Bifurcations due to small time-lag in coupled excitable systems

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Abstract

A system of ODE's is used to attempt an approximation of the dynamics of two delayed coupled FitzHugh-Nagumo excitable units, described by delay-differential equations. It is shown that the codimension 2 generalized Hopf bifurcation acts as the organizing center for the dynamics of ODE's for small time-lags. Furthermore, this is used to explain important qualitative properties of the exact dynamics for small time-delays.

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Introduction

Dynamics of a pair of excitable systems with time-delayed coupling is quite different from the dynamics with the instantaneous coupling. Also, the behaviour of coupled excitable systems differs from that of coupled oscillators with the same coupling. A prime example of the type II excitable behaviour (see [Izhikevich, 2000]) has been the system introduced by FitzHugh [FitzHugh 1955] and Nagumo et all [Nagumo et all, 1962], as an approximation of the Hodgine-Haxley model of the nerve cell membrane. One form of the FHN equations is (see [Murray, 1992]):

$$\dot{x} = -x^3 + (a+1)x^2 - ax - y + I,$$

$$\dot{y} = bx - \gamma y$$
(1)

As is well known the system (1) can operate in two regimes depending on the external current I, as an excitable system if I = 0 and

$$4\frac{b}{\gamma} < (a-1)^2,\tag{2}$$

with the stable stationary solution as the only attractor, or as a relaxation oscillator $I = const \neq 0$, with the stable limit cycle as the only attractor.

Two delayed coupled FHN excitable systems with delayed coupling given by the following equations:

$$\dot{x}_{1} = -x_{1}^{3} + (a+1)x_{1}^{2} - ax_{1} - y_{1} + c \tan^{-1}(x_{2}^{\tau}),
\dot{y}_{1} = bx_{1} - \gamma y_{1},
\dot{x}_{2} = -x_{2}^{3} + (a+1)x_{2}^{2} - ax_{2} - y_{2} + c \tan^{-1}(x_{1}^{\tau}),
\dot{y}_{2} = bx_{2} - \gamma y_{2},$$
(3)

where $x^{\tau}(t) = x(t - \tau)$, have been recently analyzed in [Burić&Todorović, 2003]. Motivation, background and the relevant literature is discussed in detail in [Burić&Todorović, 2003] and will not be repeated here.

Besides different types of oscillations induced by coupling and changed by the time-delay, the system displays two different types of excitable behaviour. The first one is described by a single stationary solution at $E_0 \equiv (0, 0, 0, 0)$ as the only attractor. The other type is described by two coexisting attractors, the stable stationary solution E_0 and a stable limit cycle corresponding to periodic exactly synchronous excitations of the two units. The later regime occurs only in a specific, relatively small, domain in the parameters (c, τ) plane. Burić&Todorović obtained bifurcation curves in (c, τ) plane by solving the characteristic equation of (3) for the non-hyperbolic roots. The bifurcation curves served as a guide for the analyzes of the system by extensive numerical calculations, which resulted in the classification of possible excitable and oscillatory dynamics.

In this letter we would like to report some analytic results aimed at better understanding of the types of bifurcations which are relevant for the two types of the excitable behaviour. To this end we shall analyze the bifurcations of the stationary solution that occur in a system related to the equations (3) in the following way. Both types of excitable behaviour happen for relatively small time-lags, and such a small time-lag induces the responsible bifurcations. Thus it might be justified to replace the time-delayed argument of the coupling function in (3) by the following approximation:

$$f(x(t-\tau)) \approx f(x-\tau \dot{x}). \tag{4}$$

and approximate the delay-differential (DDE) by ordinary differential equations. The approximate system is given by:

$$\begin{aligned} \dot{x}_1 &= -x_1^3 + (a+1)x_1^2 - ax_1 - y_1 + \\ &+ c \tan^{-1}(x_2 - \tau(-x_2^3 + (a+1)x_2^2 - ax_2 - y_2 + c \tan^{-1}(x_1))), \\ \dot{y}_1 &= bx_1 - \gamma y_1, \\ \dot{x}_2 &= -x_2^3 + (a+1)x_2^2 - ax_2 - y_2 + \\ &+ c \tan^{-1}(x_1 - \tau(-x_1^3 + (a+1)x_1^2 - ax_1 - y_1 + c \tan^{-1}(x_2))), \\ \dot{y}_2 &= bx_2 - \gamma y_2, \end{aligned}$$
(5)

Validity of the approximation (4) and (5) is not *apriori* justified even for small τ . Such type of questions have been analyzed before in general and for specific examples (see [Meinardus & Nuenberg, 1985]). More recent example of such an analyzes, for a particular system, is given in the reference [Faro & Velasco, 1997], where the approximation has been investigated using a predator-prey equations with a time-delay by comparison of numerically obtained bifurcation curves.

The main result of our analyzes is that the bifurcation which acts as the organizing center for the dynamics of the system (5) for small τ is the codimension 2 generalized Hopf (Bautin) bifurcation. Furthermore, the bifurcation occurs for quite a small time-lag where the bifurcation curves of the exact and approximate system almost coincide and the dynamics is qualitatively the same. This fact is used to explain the occurrence of the two types of excitable behaviour.

The approximate and the exact systems will be abbreviated as $\dot{X} = \mathcal{F}(X, X^{\tau})$ and $\dot{X} = \mathcal{F}_{app}(X)$ where $X \in \mathbf{R}^4$ represents the collection of coordinates x_1, y_1, x_2, y_2 .

Bifurcations of the stationary solution

We shall restrict attention only on such values of the parameters a, b, γ, c that the system \mathcal{F}_{app} for $\tau = 0$ has only one stationary solution. This occurs if

$$c < c_1 \equiv a + b/\gamma. \tag{6}$$

Futhermore, each unit is excitable when decoupled, i.e. the condition (2) is assumed satisfied. We fix the parameters a, b and γ to some arbitrary such value, and consider the bifurcations of E_0 that could occur as the parameters c and τ are varied. The bifurcation set \mathcal{B}_{E_0} is defined as the set of (c, τ) values such that the stationary solution E_0 is not hyperbolic. By an abuse of notation, we shall use the same symbol \mathcal{B}_{E_0} for the part of $\mathcal{B}_{E_0} \subset \mathbf{R}^+ \times \mathbf{R}^+$ satisfying (6), i.e.

$$\mathcal{B}_{E_0} = \left\{ (c, \tau) \in \mathbf{R}^+ \times \mathbf{R}^+ | \mathbf{Re}\lambda(c, \tau) = 0, c < c_1 \right\},\tag{7}$$

where λ is any root of the characteristic polynomial.

The set \mathcal{B}_{E_0} consists of two line segments in (c, τ) plane. Namely:

$$\mathcal{B}_{E_{0}} = \{(c,\tau) | \tau = 1/c, c < c_{1} \} \bigcup \left\{ (c,\tau) | \tau = \frac{c-a-\gamma}{c(c-a)}, c \in (a,c_{1}) \right\}$$

$$\equiv \mathcal{B}_{E_{0};p} \bigcup \mathcal{B}_{E_{0};H}.$$
(8)

Indeed, the linear part of (5)

$$A = \begin{pmatrix} F & -1 & D & E \\ b & -\gamma & 0 & 0 \\ D & E & F & -1 \\ 0 & 0 & b & -\gamma \end{pmatrix},$$
(9)

where

$$F = -a - c^2 \tau, \quad D = c + ca\tau, \quad E = c\tau \tag{10}$$

implies the following characteristic equation:

$$\Delta(\lambda) \equiv \Delta_1(\lambda)\Delta_2(\lambda) = 0 \tag{11}$$

where

$$\Delta_1(\lambda) = \lambda^2 + (\gamma - F - D)\lambda + b - F\gamma - \gamma D - bE$$

$$\Delta_2(\lambda) = \lambda^2 + (\gamma - F - D)\lambda + b - F\gamma + \gamma D + bE$$
(12)

with solutions

$$\lambda_{1,2} = \left[-\gamma + F + D \pm \sqrt{(\gamma + F + D)^2 - 4b(1 - E)} \right] / 2, \ \Delta_1(\lambda_{1,2}) = 0,$$

$$\lambda_{3,4} = \left[-\gamma + F - D \pm \sqrt{(\gamma + F - D)^2 - 4b(1 + E)} \right] / 2, \ \Delta_2(\lambda_{3,4}) = 0.$$
(13)

A nonhyperbolic root can be either equal to zero or pure imaginary. In the first case,

$$\Delta_1(0) = 0 \quad \Leftrightarrow \quad b - F\gamma - gD - bE = 0$$
$$\Leftrightarrow \quad \tau c(c\gamma - a\gamma - b) = c\gamma - a\gamma - b, \tag{14}$$

which defines the line segment $\mathcal{B}_{E_0;p}$. The second factor of the characteristic polynomial has no zero roots for any positive c and τ . In the second case

$$\Delta_1(iv) = 0, v > 0 \iff -v^2 + (\gamma - F - D)iv + b - F\gamma - \gamma D - bE = 0$$

$$\Leftrightarrow v^2 = b - F\gamma - \gamma D - bE > 0 \text{ and } (\gamma - F - D)v = 0.$$

If $c \in (a, c_1)$ then from the last condition we obtain the line segment $\mathcal{B}_{E_0;H}$ and $v = \sqrt{\gamma(a\gamma + b - c\gamma)/(c - a)}$. On the other hand, if $c \notin (a, c_1)$ there is no pure imaginary solution of $\Delta_1 = 0$. Furthermore $\Delta_2 = 0$ has no pure imaginary solutions for any positive τ and c. Thus, \mathcal{B}_{E_0} is indeed given by (8). It is illustrated in figure 1a. The point where \mathcal{B}_{E_0} intersects the c axis is denoted by c_0 . Thus:

$$c_0 = a + \gamma. \tag{15}$$

The type of bifurcations occurring for the parameters (c, τ) in $\mathcal{B}_{E_0;p}$ and $\mathcal{B}_{E_0;H}$ are described in the following two theorems.

Theorem 1 The system \mathcal{F}_{app} has a pitchfork bifurcation for any $(c, \tau) \in \mathcal{B}_{E_0;p}$.

Proof: The linear part A on $\mathcal{B}_{E_0;p}$ has a simple zero eigenvalue. The type of bifurcation at $\tau = 1/c$ is analyzed by reducing the system on the corresponding center manifold with the parameter $\epsilon = \tau - 1/c$. As we shall see, it is enough to consider the extended system, given by (5) and $\dot{\epsilon} = 0$ expended up to the third order in $x_1, x_2, y_1, y_2, \epsilon$:

$$\begin{aligned} \dot{x}_{1} &= -(a+c)x_{1} - y_{1} + (a+c)x_{2} + y_{2} + (a+1)(x_{1}^{2} - x_{2}^{2}) \\ &+ (c/3-1)(x_{1}^{3} - x_{2}^{3}) - ax_{2}^{3} - x_{2}^{2}y_{2} + cx_{2}^{2}x_{1} - c(a+1)\epsilon x_{2}^{2} + \\ &+ ac\epsilon x_{2} + c\epsilon y_{2} - c^{2}\epsilon x_{1} \end{aligned}$$

$$\dot{y}_{1} &= bx_{1} - \gamma y_{1} \\ \dot{x}_{2} &= (a+c)x_{1} + y_{1} - (a+c)x_{2} - y_{2} - (a+1)(x_{1}^{2} - x_{2}^{2}) \\ &- (c/3-1)(x_{1}^{3} - x_{2}^{3}) - ax_{1}^{3} - x_{1}^{2}y_{1} + cx_{1}^{2}x_{2} - c(a+1)\epsilon x_{1}^{2} + \\ &+ ac\epsilon x_{1} + c\epsilon y_{1} - c^{2}\epsilon x_{2} \end{aligned}$$

$$\dot{y}_{2} &= bx_{2} - \gamma y_{2} \\ \dot{\epsilon} &= 0. \end{aligned}$$
(16)

The center manifold with the parameter ϵ of the system (16), in the new coordinates (x, y, z, t, ϵ) related to the old ones by

$$\begin{aligned}
x_1 &= x - z - t, \\
y_1 &= bx/\gamma + y - bz/(\gamma + \lambda_3) - bt/(\gamma + \lambda_4), \\
x_2 &= x + z + t, \\
y_2 &= bx/\gamma + y + bz/(\gamma + \lambda_3) + bt/(\gamma + \lambda_4), \\
\lambda_{3,4} &= (-2(a + c) - \gamma \pm \sqrt{(2a + 2c - \gamma)^2 - 8b)}/2,
\end{aligned}$$
(17)

is:

$$W^{c}(0) = \{(x, y, z, t, \epsilon) | y = h_{1}(x, \epsilon), z = h_{2}(x, \epsilon), t = h_{3}(x, \epsilon); h_{i}(0, 0) = 0, Dh_{i}(0, 0) = 0, i = 1, 2, 3\}, (18)$$

where

$$h_1(x,\epsilon) = -\frac{bc}{\gamma^2}(a+b/\gamma-c)x\epsilon + \frac{b}{\gamma^2}(a+b/\gamma-c)x^3 + \frac{bc}{\gamma}(a+1)x^2\epsilon + \dots,$$

$$h_2(x,\epsilon) = 0,$$

$$h_3(x,\epsilon) = 0.$$
(19)

Restriction of (16) on the center manifold (18) is given by:

$$\dot{x} \equiv F(x,\epsilon) = c(a+b/\gamma-c)x\epsilon - (a+b/\gamma-c)x^3 - c(a+1)x^2\epsilon + \dots, \quad (20)$$

and satisfies:

$$\begin{split} \frac{\partial F(0,0)}{\partial \epsilon} &= 0, \quad \frac{\partial^2 F(0,0)}{\partial \epsilon^2} = 0, \\ \frac{\partial^2 F(0,0)}{\partial \epsilon \partial x} &= c(a+b/\gamma-c) \neq 0, \\ \frac{\partial^3 F(0,0)}{\partial x^3} &= -6(a+b/\gamma-c) \neq 0. \end{split}$$

These are the sufficient and necessary conditions for the pitchfork bifurcation. The system (5), under the condition (6) is, in a neighborhood of $(x, \epsilon) = (0, 0)$ locally topologically equivalent to $\dot{x} = \epsilon x - x^3$ (see [Arrowsmith, 1990], [Kuznetsov, 1995]). Thus, if (6) is satisfied then for $\tau \sim 1/c$, and $\tau < 1/c$ the stationary solution E_0 is stable. For $\tau > 1/c$ the stationary point E_0 is unstable but there are two new stable stationary solutions.

Theorem 2 For the parameter values $(c, \tau) \in \mathcal{B}_{E_0;H}$ the system \mathcal{F}_{app} has either the supercritical Hopf or the subcritical Hopf or the generalized Hoph bifurcation. Furthermore, there are such values of a, b and γ that the value c_B for which the system has the generalized Hopf bifurcation satisfies $c_B \in (c_0, c_1)$.

Proof: For the parameters in $\mathcal{B}_{E_0,H}$ the matrix A has a pair of purely imaginary eigenvalues $\lambda_{1,2} = \pm iv$, v > 0 and no other nonhyperbolic eigenvalues. Furthermore, for $(c, \tau) \in \mathcal{B}_{E_0;H}$

$$d \equiv \frac{d\mathbf{Re}\lambda_{1,2}}{d\tau}|_{\mathcal{B}_{E_0,H}} = \frac{1}{2}\frac{d(-\gamma + F + D)}{d\tau}|_{\mathcal{B}_{E_0,H}} = c(a-c)/2 < 0.$$
(21)

Thus, $(c, \tau) \in \mathcal{B}_{E_0;H}$ corresponds to the Hopf bifurcation. The type of the Hopf bifurcation is determined by studying the normal form of the system on the two-dimensional invariant center manifold. To obtain the normal form we use the procedure introduced in [Coullet & Spiegel 1983], and applied by Kuznetsov [Kuznetsov, 1997] to obtain the relevant coefficients in normal forms of all codimension 1 and 2 bifurcations of stationary solutions of ODE.

As we shall see, it is enough to start with the system \mathcal{F}_{app} expanded up to the terms of the third order.

$$\dot{X} = AX + \frac{1}{2}\mathcal{F}_{app,2}(X,X) + \frac{1}{6}\mathcal{F}_{app,3}(X,X,X),$$

where

$$\mathcal{F}_{app,2}(X,X) = \begin{pmatrix} (a+1)x_1^2 - c(a+1)\tau x_2^2 \\ 0 \\ (a+1)x_2^2 - c(a+1)\tau x_1^2 \\ 0 \end{pmatrix},$$

and

$$\mathcal{F}_{app,3}(X,X,X) = \begin{pmatrix} (c^2\tau/3 - 1)x_2^2 + (c\tau - c/3 - ca\tau)x_1^3 - c\tau x_1^2y_1 + c^2\tau x_2x_1^2) \\ 0 \\ (c^2\tau/3 - 1)x_2^2 + (c\tau - c/3 - ca\tau)x_1^3 - c\tau x_1^2y_1 + c^2\tau x_2x_1^2 \\ 0 \end{pmatrix}$$

First introduce a complex eigenvector $Q \in \mathbf{R}^4$ of A, i.e. AQ = ivQ with components

$$Q = \begin{pmatrix} 1 \\ (c-a)(1-iv/\gamma) \\ 1 \\ (c-a)(1-iv/\gamma) \end{pmatrix}$$

and the corresponding eigenvector of A^T : $A^T P = -ivP$

$$P = \begin{pmatrix} \frac{v+i\gamma}{4v} \\ \frac{-i\gamma}{4v(c-a)} \\ \frac{v+i\gamma}{4v} \\ \frac{-i\gamma}{4v(c-a)} \end{pmatrix}$$

normalized to $\langle P, Q \rangle = \bar{P}^T Q = 1$. Vectors Q and \bar{Q} (the complex conjugate of Q) form a basis in the center-subspace E^c of A, so any vector $R \in E^c$ can be written as $R = \alpha Q + \bar{\alpha} \bar{Q}$ where $\alpha = \langle P, R \rangle \in \mathbb{C}^1$. The relation between the original system $\dot{X} = \mathcal{F}_{app}$ and the the complex normal form of the system on the center manifold $X = H(\alpha, \bar{\alpha})$ of the following form:

$$\dot{\alpha} = iv\alpha + l_1\alpha|\alpha|^2 + l_2\alpha|\alpha|^4 + O(|\alpha|^6)$$
(22)

is contained in the corresponding homological equation:

$$\frac{\partial H}{\partial \alpha} \dot{\alpha} + \frac{\partial H}{\partial \bar{\alpha}} \dot{\bar{\alpha}} = \mathcal{F}_{app}(H(\alpha, \bar{\alpha}))$$

Substituting the Taylor expansions of the transformation H and the system \mathcal{F}_{app} into the homological equation, and collecting the terms with the same

order one gets the coefficients $l_1, l_2...$ in the normal form. The third order coefficient l_1 is given by:

$$l_{1} = \frac{1}{2} \mathbf{Re} < P, \mathcal{F}_{app,3}(Q, Q, \bar{Q}) + \mathcal{F}_{app,2}(\bar{Q}, (2ivI_{4} - A)^{-1}\mathcal{F}_{app,2}(Q, Q)) - 2\mathcal{F}_{app,2}(Q, A^{-1}\mathcal{F}_{app,2}(Q, \bar{Q})) > = \frac{1}{2} \left[-(c+3)\frac{\gamma}{c-a} + c - a - \gamma + \frac{2\gamma^{2}(a+1)^{2}}{(c-a)(b+a\gamma-c\gamma)} \right] = \frac{\gamma c^{3} + B(a, b, \gamma)c^{2} + C(a, b, \gamma)c + D(a, b, \gamma)}{2(a-c)(b+a\gamma-c\gamma)},$$
(23)

where

$$B(a, b, \gamma) = -b - 3a\gamma - 2\gamma^{2}$$

$$C(a, b, \gamma) = 2ab + 3a^{2}\gamma + 2b\gamma - 3\gamma^{2} + 3a\gamma^{2}$$

$$D(a, b, \gamma) = -a^{2}b - a^{3}\gamma + 3b\gamma - ab\gamma - 2\gamma^{2} - a\gamma^{2} - 3a^{2}\gamma^{2}.$$
(24)

If the third order coefficient $l_1 \neq 0$ the system is locally smoothly orbitally equivalent to the system

$$\dot{\alpha} = iv\alpha + l_1\alpha |\alpha|^2.$$

Since everywhere on $\mathcal{B}_{E_0,H}$ we have d < 0, the values of the parameters $(c,\tau) \in \mathcal{B}_{E_0,H}$ such that $l_1 < 0$, imply the supercitical Hopf bifurcation, if $l_1 > 0$ the bifurcation is subcritical, and if $l_1 = 0$ the bifurcation is of the generalized Hopf type. The denominator of l_1 is always negative in the considered interval $c \in (a, c_1 = a + b/\gamma)$. The numerator of l_1 always has at least one real zero c_B . Thus, there is at least one value of $c \equiv c_B$ such that the bifurcation is of the generalized Hopf type. The following choice of a, b and γ : $a = 0.25, b = \gamma = 0.02$ is an example of the values such that $c_b = 0.289024 \in (c_0, c_1) = (0.27, 1, 27)$. In this case all three alternatives occur as c is varied in the interval (c_0, c_1) .

In the case $c_B \in (c_0, c_1)$ all three types of Hopf bifurcation occur. In general, the line segment of codimension 1 subcritical Hopf bifurcations, joins with the line segment of codimension 1 supercritical Hopf bifurcations at some point (c_B, τ_B) of the codimension 2 generalized Hopf bifurcation. It is important to point out that in all numerical test that we have performed for the values of a, b and γ such that the isolated unit shows excitable behaviour, we have observed precisely the situation where $c_B \in (c_0, c_1)$ and actually is quite close to c_0 .

As is well known from the theory of the codimension 2 generalized Hopf bifurcation, besides the two lines of Hopf bifurcations of the stationary solution, there is also a line of fold limit cycle bifurcations emanating from the point (c_B, τ_B) . For the parameter values in between the lines of subcritical Hopf and fold limit cycle bifurcations the system \mathcal{F}_{app} has a stable stationary solution surrounded by an unstable limit cycle, which is surrounded by a stable limit cycle, all three lying in the manifold $x_1 = x_2, y_1 = y_2$. The generalized Hopf bifurcation at (c_B, τ_B) is illustrated in figure 1b.

Finally, let us remark that the theorems 1 and 2 are probably correct if the tan⁻¹ coupling function is replaced by any function of the sigmoid form, although we do not gave the proof in the general case because the algebra gets rather tedious. The only conditions that should be required are that: f(0) = 0, f'(0) > 0, f''(0) = 0 and $f'''(0) \neq 0$.

Approximate vs exact system

The bifurcation set in (c, τ) plane of the exact system \mathcal{F} under the same conditions (2) and (6) on the parameters a, b, γ and c, was obtained before in [Burić & Todorović, 2003]. Using the bifurcation set and the numerical test, it was conjectured that there is a domain in (c, τ) that corresponds to the death of oscillations due to time-delay. On the bases of the numerical evidence it was also conjectured that the bifurcation mechanism beyond the oscillator death is more complicated than commonly found in oscillators coupled by diffusion with delay, i.e. the inverse supercritical Hopf bifurcation (see [Reddy et. all., 1999]).

We would like to use the results about the bifurcations of the approximate system \mathcal{F}_{app} in order to discuss the time-delay death of oscillations that have been induced by coupling of excitable systems. To this end, we first compare the bifurcation sets in (c, τ) plane of the exact end the approximate system. The two sets are illustrated in figure 2. The curves denoted τ_1 and τ_2 correspond to the first and second factor of the characteristic equation of the exact system, and there $d\mathbf{Re}\lambda_{1,2}/d\tau < 0$ on τ_1 and $d\mathbf{Re}\lambda_{3,4}/d\tau < 0$ on τ_2 , where $\lambda_{1,2,3,4}$ are the solutions of the exact characteristic equation.

Few observations are in order. Firstly, the approximate systems badly fails to describe the bifurcations of the exact system for most values of the time-lag. Qualitative agreement between the dynamics of the two systems is obtained only for very small values of the time-lag. The entire family of bifurcations due to nonhyperbolicity of the second factor of the characteristic equation of the exact system is missing. The smallest time-lag for these bifurcations to occur, is to large to be capture by the approximation, for all values of $c < c_1$. Furthermore, the approximate system has a line of pitchfork bifurcations, destabilizing E_0 and introducing two new stable stationary solutions for large τ and any c. There is no analogous situation in the exact system.

On the other hand, there is a small but important domain of (c, τ) where the bifurcation curves of the exact system are well approximated by the approximate one. This is the domain precisely around the generalized Hopf bifurcation, and is indicated in the figure 2. Thus, we can use theorem 2, about the bifurcations of the approximate system, to explain the dynamics of the exact system near the bifurcation line $\tau_1(c)$. This also supports the conjecture that the mechanism involved in the death of oscillations due to time-delay in the exact system involves the line of subcritical Hopf and the line of fold limit cycle bifurcations organized by the generalized Hopf bifurcation. Consider the system for $c > c_B$ and zero or small time-lag, when it consists of two exactly synchronized oscillators (compare figures 3 and 4). The only attractor is the limit cycle in $x_1 = x_2$, $y_1 = y_2$ plane. Increasing the time-lag leads to the subcritical Hopf bifurcation for $(c, \tau) \in \mathcal{B}_{E_0,H}$ when the stationary solution becomes stable and an unstable limit cycle is created in the same plane as the stable limit cycle. The system is bi-stable with the stable stationary state and periodic excitations described by the stable limit cycle. The unstable limit cycle acts as a threshold. Further increase of the time lag leads to the disappearance of the two limit cycles in the fold limit cycle bifurcation. This corresponds to the death of oscillatory excitations. Upon further increase of τ the approximate system hits the line of pitchfork bifurcations, the stationary point becomes unstable and there are two new stable stationary solutions. Such dynamics does not occur in the exact system for any value of the time-lag. The sequence of different attractors obtained for fixed c and successively larger τ for the approximate system, illustrated in figure 3, corresponds qualitatively to the sequence in the exact system illustrated in figure 4. Large time-lags, introduce qualitatively different dynamics (figures 3d and 4d). The qualitative correspondence between the exact system and the approximation is lost.

Summary and conclusions

We have performed an analyzes of bifurcations of the stationary solution of a model of two coupled FitzHugh-Nagumo excitable systems. The model ODE's originate as a small time-lag approximation of the DDE's which explicitly include the time-delay in the transmission of excitations between the units.

The main results are given in the two theorems 1 and 2. The second theorem identifies the degenerate Hopf bifurcation as the main organizing center that is enough to explain all qualitative features of the dynamics for small time-lags. There are three possible types of dynamics in this domain. The system could be excitable, with the stable stationary solution as the only attractor, or oscillatory, when the limit cycle is the only attractor, or, finally, the system could be bi-stable. In the last case there are the stable stationary solution and the stable limit cycle. These are the three types of the dynamics that have been observed also in the exact system of DDE for small time-lags. The first theorem determines the boundary in the (c, τ) plain beyond which the dynamics of the approximate system is qualitatively different from anything that occurs in the exact system for the considered parameter values.

Our analyzes is carried out using an explicit coupling function. However, the results would probably be the same for any coupling of the same form with the function f(x) satisfying f(0) = 0, f'(0) > 0, f''(0) = 0 and $f'''(0) \neq 0$. On the other hand, different type of coupling, for example of the diffusive form, would result in different bifurcations and dynamics.

There is yet another set of codimension 2 bifurcations that occur in the exact system for larger time-delays. They happen at the intersection of Hopf bifurcation curves, and are quite important for the properties of the oscillatory dynamics at larger time-lags. This Hopf-Hopf bifurcations are not captured by the finite dimensional approximation by ODE's. In order to analyze them an infinite dimensional generalization of the method applied in theorem 2 (see [Faria & Magelhes, 1995], [Schayer & Campbell, 1998]) could be applied.

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FIGURE CAPTIONS

Figure 1: (a) Bifurcation set of the approximate system, the encircled area is enlarged in (b); (b) Dynamics near the codimension 2 generalized Hopf bifurcation.

Figure 2: Bifurcation sets of the exact (thick lines) and the approximate (thin lines) systems. τ_1 and τ_2 are Hopf bifurcation curves of the exact system, and $\tau_{H,app}$ and $\tau_{p,app}$ are Hopf and pitchfork bifurcation lines of the approximate system.

Figure 3: Projections on (x_1, x_2) of typical orbits approaching the possible attractors of the approximate system: a) One stable limit cycle (symmetric), b) stable stationary solution and the stable limit cycle (symmetric), c)one stable stationary solution, d) two stable stationary solutions.

Figure 4: Projections on (x_1, x_2) of typical orbits approaching the possible attractors of the exact system. a) One stable limit cycle (symmetric), b) stable stationary solution and the stable limit cycle (symmetric), c)one stable stationary solution, d) one stable (asymmetric) limit cycle.













