

2015 Special Issue

Self-organization of a recurrent network under ongoing synaptic plasticity

Takaaki Aoki*

Faculty of Education, Kagawa University, 1-1 Saiwai-cho, Takamatsu, Kagawa 760-8521, Japan



ARTICLE INFO

Article history:

Available online 5 June 2014

Keywords:

Spike-timing-dependent plasticity
Phase oscillators
Adaptive networks
Synchronization

ABSTRACT

We investigated the organization of a recurrent network under ongoing synaptic plasticity using a model of neural oscillators coupled by dynamic synapses. In this model, the coupling weights changed dynamically, depending on the timing between the oscillators. We determined the phase coupling function of the oscillator model, $\Gamma(\phi)$, using conductance-based neuron models. Furthermore, we examined the effects of the Fourier zero mode of $\Gamma(\phi)$, which has a critical role in the case of spike-time-dependent plasticity-organized recurrent networks. Heterogeneous layered clusters with different frequencies emerged from homogeneous populations as the Fourier zero mode increased. Our findings may provide new insights into the self-assembly mechanisms of neural networks related to synaptic plasticity.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Synaptic plasticity plays a vital role in learning in the brain, and it has been intensively investigated to understand the mechanism underlying learning. It induces changes in the structures of synaptic connections associated with neuronal activity, facilitating the organization of memory-related functional neural assemblies (Hebb, 1949). Recent neurophysiological experiments revealed that changes in synaptic connections depend on the relative spike timing between neurons during spike-timing-dependent plasticity (STDP) (Bi & Poo, 1998; Caporale & Dan, 2008; Markram, Lübke, Frotscher, & Sakmann, 1997). This observation implies that the temporal spike patterns of neurons determine synaptic patterns, raising the question of how STDP organizes neural networks into functional neuronal assemblies. This query remains an open question in the field of theoretical neuroscience, particularly when a network has rich recurrent connections.

Several numerical studies reported that STDP-organized recurrent networks exhibit interesting behaviors, including the emergence of clusters with neurons that fire synchronously (Gilson et al., 2009; Harris et al., 2003; Karbowski & Ermentrout, 2002; Maistrenko, Lysyansky, Hauptmann, Burylko, & Tass, 2007; Seliger, Young, & Tsimring, 2002; Zanette & Mikhailov, 2004) and feed-forward networks (Cateau, Kitano, & Fukai, 2008; Izhikevich, Gally,

& Edelman, 2004; Masuda & Kori, 2007; Morrison, Aertsen, & Diesmann, 2007; Song & Abbott, 2001).

The interplay between neurons and their synapses makes it difficult to analyze the dynamics of STDP-organized recurrent networks. In the presence of plasticity, the spike pattern alters the structure of the synaptic connections, resulting in the formation of new spike patterns. In other words, the synaptic connections and neuronal activities evolve simultaneously. This co-evolution presents a novel, complicated situation from the perspective of statistical physics. A conventional system is defined on the basis of a static substrate, in which several units of the system are coupled with some fixed interactions, usually denoted by a lattice, all-to-all connections, or a static network. In contrast, in a co-evolving dynamical system, the interactions change together over time with the states of the units, leading to reorganization of the interactions within the system.

To elucidate the essential nature of co-evolving neural network dynamics, we developed a simple, co-evolving dynamical model of neuronal oscillators (Aoki & Aoyagi, 2009, 2011). In this report, we demonstrate that STDP can lead to the organization of several distinct network types. In Section 2, we briefly review the phase description method and describe synapse dynamics using the phase oscillator model. In Section 3, to illustrate the typical behaviors of the model, as presented in our previous papers (Aoki & Aoyagi, 2009, 2011), we summarize the numerical results obtained by approximating $\Gamma(\phi)$ as a sine function. In Section 4, we present the main results of this paper. First, we confirm the validity of the sine approximation of $\Gamma(\phi)$, by determining the parameters of the phase oscillator model. These parameters are

* Tel.: +81 878321595; fax: +81 878321595.

E-mail addresses: takaaki.aoki.work@gmail.com, aoki@ed.kagawa-u.ac.jp.

deduced from conductance-based regular- and fast-spiking neuron models. Second, we show that the determined form of the coupling function exhibits a novel behavior, which we explain via the Fourier zero mode of the phase coupling function of the oscillator. The previous studies on phase oscillator have ignored this mode. However, we find that this constant term is critically important for STDP-organized recurrent networks, as evidenced by the result that heterogeneous layered clusters with different frequencies emerge from homogeneous populations with identical natural frequencies. Finally, we analyze the transition from homogeneous to heterogeneous layered clusters. In Section 5, we discuss and summarize our findings.

2. Materials and methods

2.1. Dynamics of neuronal oscillators

We consider the following equation of a coupled dynamical system:

$$\frac{d\mathbf{x}_i}{dt} = \mathbf{F}(\mathbf{x}_i) + \sum_j \mathbf{f}_{ij}(\mathbf{x}_i, \mathbf{x}_j),$$

where \mathbf{x}_i denotes the state of the i th neuron in a network of N neurons. The first term describes the intrinsic dynamics of the neurons (e.g. several types of ion channels) and the second term describes coupling with other neurons via synapses.

The activity of a neuron is assumed to be oscillatory, rather than random. Thus, we consider that the neuron model undergoes a limit-cycle oscillation, which is perturbed by synaptic inputs and noises. This assumption enables us to reduce the description of the neuron to a simple form with the variable ϕ . Using a standard reduction technique (Kuramoto, 1984), the coupled limit-cycle system can be described as follows:

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

where ϕ_i denotes the phase of the limit-cycle oscillation of the i th neuron in the network ($i = 1, \dots, N$), ω_i is its natural frequency, and k_{ij} is the coupling weight of the connection from the j th to the i th neuron. In Section 3 and our previous papers (Aoki & Aoyagi, 2009, 2011), the coupling function $\Gamma(\phi)$ was assumed to take the simple form $\Gamma(\phi) = -\sin(\phi + \alpha)$ for several reasons. By definition, $\Gamma(\phi_1 - \phi_2)$ is written as

$$\Gamma(\phi_1 - \phi_2) = \frac{1}{2\pi} \int_0^{2\pi} d\theta \mathbf{Z}(\theta + \phi_1) \cdot \mathbf{g}(\theta + \phi_1, \theta + \phi_2),$$

where $\mathbf{Z}(\phi)$ is the phase sensitivity function (Kuramoto, 1984), and \mathbf{g} is the coupling term between the oscillators. Near a Hopf bifurcation point involving many biological and chemical oscillators, the limit-cycle oscillation can be described by the Stuart–Landau equation. The phase sensitivity function for the oscillator is derived as $\mathbf{Z}(\phi) = (-\sin \phi - c_2 \cos \phi, \cos \phi - c_2 \sin \phi)$ where c_2 is a parameter of the oscillator. Thus, in the case of diffusive coupling between Stuart–Landau oscillators, the coupling function $\Gamma(\phi)$ can be derived analytically as the above form by Kuramoto (1984). Although $\Gamma(\phi)$ generally has higher Fourier modes, we approximate the form of the function while neglecting these higher modes. The constant term of the coupling function Γ_0 is neglected because it can be absorbed into the natural frequency term $\omega_i \rightarrow \omega_i + \frac{1}{N} \sum_j k_{ij} \Gamma_0$. Under suitable conditions, the parameter α can be regarded as the phase difference induced by a short transmission delay in the coupling (Izhikevich, 1998). For example, α can represent an axonal transmission delay in the synaptic connection or a delay in the metabolic reaction path in nerve cells.

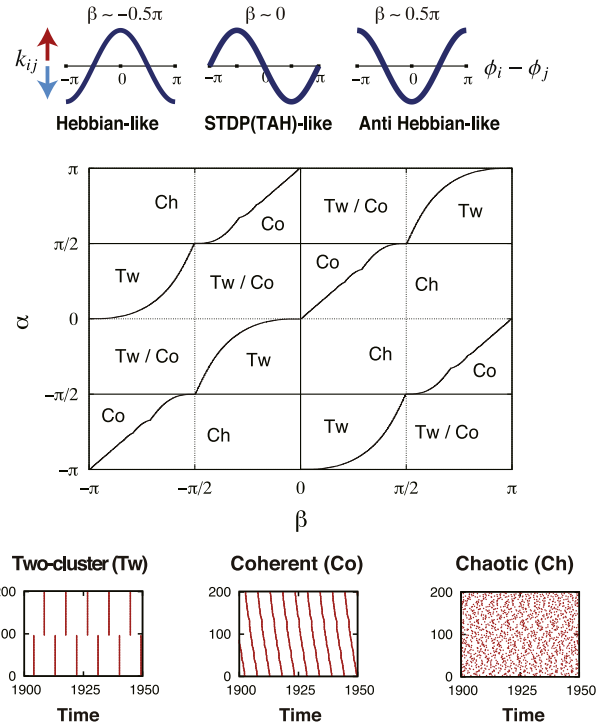


Fig. 1. Phase diagram of the dynamical system defined by Eqs. (3) and (4). Three types of asymptotic states are observed: two-cluster (Tw), coherent (Co), and chaotic (Ch).

The reduced function $\Gamma(\phi)$ can be systematically calculated from the original neuron model (Kuramoto, 1984). In Section 4, we will determine the form of $\Gamma(\phi)$ for two types of conductance-based neuron models. We will compare the results with findings from the approximated form of $\Gamma(\phi)$, to check the validity of the approximation.

2.2. Dynamics of synaptic weights

Next, we introduce the dynamics of the synaptic weights due to the plasticity. The evolution of the weights depends on the relative timing between the neurons, similar to the case with STDP:

$$\frac{dk_{ij}}{dt} = \epsilon \Lambda(\phi_i - \phi_j), \quad |k_{ij}| \leq 1. \quad (2)$$

The function $\Lambda(\phi)$, which we refer to as a learning function, determines the evolution of the weights. The learning parameter ϵ has a very small value because the dynamics of the synaptic weights are much slower than those of the neurons. The condition $|k_{ij}| \leq 1$ means that the synaptic weight is bounded. If the weight has a value outside $[1, 1]$, then the weight is immediately set to the appropriate bounded value (1 or -1). This rule is reasonable because the weight cannot increase indefinitely.

The learning function $\Lambda(\phi)$ is periodic. Therefore, for the sake of simplicity, we assume that $\Lambda(\phi)$ takes the form

$$\Lambda(\phi) = -\sin(\phi_i - \phi_j + \beta)$$

where β is the shift parameter that characterizes the learning function (top panels in Fig. 1). For example, when $\beta \sim -\pi/2$, the weights for a pair of in-phase (or anti-phase) neurons will increase (or decrease). This relationship can be considered as a Hebbian-like rule. When $\beta \sim 0$, the dependency on the relative timing becomes similar to the temporally asymmetric Hebbian rule. When $\beta \sim \pi/2$, the learning function has the opposite form to the Hebbian-like rule.

Download English Version:

<https://daneshyari.com/en/article/404156>

Download Persian Version:

<https://daneshyari.com/article/404156>

[Daneshyari.com](https://daneshyari.com)