2011 International Symposium on Nonlinear Theory and its Applications
NOLTA2011, Kobe, Japan, September 4-7, 2011

Self-organizing network of coupled neural oscillators with synaptic plasticity

Takaaki Aoki†‡, Yuri Kamitani† and Toshio Aoyagi†‡

†Graduate School of Informatics, Kyoto University, Yoshida-honcho, Sakyo-ku, Kyoto, 606-8501 Japan
‡JST CREST, Kawaguchi, Saitama 332-0012, Japan
Email: aoki@acs.i.kyoto-u.ac.jp

Abstract—We investigated a network of coupled neural oscillators in which connections between oscillators dynamically change through synaptic plasticity. We demonstrate that the co-evolving dynamics of the connections and neural oscillators yield the emergence of some specific structured connections and neural activities. We also classified these self-organized states of coupled neural networks with respect to their electrophysiological neuronal properties.

1. Introduction

Synaptic plasticity plays a vital role in learning in the brain. It induces changes in the structure of synaptic connections associated with the activity of neurons, leading to the organization of neural functional assemblies related to our memory [1]. Thus, synaptic plasticity has been intensively investigated to reveal the underlying mechanism of the learning process. Recent neurophysiological experiments [2] revealed that changes in synaptic connections depend on the relative spike timing between neurons in what is called spike-timing-dependent plasticity (STDP). This implies that the temporal spike pattern of neurons determines synaptic growth.

This experimental finding raises a question: how does STDP organize a neural network into functional neuronal assemblies? This is still an open question in theoretical neuroscience, especially in cases where a network has rich recurrent connections, although a number of numerical studies have reported that STDP-organized recurrent networks exhibit a variety of interesting behaviors [3, 4, 5].

The difficulty in analyzing the dynamics of STDP-organized recurrent networks originates from the interplay between neurons and their synapses (see Figure 1). In the presence of plasticity, the spike pattern causes the structure of synaptic connections to change, and in turn, the changes experienced by the connections cause a new spike pattern to appear. In other words, synaptic connections and neuronal activities co-evolve simultaneously, which makes the problem difficult to solve. This indicates a novel type of problem in nonlinear science. Conventional nonlinear systems are defined on static substrates: a number of units comprises the system and are coupled by some fixed interactions, which is usually denoted by a lattice, an all-to-all connection and some complex networks. In contrast, in this co-evolving dynamical system, the interactions also change in time together with the states of the units, which will lead to a new organization of the interactions and states of the units.

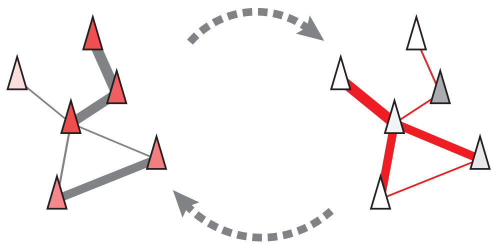

Figure 1: Schematic of an STDP-organized recurrent network. Owing to neural plasticity, the spike pattern causes the structure of synaptic connections to change, and in turn, changes experienced by the connections causes a new spike pattern to appear.

To address this problem, we will introduce a simple model of co-evolving dynamics, which consists of a population of neuronal oscillators, and analyze the asymptotic behavior of this dynamical system. We numerically and analytically demonstrate that the co-evolving dynamics of the connections and neural oscillators yields the emergence of some specific structured connections and neural activities. We have also classified these self-organized states of coupled neural networks based on their electrophysiological neuronal properties, such as regular spiking, fast-spiking, and low-threshold spiking neurons.

2. Model: Co-evolving network of coupled neural oscillators

First, let us consider a reduction of the dynamics of a single oscillatory neuron, which is usually described in a multi-dimensional dynamical system, to the one-dimensional phase oscillator model [6]. Limit-cycle oscillation is the minimal motion that represents the relative timing of the spikes of neurons, which determines STDP. Thus, let us assume that the activity of the neuron is oscillatory and not random. In other words, we consider a limit-cycle oscillator as a neuron model, which is perturbed by

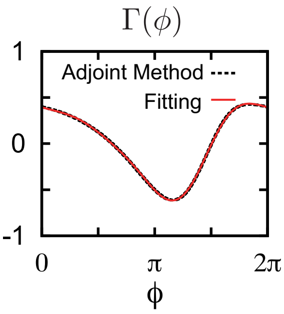

Figure 2: Example of the function $\Gamma(\phi)$ for a Hodgkin-Huxley-type neuron model coupled with α chemical synapse. The function obtained by the adjoint method can be well fitted by the first three Fourier modes.

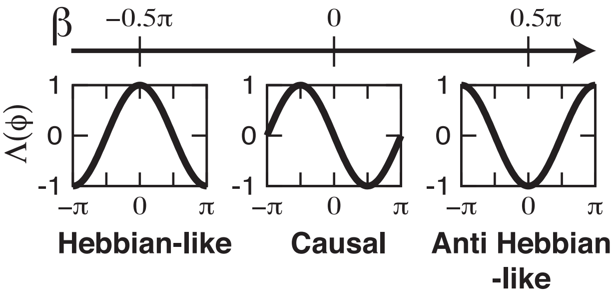

Figure 3: Learning function $\Lambda(\phi)$ is parameterized by β, which determines how the coupling weight K_{ij} evolves depending on the relative timing between the neurons i and j.

synaptic inputs and noises. This assumption has enabled us to reduce the description of the neuron to this simple form:

$$\frac{d\phi_i}{dt} = \omega_i + \frac{K_{ij}}{N}\Gamma(\phi_i - \phi_j). \quad (1)$$

The phase ϕ_i represents the state of the i-th neuron, and ω_i is its natural frequency. The later term represents the interactions caused by other neurons, and K_{ij} is the coupling weight from a neuron j to a neuron i. The function $\Gamma(\phi)$ is systematically determined from the original multi-dimensional dynamical system or by experimental methods [7, 8]. For example, in the case of the Hodgkin-Huxley neuron model coupled with α chemical synapse, the function $\Gamma(\phi)$ is calculated as in Fig. 2. $\Gamma(\phi)$ is 2π-periodic, and the first Fourier mode is usually dominant. In fact, the figure shows that $\Gamma(\phi)$ is well approximated up to the third Fourier mode. Thus, we assume that this function takes this simple form, $\Gamma(\phi) = -\sin(\phi + \alpha)$, only considering the first Fourier mode. The results based on this first Fourier mode approximation robustly hold against perturbations by additional small higher Fourier modes [9], as discussed further in Sec. 4.

Next, we introduce the dynamics of the coupling weights K_{ij} by the following equation:

$$\frac{dK_{ij}}{dt} = \epsilon\left[\Lambda(\phi_i - \phi_j)\right], \quad |K_{ij}| \leq 1. \quad (2)$$

The dynamics of the coupling weights depend on the relative timing between the neurons similar to STDP. Because the function $\Lambda(\phi)$ determines the evolution of the weights, we call it the learning function. ϵ is a parameter of the learning rate. We assume it is very small, i.e., $\epsilon \ll 1$, because the dynamics of synaptic weight is much slower than that of neurons. The additional condition, $|K_{ij}| \leq 1$, means that the synaptic weight is bounded. This condition is reasonable, because the strength of synaptic connection cannot increase indefinitely. Because the learning function $\Lambda(\phi)$ is periodic, we assume $\Lambda(\phi_i - \phi_j) = -\epsilon\sin(\phi_i - \phi_j + \beta)$, considering only the first Fourier mode. The parameter β is the shift of the sine function and is important for learning because it characterizes the properties of the weight dynamics. In Fig. 3, the graphs show the learning function $\Lambda(\phi)$, varying the parameter β. When $\beta \sim -\pi/2$ for a pair of synchronized neurons, the weights between them increase by the learning function. On the other hand, for a desynchronized pair, the weights decrease. Thus, we call it a Hebbian-like rule. If $\beta \sim 0$, the dependency on the relative timing becomes similar to the time window function of STDP, which is experimentally observed in the cortex [2]. If an oscillator precedes other, then, the connection from the preceding oscillator is potentiated and the opposite is depressed. We call this a causal rule. When $\beta \sim \pi/2$, the learning function has a form opposite to the Hebbian-like rule, thus, it is called an anti-Hebbian-like rule.

Taken together with the above equations, we eventually have the following equations of the model:

$$\frac{d\phi_i}{dt} = 1 - \frac{1}{N}\sum_j K_{ij}\sin(\phi_i - \phi_j + \alpha),$$
$$\frac{dK_{ij}}{dt} = -\epsilon\sin(\phi_i - \phi_j + \beta), \quad |K_{ij}| \leq 1, \quad (3)$$

where we assume that the natural frequencies of neurons are almost the same. Then, this model is characterized by only two parameters: α and β. Consequently, we can systematically examine the behavior of this model in a range of the parameter space.

3. Classification of neural network organization

We numerically and analytically found that the dynamical system described by equation (3) exhibits three types of asymptotic states: two-cluster, coherent, and chaotic [10]. The top three graphs in Fig. 4 are raster plots showing typical spike patterns of these states. The bottom graph depicts the phase diagram in the parameter space (α, β), which is determined by the linear stability analysis of these states. We will overlook the properties of these asymptotic states

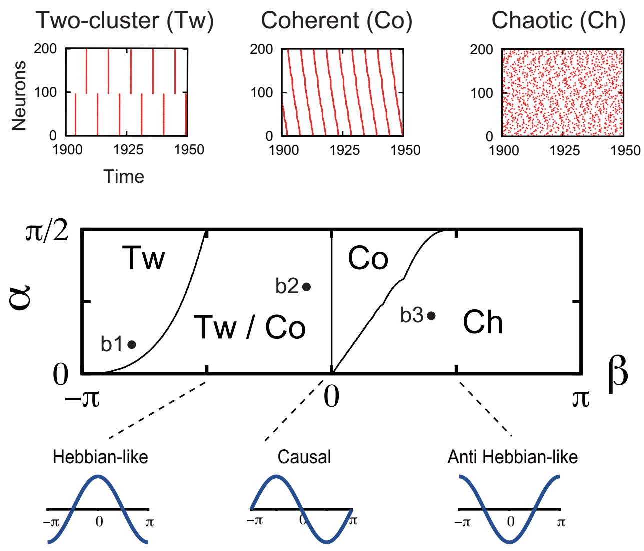

Figure 4: Phase diagram of the dynamical system defined by equation (3). This system exhibits three types of asymptotic states: two-cluster, coherent, and chaotic. Top three graphs show typical spike patterns of these states.

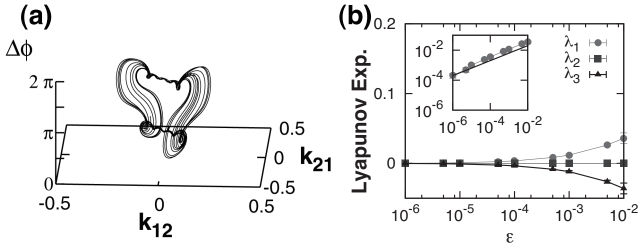

Figure 5: Chaotic behavior of the neural network characterized by positive Lyapunov exponents. **(a)** A typical trajectory of the system where a pair of neurons is reciprocally connected. **(b)** Lyapunov exponents as a function of ϵ.

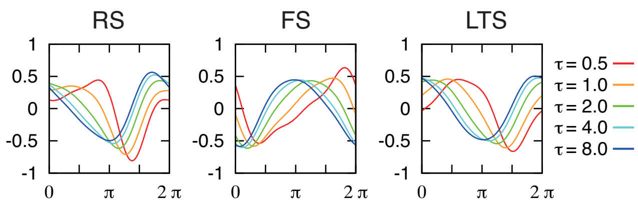

Figure 6: Obtained $\Gamma(\phi)$ of regular-spiking (RS), fast-spiking (FS), and low-threshold spiking (LTS) neurons under different conditions of synaptic transmission delay τ.

and give intuitive explanations of the mechanism of these network formations. For details, refer to [10].

The two-cluster state in which the neurons are divided into two synchronized clusters occurs when the learning function $\Lambda(\phi)$ behaves as the Hebbian-like rule. In this parameter region, if a pair of neurons is in-phase, then the weights between the neurons are increased. This will further enhance the synchronization between them. In contrast, if a pair of neurons is in anti-phase, then the weights will be decreased. In other words, in this situation, synaptic plasticity acts as a positive feedback on the synchronization of oscillators. According to this positive feedback, each pair of neurons is gradually entrained to in-phase or anti-phase synchronization, and eventually, all neurons are organized into the two-cell assemblies of synchronized neurons.

The coherent state where the neurons are arranged in a sequence as shown in Fig. 4 is observed in a parameter region where the learning function $\Lambda(\phi)$ behaves as the causal rule. In this case, plasticity is sensitive to the temporal order of spikes, and the learning function changes its weights to preserve the temporal order of oscillators. Consequently, this plasticity generates an asymmetric, feed-forward network based on the temporal order of spikes. Owing to this feed-forward connection, the relative phase relationship among neurons is stably maintained over time.

In the remaining parameter region where both the two-cluster and coherent states are unstable, we observe a chaotic behavior of the neural network characterized by positive Lyapunov exponents. In this state, the dynamical system does not settle in an ordered state. The relative spike timings of neurons and the coupling weights continue to change with time. Figure 5(a) shows a typical trajectory of the system where a pair of neurons is reciprocally connected. This system has three dynamical variables: a relative phase and two synaptic weights, and its attractor has a positive Lyapunov exponent, as shown in Fig. 5(b).

4. Network organization related to electrophysiological neuronal properties

In this section, we examine the validity of the results obtained in the previous section in the case that the neuronal oscillator is defined by neurons with realistic electrophysiological types. In Sec. 2, we assumed that the function $\Gamma(\phi)$ can be approximated only by the first Fourier mode, because it is usually dominant in the case of neuronal oscillators. However, the function $\Gamma(\phi)$, which is determined by the electrophysiological property of the neuron, includes small higher Fourier modes, and sometimes their effects are not negligible. Thus, using the adjoint method [11], we numerically determined the function $\Gamma(\phi)$ for three electrophysiological types under the different conditions of synaptic transmission delay τ: regular-spiking (RS) [12], fast-spiking (FS) [13], and low-threshold spiking (LTS) [14] neurons. We summarized the obtained $\Gamma(\phi)$ in Fig. 6. Using the obtained $\Gamma(\phi)$, we numerically study the asymptotic state of the dynamical system given by equations (1) and (2) and examine the effect of the electrophysiological prop-

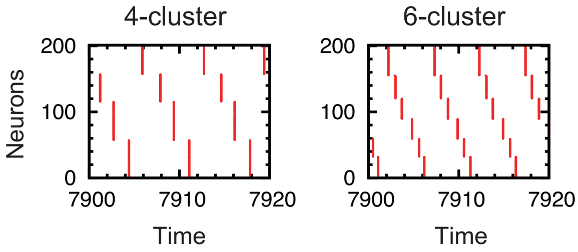

Figure 7: Spike-raster graphs of four-cluster and six-cluster states for $\Lambda(\phi)$ of FS neuron. β = -0.8 π and τ = 0.5 ms (four cluster). β = -0.1 π and τ = 1 ms (six cluster).

erties of neurons on the network organization.

Roughly speaking, we found that three types of network organizations (two-cluster, coherent, and chaotic states) are robustly observed for $\Gamma(\phi)$ of RS, FS, and LTS neurons. However, under some parameter regions, other types of network organizations are also observed (Fig. 7). In the figure, the raster plots show four or six clusters of neuronal spikes in which neurons are organized into multi-synchronized groups. These multi-cluster states are observed in the bistable region between the two-cluster and coherent states, and we found that the multi-cluster state is realized by a combination of these states [9].

5. Summary

In this paper, we have studied the self-organization of recurrent networks under STDP. STDP-organized networks are difficult to analyze because of the co-evolving dynamics of neurons and synapses. To address this problem, we introduced a simple model of the co-evolving dynamics of synaptic weights and neuronal oscillators. We found that depending on the form of the learning function, this model exhibits three distinct types of network organizations: two-cluster, coherent and chaotic states. Furthermore, we examined these network organizations with respect to to their associated electrophysiological neuronal properties, such as regular-spiking, fast-spiking and a low-threshold spiking neurons.

Acknowledgments

This work was supported by Grants-in-Aid from the Ministry of Education, Science, Sports, and Culture of Japan: Grant numbers 19GS0208, 21120002, 23115511.

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