*BIASING THE PACEMAKER IN THE BEHAVIORAL
THEORY OF TIMING*

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In the behavioral theory of timing, pacemaker rate is determined by overall rate of reinforcement. A two-alternative free-operant psychophysical procedure was employed to investigate whether pacemaker period was also sensitive to the differential rate of reinforcement. Responding on a left key during the first 25 s and on a right key during the second 25 s of a 50-s trial was reinforced at variable intervals, and variable-interval schedule values during the two halves of the trials were varied systematically. Responding on the right key during the first 25 s and on the left key during the second 25 s was not reinforced. Estimates of pacemaker period were derived from fits of a function predicted by the behavioral theory of timing to right-key response proportions in consecutive 5-s bins of the 50-s trial. Estimates of pacemaker period were shortest when the differential reinforcer rate most strongly favored right-key responses, and were longest when the differential reinforcer rate most strongly favored left-key responses. The results were consistent with the conclusion that pacemaker rate is influenced by relative reinforcer rate.

Key words: timing, temporal discrimination, behavioral theory of timing, pacemaker, differential reinforcement, key peck, pigeon

An influential theory of temporal discrimination, the behavioral theory of timing (BeT), suggests that an animal's adjunctive behavior serves as a stimulus that mediates temporal discriminations (Haight & Killeen, 1991; Killeen & Fetterman, 1988, 1993). Adjunctive behavior becomes useful as a temporal cue because of its past association with reinforcement. In terms of BeT, the adjunctive behavior is correlated with *states*. Different states occur at different points in time. Thus the adjunctive behavior correlated with a given state will occasion timing responses that are appropriate to the time the state occurred.

BeT allows a single adjunctive behavior class to be associated with multiple states or multiple adjunctive behavior classes to be associated with a single state. For example, if during the course of a working day one was

asked to decide "Is it time to go home?" the decision would be based on a discrimination of types of behavior that are highly correlated with "going home" in the past (e.g., turning off your computer) from types of behavior that are not (e.g., keeping office hours for students). Thus, the timing behavior "going home" would be more likely if one had completed the daily work routine and turned off the computer than if one was keeping office hours. Adjunctive behavior correlated with the "go home" state sets the occasion for going home. The go-home adjunctive behavior may be exhibited throughout the day (e.g., when turning off the computer because a wordprocessing application had crashed), or there may be multiple activities associated with the go-home state (e.g., checking for electronic mail messages and then turning off the computer). The timing response "going home" will be most strongly occasioned by the adjunctive behavior most highly correlated with the go-home state.

In BeT, transitions between states are caused by pulses from a hypothetical pacemaker. Note that in the model, the pacemaker does not necessarily correspond to a physical entity such as a neural process, but is a convenient shorthand description of the mathematical properties of Equation 1 below. More important, we use it here as a higher order independent variable to summarize the

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functional relation between timing and the passage of time.

The pacemaker period, τ , is assumed to vary as a function of interreinforcer interval. Bizo and White (1994a), however, formally ascribed this relation to reinforcer density, defined as reinforcer duration per session duration. Quantitative evidence for the relation between reinforcer density and pacemaker period has been variously described by Bizo and White (1994a, 1994b), Fetterman and Killeen (1991), Killeen (1991), MacEwen and Killeen (1991), and Morgan, Killeen, and Fetterman (1993). Bizo and White showed that variation of reinforcer density changes response preference for short-versus long-duration choices in a temporal discrimination, and also showed that changes in pacemaker period were associated with the change in response preference. In general, decreases in reinforcer density increase pacemaker period, and increases in reinforcer density decrease pacemaker period. Pacemaker rate equals $1/\tau$.

Bizo and White (1994a, 1994b) used a two-alternative free-operant psychophysical procedure that generated a characteristic pattern of responding across a 50-s trial, following a procedure devised by Stubbs (1968, 1979, 1980). Left-key responding of pigeons was reinforced at variable intervals during the first 25 s of a 50-s trial and was not reinforced during the second 25 s of the trial. Left-key responding occurred at higher rates during the first 25 s and then fell to lower rates during the second 25 s. Right-key responding was not reinforced during the first 25 s of the 50-s trial and was reinforced at variable intervals during the second 25 s. Right-key responding occurred at lower rates during the first 25 s and then increased to higher rates during the second 25 s.

Psychometric functions derived by dividing right-response totals in successive 5-s bins by total left and right responses in each bin over the 50-s trial were sigmoidal in form. The point at which left and right responding were equal was at approximately the midpoint of the trial (i.e., 25 s). The result of changes in pacemaker rate, achieved by varying overall reinforcer rate, was to shift the psychometric function towards shorter or longer times. That is, changes in the psychometric function corresponding to changes in pacemaker pe-

riod were reflected in *response bias* changes, with overall greater preference for responding in the first half or second half of the 50-s trial in different conditions.

Bizo and White (1994a, 1994b) manipulated overall reinforcer density but did not manipulate the relative density of reinforcers obtained by the two response alternatives. It has been well documented that response bias or preference towards one of two alternatives is determined by the differential rate of reinforcement in free-operant conditional discrimination procedures (White, 1986). Differential reinforcement in temporal discriminations has been shown to affect response bias (e.g., Davison & McCarthy, 1987; McCarthy & Davison, 1982; Raslear, 1985; Stubbs, 1976). Consequently, relative reinforcer density can be manipulated as a means of biasing behavior and possibly estimates of pacemaker period. In particular, we asked whether pacemaker rate is related to relative reinforcer rate.

Predictions from BeT

The production of pulses by the pacemaker is described by the Poisson probability density function. Killeen, Hanson, and Osborne (1978) suggested that this function can be used to describe distributions of activity and key pecking. In much the same way, Bizo and White (1994a, 1994b, in press) assumed that the Poisson probability density function could describe left- and right-key response probabilities across a 50-s trial. Following BeT, $P[N(t) = n1]$, the probability that $n1$ pulses will be produced by time t , as given by Equation 1a, is assumed to describe the distribution of left-key responses (Killeen & Fetterman, 1988). That is, when the $n1$ -th state is reached (on a probabilistic basis), the adjunctive behavior associated with that state occasions left-key responses:

$$P[N(t) = n1] = \frac{(t/\tau)^{n1} e^{-t/\tau}}{n1!}. \quad (1a)$$

Similarly, $P[N(t) = n2]$, the probability that $n2$ pulses will be produced by time t , is given by Equation 1b, and is assumed to describe the distribution of right-key responses:

$$P[N(t) = n2] = \frac{(t/\tau)^{n2} e^{-t/\tau}}{n2!}. \quad (1b)$$

Fig. 1. Left-key ($P[N(t) = n_1]$) (short-dashed curve) and right-key ($P[N(t) = n_2]$) (long-dashed curve) response probabilities generated using Equation 1 with pacemaker period $\tau = 6$ s. The probabilities of right-key responses (solid curve) were calculated by dividing right-key response probabilities by the sum of left-key and right-key response probabilities (Equation 2). n_1 was set at 1, and n_2 was set at 7.

Equations 1a and 1b, when used to describe response frequencies, need to be multiplied by a scaling parameter (Killeen & Fetterman, 1988). The smooth curves in Figure 1 show response probabilities for left-key and right-key responding predicted by Equations 1a and 1b. Figure 1 is drawn schematically to depict the relation between time in the 50-s trial, left versus right response alternatives, and changes in the relative rate of responding over the course of the trial.

Bizo and White (1994a) derived psychometric functions that described right-key responding as a function of total left- and right-key responding. A quantitative description of the psychometric function was obtained by dividing Equation 1b for right-key responding by the sum of Equation 1a for left-key re-

sponding and Equation 1b for right-key responding. Algebraic simplification yields Equation 2:

$$\begin{aligned} R/(R + L) &= \frac{P[N(t) = n_2]}{P[N(t) = n_1] + P[N(t) = n_2]} \\ &= \frac{1}{1 + \left[(t/\tau)^{n_1 - n_2} \left(\frac{n_2!}{n_1!} \right) \right]}. \end{aligned} \quad (2)$$

The solid line in Figure 1 was derived by dividing the probability of a right-key response by the total probability of both a left-key and a right-key response. Thus, Equation 2 predicts the proportion of right-key responses.

Bizo and White (1994a) made two assumptions that are implicit in Equation 2: (a) For reasons of parsimony Bizo and White fixed n_1

= 1 and allowed n_2 to vary freely. (b) The scaling parameters that are necessary to approximate left- and right-response frequencies were assumed to be equal, so that their ratio is 1.0. An advantage of fitting Equation 2 to psychometric functions generated by the present procedure is that the values of the free parameters, τ and n_2 provide higher order descriptions of the entire function, assuming that Equation 2 satisfactorily fits the data.

Bizo and White (1994a) noted that Equation 2 is applicable to data from free-operant procedures but not to those from discrete-trial choice procedures. In free-operant procedures, the sum of choice responses at any one time may vary. In discrete-trial procedures, the sum of probabilities of choice responses is 1.0. Accordingly, Raslear, Shurtleff, and Simmons (1992) assumed that in a two-alternative discrete-trial procedure, the probability of one response is 1.0 minus the probability of the other response. For the present free-operant procedure, however, the latter approach is not applicable, and the derivation of Equation 2 from Equations 1a and 1b is appropriate.

BeT predicts that changes in overall reinforcer density produce changes in pacemaker period but does not explicitly differentiate between different possible sources of reinforcement. Nevertheless, when the ratio of reinforcers obtained by responses in the first 25 s of a 50-s trial versus the second 25 s is varied, the resulting bias towards responding "short" in the first half of the trial versus responding "long" in the second half may be related to the pacemaker period. The aim of the present experiment was to examine this relation.

METHOD

Subjects

The subjects were 5 adult homing pigeons that had extensive experience in the present procedure (Bizo & White, 1994a, 1994b). A bird was weighed immediately prior to an experimental session, and if its weight did not fall within $80\% \pm 12$ g of its free-feeding weight it was excluded from that day's experimental session. When necessary, a mixture of corn, wheat, and maple peas was given at the

end of experimental sessions to maintain the bird's weight. The birds were housed individually and had free access to water and grit when not in the experimental chamber.

Apparatus

An interface panel was contained inside a sound-attenuating experimental chamber. The bird's compartment was 32 cm wide, 29 cm high, and 35 cm deep. The chamber was painted matte black. A ventilation fan mounted on the wall opposite the interface panel provided masking noise. Positioned on the interface panel were two Plexiglas response keys each 2.9 cm in diameter, 22 cm from the chamber floor and 10 cm apart. The left key could be illuminated red, and the right key could be illuminated green. Each effective response required a force of approximately 0.2 N to close a reed relay mounted behind each key; this resulted in a 50-ms blackout of the key that had been pecked. A central hopper opening above the chamber floor and midway between the two keys provided 3-s access to wheat. When wheat was available all key-lights were blacked out and the hopper was illuminated by a white light mounted in its ceiling. Experimental events were controlled and recorded by a PDP® 11/23 with SKED® software and interfacing in an adjoining room.

Procedure

Experimental sessions lasted for 48 min and were conducted 7 days a week. At the beginning of a 50-s trial, both the left and right keys were illuminated. Responses to the left key during the first 25-s component and to the right key during the second 25-s component of the trial were reinforced according to two independent constant-probability variable-interval (VI) schedules (Fleshler & Hoffman, 1962). Responses to the right key during the first 25 s and to the left key during the second 25 s of the trial were not reinforced. Reinforcers that were scheduled but not delivered during the appropriate component were held over until the next component. There were 48 trials, and trials were separated by a 10-s intertrial interval (ITI). During the ITI the chamber was blacked out and responses were not recorded.

The differential rate of reinforcement scheduled for responding on the left and

Table 1

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

Condi- tion	VI schedule (s)		Bird				
	Left	Right	L1	L2	L3	L4	L5
1	60	60	25	25	25	25	25
2	90	45	28	27	28	28	28
3	45	90	25	25	25	25	25
4	60	60	27	28	27	26	27
5	120	40	26	27	27	25	27
6	40	120	26	25	26	26	26
7	60	60	31	30	31	31	31
8	40	120	27	27	27	26	27
9	120	40	25	25	25	25	25

right keys was manipulated across conditions. Each condition was conducted until all birds had completed at least 25 sessions. In some conditions more than 25 sessions were conducted because of unscheduled delays by the experimenter in changing conditions. Table 1 presents a summary of condition changes and the number of sessions each bird completed in each condition.

Response and reinforcer frequencies for the last five sessions of each condition were averaged across replications, and all subsequent analyses were conducted on these averaged data. The probability value $p = .05$ was used as the criterion for significance for all reported statistical tests. A one-way repeated measures analysis of variance conducted on total obtained reinforcers revealed no statistically significant difference across conditions, $F(4, 16) < 1$.

RESULTS

Right-key responses were expressed as a proportion of total left- and right-key responses for 10 consecutive 5-s bins across the 50-s trial. The group mean psychometric functions in Figure 2 show that for all conditions right-key responding occurred at low rates at the beginning of the trial and increased to higher rates by the end of the trial. Figure 2 also shows that as the differential rate of reinforcement more strongly favored right-key responses, the psychometric functions shifted towards shorter times since the beginning of the trial, and key preference

more strongly favored the right key at the end of the trial.

Figure 3 shows the data for individual birds corresponding to the mean data shown in Figure 2 (i.e., the proportion of right-key responses for each bird for each condition). For each bird, as the differential rate of reinforcement more strongly favored right-key responses, the psychometric functions shifted to the left (towards shorter times), and key preference more strongly favored the right key at the end of the trial. A repeated measures analysis of variance was performed on the proportion of right-key responses. The effects of reinforcement condition, $F(4, 16) = 59.03$, 5-s bin, $F(9, 36) = 597.18$, and the interaction between condition and 5-s bin, $F(36, 144) = 27.63$, were all statistically significant.

The smooth curves in Figure 3 were derived by fitting Equation 2 to the data points using nonlinear least squares regression. Parameter estimates for the best fitting functions for individual birds are presented in Table 2. There was an excellent correspondence between the data and the fitted functions. The mean variance accounted for (VAC) was .998 ($SD = .003$), and the average mean squared error (MSE) was .0003 ($SD = .0003$).

When estimates for pacemaker period τ (Table 2) were submitted to a one-way repeated measures analysis of variance, there was a significant effect of reinforcement condition, $F(4, 16) = 4.88$. Estimates of τ were smallest when the differential rate of reinforcement most strongly favored right-key responses, and estimates of τ were largest when the differential rate of reinforcement most strongly favored left-key responses (top panel of Figure 4). There was no systematic effect of differential rate of reinforcement on estimates of $n2$, $F(4, 16) < 1.0$ (bottom panel of Figure 4).

DISCUSSION

Manipulation of the differential reinforcer rate in the present temporal discrimination procedure while keeping overall reinforcement rate constant changed estimates of pacemaker period, τ . This relation is only generally predicted by BeT, in that overall reinforcer density influences τ , as shown by previous studies (Bizo & White, 1994a, 1994b;

Fig. 2. Mean right-key responses presented as a proportion of total responses in 5-s bins based on response frequencies summed across the last 5 days of each condition and averaged across replications and subjects.

Fetterman & Killeen, 1991). The present study extends the range of reinforcer variables that influence τ to relative rate of reinforcement.

It should be noted, however, that changes in absolute reinforcer rate in both components were directly confounded with the manipulation of relative reinforcer rate. The direction of the changes in τ are consistent with BeT if absolute reinforcer rate in the right-key component determined τ . The direction of the change in τ is inconsistent with control by the left-key component. It does seem unlikely, however, that conditions in the left-key component would be totally ineffective in influencing timing.

A specific prediction for the relation between the reinforcer differential and pacemaker period can be generated by first considering the instance in which responding is equally distributed between left and right

keys (no bias). In this case the $R/(R + L)$ response proportion is 0.5 and Equation 2 can be set equal to 0.5. Solving for τ gives Equation 3, in which $t_{0.5}$ is the time since trial onset at which the right-response proportion is 0.5:

$$\tau = \frac{t_{0.5}}{\left(\frac{n2!}{n1!}\right)^{\frac{1}{(n2-n1)}}}. \quad (3)$$

Time $t_{0.5}$ is a function of the relative reinforcer differential because a higher rate of reinforcers (r_R) obtained by right-key responses in the second half of the trial will give $t_{0.5} < 25$ s, and a higher rate of reinforcers (r_L) obtained by left-key responses in the first half of the trial will give $t_{0.5} > 25$ s. We assume that the relation between $t_{0.5}$ and relative reinforcer rate for a 50-s trial is given by Equation 4:

Fig. 3. The proportion of right-key responses presented as function of trial interval in 5-s bins for each condition and for each bird. Response proportions were based on response frequencies summed across the last 5 days of each condition and averaged over replications. The smooth functions are the best fits of Equation 3 to the data.

$$t_{0.5} = \left(\frac{r_L^a}{r_L^a + r_R^a} \right) \cdot 50. \quad (4)$$

Equation 4 assumes that with equal reinforcer rates in the two components of the conditional discrimination, the time $t_{0.5}$, at which the $R/(R + L)$ response proportion is

0.5, is 25 s. With unequal reinforcer ratios, $t_{0.5}$ may differ from 25. The parameter a qualifies the effectiveness of the reinforcer differential in determining $t_{0.5}$, at which the proportion of right responses is 0.5. For example, if $a = 0$, $t_{0.5} = 25$ s, the midpoint of the trial, independently of variation in the r_L

Table 2

Parameter values (τ and $n2$) for the best fits of Equation 2 to the proportion of right-key responses based on response frequencies summed over the last 5 days of each condition for each bird. The value of $n2$ was set at 1.0 for each individual fit.

VI schedule		Bird									
Left	Right	L1		L2		L3		L4		L5	
		τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$	τ	$n2$
120	40	4.59	9	4.67	7	4.58	9	4.63	8	5.26	6
90	45	5.20	8	5.29	8	4.35	12	4.83	9	6.02	6
60	60	6.45	7	5.41	9	5.26	10	5.52	9	7.09	6
45	90	5.87	9	6.06	9	4.85	11	6.46	9	8.11	6
40	120	6.22	9	5.94	10	5.49	11	6.27	10	11.60	4

Note. τ = pacemaker period; $n2$ = state associated with right-key responses.

Fig. 4. Mean values of pacemaker period τ (top panel) and $n2$ (bottom panel) as a function of scheduled left or right VI schedule. The standard error bars are based on a single data point for each level of differential reinforcement per bird. $n2$ is the state associated with right-key responses.

and r_R reinforcer rate. If $a = 1.0$ and $r_L = r_R$, then $t_{0.5} = 25$ s.

Substitution of Equation 4 for $t_{0.5}$ in Equation 3 allows the pacemaker period τ to be modeled directly by changes in relative reinforcer rate:

$$\tau = \frac{\left(\frac{r_L^a}{r_L^a + r_R^a}\right) \cdot 50}{\left(\frac{n2!}{n1!}\right)^{\frac{1}{(n2-n1)}}} \tag{5}$$

Figure 5 shows pacemaker period as a function of the proportion of reinforcers obtained on the left key for each individual bird. The smooth curve shows Equation 5 fitted to the data. The parameter $n1$ was set at 1.0 for all fits. Equation 5 has just two free parameters a and $n2$, and provides a good description of the data. The VAC and MSE for each bird were .57, .90, .46, .93, and .84, and .25, .03, .12, .05, and .97, respectively. If $n1$ was free to vary, it would be a third parameter. Our previous fits, however, showed that in general $n1 = 1$. Fixing $n1 = 1$ is therefore parsimonious. It also assumes that the adjunctive behavior associated with the first state occasions left-key responding.

The fitted function in Figure 5 was extended beyond the range of data points to illustrate how Equation 5 behaves at extreme relative reinforcer rates. There are data that are relevant to this point. Stubbs (1979) used a temporal discrimination procedure that was similar to that of the present experiment.

Fig. 5. Pacemaker period τ plotted as a function of proportion of reinforcers obtained on the right key for each individual bird. The data points are based on response and reinforcer totals summed across the last 5 days of each condition. The smooth functions are the best fits of Equation 5 to the data. n_2 is the state associated with right-key responses; a is reinforcer sensitivity.

Fig. 6. Pacemaker period τ plotted as a function of proportion of scheduled reinforcers for "short" responses. The data were derived by Bizo and White (1994a) from fits of Equation 2 to data from Stubbs (1979, Figure 10.14, p. 365). The smooth functions are the best fits of Equation 5 to the data. n_2 is the state associated with right-key responses; a is reinforcer sensitivity.

The differential rate of reinforcement for two response alternatives was manipulated across conditions, such that the relative probability of "short" responses being reinforced was .5, .25, .05, or 0. Bizo and White (1994a) offered a reanalysis of Stubbs's experiment, in which they derived estimates of pacemaker period τ . The data points in Figure 6 show these estimates of τ plotted as a function of the proportion of scheduled reinforcers for "short" responses. The smooth curve in Figure 6 shows Equation 5 fitted to the data. The data clearly conform to the predicted function and offer confirmation of the data from the present experiment.

Bizo and White (in press) have addressed an issue concerning the model from which quantitative estimates of pacemaker period were derived in the present experiment, specifically the form of Equation 2. This model assumes that left-key responding is correlated with the state n_1 , and right-key responses are correlated with the state n_2 . This assumption does not address what the birds are doing in any intermediate states between n_1 and n_2 . Bizo and White (in press) addressed this by fitting a logistic function constrained such that its mean and standard deviation reflect

Fig. 7. Mean values of pacemaker period τ (top panel) and n_2 (bottom panel) plotted as a function of scheduled left or right VI schedule. Parameter estimates were derived from fits of the Erlang to right-key response proportions as presented in Figure 3. The standard error bars are based on a single data point for each level of differential reinforcement per bird. n_2 is the state associated with a shift in response preference from the left to the right.

ed an underlying Poisson process. This alternative model assumes no intermediate states, and produces two parameter estimates, τ and n , where n is the state at which the subject changes from left- to right-key responses. The estimates of pacemaker period Bizo and White derived using this alternative model were qualitatively similar to those derived using the model stated in Equation 2. The present data permit a test of an alternative model.

A distribution function that reflects an underlying Poisson variable is the gamma distribution; this function has been used with some success to model distributions of behavior (e.g., Fetterman & Killeen, 1991; Killeen, 1991; Killeen & Fetterman, 1993). In the spe-

cial case in which the parameter n takes only integer values, the appropriate function is the Erlang distribution.

This model makes use of just two free parameters, pacemaker period, τ , and the state n at which response preference switches from left to right. Figure 7 plots parameter estimates of τ and n , as a function of left or right VI schedule, that were derived using nonlinear least squares regression. The parameter estimates show the same functional relation to the relative reinforcer rate as shown in Figure 4. Estimates of pacemaker period increase as the ratio of scheduled reinforcers more strongly favors responses to the left key. Estimates of n are somewhat larger than expected, but this simply reflects the steepness of the psychometric functions. More important, however, estimates of n show the same functional relation to the relative reinforcer rate as shown in Figure 4. Qualitatively the results of fitting the Erlang to our data are consistent with our earlier analysis.

The results of the present experiment are generally consistent with BeT. They also suggest a modification of the relation between pacemaker period and reinforcer density specified by BeT, namely that pacemaker period is sensitive to the differential rate of reinforcement in the timing procedure.

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