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Effect of small-world connectivity on fast sparsely synchronized cortical rhythms

Sang-Yoon Kim, Woochang Lim *

Computational Neuroscience Lab., Department of Science Education, Daegu National University of Education, Daegu 705-115, Republic of Korea

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ABSTRACT

Fast cortical rhythms with stochastic and intermittent neural discharges have been observed in electric recordings of brain activity. For these fast sparsely synchronized oscillations, individual neurons fire spikings irregularly and sparsely as Geiger counters, in contrast to fully synchronized oscillations where individual neurons exhibit regular firings like clocks. We study the effect of network architecture on these fast sparsely synchronized rhythms in an inhibitory population of suprathreshold fast spiking (FS) Izhikevich interneurons (which fire spontaneously without noise). We first employ the conventional Erdös–Rényi random graph of suprathreshold FS Izhikevich interneurons for modeling the complex connectivity in neural systems, and study emergence of the population synchronized states by varying both the synaptic inhibition strength J and the noise intensity D. Fast sparsely synchronized states of relatively high degree are found to appear for large values of J and D. However, in a real cortical circuit, synaptic connections are known to have complex topology which is neither regular nor random. Hence, for fixed values of J and D we consider the Watts–Strogatz small-world network of suprathreshold FS Izhikevich interneurons which interpolates between regular lattice and random graph via rewiring, and investigate the effect of small-world synaptic connectivity on emergence of fast sparsely synchronized rhythms by varying the rewiring probability p from short-range to long-range connection. When passing a small critical value p_c^*, fast sparsely synchronized population rhythms are found to emerge in small-world networks with predominantly local connections and rare long-range connections. This transition to fast sparse synchronization is well characterized in terms of a realistic "thermodynamic" order parameter. For further understanding of this transition, we also investigate the effect of long-range connections on dynamical correlations between neuronal pairs, and find that for $p > p_c^*$, global synchronization appears in the whole population because the spatial correlation length covers the whole system thanks to sufficient number of long-range connections. The degree of fast sparse synchronization for $p > p_c^*$ is also measured in terms of a realistic "statistical–mechanical" spiking measure. As p is increased from p_c^*, the degree of population synchrony becomes higher, while the axon "wire length" of the network also increases. At a dynamical-efficiency optimal value p_{ε}^*, there is a trade-off between the population synchronization and the wiring economy, and hence an optimal fast sparsely-synchronized rhythm is found to occur at a minimal wiring cost in an economic small-world network.

* Corresponding author.
E-mail addresses: sangyoonkim@dnue.ac.kr (S.-Y. Kim), woochanglim@dnue.ac.kr (W. Lim).

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1. Introduction

Recently, brain rhythms have attracted much attention [1]. Particularly, we are interested in fast sparsely synchronized cortical rhythms, associated with diverse cognitive functions [2,3]. In some experimental data [4–10], synchronous small-amplitude fast oscillations (e.g., gamma rhythm (30–100 Hz) during awake behaving states and rapid eye movement sleep and sharp-wave ripple (100–200 Hz) during quiet sleep and awake immobility) have been observed in local field potential recordings, while individual neuron recordings have been found to show stochastic and intermittent spike discharges. Thus, single-cell firing activity differs markedly from the population oscillatory behavior. We note that these sparsely synchronized rhythms are in contrast to fully synchronized rhythms. For the fully synchronized rhythms, individual neurons fire regularly at the population frequency like the clock oscillators [11]. Hence, fully synchronized oscillations may be well described by using the conventional coupled-oscillator model composed of suprathreshold spiking neurons above a threshold in the absence of noise or for weak noise [12]. However, such coupled-oscillator models seem to be inappropriate for describing sparse synchronization because of stochastic and intermittent individual neural discharges like the Geiger counters. By taking an opposite view from that of coupled oscillators, the authors in Refs. [13–20] developed a framework appropriate for description of sparse synchronization. When the external noise is strong, suprathreshold spiking neurons discharge irregular firings as Geiger counters, and then the population state becomes unsynchronized. However, as the inhibitory recurrent feedback becomes sufficiently strong, a synchronized population state with stochastic and sparse neural discharges emerges. In this way, under the balance between strong external excitation and strong recurrent inhibition, fast sparse synchronization was found to occur in networks of suprathreshold neurons for both cases of random coupling [13–16] and global coupling [17–20]. Similar sparsely synchronized rhythms were also found to appear through cooperation of noise-induced spikings of subthreshold Morris–Lecar neurons (which cannot fire spontaneously without noise) [21–23].

In this paper, we study the effect of network architecture on fast sparsely synchronized cortical rhythms in an inhibitory population of suprathreshold fast spiking (FS) Izhikevich interneurons [24–27]. The conventional Erdös–Rényi random graph has been usually used for modeling complex connectivity occurring in diverse fields such as social, biological, and technological networks [28]. So, we first consider a random network of suprathreshold FS Izhikevich interneurons, and investigate occurrence of the population synchronized states by varying the inhibition strength and the noise intensity. Fast sparsely synchronized oscillations are found to appear when both the inhibition and the noise are sufficiently strong. Global efficiency of information transfer becomes high for random connection because its average path length (i.e., typical separation between two neurons represented by average number of synapses between two neurons along the minimal path) is short due to long-range connections [29,30]. However, random networks have poor clustering (i.e., low cliquishness of a typical neighborhood) and they are non-economic ones because the (axon) wiring cost becomes expensive due to appearance of short-range and long-range connections with equal probability [31,32]. In a real cortical circuit, synaptic connections are known to have complex topology which is neither regular nor completely random [31–39]. Hence, we consider the Watts–Strogatz model for small-world networks which interpolates between regular lattice with high clustering and random graph with short path length via rewiring [40–42]. The Watts–Strogatz model may be regarded as a cluster-friendly extension of the random network by reconciling the six degrees of separation (small-worldness) [43,44] with the circle of friends (clustering). Many recent works on various subjects of neurodynamics have been done in small-world networks with predominantly local connections and rare long-distance connections [38,45–56]. Here, we investigate the effect of small-world connectivity on emergence of fast sparsely synchronized rhythms by varying the rewiring probability p from local to long-range connections. As p is increased, long-range short-cuts that connect distant neurons begin to appear, and the average path length can be dramatically decreased only by a few short-cuts. Thus, global effective communication between distant neurons may be available via shorter synaptic paths. Eventually, when p passes a critical value p^*_c, fast sparsely synchronized rhythm emerges in the whole population because dynamical correlation length covers the whole system thanks to sufficient number of long-range connections. However, with increasing p, the (axon) wiring length also becomes longer due to appearance of long-range connections. Longer axonal projections are expensive due to their material and energy costs. Hence, we must take into account the (axon) wiring economy for the dynamical efficiency because wiring cost is an important constraint of the brain evolution [1,2,31,23,32,47,50,57–62]. At a dynamical-efficiency optimal value $p^*_{\mathcal{E}}$ an optimal fast sparse synchronization is found to occur via trade-off between synchrony and wiring cost at a minimal wiring cost in an economic small-world network [32].

This paper is organized as follows. In Section 2, we describe an inhibitory population of suprathreshold FS Izhikevich interneurons. The Izhikevich neurons are not only biologically plausible, but also computationally efficient [24–27], and they interact through inhibitory GABAergic synapses (involving the $GABA_A$ receptors). In Section 3, we first consider the conventional Erdös–Rényi random graph [28], and study appearance of the population synchronized states by varying the noise intensity D and the inhibition strength J. We fix J and D at appropriately strong values where sparsely synchronized rhythms of relatively high degree emerge. Then, we consider the Watts–Strogatz model for the small-world network which interpolates between the regular lattice and the random graph [40], and investigate the effect of the small-world connectivity on fast sparsely synchronized rhythms by increasing the rewiring probability p. For the regular connection of $p = 0$, the average path length is very long because there exist only short-range connections, and hence an unsynchronized population state appears. However, with increasing p, long-range connections begin to appear, and hence the average path length becomes shorter. Consequently, when passing a critical value p^*_c ($\simeq$0.12), the unsynchronized state is destabilized and then fast sparsely synchronized population rhythm emerges. This transition to fast sparse synchronization is well described by using a realistic "thermodynamic" order parameter, based on the instantaneous population spike rate (IPSR) [63]. In order