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Determining the largest Lyapunov exponent of chaotic dynamics from sequences of interspike intervals contaminated by noise

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Abstract. We discuss abilities of quantifying low-dimensional chaotic oscillations at the input of two threshold models from the output sequences of interspike intervals in the presence of noise. We propose a modification of the standard approach for computing the largest Lyapunov exponent from a time series that verifies the performed estimations for noisy data. We consider features of its application to different types of point processes.

1 Introduction

Point processes carrying information about systems dynamics by times of stereotype events appear in many scientific fields. An important area is neuroscience where the analysis of point processes is performed when studying information encoding by neurons and their ensembles [1]. Thus, interspike intervals (ISIs) measured at the output of a sensory neuron represent the main source of information about external stimuli. The generation of point processes is carried out due to a thresholding of an input signal and is accompanied by a partial loss of knowledge about the underlying dynamics. Nevertheless, the remaining information is enough to quantify many important features of the input signal. In particular, earlier studies [2–7] considered the problem of characterizing chaotic oscillations at the input of several threshold models including integrate-and-fire (IF) and threshold-crossing (TC) models. This characterization was based on the reconstruction of dynamical systems [8–11] from point processes. Unlike the traditional approach developed for continuous-time functions, dealing with point processes complicates the reconstruction.

Previous works [2–5] performed a thorough analysis of the IF-model, and the ability of attractor reconstruction from IF ISI series at high firing rate was proved within Sauer's embedding theorem [12,13] being an extension of the standard reconstruction technique to point processes. As it was shown in [5], an IF ISI sequence represents a nonlinear transform of the input signal if the firing rate is high, and many measures of chaotic dynamics such as the generalized dimensions or the Lyapunov exponents can easily be estimated. In order to increase the precision of their computing, some modifications of the reconstruction based on IF ISI series were applied [14–16]. The case of TC ISI series is more complicated, and there are no strict mathematical results for this type of point processes confirming the ability of reconstruction by analogy with Sauer's theorem. Due to this, quantifying metric and dynamical features of chaotic regimes from TC ISIs was carried out only in numerical studies [6,17]. However, the obtained results allowed a quantification of complex oscillatory dynamics including chaos-hyperchaos transitions using quite short series of TC ISIs [18].

The aim of the works [2–6,12–18] was to characterize low-dimensional chaotic dynamics at the input of IF- or TC-model from the output point processes for a deterministic case. The robustness of the used approaches for noisy ISI sequences was not studied in detail, although the presence of random fluctuations may essentially influence the estimated characteristics. Thus, additive noise can lead to misinterpretation of many types of non-chaotic processes as being characterized by the positive largest Lyapunov exponent (LLE) [19]. The standard algorithm for computing LLE [20] assumes but does not confirm exponential divergence of phase space trajectories. In order to reveal deterministic dynamics and to distinguish chaotic oscillations from non-chaotic noisy processes, a careful analysis of a local exponential divergence should be performed [19]. A robust estimation of LLE from time series was the subject of many studies during the past two decades [21–25] that discussed different ways for noise reduction at the stage of data preprocessing. Such preprocessing improves

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further analysis of trajectories instability in the reconstructed phase space.

From a general point of view, if noise intensity is low compared with the amplitude of a chaotic signal then an additional noise-related trajectories divergence at small scales is different from the divergence at larger scales mainly associated with the deterministic dynamics. Within the standard algorithm [20] being applied to continuous-time signals, this additional noise-related divergence of trajectories can partly be ignored by a thresholding of perturbations comparable with noise intensity. In the case of point processes such as, e.g., a series of return times into the Poincaré section, it is more complicated to determine noise intensity, since spectral methods do not allow a clear separation between components associated with noise-free dynamics and fluctuations.

Besides, a direct application of methods for noise reduction to point processes is less appropriate as compared with continuous-time functions. Due to this, the development of approaches verifying the LLE estimated from noisy point processes represents an actual problem that is discussed in this paper. ISI sequences can be contaminated by noise due to several reasons including fluctuating threshold level and a mixture of signals at the input of a threshold system when noisy processes are added to an information signal encoded into a series of spiking events. Aiming to separate effects of noise and chaotic dynamics, ideas discussed in [19] can be applied. As an alternative, we propose here an approach based on the analysis of trajectories divergence depending on the maximal orientation error. We show that point processes produced by both, IF- and TC-models, demonstrate similar features of such dependence that can be used for improving the quality of LLE estimation and determining noise intensity. The proposed approach can be applied to quite short ISI sequences for quantifying dynamical features of chaotic oscillations at the input of threshold models at the presence of noise.

The paper is organized as follows. In Section 2 we briefly describe two models of spike generation, namely, the integrate-and-fire and the threshold-crossing models. In Section 3 we consider an approach for estimating LLE from point processes including its modification for detecting noise intensity and describe features of its application to different types of point processes. In Section 4 we discuss restrictions of the used approach for noisy ISI series and principles of verification of the estimated LLE. Some concluding remarks are given in Section 5.

2 Models of spike generation

2.1 Integrate-and-fire model

IF-model is widely used as a basic model describing spiking phenomena in the dynamics of neurons [1,2]. Besides, it is also considered in many other scientific and engineering fields, e.g., within delta-sigma data converters [26]. This model describes a threshold device with an input signal $S(t)$ that is integrated up to the time moment when the integral reaches a value θ. If this threshold is reached, a spike is generated, and the value of the integral is reset to zero. The spike train T_i, $i = 1, 2, \ldots, n$ is defined by the equation

$$\int_{T_i}^{T_{i+1}} S(t)dt = \theta. \tag{1}$$

Time intervals between subsequent spikes $I_i = T_{i+1} - T_i$ are used to quantify features of the input signal $S(t)$. The problem of reconstruction based on the output spiking events consists in the following. If the sequence of time intervals I_i is known, can the chaotic attractor represented by a one-dimensional projection $S(t)$ of the phase space trajectory at the input of IF-model be restored using the output point process? When the firing rate is high and, therefore, the mean ISI $\overline{I}$ is low, the integral (1) is easily computed using the rectangular rule

$$\int_{T_i}^{T_{i+1}} S(t)dt \simeq S(T_i)I_i \quad \Rightarrow \quad S(T_i) \simeq \frac{\theta}{I_i}. \tag{2}$$

According to equation (2), the input signal is restored from an IF ISI series at time moments T_i. Larger mean ISI is associated with a reduced precision of such restoration. Errors in determining the values $S(T_i)$ at a low firing rate can be treated as adding noise to $S(t)$. When the input signal is a mixture of a chaotic process and an additive noise of relatively small intensity, the problem of quantification of the deterministic input dynamics from noisy ISI series becomes more complicated.

Let us note that the samples $S(T_i)$ are non-uniformly discretized in time. Aiming to apply standard data processing techniques, their resampling with a constant time step Δt needs to be provided. The latter is carried out by an interpolation with splines or other smooth functions. Besides the resampling, this procedure allows increasing the number of data points in the case of large $\overline{I}$ and reducing errors of vector orientations when computing LLE with the approach [20]. Since the threshold value θ is typically unknown, an arbitrary constant quantity can be used in equation (2). In particular, we may consider $\theta = 1$ that will not influence further estimations of LLE because it is convenient to perform a normalization of the attractor size to the unity interval in order to use algorithmic parameters that do not depend on the oscillations magnitude.

2.2 Threshold-crossing model

TC-model is another basic model describing a transformation of the input analogous signal $S(t)$ into the output sequence of stereotype events generated when $S(t)$ crosses a given threshold Θ. Dealing with a chaotic oscillator used as the source of a complex dynamical regime at the input of TC-model, TC ISI series can be interpreted as a sequence of return times into a Poincaré section. However, TC ISI series is a more general definition than a series of return times because it accounts for the case when a part of phase space trajectories does not intersect the secant plane given as $S(t) = \Theta$ for large Θ. In this case the corresponding secant plane does not define a Poincaré section.

Independently on the threshold Θ, the problem to be solved consists in the estimation of the attractor's characteristics associated with a chaotic dynamics $S(t)$ from the output sequence of TC ISIs for the case when the output point process is contaminated by additive noise.

3 Computing the largest Lyapunov exponent from data series

3.1 Estimation of LLE from continuous-time processes

Estimation of Lyapunov exponents from a scalar time series is often performed with the method proposed by Wolf et al. [20] that assumes a reconstruction of the phase space trajectory with the delay approach [8], although other techniques [27–31] can also be applied. The method [20] represents a standard tool for studying chaotic dynamics from time series. Due to this, here we address only those its aspects that are necessary for further description of a modified approach being applicable to noisy point processes. If $x_i = x_j(i\Delta t)$ is a time series representing the jth coordinate of the chaotic system

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{F}(\boldsymbol{x}) \tag{3}$$

discretized with the time step Δt then the delay reconstruction

$$\boldsymbol{z}_i = \left\{x_i, x_{i+k}, x_{i+2k}, \ldots, x_{i+(m-1)k}\right\} \tag{4}$$

is carried out, where m is the embedding dimension. For a weak chaotic regime with an expressed mean orbital period P, the time delay $\tau = k\Delta t$ is selected as about $P/4$. Typically, the reconstruction parameters m and τ do not essentially influence the result of LLE estimation if their selection is based on quite general requirements [8–11]. Nevertheless, a precision of LLE computing is higher if the results are averaged over variation of these parameters.

When the reconstruction is done, the mean rate of trajectories divergence is analyzed [20]. For the starting point $\boldsymbol{z}_1$ of the fiducial trajectory associated with the time moment t_1, a perturbation vector $\boldsymbol{v}_1$ of a small but finite length r_0 is selected [32]. In the direction of the maximal trajectories divergence its length increases in time as

$$r(t) = r_0 e^{\lambda_1(t_1)(t-t_1)}. \tag{5}$$

The dependence (5) characterizes a linear approach that is valid for small $r(t)$. When the perturbation increases, and the vector $\boldsymbol{v}_1$ is transformed to $\boldsymbol{v'}_1$ for which the nonlinearity of the system (3) reduces the rate of trajectories divergence, renormalizations should be performed. An optimal way for renormalizations is to choose a new perturbation in the same direction but of smaller size. Dealing with a finite amount of points $\boldsymbol{z}_i$, however, it is impossible strictly following the direction, and an orientation error occurs that influences the precision of LLE estimation. This error means that the replacement vector $\boldsymbol{v}_2$ (or $\boldsymbol{v}_k$ for further perturbations) has a component being orthogonal to the direction of the maximal divergence of trajectories. The latter component does not increase according to equation (5) and, therefore, the initial length of the vector becomes larger than in the case when the direction remains unchanged. As a result, the local value of LLE is reduced. The LLE is obtained by averaging the rate of exponential growth of perturbations along the whole fiducial trajectory.

The presence of noise in time series creates difficulties in computing λ_1. For continuous-time functions such as, e.g., a time dependence of the phase space coordinate $x(t)$ produced by the system (3), the noise level can be estimated via spectral analysis and, therefore, one can select a threshold value l_{min} for the replacement vector r_0 in such a way that the noise-related divergence of phase space trajectories is excluded (or, at least, it does not provide an essential influence). In this case one can choose a range $r_0 \in [l_{min},\ l_{max}]$ where the divergence of trajectories is caused by the dynamics of the analyzed system. Here, l_{max} sets the condition of the linear approach, i.e. an exponential divergence of trajectories. Typically, $l_{max} = 5$–10% of the attractor's size, and l_{min} is selected depending on the noise level. In order to detect and quantify chaotic dynamics associated with exponential divergence of nearby trajectories, l_{min} should be significantly less than l_{max}.

3.2 Estimation of LLE from point processes

When dealing with point processes, e.g., the sequence of return times with added noise, an estimation of noise level is a more complicated task and it may not be obvious how to correctly introduce an appropriate threshold l_{min}. Due to this reason, the problem of verifying the estimated λ_1 appears. The standard method [20] can be used for computing LLE from spike trains generated by IF- and TC-models after data preprocessing. When dealing with IF-model, this method is applied to data series $S(T_i)$ restored according to equation (2) after the interpolation with the time step Δt.

In the case of TC-model, an average instantaneous frequency is estimated before applying the method [20]. For this purpose, an approach proposed in [17] and further modified in [18] is applied. If T_i are the times of intersection of the threshold Θ by the input signal $S(t)$, and I_i are TC ISIs defined as $I_i = T_{i+1} - T_i$, then the values of the averaged instantaneous frequency can be found as

$$\omega(T_i) = \frac{2\pi}{I_i}. \tag{6}$$

Equation (6) means that averaging of the values $\omega(T_i)$ is carried out during the current time interval I_i, i.e., using a varying temporal window [17]. By analogy with IF-model, the samples $\omega(T_i)$ are interpolated by a smooth function to get a time series $\omega(j\Delta t)$ with the constant time step Δt. Although this time series does not exactly reconstruct the instantaneous frequency introduced via the Hilbert transform, it still allows estimating metric and dynamical characteristics of complex oscillations $S(t)$.

The approach [17] may lead to spurious identification of dynamical regimes if the threshold Θ is inappropriately selected (when a part of oscillations are missed) or the input signal represents a sum of different variables and the latter can produce missed events or the generation of additional spikes. To avoid spurious identification, we considered an extended method [18] that includes a preliminary data analysis for possible artifacts and additional estimations depending on the interpolation technique for point processes characterized by a broad distribution of interspike intervals. Such extensions improve the method's performance.

3.3 The proposed modified approach

In this work we propose a modified approach for estimating LLE from point processes generated by IF- and TC-models at the presence of noise. We consider the case when noise is added to the series of interspike intervals. Such noise can be of different origin, including noisy input signal and fluctuating threshold level.

In general, the algorithm [20] assumes a compromise between minimizing of both, the length of the replacement vector and the error associated with changes in phase space orientation. These goals cannot be simultaneously reached, i.e., a reduction of the angle α between the replacement vector $\boldsymbol{v}_2$ and the perturbation vector before the renormalization ($\boldsymbol{v'}_1$) restricts abilities to select an appropriate length of the vector $\boldsymbol{v}_2$. Such a restriction occurs due to a reduced number of available points in the reconstructed phase space that can be chosen as the starting points for a new perturbation providing an orientation error less than some value α, e.g., $\alpha = \pi/6$. The latter typically leads to an increased length of the replacement vector and more frequent renormalizations that need to be performed for maintaining the condition of the linear approach. Frequent renormalizations provide an accumulation of orientation errors and, therefore, an underestimated value of λ_1 that is obtained as the rate of trajectories divergence averaged along the whole data set. Within the fixed evolution time algorithm [20], the minimization of orientation changes is typically performed. The replacement vector with the length $r_0 \in [l_{min}, l_{max}]$ and the minimal angle α is searched. In the case of a deterministic dynamics, the choice of the renormalization principle is less crucial, and quite similar results are obtained for both variants, minimizing of orientation error and of the length of the replacement vector.

The proposed approach is based on the dependence of λ_1 on the maximal available angle α between the replacement vector and the vector before the renormalization when a new perturbation is chosen at the condition of minimizing the vector's length in the range $[l_{min},\ l_{max}]$. From general assumptions it is expected that large orientation errors associated with large values of α provide an underestimated LLE. Besides, very small α essentially reduces the ability to select an appropriate replacement vector. In this case, it becomes necessary to increase the length of the vector that results in trajectories divergence being out of the linear approach. Typically, this leads to a reduced length of the vector $\boldsymbol{v'}_1$ relative to $\boldsymbol{v}_1$ and underestimated λ_1. If the condition $r_0 \in [l_{min},\ l_{max}]$ is not satisfied for an available data set when α is small, the selection of a new perturbation may be provided quite arbitrarily that also reduces the estimated value of LLE. Thus, very small and large α are expected to provide an underestimated λ_1. An optimal α associated with the maximum of the dependence $\lambda_1(\alpha)$ allows for a more precise estimation of LLE from point processes. Further we shall show how a changed character of this dependence can be used to identify noise level in the analyzed data series.

4 Results and discussion

4.1 Integrate-and-fire model

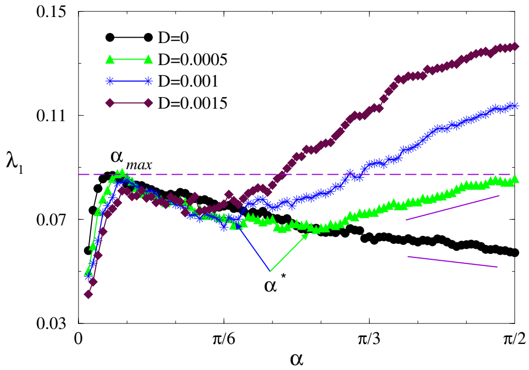
As a source of low-dimensional complex oscillations $S(t)$ at the input of IF-model we considered the Rössler system

$$\frac{dx}{dt} = -y - z,\quad \frac{dy}{dt} = x + ay,\quad \frac{dz}{dt} = b + z(x - c) \tag{7}$$

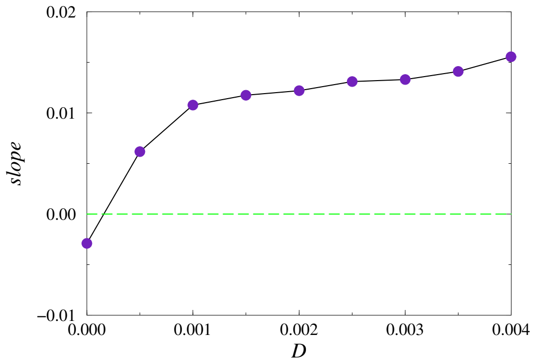
in a chaotic regime ($a = 0.15$, $b = 0.2$, $c = 10.0$). Aiming to provide a high firing rate, a translation of the dynamical variable $x(t)$ of the system (7) was performed as $S(t) = x(t) + 35$. The threshold level θ was changed to reveal restrictions of LLE computing. Noise effects were analyzed by adding a normally distributed random process $D\xi(t)$ with the intensity D to $S(t)$, i.e. the signal at the input of IF-model had the form $S(t) + D\xi(t)$.

Estimation of LLE was carried out with the approach [20] using the following renormalization principle: a replacement vector was searched with the orientation error less than α providing minimization of its length in the range $[l_{min},\ l_{max}]$. Figure 1a shows how the value of λ_1 is changed depending on α for the threshold value $\theta = 10$ and different noise intensities including the case of a deterministic dynamics.

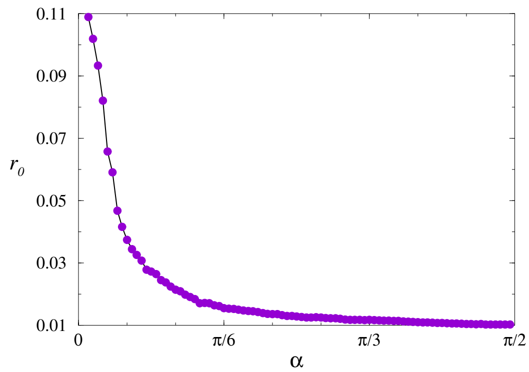
When $D = 0$, the dependence $\lambda_1(\alpha)$ demonstrates a maximum at about $\alpha_{max} \simeq \pi/25$. For angles $\alpha < \alpha_{max}$, a reduction of λ_1 is caused by frequent renormalizations. Small α leads to a low probability of selection an appropriate renormalization vector having the length close to l_{min}. Larger vectors require a reduced time duration between renormalizations. If this time duration remains unchanged, the perturbation becomes larger than l_{max} leading to underestimated LLE. Taking a shorter time duration means an increased number of renormalizations and an accumulating orientation error. When α is too small, there may be no appropriate neighboring trajectory because no point in the reconstructed phase space is satisfied



(a)



(b)



(c)

Fig. 1. Dependencies $\lambda_1(\alpha)$ estimated from IF ISI series for different noise intensities and the threshold level $\theta = 10$ leading to the firing rate about 21 spikes/period (a), slopes of these dependencies in the range $[\pi/3, \pi/2]$ (b), and mean length of the replacement vector (c). We used the following parameters: $m = 5$, $\tau \simeq P/4$, $l_{min} = 0.01$, $l_{max} = 0.1$.

to the established renormalization principle, and the requirement $r_0 \in [l_{min},\ l_{max}]$ needs to be changed to continue computation of LLE. This typically provides an underestimated λ_1.

In the region $\alpha > \alpha_{max}$, the values λ_1 are reduced with α due to increased orientation errors that result in smaller ratios $r(t)/r_0$. The corresponding dependence $\lambda_1(\alpha)$ is characterized by a negative slope in the interval $[\pi/3, \pi/2]$ (Fig. 1b). At the optimal angle α_{max}, the estimated LLE takes the value close to the expected λ_1 that is computed from the equations of the Rössler system [33]. This value is illustrated by a horizontal line in Figure 1a. The presence of an optimum at quite small angles is associated with the most precise estimations of LLE. The character of the dependence $\lambda_1(\alpha)$ (Fig. 1a, circles) is typical for deterministic sequences of IF ISIs.

When small noise is added, the dependence $\lambda_1(\alpha)$ has a different form (Fig. 1a, triangles). In the region of large α, its slope becomes positive (Fig. 1b) starting from some value α^* that depends on both, noise intensity and algorithmic parameters such as the threshold value l_{min} defining the minimal distance between the phase space trajectories. However, the existence of the optimum at α_{max} still allows better estimation of LLE. If noise intensity increases, α^* approaches to α_{max}, and the local maximum of the dependence $\lambda_1(\alpha)$ at α_{max} disappears. In such case, the estimated LLE may essentially differ from the expected value related to noise-free dynamics. Thus, a character of the dependence $\lambda_1(\alpha)$ represents a verifying marker indicating whether the LLE related to noise-free dynamics can be estimated. Additionally, the dependence $\lambda_1(\alpha)$ can be used to compare noise levels presented in the analyzed ISI series since an increased noise intensity leads to larger slopes of $\lambda_1(\alpha)$ in the region $\alpha > \alpha^*$ (Fig. 1b) and smaller values of α^*. Although the value α^* may vary depending on algorithmic parameters such as, e.g., the minimal available distance between trajectories l_{min}, the transition from negative to positive slope of the dependence $\lambda_1(\alpha)$ is kept for noisy data.

Let us point out an additional feature of the dependence $\lambda_1(\alpha)$ for noisy ISI series. When the noise intensity increases, the estimated value λ_1 related to the optimal angle α_{max} may be reduced although the values of LLE for $\alpha > \alpha_{max}$ are larger than for noise-free IF ISI series. This circumstance is probably explained by different lengths of renormalization vectors (Fig. 1c). In the range $\alpha < \alpha_{max}$ small angles reduce an ability to select appropriate perturbations. As a result, the mean length of the renormalization vector may be near the limit of the linear approach. For large vectors, effects of noise consist in a relatively small change of orientation and an increase of vector's components in the directions do not associated with the maximal divergence of trajectories. Besides, the condition of the linear approach is not satisfied between renormalizations. These two reasons lead to a reduced value of λ_1. For large angles, the mean length of the renormalization vector is significantly lower. In this case noise-induced divergence of trajectories at renormalizations can outperform their divergence caused by the dynamics. When a minimization of the perturbation is performed, there is an increased probability to select a point of a neighboring trajectory that becomes closer due to a random fluctuation. Therefore, the length of the renormalization vector is reduced as compared with the noise-free case, and the LLE increases.

The given conclusions are correct if the firing rate is high. According to the earlier studies [14–16], if the mean

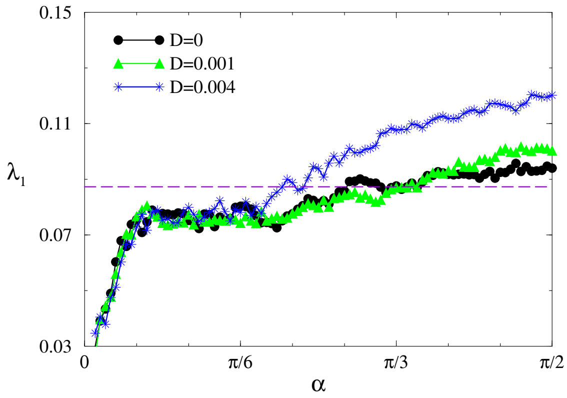
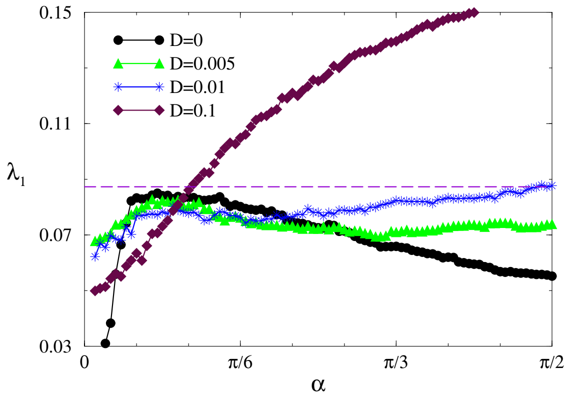
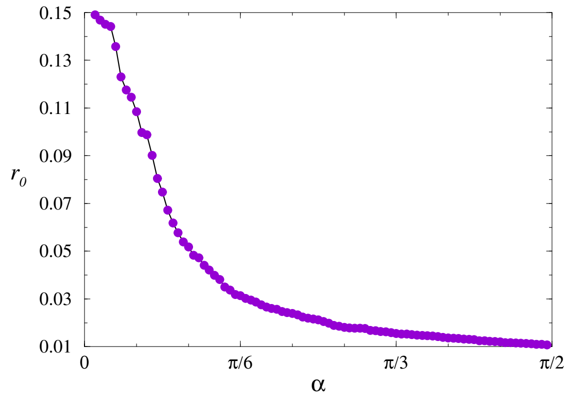


Fig. 2. Dependencies $\lambda_1(\alpha)$ estimated from IF ISI series for different noise intensities and the threshold level $\theta = 60$ leading to the firing rate about 4 spikes/period.



(a)



(b)

Fig. 3. Dependencies $\lambda_1(\alpha)$ estimated from TC ISI series for different noise intensities (a), and mean length of the replacement vector (b) for noise intensity $D = 0.01$.

ISI ($\overline{I}$) becomes less than $P/4$ where P is the mean orbital period, the corresponding sequence of IF ISIs does not allow computing dynamical characteristics of an oscillatory regime at the input of IF-model, and the variation of the amout of data does not significantly improve the performed estimations.

Let us consider the threshold level $\theta = 60$ related to the case when the requirement $\overline{I} < P/4$ is not valid. Large ISIs mean that the input signal is restored with significant errors being analogous to adding noise to IF ISI series. Due to this, even in the case of a deterministic dynamics ($D = 0$), the dependence $\lambda_1(\alpha)$ (Fig. 2) becomes similar to estimations performed for noisy input signals. The absence of an optimal value of α does not allow verifying the performed estimations of LLE. Small noise ($D = 0.0005$) does not change the character of the corresponding dependence since the values of $S(t)$ are larger as compared with the threshold level $\theta = 10$ (Fig. 1a). With increased noise level, however, the slope of $\lambda_1(\alpha)$ becomes larger similar to Figure 1a. Thus, a low firing rate has an analogy with noisy IF ISI series when computing LLE.

4.2 Threshold-crossing model

Analysis of TC ISI series reflecting the dynamics of a low-dimensional chaotic system was also performed for the Rössler model (7) with the $x(t)$ coordinate considered as the input signal, and the threshold level $\Theta = 0$. Aiming to compare effects of noise, a normally distributed random process with the intensity D was added to the sequence of TC ISIs. Figure 3a illustrates the dependences $\lambda_1(\alpha)$ estimated by analogy with the IF-model.

In the case of noise-free dynamics, $\lambda_1(\alpha)$ estimated from TC ISI series is similar to the corresponding dependence given in Figure 1a. Again, there is an optimal angle α_{max} related to the maximum of the dependence $\lambda_1(\alpha)$. LLE associated with this optimal value is nearly close to the expected value of λ_1 shown by the horizontal line in Figure 3a. Underestimated λ_1 are related to both regions, $\alpha < \alpha_{max}$ and $\alpha > \alpha_{max}$ due to a large length of renormalization vectors (Fig. 3b) and increased orientation errors, respectively.

When noise is added to TC ISI series, the form of $\lambda_1(\alpha)$ is changed. As for the IF-model, a positive slope of this dependence appears at large α, and it increases with noise intensity. Besides, the value of λ_1 becomes lower in the region of α_{max} related to the noise-free dynamics, although the estimated LLE increases at larger α. A possible explanation is analogous to the case of IF-model because the dependence of the mean length of the replacement vector on the angle α (Fig. 3b) is quite similar to the curve shown in Figure 1c. At small α, the divergence of trajectories related to the system's dynamics outperforms changes caused by noise. On the contrary, at large α noise-induced changes of the vector's length are more significant. By analogy with the IF-model, this leads to smaller initial perturbations and larger LLE. Again, a character of the dependence $\lambda_1(\alpha)$ allows confirming the estimations of λ_1 related to noise-free dynamics at the presence of an optimal α and effects of noise based on the slope of $\lambda_1(\alpha)$ at large α. Larger noise intensities increase the corresponding slope. The absence of an optimal α in the latter case does not allow estimations of λ_1 of noise-free dynamics.

4.3 Other examples

In the previous subsections, possibilities and limitations of the considered approach were examined using the Rössler system that demonstrates rather smooth oscillations. Let us now discuss other examples in order to show similarity of the observed phenomena and consider a burst oscillator described by the pancreatic β-cell model [34]

$$\begin{aligned}\frac{dV}{dt} &= \left(-I_{Ca} - I_K - g_S S\left(V - V_K\right)\right)/\tau \\ \frac{dn}{dt} &= \mu(n_\infty - n)/\tau \\ \frac{dS}{dt} &= (S_\infty - S)/\tau_S \\ I_{Ca}(V) &= g_{Ca} m_\infty (V - V_{Ca}) \\ I_K(V,n) &= g_K n(V - V_K) \\ x_\infty &= \frac{1}{1+\exp((V_x - V)/\theta_x)},\ x = m, n, S\end{aligned} \quad (8)$$

with the following parameter set: $g_{Ca} = 3.6$, $g_K = 10.0$, $g_S = 4.0$, $\tau = 20$ ms, $\tau_S = 35$ s, $V_{Ca} = 25$ mV, $V_K = -75$ mV, $V_m = -20$ mV, $V_n = -16$ mV, $V_S = -40$ mV, $\theta_m = 12$ mV, $\theta_n = 5.6$ mV, $\theta_S = 10$ mV, $\mu = 0.85$. In the model (8), V is the voltage across the cell membrane, n is the fraction of potassium channels, and S represents the intracellular calcium concentration.

Figure 4 illustrates the dependencies $\lambda_1(\alpha)$ for deterministic ($D = 0$) and noisy ($D = 0.05$) ISI series. Again, general features of these dependencies are similar to the case of the Rössler system.

In the case of noise-free quasi-periodic dynamics (Fig. 5), the dependence $\lambda_1(\alpha)$ is nearly constant with the value $\lambda_1 \approx 0.002$ for small values of α that is comparable with the available error of the method [20] for non-chaotic regimes. The absence of an optimum of $\lambda_1(\alpha)$ in the left part of the given dependence is typical for regular regimes. Noise provides a growth of the estimated λ_1 for large angles, and the behavior of $\lambda_1(\alpha)$ becomes similar to the corresponding dependence for chaotic point processes contaminated by noise (see, e.g., Fig. 3a, $D = 0.1$).

Finally, let us consider the case when the sequence of TC ISIs does not contain a low-dimensional dynamics. As an example, we may take a color noise as I_i. Figure 6 illustrates a monotonically increased dependence $\lambda_1(\alpha)$ for such ISI-series.

In the case of high dimensional chaos generated by time-delay systems such as, e.g., the Mackey-Glass model, the method does not provide estimations of λ_1 that are close to the expected value of the LLE when dealing with quite short sequences of ISIs. The latter is in accordance with the fundamental limitations for estimating Lyapunov exponents in dynamical systems [35] explaining that extremely long time series are required for the performed estimations. High-dimensional chaotic systems and intermittent chaos are discussed in [36,37].

Thus, the characteristic dependence $\lambda_1(\alpha)$ with an optimum in the range of quite small angles is typical for low-dimensional chaotic ISI-series contaminated by noise when

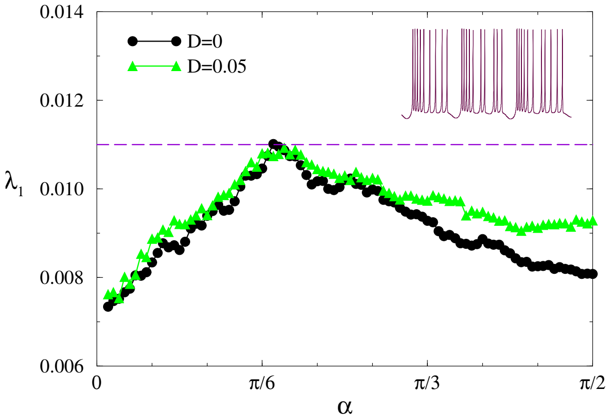


Fig. 4. Dependencies $\lambda_1(\alpha)$ estimated from TC ISI series produced by the pancreatic β-cell model for $D = 0$ and $D = 0.05$. Dashed line marks the value $\lambda_1 = 0.011$ estimated using the equations of the model (8).

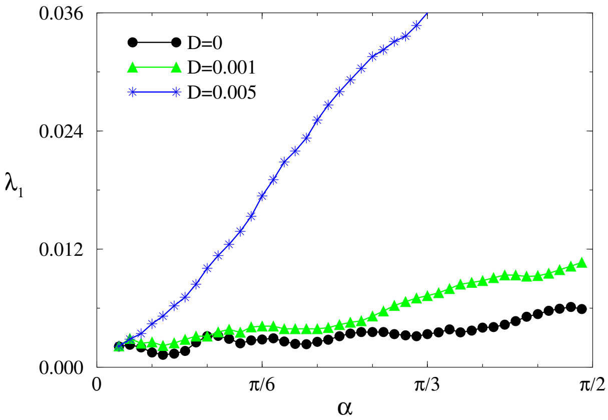


Fig. 5. Dependencies $\lambda_1(\alpha)$ estimated from TC ISI series related to noisy quasi-periodic oscillations.

noise intensity is small. Let us note that we change the range of the considered scales for perturbations by varying the angle α that is clearly seen from Figures 1c and 3b. For large α, we mainly deal with small scales, while for small α we consider significantly larger scales. However, the range of the considered scales is quite broad within the approach [20], and the dependences $r_0(\alpha)$ shown in Figures 1c and 3b illustrate the behavior of mean length of the replacement vectors. In order to analyze how the divergence of nearby trajectories depends on the scale in more detail, the concept of scale-dependent Lyapunov exponent [23–25] may be useful. It can be applied, e.g., to study the case of large noise intensities when the approach considered in the given paper provides similar results.

5 Conclusion

In this paper we discussed abilities of quantifying dynamical features of low-dimensional chaotic oscillations at the input of two threshold models (IF and TC) from the output sequences of interspike intervals at the presence

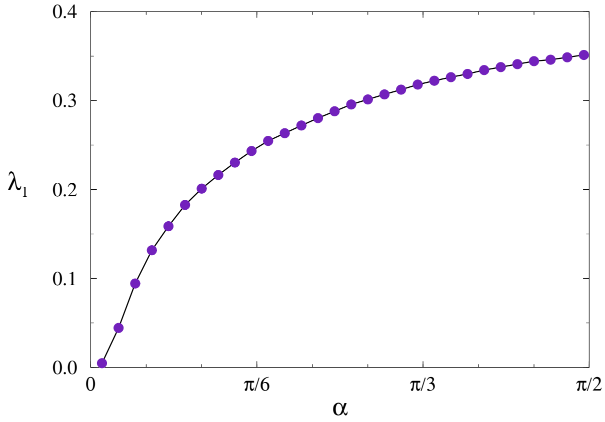


Fig. 6. Dependence $\lambda_1(\alpha)$ estimated from ISI-series representing a color noise.

of noise. For IF-model, the largest Lyapunov exponent is quite easily estimated at high firing rate in the case of a deterministic dynamics. When the firing rate is low or the output spike train is contaminated by noise, the problem of determining dynamical characteristics from point processes becomes more complicated. Here, we proposed an approach for verifying LLE estimation for noisy data that consists in computing the dependence of LLE versus the maximal available angle at renormalizations. The existence of a clear optimum of this dependence confirms the ability to estimate the characteristics of noise-free dynamics, while a positive slope of $\lambda_1(\alpha)$ is typical for noisy ISI series or for the case of low firing rate when errors in restoration of the input signal are similar to the effect of additive fluctuations.

We considered analogous features of the used approach for TC ISI series. Again, two informative signs of the dependence $\lambda_1(\alpha)$ are revealed, namely, the existence of an optimum associated with LLE that approaches the value estimated from the equations of chaotic oscillator, and a change from a negative to a positive slope of $\lambda_1(\alpha)$ at large angles for noisy data. Thus, we conclude that the proposed modification of the approach for computing LLE from ISI series can be applied to different types of point processes analyzed at the presence of fluctuations.

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Author contribution statement

All authors contributed equally to the paper.

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