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Emergenet oscillatory activities of plastic neural networks

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Abstract—How simplify modeling properties are critical for results of the simulations. In neural network simulation, post-synaptic potentials are often modeled with Dirac delta function to reduce calculation costs. To investigate the effect of PSP modeling on resultant rhythmic activities of neural networks, we constructed two types of neural networks, class 1 and class 2 excitatory neurons, and it is developed with STDP learning rule. As a result, the stable rhythms were generated only in the case of the PSP modeling with delta functions. On other modeling cases, exponential and alpha functions, the rhythms were disappeared after the sufficient long learning periods. Therefore, using simplified PSP modeling should accompany careful handling to avoid erroneous simulation results.

1. Introduction

Neurons consists networks and are connected with each other via synapses. The synapses release neurotransmitters reacting to arrivals of action potentials. The neurotransmitters trigger post-synaptic potentials (PSP). The PSPs is modeled with alpha functions in realistic simulations. For simplicity, the PSP often modeled with exponential function. In most simplest cases, the Dirac delta function is used.

Ensemble activities of neurons, for instance, synchronous firing, cell-assembly formation, and rhythms of the network, are receiving great attention. They are seemed to play significant roles in the neural signal processing. We have reported a possible emergent mechanism of the neural synchrony [9]. In this paper, we rather focus on the rhythmic activities of neural networks.

The rhythmic activities are observed in the whole brain [12, 13, 14]. The categorization of the brain rhythms are based on their frequencies [2]: delta (1.5 $\sim$ 4 [Hz]), theta (4 $\sim$ 8 [Hz]), alpha (10 $\sim$ 30 [Hz]), low gamma (30 $\sim$ 80 [Hz]), and high gamma (80 $\sim$ 200 [Hz]). In the hippocampus, the theta rhythms have a prominent role in coding of the animal's position nesting high frequency oscillations [14]. In visual cortex, the gamma rhythms are related to the attention [5]. In motor cortex, the beta rhythms are dominant and increse during motor preparation [4].

Izhikevich demonstrated that a plastic spiking neural network can generate the delta and the gamma rhythms [11]. The neural network composed of 800 regularly spiking neurons for excitatory neurons and 200 fast spiking neurons for inhibitory neurons, and the neural network develops with STDP learning. In this work, the PSPs were modeled with the delta function. However, the alternative choice of PSP modeling function might lead to different consequences. Thus, we studied the effects of the PSP modeling on the rhythmic activities.

In mammalian neocortex, six fundamental classes of firing patters are observed [3, 6, 7]: regularly spiking neurons; intrinsically bursting neurons; chattering neurons; fast spiking interneurons; low-threshold spiking neurons; and late spiking neurons. Among them, the regularly spiking neuron is most major neuron. Hodgkin stimulated the regularly spiking neurons by a constant current and observed its firing frequency [8]. By its excitability, he classified the regularly spiking neurons into two sub-categories: class 1 and class 2. The class 1 neurons start to fire with a low frequency through a critical point of firing. In contrast, the class 2 neurons start to fire with a high frequency that remains relatively constant even though the magnitude of the injected current increases. The class 1 and the class 2 excitabilities are realized by different bifurcation structures [15]: the class 1 excitability occurs when a neuron exhibits a saddle-node bifurcation; the class 2 excitability occurs when a neuron exhibits a Hopf bifurcation.

We constructed two types of neural networks with the class 1, the class 2 for excitatory neurons, and stimulate them by random inputs. The neurons are connected through chemical synapses, and the connection strength of synapses are dynamically changed depending on the activities of neurons. The dynamic change of synaptic connection is called Spike-Timing-Dependent synaptic Plasticity (STDP) [1]. To test if the choice of the PSP modeling significant effect on resultant rhythmic activities, the PSP of the class 1 or class 2 networks are modeled in delta, exponential or alpha functions. The results were compared in rater plots, power spectra, and the distributions of the plastic synaptic weights.

2. Methods

2.1. Post-synaptic potential

The PSPs were modeled in three ways: Direc delta function, exponential function, and alpha function.

2.2. Neural network

In this paper, we used a neuron model proposed by Izhikevich [10] that is described as follows:

$$\begin{cases} \dot{v} = 0.04v^2 + 5v + 140 - u + I(t), & (1) \\ \dot{u} = a(bv - u), & (2) \end{cases}$$

with an auxiliary after-spike resetting condition:

$$\text{if } v = 30[\text{mV}], \text{ then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d. \end{cases} \quad (3)$$

where v and u are dimensionless variables, a, b, c and d are dimensionless parameters, and $\dot{}$ represents d/dt, where t is the time ([ms]). The variable v represents membrane potential ([mV]) of the neuron and u represents a membrane recovery variable, which accounts for the activation of K^+ ionic currents and inactivation of Na^+ ionic currents, and it provides a negative feedback to v.

We constructed neural networks in the following way. Each network is composed of 1,000 neurons, and 80% (or 20%) of the model neurons are excitatory (or inhibitory) as in the cortex. The first neural network has the class 1 excitatory neurons. The second neural network has the class 2 excitatory neurons. Properties of the inhibitory neurons are common for both networks. Excitable property of the inhibitory neuron is the class 2 and its time constant is much faster than the excitatory neurons as in the cortex.

We applied an STDP rule (details are described below) only to excitatory-to-excitatory connections while the other connections are fixed. Each neuron connected with only 100 other neurons. For simplicity, the time is assumed to be discrete (the time step is 1[ms]). Then, the dynamics of the neural networks develops as follows:

$$\begin{cases} v_j(t+1) = v_j(t) + 0.04v_j^2(t) + 5v_j + 140 - u_j(t) + I_j(t) \\ \quad + \sum_{i=1}^{N} w_{ij} h(v_i(t - d_{ij}) - 30), & (4) \\ u_j(t+1) = u_j(t) + a_j(b_j v_j(t) - u_j(t) + e_j), & (5) \end{cases}$$

with the auxiliary after-spike resetting

$$\text{if } v_j(t) = 30[\text{mV}], \text{ then } \begin{cases} v_j(t) \leftarrow c_j \\ u_j(t) \leftarrow u_j + d_j. \end{cases} \quad (6)$$

where $v_j(t)$ is membrane potential of the j-th neuron; $u_j(t)$ is a recovery variable of the j-th neuron, and a_j, b_j, c_j, d_j and e_j are dimensionless parameters; e_j was introduced to regulate a firing rate of the neural network; For the class 1 excitatory neurons, $a_j = 0.02, b_j = -0.1, c_j = -65.0$, $d_j = 8.0$ and $e_j = -22$. For the class 2 excitatory neurons, $a_j = 0.02, b_j = 0.26, c_j = -65.0$, $d_j = 8.0$ and $e_j = 2$. For inhibitory neurons, $a_j = 0.1, b_j = 0.2, c_j = -65.0$ $d_j = 2.0$ and $e_j = 0$. w_{ij} is a synaptic connection from the i-th neuron to the j-th neuron. The synaptic weights from excitatory neurons are initially set to 6.0. The synaptic weights from inhibitory neurons are set to -5.0. If the i-th neuron and the j-th neuron are not connected, $w_{ij} = 0$. Self connection (w_{ii}) is also 0. $h(\cdot)$ is the PSP function (delta, exponential, or alpha functions). d_{ij} is a synaptic transmission delay. The delay is decided randomly between $1 \sim 20$ [ms]. $I_j(t)$(=0 or 20) represents the external input for the j-th neuron, and $I_j(t)$ follows a Poisson-process whose mean ISI is 1000 [ms].

2.3. STDP learning rule

Several experimental studies have reported window functions of the STDP learning (see e.g., Ref.[1]). In this paper, we used a typical function (Fig.**??**) [16]. The amount of synaptic weight modification (Δw) decreases exponentially with a temporal difference (Δt) between the arrival time of a pre-synaptic action potential. and the occurrence the of its corresponding post-synaptic action potential:

$$\Delta t = t_{\text{pre}} + d_{\text{pre,post}} - t_{\text{post}} \quad (7)$$

where t_{pre} is spike time of a pre-synaptic neuron, t_{post} is spike time of a post-synaptic neuron, and $d_{\text{pre,post}}$ is a delay time of spike transmission from the pre-synaptic neuron to the post-synaptic neuron. Then, synaptic modification Δw is described by the following equation,

$$\Delta w(\Delta t) = \begin{cases} A_p e^{\frac{\Delta t}{\tau_p}} & (\Delta t < 0), \\ -A_d e^{-\frac{\Delta t}{\tau_d}} & (\Delta t \geq 0), \end{cases} \quad (8)$$

where A_p and A_d are the maximum rate of modification ($A_p = 0.1, A_d = 0.12$), τ_p and τ_d are the time constants for potentiation and depression, respectively ($\tau_p = \tau_d = 20$ [ms]). We assumed that the synaptic efficacy is limited in the range of $0 \leq w_{ij} \leq 10$, because the STDP learning rule leads to further synaptic potentiation or depression to infinitely large or small synaptic weights.

3. Results

We first conducted the simulation with PSP modeling by the delta functions. Figure 1 shows raster plots of network activities. Dots on each raster plot indicate a firing of a neuron. In each raster plot, indices from 1 to 800 in vertical axis indicate the excitatory neurons, and the rests the inhibitory neurons. At the beginning of the simulations (in Fig.1, A), both the class 1 and the class 2 networks show slow rhythmic activities. These frequencies are $4 \sim 8$ [Hz]. The slow rhythms correspond to the theta rhythm ($4 \sim 8$ [Hz]) that is often observed in hippocampus [14]. With time evolution, neurons become to fire in faster rhythms. The rhythm of the class 1 neural network settles down in beta frequency bands (Fig.1 B). The power spectrum of the rhythm is shown in Fig.1 C. The plastic synaptic weights are mostly biased to the lower bound (Fig.1 F). In contrast, the class 2 neural network generates the rhythms in high frequency bands at the end of the simulations (Fig.1 F). The frequency of the fast rhythm on the class 2 network corresponds to the gamma rhythm ($30 \sim 80$ [Hz], Fig.1 F). As the same with class 1 neural network, the plastic synaptic weights are biased to the lower bound (Fig.1 H).

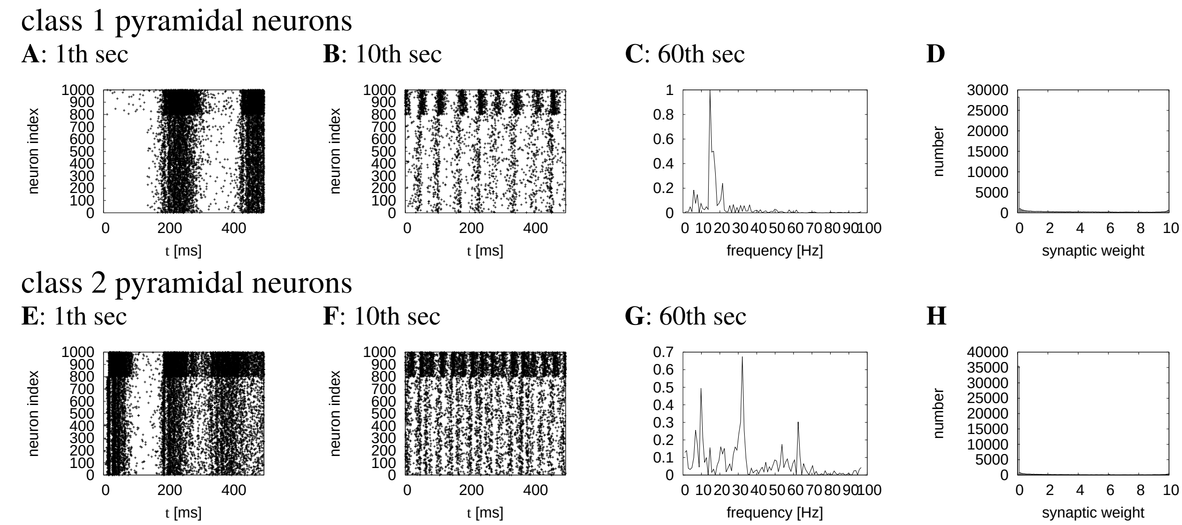

Figure 1: Oscillatory activities of (A-D) class 1 and (E-H) class 2neural networks with delta EPSP. (**A**-**B**) Raster plots at (A) 1st and (B) 60th seconds. (**C**) Power spectrum of oscillatory activities at 60th second. (**E**) The distribution of the plastic synaptic weights at 60th second. (**E**-**H**) The same as (A-D) but for class 2 neural networks.

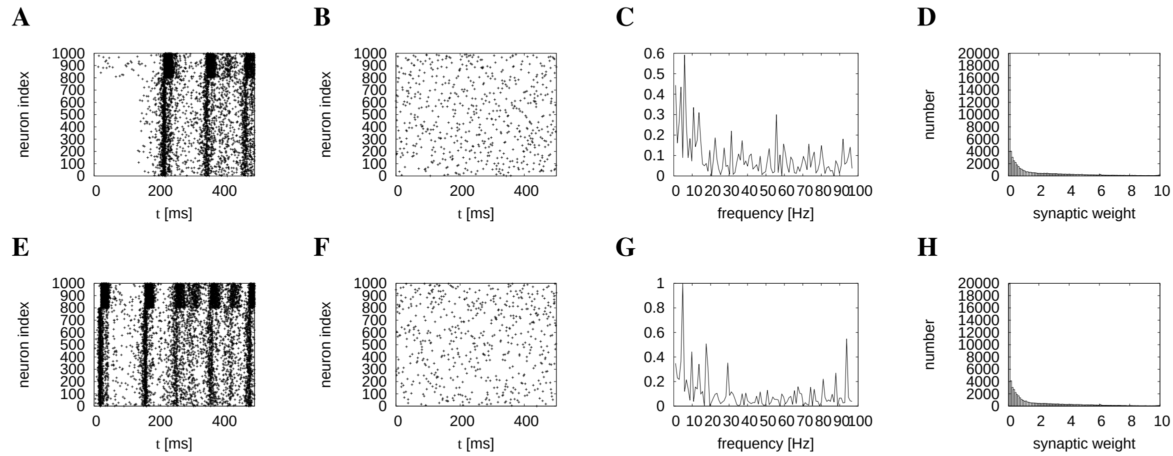

Figure 2: The same as Fig.1 but for exponential EPSP.

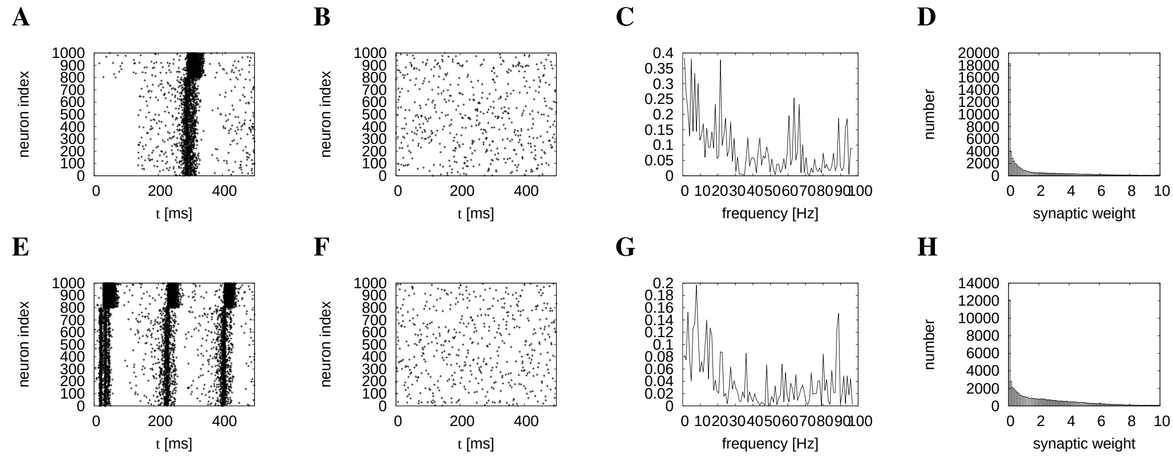

Figure 3: The same as Fig.1 but for alpha EPSP.

We then conducted the simulation with PSP modeling by the exponential functions (Fig.2). At the beginning of the simulations (Fig.2, A and E), both the class 1 and class 2 networks showed faster oscillations than delta-shaped PSP function cases. With time evolution, neurons become to less fire. Eventually, both class 1 and 2 networks become asynchrous (Fig.2 B and F). We did not observe clear peaks in power spectra (Fig.2 C and G). The plastic synaptic weights are biased to the lower bound (Fig.2 D and H).

We finally conducted the simulation with PSP modeling by the alpha functions (Fig.3). At the beginning of the simulations (Fig.3, A and E), both the class 1 and class 2 networks showed slow oscillations like in delta-shaped PSP modeling case. However, the synchrony diminished soon, and kept asynchrous (Fig.3 B and F). We did not observe clear peaks in the power spectra (Fig.3 C and G). The plastic synaptic weights are biased to the lower bound (Fig.3 D and H).

4. Discussion

We constructed two neural networks, class 1 and class 2 excitatory neurons, and investigated the effect of PSP modeling on rhythmic activities. As a result, the rhythms are stable only for the delta PSP modeling. On the other modeling cases, the rhythms were gone after the sufficient learning.

The simple modeling is often employed in simulations, to achieve faster simulations and reduces calculation costs. Our results warn to careless use of PSP modeling. The choice of modeling functions have significant effect on the consequences. Namely, the stable rhythms were observed only in delta-function PSP modeling. For realistic simulations, the alpha function should be the first choice for the PSP modeling. To use more simplified PSP modeling should accompany careful handling to avoid erroneous simulations.

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