Neuronal Avalanches Induced by Spike-Timing-Dependent Plasticity

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Abstract—Recent studies in the neuroscience have reported that neuronal avalanches are observed in cortical areas of the brain. The neuronal avalanches are considered as one of the mechanisms of memory functions in the brain. However, it still remains elusive what is a key mechanism to produce neuronal avalanches. To solve this question, we introduce spike-timing-dependent plasticity (STDP) as a candidate for the mechanism to induce the neuronal avalanches because STDP constructs functional cortical circuits. In this paper, based on this idea, we analyzed neuronal activities in networks constructed through STDP from viewpoints of neuronal avalanche.

1. Introduction

In neural systems, billions of neurons construct neural networks with synapses. It is generally believed that activities of the neural networks realize high level brain functions, for example, memories, learning, development and so on. Synfire chain is characteristic activity of the neural networks in which synchronous neuronal spikes propagate spatiotemporally [1]. Recent physiological studies have reported that synfire chains are observed in cultured slices of neocortex of rat. Distributions of event sizes and durations in the synfire chains obey a power-law with exponents $-3/2$ and -2, respectively [2, 3]. These power-law exponents are also observed in avalanches of snow mountains. Then the synfire chains with these power-law exponents are called neuronal avalanches. These power-law exponents are often reported in nonlinear dynamical systems in a critical state [4]. The previous studies suggested that the neuronal avalanches may be caused by a critical process which can optimize information processing [2]. In addition, these synchronous activity patterns in neuronal avalanches are not only highly diverse but also repeatable [3]. According to these properties, it is suggested that neuronal avalanches play important roles for the brain functions of memory.

Several neural network models have been proposed to reproduce neuronal avalanche [5]. However, it is unknown what is a key structure to produce the neuronal avalanches, and how such structures are induced. It is important to clarify such an issue to understand brain function of memory.

Synaptic connections in neural networks are modified depending on a relative spike timing between pre- and postsynaptic action potentials [6]. These synaptic modifications are called spike-timing-dependent synaptic plasticity (STDP). Neural networks with STDP have been widely analyzed in the computational neuroscience. The long-term potentiation (LTP) occurs when a postsynaptic action potential arises after a presynaptic action potential, whereas the long-term depression (LTD) occurs in a case of the reverse order of action potentials.

It is natural to expect that STDP might be one of the mechanisms of constructing characteristic structures of the neural networks and these structures can produce neuronal avalanches. Based on this idea, in this paper, we analyzed activities of neural networks with STDP from viewpoints of neuronal avalanche.

2. Methods

2.1. Neural networks with STDP transformation

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

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

where v_i and u_i are the membrane potential and the recovery variable of the ith neuron, respectively [7]. The variables $I_i^{\text{syn}}(t)$, $I_i^{\text{bg}}(t)$ and $I_i^{\text{ext}}(t)$ represent sum of synaptic inputs, background input and external input to the ith neuron at time t, respectively. The sum of synaptic inputs $I_i^{\text{syn}}(t)$ are modeled as: $\sum_j^N g_{ji} \sum_k \delta(t - t_j^k)$ where N represents the number of neurons in the network, g_{ji} represents a synaptic weight from the jth to the ith neuron, t_j^k represents the kth spike time of the jth neuron, and $\delta(\cdot)$ represents the Dirac delta function. If the variable v_i reaches 30 [mV], the ith neuron fires and the variables v_i and u_i are reset to c and d. For all neurons, we set the parameters $(b, c) = (0.2, -65)$. For excitatory neurons, we set $(a, d) = (0.02, 8)$, while $(a, d) = (0.1, 2)$ for inhibitory neurons. In the experiments, the number of neurons in the network $N = 10,000$ in which $4N/5 (= 8,000)$ neurons are excitatory and $N/5 (= 2,000)$ neurons are inhibitory. Each neuron has average $M (= 1,000)$ random connections to postsynaptic neurons. There are no connections
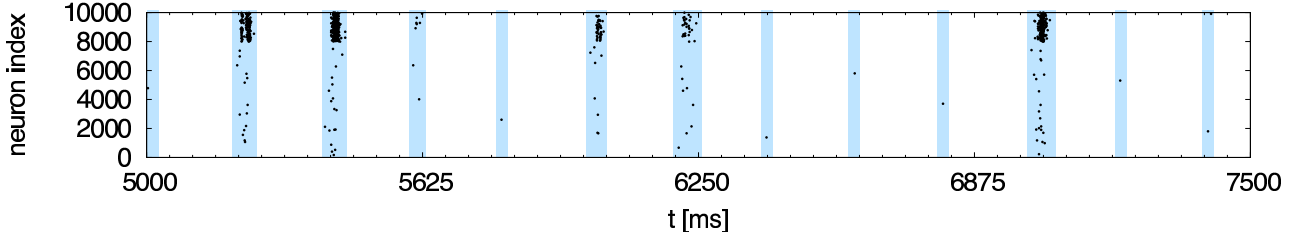
Figure 1: An example of network activities after the STDP learning. In this figure, blue regions represent neuronal avalanches and white regions correspond to blank times. In our analysis, a size of a neuronal avalanche is defined by the number of spikes included in one blue region. A lifetime of a neuronal avalanche corresponds to duration of the blue region.

between inhibitory neurons. All pacemaker neurons (see below) are excitatory. In our neural network, N_{pm} (= 100) pacemaker neurons are included. Each pacemaker neuron has M_{pm} (= 65) postsynaptic neurons which are selected randomly from excitatory neurons except for pacemaker neurons. In the neural network, synaptic weights from the jth to the ith neurons are modified depending on their activities. The synaptic modification by STDP is described by the following equation [8]:

$$\Delta g_{ji} = \begin{cases} A^+\exp(-\dfrac{t_i - t_j}{\tau}) & (t_j < t_i), \\ -A^-\exp(-\dfrac{t_j - t_i}{\tau}) & (t_j \geq t_i), \end{cases} \quad (3)$$

where A^+ (= 0.09) and A^- (= 0.1) are the learning rates of the LTP and LTD, τ (= 10 [ms]) is a time constant that determines the exponential decays of the LTP and LTD in Eq. (3), and t_i and t_j are the firing time of the ith and jth neurons, respectively [8]. In addition, nearest-neighbor spikes contribute for the long-term synaptic modifications [9]. The STDP learning is applied to only excitatory synapses from a physiological point of view [10]. The excitatory synapses are additively modified through STDP, so that we limit a range of synaptic weights with hard bounds. The range of synaptic weights is set as $g_{min} \leq g_{ij} \leq g_{max}$ where g_{min} and g_{max} are 0 and 10, respectively.

In our simulation, we introduced pacemaker neurons in the neural network. Although the pacemaker neurons are generally defined by their intrinsic property to generate rhythmic bursting activity and found in several brain regions, in our network model, the pacemaker neurons fire at a constant frequency and are not affected by inputs from the other neurons. For the pacemaker neurons we always set $I_i^{syn}(t) = 0$ and $I_i^{ext}(t) = 5$ in the neuron model we have already defined in Eq. (1).

2.2. Activities of neural network after STDP transformation

After the STDP learning for 100 [sec], we simulated the neural network without pacemaker neurons and STDP. To drive the neural network, we assumed independent Poisson-process spike trains as background inputs. We set the amplitude $I_i^{bg}(t) = 3.1$ [mV] which corresponds to sub-threshold background input. In addition, we selected an excitatory neuron from the network randomly every 200 [ms] and apply an external input to the neuron. We set the amplitude $I_i^{ext}(t) = 20$ [mV] as a supra-threshold input for evoking neuronal activities.

We analyze activities of the neural network from viewpoints of neuronal avalanche.

2.3. Measures

Figure 1 shows an example of a network activity after the STDP learning. To characterize the network activities, we use two measures, sizes and lifetimes of neuronal avalanches. In this study, we define duration not less than 4 [ms] in which no spikes are emitted as a blank time (white regions in Fig. 1). The other regions (blue regions in Fig. 1) are regarded as neuronal avalanches. Then, the size of each neuronal avalanche is the number of spikes in the blue region and the lifetime is the duration of the blue region.

3. Results

3.1. Probability distributions

The probability distributions of neuronal avalanche size and lifetime are shown in Fig. 2 when the frequency of the background inputs is varied from 200 to 400 [Hz]. From Fig. 2, the probability distributions of the neuronal avalanche sizes exhibit linearity in a log-log scale. The linearity indicates that the probability distribution obeys a power law $P(s) \sim s^\alpha$, where s is the size of neuronal avalanche, $P(s)$ is the probability of size s of the neuronal avalanche and α is a power-law exponent. In cortical networks, it is often observed that the power-law exponent is $-3/2$ [2]. Blue lines express the slope of $-3/2$ in the size distribution while green lines express the slope of α fitted by the least square approximation from data.

When we applied background inputs to the network after the STDP learning at 200 [Hz] (Fig. 2 (a) upper), the
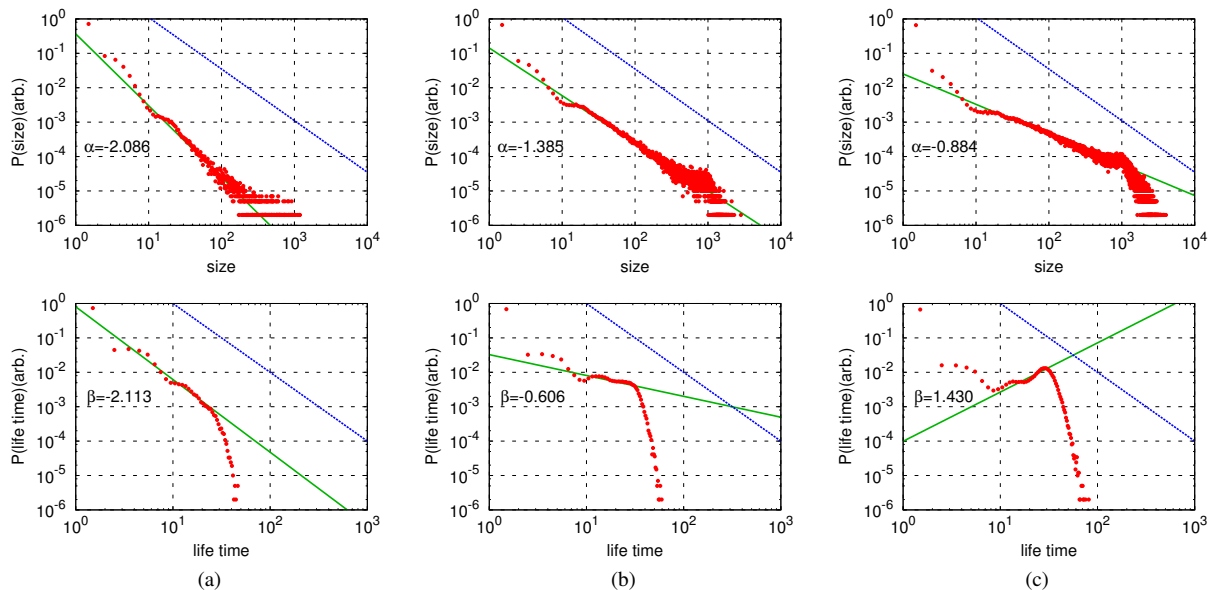
Figure 2: Size (upper) and lifetime (lower) distributions of neuronal avalanches appeared in the network after the STDP learning. Blue lines in each plot express a slope of $-3/2$ in the size distributions and -2 in the lifetime distributions. Green lines represent slopes of the distributions fitted in the range of $10 \leq s \leq 10^3$ for the size distributions and $2 \leq T \leq 40$ [ms] for the lifetime distributions. The frequencies of background inputs to the network after the STDP learning are at (a) 200, (b) 300, and (c) 400 [Hz]. These results are averaged for 50 times by changing initial network structure.

probability distribution of the neuronal avalanche size obey the power law distribution and its power law exponent of $\alpha = -2.086$ is smaller than $-3/2$, which means that large size neuronal avalanches are rarely observed. On the other hand, when we applied 400 [Hz] background inputs (Fig. 2 (c) upper), the exponent of $\alpha = -0.884$ is larger than $-3/2$, which means that large size neuronal avalanches appear more frequently than the case of 200 [Hz] background inputs. A cut-off point is around $1,000$. When we applied 300 [Hz] background inputs (Fig. 2 (b) upper), the exponent of $\alpha = -1.385$ is close to $-3/2$ up to the cut-off point around $1,000$, which means that the neuronal activities in this case shows neuronal avalanches in cortical networks.

In cortical networks, the probability distributions of the neuronal avalanche lifetime also show linearity in a log-log scale which means the probability distributions obeys a power law $P(T) \sim T^\beta$, where T is the lifetime of a neuronal avalanche, $P(T)$ is its probability and β is a power-law exponent. It is often observed that the power-law exponent is -2 [2]. Blue lines in Fig. 2 indicate slope of -2 while green lines are fitted results from our simulation. When we applied 200 [Hz] background inputs (Fig. 2 (a) lower), the probability distribution of neuronal avalanche lifetimes shows a power-law distribution. A slope of $\beta = -2.113$ is close to -2 and an exponential cut-off point is observed around 30 [ms]. These results are almost the same as those observed in the cortical networks [2]. When we applied 300 [Hz] background inputs (Fig. 2 (b) lower), the distribution of neuronal avalanche lifetimes

shows $\beta = -0.606$. This is lager than -2 and a cut-off point is observed around 30 [ms]. On the other hand, when we applied 400 [Hz] background inputs (Fig. 2 (c) lower), neuronal avalanche lifetimes do not obey power-low distributions. When the lifetimes are from about 10 to 30 [ms], the slope of the distribution is positive, which means that the longer avalanches are observed more frequently than the shorter ones in this lifetime band. From these results, the probability distribution of neuronal avalanche lifetimes is sensitive to frequencies of the background inputs.

3.2. Relationship between synaptic connections in an initial network and activities after the STDP learning

It is clear that spike propagations are always induced if neurons directly connected with pacemaker neurons begin to fire (blue dots in Fig. 3). In contrast, spike propagations do not occur when the other neurons fire (red dots in Fig. 3). In addition, neuronal spike propagations occur only among neurons which are directly connected with pacemaker neurons (Fig. 3) because they are driven by the pacemaker neurons during the STDP learning and the synapses between them are strengthened. It is considered that after the STDP learning, the synapses between them are strong enough to cause spike propagations but the others are not (Fig. 4).
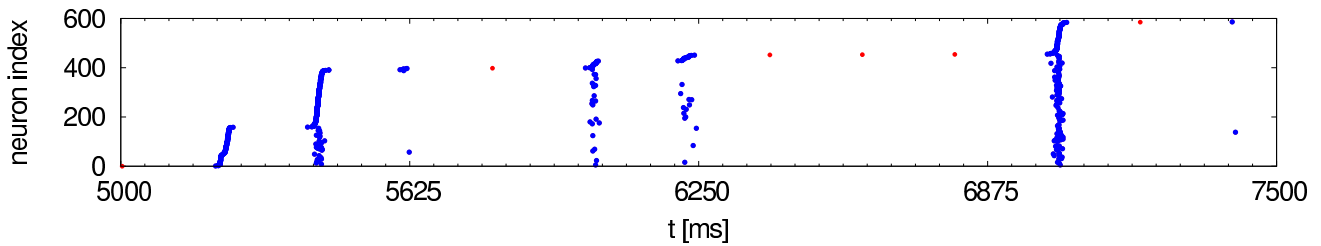
Figure 3: A raster plot whose neuron indices are sorted by the firing order. A blue dot represents a spike of a neuron connected with pacemaker neurons in the initial network structure, and a red dot represents a spike of a neuron not connected with pacemaker neurons in the initial network structure.

4. Conclusion

In this paper, we analyzed neuronal activities after the STDP learning from viewpoints of neuronal avalanche. As a result, the probability distribution of neuronal avalanche sizes and lifetimes show the power-law whose exponent is $-3/2$ and -2, respectively. In addition, we clarified that the exponents vary depending on the frequency of external inputs to the network. If frequencies of external inputs are higher, larger sizes and longer lifetimes of neuronal avalanches are more frequently appear. From these results, it is suggested that exponents of distributions of the size and the lifetime strongly depend on the frequency of background inputs. Furthermore, we show how the neuronal spike propagations occur. In addition, the neuronal spike propagations occur only among neurons which are directly connected with pacemaker neurons in the network. During the STDP learning, the neurons are driven by the pacemaker neurons and the synaptic weights between them are strengthened enough to induce the neuronal spike propagations. However, neuronal avalanches have another property; even though observation times of two neuronal avalanches are different in a few hours, their spatiotemporal patterns are highly correlated [3]. As a future work, we will investigate the correlation between spatiotemporal patterns of neuronal activities in the network after the STDP learning.
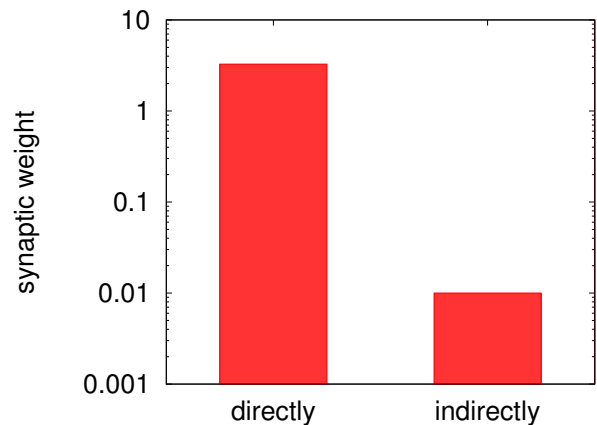

Figure 4: The mean synaptic weights between neurons which are directly connected with pacemaker neurons (left) and the others (right). The figure is plotted in a log scale.

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