On experimental predictions from a model for a neural mechanism of internal timer

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Abstract

The authors have recently proposed a model for a neural mechanism of internal timer. Here we report on predictions, which the model provides for psychological experiment of interval timing by the method of reproduction. We consider the ratio \( \gamma_k = \sqrt[k]{\mu_k} / \mu \) with \( \mu \) and \( \mu_k \) being the mean and the \( k \)th central moment of the lengths of intervals reproduced by a subject. The model predicts that for arbitrary \( k \), \( \gamma_k \) is constant for different lengths of presented intervals; the value of \( \gamma_k \) for \( k > 2 \) is uniquely determined by the experimentally observed value of \( \gamma_2 \) according to the formulae given by the model. © 2001 Elsevier Science B.V. All rights reserved.

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The method of reproduction has widely been used in psychological experiment of interval timing [2,3]. Typically, a temporal interval of a certain length, indicated by light or tone, is presented to a subject, and then the subject is told to reproduce an interval of the same length by some way, for example, pressing a key. When this experiment is repeated for a fixed length of presented intervals, although the length of a reproduced interval in each time scatters, the mean shows good agreement with the length of the presented intervals. This clearly demonstrates that humans and animals have internal timer by which they know a lapse of time.

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Furthermore, it has long been known that, when the length of presented intervals is varied, the scattering of the lengths of reproduced intervals obeys the Weber’s law [2,3]: The Weber ratio $\sigma/m$ with $\sigma$ and $m$ being the standard deviation and the mean of the length of the reproduced intervals is kept constant with the length of presented intervals. Precisely, the Weber’s law holds if the length of presented intervals is at the time scale ranging from several hundred milliseconds to several seconds. This is the time scale dealt with in the present study.

Although the existence of internal timer is thus obvious, little is experimentally established about its biological substrate. Several (but not so many) models have been proposed to theoretically examine biologically probable mechanisms of timing [5]. Some of them are based on the idea of utilizing a pacemaker. In these models, a length of an interval is represented by a chain of periods of consecutive cycles generated by a pacemaker. Indeed, oscillatory or Poisson-process-like activity that might serve as such a pacemaker is commonly observed in the brain. However, simple analysis shows that the pacemaker hypothesis is unlikely to be compatible with the Weber’s law [4,5].

According to this hypothesis, it is natural to consider that the origin of scattering of the length of represented intervals is the fluctuation in the period of each cycle. Therefore, the mean and the Weber ratio of the length of intervals represented by $n$ consecutive cycles are $\bar{m}$ and $\frac{\sigma}{\sqrt{n}\bar{m}}$, respectively, with $\sigma$ and $\bar{m}$ being the standard deviation and the mean of the cycle periods. Thus, the Weber ratio is not constant but decreases as $n$ increases.

Recently, the present authors have proposed a pacemaker-free model for a neural mechanism of internal timer [6,7]. We have considered a recurrent network of neurons, the architecture thought to describe essential features of the network structure in the cortex. Each neuron is defined as bistable; that is, it has two stable states, ‘up’ and ‘down’ states. The network activity is defined as the number of neurons staying at the up state. We have found that the stochastic dynamics of the network provides a time course of the network activity likely to represent a certain length of a temporal interval. The network activity set at the maximum at $t = 0$ remains at a large level for a certain length of an interval, and then abruptly falls. Owing to the stochastic nature of the model, the length of intervals scatters even if all the parameters in the model are fixed. It has been shown that this scattering satisfies the Weber’s law.

It goes without saying that one of the most important roles of theoretical modelling is to provide predictions for practical experiment. Indeed, our model provides predictions for psychological experiment, which can definitely be checked by the method of reproduction. Derivation of these predictions, as described below, is based on the analytical results obtained in our previous study [7].

The stochastic dynamics of our model can be given by one-step descending processes shown in Fig. 1.

The probability that the transition of the number of up-state neurons from $n$ to $n - 1$ occurs per unit time is

$$r_n = \frac{n}{1 + e^{n\sigma - \bar{m}}}.$$ (1)
(For neurophysiological origins of the parameters $\alpha$, $N$ and $n_0$, see Ref. [7].) The length of a temporal interval represented by the above-mentioned characteristic time course of the network activity is given as the stochastic variable $T_{N,n_0}$ expressing the first-passage time at which $n$, starting from $N$ at $t = 0$, decreases to $n_0$. Let $\mu_k$ be the $k$th central moment of $T_{N,n_0}$, respectively. For sufficiently large $N$, we can derive analytical expressions of $m$ (the mean of $T_{N,n_0}$) and $\mu_k$ as functions of $\alpha$, $N$ and $n_0$, as follows:

$$m = \frac{a_N}{1 - e^{-s}}, \quad (2a)$$

$$\mu_k = a_k s_k, \quad (2b)$$

where $a_N = 1/r_N$ and $s_k$ is defined by the recurrence formula

$$s_{k+1} = \frac{(k + 1)s_k \sum_{i=0}^{k} (-1)^{k+i}C_iS_i}{1 - e^{-\alpha (k+1)s}}, \quad s_0 = 1 \quad (3)$$

Let $\gamma_k = \sqrt[k]{\mu_k/m}$. Note that $\gamma_2$ is the Weber ratio. From Eq. (2), one has

$$\gamma_k = \frac{\sqrt[k]{s_k}}{1 - e^{-s}}. \quad (4)$$

From Eqs. (3) and (4), it is obvious that $\gamma_k$ depends on $\alpha$ but not on $N$ and $n_0$. Therefore, if either $N$ or $n_0$ is changed, $m$ and $\mu_k$ themselves varies according to Eq. (2), whereas $\gamma_k$ remains constant. This gives the Weber's law in the special case that $k = 2$. This, however, says more than that; the constancy is held not only for $k = 2$ but also for higher $k$'s. If we assume that in the brain, different lengths of temporal intervals are encoded by different $N'$s or $n_0$'s, we are led to the following prediction for psychophysical experiment by the method of reproduction: for arbitrary $k$, the ratio $\gamma_k$ should be constant for different lengths of presented intervals.

The above prediction is for an experimental paradigm in which the length of presented intervals is variable. Next, we demonstrate that prediction for an experimental paradigm in which the length of presented intervals is fixed can also be derived from our model. From Eqs. (3) and (4), the Weber ratio $\gamma_2$ is defined as

$$\gamma_2 = \frac{1 - e^{-s}}{\sqrt{1 - e^{-2s}}}. \quad (5)$$
Fig. 2. Dependence of \( \gamma_k \)'s for \( k = 2-6 \) on \( \alpha \) given the Eqs. (3) and (4).

Solving this equation with respect to \( \alpha \), we have

\[
\alpha = \frac{1}{2} \log \frac{1 + \gamma_k^2}{1 - \gamma_k^2}.
\]  

(6)

By substituting the experimentally observed value of the Weber ratio in the right-hand side of this equation, the value of \( \alpha \) is defined. Using this \( \alpha \), one can calculate the value of \( \gamma_k \) for \( k > 2 \) by using Eqs. (3) and (4). Our model can thus predict the value of \( \gamma_k \) for arbitrary \( k > 2 \). The probability of our model can therefore be examined by comparing this value with the experimentally observed value. The dependences of \( \gamma_k \)'s for \( k = 2, 3, 4, 5 \) and 6 on \( \alpha \) given by Eqs. (3) and (4) are shown in the Fig. 2.

Experimental predictions described above are related to the statistical properties of the order higher than the second. The method of reproduction has a long history in psychological studies of timing, but little attention has been paid to higher-order analysis of statistical properties of reproduced intervals. We hope that the experiment to quantitatively examine such higher-order statistical properties will be done in the near future. In our theory, exact expression of \( \gamma_3 \) as a function of \( \alpha \) is given by

\[
\gamma_3 = \frac{2(1 - e^{-\alpha})}{\sqrt{1 - e^{-2\alpha}}}.
\]  

(7)

Irrespective of the value of \( \alpha \), \( \gamma_3 \) is positive, which means that the distribution should be rightward skewed. Indeed, distribution of timing measured by continuation tapping, a sort of the method of reproduction, has been reported to be rightward skewed [1]. Amplifying this qualitative agreement between experiment and our model, a quantitative agreement can also be expected.

References