2016 International Symposium on Nonlinear Theory and Its Applications,
NOLTA2016, Yugawara, Japan, November 27th-30th, 2016

Analysis of Synaptic Dynamics during Infra-Slow Oscillation

Toshihiro Kobayashi†, Yutaka Shimada†,‡, Kantaro Fujiwara†,‡ and Tohru Ikeguchi†,‡

†Department of Management Science, Graduate School of Engineering, Tokyo University of Science
‡Department of Information and Computer Technology, Faculty of Engineering, Tokyo University of Science
6–3–1 Niijuku, Katsushika-ku, Tokyo, Japan

Abstract—In our brains, interaction between neurons generates a variety of rhythms, for example, alpha, delta and gamma rhythms, and so on. These rhythms are observed from mathematical neural network models with spike-timing-dependent plasticity (STDP). We have already discovered that a mathematical model with the STDP can reproduce a rhythm of very low frequency, or infra-slow oscillation. In this paper, we analyzed the synaptic dynamics during the infra-slow oscillation. As a result, it is indicated that synaptic dynamics plays a key role for reproducing the infra-slow oscillation.

1. Introduction

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

In our former study, we investigated a neural mechanism to reproduce ISO, conducting numerical simulations with changing the curvature of the STDP function[4]. In this study, we investigated the spike timing difference of presynaptic and postsynaptic neurons and temporal change in the synaptic weights of all synapses.

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 weights is decided by STDP function which is represented as follows[5]:

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

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

3. Methods

The neural network we used consists of 1,000 randomly connected Izhikevich neuron[3]. We prepared 800 excitatory neurons and 200 inhibitory neurons. In this paper, we used regular spiking neurons for the excitatory neurons, and fast spiking neurons for the inhibitory neurons. Each neuron has 100 synapses 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.

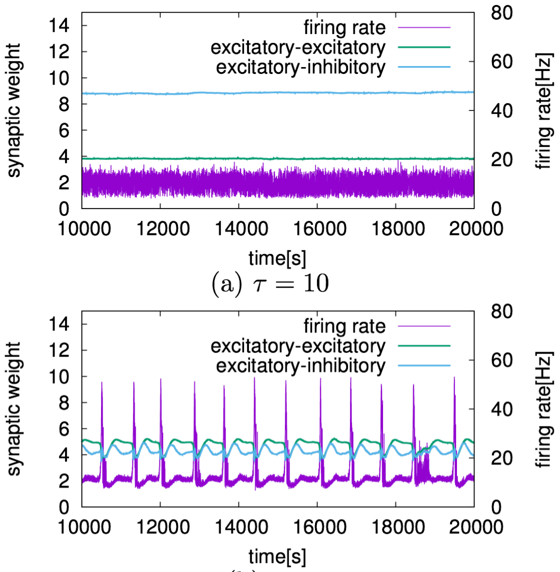
Conduction delays among all neurons are random integers between 1 [ms] and 20 [ms]. The excitatory connection obeys the STDP learning rule with every 1 second. The maximum value of LTP, A_+, is 0.1 and the maximum value of LTD, A_-, is 0.12. The initial values of the weights are set to 6, the maximum value is limited to 10, and the minimum value is limited to 0. The change of the synaptic weights adopts the nearest-neighbor spiking. The excitatory connections are updated every second by Eq. (2):

$$w_{ij}(t) = w_{ij}(t-1) + \sum_{t_i=t-1}^{t} \Delta w_{ij}(\Delta t_{ij}), \quad (2)$$

where $\Delta w_{ij}(\Delta t_{ij})$ is defined by Eq. (1) and depends on t_i and t_j. Inhibitory connection weights are fixed to -5. A randomly chosen neuron receives a pulse of 20 [mA] every 1 [ms] as a random thalamic input. With these experimental conditions, we changed the value of the parameter τ which determines the curvature of the STDP function in Eq. (1), and investigated the time series of firing rates and synaptic weights.

4. Results

4.1. Temporal Change of Firing Rates and Synaptic Weights



(a) $\tau = 10$

(b) $\tau = 1$

Figure 1: Temporal changes of firing rates and average synaptic weights[4]. 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.

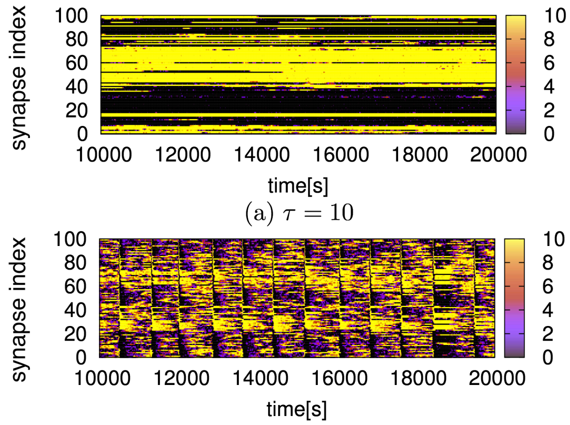
Figure 1 shows a temporal change of firing rates and average synaptic weights when $\tau = 10$ and 1. We defined the firing rate as the average firing frequency of a single neuron among all neurons every one second. Namely, we defined the firing rate by m/N [Hz], when m firings are observed from N neurons per second. 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. 1(a), when $\tau = 10$, the firing rate fluctuated with high frequency with almost constant amplitude. As shown in Fig. 1(b), when $\tau = 1$, the firing rate repeated sudden rise and fall with very slow frequency. This tendency was observed when $\tau \sim 1$.

Focusing on synaptic weights, when $\tau = 10$, the synaptic weights are constant as shown in Fig. 1(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. 1(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 $\tau = 10$.

4.2. Temporal Change of Synaptic Weights



(a) $\tau = 10$

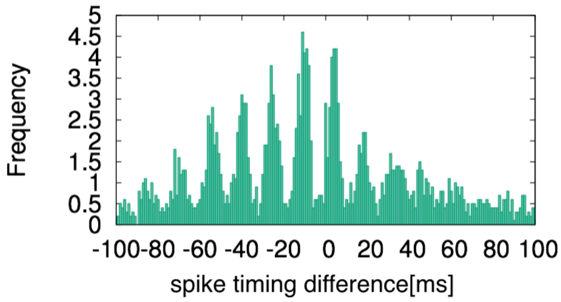
(b) $\tau = 1$

Figure 2: Temporal change of the synaptic weights in all synapses of an excitatory neuron. The horizontal axis is time[s]. The vertical axis is the synapse index. The colors show the strength of synaptic weights. The synaptic weights are almost constant and are separated into maximum and minimum value when $\tau = 10$. On the other hand, the synaptic weights change periodically and some synapses have intermediate values when $\tau = 1$.

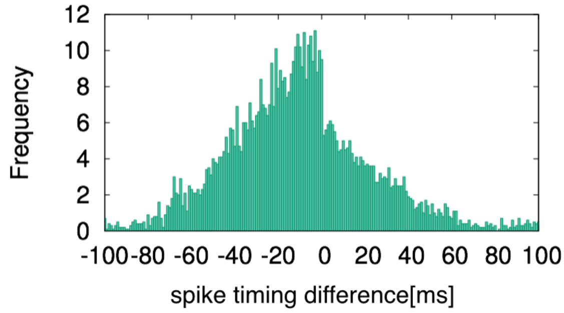
Figure 2 shows the temporal change of all synaptic weights selected from excitatory neuron arbitrarily. As shown in Fig. 2, when $\tau = 10$, the synaptic weights are almost constant and are separated into maximum and minimum values. However, when $\tau = 1$, the synaptic weights change with almost the same period as the firing rate. Some synapses have intermediate values as well as maximum and minimum values.

4.3. Histogram of Spike Timing Difference

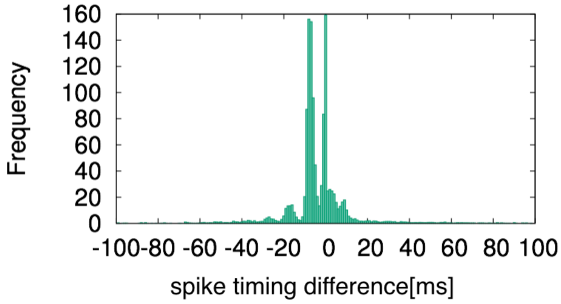
To analyze the relation between the firing of presynaptic neuron and the firing of postsynaptic neuron, we investigated the spike timing differences between presynaptic and postsynaptic neuron. In this paper, we defined spike timing difference as Δt_{ij} in Eq. (1). Figure 3(a) shows the frequency distribution of the spike timing difference when $\tau = 10$. As shown in the figure, the frequency of the spike timing difference repeats high and low values periodically. This rhythm is about 70[Hz](gamma rhythm). The appearance of the gamma rhythm has already been shown in the experiment by Izhikevich[3]. This tendency does not depend on time. Therefore, result of Fig. 3(a) is consistent with the experiment by Izhikevich[3].



(a) $\tau = 10$, low firing rate



(b) $\tau = 1$, low firing rate

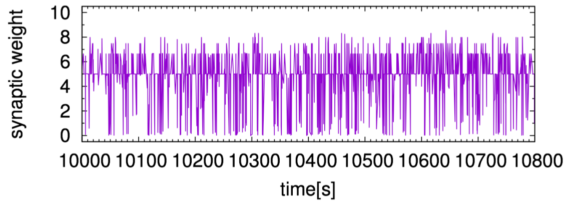


(c) $\tau = 1$, high firing rate

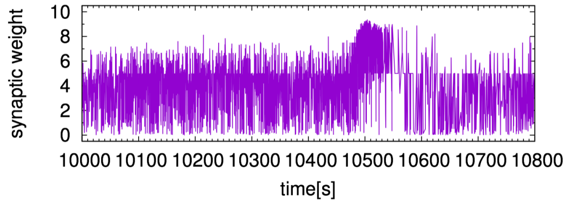
Figure 3: Frequency distributions of spike timing differences between presynaptic and postsynaptic neurons when (a)$\tau = 10$, (b)$\tau = 1$ during low firing rate and (c)$\tau = 1$ during high firing rate. The horizontal axis is difference of spike timing. The vertical axis is frequency.

Figure 3(b) and 3(c) show the histograms of the spike timing difference when $\tau = 1$. Figure 3(b) is the frequency distribution when the firing rate is low, and Fig. 3(c) is the frequency distribution when the firing rate is high. As shown in the figures, there exist more spike timing differences of negative values than those of positive values. It mean that LTD occurs more frequently than LTP. In particular, when the high firing rates appear, the number of LTD increase extremely(Fig. 3(c)).

4.4. Change of Synaptic Weights Which Induce Neuronal Firing



(a) $\tau = 10$



(b) $\tau = 1$

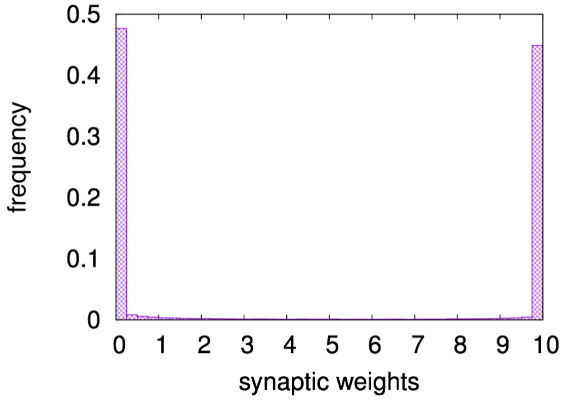
Figure 4: Temporal change of synaptic weights which induced neuronal firing. The horizontal axis is time[s]. The vertical axis is the synaptic weights. (a) shows the change when $\tau = 10$ and (b) shows the change when $\tau = 1$. When $\tau = 1$, the synaptic weights become stronger as the firing rates.

When $\tau = 1$, there are a large number of LTD during high firing rate. We investigated the reason why the firing rate becomes high despite the large number of LTD.

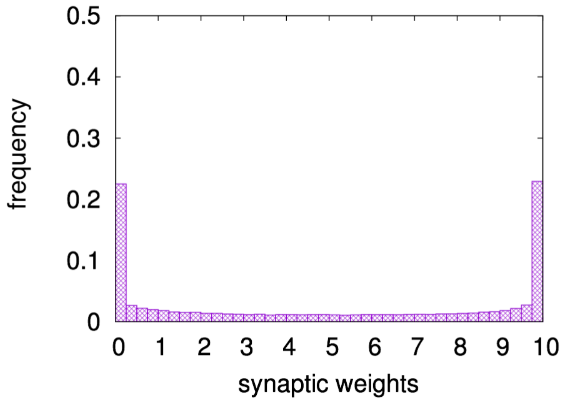
Each neuron receives a number of inputs through synapses. However such inputs do not always make the neuron fire. We focused on the synapses which induce firings of neurons. We plotted the time series of the average synaptic weight in such synapses. Figure 4 shows the temporal change of the average value of the synaptic weights in the synapses which induced neuronal firing. As shown in the figure, when $\tau = 10$ the synaptic weight fluctuates almost stationarily. When $\tau = 1$, the synaptic weight becomes stronger near 10500[s], and this corresponds to sudden rise of the firing rates as shown in Fig. 1(b). From this result, it is revealed that firing rates can be high by inputs from specific synapses even if there are more LTD than LTP in average.

4.5. Histogram of Synaptic Weights

Figure 5 shows the histogram of synaptic weights. As shown in the figure, when $\tau = 10$, the synaptic weights are almost completely separated into maximum and minimum value. On the other hand, when $\tau = 1$, the synaptic weights are not completely divided into maximum and minimum value and there are more synapses which have intermediate values.



(a) $\tau = 10$



(b) $\tau = 1$

Figure 5: Histograms of synaptic weights. The horizontal axis is synaptic weights. The vertical axis is frequency. The synaptic weights are almost completely separated into maximum and minimum values when (a)$\tau = 10$, while the synaptic weights are not completely separated into maximum and minimum values when (b)$\tau = 1$.

5. Mechanism to Generate ISO

The oscillation of the firing rate shown in Fig. 1(b) is explained by the dynamics of synaptic weights. When the value of τ is large, the STDP learning window has a large width along the temporal direction. The STDP learning with such a wide window has many chance for learning and the synaptic weights are separated into maximum and minimum values. Because the bimodal distribution does not change its shape easily by LTP and LTD, the learning converges and the firing rate becomes stable.

On the other hand, when the value of τ is small, the STDP learning window has a narrow width along the temporal direction. The STDP learning with such a narrow window has less chance for learning and the synaptic weights are not separated into maximum and minimum values completely. Because the synaptic weights of intermediate values change their values easily by LTP and LTD, the learning does not converge. The firing rates are highly influenced by the synaptic weights and exhibit sudden rise and fall. By the sudden change of the firing rates, the balance of synaptic weights breaks down significantly. Subsequently, the synaptic weights change with time by the STDP 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, or ISO, in a neural network with the STDP learning. We discovered that ISO is reproduced by the STDP learning with a narrowed window of the STDP function. With the narrow window, the learning does not converge and the synaptic weights become more influenced by the change of firing rates. From these results, it is indicated that ISO can be generated by the synaptic weights of intermediate values.

Acknowledgment

The authors would like to thank Mr. S. Ishii and AGS Corp. for their kind encouragements on this research. The research of Y.S. is supported by Grant-in-Aid for Research Activity Start-up (No. 26880020) from JSPS. The research of K.F. was supported by Grant-in-Aid for Challenging Exploratory Research (No 15K12137) from JSPS. The research of T.I. was partially supported by Grant-in-Aid for Challenging Exploratory Research (No. 24650116) from JSPS and by Grant-in-Aid for Scientific Research (C) (Generative Research Fields) (No.15KT0112) from JSPS.

References

[1] N. A. Aladjalova, Nature, Vol. **179**, pp. 957–959, 1957.

[2] S. Hughes, M. Lorincz, R. Parri and V. Crunelli, Progress in brain research, Vol.**193**, pp. 145–162, 2011.

[3] E. M. Izhikevich, Neural Computation, Vol. **18**, No. 2, pp. 245–282, 2006.

[4] T. Kobayashi, Y. Shimada, K. Fujiwara and T. Ikeguchi, Proceedings of NOLTA2015, pp. 447–450, 2015

[5] G. Bi and M. Poo, The Journal of Neuroscience, Vol. **18**, No. 24, pp. 10464–10472, 1998.