A STOCHASTIC FRAMEWORK FOR THE QUANTIFICATION OF SYNCHRONOUS OSCILLATION IN NEURONAL NETWORKS

Gaby Schneider and Danko Nikolić

1Dept. of Computer Science & Mathematics, University Frankfurt, Robert-Mayer-Str. 10, 60325 Frankfurt/Main, Germany
2Frankfurt Institute for Advanced Studies, University Frankfurt/Main, Germany,
3Max-Planck-Institute for Brain Research, Frankfurt/Main, Germany,
schneider@math.uni-frankfurt.de, danko@mpih-frankfurt.mpg.de

ABSTRACT

Synchronous oscillations are believed to be important for neuronal information processing. We use a stochastic model for parallel point processes to estimate the strength of synchrony in an oscillating network of neurons recorded in cat visual cortex. The model has the surprising ability to predict interactions between the neurons solely on the basis of the individual processes, i.e., the autocorrelograms. The strength of synchronization is defined as the mismatch between the predicted and the observed strength of interaction. This method has the advantage of distinguishing changes in the strength of synchrony from changes in the properties of the underlying processes. Thus, the model provides new approaches for the investigation of dynamical changes in the joint oscillatory activity of neuronal networks.

1. INTRODUCTION

The synchronization of oscillatory neuronal responses is likely to play an important role in cortical processing and is commonly investigated using pairwise cross-correlation histograms (CCHs; [1], Figure 1).

In a CCH, one uses either the height, the width or the area of the central peak to investigate the amount of synchronous firing. Such measures are then evaluated statistically by comparing to independent processes [2, 3, 4]. However, this null hypothesis of independent processes is insufficient to describe the nature of processes with a common oscillatory rhythm. Therefore, such methods can only indicate statistically significant deviations from independent processes and can thus be only related indirectly to the properties of the underlying processes.

In the present work, we use a stochastic spike-train model [5] that describes the oscillatory properties of the underlying processes and makes simple assumptions about their interactions. Therefore, the model offers a framework for relating the properties of individual processes, visible in the auto-correlation histograms (ACHs; [6]), to the properties of interactions between the processes, visible in CCHs. This allows for a direct measure of synchrony, which we will define here as the percentage of spike pairs that take part in the same rhythm.

2. THE SPIKE-TRAIN MODEL

2.1. Model assumptions

We use a spike-train model for parallel point processes called the ELO model (Exponential LOcking to a free oscillator), which is described in detail elsewhere [5]. The model assumes a global oscillatory rhythm (called the packet onset process, POP), shared across all processes and described by a stationary random walk \( (B_n)_{n \in \mathbb{Z}} \) with independent and normally distributed increments \( B_{i+1} - B_i \) with mean \( \mu \) and variance \( \sigma^2 \) (Figure 2, top line). An event in the POP marks the time points at which the firing intensities rise for all processes simultaneously (cycle onset). In each process \( j \), an onset \( B_i \) gives rise to an independent Poissonian spike packet with an expected number of spikes \( \alpha_j \) and exponentially decreasing firing intensity with time constant \( \tau_j \). With \( B_{n1} \) denoting the last onset before \( t \), the firing intensity of process \( j \) at time \( t \) is described by

\[
\frac{\alpha_j}{\tau_j} \sum_{i=-\infty}^{n_1} e^{-\frac{(t-B_i)}{\tau_j}} + \beta_j.
\]
The smaller $\tau_j$, the more densely the spikes cluster at the packet onsets (Figure 2, $\tau_1 < \tau_2$). Since the POP is shared by all processes, $\mu$ and $\sigma$ are global parameters. In contrast, $\alpha$ and $\tau$ may differ across units.

2.2. Cross-correlation function

Within this framework, the auto- and cross-correlation functions (ACF, CCF) of processes that comply with the model assumptions can be derived by decomposition of the processes into different packets (Figure 2, bottom panel). The CCF $F_{ab}(s)$ at shift $s \geq 0$ between processes $a$ and $b$ is then given by (for a proof see [5])

$$F_{ab}(s) = \frac{\alpha_a \alpha_b}{\mu(\tau_a + \tau_b)} \left( e^{-\frac{s}{\tau_a}} + \sum_{j \in \mathbb{Z} \setminus \{0\}} e^{\frac{s - \mu_j - \sigma_j^2}{2\tau_j^2}} \Phi \left( \frac{\mu_j - s - \sigma_j^2/\tau_j}{\sigma_j} \right) \right)$$

(2)

where $\Phi$ denotes the standard normal distribution function. $F_{ab}(s) = F_{ba}(-s)$, and the ACF of $a$ equals $F_{aa}$.

2.3. Relation between ACF and CCF

It follows that the CCH can be predicted directly from the properties of the individual ACHs because it depends on the same parameters. The smaller $\tau_a$ and $\tau_b$, the higher the respective ACH peaks, and the higher also the corresponding CCH peak.

This relation can be quantified with the first term of the CCF, $\alpha_a \alpha_b/(\mu(\tau_a + \tau_b)) e^{-\frac{s}{\tau_a}}$, which describes the intensity of spike pairs that belong to simultaneous packets and thus, determines the shape of the central peak. Since the level of the asymptotic baseline in a CCF is given by the product of the firing intensities, $\alpha_a \alpha_b/\mu$ (Figure 2), the fraction $f_h$ of the total peak height cut at baseline level is given by

$$f_h = \frac{\text{baseline peak height}}{\tau_a + \tau_b},$$

(3)

and by $f_h^{aa} = 2\tau_a/\mu$ in ACF$_a$. Thus, the simple relation

$$f_h = 1/2 \cdot (f_h^{aa} + f_h^{bb})$$

(4)

shows the direct relation between the height of the CCH peak and the respective ACHs peaks. We will use this relation to estimate the degree to which two processes are locked to the same oscillatory rhythm.

3. FITTING THE MODEL TO A DATA SET

3.1. Parameter estimation

We fitted the ELO model to a sample data set consisting of neuronal firing activity of 14 multi-units recorded in parallel in cat primary visual cortex under visual stimulation (stimuli are shown in Figure 7, see [7] for experimental methods). We first estimated the times of the global cycle onsets by smoothing the firing activity of all units with a Gaussian kernel. Packet onsets were identified as the points at which 60% of the maximum was reached (gray dots in the upper panel of Figure 3). This analysis suggested that independence and normal distribution of intervals between spike packets were appropriate assumptions for the POP. We then estimated the parameters by fitting the theoretical ACFs (Equation (2)) to the observed ACHs using a nonlinear least squares algorithm. As mentioned, $\mu$ and $\sigma$ were chosen to be identical in all units. The fitted ACFs corresponded well to the empirical ACHs (Figure 3, bottom panel). For stimulation condition 1, the parameter estimates were $\mu = 25.3$ ms, $\sigma = 7.3$ ms. The values of $\tau_1, \ldots, \tau_{14}$ were in the range of $3.5 - 8$ ms. Approximations for variances of the parameter estimates were derived both numerically by the least squares algorithm and by splitting the data into smaller groups. Both methods yielded comparable results, with standard errors smaller than 0.1 ms for $\mu$ and $\sigma$ and 0.1 - 0.9 ms for $\tau_1, \ldots, \tau_{14}$.

3.2. Prediction of interactions

With the parameters derived from the ACHs, we predicted the shape of each CCH by using Equation (2). In many cases, this prediction corresponded well to the empirically obtained CCH (Figure 4).

In some cases, the units showed nonstationary rate responses within trials that were different in both units (Figure 5, left panel). As a consequence, the observed CCHs were lower than those predicted from the ACHs (medium panel). Therefore, nonstationarity was taken into account by using a correction factor proposed in [5]: We described the firing rate of a unit as a step function, which we estimated from the overall firing rate across all trials, measured in windows of 200 ms (bold curves in the left panel of Figure 5). With the given rate estimates $\lambda_{1,a}, \ldots, \lambda_{k,a}$.
Figure 3. Investigation of model assumptions and parameter estimation. Upper panel: The spikes recorded in the 14 units show a joint oscillatory rhythm that can be described by independent and normally distributed intervals. Bottom: The observed ACHs (colors as in Figure 1) correspond well to the fitted ACFs (medium gray).

Figure 4. Observed CCHs (colors as in Figure 3) and theoretical CCFs (medium gray) predicted from the parameters derived from the corresponding ACHs.

and $\lambda_{1,b}, \ldots, \lambda_{k,b}$, the raw CCF prediction uses the product of the firing rates estimated from the ACHs,

$$\hat{\alpha}_a \hat{\alpha}_b = \sqrt{\sum_i \lambda_{i,a}^2} \sqrt{\sum_j \lambda_{j,b}^2}. \quad (5)$$

However, the correct prediction would be

$$r = \sum_i \lambda_{i,a} \lambda_{i,b}. \quad (6)$$

We therefore corrected each predicted CCF with the term

$$c_{ab} = r / \hat{\alpha}_a \hat{\alpha}_b. \quad (7)$$

Most correction factors ranged between 0.9 and 1 and resulted in good agreement between the predicted and the empirical CCHs (Figure 5, right panel).

Figure 5. Nonstationary rate responses along a trial need to be corrected when predicting a CCH. Left panel shows firing rates of units 4 (light gray) and 5 (dark gray) recorded in 20 trials in stimulation condition 1. Direct prediction leads to an erroneous height of the CCH (medium panel), which can be corrected with Equation (7).

4. THE DEGREE OF UTILIZED SYNCHRONY

A good agreement of the CCF predictions with some of the empirically obtained CCHs suggests that the model assumption about all units sharing the same oscillatory rhythm describes the data well. Therefore, this prediction can be used as a reference: The CCF predicted from the ACHs indicates the maximal possible strength of synchrony that can be obtained for the given pair of units. This predicted maximum depends on the ACHs in the following way: If ACHs have small peaks, the predicted CCH will also have a small peak and vice versa.

This perspective allows one to define the strength of utilized synchrony, which is the degree to which the observed CCH peak corresponds to the peak predicted under the above assumption that the units share the same rhythm (100% locking). Indeed, a number of CCHs showed lower peaks than predicted from their ACHs (Figure 6, bottom right panel). This indicates that the units utilize less than 100% of their potential to synchronize, indicating in turn that oscillation shared across units is weaker than the oscillation of each unit individually.

Within the spike-train model, utilized synchrony can be estimated as follows (Figure 6, upper panel): We assume that the units share the same POP only sometimes (A), while on other occasions they are locked to independent POPs with the same parameters (B). The resulting CCH is a linear combination of the CCF predicted from the ACHs (black curve in the second panel) and a flat correlogram resulting from independent processes:

$$CCH = \vartheta \cdot CCF_{predicted} + (1 - \vartheta) \cdot baseline. \quad (8)$$

The parameter $\vartheta$ indicates the percentage of spike pairs that share the same oscillatory rhythm. This number can be estimated with a least squares approach when comparing the predicted CCF to the observed CCH. When applying this measure to stimulation condition 1, the estimates of $\vartheta$ ranged between $0.4 - 0.9$, with standard errors of about 0.03. Analogous results were obtained for the other stimulation conditions.
4.1. Changes in utilized synchrony across stimuli

This method allows one to investigate whether the degree of utilized synchrony changes across stimulation conditions. Even if ACHs do not change and thus the potential to synchronize is constant, it is possible that units change utilized synchrony. This directly affects the CCH peak and can thus account for classical results based on measures of the peak height [4]. For example, we found that utilized synchrony was increased for a stimulus with one moving bar, as compared to two conflicting bars (Figure 7), which is consistent with previous reports, e.g. [8].

However, it is also possible that utilized synchrony provides a different kind of information than the classical measures. An indication of such information is shown in Figure 7 where utilized synchrony could distinguish between two groups of units, Group A (orientation preference 30°/210°) showing much higher utilization of the potential to synchronize for stimulus 5 than Group B (orientation preference 150°/330°), while Group B synchronized more strongly in stimulus 6. The functional significance of these results is yet to be investigated. However, it indicates that utilized synchrony might provide important information about the dynamics of neuronal oscillation.

5. DISCUSSION

We use a stochastic model that describes parallel processes with a joint oscillation and that can predict a CCH directly from the ACHs. By comparing the observed and the predicted CCHs, we propose to estimate to which degree units utilize their potential to synchronize. This allows one also to distinguish whether changes in a CCH are due to changes in the individual processes or to changes in utilized synchrony. The method may therefore provide new information on the dynamics of neuronal synchronization.

6. REFERENCES


