Neural Mechanism for a Cognitive Timer

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To examine a possible biological mechanism for a cognitive timer, the stochastic dynamics of a network of neurons possessing two stable states (“on” and “off” states) is studied. The fraction of on neurons existing at $t = 0$ remains large for an extended interval, and then abruptly falls. The distribution of the lengths of the interval is scale invariant in the following sense: The ratio $\sqrt[k]{\mu^2}/m$, with $m$ and $\mu^k$ being the mean and the $k$th central moment, respectively, is invariant under scale transformations of $m$ and $\mu^k$. In the special case $k = 2$, this gives Weber’s law, a hallmark of cognitive timing.

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Judging the length of an interval of time is an experimental test widely used in the psychophysical study of time perception [1]. Typically, a certain interval of time is first presented to a subject, and then he is told to judge an interval of the same length without referring to external clocks or employing a counting strategy. Indeed, subjects are able to do this with what may be considered reasonable accuracy, and this fact clearly demonstrates that humans and animals have some “internal timer” by which they can judge the lapse of time.

Inevitably, there is a difference between the length of a presented interval and that subsequently judged by a subject. It has long been known that the fluctuations in the lengths of intervals judged by a subject satisfy Weber’s law for intervals whose lengths range from several hundred milliseconds to several seconds [2–4]. The Weber ratio $\sigma/m$ with $\sigma$ and $m$ being the standard deviation and the mean of the subject-produced interval length, respectively, is independent of the presented interval length, which is generally quite close to $m$.

It might be thought that a chain of cycle periods generated by some kind of internal pacemaker provides the biological mechanism by which humans and animals judge the lengths of an interval of time [5–10]. Indeed, rhythmic or Poisson-process-like activities, which may serve as a pacemaker, are commonly observed in human and animal brains. However, such a situation seems inconsistent with Weber’s law: If the fluctuations in the subject-produced intervals did result from those of such cycle periods, the Weber ratio would scale as $1/\sqrt[m]{m}$ [9–11].

In the present study, we propose a model for a possible neural mechanism of an internal timer which does not involve a pacemaker and whose predictions are consistent with Weber’s law. This mechanism determines a particular interval of time as the duration of a state in which the system is characterized by a large network activity. This state continues from the initial time, at which the network activity is set to the maximum, until some time at which it drops suddenly. We find that the lengths of the intervals produced by this process are distributed in a scale invariant manner in the sense that the ratio of the $k$th root of the $k$th central moment to $m$ is independent of $m$ for arbitrary $k$. Weber’s law is given in the special case $k = 2$. This paper focuses upon dynamical aspects of the mechanism, and physiological implications of the model are discussed elsewhere [12].

We consider a globally coupled recurrent network of $N$ neurons with the following two properties. First, each neuron has two stable states (“on” and “off” states) if the amplitude of recurrent input remains in a particular range; a neuron in the on state outputs recurrent signals to other neurons, whereas a neuron in the off state does not. Second, each neuron is subject to stochastic noise in addition to recurrent inputs.

We describe the $i$th neuron as a two-spin Ising system defined by the Hamiltonian,

$$\mathcal{H}^{(i)} = -J\sum_{s} s_1^{(i)} s_2^{(i)} + (H - I) (s_1^{(i)} + s_2^{(i)}) ,$$

(1)

where $s_a^{(i)}$ ($a = 1, 2$) is a spin variable taking the value 0 or 1, and $J$ and $H$ are positive constants. $I$ represents the recurrent input, defined as a quantity which is proportional to $n$, the number of on neurons in the network, as

$$I = Gn ,$$

(2)

where $G$ is a coupling constant. For simplicity, the coupling constant is taken to be homogenous everywhere in the network. All neurons, hence, receive the same recurrent input $I$.

The state of each neuron is updated according to a standard algorithm for the stochastic dynamics of spin systems. At time $t$, one of $s_1^{(i)}$ and $s_2^{(i)}$ is selected at random for each $i$ ($i = 1, \ldots, N$). Then, at $t + \Delta t$, the value of the selected spin variable, say $s_a^{(i)}$, is updated by the rule

$$s_a^{(i)} = \begin{cases} 1 & \text{with probability } p_a^{(i)} = \frac{1}{1 + e^{-\beta_a \mathcal{H}^{(i)}}} , \\ 0 & \text{with probability } 1 - p_a^{(i)} , \end{cases}$$

(3)

where $\Delta_a \mathcal{H}^{(i)} = J s_b^{(i)} (t) - (H - I(t)) (a \neq b)$. 

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The state transitions of (s1i, s2i) obey the schema illustrated in Fig. 1(a). Let the values of $H^{(i)}$ for (0,0), (1,0) and (0,1), and (1,1) be $E_a$, $E_b$, and $E_c$, respectively. The relative magnitudes of $E_a$, $E_b$, and $E_c$ depend on $I$, as illustrated in Fig. 1(b). In particular, we see that, if

$$H - J < I < H,$$

the on state (1,1) and the off state (0,0) are both stable; that is, each neuron becomes bistable. (Strictly speaking, the on state is metastable, as we will see later.) On the other hand, (1,0) and (0,1) are always unstable irrespective of the value of $I$.

The time evolution of the network activity, defined by $P = n/N$, was examined by Monte Carlo simulation. The results typically obtained reveal that the network functions as a timer: The network activity, initially set at the maximum level, decreases slowly but remains fairly large for a certain period, and then suddenly falls [Fig. 2(a)]. This sudden fall can be regarded as a signal defining the end of an interval characterized by the large network activity. However, the timing generated by this timer fluctuates, owing to the inherent stochastic nature of its mechanism. Figure 2(b) displays the distribution of generated intervals, which was obtained by accumulating the results of repeated trials of the Monte Carlo simulation.

Since in this model the magnitude of $\Delta t$ represents the typical time scale of neuronal dynamics, we consider it to be of the order of a millisecond [13]. Note that $\Delta t$ is the only inherent time scale in our model. By contrast, the time scale of cognition and behavior (approximately a hundred milliseconds to a second), at which Weber’s law holds, is $10^2 - 10^3$ times greater than $\Delta t$. Given these facts, if our model exhibits emergent behavior characterized by a time scale much larger than $\Delta t$, its mechanism should be considered as representing a possible manner in which the time scale of cognition and behavior can emerge from neuronal dynamics.

The intervals generated in our model are, in fact, much longer than $\Delta t$ [in Fig. 2(a), about 1000 times longer than $\Delta t$]. An intuitive explanation for the emergence of such a long time scale is the following. Owing to stochastic noise, each neuron initially set in the on state can make a transition to the off state surmounting the potential wall between the on and off states. Therefore, if the off state is of the lower energy than the on state (this is indeed the case for the parameter values listed in the legend of Fig. 2), $n$ decreases as time passes. However, since the escape probability is generally small, this decrease proceeds very slowly. As $n$ decreases, $I$ also decreases [see Eq. (2)]. Eventually, when $I$ decreases to $H - J$, each neuron becomes monostable [Fig. 1(b)],

FIG. 1. (a) State transitions of $(s_1, s_2)$ for $I < H - J$ and $H < I$, the potential is monostable, while, for $H - J < I < H$, it is bistable.

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and the neurons which still remain in the on state rapidly move into the off state through gradient descent. The long time scale thus emerges as the long interval during which \( H - J < I \) holds.

In the following, we analytically derive the distribution of the intervals generated in our stochastic dynamics and show that it is consistent with Weber’s law. This proof is carried out in the framework of the first-passage problem [14]. We represent the states of the network by \( n \). In particular, \( n = N \) at \( t = 0 \). Then, let \( r_n \) and \( g_n \) be the probabilities per unit time for the transitions \( n \rightarrow n - 1 \) and \( n \rightarrow n + 1 \), respectively. Without losing generality, we will henceforth set \( \Delta t = 1 \). For the stochastic algorithm described above, we have \( r_n = n/4(1 + e^{(E_0-E_n)}) \) and \( g_n = n/4(1 + e^{(E_0-E_n)}) \). In the analysis below, we make the following two assumptions: First, the transition probability for \( n \rightarrow n + 1 \) is negligible compared to that for \( n \rightarrow n - 1 \), and, second, the on state is stable (strictly, metastable) at \( t = 0 \). With these assumptions, \( r_n \) can be simplified as

\[
r_n = \frac{n}{4(1 + e^{\alpha(n-\theta)})},
\]

where

\[
\alpha = \beta G, \quad \theta = \frac{H - J}{G}.
\]

Note that \( \theta \) is the value of \( n \) at which \( E_b = E_c \) holds, that is, the value at which the system changes from bistability to monostability.

Now, state transitions of the network can be described by the master equations for one-step descending processes,

\[
\frac{d}{dt} p_N(t) = -r_N p_N(t),
\]

\[
\frac{d}{dt} p_n(t) = r_{n+1} p_{n+1}(t) - r_n p_n(t) \quad (n < N),
\]

where \( p_n(t) \) is the probability that the number of neurons in the on state is \( n \) at time \( t \), satisfying the initial condition

\[
p_n(0) = \delta_{n,N}.
\]

This stochastic process is defined by the three parameters \( \alpha, \theta \), and \( \theta \).

Let \( T_{n',n''}^{(k)} \) be the stochastic variable representing the time at which \( n \), starting with \( n = n' \) at \( t = 0 \), takes the value \( n'' \) for the first time. Then, the duration of the sustained network activity is represented by \( T_{n,n_0} \) with \( n_0 \) being the maximum integer not greater than \( \theta \). For one-step descending processes defined by Eq. (7), the probability distribution density of \( T_{n,n_0} \) is given by \( f_{n,n_0}(t) = r_{n_0} p_{n_0}(t) \). The agreement of \( f_{n,n_0}(t) \) obtained by numerically solving Eq. (7) with the results of the Monte Carlo simulations [Fig. 2(b)] confirms that Eq. (7) provides a good approximation to the original stochastic dynamics given by Eq. (3).

Next, let \( m^{(k)}_{n,n_0} \) and \( \mu^{(k)}_{n_0,n} \) be the mean and the \( k \)th central moment of \( T_{n,n_0}^{(k)} \), respectively. Introducing the dimensionless quantity \( s^{(k)}_{n,n_0} = \mu^{(k)}_{n',n''}/a^k_n \) with \( a_n = 1/r_n \), we can derive the following identity:

\[
s^{(k)}_{N+1,n_0} = \sum_{u=0}^{k} C_u s^{(k-u)}_{N+1,u} \left( \frac{a_N}{a_{N+1}} \right)^u \frac{a_u}{s^{(u)}_{N,u}},
\]

Noting that \( a_N/a_{N+1} = [(N + 1)/N](1 + e^{\alpha(N-n_0)}) \) and \( s^{(u)}_{N+1,u} = k! \sum_{v=0}^{k} (-1)^v/v! \), we can rewrite this as

\[
s^{(k)}_{N+1,n_0} = \sum_{u=0}^{k} \sum_{v=0}^{k} \frac{k!}{u! v!} (-1)^v e^{-ua} s^{(u)}_{N,u},
\]

for sufficiently large \( N \). This recurrence formula expresses \( s^{(k)}_{N+1,n_0} \) as a linear combination of \( s^{(u)}_{N,u} \) \((u = 0, 1, 2, \ldots, k)\). Owing to the damping factor \( e^{-ua} \), the point \( s^{(0)}, s^{(1)}, s^{(2)}, \ldots, s^{(k)} \) converges to a fixed point \( s^{(0)}(k), s^{(1)}(k), s^{(2)}(k), \ldots, s^{(k)}(k) \) as \( N \) goes to infinity. For arbitrary \( k \) \((>0)\), \( s^{(k)}(k) \) is therefore obtained by iteratively solving

\[
s^{(k)}(k) = \frac{k^{(k-1)} + \sum_{u=0}^{k-1} C_u (-1)^u e^{-ua} s^{(u)}(a)}{1 - e^{-ka}},
\]

with \( s^{(0)}(0) = 1 \). An analytic expression for \( s^{(k)}(k) \) is, hence, given by

\[
\mu^{(k)}_{N,n_0} = a_N s^{(k)}(k).
\]

By means of similar analysis, we can also derive

\[
m^{(k)}_{N,n_0} = \frac{a_N}{1 - e^{-\alpha}},
\]

for \( N \rightarrow +\infty \).

Now, let \( \Gamma_k \) be the ratio of the \( k \)th root of \( \mu^{(k)}_{N,n_0} \) to \( m^{(k)}_{N,n_0} \):

\[
\Gamma_k = \sqrt[k]{\mu^{(k)}_{N,n_0}}/m^{(k)}_{N,n_0}.
\]

(Note that \( \Gamma_2 \) is the Weber ratio.) For \( N \rightarrow +\infty \), Eq. (11) gives

\[
\Gamma_k = (1 - e^{-\alpha})^{1/\sqrt[k]{s^{(k)}(k)}}.
\]

Since only \( \alpha \) (i.e., neither \( N \) nor \( \theta \)) appears in Eq. (10), \( s^{(k)}(k) \) and \( \Gamma_k \) depend only on \( \alpha \). Therefore, when either \( N \) or \( \theta \) is changed, \( \mu^{(k)}_{N,n_0} \) and \( m^{(k)}_{N,n_0} \) are scaled according to Eq. (11), whereas \( \Gamma_k \) is invariant. In the special case \( k = 2 \), this yields Weber’s law. From the invariance of \( \Gamma_k \) for arbitrary \( k \) under the change \((N, \theta) \rightarrow (N', \theta')\), it can be derived that this change is equivalent to the following scale transformation of time:

\[
f^{(N',\theta')}_{N,n_0}(t) = \frac{m^{(N,n_0)}_{N,n_0}}{m^{(N',\theta')}_{N,n_0}} f^{(N_{n_0})}_{N,n_0}\left(\frac{m^{(N,n_0)}_{N,n_0}}{m^{(N,n_0)^{'}}_{N,n_0}} t\right).
\]

The analytical results we obtained agree quite well with the results of the Monte Carlo simulations (Fig. 3).
In this study, we have examined a possible neural mechanism that is capable of defining an interval of time in terms of the sustained network activity of neurons. In fact, the sustained activation of neurons is widely believed to be a mechanism by which the brain encodes information in working memory during a required period [15].

Finally, we note that the mechanism proposed here is expected to be applicable not only to neural systems but also to other natural and social systems whose essence can be described by a potential function analogous to the Hamiltonian given by Eq. (1). For instance, suppose that some social trend continues as long as the number of people engaging in it is greater than some critical value. If the “pressure” tending to cause each person to engage in the trend is proportional to the number of people so engaged, the distribution of the periods during which such a trend continues will obey the statistical law elucidated here.

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