Stochastic Hierarchical Systems: Excitable Dynamics

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Abstract We present a discrete model of stochastic excitability by a low-dimensional set of delayed integral equations governing the probability in the rest state, the excited state, and the refractory state. The process is a random walk with discrete states and nonexponential waiting time distributions, which lead to the incorporation of memory kernels in the integral equations. We extend the equations of a single unit to the system of equations for an ensemble of globally coupled oscillators, derive the mean field equations, and investigate bifurcations of steady states. Conditions of destabilization are found, which imply oscillations of the mean fields in the stochastic ensemble. The relation between the mean field equations and the paradigmatic Kuramoto model is shown.

Keywords Excitable systems · Delayed integral equations ·
Time-convoluted master equations

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1 Introduction

Waiting time density functions are often used in the description of complex stochastic processes [1, 2]. One finds them in studies on random walks [3], on spin glasses [4], and on self-organized criticality [5]. Other studies that consider waiting time densities as a crucial element are devoted to reaction-transport systems [6], to turbulence [7], to quenched disorder [8] on fractals [9], and to many other contexts.

In this paper, we apply them to develop a theory of hierarchical stochastic systems that has been proposed recently [10, 11]. The generic scheme in which this notion becomes useful is a multi-state process, in the course of which a small subset of events given by a waiting time density function drives the dynamics on a higher level of structure. Let us consider an ion channel of a neuron as an example. The opening and closing of the channels control the currents which determine the membrane voltage dynamics of the cell. Each individual act of an opening or closing is the outcome of a complex interaction of many channel subunits. This interaction includes various dynamical transitions within the channel subunits, and many of these transitions do not entail changes in the current. Only the opening and closing events have relevance for the resulting membrane potential. These latter transitions are described by waiting time density functions.

The use of weighting density functions reduces the multi-state master equation governing the complete system to a low-dimensional set of evolution equations for the probability density function. The price to pay for hiding complex state dynamics in the waiting time density functions is a *non-Markovian* formulation of the problem [12]. In contrast to the case of exponentially distributed events that allow a rate formulation, the evolution operators for the stochastic dynamics depend on the past.

Nevertheless, we aim to demonstrate that waiting time densities and their evolution equations are efficient and useful tools for describing collective behavior on a certain structural level without losing information on the stochastic behavior of the underlying level. Our studies are directed to dynamical phenomena in coupled excitable dynamics [13, 14]. Noise-driven coupled excitable systems can generate spatial and temporal structures for a range of the noise intensity. These systems have been observed in different physical, chemical, biological, and sociological frameworks and are among the main topics in current complex systems research [15–23]. Many types of ion channels can be viewed as realizations of a stochastic excitable unit [15, 24, 25] and also, applications in neuron networks have been reported [2, 16].

Excitable systems can be mapped onto alternating transitions between three discrete states: a rest state, an excited (or firing) state, and an inhibited state, often also called refractory state [10, 11, 17, 26, 27]. Supplementing the discrete state scheme by waiting time density functions completes the characterization of the excitable unit.

We point out that to infer the waiting time density from the underlying dynamics, formulated by a stochastic differential equation, is a highly non-trivial task [2, 28–33]. Therefore, we have decided to model the waiting times in the discrete states by Γ -distribution densities. Parameters of the latter are adjusted to match a stochastic FitzHugh–Nagumo dynamics [10, 11, 14, 34].

A detailed description as well as a discussion of the dynamical properties of a single excitable unit is given in Section 2. Sections 3 and 4 are devoted to coupled ensembles. First, we outline a mean field theory for the occupation numbers of the three states in the globally

coupled ensemble and derive a system of integro-differential equations for their dynamics. For a paradigmatic type of coupling, we demonstrate that the onset of oscillations occurs via a Hopf bifurcation which, depending on the parameters, can be either subcritical or supercritical. Details of the bifurcation dynamics that agree with the results of the numerical simulations of coupled continuous FitzHugh–Nagumo units, are presented in Section 4. Section 5 connects the global oscillations to the paradigmatic Kuramoto model [35–40]. We show that the first two cumulants of a cumulant expansion are sufficient to formulate corresponding stochastic differential equations in the Gaussian approximation.

2 Dynamics of a Single Excitable System

The stochastic FitzHugh–Nagumo system is a prototype of excitable dynamics with continuous variables (denoted $\{u(t), v(t)\}$) [34]. It is governed by nonlinear Langevin equations and driven by additive Gaussian white noise representing external forces. An individual unit has a single stationary state $\{u^*, v^*\}$, which is stable with respect to small perturbations. However, if the perturbations $\{\delta u(t), \delta v(t)\}$ exceed a threshold, this element switches to the excited state. It performs a long excursion in phase space, which is terminated by a transition to the refractory state. The system cannot be excited out of that state. After some time, the unit returns to the initial rest state. For a neuron, the whole scenario represents a spike, and below, we will address it in this way.

In this study, we introduce a simple non-Markovian three-state model of an excitable system [13]. We define a renewal process [12, 41] with three discrete states (see Fig. 1): excited (2), refractory (3), and rest (1). As state 1 is a stable fixed point, the lifetime is modeled by an exponential density function with mean lifetime $1/\gamma$, γ being the rate of escape. The waiting time density functions in the excited and refractory states $w_2(\tau)$ and $w_3(\tau)$ are nonexponential functions, rendering the model non-Markovian [12]. We emphasize that transitions do not possess memory: The time spent in a state is independent of the time spent in the preceding states.

Thus, the time derivative of the probability to be in one of the states is determined by the balance of probability fluxes $J_i(t)$. These $J_i(t)$ are the portions of probability that leave the

Fig. 1 Three-state model of a single excitable unit. *State 1* denotes the rest state, followed by the excited or firing *state 2*. *State 3* is the refractory state. The τ s are the times elapsed after a state was entered. $w_i(\tau)$ defines the lifetimes in states $i = 1, 2, 3$, respectively

state i during the infinitesimal period dt after t . According to our assumptions, probability flows along the route $\dots \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 1 \rightarrow \dots$, and, therefore, the balance reads

$$\begin{aligned}\frac{d}{dt}P_1(t) &= J_3(t) - J_1(t), \\ \frac{d}{dt}P_2(t) &= J_1(t) - J_2(t), \\ \frac{d}{dt}P_3(t) &= J_2(t) - J_3(t).\end{aligned}\tag{1}$$

We introduce memory kernels for the probability currents from state $2 \rightarrow 3$ and from $3 \rightarrow 1$. They correspond to nonexponential distributions of pausing times in the excited and in the refractory state. In these states, the system is almost insensitive to external perturbations. Therefore, both states are left after an almost deterministic time with a small variance that increases moderately with growing noise. In contrast, the escape time out of the rest state 1 is exponentially distributed with rate γ , and its variance is as large as its mean. The dependence of the rate γ on external signals and on the states of the neighbors will be a crucial element of the model in Section 3.

Fluxes are defined as

$$\begin{aligned}J_1(t) &= \gamma P_1(t), \\ J_2(t) &= \int_0^\infty dt' J_1(t-t')w_2(t'), \\ J_3(t) &= \int_0^\infty dt' J_1(t-t')(w_2 \circ w_3)(t').\end{aligned}\tag{2}$$

where $(w_2 \circ w_3)(t) = \int_0^t dt' w_2(t')w_3(t-t')$ denotes the convolution of waiting time densities in state 2 and 3. Upon inserting these expressions for the probability currents into the master equations (1), one arrives at the integral equations for the three-state dynamics.

The introduction of the survival probabilities

$$z_i(\tau) = 1 - \int_0^\tau dt' w_i(t'),\tag{3}$$

allows a more compact representation. These functions define the probability to stay longer than τ in state i . Obviously, $z_i(0) = 1$ and $z_i(\infty) = 0$. With this abbreviation, the probability densities $P_i(t, \tau)$ that the system is in state i at time t and has entered this state at time $t - \tau$ is just the product of the probability flow $J_{i-1}(t - \tau)$ that entered at $t - \tau$ and the probability to stay there the time τ thereafter. Hence,

$$\begin{aligned}P_2(t, \tau) &= J_1(t - \tau)z_2(\tau) = \gamma P_1(t - \tau)z_2(\tau), \\ P_3(t, \tau) &= J_2(t - \tau)z_3(\tau) = \int_0^\infty dt' \gamma P_1(t - \tau' - \tau)w_2(\tau')z_3(\tau).\end{aligned}\tag{4}$$

Integrating with respect to all possible values of τ

$$P_i(t) = \int_0^\infty d\tau P_i(t, \tau)\tag{5}$$

one finally obtains integral equations for the probabilities of a single system

$$\begin{aligned} P_2(t) &= \int_0^\infty d\tau \gamma P_1(t-\tau) z_2(\tau), \\ P_3(t) &= \int_0^\infty d\tau \int_0^\infty d\tau' \gamma P_1(t-\tau'-\tau) w_2(\tau') z_3(\tau), \end{aligned} \quad (6)$$

while the equation for $P_1(t)$ follows from the normalization condition:

$$P_1(t) = 1 - P_2(t) - P_3(t). \quad (7)$$

Equations (6) and (7) are the basic constituents of the system's dynamics. They have been investigated in various applications as, for example, the characterization of coherence resonance by its power spectrum [13, 14]. For periodically varying rates, analytical characterization of stochastic resonance [42] as well as synchronization to periodic inputs [43] and delayed feedback [11] was obtained. In this paper, we take them as a basis for the derivation of mean field equations of a coupled ensemble of three-state units [10].

3 Mean Field Equations

A specific type of collective behavior of stochastic excitable media is the excitation of global oscillations accompanied by mutual synchronization of the individual units [44–52]. It is due to the amplification of an oscillatory mode that occurs at a moderate noise intensity [53–56]. Known under the name of coherence resonance [14, 57], this phenomenon is reflected by a growth of the correlation time under an increase of noise amplitude. When coupled, such units exhibit collective oscillations [14].

We consider an ensemble of N three-state systems which are globally coupled by their output. Let $\sigma_i(t)$ label the actual state of unit i at time t . In the course of time, it will assume the values 1, 2 and 3. We associate with these three states an output that equals “1” if the i -th unit is excited ($\sigma_i(t) = 2$) and “0” otherwise. Thus, the information transmitted to the neighbors is simply whether the i -th unit is excited or not. The mean field output is given by:

$$f(t) = \frac{1}{N} \sum_{i=1}^N \delta_{\sigma_i(t), 2}. \quad (8)$$

Obviously, $f(t)$ equals the relative occupation number $n_2(t)/N$ (where $n_2(t)$ is the fraction of units in state 2 at time t); hence, $f(t) \in [0, 1]$.

As mentioned above, we assume that the distributions $w_2(\tau)$ and $w_3(\tau)$ do not respond to changes of the mean field; that is, the excited and refractory times stay constant if $f(t)$ varies. We introduce a prototypical global coupling between the individual excitable elements by a dependence of the rate γ on the value of the global output $f(t)$:

$$\gamma(f(t)) = \gamma\left(\frac{n_2(t)}{N}\right). \quad (9)$$

The rate γ has the same value for all units.

To derive the mean field equations for an ensemble of N coupled units, we start with the microscopic probabilities. Let $p(\sigma_1, \dots, \sigma_j, \dots, \sigma_N, t)$ be the joint probability to find the units in states $\sigma_j(t)$ at time t with $j = 1, \dots, N$. Normalization requires

$$\sum_{\{\sigma_j\}} p(\sigma_1, \dots, \sigma_N, t) = 1 \quad (10)$$

We obtain the probability that the j th unit is in state i independently of the state of the other units by fixing the j th state and summing over all other microstates:

$$P_i^j(t) = \sum_{\{\sigma_k\}, k \neq j} p(\sigma_1, \dots, i, \dots, \sigma_N, t), \quad (11)$$

with $\sum_{j=1}^N \sum_{i=1}^3 P_i^j(t) = N$.

Equations that govern the dynamics of these probabilities are postulated in the same manner as (6). However, we have to take into account the dependence of the excitation rate γ on the states of all other units. With the definition of the microscopic probabilities, we arrive after summation at

$$P_2^j(t) = \sum_{\{\sigma_k\}, k \neq j} \int_0^\infty d\tau \gamma \left(\frac{1}{N} \sum_{i=1}^N \delta_{\sigma_i, 2} \right) \times p(\sigma_1, \dots, \sigma_{j-1}, 1, \sigma_{j+1}, \dots, \sigma_N, t - \tau) z_2(\tau), \quad (12)$$

and

$$P_3^j(t) = \sum_{\{\sigma_k\}, k \neq j} \int_0^\infty d\tau \int_0^\infty d\tau' \gamma \left(\frac{1}{N} \sum_{i=1}^N \delta_{\sigma_i, 2} \right) \times p(\sigma_1, \dots, \sigma_{j-1}, 1, \sigma_{j+1}, \dots, \sigma_N, t - \tau - \tau') z_3(\tau) w_2(\tau'). \quad (13)$$

The probability of finding n_1 units in state 1, n_2 units in state 2 and n_3 units in state 3 at time t with $n_1 + n_2 + n_3 = N$ is denoted as $p(n_1, n_2, n_3, t)$ and obeys

$$\sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} p(n_1, n_2, N - n_1 - n_2, t) = 1. \quad (14)$$

The units are indistinguishable; therefore, a relation between the microscopic and the joint probabilities is given by summation over $i = 1, 2, 3$ and $j = 1, \dots, N$:

$$\frac{1}{N} \sum_{j=1}^N \sum_{i=1}^3 P_i^j(t) = \sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} p(n_1, n_2, N - n_1 - n_2, t) = 1. \quad (15)$$

Without summation over i , we get three relations with the relative occupation numbers n_i/N under the sum on the right-hand-side:

$$\frac{1}{N} \sum_{j=1}^N P_i^j(t) = \sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} \frac{n_i}{N} p(n_1, n_2, N - n_1 - n_2, t) \quad (16)$$

$i = 1, 2, 3$

In fact, the left-hand-side is expressed as the average occupation number for all three states with given probabilities $p(n_1, n_2, n_3, t)$ for all possible relative occupations. By this rule, (12) and (13) can be rewritten in terms of the relative occupation numbers of the ensemble, yielding

$$\sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} \left[\frac{n_2}{N} p(n_1, n_2, n_3, t) - \frac{n_1}{N} \int_0^\infty d\tau \gamma\left(\frac{n_2}{N}\right) p(n_1, n_2, n_3, t - \tau) z_2(\tau) \right] = 0, \quad (17)$$

and,

$$\begin{aligned} \sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} \left[\frac{n_3}{N} p(n_1, n_2, n_3, t) - \frac{n_1}{N} \int_0^\infty d\tau \int_0^\infty d\tau' \gamma\left(\frac{n_2}{N}\right) \right. \\ \left. \times p(n_1, n_2, n_3, t - \tau - \tau') z_3(\tau) w_2(\tau') \right] = 0 \end{aligned} \quad (18)$$

with $n_3 = N - n_1 - n_2$. Next, we consider the limit of infinitely many coupled units $N \rightarrow \infty$ and neglect finite-size effects. The relative occupation numbers converge to a deterministic process $P_i(t)$ in the sense of weak convergence: we demand that the probability density function $p(n_1, n_2, n_3, t)$ becomes sharply peaked around the values $n_i = P_i(t)N$, such that an arbitrary continuous function F of the relative occupation numbers n_i/N obeys

$$\begin{aligned} \lim_{N \rightarrow \infty} \sum_{n_1=0}^N \sum_{n_2=0}^{N-n_1} p(n_1, n_2, N - n_1 - n_2, t) \times F\left(\frac{n_1}{N}, \frac{n_2}{N}, \frac{N - n_1 - n_2}{N}\right) \\ = F(P_1(t), P_2(t), P_3(t)). \end{aligned} \quad (19)$$

If the units are not coupled, their states are independent random variables, and the assumption (19) is just the law of large numbers. In this limit, we obtain from (17) and (18) the mean field equations

$$\begin{aligned} P_2(t) &= \int_0^\infty d\tau \gamma(P_2(t - \tau)) P_1(t - \tau) z_2(\tau), \\ P_3(t) &= \int_0^\infty d\tau \int_0^\infty d\tau' \gamma(P_2(t - \tau - \tau')) P_1(t - \tau - \tau') z_3(\tau) w_2(\tau'), \end{aligned} \quad (20)$$

supplemented with the normalization condition:

$$P_1(t) = 1 - P_2(t) - P_3(t). \quad (21)$$

4 Bifurcation Analysis

In the last section, we have obtained nonlinear integral equations for the probability distributions in the ensemble of coupled excitable units. In this section, we investigate briefly the linear stability of steady states of the nonlinear system of equations, which — due to the memory kernels — operates in an infinite-dimensional space. We derive the characteristic equation and show how local stable oscillations become possible.

We introduce τ_i as the mean waiting time of state i : $\tau_i \equiv \int_0^\infty d\tau z_i(\tau) = \int_0^\infty d\tau \tau w_i(\tau)$. Stationarity of the probabilities implies $P_i(t) = P_i^*$ in (20) and (21) and leads to

$$P_1^* = \frac{1/\gamma(P_2^*)}{T}, \quad P_2^* = \frac{\tau_2}{T}, \quad P_3^* = \frac{\tau_3}{T}, \quad (22)$$

with $T = 1/\gamma(P_2^*) + \tau_2 + \tau_3$ being the mean period of the process. Relations (22) are the equations for the steady states of the mean populations.

To investigate the stability of the steady states, we make the ansatz

$$P_i(t) = P_i^* + a_i \exp(\lambda t). \quad (23)$$

The amplitudes have to fulfill the normalization condition $a_1 = -a_2 - a_3$. Linearization of the rate γ yields $\gamma(P_2(t)) = \gamma(P_2^*) + \gamma'(P_2^*)a_2 \exp(\lambda t)$, and we obtain from the mean field equations the linear system of equations for the coefficients a_i :

$$\begin{aligned} a_2 &= [\gamma'(P_2^*)P_1^*a_2 - \gamma(P_2^*)(a_2 + a_3)] \hat{z}_2(\lambda) \\ a_3 &= [\gamma'(P_2^*)P_1^*a_2 - \gamma(P_2^*)(a_2 + a_3)] \hat{z}_3(\lambda) \hat{w}_2(\lambda). \end{aligned} \quad (24)$$

Here, $\lambda \in \mathbb{C}$ and

$$\hat{z}_{2,3}(\lambda) = \int_0^\infty d\tau e^{-\lambda\tau} z_{2,3}(\tau) \text{ and } \hat{w}_2(\lambda) = \int_0^\infty d\tau e^{-\lambda\tau} w_2(\tau) \quad (25)$$

are the Laplace transforms of the survival probabilities and the waiting time distributions, related by $\hat{z}_{2,3}(\lambda) = (1 - \hat{w}_{2,3}(\lambda)) / \lambda$.

Solution of (24) characterizes the eigenvalues λ of an ensemble of many coupled three-state oscillators. They obey the characteristic equation

$$0 = 1 + \frac{1}{\lambda} [\gamma(P_2^*) (1 - \hat{w}_2(\lambda) \hat{w}_3(\lambda)) - \gamma'(P_2^*) P_1^* (1 - \hat{w}_2(\lambda))]. \quad (26)$$

In general, this equation is transcendental and depends sensitively on the choice of the waiting time densities in the excited and refractory state $w_{2,3}(\tau)$. Following [10], we choose the Gamma-distribution density

$$w_k(\tau) = \frac{\alpha_k}{\tau_k \Gamma(\alpha_k)} \left(\frac{\alpha_k \tau}{\tau_k} \right)^{\alpha_k - 1} \exp \left(- \frac{\alpha_k \tau}{\tau_k} \right); \quad k = 2, 3. \quad (27)$$

These are densities with a single peak, mean value $\langle \tau \rangle = \tau_k$, and variance $\langle \Delta \tau^2 \rangle = \tau_k^2 / \alpha_k$. As a particular simple case, we consider below the integer values of α_k , yielding $\Gamma(\alpha) = (\alpha - 1)!$.

The model describes qualitatively well the properties of a stochastic FitzHugh–Nagumo system, if the values of $\alpha_{2,3}$ decrease with the noise intensity. For $\alpha_{2,3} \rightarrow \infty$ the waiting times $\tau_{2,3}$ are approximately constant at a low noise level. Growth of the variances corresponds to a higher noise level with $\alpha_{2,3} < \infty$. Eventually, in case of high noise, the transitions reduce to a rate process with $\alpha_{2,3} \rightarrow 1$. In our calculations below, we often set $\alpha_2 = \alpha_3 = \alpha$.

The Laplace transform of (27) reads:

$$\hat{w}_k(\lambda) = \left(1 + \frac{\tau_k \lambda}{\alpha_k}\right)^{-\alpha_k}. \quad (28)$$

Depending on the values of $\alpha_{2,3}$ the characteristic equation (26) possesses many (for $\alpha_{2,3} \rightarrow \infty$ infinitely many) complex roots.

An instability occurs, if (26) has solutions λ with a positive real part. It can be shown that excitatory coupling is a necessary condition for an instability. Therefore, we assume γ to be an increasing function of P_2 . A specific choice that links the three-state units to the FitzHugh–Nagumo system is an Arrhenius type of coupling:

$$\gamma(P_2(t)) = \gamma_0 \exp\left(-\frac{\Delta U_0}{D}(1 - \sigma P_2(t))\right), \quad (29)$$

where ΔU_0 is an activation constant, D is the noise intensity and σ acts as the coupling strength. Given this rate function, the implicit equation (22) for the stationary solution P_2^* reads as

$$P_2^* = \frac{\tau_2}{\tau_2 + \tau_3 + \frac{1}{\gamma_0} \exp\left(\frac{\Delta U_0}{D}(1 - \sigma P_2^*)\right)}. \quad (30)$$

In the case where all units are uncoupled, i.e. $\sigma = 0$, the rate γ is a constant, and (22) yields a unique solution. It can be shown that this solution is stable. If the units are coupled ($\sigma > 0$), we expand Eq. (26) into powers of λ , $\Phi(\lambda) = \Phi_0 + \Phi_1 \lambda + O(\lambda^2)$. By setting $\lambda = 0$, we obtain the condition for a vanishing eigenvalue: the saddle-node bifurcation. It reads $\Phi_0 = 1 + r(\tau_2 + \tau_3) - s\tau_2 = 0$, where $r = \gamma(P_2^*)$ and $s = \gamma'(P_2^*)P_1^*$. The same relation for r and s is obtained by differentiating both sides of (30) with respect to P_2^* . A saddle-node bifurcation occurs if both slopes at the intersection of two curves are equal. This situation is shown in Fig. 2II. It also shows that there is another saddle-node bifurcation at lower values of the control parameters D and σ (Fig. 2I), where two new fixed points (intersections) are created at a certain distance from the already existing fixed point.

Fig. 2 Geometric sketch of the left and right hand side of (30). The *star* indicates the stationary solution considered in the text. *Panels I and II* show a saddle-node bifurcation. *I* two fixed points are created distinct from the already existing third fixed point, $\sigma = 4.1$. *II* One of the new fixed points merges with the old one, and both disappear, $\sigma = 5.5$. *Panels III and IV* show a pitchfork bifurcation. *III* the middle fixed point is given by the inflection point of the right-hand side of (30), $\sigma = 3.6$, $D = 1.06 \cdot 10^{-4}$. *IV* two new steady states are born from the middle one, $\sigma = 4.4$, $D = 9 \cdot 10^{-5}$. Other parameters: $\gamma_0 = 0.05$, $\tau_2 = 75$, $\tau_3 = 260$, $\Delta U_0 = 0.0005$

A more complicated codimension-2 bifurcation is observed if, additionally, the second derivative of the right hand side of (30) vanishes at $P = P_2^*$ as shown in Fig. 2III and IV. At this point, two separate folds merge in a cusp catastrophe. Passage through this point of the parameter plane corresponds to a pitchfork bifurcation: two fixed points disappear, while the middle fixed point loses (in the supercritical case) or gains (in the subcritical case) stability. The fold and cusp catastrophes are visible in Fig. 3 which shows steady states as functions of D and σ .

We write (26) with the Laplace transforms (28) and integer α_i in polynomial form:

$$\left(1 + \frac{\tau_2 \lambda}{\alpha_2}\right)^{\alpha_2} \left(1 + \frac{\tau_3 \lambda}{\alpha_3}\right)^{\alpha_3} \left(1 - \frac{s}{\lambda} + \frac{r}{\lambda}\right) + \frac{s}{\lambda} \left(1 + \frac{\tau_3 \lambda}{\alpha_3}\right)^{\alpha_3} - \frac{r}{\lambda} = 0. \quad (31)$$

The passage of two complex-conjugate eigenvalues across the imaginary axis corresponds to the Hopf bifurcation and the onset of oscillations. By setting $\lambda = i\omega$ in (31), we split the real and imaginary parts of the characteristic equation:

$$R_r(\omega)r + R_s(\omega)s + C_R(\omega) = 0, \quad I_r(\omega)r + I_s(\omega)s + C_I(\omega) = 0, \quad (32)$$

where $R_r(\omega)$ and $R_s(\omega)$ denote real parts of the coefficients at r and s in (31); $I_r(\omega)$ and $I_s(\omega)$ are imaginary parts of these coefficients. Furthermore, $C_R(\omega)$ and $C_I(\omega)$ are real and imaginary parts of constant terms in (31). For r and s , we get the parametric (in terms of the critical frequency ω) representation

$$r = \frac{C_I(\omega)R_s(\omega) - C_R(\omega)I_s(\omega)}{R_r(\omega)I_s(\omega) - R_s(\omega)I_r(\omega)}, \quad s = \frac{R_r(\omega)C_I(\omega) - I_r(\omega)C_R(\omega)}{R_s(\omega)I_r(\omega) - R_r(\omega)I_s(\omega)}. \quad (33)$$

Bifurcation curves of the saddle-node and the Hopf bifurcation divide the parameter plane of $\gamma(P_2^*) = r$ and $\gamma'(P_2^*) = s(1 + r(\tau_2 + \tau_3))$ into regions with different number of unstable eigenvalues λ . These curves are shown in Fig. 4 for parameter values $\alpha = 1, 15, 20, 50$. The location of the saddle-node curve is independent of α . The point on this curve where two eigenvalues vanish simultaneously (the Takens-Bogdanov point) is the starting point of the curve of the Hopf bifurcation. Above this point, there is a unique stable steady solution. While moving along the parameter plane in direction of larger values of γ' , this state is destabilized via the Hopf bifurcation, and the system starts to oscillate [52, 58, 59]. Going further in this direction, one crosses the saddle-node curve. Below this curve, there is only one unstable solution.

The size of the parameter region with oscillatory solutions of the characteristic equation depends on the value of $\alpha = \alpha_{2,3}$: the larger the α , the larger is this region. Notably, at $\alpha \approx 15$, the geometry of the Hopf curve is dramatically changed: a turning point appears

Fig. 3 Surface of stationary solutions P_2^* over the (σ, D) -plane

Fig. 4 Number of roots of (31) with positive real part in the $\gamma\gamma'$ -plane for different α . Solid line Hopf bifurcation. Dashed line saddle-node bifurcation

upon the curve and evolves into a loop. Increasing α further (i.e., decreasing the width of the distribution peaks in the excited and refractory period) increases the area of the loop. This means that reducing the randomness in the system's dynamics supports specification among the units.

Inside the loop, there are two additional complex conjugate roots with a positive real part. When the border of the loop is crossed, the frequency of the oscillations jumps. Inside this case, hysteresis is observed (see Fig. 5) [44, 60].

The bifurcations can be related to the coupling strength σ and the noise intensity D . Both are defined by (29) and, hence, are functions of the rate $\gamma(P_2^*)$ and its derivative $\gamma'(P_2^*)$. In this way, every point from the plane of $\gamma'-\gamma$ is mapped onto the σ - D -plane.

The resulting bifurcation lines are shown in Fig. 6. Note that the figure is still incomplete, as it only contains information on bifurcations of fixed points and not on global bifurcations. Further details can be found in [10]. Numbers on the plots indicate the number of unstable eigenvalues of a fixed point. By crossing the cusp-shaped dashed curves, two new fixed points are generated or destroyed. At the Takens–Bogdanov point, the Hopf curve starts;

Fig. 5 Critical frequency at the Hopf bifurcation for different α as function of the rate $\gamma(P_2^*)$

Fig. 6 Curves of the Hopf (solid) and saddle-node (dashed) bifurcations in σ, D -space. Numbers in the regions indicate the numbers of unstable eigenvalues for steady states

its self-intersections in the σ, D plane increase the number of unstable directions in phase space.

We illustrate the results of the analysis by a schematic bifurcation diagram in Fig. 7. Our motion across the parameter space starts at low values of D . At first, there is a unique stable steady solution; below, we denote it as a primary state. Upon increasing D , at the point sn_1 , two additional unstable states are generated. Later on, at the second saddle-node bifurcation at sn_2 , one of these states merges with the primary one and vanishes. Before this event, however, the primary state is destabilized via the subcritical Hopf bifurcation at H_1 : the unstable oscillatory state collapses onto the fixed point. This oscillatory state, in its turn, has been born earlier in a tangent bifurcation at T , along with the stable limit cycle. The tangent bifurcation corresponds to the finite-amplitude onset of stable oscillations. The stable limit cycle exists in a large range of values of D . Finally, it shrinks and, over the course of the supercritical Hopf bifurcation at H_2 , transmits its stability to the only remaining steady state. Thereby, the stable limit cycle disappears and a stable steady state remains.

Time-delayed feedback has been applied in different situations to shape the dynamics of a variety of systems (see for example [11, 61–65]). In neuron networks, delay arises from the transport of information with finite propagation speed of action potentials. In the

Fig. 7 Schematic bifurcation diagram: stationary values of P_2 for steady states and averaged values of $P_2(t)$ for oscillatory states. $sn_{1,2}$ saddle-node bifurcations of steady states; $H_{1,2}$ Hopf bifurcations, T tangent bifurcation of oscillatory states

Fig. 8 Hopf bifurcation in the parameter plane of γ and γ' and corresponding frequencies without delay ($\tau_D = 0$) and with it ($\tau_D = 5$)

ensemble of three-state models, it means that the rate now becomes a function of an earlier value of the global output: $\gamma = \gamma(P_2(t - \tau_D))$.

Let us again look at the linear stability of the stationary fixed point given by (22). The expansion of the rate is now changed by a factor $e^{-\lambda\tau_D}$

$$\gamma(P_2(t - \tau_D)) = \gamma(P_2^* + a_i e^{\lambda(t - \tau_D)}) = \gamma(P_2^*) + e^{-\lambda\tau_D} \gamma'(P_2^*) a_i e^{\lambda t}. \quad (34)$$

Accordingly, in the case of delayed feedback, only the coefficient $s = \gamma'(P_2^*)P_1^*$ in the characteristic equation has to be changed: $s \rightarrow s e^{-\lambda\tau_D}$. Figure 8 shows the bifurcation diagram in the parameter plane of γ and γ' with the Hopf curves for values of the sharpness parameter $\alpha = 14$ and $\alpha = 20$. Oscillatory behavior (loops of the curves) is reinforced by the delayed feedback, provided it is contained in the dynamics without delay as well ($\alpha = 20$). Thus, for the selected parameters, we observe a quantitative but no qualitative change.

5 Diffusion Approximation of the Three-State Dynamics

In the following we outline the reduction of the model to Langevin dynamics governed by drift and diffusion properties of the three-state dynamics. It can be considered as a diffusion approximation of a renewal process with statistically independent time intervals between subsequent discrete events. The important information on such a process describing the temporal evolution of the number of events is provided by two quantities: (1) the rate of occurrence of events and (2) its effective diffusion coefficient. The latter quantity describes, how the variance of the number of events grows in time. We map the number of events on a random continuous phase increasing by 2π if an event occurs. The rate of events is just the increment of the phase per unit time or the angular frequency. The increment of the variance per unit time gives the phase diffusion coefficient. Thus, both increments can be used as a measure of the periodicity and regularity of the process in the diffusion approximation.

In [66], a method was proposed to calculate this mean frequency and effective diffusion coefficient of a renewal process in terms of its waiting time distribution $w(\tau, t)$, where τ is the waiting time and t is the absolute time at which the last event happened. To calculate

the moments of discrete events, a continuous envelope $P(\phi, t)$ of the discrete probabilities $P_k(t)$ was introduced. Also the probability currents $j_k(t)$ were related to an envelope $J(\phi, t)$.

The continuous envelope $P(\phi, t)$ obeys the Kramers–Moyal equation

$$\frac{\partial}{\partial t} P(\phi, t) = \sum_{n=1}^{\infty} \frac{(-1)^n}{n!} D^{(n)}(t) \left(\frac{\partial}{\partial \phi} \right)^n P(\phi, t). \quad (35)$$

The continuous variable ϕ can now be interpreted as a phase ϕ : the dynamics of which describe the evolution of the three-state oscillators as a continuous motion along a circle from 0 to 2π . By restricting further the dynamics to the first two terms in (35), one obtains a Smoluchowski equation for the probability density $P(\phi, t)$. In this so-called diffusion approximation the continuous phase of a single unit is governed by a Langevin equation with constant drift and noise:

$$\frac{d}{dt} \phi = D^{(1)} + \sqrt{D^{(2)}} \xi(t). \quad (36)$$

We use the Ito definition of the stochastic differential equation. $\xi(t)$ is Gaussian white noise with an intensity equal to 1. The drift and diffusion coefficients are given by the first and second moments of the renewal process for one rotation [66]

$$D^{(1)} = \frac{2\pi}{\langle T \rangle}, \quad D^{(2)} = (2\pi)^2 \frac{\langle T^2 \rangle - \langle T \rangle^2}{\langle T \rangle^3}, \quad (37)$$

where T denotes one period of the three-state dynamics with mean $\langle T \rangle = \bar{\tau}_1 + \bar{\tau}_2 + \bar{\tau}_3$. The phase ϕ increases by $\Delta\phi = 2\pi$ during one rotation.

In the three-state model the corresponding moments in (37) can be calculated easily. The mean of τ_1 is $1/\gamma$ and its variance $1/\gamma^2$ and the other transitions are described by the Gamma-distribution densities (27) with mean $\tau_{2,3}$ and variance $\tau_{2,3}^2/\alpha_{2,3}$. Hence we obtain for the drift and diffusion coefficients of single independent units

$$D^{(1)} = \frac{2\pi}{1/\gamma + \tau_2 + \tau_3}, \quad D^{(2)} = (2\pi)^2 \frac{1/\gamma^2 + \tau_2^2/\alpha_2 + \tau_3^2/\alpha_3}{(1/\gamma + \tau_2 + \tau_3)^3}. \quad (38)$$

The solution of the Smoluchowski equation (36) yields a Gaussian distribution; its mean values and variance increase in time as $D^{(1)}(t - t_0)$ and $D^{(2)}t$, respectively.

In Section 3 we derived the mean field equations. They have a structure similar to the kinetic equations of single units but with the rate γ depending on the global output $f(t)$. Therefore, it is straightforward to assume for the continuous phase dynamics of the ensemble the same dependence as for the single unit. Hence, we formulate the Ito–Langevin equations in the diffusion approximation for the individual phases ϕ_i of the N units in the ensemble. In these equations, the rate γ should depend on the mean output $f(t)$. Similar to the discrete case, the Ito–Langevin equations for the phases in the coupled network read

$$\frac{d}{dt} \phi_i = D^{(1)}(f) + \sqrt{D^{(2)}(f)} \xi(t). \quad (39)$$

The ensemble is connected through the global output $f(t)$ which still has to be defined. We will use a nonrigorous but simple continuous prescription for relating this output to the continuous phases. We postulate the output of a unit to be

$$s_i(t) = \frac{1 + \cos(\phi_i)}{2}. \quad (40)$$

It would be an exact mapping if the phases $\pm\pi/2$ correspond to state 1 and 3 and phase $\phi = 0$ to state 2. In that sense, (40) has similar properties as the output defined for the three state systems, and we will use it as the link between the different elements in the continuous description.

With (8), the global output is then expressed in the continuous description by

$$f(t) = \frac{1}{2N} \sum_{i=1}^N (1 + \cos(\phi_i)). \quad (41)$$

The rate γ is given by

$$\gamma(f) = \gamma_0 e^{-\frac{\Delta U}{D}(1-\sigma f)} \approx \gamma_0 e^{-\frac{\Delta U}{D}} \left(1 + \frac{\Delta U \sigma}{2DN} \sum_{i=1}^N (1 + \cos \phi_i) \right), \quad (42)$$

and for the expansion, we assume the coupling strength σ to be sufficiently small. Then, the drift coefficient can be approximated by:

$$D^{(1)}(f) = \frac{2\pi}{\frac{1}{\gamma_0 e^{-\frac{\Delta U}{D}(1-\sigma f)}} + \tau_2 + \tau_3} \approx \frac{1}{\omega_0^{-1} - e^{-\frac{\Delta U}{D}} \frac{A}{\gamma_0} \sum_{i=1}^N (1 + \cos \phi_i)}, \quad (43)$$

with $\omega_0^{-1} = \frac{1}{2\pi} \left(\frac{1}{\gamma_0} e^{\frac{\Delta U}{D}} + \tau_2 + \tau_3 \right)$ and $A = \frac{\Delta U \sigma}{4\pi ND}$. Further expansion gives:

$$\begin{aligned} D^{(1)}(f) &= \frac{\omega_0}{1 - e^{-\frac{\Delta U}{D}} \frac{A\omega_0}{\gamma_0} \sum_{i=1}^N (1 + \cos \phi_i)} \\ &\approx \omega_0 + e^{-\frac{\Delta U}{D}} \frac{A\omega_0^2}{\gamma_0} \sum_{i=1}^N (1 + \cos \phi_i). \end{aligned} \quad (44)$$

For the determination of the diffusion coefficient, we take the case of a deterministic switching in the excited and refractory state and set $\alpha_{2,3} = \alpha \rightarrow \infty$. Then, these steps do not contribute to the variance, which is valid for lower noise levels. That results in:

$$\sqrt{D^{(2)}(f)} = \frac{2\pi}{\gamma \langle T \rangle^{3/2}}. \quad (45)$$

In the first approximation, one sets $1/\langle T \rangle^{3/2} = \omega_0^{3/2} + \dots \approx \omega_0^{3/2}$ and obtains

$$\sqrt{D^{(2)}(t)} \approx \frac{\omega_0^{3/2}}{\gamma_0} e^{-\frac{\Delta U}{D}} \left(1 - A \sum_{i=1}^N (1 + \cos \phi_i) \right). \quad (46)$$

Given these approximations, we arrive at the Langevin equation for the phase ϕ_j in the following form:

$$\begin{aligned} \frac{d}{dt} \phi_j &= \omega_0 + e^{-\frac{\Delta U}{D}} \frac{A\omega_0^2}{\gamma_0} \sum_{i=1}^N (1 + \cos \phi_i) \\ &\quad + \frac{\omega_0^{3/2}}{\gamma_0} e^{-\frac{\Delta U}{D}} \left(1 - A \sum_{i=1}^N (1 + \cos \phi_i) \right) \xi_i(t). \end{aligned} \quad (47)$$

In this way we have derived a Kuramoto-like equation of the kind that has been often used for the description of transitions in active rotator models. The first term is the mean frequency of rotation.

6 Conclusions

We have introduced a non-Markovian discrete model to study ensembles of globally coupled units with excitable dynamics. Dynamics of such units is characterized through the waiting time densities of the discrete states. Their determination is not limited to the FitzHugh–Nagumo system that we have used here. As a starting point for the formalism of the waiting time densities, one can take an arbitrary dynamical system in which an excitation of the single steady state is followed by a long excursion in the phase space and a subsequent refractory time. Neither is the approach restricted to the specific type of coupling we have introduced.

For the first time, we included in our model a delayed feedback and found that it results in shifts of the bifurcation diagrams. For other parameter values one should expect a much more complex collective behavior as a consequence of delayed feedback: for a fixed point (steady state), the number of unstable directions in the phase space can become arbitrarily high.

Future work will be necessary to develop simple models with arbitrary coupling. For applications in neuroscience and in biophysics, globally interacting ensembles can give only a first insight into multiple possible complex spatial and temporal structures. The introduction of local diffusive coupling or the consideration of dynamical systems on networks for stochastic models as the considered three-state model remains a challenge for the future.

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