

BIFURCATIONS OF FITZHUGH-NAGUMO EXCITABLE SYSTEMS WITH CHEMICAL DELAYED COUPLING

Dragana Ranković

Abstract. System of delayed differential equations is used to model a pair of FitzHugh-Nagumo excitable systems with time-delayed fast threshold modulation coupling. The Hopf bifurcation of the stationary solution, due to coupling is completely described. The critical time delays, that include indirect and direct Hopf bifurcations, and conditions on the parameters for such bifurcations are found. It is shown that there is a domain for values of time lags and coupling strength where instability of the equilibrium introduced by coupling can disappear due to interaction delay.

1. Introduction

In modelling realistic neuronal networks it is useful and also important to use explicitly the time-delays in the description of the transfer of information between the neurons. The system of delayed differential equations (DDE's) provide a quite natural and common mathematical framework for such models. It is an infinite dimensional dynamical system and its qualitative analysis requires generalization of the tools available for finite systems.

Two general types of synaptic connection between neurons are electrical and chemical. In our previous investigations [6, 4] we considered sigmoid and electrical connection between neurons, namely we studied bifurcations of FitzHugh-Nagumo systems with electrical delayed coupling. The chemical synapses are much more common, and the synaptic transmission time is especially significant of synapses of the chemical type. It is well known that time-delay can change qualitatively the dynamical features of the system [5, 8].

In this paper we shell analyze two coupled FHN excitable systems with delayed

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coupling, given by the following delay-differential equations:

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

where $x_i^\tau(t) \equiv x_i(t - \tau)$, the delay τ is positive.

In order to model the coupling among neurons by a chemical synapse, we shall use the so-called fast threshold modulation scheme proposed by Somers and Kopell in 1993 [13] and often used by others, e.g., [3]. The form of the FTM coupling that we shall use, is given by the following function:

$$f(x_1, x_2^\tau) = -(x_1 - V_s) \frac{1}{1 + e^{-k(x_2^\tau - \theta_s)}} - \frac{V_s}{1 + e^{k\theta_s}}.$$

This function explicitly includes the time delay in the synaptic transmission. The variable parameter c is the coupling strength between the first neuron at time t and its neighbor at some previous time $t - \tau$, so it is real and positive. The coupling model (1) when $\tau = 0$ is called fast, because it does not incorporate any real synaptic dynamics. The model exhibits either a hard or a more gradual thresholdlike behavior, depending on the size of the parameter k , with $k \rightarrow \infty$ corresponding to the hard threshold. The synaptic reversal potential is denoted as V_s and x is synaptic potential. A positive or negative sign of the difference between V_s and x , corresponds to an excitatory or inhibitory effect of the synapse. In this paper the values of the parameters θ_s , V_s , and k will be held fixed as $\theta_s = -0.25$, $V_s = 2$, and $k = 10$.

The dynamics of the complex system depends on the properties of each of the units and on their interactions. A single neuron as one unit of the complex system displays excitable behavior. Prime example of the excitable behavior is the system introduced by FitzHugh [9] and Nagumo et al. [12] as an approximation of the Hodgkin-Huxley model of the nerve cell membrane:

$$\begin{aligned} \dot{x} &= -x^3 + (a+1)x^2 - ax - y \\ \dot{y} &= bx - \gamma y, \end{aligned} \tag{2}$$

where a , b and γ are positive parameters. We shall use the system (2) for parameter range, when system displays the excitable behavior. Point $(x, y) = (0, 0)$ is the stationary solution for any value of the parameters a , b , γ . Furthermore, it is always a stable stationary point, which could be a node, if $a - \gamma \geq 2\sqrt{b}$, or a focus, when $a - \gamma < 2\sqrt{b}$. We shall restrict our attention to the case when it is the only stationary solution. This is the case if $4b/\gamma > (a - 1)^2$.

We shall analyze local stability and bifurcations of the stationary solutions of (1).

2. Local stability and bifurcations of the stationary solution

In this section we study stability and bifurcations of the stationary solution $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$ of the system (1) for varying values $c > 0$ and $\tau > 0$. Parameters a, b and γ are fixed on values such that each of the units displays the excitable behavior.

2.1. Instantaneous coupling $\tau = 0$

Consider the system (1) in the case of instantaneous coupling.

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

THEOREM 2.1. *Stationary solution $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$ of the system (3) is:*

- 1° for $a - \gamma \geq 2\sqrt{b}$, stable node-node for every $0 < c < \frac{a - \gamma - 2\sqrt{b}}{q - p}$ and for every $\frac{a - \gamma - 2\sqrt{b}}{q - p} < c < \frac{a + \gamma}{q - p}$, stable focus-node;
- 2° for $a - \gamma < 2\sqrt{b}$, stable focus-focus for every $0 < c < \frac{2\sqrt{b} - a + \gamma}{p + q}$ and for every $\frac{2\sqrt{b} - a + \gamma}{p + q} < c < \frac{a + \gamma}{q - p}$, stable focus-node.

In both of these cases 1° and 2° system has subcritical Hopf bifurcation for parameter value

$$c = c_0 = \frac{a + \gamma}{q - p}.$$

Proof. Local stability of the stationary solution is determined by analyzing the system linearized at $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$.

$$\begin{aligned} \dot{x}_1 &= -ax_1 - y_1 + c \frac{\partial f}{\partial x_1}(0, 0)x_1 + c \frac{\partial f}{\partial x_2}(0, 0)x_2, \\ \dot{y}_1 &= bx_1 - \gamma y_1, \\ \dot{x}_2 &= -ax_2 - y_2 + c \frac{\partial f}{\partial x_1}(0, 0)x_2 + c \frac{\partial f}{\partial x_2}(0, 0)x_1, \\ \dot{y}_2 &= bx_2 - \gamma y_2. \end{aligned} \tag{4}$$

Linear part of (4),

$$\begin{bmatrix} -a - cp & -1 & cq & 0 \\ b & -\gamma & 0 & 0 \\ cq & 0 & -a - cp & -1 \\ 0 & 0 & b & -\gamma \end{bmatrix}$$

where $p = \frac{1}{1 + e^{k\theta}}$, $q = \frac{kVe^{k\theta}}{(1 + e^{k\theta})^2}$ implies the following characteristic equation:

$$\Delta(\lambda) \equiv \Delta_1(\lambda)\Delta_2(\lambda) = 0 \tag{5}$$

where

$$\begin{aligned}\Delta_1(\lambda) &= \lambda^2 + (a + cp + \gamma - cq)\lambda + (a + cp - cq)\gamma + b, \\ \Delta_2(\lambda) &= \lambda^2 + (a + cp + \gamma + cq)\lambda + (a + cp + cq)\gamma + b\end{aligned}\quad (6)$$

with solutions

$$\begin{aligned}\lambda_{1,2} &= \frac{1}{2}[-(a + cp + \gamma - cq) \pm \sqrt{(a + cp - \gamma - cq)^2 - 4b}], \\ \lambda_{3,4} &= \frac{1}{2}[-(a + cp + \gamma + cq) \pm \sqrt{(a + cp - \gamma + cq)^2 - 4b}].\end{aligned}\quad (7)$$

The sign of the real part of the four eigenvalues (7) determines the stability type of the trivial stationary point. If $a - \gamma \geq 2\sqrt{b}$, the point is stable node-node for every $0 < c < \frac{a - \gamma - 2\sqrt{b}}{q - p}$, and if c is larger the eigenvalue $\lambda_{1,2}$ becomes complex and the point becomes stable focus-node. Otherwise, if $a - \gamma < 2\sqrt{b}$, the point is stable focus-focus for every $0 < c < \frac{2\sqrt{b} - a + \gamma}{p + q}$ and for larger c the eigenvalue $\lambda_{3,4}$ becomes real and the point is again stable focus-node. Now, for any parameter a , b and γ eigenvalues $\lambda_{1,2}$ becomes pure imaginary for

$$c = c_0 = \frac{a + \gamma}{q - p},$$

where

$$d = \operatorname{sgn} \left(\frac{d \operatorname{Re} \lambda_{1,2}}{dc} \right)_{c=c_0} = \operatorname{sgn} \left(\frac{q - p}{2} \right) > 0.$$

The type of bifurcation at $c = c_0$ is analyzed by reducing the system (3) on the corresponding center manifold. The first step is to transform the coordinates (x_1, y_1, x_2, y_2) into the new ones (x, y, z, t) , by using the eigenvectors correspondents to eigenvalues $\lambda_{1,2,3,4}$. This transformation is given with the following equations

$$\begin{aligned}x_1 &= y + z + t, \\ y_1 &= -\omega x + \gamma y - \frac{b}{\lambda_3 + \gamma} z - \frac{b}{\lambda_4 + \gamma} t, \\ x_2 &= y - z - t, \\ y_2 &= -\omega x + \gamma y - \frac{b}{\lambda_3 + \gamma} z - \frac{b}{\lambda_4 + \gamma} t,\end{aligned}$$

where $\omega = \sqrt{b - \gamma^2}$ ($b > \gamma^2$ for considered values of parameters). The system (3), in the new coordinates and for $c = c_0$ is:

$$\begin{aligned}\dot{x} &= -\omega y + f_1(x, y, z, t), \\ \dot{y} &= \omega x + f_2(x, y, z, t), \\ \dot{z} &= \lambda_3 z + g_1(x, y, z, t), \\ \dot{t} &= \lambda_4 t + g_2(x, y, z, t)\end{aligned}\quad (8)$$

where

$$\begin{aligned} f_1(x, y, z, t) &= \frac{\gamma}{2\omega}(F(y+z+t, y-z-t) + F(y-z-t, y+z+t)), \\ f_2(x, y, z, t) &= \frac{1}{2}(F(y+z+t, y-z-t) + F(y-z-t, y+z+t)), \\ g_1(x, y, z, t) &= -\frac{\lambda_3 + \gamma}{2(\lambda_4 - \lambda_3)}(F(y+z+t, y-z-t) - F(y-z-t, y+z+t)), \\ g_2(x, y, z, t) &= \frac{\lambda_4 + \gamma}{2(\lambda_4 - \lambda_3)}(F(y+z+t, y-z-t) - F(y-z-t, y+z+t)) \end{aligned}$$

and where

$$F(x_1, x_2) = cf(x_1, x_2) + cpx_1 - cqx_2 - x_1^3 + (a+1)x_1^2.$$

The center manifold with parameter $\epsilon = c - c_0$ is:

$$\begin{aligned} W^c(0) &= \{(x, y, z, t, \epsilon) \mid z = h_1(x, y, \epsilon), t = h_2(x, y, \epsilon), \|(x, y, \epsilon)\| < \eta, \\ &h_i(0, 0, 0) = 0, Dh_i(0, 0, 0) = 0, i = 1, 2\} \end{aligned}$$

Using the fact that the center manifold is invariant under the dynamics generated by (8), we obtain

$$\begin{aligned} \dot{x} &= -\omega y + f_1(x, y, h_1, h_2, \epsilon), \\ \dot{y} &= \omega x + f_2(x, y, h_1, h_2, \epsilon), \\ \dot{z} &= Dh_1 \dot{x} = \lambda_3 h_1 + g_1(x, y, h_1, h_2, \epsilon), \\ \dot{t} &= Dh_2 \dot{y} = \lambda_4 h_2 + g_2(x, y, h_1, h_2, \epsilon) \end{aligned}$$

which yields the following quasilinear partial differential equation for h_1 and h_2 :

$$\begin{aligned} Dh(x, y, \epsilon) \left(\begin{bmatrix} 0 & -\omega \\ -\omega & 0 \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} + \begin{bmatrix} f_1(x, y, h_1, h_2, \epsilon) \\ f_2(x, y, h_1, h_2, \epsilon) \end{bmatrix} \right) - \\ \begin{bmatrix} \lambda_3 & 0 \\ 0 & \lambda_4 \end{bmatrix} \begin{bmatrix} h_1 \\ h_2 \end{bmatrix} - \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} = 0 \quad (9) \end{aligned}$$

Using the theorem about approximation of the center manifold [2] we obtain $h_1(x, y, \epsilon) = 0$ and $h_2(x, y, \epsilon) = 0$. Hence,

$$W_{loc}^c(0) = \{(x, y, z, t) \mid z = 0, t = 0\}$$

or in the old coordinates the center manifold is in fact a plane given by equations $x_1 = x_2$ and $y_1 = y_2$. The dynamics on the center manifold is then given by

$$\begin{aligned} \dot{x} &= -\omega y + \frac{\gamma}{\omega} F(y, y, \epsilon), \\ \dot{y} &= \omega x + F(y, y, \epsilon) \end{aligned}$$

where

$$F(y, y, \epsilon) = (c_0 + \epsilon)f(y, y) + (c_0 + \epsilon)py - (c_0 + \epsilon)qy - y^3 + (a+1)y^2.$$

After using the method of normal forms [1, 7, 11], and change of coordinates $x = r \cos \theta$, $y = r \sin \theta$ the dynamics on the center manifold for small ϵ is given by the normal form of the Hopf bifurcation

$$\begin{aligned}\dot{r} &= d\epsilon r + \alpha r^3 + O(\epsilon^2 r, \epsilon r^3, r^5), \\ \dot{\theta} &= \omega + e\epsilon + \beta r^2 + O(\epsilon^2, \epsilon r^2, r^4),\end{aligned}\tag{10}$$

where $\omega = \sqrt{b - \gamma^2}$, $d = \frac{q-p}{2}$, $e = -\frac{\gamma(q-p)}{2\omega}$,

$$\begin{aligned}\alpha &= \frac{1}{16} \left[\frac{c_0 k^2 e^{k\theta} (1 + kV - 4kV e^{k\theta} + e^{2k\theta} (kV - 1))}{(1 + e^{k\theta})^4} - 6 \right] \\ &\quad + \frac{\gamma}{16\omega^2} \left[2(a + 1) - \frac{c_0 k^2 V e^{k\theta} (1 - e^{k\theta})}{(1 + e^{k\theta})^3} \right]^2 \\ \beta &= \frac{\gamma}{16\omega} \left[6 - \frac{c_0 k^2 e^{k\theta} (1 + kV - 4kV e^{k\theta} + e^{2k\theta} (kV - 1))}{(1 + e^{k\theta})^4} \right] \\ &\quad - \frac{1}{48\omega^3} \left[2(a + 1) - \frac{c_0 k^2 V e^{k\theta} (1 - e^{k\theta})}{(1 + e^{k\theta})^3} \right]^2 (5\gamma^2 - 2\omega^2).\end{aligned}$$

Since $d > 0$ and $\alpha > 0$ stationary point for $c = c_0$ has subcritical Hopf bifurcation and that completes the proof of the theorem. ■

Thus, whatever the stability type of the stationary point in the uncoupled case might be, there is the corresponding value of the coupling constant c such that the point becomes focus-node. Then for small values $\epsilon = c - c_0$ less than zero, the stationary point is stable and surrounded with an unstable limit cycle. This limit cycle disappears through subcritical Hopf bifurcation when c reach the value c_0 . Then, for small $\epsilon = c - c_0 > 0$ stationary point becomes unstable. Furthermore, numerical calculations shows that at some value c less than c_0 system has the stable stationary solution surrounded by a unstable limit cycle, which is surrounded by stable limit cycle. This unstable limit cycle disappear and stationary solution becomes unstable at $c = c_0$ due to Hopf bifurcation. However the Hopf bifurcation does not affect the stability of the large limit cycle. The stable limit cycle disappears for some value of the coupling constant $c = c_1$ larger than c_0 , when there appears other stable stationary solutions.

Let us now discuss the zero solution of (5). Such solution would imply that $c = \frac{a\gamma+b}{\gamma(q-p)}$. For all physically relevant values of parameters a , b and γ such that the isolated unit shows excitable behavior, this value of c is always larger than c_1 , i.e. there is nonzero stable stationary solution. So we disregard such solutions of the characteristic equation (5), and concentrate only on the Hopf bifurcations.

2.2. Delayed coupling $\tau > 0$

Consider the system (1) in the case of delayed coupling. As in the previous case, local stability of stationary solution is determined by analyzing the system linearized at $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$.

THEOREM 2.2 *The system (1) undergoes a Hopf bifurcation at equilibrium $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$ for critical time delays given by:*

1° *If $\sin(\omega\tau) = \frac{-\omega_{\pm}^3 + (b-\gamma^2)\omega_{\pm}}{cq(\omega_{\pm}^2 + \gamma^2)} > 0$, then*

$$\tau_{1,\pm}^j = \frac{1}{\omega_{\pm}} \left[2j\pi + \arccos \frac{(a+cp)\omega_{\pm}^2 + \gamma(b+a\gamma+cp\gamma)}{cq(\omega_{\pm}^2 + \gamma^2)} \right], j = 0, 1, 2, \dots$$

and if $\sin(\omega\tau) = \frac{-\omega_{\pm}^3 + (b-\gamma^2)\omega_{\pm}}{cq(\omega_{\pm}^2 + \gamma^2)} < 0$ then

$$\tau_{1,\pm}^j = \frac{1}{\omega_{\pm}} \left[(2j+2)\pi - \arccos \frac{(a+cp)\omega_{\pm}^2 + \gamma(b+a\gamma+cp\gamma)}{cq(\omega_{\pm}^2 + \gamma^2)} \right], j = 0, 1, 2, \dots$$

2° *If $\sin(\omega\tau) = \frac{\omega_{\pm}^3 - (b-\gamma^2)\omega_{\pm}}{cq(\omega_{\pm}^2 + \gamma^2)} > 0$ then*

$$\tau_{2,\pm}^j = \frac{1}{\omega_{\pm}} \left[2j\pi + \arccos \frac{-(a+cp)\omega_{\pm}^2 - \gamma(b+a\gamma+cp\gamma)}{cq(\omega_{\pm}^2 + \gamma^2)} \right], j = 0, 1, 2, \dots$$

and if $\sin(\omega\tau) = \frac{\omega_{\pm}^3 - (b-\gamma^2)\omega_{\pm}}{cq(\omega_{\pm}^2 + \gamma^2)} < 0$ then

$$\tau_{2,\pm}^j = \frac{1}{\omega_{\pm}} \left[(2j+2)\pi - \arccos \frac{-(a+cp)\omega_{\pm}^2 - \gamma(b+a\gamma+cp\gamma)}{cq(\omega_{\pm}^2 + \gamma^2)} \right], j = 0, 1, 2, \dots$$

where

$$\omega_{\pm} = \sqrt{\frac{-A \pm \sqrt{A^2 - 4B}}{2}}$$

$$A = (a+cp)^2 + \gamma^2 - 2b - c^2q^2, \quad B = (b+a\gamma+cp\gamma)^2 - c^2q^2\gamma^2,$$

$$p = \frac{1}{1+e^{k\theta}}, \quad q = \frac{kV_s e^{k\theta}}{(1+e^{k\theta})^2}.$$

Proof. Linearization of the system (1) at $(x_1, y_1, x_2, y_2) = (0, 0, 0, 0)$

$$\begin{aligned} \dot{x}_1 &= -ax_1 - y_1 - px_1 + cqx_2^{\tau}, \\ \dot{y}_1 &= bx_1 - \gamma y_1, \\ \dot{x}_2 &= -ax_2 - y_2 + cqx_1^{\tau} - px_2, \\ \dot{y}_2 &= bx_2 - \gamma y_2. \end{aligned} \tag{11}$$

where $p = -\frac{\partial f}{\partial x_1}(0, 0) = \frac{1}{1+e^{k\theta_s}}$ and $q = \frac{\partial f}{\partial x_2}(0, 0) = \frac{kV_s e^{k\theta_s}}{(1+e^{k\theta_s})^2}$. Substitution $x_i(t) = A_i e^{\lambda t}$, $y_i(t) = b_i e^{\lambda t}$, $x_i(t-\tau) = A_i e^{\lambda(t-\tau)}$, $i = 1, 2$, results in a system of algebraic equations for constants A_i and B_i . This system has a nontrivial solution if the following is satisfied:

$$\Delta(\lambda) \equiv \Delta_1(\lambda)\Delta_2(\lambda) = 0 \tag{12}$$

where

$$\begin{aligned}\Delta_1(\lambda) &= \lambda^2 + (a + cp + \gamma)\lambda + (a + cp)\gamma + b - cq\lambda e^{-\lambda\tau} - cq\gamma e^{-\lambda\tau}, \\ \Delta_2(\lambda) &= \lambda^2 + (a + cp + \gamma)\lambda + (a + cp)\gamma + b + cq\lambda e^{-\lambda\tau} + cq\gamma e^{-\lambda\tau}\end{aligned}\quad (13)$$

Equation (12) is the characteristic equation and corresponds to the system (11). Infinite dimensionality of the system is reflected in the transcendental character of (12). However, the spectrum of the linearization of (1) is discrete and can be divided into infinite-dimensional hyperbolic and finite-dimensional nonhyperbolic parts [10]. As in the finite-dimensional case, the stability of the hyperbolic stationary point is determined by the signs of the real part of the roots of (12). Exceptional roots, equal to zero or with zero real part, correspond to the finite-dimensional center manifold where the local stability depends on the nonlinear terms.

Bifurcations due to a nonzero time lag occur when some of the roots of (12) cross the imaginary axes. Let us first discuss the nonzero pure imaginary roots. Substitution $\lambda = i\omega$ into Δ_1 gives

$$\begin{aligned}\sin(\omega\tau) &= \frac{-\omega^3 + (b - \gamma^2)\omega}{cq(\omega^2 + \gamma^2)}, \\ \cos(\omega\tau) &= \frac{(a + cp)\omega^2 + \gamma(b + (a + cp)\gamma)}{cq(\omega^2 + \gamma^2)}\end{aligned}\quad (14)$$

or into Δ_2 gives

$$\begin{aligned}\sin(\omega\tau) &= \frac{\omega^3 - (b - \gamma^2)\omega}{cq(\omega^2 + \gamma^2)}, \\ \cos(\omega\tau) &= \frac{-(a + cp)\omega^2 - \gamma(b + (a + cp)\gamma)}{cq(\omega^2 + \gamma^2)}.\end{aligned}\quad (15)$$

Squaring and adding the above two pairs of equations, (14) and (15), results in the same equation

$$\omega^6 + (A + \gamma^2)\omega^4 + (A\gamma^2 + B)\omega^2 + B\gamma^2 = 0, \quad (16)$$

where

$$A = (a + cp)^2 + \gamma^2 - 2b - c^2q^2, \quad B = (b + a\gamma + cp\gamma)^2 - c^2q^2\gamma^2.$$

Since $\omega^2 \neq -\gamma^2$, the term $\omega^2 + \gamma^2$ can be factored out from (16) to obtain

$$\omega^4 + A\omega^2 + B = 0. \quad (17)$$

Solutions of (17) give the frequencies ω_{\pm} of possible nonhyperbolic solutions

$$\omega_{\pm} = \sqrt{\frac{-A \pm \sqrt{A^2 - 4B}}{2}}.$$

The corresponding critical time lag follows from (14) and (15). Consider the pair of equations (14) we obtain 1° in the statement of the theorem, and consider the pair of the equations (15) we obtain 2° in the statement of the theorem.

We denote any bifurcation value of the time lag by τ_c . Differentiation of the characteristic equation

$$\Delta_1(\lambda(\tau), \tau) \cdot \Delta_2(\lambda(\tau), \tau) = 0$$

gives

$$\left(\frac{\partial \Delta_1}{\partial \lambda} \Delta_2 + \Delta_1 \frac{\partial \Delta_1}{\partial \lambda} \right) \frac{d\lambda}{d\tau} = - \frac{\partial \Delta_1}{\partial \tau} \Delta_2 - \Delta_1 \frac{\partial \Delta_2}{\partial \tau}$$

and

$$\operatorname{sgn} \left(\frac{d \operatorname{Re} \lambda}{d\tau} \right)_{\tau=\tau_c} = \operatorname{sgn} \left\{ \operatorname{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\tau=\tau_c} = \operatorname{sgn} \left(\frac{2\omega^2 + A}{c^2 q^2 (\omega^2 + \gamma^2)} \right).$$

Substitution of $\omega = \omega_{\pm}$ finally gives

$$\left(\frac{d \operatorname{Re} \lambda}{d\tau} \right)_{\tau=\tau_+} > 0, \quad \left(\frac{d \operatorname{Re} \lambda}{d\tau} \right)_{\tau=\tau_-} < 0. \quad \blacksquare$$

The formulas for critical time-lags give bifurcation curves in plane (τ, c) for fixed values of parameters a, b and γ . For the first few $j = 0, 1, 2$, and for parameters a, γ and b fixed at some typical values, the bifurcation curves are shown in Fig. 1.

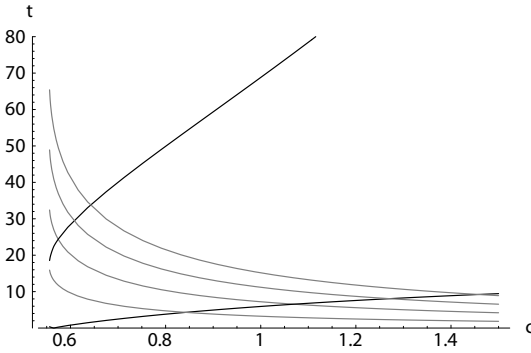


Fig. 1. First few branches of the bifurcation curves $\tau_c(c)$ given by Theorem 2.2, for parameters $a = 0.25, b = 0.02, \gamma = 0.02$. The grey ones corresponds to the curves denoted as τ_+ and the curves denoted as τ_- are black.

The expressions for ω_{\pm} in Theorem 2.2 are valid if coupling constant c satisfies $A^2 - 4B \geq 0$. For the other values of c we proved the following theorem.

THEOREM 2.3. *If the parameter c in the system (1) satisfies*

$$A^2 - 4B < 0 \tag{18}$$

where

$$A = (a + cp)^2 + \gamma^2 - 2b - c^2 q^2, \quad B = (b + a\gamma + cp\gamma)^2 - c^2 q^2 \gamma^2,$$

$$p = \frac{1}{1 + e^{k\theta}}, \quad q = \frac{kV e^{k\theta}}{(1 + e^{k\theta})^2},$$

than the trivial stationary solution is stable for all time lags $\tau > 0$.

Proof. Let us start with the characteristic function (13) in the form

$$\phi(z) = [(z + \gamma)(z + a + cp) + b]^2 - c^2 q^2 (z + \gamma)^2 e^{-2z\tau}$$

and consider the following expression:

$$f(z) = \frac{\phi(z)}{P_4(z)} = 1 - \frac{c^2 q^2 (z + \gamma)^2}{P_4(z)} e^{-2z\tau},$$

where $P_4(z) = [(z + \gamma)(z + a + cp) + b]^2$ is actually squared the characteristic function of the single noncoupled unit.

Consider contour C_R in the complex half plane $\operatorname{Re} z > 0$, formed by segment $[-iR, iR]$ of imaginary axis and semicircle with radius R centered at the origin. We assumed that the system (2) has only one stationary solution $(x, y) = (0, 0)$ ($4(b/\gamma) > (a - 1)^2$) which is always stable. Then we can conclude that the polynomial $P_4(z)$ has no zeros in the half plane $\operatorname{Re} z > 0$. In that case, the number of poles of $f(z)$ is $P_c = 0$. Using the argument principle we infer the number of zeros N_{C_R} of $f(z)$. If $\lim_{R \rightarrow \infty} N_{C_R} = 0$, then all the roots of the characteristic function $\phi(z)$ satisfy $\operatorname{Re} z < 0$. Thus, we need to find the condition on parameter c , such that the image of contour C_R when $R \rightarrow \infty$ by the function does not encircle point $z = 0$. For such values of parameter c the variation of the argument is zero, so $\lim_{R \rightarrow \infty} N_{C_R} = 0$.

It is enough to consider the image of segment $[-iR, iR]$ by the function

$$\omega_\tau(z) \equiv \frac{c^2 q^2 (z + \gamma)^2}{P_4(z)} e^{-2z\tau},$$

because the image of the semicircle shrinks to a point as $R \rightarrow \infty$. Since $|\omega_\tau(iy)| < 1$ if and only if $|\omega_0(iy)| < 1$, we now consider only $|\omega_0(iy)|$.

Since

$$\begin{aligned} |\omega_0(iy)| &= \left| \frac{cq(iy + \gamma)}{(iy + \gamma)(iy + a + cp) + b} \right|^2 \\ &= \frac{c^2 q^2 (\gamma^2 + y^2)}{y^4 + ((a + cp)^2 + \gamma^2 - 2b)^2 y^2 + (a\gamma + cp\gamma + b)^2} \end{aligned}$$

we obtain that $|\omega_0(z) < 1|$ is equivalent with

$$y^4 + Ay^2 + B > 0. \quad (19)$$

where A and B are given by the same formula as in (17), i.e.,

$$A = (a + cp)^2 + \gamma^2 - 2b - c^2 q^2, \quad B = (b + a\gamma + cp\gamma)^2 - c^2 q^2 \gamma^2.$$

$A^2 - 4B < 0$ is satisfied for all c , consequently (19) is true so the stationary solution is stable for all $\tau > 0$. ■

Let us now discuss $A^2 - 4B < 0$, condition in Theorem 2.3. For $c = 0$ this condition is equivalent with condition on parameter a , b and γ , $(a - \gamma) < 2\sqrt{b}$,

i.e., when uncoupled units have focus-focus stationary point. In that case in the coupled system there is the range on parameter c , $c \in (0, c^\tau)$ when the stationary point is stable for any τ (see fig. 1). For some value c^τ we have $\omega = \omega_+ = \omega_-$ so our bifurcation curves given by Theorem 2.2 should coincide in this point. In the other case we don't need Theorem 2.3 because for all small $c > 0$ condition $A^2 - 4B < 0$ is not satisfied. In both of this cases we have range on parameter c , $c \in (c^\tau, c_0)$ or in the other case $c \in (0, c_0)$ when increasing the time lag τ results in the destabilization of the stationary point.

Next we consider the range of coupling $c \in (c_0, c_1)$. Then, for sufficiently small $\tau > 0$, there is only one pair of roots of (12) in the right half plane, and the other roots have negative real parts. There is an unstable stationary solution and the stable limit cycle.

3. Summary and conclusions

We have performed an analysis of bifurcations of the stationary solution of a model of two coupled FitzHugh-Nagumo excitable systems.

Bifurcation analysis of the system of ordinary differential equations, shows that the instantaneous coupling can introduce instability of the stationary solution. This result is given in Theorem 2.1. There is the critical value of the coupling constant $c = c_0$ when system has subcritical Hopf bifurcation. We explicitly get the equations that determines the dynamics on the center manifold. For small and negative parameter $\epsilon = c - c_0$ in the plane $x_1 = x_2$, $y_1 = y_2$ there is unstable limit cycle with radius $\sqrt{-\frac{d\epsilon}{\alpha}}$, and stable stationary solution. From numerical calculations we know that for the same values of the parameter ϵ , there is a stable limit cycle with bigger radius than the unstable. The unstable limit cycle acts as a threshold. For small and positive ϵ the unstable limit cycle disappears and the stationary solution is unstable.

Further results of analyzes of the system of delayed differential equations are given in Theorems 2.2 and 2.3. For small coupling constant and small time lags there is only one attractor in the form of the stable stationary solution. Theorem 2.3 proves that in the case when uncoupled units have focus-focus stationary solution there is the range on parameter $c \in (0, c^\tau)$ when the stationary solution is stable for any value of the time lag. From the bifurcation curves given in Theorem 2.2 we know that for $c \in (c^\tau, c_0)$ in one case or for $c \in (0, c_0)$ in the other and small time lags the stable stationary point is the only attractor. But, as time lag is increased the stationary solution becomes unstable due to Hopf bifurcation. Further increasing of the time lag τ could lead to stabilization of the stationary point. For $c > c_0$ the stationary solution is unstable. For small τ there is only one pair of the roots of characteristic equation in the right half plane. Increasing the τ , every critical value denoted with τ_+ gives us one more pair of the roots with positive real parts or one more unstable direction and critical values τ_- turns one unstable direction into the stable direction. In the fig. 1 we can see that for small values $c - c_0$ there is the region in (c, τ) plane where the stationary solution could be stable.

Our results are important in modelling neuronal dynamics with synaptic delays explicitly included.

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Department of Physics and Mathematics, Faculty of Pharmacy University of Belgrade, Vojvode Stepe 450, Beograd, Serbia

E-mail: draganat@pharmacy.bg.ac.rs