



Stability and Hopf bifurcation in leech heart interneuron model

F. Parvizi*, M. Razvan and Y. Alipour Fakhri

Abstract

This article investigates the activity regimes of a realistic neuron model (as a slow-fast system). The authors study this model using the dynamical systems theory, for example, qualitative theory methods of slow-fast systems. The authors obtain the stability conditions of equilibria in leech heart interneurons under defined pharmacological conditions and following Hodgkin–Huxley formalism. Although in neuronal models, the membrane is usually considered capacitance as a fixed parameter, the membrane capacitance parameter is assumed as a control parameter to guarantee the existence of Hopf bifurcation using the Routh–Hurwitz criteria. The authors investigate the transition mechanism between the silent phase and tonic spiking mode. Furthermore, some simulations are provided using XPPAUT software for analytical results.

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*Corresponding author

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Fatemeh Parvizi

Department of Mathematics, Payame Noor University(PNU), Tehran, Iran. e-mail: Parvizifa@gmail.com

Mohammadreza Razvan

Department of Mathematics, Faculty of Mathematical Sciences, University of Sharif, Tehran, Iran. e-mail: razvan@sharif.ir

Yousef Alipour Fakhri

Department of Mathematics,, Payame Noor University(PNU), Tehran, Iran. e-mail: y-alipour@pnu.ac.ir

1 Introduction

Periodic orbits play an important role in nonlinear dynamical models, especially in computational neuroscience from the point of view of their topology. Now one of the models that pay attention to researchers, is neuron models whose topology is associated with specific and regular activities such as tonic spiking, bursting, and resting.

Most neurons show potential membrane oscillations as endogenous or in terms of external perturbations. Many kinds of activities on neuronal models based on models following the formalism of Hodgkin–Huxley were described in terms of the qualitative theory of fast-slow systems [1, 11]. Fast-slow systems are a special class of dynamical systems with at least two distinct time scales. The solutions of fast-slow systems possess features that are constrained to stay near the slow-motion manifolds, composed of equilibria and periodic orbits of the fast subsystem. If both manifolds are transient for the solutions of the corresponding neuron model, then it exhibits a bursting behavior, a repetitive alternation of tonic spiking and quiescent periods. Otherwise, the model indicates the tonic spiking activity if there is a stable periodic orbit on the tonic spiking manifold, or it shows no oscillations when solutions are attracted to a stable equilibrium state on the quiescent manifold [12].

Classifying transition mechanisms between various regimes is a fundamental problem of the theory of dynamical systems and neuroscience. Real neurons can show various types of firing patterns, such as tonic spiking, bursting oscillations, and silent states, that are frequently observed in neuronal electrophysiological experiments. We investigate the stability of the silent phase and the existence of periodic solutions in the Leech heart interneuron model.

Malashchenko, Shilnikov, and Cymbalyuk [14] described that the leech heartbeat is one of the best-studied invertebrate neuronal networks with an identified function, a set of identified participating neurons, and well-developed biophysically accurate models. It consists of a small number of interneurons distributed over several ganglia. Those located in ganglia 3 and 4 are responsible for generating basic rhythm [2]. Here we focus on the dynamics of a single interneuron from either ganglion 3 or 4. The canonical model has proved itself as a powerful tool for predicting phenomena.

This model has already been studied by Shilnikov and Cymbaluk [19] and Wanga et al. [21]. They consider different parameters, for example, V_{K2}^{shift} or E_l, g_l , as a control parameter with different initial conditions and investigated the existence of different codimension-one or two bifurcations. Researchers found the parameter regimes in which bursting, tonic spiking, and silence are stable. They located several kinds of multi-stability in which more than one activity is stable, such as bi-stability in which bursting coexistent with tonic spiking, bursting coexistent with silence, and tonic spiking with silence.

Cymbalyuk et al. [4] have examined the single heart interneuron model. Using extracellular recording methods, they demonstrated that oscillator and

premotor cardiac interneurons continue to burst when pharmacologically isolated with bicuculline, albeit in certain preparations, the bursting is not strong. They performed a bifurcation analysis of their model using the leak conductance g_l and reversal potential E_l as parameters. The bifurcation diagram shows a narrow strip of parameter values, where bursting occurs, separating large zones of tonic spiking and silence. Moreover, the authors found multi-stability zones, which are regions where the major activities co-exist. They propounded how robustness is achieved in this system, how critical variables such as period and duty cycle may be controlled, and how modulation may affect this control.

Shilnikov and Cymbalyuk [19] showed how two different codimension-one bifurcations of a saddle-node periodic orbit with homoclinic orbits could explain a scenario of transitions between tonic spiking and bursting activities in neuron models following Hodgkin–Huxley formalism. They also found the co-existence of tonic spiking and bursting modes, which are separated by a saddle periodic orbit. This mechanism is based on a Lukyanov–Shilnikov bifurcation for a saddle-node periodic orbit with noncentral homoclinic orbits. They showed that as a bifurcation parameter is varied, the unstable periodic orbit separates the basins of attraction of two co-existing modes: the tonic spiking periodic orbit and bursting regime.

Cymbalyuk and Shilnikov [5] presented conditions under which this model demonstrates another kind of bi-stability with two coexistent tonic spiking modes. They developed a geometrical framework for Pontryagin’s averaging method of singularly perturbed systems and located periodic orbits and studied their bifurcations. Pontryagin’s averaging method gives a clear geometrical interpretation of this mechanism. They showed that as a bifurcation parameter is varied, the unstable periodic orbit separates the basins of attraction of two co-existing modes: tonic spiking regime coexisting with another spiking regime.

Furthermore, by synchronization of Wanga et al. [21] in gap-junction, coupled neurons with co-existing attractors of spiking and bursting firings are investigated as the coupling strength gets increased for this model. Kolomiets and Shilnikov [12] considered this model as an example to investigate generic mechanisms of transition between distinct patterns of activity in it. They considered neuronal bursting as a modular activity consisting of different limiting branches corresponding to oscillatory and equilibrium regimes from the fast subsystem, based on the Poincaré return map to analyze nonlocal bifurcation to understand better and determine what makes bursting and spiking attractors fluctuate their shape and stability.

The lipid bilayer of the cell membrane is a dielectric that creates a capacitance by separating charge inside and outside the cell. Such capacitance behavior is represented in electrical equivalent circuit models of the cell membrane with an electrical capacitor element [16]. The membrane-specific capacitance is considered constant and ubiquitous [6]. Moreover, myriad models of excitable cells and axons incorporate a constant membrane capacitance

[16]. However, the dielectric properties of living tissues exhibit frequency-dependent behavior [7].

Howell et al. [10] checked out the effect of a frequency-dependent capacitance on neuronal excitability. They found that the effect of dielectric dispersion on the sinusoidal stimulation thresholds depended on the electrical properties of the neuronal membrane. Moreover, dielectric dispersion increased action potential conduction velocity. When analyzing the response qualities of brain elements at various frequencies, it is necessary to account for the influence of frequency-dependent capacitance. Furthermore, in this paper, we consider the membrane capacity as a control parameter in the neuronal model. To the best of our knowledge, this is the first work that shows how to occur Hopf bifurcation in this model when the membrane capacitance parameter varies.

The concept of Hopf bifurcation, which is known as the Poincaré–Andronov–Hopf bifurcation, seems complicated and abstract. However, this theory applies to many real problems. Furthermore, the application of Hopf bifurcation theory is quite wide. This theory is applied in tests of various oscillations caused by wind gusts (which is very important in the field of construction), LCR oscillations in electrical circuits, transitions among neuronal activity regimes in neuronal models, periodic generation of nerve impulses in the nervous system, as well as, for instance in epidemiological models that describe fluctuations in the number of patients with an infectious disease. Through experimental measurements, the researchers found that the membrane capacity decreases with increasing frequency.

In many neuronal models, Hopf bifurcation occurs by changing various parameters. Using computer software, the Hopf bifurcation can be determined in multidimensional dynamical systems that depend on certain parameters. The presence of Hopf bifurcation is proved, and the bifurcation parameter value is estimated using the Routh–Hurwitz criterion, which determines the difference of this research.

This manuscript considers a model of a pharmacologically isolated heart-beat interneuron when the membrane capacitance is the control parameter. Then, the transition mechanism between the silent phase and tonic spiking mode is investigated. Hopf bifurcation occurs when a periodic solution or boundary cycle, which surrounds the equilibrium point, appears or disappears with a change in the parameter value. This type of Hopf bifurcation occurs where a pair of complex conjugate eigenvalues of the Jacobian matrix passes through the imaginary axis while all other eigenvalues have negative real parts. Furthermore, the existence of this type of Hopf bifurcation leads limit cycle losing stability and disappearing when changing a control parameter. First, we find that such a region for the existence of periodic solutions and Hopf bifurcation is being investigated. The type of bifurcation can be determined analytically, but it is very complicated. However, using computers (numerical experiments), we determine the type of bifurcation much faster and easier. The trajectories of this model were obtained using Dormand–Prince solvers, which are related to Runge–Kutta and are adaptive method

of solving ODE. The integration and bifurcation analysis was performed utilizing Mathematica and XPPAUT. These simulations present our theoretical results.

The manuscript is organized as follows: first, we provide some necessary preliminaries. Then we introduce the neuronal model and specify the parameters and the initial condition. In Section 3, we investigate a general geometrical framework for the analysis of (equilibrium points of a system) solutions to slow-fast dynamical systems. In the last section, we present some simulations to illustrate analytical results.

2 Preliminaries

2.1 Routh–Hurwitz criterion for the existence of Hopf bifurcation

In this section, an important criterion, which is known as the Routh–Hurwitz criterion, is presented that gives necessary and sufficient conditions for all roots of the characteristic equation that real parts of eigenvalues are negative. This criterion is stated in the next theorem; see [20, 17].

Theorem 1 (Routh–Hurwitz criterion). Consider a polynomial as follows:

$$\alpha_k x^k + \alpha_{k-1} x^{k-1} + \alpha_{k-2} x^{k-2} + \cdots + \alpha_1 x + \alpha_0,$$

when $\alpha > 0$, the polynomial has all roots with negative real parts if and only if all the leading principal minors of the $k \times k$ matrix

$$A = \begin{pmatrix} \alpha_1 & \alpha_0 & \cdots & 0 \\ \alpha_2 & \alpha_1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{2k-1} & \alpha_{2k-2} & \cdots & \alpha_k \end{pmatrix}$$

are positive and $\alpha_k > 0$. We assume that $\alpha_j = 0$ if $j < 0$ or $j > k$.

Let us consider a system

$$\dot{x} = f(x, \mu), \quad x \in \mathbb{R}^n, \quad \mu \in \mathbb{R}^1, \quad (1)$$

with an equilibrium (x_0, μ_0) and $f \in C^\infty$.

There is another theorem, which shows the existence of Hopf bifurcation in system (1).

Theorem 2. Assume that system (1) has an equilibrium $(x_0; \mu_0)$ at which the following properties are satisfied:

(SH1) $D_x f_{\mu_0}(x_0)$ has a simple pair of pure imaginary eigenvalues and other eigenvalues have negative real parts.

Thus, there exists a smooth curve of equilibria $(x(\mu); \mu)$ with $x(\mu_0) = x_0$. The eigenvalues $\lambda(\mu); \bar{\lambda}(\mu)$ of $D_x f_{\mu_0}(x(\mu))$ which are imaginary at $\mu = \mu_0$ vary smoothly with μ . In addition, if

(SH2) $d(Re(\lambda(\mu)))/d\mu \neq 0$,

then a simple Hopf bifurcation will occur.

Proof. See [8]. □

Moreover, researchers can apply n principal sub-determinants to obtain a parameter value for Hopf bifurcation Theorem. It should be noted that the characteristic polynomial of the Jacobian matrix $J(\mu)$ of system (1) is denoted as follows:

$$P(\lambda; \mu) = \det(\lambda I_n - J(\mu)) = p_0(\mu) + p_1(\mu)\lambda + \cdots + p_n(\mu)\lambda^n,$$

where every $p_i(\mu)$ is a smooth function of μ , and $p_n(\mu) = 1$. We consider the case $p_0(\mu) > 0$, because there is not any nonnegative real root. Let

$$L_n(\mu) = \begin{pmatrix} p_1(\mu) & p_0(\mu) & \cdots & 0 \\ p_2(\mu) & p_1(\mu) & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ p_{2n-1}(\mu) & p_{2n-2}(\mu) & \cdots & p_n(\mu) \end{pmatrix}$$

where $p_i(\mu) = 0$ if $i < 0$ or $i > n$. Moreover, when $p_0(\mu) > 0$, according to the Routh–Hurwitz criterion, the polynomial $P(\lambda; \mu)$ of λ has all roots with negative real parts if and only if the following n principal subdeterminants of $L_n(\mu)$ are positive:

- $D_1(\mu) = \det(L_1(\mu)) = p_1(\mu) > 0$,
- $D_2(\mu) = \det(L_2(\mu)) = \det \begin{pmatrix} p_1(\mu) & p_0(\mu) \\ p_3(\mu) & p_2(\mu) \end{pmatrix} > 0$,
- \vdots
- $D_n(\mu) = \det(L_n(\mu)) > 0$.

Since $D_n(\mu) = p_n(\mu)D_{n-1}(\mu)$ and for characteristic equation $p_n(\mu) = 1$, the Routh–Hurwitz criterion conditions can be formulated as

$$p_0(\mu) > 0, D_1 > 0, D_2 > 0, \dots, D_{n-1} > 0.$$

Theorem 3. Suppose that there is a smooth curve of equilibria $(x(\mu), \mu)$ with $x(\mu_0) = x_0$ for (1). Then conditions (SH1) and (SH2) for a simple Hopf bifurcation are equivalent to the following conditions on the coefficients of the characteristic polynomial $P(\lambda; \mu)$:

1. $p_0(\mu_0) > 0; D_1(\mu_0) > 0; \dots; D_{n-2}(\mu_0) > 0; D_{n-1}(\mu_0) = 0,$
2. $\frac{dD_{n-1}(\mu_0)}{d\mu} \neq 0.$

Proof. see [13]. □

2.2 Neuron model

Because a complete study of a neuronal model including all the currents identified experimentally is very complex, we study the dynamics of a reduction of the canonical leech heart interneuron model. Depending on the parameter values, the model may display several regimes, including tonic spiking, bursting, and quiet phase. These regimes represent the intricacy of the dynamics of diverse membrane ionic currents acting on distinct time scales. These neurons are particularly attractive for analysis in terms of the theory of dynamical systems since their membrane ionic currents were measured via voltage-clamp experiments and well described by a canonical model using the Hodgkin–Huxley formalism. We focus on the dynamics of a single interneuron when isolated pharmacologically from the rest of the network. In these neurons, eight voltage-dependent ionic currents have been well identified and characterized [18, 9]. These currents are separated into four groups and classified by their ionic specificity in Table 1. Moreover, “C.N.” is the abbreviation of current names. The model equations for I_{Na} current were

Table 1: Ionic currents in leech heart interneuron model

Ion	C.N.	Description	Method of quantify
Na	I_{Na}	fast sodium current	Hodgkin–Huxley Voltage clamp
	I_{NaP}	persistent sodium current	
K	I_{K1}	delayed rectifier-like potassium current	Voltage clamp
	I_{K2}	persistent potassium current	
	I_{Ka}	fast transient potassium	
Ca	I_{CaF}	rapidly inactivating current	Voltage clamp
	I_{CaS}	slowly inactivating current	
Na, K	I_h	hyperpolarization activated current	Voltage clamp

borrowed from the original work by Hodgkin and Huxley, which adjusted for leech kinetics. These currents are independent of the intracellular concentration of any particular ion. A canonical model of a single neuron was

described by a system of 14 differential equations running at multiple time scales which vary from a few milliseconds through seconds. As pointed out before, a complete investigation of this concept would be exceedingly tough and difficult. By blocking clusters of currents in live cardiac interneurons and exploiting their distinctive characteristics, neuronal dynamics are simplified. From the standpoint of the theory of dynamical systems, these distinctive behaviors provide intriguing phenomena for investigation [19].

Shilnikov and Cymbalyuk [19] removed from the 14-D canonical model developed in [9] the equations and terms describing blocked currents: I_{CaF} , I_{CaS} , and I_h . For simplicity, they assumed that the partial block of outward currents completely removes I_{K1} , as well as I_{KA} , and the current I_{NaP} is ignored, whereas it reduces I_{K2} . Now, the neuron can be described by the model based on just two currents activation of I_{K2} as m_{K2} and inactivation of I_{Na} as h_{Na} and V as the membrane potential. Therefore the resulting model described in [3] is as follows:

$$\begin{cases} CV' = -(\bar{g}_{K2}m_{K2}^2(V - E_K) + g_l(V - E_l) \\ \quad + \bar{g}_{Na}f(-150, 0.0305, V)^3h_{Na}(V - E_{Na})), \\ m'_{K2} = \frac{f(-83, 0.018 + V_{K2}^{shift}, V) - m_{K2}}{\tau_{K2}}, \\ h'_{Na} = \frac{f(500, 0.03391, V) - h_{Na}}{\tau_{Na}}, \end{cases} \quad (2)$$

where the variables V , m_{K2} , and h_{Na} display as membrane potential, activation of I_{K2} , and an inactivation of I_{Na} , respectively.

Moreover, f is a Boltzman function: $f(x, y, z) = \frac{1}{(1 + e^{x(y+z)})}$ and other

Table 2: Electrical properties of the leech heart interneuron Model

Parameter	Description	Unit(s)	Value
C	Membrane capacitance	nF	B.P.
\bar{g}_{Na}	Maximum conductance of I_{Na}	nS	200
\bar{g}_{K2}	Maximum conductance of I_{K2}	nS	30
g_l	Leakage conductance of current	nS	8
E_{Na}	Sodium reversal voltage	mV	45
E_{K2}	Potassium reversal voltage	mV	-70
E_l	Leakage reversal voltage	mV	-46
V_{K2}^{shift}	Shift of the membrane potential of half-inactivation of I_{K2} from its canonical value	mV	-25.98
τ_{Na}	Time constants of inactivation of I_{Na}	S	0.0405
τ_{K2}	Time constants of activation of I_{K2}	S	0.9

parameters are described in Table 2. As we noted before, we use C as a bifurcation parameter or (B.P.) in system (2).

3 Main results

Now, we replace the parameter values are given in Table 2 in system (2) and compute its equilibrium points. These points are as follows:

$$q_1 = (0.004327, 0.424776, 0), \quad q_2 = (-0.02793, 0.04831, 0.04788).$$

To investigate the dynamical behavior of equilibrium points, we need to get the Jacobian matrix of system (2) at these points. For this aim, we obtain the Jacobian matrix of system (2) as follows:

$$\begin{pmatrix} -\frac{200z}{(a+1)^3} - \frac{90000a(x-0.045)z}{(a+1)^4} - 30y^2 - 8 & -60(x+0.07)y & -\frac{200(x-0.045)}{(a+1)^3} \\ \frac{92.2222Ce^{-83(x-0.00798)}}{(e^{-83(x-0.00798)}+1)^2} & -1.11111C & 0 \\ -\frac{12345.7Ce^{500(x+0.03391)}}{(e^{500(x+0.03391)}+1)^2} & 0 & -24.6914C \end{pmatrix},$$

where $(V, m_{K2}, h_{Na}) = (x, y, z)$ and $a = e^{-150(x+0.0305)}$. The Jacobian matrix and the characteristic equation of system 2 at q_1 and q_2 are computed below

- at q_1

$$A_{q_1}(C) = \begin{pmatrix} -13.4131 & -1.89443 & 8.00404 \\ 22.5345C & -1.11111C & 0 \\ -0.0000613486C & 0 & -24.6914C \end{pmatrix},$$

$$P_{q_1}(\lambda, C) = 1422.06C^2 + (27.4349C^2 + 388.782C)\lambda + (13.4131 + 25.8025C)\lambda^2 + \lambda^3,$$

- at q_2

$$A_{q_2}(c) = \begin{pmatrix} 16.7353 & -0.121944 & 3.07555 \\ 4.24029C & -1.11111C & 0 \\ -562.805C & 0 & -24.6914C \end{pmatrix},$$

$$P_{q_2}(\lambda, c) = 1476.9C^2 + (1299.64C + 27.4349C^2)\lambda + (25.8025C - 16.7353)\lambda^2 + \lambda^3.$$

Now, we investigate the stability of equilibria by the Routh–Hurwitz criterion. Therefore we need to compute $L_i(C), i = 1, 2$ and find where the coefficients of the characteristic polynomials are positive. In the following, we denote the coefficients of $P_{q_i}(\lambda, C)$ by P_{ij} , where j shows the power of λ parameter. Hence the Routh–Hurwitz criterion holds for $P_{q_1}(\lambda, C)$ if

$$\begin{aligned}
P_{10} &= 1422.06C^2 > 0; \\
P_{11} &= 27.4349C^2 + 388.782C > 0; \\
P_{12} &= 25.8025C + 13.4654 > 0; \\
P_{13} &= 1 > 0;
\end{aligned}$$

- $D_1(C) = \det(L_1(C)) = p_1(C) = 27.4349C^2 + 388.782C > 0;$
- $D_2(C) = \det(L_2(C))$
 $= \det \begin{pmatrix} 27.4349C^2 + 388.782C & 1422.06C^2 \\ 1 & 25.8025C + 13.4654 \end{pmatrix} > 0.$

We have similar conditions for $P_{q_2}(\lambda, C)$ as follows:

$$\begin{aligned}
P_{20} &= 1476.9C^2 > 0; \\
P_{21} &= 27.4349C^2 + 1299.64C > 0; \\
P_{22} &= 25.8025C - 16.7353 > 0; \\
P_{23} &= 1 > 0;
\end{aligned}$$

- $D_1(C) = \det(L_1(C)) = p_1(C) = 27.4349C^2 + 1299.64C > 0;$
- $D_2(C) = \det(L_2(C))$
 $= \det \begin{pmatrix} 27.4349C^2 + 1299.64C & 1476.9C^2 \\ 1 & 25.8025C - 16.7353 \end{pmatrix} > 0.$

By the above computations, we have the following theorem.

Theorem 4. Let $q_1 = (0.00433, 0.42478, 0)$ and $q_2 = (-0.02793, 0.04831, 0.04788)$ be the equilibrium points of system (2). Then

1. q_1 is unstable for $0 < C \leq 1$,
2. q_2 is stable for $C > 0.678033$ and unstable for $C < 0.678033$.

Proof. It is trivial. □

If we put $C_0 = 0.678033$ at $q_2 = (-0.02793, 0.04831, 0.04788)$, then we get the following relations:

$$\begin{aligned}
P_{20}(0.678033) &= 1476.9(0.678033^2) > 0; \\
P_{21}(0.678033) &= 27.4349(0.678033^2) + 1299.64(0.678033) > 0; \\
D_2(0.678033) &= \det \begin{pmatrix} 27.4349C_0^2 + 1299.64C_0 & 1476.9C_0^2 \\ 1 & 25.8025C_0 - 16.7353 \end{pmatrix} \\
&= 707.889C_0^2 + 31597.9C_0 - 21749.9 \simeq 0;
\end{aligned}$$

$$\begin{aligned} \left. \frac{dD_2(C)}{dC} \right|_{C=C_0} &= \left. \frac{d(707.889C^2 + 31597.9C - 21749.9)}{dC} \right|_{C=0.678033} \\ &= 1415.778(0.678033) + 31597.9 \neq 0. \end{aligned}$$

Therefore, according to these results we can state the following theorem.

Theorem 5. Suppose that for $C_0 = 678033$ and equilibrium point $q = q_2$ of system (2) the following relations satisfy:

1. $P_{20}(C_0) = 1476.9C_0^2 > 0$;
2. $P_{21} = 27.4349C^2 + 1299.64C_0 > 0$;
3. $D_2(C_0) \simeq 0$;
4. $\left. \frac{dD_2(C)}{dC} \right|_{C=C_0} \neq 0$.

Then C_0 is a simple Hopf bifurcation value for system (2) at the equilibrium point $q = q_2$.

4 Numerical simulation

In this section, several numerical simulations are presented to verify the efficiency of our analytical results. In addition, we draw the bifurcation diagram that shows periodic orbits crossing the plane $V = -0.025$. The simulation parameter values are shown in Table 3. We study the stability of the system's equilibrium points for particular C parameter values satisfying Theorems 4 and 5.

If we consider the starting point $p_1 = (0.0043, 0.42, 0.0001)$ near equilib-

Table 3: C parameters values and initial values

C	Initial value	Figure
0.64	(0.004,0.413,0.001)	Figure 1
0.685	(-0.0266,0.0478,0.0475)	Figure 2
0.6	(-0.0266,0.0478,0.0475)	Figure 3

rium point q_1 , for $C = 0.64$, then it is observed that the equilibrium point is unstable; see Figure 1.

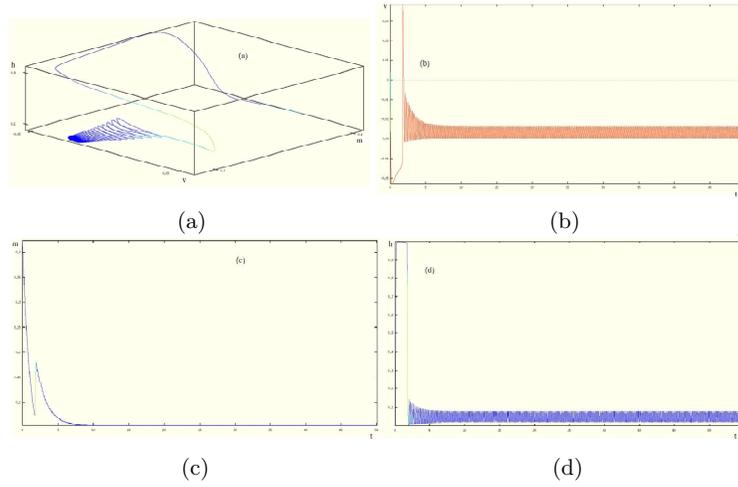


Figure 1: (a). Phase portrait in the space (V, m_{K2}, h_{Na}) at $(0.0043, 0.42, 0.0001)$ and $C = 0.64$. (b), (c), and (d). Time history of the neuronal model in terms of V, m_{K2} and h_{Na} , respectively.

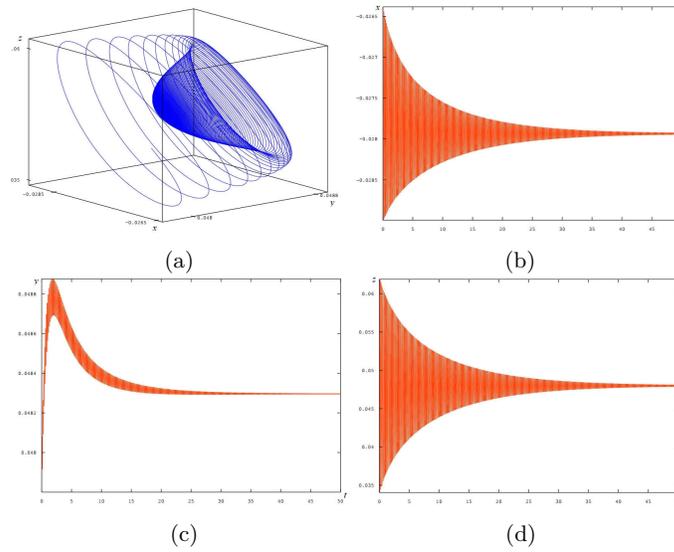


Figure 2: (a). Phase portrait in the space (V, m_{K2}, h_{Na}) at $(-0.0266, 0.0478, 0.0475)$ and $C = 0.685$. (b), (c), and (d). Time history of the neuronal model in terms of V, m_{K2} and h_{Na} , respectively.

Now suppose that the starting point $p_2 = (-0.0266, 0.0478, 0.0475)$ near equilibrium point q_2 , for parameter $C = 0.64$. Then it is observed that the equilibrium point is unstable; see Figure 2.

Therefore, by Theorem 5, $C_0 = 0.678033$ is a Hopf bifurcation value

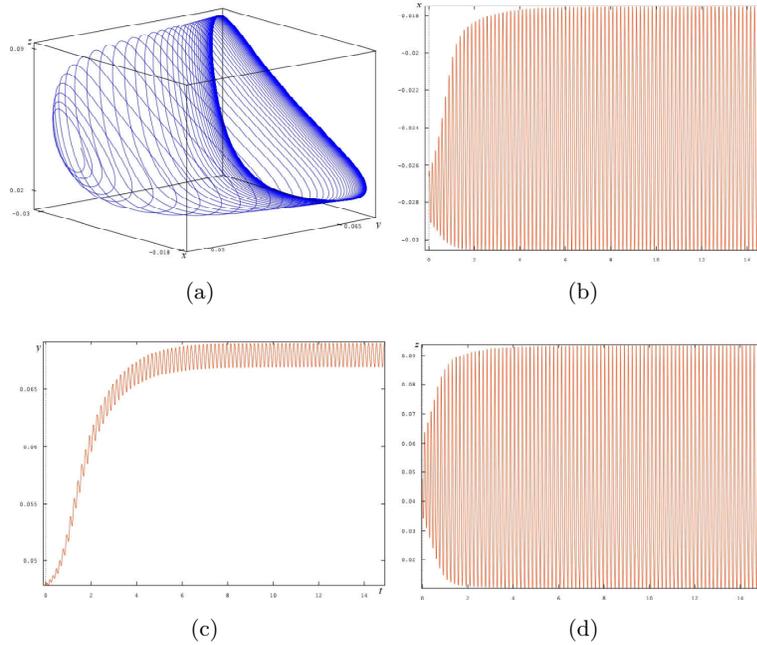


Figure 3: (a). Phase portrait in the space (V, m_{K2}, h_{Na}) at $(-0.0266, 0.0478, 0.0475)$ and $C = 0.6$. (b), (c), and (d). Oscillatory waveforms generated by the neuron model (2) in terms of V, m_{K2} and h_{Na} , respectively.

for equilibrium q_2 of leech heart interneuron model. Furthermore, for C_0 , the Jacobian matrix $A_{q_2}(C_0)$ has a pair of pure imaginary eigenvalues $\lambda_1; \lambda_2 \simeq \pm 29.842209i$, and a negative real eigenvalues $\lambda_3 = -0.762921$.

We solved equation (2) by means of the fourth and fifth-order Runge–Kutta (RK-45) method. To show the occurrence of Hopf bifurcation, we present some numerical simulations. The related trajectories in the phase space (V, m_{K2}, h_{Na}) and the oscillatory waveforms generated by the neuronal model (2) for different values of parameter C are presented in Figures 3 and 4.

In Figure 5, we show that by considering a fixed point and changing C , the periodic orbit at the bifurcation value disappeared. As it is illustrated in Figure 4, the equilibrium point

$$q_2 = (-0.02793, 0.04831, 0.04788)$$

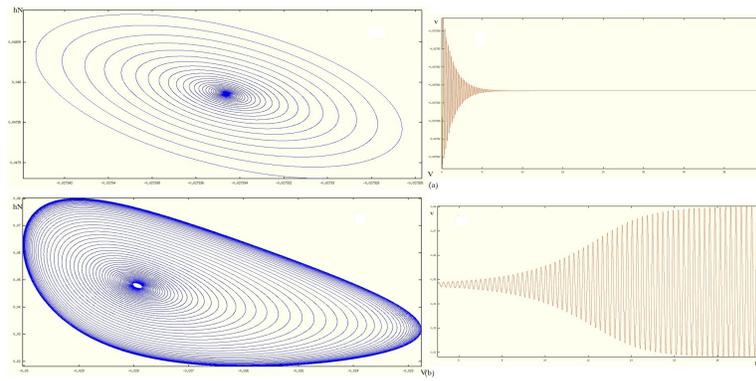


Figure 4: Comparison between phase portraits and oscillatory waveforms in (V, h_{Na}) -space for $C = 0.645$ and $C = 0.72$.

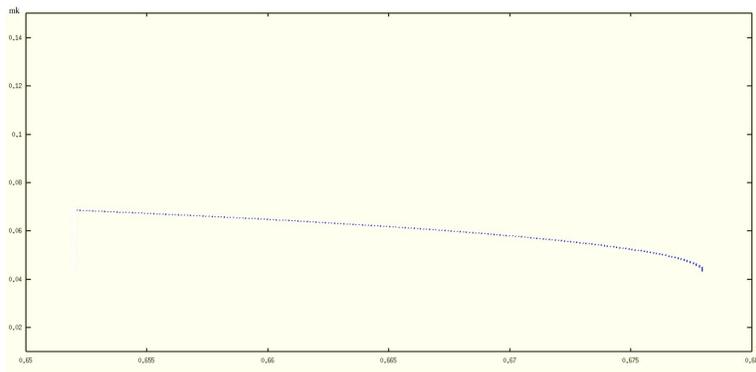


Figure 5: Bifurcation diagram of system (2)

is a stable focus when the membrane capacitance is bigger than C_0 . In this case, through time, the amplitude of oscillatory waveforms will vanish. While for $C < C_0$, the equilibrium point q_2 turns out to be an unstable focus surrounded by a stable limit cycle.

This subsystem exhibits either tonic spiking, which corresponds to a stable limit cycle or quiescence which corresponds to a stable equilibrium point. Stability loss of the stable limit cycle in the fast subsystem gives rise to a stable equilibrium through a supercritical Andronov–Hopf bifurcation. When a stable limit cycle shrinks into an unstable equilibrium, then the equilibrium becomes stable. That is, the equilibrium undergoes supercritical Andronov–Hopf bifurcation.

5 Conclusion

Since finding bifurcations, such as Hopf bifurcations in dynamical systems, is not an easy task, mathematical researchers are looking for computer tools and methods to observe Hopf bifurcations and estimate the number of bifurcation parameters.

In this paper, a leech heart interneurons model has been considered when membrane capacitance is the control parameter. Then by using the Routh–Hurwitz criteria, the sufficient conditions have been examined such that under which the system undergoes supercritical Andronov–Hopf bifurcation. Hence, in this model, the transition between the silent phase and tonic spiking mode was through Hopf bifurcation. Moreover, the authors introduced an interval in the parameters space in which the system has a stable limit cycle in which the neuron is in a tonic spiking mode. Numerical simulations were carried out using the fourth and fifth-order Runge–Kutta method to support our analytical results. In fact, by simulations and Hopf bifurcation theory, we showed that the stable limit cycle could be disappeared.

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