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Temporal evolution of spatial structures in neural networks through STDP

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Abstract— Spike-timing-dependent plasticity (STDP) has been experimentally observed in several areas of the brain and theoretically analyzed in model studies. In particular, temporal development and equilibrium states of synaptic distributions have been enthusiastically analyzed. Although these analyses are important to understand mechanisms of STDP in neural networks, it has not been yet fully clarified what kind of spatial structures STDP organizes. In this paper, analyzing spatial structures in neural networks developed through STDP, we investigated effects of such structures for neuronal activities. As a result, depending on the mean inter-spike interval (ISI) of external inputs, STDP generates different network structures. Furthermore, neuronal activities in the network also change as the mean ISI of external inputs varies.

1. Introduction

Billions of cells interact with each other mainly through chemical synapses in the brain. Cells in the brain construct extremely complex networks with synaptic connections and effectively process huge amount of information using such complex structures. In addition, for memories, learning, and development, it is generally considered that synaptic plasticity plays an important role in the brain.

Recent studies in the field of the neuroscience have revealed that the long-term synaptic modifications arise depending on precise relative spike timings between pre- and postsynaptic action potentials, which is called spike-timing-dependent plasticity (STDP). STDP has been experimentally observed in several areas of many kinds of species [1–6]. The long-term potentiation (LTP) occurs when a postsynaptic action potential follows a presynaptic one within tens milliseconds while the reverse order of action potentials between pre- and postsynaptic neurons leads the long-term depression (LTD) [1, 3, 5, 6].

Triggered by these experimental studies, basic mechanisms of STDP have been widely analyzed in the computational neuroscience. In particular, temporal evolution and equilibrium states of synaptic distribution have been computationally and theoretically analyzed [7–11]. These analyses are indispensable to understand the basic mechanisms and properties of STDP. However, in these analyses, networks have particular forms: many presynapses and one postsynaptic neuron. Analyses of the synaptic distribution are appropriate because of a simple network structure used in the analyses, but are not enough when we analyze the works of STDP in recurrent neural networks. Then, many scientists begin to be interested in mechanisms and properties of STDP in the recurrent neural networks [12–17], but it has been unclear how structures are constructed through STDP yet.

In this paper, we analyze temporal evolution of the spatial structures in a recurrent spiking neural network organized through STDP from viewpoints of the complex network theory. In addition, we also analyze the neuronal activities and relation between the structures and the neural activities in the neural networks organized through STDP.

2. Methods

Anatomical findings in cortices show that the ratio of the number of excitatory and inhibitory cells is $4:1$. Then, a neural network is constructed from N cells in which $4N/5$ cells are excitatory and $N/5$ ones are inhibitory. In the neural network, each cell is connected with M other cells through synapses where M postsynaptic cells are randomly selected and there are no connections between inhibitory cells. Dynamics of the jth cell is represented by the following 2-dimensional ordinary differential equations:

$$\dot{v}_j = 0.04v_j^2 + 5v_j + 140 - u_j + I_j(t), \quad (1)$$

$$\dot{u}_j = a_j(b_j v_j - u_j), \quad (2)$$

with the auxiliary after-spike resetting:

$$\text{if } v_j \geq 30\,[\text{mV}], \text{ then} \begin{cases} v_j \leftarrow c_j \\ u_j \leftarrow u_j + d_j \end{cases} \quad (3)$$

where v_j and u_j are the membrane potential and the recovery variable of the jth cells, respectively [18]. The variable I_j is the sum of an external input and presynaptic inputs into the jth cell: $I_j(t) = I^{\text{ext}}\delta(t - t_j^{\text{ext}}) + \sum_{i\neq j}^{N} w_{ij}\delta(t - t_i - d_{ij})$ where I_j^{ext} represents the strength of an external input into the jth cell, w_{ij} is a weight of synaptic connection from the ith to jth cells characterized by the postsynaptic potential, t_i is the firing time of the ith cell, d_{ij} represents an axonal conduction delay from the ith to jth cells, and $\delta(t)$ represents the delta function. The model described in Eqs. (1)–(3) is computationally effective as well as the leaky-integrate and fire model but realizes rich firing patterns with varying the parameters a_j, b_j, c_j, and d_j [19].

Synaptic weights between excitatory cells change through STDP and an STDP window function is described as

$$\Delta w_{ij} = \begin{cases} A_+ \cdot e^{-|\Delta t_{ij}|/\tau_+} & \Delta t_{ij} > 0 \\ -A_- \cdot e^{-|\Delta t_{ij}|/\tau_-} & \text{otherwise} \end{cases} \quad (4)$$

where A_+ and A_- are the learning rates of the LTP and LTD, and τ_+ and τ_- are the time constants determining the exponential decays of the LTP and the LTD in the window function [8, 20]. In Eq. (4), $\Delta t_{ij} (= t_j - d_{ij} - t_i)$ represents a relative spike timing between the ith and jth cells where t_i is the firing time of the ith cell. The ith and jth cells correspond to a pre- and a postsynaptic cells, respectively. In addition, nearest spikes contribute for the long-term synaptic modifications [21].

In the following analysis, the number of cells in the spiking neural network is fixed to $1,000$. We use the regular spiking type as excitatory cells while the fast spiking type as inhibitory ones. We use the same parameter values in Eqs. (1)–(3) as in Ref. [18]. The strength of external inputs $I^{\text{ext}} = 20$ [mV] for all the cells in the network, and we assume that external inputs for each cell is the Poissonian random input. The delay d_{ij} is set to $[0, 10]$ [ms] for excitatory synapses, which is uniformly distributed while d_{ij} is set to 1 [ms] for inhibitory ones. In the initial condition, the weights w_{ij} for excitatory and inhibitory synapses are set to 6 and -5 [mV], respectively. We limit the range of synaptic weights for STDP between 0 and $w_{\max} (= 10)$ [mV]. In Eq. (4), A_+ and A_- are set to 0.1 and 0.12, and $\tau_+ = \tau_- = 20$ [ms].

To investigate network structures, we use the degree which is one of the basic measures for the complex network theory. We can define two types of the degree because the network is a digraph. in- and outdegree. The indegree k_i^{in} and outdegree k_i^{out} of the ith cell are defined as follows:

$$k_i^{\text{in}} = \sum_j H_0(w_{ji}/w_{\max}) \text{ and } k_i^{\text{out}} = \sum_j H_0(w_{ij}/w_{\max}) \quad (5)$$

where $H_0(w)$ represents the Heviside step function. In this paper, to simplify our analysis, we only focus on synaptic connections between excitatory cells. Moreover, we also use the strength, a natural extension of the degree for weighted networks. There are two types of strength as well as the degree, and the instrength s_i^{in} and the outstrength s_i^{out} are defined by

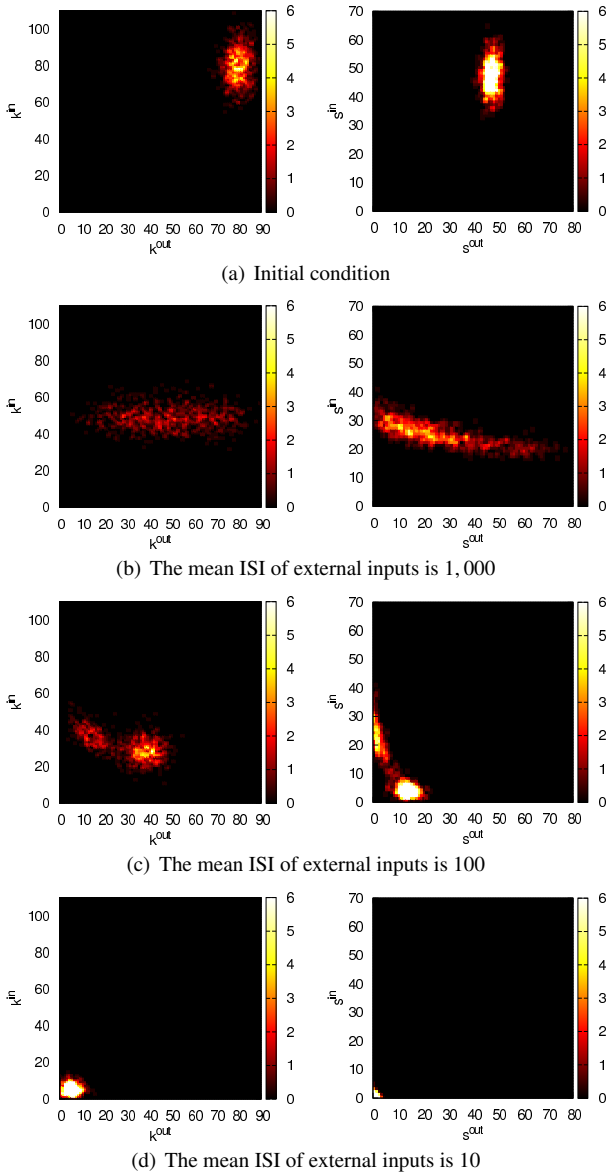
$$s_i^{\text{in}} = \sum_j w_{ji}/w_{\max} \text{ and } s_i^{\text{out}} = \sum_j w_{ij}/w_{\max}. \quad (6)$$

In addition, we use the coefficient of variation (C_V) [22] and the local variation (L_V) [23] as statistics for evaluating neuronal activities. The C_V and L_V are defined as follows:

$$C_V = \frac{\overline{T}}{\Delta T}, \quad (7)$$

$$L_V = \frac{1}{n-1} \sum_{i=1}^{n-1} \frac{3(T_i - T_{i+1})^2}{(T_i + T_{i+1})^2} \quad (8)$$

where $\overline{T} = \frac{1}{n}\sum_{i=1}^{n} T_i$ and $\Delta T = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(T_i - \overline{T})^2}$ are the mean value and the standard deviation of n inter-spike intervals (ISIs) and T_i is the ith ISI.



(a) Initial condition

(b) The mean ISI of external inputs is $1,000$

(c) The mean ISI of external inputs is 100

(d) The mean ISI of external inputs is 10

Figure 1: Joint degree (left) and strength (right) distribution matrices of self-organized neural networks through STDP.

3. Results

3.1. Network structures

The results are depicted by the joint degree distribution matrix (JDDM) or the joint strength distribution matrix (JSDM) [24] (Fig. 1). The JDDMs (JSDMs) are 2-dimensional images whose vertical and horizontal axes are indegree (instrength) and outdegree (outstrength), respectively. Color bars represent corresponding frequency. To

capture distribution characteristics easily the frequencies above 6 are included into 6.

In the initial condition, both JDDM and JSDM show the Poissonian distribution because cells are randomly connected with synapses (Fig. 1(a)). In the case of the self-organized neural network driven by external inputs whose mean ISI is 1,000 [ms], both the outdegree and the outstrength widely distribute although both the indegree and the instrength of all cells take almost the same value (Fig. 1(b)). In addition, frequencies of the low outstrength become high (Fig. 1(b) right). Then, STDP generates the network structure in which all the cells are affected from almost the same number of other cells by the same strength but the attention depends on each cell when the neural network is stimulated by external inputs whose mean ISI is 1,000 [ms].

When the mean ISI is 100 [ms], the distribution range of the indegree is similar to the case of 1,000 [ms], but that of outdegree becomes about a half (Fig. 1(c) left). In addition, the outdegree of many cells becomes high and the distribution of the outdegree is biased in the neural networks. We can see many cells affect about 40 other cells. Interestingly, we can see two groups emerge in the neural network from the result of the JSDM (Fig. 1(c) right). In the first group, the instrength is high but outstrength is low. In contrast, the outstrength is high but instrength is low in the second group. The cells belonging to the first group are strongly affected from the other cells but weakly affect to the other cells. It means that these cells mainly process information inside the network. The cells belonging to the second group are weakly affected from the other cells but strongly affect to the other cells, which indicates that these cells are mainly activated by external inputs, then, the activities of these cells should reflect the external inputs. Namely, these cells play a role of receiver for external information and distribute the information.

When the mean ISI of external inputs is 10 [ms], both the indegree and the outdegree are low (Fig. 1(d)). In this case, all the cells interact no more than 30 other cells. In addition, from the JSDM, all the cells are weakly connected to the other cells, so that neuronal activities are controlled by external inputs and an assembly of cells no longer behaves as a network.

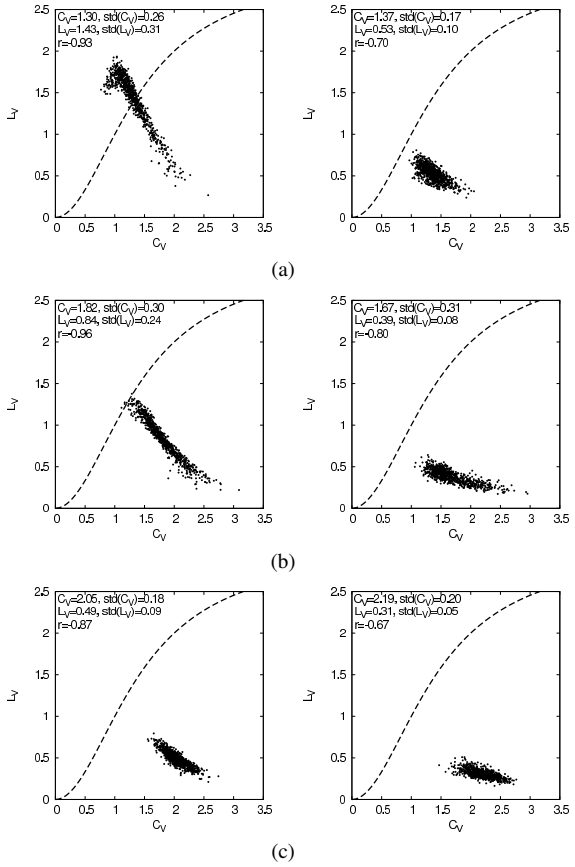


Figure 2: Scattergrams of the coefficient of variation (C_V) and the local variation (L_V). Dashed curves represent the expected values of the C_V and the L_V for the Gamma process represented by the family of distribution functions $p_z(T) = a^z T^{z-1} \exp(-aT)/\Gamma(z)$ where $\Gamma(z) = \int_0^\infty dt\ t^{z-1} \exp(-t)$ [23]. The variable r indicates the correlation coefficient of the C_V and the L_V. In each figure, left and right panels depict the results of the initial condition and after the learning. The mean ISIs of external inputs are (a) 1,000, (b) 100, and (c) 1 [ms].

3.2. Neural activities

The results of neuronal dynamics are described as the scattergrams of the C_V and the L_V (Fig. 2). In each figure, the left panel is the result of the network structure in the initial condition while the right one is for the network after the learning. Dashed lines represent the expected values of the C_V and the L_V for the Gamma process. The mean values and the standard deviations of the C_V and the L_V are shown in each figure. The correlation coefficient between the C_V and the L_V is also shown in each figure. To compute the values of both the C_V and the L_V, we use n (= 100) ISIs for all the cells following Ref. [23]. To generate ISIs, we stop applying STDP to the network but continue to simulate the organized network with the random external inputs.

From the result of 1,000 [ms] mean ISI, the mean values of both the C_V and the L_V take high values in the initial condition (Fig. 2(a) left). Then, many cells fire irregularly in the network. However, the correlation coefficient r between the C_V and the L_V is negative. It means that a few cells exhibit global irregular firing but local regular firing. In addition, the standard deviations of both the C_V and the L_V are large, which indicates that neuronal activities are diverse. Comparing to the result of the initial condition, the mean value of the C_V slightly increases but that of the L_V decreases after the learning (Fig. 2(a) right). Then, STDP leads global irregularity and local regularity to neuronal ac-

tivities when external inputs whose mean ISI is $1,000$ [ms] are injected. The decrease of the standard deviation of the C_V and the L_V indicates the decrease of the diversity of neuronal activities in the network.

When the mean ISI of external inputs is 100 [ms], the mean value of the C_V is larger than that of the case of $1,000$ [ms] mean ISI while the mean value of the L_V is smaller than that of the case of $1,000$ [ms] (Fig. 2(b) left). Then, global irregularity strengthens but local one weakens and the other tendency is almost the same as the result of $1,000$ [ms] mean ISI in the initial condition (Fig. 2(a) left). After the learning, both the mean values of the C_V and the L_V decrease from the initial condition (Fig. 2(b) right). It is intriguing that for the external inputs whose mean ISI is 100 [ms], STDP reduce not only the global irregularity but also the local irregularity of neuronal activities.

When cells are stimulated by external inputs with 10 [ms] mean ISI, the mean value of the C_V is larger and that of the L_V is smaller than two other cases in the initial condition (Fig. 2(c) left). Taking account of the results shown in Figs. 2(a) and 2(b), the global irregularity of neuronal activities becomes stronger if the mean ISI of external inputs is shorter. In contrast, the shorter the mean ISI of external inputs is, the stronger their local regularity becomes. In addition, comparing to the other cases, the standard deviations of both C_V and L_V are smaller. Then, the neuronal activities in the network lose their diversity. After the learning, the mean value of C_V becomes larger but that of L_V becomes smaller than those of the initial condition as well as the result of $1,000$ [ms] (Fig. 2(c) right).

4. Conclusion

In this paper, we analyzed temporal evolution of self-organized neural network structures through spike-timing-dependent plasticity (STDP) from viewpoints of the complex network theory. As the results, we find that depending on the mean ISI of external inputs, spatially different structures are constructed by the STDP In particular, STDP generates a specific structure for external inputs whose mean ISI is 100 [ms] in our analysis. In such a structure, the neural networks may accommodate the information from the other areas and efficiently process the information in the neural network. In addition, the similar structures emerge if the mean ISI of external inputs resides so called the gamma frequency (results are not shown). It is widely acknowledged that the Gamma oscillation plays an important role for memories and learning. Then, we expect that the network structures we showed in this paper might be useful for the memories or the learning. In addition, we showed that the local irregularity of neuronal activities decreases through STDP. However, the results of the global irregularity are different from those of the local one. In particular, the global irregularity decreases only when external inputs of 100 [ms] mean ISI drives the STDP neural network. Taking into account the results of the networks structure, the mean ISI is of 100 [ms] meaningful for the STDP neural network.

As a future work, we will investigate the neural network structures constructed through STDP if the other parameters are varied.

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