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ScienceDirect
Behavioural Processes 75 (2007) 188–198
BEHAVIOURAL PROCESSES
www.elsevier.com/locate/behavproc

Short communication

Applications of timing theories to a peak procedure

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Received 6 September 2006; received in revised form 14 December 2006; accepted 23 January 2007

Abstract

This article describes applications of scalar expectancy theory (SET), learning-to-time theory (LeT), and Packet theory to data from a peak procedure. Twelve rats were trained in a multiple cued-interval procedure with two fixed intervals (60 and 120 s) signaled by houselight and white noise. Twenty-five percent of the cycles were nonfood cycles, which were 360 s long and had no reinforcement. Mean and individual response rates on nonfood cycles were fitted with explicit solutions of SET, LeT and Packet theory. Applications of the three timing theories were compared in terms of goodness of fit and complexity.

Keywords: LeT; Packet theory; Peak procedure; SET

1. Introduction

Two mathematical theories of timing behavior, scalar expectancy theory (SET; Gibbon et al., 1984) and learning-to-time theory (LeT; Machado, 1997) use different approaches to explain the behavior of animals on timing procedures. A more recent account, Packet theory (Kirkpatrick, 2002) integrates the two approaches with the inclusion of multiple variance sources (as in SET) and vector memories (as in LeT). Although these theories were constructed in different ways, each of them includes three common components: a representation of physical time, a storage mechanism that contains information about when reinforcers are delivered, and a response rule to generate predictions (Church, 1999).

SET (Gibbon et al., 1984) is a cognitive account in terms of perception, memory and decision. The number of pulses generated by a pacemaker represents physical time since a time signal, which is recorded in an accumulator. The number of pulses at the time of reinforcement, multiplied by a memory coefficient, is stored in a distribution memory. A new number from the accumulator will be compared to a remembered value and, when they are "close enough," operant responses occur. This theory emphasizes multiple variance sources and that variability in timing is proportional to the mean of the interval being timed, which is known as the scalar property of timing.

An alternative theory, LeT (Machado, 1997), derived originally from BeT (Killeen and Fetterman, 1988), assumes that the temporal regulation of operant behavior is derived from a sequence of behavioral states that is the representation of physical time. Information about when reinforcers are delivered is encoded by an associative component. Operant response rate depends on both activation of behavioral states and their associative strength. One major success of LeT is that it generates accurate predictions for acquisition of timing behavior, and these predictions converge to an appropriate description of steady-state behavior (Machado, 1997; Machado and Cevik, 1998).

Packet theory was first proposed by Kirkpatrick and Church in 2002 and 2003, and has been modified somewhat since then (Guilhardi et al., 2005, in press). The name comes from the observation of bouts of responses which result from packets of responses issued by the theory (Kirkpatrick and Church, 2003). A current version of Packet theory (Guilhardi et al., in press) has a storage mechanism that consists of two separate memories, pattern memory and strength memory, dealing with response pattern and response rate, respectively. The two memories are combined with an operant level to initiate packets. Packet theory combines SET's multiple variance sources and LeT's vector memories, which allows this theory to account not only for scalar properties of steady-state responding, but also for acquisition and extinction (Guilhardi et al., in press).

The peak procedure is commonly used to study temporal generalization (Catania, 1970; Roberts, 1981). In a simple peak procedure, fixed-interval (FI) cycles and nonfood cycles are presented in a random order. A nonfood cycle is much longer than

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doi:10.1016/j.beproc.2007.01.010

an FI cycle and has no reinforcement. The data analyses usually focus on the behavior on nonfood cycles. Studies show that data from peak procedures can be well fitted by the explicit solutions of SET (e.g., Gibbon et al., 1984) and LeT (e.g., Machado, 1997). The explicit solution of Packet theory was recently developed (Yi, 2006) and has not previously been applied to the peak procedure. In the present analysis, steady-state data from a peak procedure with multiple cued intervals were fitted with the explicit solutions of the three theories.

2. Materials and methods

2.1. Animals

Twelve experimentally naïve male Sprague–Dawley rats (Taconic Laboratories, Germantown, NY) were used. Each animal received 5 g of Dustless Precision Pellets (Bio-Serv, Rodent Grain-Base Formula, Frenchtown, NJ) that were delivered as reinforcers during the experiment and an additional 15 g of FormuLab 5008 food in its home cage every day after its testing session.

2.2. Apparatus

Each of the 12 chambers (25 cm × 30 cm × 30 cm) was equipped with a pellet dispenser, a left lever, a right lever, and a water bottle. The pellet dispenser (Model ENV-203) delivered 45-mg pellets into the food cup that was located midway between the left lever and the right lever. The two levers (Model ENV-112) were located 12 cm apart, placed 7 cm above the floor grid, and measured 4.5 cm wide, 1 mm thick, 2 cm expanded into the box, and required a force of 18 g to operate. On the wall opposite to the levers and the food cup, one water bottle was mounted outside of the box with a tube that protruded through a hole in the wall. An audio amplifier (Model ANL-926) was located outside of the wall with the water bottle, which was used to produce 70-dB white noise. A houselight (Model ENV-227M) was located near the ceiling of the box and was used to produce 200 Lux light. Each chamber was located inside a ventilated box (74 cm × 38 cm × 60 cm) that was used for noise attenuation. Four Gateway Pentium®III/500 computers running Med-PC Medstate Notation Version 2.0, controlled experimental events and recorded the time at which each event and response occurred with 2-ms precision.

2.3. Procedure

Phase 1. Two fixed intervals (60 and 120 s) were signaled by two stimuli, white noise and houselight, counterbalanced across rats. Only one lever, either the left or right lever, was used for responding (the assignment of levers was counterbalanced across rats). A cycle started with the onset of the stimulus (or stimuli). If the two stimuli were presented individually, the cycle type was referred to as FI 60 s or FI 120 s, in which the first press 60 s after the onset of the short stimulus, or the first press 120 s after the onset of the long stimulus, was reinforced with a food pellet and terminated the stimulus. If the two stimuli were presented together, the cycle type was referred to as the compound condition, in which the first press 60 s after the onset of the short stimulus was reinforced with a food pellet and terminated the short stimulus, and the first press 120 s after the onset of the long stimulus was reinforced with one more pellet and terminated the long stimulus. After 20 s without stimuli, a new cycle started. A session ended with 14 cycles of FI 60 s, 14 cycles of FI 120 s, and 28 cycles of the compound condition. The three cycle types were mixed and presented in a random order. Rats were trained for 100 sessions (Session 1–100).

Phase 2. After Phase 1 the same rats were exposed to the peak procedure. Twenty-five percent of the cycles were nonfood cycles. The remaining were food cycles as the same as in Phase 1. Food cycles and nonfood cycles were randomly presented. On the nonfood cycles of FI 60 s and 120 s (i.e., Peak 60 and 120 s), the stimulus lasted 360 s and no food was delivered. On the nonfood cycles of the compound condition, the two stimuli terminated simultaneously 360 s after the cycle start and no food was delivered for either of them. Rats were trained for another 100 sessions (Session 101–200). The compound condition in Phase 1 and 2 was designed for simultaneous timing of multiple intervals and the data were not included in the present analysis.

2.4. Data analyses

The data from all nonfood cycles of FI 60 and 120 s (i.e., Peak 60 and 120 s) were used for the analyses. Mean and individual response rate were fitted with the explicit solutions of SET, LeT and Packet theory (see Appendix A for details). Parameters were estimated by the "NLINFIT" function in MatLab 7.0 (R14) (MathWorks, Natick, MA) with the Gaussian–Newton algorithm.

3. Results

The mean response rate on nonfood cycles as a function of time since stimulus onset is shown in the left panels of Fig. 1 (filled and open circles). The response rate increased gradually when the stimulus began and, after a maximum that was close to the time of reinforcement, the gradient declined gradually in a slightly asymmetric fashion. After the response rate declined, the rats continued responding with a low steady rate. The mean relative response rate (normalized by maximum) as a function of relative time (normalized by peak time) on Peak 60 and 120 s approximately superposed (not shown). A similar response pattern has been observed in many peak studies (e.g., Roberts, 1981; Roberts et al., 1989; Church et al., 1994). This suggested that the compound condition did not have a substantial effect on the responding during Peak 60 and 120 s cycles.

The solid lines near the filled and empty circles in the left panels of Fig. 1 are the fits of the three theories to the mean data. Table 1 provides the corresponding parameters and the goodness of fits as measured by ω^2 (the proportion of variance explained). The residuals, defined as the difference between the mean data and the predicted values, are shown as a function of time since stimulus onset in the right panels of Fig. 1. The residuals from

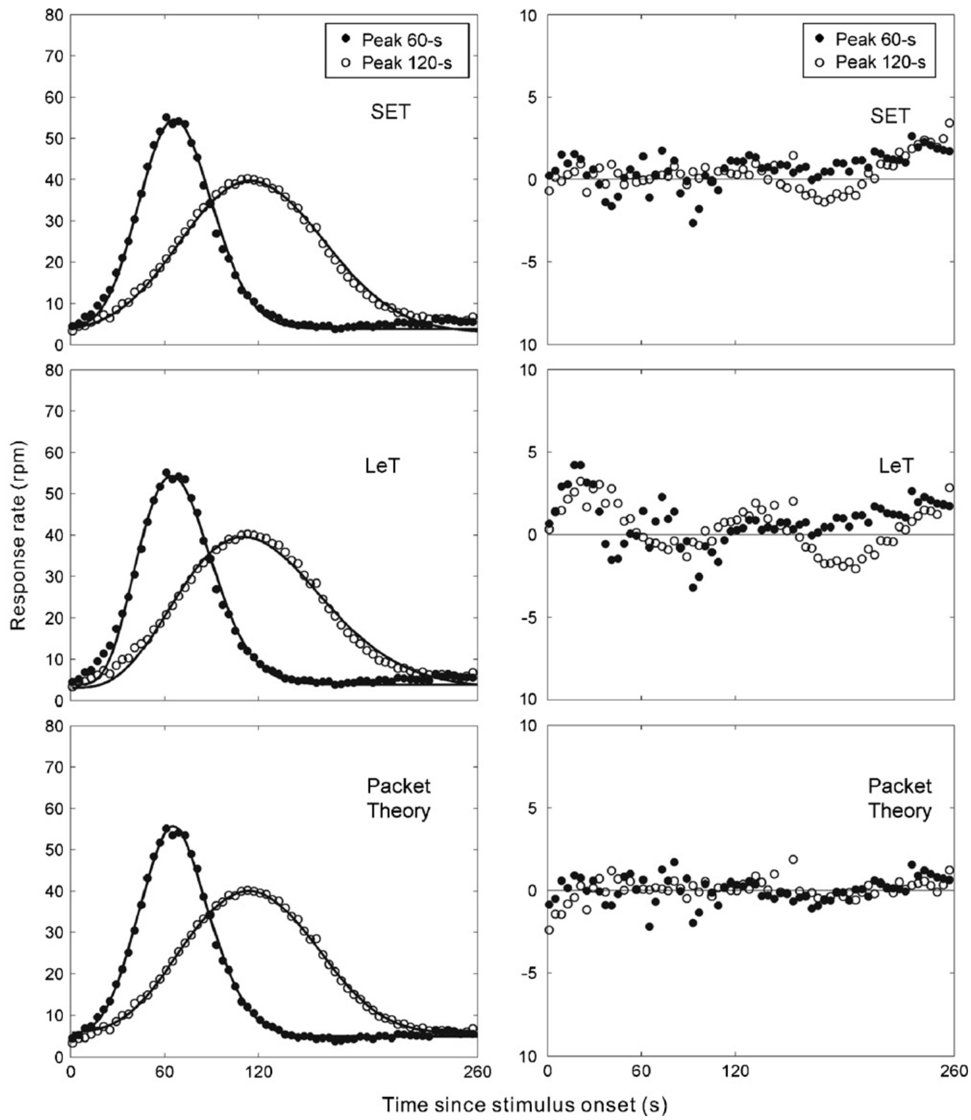

Fig. 1. Mean response rate on nonfood cycles on Peak 60 s (filled circles on left panels) and 120 s (open circles on left panels), predictions of three theories (solid lines across circles on left panels) and the corresponding residuals (right panels).

fits of the models to the individual data were very similar to the residuals from their fits to the mean (not shown).

3.1. Scalar expectancy theory (SET)

SET (Gibbon et al., 1984) assumes that a pacemaker generates pulses that are stored in an accumulator. The accumulated number of pulses since a time signal, denoted by $m(t)$, is the representation of current elapsed time. When reinforcement occurs, the accumulated number is transferred into reference memory. A distribution memory for the time of reinforcement is built up with many cycles of training. m_{m} indicates a random sample from this distribution memory.

The comparison rule of SET (Gibbon et al., 1984) is

$$\left|\frac{m_{\mathrm{m}} - m(t)}{m_{\mathrm{m}}}\right| < b \quad (1)$$

where b is a threshold. Let E denote the event that the inequality in Eq. (1) is satisfied and $\bar{E}$ denote the event that it is not (i.e., $|m_{\mathrm{m}} - m(t)|/m_{\mathrm{m}} \geq b$). Then the probability of response, $P[R(t)]$, is

$$P[R(t)] = P[R(t)|E]P(E) + P[R(t)|\bar{E}]P(\bar{E}) \quad (2)$$

The original account of SET (Gibbon et al., 1984) assumed that the probability of response was 1 when Eq. (1) was true (i.e., $P[R(t)|E] = 1$) and that the probability of response was 0 when Eq. (1) was false (i.e., $P[R(t)|\bar{E}] = 0$). As such, it cannot account for the low, steady rate of responding observed in the latter portion of peak cycles. In this analysis, the theory was slightly modified: When Eq. (1) was not satisfied, responses still occurred with a low probability P_{R_0} (i.e., $P[R(t)|\bar{E}] = P_{R_0}$). Because $P(E) + P(\bar{E}) = 1$, Eq. (2) can be rewritten as

$$P[R(t)] = (1 - P_{R_0})P(E) + P_{R_0} \quad (3)$$

Table 1
Parameters used by the three theories

		Equation[a]	Peak 60	Peak 120
SET				
Λ	Mean pacemaker rate	(A1)	5.000	5.000
γ_λ	Coefficient of variation of pacemaker rate	(A2)	.020	.020
T_0	Mean switch delay	(A1)	0	0
σ_0	Standard deviation of switch delay	(A2)	7.316	8.616
K_m	Mean memory multiplier	(A3)	1.000	.950
γ_k	Coefficient of variation of memory multiplier	(A4)	.312	.123
B	Mean threshold	(A5)	.158	.345
γ_b	Coefficient of variation of threshold	(A6)	.713	.815
A	Scale parameter	(A8)	154.616	52.649
P_{R_0}	Probability of response at low state	(A8)	.030	.041
ω^2	Proportion of variance accounted for		**.996**	**.992**
LeT				
λ	Spreading rate of activation of behavioral states	(A9)	.288	.106
γ	Learning parameter	(A11)	.035	.017
A	Scale parameter	(A12)	119.75	94.734
R_0	Operant level	(A12)	3.858	3.072
ω^2	Proportion of variance accounted for		**.991**	**.986**
Packet theory				
K	Mean memory coefficient	(A13)	1.100	.960
γ_k	Coefficient of variation of memory coefficient	(A13)	.111	.083
Φ	Mean threshold percentage	(A15)	31.590	41.634
γ_b	Coefficient of variation of threshold	(A15)	.884	.565
A	Scale parameter	(A18)	64.964	37.277
R_0	Operant level	(A18)	4.946	5.557
ω^2	Proportion of variance accounted for		**.998**	**.997**

[a] The equations in Appendix A.

In this analysis, P_{R_0} was viewed as a parameter. To fit the response gradient, a scale factor A with units s^{-1} was required to translate the probability of response $P[R(t)]$ into response rate $R(t)$:

$$R(t) = AP[R(t)] \tag{4}$$

This modified SET fit the mean response rate gradient very well ($\omega^2 = .996$ for Peak 60 s and $\omega^2 = .992$ for Peak 120 s). The residuals between the mean response rate and the prediction of SET were small but slightly systematic (top right panel of Fig. 1). The mean ω^2 of individual fits was .960 (S.D. = .019) for Peak 60 s and .937 (S.D. = .032) for Peak 120 s.

3.2. Learning-to-time theory (LeT)

Machado's (1997) LeT consists of three components: a series of behavioral states, the operant response, and the association between the behavioral states and the operant response. At time t, the activation of behavioral state j is $X(t,j)$, and the strength of its association with the operant response is $W(t,j)$. The rate of operant response $R(t)$ depends on the activation and the associative strength of all behavioral states:

$$R(t) = A\sum_{j=1} X(t, j)W(t, j) \tag{5}$$

where A is the scale parameter with units s^{-1}. Because this response rule also cannot account for responses during the low state of responding, it was modified by the inclusion of an operant level R_0:

$$R(t) = A\sum_{j=1} X(t, j)W(t, j) + R_0 \tag{6}$$

Because the peak of prediction of LeT was consistently later than the time of reinforcement when probability of reinforcement is high (see Machado, 1997, for details), the representation for the time of reinforcement (or target time) was set earlier than the actual target time. For example, to fit the mean data, the target time was 57 s for Peak 60 s and 102 s for Peak 120 s.

The fit of LeT to the mean response rate gradient was $\omega^2 = .991$ for Peak 60 s and $\omega^2 = .986$ for Peak 120 s. The residuals between the mean response rate and the prediction of LeT oscillated around zero, and the oscillation frequency on Peak 60 s was approximately twice the frequency on Peak 120 s (right middle panel of Fig. 1). The mean ω^2 of individual fits was .940 (S.D. = .027) for Peak 60 s and.935 (S.D. = .035) for Peak 120 s.

3.3. Packet theory

In Packet theory, the information about when reinforcers are delivered is stored in a vector memory denoted by $m(t)$, which is compared with a threshold b to generate a variable called response state $h(t)$:

$$h(t) = \begin{cases} 1 & \text{if } |m(t)| < b \\ 0 & \text{if } |m(t)| \geq b \end{cases} \tag{7}$$

The expected value of $h(t)$ (expressed as $E[h(t)]$, see Eq. (A16) in Appendix A) was calculated based on the combination of two scalar sources: the remembered time of reinforcement and the threshold. Steady-state responding was determined by $E[h(t)]$:

$$R(t) = AE[h(t)] + R_0 \tag{8}$$

where R_0 is the operant level, which is similar to the operant level that has been added to LeT, and A is the scale parameter with units s^{-1}.

Results showed that Packet theory fit the mean data accurately: $\omega^2 = .998$ for Peak 60 s and $\omega^2 = .997$ for Peak 120 s. The residuals between the mean response rate and the prediction of Packet theory were small (right bottom panel of Fig. 1). The mean ω^2 of individual fits was .976 (S.D. = .013) for Peak 60 s and .950 (S.D. = .035) for Peak 120 s.

The goodness of fit of the three theories was compared by entering ω^2 values from fits to individual data into a repeated-measures ANOVA, followed by pairwise t-tests. For Peak 60 s, the goodness of fit of the three theories were significantly different ($F_{(2,22)} = 19.958, p < .001$), the fit of Packet theory was higher than LeT ($t_{(11)} = 5.399$, $p < .001$) and SET ($t_{(11)} = 3.011$, $p < .05$), and the fit of SET was higher than LeT ($t_{(11)} = 4.035$, $p < .01$). For Peak 120 s, the difference between the goodness of fit of the three theories was not significant ($F_{(2,22)} = 1.402$, $p = .267$), the fit of Packet theory was higher than LeT ($t_{(11)} = 3.316$, $p < .01$) but not different from SET ($t_{(11)} = 1.240$, $p = .241$), and the fits of SET and LeT were similar ($t_{(11)} = .140$, $p = .892$).

4. Discussion

A basis for comparison of the three theories (SET, LeT, and Packet theory) is required to determine which provided the best account of the data. Although a number of criteria have been proposed to be important for theory comparison, three are widely accepted and frequently used: goodness of fit, complexity and generality.

4.1. Goodness of fit

All three theories described the data very well, accounting for approximately 99 percent of the variance in the mean response rate gradients (shown in the left panels of Fig. 1), and over 90% of the variance in the individual response rate gradients.

The residuals (shown in the right panels of Fig. 1) refer to the differences between the observed and predicted data. Random residuals indicate unexplained variability that may be due to random fluctuations or measurement errors; systematic residuals indicate unexplained variability and suggest limitations of the theory. The residuals from a good theory should be small and randomly distributed about zero. The observed residuals from the three timing theories were small but systematic. This suggests modifications of the theories that should be considered.

The systematic residuals in the latter portion of peak cycles with all three theories may have been due to the assumption that a constant operant level accounted for the response rate during the low state of responding that, in fact, increased slowly with time. The oscillating residuals of LeT may have been due to the predictions of this theory that produced gradients more skewed than the data.

4.2. Complexity

In addition to goodness of fit, the complexity of a theory is an important basis for theory evaluation. An unnecessarily complex theory will overfit the data and increase the variability in parameter estimation (Myung, 2000).

In this analysis, SET used 10 parameters, LeT used 4 and Packet theory used 6 (Table 1). If all parameters were estimated by free searching, theories with many parameters would probably obtain variable parameter estimates (discussed later). To reduce the risk of overfitting data, some parameters were fixed with empirical values. For example, the operant level (R_0) in LeT and (AP_{R_0}) in SET were represented by the response rate at time $t = 0$; the mean pacemaker rate (Λ) in SET was 5 and the coefficient of variation (γ_λ) was .02, and the mean switch delay (T_0) was 0; the mean memory multiplier (K_m) in SET and the mean memory coefficient (K) in Packet theory were 1 or

Table 2
Comparison of complexity

	SET	LeT	Packet theory
(a) ω^2s in cross-validation			
Peak 60 s			
Calibration	.991	.987	.996
Validation	.972	.969	.951
Difference = $C - V$	.019	.018	.045
Peak 120 s			
Calibration	.991	.986	.991
Validation	.899	.895	.860
Difference = $C - V$	.092	.091	.131

	A	B	γ_b	γ_k	T_0	σ_0
(b) Coefficient of variation in parameter estimation						
SET						
Peak 60 s	.530	.406	.499	2.172	.120	.107
Peak 120 s	.304	.230	.444	.460	3.150	.216

	A	λ	γ
(b) Coefficient of variation in parameter estimation			
LeT			
Peak 60 s	.333	.120	.509
Peak 120 s	.510	.204	.712

	A	Φ	γ_b	γ_k	R_0
(b) Coefficient of variation in parameter estimation					
Packet theory					
Peak 60 s	.166	.122	.215	.257	.292
Peak 120 s	.332	.500	.679	.418	.456

close to 1. (These parameters are defined in Appendix A.) The remaining parameters, estimated with free searching, are listed in Table 2b. SET, LeT and Packet theory used 6, 3, and 5 free parameters, respectively.

Cross-validation was used to measure overfitting due to theory complexity. The general approach was as follows: (a) a data set was divided into a calibration sample (e.g., the data from odd sessions) and a validation sample (e.g., the data from even sessions), (b) the values of the parameters that minimized the sum of squared deviations between the calibration sample and the predictions of the theory were determined, and then (c) these parameters were used to fit the validation sample. The decrement of goodness of fit of validation sample relative to the calibration sample is a measure of overfitting. Table 2a provides the mean ω^2s across individual rats based on the calibration and validation samples and the difference between them. It shows that the mean ω^2s on validation did not decline much for SET or LeT. But Packet theory had the largest decrement on Peak 60 s (4.3%) and Peak 120 s (13.2%), which suggests it had a tendency to overfit the data.

Complexity also affects the variability in parameter estimation. An overly complex theory can successfully fit one data set regardless of errors in the parameters. When such a theory is used to fit another sample, the parameter values will change dramatically to get the excellent fit, but those unstable parameter values carry very little information. To measure the variability of parameter estimation, the whole data set in this analysis was divided into 10 subsets. (Subset j contains the $(10i+j)$th sessions; $i=0, 1, 2, \ldots, 9$; $j=1, 2, \ldots, 10$.) and the mean response rate gradient of each set was fitted by the three theories. Table 2b shows the coefficient of variation (the standard deviation divided by the mean, or CV) of each free parameter across 10 samples. It shows that most parameters of LeT and Packet theory are very stable. But some parameters of SET, such as γ_k and T_0, are more variable.

4.3. Generality

The generality of a theory should be composed of its input generality and output generality. Input generality refers to the range of procedures the theory can explain, and the output generality refers to the range of measures the theory can fit. The goal of all theories is to account for a wide range of procedures and be suitable for a wide range of dependent measures. Because it is not the major issue of this analysis, the generality of the three theories is not further discussed.

The comparison of three timing theories reveals that each of them has particular strengths and weaknesses. SET generated excellent fits, but was overly complex. LeT was parsimonious and its fits were good, but there were systematic errors. Packet theory combined some good features of SET and LeT, which allowed it to fit data well without using many parameters. Although this analysis described the applications of the three theories to only a single dependent variable (the response rate gradient) of a single procedure (the peak procedure), at asymptote, the successes of these theories suggest that much progress has been made towards the development of an accurate, general, and parsimonious account of timing behavior.

Acknowledgements

This analysis was supported by National Institute of Mental Health Grant MH44234 to Brown University. The author appreciated the guidance and support of Russell Church during the preparation of this article. She also thanks Mika MacInnis and Richard Keen for help in design and execution of the experiment.

Appendix A. Explicit solutions of three theories

A peak procedure is a mixture of food cycles with a probability of p and nonfood cycles with a probability of $1-p$. On food cycles, the first response after a fixed interval T_1 since the onset of a stimulus (e.g., houselight) is reinforced with the delivery of food for a fixed duration d, and it terminates the stimulus. On nonfood cycles, the stimulus goes off T_2 after the stimulus onset without food. The short delay between the food availability and its delivery following a response on food cycles is not under the consideration of this analysis.

A.1. SET

In SET, the probability of response $P[R(t)]$ is largely determined by the probability of $|m_\mathrm{m}-m(t)|/m_\mathrm{m}<b$, denoted by $P(E)$.

The number of pulses in the accumulator, $m(t)=\lambda\tau$, is a Poisson distribution. The pacemaker rate λ is a normally distributed random variable with a mean Λ and standard deviation, $\sigma_\lambda=\gamma_\lambda\Lambda$, where γ_λ is the coefficient of variation of λ. The switch is assumed to have some latency (t_1) to close after the stimulus turns on and some latency (t_2) to open after the stimulus turns off. The difference between the two latencies, $t_0=t_1-t_2$, is normally distributed with a mean T_0 and standard deviation σ_0. The effective switch closure time, τ, is the difference between the actual time t and t_0: $\tau=t-t_0$. Then, the expected value of $m(t)$ is

$$E[m(t)] = \Lambda(t-T_0) \tag{A1}$$

and the variance is

$$\mathrm{Var}[m(t)] = (1+\gamma_\lambda^2)(\Lambda\sigma_0)^2 + \Lambda(t-T_0) + \gamma_\lambda^2\Lambda^2(t-T_0)^2 \tag{A2}$$

The number of pulses at the time of reinforcement ($t=T_1$) is m_T. It is stored in memory as m_m, multiplied by a variable k_m (i.e., $m_\mathrm{m}=k_\mathrm{m}m_\mathrm{T}$). k_m is a normally distributed random variable with a mean K_m and standard deviation $\sigma_\mathrm{m}=\gamma_k K_\mathrm{m}$, where γ_k is the coefficient of variation of k_m. Then, the expected value of m_m is

$$E(m_\mathrm{m}) = K_\mathrm{m}\Lambda(T_1-T_0) \tag{A3}$$

and the variance is

$$\begin{aligned}\mathrm{Var}(m_\mathrm{m}) = K_\mathrm{m}^2[&(1+\gamma_\lambda^2)(1+\gamma_k^2)(\Lambda\sigma_0)^2 + (1+\gamma_k^2)\Lambda(T_1-T_0) \\ &+((1+\gamma_\lambda^2)(1+\gamma_k^2)-1)\Lambda^2(T_1-T_0)^2]\end{aligned} \tag{A4}$$

The threshold b is a normally distributed random variable with a mean B and standard deviation $\gamma_b B$, where γ_b is the coefficient of variation of b.

The three variance sources, $m(t)$, m_m, and b, can be combined. Define $x_i(t)=m(t)-[1+(-1)^i b]m_\mathrm{m}$, $i=1, 2$. The expected value of $x_i(t)$ is

$$E[x_i(t)] = \Lambda(t-T_0) - [1+(-1)^i B]K_\mathrm{m}\Lambda(T_1-T_0) \tag{A5}$$

and the variance is

$$\begin{aligned}\mathrm{Var}[x_i(t)] = {}&\sigma_\mathrm{m}^2 + \sigma_{\mathrm{m_m}}^2(\gamma_b^2B^2 + [1+(-1)^i B]^2) \\ &+[K_\mathrm{m}\Lambda(T_1-T_0)]^2\gamma_b^2B^2\end{aligned} \tag{A6}$$

where $\sigma_\mathrm{m}^2 \equiv \mathrm{Var}[m(t)]$ and $\sigma_{\mathrm{m_m}}^2 \equiv \mathrm{Var}(m_\mathrm{m})$ (Eqs. (A2) and (A4)).

Define $Z_i = -E[x_i(t)]/\sqrt{\mathrm{Var}[x_i(t)]}$, $i=1, 2$. Z_1 and Z_2 are the corresponding z values of zero on the distribution of x_1 and x_2, respectively. Because the distribution of $x_i(t)$ is approximately normal (see Appendix in Gibbon et al., 1984, for details), the distribution of Z_i is approximately a standard normal distribution with a mean of zero and standard deviation of one. Then, the probability of $|m_\mathrm{m}-m(t)|/m_\mathrm{m}<b$ is

$$P(E) = \Phi(Z_2) - \Phi(Z_1) \tag{A7}$$

where Φ is the distribution function of standard normal distribution:

$$\Phi(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} \exp\left(-\frac{u^2}{2}\right) du$$

The probability of response $P[R(t)]$ is calculated by $P[R(t)] = P(E)P[R(t)|E] + P(\bar{E})P[R(t)|\bar{E}]$, where $P[R(t)|E]$ refers to the probability of response given $|m_{\mathrm{m}} - m(t)|/m_{\mathrm{m}} < b$, and $P[R(t)|\bar{E}]$ refers to the probability of response given $|m_{\mathrm{m}} - m(t)|/m_{\mathrm{m}} \geq b$. Because $P[R(t)|E] = 1$, $P[R(t)|\bar{E}] = P_{R_0}$, and $P(\bar{E}) + P(\bar{E}) = 1$, the probability of response is rewritten as $P[R(t)] = (1 - P_{R_0})P(\bar{E}) + P_{R_0}$, which is translated to response rate by a scale parameter A:

$$R(t) = A[(1 - P_{R_0})P(E) + P_{R_0}] \tag{A8}$$

A.2. LeT

LeT has three components: behavioral states, operant response, and the association between the behavioral states and the operant response.

The activation of behavioral state j at time t is

$$X(t, j) = \frac{\exp(-\lambda t)(\lambda t)^j}{j!} \tag{A9}$$

where λ is the parameter that refers to the speed of the activation spreading across the states.

The associative strength at the beginning of $(n+1)$th cycle is

$$W_{n+1}(0, j) = \underbrace{pW_n(T_1 + d, j)}_{\text{food cycle}} + \underbrace{(1 - p)W_n(T_2, j)}_{\text{nonfood cycle}} \tag{A10}$$

$W_n(T+d,j)$ is obtained through the reinforcement dynamic process (Eq. (6) in Machado, 1997) with $t = T_1 + d$ (i.e., the previous cycle is food cycle), and $W_n(T_2,j)$ is obtained through the no-reinforcement dynamic process (Eq. (5) in Machado, 1997) with $t = T_2$ (i.e., the previous cycle is nonfood cycle). Both of them can be written as a function of $W_n(0,j)$. Then, Eq. (A10) becomes a linear difference equation: the left-hand side is $W_{n+1}(0,j)$ and the right-hand side only contains $W_n(0,j)$. The solution of $W_n(0,j)$ can be calculated and its steady-state distribution, denoted by $W(j)$, is

$$W(j) \approx \frac{X(T_1, j)}{X(T_1, j) + \gamma \int_0^{T_1} X(\tau, j)\,d\tau + \gamma(1 - p/p) \int_0^{T_2} X(\tau, j)\,d\tau} \tag{A11}$$

where $\gamma = \alpha/\beta d$. α and β are the learning parameters during reinforcement and no-reinforcement, respectively. LeT assumes that $W_n(t,j)$ at steady state does not change appreciably with time on a single cycle, such that $W_n(t,j) \approx W_n(0,j)$. Then, $W(j)$ in Eq. (A11) is an approximation of the steady-state distribution of $W_n(t,j)$.

The modified response rule is

$$R(t) = A \sum_{j=1} X(t, j)W(j) + R_0 \tag{A12}$$

with a scale parameter A and operant level R_0.

A.3. Packet theory

The explicit solution of Packet theory presented in this Appendix is a condensed version, with a full account to be provided elsewhere (Yi, 2006). At steady state, the storage mechanism contains the remembered time of reinforcement $\hat{T}_1$, reference memory $m(t)$ and strength memory $w(t)$.

$\hat{T}_1$ is a normally distributed random variable with a mean KT_1 (K, the mean of memory coefficient and T_1 is the time of reinforcement) and standard deviation $\gamma_k KT_1$ (γ_k, the coefficient of variation of memory coefficient). Then the density function of $\hat{T}_1$ is

$$g(y) = \frac{1}{\gamma_k KT_1 \sqrt{2\pi}} \exp\left(\frac{-(y - KT_1)^2}{2\gamma_k^2 (KT_1)^2}\right) \tag{A13}$$

The steady-state reference memory $m(t)$ is

$$m(t) = \hat{T}_1 - t \quad (0 \leq t \leq T_2), \qquad m(t) = m_0 \quad (t > T_2) \tag{A14}$$

where m_0 is the initial memory. The steady-state strength memory $w(t)$ is approximately constant.The threshold b is normally distributed with a mean B and standard deviation $\gamma_b B$, where γ_b is the coefficient of variation of b. Then the density function of b is

$$f(x) = \frac{1}{\gamma_b B \sqrt{2\pi}} \exp\left(\frac{-(x - B)^2}{2\gamma_b^2 B^2}\right) \tag{A15}$$

where B is the φth percentile of $m(t)$ (for $m(t) \geq 0$). Because $m(t)$ is a function of $\hat{T}_1$ (Eq. (A14)), B is also a function of $\hat{T}_1$, expressed as $B(\hat{T}_1)$.

The response state $h(t)$ is based on the comparison of $|m(t)|$ with b: when $|m(t)|$ is less than b, the high response state $h(t)$ is true (i.e., $h(t) = 1$), otherwise, it is false (i.e., $h(t) = 0$). The convolution of $\hat{T}_1$ and b is calculated to obtain the expected value of $h(t)$:

$$E[h(t)] = \frac{1}{2\pi\gamma_k\gamma_b KT_1} \int_0^{\infty} dy \int_{|y-t|}^{\infty} dx \frac{1}{B(y)} \times \exp\left(\frac{-(x - B(y))^2}{2\gamma_b^2 B^2(y)}\right) \exp\left(\frac{-(y - KT_1)^2}{2\gamma_k^2 (KT_1)^2}\right) \tag{A16}$$

The packet initiation rate $r(t)$ depends on the response state $h(t)$, the strength memory $w(t)$, and the operant level of packet initiation r_0:

$$r(t) = ah(t)w(t) + r_0 \tag{A17}$$

where a is a scale parameter. To translate packet initiation rate to response rate, the number of responses per packet u is required: $R(t) = ur(t)$. Because the mean of u and $w(t)$ are constant, or approximately constant, the expected value of response rate is

$$E[R(t)] = AE[h(t)] + R_0 \tag{A18}$$

where $A = auw(t)$, and R_0 is the operant level of response rate.

Appendix B. MatLab code

```
%%These functions for applications of theories to a peak procedure
%%    Scalar Expectancy Theory: setpeak
%%    Learning-to-time Theory: letpeak
%%    Packet Theory: packetpeak

%% Scalar Expectancy Theory

function R = setpeak(t,T,parameters)
%% Inputs
%% t = a temporal vector (integers)
%% T = time of reinforcement (an integer)
%% parameters = a vector that contains 10 parameters
%% Outputs
%% R = model prediction; a vector with the same size of t
%% e.g. for peak 120
%% t = 1:260; bin size is 1 s
%% T = 120;
%% parameters = [5 0.02 0 8.676 0.95 0.123 0.345 0.8146 52.6489 0.041];

%%%%%%%%%%%% parameters %%%%%%%%%%
Lammda = parameters(1); % mean pacemaker rate
gammaLammda = parameters(2); % cv. of pacemaker rate
T0 = parameters(3); % mean switch latency
Sigma0 = parameters(4); % SD. of switch latency
Km = parameters(5); % mean memory multiplier
gammaKm = parameters(6); % cv. of memory multiplier
B = parameters(7); % mean threshold
gammaB = parameters(8); % cv. of threshold
A = parameters(9); % scale parameter
Pr0 = parameters(10); % Probability of response at low state

%%%%%%%%%%%% model %%%%%%%%%%%%%
%%% accumulator %%%
D = t - T0; %% effectual switch closure duration
Dt = T - T0; %% effectual reinforcement time
E_Mt = Lammda*D; %% mean of Mt in Eq.A1
Var_Mt = (1+gammaLammda^2).*(Lammda*Sigma0).^2+Lammda*D+
gammaLammda^2.*(Lammda*D).^2; %% variance of Mt in Eq.A2

%%%% memory %%%
E_Mm = Km*Lammda*Dt; %% mean of Mm in Eq.A3
Var_Mm = Km^2.*[(1+gammaLammda^2).*(1+gammaKm^2).*(Lammda*Sigma0).^2 +
(1+gammaKm^2).*Lammda.*Dt+((1+gammaLammda^2).*(1+gammaKm^2)-
1).*(Lammda*Dt).^2]; %% variance of Mm in Eq.A4

%%% decision %%%
%% combination of Mt, Mm and b
Sigmab = B*gammaB; %% SD. of b
W1 = 1-B;
W2 = 1+B;
E_x1 = E_Mt - E_Mm*W1; %% Eq.A5
E_x2 = E_Mt - E_Mm*W2; %% Eq.A5
Var_x1 = Var_Mt+Var_Mm*(Sigmab^2 + W1^2)+(E_Mm^2).*(Sigmab.^2);%%Eq.A6
Var_x2 = Var_Mt+Var_Mm*(Sigmab^2 + W2^2)+(E_Mm^2).*(Sigmab.^2);%%Eq.A6
Z1 = -E_x1./sqrt(Var_x1);
Z2 = -E_x2./sqrt(Var_x2);

%%% response %%%
Pr = normcdf(Z2)-normcdf(Z1); %% Eq.A7
R = A*((1-Pr0)*Pr+Pr0); %% response rate in Eq.A8
```

```
%% Learning-to-time Theory

function R = letpeak(t,T,parameters)
%% Inputs
%% t = a temporal vector (integers)
%% T = time of reinforcement (an integer)
%% parameters = a vector that contains 4 parameters
%% Outputs
%% R = model prediction; a vector with the same size of t
%% e.g. for peak 120
%% t = 1:260; bin size is 1 s
%% T = 102; % see results
%% parameters = [0.106 0.017 94.734 3.072];

%%%%%%%%%%%% parameters %%%%%%%%%%
Lammda = parameters(1); % spreading rate of activation
Gamma = parameters(2); % learning rate
A = parameters(3); % scale parameter
R0 = parameters(4); % operant level

%%%%%%%%%%%% procedure %%%%%%%%%%%%
T2 = 360; %% the length of nonfood cycle
p = 0.75; %% the probability of food

%%%%%%%%%%%% model %%%%%%%%%%%%
jx = 1; %% the 1st behavioral state
for j = 1:80
    %% activation of behavioral states, X(t,j), in Eq.A9
    jx = jx*j; %% j!, j-factorial
    X(t,j) = exp(-Lammda*t).*(Lammda*t).^j./jx;
    Xt = exp(-Lammda*T).*(Lammda*T).^j./jx; %% when t=T, X(T,j)

    %% integration 1 in Eq.A11: if the last cycle is food cycle
    Xr1 = 0;
    for i = 0:T
        Xs= exp(-Lammda*i).*(Lammda*i).^j./jx;
        Xr1 = Xr1 + Xs;
    end
    Xr1 = 1*Xr1;

    %% integration 2 in Eq.A11: if the last cycle is nonfood cycle
    Xr2 = 0;
    for i = 0:T2
        Xs= exp(-Lammda*i).*(Lammda*i).^j./jx;
        Xr2 = Xr2 + Xs;
    end
    Xr2 = 1*Xr2;

    %% associative strength in Eq.A11
    W = Xt/(Xt + Gamma*Xr1 +Gamma*(1-p)/p*Xr2);
    r(t,j) = W*X(t,j);
end

%% response rate in Eq.A12
R = A*sum(r,2)+R0;
```

```
%% Packet Theory

function R = packetpeak(t,T,parameters)
%% Inputs
%% t = a temporal vector (integers)
%% T = time of reinforcement (an integer)
%% parameters = a vector that contains 6 parameters
%% Outputs
%% R = model prediction; a vector with the same size of t
%% e.g. for peak 120
%% t = 1:260; if bin size is 1 s
%% T = 120;
%% parameters = [0.96 0.083 41.634 0.565 37.277 5.557];

%%%%%%%%%%%% parameters %%%%%%%%%%
K = parameters(1); % mean memory coefficient
gammaK = parameters(2); % cv. of memory coefficient
Phi = parameters(3); % mean threshold percentage
gammaB = parameters(4); % cv. of threshold
A = parameters(5); % scale parameter
R0 = parameters(6); % operant level

%%%%%%%%%%%% procedure %%%%%%%%%%%%%
T2 = 360; %% the length of nonfood cycle

%%%%%%%%%%%% model %%%%%%%%%%%%%
ht(t) = 0; %% initial response state

for i = 1:T2
    %% distribution function of T^hat in Eq.A13
    T_density =
    exp(-(i-K*T)^2/(2*(gammaK*K*T)^2))/(sqrt(2*pi)*gammaK*K*T);

    %% reference memory in Eq.A14
    Mt = i-t;

    %% the mean threshold
    B = prctile(Mt(find(Mt>=0)),Phi);

    %% distribution function of b in Eq.A15
    B_density = 1 - normcdf(abs(Mt),B,B*gammaB+eps);

    %% response state, h(t), in Eq.A16
    Ph = B_density*T_density;
    ht = ht + Ph;
end

%% response rate in Eq.A18
R = [A*ht + R0]';
```

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