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Spike timing-dependent plasticity in sparse recurrent neural networks

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Abstract— Spontaneous neuronal activity is observed in many areas of the brain and an important property of cortical and hippocampal neural circuits. Neuronal avalanche is a quite interesting phenomenon and much paid attention in both experimental and theoretical studies. In some theoretical works, neuronal avalanche reproducible network models were proposed, that are constructed using a specific wiring manner. However, how neuronal circuits organize such a network architecture?

In this study, we address to this question from a viewpoint of self-organization of neural networks with Hebbian plasticity, and show that spike timing-dependent plasticity (STDP) provides an architecture that can reproduce neuronal avalanches. The point in this study is that applied input is spatiotemporally patterned and some neurons share the applied input. Our results suggest that the spatiotemporally patterned neuronal firings observed in the cortices and hippocampus play a crucial role for organization of avalanche reproducible neural circuits.

1. Introduction

Recent studies revealed a novel mode of neuronal activity in which synchronized firings were propagated, that was termed *neuronal avalanche* because of its similarity of the size and duration properties to the avalanche in mountains [1]. The neuronal avalanches were observed not only *in vitro* [1, 2] but also *in vivo* [3, 4], and considered as phenomena related to the memories and behaviors since the avalanches were reproducible in the scale of hours [5].

In the theoretical studies, there are a number of studies showing the scaling manner in the neuronal activity [6–9]. In 2007, a network model that could reproduce the statistics of neuronal avalanches with a spiking neuron model was proposed [8]. In the model, some feedforward sub-networks were embedded and a few feedback connections were added in accordance with a specific wiring manner, however, this study gives rise to a new question: how do neural circuits obtain such an architecture?

One of the possibilities is the learning. Some recent theoretical studies showed that STDP could be a source of feedforward architectures when neurons in networks behaved as oscillators [10–14]. These studies are quite interesting with respect to the organization of feedforward

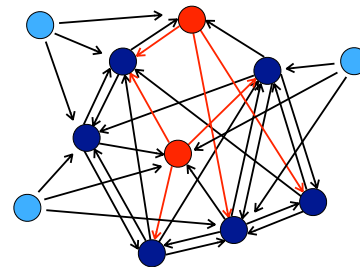


Figure 1: Schematic diagram of our network model. Blue and red nodes represent excitatory and inhibitory neurons. Light blue nodes correspond to external neurons. Black and red arrows are excitatory and inhibitory synaptic connections, respectively.

architectures, but it seems to be impossible to observe neuronal avalanches because, different from the model in Ref. [8], only one large feedforward architecture is organized. In addition, cortical and hippocampal neurons irregularly fire and do not behave as oscillators [15]. In the case where neurons in networks are under excitable state, it was shown that spatiotemporally patterned input made network architecture feedforward-like [16].

Taking into account these studies, we proposed a model that was a neuronal avalanche reproducible network [17, 18]. This network model did not need any specific wiring manners and spontaneously organized through STDP. In this model, it was successful in achieving a certain level of realizing the scaling property in size and lifetime of avalanches, but the model left room for improvement. One of the aims of this study is improving this model. Based on the model, we remodel neural networks that are spontaneously organized and able to realize the statistics of neuronal avalanches. In addition to the improvement, we analyze influences of the noisy input rate during and after the learning on the construction of the neuronal avalanche reproducible networks.

2. Materials and Methods

A network model considered in this study includes $N(= 10,000)$ excitatory neurons (blue nodes in Fig. 1) and $N/4$ inhibitory neurons (red nodes in Fig. 1), and these neurons are interacted through chemical synapses (arrows in Fig. 1). The connection probability is 10% and neurons are randomly connected, but connections between inhibitory neurons are avoided. The dynamics of each neuron is described by the following equations

$$\begin{aligned} \dot{v}_j &= 0.04v_j^2 + 5v_j + 140 - u_j + I_j(t), \\ \dot{u}_j &= a_j(b_jv_j - u_j), \end{aligned} \quad (1)$$

where v_j and u_j are respectively reset to c_j and $u_j + d_j$, when v_j reaches 30 mV. In Eq. (1), v_j and u_j are the membrane potential and the recovery variable [19]. In the initial condition, the variables v_j and u_j are set as $v_j \in [-70, -50]$ and $u_j \in [-8, -6]$, respectively. To achieve heterogeneity, for excitatory neurons, $(a_j, b_j) = (0.02, 0.2)$ and $(c_j, d_j) = (-65, 8) + (15, -6)r^2$, while $(a_j, b_j) = (0.02, 0.25) + (0.08, -0.05)r$ and $(c_j, d_j) = (-65, 2)$ for inhibitory neurons, where r represents a random number [19]. Synaptic current is modeled as $I_j(t) = \sum_i w_{ij}\delta(t - t_i^k)$, where w_{ij} is the synaptic strength from the i th neuron to the j th neuron, and t_i^k is the k th spike of the i th neuron of the j th neuron.

Each neuron is stimulated by noisy input that obeys the independent Poissonian manner at f Hz. The strength of each pulse input is fixed during the simulation and set to 3.1 and 3.41 for excitatory and inhibitory neurons, respectively.

In addition to the noisy input, $n(= 125)$ external neurons (light blue nodes in Fig. 1) also stimulate neurons in the network. The dynamics of the external neurons is also given by Eq. (1), but the input is different from neurons in the network. The input to the external neurons is constant and its strength is 5, which induces periodical firings. In order to avoid synchronization, the initial values of v_j and u_j of the external neurons are varied as $v_j \in [-120, -50]$ and $u_j \in [-8, 100]$. Each external neuron has $m(= 65)$ feed-forward connections to neurons in the network, that is, m neurons in the network receive the input from an external neuron at the same time.

Connections only between excitatory neurons, including external neurons, are modified by STDP with an asymmetric window [20]. When the temporal interval between the i th (presynaptic) neuron and j th (postsynaptic) neuron, $\Delta t \equiv t_j - t_i$, is positive, a synaptic strength w_{ij} increases by $A_+e^{-|\Delta t|/\tau}$ but decreases by $A_-e^{-|\Delta t|/\tau}$ for the other cases, where $A_+(= 0.1)$ and $A_-(= 1.05A_+)$ are the maximum synaptic modifications of long-term potentiation and depression, and $\tau(= 20$ ms) is the time constant. Plastic synaptic strengths are constrained with hard bounds of $w_{ij} \in [0, 20]$ for connections from external neurons, and of $w_{ij} \in [0, 7]$ for the other plastic connections. Inhibitory synaptic strengths in the network are set to -0.05 . Excitatory connections from excitatory neurons to inhibitory

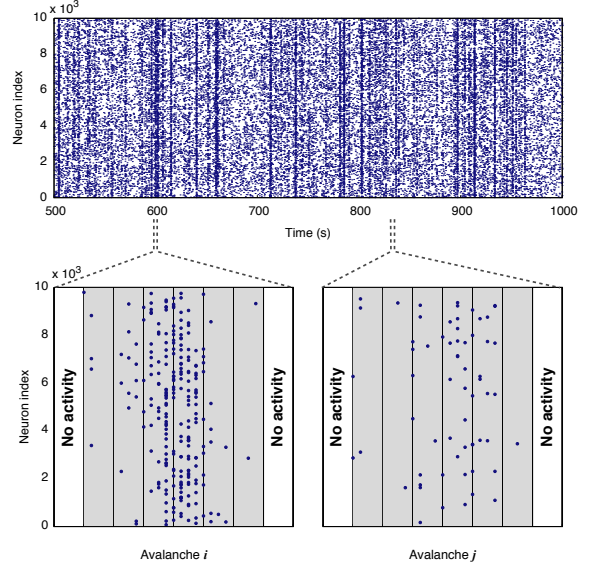


Figure 2: Examples of neuronal avalanches. The upper panel is long-term avalanche data from 500 s to 1,000 s. The two lower panels are enlargements of parts of the upper panel and show avalanches i and j . The vertical lines indicate bin width B ms and the gray areas represent neuronal avalanches. The size of a neuronal avalanche is defined as the number of firing neurons in a gray area. The lifetime is a period from the first spike to the last spike in a gray area. The white areas represent the period in which neurons in the network do not fire.

neurons are set to 4 and fixed during the learning, whereas ones between excitatory neurons are initially set to 0.01 and change obeying to the learning rule. Synaptic strengths from external neurons are set to 20 in the initial condition.

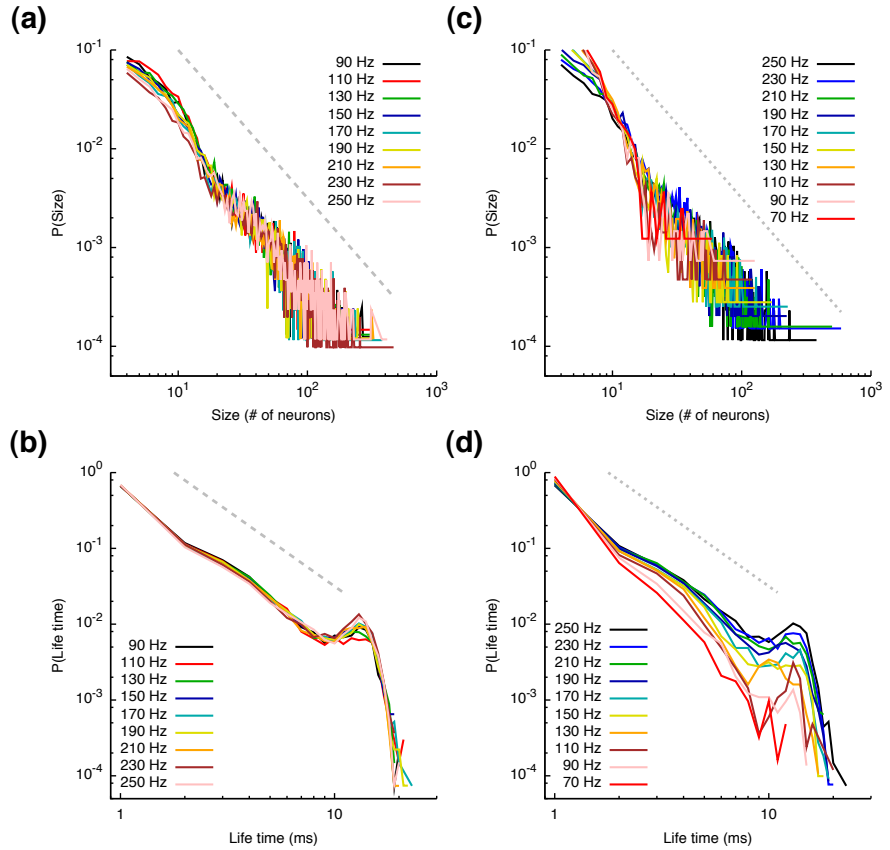
After long time enough to converge the distribution of plastic synapses, external neurons are removed and noisy input at f_{aft} Hz is applied to all neurons in the network. The present model does not have any mechanisms for the induction of synchronous activity in the network, then, as a trigger of a neuronal avalanche, a strong pulse input, whose strength is 20, is injected to $k(= 3)$ excitatory neurons in the network at every 200 ms. For 5,000 s, this procedure is continued.

Probability distributions of size (the number of neurons) and lifetime (the duration) of avalanches are generated from spike data after removing external neurons. The way to identify neuronal avalanches is same as in Ref. [1] (See also Fig. 2).

3. Results

Even though the impulse input is injected to the same number of neurons (3 neurons) at every 200 ms, diverse sizes and lifetimes of avalanches appear (Fig. 2). This re-

Figure 3: Size and lifetime distributions of neuronal avalanches display the power laws (a),(b) when f is varied from 90 Hz to 250 Hz and f_{aft} is fixed to 250 Hz. (c),(d) Same as (a),(b), but f is fixed to 170 Hz and f_{aft} is varied from 70 Hz to 250 Hz. In the size and lifetime distributions, the gray dashed lines are guidelines of the power law exponents -1.5 and -2 . The bin width B is set to 1 ms.



sult indicates that some specific subnetworks are spontaneously architected by STDP and spatiotemporal patterned input.

The size and lifetime distributions observed from our model display the power laws and their exponents are -1.5 and -2 , respectively (Fig. 3(a),(b)). This nature is robust for the firing rate f of noisy input during the learning because the construction of subnetworks is mainly due to the spatiotemporally patterned input from external neurons.

In contrast to the parameter f , the firing rate f_{aft} of noisy input affects on both size and lifetime distributions (Fig. 3(c),(d)). The lower f_{aft} is, the smaller exponents of the power law distributions are. This fact indicates that large and long-lasting avalanches are harder to occur as f_{aft} is lower. In cases of high f_{aft} , the input leads to high sub-threshold membrane potential of neurons and they keep the condition where they easily emit spikes. In cases of low f_{aft} , however, the membrane potential of neurons is far from firing threshold, therefore, it is hard that the long-lasting or large size of avalanches arise in the network. The high rate weak input supports the generation of large and long-lasting neuronal avalanches by raising the membrane potential of neurons. Nevertheless, the power law distributions are preserved in any case. From this fact, it is suggested that the organized network structure, that is guessed

to be feedforward architecture, plays a crucial role to induce the power law distributions in avalanche size and lifetime.

Compared with our previous model, the scaling property in both size and lifetime distributions is improved (Fig. 3(a),(b) and Refs. [17, 18]). In particular, when sizes and lifetimes are small, the undulation disappears and both size and lifetime distributions form more straight.

4. Discussions

In this paper, we showed that STDP is one of the possibilities to construct networks that can induce neuronal avalanches. In our results, the distributions of the size and lifetime well fit to the power laws, and their exponents are -1.5 and -2 , as observed in Ref. [1]. The point in this study is spatiotemporal patterned input and sharing common inputs. The assumption of such an input is appropriate because, in fact, spatially patterned firings were observed in many areas of the brain [21, 22], which could be inputs for the other neurons, and besides, it is well known that some neurons share presynaptic inputs [23, 24].

Although, in previous theoretical studies, the 4-ms-bin width was used to identify neuronal avalanches [8, 17, 18] according to main results in Ref. [1], we took the 1-ms one.

Our choice was seemingly more appropriate than that of the other works because the definition of the avalanche size in the theoretical studies, including our study, is the number of firing neurons in an avalanche. In the main results in Ref. [1], avalanches were identified using the 4-ms-bin width but the size was defined by the number of electrodes. Under this definition, there was no longer the amplitude information of local field potentials (LFPs). The number of firing neurons is proportional to the amplitude of LFPs rather than the number of electrodes. In fact, the 1-ms-bin width was adopted when the size of an avalanche was defined as the amplitude of LFPs in Ref. [1] as well. In this sense, the 1-ms-bin width might be a better choice.

Although we showed that the proposed model was able to reproduce the neuronal avalanche statistics, neuronal avalanches have another property that is the reproducibility [5]. In our previous model, the reproducibility was evaluated using the cross-correlation between pairs of avalanches as the similarity of spatiotemporal patterns [18]. Actually, we observed the reproducibility of neuronal avalanches at the spike level, however, there was no diversity as observed in Ref. [5]. The model proposed in this study should be evaluated and this is our future work.

In addition, we should also investigate the organization mechanisms of neuronal avalanches via STDP with spatiotemporal input. These things might be important to understand the neural information processing in the brain.

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