Reinforcement context and pacemaker rate in the behavioral theory of timing

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In the present experiment, an attempt was made to extend the base of evidence for the assumption of the behavioral theory of timing that pacemaker rate is determined by reinforcement rate. Pigeons discriminated the first half from the second half of a 50-sec trial in a free-operant psychophysical procedure. Left-key responding was reinforced at variable intervals during the first 25 sec, and right-key responding was reinforced at variable intervals during the second 25 sec. The rate of "extraneous" reinforcers delivered at variable intervals following responses to a center key was manipulated independently of performance in the temporal discrimination. Quantitative estimates of pacemaker rate were not directly proportional to extraneous rate of reinforcement, whether extraneous reinforcers were available during the intertrial interval, the entire session, or the trial only. Instead, estimates of pacemaker rate were inversely related to the rate of extraneous reinforcement, which suggests that pacemaker rate is determined by the ratio of the rate of reinforcement for the timing response relative to other sources of reinforcement.

The behavioral theory of timing (BeT) provides a successful account of animal timing (Killeen, 1991; Killeen & Fetterman, 1988, 1993). Several propositions are fundamental to BeT. First, individuals possess an internal pacemaker. Second, pacemaker pulses cause transitions between hypothetical sequential "adjunctive states." Third, Killeen and Fetterman (1988, 1993) have suggested that adjunctive behavior becomes correlated with the sequential states. In particular, the adjunctive behavior correlated with state n serves as a discriminative stimulus that occasions the timing response required at time t . The adjunctive behavior gains utility as a discriminative stimulus by virtue of the selective action of reinforcement that follows the timing response. Mathematically, the model predicts the time at which state n occurs. Behaviorally, the timing response is occasioned by the adjunctive behavior that occurs at about time t , that is, when in state n . The time at which state n is reached depends on the pacemaker period. Thus, timing consists of a conditional discrimination based on the adjunctive behavior. For example, if an individual is in a state correlated with a "long" duration as opposed to some shorter duration and is asked to make a temporal

discrimination, it would be more likely to respond "long" if it is engaged in behavior previously correlated with the "long" state than if it is engaged in behavior that is not well correlated with being in the "long" state.

BeT assumes that pacemaker pulses cause transitions between hypothetical sequential states according to the Poisson process given by

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

$P[N(t) = n]$ gives the probability that by time t the number of pulses registered is n . The average pacemaker period is τ , and pacemaker rate is $1/\tau$.

A major assumption of BeT is that pacemaker rate varies as a positive linear function of reinforcer rate. More generally, the linear relationship between reinforcer density D and pacemaker rate is well described by Equation 2 (Bizo & White, 1994b). In Equation 2, the intercept is the resting pacemaker rate $1/\tau_0$, which is independent of the experimental context.

$$\frac{1}{\tau} = kD + \frac{1}{\tau_0} \quad (2)$$

Reinforcer density D is measured in terms of total reinforcer duration per total session duration. Reinforcer duration can be calculated for a range of manipulations that affect total reinforcer duration per session. Pacemaker rate has been shown to vary as a function of reinforcer frequency (Bizo & White, 1994a; Fetterman & Killeen, 1991; MacEwen & Killeen, 1991; Morgan, Killeen, & Fetterman, 1993), reinforcer duration (Bizo & White, 1994b; Fetterman & Killeen, 1991; MacEwen & Killeen, 1991), and intertrial interval (ITI) duration (Bizo & White, 1994b; Fetterman & Killeen, 1991; Raslear, Shurtleff, & Simmons, 1990).

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In all previous experiments, the variables that determined pacemaker rate were directly related to the density of reinforcers maintaining the discriminative timing response. In the present experiment, the question asked was whether pacemaker rate was sensitive to the global reinforcement context—that is, whether it was influenced by reinforcers unrelated to the temporal discrimination. If the pacemaker is driven by reinforcers from all sources in the experimental session, there should be a direct relationship between the rate of extraneous reinforcement and pacemaker rate.

In the present experiment, reinforcers were scheduled for responding on a third (center) key, unrelated to the temporal discrimination, during the ITI, the entire session, or the trial only. We described the reinforcers obtained by center-key responses as “extraneous reinforcers” by analogy with sources of background or extraneous reinforcement that are concurrently available but unrelated to reinforcement for operant responding in the main task (Herrnstein, 1970). The rate of extraneous reinforcement was manipulated in an attempt to vary overall reinforcement density independently of reinforcement density for the timing response. It was predicted that pacemaker rate would vary as a direct linear function of changes in extraneous reinforcement density according to Equation 2.

The free-operant psychophysical procedure in the present experiment, which was the same as that used by Bizo and White (1994a, 1994b), was based on a procedure used by Stubbs (1968, 1979, 1980). This procedure involves the discrimination of the first half of a 50-sec trial from the second half of the trial. Responses to the left key were reinforced at variable intervals during the first 25 sec after trial onset, and responses to the right key were reinforced during the second 25 sec after trial onset. This procedure typically results in a pattern of responding in which left-key response rates are high at the start of the trial and fall to lower levels by the end of the trial. Responding on the right key is infrequent at the beginning of the trial and increases to higher rates by the end of the trial. Sigmoidal psychometric functions are generated by taking right responses as a proportion of total left- and right-key responses (Bizo & White, 1994a, 1994b). The question of interest was whether the values of pacemaker period (the inverse of pacemaker rate), obtained by fitting predictions based on Equation 1 to the psychometric functions, were inversely related to the rate of “extraneous” reinforcers.

METHOD

Subjects

The subjects were 5 adult homing pigeons with experimental histories in category discrimination procedures but not in temporal discrimination. The birds were housed individually and had free access to water and grit. Their weights were kept at $80\% \pm 12$ g of their free-feeding weights; when required, the birds were fed corn, wheat, and maple peas, after experimental sessions, to maintain their weights within the specified range. Birds were not included in the day's experimental session if their weights exceeded the specified range immediately prior to an experimental session.

Apparatus

An interface panel, with internal dimensions of 32 cm wide $\times$ 35 cm deep $\times$ 29 cm high, was mounted inside a sound-attenuating experimental chamber. The interior of the chamber was painted matte black, and a ventilation fan was situated in the rear of the chamber on the wall opposite the interface panel. Two Plexiglas keys, 2.9 cm in diameter, were mounted on the interface panel. The keys were 10 cm apart and 22 cm from the chamber floor. A center key, 2 cm in diameter, was mounted 22 cm above the grid floor in the center of the interface panel and 8.5 cm above the top of the hopper opening. An IEE stimulus projector was mounted behind the center key. Both side keys could be illuminated green, and the center key could be illuminated red. A force of approximately 0.2 N was needed to operate a reed relay mounted behind the side keys; one of 0.15 N was needed to close a microswitch behind the center key. Effective responses caused a 50-msec blackout of the key to which the response was directed. When a central hopper provided access to reinforcement (2.5-sec access to wheat), all response keys were turned off and a white light in the ceiling of the hopper opening illuminated the hopper opening. Experimental events were programmed and recorded via a PDP-11/23 and SKED software and interfacing in an adjacent room.

Procedure

Initial training. Initially the birds were trained to discriminate between the first and second halves of a 50-sec trial. Experimental sessions were scheduled for 7 days a week. Short blackout periods preceded and followed each session, and responses were not recorded. At the start of the 50-sec trial, two side keys were illuminated green. Reinforcement was delivered according to a variable interval (VI) 30-sec schedule contingent on responses to the left key during the first 25 sec of the 50-sec trial; responses to the right key were in extinction during the first 25 sec of the trial. After 25 sec, the reinforcement contingencies were reversed, with left-key responses in extinction and right-key responses reinforced according to a VI 30-sec schedule. The constant-probability VI schedules (Fleshler & Hoffman, 1962) in the different components were independent. Trials were separated by a 10-sec ITI and the side keys were turned off. Each session lasted for 48 trials and finished with a 10-sec ITI. The birds received between 123 and 154 days of initial training (Table 1).

Conditions 1–3. After initial training, the VI schedules on the side keys were changed to VI 60. All other aspects of the temporal discrimination task on the left and right keys remained the same as in initial training. During the 10-sec ITI, the side keys were turned off and the center key was illuminated red. Reinforcement was delivered according to a VI schedule, contingent on responses to the center key. The constant-probability VI schedule for center-key responding was independent of the schedules in the discrimination task. Each experimental session lasted for 48 trials and finished with an ITI. An experimental condition was completed after all birds had completed at least 25 sessions. The VI schedule on the center key during the ITI was varied across three conditions, the values of which were VI 10 (Condition 1), VI 120 (Condition 2), and VI 10 (Condition 3). A summary of condition changes and the number of sessions in each condition for each bird is given in Table 1.

Conditions 4–9. After a short break, the birds were introduced to Conditions 4–9. The procedure was the same as that used in Conditions 1–3, except that reinforcement was delivered according to independent VI 50-sec schedules contingent on responses to the left key during the first 25 sec of the 50-sec trial or contingent on responses to the right key during the second 25 sec of the 50-sec trial. Center-key responses were reinforced intermittently according to a VI schedule throughout both the trial and ITI. All three keys were illuminated during the 50-sec trial. The side keys were turned off and the center key remained illuminated during the 10-sec ITI. The VI schedule on the center key was varied over extinc-

Table 1
Summary of Conditions and the Number of Sessions
Completed by Each Bird in Each Condition

Condition	Center VI	Bird				
		H1	H2	H3	H4	H5
Initial training		147	123	125	130	154
1	10	39	39	37	34	35
2	120	28	28	27	28	28
3	10	28	29	29	28	28
4	120	28	28	28	29	25
5	240	25	26	26	26	26
6	120	27	28	27	25	27
7	60	26	26	27	27	25
8	Ext	28	28	28	25	27
9	30	36	35	34	32	44
10	240	28	32	31	26	30
11	30	28	28	27	28	28
12	Ext	26	28	28	26	26
13	60	25	27	29	27	30
14	240	28	34	42	35	71

Note—For Conditions 1–3, extraneous reinforcers were available during the intertrial interval only. For Conditions 4–9, extraneous reinforcers were available throughout the entire session. For Conditions 10–14, extraneous reinforcers were available during the trial only. VI, variable interval; Ext, extinction.

tion, VI 240, VI 120, VI 60, and VI 30 in six different conditions (see Table 1).

Conditions 10–14. The apparatus was the same as that used in Conditions 1–9, except that experimental events were programmed and recorded by a 386 microcomputer, using Med-PC 2.00 software. (After completion of Conditions 1–9, the laboratory in which the experiment was conducted had been relocated to a different building.)

The procedure was similar to that used in the previous conditions. Reinforcement was delivered according to independent VI 50-sec schedules contingent on responses to the left key during the first 25 sec of the 50-sec trial or contingent on responses to the right key during the second 25 sec of the 50-sec trial. Center-key responses were reinforced according to an independent VI schedule throughout the trial but not during the ITI. Both of the side keys and the center key were illuminated during the 50-sec trial. During the 10-sec ITI, all keys were turned off. The VI schedule on the center key was varied over extinction, VI 240, VI 60, and VI 30 in five different conditions. Table 1 summarizes the condition changes and the number of sessions conducted for each bird in each condition.

Analysis

For all conditions, effective keypecks to the left and right keys were recorded in twelve 5-sec bins during each trial. These response frequencies were summed over the total number of trials for each daily session for the last 5 days of each condition. These response totals were used as the basis for subsequent analysis; responses recorded during the ITI, however, were not used in the present analysis. Reinforcement time was not subtracted from the time base for the trial. The value of $p = .05$ was used as the criterion of significance for all statistical tests.

The present procedure yields psychometric functions that describe right-key responding as a function of total left- and right-key responding in ten 5-sec bins across the 50-sec trial (Bizo & White, 1994a, 1994b). Because Equation 1 can be used to separately describe left- and right-key responding, Bizo and White obtained a quantitative description of the psychometric function by

dividing Equation 1 for right-key (R) responding (with $n = n2$) by the sum of Equations 1 for right- and left-key responding (L) (with $n = n1$). Algebraic simplification yields Equation 3:

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

Equation 3 was fit to psychometric functions for each condition for individual birds. For reasons of parsimony and because preliminary fits with $n1$ as a free parameter frequently yielded $n1 = 1.0$, the parameter $n1$ was set at 1.0 for all fits. The remaining two parameters, τ and $n2$, were allowed to vary freely until they settled on values that maximized the variance accounted for. Values of τ and $n2$ therefore provided higher order dependent variables in that they allowed a quantitative description of the psychometric functions as fitted by Equation 3. Because the inverse of τ is pacemaker rate, τ is the pacemaker period. The number of the state that signals occurrence of the discriminative timing response is $n2$.

In the three sets of conditions, fits of Equation 3 accounted for the obtained psychometric functions very well. The average variances accounted for were 0.987 ($SD = 0.014$), 0.968 ($SD = 0.013$), and 0.979 ($SD = 0.026$) for the sets of Conditions 1–3, 4–9, and 10–14, respectively. The average mean squared errors for the three sets of conditions were 0.001 ($SD = 0.0003$), 0.002 ($SD = 0.0005$), and 0.002 ($SD = 0.0014$), respectively. The excellent fits of Equation 3 to the individual psychometric functions therefore justified the use of τ and $n2$ as higher order dependent measures of temporal discrimination performance.

Because it was important to establish that reinforcer rates for responses in the temporal discrimination task had remained constant, obtained reinforcers per trial on left and right keys were examined as a function of the rate of extraneous reinforcement in the different sets of conditions. In Conditions 1–3, 4–9, and 10–14, mean obtained reinforcers per trial were 0.77, 0.89, and 0.81, respectively. A repeated measures analysis of variance showed that within sets of conditions the obtained reinforcers did not vary significantly as a function of the center-key reinforcement schedules. Additionally, obtained reinforcers did not differ between left and right keys, and there was no interaction between left versus right key and center-key reinforcement schedule. We therefore conclude that obtained left-key and right-key reinforcer frequencies in the temporal discrimination task were not affected by variation in extraneous reinforcers obtained by center-key responses.

RESULTS

To show that performance in the temporal discrimination was generally consistent with prior data (Bizo & White, 1994a, 1994b) and was influenced by extraneous reinforcement in the ITI and during the trial, Figure 1 shows absolute response rates during the trial averaged over birds for the leanest (top panel) and richest (middle panel) center-key reinforcement-rate conditions for each of the three sets of conditions. Figure 1 shows high rates of response on the left key during the first 25 sec of the trial and high rates of response on the right key during the second 25 sec of the trial, as expected according to the procedural contingencies of the temporal discrimination task. Figure 1 also shows a similar pattern of responding when extraneous reinforcement was scheduled for center-key responding, but with lowered absolute left- and right-key response rates when center-key reinforcers were obtained during the trial.

Figure 1. Mean absolute response frequencies and proportions of right-key responses for conditions in which lean (filled symbols) or rich (unfilled symbols) rates of reinforcement were arranged for center-key responses during the ITI only (Conditions 2, 3), during the ITI and trial (Conditions 8, 9) and during the trial only (Conditions 11, 12). Mean absolute left-key (circles), center-key (squares), and right-key (triangles) responses are shown in the top and middle panels. Right-key responses as a proportion of total left and right responses were based on data in the top and middle panels and are shown in the bottom panel. VI, variable interval; ITI, intertrial interval.

The bottom panels of Figure 1 show psychometric functions for the absolute response-rate data presented in the top and middle panels of Figure 1. The psychometric functions were flatter for the rich center-key reinforcement conditions than for the lean conditions. The differences illustrated in Figure 1 are consistent with the data for other conditions, and their statistical significance was verified by analysis of variance. The main focus of the present paper, however, is on changes in pacemaker period, τ .

For Conditions 1–3, comparison of τ values (Table 2) across conditions shows that, when the center-key reinforcement rate during the ITI was decreased or increased, the change in pacemaker period τ varied inversely with the

change in reinforcer rate for 2 of 10 condition changes (significant using the binomial statistic).

For Conditions 4–9, obtained τ values were compared across conditions when center-key reinforcers were available through the whole session (ITI plus trial) (Table 2). When the center-key reinforcement rate was increased, τ decreased, and when reinforcement rate was decreased, τ increased for 7 of 25 condition changes (significant using the binomial statistic).

When obtained τ values were compared across condition changes for Conditions 10–14 (when extraneous reinforcers were available only during the trial, Table 2), when the center-key reinforcement rate was increased, τ decreased, and when reinforcement rate was decreased,

Table 2
Obtained Parameter Values (τ and $n2$) for the Best Fit of Equation 3 to Right-Key
Response Proportions Based on Absolute-Response Frequencies
Summed Over the Last 5 Days of Each Condition

Condition	Bird									
	H1		H2		H3		H4		H5	
	τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$
1 VI 10	9.05	4	7.03	5	9.15	3	6.83	5	15.46	3
2 VI 120	8.24	5	5.50	5	8.18	5	6.99	5	8.24	4
3 VI 10	6.59	5	6.44	6	9.83	3	8.05	5	31.45	2
4 VI 120	11.03	3	4.63	5	11.28	2	8.23	2	10.65	3
5 VI 240	5.93	6	7.26	3	8.62	3	7.96	4	9.11	4
6 VI 120	6.51	5	3.30	3	11.46	2	7.50	3	7.25	4
7 VI 60	6.73	4	4.82	4	10.07	3	10.15	3	11.65	3
8 Ext	6.36	7	7.95	4	6.98	5	9.92	4	6.33	6
9 VI 30	10.22	2	5.79	4	9.60	3	11.41	2	8.78	5
10 VI 240	5.40	6	4.80	8	6.86	5	7.00	6	5.60	7
11 VI 30	9.42	3	5.47	5	8.41	4	8.55	5	6.69	7
12 Ext	7.63	5	6.83	6	6.07	6	6.45	6	6.04	6
13 VI 60	7.24	2	6.74	5	7.03	4	5.69	5	5.33	8
14 VI 240	9.09	2	7.11	3	6.17	3	9.02	3	6.11	7

Note—The value of $n1$ was set at 1 for individual birds. VI schedule on center key. τ , average pacemaker period; $n1$, state associated with left-key responses; $n2$, state associated with right-key responses; VI, variable interval; Ext, extinction.

τ increased for 9 of 20 condition changes (which was not significant using the binomial statistic).

The results of the present experiment failed to support the prediction that pacemaker period τ should vary as an inverse function of the rate of extraneous reinforcers obtained by center-key responses. In fact, the changes in pacemaker period τ appeared to be opposite initial predictions. Over the three sets of conditions, changes in τ between one reinforcer rate condition and the next were in the direction opposite that initially predicted for a total of 37 of 55 condition changes (which is significant using the binomial statistic). Figure 2 (top panel) shows mean values of pacemaker period plotted as a function of obtained rate of reinforcement from timing and extraneous sources. Clearly, this relation is a positive increasing function and not the inverse function initially predicted. This positive relationship between extraneous reinforcement rate and pacemaker period is better illustrated when mean values of pacemaker period are plotted as a function of the rate of reinforcement for the temporal discrimination relative to overall rate of reinforcement for the temporal discrimination and from extraneous reinforcement (Figure 2, bottom panel).

Changes in the values of $n2$ across center-key reinforcement conditions (Table 2) were examined in relation to recalibration. Recalibration refers to a reconditioning of adjunctive behaviors associated with some criterion state to some new state following a change in pacemaker rate. Such a change would improve timing performance following a change in pacemaker rate, and results in an inverse relationship between τ and $n2$ (Bizo & White, 1994a, 1994b; Haight & Killeen, 1991; Killeen, 1991; Killeen & Fetterman, 1988). For Conditions 1–3, 4–9, and 10–14, the significant Spearman's rank order correlations between τ and $n2$ were, respectively, -0.88 ($N = 15$), -0.68 ($N = 30$), and -0.73 ($N = 25$). The in-

verse relationship between τ and $n2$, also shown in Figure 3, therefore supports the occurrence of recalibration. The specific relationship between τ and $n2$ predicted by BeT at the point of subjective equality can be found by setting Equation 3 = 0.5 and solving for τ with $t = 25$ (the midpoint of the trial) and $n1 = 1$ (Bizo & White, 1994b). That is,

$$\tau = 25 * \left(\frac{n2!}{n1!} \right)^{1/(n1-n2)} \quad (4)$$

The function described by Equation 4 with $n1 = 1$ is drawn as the smooth curve in Figure 3. There is a reasonable concordance between the data and Equation 4.

DISCUSSION

BeT assumes that pacemaker rate $1/\tau$ is a direct function of the reinforcement density. The present experiment attempted to clarify the issue of the sources of reinforcers that might contribute to the calculation of reinforcement density. Specifically, is pacemaker rate proportional to global reinforcement density, that is, reinforcers from all possible sources, or is it directly related to the reinforcement rate specific to the temporal discrimination exclusive of other sources? Because BeT does not specify the exact context of reinforcement over which reinforcement density is estimated, it was predicted that pacemaker rate would vary as a positive function of extraneous reinforcer rate in that it contributes to global reinforcement density.

The present experiment tested these possibilities by providing "extraneous" reinforcers, which were unrelated to the timing task, during the ITI, throughout the entire session, and during the trial only. If the extraneous reinforcers are included in the individual's estimate of re-

Figure 2. The top panel shows mean values of pacemaker period, τ plotted as a function of obtained rate of reinforcement from timing and extraneous sources. The bottom panel shows mean values of pacemaker period, τ plotted as a function of the rate of reinforcement for the temporal discrimination relative to overall rate of reinforcement for the temporal discrimination and from extraneous reinforcement. The means are based on the data in Table 2. The standard-error bars are based on a single mean data point per bird. VI, variable interval; Ext, extinction.

inforcer density, increases in overall reinforcer density should speed the pacemaker (decrease τ) and decreases in reinforcer density should slow the pacemaker (increase τ).

In the present experiment extraneous reinforcers were arranged by intermittently reinforcing responses on a third (center) key, independently of the temporal discrimination that involved responding on left and right keys. When extraneous reinforcer rate was varied in the ITI (Conditions 1-3), pacemaker period τ changed in the opposite direction to that initially predicted in 8 of 10 comparisons of τ for one condition with τ for the next. When extraneous reinforcer rate was varied during both the ITI and trial (Conditions 4-9), τ changed in the direction opposite to that predicted for 18 of 25 comparisons, and when extraneous reinforcer rate was varied only during the trial (Conditions 10-14), τ changed in the direction opposite to that predicted for 11 of 20 comparisons. The changes in pacemaker period between one reinforcer-rate condition and the next varied as positive linear function of extraneous reinforcement rate, for a

total of 37 of 55 condition changes over the three sets of conditions. It cannot be concluded, therefore, that pacemaker rate is directly related to global reinforcer rate calculated by taking account of both extraneous and task-related reinforcers. In terms of an effect on pacemaker period, extraneous reinforcers during the trial were not clearly differentiated in their effects from extraneous reinforcers during the ITI (Figure 2).

The present data are consistent with the view that pacemaker rate is a direct function of the density of reinforcers scheduled for timing responses, relative to other (extraneous) sources of reinforcers. By virtue of their effect on reinforcer relativity, an increase in the rate of extraneous reinforcers decreases pacemaker rate and, as illustrated by Figure 2 (bottom panel), pacemaker rate (the inverse of pacemaker period) is inversely related to the rate of extraneous reinforcement. That is, pacemaker rate is sensitive to the context for reinforcement (cf. Herrnstein, 1970). Pacemaker rate may therefore show the same inverse relationship to the rate of alternative reinforcers that has been found for concurrent choice. That is, the absolute rate of responses maintained by reinforcers delivered at a constant rate is inversely related to the rate of reinforcers produced by an alternative response (White, McLean, & Aldiss, 1986). Because this contextual relationship has extensive generality (de Villiers & Herrnstein, 1976), a parsimonious assumption is that pacemaker rate is also determined by reinforcers for the timing response relative to all other reinforcers.

An experiment by Morgan et al. (1993) initially appears inconsistent with the results of the present experiment. Morgan et al. provided pigeons with several sessions of access to response-independent food on a fixed-time schedule interspersed with blocks of sessions

Figure 3. Parameter values of average pacemaker period, τ plotted as a function of $n2$ (see Table 2). The smooth curve is predicted by Equation 4. VI, variable interval; $n2$, state associated with right-key responding.

in a temporal discrimination. The fixed-time schedule provided access to food at a higher rate following a 10-sec red-key-light stimulus or a lower rate following a 60-sec stimulus (red light was the stimulus used to signal duration in the temporal discrimination) than they had previously experienced during the temporal discrimination. When returned to the temporal discrimination, the pigeons that had previously experienced high rates of response-independent food judged the standard durations to be longer than those returning from a low rate of response-independent food. Morgan et al. used the same stimulus to signal the fixed-time schedule (extraneous food) as was used to signal duration in the temporal discrimination to induce changes in pacemaker rate. It would be interesting, however, to see if Morgan et al.'s result would be replicated if the extraneous food had been signaled by a stimulus unrelated to the temporal discrimination. We would predict that pacemaker rate would vary inversely with the rate of extraneous reinforcers. Related to this point, there are two studies that have demonstrated that prefeeding rats appeared to slow the pacemaker (Meck & Church, 1987; Roberts, 1981) apparently contrary to predictions of BeT that increases in global reinforcement density (i.e., prefeeding) should increase pacemaker rate. These studies are consistent, however, with the conclusion that pacemaker rate should vary inversely with the rate of alternative reinforcers.

A conceptual issue raised by our analysis has to do with our assumption that all left-key responses are correlated with state $n1$ and all right-key responses occur during state $n2$. This begs the question as to what behavior an individual is engaged in during the intermediate states. An alternative approach would be to assume that left- and right-key responding is correlated with a range of states, and that there is some state n at which response preference switches from left to right. This would simply involve fitting the present data with a cumulative probability function constrained such that it reflected an underlying Poisson process. The logistic function was fit to the present data, constrained such that $\mu = n\tau$ and $\sigma = \sqrt{n\tau}$. Qualitatively, the results of these fits are consistent with our earlier analysis. Estimates of pacemaker rate varied inversely with the rate of extraneous reinforcement for 43 of 55 condition changes.

The present experiment suggests that the relationship between pacemaker rate and reinforcement density is dependent on the context for reinforcement. That is, changes in extraneous reinforcement rate did not contribute functionally to global reinforcement density. Instead, the data suggest that pacemaker rate is specific to the rate of reinforcers for the timing response, relative to all other sources of reinforcers, over both the trial and ITI. The present data suggest the qualification of the behavioral theory of timing, such that pacemaker rate is determined by the

density of reinforcers for the timing response, relative to other sources of reinforcement, consistent with the ubiquitous importance of the reinforcement context in studies of choice.

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