Journal of Veterinary Science & Technology manuscript No.
(will be inserted by the editor)

Small deviations from the scalar property and carry-over effects

J Veterinar Sci Technolo 2016, Volume 7 Isuue 1
doi: 10.4172/2157-7579.1000294

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Received: January 16, 2016 / Accepted: January 27, 2016 / Published: January 29, 2016

Abstract In order to measure the extent to which timing behavior diverges from a scalar property, the authors tested their recently published model of timing behavior (Hasegawa, T., & Sakata, S., 2015, *Journal of Computational Neuroscience*, 38, 301–313).

With rats as subjects, peak-interval procedures were performed. For each interval length presented to subjects, the model was used to identify the length of the basic clock period and the weight of the clocks. A carry-over effect was observed on the basic clock period, suggesting the uniqueness of the clock (stopwatch) system. Analysis indicated that, when coping with peak-interval procedures of different lengths, the rats changed not only the basic clock period but also the weights of the clocks. It was the changes in the clocks' weights that led to the observed small deviations from the scalar property, and this also suggested the uniqueness of the clock (stopwatch) system in the range tested in the experiment.

Keywords Scalar property · Peak procedure · Basic clock period · Weights of clocks

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1 Introduction

The data used in this study are the same as in our recently published study, Hasegawa and Sakata (2015), in which the focus was primarily on the mathematical model. In the current study, we apply that model and method to an analysis of the timing behavior of animals.

1.1 Peak-interval procedure and scalar property

A fixed-interval (FI) schedule of reinforcement can be used as a part of a set of temporal discrimination procedures. In an FI procedure, a hungry subject is reinforced at the time of the first response after a fixed interval of time has elapsed since the last previous reinforcement. A peak-interval (PI) procedure includes both FI trials and probe trials, in which no reward is given, and it is widely used to study interval timing[1].

Empirical results show that the timing behavior of an animal has a scalar property, consistent with Weber's law for timing, and it demonstrates timescale invariance (superposition) (Church 2003; Gibbon 1991; Gibbon 1977). Mathematically, this property is demonstrated when the graphs of the timing response functions of an animal are identical to a linear transformation expressed by some matrix $\begin{pmatrix} a & 0 \\ 0 & b \end{pmatrix}$, where a and b are nonzero real numbers; this is true even if their functions are created under different FI durations in the PI schedule.

[1] Abbriviations. FI schedule, fixed interval schedule; PI procedure, peak-interval procedure.

1.2 Scalar expectancy theory

The scalar property is one of the starting points of the scalar expectancy theory (SET), which was developed by Gibbon and colleagues (Gibbon 1977; Gibbon et al. 1984)[2].

In SET, the operant response function describing behavior during a PI procedure is expressed by

$$R(t) = a \exp\left\{-\frac{1}{2}\left(\frac{t-t_0}{b}\right)^2\right\} + R_0 \quad (t \geqq 0), \qquad (1)$$

where $R(t)$ is the operant response function, which measures the time at which a behavior appears that indicates that the subject perceives that the interval has elapsed, t_0 is the t-coordinate of the vertex of the graph of $R(t)$, b is the standard deviation, and a and R_0 are parameters. This is a modification of the density function for the normal distribution.

1.3 Poisson decomposition

We were inspired by the behavioral theory-of-timing (BeT) model (Killeen and Fetterman 1988) and the learning-to-time (LeT) model (Machado 1997) to develop a model of interval-timing behavior (Hasegawa and Sakata 2015).

Let λ be a constant, and let

$$X_n(t) = \frac{\exp(-\lambda t)\cdot(\lambda t)^n}{n!} \quad (t \geqq 0;\ n = 0, 1, 2, 3, \ldots),$$

where $X_n(t)$ $(n = 0, 1, 2, 3, \ldots)$ are the gamma density functions, which are the density functions of the Poisson distribution. In the new model, the explicit solution of a peak-interval procedure is

$$\underline{\overline{R_s(t)}} = \begin{cases} 1 & (\text{if } R_s(t) > 1), \\ R_s(t) & (\text{if } 0 \leqq R_s(t) \leqq 1), \\ 0 & (\text{if } R_s(t) < 0), \end{cases} \qquad (2)$$

where

$$\begin{aligned} R_s(t) &= \sum_{n=0}^{3} c_n(s) X_n(t) \\ &= c_0(s)X_0(t) + c_1(s)X_1(t) \\ &\quad + c_2(s)X_2(t) + c_3(s)X_3(t), \end{aligned} \qquad (3)$$

and the $c_n(s)$ $(s = 1, 2, 3, \ldots)$ are the constant weights of $X_n(t)$ for each session s. We will call both this model and this method of analysis *Poisson decomposition* (PD)[3].

[2] Abbriviation. SET, the scalar expectancy theory.

[3] Abbriviation. PD, Poisson decomposition.

We have observed that the behaviors across PI schedules with different interval lengths do not always exhibit the scalar property in an exact sense. The current study attempts to measure these small deviations by using our model to provide an improved description of the timing behavior of the subjects. The results suggest that a single clock (stopwatch) system is involved within the range of intervals considered in the following experiment.

2 Materials and methods

2.1 Animals

Twelve experimentally naïve male Wistar rats (Cr1j; Japan Charles River Laboratories, Yokohama, Japan) about 15 weeks of age were used: [group RatsA] RatA1, RatA2, ..., RatA6; [group RatsB] RatB1, RatB2, ..., RatB6.

The rats were housed individually in an environment with a constant room temperature of 23°C. The ratio of light to darkness was 1 : 1. Lights were on from 8 a.m. to 8 p.m.; otherwise, lights were off. Each animal received 1.35 g (= 30 × 45 mg) of Dustless Precision Pellets (F0165; Bio-Serv, NJ, USA) as reinforcers during the experiment. Additional food (CE-2; Clea Japan, Inc., Tokyo, Japan) and water were provided in the subjects' home cages after the daily experimental session; this diet was presented at the same time each day. This post-session feeding was the amount necessary to maintain each subject at 85% of their free-feeding weight.

This study was approved by the Animal Experimental Committee of Hiroshima University (Hiroshima, Japan) and was performed in accordance with the National Institutes of Health Guidelines on the Use of Laboratory Animals.

2.2 Apparatus

Each of the 6 operant chambers (25 cm × 30 cm × 30 cm) was equipped with a pellet dispenser, a lever, a light, and a charge-coupled device (CCD) camera. The front and back walls were aluminum; the side walls and the ceiling were transparent acrylic. The floor was made up of 16 parallel stainless steel bars.

The pellet dispenser (PD-50; Oharamedic, Tokyo, Japan) delivered 45 mg pellets into a food cup, which was attached to the front wall near the floor grid. The lever (H23-17RA; Coulbourn, PA, USA) was located in the front wall about 2.5 cm above the floor grid. A one-watt light was located on the ceiling. The CCD camera (KCB-401P; Mother Tool, Nagano, Japan) was

Table 1 Duration of PI to which RatsA and RatsB were exposed (adopted from Hasegawa and Sakata 2015)

Sessions	1–30	31–40	41–50	51–60	61–70
RatsA	PI-30	PI-20	PI-30	PI-45	PI-30
RatsB	PI-30	PI-45	PI-30	PI-20	PI-30

located near the light. The behavior of the rats was monitored remotely by a liquid crystal display placed outside the experiment room. Each chamber was located inside a ventilated box (40 cm × 62 cm × 46 cm) that was used for sound and light reduction. One computer (Endeavor VZ-4000; EPSON, Tokyo, Japan) controlled all the experimental events and recorded the times at which each event and response occurred for each individual in each experiment. Another computer (VAIO PCV-RX62K; SONY, Tokyo, Japan), which was connected to audio amplifiers, produced tone stimuli: pulses of 2000 Hz, on/off every 250 ms (i.e., 4 Hz) and at 80 dB.

2.3 Procedure

Let PI-T denote a peak-interval procedure of T s duration, where $T = 20$, 30, or 45. The rats were initially trained by autoshaping and hand shaping to press the lever; after the initial training, the rats were exposed to the PI procedures. The parameter values used and the sessions during which they were presented are presented in Table 1.

Each group began and ended this sequence of five conditions with PI-30. For group RatsA, the middle three conditions were an ascending series of PI durations with a common ratio of $\frac{3}{2}$ (PI-20, PI-30, and PI-45); we note that on a logarithmic scale (subjective scale), 20, 30, and 45 are equidistant. For group RatsB, the middle three conditions were the same but in descending order; thus, their common ratio was $\frac{2}{3}$, and they remain equidistant on a logarithmic scale.

Each FI trial started with a tone stimulus. In an FI trial of T s, the subject (rat) received a pellet reinforcer when it pressed the lever for the first time when $T < t < 3T$. The tone stimulus stopped when the rat received reinforcement, and this was followed by a silent intertrial interval (ITI) that lasted for T s[4]. If the rat did not respond while $T < t < 3T$, then a silent ITI of T s was presented without reinforcement. During probe trials, the tone stimulus lasted $3T$ s, and a silent ITI of T s followed.

One session consisted of 100 FI trials and 30 probe trials. The order was pseudorandom: the initial 10 trials were FI trials; and the remaining 120 trials consisted of 30 units of four trials each, where each unit included one probe trial and three FI trials in random order. Sessions occurred once per day for 70 days.

[4] Abbriviation. ITI, intertrial interval.

2.4 Data analysis

Analyses were based on the data from all of the probe trials (i.e., the non-food cycles), in the 21st through 70th sessions.

The mean of the individual subjects' response rates during each session were fitted with the explicit solutions of SET and of the PD with eq. (3).

The computer we used was a Pentium 4 PC (Endeavor AT930C, Intel Pentium 4 CPU 2.40 GHz, 504 MB RAM; EPSON, Tokyo, Japan). The software MATLAB (MathWorks, MA, USA) was used to fit the models to the data.

3 Results

3.1 Fits using Pearson's correlation coefficient and AIC

The Akaike information criterion (AIC) is defined to be

$$\begin{aligned}\mathrm{AIC} = &- 2\ln(\text{maximum likelihood}) \\ &+ 2(\text{number of adjusted parameters}).\end{aligned}$$

This criterion indicates which of two models best describes a given data set; the model with a smaller value is the better model (Akaike 1974)[5]. In our first PD for each session s, there are five free parameters (λ, $c_0(s)$, $c_1(s)$, $c_2(s)$, and $c_3(s)$), and thus

$$\mathrm{AIC} = -2\ln(\text{maximum likelihood}) + 10.$$

We used Pearson's product-moment correlation coefficient (r) and the AIC value to assess which of the two mathematical models, SET or PD, provided the better fit. As an example, we present in Figure 1 the data for one session with one subject, as fitted by both SET and PD.

3.2 Basic period of clocks as determined by PD

In our proposed PD model, $\frac{1}{\lambda}$ (s) represents the basic period of the clock (stopwatch) that the subject used to time the PI interval. Its reciprocal, λ (1/s), represents the basic speed of the clock (stopwatch). The basic period $\frac{1}{\lambda}$ (s) of each session is shown in Figure 2, and the means of $\frac{1}{\lambda}$ (s) are shown in Figures 3 and 4.

[5] Abbriviation. AIC, the Akaike information criterion.

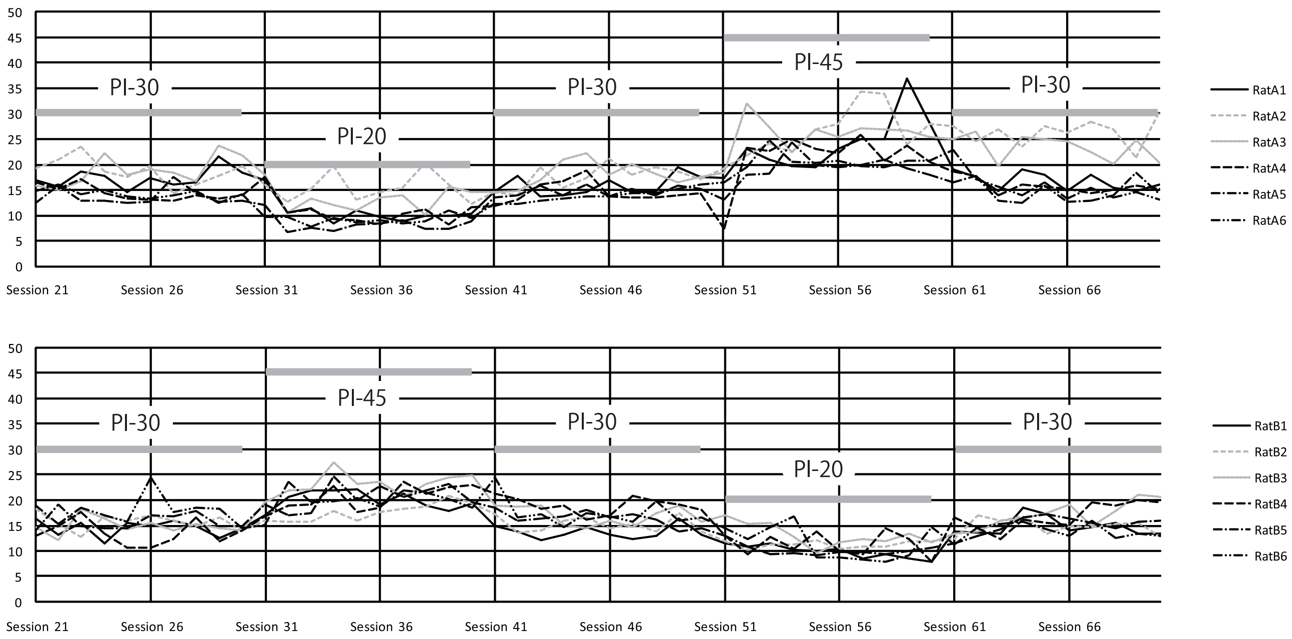

Fig. 2 Basic clock period $\frac{1}{\lambda}$ (s) for 12 rats in the sessions 21 through 70 (adopted from Hasegawa and Sakata 2015)

3.3 Weights of clocks by as determined by PD

Using PD, coefficients $c_n(s)$ ($n = 0, 1, 2, 3$; $s = 21, 22, 23, \ldots, 70$) were extracted from the data. The means and standard deviations of $c_n(s)$ for each subject are presented in Table 2.

4 Discussion

4.1 Basic period of clocks, as determined by PD

In PI-30, for example, if the basic period $\frac{1}{\lambda} = 15$ (s), then we may say that a rat times the interval of 30 s using the 15 s and 45 s clocks for inhibition, in addition to their primary use of the 30 s clock (Hasegawa and Sakata 2015).

We observed that the basic clock period did not change proportionally to the FI length during the current peak procedure (Figure 3). A closer analysis revealed that the first half of each 10 sessions under the same condition was more influenced by the previous FI length than was the latter half of the sessions (Figure 4). This carry-over effect suggests that a single clock system (stopwatch system) was involved in timing within this range (between 20 s and 45 s).

We investigated whether the peak time length and the basic period in a given condition were influenced by the PI duration during the condition immediately preceding it, and whether the sequence in which conditions were presented affected how successfully either model (SET and PD) described these data. For this analysis, we included the five sessions before and after each change in the PI length. Table 3 lists the sessions that formed part of these ascending and descending sequences. Figure 5 presents a scatter diagram of the behavioral subjective peak time t_0 that was identified after fitting SET for sessions forming part of a descending sequence (top panel), and an ascending sequence (bottom panel). Figure 6 presents the basic period $\frac{1}{\lambda}$ (s) that was identified after fitting PD for the same two categories of sessions.

Both Figure 5 and Figure 6 show that the slope of the line fitted to the descending sequence was higher than that fitted to the ascending sequence. This indicates that changes in the PI length made in a descending sequence had a greater effect on the subjects' subjective estimates of the length of the interval than did the changes made in an ascending sequence. The emotional drive of subjects to obtain food quickly might have been expressed in this ratio.

Looking at $\frac{a_D}{a_A}$ in Table 4, we see that the sensitivity of the PD (11.2%) to the sequence in which the conditions are presented is a little greater than that of SET (6.7%), but the variances in the parameter values identified by PD are bigger than those identified by SET, as seen in Figures 5 and 6. We will discuss this below in Section 4.3.

4.2 Transposition (as in Hasegawa and Sakata 2015)

In Section 1.3, we defined the weights $c_n(s)$ as constant for a given session. Moreover, the data presented in Table 2 indicate that the values of $c_0(s)$, $c_1(s)$, $c_2(s)$, and $c_3(s)$ are stable against changes in FI length and that they are almost constant within each rat in the 21st through 70th sessions. This indicates that rats cope with changes of FI length primarily by changing the basic period of the clocks (stopwatch) used to time the FI interval. The weights of $c_0(s)$, $c_1(s)$, $c_2(s)$, and $c_3(s)$ indicate the subjects' relative usage of clocks $X_0(t)$, $X_1(t)$, $X_2(t)$, and $X_3(t)$, and the clock weights were almost constant, which implies a transposition. It can be shown mathematically that the system of functions $R_s(t)$ in eq. (3) has the scalar property if and only if $c_n(s)$ $(n = 0, 1, 2, 3)$ do not change their ratio. Generally speaking, the system of $\overline{R_s(t)}$ does not have the scalar property (as can be seen in the bottom panel of Figure 1), but if $R_s(t) \leqq 1$ in its entire domain, which is observed in most cases, then $\overline{R_s(t)}$ has the scalar property. With $c_0(s)$, $c_1(s)$, $c_2(s)$, and $c_3(s)$ fixed at the values presented in Table 2, PD produced fits that had better AICs than did SET (Hasegawa and Sakata 2015). Let PD($\overrightarrow{c}$) denote such models.

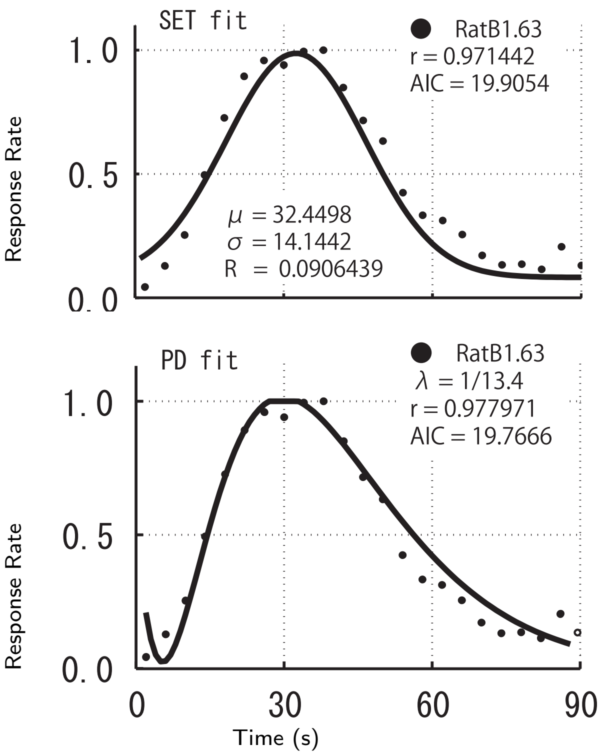

Fig. 1 Examples of the fit with SET (top panel) and with PD (lower panel) for the data from session 63 for RatB1. The rate of response $R(t)$ or $\overline{R_{63}(t)}$ is plotted on the vertical axis. The time t since the onset of the stimulus is plotted on the horizontal axis. Dots represent the mean rate at intervals of 4 s. The correlation coefficients (r) of these fits are 0.971 (SET) and 0.978 (PD), the Akaike information criterion (AIC) values are 19.91 (SET) and 19.77 (PD). For SET and PD, the values of r and AIC are similar and both models give a good fit. Although they are almost equally good as mathematical models for this data set, we can easily observe a difference in the shapes of the curves (adopted from Hasegawa and Sakata 2015)

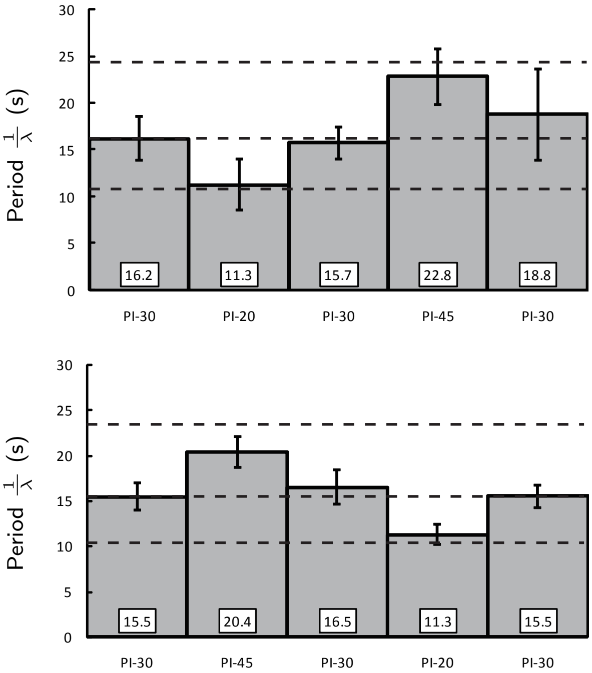

Fig. 3 Mean basic clock period $\frac{1}{\lambda}$ (s), by PI length. Error bars present the standard deviations. Broken lines indicate $\frac{3}{2} \cdot \frac{1}{\lambda_0}$, $\frac{1}{\lambda_0}$, and $\frac{2}{3} \cdot \frac{1}{\lambda_0}$, where $\frac{1}{\lambda_0}$ is the basic period of the first PI-30 in sessions 21 through 30. The top and bottom panels present these values for groups RatsA and RatsB, respectively

4.3 Peak shifts

In eq. (1) of SET, t_0 is assumed to express the peak time of a subject's subjective behavior. Figure 7 is a scatter diagram of the basic period $\frac{1}{\lambda}$ (s) of the PD fit and the peak time t_0 (s) obtained by the SET fit. The averages for five-session blocks are presented, as in Figure 4.

In Figure 7, we can clearly see three disjoint groups of points. Each group corresponds to one of the three PI durations presented. In a previous paper (Hasegawa and Sakata 2015), we conservatively compared SET and PD: "*we propose that* PD *and* PD($\overrightarrow{c}$) *may be useful additions to* SET *in the analysis of timing behaviour.*" Besides the reasons presented in that paper, Figure 7

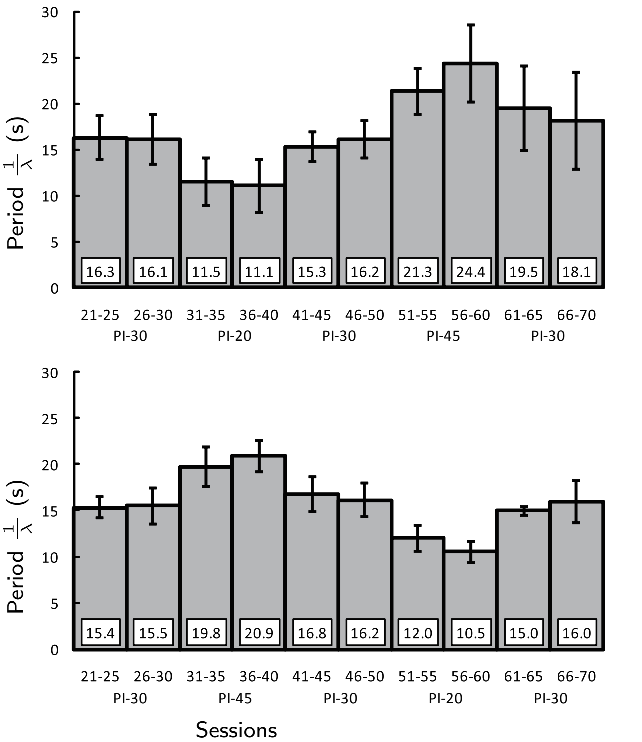

Fig. 4 Mean basic clock period $\frac{1}{\lambda}$ (s), in five-session bins. Error bars present the standard deviations. The top and bottom panels present data from groups RatsA and RatsB, respectively

gives an additional reason and shows why we were careful; in truth, it is necessary to include the use of SET for this study.

The average basic clock period $\frac{1}{\lambda}$ (s) and the average clock weights $c_n(s)$ $(n = 0, 1, 2, 3)$ for PI-20 (120 sessions), PI-30 (360 sessions; the baseline), and PI-45 (120 sessions) are shown in Table 5.

The graphs of $\overline{R_s(t)}$ for these averages are presented in Figure 8. The ratio of $c_1(s)$ and $c_3(s)$, i.e., the ratio of the weights of $X_1(t)$ and $X_3(t)$, are different for each graph. Broken curves express $c_1(s)X_1(t)$ (left) and $c_3(s)X_3(t)$ (right), which change the shape of the response graph (bold) and causes the peaks to shift (Spence 1937; Mazur 2006; Hasegawa and Sakata 2015). Since PD features have sufficient resolution, we again propose that PD and PD($\overrightarrow{c}$) may be useful additions to SET in the analysis of timing behavior.

The weights $c_n(s)$ calculated using PD are approximately constant. Even with this approximation, PD($\overrightarrow{c}$) fitted slightly better than SET, as assessed by Pearson's correlation coefficient and the AIC. With this assumption, the scalar property can be considered to be a kind of transposition.

A detailed investigation, however, revealed that the weights $c_n(s)$ were not constant. Rather, they were affected by the interval length that was presented during

Table 2 Means and standard deviations of the coefficients $c_n(s)$ for all 12 rats (adopted from Hasegawa and Sakata 2015)

Mean	$c_0(s)$	$c_1(s)$	$c_2(s)$	$c_3(s)$
RatA1	0.46	−2.81	9.28	−4.60
RatA2	0.34	−2.11	9.02	−5.45
RatA3	0.57	−3.22	9.98	−5.17
RatA4	0.50	−2.80	8.25	−3.09
RatA5	0.50	−2.81	8.57	−3.51
RatA6	0.49	−2.89	8.68	−3.56
RatB1	0.29	−1.30	5.15	−0.57
RatB2	0.40	−2.29	7.23	−2.28
RatB3	0.47	−2.82	8.92	−4.06
RatB4	0.29	−1.81	7.67	−3.54
RatB5	0.39	−2.50	8.37	−3.62
RatB6	0.32	−2.24	8.15	−3.65
S.D.				
RatA1	0.13	0.49	0.93	1.12
RatA2	0.13	0.64	1.13	1.77
RatA3	0.12	0.48	1.16	1.57
RatA4	0.21	0.64	1.17	1.37
RatA5	0.21	0.78	0.97	0.89
RatA6	0.18	0.53	0.90	1.00
RatB1	0.17	0.84	1.12	0.95
RatB2	0.15	0.78	1.61	1.60
RatB3	0.15	0.58	1.22	1.50
RatB4	0.11	0.59	0.87	1.13
RatB5	0.12	0.47	1.01	1.09
RatB6	0.12	0.56	1.05	1.38

Table 3 Sessions included in the analysis presented in Figure 7. The top half of the table presents sessions that form part of a descending sequence of PI lengths for each group, and the bottom half presents those that form part of an ascending sequence

Descending	From		To
RatsA	26–30	$\searrow$	31–35
	56–60	$\searrow$	61–65
RatsB	36–40	$\searrow$	41–45
	46–50	$\searrow$	51–55

Ascending	From		To
RatsA	36–40	$\nearrow$	41–45
	46–50	$\nearrow$	51–55
RatsB	26–30	$\nearrow$	31–35
	56–60	$\nearrow$	61–65

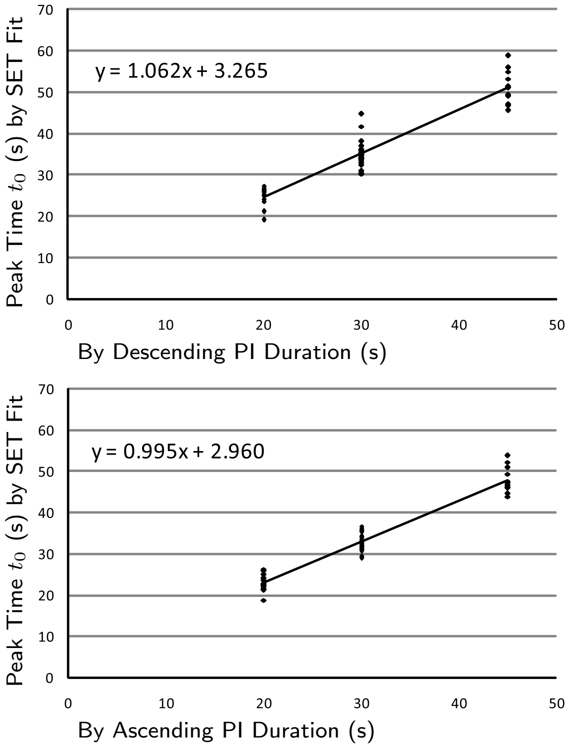

Fig. 5 Scatter diagrams of the peak time t_0, identified by fitting SET to the data. Data from sessions forming part of a descending sequence are presented in the upper panel, and those forming part of an ascending sequence are presented in the lower panel. See Table 3 for the exact number of sessions of each type for each group of subjects

Table 4 Slope a of the linear approximations in Figures 5 and 6 and their ratio

a	SET	PD
a_D: descending	1.062	0.426
a_A: ascending	0.995	0.383
a_D/a_A	1.067	1.112

the PI procedure. The changes in the weights reflected the shape of the response graph and caused the peaks to shift. This could be an example of where the behavior does not have the scalar property, in an exact sense.

Table 5 Average basic clock periods $\frac{1}{\lambda}$ and average clock weights $c_n(s)$ $(n = 0, 1, 2, 3)$ of PI-20, PI-30, and PI-45

	PI-20	PI-30	PI-45
$\frac{1}{\lambda}$	11.28	16.36	21.60
$c_0(s)$	0.25	0.47	0.45
$c_1(s)$	-1.81	-2.63	-2.63
$c_2(s)$	7.44	8.62	8.07
$c_3(s)$	-3.21	-3.92	-3.03

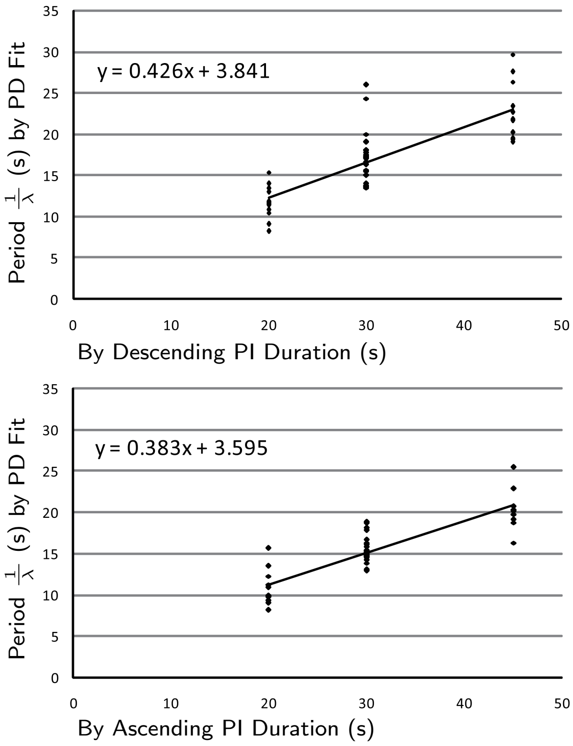

Fig. 6 Scatter diagrams of the basic clock period $\frac{1}{\lambda}$, identified by fitting PD to the data. Data from sessions forming part of a descending sequence are presented in the upper panel, and those forming part of an ascending sequence are presented in the lower panel. See Table 3 for the exact number of sessions of each type for each group of subjects

Rats changed both the basic periods and the weights of the clocks in order to cope with changes in the durations of the PIs. This may be why the variances in the basic period, as determined by PD, were bigger than the variances of the subjective peak times, as determined by SET (see Section 4.1).

The set of values of $c_0(s)$, $c_1(s)$, $c_2(s)$, and $c_3(s)$ shown in Table 5 represent measurements of the extent to which behavior diverged from the scalar property.

In addition to the carry-over effect discussed in Section 4.1, the transformation of the parameters in the PI procedures support the idea that each subject's clock system (stopwatch system) is unique in range, at least in when we consider durations between 20 s and 45 s. These results do not indicate the existence of separate clocks for 20 s, 30 s, and 45 s. The brain sections that become activated when a subject performs tasks that are related to PIs in the range of 20 s to 45 s can be considered to be a set of components of a clock (stopwatch).

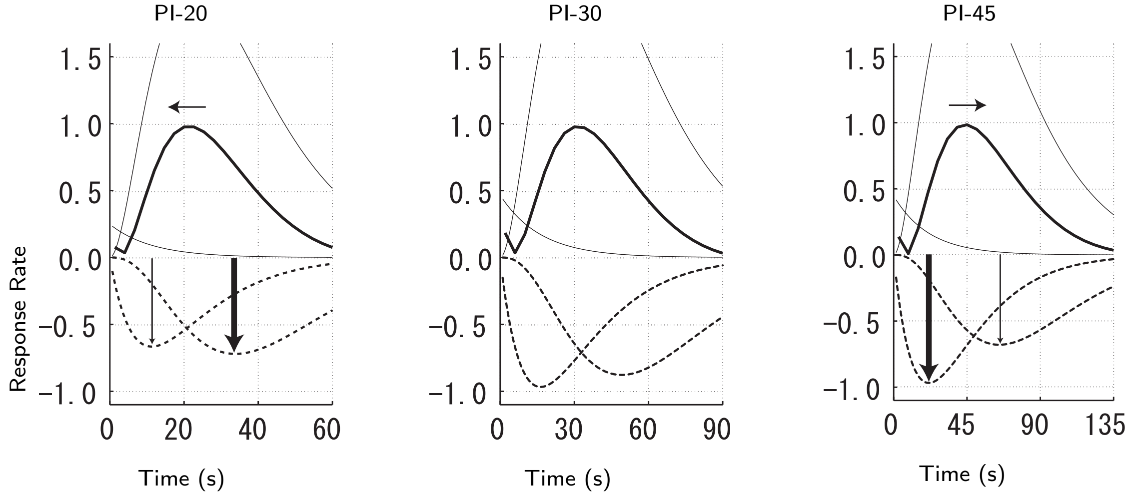

Fig. 8 Graphs of $\overline{R_s(t)}$ (bold curve). Data are those presented in Table 5. The two broken curves are the graphs of $c_1(s)X_1(t)$ (left, each) and $c_3(s)X_3(t)$ (right, each), whose ratio determines the shape of $\overline{R_s(t)}$. See Hasegawa and Sakata 2015, Figures 7 and 8, for an explanation of the shifts in the peaks

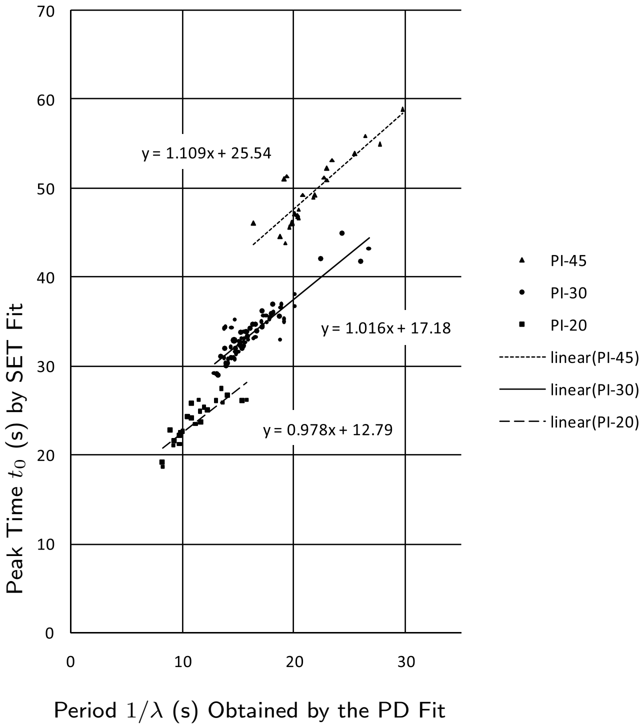

Fig. 7 Scatter diagram of the period $\frac{1}{\lambda}$, based on the PD model, against the peak time t_0 identified by fitting the SET. We see three groups of points without intersection, each corresponding to one of the three PI durations that we used

References

1. Akaike H (1974). A new look at the statistical model identification. IEEE Transaction Automatic Control, 19: 716-723.
2. Church RM (2003). A concise introduction to scalar timing theory. In Meck WH (Ed.), Functional and Neural Mechanisms of Interval Timing. Boca Raton, Florida: CRC Press pp: 3-22
3. Gibbon J (1977). Scalar expectancy theory and Weber's law in animal timing. Psychological Review, 84: 279-325.
4. Gibbon J, Church RM, Meck WH (1984). Scalar timing in memory. Annals of the New York Academy of Sciences, 423: 52-77.
5. Gibbon J (1991). Origins of scalar timing. Learning and Motivation, 22: 3-38.
6. Hasegawa T, & Sakata S (2015). A model of multi-second timing behaviour under peak-interval procedures. Journal of Computational Neuroscience, 38: 301-313, doi: 10.1007/s10827-014-0542-4
7. Killeen PR, & Fetterman, JG (1988). A behavioral theory of timing. Psychological Review, 95: 274-295.
8. Machado A (1997). Learning the temporal dynamics of behavior. Psychological Review, 104: 241-265.
9. Mazur JE (2006). Learning and behavior. 6th ed. Upper Saddle River, NJ: Prentice Hall.
10. Spence KW (1937). The differential response in animals to stimuli varying within a single dimension. Psychological Review, 44: 430-444.