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Realistic thermodynamic and statistical-mechanical measures for neural synchronization

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HIGHLIGHTS

- We employ the instantaneous population spike rate (IPSR) which can be obtained in experiments.
- We develop realistic thermodynamic and statistical-mechanical measures for neural synchronization, based on IPSR.
- The realistic thermodynamic and statistical-mechanical measures make practical characterization of the neural synchronization in both computational and experimental neuroscience.
- More accurate characterization of weak sparse spike synchronization can be achieved in terms of realistic statistical-mechanical IPSR-based measure.

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ABSTRACT

Synchronized brain rhythms, associated with diverse cognitive functions, have been observed in electrical recordings of brain activity. Neural synchronization may be well described by using the population-averaged global potential V_G in computational neuroscience. The time-averaged fluctuation of V_G plays the role of a "thermodynamic" order parameter $\mathcal{O}$ used for describing the synchrony–asynchrony transition in neural systems. Population spike synchronization may be well visualized in the raster plot of neural spikes. The degree of neural synchronization seen in the raster plot is well measured in terms of a "statistical-mechanical" spike-based measure M_s introduced by considering the occupation and the pacing patterns of spikes. The global potential V_G is also used to give a reference global cycle for the calculation of M_s. Hence, V_G becomes an important collective quantity because it is associated with calculation of both $\mathcal{O}$ and M_s. However, it is practically difficult to directly get V_G in real experiments. To overcome this difficulty, instead of V_G, we employ the instantaneous population spike rate (IPSR) which can be obtained in experiments, and develop realistic thermodynamic and statistical-mechanical measures, based on IPSR, to make practical characterization of the neural synchronization in both computational and experimental neuroscience. Particularly, more accurate characterization of weak sparse spike synchronization can be achieved in terms of realistic statistical-mechanical IPSR-based measure, in comparison with the conventional measure based on V_G.

1. Introduction

Recently, much attention has been paid to brain rhythms observed in scalp electroencephalogram and local field potentials (Buzsáki, 2006). These brain rhythms emerge via synchronization between individual firings in neural circuits. This kind of neural synchronization may be used for efficient sensory and cognitive processing such as sensory perception, multisensory integration, selective attention, and memory formation (Wang, 2010, 2003; Gray, 1994), and it is also correlated with pathological rhythms associated with neural diseases (e.g., epileptic seizures and tremors in the Parkinson's disease) (Traub and Whittington, 2010). Here, we are interested in characterization of these synchronized brain rhythms (Golomb, 2007; Kreuz, 2011a,b).

A neural circuit in the major parts of the brain is composed of a few types of excitatory principal cells and diverse types of inhibitory interneurons. By providing a coherent oscillatory output to the principal cells, interneuronal networks play the role of the backbones of many brain rhythms (Buzsáki, 2006; Wang, 2010, 2003; Buzsáki et al., 2004). In this paper, we consider an inhibitory population of fast spiking (FS) Izhikevich subthreshold interneurons (Izhikevich, 2003, 2004, 2007, 2010). Sparsely synchronized neural oscillations are found to appear in an intermediate range of noise intensity. At the population level, fast synchronized rhythms emerge, while at the cellular level, individual neurons discharge

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stochastic firings at low rates than the population frequency. Fast cortical rhythms [e.g., beta (15–30 Hz), gamma (30–100 Hz), and ultrafast (100–200 Hz) rhythms], associated with diverse cognitive functions, typically exhibit sparse synchronization (Wang, 2010; Brunel and Hakim, 2008, 1999; Brunel, 2000; Brunel and Wang, 2003; Geisler et al., 2005; Brunel and Hansel, 2006). The main purpose of our work is to make practical characterization of synchronized cortical rhythms by using realistic measures applicable in both computational and experimental neuroscience.

Neural synchronization may be well described in terms of the population-averaged global potential V_G in computational neuroscience. For a synchronous case, an oscillating global potential V_G appears; otherwise (i.e., V_G is stationary) the population state becomes unsynchronized. Thus, the mean square deviation of V_G plays the role of an order parameter $\mathcal{O}$ used for describing the synchrony–asynchrony transition in neural systems (Manrubia et al., 2004; Hansel and Mato, 2003; Golomb and Rinzel, 1994; Hansel and Sompolinsky, 1992; Ginzburg and Sompolinsky, 1994; Lim and Kim, 2007, 2009, 2011; Hong et al., 2011). The order parameter $\mathcal{O}$ can be regarded as a "thermodynamic" measure because it concerns just the macroscopic global potential V_G without considering any quantitative relation between V_G and the microscopic individual potentials. Through calculation of $\mathcal{O}$, one can determine the region of noise intensity where synchronized rhythms appear. Population spike synchronization may be well visualized in the raster plot of neural spikes (i.e., a spatiotemporal plot of neural spikes) which can be directly obtained in experiments. For the synchronous case, "stripes" (composed of spikes and indicating population synchronization) are found to be formed in the raster plot. Due to synchronous contribution of spikes, local maxima of the global potential V_G appear at the centers of stripes. Recently, a "statistical-mechanical" spike-based measure M_s was introduced by taking into consideration both the occupation pattern and the pacing pattern of spikes in the stripes of the raster plot (Lim and Kim, 2007, 2009, 2011; Hong et al., 2011). Particularly, the pacing degree between spikes is determined in a statistical-mechanical way by quantifying the average contribution of (microscopic) individual spikes to the (macroscopic) global potential V_G. The global potential V_G is thus used to provide a reference global cycle for the calculation of both the occupation and the pacing degrees. Hence, V_G becomes an important population-averaged quantity because it is involved in calculation of both $\mathcal{O}$ and M_s. However, to directly obtain V_G in real experiments is very difficult. To overcome this difficulty, instead of V_G, we use an experimentally obtainable instantaneous population spike rate (IPSR) which is often used as a collective quantity showing population behaviors (Wang, 2010; Brunel and Hakim, 2008, 1999; Brunel, 2000; Brunel and Wang, 2003; Geisler et al., 2005; Brunel and Hansel, 2006), and develop realistic thermodynamic and statistical-mechanical measures, based on IPSR, to make practical characterization of the neural synchronization in both computational and experimental neuroscience. These realistic thermodynamic and statistical-mechanical measures are in contrast to conventional "microscopic" synchronization measures such as the correlation-based measure (based on the cross-correlation between the microscopic individual potentials of pairs of neurons) (Wang and Buzsáki, 1996; White et al., 1998) and the spike-based measures based on the spike-distance (Victor and Purpura, 1996, 1997; van Rossum, 2001; Kreuz et al., 2011, 2013) and the ISI (interspike interval)-distance (Kreuz et al., 2007) between the microscopic individual spike trains of pairs of neurons). The correlation-based and the spike-based measures are microscopic ones because both of them concern just the microscopic individual potentials or spike-trains without taking into account any quantitative relation between the microscopic quantities and the global activities (e.g., V_G and IPSR). In addition to characterization of population spike synchronization, the conventional spike-based measures are also used to quantify the reliability of spike timing (Mainen and Sejnowski, 1995; Tiesinga et al., 2002; Schreiber et al., 2003; Gutkin et al., 2003; Brette, 2003; Rodriguez-Molina et al., 2007; Galán et al., 2008; Lin et al., 2009; Yu et al., 2013) and the reliability of stimulus discrimination (Hernández et al., 2000; Schaefer et al., 2006; Narayan et al., 2006; Wang et al., 2007; Schmuker and Schneider, 2007; Chicharroa et al., 2011).

This paper is organized as follows. In Section 2, we describe a biological globally coupled network composed of FS Izhikevich subthreshold neurons. The Izhikevich neurons are not only biologically plausible, but also computationally efficient (Izhikevich, 2003, 2004, 2007, 2010), and they interact through inhibitory GABAergic synapses (involving the $GABA_A$ receptors). In Section 3, we develop realistic thermodynamic and statistical-mechanical measures, based on IPSR, which are applicable in both the computational and the experimental neuroscience. Their usefulness for characterization of neural synchronization is shown in explicit examples. Through calculation of the realistic thermodynamic order parameter, we determine the range of noise intensity where sparsely synchronized neural oscillations occur. In the synchronous region of noise intensity, we also characterize synchronized rhythms in terms of realistic statistical-mechanical spiking measure M_s. It is thus shown that M_s is effectively used to characterize sparse synchronization shown in partially occupied stripes of the raster plot. For examination on effectiveness of realistic statistical-mechanical measure M_s, we have also successfully characterized neural synchronization in another population of FS Wang–Buzsáki suprathreshold interneurons (Wang and Buzsáki, 1996) in Section 4. Furthermore, it has been shown that more accurate characterization of weak sparse spike synchronization can be achieved in terms of statistical-mechanical IPSR-based measures, in comparison with the conventional statistical-mechanical V_G-based measures. Finally, a summary along with discussion on the applicability of realistic statistical-mechanical measure to real experimental data is given in Section 5.

2. Inhibitory population of FS Izhikevich subthreshold neurons

We consider an inhibitory population of N globally coupled subthreshold neurons. As an element in our coupled neural system, we choose the FS Izhikevich interneuron model which is not only biologically plausible, but also computationally efficient (Izhikevich, 2003, 2004, 2007, 2010). The population dynamics in this neural network is governed by the following set of ordinary differential equations:

$$C\frac{dv_i}{dt} = k(v_i - v_r)(v_i - v_t) - u_i + I_{DC} + D\xi_i - I_{syn,i}, \quad (1)$$

$$\frac{du_i}{dt} = a\{U(v_i) - u_i\}, \quad (2)$$

$$\frac{ds_i}{dt} = \alpha s_\infty(v_i)(1 - s_i) - \beta s_i, \quad i = 1, \ldots, N, \quad (3)$$

with the auxiliary after-spike resetting:

$$\text{if } v_i \geq v_p, \quad \text{then } v_i \leftarrow c \text{ and } u_i \leftarrow u_i + d, \quad (4)$$

where

$$U(v) = \begin{cases} 0 \text{ for } v < v_b \\ b(v - v_b)^3 \text{ for } v \geq v_b \end{cases}, \quad (5)$$

$$I_{syn,i} = \frac{J}{N-1}\sum_{j(\neq i)}^{N} s_j(t)(v_i - V_{syn}), \quad (6)$$