JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1999, **71,** 215–251 NUMBER 2 (MARCH)

TIME AND MEMORY: TOWARDS A PACEMAKER-FREE THEORY OF INTERVAL TIMING

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A popular view of interval timing in animals is that it is driven by a discrete pacemaker-accumulator mechanism that yields a linear scale for encoded time. But these mechanisms are fundamentally at odds with the Weber law property of interval timing, and experiments that support linear encoded time can be interpreted in other ways. We argue that the dominant pacemaker-accumulator theory, scalar expectancy theory (SET), fails to explain some basic properties of operant behavior on interval-timing procedures and can only accommodate a number of discrepancies by modifications and elaborations that raise questions about the entire theory. We propose an alternative that is based on principles of memory dynamics derived from the multiple-time-scale (MTS) model of habituation. The MTS timing model can account for data from a wide variety of time-related experiments: proportional and Weber law temporal discrimination, transient as well as persistent effects of reinforcement omission and reinforcement magnitude, bisection, the discrimination of relative as well as absolute duration, and the choose-short effect and its analogue in number-discrimination experiments. Resemblances between timing and counting are an automatic consequence of the model. We also argue that the transient and persistent effects of drugs on time estimates can be interpreted as well within MTS theory as in SET. Recent real-time physiological data conform in surprising detail to the assumptions of the MTS habituation model. Comparisons between the two views suggest a number of novel experiments.

Key words: timing, clock, habituation, recall, Weber law, choose short, pacemaker

There is a developing consensus that interval timing in animals is driven by a discrete pacemaker-accumulator mechanism that yields a linear scale for encoded time (e.g., Gibbon, 1991). But these mechanisms are fundamentally at odds with the Weber law property of interval timing, and experiments that support linear time can be interpreted in other ways. In this article we first review the experimental and theoretical evidence for the dominant pacemaker-accumulator theory, scalar expectancy theory (SET; Gibbon, 1977). This review does not deal with the major competitor to SET, the behavioral theory of timing (BeT: Killeen & Fetterman, 1988). Both theories confront the Poisson variability (Weber law) problem, but BeT solves it in a less ad hoc (and more easily disprovable) way than SET (Bizo & White, 1995, 1997). We focus on SET to limit the length of this paper, because some critiques of BeT already exist (e.g., Church, Meck, & Gibbon, 1994; Gibbon & Church, 1992) and because in terms of citations and numbers of published papers, SET is by far the most popular theory of interval timing. The review concludes that SET fails to explain some basic properties of operant behavior on interval-timing procedures and can only accommodate a number of quantitative discrepancies by modifications and elaborations that raise questions about the entire theory. The second part of the paper suggests an alternative approach based on known principles of memory dynamics. This alternative lacks the formal analytic base of SET, but is pacemaker free, is simpler in concept, and addresses a wider range of data.

SCALAR EXPECTANCY THEORY

The scalar expectancy theory of timing (Gibbon, 1977; Gibbon & Church, 1984; Treisman, 1963) has provided a valuable framework for the study of interval timing in animals. The theory has motivated and or-

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We thank Melissa Bateson, Alex Kacelnik, Warren Meck, and their timing research group for several helpful discussions of the issues raised in this paper. Juan Delius, John Gibbon, and Peter Killeen also commented on earlier versions of the present paper. A summary of the main argument was presented at the November 1997 meeting of the Psychonomic Society in Philadelphia. We are grateful to the National Science Foundation, the National Institutes of Mental Health and Drug Abuse, and the Alexander von Humboldt Foundation for research support. J. J. Higa is now at Texas Christian University.

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ganized the majority of recent behavioral experiments on interval timing (cf. Gibbon, 1991). It has also provided suggestive insights into pharmacological effects (e.g., Meck, 1996). We believe that two features of SET may well be retained by future theories of interval timing: the idea that the current time estimate and the memory for times reinforced in the past follow independent laws; and the notion that behavior is driven by some kind of comparison between current and remembered time of reinforcement. Nevertheless, we will argue that despite its formal structure and proven usefulness, SET is unnecessarily elaborate and redundant, and it faces empirical shortcomings that are sufficient to motivate the search for an alternative.

SET was devised to explain two things: (a) that steady-state measures of time discrimination such as wait time (or, more precisely, *break point*; Schneider, 1969) on fixed-interval (FI) schedules or peak-rate time (on the peak procedure) are proportional to the to-be-timed interval (*proportional timing*; Dews, 1970); and (b) that the standard deviations of such dependent measures are proportional to their means (e.g., Catania, 1970; Staddon, 1965). The latter property is just Weber's law applied to the dimension of time (*Weber timing*). In the SET context it is termed *scalar timing* (Gibbon, 1977).

In fact, there is some confusion between the terms *scalar* and *proportional* in the literature, which is why we reserve the term *proportional timing* for any linear relation between an independent temporal variable (like interfood interval) and a dependent variable (like wait time or peak time), and *scalar* (Weber law) *timing* for the constant ratio between the mean and standard deviation of a dependent temporal variable.

The essence of scalar expectancy theory is straightforward: A Poisson-variable ''pacemaker'' begins emitting pulses a short time after the onset of the time marker, and these are accumulated until a short time after reinforcement, at which point the value of the accumulator is stored in a *reference memory* and the accumulator is reset to zero. Parameters in the simple theory are the start and stop delays and the rate of the pacemaker (which determines the variability of time estimates). To generate behavior, the stored accumulator total is compared with the current total, and when the difference falls below a threshold (which may also vary), responding at a steady rate begins. There is not yet consensus about the learning process: how many values are stored in reference memory, how these are selected for comparison, and so forth (Brunner, Fairhurst, Stolovitsky, & Gibbon, 1997). The credit-assignment problem—how does the system ''know'' what stimulus to use to reset the accumulator (i.e., how does it identify the time marker?)—is left open by SET. We will see in a moment that a related problem—how does the system recognize a trial?—is also not addressed by SET.

The pacemaker concept has always been troubling, because the properties of real timing are fundamentally at odds with it. The problem is that timing with a pacemaker-accumulator implies greater relative accuracy at longer time intervals. If there is no error in the accumulator, or if the error is independent of accumulator value, and if there is pulse-by-pulse variability in the pacemaker rate, then by the law of large numbers, relative error (standard deviation divided by mean, coefficient of variation) must be less at longer time intervals. This relative improvement with absolute duration is independent of the type of variability in the pacemaker. In fact, coefficient of variation is approximately constant (Weber's law, the scalar property) over a limited range of times. At longer times the coefficient of variation tends to increase (rather than decrease) with the duration of the timed interval (e.g., Gibbon, Malapani, Dale, & Gallistel, 1997; Zeiler, 1991). Gibbon (1977) was aware of this problem early on, but chose to deal with it in ways that preserve the pacemaker-accumulator properties of SET.

In an exploration of ways to reconcile the pacemaker-accumulator idea with Weber's law, Gibbon and Church (1984) showed that the simple pacemaker-accumulator model needs to be modified if it is to match the data. First, Gibbon and Church acknowledge that Poisson variance alone does not yield the scalar property: ''In the Poisson system, variance increases directly with the mean, so that the system is more efficient, i.e., the ratio of standard deviation to mean is lower at long times than at short times'' (1984, p. 475); and later, ''These results, we feel, rule out Poisson variance acting alone'' (p. 477). Then, they go on to deal with the pacemaker-accumulator problem as follows:

> An alternative [to pulse-by-pulse variability] source of pacemaker variance is a drifting rate. Imagine that the time between pulses . . . is fixed on any trial, but from trial to trial, the pulse rate . . . varies normally around a mean. . . . A more realistic version might allow rapid variation of local pulse rate both within and between trials, but *for our present purposes, it is simplest to think of a locally constant rate which varies from trial to trial* [italics added] . . . we show that assuming a normal form for local rate . . . we arrive at a system that is linear in real time with the scalar property: variance in the accumulator, and therefore the memory, increases approximately as the square of the mean. (p. 477)

So, rather than give up the pacemaker idea, a core assumption of the theory, Gibbon and Church reconcile it with the scalar property by means of two additional assumptions: that pacemaker rate varies (a) only from trial to trial (even though the system has no principled way to distinguish trial-onset stimuli from other stimuli) rather than simply pulse by pulse, and (b) normally rather than Poisson (note that normal variation in pulse *rate* assumes a much more complex process than random—Poisson—variation in *time of occurrence* of each pulse).

Given these constraints on the pacemaker, it is not clear why it is needed at all. Why not just assume a linear time code (no counts) with a slope that varies normally from trial to trial? In this bald form the arbitrariness of the assumption of trial-by-trial variation would be more apparent. We argue below that current expositions of the theory in fact take something close to this form, but because the pacemaker-accumulator framework is retained, the redundancy of the pacemaker assumption is not obvious.

It is worth noting that the accumulator assumption is itself problematic, because it implies a biological process that can increase without limit. SET assigns no upper bound to the duration of intervals that can be timed, so if the time code is linear, there is no limit on the accumulator total.

The fundamental contradiction between the pacemaker-accumulator idea and the Weber law property of timing should be fatal to any pacemaker-accumulator theory. Why has SET thrived in spite of this difficulty? One reason is surely because the pacemaker notion is so intuitively plausible: Modern clocks (but not older devices such as the hourglass and the clepsydra) all rely on the counting of discrete pulses. Neurophysiology also provides ample evidence for pacemakers with periods in the SET range (1 to 50 per second) (e.g., Spitzer & Sejnowski, 1997). But traces, integrators, and long-period oscillators are also widespread in neural and other tissue, even at the level of individual cells (Bünning, 1973; Kondo et al., 1997). Physiology is rich enough to support almost any hypothetical mechanism, so that physiological plausibility rarely distinguishes among behavioral theories (Staddon & Zanutto, 1998). Many drug effects find a natural interpretation within SET (e.g., Meck, 1996), but they can also be explained (we will argue) by competing theories, so this evidence is also not decisive.

We suspect that the main reason the Poisson pacemaker is accepted despite its theoretical inconvenience is that in recent expositions of SET it receives only lip service: It is assumed but not really used. For example, it is often suggested that the Poisson pacemaker has a ''high rate'' (Gibbon, 1991, p. 22) so that ''Poisson [pacemaker] variance rapidly becomes swamped by scalar variance [i.e., the noisy multiplier]'' (Leak & Gibbon, 1995, p. 18). Gibbon (1992) has shown how assumptions about memory encoding and decoding ''allow multiplicative random variables to intervene . . . between the value of a count in the accumulator at reinforcement time and its value after retrieval when it is used for comparison'' (1992, p. 289). He concludes, ''Scalar variance is induced by randomizing the Poisson mean with bias, or encoding the retrieval variance in the memory system. The components of variance multiply the representation of criterion times and hence induce the scalar property'' (p. 293). And, most recently and simply, ''We have proposed that [Weber's law in timing] reflects an underlying random variation in a multiplicative noise variable'' (Gibbon et al., 1997, p. 170). Thus, the awkward property of any pacemaker-accumulator system—increasing relative accuracy at longer times—is sidestepped, because variance due to pacemaker rate variation is a trivial part of the whole. In both early and current versions of SET, the Poisson pacemaker assumption is redundant: Either the Poisson property is replaced by a constant rate that varies from trial to trial, or, alternatively, residual Poisson variability is deemed to make a negligible contribution to total variance.

The core assumptions of SET as it is actually used seem to be something like the following. SET, and perhaps any theory of operant timing, seems to require *three* time-related variables: real elapsed time, the encoded value of current time, and the remembered value for times encoded in the past. We denote real time as t_i, where i indicates the relevant time marker. The encoded value for t_i is τ_i. The remembered value for a past τ_i we indicate by τ_i'. An asterisk denotes the value of each variable that is associated with reinforcement. The internal variable for current time, τ_i, is always referred to in SET as "number of pulses," but because the pacemaker-accumulator assumption is in fact unnecessary, it could simply be any internal variable proportional to real time.

SET assumes that the relation between remembered time and real time is linear (cf. Figure 3, below; Leak & Gibbon, 1995, Figure 1, and many such figures in earlier papers). Formally, $\tau' = kt$ (subscripts neglected for simplicity); that is, remembered time, τ', is proportional to real time, t, and k is a constant of proportionality. But this cannot be a direct relation, because remembered time, τ', is not stored directly—what is stored is encoded time, τ—and indeed Gibbon (1991) writes "When, on a given trial, reinforcement is obtained at a time t^*, the value for accumulated pulses [i.e., τ, encoded current time, in our terminology] stored in working memory on that trial is translated to reference memory [i.e., converted from τ^* to τ'^*] via the proportionality constant, k [our symbols]" (p. 23). So the correct relations must be

$$\tau' = k\tau \tag{1a}$$

and

$$\tau = \lambda t, \tag{1b}$$

so that

$$\tau' = k\lambda t, \tag{1c}$$

where λ denotes the pacemaker rate or, in our terms, the scale relation between linearly coded internal time τ and real time t. Gibbon concludes, "The variation induced by these parameters [k and λ] scales with t^* so that the distributions on memory are (nearly) scale transforms of each other" (1991, p. 23). As we have seen, the variation in pacemaker rate, λ, is assumed to be negligible; hence, the major contribution to these distributions is variation in parameter k. Because k is a multiplier, any variation in τ' will automatically be proportional to t (i.e., scalar, in SET terminology). Thus, SET explains the scalar property by assuming (a) that there is a multiplicative transformation between encoded time and remembered time; (b) that temporal judgments represent a comparison between long-term remembered time and short-term-encoded current time; and (c) that most of the variability in remembered time is due to the multiplicative relation (k) between encoded and remembered time. The Poisson pacemaker-accumulator system seems to be completely redundant in this most recent version of SET. The effect of independent variables such as drugs on a previously learned performance is attributed either to a change in k (the translation between working and reference memory), a change in the slope of Equation 1b (i.e., in the more or less constant pacemaker rate), or a change in τ'^*, the remembered time of reinforcement (in reference memory).

Response rule. Predictions of response pattern versus time (and sources of variability) are obtained through a threshold assumption (note that the assumption that response rate stops and starts around the time of reinforcement is tied very much to a particular experimental procedure, the peak procedure, discussed below, because response rate is not so simply related to t^* on other interval-timing schedules):

$$\begin{cases} \text{if } |\tau'^* - \tau| < \theta, & \text{response rate} = x, \\ \text{otherwise}, & \text{response rate} = 0, \end{cases} \tag{2a}$$

where x is a constant and θ is a threshold. Because both τ' and τ are linear with respect to real time (Equation 1), t may be substituted so that Equation 2a is thus shorthand for (λ cancels)

$$\begin{cases} \text{if } |kt^* - t| < \theta, & \text{response rate} = x, \\ \text{otherwise}, & \text{response rate} = 0. \end{cases} \tag{2b}$$

Although Equation 2a is the simplest form of threshold assumption, in most expositions of SET (cf. Church & Gibbon, 1982, Equation 1; Gibbon, 1991, Equation 1) a ratio version is preferred:

$$\begin{cases} \text{if } |(kt^* - t)/kt^*| < \theta, & \text{response rate} = x, \\ \text{otherwise,} & \text{response rate} = 0. \end{cases} \tag{2c}$$

Equation 2c, linear time encoding with a ratio response rule, is equivalent to logarithmic time with a difference response rule:

$$|(kt^* - t)/kt^*| < \theta$$
$$= |t/kt^*| < \theta + 1 = |\ln t - \ln t^*| < \theta', \tag{2d}$$

where θ' is a threshold value. Nevertheless, the ratio-rule-with-linear-time version is preferred in SET because of the commitment to a pacemaker.

The essential features of SET as it has been used in recent papers are thus relatively simple: linear encoded and remembered time, related multiplicatively, and all-or-none behavior generated via a thresholded comparison between them. We will argue in a moment that time is in fact encoded approximately logarithmically, as Equation 2d implies.

Alternatives to Linear Encoded Time

It is important to recognize that the only necessary requirement for interval-time discrimination is some internal variable that changes in a reliable monotonic way with time elapsed since a time marker. Moreover, as long as there is a unique value of the variable for each time, it makes no difference whether the variable increases or decreases with time. Given such a monotonic function, time can be told by associating specific values of the variable with reinforcement or its absence and responding accordingly. Given that SET-type theories of timing are essentially a comparison between some internal time-related variable, $\tau = f(t)$, and the remembered value of that variable at the time of reinforcement, there is no up-front reason to restrict such models to a linear function. A couple of nonlinear possibilities are exponential,

$$\tau = e^{-at}, \tag{3}$$

and logarithmic,

$$\tau = k_1 - k_2\ln(t), \tag{4}$$

where a and k_i are constants. Exponential decay is not consistent with Weber's law but, as Fechner showed many years ago, a logarithmic function like Equation 4 is. If internal noise, ϵ, is independent of τ [i.e., $\tau = k_1 - k_2\ln(t) + \epsilon$], then Weber's law (the scalar property) can be obtained directly, just from the form of τ, because the slope of Equation 4 is inversely related to t: $d\tau/dt = -k_2/t$. [Because it does not matter whether $f(t)$ is increasing or decreasing, we use the decreasing form of log function for comparability with the other decreasing functions, and because we will later introduce the idea of a decreasing memory trace as a basis for the timing function.] Given a constant variation in response threshold, therefore, the variation in the time of onset of responding (Equation 2) will be proportional to the slope of $f(t)$, hence (for the log function) proportional to t. This is less ad hoc than the early version of SET, which assumes linear $f(t)$ plus trial-locked variation in pacemaker rate to achieve the same result. It is more complicated than the later SET, which uses a multiplicative translation from working to reference memory (k), but that version runs into difficulties with bisection data.

The log-time assumption is consistent with temporal bisection data, which show that animals judge an event of duration x to be equally like two comparison durations y and z if $x \cong \sqrt{yz}$, that is, at the geometric mean (e.g., Church & Deluty, 1977; Stubbs, 1968). In a typical bisection experiment the organism has two choices and is presented on each trial with one of two stimulus durations, T_S and T_L. Reinforcement is delivered for Response A following the short duration, T_S, and Response B following the long, T_L. In occasional probe trials, intermediate durations are presented. The typical finding is that subjects are indifferent between A and B when the probe duration, T_P, is equal to the geometric mean of T_S and T_L, $T_P = (T_S \cdot T_L)^{½}$. This is what would be expected given symmetrical variation around T_S and T_L on a logarithmic psychological time scale: Responses A and B should have equal strength (point of subjective equality) at the geometric mean of the short and long training times. This result is different from what would be predicted by SET (cf. Gibbon, 1981; Leak & Gibbon, 1995, Figure 1). For example, given $T_S = 1$ and T_L

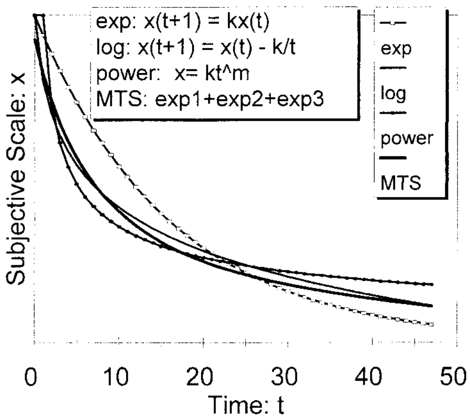

Fig. 1. Some memory-decay functions. Parameters (Equation 16): $a_i = .7$, .9, and .994, for three cascaded integrators; $b = .2$. $k = .94$ (exp). $k = .2$ (log). $m = -.5$ (power). The MTS function is derived from the recovery portion of a habituation series. Scale parameters are ignored. Note that the power and MTS functions are very similar.

$= 2$, logarithmic time predicts bisection at $T_P = 1.414$ and scalar timing at $T_P = 1.33$, the harmonic mean (linear time would place the point of subjective equality at 1.5).

There are several other functions that have very similar properties to the logarithmic: power (e.g., Staddon, 1984), the sum of exponentials (multiple time scale: MTS[1]; Staddon, 1997; Staddon & Higa, 1996), and others. Four functions are shown in Figure 1. The logarithmic, power, and MTS (but not the single-exponential) functions can approximate both Weber's law and necessary memory properties such as Jost's law. The power function is the candidate offered by Wixted and Ebbesen (1991, 1997) for the forgetting function in a range of species. The log and power functions were the best fits to the large human-forgetting-curve data set reviewed by Rubin and Wenzel (1996; they did not look at MTS-type functions). The resemblance between the MTS and power functions will become relevant when we present a memory-based approach to time discrimination in the second half of the paper.

Argument Against Log Time

Given the apparent equivalence of models with a linear time scale and a ratio-difference response rule versus a logarithmic scale and a constant-difference response rule, it is obviously important for SET to rule out the hypothesis that time is encoded logarithmically. The main argument against the assumption that time is encoded in a log-like way is based on "time-left" choice experiments (Gibbon & Church, 1981). In the time-left procedure, rats or pigeons must choose between a short fixed delay and a longer fixed delay that has already partly elapsed (time left). In their Experiment 1, for example, rats chose between two levers, one fixed and the other retractable, representing different delays until food reinforcement. The fixed lever signaled a fixed delay, C_{TO} (timed from trial onset), until food. The delay on the retractable lever, S_{LP} (timed from lever presentation), presented T_{TO} s into the trial, was also fixed, but shorter than C_{TO}. The experimental question is: How will preference for fixed delay S_{LP} versus time-left delay $C_{TO} - T_{TO}$ change as a function of T_{TO}? In particular, will the animals prefer the time-left lever when $C_{TO} - T_{TO} = S_{LP}$? In fact, rats are indifferent when delays to food are equal on both levers, which Gibbon and Church take as evidence against logarithmic coding of time: "A logarithmic or indeed any curvilinear subjective time scale ought to result in a greater preference for the time-left side of the choice when the real time left to food is equal on both alternatives" (p. 92).

This argument is equivalent to saying that because the log form for τ changes less during the second half of a timed interval than during the first half, the second half is more valuable to the animal, because it is objectively smaller than a half-length interval just beginning (cf. Gibbon & Church's, 1981, discussion of Figure 2). Thus, if a 30-s lever ($S_{LP} = 30$) is introduced half way through the interval on a 60-s lever ($C_{TO} = 60$), the animal is supposed to compare the small upcoming difference, $\Delta\tau$, between τ_{30} and τ_{60} on the 60-s lever with the larger upcoming difference between τ_0 and τ_{30} on the inserted lever and choose the 60-s lever, rather than be indifferent between the two as linear timing would require.

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[1] But note that because of the nonlinear dynamics of the MTS model, the form of the function is not invariant, but depends on the system history. For example, see how the MTS trace declines more slowly after a history of low-rate stimuli versus a history of high-rate stimuli in Figure 5, below.

This analysis is flawed, because it takes an assumption about the form of an internal "time-coding" variable and then assumes a direct relation between that variable and reinforcement value: the smaller $\Delta\tau$, the greater the value.[2] The problem is that a theory about how time is encoded [e.g., the assumption that $\tau = f(t)$] says nothing at all about how an animal will *act* with respect to a given change in τ. Nor does it say whether a given change always has the same value, independent of the starting value for τ. For example, it is possible that the animal will evaluate the 30-s alternative in a conditional way, depending on when it occurs during the 60-s interval, or that it will begin timing both outcomes from the beginning of the 30-s interval once the 30-s lever is introduced. Moreover, Gibbon and Church's (1981) assumption that value is inversely related to $\Delta\tau$, independently of the starting value, leads to obvious counterfactuals. After a very long time, even a large time-left delay (very small $\Delta\tau$ at that long time) should be preferred to a short comparison delay (large $\Delta\tau$), for example. Either the log-time assumption is wrong, or the assumption that value is inversely related to encoded (as opposed to real) time is wrong.

Gibbon and Church (1981) have a second argument for the linear time assumption:

> The increase in preference for time left over indifference when the standard lever entered at 45 sec was the same as the decrease in preference for time left when the standard lever entered at 15 sec. Thus, preference was symmetrical around indifference. These results strongly suggest that time is appreciated in a linear fashion in both intervals. A logarithmic or indeed any curvilinear subjective time scale ought to result in a greater preference for the time-left side of the choice when the real time to food is equal on both alternatives. (p. 92)

They do acknowledge a potential problem with this interpretation: "Suppose that each of the three entry points [i.e., 15 s, 30 s, and 45 s] is learned separately *as a paired-associate subtask* [italics added]. Were this the case, the performances should be comparable with ones in which a 45-sec FI is pitted against a 30-sec FI, two 30-sec FIs are pitted against each other, etc." On this basis they conclude that "The mechanism for producing an appropriate performance in each of the three subproblems then might be of almost any sort, independently of the character of the subjective time scale" (p. 93). Nevertheless, they reject this line of reasoning because preference for the 60-s lever when the 30-s choice is inserted at 15 s (45 vs. 30 s to food) is the same as the preference for the 30-s lever when it is inserted at 45 s (15 s vs. 30 s to food). But this argument is also not decisive, because the supposedly symmetrical data (their Figure 3) are not very convincing (there is much individual variability among the 4 rats), and because such a result is in any case not quite what we would expect from other choice data. In other experiments with delayed reward (e.g., Chung & Herrnstein, 1967; Shull, Mellon, & Sharp, 1990) preference is proportional to *relative immediacy*. Thus, given two delays on left and right d_L and d_R, the ratio of responding, $B_L/B_R = (1/d_L)/(1/d_R) = d_R/d_L$. Hence, in the time-left experiment, we might expect $B_{45}/B_{30} = 30/45 = .67$, whereas $B_{30}/B_{15} = 15/30 = .5$, that is, the two ratios should not be the same, as Gibbon and Church contend. They did not test between these two possibilities in this experiment, but in a later ones (Brunner, Gibbon, & Fairhurst, 1994; Gibbon, 1986) they confirmed that reinforcement delays conform to the idea that the animals value a choice according to relative immediacy. Thus, in the Gibbon (1986) experiment, pigeons were roughly indifferent between two equiprobable delays of 15 and 240 s (harmonic mean: 28 s) and a fixed delay of 30 s.

There are at least two other ways to interpret the time-left experiment that can reconcile these results with nonlinear encoded time:

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[2] Gibbon and Church's argument is deceptively similar to the optimality argument that derives risk aversion from decreasing marginal utility. The crucial difference is that the risk-aversion argument derives from a plot of subjective value versus objective quantity, whereas their argument derives from a plot of objective time code versus objective real time. The problem in their analysis is that *subjective* is not the same as *encoded*. Time may well be (and is, we contend) encoded nonlinearly, in the sense that it is mapped onto some internal variable that increases with elapsed time in a negatively accelerated way. Nevertheless, subjective time, like subjective weight and other examples, is roughly proportional to real time. We argue that encoding determines experimental results that depend on discriminability, but subjective value determines results that depend on value (e.g., choice experiments).

First, consider Gibbon and Church (1981), Experiment 2 (Figure 6). There are two choices, each available at a variable time after trial onset (TO): call that time T_{TO}. Choice W gives food after a time, C_{TO}, that is variable from the time of choice presentation, but is fixed from the onset of the trial. Thus the time marker for Choice W is trial onset. For this choice, therefore, we have a real time, t_{TO}, and an encoded time, τ_{TO}, both measured from time marker TO. On a given trial, at time T the *value* of Choice W is given by the *immediacy* of food on that choice (according to numerous delay-of-reinforcement experiments, e.g., Chung & Herrnstein, 1967), which is given by the difference between the time at which the choice must be made, T_{TO}, and the time when food is predictably delivered, C_{TO}. Because $\tau = f(t)$, this value function is just

$$V(T) = V(\tau_C - \tau_T) = 1/[f^{-1}(\tau_C) - f^{-1}(\tau_T)] \cong 1/(C_{TO} - T_{TO}), \quad (5)$$

where f^{-1} denotes the inverse function. The situation for the other choice in this experiment, Choice G, is simple: Food arrives after a fixed delay time, S, from choice presentation (CP, not trial onset) which is independent of T. Thus,

$$V(T) = V(\tau_S) = 1/f^{-1}(\tau_S) \cong 1/S_{CP}. \quad (6)$$

The choice then is trivial: Choose the shorter real-time delay, which is what the animals do.

In other words, although time is coded according to some function $f(t)$ that determines the accuracy of time discrimination (this is a *confusion scale* in the traditional psychophysical terminology), behavioral actions are determined by the inverse function, which is the animal's estimate of real time—the ecologically relevant variable. The claim is that no matter what the animal's internal code for elapsed time, it will also have some kind of compensatory perceptual constancy mechanism (we suggest a specific possibility below) that allows it to behave appropriately with respect to the real world (i.e., real time). This way of doing it avoids the non sequitur of assuming that just because long times cannot be estimated as accurately as short times, time intervals long delayed from a time marker are somehow more valuable than time intervals little delayed from a time marker.

There is a second way to look at the time-left experiment. First, we must acknowledge that an organism may be able to assess (i.e., respond selectively to) the rate of occurrence of an event like food reinforcement without being directly sensitive to the time at which food occurs. For example, a simple organism whose behavior is guided by a leaky integrator can assess reinforcement rate via the state of the integrator but may nevertheless be unable to anticipate a periodic event (cf. many stochastic learning models, beginning with Bush & Mosteller, 1955). Second, we assume that the organism can learn the association between particular stimuli and particular rates of reinforcement.

Now consider the decaying "memory" of a time marker. At different delay times, 1, 2, 3, and so on, this memory takes on different values, τ_1, τ_2, τ_3, and so on. On the time-left choice, each of these "memories" is a discriminative stimulus for an outcome that has a certain rate of reinforcement (the reciprocal of the time left). (This is a "paired-associate subtask," in the words of Gibbon and Church, 1981.) The reinforcement rate signaled by each stimulus value can therefore be compared with the rate signaled by the fixed-delay "standard" stimulus. Clearly, the animal should be able to choose either the time-left stimulus, τ_i, or the standard stimulus, depending on which is associated with the higher rate of reinforcement. This interpretation is independent of the particular form of memory-decay function. Perhaps this is what Gibbon and Church meant when they write (correctly, in our view) that "The mechanism for producing an appropriate performance in each of the three subproblems then might be of almost any sort, independently of the character of the subjective time scale" (1981, p. 93).

The essential feature of our second argument against Gibbon and Church's interpretation of the time-left experiment is separation between the animal's capacity to assess reinforcement rates and its capacity to use a decaying memory trace as a stimulus. There is in fact no necessary relation between an organism's ability to learn to identify a particular point in time and its sensitivity to rates of reinforcement The theoretical proof is the existence of reinforcement-rate-sensitive learning models that lack any timing capability (e.g., Dragoi & Staddon, in press). The empirical proof is that even in situations where time discrimination is possible, such as concurrent variable-interval variable-interval choice, time discrimination (momentary maximizing), and choice performance often operate independently (cf. Hinson & Staddon, 1983; Williams, 1988); and some organisms—some fish, for example—are able to choose on the basis of reinforcement rate but seem to be rather poor at estimating time intervals (Rozin, 1965). Thus, Gibbon and Church's interpretation of the time-left procedure is by no means forced. Hence their data do not constitute evidence against the idea that encoded time is nonlinear.

These examples are just illustrative. The fundamental flaw in the time-left argument is in fact *conceptual*—namely the assumption that an organism has access to (and its behavior is directly determined by) the objective properties of its own internal representation, or, to put the same thing in more ''psychological'' terms, that subjective (how long a time appears to be to the animal) equals objective (how much its internal time code changes). This is an old error in psychology, and there are numerous illustrations. For example, in the neural homunculus in the human brain, the representation of the hands is much larger than the representation of the back, and this is reflected in the smaller two-point threshold on the hands. But we do not feel that our hands are larger than our back. Peripheral visual resolution is much worse than foveal, but the periphery does not appear smaller than the area observed by the fovea. In the discrimination of weight (Weber's original experiment, and the basis for his law), few doubt that the internal coding is logarithmic. Yet there is also no doubt that although the just-noticeable-difference (jnd) for a 1 lb weight is about 0.2 lb and the jnd for a 10 lb weight is about 2 lb, the subject knows perfectly well that the second increment is larger than the first. As Stevens wrote many years ago, ''the jnd's for loudness are unequal in subjective value. The same appears to be true of other intensive attributes like subjective weight, brightness and taste'' (1951, p. 36). The general point is that discriminability does not determine perceived value. Every sensory dimension is processed in a way that usually preserves a measure of perceptual constancy (cf. the first interpretation, above). Thus, we may be less accurate at large values (weights, times) than short, but we know perfectly well that a weight or a time has approximately doubled in value, even though our internal code has changed by less than a factor of two.[3]

Argument for Log Time

The time-left experiments are not a convincing argument against logarithmic encoding of time. Is there any evidence in favor of log-like encoding, beyond the Weber law standard-deviation property and geometric-mean bisection data? There is some indirect supporting evidence that derives from the widespread finding of power-law relations in interval-timing experiments. Platt (1979) has reviewed numerous studies showing a power-law relation between temporal dependent and independent variables in temporal differentiation and discrimination experiments:

$$b = qt^{s}, \qquad (7)$$

where b is the observed behavior (e.g., response duration, waiting time), t is the required duration, q is a constant, and s is an exponent (usually close to one). Power-function relations with exponents different from unity cannot easily be reconciled with SET, but there is a theoretical argument that ties them to logarithmic internal coding. The argument is as follows.

First assume that temporal discrimination is a comparison process in which an internal, logarithmic temporal variable (reference memory) is compared with an output variable (working memory: encoded elapsed time) that is also logarithmic: ''Investigators . . . have suggested that performance in scaling experiments results from the subject

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[3] John Gibbon (personal communication) has pointed out an apparent contradiction between the geometric-mean bisection data, which are consistent with a log scale, and the time-left and other similar choice data, which are consistent with linear time. The difference is that in the bisection case, the animal is judging the duration of a single past event (the sample time) and therefore chooses based on the log-scale point of subjective equality, which is the geometric mean. But in a choice experiment (e.g., preference for a fixed delay, x, vs. two equiprobable delays, y and z) the animal is choosing between different expected rates of reinforcement, so that choice is at the value point of subjective equality, which is the harmonic mean: $x = ½(y + z)/yz$.

matching an internal representation of the stimulus to an internal representation of the response. If both of these representations are logarithmically related, the power law results'' (Platt, 1979, p. 19; see Ekman, 1964; MacKay, 1963). In other words, if memory for a time interval is encoded logarithmically and if current elapsed time is also encoded logarithmically, and if behavior involves comparison between the two, then the empirical relation between temporal independent and dependent variables will take the power form.

This interpretation of the psychophysical power law was extended by Staddon (1978) and the argument can be applied to time discrimination. We assume that the internal effects, *dz,* of both remembered time (represented in Equation 8) and elapsed time (represented by Equation 9) show Weber law sensitivity, according to sensitivity coefficients (Weber fractions), w_t and w_b:

$$\frac{dt}{t} = w_t dz_t \tag{8}$$

and

$$\frac{db}{b} = w_b dz_b. \tag{9}$$

The first equation simply states that a small change in real time, *dt,* has a psychological effect, *dz*, that is inversely related to *t* and the Weber fraction w_t: $dz = dt/w_t t$; and similarly for the second equation (Staddon, 1978).

Integrating both sides of Equations 8 and 9 yields

$$\ln t + K_1 = w_t z_t \tag{10}$$

and

$$\ln b + K_2 = w_b z_b, \tag{11}$$

a logarithmic relation between both remembered time, *t*, and elapsed time, *b*, and their internal effects, z_t and z_b. K_1 and K_2 are constants of integration. In temporal discrimination experiments, the internal effects of remembered and elapsed time are equated, $z_t = z_b$, which allows us to eliminate *z* from Equations 10 and 11. Rearranging yields the power relation (Equation 7), with

$$q = \exp(w_b K_1/w_t - K_2) \tag{12}$$

and

$$s = w_b/w_t. \tag{13}$$

The two constants, K_1 and K_2, are scale factors (Staddon, 1978), assumed to be constant across different experimental procedures.

Notice that if the sensitivities (Weber fractions) of remembered time and elapsed time are the same, the exponent, *s*, is unity, and behavior (waiting time), *b*, is linearly related to elapsed time, *t*. This is a common, but not universal, result in temporal experiments. The exponent for the function relating waiting time to FI duration in steady-state parametric FI experiments is usually close to one. But the exponent in steady-state tracking experiments, in which the animal is repeatedly subjected to cyclically varying interfood intervals, is typically less than one. This is just what we would expect, given that the exponent $s = w_b/w_t$ and that it is harder for the animal to remember the upcoming interfood interval when several are intermixed in each session than when all the intervals are the same from session to session. If w_t, the Weber fraction for remembered time, increases (i.e., poorer discrimination), then the exponent *s* should decrease. As this argument suggests, Innis and Staddon (1971) found a less-than-one power-function exponent of .824 in an early interval-tracking experiment in which pigeons were repeatedly exposed to a cycle of seven ascending and seven descending interfood intervals. They also found that the exponent increased to .894 when different discriminative stimuli signaled the ascending and descending parts of the cycle and presumably reduced memory interference among remembered intervals (cf. Staddon, 1974b).

If different experimental arrangements affect sensitivities and the two sensitivities are affected differentially, then the power-function exponent will be different in different experiments. It follows from Equations 12 and 13 that the slopes and intercepts of a set of such functions will be linearly related:

$$\ln q = sK_1 - K_2, \tag{14}$$

which is a testable empirical prediction. DeCasper (1974, cited in Platt, 1979) plotted the slopes and intercepts of power functions obtained in four different temporal differentiation experiments, with the results shown

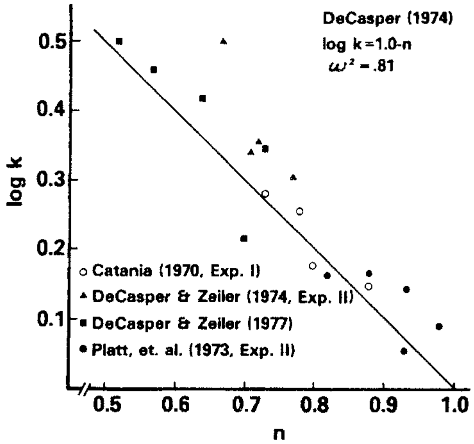

Fig. 2. Log intercept (*k*) versus exponent (*n*) for four temporal differentiation experiments reanalyzed by DeCasper (1974).

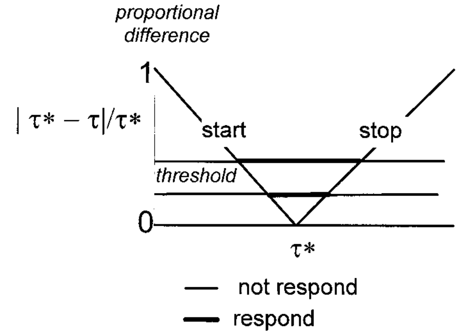

Fig. 3. Scalar timing and the threshold response rule. Responding at a constant rate starts and stops when the difference line exceeds or falls below the threshold. The scalar assumption means that the difference line always begins at 1 and ends at 0 (when $\tau^* = T$, for any T); the linear subjective time assumption means the line is straight.

in Figure 2. The slopes and exponents show a reasonably good linear fit to Equation 14.

On the basis of the DeCasper analysis, Platt (1979) is almost ready "to conclude that the power law for temporal differentiation schedules indicates a logarithmic internal representation for time" (p. 20), but he draws back because

> There are . . . two great logical gaps in the attempt to view temporal differentiation schedules as analogous to psychophysical scaling procedures: (1) what is the stimulus whose internal representation is controlling responding and (2) how can the relationship between that stimulus and its internal representation be inferred from responding which may be the result of additional transformations required by the reinforcement contingencies? (p. 21)

We have answered the first question. The "stimulus" is just the logarithmically transformed value of current elapsed time. Its "internal representation" is the reference memory for past encoded times. The meaning of Platt's second question is not totally clear to us in this context, but we do take up the issue of reinforcement contingencies later in connection with several specific examples. In any event, we do not believe that Platt's objections to the log-log account of power-law data are conclusive. Taken all together, the data and arguments in favor of time coding that is approximately logarithmic are stronger than for any other simple function.

Individual Trials: Correlation Data and Distributions

In the SET analysis of individual trials on the peak procedure (Church et al., 1994), well-trained rats are said to learn on each trial to wait for a certain time (the *start time*) until they begin pressing the lever at a constant rate, which they maintain until they eventually stop responding (at the *stop time*). The constant-rate assumption is only approximately true, at least for pigeons. For example, Cheng and Westwood (1993) presented peak-procedure data showing that "within the run phase was an inner run phase at a yet higher rate" (p. 56). And much earlier, Staddon and Frank (1975) showed that on FI schedules, pigeons respond faster the later they begin responding within an interval. Nevertheless, granted the stop–constant-run–stop pattern for rats, the threshold assumption of SET (Equation 2, above), together with the scalar assumption and the assumption of linear encoded time, makes some clear predictions about the correlations among start time (t_{start}), stop time (t_{stop}), and spread ($t_{\text{stop}} - t_{\text{start}}$) on the peak procedure. These predictions are illustrated in Figure 3 (a modified version of Church et al.'s, 1994, Figure 2). The figure shows the value of the difference between τ (encoded time) and τ'^*, the remembered time at which reinforcement occurs (corresponding to T in real time, when there is no reference-memory variance) as t increases from zero, through T (the time of reinforcement) and beyond (V-shaped pair of lines). The threshold is assumed by SET to vary, and two threshold values (horizontal lines) are shown, with two start and stop times. When the threshold is low, start time is long and the time between start and stop is short; conversely, when the threshold is high, start time is short and the time between start and stop times is long. In simple SET, therefore, the correlation between t_{start} and *both* t_{stop} *and* $t_{\text{stop}} - t_{\text{start}}$ (spread) is negative.

The data agree only partially: The correlation between start and spread is indeed negative, as SET, and some other theories (Killeen & Fetterman, 1993; Staddon, 1972a; Staddon & Ayres, 1975) predict ($M = -0.33$, Church et al., 1994, Table 2). But the correlation between start and stop is in fact positive ($M = 0.31$), as predicted by response-competition theories (e.g., Staddon & Ayres, 1975); not negative as predicted by this version of SET. Church et al. (following Gibbon & Church, 1990) interpret the positive start–stop correlation as evidence for memory variance (the once-per-trial sampling of τ'^*, discussed earlier) plus different stop and start thresholds; that is, they reconcile model and data by adding another process and parameter. In their final statement on this problem, Church et al. (1994) conclude that the covariance data support a ''scalar timing model in which animals used on each trial a single sample from memory of the time of reinforcement and separate response threshold to decide when to start and stop responding'' (p. 135)—a total of five parameters. Even without the second threshold, Gibbon and Church (1990) concluded that ''The flexibility of the surviving [SET] models is of course bought at some cost, since additional assumptions ineluctably lead to additional parameters'' (p. 53). Perhaps for this reason, the single-threshold, linear-difference, no-memory-variance model continues to be used (e.g., Leak & Gibbon, 1995, Figure 1) despite its inconsistency with the correlation data.

Figure 3 makes other predictions about peak-procedure data. For example, if the only source of variance in the model is variation in the single threshold, then, because of the linear time assumption, distributions of start and stop times should be symmetrical with the same standard deviation. They are neither. Church et al. (1994) report that the standard deviation of start times is less than the standard deviation of stop times (for the same T value; see their Figure 8). At least one other study seems to show larger standard deviations for start than for stop times, and the start distribution is highly skewed (Brunner et al., 1997, Figure 2). Zeiler and Powell (1994) report that when only individual-subject data are considered, start and stop times (measured by Schneider's, 1969, break-point procedure) show constant coefficient of variation, consistent with the scalar property, but pause (time to first response) and peak-rate time (the preferred variable in SET peak-procedure experiments) show coefficient of variation increasing as a function of schedule FI value. They also show a number of power-function (rather than linear) relations between temporal dependent and independent variables (as have a number of other investigators, cf. Platt, 1979). Zeiler and Powell conclude, ''Existing theory does not explain why Weber's law so rarely fits the results or why each type of behavior seemed unique'' (p. 1). These findings are not consistent with the simple threshold analysis, although doubtless all could be reconciled with SET by ''an appropriate selection of a response rule and an adroit introduction of variance in the structures we describe'' (Gibbon & Church, 1984, p. 482).

One problem with Figure 3 seems to be the assumption that start and stop times are set by the same process, whereas the obvious dependence of both on the schedule parameters implies that they are determined separately. (The separate determination of start and stop is recognized by the two-threshold version of SET, but the values of the two thresholds are not explicitly linked to schedule parameters, as the data suggest they should be.) Reinforcement-omission experiments suggest that the default pattern on strictly periodic reinforcement schedules is for responding to continue indefinitely once it has begun (i.e., ''stop'' time → ∞). On standard FI schedules, the animal rarely experiences T values greater than the FI value, so the default pattern shows up when reinforcers are occasionally omitted (Staddon, 1974b; Staddon & Innis, 1966). On the peak procedure, start time is determined by T, the time when the earliest reinforcement can occur, but stop time is determined by T plus the intertrial interval (i.e., by the time when the next reinforcement opportunity will occur). This dependence is acknowledged in later papers (Brunner et al., 1997; Church, Miller, Meck, & Gibbon, 1991; Leak & Gibbon, 1995), but has not yet led to a comprehensive revision of the earlier approach.

Figure 3 also illustrates a deeper problem with SET: that the scalar property (which is admittedly difficult to derive from a pacemaker-accumulator mechanism) is treated as an axiom rather than as a derived result. Leak and Gibbon (1995), for example, deal with simultaneous timing of two intervals by drawing a version of Figure 3 for each interval (see their Figure 1), rather than by reapplying the full pacemaker-accumulator model, with its various thresholds and sources of variance, to two timed intervals.

Summary: Theoretical Strategies

These problems with SET, and its advocates' responses to them, illustrate one of two quite different approaches to theorizing. One approach is to assume, on a priori or intuitive grounds, the existence of some process, like a pacemaker-driven internal clock. Research then proceeds in two steps. The first step is to refine an experimental paradigm that is presumed to provide a "pure" measure of clock properties (the peak procedure, with suitable choices of probe-trial probability and duration and intertrial-interval distribution). The next step is to derive increasingly precise predictions about the quantitative properties of behavior in this situation. If these are confirmed, the theory is supported. If not, the theory is modified, usually by adding nonlinear elements (thresholds, multipliers) or sources of variance, until the new data are accommodated. There is little concern for uniqueness. For example, the SET literature abounds with phrases like "Here, we describe the version of the model used in fitting the data from the two experiments" (Allan & Gibbon, 1991, p. 41); "I consider here two response rules, both of which have been used in different contexts" (Gibbon, 1991, p. 25); or "I begin with a general model which applies to any of the timing performances . . . but with differing instantiations in the components" (Gibbon, 1991, p. 21). The reader gets the impression that the model is assumed to be true, and the task of the experiment is to identify sources of variance within the model framework: "The estimate of a time interval may reflect sources of variance in the clock, memory, or comparator." The authors go on to acknowledge that "The estimate may also reflect sources of variance that are independent of the timing process" (Church et al., 1991, p. 207), but the assumption that there *is* a separate "timing process" is never questioned. The model itself is treated like a set of interchangeable parts that in different combinations can fit data from almost any interval-timing experiment. The usual scientific strategy of looking for *the* theory for a given set of phenomena has been abandoned in favor of a sort of erector-set approach whose objective is not to find *one* explanation but *some* explanation, within the flexible range of possibilities defined by SET.

This is not necessarily a bad strategy—after all, living organisms are also constructed from a limited number of parts assembled in different combinations, and much neural net theorizing has this quality. The SET approach has also been helpful in designing and organizing experiments and can give a sense of closure to the analysis of puzzling data. But it has pitfalls. First, because the initial pacemaker-accumulator-clock hypothesis was grounded largely in intuition and a priori, and not on demonstrated power to explain preexisting data, the likelihood that it is on the right lines may be very small. Second, because the approach is so flexible and the data set is relatively limited, the research program does not—and perhaps cannot—lead to abandonment of the original theory, which can almost always be preserved via modification and elaboration. But for the disinterested observer, each new discrepancy and each new elaboration of the theory increasingly raise the question of whether this is the right approach at all.

The alternative is to proceed first inductively, to try to find a general rule or process that can explain a wide range of existing data on time-related reinforcement schedules. By beginning with a process that has a substantial inductive base, we may have a better chance that refinement through experiment will lead to a better theory, not just one more resistant to disproof.

A MEMORY-BASED TIMING PROCESS

A rat is not a psychophysical instrument, although, given appropriate training, it can behave like one. On periodic food-reinforcement schedules, rats, pigeons, and many other animals engage in a variety of interim activities in addition to the terminal operant response that yields the food (Shettleworth, 1975; Staddon & Simmelhag, 1971; Timberlake, 1983). These activities seem to compete, with each other and with the operant response (Staddon, 1972a, 1977; Staddon & Frank, 1975). For example, restrained pigeons wait a shorter time until the first postfood FI response than do unrestrained animals that can move around and engage in interim activities (Frank & Staddon, 1974). An interim activity like wheel running seems to delay the terminal response of lever pressing; omitting the wheel causes lever pressing to begin earlier in the timed interval (Staddon & Ayres, 1975). Each activity has its own internal dynamic, and each seems also to be sensitive to temporal cues. For example, in a well-trained animal, each activity seems to occur for a characteristic time. Consequently, when an activity begins late in the interfood interval it tends also to end late. This may be the explanation for the reliably positive start-stop correlation in peak-procedure experiments discussed earlier. Conversely, when an activity begins early, it can continue longer, because the next activity in the sequence (which has its own temporal causal factors) does not cut in until its proper time. This may account for the negative start-spread correlations discussed earlier. Patterns of correlations support the idea that each activity is separately controlled. For example, the later an activity ends in an interfood interval, the shorter the delay between its offset and the onset of the next activity in the sequence; the sequence of acts does not constitute a chain (Staddon & Ayres, 1975; Staddon & Frank, 1975). In sum, even on strictly periodic reinforcement schedules, postfood time is only one of several causal factors acting on the operant response.

But most experiments on interval timing in recent years have not stuck to strictly periodic schedules. The modal study is much more likely to use something like the peak procedure (perhaps with two or three response alternatives), or some kind of comparison method such as bisection, than a simple FI schedule. The aim, of course, is to assess the "time sense" in an exact way that parallels human psychophysics. But under these conditions, the identity of the time marker is often uncertain. As Stubbs et al. (1994) point out, "with complex stimulus arrangements, like those used in much current nonhuman animal research, multiple aspects of complex stimuli affect behavior and complex stimuli exert multiple effects on behavior" (p. 31). Given the complex response and stimulus properties of interval-timing experiments, it may be a mistake, therefore, to expect the kind of exclusive control by time (measured from a single time marker) that is taken for granted by SET and some other timing theories.

Nevertheless, post-time-marker time is *one* of the factors controlling a temporal dependent variable such as peak time or postreinforcement pause. But because it is unlikely to be the only one, we may have to lower our expectations about the degree of quantitative predictive precision to be expected from any theory that deals with time alone. With this caveat in mind, in the second half of this paper we outline a memory-based approach to temporal control.

Our theory shares two features with SET: a separation between the animal's estimate of current time and its memory for times reinforced in the past; and the idea that interval timing involves some kind of comparison between remembered and current time.

As we showed earlier, the arguments against log-like encoded time offered by SET are not compelling. There are other possibilities for $f(t)$, such as the power and MTS functions, that share with the log function the property that they decline rapidly at first and more slowly later (e.g., Dreyfus, Fetterman, Smith, & Stubbs, 1988; Staddon, 1983, 1984, 1997; Stubbs et al., 1994). Moreover, SET is designed primarily to deal with steady-state data. It has no intrinsic dynamics and does not attempt to solve the assignment-of-credit problem. Here we discuss a memory-based alternative to pacemaker-accumulator models that is intrinsically dynamic, suggests ways to deal with assignment of credit, and also implies logarithmic-like temporal encoding derived from data on memory. We propose that there may be no ''internal clock'' as such at all; that interval time discrimination is just like any other discrimination, the only difference being in what is discriminated. In time discrimination, we will argue, animals are learning to discriminate between memories of different ages and thus of different ''strengths.''

The role of the time marker. All interval timing is timing with respect to some stimulus, such as food reinforcement or the intertrial interval, that acts as a *time marker.* (Multiple stimuli may act as time markers under some conditions, but we do not deal with that possibility here.) The time marker initiates the interval that is to be timed. The time marker, and the different properties of different kinds of time marker, are largely ignored by SET and other cognitive timing theories (but see Mellon, Leak, Fairhurst, & Gibbon, 1995), even though there is abundant evidence that timing is more effective with respect to some time markers than others. Reinforcement, or a stimulus that signals reinforcement, is more effective than neutral stimuli, for example (S. Roberts & Holder, 1984; Spetch & Wilkie, 1981; Staddon & Innis, 1969; Starr & Staddon, 1974).

A time marker, like any stimulus, changes the state of the organism. Some aspects of that change may be more or less permanent, but other aspects continue to change with time, typically to grow weaker as their effects (short-term memory) decay. (There are also interactions among memories: retroactive and proactive interference. There is evidence for proactive interference between time markers, Staddon, 1974b, 1975. We discuss some below, but we focus here on the decay aspect.) If the organism is sensitive to the changing aspects of a memory, if we can discover a quantitative form for the change in the memory variable with time, and if the organism can learn to associate specific actions with specific values of the memory variable, then we have provided the organism with a potential ''interval clock.'' Moreover, we have done so by making use of a familiar process—short-term memory—rather than through the postulation of a pacemaker-accumulator ''clock.'' There may also be an internal clock that is independent of memory. But it is more parsimonious to see first how well we can explain interval timing with known processes, before resorting to an assumption whose main basis is the phenomenon it is supposed to explain.

We here develop a memory-based theory of interval timing in answer to two questions: What is an appropriate paradigm for event memory? And, what does this paradigm tell us about the way that stimulus effects change with time?

The Event-Memory Paradigm

The most elementary effect of stimulus presentation is *habituation*, the waning of a reflex response to successive presentations of a stimulus. Habituation is our paradigm for event memory. We assume that even stimuli that elicit no reflex response have memorial effects that resemble those of stimuli that do elicit a response. Thus, the dynamics of habituation provide an objective answer to our second question: How do the effects of stimulus presentation change with time?

Habituation is widely observed with many different responses and stimuli and across species ranging from protists to humans (Eisenstein & Peretz, 1973; Jennings, 1906/1976; Peeke & Herz, 1973; Peeke & Petrinovich, 1984; Thompson & Spencer, 1966; Wood, 1970). Habituation has an important dynamic property, termed *rate sensitivity* (Byrne, 1982; Carew, Pinsker, & Kandel, 1972; Davis, 1970; Staddon, 1993; Staddon & Higa, 1996). Rate sensitivity is the surprising fact that although habituation is more rapid and complete when interstimulus intervals are short than when they are long, recovery from habituation is also more rapid after short interstimulus intervals. Rate sensitivity puts certain constraints on the dynamics of short-term memory.

Habituation can be duplicated by a process in which response strength is the difference between a constant stimulus effect and a leaky-integrator short-term stimulus memory (Figure 4: θ is a threshold, usually zero, X is the stimulus input, V_I is the inhibitory integrator ''charge,'' and V_O is the response output). This scheme (termed *feedforward habituation*; Staddon & Higa, 1996) is a formalization of a well-known proposal by Sokolov (1963). As successive stimuli are presented, the accumulated charge of the integrator (short-term memory for the stimulus) increases. Because

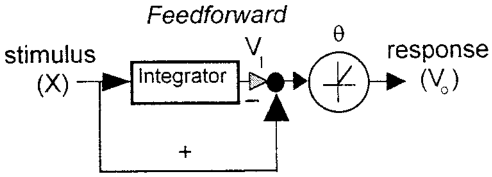

Fig. 4. Single-unit feedforward habituation model. Integrated effects of past stimuli, V_I, are subtracted from the direct effects, X, and the above-threshold difference, $X - V_I - \theta$, determines the response strength V_O.

response output is the difference between the integrator charge and the constant stimulus input, output response strength decreases as successive stimuli are presented and memory strength builds up. If the interstimulus interval is too large, however, the integrator "discharges" ("forgets") between stimulus presentations and the system does not habituate. Thus, the degree of habituation in the model, as in nature, is less at longer interstimulus intervals.

The single-unit model habituates less at long interstimulus intervals than at short ones, but posthabituation recovery is just as rapid, because only one time constant is involved. Staddon (1993) showed that a series of at least two cascaded habituation units (the output of the first being the input to the second, and the second slower than the first) is necessary to reproduce the rate-sensitive property (earlier habituation models by Gingrich & Byrne, 1985, and Treisman, 1984, also incorporate two stages). Staddon and Higa (1996) showed that this type of model can be extended to any number of stages.

Equations. Formally, in discrete-time notation, the single-unit feedforward model is

$$V_O(t) = X(t) - V_I(t) - \theta, \quad \text{if } V_O > 0,$$
$$= 0 \quad \text{otherwise.} \qquad (15)$$

(Equivalently, $V_O = \boldsymbol{\theta}(X - V_I)$, where $\boldsymbol{\theta}$ denotes a threshold function.)

$$V_I(t+1) = a_I V_I(t) + b_I X(t),$$
$$0 < a_I < 1, \qquad b_I > 0, \qquad (16)$$

where V_I is the integrated inhibitory effect of past stimuli, V_O is response strength, θ is the output threshold (usually zero, to avoid negative responding), a is a time constant that reflects the period over which past stimuli contribute to habituation, $X(t)$ is the effect of a stimulus at time t, and b is the weighting of the stimulus effect. If a is small, only recent stimuli contribute, and habituation is rapid if the stimulus spacing is short enough. If a is large, even stimuli that occurred a while ago contribute: Habituation will occur even if stimuli are widely spaced. Parameter b affects habituation rate but not recovery rate, which is determined entirely by a.

Reflex strength, V_R, is the *potential* response strength at any time, given a standard stimulus (set by convention at unity). Reflex strength is the response strength that would have been measured, had a stimulus been given at time t. Thus, when a stimulus *is* given, response strength equals reflex strength. Reflex strength for the single-unit leaky-integrator habituation model with zero threshold is just $V_R = 1 - V_I$, where V_I is the state of the single integrator and 1 is the value of the standard stimulus. When the stimulus presented is the standard unit stimulus, response strength is equal to the suprathreshold part of reflex strength at the instant of stimulus presentation. A plot of theoretical reflex strength during habituation will be a sawtooth, rising between stimulus presentations, and declining suddenly following each stimulus. The low point of each sawtooth corresponds to the response strength (i.e., the actual response level when a stimulus is presented), and these points decline to a lower asymptote as the stimulus series progresses. When stimuli cease, reflex strength rises smoothly to an upper asymptote (spontaneous recovery).

Any number of habituation units can be cascaded, with the output of the jth unit, V_{Oj}, being the stimulus input, X_{j+1}, to unit $j + 1$. The final output is just the output of the last integrator in the chain.

In a cascade with zero thresholds and unit stimulus input, it is easy to show that the net reflex strength at the last integrator (N) in the cascade (i.e., reflex strength of the whole system) is just

$$V_R = 1 - \sum_{j=1}^{N} V_{Ij}. \qquad (17)$$

Memory-trace strength. Spontaneous recovery, the increase in reflex strength as a function of time in the absence of further stimulation, is the reflex counterpart of forgetting.

For a habituated reflex, response strength recovers with time as memory for the stimulus fades. For a memory, strength decreases with time. In the cascaded-integrator model, memory-trace strength—the recallability of a stimulus—is thus the complement of reflex strength:

$$V_{\mathrm{M}} = 1 - V_{\mathrm{R}} = \sum_{j=1}^{N} V_{\mathrm{I}j}, \qquad (18)$$

where V_{M} is memory-trace strength.

The MTS forgetting curve in Figure 1 was generated by a three-unit system of the sort described by Equations 15 through 18. The curve shows V_{M} during spontaneous recovery after a habituation series.

MTS Memory Timing Model

The basic idea of the multiple-time-scale (MTS) model is that what is learned on periodic schedules is the reinforced and nonreinforced values of the animal's memory for the time marker (i.e., the values of V_{M} that are associated with reinforcement and nonreinforcement). (Note that some V_{M} values never occur: those corresponding to post-time-marker times longer than the longest interfood interval. Neither reinforcement nor nonreinforcement can be associated with those values.) The obvious objection to any memory model is that, as we have just shown, if "noise" is assumed to be constant, independent of the memory value, Weber law timing requires a logarithmic memory. But in fact, the kind of memory function necessary to match data on rate-sensitive habituation and Jost's forgetting law is very close to the logarithmic form necessary to account for the Weber's law and time-discrimination and differentiation data: rapid deceleration at first, followed by slower deceleration. Moreover, as we will see in a moment, the data suggest that the correct memory-decay function is only approximately logarithmic, although in Weber law and bisection experiments with moderate stimulus ranges, the log and MTS functions are probably not distinguishable (see Figure 1). The MTS approach to timing offers the possibility of integrating a wide range of phenomena—habituation, rate sensitivity, partial reinforcement effects, Jost's law, Weber law timing, the psychophysics of temporal choice, and many properties of time-based reinforcement schedules (cf. Staddon, 1993, 1997; Staddon & Higa, 1996)—by means of a single event-memory process.

The assumption that timing depends on the same mechanism as habituation may also help to solve the credit-assignment problem (i.e., identification of the time marker). The theorist need not assume that the animal "knows" the relevant time marker. Now, every discriminable event will have its own trace, and remembered reinforced values will compete for control of the response. Only good predictors will compete effectively, presumably (see Staddon & Zhang, 1991, and Dragoi & Staddon, in press, for explicit competition models of credit assignment that might be applied to this problem). Moreover, "reset" will not be absolute in this type of model (as it is in SET, absent ad hoc assumptions; see our discussion of reinforcement omission, below). Events preceding the most recent time marker affect V_{M}; hence, they affect the animal's "time estimate." There are similar effects on reinforcement schedules: For example, the postfood response profile shows proactive interference effects on some temporal schedules (e.g., Lejeune, Ferrara, Simons, & Wearden, 1997; Staddon, 1974a, 1974b), and the effects of successive reinforcers have been shown to cumulate under some conditions (Horner, Staddon, & Lozano, 1997). The fact that events have cumulative effects in the MTS model automatically subsumes timing and counting under the same theory, as we show in a moment.

In this section of the paper, we apply the MTS model to static phenomena of interval timing: proportional timing, Weber's law, the reinforcement-magnitude effect, the reinforcement-omission effect, duration-discrimination experiments, and timing and counting experiments. We also describe how some drug effects on timing, usually interpreted in terms of SET, can as easily be fitted into the MTS framework. Finally, we briefly describe intriguing preliminary data on the neural basis of habituation dynamics that also mesh very well with the MTS model. The MTS approach has implications for schedule dynamics as exemplified, for example, by the rich but puzzling data set on cyclic-interval schedules (e.g., Higa & Staddon, 1997; Innis & Staddon, 1971; Staddon, 1969; Staddon & Higa, 1991), but this analysis requires discus-

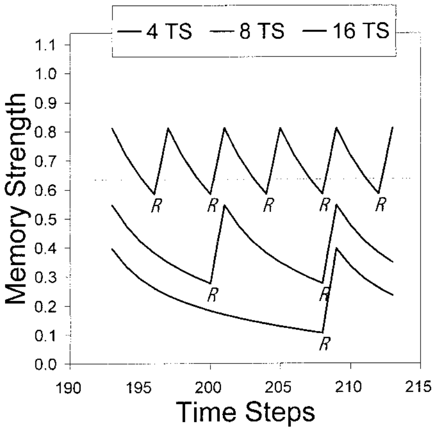

Fig. 5: Steady-state memory traces for a three-stage MTS model for three FI schedules with reinforcers presented at four, eight, and 16 time-step intervals. R denotes the trace value at the instant of reinforcement. The horizontal line represents a hypothetical start response threshold on the four time-step schedule.

sion of learning mechanisms, which we defer until a later paper.

Proportional timing. Any variable that changes monotonically with time elapsed since a time marker can serve as an internal clock. Figure 5 shows steady-state memory traces from a three-stage MTS model at three FI values; the time at which reinforcement occurs is indicated by R in each record. Clearly, on each schedule there is a unique V_M value associated with reinforcement. For this particular MTS model, the V_M value at the instant of reinforcement is inversely related to the FI value, but this need not always be true, nor is it necessary for time discrimination. All that *is* necessary for proportional timing is that the trace change in the same monotonic way from one time marker to the next on a given schedule.

After some exposure to a given periodic schedule, reinforcement will be associated with a small range of V_M values, which allows the animal to learn a given response criterion, illustrated for the four time-step series by a horizontal line in Figure 5. When the trace falls below the criterion, responding begins. (Actual responding on FI schedules is not always break and run, of course; something more than this simple rule will be needed for a comprehensive truly dynamic model of temporal discrimination.) If the threshold is set a fixed distance from the value of V_M*, the V_M value associated with reinforcement, then the post-time-marker waiting time will be approximately a fixed fraction of t*, the to-be-timed interval, as long as V_M is approximately logarithmically related to time.

The curves in Figure 5 look like simple traces, but the MTS model differs from most trace models (but not all; Killeen's, 1979, arousal theory has similar properties) in two respects. We have already mentioned one: Successive stimuli have cumulative effects (and the magnitude of the trace is proportional to stimulus magnitude). But the second property is more subtle: The *form* of the trace depends on the system history. To see this, consider two histories. One is a long series of short FIs, say four time steps; the other is a comparable series of longer intervals, say 32 time steps. Now imagine a three-unit MTS model, with the first two units being "fast" (small *a* values, e.g., .5, .8) and the last unit slow (e.g., .999). After four time steps, the first two units will still retain much of the initial value, so that each new stimulus (reinforcer) will add only a small increment to the last, slow unit. The trace,

$$V_M = \sum_{j=1}^{N} V_{1j},$$

will therefore decline relatively rapidly, because its decay rate will be dominated by the faster units. Conversely, after a history of 32 time-step interstimulus intervals, each stimulus will deliver a substantial increment to the slow unit because the faster units will have lost much of their initial value after 32 time steps. Hence, the trace decay will be dominated by the slow unit. In short, memory traces after a history of frequent reinforcement will decay faster than after a history of infrequent reinforcement, "tuning" the trace to the prevailing interstimulus interval. The difference in decay rates is not large, but it makes the system more efficient in dealing with a wide range of interstimulus intervals than a simple, fixed-trace model. As we show next, it also holds the Weber fraction approximately constant over a substantial range of timed intervals.

Weber's law (the scalar property). The Weber fraction, *W*, is defined as the change in physical stimulus value that corresponds to a small fixed change in the value on the psychologi-

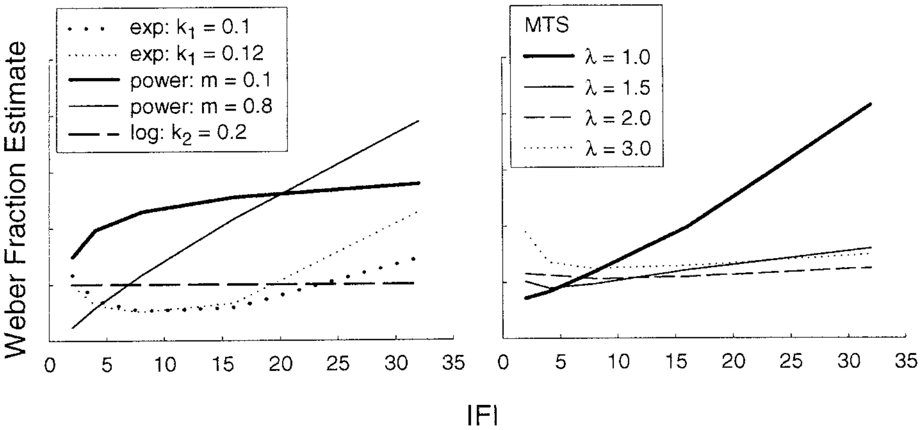

Fig. 6. How the Weber fraction changes with interfood interval, according to different trace models. The Weber fraction estimate is $dt/|df(t)t|$, that is, $1/|$*slope*interfood interval*$|$, where *slope* $= V_M(t+1) - V_M(t)$. The abscissa shows interfood intervals from two to 32 time steps. Left panel: Exponential, log, and power functions: $f(t) = \exp(-k)$, $f(t) = \ln t$, $f(t) = t^m$. Parameter values are shown in the legend. Right panel: A three-stage MTS model. Parameter λ determines the three rate parameters, a_i (Equation 16), according to the relation $a_i = 1 - \exp(-\lambda i)$ (Staddon & Higa, 1996, Equation 5); parameter $b_i = .1$.

cal scale at that point, divided by the stimulus value. Thus,

$$W(x) = dx/x, \tag{19}$$

where $W(x)$ is the Weber fraction at point x on the stimulus scale and dx is the stimulus change necessary to produce a just-noticeable change in the psychological scale. Given a particular psychological scale, $z(x)$, with slope $S(x) = dz/dx$ at point x, therefore, $dx = dz/S(x)$. By the jnd assumption, dz is constant. Therefore we can substitute for dx in Equation 19, $dx = k/S(x)$, so that the Weber fraction is

$$W(x) = k/xS(x), \tag{20}$$

or, in words, the Weber fraction is inversely proportional to slope times stimulus value. We therefore term the quantity 1/|slope*value| the *Weber fraction estimate* for a given psychological scale.

Fechner's insight was to notice that Weber's law—the constancy of the Weber fraction—follows from two ideas: that sensory dimensions are encoded logarithmically, and that internal noise is constant (independent of the encoded value). Logarithmic encoding means that the slope of the internal variable is inversely proportional to its value, so that the absolute value of the slope multiplied by value is a constant that is inversely proportional to the Weber fraction. Figure 6 shows how the Weber fraction estimate varies as a function of interfood interval for a variety of trace models. The left panel compares the log function with power and exponential functions. As you can see, the exponential function always violates Weber's law, because after an initial decrease, the Weber fraction increases with interfood interval. The Weber fraction estimate also increases with interfood interval for power functions, but after an initial rise, further increase is gradual for small exponents ($0 > m > -.3$). The right panel shows trace functions from a three-unit MTS model. For each function, we computed the Weber fraction estimate at the instant of reinforcement, in the steady state (i.e., after exposure to a number of interfood intervals). The parameter, λ, determines how the rate constant, a_i, changes from the first unit to the last. The Weber fraction estimate increases with interfood interval for the MTS model, but relatively slowly for λ values greater than 1.5, which is the range we have used to model habituation data (Staddon & Higa, 1996). By increasing the number of habituation units (we used three, but physiological data discussed below suggest that humans, at least, may have 10 or more), the constancy of the Weber fraction can be extended to indefinitely large durations. Both power and MTS models are consistent with existing data, which show a slow increase in the Weber frac-

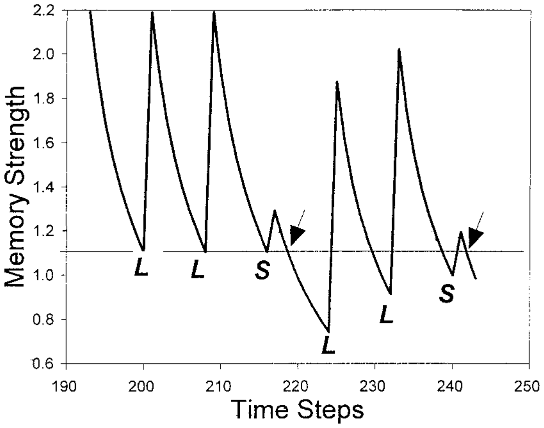

Fig. 7. Steady-state memory-trace strength on an eight time-step FI schedule with large (L) reinforcers. Small (S) reinforcers are substituted at the end of two intervals. Horizontal line is the trace strength at which reinforcement normally occurs. This level is reached sooner following the small reinforcers (arrows).

tion (coefficient of variation) with duration of the timed interval (Gibbon et al., 1997; Zeiler, 1991; Zeiler & Powell, 1994).

Reinforcement-magnitude effects. A counterintuitive implication of the MTS theory is that on FI and similar interval-timing procedures with reinforcement as the time marker, occasional briefer-than-usual reinforcements should reduce postreinforcement pause or break point ("reduce the animal's subjective estimate of time to reinforcement," in the language of timing theories). The prediction is counterintuitive because it implies that an animal will systematically misjudge time to food on account of an objectively irrelevant variable: the magnitude of the time marker. This prediction is illustrated in Figure 7. The horizontal line indicates the value of V_M (i.e., τ^*, in our previous notation, where τ is the encoded value of elapsed time) that corresponds to the usual time of food delivery. Because the small food deliveries increase V_M less than the large, V_M will reach τ^* sooner after a small reinforcement than after a large one. Hence, the animal should begin responding sooner after a small reinforcement than after a large one, and this effect should be immediate. In experiments that have intermixed reinforcements of different durations, postreinforcement pause is directly related to reinforcement duration, just as this analysis implies (e.g., Lowe, Davey, & Harzem, 1974; Meltzer & Brahlek, 1970; Staddon, 1970a; see also Perone & Courtney, 1992), and the effect shows up during the first session under the mixed-duration procedure. The data also show, as this model predicts, that the effect is a reduction in pause after the smaller reinforcement durations, rather than an increase after the long.

This analysis implies certain sequential dependencies. For example, for the system in Figure 7, if a small reinforcer initiates interval N and the next interval begins with a large reinforcer, waiting time in interval $N + 1$ should also be shorter than the average post-large wait, though not as short as the wait in interval N. Dependencies of this sort have not been studied extensively.

Note, however, that the shorter reinforcement, shorter pause effect is *not* to be expected if *all* reinforcements are brief. Under those conditions, the horizontal line in Figure 7 that represents the reinforced V_M value will simply be lower, and postreinforcement pause will be adjusted to that level. In conformity with this prediction, chronic FI experiments with large or small reinforcers show more or less the same postreinforcement pause (Bonem & Crossman, 1988; MacEwen & Killeen, 1991). (The effect should, and does, occur during transitions from one reinforcement duration to another, however.)

Reinforcement-omission effect. If a pigeon or a rat is well trained on an FI schedule, and a reinforcement (R) is occasionally omitted at the end of the interval and is replaced by a neutral nonreinforcement stimulus (N) such as a timeout or keylight change equal in length to the reinforcement itself, responding in the subsequent interval begins sooner than usual. This reduction in post-time-marker waiting time is known as the *reinforcement-omission effect* (Staddon & Innis, 1966). Like the reinforcement-magnitude effect just described, it is counterintuitive, because in all of these experiments the time to food signaled by reinforcement and by the stimulus presented in its place is always the same. Nevertheless, as long as the omission is not too frequent (no more than 50% of intervals) the omission effect persists almost indefinitely, in both rats and pigeons (there are some second-order differences between rats and pigeons, however; see Staddon & Innis, 1969).

The simplest way to conceptualize reinforcement omission is to assimilate it to a reduction in reinforcement magnitude: Reinforcement suppresses responding (i.e., produces a postreinforcement pause) on FI schedules; events similar to reinforcement suppress it less (stimulus generalization decrement). The experimental evidence for the generalization decrement interpretation is very strong (cf. Kello, 1972; Staddon, 1970b, 1972b; Staddon & Innis, 1969). In this case, Figure 7 can be used to illustrate reinforcement omission as well as reinforcement reduction. In both cases, the estimated time to reinforcement is reduced, the animal begins responding too early in the interfood interval and response rate across the whole interval is higher than usual (the omission effect). Figure 7 also resembles the ''incomplete reset'' explanation for the omission effect proposed by SET: ''If the reset [of the accumulator] is not complete when reinforcement does not occur, then the next trial would show a shorter pause before the break point'' (Gibbon, 1991, p. 23). The difference between this interpretation and the MTS account is that SET says nothing about *why* small reinforcers should be less effective time markers than large ones, whereas reinforcer magnitude (however measured) is the input variable to the MTS theory. The MTS account is also an advance over the generalization decrement interpretation, because it suggests why these effects are persistent rather than transient. (SET is likewise silent on the onset properties and persistence of the omission and reinforcement-magnitude effects.)

Nevertheless, there is a problem with the assimilation of reinforcement omission to a reduction in reinforcer magnitude: The reinforcement-omission effect depends on the absolute value of the timed interval.[4] In well-trained pigeons, there is negligible omission effect at short (<60 s) interfood intervals (Starr & Staddon, 1974). Yet the effect shown in Figure 7 should occur with any interfood interval. This dependence on absolute interfood-interval value is one reason that the omission effect has been interpreted as a sort of proactive memory interference (Staddon, 1974b). A short time after the omission stimulus (the argument goes), the not-so-memorable omission stimulus can still exert influence and control waiting time. But at longer intervals, the influence of the prior reinforcement overshadows the influence of the omission stimulus and, because time since reinforcement is necessarily longer than the interfood interval, responding begins too soon, producing the omission effect. (Note the resemblance between this interpretation of the omission effect and Jost's memory law: An older, initially weaker memory for the most recent reinforcer with time overtakes the newer, initially stronger memory for the omission stimulus.)

In terms of the MTS model, the proactive interference interpretation requires not one trace but two, one for reinforcements and one for omission stimuli. The two-trace assumption is not unreasonable, because the two events, food and a neutral stimulus, differ in at least two dimensions, not just one as in the reinforcement-magnitude effect. Granted that there are separate traces for N and R, the theoretical questions are: How will the traces differ? And, to which trace should the organism attend (i.e., which one will control behavior) or will both exert some influence? There are obviously several ways to answer the second question, but the simplest is just to take the traces at face value: As in the MTS interpretation of Jost's law (Staddon, 1997), let the higher trace be the controlling one.[5]

The first question, how should the traces differ, is trickier. It will not do to simply make the N trace weaker, because this will not capture the absolute time dependence of the omission effect. The assumption of a weaker N trace also permits the R trace to be higher than the N trace even immediately after the N stimulus under some conditions, which violates our intuition that even a feeble stimulus can be perfectly recalled right after its occurrence. The answer is that the N trace must be not weaker than the R trace, but less persistent. One way to implement this idea in

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[4] We note, however, that no experiment seems to have been done to see whether the reinforcement-magnitude effect is in fact independent of interfood interval. We assume that there is no effect, but we may be wrong, in which case the account in this section will need to be revised.

[5] This assumes that reinforcement and the omission stimulus are equally good predictors. A strong trace that is a poor predictor of reinforcement will presumably be less effective as a controlling stimulus than a weaker trace that is a good predictor.

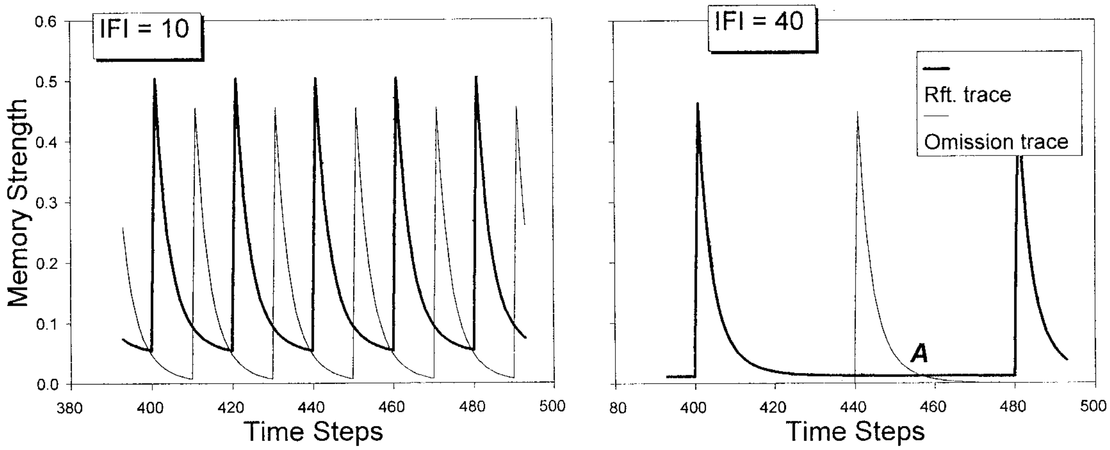

Fig. 8. Memory traces during reinforcement omission. Heavy solid line: trace following reinforcement (R). Light line: trace following omission stimulus (N). Left panel: 10 time-step interfood interval, with alternate reinforcements omitted. Note that the N trace is higher than the R trace throughout the post-N interval. Right panel: 40 time-step interval. Note that the R trace overtakes the N trace early in the interval (point A). Parameters: $b_i = 1 - a_i$; $a_1 = .7$, $a_2 = .85$, $a_3 = .999$. All thresholds were zero, except the threshold between the second and third integrator in the omission cascade, which equaled .75; the threshold affected only input to the integrator, and the memory-trace strength was computed the same way for both traces (Equation 18). Reinforcement and omission magnitude both equaled 1.

our scheme is shown in Figure 8, which shows the trace configuration for an alternating NRNR sequence at two interval durations, 10 and 40 time steps. Note that in the left panel, although the N trace is generally lower than the R trace, nevertheless in each post-N interval, the N trace is higher than the R trace throughout the interval. On the other hand, in the 40 time-step intervals, the two traces cross over early in the interval, that is, the N trace loses to the preceding R trace part way through each interval. Because the R trace after it crosses over is well below the value associated with reinforcement, responding begins too soon in post-N intervals, which is the omission effect.

In order to obtain the result in Figure 8, it was necessary only that the N and R processes differ in the threshold between the second and third integrators. In the example, θ_2 for the N process is greater than zero, which has the effect of limiting the input to the third, and slowest, integrator in the cascade, making the N trace intrinsically less persistent than the R trace.[6] This change makes little difference when the interfood interval is short, because the V value for the third integrator is small for both N and R traces, so that there is little difference between them, and no omission effect. But when the interfood interval is long, V_3 is substantial for the R trace but (because of the threshold) small for the N trace, yielding the omission effect.

Bisection and relative-duration discrimination. As we have seen, bisection at the geometric mean is consistent with log-like encoding of time and inconsistent with scalar timing (Gibbon, 1981), although a later version of SET, with some additional assumptions, is able to fit these data (Allan & Gibbon, 1991). But SET does not seem to have been applied to extensive data on relative-duration discrimination reported by Stubbs and his associates (e.g., Dreyfus et al., 1988; Stubbs et al., 1994). The main features of these data are consistent with a trace model that is not precisely logarithmic. The power function, with small exponent (which is a static approximation to the MTS model), provides the best static account.

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[6] It may seem odd to make threshold a function of the stimulus, but what this means in practice is just that a stimulus, such as N or R, cannot be adequately characterized by a single number. At least two are required, one corresponding to our stimulus strength variable, X, and the other to persistence of effect (“memorability,” if you like). The threshold vector is then a function of the memorability variable.

The usual procedure in these experiments is for pigeons to peck a center key to produce a red light of one duration that is followed immediately by a green light of another duration. When the green center-key light goes off, two yellow side keys light up. The animals receive food reinforcement for pecking the left side key if the red light was longer, and receive food for pecking the right side key if the green light was longer; this is a relatively simple task that pigeons master easily.

How does discrimination accuracy depend on both relative and absolute duration of the stimuli in these experiments? The main effects are that discriminability is directly related to the ratio of the two stimuli and is inversely related to the duration of the second stimulus. For example, average discriminability when the short and long stimuli are in 4:1 ratio is higher than when they are in 2:1 ratio. But if we look at 4:1 pairs when the 4 stimulus is first and the 1 stimulus second, versus the opposite order with 1 stimulus first followed by 4, accuracy is better in the case in which the 4 stimulus is first. As Stubbs et al. point out, the second finding is consistent with a memory account, because memory for the first stimulus will be weaker when the second stimulus is the longer of the two. The first finding, of course, follows from log-like temporal encoding.

These experiments show the importance of a plausible theory for settling on a principled (i.e., nonarbitrary) response rule. In the case of procedures like FI schedules or the peak procedure, the response rule is relatively straightforward: Respond at times when food is probable and not at other times. No comparison (other than between remembered and current time of reinforcement) is required. But in the Stubbs et al. (1994) studies, the animal must somehow compare encoded red and green time intervals and respond differentially depending on the outcome of the comparison. A formal analysis must first identify the type of comparison and then show how it is applied to reduce the comparison problem to a decision on a single decision axis (just like the threshold analysis in SET, where the decision axis is linear encoded time and a threshold makes the respond/not-respond decision).

In the MTS theory, the transformation of actual time, *t*, into encoded time, $f(t)$, is approximately logarithmic (only approximately, because we know that the Weber fraction increases slowly with absolute time rather than remaining constant, as pure logarithmic encoding requires). As we saw, both the power function (with small exponent) and the MTS model have this property (Figure 6). The power function

$$f(t) = kt^{w}, \quad w < 0, \tag{21}$$

where k is a constant and w is an exponent on the order of -0.1 was used by Stubbs et al. (1994) and Dreyfus et al. (1988; see also Staddon, 1984) to analyze their data, and we present a slightly expanded version of their account here. The response rule can be derived by asking: What simple transformation of trace values (of the onset and offset times of the red and green stimuli) at the time of choice best predicts reinforcement on this procedure? The answer, for log-like functions, is that the *difference* between traces provides a good estimate of relative stimulus duration.

Let T_R and T_G be the durations of the red and green stimuli on a given trial. The reinforcement contingencies are: If $T_R/T_G < 1$, reinforcement is contingent on Response A; if $T_R/T_G > 1$, reinforcement is contingent on Response B. To estimate T_R and T_G, the organism presumably has available traces corresponding to every discriminable change in stimulation. In this case, the relevant events are trial onset and the offset of the red stimulus (i.e., the time of the red-green transition). The values at time of choice of traces initiated by these events constitute the input to the decision process. Traces for two trial types in which $T_R + T_G$ = constant are illustrated in Figure 9. Trace A is the trace for trial onset; Traces B and B′ are for the time of the red-green transition: B is for the case in which the red stimulus is shorter and B′ is for the case in which it is the longer. C represents the time of choice (green stimulus offset).

At the time of choice (i.e., just after the green stimulus goes off), the value of the trial-onset trace is $f(T_R + T_G)$ and the value of the red-offset trace is $f(T_G)$, where f is the log-like time-encoding function. Perhaps the simplest theoretical assumption we can make is that the organism is able, in effect, to compute the difference between pairs of traces.

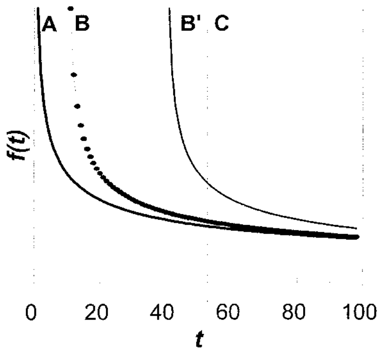

Fig. 9. Relative-duration discrimination. The graph shows hypothetical memory traces, $f(t)$, for three stimulus onsets. A is the time of onset of the red stimulus (Stubbs et al., 1994), which ends either at B or B′, depending on whether red is shorter than green or the reverse. In either case, the green stimulus ends at C. On each trial the subject must base his choice at time C on two trace values: the trace of trial onset, beginning at time A, and the trace of the red-green transition, whose trace begins at time B or B′, depending on whether green or red is longer.

This is done for the log and power functions for f (Equation 21) in Figure 10, which conveys the same information as the top panel of Figure 6 in Stubbs et al. (1994). Each curve is for a given base duration, from 2 to 24 s. Each base duration is compared with five comparison durations in ratios of 0.25, 0.5, 1, 2, and 4—approximately the range studied in the Stubbs et al. experiment. The vertical line at 1 on the abscissa divides pairs in which red is longer than green from those in which green is longer than red. The horizontal dashed line is a possible criterion: Above criterion make Response A, below make Response B.

The first thing to notice is that with pure log encoding (heavy line), performance is the same at a given red-green ratio, independent of the absolute time values. This is inconsistent with the pattern in the data, which shows differences between long and short absolute durations even if their ratio is the same (Stubbs et al., 1994, Figure 6). The pattern in the data is closer to what is predicted by the power form (light lines): At a given duration ratio, performance accuracy (the slope of the difference function) is always higher for shorter absolute durations. Second, for a reciprocal pair of red-green durations (equidistant from the 1:1 line on the log scale in the figure), such as 1:2 or 2:1, the distance to the criterion (i.e., accuracy) is always greater for the 2:1 pair than for the 1:2 pair: Accuracy is better when the shorter stimulus is second. Because it is also concave upward, like the MTS functions, this prediction is true for the log function also. Third, because the func-

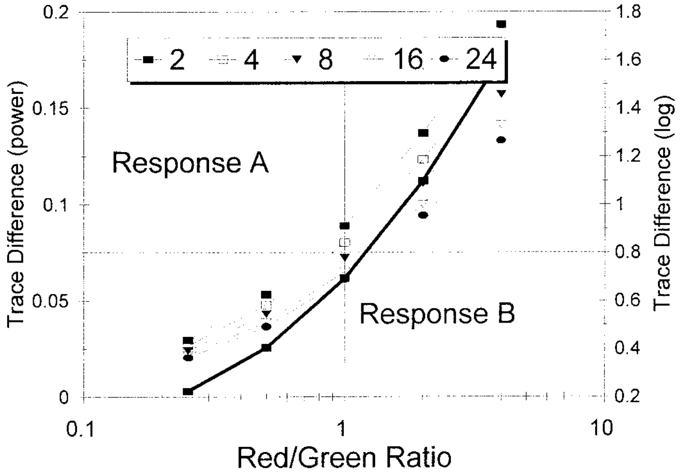

Fig. 10. Trace difference versus ratio of red-green durations in the Stubbs et al. (1994) experiment. Light lines: Prediction from a power-function trace. Trace difference was computed as $|f(t_{R+G}) - f(t_G)|$, where $f(t) = t^{.15}$, $f(t_{R+G})$ is the trace of trial onset, and $f(t_G)$ is the trace of the onset of the green stimulus (i.e., the second stimulus in the red-green sequence). Each curve is for the same set of red-green ratios but a different absolute value for the base duration, from 2 to 24 s. Heavy line: Prediction for the log function $f(t) = \ln t$. The absolute-duration functions collapse into a single function, because only duration ratio matters for the log trace. Note the logarithmic abscissa.

tions with longer base durations are lower, the theory predicts an increasing tendency to make Response B (''red shorter'') at longer absolute durations (when the red-green ratio is held constant), a shift in bias also seen in the data (Dreyfus et al., 1988; Stubbs et al., 1994). Finally, the smaller the red-green ratio (i.e., the longer the second stimulus in relation to the first), the less the effect of base duration; Stubbs et al. report good agreement with data on this point also.

The data of Stubbs et al. (1994) do contain one apparent anomaly: In a comparison of broad and restricted ranges of times, they report that performance on individual pairs in the restricted-range condition was worse than in the extended-range condition, a result incompatible with any analysis that treats each pair in isolation. They suggest that the longer trial duration under the restricted-range condition may be responsible. We have two comments. First, a dynamic MTS analysis may give predictions that deviate slightly from the static power-function approximation and so may explain the range effect, because any dynamic analysis will carry over some information from one comparison pair to the next. We are not yet ready to present such an analysis for this situation, because of uncertainty about the proper learning rule (see below). We have intentionally restricted discussion so far to situations that require only minimal assumptions about learning. Second, our explanation depends upon the assumption that subjects in this situation learn, in effect, to apply a differencing rule. The competing rule is an absolute one (Dreyfus, Fetterman, Stubbs, & Montello, 1992): to learn to link Responses A and B to specific green durations. Although Stubbs et al. found little evidence for control of behavior by absolute stimulus duration, it is still conceivable that learning the differencing rule is easier given a larger set of exemplars (i.e., in the extended-range condition). Again, without some formal model of the process by which the animal selects among response rules, this can only be a conjecture.

Our trace-difference analysis explains relative-duration discrimination by means of a single response criterion on a trace-difference decision axis. Notice that this process is *not* sufficient to discriminate among three alternatives, which is what is required in the temporal version of the ''intermediate-size problem'' (i.e., learning to make one of three responses depending on whether an intermediate duration appears first, second, or last in a sequence of three durations). Given three durations and three traces, a single criterion is sufficient to identify the longest or the shortest, but a second criterion is required to identify the intermediate duration. Fetterman (1998) has recently reported that pigeons can indeed identify the longest or the shortest in a series of three but fail to perform reliably above chance (or to show transfer to novel durations) in identifying the intermediate duration. Apparently pigeons are limited to a single criterion.

Overall, our analysis makes two important theoretical points: (a) The event trace is log-like, but two kinds of empirical data show that it deviates systematically from the log form: the gradual increase in the Weber fraction at long times, and the effect of absolute time on performance at the same red-green ratio in the Stubbs procedure. Both the power and MTS trace functions satisfy these conditions. (b) The response rule and memory-trace form are to a degree complementary. We think that differencing is a simpler assumption than the forming of ratios and is thus theoretically preferable. Nevertheless, a log trace with a differencing response rule gives similar results to linear time and a ratio response rule. The problem for SET is that deviations from Weber's law and absolute-time effects in relative-duration-discrimination data require systematic deviations from the log form, which are easily accommodated within the trace framework but not so easily within the linear-time framework of SET.

We are not sure how to apply SET to relative-duration experiments. Given that two times must be compared, must SET assume two separate accumulators? Presumably the values of the red and green accumulators must then be compared with two reference-memory values. What response rule would be appropriate? Because encoding is linear, a differencing response rule could satisfy the reinforcement contingencies. There is an experimental test of the view that performance in the Stubbs procedure is driven by computation of differences between linearly encoded times, because such a model gives no special status to zero difference. In other words, differencing animals should be able to learn easily to discriminate between two randomly chosen times, *x* and *y*, that differ by a fixed amount *z* versus two randomly chosen times that differ by 0 or 2*z*. But because this discrimination cannot be done by any simple operation on log-like traces, our theory must predict that pigeons should fail at it. Conversely, animals should have no difficulty discriminating on the basis of duration ratios (e.g., discriminating between randomly chosen times in fixed ratio, $x/y = k$, vs. ratios of $0.5k$ and $2k$). The first experiment does not appear to have been done, but Fetterman, Dreyfus, and Stubbs (1989) have done a ratio-discrimination experiment. They have shown that pigeons can learn to make one response if two successive durations are in a ratio greater than 2:1 and a different response if the ratio is less than 2:1, for example. Moreover, the pigeons showed much the same accuracy at a range of different criterion ratios, a result that is perfectly compatible with our single-criterion log-like trace model.

Absolute duration discrimination and the "choose-short" effect. There is an interesting asymmetry in time discrimination that provides very strong support for a decaying-trace model. In a version of the delayed matching-to-sample procedure, pigeons and rats can readily learn to make one response following a short (e.g., 2-s) stimulus and another response following a long (e.g., 8-s) stimulus, even if the opportunity to respond is delayed slightly after stimulus offset (e.g., Church, 1980; Spetch, 1987; Spetch & Wilkie, 1982). But if longer choice delays are occasionally introduced, performance worsens dramatically and in a biased way: The frequency of "short" errors increases with delay. This is known as the *choose-short effect* (Grant, Spetch, & Kelly, 1997; Spetch & Wilkie, 1982). As Stubbs et al. (1994) point out, this result is almost trivially explained by our theory. In delayed match-to-sample duration-discrimination experiments, the only reliable correlate of stimulus duration is the difference in strength (at the time of the response) between the trace of stimulus offset and the trace of trial onset. Formally, $\delta_S = f(D) - f(T_S + D)$ for the short stimulus and $\delta_L = f(D) - f(T_L + D)$ for the long, where T_S and T_L are the stimulus durations and D is the choice delay. With the power form for f, this difference, δ, will obviously always be larger for the long stimulus than for the short, $\delta_L > \delta_S$. But if D is suddenly increased, δ_L will decrease much more than δ_S and will move in the direction of δ_S*, the reinforced value of δ_S (i.e., the situation will seem more similar to the situation in which a short response is appropriate). The argument is illustrated graphically in Figure 11.

This analysis predicts the opposite effect if D is *decreased*, however, because reducing D shifts δ_S in the direction of δ_L*, the reinforced value of δ_L. To see this, imagine that $D2$ (rather than $D1$) in Figure 11 is the training delay and $D1$ is the testing value. In an experiment with $T_S = 2$ s, $T_L = 8$ s, and $D = 10$ s, Spetch (1987) has shown that pigeons perform accurately at the training delay, show a short bias when occasional longer delays are introduced, but show choose-long errors when *shorter* delays are introduced. The symmetry between the choose-short and choose-long effects strongly supports our trace analysis. Note that this analysis implies that pigeons trained with two values for D in a situation will perform worse on trials with the longer D value than they would if trained with that value alone, because there is no longer a unique reinforced trace value for the short and long samples. (In designing such an experiment, care will need to be taken to ensure that the animals cannot use prospective encoding; cf. Grant et al., 1997.)[7]

The symmetry between timing and counting. There are close resemblances between the discrimination of time and number. SET explains timing as a sort of counting (of pacemaker pulses), which implies obvious similarities between the two and appears to support

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[7] Spetch and Rusak (1992) and Sherburne, Zentall, and Kaiser (in press) have found that the choose-short effect is abolished if the intertrial-interval stimulus and the stimulus during the retention interval are different. At least two explanations—"confusion" (Sherburne et al.) and the "relative-duration hypothesis" (Spetch & Rusak)—have been offered for this effect. But only our trace account, as far as we know, can account for both the choose-short and choose-long effects and the symmetrical choose-small effect in number discrimination (no one seems to have yet demonstrated a choose-large effect). We conjecture that the differential-stimuli effect may reflect stimulus-specific prospective encoding (i.e., remembering the correct response rather than the experienced duration), which is possible when intertrial-interval and retention-interval stimuli are different but not when they are the same.

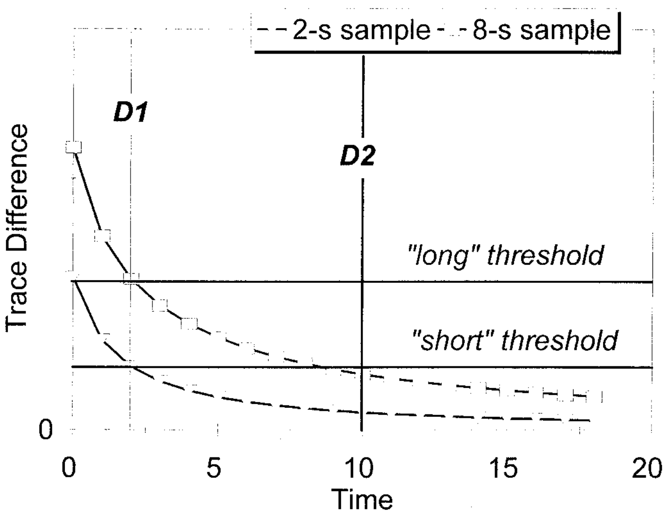

Fig. 11. The choose-short effect. The curves show the difference between the power-form traces of stimulus offset and trial onset for a short (2-s) and a long (8-s) stimulus. Vertical line *D*1 is the usual delay before a response is made, and the two threshold lines, labeled long threshold and short threshold, are learned appropriate to *D*1. A simple response rule is: Respond long if the trace value is closer to the long threshold, respond short if it is closer to the short threshold. If a long delay, *D*2, is occasionally introduced, the trace value for the long stimulus is now in the vicinity of the short threshold, so the subject will respond short to the long stimulus. The trace for the short stimulus has moved below the short threshold, but is still closer to the short than to the long threshold, so short will be the response here also.

the pacemaker-accumulator approach. Meck, Church, and Gibbon (1985) proposed that the same process might underlie both types of discrimination—an extension of SET that, in its most recent version, allows a single accumulator to count both pacemaker pulses and events. The input to the accumulator is controlled by what Meck terms a "mode switch" that "gates the pulses to the accumulator in one of three different modes depending on the nature of the stimulus, giving this mechanism the ability to act as both a counter and a timer based on the representation of the variable in the accumulator" (Meck, 1997, pp. 141–142). The three modes are "run," "stop," and "event." "Run" accumulates pulses from stimulus onset until its end; "stop" accumulates pulses as long as a stimulus is present (i.e., it accumulates across successive stimulus occurrences); and "event" counts events. By suitably combining these modes, the mode-control version of SET can model the many similar psychophysical properties of time and number discrimination.

W. Roberts (1997) applied an earlier, "dual-mode" version of the Meck et al. (1985) mode-control model, with two accumulators, one for time and one for number, and two independent switches, to experiments on number discrimination. This model can count pacemaker pulses (time), events (number), or both (or, presumably, neither), depending on the switch settings. Roberts gives a good summary of the workings of this system:

> In order to store the time or number of events recorded in an accumulator, numbers of pulses are sent from the accumulators to . . . working memory; values stored in working memory at the time of reward are transmitted to the reference memory for long-term storage. Finally, response decisions are made in a comparator. The comparator is fed information from both working and reference memory. From the working memory, it continuously receives a record of the number of pulses stored in the accumulators. From reference memory, it retrieves criterion quantities of pulses for comparison with . . . working memory. Comparison is based on a ratio of the absolute difference between the criterion value from reference memory (RM) and the current value in working memory (WM) divided by the RM value. (W. Roberts, 1997, p. 192)

When the ratio of $|\mathrm{RM} - \mathrm{WM}|/\mathrm{RM}$ crosses a

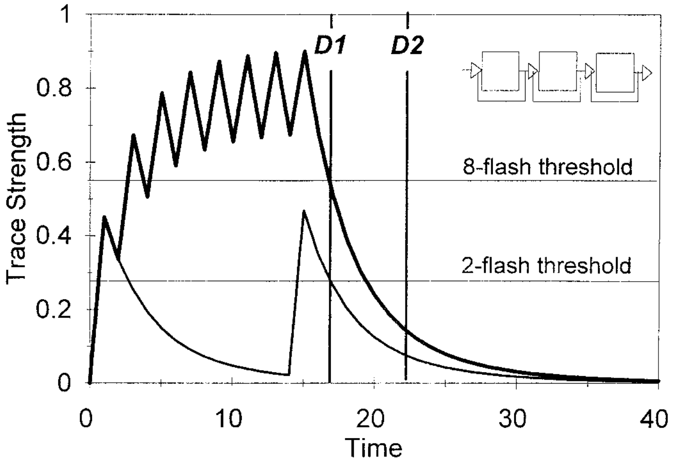

Fig. 12. The choose-small effect, simulated by a three-unit habituation model (inset). Animals are trained at short response delay *D*1 and set their response criteria accordingly (two- and eight-flash thresholds). When tested at a longer delay, *D*2, trace strength following the eight-flash stimulus shifts in the direction of the criterion for the two-flash stimulus, producing a choose-small bias.

threshold, responding is triggered, as already described.

W. Roberts (1997) uses an augmented version of dual-mode SET to account for the number-discrimination equivalent to the choose-short effect in time discrimination (Fetterman & MacEwen, 1989). He trained pigeons to make one response following a series of eight flashes and another after two flashes, both series occurring over a 4-s period to eliminate time as a cue. After training, the opportunity to respond was delayed for 2, 5, or 10 s, with dramatic results: Responses to the two-flash stimulus remained high, but responses to the eight-flash stimulus rapidly declined with increasing delay, a choose-small effect. Roberts explains this effect by adding a "loss" assumption to the dual-mode model: the idea that working memory loses pulses over time. (His assumption of a fixed-fractional loss per unit time [p. 199] amounts in fact to exponential decay.) Roberts goes on to make the argument that as time elapses, the number of pulses in the accumulator after the eight-flash stimulus will approach the criterion for the two-flash stimulus, hence the increase in small responses as the response opportunity is increasingly delayed. He concludes that the data "support the ideas that time and number are represented by the common mechanism of accumulated pulses and that pulses are progressively lost from both time and number accumulators over a retention interval" (pp. 200–201).

What these data in fact support is simply the idea of memory-trace decay. Nothing in the choose-small effect demands pulses or dual accumulators. Because the MTS model is driven by events and its output accumulates their decaying effects, the MTS model automatically explains the resemblances between time and number discrimination. It explains the choose-small effect directly, without any additional assumptions and with none of the elaborate apparatus postulated by the mode-control versions of SET. The argument is trivial. Each flash is an input event and increments the integrator cascade. Two flashes in 4 s produce a lower output (trace value) than eight flashes in 4 s. If the criteria for choice are set for a short response delay, then at longer delays, the trace value following eight flashes will approach the two-flash criterion; hence, responding will increasingly be to the 2-s key: the choose-small effect. The MTS account is illustrated in Figure 12.

Because it is real time, the MTS account makes specific predictions about the effects on choice of the temporal pattern of flashes within the counting period. We do not know how well these predictions will match the data, because the necessary experiments remain to be done. But it is already clear that known similarities between timing and count-

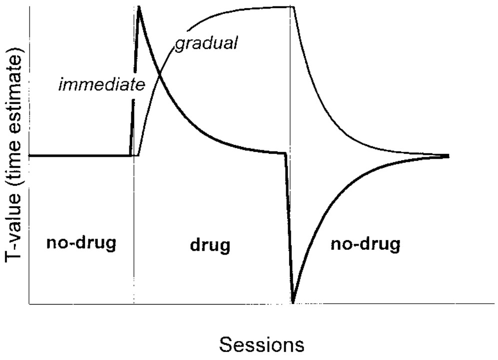

Fig. 13. Immediate-transient (heavy line) and gradual-persistent (light line) effects of dopaminergic and cholinergic drugs, according to Meck (1996). Only effects to increase *T* are shown; there are also effects of both kinds that decrease *T*.

ing, such as Weber law variance and the choose-small effect, are immediately implied.

Drug effects. Dopaminergic and cholinergic drugs can affect timing behavior. Meck (1983, 1996) has identified two main kinds of effect on a temporal dependent variable (call it *T*) such as peak time in the peak procedure: *T* can either increase or decrease under the influence of the drug, and these effects can be either immediate (*T* increases or decreases soon after the drug is administered, with an inverse rebound when drug administration ceases) and transient (*T* returns to the predrug level under continued administration, and following the rebound when administration ceases); or gradual (the change in *T* occurs over several days), in which case it usually persists until the drug is no longer administered, when *T* slowly returns to the predrug level. Interestingly, there seem to be no examples of the other two logical possibilities: immediate, persistent effects or gradual effects that eventually dissipate. Two of these effects—immediate-transient increase in *T* and gradual-persistent increase in *T*—are shown schematically in Figure 13 (see Meck, 1996, Figures 4 and 5 for comparable data showing decreases as well as increases).

The immediate-transient change is usually termed a clock-type effect in SET. It is attributed to a change in "clock speed." If the clock runs faster under the drug than previously, the animal's estimate of reinforcer time will be reached too soon: *T*, the temporal dependent variable, will therefore decrease. Dopaminergic agonists such as methamphetamine have this speeding-up effect. Conversely, dopaminergic antagonists such as haloperidol have the opposite effect: Clock speed is decreased so that *T* increases (Figure 13, heavy line).

The gradual-persistent effect is usually termed a reference-memory-type change in SET. The interpretation here is that "memory-storage speed" is altered by the drug. There is no immediate change in performance "because the vast majority of time values stored in reference memory were accumulated during baseline training under conditions of normal memory-storage speed, not one distorted by drug administration" (Meck, 1996, p. 237). As the distorted memories accumulate during training under the drug, *T* shifts appropriately. The cholinergic antagonist physostigmine produces a slow decrease in *T*, whereas the agonist atropine produces a slow increase in *T* (Figure 13, light line).

Our theory provides alternative interpretations for these effects. The immediate-transient change resembles the reinforcement-magnitude effects discussed earlier. Reducing reinforcement magnitude, for example, produces a transient decrease in *T*; increasing reinforcement magnitude produces a transient increase. Thus, one alternative interpretation of so-called clock-speed effects is that they cause an immediate change in the memorability of the time marker. Tests of drugs that produce these effects with a variety of different time markers may therefore produce quantitatively different effects on *T*: A given drug and dose may produce a large effect with a not-very-salient time marker like a neutral timeout and a much smaller effect with a highly salient time marker like a large reinforcer. It is also possible that immediate-transient changes reflect changes in the time constants of the integrator chain. This interpretation is close to the SET clock-speed-change interpretation of these effects. In this case, differences between different time markers should be minimal. Quantitative experimental data, showing the effects of different dopaminergic drugs at different *T* values, could help decide this issue.

Another prediction is that other drugs known to affect short-term memory (e.g., in delayed match-to-sample experiments) should also produce immediate-transient effects on time discrimination.

The gradual-persistent effect is much the same as if the to-be-timed interval were to be changed. The change in T here is also usually (but see Higa & Staddon, 1997) gradual, but persists as long as the new interval is maintained. In the MTS model a gradual-persistent effect would be interpreted as a change in the remembered value of V_M*, V_M'*, the trace value associated with reinforcement. Under normal conditions, V_M'* is approximately equal to V_M*, which is why the relation between T and the actual to-be-timed interval is usually a power function with unit slope, that is, linear (see the discussion of power functions and log time, above). If long-term memory is imperfect, however, the two values may drift apart, so that at the time of testing, the animal may show a too-long or too-short value of T, depending on the direction of drift. This interpretation suggests that the amount of "memory shift" under a given drug regimen may depend on the time between experimental sessions (i.e., the time allowed for drift). If sessions are closely spaced there may be less drift than if they are 24 or 48 hr apart. It will also be interesting to look at the power-function exponent when steady-state T values under drug and no-drug conditions are compared.

Drug versus no-drug performance on cyclic interval schedules, in which interfood interval N depends on the duration of preceding interfood interval $N - 1$ (Higa & Staddon, 1997; Innis & Staddon, 1971), might also shed light on these two hypotheses. On periodic schedules, according to SET, reference memory contains many values of the time of reinforcement, t*, which is why cholinergic drugs, which distort the translation from working to reference memory, take some time to have an effect on temporal performance (gradual-persistent effects), "because the vast majority of time values stored in reference memory were accumulated during baseline training under conditions of normal memory-storage speed, not one distorted by drug administration" (Meck, 1996, p. 237). On cyclic schedules, however, performance is strongly determined by the preceding interfood interval, which implies that reference memory under these conditions contains few t* values. Consequently, if we read SET correctly, on cyclic schedules cholinergic drugs should have their effect within a few intervals, rather than taking several sessions. MTS theory seems to make a similar prediction, albeit from different premises. If we interpret gradual-persistent effects as drift in V_M'*, then the time for drift on cyclic schedules is much less than on regular FI schedules; hence, the effect of the drug should be less.

There are probably other interpretations within both frameworks. Our point here is simply that there seems to be nothing in these drug data that uniquely favors the SET interpretation.

Brain mechanisms. We believe that behavioral theories stand on their own feet. They are valid to the extent that they describe behavioral data accurately and economically. We argued earlier that given the richness of physiology, the notion of "biological plausibility" is a slippery one. Is a counter and pacemaker more or less plausible than a leaky integrator? Is a system made up of artificial neurons more "physiological" than one composed of thresholds and capacitors? Questions like these seem destined to be inconclusive. All that really matters in science, we suspect, is how much can be explained with how little (Staddon & Zanutto, 1998). Nevertheless, the pacemaker-accumulator assumptions of SET have inspired a vigorous, and to some degree successful (Gibbon et al., 1997; Meck, 1996), search for underlying physiological mechanisms. It is worth mentioning, therefore, some recent real-time physiological data that seem to fit remarkably closely the basic assumptions of MTS theory.

MTS timing theory is based on five ideas, one about timing and four about habituation: (a) temporal learning uses short-term memory traces as discriminative stimuli; (b) the properties of short-term memory can be understood through the mechanisms of habituation; (c) habituation is a process in which responding is inhibited by a leaky integrator system driven by stimulus input; (d) habituation units are cascaded; and (e) the faster units are on the periphery and the slower ones are further downstream. In a recent report, Glanz (1998) describes a study reported to the American Physical Society by Williamson and his colleagues that has identified physiological counterparts for the last three assumptions. Williamson's group used a superconducting quantum interference device (SQUID) to detect tiny changes in human brain magnetic activity. Their system recorded maps of whole-brain activity that could be updated every few milliseconds. In the simplest experiment, they looked at brain activity following a single 0.1-s stimulus: ''In quick succession, over less than half a second, about a dozen patches lighted up like pinball bumpers, starting with the primary visual cortex in the occipital lobe at the back of the brain'' (p. 37). This activation in rapid succession is precisely what we would expect from a series of cascaded units, where the SQUID is detecting changes in V_i, the activation of each integrator. In a second experiment that was in effect a two-trial habituation study with brain activity as the reflex response, subjects were presented twice with a brief (0.1-s) checkerboard stimulus.

> They showed the checkerboard twice, with a varying time interval between the displays, to see whether the first stimulus had left any kind of impression along the way. For very brief intervals—10ths of a second—only the areas of initial processing in the back of the brain fired on the second flash, while the others were silent. . . . But as the interval was increased to 10, 20, or even 30 seconds, the downstream areas began firing on the second flash, with a strength finally approaching that of the initial pop. . . . The data imply, says Williamson, that each site has a distinct ''forgetting time,'' ranging from 10ths of a second in the primary visual cortex—the first stage of raw processing—to as long as 30 seconds farther downstream. (p. 37)

Again, this is precisely the behavior of our cascade of habituation units. Because the initial units have fast time constants, they block input to the later, slower units as long as the interstimulus interval is short enough that they have not had time to discharge (''forget'') between stimuli; hence, no response of the ''downstream'' units to the second flash at a short interstimulus interval. But when the interstimulus interval is long, the initial units have already discharged, allowing the stimulus to pass through to later units, which can therefore respond. Williamson continues, ''The memories decayed with the simplicity of a capacitor discharging electricity—exponentially with time—and the later an area's place in the processing queue, the longer its memory time was'' (p. 37). Apparently brain ''memories,'' like our leaky integrators, forget exponentially.

Whether other studies will provide additional physiological counterparts for the MTS theory remains to be seen. But we do believe that the jury is still out on whether pacemaker-accumulator theories or the MTS theory have the stronger claim to biological plausibility.

CONCLUSION

The ability to discriminate between stimuli of different durations and to respond differentially at times associated with the presence or absence of reinforcement is widespread in the animal kingdom. The clock-like properties of this behavior, which can be much improved with suitable training, has made the inference of a real ''internal clock'' almost irresistible. There are many kinds of clock, but the best ones operate by counting regular (or even irregular) pulses. Unfortunately, the very power of pacemaker-accumulator clocks is the main argument against them as models for temporal discrimination. The property that the longer the interval (and the larger the number of accumulated counts), the more accurate pacemaker-accumulator clocks become, is quite different from the most reliable feature of animal timing, which is that relative accuracy is essentially constant over a limited range of times, and actually declines over longer ranges. The Weber law property can be reconciled with Poisson variability in the pacemaker only by additional assumptions—that rate variation occurs only between and not within trials—or by assuming such a fast pacemaker that other, ''scalar'' sources of variance make the major contribution and the pacemaker-accumulator feature becomes irrelevant. In either case, the real theoretical work is being done by something other than the pacemaker-accumulator mechanism, because of its fundamental incompatibility with Weber's law.

What is left in scalar expectancy theory, once the pacemaker-accumulator property has been sidelined, is the assumption that time is encoded linearly, with scalar variance. But as we have seen, the experiments that appear to argue for linear (rather than log-like) encoding of time are open to alternative interpretations and cannot prove their point. Moreover, there are several lines of argument that favor log-like encoding: bisection data, a theoretical argument that derives power-function empirical relations from log-like encoding of working and reference memory, and data on absolute and relative temporal discrimination. The choose-short effect provides very strong evidence for a trace interpretation of time discrimination and is incompatible with pacemaker-accumulator-type models, absent auxiliary assumptions. Other data that appear to support SET—start and stop distributions and start-stop and start-spread correlations in the peak procedure, for example—only partially confirm the simple version of SET, can only be partially accommodated via extra assumptions (thresholds, variation in reference memory), but can also be explained in other ways. Drug effects compatible with SET are also compatible with the MTS approach, and both approaches seem to make some sense physiologically.

What remains by way of direct support for the pacemaker-accumulator account are the many very precise quantitative matches between empirical distributions of peak times and related measures and predictions from versions of SET (e.g., Church & Gibbon, 1982). The most striking fact about these distributions (e.g., in peak-procedure experiments) is that they are more or less symmetrical, rather than skewed, as would be expected if the response distribution were directly derived from normal variation on a log-like internal code. We have not discussed these distributions in detail in this article for two reasons, one general, the other specific. The specific reason is suggested by Platt's (1979) comment quoted earlier: ''How can the relationship between [a] stimulus and its internal representation be inferred from responding which may be the result of additional transformations required by the reinforcement contingencies?'' (p. 21). That is, granted we know that the distribution of responses in time in procedures like the peak procedure can be molded by varying the probability of reinforcement and nonreinforcement at different times, how can we settle on a particular distribution as *the* correct one? The problem can perhaps be clarified comparing some experimental results. An FI schedule requires the specification of a single parameter, the interval duration, but the peak procedure requires us to specify more than four parameters: the to-be-timed interval duration, the duration and probability of ''empty'' trials, and the duration of the intertrial interval. The additional parameters specify the distribution of the intertrial interval if it is variable. Now consider the peak procedure with zero intertrial interval and very rare empty intervals. This is the same thing as FI with occasional reinforcement omission. We know that the postfood distribution of responses will be highly asymmetrical: an ogival (on average) increase in responding that remains flat and high for a time at least equal to twice the FI (cf. Kello & Staddon, 1974). As an intermediate case, consider what will happen if we increase the intertrial interval until it is roughly equal to the to-be-timed interval and increase the frequency of empty trials. Now the distribution of responding becomes bimodal but still asymmetrical, and is best modeled by a slightly skewed Gaussian plus a linear ramp through the origin (Cheng & Westwood, 1993). Finally, let us further increase both the duration and frequency of empty intervals. Now the distribution of responding looks almost Gaussian, with perhaps a small additive constant (e.g., Church et al., 1994). The question is, which of these three distributions represents the ''real'' psychological scale? Our answer is that there may be no ''real'' distribution, only a learning process that operates under the environmental constraints provided by the reinforcement schedule. Church et al. (1991), on the other hand, in their exploration of procedural variables, have no doubt that the ''real'' distribution is symmetrical: ''It is readily shown that, if only one [Gaussian source of variance] is operating, the result is symmetry in the function'' (p. 213). They therefore rephrase Platt's question as, what are the sources of variance that distort the underlying symmetric distribution? Deviations from symmetry are attributed to ''anticipation'' of the next trial or ''checking'' responses, but because these suggestions are not given the same kind of formal expression as the SET assumptions, we cannot be sure that they work as intended. A more principled theoretical answer to the question of how contingencies affect timing behavior might be a version of SET that relates the various theoretical parameters to the four or more parameters that define the peak procedure, but this does not seem to have been attempted.

The general reason for deferring discussion of distribution form is that Gaussian-type distributions commonly appear whenever repetitive observations are averaged or when dealing with a multistage process. Both these conditions are fulfilled by temporal discrimination experiments. The usual data in SET-type experiments are averages across hundreds of trials and often from 10 or more animals. The preferred measure for demonstrating symmetrical timing functions is peak time (i.e., the peak of the response rate vs. time distribution—the average of the wait-run-stop pattern generated on each empty trial), which is demonstrably more symmetrical than the distributions of start and stop times that underlie it (cf. Brunner et al., 1997, Figure 2).

Timing itself involves at least three stages—encoding of real time, ''storage'' (which may be gradual or, as SET proposes, rapid) and some kind of ''retrieval''—so that the preference distributions in a bisection experiment, for example, reflect output as well as input transformations and whatever process of transformation exists between them. Granted that variability affects each of these stages, nonlinear effects in each stage are likely to be washed out in the aggregate, leading to approximately symmetric output distributions. Consequently, we believe that the existence of symmetrical Gaussian distributions constitutes only weak evidence for the fundamental linearity of the underlying processes.

Proving this claim in detail is likely to be a lengthy process whose validity necessarily depends on the validity of our model for the entire process of temporal discrimination: time encoding, long-term memory, response rule, and all the transformations in between. We do not yet have such a comprehensive model. We defer discussion to another occasion for this reason, but also because we believe there are more powerful ways to test behavioral theories than through precise quantitative correspondence between parameter-rich predictions and highly averaged data. It is a better strategy, we argue, to look first at individual animals and data from a wide range of timing situations, and begin with qualitative (rather than quantitative) predictions from a theory that uses as few a priori theoretical concepts as possible. Detailed quantitative predictions may be appropriate once a qualitative match between theory and a broad range of data gives us confidence that the major assumptions are correct. We are not yet at that stage, particularly as far as assumptions about learning (associative) mechanisms are concerned. Consequently, even though our ultimate objective is to come up with a fully dynamic, real-time theory, our focus in the second part of the paper has been on static phenomena and effects that can be explained without commitment to any but the most general learning principle.

We have shown in the second part that a MTS memory model, derived from ubiquitous data on rate-sensitive habituation, can account for the major features of data from a wide variety of time-related experiments: proportional and Weber law temporal discrimination, transient as well as persistent effects of reinforcement omission and reinforcement magnitude, bisection, the discrimination of relative as well as absolute duration, and the choose-short effect and its analogue in counting experiments. The many resemblances between timing and counting are an automatic consequence of the MTS model. Absolute-duration effects in experiments on the discrimination of relative duration show that the static form of trace left by a time marker is better approximated by a power function than a log function. Either function, as well as the dynamic MTS function, is consistent with data from human and animal memory experiments. In almost every case, the MTS model suggests new experimental tests. We also argue that many of the interesting transient and persistent effects of drugs on time estimates can be as well interpreted within our scheme as in SET, and the comparison also suggests novel experiments. The key feature of both accounts for the interpretation of these drug effects seems to be the separation between working and reference memory—the pacemaker-accumulator features of SET are unnecessary and even misleading. Moreover, the role of memory as a timer in the MTS account immediately suggests direct links between time discrimination effects and mnemonic effects of drugs.

The major uncertainties in the MTS approach have to do with learning and long-term (associative) memory. How are trace values ''learned''? When, and how, are trace values ''stored'' and ''retrieved''? Indeed, are these metaphors even appropriate? Only when the learning issue is settled can we begin to apply the theory to experiments that deal with expectations—choice between delayed reinforcers, the time-left procedure, and so forth—and with true dynamic effects, such as the rapid effects recently reported in the timing literature (e.g., Lejeune et al., 1997; Wynne & Staddon, 1988) as well as older data on cyclic temporal schedules (e.g., Staddon, 1969; Staddon & Higa, 1991), orderly facts that are still not understood and are widely ignored by SET and most other contemporary theories of timing.

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Received December 8, 1997
Final acceptance August 27, 1998