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Increase of coherence in excitable systems by delayed feedback

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Abstract
The control of coherence and spectral properties of noise-induced oscillations by time-delayed feedback is studied in a FitzHugh–Nagumo system which serves as a paradigmatic model of excitable systems. A semianalytical approach based on a discrete model with waiting time densities is developed, which allows one to predict quantitatively the increase of coherence measured by the correlation time, and the modulation of the main frequencies of the stochastic dynamics in dependence on the delay time. The analytical mean-field approximation is in good agreement with numerical results for the full nonlinear model.

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1. Introduction

This work is concerned with single excitable units under random impacts. These stochastic systems show noise-induced oscillations, whose coherence can be improved by application of time-delayed feedback. Originally, this technique has been proposed to control the dynamics of systems exhibiting deterministic chaos [1]. Stabilization of unstable periodic orbits embedded in a chaotic attractor was found [2] by using as control signal the difference between the instantaneous system variable $\sigma(t)$ and its delayed value $\sigma(t-\tau_D)$. Such a delayed feedback was also applied to self-oscillators in the presence of noise in order to increase the coherence of limit cycles [3]. In particular, the FitzHugh–Nagumo model in the oscillatory regime was prototypically investigated in this context [4–8]. Delayed feedback has also been considered for merely noise-induced dynamics in bistable systems [9, 10], monostable systems close to a Hopf bifurcation or excitable systems [11–15] as well as spatially extended systems [16, 17]. While analytical approaches have been successfully used to calculate spectral and coherence properties for stochastic systems below a Hopf bifurcation [13, 14] and in the

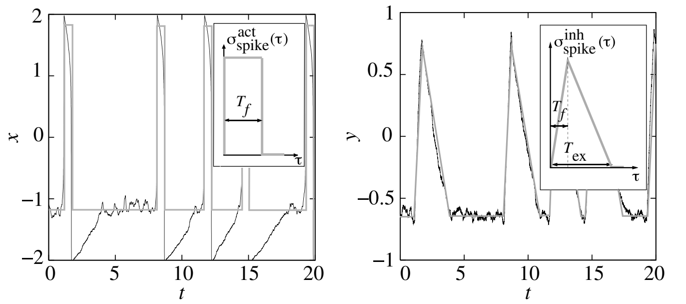

Figure 1. Spike train of the FHN model, equation (1) (black lines). Left: $x(t)$, right: $y(t)$. Grey lines and insets show spike approximations as considered in the discrete model. ($a = 1.1$, $\epsilon = 0.01$, $D = 0.004$, and no signal $s = 0$.)

case of bistable-delayed coupled systems [9], analytical concepts have not been developed for excitable systems so far.

It is the purpose of this paper to present such an analytical approach based on a discrete description of excitable systems [18–20], which we modify for delayed-feedback control. This approach, based on the definition of waiting time densities for two discrete states of an excitable unit, allows us to predict quantitatively the increase of coherence for excitable systems under time-delayed feedback. We note that similar discrete spike-response models were earlier considered, albeit without delayed-feedback control, by Gerstner *et al* [21, 22] and Kistler *et al* [23]. A linear stability analysis of neuron models with waiting time distributions was discussed in [24–26].

2. The FitzHugh–Nagumo model

Excitable systems have a single stable fixed point, and small perturbations are damped out. If, however, the system is kicked beyond some threshold, it responds with a large excursion in phase space, corresponding to *excitation* or *spiking*, before returning to the rest state. Another excitation is only possible after a certain recovery time has elapsed. A prototype model that is widely used in physics, chemistry and biology to describe this behavior [27] is the FitzHugh–Nagumo (FHN) model which in a simplified form reads as

$$\epsilon \dot{x} = x - \frac{x^3}{3} - y, \qquad \dot{y} = x + a - s(t) + \sqrt{2D}\xi(t). \tag{1}$$

A Gaussian white noise source $\xi(t)$ with $\langle \xi(t) \rangle = 0$ and $\langle \xi(t+\tau)\xi(t) \rangle = \delta(\tau)$ and strength D, and a control signal $s(t)$ have been added to the dynamics of the inhibitor variable y. In the following we will choose this signal as the time-delayed feedback control.

The instantaneous value of an input or signal $s(t)$ shifts the position of the corresponding nullclines of the dynamics. It acts as alteration of the activation threshold a and, consequently, the rate of activation of new spikes varies significantly with s. But otherwise, in the case of strong time scale separation, i.e., small ϵ, and sufficiently small signals $s(t)$ the excursion path in the phase space is unaffected. The shape of the spikes is robust so that the output $x(t)$ and $y(t)$ will consist of a series of essentially identically shaped spikes at discrete times t_i (figure 1).

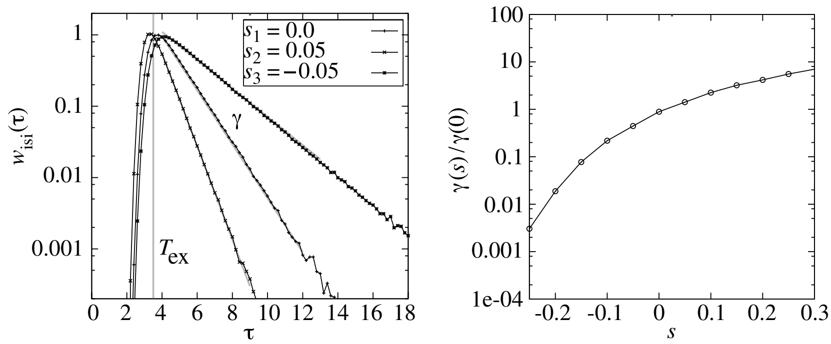

Figure 2. Left: ISI density w_{isi} (logarithmic scale) of the FHN system (equation (1)) with parameters $a = 1.1$, $\epsilon = 0.01$ and $D = 0.004$ for different constant values of $s = s_i (i = 1, 2, 3)$. Right: excitation rate $\gamma(s)$ as a function of the constant signal s. Empty circles are the results of simulations.

2.1. The FHN model with feedback by activator or inhibitor

Recently, we have proposed a discrete model for the dynamics of excitable system [18, 19]. Denoting the times when an excitation happens by t_i, we can approximate the output of the system by a series of identical spikes $\sigma_{\text{spike}}(\tau)$ (insets of figure 1):

$$\sigma(t) = \sigma_{\text{fix}} + \sum_i \sigma_{\text{spike}}(t - t_i), \tag{2}$$

where σ_{fix} denotes the rest state, i.e., when no excitation happens, and σ may be chosen as the activator variable x or the inhibitor variable y. Then the dynamics is characterized by the properties of the interspike intervals (ISI), i.e., the periods between the two spikes, and by the shape of the spike.

The inspection of figure 1 suggests distinguishing between the activator $x(t)$ and the inhibitor $y(t)$. In the case of $x(t)$ we will approximate a single spike as a rectangular pulse with height σ^{act}, i.e.,

$$\sigma^{\text{act}}_{\text{spike}}(\tau) \approx \sigma^{\text{act}} \times \begin{cases} 1 & \tau < T_f \\ 0 & \tau \geqslant T_f \end{cases} \tag{3}$$

Alternatively, for the inhibitor a sawtooth-like shape of the spike with the maximal value σ^{inh} is chosen, i.e.,

$$\sigma^{\text{inh}}_{\text{spike}}(\tau) \approx \sigma^{\text{inh}} \times \begin{cases} \dfrac{\tau}{T_f} & \tau < T_f \\[2mm] \dfrac{T_{\text{ex}} - \tau}{T_{\text{ex}} - T_f} & T_f \leqslant \tau < T_{\text{ex}} \\[2mm] 0 & \tau > T_{\text{ex}} \end{cases} \tag{4}$$

where T_f is the firing time, and T_{ex} is the excursion time (see figure 1). Obviously $T_f < T_{\text{ex}}$.

3. The distribution of interspike intervals

To obtain the ISI characteristics we have simulated the FHN model and generated long sequences of spikes. The results of ISI distribution densities for three fixed values of the signal $s = s_i (i = 1, 2, 3)$ are shown in figure 2. We observe that the ISI distribution consists of two components: an approximately fixed time which after excitation is needed to return back to the fixed point (T_{ex}), and an exponentially distributed activation period. The excursion time T_{ex} in the first approximation is not influenced by signals $s(t)$, whereas the activation process out of the fixed point is more sensitive to perturbations of the effective threshold $a - s(t)$. Our simulation shows that the stochastic dynamics of the activation can be considered as a Markovian rate process whose rate γ depends on the signal s. We assume that this signal will be the single source creating correlations between subsequent excitations.

The corresponding ISI distribution density will be denoted as $w_{isi}(\tau, t)[s]$ indicating the dependence on the signal $s(t)$. It means that $w_{isi}(\tau, t)[s]\,d\tau$ gives the probability of having an ISI in $(\tau, \tau + d\tau)$ starting at time t for a given signal $s(\cdot)$. Then the probability $j(t)\,dt$ that the system is activated and a spike starts within the interval $(t, t + dt)$ obeys

$$j(t) = \int_0^\infty d\tau\, w_{isi}(\tau, t - \tau)[s]\, j(t - \tau). \tag{5}$$

Here, we assume that the ISIs are correlated only due to the external signal. Equation (5) defines a renewal process controlled by the signal.

Next, we take into account the fact that each ISI is the sequence of the activation time out of the fixed point followed by the excursion period. Both are independent of each other and, therefore, $w_{isi}(\tau, t)[s]$ is expressed as the convolution

$$w_{isi}(\tau, t)[s] = \int_0^\tau d\tau' w_{fix}(\tau', t + \tau - \tau')[s] w_{ex}(\tau - \tau'). \tag{6}$$

Here, the distribution density of excursion periods $w_{ex}(\tau'')$ is independent of the signal s. In particular, we assume that the excursion periods are deterministic

$$w_{ex}(\tau) = \delta(\tau - T_{ex}), \tag{7}$$

which is a good approximation for a low noise level. The second distribution density $w_{fix}(\tau, t)[s]$ multiplied by $d\tau$ yields the probability of having an activation time in the interval $(\tau, \tau + d\tau)$ starting at time t for a given signal $s(\cdot)$. The probability $W(\tau, t)[s]$ of generating no spike in the interval τ if the interval starts at time t is assumed as

$$W(\tau, t)[s] = \exp\left(-\int_0^\tau d\tau' \gamma(s(t + \tau'))\right). \tag{8}$$

This waiting time distribution describes the survival probability in a discrete state at τ which has been entered at time t and which can be left with the rate $\gamma(s(t))$ dependent on the instantaneous signal $s(t)$. Then the probability density to have a spike in the interval $(\tau, \tau + d\tau)$ reads

$$w_{fix}(\tau, t)[s] = -\frac{W(\tau, t)[s]}{d\tau} = \gamma(s(t + \tau)) \exp\left(-\int_t^{t+\tau} d\tau' \gamma(s(\tau'))\right), \tag{9}$$

which is in good accordance with the simulations. Later on, if comparing theory and simulations, we will choose an Arrhenius-like dependence on the signal

$$\gamma(s) = \gamma(0) \exp\left(\frac{\gamma'(0)}{\gamma(0)} s\right), \tag{10}$$

which is in accordance with our simulations as presented in the right panel of figure 2, and $\gamma'(0)$ is the linear slope in figure 2 at $s = 0$. The assumption that the rate depends only on the instantaneous signal and neither on its history nor on the waiting time τ is an approximation and serves as a rough estimate. It is valid if the relaxation is fast compared to both the activation and the variation of the signal [29].

Eventually, our aim is to introduce a time-dependent signal $s(t)$ via time-delayed feedback: in the FHN model it is assumed to be proportional to the difference of the activator

$K_x(x(t) - x(t - \tau_D))$ or the inhibitor $K_y(y(t) - y(t - \tau_D))$ with some earlier value shifted by the delay time τ_D. K_x and K_y are the feedback amplitudes.

In the discrete model we take the signal to be proportional to the difference between the instantaneous output $\sigma(t)$ and the delayed output $\sigma(t - \tau_D)$ yielding with control parameter K

$$s(t) = K(\sigma(t) - \sigma(t - \tau_D)) \tag{11}$$

where $\sigma(t)$ may be the activator or the inhibitor. We will use the expression from equation (3) or from equation (4), respectively.

Let us underline that our specific example, i.e., the FHN model, is not a limitation of the proposed approach. In the case of other excitable models the corresponding ISI densities with adapted dependences on the instantaneous signal have to be inserted. The particular shape of the feedback has to be chosen in accordance with the model under consideration.

4. Characteristic frequencies of the FHN model

In the following we estimate the characteristic frequencies and coherence properties of the discrete excitable system. These frequencies are given by the main peaks of the spectral power density. Coherence properties can be quantified by the correlation time

$$t_{\text{corr}} \equiv \frac{1}{c_{\sigma,\sigma}(0)} \int_0^\infty \mathrm{d}\tau |c_{\sigma,\sigma}(\tau)| \tag{12}$$

with $c_{\sigma,\sigma}(\tau) = \langle(\sigma(t+\tau) - \langle\sigma\rangle)(\sigma(t) - \langle\sigma\rangle)\rangle$. To this end we consider equation (5) for the excitation probability density $j(t)$, which reads with the convoluted ISI density (see equation (6))

$$j(t) = \int_0^\infty \mathrm{d}\tau \int_0^\tau \mathrm{d}\tau'\, w_{\text{fix}}(\tau', t - \tau')[s] w_{\text{ex}}(\tau - \tau') j(t - \tau). \tag{13}$$

Exchanging the two integrals and substituting the integration variable τ by $\tau'' = \tau - \tau'$ yields after renaming $\tau' \to \tau, \tau'' \to \tau'$:

$$j(t) = \int_0^\infty \mathrm{d}\tau \int_0^\infty \mathrm{d}\tau'\, w_{\text{fix}}(\tau, t - \tau)[s] w_{\text{ex}}(\tau') j(t - \tau - \tau'). \tag{14}$$

Let us express this equation in words. The density $j(t)$ to generate a new spike at time t equals the probability of having a spike at a previous time $t - \tau - \tau'$ multiplied by the probability for an excursion lasting τ' and the probability of a time τ needed for a new activation out off the fixed point. At time $t - \tau$ the system returns from the excursion when the signal s approaches the value $s(t - \tau)$. This signal in $w_{\text{excite}}(\tau, t - \tau)[s]$ is selected as in equation (11) and realizes the delayed feedback.

We approximate in equation (13) the output σ by its mean value, i.e., we replace

$$\sigma(t) \approx \bar{\sigma}(t) = \sigma_{\text{fix}} + \int_0^\infty \mathrm{d}\tau'' j(t - \tau'')\sigma_{\text{spike}}(\tau''), \tag{15}$$

which closes the set of equations in a nonlinear way. When substituted into equation (5), it describes an ensemble of N ($N \to \infty$) excitable systems coupled via a delayed mean field.

The stationary mean-field equation has a singular stationary solution obeying

$$j_{\text{st}} = \frac{1}{\bar{\tau}_{\text{ex}} + \bar{\tau}_{\text{fix}}}. \tag{16}$$

Here, $\bar{\tau}_{\text{ex}} = \int_0^\infty \mathrm{d}\tau\, \tau w_{\text{ex}}(\tau)$ and $\bar{\tau}_{\text{fix}} = \int_0^\infty \mathrm{d}\tau\, \tau w_{\text{fix}}(\tau, t - \tau)[0] = 1/\gamma(0)$ are the mean excursion time and mean time in the fixed point. Note that in the stationary state the feedback is constant, namely zero, and the activation time thus does not depend on the actual time.

A linear stability analysis of the stationary solution can be performed by putting $j = j_{st} + \delta j$ in equation (13) . Linearizing for small variations gives

$$\delta j(t) = \int_0^\infty \mathrm{d}\tau \int_0^\infty \mathrm{d}\tau'\, w_{\mathrm{fix}}(\tau, t-\tau)[0] w_{\mathrm{ex}}(\tau')\delta j(t-\tau-\tau') + j_{st}\int_0^\infty \mathrm{d}\tau \int_0^\infty \mathrm{d}\tau'\, w_{\mathrm{ex}}(\tau') \frac{\partial w_{\mathrm{fix}}(\tau, t-\tau)[s]}{\partial s}\bigg|_{s=0} \delta s(\cdot) \quad (17)$$

The variation of j induces a variation of the feedback, i.e., a change in the signal δs at various times due to the memory of the process. In the probability density of activation (9) the variation of the signal occurs both in the prefactor and in the exponent

$$\delta w_{\mathrm{fix}}(\tau, t-\tau)[s] = \delta\gamma(s(t))\, \mathrm{e}^{-\int_{t-\tau}^t \mathrm{d}\tau' \gamma(s(\tau'))} + \gamma(s(t))\delta\, \mathrm{e}^{-\int_{t-\tau}^t \mathrm{d}\tau' \gamma(s(\tau'))}. \quad (18)$$

In particular it follows with derivatives

$$\frac{\partial w_{\mathrm{fix}}(\tau, t-\tau)[s]}{\partial s}\delta s(\cdot) = \frac{\partial \gamma(s)}{\partial s}\, \mathrm{e}^{-\int_{t-\tau}^t \mathrm{d}\tau' \gamma(s(\tau'))}\delta s(t) + \gamma(s(t))\, \mathrm{e}^{-\int_{t-\tau}^t \mathrm{d}\tau' \gamma(s(\tau'))}\left(-\int_{t-\tau}^t \mathrm{d}\tau' \frac{\partial\gamma(s)}{\partial s}\delta s(\tau')\right). \quad (19)$$

Putting $s = 0$ leads to

$$\frac{\partial w_{\mathrm{fix}}(\tau, t-\tau)[s]}{\partial s}\bigg|_{s=0}\delta s(\cdot) = \gamma'(0)\, \mathrm{e}^{-\gamma(0)\tau}\left(\delta s(t) - \gamma(0)\int_{t-\tau}^t \mathrm{d}\tau'\, \delta s(\tau')\right). \quad (20)$$

Here $\gamma'(0) = \partial\gamma(s)/\partial s|_{s=0}$ and $\delta s(\cdot)$ are the variations of the signal as a consequence of the feedback giving

$$\delta s(\cdot) = K\int_0^\infty \mathrm{d}\tau''(\delta j(\cdot - \tau'') - \delta j(\cdot - \tau_D - \tau''))\sigma_{\mathrm{spike}}(\tau'').$$

As usual $\delta j \propto \mathrm{e}^{\lambda t}$ which yields the characteristic equation for the eigenvalues λ,

$$1 = \hat{w}_{\mathrm{ex}}(\lambda)\hat{w}_{\mathrm{fix}}(\lambda)[0] + j_{st}K\hat{\sigma}_{\mathrm{spike}}(\lambda)(1 - \mathrm{e}^{-\lambda\tau_D})\delta w_{\mathrm{fix}}(\lambda)[0]. \quad (21)$$

Here $\hat{f}(\lambda) = \int_0^\infty \mathrm{d}\tau\, \mathrm{e}^{-\lambda\tau} f(\tau)$ denotes the Laplace transform and with the probability densities in equations (7) and (9) we obtain

$$\hat{w}_{\mathrm{fix}}(\lambda)[0] = \frac{\gamma(0)}{\gamma(0)+\lambda}, \qquad \hat{w}_{\mathrm{ex}}(\lambda) = \exp(-\lambda T_{\mathrm{ex}}).$$

Substituting equation (20) into equation (17) and performing the integrations with the exponential ansatz for δj defines the last item of the characteristic equation (21). Therein we have abbreviated

$$\delta w_{\mathrm{fix}}(\lambda)[0] = \gamma'(0)\frac{\lambda}{\gamma(0)(\lambda + \gamma(0))}. \quad (22)$$

Calculating Laplace transforms $\hat{\sigma}^{\mathrm{act}}(\lambda)$ and $\hat{\sigma}^{\mathrm{inh}}(\lambda)$ from equations (3) and (4) we finally obtain for activator feedback the characteristic equation

$$\lambda + \gamma(0)(1 - \mathrm{e}^{-T_{\mathrm{ex}}\lambda}) + \frac{K\gamma'(0)(1 - \mathrm{e}^{-\lambda\tau_D})}{1 + \gamma(0)T_{\mathrm{ex}}}\sigma^{\mathrm{act}}(1 - \mathrm{e}^{-\lambda T_f}) = 0. \quad (23)$$

In the case of inhibitor feedback the characteristic equation reads

$$\lambda + \gamma(0)(1 - \mathrm{e}^{-T_{\mathrm{ex}}\lambda}) + \frac{K\gamma'(0)(1 - \mathrm{e}^{-\lambda\tau_D})}{1 + \gamma(0)T_{\mathrm{ex}}}\sigma^{\mathrm{inh}} \times \left(\frac{T_f - T_{\mathrm{ex}} + \mathrm{e}^{-\lambda T_f}T_{\mathrm{ex}} - \mathrm{e}^{-\lambda T_{\mathrm{ex}}}T_f}{\lambda T_f(T_f - T_{\mathrm{ex}})}\right) = 0. \quad (24)$$

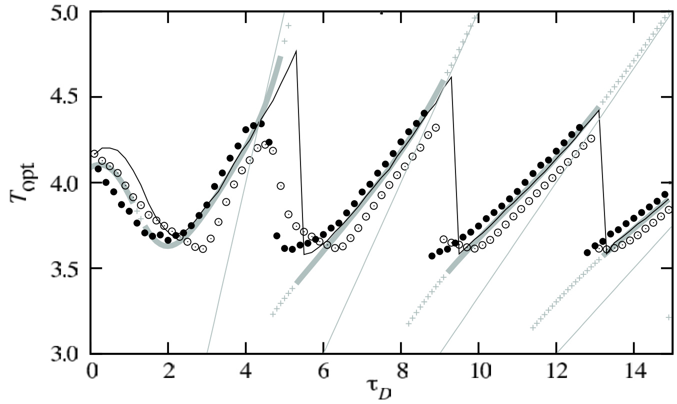

Figure 3. Characteristic times for delayed inhibitor feedback versus delay time τ_D. The plot shows times corresponding to the following: thick gray line—the least stable eigenvalue as a solution of equation (24); gray crosses (+)—other eigenvalues. Empty circles (○)—maxima of the spectral power density of a single discrete system (numerical simulations). Thin black line—maximum of the spectral power density of an ensemble of 200 delayed mean-field coupled discrete systems (numerical simulations). Full circles (•)—maxima of the spectral power density of the FHN system equation (1) with delayed feedback. Thin straight gray lines: $T_{\rm opt} = \tau_D/n$ with $n = 1, 2, 3, 4$. Parameters: $a = 1.1$, $D = 0.004$, $\epsilon = 0.01$; discrete model: $T_{\rm ex} = 3.34$, $T_f = 0.56$, $\gamma(0) = 0.4$, $\gamma'(0) = 5$; $\sigma^{\rm inh} = 1.4$, $K = K_y = -0.1$.

Equations (23) and (24) incorporate several time scales and dependences on the shape of the spike. They distinguish between activating or inhibiting feedback (sign of K) as well. Hence their transcendental structure does not allow an analytic treatment, as was done previously in [11, 12] for a delayed van der Pol oscillator. In the following section we, therefore, investigate numerically the roots of these characteristic equations and compare them with results of simulations.

5. The coherence properties of the FHN model

The structure of eigenvalues resulting from the characteristic equations contains the necessary information about the dynamics of the delayed excitable system. Namely, the imaginary part of the least stable eigenvalue corresponds to the frequency of the peak spectral power density while the coherence properties are related to the real part of the least stable eigenvalue. Therefore, in the following we compare the frequencies of the maximum spectral power densities, obtained from numerical simulations of the discrete model as well as from simulations of the delayed FHN model, with the frequencies of the least stable eigenvalue as solutions of the mean-field characteristic equation (23) and (24), respectively. The coherence properties are investigated as well by simulating the delayed FHN system and computing the correlation time (12), and comparing it with the inverse of the real part of the least stable eigenvalue from the corresponding characteristic equation.

5.1. Delayed feedback by inhibition

Figure 3 shows the characteristic time scales of the excitable dynamics versus delay time τ_D in the case of delayed inhibitor feedback $s(t) = K(y(t - \tau_D) - y(t))$. We choose $K < 0$, which turns out to be particularly effective, since then the activation threshold is diminished in the fixed point whenever $y(t - \tau_D) > y(t)$. In contrast, in [11] $K > 0$ was considered.

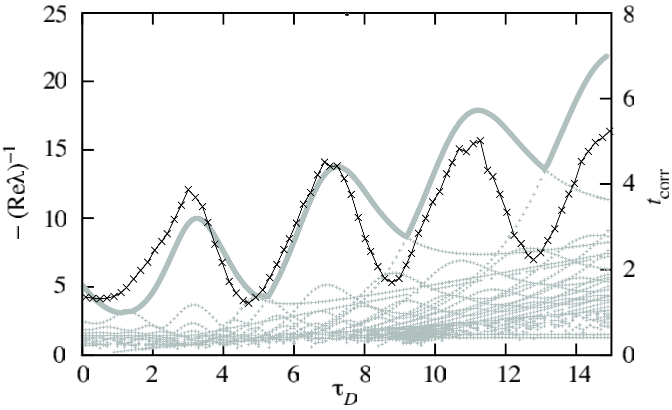

Figure 4. Coherence properties in the case of delayed inhibitor feedback versus delay time τ_D. Thick gray line: inverse of the negative real part of the least stable eigenvalue. The thin gray lines show the same for other, lower eigenvalues. Crosses ($\times$): correlation time t_{corr} of the inhibitor y of the FHN model (right scale). Parameters as in figure 3.

The thick gray lines denote $T_{opt} = 2\pi/\omega$, where ω is the imaginary part of the least stable eigenvalue $\lambda = \lambda' + i\omega$ of the characteristic equation (24), i.e., the eigenvalue with the smallest value of the real part $|\lambda'|$ (thick gray line in figure 4). A time delay generally creates infinitely many complex eigenvalues, which in our case all have negative real parts. Their inverse $|\lambda'|^{-1}$ is shown as thin gray lines in figure 4, oscillating as a function of τ_D, as generally found in the eigenvalue spectrum of linear delay equations [11–14]. Whenever the real parts of the two eigenvalue branches cross over, and another eigenvalue branch becomes the least stable one, the corresponding imaginary part jumps to the new branch. These jumps between the thick gray lines are clearly visible in figure 3, where the continuation of those least stable branches beyond the crossover points is indicated by thin gray crosses. The leading eigenvalue periods $T_{opt} = 2\pi/\omega$ coincide quite well with the dominant oscillation periods extracted from the main peak of the power spectral densities of the full FHN system (full circles) and of the approximate discrete systems (empty circles: single system; thin black line: ensemble of 200 discrete systems). It is remarkable that the approximately piecewise linear variation of the dominant oscillation period with delay time in the excitable system can be roughly estimated from the behavior found in systems near Hopf bifurcations, where the piecewise linear variation follows the law [11, 12] $T_{opt} = \tau_D/n$ with $n = 1, 2, 3, \ldots$, depicted by the thin straight gray lines in figure 3.

Figure 4 depicts the modulation of the coherence of the noise-induced oscillations in dependence upon the time delay. The correlation time t_{corr} calculated from the full nonlinear FHN model shows a nonmonotonic modulation with τ_D which is matched very well by the modulations of the inverse real part of the least stable eigenvalue of the mean-field approximation. There is a strong overall increase of coherence with increasing delay times.

Thus, for the inhibitor feedback we find reasonable agreement between the approximate theory of the discrete model and the full FHN system using the parameters of the uncontrolled system from figure 1. The characteristic frequencies of the FHN system agree well with the frequencies associated with the least stable eigenvalues of the discrete mean-field model (figure 3), thus making it a useful tool for semianalytical calculations in excitable systems with delayed feedback. Generally the results agree the better, the larger the delay time τ_D is. Also, the modulation of the coherence of the FHN system with varying delay time τ_D can be well understood using this theory. Namely, a maximum correlation time is observed for those

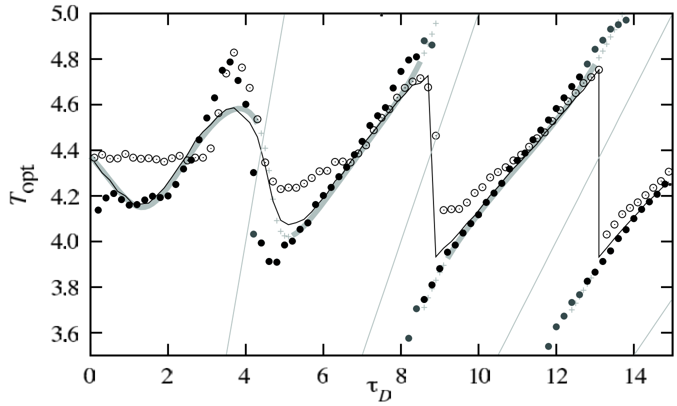

Figure 5. Characteristic times in the case of delayed activator feedback versus delay time τ_D. Symbols as in figure 3. Parameters: FHN model: $a = 1.1$, $D = 0.004$, $\epsilon = 0.01$, $K_x = 0.05$; discrete model: $T_{ex} = 3.34$, $T_f = 0.56$, $\gamma(0) = 0.4$, $\gamma'(0) = 5$, $\sigma^{act} = 3$, $K = K_x = 0.05$.

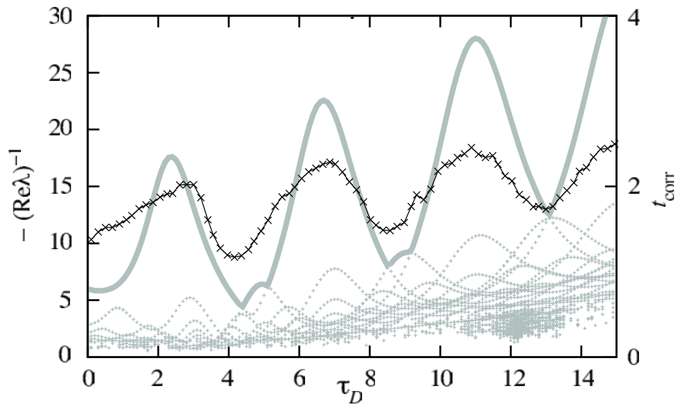

Figure 6. Coherence properties in the case of delayed activator feedback versus delay time τ_D. Symbols as in figure 4. Parameters as in figure 5.

delay times τ_D for which the eigenvalues of the characteristic equation are least stable, i.e., the inverse modulus of their real part is largest. Minimum correlation times are found for such τ_D for which the real parts of two branches of the eigenvalue spectrum cross over, leading to two different competing frequencies (see figure 4). The striking coincidence between the real part λ' of the leading eigenvalue and the correlation time, up to a constant factor, can be understood by noting that in the linear approximation the half-width of the main Lorentzian peak of the power spectral density is $|\lambda'|$, and $t_{cor} \sim |\lambda'|^{-1}$ [13].

5.2. Delayed feedback by activation

For the activating feedback a spike is most likely excited at time t if at $t - \tau_D$ in the past there was also a spike, thus leading to a small feedback term during an excursion. Therefore, the spike parameters estimated without feedback fit well when used in the discrete model with feedback (see figure 5 for the characteristic times and figure 6 for the correlation time in the case of delayed activator feedback).

It should be noted that the agreement between the approximate discrete model and the full FHN system in the case of the inhibitor feedback can be improved by choosing a larger excursion time $T_{\mathrm{ex}} \approx 3.6$. This is due to the fact that a signal independent excursion time is only a rough approximation. In contrast to the activator feedback, with the inhibitor feedback a spike is most likely generated if there was no spike at time $t - \tau_D$. Therefore, the control force $K(x(t) - x(t - \tau_D))$ is positive during the motion on the right stable branch of the cubic x nullcline and negative during the motion on the left stable branch, thus in both cases decreasing the absolute value of $\dot{y}$ in the FHN dynamics equation (1), which leads to an increased excursion time.

6. Conclusions

We have presented a new approach to semianalytically estimate coherence and spectral properties in excitable systems with time-delayed feedback. It is based on a discrete model which depends on characteristic parameters of the corresponding waiting time distributions, i.e., the mean excursion time T_{ex} and the firing time T_f, the spike shape $\sigma_{\mathrm{spike}}(t)$, the activation rate without feedback $\gamma(0)$ and its sensitivity $\gamma'(0)$ with respect to a signal. The proposed mean-field approximation of the feedback describes well the dynamic behavior given by the leading eigenvalue periods T_{opt} in the case of a large population of globally delayed coupled excitable systems (as demonstrated by our simulations with 200 delayed units in figures 3 and 5). It also reproduces quantitatively the characteristic frequencies of a single excitable system with delayed feedback. Furthermore, it explains the modulation and strong increase in coherence, as measured by the correlation time t_{corr}, with varying time delay τ_D (see figures 4 and 6). Since the FitzHugh–Nagumo model is a paradigmatic model of an excitable system, our analytical description can be readily applied also to other systems of this class. Our method uses a parameterization of the shape of the spikes, equations (3), (4), and of the interspike interval distribution w_{ISI} only, see figure 2. Thus the control concepts are potentially important for a wide range of excitable systems in physics, chemistry, biology and medicine, e.g., lasers, chemical reaction systems, neural systems.

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