How spurious correlations affect a correlation-based measure of spike timing reliability

Jan A. Freund \(^{a,b,*}\), Alexander Cerquera \(^c\)

\(^a\) Theoretical Physics/Complex Systems Research Group, ICBM, Carl von Ossietzky Universität Oldenburg, D-26111 Oldenburg, Germany
\(^b\) Research Center Neurosensory Science, Carl von Ossietzky Universität Oldenburg, D-26111 Oldenburg, Germany
\(^c\) Faculty for Electronic and Biomedical Engineering, Complex Systems Research Group, Antonio Nariño University, Bogotá, Colombia

1. Introduction

Neurons transmit information about a stimulus via spike trains. The specific way stimulus features shape these spike trains is the essence of a neural code. In theoretical approaches to neural coding [1–3] two dichotomies play a prominent role: rate code vs. spike timing code and single unit code vs. population code. Rate codes are robust against spike jitter and shuffling of spikes but a rather inefficient way of coding [4], in particular for short evaluation times.

The specific way stimulus features shape these spike trains is the importance for fast coding strategies, i.e. when stimulus features have to be reconstructed within a short time span allowing at most one spike per neuron to be elicited. Under such circumstances a single unit rate estimate must necessarily be highly unreliable. On the contrary, a population rate is less prone to estimation errors because of mitigating ensemble statistics. However, many redundant neurons would be needed to suppress statistical fluctuations sufficiently which makes this short-time population rate code highly inefficient [4]. An improvement is achieved by evaluating the timing (or just the rank-order [5]) of all those spikes across the population which are triggered by the stimulus. Admittedly, in a single trial situation stimulus-induced spikes cannot be easily separated from spontaneous spikes. However, in trials with repeated presentations of the same stimulus a significant similarity of spike trains across the trial ensemble can be seen as an indication of a stimulus selective neuron. It is evident that stimulus selectivity is beneficial for stimulus reconstruction. Therefore, the task to build optimal subpopulations means to separate stimulus selective neurons from non-selective ones. A constructive way to reach this goal is to assess stimulus selectivity of each neuron by measuring its reliability, i.e. the spike train similarity of the repeated trial ensemble can be seen as a correction is essential before comparing neurons with distinctly different spike rates. Such a comparison may, for instance, guide the choice of stimulus selective sensory neurons that are pooled to repeated presentations of the same stimulus. Spike jitter as well as additional or missing spikes are caused by neuronal noise and have the effect of limiting spike timing reliability.

The dichotomy of single unit vs. neuronal populations gains importance for fast coding strategies, i.e. when stimulus features have to be reconstructed within a short time span allowing at most one spike per neuron to be elicited. Under such circumstances a single unit rate estimate must necessarily be highly unreliable. On the contrary, a population rate is less prone to estimation errors because of mitigating ensemble statistics. However, many redundant neurons would be needed to suppress statistical fluctuations sufficiently which makes this short-time population rate code highly inefficient [4]. An improvement is achieved by evaluating the timing (or just the rank-order [5]) of all those spikes across the population which are triggered by the stimulus. Admittedly, in a single trial situation stimulus-induced spikes cannot be easily separated from spontaneous spikes. However, in trials with repeated presentations of the same stimulus a significant similarity of spike trains across the trial ensemble can be seen as an indication of a stimulus selective neuron. It is evident that stimulus selectivity is beneficial for stimulus reconstruction. Therefore, the task to build optimal subpopulations means to separate stimulus selective neurons from non-selective ones. A constructive way to reach this goal is to assess stimulus selectivity of each neuron by measuring its reliability, i.e. the spike train similarity of the repeated trial ensemble, and then rank and threshold the population with respect to this measure (cf. the discussion in Section 5).

Severe measures of spike train similarity exist, e.g. [6–11]. Paiva et al. [12] reported a comparison of binless spike train measures. Using measures without binning the time axis avoids boundary effects due to quantization of spike trains and is favorable for estimation. In the same publication three of these binless measures, Victòr’s and Purpura’s spike train metrics [6], van Rossum’s distance [7] and Schreiber et al.’s correlation measure, were put in a unifying perspective through a formulation via different kernel functions. Notwithstanding the fact that these methods are binless the kernel width introduces a
smoothing parameter that controls the importance of spike timing precision.

Here we want to point out that in a comparative spike train reliability analysis of neurons with different rates the choice of this kernel width strongly influences the level of statistical significance which can be seen as a kind of bias. Statistical significance comes into play when assessing the reliability value observed for a specific neuron against the backdrop of spurious correlations occurring in reference ensembles of spike trains that are constructed in accordance with a null-hypothesis. In the case of comparatively short observation times that we have in mind the reference ensemble will be given by Poisson spike trains of a (constant) firing rate identical to the related estimate of the analyzed neuron. Generalizations to longer spike trains will be discussed in Section 6. Our presentation will be focused on Schreiber et al.'s correlation measure, however, the mentioned considerations of spike timing reliability are constructed in accordance with a null-vector. Since the numerator of (3) balances only non-vanishing segments of smoothed spike trains we choose to define

\[
\langle \hat{s}_i \cdot \hat{s}_j \rangle = 0 \quad \text{if} \quad |\hat{s}_i| = 0 \lor |\hat{s}_j| = 0.
\]

As pointed out by Schreiber et al. [8] \( R \) accounts for the similarity of spike trains and, contrary to PTH-based measures, is sensitive to slow variations in firing rate across cell trials.

### 3. Spurious correlations between independent Poisson spike trains

The use of the correlation-based measure (3) as a measure of spike timing reliability is justified whenever the quantified similarity of spike trains is beyond the accidental similarity of statistically independent spike trains. However, because of the non-negativity of the correlation-based measure spurious correlations reflecting such accidental similarities must necessarily be reflected by positive values. Therefore, these positive deviations from zero constitute a kind of bias that should be excluded from considerations of spike timing reliability.

To see how the bias statistics depends on the spike rate \( \tau \) of the neuron and on the choice of parameters we consider an ensemble of independent Poisson spike trains. These are constructed by concatenation of interspike-intervals \( t_i \) chosen independently according to

\[
\tau_i = \frac{\ln \left( \frac{1}{\tau} \right)}{\lambda},
\]

where \( \zeta_i \) is a random number equidistributed in the unit interval. We thus generate a sequence of independent ISIs that are exponentially distributed, i.e.

\[
p(t) = \lambda e^{-\lambda t}.
\]

Both mean and standard deviation of the ISI distribution are given by \( \lambda^{-1} \) which, therefore, is the characteristic time scale of the neuron. In Fig. 1 we show an ensemble of 10 independent spike trains that results from concatenation of such ISIs together with the signal traces resulting from the Gaussian filter. When comparing the spike timing reliability of a population of neurons with vastly different spike rates one is left with two options:

- use of the correlation-based measure (3) with a population specific constant \( \sigma_e \). This choice is reasonable if from physiological considerations the spike timing precision is identical for all neurons of the population, notwithstanding the fact that they might possess significantly varying spike rates. In case no such

---

**Section 2**

### The correlation-based measure

We assume that \( N \) spike trains were recorded from a single neuron subjected to repeated presentations of the same stimulus. The method proposed by Schreiber et al. [8] proceeds as follows:

- A spike train, characterized by the sequence of \( M \) spike times \( t_1, \ldots, t_M \), is convoluted (smoothed) with a Gaussian filter of temporal width \( \sigma_c \) yielding the signal

\[
s(t) = \frac{1}{\sqrt{2\pi\sigma_c^2}} \exp \left( -\frac{(t-t_i)^2}{2\sigma_c^2} \right).
\]

The parameter \( \sigma_c \) must be chosen by the experimenter and should match the estimated temporal timing precision of spikes. Therefore, it is characteristic for a specific (type of)

- Binning: the time-continuous signal \( s(t):0 \leq t \leq T \) is then converted to a vector \( \mathbf{s} = (s_1, \ldots, s_K) \) by choice of a bin width \( \Delta t \) and by the definition of the \( k \)-th vector component as the mean value

\[
s_k = \frac{1}{\Delta t} \int_{(k-1)\Delta t}^{k\Delta t} s(t) \, dt \quad \text{for} \quad k = 1, \ldots, K.
\]

Here the number \( K \) of vector components is related to the bin width \( \Delta t \) and the total observation time \( T \) by \( K = \lceil T/\Delta t \rceil \) (where \( \lceil \ldots \rceil \) indicates the nearest smaller integer). Choosing \( \Delta t < \sigma_c \) makes the integrand in (2) a mildly varying function. Hence, for any \( 0 \leq \theta \leq 1 \), \( s_k = s((k-\theta)\Delta t) \) is an equally valid choice. In all of our calculations we fixed \( \Delta t = 1 \) ms, the shortest interspike interval reflecting absolute neuronal refractory time. Such a small bin width substantially reduces quantization effects, even more so, since binning is performed after smoothing.
estimate for the spike timing precision exists a characteristic time scale of the population may be chosen, for instance, as a tenth of \(1/(\tau^2) \text{est} \), where the trial and population average \(\langle \tau^2 \rangle_{\text{est}} = \langle \tau^2 \rangle_{\text{pop}} \) is an estimator for the average population spike rate.

\(B\): use of the correlation-based measure \((3)\) with a neuron specific constant \(\sigma_c\). This situation applies if information on the scaling of spike timing precision with spike rate \(\sigma_c(z)\) is available. Lacking this knowledge one could choose a neuron specific characteristic time scale, for instance, a tenth of \(1/\tau_{\text{est}}\), where the trial average \(\tau_{\text{est}} = N/1\) is an estimator for the spike rate of a single cell.

In Fig. 2 we show how these two options shape the correlation-based measure in application to independent Poisson spike trains. For a given average spike rate \(z\) simulations were done with 80 replicates of trial ensembles of 80 independent spike trains. Each spike train was generated by simulation of a Poisson model neuron with constant spike rate \(z\). As shown in Fig. 1 the observation time was \(T=200\) ms and the bin width chosen as \(\Delta t=1\) ms. In the left panel of Fig. 2 (case \(A\)) we see that the choice of a constant \(\sigma_c = 5\) ms leads to a pronounced increase of \(R\) with increasing spike rate \(z\). For spike rates much higher than 50 Hz the curve must reach saturation at the value one because \(\sigma_c^2 \geq 1\). In the right panel of Fig. 2 (case \(B\)) an initial increase is followed by a saturation at around a value of 0.25 (below one). The constancy of the flat part is a consequence of adapting \(\sigma_c\) to the trial average estimate of the spike rate \(\tau_{\text{est}}\) via the hyperbola

\[
\sigma_c = \frac{1}{10\tau_{\text{est}}} = \frac{T}{10N_z}, \quad \text{for} \left(\frac{1}{T} \leq \tau_{\text{est}} \leq \frac{1}{10\Delta t} \Rightarrow 1 \leq N_z \leq \frac{T}{10\Delta t}\right).
\]

(7)

In the case of \(\tau_{\text{est}} < T^{-1} = 5\) Hz, which corresponds to the average observation of less than one spike, we freeze \(\sigma_c\) at the value \(T/10=20\) ms. Using Gaussian filters with broader widths does not seem reasonable since a single spike would be smeared across all of the recording window. In the other extreme of spike rates larger than \(1/(10\Delta t) = 100\) Hz the connection via the hyperbola \((7)\) would select \(\sigma_c < \Delta t = 1\) ms, i.e. below all physiologically reasonable limits of spike timing precision. Therefore, we freeze \(\sigma_c = 1\) ms for spike rates larger than 100 Hz. The consequence is that beyond this spike rate the plateau would be traded again for an increasing curve approaching the saturation limit at one in the ultra-high spike rate limit. At least for spike rates in the range between 5 Hz and 100 Hz through our choice \((7)\) we can arrange for a constant bias.

The grey bands flanking the average (fat solid line) shown in both upper panels of Fig. 2 indicate the central 90% percentiles of \(R\). Their values are computed from 80 replicates (of 80 trial ensembles) and thus give an idea about the range of values that have to be expected for the bias. Of course, the width of this range depends on the number of trials, i.e. it will shrink [increase] with increasing [decreasing] the number of trials. On the one hand, values below these grey bands indicate significant deviations and characterize spike train ensembles that are much dissimilar than our constructed Poissonian ensembles. Such ensembles with dissimilarity beyond the chance level may arise as copies of a consensus spike train which are temporally shifted with respect to each other by an amount \(\text{jitter}\) that exceeds the filter width \(\sigma_c\) but remains less than the average interspike distance. On the other hand, the range above the grey bands corresponds to spike train ensembles which exhibit similarity beyond the chance level. This is the range where values, indeed, can be used to identify and quantify spike timing reliability.

When it comes to quantifying spike train similarity beyond chance level it is clear that the bias should be subtracted

\[
R_{\text{corrected}} = R_{\text{uncorrected}} - R_{\text{chance}}. \tag{8}
\]

Graphically this means to quantify reliability not with reference to the abscissa but with reference to the fat solid lines seen in the upper panels of Fig. 2. In the following Section 4 we derive an approximate mathematical expression for \(R_{\text{chance}}\) permitting an easy and fast correction.

4. Analytic considerations

In the literature on stochastic processes (e.g. p. 149 in [13]) a Poisson process filtered with \(w(t)\), i.e.

\[
X(t) = \sum_{m=-\infty}^{\infty} w(t-T_m), \tag{9}
\]

is known as a shot noise process. Campbell's theorem states that\(^2\)

\[
\langle X(t) \rangle = z \int_{-\infty}^{\infty} w(s) ds, \tag{10}
\]

\[
\text{Cov}[X(t),X(t+\tau)] = z \int_{-\infty}^{\infty} w(s)w(s+\tau) ds \tag{11}
\]

with \(z\) being the rate (intensity) of the Poisson process. Therefore, the signal defined by \((1)\) is a segment of a shot noise process with \(w(t)\) being a Gaussian with mean zero and variance \(\sigma_w^2\). As a consequence of Campbell's theorem we find

\[
\langle s(t) \rangle \approx z, \tag{12}
\]

\[
\text{Cov}[s(t),s(t+\tau)] \approx z \frac{\tau}{\sqrt{2\pi}\sigma_c} \exp \left( -\frac{\tau^2}{4\sigma_c^2} \right). \tag{13}
\]

The approximate applicability of this formula is limited to segments which are long in comparison to the filter width \(\sigma_c\). In the context of our considered spike trains this translates into the

\[^1\] We denote a trial average of \(N_z\) by the overbar \(\bar{N}\), and a population average by brackets \(\langle N_z \rangle\), hence a trial and population average by \(\langle \bar{N} \rangle\).

\[^2\] \(\langle X \rangle\) and \(\text{Cov}[X,Y]\) denote expectation value and covariance of random variables \(X\) and \(Y\) respectively.
demand that \( \sigma_c \) should be considerably smaller than the observation time \( T=200 \text{ ms} \).

Making the step to the \( N \) trial vectors \( \{\tilde{s}_1, \ldots, \tilde{s}_N\} \) we denote by

\[
\tilde{s}_{i,n} = x + \delta x_{i,n}
\]

the \( n \)-th vector component \((n=1, \ldots, K)\) of the \( i \)-th trial \((i=1, \ldots, N)\). The statistics of fluctuations \( \delta x_{i,n} \) is described by

\[
\text{Cov}[\delta x_{i,n}, \delta x_{j,n-1}] \approx \frac{X}{2\sqrt{\pi}\sigma_c} \exp\left(-\frac{(k at)^2}{4\sigma_c^2}\right) \delta_{ij},
\]

where the Kronecker \( \delta_{ij} \) in (16) expresses the independence of Poisson spike trains. Notice that the fluctuations are correlated up to a typical index length \( k \sim O(2\sigma_c/\Delta t) \).

Given an ensemble \( S \) of \( N \) independent Poisson spike trains we compute the correlation-based measure (3) as follows

\[
\mathcal{R}(S) = \frac{2}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} \frac{1}{K} \left[ \sum_{m=1}^{K} \delta_{i,m} \delta_{j,m} \right] \left[ \sum_{m=1}^{K} \delta_{i,m} \right] \left[ \sum_{m=1}^{K} \delta_{j,m} \right].
\]

By definition of \( \eta_{ij} = \delta x_{ij}/\sigma \) we find

\[
\mathcal{R}(S) = \frac{2}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} \frac{1 + \sum_{m=1}^{K} \delta_{i,m} + \delta_{j,m} + \delta_{i,m} \delta_{j,m}}{1 + \sum_{m=1}^{K} \delta_{i,m} + \delta_{j,m} + \delta_{i,m} \delta_{j,m}}.
\]

The quantity \( \mathcal{R}(S) \) is a random variable that is distributed in accordance with the various realizations of Poissonian ensembles. Above we have sampled this distribution through our numerical simulations of 80 replicates and estimated its 90% percentile. Therefore, we identify the bias with the replicate mean

\[
\mathcal{R}_{\text{change}} = \langle \mathcal{R}(S) \rangle_{\text{replicates}}.
\]

A rigorous calculation of this expression seems very tedious (if feasible at all). However, a considerable simplification can be reached through the observation that the weighted sums in (18) already constitute a trial \((i<j=1, \ldots, N)\) and temporal \((n,m,\tilde{m}=1, \ldots, K)\) average respectively. While the idea of a temporal average is challenged by the autocorrelation (16) the restriction \( \sigma_c < T \) imposed by applicability of Campbell's theorem again supports this interpretation. The trial average is an expression of the type

\[
\langle X \rangle \approx \langle X \rangle + \frac{1}{1 + 2\sqrt{\pi}\sigma_c} \langle \delta X \rangle\langle \delta X \rangle + O(\langle \delta X \rangle^2)
\]

where \( \langle \delta X \rangle \) denotes all terms obtained via a Taylor expansion. Although the average of a nonlinear function is not the nonlinear function of its averaged arguments we found that the leading term in (21) still renders a satisfactory approximation

\[
\mathcal{R}_{\text{change}} \approx \frac{1}{1 + 2\sqrt{\pi}\sigma_c} \frac{1}{1 + 2\sqrt{\pi}\sigma_c} = \frac{2}{1 + 2\sqrt{\pi}\sigma_c}
\]

where we have used \( \langle \eta_{ij} \rangle = 0, \langle \eta_{ij} \eta_{kl} \rangle = \delta_{ij} \delta_{kl} \) and \( \langle \delta_{ij} \rangle = 0 \) and that \( \text{Var}[\eta_{ij}] \) is given by (16) for \( i=j, k=0 \) and divided by \( x^2 \). A numeric evaluation of formula (22) is plotted in Fig. 2 with grey dashed curves.

Before we turn to an application of our approach we briefly mention that an alternative to subtracting the mean reliability \( \mathcal{R}_{\text{change}} \) of the Poisson ensemble (cf. (8)) is to subtract the mean \( \langle s(t) \rangle \) of the filtered Poisson spike trains from the signal \( s(t) \) and to use \( s(t) - \langle s(t) \rangle \) in the correlation measure yielding

\[
\hat{\mathcal{R}}_{\text{corrected}} = \frac{2}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} \frac{1}{K} \left[ \sum_{m=1}^{K} \delta_{i,m} \delta_{j,m} \right] \left[ \sum_{m=1}^{K} \delta_{i,m} \right] \left[ \sum_{m=1}^{K} \delta_{j,m} \right].
\]

Since our filtered stationary Poissonian reference ensemble has a mean given by Campbell’s theorem (12) the effect will be to arrive at

\[
\hat{\mathcal{R}}_{\text{corrected}(S)} = \frac{2}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} \frac{1}{K} \left[ \sum_{m=1}^{K} \delta_{i,m} \delta_{j,m} \right] \left[ \sum_{m=1}^{K} \delta_{i,m} \right] \left[ \sum_{m=1}^{K} \delta_{j,m} \right].
\]
between $\delta z_{i,n}$ and $\delta z_{j,n}$ across trials $i$ and $j$ and thus can build up positive values.

It should be clear that due to the nonlinearity of the cosine both ways to remove the bias generate different statistics. However, an elaboration of the precise differences appears cumbersome and is left to future research. Aside from residual fluctuation statistics we see no substantial differences in the ability of both methods to remove the bias. Since the essential point is to remove the bias at all we choose to employ the well-established formula (3) generating values in the unit interval and then subtract the value of $R_{\text{chance}}$.

5. Application to an ensemble of retinal ganglion cells

Being equipped with a method and a formula to quantify the bias of the spike timing reliability measure we demonstrate its consequences in application to a retinal ganglion cell (RGC) ensemble. Stimulus induced activity of an isolated turtle retina was recorded with a multi-electrode array and a total of 107 RGCs were identified through a spike sorting procedure; experimental details can be found in [14]. The stimulus was a complex light pattern that was moved linearly (back and forth) across the retina at varying speeds. The task was to reconstruct these varying speeds and motion direction from the recorded spike response of RGC ensembles. Considering reconstructions with small sub-populations raises the question how to select RGCs preferentially. One of the hypotheses guiding cell selection might be that a high reliability of spike train response is an indication for stimulus selective cells and, hence, for better reconstruction performance. As discussed in [14] reliability is only one factor influencing stimulus selectivity while responsivity, i.e. the degree of changes induced by a shift of the stimulus, is another. A highly reliable but rather “stiff” neuron might not be well suited for reconstruction. Intuitively one expects a trade-off between reliability and responsivity for if a stimulus easily shifts spikes neuronal noise probably will do as well. A quantity like $d'$ balancing these counteracting tendencies does exist for spike counts but, to the best of our knowledge, not yet for whole spike trains. Therefore, spike timing reliability and responsivity were assessed separately.

The variation of spike rates with stimulus velocities is evaluated in the form of cell specific tuning curves. From the above analyses we expect that similar tuning curves should be found for the spike timing reliability before bias subtraction. Indeed, as seen in Fig. 3 the uncorrected curves seem to indicate that spike train response to faster motion is more reliable than that for slowly moving visual patterns. As can be found from the corrected curves this is actually only true for one neuron but not for the other one which prior to correction even seems to be the more reliable of the two.

This is also found when computing the spike timing reliability measure for the complete set of neural spike trains, i.e. for all 107 RGCs.
RGCs and all nine stimulus velocities (ranging from $-2.5$ mm/s (leftward) to $2.5$ mm/s (rightward)) depicted in Fig. 4. All experiments and evaluation parameters were identical to the ones used before: $\Delta t = 1$ ms, $T = 200$ ms, $\sigma_T = 5$ ms.

While prior to bias correction highest spike rates seem to indicate highest spike timing reliability, after bias correction it becomes obvious that only responses with approximately two spikes per 200 ms are reliable beyond the chance level. Therefore, when selecting cells in accordance with maximum spike timing reliability bias subtraction will significantly alter resulting small sub-populations [14].

6. Conclusions

We have shown that spurious correlations may lead to a misinterpretation of the correlation-based measure (3) of spike timing reliability [8]. The effect of spurious correlations becomes more pronounced for neurons with higher spike rate. Within limits set by the observation time $T$, i.e. the length of spike trains, and the bin width $\Delta t$, i.e. an estimate for spike timing precision, the bias increase of the measure towards higher spike rates can be compensated by choice of a filter width $\sigma_T$ that varies inversely with the estimated spike rate. Moreover, it is possible to estimate and subtract the bias from measured values thus allowing for a better comparison of neurons with significantly varying spike rates. Of course, a bias approaching its theoretical upper bound at one means that an actually reliable spike response cannot be distinguished from a random spike pattern just because the parameters $\sigma_T$, $\Delta t$ and $T$ are chosen inappropriately. Alternatively, the mean spike rate can be subtracted prior to computing the correlation measure.

In the considered case of short spike trains (200 ms) with few spikes the reference ensemble was composed of Poisson spike trains with constant estimated firing rate. For spike trains that are long in comparison with the inverse firing rate, i.e. with average many spikes, temporal variations of the firing rate might become important. Such a situation was already considered for recurrent neural networks [16] where spurious correlations due to shared and correlated input could be removed by including the local firing rates. In our case we have highly correlated inputs (stimulus repetitions + noise) that are shared by all members of the trial ensemble. The equivalent treatment would correspond to the construction of spike train ensembles generated via independent Poisson neurons that share a common local firing rate. The reliability statistics of this reference ensemble could be easily generated via simulations and one may again be subtracted. Analytic reasoning, albeit straightforward, will be more involved and must include non-stationary shot noise and generalizations of Campbell’s theorem (cf. 4–5, Complements 5C, p. 156 of [13]).

Changing the filter width in dependence on the firing rate also impacts the scale of temporal precision on which reliability is computed. It is a matter of interpretation whether a neuron with a temporal precision of 5 ms and a firing rate of 50 Hz should be considered equally as or less reliable than a neuron with the same temporal precision of 5 ms at a firing rate of only 5 Hz. In our judgment the final answer must be given in accordance with the physiology of involved neurons. The H1 neuron of a fly, for instance, can generate spikes at a rate of 50 Hz and with a timing precision in the (sub-)millisecond range [15]. In case a good estimate $\sigma_{\Delta t}^2(t)$ of the local firing rate can be given (for longer spike trains) it is also thinkable to use a local filter width $\sigma_{\Delta t}(t) = 1/(10\sigma_{\Delta t}^2(t))$.

A more refined evaluation of the residual fluctuation statistics of (19) and (24) remains to be done. Its result would allow to choose the more efficient of both methods and facilitate a fast, yet more realistic bias correction in the range of low spike rates.

Acknowledgments

The authors acknowledge support by the German Research Foundation (DFG) in the framework of the Research Unit FOR 701. A.C. was supported by the ALECOL Program (Antonio Nariño University in Colombia/Ictex/Coleciencias/Colombian Education Ministry/German Academic Exchange Service (DAAD)) and the International Graduate School for Neurosensory Science and Systems (InterGK). Helpful hints by an anonymous referee are acknowledged.

References

Alexander Cerquera was born in Bogotá, Colombia, on August 1978. He received his undergraduate degree in Biomedical Engineering from the Antonio Nariño University in Bogotá in August of 2002. In February 2006 he received his M.Eng. in Industrial Automation from the National University of Colombia Manizales Head-quarter. In July of 2010 he finished his doctoral studies at the Carl von Ossietzky University in Oldenburg, Germany, in the framework of the Ph.D. Program “Neurosensory Science and Systems”. In his dissertation project he analyzed multi-electrode recordings of the turtle retina with the aim to reconstruct motion stimuli and compare several coding hypotheses. Presently, he works as an Assistant Professor at the Faculty for Electronic and Biomedical Engineering at the Antonio Nariño University in Bogotá, as well as with the Research Group Complex Systems of the same institution. His current research topics are in the fields of biomedical signal and image processing.