A model for neural representation of temporal duration

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Abstract

To address how temporal duration is encoded in neural systems, we put forward a simple model for recurrent neural networks. Particular assumptions are only the following two: (1) neuronal bistability and; (2) environmental effects described by a heat bath. The results of Monte Carlo simulation show that population activity triggered at an initial time continues for a prolonged duration, followed by an abrupt self-termination. This time course seems highly suitable for neural representation of temporal duration. The time scale of this prolonged duration is much longer than the time scale of neuronal firing which is of the order of ms. The former time scale implies that of interval timing in cognition and behaviour. Thus, the model provides a possible explanation for a link between these two separated time scales. The Weber law, a hallmark of humans and animals' interval timing, can also be reproduced in our model.

Keywords: Neural representation; Temporal duration; Interval timing; Bistability; Random noise; Weber law

1. Introduction

That humans and animals are capable of interval timing seems obvious as demonstrated by numerous cognitive and behavioural studies. For instance, interval timing between conditioned stimulus and delayed delivery of reward (reinforcement) is one of the most frequently used experimental paradigms for these studies (Gibbon and Balsam, 1981).

Interval timing involves several processes such as detection, storage or recall of temporal duration. Undoubtedly neural coding of temporal duration in some way must be working underlying these processes. Then, how is temporal duration encoded in neural systems?

Despite that several lines of experimental studies have already been conducted to address neural mechanisms of interval timing (for example, see Niki and Watanabe, 1979; Buonomano et al., 1997; Schultz et al., 1997; Chang et al., 1999), we still have little evidence decisive for concluding. A number of hypothetical models have been proposed up to now (for review, see Ivry 1996; Miall, 1996). As reviewed by Ivry (1996), they can be
classified into two categories: clock-counter models and interval models.

In clock-counter models, outputs generated by a pacemaker accumulate in a task-specific counter. The number of outputs accumulated in the counter represents temporal duration. The scalar expectancy theory (SET), which is a dominant hypothesis in cognitive and behavioural studies of interval timing, belongs to this category, (Gibbon 1971, 1972, 1977; Gibbon and Church 1981; Church and Gibbon, 1982; Gibbon and Church 1984; Gibbon et al., 1984). The model recently proposed by Bugmann (1998), which utilizes dwindling but not accumulating, is considered to be a modified version of a clock-counter model.

In interval models, different time intervals are represented by distinct elements or by different combinations of distinct elements, each element or combination corresponding to a specific interval. There are a variety of models considered belonging to this category (for example, Sutton and Barto, 1981; Tank and Hopfield, 1987; Grossberg and Schmajuk, 1989; Miall, 1989; Church and Broadbent, 1990a,b; Ivry, 1996; Montague et al., 1996; Staddon and Higa, 1999).

Several augments have been raised against clock-counter models (see Ivry 1996; Staddon and Higa, 1999). The main objection is that naïve versions of clock-counter models are incompatible with the Weber law, a hallmark of humans and animals’ interval timing (for the Weber law, see Section 2.1). It should, however, be noticed that there is an additional problem that has been overlooked not only by clock-counter models but also by interval models. This refers to the problem of time scale. Time scales characterizing the dynamics of neuronal firing are of the order of ms, whereas time scales from several hundred ms to several s, sometimes to several min, characterize interval timing in cognition and behaviour. Hence, if we adhere to the doctrine that ‘everything can be traced back to neuronal firing’, it becomes necessary to explain a link between these two separated time scales (Miall, 1996). How do time scales much longer than ms emerge from the dynamics characterized by time scales of ms?

In the present study, we put forward a model for neural representation of temporal duration, which is pacemaker-free as well as providing a possible solution to the problem of time scale. The model also reproduces the Weber law, an experimental hallmark of humans and animals’ interval timing.

2. Theory

2.1. Criterion

We set the criterion that the model should satisfy three requirements described in the following.

The most probable neural representation of temporal duration may be as follows: Activity of a population of neurons triggered at an initial time long-lastingly continues, followed by a self-termination at the end of the duration to be represented (Miall, 1996). This view is partly supported by electrophysiological recordings from prefrontal and cingulate cortex during timing behaviour in the monkey (Niki and Watanabe, 1979). The first requirement is therefore that the model should generate the time course of population activity as stated above.

The second requirement is that the model should present a possible solution to the problem of time scale.

The third requirement is that the model should reproduce the Weber law, a well-established experimental hallmark of humans and animals’ interval timing. The Weber law states that the standard deviation $\sigma$ of the distribution of timed response is a linear function of the averaged time $\mu$; that is, the Weber ratio $\sigma/\mu$ is constant with respect to $\mu$ (see, for review, Gibbon et al., 1997; Bugmann, 1998). The plausibility of the model can therefore be examined by testing whether it can reproduce the Weber law.

2.2. Model

The model examined by us is extremely simple. We considered recurrent networks of $N$ neurons (Fig. 1). Particular assumptions are only the following two.
The first assumption is that: Each neuron is bistable if sufficient recurrent input is provided. This means that the firing rate of a neuron is high/low if this neuron is at the up/down state (Fig. 1). It has been proposed in the recent theoretical study that the voltage dependence of NMDA conductance coupled with GABAergic conductance can generate bistability of the membrane potential (Lisman et al., 1998; see also Camperi and Wang, 1998). This may provide possible mechanisms responsible for the neuronal bistability postulated in our model.

The recurrent networks illustrated in Fig. 1 abstract a network structure in some brain region involved in temporal-duration coding, which is presumably located in the prefrontal cortex (Fuster, 1997). In general, each brain region interacts with a lot of other brain regions by signal transmissions. The recurrent networks in our model should therefore be considered not as a closed system but as an open system interacting with environments. The simplest but effective way to incorporate the environmental effects is to describe them as a heat bath. Hence the second assumption is that: each neuron receives random noise input in addition to recurrent input (Fig. 1).

2.3. Mathematical formulation of the model

Basically, the time course of the membrane potential of each neuron should be described by the Hodgkin–Huxley equation. However, essential points of our model are the neuronal bistability and randomness. Without spoiling these essences, we devised to simplify the mathematical formulation. Instead of the Hodgkin–Huxley equation, we used a two-spin Ising system to describe each neuron.

The two-spin Ising system describing the \( n \)-th neuron is defined by the Hamiltonian

\[
H^{(n)} = -w s_1^{(n)} s_2^{(n)} + (\theta - I)(s_1^{(n)} + s_2^{(n)})
\]

where \( s_i^{(n)} (i = 1 \text{ or } 2) \) is a spin variable that takes 1 or 0; \( I \) represents recurrent input to this neuron, which is given by

\[
I = G \frac{N_{\text{up}}}{N}
\]

with \( G \) and \( N_{\text{up}} \) being the synaptic strength and the number of neuron at the up state, respectively. Just for simplicity, the synaptic strength has been set equal everywhere in the networks. If \( I \) satisfies

\[
\theta - w < I < \theta
\]

the system has two stable states: \((s_1^{(n)}, s_2^{(n)}) = (1, 1)\) and \((s_1^{(n)}, s_2^{(n)}) = (0, 0)\). The up state of the \( n \)-th neuron can be assigned to the former and the down state to the latter. Thus, the description by the two-spin Ising system satisfies the neuronal bistability.

The randomness can also be incorporated into the model if the following stochastic algorithm defines the dynamics of each neuron:

\[
s_i^{(n)}(t + \Delta t) = 1 \quad \text{with probability} \quad p_i^{(n)}(t)
\]

\[
s_i^{(n)}(t + \Delta t) = 0 \quad \text{with probability} \quad 1 - p_i^{(n)}(t)
\]

This is just the same as the algorithm of the Boltzmann machine (Ackley et al., 1985). The time step \( \Delta t \) defines the time scale of neuronal firing. Hence \( \Delta t \) is of the order of ms.

The mathematical formulation of our model is ready in the above. Notice that time scales much
Fig. 2. Time course of population activity $P$ calculated by Monte Carlo simulation according to the stochastic algorithm. The figure shows the results obtained for the following parameter values: $N = 500$; $w = 10$; $\theta = 30$; $\beta = 2.0$; $\Delta t = 0.002$ s; $G = 24.8$.

$P = \frac{N_{up}}{N}$ \hspace{1cm} \hspace{1cm} (5)

Fig. 2 shows the time course of $P$ obtained by Monte Carlo simulation according to the stochastic algorithm (4). The population activity triggered at an initial time is sustained for a prolonged duration, followed by an abrupt self-termination. This is just the desired time course as required in the criterion (see Section 2.1). Notice that the duration is much longer than ms.

Even if all the parameters including the synaptic strength $G$ are fixed, the duration scatters because of the stochastic nature of the model. Distribution of the duration is shown in Fig. 3, which is obtained by accumulating the results of a large number of trials, each with different random numbers.

The mean duration is a monotonic increasing function of the synaptic strength $G$ (data not shown). The mean duration can therefore be adopted to match the duration to be coded by adjusting $G$. We further calculated the Weber ratio ($\sigma/\mu$) for different $G$'s. The ratio appears to be constant irrespective of $\mu$ (Fig. 4). Thus, our model can reproduce the Weber law.

Fig. 3. Distribution of the duration of population activity. The distribution was obtained by accumulating results of a number of trials, each with different random numbers. The parameter values used in these trials are the same with Fig. 2.

Fig. 4. Reproduction of the Weber law. For each of the different values of $G$, the mean ($\mu$) and the standard deviation ($\sigma$) of the duration of population activity were calculated by sampling 500 trials, each performed with different random number. The results show that the Weber ratio ($\sigma/\mu$) is constant with $\mu$. The parameter values used in these calculations are the same with Fig. 2 except for $G$.

longer than ms are not explicitly postulated in this formulation.

3. Results

Let $P$ be the population activity defined by the ratio of the up-state neurons to the total neurons:
Fig. 5. Schematic description of the mechanisms responsible for the emergence of prolonged time scales from the dynamics characterized by much shorter time scales. For detailed description, see the text.

4. Summary and discussion

A model for recurrent networks of bistable neurons, each with random noise input, was examined to address possible mechanisms for neural coding of temporal duration. We have obtained the time course of population activity, which is quite suitable for neural representation of temporal duration (Fig. 2). The Weber law, a hallmark of humans and animals’ interval timing, is also reproduced in our model, which confirms the plausibility of our model.

Mechanisms responsible for the emergence of the time course of population activity with prolonged time scales much longer than ms can be accounted for as illustrated in Fig. 5. At the initial time, all neurons are set at the up state. If it were not for the random noise input, each neuron would eternally remain at the up state because of the potential wall between the up and down states. However, since randomness is assumed in our model, each neuron has a chance to escape from the up to down states crossing the potential wall. The escape probability is yet very small but not zero. As time proceeds, the number of up state neurons therefore gradually decreases. Accordingly, recurrent input \( I \) also decreases (see Eq. (2)).

Since bistability of each neuron is sustained by recurrent input (see the condition (3)), bistability becomes dulled as \( I \) decreases. Finally, at the point where \( I \) crosses the value \( \theta - w \), the potential becomes monostable. Just then, all remaining up-state neurons transit to down state by gradient descent. This is just analogous to first-order phase transition in statistical physics.

Escape of neurons from the up to down states with the help of random noise (stage 1 in Fig. 5) proceeds asynchronously and very slowly. In contrast, transition of the remaining neurons from the up to down states by gradient descent (stage 2 in Fig. 5) happens almost synchronously and very quickly. These are the reason for the emergence of the time course of population activity like that shown in Fig. 2 with prolonged time scales much longer than ms.

Randomness is thus crucial in our model. In previous models, in contrast, randomness was not essential for temporal-duration coding itself but merely added in order to introduce a stochastic nature and to examine their reproducibility of the Weber law (Gibbon, 1977, 1981; Gibbon and Church, 1984; Church and Broadbent, 1990a,b; Allan and Gibbon, 1991; Gibbon, 1992; Gibbon et al., 1997). Our model clears the criterion posed in Section 2.1 with fewer assumptions.

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References


