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A spike train analysis for detecting temporal integration in neurons

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Abstract

A multi-unit spike train analysis technique is developed to deduce the number of incoming spikes that are temporally integrated to produce the next spike firing by examining the dependency of spike firing in a given neuron with respect to the sequence of firings in another neuron. This analysis considers the contribution of temporal summation of multiple spikes in one neuron that is correlated to the probability of spike firing in another neuron. These simulation results show that the analysis can extract the number of spikes and the duration of temporal integration. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Spike train analysis; Temporal integration; Correlation analysis

1. Introduction

We present a new multi-unit spike train analysis technique to detect the contribution of temporal integration to the generation of spikes in neurons. This spike train analysis provides an efficient method to deduce the likelihood of spike generation in one neuron that is correlated with the temporal integration of incoming spikes from another neuron. Although temporal integration is a well-known phenomenon in neurophysiology, the signal processing functions of temporal integration 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 spike generation probability can be correlated with temporal integration based on spike

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trains recorded extracellularly from neurons. This enables experimentalists to study the contribution of temporal integration in neural processing without a need for intracellularly recording from multiple neurons to obtain the subthreshold potentials that deduce the contribution of temporal integration.

The present analysis introduced in this paper establishes the spike firing probability conditioned on the temporal integration period of *multiple* incoming spikes. This analysis estimates the conditional probability by establishing the covariant statistics of the multiple interspike interval (ISI) and cross-interval (CI). In contrast, the traditional auto-correlation technique [5] and cross-correlation technique [6] establish the univariant statistics ISIs and CIs, respectively. Although other covariant statistics of the derivative measures of ISIs and CIs have also been introduced to analyze the spike trains, such as the scaled cross-coincidence histogram [3], the cross-covariance histogram [4], the joint peri-stimulus time histogram [1], the cross-interspike-interval histograms [11,12], the pre-conditional cross-interval histogram [2], and the post-conditional cross-interval histogram [13], these statistics are not specifically designed to extract the contribution of temporal integration. Specifically, the contribution of *multiple-spikes* firing to a single-spike coupled-firing is yet to be addressed. This analysis is an extension of the doublet (two spikes) integration analysis introduced earlier [10] so that the contribution of *multiple* spikes arriving within the integration period can be correlated with the spike firing.

2. Theoretical methods

Let the reference spike train, A, with a total of N_A spikes be represented by

$$f_A(t) = \sum_{n=1}^{N_A} \delta(t - t_n) \quad \forall t_n \text{ such that } t_n < t_{n+1} \tag{1}$$

and the compared spike train, B, with a total of N_B spikes be represented by

$$f_B(t') = \sum_{m=1}^{N_B} \delta(t' - t'_m) \quad \forall t'_m \text{ such that } t'_m < t'_m + 1, \tag{2}$$

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.

The first-order pre-interspike interval (pre-ISI, τ_{n-1}) relative to the nth reference spike in the reference spike train A is defined as

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

and the kth-order pre-ISI is defined as

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

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 $t'_m \le t_n \le t'_{m+1}$.

The probability of firing the next spike is given by the probability density function (pdf). The joint probability density function (joint pdf) of the next cross-spike firing in the compared neuron 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

$$\begin{aligned} P(\tau_x \cap \tau'_y) &= \frac{\sum_{n=1}^{N_A-k} \delta(t_n - t_{n-k} - \tau_x)\delta(t'_{m+1} - t_n - \tau'_y)}{\sum_{n=1}^{N_A-k} \delta(t_n)} \\ &= \frac{\sum_{n=1}^{N_A-k} \delta(\tau_n^{(k)} - \tau_x)\delta(\tau'_{n,\,m+1} - \tau'_y)}{N_A - k} \\ &\qquad \forall t_n, t'_m \text{ such that } t'_m \le t_n \le t_{m+1} \text{ and } t_{n-1} < t_n, \end{aligned} \tag{6}$$

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

The joint pdf can be represented graphically by a two-dimensional function displayed in an xy-plot. Traditionally, the xy-plot representing the numerator of (6) is used in most spike train analyses. This representation is similar to the plots in the joint interspike interval (JISI) analysis [7] or "return map" analysis [8,9], pre-conditional cross-interspike-interval analysis [12] and post-conditional cross-interval analysis [10,13].

A "pre-ISI vs. post-CI scatter plot" is produced by taking each spike in the reference spike train as the reference spike and plotting the corresponding coordinate (τ_x, τ'_y) on the xy-plot. A three-dimensional "pre-ISI vs. post-CI joint pdf plot" can also be obtained to visualize the distribution by building a two-dimensional histogram from the scatter plot.

3. Theoretical interpretations

The spike firing probability that is correlated with the temporal integration period can be obtained from the three-dimensional distribution. A horizontal "ridge" indicates that temporal integration is correlated with the next spike generation. The "length" of the ridge represents the duration of the temporal integration period. The number of spikes contributing to the temporal integration 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 temporal integration.

4. Simulation results

To illustrate how this analysis can be used to extract the number of spikes contributing to temporal integration, Fig. 1 shows the "second-order pre-ISI vs. post-CI joint pdf plot" for neuron A (the reference neuron) correlated with neuron B (which is driven by neuron A) with a discrete well-defined integration period. A narrow horizontal ridge is found parallel to the x-axis (the pre-ISI axis) in this plot. The length of this ridge reveals the temporal integration period that is correlated with the next spike firing. It lasts between 5 and 35 ms. This is the period in which multiple incoming spikes are integrated before a spike is generated

The narrow ridge of high probability of firing corresponds to the 2.5 ms in the y-axis (the post-CI axis). This suggests that the two neurons are tightly coupled at 2.5 ms latency, but are not unlikely to be coupled at other latencies. Thus, this analysis reveals the coupling between the two neurons as well as the duration of integration for spike generation.

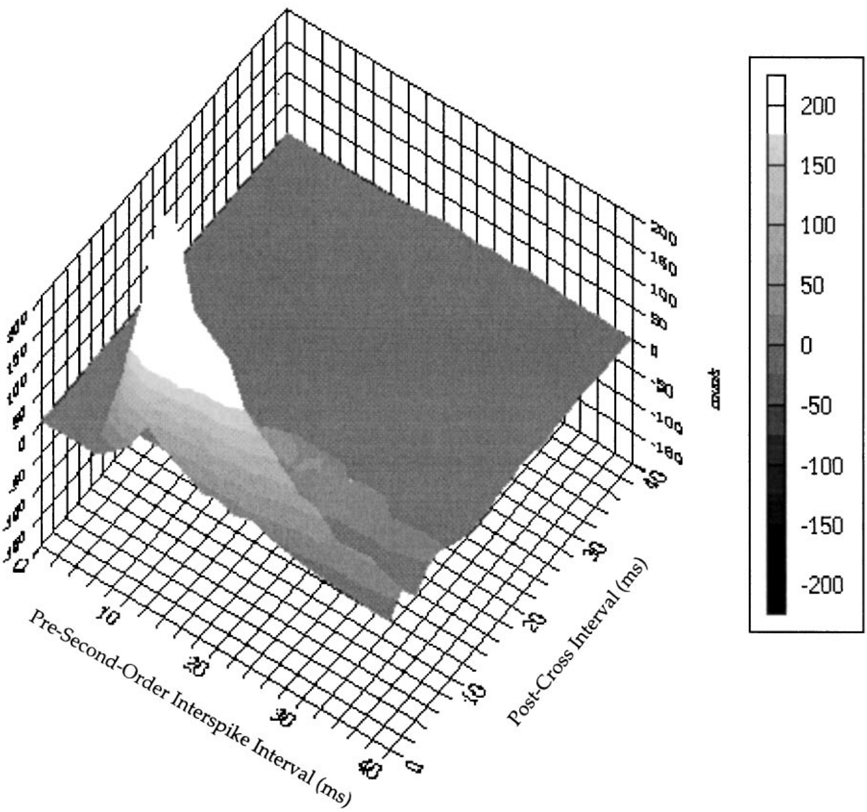

Fig. 1. Second-order pre-ISI vs. post-CI joint pdf plot for neuron A (the reference neuron) correlated with neuron B (which is driven by neuron A) with a discrete well-defined integration period shown by the narrow ridge of increased conditional probability of spike firing.

The number of spikes involved in temporal integration is also quantified by this analysis. In this case, a ridge is found in the second-order joint pdf plot, which indicates that three ($k+1$, where $k=2$) spikes are needed to produce this temporal integration.

5. Conclusions

We present a new spike train analysis technique to extract the temporal summation of multiple consecutive spikes contributing to the next spike firing. These simulation results show that not only the temporal integration period can be extracted from this method, but also the number of spikes required for this integration.

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