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# Thermodynamic order parameters and statistical–mechanical measures for characterization of the burst and spike synchronizations of bursting neurons

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## HIGHLIGHTS

- We are interested in characterization of population synchronization of bursting neurons which exhibit both the slow bursting and the fast spiking timescales.
- We separate the slow bursting and the fast spiking timescales via frequency filtering, and extend the thermodynamic order parameter and the statistical-mechanical measure based on the experimental-obtainable instantaneous population firing rate (IPFR) $R(t)$ to the case of bursting neurons.
- We show that both the order parameters and the statistical-mechanical measures may be effectively used to characterize the burst and spike synchronizations of bursting neurons.

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## ABSTRACT

We are interested in characterization of population synchronization of bursting neurons which exhibit both the slow bursting and the fast spiking timescales, in contrast to spiking neurons. Population synchronization may be well visualized in the raster plot of neural spikes which can be obtained in experiments. The instantaneous population firing rate (IPFR) $R(t)$, which may be directly obtained from the raster plot of spikes, is often used as a realistic collective quantity describing population behaviors in both the computational and the experimental neuroscience. For the case of spiking neurons, realistic thermodynamic order parameter and statistical–mechanical spiking measure, based on $R(t)$, were introduced in our recent work to make practical characterization of spike synchronization. Here, we separate the slow bursting and the fast spiking timescales via frequency filtering, and extend the thermodynamic order parameter and the statistical–mechanical measure to the case of bursting neurons. Consequently, it is shown in explicit examples that both the order parameters and the statistical–mechanical measures may be effectively used to characterize the burst and spike synchronizations of bursting neurons.



## 1. Introduction

In recent years, brain rhythms which are observed in scalp electroencephalogram and local field potentials have attracted much attention [1]. These brain rhythms emerge via synchronization between individual neuronal firings. Synchronization

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of firing activities may be used for efficient sensory and cognitive processing (e.g., feature integration, selective attention, and memory formation) [2–4]. This kind of neural synchronization is also correlated with pathological rhythms associated with neural diseases such as epilepsy, Parkinson's disease, and Alzheimer's disease [5–7]. Here, we are interested in characterization of these synchronous brain rhythms.

There are two basic types of neuronal firing activities, spiking and bursting [8]. We are concerned about synchronization of bursting neurons. Bursting occurs when neuronal activity alternates, on a slow timescale, between a silent phase and an active (bursting) phase of fast repetitive spikings [9–13]. Thanks to a repeated sequence of spikes in the bursting, there are several important bursting activities in the neural information transmission [10,14–17]. For example, (1) bursts are necessary to overcome the synaptic transmission failure, (2) bursts are more reliable than single spikes in evoking responses in postsynaptic neurons, and (3) bursts can be used for selective communication between neurons, where the interspike frequency within the bursts encodes the channel of communication. Intrinsically bursting neurons and chattering neurons in the cortex [18,19], thalamocortical relay neurons [20,21], thalamic reticular neurons [22], hippocampal pyramidal neurons [23], Purkinje cells in the cerebellum [24], pancreatic $\beta$-cells [25–27], and respiratory neurons in pre-Botzinger complex [28,29] are representative examples of bursting neurons. These bursting neurons exhibit two different patterns of synchronization due to the slow and fast timescales of bursting activity. Burst synchronization (synchrony on the slow bursting timescale) refers to a temporal coherence between the active phase onset or offset times of bursting neurons, while spike synchronization (synchrony on the fast spike timescale) characterizes a temporal coherence between intraburst spikes fired by bursting neurons in their respective active phases [30,31]. Recently, many studies on the burst and spike synchronizations have been made in several aspects (e.g., chaotic phase synchronization, transitions between different states of burst synchronization, effect of network topology, effect on information transmission, suppression of bursting synchronization, effect of noise and coupling on burst and spike synchronizations, and delay-induced synchronization) [32–48].

In this paper, we are concerned about practical characterization of the burst and spike synchronizations of bursting neurons. For illustration of burst and spike synchronizations, refer to Fig. 3 of Ref. [31] where two coupled Hindmarsh–Rose neurons were considered. For small coupling, there are no burst and spike synchronization (see the first column), while burst and spike synchronizations occur when the coupling parameter passes a threshold (see the third column). Population synchronization may be well visualized in the raster plot of neural spikes which can be obtained in experiments. Instantaneous population firing rate (IPFR), $R(t)$, which is directly obtained from the raster plot of spikes, is a realistic collective quantity describing population behaviors in both the computational and the experimental neuroscience [2,49–54]. In our previous work on spiking neurons [55], we employed $R(t)$ as a population quantity, and developed realistic measures, based on $R(t)$, to make practical characterization of synchronization of spiking neurons in both the computational and the experimental neuroscience. The mean square deviation of $R(t)$ plays the role of an order parameter $\mathcal{O}$ used for characterizing synchronization transition of spiking neurons [56]. The order parameter $\mathcal{O}$ can be regarded as a "thermodynamic" measure because it concerns just the macroscopic quantity $R(t)$ without considering any quantitative relation between $R(t)$ and the microscopic individual spikes. Through calculation of $\mathcal{O}$, one can determine the threshold value for the spike synchronization. Moreover, to quantitatively measure the degree of spike synchronization, a "statistical–mechanical" spiking measure $M_s$ was introduced by taking into consideration both the occupation pattern and the pacing pattern of spikes in the raster plot. Particularly, the pacing degree between spikes was determined in a statistical–mechanical way by quantifying the average contribution of (microscopic) individual spikes to the (macroscopic) IPFR $R(t)$. Consequently, synchronization of spiking neurons may be well characterized in terms of these realistic thermodynamic order parameter and statistical–mechanical measure, $\mathcal{O}$ and $M_s$, based on $R(t)$.

The main purpose of our work is to characterize the burst and spike synchronizations of bursting neurons by extending the thermodynamic order parameter and the statistical–mechanical measure of spiking neurons [55] to the case of bursting neurons. Through the fast–slow burster analysis, a bursting system is separated into a fast and a slow subsystem [11,57–59]. Thus, fast variables of the bursting system are extracted and then slow variables are used as bifurcation parameters for bifurcation analysis of the bursting system. For our case, to characterize the burst and spike synchronizations we separate the slow and fast timescales of the bursting activity via the frequency filtering, and decompose the IPFR $R(t)$ into $R_b(t)$ (the instantaneous population burst rate (IPBR) describing the bursting behavior) and $R_s(t)$ (the instantaneous population spike rate (IPSR) describing the intraburst spiking behavior). Then, the mean square deviations of $R_b$ and $R_s$ play the role of realistic thermodynamic order parameters, $\mathcal{O}_b$ and $\mathcal{O}_s$, used to determine the bursting and spiking thresholds for the burst and spike synchronization, respectively. We also consider another raster plot of bursting onset or offset times for more direct visualization of bursting behavior. From this type of raster plot, we can directly obtain the IPBR, $R_b^{(on)}(t)$ or $R_b^{(off)}(t)$, without frequency filtering. Then, the time-averaged fluctuations of $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ also play the role of the order parameters, $\mathcal{O}_b^{(on)}$ and $\mathcal{O}_b^{(off)}$, for the bursting transition. These bursting order parameters $\mathcal{O}_b^{(on)}$ and $\mathcal{O}_b^{(off)}$ are more direct ones than $\mathcal{O}_b$ because they may be obtained directly without frequency filtering and they yield the same bursting threshold which is obtained through calculation of $\mathcal{O}_b$. As a next step, in the whole region of burst synchronization, the degree of burst synchronization seen in the raster plot of bursting onset or offset times may be well measured in terms of a statistical–mechanical bursting measure $M_b$, introduced by considering both the occupation and the pacing patterns of bursting onset or offset times in the raster plot. In a similar way, we also develop a statistical–mechanical spiking measure $M_s$, based on $R_s$, to quantitatively measure the degree of the intraburst spike synchronization. Consequently, through separation of the slow bursting and the fast spiking timescales, burst synchronization may be well characterized in terms of both the bursting order parameters ($\mathcal{O}_b$,