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STDP Learning Can Reproduce Infra-Slow Oscillation

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Abstract—In our brains, interaction between neurons generates a variety of rhythms such as delta rhythms and gamma rhythms. These rhythms are numerically observed in a mathematical model of a neural network with spike-timing-dependent plasticity (STDP). In this paper, we discovered that a mathematical model with the STDP can reproduce infra-slow oscillation, or rhythm of very low frequency, by changing parameters of the STDP learning.

1. Introduction

Billions of neurons exist in our brains and their interaction generates a variety of rhythms. Among them, infra-slow oscillation (ISO) is one of the rhythms generated in the brains. ISO was discovered by Aladjalova[1] with a local field potential recorded from the rabbit neocortex. Since then, ISO has been observed in various kinds of mammalian brains[2]. However, its generation mechanism remains unknown. On the other hand, delta rhythms (2–4[Hz]) and gamma rhythms (30–100[Hz]) are numerically reproduced by a mathematical model of a neural network with axonal conduction delays and spike-timing-dependent plasticity (STDP)[3].

In this paper, we investigated a neural mechanism to reproduce ISO. To reveal the mechanism, we conducted numerical simulations by changing the curvature of the STDP function and by biasing change rates of the synaptic weights in the STDP learning.

2. STDP learning

We used the STDP rule for learning of the neural network. In the STDP, the magnitude of change rates in synaptic weights depends on the timing of spikes: if a presynaptic spike arrives at the postsynaptic neuron before the postsynaptic neuron fires, the synapse is potentiated (long-term potentiation, LTP). If the presynaptic spike arrives at the postsynaptic neuron after the postsynaptic neuron fired, the synapse is depressed (long-term depression, LTD). The magnitude of the change in synaptic weight is decided by STDP[4] function which is represented as follows:

$$\Delta w_{ij}(\Delta t_{ij}) = \begin{cases} A_+ \exp(-\frac{\Delta t_{ij}}{\tau})\ (\Delta t_{ij} > 0), \\ -A_- \exp(\frac{\Delta t_{ij}}{\tau})\ (\Delta t_{ij} < 0), \end{cases} \quad (1)$$

where $\Delta t_{ij} = t_i - t_j$, t_i is the firing time of postsynaptic neuron i, t_j is the firing time of presynaptic neuron j, A_+ is the maximum value of LTP, A_- is the maximum value of LTD. τ is the time constant of LTP and LTD.

3. Methods

In this experiment, we used the Izhikevich neuron model[3] as a processing element of a neural network. The neuron i in the neural network is expressed by Eq. (2):

$$\dot{v_i} = 0.04{v_i}^2 + 5v_i + 140 - u_i + \sum_{j \in S_i} w_{ij} H(v_j - 30), \quad (2)$$

where S_i is a set of neurons which are connected to the neuron i, w_{ij} is a synaptic weight from the neuron j to neuron i, and $H(x)$ is a step function ($H(x) = 0$ if $x < 0$, and $H(x) = 1$ if $x \geq 0$). When $v_j \geq 30$, that is, when neuron j connecting to neuron i fires, the value of the synaptic weight w_{ij} is applied to the neuron i.

The neural network consists of 1,000 randomly connected neurons. We prepared 800 excitatory neurons and 200 inhibitory neurons. In the experiments, we used regular spiking neurons for excitatory neurons, and fast spiking neurons for inhibitory neurons. Each neuron has 100 synapses to be connected to other neurons. Every excitatory neuron is connected to 100 neurons that are randomly chosen from all neurons, while every inhibitory neuron is connected to 100 neurons that are randomly chosen from excitatory neurons.

Conduction delays among neurons are random integers between 1 [ms] and 20 [ms]. The excitatory connection obeys the STDP learning rule with every 1 second. The maximum value of LTP, A_+, is 0.1 and the maximum value of LTD, A_-, is 0.12. The initial values of the weights are set to 6, the maximum value is limited to 10, and the minimum value is limited to 0.

The excitatory connections are updated every second by Eq. (3):

$$w_{ij}(t) = w_{ij}(t-1) + \sum_{t_i=t-1}^{t} \Delta w_{ij}(t_i, t_j), \quad (3)$$

where $\sum_{t_i=t-1}^{t} \Delta w_{ij}(t_i, t_j)$ is the sum of the change in synaptic weights $\Delta w_{ij}(t_i, t_j)$ from time $t-1$ [s] to t

[s]. Inhibitory connection weights are fixed to -5. A ramdomly chosen neuron receives a pulse of 20 [mA] every 1 [ms] as a random thalamic input. With these experimental conditions, we carried out the following two experiments and investigated the time series of firing rates and synaptic weights.

- Experiment 1: We changed the value of the parameter τ which determines the curvature of the STDP function in Eq. (1).
- Experiment 2: We biased the change of the synaptic weights in the STDP learning. Namely, we used Eqs. (4) and (5) instead of Eq. (3). Equation (4) updates the synaptic weights from excitatory neurons to excitatory neurons, and Eq. (5) updates the synaptic weights from excitatory neurons to inhibitory neurons. We conducted the experiments by changing the values of δ_e and δ_i.

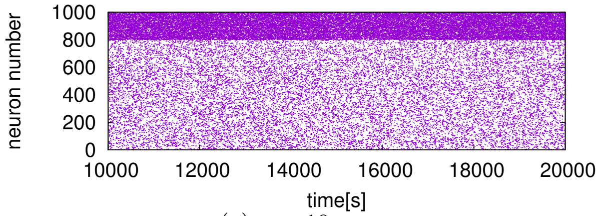
$$w_{ij}(t) = w_{ij}(t-1) + \sum_{t_i=t-1}^{t} \Delta w_{ij}(t_i, t_j) + \delta_e \qquad (4)$$

$$w_{ij}(t) = w_{ij}(t-1) + \sum_{t_i=t-1}^{t} \Delta w_{ij}(t_i, t_j) - \delta_i \qquad (5)$$

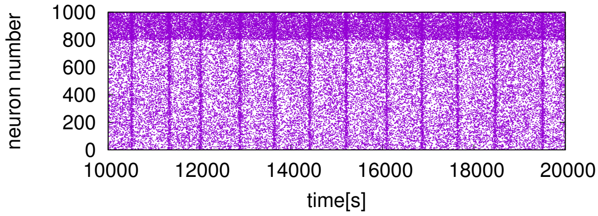
4. Results

4.1. Results of Experiment 1

Figure 1 shows the raster plots when the parameter τ takes the values $\tau = 10$ [ms] and $\tau = 1$ [ms]. As shown in Fig. 1, when $\tau = 10$, no rhythmic activity of neurons can be observed. However, when $\tau = 1$, we observed a very slow rhythm (synchronous firing approximately every 800 [s]) in the neural network model.

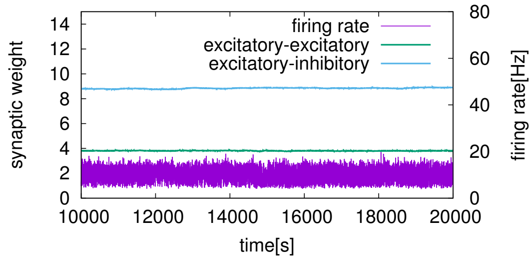


(a) $\tau = 10$.

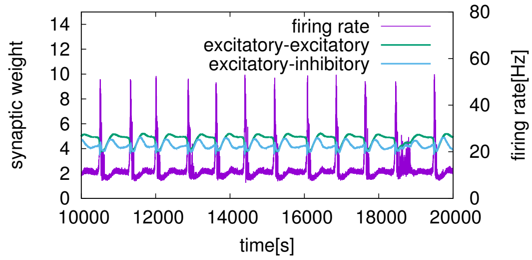


(b) $\tau = 1$.

Figure 1: Raster plots when (a) τ =10 [ms] and (b) τ =2 [ms]. The horizontal axis is time [s]. The vertical axis is the neuron number: the number 1 – 800 are excitatory neurons and the number 801 – 1000 are inhibitory neurons.



(a) $\tau = 10$



(b) $\tau = 1$

Figure 2: Temporal changes of firing rates and average synaptic weights. The horizontal axis is time [s], the left vertical axis is the synaptic weight and the right vertical axis is the firing rate [Hz]. When $\tau = 1$, the firing rate and the synaptic weight oscillate with very slow rhythms. Both excitatory to excitatory and excitatory to inhibitory synaptic weights take almost the same values.

Figure 2 shows a temporal change of firing rates and average synaptic weights when $\tau = 10$ and 1. We defined the firing rate as the average firing frequency of a single neuron among all neurons every one second. Namely, when m firings are observed from N neurons per second, the firing rate (average frequency) is defined by m/N [Hz]. The average synaptic weight is the average value of synaptic weights of all connections including excitatory and inhibitory connections in every second.

As shown in Fig. 2(a), when $\tau = 10$, the firing rate oscillated with high frequency with almost constant amplitude. As shown in Fig. 2(b), when $\tau = 1$, the firing rate repeated sudden rise and fall with very slow frequency. This tendency was observed when $\tau \sim 1$.

Figure 3 shows time series of firing rates when the value of τ is decreased from 10 to 1. When the values of τ become smaller, the amplitudes of the firing rate become larger (Fig. 3(a)(b)(c)). By decreasing the value of τ further, the amplitudes change irregularly and sometimes the firing rates rise suddenly (Fig. 3(d)(e)(f)(g)). When $\tau = 1.2$, the sudden rise of firing rates appeared periodically (Fig. 3(h)).

Focusing on synaptic weights, when $\tau = 10$, the synaptic weights are constant as shown in Fig. 2(a). The synaptic weights between excitatory and inhibitory neurons are stronger than that of excitatory and excitatory neurons.

On the other hand, as shown in Fig. 2(b), the synaptic weights oscillate with the same period as the firing rate when $\tau = 1$. The synaptic weights from excitatory to inhibitory neurons became smaller than that from excitatory to excitatory neurons. The difference between excitatory–inhibitory synaptic weights and excitatory–excitatory synaptic weights is smaller when $\tau = 1$ than when $\tau = 10$.

This can be explained as follows. In this experiment, we used the regular spiking neurons as excitatory neurons and the fast spiking neurons as inhibitory neurons. Namely, while an excitatory neuron fires once, an inhibitory neuron fires more than once.

When the value of τ is large, a learning window of the STDP learning has a large width along temporal direction. Then connections with various values of firing time lags can interact with each other. Thus, the inhibitory connections are strengthened more frequently than the excitatory connections because of high firing frequency of inhibitory neurons. Therefore, the synaptic weights to inhibitory neurons become stronger than that to excitatory neurons.

When the value of τ is small, the learning window has a narrow width along temporal direction. Then, connections with small time lags can only interact with each other. Thus, the connections to inhibitory neurons are strengthen fewer times than the case of large τ. These mechanisms make the synaptic weights to inhibitory neurons as strong as that to excitatory neurons.

4.2. Results of Experiment 2

From the results of **4.1**, we show that when $\tau = 1$, ISO could be observed. However, the parameter value of $\tau = 1$ [ms] is physiologically implausible, because τ is reported to range from 10 [ms] to 40 [ms] in mammals[5][6]. Then, in this section, we investigated whether ISO can be observed with physiologically plausible parameter ranges.

When ISO was observed, no large difference exists between synaptic weights to excitatory neurons and inhibitory neurons (Fig. 2). On the other hand, when $\tau = 10$, the synaptic weights to inhibitory neurons are stronger than that to excitatory neurons.

Therefore, we used a biased STDP rule to weaken the inhibitory synaptic weights and to strengthen the excitatory synaptic weights. The biased update of the excitatory synaptic weight is expressed by Eq. (4), and the update of the inhibitory synaptic weight is expressed by Eq. (5). Under this condition, we changed the values of δ_e and δ_i to examine whether ISO appears when $\tau = 10$.

As shown in Figs. 4 and 5, when $\delta_e = 0.300$ and $\delta_i = 0.308$, we observed ISO. The firing rates increase and decrease with very low oscillation frequency. The average synaptic weights also oscillate almost with the same frequency (~ 0.0005[Hz]).

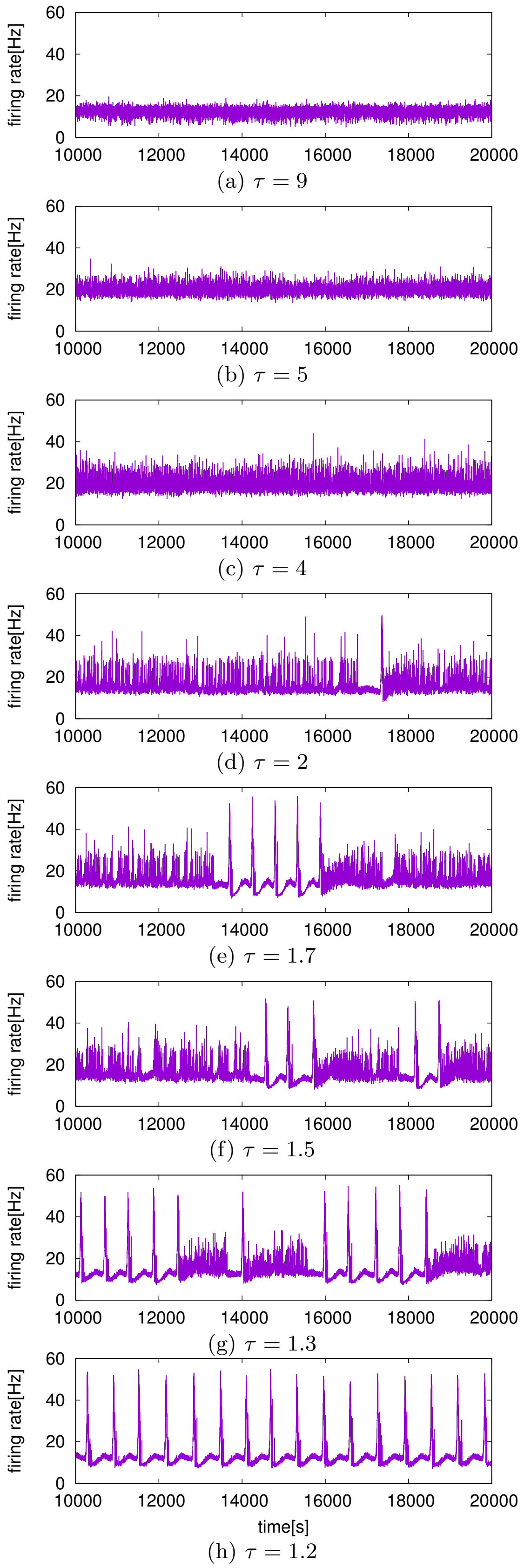


Figure 3: Temporal change of firing rates. The horizontal axis is time [s] and the vertical axis is the firing rate [Hz].

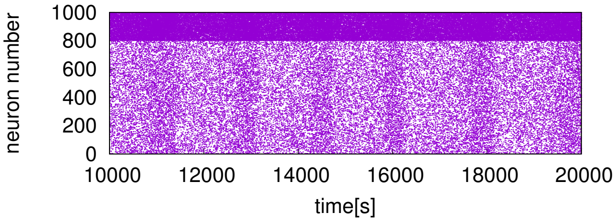


Figure 4: Raster plot when $\tau = 10$, $\delta_e = 0.300$ and $\delta_i = 0.308$. The horizontal axis is time [s] and the vertical axis is the neuron number. We can see rhythmic activities of neurons.

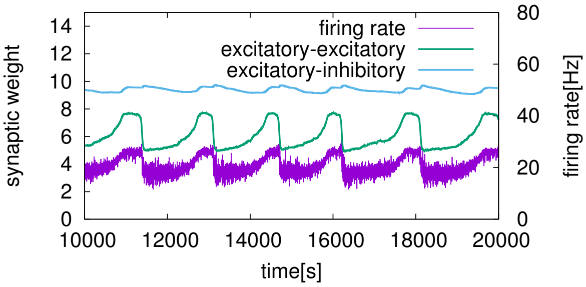


Figure 5: Temporal change of firing rates and average synaptic weights ($\tau = 10$, $\delta_e = 0.300$ and $\delta_i = 0.308$). The horizontal axis is time [s], the left vertical axis is the synaptic weight and the right vertical axis is the firing rate [Hz]. The firing rate and the synaptic weight oscillate with very slow frequency($\sim$ 0.0005 [Hz]).

5. Mechanism to Generate ISO

The oscillation of the firing rate in Figs. 2(b) and 5, is explained by the difference between the synaptic weights to excitatory neurons and that to inhibitory neurons. When the synaptic weights to excitatory neurons are strong, excitatory neurons fire more easily. Then, the whole firing rates become higher. When the synaptic weights to inhibitory neurons are strong, inhibitory neurons fire more easily. Then, the whole firing rates become lower.

On the other hand, when the synaptic weights to excitatory neurons and inhibitory neurons are balanced, the firing rate can be both high and low. Therefore, when the synaptic weights change by the STDP learning, the firing rate changes with time.

Considering these modulation of synaptic weights, we can explain the mechanism to generate ISO as follows. First, the synaptic weights change with time by the STDP learning. About learning of excitatory–excitatory neurons and excitatory–inhibitory neurons, if the chance for the learning is one–sided (this is the case of Fig. 2(a)), the learning converges and the firing rate becomes stable. For example, if there is a high chance for the learning of excitatory–inhibitory (excitatory–excitatory) neurons than that of excitatory–excitatory (excitatory–inhibitory) neurons, the synaptic weights to inhibitory (excitatory) neurons become stronger than that to excitatory (inhibitory) neurons. Then, the firing rate becomes stable at a low (high) value.

However, if the chance for the learning of excitatory–inhibitory neurons and that of excitatory–excitatory neurons is balanced (this is the case of Figs. 2(b) and 5), the learning does not converge and the synaptic weights keep changing. Changing synaptic weights make the firing of excitatory and inhibitory neurons out of balance. Then the firing rates change suddenly. By the sudden change of the firing rates, the synaptic weight balance breaks down significantly. Subsequently, the synaptic weights change with time by learning, which causes sudden change of firing rates again. By repeating these processes, ISO is reproduced.

6. Conclusion

In this paper, we investigated the occurrence of slow oscillation in a neural network with the STDP learning. We discovered that ISO can be reproduced by the STDP learning with balanced weights of connections (which connect to excitatory neurons and inhibitory neurons). From these results, two possible neuronal mechanisms for generating ISO are indicated: (1)change the curvature of the STDP function and (2)bias the learning to balance the synaptic weights.

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