Small Deviations from the Scalar Property and Carry-Over Effects

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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 [1]. 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

Abbreviations: FI schedule: Fixed interval schedule; PI: procedure peak-interval procedure; SET: the scalar expectancy theory; AIC: the Akaike information criterion; PD: Poisson decomposition; ITI: Intertrial interval;

Introduction
The data used in this study are the same as in our recently published study by Hasegawa and Sakata [1], 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.

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.
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) [2-4]. 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 \( \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix} \); 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.

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 [4,5]. In SET, the operant response function describing behavior during a PI procedure is expressed by

\[
R(t) = a \exp \left( \frac{1}{2} \left( \frac{t-t_0}{b} \right)^2 \right) + R_0 \quad (t \geq 0)
\]

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.

Poisson decomposition
We were inspired by the behavioral theory-of-timing (BeT) model [6] and the learning-to-time (LeT) model [7] to develop a model of interval-timing behavior [1].

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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 this model and this method of analysis Poisson decomposition (PD)1.

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.

Materials and methods

Animals

Twelve experimentally naive male Wistar rats (Crj; 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 1.35g (=30 × 45 mg) of Dustless Precision Pellets (FD0165; Bio-Serv, NJ, USA) as reinforcers during the experiment. Additional food (CE-2; Clea Japan, Inc., Tokyo, Japan) and water (F0165; Bio-Serv, NJ, USA) 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.

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 located 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 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.

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 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 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 reinforce 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 inter-trial interval (ITI) that lasted for T4s. 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.

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 subject’s 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, 504MB RAM; EPSON, Tokyo, Japan). The software Matlab (MathWorks, MA, USA) was used to the models to the data.

Results

Fits using Pearson’s correlation coefficient and AIC

The Akaike information criterion (AIC) is defined to be

\[
AIC = -2 \ln (\text{maximum likelihood}) + \text{number of adjusted parameters}.
\]

This criterion indicates which of two models best describes a given data set; the model with a smaller value is the better model [10]. In our first PD for each session s, there are five free parameters \( (\lambda, c_0 (s), c_1 (s), c_2 (s), c_3 (s)) \), and thus

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

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.

Basic period of clocks as determined by PD

| 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 |

Table 1: Duration of PI to which RatsA and RatsB were exposed (adopted from Hasegawa and Sakata).
In our proposed PD model, $1/\lambda (s)$ represents the basic period of the clock (stopwatch) that the subject used to time the PI interval. It’s reciprocal, $\lambda (1/s)$, represents the basic speed of the clock (stopwatch). The basic period $1/\lambda (s)$ of each session is shown in Figure 2, and the means of $1/\lambda (s)$ are shown in Figures 3 and 4.

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.

Discussion

Basic period of clocks, as determined by PD

In PI-30, for example, if the basic period $1/\lambda=15$ (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, $1/\lambda(s)$ that was identified after fitting PD for the same two categories of sessions.

Both Figures 5 and 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 $aD/aA$ 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.
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 subject’s 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 does not have the scalar property (as can be seen in the bottom panel of Figure 1), but if ≤1 in its entire domain, which is observed in most cases, then $R_s(t)$ 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 denote such models.

Peak shift

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 $\lambda$ (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.

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
### 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.

| Group   | From  | To    |
|---------|-------|-------|
| RatsA   | 26-30 | 31-35 |
|         | 56-60 | 61-65 |
| RatsB   | 36-40 | 41-45 |
|         | 46-50 | 51-55 |
| Ascending | From  | To    |
| RatsA   | 36-40 | 41-45 |
|         | 46-50 | 51-55 |
| RatsB   | 26-30 | 31-35 |
|         | 56-60 | 61-65 |

The graphs of 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 $c_1(s)$ for $X_1(t)$ (left) and $c_3(s)$ for $X_3(t)$ (right), which change the shape of the response graph (bold) and causes the peaks to shift [1,8,9]. Since PD features have sufficient resolution, we again propose that PD and PD may be useful additions to SET in the analysis of timing behavior.

The weights $c_n(s)$ calculated using PD is approximately constant. Even with this approximation, PD 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 the PI procedure. The changes in the weights reflected the shape of the response graph and caused the peaks to shift.
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 (stop-watch).

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