

Phase switching in Hindmarsh-Rose relay neurons

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Abstract. A system of Hindmarsh-Rose relay neurons with time delay coupling is considered in which the relay (central) neuron has an additional feedback term that represents the interaction activity with a local environment. The strength of environmental coupling with the central neuron plays an important role in inducing synchronization and de-synchronization between the outer neurons. The strength of feedback developed from the environmental coupling has created a gradual quenching in the oscillations of the central neuron. At a higher feedback coupling strength, oscillation of the central neuron is suppressed drastically and a transition from a regime of synchronization to out-of-phase synchronization take place between the oscillations of the two outer neurons.

1 Introduction

The phenomenon of synchronization is ubiquitous in neuronal systems [1]. Synchronization of neuronal activity in cortical areas is thought to underlie many aspects of cognition [2,3] and it has been proposed as an integrative mechanism, by bringing widely distributed neurons in order to have a coherent output [4]. Studies investigating interplay between topology and dynamics in complex networks have shown that certain network motifs combined with the intrinsic dynamics of the nodes, and the rules of interaction between them govern the kind of dynamical activities that are possible on the network [5].

Occurrences of synchronization in brain rhythms such as gamma and theta oscillations between spatially separated brain areas suggested that stable information processing between two hemispheres is achieved through thalamus by relaying signals [6]. This hypothesis is supported by the anatomical structure of brain. There are thick band of nerve fibers called corpus callosum through which the two hemispheres of the brain communicate through thalamus, and relay signals to the cerebral cortex [6,7]. Experiments with lasers and neuronal oscillators that are not directly coupled but through a relay have also shown that synchronization could arise between spatially separated oscillators, when time-delays are incorporated in the coupling [8–11]. Time delays arise in natural systems due to finite velocity of the propagation of signals, and delays are abundant in neuronal systems.

In contrast to phenomenon of synchronization, coupled natural systems can also exhibit another phenomenon called amplitude death where the oscillations of coupled

system are quenched [12,13]. Examples of amplitude death in natural systems can be drawn from chemical systems, electronic systems, neuronal systems etc. [12]. Theoretical and experimental studies have shown that time-delay has induced amplitude death in a network of coupled identical oscillators [14,15]. When the network consists of dissimilar oscillators, a dynamical regime known as partial amplitude death can exist where oscillations in some part of the network are quenched while the rest continue to oscillate [16].

In many physical or biological systems, environment plays an important role in changing the activity of a system. In neurodegenerative disease like Alzheimer, neuronal activities are found to be suppressed in some parts of the brain thereby indicating that some of the brain cells are failed to perform their respective activities. What exactly causes the failure of neurons in Alzheimer's disease is not yet completely known. However, various experiments have established that production of certain proteins like Beta-Amyloid and Tau proteins lead to the accumulation over some groups of neurons that might cause this disorder [17]. It has been shown that dipole moments can be induced in such proteins by the electrical activities of the neurons [18], and these induced activities make a feedback loop to affect the electrical properties of neurons. More production and accumulation of these proteins on neurons lead to the death of nerve cells [17].

Motivated by the physiological evidence of Alzheimer's disease, this paper studies the effects of environmental coupling to a group of identical neurons operating in time-delay relay network. Neural activity is a co-operative process of neurons, where information transfer between them takes place with finite speed. This finite speed of signal transmission over a distance give rise to a finite delay e.g. the speed of signal conduction through unmyelinated axonal fibers is of the order of 1 ms resulting in the time delay of upto about 100 ms for propagation through cortical network. Thus, consideration of time delay in the network of neurons is a more realistic way.

This study has shown that environmental coupling to the central neuron of the relay network can induce partial amplitude death (gradual quenching of oscillation of the central oscillation) [16] leading to various dynamical regimes of synchronization and desynchronization between spatial separated oscillators. This partial amplitude death occurs during the time when the oscillation of the central neuron is suppressed by the feedback coupling with an external environment [17]. However, oscillations of the spatially separated neurons remain intact with a phase lag. In the relay network, even though identical neurons were considered as the dynamical units, the presence of feedback term to central neuron makes the system appear to be inhomogeneous. The already existing framework of time-delay coupling of dissimilar oscillators [16] allowed us to understand the occurrence of partial amplitude death. However, it did not explicitly provide any information about the coupling scheme between a system and a local environment. And there were no information about phase relationships of the oscillators.

In the present study, we study a model of time delay relay network of Hindmarsh-Rose (HR) neurons with a simple linear feedback coupling and illustrate the findings through numerical simulations. We have shown that a simple direct environmental coupling is also effective in order to induce partial amplitude death in a relay network system thereby resulted into the presence of a phase shift between spatially separated oscillators. In this paper, we will show the results of numerical simulations of the system and investigate the dynamics involved through the computation of Lyapunov exponents of the coupled HR neurons together with the feedback coupling.

The paper is organized as follows: An equation of time-delay coupled nonlinear systems and a scheme of environmental coupling is considered in Sect. 2. In Sect. 3, the study of dynamical behavior of time-delay coupled Hindmarsh-Rose relay neurons

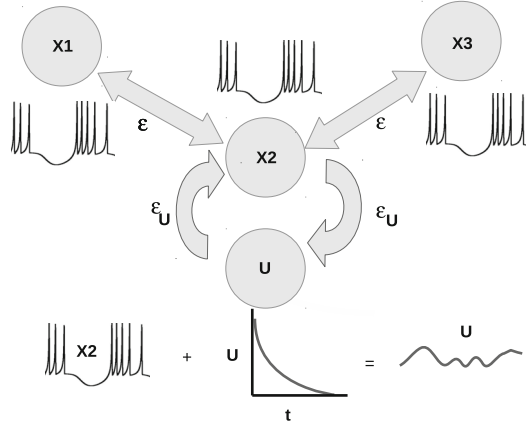


Fig. 1. A schematic representation of a system consisting of three relay neurons are shown where, the central neuron interacts with a local environment. The electrical activity of the central neuron induces dipole moments to the surrounding medium, which in turn provide an electrical signal back to the neuron forming a closed loop and this interaction also enables to keep the activities of the surrounding medium in a sustainable way. However, the activity of such local medium will decay in case of the absence of this interaction.

with environmental coupling and its results are given in Sect. 4. And, summary and discussion are given in Sect. 6.

2 Relay oscillators with feedback environmental coupling

Biological systems at phenomenological level interact with each other via diffusive process and signals are propagated with finite velocity. A system of time delay coupled relay oscillators can be defined by the following set of equations,

$$\begin{aligned}
 \frac{d\mathbf{X}_1}{dt} &= \mathbf{F}(\mathbf{X}_1, \mathbf{p}) + \varepsilon(\mathbf{X}_2(t - \tau) - \mathbf{X}_1(t)) \\
 \frac{d\mathbf{X}_2}{dt} &= \mathbf{F}(\mathbf{X}_2, \mathbf{p}) + \varepsilon(\mathbf{X}_1(t - \tau) - \mathbf{X}_2(t)) + \varepsilon(\mathbf{X}_3(t - \tau) - \mathbf{X}_2(t)) \\
 \frac{d\mathbf{X}_3}{dt} &= \mathbf{F}(\mathbf{X}_3, \mathbf{p}) + \varepsilon(\mathbf{X}_2(t - \tau) - \mathbf{X}_3(t))
 \end{aligned} \tag{1}$$

where \mathbf{X}_1 , \mathbf{X}_2 , and \mathbf{X}_3 represent of the three sub-systems in the relay network. Here \mathbf{X}_1 and \mathbf{X}_3 are the outer oscillators while \mathbf{X}_2 acts as the central oscillator. The function \mathbf{F} determines the dynamical evolution and \mathbf{p} represents the parameter that determines the dynamical behavior of each of the oscillators in the system. The strength of interaction is determined by ε , and τ represents the time-delay in the propagation of signals between the oscillators.

In this system, the central oscillator acts as the main component to transmit signal between the peripheral oscillators and therefore, we are interested in understanding the effect of interaction between the surrounding medium and the central oscillator (see Fig. 1). The dynamical equation of the central oscillator with the environmental

coupling is given by

$$\begin{aligned}\frac{d\mathbf{X}_2}{dt} &= \mathbf{F}(\mathbf{X}_2, \mathbf{p}) + \varepsilon((\mathbf{X}_1(\mathbf{t} - \tau) - \mathbf{X}_2(\mathbf{t})) + \varepsilon((\mathbf{X}_3(\mathbf{t} - \tau) - \mathbf{X}_2(\mathbf{t})) + \varepsilon_U \mathbf{U} \\ \frac{d\mathbf{U}}{dt} &= -k\mathbf{U} - \varepsilon_U \mathbf{X}_2\end{aligned}\quad (2)$$

where, the variable \mathbf{U} represents the induced activity at the surrounding medium [19] and ε_U is the strength of interaction arises from the environmental coupling. In the presence of the interaction between the central oscillator and surrounding medium, the dynamics of the surrounding medium has a sustained activity. Without the input from the central oscillator, local activity of the surrounding medium will decay exponentially with a rate k (see Fig. 1).

3 System of Hindmarsh-Rose neurons with feedback environmental coupling

We consider Hindmarsh-Rose (HR) neurons [20] as the dynamical units of the relay system. The two spatially separated HR neurons are described by the following dynamical equations,

$$\begin{aligned}\frac{dx_{1,3}}{dt} &= y_{1,3} - ax_{1,3}^3 + bx_{1,3}^2 - z_{1,3} + I_{ext} \\ \frac{dy_{1,3}}{dt} &= c - dx_{1,3}^2 - y_{1,3} + \varepsilon(y_2(t - \tau) - y_{1,3}(t)) \\ \frac{dz_{1,3}}{dt} &= r[s(x_{1,3} - x_0) - z_{1,3}].\end{aligned}\quad (3)$$

The central neuron together with feedback coupling of local environment is described by the following equations,

$$\begin{aligned}\frac{dx_2}{dt} &= y_2 - ax_2^3 + bx_2^2 - z_2 + I_{ext} + \varepsilon_U U \\ \frac{dy_2}{dt} &= c - dx_2^2 - y_2 + \varepsilon(y_1(t - \tau) - y_2(t)) + \varepsilon(y_3(t - \tau) - y_2(t)) \\ \frac{dz_2}{dt} &= r[s(x_2 - x_0) - z_2] \\ \frac{dU}{dt} &= -kU - \varepsilon_U x_2.\end{aligned}\quad (4)$$

Here, the central neuron induces activities to the surrounding medium, and the surrounding medium provides a feedback to the central neuron establishing a loop in order to affect its membrane voltage. In the above equations, the variable x is the membrane potential, y is the fast current (associated with Na^+ or K^+), and z is the slow current (associated with Ca^+). The system parameters are set at $k = 1$, $a = 1.0$, $b = 3.0$, $c = 1.0$, $d = 5.0$, $s = 4.0$, $r = 0.006$, and $x_0 = -1.60$. I_{ext} is the external current. Depending on the value of I_{ext} , the system shows steady state behavior, periodic spiking, chaotic spiking or bursting. In the parameter range $2.92 < I_{ext} < 3.4$, the system exhibit chaotic behaviour [20]. The behaviors of the uncoupled chaotic HR neurons and decay activity of the local activity are shown in Fig. 4(a) and (b).

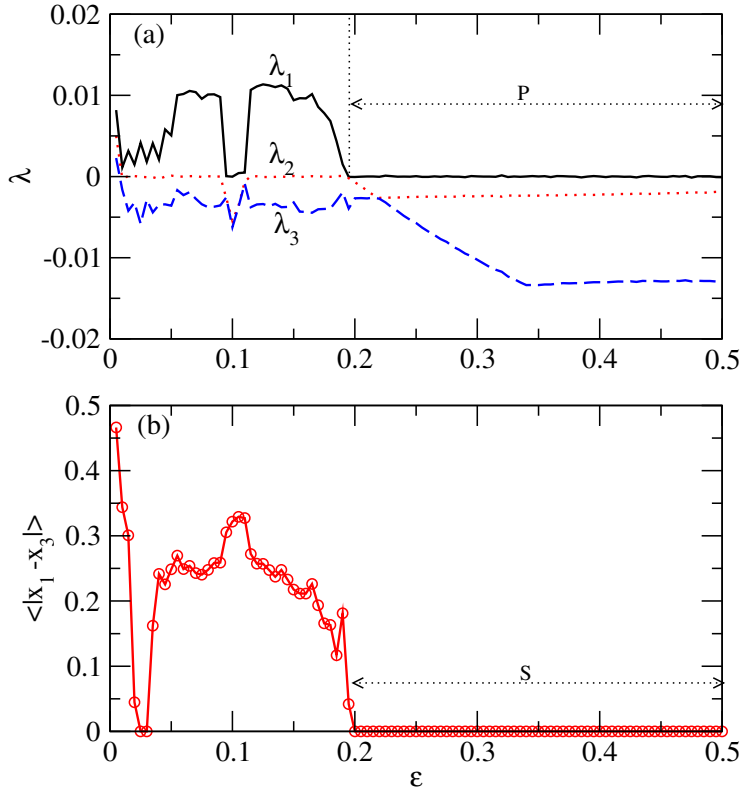


Fig. 2. Dynamics of the three HR relay neurons with time delay coupling ($\tau = 1.5$) showing as a function of coupling strength. (a) Variation of the three largest Lyapunov exponents ($\lambda_1, \lambda_2, \lambda_3$) vs. coupling strength ε . P denotes the periodic regime. (b) Average absolute difference of the membrane voltages of the two outer neurons \mathbf{X}_1 and \mathbf{X}_3 . S denotes the region of synchronization between outer oscillators.

4 Results

4.1 Dynamical behavior of three HR relay neurons without environmental coupling

The presence of time-delay in Eqs. (3) and (4) makes the system infinite dimensional since initial conditions over a continuous interval τ are needed to define a solution. In order to solve the delay differential equations, we employ standard numerical technique [23] and calculated the three largest Lyapunov exponents (LEs) of the system. Each oscillator is set in the chaotic regime at $I_{ext} = 3$ [20] and coupled them with time delay, $\tau = 1.5$. Figure 2 shows the behavior of time delay coupled HR relay neurons as a function of coupling strength ε between them. The behavior of Lyapunov exponents (LEs) are shown in Fig. 2(a) and the average difference of membrane potentials (synchronization error) $\langle |x_1 - x_3| \rangle$ between the outer neurons is shown in Fig. 2(b). This figure articulates that the onset of synchronization is achieved [24] at around the critical coupling strength $\varepsilon \sim 0.2$, where synchronization error goes to zero. At this value of coupling strength, the largest Lyapunov exponent (λ_1) have a transition from positive to zero value, while the second and third largest exponent ($\lambda_{2,3}$) become negative (Fig. 2(a)).

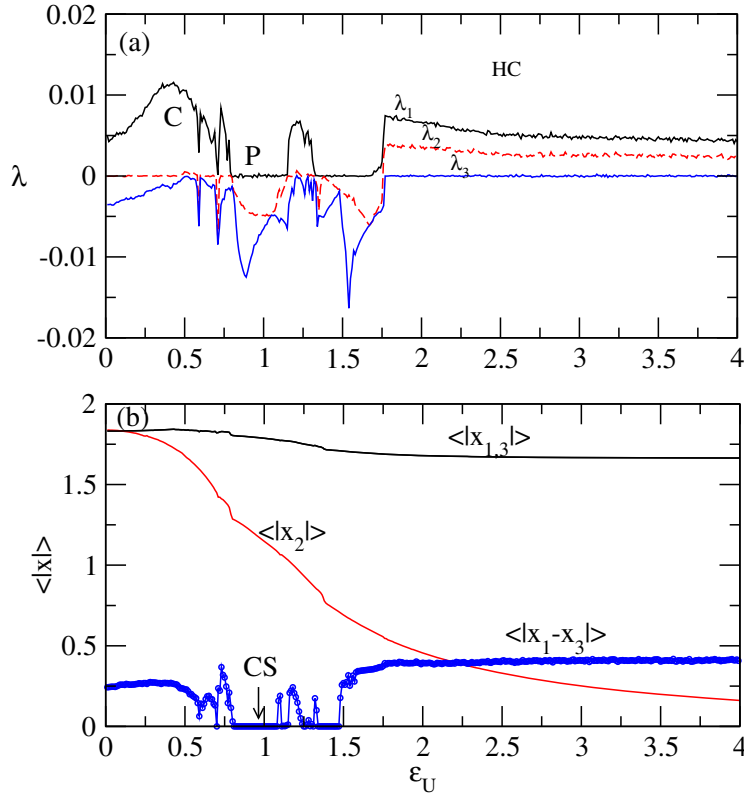


Fig. 3. Dynamics of the global system as a function of the strength of feedback dynamics. (a) Variation of the largest three Lyapunov exponents ($\lambda_1, \lambda_2, \lambda_3$) vs. ε_U . C denotes the regions where the largest Lyapunov exponent is positive (chaotic region), P denotes the regions where $\lambda_1 = 0$ (periodic region), and HC denotes the regions where $\lambda_{1,2} > 0$ (hyperchaotic region). (b) Variation of the maximum value of the membrane voltages (black and red curves) of the three neurons and the average difference (blue curve) of the membrane voltages between spatially separated oscillators.

4.2 Effect of feedback environmental coupling

To study the effect of interactions between the central neuron and the surrounding medium, we set the coupling between the neurons at $\varepsilon = 0.05$ while the HR neurons are operating in chaotic regime (see Fig. 2(a)). All other parameters are kept same as mentioned above. The decay rate of local activity in Eq. (4) is set at $k = 1$.

The variation of largest Lyapunov exponent vs. strength of the feedback environmental coupling ε_u is shown in Fig. 3(a). As the value of ε_u increases, chaotic dynamics ($\lambda_1 > 0$) gets stabilized provided that regions of periodic dynamics ($\lambda_1 = 0$) are appeared. At higher coupling strength, a regime of hyperchaos ($\lambda_{1,2} > 0$) is appeared. The variations of the maximum amplitude of membrane voltages of the three neurons are shown in Fig. 3(b). In this figure, the amplitude of the central neuron is found to be suppressed at a significant level comparing to the amplitudes of the two outer neurons. It is therefore clearly shown that feedback environmental coupling can induce partial amplitude death in the system. The difference of membrane voltages of the two outer neurons $\Delta x = \langle |x_1 - x_3| \rangle$ (blue curve) is also shown in Fig. 3(b).

Synchronization between the two outer neurons is achieved inside the region, where the neurons operate in the established periodic regime (see Fig. 3(a) and (b)). The

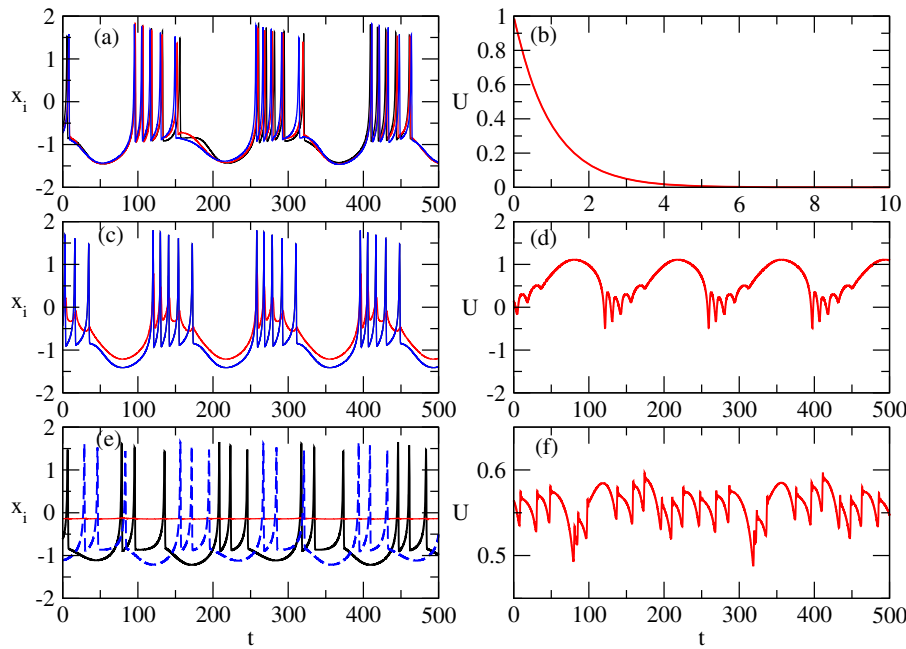


Fig. 4. Membrane voltages of three relay HR neurons and dynamics local environment. The left panel shows the membrane potentials of the neurons at different feedback coupling strength. The right panel shows the behavior of the corresponding dynamics of local environment. (a) Chaotic oscillations of the neurons (blue, red and black colors) at $\varepsilon_U = 0$. (b) Activity of local environment. (c) Oscillations of three relay HR neurons at feedback coupling $\varepsilon_U = 0.916$. The two spatially separated neurons are in complete synchronization (blue and black). The oscillations of the central neuron (red) is now quenched due to the feedback dynamics. (d) Periodic dynamics of induced oscillations at $\varepsilon_U = 0.916$. (e) Out-of-phase oscillations of spatially separated neurons (black and blue dashed lines) and quenched oscillation of central neuron (red) at high feedback coupling $\varepsilon_U = 4$. (f) Chaotic dynamics of induced oscillations at $\varepsilon_U = 4$.

presence of time-delay in the coupling stabilized the unstable periodic orbits (UPOs) which are present in the system [21, 22]. Δx is zero when there is complete synchronization, and Δx has a non-zero value when complete synchronization is disturbed. When parameter mismatch were introduced the neurons or noise added to the external current parameter I_{ext} , complete synchronization were also lost in all cases.

Periodic oscillations of the neurons and sustained activity of the surrounding medium at coupling strength $\varepsilon_u = 0.916$ are shown in Fig. 4(c) and (d) respectively. The quenched oscillation of the central neuron is also shown in Fig. 4(c). As the strength of feedback environmental coupling ε_u increases, amplitude of the central neuron drastically decreases into a consequential transition from a complete synchrony to a regime of phase-lag between the two outer neurons. The behaviour of phase-lag of the two outer neurons at $\varepsilon_u = 4$ is shown in Fig. 4(e). Above, the horizontal line in the figure shows the membrane voltage of the central neuron in a quenched state. This situation where, oscillations of the central neuron are quenched by locally induced feedback dynamics of the surrounding environment though the outer neurons continue to oscillate leads to the phenomenon of partial amplitude death. In addition, the activity of the surrounding environment remains in a chaotic regime at times of partial amplitude death as is shown in Fig. 4(f).

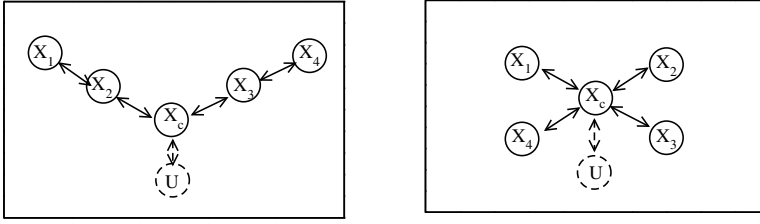


Fig. 5. Schematic diagram of HR neurons in chain and star topology where the central neuron is interacting with the local environment.

4.3 System of five Hindmarsh-Rose neurons where the central neuron interacts with local environment

Many networks occurring in nature are characterized by the presence of hubs as in the case of scale free and star networks where few central nodes (hubs) have large connectivity or links [25,26]. Since we are interested in the study of the effect of feedback environmental coupling to the central neuron of neuronal networks, we now consider networks consisting five HR neurons. Two possible network topologies are linear relay and star networks. Star network is a special relay network where the central oscillator forms the hub of the network and interacts with all other oscillators at periphery.

A schematic representation of these networks where the central neuron is interacting with the surrounding medium is shown in Fig. 5. The similarity and difference of the oscillating patterns of the neurons and the local activity that arises in these networks at various coupling strengths between the central neuron and environment are shown in Fig. 6. The coupling strength between neurons and time delay are kept same as in the case of three neurons ($\varepsilon = 0.05$ and $\tau = 1.5$).

The right and left panels in Fig. 6 show the oscillations of HR neurons in both star and chain networks. This shows that a transition from synchronization to de-synchronization take place between the peripheral neurons at different feedback coupling strengths. At feedback coupling strength $\varepsilon_U = 1$, the peripheral neurons in both star and chain networks are in complete synchronization. Figures 6(a) and (e) show the synchronized oscillations of the peripheral neurons. The oscillations of the central neurons are shown in Fig. 6(b) and (f) respectively. At higher coupling strength $\varepsilon_U = 5$, the oscillations of the central neuron are drastically quenched (see Fig. 6(d) and (h)). These oscillations quenching in central neurons result in de-synchronization between the peripheral neurons in both star and chain networks (see Fig. 6(c) and (d)).

In the case of star network, oscillations of the peripheral neurons are completely de-synchronized. However for the case of chain network, there is a formation of two clusters consisting of two neurons each. Neurons on the left of central oscillator are in one cluster, and neurons on the right are in another cluster. Both neurons in each cluster oscillate in synchrony while neurons in the other clusters oscillate with a phase lag [27,28] as shown in Fig. 6(g). Star network provides an effective topology for synchronization and optimization of output power in the context of optical communications [29].

5 Summary

We have studied the effect of feedback environmental coupling to the central neuron of time delay coupled HR relay neurons. The strength of the feedback interaction

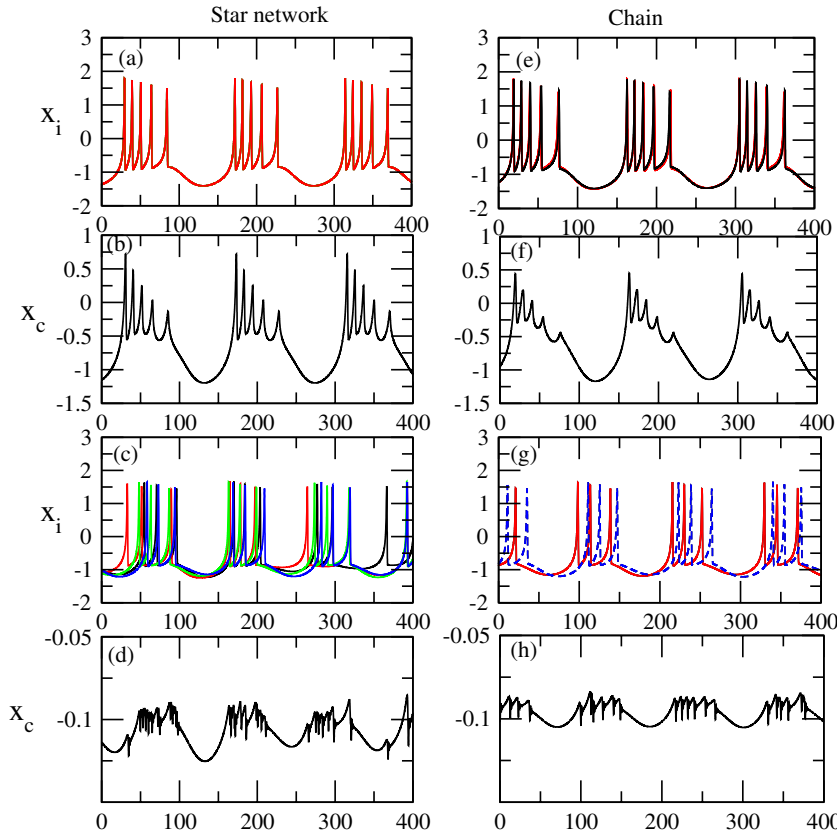


Fig. 6. Dynamics of five HR neurons in relay networks where the central neuron has feedback coupling. Left panels show the oscillations of HR neurons in star network. (a) Synchronized oscillations of peripheral HR neurons in star network at feedback coupling strength $\varepsilon_U = 1$. (b) Oscillations of central neuron at $\varepsilon_U = 1$. (c) Desynchronized oscillations (red, green, blue and black colors) of the peripheral neurons at $\varepsilon_U = 5$. (d) Quenched oscillations of central neuron at $\varepsilon_U = 5$. Right panel show the corresponding oscillations of the HR neurons in chain topology. (e) Synchronized oscillations of peripheral HR neurons and (f) oscillations of central neuron at $\varepsilon_U = 1$. (g) Synchronization of oscillators in two clusters at $\varepsilon_U = 5$. Red and dashed blue lines are the synchronized oscillations in each clusters. (h) Subthreshold oscillations of central neuron at $\varepsilon_U = 5$.

with local environment plays an important role in quenching the oscillations of the central neuron [30] resulting in a dynamical regime of partial amplitude death, and along the route, a transition from synchronization to de-synchronization takes place between the peripheral neurons.

Our study suggest that local external medium can play an important role in switching signals on and off leading to various emergent dynamics and such result may help in understanding gene regulation and control of gaits [31]. A simple linear feedback environmental coupling provides an effective strategy to suppress oscillations in particular node(s) of network, and this mechanism is quite robust.

The dynamical regime of partial amplitude death where there is coexistence of neurons which are oscillating and neuron(s) with quenched oscillations may be a plausible candidate that could bring an insight to understand partial memory loss [32]. Memory loss is associated with the failure of a group of neurons whose

synchronous spiking patterns represent a memory. In this context, failure of a neuron firing resulting to disruption of synchrony in a group of neurons may eventually lead to partial loss of memory. While the knowledge of synchronization [33] is accumulating, understanding of how oscillations are disturbed and how phase switching between groups of neurons emerges from the interaction of neuron(s) and local environment is still immature. Experiments have gone much more rapidly, and there is a need to study the observations through modeling and understand them within the existing theoretical framework. We expect that such study will guide us a way to implement practical application in control as the proposed model is simple and they can be easily implemented.

Recently, reservoir computing (RC) has been implemented by using a single nonlinear node with delayed feedback [34]. In the working paradigm of RC, a higher dimensional system is required to process information between the input and output state. When a single delayed feedback is introduced to a nonlinear node, the state space become infinite dimensional, and such system fulfils the properties of reservoirs for proper operation [34]. Time-delay systems provide an important class of dynamical systems, and we expect many interesting and important applications in the future.

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