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A multi-unit spike train analysis for quantifying phase relationships of near-synchrony firings

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Abstract

A multiple single-unit spike train analysis technique is introduced to quantify the phase relationships of spike firings in a subset of three neurons within a neural network. Synchronized firings in neurons had been implicated in neural processing, yet the phase relationships between firing of neurons may also be important for processing. A phase-plane plot is used to determine the phase-locking and phase-shifting characteristics of neural firings among this set of three simultaneously recorded neurons. The trajectories of points in the three-neuron phase-plane provide a signature of the phase-shift characteristics in these neurons participating in synchronized firing. © 2001 Published by Elsevier Science B.V.

Keywords: Spike train analysis; Phase relationship; Near synchrony

1. Introduction

Recently, there have been increasing interests in neuroscience to apply spike train analysis to detect the relationship of spike firings among neurons. A number of novel spike train analyses have been introduced recently to detect the spike firing patterns [2,7,8].

Synchronized firing had been implicated in the processing of neural signals within a network. Yet the phase relationship among the firings of different neurons may also be important in the neural processing, since synchronized firings are often referred to near synchrony within a small finite time-window rather than absolute simultaneity of firings within a millisecond.

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The spike train analysis technique introduced in this paper is developed to address the specific phase relationship of spike firings that may be characteristic of a particular synchronized firing pattern. A two-dimensional phase-plane plot is used to quantify the phase relationships among three simultaneously recorded neurons. The trajectory of the points in this three-neuron phase-plot will be used to characterize how the phase relationship among these neuron changes in time, thus providing a signature of the coupled-firing relationships among them.

2. Overview of the spike train analysis

In summary, this three-neuron spike train analysis is a graphical quantitative measure based on the phase differences of spike firings among these three neurons. Let us assume that we select three neurons from a pool of neurons within a network for analysis first, and then apply the same analysis for all neurons within the network systematically. Let the three selected neurons be A, B and C. The time stamp of each spike is recorded for each neuron.

The phase difference between the spike firings of neurons A and B can be quantified as the lead time or lag time depending on sign of the time difference between neuron A and neuron B's firing. [For simplicity of terminology, we will use the term "phase difference" to represent the "time difference" between the neurons' firings, even though technically speaking phase difference refers to the phase angle of the firing cycle rather than the time, in accordance with the usage of the intuitive term phase plot rather than time plot.] This time difference is plotted on the x-axis of the phase plot.

Similarly, the lead time and lag time between the spike firings of neurons A and C can be quantified and plotted on the y-axis of the phase plot. Thus, the lead time and lag time between the spike firings of neurons B and C with respect to neuron A can be graphically represented in a two-dimensional plot rather than a three-dimensional plot.

This phase-plane analysis is different from the "snow-flake diagram" of Perkel et al. [3] since it requires two axes rather than the three-axis snow-flake representation. It is different from the joint-peri-stimulus time histogram (JPSTH) of Aertsen et al. [1] since it does not require any external stimulus to the network, and the origin of the plot does not represent the onset of the stimulus as in the JPSTH. It is different from the generalized cross-correlogram in that only the time relationships of the succeeding spikes among neurons are plotted to quantify the near synchrony of spike firings only, whereas the generalized cross-correlogram correlates all spike occurrences. It is different from the joint-interspike (JISI) analysis of Rodieck et al. [4] or the nonlinear analysis return map [5,6] since JISI and return-map analyses describe the timing relationship of a single neuron rather than three-neuron within the phase plot.

3. Theoretical methods

Let there be three spike trains, $a(t)$, $b(t)$, and $c(t)$, recorded simultaneously. Let $a(t)$ be the reference spike train with a total of N spikes represented by

$$a(t) = \sum_{n=1}^{n=N} \delta(t - t_n) \tag{1}$$

and the compared spike trains, $b(t)$ and $c(t)$ with a total of L and M spikes, respectively, be represented by

$$b(t) = \sum_{l=1}^{l=L} \delta(t - t_l),$$
$$c(t) = \sum_{m=1}^{m=M} \delta(t - t_m), \tag{2}$$

where t_n, t_1 and t_m are the occurrence times of nth, lth and mth spikes in spike trains $a(t)$, $b(t)$ and $c(t)$, respectively, and $\delta(t)$ is a delta function denoting the occurrence of a spike at time t.

The cross-interval, CI, between two neurons can be defined as the time interval between spikes in these two spike trains. Let us also define the "pre-cross-interval" as the CI before the reference spike, and the "post-cross-interval" as the CI after the reference spike. Then, the kth order pre-cross-intervals relative to the nth reference spike in the reference spike train, $a(t)$, with respect to spike trains $b(t)$ and $c(t)$ are defined as

$$\tau'_{n,-k} = |t'_{l-k+1} - t_n| = t_n - t'_{l-k+1}\,,$$
$$\tau'_{m,-k} = |t'_{m-k+1} - t_n| = t_n - t'_{m-k+1}\,, \tag{3}$$

respectively. These joint pair of number will be plotted as the coordinate in the two-dimensional phase plot. The post-cross-intervals can similarly be defined.

Let the probability density function (pdf), of the kth order pre-CI between the compared train, $b(t)$, and the nth spike in the reference train $a(t)$ be defined as

$$f(\tau'_{i,-k}) = \int_{-\infty}^{\infty} \delta(t - \tau'_{n,l,-k})\,\mathrm{d}t \quad \forall n. \tag{4}$$

taking all spikes into account, and the pdf of the kth order pre-CI between the compared train, $c(t)$, and the nth spike in the reference train $a(t)$ is similarly defined as

$$f(\tau'_{j,-k}) = \int_{-\infty}^{\infty} \delta(t - \tau'_{n,m,-k})\,\mathrm{d}t \quad \forall n. \tag{5}$$

4. Theoretical interpretations

The relationship between how the sequential near-synchronous firings in the compared neurons b and c can be characterized by the trajectories of points in the two-dimensional phase plot. Clustering of points indicates that the neurons are phase-locked together at a specific lag-time (or lead-time) as revealed by the coordinate of the points.

Vertical band of points indicates tight coupling between neurons a and b but not with neuron c . Horizontal band of points indicates tight coupling between neurons a and c but not with neuron b. Thus, the near-synchrony relationship can be characterized based on the time differences between spike firings in these neurons.

If the points are found to follow a cyclic trajectory in the phase plot, it indicates that the three neurons are changing their firing relationships in a coordinated fashion that is dynamical with time. This may represent specific neural processings that are time varying rather than constant.

5. Results

The results of the phase-plot analysis as described above can be used to deduce the dynamical firing relationship among a three-neuron group. The signature of the phase relationship (or the time differences in the lead time and/or lag time) can be characterized uniquely in the phase plot based on the trajectory of the points. Thus, the intriguing fine detail of firing times in near-synchronous firings may represent more specific and precise neural processing than formerly recognized. The three-dimensional pdf's (representing the density of points) in the phase plot provide the conditional firing probability at those lead times and lag times.

6. Summary

A phase-plot analysis is introduced to describe the firing relationships among three neurons. The mathematical descriptions of the multiple single-unit spike train analysis are given. The phase-plane analysis provides a graphical representation of the correlation of spike firings among three neurons as characterized by the clustering of points in the graph representing the pdf's.

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Dr. 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.