and gap. For baseline probe trials, only the left yellow keylight was presented. For S+, S-, and gap trials, intruded events were presented at 3 (early, E), 9 (middle, M), or 15 (late, L) s after trial onset. For both S+ and S- trials, the intruded event was the illumination of the center key light for 6 s and the left yellow key light remained illuminated. For gap trials, the intruded event was the termination of the left yellow key light (see Figure 1). There were 3 baseline probe trials in a session. There were 12 S+, 9 S-, and 9 gap trials; early, middle, and late S+, S-, and gap trials were presented equally often for each probe trial type. A peck to the S+ could be reinforced on 1 of the 4 S+ trials for each temporal location, selected randomly; therefore the nominal rate of reinforcement was the same as that on the RI 24-s training schedule. When available, reinforcement could be earned in a randomly selected 1-s bin of the 6-s S+ key presentation. Once the reinforcer was programmed in a bin, it remained available on successive bins within a trial until earned. As in the PI training sessions, the order of FI and probe trials were randomized within blocks of 10 trials. The order of probe trial type was completely random. Each session began with two reinforced FI trials prior to the initiation of the block randomized trial sequence. The proportion of FI and probe trials was identical to the ratio in the study by Aum et al. (2004) (i.e., 70 % FI and 30 % probe trials), and the RI schedule on the S+

Figure 1. Procedure diagrams for trial events during all experimental phases. Values represent seconds. E, M, and L represent early, middle, and late, respectively.


Time
30
120 s
FI Trials
FI-key light
Baseline Trials
FI-key light
E S+/S- Trials
FI-key light
Center-key light
3
6
M S+/S- Trials
FI-key light
Center-key light
9
6
L S+/S- Trials
FI-key light
Center-key light
15
6


E Gap Trials
FI-key light
3
6
M Gap Trials
FI-key light
9
6
L Gap Trials
FI-key light
15
6

trials was also the same as that in that study. Compared to the study by Aum et al., the number of baseline probe trials was reduced from 6 to 3 per session in order to accommodate additional test trials (i.e., S- and gap trials).

Extinction phase (25 sessions). Conditions were identical to those of the task/gap phase 1 except that no reinforcer was scheduled during the presentation of the S+ cue.

Alternated PI and discrimination training phase 2 (11 PI and 10 discrimination training sessions). The Alternated PI and discrimination training phase was reinstated during these sessions.

Task/gap phase 2 (30 sessions). The procedure was the same as that during task/gap phase 1.

Table 1 summarizes the sequence of phases and number of sessions in each phase of the experiment. Equipment failures occurred in session 1, 14, and 15 of the task/gap phase 1 for bird 7, 8, and 3, respectively. In addition, the data for one session (session 6) of the extinction phase were lost for bird 6 and 8. In those cases, one additional session was run to replace the error session or lost session data.

Data Recording and Analysis

During the PI sessions, and the three experimental phases (task/gap phase 1, extinction phase, task/gap phase 2), keypecks to the left key were recorded in 1-s bins during the entire 120-s probe trial. Total numbers of keypecks to the center key during the presentation of S+ and S- were recorded during RI training, discrimination training, and the three experimental phase sessions. Unless otherwise indicated, in the analysis of

Table 1

Sequence of phases and number of sessions in each phase (or the range of the number of sessions from minimum to maximum).

Phase	Number of Sessions
Pretraining	
Magazine training	6-7
Autoshaping	2-9
Fixed-ratio1	1
Fixed-ratio 2	1
Fixed-interval 30 s training	5
Peak-interval training	51
Random-interval training	
Autoshaping	1-2
Random-interval 1 s	1
Random-interval 2 s	1
Random-interval 12 s	1-2
Random-interval 24 s	1-2
Discrimination training	3-4
Alternated peak-interval and discrimination training phase 1	
Peak-interval training	29
Discrimination training	28

Task/gap phase 1	25
Extinction	25
Alternated peak-interval and discrimination training phase 2	
Peak-interval training	11
Discrimination training	10
Task/gap phase 2	30

PT during the task/gap phases, S+ trials on which reinforcers were programmed for responses on the S+ key light were excluded.

Because S+, S-, and gap events were presented on probe trials in which pecks to the FI key were not reinforced, response rates to the FI key on those trials tended to decrease across test sessions. The decrease was greater on the S+ trials than on the S- and gap trials (see Appendix H for the comparison of peak rate among the S+, S-, and gap trials). On the other hand, relatively high response rates to the FI key on baseline probe trials tended to be maintained over sessions. The decrease in response rate on task and gap trials was accompanied by flattening of the peak interval functions, and indeterminate PTs for some birds (see Appendix B, C, and E for individual bird's temporal pattern of performance on baseline, task, and gap trials during the task/gap phase 1, extinction, and task/gap phase 2, respectively). Therefore, differential responding between baseline probe trials and task and gap trials was evaluated by computing a discrimination index (DI). The DI was calculated as mean response rate to the FI key on intruded event trials divided by mean response rate on the baseline probe trials throughout the 120-s probe trial period. Presentation of the intruded event occasioned an abrupt decrease in the response rate to the FI key. To avoid an artifact of the task cue or gap presentation the DI was based on mean response rate to the FI key on task or gap trials throughout the post-task cue or gap event period. A criterion DI was set at 0.5, and any birds whose early, middle, or late S+, S-, or gap probe trial data produced a DI lower than 0.5 were not included in the calculation of PT (see Appendix F for individual bird's DIs on early, middle, and late S+, S-, and gap trials during the task/gap phase 1 and 2 and the extinction phase). Bird 10 died after session 13 of the extinction phase, and its data were not included in the data analyses for the extinction phase. Accordingly, for the analyses of PT, the data of birds 1, 2, 3, 4, 5, 7, 8, and 10 were included in the task/gap phase 1; data of birds 1, 2, 4, 5, 7, and 8 in the extinction phase; and data of birds 2, 4, 5, 7, and 9 in the task/gap phase 2.

In the calculation of PT, the iterative median method used in the previous studies (Aum et al., 2004; Roberts, 1981) could not be applied to the data of the present experiment owing to asymmetrical peak interval functions. For some birds, response rates in the end of the probe trials tended to rise again after the occurrence of a peak earlier in the trial. In those cases, the median method produced overestimated PTs that did not conform to the peak time evident upon visual inspection. As an alternative measure, the time at which a maximum response rate occurred was identified as PT in the present experiment. To avoid the artifact of the task cue or gap presentation, PTs on task (S+ and S-) and gap trials were based on performance after the termination of the task or gap event, in the maximum rate method of PT calculation. In that method, first, mean response rates in sliding blocks of 20 s (1-20 s, 2-21 s, etc) were calculated. Second, the best-fit regression line was found for each 20-s sliding block. Third, the 20-s sliding time block for which the slope of the regression line was the maximum negative value was identified. Finally, the 20-s time block for which the mean response rate was the maximum (peak rate) was identified between the time block following the termination of the intruded event and the time block with the maximum negative slope. Peak time was defined as the mid time point of the 20-s sliding time block at which the mean response rate was the maximum. In order to reduce variability, data were averaged across 5-session blocks. Based on the changes in the temporal pattern of the response rate function as a function of 5-session blocks, data during blocks 1 and 2, and data during blocks 3, 4, and 5 were averaged and PTs were calculated based on the resulting mean response rate functions.

All inferential statistical analyses were based on an α level of .05; all t-tests were two-tailed unless otherwise indicated.

Results

Alternated PI and Discrimination Training Phase 1

When animals were trained under the PI procedure, response rate within a trial tended to increase up to the programmed FI value of 30 s since trial onset, and then fell gradually to a level above 0. Figure 2 shows the group mean temporal pattern of performance on the probe trials during the last 10 PI sessions in the alternated PI and discrimination training phase 1 (see Appendix A for individual bird's temporal pattern of performance in this phase). The group function was unimodal and the mode was centered around 30 s. Individual birds' PTs on the probe trials were 32.5, 27.5, 16.5, 34.5, 28.5, 20.5, 28.5, 28.5, 33.5, and 29.5 s for bird 1 to 10, respectively. Group mean PT, 28.0 s, was not significantly different from the programmed FI value, 30.0 s ($t(9) = 1.12$, $p = .29$).

During the discrimination training sessions in the alternated PI and discrimination training phase 1, birds' discrimination performance between the S+ cue and S- cue was maintained as in the previous discrimination training phase. Figure 3 shows the group mean center-key peck rate (responses per second) in the presence of S+ and S- cues (top panel) and the group mean discrimination ratio (bottom panel) during 28 discrimination

Figure 2. Group mean (n=10) FI-key peck rate (responses per second) as a function of elapsed probe-trial time during the last 10 PI sessions of the alternated PI and discrimination training phase 1.

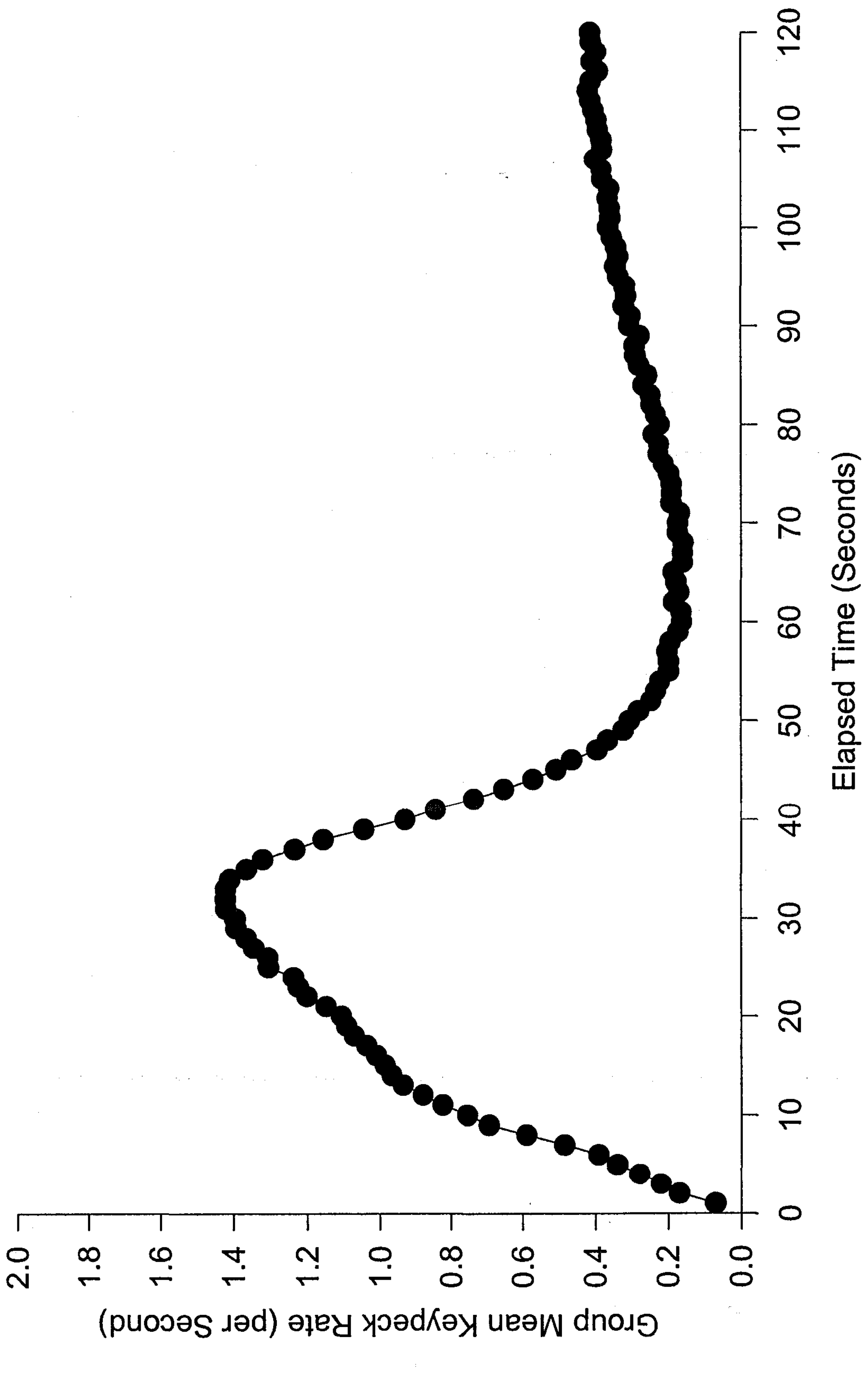
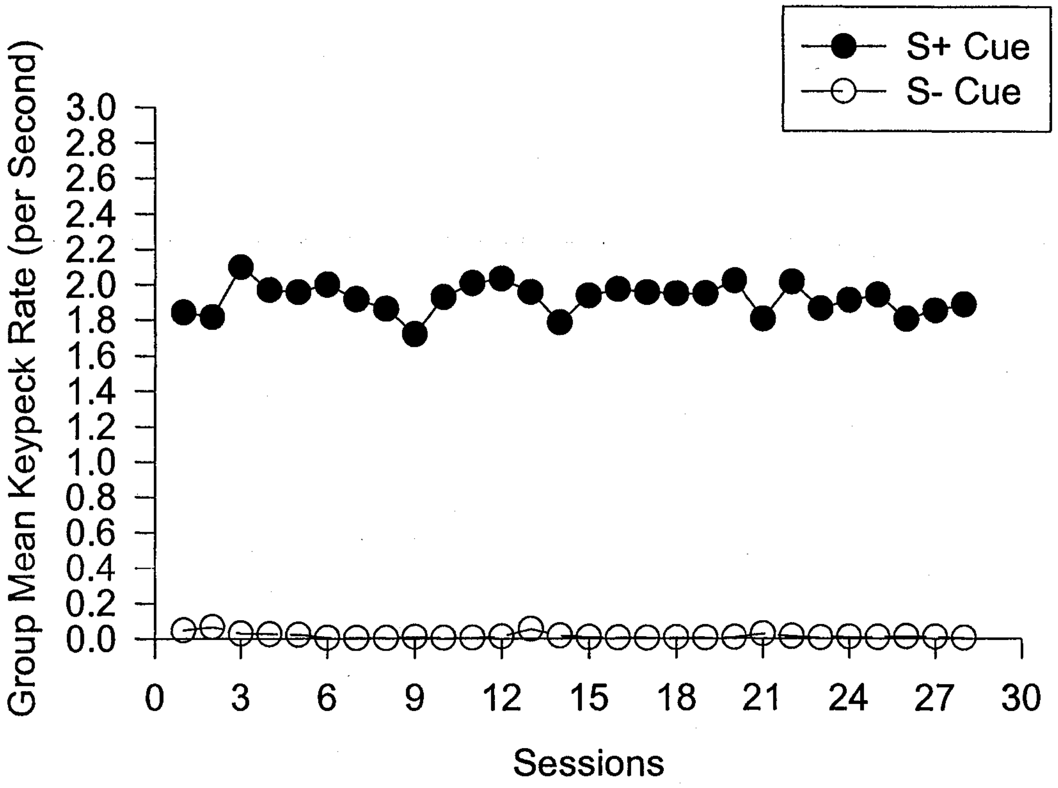
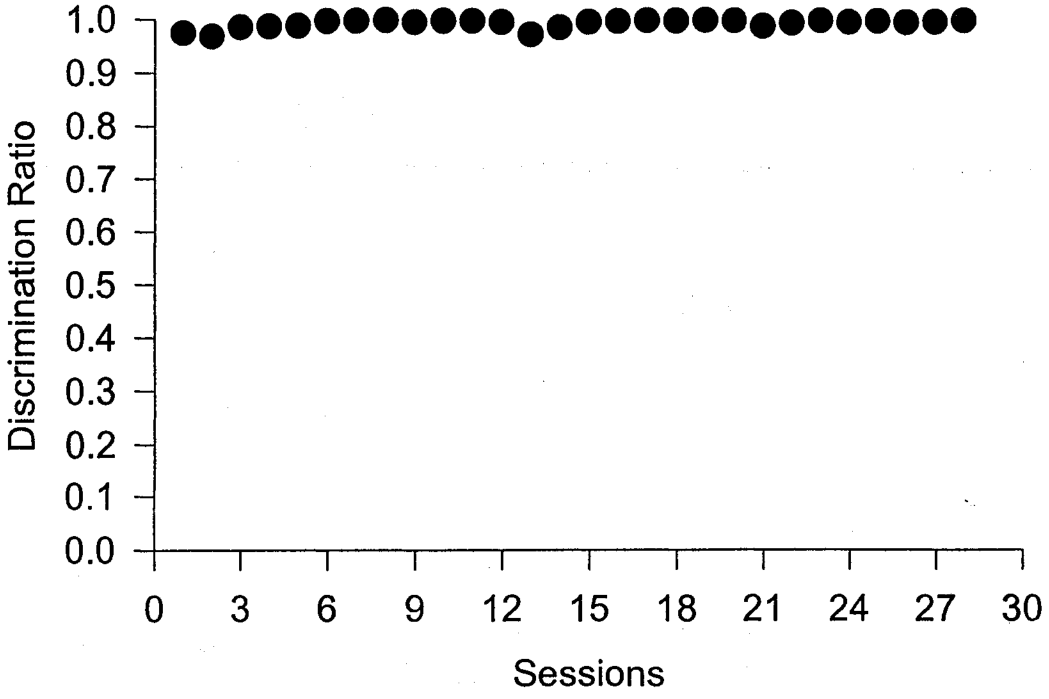

Group Mean Keypeck Rate (per Second)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Elapsed Time (Seconds)
0
10
20
30
40
50
60
70
80
90
100
110
120

Figure 3. Group mean (n=10) center-key peck rate (responses per second) (top) and discrimination ratio (bottom) during discrimination training sessions of the alternated PI and discrimination training phase 1.


S+ Cue
S- Cue
Group Mean Keypeck Rate (per Second)
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
3
6
9
12
15
18
21
24
27
30
Sessions

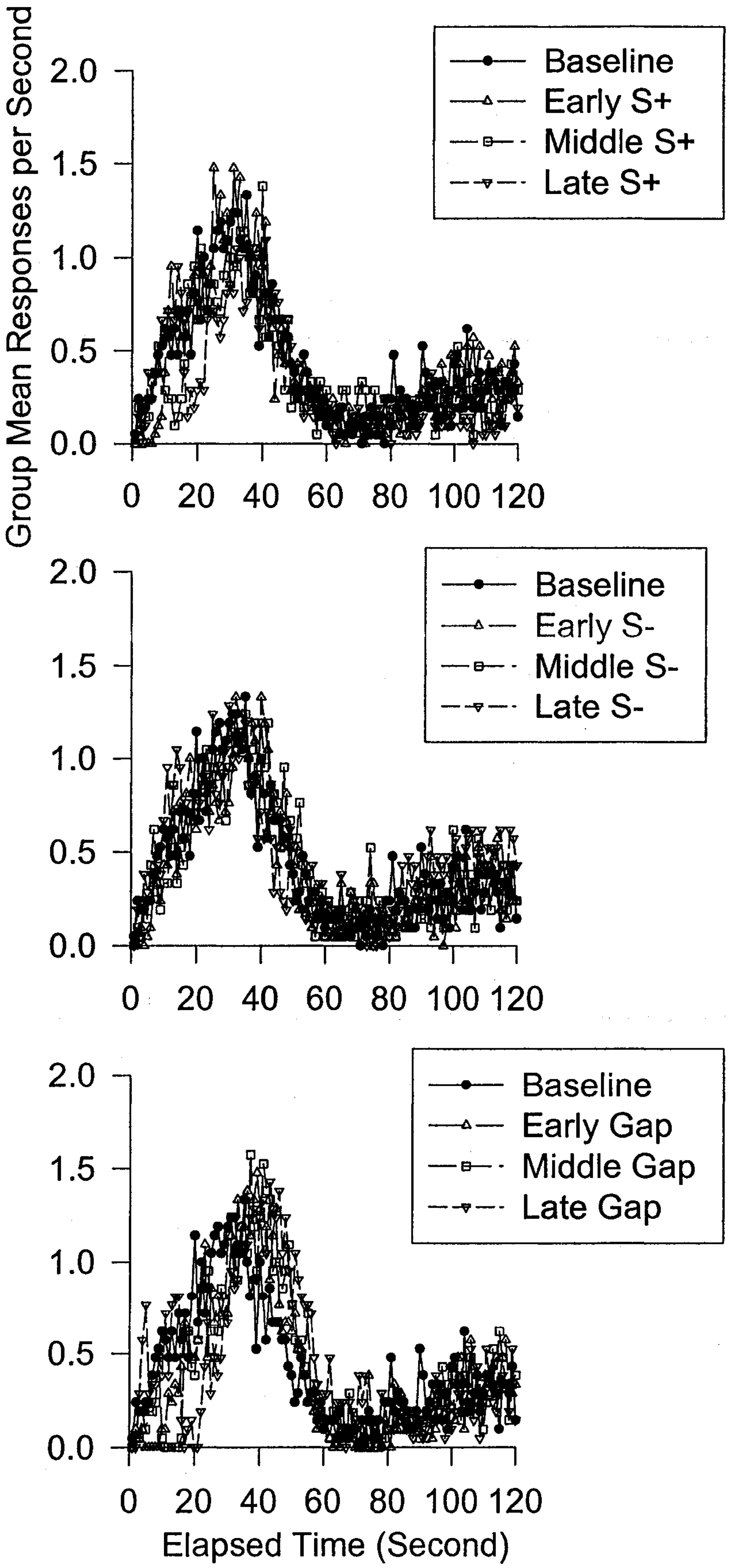

Discrimination Ratio
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
3
6
9
12
15
18
21
24
27
30
Sessions

training sessions in the alternated PI and discrimination training phase 1. In all discrimination training sessions, most center-key pecks occurred on S+ trials and almost no responding occurred on S- trials. Accordingly, group mean DRs in all discrimination training sessions were either close to or equal to 1 (group mean range: 0.97 - 1.00), indicating stable and well established discrimination performance. The overall group mean center-key peck rates on S+ and S- trials over the 28 discrimination training sessions were 1.92 and 0.02 responses per second, respectively, and the overall group mean DR was 0.99.

Task/gap phase 1

Responding directed toward the left (FI) key. During the first session there appeared to be little if any effect of S+ cue presentation on birds' performance on the FI key. Figure 4 presents the group mean (n=7) temporal pattern of performance on the FI key on baseline probe trials and S+ (top panel), S- (middle panel), and gap (bottom panel) probe trials at each of the three temporal locations (early, middle, and late) of the task cue or gap event during the first session of the task/gap phase 1. There was a system failure for bird 7 in the first session and bird 6 and 9 did not meet the DI criterion on this session. Therefore, the data in Figure 3 are based on the remaining birds (n=7). Even though the birds tended to stop responding to the FI key in the presence of S+ cue, which is indicated by the abruptly decreased response rate, the effect of the S+ cue on timing was not detrimental. For the S+ trials, compared to the response rate function for the baseline probe trials, there was a rightward shift in the response rate function (that is, PT shift toward a longer time) only at the late location of the S+ cue ($t(6) = 2.56$, $p < .05$), indicating overestimation of the reinforcer delivery time. For the S- trials, the response

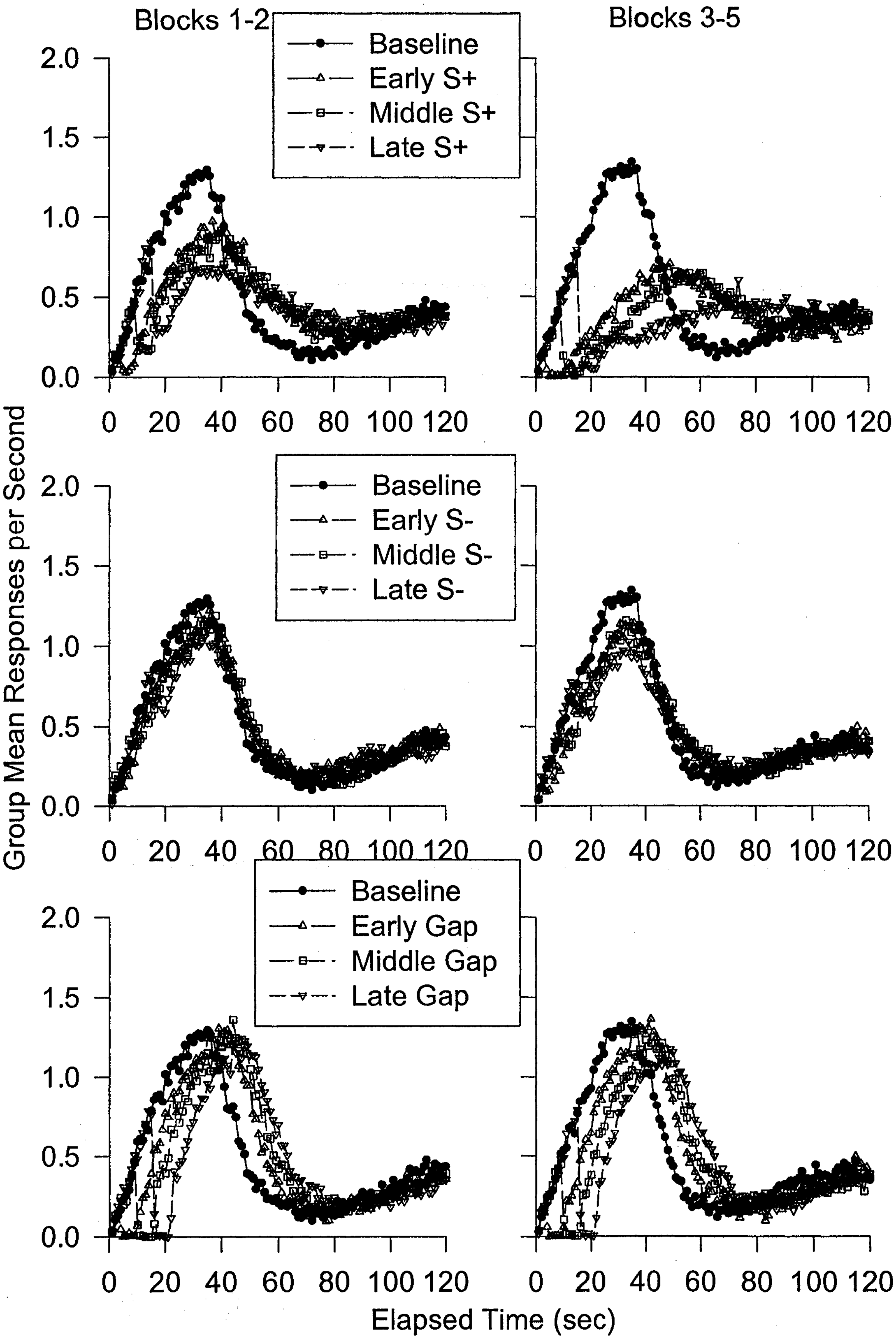
Figure 4. Group mean (n=8) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session 1 of the task/gap phase 1. Data are shown separately for early, middle, and late locations of the S+, S-, and gap events.


Group Mean Responses per Second
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Elapsed Time (Second)

rate functions were superimposed on the baseline function. For the gap trials, compared to the baseline function there were rightward shifts in the response rate functions at all three locations of the gap event ($t(6) \geq 2.57$, $p < .05$), indicating a clear effect of the gap event on timing in the first session.

As test sessions continued, clear shifts in the response rate functions were also observed at all three locations of the S+ cue. Figure 5 presents the group mean (n=8) temporal pattern of performance on the FI key on baseline probe trials and S+ (top panels), S- (middle panels), and gap (bottom panels) probe trials at each of the three temporal locations (early, middle, and late) of the task cue or gap event during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase1 (see Appendix B for individual bird's temporal pattern of performance in this phase). Birds' timing performance on the baseline probe trials was maintained as in the PI sessions of the previous phase. For the group mean response rate function on the baseline probe trials the mode was centered around 30 s during both blocks 1-2 and 3-5. For the task and gap trials, there was abrupt decrease in the response rate to near zero when the S+ cue or gap event was presented, whereas there was less of a decrease when the S- cue was presented. Compared to the baseline function, the response rate functions for the S+ and gap trials shifted to the right. The response rate functions for the S- trials shifted only slightly. During both blocks 1-2 and 3-5, the degree of the shift on the S+ trials was greater than that on the S- trials. In addition, during both blocks 1-2 and 3-5 the degree of the shift on the S+ and gap trials tended to increase as a function of the temporal location of the S+ cue and gap events; no differential shift was observed across temporal locations of the S- cue on the S- trials. Figure 4 also suggests differences in peak rates among probe trial types. In general, peak

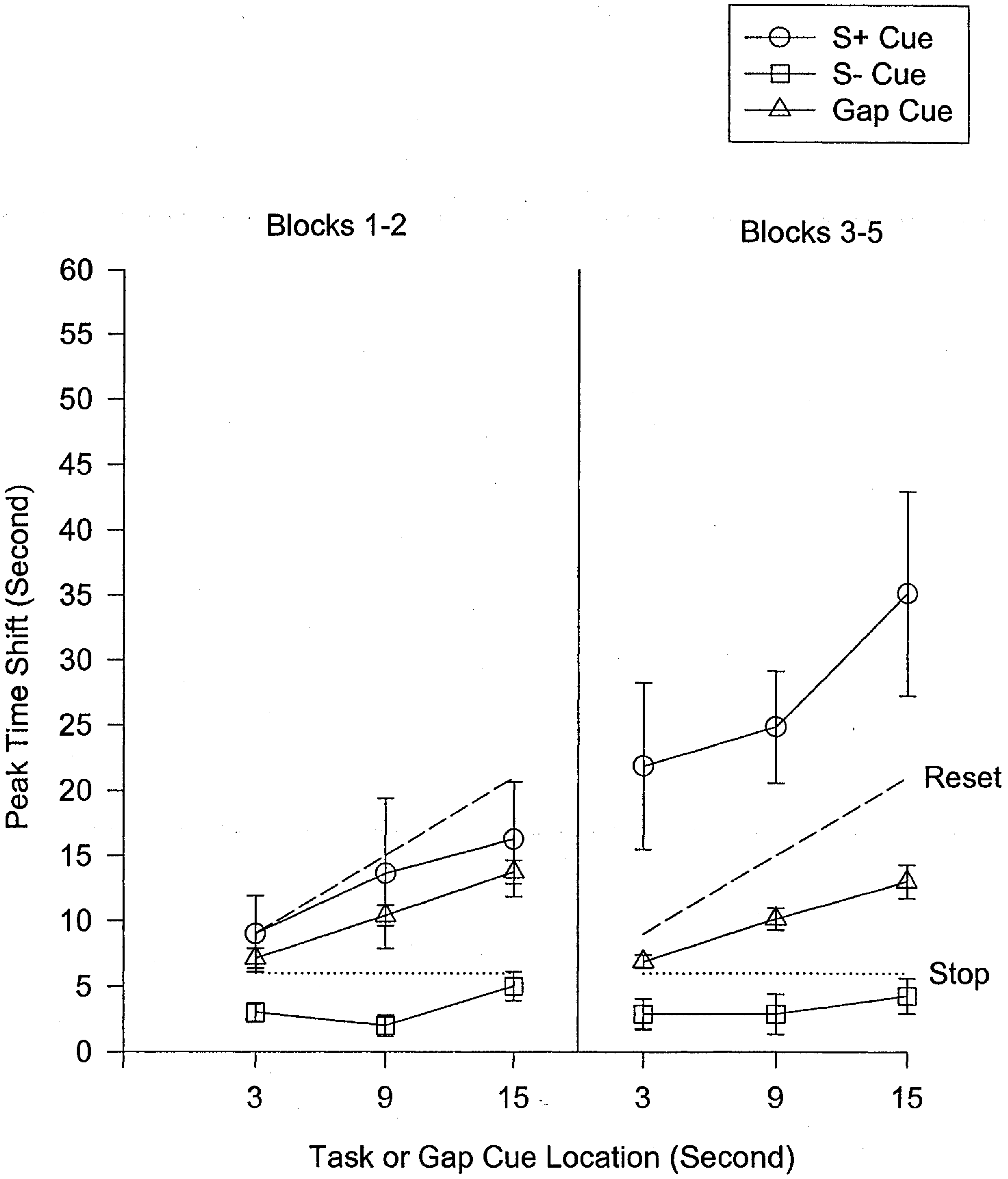
Figure 5. Group mean (n=8) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase1. Data are shown separately for early, middle, and late locations of the S+, S-, and gap events.


Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Group Mean Responses per Second
Elapsed Time (sec)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

rate on S+ trials was lower than peak rates on baseline, S-, and gap trials. Quantitative analysis of peak rate is presented in Appendix H.

For quantitative analysis of the shift in the response rate functions on S+, S-, and gap trials, the magnitude of the shift (PT shift) was calculated by subtracting the PT on baseline probe trials from PT on S+, S-, or gap trials. Figure 6 shows the obtained group mean PT shift (±SEM) at each task cue or gap event location on S+, S-, and gap trials during session blocks 1-2 and 3-5 of the task/gap phase 1 (see Appendix G for each individual bird's PT on baseline, S+, S-, and gap trials in this phase). The broken lines represent the predicted PT shift based on the stop or reset mode of clock switch. At all three locations of the S+, S-, and gap events PT shift was greater than 0 during both blocks 1-2 and 3-5 ($ts(7) \geq 2.49$) except for the PT shifts at the middle location of the S+ cue during blocks 1-2 and at the middle location of the S- cue during blocks 3-5. Peak time shift on the S+ trials was greater than that on the S- trials during both blocks 1-2 and 3-5. In addition, during both blocks 1-2 and 3-5, PT shift on the S+ and gap trials increased as a function of the temporal location of the S+ cue and gap event; PT shift on the S- trials was stable across the locations. For the group mean functions, Pearson correlation coefficients between location and PT shift on the gap trials during both blocks 1-2 and 3-5 were greater than 0.999, implying a linear relationship. The correlation coefficients applied to the S+ trials during blocks 1-2 and 3-5 were lower than those on the gap trials. Peak time shift on the S+ trials increased over session blocks; stable PT shifts were obtained over session blocks on the S- and gap trials. A session block x trial type x location ANOVA of PT shift yielded significant effects of session block, $F(1, 7) =$

Figure 6. Group mean (n=8) peak-time shift (± SEM) as a function of the location of S+, S-, and gap events during sessions blocks 1-2 and 3-5 of the task/gap phase 1. Dotted and dashed lines refer to stop and reset predictions, respectively.

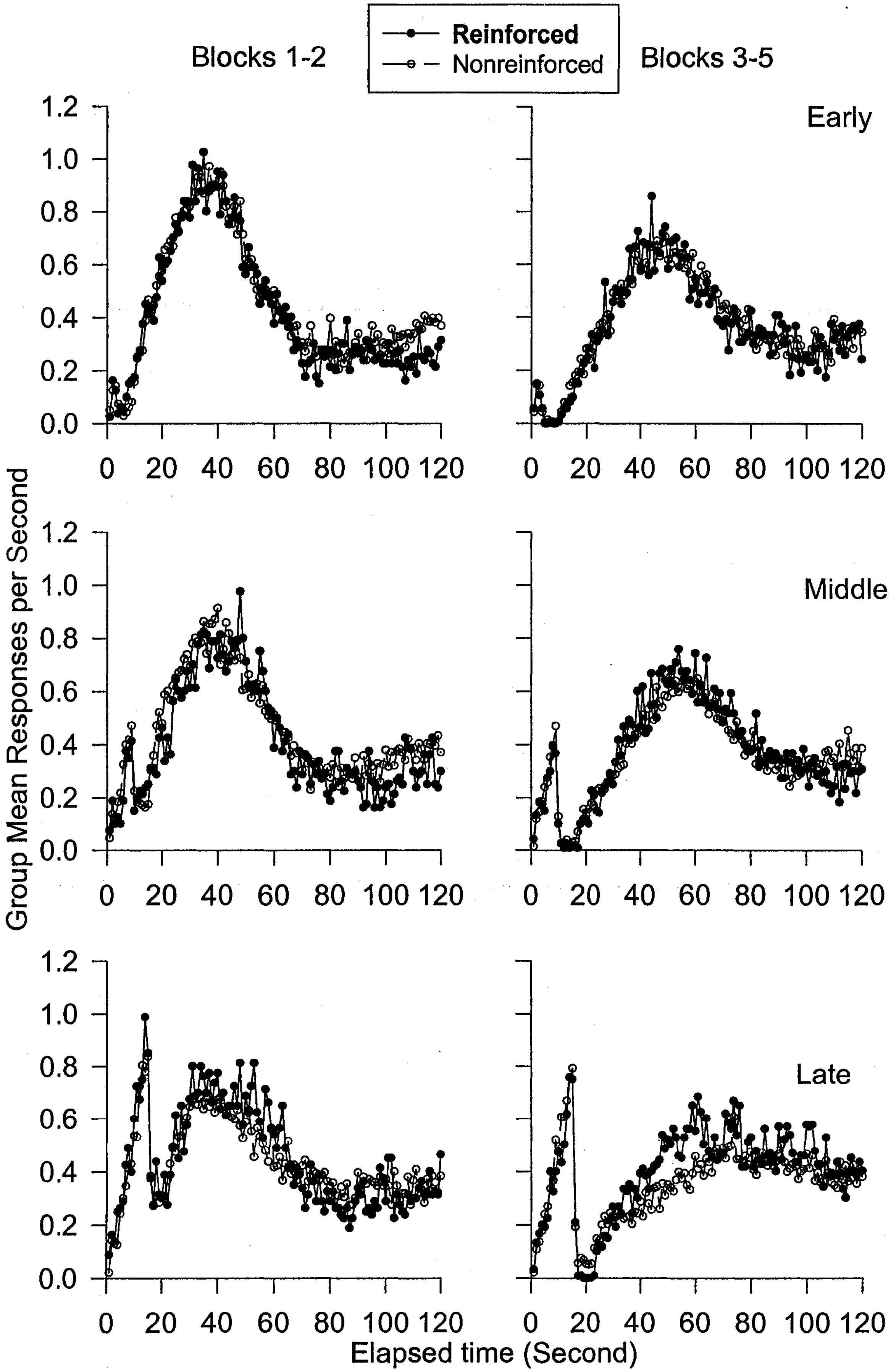

S+ Cue
S- Cue
Gap Cue
Blocks 1-2
Blocks 3-5
Peak Time Shift (Second)
0
5
10
15
20
25
30
35
40
45
50
55
60
Reset
Stop
3
9
15
3
9
15
Task or Gap Cue Location (Second)

11.53, trial type, *F*(2, 14) = 9.33, and location, *F*(2, 14) = 16.03; the session block x trial type interaction, *F*(2, 14) = 44.87. The trial type x location interaction was not significant, *F*(4, 28) = 2.39, *p* = .08, nor were other interaction effects significant. When the trial type effect was analyzed separately for blocks 1-2 and 3-5, it was significant for both blocks 1-2 (*F*(2, 14) = 4.07) and 3-5 (*F*(2, 14) = 15.36). Subsequent tests indicated that the PT shift on the S+ trials was greater than that on the S- trials, but not gap during blocks 1-2, and greater than the PT shifts on both S- and gap trials during blocks 3-5. When the session block effect was analyzed separately for each trial type, PT shift during blocks 3-5 was greater than that during blocks 1-2 for the S+ trials (*F*(1, 7) = 28.81). In contrast, PT shifts were not significantly different between blocks for the S- and gap trials. The greater PT shift on the S+ trials than on the S- trials is consistent with the predicted PT shift when the role of reinforcement history (that is, training history) is assumed to be critical in relation to the effect of the concurrent task cue.

To relate the obtained PT shifts on the task and gap trials to the temporal information processing model, the obtained PT shifts were compared to the stop and reset predictions. If the switch of the animal's internal clock operated with a stop mode during the presentation of the task cue or gap event, the PT shifts would be equal to the duration of the task cue or gap event (stop prediction) regardless of the temporal location of the cue or the event. On the other hand, if the switch operated with a reset mode, the PT shifts would be equal to the time elapsed before the onset of the task cue or gap event plus the duration of the cue or the event (reset prediction). Accordingly, the PT shift would increase as a function of the temporal location of the task cue or gap event. During blocks 1-2, PT shift on the S+ trials was not significantly different from either stop or reset prediction at all three locations. Peak time shift on the S- trials was lower than the stop prediction at the early and middle locations of the S- cue (*t*s(7) ≥ 4.10) and lower than the reset prediction at all three locations (*t*s(7) ≥ 8.20). Peak time shift on the gap trials was greater than the stop prediction at the middle and late locations of the gap event (*t*s(7) ≥ 5.63), but lower than the reset prediction at all three locations (*t*s(7) ≥ 2.45). During blocks 3-5, PT shift on the S+ trials was greater than the stop prediction (*t*s(7) ≥ 2.48), but not significantly different from the reset prediction at all three locations of the S+ cue. A one-tailed *t* test, however, showed that PT shift at the early and middle locations of the S+ cue was significantly greater than the reset prediction (*t*(7) ≥ 2.01). Peak time shift on the S- trials was lower than the stop prediction at the early location of the S- cue (*t*(7) = 2.74) and lower than the reset prediction at all three locations (*t*s(7) ≥ 5.37). Peak time shift on the gap trials was greater than the stop prediction at the middle and late locations of the gap event (*t*s(7) ≥ 4.95), but lower than the reset prediction at all three locations (*t*s(7) ≥ 4.12). The PT shift on the S+ trials during blocks 3-5, which exceeded both stop and reset predictions, and the PT shift on the gap trials, which tended to fall between stop and reset predictions, replicated PT shifts on concurrent task and gap trials in previous studies (Aum et al., 2004; Cabeza de Vaca et al., 1994).

To determine whether there was any effect of the reinforcer presented to the center-key pecks in the presence of the S+ cue on PT, response rate functions on reinforced S+ trials were compared to those on nonreinforced S+ trials. Figure 7 shows the group mean temporal pattern of performance on the FI key on the reinforced and nonreinforced S+ trials at early (top panels), middle (middle panels), and late (bottom panels) locations of the S+ cue in task/gap phase 1. The left and right panels represent

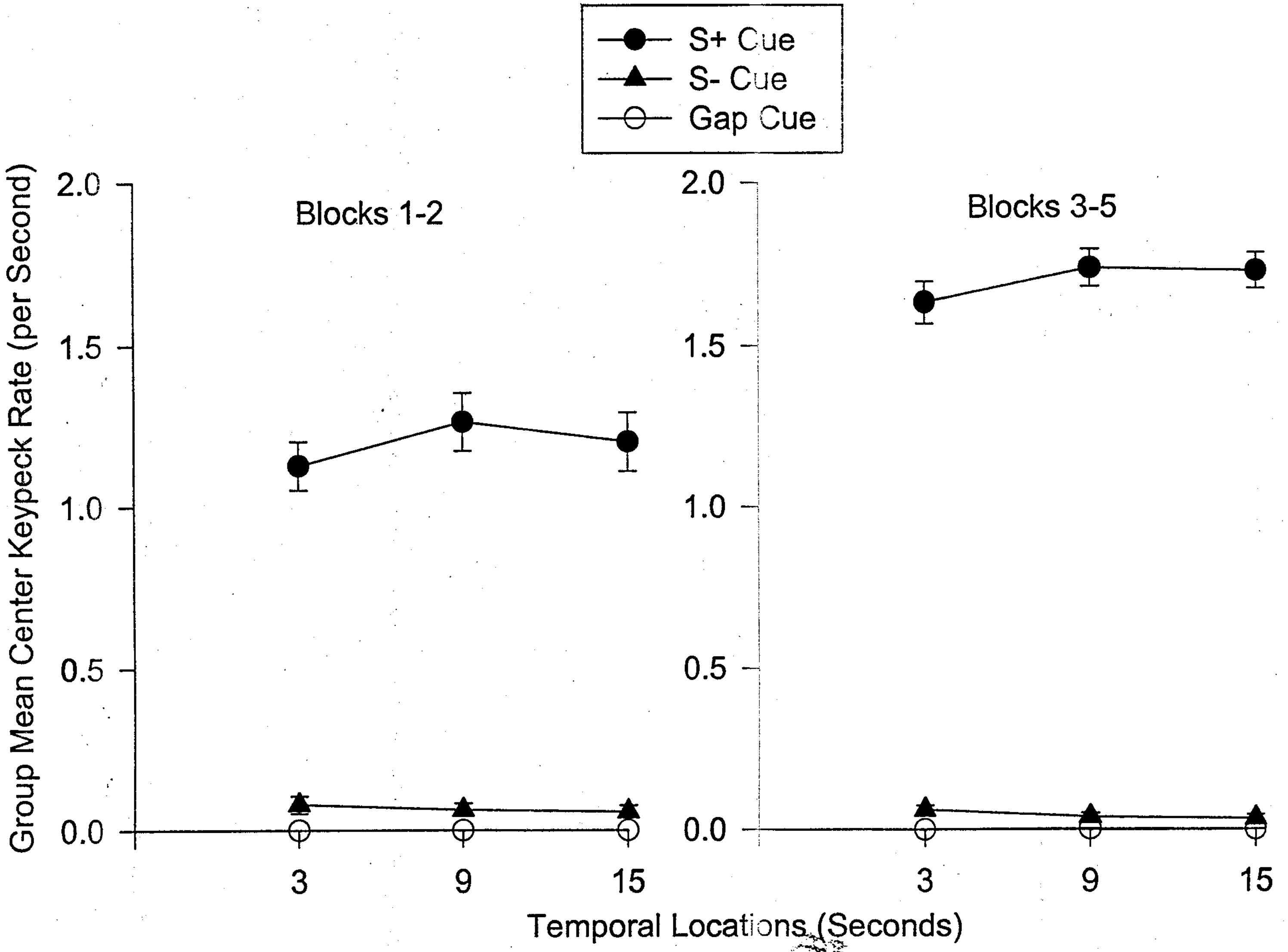
Figure 7. Group mean (n=8) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on reinforced and nonreinforced S+ trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase1. Data are shown separately for early (top), middle (middle), and late S+ trials (bottom).


Reinforced
Nonreinforced
Blocks 1-2
Blocks 3-5
Early
Middle
Late
Group Mean Responses per Second
Elapsed time (Second)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
20
40
60
80
100
120

birds' performance during session blocks 1-2 and 3-5, respectively. During both blocks 1-2 and 3-5, the reinforced and nonreinforced response rate functions at each temporal location of the S+ cue tended to overlap, implying that the reinforcer presented on the center key on the S+ trials did not affect PT.

Responding directed toward the center key. Compared to the center-key peck rate in the presence of the S+ cue during the discrimination training sessions in the previous phase (1.92 responses per second), center-key peck rate during blocks 1-5 in the task/gap phase 1 (1.57 responses per second) was significantly lower, *t*(7) = 3.68. Birds' discrimination performance between the S+ and S- cues was, however, maintained as in the previous phase. That is, animals tended to peck the center key only in the presence of the S+ cue. Figure 8 shows the group mean center-key peck rate (responses per second) during the presentation of the S+, S-, or gap event as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the task/gap phase 1. During both blocks 1-2 and 3-5, center-key peck rate was highest during the presentation of the S+ cue. Very low and near zero center-key peck rate occurred during the presentation of the S- cue and gap event, respectively. Accordingly, birds' DRs were very high in both blocks 1-2 (group mean DR=0.93) and 3-5 (group mean DR=0.97). In addition, center-key peck rate at all three locations of the S+ cue tended to increase across session blocks. A session block x trial type x location ANOVA applied to the center-key peck rate yielded significant effects of the trial type, *F*(2, 14) = 69.00, and session block x trial type interaction, *F*(2, 14) = 3.92. No other main or interaction effects were significant. A separate one-way ANOVA to test the session block effect for each trial type did not show

Figure 8. Group mean (n=8) center-key peck rate (responses per second) during the presentation of the S+, S-, and gap events as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the task/gap phase 1.

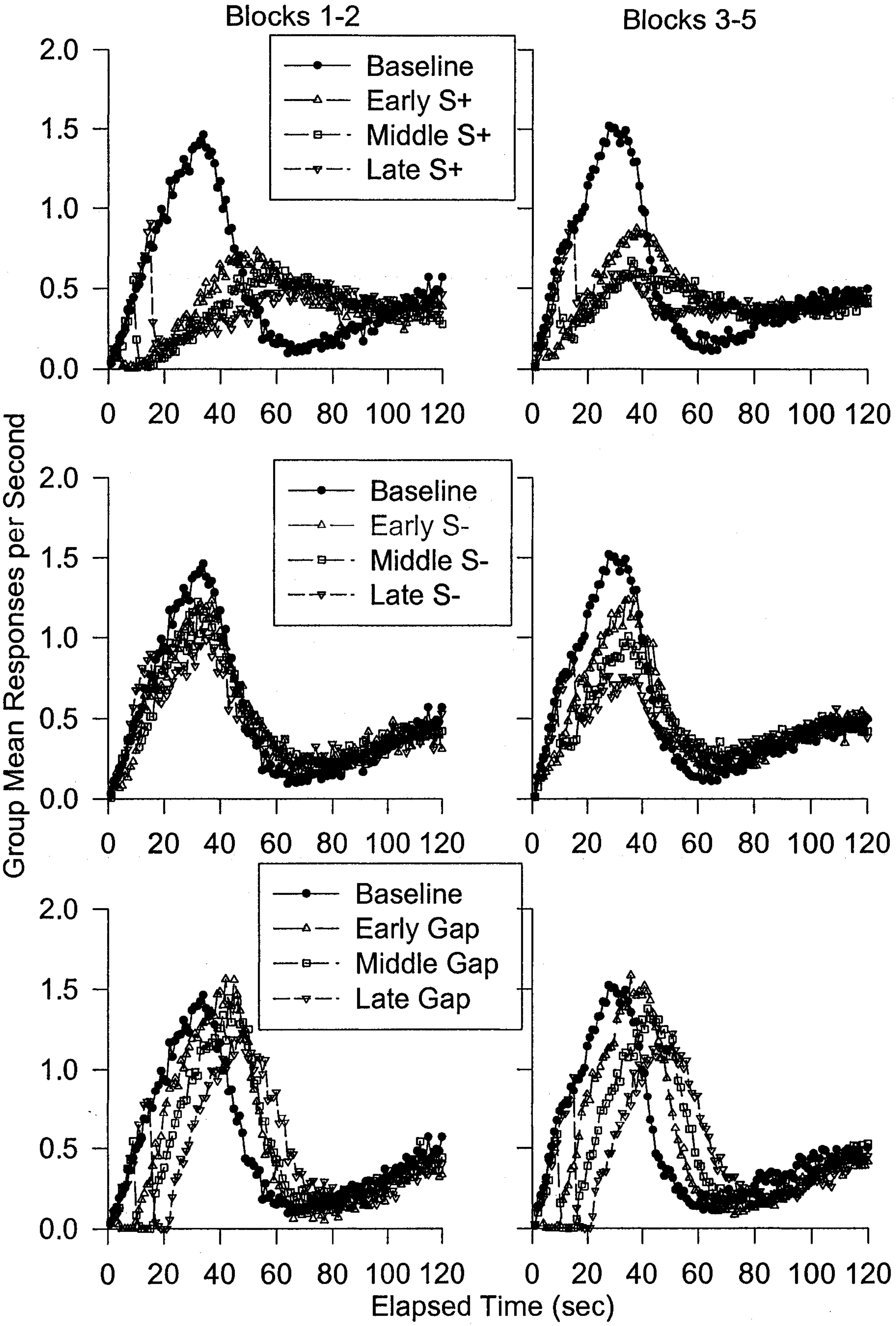

S+ Cue
S- Cue
Gap Cue
Blocks 1-2
Blocks 3-5
Group Mean Center Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
2.0
1.5
1.0
0.5
0.0
3
9
15
3
9
15
Temporal Locations (Seconds)

any significant session block effect for any trial type. A nonparametric test, however, revealed that 7 birds among 8 birds showed increases in the center-key peck rate across type effect for both blocks 1-2 and 3-5, *F*(2, 14) ≥ 22.04. The group mean center-key peck rates during the presentation of the S+ cue were 1.20 and 1.70 responses per second during blocks 1-2 and 3-5, respectively. While both group mean PT shift and center-key peck rate on the S+ trials increased over session blocks, these variables were not related across birds. That is, correlation of center-key peck rate change with PT shift change from session blocks 1-2 to 3-5 was not significant (r = -0.70, n=8).

Extinction Phase

Responding directed toward the FI key. If the reinforcement history of the concurrent task cue was critical in the obtained PT difference between S+ and S- trials during the task/gap phase 1, the extinction of the S+ cue might be expected to reduce the PT on the S+ trials. Figure 9 shows the group mean (n=6) temporal pattern of performance on the FI key on baseline probe trials and S+ (top panels), S- (middle panels), and gap (bottom panels) probe trials at each of the three temporal locations (early, middle, and late) of the task cue or gap event during session blocks 1-2 (left) and 3-5 (right) of the extinction phase (see Appendix C for individual bird's temporal pattern of performance in this phase). Birds' timing performance on the baseline probe trials was maintained as in the sessions of the task/gap phase 1. For the group mean response rate function on the baseline probe trials, the mode was centered around 30 s during both blocks 1-2 and 3-5. Compared to the baseline function, the response rate functions for the S+ and gap trials shifted to the right during both blocks 1-2 and 3-5. The degree of the shift was, however, reduced across session blocks for the S+ trials; a similar degree of

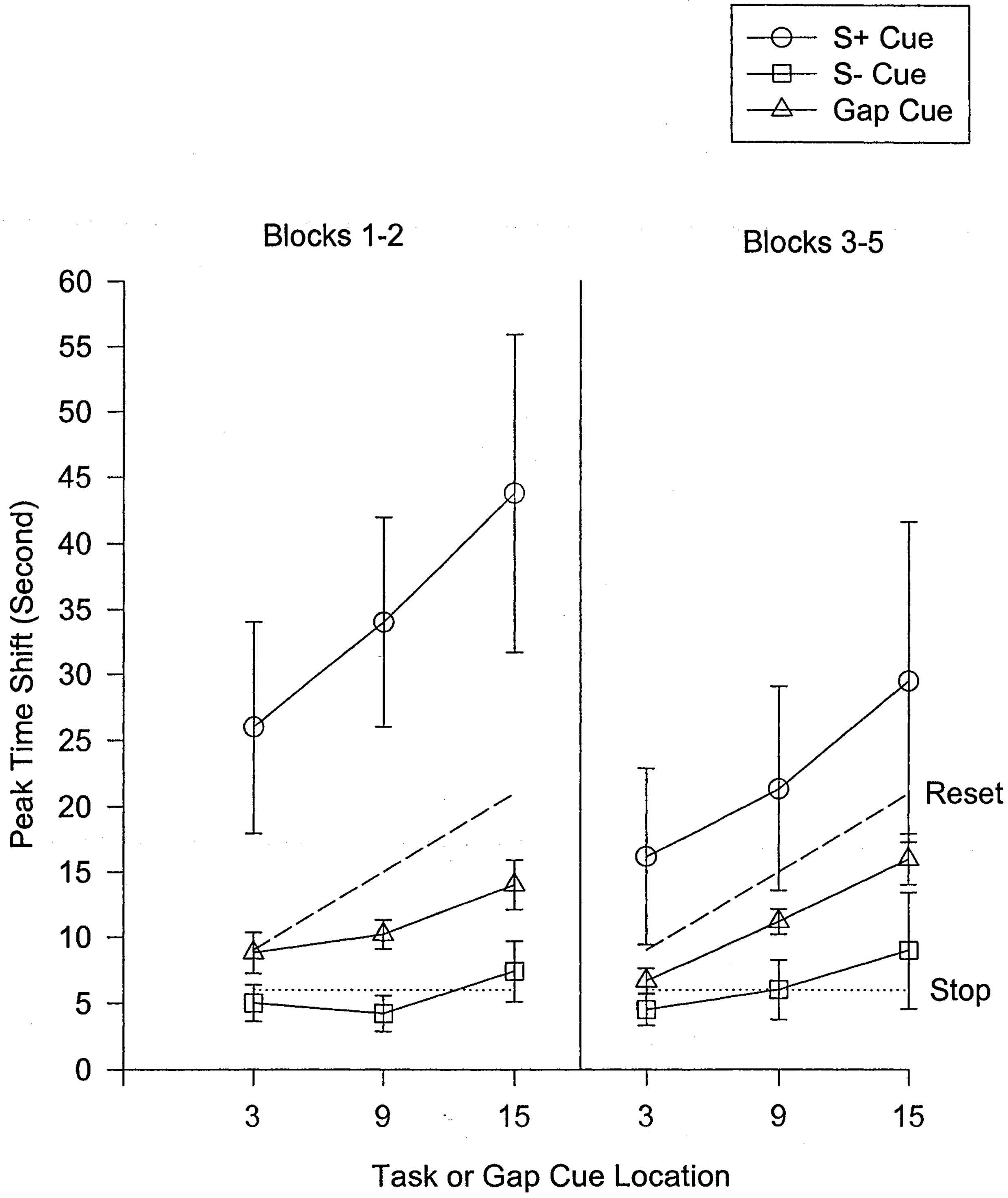
Figure 9. Group mean (n=6) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the extinction phase. Data are shown separately for early, middle, and late locations of the S+, S-, and gap events.


Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Early S-
Middle S-
Late S-
Early Gap
Middle Gap
Late Gap
Group Mean Responses per Second
2.0
1.5
1.0
0.5
0.0
0 20 40 60 80 100 120
Elapsed Time (sec)

the shift was observed across session blocks for the gap trials. For the S- trials, there were slight rightward shifts in the response rate functions from blocks 1-2 to 3-5. Figure 9 also suggests differences in peak rates among probe trial types. In general, peak rate on S+ trials was lower than peak rates on baseline, S-, and gap trials (see Appendix H for quantitative analysis of peak rate).

Figure 10 shows the obtained group mean PT shift (±SEM) at each task cue or gap event location on S+, S-, and gap trials during session blocks 1-2 and 3-5 of the extinction phase (see Appendix G for each individual bird's PT on baseline, S+, S-, and gap trials in this phase). The broken lines represent the predicted PT shift based on the stop or reset mode of clock switch. For the S+ trials, during blocks 1-2, PT shift at all three locations of the S+ cue was greater than 0, $ts(5) \geq 3.55$. However, during blocks 3-5, only the PT shift at the middle location of the S+ cue was greater than 0, $ts(5) = 2.75$. For the S- trials, during blocks 1-2, only the PT shift at the early location of the S- cue was greater than 0, $t(5) = 2.98$. During blocks 3-5, PT shift at the early and middle locations of the S- cue was greater than 0, $ts(5) \geq 2.67$. For the gap trials, during both blocks 1-2 and 3-5, PT shift at all three locations of the gap event was greater than 0, $ts(5) \geq 5.74$. During blocks 1-2, the PT shift on the S+ trials was greater than that on the S- and gap trials. However, as the extinction sessions continued, PT shift on the S+ trials tended to decrease; stable PT shifts were obtained on the S- and gap trials. Accordingly, during blocks 3-5, PT shift on the S+ trials was not significantly different from that either on the S- or gap trials. A session block x trial type x location ANOVA of PT shift yielded significant main effects of trial type ($F(2, 10) = 7.15$), location ($F(2, 10) = 6.61$),

Figure 10. Group mean (n=6) peak-time shift (± SEM) as a function of the location of S+, S-, and gap events during session blocks 1-2 and 3-5 of the extinction phase. Dotted and dashed lines refer to stop and reset predictions, respectively.

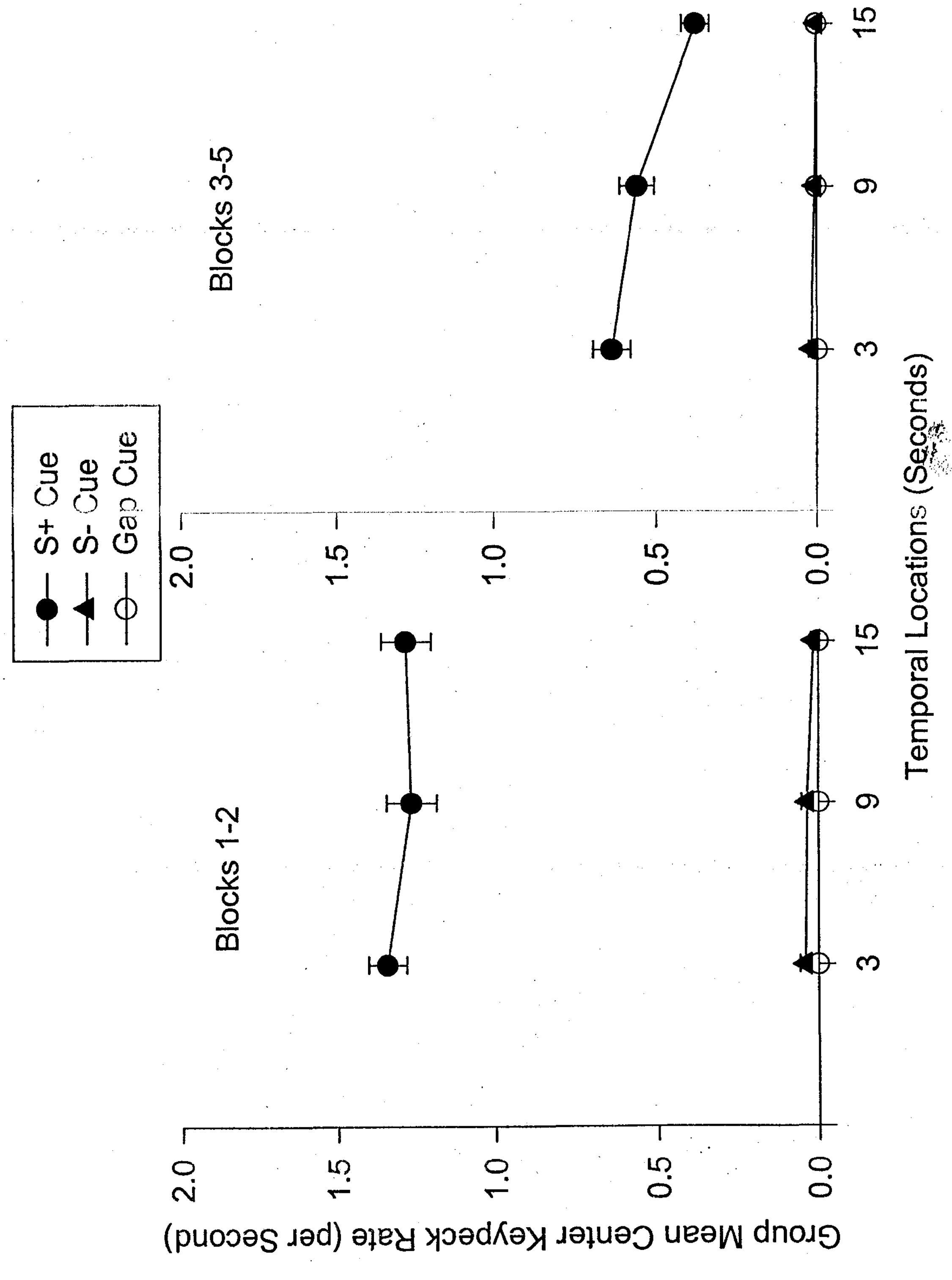

S+ Cue
S- Cue
Gap Cue
Blocks 1-2
Blocks 3-5
Peak Time Shift (Second)
60
55
50
45
40
35
30
25
20
15
10
5
0
3
9
15
3
9
15
Reset
Stop
Task or Gap Cue Location

and session block x trial type interaction, $F(2, 10) = 8.05$. Other main and interaction effects were not significant. When the trial type effect was analyzed separately for blocks 1-2 and 3-5, it was significant only for blocks 1-2, $F(2, 10) = 13.12$. Subsequent tests indicated that PT shift on the S+ trials was greater than PT shifts on both S- and gap trials during blocks 1-2. When the session block effect was analyzed separately for each trial type, PT shift did not differ significantly between blocks 1-2 and 3-5 for any of the three trial types. A nonparametric test, however, revealed that all 6 birds showed decreased PT shift on early and middle S+ trials across session blocks (sign test, $p = .02$). The decrease in the PT shift on the S+ trials over session blocks and the reduction in the difference of the PT shift magnitude between S+ and S- trials in the later session blocks were consistent with the prediction based on the critical role of reinforcement in the effect of the concurrent task cue on timing.

During blocks 1-2, PT shift on the S+ trials was greater than the stop prediction ($ts(5) \geq 2.67$), but not significantly different from the reset prediction at all three locations of the S+ cue. Peak time shift on the S- trials was not significantly different from the stop prediction, but was lower than the reset predictions at all three locations of the S- cue, $ts(5) \geq 3.45$. Peak time shift on the gap trials was greater than the stop prediction ($ts(5) \geq 4.69$), but was lower than the reset prediction at the middle and late locations of the gap event, $ts(5) \geq 2.98$. During blocks 3-5, PT shift on the S+ trials was not significantly different from either stop or reset prediction at all three locations of the S+ cue. Peak time shift on the S- trials was not significantly different from the stop prediction, but was lower than the reset prediction at all three locations of the S- cue, $ts(5) \geq 2.71$. Peak time shift on gap trials was greater than the stop prediction only at the middle and late gap locations (*t*s(5) ≥ 5.09), and was lower than the reset prediction only at the middle location (*t*(5) = 4.05). The fact that the PT shift on S+ trials in the later blocks did not differ significantly from stop prediction suggests that extinction of the concurrent task cue decreased its disruptive effect on timing.

Responding directed toward the center key. The extinction schedule on the center key during the presentation of the S+ cue had a clear effect on the center-key peck rate. Figure 11 shows the group mean center-key peck rate (responses per second) during the presentation of the S+, S-, or gap event as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the extinction phase. During both blocks 1-2 and 3-5, center-key peck rate was highest during the presentation of the S+ cue. Very low and near zero center-key peck rate occurred during the presentation of the S- cue and gap event, respectively. Accordingly, birds' DRs were very high in both blocks 1-2 (group mean DR = 0.98) and 3-5 (group mean DR = 0.88). However, center-key peck rate at all three locations of the S+ cue decreased across session blocks. Interestingly, during blocks 3-5, center-key peck rate on the S+ trials decreased as a function of the temporal location of the S+ cue. A session block x trial type x location ANOVA applied to the center-key peck rate yielded significant trial type (*F*(2, 10) = 55.85), and session block (*F*(1, 5) = 72.44) main effects. Session block x trial type (*F*(2, 10) = 97.51), session block x location (*F*(2, 10) = 5.98), and session block x trial type x location (*F*(4, 20) = 5.10) interactions were also significant. No other main or interaction effect was significant. When the block effect was analyzed separately for each trial type (S+, S-, or gap trial type), it was significant only for the S+ trial type, indicating decreased center-key peck rate across the extinction session blocks on S+ trials. The three-way interaction

Figure 11. Group mean (n=8) center-key peck rate (responses per second) during the presentation of the S+, S-, and gap events as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the extinction phase.


Blocks 1-2
Blocks 3-5
S+ Cue
S- Cue
Gap Cue
Group Mean Center Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
2.0
1.5
1.0
0.5
0.0
3
9
15
3
9
15
Temporal Locations (Seconds)

indicated that there was a location x block interaction only for the S+ trials (*F*(2, 10) = 6.02), not for the S- and gap trials . When the location effect on S+ trials was analyzed separately for blocks 1-2 and 3-5, there was a significant location effect only for blocks 3-5, *F*(2, 10) = 5.45. Subsequent tests indicated that during blocks 3-5 center-key peck rates at the early and middle locations of the S+ cue were greater than that at the late location of the S+ cue. The group mean center-key peck rates during the presentation of the S+ cue were 1.29 and 0.52 responses per second during blocks 1-2 and 3-5, respectively. While both group mean PT shift and center-key peck rate decreased over session blocks on the S+ trials, these variables were not related across birds. That is, correlation of center-key peck rate change with PT shift change from session blocks 1-2 to 3-5 was not significant ($r = 0.35$, n=6).

Alternated PI and Discrimination Training Phase 2

To recover the extinguished center-key pecks on the S+ trials prior to return to the task/gap phase, animals were again exposed to the alternated PI and discrimination training phase. Figure 12 shows the group mean temporal pattern of performance on the probe trials during the last 10 PI sessions (sessions 2-11) in the alternated PI and discrimination training phase 2. (see Appendix D for individual bird's temporal pattern of performance in this phase). The group function was unimodal and the mode was centered around 30 s. Individual birds' PTs on the probe trials were 35.5, 29.5, 24.5, 33.5, 34.5, 22.5, 26.5, 27.5, and 32.5 s for birds 1 to 9, respectively. Group mean PT, 29.6 s, was not significantly different from the programmed FI value, 30 s, ($t(8) = 0.25, p = .81$).

Figure 12. Group mean (n=9) FI-key peck rate (responses per second) as a function of elapsed probe-trial time during the last 10 PI sessions of the alternated PI and discrimination training phase 2.

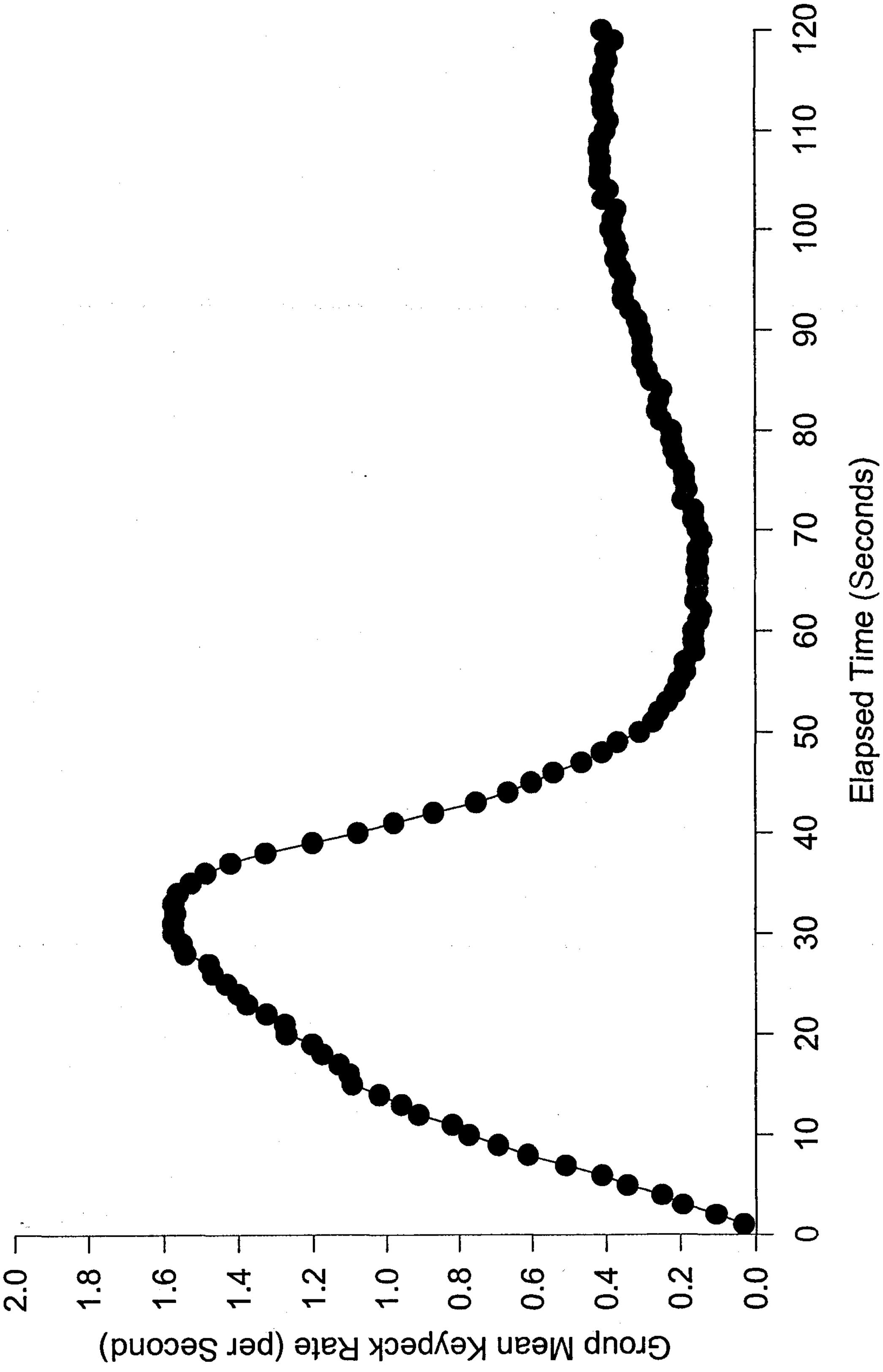
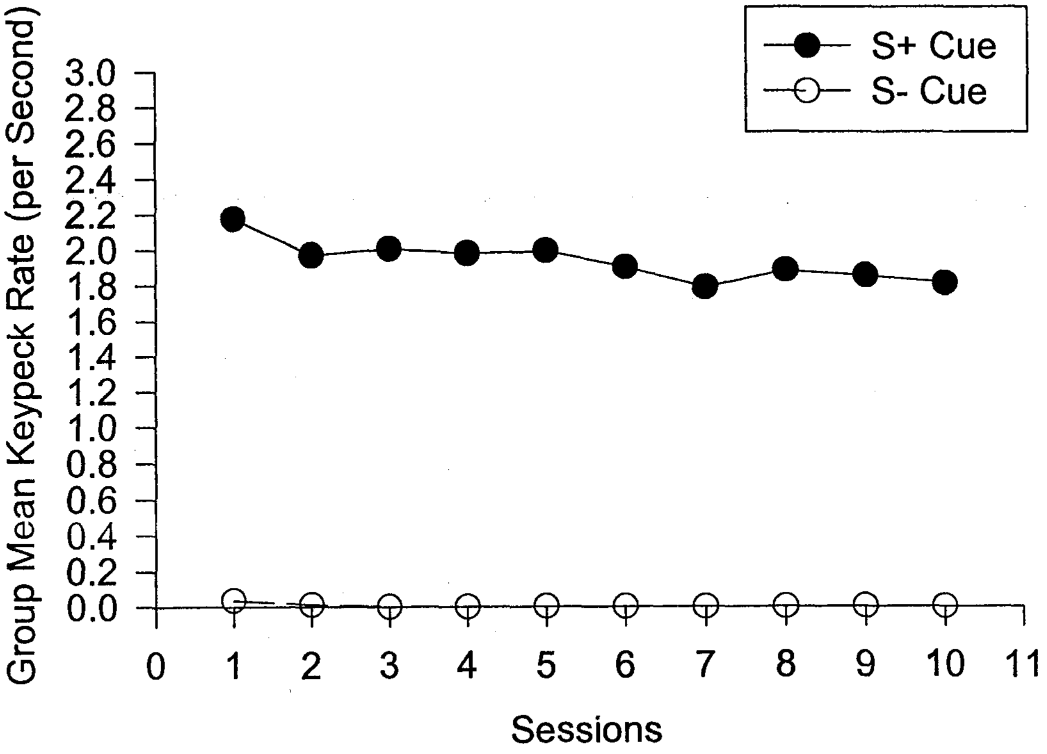

Group Mean Keypeck Rate (per Second)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Elapsed Time (Seconds)
0
10
20
30
40
50
60
70
80
90
100
110
120

Figure 13 shows the group mean center-key peck rate (responses per second) in the presence of S+ and S- cues (top panel) and the group mean discrimination ratio (bottom panel) during the 10 discrimination training sessions in the alternated PI and discrimination training phase 2. In all discrimination training sessions, most center-key pecks occurred on S+ trials and almost no responding occurred on S- trials. Accordingly, group mean DRs in all sessions were either close to or equal to 1 (group mean rage: 0.98 - 1.00). The overall group mean center-key peck rates on S+ and S- trials over the 10 discirmination training sessions were 1.94 and 0.01 responses per second, respectively, and the overall group mean DR was 1.

Task/gap phase 2

Responding directed toward the FI key. Figure 14 presents the group mean (n=5) temporal pattern of performance on the FI key on baseline probe trials and S+ (top panels), S- (middle panels), and gap (bottom panels) probe trials at each of the three temporal locations (early, middle, and late) of the task cue or gap event during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase 2 (see Appendix E for individual bird's temporal pattern of performance in this phase). Birds' timing performance on the baseline probe trials was maintained as in the previous task/gap phase 1. For the group mean response rate function on the baseline probe trials the mode was centered around 30 s during both blocks 1-2 and 3-5. Compared to the baseline function, the response rate functions for the S+ and gap trials shifted to the right. The response rate functions for the S- trials shifted to the right only slightly. During both blocks 1-2 and 3-5, the degree of the shift on the S+ trials was greater than the shifts on the S- and gap trials. In addition, the degree of the shift on the S+ trials was greater in the later blocks (3-5) than in the

Figure 13. Group mean (n=9) center-key peck rate (responses per second) (top) and discrimination ratio (bottom) during discrimination training sessions of the alternated PI and discrimination training phase 2.


S+ Cue
S- Cue
Group Mean Keypeck Rate (per Second)
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
6
7
8
9
10
11
Sessions

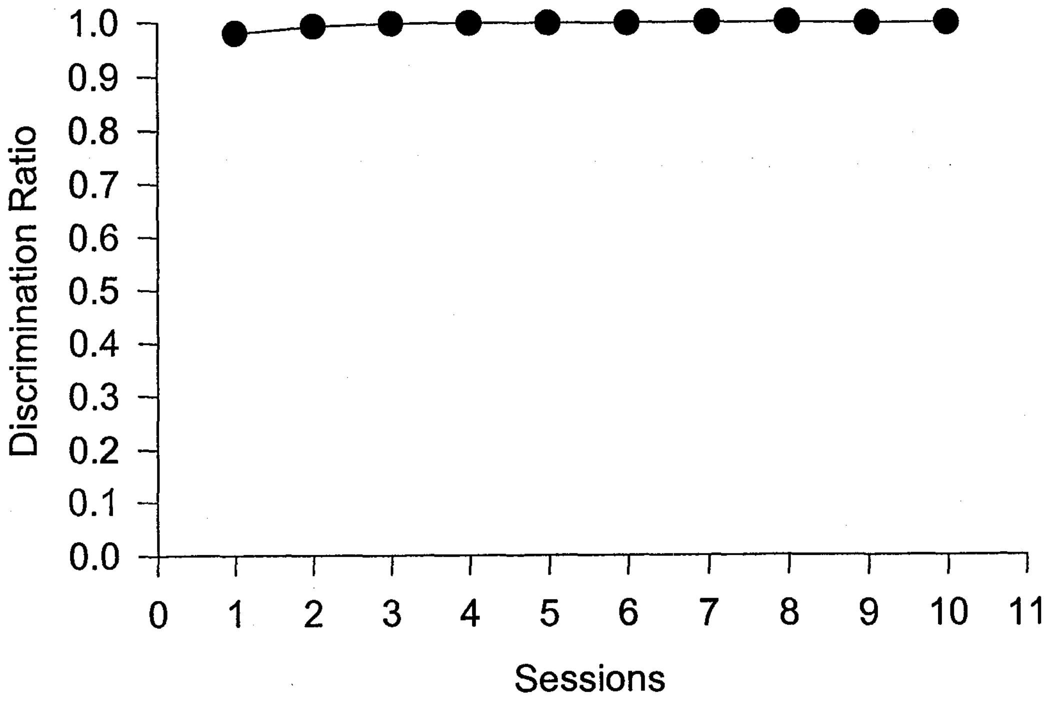
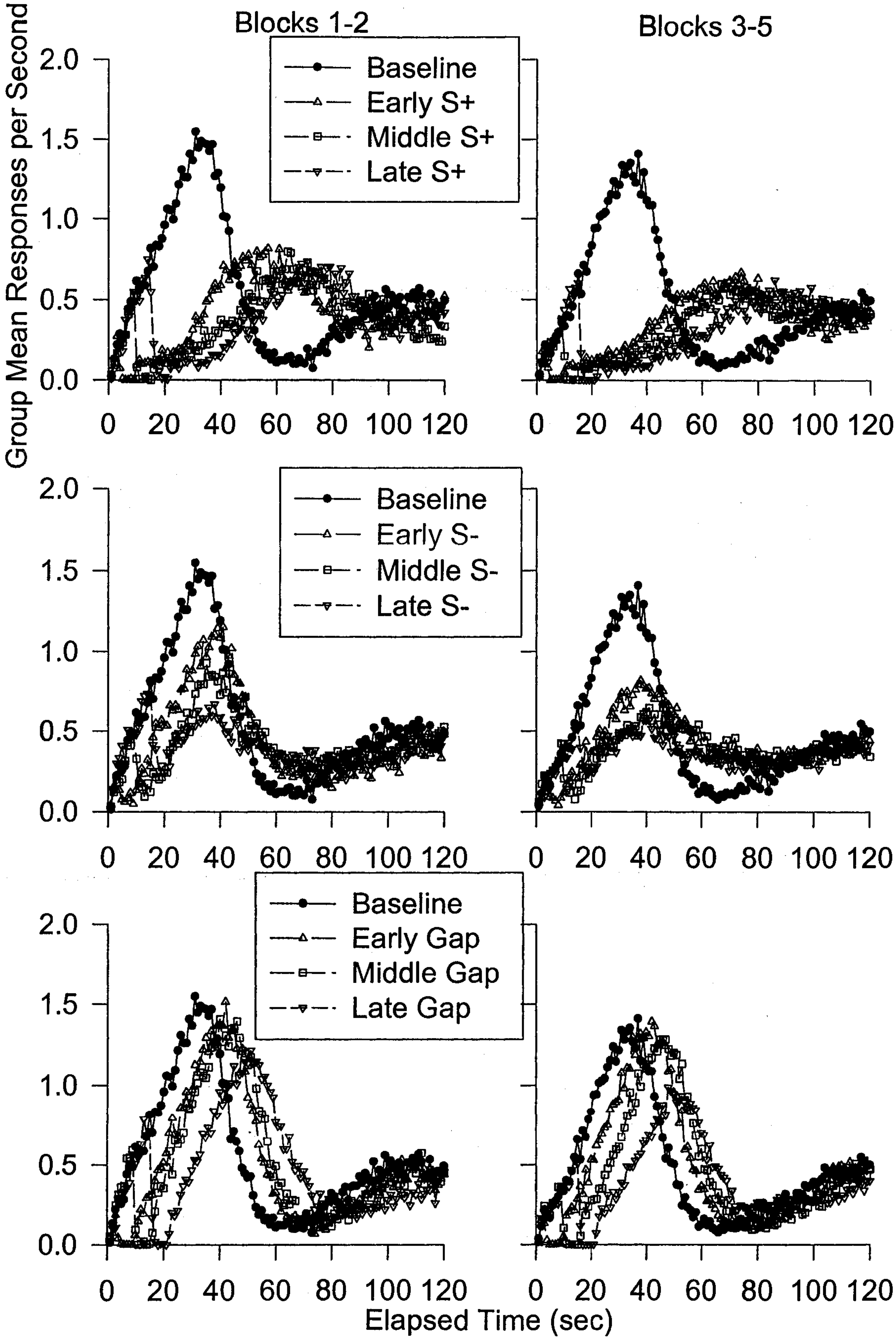

Discrimination Ratio
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
6
7
8
9
10
11
Sessions

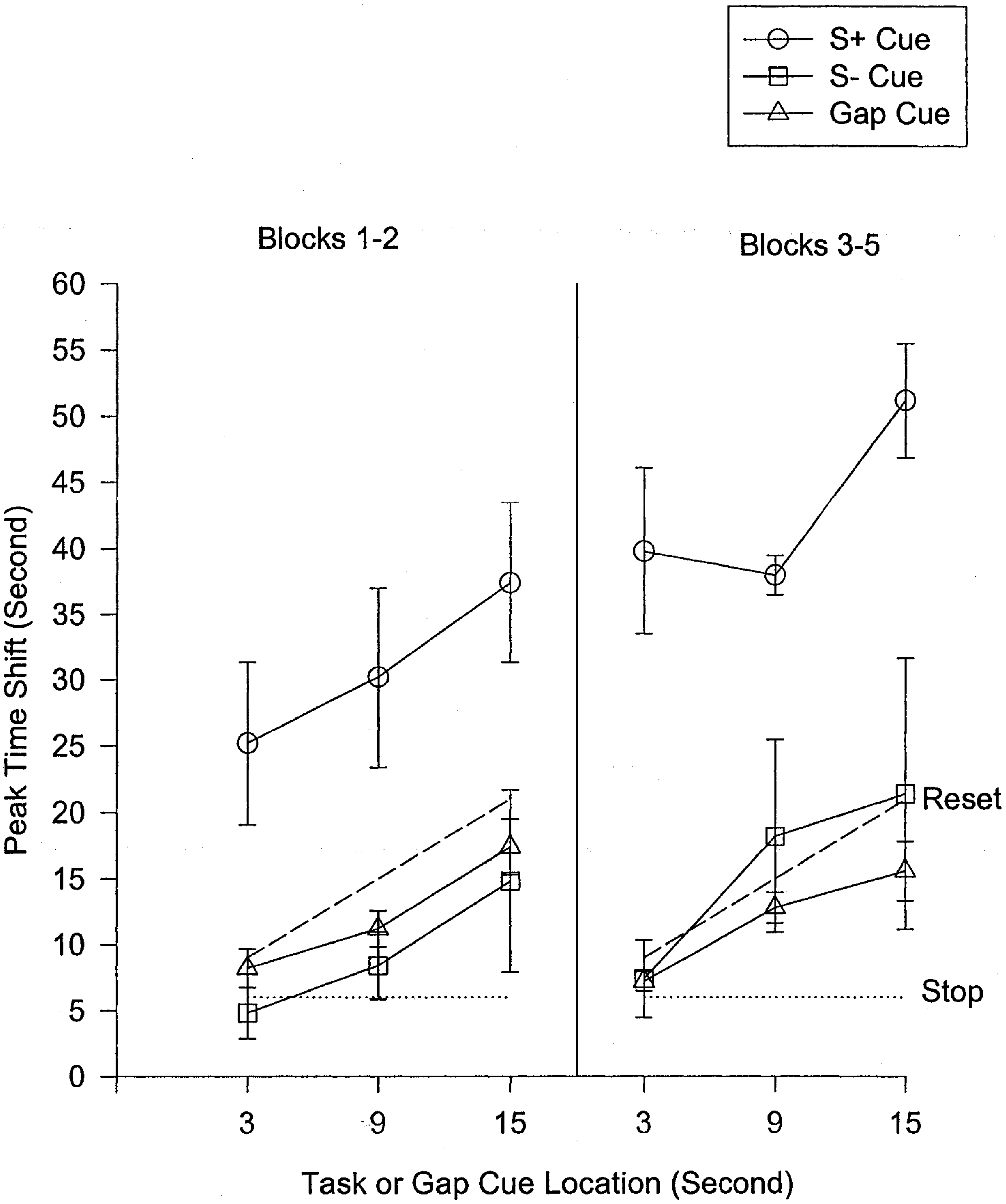
Figure 14. Group mean (n=5) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase 2. Data are shown separately for early, middle, and late locations of the S+, S-, and gap events.


Blocks 1-2
Blocks 3-5
Group Mean Responses per Second
2.0
1.5
1.0
0.5
0.0
Baseline
Early S+
Middle S+
Late S+
Early S-
Middle S-
Late S-
Early Gap
Middle Gap
Late Gap
0 20 40 60 80 100 120
Elapsed Time (sec)

earlier blocks (1-2); the degree of the shift on the S- and gap trials was similar across session blocks. During both blocks 1-2 and 3-5, the degree of the shift on the S+ and gap trials tended to increase as a function of the temporal location of the S+ cue and gap event; no differential shift was observed across temporal locations of the S- cue on the S- trials. Figure 14 also suggests differences in peak rates among probe trial types. In general, peak rates on S+ and S- trials were lower than peak rate on baseline probe trials (see Appendix H for quantitative analysis of peak rate).

Figure 15 shows the obtained group mean PT shift (±SEM) at each task cue or gap event location on S+, S-, and gap trials during session blocks 1-2 and 3-5 of this phase (see Appendix G for each individual bird's PT on baseline, S+, S-, and gap trials in this phase). The broken lines represent the predicted PT shift based on the stop and reset mode of the clock switch. At all three locations of the S+ cue and gap event PT shift was greater than 0 during both blocks 1-2 and 3-5 ($ts(4) \geq 4.12$). At all three locations of the S- cue, PT shift during both blocks 1-2 and 3-5 was not significantly different from 0, except for the PT shift at the middle location of the S- cue during blocks 1-2 which was greater than 0. The PT shift on the S+ trials was greater than PT shifts on the S- and gap trials during both blocks 1-2 and 3-5. In addition, during both blocks 1-2 and 3-5 PT shifts on S+ and gap trials tended to increase as a function of the temporal location of the S+ cue and gap event. Peak time shift on the S+ trials increased over session blocks; stable PT shifts were obtained over session blocks on the gap and S- trials. A session block x trial type x location ANOVA of PT shift yielded significant effects of trial type, $F(2, 8) = 12.28$, and location, $F(2, 8) = 13.44$, and session block x trial type interaction, $F(2, 8) = 7.16$. The trial type x location interaction was not significant, ($F(4, 16) = 0.49$,

Figure 15. Group mean (n=5) peak-time shift (± SEM) as a function of the location of S+, S-, and gap events during sessions blocks 1-2 and 3-5 of the task/gap phase 2. Dotted and dashed lines refer to stop and reset predictions, respectively.


S+ Cue
S- Cue
Gap Cue
Blocks 1-2
Blocks 3-5
Peak Time Shift (Second)
60
55
50
45
40
35
30
25
20
15
10
5
0
Reset
Stop
3
9
15
3
9
15
Task or Gap Cue Location (Second)

$p = .74$), nor were other main and interaction effects significant. When the trial type effect was analyzed separately for blocks 1-2 and 3-5, it was significant during both blocks 1-2 ($F(2, 8) = 8.15$) and 3-5 ($F(2, 8) = 15.21$). Subsequent tests indicated that the PT shift on the S+ trials was greater than the PT shifts on the S- and gap trials during both blocks 1-2 and 3-5. When the session block effect was analyzed separately for each trial type, PT shift during blocks 3-5 was greater than that during blocks 1-2 for the S+ trials ($F(1, 4) = 12.48$). In contrast, peak time shifts were not significantly different between blocks for the S- and gap trials. The greater PT shift on the S+ trials than on the S- trials in this phase was consistent with the predicted PT shift when the role of reinforcement history is assumed to be critical in relation to the effect of the concurrent task cue.

During blocks 1-2, PT shift on the S+ trials was greater than the stop prediction at all three locations of the S+ cue ($ts(4) \geq 3.14$), but were not significantly different from the reset prediction. Peak time shift on the S- trials was not significantly different from either the stop or reset prediction at all three locations of the S- cue. Peak time shift on the gap trials was greater than the stop prediction at the middle and late locations of the gap event ($ts(4) \geq 3.83$), but was lower than the reset prediction only at the middle location of the gap event ($t(4) = 2,80$). During blocks 3-5, PT shift on the S+ trials was greater than both stop and reset predictions at all three locations of the S+ cue ($ts(4) \geq 4.90$). Peak time shift on the S- trials was again not significantly different from either the stop or reset prediction at all three locations of the S- cue. Peak time shift on the gap trials was greater than the stop prediction at the middle and late locations of the gap event ($ts(4) \geq 4.27$), but was not significantly different from the reset prediction at all three locations. The PT shift on the S+ trials that was greater than the reset prediction during blocks 3-5 in this phase again replicated the PT shift previously observed on concurrent task trials (Aum et al., 2004), and showed the effect of the present manipulation-reinforcement history of the concurrent task cue.

As in the previous task/gap phase 1, the degree of the shift in the response rate functions between reinforced and nonreinforced S+ trials was similar in the task/gap phase 2. Figure 16 shows the group mean temporal pattern of performance on the FI key on the reinforced and nonreinforced S+ trials at early (top panels), middle (middle panels), and late (bottom panels) locations of the S+ cue in task/gap phase 2. The left and right panels represent birds' performance during session blocks 1-2 and 3-5, respectively. During both blocks 1-2 and 3-5, the reinforced and nonreinforced response rate functions at each temporal location of the S+ cue tended to overlap, implying that the reinforcer presented on the center key on the S+ trials did not affect PT.

Responding directed toward the center key. Figure 17 shows the group mean center-key peck rate (responses per second) during the presentation of the S+, S-, or gap event as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the task/gap phase 2. During both blocks 1-2 and 3-5 center-key peck rate was highest during the presentation of the S+ cue. Very low and near zero center-key peck rate occurred during the presentation of the S- cue and gap event, respectively. Accordingly, birds' DRs were very high in both blocks 1-2 (group mean DR = 0.97) and 3-5 (group mean DR = 0.97). A session block x trial type x location ANOVA applied to the center-key peck rate yielded a significant trial type main effect, *F*(2, 8) = 44.11. No

Figure 16. Group mean (n=5) FI-key peck rate (responses per second) as a function of elapsed probe-trial time on reinforced and nonreinforced S+ trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase2. Data are shown separately for early (top), middle (middle), and late S+ trials (bottom).

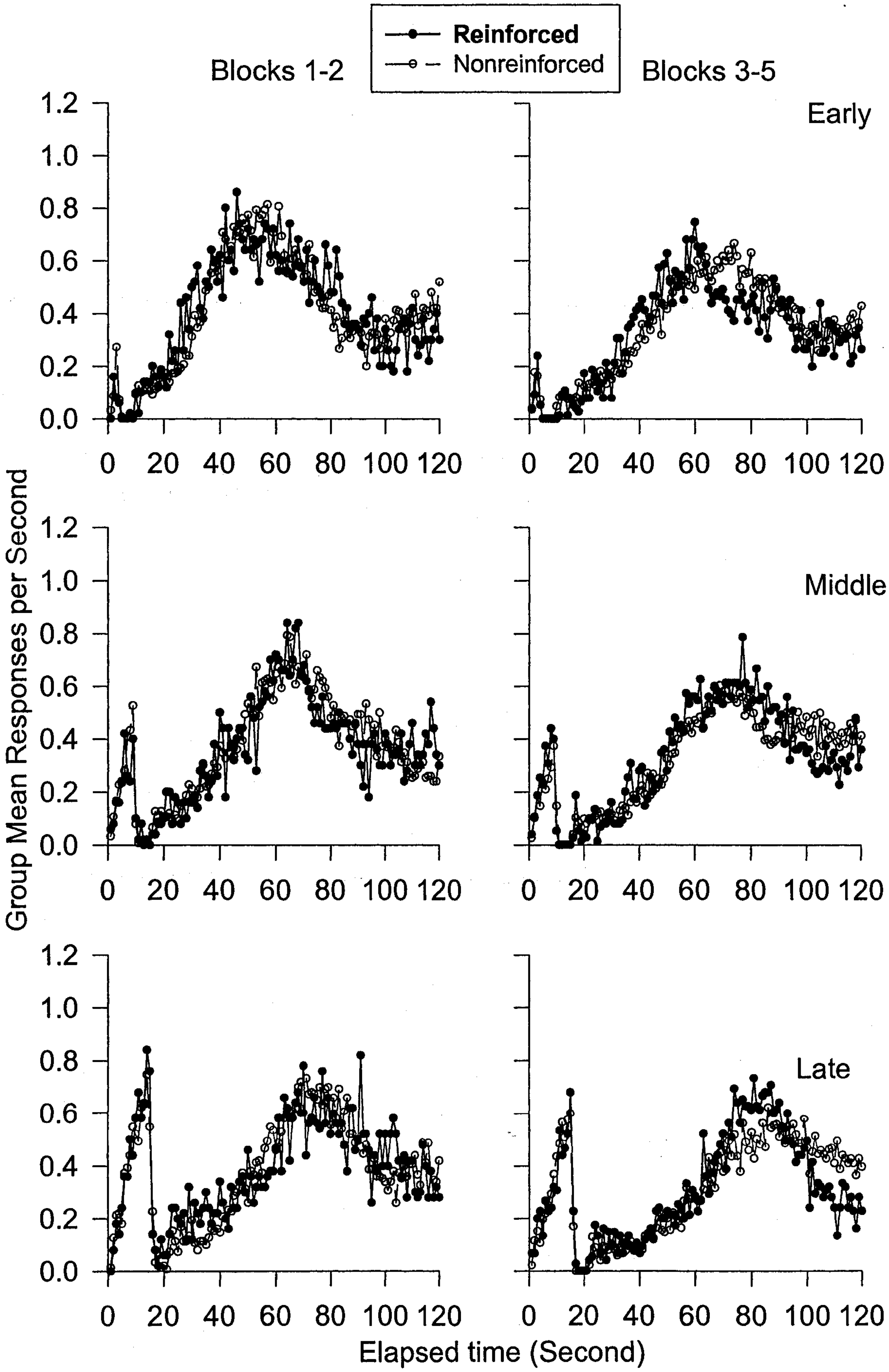
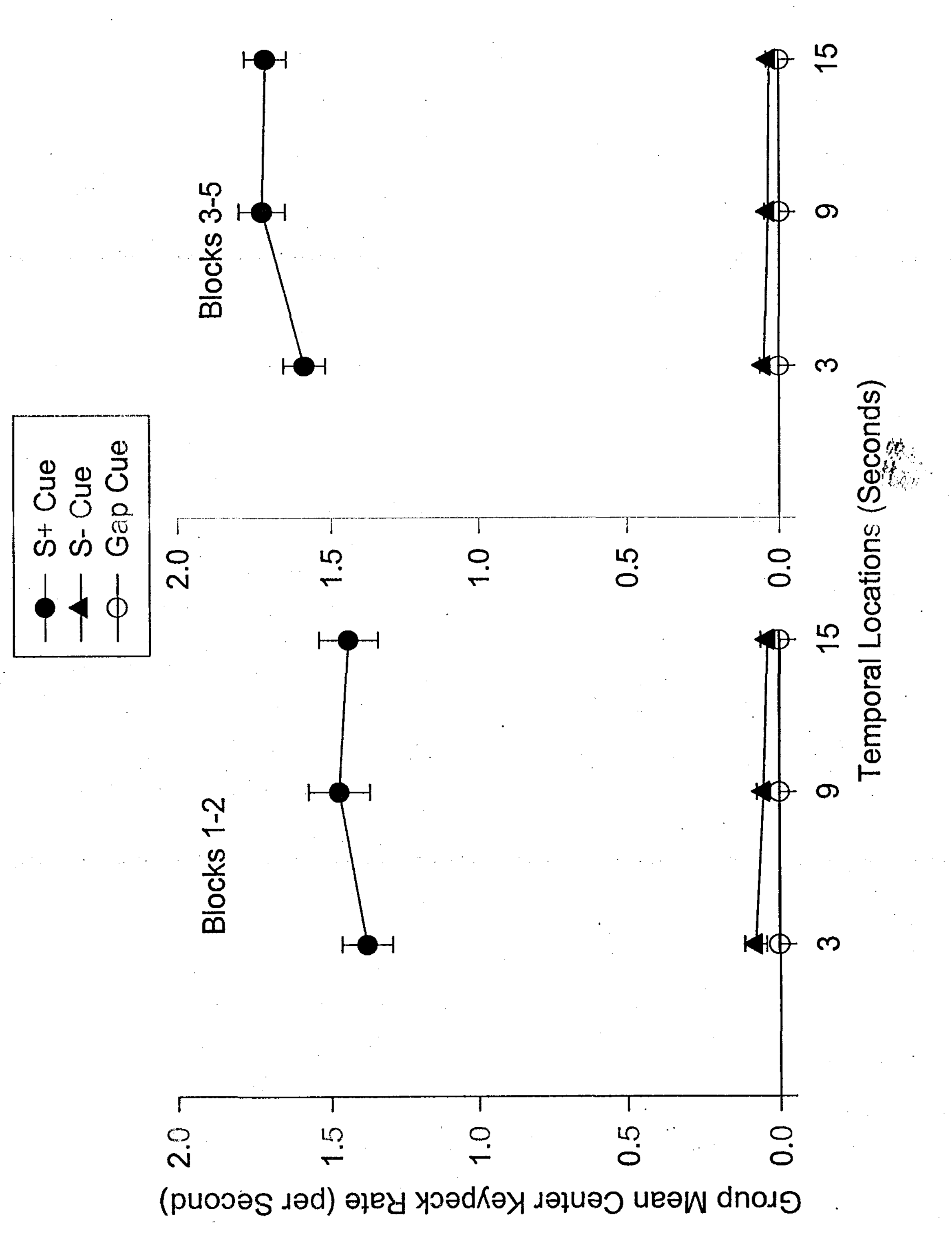

Reinforced
Nonreinforced
Blocks 1-2
Blocks 3-5
Early
Middle
Late
Group Mean Responses per Second
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
Elapsed time (Second)

Figure 17. Group mean (n=8) center-key peck rate (responses per second) during the presentation of the S+, S-, and gap events as a function of the temporal location of the event during session blocks 1-2 and 3-5 of the task/gap phase2.


Blocks 1-2
Blocks 3-5
S+ Cue
S- Cue
Gap Cue
Group Mean Center Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
3
9
15
Temporal Locations (Seconds)

other main or interaction effects were significant. The group mean center-key peck rates during the presentation of the S+ cue were 1.53 and 1.68 responses per second during blocks 1-2 and 3-5, respectively. The correlation of center-key peck rate change with PT shift change from session blocks 1-2 to 3-5 was not significant (r = -0.30, n=5).

Discussion

The results of the present experiment on the effect of the gap and concurrent task cue on animals' timing were consistent with the results of previous studies. First, under the PI procedure, the brief termination of the timing cue (gap) on probe trials resulted in a rightward shift of animals' temporal pattern of responding to the timing cue compared to that on baseline probe trials in which no gap occurred (PT shift). Specifically, the PT shift on the gap trials was greater than the stop prediction but less than the reset prediction (Cabeza de Vaca et al., 1994; Roberts, 1981). Second, under the PI procedure, presentation of the concurrent task cue (S+), which was highly correlated with reinforcement, also resulted in a rightward shift of animals' temporal pattern of responding to the timing cue compared to that on baseline probe trials. The PT shift on the S+ trials tended to be greater than the reset prediction (Aum et al., 2004). Third, the PT shift increased as a function of the temporal location of the gap event and S+ cue.

The main purpose of the present experiment was to identify the variable that is responsible for the difference in PT shift between gap and S+ concurrent task probe trials. For that purpose, reinforcement history was manipulated for the two cues--S+ and S- cues--while the stimulus property was controlled by balancing the color of the S+ and S- cues across birds. For both S+ and S- cues, PT shifts were observed. However, the PT shift was much greater on the S+ trials compared to that on the S- trials. Furthermore, when reinforcers were no longer available for responding to the center key on the S+ trials (extinction phase), the PT shift on the S+ trials tended to decrease across extinction sessions. In addition, the PT shift on the S- trials tended to be lower than the stop prediction, whereas the PT shift on the gap trials was greater than the stop prediction in the present experiment (see Figure 5 for the comparison in PT shift between S- and gap trials). If the difference in the PTs between the S+ and gap trials in Aum et al. (2004) was due only to differences in stimulus properties (e.g., stimulus salience), PT shift on the S- trials would exceed that on the gap trials in the present experiment as PT shift on the S+ trials does. In that sense, the results of the PT shift on the S- and gap trials in the present study refute the stimulus property explanation and provide converging evidence for a reinforcement history effect. That is, reinforcement history imposed on the concurrent task cue is critical in producing the observed substantial PT shift on the S+ trials.

Reinforcement history with respect to intruded stimulus events also appeared to affect response rate on the timing cue. Peak rate at each location of the S+ cue was lower than that on the S- and gap cue (Appendix H), implying that the S+ cue was a more salient discriminative signal of nonreinforcement on the FI key than was the S- cue. As the role of color was balanced across S+ and S- cues, the difference in salience is attributable to the functional properties of these cues rather than to their physical properties.

The PT shift on S+ trials that exceeded the reset prediction in the present study could not be explained by the memory decay account, which has been used to explain the effect of a gap on animal timing performance (Cabeza de Vaca et al., 1994). In that account, the maximum PT shift on concurrent task trials occurs when memory of the pretask cue period decays completely, and the clock stops during the cue period. Accordingly, the maximum possible PT shift on concurrent task trials would be equal to the duration of the pretask cue period plus the task cue duration, which is consistent with the reset prediction. The fact that the PT shift on S+ trials in the present experiment exceeded the reset prediction is not consistent with the memory decay account.

In explaining the interference effect of a concurrent task on human timing, an attentional competition account has been prevalent (e.g., Brown, 1997; Zakay, 1989). Sutton and Roberts (2002) used an attentional competition (divided attention) account for the disruption in their pigeons' timing in the presence of a coextensive concurrent task (e.g., pattern matching, spatial discrimination). According to that account, the concurrent task competes with the timing task for limited attentional resources. Disruption in timing occurs mainly during the presentation of the concurrent task cue, that is, it is an intracue effect. If this sort of inference is applied to the present procedure, the predicted PT shift on the concurrent task cue trials would be the same as the stop prediction. Therefore, the PT shift on the S+ trials in the present experiment is not consistent with the attentional competition account.

Compared to the attentional competition account, the expectancy account of the concurrent task effect states that attentional competition between the timing and concurrent tasks can occur before the presentation of the concurrent task. That is, once the task cue trials are introduced in the task/gap phase, attention during the timing cue is diverted between timing and expectation of the task cue. That expectancy retards accumulation of subjective time throughout the pretask cue time period, resulting in underestimated duration (Lejeune et al., 1999). In the expectancy account, the greatest PT shift on the concurrent task cue trials is predicted when no subjective time has been accumulated before the concurrent task cue and animals stop timing during the concurrent task cue presentation, consistent with the reset prediction. In addition, the expectancy effect should also appear on the baseline probe trials once the task cue has been introduced in the task/gap phase. Accordingly, compared to the PTs on the probe trials in the previous PI sessions, PTs on the baseline probe trials in the task/gap phase sessions are predicted to occur later, at least during the initial sessions of that phase. Indeed, the expectancy effect during that phase would be greatest when the task cue is omitted, as on baseline probe trials. Accordingly, latest PTs would be predicted on the baseline probe trials compared to the PTs on the task and gap trials (see Fortin and Masse, 2000, for the expectancy account on human timing under the gap procedure). The results of the present experiment, however, showed that PTs on the baseline probe trials in the task/gap phase were not different from PTs on the probe trials in the previous PI sessions, and occurred earlier than those on the task and gap trials, an outcome that is not in line with the expectancy account.

One alternative explanation for the PT shift on the S+ trials obtained in the present experiment is the delay in resumption of timing after the concurrent task cue presentation, represented by an opened switch. Aum et al. (2004) proposed that on S+ trials timing is suspended not only during the presentation of the task cue but also after the termination the cue, a postcue effect. In that account, the delay in resumption of timing is considered to be related to off-task behavior engendered by the task cue.

Accordingly, animals may stop responding to the timing cue or stop engaging in temporal processing for a substantial time period after the presentation of the task cue.

The sustained off-task behavior after the termination of the S+ cue might be related to the reinforcement history of the S+ cue. It has been reported that animals engage in a form of off-task behavior after the termination of the reinforcer (Cohen & Campagnoni, 1989; Staddon & Simmelhag, 1971). For example, Staddon and Simmelhag (1971) observed pigeons' turning away from facing the reinforcer dispenser in the period following the reinforcer presentation under an intermittent reinforcement schedule. Cohen and Campagnoni also observed pigeons' spatial retreat to the rear of the chamber (away from the reinforcer dispenser) during the interreinforcer interval when their pecking was maintained under either a continuous fixed ratio or fixed interval reinforcement schedule. The probability of the pigeon's location in the rear of the chamber was greatest in the time period soon after the presentation of the reinforcer (postreinforcer period). It could be argued that the postreinforcer period has negative discriminative stimulus properties. Withdrawal behavior has been observed in the presence of cue explicitly uncorrelated with reinforcement (Brown, Coleman, & Elefant, 1983; Hearst & Franklin, 1977). In the present experiment, birds' behavior after the termination of the S+ cue was not systematically measured. Informal observation by the experimenter, however, indicated that pigeons moved away from the front wall of the chamber where the FI and S+ cues were presented, and on some occasions engaged in wing flapping after the termination of the S+ cue.

Off-task behavior might account, in part, for the reduction in response rate on the FI key during the S+ trials as compared to baseline trials. It could be argued that the PT shift observed on the S+ trials is an artifact resulting from suppression of responding to the timing cue by competing behavior. On that account, the observed response rate on the S+ trials on the timing cue would represent a net rate following a reduction of response rate from that observed on baseline trials. Thus, the resultant response rate to the timing cue on the S+ trials would not exceed the response rate on the baseline trials. However, the response rate on the S+ trials exceeded that on the baseline trials at later times within the probe interval, refuting the idea of an artifactual PT shift.

The delay in resumption of timing after the task cue presentation alone cannot explain the location effect of the S+ cue on the PT shift observed in both Aum et al. (2004) and present studies. In both studies, the PT shift on S+ trials increased as a function of the location of the S+ cue. If animals just delayed their resumption of timing after the task cue presentation by a certain time period, the PT shift would be equal to the delay interval regardless of the location of the task cue, and no location effect of the task cue on the PT shift would be predicted. In that sense, the observed location effect suggests that at least some resetting occurred in the animals' clock after the presentation of the S+ cue in conjunction with the delay in resumption of timing. In relation to that inference, Roberts (1981) showed that animals' internal clock is reset by food to some extent. In his study (Experiment 4, 1981), rats were trained under a PI procedure composed of food and empty trials which were randomly mixed. Trials were separated by an ITI. On a random half of the food trials, food was delivered when rats pressed the lever after 40 s had elapsed since the trial onset and the trial then ended (ordinary food trials). On the other half of the food trials, food was not delivered when rats pressed the lever after 40 s had elapsed and the trial ended without reinforcement (omitted food trials). Some empty trials were presented following ordinary food trials (baseline empty trials), whereas other empty trials followed the omitted food trials (omission empty trials). Compared to the response rate function on the baseline empty trials, the response rate function on the omission empty trials shifted to the left, indicating that animal's internal clock was reset to a lesser extent than usual in the end of the previous omitted food trials. Based on the results, Roberts argued that animals' internal clock is reset partially by food. The S+ cue in the present experiment might have acquired a conditioned reinforcer function through its association with a high probability of food reinforcement in its presence. In that case, reset clock mechanism at the end of the S+ cue is very plausible. Accordingly, the PT shift on the S+ trials obtained in the present experiment can be explained by the combination of the delay in resumption of timing after the task cue presentation and reset clock at the end of the task cue.

Another more simple explanation for the PT shift on the S+ trials obtained in the present experiment is a reduction in clock rate after the presentation of the S+ cue. That is, if the S+ cue decreases the clock speed, less subjective time is accumulated per unit of physical time, and a longer time must elapse before the accumulated subjective time is close to the remembered reinforced time, producing a PT shift to the right on those S+ trials. Changes in clock speed by some manipulations have been reported in both animals (Meck, 1983) and humans (Penton-Voak, Edwards, Percival, & Wearden, 1996; Wearden & Penton-Voak, 1995). Using a matching-to-sample procedure, Meck showed that the psychophysical function which relates the proportion of choosing a "long" response to the signal duration shifted to the left when rats trained under saline condition were tested under methamphetamine condition, that is, their PSE decreased. Using a temporal generalization procedure, Penton-Voak et al. (Experiment 1) showed that presentation of a brief period of repetitive clicks, which is assumed to be mildly arousing, prior to the timing stimulus shortens subjective time estimate. In their study, after participants experienced a standard duration (400 ms) of the tone stimulus, which was preceded by a period of 5-s silence, they were given one of seven test durations (250, 300, 350, 400, 450, 500, and 550 ms) of the comparison tone. The comparison tone was preceded by a 5-s click train of the specified frequency or 5-s silence. Participants' task was to judge whether the comparison stimulus was the same duration as the standard tone by pressing "Y" ("Yes" response) or "N" ("No" response) key on the keyboard. For data analysis, the proportion of "Yes" responses to the comparison stimulus was plotted as a function of the comparison stimulus duration (temporal generalization gradient). Compared to the silence condition, temporal generalization gradient shifted in a direction (left) indicating shorter time judgment in the presence of the click train. The results of both Meck and Penton Voak et al's studies were explained in terms of the increased clock speed. Penton Voak et al. proposed that the click train increased the speed of the clock through the increase in the arousal level of the participants. In the present experimental preparation, the presentation of the S+ cue, as a signal for reinforcement, might be expected to increase arousal level, and therefore clock speed because of its association with a relatively high probability of reinforcement (see Killeen & Fetterman, 1988). Therefore, the reduction in clock rate after the presentation of the S+ cue is not a plausible explanation for the PT shift on the S+ robe trials obtained in the present experiment.

The PT shift on the gap trials, which was greater than the stop prediction but lower than the reset prediction in the present experiment, is consistent with the memory decay account. That is, timing stops during the gap and the subjective time accumulated before the gap is gradually lost during the gap period (Cabeza de Vaca et al., 1994). In particular, the linear increase in PT as a function of the temporal location of the gap in the present study as in the study by Cabeza de Vaca et al. suggests power or exponential decay function in which the amount of the decay during the gap period varies directly with the time accumulated in the animals' internal clock prior to the gap. That is, more decay occurs when more time has been accumulated before the gap.

Even though there were PT shifts toward longer PTs on the S- trials compared to that on the baseline probe trials, the shifts tended to be lower than the stop prediction in the present experiment. As a cue that was never paired with reinforcement, S- may be compared to a novel cue. In a study by Roberts (Experiment 2, 1981), rats were trained under a PI procedure with a light stimulus which signaled an FI 40-s reinforcement schedule on food trials. Then, a novel sound turned on for 10 s starting at 10 s. Initially, the sound had little effect on the rats' timing performance. Gradually the interruption of the timing stimulus with the sound was found to increase peak time on the sound probe trials over sessions. In the final sessions the PT shift on the sound probe trials was greater than the stop prediction but tended to be lower than the reset prediction. Compared to the PT shift on the sound probe trials in Roberts' study, the shift on the S- trials in the present experiment was smaller, suggesting that the effect of a task cue which has a history of nonreinforcement is different from the effect of a novel cue on timing.

In addition to the minimum PT shift on the S- trials, no location effect was observed in the present experiment, excluding the possibility of clock reset after the presentation of the S- cue. The minimal effect of the S- cue in the present experiment might be related to the conditioned inhibitory function of the S- cue. During the discrimination training sessions in the present experiment, the S- cue was explicitly associated with nonreinforcement, whereas the S+ cue was associated with reinforcement. That discrimination training might have endowed the S- cue a conditioned inhibitory function. Previous studies (e.g., Rescorla, 1969, 1971) showed that the conditioned inhibitory function is acquired for a cue by making the cue differentially signal a lower probability of reinforcement or nonreinforcement. Although the conditioned inhibitory function of the S- cue was not tested explicitly, the discrimination training procedure suggests at least that the S- cue was not a neutral stimulus when the cue was presented in the task/gap phase sessions, and likely possessed conditioned inhibitory properties.

The increased PT shift on the S+ trials as a function of the temporal location of the cue could not be attributed to the difference in the center-key peck rate among the three locations in the present experiment. No consistent increase in the center-key peck rate as a function of the location of the S+ cue was observed, providing no evidence for differences in the excitatory strength of the S+ cue among the three locations. The location effect is consistent with clock reset at all locations, and with the possibility that the properties of the key that engender keypecking are also related to engagement of the reset mode.

As in Aum et al. (2004), the effect of the S+ cue on PT emerged over sessions in the present study. On session 1, the effect was observed only at one location of the S+ cue. In contrast, the effect of the gap on PT was evident at all three locations of the gap event from the outset of testing, as in Aum et al. (2004) and Cabeza de Vaca et al. (1994). It is likely that the immediacy of the gap effect in contrast to the delayed emerging S+

cue effect could be traced to the initial detectability of the cue. That is, the gap is an interruption of the timing cue to which the animals were oriented; the S+ cue was presented in a separate location from the timing cue. Accordingly, the gap was more detectable than the S+ cue during the initial sessions. The increased center-key peck rate during the presentation of the S+ cue over sessions is consistent with the increased detectability of the S+ cue over sessions.

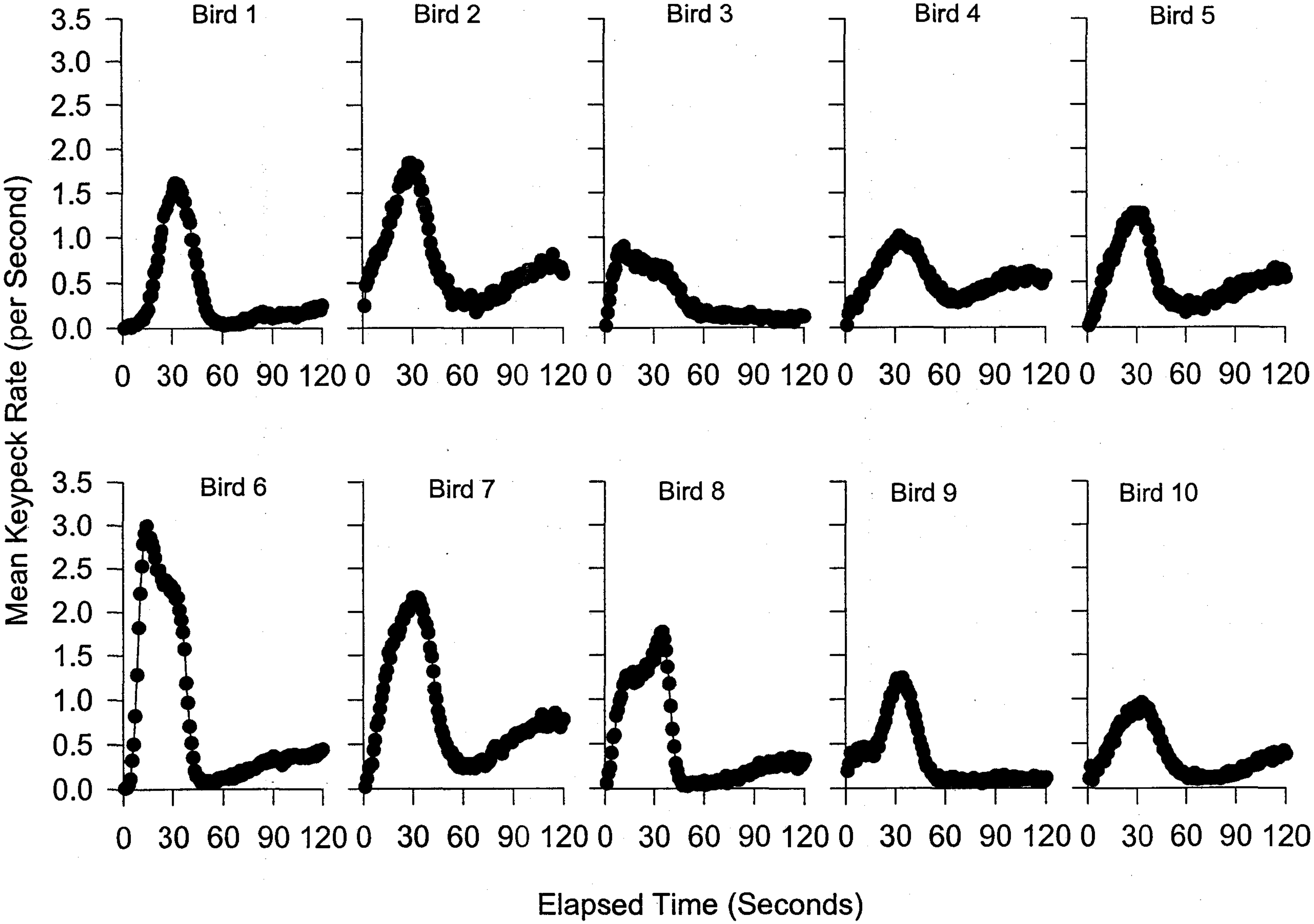
The observed PT shifts on S+ and gap trials in the present experiment are in contrast to the results of Meck and Church (1984) and Dews (1962) who found no effect of an intruded event on temporal control. However, in both previous studies, the effect of the intruded event was evaluated under maintained reinforcement conditions. That is, the reinforcer was still presented for responding to the timing cue on the intruded event trials. Therefore, the difference in the results can be attributable to the procedural difference.

The PT shift on S+ trials that indicates shortened perceived time in the presence of the concurrent task cue is consistent with humans' time underestimation under dual task situations (see Brown, 1997, for the underestimation of human timing under various concurrent nontemporal tasks). Presumably, the S+ cue in the present experiment is similar to the concurrent nontemporal task that competes with the timing task for limited attentional resources in the human timing literature. In contrast to the discrete concurrent task cue used in the present study, the concurrent task is given coextensively with the timing task from the beginning of the interval in most human timing studies. Accordingly, the suspension of timing after the termination of the concurrent task could not be studied with the kind of the concurrent nontemporal task employed in those studies. Human timing studies using a discrete concurrent task cue which has a hedonic value would be worth studying in regard to possible common timing mechanism in animal and human performance. In addition, even though similar results were obtained between animal and human studies on the effect of a concurrent task on timing, the number of animal studies is still sparse. Also, as Sutton and Roberts (2002) indicated, the types of nontemporal tasks used in animals have been limited (e.g., VR task), whereas many different types of nontemporal tasks were used in humans. In that sense, more future animal studies using a variety of different nontemporal tasks are needed to compare animal timing under dual task situations with human timing.

In summary, the results of the present study showed that the disruptive effect of the concurrent task cue on animal timing performance was mainly dependent on the reinforcement history of the concurrent task cue, rather than the physical stimulus properties (e.g., salience) of the cue. The obtained PT shift on the concurrent task trials, which was greater than that predicted by the reset clock mechanism, is considered to be the result of the combination of the delay in resumption of timing after the task cue presentation and clock reset at the end of the task cue. Specifically, it is suggested that a delay in resumption of timing is attributable to off-task behavior after the termination of the task cue (a post-cue effect). Compared to the PT shift obtained when the timing cue was briefly interrupted with a gap or S-, the greater PT shift on S+ trials in the present study suggests that the reinforcement history of the S+ cue produced such a post-cue effect. However, other properties of the concurrent task cue (e.g., the termination of the task cue signaling unavailability of reinforcement) might also produce a post-cue effect . In future studies, manipulation of the hedonic value of the concurrent task cue would be valuable in assessing the nature of the post-cue effect.

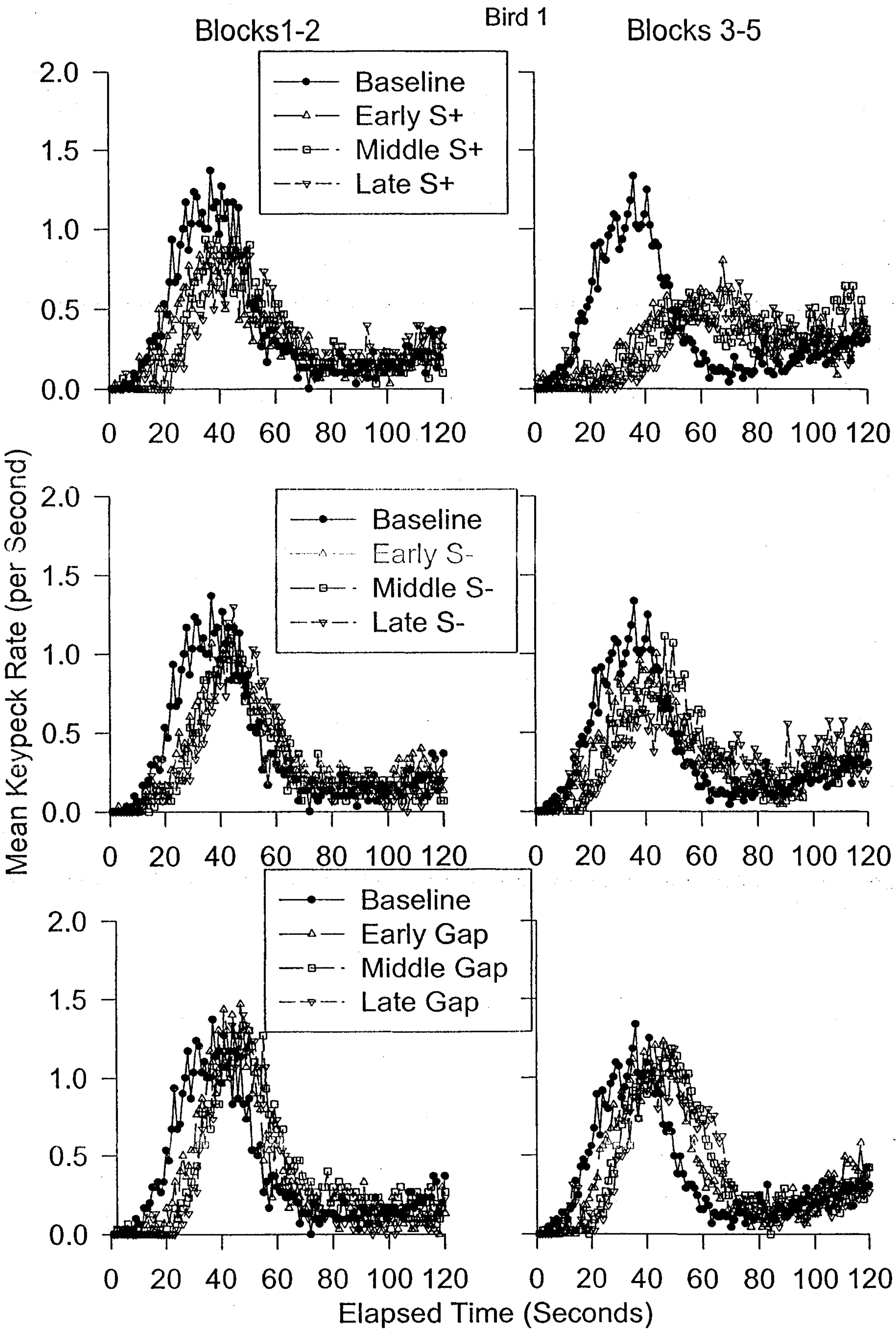
Appendix A

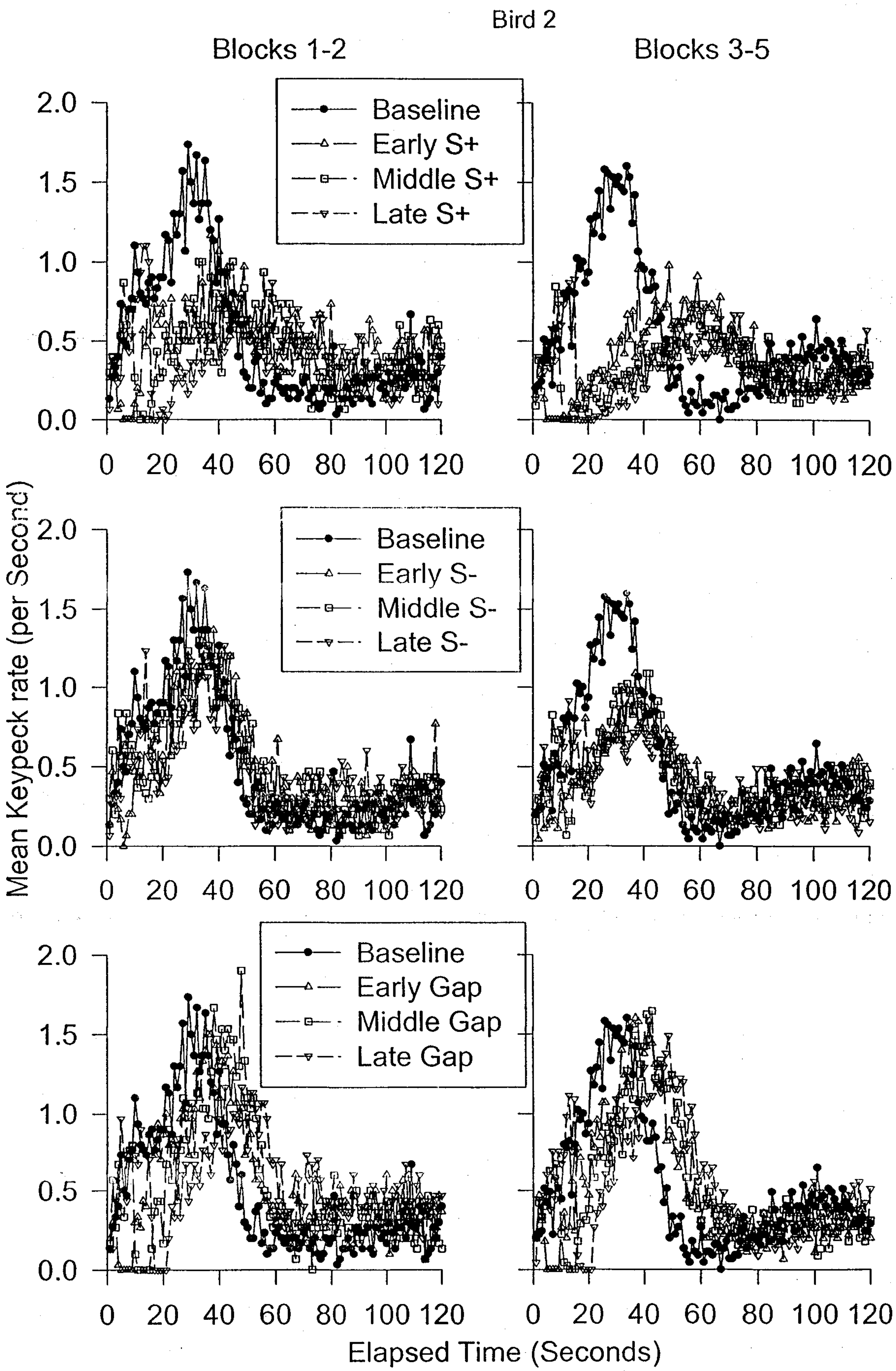
Individual bird's FI-key peck rate (responses per second) as a function of elapsed probe-trial time during the last 10 PI sessions of the alternated PI and discrimination training phase 1.

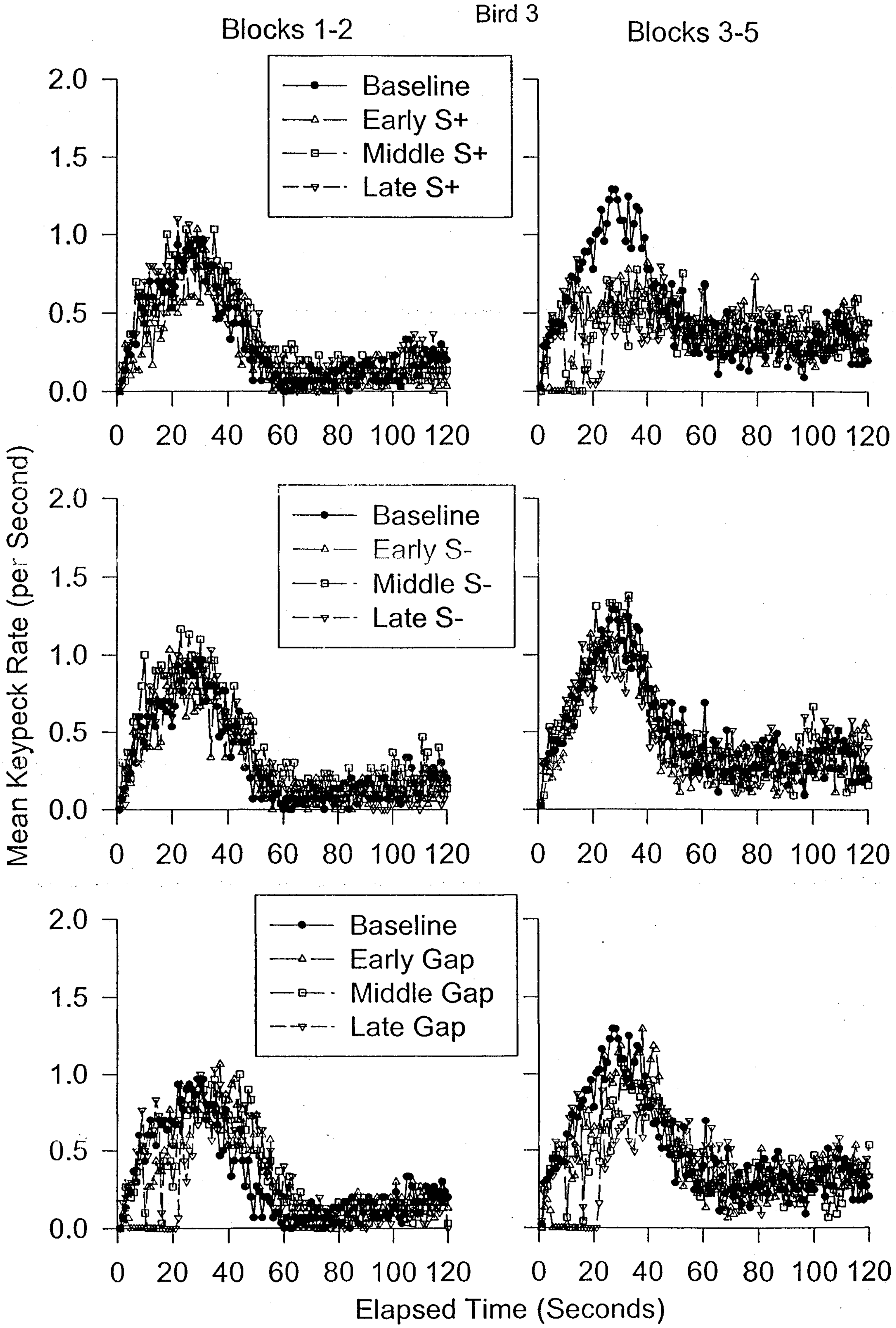

Bird 1
Bird 2
Bird 3
Bird 4
Bird 5
Bird 6
Bird 7
Bird 8
Bird 9
Bird 10
Mean Keypeck Rate (per Second)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
30
60
90
120
Elapsed Time (Seconds)

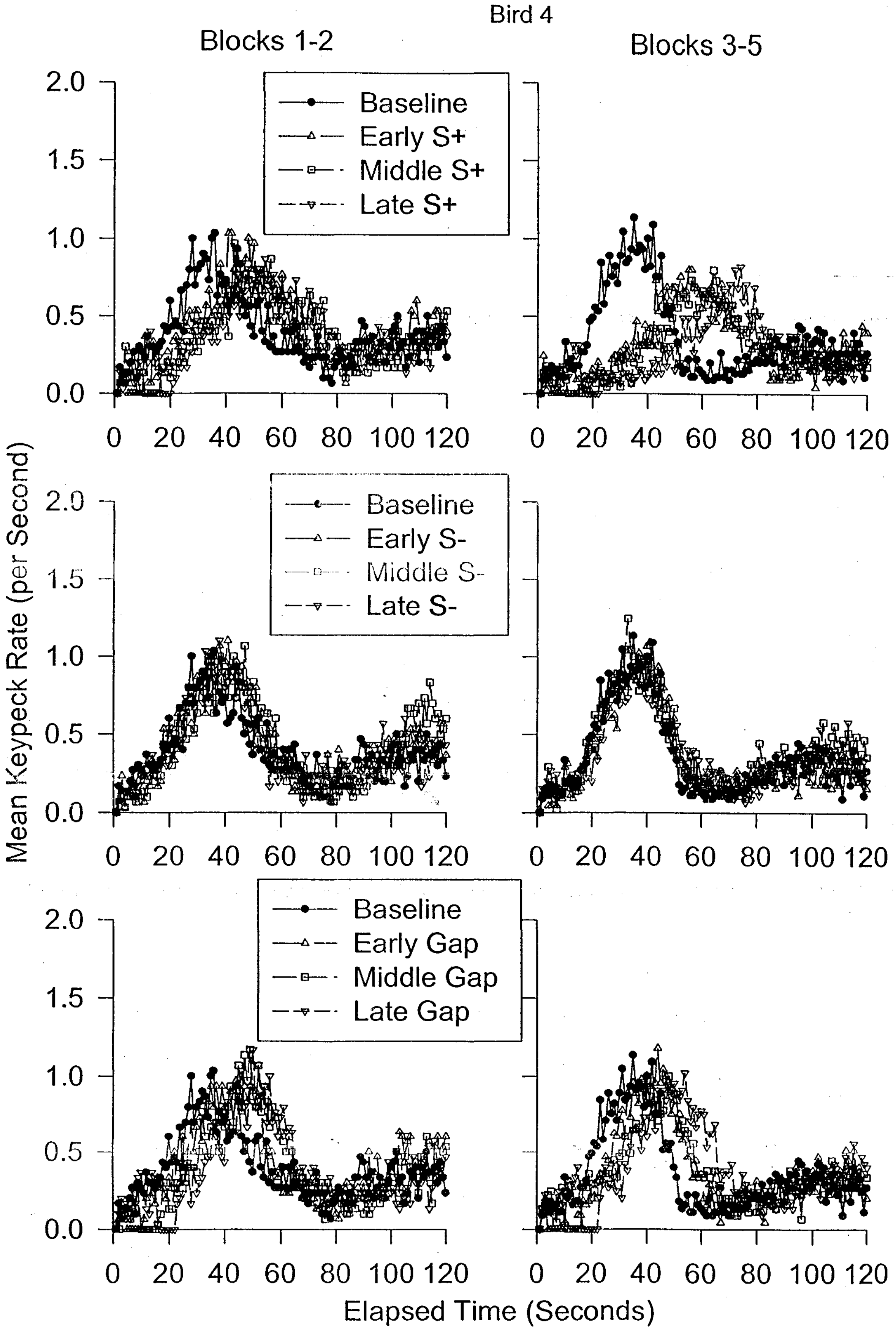
Appendix B

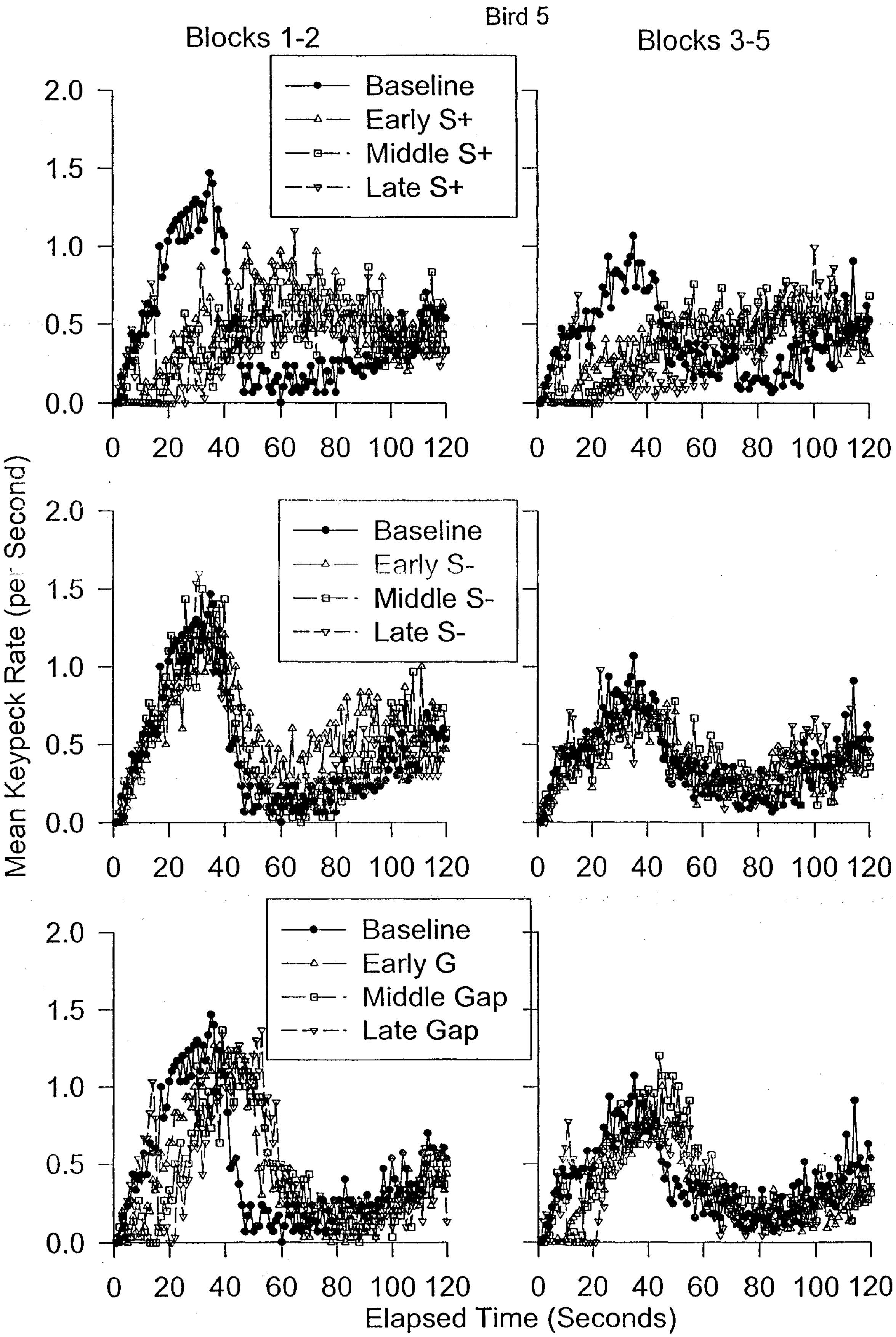
Individual bird's mean FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase 1.

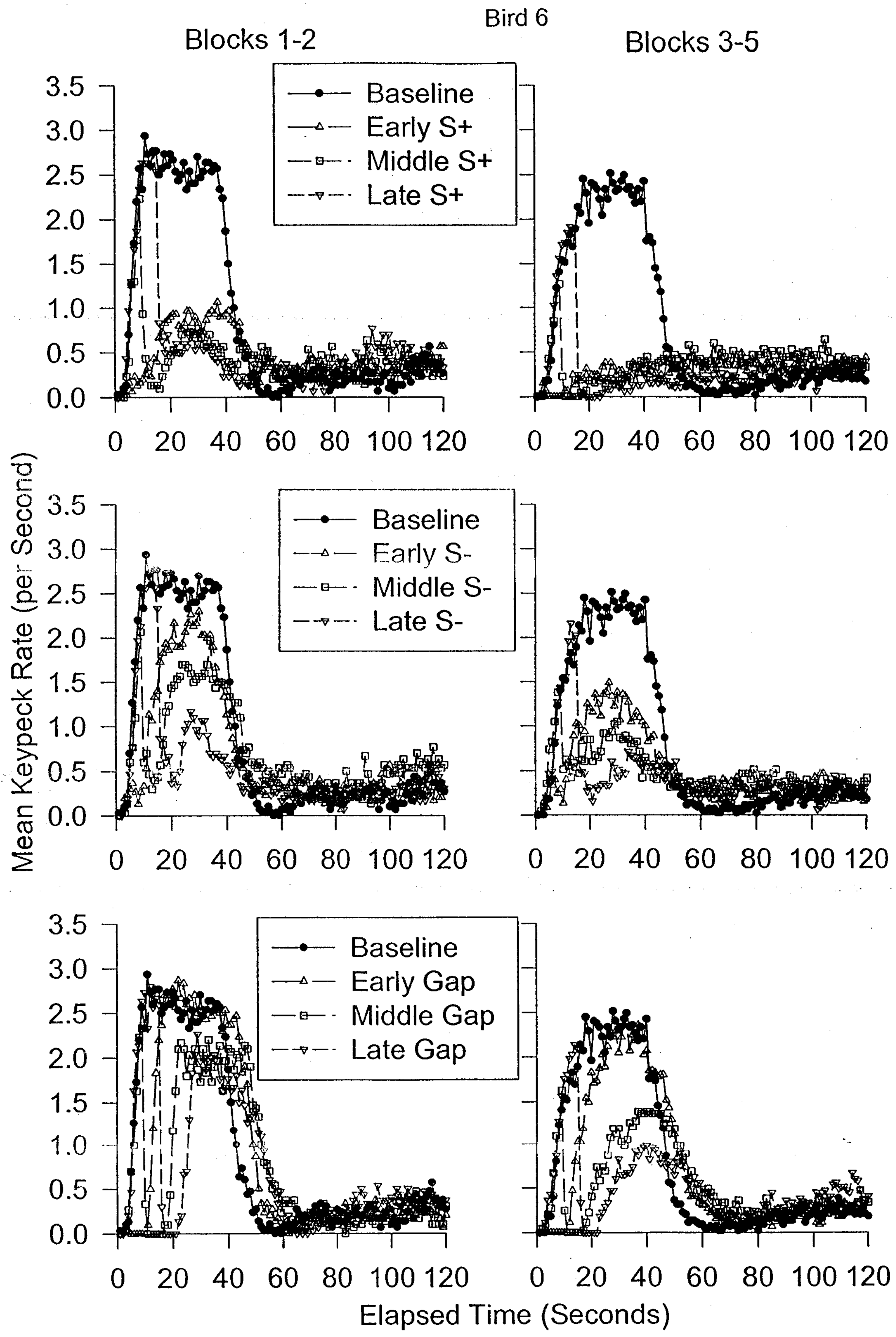

Bird 1
Blocks1-2
Blocks 3-5
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

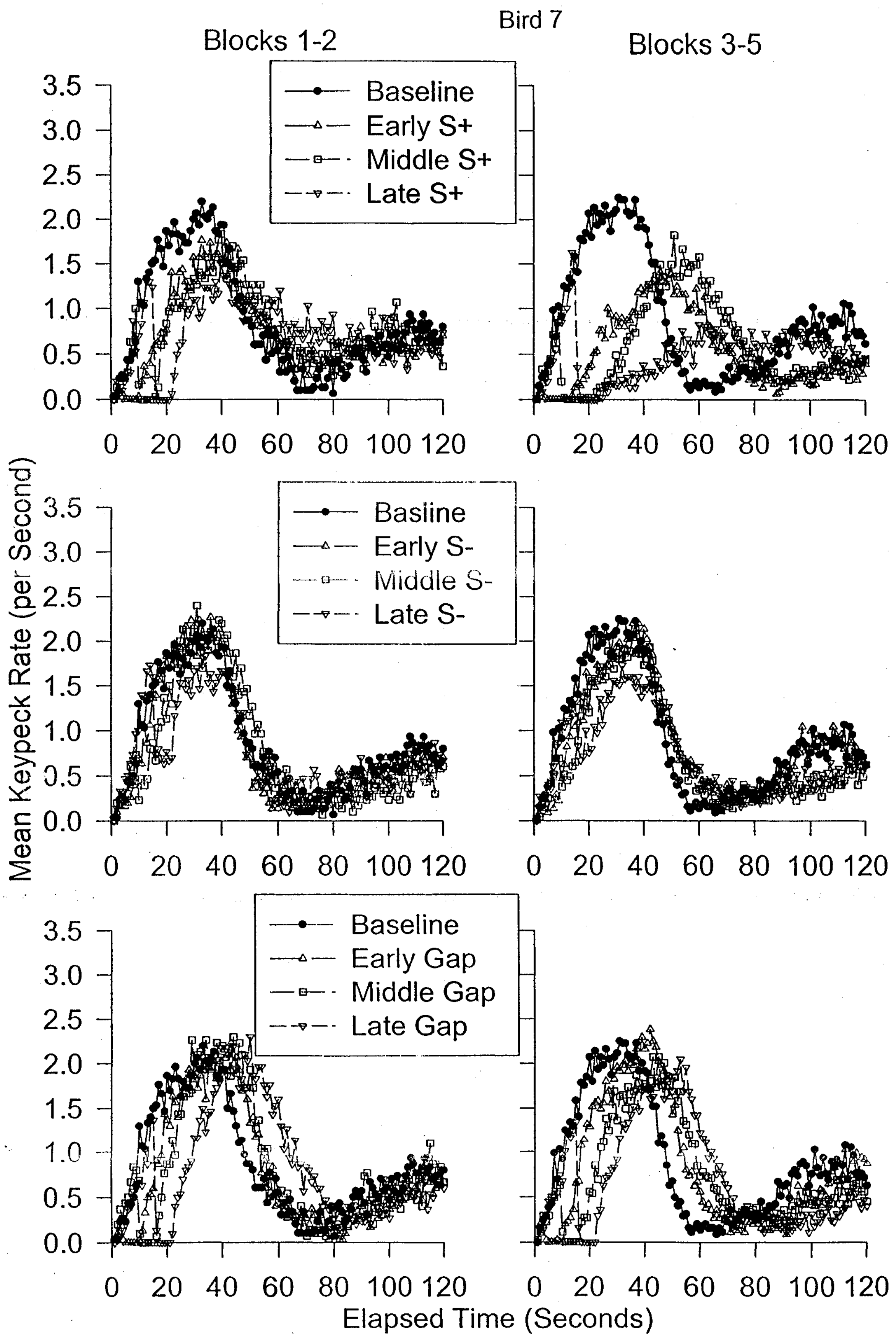

Bird 2
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
2.0
1.5
1.0
0.5
0.0
0 20 40 60 80 100 120
Mean Keypeck rate (per Second)
Elapsed Time (Seconds)

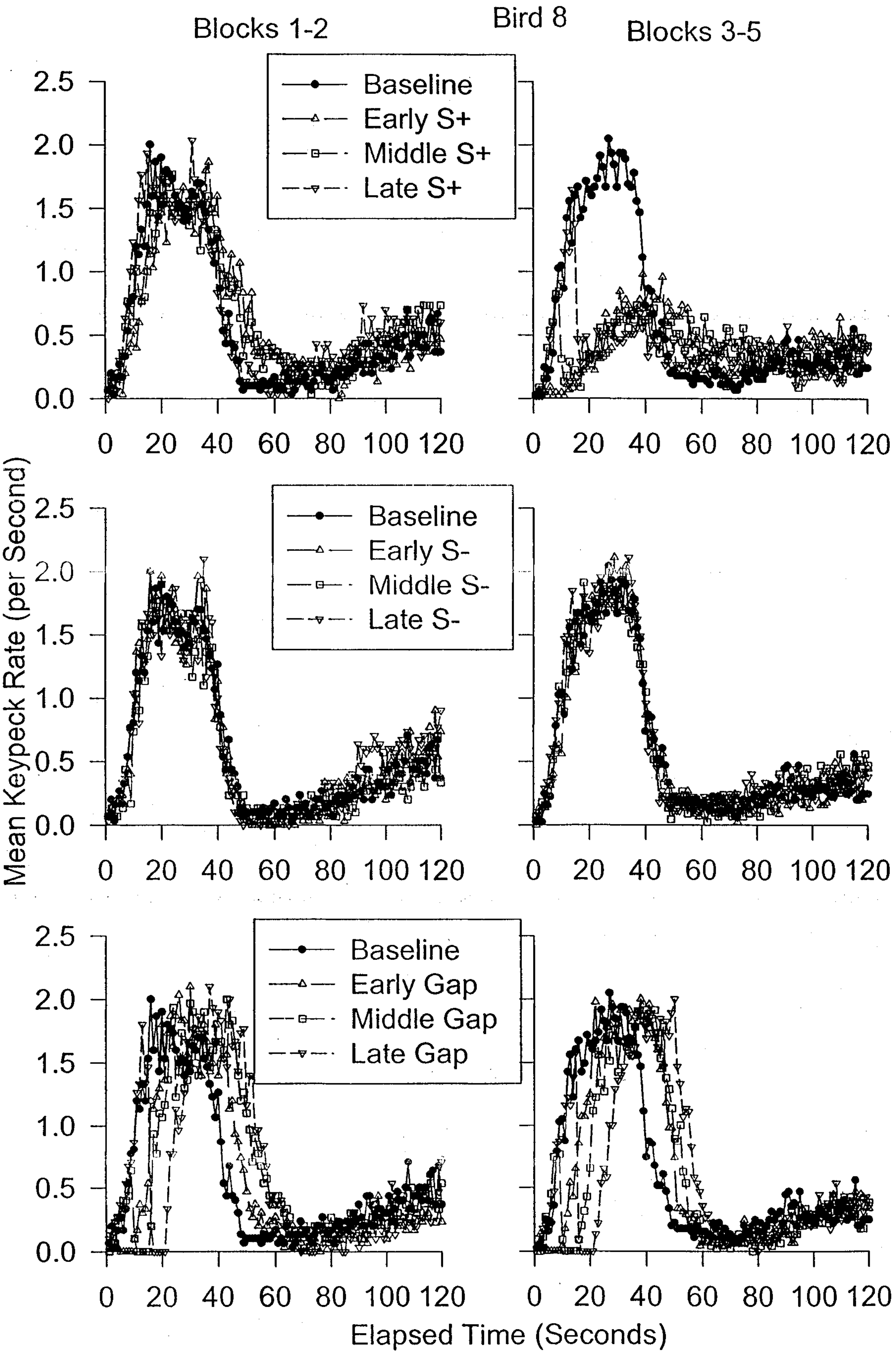

Bird 3
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

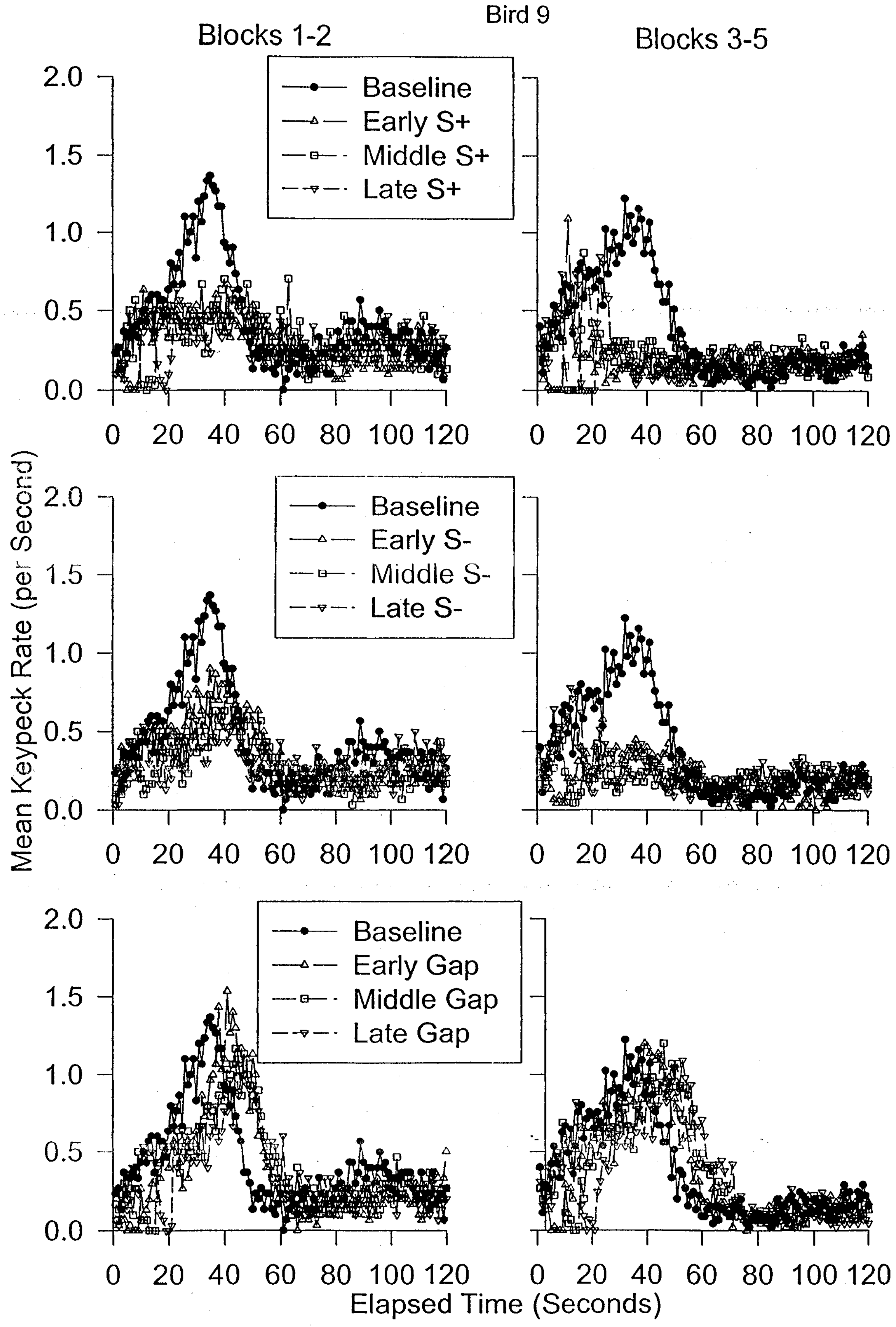

Bird 4
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
0 20 40 60 80 100 120
Elapsed Time (Seconds)

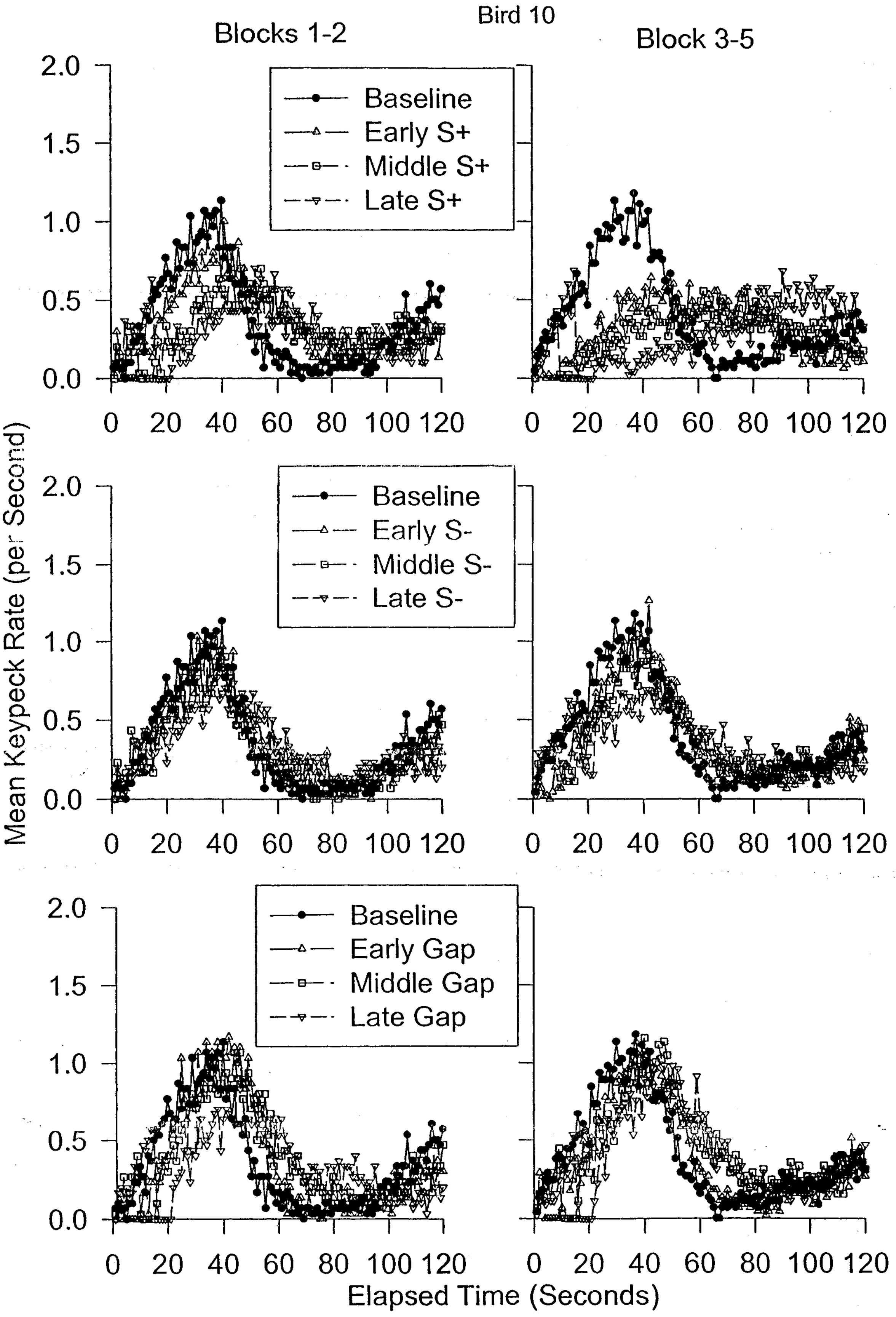

Bird 5
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early G
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 6
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120


Bird 7
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Basline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
20
40
60
80
100
120
Elapsed Time (Seconds)

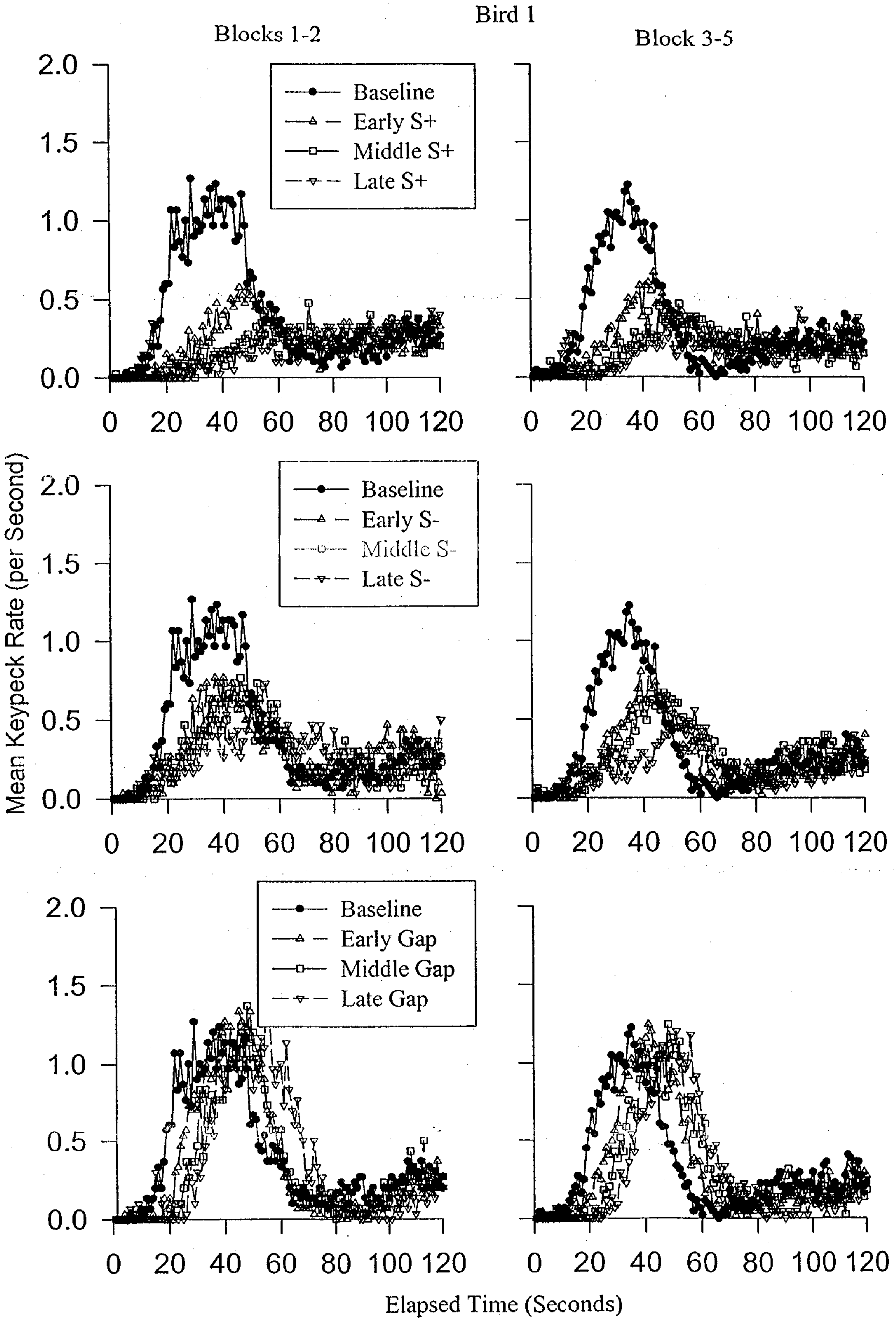

Bird 8
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
0 20 40 60 80 100 120
Elapsed Time (Seconds)

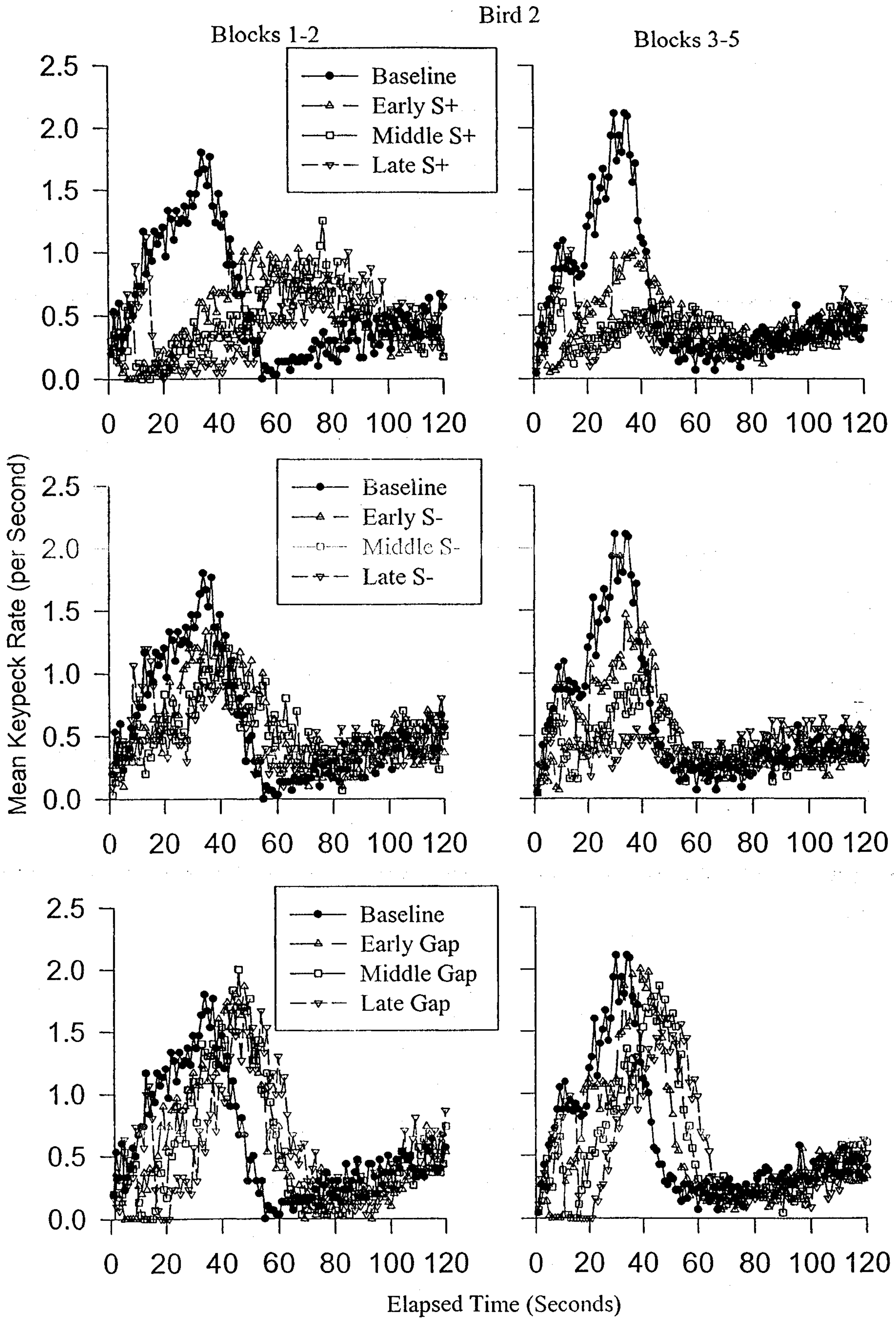

Bird 9
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

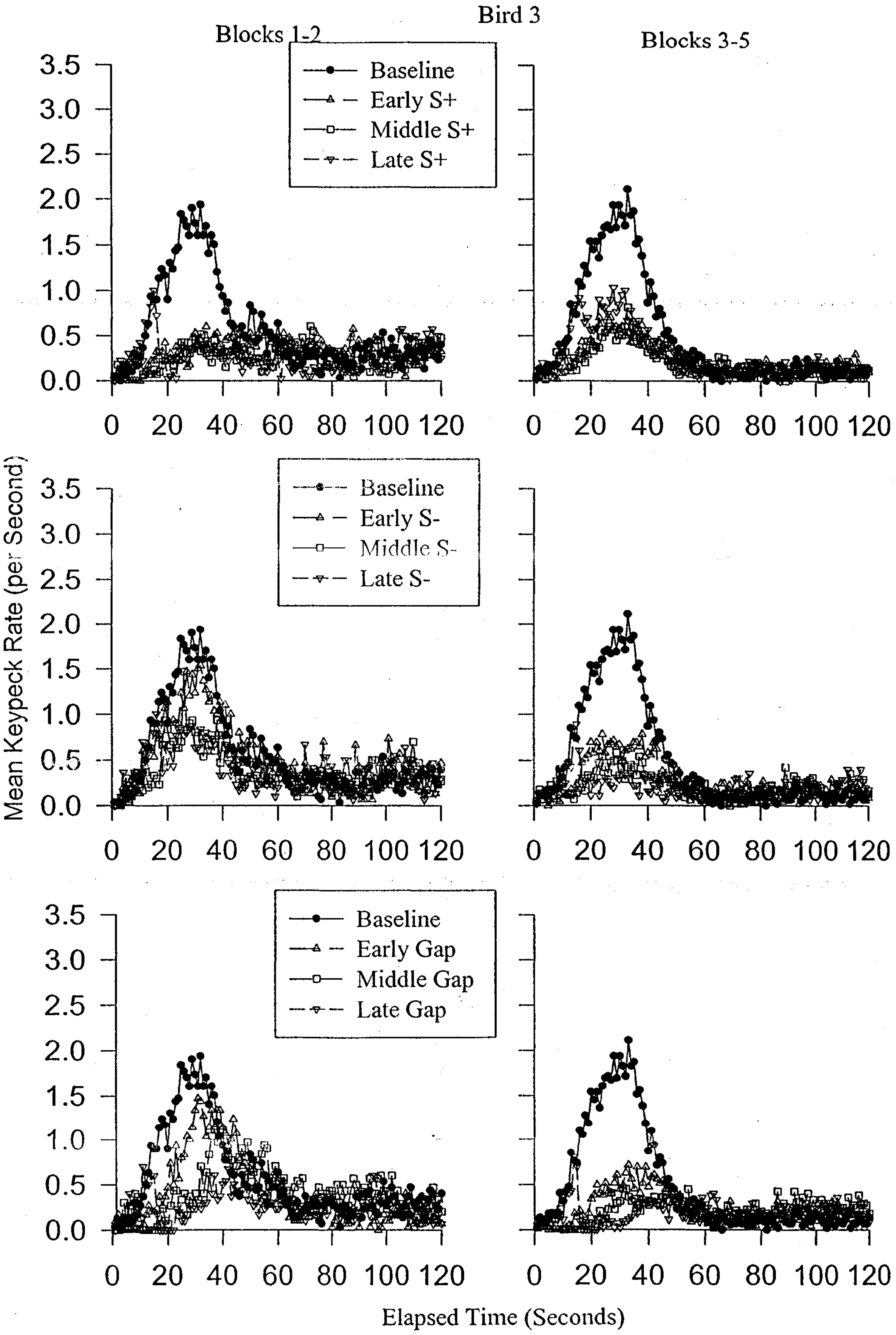

Bird 10
Blocks 1-2
Block 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

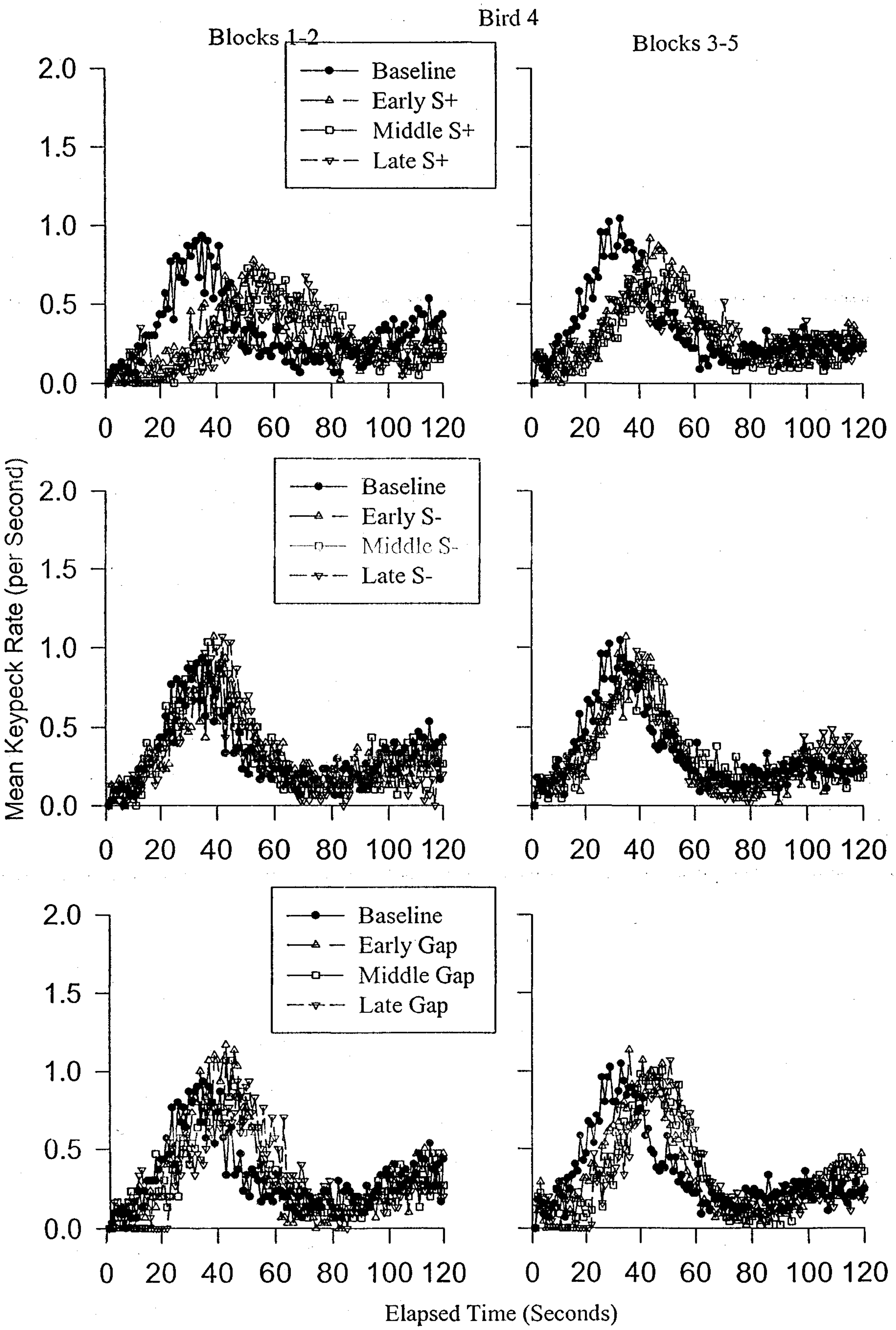
Appendix C

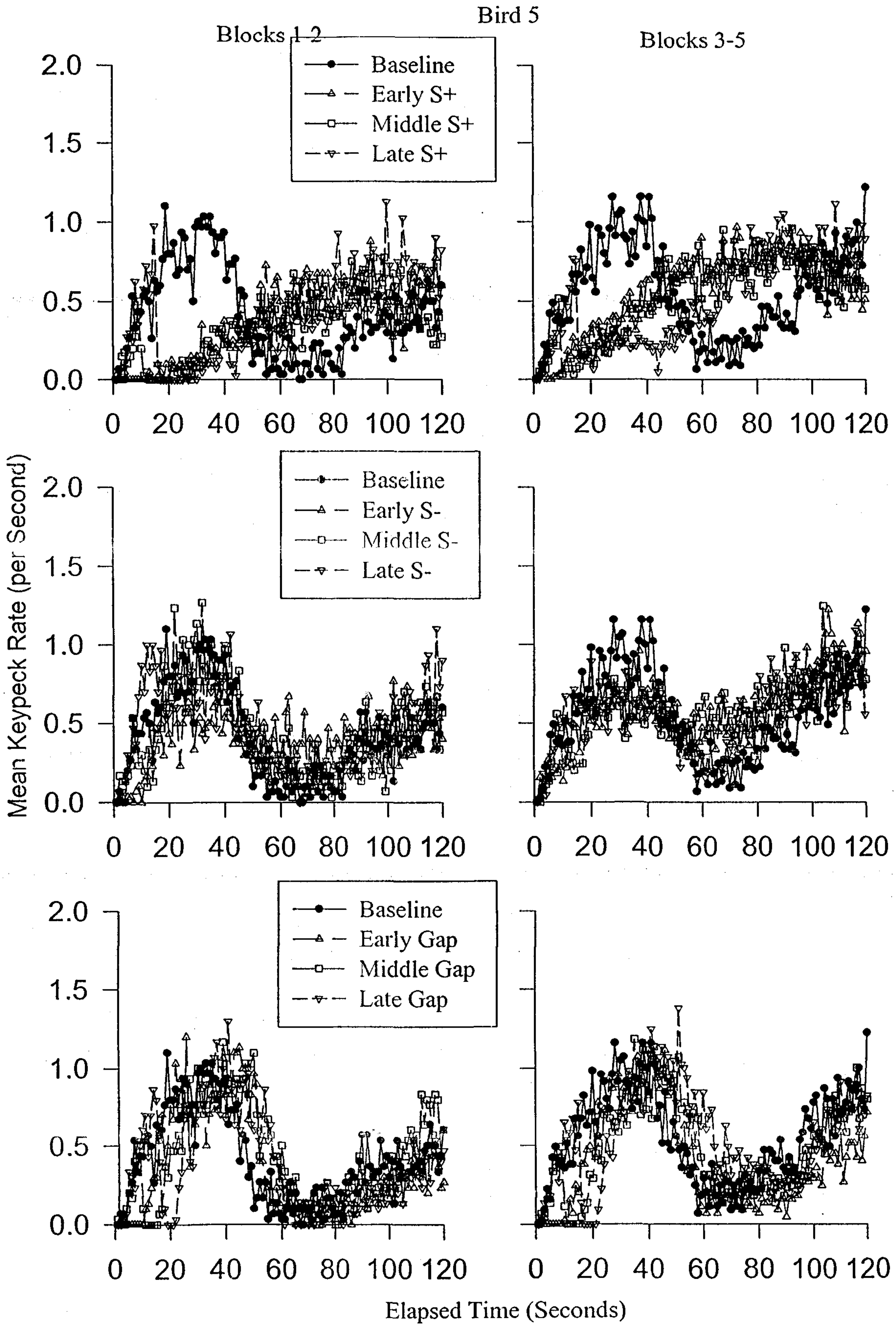
Individual bird's mean FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the extinction phase.

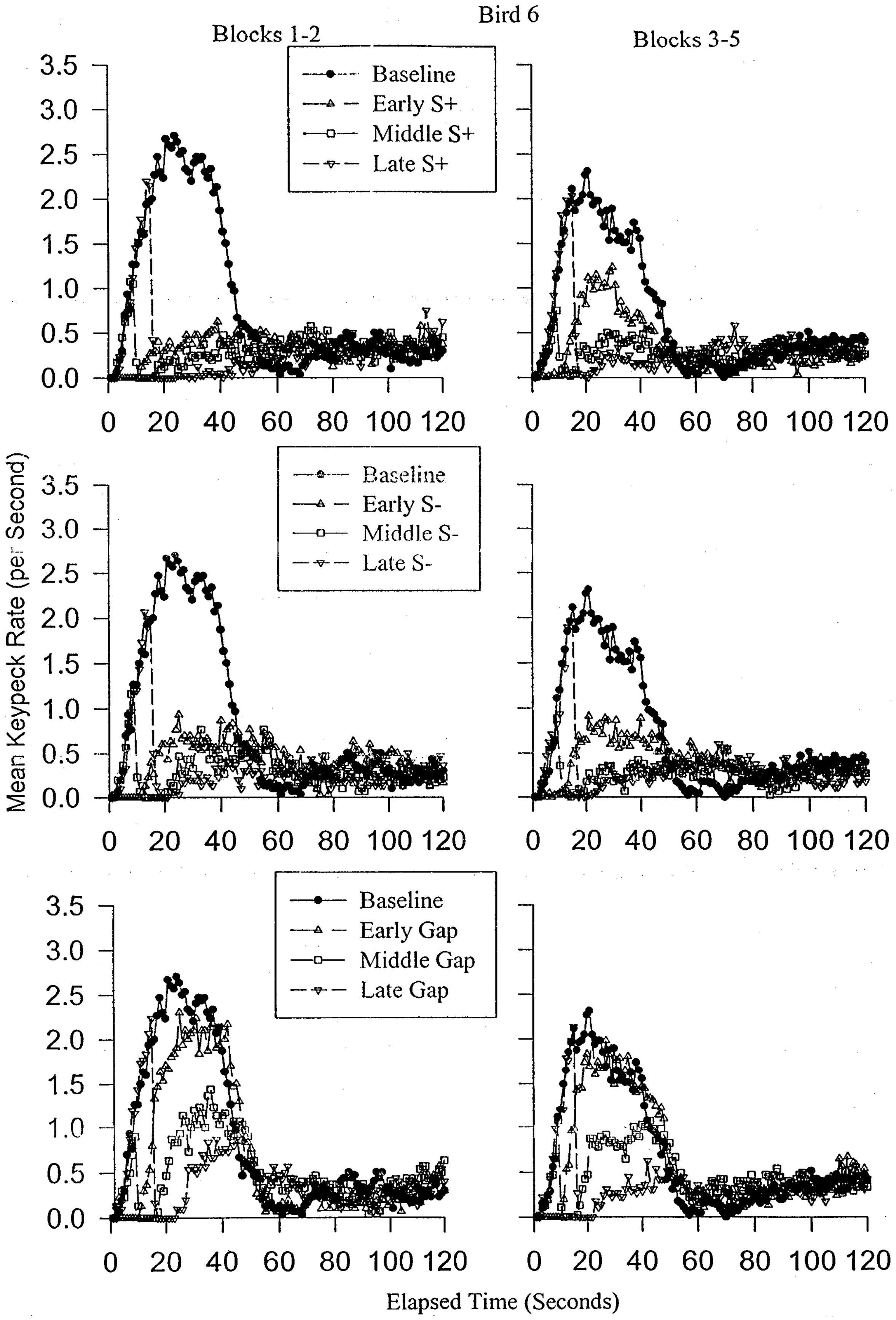

Bird 1
Blocks 1-2
Block 3-5
Baseline
Early S+
Middle S+
Late S+
Early S-
Middle S-
Late S-
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120

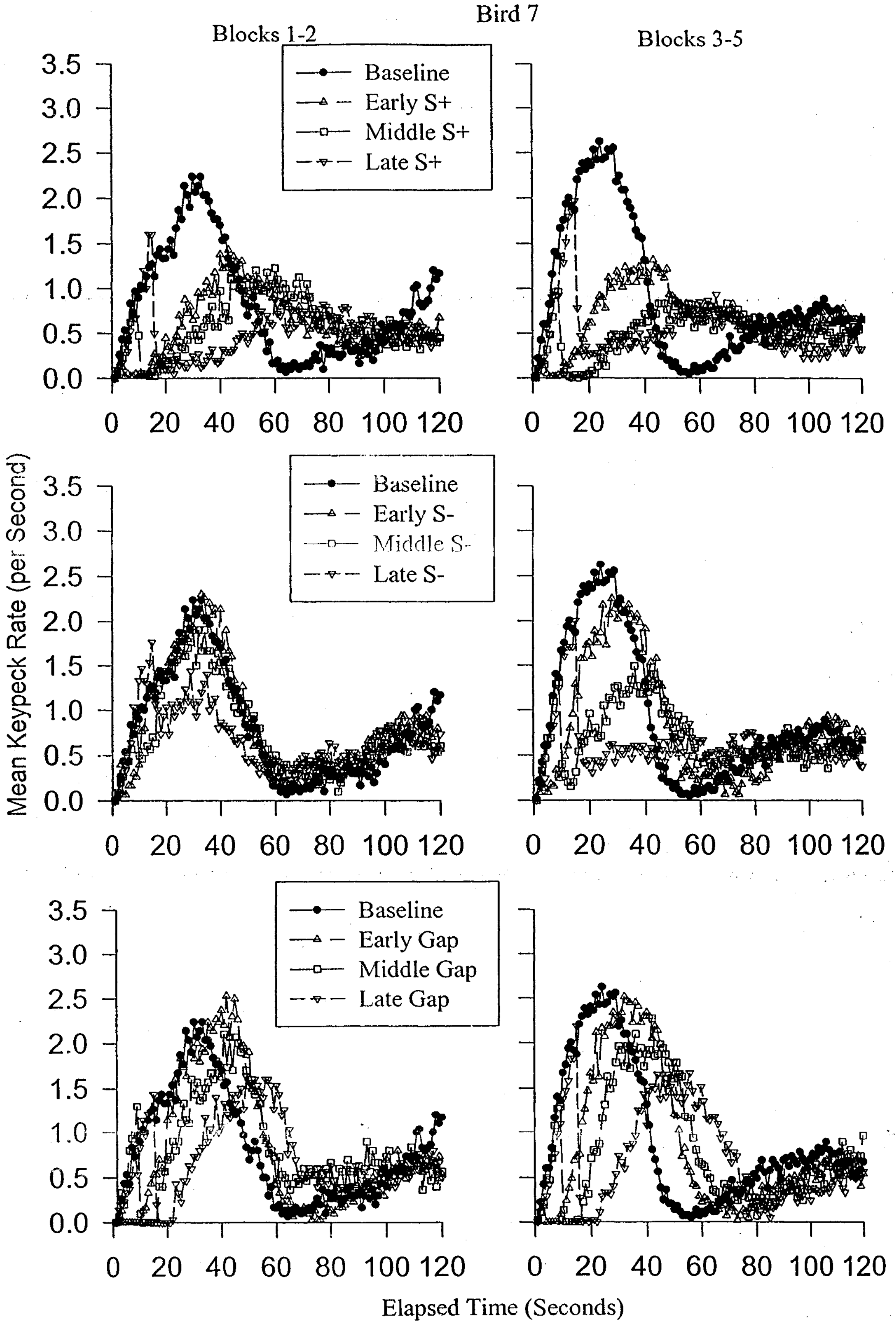

Bird 2
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)

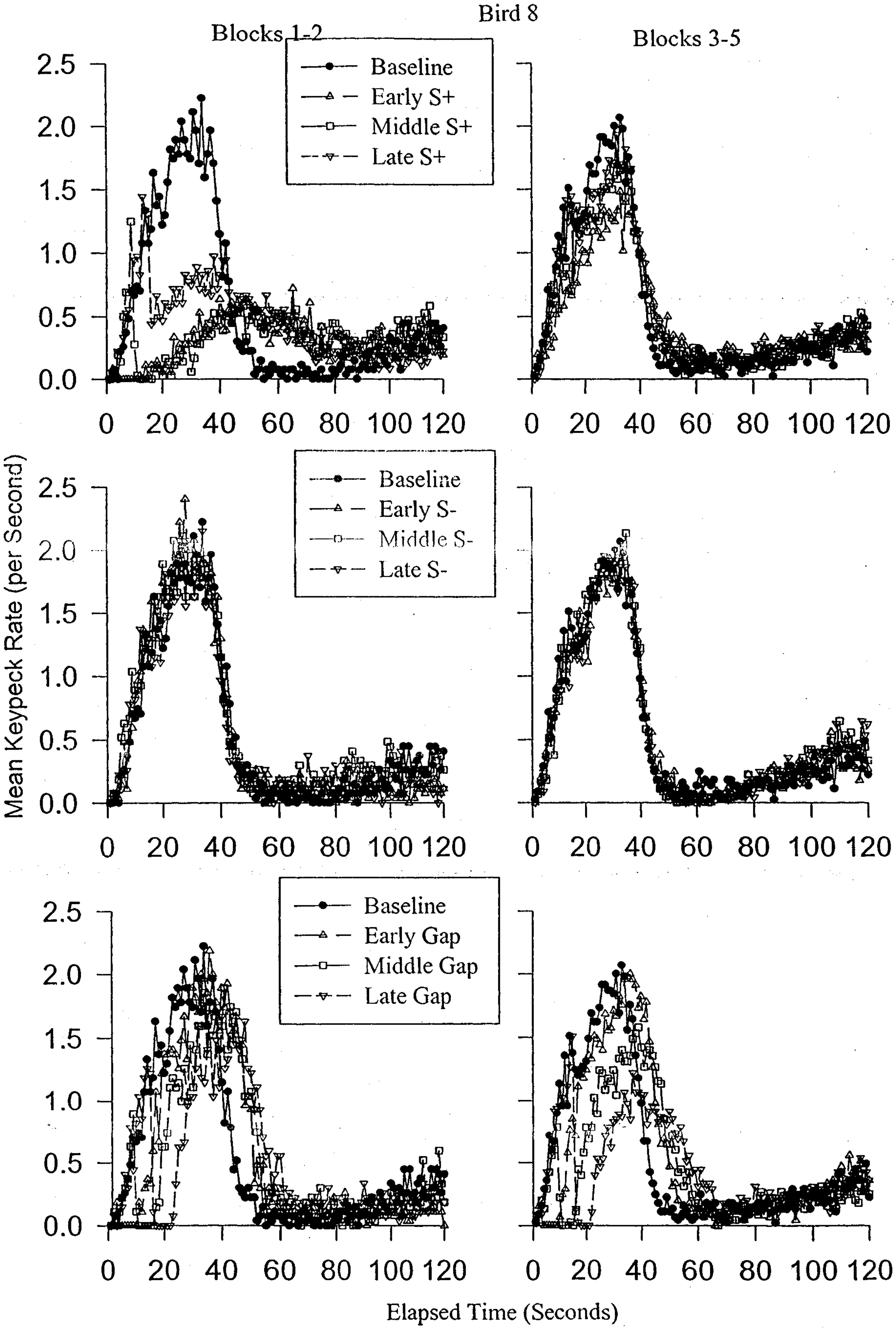

Bird 3
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
20
40
60
80
100
120
Elapsed Time (Seconds)

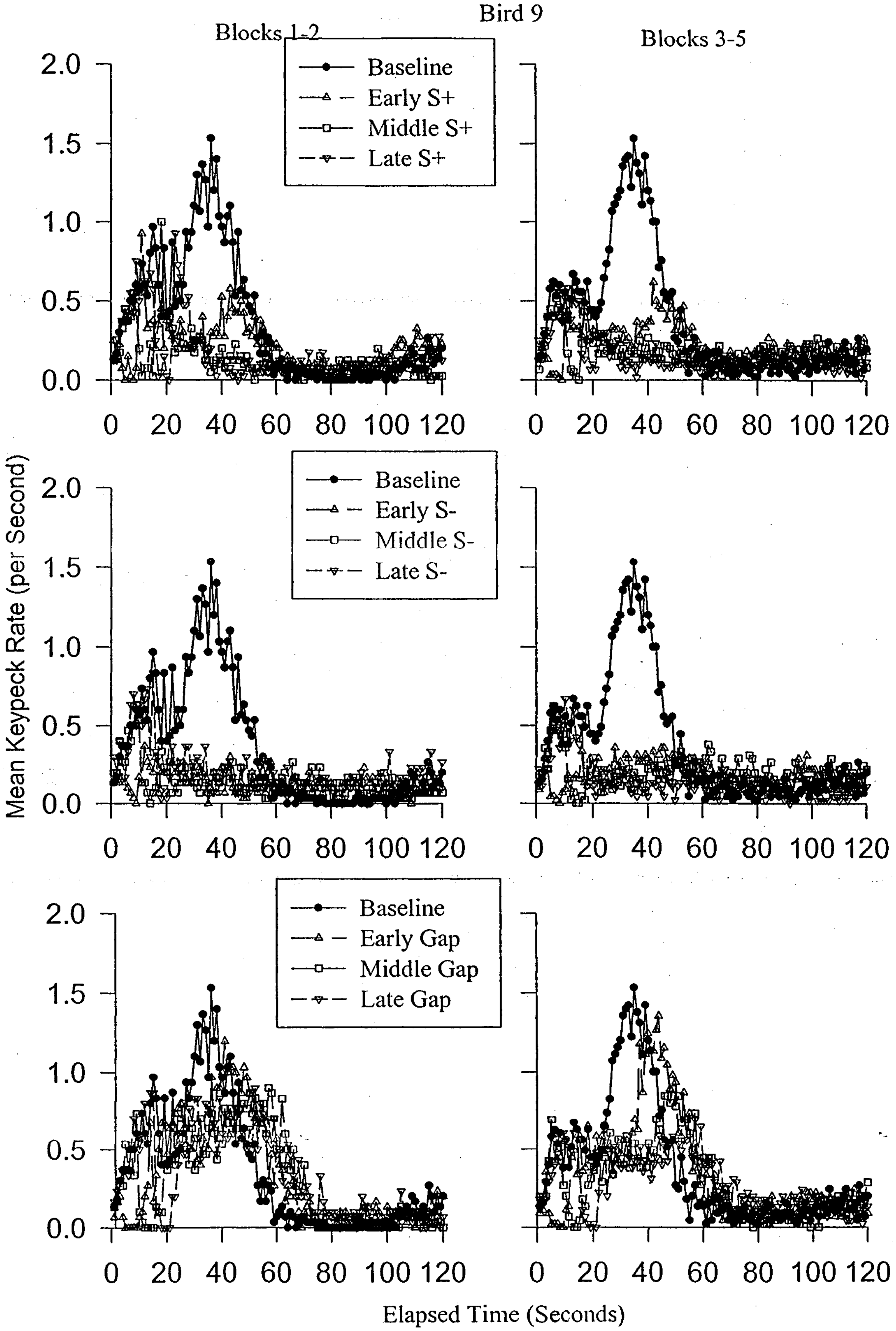

Bird 4
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 5
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 6
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
20
40
60
80
100
120

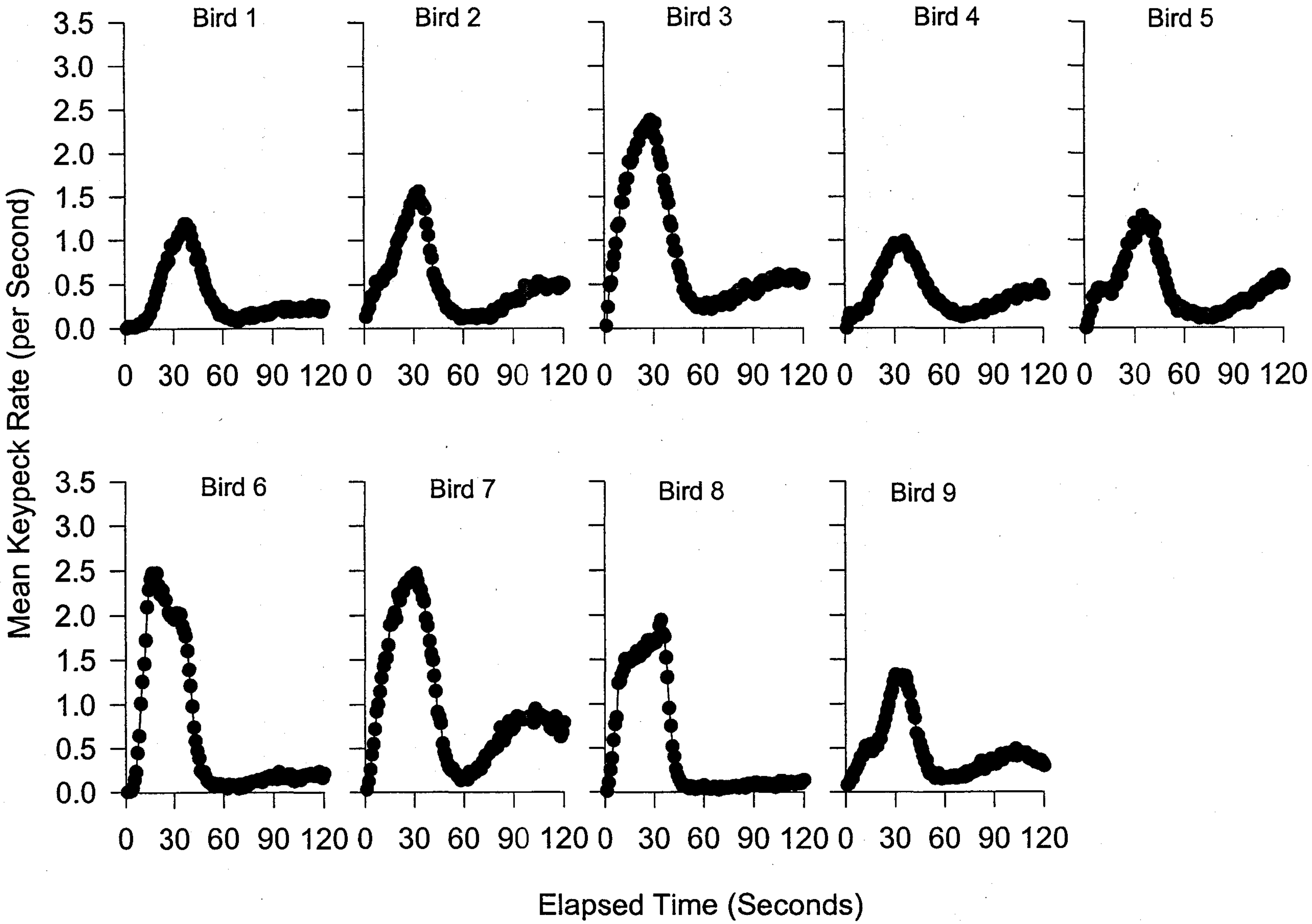

Bird 7
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 8
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 9
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)

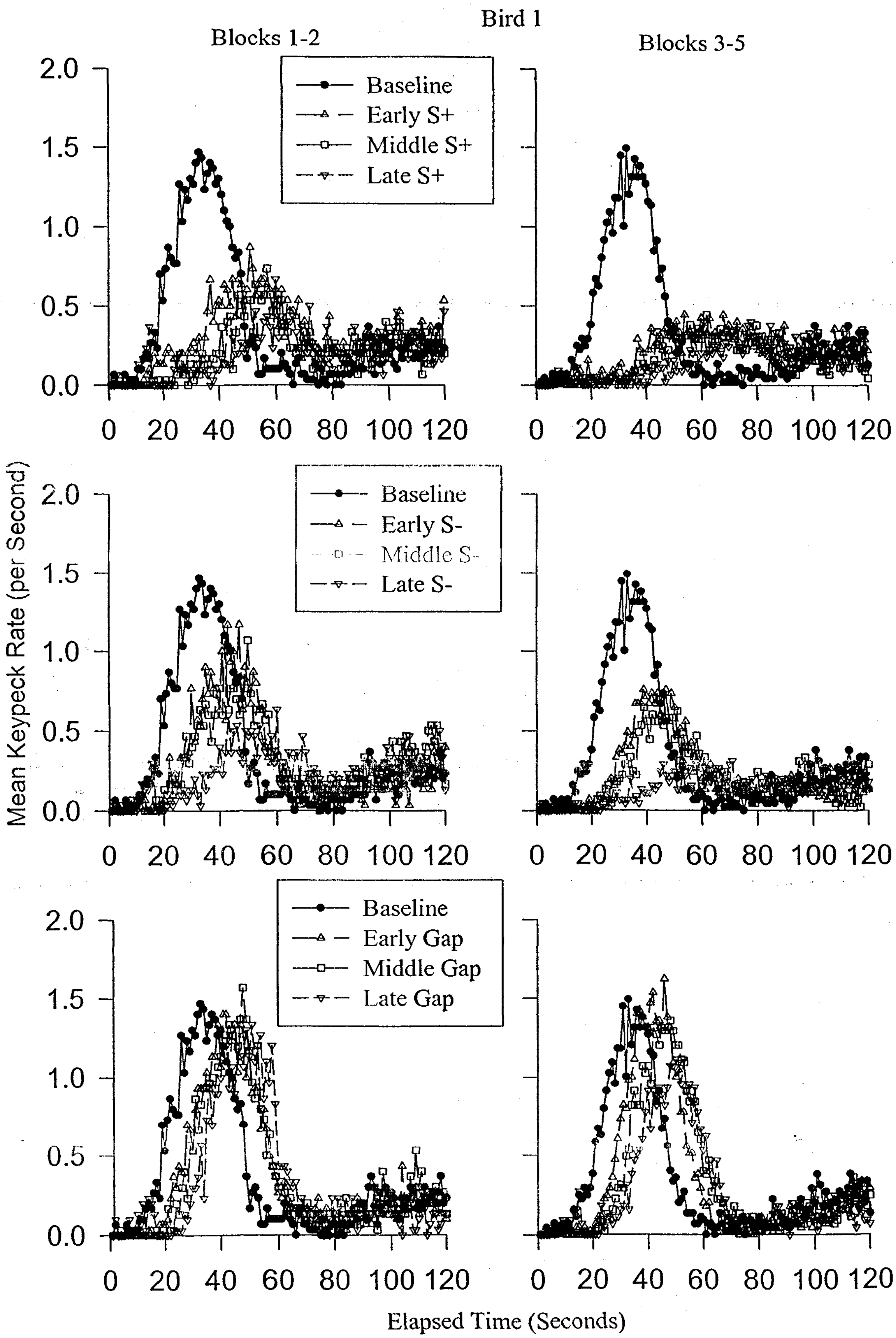
Appendix D

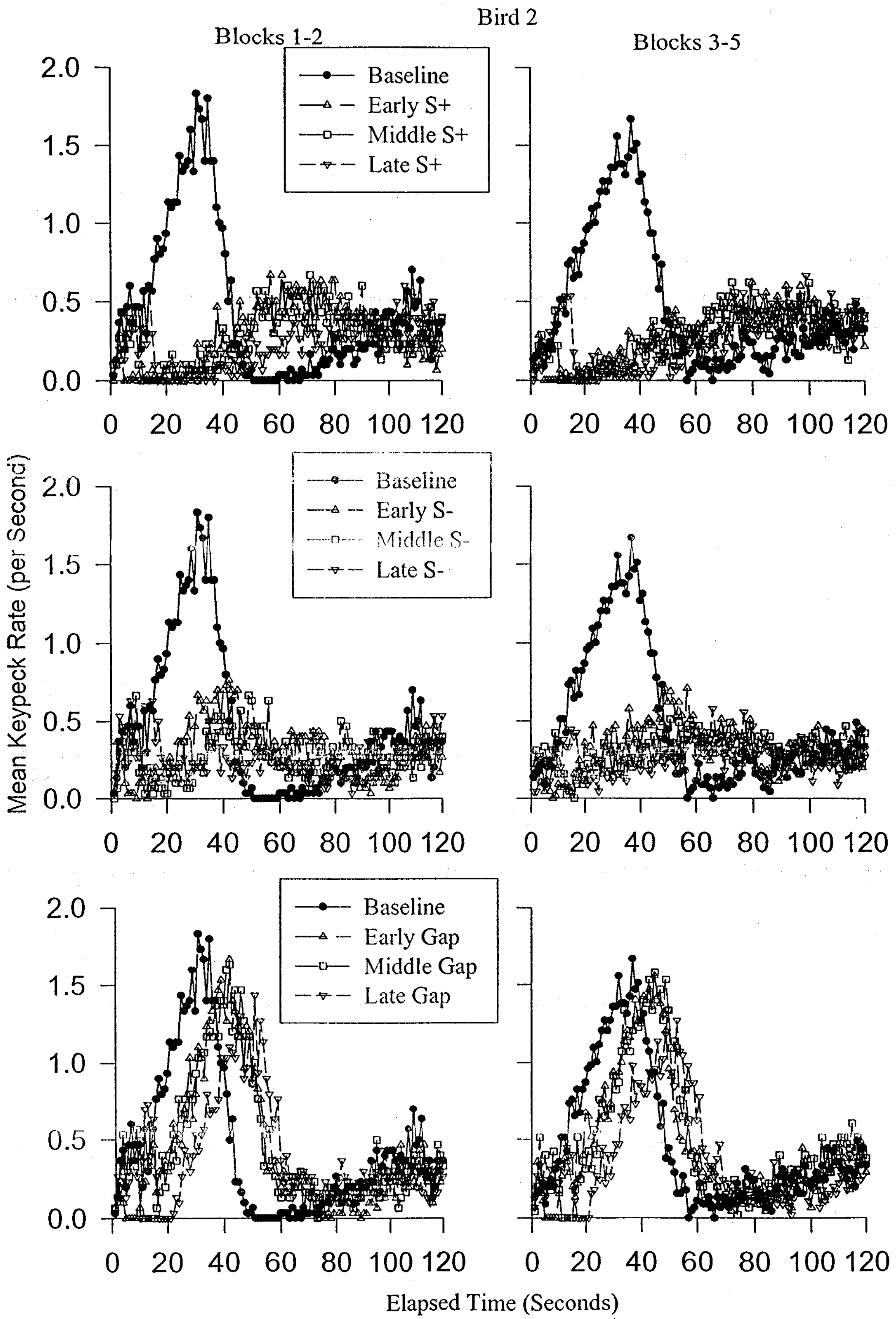
Individual bird's FI-key peck rate (responses per second) as a function of elapsed probe-trial time during the last 10 PI sessions of the alternated PI and discrimination training phase 2.

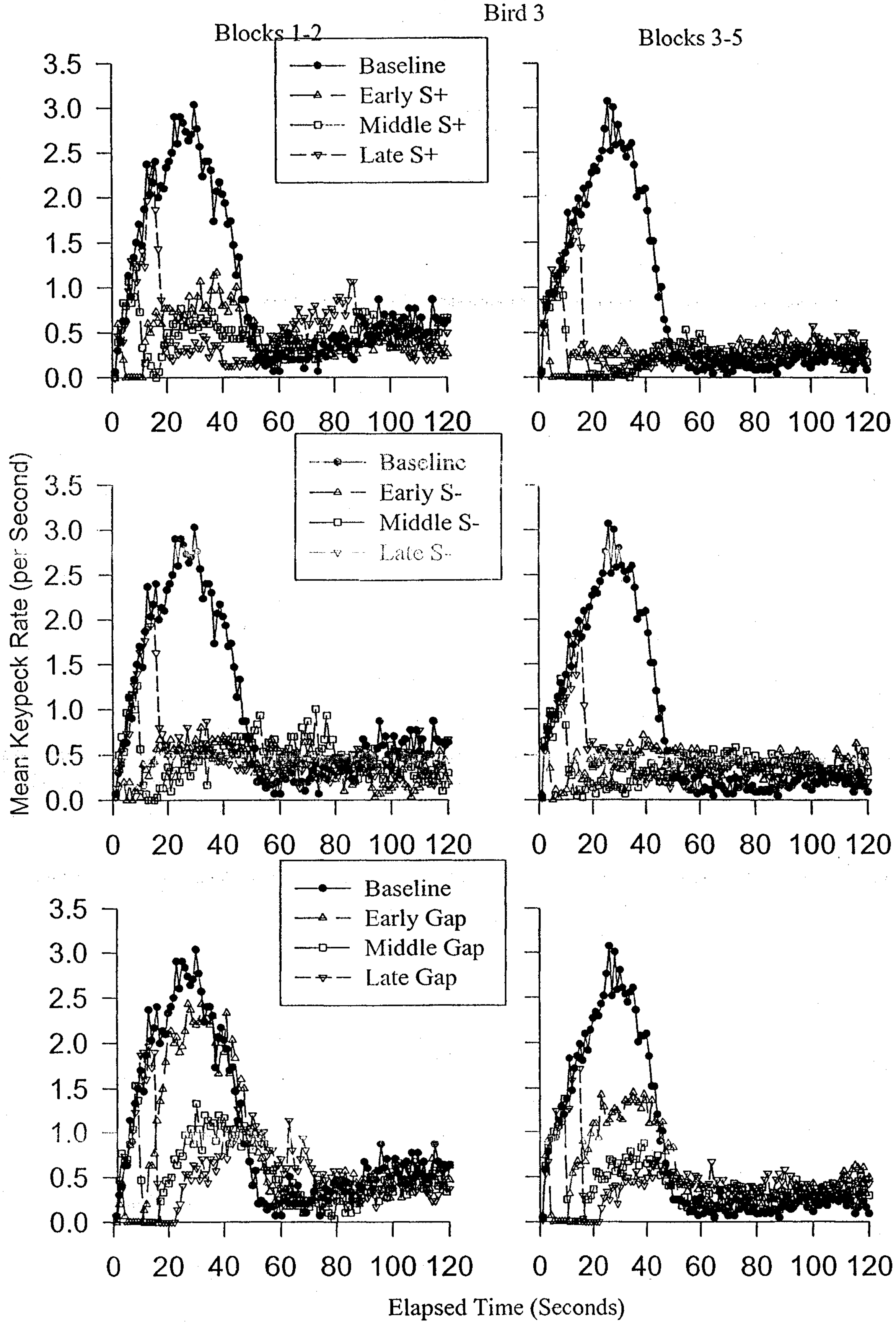

Bird 1
Bird 2
Bird 3
Bird 4
Bird 5
Bird 6
Bird 7
Bird 8
Bird 9
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
30
60
90
120
Elapsed Time (Seconds)

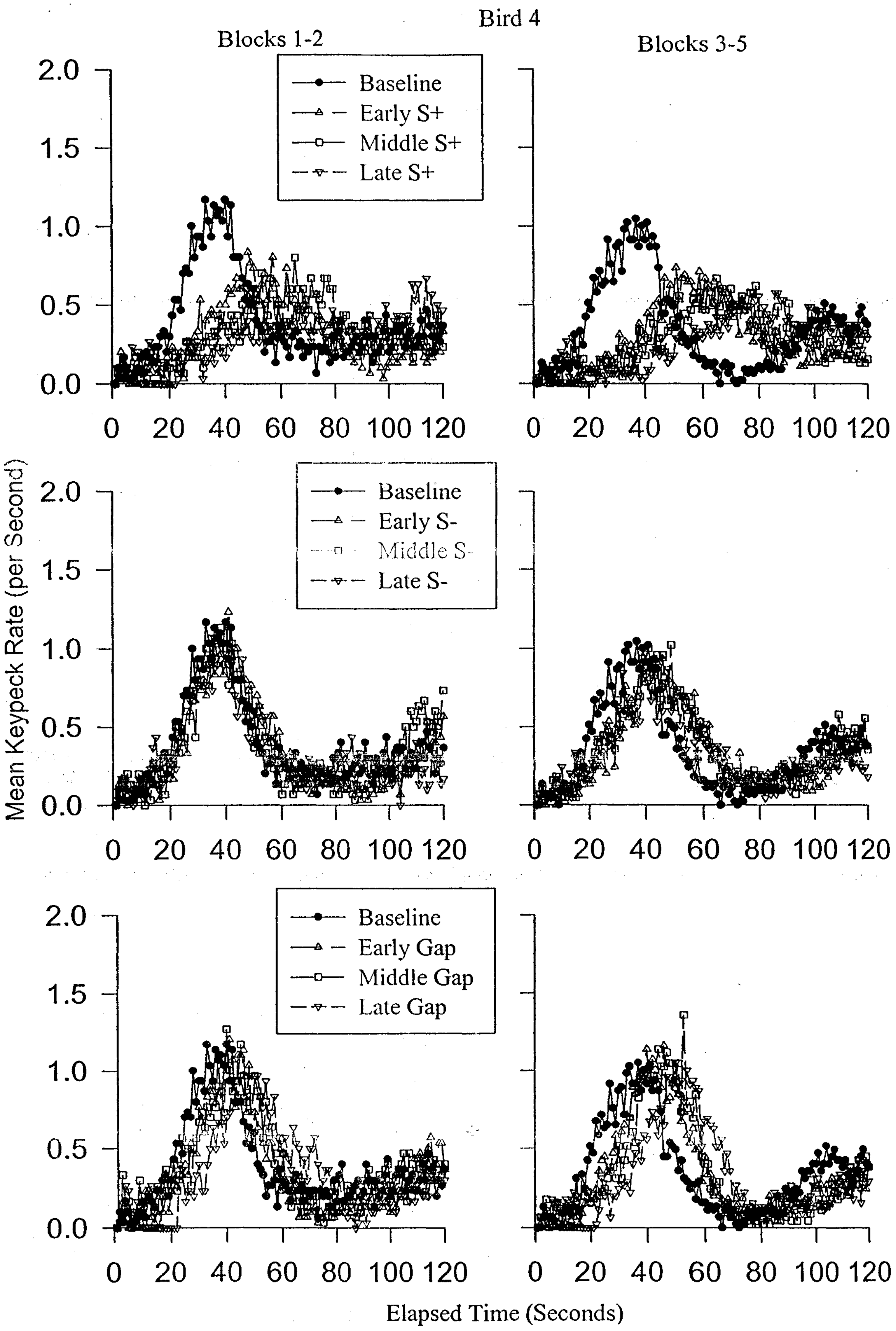
Appendix E

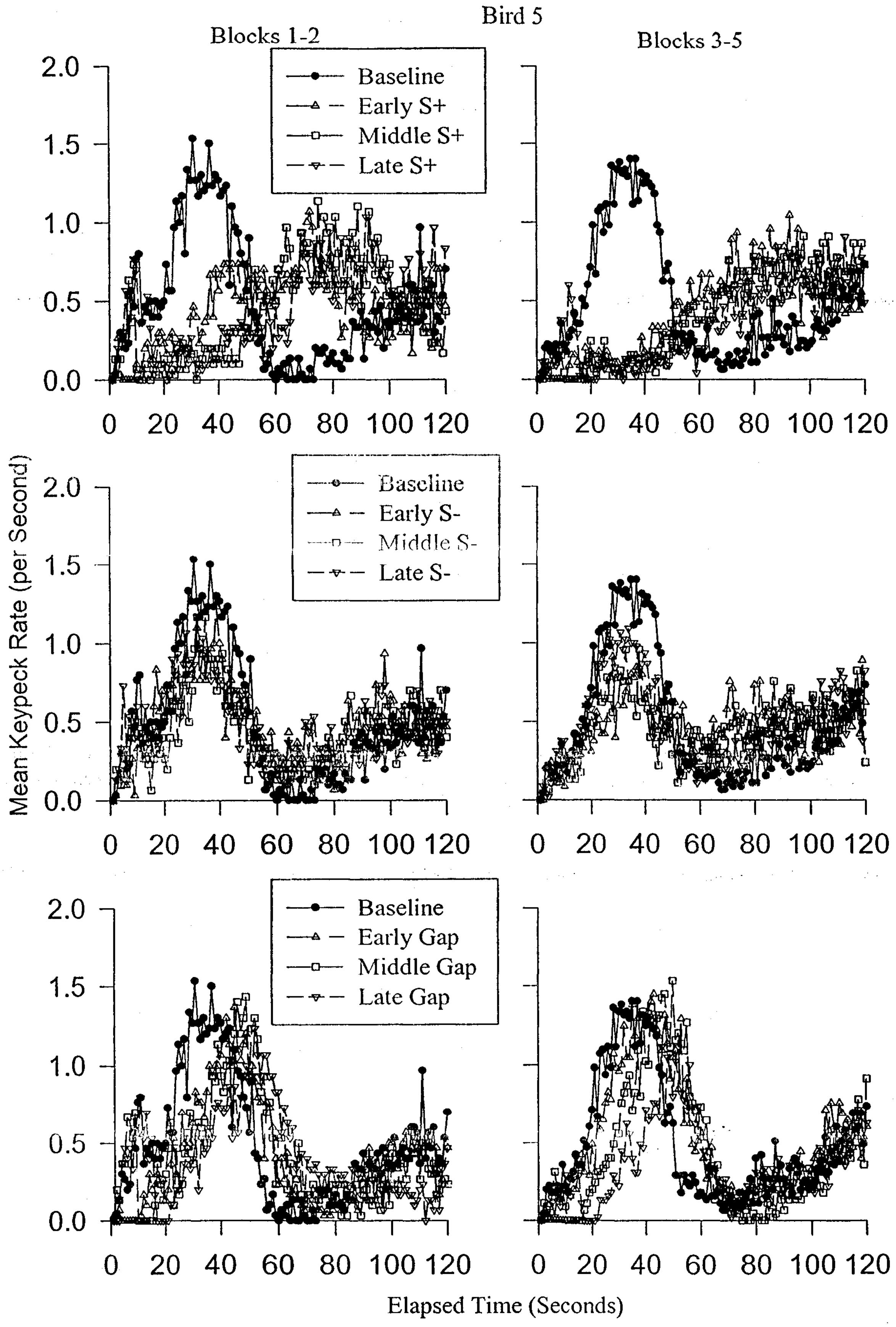
Individual bird's mean FI-key peck rate (responses per second) as a function of elapsed probe-trial time on baseline, S+ (top), S- (middle), and gap (bottom) probe trials during session blocks 1-2 (left) and 3-5 (right) of the task/gap phase 2.

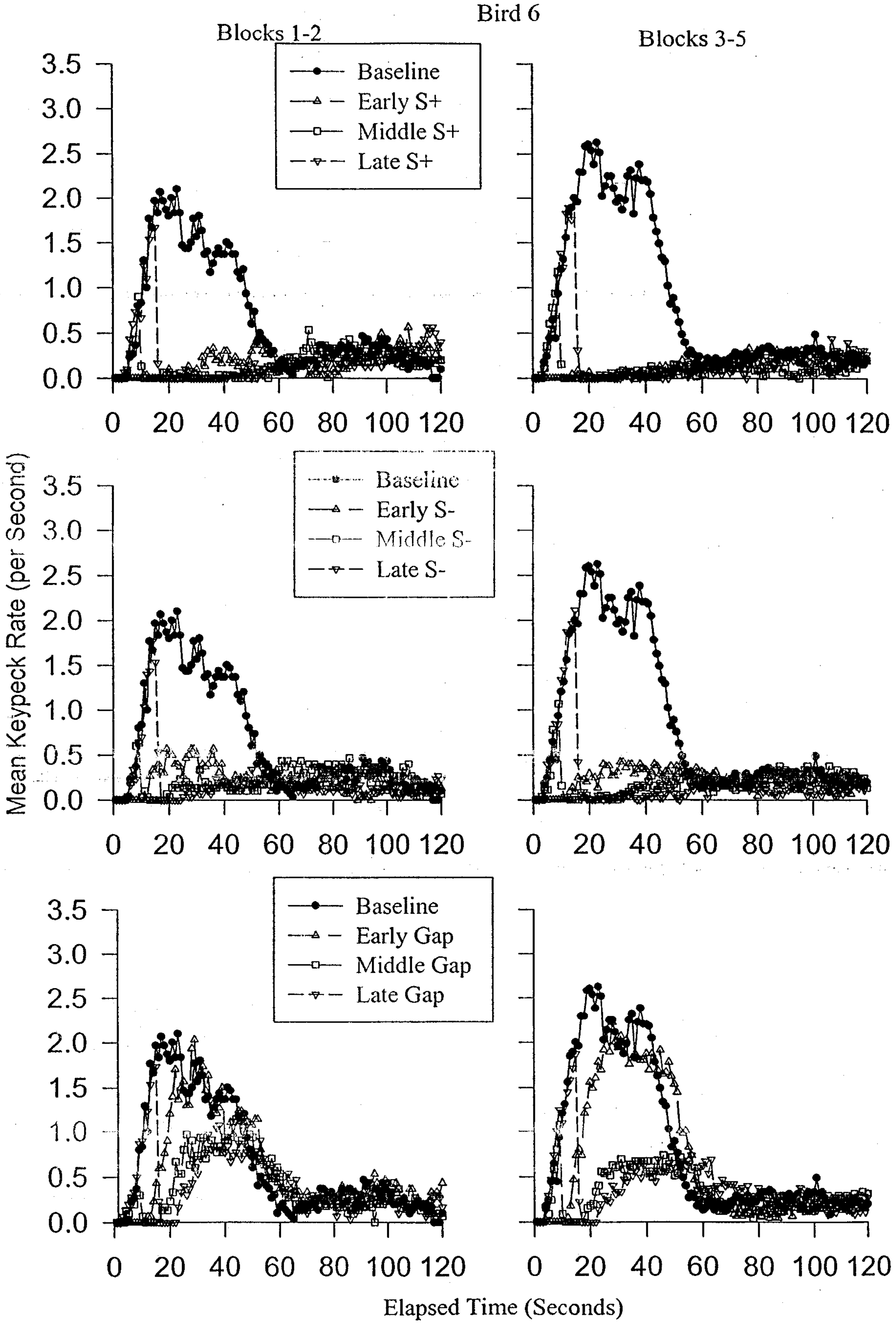

Bird 1
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
0 20 40 60 80 100 120
Elapsed Time (Seconds)

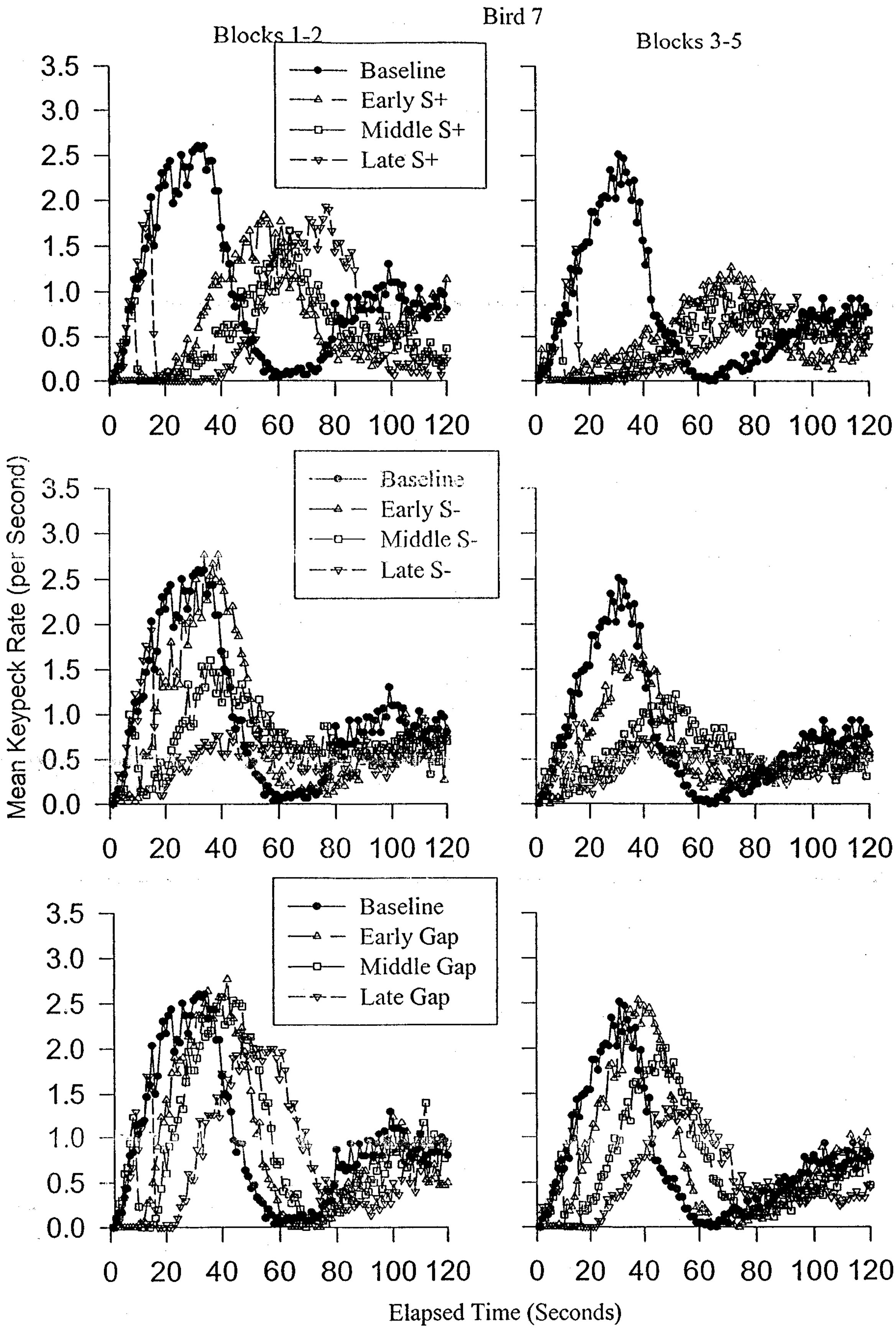

Bird 2
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
0 20 40 60 80 100 120
Elapsed Time (Seconds)

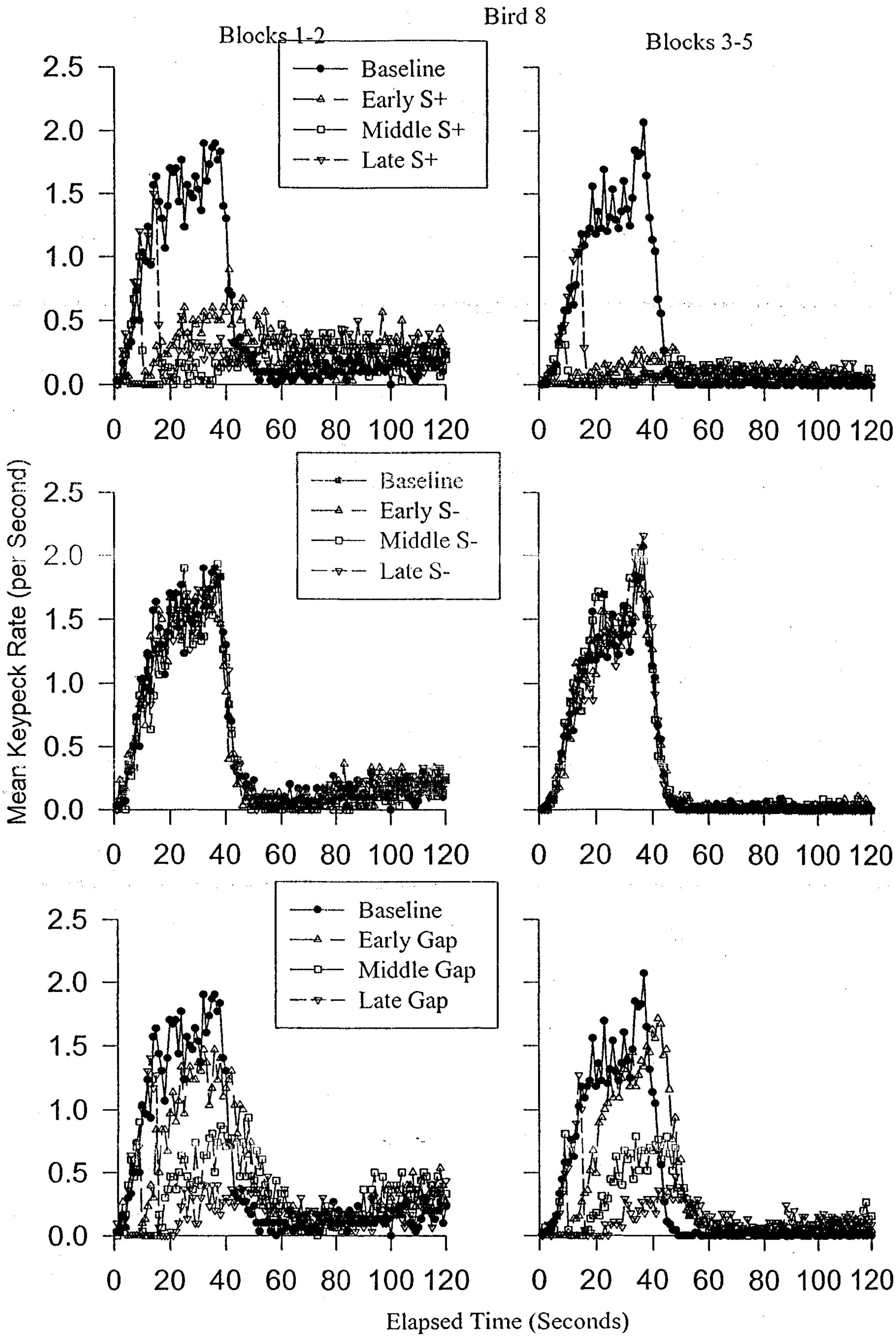

Bird 3
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0 20 40 60 80 100 120
Elapsed Time (Seconds)

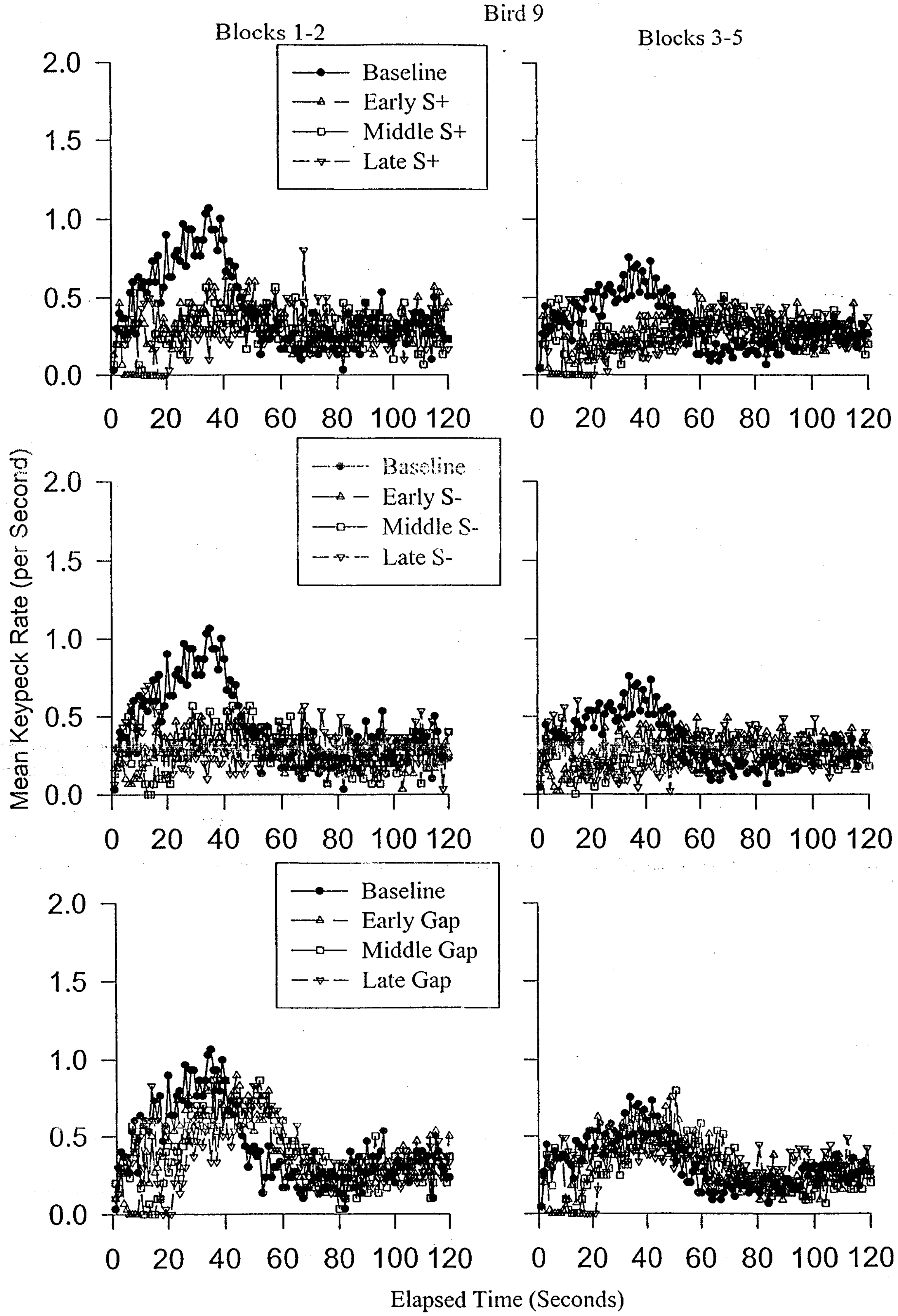

Bird 4
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
0 20 40 60 80 100 120
Elapsed Time (Seconds)


Bird 5
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
Elapsed Time (Seconds)
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
120


Bird 6
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 7
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 8
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
Elapsed Time (Seconds)


Bird 9
Blocks 1-2
Blocks 3-5
Baseline
Early S+
Middle S+
Late S+
Baseline
Early S-
Middle S-
Late S-
Baseline
Early Gap
Middle Gap
Late Gap
Mean Keypeck Rate (per Second)
2.0
1.5
1.0
0.5
0.0
0 20 40 60 80 100 120
Elapsed Time (Seconds)

Appendix F

Birds' discrimination indexes to represent differential responding on baseline and test (S+, S-, and gap) probe trials during blocks 1-2 (top) and 3-5 (bottom) of the task/gap phase 1, extinction phase, and task/gap phase 2.

Task/gap phase 1

	Blocks 1-2								
Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.842	0.895	0.929	0.978	0.913	0.967	0.980	1.137	1.014
2	0.945	0.902	0.783	0.991	0.968	0.929	1.167	1.136	1.113
3	0.827	1.085	0.960	0.930	1.196	0.898	1.050	1.020	0.951
4	1.083	1.020	1.045	1.123	1.210	1.115	1.124	1.125	1.060
5	1.081	0.979	0.911	1.354	1.179	1.081	1.012	0.959	1.015
6	0.512	0.444*	0.419*	0.800	0.810	0.426*	1.028	0.822	0.754
7	0.898	0.956	0.914	0.994	0.966	0.848	0.968	1.017	1.062
8	1.124	1.140	0.956	1.052	0.908	0.942	1.029	1.186	1.076
9	0.670	0.772	0.728	0.818	0.709	0.717	0.909	0.951	0.886
10	1.052	0.951	0.853	1.020	0.907	0.971	1.076	1.155	1.039
Mean	0.903	0.915	0.850	1.006	0.977	0.889	1.034	1.051	0.997

Blocks 3-5

Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.838	0.869	0.822	0.990	1.002	1.026	1.134	1.162	1.130
2	0.743	0.631	0.620	0.785	0.818	0.738	1.020	1.037	1.054
3	0.809	0.789	0.830	0.968	0.999	0.887	0.957	0.864	0.886
4	0.891	0.874	0.812	1.039	1.203	1.102	1.112	1.053	1.199
5	0.979	1.021	0.896	0.998	0.997	1.092	0.887	1.075	0.934
6	0.366*	0.470*	0.275*	0.670	0.570	0.449*	0.974	0.694	0.577
7	0.633	0.704	0.550	1.031	0.865	0.801	0.967	0.901	0.861
8	0.693	0.648	0.584	1.004	0.973	0.896	1.051	1.002	1.040
9	0.488*	0.573	0.476*	0.514	0.509	0.576	1.030	1.020	0.999
10	0.827	0.773	0.780	0.994	0.990	0.890	1.006	1.156	1.091
Mean	0.727	0.735	0.665	0.899	0.892	0.846	1.014	0.996	0.977

Extinction phase

	Blocks 1-2								
Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.636	0.516	0.520	0.745	0.756	0.774	0.934	0.906	1.030
2	0.852	0.796	0.732	0.980	0.963	0.821	1.042	1.041	1.026
3	0.619	0.486*	0.451*	0.976	0.743	0.662	0.752	0.800	0.503
4	0.874	0.849	0.798	1.063	1.055	1.057	1.093	1.065	1.094
5	0.914	0.922	1.068	1.007	1.129	1.093	0.949	1.155	0.953
6	0.421*	0.361*	0.281*	0.532	0.360*	0.312*	0.846	0.633	0.464*
7	0.799	0.774	0.630	1.111	1.005	0.769	1.068	1.075	0.961
8	0.583	0.642	0.747	1.024	1.076	0.863	1.057	0.999	0.923
9	0.600	0.350*	0.373*	0.373*	0.339*	0.416*	0.974	0.885	0.892
Mean	0.700	0.633	0.622	0.868	0.825	0.752	0.968	0.951	0.872

Blocks 3-5

Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.741	0.601	0.578	0.773	0.883	0.702	1.014	1.068	0.995
2	0.749	0.597	0.550	0.865	0.709	0.672	1.012	0.984	0.934
3	0.464*	0.435*	0.561	0.577	0.439*	0.376*	0.496*	0.474*	0.382*
4	0.952	0.876	0.950	0.943	1.014	1.041	1.025	1.061	1.050
5	1.066	1.061	1.047	1.101	1.103	1.079	0.792	0.962	1.110
6	0.520	0.416*	0.406*	0.624	0.382*	0.392*	0.980	0.716	0.458*
7	0.782	0.603	0.537	0.961	0.769	0.616	0.986	0.940	0.794
8	0.886	0.933	0.928	1.014	1.016	0.920	1.066	0.899	0.808
9	0.605	0.431*	0.300*	0.483*	0.470*	0.272*	0.947	0.766	0.735
Mean	0.752	0.661	0.651	0.816	0.754	0.674	0.924	0.875	0.807

Task/gap phase 2

	Blocks 1-2								
Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.864	0.659	0.605	0.819	0.907	0.724	1.026	1.070	1.015
2	0.659	0.637	0.513	0.688	0.632	0.546	0.994	1.062	0.975
3	0.488*	0.451*	0.439*	0.404*	0.454*	0.412*	0.870	0.537	0.558
4	0.845	0.909	0.862	0.951	1.031	1.008	0.967	1.079	1.018
5	0.967	0.938	0.979	1.005	0.938	1.009	0.909	0.903	0.865
6	0.269*	0.231*	0.241*	0.329*	0.342*	0.209*	0.945	0.634	0.598
7	0.722	0.600	0.645	0.908	0.779	0.574	0.976	1.031	0.908
8	0.597	0.380*	0.479*	0.993	0.852	0.828	0.939	0.700	0.414*
9	0.774	0.719	0.721	0.672	0.665	0.690	0.999	0.954	0.876
Mean	0.687	0.614	0.609	0.752	0.733	0.667	0.958	0.885	0.803

Blocks 3-5

Bird	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	0.603	0.542	0.505	0.668	0.660	0.466*	1.053	1.070	0.950
2	0.595	0.604	0.537	0.693	0.644	0.569	1.007	1.111	0.881
3	0.319*	0.267*	0.298*	0.494*	0.393*	0.397*	0.701	0.457*	0.481*
4	0.850	0.851	0.850	0.994	1.113	1.035	1.000	1.020	1.043
5	0.890	0.872	0.782	1.013	1.006	1.075	1.129	0.989	0.829
6	0.150*	0.110*	0.171*	0.275*	0.218*	0.118*	0.835	0.402*	0.427*
7	0.664	0.592	0.552	0.873	0.748	0.590	1.082	0.953	0.793
8	0.274*	0.179*	0.205*	1.057	1.054	0.850	1.004	0.550	0.381*
9	0.869	0.832	0.813	0.913	0.804	0.755	0.990	0.948	1.024
Mean	0.579	0.539	0.524	0.775	0.738	0.651	0.978	0.833	0.756

Note. "*" indicates discrimination index values which are lower than 0.5.

Appendix G

Birds' PTs on baseline and test (S+, S-, and gap) probe trials during blocks 1-2 (top) and 3-5 (bottom) of the task/gap phase 1, extinction phase, and task/gap phase 2.

Task/gap phase 1

Blocks 1-2

Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	37.5	36.5	41.5	46.5	43.5	42.5	47.5	42.5	46.5	46.5
2	30.5	40.5	40.5	45.5	34.5	34.5	36.5	36.5	41.5	47.5
3	25.5	32.5	26.5	31.5	27.5	25.5	31.5	35.5	34.5	37.5
4	35.5	50.5	51.5	50.5	39.5	40.5	36.5	43.5	48.5	50.5
5	30.5	56.5	82.5	74.5	35.5	30.5	31.5	40.5	43.5	43.5
7	31.5	36.5	39.5	42.5	31.5	32.5	34.5	36.5	38.5	47.5
8	24.5	30.5	28.5	31.5	25.5	25.5	31.5	29.5	36.5	39.5
9	32.5	36.5	46.5	55.5	34.5	32.5	38.5	40.5	41.5	45.5
Mean	31.0	40.0	44.6	47.3	34.0	33.0	36.0	38.1	41.4	43.9

Blocks 3-5										
Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	35.5	61.5	55.5	67.5	39.5	46.5	45.5	43.5	45.5	44.5
2	30.5	57.5	62.5	62.5	36.5	36.5	35.5	37.5	42.5	48.5
3	29.5	32.5	43.5	36.5	26.5	27.5	31.5	33.5	36.5	39.5
4	35.5	52.5	58.5	71.5	38.5	35.5	35.5	42.5	44.5	51.5
5	33.5	95.5	83.5	97.5	37.5	36.5	32.5	40.5	45.5	42.5
7	29.5	47.5	51.5	69.5	35.5	33.5	35.5	38.5	43.5	46.5
8	27.5	39.5	38.5	32.5	26.5	25.5	31.5	34.5	35.5	41.5
10	33.5	43.5	60.5	98.5	37.5	36.5	41.5	39.5	42.5	44.5
Mean	31.9	53.8	56.8	67.0	34.8	34.8	36.1	38.8	42.0	44.9

Extinction phase

				Blocks 1-2						
Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	38.5	47.5	61.5	81.5	41.5	42.5	54.5	42.5	44.5	50.5
2	31.5	58.5	68.5	84.5	37.5	39.5	38.5	42.5	43.5	52.5
4	31.5	51.5	54.5	69.5	40.5	37.5	38.5	40.5	42.5	46.5
5	28.5	84.5	92.5	108.5	34.5	31.5	32.5	41.5	40.5	38.5
7	32.5	47.5	53.5	78.5	32.5	30.5	31.5	37.5	43.5	53.5
8	28.5	46.5	51.5	33.5	29.5	28.5	31.5	35.5	38.5	40.5
Mean	31.8	56.0	63.7	76.0	36.0	35.0	37.8	40.0	42.2	47.0

				Blocks 3-5						
Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
1	34.5	43.5	51.5	99.5	41.5	45.5	53.5	41.5	46.5	49.5
2	29.5	39.5	45.5	34.5	35.5	39.5	34.5	39.5	42.5	46.5
4	33.5	46.5	49.5	37.5	39.5	38.5	35.5	40.5	45.5	48.5
5	32.5	81.5	89.5	96.5	36.5	31.5	31.5	36.5	42.5	44.5
7	25.5	38.5	47.5	61.5	30.5	36.5	51.5	33.5	38.5	50.5
8	28.5	31.5	28.5	31.5	27.5	28.5	31.5	32.5	35.5	40.5
Mean	30.7	46.8	52.0	60.2	35.2	36.7	39.7	37.3	41.8	46.7

Task/gap phase 2

				Blocks 1-2						
Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
2	30.5	70.5	61.5	71.5	39.5	46.5	44.5	40.5	39.5	46.5
4	35.5	49.5	69.5	60.5	39.5	39.5	36.5	42.5	42.5	47.5
5	33.5	70.5	79.5	87.5	31.5	35.5	32.5	44.5	46.5	50.5
7	27.5	53.5	62.5	72.5	35.5	39.5	52.5	37.5	41.5	52.5
9	32.5	41.5	37.5	54.5	37.5	40.5	67.5	35.5	45.5	49.5
Mean	31.9	57.1	62.1	69.3	36.7	40.3	46.7	40.1	43.1	49.3

Blocks 3-5										
Bird	BL	ES+	MS+	LS+	ES-	MS-	LS-	EGP	MGP	LGP
2	32.5	87.5	72.5	92.5	50.5	62.5	70.5	40.5	43.5	48.5
4	35.5	56.5	67.5	79.5	44.5	45.5	41.5	43.5	47.5	51.5
5	35.5	86.5	75.5	93.5	36.5	31.5	32.5	41.5	45.5	49.5
7	30.5	71.5	69.5	86.5	35.5	48.5	44.5	39.5	45.5	53.5
9	34.5	65.5	73.5	72.5	38.5	71.5	86.5	39.5	50.5	43.5
Mean	33.7	73.5	71.7	84.9	41.1	51.9	55.1	40.9	46.5	49.3

Appendix H

Group Mean Peak Rate on Baseline, S+, S-, and Gap Probe Trials during Session Blocks 1-2 and 3-5 of the Task/gap Phase 1, Extinction, and Task/gap Phase 2, and Statistical Analysis Results.

Group mean peak rate

Trial types	Task/gap phase 1		Extinction phase		Task/gap phase 2	
	1-2	3-5	1-2	3-5	1-2	3-5
Baseline	1.20	1.24	1.28	1.40	1.35	1.21
Early S+	0.94	0.69	0.70	0.87	0.78	0.65
Middle S+	0.91	0.65	0.64	0.73	0.70	0.56
Late S+	0.80	0.56	0.62	0.71	0.69	0.55
Early S-	1.14	1.09	1.13	1.14	0.99	0.77
Middle S-	1.14	1.09	1.10	0.94	0.78	0.64
Late S-	1.04	0.93	0.93	0.76	0.60	0.59
Early Gap	1.22	1.23	1.38	1.40	1.26	1.22
Middle Gap	1.21	1.16	1.24	1.24	1.25	1.14
Late Gap	1.13	1.08	1.13	1.10	1.06	0.85

Results of Analysis of Variance for Peak Rate

Task/gap phase 1

Source	*df*	*F*
Trial type	2	25.23*
Session block	1	9.08*
Trial type x Session Block	2	1.97

Extinction phase

Source	*df*	*F*
Trial type	2	9.89*
Session block	1	0.01
Trial type x Session block	2	1.27

Task/gap phase 2

Source	*df*	*F*
Trial type	2	11.12*
Session block	1	2.02
Trial type x Session block	2	0.07

*$P < .05$

Post-hoc Test Results for Trial Type and Peak Response Rate

Task/gap phase 1 Session blocks 1-2

Grouping		Mean Peak rate	N	Trial type
	A	1.22187	8	E Gap
	A	1.21125	8	M Gap
	A	1.19958	8	Baseline
B	A	1.14229	8	M S-
B	A	1.13813	8	E S-
B	A	1.13354	8	LGap
B	C	1.03667	8	L S-
D	C	0.93583	8	E S+
D	E	0.90563	8	M S+
	E	0.79521	8	L S+

Session blocks 3-5

Grouping		Mean Peak rate	N	Trial type
	A	1.24306	8	Baseline
	A	1.22819	8	E Gap
	A	1.15903	8	M Gap
B	A	1.09236	8	E S-
B	A	1.08667	8	M S-
B	A	1.07694	8	L Gap
B		0.93000	8	L S-
	C	0.69236	8	E S+
	C	0.64875	8	M S+
	C	0.56347	8	L S+

Extinction phase Session blocks 1-2

Grouping			Mean Peak rate	N	Trial type
	A		1.3799	6	E Gap
B	A		1.2819	6	Baseline
B	A		1.2410	6	M Gap
B	A	C	1.1346	6	L Gap
B	A	C	1.1315	6	E S-
B		C	1.1037	6	M S-
D	C		0.9255	6	L S-
E	D		0.6974	6	E S+
E			0.6356	6	M S+
E			0.6161	6	L S+

Grouping				Session blocks 3-5 Mean Peak rate	N	Trial type
A				1.4044	6	E Gap
A				1.4035	6	Baseline
B		A		1.2433	6	M Gap
B		A	C	1.1354	6	E S-
B	D	A	C	1.0952	6	LGap
B	D	E	C	0.9441	6	M S-
D	E	C		0.8719	6	E S+
D	E			0.7624	6	L S-
E				0.7301	6	M S+
E				0.7094	6	L S+

Task/gap phase 2 Session blocks 1-2

Grouping			Mean Peak rate	N	Trial type
	A		1.3473	5	BL
B	A		1.2597	5	EGP
B	A		1.2460	5	MGP
B	A	C	1.0627	5	LGP
B	D	C	0.9880	5	ES-
E	D	C	0.7847	5	ES+
E	D	C	0.7787	5	MS-
E	D		0.6990	5	MS+
E	D		0.6897	5	LS+
E			0.5990	5	LS-

Session blocks 3-5			
	Mean		
Grouping	Peak rate	N	Trial type
A	1.2164	5	8
A	1.2142	5	1
A	1.1416	5	9
B	0.8529	5	10
C B	0.7664	5	5
C B	0.6527	5	2
C B	0.6387	5	6
C B	0.5889	5	7
C	0.5587	5	3
C	0.5471	5	4

Note. Mean peak rates corresponding to the same grouping letter do not differ significantly; otherwise differences are significant (α = .05). N refers to number of subjects.

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