

Delay-induced stochastic bursting in excitable noisy systemsChunming Zheng¹ and Arkady Pikovsky^{1,2}¹*Institute for Physics and Astronomy, University of Potsdam, Karl-Liebknecht-Strasse 24/25, 14476 Potsdam-Golm, Germany*²*Research Institute for Supercomputing, Nizhny Novgorod State University, Gagarin Avenue 23, 606950 Nizhny Novgorod, Russia*

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We show that a combined action of noise and delayed feedback on an excitable theta-neuron leads to rather coherent stochastic bursting. An idealized point process, valid if the characteristic timescales in the problem are well separated, is used to describe statistical properties such as the power spectral density and the interspike interval distribution. We show how the main parameters of the point process, the spontaneous excitation rate, and the probability to induce a spike during the delay action can be calculated from the solutions of a stationary and a forced Fokker-Planck equation.

DOI: [10.1103/PhysRevE.98.042148](https://doi.org/10.1103/PhysRevE.98.042148)**I. INTRODUCTION**

Time-delayed feedback and noise are factors that substantially contribute to complexity of the dynamical behaviors. While noise generally destroys coherence of oscillations, there are situations (e.g., stochastic and coherence resonances) where it plays a constructive role leading to a quite regular behavior [1,2]. Also delayed feedback can either increase or suppress coherence of oscillators [3–5]. Interplay of delay and noise is important for neural systems, where it has been studied both on the level of individual neurons [6], of networks of coupled neurons [7], and of rate equations [8].

A significant progress in understanding of an interplay of noise and delayed feedback has been achieved for bistable systems [9,10]. Furthermore, variants of the bistable dynamics with highly asymmetric properties of the two states have been adopted to describe excitable systems under delay and noise [6,7,11]. In this paper we develop another approach to the dynamics of excitable noisy systems with a delayed feedback. We investigate a theta-neuron model [12], which is a paradigmatic example of an excitable system in mathematical and computational neuroscience. Under the action of a small noise, this system demonstrates a random, Poisson sequence of spikes. For the stochastic excitable theta neuron model, the interspike interval distribution and the coefficient of variation have been analyzed analytically in Refs. [13,14]. We will show that a small additional delayed feedback (large feedback can significantly modify the dynamics, see, e.g., Ref. [15]) leads to an interesting partially coherent spike pattern which we call *stochastic bursting*. Bursting describes a general phenomenon with quiescent periods following periods of rapid repeated firing and is thought to be important in communication between neurons and synchronization [16]. In our present paper, the bursts themselves appear at random instants of time and have random duration, but inside each burst the spikes are separated by nearly constant time intervals. Contrary to the bistable models, in our description we consider only the excitable state as stochastic one, while the excitation itself is deterministic.

The paper is organized as follows. We first formulate the basic model in Sec. II. Then, in Sec. III we formulate a point process description of the stochastic bursting, and derive statistical properties such as the distribution of inter-spike intervals and the power spectral density. In this description there are two parameters, the rate of excitation and the probability for delayed feedback to induce a spike. The latter quantity is nontrivial, and we describe approaches to its calculation in Sec. IV. We discuss the results in Sec. V.

II. MODEL FORMULATION

In this paper we study the dynamics of an excitable system subject to noisy input and delayed feedback. The model is described by a scalar variable θ defined on a circle:

$$\dot{\theta} = a + \cos \theta + \epsilon[a + \cos \theta(t - \tau)] + \sqrt{D}\xi(t). \quad (1)$$

Here parameter a defines the excitability properties, parameter D describes the level of external noise [which we assume to be Gaussian white one, $\langle \xi(t) \rangle = 0$, $\langle \xi(t)\xi(t') \rangle = 2\delta(t - t')$], and ϵ is the amplitude of a delayed feedback. The feedback is chosen to vanish in the steady state of the system. Model Eq. (1), without delayed feedback, is very close to the theta-neuron model [12], extensively explored in different contexts in neuroscience (where inclusion of noise is very natural, while a delayed feedback is often attributed to the autapse effect, cf. [17]), and to the active rotator model [18]. In Eq. (1) we assume a simple additive action of the delayed feedback and of noise. For theta-neurons, one quite often explores multiplicative forcing, where the force terms are multiplied with factor $(1 - \cos \theta)$ (cf. Ref. [19]; notice that our variable is shift by π to the variable used in Ref. [19]). However, as will be clear from the analysis below, this brings only small quantitative corrections to the results, while the main qualitative conclusions remain valid – because the most sensitive to forcing region in the phase space is around $\theta \approx -\pi$, and in this domain the factor $(1 - \cos \theta)$ is nearly a constant.

For $|a| \lesssim 1$ the autonomous theta-neuron (without noise and feedback) is in an excitable regime: there are two nearby

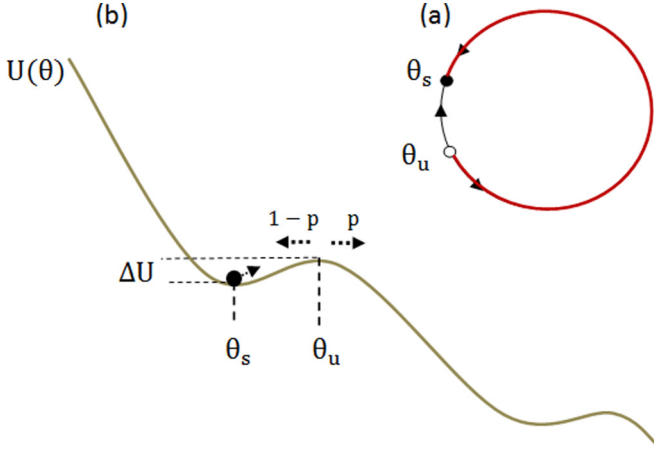


FIG. 1. A sketch of the theta-neuron model Eq. (1). In (a), the red trajectory from θ_u to θ_s represents a spike, while the black curve shows relaxation without a spike. Panel (b) depicts how the “phase particle” evolves in the effective potential $U(\theta)$, either overcoming the barrier (with probability p), or returning back to the equilibrium θ_s (with probability $1 - p$).

stationary states, one stable and one unstable. Both noise and the feedback can kick the system from the stable equilibrium so that it produces a “spike.” Our goal in this paper is to describe statistical properties of the appearing spike train. Prior to the full analysis, we briefly outline relatively simple cases of the purely deterministic dynamics (no noise) and of the purely noisy dynamics (no delayed feedback).

A. Deterministic case

An autonomous theta-neuron (one sets $\epsilon = D = 0$ in (1)) with $|a| \lesssim 1$ is an excitable system with one stable fixed point at $\theta_s = \arccos(-a)$ and another unstable fixed point at $\theta_u = 2\pi - \arccos(-a)$. One can represent the dynamics as an overdamped motion in an inclined periodic potential

$$\dot{\theta} = -\frac{dU}{d\theta}, \quad U(\theta) = -a\theta - \sin\theta, \quad (2)$$

for which θ_s is a local minimum and θ_u is a local maximum; see Fig. 1. As parameter a is close to the value of a SNIC bifurcation $a = 1$, the distance $\theta_u - \theta_s$ is small (correspondingly, the barrier of the potential is small as well) and already a small external perturbation can produce a nearly 2π -rotation of θ . The form of the spike can be represented as a trajectory that starts at θ_u , ends at θ_s , and reaches the maximal value at time instant t_0 :

$$\Theta_{\text{sp}}(t) = 2 \arctan \left[\sqrt{\frac{1+a}{1-a}} \tanh \left(\frac{\sqrt{1-a^2}}{2} (t - t_0) \right) \right]. \quad (3)$$

Let us now consider deterministic model (1) with delay, i.e., the case $D = 0$. The system still has a locally stable equilibrium θ_s . However, for large enough ϵ it can possess stable periodic oscillations. Indeed, a perturbation of the equilibrium can result in a spike Eq. (3). After the delay time τ , a force

$$\epsilon H(t) = \epsilon [a + \cos \Theta_{\text{sp}}(t)] \quad (4)$$

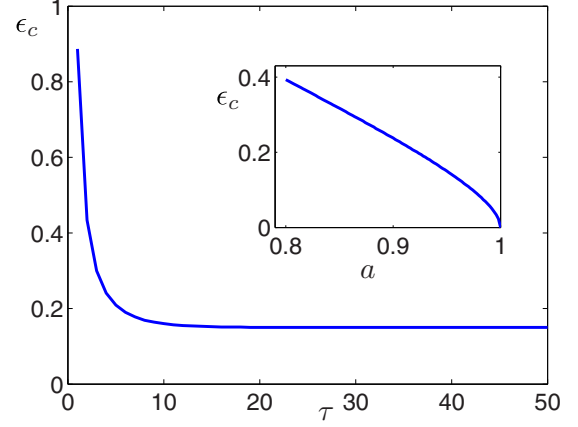


FIG. 2. Critical value of ϵ in dependence on the delay time τ in the deterministic case with $a = 0.95$. The inset is the asymptotic value at large delay times ϵ_c in dependence on excitability parameter a .

will act on the theta-neuron. For a sufficiently large value of ϵ it will produce a new spike, etc. In Fig. 2 we show critical values of ϵ that depend on the delay time τ as well as the excitability parameter a . Clearly, $\epsilon_c \rightarrow 0$ if the excitability parameter a approaches the bifurcation value $a_{\text{SNIC}} = 1$. Dependence on the delay time is also rather obvious: for large delays the critical value ϵ_c is delay-independent, while for delays comparable to the pulse duration [which is, according to Eq. (3), $\sim (1 - a^2)^{-1/2}$] there is a blocking effect which mimics a refractory period for a neuron after a spike.

B. Noisy case

If there is no time-delay feedback, i.e., $\epsilon = 0$, but noise is present, $D > 0$, the spikes can be induced by noise. The model is well-described in the literature [20], here we briefly outline the features required for consideration of the more complex case with delay. The dynamics is especially simple for small noise: in this case, most of the time the system stays in a neighbourhood of the stable state θ_s , and the excitations are rare. The sequence of spikes builds a Poisson process with a constant spiking rate λ , which is equal to the probability current J of the corresponding Fokker-Planck equation

$$\frac{\partial P(\theta, t)}{\partial t} = -\frac{\partial J}{\partial \theta} = -\frac{\partial}{\partial \theta} [(a + \cos \theta)P(\theta, t)] + D \frac{\partial^2 P(\theta, t)}{\partial \theta^2}. \quad (5)$$

The stationary solution of Eq. (5) is

$$P_{\text{st}}(\theta) = C \int_{\theta}^{\theta+2\pi} \frac{d\psi}{D} e^{-\int_{\theta}^{\psi} \frac{a+\cos\varphi}{D} d\varphi}. \quad (6)$$

Here C is the normalization constant, so the current is represented as

$$\lambda = J = C \left(1 - e^{-\int_0^{2\pi} \frac{a+\cos\theta}{D} d\theta} \right). \quad (7)$$

In the limit of small noise, this exact expression reduces to the Kramers escape rate over the potential barrier: $\lambda \approx \frac{1}{2\pi} \sqrt{U''(\theta_s)|U''(\theta_u)|} \exp\{-\Delta U/D\}$.

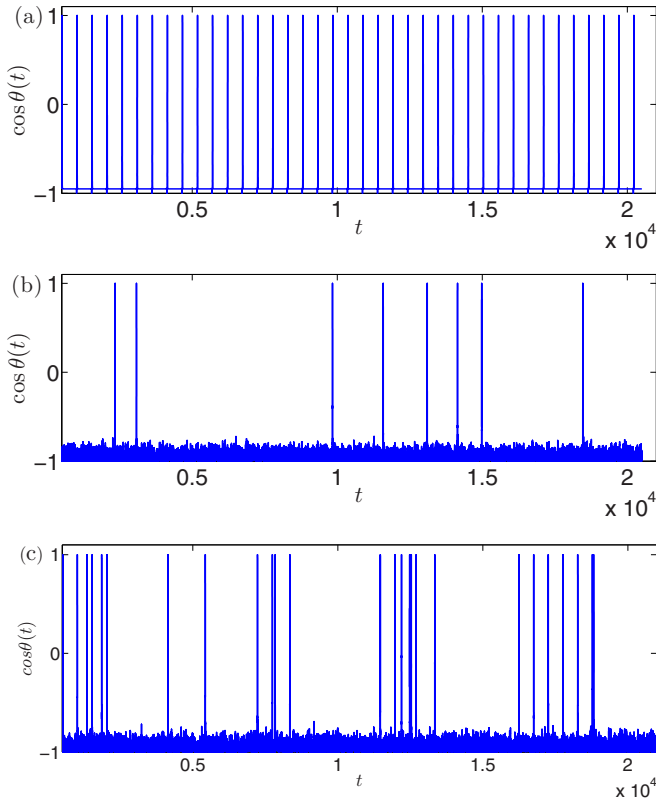


FIG. 3. Panel (a) is the periodic solution in the deterministic case when $\epsilon > \epsilon_c$. In this deterministic case we simulate Eq. (1) by the Euler method with discrete time interval $dt = 0.01$. Panel (b) shows the noisy case without delayed feedback, i.e., $\epsilon = 0$, with the spike train obeying the Poisson statistics. Panel (c) is the case with both noise ($D = 0.005$) and delayed feedback ($\epsilon = 0.14$), showing the *stochastic bursting* phenomenon. Spike trains in panels (b) and (c) are obtained through simulation Eq. (1) by the Euler-Maruyama method with discrete time interval $dt = 0.01$. Many spikes with the interval close to τ are induced, depending on the delay force amplitude. The parameters are $a = 0.95$, $\tau = 500$.

III. DELAY AND NOISE-INDUCED BURSTING AS A POINT PROCESS

Our main interest here is in the combination effect of time delay and noise with $D \neq 0$, $\epsilon \neq 0$. We illustrate the dynamics in Fig. 3(c), where we compare it with the purely periodic dynamics in the deterministic case [Fig. 3(a)] and with the Poisson sequence of spikes for delay-free case [Fig. 3(b)]. In Fig. 3(c) one can see randomly appearing spikes, like in case Fig. 3(b), and “bursts” of several spikes separated by the delay time τ [like in case Fig. 3(a)]. Qualitatively, this picture illustrates the two sources of spike formation: (i) due to a fluctuation of the noise driving, this source is delay-independent, and (ii) delay-induced spikes which appear due to a combinational effect of delay forcing and noise. We call the former spikes “spontaneous” ones, or “leaders,” and the latter spikes as “induced” ones, or “followers.” An exact analytic approach to the noisy dynamics is hardly possible, because in presence of delay feedback and noise, the system is non-Markovian. Therefore we will next formulate an idealized point process model, which generalizes the Poisson point process in absence

of the delayed feedback. Then, in Sec. IV we will discuss how to calculate parameters of this point process. Since the possibility of applying the point process model is based on the separation of timescales, it is required that the length of the pulse is much smaller than the characteristic interspike interval, which is either the delay time, or the characteristic time interval between the spontaneous spikes. We assume this conditions to be fulfilled, and use in numerical examples the parameters that ensure the timescale separation.

A. Point process model

Point processes are widely used to mathematically model physical processes that can be represented as a stochastic set of events in time or space, including spike trains. The spike train can be viewed as a sequence of pulses, fully determined via the spike appearance times t_j . In the case each spike is considered as a δ pulse, we have $\sum_j \delta(t - t_j)$; more generally we can write $\sum_j H(t - t_j)$, where H is the waveform Eq. (4). In our model, we adopt the leader-follower relationship to describe the spiking pattern of type shown in Fig. 3(c). The spikes which appear when the delay feedback is weak, i.e., solely due to a large fluctuation of noise, we call “spontaneous” ones. As delay plays no role for these spikes, they form a Poisson process with rate λ , as described in Sec. II B. Each spontaneous spike produces, after delay time τ , forcing Eq. (4). During this pulse forcing, the potential barrier decreases and there is an additional enlarged probability to overcome the barrier and to produce a “follower” spike. We denote the total probability to induce the follower spike as p (correspondingly, the probability to have no follower is $1 - p$). Of course, each induced spike can also produce a follower, with the same probability p . Thus, a leader spike induces a sequence of exactly L followers with probability $\varrho(L) = p^L(1 - p)$.

The two parameters, λ and p , fully describe the point process, consisting of “bursts” as shown in Fig. 4. Each burst starts with a leader, which appears with a constant rate λ , these leaders form a Poisson process. The followers are separated by the time interval τ , their number in the burst is random according to the distribution $\varrho(L)$. Noteworthy, the bursts can overlap.

Below we discuss statistical properties of the point process following from the described model. It is rather simple to obtain the overall density of spikes. Indeed, the average number of followers of a leader is $\sum_{L=0}^{\infty} L \varrho(L) = \frac{p}{1-p}$, and hence the overall spike rate is

$$\mu = \lambda \left(1 + \frac{p}{1-p} \right) = \frac{\lambda}{1-p}. \quad (8)$$

Because the process is stationary, the probability to have a spike in a small time interval $(t, t + \Delta)$ does not depend on t and is equal to $\mu \Delta$. Correspondingly, the probability that in a finite time interval T there is no one spike is $\exp[-\mu T]$.

B. Interspike interval distribution

Now we derive the interspike interval (ISI) distribution, employing the renewal theory [21,22]. Given a spike at time t and the next spike at time t' , the probability to have no

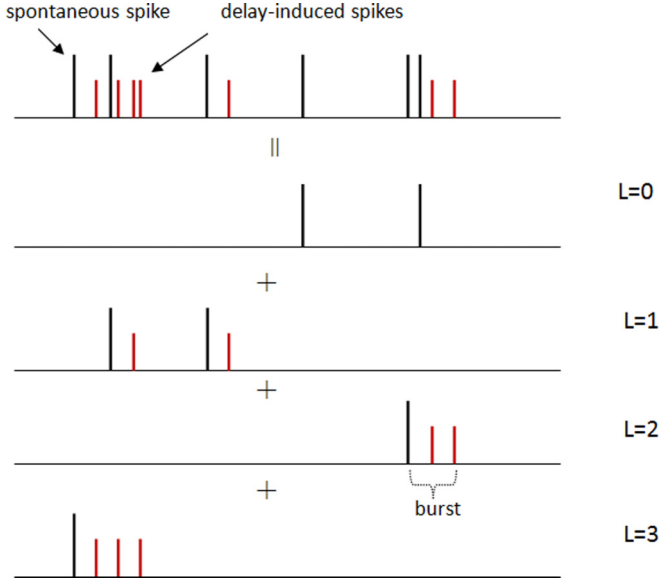


FIG. 4. Schematic description of the point process. The black high pulses represent the spontaneous spikes (leaders) while the red low ones represent the delay-induced spikes (followers) (the difference in the height of spikes is just a schematic way to classify the events into leaders and followers, while they are of the same height in reality). A leader with a random number of its followers form a burst. The whole process can be viewed as a superposition of sub-processes with a fixed number of followers.

spike in the interval $[t, t']$ is called survival function. Let us separate the ISI, i.e., $T = t' - t$, into three different cases, namely, $T > \tau$, $T = \tau$ and $T < \tau$. If $T < \tau$, the spikes at t and t' can be either spontaneous (leader) or delay-induced ones (followers of spikes preceding that at t), so the survival function is determined by the full rate μ : $S(T) = \exp(-\mu T)$. In contradistinction, for the case $T > \tau$, the next spike can be only a spontaneous one. The probability that there is no spike in $[t, t']$ is the product of three terms: the probability to have no spikes in the interval $[t, t + \tau)$ with survival function $S_{\tau b} = \exp(-\mu\tau)$, the probability $(1 - p)$ not to have a follower for the spike at t , and the probability to have no spike in the interval $[t + \tau, t']$, where only the spontaneous rate λ applies with the survival function $S_{\tau a} = \exp(-\lambda(T - \tau))$. Thus, the survival function for the case $T > \tau$ is $S(T) = S_{\tau b}(1 - p)S_{\tau a} = (1 - p)e^{-\mu\tau - \lambda(T - \tau)}$. Based on the above description and the relationship between the cumulative ISI distribution $Q(T)$ and the survival function $Q(T) = 1 - S(T)$, the cumulative ISI distribution can be obtained as follows:

$$Q(T) = \begin{cases} 1 - e^{-\mu T}, & T < \tau, \\ 1 - (1 - p)e^{-\mu\tau - \lambda(T - \tau)}, & T \geq \tau. \end{cases} \quad (9)$$

According to the relationship between the cumulative ISI distribution and the ISI distribution density $P(T) = Q'(T)$, we can also obtain the ISI distribution density:

$$P(T) = \begin{cases} \mu e^{-\mu T}, & T < \tau, \\ p e^{-\mu\tau} \delta(T - \tau), & T = \tau, \\ \lambda(1 - p)e^{-\mu\tau - \lambda(T - \tau)}, & T > \tau. \end{cases} \quad (10)$$

We compare the obtained ISI distribution with the numerical result in Fig. 5.

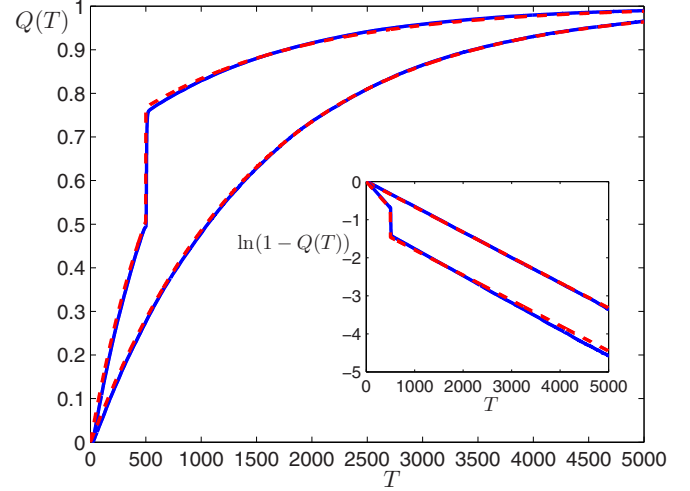


FIG. 5. Cumulative ISI distribution $Q(T)$ vs T . The blue curve shows numerical simulations of Eq. (1), the dashed red curve corresponds to the point process with Eq. (9), where $\lambda = 6.64 \times 10^{-4}$ is calculated from Eq. (7) and $p = 0.53$ is calculated from Eq. (20). The upper two curves with a jump at $T = \tau$ correspond to the delay case with $\epsilon = 0.14$, while the lower two ones correspond to the case without delay, i.e. $\epsilon = 0$. The inset in a logarithmic scale is to show the coincidence of the slopes, which validates the point process representation of the original model. Parameters are $a = 0.95$, $D = 0.005$, and $\tau = 500$.

C. Power spectral density

Next, we discuss correlation properties of the point process. The spike train in our model can be represented as a superposition of sub-trains having a fixed number L of followers; see Fig. 4 for an illustration of this superposition. Let us denote $H(t)$ the shape of a spike [it is a δ function for the point process model, but for a real process it is given by Eq. (3)]. Then the time series can be written as sum of subseries of bursts of size $L + 1$:

$$x(t) = \sum_{L=0}^{\infty} G_L(t) \otimes Y_L(t) \otimes H(t), \quad (11)$$

where terms G_L and Y_L describe the leaders and the followers for the bursts of size $L + 1$:

$$G_L(t) = \sum_i \delta(t - t_L^i); \quad Y_L(t) = \sum_{l=0}^L \delta(t - l\tau). \quad (12)$$

The leaders of a sub-series of bursts of size $L + 1$ form a Poisson process with the rate $\lambda\varrho(L)$, and the followers form a periodic set of spikes with separation τ . Here symbol \otimes denotes a convolution.

According to the property of convolution and the independence of the subseries for different L , the power spectral density is the sum of spectral densities of the series; inside each subseries we have a product of spectral functions:

$$S_x(\omega) = \sum_{L=0}^{\infty} S_{G_L}(\omega) S_{Y_L}(\omega) S_H(\omega). \quad (13)$$

Here $S_{G_L}(\omega)$ is the power spectral density of the spontaneous spikes, which have the Poisson statistics. The power spectral density of the Poisson process is a constant [23]:

$$S_{G_L}(\omega) = \lambda \varrho(L) = \lambda(1-p)p^L. \quad (14)$$

The term $S_{Y_L}(\omega)$ is the power spectral density of the set of L points separated by time interval τ , i.e.,

$$S_{Y_L}(\omega) = \left| \int_0^\infty Y_L(t) e^{-i\omega t} dt \right|^2 = \frac{1 - \cos(L+1)\omega\tau}{1 - \cos\omega\tau}. \quad (15)$$

Finally, $S_H(\omega)$ is the power spectral density of the shape function

$$S_H(\omega) = \left| \int_{-\infty}^\infty H(t) e^{-i\omega t} dt \right|^2.$$

Summarizing, we obtain the following expression for the power spectral density of the spike train:

$$\begin{aligned} S_x(\omega) &= \sum_{L=0}^{\infty} \frac{1 - \cos(L+1)\omega\tau}{1 - \cos\omega\tau} \lambda(1-p)p^L S_H(\omega) \\ &= \frac{\lambda(1+p)}{1 + p^2 - 2p \cos\omega\tau} S_H(\omega). \end{aligned} \quad (16)$$

The most important part of the spectrum is the first factor, thus we discuss the spectrum for the case of δ -pulses $S_H = 1$. For the limiting delay-free case, when $p = 0$, we have $S_x(\omega) = \lambda S_H(\omega)$, which corresponds to a purely Poisson process of spontaneous spikes. In another limiting case of extensive bursting $p \rightarrow 1$, the power spectral density becomes a periodic sequence of narrow Lorentzian-like peaks at frequencies $\omega = 0, \frac{2\pi}{\tau}, \frac{4\pi}{\tau}, \dots$. The width of a peak is $\sim (1-p)$, while the amplitude scales $\sim (1-p)^{-2}$ (the total power of a peak diverges in this limit because the density of spike diverges).

In Fig. 6 we compare the obtained expression for the spectral density with direct numerical modeling of Eq. (1).

IV. PROBABILITY TO INDUCE A SPIKE

As have been shown in the Sec. III above, in our model, from the viewpoint of a point process, there are only two parameters: the spontaneous spiking rate λ (or J) and p , the probability to induce a spike by a delay force and noise. The expression for λ is given by Eq. (7). The main challenge that is discussed in this section, is an analytical calculation of p .

From the simulations of Eq. (1), where the delay force can be switched off and on (corresponding to $\epsilon = 0$ and $\epsilon \neq 0$, respectively), the probability to induce a spike follows from the relation Eq. (8):

$$p = \frac{\langle n \rangle - \langle n_0 \rangle}{\langle n \rangle}. \quad (17)$$

Here $\langle n_0 \rangle$ is the average number of spikes within a large time interval without the time-delayed force, while $\langle n \rangle$ is the average number of spikes in presence of the delayed force within the same time interval.

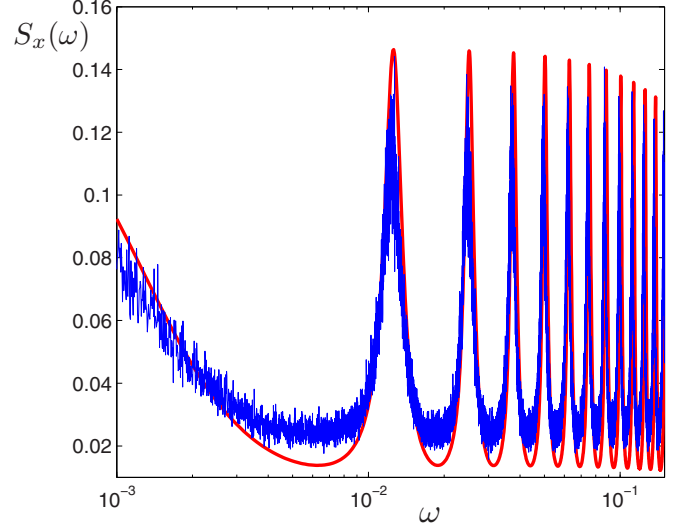


FIG. 6. The power spectral density from the simulations (blue curve) and from the point process (red curve) described by Eq. (16), in which $\lambda = 6.64 \times 10^{-4}$, $p = 0.53$ are calculated from Eq. (7) and Eq. (20), respectively. The shape function is as Eq. (4) describes. Values of a , D and τ are the same as in Fig. 5, i.e., $a = 0.95$, $D = 0.005$, and $\tau = 500$.

A. Induced probability from the solution of the Fokker-Planck equation

Due to the nonlinear force and non-Markovian property of Eq. (1), it is hard to obtain the exact solution analytically, e.g., formulating it in terms of delay Fokker-Planck equation. However, since a is close to 1 and the noise intensity is small, we can approximate the delay force with a deterministic time-dependent force based on the spike solution Eqs. (3) and (4). Thus, the problem reduces to consideration of a deterministically driven stochastic model,

$$\dot{\theta} = a + \cos\theta + \epsilon H(t) + \sqrt{D}\xi(t), \quad (18)$$

where the force term is given by Eq. (4). The corresponding Fokker-Planck equation reads

$$\begin{aligned} \frac{\partial P(\theta, t)}{\partial t} &= -\frac{\partial}{\partial \theta} \{ [a + \cos\theta + \epsilon H(t)] P(\theta, t) \} \\ &\quad + D \frac{\partial^2 P(\theta, t)}{\partial \theta^2}. \end{aligned} \quad (19)$$

To properly formulate the setup for this equation, we need to describe its dynamics qualitatively. As a starting state prior to incoming pulse $H(t)$, we can take a stationary distribution of the equation with $\epsilon = 0$, i.e., the stationary solution (6): $P(\theta, -T) = P_{st}(\theta)$, for $0 \leq \theta < 2\pi$. Here $-T$ is a starting point of pulse action. Under action of the pulse, this state evolves, and $P(\theta, t)$ shifts in positive direction of θ , and a flux of probability through the point $\theta = 0$ increases—this exactly describes increased local rates of a spike excitation during the action of the pulse. To control “multiple” pulse excitation (generation of two or more spikes during one acting pulse) it is convenient to choose the period of domain as 8π instead of 2π . Then, after the action of the pulse $H(t)$, a state $P(\theta, T)$ is reached. The net probability within the domain $[2\pi, 4\pi]$ can

be interpreted as the probability to induce just one spike by the force $\epsilon H(t)$ as follows:

$$p = \int_{2\pi}^{4\pi} [P(\theta, T) - P_0(\theta, T)]d\theta. \quad (20)$$

Here $P(\theta, T)$ is the solution of Eq. (19), while $P_0(\theta, T)$ is the corresponding solution of the unforced Fokker-Planck equation (i.e., of Eq. (19) with $\epsilon = 0$)—it describes spontaneous spikes. The total probabilities in domains $[4\pi, 6\pi]$ and $[6\pi, 8\pi]$ (they correspond to the probabilities to induce 2 or 3 spikes) are actually very close to zero and therefore can be neglected.

Practically, we solve Eq. (19) with a spectral method. We represent the probability density as a (truncated) Fourier series as $P(\theta, t) = \sum_{m=-N}^N C_m(t)e^{i\frac{m}{4}\theta}$, and substitute it into the Fokker-Planck equation. In this way we obtain a large system of nonautonomous ODEs for the Fourier modes

$$\begin{aligned} \frac{dC_m}{dt} = & \frac{m}{8i}C_{m-4} - \left[\frac{i}{4}ma + \frac{i}{4}m\epsilon H(t) + \frac{m^2}{16}D \right] C_m \\ & + \frac{m}{8i}C_{m+4}. \end{aligned} \quad (21)$$

We truncated this system at $N = 400$ and solved the above ODEs by the fourth-order Runge-Kutta method with time step 0.001.

As Fig. 7 depicts, the numerical method described fits well with the simulation results. We also investigated how the noise intensity influences the probability to induce a spike. To analyze the role of noise and delay, we compare the results in presence of noise with the deterministic case, where there is a critical value of ϵ to induce periodic spikes. Generally speaking, for $\epsilon < \epsilon_c$, noise enhances the spiking by

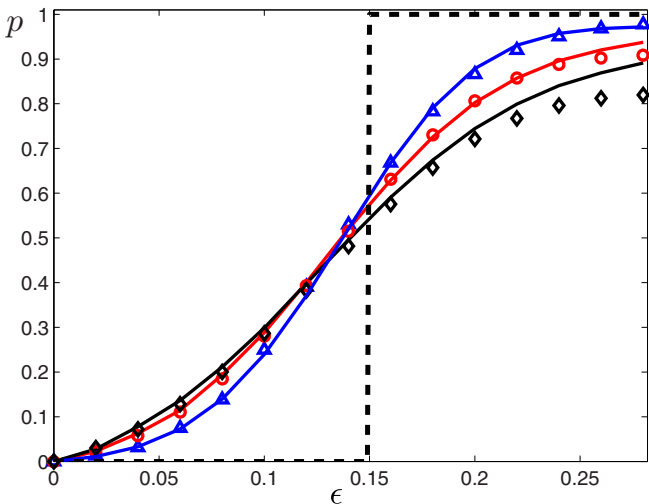


FIG. 7. Probability to induce a spike by time delayed feedback for different delay force amplitudes. The blue triangles, red circles, and black diamonds represent the simulation results of Eq. (17) for $D = 0.005, 0.007, 0.009$ [we used the Euler-Maruyama method with time step $dt = 0.01$, integration interval was 5×10^5 , and additionally averaging over 200 realizations was performed]. The solid lines with the same color is the corresponding numerical results of Eq. (20). The black dashed line is the deterministic solution with $\epsilon_c = 0.15$. Parameters are chosen as $a = 0.95, \tau = 500$.

cooperation with the delay feedback, while for $\epsilon > \epsilon_c$ noise can prevent spikes otherwise induced by the delay feedback.

B. Analytic approaches to calculate induced probability

As we have shown above, the problem reduces to the analysis of a pulse-driven Fokker-Planck equation. Such an analysis can be performed analytically in the limiting cases of an adiabatic (very long) pulse, and of a kicked (δ -function) driving. The adiabatic approximation appears to be rather bad, while for a narrow pulse, as we show below, the approximation of a δ -kick appears to be satisfactory.

It is convenient to introduce a parameter to control the width of the forcing pulse. Therefore, Eq. (1) is modified into the following one:

$$\dot{\theta} = a + \cos \theta + \epsilon C_q [a + \cos \theta(t - \tau)]^q + \sqrt{D}\xi(t). \quad (22)$$

Here parameter q determines the effective width of the pulse, and C_q is the normalization coefficient defined as

$$C_q = \frac{1}{\int_{-\infty}^{\infty} (a + \cos \Theta_{sp}(t))^q dt},$$

being consistent with Eq. (1) when $q = 1$. For large values of q , the force in Eq. (22) is nearly a δ -pulse.

The analysis can be performed in terms of the so-called splitting probability. We start with an equilibrium solution of the autonomous Fokker-Planck Eq. (6), which for small noise is concentrated around the stable state (minimum of the potential). During the δ -kick, the static potential and diffusion term do not play a role, and hence the effective evolution of the probability density from τ^- to τ^+ is just the shift:

$$P(\theta, \tau^+) = e^{-\epsilon \frac{\partial}{\partial \theta}} P(\theta, \tau^-) = P_{st}(\theta - \epsilon). \quad (23)$$

Due to the noisy environment, the following evolution is a relaxation, described by the autonomous Fokker-Planck equation. During this evolution, a “particle” can overcome the potential barrier, thus producing a spike, or return back to the stable state, this corresponds to not inducing a spike. The main contribution is from the points around $\theta_s + \epsilon$, for which we can approximate the potential by the inverted parabolic one. Evolution in such a potential is known as the splitting problem [24]. If the “phase particle” is initially at the position θ , the probability to eventually be right to the maximum θ_u is

$$\rho(\theta) = \frac{1}{2} \left(1 - \operatorname{erf} \left[(\theta_u - \theta) \sqrt{\frac{|U''(\theta_u)|}{D}} \right] \right). \quad (24)$$

Thus, the probability to induce a spike is

$$p(\epsilon) = \int_{\epsilon}^{2\pi+\epsilon} P_{st}(\theta - \epsilon) \rho(\theta) d\theta = \int_0^{2\pi} P_{st}(\theta) \rho(\theta + \epsilon) d\theta. \quad (25)$$

In Fig. 8 we compare the analytical expression for the δ pulse with simulations for different values of parameter q . For $q = 1$ the analytic formula is not a good approximation, but for $q = 5$ and larger values, it fits numerics rather well.

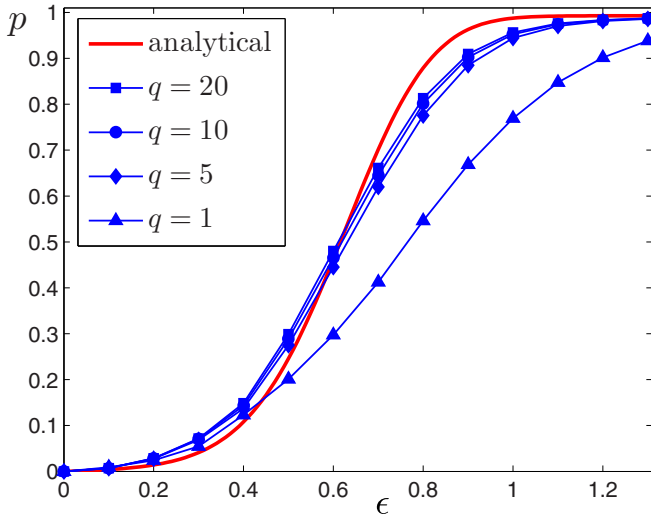


FIG. 8. Probability to induce a spike by delayed pulses with different sharpness vs. the amplitude of the delay force. The blue triangles, diamonds, circles, and rectangles represent the simulation results of Eq. (17) with $q = 1, 5, 10,$ and $20,$ respectively. The red curve is the analytical result from Eq. (25) for the δ -pulse. Parameters are chosen as $a = 0.995, D = 0.005,$ and $\tau = 500.$

V. CONCLUSIONS

We have demonstrated that the combinational effect of time delay and noise can lead to interesting spike patterns in excitable neurons. We have shown that a weak positive (excitatory) time-delay feedback on the excitable neuron in a noisy environment leads to delay-induced stochastic bursting. As an ideal mathematical model to describe the spiking pattern we adopted a point process with the leader-follower relationship. The main restriction in the applicability of this model is a separation of timescales, which requires noise to be weak and the delay to be long. The model contains just two parameters, the rate λ of appearance of spontaneous spikes, and the probability p to induce a follower spike. Roughly, the bursting pattern can be described as a sequence with randomly appearing bursts (with average inter-burst interval λ^{-1}), having random durations [as an average, each burst has $p(1-p)^{-1}$ spikes].

It is instructive to analyze the roles noise and time delay play in the model. When the amplitude of the delay force is below the critical value of onset of delay-induced oscillations (i.e., $\epsilon < \epsilon_c$), noise and delay jointly induce spikes: delayed

feedback reduces temporarily the potential barrier to overcome due to noisy forcing. However, if the amplitude of the delay force is above the critical value, i.e., $\epsilon > \epsilon_c$, and delay feedback is large enough to induce spikes in the deterministic case, noise makes the probability to induce spikes to be less than one, so that the bursts remain finite. As a very rough estimation, one can say that exactly at $\epsilon = \epsilon_c$ the delayed force brings the system to the unstable state (maximum of the effective potential), from which noise can produce a spike with probability $1/2$. This estimate is confirmed by numerical results presented in Fig. 7, where the dashed line crosses the probability p curves at $p \approx 1/2$.

As we have shown in the paper, two essential parameters determine statistical properties of the stochastic bursting: the spontaneous excitation rate λ and the probability to induce a spike during the feedback p . While the former is the standard quantity, easily calculated from the stationary solution of the autonomous Fokker-Planck equation, the latter probability could be found only numerically (from the solution of forced Fokker-Planck equation) or with some additional approximations. We have found that adiabatic approximation is not adequate for the theta-neuron considered, while the approximation of a narrow, δ -function-like pulse gives a qualitatively good result. A quantitative correspondence could be achieved, however, only when we modified the form of the delayed force making it narrower than in the original formulation.

Our basic system in this paper was a one-dimensional equation similar to that of a theta-neuron. This significantly simplified the analysis based on the Fokker-Planck equation. However, we expect that the point process model of the dynamics will be valid in other, more realistic systems of Hodgkin-Huxley type, like the the noisy FitzHugh-Nagumo system with delayed feedback, provided the above mentioned separation of the characteristic timescales is valid.

Finally, we hope that the approach based on the point process model can be extended to networks of delay-coupled noisy theta-neurons, which is one of the future subjects.

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