Consistency in neuronal avalanche induced by spike-timing-dependent plasticity

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Abstract—Recent studies in the field of neuroscience have reported the observation of neuronal avalanches in cultured cortical slices of the brain. The neuronal avalanches are considered as one of the mechanisms of memory functions in the brain.

We have already shown that the spike-timing-dependent plasticity (STDP) can reproduce network activities with neuronal-avalanche properties, which indicates that STDP is one of the mechanisms to produce neuronal avalanches. On the other hand, "consistency" is another essential key for information transmission in biological and physiological systems and also for the reproducibility of spatiotemporal patterns in the brain activities. Therefore, one of the possible hypotheses is that the neuronal avalanche is a kind of consistency in the brain. In this paper, to investigate whether the neuronal avalanches show consistency or not, we analyze the activity patterns emerging in the STDP network from the viewpoint of consistency. As a result, it is shown that the activity patterns in the STDP network have high consistency and STDP transformation increases the consistency of the avalanche patterns.

1. Introduction

Recently, much attention has been paid to neuronal avalanche in cortical areas because of its possible functional roles to realize the memory in the brain [1], [2]. It is widely acknowledged that one of the characteristic properties of the neuronal avalanche is quantified by event sizes and durations of network activity patterns that form power-law distributions with exponents -1.5 and -2, respectively [1]. These power-law exponents are also observed in avalanches on snow mountains. Accordingly, the activities with these power-law exponents are named neuronal avalanche after the avalanches in the snow mountains. These power-law exponents are often reported in nonlinear dynamical systems in a critical state [3]. The previous studies suggested that the neuronal avalanches may be caused by a critical process where information processing can be optimized [1]. In addition, activity patterns in the neuronal avalanches are not only highly diverse but also reproducible [2]. According to these properties, it is suggested that the neuronal avalanches play important roles for the brain functions of memory [1], [2].

Modification of synaptic connections in neural networks depends on relative spike timing between pre- and postsynaptic action potentials [4]. These synaptic modifications are called spike-timing-dependent plasticity (STDP). The long-term potentiation (LTP) occurs when a postsynaptic action potential arises repetitively after a presynaptic action potential, whereas the long-term depression (LTD) occurs in the case of the reverse order of action potentials.

It is natural to expect that STDP is one of the mechanisms of constructing the characteristic structures of the neural networks, and such structures can produce the neuronal avalanches. Based on this idea, we have already shown STDP realize the properties of the neuronal avalanches [5], [6], [7].

"Consistency" [8] is one of the most interesting theory in the nonlinear dynamical systems. Consistency is defined as reproducibility of the response from a nonlinear dynamical system repeatedly driven by the input, despite starting from different initial internal states of the dynamical system [8]. Consistency is considered as an essential for information transmission in biological systems and for reproducibility of spatiotemporal patterns in the brain activities [8]. In the previous study [7], we have shown that spatiotemporal firing patterns can be reproduced in the STDP network. However, the reproducibility of the spatiotemporal firing patterns has not produced by repetitive inputs. Therefore, it is not clear whether the consistency is an underlying phenomenon to produce the neuronal avalanche in the brain system. In this paper, to investigate whether the avalanche activities show consistency or not, we analyze the activity patterns emerging in the STDP network with repeatedly driven external inputs.

2. Methods

2.1. Neural networks with STDP

In our numerical experiments, we used a neuron model whose dynamics is represented by 2-dimensional ordinary differential equations. The dynamics of the *i*th neuron is defined as follows:

$$\dot{v}_i = 0.04v_i^2 + 5v_i + 140 - u_i + I_i^{\text{syn}}(t) + I_i^{\text{ext}}(t) + I_i^{\text{bg}}(t), (1)$$

$$\dot{u}_i = a(bv_i - u_i), \tag{2}$$

where v_i and u_i are the membrane potential and the recovery variable of the *i*th neuron, respectively [9]. The variables $I_i^{\text{syn}}(t)$, $I_i^{\text{ext}}(t)$ and $I_i^{\text{bg}}(t)$ represent sum of synaptic inputs, external inputs and background inputs to the *i*th neuron at time *t*, respectively. The sum of synaptic inputs $I_i^{\text{syn}}(t)$ are modeled as: $\sum_j^N \sum_k g_{ji} \delta(t - t_j^k)$ where *N* represents the number of neurons in the network, g_{ji} represents a synaptic weight from the *j*th to the *i*th neuron, t_j^k represents the birac delta function. If the variable v_i reaches 30 [mV], the *i*th neuron fires and the variables v_i and u_i are reset to *c* and $u_i + d$. For all the neurons, we set the parameters

(b, c) = (0.2, -65). We set (a, d) = (0.02, 8) for excitatory neurons, while (a, d) = (0.1, 2) for inhibitory neurons. In the experiments, we set the number of neurons in the network N = 10,000 of which 8,000 neurons are excitatory and 2,000 neurons are inhibitory. In our network, pacemaker neurons activate the network [10]. In this paper, the pacemaker neurons are defined to fire at a constant frequency and are not affected by inputs from the other neurons. For the pacemaker neurons, we always set $I_i^{\text{ext}}(t) = 5$ and $I_i^{\text{bg}}(t) = 0$, while for other neurons we set $I_i^{\text{ext}}(t) = 0$ and $I_i^{\text{bg}}(t)$ as independent Poisson-process spike trains with firing rate λ with amplitude 3.1 [pA]. We used 100 excitatory neurons as pacemaker neurons. Each pacemaker neuron projects to 65 excitatory neurons that are randomly selected. Other neurons have average 1,000 random connections with other neurons. Inhibitory neurons are connected only to excitatory neurons except pacemaker neurons.

In the neural network, synaptic weights from the presynaptic neuron j to the postsynaptic neuron i are modified depending on pre- and postsynaptic activities. The synaptic modification by the STDP is described by the following equations [11]:

$$\Delta g_{ji} = \begin{cases} A^{+} \exp(-\frac{t_{i} - t_{j}}{\tau}) & (t_{j} < t_{i}), \\ -A^{-} \exp(-\frac{t_{j} - t_{i}}{\tau}) & (t_{j} \ge t_{i}), \end{cases}$$
(3)

where A^+ (= 0.09) and A^- (= 0.1) are the learning rates of the LTP and the LTD, τ (= 10) [ms] is a time constant that determines the exponential decays of the LTP and LTD, and t_i and t_j are the firing time of the *i*th and *j*th neurons, respectively [11]. In the simulation, nearestneighbor spikes contribute to the long-term synaptic modifications [12]. The STDP learning is applied only to excitatory synapses from a physiological point of view [13]. The excitatory synapses are additively modified through STDP, thus we limit a range of synaptic weights with hard bounds. The range of synaptic weights is set as $g_{\min} \le g_{ji} \le g_{\max}$ where g_{\min} and g_{\max} are 0 and 10, respectively. Initial synaptic weights are 0.01 for excitatory connections, and -0.03 for inhibitory connections. The synaptic weights of connections from the pacemaker neurons are 20.

After the STDP learning for 100 [s], we eliminate the pacemaker neurons. To drive the neural network, we randomly select N_d excitatory neurons $(i_1, i_2, ..., i_{N_d})$ from the network and apply a supra-threshold input of $I_i^{\text{ext}}(t) = 20$ [pA] to one of the neurons every T (= 200) [ms] by turns. After we apply an input to the i_{N_d} th neuron, the i_1 th neuron is driven again. Therefore, neurons are repeatedly driven by a supra-threshold input every $N_d \times T$ [ms].

2.2. Consistency analysis of avalanche patterns

To investigate the consistency of the STDP-network activities, we quantified the similarity of avalanche patterns. To quantify similarity, we transformed the firing patterns to vectors (Fig. 1). At first, we observe N spike sequences for $\mathcal{T} (= 10^3)$ [s] from the network. Each spike sequence is divided by bins whose width is $\Delta t (= 4)$ [ms]. Thus, we obtain $n = \lfloor \mathcal{T} / \Delta t \rfloor$ bins for each spike sequence, where $\lfloor \cdot \rfloor$ represents the floor function. Let us describe the spike sequence of the *i*th neuron as $\{b_i(1), b_i(2), \ldots, b_i(n)\}$. From this description, we can write an instantaneous spatial pattern of the network activity with a vector $\mathbf{b}(i) =$ $(b_1(i), b_2(i), \ldots, b_N(i))^T$. A neuron in the network is activated by the external inputs every T [ms], so that we regard the network activity for T [ms] as a block. Thus, the *j*th spatiotemporal pattern of the network can be written as a combination of vectors $\mathbf{B}_j = (\mathbf{b}(j \times T + 1), \mathbf{b}(j \times T + 2), \ldots, \mathbf{b}(j \times T + T))$. This vector represents single neuronal avalanche. Accordingly, we compute a correlation coefficient to quantify the similarity between vectors. The correlation coefficient between vectors \mathbf{A} and \mathbf{B} is defined by the following equation:

$$C(\mathbf{A}, \mathbf{B}) = \frac{E(\mathbf{A}\mathbf{B}) - E(\mathbf{A})E(\mathbf{B})}{\sigma(\mathbf{A})\sigma(\mathbf{B})},$$
(4)

where $E(\cdot)$ is the average value, $\sigma(\cdot)$ is the standard deviation, and **AB** is the vector dot product.

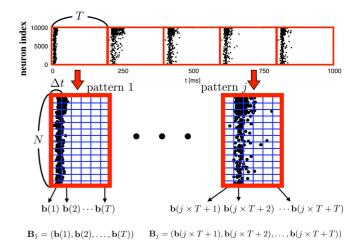


Figure 1: Transformation from firing patterns to a vector.

3. Results

We show the correlation matrices in Fig. 2. The *ij*th element of the correlation matrix represents the correlation coefficient between the *i*th and *j*th avalanche patterns with color bar. We applied a paired clustering algorithm to all the correlation matrices [2] to obtain similar avalanche patterns. From Fig. 2 (a) left, it is clear that some highlycorrelated clusters exist. These clusters mean that high similarity patterns repeatedly emerged. From Fig. 2 (a) middle and right, it is clear that most of the highly-correlated clusters vanished. These results of correlation matrices indicate that if avalanche patterns emerged in early periods, they have higher reproducibility and in later periods do not. Figure 2 (b) left, similar to Fig. 2 (a) left, shows the existence of some high correlation clusters. Figure 2 (b) middle and right, unlike Fig. 2 (a) middle and right, show that high correlation clusters remain. However, most of the clusters are merged into one large cluster (Fig. 2 (b) middle), subsequently, the correlation of the cluster gets lower (Fig. 2 (b) right). These correlation matrices in Fig. 2 (a) and (b) indicate that, when $N_d = 10$, the reproducibility of the avalanche patterns decays with time. Figure 2 (c) left shows that some high correlation clusters exist in a few avalanche patterns. These correlation clusters mean that most of the avalanche patterns emerging in the early period have low reproducibility, but some avalanche patterns have high reproducibility. Unlike middle and right panels

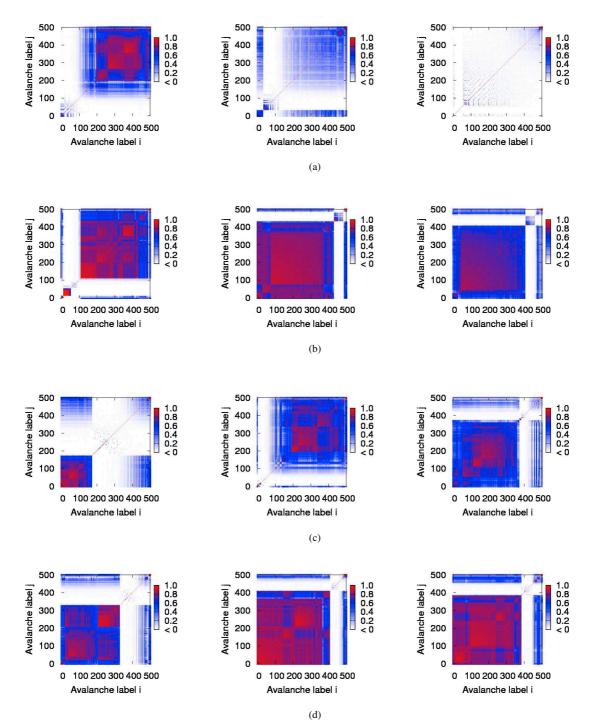


Figure 2: Correlation matrices sorted by the clustering algorithm [2]. The number of neurons driven by the external input N_d and the frequencies of background inputs applied to the network λ were set to (a) 10, 300, (b) 10, 400, (c) 50, 300, (b) 50, 400. Left, middle and right panels are produced by avalanche patterns recorded in the periods [0, 100], [500, 600] and [900, 1000] [s], respectively.

in Fig. 2 (a) and (b), Fig. 2 (c) middle and right panels show that some high correlation clusters remain and are not merged into a single cluster with time. Similar to Fig. 2 (c), Fig. 2 (d) shows that the correlation matrices produced by avalanche patterns emerging in each period have some high correlation clusters. These correlation matrices in Fig. 2 (c) and (d) indicate that, when $N_d = 50$, high reproducibility in the avalanche patterns is kept during the whole period in our simulation. From these results in Fig. 2, it is suggested that the avalanche patterns emerging in early period have high reproducibility, and developments of the reproducibility depend on the number of neurons which an external input is applied.

To investigate how the developments of the reproducibility depend on N_d , we plot temporal changes of averaged correlation coefficients. At first, in Fig. 3 (a), we plot the averaged correlation coefficients in each period when $N_d = 5$, 50 and $\lambda = 300$, 400 [Hz], respectively. When $N_d = 5$, averaged correlation coefficients get lower with time in both $\lambda = 300$ and 400. On the other hand, when $N_d = 50$, averaged correlation coefficients get higher with time in both $\lambda = 300$ and 400. Next, in Fig. 3 (b), we plot averaged correlation coefficients in the period [900, 1000] by changing N_d from 5 to 50. When $\lambda = 300$ and 400, averaged correlation coefficients increase with N_d until $N_d = 30$. These results in Fig. 3 show that correlation matrices produced by avalanche patterns with large N_d have average correlations increasing with time.

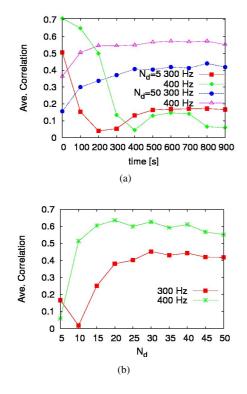


Figure 3: Averaged correlation coefficients of correlation matrices. (a) Averaged correlation coefficients calculated in a matrix produced by avalanche patterns recorded in the period [t, t + 100] are plotted at t. N_d = 10, 50 and λ = 300, 400. (b) Averaged correlation coefficients calculated in a matrix produced by avalanche patterns recorded in the period [900, 1000] are plotted by changing N_d from 5 to 50.

4. Conclusion

In this paper, we analyzed neuronal activities after the STDP learning from the viewpoints of neuronal avalanches. We investigated if the activity patterns in neuronal avalanches have high consistency, namely, whether or not a firing of the same external-input neuron could reproduce the activity patterns. As a result, correlation matrices produced by avalanche patterns emerged from the same external-input neuron showed high reproducibility. Furthermore, the average correlation coefficients in correlation matrices increase with time if the network was driven with large $N_{\rm d}$, while, they decrease with time if driven with small $N_{\rm d}$. From these results, it is clarified that avalanche patterns have high consistency and STDP transformation to the neural network evoked by activity patterns with large $N_{\rm d}$ strengthens consistency in the avalanche patterns. It is suggested that STDP transformation can enhance the consistency in the avalanche patterns under the various conditions of the external input patterns.

In this paper, we analyzed consistency of the activities in the network after STDP transformation, but did not mention the network structures. Thus, it is an important future problem to investigate how the neural network structures affect consistency of activity patterns.

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