

A Behavioral Theory of Timing

Peter R. Killeen and J. Gregor Fetterman
Arizona State University

We base a theory of timing on the observation that signals of reinforcement elicit adjunctive behaviors. The transitions between these behaviors are well described as a Poisson process, with a rate constant proportional to the rate of reinforcement in the experimental context. These behaviors may come to serve as the basis for conditional discriminations of the passage of time. Varying the rate of reinforcement will generate distributions of behavior whose mean and standard deviation vary proportionately. Holding the rate of reinforcement constant while manipulating the intervals to be judged will generate different functional relations between the mean and standard deviation, and these will lead to bisection at or slightly above the geometric mean, depending on the measure of bisection employed. The correlation between the rate of the Poisson process and the rate of reinforcement implies that psychometric functions should be affected by the rate of reinforcement. This prediction is confirmed. We extend the models derived from this theory to other phenomena, such as temporal generalization and discrimination, subjective shortening, and paired comparisons of intervals. Current models of choice between delayed reinforcers are consistent with our theory of timing.

We propose a simple theory of timing based on the following premises: Stimuli that signal reward engender responses. These responses may be elicited or emitted, interim or terminal. We shall generically call them adjunctive, recognizing that traditional usage restricts the term *adjunctive* to behaviors that are not instrumental. We use the term in a broader sense in this article because the literature shows that there are elicited properties to responses formerly treated as operant (e.g., Moore, 1973). Furthermore, we do not believe that the collateral behaviors of which we speak emerge *because* they are instrumental in aiding timing; however, their utility in that role may affect the rate of reinforcement and thus feed back on and shape their expression, either beneficially or detrimentally.

We hold that transitions between adjunctive behaviors are caused by pulses from an internal clock. Impressive evidence for the existence and properties of such a clock has been adduced by Church and his associates (see, e.g., Church, 1984). For convenience in describing our basic model, we speak of states corresponding to each class of adjunctive responses, with each pulse that is registered moving the system from one state to the next. Each of the states may be of variable duration, and the responses associated with it may occur at different rates,

including a rate of zero. The states are not taken as a cause of the behavior. An efficient cause of the behavior in state $n + 1$ is the reception of a pulse while the animal was engaged in a behavior corresponding to state n . A material cause is the presence of an environment that will support the behaviors of a suitably motivated organism. We eschew specification of any final cause, such as the presumption that the adjunctive behaviors evolved to assist the animal in making temporal judgments. A formal cause is described by our theory.

We presume that the adjunctive behaviors may come to serve as discriminative stimuli for subsequent responses. In timing experiments, if an animal is interrupted while in some state and asked to respond *short* or *long*, it will make whichever response has been most often associated with reinforcement in the context of the behaviors associated with that state. Choice responses thus constitute the end of a simple chain of behavior. When asked to judge whether a stimulus is longer than a standard, the animal will make the choice response *long* if, at the time of the question, it was in the state it had come to associate with the long training stimulus. Likewise, early adjunctive states may become conditioned to *short* responses. Intermediate states will be unreliable predictors of reinforcement, and *short* and *long* responses will be probabilistically reinforced in the context of them.

Although it might be possible for animals to use the pulses alone as a cue, the pulses are presumed to be of brief duration and indiscriminable from one another. Conditioning to the adjunctive behavior that characterizes the state aids counting, in much the same manner as does the use of fingers and feet by civilizations not blessed with numbers.

This behavioral theory of timing constitutes a formalization of the view that behavior is the mediator of temporal control (see Richelle & Lejeune, 1980, for an excellent discussion of the role of collateral behavior in temporal control). Other explana-

This research was supported in part by National Institute of Mental Health (NIMH) Grant MH39496 to Peter R. Killeen and in part by an NIMH NRS Award F32 MH09306 to J. Gregor Fetterman.

We thank J. R. Platt, N. Weiss, and an anonymous reviewer for their comments on an earlier draft of this article. The present form of this article owes much to the careful eye of J. Gibbon. None of these colleagues are responsible for any remaining errors, nor do they necessarily agree with all the points we make.

Correspondence concerning this article should be addressed to either Peter R. Killeen or J. Gregor Fetterman, Department of Psychology, Arizona State University, Tempe, Arizona 85287.

tions of the timing process have implicated internal operations and comparisons as the basis of animals' perception of time (see, e.g., Gibbon & Allan, 1984). We do not talk about the perception of time or subjective scales of it, or of ratio comparisons of one memorial representation with another, but rather of simple conditional discriminations. The strength of the present approach derives from the explicit models on which it is based and from the explicit predictions that they afford.

Specification of the Model

The way in which behavior changes throughout the interval between reinforcers may be seen in Figure 1. Killeen (1975) described such processes as a cascade of behavior, with the first state in an interval having a constant probability of being initiated over time and a second, smaller, probability of being displaced by a response from a succeeding state. But when more than two or three behaviors are involved, the solution of this Markov process becomes unwieldy (McGill & Gibbon, 1965). Killeen, Hanson, and Osborne (1978) showed that a simpler model described most of the data. They assumed that transitions between states occurred with constant probability and may be treated as coincident with pulses from an internal pacemaker. We then may ask, What is the probability at any instant t that an animal is in the state correlated with a particular behavior (e.g., running in the wheel or pacing the front wall)? If each pulse has a constant probability of occurring, the appropriate model is a Poisson process, and the equation that embodies it is the density function of the Poisson distribution (McGill, 1963):

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

where $p(N(t) = n)$ signifies the probability that the number of pulses registered by time t equals n , with τ the average time between pulses. Because the different behaviors may be measured in different ways within each of these states, Equation 1 must be multiplied by a scale factor (A) to predict response rates. This model is appropriate even if the organism stays in each state for a random number of counts; all that changes then is the nominal value of τ (Bush & Mosteller, 1955).

The Poisson process is usually distributed over n : The question then asked is, What is the probability that exactly n events will occur in a given time or space?, with various values of n as the abscissae. But we are interested in distributing Equation 1 over t , with n as the parameter. The question that this addresses is, What is the probability that an animal is in state n at time t ? Distributed over t this way, Equation 1 is closely related to the gamma distribution, which asks, What is the probability that an animal leaves the n th state at time t ? (see Appendix; Cox & Miller, 1965); that is, what is the distribution of times at which the n th pulse occurs. Equation 1 describes the probability of being in the n th state at a particular time, not the probability of leaving it.

Equation 1 provides a good account of the time course of interim and terminal behavior, as demonstrated in Figure 2, where it is applied to the general activity and key pecking of pigeons reinforced on fixed interval (FI) schedules of 30 s, 100 s, and 300 s (from Killeen et al., 1978). The solid curves

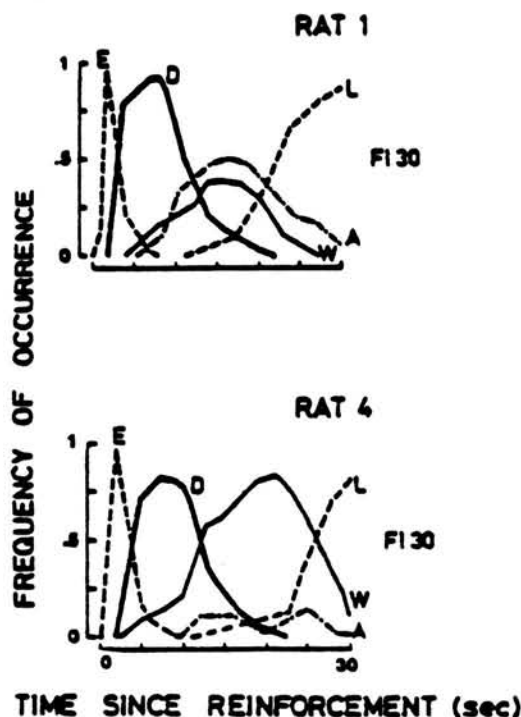


Figure 1. Frequency of occurrence of different activities for two rats as a function of time since reinforcement on a fixed-interval 30-s schedule. (E = eat, D = drink, A = general activity, W = in running wheel; L = contact lever. From "Diversity and Substitutability of Adjunctive Activities Under Fixed-Interval Schedules of Food Reinforcement" by T. J. Roper, 1978, *Journal of the Experimental Analysis of Behavior*, 30, pp. 83-96. Copyright 1978 by the Society for the Experimental Analysis of Behavior, Inc. Reprinted by permission of the publisher and author.)

through the data are from Equation 1. It was assumed that the rate of the internal clock remained constant within each condition. Figure 3 shows how the rate of the clock varied between conditions as a function of the rate of reinforcement. This proportional relation between the average time between reinforcers and the average time between counts has been used to explain the partial reinforcement extinction effect and to develop a model of autoshaped responding (Killeen, 1982, 1984). It forms a central part of the current theory of timing. The theory will be elaborated as necessary to deal with different experimental paradigms as they arise in this review.

The slope of the line in Figure 3 is 3.6, indicating that for pigeons in this type of situation, about 3 or 4 pulses will have occurred by the end of the interval, with the average number over many trials being 3.6. Other experiments suggest that the pacemaker may run faster for rats and thus support a greater number of states and their corresponding adjunctive behaviors. However, one cannot estimate the number of states during an interval simply by counting the number of different behaviors, because in some environments a single adjunctive behavior (such as schedule-induced polydipsia) may be supported by several consecutive states.

Applications to Timing

Equation 1 provides an accurate account of the changes in response rates over time, but many other different procedures

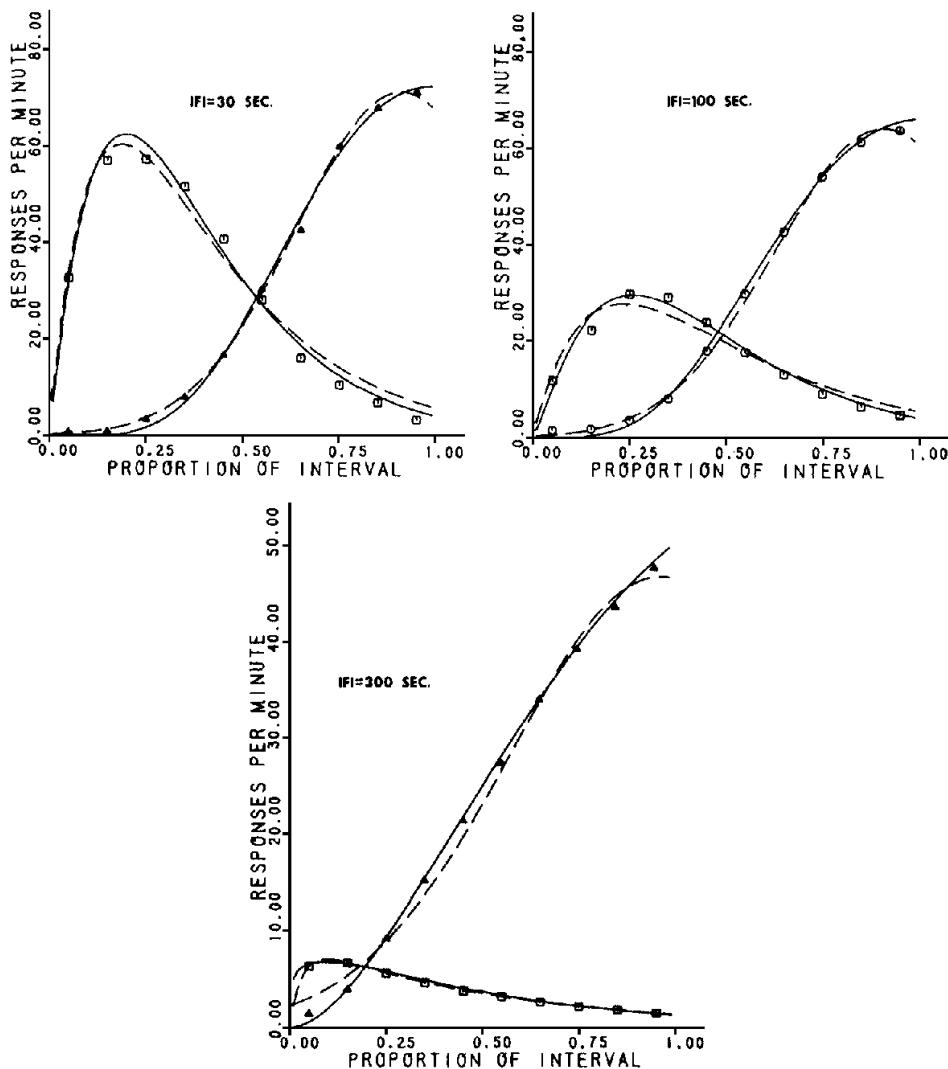


Figure 2. Distributions of activity and key-pecking responses averaged over three pigeons. (The continuous curves are from Equation 1; the rising dashed curves are from the normal density function; IFI = inter-food interval. From "Arousal: Its Genesis and Manifestation as Response Rate" by P. R. Killeen, S. J. Hanson, and S. R. Osborne, 1978. *Psychological Review*, 85, 571-581. Copyright 1978 by the American Psychological Association. Reprinted by permission of the publisher and authors.)

have been designed to assess timing in animals (for reviews, see Platt, 1979; Stubbs, 1979). A useful way of sorting these designs into types is to ask whether the responses that are measured reflect the flow of behavior in real time, are contingent responses based on a time interval that has elapsed, or anticipate a time interval about to occur. We label these types as *immediate*, *retrospective*, and *prospective* timing. Many of the schedule-based procedures (Figures 1 and 2) are of the first type, many of the psychophysical-trials procedures are of the second type, and many of the delay of reinforcement procedures and operant choice procedures are of the third type.

Immediate Timing

We may diagram this procedure with the paradigm of Figure 4. Compare that paradigm with the data resulting from it (Fig-

ures 1 and 2). The most complete description of such data is provided by Equation 1, with the parameter n taking different values for each of the different behaviors, and with τ remaining constant for all behaviors from any particular interval. But there are more traditional treatments of such data that should be reconciled with this model. For instance, the data in Figure 2 came from a study by Hanson and Killeen (1981) that analyzed the use of the latency of the first response (the postreinforcement pause, or PRP) on FI schedules as a measure of temporal discrimination. It had been shown that the PRP increases with the mean value of the FI schedule (T), but that it is a concave rather than linear function of it (e.g., Harzem, Lowe, & Spencer, 1978). Harzem et al. found that the PRP could be characterized as a power function of T with an exponent of 0.74, and that value was replicated by Hanson and Killeen.

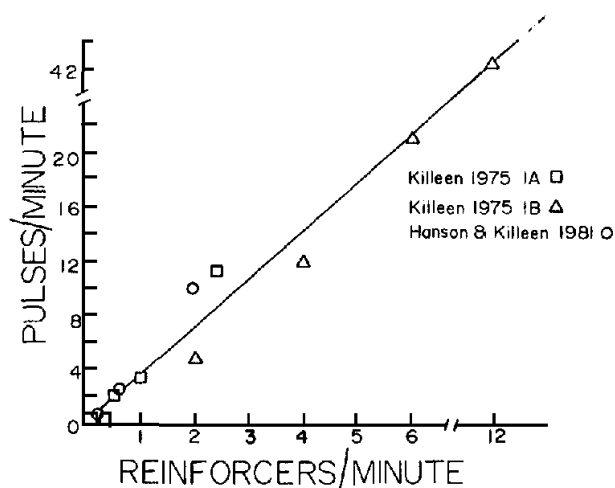


Figure 3. The inferred rate of the pacemaker as a function of the rate of reinforcement. (The data are values of $1/\tau$ from Equation 1, recovered from distributions of activity rates and key-pecking rates for pigeons as reported by Killeen, 1975, and Hanson and Killeen, 1981. The straight line through the data has a slope of 3.6.)

However, other ways of measuring the point in the fixed interval at which substantial responding begins (e.g., Schneider's breakpoint analysis, 1969) show a proportional relation to T . That finding was also replicated by Hanson and Killeen. Thus, two putative measures of "timing" show different functional relations to the interval said to be timed.

In fact, neither the PRP nor the breakpoint is an ideal measure of timing. Those indices were originally designed simply to describe schedule performance (Platt, 1979), but as Stubbs and Dreyfus (1981) noted, these schedules provide no standardized contingencies to discourage errant "early" responses. The PRP is biased by the overall level of responding and by the duration of the opportunity to respond. Thus, if there is a random likelihood of responding that results in a 1% probability of a response every second, it would have little effect on measured PRPs of a 30 s FI, but it would cause the PRP of a 300 s FI to terminate much earlier than "expected." Such a random component to responding would be sufficient to bring about the concave relation observed between PRP and T .

The breakpoint separates intervals into periods of low and high response rates in a way that avoids the problem of nonzero rates in the first period. Its implementation is inconvenient, however, because it requires a curve-fitting procedure for every interval constituting a session. Nonetheless, it does provide a test of our theory of timing. If that theory is correct, animals should switch into a terminal response state after some number of pulses from the pacemaker, and thus the breakpoints should be distributed as a gamma density (McGill, 1967). Hanson and Killeen (1981) showed that the gamma provided a good fit to the distribution of breakpoints. Furthermore, if the rate of the pacemaker is proportional to the rate of reinforcement (as shown in Figure 3) then $\tau = kT$ and both the mean of the breakpoint distribution ($(n + 1)\tau$) and its standard deviation ($\sqrt{n + 1}\tau$) should covary with T . Again, Hanson and Killeen

showed this to be the case. Gibbon (1977) demonstrated proportionality between the mean temporal estimate and its standard deviation in this and many other sets of data, and took that relation as a core assumption in his scalar expectancy theory (SET) of timing.

If the assumptions of our theory are correct, they make possible more convenient and efficient measures of temporal control in these situations: The mean and variance of the distribution of responses over time will use all of the data and thus provide efficient indices of behavior. Unfortunately, the direct calculation of these indices requires that the entire distribution be available, uninterrupted by the delivery of reinforcement. Two solutions to this inconvenience have been used: One is to use the theory to determine a mean based on only the left limb of the distribution; the other is to probabilistically reinforce the animal and record data for the right limb of the distribution on unreinforced trials. Using the first approach, Lowe and Harzem (1977) found that the normal density function provided a good description of the data from rats and pigeons, with the means and standard deviations of the distributions increasing with T for both species.

The second solution to this problem has been called the *peak procedure* (Catania, 1970; Mechner, 1958; Roberts, 1981). In the peak procedure food deliveries are arranged periodically, as with FI schedules, but food is omitted on some trials and the animal is permitted to respond beyond the point at which food is usually given. Roberts recorded response rates in successive segments of the interval on these omission trials and found that (a) response rates decreased smoothly on either side of the peak rate and were well described by normal distributions, and (b) peak rates occurred at approximately the point at which food was normally given.

Why should the normal density function describe these data? When several states occur before the state supporting the measured response, Equation 1 looks much like a normal distribution. The central limit theorem asserts that this similarity will increase as n increases; the rising dashed curves in Figure 2 show that the approximation is not bad for values of n as low as 3. The use of Equation 1 entails that the animals are in the response state only until the next pulse from the pacemaker. That is an adequate assumption for the asymptotic data reviewed so far, with any insufficiencies being accommodated by the scale factor. But the first few times food is omitted, animals persist



Figure 4. Schematic of the immediate timing paradigm. (T = time, R = responses, S = reinforcers. Subscripts identify different classes of activities; vertical lines indicate the occurrence of responses.)

in responding much longer than predicted by the symmetric normal distribution. Such data call for a more general treatment that permits residence in the response state(s) for several pulses. The Appendix provides a simple model for that generalization.

The assumption of an underlying Poisson process forces a certain relation between changes in the mean ($(n+1)\tau$) and changes in the variance ($(n+1)\tau^2$) of the normal approximation (see the Appendix for the derivation of those parameters). If the mean is doubled by increasing n , then the variance should also double. But if the mean is doubled by doubling τ , then the variance should quadruple. In his SET, Gibbon (1977) argued that the latter situation is the general case—the variance is proportional to the square of the interval timed (and thus the standard deviation is proportional to the interval)—and took this as evidence against a Poisson process. He did so because in his model the rate of the pacemaker is not a function of the duration of the interval being timed, so changes in the mean for a Poisson system could only be caused by changes in n . Our theory, however, does not so restrict the system, but rather holds that τ is driven by the rate of reinforcement in the context (Figure 3).

In Roberts's (1981) peak procedure, the rate of reinforcement in real time remains constant. If that context comprises all of the time in the chamber, τ should also remain constant. Under these assumptions the animals can accommodate to longer values of t only by shifting the state that serves as a cue for their lever pressing, causing the variance to increase proportionately with T , not with its square.¹ Roberts's data do not clearly discriminate between these two possibilities: The ratio of the means for the 40-s versus the 20-s conditions was not quite two to one (1.91:1), and that of the variances was 2.95:1. The latter is greater than the 1.91:1 predicted by a constant τ , less than the 3.65:1 predicted by SET.

For all the equivocality of variance ratios, the normal density with parameters derived from the assumption of a Poisson process provides a very good fit to these data: Fixing τ at 5.6 s, fixing n at 3.7 and 7.4, respectively, for the 20-s and 40-s stimuli, and with a scale factor of 140 responses per minute, that model accounts for 98% of the variance in the 32 data points. (The generalization for multiple pulses in the response state (see the Appendix), with m set to 1, provides an equally good fit to the data.)

These studies highlight the importance of distinguishing between within-condition comparisons such as the aforementioned, where rate of reinforcement, and thus τ , remains constant, and between-conditions comparisons, where rate of reinforcement, and thus τ , varies. The extent to which τ is locked to rate of reinforcement in real time (i.e., averaged over stimuli and blackouts) is an important empirical question to which we shall return.

Retrospective Timing

Although the results described above support our theory of timing, it is problematic whether the flow of behavior over time measured in schedule-based situations should be called "timing," any more than the tides should be said to time the moon. To say that an organism is timing usually implies that some type

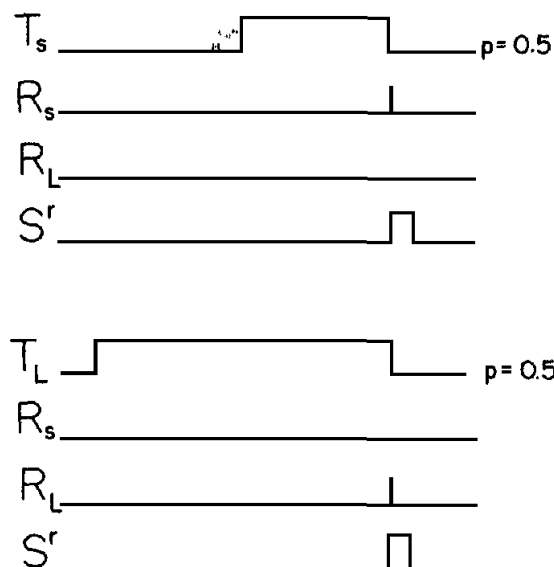


Figure 5. Schematic of the retrospective timing paradigm. (T = time, R = responses, S = reinforcers. The subscripts S and L identify short and long intervals, respectively, and the responses appropriate to them. In most experiments the probability of a short stimulus [top set of traces] or a long stimulus [bottom set of traces] is 0.5.)

of chronometer is used to measure a time interval and that subsequent instrumental performance is guided contingent on the measure obtained. Behavior in retrospective timing experiments, in which animals are asked to judge the duration of an elapsed interval (see Figure 5), comes closer to that construction of the term *timing* than does behavior under the free-operant procedures.

Nonetheless, it is the essence of our theory that animals do not make temporal "judgments," as implied by many of the descriptions of data issuing from these procedures: That is, they do not isolate the stimuli to be timed from other events in their environment and then compare them in some way. Instead, timing experiments and the stimuli in them elicit various behaviors (which we have labeled *adjunctive behaviors*) from animals, and they do so as a function of the stimulus's average temporal proximity to reinforcement. When a temporal judgment is required, animals make a differential response based on the adjunctive responses they were engaged in at that time. In effect, if the animal was, say, pacing when the choice was called for, it would choose *short*; if it was pecking at the front wall, it would choose *long*; if it was doing neither, it would select the alternative most often associated with reward in the context of the ongoing behavior. Note clearly that this is a model of an unsophisticated organism, one that does not compare similarities, take ratios, or calculate relative proximity. The animal merely responds one way if interrupted while doing one thing, the other way if interrupted while doing some other thing.

¹ Of course, in this case the shift cannot be smooth, but must occur in quanta that are multiples of τ . Meck, Komeily-Zadeh, and Church (1984) have adduced evidence for such quantal adjustments in timing.

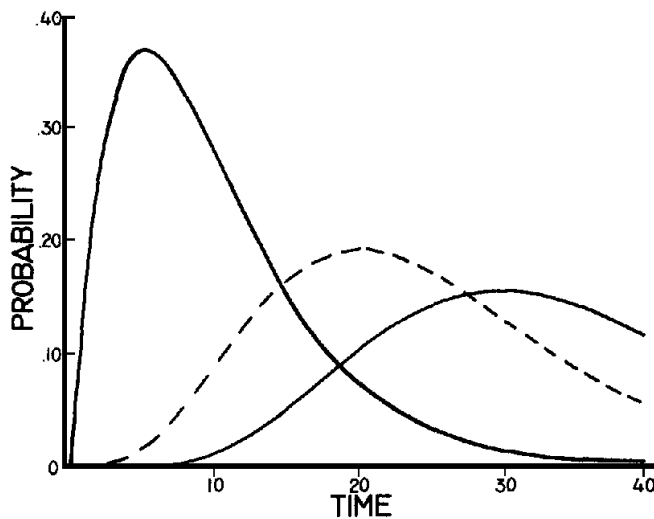


Figure 6. Illustration of the transition between underlying adjunctive states. (The distributions are based on Equation 1, with $\tau = 8$ and $n = 1, 4$, and 6 for the successive curves. The mean time of the first distribution is 8, of the last is 48; the point at which they cross is approximately their geometric mean, around 20. The dashed curve has close-to-equal abscissae over 8 and 48 s, and so may represent transitional behaviors such as "switching over." Its mean of 24 is close to the point of subjective equality predicted by Equation 6, which is 22.)

We shall take as the prototype of the retrospective approach an experiment by Church and Deluty (1977). These investigators trained rats to make a response to one lever if a preceding signal was short and a response to a different lever if the signal was long. In different phases of the experiment the short and long stimuli were 1–4, 2–8, 3–12, and 4–16 s. They then tested the animals by presenting five durations intermediate to the training stimuli and derived the points at which the relative probability of a long response was just 0.50 (i.e., the point of subjective equality, or PSE). We now develop a model based on our theory to predict them. Picture a distribution of adjunctive behaviors centered over the short training stimulus (t_s) and another centered over the long training stimulus (t_L ; see Figure 6). (There may be other intermediate adjunctive behaviors that are probabilistically associated with t_s and t_L , but we shall defer consideration of them until necessary.) We ask at what point the descending limb of the *short* response distribution crosses the ascending limb of the *long* response distribution. That is, for what value of t are the ordinates of two Poisson functions equal, such that

$$p(N(t) = n_s) = p(N(t) = n_L). \quad (2)$$

where $p(N(t) = n)$ is defined as in Equation 1, n_s is the number of pulses associated with the state underlying responses to the short alternative, and n_L is the number of pulses associated with the state underlying responses to the long alternative. The scale factor A does not appear because we presume that the measured responses will have the same topography and thus A will cancel out of both sides.

It is not necessary to solve Equation 1 as it stands; instead

one can set the two versions of it equal to each other, as in Equation 2, and simplify. But the result involves estimating three parameters (τ , n_s , and n_L). A simpler prediction is possible if we rely on the normal approximation to the Poisson and on one additional assumption: that the numbers of the states (n_s and n_L) are proportional to the values of t_s and t_L . This assumption must be true if the means of the response distributions are centered over their training stimuli and the value of τ is constant. Because this is a within-condition comparison, τ must be constant. The distributions would then have means equal to each of the training stimuli: $(n_i + 1)\tau = t_i$, so that $n_s = t_s/\tau - 1$, and $n_L = t_L/\tau - 1$. Substituting, we find the standard deviation of these distributions ($\sqrt{n + 1}\tau$) to be $(t_s\tau)^{1/2}$ and $(t_L\tau)^{1/2}$.

The point at which the two functions cross, t' , is the point at which the Z scores of the two normal approximations are equal. In Figure 6, this is around 20 s. We set the Z score for t' with respect to the short distribution centered on t_s equal to the Z score for t' with respect to the long distribution centered on t_L :

$$(t' - t_s)/(t_s\tau)^{1/2} = -(t' - t_L)/(t_L\tau)^{1/2}. \quad (3)$$

We may solve this equation for t' , and after some tedious manipulation we find the solution to be simply that

$$t' = (t_s t_L)^{1/2}. \quad (4)$$

Equation 4, the geometric mean of the training stimuli, affords a parameter-free prediction of the point at which animals should make a transition from behavior conditioned to the *short* response to behavior conditioned to the *long* response. The value of τ cancels out in its derivation, so that it should hold over various rates of reinforcement. Its accuracy may be evaluated in Table 1, where the values of t_s , t_L , and their geometric means are listed.

Gibbon (1981b) also demonstrated that if the standard deviation increases with the square root of t , then given a logic similar

Table 1
Training Stimuli (t_s and t_L), Obtained Points of Subjective Equality as Measured by Equality of Rates (Rate) and Average Switching Point (Switch), and Predictions from Equations 4 and 6

t_s	t_L	Rate	Equation 4	Switch	Equation 6
Church & Deluty (1977)					
1	4	2.2	2.0		
2	8	4.1	4.0		
3	12	6.0	6.0		
4	16	8.3	8.0		
Platt & Davis (1983)					
10	20	13	14	15	14
10	40	17	20	23	22
10	80	23	28	33	34
10	160	28	40	68	54
20	160	41	57	69	67
40	160	84	80	88	87
80	160	108	113	100	115

to ours (i.e., that the discrimination process is based on a likelihood ratio rule, implicit in Equation 2), the animals should bisection at the geometric mean. He rejected this Poisson model because it violated Weber's law—the stipulation that the standard deviation should be proportional to the mean. Our approach can encompass both bisection at the geometric mean and Weber's law, because we require that τ be driven by the rate of reinforcement. When that is varied, as it is in most immediate timing experiments, we expect Weber's law to hold. When the comparison is between two time intervals within the same reinforcement context, τ remains constant, variance grows more slowly with time, and bisection at the geometric mean is both predicted and observed.

An experiment of Platt and Davis (1983) confirms the previous results, provides a good demonstration of techniques that are a blend of immediate and retrospective timing, and provides an opportunity to extend our model. These investigators trained pigeons on a continuous choice procedure where food was available for one response a short time ($S = t_s$) after trial onset or for a different response at a longer time ($L = t_L$) after trial onset (see Figure 7). Their pigeons responded to the S alternative early in each trial, and then switched over to the L response later in the trial. Both response alternatives were continuously available, and the investigators measured the point at which the long and short response rates were equal, the PSE. Data from their first experiment “clearly support Stubbs's (1976) conclusion that pigeons are indifferent between two temporal intervals at the geometric mean of those intervals and eliminate any possibility that this result is an artifact of control solely by the S interval” (Platt & Davis, 1983, p. 165). Their results greatly extended the range of geometric means that had been shown to predict bisection and did “not depend on the realization of the ideal of one switch from the S to the L response per trial” (p. 165), as their pigeons switched an average of 4.4 times during each trial. To further test the predictive utility of the geometric mean, in their second experiment these investigators greatly increased the relative distance between the two stimuli (S and L). Table 1 lists their stimuli and the resulting PSEs. Equation 4 continues to provide a reasonable prediction of their data, but as the stimuli diverge, bisection points fall progressively below the predictions.

This limitation on the geometric mean also follows from our theory. In the case of $t_s = 10$, $t_L = 160$, for example, the states centered over those training values have no substantial likelihood of occurring near the geometric mean—both ordinates will be very close to zero and unable to support any behavior. And thus it was: In this condition “response-rates to both keys were at near-zero values for a period of time beginning at approximately twice the duration of the S interval” (Platt & Davis, 1983, p. 168). The locus of “bisection” will depend on whether one measures the point where the curves first meet at zero or where they later diverge from zero. In this situation the conditions for inferring PSE from equality of rates are unsatisfactory, for the animal is clearly saying “no” to both. But there is a different way of estimating PSE in these situations, to which we turn.

It has already been noted that more than one switching response was made per interval. This could be a problem for our

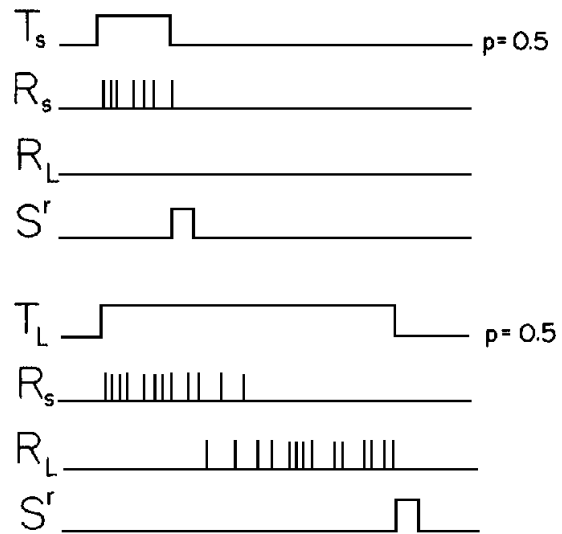


Figure 7. Schematic of the procedure for the Platt and Davis (1983) experiment. (T = time, R = responses, S = reinforcers. The subscripts S and L identify short and long intervals, respectively, and the responses appropriate to them. The vertical lines indicate the occurrence of responses.)

theory if a switch from key S to key L meant a transition from state S to state L, because then our theory would not allow the animals to get back to S, as in fact they did. But it is not a problem if one recognizes that switching itself may become a response class. In studies of choice it has historically been treated as such, and special contingencies of reinforcement are used to manipulate it independently of continuing responses on the choice keys (Herrnstein, 1961; Shull & Pliskoff, 1967). But if we are to construe switching this way, as we must, it forces a new prediction on us. If switching is treated as an adjunctive response in its own right, to which state does it correspond? It is obviously a transition between S and L. We may therefore ask which of the intermediate states is likely to have received approximately equal reinforcement from the short training stimulus and from the long training stimulus. (That is, we ask for what values of τ and n the function for switching (Equation 1) has equal ordinates at t_s and t_L .) Earlier states will be conditioned to the short response, later states to the long response, and the switching point will lie somewhere near the middle of the state in question (see Figure 6).

We implement this analysis by solving the following equation:

$$p(N(t_s) = n) = p(N(t_L) = n), \quad (5)$$

where again $p(N(t) = n)$ is defined as in Equation 1. Although this equation resembles Equation 2, it is actually quite different. Equation 2 asked at what point two different functions, characterized by n_s and n_L pulses, had ordinates of the same height. Equation 5 asks for the specification of a single function, characterized by n pulses, that has ordinates of equal height over both training stimuli t_s and t_L . This distinction is clarified by inspection of Figure 6. Solving Equation 5, we obtain the following:

$$\tau n = (t_L - t_S) / \ln(t_L/t_S). \quad (6)$$

This has not given us n , the number of the state, but nonetheless provides a valuable prediction concerning switching. The quantity on the left-hand side of the equation is the mode of the gamma distribution corresponding to Equation 1. It is thus a reasonable (if slightly biased) estimate of the average switching point. Fortunately, Platt and Davis (1983) measured not only the points at which rates of adjunctive behaviors were equal, but also the median points at which the animals switched from one response to the other. Table 1 shows that Equation 6 provides good predictions of those points (although, as expected because the mode is less than the median, it tends to slightly underestimate them). It can be seen that the switching points generally occur later in the interval than the crossover of the rate curves, as predicted by our models.

This analysis then resolves the relation between two different measures of bisection and the intervals that control those responses. The point at which the response rates supported by different states are equal is well predicted by the geometric mean, as long as response rates are above noise level. The appropriateness of the geometric mean (the average of the logarithms of t_S and t_L) has misled some investigators into positing a logarithmic transformation to get to the underlying time scale. This misperception has been exacerbated by the fact that in most immediate timing situations τ varies proportionately with the average interreinforcement interval. Since the standard deviation of Equation 1 is proportional to τ , a logarithmic transformation of the abscissae would keep the standard deviation approximately invariant in these situations and would tend to correct the positive skew of Equation 1 (Johnson, 1949). According to the assumptions of Thurstonian scaling, this would identify the logarithm of time as the appropriate psychological scale. However, we emphasize that our analysis does *not* posit an underlying time scale that is logarithmic. On the contrary, we assumed throughout, and especially in deriving Equations 4 and 6, that the only scale of time relevant to these investigations is a linear function of real time. Our analysis does not require "subjective" scales of time, and is inconsistent with any hypothesis that a nonlinear transformation of time plays a causal role in the governance of behavior.

Psychometric Functions

The psychometric function describes the relative probability of responding *long* following stimuli intermediate to the training values. This function provides a more detailed accounting of behavior than the PSE, which is the single point of time at which the relative probability is 0.50. Our theory requires that the psychometric function be affected by the period of the pacemaker, τ , in two ways. If the time between reinforcers is increased (say, by lengthening t_S or t_L) τ will increase, and the PSE along with the rest of the psychometric function will gradually shift to longer values of t . But with continued reinforcement, as different states become better predictors of the correct choice, animals will recondition the states underlying long and short responses. Such an assumption was implicit in the development of Equations 4 and 6, which cannot be accurate unless such

adjustments have occurred. But such compensations will not be immediate, and will not always be exact, so that transient shifts in the psychometric function should be visible when the rate of reinforcement is altered. The second effect of such manipulations is that the standard deviation should increase with increases in τ , and the resulting decrease in accuracy should be durable.

In the case of a retrospective timing study by Raslear (1983), the test stimuli were spaced logarithmically in some of the conditions and arithmetically in other conditions. The rate of reinforcement varied substantially between the two conditions—the average duration of the trials was 10 s in the logarithmic series and 20 s in the arithmetic series. In his Figure 4, Raslear displayed the psychometric functions for those two conditions. Those data are reproduced in Figure 8, along with psychometric functions derived from our theory. Because t_S was very brief (100 ms), it is reasonable to expect that the state supporting the judgment *short* corresponded to the time during which no pulses had yet been registered. The most parsimonious model is provided by further assuming that the rats always respond *long* after a single pulse is registered. The probability of being in the state in which no pulses have yet been registered ($n = 0$ in Equation 1) is the exponential decay function $\exp(-t/\tau)$. The psychometric function, the probability of saying *long*, is then simply $1 - \exp(-t/\tau)$. As predicted by our theory, τ shifted appropriately with the change in rate of reinforcement: from 1.9 s per pulse in the logarithmic condition to 3.3 s per pulse in the arithmetic condition. This decreased speed of the pacemaker shifted the PSE to the right and decreased the slope of the psychometric function (the latter effect not obvious because of the logarithmic x-axis). The model's predictions follow the course of the data (see Figure 8) and clearly reflect the impact of variation in rate of reinforcement on the psychophysical discrimination of time.

What context serves as the basis for the calibration of the clock? The assumption that the speed of the clock is proportional to the rate of reinforcement will constrain the possibilities. In Raslear's experiment, the ratio of the speeds in the two conditions was 1.7:1. What potential time bases have the same ratio? The ratio of stimulus durations, including a choice time of about 4 s, and excluding the intertrial interval (ITI), is 1.7:1. Taking this as the context implies that the pacemaker delivers on the average seven pulses per reinforcer.

Additional information is provided by a subsequent experiment in which Raslear, Shurtleff, and Simmons (1987) tested Weber's law using a wider range of stimuli (0.10 s to 20 s). They reported the index of detectability derived from signal detection theory, d' , which is the distance in Z score units between the centers of two normal densities that represent the spread of subjective effect of the stimuli (Green & Swets, 1966). They concluded, "Weber's law is not valid for rat duration discriminations when a sufficiently wide range of stimuli is used" (p. 5), because for equal ratios of S:L, accuracy still depended on the absolute values of the stimuli. This is what we predict: Using the preceding model with a single pulse criterion for responding *long*, we obtain the predictions shown in Figure 9. The time base assumed was the trial duration, including 4 s for the choice response and excluding the ITI. The constant of proportionality

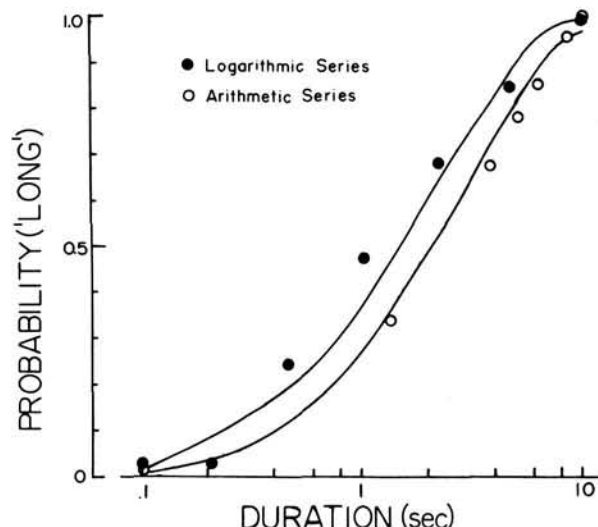


Figure 8. Psychometric functions for rats discriminating between a 0.1-s stimulus and a 10.0-s stimulus. (Filled circles are from a condition in which the intermediate test stimuli were spaced logarithmically; unfilled circles are from a condition in which the test stimuli were spaced arithmetically. The data are from Raslear, 1983. The smooth curves through the data are based on the assumption that the subjects responded *short* until they received one pulse from the pacemaker, after which they responded *long*. Two different functions are predicted because the different rates of reinforcement under the two conditions forced different speeds of the pacemaker. Note the logarithmic spacing of the abscissae.)

between pacemaker speed and reinforcement rate was set to six pulses per interval. The errors of prediction occurred primarily where accuracy was above 96% (the top 3 points), where the use of d' exaggerated discrepancies that did not exceed 2 percentage points.

The notion that the rate of reinforcement should affect the psychometric function is surprising and needs a direct test. This was provided by Fetterman, Killeen, and Evans (1986), who trained four pigeons on a timing task where pecks to the *main* response key, which could be lit by red or green light, could produce food 8 s (t_s) or 24 s (t_L) after a trial began. On half the trials, food was available after t_s , providing that the main key color was red; on the remaining trials the food was available after t_L if the main key color was green. The change in key color was produced by a peck to a second, *changeover* key, at which time the changeover key became dark and inoperative for the remainder of the trial. Two of the pigeons were trained with an ITI of 15 s, the other two with an ITI of 180 s. Insofar as the ITI was included in the reinforcement context, the rate of reinforcement and thus τ differed in the two conditions. After 20 sessions of training the ITI values were reversed.

Our predictions are straightforward: The decrease in the rate of reinforcement experienced by the 15 \rightarrow 180 group should, if anything, increase τ and produce a shift to the right in the psychometric function. The increase in the rate of reinforcement experienced by the 180 \rightarrow 15 group should decrease τ and produce a shift to the left in the psychometric function.

Figure 10 displays the relevant data. It shows the probability of changing the key color to green (*long*) as a function of time for initial training conditions (filled circles) and for the first session after the shift (unfilled circles). All pigeons showed the predicted effects; the data are averaged over pairs within each group. The psychometric functions shifted to the right when the ITI was increased and to the left when the ITI was decreased. We did not expect the shift in the PSE to be sustained because the animals should eventually recondition the states that support the changeover response, so that the shift should be transient, with the PSE returning to about the geometric mean after a few sessions. This was the case. The standard deviation of the group trained under the low rate of reinforcement was greater than that trained under the high rate (3.2 vs. 2.8), as predicted. After the shift variability increased (the slope of the psychometric functions decreased) for both groups. However, the slope for the group that shifted to the high rate of reinforcement did not subsequently recover, as we predicted it would. Furthermore, the shifts were not proportional to the shifts in rate of reinforcement in real time, suggesting that for pigeons, the duration of the ITI is discounted in calibrating τ (but not completely discounted, as it appears to be for rats).

These are not the first data to show an effect of rate of reinforcement (or of arousal; Triesman, 1963) on temporal estimates. Catania (1970) trained pigeons on various schedules that imposed a minimum response latency and found that as he decreased the ITI, the delay until the first response also decreased. Roberts and Holder (1985) trained rats to make one response

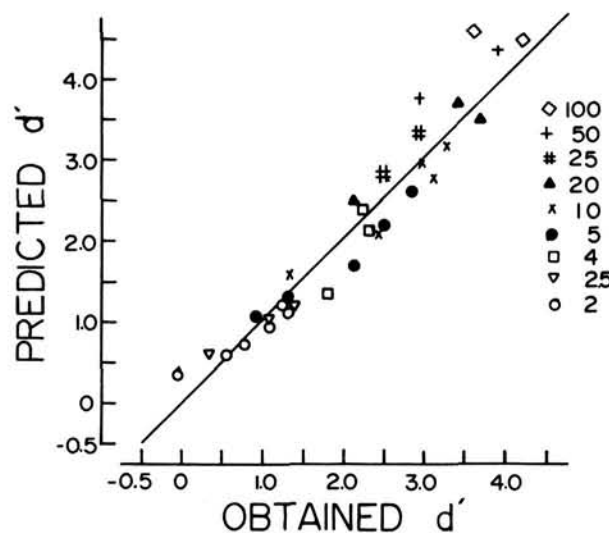


Figure 9. Predicted versus obtained d' scores for rats discriminating between two stimulus durations; the ratio of these durations is keyed to the different symbols. (The model is the same as that used to generate the psychometric functions in Figure 8, with the predicted probabilities of R_L [long response] given t_L [long training stimulus] and R_L given t_s [short training stimulus] converted to the d' index. Figure adapted from *Weber's Law and Time Discrimination in the Rat* by T. G. Raslear, D. Shurtleff, and L. Simmons, a paper presented at the meeting of the Eastern Psychological Association, Arlington, VA, April 1987. Adapted by permission of the author.)

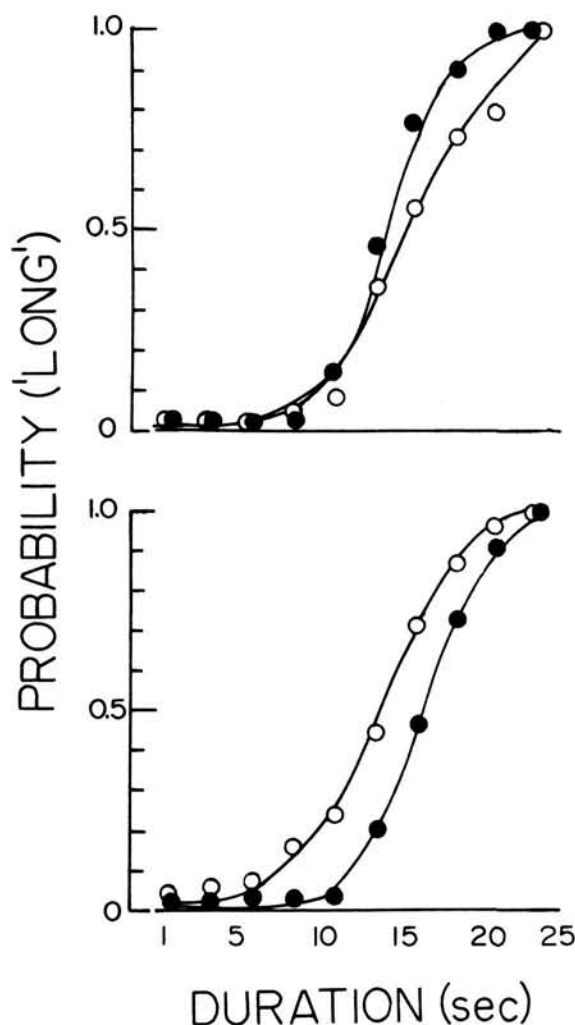


Figure 10. The probability of switching to long as a function of time. (The filled circles are from the last five sessions of baseline training. The unfilled circles are from the first session of postshift testing. The top panel shows the average data from two pigeons shifted from an intertrial interval (ITI) of 15 s to one of 180 s; the bottom panel shows the average data from two pigeons shifted from an ITI of 180 s to one of 15 s.)

after a signal of short duration and another response after a signal of long duration and then manipulated the rate of reinforcement during the signals. In the first experiment following training, 80% of the choice trials were replaced by extinction or pairing trials. During the extinction trials, the signals were presented for 15 s followed directly by the ITI. During the pairing trials the signals were presented for 15 s followed by a food pellet and then the ITI. Roberts and Holder found that the extinction condition produced a significant increase in the bias for reporting a signal short, but that the pairing trials did not.

There were trends within sessions that suggested that the speed of the pacemaker was accommodating to the experimental manipulations. However, the major effects on bias occurred more rapidly than we believe the pacemaker can readjust. Conditioning and extinction of the stimuli will also affect the ad-

junctive behaviors on which temporal judgments are contingent. Extinguishing responses to t_L will decrease the very behaviors that support the conditional discrimination long. Accuracy for long stimuli should decrease, and this is what Roberts and Holder (1985) found. Extinction trials for signals of duration t_S will both decrease the behaviors that support the conditional discrimination short and disrupt the subsequent chain of adjunctive responses that leads to the conditional discrimination long, so that accuracy for both should decrease. This is again what Roberts and Holder found. Pairing trials increase the likelihood of animals' engaging in adjunctive behaviors, but they do not enhance the conditional discrimination, so that they should improve neither short nor long accuracy. In fact, pairing decreased accuracy for both. Numerous other conditions were run, some of whose results are not obvious consequences of this analysis. These experiments demonstrate the complex effects that may be obtained when the rate of the pacemaker is varied at the same time that the adjunctive behaviors underlying temporal judgments are conditioned and extinguished.

Cumulative Normal Distribution

Analysis of Raslear's (1983; Raslear et al., 1987) data was simple because the psychometric function was the cumulative exponential. When the number of the states exceeds two or three, it becomes possible to represent the predicted psychometric functions as cumulative normal distribution (CND) functions (see Appendix). Laming noted, "Everyone agrees that the psychometric function for a differential discrimination is approximately a normal integral" (Laming, 1973, p. 65). The CND values are easily obtained by referring to a table. Where more analytic convenience is required, the logistic function provides an approximation to the normal that is adequate for most purposes (Bush, 1963). Molenaar (1970) provided some improvements on the normal approximation when more accuracy is required.

Our analysis presumes that animals not only enter a state, but also exit from it some time later. If they enter the state conditioned to long on the third pulse and exit from it on the fourth, a Poisson function with $n = 3$ will capture the data. But if more than one state is conditioned to long, then the sum of the Poissons for $n = 3, 4, \dots, n + m$ is needed. In the Appendix it is noted that this sum may be approximated by the difference of two distribution functions for the gamma or, more simply, the difference of two CNDs. Then the probability of being in any one of the states conditioned to the long stimulus n_L , is $p(N(t) = n_L)$:

$$p(N(t) = n_L) = \Phi(\mu, \sigma) - \Phi(\mu', \sigma'), \quad (7)$$

where $\Phi(\mu, \sigma)$ is a cumulative normal distribution of mean μ and variance σ^2 . If we assume that the underlying process is Poisson, then $\mu = (n + 1)\tau$, $\sigma = \sqrt{n + 1}\tau$, and $\mu' = (n + m + 1)\tau$, $\sigma' = \sqrt{n + m + 1}\tau$.

Because the CND is the limiting distribution for many different models of the timing process, our ability to use Equation 7 as an accurate description does not, unfortunately, elucidate the nature of the underlying process. Some of these potential models are listed in the Appendix. Some constraint on them

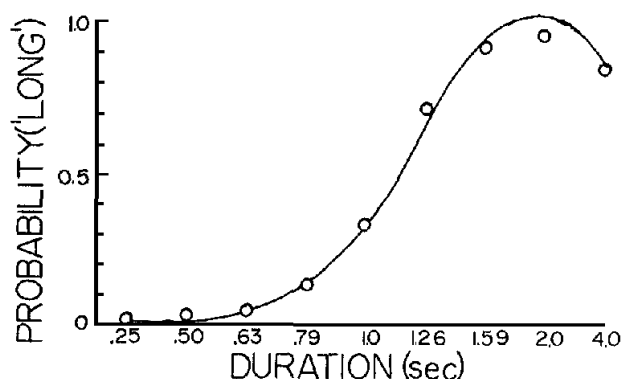


Figure 11. The psychometric function for pigeons discriminating between a 0.5-s stimulus and a 2.0-s stimulus. (The data are averaged over four animals. The curve through the data is derived from Equation 7.)

is provided by the relation between the mean and the standard deviation of the CND, which may help delimit our choice of underlying processes.

Unconditioned States

Psychometric functions are usually thought of as monotonically increasing ogives, but Equation 7 permits them to decrease toward zero for durations sufficiently longer than those to which the animals have been conditioned. Siegel (1986; Siegel & Church, 1984) reported such data, which showed the psychometric function bending back toward chance for test stimuli outside the range of training stimuli. We replicated those results with pigeons, which were trained under a psychophysical trials procedure to discriminate between 0.5-s and 2.0-s periods of darkness that were initiated by a peck to a central response key. At the offset of the duration, the two side keys were illuminated, and responses to the left were reinforced following a short duration, and responses to the right were reinforced following a long duration. Probe durations were introduced at intermediate and extreme values. Figure 11 shows the data, with clear evidence for a downturn at long test values.

What will an animal do when a choice is called for at a time when no mediating behavior has been conditioned to either long or short, that is, for $t \gg t_L$ and for $t \ll t_S$? Latency will increase, and responding may occur at random. But random does not mean zero probability of responding to the *long* lever. Therefore Equation 7 will need to be modified to allow for guessing. One such modification for temporal generalization data was offered by Church and Gibbon (1982).

Church and Gibbon found nonmonotonic psychometric functions when they rewarded rats for pressing levers after signals of a certain duration (in various conditions 2 s, 4 s, and 8 s) but not after signals of other durations. Church and Gibbon modeled the data with the difference between two normal distributions and took a high baseline level of responding into account by adding parameters indicating the probability of paying attention and of responding (operant level), given that the animal wasn't attending. We may account for the data using Equation 7 and the assumption that the rats always chose *long* when

in states 4 through 12, and otherwise chose *long* with probability *pl*. We set *pl* to 0.36 for the two shortest conditions and to 0.45 for the 8-s condition. If we presume as usual that the rats did not take ITI into account in calibrating their pacemaker, which was otherwise proportional to rate of reinforcement, then our model accounts for over 96% of the variance in the data.

Under certain conditions, in particular $t_S \gg 0$ and t_L relatively close to t_S , the value of τ will be small relative to t_S . Then it is possible for one or more states to regularly occur before t with little chance of being conditioned to short. In these circumstances we would expect an upturn of the psychometric function toward chance for very short values of t (i.e., for $t < t_S$).

In many situations it is possible for animals to use a simple criterion such as the following: During adjunctive behavior corresponding to state 0, choose *short*; otherwise choose *long*. This was the rule assumed in analyzing Raslear's (1983) and Raslear et al.'s (1987) data, where $t_S \approx 0$. There will be a tendency toward such heuristics not only because of their simplicity, but also because fewer states will occur around t_S than around t_L (because the variance in the time at which an animal leaves a state increases proportionately with n). This will permit conditioning to *short* to occur more rapidly than conditioning to *long*. Because of this asymmetry of conditioning, we expect that early in many temporal generalization experiments the right limb of the psychometric function will remain quite high and will move toward an approximately symmetric position only after repeated extinction of long responses at times $t > t_L$.

Psychometric Functions as Generalization Gradients

An old question in psychophysics concerns the relation of generalization gradients to the animal's ability to discriminate stimuli along the dimension that is manipulated (Guttman & Kalish, 1956; Kimble, 1961; Lashley & Wade, 1946; Shepard, 1965; Terrace, 1966). Most investigators conclude that there is a relationship, but that the two are not the same thing: Animals will generalize between similar stimuli unless there is a good reason to discriminate between them. Although the slope of the psychometric function may be taken as a measure of the extent to which an animal is discriminating between stimuli, it is not an unbiased measure of the extent to which it could discriminate, that is, of the ultimate discriminability of those stimuli. Only when an animal is pressed by scheduling of stimuli, reinforcement contingencies, and so on, to make as fine a distinction as possible do we expect to get close to a measure of discriminability. Therefore we should not be surprised that if suitably reinforced, animals can do better than predicted by our Poisson model of timing, in that it posits a clock with minimal reliability—the probability of a pulse at any instant is independent of how long it has been since the last pulse. Our theory of timing is to this point a theory of temporal generalization.

How might animals do better? We have watched pigeons on periodic schedules of feeding turn to the left wall, pace back and forth about four times, turn to the back wall, pace about four times, and so on past the other side and to the front wall. Thus the adjunctive behaviors that we lump into three to seven distributions have structure to them, and it is possible that subjects

may utilize that structure to improve resolution. Killeen and Weiss (1987) have found that under a broad range of assumptions concerning the nature of the distributions of τ and the nature of error in the counter/accumulator, it is to the individual's advantage to segment the interval into subintervals. The Appendix gives examples of specific model systems in which this is done. The theoretical functions in Figures 10 and 11 are CNDs that require greater accuracy than is plausible from a Poisson process and for which one of those alternate models might be appropriate. Equation 7 may be used as an approximation for most of those renewal process models and thus offers a general model for discrimination and generalization experiments.

Paired Comparison Experiments

Fetterman and Dreyfus have recently (1986, 1987) introduced a new procedure for the study of retrospective timing in animals that presses the animals to make accurate discriminations and provides an opportunity to demonstrate how one model of discrimination might be developed within our framework. Using a trials procedure, they presented pigeons with a red light of duration t_1 followed by a green light of duration t_2 . After the offset of the second stimulus, responses to key A were reinforced if $t_1 > t_2$ and responses to key B were reinforced if $t_2 > t_1$. Pigeons were surprisingly accurate on this difficult task, with the typical animal being correct about 85% of the time. Fetterman and Dreyfus also observed negative time-order errors in these experiments. Such errors result when the first stimulus of a duration pair is underestimated relative to the second and are a common bias in human time estimates (Hellstrom, 1985). This error is reflected in Fetterman and Dreyfus's data as a bias to call the second stimulus long. Some of their results are displayed in Figure 12.

These data, and others on temporal integration reported by Stubbs, Dreyfus, and Fetterman (1984) and by Meck and Church (1983), require a new hypothesis about the behaviors within a state that may serve as discriminative stimuli for choice responses. We propose that the animals engage in adjunctive behavior during the intervals in a manner that may serve as an add-subtract counter. An example of this behavior might be gradual movement toward the side that is associated with t_1 long increasingly as that stimulus is on, and then gradual movement back toward the other side increasingly as the second stimulus is on (suggested by J. R. Platt, May 1983). If when the choice keys come on the subject is pecking to one side of some central mark, it chooses t_2 long; otherwise it chooses t_2 short. Alternatively, the animals might peck the stimulus key at a slower and slower rate through t_1 and peck the stimulus key at a faster and faster rate through t_2 . If, when the choice keys come on the subject is pecking above some criterion rate, it chooses t_2 long; otherwise it chooses t_2 short. The sign-tracking, approach/retreat, and goal-tracking behaviors reported for animals in conditioning situations (see, e.g., Eldridge & Pear, 1987; Locurto, Gibbon, & Terrace, 1981) could easily serve as the conditioning mechanism for this mediator.

To fix ideas we picture the animal moving to the "left" with probability pl for t_1 s, with increments in distance every unit of

time, and then "right" with probability pr for t_2 s with increments every unit of time. The final position of the animal does not depend on the strict sequential ordering of these directional movements. This is good for two reasons. The first is that it permits us to use a simple Markov model of the process; the second is that it permits us to account for the temporal integration data of Stubbs et al. (1984), wherein accurate discriminations were maintained even though the stimuli to be compared were segmented into many interlaced chunks. The average distance the animal moves during t_1 is proportional to plt_1 , with variance $t_1p/(1-p)$. The distribution of distances may be approximated by the normal distribution with appropriate mean and variance. A similar treatment holds for the distance moved during t_2 . The difference of these normally distributed random variables is itself a normally distributed random variable with mean equal to $plt_1 - prt_2$ and variance equal to the sum of the constituent variances.

The predictions are shown as solid lines in Figure 12; the parameters for the left panel are $pl = 0.78$, $pr = 0.80$; for the right panel: $pl = 0.54$, $pr = 0.65$. The smaller values for the second condition suggest that the animal's timing behavior was less vigorous (and therefore less accurate) for those longer intervals. The larger values for pr within conditions suggest that the animals returned to the center line more quickly than they left it, resulting in a bias to call the first stimulus shorter than it actually was (the negative time-order error). The model accounts for 97% of the variance in each of the two conditions. To support such accurate performance, the implicit rate of the animal's movement must be high, on the order of 1 unit every 1 or 2 s. Just how this rate is related to the rate of the pacemaker is unclear, although both decrease as the rate of reinforcement decreases.

Blank Trials and Delayed Reports

The first state in the sequence of states is likely to be correlated with pausing and to control types of adjunctive behavior that are not manifest in overt responding. If testing is arranged so that responding is discouraged, such as by presenting trials with no stimuli or trials in which testing is delayed by a timeout, we might expect choice responses in those situations to favor the alternative that is usually correlated with such quiescent states—the *short* response. This bias to respond *short* has been shown for the no-stimulus experiment (Church, 1980; Roberts, 1982), and a choose-short bias has also been demonstrated for delayed testing (Kraemer, Mazmanian, & Roberts, 1985; Spetch & Wilkie, 1982, 1983). The bias to respond *short* should increase monotonically with delay, as the probability of being in a state conditioned to *long* responses continuously decreases. If reinforcement is continued for correct responses, we would expect the animals to accommodate the delays by reconditioning the states associated with *short* and *long* responses—that is, by shifting their values of n_s and n_l , causing a transience in the effect. We shall now elaborate the model to transform these qualitative predictions into quantitative ones.

Figure 13 displays the subjective shortening data of Spetch and Wilkie (1982). These investigators trained pigeons to make one response after a short-duration (2 s) stimulus and a different

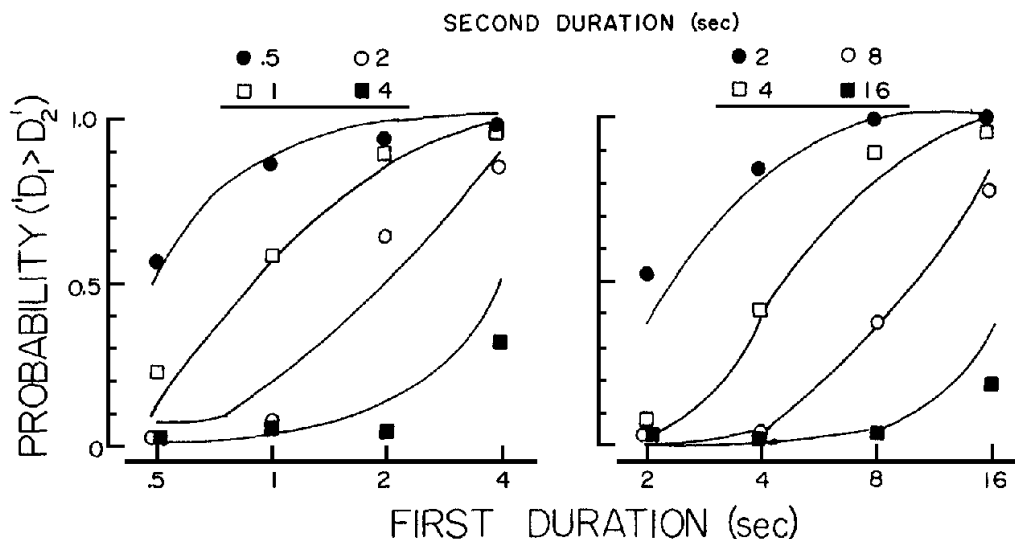


Figure 12. The probability of responding *long* as a function of the duration of the first stimulus, t_1 , in a paired comparison experiment. (The parameter is the duration of the second stimulus, t_2 . The data are averaged over 4 subjects. The left panel shows data from the first condition, which used a smaller range of stimuli, and the right panel shows data from the second condition, which used a greater range of stimuli. The continuous curves come from a random walk model, with the two parameters representing the rate of movement away from and back toward a central point. Figure adapted from "Pair Comparison of Duration" by J. G. Fetterman and L. R. Dreyfus. *Behavioural Processes*, 1986, 12, pp. 111–123. Adapted by permission of the publisher and author.)

response after a long-duration (10 s) stimulus. The stimuli were presentations of either a light or food. Delays were then interposed between stimuli and choice, and accuracy declined to chance with delays of 20 s. All pigeons showed a bias to choose *short* when delays exceeded 10 s. Spetch and Wilkie interpreted this bias as resulting from a subjective shortening of time in memory.

Our theory does not require a memorial representation, let alone one that is shortened with interposed delays. It does require that adjunctive behaviors correlated with the response *long* grow in a cumulative fashion over time. The use of the CND is convenient and provides an accurate representation of the data. During the delay period we assume that the next pulse of the pacemaker will carry the animal out of the conditioned states and that the animal will then allocate its behavior to the two choice keys with a biased probability. Figure 14 gives a pictorial representation of these processes. In it we show the probability of being in the state associated with a *long* response as a function of time through the trial and ensuing delay for the long-duration stimulus (top panel) and the short-duration stimulus (middle panel). At the onset of the delay the animal is in either the *long* state or the *short* one. It exits from those states as an exponentially decreasing function of time during the delay. If it is in neither of those states, it will respond with biased guessing. The dashed lines in the top two panels show the probability of reporting *long* as a function of delay, with a bias to guess *long* of 0.36 when in neither state. The bottom panel shows the resulting probability of being correct after a long or short stimulus.

To accommodate the data of Spetch and Wilkie, we must as-

sume in both the light and food conditions that on the average the animals switched to the *long* state after 6 s and that the probability of guessing *long* when not in a conditioned state was 0.36. The standard deviation for the light stimulus was 5.5 s, and τ was 9.2 s. The standard deviation for the food stimulus was 3.3 s, and τ was 7.5 s. (The decrease in τ and the concomitant decrease in the standard deviation were expected, given that the food stimulus must also function as a source of arousal and thus accelerate the animal's pacemaker.) Figure 13 shows the predictions of the model as curves through the data.

Figure 15 displays the data of Kraemer et al. (1985). These investigators replicated the choose-short result and in addition modified the task to differentiate between explanations based on a shortening of subjective time and one based on coding. The coding explanation holds that durations are "labeled" immediately after their termination and that these labels are forgotten during the delay. Short and long presentations of a light stimulus were intermixed with trials during which no stimulus was presented, and three choice alternatives were provided that were reinforced on short, long, and no-sample trials. Delays between sample stimuli and choice produced a pattern of preferences that was held to be inconsistent with the subjective shortening hypothesis: There was no delay at which the long stimulus came to look sufficiently like a short stimulus to cause a substantial increase in responses to the short key. There were problems with the coding hypothesis as well, both in articulation (why should forgotten stimuli not be randomly called short or absent, rather than just absent as the authors suggest?) and empirically (as the authors noted, it does not predict the concavity in choices of the long key after a short stimulus, nor the difference

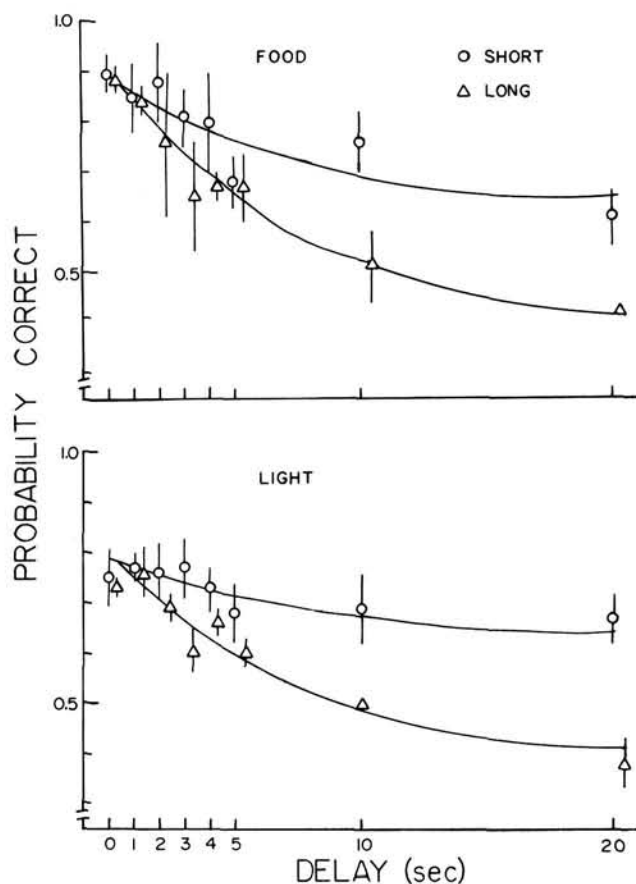


Figure 13. The probability of a correct judgment as a function of the delay after the interval to be judged and before choice. (The data are from Spetch and Wilkie, 1982, who used a short stimulus of 2 s and a long stimulus of 10 s. The stimuli were a change in illumination [bottom panel] or the availability of food [top panel]. The vertical bars indicate \pm the standard error of the mean over subjects. The curves through the data are derived from our theory; see Figure 14 for its explication. Figure adapted from "A Systematic Bias in Pigeons' Memory for Food and Light Duration" by M. L. Spetch and D. M. Wilkie. *Behaviour Analysis Letters*, 1982, 2, pp. 267-274. Adapted by permission of the publisher and author.)

in slopes of the correct responses). None of the hypotheses provided quantitative predictions.

The model that we developed for Spetch and Wilkie (1982) will accommodate the data of Kraemer et al. (1985) if we make the following assignments to the parameters: The animal typically switches to the *long* state after 4.8 s, τ is 8.3 s, and the standard deviation is 3.5 s. If the animal finds itself in a state not associated with reward, the probability of responding *long* is 0.18. The results of these calculations are shown by the curves through the data in Figure 15.

Prospective Timing

In prospective timing, an animal's responses are under the control of a delay that is about to occur. If the end of that delay

is signaled by reinforcement, the situation is a classic delay of reinforcement paradigm (see Figure 16). Because most of the available prospective timing data are derived from this variation, we shall focus on it.

A critical assumption of our treatment of these data concerns the manner in which the delayed primary reinforcer makes con-

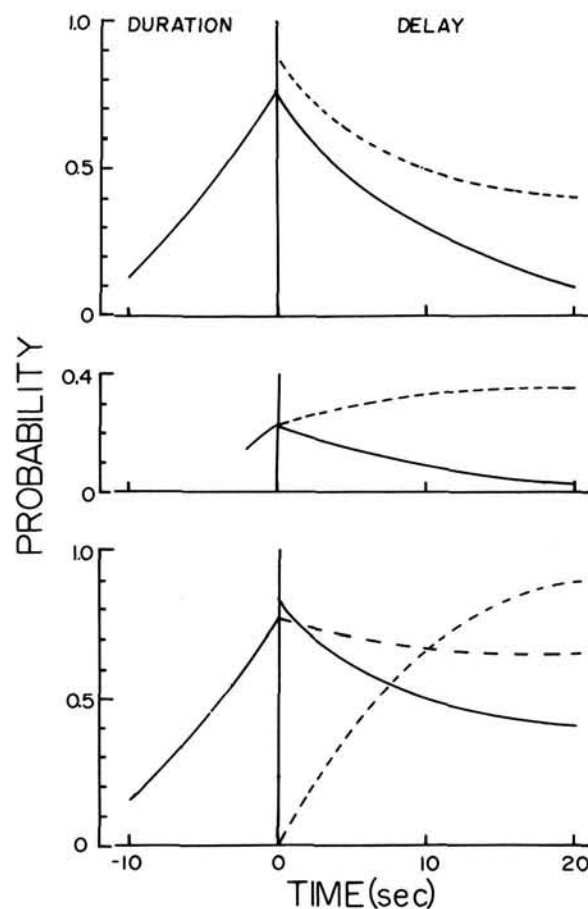


Figure 14. Hypothetical processes underlying the "subjective shortening" effect. (The curves are those used to generate the predictions for the light stimulus condition of Spetch and Wilkie, 1982, in Figure 13. In the top panel, the continuous curves show the probability of being in a state associated with the response *long* as a function of time through the presentation of the stimulus and during the delay after it. When not in a state associated with the *short* or *long* response, the animals guess *long*, with a probability of 0.36. The dashed curve shows the probability of choosing *long*, for either reason, during the delay [a hit]. In the middle panel, the continuous curve shows the probability of being in the *long* state, during and after the short stimulus, and the dashed curve shows the probability of choosing *long* [a false alarm]. The bottom panel shows the probability of being correct after a long stimulus [continuous curve; from the dashed curve of the top panel] and the probability of being correct after a short stimulus [heavy dashed curve; the complement of the dashed curve in the middle panel]. The bottom panel also shows the probability of being in neither of the conditioned states as a function of time through the delay [rising dashed curve]. If given the choice of a third key on which to report *neither*, responses to it should grow proportionately with that curve [see Figure 15].)

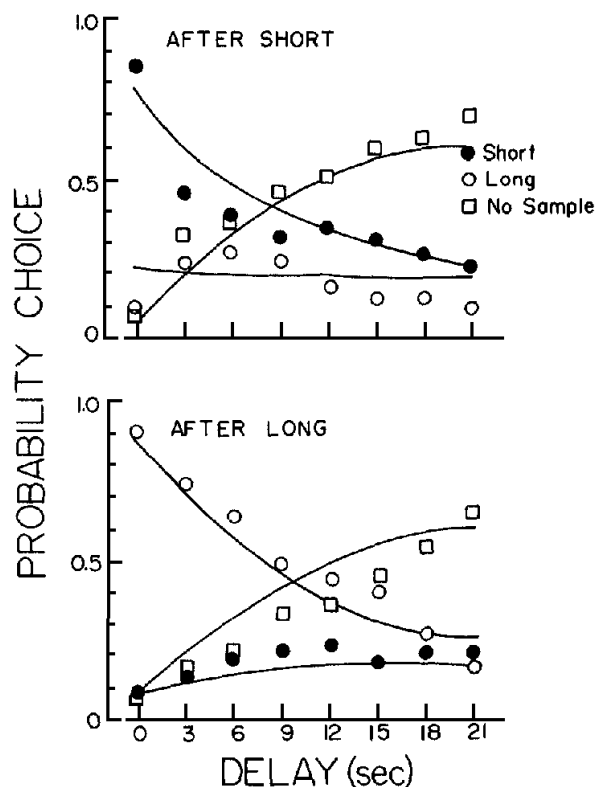


Figure 15. The probability of reporting *short*, *long*, or *neither* as a function of the delay of the question, following short stimuli (top panel) or long stimuli (bottom panel). (The data are from Kraemer, Mazmanian, and Roberts, 1985, averaged over four subjects. The smooth curves come from our theoretical model. See Figure 14 for explication.)

tact with behavior. We do not believe that a reinforcer can act "backwards in time," and therefore hold that the "delay of reinforcement gradients" that are often drawn as concave rising curves between a response and a delayed reinforcer are misleading. Our theory holds that the animal has a constant probability of leaving the state associated with the response that initiated the delay. If it remains in that state, the responses that typify that state receive the full effect of the primary reinforcer (nominally, 1.0). If it leaves the state and engages in other responses, it is those other responses that are strengthened. The mean residence time in each state is τ . Therefore the contribution from primary reinforcement to the response state present when the delay began is $\exp(-t/\tau)$, where t is the delay to reinforcement.

The animal's choice behavior may also be strengthened by conditioned reinforcement afforded by the immediate change of stimuli that usually occurs at the start of the delay. The relation between the strength of a conditioned reinforcer and the delay of reinforcement that it signals is likely to be a monotone decreasing function, and we choose the simplest of those, $1/t$, $t > 0$. The combined contribution from primary and secondary reinforcement then is as follows:

$$S = \exp(-t/\tau) + 1/t, \quad t > 0. \quad (8)$$

This model may be tested against data collected by Mazur

(1984), who used an adjusting procedure to measure pigeons' choices between fixed and variable delays to reinforcement. Responses to one key led to a delay that was constant within the condition, whereas pecks to the other key led to a delay whose value was adjusted until the pigeons became indifferent between the two delays. To evaluate our model, we calculate S for each of the intervals composing the schedule on the standard key and then determine what is the value of t for the adjusting key that would generate an approximately equal value of S . This process is repeated for various values of two free parameters, S and a key bias parameter that multiplies the value of S for the standard key. Values of 0.85 for bias and 4.5 s for τ minimize the deviation between obtained and predicted values of the adjusting schedule, and account for 98% of the data variance.

Equation 8 is the sum of two very similar functions of time, each in its turn very similar to Mazur's (1984) model for the delay of reinforcement gradient: $S = A/(1 + KD)$, where A is a measure of the amount of reinforcement, K is a free parameter, and D is the delay in question. A Taylor series expansion of the exponential term in Equation 8 is $1/(1 + t/\tau)$, so that his D is our t and his K is the reciprocal of our τ . The two models will not be empirically discriminable over their range, but the additive conditioned reinforcement factor in Equation 8 makes a test possible. Dunn, Williams, and Royalty (1987) recently analyzed the role of conditioned reinforcement in concurrent-chain paradigms and concluded, "The results clearly reveal the inadequacy of any account of choice that does not include provision for the role of the terminal-link stimuli" (p. 126).

The value of 4.5 s for τ is similar to that found in other studies of the delay of reinforcement gradient. Killeen and Smith (1984) asked pigeons to discriminate whether a change in key

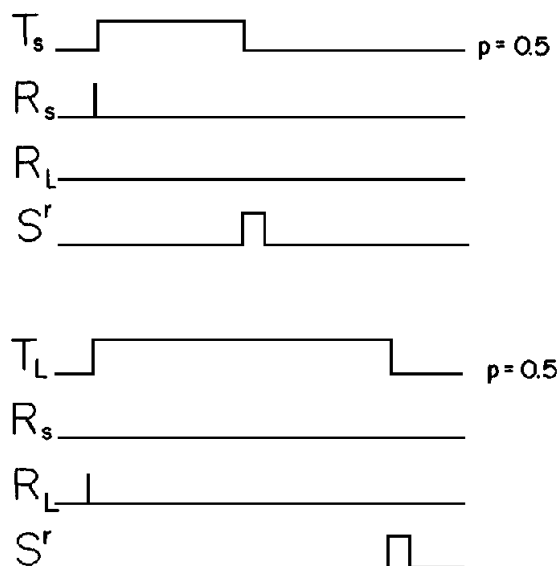


Figure 16. Schematic of the prospective timing paradigm. (T = time, R = responses, S = reinforcers. The subscripts S and L identify short and long intervals, respectively, and responses appropriate to them. In most experiments the probability of a short stimulus [top set of traces] or a long stimulus [bottom set of traces] is 0.5.)

lights was caused by their peck or was unrelated to their peck. Accuracy decreased as a function of the delay of the question, and the authors described this decrease as an exponential decay with a time constant of 7.5 s. When the animals were fed during the delay, the decay was much faster, with accuracy at chance level after 4 s of delay. It is curious, in a sense, that the longer the reward for a peck, the less able the animals were to say afterward whether their peck caused the reward. However, although the animals were unable to discriminate the provenance of reward, this does not indicate that the reward did not strengthen the peck that brought it about. It was the integral of area under the decay curve that acted on the peck response, not the ordinate of the curve (i.e., the marginal strength of the trace) at the end of the feeding.

Our interpretation of the delay of reinforcement gradient will not handle all paradigms, such as the taste-illness associations that have time constants on the order of hours rather than seconds (Revusky, 1968). It is consistent, however, with the early research showing the importance of postural cues in delayed choice experiments (e.g., Blough, 1959) and the importance of conditioned reinforcement mediators (Grice, 1948).

Most experiments designed to study choice between delays of reinforcement use a free-operant concurrent chains procedure, in which animals make many choice responses in the initial links before they gain access to the terminal links constituting the delays. Analyses of the contingencies of reinforcement that favor switching between the alternatives have given rise to a vigorous controversy on the proper characterization of such choice behavior (Commons, Herrnstein, & Rachlin, 1982; Nevin, 1979; Shimp, 1966). We shall not attempt to take our behavioral theory of timing into this foray, beyond noting that Equation 8 is the kernel of one model of concurrent-chain performance (Killeen, 1982) and is reducible to the kernel of another (Fantino's delay reduction theory; Fantino, 1969, 1977; Squires & Fantino, 1971). The interaction of t and τ in our basic equations reconciles our approach with Fantino's emphasis on the importance of the delay of reinforcement being considered relative to the average delay in the experimental context.

The Clock and the Counter

Our theory relies on a classic model of timing, the clock-counter or pacemaker-accumulator system, in which an oscillator of some type generates pulses that are summed by an accumulator. Killeen and Weiss (1987) have generalized the system to one in which variability may arise not only from inaccuracy in the pacemaker, but also from errors in the counter, and have shown that the generalized model is consistent with many of the data on relative accuracy in human time perception. The clock and the counter have been key hypothetical constructs in our behavioral theory of timing. What do we take to be the physical realization of them?

The Counter/Accumulator

It is possible to maintain our behavioral orientation in treatment of the accumulator (and that is an orientation we adopt out of parsimony rather than ideology). The counter we take

to be simply the animal's ability to use various action states—behaviors such as pacing the side wall that are correlated with successive states in our Poisson model—as conditional stimuli on which to base a choice response. When pressed for greater accuracy, the animal may use the physical location of responses within one of these action states as a temporal map, as we successfully presumed in analyzing the paired comparison data in Figure 12. The assumption that the counter is embodied in physical activity or location has some observational support: "We noted that the rhythmic, stereotyped behavior of the two subjects with better discrimination was more rapid than that of the subject with poorer discrimination and also that the behavior during the signal was the same as the behavior during the intertrial interval only for the subject with the poorer discrimination" (Church, Getty, & Lerner, 1976, p. 310). Furthermore, the assumption is testable: For example, discrimination of time within an action class should be poorer than discrimination of time across action classes; if animals "mistakenly" reenter a state correlated with an early adjunctive response, their temporal estimates should be likewise warped. If they "miss" counts while engaged in a strong behavior such as schedule-induced polydipsia, time will not seem to have passed. If they are pulled out of one state into the next by external stimuli, time will have moved quickly. It may be that observation of such mediating behavior will take a mother's eye, especially in the case of very fine and quick temporal estimates. We hope not, but the models will stand nonetheless.

The Clock/Pacemaker

For our characterization of the pacemaker we are immediately driven inside the organism. Fortunately, excellent experimentalists have been there before us and have provided valuable information on the functional nature of the clock. Church (1984) summarized some of the data that he and his associates have collected (note that these investigators use *clock* to refer to the whole pacemaker-accumulator system). For instance, Roberts and Church (1978; see also Roberts, 1981) found that the rat's clock can be stopped; time before stopping can be added without loss to time after stopping; and the clock times signals from different modalities times up, and times intervals of different lengths using the same rate. This last conclusion was based on an experiment similar to the bisection paradigm and is consistent with our presumption of constant τ wherever rate of reinforcement is constant. The other conclusions are also consistent with our theory, if we presume that rats do not register pulses and do not advance through the states during a timeout. Maricq, Roberts, and Church (1981) and Meck (1983, 1986) have quantified the effects of various pharmacological agents on the pacemaker. Repetitive stimuli may drive the counter just as do pulses from the pacemaker, although perhaps less effectively, in that it requires five external pulses to move the animal as far along as one second of the internal pulses (Meck, Church, & Gibbon, 1985).

The pacemaker itself is almost certainly a biological oscillator (Hoagland, 1935), probably of the relaxation type (Sollberger, 1965). It is affected by body temperature, drugs, and time of day (Poppel, 1972). And it is affected by level of arousal (Treisman,

1963), a construct that we have elsewhere taken to be directly proportional to the rate of reinforcement (Killeen et al., 1978).

Remaining Issues

Relation to Scalar Expectancy Theory

For Gibbon and his associates (Gibbon, 1977; Gibbon and Church, 1981; Gibbon, Church, & Meck, 1984) the internal clock is an information processing system that contains a number of components such as the pacemaker, a switch that may connect the pacemaker to an accumulator, a working (short-term) memory, and a reference (long-term) memory. The rate of the pacemaker is not tied to the rate of reinforcement, as it is in our theory, although it may vary randomly between intervals that are being timed. The number of counts accumulates as long as the animal is "timing" a stimulus. Temporal judgments (e.g., choice responses) are based on the output of a comparator that matches the number of accumulated pulses with the number in reference memory. The comparison is made according to a relative proximity rule in which the subject calculates the ratio of the difference between remembered and experienced durations, relative to the remembered duration (Gibbon, 1981a). This relative proximity measure is assessed against a criterion ratio, and if it exceeds the criterion, a response is made. A core assumption is that of scalar timing—the standard deviation should be proportional to the mean of the remembered durations ("The scalar property applies to the memory for time, not necessarily to real time"; Gibbon, Church, & Meck, 1984, p. 66). The form that is used to fit the data is often a CND, or the difference between two CNDs. Because the normal approximation is the bottom line to many different types of underlying timing mechanisms, including those we have outlined in this paper, it does not in itself serve to distinguish the approaches. They are discriminable on two other counts. We hold that the rate of the pacemaker should vary with the rate of reinforcement in the experimental context, whereas SET does not. We eschew models that require complex similarity judgments, memorial representations, and subjective transformations, whereas SET does not. It is perhaps inevitable that our behavioral theory of timing will become more complex, and perhaps more cognitive, as it is extended to new experimental results, but for now its simplicity suffices.

The Time Base for τ

One issue on which we have not yet achieved closure is the time base to which τ is calibrated and the mechanism for updating τ . One of us has speculated elsewhere on possible models for the updating process (Killeen, 1981, 1984; see also McNamara & Houston, 1987). It appears that rats base their estimates primarily on times when reinforcement is potentially available, weighting less heavily, or not at all, times when reinforcement is unavailable, such as the ITI, and times out of the experimental context, such as time in the home cage. (But see Bacotti, 1976, who showed that rats may anticipate home-cage feeding.) Perhaps the updating is done only while the rat is in a "foraging" mode (see Commons, Kacelnik, & Shettleworth, 1987, for data

and models of the updating process in foraging situations). Contextual boundaries appear somewhat less precise for pigeons; the results shown in Figure 10 suggest that pigeons are less able to exclude the ITI from their time base. This distinction may provide the basis for understanding species differences in contrast and autoshaping effects.

The fact that an animal's pacemaker may be sensitive to overall rate of reinforcement in its environment provides the mechanism sufficient for many of the abilities that have been observed or postulated in animals. A faster pacemaker due to higher overall rate of reinforcement means less residence time in any particular state and thus steeper delay of reinforcement gradients. It means that the amount of time an animal perseveres in any food patch or foraging activity will be related to the overall density of food in its environment. It means that animals will extinguish more quickly after dense schedules of reinforcement than after thin ones. It means that delayed reinforcers will have a larger impact in the context of infrequent overall rate of reinforcement than in the context of frequent reinforcement. It means that reduction of the overall rate of reinforcement by the introduction of a signaled period of extinction will generate a contrasting increase in the response rate in the unchanged component. Finally, it means that animals drift through a relativistic world in which they have little access to absolute measures of time other than gross circadian rhythmicity. The task now is to provide specific models, based on a theory such as the present one, to make exact predictions. If successful, diverse phenomena differing in their manifestation among species may be related to one unitary mechanism.

Summary and Conclusions

Let us review the premises and products of our theory. Signs of reinforcement elicit adjunctive behaviors, which we characterize as cohering in a state, or class. In the presence of stimuli that are extended in time and signal reinforcement, a series of these states occurs. The transition from one state to the next in the series occurs with some probability as a function of time. For the simplest model, the Poisson process, this probability is independent of time. That simplest model was effective in describing the time course of adjunctive behaviors, including operant responding. In fitting the data, we found that the average time spent in each of the states, τ , was proportional to the average time between reinforcers in that context. In many situations this implies that the standard deviation of the probability distributions of these states will be proportional to the period of food delivery, a relationship called *scalar timing*. If, however, the rate of reinforcement is held constant, say by comparing two different intervals within the same session, the standard deviation of the distributions will vary as the square root of the interval in which they occur. In this case we predict the PSE by showing that the probability of being in either of two adjunctive states, each centered over one of the intervals to be timed, is equal at the geometric mean of those times.

In experiments involving retrospective timing, where animals must respond differentially on the basis of time elapsed since the onset of a signal, we presumed that these judgments are based on discriminations of the adjunctive states in effect at

the time of the question. Again the Poisson model was useful in some analyses, but the CND was introduced because of its greater convenience and flexibility. The CND will be appropriate as a limiting distribution even where the pacemaker that governs residence in a state is more accurate than allowed by the Poisson assumptions. Several alternate models of the underlying process that dovetail with the CND are described in the Appendix.

This model of retrospective timing provided good descriptions of psychometric functions and a parameter-free prediction that animals should on the average switch between schedules at a point in time slightly above the geometric mean (Equation 6). Furthermore, in transitional conditions in which the animals have not readjusted the states that served as the basis of their temporal discrimination, the psychometric function should be affected by the rate of reinforcement in the context. This prediction was shown to hold.

More complex performances are possible, such as delayed judgment, and comparison of the relative duration of two or more durations. Models may be developed from our theory that address these situations specifically. In the case of delayed choices, the models allow a subjective shortening effect, found by several investigators. In the case of comparative judgment, we presumed that the durations are mapped against movement motivated by differential approach to signs of reinforcement. This hypothesis permits a model of comparative judgment that forces Weber's law to hold, permits the segmentation of the intervals into an arbitrary number of components, and has numerous implications for the arrangement of experimental stimuli and response locations. It highlights the distinction between temporal generalization experiments in which imprecise Poisson timing mechanisms may operate, and discrimination experiments in which more precise mechanisms may be recruited by the subjects.

Delayed reinforcement is often pictured as working backward in time to affect the response that brought it about, but of course that is impossible. Traces of the response that brought about the reinforcer must linger, so that there is something to be affected by reinforcement when it occurs. The probability of lingering in the state that supported the instrumental response correlated with reinforcement is an exponential decay function of time, with a time constant of τ . This fundamental assertion may be developed into a prototype model of choice for delayed reinforcement; depending on several contingent ways of further developing the prototype, one arrives at Mazur's (1984), Fantino's (1977), or Killeen's (1982) model of choice.

The correlation between pacemaker speed and the richness of the environment may serve as the adaptation level mechanism that mediates foraging strategies and contrast effects, as well as second-order effects such as the filled-interval illusion. It may ultimately be found to underlie the transient impressions of the differences in pace of life as organisms enter, and then adapt to, new environments.

References

- Allan, L. G., Kristofferson, A. B., & Wiens, E. W. (1971). Duration discrimination of brief light flashes. *Perception and Psychophysics*, 9, 327-334.
- Bacotti, A. V. (1976). Home cage feeding controls responding under multiple schedules. *Animal Learning & Behavior*, 4, 41-44.
- Blough, D. S. (1959). Delayed matching in the pigeon. *Journal of the Experimental Analysis of Behavior*, 2, 151-160.
- Bush, R. R. (1963). Estimation and evaluation. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology* (Vol. 1), pp. 429-469. New York: Wiley.
- Bush, R. R., & Mosteller, F. (1955). *Stochastic models for learning*. New York: Wiley.
- Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1-42). New York: Appleton-Century-Crofts.
- Church, R. M. (1980). Short-term memory for time intervals. *Learning and Motivation*, 11, 208-219.
- Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception* (pp. 566-582). New York: New York Academy of Sciences.
- Church, R. M., & Deluty, M. Z. (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 216-228.
- Church, R. M., Getty, D. J., & Lerner, N. D. (1976). Duration discrimination by rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 303-312.
- Church, R. M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, 8, 165-186.
- Commons, M. L., Herrnstein, R. J., & Rachlin, H. (Eds.). (1982). *Quantitative analyses of behavior: Vol. II. Matching and maximizing accounts*. Hillsdale, NJ: Erlbaum.
- Commons, M. L., Kacelnik, A., & Shettleworth, S. (Eds.). (1987). *Quantitative analyses of behavior: Vol. VI. Foraging*. Hillsdale, NJ: Erlbaum.
- Cox, D. R. (1962). *Renewal theory*. London: Methuen.
- Cox, D. R., & Miller, H. D. (1965). *The theory of stochastic processes*. New York: Wiley.
- Dunn, R., Williams, B., & Royalty, P. (1987). Devaluation of stimuli contingent on choice: Evidence for conditioned reinforcement. *Journal of the Experimental Analysis of Behavior*, 48, 117-131.
- Eldridge, G. D., & Pear, J. J. (1987). Topographical variations in behavior during autoshaping, automaintenance, and omission training. *Journal of the Experimental Analysis of Behavior*, 47, 319-333.
- Fantino, E. (1969). Choice and rate of reinforcement. *Journal of the Experimental Analysis of Behavior*, 12, 723-730.
- Fantino, E. (1977). Conditioned reinforcement: Choice and information. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 313-339). Englewood Cliffs, NJ: Prentice-Hall.
- Fetterman, J. G., & Dreyfus, L. R. (1986). Pair comparison of duration. *Behavioural Processes*, 12, 111-123.
- Fetterman, J. G., & Dreyfus, L. R. (1987). Duration comparison and the perception of time. In M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin (Eds.), *Quantitative analyses of behavior: Vol. 5. Reinforcer value—the effect of delay and intervening events* (pp. 3-27). Hillsdale, NJ: Erlbaum.
- Fetterman, J. G., Killeen, P. R., & Evans, T. (1986). [Timing and rate of reinforcement]. Unpublished data.
- Fetterman, J. G., Stubbs, D. A., & Dreyfus, L. R. (1986). Scaling of events spaced in time. *Behavioural Processes*, 13, 53-68.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, 84, 279-325.
- Gibbon, J. (1981a). Two kinds of ambiguity in the study of psychological time. In M. L. Commons & J. A. Nevin (Eds.), *Quantitative analysis*

- ses of behavior: Vol. 1. Discriminative properties of reinforcement schedules (pp. 157-189). Cambridge, MA: Ballinger.
- Gibbon, J. (1981b). On the form and location of the psychometric bisection function for time. *Journal of Mathematical Psychology*, 24, 58-87.
- Gibbon, J., & Allan, L. (Eds.). (1984). *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception*.
- Gibbon, J., & Church, R. M. (1981). Time left: Linear versus logarithmic subjective time. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 87-108.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception* (pp. 52-77).
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Grice, G. R. (1948). The relation of secondary reinforcement to delayed reward in visual discrimination learning. *Journal of Experimental Psychology*, 38, 1-16.
- Guttman, N., & Kalish, H. I. (1956). Discriminability and stimulus generalization. *Journal of Experimental Psychology*, 51, 79-88.
- Hanson, S. J., & Killeen, P. R. (1981). Measurement and modeling of behavior under fixed-interval schedules of reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 129-139.
- Harzem, P., Lowe, C. F., & Spencer, P. T. (1978). Temporal control of behavior: Schedule interactions. *Journal of the Experimental Analysis of Behavior*, 30, 255-270.
- Hellstrom, A. (1985). The time-order error and its relatives: Mirrors of cognitive processes in comparing. *Psychological Bulletin*, 97, 35-61.
- Herrnstein, R. J. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior*, 4, 267-272.
- Hoagland, H. (1935). *Pacemakers in relation to aspects of behavior*. New York: Macmillan.
- Hopkins, G. W. (1984). Ultrastable stimulus-response latencies: Towards a model of response-stimulus synchronization. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception* (pp. 16-29). New York: New York Academy of Sciences.
- Johnson, N. L. (1949). Systems of frequency curves generated by methods of translation. *Biometrika*, 36, 149-176.
- Killeen, P. R. (1975). On the temporal control of behavior. *Psychological Review*, 82, 89-115.
- Killeen, P. R. (1979). Arousal: Its genesis, modulation, and extinction. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behavior: Vol. 1. Reinforcement and the organization of behavior* (pp. 31-78). London: Wiley.
- Killeen, P. R. (1981). Averaging theory. In C. M. Bradshaw, E. Szabadi, & C. F. Lowe (Eds.), *Quantification of steady-state operant behaviour* (pp. 21-34). New York: Elsevier.
- Killeen, P. R. (1982). Incentive theory. In D. J. Bernstein (Ed.), *Nebraska Symposium on Motivation 1981: Vol. 29. Response structure and organization* (pp. 169-216). Lincoln: University of Nebraska Press.
- Killeen, P. R. (1984). Incentive theory III: Adaptive clocks. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception* (pp. 515-527). New York: New York Academy of Sciences.
- Killeen, P. R., Hanson, S. J., & Osborne, S. R. (1978). Arousal: its genesis and manifestation as response rate. *Psychological Review*, 85, 571-581.
- Killeen, P. R., & Smith, J. P. (1984). Perception of contingency in conditioning: Scalar timing, response bias, and the erasure of memory by reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 335-345.
- Killeen, P. R., & Weiss, N. A. (1987). Optimal timing and the Weber function. *Psychological Review*, 94, 455-468.
- Kimble, G. A. (1961). *Hilgard and Marquis' conditioning and learning*. New York: Appleton-Century-Crofts.
- Kraemer, P. J., Mazmanian, D. S., & Roberts, W. A. (1985). The choose-short effect in pigeon memory for stimulus duration: Subjective shortening versus coding models. *Animal Learning and Behavior*, 13, 349-354.
- Kristofferson, A. B. (1977). A real-time criterion theory of duration discrimination. *Perception and Psychophysics*, 21, 105-117.
- Kristofferson, A. B. (1980). A quantal step function in duration discrimination. *Perception and Psychophysics*, 27, 300-306.
- Kristofferson, A. B. (1984). Quantal and deterministic timing in human duration discrimination. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*, Vol. 423. *Timing and time perception* (pp. 3-15). New York: New York Academy of Sciences.
- Laming, D. (1973). *Mathematical psychology*. London: Academic Press.
- Lashley, K. S., & Wade, M. (1946). The Pavlovian theory of generalization. *Psychological Review*, 53, 72-87.
- Locurto, C. M., Gibbon, J., & Terrace, H. S. (1981). *Autoshaping and conditioning theory*. New York: Academic Press.
- Lowe, C. F., & Harzem, P. (1977). Species differences in temporal control of behavior. *Journal of the Experimental Analysis of Behavior*, 28, 189-201.
- Maricq, A. V., Roberts, S., & Church, R. M. (1981). Methamphetamine and time estimation. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 18-30.
- Mazur, J. E. (1984). Tests of an equivalence rule for fixed and variable delays. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 426-436.
- McGill, W. J. (1962). Random fluctuations in response rate. *Psychometrika*, 27, 3-17.
- McGill, W. J. (1963). Stochastic latency mechanisms. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology*, Vol. 1, (pp. 309-360). New York: Wiley.
- McGill, W. J. (1967). Neural counting mechanisms and energy detection in audition. *Journal of Mathematical Psychology*, 4, 351-376.
- McGill, W. J., & Gibbon, J. (1965). The general-gamma distribution and reaction times. *Journal of Mathematical Psychology*, 2, 1-18.
- McNamara, J. M., & Houston, A. I. (1987). Memory and the efficient use of information. *Journal of Theoretical Biology*, 125, 285-395.
- Mechner, F. (1958). Probability relations within response sequences under ratio reinforcement. *Journal of the Experimental Analysis of Behavior*, 1, 109-121.
- Meck, W. H. (1983). Selective adjustment of the speed of internal clock and memory processes. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 171-201.
- Meck, W. H. (1986). Affinity for the dopamine d2 receptor predicts neuroleptic potency in decreasing the speed of an internal clock. *Pharmacology, Biochemistry, & Behavior*, 25, 1185-1189.
- Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 320-334.
- Meck, W. H., & Church, R. M. (1984). Simultaneous temporal processing. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 1-29.
- Meck, W. H., Church, R. M., & Gibbon, J. (1985). Temporal integration in duration and number discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, 11, 591-597.
- Meck, W. H., Komeily-Zadeh, F. N., & Church, R. M. (1984). Two-step

- acquisition: Modification of an internal clock's criterion. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 297-306.
- Molenaar, W. (1970). Normal approximations to the Poisson distribution. In G. P. Patil (Ed.), *Random counts in biomedical and social sciences* (pp. 237-254). University Park: Pennsylvania State University Press.
- Moore, B. R. (1973). The role of directed Pavlovian reactions in simple instrumental learning in the pigeon. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 206-230). New York: Appleton-Century-Crofts.
- Nevin, J. A. (1979). Overall matching versus momentary maximizing: Nevin (1969) revisited. *Journal of Experimental Psychology: Animal Behavior Processes*, 5, 300-306.
- Platt, J. R. (1979). Temporal differentiation and the psychophysics of time. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behavior: Vol. 1. Reinforcement and the organization of behavior* (pp. 1-29). London: Wiley.
- Platt, J. R., & Davis, E. R. (1983). Bisection of temporal intervals by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 160-170.
- Poppel, E. (1972). Oscillations as possible basis for time perception. In J. T. Fraser, F. C. Haber, & G. H. Muller (Eds.), *The study of time* (pp. 219-241). New York: Springer-Verlag.
- Raslear, T. G. (1983). A test of the Pfanzagl bisection model in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 49-62.
- Raslear, T. G., Shurtleff, D., & Simmons, L. (1987, April). *Weber's law and time discrimination in the rat*. Paper presented at the meeting of the Eastern Psychological Association, Arlington, VA.
- Revusky, S. (1968). Aversion to sucrose produced by contingent X-radiation: Temporal and dosage parameters. *Journal of Comparative and Physiological Psychology*, 65, 17-22.
- Richelle, M., & Lejeune, H. (1980). *Time in animal behaviour*. Oxford, England: Pergamon Press.
- Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 242-268.
- Roberts, S. (1982). Cross-modal use of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 8, 2-22.
- Roberts, S., & Church, R. M. (1978). Control of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 4, 318-337.
- Roberts, S., & Holder, M. D. (1985). Effects of classical conditioning on an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 11, 194-214.
- Roper, T. J. (1978). Diversity and substitutability of adjunctive activities under fixed-interval schedules of food reinforcement. *Journal of the Experimental Analysis of Behavior*, 30, 83-96.
- Schneider, B. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior*, 12, 667-687.
- Shepard, R. N. (1965). Approximation to uniform gradients of generalization by monotone transformation of scale. In D. I. Mostofsky (Ed.), *Stimulus generalization* (pp. 94-110). Stanford, CA: Stanford University Press.
- Shimp, C. P. (1966). Probabilistically reinforced choice behavior in pigeons. *Journal of the Experimental Analysis of Behavior*, 9, 443-455.
- Shull, R. L., & Pliskoff, S. S. (1967). Changeover delay and concurrent schedules: Some effects on relative performance measures. *Journal of the Experimental Analysis of Behavior*, 10, 517-527.
- Siegel, S. F. (1986). A test of the similarity rule model of temporal bisection. *Learning and Motivation*, 17, 59-75.
- Siegel, S. F., & Church, R. M. (1984). The decision rule in temporal bisection. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences, Vol. 423. Timing and time perception* (pp. 643-645). New York: New York Academy of Sciences.
- Sollberger, A. (1965). *Biological rhythm research*. New York: Elsevier.
- Spetch, M. L., & Wilkie, D. M. (1982). A systematic bias in pigeons' memory for food and light duration. *Behaviour Analysis Letters*, 2, 267-274.
- Spetch, M. L., & Wilkie, D. M. (1983). Subjective shortening: A model of pigeons' memory for event duration. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 14-30.
- Squires, N. K., & Fantino, E. (1971). A model for choice in simple concurrent and concurrent-chains schedules. *Journal of the Experimental Analysis of Behavior*, 15, 27-38.
- Stubbs, D. A. (1976). Scaling of stimulus duration by pigeons. *Journal of the Experimental Analysis of Behavior*, 26, 15-25.
- Stubbs, D. A. (1979). Temporal discrimination and the psychophysics of time. In M. D. Zeiler & P. Harzem (Eds.), *Advances in the analysis of behavior: Vol. 1. Reinforcement and the organization of behavior* (pp. 341-369). London: Wiley.
- Stubbs, D. A., & Dreyfus, L. R. (1981). Temporal discrimination: From psychophysics to reinforcement schedules. In M. L. Commons & J. A. Nevin (Eds.), *Quantitative analyses of behavior: Vol. 1. Discriminative properties of reinforcement schedules* (pp. 137-156). Cambridge, MA: Ballinger.
- Stubbs, D. A., Dreyfus, L. R., & Fetterman, J. G. (1984). The perception of temporal events. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences, Vol. 423. Timing and time perception* (pp. 30-42). New York: New York Academy of Sciences.
- Terrace, H. S. (1966). Stimulus control. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 271-344). New York: Appleton-Century-Crofts.
- Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock." *Psychological Monographs*, 77 (Whole No. 576).

(Appendix follows on next page)

Appendix

Models of the Pacemaker-Accumulator System

Equation 1 in the text is the model of a timing machine called a clock-counter or pacemaker-accumulator system. In these systems one device generates pulses and another accumulates them and then signals when they equal or exceed some preset value. For us, the "accumulation" is done by the animal's transit from one behavioral state to the next when a pulse is registered. Although this Poisson process has proved useful in our analyses, it invokes unnecessarily strong assumptions about timing. In particular, it presumes that the pacemaker is as inaccurate as a timing device can be, with the probability of emitting a pulse at any point in time independent of how long it has been since the last pulse. Furthermore, it assumes that the accumulator is flawless—variability or error in counting (i.e., in making transitions between behavioral states) is assumed to be zero. These assumptions were made because the resulting Poisson process is well understood and because when we are adding up a number of random variables, the resulting models are often robust over erroneous assumptions concerning the location of the error in the system. Thus, the sum of a random number of random variables will tend toward a normal distribution, independent of the contributions of timing or counting error and independent of the distribution of the variables themselves. What will change in these cases is the relation between the mean number of pulses (n) and their variance. The appropriateness of the underlying models as the basis for the cumulative normal distribution (CND) approximation may be evaluated in part by the relationship they force between the standard deviation and the mean, as reflected in the ratio of those two parameters, the coefficient of variation (CV).

It is possible to generalize the clock-counter model to permit error in counting, following the logic of Killeen and Weiss (1987). However the data at hand do not require the general case. Therefore various models for the pacemaker shall be examined first, followed by a brief description of a method for including counting error.

The Poisson Process

The Poisson distribution tells us the probability that exactly n events have occurred in the interval of time between 0 and t . It is usually distributed over n . However, we may compute Equation 1 for various values of t , and this will give us the probability that the animal will be in the n th state at time t . Used this way, Equation 1 is not a distribution, because the area under the curve does not equal 1.0; integration of Equation 1 shows that the area equals τ . Correcting for the area by dividing by τ transforms Equation 1 into a gamma density with mean of $(n+1)\tau$ and standard deviation of $\sqrt{n+1}\tau$. The CV of the model is thus $(n+1)^{-1/2}$.

The response envelopes predicted by Equation 1 presume that response rate within a state is constant and that the averaged data look like a gamma density because many rectangular distributions with random start and stop times are averaged. However, Killeen (1979) showed that Equation 1 also provides an excellent fit to simulated data in which response rates increase linearly throughout the response state.

Equation 1 is correct only when the animal leaves the response state after a single additional pulse. If it stays for m additional pulses, then Equation 1 must be summed over each of those values for n through $n+m$. A simpler approach is to calculate the distribution of times at which the animal enters the response state, which will be a gamma distribution with parameters n and τ , and the times at which the animal leaves the response state, which will be a gamma distribution with parameters $n+m$ and τ . Then the probability that the animal is in the response state is the difference between those two functions (see Cox

& Miller, 1965, section 9.2). The cumulative normal distribution is an excellent approximation to the gamma distribution and may be used in its place.

Strictly speaking, the Poisson distribution is defined only for integer values of the count parameter, n . However, most of the data analyzed is derived from averages over subjects or sessions and thus may represent mixtures of Poisson functions with different indices. Although the mixture of Poissons with indices of, say, 3 and 4, is not precisely represented by a Poisson with an index of 3.5, the latter provides a good approximation, accounting for 98% of the variance in the distributions derived from simulations of such situations.

Quantal Timing

Temporal quantum theory lies at the other boundary of assumptions concerning the location of errors in the timing process, in that it assumes zero variance in the period of the pacemaker. Kristofferson (1984) has reviewed a program of research conducted by himself and colleagues on a real-time criterion theory (RTC) of timing (Kristofferson, 1977; Hopkins, 1984), which has at its heart a quantal model for the pacemaker. This model assumes that the pacemaker has zero variance, but that it is free running, rather than synchronized with the onset of the stimulus to be timed. Variance is introduced by the truncation errors incurred at onset and offset of the stimulus. Because the pulses (quanta) occur at regular intervals, each of the truncation errors has a rectangular distribution, and the net error has a triangular distribution (the convolution of two rectangular distributions). Additional errors may be introduced by afferent and efferent conduction times. As with the Poisson model, counting is assumed to be otherwise error free. Kristofferson and his associates have amassed convincing data for the appropriateness of this model for well-practiced subjects. Furthermore, the psychometric function predicted by this theory closely resembles the cumulative normal distribution.

There is much in Kristofferson's RTC theory that is consistent with our behavioral theory of timing. Both theories reject the interval-measure hypothesis, which holds that some input mechanism takes a measure of the temporal extent of the stimulus, which then may be compared with other measures. Both our behavioral theory and RTC theory hold that choice response S is made if the external stimulus terminates before a criterion is reached and that response L is made otherwise. For Kristofferson, that criterion is a fixed number of counts from an error-free pacemaker. For us that criterion is whether the animal is in a state conditioned to the L response—and what puts it in that state is a fixed number of pulses from a pacemaker. We have assumed the pacemaker to be extremely variable, but that is not an essential part of our theory. Kristofferson presumes, on the basis of substantial data, that for well-practiced subjects the size of the temporal quantum is invariant within ranges of stimulus durations. We would make that presumption only if arousal, and thus τ , remained constant.

(The constancy of the quantum is a separate assumption from that of zero variance in the pacemaker from trial to trial. It entails that Weber's law is false—that error in timing should be constant, not proportional to the magnitude of the stimulus. Allan, Kristofferson, and Wiens (1971) provided evidence that over limited ranges of stimuli the fixed-quantum assumption is correct for well-trained human subjects. Outside those ranges, though, quantal size does change. Kristofferson (1980, 1984) has demonstrated that for untrained subjects the standard deviation of estimates is proportional to t , but that for well-trained subjects variability grows as a step-function of the duration of stimuli evaluated—con-

stant over a range, then increasing as a multiple of the mean duration of the next range. It is as though the period of the pacemaker remains constant within each range and then doubles as the duration of the stimulus increases past some threshold.)

If we presume that the rate of the pacemaker varies with the rate of reinforcement, and we identify its period, τ , with the temporal quantum, then RTC theory provides a potential foundation for the CND models used in this article. The CV of the quantal timing model is $0.41/n$.

Random Fluctuations in Period

We seldom wish to presume either a perfectly random timer (the Poisson emitter) or a perfectly accurate timer (the quantal emitter). The difficulty arises in finding a statistical model for the general case. McGill (1962) constructed a mechanism to analyze systems whose "intervals resemble the ticking of a watch . . . more stable than a purely random sequence, but less stable than a completely periodic system. Moreover they will have the capacity to take on any one of the wide range of possibilities between these extremes" (p. 3). McGill's mechanism consisted of a pacemaker with a strictly periodic beat but a random delay between the emission of the pulse and its registration by the accumulator. If the random component is large compared with the period of the pacemaker, the system will approach the Poisson model; if it is small compared with the period, the system will converge on one resembling Kristofferson's quantal model. Let the period of the pacemaker be τ , the average delay between an excitation and registration be δ and ν be a measure of the relative error: $\nu = \exp(-\tau/\delta)$. Then the average interval between registered counts (d) will be as follows:

$$d = \tau/(1 - \nu), \quad (A1)$$

with a variance of

$$\sigma_d^2 = 2\delta^2 - \nu\tau^2/(1 - \nu)^2. \quad (A2)$$

If δ is small relative to τ , the variance is approximately thus:

$$\sigma_d^2 = 2\delta^2. \quad (A3)$$

Because this approach permits error in the pacemaker to range from zero to that appropriate to a Poisson process, it provides a general and flexible model. However, with this model there is no obvious way to justify a relation between timing error and the period of the pacemaker, and such a correlation is a fundamental reality of the data. The CV is approximately $1.4\delta/d$, and from Equation A1 we see that it decreases as a function of τ .

Hierarchical Timing

Presume that before a transition is made from one state to the next, exactly n' pulses must be registered. An example of this system is provided by the common practice of counting "One-thousand-one, one-thousand-two . . ." when attempting to time intervals without a chronometer. Here, four syllables must be registered before the counter is advanced. The variance in the duration of the subintervals is $n'd^2$, with a mean of $\tau = n'd$. The mean time of exit from the n th state is $nn'd$, with variance $\sigma^2 = nn'd$. The CV is $(nn')^{-1/2}$.

The assumption of hierarchical counting reduces the number of states through which the animal moves by requiring multiple pulses for each transition. It assumes structure within each state that can serve as

a "mini-accumulator": one example might be the pacing of an animal across the walls, with, say, five paces to go across each wall ($n' = 5$), and $n = 4$ for the four walls. In this example the variance in the interpace interval is likely to be less than that of a Poisson process. If that is the case, or if there is some error involved in counting the paces, the more general model that follows must be employed. Behavior that might be interpreted as reflecting hierarchical timing has been reported by Meck and Church (1984).

General Case: Error in Timing and Counting

In the Poisson process, the intervals between successive events are independently exponentially distributed. An important generalization is to allow the intervals to be independently and identically distributed with an arbitrary density function. The resulting series of events is called a renewal process (Cox & Miller, 1965; Cox, 1962). If we let S_n stand for the time up to the n th event, application of the central limit theorem shows that S_n is asymptotically normally distributed with mean $n\tau$ and variance $n\sigma_\tau^2$, where τ and σ_τ^2 are the mean and variance of the underlying random variables.

If there is error in the counter, then the variance of S_n will be (Killeen & Weiss, 1987) as follows:

$$\sigma_{S_n}^2 = n\sigma_\tau^2 + \tau^2\sigma_n^2, \quad (A4)$$

with coefficient of variation:

$$CV = \left(\frac{\sigma_\tau^2}{n\tau^2} + \frac{\sigma_n^2}{n^2} \right)^{1/2}. \quad (A5)$$

Specification of the constituent variances requires models for those processes. As is the case with timing, there are many possible models for the error in the counter. Consider the case in which both variances grow proportionally with the square of their mean (Weber's law). Then the CV is simply $(k/n + k')^{1/2}$, where k is the Weber fraction for time and k' the Weber fraction for number. Note that this equation predicts that for large values of T (and thus, presumably, large values of n), relative timing error is due primarily to variability in the accumulator, as indexed by k' .

Consider next the case in which there is a constant probability p of registering a count, with $0 < p < 1$. For this model, the number of counts up to the n th registration is Pascal distributed, with a mean of n/p and variance of $n(1 - p)/p^2$. Then Equation A4 becomes the following:

$$\sigma_{S_n}^2 = n/p\sigma_\tau^2 + n\tau(1 - p)/p^2, \quad (A6)$$

with coefficient of variation:

$$CV = [(p\sigma_\tau^2)/(n\tau^2) + (1 - p)/n]^{1/2}. \quad (A7)$$

For the Poisson emitter, $\sigma_\tau^2 = \tau^2$, so that Equation A7 reduces to $n^{-1/2}$.

This general approach provides a flexible and realistic basis for analysis of the processes underlying the CND. With further experiments (such as Fetterman, Stubbs, & Dreyfus, 1986; Meck & Church, 1983), it should become possible to more precisely specify likely values for σ_τ^2 and σ_n^2 and the variables of which they are a function.

Received January 6, 1987

Revision received October 1, 1987

Accepted August 21, 1987 ■