On similarity measures for spike trains

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Abstract. A variety of (dis)similarity measures for one-dimensional point processes (e.g., spike trains) are investigated, including the Victor-Purpura distance metric, the van Rossum distance metric, the Schreiber *et al.* similarity measure, the Hunter-Milton similarity measure, the event synchronization proposed by Quiroga, and the stochastic event synchrony measures (SES) recently proposed by Dauwels *et al.*

By analyzing surrogate data, it is demonstrated that most measures are not able to distinguish timing precision and event reliability, i.e., they depend on both aspects of synchrony. There are two exceptions: with appropriate choice of parameters, event synchronization quantifies event reliability, independently of timing precision; the two SES parameters quantify both timing precision and event reliability separately. Before one can apply the (dis)similarity measures (with the exception of SES), one needs to determine potential lags between the point processes. On the other hand, SES deals with lags in a natural and direct way, and therefore, the SES similarity measures are robust to lags.

As an illustration, neuronal spike data generated by the Morris-Lecar neuron model is considered.

1 Introduction

In the last years, the problem of detecting correlations between neural signals has attracted quite some attention in the neuroscience community (e.g., [14]). Several studies have related neural synchrony to attention and cognition (e.g., [2]); recently, it has been demonstrated that patterns of neural synchronization flexibly trigger patterns of neural interactions [18]. Moreover, it has frequently been reported that abnormalities in neural synchrony lie at the heart of a variety of brain disorders such as Alzheimer's and Parkinson's disease (e.g., [15]).

In this paper, we focus on the synchrony of pairs of spike trains. We consider two different aspects of synchrony: timing precision and reliability. Those concepts can be understood from the following analogy; when you wait for a train in the station, the train may come at the station or it may not come at all, for example, it may be out of service due to some mechanical problem. If the train comes, it may or may not be on time. The former uncertainty is related to reliability, whereas the latter is related to precision.

We will compare and assess a variety of classical and recently proposed spiking synchrony measures, including the Victor-Purpura distance metric [17], the van Rossum distance metric [16], the Schreiber *et al.* similarity measure [12], the

Hunter-Milton similarity measure [7], the event synchronization measure proposed in [10], and the stochastic event synchrony measures (SES) proposed by Dauwels *et al.* [3].

We assess those measures by means of surrogate data, which allows us to investigate the statistical properties of those measures; such study, albeit important, does not seem to have been carried out before. Next we apply those measures to quantify the spiking synchrony of Morris-Lecar neurons. (This paper summarizes some of the results, we refer to [4] for a longer manuscript.)

This paper is organized as follows. In the next section, we review the (dis)similarity measures for one-dimensional point processes considered in this study. In Section 3 we investigate the robustness and reliability of those (dis)similarity measures by means of surrogate data. In Section 4 we apply those measures to quantify the firing reliability of Morris-Lecar type I and type II neurons. We offer some concluding remarks in Section 5.

2 Review of Similarity Measures

In this section, we review the (dis)similarity measures considered in this paper. All measures are applied to pairs of point processes x and x'. For the sake of definiteness, we will consider point processes in time, e.g., spike trains.

2.1 Victor-Purpura Spike Train Metric

The distance metric D_V of [17] defines the distance between two point processes as the minimum cost of transforming one point process into the other. This transformation is carried out by combining three basic operations: event insertion, event deletion, and event movement. The cost of deleting or inserting of an event is set to one, whereas the cost of moving an event in time is proportional to the time shift. The inverse of the proportionality constant C_V , denoted by $\tau_V = 1/C_V$, defines the time scale of distance metric D_V . If and only if the point processes x and x' are identical, the distance metric $D_V = 0$.

2.2 Van Rossum Similarity Measure

In the approach of [16], the two point processes are converted into continuous time series. In particular, each event of x is convolved with an exponential function $\exp(t-x_k/\tau_R)$ (with $t>x_k$), resulting in the time series s(t). Likewise each event of x' is convolved with this exponential function, leading to the time series s'(t). From the time series s(t) and s'(t), the van Rossum distance measure [16] is computed as:

$$D_R = \frac{1}{\tau_R} \int_t [s(t) - s'(t)]^2 dt.$$
 (1)

Note that $D_R(\sigma_S) = 0$ if and only if x and x' are identical. The time scale of this distance measure is determined by the time constant τ_R .

2.3 Schreiber et al. Similarity Measure

Also in the approach proposed in [6] and [12], the two point processes x and x' are first convolved with a filter, resulting in time series s(t) and s'(t). The

filter may for example be exponential [6] or Gaussian [12], and it has a certain width τ_S . Next the pairwise correlation between the time series s(t) and s'(t) is computed:

$$S_S = \frac{\int_t s(t)s'(t) dt}{\sqrt{\int_t s^2(t) dt} \sqrt{\int_t s'^2(t) dt}}.$$
 (2)

It is noteworthy that the width τ_S of the filter defines the time scale of interaction between the two point processes. We also wish to point out that if and only if x and x' are identical, we have $S_S = 1$.

2.4 Hunter-Milton Similarity Measure

An alternative similarity measure was proposed in [7]. For each event x_k , one identifies the nearest event $x'_{k'(k)}$ in the point process x'. The degree of coincidence between those two events is determined as $d(x_k) = \exp(-|x_k - x'_{k'(k)}|/\tau_H)$. Along the same lines, one identifies for each $x'_{k'}$ the nearest event $x_{k(k')}$ in the point process x, and determines the degree of coincidence $d(x'_{k'})$. The similarity S_H between x and x' is then computed as:

$$S_H = \frac{\frac{1}{N} \sum_{k=1}^{N} d(x_k) + \frac{1}{N'} \sum_{k'=1}^{N'} d(x_k')}{2}.$$
 (3)

The parameter τ_H sets the time scale for event coincidence. If x and x' are identical, we have $S_H = 1$.

2.5 Event Synchronization

Event synchronization [10] defines similarity in terms of coincident events. Two events are considered to be coincident if their timing offset is smaller than a maximum lag τ_Q . This lag can be extracted automatically from the point processes x and x':

$$\tau_Q(k, k') = \min(x_{k+1} - x_k, x_k - x_{k-1}, x'_{k'+1} - x'_{k'}, x'_{k'} - x'_{k'-1})/2.$$
 (4)

One computes the number of times an event appears in x shortly after an event appears in x':

$$d(x|x') = \sum_{k=1}^{N} \sum_{k'=1}^{N'} J_{kk'}, \tag{5}$$

where

$$J_{kk'} = \begin{cases} 1 & \text{if } 0 < x_k - x'_{k'} \le \tau_Q \\ 1/2 & \text{if } x_k = x'_{k'} \\ 0 & \text{else.} \end{cases}$$
 (6)

Similarly one can define d(x'|x), and eventually, event synchronization is determined as:

$$S_Q = \frac{d(x|x') + d(x'|x)}{\sqrt{NN'}}. (7)$$

If and only if all events in x and x' are coincident, we have $S_Q = 1$.

2.6 Stochastic Event Synchrony

Stochastic event synchrony (SES) [3] considers two point processes x and x' as synchronous if they are identical apart from: (i) a time shift δ_t ; (ii) small deviations in the event occurrence times; (iii) a few event insertions and/or deletions.

At the heart of SES lies a statistical model $p(x, x', \delta_t, s_t)$ that describes how the two point processes x and x' may be generated, as illustrated in Fig. 1: one first generates a point process v of length ℓ , next one makes two identical copies of v and shifts those over $-\delta_t/2$ and $\delta_t/2$ respectively; the events of the resulting point process are randomly shifted (with variance $s_t/2$), and some of those events are deleted, independently with probability p_d (indicated by minus sign), resulting eventually in x and x'. As a result of those deletions (or equivalently, insertions), some events in x are non-coincident (marked in red), i.e., they can not be associated to an event in x' and vice versa.

More specifically, SES is defined as the triplet (δ_t, s_t, ρ) , where ρ is the percentage of non-coincident events. We will denote the standard deviation of the (event) timing jitter by σ_t , and hence $s_t = \sigma_t^2$. The SES parameters are computed by conducting statistical inference in the model $p(x, x', \delta_t, s_t)$, more precisely, by coordinate descent and dynamic programming [3].

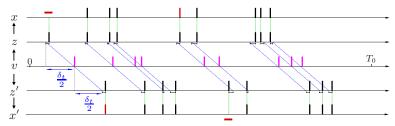


Fig. 1. Stochastic event synchrony: procedure relating x to x'.

2.7 Discussion

It is noteworthy that the above mentioned approaches do not discretize the time axis; therefore they avoid the tricky issue of choosing the bin width.

Most of the above measures depend on a parameter that defines the time scale of the interaction between the point processes. Event synchronization, however, adapts its time scale automatically, the user does not need to specify it. The same holds for SES: the time scale is determined by the parameter s_t , which is computed by the inference algorithm, and does not need to be specified a priori.

There might be a delay between the two point processes x and x'. Before the above mentioned measures (except SES) can be applied, one first needs to estimate potential delays, and shift the point processes accordingly. On the other hand, SES directly handles delays, and it does not require a separate procedure to estimate delays.

3 Analysis of Surrogate Data

In order to benchmark the different measures, we apply them to surrogate data. We randomly generated 10'000 pairs of one-dimensional point processes (x, x')

according to the procedure depicted in Fig. 1. We considered several values of the parameters ℓ , p_d , δ_t and s_t (σ_t). More specifically, the length ℓ was chosen as $\ell = \ell_0/(1-p_d)$, where $\ell_0 \in \mathbb{N}_0$ is a constant. With this choice, the expected length of x and x' is ℓ_0 , independently of p_d . We considered the values $\ell_0 = 100$, $p_d = 0, 0.1, \ldots, 0.4$, $\delta_t = 0$ ms, 25ms, 50ms, and $\sigma_t = 10$ ms, 30ms, and 50ms.

The constant C_V of the Victor-Purpura metric was set to $0.001 \, \mathrm{ms}^{-1}$, and the time constants τ_R , and τ_S , τ_H , and τ_Q were set of 20ms. Those values seemed to yield the most reasonable results. In order to assess the (dis)similarity measures, we compute for each above mentioned parameter setting and for each measure S the expectation $E\{S\}$ and normalized standard deviation $\overline{\sigma}\{S\} = \sigma\{S\}/E\{S\}$. Those statistics are computed by averaging over 10'000 pairs of point processes (x, x'). Some of the results are summarized in Fig. 2. In particular, that figure contains results for SES, the Victor-Purpura metric, and the Schreiber et al. measure; the other measures of Section 2 lead to similar results as the Schreiber et al. measure. Note that Fig. 2(a) to Fig. 2(d) show curves for $\delta_t = 0 \, \mathrm{ms}$, 25ms, 50ms; the curves are practically coincident, except in Fig. 2(b). For the sake of clarity, the other figures only contain curves for $\delta_t = 0 \, \mathrm{ms}$, the curves for different δ_t are not coincident.

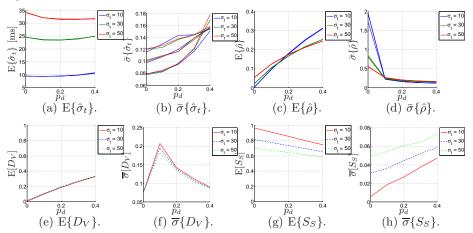


Fig. 2. Results for SES, Victor-Purpura metric D_V and Schreiber *et al.* measure S_S . From this study of surrogate data, we can conclude the following:

- The measures considered in this paper are reliable in the sense that their statistical fluctuations are relatively small; their normalized standard deviation is typically below 30%, and often even below 20%.
- Most measures depend on both p_d and s_t , and therefore, they are not able to separate the two key aspects of synchrony, i.e., timing precision and event reliability. There are two exceptions: the distance metric D_V grows with p_d independently of s_t (cf. Fig. 2(e)). The same holds for the SES parameter ρ (cf. Fig. 2(c)); both D_V and ρ are measures of event reliability. Note that ρ is robust to lags δ_t , in contrast to D_V . The SES parameter s_t is largely independent of p_d (cf. Fig. 2(a)), it is a robust measure for timing dispersion.

- SES is insensitive to lags: the curves in Fig. 2(a) and 2(c) for different values of δ_t are coincident. The other measures strongly depend on δ_t (see Fig. 3(a)), the similarity (dissimilarity) substantially decreases (increases) with δ_t ; therefore, one needs to estimate potential lags before they can be applied.
- There exists a classical procedure to estimate the timing dispersion based on the Schreiber et al. measure S_S (see, e.g., [14]). One computes S_S for a range of values of τ_S . The value of τ_S at which $S_S = 0.5$ is considered as an estimate σ_S of the timing dispersion. It is important to realize, however, that since the Schreiber et al. measure S_S significantly depends on p_d , also the resulting estimates of timing dispersion will significantly depend on p_d (see Fig. 3(b)). In contrast, the estimate \hat{s}_t of the SES parameter s_t does not suffer from those shortcomings (see Fig. 2(a)).

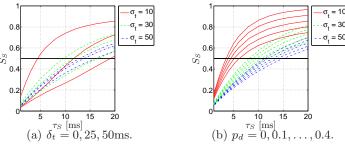


Fig. 3. Sensitivity of the Schreiber *et al.* measure S_S to δ_t and p_d .

4 Firing Reliablity of a Neuron

In this section, we use the (dis)similarity measures to quantify the firing reliability of neurons. We consider the Morris-Lecar neuron model [9], which exhibits properties of type I and II neurons [5]. The spiking behavior differs in both neuron types, as illustrated in Fig. 4.

In our experiments, the input current of the Morris-Lecar neuron consists of a baseline, a sinusoidal component, and zero-mean additive white Gaussian noise. The sinusoidal component forces the neuron to spikes regularly, however, the precise timing varies from trial to trial due to the Gaussian noise (see Fig. 4). Our objective is to investigate how the noise affects the spike timing and the tendency to drop spikes. We are especially interested in how the effect of noise differs in both neuron types. In type II neurons, the timing jitter is small, but spikes tend to drop out. In type I neurons, on the other hand, fewer spikes drop out, but the dispersion of spike times is larger. In other words, type II neurons prefer to stay coherent or to be silent, on the other hand, type I neurons follow the middle course between those two extremes [11].

We computed the similarity measures for each pair of 50 trials. Next we averaged those parameters over all pairs; since there are 50 trials, we have 1225 such pairs in total. A similar approach was followed in [12, 7].

SES results in the estimates $(s_t, \rho) = ((15.2 \text{ms})^2, 0.029)$ and $(s_t, \rho) = ((2.7 \text{ms})^2, 0.27)$ for type I and type II neurons respectively. This agrees with our intuition: since in type II neurons spikes tend to drop out, ρ should be large. On the other

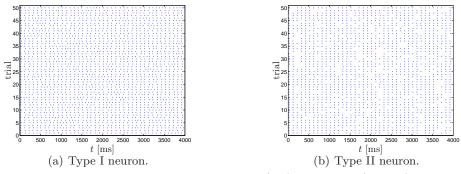


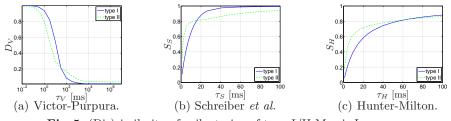
Fig. 4. Raster plots of spike trains from type I (top) and type II (bottom) neurons.

hand, since the timing dispersion of the spikes in type I is large, we expect s_t to be large in those neurons.

The results for the other measures are summarized in Fig. 5; it can be seen that the similarity measures S_S and S_H are larger for type II neurons than for type I neurons for small time constants τ_S and τ_H , whereas for large time constants, the opposite holds. This can be explained as follows: since the timing dispersion in type I neurons is fairly large, many spikes of type I neurons will be treated as non-coincident (non-overlapping) for small τ_S and τ_H . On the other hand, for large time constants, most spikes of type I neurons will be considered as coincident (overlapping). In contrast, type II neurons have high timing precision, and therefore, the similarity measures S_S and S_H grow quickly with the time constants τ_S and τ_H . However, the measures converge to relatively small values: due to the large number of drop-outs in spike trains of type II neurons, a substantial amount of spikes are treated as non-coincident; therefore, as the time constants grow, the similarity measures S_S and S_H attain smaller values than in type I neurons.

The results of the Victor-Purpura distance metric D_V and the van Rossum distance metric D_R (not shown here) can be understood along the same lines.

As we pointed out earlier, SES adjusts its time scale automatically. The same holds for event synchronization [10]: one may adapt the time constant τ_Q according to (4). With this adaption rule for τ_Q , we obtained $S_Q=0.96$ for type I neurons and $S_Q=0.83$ for type II neurons. This can be understood as follows: since for the data at hand, the adaptive time constant τ_Q is typically about 50ms or larger, the value of S_Q is the lowest in type II neurons due to the frequent drop-outs.



 ${\bf Fig.\,5.}$ (Dis) similarity of spike trains of type I/II Morris-Lecar neurons.

This analysis underlines an important issue: most classical measures depend on a time constant, and in many practical situations, it is not obvious how to choose the "optimal" value of those time constants. Indeed, Fig. 5 suggests that one should compute the measures for a range of values of the time constants. As a result, one obtains not just one single measure of similarity, but a similarity function $S(\tau)$. Such function may not always be easy to interpret, compare, or manipulate in practice. As we pointed out earlier, event synchronization and SES do not suffer from this shortcoming, since they automatically determine the appropriate time scale.

Conclusions

We compared various classical and recently proposed measures for spike synchrony. We have shown that most measures are not able to distinguish timing precision and event reliability, with two notable exceptions: with appropriate choice of parameters, event synchronization quantifies event reliability, independently of timing precision; the two SES parameters quantify both timing precision and event reliability separately. Moreover, all measures require the separate procedures to estimate potential lags between the point processes, except SES, which deals with lags in a natural and direct way, and consequently, the SES similarity measures are robust to lags.

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