Measuring synchrony of spiking neurons with correlation functions: Effect of different time constants

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Abstract

It was pointed out recently that the magnitude of the main peak in a shuffled cross-correlogram is not always a good indicator of synchrony. Here a synchrony of two spiking neurons firing periodically is studied using both regular (appropriately normalized) and shuffled cross-correlation functions. The dependence of both functions on different time constants (membrane, synaptic, current correlations) is determined. Based on this and on another argument it is suggested that the normalized regular cross-correlogram provides more suitable measure of synchrony in cases involving spiking neurons firing periodically.

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It is common to measure neural synchrony using cross-correlation functions. Brody [1] argued that caution must be taken when using one of such functions, namely shuffled cross-correlogram. He pointed out that the hight of the main peak in this function is not always a good measure of synchrony. As a remedy, Brody suggested that also other measures (like autocorrelation functions) should be taken into account to judge about synchrony. However, his analysis does not provide much information in the case of fast neural oscillations, such as the gamma rhythm present in many parts of the cortex. In particular, one would like to know how the basic characteristics of the main peak depend on different time constants and what is the relationship between those characteristics and the precision of synchrony.

This paper addresses these questions and additionally it suggests that in the case of rapid periodic neural firing a better and more natural measure of synchrony provides a regular cross-correlogram that is appropriately normalized. We define this quantity $C_{12}^{nor}(\tau)$ in the following way:

$$C_{12}^{nor}(\tau) = \frac{\int dt \ < s_1(t+\tau)s_2(t) >}{\sqrt{< M_1 >< M_2 >}}, \tag{1}$$

where $s_i(t)$ is a signal characterizing the occurance of a spike in neuron i ($i = 1, 2$) at time t and $s_i(t) = (1/\sqrt{\pi}\sigma) \sum_k \exp[-(t - t_i^{(k)})^2/\sigma^2]$, where σ is a temporal width of a spike and $t_i^{(k)}$ is a time of its occurance. $< M_i >$ is average number of spikes fired by neuron i in a certain time interval T, i.e. $< M_i >= \int dt < S_i >$. Symbol $< ... >$ denotes averaging over trials or equivalently over fluctuations in the input current. The value of the quantity $C_{12}^{nor}(0)$ is restricted to the interval (0,1), and the degree of synchrony is maximal if $C_{12}^{nor}(0) \mapsto 1$.

The shuffled cross-correlogram $SC(\tau)$ is defined as

$$SC_{12}(\tau) = \frac{1}{T} \int dt < \delta s_1(t+\tau)\delta s_2(t) >, \tag{2}$$

where $\delta s_i(t) = s_i(t) - < s_i(t) >$ is a fluctuation in a signal over average at time t. (One can write $SC_{12}(\tau)$ equivalently as $SC_{12}(\tau) = (1/T) \int dt < s_1(t+$

$\tau)s_2(t) > -(1/T) \int dt < s_1(t+\tau)s_2(t) >$). From the above definition, eq. (2), it is apparent that the shuffled cross-correlogram measures correlations occuring in the fluctuations in the signals. The hight of the main peak in $SC_{12}(\tau)$ is a measure of coincidence (synchrony) in the fluctuations around the average value. In the case of two neurons firing regularly in phase with the same frequency, fluctuations are small and as a consequence the main peak of SC_{12} is tiny. This happens despite the fact that such neurons have very high percentage of simultaneous spikes. Clearly, in such instances the shuffled cross-correlogram cannot be the proper measure of synchrony.

The normalized regular cross-correlogram is advantageous over the shuffled cross-correlogram in several respects. First, the hight of the main peak in it is directly proportional to the ratio of simultaneously occuring spikes ("synchronous" spikes) in two neurons to the total number of fired spikes. Second, the width of the main peak is a direct measure of the precision of synchrony (the wider the peak the more sloppy synchrony is). This is important when we deal with fast oscillations and 1 *msec* synchrony. Third, there is no need to consider additional quantities as in the case of the shuffled cross-correlogram.

As an example consider two local circuits, each containing two integrate-and-fire neurons (one inhibitory and one excitatory) firing periodically. The circuits are not synaptically connected but they receive (excitatory neurons only) the same *average* amount of excitation. This excitation comes from non-local neurons and possibly from a stimulus. The total amount of excitation received by the excitatory neuron in each circuit is greater then the amount of local inhibition. The magnitude of the excitatory current fluctuates in both circuits and this is described by a current-current correlation function $< \delta I_i(t+\Delta t)\delta I_j(t) > \sim \exp(-\Delta t/\tau_{ij})$, where τ_{ij} is a correlation time constant or a measure of "memory" in the current fluctuations between neuron i and j (when $i = j$ then τ_{ii} provides a memory for current fluctuations solely in neuron i).

Taking the above into account we are able to obtain analytic expressions [2] for $C_{12}^{nor}(\tau)$ and $SC_{12}(\tau)$. These expressions provide explicit dependence of the hight and the width of the main peak on the different time constants. It turns out that for a very small effective membrane time constant τ_m, the hight of the main peak of the shuffled cross-correlogram $SC_{12}(0) \sim \tau_m^2 \mapsto 0$. Small effective membrane time constants can be found in cases involving high level of excitation during gamma oscillations [3]. Similarly, if the correlation time constants for fluctuating excitation (τ_{12}, τ_{11}, τ_{22}) are small, we again obtain that the shuffled cross-correlogram peak $SC_{12}(0) \mapsto 0$. On the other hand, the normalized cross-correlogram $C_{12}^{nor}(\tau)$ does not display such sensitivity on the above time constants. The hight of the main peak is always pronounced when the degree of synchrony is high, regardless of the time constants. Interesting result is that the width of the main peak, corresponding to the precision of the synchrony is getting thinner as the membrane time constant τ_m and the correlation time constant τ_{12} increase.

References

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[3] R.D. Traub and R. Miles, J. Comp. Neuroscience, **2**, 291 (1995).