Effects of intratrial stimulus change on fixed-interval performance: The roles of clock and memory processes

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In two experiments, pigeons were exposed to differentially cued training trials of fixed interval (FI) 30 and 60 sec. In addition, shift trials were presented in which the cue associated with one FI value was presented for a prearranged duration at trial onset, followed by offset of that cue and presentation of the other cue. Response-contingent reinforcement was scheduled during the second cue. During the first shift phase, the FI 30-sec cue was shifted to the FI 60-sec cue; in a second phase, the order of the cue shift was reversed. Inferences about accumulator and memory functions of the internal clock were based upon behavior during both training trials and shift trials. At the end of both shift phases, test-trial FI functions generally superimposed in a manner consistent with accumulator reset on cue shift. Individual differences in clustering of functions were accommodated by variation in reference-memory storage across subjects. This interpretation was tested in Experiment 2 by constraining reference-memory storage on shift trials. These conditions yielded a decrease in between-subject variability and provided data consistent with accumulator reset and control by a single reference-memory value on shift trials.

Recent research on animal timing has been guided by psychological models of timing, usually referred to as internal clock models (Treisman, 1963). The present research is based on the three-process model of timing proposed by Gibbon and Church (1984). The model includes a clock process in which pulses generated by a pacemaker can be gated to an accumulator by a switch. The position of the switch, open or closed, determines whether the clock is stopped or running, respectively.

The value of the accumulator at any moment is a cumulative sum of pulses—that is, the clock is an “up timer” (Church, 1978; S. Roberts & Church, 1978). The accumulator is assumed to reset to zero at reinforcement. The momentary value of the accumulator is stored in the working-memory component of the memory process. The memory process also includes a reference memory in which values contained in the accumulator at the time of reinforcement are stored. The relation between the clock and behavior is governed by the decision process. A comparator continually compares the value contained in working memory with a value stored in reference memory. Responding depends upon the similarity between these two values.

The present research focuses on accumulator and reference-memory processes when the animal is presented with two consecutive temporal events on a given trial. Data bearing on accumulator function have been described by S. Roberts and Church (1978), Cheng and W. A. Roberts (1989), and W. A. Roberts, Cheng, and Cohen (1989). S. Roberts and Church exposed rats to training trials that consisted in presentation of a differentially cued discrete-trial fixed-interval (FI) schedule. Two FI values were trained. On test trials (or shift trials), one FI cue was presented at trial onset, followed by an abrupt shift to the other FI cue. Reinforcement was primed after total elapsed trial time was equal to that on training trials with the postshift cue. Behavior during the postshift cue was examined as a function of duration of the preshift cue, and inferences were drawn regarding accumulator function at the moment of a shift. S. Roberts and Church concluded that pulses accumulated during the first signal were retained in the accumulator and that pulses continued to accumulate until reinforcement occurred. A different conclusion was reached by W. A. Roberts, Cheng, and Cohen, who exposed pigeons to shift trials. In their study, shifts occasioned resetting of the accumulator to zero (but see Cheng & W. A. Roberts, 1989, for a different conclusion). W. A. Roberts et al. tentatively attributed these differences in accumulator function to species effects, although procedural details of the studies also differ. One goal of the present study was systematic replication with pigeons of the procedure used by S. Roberts and Church with rat subjects.

A second important implication can be drawn from these studies. Using the procedure described by S. Roberts and

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Church as a reference, it can be seen that differences in accumulator mode (reset or nonreset) at shift time determine not only the contents of working memory, and therefore performance, on shift trials, they also imply differences in the information stored in long-term (reference) memory at reinforcement on shift trials. In the case of nonresetting, a duration equal to total elapsed trial time will be stored. In the case of resetting at shift time, the accumulator value present at reinforcement will differ as a function of preshift duration. It will also differ from (be shorter than) the training duration associated with the post-shift cue. Therefore, the reset mode will increase the variability among stored durations associated with the post-shift cue. This, in turn, will influence the decision process on individual trials, as the comparator samples an increasingly variable set of remembered durations. Thus, under certain conditions, the clock model predicts change in shift trial and FI training-trial performance during the postshift cue as a function of repeated exposure to shift trials. Specifically, as variability of reinforced duration increases, performance should come to resemble that associated with variable-interval (VI) schedules (Catania & Reynolds, 1968; Lund, 1976).

The present research tested the foregoing predictions of the internal clock model. In Experiment 1, pigeons were exposed to the procedure employed by S. Roberts and Church (1978). Accumulator mode (resetting or nonresetting) on shift trials was assessed quantitatively. In a novel aspect of the present study, a second, independent assessment of reference-memory function was achieved by comparing performance on training trials before and after introduction of test trials. If resetting is indicated, and reference memory is accessed under poor stimulus control, then training-trial performance during the post-shift cue should change to reflect storage of a range of durations shorter than the FI parameter.

In Experiment 2, the predictive strength of the internal clock model was evaluated. This experiment was prompted in part by the results of Experiment 1 and those reported by Cheng and W. A. Roberts (1989), which were similar in demonstrating between-subject variability in shift-trial performance. Application of the clock model to these data implicated variability in reference-memory storage under a reset mode as the source of the variability in both studies. This interpretation was tested by exposing the subjects from Experiment 1 to a procedure designed to constrain the range of durations stored in reference memory on shift trials. As in Experiment 1, performance on shift trials was assessed for accumulator mode, and training-trial data were analyzed as an index of reference-memory function.

EXPERIMENT 1

Method

Subjects

Four adult White Carneau hen pigeons were maintained at 80% of their free-feeding weights. They were housed in individual home cages with grit and water continuously available, under a 14:10

light:dark cycle. All 4 pigeons had experimental histories in an auto-shaping experiment with colors and patterns as stimuli. One bird (Bird 4749) died during a 21-month interval between phases Shift 30-60 and Baseline 2.

Apparatus

The experiment was conducted in a locally made pigeon chamber having the same dimensions as BRS/LVE Chamber Model SEC-002. A three-key intelligence panel was employed that had the same dimensions and components as BRS/LVE Model PIP-016. Only the center key was used. An IEE stimulus projector (Model 00010-01-B272-1820) could transilluminate the center key with red or green light. Masking noise was provided by a ventilation fan and a white-noise generator. An IMSAI microcomputer, located in an adjacent room, arranged the experimental contingencies and recorded data.

Procedure

Baseline 1 phase (Sessions 1-40). In this phase, discrete trials of FI 30 sec and FI 60 sec were presented. Forty of these training trials were presented in each session, 20 of each type randomly mixed. For 2 pigeons (Birds 5400 and 1292), FI 30-sec trials were signaled by the red keylight; FI 60-sec trials were signaled by the green keylight. For the other 2 pigeons, the colors were reversed. A trial began with the presentation of either red or green on the center key. After 30 or 60 sec, food was primed. The next peck on the center key produced food and turned the keylight off to end the trial. The mean intertrial interval was 20 sec (15-sec minimum plus a 5-sec mean of a geometric distribution). The houselight, located above the center key, was continuously illuminated during experimental sessions.

Shift 30-60 phase (Sessions 41-66). During this condition, sessions included 10 shift trials and 30 training trials in random order (20 trials of FI 30 sec and 10 trials of FI 60 sec). A shift trial started with the FI 30-sec signal and shifted to the FI 60-sec signal, which remained on for the rest of the trial. Shifts could occur 6, 12, 18, 24, or 30 sec after trial onset, and food was primed 60 sec after the trial began.

Baseline 2 phase (Sessions 67-87). During the next 21 sessions, Baseline 1 conditions were reinstated.

Shift 60-30 phase (Sessions 88-113). The procedure was similar to that described for phase Shift 30-60, except that shifts now occurred from the FI 60-sec signal to the FI 30-sec signal. In each session, 10 FI 30-sec, 20 FI 60-sec, and 8 shift trials were randomly mixed. Shift trials began with the FI 60 signal and shifted to the FI 30 signal after 6, 12, 18, or 24 sec from trial onset. Food was primed 30 sec after the trial began.

Throughout all phases of Experiments 1 and 2, the first 10 trials of a session consisted of 5 FI 30-sec and 5 FI 60-sec training trials, randomly mixed. Data from these trials were not included in any analyses. Pecks to the center key were recorded in 1-sec bins.

Results and Discussion

Figure 1 presents mean responses per minute plotted against trial time (scaled in successive 3-sec intervals) during the last 10 sessions of the Baseline 1 phase. The 4 birds showed similar patterns: Response rate generally increased during the trial, except for the nonmonotonic function on the 30-sec trial for Bird 5400. For all birds, rates on 30-sec trials were higher than those on 60-sec trials.

Shift 30-60

Performance of individual birds during the last 10 sessions of the Shift 30-60 phase is presented in Figure 2, which shows response rate as a function of time, sepa-

Figure 1. Mean rate of responding as a function of elapsed trial time during the last 10 sessions of the baseline phase of Experiment 1. Rate is plotted separately for FI 30-sec and FI 60-sec trials.

ately for 30-sec and 60-sec training trials and for each of the test trials designated by duration of the preshift period. Only postshift data are shown for test trials. In the left panel, test-trial functions are plotted with respect to time since trial onset (trial time); in the right panel, time begins with the occurrence of the stimulus change (shift time). In both panels, data from training trials (FI 30-sec and FI 60-sec trials) are presented with respect to trial time, for comparison.

Accumulator process. Performance on test trials should reflect resetting versus nonresetting of the accumulator upon a cue shift. If the accumulator does not reset, then subjective time following the shift should be equivalent to subjective elapsed time from trial onset. In that case, postshift performance on all test trials should resemble performance on the long-delay training trial when data are plotted in trial time (i.e., the functions should superimpose). For Bird 1292, cue shifts produced abrupt, transient decrements in response rates, which subsequently rose to converge uniformly upon the 60-sec training function. The data for this bird support the inference that the accumulator did not reset, since test functions plotted against trial time showed greater superposition than when plotted against shift time.

If the accumulator does reset upon a cue shift, then, at a given elapsed time from trial onset, subjective times following the shift should differ among test trials, and

functions should diverge when plotted in trial time. Since subjective time reckoned from the shift should be equivalent, however, test functions may be expected to superimpose when plotted in shift time. Figure 2 indicates a greater degree of clustering of test-trial functions for Birds 4167, 5400, and 4749 when plotted in shift time than when plotted in trial time, supporting a reset interpretation for those birds.

A quantitative analysis was undertaken to provide a numerical index of superposition (S. Roberts, 1981). Total variance of test-trial function values was partitioned into variance attributable to the mean of the functions at different points in time and remaining, or error, variance. The index of superimposition was taken as the proportion of variance accounted for by the mean (i.e., explained variance/total variance). Rates entered the computation for each second in which data were available for two or more trial types. Calculations were made separately with and without inclusion of the 60-sec training-trial function, since it is possible that test functions may cluster around values that differ from those of the training function. The first and second index values presented in each panel of Figure 2 are computed with and without the training-trial function, respectively. Results were in line with visual inspection of the data. For Bird 1292, the superposition index was maximal for the trial-time plot with inclusion of the training trial. For Birds 4167 and 4749, the indices were max-

Figure 2. Individual birds' performance on training and test trials during the last 10 sessions of Experiment 1, phase Shift 30-60. Rate is plotted as a function of elapsed trial time in the left panel and as a function of postshift time in the right panel. The functions include performance on the FI 30-sec and FI 60-sec training trials, and rate during the postshift, FI 60-sec stimulus on shift trials. The legend indicates duration of preshift time for each shift-trial function. For example, "Sh 6" refers to data from trials on which the shift occurred 6 sec after trial onset. Bird numbers are indicated in the upper left corner of each panel, and superposition indices (see text for explanation) are presented in the lower right corners.

imal for shift-time plots with inclusion of the training trial. For Bird 5400, the index marginally favored accumulator reset (shift-time plot) without inclusion of the training trial.

Initial test performance for the group of birds was also examined. On the first two sessions (four test trials of each type), group mean data indicated nonresetting: Superposition indices (training trial included) were .74 and .50 for trial and shift time, respectively. Three of the 4 birds yielded individual functions in line with the group means; however, data for Bird 4167 suggested resetting of the clock. Thus, a nonreset mode may be supplanted by the reset mode with increased amounts of training.

Memory process. Adoption of a reset mode on test trials implies that reinforcer delivery will occur at accumulator values shorter than the 60-sec duration associated with the long-delay cue on training trials. Thus, novel reference times will be stored following test trials. Test-trial performance should depend upon how reference-memory access is achieved among a range of alternatives. At one extreme, the long-delay cue may control storage (and retrieval) of subjective times on training and test trials alike, resulting in the establishment of a single, heterogeneous set of stored times. In this case, sampling from reference memory on all trials with the long-delay cue would yield a wide range of values, and response-rate functions might be expected to resemble behavior on a VI schedule with little or no evidence of "timing." Moreover, training- and test-trial functions should superimpose when plotted in shift time. The relatively flat superimposed functions in the shift-time plots for Birds 4167 and 4749 conform to this pattern.

At the other extreme, subjective times of reinforcement on each of the test trials and the training trial may be stored (and retrieved) under stimulus control by preshift cue duration. In this case, different homogeneous sets of stored times would be accessed across trial types, although the degree of stimulus control implied by this alternative may require large amounts of overtraining. Intermediate degrees of stimulus control are possible. For instance, discrimination between test trials and the long-delay training trial would establish two sets of stored times, leading to VI performance on test trials while preserving temporal control on the training trial. The performance of Bird 5400 appears to reflect resetting of the accumulator with retrieval under this sort of stimulus control.

In the present design, inferences based on the superposition of functions are independently verifiable from a comparison of performance on training trials during baseline and test-trial phases. There are two conditions under which training-trial performance should remain unaffected by test trials. One occurs when the accumulator does not reset upon a cue shift, and the second obtains when the accumulator does reset, but reference memory is differentially accessed on training and test trials. In both cases, reference-memory storage and retrieval remain unchanged following the introduction of test trials, and temporal control characteristic of the FI schedule on training trials

should not be adversely affected. These conditions held, respectively, for Birds 1292 and 5400, according to the foregoing analyses.

On the other hand, if the accumulator resets upon a cue shift, and reference memory is accessed identically on training and test trials, then temporal control on training trials should resemble VI performance during the test phase. Thus, when overlap is found between training- and test-trial functions, as indicated in the foregoing analysis for Birds 4167 and 4749, the training-trial function should be affected in two ways. First, while both simple- and discrete-trial FI schedules produce well-behaved increasing rate functions over time, VI schedules yield stable rates (Ferster & Skinner, 1957). Thus, the training-trial function should be steeper during baseline phases than during testing phases. Second, overall rate of response should be affected. VI schedules tend to maintain higher average rates than do FI schedules when schedule values are identical (Catania & Reynolds, 1968; Lund, 1976; Mandell, 1980). In fact, in the present case, the variable intervals generate an average interval shorter than the fixed interval on the training trial. For both reasons, training-trial functions should exhibit higher overall rates during testing phases than during baseline phases.

Effects upon training-trial performance were evaluated quantitatively from an analysis of interval schedule performance provided by Lund (1976). In that analysis, behavior on FI and VI schedules was described in terms of the relation, $R = aT^k$, where R is momentary rate of response and T is elapsed time since the start of an interval. Lund exposed pigeons to two manipulations that yielded continua along which schedule properties moved from VI to FI. Expected variations in momentary-rate functions were produced: Relatively sharply rising functions under FI conditions gave way to flatter functions as VI endpoints were approached, largely as a result of rate increases occurring earlier in the interreinforcer interval. These effects were captured, respectively, by the constants k and a of the power function, determined as least squares estimates. As sensitivity to elapsed time, k , decreased, a varied inversely.

Lund's analysis was applied to the training-trial behavior in the present study to determine if response characteristics shifted from FI- to VI-like performance between the last 10 sessions of baseline and test phases. Constants were obtained by a linear regression analysis after log transforms of elapsed-time values (1-60 sec) and corresponding momentary rates. Estimates of both constants, explained variance, and overall rate for the 60-sec training function in each phase are presented in Table 1. The results indicate agreement between conclusions suggested by inspection of test-trial performance and changes in the training-trial function from baseline to test phase. The 2 birds (Birds 4167 and 4749) whose data clearly indicated a reset mode with clustering of training and test functions also exhibited changes in a , k , and overall rate consistent with the development of VI-like performance in the test phase. No deterioration in FI performance was

Table 1
Parameter Estimates in the Relation $R = aT^k$
and Overall Rates for Training-Trial Functions

Bird	Condition	<i>a</i>	<i>k</i>	<i>r</i> ²	Rate (rpm)
Experiment 1: Shift 30–60 Phase					
1292	Baseline	6.37	.81	.97	97
	Testing	7.23	.87	.86	131
4167	Baseline	1.71	1.01	.96	52
	Testing	2.48*	.93*	.91	58
5400	Baseline	2.27	.95	.97	56
	Testing	.78*	1.23*	.95	52
4749	Baseline	1.95	.94	.97	47
	Testing	12.64*	.49*	.64	64
Experiment 1: Shift 60–30 Phase					
1292	Baseline	26.03	.70	.81	166
	Testing	23.55	.70	.87	150
4167	Baseline	12.54	.86	.81	124
	Testing	110.52*	.13*	.25	155
5400	Baseline	2.86	1.10	.90	56
	Testing	13.31*	.88*	.74	142
Experiment 2					
1292	Baseline	11.64	.98	.85	165
	Testing	6.45*	1.14	.88	146
4167	Baseline	9.47	.87	.82	99
	Testing	4.38*	1.06	.78	80
5400	Baseline	2.37	1.28	.97	80
	Testing	1.99	1.33	.95	79

Note—For Experiment 1, Shift 30–60 phase, 60-sec training trials are represented; for remaining entries, data refer to 30-sec training trials.

*A reliable difference between parameter values (see text).

found or expected for the remaining two birds. For one of these birds (5400), reliable changes were obtained in parameter values in the direction of sharpened temporal control. Reliability of the change in parameter values between phases was calculated with one-tailed *t* tests at the .05 significance level. The denominator of *t* was calculated as the square root of the sum of squared standard errors of parameter estimates from each phase. Degrees of freedom were 116 and 58, respectively, for comparisons involving 60- and 30-sec training-trial durations.

Shift 60–30

Figure 3 shows performance for individual birds during the last 10 sessions of the Shift 60–30 phase. For all 3 birds, response-rate functions showed clearly greater clustering when plotted against shift time than when plotted against trial time, indicating a reset mode in each case. Thus, adoption of the reset mode does not appear to depend upon the direction of change in signaled delay to reinforcement under the conditions of the present experiment.

However, performance differed among birds. For Subjects 4167 and 5400, the training- and test-trial functions were clustered; however, for Bird 1292, the superimposed set of test functions was well separated from the short-delay training function. The superposition indices support the visual impressions that a reset mode was adopted by all 3 birds and that Birds 4167 and 5400 accessed reference memory identically on training and test trials, whereas

Bird 1292 accessed long-term memory differentially under stimulus control.

The foregoing inferences imply that temporal control on training trials should deteriorate during the Shift 60–30 phase relative to the Baseline 2 phase for Birds 4167 and 5400, but not for Bird 1292. These expectations were confirmed in regression analyses of the short-delay training-trial functions in both phases. As indicated in Table 1, parameter values for birds changed in the direction of VI-like performance for Subjects 4167 and 5400, but not for Bird 1292.

Conclusions

The results of Experiment 1 indicate that species is clearly not the only determinant of accumulator mode. Three of 4 pigeons in Experiment 1 initially exhibited non-resetting, as reported for rats (S. Roberts & Church, 1978). However, following additional training under identical conditions, only 1 bird retained the nonreset mode. Furthermore, at the end of the second shift phase, all 3 birds exhibited reset behavior. Thus, the accumulator mode is subject to modification within subjects. One possible determinant of mode may be amount of training. The nonreset mode has been observed generally in naive subjects or early in training (Gibbon & Balsam, 1981, split-trials procedure; S. Roberts, 1981, Experiments 2 and 5; S. Roberts & Church, 1978), whereas the reset mode has appeared following more extensive training (Cheng & W. A. Roberts, 1989; W. A. Roberts et al., 1989), a pattern of results in line with that of Experiment 1.

These and other data indicating resetting on stimulus change in pigeons may be contrasted with data (Dews, 1962; Gibbon & Balsam, 1981; Stubbs, Dreyfus, & Fetterman, 1984) and theory (Gibbon & Balsam, 1981) supporting temporal integration in pigeons. For example, using a conditional discrimination task based on stimulus duration, Stubbs et al. reported evidence of temporal summation of like-component durations in an ABAB stimulus sequence. Temporal integration of such events implies a clock that does not reset when a stimulus change occurs. Numerous procedural differences distinguish these studies, but one feature common to them is the repeated presentation of the target cues prior to reinforcement. In contrast, studies reporting resetting have employed successive stimulus compounds of nonrecurring components. The roles of stimulus sequence and training history in resetting remain to be determined, but it is clear from the existing data that accumulator mode, like other clock functions (Church, 1984), is not fixed.

Although terminal performance in Experiment 1 strongly supported resetting, substantial individual differences among birds on test trials indicate that accumulator mode does not account for all the variance observed in test-phase behavior. It is proposed that such differences may be explained by differences among birds in accessing long-term memory. Comparisons of training-trial performance during baseline and shift phases independently confirmed inferences concerning storage/retrieval patterns. This

Figure 3. Performance of individual birds on training and test trials during the last five sessions of Experiment 2. The format of this figure is identical to that of Figure 2.

analysis was pursued in Experiment 2, which tested the implication of constraints on the memory process under conditions of accumulator reset.

EXPERIMENT 2

While the present data and those of W. A. Roberts et al. (1989) provide considerable evidence for accumulator reset when pigeons are exposed to a stimulus shift, an alternate interpretation has been advanced by Cheng and W. A. Roberts (1989), who also studied pigeons under a shift procedure. Cheng and W. A. Roberts concluded

that their subjects did not reset at shift time. Rather, the birds were said to time both the entire trial and the post-shift duration, with performance being governed by a weighted average of these durations. Although their account does not anticipate the evidence for stimulus control of timing behavior found in the present study, it bears consideration. Therefore, in Experiment 2, we sought additional evidence for accumulator reset upon cue shift.

A second purpose of Experiment 2 was to rule out non-temporal factors as the source of individual variability observed in Experiment 1. On the present analysis, individual differences in performance resulted from differences

in accessing long-term memory of postshift duration. Alternatively, individual differences unrelated to clock function may have produced these effects. In Experiment 2, we sought to substantially reduce individual variability in performance by constraining the range of durations available for storage on test trials. Test trials were administered as in the last phase (Shift 60–30) of Experiment 1, except that postshift cue duration was held constant at 30 sec. If the accumulator is reset upon cue shift, a constant 30-sec duration will be represented in the accumulator at reinforcement during shift trials. Therefore, only one set of homogeneous durations should be stored and retrieved by the postshift cue on training and test trials, regardless of preshift duration. Training- and test-trial performance should therefore conform to the pattern of responding normally associated with the FI schedule presented on training trials. Of course, if animals do not reset upon cue shift, as suggested by Cheng and W. A. Roberts, performance should be consistent with storage and retrieval of a heterogeneous set of durations.

Method

Subjects and Apparatus

The subjects and apparatus were the same as those of Experiment 1.

Procedure

Baseline conditions (training trials only) were reinstated for the first 29 sessions. During Sessions 143–168, shift trials were introduced. There were 8 shift trials, 10 FI 30-sec trials, and 20 FI 60-sec trials, randomly mixed, each session. Shift trials were identical to those in the Shift 60–30 phase of Experiment 1, except that the postshift (FI 30-sec) signal was always 30 sec in duration. Therefore, food was primed at different elapsed trial times depending on the shift point: 36, 42, 48, or 54 sec after trial onset.

Results and Discussion

Performance during the last 10 sessions is shown in Figure 4. Although each test trial lasted 30 sec, functions were truncated for purposes of comparison at the values appropriate to Experiment 1. As expected, the results clearly supported the reset mode for all 3 birds. In addition, superposition indices for calculations with and without the training trial were close for all 3 birds, as would be expected if a common reference-memory value were accessed on both training and test trials.

A second source of evidence regarding reference memory is provided in Table 1 by the parameter estimates from the power-function analysis of the training-trial function during baseline and test phases. Even if birds accessed different reference-memory values on training and test trials, as some appeared to do in Experiment 1, the use of a constant delay in Experiment 2 should have severely constrained the range of stored delays, identically for baseline and test phases. The parameter estimates in Table 1 support this outcome: the values indicated that temporal control was not disrupted for any bird in the training-to-test transition. Indeed, all 3 birds exhibited enhanced control by parameter value changes (increase in k , decrease

in a), differences in a being reliable for 2 of the birds (Birds 1292 and 4167). Response rates also changed in a congruent direction. Although these changes are not necessarily predicted by the reference-memory process, they are not at variance with it, and they may be expected as an instance of enhanced temporal control resulting from extended exposure to an FI schedule (Cumming & Schoenfeld, 1958; Schneider, 1969).

Comparisons of Figures 3 and 4 reveal greater agreement among birds in response patterns in Experiment 2, as predicted from the imposed schedule constraint on values stored on shift trials. Moreover, consistent with the present analysis, maximum superposition indices were higher in Experiment 2 for each bird. Thus, the data support the interpretation of individual differences in Experiment 1 in terms of variability in values stored in reference memory, while rejecting nonclock-related variance as the source of this effect.

An unanticipated result was the elevation of test-trial rates relative to the training-trial function in the shift-time figures. It is possible that these differential rates reflect differences in the prevailing response rate on the 60-sec cue at the moment of stimulus change. Pearson correlations calculated between rates on the first postshift 1-sec bin and on the preceding preshift bin at each of the four test-trial durations yielded high positive correlations for each bird ($r = .87, .98$, and $.84$, for Birds 1292, 4167, and 5400, respectively). Thus, initial differences in postshift response rates among test trials are not incompatible with the conclusion that experimental control of timing function was demonstrated in Experiment 2.

GENERAL DISCUSSION

The present findings suggest that performance following a shift between signals for different FI schedules may be understood in terms of two internal clock processes—accumulator and reference-memory processes. Evidence concerning both was obtained from measures of superposition of postshift test-trial functions with training-trial functions, as in S. Roberts and Church (1978). Inferences about reference memory were also based on separate assays of changes in training-trial functions between baseline and test phases. Resetting upon a stimulus shift in most instances was the clock mode favored by the data. Reference-memory functions exhibited substantial variability across birds and conditions; however, procedural constraints on the range of values stored in reference memory greatly curtailed interbird differences in performance.

In a study related procedurally to the present one, Cheng and W. A. Roberts (1989) drew somewhat different conclusions. In their Experiment 2, pigeons were exposed to reinforced segmented trials. The first, differentially cued segment was either 9 or 21 sec in duration, and the second segment was 21 or 9 sec in duration, for a total trial duration of 30 sec in both cases. Response-contingent reinforcement was available at the end of each trial. Timing

Figure 4. Performance of individual birds on training and test trials during the last five sessions of Experiment 2. The format of this figure is identical to that of Figure 2.

was assessed by means of the peak procedure (S. Roberts, 1981). On empty, segmented test trials, Segment 1 duration varied from 3 to 27 sec. As in the present study, Cheng and W. A. Roberts's subjects showed individual differences in apparent timing strategy. The authors accounted for these differences by suggesting that birds "were partly timing the entire complex event of 30-s duration and partly timing only the second signal of the event" (Cheng & W. A. Roberts, 1989, p. 363). Performance on individual test trials was said to be governed by the birds' retrieving the remembered duration of the complex event (30 sec) and a remembered duration associated with

the Segment 2 cue. A weighted average of these two durations served as a criterion for timing on that trial. Individual differences were attributed to differential weights assigned to the two retrieved durations. The model assumes a single clock with a reset process that does not empty the accumulator upon a cue shift, but, instead, adjusts the criterion value through weighted averaging.

The alternate view adopted here differs in three important ways from the analysis of Cheng and W. A. Roberts. First, we argue that data indicating timing of the post-shift cue (Cheng & W. A. Roberts, 1989; W. A. Roberts et al., 1989; see also the results of the present study) im-

ply resetting the accumulator at shift time. Evidence that animals time the postshift cue duration implies prior storage of that duration. Given a single-clock model, the duration of the second event can be stored only if the accumulator resets to zero at shift time. Second, we argue that the comparator process selects remembered durations based only upon the prevailing cue. On a shift trial, the criterion initially selected is based upon remembered time of reinforcement in the presence of the preshift cue. When a cue shift occurs, the previous criterion is replaced by one based upon remembered reinforcement times associated with the postshift cue. Finally, we suggest that the specific duration sampled on a trial will vary, depending upon the extent to which storage and retrieval are under stimulus control of preshift events. If stimulus control is poor, the range of durations sampled is directly related to the programmed range of delays to reinforcement in the presence of the postshift cue (i.e., sampling is made from a heterogeneous set of criterion values). If stimulus control is well established, the range of durations is correspondingly reduced to those associated with the individual retrieval cues on previous trials.

Cheng and W. A. Roberts reject this view, but aspects of their findings (Experiment 2) are compatible with it. Their data may be interpreted as reflecting invariable clock reset upon a cue shift and sampling of a single criterion value on each trial. On this account, criterion values of 9 or 21 sec are accessed under stimulus control by preshift cues; response-rate functions represent averages of response rates based on the sampling of different reference-memory values across trials, not averages of memory values taken within trials. Examination of their data for individual birds indicates that the relations of peak time to preshift cue duration are consistent with accumulator resetting and indicates a change in likelihood of sampling 9-sec versus 21-sec criterion values as preshift duration increases, with individual differences reflecting variation in degree of stimulus control. Moreover, if stimulus control of reference-memory selection by preshift cues were imperfect, reference-memory value would be sampled from a heterogeneous set, leading to more variable time estimates than would be expected from sampling a homogeneous set. Variability of birds' time estimates based on widths of the peak-rate functions support this inference: widths for 4 out of 5 birds in Experiment 2 were greater than those under previous conditions (Experiment 1) in which only one postshift delay to reinforcement had been scheduled.

The present proposal seems parsimonious. First, it requires a simple assumption that durations stored are based upon the contents of the accumulator (or working memory) at the time of reinforcement. Second, no mechanism is required to govern the partial timing of the complex event and the postshift cue. Finally, no special assumptions are required to account for the retrieval and processing of two remembered durations on a single trial. Individual differences are attributed solely to familiar principles of stimu-

lus control, as supported by the analysis of training-trial performance in the present study.

The appeal to stimulus control of storage/retrieval functions is in line with encoding specificity of long-term human and animal memory (e.g., Spear, 1973; Tulving & Thomson, 1973). In the present context, encoding cues refer to variable-duration preshift stimuli, representations of which must be available at the time of storage later in a trial upon reinforcer occurrence. While evidence of short-term memory for duration in pigeons is affirmative (e.g., Church, 1980; Spetch & Rusak, 1989), the data indicate that functional encoding cues may have been no more specific than presence versus absence of the preshift cue, under conditions of the present study.

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Forthcoming *Animal Learning & Behavior* Articles

The following is a list of forthcoming *Animal Learning & Behavior* articles that are currently in press. They are given in approximate order of acceptance. Each entry includes the name and address of the author with whom to communicate for further prepublication information.

- "Comparing spatial memory in two species of tit: Recalling a single positive location" by S.D. Healy & J.R. Krebs (S.D.H., Edward Grey Inst. of Field Ornithology, South Parks Road, Oxford OX1 3PS, U.K.)
- "Variations in the retention of taste aversions: Evidence for retrieval competition" by W.R. Batsell, Jr., & M.R. Best (W.R.B., Dept. of Psychology, Southern Methodist Univ., Dallas, TX 75275)
- "Context sensitivity of conditioned suppression following preexposure to the conditioned stimulus" by D. Swartztruber & M.E. Bouton (D.S., Dept. of Psychology, Univ. of Pennsylvania, 3815 Walnut St., Philadelphia, PA 19104)
- "The form of timing distributions in pigeons under penalties for responding early" by K. Cheng (Dept. of Psychology, Univ. of Toronto, Toronto, ON, Canada M5S 1A1)
- "Rate of reinforcement and session duration as determinants of within-session patterns of responding" by F.K. McSweeney (Dept. of Psychology, Washington State Univ., Pullman, WA 99164-4820)
- "Extinction of stimulus elements decreases the rate of conditional discrimination learning" by B.A. Williams & B.O. Ploog (B.A.W., Dept. of Psychology, Univ. of California, San Diego, La Jolla, CA 92093-0109)
- "Fear potentiation of the acoustic startle reflex in rats using noises of various spectral frequencies" by S. Campeau & M. Davis (M.D., Dept. of Psychiatry, Yale Univ. School of Medicine, 34 Park St., New Haven, CT 06508)