

THEORETICAL AND REVIEW ARTICLES

A modular theory of learning and performance

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We describe a theory to account for the acquisition and extinction of response rate (conditioning) and pattern (timing). This modular theory is a development of packet theory (Kirkpatrick, 2002; Kirkpatrick & Church, 2003) that adds a distinction between pattern and strength memories, as well as contributing closed-form equations. We describe the theory using equations related to a flow diagram and illustrate it by an application to an experiment with repeated acquisitions and extinctions of a multiple-cued-interval procedure using rats. The parameter estimates for the theory were based on a calibration sample from the data, and the predictions for different measures of performance on a validation sample from the same data (cross-validation). The theory's predictions were similar to predictions based on the reliability of the behavior.

A great deal is known about the determinants of the behavior of rats and pigeons in Skinner boxes. The procedures developed and described by Skinner (1938) have been effectively used for research on many psychological processes, including perception (Blough, 1956), conditioning (Rescorla & Wagner, 1972), timing (Gibbon, 1977), and choice (Herrnstein, 1974). One purpose of that research has been to describe and organize the determinants of behavior. The research has identified a large number of replicable results, so that, under many procedures, it is possible to predict the behavior of an animal (Ferster & Skinner, 1957). The research has also led to general principles—for example, the scalar timing principles (Gibbon, 1977) and the matching law (Davison & McCarthy, 1987)—that permit prediction of behavior under a wide range of conditions.

Early attempts to develop a general process model of animal learning and performance (e.g., Hull, 1943) were regarded as premature, primarily because of insufficient data on which to base such a model. Before extensive data became available, a more productive path was to develop separate models for different psychological processes, such as perception, conditioning, timing, and choice. For example, theories of conditioning were developed in order to account for response strength as a function of the amount of training, and theories of timing were developed for response rate as a function of time since onset of a time marker. The Rescorla–Wagner model is one heavily cited model of conditioning (Rescorla & Wagner, 1972); on September 26, 2006, a search of PsychINFO generated 188 citations including the words *Rescorla*, *Wagner*, and *model*. Likewise, scalar timing theory is a heavily cited

model of timing (Gibbon, 1977); on the same day, a search of PsycINFO generated 117 citations for *scalar timing theory* or *scalar expectancy theory*.

The Rescorla–Wagner model was developed to account for the results of experiments on acquisition and extinction of classical conditioning, especially those involving multiple stimuli. The model has been stable, so that the original equation and assumptions are still being used (Rescorla & Wagner, 1972, pp. 75–77):

$$\Delta V_i = \alpha_i \beta_j (\lambda_j - V), \quad 0 \leq \alpha_i \leq 1 \text{ and } 0 \leq \beta_j \leq 1,$$

where the change in the associative strength of stimulus i (ΔV_i) is proportional to the product of the learning rate of the stimulus (α_i), the strength of reinforcer j (β_j), and the difference between the asymptotic associative strength of the reinforcer (λ_j) and the sum of the strength of all stimuli present (V). The assumption is that the magnitude or probability of conditioned responding is ordinally related to V . This was developed only as a model of conditioning; it does not account for timing.

Scalar timing theory was developed to account for the result of experiments in which behavior is a function of the time between stimuli, responses, and reinforcers (Gibbon, 1977). The theory initially referred to the basic principles of scalar timing—that is, the proportional relationship between the mean time of response and physical time, the linear relationship between the standard deviation of the time of response and physical time, the constant coefficient of variation (Weber's law), and the superposition of behavioral functions at different times. Later on it referred to a process model that included modules for temporal perception, memory, and decision processes

(Gibbon, Church, & Meck, 1984). However, scalar timing theory was developed as a model of timing, and so does not account for the acquisition and extinction of response strength.

In an attempt to account for both the timing and conditioning produced by many procedures, both the Rescorla–Wagner model and scalar timing theory have been expanded. Real-time learning models were developed as extensions of the Rescorla–Wagner model to account for timing as well as conditioning (Sutton & Barto, 1981), and rate expectancy theory was combined with scalar timing theory to account for conditioning as well as timing (Gallistel & Gibbon, 2000). The learning-to-time model (Machado, 1997) and packet theory (Kirkpatrick, 2002; Kirkpatrick & Church, 2003) have provided integrated approaches to account for both timing and conditioning.

An Overview of Packet Theory

This article will describe and evaluate a modified version of packet theory. This is a modular theory of learning and performance that contains parts that may be labeled *perception*, *memory*, and *decision*. The theory combines ideas from scalar timing theory (Gibbon et al., 1984), the learning-to-time model (Machado, 1997), conditioning theories (Bush & Mosteller, 1955; Rescorla & Wagner, 1972), as well as from several additional sources. Like scalar timing theory, it considers a clock as an accumulation process and uses a threshold for comparison of clock and memory. Like the learning-to-time model, it considers perception and memory as vectors. Like conditioning theories, it uses combinations of values with a linear operator rule.

Packet theory is not unique in being a modular theory: Many theories of conditioning and timing may be regarded as modular (Church & Kirkpatrick, 2001). This feature, however, may be the most important one for the development of theoretical improvements. The name *packet theory* derives from a focus on the decision module, which provides the basis for bouts of responses. Thus, with this theory, it is possible to compare the output of the theory with the primary behavioral data (i.e., precise times of occurrence of individual responses). The perception and memory modules, however, are just as important as the decision module, so it may be more balanced to consider ours a “modular model,” rather than a revised version of packet theory.

Packet theory has been previously simulated to account for data from random-interval, fixed-interval, and tandem random-plus-fixed-interval procedures (Kirkpatrick, 2002; Kirkpatrick & Church, 2003). In these previous experiments, differences in the reinforcement rate produced changes in the overall response rate, and differences in the reinforcement distribution produced changes in the response pattern. Packet theory has also been simulated to account for the data from procedures in which more than one cue (time marker) is used to signal availability of the reinforcer (Guilhardi, Keen, MacInnis, & Church, 2005). In these procedures, changes in the rate of responding (e.g., an abrupt reduction in response rate followed by a slow increase in response rate) and in the overall slope of

the response rate gradient following the occurrence of an additional time marker have suggested that rats time multiple intervals simultaneously (Church, Guilhardi, Keen, MacInnis, & Kirkpatrick, 2003; Leak & Gibbon, 1995; Meck & Church, 1984). The addition of rules that describe how rats combined different temporal cues increased the generality of the predictions of the model. In addition to asymptotic performance, packet theory was also simulated with a single set of parameters to account for many different patterns described by different functional forms of different dependent measures of the dynamics of temporal discrimination (Guilhardi & Church, 2005). In some cases, the predictions of the theory were evaluated via a qualitative comparison of the predictions to the data (Kirkpatrick, 2002; Kirkpatrick & Church, 2003). In other cases, the theory predictions were superposed onto the data and a quantitative index of goodness of fit, such as the variance accounted for, was reported (Guilhardi & Church, 2005; Guilhardi et al., 2005). The modularity of the theory facilitates the evaluation and extensions of the models to different procedures.

This article is an extension of packet theory based on earlier versions of that theory. It adds a distinction between pattern and strength memory—that is, the use of separate memory structures sensitive to both the times of reinforcers relative to time markers (“pattern memory”) and the rate of reinforcement (“strength memory”). It also includes the use of an operant baseline rate and specifications of the characteristics of a packet of responses, which makes it possible to make predictions of the time of responses. This new model extends packet theory by (1) applying it in order to account for the dynamics of the pattern and rate during extinction for fixed-interval procedures and (2) providing closed-form equations of packet theory for fixed-interval procedures.

A Description of Packet Theory

Figure 1 is a flow diagram of packet theory. It contains the basic elements of the theory and the inputs and outputs of each of the elements. The *time marker* refers to stimuli,

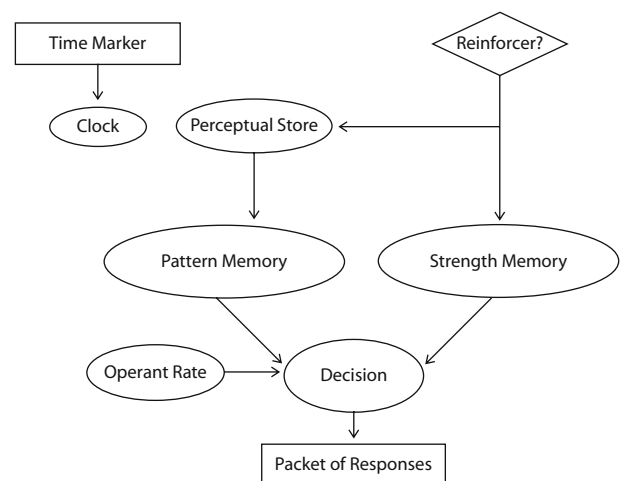


Figure 1. A flow diagram of a packet theory of behavior.

reinforcers, or responses that are inputs to a clock; the reinforcer also has characteristics that affect the *perceptual store*, a function that relates the time of onset of a time marker to the time of reinforcement, and *strength memory*, a function that is affected by the rate of reinforcement. The perceptual store is the input to *pattern memory*, which is a function related to the expected time to the next reinforcement as a function of time since the onset of a time marker based on previous experience. A *decision to respond* is based on pattern and strength memories, and an operant rate. If a decision to respond occurs, it produces a packet of responses.

Figure 2 provides a more detailed flow diagram of packet theory. The notation for the variables and parameters of packet theory is given in Appendix A. The process is divided into five stages, represented by the five rows of elements for (respectively) procedure, perception, memory, decision, and response. A *procedure* consists of the specifications of the conditions under which time markers (such as stimuli) and reinforcers will be delivered. A clock transforms the physical time (t) into subjective time (t).

This perceptual representation of time is available to the entire system at all times. At the delivery of a reinforcer, the perceptual store is updated. *Memory* consists of a pattern memory and a strength memory that represent the way that the system is altered by previous experience. The state of pattern memory is affected by the reference memory, which provides a record of the times of reinforcement relative to a time marker (from the perceptual store), and by a threshold. Strength memory is affected by the occurrence or nonoccurrence of a reinforcer at any time and provides a record of the reinforcement rate (relative to the configuration of stimuli present). A *decision* is based on the state of pattern memory, strength memory, and an operant rate. If the decision is to respond, a packet of responses is initiated. Each of the boxes in Figure 2 contains the number of the equation in the text that describes the transformation of the input(s) of the box into its output(s). The function forms for pattern and strength memory and packet initiation are for a discriminative fixed-interval (FI) procedure.

Procedure. In a discriminative FI procedure, the first response (e.g., head entry) after a fixed time (T) since the

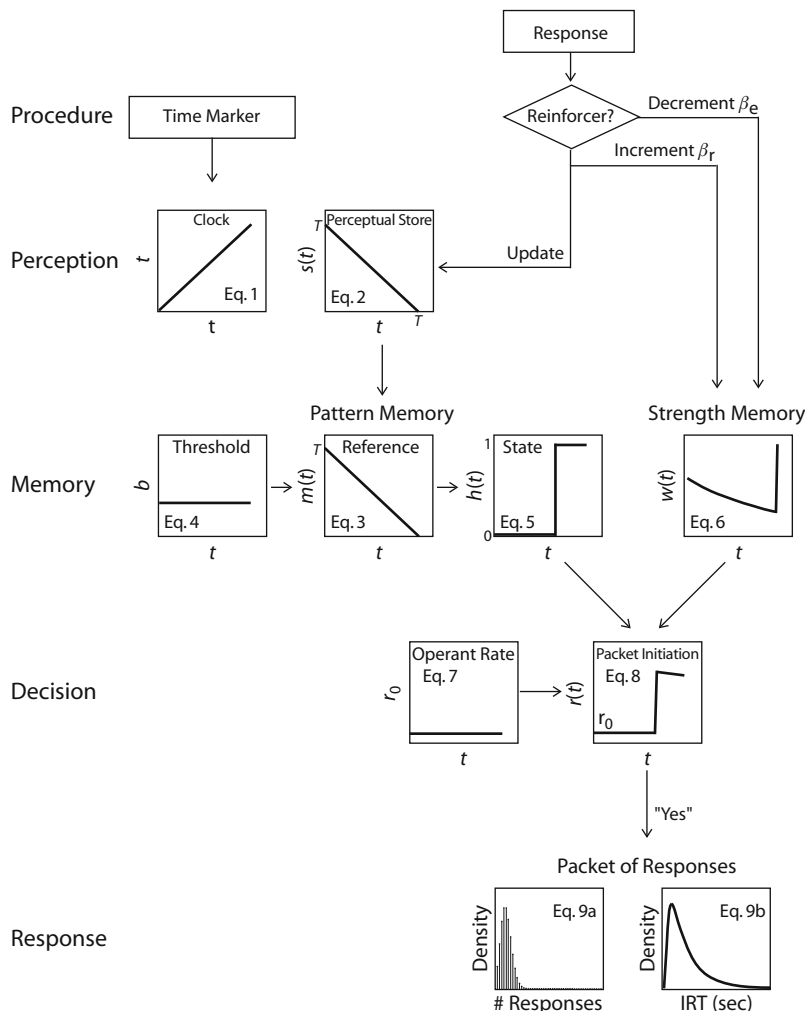


Figure 2. A detailed flow diagram of the processes of perception, memory, decision, and response in packet theory. The equation numbers refer to the equations in the text.

onset of a stimulus (e.g., a houselight) is reinforced with the delivery of food for a fixed duration (d). The delivery of food initiates a period with no stimulus, after which the stimulus is presented again.

Perception. The onset of the stimulus, response, or reinforcer is used as a time marker that restarts an internal clock that increases as a linear function of time. This process serves as the perceptual representation of time that is available to the entire system at all times:

$$t = c \cdot \tau, \quad (1)$$

where τ is physical time, c is clock rate, and t is subjective time. Note that subjective variables and parameters are italicized consistently throughout the text, but physical and procedural variables and parameters are not. The perceptual representation of time with clock rate $c = 1$ is shown in Figure 2 (Equation 1) as a linear increasing function that relates subjective time and physical time beginning at the onset of a time marker.

When the reinforcer is delivered, a new expected time to reinforcer in the perceptual store is generated by a simple transformation of the perceptual representation of time (t , Equation 1) into an expected time to reinforcement, as expressed in Equation 2:

$$s_n(t) = \begin{cases} T_n - t, & 0 < t \leq T_n, \\ 0, & T_n < t \leq T_n + d_n, \end{cases} \quad (2)$$

where T_n and d_n are the perceived time of reinforcement and the perceived reinforcement duration on cycle n , respectively. The perceptual store, with $c = 1$ and $T_n = T$, is shown in Figure 2 (Equation 2) as a linear decreasing function that relates expected time to reinforcement and subjective time beginning at a time marker and ending at the time of the reinforcer delivery. If different types of time markers occur, each is independently perceived and, after reinforcement, stored as different entities in the perceptual store.

Pattern memory. If a reinforcer is delivered, pattern memory is updated. This includes the updating of reference memory and the generation of a thresholded response state. Reference memory is the weighted mean of the values in the current perceptual store and in the previous reference memory, as expressed in Equation 3:

$$m_n(t) = \alpha_m s_n(t) + (1 - \alpha_m) m_{n-1}(t), \quad 0 \leq \alpha_m \leq 1, \quad (3)$$

where $m_{n-1}(t)$ is the reference memory containing information about the experience before cycle n , and α_m is a learning rate parameter that varies between 0 and 1. The reference memory at the steady state is shown in Figure 2 (Equation 3) as the same function that is in perceptual store. This occurs because the times from the onset of the time marker to the reinforcement are the same in every cycle in the example of an FI procedure. The short delay between the food availability and its delivery following a response in the FI procedure is not being considered in the present analysis.

Response state on a cycle is based on the comparison of reference memory with a threshold. The threshold is set

at some percentile of the reference memory, as expressed in Equation 4:

$$b_n = [m_n(t)]_\phi, \quad (4)$$

where the subscript ϕ refers to the ϕ th percentile. The threshold percentile ϕ is a normal random variable with a mean Φ and a coefficient of variation γ . The variation of b_n is primarily determined by the distribution of ϕ (see Appendix B for details). The threshold on a cycle is shown in Figure 2 (Equation 4) as a constant value.

Response state (high or low) depends on whether reference memory is below or above the threshold, as expressed in Equation 5:

$$h_n(t) = \begin{cases} 1, & m_n(t) \leq b_n, \\ 0, & m_n(t) > b_n. \end{cases} \quad (5)$$

The response state on a cycle is shown in Figure 2 (Equation 5) as a step function that begins at 0 and switches to 1. The threshold b_n was set at some percentile of $m_n(t)$ in order to keep the area under the step function constant across reinforcement rates that are the same but have different distributions (e.g., fixed and random intervals). Reinforcement distribution has been reported to affect pattern of responding but not rate of responding, whereas reinforcement rate has been reported to affect rate but not pattern of responding (Kirkpatrick & Church, 2003).

Strength memory. Strength memory is updated in time. If no reinforcer is delivered, the strength memory, denoted by $w(t)$, is decremented (Equation 6a); if a reinforcer is delivered, it is incremented (Equation 6b):

with no reinforcement,

$$\frac{dw_n(t)}{dt} = \beta_e [0 - w_n(t)], \quad 0 < t \leq T_n, \quad (6a)$$

with reinforcement,

$$\frac{dw_n(t)}{dt} = \beta_r [1 - w_n(t)], \quad T_n < t \leq T_n + d_n, \quad (6b)$$

where β_e and β_r are the learning rates during no reinforcement and reinforcement, respectively. The strength memory on a cycle is shown in Figure 2 (Equation 6) as a decreasing function of time since the onset of the time marker when no reinforcer is given, with a large increment at the time of delivery of a reinforcer.

Decision. The operant rate of packet initiation $r_0(t)$ is a decision component that is not affected by pattern or strength memories. It is, at present, a parameter simply estimated by a constant, as described in Equation 7 and shown in Figure 2 (Equation 7):

$$r_0(t) = r_0. \quad (7)$$

The decision to initiate a packet of responses is described in Equation 8. It is a function of response state $h_n(t)$ (Equation 5), strength memory $w_n(t)$ (Equation 6), operant rate of packet initiation r_0 (Equation 7), and a rate parameter A . Because of the addition of a constant operant rate of packet initiation, the decision to respond occurs in a two-state fashion: a low rate (r_0) and a high

rate ($A \cdot w_n(t) + r_0$). The decision to initiate a packet of responses function is shown in Figure 2 (Equation 8):

$$r_n(t) = A \cdot h_n(t)w_n(t) + r_0. \quad (8)$$

Response. When responses are generated, they usually occur in bouts. Bouts are the observed clusters of responses that are generated on the basis of a theoretical structure of bursts of responses called *packets*. The structure of packets of responses, which is not affected by temporal procedure, is measured by the number of responses per packet and the interresponse interval in a packet.

The number of head entry responses in a packet is assumed to follow a Poisson distribution, as expressed in Equation 9a:

$$P(u) = \mu^u \frac{e^{-\mu}}{u!}, \quad u = 0, 1, 2, \dots, \quad (9a)$$

where u is the number of responses in a packet, μ is the mean response number, and $P(u)$ refers to the probability that a packet contains u responses. The interresponse interval of head entry responses is assumed to be an inverse-Gaussian (Wald) distribution, as expressed in Equation 9b:

$$P(x) = \sqrt{\frac{\lambda_w}{2\pi x^3}} \cdot \exp\left[-\frac{\lambda_w(x - \mu_w)^2}{2\mu_w^2}\right], \quad x \geq 0, \quad (9b)$$

where x is the interresponse interval in a packet, μ_w is the mean interresponse interval, and λ_w is a scale parameter. The functions of number of responses in a packet and interresponse time (IRT) are shown in Figure 2 (Equations 9a and 9b, respectively).

Closed-Form Equations for Packet Theory

In this section, the equations used for fitting data are described. A more complete development of the closed-form equations for the summary measures used in this article can be found in Appendix B. Response rate is generated by the combination of packet initiation and packet structure, as expressed in Equation 10:

$$R_n(t) = [A \cdot h_n(t)w_n(t) + r_0] \cdot u. \quad (10)$$

Packet theory claims that the separation of response pattern and response rate results from the independence of pattern memory and strength memory. (See the proof in Appendix B.)

The mean response rate as a function of time, $R_n(t)$, at steady state is determined by pattern memory. The mean number of responses in a packet is μ , the steady state $w_n(t)$ is approximately constant and denoted by w , and $h_n(t)$ is derived as an integral of the density function of the threshold distribution from the current memory to infinity (see Appendix B for details). Thus, the mean response rate as a function of time at the steady state is

$$R_n(t) = A_{uw} \int_{m_n(t)}^{\infty} f(b) db + R_0, \quad (11)$$

where A_{uw} is the product of A , μ , and w ; R_0 is the product of r_0 and μ ; and $f(b)$ is the density function of threshold. Equation 11 suggests that the response pattern at steady

state is determined by pattern memory. Thus, it can be described by the parameters of the threshold distribution.

The mean response rate as a function of cycles, $R_n(\bar{t})$, is determined by strength memory. The value of $w_n(\bar{t})$ approximates $w_n(0)$, and $h_n(\bar{t})$ is a constant (see Appendix B for details). Thus, the mean response rate as a function of cycles is

$$R_n(\bar{t}) = A_{uh} \cdot w_n(0) + R_0, \quad (12)$$

where A_{uh} is the product of A , μ , and $h_n(\bar{t})$. The rate parameters A_{uh} (Equation 12) and A_{uw} (Equation 11) may have slightly different values, but both are measures of response rate. Equation 12 suggests that the overall response rate is determined by strength memory. Thus, it can be described by the strength memory parameters β_r and β_e .

An Application of a Packet Theory of Acquisition and Extinction

In the sections below, successive acquisitions and extinctions of three discriminative FIs are described and predictions of packet theory are compared with the observed data. The goals were (1) to predict the rate and pattern of appetitive behavior during the acquisition and extinction of discriminative FIs; (2) to determine the effects of extinction on the memory for the pattern of behavior; and (3) to compare the learning rates of acquisition and extinction of discriminative FIs.

METHOD

Animals

Twelve male Sprague Dawley rats with no previous experience were used in the experiment. The rats were housed individually in a colony room on a 12:12-h light:dark cycle (lights off at 8:30 a.m. so that testing occurred during the dark phase of the light:dark cycle). Dim red lights provided illumination in the colony room and the testing room. The rats were fed a daily ration that consisted of 45-mg Noyes pellets (Improved Formula A) that were delivered during the experimental session, and an additional 15 g of FormuLab 5008 food given in the home cage after the daily sessions. Water was available ad libitum in both the home cages and the experimental chambers. The rats arrived in the colony at 35 days of age and were 187 days of age when training began.

Apparatus

The 12 boxes (25 × 30 × 30 cm) were located inside ventilated, noise-attenuating enclosures (74 × 38 × 60 cm). Each box was equipped with a food cup and a water bottle. Three stimuli, referred to as “noise,” “light,” and “clicker,” were generated by modules from Med Associates (St. Albans, VT). The noise was a 70-dB white noise, with an onset rise time and termination fall time of 10 msec, that was generated by an audio amplifier (Model ANL-926). The light was a diffused houselight (Model ENV-227M) rated to illuminate the entire chamber over 200 Lux at a distance of 3 in. The clicker (Model ENV-135M) was a small relay mounted on the outside of the box that was used to produce auditory clicks at a rate of 1/sec. A pellet dispenser (Model ENV-203) delivered 45-mg Noyes pellets into the food cup on the front wall. Each head entry into the food cup was detected by an LED photocell. A water bottle was mounted outside the box; water was available through a tube that protruded through a hole in the back wall of the box. Two Gateway Pentium III/500 computers running Med-PC Medstate Notation Version 2.0 (Tatham & Zurn, 1989) controlled experimental events and recorded the time at which events occurred with 2-msec resolution.

Procedure

The animals received training in the multiple-cued-interval procedure (Guilhardi & Church, 2005). A cycle in this procedure consisted of a 20-sec period in which the discriminative stimulus was off, followed by a fixed interval with the discriminative stimulus on. Food was primed at the end of this FI. Immediately after the next head entry into the food cup (measured as the time of the breaking of a photo beam in the food cup), food was delivered, the discriminative stimulus was turned off, and the next cycle began. The daily sessions were composed of 60 cycles.

The experiment had four phases: acquisition, extinction, reacquisition, and repeated acquisitions and extinctions.

Acquisition. In the first phase, all rats were trained for 30 sessions under 30-, 60-, and 120-sec FI schedules of reinforcement differentially signaled by white noise, light, or clicker. The assignment of stimuli to intervals was counterbalanced across animals. One of the three possible intervals (30, 60, or 120 sec) was presented randomly with equal probability on every cycle.

Extinction. In the 35 sessions of the second phase, head entry responses were not reinforced after one of the intervals, and the stimulus terminated after 30, 60, or 120 sec (i.e., the time at which food would be available). The 12 rats were randomly partitioned into three groups of 4 rats. One randomly selected group had responses to the 30-sec interval extinguished, another had responses to the 60-sec interval extinguished, and the remaining group had responses to the 120-sec interval extinguished. Thus, for each rat, responses to one of the three intervals were extinguished, and the conditions of acquisition were maintained on the other two intervals. The stimulus-to-interval assignment was counterbalanced across groups and randomized when counterbalancing was not possible.

Reacquisition. In the 10 sessions of the third phase, the conditions were identical to those in the acquisition phase for all rats.

Repeated acquisitions and extinctions. In the final phase of 45 sessions, there was extinction of responses to one of the three intervals, as in the extinction phase. However, responses to a different interval, and therefore to a different discriminative stimulus, were extinguished on every session. On the first session of this phase, one of the three intervals was randomly chosen with equal probability. For each of the remaining sessions, one of the three intervals was randomly selected with equal probability, with the restriction that the interval during which responses of head entry were extinguished did not repeat on two consecutive sessions.

RESULTS

Response Rates During Acquisition, Extinction, and Reacquisition

Overall response rate as a function of sessions increased when the first response after the FI was followed by reinforcement during acquisition, plotted on a logarithmically spaced scale in Figure 3 (left panels). The overall response rate was defined as the mean response rate during the stimulus-on period. In contrast, overall response rate as a function of sessions decreased when responses after the FI were not followed by reinforcement during extinction for the FIs of 30 sec (top center panel), 60 sec (middle center panel), and 120 sec (bottom center panel).

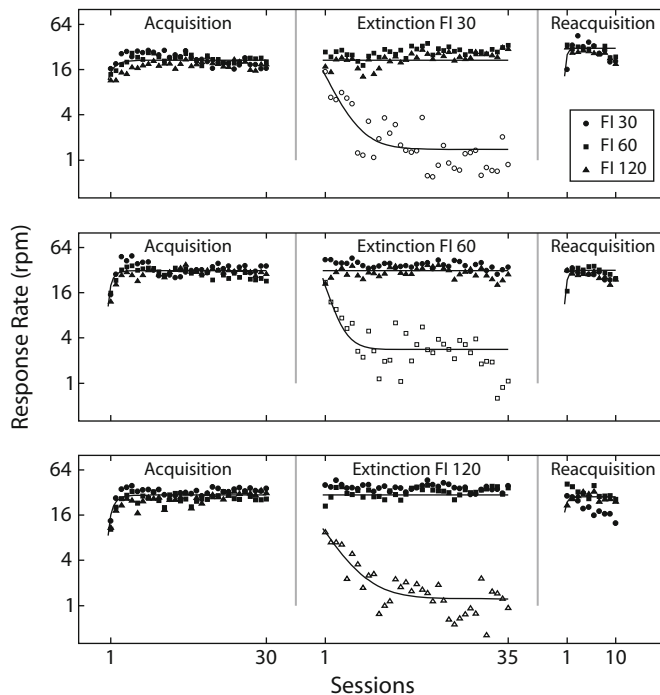


Figure 3. Response rate. Response rate during the stimulus as a function of sessions, during acquisition (left panels), extinction (fixed interval [FI] 30 sec, top center panel; FI 60, middle center panel; FI 120, center bottom panel), and reacquisition (right panels). The empty symbols indicate intervals with no reinforcement. The data are averaged across rats, and the smooth lines are the fits of Equation 12 to the data. Note that the y-axis is scaled logarithmically.

During reacquisition, overall response rate rapidly increased to levels similar to those at the end of acquisition. The smooth lines in Figure 3 are the fits of packet theory (Equation 12) to the mean data across intervals and rats during acquisition; to the interval extinguished and the mean of the remaining two intervals during extinction, averaged across rats; and to the previously extinguished FI averaged across rats during reacquisition. The estimated parameters were for the reinforcement learning rate (β_r), the no-reinforcement learning rate (β_e), the rate parameter (A_{uh}), and the operant rate (R_0). The proportion of variance accounted for (ω^2) was .87, .88, and .88 for the FIs 30 sec (top panels), 60 sec (center panels), and 120 sec (middle panels), respectively.

Fits of the equation to individuals made it possible to compare the treatment conditions. The rate of learning during reinforcement (β_r) was faster than the rate of learning during no reinforcement (β_e) for all FIs during both acquisition and reacquisition phases [$F(1,9) = 42.15, p < .001$]; the rate of learning (β_r) in reacquisition was faster than during acquisition [$F(1,9) = 7.33, p < .05$]. An ANOVA with phases (acquisition, extinction, and reacquisition) as a within-subjects factor and FI (30, 60, and 120 sec) as a between-subjects factor showed that the extinction learning rate β_e was similar across FIs [$F(2,9) = 0.60, p = .568$] and phases [$F(2,18) = 3.17, p = .066$]. There was no phase versus FI interaction [$F(4,18) = 0.68, p = .615$].

Response Pattern During Acquisition, Extinction, and Reacquisition

The patterns of responding at asymptote during acquisition, extinction, and reacquisition are shown in Figure 4. The arrows indicate the response rate gradients for the interval durations during which responses were extinguished (30 sec, top center panel; 60 sec, middle center panel; and 120 sec, bottom center panel). Response rate increases as a function of time since stimulus onset during the FIs of 30, 60, and 120 sec. The increase in response rate is particularly pronounced for the stimuli during which reinforcement was delivered. The smooth lines are the fits of packet theory (Equation 11) to the mean data across rats.

The smooth functions in Figure 4 show the estimated response rates as a function of time since stimulus onset during the acquisition, extinction, and reacquisition phases. They are based on fits of Equation 11 using the rate parameter (A_{uw}), the mean of the threshold percentile (Φ), the coefficient of variation of the threshold percentile (γ), and operant rate (R_0). The proportions of variance accounted for by the model (ω^2) were .988, .989, and .989 for the FIs 30 (top panels), 60 (middle panels), and 120 sec (bottom panels), respectively.

A measure of overfitting due to excessive complexity by the model was determined by cross-validation. The parameters of the model were estimated for each rat, and ω^2 determined, using a calibration sample composed of half

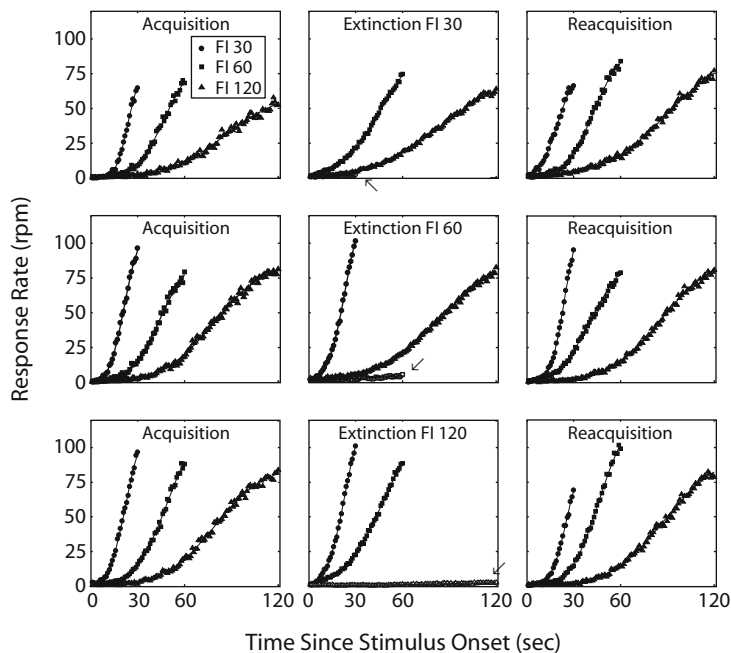


Figure 4. Response pattern. Response rate as a function of time since stimulus onset during acquisition (left panels), extinction (fixed interval [FI] 30 sec, top center panel; FI 60, middle center panel; FI 120, bottom center panel), and reacquisition (right panels). The arrows in the center panels indicate the gradients at the intervals during which no food was delivered. The data are averaged across rats during Sessions 21–30 of acquisition, 11–35 of extinction, and 1–10 of reacquisition. The smooth lines are the fits of Equation 11 to the data.

of the data (e.g., even sessions). The proportions of variance accounted for by the model relative to the calibration sample (ω^2 calibration) averaged across rats were .975, .981, and .984 for the FIs 30, 60, and 120 sec, respectively. Another ω^2 was determined for each rat from the fits of the initial model fit (with parameters determined by the calibration sample) to the validation sample composed of the second half of the data (e.g., odd sessions). The proportions of variance accounted for by the model relative to the validation sample (ω^2 validation) averaged across rats were .944, .958, and .962 for the FIs 30, 60, and 120 sec, respectively. The ratios between ω^2 validation and calibration, a measure of overfitting, were 0.968, 0.977, and 0.978 for the FIs 30, 60, and 120 sec, respectively. A ratio close to 1 indicated little overfitting by the model. The ratios averaged across intervals were less than 1 [$t(11) = 5.58, p < .001$], indicating some overfitting by the model. In addition, a measure of the reliability between the calibration and validation data samples was determined. The proportions of variance accounted for by the calibration sample relative to the validation sample (ω^2 reliability) were .917, .944, and .944 for the 30-, 60-, and 120-sec FIs, respectively. The ratios between ω^2 validation and reliability were 1.029, 1.015, and 1.019 for the 30-, 60-, and 120-sec FIs, respectively. A ratio close to 1 indicated that the variabilities of the model and the data were similar. The ratios averaged across intervals were greater than 1 [$t(11) = 5.58, p < .001$], indicating a greater variability in the data relative to the model.

One measure of response rate, the parameter A_{uv} (the rate parameter determined from the fits of Equation 11), was greatly affected by reinforcement treatment during each experimental phase but not affected by the FI. An ANOVA with phases (acquisition, extinction, and reacquisition) as a within-subjects factor and FI (30, 60, and 120 sec) as a between-subjects factor was performed on the rate parameter A_{uv} . The parameter was much lower for extinction than for acquisition and reacquisition [$F(2,18) = 105.37, p < .001$] and was similar across FIs [$F(2,9) = 0.70, p = .522$].

Two measures of the pattern of responses, the mean threshold percentile (Φ) and the coefficient of variation of the threshold percentile (γ), and another measure of rate of responses, the operant rate (R_0), were not affected by reinforcement treatment (acquisition, extinction, and reacquisition) or by the FI. Φ was similar across phases (acquisition, extinction, and reacquisition) [$F(2,18) = 0.57, p = .577$], and across FIs (30, 60, and 120 sec) [$F(2,9) = 0.31, p = .743$]. γ was also similar across reinforcement treatments [$F(2,18) = 0.21, p = .808$] and across FIs [$F(2,9) = 0.24, p = .794$]. Moreover, R_0 was also similar across phases [$F(2,18) = 1.24, p = .335$] and across FIs [$F(2,9) = 0.61, p = .553$].

The similarity of the patterns of response rate gradients during conditions in which responses were and were not followed by reinforcement (indicated by the arrows in Figure 4) are shown in Figure 5, with response rate during extinction plotted in a relative scale. Relative response rate (response rate relative to the mean response rate) in-

creased as a function of time since stimulus during the 30-, 60-, and 120-sec FIs. The thin lines are the fits of packet theory (Equation 11) to the mean data across rats.

Response Rate During Repeated Acquisitions and Extinctions

In every session during repeated acquisitions and extinctions, reinforcers were once again delivered at the fixed interval extinguished during the previous sessions (repeated acquisition sessions) and removed for one of the two FIs that had been reinforced during the previous session (repeated extinction sessions).

The response rate as a function of sessions of repeated acquisitions (top panel) and repeated extinctions (bottom panel) during the FIs 30, 60, and 120 sec are shown in Figure 6. The mean response rate during sessions of repeated acquisitions was greater than that during sessions of repeated extinctions for all of the FIs. An ANOVA with reinforcement treatment during the repeated acquisitions and extinctions phase and FI as between-subjects factors showed an effect of reinforcement treatment [$F(1,11) = 73.07, p < .001$]. In addition, the mean response rate was inversely related to the FI: The mean rates during repeated acquisitions were 77.4, 62.8, and 55.1 responses/min for the FIs 30, 60, and 120 sec, and the mean rate during repeated extinctions was 52.5, 48.3, and 35.4 responses/min, respectively, for the three FIs. There was an effect of FI [$F(2,22) = 4.52, p < .05$].

The slopes of the response rate as a function of sessions of repeated acquisitions and extinctions were relatively flat. The lines shown in Figure 6 are at the mean response rates for the 30-, 60-, and 120-sec FIs during the sessions of repeated acquisitions (top panel) and repeated extinctions (bottom panel).

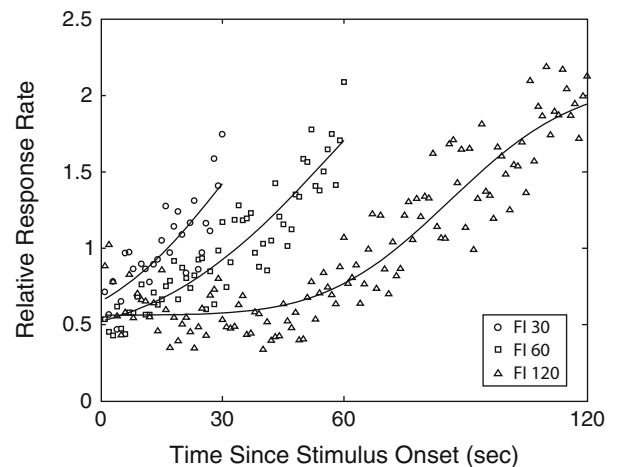


Figure 5. Response pattern during extinction. Relative response rate (proportion of the mean response rate) as a function of stimulus onset for the fixed interval (FI) 30-, 60-, and 120-sec conditions, during which responses were not followed by reinforcement, in the last 25 sessions of extinction. The smooth lines are the fits of Equation 11 to the data.

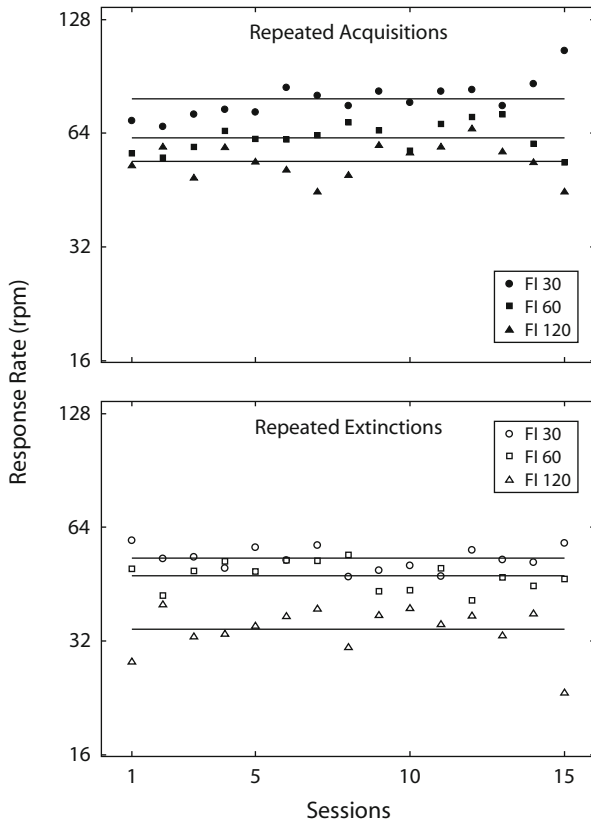


Figure 6. Response rate. Response rate as a function of sessions during the repeated acquisitions (top panel) and repeated extinctions (bottom panel) for the fixed intervals (FIs) 30, 60, and 120 sec. The data are mean response rates during the final portion of the stimulus presentation (the last 5, 10, and 20 sec for the FI 30, 60, and 120 conditions) during Cycles 2–15, averaged across rats. The smooth lines are the fits of Equation 12 to the data. Note that the y -axis is scaled logarithmically.

Response Pattern During Repeated Acquisitions and Extinctions

Figure 7 shows that the response pattern was also maintained during the repeated extinctions and acquisitions. Response rate increased as a function of stimulus onset during the FIs 30, 60, and 120 sec. The smooth lines are the fits of Equation 11 to the data averaged across rats. The proportion of variance accounted for by the model (ω^2) averaged across rats, intervals, and repeated acquisitions and extinctions was .981. A measure of overfitting due to excessive complexity by the model was determined by cross-validation. The parameters of the model were estimated for each rat, and ω^2 was determined using a calibration sample composed of half of the data (e.g., even sessions). The proportion of variance accounted for by the model relative to the calibration sample (ω^2 calibration), averaged across rats, intervals, and repeated acquisitions and extinctions, was .967. Another ω^2 was determined for each rat from the fits of the initial model fit (with parameters determined by the calibration sample) to the validation sample composed of the second half of the data (e.g., odd sessions). The proportion of variance accounted for by

the model relative to the validation sample (ω^2 validation), averaged across rats, intervals, and repeated acquisitions and extinctions, was .907. The ratio between ω^2 validation and calibration, a measure of overfitting, was 0.938. This ratio was less than 1 [$t(11) = 5.12, p < .001$], indicating some overfitting by the model. In addition, a measure of the reliability between the calibration and validation data samples was determined. The proportion of variance accounted for by the calibration sample relative to the validation sample (ω^2 reliability) was .877. The ratio between ω^2 validation and calibration was 1.034. This ratio was greater than 1 [$t(11) = 2.43, p < .001$], indicating more variability across data samples than across a model and a data sample.

One measure of response rate, the parameter A_{rw} (determined from the fits of Equation 11), was greatly affected by reinforcement treatment during repeated acquisitions and extinctions, and was also affected by the FI. An ANOVA with reinforcement treatment (repeated acquisitions and extinctions) as a within-subjects factor and FI (30, 60, and 120 sec) as a between-subjects factor was performed on the rate parameter A_{rw} . The parameter was lower for repeated extinctions than for repeated acquisitions [$F(1,11) = 51.52, p < .001$] and was a function of FI [$F(2,22) = 3.46, p < .05$]; there was no interaction [$F(2,22) = 0.79, p = .467$].

A measure of the pattern of responses, the mean threshold percentile (Φ), was similar across reinforcement treatments [$F(1,11) = 3.69, p = .081$] and was a function of FI [$F(2,22) = 4.19, p < .05$], and there was no reinforcement treatment versus FI interaction [$F(2,22) = 0.93, p = .409$]. Another measure of the pattern of responses, the coefficient of variation of the threshold percentile (γ), differed across reinforcement treatments [$F(1,11) = 7.13, p < .05$] and was similar across FIs [$F(2,22) = 2.05, p = .153$], but

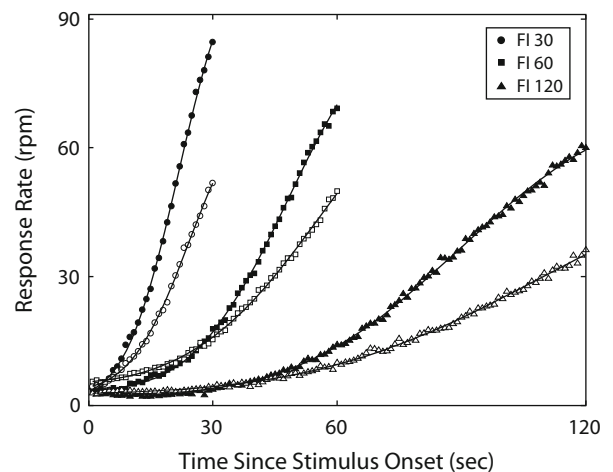


Figure 7. Response pattern. Response rate as a function of time since stimulus onset during the fixed interval (FI) 30-, 60-, and 120-sec conditions across sessions of repeated acquisitions and extinctions. The data are average response rates across rats and sessions during which the intervals were reinforced (filled symbols) and not reinforced (empty symbols). The smooth lines are the fits of Equation 11 to the data.

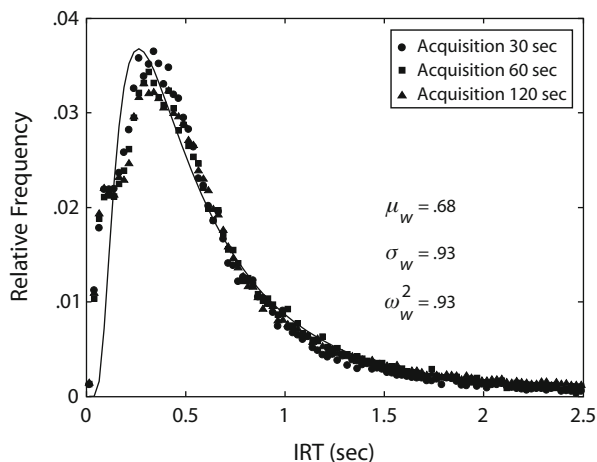


Figure 8. Response bouts. Interresponse time (IRT) distributions for the 30-, 60-, and 120-sec stimulus durations during the last 20 sessions of acquisition (Sessions 11–30). The data are averaged across rats, and the smooth line is the fit of Equation 9b to the mean data across rats and stimulus durations.

again there was no interaction [$F(2,22) = 1.30, p = .293$]. Another measure of rate, the operant rate (R_0), was similar across reinforcement treatments [$F(1,11) = 0.94, p = .353$] and across FIs [$F(2,22) = 1.21, p = .318$], and there was no interaction [$F(2,22) = 0.13, p = .876$].

Response Bouts

Although the averaged response pattern was well characterized by smooth functions (Equation 11), responses were organized in bouts. Moreover, the bouts were similar across stimulus durations. The interresponse time (IRT) distributions for the 30-, 60-, and 120-sec FIs during the last 20 sessions of acquisition (Sessions 11–30) are shown in Figure 8. The data are averaged across rats, and the smooth line is the fit of Equation 9b to the mean data across rats and stimulus durations. Equation 9b was also used to fit the IRT distributions of individual rats for the 30-, 60-, and 120-sec FIs. The center (μ_w) and scale (λ_w) parameters of the Wald distribution were similar across stimulus durations [$F(2,22) = 0.96, p = .397$ and $F(2,22) = 0.14, p = .872$, respectively]. Although the variance accounted for (ω^2) by the fit of the Wald distribution to the IRT distribution averaged across fixed intervals was .93, there were systematic deviations of the data from this function form. The bimodal pattern was observed in all three intervals for half of the rats.

DISCUSSION

This article describes an experiment that investigated the dynamics of acquisition and extinction. The results from this experiment were consistent with the results previously described: Rate of acquisition was faster than rate of extinction (Guilhardi, Yi, & Church, 2006; Rescorla, 2002); rate of reacquisition was faster than the rate of initial acquisition (Guilhardi & Church, 2005); and memory for interval duration was preserved after extinction (Guil-

hardi & Church, 2006; Ohyama, Gibbon, Deich, & Balsam, 1999; Rescorla, 1996, 2001). In the present experiment, the hypothesis that memory for interval duration was preserved after extinction was based on the fact that the response rate gradients were still related to interval duration during extinction. When the rate and pattern parameters of the model were free to vary, the rate parameter of the model (A) was greatly affected by extinction, but the pattern parameters (mean and coefficient variation of the threshold) were not. (One of the pattern parameters, the coefficient of variation of the threshold, had a marginally significant effect only in repeated extinctions; see Figure 7.)

In addition, the results of this experiment showed no evidence that the speed of extinction of response strength increased after successive acquisitions and extinctions (Figure 6). These results are surprising considering that, under many conditions of successive conditional discrimination learning, animals develop learning sets referred to as the ability of “learning to learn” (Harlow, 1949).

This article also describes a modular theory of learning and performance, its application to a multiple-cued-interval procedure, and the bases for its evaluation. The model described here is a modified version of packet theory whose features include modularity, specificity in its behavioral output, and the availability of closed-form equations. The bases for evaluation of the model include a comparison of the goodness of fit based on the model relative to other samples of the data, as well as input and output generality, complexity, and predictive value.

Modularity

The modularity of the model is shown by the flow diagram (Figure 2), with separate modules for perception, memory, decision, and response. The equation number in each of the boxes specifies the transformation rules for each module.

Probably the most important new feature of this model is the use of separate pattern and strength memories. Pattern memory is updated by reinforcement, but its content is determined by current perception and previous memory. Since pattern memory is only updated when reinforcement occurs, the response pattern is maintained during extinction. These predictions of the model are consistent with experiments that have described the pattern of responses during extinction (Drew, Yang, Ohyama, & Balsam, 2004; Guilhardi & Church, 2006; Guilhardi et al., 2006), and also consistent with the maintenance of associations during extinction (Rescorla, 1996, 2001). These predictions, however, are not consistent with experiments that have shown pattern learning during extinction (Guilhardi & Church, 2006, Experiment 2). Improvements in the pattern memory of this module are still necessary.

Strength memory is increased by reinforcement and decreased by nonreinforcement. The implementation of this process was adapted from an application of the Rescorla–Wagner model to a procedure (Rescorla, 2002) in which the rates of acquisition and extinction were compared (Guilhardi et al., 2006). In this experiment, the authors described the effects of successive acquisitions and ex-

inctions on response rate and pattern, and showed that a simple linear mapping of response rate to the response strength variable of the Rescorla–Wagner model was sufficient to fit the response rate results.

This open architecture should facilitate modification and improvements in the model. For example, the present version of the model contains a representation of time that is proportional to physical time. Various alternatives have been proposed that could be explored in an overall model that was not otherwise changed. These alternatives might include a diffusion model that has been effectively used for reaction time (Ratcliff, Van Zandt, & McKoon, 1999); various pulse distributions, including the Raleigh distribution that directly produces the scalar properties (Reid & Allen, 1998); and oscillatory sources that produce small but systematic deviations from linearity in perceived time (Crystal, 2001).

Closed-Form Equations

Many quantitative models of behavior may be described with difference equations (for discrete trials) or differential equations (for continuous time) in which one of the factors required for the prediction of behavior is the behavior on the previous cycle session (or at a previous time). Thus, such models provide statements about the change in behavior, not directly about the behavior itself. To obtain information about behavior on the n th cycle, it is necessary to calculate all previous cycles. Computer simulations of these models can be easily done, but there is a trade-off between the time required for a simulation and the accuracy obtained.

A closed-form equation is one that can be expressed in terms of elementary or well-known functions. Specifically, it may require an input of a trial number or a temporal duration, but it will not include a measure of the behavior on the previous trial (or time). This type of equation requires much less calculation, which can be done more rapidly and accurately.

Closed-form equations have been developed for other theories of timing and conditioning, such as scalar timing theory (Gibbon et al., 1984) or the learning-to-time model (Machado, 1997), and they are available for the asymptotic value in the Rescorla–Wagner model (Yamaguchi, 2006). Closed-form equations for packet theory are described in the present article.

Specificity of Behavioral Output

The primary data consisted of the times of head entries into the food cup, the times of onset and termination of the stimuli, and the time of food delivery. From the primary data, various standard summary measures of performance were calculated. These measures reflected the response rate, response pattern, and response bouts. Response rate was examined as a function of sessions and treatment conditions; response pattern was examined as a function of the absolute and relative local response rates as a function of time since stimulus onset, and response bouts were characterized by the frequency distribution of interresponse intervals as a function of treatment conditions. These summary measures had quite different func-

tional forms, so it is clear that a successful prediction was not based on curve fitting of a particular function (such as an exponential, logistic, or normal function). Presumably, a successful prediction of the different shapes of different summary measures required a valid process model. For example, additional dependent measures of FIs (Guilhardi & Church, 2004), such as postreinforcement pause and curvature index, could be used to describe performance under acquisition and extinction. The functional forms here described could not be directly used to predict these new functional forms, but the new forms could be derived, with no additional assumptions or parameters, from those originally used to describe the pattern and rate modules.

A goal of packet theory is to account for times of responses, and if that is achieved, it will obviously be possible to account for any summary measure. In fact, the predictions of multiple functional forms described by multiple dependent measures with a single set of assumptions have been described for acquisition using a simulation of packet theory (Guilhardi & Church, 2005).

Generality

Output generality. Packet theory has been applied to various standard summary measures of the primary data. Ideally, for output generality, it should be extended to a sample of all summary measures of the primary data in a specified universe.

Finally, packet theory has been applied to two specific responses (leverpressing and head entry). Ideally, it should be extended to additional features of these responses (e.g., dwell time) and to other behavior that occurs in the box (such as drinking, types of grooming, and types of exploration). Through online analysis of digital video, continuous automatic monitoring of the behavioral state should be feasible.

Input generality. At present, packet theory has been applied to various specific procedures. Ideally, for input generality, it should be extended to a sample of all procedures in a specified universe.

Goodness of Fit

Typically, *goodness of fit* refers to the percentage of variance accounted for by a model. It involves a comparison of the predictions of the proposed model with a null hypothesis. This is usually considered to be a necessary, but certainly not a sufficient, basis for model selection (Myung & Pitt, 2002, pp. 443–453; see also Myung, 2000; Pitt, Myung, & Zhang, 2002). In some cases, however, it may not even be necessary. Consider the extensive evidence that, under certain conditions, animals and people may respond in a nearly random manner (Neuringer, 2002). A good model of this process should also produce nearly random output, but the goodness of fit would be near 0. This is a serious limitation of a goodness-of-fit criterion that compares the fit of a proposed model with the fit of the null hypothesis.

Generalizability should refer to the ability of a model to mimic, not only a particular sample, but also other samples from the same process. An appropriate criterion for a successful prediction would be its similarity to the reli-

ability of the behavior: The differences between the model and the data should be neither more nor less variable than the differences between two samples of the data. This is implicit in the use of a Turing test for the evaluation of a model (Church & Guilhardi, 2005).

Improvement of the fit. The theory should be modified when systematic deviations of the data from the predictions are identified. In the present article, these are most clearly seen in the frequency distribution showing the bouts (Figure 8). Of course, any modifications in the model should be tested for backward compatibility. The goal of a theory is to predict behavior at least as well as one sample of behavior can predict another (the reliability of behavior). In the present article, the ω^2 validation was slightly greater than the ω^2 reliability (Figures 4 and 7). This undoubtedly reflects the fact that the mean of the model does not reflect the sampling error in the calibration and the validation sets.

This is undesirable if one is trying to produce a model that is indistinguishable from the data, and may be corrected in two ways: by changes in the evaluation procedure (e.g., selection of dependent variables that represent the variability of the predictions of the model) or by corrections in the model (e.g., change in the variability levels of the model predictions).

Decrease in Complexity

Because of the low amount of random variability in the data, there was no serious overfitting problem. Thus, the percentage variance accounted for by the model with cross-validation was only slightly lower than that without (Figures 4 and 7). Nonetheless, unnecessary complexity should be eliminated whenever possible. The modularity also facilitates the determination of ways to reduce the complexity of the model. Perhaps some modules are not necessary, or perhaps the function forms or the number of parameters can be reduced.

Predictive Value

Data archives. Primary data from animal cognition research (Kurtzman, Church, & Crystal, 2002; Vaughan, 2004) have increasingly been made available by scientific societies, such as the Psychonomic Society (www.psychonomic.org/archive) and the Society for Neuroscience (big.sfn.org/NDG/site); by research institutes, such as the Massachusetts Institute of Technology (libraries.mit.edu/guides/subjects/data); and by researchers' personal Web sites (e.g., www.brown.edu/Research/Timelab and www.uga.edu/animal-cognition-lab). These archives often include the times of all recorded behavioral and procedural events, as well as documentation of codes and other conventions. They are efficient resources for testing theoretical predictions prior to conducting experiments. At present, various related topics, such as conditioning, timing, and choice, are often explained with different theories. With increased availability of mathematical theories of behavior in the archives, it will be feasible to develop more unified theories based on secondary data analysis.

Diagnosis. If prediction from a model is successful, there is a possibility that the theory can also be used for

diagnosis. The prediction task is to infer the behavior from the input; the diagnosis task is to infer the input from the behavior. Thus, on the basis of the observed behavior and a theory, the problem would be to identify the conditions that produced the behavior. This is a more difficult task, but one that may be of greater practical importance.

Novel predictions. Most of the applications of packet theory have been to standard procedures that usually produce (at least qualitatively) standard results. Conditions under which standard procedures occasionally produce nonstandard predictions should also be examined, and the theory should be tested with some new procedures. A theory that makes no novel predictions serves only to organize the results; a theory that does make some novel predictions may simply need to be improved, but it might also lead to new discoveries.

Conclusions

A development of packet theory was described, with the additions of modularity, a distinction between pattern and strength memories, and closed-form equations. In addition to accounting for the dynamics of acquisition, this article extended the application of the theory to account for the dynamics of extinction. Goodness of fit of the theory was based on cross-validation: A calibration sample from the data was used for parameter estimates, and a validation sample from the same data was used to estimate goodness of fit. The predictions based on the theory were similar to predictions based on the reliability of the behavior.

AUTHOR NOTE

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FILE: Guilhardi-PB&R-2007.zip.

DESCRIPTION: The compressed archive file contains .txt data files (1,417) for individual rats on individual sessions. The primary data are the times (column 1) of events (column 2) that occurred during the experimental session. A readme file is also contained (readme.pdf). The readme file contains a description of the supplementary material such as, content, file formats, and file naming conventions.

LINK: www.brown.edu/Research/Timelab.

DESCRIPTION: Contains additional data in the same format, documentation of the procedures and formats, and references to publications that analyze aspects of these additional data.

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APPENDIX A
Notation

Module	Variable	Parameter	Name	Equation
Perception	t		Physical time	
	t		Perceived time	
	T		Target time	
	T		Perceived target time	
Pattern memory		c	Clock rate	1
	$s_n(t)$		Expected time to reinforcer in perceptual store	
	$m_n(t)$		Reference memory	
	$h_n(t)$		Response state	
	b_n		Threshold	
			α_m	Memory learning rate
		$\phi(\Phi, \gamma)$	Threshold percentile (mean and coefficient of variation)	4
Strength memory	$w_n(t)$		Strength memory	
	$w_n(0)$		Zero-time strength memory	
		β_c	Learning rate during no reinforcement	6
		β_r	Learning rate during reinforcement	6
Decision	$r_n(t)$		Packet initiation	
	$R_n(t)$		Response rate	
		$A(A_{ih}, A_{iw})$	Rate parameter	
		r_0	Operant baseline rate of packet initiation	8
		R_0	Operant baseline rate of response	10
Response	u		Number of responses in a packet	
	x		Interresponse interval in a packet	
		μ	The mean response number in a packet	
		λ_w	The scale parameter in Wald distribution	
		μ_w	The center parameter in Wald distribution	
Others	n		Cycle number	
	\bar{n}		The average across cycles	
	\bar{t}		The average across some interval	

APPENDIX B

An Application of Packet Theory

The equations and proofs of packet theory in this appendix are based on a fixed-interval procedure (FI). In this procedure, the first response after a fixed interval from the onset of a time marker produces a reinforcer; a *cycle* refers to the interval between the onset of the time marker and termination of the reinforcer. In this application, the time between the fixed interval and the time of reinforcement is approximated by setting it to 0, as in a fixed-time procedure. Observed procedural and response variables are written in standard font; intervening variables, such as perception, memory, and decision variables, are written in italics. Parameters are written either in italics or Greek letters.

The first goal of this appendix is to describe the response rate as a function of time since the onset of a time marker for each cycle of each individual rat (Equation B19). The second goal is to describe the mean response rate as a function of time since the onset of the time marker (across cycles) and the mean response rate as a function of cycles (across time within the interval). The mean response rate as a function of cycles is given in Equation B20b; the mean response rate as a function of time is given in Equation B21b. The approach is to follow the organizational scheme diagrammed in Figure 2.

Perception

The perceived time t is proportional to the physical time t :

$$t = c \cdot t. \quad (\text{B1, Equation 1})$$

According to Equation B1, the perceived time of reinforcement is

$$T = c \cdot T \quad (\text{B2a})$$

APPENDIX B (Continued)

and the perceived reinforcement duration is

$$d = c \cdot d \quad (\text{B2b})$$

when $c = 1$, $t = t$, $T = T$, and $d = d$. The expected time to reinforcement, $s_n(t)$, is

$$s_n(t) = \begin{cases} T - t, & 0 < t \leq T; \\ 0, & T < t \leq T + d. \end{cases} \quad (\text{B3, Equation 2})$$

Because in the FI procedure $s_n(t)$ does not change with cycle, it can be simply written as $s(t)$.

Memory

Pattern memory. Reference memory, $m_n(t)$, is updated when a reinforcer is delivered.

$$m_n(t) = \alpha_m s(t) + (1 - \alpha_m) m_{n-1}(t), \quad 0 \leq \alpha_m \leq 1, \quad (\text{B4, Equation 3})$$

where α_m is the pattern learning rate parameter. According to Equation B4, $m_n(t)$ is a weighted mean of $s(t)$ and $m_{n-1}(t)$. Similarly, $m_{n-1}(t)$ is a weighted mean of $s(t)$ and $m_{n-2}(t)$, $m_{n-2}(t)$ is a weighted mean of $s(t)$ and $m_{n-3}(t)$, and so on and so forth. Given the initial condition, $m_0(t) = m_0$, $m_n(t)$ can be derived:

$$m_n(t) = \left[1 - (1 - \alpha_m)^n \right] s(t) + (1 - \alpha_m)^n m_0. \quad (\text{B5})$$

The situation in which the animal fails to learn, in which $\alpha_m = 0$ and $m_n(t) = m_0$, requires no further development. If learning occurs, $0 < \alpha_m \leq 1$ or, equivalently, $0 \leq 1 - \alpha_m < 1$; after sufficient training, $(1 - \alpha_m)^n$ is close to 0 and $m_n(t)$ converges to $s(t)$. Thus, $s(t)$ is the asymptote of $m_n(t)$.

Threshold, b_n , is set at the ϕ th percentile of reference memory,

$$b_n = \lceil m_n(t) \rceil_\phi, \quad (\text{B6, Equation 4})$$

such that the probability that $m_n(t) \leq b_n$ is $\phi/100$. At steady state, the threshold is not affected by n , and thus $b_n = b$. The threshold b is normally distributed with a mean $B = [s(t)]_\phi$ (the Φ th percentile of $s(t)$; Φ , the mean of ϕ) and a standard deviation γB (γ , the coefficient of variation of ϕ). The density function of b is

$$f(b) = \frac{1}{\gamma B \sqrt{2\pi}} \cdot \exp\left(\frac{-(b - B)^2}{2\gamma^2 B^2}\right).$$

Response state, $h_n(t)$, is based on the comparison of $m_n(t)$ and b_n .

$$h_n(t) = \begin{cases} 1, & m_n(t) \leq b_n; \\ 0, & m_n(t) > b_n. \end{cases} \quad (\text{B7, Equation 5})$$

According to the definition of threshold, on a single cycle the probability that $h_n(t) = 1$ is $\phi/100$, and the probability that $h_n(t) = 0$ is $1 - \phi/100$. Thus, the mean response state on single cycles is a constant:

$$h_n(\bar{t}) = 1 \cdot \phi/100 + 0 \cdot (1 - \phi/100) = \phi/100. \quad (\text{B8})$$

At steady state, the mean (expected value) of $h_n(t)$ across the cycles is

$$h_n(t) = 1 \cdot P[s(t) \leq b] + 0 \cdot P[s(t) \geq b]. \quad (\text{B9a})$$

Because the density function of b is $f(b)$,

$$P[s(t) \leq b] = \int_{s(t)}^{\infty} f(b) db.$$

Then,

$$h_n(t) = \int_{s(t)}^{\infty} f(b) db. \quad (\text{B9b})$$

Strength memory. Strength memory, $w_n(t)$, is decremented if no reinforcer is delivered; it is increased if a reinforcer is delivered.

$$\text{no reinforcement, } \frac{dw_n(t)}{dt} = \beta_e [0 - w_n(t)], \quad 0 < t \leq T; \quad (\text{B10, Equation 6a})$$

$$\text{reinforcement, } \frac{dw_n(t)}{dt} = \beta_r [1 - w_n(t)], \quad T < t \leq T + d. \quad (\text{B11, Equation 6b})$$

Two assumptions are required to connect Equations B10 and B11 together continuously. The first assumption is that the strength memory just before a reinforcement equals the strength memory at the beginning of the reinforcement. Consider a small interval Δ , such that $T - \Delta$ is just prior to reinforcement, so that $w_n(T - \Delta)$ is determined by Equation B10, and that $T + \Delta$ is at the beginning of reinforcement, so that $w_n(T + \Delta)$ is determined by Equation B11. When Δ is close to 0, $w_n(T - \Delta) \approx w_n(T + \Delta)$, such that

$$\lim_{\Delta \rightarrow 0} w_n(T - \Delta) = \lim_{\Delta \rightarrow 0} w_n(T + \Delta). \quad (\text{B12})$$

APPENDIX B (Continued)

The second assumption is that the strength memory at the end of cycle n equals the strength memory at the beginning of cycle $n+1$. Similarly, consider a small interval Δ , such that $T + d - \Delta$ on cycle n is close to the end of reinforcement, so that $w_n(T + d - \Delta)$ follows Equation B11, and that $0 + \Delta$ on cycle $n+1$ is just after reinforcement, so that $w_{n+1}(0 + \Delta)$ follows Equation B10. When Δ is close to 0,

$$w_n(T + d - \Delta) \approx w_{n+1}(0 + \Delta)$$

and

$$\lim_{\Delta \rightarrow 0} w_n(T + d - \Delta) = \lim_{\Delta \rightarrow 0} w_{n+1}(0 + \Delta). \quad (\text{B13})$$

Solve $w_n(t)$ from Equation B10, and one can get

$$w_n(t) = w_n(0)e^{-\beta_e t}, \quad 0 < t \leq T. \quad (\text{B14})$$

Solve $w_n(t)$ from Equation B11, and one can get

$$w_n(t) = Ce^{-\beta_r t} + 1, \quad T < t \leq T + d, \quad (\text{B15a})$$

where C is a constant that can be obtained following the first assumption (Equation B12), $C = w_n(0)e^{(\beta_r - \beta_e)T} - e^{\beta_r T}$. Then,

$$w_n(t) = w_n(0)e^{(\beta_r - \beta_e)T - \beta_r t} - e^{\beta_r(T-t)} + 1, \quad T < t \leq T + d. \quad (\text{B15b})$$

Because β_e and β_r are very small (β_e and $\beta_r \ll 0.1$), $e^{-\beta_e t}$, $e^{(\beta_r - \beta_e)T - \beta_r t}$, and $e^{\beta_r(T-t)}$ are close to 1. Thus, $w_n(t)$ approximates $w_n(0)$.

Following the second assumption (Equation B13), Equations B14 and B15b can be combined:

$$w_n(0)e^{(\beta_r - \beta_e)T - \beta_r(T+d)} - e^{\beta_r(T-T-d)} + 1 = w_{n+1}(0). \quad (\text{B16})$$

Given the initial condition $w_0(0) = w_0$, $w_n(0)$ can be solved from this difference equation.

$$w_n(0) \approx w + (w_0 - w)(1 - \beta_r d - \beta_e T)^n, \quad (\text{B17})$$

where

$$w = \frac{\beta_r d}{\beta_r d + \beta_e T}.$$

Because β_e and β_r are very small, the value of $1 - \beta_r d - \beta_e T$ is between 0 and 1, and after sufficient training, $(1 - \beta_r d - \beta_e T)^n$ is close to 0. Thus, w is the asymptote of $w_n(0)$. Because $w_n(t)$ is approximately equal to $w_n(0)$ as demonstrated before, w is approximately equal to the asymptote of $w_n(t)$.

This application assumes that strength memory and pattern memory are independent of each other. Event A and Event B are claimed to be independent if and only if

$$(i) \quad P(AB) = P(A)P(B), \text{ or equivalently,}$$

$$(ii) \quad P(A | B) = P(A), \text{ given } P(B) \neq 0.$$

The probability that $w_n(t)$ increases and the probability that $w_n(t)$ decreases are denoted by $P(w \uparrow)$ and $P(w \downarrow)$. The probability that $h_n(t) = 0$ and the probability that $h_n(t) = 1$ are denoted by $P(h = 0)$ and $P(h = 1)$. During no reinforcement ($0 < t \leq T$), $w_n(t)$ decreases, regardless of response state. Then,

$$P(w \downarrow | h_n = 0) = P(w \downarrow | h_n = 1) = P(w \downarrow) = 1$$

and

$$P(w \uparrow | h_n = 0) = P(w \uparrow | h_n = 1) = P(w \uparrow) = 0.$$

Thus, according to Condition ii, $w_n(t)$ and $h_n(t)$ are independent during no reinforcement. During reinforcement ($T < t \leq T + d$), $w_n(t)$ increases and response state is high. Then,

$$P(w \uparrow \cap h = 1) = P(w \uparrow)P(h = 1) = 1,$$

$$P(w \downarrow \cap h = 0) = P(w \downarrow)P(h = 0) = 0,$$

$$P(w \uparrow \cap h = 0) = P(w \uparrow)P(h = 0) = 0,$$

and

$$P(w \downarrow \cap h = 1) = P(w \downarrow)P(h = 1) = 0.$$

Thus, according to Condition i, $w_n(t)$ and $h_n(t)$ are independent during reinforcement. However, because both of them are affected by the perceived time of reinforcement, T , $w_n(t)$ and $h_n(t)$ may not be independent on a complete cycle ($0 < t \leq T + d$). Because the perceived reinforcement duration d is very short and the response rate analysis focuses on the interval before the reinforcement, in this application $w_n(t)$ and $h_n(t)$ are approximately independent of each other.

APPENDIX B (Continued)

Decision

Packet initiation is determined by three factors: response state $h_n(t)$, strength memory $w_n(t)$, and operant rate of packet initiation r_0 (see Equation 7 in text).

$$r_n(t) = A \cdot h_n(t)w_n(t) + r_0, \tag{B18, Equation 8}$$

where A is a rate parameter. The number of responses per packet, u , is required to translate the rate of packet initiation $r_n(t)$ to the rate of response $R_n(t)$.

$$R_n(t) = A \cdot u \cdot h_n(t)w_n(t) + r_0 \cdot u. \tag{B19, Equation 10}$$

Fitting of Packet Theory to Summary Measures

Several properties of expectation (or mean) are used to derive the two means: the mean response rate as a function of cycles and the mean response rate as a function of time. Given two random variables x and y ,

- (1) $E(x + a) = E(x) + a$, given a is a constant;
- (2) $E(ax) = aE(x)$, given a is a constant;
- (3) $E(x \cdot y) = E(x) \cdot E(y)$, if x and y are independent.

The mean response rate as a function of cycles can thus be obtained. The assumptions of independence for the variables of Equation B19 are that A and r_0 are constants, u is independent of any temporal component, and, as demonstrated above, $w_n(t)$ and $h_n(t)$ are approximately independent of each other. Then, according to Properties 1, 2, and 3, one can obtain

$$R_n(\bar{T}) = A_u \cdot h_n(\bar{T})w_n(\bar{T}) + R_0, \tag{B20a}$$

where A_u and R_0 are the products of μ (the mean of u , see Equation 9a in text) with A and with r_0 , respectively. $w_n(\bar{T})$ is approximately equal to $w_n(0)$, and $h_n(\bar{T})$ equals $\phi/100$. Then, Equation B20a can be rewritten as

$$R_n(\bar{T}) = A_{uh} \cdot w_n(0) + R_0, \tag{B20b, Equation 12}$$

where A_{uh} is the product of A_u and $\phi/100$. Equation B20b is the equation that generates the fits in Figure 4. It suggests that the mean response rate as a function of cycles is determined by strength memory.

The mean response rate as a function of time can also be obtained on the basis of the same assumptions of independence about the variables and the three properties of expectation used to obtain Equation B20a:

$$R_{\bar{n}}(t) = A_u \cdot h_{\bar{n}}(t)w_{\bar{n}}(t) + R_0. \tag{B21a}$$

At steady state, $w_{\bar{n}}(t)$ is approximate to a constant

$$w = \frac{\beta_i d}{\beta_i d + \beta_e T},$$

and $h_{\bar{n}}(t)$ is given by Equation B9b. Then, Equation B21a can be rewritten as

$$R_{\bar{n}}(t) = A_{uw} \int_{s(t)}^{\infty} f(b) db + R_0, \tag{B21b, Equation 11}$$

where A_{uw} is the product of A_u and w . Equation B21b is the equation that generates the fits in Figure 5. It suggests that the mean steady-state response rate as a function a time is determined by pattern memory.