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# Estimating the correlation between bursty spike trains and local field potentials

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ABSTRACT

To further understand rhythmic neuronal synchronization, an increasingly useful method is to determine the relationship between the spiking activity of individual neurons and the local field potentials (LFPs) of neural ensembles. Spike field coherence (SFC) is a widely used method for measuring the synchronization between spike trains and LFPs. However, due to the strong dependency of SFC on the burst index, it is not suitable for analyzing the relationship between bursty spike trains and LFPs, particularly in high frequency bands. To address this issue, we developed a method called weighted spike field correlation (WSFC), which uses the first spike in each burst multiple times to estimate the relationship. In the calculation, the number of times that the first spike is used is equal to the spike count per burst. The performance of this method was demonstrated using simulated bursty spike trains and LFPs, which comprised sinusoids with different frequencies, amplitudes, and phases. This method was also used to estimate the correlation between pyramidal cells in the hippocampus and gamma oscillations in rats performing behaviors. Analyses using simulated and real data demonstrated that the WSFC method is a promising measure for estimating the correlation between bursty spike trains and high frequency LFPs.

## 1. Introduction

The advent of multi-electrode arrays has facilitated the simultaneous recording of the spiking activity of multiple neurons and neural ensembles, which provides an important method for investigating the fundamental issues related to neural coding (Claverol-Tinture, Cabestany, & Rosell, 2007; Galashan et al., 2011; Schwartz, 2004; Stafford, Sher, Litke, & Feldheim, 2009). The voltage signals obtained are generally separated into two types: the spikes or action potentials, which are fired by neurons and identified by high-pass filtering, detection, and sorting; and the local field potentials (LFPs), which are the total synaptic currents in the neuronal circuit and are obtained by low-pass filtering the original wideband signal (Mizuseki, Sirota, Pastalkova, & Buzsaki, 2009; Perelman & Ginosar, 2007). The interactions between the spikes of single neurons, i.e., spike trains, and the ongoing LFP oscillations are becoming hot topics in neuroscience because they allow us to study how the activities of individual neurons are related to those of the larger-scale networks in which they are embedded. Their significance has been shown to be associated with high-level brain functions, such as attention (Chalk et al., 2010; Fries, Reynolds, Rorie, & Desimone, 2001), memory (Harris et al., 2002; Lee, Simpson, Logothetis, & Rainer, 2005; Le Van Quyen et al., 2008), motor tasks (Courtemanche, Pellerin, & Lamarre, 2002; Hagan, Dean, & Pesaran, 2012; van Wingerden, Vinck, Lankelma, & Pennartz, 2010), and sensory processing (Eggermont & Smith, 1995; Fries, Roelfsema, Engel, Konig, & Singer, 1997; Pienkowski & Eggermont, 2011; Xu, Jiang, Poo, & Dan, 2012).

To quantify the correlation between spike trains and LFPs, a wide variety of spike–LFP measures have been introduced in the past few years, e.g., the phase histogram, which is calculated by summing spikes that occur at different LFP phases (Csicsvari, Jamieson, Wise, & Buzsaki, 2003); the pairwise phase consistency, which is a bias-free measure of rhythmic neuronal synchronization (Vinck, Battaglia, Womelsdorf, & Pennartz, 2012; Vinck, van Wingerden, Womelsdorf, Fries, & Pennartz, 2010); phase locking, which is evaluated by applying the Rayleigh test for circular uniformity to the spike phase distribution (Colgin et al., 2009; Siapas, Lubenov, & Wilson, 2005; Sirota et al., 2008); and coherency,

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which is obtained by normalizing the cross-spectrum of each process (spike train and LFP) with the spectrum of each process (Chalk et al., 2010; Gregoriou, Gotts, Zhou, & Desimone, 2009; Jarvis & Mitra, 2001; Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002). In addition, another commonly used method for studying spike–LFP interactions is the spike field coherence (SFC), which measures the synchronization between spike trains and LFPs as a function of the frequency, where it takes values between 0% (complete lack of synchronization) and 100% (complete synchronization) (Fries et al., 2001, 1997). The SFC can be used to describe the strength of synchronization between spike times and a particular phase of the LFP oscillation at a certain frequency. The SFC has been employed to investigate memory formation in humans (Rutishauser, Ross, Mamelak, & Schuman, 2010), the neural mechanism of visual attention in macaque monkeys (Chalk et al., 2010; Fries et al., 2001), stimulus-specific synchronization in the primary visual cortex of awake cats exhibiting behaviors (Siegel & Konig, 2003), and other brain functions (Fries, Schroder, Roelfsema, Singer, & Engel, 2002; Issa & Wang, 2011; Lewandowski & Schmidt, 2011; Tiesinga, Fellous, Salinas, Jose, & Sejnowski, 2004; Wang, Iliescu, Ma, Josic, & Dragoi, 2011). However, this method also has the drawback that the estimated coherence is biased when only a small number of spikes are available (Grasse & Moxon, 2010; Vinck, Lima et al., 2010; Vinck, van Wingerden et al., 2010). Recently, a new pairwise measure that is not biased by the number of spikes was developed to address this problem (Vinck et al., 2012). In addition to the spike number, the temporal structure of spike trains has an effect on the SFC calculation. Bursts, i.e., short episodes of high-frequency spike firing (Mammone & Morabito, 2008), are commonly observed structures in spike trains. In the present study, we modified the SFC method for bursty spike trains and LFPs to estimate correlations. Given that the coherence is generally used to measure the linear association between two signals in the frequency domain, we use the correlation to denote the relationships between spike trains and LFPs in the present study, which emphasizes the synchronization of the LFP segments around the spike times.

If all the spikes in the bursts are used to calculate the coherence, the SFC values will decrease, even if there is a strong phase-locked synchronization between bursty spike trains and LFPs at high frequency bands. To overcome this drawback, we propose an improvement to the SFC algorithm. The manipulation is analogous to the process of weighting, thus the modified approach is referred to as weighted spike field correlation (WSFC). The weighting process emphasizes the contributions of some aspects of a dataset to the final result by allocating them greater weight during the analysis. When calculating the WSFC, only the first spike in each burst is employed to compute the SFC. The number of times that the first spike used is determined by the number of spikes per burst. This manipulation emphasizes the firing time of the first spike in a burst and highlights the difference between a burst and an individual spike. To evaluate the performance of the proposed method, we applied it to simulation data and real neurobiological signals recorded in the hippocampus of rats.

## 2. Materials and methods

### 2.1. Methods

The SFC is a function of frequency, which is obtained by computing the ratio of the power spectrum for the spike-triggered average (STA) over the average power spectrum of the LFP fractions (Fries et al., 1997). Thus, the SFC is dependent on the LFP power and the spike number. Suppose that the spike train of a neuron is denoted as $S = [s_1, s_2, \ldots, s_m]$, where $m$ is the spike number. $V = [v_1, v_2, \ldots, v_m]$ is the set of LFP segments, where $v_i$ is the sample of the LFP signal in the time window $[s_i - T/2, s_i + T/2]$, and $T$ is the duration of the LFP segments. The STA is constructed by averaging the LFP fractions within the windows centered on the spikes. The power spectrum of STA (PSTA) is defined as:

$$\sigma = \Psi\left(\frac{1}{m}\sum_{i=1}^{m} v_i\right), \tag{1}$$

where $\Psi$ denotes the operation used to calculate the power spectrum. To describe the power of every frequency component in the LFP segments used to construct the STA, i.e., $v_i$ with $i = 1, 2, \ldots, m$, the average power spectrum of $v_i$ is:

$$\omega = \frac{1}{m}\sum_{i=1}^{m}[\Psi(v_i)]. \tag{2}$$

This is also referred to as the spike-triggered power spectrum or STP (Fries et al., 1997; Rutishauser et al., 2010), and the SFC is defined as (Fries et al., 1997):

$$\delta_{\mathrm{SFC}} = \frac{\sigma}{\omega} \times 100\%. \tag{3}$$

The STP and PSTA can be computed using many methods. For example, multitaper analysis is a powerful and robust method for estimating a single-trial spectrum (Jarvis & Mitra, 2001), which can be performed using the Chronux toolbox (Bokil, Andrews, Kulkarni, Mehta, & Mitra, 2010). The multitaper method is employed in the present study to analyze the spectra of the simulated and experimentally recorded LFP signals.

The SFC reflects the synchronization between spike trains and LFPs at different frequencies. However, it does not function well with bursty spike trains and LFPs at high frequency bands, as shown in the following section. A burst can be defined as a temporary increase in the firing rate of spikes relative to the background activity (Cocatre-Zilgien & Delcomyn, 1992; Palm, 1981; Robin et al., 2009). As the mechanism for generating bursts has been mentioned, it is commonly accepted that small depolarization keeps the cell silent, moderate depolarization makes the cell fire single spikes, and high depolarization causes the cell to discharge in burst mode (Harris, Hirase, Leinekugel, Henze, & Buzsáki, 2001). Thus, bursts code the same neural information as single spikes but with higher reliability (Harris et al., 2001; Lisman, 1997). Based on this concept, the first spike in each burst is selected and used to represent the burst as an event (Kepecs & Lisman, 2003; Swadlow & Gusev, 2001).

The present study focuses on the approach used to quantify the level of synchronization between spike trains and LPFs. Thus, we propose the WSFC method, which allows only the first spike in each burst to be utilized in the computation of the PSTA and STP. To emphasize the difference between single spikes and bursts, the first spikes in the bursts are used multiple times. The number of times is equal to the number of spikes per burst. In this manner, the first spike timing represents the occurrence of the burst and the weighting procedure (using the first spike multiple times) reflects the properties of the burst. Suppose that a bursty spike train is $S_B = [s_1, \ldots, s_m, b_{11}, \ldots, b_{1k_1}, b_{21}, \ldots, b_{2k_2}, \ldots, b_{n1}, \ldots, b_{nk_n}]$, where $s$ denotes single spikes, $b$ represents bursts, $m$ is the number of single spikes, $n$ is the number of bursts, and $k$ is the spike number per burst. The power spectrum of the weighted STA is

$$\sigma_w = \Psi\left(\frac{1}{m+\sum k}\left(\sum_{i=1}^{m} v_i + \sum_{j=1}^{n} k_j \times v_{j1}\right)\right), \tag{4}$$

and the weighted spike triggered power spectrum of LFP is

$$\omega_w = \frac{1}{m+\sum k}\Psi\left(\sum_{i=1}^{m} v_i + \sum_{j=1}^{n} k_j \times v_{j1}\right), \tag{5}$$