Pacemaker Rate in the Behavioral Theory of Timing

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The assumption by the behavioral theory of timing that pacemaker rate is proportional to reinforcer density was tested in 2 experiments. Pigeons discriminated between the 1st and 2nd halves of a 50-s trial. Responses on a left key were reinforced at variable intervals for the first 25 s of the trial, and right-key responses were reinforced at variable intervals during the second 25 s. In Experiment 1, overall reinforcement rate was varied by manipulating the intertrial interval (ITI) duration. Pacemaker rate, estimated by fitting predictions to psychometric functions, was an inverse function of ITI. In Experiment 2, reinforcer duration was manipulated as a means of altering reinforcer density. Pacemaker rate was found to be directly related to reinforcer duration. The present results support the assumption that pacemaker rate is determined by reinforcer density.

The *behavioral theory of timing* (BeT), which was proposed by Killeen and Fetterman (1988, 1993), offers a behaviorally mediated timing model. BeT proposes that sequential states are correlated with classes of adjunctive behavior. The adjunctive behaviors can serve as conditional discriminative stimuli for temporal discriminations. Because a discriminative response is cued or mediated by an adjunctive behavior, and the effective adjunctive behavior is associated with a given state or states, the occurrence of discriminative responses depends on transitions between states. BeT does not, however, suggest that sequences or chains of adjunctive behaviors are the basis of timing (Killeen & Fetterman, 1993).

Transitions between states are driven by pulses produced by a pacemaker. Generation of these pulses is described by the Poisson process given in Equation 1:

$$p[N(t) = n] = \frac{[(t/\tau)^n e^{-t/\tau}]}{n!}. \tag{1}$$

Equation 1 gives the probability $p[N(t) = n]$ that a number n of pacemaker pulses is produced by time, t. τ is the average interpulse time of the pacemaker. The pacemaker rate is therefore given by the inverse of τ. Because the pacemaker is part of the hypothetical Poisson process, the pacemaker rate, $1/\tau$, is, in essence, an intervening variable. When the Poisson process reaches the nth state, the adjunctive behaviors associated with the nth state will cue the appropriate discriminative response. Equation 1 has been shown to account well for various response distributions

generated by fixed-interval schedules (Killeen, 1975; Killeen, Hanson, & Osborne, 1978) and timing in a free-operant psychophysical procedure (Bizo & White, 1994).

BeT assumes that pacemaker rate is determined by reinforcement rate; that is, the average time between pacemaker pulses τ is a function of interreinforcer interval, T (Killeen & Fetterman, 1988). This relationship is described by Equation 2 and suggests that reinforcement rate influences temporal discrimination:

$$\tau = kT. \tag{2}$$

There is clear evidence that motivational factors influence temporal discriminations. Killeen et al. (1978) showed that response rate increases with shorter interfood intervals. Killeen et al. interpreted this finding in terms of an increase in arousal caused by reinforcing events. Zeiler (1991) showed that timing behavior is affected by whether the reinforcement economy is open or closed. In closed-economy conditions, pigeons' weights were higher than they were in an open economy. Levels of arousal may therefore have been different for the two economy types. Zeiler considered the differences in timing performance for the two groups as consistent with BeT "to the extent that the kind and magnitude of adjunctive behavior varies with frustration, and timing mechanisms can differ with the feeding economy and timing behavior would change" (p. 23).

Killeen and Fetterman (1988) argued that the relation between reinforcement rate and pacemaker rate is consistent with a shift of the point of subjective equality (PSE) of psychometric functions for temporal discriminations when reinforcement rate is changed. The psychometric function describes the probability of reporting one of two durations. The PSE is the point at which the probability of making a response such as *long* (vs. *short*) is 50%. Both the PSE and the variance of such a psychometric function are related to the interpulse time, τ, and hence to the number of pulses, n, that are registered by some time, t (cf. Equation 1). BeT makes specific predictions about the manner in which psychometric functions should be affected by changes in reinforcement rate (Killeen & Fetterman, 1988). For example,

when reinforcement rate is increased, pacemaker rate should increase. This produces a choose-long preference and shifts the PSE to shorter durations. A change in the pacemaker rate should also affect the variance (slope) of the psychometric function. In this instance, a faster pacemaker would decrease the variance and would steepen the slope of the psychometric function. In general, changes in PSE can be thought of as a change in response bias, and changes in variance can be thought of as a result of a change in discriminability. These changes in the PSE of the psychometric function after a change in reinforcement rate, however, are not assumed to be permanent, as the behaviors supporting the discrimination are assumed to recalibrate, as discussed below (Killeen & Fetterman, 1988).

A growing number of researchers have investigated the role of reinforcement rate in determining pacemaker rate. Fetterman and Killeen (1991) trained pigeons to discriminate between a short (4-s) duration and a long (12-s) duration. Five intermediate probe durations were then presented on 20% of the trials, and choices were not reinforced. Correct choice responses to short and long stimuli on training trials were reinforced to maintain reinforcement probability at .8 or .2 for both training and probe trials. Reinforcement probability was varied every 10 sessions. Sessions ended after 60 reinforcers in the .8 condition and after 40 reinforcers in the .2 condition. Fetterman and Killeen's procedure generated psychometric functions relating the proportion of long choices to stimulus duration. They found that, contrary to the predictions of BeT, reinforcement probability produced no systematic variation in either PSE or the standard deviation of the psychometric functions.

Fetterman and Killeen (1991) also examined the effect of intertrial interval (ITI) on temporal discrimination. They used the same discrimination as described above, except the probability of reinforcing a correct choice response was .50. On 20% of the trials five intermediate probe durations were presented, and choice responses were not reinforced. ITIs were either 10 s or 100 s. Fetterman and Killeen found little systematic effect of ITI duration on the variance or PSE of obtained psychometric functions. They suggested that ITI may act differently on responding in a free-operant choice procedure compared with a psychophysical choice procedure. Their results contrast with those of Raslear, Shurtleff, and Simmons (1992), who trained rats to discriminate between short (0.1-s) and long (10-s) durations with a 5-s ITI. They then varied ITI across a series of five ITI durations on probe days while keeping the discrimination task the same. Rate of reinforcement decreased as ITI duration was increased. Raslear et al. found a decrease in discriminability (A') and an increase in bias to respond long (B") as the ITI duration was increased, as predicted by BeT. In view of an absence of a clear effect of ITI duration on the PSE or on the variance of psychometric functions in Fetterman and Killeen's study, however, it is important to establish whether ITI duration influences pacemaker rate.

The effect of reinforcement probability on timing behavior has also been investigated with the peak procedure (MacEwen & Killeen, 1991): After training in which re-

sponses on each trial are reinforced at fixed intervals, probe trials are introduced that are about twice the duration of the fixed interval used in training; responding during probe trials is not reinforced. MacEwen and Killeen manipulated reinforcement rate in two ways—by varying the duration of the fixed interval and by randomly inserting time-out periods. MacEwen and Killeen found that, for both manipulations, pacemaker rate was proportional to reinforcement rate.

Morgan, Killeen, and Fetterman (1993) trained pigeons to discriminate short (10-s) from long (20-s) durations in a discrete-trial choice procedure. In separate conditions, the rate of reinforcement was increased or decreased compared with baseline training by high or low probability response-independent food presentations. Morgan et al. found that when the pigeons were returned to the temporal discrimination, the birds that had experienced the richer condition of free food were more likely to judge the stimulus durations as longer than when they had experienced the leaner condition of free food. This result is consistent with BeT's predictions that changes in the rate of reinforcement should alter the speed of the pacemaker. Hence a faster pacemaker should result in a bias to respond long, and a slower pacemaker should result in a bias to respond short.

Bizo and White (1994) found clear effects of reinforcement rate on pacemaker rate. They varied the rate of variable-interval (VI) reinforcement for pigeons, maintaining the timing behavior in components of a free-operant psychophysical procedure. This procedure involved the discrimination of the first half of a 50-s trial from the second half. Decreases in reinforcement rate decreased pacemaker rate, and increases in reinforcement rate increased pacemaker rate, as predicted by BeT. When reinforcement rate is varied as in the above studies, however, there is always the possibility that changes in response distributions are influenced by the discrimination of reinforcer delivery although Bizo and White showed that this is not a factor.

Alternatives to varying overall reinforcement rate without changing absolute reinforcement frequency should be examined. Alternative means of varying reinforcement rate will provide generality for BeT's assumption that pacemaker rate is proportional to reinforcer rate (see Equation 2). In the present experiments, we attempted to manipulate overall reinforcement rate independent of reinforcement frequency by varying ITI duration (Experiment 1) and by varying reinforcer duration (Experiment 2).

Experiment 1

Variation in ITI duration results in a change in overall reinforcement rate, when rate is calculated in terms of reinforcers per session. Such a manipulation allows reinforcement rate for individual trials to remain constant.

The procedure in the present experiments was the one used by Bizo and White (1994). It generated a psychometric function that related the proportion of right-key responses to the time since the trial began. Bizo and White showed that the form of this psychometric function was affected by

reinforcement rate, as predicted by BeT. The procedure was based on the free-operant psychophysical procedure used by Stubbs (1968, 1979, 1980), which involves presenting two keys concurrently during a 50-s trial, with trials being separated by an ITI. For the first 25 s of the trial, reinforcers are scheduled for responses on the left key at variable intervals. For the remaining 25 s of the trial, reinforcers are scheduled for responses to the right key.

In Bizo and White's (1994) study, and in the present experiments, the proportion of right-key responses was calculated by dividing right-response frequencies by the sum of left- and right-response frequencies. Bizo and White generated quantitative predictions of proportions of right responses by dividing Equation 1 for right responses with $n = n2$ by the sum of Equation 1 for right responses and Equation 1 for left responses with $n = n1$. Algebraic simplification yields Equation 3, which predicts right responses (R) as a proportion of total right and left (L) responses:

$$(R/R + L) = \frac{1}{1 + ([t/\tau]^{n1 - n2} * n2!/n1!)}. \qquad (3)$$

This approach is appropriate for a free-operant procedure in which the sum of left and right responses is variable across time compared with a discrete-trial procedure in which the sum of the proportions of left and right responses is 1.0 (Raslear et al., 1992). In a discrete-trial procedure, one could assume that the probability of a right response is equal to 1 minus the probability of a left response.

The top panel of Figure 1 shows predicted probabilities of left and right responses as derived from Equation 1 for two values of n, 1 and 7, and the same value of interpulse time, $\tau = 5$ s. These predicted functions are comparable in form to data obtained from several procedures as described by Killeen (1991) and to data obtained from the present procedure (Bizo & White, 1994).

The bottom panel of Figure 1 shows the psychometric function derived from Equation 3 using the parameter values given in the top panel (solid line). A second function (dashed line) is given for comparison to show the predicted effect of an increase in τ (slowing of the pacemaker) on the psychometric function. A longer ITI would be expected to generate functions similar to that for $\tau = 6$ s in the bottom panel of Figure 1 because of a slowing of the pacemaker. Note that a unit change in τ produces a sizable effect on the psychometric function. In Experiment 1, we investigated the effect of ITI duration on pacemaker rate as measured by the inverse of interpulse time τ.

Method

Subjects. The subjects were 5 locally supplied adult homing pigeons *(Columba livia),* 3 of which were female. The birds had previous experimental histories in multiple-concurrent schedules and conditional discriminations and in the procedure used in the present experiment (Bizo & White, 1994). The birds' weights were kept at 80% ± 12 g of their free-feeding weights. If a bird's weight exceeded the specified range immediately before an experimental session, the bird was not included in that session. The birds were
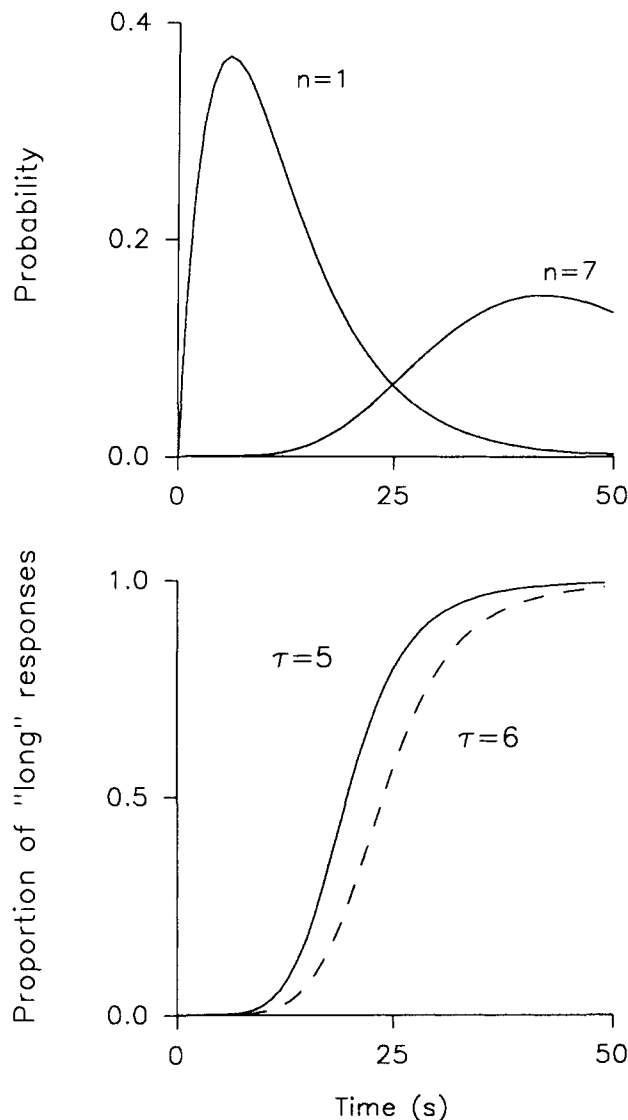
Figure 1. The smooth functions (top panel) show probability functions of responses associated with hypothetical "short" response states $(n = 1)$ and with "long" response states $(n = 7)$. The functions are based on Equation 1 solved for $\tau = 5$ s, with $n = 1$ and 7 for the respective functions. The bottom panel shows Equation 3 distributed over t and solved for $n1 = 1$ and $n2 = 7$, with $\tau = 5$ s (solid curve) and $\tau = 6$ s (dashed curve). Pacemaker rate $= 1/\tau$. n = number of pacemaker pulses; τ = average interpulse time of the pacemaker; t = time; $n1$ = state associated with left-key responses; $n2$ = state associated with right-key responses.

housed individually and had free access to water and grit. If necessary, supplementary feed of corn, wheat, and maple peas was given after experimental sessions to maintain the weights within the specified range.

Apparatus

An interface panel, 32 cm wide and 29 cm high, formed one wall of a 35-cm deep sound-attenuating experimental chamber.

The interior of the chamber was painted matte black. A ventilation fan was situated in the rear of the chamber on the wall opposite the interface panel and provided masking noise during the experimental sessions. Two Plexiglas keys, 2.9 cm in diameter, were mounted on the interface panel, 22 cm from the chamber floor and 10 cm apart. The left and right keys could be illuminated orange. A force of approximately 0.2 N was required to operate a reed relay mounted behind the key, and an effective response caused a 50-ms blackout of the pecked key. A central hopper could provide 3-s access to wheat. When the hopper was raised, the response keys were turned off and a white light illuminated the hopper. Experimental events were programmed and recorded by a DEC computer (Model PDP 11/23) and SKED software (Kalamazoo, MI) and interfacing in an adjacent room.

Procedure

Each experimental session lasted for 48 min. Experimental sessions were scheduled for 7 days a week. Each trial lasted for 50 s. A short blackout period preceded and followed each session, and no responses were recorded during these periods. Trials began with the orange illumination of the left and right keys. Apart from a 50-ms offset of a key light following each effective response, the illumination of the keys did not change across the 50-s trial. During the first 25 s of the 50-s trial, left-key responses were reinforced according to a VI 30-s schedule, and right-key responses were extinguished. After 25 s the contingencies were reversed; right-key responses were reinforced periodically according to a VI 30-s schedule, and left-key responses were extinguished. The constant-probability VI schedules in the different components (Fleshler & Hoffman, 1962) were independent. Scheduled reinforcers not delivered in a trial were held over until the next trial. There was an ITI after each trial during which all key lights were blacked out, and no responses were recorded. Experimental conditions were conducted until all birds had completed at least 25 sessions. The duration of the ITI was varied across conditions (see Table 1). In Conditions 1, 3, 5, 7, and 9 there was a 10-s ITI, and there were 48 trials per session. In Condition 2, there was a 70-s ITI, and there were 24 trials per session. In Conditions 4, 6, and 8 there was a 190-s ITI, and there were 12 trials per session. After Condition 4 and before Condition 5 a separate experiment was conducted using a similar procedure. Table 1 is a summary of the condition changes and the number of sessions each bird experienced in each condition in Experiment 1.

Effective key pecks to the left and right keys were recorded in
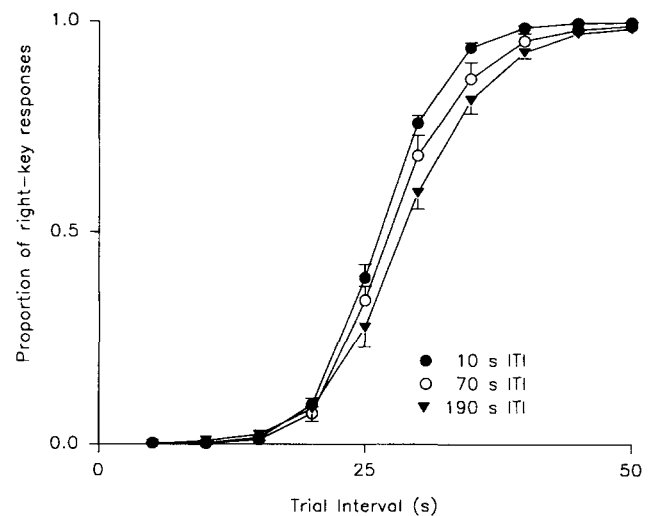
5-s bins during each trial and were summed over all trials for each daily session. These response totals were used as the basis for analysis. Reinforcement time was not subtracted from the time base for the trial. The proportion of right-key responses as a function of total responses was calculated for each 5-s bin for responses summed over the last 5 days of each condition. The level of significance used for all statistical tests was $p = 0.05$.

Results

Figure 2 shows the mean response proportions averaged for the different ITI conditions for consecutive 5-s bins of 50-s trials. The standard error bars in Figure 2 are based on single data points for each condition for each bird ($N = 5$); that is, data for replications of each condition were averaged for each bird before the group mean was calculated. The psychometric functions for longer ITIs are displaced toward longer times. The mean response proportions for the different sets of ITI conditions for each bird were submitted to a repeated measures analysis of variance (ANOVA). There were significant effects of ITI, $F(2, 8) = 4.95$; and 5-s bin, $F(9, 36) = 1,178$; and a significant interaction between ITI and 5-s bin, $F(18, 72) = 3.82$. The significant interaction, combined with the significant effect of ITI, supports the conclusion that the psychometric functions were shifted to the right for longer ITIs.

This conclusion was further supported by the analyses of data for individual birds. Figure 3 shows the proportion of right-key responses for successive 5-s bins of the 50-s trial for individual birds for the first two conditions (10- and 70-s ITI) and the last two conditions (190- and 10-s ITI). The two 10-s conditions and the 190-s condition are very typical of other 10- and 190-s conditions. In all cases, these proportions of right-key responses clearly follow a sigmoidal function.

Table 1
Summary of Condition Changes and the Number of Experimental Sessions Each Bird Completed in Each Condition in Experiment 1

	ITI	Bird				
Condition	(in seconds)	L1	L2	L3	L4	L5
1	10	25	30	30	30	30
2	70	25	25	25	26	26
3	10	25	36	36	35	32
4	190	26	26	25	26	26
5	10	25	28	28	28	28
6	190	27	27	27	25	27
7	10	28	28	28	29	28
8	190	26	27	26	26	26
9	10	25	26	26	25	25

Note. ITI = intertrial interval.

Figure 2. Mean right-key response proportions averaged over birds for each intertrial interval (ITI) condition and averaged across replications for Experiment 1. (The standard error bars are based on a single mean data point per bird).
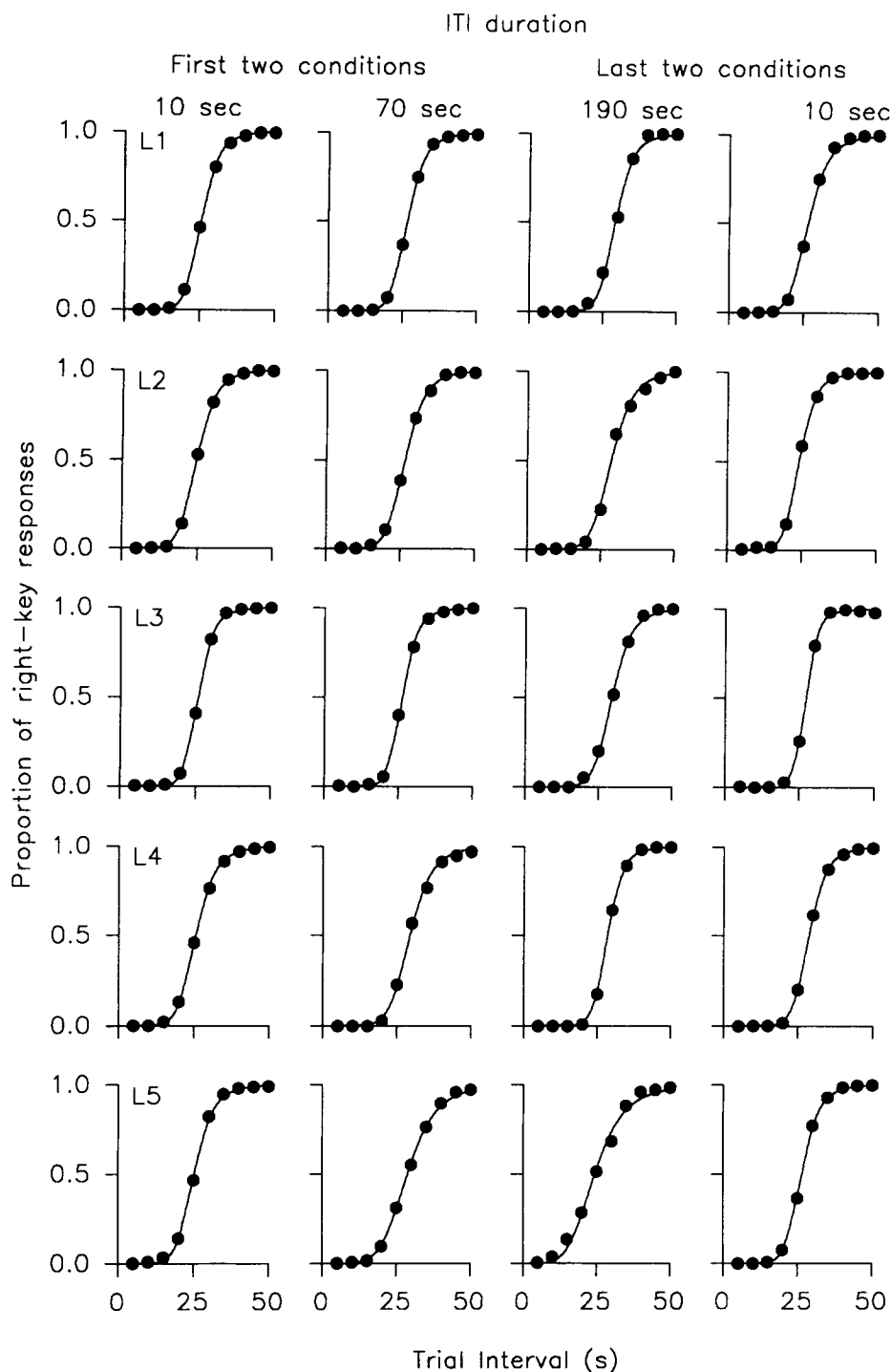
Figure 3. Proportions of right-key responses in 5-s bins based on response totals over the last five sessions of the first two intertrial interval (ITI) conditions (10- and 70-s) and the last two intertrial interval conditions (190- and 10-s) for each bird for Experiment 1. The smooth psychometric functions are best-fitting functions predicted by Equation 3. The order of conditions (in seconds) was 10, 70, 10, 190, 10, 190, 10, 190, and 10 (see Table 1).

We evaluated the extent to which the functions in Figure 3 moved toward shorter or longer durations in terms of the interpulse time parameter τ in Equation 3 (cf. Figure 1, bottom panel); that is, τ was used as a higher order dependent variable. The smooth curves in Figure 3 are the best fits of Equation 3 to the data points fitted by a nonlinear least

squares regression. In fitting Equation 3, parameter $n1$ was set at 1, and parameters τ and $n2$ were allowed to vary freely. Setting $n1$ equal to 1 limited the number of free parameters in Equation 1 to 2 and was consistent with the assumption that adjunctive behaviors associated with the first state were highly likely to cue left-key responses. The smooth functions shown in Figure 3 are typical of all conditions and show that Equation 3 accounted for the data well. The mean variance accounted for was 0.999 (SD = 0.0016), and it fell below 0.995 on only two occasions, once for Bird L3 and once for Bird L5. The average mean square error was 0.0002 (SD = 0.0003).

The parameter values for the best-fitting functions are presented in Table 2. A comparison of the obtained τ value for a condition with the τ value for the next condition shows that when the ITI was increased or decreased, τ increased or decreased according to BeT predictions for 27 of the 35 condition changes, which was significant using the binomial statistic. Note that, because of the break between Conditions 4 and 5, a comparison between these two conditions was not included.

A comparison of the obtained $n2$ value for a condition with the $n2$ value for the next condition revealed no systematic variation (see Table 2) and showed that when the ITI was increased or decreased, $n2$ increased or decreased in a direction opposite to the changes in τ predicted by BeT for 18 of 35 condition changes (not significant with the binomial test).

Recalibration and PSE changes. An inverse relation between τ and $n2$ is evidence for recalibration (Bizo & White, 1994; Killeen, 1991; Killeen & Fetterman, 1988). Although no systematic change in $n2$ corresponded with the change in ITI, there was a consistent inverse relation between τ and $n2$ for each bird. For each of the 5 birds, Pearson product–moment correlations between τ and $n2$ were $-.67$, $-.96$, $-.83$, $-.86$, and $-.93$. The changes in $n2$ during the course of a condition should occur because of compensation for the changes in τ produced by the change in overall reinforcement rate. That is, with increased pacemaker speed, there is a change in the number of states that

occur before reaching the state associated with the adjunctive behavior that cues the timing response. Because changes in criterion restore accuracy by compensating for changes in τ, it should not be surprising to find that changes in the PSE are less sensitive to the manipulations than are either n or τ by themselves. The PSE may be calculated by setting Equation 3 to 0.5 and solving for t (Bizo & White, 1994). That is,

$$PSE = \tau * \left(\frac{n2!}{n1!} \right)^{\frac{1}{(n2 - n1)}}. \tag{4}$$

Equation 4 provides a measure of PSE that is based on all the data points contributing to the psychometric function rather than just the points in the vicinity of the PSE. Table 2 presents values of the PSE calculated using Equation 4.

A comparison of the obtained PSE value for a condition with the PSE value for the next condition shows that when the ITI was increased or decreased, PSE decreased or increased respectively, for 30 out of 35 condition changes, which was significant using the binomial statistic. (Because of the break between Conditions 4 and 5, a comparison between these two conditions was not included.) The systematic change in PSE after changes in ITI, combined with the absence of systematic changes in $n2$, suggests that the behavior underlying the conditional discrimination may not have completely recalibrated to new states by the end of a condition.

Figure 4 is a summary of the changes in τ, $n2$, and PSE given in Table 2 for each bird. Values of τ, $n2$, and PSE were averaged for repetitions of the same ITI conditions for each bird, and these values were averaged across each bird for each ITI. The top panel of Figure 4 shows that the mean value of τ increased as ITI was increased, as predicted by BeT. This increase was statistically significant, $F(2, 8)$ = 4.45. The middle panel of Figure 4 shows that the mean value of $n2$ decreased as ITI was increased, but this decrease was not statistically significant, $F(2, 8)$ = 2.02. The bottom panel of Figure 4 shows the mean values of PSE that did not increase significantly as ITI was increased, $F(2, 8)$ = 3.76.

Table 2

Obtained Parameter Values (τ, n2) for the Best Fit of Equation 3 to Right-Key Response Proportions, Based on Response Rates Summed Over the Last 5 Days of Each Condition, for Experiment 1

| Length of ITI (in seconds) | Bird | | | | | | | | | | | | | | |
| | L1 | | | L2 | | | L3 | | | L4 | | | L5 | | |
	τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE
10	4.76	10	25.48	5.00	9	24.75	4.49	11	25.83	5.16	9	25.59	5.08	9	25.16
70	4.95	10	26.50	5.33	9	26.43	4.55	11	26.17	5.92	9	29.32	6.93	7	28.69
10	5.65	9	28.01	5.15	9	25.49	4.70	10	25.16	5.15	10	27.57	5.05	10	27.05
190	5.30	9	26.24	5.73	8	26.07	5.23	11	30.07	5.84	9	28.94	7.53	6	28.05
10	4.73	10	25.32	4.91	10	26.27	4.20	13	27.51	4.65	11	26.77	6.18	7	25.61
190	4.77	12	29.35	7.30	6	27.22	6.78	9	33.58	5.35	10	28.68	8.66	5	28.65
10	4.99	10	26.70	4.68	10	25.06	4.20	13	27.56	5.53	9	27.41	5.56	8	25.29
190	5.07	11	29.20	5.76	9	28.52	5.51	10	29.52	4.64	12	28.54	6.55	6	24.40
10	5.33	9	26.42	4.50	10	24.12	3.89	14	27.02	4.98	11	28.66	4.93	10	26.41

Note. ITI = intertrial interval; τ = average interpulse time; $n1$ = state associated with left-key responses; $n2$ = state associated with right-key responses; PSE = point of subjective equality. $n1$ was set at 1 for individual birds; PSEs were calculated using Equation 4.
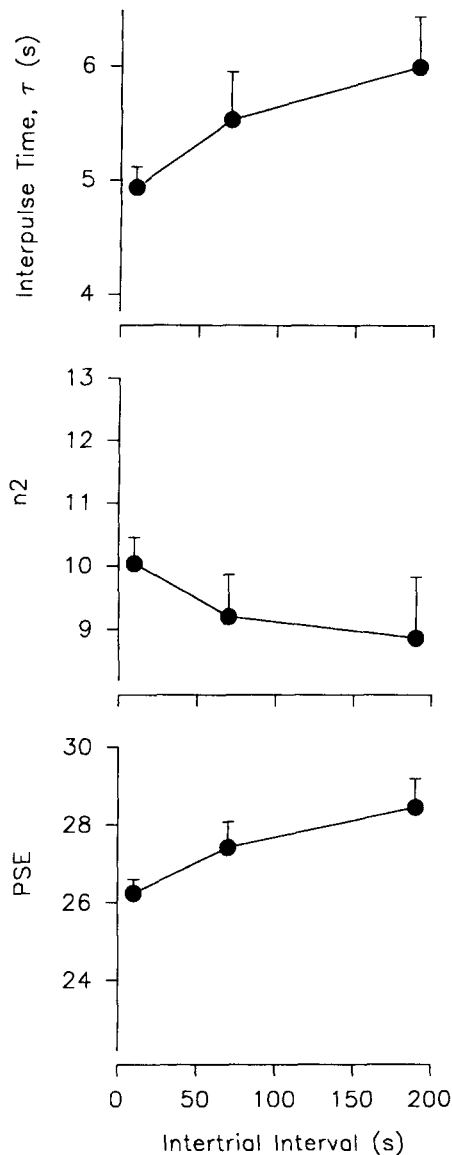
Figure 4. Mean values of average interpulse time τ (top panel), mean values of $n2$ (state associated with right-key responses; middle panel), and mean points of subjective equality (PSEs; bottom panel) plotted as a function of intertrial interval for Experiment 1. The means are based on the data in Table 2. The standard error bars are based on a single mean data point per bird. Pacemaker rate = $1/\tau$.

Obtained reinforcers. We submitted the mean obtained reinforcers per trial, averaged across replications of the same ITI condition for each condition and for each bird, to a repeated measures ANOVA, which revealed a statistically significant difference in obtained reinforcers per trial across ITI conditions, $F(2, 8) = 27.30$, with longer ITIs yielding less frequent reinforcement. The mean reinforcers per trial for the 10-, 70-, and 190-s ITI conditions were 1.60, 1.58, and 1.48, respectively. When we analyzed reinforcers per trial in terms of which key they were obtained on, we found

a significant effect of key, $F(1, 4) = 8.68$, with more reinforcers obtained on the right than on the left. The mean left reinforcers per trial for the 10-, 70-, and 190-s ITI conditions were 0.79, 0.79, and 0.72, respectively, and the mean right reinforcers per trial were 0.81, 0.80, and 0.76, respectively.

The small but consistent differences in obtained reinforcers per trial for the long versus short ITI durations were the result of a reduction in response rate in the long ITI conditions. There was a significant effect of ITI condition on overall responses per trial, $F(2, 8) = 4.60$. The mean responses per trial across the 10-, 70-, and 190-s ITI conditions were 79.31, 81.39, and 69.52, respectively. The reduction in response rate in the 190-s ITI occurred for both the first and the second components of the trial. The decreased response rate is likely to account for the reduction in reinforcers per trial for the 190-s ITI condition. However, these changes in interpulse time were not directly proportional to changes in interreinforcer interval, as predicted by Equation 2.

Discussion

At a qualitative level, the assumption by BeT that reinforcement rate determines pacemaker rate was confirmed by the shift in the psychometric function toward longer durations under conditions in which overall reinforcement was decreased by lengthening the ITI (Figure 2). Strong quantitative support was also provided by fitting Equation 3 to the data for individual birds. Not only were the fits of the predicted functions to the data excellent (Figure 3), but also the estimate of the parameter τ changed as expected according to BeT. Specifically, as ITI increased, thereby decreasing overall reinforcement rate, values of the interpulse time parameter τ increased, consistent with a slowing of the pacemaker (Figure 4).

In BeT, the parameter n is the number of the state associated with the adjunctive behavior that cues the timing response. For reasons of parsimony and consistency with our preliminary analyses, n was set at 1 for left responses and varied freely for right responses. We expected that a shift from one pacemaker rate to another would be associated with a change in n for right responses, owing to recalibration (Killeen & Fetterman, 1988). For example, a faster pacemaker would result in arriving at the nth state sooner. To maintain accurate performance, new behaviors become associated with a later state and serve as cues for timing. Such recalibration would result in an inverse relation between τ and $n2$. This has been reported by Bizo and White (1994), Killeen and Fetterman (1988), Haight and Killeen (1991), and Morgan et al. (1993). Figure 4 shows a clear inverse relation between τ and $n2$, although the change in $n2$ with ITI was not statistically significant. In particular, there were significant negative correlations between τ and $n2$ for each bird. The present evidence for recalibration thus constitutes strong support for BeT.

There are two qualifications of the interpretation of the results of Experiment 1. First, the relation between inter-

pulse time τ and the interreinforcer interval was not strictly proportional, contrary to the assumption of BeT. This deviation from a strictly proportional relationship would result if the ITI were discounted in the time base for an animal's estimate of the reinforcement density (Fetterman & Killeen, 1991).

Second, obtained reinforcers per trial were consistently fewer in the 190-s ITI conditions than in the other conditions. It seems that the reduction in reinforcers per trial resulted from an overall reduction in response rate. The change in reinforcers per trial may therefore have contributed to the slowing of the pacemaker rate in the 190-s ITI condition (cf. Bizo & White, 1994). The absolute change in reinforcers per trial was small (although consistent), however, and the presence of a difference in τ between the 10-s and 70-s ITI conditions, despite no change in reinforcers per trial, suggests that reinforcers per trial may not have been a contributing factor. Insofar as longer ITI durations result in a reduction in response rate with a concomitant reduction in reinforcement rate, it remains important to find ways of changing reinforcement density within a trial without changing reinforcement rate. We did this in Experiment 2 by manipulating reinforcer duration.

Experiment 2

In Experiment 2, we investigated the effect of reinforcer duration on pacemaker rate. In general, we expected that increases in reinforcer duration would increase pacemaker rate, as indicated by a decrease in average interpulse time τ.

We chose reinforcer duration as a means of manipulating reinforcement density because, as Nevin (1974) has pointed out, "magnitude of reinforcement has a number of effects that are strikingly parallel to those of frequency of reinforcement" (p. 395). Studies of concurrent-schedule performance, however, have suggested that undermatching of choice to relative reinforcer duration may be greater than undermatching for relative reinforcer frequency (Davison & Hogsden, 1984). Fetterman and Killeen (1991) pointed out there are few studies that address the effect of reinforcer magnitude on timing. A main advantage of manipulating reinforcer magnitude or duration as a test of BeT is that reinforcer frequency remains constant and is not confounded with changes in reinforcer duration as a means of manipulating reinforcement density.

To date, manipulations of reinforcer duration have provided little direct support for BeT. Fetterman and Killeen (1991) tested the assumption that reinforcer density determines interpulse time by manipulating reinforcer duration. Their task involved the discrimination of two successive durations. Probe durations were randomly presented on half the trials. BeT's prediction was that the longer the reinforcer duration, the smaller the variance of the psychometric function and the further the shift in the PSE toward shorter durations (smaller PSEs). This prediction follows from the direct relation between the mean and variance of the Poisson distribution. There was an increase in variance following a decrease in reinforcer duration and a decrease in

variance after an increase in reinforcer duration, consistent with BeT's predictions. Of 12 condition changes, 11 exhibited the predicted increase or decrease in the standard deviation of the psychometric functions, which was significant using the binomial statistic. However, a comparison of PSEs across the same condition changes revealed no systematic variation, contrary to the predictions of BeT. Accordingly, it is not possible to conclude whether reinforcer duration influenced pacemaker rate. Furthermore, MacEwen and Killeen (1991) used the peak procedure and manipulated reinforcer density by varying the duration of reinforcers that followed a correct response after some fixed interval. They found that reinforcer duration did not affect the average interpulse time.

In Experiment 2, we studied the effect of reinforcement duration using the procedure of Experiment 1. Bonem and Crossman (1988) noted that when reinforcer duration is manipulated, the time base for the occurrence of events is also changed, thus introducing a potential confound. Because in the present procedure variations in reinforcer duration would alter the time base for a trial, analyses were based on responses produced in trials in which no reinforcers were delivered (unreinforced trials).

Method

Subjects. The subjects were the same as those used in Experiment 1, but they had completed another experiment, which used the current procedure, before the present experiment.

Apparatus. The apparatus was same as that used in Experiment 1, except that experimental events were controlled and recorded by an NEC 80386 microcomputer with Med–PC 2.00 software (Med Associates, East Fairfield, VT) and interfacing located in an adjacent room.

Procedure. The general procedure was the same as that used in Experiment 1, except that trials began with the red and green illumination of the left and right response keys, respectively. Experimental conditions were conducted until all birds had completed at least 25 sessions. Reinforcer duration was varied between conditions. Trials without reinforcers were not deliberately programmed, nor were they signaled in any way, but occurred at the different times during the session when long interreinforcer intervals were arranged by the VI schedules. Table 3 is a summary of the condition changes and the number of sessions conducted for each bird in each condition, as well as the number of trials without reinforcers for each bird in the last five sessions of each condition. In general, about half of the trials within a session were without reinforcers. Birds L2 and L3 responded at low rates in the 1.5-s reinforcer-duration conditions and hence experienced many more unreinforced trials than the other birds. There were, however, no statistically significant differences in obtained reinforcer totals for the different reinforcer-duration conditions, $F(1, 4) = 2.60$.

Key pecks to the left and right keys were recorded in 5-s bins during each trial and were summed over the total number of trials without reinforcers for each daily session. These response totals were used as the basis for calculating response proportions (which did not depend on total available trial time within a session). We calculated the proportion of right-key responses as a function of total responses for each 5-s bin for responses summed over the last 5 days of each condition.

Table 3

Summary of Conditions and the Number of Experimental Sessions Completed by Each Bird in Each Condition in Experiment 2

Condition	Reinforcer duration (in seconds)	Bird				
		L1	L2	L3	L4	L5
1	4	29 (114)	31 (116)	30 (113)	29 (106)	28 (106)
2	1.5	32 (107)	30 (162)	27 (208)	31 (114)	31 (124)
3	4	26 (106)	26 (115)	26 (112)	25 (113)	26 (114)
4	1.5	30 (110)	25 (177)	28 (232)	31 (113)	30 (118)

Note. Numbers in parentheses are total trials without reinforcers summed over the last five sessions (of a possible 240).

Results

Figure 5 shows the mean right-key response proportions averaged across replications of the same reinforcer duration for consecutive 5-s bins of the 50-s trials. We performed a repeated measures ANOVA for the factors of reinforcer duration, replications of each reinforcer-duration condition, and consecutive 5-s bin on the right-key response proportions. There was a statistically significant main effect of 5-s bin, $F(9, 36) = 144.98$. There were no statistically significant main effects of reinforcer duration or replication, both $Fs(1, 4) < 1$. More important, there was a statistically significant interaction between reinforcer duration and 5-s bin, $F(9, 36) = 3.37$, showing that the psychometric functions differed among the reinforcer-duration conditions. There was no significant interaction between replication and 5-s bin, $F(9, 36) < 1$. The differences in the sigmoidal functions in Figure 5 were therefore consistent across replications. The psychometric functions were flatter and further shifted to the right for the 1.5-s reinforcer duration conditions than for the 4-s reinforcer duration conditions.
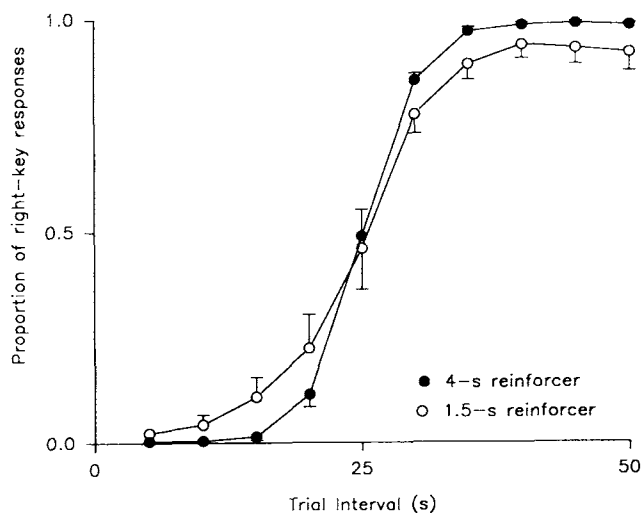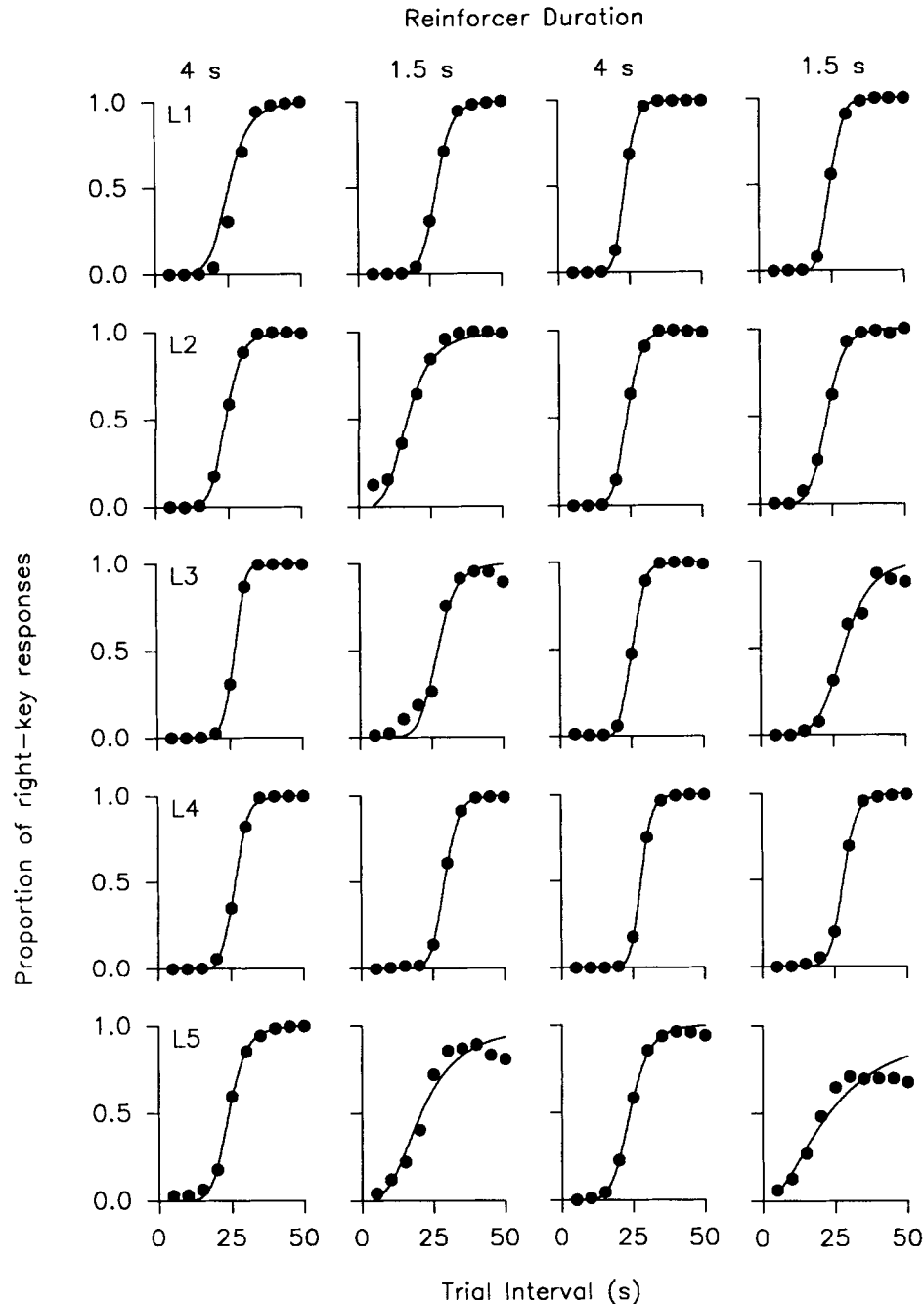

Figure 5. Mean right-key response proportions averaged over birds for each reinforcer-duration condition and averaged across replications for Experiment 2. The standard error bars are based on a single mean data point per bird.

Figure 6 shows that the proportion of right-key responses increased across the trial according to a sigmoidal function. The smooth curves in Figure 6 are the best fits of Equation 3 to the data for $n1$ set at 1. Table 4 shows the parameter values τ and $n2$ for the best fits of Equation 3 to the proportion of right-key responses. The mean variance accounted for by Equation 3 was 0.989 ($SD = 0.0228$), and it was at least 0.995, except in five instances—once for Bird L2 and twice each for Birds L3 and L5. The average mean square error was 0.0012 ($SD = 0.0020$). Table 4 also shows PSEs calculated with Equation 4.

A comparison of τ values for psychometric functions from consecutive conditions shows that τ values changed in the direction predicted by BeT for 14 of 15 condition changes, which was significant using the binomial statistic. Similarly, $n2$ values for functions from consecutive conditions revealed that $n2$ values changed in the direction of the changes in τ predicted by BeT for 13 of 15 condition changes, which was significant using the binomial statistic. There was no systematic variation in PSE across consecutive conditions, and the values changed in a direction consistent with changes in τ for only 6 of 15 condition changes (not significant with the binomial statistic). This suggests that in the present experiment, the PSE was a less sensitive measure of timing behavior than the parameter values τ and n.

Figure 7 is a summary of the changes in τ, $n2$, and PSE given in Table 4 for each bird. The top panel of Figure 6 shows that the mean value of τ decreased as reinforcer duration was increased, as predicted by BeT, and was significant with the Friedman test, $T(3) = 8.28$. The middle panel of Figure 7 shows that the mean value of $n2$ increased as reinforcer duration was increased, although this increase was not statistically significant, $T(3) = 5.82$. The bottom panel of Figure 7 shows that the mean values of PSE increased a small but statistically nonsignificant amount as reinforcer duration was increased, $T(3) = 2.04$.

There were 10 comparisons between 1.5- and 4-s reinforcer durations for τ and $n2$ parameter values over the 5 birds. For these 10 comparisons, changes in τ and $n2$ were in opposite directions for 8 cases, which was significant with the binomial test. For 2 cases, $n2$ did not differ; that is, there was a significant inverse relation between τ and $n2$. For each of the birds, the Pearson product–moment correlations between τ and $n2$ were $-.98$, $-.95$, $-.97$, $-.89$, and

Reinforcer Duration

Figure 6. Proportions of right-key responses in 5-s bins based on response totals over the last five sessions of each condition for each bird for Experiment 2. The smooth curves are the best nonlinear least squares fits of Equation 3 to the data.

−.95, respectively. The inverse relation between τ and $n2$ is consistent with recalibration of the behavior underlying the temporal discrimination (see below).

Discussion

The results of Experiment 2 further support the assumption by BeT that reinforcement density determines pace-

maker rate. Psychometric functions were flatter for the 1.5-s reinforcer duration conditions than for the 4-s reinforcer duration conditions and were shifted toward longer durations (see Figure 5). The quantitative fits of Equation 3 to the data were uniformly excellent, and the parameter τ decreased as reinforcer duration was increased and increased when reinforcer duration was decreased, in accordance with the prediction of BeT. Also, evidence of reca-

Table 4

Obtained Parameter Values (τ, n2) for the Best Fit of Equation 3 to Right-Key Response Proportions, Based on Response Rates Summed Over the Last Five Sessions of Each Condition, for Trials Without Reinforcement for Experiment 2

| | Reinforcer duration (in seconds) | Bird | | | | | | | | | | | | | | |
| | | L1 | | | L2 | | | L3 | | | L4 | | | L5 | | |
Condition		τ	n2	PSE	τ	n2	PSE	τ	n2	PSE	τ	n2	PSE	τ	n2	PSE
1	4	5.55	8	25.25	4.47	10	23.94	3.42	16	26.39	4.01	13	26.82	4.82	9	23.90
2	1.5	4.73	11	27.25	5.06	5	16.74	5.44	9	26.94	4.42	13	28.93	7.10	4	20.47
3	4	3.58	13	26.07	4.12	11	30.49	3.85	13	24.40	3.60	16	31.90	5.22	8	24.89
4	1.5	3.75	13	24.55	4.66	9	23.10	6.91	7	28.61	4.27	13	27.96	9.32	3	22.83

Note. τ = average interpulse time; n1 = state associated with left-key responses; n2 = state associated with right-key responses; PSE = point of subjective equality. n1 was set at 1 for individual birds; PSEs were calculated using Equation 4.

libration of the adjunctive behavior to the states that underlie the discrimination was provided by the strong inverse relationship between τ and n2, coupled with non-systematic variation of the PSE (see Figure 7).

General Discussion

BeT, as proposed by Killeen and Fetterman (1988), offers a timing model that places a special utility on the role of behavior in mediating temporal discriminations. BeT holds that pulses from a hypothetical pacemaker move the organism through sequential states. The transitions between states is described by a Poisson process (see Equation 1). Adjunctive behaviors correlated with the nth state may precede reinforcement of the discriminative response. The adjunctive behaviors then provide the basis for the organism's conditional discrimination as to its position in time.

BeT also holds that pacemaker rate is a direct function of reinforcer density and is sensitive to motivational parameters. The period of the pacemaker, τ (interpulse time), is assumed to be directly related to interreinforcer interval T (Equation 2) and therefore inversely related to reinforcement rate. That is, increased levels of reinforcement density speed the pacemaker, and decreased density slows the pacemaker (Bizo & White, 1994; Fetterman & Killeen, 1991; Killeen & Fetterman, 1988, 1993; MacEwen & Killeen, 1991; Morgan et al., 1993).
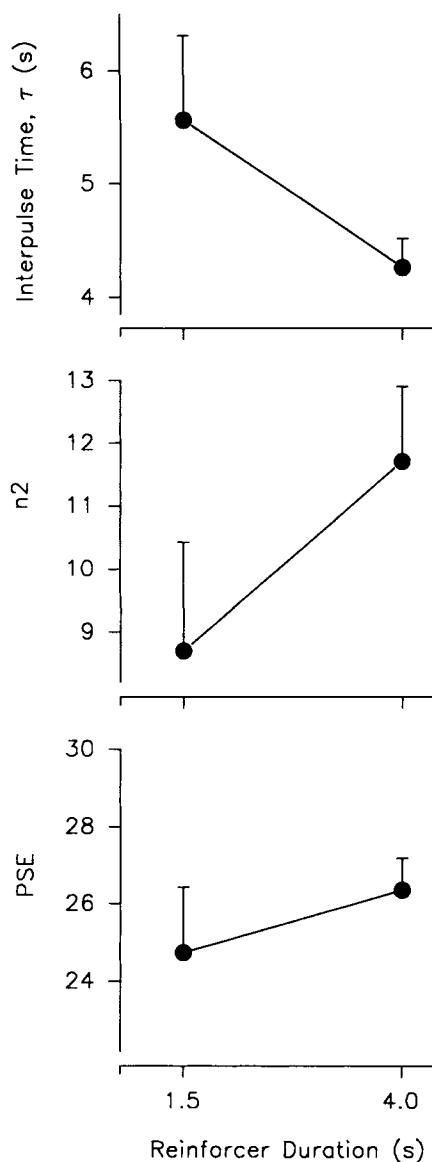
The results of Experiment 1 support the hypothesis that pacemaker rate is determined by reinforcement density. In Experiment 1, we manipulated reinforcement density by varying the duration of the ITI. Reinforcement density was therefore defined in terms of reinforcers per session, with longer ITIs associated with lower rates of reinforcement and hence larger values of interpulse time (slower pacemaker). The hypothesis that ITI would influence interpulse time is confirmed by the data in Figure 2, which show that the longer the ITI, the further the psychometric function is shifted toward longer durations, consistent with a slowing of the pacemaker. The change in mean values of interpulse time obtained by fitting predictions from BeT to the psychometric functions is confirmed by the data in Figure 4, which show that interpulse time increases as ITI increases. This support for BeT is qualified, however, by the reduction

in reinforcers per trial that was associated with the largest ITI. That is, the slowing of the pacemaker could have resulted from reduced reinforcers per trial, although the absence of a change in reinforcers per trial across the two shorter ITI durations suggests that in this case reinforcers per trial did not contribute to pacemaker rate. Instead, overall reinforcement rate is the important variable. One should also note that the strict proportional relationship specified by Equation 2 was not observed.

The results of Experiment 2 also support the assumption that pacemaker rate is a function of reinforcement density. Estimates of interpulse time τ varied according to BeT's predictions. When reinforcer duration was increased, interpulse time decreased, and when reinforcer duration was decreased, interpulse time increased. When interpulse time was plotted against reinforcer duration (see Figure 7, top panel), interpulse time was an inverse function of reinforcer duration. As with Experiment 1, this relation was not strictly proportional.

Previous research usually has failed to find a relation between pacemaker rate and reinforcer duration (Fetterman & Killeen, 1991; MacEwen & Killeen, 1991). Why this should be the case is unclear. It is possible that manipulations of reinforcer duration do not affect reinforcer density to the same extent as reinforcer frequency. This possibility is consistent with previous studies of concurrent choice in which reinforcer duration was less effective than reinforcer frequency (Davison & Hogsden, 1984; Schneider, 1973; Todorov, 1973). Also, in the previous studies food was delivered after the interval that was timed (Fetterman & Killeen, 1991; MacEwen & Killeen, 1991), whereas in the present study reinforcers occurred during the timed interval. Accordingly, the present procedure may have increased the salience of reinforcer duration.

Because BeT assumes that pacemaker rate is determined by reinforcement rate, specification of the time base for reinforcement is fundamental to BeT. The present test of the prediction that pacemaker rate is determined by ITI depends on the assumption that ITI and trial duration contribute equally to the time base for the calculation of reinforcement density (Equation 2). More generally, any definition of reinforcer density would need to take account of intratrial interreinforcer interval, ITI, and reinforcement duration, all

ample, Equation 5 assumes that pacemaker rate $1/\tau$ is a linear function of reinforcer density D, where density is measured in terms of total reinforcement duration per total session duration. D can be multiplied by a scaling constant, which equals 1.0 in the present case.

$$\frac{1}{\tau} = D + \frac{1}{\tau_0} \tag{5}$$

Figure 8 shows pacemaker rate plotted as a function of reinforcement density, measured as total seconds of reinforcer duration per total session duration (in seconds) for Experiments 1 and 2 and for Bizo and White's (1994) Experiment 2. Equation 5 explains the data well, with 88% of the variance accounted for. Figure 8 shows that pacemaker rate is linearly related to the density of reinforcement. Fetterman and Killeen (1991) also plotted pacemaker rate as a function of reinforcement density and found a linear relationship with a positive value of $1/\tau_0$.

Killeen and Fetterman (1988) suggested that after a change in reinforcement density, the pacemaker rate should change and that any resulting changes in the PSE should be transient. For example, a faster pacemaker would result in arriving at the nth state sooner. In an attempt to maintain accurate performance, however, new behaviors would become associated with a later state and would serve as the cue for discriminative responses. That is, as τ decreases, the values of n increase. Recalibration thus results in changes in n that are the inverse of changes in the interpulse time τ. Recalibration refers to the reconditioning of "the behaviors

Figure 7. Mean values of average interpulse time, τ (top panel), mean values of $n2$ (state associated with right-key responses; middle panel), and mean points of subjective equality (PSEs; bottom panel) plotted as a function of reinforcer duration for Experiment 2. The means are based on the data in Table 4. The standard error bars are based on a single mean data point per bird. Pacemaker rate $= 1/\tau$.

of which may contribute to the time base for the reinforcement rate and hence to the interpulse time τ. That is, the effective time base for the calculation of pacemaker rate is total session duration. One can further argue that, because Experiments 1 and 2 did not support a strictly proportional relation between pacemaker rate and reinforcement density, the relation between pacemaker rate and reinforcement rate may be linear rather than strictly proportional. This can be achieved by assuming a resting pacemaker rate of $1/\tau_0$, which is independent of the experimental context. For ex-

Figure 8. Mean values of pacemaker rate $(1/\tau)$ plotted as a function of reinforcement density (reinforcer seconds per second of session duration) for the present Experiments 1 and 2 and for Bizo and White's (1994) Experiment 2. The straight line shows Equation 5 fitted to the data. ITI $=$ intertrial interval; VAC $=$ variance accounted for.

that support the choice responses 'short' and 'long' " (Fetterman & Killeen, 1991, p. 236).

Previous support for recalibration is mixed; it has been reported by Bizo and White (1994), Haight and Killeen (1991), Killeen and Fetterman (1988), and Morgan et al. (1993) and may be inferred from Raslear et al. (1992). Fetterman and Killeen (1991) have reported its absence. The present experiments offer some support for recalibration. In Experiment 1 there was an inverse relationship between average interpulse time τ and $n2$. However, there was also a systematic change in PSEs after changes in the ITI. Because BeT predicts that owing to recalibration the PSE should shift back to some central value given prolonged exposure to a new ITI condition, recalibration may not have been complete in Experiment 1.

In Experiment 2 there was also an inverse relation between average interpulse time τ and $n2$. The interpretation of this inverse relation is that in response to an overall faster or slower pacemaker, the behaviors that support discriminative responding become associated with new states, as evidenced by the change in $n2$. This conclusion is further supported by the nonsystematic variation of the PSEs as a result of variations in reinforcement duration. As a result of recalibration, the PSE may not be as sensitive a measure of changes in timing behavior as τ or n (Bizo & White, 1994).

In addition to the support for recalibration from the negative correlations between τ and $n2$ in Experiments 1 and 2, quantitative evidence is provided by the correspondence

between the data and Equation 4. When Equation 4 is rearranged to express τ as a function of $n2$, and $n1$ is set at 1, the single free parameter is the PSE. The relation is a family of near-parallel monotonically decreasing curves with PSE as the parameter. The curve for PSE = 25 s (the midpoint of the trial) is shown in Figure 9. Also shown in Figure 9 are individual values of τ plotted as a function of $n2$ for each condition and for each bird in Experiments 1 and 2. Although the smooth curve in Figure 9 has no free parameters, there is a strong degree of concordance between the smooth curve predicted by Equation 4 (for PSE = 25 s) and the obtained data points across a range of conditions and different birds in the present experiments. Figure 9, therefore, offers strong support for BeT.

The present experiments expand the base of experimental support for BeT. Interpulse time varied as an inverse function of ITI and reinforcer duration. This suggests that the birds included ITI and reinforcer duration in their estimate of reinforcement density, although this relation was not strictly proportional (see Figure 8). There also appeared to be a recalibration of the relation between sequential states and adjunctive behavior to compensate for a slower or faster pacemaker, as suggested by an inverse relationship between $n2$ and interpulse time for Experiment 2.

References

Bizo, L. A., & White, K. G. (1994). The behavioral theory of timing: Reinforcer rate determines pacemaker rate. *Journal of the Experimental Analysis of Behavior, 60,* 19–33.
Bonem, M., & Crossman, E. K. (1988). Elucidating the effects of reinforcement magnitude. *Psychological Bulletin, 104,* 348–362.
Davison, M., & Hogsden, I. (1984). Concurrent variable-interval schedule performance: Fixed versus mixed reinforcer durations. *Journal of the Experimental Analysis of Behavior, 41,* 169–182.
Fetterman, J. G., & Killeen, P. R. (1991). Adjusting the pacemaker. *Learning and Motivation, 22,* 226–252.
Fleshler, M., & Hoffman, H. S. (1962). A progression for generating variable-interval schedules. *Journal of the Experimental Analysis of Behavior, 5,* 529–530.
Haight, P. A., & Killeen, P. R. (1991). Adjunctive behavior in multiple schedules of reinforcement. *Animal Learning & Behavior, 19,* 257–263.
Killeen, P. R. (1975). On the temporal control of behavior. *Psychological Review, 82,* 89–115.
Killeen, P. R. (1991). Behavior's time. In G. Bower (Ed.), *The psychology of learning and motivation* (Vol. 27, pp. 294–334). San Diego, CA: Academic Press.
Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review, 95,* 274–295.
Killeen, P. R., & Fetterman, J. G. (1993). The behavioral theory of timing: Transition analyses. *Journal of the Experimental Analysis of Behavior, 59,* 411–422.
Killeen, P. R., Hanson, S. J., & Osborne, S. R. (1978). Arousal: Its genesis and manifestation as response rate. *Psychological Review, 85,* 571–581.
MacEwen, D., & Killeen, P. (1991). The effects of rate and amount of reinforcement on the speed of the pacemaker in pigeons' timing behavior. *Animal Learning & Behavior, 19,* 164–170.
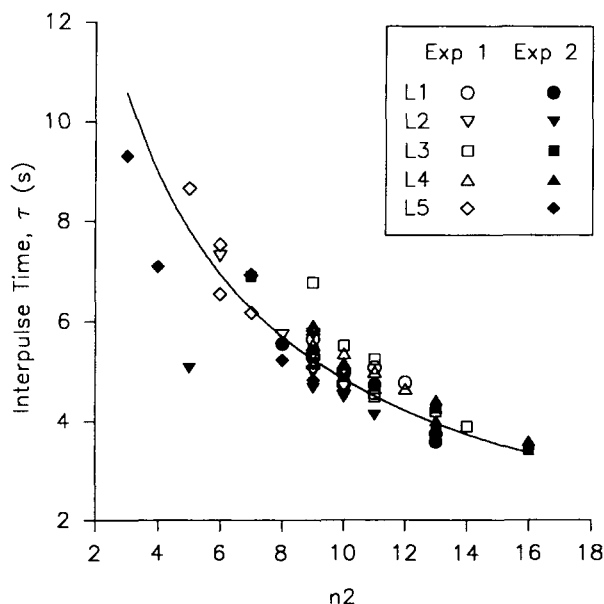Morgan, L., Killeen, P. R., & Fetterman, J. G. (1993). Changing

Figure 9. The relation between obtained values of the parameters τ and $n2$ (state associated with right-key responses), for each bird (L1–L5), in Experiments 1 and 2 (see Tables 2 and 4). The smooth curve plots τ as a function of $n2$, predicted by rearranging Equation 4 with point of subjective equality set at 25 s and $n1$ = 1. The proportion of variance in the data points accounted for by the smooth curve is .68. $n1$ = state associated with left-key responses.

rates of reinforcement perturbs the flow of time. *Behavioural Processes, 30,* 259–272.

Nevin, J. A. (1974). Response strength in multiple schedules. *Journal of the Experimental Analysis of Behavior, 21,* 389–408.

Raslear, T. G., Shurtleff, D., & Simmons, L. (1992). Intertrial–interval effects on sensitivity (A') and response bias (B") in a temporal discrimination by rats. *Journal of the Experimental Analysis of Behavior, 58,* 527–535.

Schneider, J. W. (1973). Reinforcer effectiveness as a function of reinforcer rate and magnitude: A comparison of concurrent performances. *Journal of the Experimental Analysis of Behavior, 20,* 461–471.

Stubbs, A. (1968). The discrimination of stimulus duration by pigeons. *Journal of the Experimental Analysis of Behavior, 11,* 223–238.

Stubbs, D. A. (1979). Temporal discrimination and psychophysics.

In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behavior: Vol. 1. Reinforcement and the organization of behavior* (pp. 341–369). New York: Wiley.

Stubbs, D. A. (1980). Temporal discrimination and a free-operant procedure. *Journal of the Experimental Analysis of Behavior, 33,* 167–185.

Todorov, J. C. (1973). Interaction of frequency and magnitude of reinforcement on concurrent performances. *Journal of the Experimental Analysis of Behavior, 19,* 451–458.

Zeiler, M. D. (1991). Ecological influences on timing. *Journal of Experimental Psychology: Animal Behavior Processes, 17,* 13–25.