



Hopf bifurcations in dynamics of excitable systems

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Abstract

A general FitzHugh–Rinzel model, able to describe several neuronal phenomena, is considered. Linear stability and Hopf bifurcations are investigated by means of the spectral equation for the ternary autonomous dynamical system and the analysis is driven by both an admissible critical point and a parameter which characterizes the system.

Keywords FitzHugh Rinzel model · Linear stability · Hopf bifurcations · Neuron bursting frequency

Mathematics Subject Classification 34C23 · 92B05 · 92Bxx

1 Introduction

The physiological and chemical properties that characterize neurons make them able to receive, process and transmit electrical signals that, associated with ionic currents, cross the membrane of the neuron. These electrical signals are called nerve impulses, while the difference in electrical charge that exists between the inside and outside of the neuronal cell is called membrane potential. The variation in the membrane potential is called action potential and it travels along the axon and is transmitted unchanged to other neurons in the form of electrical impulses. In this way, information is transmitted from one neuron to another, forming what is known as synapse. This phenomenon is well known in literature and an extensive bibliography exists in regard [1–3]. A reference point for these studies are the works of Hodgkin and Huxley [HH], who developed the model of the propagation of an electrical signal along a squid axon (an axon so great to be called giant). Their model consists of a system of four differential equations describing the dynamics of the membrane potential and the three

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fundamental ionic currents: the sodium current, the potassium current and the leakage current, which is mainly due to chlorine but also considers the effect of other minor ionic currents. However, the non linearity and high dimensionality of the HH model made the analysis too complicated, so that simpler models were introduced to allow the essential aspects of the dynamics of models to be captured.

One of these models is the FitzHugh-Nagumo system (FHN) where, indicating by $U(x, t)$ the transmembrane potential and by $W(x, t)$ a variable associated with the contributions to the membrane current from sodium, potassium and other ions, it is given by

$$\begin{cases} \frac{\partial U}{\partial t} = D \frac{\partial^2 U}{\partial x^2} - W + f(U) \\ \frac{\partial W}{\partial t} = \varepsilon(-\beta W + c + U). \end{cases} \quad (1)$$

Constant $D > 0$ is a diffusion coefficient related to the axial current in the axon. It follows from the HH theory where, denoting by d the diameter of the axon and by r_i the resistivity, the spatial variation of the potential V gives the term $(d/4r_i)V_{xx}$ from which the term $D U_{xx}$ is deduced [3]. Furthermore ε , c , and β are constants that characterize the model's kinetic.

The documentation is numerous and the analysis is extensive (see, for instance, [4, 5] and references therein).

As for function $f(U)$, it depends on the reaction kinetics of the model and can assume various expressions such as a piecewise linear form, or $f(U) = U - U^3/3$. Besides, more in general, function $f(U)$ assumes the following form [1, 2]:

$$f(U) = U(a - U)(U - 1). \quad (2)$$

The cubic term is due to an instantaneous inversion of the sodium permeability and can be thought to play the same role as the m variable in the HH model, where the variable of activation of the channels of sodium is considered. Hence, a represents a threshold constant and is an excitability parameter [6]. In addition, a can take both positive and negative values (see, f.i. [7]) and cases with function $a(x)$ are considered in [8] for inhomogeneous means.

Besides, one aspect worth noting is the existence of an equivalence between the FHN model and the third-order equation characterizing Josephson junctions in superconductivity [9–11]. It follows that the analysis of such models is reflected in both biological and superconducting phenomena and, in addition, in dissipative problems [12–14].

Similarly, in order to investigate other phenomena such as, for example, bursting oscillations, the well known system of FitzHugh–Rinzel (FHR) can be considered [15–19]. This model is derived from the FHN model and, unlike the latter, has an additional variable that changes periodically from a rapid spike oscillation to a silent phase during which the membrane potential changes slowly [1].

Indeed, bursting phenomena occur in various scientific fields (see, f.i. [20] and references therein), and many devices are being built to mimic the behavior of a

biological synapse, suggesting that electronic synapses may be introduced in the future to directly connect neurons [21]. As a result, the FHR system is increasingly being studied to provide a mathematical description of physical phenomena occurring in organisms.

The FitzHugh–Rinzel model considered in this paper is the following one:

$$\begin{cases} \frac{dU}{dt} = -aU + U^2 \left(a + 1 - \frac{1}{k}U \right) - W + Y + I \\ \frac{dW}{dt} = \varepsilon(-\beta W + c + U) \\ \frac{dY}{dt} = \delta(-U + h - dY) \end{cases} \quad (3)$$

where the physical variables (U, W, Y) represent, respectively, the transmembrane potential, the recovery variable and the slow current in the dendrite. Moreover, the parameter ε specifies the relationship between the time constants of the activator and inhibitor [6], and c and β can be related to the number of cell membrane channels open to sodium and potassium ions, respectively [22]. Constant I measures the amplitude of the external stimulus current and is modulated by the variable Y on a slower time scale [1]. In addition, if $\beta\varepsilon$ and δd are positive constants, they can be regarded as the coefficients of viscosity [23].

When $k = 3$ and $a = -1$, (3) turns into this model:

$$\begin{cases} \frac{dU}{dt} = U - U^3/3 + I - W + Y \\ \frac{dW}{dt} = \varepsilon(-\beta W + c + U) \\ \frac{dY}{dt} = \delta(-U + h - dY). \end{cases} \quad (4)$$

often studied in literature (see, f.i. [15, 18, 23] and references therein).

Aim of the paper is to analyze the linear stability of the critical points of the FHR system, as well as to highlight the cases of Hopf bifurcations. Considering the spectrum equation, and its eigenvalues, stability is evaluated by the Lienard-Chipart criterion. Furthermore, for what concerns instability, showing that the problem can be expressed by way of a positive parameter R , the steady and/or oscillatory Hopf bifurcations cases are determined by means of the instability coefficient power (ICP) method introduced by Rionero (see, f.i. [23, 24] and references therein). The plan of the paper is the following one: Sect. 2 highlights some premises by which the subsequent theorems will be proved. In Sect. 3 the mathematical problem and linear operator L with its

invariants is given. Finally, in Sects. 4 and 5, Hopf bifurcations driven by critical point \bar{U} and driven by coefficient $-\eta = -\varepsilon\beta$ are evaluated.

2 Some premises

Due to the oscillatory activities of neurons, the onset of oscillatory bifurcations has gained the attention of many researchers. Regarding the study of Hopf's bifurcations, an extensive literature exists (see, f.i. [23–26] and references therein). In order to justify the results stated here, some introductory considerations will be required.

Indeed, in relation to linear stability, according to [26] when a phenomenon is modelled by the system:

$$\frac{d\mathbf{U}}{dt} = \mathbf{F} \quad t \geq 0, \quad \mathbf{U}(0) = \mathbf{U}_0 \quad (5)$$

introducing a fixed solution \bar{U} and the perturbation $\mathbf{u} = \mathbf{U} - \bar{U}$, the behaviour of \mathbf{u} is governed by:

$$\frac{d\mathbf{u}}{dt} = L\mathbf{u} + N\mathbf{u}, \quad t \geq 0, \quad \mathbf{u}(0) = \mathbf{u}_0 \quad (6)$$

with \mathbf{u}_0 initial perturbation to \bar{U} and $(N\mathbf{u})_{\mathbf{u}_0} = 0$.

Considering the linear operator

$$\begin{cases} L = \| a_{i,j} \|, & (i, j = 1, 2, \dots, n) \\ a_{i,j} = \text{const.} \in \mathcal{R} \text{ and independent from } t, \end{cases} \quad (7)$$

the stability and instability of \bar{U} is called linear if it is evaluated via the linear system

$$\frac{d\mathbf{u}}{dt} = L\mathbf{u}, \quad t \geq 0, \quad \mathbf{u}(0) = \mathbf{u}_0 \quad (8)$$

neglecting the nonlinear contribution $N\mathbf{u}$.

In this regard, some theorems can be provided.

Theorem 1 *If*

$$\det(a_{i,j} - \lambda \delta_{i,j}) = 0 \quad \delta_{i,j} = \text{Kronecker numbers} \quad (9)$$

is the spectral equation whose eigenvalues of the $n \times n$ matrix $\|a_{i,j}\|$ are λ_i ($i = 1, 2, 3, \dots, n$), and if and only if all the eigenvalues have negative real parts, then $\mathbf{u} = \mathbf{0}$ is linearly globally attractive and asymptotically exponentially stable. Otherwise, if there exists at least an eigenvalue with positive real part, then $\mathbf{u} = \mathbf{0}$ is unstable. \square

In addition, as proved in [26], for a system formed by three equations such as the FHR model, the spectrum equation (9) of L is reduced to the following expression:

$$\mathcal{P}(\lambda) = \lambda^3 - I_1\lambda^2 + I_2\lambda - I_3 \quad (10)$$

where

$$I_1 = a_{11} + a_{22} + a_{33}; \quad I_3 = \det \| a_{i,j} \|, \quad (11)$$

$$I_2 = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} + \begin{vmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{vmatrix} + \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix}, \quad (12)$$

represent the invariants of L whose spectrum is the set $\sigma = \{\lambda_1, \lambda_2, \lambda_3\}$ of its eigenvalues. Moreover, connected to the invariants $I_i (i = 1, 2, 3)$, we can introduce the quantities:

$$A_1 = -\text{trace of } L = -(\lambda_1 + \lambda_2 + \lambda_3) = -I_1; \quad (13)$$

$$A_2 = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} + \begin{vmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{vmatrix} + \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} = \lambda_1(\lambda_2 + \lambda_3) + \lambda_2\lambda_3 = I_2 \quad (14)$$

and

$$A_3 = -\det \text{ of } L = -\lambda_1\lambda_2\lambda_3 = -I_3 \quad (15)$$

and, according to [23], the following Lienard-Chipart criterion holds:

Theorem 2 *If and only if*

$$A_k > 0, \quad (k = 1, 2, 3) \quad \text{and} \quad A_0 = A_1 A_2 - A_3 > 0, \quad (16)$$

all the eigenvalues have negative real part. In particular, each of the conditions:

$$A_1 > 0, \quad A_2 > 0, \quad A_3 > 0, \quad (17)$$

is necessary for all the roots to have negative real parts. Otherwise some roots will have positive real parts. \square

Moreover, taking into account that the instability can occur only via a zero eigenvalue ($\lambda = 0 \Leftrightarrow A_3 = 0$) or via a pure imaginary eigenvalues, $\lambda_{1,2} = \pm i\omega$ (i imaginary unit, $\omega \in \mathfrak{R}^+$) such that $\mathcal{P}(i\omega, R) = 0$, the onset of instability will be defined either as steady bifurcation or Hopf bifurcation depending on whether the instability occurs through a steady or oscillatory state [26].

When the problem at issue depends on a positive parameter R , let denote by R_{c_k} the lowest roots of value of R such that $A_k(R) = 0$ for $k = 1, 2, 3$. According to [23], it is possible to introduce the

$$\text{"instability coefficient power"}(ICP)_k \text{ of } A_k : (ICP)_k = \frac{1}{R_{C_k}} \quad (18)$$

and the following theorem holds:

Theorem 3 Let $A_{\bar{k}}$ be the spectrum equation coefficient with the biggest ICP and let the critical point \bar{C} be linearly asymptotically stable at $R = \bar{R} = 0$. Then, at the growing of R from $R = 0$, the instability occurs at $R = R_{C_{\bar{k}}}$ and one has a steady bifurcation if $\bar{k} = 3$, while an oscillatory bifurcation occurs at an $R \in]0, R_{C_{\bar{k}}}[$ if $k < 3$. \square

3 Mathematical model

Let consider the FHZ system (3) and assuming

$$\eta = \beta \varepsilon; \quad \gamma = \delta d \quad (19)$$

it results:

$$\begin{cases} \frac{dU}{dt} = -aU + U^2(a+1) - \frac{1}{k}U^3 - W + Y + I \\ \frac{dW}{dt} = -\eta W + \varepsilon c + \varepsilon U \\ \frac{dY}{dt} = -\delta U + \delta h - \gamma Y \end{cases} \quad (20)$$

If $C = (\bar{U}, \bar{W}, \bar{Y})$ is an admissible critical point, considering:

$$u = U - \bar{U}; \quad w = W - \bar{W}; \quad y = Y - \bar{Y} \quad (21)$$

as the perturbation vector, from (20) one obtains:

$$\begin{cases} \frac{du}{dt} = -\frac{1}{k}u^3 - \frac{3}{k}u^2\bar{U} - \frac{3}{k}u\bar{U}^2 - au + (a+1)(u^2 + 2u\bar{U}) - w + y \\ \frac{dw}{dt} = \varepsilon u - \eta w \\ \frac{dy}{dt} = -\delta u - \gamma y. \end{cases} \quad (22)$$

Linearizing about C , it results:

$$\begin{cases} \frac{du}{dt} = u \left[-\frac{3}{k} \bar{U}^2 - a + 2(a+1) \bar{U} \right] - w + y \\ \frac{dw}{dt} = \varepsilon u - \eta w \\ \frac{dy}{dt} = -\delta u - \gamma y. \end{cases} \quad (23)$$

Denoting by

$$L = \begin{pmatrix} -3\frac{1}{k}\bar{U}^2 + 2(a+1)\bar{U} - a - 1 & 1 & 0 \\ \varepsilon & -\eta & 0 \\ -\delta & 0 & -\gamma \end{pmatrix} \quad (24)$$

the linear operator, according to (11)–(12), for $k = 3$, one has:

$$\begin{cases} I_1 = -\left[\bar{U}^2 - 2(a+1)\bar{U} + a + \eta + \gamma \right] \\ I_2 = -(\eta + \gamma) \left[-\bar{U}^2 + 2(a+1)\bar{U} - a \right] + \varepsilon + \delta + \eta\gamma \\ I_3 = -\left\{ \gamma \left[\eta \left(\bar{U}^2 - 2(a+1)\bar{U} + a \right) + \varepsilon \right] + \delta\eta \right\} \end{cases} \quad (25)$$

as the invariants of L . Besides, taking into account (13)–(15) one deduces:

$$\begin{cases} A_1 = \bar{U}^2 - 2(a+1)\bar{U} + a + \eta + \gamma \\ A_2 = -(\eta + \gamma)(-\bar{U}^2 + 2(a+1)\bar{U} - a) + \varepsilon + \delta + \eta\gamma \\ A_3 = \gamma [\eta(\bar{U}^2 - 2(a+1)\bar{U} + a) + \varepsilon] + \delta\eta, \end{cases} \quad (26)$$

and letting

$$\Gamma = \bar{U}^2 - 2(a+1)\bar{U} + a, \quad (27)$$

one obtains

$$\begin{cases} A_1 = \Gamma + \eta + \gamma \\ A_2 = (\eta + \gamma)\Gamma + \varepsilon + \delta + \eta\gamma \\ A_3 = \gamma\eta\Gamma + \gamma\varepsilon + \delta\eta \\ A_0 = A_1A_2 - A_3 = (\Gamma + \eta + \gamma)[(\eta + \gamma)\Gamma + \varepsilon + \delta + \eta\gamma] - (\gamma\eta\Gamma + \gamma\varepsilon + \delta\eta). \end{cases} \quad (28)$$

4 Hopf bifurcations driven by \bar{U}

The FHR system depends on several parameters, and according to each coefficient, various Hopf bifurcations conditions can be obtained.

In order to study Hopf bifurcations driven by critical point \bar{U} , the attention is focused on

$$\Gamma = \bar{U}^2 - 2(a + 1)\bar{U} + a$$

already introduced in (27), and the following theorem for linear stability can be proved:

Theorem 4 *Let $\bar{C} = (\bar{U}, \bar{W}, \bar{Y})$ be an admissible critical point and let assume constants $(\varepsilon, \delta, d, \beta)$, be positive. Then, whatever the value of variable $a \in \mathcal{R}$ may be, if*

$$\begin{cases} \bar{U} \leq -\sqrt{a^2 + a + 1} + a + 1 \\ \text{or} \\ \bar{U} \geq \sqrt{a^2 + a + 1} + a + 1, \end{cases} \quad (29)$$

then the critical point \bar{C} is linearly, globally attractive and asymptotically exponentially stable.

Proof Condition (29) ensures that $\Gamma \geq 0$, and it is possible to prove that the positiveness of the FHR system's constants implies that A_k , ($k = 0, 1, 2, 3$), determined in (28), are all non-negative. Moreover, they are increasing functions of Γ .

This ensures that conditions (16) of theorem 2 state, and hence theorem holds. \square

When conditions (29) are not satisfied, i.e the critical point \bar{U} is such that the following inequality:

$$-\sqrt{a^2 + a + 1} + a + 1 < \bar{U} < \sqrt{a^2 + a + 1} + a + 1 \quad \forall a \in \mathcal{R} \quad (30)$$

holds, then it results $\Gamma < 0$ and in this case it is possible to introduce a positive parameter R as “bifurcation parameter”. Indeed if we let:

$$\begin{cases} R = -\Gamma = -[\bar{U}^2 - 2(a+1)\bar{U} + a] > 0 \\ c_1 = \eta + \gamma \\ c_2 = \frac{\varepsilon + \delta + \eta\gamma}{\eta + \gamma} \\ c_3 = \frac{\gamma\varepsilon + \eta\delta}{\eta\gamma} = \frac{d + \beta}{\beta d} \end{cases} \quad (31)$$

it results:

$$\begin{cases} A_1 = -R + c_1 \\ A_2 = -c_1 R + c_1 c_2 \\ A_3 = -\gamma \eta R + c_3 \gamma \eta \end{cases} \quad (32)$$

with:

$$A_1 = 0 \Leftrightarrow R = c_1; \quad A_2 = 0 \Leftrightarrow R = c_2; \quad A_3 = 0 \Leftrightarrow R = c_3. \quad (33)$$

So that, denoting by R_{c_k} the lowest roots of value of R such that $A_k = 0$ for $k = 1, 2, 3$, one has:

$$R_{c_k} = \min_{(\beta, d, \varepsilon, \delta) \in R^+} c_k \quad k = 1, 2, 3 \quad (34)$$

and the following theorem holds:

Theorem 5 *In the hypothesis (30), let $R = -\Gamma = -[\bar{U}^2 - 2(a+1)\bar{U} + a] > 0$ and let constants $(\varepsilon, \delta, d, \beta)$, be positive.*

Then, at the growing of R from $R = 0$, conditions

$$\eta + \gamma < \frac{\varepsilon + \delta + \eta\gamma}{\eta + \gamma}; \quad \eta + \gamma < \frac{d + \beta}{\beta d}; \quad (35)$$

ensure that a simple oscillatory bifurcation occurs at a $\bar{R} \in]0, R_{C_1}[$, with a frequency $\frac{\varphi}{2\pi}$ where $\varphi^2 = \frac{A_3(\bar{R})}{A_1(\bar{R})} = A_2(\bar{R})$.

If, in particular

$$\eta + \gamma = \frac{\varepsilon + \delta + \eta\gamma}{\eta + \gamma}; \quad \eta + \gamma < \frac{d + \beta}{\beta d} \quad (36)$$

a simple oscillatory bifurcations occurs at a $\bar{R} \in]0, R_{C_1} = R_{C_2}[$.

Otherwise, if

$$\eta + \gamma = \frac{d + \beta}{\beta d} < \frac{\varepsilon + \delta + \eta \gamma}{\eta + \gamma} \quad (37)$$

a steady + oscillatory bifurcation appears with a frequency given by $\varphi = (2\pi)(\sqrt{A_2})_{R_{C_1}}$.

Moreover, if

$$\frac{\varepsilon + \delta + \eta \gamma}{\eta + \gamma} < \eta + \gamma < \frac{d + \beta}{\beta d} \quad (38)$$

a simple oscillatory bifurcation occurs at a $\bar{R} \in]0, R_{C_2}[$.

Proof When $R = -\Gamma = 0$, it results:

$$\begin{aligned} A_0|_{\Gamma=0} &= A_1 A_2 - A_3|_{\Gamma=0} = (\eta + \gamma)(\varepsilon + \delta + \eta \gamma) - (\gamma \varepsilon + \delta \eta) \\ &= \eta \varepsilon + \gamma \delta + (\eta + \gamma)\eta \gamma > 0 \end{aligned}$$

with $A_k > 0$ ($k = 1, 2, 3$). So, the critical point is linearly, asymptotically stable for $R = 0$.

Besides, when inequalities (35) hold, it means that

$$R_{C_1} < R_{C_2}; \quad R_{C_1} < R_{C_3};$$

i.e. A_1 is the spectrum equation coefficient with the biggest instability coefficient power, so that at $R = R_{C_1}$, it results:

$$A_1 = 0, \quad A_3 = \gamma \eta (-c_1 + c_3) > 0; \quad A_0 = A_1 A_2 - A_3 < 0$$

and hence, in view of the continuity of $A_1 A_2 - A_3$, there exists a $\bar{R} \in]0, R_{C_1}[$ such that

$$A_1(\bar{R})A_2(\bar{R}) - A_3(\bar{R}) = 0,$$

being \bar{R} the lowest root of $A_1 A_2 = A_3$ in $]0, R_{C_1}[$ and it results

$$P(i\varphi, \bar{R}) = 0 \Leftrightarrow [\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3]_{i\varphi} = 0 \quad (39)$$

and hence

$$-i\varphi^3 - A_1(\bar{R})\varphi^2 + iA_2(\bar{R})\varphi + A_3(\bar{R}) = 0 \quad (40)$$

with

$$\varphi^2 = \frac{A_3(\bar{R})}{A_1(\bar{R})} = A_2(\bar{R}). \quad (41)$$

Besides, conditions (36) imply that $R = R_{C_1} = R_{C_2} < R_{C_3}$ that means $A_1 = A_2 = 0$ and

$$A_3(R_{C_1}) = -\gamma \eta c_1 + c_3 \gamma \eta > 0$$

Consequently, the spectrum equation is reduced to:

$$\lambda^3 + A_3 = (\lambda + A_3^{1/3})(\lambda^2 - \lambda A_3^{1/3} + A_3^{2/3}) = 0 \quad (42)$$

and hence

$$\lambda_1 = -A_3^{1/3} \quad \lambda_{2,3} = (1 \pm i\sqrt{3})A_3^{1/3}/2.$$

This means that a simple oscillatory bifurcation occurs at a $\bar{R} \in]0, R_{C_1} = R_{C_2}[$.

Instead, when (37) holds, $R_{C_1} = R_{C_3} < R_{C_2}$; and hence one obtains $A_1 = A_3 = 0$. So, from the spectrum equation it results:

$$P(i\varphi) = 0 \Leftrightarrow [\lambda(\lambda^2 + A_2)]_{i\varphi} = 0 \Leftrightarrow \lambda = 0; \varphi = (\sqrt{A_2})_{R_{C_1}} = \sqrt{c_1(c_2 - c_1)} \quad (43)$$

and a steady ($\lambda = 0$) + oscillatory bifurcation of frequency φ/π with $\varphi = (\sqrt{A_2})_{R_{C_1}}$ occurs.

Analogous results can be obtained if we suppose R_{C_2} to be the biggest ICP and hence (38) is proved, too. \square

5 Hopf bifurcations driven by $-\eta = -\varepsilon \beta > 0$

The previous bifurcation criterion required that $\Gamma \leq 0$. In the present section, we prove that, by choosing $\eta = \varepsilon \beta$ as bifurcating parameter and letting $\eta \leq 0$, the Hopf bifurcation can arise with $\Gamma \geq 0$.

Indeed, the following theorem states:

Theorem 6 *Let consider a critical point \bar{C} such that:*

$$\bar{U} \leq -\sqrt{a^2 + a + 1} + a + 1 \text{ or } \bar{U} \geq \sqrt{a^2 + a + 1} + a + 1 \quad (44)$$

and let constants (ε, δ, d) , be positive. Assuming $R = -\eta = -\varepsilon \beta > 0$, then, at the growing of R from $R = 0$, conditions

$$\Gamma + \gamma \leq \frac{\gamma \Gamma + \varepsilon + \delta}{\Gamma + \gamma}; \quad \Gamma + \gamma < \frac{\gamma \varepsilon}{\gamma \Gamma + \delta} \quad (45)$$

ensure that a simple oscillatory bifurcation occurs at a $\bar{R} \in]0, R_{C_1}[$, while if

$$\Gamma + \gamma = \frac{\gamma\varepsilon}{\gamma\Gamma + \delta} < \frac{\gamma\Gamma + \varepsilon + \delta}{\Gamma + \gamma} \quad (46)$$

a steady+oscillatory bifurcation appears.

Moreover, if

$$\frac{\gamma\Gamma + \varepsilon + \delta}{\Gamma + \gamma} < \eta + \Gamma < \frac{\gamma\varepsilon}{\gamma\Gamma + \delta}, \quad (47)$$

a simple oscillatory bifurcation occurs at a $\bar{R} \in]0, R_{C_2}[$.

Proof Condition (44) ensures that Γ , defined in (27), is positive. Moreover, since (28), when $\eta = 0$, it results $A_k > 0$ ($k = 1, 2, 3$) and

$$A_0]_{\eta=0} = A_1 A_2 - A_3]_{\eta=0} = (\Gamma + \gamma)(\Gamma\gamma + \varepsilon + \delta) - \gamma\varepsilon > 0.$$

So, the critical point $\bar{C} = (\bar{U}, \bar{W}, \bar{Y})$ is linearly, asymptotically stable for $R = \bar{R} = 0$. In addition, denoting by

$$c_1 = \Gamma + \gamma; \quad c_2 = \frac{\gamma\Gamma + \varepsilon + \delta}{\Gamma + \gamma}; \quad c_3 = \frac{\gamma\varepsilon}{\gamma\Gamma + \delta} \quad (48)$$

from (28) it results

$$A_1 = 0 \Leftrightarrow R = c_1; \quad A_2 = 0 \Leftrightarrow R = c_2; \quad A_3 = 0 \Leftrightarrow R = c_3, \quad (49)$$

and so, by retracing the analysis set forth in the previous bifurcation cases, this theorem can also be proved. \square

6 Remarks and discussion

As it is well known, the phenomenon related to Hopf bifurcations is of great importance and it is widely studied. In this paper, the FHR model (3) considered also depends on the variable a generally not present in the bifurcations studies and it generalizes the FHR system (4), which, on the contrary, is more often considered in literature.

Moreover, the results obtained [see, f.i. Theorems 4–5 and condition (30)] do not require any assumptions for the real variable a and this implies that the analysis can certainly be directed to a wider set of physical cases.

Furthermore, the equivalence that such a mathematical model creates between biological problems and superconducting processes of Josephson junctions or vis-

coelasticity, suggests that the analysis of such models is reflected in a large number of realistic mathematical models.

In this paper the onset of Hopf bifurcations, driven by specific parameters, is considered. In particular an analysis on the onset of steady and oscillatory bifurcations has been performed driven by both an admissible critical point \bar{U} and a coefficient characterized the FHR system.

Looking forward, in order to obtain a more comprehensive view of the stability and instability of critical points, the analysis can be extended to evaluate Hopf bifurcations driven by all other coefficients that characterize the FHR system. Moreover, it will be possible to determine explicit critical points at particular values of the FHR system variables and also evaluate the explicit value of the bifurcation parameters R .

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Declarations

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