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Mean Field Dynamics of Networks of Delay-coupled Noisy Excitable Units

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Abstract. We use the mean-field approach to analyze the collective dynamics in macroscopic networks of stochastic Fitzhugh-Nagumo units with delayed couplings. The conditions for validity of the two main approximations behind the model, called the Gaussian approximation and the Quasi-independence approximation, are examined. It is shown that the dynamics of the mean-field model may indicate in a self-consistent fashion the parameter domains where the Quasi-independence approximation fails. Apart from a network of globally coupled units, we also consider the paradigmatic setup of two interacting assemblies to demonstrate how our framework may be extended to hierarchical and modular networks. In both cases, the mean-field model can be used to qualitatively analyze the stability of the system, as well as the scenarios for the onset and the suppression of the collective mode. In quantitative terms, the mean-field model is capable of predicting the average oscillation frequency corresponding to the global variables of the exact system.

INTRODUCTION

One of the extraordinary properties of excitable systems lies in their ability to synchronize. Appreciating the wealth of complex synchronization phenomena and spatiotemporal pattern activity, the macroscopic systems of coupled excitable units have now been recognized as a distinct class of dynamical systems [1]. The dynamics of such systems typically involves multiple characteristic spatial and temporal scales, which results in different forms of perturbation and fluctuations of intrinsic parameters. Such influences are described by introducing noise into pertaining models. Further, modeling of macroscopic systems of excitable units requires one to explicitly take into account the effects of interaction delays, which derive from finite signal velocities and/or latency in units' responses.

In mathematical terms, these models are given by systems of nonlinear stochastic delay-differential equations ($SDDE$s), whose stability and bifurcations are difficult to analyze. In particular, the approach to stability analysis based on Fokker-Planck formalism is hampered by the non-Markovian character of the underlying process, whereas the phase reduction techniques are not applicable, as the phase variable cannot be attributed to systems lying in equilibrium. Nonetheless, one should further be able to account for the stochastic bifurcations that the global variables may undergo, which is accompanied by a qualitative change of the relevant asymptotic probability distributions or the associated power spectra [2]. For these reasons, it has become necessary to develop approximate models, that (i) can allow one to analyze the stability and stochastic bifurcations of the described systems, and (ii), are self-contained, in a sense that the parameter domains where the model applies or fails are mathematically tractable.

In this paper, we consider assemblies of noisy Fitzhugh-Nagumo (FHN) units, whose dynamics is canonical for type II excitability class. The goal is to make an overview of results demonstrating that the two requirements stated above are satisfied by the mean-field (MF) model which combines the cumulant approach with the Gaussian approximation. The paper is organized as follows. In Sec. 1, we present the MF model for an assembly of FHN units and discuss the conditions under which its two core approximations are fulfilled. In Sec. 2 we examine the setup consisting of two delay-coupled networks of FHN units and analyze its stability and bifurcations.

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MF APPROXIMATIONS AND THEIR VALIDITY

Let us consider a network of delay-coupled *FHN* units with noise terms added to the slow variables ("internal noise"). For simplicity, we assume that the network is homogeneous and that the units are coupled in the all-to-all fashion. The couplings are characterized by the strength c and the delay τ. The local dynamics is then given by:

$$\begin{aligned}\varepsilon dx_i &= (x_i - x_i^3/3 - y_i)dt + \frac{c}{N}\sum_{j=1}^{N}(x_j(t-\tau) - x_i)dt \\ dy_i &= (x_i + b)dt + \sqrt{2D}dW_i, i = 1, \ldots N,\end{aligned} \tag{1}$$

where $\varepsilon = 0.01$ is the separation ratio between the fast and the slow characteristic time scale, $b = 1.05$ denotes the bifurcation parameter, while dW_i are stochastic increments of independent Wiener processes. The Hopf bifurcation occurs at $b = 1$, and the units are in excitable regime for $b > 1$.

Starting from the original system of $2N$ *SDDE*s, the *MF* model reduces the description of collective dynamics to a set of just 5 deterministic delay-differential equations for the means $m_x(t) = \langle x_i(t)\rangle \equiv \lim_{N\to\infty}(1/N)\sum_{i=1}^{N} x_i(t), m_y(t) = \langle y_i(t)\rangle$, the variances $s_x(t) = \langle(\langle x_i(t)\rangle - x_i(t))^2\rangle, s_y(t) = \langle(\langle y_i(t)\rangle - y_i(t))^2\rangle$ and the covariance $u(t) = \langle(\langle x_i(t)\rangle - x_i(t))(\langle y_i(t)\rangle - y_i(t))\rangle$, whereby D plays the role of an additional bifurcation parameter. The fact that the system comprises only the equations for the first and the second order moments is consistent with the Gaussian approximation, which is required as a closure hypothesis due to nonlinearity of the original system (1). In order to ensure that the model is analytically tractable, one may further introduce "adiabatic approximation", by which the variances and the covariances are replaced by their stationary values [3, 4]. This is physically justified as the corresponding relaxation times are typically small. The *MF* model then contains just two equations for the means [3, 4]:

$$\begin{aligned}\varepsilon\frac{dm_x(t)}{dt} &= m_x(t) - m_x(t)^3/3 - \frac{m_x(t)}{2}\left\{1 - c - m_x(t)^2 + \sqrt{[c-1+m_x(t)^2]^2 + 4D}\right\} - m_y(t) + c[m_x(t-\tau) - m_x(t)], \\ \frac{dm_y(t)}{dt} &= m_x(t) + b.\end{aligned} \tag{2}$$

The form (2) is convenient because for $\tau = 0$ one may apply the phase plane analysis, showing that for conditions where the *MF* model holds, the whole assembly acts as a macroscopic excitable system, cf. Fig. 1(a). It is further possible to directly compare the features of excitable dynamics (such as threshold-like behavior) for a single *FHN* unit and the assembly. Another important point is that the bifurcation analysis of the *MF* model can be carried out analytically [3]. In particular, system (2) is found to undergo a sequence of direct and inverse Hopf bifurcations, see the $\tau(D)$ bifurcation diagram in Fig. 1(b), whereby the former (latter) are always supercritical (subcritical). The system's behavior is also strongly affected by the global fold-cycle bifurcation. Due to interplay between the local bifurcations and the global bifurcation, there are parameter domains where the *MF* model is bistable, exhibiting coexistence between the stationary and the oscillatory state or between two oscillatory solutions.

An issue relevant for the application of *MF* model is to identify the parameter domains where it provides qualitatively accurate predictions. This depends on the range of validity of *MF* approximations (*MFA*s). In our recent paper [3], we have singled out the Quasi-independence Approximation (*QIA*) and the Gaussian Approximation (*GA*) as the key ingredients for the model (2), providing their precise formulations. Here we briefly address two conceptual points regarding the *MFA*s: (i) whether they are "universal", or they should be adapted to the considered class of systems, and (ii) whether the dynamics of the *MF* model can itself point to parameter domains where the *MFA*s fail.

The *MFA*s are often regarded as if they were independent on the class of systems which the particular model belongs to. Within such simplified view, one would expect the *MF* model to break down above the stochastic bifurcation underlying transition from the stochastically stable fixed point to continuous oscillations, which is accompanied by the loss of Gaussian property for the *asymptotical* distribution of the global variables $X = (1/N)\sum_{i=1}^{N} x_i(t), Y = (1/N)\sum_{i=1}^{N} y_i(t)$. However, the *MF* model holds in the supercritical state and its oscillation frequency above the Hopf bifurcation matches quite closely the average frequency of the noise-induced oscillations for the (X,Y) variables. This indicates that formulation of *GA* should be adapted to class II excitable systems. We have shown that it is crucial to take into account the relaxation character of pertaining oscillations [3]. Such refined formulation of *GA* does not require the $x_i(t)$ and $y_i(t)$ to be Gaussian processes over asymptotically large time intervals, but rather to be Gaussian over small intervals $(t, t+\delta t)$, whereby the latter should hold for most t. Use of *GA* in the supercritical state relies on that the fraction of time where this condition is not satisfied does not lead to significant deviations of the *MF* dynamics relative to the exact system.

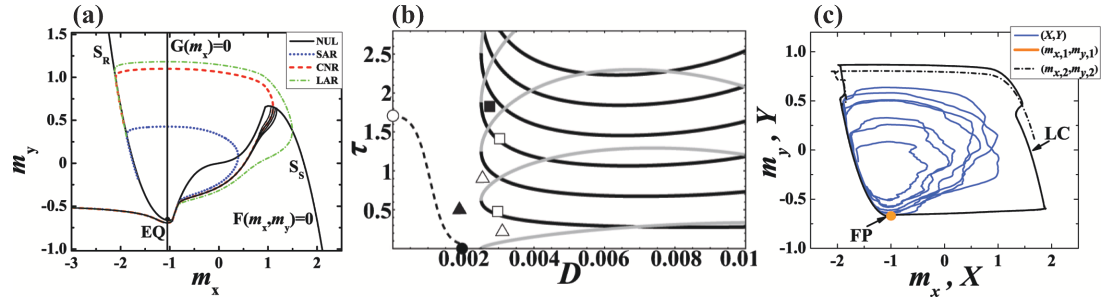

FIGURE 1. (a) Phase plane analysis of the *MF* model (2) for $b = 1.05, c = 0.1, \varepsilon = 0.07, \tau = 0$. The boundary between the initial conditions leading to small (*SAR*) or large amplitude responses (*LAR*) is given by a canard-like (*CNR*) trajectory ("ghost separatrix"). (b) Bifurcation diagram for the *MF* model (2). The direct (inverse) Hopf bifurcations are shown by the black (gray) solid lines, whereas the dashed line indicates the parameter values that give rise to fold-cycle bifurcation. The regions admitting bistability between the fixed point (FP) and the limit cycle (*LC*), or between two *LC*s are denoted by triangles (squares). (c) Illustration of the scenario where *QIA* fails. The stochastic orbit of the exact system (blue line) fluctuates between the coexisting solutions of the *MF* model, the FP and the *LC*. The parameter set is $(c, D, \tau) = (0.1, 0.0029, 0.3)$.

Detailed analysis shows that *GA* is satisfied if there is qualitative matching between the attractors for local variables (x_i, y_i) and the respective averages over an ensemble of stochastic realizations. As for validity of *QIA*, the key point lies in that the dynamics of the *MF* model may indicate in a self-consistent fashion the parameter domains where *QIA* no longer holds. In particular, we have shown that the *noise-induced bistability* in the *MF* dynamics is a necessary condition for the failure of *QIA* [3]. The key step to this inference is to realize that *QIA* implies the validity of Gaussian approximation for the *global* variables (X, Y) over an ensemble of stochastic realizations. What we have demonstrated is that the stochastic fluctuations of (X, Y) are no longer Gaussian when the *MF* model displays coexistence between the fixed point and the limit cycle or between two limit cycles. For the parameter domains admitting these scenarios, the typical orbits of the exact system exhibit large fluctuations that qualitatively appear as stochastic switches between the two solutions of the *MF* model, see Fig. 1(c). Note that the violation of *QIA* may point to complex self-organization phenomena, such as the cluster-states [5, 6].

MF MODEL FOR TWO DELAY-COUPLED ASSEMBLIES

Our main point concerns the potential extending of the *MF* approach to hierarchical and modular networks. To this end, we consider a paradigmatic setup involving two interacting networks of globally coupled FHN units. Such a block may serve as a nucleus for the "network of networks" [7, 8], which can either be realized as a hierarchy of multiple networks, or it can be seen as an idealization of a network with strong modular structure and a large number of elements in each community. Both types of configurations are quite common in biological systems.

In our setup, the populations are assumed to be homogeneous, and the coupling between the assemblies is given by a nonlinear threshold-like function of the respective global variables. The inter-population couplings are characterized by the strength $g_{c,i}$, where i refers to the population index, and the delay $\tau_{c,i}$. The interactions within the populations are linear, and are described by $g_{in,i}$ and $\tau_{in,i}$, $\tau_{in,i} < \tau_{c,i}$. The equations for the local dynamics then read:

$$\begin{aligned}
\varepsilon dx_{i,k} &= (x_{i,k} - x_{i,k}^3/3 - y_{i,k})dt + \frac{g_{in,k}}{N}\sum_{j=1}^{N}[x_{j,k}(t-\tau_{in,k}) - x_{i,k}(t)]dt + g_{c,k}\arctan[X_l(t-\tau_{c,k}) + b_l]dt, \\
dy_{i,k} &= (x_{i,k} + b_k)dt + \sqrt{2D_k}dW_{i,k},
\end{aligned} \tag{3}$$

where k, l denote population indices ($k, l \in \{1, 2\}, k \neq l$). Applying the method described in Sec. 1, we arrive at the *MF* model for two delay-coupled assemblies [4]:

$$\begin{aligned}
\varepsilon \frac{dm_{x,i}(t)}{dt} &= m_{x,i}(t) - \frac{m_{x,i}(t)^3}{3} - \frac{m_{x,i}(t)}{2}(1 - g_{in,i} - m_{x,i}(t)^2 + \sqrt{(g_{in,i} - 1 + m_{x,i}(t)^2)^2 + 4D_i}) - m_{y,i}(t) \\
&\quad + g_{in,i}(m_{x,i}(t-\tau_{in,i}) - m_{x,i}(t)) + g_{c,i}\arctan(m_{x,j}(t-\tau_{c,i}) + b_j) \\
\frac{dm_{y,i}(t)}{dt} &= m_{x,i}(t) + b_i, \qquad (i, j \in \{1, 2\}, i \neq j).
\end{aligned} \tag{4}$$

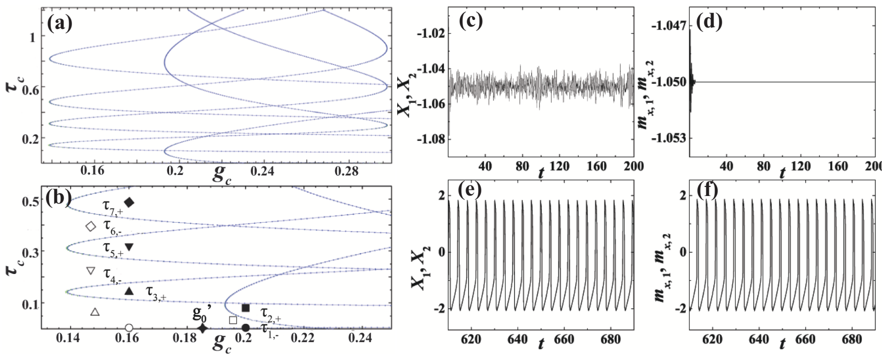

FIGURE 2. (a) Hopf bifurcation curves $\tau_c(g_c)$ for model (4). The internal parameter values are $\tau_{in} = 0.3$ $g_{in} = 0.1$ and $D = 0.0001$. (b) provides a close-up view of (a), focused on the parameter region where the stability of the equilibrium changes. (c), (d), (e) and (f) show the time series of the exact system (3) and the approximate system (4) below ($g_c = 0.16, \tau_c = 0.06$) and above ($g_c = 0.16, \tau_c = 0.14$) the curve $\tau_{3,+}$ from (b). The left (right) column refers to the exact (approximate) system, whereas the top (bottom) row corresponds to states below (above) $\tau_{3,+}$.

Since our main interest lies with the effects of $g_{c,i}$ and $\tau_{c,i}$, let us suppose that the intra-coupling parameters of both assemblies are identical and are set to g_{in} and τ_{in} which admit the stationary state. As for a single population, the bifurcation analysis shows that the approximate model (4) undergoes a sequence of direct and inverse supercritical and subcritical Hopf bifurcations, such that the direct (inverse) bifurcations lead to destabilization (stabilization) of the stationary state [4]. The sequence *per se* depends on the details of system configuration, like the symmetrical/asymmetrical character of the cross-population terms.

The main result refers to the symmetrical case $g_{c,1} = g_{c,2} = g_c, \tau_{c,1} = \tau_{c,2} = \tau_c$, see the $\tau_c(g_c)$ bifurcation diagram in Fig. 2(a). In particular, we demonstrate that the equilibrium may lose stability via two different scenarios depending on g_c [4]. This is associated to the fact that apart from the local Hopf bifurcations, the *MF* model also undergoes a global fold-cycle bifurcation at $(g_c, \tau_c) = (g_0^{'}, 0)$, whereby a saddle cycle and a large stable limit cycle are born. For $g_c < g_0^{'}$, the equilibrium is destabilized via the direct supercritical Hopf bifurcation, cf. the corresponding time series in Fig. 2(c)-(f). Note that such a scenario can also be realized for *instantaneous* couplings solely by increasing g_c. The other scenario ($g_c > g_0^{'}$) unfolds via the direct subcritical Hopf bifurcation, and is immediately tied to the global bifurcation. In fact, sufficiently away from the Hopf bifurcation, the only remaining attractor is the large cycle born in the fold-cycle bifurcation. An interesting ingredient to the second scenario is that for $g_c \simeq g_{in}$ there exists a time-lag threshold necessary to destabilize the equilibrium. Apart for facilitating the qualitative analysis on stability of the exact system, as well as the scenarios for onset and suppression of the collective mode, the *MF* model (4) also provides accurate predictions on the average frequency of oscillations of the exact system (3).

The future work will focus on the analysis of finite-size effects and building the *MF* model appropriate for networks with complex topology of interactions.

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