ORIGINAL PAPER



Chaotic resonance in Hodgkin-Huxley neuron

Veli Baysal · Zehra Saraç · Ergin Yilmaz

Received: 26 February 2019 / Accepted: 3 June 2019 / Published online: 13 June 2019 © Springer Nature B.V. 2019

Abstract Chaotic Resonance (CR), whereby the response of a nonlinear system to a weak signal can be enhanced by the assistance of chaotic activities that can be intrinsic or extrinsic, has recently been studied widely. In this paper, the effects of extrinsic chaotic signal on the weak signal detection performance of the Hodgkin-Huxley neuron are examined via numerical simulation. The chaotic signal has been derived from Lorenz system and is injected to neuron as a current. Obtained results have revealed that the H-H neuron exhibits CR phenomenon depending on the chaotic current intensity. Also, we have found an optimal chaotic current intensity ensuring the best detection of the weak signal in H-H neuron via CR. In addition, we have calculated the maximal Lyapunov exponent to determine whether the H-H neuron is in chaotic regime. After determining the state of the neuron, we have shown that the H-H neuron can be able to detect the weak signal even if it is in the chaotic regime. Finally, we have investigated the effects of chaotic activity on the collective behavior of H-H neurons in small-world networks and have concluded that CR effect is a robust phenomenon which can be observed both in single neurons and neuronal networks.

V. Baysal · E. Yilmaz (⊠)
Department of Biomedical Engineering, Bülent Ecevit
University, 67100 Zonguldak, Turkey
e-mail: erginyilmaz@yahoo.com

Z. Saraç

Department of Electrical-Electronics Engineering, Bülent Ecevit University, 67100 Zonguldak, Turkey

Keywords Chaotic resonance · H–H neuron · Lorenz system

1 Introduction

The concept of resonance in nonlinear systems can be described by detection of weak signals, believed to carry information, with the help of various kinds of external forcing. A well-known example of this forcing is noise. It is known that the presence of noise in dynamical systems is essential in order for the system response to weak periodic signal to be enhanced by random fluctuations. This phenomenon is known as Stochastic Resonance (SR) [1]. The SR has been found to occur in a wide variety of nonlinear systems, including electrical, optical, mechanical, chemical and biological systems [1–7]. As an example of biological systems, SR is pervasive in nervous system [8–13]. Several experimental and numerical studies showed that neural systems utilize external noise to improve the ability of weak signals detection [14–19].

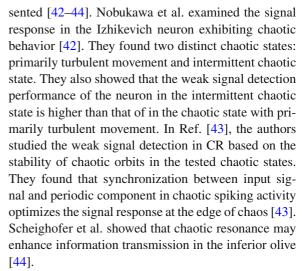
On the other hand, neural units operate over a wide frequency range between low-frequency and high-frequency spiking modes, such as regular spiking and fast spiking, also bursting neurons may exhibit two widely different time scales [20]. This indicates that neurons are under the influence of bichromatic signals. Based on this fact, it has been shown that the response of some dynamical system to a low-frequency weak signal can be optimized via a high-frequency signal,



which can be another candidate for external forcing instead of noise. This phenomenon is called Vibrational Resonance (VR) [21]. The role of VR in different processes of brain is capital, and much attention has been given to this phenomenon in neuroscience [22–24].

In the last few decades, in animal experiments, researchers have observed that temporally irregular firings of neurons are present in both during ongoing spontaneous activity and when driven at high firing rates [25–27]. Moreover, it is believed that most of cognitive brain functions, such as working memory [28], selective attention [29] and sensory coding [30], are fulfilled by irregular neuronal firings. Researchers also observed that chaotic neuronal activity takes place at several hierarchical levels, from the electrical response of a single neuron to the activity of the entire brain [31–34]. Hayashi et al. studied the response of the Onchidium pacemaker neuron to a sinusoidal current [35]. They reported that Onchidium pacemaker neuron exhibits irregular firings including three chaotic states: chaos, intermittency and random alternation. Freeman studied to find an evidence of chaotic itinerancy in human brains via recording of the electroencephalogram (EEG) from the scalp of normal subjects [36–38]. In his various studies, neuronal chaotic itinerancy based on the results of electroencephalogram (EEG) from the scalp of normal subjects was reported. Paul et al. investigated neuronal network oscillations in sleep and wakefulness states via a computational model based on physiological recordings and physiologically realistic parameters of a three-neuron network that consisted of a thalamocortical cell, a thalamic reticular neuron, and a corticothalamic cell [39]. They found that, during the transition period between sleep and wakefulness state, the thalamic and cortical neurons exhibited chaotic dynamics, based on the behaviors of strange attractors, the positive Lyapunov exponents and fractal dimensions of spike trains.

Considering aforementioned studies about chaotic activity in neuronal system, it is evident that neurons are under the influence of chaotic signals. Amplifying the response to a weak signal by the assistance of chaotic activities instead of noise or high-frequency driving is called Chaotic Resonance (CR) [40,41]. The CR occurs through two different ways: One is the use of external chaotic signal instead of noise utilized in SR, and the other is the use of intrinsic chaotic activities in place of external chaotic signal. Recently, many studies of CR based on intrinsic chaotic activities have been pre-



Several neuron models that mimic the behaviors of actual neuron reflect chaotic behavior at appropriate values of system parameters [33,43]. Although neurons are exposed to both external and intrinsic chaotic activity, the effects of external chaotic activity on the weak signal detection performance of the H–H neuron have yet to be investigated. Considering the gap in the literature, in this paper, we have elaborately investigated the effects of external chaotic activity on the weak signal detection performance of the H–H neuron by assuming that the chaotic signal is derived from the Lorenz system.

2 Model and methods

In the presence of a weak signal and a chaotic signal, the H–H model [45] is defined by the below equation:

$$C_{m} \frac{dV}{dt} + g_{K}^{\text{max}} n_{i}^{4} (V - V_{K}) + g_{\text{Na}}^{\text{max}} m^{3} h (V - V_{\text{Na}})$$

+ $g_{L} (V - V_{L}) = I_{\text{syn}} + I_{\text{ext}}$ (1)

where $C_m = 1 \, \mu \, \text{F/cm}^2$ is the capacity and V is the potential of cell membrane. $g_{\text{K}}^{\text{max}} = 36 \, \text{mS/cm}^2$, $g_{\text{Na}}^{\text{max}} = 120 \, \text{mS/cm}^2$ and $g_{\text{L}} = 0.3 \, \text{mS/cm}^2$ denote the maximal potassium, sodium and leakage conductance per unit area of the cell, respectively. $V_{\text{K}} = -12 \, \text{mV}$, $V_{\text{Na}} = 120 \, \text{mV}$, $V_{\text{L}} = 10.6 \, \text{mV}$ are reversal potentials for potassium, sodium and leakage ion channels, respectively. m, h, and n are three gating variables, which obey the following Langevin equation [45]:

$$\frac{\mathrm{d}\gamma}{\mathrm{d}} = \alpha_{\gamma}(V)(1-\gamma) - \beta_{\gamma}(V)\gamma, \quad \gamma = m, \ n, \ h \quad (2)$$



where

$$\alpha_m = \frac{0.1(V+40)}{1 - \exp[(-V+40)/10]} \tag{3}$$

$$\beta_m = 4\exp[-(V + 65)/18] \tag{4}$$

$$\alpha_n = \frac{0.01(V+55)}{1-\exp[(V+55)/10]} \tag{5}$$

$$\beta_n = 0.125 \exp[-(V + 65)/80] \tag{6}$$

$$\alpha_h = 0.07 \exp[-(V + 65)/20)]$$
 (7)

$$\beta_h = \frac{1}{[1 + \exp(-(V + 35)/10)]} \tag{8}$$

In Eq. (1), $I_{\text{ext}} = A\sin(\omega t)$ is the weak signal that is applied to H–H neuron. A is the amplitude, and ω is the frequency of the weak signal. $I_{\rm syn}=I_0+I_{\rm chaos}$ represents the total synaptic input received from environmental neurons and has two parts: the slowly changing part or the constant part (I_0) and the fast changing part (I_{chaos}). At the same time, I_0 controls the excitability level of the neuron. Unless otherwise specified, we set $A = 1 \,\mu\text{A/cm}^2$ and $I_0 = 0$. $I_{\text{chaos}} = \varepsilon x$ denotes the chaotic current which is supposed to stem from the chaotic activities of environmental neurons. ε is chaotic current intensity, and x is external chaotic signal based on Lorenz system. There is no specific reason in choosing Lorenz system as a chaotic signal source. Other chaotic sources can also be utilized. Here, the Lorenz system used for producing the chaotic signal is given by the equations as follows [46].

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \sigma(y - x) \tag{9}$$

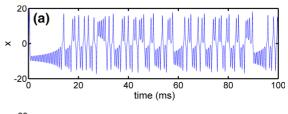
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \rho x - y - xz \tag{10}$$

$$\frac{\mathrm{d}z}{\mathrm{d}t} = xy - \beta z \tag{11}$$

The external chaotic current is obtained from Eq. (9) with the chaotic system parameters of $\beta = 8/3$, $\sigma = 10$, $\rho = 28$. The chaotic signal x produced with Eq. (9) and x - z phase plane are illustrated in Fig. 1.

To quantitatively determine the correlation between the weak periodic signal and the output activity of the H–H neuron in the presence of chaotic signal, we calculate the Fourier coefficient (Q) during N=1000 periods of weak signal as follows [22]:

$$Q_{\sin} = \frac{\omega}{2N\pi} \int_{0}^{2N\pi/\omega} 2V(t)\sin(\omega t) dt$$
 (12)



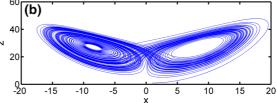


Fig. 1 a Time series of Lorenz system; b Phase diagram of chaotic Lorenz system

$$Q_{\cos} = \frac{\omega}{2N\pi} \int_0^{2N\pi/\omega} 2V(t)\cos(\omega t) dt$$
 (13)

$$Q = \sqrt{Q_{\sin}^2 + Q_{\cos}^2} \tag{14}$$

where ω is the frequency of weak signal. In Eq. (14), the bigger Q means the higher correlation between the weak periodic signal and the output activity of the H–H neuron. To determine whether the H–H neuron is in chaotic regime, we calculate the maximal Lyapunov exponent (λ) during N=21,000 steps as follows.

$$\lambda = \frac{1}{N\delta t} \sum_{i=1}^{N} \ln \frac{\Delta_i}{\Delta} \tag{15}$$

where Δ is a small value added to the initial conditions of the original trajectory. Δ_i is the deviation from the original trajectory at the step i. We use the algorithm given in Ref. [47] to examine the λ . The schematic representation of the calculation procedure for Lyapunov exponent is given in Fig. 2.

To explain the collective behavior of the excitable H–H system under the effects of chaotic activity, we use the Newman–Watts model of small-world (SW) network consisting of identical H–H neurons. The network is composed of M=60 identical neurons with initially each having k=2 connectivity. In SW neuronal networks, the membrane potential of each neuron in the presence of chaotic activity is given with the following equation:



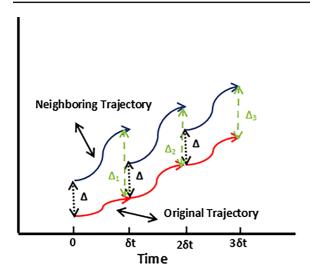


Fig. 2 The schematic representation of the calculation procedure of Lyapunov exponent

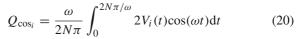
$$C \frac{dV_{i}}{dt} = g_{K}^{\max} n_{i}^{4} (V_{K} - V_{i}) + g_{Na}^{\max} m_{i}^{3} h_{i} (V_{Na} - V_{i}) + g_{L} (V_{L} - V_{i}) + I_{\text{ext}_{i}} + I_{\text{chaos}} + \sum_{j=1, i \neq j}^{M} \kappa_{ij} (V_{i} - V_{j})$$
(16)

$$\frac{\mathrm{d}\gamma_i}{\mathrm{d}t} = \alpha_{\gamma i}(V_i)(1 - \gamma_i)
-\beta_{\gamma i}(V_i)\gamma_i, \gamma = m, n, h$$
(17)

where V_i and V_j are the membrane potentials for neuron i and neuron j, respectively. κ_{ij} is the coupling strength between neuron i and neuron j. If neuron i and j are connected, $\kappa_{ij} = \kappa = 0.05$, otherwise $\kappa_{ij} = 0$. $I_{ext_i} = A\sin(\omega t)$ is weak signal that is applied to neuron i. In this paper, we introduce an f parameter which determines proportion of neurons exposed to weak signal in the network. If the weak signal is applied to neuron i $A = 1 \, \mu \, A/\text{cm}^2$, otherwise A = 0. To measure the propagation of CR in the network, we calculate Fourier coefficient Q as an average of the individual Q_i values as follows:

$$Q = \frac{1}{M} \sum_{i=1}^{M} Q_i \tag{18}$$

$$Q_{\sin_i} = \frac{\omega}{2N\pi} \int_0^{2N\pi/\omega} 2V_i(t)\sin(\omega t) dt$$
 (19)



$$Q_i = \sqrt{Q_{\sin_i}^2 + Q_{\cos_i}^2} \tag{21}$$

where Q_i is the Fourier coefficient of neuron i. Also, results given in the all figures are obtained by averaging over 20 different network realizations for ensuring statistical consistency.

3 Results and discussion

We systemically analyze the impacts of external chaotic activity, derived from Lorenz system, on the weak signal detection performance of the H–H neuron by computing the Fourier coefficient Q. For this aim, the parameters of the Lorenz system are set to ensure chaotic oscillation. Then, the H–H neuron is exposed to this chaotic signal as well as the weak periodic signal. The response measure Q is calculated during 1000 periods of the weak signal depending on the chaotic current intensity for various frequency of the weak signal as shown in Fig. 3. Also, in Fig. 3, the weak signal and the membrane potential of the H–H neuron are plotted as a function of time for: small, intermediate and high values of the chaotic current intensity ε .

As shown in Fig. 3a, regardless of the weak signal frequency ω , the Q curves exhibit a bell-shaped dependence on the chaotic current intensity, indicating the clear signature of the chaotic signal-induced resonance or CR in a single H–H neuron. Also, there is an optimal chaotic current intensity, equaling approximately $\varepsilon \approx 0.5$, for the best detection of weak signal. Moreover, it is seen in the inset of Fig. 3a the weak signal detection performance of the H-H neuron exhibits resonance-like dependence on the frequency of weak signal for the optimal chaotic current intensity ($\varepsilon = 0.5$), where the highest Q is obtained at $\omega = 0.3 \, \mathrm{ms}^{-1}$. For small values of ε in Fig. 3b, it is seen that the H-H neuron is mostly in its quiescent state, and therefore, it is not able to detect the weak signal for the given amplitude A. However, for an optimal value of ε (Fig. 3c), H–H neuron fires in a strongly correlated manner with the weak signal resulting in a high encoding performance for the neuron. Finally, with a further increase in the chaotic current intensity (Fig. 3d), the correlation between the spiking activity of H-H neuron and the weak signal is destroyed. The neuron produces spikes, being uncorrelated with the weak signal, under



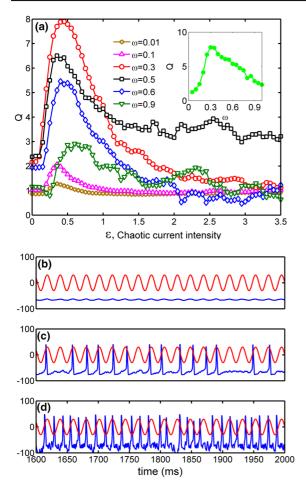


Fig. 3 Response of the H–H neuron to the weak signal. **a** Q is plotted as a function of ε for different frequencies of the weak signal. Inset shows the maximal Q depending on the frequency of the weak signal, ω . The membrane potential of the H–H neuron and the weak signal (the amplitude of weak signal is magnified 30 times for visibility) are plotted for three different chaotic current intensities: $\mathbf{b} \, \varepsilon = 0.1$, $\mathbf{c} \, \varepsilon = 0.45$, $\mathbf{d} \, \varepsilon = 3$. It is seen that the most coherent firings with the weak signal occur at the intermediate level of chaotic current intensity ($A = 1 \, \mu \text{A/cm}^2$, $\omega = 0.3 \, \text{ms}^{-1}$, $I_0 = 0 \, \mu \text{A/cm}^2$)

the effect of the chaotic current intensity which is large enough to enable the neuron to fire spike in the absence of weak signal.

To present a global pint of view on how the weak signal detection performance of the H–H neuron is modulated by the chaotic current intensity ε depending on the frequency of weak signal ω , we calculate the Fourier coefficient Q in a wide range of the chaotic current intensity $\varepsilon[0-3.5]$ and the frequency of weak signal $\omega[0.001-1~{\rm ms}^{-1}]$. Obtained results are given as

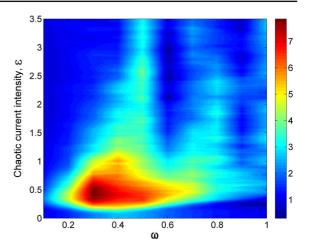


Fig. 4 The dependence of Q on the chaotic current intensity and the weak signal frequency $(A = 1 \,\mu\text{A/cm}^2, I_0 = 0 \,\mu\text{A/cm}^2)$

a parameter plane plot in Fig. 4. The results shown in Fig. 4 clarify the findings which are given in Fig. 3. When the results in Fig. 4 are analyzed, the presence of an island (red-shaded region) where the weak signal can be optimally detected by the H–H neuron is observed. From the results in Fig. 4, it has been unearthed that neither too weak chaotic current nor too strong one is useful for the neuron to detect the weak signal efficiently. There must be an optimal intermediate level of chaotic activity in the system for the efficient detection of weak signal. This result is similar to the presence of an intermediate level of noise, ensuring the best detection in SR [7,16].

To provide some perspective and clarity to the given results in Fig. 4, we present the inter-spike interval histograms (ISIHs) of the neuronal firings computed from 10000 ISIs for different chaotic current intensities at the frequency of weak signal $\omega = 0.3 \,\mathrm{ms}^{-1}$ in Fig. 5. In Fig. 5a, when the chaotic current intensity is small, the neuron exhibits a multi-modal ISIH with various peaks occurring approximately at the period of the weak signal and at its harmonics. In this case, it is expected that Q reaches higher values but in the obtained results Q is very small. This can be explained by the fact that the peak of ISIH appearing at the weak signal period is quite small. Actually, firing rate of the H–H neuron is extremely low with small value of the chaotic current intensity. The H–H neuron generally skips firing because of low chaotic current intensity at the positive cycle of weak signal. Moreover, the H–H neuron mostly falls into a quiescent state. As a result,



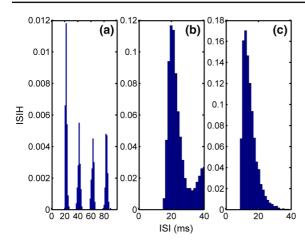


Fig. 5 Presented are inter-spike interval histograms (ISIHs) of the H–H neuron obtained from 10000 inter-spike intervals **a** $\varepsilon = 0.1$, **b** $\varepsilon = 0.45$ **c** $\varepsilon = 3$. The chaotic activity can affect the dominant period of the firings in the H–H neuron ($\omega = 0.3$, $A = 1 \,\mu\text{A/cm}^2$, $I_0 = 0 \,\mu\text{A/cm}^2$). Readers should pay attention to the axis scales of figures, which are given in different ranges for visibility

the weak signal detection performance of the H-H neuron is significantly diminished. For a modest value of ε in Fig. 5b, there is an increase at the peak of ISIH occurring at the period of the weak signal, and it is observed that the H-H neuron fires in a strongly correlated manner with the weak signal (Fig. 3c). The reason of this harmony between the H–H neuron firing activity and the weak signal is that the timescale of the intrinsic oscillations, caused by weak signal, and the one added to neuronal dynamics by chaotic activity match relatively more proper way. Hereby, the weak signal is encoded efficiently by the neuron. Further increasing of chaotic current intensity results in a distinct sharp peak in ISIH occurring at around 10 ms as shown in Fig. 5c. However, it is not coherent with period of weak signal $(T \approx 21 \text{ ms})$, so we obtained small Q values.

Thus far, we have performed all simulations with the assumption that the bias current $I_0=0\,\mu\text{A/cm}^2$. However, the excitability level of the neuron may have important effects on the neuronal dynamics and may induce different responses. We calculate the Fourier coefficient Q in a parameter space spanned by the chaotic current intensity and I_0 current to show the effects of excitability level of the neuron on the weak signal detection performance in the H–H neuron in Fig. 6. It is clearly seen that the weak signal detection performance of the H–H neuron displays a resonance-

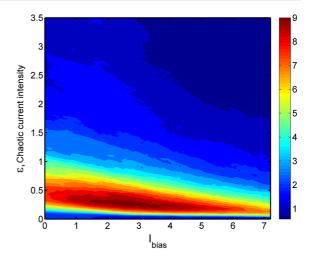


Fig. 6 The dependence of Q on the chaotic current intensity and the excitability level of the H–H neuron ($A=1\,\mu\text{A/cm}^2$, $\omega=0.3\,\text{ms}^{-1}$)

like dependence on the chaotic current intensity for all values of I_0 . From this result, we may infer that the CR is a robust phenomenon which occurs independently from the level of excitability. Also, with the increasing of the excitability of neuron, the range of chaotic current intensity in which the weak signal can be detected optimally by the H-H neuron narrows. Moreover, the chaotic current intensity ensuring the best detection performance slightly decreases, with the increasing of excitability. When the chaotic current intensity set to a value within the range warranting high detection performance, with the increasing of bias current, Q first increases and reaches an optimal value, then decreases with the further increase in I_0 . These results indicate the presence of resonance-like behavior occurring depending on I_0 .

On the other hand, recent experimental studies have shown that there exists a certain frequency range in which the weak signal is effectively encoded by the neuron [48]. At the same time, it is also found that the signal transduction capacity of a neuron is dependent on not only the frequency of periodic driving but also the amplitude of this force. These findings indicate that neurons do not have a particular firing threshold regarding to the amplitude of the periodic signal. This inference is confirmed in Ref. [49], where the authors determined the amplitude border distinguishing subthreshold and suprathreshold regimes for each frequency of periodic forcing in the excitable Hodgkin–Huxley system. By considering this information, the



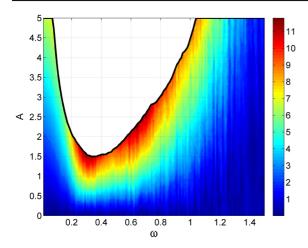


Fig. 7 The dependence of the weak signal detection performance of the neuron (Q) on the frequency and amplitude of the weak signal in the presence of the optimal chaotic activity $(\varepsilon=0.45)$

signal amplitude used in the results obtained so far is more close to suprathreshold regime for particular frequencies around $\omega = 0.3 \, \text{ms}^{-1}$, while the same value is extremely far for the rest of the frequency band. To investigate the effects of the amplitude and the frequency of weak signal on Q, first, in the absence of chaotic signal, we obtained the characteristic curve (depicted with solid black line) separating the subthreshold and suprathreshold regimes in amplitudefrequency parameters plane in Fig. 7, as in ref [49]. Then, for the optimal chaotic current intensity, the Q is calculated for each amplitude–frequency pairs that ensures the obtained signal is within the subthreshold regime. In the previous works, it is found that the H–H neuron could be in a sensitive state for firing a spike in precise frequency range of periodic driving [50] and this range allows intrinsic dynamics of the neuron to resonate with input signals [51]. In line with these results, it is seen that the chaotic activity significantly enhances Q when the amplitude of weak signal is close to suprathreshold regime for the frequency range of $0.2 \text{ms}^{-1} < \omega < 1.05 \text{ ms}^{-1}$. The weak signal detection performance of H-H neuron decreases with the increasing frequency on the right side of this range. However, it is not possible to obtain high Q values for very small frequencies before the given range. Finally, it can be concluded that the closer the amplitude of the weak signal to the curve, the better the weak signal detection performance of H-H neuron via chaotic activity in its frequency sensitive state.

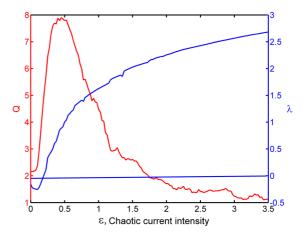


Fig. 8 The dependence of Q and λ on the chaotic current intensity $(A = 1 \,\mu\text{A/cm}^2, \, \omega = 0.3 \,\text{ms}^{-1}, \, I_0 = 0 \,\mu\text{A/cm}^2)$

In experimental and numerical studies, it has been found that periodically varying stimuli induces a rich variety of response behaviors in the H-H model such as mode-locked (periodic), chaotic, and quasiperiodic oscillations of membrane voltage [53–60]. In recent years, there has been a growing interest in studies on how the chaotic regime in neuron models occurs [42]. However, it is not clear whether neuron can process weak signal in the chaotic regime, and from which factors its detection performance is affected in this state. To investigate the weak signal detection performance of the H–H neuron in chaotic regime, we calculate Q and maximal Lyapunov exponent, λ , depending on the chaotic current intensity for $\omega = 0.3 \,\mathrm{ms}^{-1}$ in Fig. 8. For small values of the chaotic current intensity, it is seen that λ is negative (meaning that neuron is not in chaotic regime) and the weak signal detection performance of H–H neuron is quite low. With this parameter setting, it is also shown that H-H neuron becomes a silent regime with mostly no spike, and there are subthreshold oscillations (see Fig. 3b). With the increasing of the chaotic current intensity, the λ becomes positive (referring to a chaotic activity); however, Q is still low. With further increasing in the chaotic current intensity, both λ and Q rise. Increased λ means that chaotic behavior grows in the dynamics of the H-H neuron. On the other hand, when the chaotic current intensity is still further increased, the λ continues to increase, but Q decreases. Based on these results, it is concluded that there is an optimal chaotic regime in H-H neuron for the best detection of the weak signal. These results confirm that neuronal system operates at a critical point



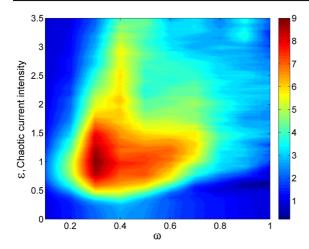


Fig. 9 The dependence of Q on the chaotic current intensity and the weak signal frequency when using Chen chaotic system as a source of chaotic activity ($A = 1 \mu A/cm^2$, $I_{bias} = 0 \mu A/cm^2$)

between order and chaos for an optimum information processing [61,62].

Up to now, we have utilized Lorenz chaotic attractor as a chaotic activity source to show the effects of chaotic activity on the weak signal detection performance of H-H neuron. In fact, chaotic activity in the brain may not be exactly the same with Lorenz chaotic attractor. Therefore, it is important to observe the effects of different chaotic attractors on the weak signal detection performance of the H-H neuron. For this aim, we utilize Chen [63] and Chua [64] chaotic attractors as a source of chaotic activity to generalize the impacts of chaotic activity on neuron dynamics. As seen in Figs. 9 and 10, when using Chen and Chua system, respectively, there is a range of chaotic current intensity that enhances the weak signal detection performance of H-H neuron significantly. These results show that the weak signal detection performance of H-H neuron can be increased via chaotic activity regardless of its source.

We have examined the effects of chaotic activity on the weak signal detection performance of H–H neurons at single neuron level so far. But, when it is considered that the human brain contains more than 100 billion neurons, it is important that any phenomena occurring in a single neuron emerge at the network level. In this context, we analyze the effects of chaotic activity at the network level to explain how the collective behavior of H–H neurons is affected by chaotic activity. For this aim, we analyze the effects of chaotic current intensity on the weak signal detection performance of networked

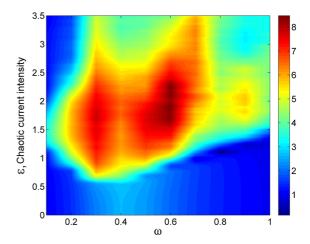


Fig. 10 The dependence of Q on the chaotic current intensity and the weak signal frequency when using Chua chaotic system as a source of chaotic activity ($A = 1 \,\mu\text{A/cm}^2$, $I_{\text{bias}} = 0 \,\mu\text{A/cm}^2$)

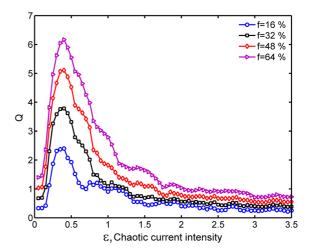


Fig. 11 The Q is plotted as a function of ε for different f values in Newman–Watts SW networks ($p=0.05, \kappa=0.05, A=1\,\mu\text{A/cm}^2, I_{\text{bias}}=0\,\mu\text{A/cm}^2, \omega=0.3\,\text{ms}^{-1}$)

neurons for different f values with the probability of adding link p=0.05 and coupling strength $\kappa=0.05$. Obtained results are presented in Fig. 11. As seen in Fig. 11, the Q curves exhibit resonance-like behaviors depending on chaotic current intensity regardless of the f values. Also, the optimal chaotic current intensity ensuring the best detection of weak signal on the network approximately equals to $\varepsilon=0.45$ for all f values. Moreover, the resonance amplitude enhances with the increasing f values when the chaotic current intensity has its optimal value.



4 Conclusions

In experimental studies, it is found that human brain operates at a critical point between order and chaos that is known as edge of chaos in order to optimize information transfer [61]. Also, it is shown that neurons exhibit chaotic behavior based on different factors which arise from neuronal medium such as stimuli type, network structure and synaptic strength [33]. Therefore, in the present study, the weak signal detection performance of the H-H neuron is investigated in the presence of extrinsic chaotic activities. Also, we have examined the maximal Lyapunov exponent to determine the state of the neuron. The obtained results have shown that the chaotic current intensity and the frequency and amplitude of the weak signal can significantly influence the weak signal detection performance of the H-H neuron. It is revealed that the weak signal detection performance of H-H neuron can be optimized by chaotic signal, instead of noise and high-frequency stimuli. Here, the chaotic signal injected into neuron plays a role which is similar to the ones acted by noise in stochastic resonance and high-frequency signal in VR. We show the existence of an optimal chaotic current intensity $(\varepsilon = 0.45)$ at which the weak signal detection performance of H-H neuron significantly enhances. Also, there is an optimal frequency ($\omega = 0.3 \,\mathrm{ms}^{-1}$) for the best detection of weak signals. On the other hand, it is observed that the more the amplitude of weak signal is close to the border that separates suprathreshold and subthreshold signals, the more the weak signal detection performance is obtained in H–H neuron. Besides, the smallest amplitude value ensuring an optimal detection performance is obtained when weak signal frequency set $\omega = 0.3 \, \text{ms}^{-1}$. Moreover, we find that the chaotic current intensity ensuring optimal detection performance decreases with increasing of excitability of the H-H neuron. We demonstrate that the H-H neuron is able to detect efficiently the weak signal even if it is in chaotic regime. We also analyze the effects of different chaotic sources on the weak signal detection performance of the neuron by using Chua system and Chen system as a source of chaotic signal. Obtained results have shown that Chua and Chen chaotic systems have similar effects to Lorenz chaotic system on the weak signal detection performance of the H–H neuron. Finally, we show that CR emerges in SW networks. These results indicate that CR is robust phenomena.

In the current study, we examine the effects of chaotic activity on the weak signal detection performance of single neurons and neuronal networks using Fourier coefficients. However, in the literature there are many phenomena occurring in single neurons and neuronal networks such as first spike latency and firing rate; therefore, in the future studies, it is worth to investigate the effects of chaotic activities on these phenomena in complex neuronal networks having different topologies.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

References

- Gammaitoni, L., Hänggi, P., Jung, P., Marchesoni, F.: Stochastic resonance. Rev. Mod. Phys. 70(1), 223–287 (1998)
- Russell, D.F., Wilkens, L.A., Moss, F.: Use of behavioural stochastic resonance by paddle fish for feeding. Nature 402(6759), 291–294 (1999)
- Douglass, J.K., Wilkens, L., Pantazelou, E., Moss, F.: Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance. Nature 365(6444), 337–340 (1993)
- Anishchenko, V.S., Neiman, A.B., Moss, F., Schimansky-Geier, L.: Uspekhi Fizicheskih Nauk. Sov. Phys. Usp. 42, 7 (1999)
- McNamara, B., Wiesenfeld, K.: Theory of stochastic resonance. Phys. Rev. A 39(9), 4854–4869 (1989)
- Palonpon, A., Amistoso, J., Holdsworth, J., Garcia, W., Saloma, C.: Measurement of weak transmittances by stochastic resonance. Opt. Lett. 23(18), 1480–1482 (1998)
- Hänggi, P.: Stochastic resonance in biology how noise can enhance detection of weak signals and help improve biological information processing. ChemPhysChem 3(3), 285–290 (2002)
- Wiesenfeld, K., Moss, F.: Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDs. Nature 373(6509), 33–36 (1995)
- Wiesenfeld, K., Jaramillo, F.: Minireview of stochastic resonance. Chaos 8(3), 539–548 (1998)
- Longtin, A.: Stochastic resonance in neuron models. J. Stat. Phys. 70(1–2), 309–327 (1993)
- Moss, F., Ward, L.M., Sannita, W.G.: Stochastic resonance and sensory information processing: a tutorial and review of application. Clin. Neurophysiol. 115(2), 267–281 (2004)
- Yasuda, H., Miyaoka, T., Horiguchi, J., Yasuda, A., Hänggi, P., Yamamoto, Y.: Novel class of neural stochastic resonance and error-free information transfer. Phys. Rev. Lett. 100(11), 118103–118106 (2008)
- Yilmaz, E., Uzuntarla, M., Ozer, M., Perc, M.: Stochastic resonance in hybrid scale-free neuronal networks. Physica A 392(22), 5735–5741 (2013)



 Collins, J.J., Imhoff, T.T., Grigg, P.: Noise-enhanced tactile sensation. Nature 383(6603), 770 (1996)

- Russell, D.F., Wilkens, L.A., Moss, F.: Use of behavioural stochastic resonance by paddle fish for feeding. Nature 402(6759), 291–294 (1999)
- Perc, M.: Stochastic resonance on excitable small-world networks via a pacemaker. Phys. Rev. E 76(6), 066203–6 (2007)
- Bezrukov, S.M., Vodyanoy, I.: Noise-induced enhancement of signal transduction across voltage-dependent ion channels. Nature 378(6555), 362–364 (1995)
- Schmid, G., Goychuk, I., Hänggi, P.: Stochastic resonance as a collective property of ion channel assemblies. EPL (Europhysics Letters) 56(1), 22–28 (2001)
- Guo, D., Li, C.: Stochastic resonance in Hodgkin-Huxley neuron induced by unreliable synaptic transmission. J. Theor. Biol. 308, 105–114 (2012)
- Izhikevich, E.M.: Simple model of spiking neurons. IEEE Trans. Neural Netw. 14(6), 1569–1572 (2003)
- Landa, P.S., McClintock, P.V.: Vibrational resonance. J. Phys. A: Math. Gen. 33(45), L433 (2000)
- Ullner, E., Zaikin, A., Garcia-Ojalvo, J., Bascones, R., Kurths, J.: Vibrational resonance and vibrational propagation in excitable systems. Phys. Lett. A 312(5–6), 348–354 (2003)
- Deng, B., Wang, J., Wei, X., Tsang, K.M., Chan, W.L.: Vibrational resonance in neuron populations. Chaos 20(1), 013113 (2010)
- Yu, H., Wang, J., Liu, C., Deng, B., Wei, X.: Vibrational resonance in excitable neuronal systems. Chaos 21(4), 043101 (2011)
- Stiefel, K.M., Englitz, B., Sejnowski, T.J.: Origin of intrinsic irregular firing in cortical interneurons. Proc. Natl. Acad. Sci. 110(19), 7886–7891 (2013)
- Fellous, J.M., Rudolph, M., Destexhe, A., Sejnowski, T.J.: Synaptic background noise controls the input/output characteristics of single cells in an in vitro model of in vivo activity. Neuroscience 122(3), 811–829 (2003)
- Destexhe, A., Rudolph, M., Paré, D.: The high-conductance state of neocortical neurons in vivo. Nat. Rev. Neurosci. 4(9), 739–751 (2003)
- Hansel, D., Mato, G.: Short-term plasticity explains irregular persistent activity in working memory tasks. J. Neurosci. 33(1), 133–149 (2013)
- Ardid, S., Wang, X.J., Gomez-Cabrero, D., Compte, A.: Reconciling coherent oscillation with modulation of irregular spiking activity in selective attention: gamma-range synchronization between sensoryand executive cortical areas. J. Neurosci. 30(8), 2856–2870 (2010)
- Doron, G., von Heimendahl, M., Schlattmann, P., Houweling, A.R., Brecht, M.: Spiking irregularity and frequency modulate the behavioral report of single-neuron stimulation. Neuron 81(3), 653–663 (2014)
- Arbib, M.A., Fellous, J.M.: Emotions: from brain to robot. Trends. Cogn. Sci. 8(12), 554–561 (2004)
- Freeman, W.J.: Evidence from human scalp electroencephalograms of global chaotic itinerancy. Chaos 13(3), 1067–1077 (2003)
- Korn, H., Faure, P.: Is there chaos in the brain? II. Experimental evidence and related models. C. R. Biol. 326(9), 787–840 (2003)

- 34. El Boustani, S., Destexhe, A.: Brain dynamics at multiple scales: can one reconcile the apparent low-dimensional chaos of macroscopic variables with the seemingly stochastic behavior of single neurons? Int. J. Bifurc. Chaos 20(06), 1687–1702 (2010)
- Hayashi, H., Ishizuka, S., Hirakawa, K.: Chaotic response of the pacemaker neuron. J. Phys. Soc. Jpn. 54(6), 2337–2346 (1985)
- 36. Freeman, W. J.: On the problem of anomalous dispersion in chaoto-chaotic phase transitions of neural masses, and its significance for the management of perceptual information in brains. In: Synergetics of cognition (pp. 126-143). Springer, Berlin (1990)
- Freeman, W.J.: A proposed name for aperiodic brain activity: stochastic chaos. Neural Netw. 13(1), 11–13 (2000)
- Freeman, W.J., Burke, B.C., Holmes, M.D.: Aperiodic phase re-setting in scalp EEG of beta-gamma oscillations by state transitions at alpha-theta rates. Hum. Brain Mapp. 19(4), 248–272 (2003)
- Paul, K., Cauller, L.J., Llano, D.A.: Presence of a chaotic region at the sleep-wake transition in a simplified thalamocortical circuit model. Front. Comput. Neurosci. 10, 91 (2016)
- Carroll, T.L., Pecora, L.M.: Stochastic resonance and crises. Phys. Rev. Lett. 70(5), 576–579 (1993)
- Carroll, T.L., Pecora, L.M.: Stochastic resonance as a crisis in a period-doubled circuit. Phys. Rev. E 47(6), 3941–3949 (1993)
- Nobukawa, S., Nishimura, H., Yamanishi, T., Liu, J.Q.: Analysis of chaotic resonance in Izhikevich neuron model. PloS ONE 10(9), e0138919 (2015)
- Nobukawa, S., Nishimura, H., Yamanishi, T., Liu, J.Q.: Chaotic states induced by resetting process in Izhikevich neuron model. JAISCR 5(2), 109–119 (2015)
- Schweighofer, N., Doya, K., Fukai, H., Chiron, J.V., Furukawa, T., Kawato, M.: Chaos may enhance information transmission in the inferior olive. Proc. Natl. Acad. Sci. 101(13), 4655–4660 (2004)
- Hodgkin, A. L., Huxley, A. F.: Movement of sodium and potassium ions during nervous activity. In: Cold Spring Harbor symposia on quantitative biology (Vol. 17, pp. 43–52). Cold Spring Harbor Laboratory Press (1952)
- Ma, J., Ying, H.P., Pu, Z.S.: An anti-control scheme for spiral under Lorenz chaotic signals. Chin. Phys. Lett. 22(5), 1065– 1068 (2005)
- Wilson, H. R.: Spikes, decisions, and actions: the dynamical foundations of neurosciences. (1999)
- Levin, J.E., Miller, J.P.: Broadband neural encoding in the cricket cereal sensory system enhanced by stochastic resonance. Nature 380(6570), 165 (1996)
- Pankratova, E.V., Polovinkin, A.V., Mosekilde, E.: Resonant activation in a stochastic Hodgkin–Huxley model: interplay between noise and suprathreshold driving effects. Eur. Phys. J. B 45(3), 391–397 (2005)
- Yu, Y., Liu, F., Wang, W.: Frequency sensitivity in Hodgkin– Huxley systems. Biol. Cybern. 84(3), 227–235 (2001)
- Wang, W., Wang, Y., Wang, Z.D.: Firing and signal transduction associated with an intrinsic oscillation in neuronal systems. Phys. Rev. E 57(3), R2527 (1998)



- Xie, Y., Chen, L., Kang, Y.M., Aihara, K.: Controlling the onset of Hopf bifurcation in the Hodgkin–Huxley model. Phys. Rev. E 77(6), 061921 (2008)
- Kaplan, D.T., Clay, J.R., Manning, T., Glass, L., Guevara, M.R., Shrier, A.: Subthreshold dynamics in periodically stimulated squid giant axons. Phys. Rev. Lett. 76(21), 4074 (1996)
- Matsumoto, G.: Periodic and Nonperiodic responses of membrane potentials in squid giant axons during sinusoidal current stimulation. J. Theor. Neurobiol. 3, 1–14 (1984)
- Aihara, K.: Chaos in neurons. Scholarpedia 3(5), 1786 (2008)
- Guttman, R., Feldman, L., Jakbsson, E.: Frequency entrainment of squid axon membrane. J. Membr. Biol. 56(1), 9–18 (1980)
- Lee, S.G., Kim, S.: Bifurcation analysis of mode-locking structure in a Hodgkin–Huxley neuron under sinusoidal current. Phys. Rev. E 73(4), 041924 (2006)
- Borkowski, L.S.: Bistability and resonance in the periodically stimulated Hodgkin–Huxley model with noise. Phys. Rev. E 83(5), 051901 (2011)
- Borkowski, L.S.: Response of a Hodgkin–Huxley neuron to a high-frequency input. Phys. Rev. E 80(5), 051914 (2009)

- Parmananda, P., Mena, C.H., Baier, G.: Resonant forcing of a silent Hodgkin–Huxley neuron. Phys. Rev. E 66(4), 047202 (2002)
- Bassett, D.S., Meyer-Lindenberg, A., Achard, S., Duke, T., Bullmore, E.: Adaptive reconfiguration of fractal smallworld human brain functional networks. Proc. Natl. Acad. Sci. 103(51), 19518–19523 (2006)
- Kitzbichler, M.G., Smith, M.L., Christensen, S.R., Bullmore, E.: Broadband criticality of human brain network synchronization. PLoS Comp. Biol. 5(3), e1000314 (2009)
- Lü, J., Chen, G.: Generating multiscroll chaotic attractors: theories, methods and applications. Int. J. Bifurcat. Chaos 16(04), 775–858 (2006)
- Chua, L.E.O.N.O., Komuro, M., Matsumoto, T.: The double scroll family. IEEE Trans. Circuits Syst. 33(11), 1072–1118 (1986)

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

