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Research paper

Improving the quality of extracting dynamics from interspike intervals via a resampling approach

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ABSTRACT

We address the problem of improving the quality of characterizing chaotic dynamics based on point processes produced by different types of neuron models. Despite the presence of embedding theorems for non-uniformly sampled dynamical systems, the case of short data analysis requires additional attention because the selection of algorithmic parameters may have an essential influence on estimated measures. We consider how the preliminary processing of interspike intervals (ISIs) can increase the precision of computing the largest Lyapunov exponent (LE). We report general features of characterizing chaotic dynamics from point processes and show that independently of the selected mechanism for spike generation, the performed preprocessing reduces computation errors when dealing with a limited amount of data.

1. Introduction

Quantifying dynamical features of complex oscillations with Lyapunov exponents is a commonly used approach that has various scientific and engineering applications. It can be applied to estimate the Lyapunov spectrum with a required accuracy if the mathematical model of the analyzed system is known and there are no restrictions of its study [1,2]. When this information is unavailable, and only a single phase space variable is measured, this task can be solved via the reconstruction technique [3–5] which is based on the assumption that the temporal dependence of the analyzed variable is related to an attractor, and the considered length of the phase trajectory is sufficient to get required information about properties of this attractor. The latter is especially important for inhomogeneous attractors in which the rate of divergence or convergence of nearby phase space trajectories significantly varies depending on the selected region.

In general, the less information about the system is known, the less precision of its quantification can be reached. However, even under the condition of very limited information such as in the case of point processes, the analyzed complex dynamics can be appropriately characterized. This type of deterministic or stochastic processes carries information about the system's behavior by times of stereotype events [6]. Point processes are widely studied in neuroscience in the context of information encoding provided by neuronal systems [7,8]. In neurophysiological studies, an action potential sequence, or spike train, is the only source of information about the sensory input, and the debate between rate and time coding is still on-going [9].

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In order to understand how sensory input can be characterized from the output spike train, a series of theoretical studies with different neuron models was performed. Among these studies, several key theoretical results should be mentioned including Sauer's embedding theorem [10,11] being an extension of the Takens theorem [4] for point processes. It was proved for interspike intervals generated by an integrate-and-fire (IF) neuron model at high firing rate. According to this theorem, the output ISI series allows reconstruction of the attractor related to the input of IF-model. Although the ISI series represent a non-uniform sampling case, delay vectors of ISIs keep information about low-dimensional dynamical systems producing input signals. Numerical investigation performed in [12] confirmed the ability to recover dynamical information from ISI-series for different neuron models driven by chaotic oscillations. This confirmation was based on the predictability of ISI-series that has a close relation to reconstruction. The paper [13] extended the existing knowledge about reconstruction of non-uniformly sampled dynamical systems including not only the integrate-and-fire mechanism, but also many other cases. Thus, there is an essential theoretical background to recover dynamics of the input of neuron models from the output spike trains. This background allows us to expect that dynamical features of chaotic oscillations driving the neuron models can be characterized from the output point processes using the standard numerical techniques [14–20].

Despite the achieved progress in the analysis of non-uniformly sampled dynamical systems, the case of short dataset needs to be discussed in more detail. Actually, at the restrictions of available data the quality of reconstruction and, therefore, the precision of computing the Lyapunov exponents or other numerical characteristics may essentially depend on the used method and on the selection of its parameters. Embedding theorems do not guarantee a "good" reconstruction if the available ISI series contains a limited amount of samples. In order to improve the quality of recovering the input dynamics from short sequences of interspike intervals, their preliminary processing may be useful. Here we discuss, how such preprocessing allows increasing the accuracy of computing the largest LE (λ_1). The paper is organized as follows. Section 2 describes several neuron models and the approaches used for analysis of ISI series produced by these models. A comparative analysis of results obtained in both cases, with and without data preprocessing, is performed in Section 3. Main concluding remarks are given in Section 4.

2. Models and methods

2.1. Generic IF model

Let us start from the generic IF-model that has been widely studied in many relevant publications (see, e.g., [10–15]). This model provides a transformation of an input signal $S(t)$ into an output spike train according to the following procedure. The signal $S(t)$ is integrated from a time moment T_0

$$V(t) = \int_{T_0}^{t} S(t')dt'. \tag{1}$$

When the integral reaches a threshold Θ, a short-lasting impulse (spike) is generated, and the value of $V(t)$ is reset to zero (Fig. 1a). The resulting spike train is obtained according to the following mathematical definition

$$\int_{T_i}^{T_{i+1}} S(t)dt = \Theta, \tag{2}$$

where T_i are the times of consequent spikes used to get ISI series $I_i = T_{i+1} - T_i$ (Fig. 1b).

Here we consider the chaotic oscillations $S(t) = x(t) + 35$ as a driving signal for the generic IF model, where $x(t)$ is the phase variable of the Rössler system [21]

$$\begin{aligned} \frac{dx}{dt} &= -(y+z), \\ \frac{dy}{dt} &= x + ay, \\ \frac{dz}{dt} &= b + z(x-c) \end{aligned} \tag{3}$$

with the parameters $a = 0.15,\ b = 0.2,\ c = 10.0$, and the offset is used to avoid negative values of $x(t)$. Aiming to increase the precision of estimating the times T_i, the integration step in Eq. (1) is reduced when $V(t)$ crosses the threshold, and the integration near the value Θ is repeated. We used a fourth-order Runge–Kutta method with the time step $h = 10^{-3}$ when performing the initial integration, and $h = 10^{-5}$ for a more precise detection of firing times.

At high firing rate leading to small ISIs, the integral (2) is easily computed using the rectangular rule

$$\int_{T_i}^{T_{i+1}} S(t)dt \simeq S(T_i)I_i \tag{4}$$

that provides the following way for restoration of the chaotic input $S(t)$ from the output ISI series

$$S(T_i) \simeq \frac{\Theta}{I_i} \tag{5}$$

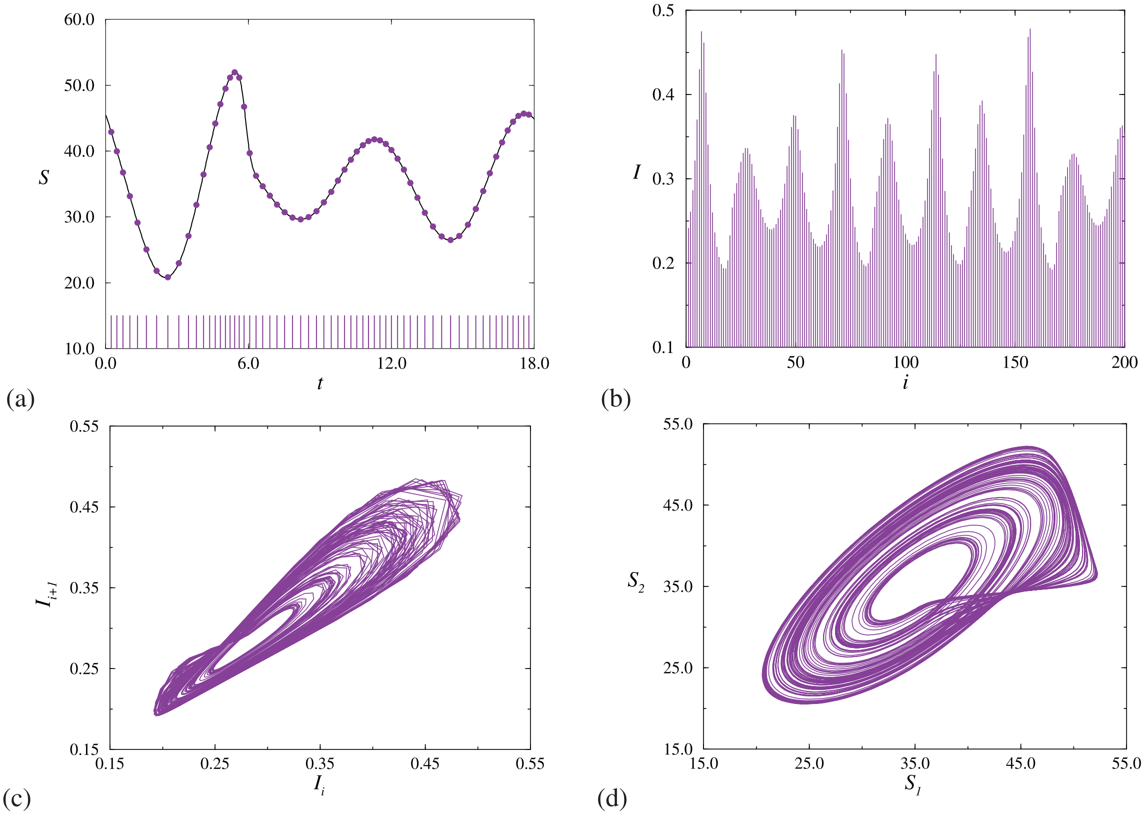

Fig. 1. The generic IF model: (a) an input signal and the output spike train (times of spike generation are shown by circles); (b) the ISI sequence; (c, d) attractors restored using 3000 ISIs without and with the resampling approach, respectively, where $S_1 = S(t)$, $S_2 = S(t+d)$, and d is the time delay.

and, correspondingly, the dynamical properties of $S(t)$ are estimated based on information contained in the IF ISI series (the scaling coefficient Θ is selected arbitrarily because it does not influence LEs).

Attractor reconstruction using I_i can be provided with the embedding delay equal to one ISI [10], and such reconstruction keeps metrical and dynamical invariants of the original attractor. When characterizing dynamical properties of the chaotic signal $S(t)$ from the ISI series with the standard approach for computing LEs [22], the divergence of nearby trajectories in the reconstructed phase space is analyzed. The accuracy of such an estimation may be reduced if time intervals between the successive spikes I_i are characterized by a broad distribution and the considered amount of data is limited.

Alternatively, we may realize a resampling of the analyzed dataset with a constant time step. As we show in Section 3, such data preprocessing improves the estimations of Lyapunov exponents when dealing with short recordings. For the ISI sequence produced by the generic IF model, the resampling is easily provided via the interpolation of the samples (5) with a smooth function, e.g., a cubic spline. Thus, a transition from the values $S(T_i)$ to a time series $S(i\Delta t)$, $i = 1, \dots, N$ is performed. Besides introducing a uniform sampling, such approach increases the number of points in the reconstructed phase space. Fig. 1c and d shows the restored attractors for both the considered cases.

2.2. Glass–Mackey IF model

By analogy with the study [12], we discuss another variant of the integrate-and-fire dynamics. Unlike the generic IF model, the Glass–Mackey model [23,24] demonstrates periodic firings in the absence of a driving signal, and the added chaotic process $S(t)$ provides a modulation of the threshold resulting in variations of ISIs. The neural activity is described by a linear dependence

$$V(t) = \alpha t + \beta \tag{6}$$

between the spiking events. When $V(t)$ reaches the threshold, i.e., $V(t) = S(t)$, a spike is generated, and the value of $V(t)$ is reset to zero (Fig. 2a). By analogy with the generic IF model, detection of spiking events with higher precision can be provided. For this purpose, interpolation of the input signal $S(t)$ is realized. High firing rate is related to large values of α. For smaller α, time intervals between spiking events increase which may lead to a loss of nonlinear forecastability.

Taking $\beta = 0$, the following relation between the ISIs and the samples of the signal $S(t)$ is obtained

$$S(T_i) = \alpha (T_i - T_{i-1}) = \alpha I_{i-1}. \tag{7}$$

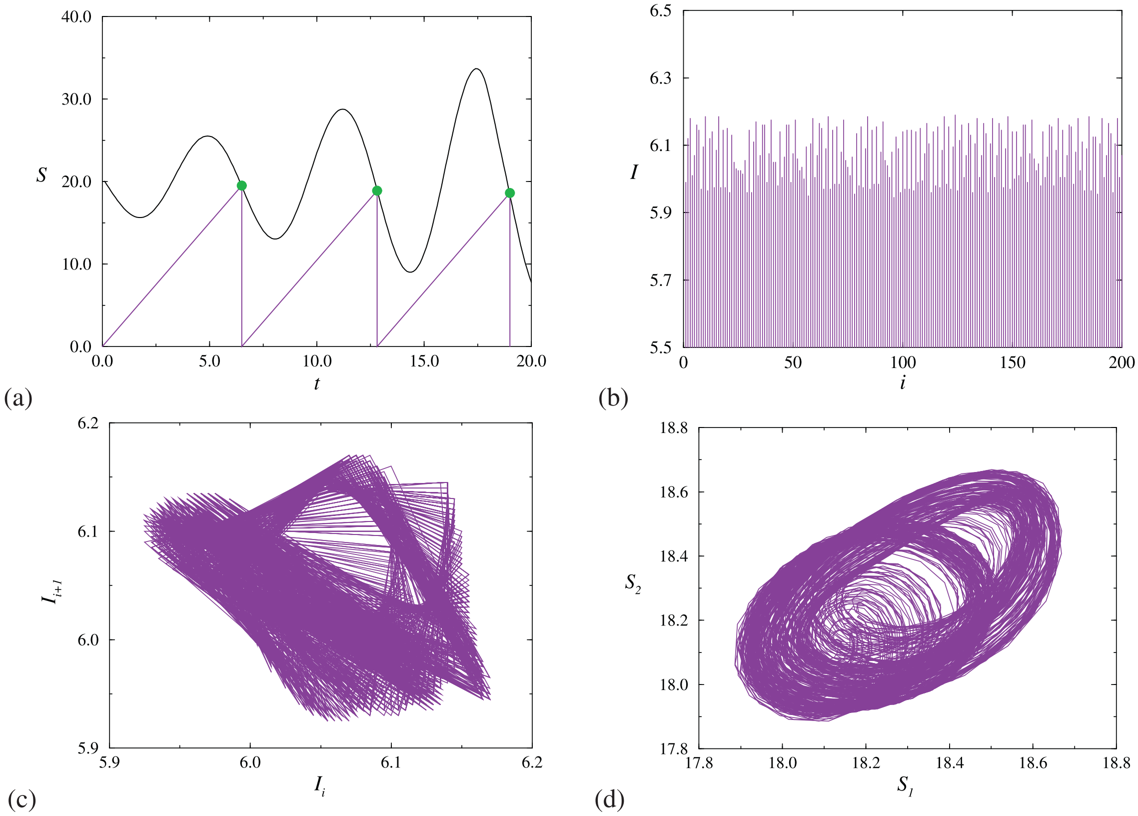

Fig. 2. The Glass–Mackey IF model: (a) an input signal and the times of spike generation ($\alpha = 3$); (b) the sequence of interspike intervals; (c, d) attractors restored using 3000 ISIs without and with the resampling approach, respectively.

Again, we may reconstruct the attractor using the ISI sequence I_i (Fig. 2b) with the embedding delay equal to one ISI or perform a preliminary transition to the values $S(T_i)$ and their further resampling with the constant time step Δt that provides a time series $S(i\Delta t)$, $i = 1, \ldots, N$ used for reconstruction. The corresponding phase portraits are shown in Fig. 2c and d.

2.3. Threshold-crossing model

Threshold-crossing (TC) model describes the generation of neuron firings when the input signal $S(t)$ crosses the threshold level Θ in one direction, e.g., upwards. Considering the same example of driving signal as for the IF-models, namely, the chaotic oscillations produced by the Rössler system, we take $S(t) = x(t)$ and set the threshold value Θ in such a way that its intersection occurs during each oscillation of the signal $S(t)$ (Fig. 3a).

Time moments when the selected threshold value is reached are related to times of intersection of the Poincaré section $x(t) = \Theta$. From this point of view, the sequence of TC ISIs represents the sequence of times when the phase trajectory returns to the secant plane (Fig. 3b). The considered type of point processes enables reconstruction by analogy with the ISI sequences produced by the IF-models [25,26]. Let us note, however, that the process of spike generation described by the TC-model is accompanied by the generation of a single spike per oscillation. This is a more complicated case as compared with the IF-models where several spikes are related to one oscillation of the input signal (at high firing rate), and the more spikes per oscillation are produced, the higher the quality of the attractor reconstruction is provided. Despite the reduced amount of information about the driving signal contained in TC ISI sequences, the embedding with the delay equal to one ISI enables computing metrical and dynamical characteristics of the original attractor associated with the input signal $S(t)$.

An alternative approach to reconstruction was proposed in [16,19] and consists in the transition from TC ISIs to the values of the instantaneous frequency averaged during a return time $I_i = T_{i+1} - T_i$

$$\omega(T_i) = \frac{2\pi}{I_i} \tag{8}$$

For chaotic oscillations associated with a phase-coherent dynamics, the dependence of the averaged instantaneous frequency is rather close to the dependence of the instantaneous frequency estimated from the input signal $S(t)$ via the Hilbert transform [16].

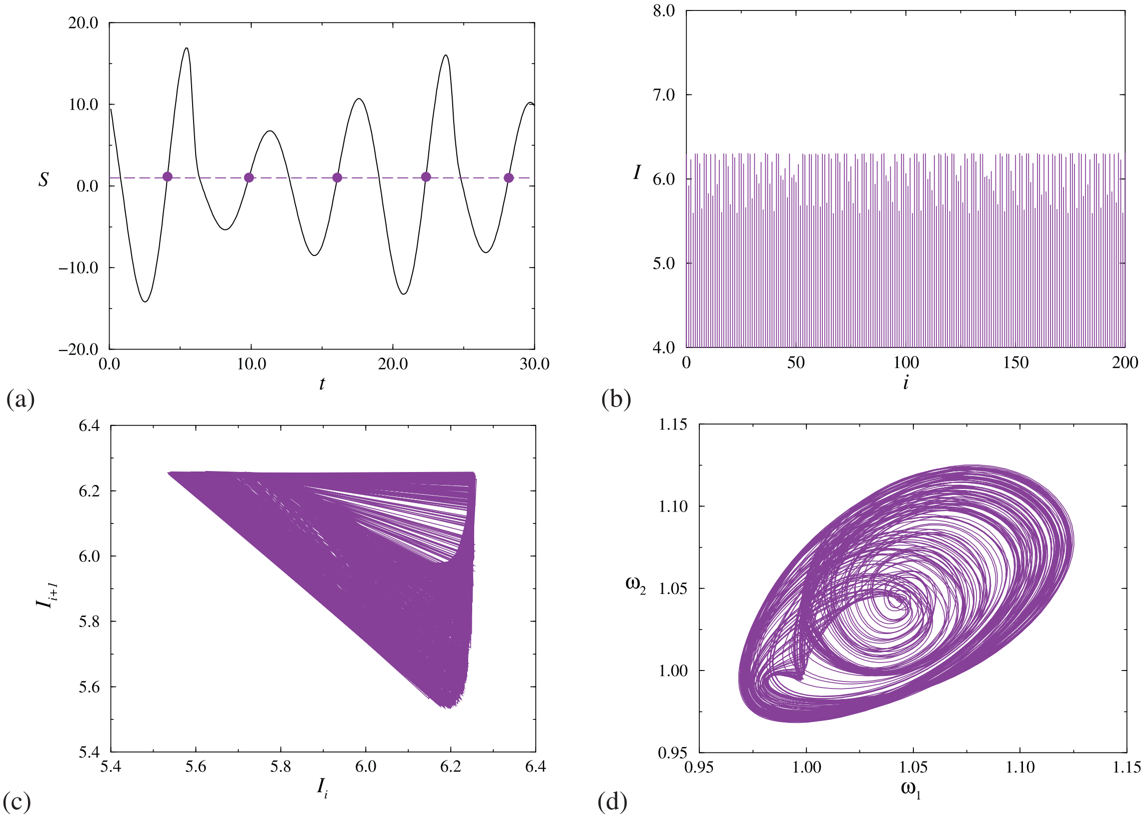

Fig. 3. The threshold-crossing model: (a) an input signal and the times of spike generation; (b) the sequence of interspike intervals; (c, d) attractors restored using 3000 ISIs without and with the resampling approach, respectively, where $\omega_1 = \omega(t)$, $\omega_2 = \omega(t+d)$, and d is the time delay.

The samples $\omega(T_i)$ can be used for the attractor reconstruction similar to the IF ISIs (Fig. 3c), and the latter will provide, e.g., the same value of the largest LE since λ_1 is invariant to nonlinear transformation of the signal. Another possibility consists in the resampling of the values $\omega(T_i)$ through interpolation with a constant time step Δt. This means that we transform a non-uniformly sampled point process into a uniformly sampled temporal dependence of the instantaneous frequency that enables restoration of the chaotic attractor using the standard embedding technique [19,27] (Fig. 3d).

2.4. Chaotic bursting

Up to now, we discussed neuron models driven by oscillations generated by the Rössler system in a phase-coherent chaotic regime. Let us consider a more complicated problem of highly-nonlinear oscillations, when the phase trajectory includes intermittent segments with fast and slow dynamics. As the corresponding example, the β-cell model is chosen [28] that generate chaotic bursts of impulses with varying time intervals between them (Fig. 4a and b):

$$\frac{dV}{dt} = (-I_{Ca} - I_K - g_P P(V - V_K))/\tau,$$
$$\frac{dn}{dt} = \mu(n_\infty - n)/\tau,$$
$$\frac{dP}{dt} = (P_\infty - P)/\tau_P, \tag{9}$$

$$I_{Ca}(V) = g_{Ca} m_\infty (V - V_{Ca}),$$
$$I_K(V,n) = g_K n(V - V_K),$$
$$x_\infty = \frac{1}{1 + \exp((V_x - V)/\varphi_x)}, \quad x = m, n, P. \tag{10}$$

Here, V is the voltage at the membrane, n describes the fraction of open potassium channels, and P is a slow variable associated with the calcium concentration. The model (9) was considered under the following parameter set: $g_{Ca} = 3.6$, $g_K =$

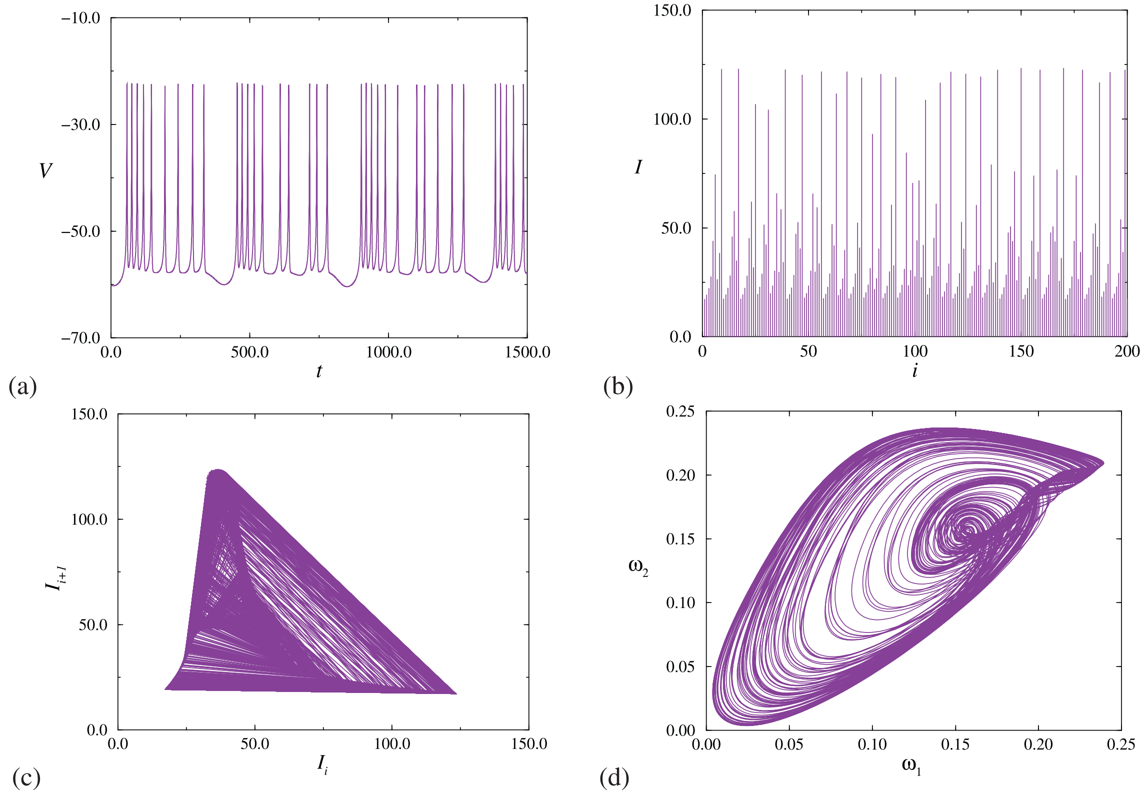

Fig. 4. The β-cell model: (a) the chaotic bursts described by (9); (b) the sequence of time intervals between firing events; (c, d) attractors restored using 3000 ISIs without and with the resampling approach, respectively.

10.0, $g_P = 4.0$, $\tau = 20$ ms, $\tau_P = 35$ s, $V_{Ca} = 25$ mV, $V_K = -75$ mV, $V_m = -20$ mV, $V_n = -16$ mV, $V_P = -40$ mV, $\varphi_m = 12$ mV, $\varphi_n = 5.6$ mV, $\varphi_P = 10$ mV, $\mu = 0.85$. Analysis of its dynamics was performed based on the series of time intervals between the firing events. Two variants of the attractor restoration were analyzed: the direct reconstruction using the series of time intervals between consequent events (I_i), and the transition to the averaged instantaneous frequency $\omega(i\Delta t)$ performed by analogy with the TC model (Fig. 4c and d).

3. Results and discussion

3.1. Generic IF model

A comparative study of different methods for the attractor reconstruction was performed starting from the generic IF model being the simplest example of the spike generation mechanism. Here and further, estimation of the largest LE from point processes is based on the standard numerical technique proposed by Wolf et al [22]. Fig. 5 shows dependencies of the largest LE (λ_1) for two cases: the reconstruction using the original IF ISI series by selecting the embedding delay equal to one ISI (circles), and the reconstruction using resampled data after the transition to the values of the driving signal as described in Section 2.1 (triangles). According to the performed estimations, the precision is higher for the second approach that provided an averaged error $E_2 = 1.4\%$ vs. $E_1 = 2.9\%$ for the first reconstruction method. Here, we compared the values λ_1 estimated from the output point process and from the corresponding input signal $S(t)$ with the same method for LE computing [22]. These estimations are fairly close to the values computed using the equations of the Rössler system [1,2,29].

Besides a reduction of the computation error, the resampling approach demonstrates a higher stability to fluctuations. To show this, we added a normally distributed random process with the intensity $D = 10^{-3}$ to the ISI sequence and performed a comparison of the considered two methods for noisy data. The distinction between the values λ_1 estimated using the interpolated dependence $\omega(i\Delta t)$ was significantly less than for estimations performed using the original ISI sequence I_i (1.1% and 4.3%, respectively).

The latter may be explained by a reduction of orientation errors when computing the largest LE that have strong influence on the estimated quantity. Despite the new samples introduced via the interpolation are not exactly known, and their consideration may be treated as adding small noise to the phase trajectory, an increased number of points in the reconstructed phase space (we considered 5–10 times larger amount of data after the interpolation of samples (5) provides

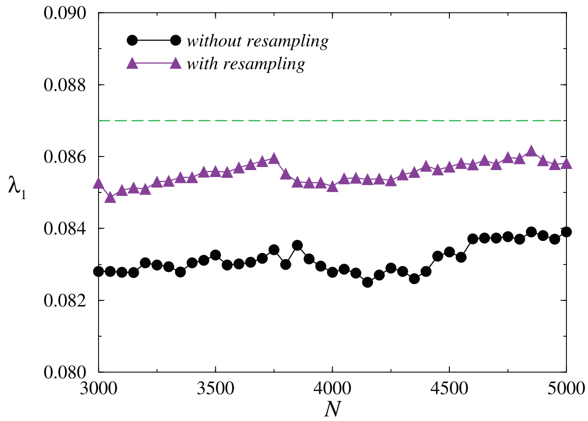

Fig. 5. The largest LE estimated from the ISI sequences produced by the generic IF model using two variants of the attractor reconstruction: the standard (without resampling) and the proposed approach (with resampling). Dashed line indicates the value computed using the input signal.

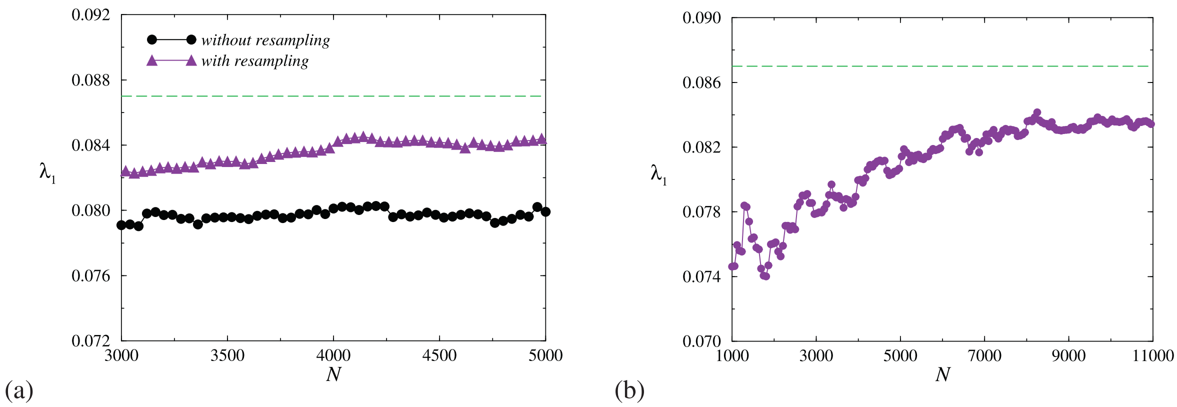

Fig. 6. (a) The largest LE estimated from the ISI sequences generated by the Glass–Mackey IF model using two variants of the attractor reconstruction at high firing rate ($\alpha = 11$); (b) estimations performed with the resampling approach at low firing rate ($\alpha = 3$).

a higher probability of keeping the direction for the perturbation vectors and reduces projections of these vectors in the directions being orthogonal to the direction of the maximal divergence of nearby trajectories. The latter effect may be more important as compared with the insignificant lack of precision caused by the interpolation. Besides, when performing the reconstruction directly from the ISI sequence, the time interval between consequent samples is taken as equal to the mean ISI value. If ISIs are characterized by a narrow distribution, their individual distinctions can be ignored. For broader distribution of ISIs, differences in time intervals will have an additional influence on the precision of computing the rate of trajectories instability in the reconstructed attractor.

3.2. Glass–Mackey IF model

Similar results are obtained for the Glass–Mackey IF model considered at high firing rate ($\alpha = 11$, Fig. 6a). Direct application of the method [22] to the attractor restored using the delayed ISI sequence provides an error $E_1 = 7.8\%$. The reconstruction performed from the resampled dataset with the preliminary interpolation of samples reduces this error to $E_2 = 3.6\%$. Let us note that high firing rate is a necessary condition that influences the predictability of the ISI series. According to Racicot and Longtin [12], a decreased α which provides a reduction of the firing rate is associated with a growth of the normalized prediction error, i.e., a reduced nonlinear forecasting. Nevertheless, if the considered firing rate does not relate to missed oscillations of the driving signal, the largest LE can be estimated with the resampling approach, but a “good” estimation is provided for longer datasets. Fig. 6b illustrates how λ_1 varies with the duration of the ISI series. The largest LE approaches the expected value with increased amounts of data. Its estimation for short ISI sequence provides a computation error $E_2 \simeq 15\%$ when processing sequences of about 1000 samples.

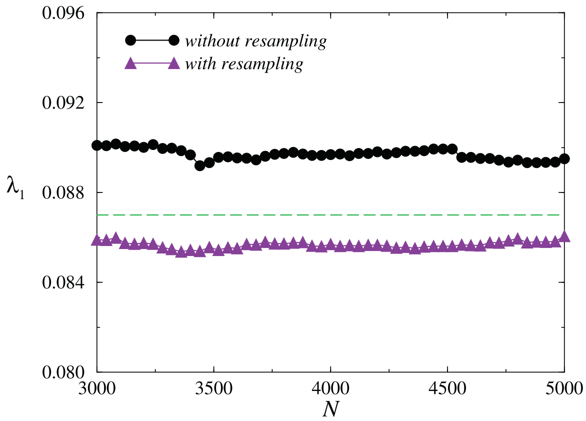

Fig. 7. The largest LE estimated from the ISI sequences produced by the TC model using two variants of the attractor reconstruction.

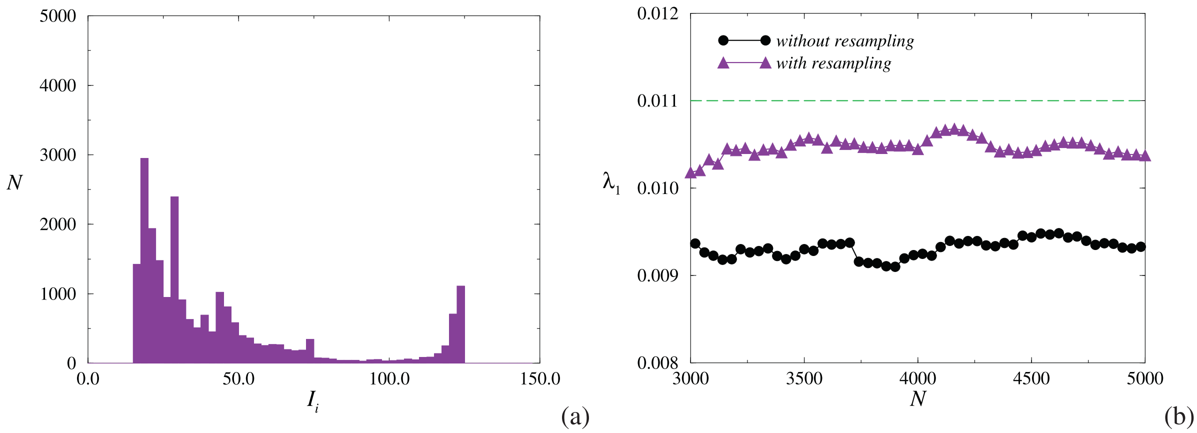

Fig. 8. (a) The distribution of time intervals between firing events in the dynamics of the β-cell model; (b) the largest LE estimated using two variants of the attractor reconstruction.

3.3. Threshold-crossing model

Consideration of the TC model confirms the advantages of the approach based on the resampled ISI series. Unlike the IF-model, the preliminary processing of the TC ISIs is based on the approximation of the instantaneous frequency of the input signal instead of the restoration of the driving process itself. Although the reconstruction using the initial ISI sequence is able to quantify dynamical properties of chaotic oscillations (Fig. 7, $E_1 = 2.6\%$), the resampling-based approach provides a better precision ($E_2 = 1.7\%$). These results are obtained in the course of averaging over standard parameters used within the method [22], such as embedding dimension, renormalization time, length of perturbation vector, etc. Additionally, time delay was varied within the second approach near the recommended value of 1/4 part of the characteristic period for chaotic oscillations. By analogy with the IF-model, this approach provided a smaller distinction between estimations performed for deterministic ISI sequences and ISI sequences contaminated by additive noise. By selection of the normally distributed random process with the intensity $D = 10^{-3}$ we observed distinctions of λ_1 between noisy and noise-free ISI sequences taking about 1.9% for the approach with resampling and interpolation, and about 2.8% for the direct method without data preprocessing.

3.4. Chaotic bursting

Finally, let us consider a more complex dynamics produced by the burst oscillator (9). Despite the presence of a broad and bimodal distribution of time intervals between spiking events (Fig. 8a) that includes both, interspike intervals (within a single burst) and interburst intervals (between consecutive bursts), the resulting point process enables a fairly good estimation of λ_1 (Fig. 8b) even for relatively short amount of data. Again the method with the resampling of the analyzed dataset provided a better quantification of the underlying dynamics ($E_2 = 5.3\%$) unlike the direct application of the reconstruction technique to the output point process ($E_1 = 12.1\%$).

Table 1
Computation error of the considered methods (estimation performed using 5000 ISIs).

Model system	Error, %	
	Without resampling	With resampling
Generic IF	2.9	1.4
Glass–Mackey IF	7.8	3.6
Threshold-crossing	2.6	1.7
β-cell	12.1	5.3

3.5. A comparative analysis

Table 1 summarizes the results of the considered two methods (without and with data preprocessing) for all four model systems. The approach based on the resampling of the ISI-sequences demonstrates a higher quality of the characterizing chaotic dynamics from point processes.

A larger error of the λ_1 estimation in the case of the β-cell model compared with the chaotic oscillations of the Rössler system considered within the previous models is explained by the inhomogeneity of the restored attractor since the presence of distinct time scales results in the appearance of regions with clearly different rate of trajectories divergence, and the latter increases errors caused by renormalizations of the perturbation vectors.

Note that the systematic biases observed in Figs. 5–8 are explained by errors associated with changes in the phase space orientation. A limited amount of available points in the reconstructed phase space reduces an ability to select appropriate perturbations when computing LEs, and the latter leads to an increase of vector components in the directions do not associated with the maximal divergence of trajectories. Typically, this effect is more pronounced for initial distances between the phase space trajectories, and due to the related growth of the renormalization vector, the resulting LE is underestimated.

4. Conclusion

In this study we considered the problem of computing the largest Lyapunov exponent from point processes who are the output of different types of neuron models. The existing theoretical background confirms the ability of reconstruction of non-uniformly sampled dynamical systems including for dynamics of sensory neurons, as well as many other cases. In practice, however, dealing with a limited (and often quite small) amount of data results in a reduced precision of estimations. Depending on the selected parameters, reconstruction can lead to different distortions of the restored attractor. In order to reach the attractor structure despite these distortions, the selection of algorithmic parameters is an important issue. Besides, a preliminary data processing may be useful to improve the characterization of attractor properties. Here, we considered two variants of such preprocessing for IF- and TC-mechanisms. For IF models, a restoration of the input signal was done using the output point process including an interpolation of the estimated values which provided a uniform sampling. For the TC model, a restoration of the instantaneous frequency of chaotic oscillations was realized with a resampling procedure.

The performed analysis give an opportunity to formulate some general features of characterizing chaotic dynamics from point processes produced by distinct neuron models. Independently of the selected model, the considered preliminary processing of the output ISI sequences provided a higher precision of computing λ_1 when dealing with a limited amount of data. For long dataset the latter conclusion is less important because orientation errors occurring during the computing of λ_1 are reduced with the increased amount of data, and depending on the required precision of estimations we may adjust the length of the processed ISI sequence. However, the considered approach may significantly reduce computation errors for short datasets.

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