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How rats combine temporal cues

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Abstract

The procedures for classical and operant conditioning, and for many timing procedures, involve the delivery of reinforcers that may be related to the time of previous reinforcers and responses, and to the time of onsets and terminations of stimuli. The behavior resulting from such procedures can be described as bouts of responding that occur in some pattern at some rate. A packet theory of timing and conditioning is described that accounts for such behavior under a wide range of procedures. Applications include the food searching by rats in Skinner boxes under conditions of fixed and random reinforcement, brief and sustained stimuli, and several response-food contingencies. The approach is used to describe how multiple cues from reinforcers and stimuli combine to determine the rate and pattern of response bouts.

Keywords: Packet theory; Temporal cues; Time perception; Time estimation

We describe a quantitative model of timing that generates times of responses (i.e., *behavior*) given the times of onsets and terminations of stimuli and reinforcers (i.e., the *procedure*), and determines how information from multiple time-markers (e.g., *stimulus onset*, *stimulus termination*, and *delivery of reinforcer*) are combined to control behavior. From simulated data, a large number of summary measures can be calculated that can be compared with corresponding measures obtained from animal experimental data.

The behavior of animals is often characterized by clusters of responses (i.e., bouts of responses) such as food searching by rats in an operant chamber (Shull et al., 2001), and the patterns of feeding in cows (Tolkamp and Kyriazaki, 1999). The rates and patterns of bouts are controlled by the particular procedure imposed. The packet theory of timing and conditioning described in this article is a small modification of the one previously used to account for the pattern and rate of bout initiation, and bout characteristics (Kirkpatrick, 2002; Kirkpatrick and Church, 2003).

1. Simple procedures for the study of conditioning and timing

Many standard procedures involve multiple time-markers. This section begins with a description of an operant trace procedure involving three time-markers that we proceed to decompose in order to develop the model.

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1.1. Three time-markers

The primary data produced by any conditioning procedure are the times of the onsets and terminations of stimuli, responses, and reinforcers. The top panel of Fig. 1 shows an operant trace procedure in which a noise stimulus is followed by a time interval before food is delivered. This interval is referred to as the "trace" interval. In this procedure, food is delivered at the time of the first response after a fixed time from stimulus termination. In this panel, the time that the reinforcer is available is indicated by the open triangles (i.e., prime), the time that the reinforced response occurs is indicated by an arrow, and the time of food delivery is indicated by a filled triangle. This procedure contains three time-markers for food: the time of the previous food, the time of noise onset, and the time of noise termination.

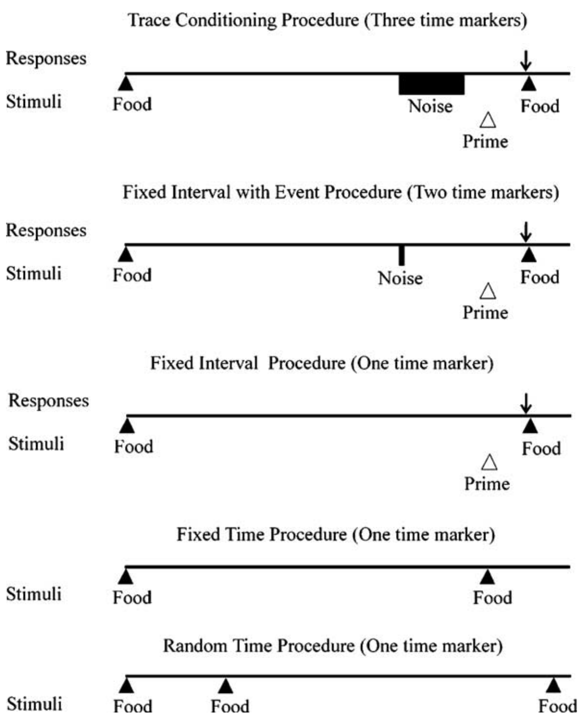

Fig. 1. Procedures with three time-markers (a trace conditioning procedure), two time-markers (a fixed interval with one event procedure) and one time-marker (fixed interval, fixed time, and random-time procedures). The complexity of the procedures decreases from top to bottom. The symbols indicate food delivery (filled triangle), prime of food delivery (empty triangle), responses necessary for food delivery (arrow), and noise stimulus (filled rectangles).

1.2. Two time-markers

A slightly simplified version of an operant trace procedure, shown in the second panel of Fig. 1, contains a brief pulse of noise with the onset and termination of the noise occurring almost simultaneously (Dews, 1962). Thus, this procedure contains two time-markers for food: the time of the previous food, and the time of the noise pulse.

1.3. One time-marker

A further simplification of this procedure is shown in the third panel of Fig. 1. The noise stimulus is omitted and food is signaled by a single time-marker: the time of previous food. This is usually referred to as a fixed-interval schedule (Ferster and Skinner, 1957; Schneider, 1969).

An additional simplification of the fixed-interval procedure is to eliminate the dependency of food delivery on a response, as shown in the fourth panel of Fig. 1. A procedure in which food is delivered at fixed times, regardless of the occurrence of any responses, is usually referred to as a "fixed-time procedure," or "temporal conditioning" (Pavlov, 1927). Food may also be delivered at random times with the same mean duration, as shown in the bottom panel of Fig. 1 (La Barbera and Church, 1974). Other reinforcement distributions can also be used to determine the times at which the animals obtain food.

2. Behavior in a fixed-time procedure

In this section we apply the packet theory to procedures with a single time-marker; in subsequent sections we extend the theory to procedures with two or three time-markers. In procedures with more than one time-marker, a combination rule for the multiple time-markers is necessary.

Six rats were trained for 30 sessions on a fixed-time procedure with food delivered every 120 s and head entries into the food cup were recorded. This procedure is shown in the top panel of Fig. 2. A sample of responses from one rat during Session 21 is shown in the second panel of Fig. 2 as a function of session time for 20 blocks of 20 s. The sequence of blocks represents 400 s of the session; each block is not systematically related to procedural events. Although in some cases a response occurred by itself, in most cases the responses were clustered together, suggesting that they occurred in bouts. The interresponse time distribution for the 30 sessions of training is shown in the third panel of Fig. 2. The distribution was positively skewed with the most frequent interresponse time occurring at 0.282 s. Response rate as a function of time since food (response gradient) for the last 10 sessions is shown in the fourth panel of Fig. 2. The response gradient was initially high, decreased rapidly, and later increased as the time of the next food approached. The initial segment of the curve (i.e., the sharp decrease in response rate) was related to the consumption of the food pellet, and the final segment of the curve (i.e., the gradual increase in response rate) was related to the anticipation of the delivery of the next food. The behavior in this fixed-time procedure was orderly: responses occurred in bouts, and the pattern and rate of responses were controlled by the procedure.

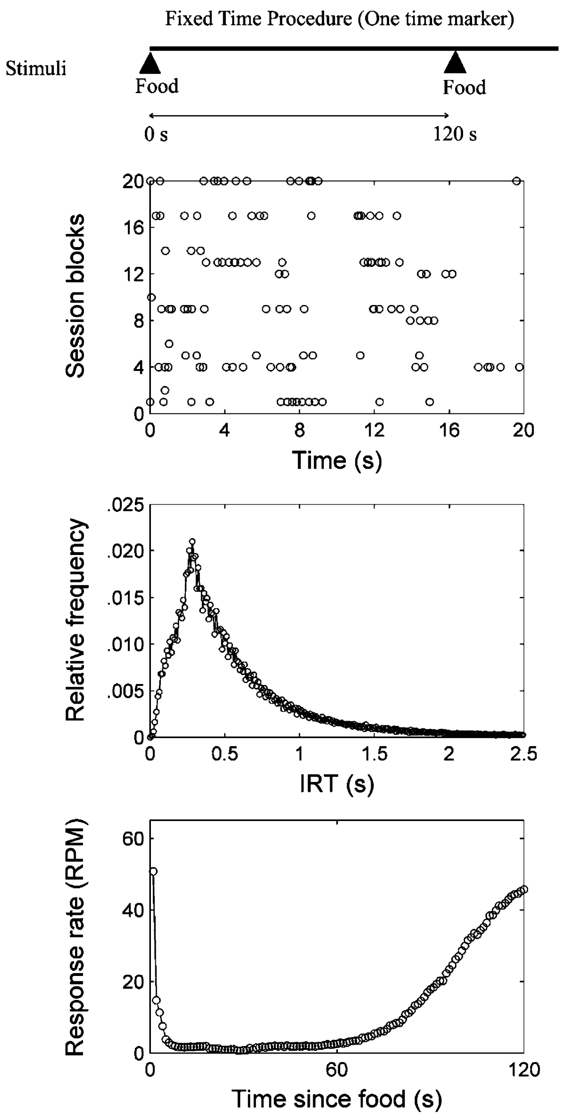

Fig. 2. Top panel: fixed time 120 s procedure (one time-marker). Second panel: head entries of rats as a function of session time. Third panel: interresponse time distribution. Bottom panel: response rate as a function of time since food.

3. Description of a packet theory of conditioning and timing

In this section, packet theory will be described with respect to the fixed-time procedure. In the following section, the predictions of the model regarding bouts, patterns, and rates will be compared with experimental data.

The input to this model is a procedure, such as the fixed-time procedure shown in the top panel of Fig. 2. The procedural inputs are the times of the onsets and terminations of stimuli (e.g. white noise, clicker, and light), and the times of occurrences of reinforcers (e.g. food). The outputs from packet theory are the times of responses. The way packet theory processes the procedural inputs is described in four modules: perception, memory, decision, and responses (see Fig. 3).

3.1. Perception

Perception follows directly from the procedure. In the fixed-time procedure there is only a single input, the time of food delivery, which serves as a time-marker for the next food delivery. At any instant between food deliveries, the animal keeps track of the time since the previous delivery in a manner proportional to physical time. Thus, at the time of reinforcement, the duration between the successive food deliveries, d, is available and the perception of that elapsed interval, $s(t)$, can be determined as described in Eq. (1):

$$s(t) = d - t \quad (1)$$

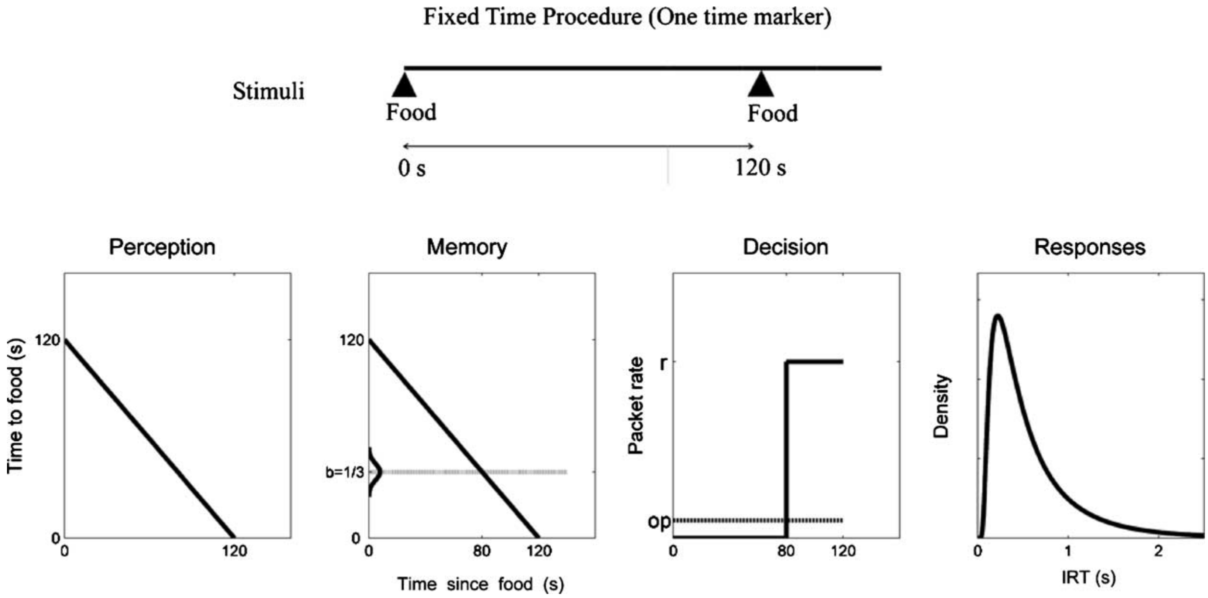

Fig. 3. Top panel: fixed-time 120 s procedure. Bottom panel: perception, memory, decision, and interresponse time distribution modules of packet theory applied to the fixed-time procedure.

where t is time since the last food. The bottom left panel of Fig. 3 shows perception based on a single duration, when the duration from the time-marker to the delivery of reinforcement is 120 s.

3.2. Memory

At the time of reinforcement, the perception $s(t)$ is determined, and added to a memory. Memory is a weighted mean of the individual perceptions as described in Eq. (2):

$$E_{n+1}(t) = \alpha s(t) + (1 - \alpha) E_n(t) \qquad (2)$$

where $E(t)$ is the memory, $s(t)$ the perception of the duration of the last interfood interval (d), α the learning parameter, and n the current number of reinforcements. At time of reinforcement $E(0)$ is the expected duration to the next food.

Memory is a weighted mean of all past perceptions and the current perception. This idea was used by Bush and Mosteller (1955) to describe the learning of the probability of a response, and it is used here to describe the learning of expected durations to reinforcement as a function of physical time.

Both the perception, $s(t)$, and the memory, $E(t)$, are conditional expectations, the expected time to the next food as a function of time since the previous food. In the case of the fixed-time procedure, the memory at asymptote equals the perception, as shown by the two solid lines in the perception and memory panels of Fig. 3. Although this equality holds for fixed-time distributions, it does not hold for procedures in which the interfood intervals come from uniform or exponential distributions (i.e., variable or random time schedules; see Section 6). The explicit expression for the asymptotic memory function, given the distribution of interfood intervals, is in Kirkpatrick (2002) and Kirkpatrick and Church (2003). Presumably it will be possible to develop a complete explicit solution for the times of occurrence of responses given a procedure, but that is not now available. Therefore, the comparison of the data with the predictions of packet theory will be based on simulations.

3.3. Decision

In packet theory, responses are generated by packets that are determined by the memory and a constant operant level of responding. The process used in the present analysis is described below.

3.3.1. Threshold

A threshold transforms the continuous pattern in memory into a pattern with two states: A high state with rate (r) of initiating packets of responses and a low state with no initiation of new packets of responses. In every cycle, a single random sample (b) is taken from a normal distribution (η) with a mean between 0 and 1 (μ_b) and some coefficient of variation (γ_b) as described in Eq. (3):

$$b = \eta(\mu_b, \gamma_b) \quad (0 \leq \mu_b \leq 1) \tag{3}$$

If the sample is below 0, b is resampled, and if it is above 1 it is set to 1. Thus, b is a proportion between 0 and 1. The threshold B is defined in Eq. (4):

$$B = P_b(E(t)) \quad (0 \leq t \leq E(0)) \tag{4}$$

where P_b is the bth percentile of the memory function $E(t)$ when t is between 0 and $E(0)$. The threshold (B) is a time such that, when memory is above B, the decision function is in the low state and when memory is below B the decision function is in the high state.

For example, if the sampled b were 1/3, the threshold B for the memory of a fixed interval of 120 s would be at 80 s (see memory panel of Fig. 3). Note that 1/3 of the memory, for t between zero and $E(0)$, is below the threshold (high responding state) and 2/3 are above (low responding state).

In the fixed-time procedure, the decision based on memory is a single step function that changes from zero to a high (r) probability of occurrences of packets of responses. The respective decision step function is the solid line also shown in the decision panel of Fig. 3. In a fixed-time procedure the threshold is a fixed proportion of memory and its variability is dependent on the mean interval duration between the time-marker and delivery of food (constant coefficient of variation), so the scalar property is embedded in the theory.

3.3.2. Operant level (op)

The operant level, represented by the dotted line shown in the decision panel at the bottom of Fig. 3, is the rate of emitting a packet of responses for many possible reasons, such as the smell of food in the food cup and random exploratory behavior. It consists of packets of responses that are generated with a constant low probability throughout an interval.

3.3.3. Combination of two rates for decision

The rate of packet initiation is the sum of the packet rate determined by the threshold (r) and the packet rate determined by the operant level (op).

3.4. Responses

3.4.1. Packets versus bouts

A packet consists of a variable number of responses with variable interresponse times. Packets of responses are theoretical; bouts are observed clusters of responses. Packets of responses can result in overlapping bouts of responses. Thus, the observed response bouts can differ from the theoretical packets of responses.

3.4.2. Number of responses in a packet

The number of responses per packet has a Poisson distribution with a mean of five responses per packet. The mean number of responses per packet was an approximation from the observations of Kirkpatrick (2002) and Kirkpatrick and Church (2003).

3.4.3. Interresponse distribution in a packet

The interresponse times within a packet were sampled from a Wald (Inverse Gaussian) distribution as described in Eq. (5):

$$f(x) = \left(\frac{\lambda}{2\pi x^3}\right)^{1/2} \exp\left(\frac{-\lambda(x-\mu)^2}{2\mu^2 x}\right) \tag{5}$$

where μ is the center parameter and λ the scale parameter. The parameter μ was set to 0.60 and λ set to 0.77 for simulations of all procedures. The Wald density function with these parameters is shown on the response panel of Fig. 3 for interresponse times ranging from 0 to 2.5 s. The Wald distribution can arise from a random-walk process with one absorbing barrier (Luce, 1986), but some additional or different processes may be involved to account for the small but systematic discrepancies between the observed and predicted interresponse interval distributions.

Table 1
Parameters of packet theory of timing and conditioning used for the simulation of the procedures with single and multiple time-markers

Procedure	Parameters											
	Bout			Pattern							Rate	
	#R	μ_w	σ_w	op	α	μ_b	γ_b	w_1	w_2	w_3	r	p_r
Single time-marker												
(1) One time-marker												
(a) Fixed time (Fig. 4)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.24	0.51	1	–	–	0.14	0.4
(b) Random Time (Fig. 7)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.24	0.51	1	–	–	0.05	0.4
(c) Fixed interval (Fig. 8)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.28	0.51	1	–	–	0.33	0.4
(d) Fixed interval (Fig. 10, top)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.24	0.55	1	–	–	0.33	0.4
(e) Fixed interval (Fig. 11, top)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.19	0.92	1	–	–	0.30	0.4
Multiple time-markers												
(2) Two time-markers												
(a) FI with event (Fig. 10, bottom)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.24	0.55	1	0.60	–	0.33	0.4
(2) Onset-to-food	5	0.60	0.77	0.004	0.05	0.53	0.55	–	0.40	–	0.33	0.4
(b) FI with event (Fig. 11, second)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.19	0.92	1	0.60	–	0.30	0.4
(2) Onset-to-food	5	0.60	0.77	0.004	0.05	0.40	0.92	–	0.40	–	0.39	0.4
(3) Three time-markers												
(a) FI with two events (Fig. 11, third)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.19	0.92	1	0.60	0.36	0.30	0.4
(2) Onset-to-food	5	0.60	0.77	0.004	0.05	0.40	0.92	–	0.40	0.24	0.39	0.4
(3) Termination-to-food	5	0.60	0.77	0.004	0.05	0.80	0.38	–	–	0.40	0.49	0.4
(b) FI with state (Fig. 11, bottom)												
(1) Food-to-food	5	0.60	0.77	0.004	0.05	0.19	0.92	1	0.60	0.36	0.30	0.4
(2) Noise-to-food	5	0.60	0.77	0.004	0.05	0.40	0.92	–	0.40	0.24	0.39	0.4
(3) Click-to-food	5	0.60	0.77	0.004	0.05	0.80	0.38	–	–	0.40	0.49	0.4

3.4.4. *Reactive packets*

In addition to response packets generated from the decision function and by the operant level, reactive response packets were generated with probability p_r for each delivery of food. These packets also have a Poisson distribution with a mean of five responses and an interresponse time distribution determined by a Wald density function as described in Eq. (5). The same parameter values used for the response packets generated from the decision function and the operant level were used for the reactive packets. Reactive response packets replaced any anticipatory response that had yet not occurred. The parameters used in the simulation of all procedures are presented in Table 1.

3.5. *Summary of packet theory*

In packet theory, responses are organized in packets. The probability of initiating a packet depends on three factors, the operant level, whether food was delivered or not, and the memory function (via a noisy threshold).

Once a packet starts, a variable, Poisson-distributed number of responses is emitted, with consecutive responses separated by variable, Wald-distributed time intervals.

4. Application of packet theory to a fixed-time procedure

Next we show the results of a simulation of packet theory in a fixed-time procedure. Packet theory was simulated for the fixed-time procedure shown in the top panel of Fig. 4. A sample of the output of the simulation is shown as a function of time for 20 blocks of 20 s observed during the last half of the simulation (Fig. 4, second panel). Although in some cases a response occurred by itself, in most cases responses were clustered together, suggesting that they occurred in bouts. The pattern obtained from the simulation resembled the pattern observed in the data (Fig. 2, second panel).

The interresponse time distribution observed in the data (empty circles), in the simulation (filled circles) and the theoretical Wald density function with the parameter μ set to 0.60 and λ set to 0.77 are shown in the third panel of Fig. 4. The most frequent interresponse times occurred at 0.192 s for the simulated distribution, 0.222 s for the theoretical distribution, and 0.282 s for the data distribution. The simulated interresponse time distribution (generated by the model) and the observed interresponse time distribution (generated by the animal) were both very similar to the theoretical Wald function.

Response rate (rpm) as a function of time since food (s) observed in the data (empty circles) and in the simulation (solid line) was high initially, decreased rapidly, and later increased as the time of the next food approached, as shown in the bottom panel of Fig. 4. The proportion of variance accounted for by the model (ω^2) was 0.96.

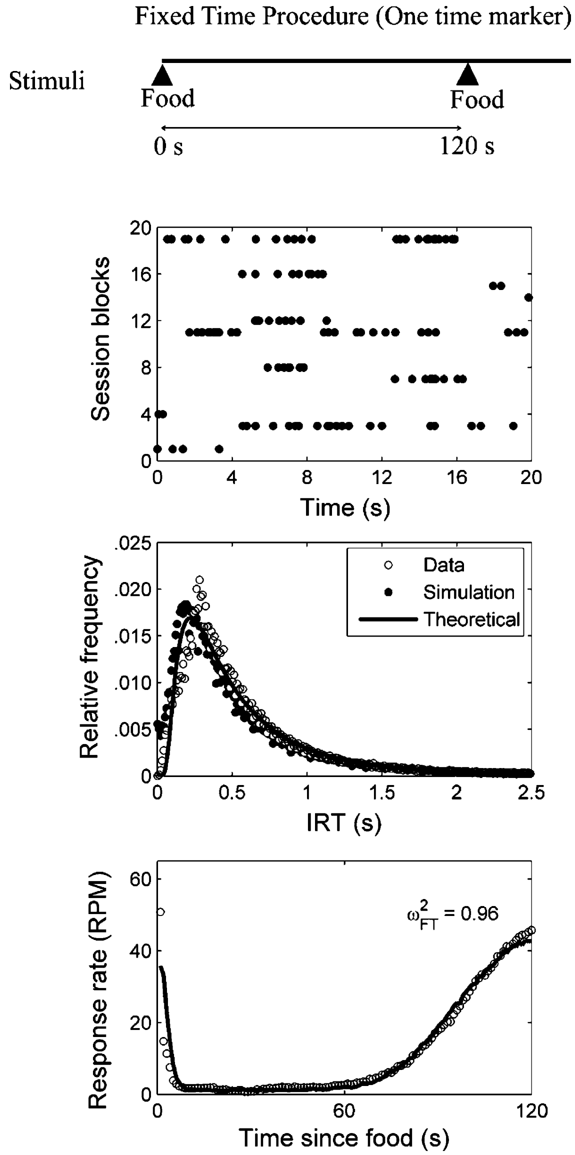

Fig. 4. Top panel: fixed time 120 s procedure. Second panel: simulated responses as a function of session time. Third panel: interresponse time distribution observed (empty circles), simulated (filled circles) and theoretical (solid line). The theoretical function was a Wald distribution with the location parameter (μ) set to 0.60 and the scale parameter (σ) set to 0.77. Bottom panel: response rate observed (empty circles) and response rate predicted by the model (solid line) as a function of time since food. The response was a head entry into a food cup by rats on a fixed-time procedure.

5. Similarity of bouts under different procedures

The bouts of behavior observed during the fixed-time procedure were well characterized by the Wald distribution shown by the solid line in third panel of

Fig. 4. The generality of the Wald distribution to describe the interresponse times within a bout of head entry responses by rats for many procedures is shown in Fig. 5. The relative frequency of interresponse times for classical procedures with fixed and random reinforcement distributions (fixed time, FT, and random time, RT), for procedures with different response contingencies (fixed and random time, FT and RT, and fixed interval, FI), and for different interval durations (45, 90, 120, and 180 s) was compared to the Wald distribution (with the same parameters used in the third panel of Fig. 4). The theoretical line fit to the mean of the six data functions accounted for 95% of the variance. The fit of the Wald distribution was impressive, because the same parameters were used for a wide range of procedures.

The extent to which packet theory can be generalized to simulate response rate curves from different procedures, such as the random-time (change in reinforcement distribution) and fixed-interval (change in response contingency) procedures, with no changes in its assumptions and few changes in parameter settings, is described next.

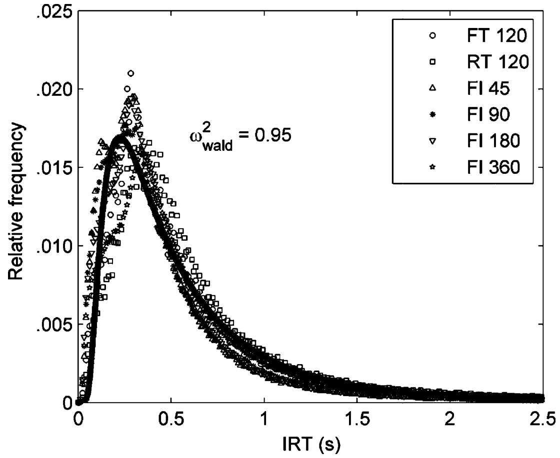

Fig. 5. Interresponse time distribution in classical conditioning procedures for different reinforcement distributions (fixed time, FT, and random time, RT), operant conditioning procedures (fixed interval, FI) and for different interval durations (45, 90, 120, 180 and 360 s). The response was a head entry into the food cup by rats. The solid line is the theoretical Wald distribution functions with the location parameter (μ) set to 0.60 and the scale parameter (σ) set to 0.77. Data from the four fixed-interval functions were provided by Elizabeth Kyonka.

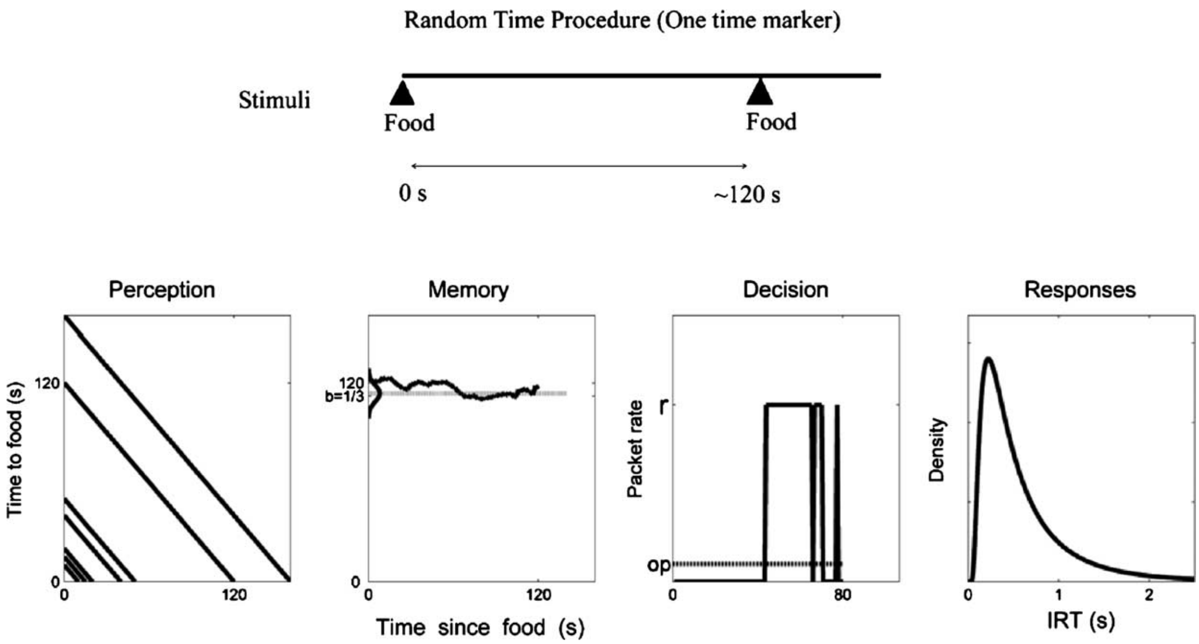

Fig. 6. Top panel: random time 120 s procedure. Bottom panel: perception, memory, decision, and response modules of packet theory applied to the random-time procedure.

6. Application of packet theory to a random-time procedure

The random-time procedure, shown in the top panel of Fig. 6, is identical to the fixed-time procedure, except that the times of food deliveries are distributed randomly (a random sample from an exponential distribution with a single parameter, μ). Packet theory for the random-time procedure is identical to the one for the fixed-time procedure. The differences in the output of the model follow from the difference in the procedure (reinforcement distribution). This is illustrated in Fig. 6. The perceptions may be greater or less than 120 s. When these are combined in memory, using the same equations as in the fixed case (Eq. (2)), the asymptotic memory function approaches a flat line near 120 s. In this example, as in the fixed-time procedure, the proportion of the memory below the threshold B is 1/3 (see Eqs. (3) and (4)). On a particular cycle, the packet rate varies from the operant level to r more than once per cycle (see decision panel of Fig. 6). As in the fixed case, when a packet is initiated, it consists of a mean of five responses with interresponse times approximated by a Wald function (Eq. (5)).

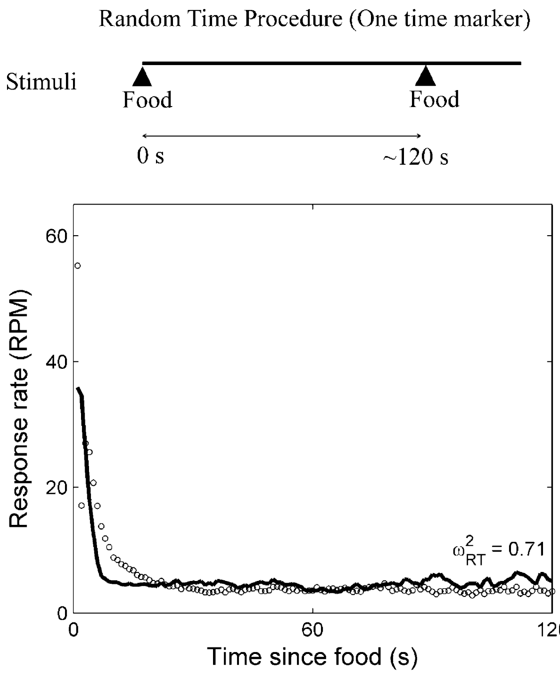

Fig. 7. Top panel: random-time procedure (one time-marker). Bottom panel: response rate observed (empty circles) and response rate predicted by the model (solid line) as a function of time since food (s). The response was a head entry into a food cup by rats on a random-time procedure.

Six rats were trained for 30 sessions on a random-time procedure with food delivered at times that were exponentially distributed with a mean of 120 s (Fig. 7, top panel). Head entries into the food cup were recorded. The bout structure of responding by the rats (interresponse time distribution) on the random-time procedure with a mean of 120 s is shown in Fig. 5 with open squares for the data (RT 120) and the solid line for the Wald distribution used for all the procedures. Fig. 7 shows the response gradients from data of the last half of training for the rats (open circles) and for the simulation (solid line). The behavior is characterized by a reaction to food, followed by a low and relatively constant response rate until the next food delivery. The simulated and observed response gradients were very similar. The proportion of variance accounted for by the model (ω^2) was 0.71, a value that is satisfactory considering that the mean is a reasonable estimate of the gradient.

7. Application of packet theory to a fixed-interval procedure

The fixed-interval procedure is identical to the fixed-time procedure, except that the food deliveries are dependent upon a response after termination of the interval (Fig. 8). Packet theory for the fixed-interval procedure is identical to the one for the fixed-time procedure; the differences in the output of the model follow from the difference in the procedure (response dependency). The addition of a response dependency produces a short but consistent delay between the reinforcer availability (prime) and reinforcer delivery. The interval perceived from a time-marker to food is based on the actual delivery of food and not on food availability. Therefore, the distribution in memory will be slightly longer and more variable for a fixed-interval than for a fixed-time procedure. As in the fixed-time and random-time procedures, if a packet is initiated, it consists of a mean of five responses with interresponse times approximated by a Wald function (Eq. (5)).

Six rats were trained for 30 sessions on a fixed-interval procedure with food primed 120 s following

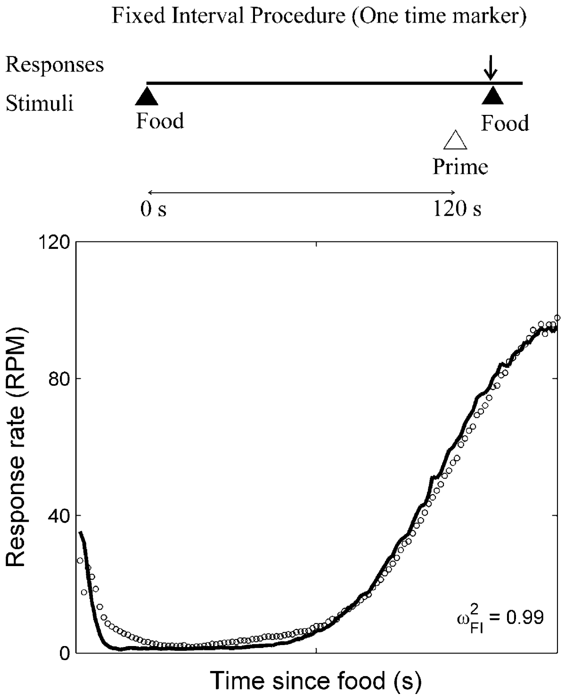

Fig. 8. Top panel: fixed-interval procedure (one time-marker). Bottom panel: response rate observed (empty circles) and response rate predicted by the model (solid line) as a function of time since food (s). The response was a head entry into the food cup by rats on a fixed-interval procedure.

the previous food delivery (Fig. 8, top panel) and delivered at the first head entry response after prime. Head entries into the food cup were recorded. The bottom panel of Fig. 8 shows the response gradients from data of the last half of training for the rats (open circles) and for the simulation (solid line). As in the fixed-time procedure, the behavior was characterized by a reaction to food, followed by a low rate that increased as the time of the next food approached. The simulated and observed response gradients were very similar. The proportion of variance accounted for by the model (ω^2) was 0.99.

8. Combination rules for multiple time-markers

The fixed-time, random-time, and fixed-interval procedures have one time-marker that indicates when the next food will be delivered. Packet theory accounted for the pattern, rate, and bout structures in the data under these procedures. In most procedures there is more than one time-marker. The problem is how these multiple sources of information affect the animals' behavior (Church et al., 2003; Meck and Church, 1984). In the next section, additional data will be described for cases in which multiple time-markers are present. Three ways in which different time-markers can be combined to generate packets of responses will be described. These alternative combination rules will be compared with the results of procedures with two and three time-markers.

The procedure shown in Fig. 9 (top panel) is a fixed-time 120 s procedure with the addition of a brief noise stimulus 90 s after food delivery. As in the case of a fixed-time procedure with no additional stimulus, the previous food is a time-marker for the next food delivery. This interval is called the food-food interval, which in this example, is 120 s. In this procedure, the noise is a second source of information about the time at which the next food will be available. This interval between the noise and food is referred to as noise–food interval, which in this example, is 30 s. The two intervals may be treated independently in the sense that each generates an expectation function in memory.

The decision function (rate of initiating packets of responses) described in the fixed-time case is a step function determined by the threshold B. For the two-event procedure described above, the food–food and noise–food functions occur together; they start at different times but overlap in time. (In this example, the functions overlap from 90 s until the time of food delivery, 120 s.) The functions are shown in the middle panels of Fig. 9 and are labeled food–food (FF) and noise–food (NF). A combination rule specifies the rate of packet generation at times when the functions overlap. Three ways that two decision functions can be combined (most recent, weighted mean, and sum) are shown in the bottom panels of Fig. 9. In all three cases, the generation of packets by the model can be defined by the summation of the packets generated by the two decision functions, each weighted by a constant (w). With different values of w, the changes in w determine whether the combination rule is "most recent," "weighted mean," or "sum".

Most recent (bottom of Fig. 9, left panel). The decision function that represents the most recent time-marker is used exclusively to generate packets (i.e., the weight of the function generated by the most recent time-marker NF is set to equal 1 and the weight of the function determined by the previous time-marker FF set to 0 following the presentation of the noise event). This is the simplest combination rule with no free parameters.

Weighted mean (bottom of Fig. 9, center panel). The weighted mean is a linear average of the two decision functions. The weights range between 0 and 1, and the sum of the two weights is equal to 1 (one free param-

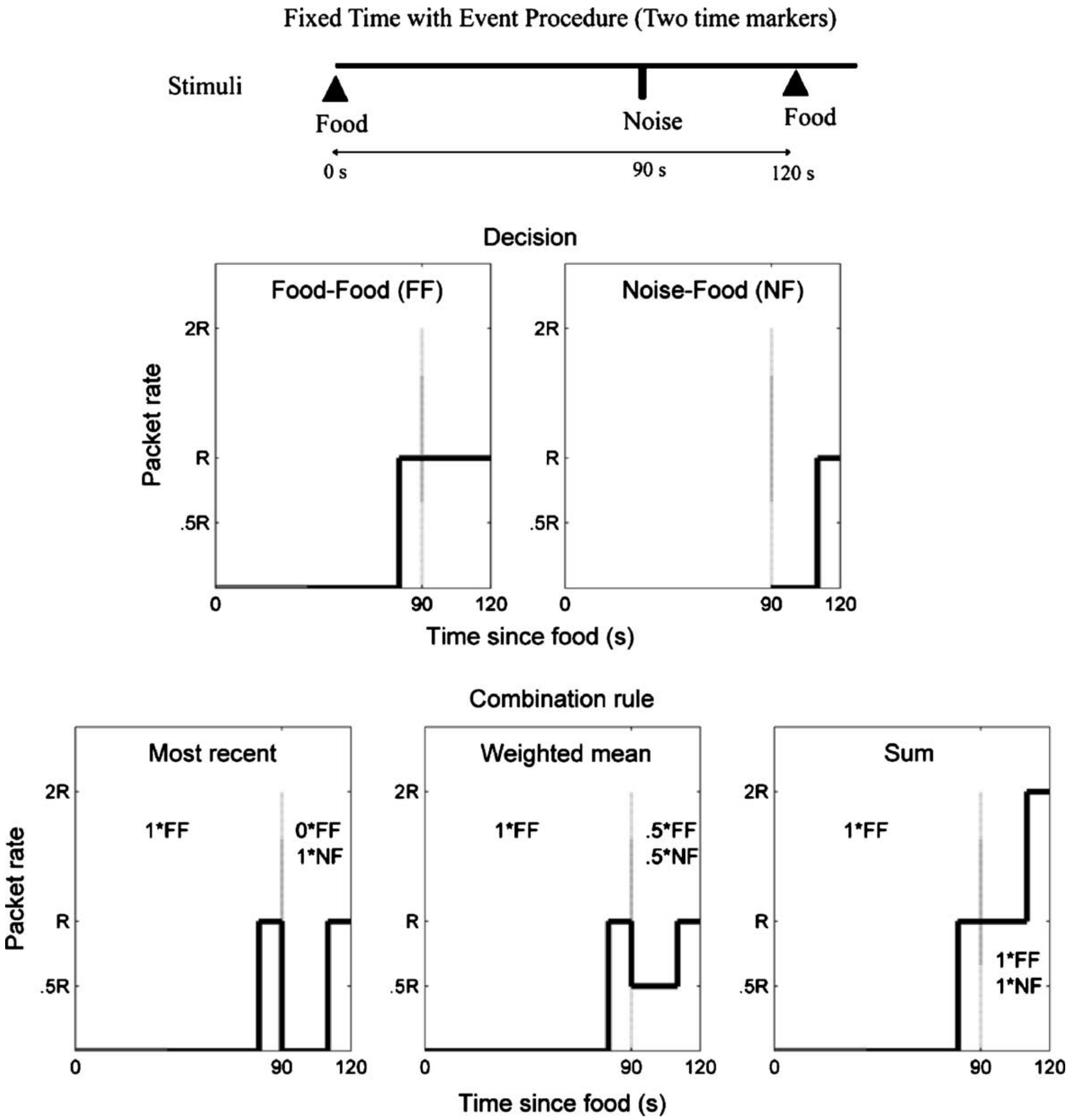

Fig. 9. Top panel: fixed interval with event procedure (two time-markers). Middle panels: decision module of packet theory for two time-markers: the preceding food (left panel) and brief presentation of noise (right panel). Bottom panels: three possible combination rules based on the decision functions of the two time-markers: most recent (left panel), weighted mean (center panel), and sum (right panel). See text for details.

eter). The center panel in Fig. 9 shows an example in which the weight of the FF was set to 0.5; thus, the weight of the NF was 0.5.

Sum (bottom of Fig. 9, right panel). The combination rule is a sum of the two decision functions each weighted independently. The two parameters are not constrained (i.e., there were two free parameters). The right panel in Fig. 9 shows an example in which the weight of the FF is set to 1 and the weight of the NF is also set to 1.

The combination rules described above were used to simulate packet theory for procedures with two and three time-markers. In the case of three time-markers, there are two additional free parameters for the weighted mean and the sum combination rules. The comparison between the data and model simulation was conducted and the choice among combination rules was based on an informal criteria that maximized the goodness of fit, and minimized the complexity (defined by the number of free parameters) of the combination rule. The simulations of the procedures with two and three time-markers are described in the next two sections.

9. Application of packet theory to two time-markers

Ten rats were trained for 30 sessions on a fixed-interval-with-event procedure (two time-markers) as shown in the left panels of Fig. 10. In this procedure, food was delivered dependent upon a head entry into the food cup after 120 s (standard fixed-interval procedure, top left panel). On some occasions ($p = 0.63$), a 1 s presentation of white noise occurred 90 s after the previous food delivery, and provided an additional signal for the time of the next food availability (bottom left panel). During these occasions, the procedure was a fixed interval with the addition of a signal at 90 s. Note

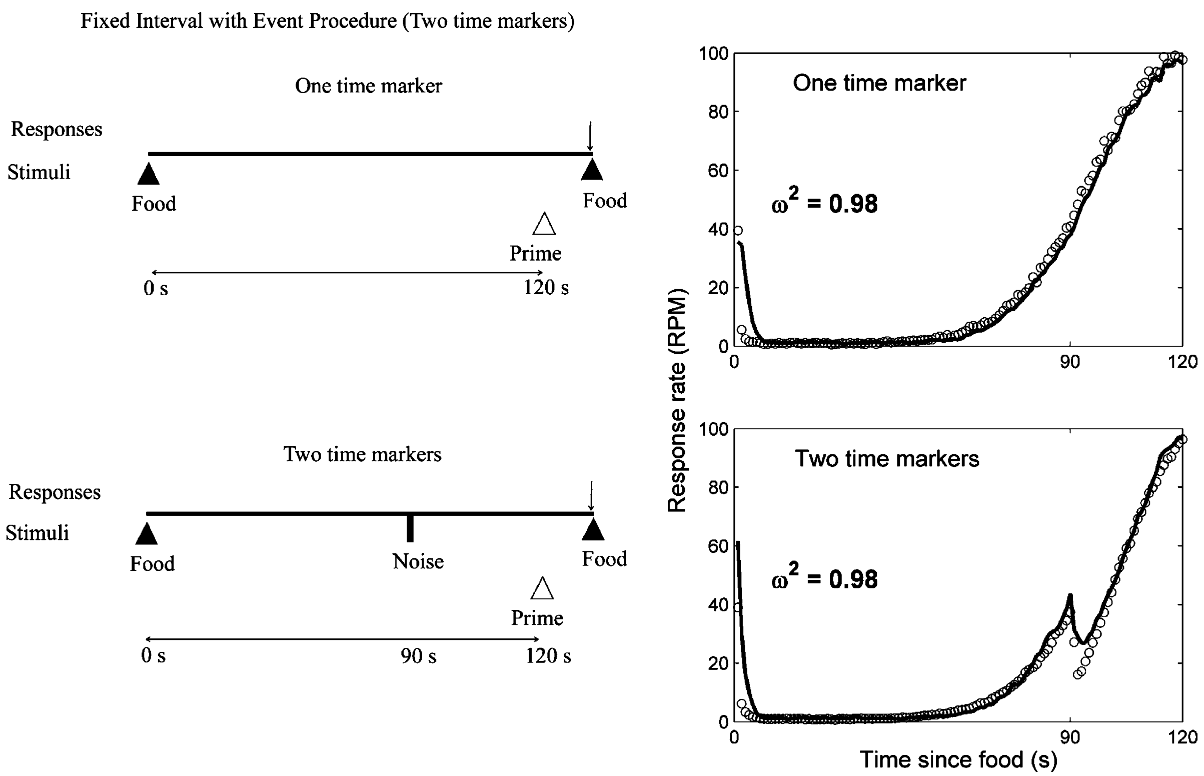

Fig. 10. Left panels: fixed interval with event procedure with no signal (top) and with signal (bottom). Right panels: response rate observed (empty circles) and response rate predicted by the model (solid line) as a function of time since food for the occasions with no signal (top) and occasions with signal (bottom).

that this procedure is the same as that described in Fig. 9 with the introduction of a response dependency and is also referred to as a tandem FT–FI schedule (Marr and Zeiler, 1974).

The results of the last 10 sessions of training are shown in the right panels of Fig. 10. When there was no signal (one time-marker), response rate initially decreased and then increased as the time of the next food approached (empty circles, top right panel). On the occasions in which there was a signal at 90 s, response rate also decreased initially and then increased as the time of the next food approached. In addition, there

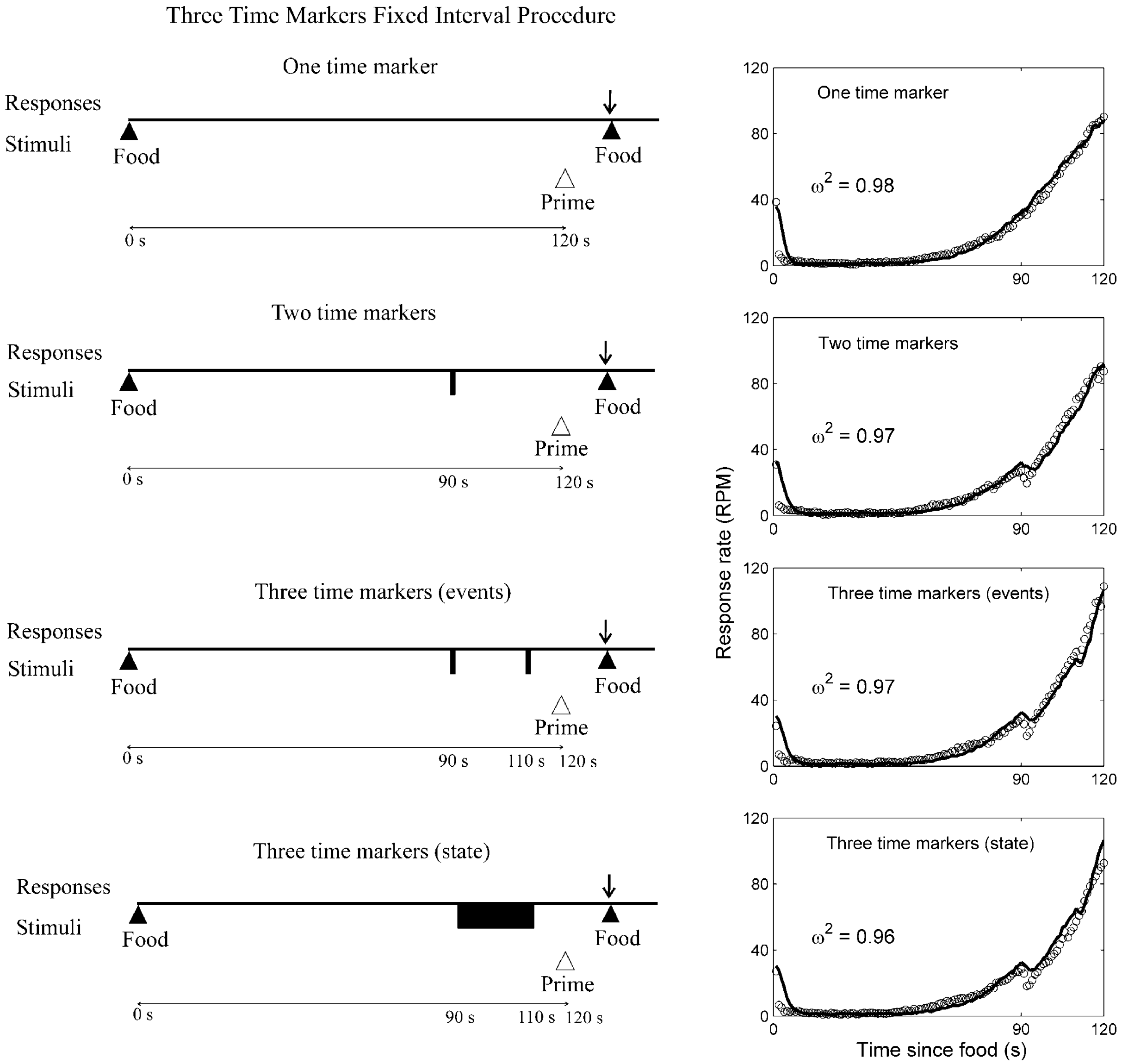

Fig. 11. Left panels: trace procedure with cycles with no signal (top panel), cycles with one brief event (second panel), cycles with two brief events (third panel), and cycles with the presentation of a stimulus state (bottom panel). Right panels: response rate observed (empty circles) and response rate predicted by the model (solid line) as a function of time since food(s) for the cycles with no signal (top panel), cycles with one brief event (second panel), cycles with two brief events (third panel), and cycles with a stimulus state (bottom panel).

was a dip at the time at which the brief signal occurred. That is, at the time of the signal, there was a sudden decrease in response rate, followed by an increase in the slope of the function (bottom right panel). The decrease in response rate following the signal is consistent with results previously described (Kelleher, 1966; Marr and Zeiler, 1974).

The solid lines are the simulation of packet theory to the data. On the occasions in which no signal occurred, packet theory is identical to that for the fixed-time, random-time, and fixed-interval procedures. The variance accounted for (ω^2) by the model was 0.98. On the occasions in which a signal occurred, packet theory is also identical to that for the fixed-time, random-time, and fixed-interval procedures with the addition of a perception, a memory, and a decision module for the additional time-marker, and the addition of a combination rule. On the occasions in which the two decision functions were generating packets, the weights were 0.6 for the food-to-food function and 0.4 for the noise-to-food function. The weighted average combination rule predicted the data well with one free parameter (see Table 1). Note that the parameters for the common function (food–food) for the two time-marker case and the one time-marker case were the same. Moreover, the combination rule parameters (w) were the same for the two time-marker procedures (Figs. 10 and 11). The variance accounted for by the model (ω^2) was 0.98.

10. Application of packet theory to three time-markers

Twenty-four rats were trained for 20 sessions on a trace conditioning procedure (3 time-markers fixed-interval procedure) as shown in the left panels of Fig. 11. In this procedure, food was delivered dependent upon a head entry response into the food cup 120 s after the previous food (standard fixed-interval procedure, top left panel). On some occasions ($p = 0.2$), a 0.5 s presentation of white noise occurred 90 s after the previous food delivery and provided an additional signal for the time of next food (second left panel). On other occasions ($p = 0.2$), in addition to the noise, another 0.5 s presentation of a clicker occurred at 110 s after the previous food and provided an additional signal for the time of the next food (third left panel). On other occasions ($p = 0.2$), a white noise started at 90 s and ended at 110 s after the previous food, providing two additional signals (stimulus onset and termination) for the time of the next reinforcement (fourth left panel). Note that on some occasions there was only one time-marker (top panels), on other occasions there were two time-markers (second panels), and still on others, three time-markers (third and bottom panels).

The results for the last five sessions of training are shown in the right panels of Fig. 11. When there was no signal (one time-marker), response rate initially decreased and then increased as the time of the next food approached (empty circles, top right panel). On the occasions in which there was a signal at 90 s response rate also decreased initially and then increased as the time of the next food approached. In addition, at the time of the signal, there was a sudden decrease in response rate followed by an increase in rate with an increase in the slope of the function (empty circles, second right panel). On the occasions in which there were two time-markers (either the noise and clicker, or onset and termination of the noise), response rate initially decreased and then increased as the time of the next food approached. In addition, at the times of the two signals, there was a sudden decrease in response rate followed by an increase in response rate with an increase in the slope of the function after each time-marker (empty circles, third and bottom panels).

The solid lines are the simulation of packet theory to the data. On the occasions in which no signal occurred, packet theory was identical to that for the fixed-time, random-time, and fixed-interval procedures. The variance accounted for (ω^2) by the model was 0.98. On the occasions in which two time-markers occurred, packet theory is identical to that described in the previous section for the two time-marker case. The weighted average combination rule predicted the data well with one free parameter (see Table 1). The variance accounted for by the model (ω^2) was 0.97.

On the occasions in which three time-markers occurred, packet theory is identical to the two time-marker theory with the addition of a perception, a memory, and a decision module for the third time-marker, and the addition of one parameter to the weighted average combination rule (see Table 1). The weight parameters (w) were the same as in the two time-marker cases, whenever there were two decision functions generating packets of responses. When there was an additional decision function (either determined by the termination of the noise, or a click sound) the parameters were 0.36 for the food-to-food, 0.24 for the onset-to-food, and 0.4 for the termination-to-food. The weighted average combination rule predicted the data well with one free parameter. The variance accounted for (ω^2) by the model was 0.96.

11. Discussion

Packet theory provides a quantitative account of the times of responses of rats in procedures that differed on four dimensions—the distribution of times between successive reinforcers (fixed or random), the interval between reinforcers (45, 90, 120, 180, 360 s), the contingency between response and reinforcer (classical or operant), and the number of time-markers (1, 2 or 3).

11.1. Comparison of behavior in different procedures

11.1.1. Similarities

In all these procedures, the characteristics of the bouts, the operant rate, and the learning rate were similar. The distribution of head entries within a bout could be characterized by a Wald distribution with the location parameter equal to 0.60 s and the scale parameter equal to 0.77 s. The same low operant rate (0.004 responses per minute) was used for all procedures. The same learning rate (0.05) was also used for all procedures, although the actual learning rate, α, could not be identified by the analyses that were conducted on asymptotic data. The 0.05 learning rate was close to the learning rate previously used to describe initial acquisition of fixed intervals and transitions from one fixed interval to another (Guilhardi and Church, in press). It could also be set close to 1 to account for the dependency of the post-reinforcement pause on the just-preceding interfood interval, especially when the interfood interval is short (Wynne and Staddon, 1992).

11.1.2. Differences

The effects of the procedures on behavior were primarily due to their effects on the pattern and rate of responding. The procedures affected the mean and coefficient of variation of the threshold, and the rate of packet generation. A single parameter, rate of packet generation (r), was sufficient to account for the differences between the fixed- and random-time procedures. The three interval procedures were simulated with variations in the rate of packet generation and the mean and variability of the threshold. These three parameters were also varied to account for the data in the procedures with multiple time-markers. Ideally all the parameters would be the same across all conditions, or there would be a simple rule to account for the effects of the procedures on the parameters that were different under different conditions.

11.2. Combination rules

In procedures involving two or three time-markers, the observed behavior was a result of a combination of the effects of the individual time-markers, including the possibility of interactions between time-markers. For the procedures involving multiple time-markers, a weighted average combination rule was sufficient to account for the data. This consisted of a weight for each of the time-markers that had occurred at a given time during the cycle, with the sum of the weights equal to 1.0. The weights were consistent across procedures.

11.3. Evaluation of packet theory

11.3.1. Fit of the data by the model

The data was reasonably fit by the model. The percentage of variance accounted for was high and approximately the same in 9 of the 10 functions shown in Figs. 4, 5, 8, 10 and 11 (0.95, 0.96, 0.96, 0.97, 0.97, 0.98, 0.98, 0.98, and 0.99). In the case of the random procedure (Fig. 7), the percentage of variance accounted for was only 0.71, but the theory had segments appropriate to the reaction to food and the constant expected time to food. The measure of percentage of variance accounted for is not particularly useful for flat functions since it is a comparison of the unexplained variance of the data relative to the unexplained variance of the mean of the data. In this case, the mean of the data is a good approximation of the data.

11.3.2. Simplicity of the model

One of the strengths of this model was that it was possible to use the same values for many of the parameters across all the procedures. The three parameters that were used to simulate the data accounted for 1080 data points in the gradients (120 data points in each of 9 figures). The 3000 data points in the 6 relative distributions of the interresponse intervals shown in Fig. 5 (500 data points for each of 6 conditions) did not require any parameter adjustment across different procedures. Because of the high ratio of data points to adjusted parameters, the model is reasonably simple.

11.3.3. Generality of the model

The generality of the model refers both to the generality of the input that the model can accept, and the generality of the output that the model can deliver. The generality of the input to the model refers to the range of procedures that are fit by the model. Packet theory was applied to procedures involving one, two, and three time-markers in classical and instrumental procedures with different time intervals and reinforcement distributions. Thus, the model is reasonably general in terms of the input it can accept.

The generality of the output of the model refers to the range of measures of behavior that it fits. The potential generality of the model is considerable. Because the model predicts times of responses, the simulation can be used to estimate any dependent measure that can be calculated from the original data (e.g., interresponse time distributions, response gradients, and discrimination ratios). The original data containing times of onset and termination of stimuli and responses generated by the rats, as well as the times of onset and termination of stimuli and responses generated by the model are available. In the present paper, fits from the simulation are presented only for the interresponse time distribution and the response gradients, but a model that can pass a Turing test (Church, 2001) must fit all other dependent measures as well (Guilhardi and Church, in press).

Although the variance accounted for by the model was high in most of the procedures described, a more sensitive evaluation of the model will show the necessity of improvements. Church and Guilhardi (in press) showed that although the fit of the model on a fixed-interval procedure was excellent, the model is still distinguishable from the real data using a Turing test.

11.3.4. Fits to individual animals

The primary data consists of the times of responses between individual interfood intervals. The primary data may be averaged across a session, multiple sessions, and across rats. The averaging across multiple observations can produce changes in the function shape, as well as reductions in variability. The change in function shape produced by averaging is particularly apparent when the primary data is averaged across a session of individual rats. For example, the primary data of fixed-interval responding is a step function which, when averaged across interfood intervals, produces an ogival function (Schneider, 1969). The primary simulated data of packet theory consists of step functions similar to those produced by individual animals on individual interfood intervals.

The simulation of packet theory produced the primary data for approximately the same amount of training received by an individual rat on any procedure. Thus, it would be possible to compare the theory to the primary data or averaging across multiple observations on a single session, across sessions, or across individuals. The original data and the simulated data are available at http://www.brown.edu/Research/Timelab.

11.4. Comparison of this version with the previous version of packet theory

The version of packet theory used in this article is a slightly modified version of the one described by Kirkpatrick (2002) and Kirkpatrick and Church (2003). It will be called “Version 2” to distinguish it from the original version that will be called “Version 1”.

The major change to Version 2 is that a threshold with a mean and coefficient of variation was introduced. In Version 1 the probability of packet initiation was linearly related to the memory of the time since food; the threshold in Version 2 provides the flexibility for other relationships (such as a step function) between the memory of the time since food and the probability of packet initiation. The simulated mean response rate over many cycles is ogival in shape. A second change in Version 2 was in the use of a Wald distribution for the description of the bouts of behavior. This had only a small effect on the predicted times of responses, but it was more consistent with the data.

11.5. Further developments of the model

The generality of the model must be examined further. This involves comparing the predictions of the model to experimental results, with many additional procedures (input generality), and on many measures of head entries as well as other classes of responses (output generality). This research will undoubtedly identify failures of the present version of the model that will need to be rectified. In some cases, these changes may not make the model more complex, such as a change in the bout-generating function. In other cases, however, it may be necessary to introduce an additional concept with free parameters. For example, it may be necessary to introduce some perceptual variability to account for quantitative results in various procedures, such as the peak procedure.

The meaning of the parameter values (shown in Table 1) must also be examined further. The parameters that are constant across all procedures may be regarded as characteristic of the animal, but what is the meaning of those that are different for different procedures? In the present analysis these parameters include the mean and standard deviation of the threshold, and the rate of packet elicitation. In some cases, the amount of training or the reinforcement rate may be the cause, but these influences must be identified explicitly to be satisfactory. Otherwise, one must assume that the animal has a procedure detector that it can use to set its parameters. Although not described in this article, the model can be applied to individual animals. When this is done, it is clear that there are reliable individual differences in the parameters across animals. Ideally, individuals would maintain consistent parameter values across many procedures.

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References

Bush, R.R., Mosteller, F., 1955. Stochastic Models for Learning. Wiley, New York.

Church, R.M., 2001. A Turing test for computational and associative theories of learning. Curr. Dir. Psychol. Sci. 10, 132–136.

Church, R.M., Guilhardi, P., Keen, R., MacInnis, M., Kirkpatrick, K., 2003. Simultaneous temporal processing. In: Helfrich, H. (Ed.), Time and Mind II: Information Processing Perspectives. Hogrefe & Huber Publishers, Göttingen, Germany, pp. 3–19.

Church, R.M., Guilhardi, P., in press. A Turing test of a timing theory. Behav. Process.

Dews, P.B., 1962. The effects of multiple S^{Δ} periods on responding on a fixed-interval schedule. J. Exp. Anal. Behav. 5, 369–374.

Ferster, C.B., Skinner, B.F., 1957. Schedules of Reinforcement. Appleton-Century-Crofts, New York.

Guilhardi, P., Church, R.M., in press. Dynamics of temporal discrimination. Learn. Behav.

Kelleher, R.T., 1966. Conditioned reinforcement in second-order schedules. J. Exp. Anal. Behav. 9, 475–485.

Kirkpatrick, K., 2002. Packet theory of timing and conditioning. Behav. Process. 57, 89–106.

Kirkpatrick, K., Church, R.M., 2003. Tracking of the expected time to reinforcement in temporal conditioning procedures. Learn. Behav. 31, 3–21.

La Barbera, J.D., Church, R.M., 1974. Magnitude of fear as a function of expected time to an aversive event. Anim. Learn. Behav. 2, 199–202.

Luce, R.D., 1986. Response Times: Their Role in Inferring Elementary Mental Organization. Oxford University Press, New York.

Marr, M.J., Zeiler, M.D., 1974. Schedules of response-independent conditioned reinforcement. J. Exp. Anal. Behav. 21, 433–444.

Meck, W.H., Church, R.M., 1984. Simultaneous temporal processing. J. Exp. Psychol. Anim. Behav. Process. 10, 1–29.

Pavlov, I.P., 1927. Conditioned Reflexes (Transl.; G.V. Anrep). Oxford University Press, New York.

Schneider, B.A., 1969. A two-state analysis of fixed-interval responding in the pigeon. J. Exp. Anal. Behav. 12, 677–687.

Shull, R.L., Gaynor, S.T., Grimes, J.A., 2001. Response rate viewed as engagement bouts: effects of relative reinforcement and schedule type. J. Exp. Anal. Behav. 75, 247–274.

Tolkamp, B.J., Kyriazaki, I., 1999. To split behaviour into bouts, log-transform the intervals. Anim. Behav. 57, 807–817.

Wynne, C.D.L., Staddon, J.E.R., 1992. Waiting in pigeons: the effects of daily intercalation on temporal discrimination. J. Exp. Anal. Behav. 58, 47–66.