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Emergence of self-organized structures in a neural network using two types of STDP learning rules

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Abstract—Recent numerical experiments reveal that in a neural network with the spike-timing dependent synaptic plasticity (STDP) learning emerges a functional complex network structure. The functional complex network structure has the small-world property and the scale-free property. However, experimental settings in the previous report are physiologically inappropriate. In addition, although there are two types of STDP learning rules, only one rule is used in the previous experiments. Thus, in this paper, we analyzed how the neural network structure self-organize and what kinds of complex neural network structure emerge with physiologically appropriate settings, if the two types of STDP learning, the additive and the multiplicative learning rules, are applied.

1. Introduction

Billions of neurons exist in our brain. These neurons interconnect with each other through synapses or gap junctions, then they construct complex neural network structure in the brain. Using such a complex neural network structure, huge amounts of information are effectively processed.

Recent studies in the field of the neuroscience show that a new kind of synaptic plasticity is used in our brains: the spike-timing dependent synaptic plasticity (STDP), which has experimentally been observed in several regions of the brain from different kinds of species[7]. It is called a pre-neuron which transmits a spike. On the other hand, it is called a post-neuron which receives a spike. The long term synaptic modification depends on the firing timing between the pre-neuron and post-neuron, and it arises within approximately a few milliseconds. Then, a synapse is strengthened if the post-synaptic spike follows the pre-synaptic spike. This synaptic modification is called the long-term potentiation (LTP, see Fig.1). On the other hand, a synapse is weakened if the pre-synaptic spike follows the post-synaptic spike, it is called the long-term depression (LTD, see Fig.2).

Since a seminal paper by Bi and Poo[6], experimental and theoretical studies have been devoted to analyze the fundamental properties induced by the STDP learning. Then, it is widely acknowledged that the frequency distribution of synaptic weights by the STDP learning gradually converges to a bimodal distribution. However, it is not only interesting but also important to analyze what kinds of spatial structure of the synaptic weight will emerge: regular, random, or complex structure?

Until 1998, in the graph theory mainly analyzed are regular networks and random networks. A regular network has a specific structure, but its network size is large. On the other hand, a random network has a small network size but no specific structure. However, it has been shown that real networks often exhibit a small network size even though they still keep clusters. To model these characteristics, Watts and Strogatz[2] recently proposed an interesting new concept, the small-world network and they showed that the small-world networks have different characteristic from regular networks or random networks: a short characteristic path length but a large clustering coefficient. They also showed that the small-world networks exist in many real networks: for example, the co-acting relationship in movie films, the power grid networks, and the anatomical structure of *C. elegans*. Neural networks in our brain may also have the small-world network structure, however, it has yet been clarified how a neural network self-organizes to evolve such a functional complex network.

Recently, Shin and Kim[1] and Suzuki and Ikeguchi[11] reported almost at the same time a relation between the STDP learning and the complex network structure of a neural network. They[1, 11] showed a possibility that a self-organization of the small-world network structure in a neural network could be caused by the STDP learning. Although their results[1, 11] sound interesting, two fundamental problems still remain. Firstly, experimental settings are physiologically inappropriate[1]. Secondly, they only used a single type of STDP learning rule, although there are different types of learning rules in the STDP, such as an additive learning rule and a multiplicative learning rule.

Thus, in this paper, using more physiological settings we evaluated a possible complex structure of the neural network with the STDP learning. More physiological settings mean that we distingish excitatory and inhibitory neurons, and we give 10 Hz external inputs to a neural network. We also evaluate what kind of difference will emerge in a neural network structure if different types of the STDP learning rule, such as the additive and the multiplicative STDP rules, are applied.

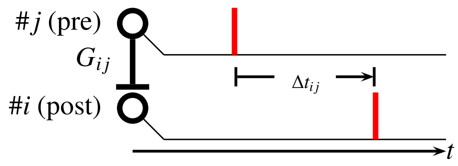

Figure 1: Two nodes express pre- and post-neurons. The edge is a synaptic connection from the j-th node to the i-th node. G_{ij} is a synaptic weight from the j-th neuron to the i-th neuron. This figure represents that the j-th post-neuron fires after the i-th pre-synaptic neuron fires. Then, the synaptic connection between the j-th (pre) neuron and the i-th (post) neuron is strengthened, which is call the long-term potentiation.

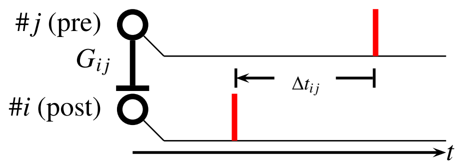

Figure 2: The same as Fig.1, but for the long-term depression. The firing timing of two spikes is reversed.

2. Neuron model

In this paper, we used the FitzHugh-Nagumo neuron model (a two-dimensional relaxation oscillator)[9, 1] as an element of a neural network. The i-th neuron in the neural network is defined as follows:

$$\begin{array}{rcl} \epsilon \dot{v}_i & = & I_{\text{ion}} + I_{\text{syn}} + I_{\text{ext}}, \\ \dot{w}_i & = & v_i - w_i - b, \\ I_{\text{ion}} & = & v_i(v_i - a)(1 - v_i) - w_i, \end{array} \tag{1}$$

where v_i is a fast voltage variable of the i-th neuron; w_i is a slow recovery variable of the i-th neuron if $\epsilon \ll 1$; a, b, and ϵ are parameters; I_{ion} is an ionic current through membrane and I_{ext} is an external stimulus: a neuron is connected from the other neurons with synapses, then, if pre-synaptic neurons emit spikes, a synaptic current is transmitted from the pre-synaptic neurons to a post-synaptic neuron. This synaptic current I_{syn} to the i-th neuron at time t is described as follows:

$$I_{\text{syn}}(t) = \sum_{j=1, j\neq i}^{N} \{g_{ij}(t)(V - v_i(t)) + \bar{g}_{ij}(t)(\bar{V} - v_i(t))\}, \tag{2}$$

where N is the number of the neurons in the neural network; g_{ij} ($\bar{g}_{ij}$) is a synaptic conductance from the j-th neuron to the i-th neuron and V ($\bar{V}$) is synaptic reversal potential only for the excitatory (inhibitory) neuron. The excitatory neuron accelerates its post-synaptic firings. The inhibitory neuron depresses its post-synaptic firings. The synaptic conductance between the i-th and j-th neurons is defined as follows:

$$\tau_{\text{syn}} \frac{\mathrm{d}g_{ij}}{\mathrm{d}t} = -g_{ij}, \tag{3}$$

$$\bar{\tau}_{\text{syn}} \frac{\mathrm{d}\bar{g}_{ij}}{\mathrm{d}t} = -\bar{g}_{ij}, \tag{4}$$

where τ_{syn} ($\bar{\tau}_{\text{syn}}$) is an excitatory (inhibitory) time constant of the decay. The synaptic conductance between the i-th and j-th neuron decays exponentially if the j-th pre-synaptic neuron does not emit a spike.

If the j-th pre-synaptic neuron fires at time t^*, the synaptic conductance is updated as follows:

$$g_{ij} \to g_{ij} + \frac{G_{ij}(t^*)}{N-1}, \tag{5}$$

$$\bar{g}_{ij} \to \bar{g}_{ij} + \frac{\bar{G}_{ij}(t^*)}{N-1}, \tag{6}$$

where G_{ij} ($\bar{G}_{ij}$) is a maximum excitatory (inhibitory) conductance from the j-th neuron to the i-th neuron. In this paper, we set $\bar{G}_{ij}$ as constant, and G_{ij} is modified by the STDP learning rules.

3. STDP learning rules

The STDP learning rule is a temporally asymmetric Hebbian plasticity. This learning rule modifies the maximum conductance from the j-th neuron to the i-th neuron in case that the j-th pre-synaptic neuron is excitatory. Then G_{ij} is strengthened if the i-th post-synaptic neuron fires after the j-th pre-synaptic neuron emits a spike. This synaptic modification is called the long-term potentiation (LTP, see Fig.1). On the other hand, G_{ij} is weakened if the i-th post-synaptic neuron fires before the j-th pre-synaptic neuron emits a spike. This synaptic modification is called long-term depression (LTD, see Fig.2). The amounts of the synaptic modification is decided by a temporal difference between the two spikes. If the temporal-spike interval is short, the synaptic modification becomes large.

Let us describe t_j as a firing time of the j-th pre-synaptic neuron, and t_i as that of the i-th post-synaptic neuron. Then, the STDP function is defined quantitatively as

$$F(\Delta t_{ij}) = \begin{cases} A_+ e^{\frac{-\Delta t_{ij}}{\tau_+}} & \text{if } \Delta t_{ij} > 0, \\ -A_- e^{\frac{\Delta t_{ij}}{\tau_-}} & \text{if } \Delta t_{ij} < 0, \end{cases} \tag{7}$$

where $\Delta t_{ij} = t_i - t_j$ and $F(\Delta t_{ij}) = 0$ if $\Delta t_{ij} = 0$. The parameters τ_+ and τ_- determine a temporal window of the STDP, and A_+ and A_- are the maximum amounts of the synaptic modification in the STDP. The upper equation expresses the LTP and the lower one expresses the LTD.

In the STDP, there are two types of the leaning rules. The first one is an additive rule and the second one is a multiplicative rule. The additive STDP learning rule is described by

$$\Delta G_{ij} = F(\Delta t_{ij}) \tag{8}$$

where ΔG_{ij} is the amount of synaptic modification. Eq.(8) means that the value of the STDP function corresponds to the amount of the synaptic modification. On the other hand, the multiplicative STDP learning rule is described by

$$\Delta G_{ij} = G_{ij} F(\Delta t_{ij}). \tag{9}$$

In the multiplicative learning rule, the product of the value of the STDP function and the maximum excitatory conductance corresponds to the amount of the synaptic modification.

4. Measures

To evaluate whether the network has the small-world property or not, the average connection probability $\langle k/n \rangle$, the characteristic path length L, and the clustering coefficient C are often used. These measures are defined as follows:

$$\langle k/n \rangle = \frac{1}{n} \sum_{i=1}^{n} \frac{k_i}{n}, \tag{10}$$

$$L = \frac{1}{n(n-1)} \sum_{j=1}^{n} \sum_{i=1, i \neq j}^{n} d_{ij}, \tag{11}$$

$$C = \frac{1}{n} \sum_{i=1}^{n} C_i, \tag{12}$$

where n is the number of nodes (neurons) in a network; d_{ij} is the shortest distance from the i-th node to the j-th node; k_i is a degree (the number of synaptic connections) of the i-th node; C_i is the clustering coefficient of the i-th node and defined as

$$C_i = \frac{\sum_{l=1}^{k_i} \sum_{m=l+1}^{k_i} c_{v_i(l) v_i(m)}}{{}_{k_i}\mathrm{C}_2}, \tag{13}$$

where $v_i(l)$ is the l-th adjacent node of the i-th node. $c_{v_i(l) v_i(m)}$ takes 1 if the node $v_i(l)$ and the node $v_i(m)$ are connected, and takes 0 if they are not connected.

5. Structural property of a neural network as an undirected and unweighted graph

If a neural network has a small-world property, the characteristic path length becomes short but the clustering coefficient becomes high. However, these measures are usually applied to undirected and unweighted network. What is important here is that neural networks are generally represented by a directed and weighted networks. Although several interesting measures are proposed to evaluate such directed and weighted networks, we transform from a directed and weighted neural network to an undirected and unweighted network in this paper. The main reason is that after applying the STDP learning rules, the distribution of synaptic weights in the self-organized neural network using the STDP learning rule becomes bi-modal, which means that some population of synapses are strengthened to the maximum conductance while the others are weakened to zero. It is very natural to consider that the strengthened synapses express the functional connections, which support strong influences between two neurons. Then, we defined that the i-th and j-th neurons are connected if $G_{ij} > 0.99 G_{\max}$ or $G_{ji} > 0.99 G_{\max}$, and in the other cases, they are not connected. $G_{\max}$ is the maximum synaptic weight of G_{ij}. We call such an undirected and unweighted network the STDP network.

6. Construction method of random networks

To evaluate whether the STDP network has the small-world property or not, we have to compare the STDP network with its randomized network. We generated a randomized network of the STDP network with a random rewiring. Namely, we randomly rewired the edges of the STDP network. How to construct a randomized network is described as follows:

1. An end of the edge between the i-th and j-th nodes is cut off with the probability 0.5, and

2. If the end is cut to which the i-th node was connected yet, we randomly selected the $k(\neq i)$-th node. Then, if the j-th node and k-th node are not connected, the j-th node and the k-th node are connected,

3. Repeat the above steps 1 and 2 until all the edges are rewired.

7. Computational simulation

7.1. Experimental settings

We used a neural network with 1,000 neurons. We also set the number of excitatory neurons to 800, and inhibitory neurons to 200. Each neuron has synaptic connections to all neurons without itself. We set the synaptic weight of G_{ij} to $(0, 0.1]$ using uniform distributed random numbers as an initial condition. If the j-th neuron is inhibitory, we also set the synaptic weight of $\bar{G}_{ij}$ to 0.03. We applied the STDP learning rule to G_{ij} at every firing event. Then, the self-organized neural network produced by the STDP learning is undirectionalized and unweighted. Let us define $L_{\rm s}(t)$ and $C_{\rm s}(t)$ as the characteristic path length and the clustering coefficient of the STDP network at time t, respectively. We also defined the characteristic path length and the clustering coefficient of the random network, $L_{\rm r}(t)$, $C_{\rm r}(t)$, respectively. Then, we calculated $L_{\rm s}(t)/L_{\rm r}(t)$ and $C_{\rm s}(t)/C_{\rm r}(t)$. We repeated these procedures from 0 to 600 [sec]. Moreover, we simulate in both cases of the additive and the multiplicative rules.

We set the parameters of Eqs. (1)–(7) as follows: $\epsilon = 0.005$, $a = 0.5$, $b = 0.12$, $I_{\rm ext} = 0.2$, $V = 0.7$, $\bar{V} = 0.0$,

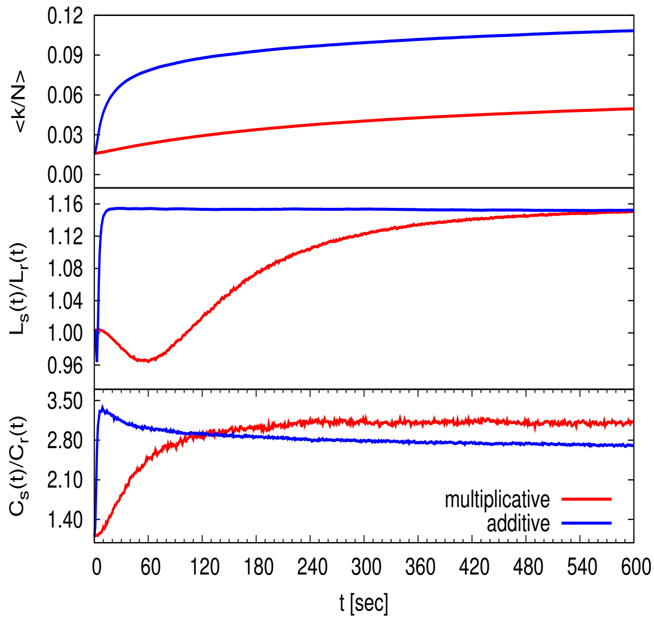

Figure 3: Transition of $\langle k/N \rangle$, $L_s(t)/L_r(t)$, and $C_s(t)/C_r(t)$. A horizontal axis is a time at which the STDP learning rules is applied to the neural network. The vertical axes show the values of $\langle k/N \rangle$(top), $L_s(t)/L_r(t)$(middle), and $C_s(t)/C_r(t)$(bottom), respectively. The red lines the results by the multiplicative STDP rule, and the blue lines represent those of the additive STDP learning rule.

$\tau_{\text{syn}} = \bar{\tau}_{syn} = 0.2$, $A_+ = 0.01$, $A_- = 0.006$, $\tau_+ = 1.0$, and $\tau_- = 2.0$.

7.2. Results

The results are shown in Fig.3. A network has the high small-world property if the average connection probability $\langle k/N \rangle$ is small, $L_s(t)/L_r(t) \simeq 1$, and $C_s(t)/C_r(t) \gg 1$. In Fig.3, as the average connection probability is small, the values of $L_s(t)/L_r(t)$ of the additive and the multiplicative learning rules are close to 1, and the values of $C_s(t)/C_r(t)$ are much larger than one. These results indicate that the STDP networks using both additive and multiplicative STDP learning rules self-organize to evolve to a small-world network.

The average connection probability $\langle k/N \rangle$ of the multiplicative rule is always smaller than that of the additive one. In addition, we can see that the characteristics of the multiplicative rule increase slowly, while those of the additive rule increase rapidly. The values of $L_s(t)/L_r(t)$ for both learning rules finally converge to 1.15. In addition, although $C_s(t)/C_r(t)$ of the multiplicative rule is smaller than that of the additive rule between 0 [sec] and 120 [sec], the value of $C_s(t)/C_r(t)$ of the multiplicative rule becomes larger than that of the additive rule after 120 [sec]. From these results, the STDP network using the multiplicative STDP learning rule has the higher small-world property than that of the additive STDP learning rule.

8. Conclusions

In this paper, we analyzed a complex functional structure of a neural network which evolves by additive and multiplicative STDP leaning rules. We conducted numerical simulations with more physiologically appropriate experimental conditions. From the results, we discovered that the neural networks have the small-world property by both STDP learning rules and that the self-organized neural network using the multiplicative STDP learning rule has higher small-world property than the additive learning rule. We also confirmed that the neural network with the additive STDP learning rule rapidly constructs a complex structure of the small-world network. In the future works, we consider to analyze directed and weighted neural networks in order to capture the characteristics more precisely.

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