

SIGNALS AND SYSTEMS IN LEARNING AND MEMORY

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Abstract. An oscillation in the brain is characterized by four physical quantities; *amplitude, frequency, phase and entropy*. While the first three quantities correspond to its activity in environment where the background noise is at low levels, the last quantity reveals its state in noisy real world conditions. We explored models pertaining to the first case. As far as functionality of healthy brain is concerned, phase information is most crucial. We report existence of nonlinear oscillations which preserve phase in single neuron systems; modified Morris-Lecar (M-L) and Hindmarsh-Rose (H-R) models. The bifurcation analysis of both single neural systems is presented. The bifurcation scenarios suggest that these systems support interesting dynamical transitions in parameter ranges which are disjoint. Phase-coupled oscillations represented by limit cycles in the phase space of the system and synchronization analysis of the complex network of neuron models are believed to play a crucial role in information transport. The phase-coupled oscillations also plays important role in learning and memory processes. Time trajectories originating for different initial conditions lag behind each other while expected behavior is that these would overlap. The complex connections of network and coupling strength present significant results and which are very efficient to clinical medical research. .

Keywords. Spiking bursting. Morris-Lecar model. Hindmarsh-Rose model. Bifurcation. Phase-coupled oscillations. Network connections. Synchronization.

1 Introduction

Oscillatory brain activity shapes the functional architecture of the working brain. Neuronal networks displaying oscillations in different bands are selectively distributed in the brain. This activity is explored in neuronal models. A memory process involves perception of a sensory input which is similar in information content to already stored in neuronal cells. Basar et al. [1] have argued that sensory perception is the result of interplay between cognition and memory. Rai et al. [2] studied a model based on new kind of oscillations (phase coupled) in brain which carry amplitude, phase and time information. These phase-

coupled oscillations were discovered in an extended version of a Morris-Lecar model [3] which is derived from the Hodgkin-Huxley model [4].

There are three stages of memory: sensory, short-term and long-term [5]. Sensory memory is classified into three categories: visual, auditory and olfactory. Short-term memory stores single or chunked items for 30 seconds without repetition. The reasoning process is an essential component of short-term memory. The learning process [6, 7] involves transfer of information from short to long term memory. Encoding happens while information is repeatedly processed in the hippocampus. In rapid eye movement (REM) [8, 9], memories are replayed and reinforced in the hippocampus. Permanent memory traces are stored where sensory inputs first occurred. They are connected through neuronal networks. Memories are stored in complex neuronal networks spread over the entire brain surface.

Hodgkin and Huxley [4] developed a model for generation of action potential in the axon of the squid in terms of time and voltage-dependent sodium and potassium conductance G_{Na} . is decided by three activation particles m and one inactivating particle h . The potassium conductance is governed by four activating particles, n . It was observed by Fitzhugh and Nagumo [10] independently that the membrane potential, $v(t)$ and sodium activation, $m(t)$ evolves on similar time-scales during action-potentials. On the other hand, sodium inactivation, $h(t)$ and potassium activation, $n(t)$ change on slower time-scales. Fitzhugh-Nagumo model does not serve as a description of dynamic behavior of realistic neurons; e. g., rapid firing of the neuron. Hindmarsh and Rose [11] modified the Fitzhugh-Nagumo model by replacing the linear function, $g(x)$ with a quadratic function. The model produces spikes when being stimulated by a positive current. It is possible to switch between the stable resting state and stable limit cycle by changing the applied current.

A biological neuron does not fire with a constant frequency, but the firing slows down in due course of time and eventually terminates. This is called firing frequency adaptation [12, 13]. This is achieved by adding an extra variable to the two dimensional system of Hindmarsh-Rose dynamical equations. This extra variable represents a slowly varying hyperpolarizing current. Suitable choices of model parameters lead to biological phenomenon of bursting and chaotic bursting. While the activity of neu-

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rons alternates between a quiescent state and repetitive spiking, the activity is called bursting. Generally it is caused by a slow voltage or calcium dependent process that can modulate fast spiking activity. The two important bifurcations associated with bursting are: bifurcation of a quiescent state that leads to repetitive spiking and bifurcation of a spiking attractor that leads to quiescence [14].

The synchronization analysis of neural networks has been very important problem in computational neuroscience. The complex behavior of connections of network and the coupling mechanism synchronization present significant results and very efficient to clinical research such as epilepsy and Parkinsons disease. The spiking and different types bursting behavior are the characteristics and nonlinear phenomena of the neurons [15]. Neurons information coding is generated by firing action potentials [16]. The bursting behavior of neurons exhibits two types of states between repetitive firing behavior and short resting behavior. The inter spike interval (ISI) plays significant role in information processing [17]. There are some papers [18, 19, 20, 21] in which synchronization of neuron network were studied. However, it is not completely known the types of connections of neurons in a network and the parameters of the network whether they are identical or nonidentical in the brain. There are mainly two types of coupling chemical and electrical synapses. The chemical synapses can excitatory or inhibitory or both and electrical synapses are bidirectional coupling [20, 22]. Belykh et al. [22] has presented the chemically coupled neuron network that affects the state of the networks. Some types of neural networks, the complete synchronous behavior of a bursting neuron network depends on the coupling strength, network structure and number of neurons [22]. There are other types of neuron networks whose synchronous behavior depends only on coupling strength and network structure [18, 19, 20]. However, we are only interested the bursting neuron networks of identical M-L neurons and H-R neurons in which the coupling strength is the key feature. An algorithm is proposed [19, 20] for numerical simulation of synchronization analysis to present the burst synchronization of network of neurons. In our work, we have observed that the value of minimal coupling strength which is needed to obtain the synchronized behavior depends on the network structure and the number of neurons for a particular set of parameters. We have also reported the bifurcation analysis of two neural systems, demonstrating the phase-coupled oscillations with and without bursting and synchronization of network of M-L and H-R neurons for two types of network structures.

The paper is organized as follows. In section 2, modified Morris-Lecar and 3D Hindmarsh-Rose models are presented. Section 3 is devoted to methodology used to investigate the rich dynamical repertoire of these two models. Section 4 gives an account of the simulations performed. Section 5 discusses about both the neural mod-

els why the models are selected for computation. The last section summarizes salient results obtained during the course of the study and concludes with a few directions for future research.

2 Single neuron models

2.1 Spiking bursting M-L model

Morris-Lecar model is a two dimensional representation of a four dimensional Hodgkin- Huxley system. This reduced order description of a single neuron dynamics is based on the fact that Na^+ conductivity is exceptionally high in comparison to Ca^{+2} and K^+ conductance in the pyramidal cells. Wang et al. [23] proposed and studied bursting and synchronization in an extended Morris-Lecar model which was obtained by adding an extra variable to the two dimensional Morris-Lecar system. This system is described by the set of coupled nonlinear ordinary differential equations [14, 23].

$$\frac{dV}{dt} = 0.5g_{Ca} \left\{ 1 + \tanh \left(\frac{V - V_1}{V_2} \right) \right\} (1 - V) + g_K W (V^K - V) + g_L (V^L - V) + I, \quad (1a),$$

$$\frac{dW}{dt} = \varphi \cosh \left(\frac{V - V_3}{2V_4} \right) \left\{ 0.5 \left(1 + \tanh \left(\frac{V - V_3}{V_4} \right) \right) - W \right\}, \quad (1b),$$

$$\frac{dI}{dt} = -\varepsilon (V_0 + V), \quad (1c),$$

where V is the membrane potential, W is the fraction of open potassium channel at any point of time (i.e., W is the recovery variable: the probability that the potassium channel is conducting). I is the external current being input to the neuronal cell. g_{Ca} , g_K and g_L are conductivities for the population of Calcium, Potassium and Leak channels. V_1 sets the threshold value for the tangent hyperbolic function which measures the rate of change of mean membrane potential due to transport of Calcium ions and V_2 is the steepness parameter for the same function. V_3 and V_4 are midpoint potentials at which the Calcium and Potassium currents are half-activated. φ is a temperature scaling factor. The rate of decay of external current I is assumed to be linearly proportional to the membrane potential. The current I represents relatively slow subsystem that controls fast spiking behavior. The small parameter value ε ($0 < \varepsilon \ll 1$) represents time scale relation between spiking and modulation behavior. There are different types of bursting for different parameter regimes shown by the above neural system. Different bursting behavior occurs by the current parameter I , for different values of ε and the equilibrium potential V^K .

2.2 Hindmarsh-Rose model

The three dimensional model proposed by Hindmarsh and Rose [11, 12] is famous for its bursting behavior. It is

represented by following set of nonlinear ordinary coupled differential equations.

$$\frac{du_1}{dt} = u_2 - u_1^3 + au_1^2 - u_3 + I, \quad (2a)$$

$$\frac{du_2}{dt} = 1 - 5u_1^2 - u_2, \quad (2b)$$

$$\frac{du_3}{dt} = c \{d(u_1 + 1.6) - u_3\}, \quad (2c)$$

where u_1 is the membrane potential, u_2 represents the rate of transport of sodium and potassium ions and the variable u_3 measures the rate of transport of other ions. Sodium and Potassium ions are transported through fast ion channels and other ions are transported through slow ion channels. The parameter a governs bursting and spiking behavior. I is the external current which is a control parameter of the system. c is the parameter which controls the speed of variation of the slow variable u_3 i.e., the efficiency of slow channels in exchanging ions. This parameter also controls the number of spikes per burst. The parameter d governs adaptation. It is a fast-slow system. The first two equations represent the fast subsystem and the last equation corresponds the slow system.

3 Methodology

Values of system parameters are set in such a way that the unmodified Morris-Lecar system performs self-sustained tonic spiking. Since I is a slow variable, parameter ε ($0 < \varepsilon \ll 1$) taken to be 0.001. At the following set of values of the model parameters, the modified Morris-Lecar system performs busting activity with two bursts per spike.

$g_{Ca} = 1.2$, $V_1 = -0.01$, $V_2 = 0.15$, $g_K = 2$, $V^K = -0.7$, $g_L = 0.5$, $V^L = -0.5$, $V_0 = 0.2$, $\varphi = 1/3$, $V_3 = 0.1$, $V_4 = 0.05$ and $\varepsilon = 0.001$.

At this value of the parameter ε , the time series starting from two nearby initial conditions overlap each other. The value of this parameter is varied to investigate single neuron dynamics of the modified Morris-Lecar system. We show phase plane analysis and synchronization analysis of network of neurons for the above parameter values at $\varepsilon = 0.005$. For Hindmarsh-Rose system, the same methodology is followed. At the following set of values of the parameters $a = 3$, $c = 0.003$, $d = 5$, $I = 2.0$, the single neuron system exhibits bursting activity with two bursts per spike. The value of the applied current is varied on both sides of the base value in a specified range. We also present the phase plane analysis and synchronization analysis for network of neurons for the above parameter values with $I = 3.25$.

We now present the stability analysis and bifurcation analysis [24, 25, 26, 27] of both the neural systems through the control parameters. The M-L system has no zero equilibrium point. At the value $\varepsilon = 0.005$, the nonzero equilibrium point is derived. The equilibrium

point is $(V^*, W^*, I^*) = (-0.2, 0.0000061, 0.0441)$. Corresponding variational matrix is given by

$$J_1 = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

where $a_{11} = 0.5g_{Ca}\{-1 + \tanh((V - V_1)/V_2)\} + (1/V_2)(1 - V) \sec h^2((V - V_1)/V_2)\} - g_K W - g_L$, $a_{12} = g_K(V^K - V)$, $a_{13} = 1$, $a_{21} = 0.5(1/V_4)\varphi \cosh((V - V_3)/2V_4) \sec h^2((V - V_3)/V_4) + \varphi(1/2V_4) \sinh((V - V_3)/2V_4)\{0.5(1 + \tanh((V - V_3)/V_4)) - W\}$, $a_{22} = -\varphi \cosh((V - V_3)/2V_4)$, $a_{23} = 0$, $a_{31} = -\mu$, $a_{32} = 0$, $a_{33} = 0$. The value of the above variational matrix at the equilibrium point (V^*, W^*, I^*) is derived to find the eigen values of the matrix. The eigen values are $\lambda_1 = 0.7129$, $\lambda_2 = 0.0070$, $\lambda_3 = -3.3557$. Now, the stability condition of the nonzero equilibrium point of the system is derived. The equilibrium point is a saddle point as λ_1, λ_2 are positive. For the modified Morris-Lecar model system (1a) – (1c), we take the control parameters as V^K and ε . For the Hindmarsh-Rose model system (2a) – (2c), we take the control parameters as I , d and c [28]. Now, we show the Hopf-bifurcation analysis of neural system (2a) – (2c) against the parameter c which controls the speed of variation of the slow variable u_3 at the non zero equilibrium point $(x^*, y^*, z^*) = (-0.9366, -3.3861, 3.3170)$ for the following set of parameter values $a = 3$, $d = 5$, $I = 3.25$. We use the Liu [29] technique to show the bifurcation analysis for the nonlinear neural system (2a) – (2c). The variational matrix about the nonzero equilibrium point is described as follows:

$$J_2 = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

where $a_{11} = -3x^{*2} + 6x^*$, $a_{12} = 1$, $a_{13} = -1$, $a_{21} = -10x^*$, $a_{22} = -1$, $a_{23} = 0$, $a_{31} = 5c$, $a_{32} = 0$, $a_{33} = -c$.

The characteristic equation of the matrix J_2 is given by

$$p(\lambda; c) = \lambda^3 + p_2(c)\lambda^2 + p_1(c)\lambda + p_0(c) = 0$$

where $p_0(c) = -(a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{13}a_{31}a_{22})$, $p_1(c) = -(a_{11}a_{33} - a_{11}a_{22} - a_{22}a_{33} + a_{12}a_{21} + a_{13}a_{31})$, $p_2(c) = -(a_{11} + a_{22} + a_{33})$.

Now, the above expressions are of the form

$$p_0(c) = -\{c((-3x^{*2} + 6x^*) - 10x^* - 5)\},$$

$$p_1(c) = -((-3x^{*2} + 6x^*)(c + 1) - 10x^* - 6c),$$

$$p_2(c) = -((-3x^{*2} + 6x^*) - c - 1).$$

Hopf-bifurcation occurs at $c = c_0$ about the non-zero equilibrium point if the following conditions are satisfied. The conditions are

$$\begin{cases} p_0(c = c_0) > 0, p_1(c = c_0) > 0, \\ A(c = c_0) = p_1(c = c_0)p_2(c = c_0) - p_0(c = c_0) = 0, \\ dA(c = c_0)/dc \neq 0. \end{cases} \quad (3)$$

The non-zero equilibrium point is locally asymptotically stable if $p_0 > 0, p_1 > 0, p_2 > 0$ and $p_1 p_2 - p_0 > 0$ by Routh-Hurwitz condition. The control parameter c appears in the terms a_{31}, a_{33} . We derived the value of c from the condition $A(c = c_0) = p_1 p_2 - p_0 = 0$ (Eq. (3)). The critical value is $c = c_0 = 0.08157$. At this value, all conditions of Eq. (3) are satisfied for the bifurcation analysis which is presented in Fig. 4((i), (ii)). The control parameter c controls the speed of variation of the slow variable u_3 . This parameter controls the difference between fast and slow subsystem of the H-R model i.e., the efficiency of slow channels in exchanging ions. The bifurcation scenario (Fig. 4(i)) presents the behavior of solution of evolution of the parameter c from 0 to 0.09 and for fixed value of $I = 3.25$. It represents reverse period double bifurcations as c takes larger values in the range. The parameter I which controls the dynamics of the model system has been shown in simulation results. Now, a network of coupled n neurons is considered for the structure [19, 20]. The network is supposed for the j -th M-L neuron as

$$\frac{dx_j}{dt} = 0.5g_{Ca} \left\{ 1 + \tanh \left(\frac{x_j - V_1}{V_2} \right) \right\} (1 - x_j) + g_K y_j (V^K - x_j) + g_L (V^L - x_j) + z_j + g_s \sum_k p_{jk} (x_k - x_j), \quad (4a)$$

$$\frac{dy_j}{dt} = \varphi \cosh \left(\frac{x_j - V_3}{2V_4} \right) \left\{ 0.5 \left(1 + \tanh \left(\frac{x_j - V_3}{V_4} \right) \right) - y_j \right\}, \quad (4b)$$

$$\frac{dz_j}{dt} = -\varepsilon (V_0 + x_j). \quad (4c)$$

The above system can be written as

$$\dot{Y}_j = G(Y_j) + g_s \sum_k p_{jk} (Y_k - Y_j) J, \quad (5)$$

where $Y_j = (x_j, y_j, z_j)$ represents the state variables of the j -th neuron of the network system. $G(Y_j) = (g_1(Y_j), g_2(Y_j), g_3(Y_j))$ are the right hand side nonlinear functions of the above system (4a) – (4c). g_s is the coupling strength. J is the 3×3 matrix represents that the neurons in the network are connected with the first state variable. The neurons in the network are coupled through the membrane potential of the neural system,

$$J = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

The $n \times n$ matrix p_{jk} represents that the j -th neuron is connected with the k -th neuron when $j \neq k$. The connection is represented by the elements of p_{jk} . The condition is $p_{jk} = p_{kj} = 1$, if the two neurons are connected, $p_{jk} = p_{kj} = 0$, if not connected. The diagonals of the matrix p_{jk} are represented by the following condition

$$p_{jj} = - \sum_{k=1, k \neq j}^n p_{jk}, \quad j = 1, 2, \dots, n.$$

The most important condition of the synchronized behavior is when state variables of the network system follows the relationship $Y_1(t) = Y_2(t) = \dots = Y_n(t) = Y(t)$ as time tends to infinity. Then the neuron network reaches the synchronization state. The synchronization error system is defined as $e_j = Y_{j+1} - Y_j$, for $j = 1, 2, \dots, n$, where $e_j = (e_{j1}, e_{j2}, e_{j3})$. If all the neurons in the network are synchronized, it is shown that the error e_j tends to zero as time goes to infinity. There are many types of symmetrical network structure such as chain network, ring type network, global network and star network structure etc. In this paper, we are interested in the chain and global type network structure [19, 20, 22]. For an example, it is provided that three neurons are connected through chain and global network. The coupling matrices p_{jk} for different networks are different. Now, the coupling matrices p_{jk} for the connection in the network of $n = 3$

$$\text{neurons are written as } p_{chain} = \begin{pmatrix} -1 & 1 & 0 \\ 1 & -2 & 1 \\ 0 & 1 & -1 \end{pmatrix}$$

$$\text{and } p_{global} = \begin{pmatrix} -n+1 & 1 & 1 \\ 1 & -n+1 & 1 \\ 1 & 1 & -n+1 \end{pmatrix}.$$

The coupling strengths g_s are changed to show the synchronization states for the minimal coupling strength for a particular parameter set of both the neural models. The network of model neurons is chosen as identical. The synchronized behavior depends on the coupling strengths and the network structure. The simulation results of the synchronized behavior of the network system are presented in Section 4.

4 Simulations

Phase space analysis (cf. Figs. 1 and 3) is supplemented with bifurcation diagrams to figure out possibilities of dynamical transitions in the neural system as a system parameter is varied. The complexity of the system presents a challenging suit of new possibilities which are presented in Figs. 2 and 4. Disjoint branches of bifurcation phenomena reveal that the parameter values supporting different dynamical transitions are also disjoint.

Two model systems were extensively simulated to scan for phase-coupled oscillations [2] in these single neuron systems. A distinguishing feature of these nonlinear oscillations is that phase information is preserved while the memories are created and stored. The membrane potential is the relevant variable which is plotted against time. As ε is increased to 0.002, number of bursts per unit spike is reduced and two signals still overlap. Phase-coupled oscillations appear at $\varepsilon = 0.003$. When the value of the parameter ε is increased further, some of the spikes belonging to different signals overlap. At $\varepsilon = 0.006$, two signals overlap each other. At $\varepsilon = 0.007$, number of spikes per burst is reduced while the two signals completely overlap each other. As ε is increased further, phase-coupled

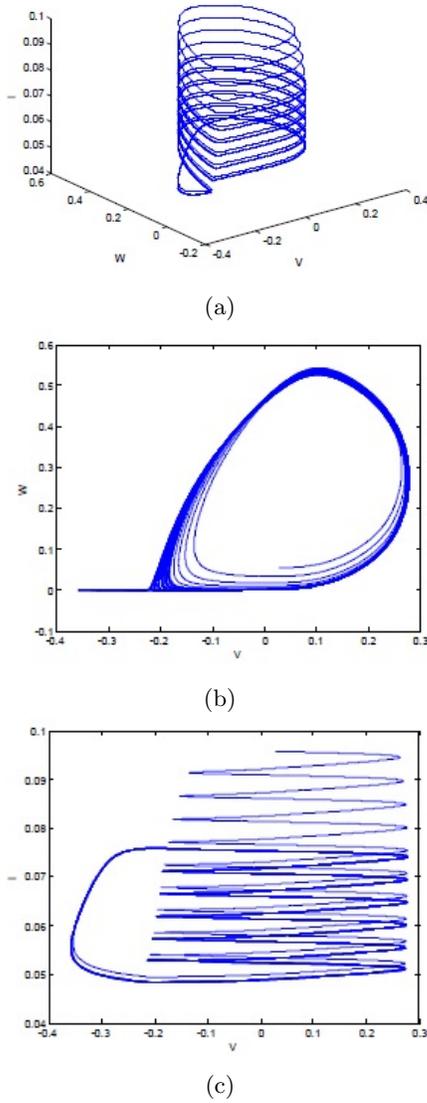


Figure 1: Phase plane analysis of the spiking-bursting neural model system (1a) – (1c). (a) 3D phase plot, (b) phase plot of V vs W and (c) V vs I .

oscillations reappear with less number of bursts per unit spike. Phase-coupled oscillations in the modified Morris-Lecar system are shown in Fig. 5.

As the applied current is decreased to the Hindmarsh-Rose neuron, signals for two nearby initial conditions separate each other. At $I = 1.7$, true phase-coupled oscillations show up. When the value of the applied current is increased, number of bursts per spike is increased with disappearance of phase-coupled oscillations. Phase-coupled oscillations reappear at $I = 2.8$. As the value of the applied current is increased further, number of bursts per unit spike increases for $I = 3.1$. Phase-differences between bursts belonging to two signals are not maintained, thus, the phase-coupling is lost. At $I = 3.7$, chaotic bursting manifests itself. Phase-coupled oscillations reappear at $I = 4.1$ with increased number of bursts per spike. The

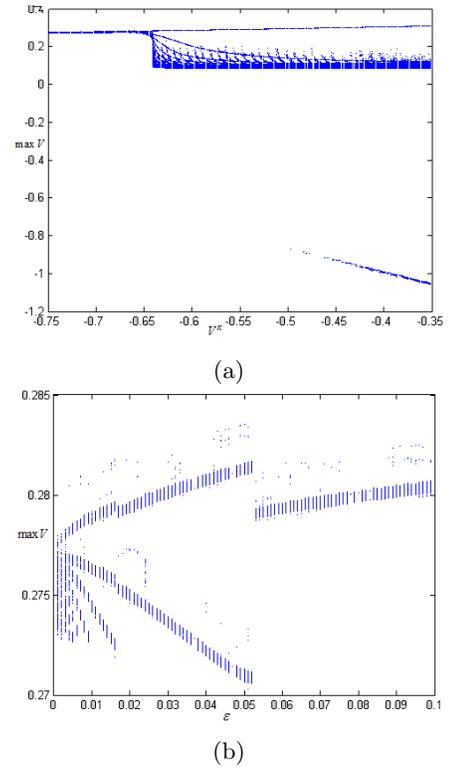


Figure 2: Bifurcation analysis of the spiking-bursting neural model system (1a) – (1c). (a) Bifurcation plot of V^K vs $\max V$ and (b) ε vs $\max V$.

bursting behavior is altogether lost as the applied current is increased further. At $I = 4.3$, tonic spiking is observed. Phase-coupled oscillations without bursting are observed in the interval (4.4, 4.6). Phase-coupled oscillations are shown in Fig. 6.

We are interested in synchronization behavior of network of identical neurons. For the chain network of M-L neurons, the coupling strengths for complete synchronous behavior is $g_s = 2.2$ (Fig. 7) and for global networks the minimal coupling strength is $g_s = 2.3$ (Fig. 9) which are close to each other. The phases of synchronization states are presented in Figs. 8 and 10 which show the targeted synchronization from transition state desynchronization to complete synchronization. The coupling strengths g_s are changed to show the synchronization states for the minimal coupling strength for a particular parameter set of both the identical neural models. For the H-R model only global network scheme is presented to show the synchronous states. As both the network types (chain and global) the complete synchronous states obtain at synaptic coupling strengths close to 0.9 for network of three neurons. The transition states for complete synchronous behavior for different coupling strengths are presented in Fig. 11. The phase plane behavior (Fig. 12) confirms the existence of complete synchronous behavior.

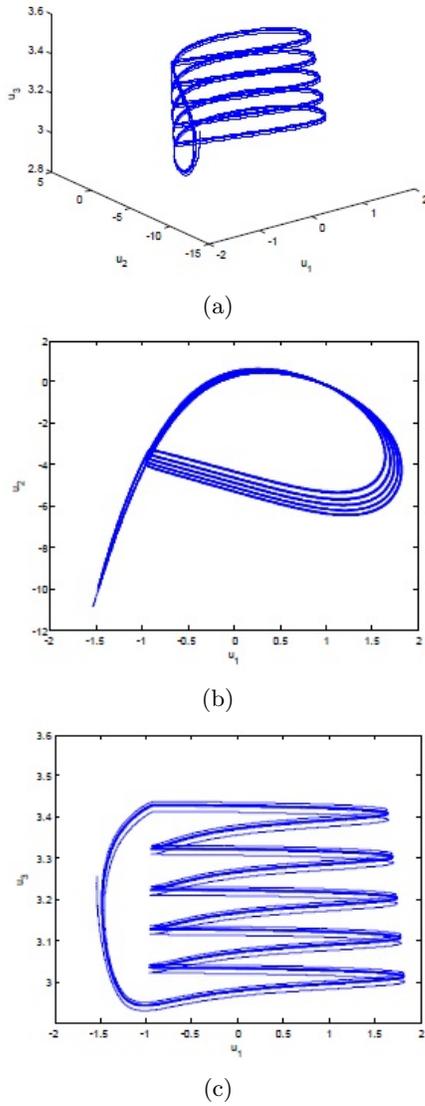


Figure 3: Phase plane analysis of the spiking-bursting neural model system (2a) – (2c). (a) 3D phase plot, (b) phase plot of u_1 vs u_2 and (c) u_1 vs u_3 .

5 Discussion

Bursting is indispensable for information processing and signal transduction. It is also important for intercellular ionic signaling. It consists of periodic clustering of electrical impulses. It occurs in several nerve and endocrine cells; e. g., thalamic neurons, hypothalamic neurons, cortical neurons and the spinal cord. It encodes two time scales. It can amplify neurotransmitter secretion and be helpful in relieving presynaptic inhibition. A neuron is said to be fast-slow burster if the bursting behavior can be expressed as a singularly perturbed model system of the form $\dot{x} = f(x, \mu)$ (for Fast Spiking) and $\dot{y} = \mu g(x, y)$ (for Slow Modulation), where $\mu \ll 1$ represents the ratio of time scale between the two behaviors spiking and modulation. The vector $x \in R^m$ represents relatively fast processes associated with the action potential generation

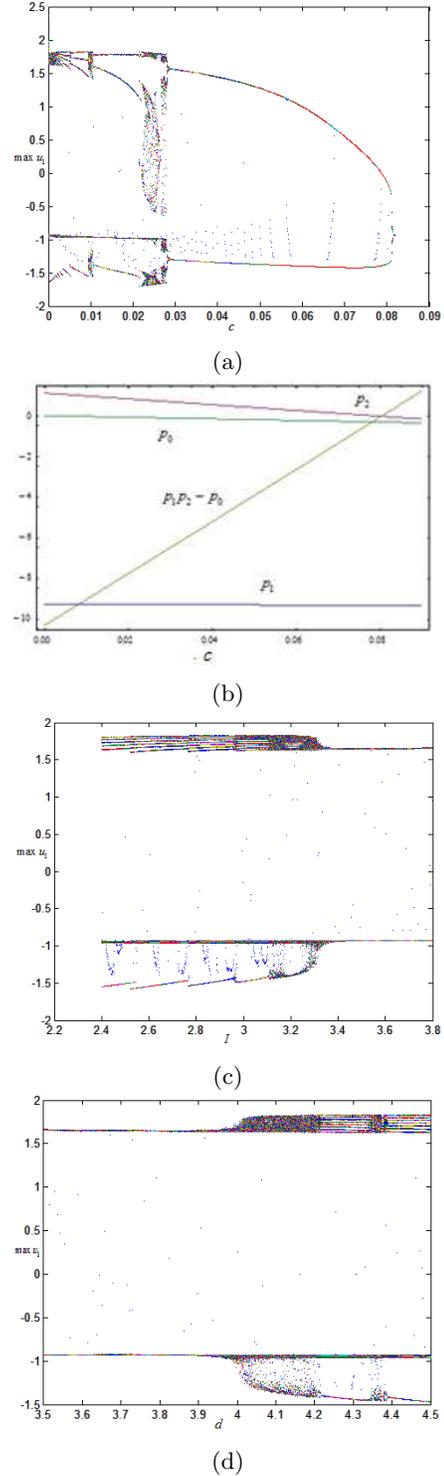


Figure 4: Bifurcation analysis of the spiking-bursting neural model system (2a) – (2c). (a) Bifurcation diagrams of c vs $\max u_1$, (b) parameter c vs $p_0, p_1, p_2, p_1 p_2 - p_0$, (c) I vs $\max u_1$ with $d = 4$ and (d) d vs $\max u_1$ with $I = 3.32$.

and $y \in R^k$ means slow processes that modulate x . Both the fast and slow systems constitute the method of dissection of neuronal bursting [30]. While it is a common

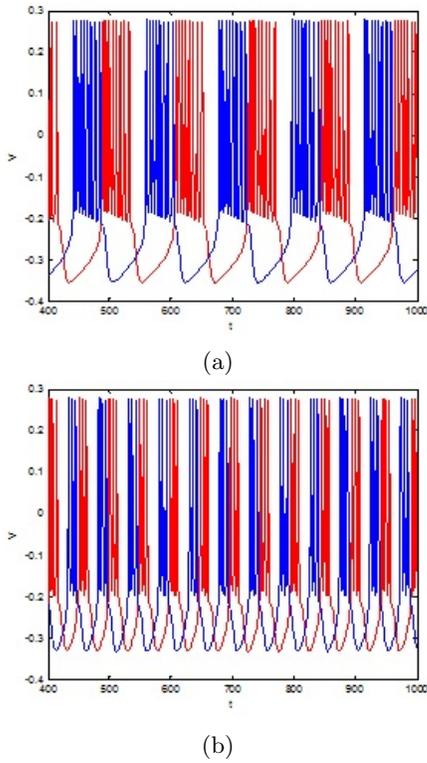


Figure 5: Phase-coupled oscillations in Modified Morris-Lecar Single Neuron system at $\varepsilon = 0.003$ and 0.01 respectively. Red and blue signals are generated for two nearby initial conditions.

neuronal activity, two dimensional models cannot support such a behavior. This is the reason why we consider two three dimensional models with different neurological attributes. In the first, the applied current was taken to be a slow dynamical variable with linear feedback. The other model explored was a Hindmarsh-Rose neuron with an extra variable, which represents bursting. We have reported phase-coupled oscillations with tonic bursting in both modified Morris-Lecar and Hindmarsh-Rose single neurons [31].

These phase-coupled oscillations provide an energy efficient way of information processing in the central nervous system (CNS) [2]. Authors proposed a working memory (WM) model which propounded that PCOs are carriers of information to the Central Executive. These nonlinear oscillations represent stimulus triggered response of different neurotransmitters. The genesis of phase-coupled oscillations can be understood in terms of a single neurotransmitter as well. The functioning of central executive results from interactions of neural networks in different regions of the brain. Populations of Hillar cells encode the identity of the stimulus. The cellular basis of hippocampus dependent memory is represented by stimulus-evoked up-states in the dentate gyrus. The working memory formation in the dentate gyrus is regulated by semilunar granule cells (SCGs) [32].

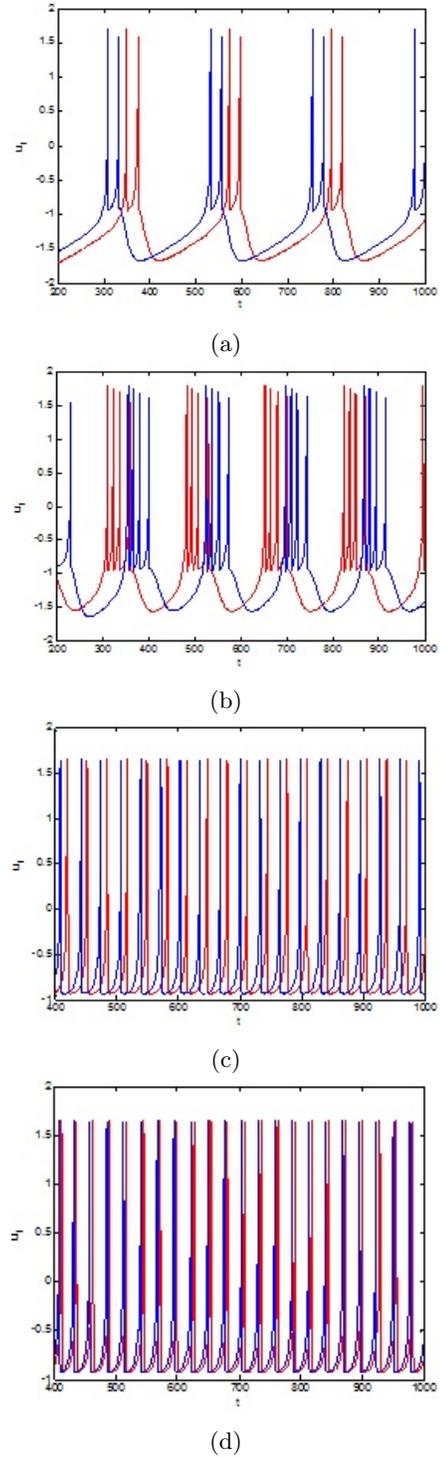


Figure 6: Phase-coupled oscillations in Hindmarsh-Rose Single Neuron system at $I = 1.7, 2.8, 4.4$ and 4.6 respectively. Red and blue signals are generated for two nearby initial conditions.

Now, the biophysical features and mathematical computational efficiencies of the two above mentioned spiking and bursting neural models i.e., M-L and H-R models are discussed for synchronized behavior. The applications of

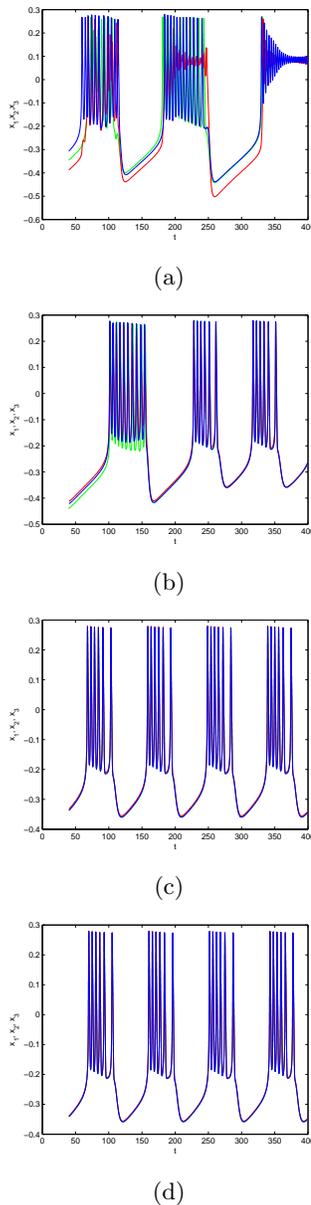


Figure 7: Time series analysis for synchronization behavior of chain network of three M-L neuron system at the coupling strengths $g_s = 0.1, 0.3, 2.1$ and 2.2 respectively. Green, Red and blue signals are generated for three coupled identical neurons.

the two models are investigated and compared by using mathematical simulation results and graphical representations. Many research papers discovered that spike timing pulse-coupled neural networks is an important component for information processing system in the neurons [31].

In the neural network system, there are mainly two important questions. One is what type of neural model is considered for the spiking behavior of the neuron and another is how they are connected with each other. The mathematical neural models (M-L and H-R model)

present neuro-computational behavior of real neurons and have significant contribution in information processing and temporal coding. Two models have many same type features which are efficient in real computational field. The neurons are excitable in nature. When they are stimulated by using dc current they can exhibit different spiking and bursting behavior. M-L and H-R neuron models present tonic spiking and tonic bursting behavior. They are both class I and class II excitable. They have spike latency and sub threshold oscillations for different external stimulus values. They are also integrators. The different spiking behavior is observed in M-L neurons. However, it exhibits tonic bursting behavior when the extra equation is added i.e., the applied stimulus is considered as variable. In real neurons, the tonic spiking behavior is observed in low threshold spiking neurons, regular spiking excitatory neurons [31, 33, 34, 35] etc. For example cat neocortex chattering neurons [36] shows tonic bursting patterns. Some types of neurons such as the neocortical regular spiking excitatory neurons can exhibit low frequency spiking behavior (range 2-200 Hz) for weak stimulus which is called class I excitable neurons [14, 15, 31]. When the neurons present regular spiking behavior only for large frequency input stimulus, they are called class II excitable neurons. Depending on the appropriate choices of the functions and parameters the two above mentioned neural models produce above neuro computational features which are happened in real neurons and since we are concerned with the simulations of the behavior of action potentials. In spite of these above properties of the two neurons both the models have other similar and non similar properties [14, 31] which are not included here.

6 Conclusion

Unlike bi-stability (two different types of dynamical behaviors exist at the same set of parameter values for two different sets of initial conditions), the phase-coupled oscillations are manifested by maintenance of a phase-difference between two signals representing same kind of dynamical behavior. These phase-coupled oscillations [2] were first detected in a Morris-Lecar Neural system which described the interaction of excitatory neuronal cells with local interneurons. The existence of phase-coupled oscillations with bursting behavior of single neurons suggests that these oscillations play a fundamental role in how information is transported and processed in the brain. As bursts are crucial to rectify the synaptic transmission failure and reduction of neuronal noise, they are used in selective communication between neurons [31]. The existence of phase-coupled oscillations in single neuron systems studied in this paper indicates that the bursting neurons play a vital role in communication between networks of cortical neurons. A further research activity would be to study synchronization phenomena between phase-coupled oscillations generated in response to a stimulus in neural networks in different brain regions at the same time. This will help to unearth functional coupling of different brain regions. Many poorly understood aspects of brain dynamics needs to be explored in terms of these new kinds of nonlinear oscillations. The networks of the computationally efficient spiking neurons interconnected through different network structure which are biologically relevant and exposed to how the information is processed in the brain. According to the different characteristics of the computational neuro physiology of brain, the complete patterns and total types of network structures are not explored. Therefore, a realistic and biologically efficient network of spiking neurons can be explored for the information processing system.

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References

- [1] E. Basar, C. Basar-Eroglu, S. Karakas, and M. Schurmann, "Brain Oscillations in Perception and Memory," *Intern. J. Physiol.*, vol. 35, pp. 95-124, 2000.
- [2] V. Rai, S.R. Nadar, and R.A. Khan, "Phase coupled oscillations in the brain: nonlinear phenomena in cellular signaling," *ISRN Biomathematics*, 2013, article I. D. 194239, pp. 1-7, 2013.
- [3] C. Morris and H. Lecar, "Voltage oscillations in the barnacle giant muscle fiber," *Biophysical Journal*, vol. 35, pp. 193-213, 1981.
- [4] A.L. Hodgkin and A.F. Huxley, "A quantitative description of membrane current and application to conduction and excitation in nerve," *J. Physiol. (London)*, vol. 117, pp. 500-544, 1952.
- [5] S.A. Mcleod, "Stages of Memory Encoding, Storage, and Retrieval," Np. 2007, Web Oct. 3, 2014.
- [6] J.R. Anderson, *Learning and Memory: an Integrated Approach*, New York, USA: John Wiley and Sons, Inc., 2000.
- [7] Q. Yu, H. Tang, K.C. Tan, and H. Yu, "A brain-inspired spiking neural network model with temporal encoding and learning," *Neurocomputing*, vol. 138, pp. 3-13, 2014.
- [8] P. Maquet, J. M. Peters, J. Alerts, G. Delfiore, C. Degueldre, A. Luxen, and G. Franck, "Functional Neuro-anatomy of rapid eye movement sleep and dreaming," *Nature*, vol. 383, pp. 163-166, 1996.
- [9] D. Coon and J.O. Mitterer, *Introduction to Psychology: Gateways to Mind and Behavior*, Boston, MA, USA: Cengage Learning, 2013.
- [10] E.M. Izhikevich, *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting*, Cambridge MA, USA: The MIT Press, 2007.
- [11] J. L. Hindmarsh and R.M. Rose, "A model of the nerve impulse using two first order differential equations," *Nature (London)*, vol. 296, pp. 162-164, 1982.
- [12] J. L. Hindmarsh and R.M. Rose, "A model of neuronal bursting using three coupled first order differential equations," *Proc. R. Soc. Lond. Series B*, vol. 221, pp. 87-102, 1984.
- [13] K. Christof, *Biophysics of Computation*, Don Mills, On, Canada: Oxford University Press, pp. 142-172, 1999.
- [14] E.M. Izhikevich, "Neural excitability, spiking and bursting," *Int. J. Bifurc. Chaos*, vol. 10, pp. 1171-1265, 2000.
- [15] E. M Izhikevich, "Bursts as a unit of neural information: selective communication via resonance," *Trends in Neuroscience*, vol. 26. pp. 161-167, 2003.
- [16] J.E Liman, "Bursts as a unit of neural information: making unreliable synapses reliable," *Trends in Neuroscience*, vol. 20, pp. 38-43, 1997.
- [17] W. Ying, X. Jianxue, H. Daihai, and J. Wuyin, "Study on nonlinear characteristics of two synchronizing uncoupled Hindmarsh-Rose neurons," *Acta Physica Sinica*, vol. 54, pp. 3457-3464, 2005.
- [18] N. Corson, S. Balev, and M. A. Aziz-Alaoui, "Detection of Synchronization Phenomena in Networks of Hindmarsh-Rose Neuronal Models," *ECCS'10: European Conference on Complex Systems, Lisbon*, pp.1-6, 2010.
- [19] Q. Jia and Z. Chen, "Coupled network synchronization of non-identical Hindmarsh-Rose model, Modelling, Identification and Control (ICMIC)," *Proceedings of 2011 International Conference*, pp. 246-251, 2011.
- [20] F. J. Zhou, J. Juang, and Y. H. Liang, "Multistate and multistage synchronization of Hindmarsh-Rose neurons with excitatory and electrical synapses," *IEEE Transactions on Circuits and Systems*, vol. 59, pp. 1335-1347, 2012.

- [21] S. R. D. Djeundam, R. Yamapi, G. Filatrella, and T. C. Kofane, "Stability of the synchronized network of Hindmarsh-Rose neuronal models with nearest and global couplings," *Commun. Nonlinear Sci. Numer. Simul.*, vol. 22, pp. 545-563, 2015.
- [22] I. Belykh, E. de Lange, and M. Hasler, "Synchronization of bursting neurons: what matters in the network topology," *Phys. Rev. Lett.*, vol. 94, 188101, 2005.
- [23] H. Wang, Q. Lu, and Q. Wang, "Bursting and synchronization transition in the coupled modified ML neurons," *Commun. Nonlinear Sci. Numer. Simul.*, vol. 13, pp. 1668-1675, 2008.
- [24] J. Zhang, C. Wang, M. Wang, and S. Huang, "Firing patterns transition induced by system size in coupled Hindmarsh-Rose neural system," *Neurocomputing*, vol. 74, pp. 2961-2966, 2011.
- [25] K. Tsumoto, H. Kitajima, T. Yoshinaga, K. Aihara, and H. Kawakami, "Bifurcations in Morris-Lecar neuron model," *Neurocomputing*, vol. 69, pp. 293-316, 2006.
- [26] N. Corson, M. A. Aziz-Alaoui, R. Ghnemat, S. Balev, and C. Bertelle, "Modelling the Dynamics of Complex Interaction Systems: from Morphogenesis to Control," *Int. J. Bifur. Chaos*, vol. 22, 1250025, 2012.
- [27] S.R. D. Djeundam, R. Yamapi, T. C. Kofane, and M.A. Aziz-Alaoui, "Deterministic and stochastic bifurcations in the Hindmarsh-Rose neuronal model with and without random signal," *CHAOS. An Interdisciplinary Journal of Nonlinear Science*, vol. 23, 033125, 2013.
- [28] N. Corson and M. A. Aziz-Alaoui, "Asymptotic Dynamics for Slow-Fast Hindmarsh-Rose Neuronal System," *Dynamics of Continuous, Discrete and Impulsive Systems, series B*, vol. 16, pp. 535-549, 2009.
- [29] W. M. Liu, "Criterion of Hopf-bifurcations without using eigen values", *J. Math. Anal. Appl.*, vol. 182, pp. 250-256, 1994.
- [30] J. Rinzel and Y. S. Lee, "Dissection of a model for neuronal parabolic bursting," *J. Math. Biol.*, vol. 25, pp. 653-675, 1987.
- [31] E. M. Izhikevich, "Which model to use for cortical spiking neurons?," *IEEE Trans. neural netw.*, vol. 15, pp. 1063-1070, 2004.
- [32] D.D. Fraser and B.A. Macvicar, "Cholinergic dependent plateau potential in hippocampus CA1 pyramidal neurons," *J. Neurosci.*, vol. 16, pp. 4113-4128, 1996.
- [33] B. W. Connors and M. J. Gutnick, "Intrinsic firing patterns of diverse neocortical neurons," *Trends Neurosci.*, vol. 13, pp. 99-104, 1990.
- [34] J. R. Gibson, M. Belerlein, and B. W. Connors, "Two networks of electrically coupled inhibitory neurons in neocortex," *Nature*, vol. 402, pp. 75-79, 1999.
- [35] J. Rinzel and G. B. Ermentrout, *Analysis of neural excitability and oscillations*, in *Methods in Neuronal Modeling*, C. Koch and I. Segev, Eds. Cambridge, MA: MIT Press, 1989.
- [36] C. M. Gray and D. A. McCormick, "Chattering cells: Superficial pyramidal neurons contributing to the generation of synchronous oscillations in the visual cortex," *Science*, vol. 274, pp. 109-113, 1996.

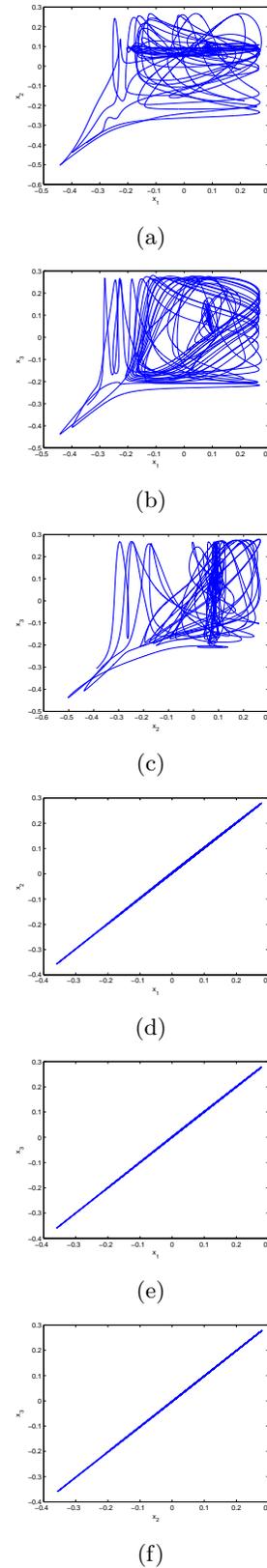


Figure 8: Phase-plane analysis of the chain network of three identical M-L neural system. First three diagrams are the phase plane scenarios for $g_s = 0.1$ and last three for $g_s = 2.2$ respectively.

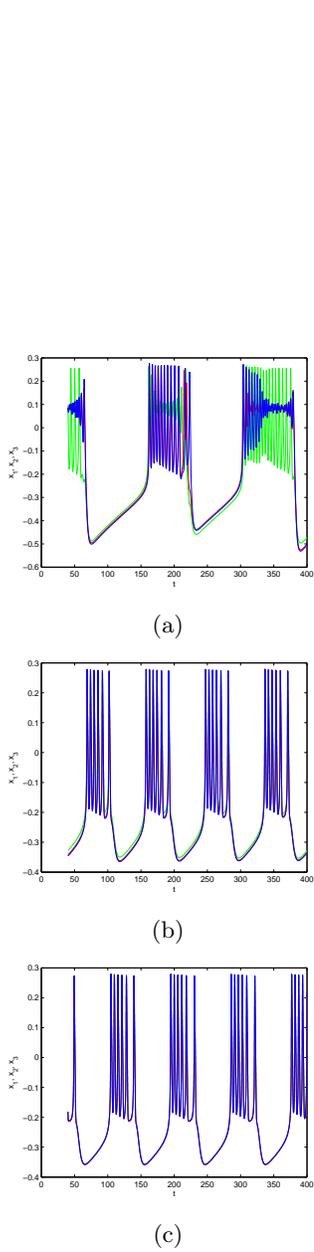


Figure 9: Time series analysis for synchronization behavior of global network of three M-L neuron system at the coupling strengths $g_s = 0.1, 0.7$ and 2.3 respectively. Green, Red and blue signals are generated for three coupled identical neurons.

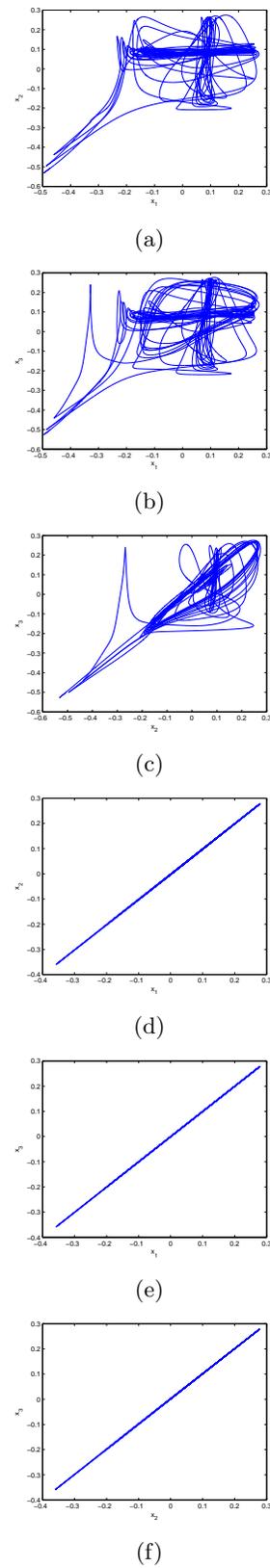


Figure 10: Phase-plane analysis of the global network of three identical M-L neural system. First three diagrams are the phase plane scenarios for $g_s = 0.1$ and last three for $g_s = 2.3$ respectively.

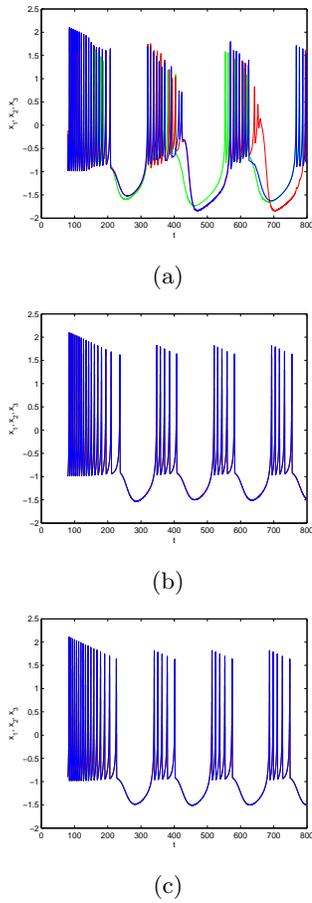


Figure 11: Time series analysis for synchronization behavior of global network of three H-R neuron system at the coupling strengths $g_s = 0.1, 0.6$ and 0.9 respectively. Green, Red and blue signals are generated for three coupled identical neurons.

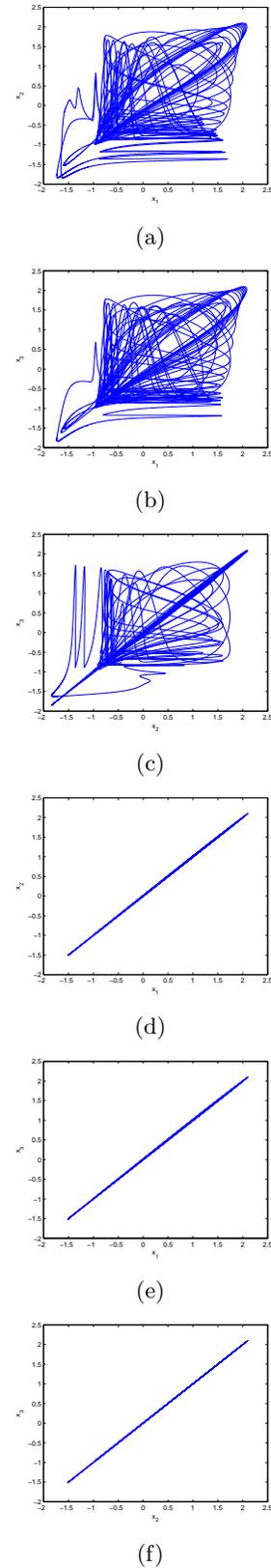


Figure 12: Phase-plane analysis of the global network of three identical H-R neural system. First three diagrams are the phase plane scenarios for $g_s = 0.1$ and last three for $g_s = 0.9$ respectively.