Neural Networks 97 (2018) 92–106

Contents lists available at ScienceDirect

Neural Networks

journal homepage: www.elsevier.com/locate/neunet

Stochastic spike synchronization in a small-world neural network with spike-timing-dependent plasticity

Sang-Yoon Kim, Woochang Lim *

Institute for Computational Neuroscience and Department of Science Education, Daegu National University of Education, Daegu 42411, Republic of Korea

HIGHLIGHTS

- An excitatory small-world network of subthreshold neurons is considered.
- Effect of spike-timing-dependent plasticity on spike synchronization is investigated.
- Both the additive and the multiplicative case are considered.
- A “Matthew” effect in synaptic plasticity is found to occur.
- Emergence of potentiation and depression is investigated via microscopic studies.

ARTICLE INFO

Article history:
Received 13 April 2017
Received in revised form 17 August 2017
Accepted 29 September 2017
Available online 12 October 2017

Keywords:
Spike-timing-dependent plasticity
Stochastic spike synchronization
Small-world network
Subthreshold neurons

ABSTRACT

We consider the Watts–Strogatz small-world network (SWN) consisting of subthreshold neurons which exhibit noise-induced spikings. This neuronal network has adaptive dynamic synaptic strengths governed by the spike-timing-dependent plasticity (STDP). In previous works without STDP, stochastic spike synchronization (SSS) between noise-induced spikings of subthreshold neurons was found to occur in a range of intermediate noise intensities. Here, we investigate the effect of additive STDP on the SSS by varying the noise intensity. Occurrence of a “Matthew” effect in synaptic plasticity is found due to a positive feedback process. As a result, good synchronization gets better via long-term potentiation of synaptic strengths, while bad synchronization gets worse via long-term depression. Emergences of long-term potentiation and long-term depression of synaptic strengths are intensively investigated via microscopic studies based on the pair-correlations between the pre- and the post-synaptic IISRs (instantaneous individual spike rates) as well as the distributions of time delays between the pre- and the post-synaptic spike times. Furthermore, the effects of multiplicative STDP (which depends on states) on the SSS are studied and discussed in comparison with the case of additive STDP (independent of states). These effects of STDP on the SSS in the SWN are also compared with those in the regular lattice and the random graph.

1. Introduction

In recent years, much attention has been paid to brain rhythms (Buzsáki, 2006; Traub & Whittington, 2010). These brain rhythms emerge via population synchronization between individual firings in neural circuits. This kind of neural synchronization is associated with diverse cognitive functions (e.g., multisensory feature integration, selective attention, and memory formation) (Gray, 1994; Wang, 2010), and it is also correlated with pathological rhythms related to neural diseases (e.g., tremors in the Parkinson’s disease and epileptic seizures) (Hammond, Bergman, & Brown, 2007; Uhlhaas & Singer, 2006). Population synchronization has been intensively investigated in neural circuits composed of spontaneously-firing suprathreshold neurons exhibiting regular discharges like clock oscillators (Wang, 2010). In contrast to the case of suprathreshold neurons, the case of subthreshold neurons (which cannot fire spontaneously) has received little attention. The subthreshold neurons can fire only with the help of noise, and exhibit irregular discharges like Geiger counters. Noise-induced firing patterns of subthreshold neurons have been studied in many physiological and pathophysiological aspects (Huber & Braun, 2006). For example, sensory receptor neurons were found to use the noise-induced firings for encoding environmental electric or thermal stimuli through a “constructive” interplay of subthreshold oscillations and noise (Braun, Wissing, Schäfer, & Hirsh, 1994). These noise-induced firings of a single subthreshold neuron become most coherent at an optimal noise intensity, which is called coherence resonance (Longtin, 1997). Moreover, array-enhanced coherence resonance was also found to occur in a population of subthreshold

---

* Corresponding author.
E-mail addresses: sykim@icn.re.kr (S.-Y. Kim), wclim@icn.re.kr (W. Lim).

https://doi.org/10.1016/j.neunet.2017.09.016

neurons (Hu & Zhou, 2000; Shinohara, Kanamaru, Suzuki, Horita, & Aihara, 2002; Wang, Chik, & Wang, 2000; Zhou & Kurths, 2002; Zhou, Kurths, & Hu, 2001). In this way, in certain circumstances, noise plays a constructive role in the emergence of dynamical order, although it is usually considered as a nuisance, degrading the performance of dynamical systems.

Here, we are interested in stochastic spike synchronization (SSS) (i.e., population synchronization between complex noise-induced firings of subthreshold neurons) which may be correlated with brain function of encoding sensory stimuli in the noisy environment. Recently, such SSS has been found to occur in an intermediate range of noise intensity via competition between the constructive and the destructive roles of noise (Lim & Kim, 2007, 2009, 2011). As the noise intensity passes a lower threshold, a transition to SSS occurs because of a constructive role of noise to stimulate coherence between noise-induced spikings. However, when passing a higher threshold, another transition from SSS to desynchronization takes place due to a destructive role of noise to spoil the SSS. In the previous works on SSS, synaptic coupling strengths were static. However, in real brains synaptic strengths may vary to adapt to the environment [i.e., they can be potentiated (Hebb, 1949; Kornoski, 1948; Shatz, 1992) or depressed (Bienenstock, Cooper, & Munro, 1982; Sejnowski, 1977; Stent, 1973; von der Malsburg, 1973)]. These adjustments of synapses are called the synaptic plasticity which provides the basis for learning, memory, and development (Abbott & Nelson, 2000). Regarding the synaptic plasticity, we consider a Hebbian spike-timing-dependent plasticity (STDP) (Bi & Poo, 1998, 2001; Caporale & Dan, 2008; Dan & Poo, 2004, 2006; Debanne, Gähwiler, & Thompson, 1998; Egger, Feldmeyer, & Sakmann, 1999; Feldman, 2000, 2012; Gerstner, Kempter, van Hemmen, & Wagner, 1996; Kepecs, van Rossum, Song, & Tegner, 2002; Markram, Gerstner, & Sjöström, 2012; Markram, Lübke, Frotscher, & Sakmann, 1997; Song, Miller, & Abbott, 2000; Tzounopoulos, Kim, Oertel, & Trussell, 2004; Wittenberg & Wang, 2006; Zhang, Tao, Holt, Harris, & Poo, 1998). For the STDP, the synaptic strengths vary via a Hebbian plasticity rule depending on the relative time difference between the pre- and the post-synaptic spike times. When a pre-synaptic spike precedes a post-synaptic spike, long-term potentiation occurs; otherwise, long-term depression appears. The effects of STDP on population synchronization in networks of (spontaneously-firing) suprathreshold neurons were studied in various aspects (Borges et al., 2016, 2017; Popovych & Tass, 2012; Popovych, Yanchuk, & Tass, 2013).

In this paper, we consider an excitatory Watts–Strogatz small-world network (SWN) of subthreshold neurons (Strogatz, 2001; Watts, 2003; Watts & Strogatz, 1998), and investigate the effect of additive STDP (independent of states) on the SSS by varying the noise intensity D. A Matthew effect in synaptic plasticity is found to occur due to a positive feedback process. Good synchronization gets better via long-term potentiation of synaptic strengths, while bad synchronization gets worse via long-term depression. As a result, a step-like rapid transition to SSS occurs by changing D, in contrast to the relatively smooth transition in the absence of STDP. Emergences of long-term potentiation and long-term depression of synaptic strengths are intensively studied through microscopic investigations based on both the distributions of time delays between the pre- and the post-synaptic spike times and the pair-correlations between the pre- and the post-synaptic IISRs (instantaneous individual spike rates). Moreover, the effects of multiplicative STDP (which depends on states) on the SSS are also studied (Popovych & Tass, 2012; Rubin, Lee, & Sompolinsky, 2001). For the multiplicative case, a change in synaptic strengths scales linearly with the distance to the higher and the lower bounds of synaptic strengths, and hence the bounds for the synaptic strength become "soft", in contrast to the hard bounds for the additive case. The effects of STDP for the multiplicative case with soft bounds are discussed in comparison with the additive case with hard bounds. Moreover, the effects of additive and multiplicative STDP on the SSS in the SWN are also compared with those in the regular lattice and the random graph.

This paper is organized as follows. In Section 2, we describe an excitatory Watts–Strogatz SWN of subthreshold Izhikevich regular spiking neurons (Izhikevich, 2003, 2004), and the governing equations for the population dynamics are given. Then, in Section 3 we investigate the effects of STDP on the SSS for both the additive and the multiplicative cases by varying D. Finally, in Section 4 a summary is given.

2. Excitatory small-world network of subthreshold neurons with synaptic plasticity

We consider an excitatory directed Watts–Strogatz SWN, composed of N subthreshold regular spiking neurons equidistantly placed on a one-dimensional ring of radius $N/2\pi$. The Watts–Strogatz SWN interpolates between a regular lattice with high clustering (corresponding to the case of $p = 0$) and a random graph with short average path length (corresponding to the case of $p = 1$) via random uniform rewiring with the probability p (Strogatz, 2001; Watts, 2003; Watts & Strogatz, 1998). For $p = 0$, we start with a directed regular ring lattice with N nodes where each node is coupled to its first M_{syn} neighbors ($M_{syn}/2$ on either side) via outward synapses, and rewire each outward connection uniformly at random over the whole ring with the probability p (without self-connections and duplicate connections). This Watts–Strogatz SWN model may be regarded as a cluster-friendly extension of the random network by reconciling the six degrees of separation (small-worldness) (Guare, 1990; Milgram, 1967) with the circle of friends (clustering). Many recent works on various subjects of neurodynamics have been done in SWNs with predominantly local connections and rare long-distance connections (Achard & Bullmore, 2007; Kaiser & Hilgetag, 2006; Kim & Lim, 2015; Kwon & Moon, 2002; Lago-Fernández, Huerta, Corbacho, & Sigüenza, 2000; Lizier, Pritam, & Prokopenko, 2011; Ozer, Perc, & Uzuntarla, 2009; Riecke, Roxin, Madruga, & Solla, 2007; Roxin, Riecke, & Solla, 2004; Shanahan, 2008; Wang, Duan, Perc, & Chen, 2008; Wang, Perc, Duan, & Chen, 2010; Yu, Huang, Singer, & Nikolie, 2008). As elements in our SWN, we choose the Izhikevich regular spiking neuron model which is not only biologically plausible, but also computationally efficient (Izhikevich, 2003, 2004).

The following Eqs. (1)–(6) govern the population dynamics in the SWN:

$$\frac{dv_i}{dt} = F(v_i) - u_i + I_{DC,i} + D\xi_i - I_{syn,i}, \tag{1}$$

$$\frac{du_i}{dt} = a\,(bv_i - u_i), \quad i = 1, \ldots, N, \tag{2}$$

with the auxiliary after-spike resetting:

$$\text{if } v_i \geq v_p, \text{ then } v_i \to c \text{ and } u_i \to u_i + d, \tag{3}$$

where

$$F(v) = 0.04v^2 + 5v + 140, \tag{4}$$

$$I_{syn,i} = \frac{1}{d_i^{(in)}} \sum_{j=1 (j \neq i)}^{N} J_{ij}\, w_{ij}\, s_j(t)\,(v_i - V_{syn}), \tag{5}$$

$$s_j(t) = \sum_{f=1}^{F_j} E(t - t_f^{(j)} - \tau_l);$$