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Unbiased and robust quantification of synchronization between spikes and local field potential

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HIGHLIGHTS

- We proposed a new method, spike-triggered correlation matrix synchronization, for characterizing the synchronization between spike trains and rhythms present in LFP.
- The method is not sensitive to the total number of spikes in the calculation.
- The method is superior to an existing unbiased measure (PPC) in resisting spike noise arising from jitter and extra spikes.
- We demonstrated that spike–LFP synchronization can be used to explore interesting information on the mechanism of orientation selectivity in the primary visual cortex.

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ABSTRACT

Background: In neuroscience, relating the spiking activity of individual neurons to the local field potential (LFP) of neural ensembles is an increasingly useful approach for studying rhythmic neuronal synchronization. Many methods have been proposed to measure the strength of the association between spikes and rhythms in the LFP recordings, and most existing measures are dependent upon the total number of spikes.

New method: In the present work, we introduce a robust approach for quantifying spike–LFP synchronization which performs reliably for limited samples of data. The measure is termed as spike-triggered correlation matrix synchronization (SCMS), which takes LFP segments centered on each spike as multi-channel signals and calculates the index of spike–LFP synchronization by constructing a correlation matrix.

Results: The simulation based on artificial data shows that the SCMS output almost does not change with the sample size. This property is of crucial importance when making comparisons between different experimental conditions. When applied to actual neuronal data recorded from the monkey primary visual cortex, it is found that the spike–LFP synchronization strength shows orientation selectivity to drifting gratings.

Comparison with existing methods: In comparison to another unbiased method, pairwise phase consistency (PPC), the proposed SCMS behaves better for noisy spike trains by means of numerical simulations.

Conclusions: This study demonstrates the basic idea and calculating process of the SCMS method. Considering its unbiasedness and robustness, the measure is of great advantage to characterize the synchronization between spike trains and rhythms present in LFP.

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1. Introduction

In neuroscience, rhythmic synchronization has been proposed as a candidate mechanism for neuronal communication, assembly formation, and neural coding (Buzsaki, 2010; Fries, 2005; Siegel et al., 2009). Generally, quantifying the consistent phase-relationship in a particular frequency band of signals generated by

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two separate sources is used to characterize their rhythmic synchronization. A recent interest is to estimate the synchronization between the spiking activity of individual neurons and the local field potential (LFP) of neural ensembles (Ray, 2014).

Spikes and LFP can be obtained from the signal recorded by a microelectrode. The former are fired by neurons and identified by high-pass filtering, detection, and sorting. The latter reflects the total effects of the synaptic currents in the neuronal circuit and is obtained by low-pass filtering the original wideband signal. Several rhythms of the LFP are generated through inhibitory networks that produce periodic fluctuations in the intracellular potential of the target post-synaptic neurons such that the excitability of these neurons varies within one period of the rhythm, which can be used to synchronize the spiking of neurons (Buzsaki and Wang, 2012; Ray, 2014). Also, it is reported that spikes can be inferred from the LFP in the primary visual cortex of monkeys (Rasch et al., 2008). Furthermore, the LFP is thought to mainly reflect the summed transmembrane currents flowing through the neurons within a local region around the microelectrode tip (Buzsaki et al., 2012; Reimann et al., 2013) and its phase is widely adopted to characterize the spike–LFP synchronization (Colgin et al., 2009; Csicsvari et al., 2003; Fries et al., 2001). In view of the above considerations, we suggest that there exists a correlation between the variation of LFP phase and the neural firing which generates the spike–LFP synchronization.

Several spike–LFP synchronization measures have been introduced in the past few years, e.g., the phase histogram (Csicsvari et al., 2003), phase locking (Colgin et al., 2009), spike field coherence (Fries et al., 2001), and coherency (Pesaran et al., 2002). However, these measures are dependent upon the total number of spikes, which renders comparison of spike–LFP synchronization across experimental contexts difficult. Often, different experimental conditions yield substantially different number of spikes. Thus, it is necessary and urgent to develop an unbiased measure for characterizing the synchronization between spikes and LFP. Recently, a circular statistic, pairwise phase consistency (PPC), has been proposed. It is a bias-free and consistent estimator of spike–LFP synchronization (Vinck et al., 2010). Unfortunately, the performance of PPC severely deteriorates in the presence of spike noise. In this study, we present a new measure for estimating spike–LFP synchronization, which is independent of the total number of spikes and robust against spike noise.

2. Materials and methods

2.1. The spike-triggered correlation matrix synchronization

The main idea of the proposed method is to take LFP segments centered on each spike (spike-triggered LFPs) as multi-channel signals and calculate the index of spike–LFP synchronization by constructing a correlation matrix. Thus, we refer to this new method as spike-triggered correlation matrix synchronization (SCMS). A detailed description of the algorithm is in the following.

First, it is necessary to filter the LFP in certain frequency band of research interest with zero-phase-shift filters. Then, compute the instantaneous phase of the whole filtered LFP signal by Hilbert transform. For a signal $v(t)$, the analytic signal $\zeta(t)$ is a complex function of time, and it is defined as:

$$\zeta(t) = v(t) + j\tilde{v}(t) = A(t)e^{j\phi(t)}, \tag{1}$$

where the function $\tilde{v}(t)$ is the Hilbert transform of $v(t)$:

$$v(t) = \frac{1}{\pi}\text{P.V.} \times \int_{-\infty}^{+\infty} \frac{v(t)}{t-\tau}\text{d}\tau. \tag{2}$$

P.V. indicates that the integral is taken in the sense of Cauchy principal value (Rosenblum et al., 1996). Suppose that the spike train (i.e., a series of spikes) fired by a neuron is denoted as $S = [s_1, s_2, \ldots, s_n]$, where s_i $(i = 1, 2, \ldots, n)$ is the spiking time and n is the number of spikes. $W = [w_1, w_2, \ldots, w_n]$ is the set of LFP segments, where $w_i\,(i = 1, 2, \ldots, n)$ denotes the samples of the LFP signal in the time window $\left[s_i - T/2,\ s_i + T/2\right]$ and T is the duration of the LFP segments. Thus, the set of phase signals $\Phi = [\phi_1, \phi_2, \ldots, \phi_n]$ corresponding to the set of LFP segments can be obtained.

Second, construct the correlation matrix **C** by calculating the phase locking value (PLV) between pairs of LFP segments, i.e.,

$$c_{kl} = \left|\frac{1}{N}\sum_{i=1}^{N} e^{j(\phi_k(t_i)-\phi_l(t_i))}\right|, \tag{3}$$

where N denotes the number of samples in the time window. All entries of matrix **C** range from 0 to 1: when $c_{kl} = 1$, there is a perfect phase synchronization between the k and l LFP segments; and when $c_{kl} = 0$, there is no synchronization. Thus **C** is a real symmetric matrix and all diagonal elements are equal to 1. Then, the eigenvalue decomposition of **C** is given by

$$Cu_i = \lambda_i u_i, \tag{4}$$

where λ_i are the eigenvalues, with $\lambda_1 \geq \lambda_2 \geq \ldots \geq \lambda_n$, u_i are the eigenvectors corresponding to λ_i. The eigenvalues have the following properties: (1) all eigenvalues are real numbers and the sum of the eigenvalues equals the number of LFP segments. (2) If the LFP segments are fully nonsynchronized, **C** will approximate to an identical matrix and all of the eigenvalues will distribute around 1 which indicates the random synchronization between the LFP segments. (3) Once all of LFP segments are perfectly synchronized, the elements of **C** will be equal to 1. The maximum eigenvalue is equal to the number of LFP segments n and other eigenvalues falls to zero. Thus, eigenvalues can provide information about the synchronization between the LFP segments (Li et al., 2007).

Finally, in order to obtain a normalized value of spike–LFP synchronization which is independent of the number of spikes, we randomize all spike-triggered LFP segments to compute a surrogate correlation matrix **R** (Li et al., 2007). The surrogate data is generated by randomly shuffling the order of the original signals (Theiler et al., 1992). Similarly, we can obtain the ordered eigenvalues of matrix **R**. Repeating this randomization and computation M times (we select $M = 100$ in this work), the mean and standard deviation (SD) of the maximum eigenvalues are denoted as $\bar{\lambda}'_1$ and σ_1, respectively. Then, the normalized spike–LFP synchronization can be computed by the following equation:

$$\eta = \begin{cases} \left(\dfrac{\lambda_1 - \bar{\lambda}'_1}{n - \bar{\lambda}'_1}\right) & \text{if } \lambda_1 > \left(\bar{\lambda}'_1 + K \times \sigma_1\right) \\ 0 & \text{otherwise} \end{cases}, \tag{5}$$

where K is a constant that determines the threshold, and $K = 3$ is selected for 99% confidence intervals (Li et al., 2007).

The reason for the choice of the maximum eigenvalue (λ_1 and $\bar{\lambda}'_1$) is in the following. Li et al. (2007) noted that when multi-channel signals are acquired from a local region, the first synchronization index, which corresponds to the maximum eigenvalue, is appropriate for indicating the global synchronization. Moreover, as spikes and LFP are recorded by the same microelectrode, the spike-triggered LFPs can be considered as multichannel signals from one region of synchronization. Thus, it is justifiable to use the first synchronization index to characterize the spike–LFP synchronization.

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