A new correlation-based measure of spike timing reliability

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Abstract

We introduce a new correlation-based measure of spike timing reliability. Unlike other measures, it does not require the definition of *a posteriori* "events". It relies on only one parameter, which directly relates to the timescale of spike timing precision. We test the measure in a complex reliability classification task, where model neurons of different dynamics are driven by stimuli with different frequency content and amplitudes. We find that the measure is efficient and faithful in characterizing spike timing reliability, and that it performs as well as the widely used histogram-based measures.

1 Introduction

The precise and reliable timing of spikes is the focus of many recent studies (see for example (Mainen and Sejnowski, 1995; Hunter *et al.*, 1998)). Different measures have been used to quantify the reliability of spike timing in the context of various neuronal systems. Most of them are initially based on the post stimulus histogram (PSTH), but differ in the way the reliability is calculated from the histogram. Histogram measures have at least two independent parameters, both of which have to be carefully adapted. In this study, we introduce a correlation-based measure that characterizes spike timing reliability. It performs equally well as the histogram measures, but relies only on one, very intuitive parameter. We apply it to a complex reliability classification task, where stimuli have different frequency content, different amplitudes and where the dynamics of the spike generation are varied. The spike data is obtained from model neurons with different leak channel densities. The results are compared to those that are obtained with a histogram measure.

2 Methods

2.1 The Reliability measures

The reliability is calculated from the spike trains that a cell elicits in response to repeated presentations of the same stimulus. For histogram measures, the PSTH or a smoothed version of it is used to define firing "events" and reliability is then extracted as the ratio between spikes occuring within events and the total number of spikes. The definitions of events vary widely, and the subtle differences between event definitions make it difficult to compare the results. Most studies apply a threshold to the PSTH, singling out time bins with spike counts above threshold as associated to events. The threshold values can be defined in absolute terms, relative to the number of trials contributing to the PSTH, as a percentage of the peak (or the minima) in the histogram, or relative to the mean firing rate of the neuron. All these measures may represent reliability faithfully, if carefully adapted to the neuronal data. However, histogram-based measures are not sensitive to slow variations in firing rate across cell trials, which might be characteristic of certain cells (e.g. stochastic switches between bursts and single spikes). A correlation measure, because it relies on individual trials rather than their average, is sensitive to such variations.

We define the correlation measure as follows: The spike trains obtained from N repeated presentations of the same stimulus are smoothed with a Gaussian filter of a given width, pairwise correlated, and the normalized value of the correlation is averaged over all pairs. Thus no explicit definition of events is necessary. If we represent the smoothed spike trains $\vec{s_i}(i = 1, ..., N)$ as individual vectors, the measure R_{corr} reads

$$R_{corr} = \frac{2}{N(N-1)} \sum_{i=1}^{N} \sum_{j=i+1}^{N} \frac{\vec{s_i} \cdot \vec{s_j}}{|\vec{s_i}||\vec{s_j}|},$$

and can mathematically be interpreted as the averaged value of the cosine of the angle between the smoothed spike vectors. The normalization ensures that $R_{corr} \in [0; 1]$. The only parameter of this measure is the width of the Gaussian filter, which defines the timescale of reliability.

2.2 The model

In order to test the correlation measure, a one-compartmental pyramidal neuron was implemented in NEURON. It includes a fast sodium current, a delayed-retifier potassium current, a leak current, a persistent sodium current, and a slow potassium current.

The stimuli consist of three additive components: a DC current which is kept fixed over all trials, a sine wave (50 different frequencies and three different amplitudes are tested), and Gaussian noise of small variance (representing the membrane noise of the cell). For each frequency and

amplitude combination, spikes for $N = 20$ repeated trials of stimulus presentation are recorded. The stimuli only differ in the realization of the Gaussian noise. Both, histogram and correlation reliability measures, are then applied to characterize the reliability of spike timing for one set of N trials. The reliability values of all sets of stimuli can be summarized in an Arnold plot, which depicts the reliability as a function of the frequency and amplitude of the sine component of the stimulus for one model cell.

The reliability of spike timing depends on the frequency content of the stimulus (Hunter *et al.*, 1998; Fellous *et al.*, 2001). We therefore expect that a plot of reliability as a function of the frequency and the amplitude of the sine component (Arnold plot), will reveal frequencies, where spike timing is especially reliable (resonance frequencies), see also Fig. 1. A faithful reliability measure should capture the resonances and also show an increase of reliability with higher amplitudes of the sine waves.

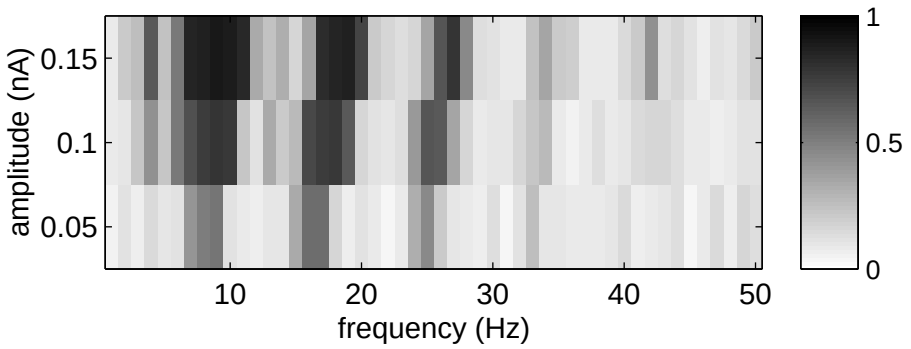

Figure 1: *Arnold plot showing the reliability (colorcoded) using the new correlation-based measure. The resonance frequencies are clearly visible at all three amplitudes. Note also that reliability increases with amplitude.*

3 Results

We constructed surrogate data sets and compared the correlation-based measure to the histrogram-based measure. We paid particular attention to the influence of missing spikes, additional noisy spikes, and spike jitter. Overall, because the correlation-based measure does not rely on the definition of events, it was found to be more robust and show smoother degradation than the histogram-based measures.

Spike timing reliability for the set of stimuli described above was evaluated with both the correlation and the histogram measures. The parameters of the measures were adapted to give similar values of reliability for all sets of stimuli and at the same time to represent the frequency and amplitude dependence expected from the raster plots. For the histogram measure this meant adaptation of both, the bin size and the event threshold (which was implemented as a percentage

of the peak in the PSTH). For the correlation measure only the width of the Gaussian smoothing filter was adjusted. We found quantitatively that both measures performed equally well and the resonance frequencies were clearly distinguishable.

As expected, we observed Arnold tongues (tongue-shaped regions of higher reliability). We found that the reliability at a resonance frequency was lower for smaller amplitudes and became more pronounced at higher amplitude levels. The location of the Arnold tongues in frequency space defined the resonance frequency. The most pronounced resonance was found at a 1:1 locking to the stimulus, where each maximum of the sine wave elicited one spike. The other resonances occured at multiples of the dominant resonance frequency (see Fig. 1).

We also varied the density of the leak channels in the model neuron. Using both measures, we observe a shift in the dominant resonance frequency from higher to lower frequencies with rising leak channel densities.

4 Conclusions

The correlation measure is well suited to faithfully characterize spike timing reliability. It has proven stable over a broad range of frequency content, amplitudes and also over cells with different intrinsic properties, as modeled by various channel densities. It only relies on one parameter, which determines the jitter of individual spikes that is still considered reliable and therefore related to the timescale of spike timing precision. The measure is computationally efficient (in case of a very high resolution of the spike times, bin width can be traded for filter width and we find that it is in principle not necessary to average over more than N randomly chosen pairs of trials, instead of all $N(N-1)/2$ pairs). Interestingly, the dominant resonance frequency shifts from higher to lower values when the leak channel density increases. Biologically, neuromodulators might change the effective channel density of a neuron (including the leak) and thus tune the resonance frequency to the dominant frequency in the input. Using the correlation measure, we will explore the functional significance of such frequency shifts in a different study.

References

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