THE BEHAVIORAL THEORY OF TIMING: REINFORCER RATE DETERMINES PACEMAKER RATE

Lewis A. Bizo and K. Geoffrey White

UNIVERSITY OF OTAGO, NEW ZEALAND

In the behavioral theory of timing, pulses from a hypothetical Poisson pacemaker produce transitions between states that are correlated with adjunctive behavior. The adjunctive behavior serves as a discriminative stimulus for temporal discriminations. The present experiments tested the assumption that the average interpulse time of the pacemaker is proportional to interreinforcer interval. Responses on a left key were reinforced at variable intervals for the first 25 s since the beginning of a 50-s trial, and right-key responses were reinforced at variable intervals during the second 25 s. Psychometric functions relating proportion of right-key responses to time since trial onset, in 5-s intervals across the 50-s trial, were sigmoidal in form. Average interpulse times derived by fitting quantitative predictions from the behavioral theory of timing to obtained psychometric functions decreased when the interreinforcer interval was decreased and increased when the interreinforcer interval was increased, as predicted by the theory. In a second experiment, average interpulse times estimated from trials without reinforcement followed global changes in interreinforcer interval, as predicted by the theory. Changes in temporal discrimination as a function of interreinforcer interval were therefore not influenced by the discrimination of reinforcer occurrence. The present data support the assumption of the behavioral theory of timing that interpulse time is determined by interreinforcer interval.

Key words: timing, temporal discrimination, behavioral theory of timing, psychometric function, interreinforcer interval, variable-interval schedules, key peck, pigeon

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The behavioral theory of timing (BeT) emphasizes the role of behavior in temporal discrimination (Killeen & Fetterman, 1988, 1993). According to BeT, certain kinds of adjunctive behavior, whether elicited, emitted, interim, or terminal, occur in a consistent fashion such that they are temporally related to reinforcer delivery. These kinds of behavior may then act as conditional discriminative stimuli when an animal is required to make a temporal discrimination. In BeT, classes of adjunctive behavior are associated with hypothetical states. One class of behavior can be associated with several states, and several types of behavior maybe associated with a single state. Pulses from a hypothetical "pacemaker" drive transitions from one state to the next, according to a Poisson process. The probability that

n pulses will be produced by time t, $P[N(t) = n]$, is given by Equation 1:

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

In Equation 1, τ is the average interpulse time, and in effect is an intervening variable because of the hypothetical nature of the pacemaker. Equation 1 has been successful in describing several distributions of behavior over time (e.g., Killeen, 1975, 1991; Killeen, Hanson, & Osborne, 1978). The temporal distribution of timing response depends on the number of pulses (n) produced by time t and also by the average interpulse time (τ). A core assumption of BeT is that average interpulse time is a linear function of the average interreinforcer interval, T:

$$\tau = kT. \quad (2)$$

Interreinforcer interval (IRI) thus determines the average interpulse time, which in turn determines the average rate of transitions between states. When the Poisson process reaches the nth state, the adjunctive behavior correlated with that state will occasion the appropriate timing behavior.

Evidence that IRI determines average interpulse time has been drawn by Killeen and Fetterman (1988) from the shift of the point of subjective equality (PSE) of psychometric

functions for temporal discriminations. Killeen and Fetterman described a timing task in which pecking a main response key produced food 8 s (when the key was red) or 24 s (when the key was green) after a trial had begun. Food was available after 8 s on half the trials in a session and after 24 s on the other half. Key color could be changed by pecks on a changeover key that then became inoperative for the remainder of the trial. The IRI was varied indirectly by varying the duration of the intertrial interval (ITI). For 2 birds the ITI was initially 15 s, and for the other 2 it was initially 180 s. ITI conditions were reversed after 20 sessions. Psychometric functions, which presented the probability of changing to the "long" choice response (green key) as a function of time, shifted to the longer durations (larger PSEs) when the ITI was increased, consistent with an increase in the interpulse time, as predicted by BeT. The psychometric functions shifted to the shorter durations (smaller PSEs) when the ITI was decreased, consistent with a decrease in the interpulse time. The variance of the psychometric functions increased following an increase in ITI, as predicted by BeT. An increase in the variance of the psychometric function also occurred when the ITI was decreased, but this was not predicted by BeT because the mean and variances of the Poisson process should be directly related.

Fetterman and Killeen (1991) tested more directly the assumption that IRI determines interpulse time by varying reinforcement probability. The task involved the discrimination of a short 4-s duration and a long 12-s duration. Probe durations were randomly presented on half the trials. Reinforcer probability was manipulated by reinforcing timing responses on 20% or 80% of the trials. Psychometric functions were expected to shift towards longer durations and flatten out with the lower probability of reinforcement, and hence the standard deviation of the psychometric function should increase. PSEs were predicted to increase with decreases in reinforcement probability, and PSEs were expected to decrease with increases in reinforcement probability. The changes in standard deviation of the psychometric functions following a change in reinforcement probability were as predicted for only 2 of the 4 birds, with larger standard deviations for the low reinforcement-probability condition compared to the high proba-bility condition. There was no systematic change in the PSEs of the psychometric functions as a result of manipulating reinforcement probability.

In Fetterman and Killeen's (1991) experiment, session duration differed between high and low reinforcer-probability conditions. Sessions ended after 60 reinforcers in the 80% condition and after 40 reinforcers in the 20% condition. Because reinforcers per session duration may have influenced timing, the predicted effect of IRI may have been clearer with constant session duration. Also, the experimental conditions lasted for just 10 sessions. With longer conditions, a change of reinforcement probability may have had a greater effect on behavior. The evidence from Fetterman and Killeen's study for a relation between IRI and interpulse time is therefore not compelling.

In another study, MacEwen and Killeen (1991) manipulated IRI in the peak procedure. In this procedure, responses are reinforced at some fixed interval after the beginning of the trial. On test trials, reinforcers are omitted and the trial continues for about twice the fixed-interval duration. Distributions of responses on test trials peak at about the value of the fixed interval used in training. MacEwen and Killeen found that increasing the fixed-interval duration increased estimates of the average interpulse time, as predicted by BeT.

Killeen (1991) described an unpublished study in which reinforcement was contingent on responses to a left key 8 s after the start of a trial, to a center key 16 s after the start of a trial, and to a right key 32 s after the start of a trial. The proportion of trials with reinforcement was manipulated. Reinforcement probability was initially 1.0, then .75, and finally 1.0. When overall IRI was increased (in the .75 condition), the distributions of responses as a function of time since trial onset for each of the three keys shifted towards longer durations, and the variance of the distributions increased, compared to response distributions for both 1.0 conditions. An increase in estimated interpulse time was proportional to the decrease in reinforcement probability.

The present experiments were designed to examine further the effects of interreinforcer interval on interpulse time, in view of the mixed evidence for BeT from the previous studies in which IRI was manipulated. A timing procedure was used in which two keys were con-

currently available following a short intertrial interval. This procedure was based on the free-operant psychophysical procedures used by Stubbs (1968, 1979, 1980). In this procedure, for the first 25 s after trial onset, reinforcers followed responses on one key at variable intervals (VI). During the period from 25 s to 50 s after trial onset, reinforcers followed responses on a second key. Optimal timing was shown by a switch from one key to the other at 25 s. The procedure generates a psychometric function that relates the proportion of responses on one key as a function of total responses to time since the beginning of the trial. The PSE of this sigmoidal function occurs at about 25 s. That is, at about 25 s after trial onset, the proportion of responses on one key is .5.

Equation 1 can be used to predict the absolute rates of responses on left and right keys in the timing procedure. The absolute rate predictions are similar to those described by Killeen (1991), although for a different procedure. The functions in the top panel of Figure 1 illustrate the typical pattern of responding in the present timing procedure, with left-key response rates being higher in the first 25 s than in the second 25 s, and with right-key responses showing the converse pattern. The data points are the sum of absolute responses for the last five sessions from the first condition for Bird L1 in the present Experiment 1; they illustrate the close correspondence between actual response frequencies and the functions predicted by Equation 1 (smooth curves). The two smooth curves show that with the assumptions of a common value for interpulse time τ and two different values for n, Equation 1 satisfactorily describes absolute left and right response frequencies.

In the middle panel of Figure 1, the data points were derived by taking right responses as a proportion of total responses. Predictions for the psychometric function (smooth curve) in the second panel of Figure 1 were generated in the following way. Absolute right-response frequencies or rates are predicted by Equation 1 with $n = n2$, and absolute left-response frequencies or rates are predicted by Equation 1 with $n = n1$. The same value of average interpulse time τ is assumed for both versions of Equation 1. Because the proportion of right responses in the actual data is calculated by dividing right response frequencies by the sum of left and right response frequencies, predic-

tions of proportions of right responses were generated in the same way. That is, the proportion of right responses is predicted 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 ($n = n1$). Following algebraic simplification, right responses (R) as a proportion of total right and left (L) responses is given by Equation 3[1]:

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

This equation is based on separate predictions for absolute rates of left and right responses. It is applicable to free-operant procedures in which the sum of choice responses at any one time may vary, unlike discrete-trial procedures in which the sum of frequencies of choice responses is constant and their probabilities sum to 1.0 (Raslear, Shurtleff, & Simmons, 1992).

The third panel of Figure 1 shows two psychometric functions, one for $\tau = 6.5$ and the other for $\tau = 5.5$. (The difference between these values is of the same order as the difference between τ values in the present Experiment 1.) This panel illustrates the predicted shift in the function that would result from a decrease in the average interpulse time, τ. The difference between the two functions is the predicted effect of different interreinforcer intervals, with a reduced IRI generating the function for $\tau = 5.5$. The shift to shorter durations steepens the function and decreases its variance (cf. Killeen & Fetterman, 1988).

EXPERIMENT 1

In Experiment 1, we examined the effect of average IRI on average interpulse time by varying the VI schedule that maintained responding on the left and right keys in the two-

key timing procedure. The ratio of scheduled reinforcement for responses to the left and right keys was always 1.0. The general prediction was that the psychometric function should shift towards longer durations with longer IRIs. In terms of Equation 3, estimates of average interpulse time derived from the psychometric function should be greater for the longer VI values.

METHOD

Subjects

Subjects were 5 adult homing pigeons. All birds had previous experimental histories in multiple-concurrent schedules with color, line-tilt (White, 1986), and shape stimuli. The birds were maintained at 80% of their free-feeding weights. If their weights did not fall within ±12 g of the prescribed weight immediately prior to an experimental session, they were not included in that day's experimental session. All birds were housed individually and had free access to water and grit. Supplementary feed was given after experimental sessions and consisted of a mix of wheat, corn, and maple peas.

Apparatus

A sound-attenuating experimental chamber, 32 cm wide, 35 cm deep, and 29 cm high on the inside, contained an interface panel. The interior of the chamber was painted matte black. A ventilation fan provided masking noise during experimental sessions. Two Plexiglas response keys were mounted on the interface panel 22 cm from the chamber floor and 10 cm apart. The keys were both 2.9 cm in diameter. The left key could be illuminated red and the right key green. Each key required a force of approximately 0.2 N to operate a reed relay mounted behind the key. Each effective response resulted in a 50-ms blackout of the pecked key. The central hopper opening provided 4-s access to wheat. When wheat was available, the response keys were turned off and a white light inside the top of the hopper opening illuminated the grain hopper. A PDP® 11/23 with SKED® software and interfacing in an adjacent room controlled and recorded the experimental events.

Procedure

Experimental sessions were usually conducted 7 days a week. Sessions lasted for 48 min. A short blackout period preceded and
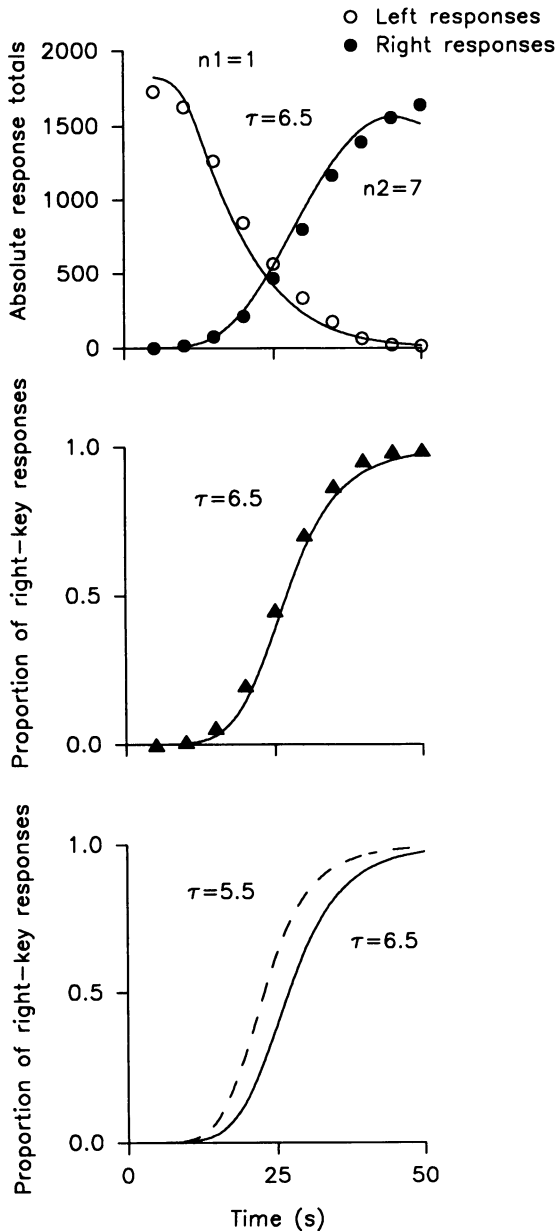
Fig. 1. The smooth functions show predictions from Equation 1 of frequencies of left- and right-key responses in the present procedure (top panel) and predictions from Equation 3 for response proportions (middle panel) using the same parameter values as for predictions of response frequencies. Predictions from Equation 3 for different values of τ are also shown (bottom panel). The data points in the top panel are the absolute response totals from the last five sessions of Condition 1 of Experiment 1 for Bird L1, chosen arbitrarily to illustrate the correspondence between predictions from Equation 1 and actual data. Data points in the middle panel are response proportions calculated from the absolute rates in the top panel.

followed each session, and responses were not recorded during the blackouts. The chamber and all keys were dark during blackout periods. The birds were trained on a schedule that consisted of a 50-s trial with a 10-s ITI. During the ITI, the keys and the chamber were dark and responses were ineffective. The stimuli on left and right keys remained unchanged throughout each trial. For the first 25 s, responses to the left key were reinforced according to a VI schedule and responses to the right key were extinguished. After 25 s, the VI and extinction components were reversed, so that responses to the right key were reinforced according to a VI schedule and responses to the left key were extinguished. The constant-probability VI schedules (Fleshler & Hoffman, 1962) in the different components were independent. Reinforcers set up but not obtained in the left or right components of one trial were held over until the next. Each session lasted for 48 trials.

During initial training, the VI schedule was VI 25 s for 4 days, followed by VI 30 s for 40 days. Thereafter, the VI schedule was manipulated across the five conditions listed in Table 1. The criterion for completion of a condition was that all birds were to have completed a minimum of 25 sessions. In the VI 15-s condition especially, there were sessions when some birds were overweight and were not tested. As a result, other birds completed many more than the minimum 25 sessions per condition (Table 1). The last condition was inadvertently conducted for fewer sessions (see Table 1). Table 1 summarizes the condition changes and the number of sessions for which each condition was conducted for each bird.

RESULTS

Key pecks to the left and right keys were recorded in 5-s bins during each trial. These were summed over the 48 trials for each daily session. All analyses were based on these response totals, and reinforcement duration was not subtracted from the 50-s time base for each trial. Absolute right-key response distributions were S shaped; they started low and increased to a maximum by the end of the trial. Left-key response distributions were reverse-S shaped; they started high and decreased to a minimum by the end of the trial. The absolute response totals in the top panel of Figure 1 for the last five sessions of the first condition for

Table 1

Summary of conditions and the number of sessions completed by each bird in each condition of Experiment 1.

Condi-tion	VI	Bird				
		L1	L2	L3	L4	L5
1	30	27	27	27	27	27
2	120	25	25	25	25	25
3	15	25	36	47	46	25
4	120	25	26	26	26	25
5	30	16	20	20	20	18

Bird L1 are typical of those for other birds and other conditions. Absolute rate functions were similar to those reported by Stubbs (1979, 1980). The proportion of right-key responses as a function of total responses was calculated for each 5-s bin of each trial for the 1st day, 2nd day, 5th day, last day, and for the sum of last 5 days of each condition.

Figure 2 shows the proportion of right responses in 10 consecutive 5-s bins for responses summed over the last 5 days of each condition (columns) for each bird (rows). Figure 2 shows that the response proportion systematically increased according to a sigmoidal function. As will be shown by the quantitative analysis below, the functions for the VI 120-s conditions are displaced towards longer times since the start of the trial and are less steep than are the functions for the VI 15-s and VI 30-s conditions.

The functions for the different conditions (Figure 2) were compared in terms of the estimates of the parameters of Equation 3 that best fitted the data. The data in Figure 2 were fitted using a nonlinear least squares regression. Initial fits of Equation 1 to absolute left-key response frequencies revealed that n rarely settled on any other value than 1. Because a reduction in the number of free parameters in Equation 3 is in the interests of parsimony, the parameter $n1$ was kept at 1, and the other two parameters, τ and $n2$, varied freely. Setting $n1 = 1$ assumes that the classes of adjunctive behavior that occasion left responses, or the left responses themselves, are all associated with the first state in the Poisson process. The best fitting functions are shown as smooth curves in Figure 2.

Table 2 presents obtained parameter values derived from fitting Equation 3 to the proportion of right-key responses for the last 5 days. The average variance accounted for
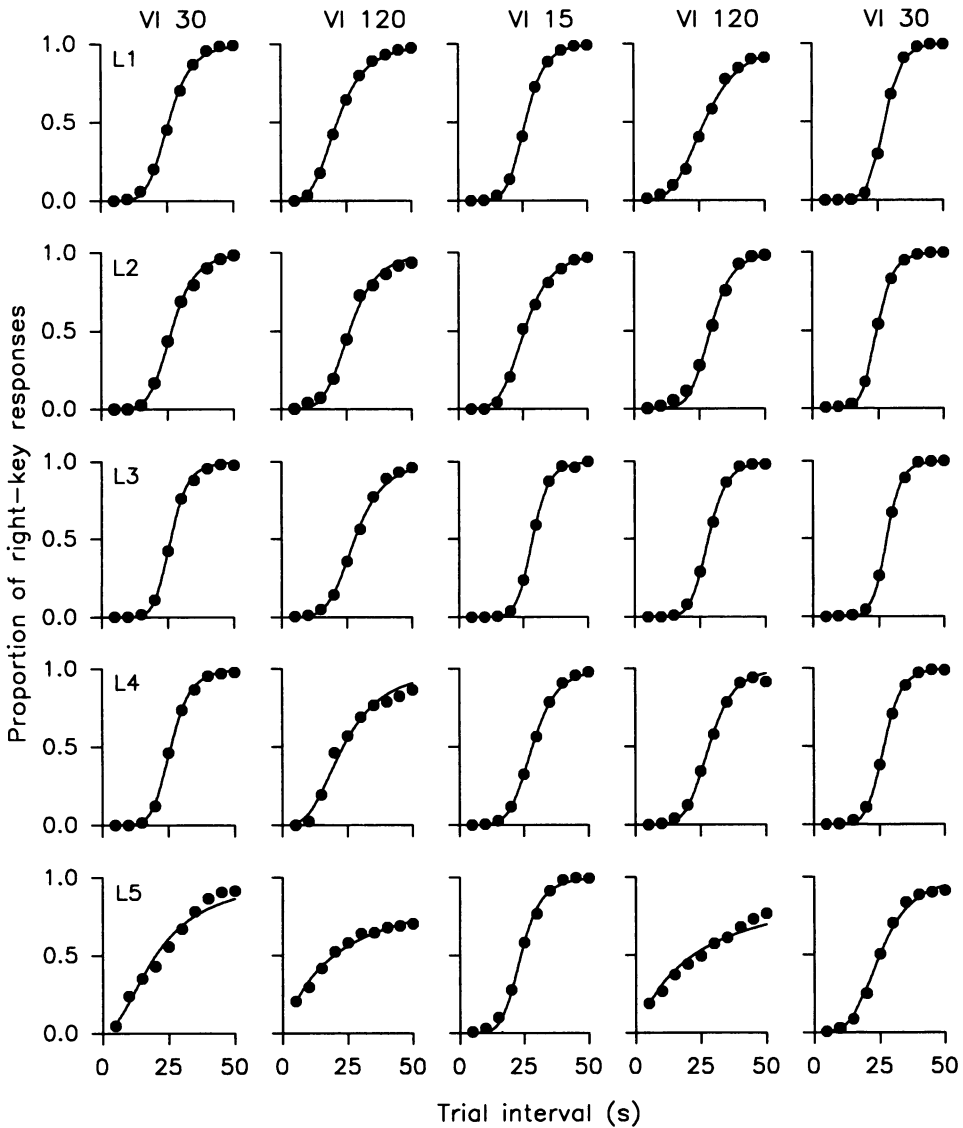
Fig. 2.   Proportion of right-key responses in 5-s bins based on response totals over last five sessions of each condition for each bird in Experiment 1. The smooth curves are the best fitting functions of Equation 3 fitted to the data.

(VAC) was .994, with a standard deviation (*SD*) of .01. Except for four instances, the variance accounted for was always better than .995. The average mean squared error was 0.0005 (*SD* = .0006). The fits of Equation 3 to the individual functions were therefore uniformly excellent.

A comparison of the last 5 days of each condition with the last 5 days of the immediately following condition in Table 2 shows that there was an increase in the average interpulse time, τ, following an increase in the average interreinforcer interval, and a decrease in τ following a decrease in the average interreinforcer interval. These trends occurred for 18 of the 20 condition changes, which is statistically significant with a binomial probability of $p = .0002$. When IRI was increased, 8 of 10 condition changes showed the predicted increase in τ, which is statistically significant using the binomial test, $p < .05$. When the IRI was decreased, 10 of 10 condition changes showed the predicted decrease in τ. These directional changes are in accordance with the prediction of BeT.

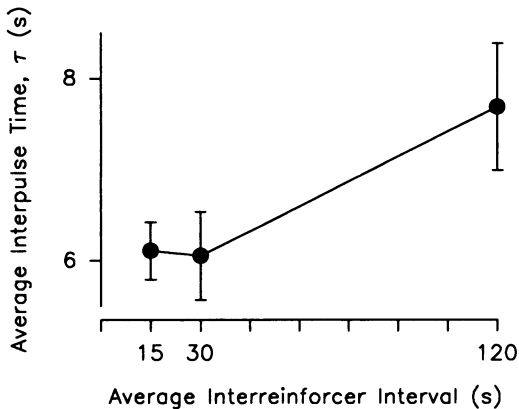Figure 3 shows group average values of τ

Fig. 3. Mean values of average interpulse time, τ, as a function of scheduled interreinforcer interval, for data based on response totals for the last 5 days of each condition in Experiment 1. The error bars are ±1 *SEM*.

as a function of average interreinforcer interval, based on the individual data presented in Table 2 (values of τ for the replications of the VI 30-s and VI 120-s conditions were initially averaged for each bird). Figure 3 summarizes the general result that τ is a positively increasing function of interreinforcer interval. A repeated measures analysis of variance on the data in Figure 3 indicated that the effect of IRI was statistically significant, $F(2, 8) = 4.53$, $p < .05$.

The change in values of τ from one condition to the next, and the stability of τ values across a condition, were examined by fitting Equation 3 to the proportion data for selected individual sessions. The sessions included the 1st, 2nd, 5th, and last days of each condition. The average variance accounted for was .993 ($SD = .009$), and the average mean squared error was 0.0009 ($SD = .0008$). Fits of Equation 3 to the data for individual sessions were therefore excellent. There was no statistically significant

group difference between τ values for the last day of each condition and the τ values for the last 5 days of each condition, $F(4, 16) < 1$.

Table 3 presents τ and $n2$ values for the best fits of Equation 3 to the proportion data for the selected individual sessions. A comparison of obtained τ for the last day of a condition with the 1st day of the next condition shows that following an increase in interreinforcer interval, interpulse time increased, as predicted by BeT. Likewise, following a decrease in interreinforcer interval, τ decreased. These predicted trends occurred for 14 of the 20 condition changes over birds (binomial probability, $p < .05$).

Figure 4 (top panel) shows τ values averaged over birds (based on individual data in Table 4) and plotted for the first, second, fifth, and last sessions of each condition. In order to assess changes in τ during each condition, taking as a beginning point the last session of the previous condition, regression lines were fitted to the four data points for each condition plus the last session of the previous condition (except in the case of the very first condition). Positive and negative slopes of the regression lines provide an indication of whether τ increased or decreased over the course of a condition. There were clear increases in the value of τ during the VI 120-s conditions and less clear decreases in τ during the VI 30-s and VI 15-s conditions. A repeated measures analysis of variance comparing values of τ for schedule condition and individual session revealed that the interaction between schedule condition and individual session was statistically significant, $F(12, 48) = 2.711$, $p < .05$. In terms of BeT, the hypothetical pacemaker slowed down in the lean schedules and speeded up in the rich schedules.

Figure 4 (middle panel) also shows changes in $n2$, the number of pulses determining hy-

Table 2

Obtained parameter values (τ, $n2$) for the best fit of Equation 3 to response proportions based on response rates summed over the last 5 days of each condition in Experiment 1. The value of $n1$ was set at 1 for each fit.

Condition	Bird L1		Bird L2		Bird L3		Bird L4		Bird L5	
	τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$
VI 30	6.19	7	6.39	7	5.26	9	5.68	8	8.17	4
VI 120	6.50	5	6.98	6	7.50	6	8.05	4	9.76	2
VI 15	5.76	8	6.88	6	5.34	10	6.84	7	5.72	7
VI 120	8.20	5	6.40	8	5.67	9	6.80	7	11.04	2
VI 30	5.14	10	5.95	9	4.85	11	5.38	9	7.54	5

Table 3

Obtained parameter values (τ and $n2$) for the best fit of Equation 3 to the data of the 1st day, 2nd day, 5th day, and last day of each condition for each bird in Experiment 1. PSEs calculated using Equation 4 are also given.

Condi-tion	Day	Bird L1			Bird L2			Bird L3			Bird L4			Bird L5		
		τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE	τ	$n2$	PSE
VI 30	1st	5.48	7	22.71	4.39	8	19.98	6.23	7	25.78	5.65	9	27.99	6.86	4	19.79
VI 30	2nd	5.49	7	22.74	6.01	7	24.90	7.02	7	29.06	6.03	8	27.44	6.07	4	17.52
VI 30	5th	6.05	6	22.55	5.24	8	23.85	4.28	9	21.20	7.13	8	32.45	7.64	4	22.05
VI 30	last	5.08	9	25.17	5.63	8	25.59	5.24	9	25.93	5.22	10	27.97	7.21	4	20.79
VI 120	1st	6.69	6	24.93	5.39	9	26.71	6.22	7	25.77	5.87	8	26.69	6.81	3	16.69
VI 120	2nd	5.88	7	24.35	7.10	6	26.49	5.52	8	25.10	6.53	8	29.69	5.98	3	14.65
VI 120	5th	7.25	6	27.04	5.79	7	23.98	6.09	6	22.69	7.77	6	28.98	9.40	2	18.80
VI 120	last	6.54	6	24.37	7.39	6	27.54	7.02	6	26.16	8.75	3	21.44	13.80	2	27.60
VI 15	1st	5.49	8	24.96	6.38	5	21.11	8.26	6	30.79	9.47	4	27.31	10.05	3	24.61
VI 15	2nd	5.30	7	21.95	5.72	7	23.67	6.02	7	24.93	8.19	4	23.62	9.47	3	23.20
VI 15	5th	5.84	8	26.58	7.25	6	27.04	6.23	8	28.35	9.90	3	24.25	10.48	3	25.68
VI 15	last	5.17	9	25.60	7.27	6	27.10	4.43	12	27.26	6.74	4	30.67	6.27	6	23.36
VI 120	1st	6.18	7	25.58	6.11	7	25.29	4.68	10	25.04	7.93	5	26.25	5.89	5	19.51
VI 120	2nd	7.09	7	29.34	5.72	8	26.02	5.85	7	24.21	6.54	5	21.64	7.66	4	22.09
VI 120	5th	6.09	6	22.71	7.22	6	26.90	7.03	6	26.22	6.15	8	27.97	7.67	4	22.14
VI 120	last	7.94	7	32.86	6.60	8	30.03	5.91	10	31.64	6.69	7	27.71	11.25	3	27.56
VI 30	1st	6.53	7	27.06	6.05	6	22.54	4.99	10	26.72	5.73	7	23.71	6.04	7	25.00
VI 30	2nd	4.90	10	26.26	4.37	9	21.63	4.34	11	24.96	6.26	8	28.48	6.31	6	23.52
VI 30	5th	5.45	9	27.02	5.64	9	27.92	5.49	9	27.17	6.32	7	26.18	8.27	4	23.86
VI 30	last	4.85	10	26.00	5.62	8	25.55	5.15	11	29.64	5.29	9	26.22	8.56	5	28.34

pothetical state transitions associated with right-key responses, over the course of the component. There were clear decreases in the value for $n2$ during the VI 120-s conditions and clear increases in $n2$ during the VI 30-s and VI 15-s conditions. A repeated measures analysis of variance comparing values of $n2$ for schedule condition and individual session revealed that the interaction between schedule condition and individual session was statistically significant, $F(12, 48) = 2.792$, $p < .05$.

The systematic increase and decrease in the mean values for $n2$ during the course of rich and lean components, respectively, are taken as evidence for recalibration (Killeen, 1991;

Killeen & Fetterman, 1988). That is, the changes in $n2$ during the course of a condition result from an adjustment that compensates for changes in τ produced by the change in average IRI. As a result of recalibration, measurement of PSE may not always reveal changes predicted by BeT (Fetterman & Killeen, 1991). The PSEs may be calculated by setting Equation 3 to .5 and solving for t. That is,

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

Equation 4 provides a measure of PSE that is

Table 4

Summary of condition changes and the number of sessions completed by each bird in each condition of Experiment 2. The number of no-reinforcement trials summed over the last five sessions (of a possible 240 trials) is given in parentheses.

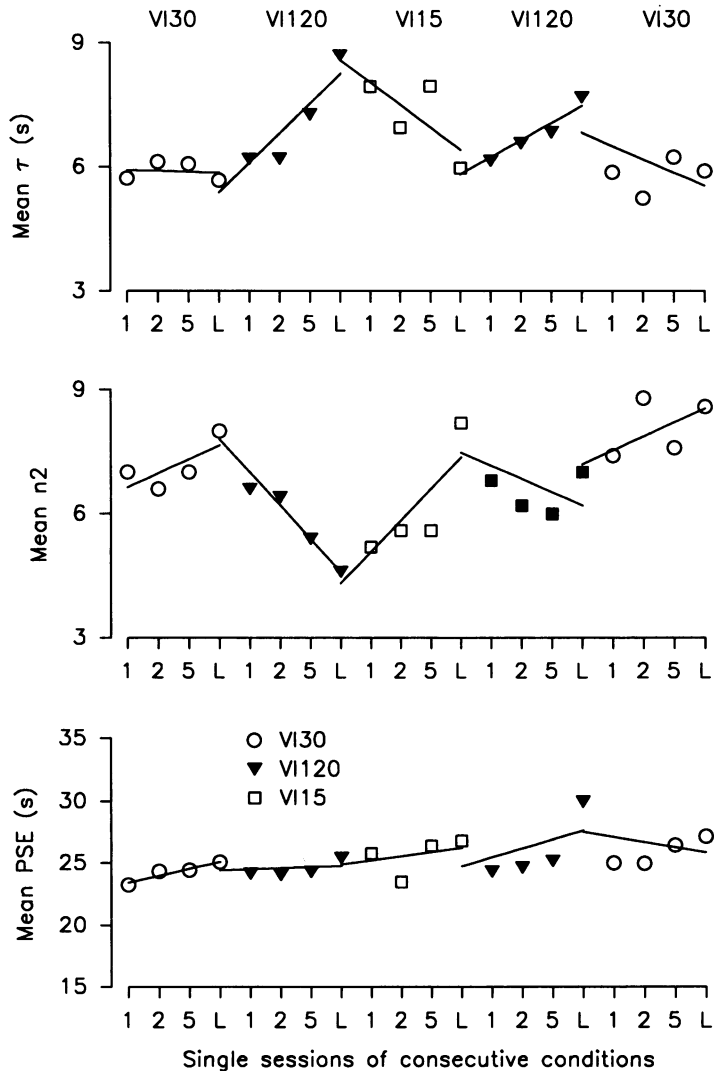| Condi-tion	VI	Bird				
		L1	L2	L3	L4	L5
1	30	28 (56)	29 (48)	31 (42)	31 (51)	26 (45)
2	120	28 (170)	28 (167)	28 (174)	28 (164)	27 (169)
3	15	25 (5)	25 (12)	41 (8)	34 (11)	25 (5)
4	120	29 (161)	30 (163)	31 (160)	31 (154)	28 (174)
5	30	29 (49)	31 (41)	42 (43)	40 (48)	31 (52)

Fig. 4. The top panel shows group average τ values (based on data in Table 3) for the 1st, 2nd, 5th, and last days of each condition in Experiment 1. The middle panel shows group average $n2$ values (based on data in Table 3) for the 1st, 2nd, 5th, and last days of each condition. The bottom panel shows group average PSE values (based on data in Table 3). The straight lines in each panel were fitted using linear regression.

based on all the data points contributing to the psychometric function, rather than just the points in the vicinity of the PSE. Table 3 presents values of the PSE calculated using Equation 4 for individual birds; the group means are shown in Figure 4 (bottom). A repeated measures analysis of variance comparing values of the PSE for schedule condition and individual session revealed no statistically significant interaction between schedule condition and individual session, $F(12, 48) < 1$. This suggests that the PSE is a less sensitive mea-

sure of timing behavior than the parameter values τ and n.

EXPERIMENT 2

Experiment 1 clearly showed that the average hypothetical interpulse time was determined by interreinforcer interval. Although this result is in accordance with BeT, an alternative account for the result must be considered. Because the two-key timing procedure involved the delivery of reinforcers during the interval

to be timed, a period without reinforcers on the left (after 25 s) may have served as a discriminative stimulus to switch to the right. Therefore, on leaner schedules the birds may change over sooner, because the likelihood of a trial without reinforcers is higher the leaner the schedule. This prediction is contradicted by the results of Experiment 1, and is opposite to the prediction of BeT that switches should occur sooner on richer schedules, in that average interpulse time is shorter. An alternative view is that the difficulty in detecting changes in the occurrence of reinforcers on leaner schedules may result in switches occurring later. In either case, the discrimination of reinforcer occurrence within trials may be an important factor.

Because previous studies used procedures different from that used in the present experiments and did not include reinforcers in the interval to be timed (Fetterman & Killeen, 1991; MacEwen & Killeen, 1991), it was deemed important to examine whether the temporal discrimination in Experiment 1 was influenced by the discrimination of reinforcer occurrence. In Experiment 2, therefore, the procedure and conditions of Experiment 1 were replicated, except that responses were recorded separately for trials that naturally included reinforcers and those that did not (trials that did not contain reinforcers are labeled *no-reinforcement trials,* and trials with reinforcers are labeled *reinforcement trials*). If, as predicted by BeT, average interpulse time is a function of overall interreinforcer interval, changes in average interpulse time should still be evident for both reinforcement and no-reinforcement trials.

METHOD

Subjects

The subjects were the same birds used in Experiment 1. They had completed two other experiments, using a similar procedure, between Experiment 1 and Experiment 2.

Apparatus

The apparatus was the same as in Experiment 1, except that experimental events were programmed and recorded by a 386 microcomputer, using Med-PC® 2.00 software. Since completing Experiment 1, the laboratory in which the experiments were conducted had been relocated to a different building.

Procedure

The procedure was the same as that in Experiment 1. Data were recorded separately for no-reinforcement and reinforcement trials. No-reinforcement trials were not specifically programmed nor were they signaled in any way, but they occurred at various points in the session when long interreinforcer intervals were arranged by the VI schedules. Table 4 summarizes the condition changes and the number of sessions conducted for each bird in each condition, as well as the number of no-reinforcement trials for each bird in the last five sessions of each condition.

RESULTS

The proportion of total responses made on the right key was calculated for each 5-s bin of the last 5 days of each condition for each bird. Separate psychometric functions relating the proportion of right responses to consecutive 5-s intervals of the 50-s trial, for trials with and without reinforcers, were very similar to those shown in Figure 2.

The fits of Equation 3 to the individual psychometric functions for reinforcement and no-reinforcement trials were excellent, and again were similar to those shown in Figure 2. For reinforcement trials, the mean variance accounted for was .999 (SD = .0008), and average mean squared error was 0.0002 (SD = .0001). For no-reinforcement trials, the mean variance accounted for was at least .997 (SD = .0072), and average mean squared error was 0.0006 (SD = .0012).

Table 5 presents the parameter values, τ and $n2$, obtained from fitting Equation 3 to the proportional right-key response data for reinforcement and no-reinforcement trials, with $n1$ set at 1. Comparison of τ values for the last 5 days of a condition with τ values for the last 5 days of the next condition for reinforcement trials showed the change in τ following a change in IRI expected according to BeT in 13 of 20 cases (binomial p = .07). Comparison of τ values for the least 5 days of a condition with those of the last 5 days of the next condition for no-reinforcement trials showed the change in τ predicted by BeT in 19 of 20 cases (binomial p < .0002). Table 5 also shows that obtained τ was consistently smaller for no-reinforcement trials than for reinforcement trials for 19 of 25 individual comparisons (binomial p < .0053).

Table 5

Obtained parameter values (τ and $n2$) for the best fit of Equation 3 to response proportions based on response rates summed over the last 5 days of each condition of Experiment 2, for reinforcement and no-reinforcement trials. The value of $n1$ was set at 1 for each fit.

Bird	Condition	Reinforcement trials		No-reinforcement trials	
		τ	$n2$	τ	$n2$
L1	VI 30	4.80	10	3.98	11
	VI 120	4.38	11	4.21	11
	VI 15	4.19	11	2.20	22
	VI 120	4.77	11	4.87	10
	VI 30	4.47	10	4.06	10
L2	VI 30	5.32	9	4.51	11
	VI 120	5.42	9	4.88	11
	VI 15	4.89	9	3.31	13
	VI 120	4.01	14	4.15	13
	VI 30	4.36	10	3.60	13
L3	VI 30	4.13	13	3.87	14
	VI 120	4.79	13	5.20	11
	VI 15	4.95	10	3.94	12
	VI 120	4.41	12	4.56	12
	VI 30	5.04	11	4.26	14
L4	VI 30	4.88	10	4.30	12
	VI 120	5.41	10	5.15	10
	VI 15	4.87	9	3.83	12
	VI 120	5.16	10	4.62	12
	VI 30	4.60	12	3.29	17
L5	VI 30	6.44	7	6.19	7
	VI 120	6.85	7	6.15	7
	VI 15	4.62	10	2.68	19
	VI 120	5.15	9	7.31	6
	VI 30	5.20	8	5.86	7

Fig. 5. Mean values of average interpulse time, τ, as a function of the scheduled interreinforcer interval for data based on the last five sessions of each condition in Experiment 2. The error bars are ± 1 *SEM*.

Figure 5 shows mean values of τ, based on the parameter values for individual birds in Table 5, plotted against average IRI for reinforcement and no-reinforcement trials. According to a repeated measures analysis of variance, the mean values for τ were greater for reinforcement trials than for no-reinforcement trials, $F(1, 4) = 32.25$, $p < .01$, and changed as a function of IRI, $F(2, 8) = 4.77$, $p = .05$, thus replicating the main result of Experiment 1. There was a statistically significant interaction, however, between the effects of IRI and reinforcement versus no-reinforcement trials, $F(2, 8) = 15.59$, $p < .01$. Further analysis showed that the effect of IRI was not statistically significant for reinforcement trials, $F(2, 8) < 1$, but was statistically significant for no-reinforcement trials, $F(2, 8) = 7.48$, $p < .05$. The increase in interpulse time from increasing IRI was obtained for 2 of 5 birds on reinforcement trials and for 5 of
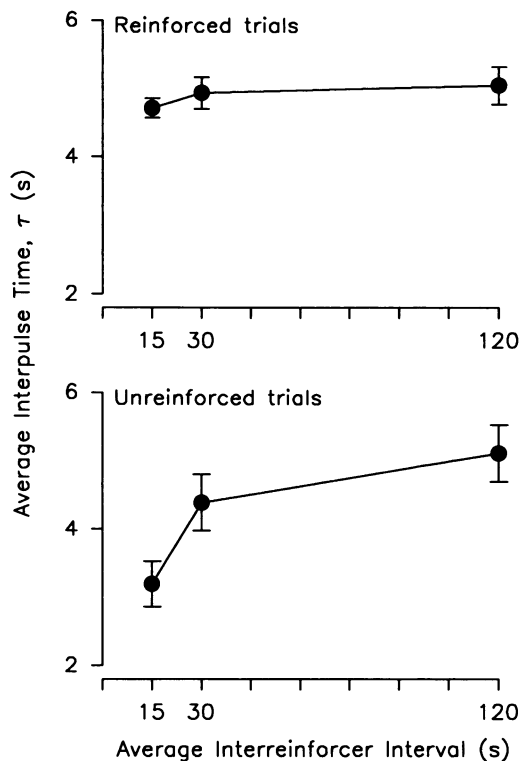
5 birds on no-reinforcement trials (Table 5). The positive relation between average interpulse time and IRI demonstrated in Experiment 1 was therefore confirmed in Experiment 2 only for no-reinforcement trials.

DISCUSSION

In BeT, timing is mediated by behavior (Killeen & Fetterman, 1988). This model proposes that classes of behavior correlated with hypothetical states serve as discriminative stimuli for timing behavior. Transitions between states are generated by pulses from a pacemaker according to a Poisson process (Equation 1). The occurrence of a given timing response is therefore related to average interpulse time of the pacemaker, τ, which in turn is determined by the average interreinforcer interval, T (Equation 2).

Experiment 1 tested the prediction that changes in absolute interreinforcer interval would produce changes in interpulse time.

When IRI was decreased, interpulse time decreased, consistent with a speeding up of the pacemaker. When IRI was increased, interpulse time increased, consistent with a slowing of the pacemaker. The relationship between interpulse time and IRI is best illustrated by Figure 3, which shows interpulse time increasing with larger interreinforcer intervals, as predicted by BeT. This finding is consistent with past research in which a similar relation has been reported (Fetterman & Killeen, 1991; Haight & Killeen, 1991; Killeen, 1991; Killeen & Fetterman, 1988; MacEwen & Killeen, 1991). In Experiment 1 the effect was consistent across individual birds, although it was relatively small in magnitude, with an increase in IRI duration from 15 s or 30 s to 120 s generating a 27% increase in average interpulse time compared to a much larger increase in IRI duration. The strict proportionality required by Equation 2 was therefore not obtained.

An alternative explanation for the relationship between interpulse time and interreinforcer interval was that the birds were discriminating reinforcer occurrence. Consequently, Experiment 2 separately recorded responses for trials with and without reinforcers. Obtained values of interpulse time for trials without reinforcement varied with interreinforcer interval in a manner consistent with predictions of BeT, and for both types of trials combined in Experiment 1 (Figures 3 and 5). In Experiment 2, there was a 66% increase in average interpulse time when IRI was increased from 15 s to 120 s for trials without reinforcement. The relation between interpulse time and IRI for no-reinforcement trials in Experiment 2 demonstrates that the relation cannot be accounted for in terms of discrimination of reinforcer occurrence.

The present result is consistent with the results of an experiment by Raslear et al. (1992), in which IRI was varied by varying intertrial interval in a discrete-trial temporal discrimination. Their task involved the discrimination of two durations of houselight. As ITI duration was increased, there was an increasing bias towards reporting the longer of the two sample durations, as predicted by BeT (cf. Equation 1). The change in bias (measured by the nonparametric index B″) is consistent with the present result, because a shift in the

present psychometric functions towards longer durations is the result of a higher probability of choosing the alternative associated with the longer duration. That is, a shift in the psychometric function is a bias change, whereas a change in the slope of the function is a discriminability change.

The present result is also generally consistent with a result reported by Dreyfus (1991). In one set of conditions, the concurrent reinforcer ratio in the first 10 min of the session was reversed for the second 10 min. That is, the first 20 min of one session was analogous to one 50-s component of the present procedure. When absolute reinforcer rate was high, concurrent response proportions more closely matched concurrent reinforcement proportions than when absolute rates were low. That is, response proportions were under greater control by the time since the beginning of the session when absolute reinforcer rate was high than when it was low. However, Dreyfus's results did not allow an assessment of whether the leaner reinforcer rate resulted in a lag in the time that response proportions followed the change in reinforcer proportions at the end of the first component.

Further support for the present result is provided by a recent study by Morgan, Killeen, and Fetterman (in press). Pigeons were required to choose the left key following a 10-s center-key stimulus or the right key following a 20-s stimulus in a discrete-trial procedure. Interreinforcer interval was manipulated by changing the rate of delivery of free reinforcers above or below the baseline reinforcer rate. A 14-s no-reinforcement probe trial was presented on 25% of trials. As predicted by BeT, decreasing the IRI led to a choose-long bias and increasing the IRI led to a choose-short bias. Under an extinction condition, Morgan et al. found a choose-short bias and attenuated discrimination, consistent with a slowing of the pacemaker.

In the present Experiment 2, however, the predicted changes in interpulse time for different IRI conditions were not clearly present for trials that included reinforcement. One possibility is that for rich schedules, the birds would have spent a greater proportion of the trial eating rather than responding; this may have changed the molar response distributions. Nevertheless, the proportion of right-key re-

sponses should have remained unchanged regardless of whether reinforcer time was subtracted from the time base of the trial.

Another possibility is related to the distinction among three types of trials that comprised trials with reinforcement: reinforcement on the left key only, reinforcement on the right key only, and reinforcement on both keys for individual trials. Differences in the proportion of each type of reinforced trial between the lean and rich conditions, combined with differences in response distributions for each trial type, may have differentially affected the obtained response distributions, in that overall response rates were summed over the various trial types. This explanation receives some post hoc support from our reanalysis of data reported by Stubbs (1979). Stubbs varied reinforcement probability for two response alternatives (red and green) using a procedure similar to that of the present experiment. Responses to the red choice key were reinforced during the first 20 s after trial onset, and responses to the green choice key were reinforced between 20 s and 30 s after trial onset. Reinforcement probability for choices of the green key relative to reinforcers for choices of red was increased over conditions from .50 to 1.0. Figure 6 shows data points (probability of a green-key response) estimated from Stubbs' Figure 10.14 (1979, p. 365). When relative reinforcement probability was .50, the resulting psychometric function was similar to those in the present study. When relative reinforcement probability was 1.0, choice responses predominantly favored the longer duration. The smooth curves are fits of Equation 3 to the data, with $n1$ set at 1 and $n2$ set at 7. Interpulse time was allowed to vary freely. Equation 3 accounts for the data well. Figure 6 shows that response preference clearly shifts to the longer of the two response alternatives as the relative reinforcement rate favors the longer alternative. This shift is reflected as a decrease in hypothesized interpulse time with increasing reinforcement probability.

Another explanation for the absence of an effect of interreinforcer interval in interpulse time for trials with reinforcement may be that reinforcement time is not included in the time base for a trial, and that the psychometric function depends on the obtained time for a trial. Hence, on rich schedules, a fast pacemaker
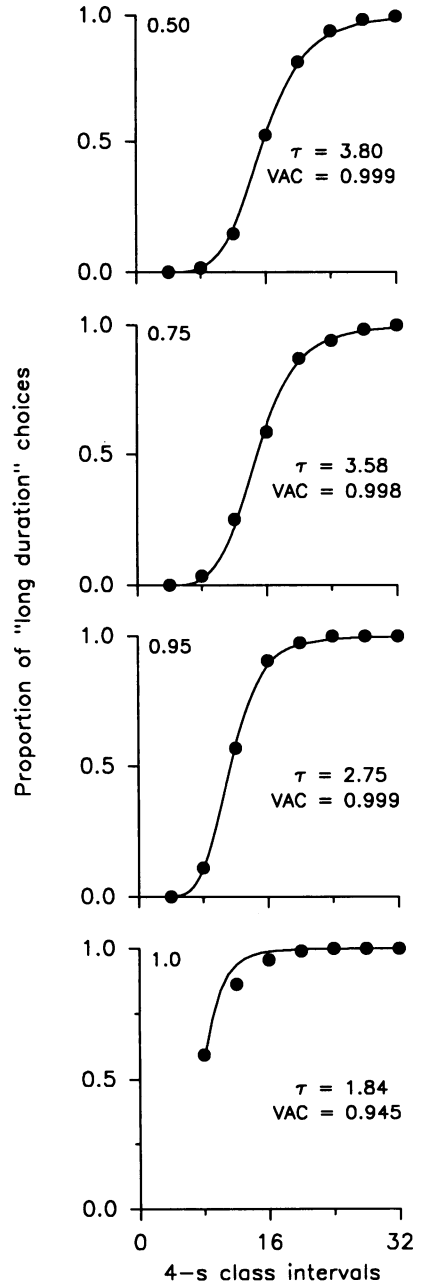

Fig. 6. Fits of Equation 3 (smooth curve) to data from Stubbs (1979, Figure 10.14, p. 365). The data are proportion of responses to the green choice key in 4-s bins, in a procedure similar to that of the present experiments. Each panel shows in descending order the different rates of differential reinforcement for the red key. Values of $n1$ and $n2$ were held at 1 and 7, respectively. Values of the free parameter τ and the variance accounted for (VAC) are given for each fit.

that pushes the psychometric function to longer durations would be balanced by reinforcement time being subtracted from the time base for the trial that would push the psychometric function to shorter durations. The result of such a process would be no observed change in measurable interpulse time as manifested in response distributions. It is also possible that the different processes described above as explanations for the failure of the data from trials with reinforcement to support the predictions of BeT are all present at once, with each process making its own differential contribution to the estimate of average interpulse time (τ) for the various conditions of reinforcement. To test this probability would require more detailed recording of responding within the different trial types than was undertaken in the present experiment.

The present data also allow the notion of recalibration to be addressed. Killeen and Fetterman (1988) suggested that following a change in interreinforcer interval, interpulse time should change, but that changes in the PSE should be transient. For example, a faster pacemaker would result in arriving at the nth state sooner. In order to maintain accurate performance, new kinds of behavior become associated with a later state and serve as the cue for timing. That is, the value of n increases. Hence, recalibration results in changes in n that are the inverse of changes in interpulse time, τ. Recalibration is expected because "with continued reinforcement, as different states become better predictors of the correct choice, animals will recondition [recalibrate] the states underlying long and short responses" (Killeen & Fetterman, 1988, p. 281). Recalibration may not be immediate, and BeT does not predict the time by which it should occur. Hence, the notion of recalibration is difficult to test. Support for recalibration is mixed. It was reported by Killeen and Fetterman (1988), Haight and Killeen (1991), and Morgan et al. (in press), and its absence was reported by Fetterman and Killeen (1991). When recalibration was absent, the predicted changes in interpulse time did not occur.

The present data provide clear evidence for recalibration. The middle panel of Figure 4 shows $n2$ changing in the opposite direction to interpulse time within conditions (top panel). Because the result of recalibration is the maintenance of accuracy, the PSEs remain relatively invariant (see bottom panel of Figure 4).

Taken together, Experiments 1 and 2 provide support for BeT. Interpulse time τ was positively related to the interreinforcer interval (Figures 3 and 5), although strict proportionality was not observed in the relation between τ and interreinforcer interval, and the relation was not clearly manifested on trials with reinforcement. Nevertheless, there were orderly changes in the psychometric functions as quantified in terms of interpulse time. The changes were consistent with BeT's assumptions about pacemaker rate. The predictions about the effects of interreinforcer interval on timing behavior may prove to be BeT's strength.

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