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A spike train analysis for correlating burst firings in neurons

David C. Tam*

Department of Biological Sciences, University of North Texas, Denton, TX 76203, USA

Abstract

We introduced a multiple single-unit spike train analysis technique to deduce the burst firing patterns in one neuron that are temporally correlated to the spike generation in another neuron. This analysis considers the contribution of temporal summation of burst firings in one neuron that is correlated to the probability of spike firing in another neuron. The result shows that the analysis can extract the number of spikes and the duration of burst pattern. © 2001 Published by Elsevier Science B.V.

Keywords: Spike train analysis; Correlation; Burst firing

1. Introduction

We provide a new multiple single-unit spike train analysis technique to detect the relationship of burst firing to the generation of spikes in neurons. This spike train analysis deduces the likelihood of spike firing in one neuron correlated with the burst firing of incoming spikes from another neuron.

Burst-firing is a well-known phenomenon in neurophysiology. Yet, the signal processing functions of burst in neuroprocessing have not been examined or demonstrated with respect to the spike trains recorded in a network. This method will provide a statistical measure so that the probability of spike generation can be correlated with burst firing based on spike trains recorded extracellularly from neurons rather than intracellular recordings. By providing a spike train analysis method for detecting subthreshold events, experimentalists can study the contribution of bursts in neural processing without needing to record intracellularly.

* Tel.: + 1-940-565-3261; fax: + 1-940-565-4136.
E-mail address: dtam@unt.edu (D.C. Tam).

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Although a lot of traditional spike train analysis do exist, such as the auto-correlation technique [2] and cross-correlation technique [3] establish the univariant statistics ISIs and CIs, respectively, the current analysis extends the traditional cross-correlation analysis and the doublet (double spikes) integration analysis introduced by Tam [8].

2. Theoretical methods

This burst analysis estimates the spike firing probability density function (pdf) based on the temporal integration period of the incoming spikes in bursts. In other words, it establishes the conditional probability by using the covariant statistics of the interspike interval (ISI) and cross-interval (CI).

Let us assume that there are two spike trains recorded simultaneously. Furthermore, let us denote one of the spike train as the reference spike train, A, with a total of N_A spikes be represented by

$$A(t) = \sum_{n=1}^{N_A} \delta(t - t_n). \tag{1}$$

The other spike train is considered as the compared spike train, B, with a total of N_B spikes be represented by

$$B(t') = \sum_{m=1}^{N_B} \delta(t' - t'_m), \tag{2}$$

where t_n and t'_m are the occurrence times of nth and mth spikes in spike trains A and B, respectively, and $\delta(t)$ is a delta function denoting the occurrence of a spike at time t.

Let us further define the pre-interspike interval (pre-ISI, τ_{n+1}) as the interspike interval before the reference spike. There are many pre-ISIs relative to the reference spikes, the first-order pre-ISI to the kth order pre-ISI. Thus, we can define the first-order pre-ISI with respect to the nth reference spike in the reference spike train A as

$$\tau_n^{(1)} = t_n - t_{n-1} \tag{3}$$

and the kth-order pre-ISI as

$$\tau_n^{(k)} = t_n - t_{n-k}. \tag{4}$$

Similarly, the post-cross-interval (post-CI) between the compared and reference spike trains relative to the nth reference spike in spike train A is defined as

$$\tau'_{n,m+1} = t'_{m+1} - t_n \tag{5}$$

such that $t'_m \leqslant t_n \leqslant t'_{m+1}$.

The contribution of the bursts (the number of consecutive spikes) to the next spike firing in a neuron can be established by the joint probability density function (joint pdf) of firing of the next spike relative to the reference spike based on the pdf's of the kth order ISI and the next CI. The number of spikes in the burst, k, is implicitly included in the kth order ISI used in the analysis.

At lag-time τ'_y (= post-CI), given that k preceding spikes have fired in the reference spike train before the reference spike at lead-time τ_x (= pre-ISI), is given by

$$P(\tau_x, \bigcap \tau'_y) = \frac{\sum_{n=1}^{N_A - k} \delta(t_n - t_{n-k} - \tau_x)\delta(t'_{m+1} - t_n - \tau'_y)}{\sum_{n=1}^{N_A - k} \delta(t_n)},$$

$$= \frac{\sum_{n=1}^{N_A - 1} \delta(\tau_n^k - \tau_x)\delta(\tau'_{n,m+1} - \tau'_y)}{N_A - 1}, \tag{6}$$

$$\forall t_n, t'_m \quad \text{such that } t'_m \leqslant t_n \leqslant t_{m+1} \text{ and } t_{n-1} < t_n,$$

where τ_x is the "lead-time" and τ'_y is the "lag-time" as defined in conventional correlation terminology.

We represent this burst firing kth order joint-pdf by a two-dimensional probability density plot similar to the plots for a single neuron in the joint interspike interval (JISI) analysis [4], "return map" analysis [5,6], the joint interspike interval difference (JISID) analysis [1], or the two-dimensional plot for two-neuron pair for C-I analysis [7], doublet analysis [8], and temporal integration analysis [9].

This two-dimensional burst firing joint-pdf is obtained by plotting the kth order pre-ISI vs. post-CI. The density of the points in this two-dimensional plot represents the joint-pdf. Alternatively, a three-dimensional joint-pdf graph can be used to visualize the point density by constructing a two-dimensional histogram based on the distributed points on the x–y plane.

In order to reveal the difference between the correlated spike firing with temporal integration and without temporal integration (i.e., with bursts and without bursts) a "difference joint-pdf plot" can be constructed by subtracting the above conditional joint pdf from the baseline "unconditional" joint pdf. The unconditional joint pdf is obtained by forming the joint-product of the pre-ISI and post-CI distributions.

3. Theoretical interpretations

The number of spikes in a burst, $k + 1$, is implicitly included in the kth order pre-ISI vs. CI analysis, because the temporal integration period used in the analysis before the spike is correlated with the next spike firing is given by the kth pre-ISI. Therefore, the joint-pdf of the kth order graph represents the potential contribution of k consecutive spikes summated temporally before the next spike is fired. If the joint-pdf of the kth order pre-ISI vs. CI does not differ from the joint-pdf of the $(k - 1)$th order pre-ISI vs. CI, then the additional spike does not significantly add to the contribution (correlate) to the next spike generated.

By iterating this analysis from the first-order pre-ISI, the second-order pre-ISI up to the kth order pre-ISI until the joint-pdf does not differ significantly from the previous one, we can deduce that $k+1$ spikes are involved in the burst that are potentially summated temporally to produce the next spike firing.

4. Results

The three-dimensional distribution of the "difference joint-pdf" provides a better representation of the contribution of the burst to the next spike firing by subtracting the baseline pdf that is due to mere chance coincidence in the correlation. It is important to correct for the chance correlation to eliminate the null hypothesis of uncorrelated spike events due to random coincidence. With the difference joint-pdf, the comparison between the joint-pdf of the kth order pre-ISI vs. CI and the joint-pdf of the $(k-1)$th order pre-ISI vs. CI can easily be made.

When this conditional probability of spike firing is subtracted from the baseline uncorrelated conditional probability, the level of excitation or suppression of firing in relation to the preceding summated spikes can be extracted.

Furthermore, the burst period can be obtained from the kth order pre-ISI vs. CI plot. A ridge indicates that there are $k+1$ spikes in the burst that correlate with the next spike generation. The width of the ridge indicates the bursting period. The number of spikes contributing to the burst can be deduced from the ridge found in the kth order joint-pdf. Specifically, if a ridge is found in the kth order joint pdf, then $k+1$ spikes are required to summate in order to generate a spike by burst.

5. Summary

A burst firing spike train analysis is introduced to detect the statistical contribution of burst to the next spike firing. It provides a method to detect the number of spikes in the burst that correlates with the next spike generation. The joint-pdf provides an estimate of this correlated firing probability. The difference joint-pdf provides the probability of firing in relation to the incoming burst corrected for mere chance coincidence.

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David C. Tam is an associate professor at the University of North Texas. He holds a Ph.D. in physiology, and three B.S. degrees in computer science, physics and astrophysics, all from the University of Minnesota. His current research interest is developing statistical multiple spike trains analysis techniques and applying these analytical methods to both simulated and experimental neurophysiological data to understand the signal processing functions of the central nervous system (CNS) as well as extracting the encoding schemes used by the CNS.