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Stochastic resonance in hybrid scale-free neuronal networks

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HIGHLIGHTS

- Hybrid scale-free neuronal networks exhibit stochastic resonance.
- Electrical synapses are more efficient than chemical synapses in the hybrid alliance.
- There exists an optimal density of connections for the response to the input signal.
- The system size is irrelevant for the stochastic resonance on hybrid neuronal networks.
- Hybrid coupling promises new noise-induced phenomena in neuronal networks.

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ABSTRACT

We study the phenomenon of stochastic resonance in a system of coupled neurons that are globally excited by a weak periodic input signal. We make the realistic assumption that the chemical and electrical synapses interact in the same neuronal network, hence constituting a hybrid network. By considering a hybrid coupling scheme embedded in the scale-free topology, we show that the electrical synapses are more efficient than chemical synapses in promoting the best correlation between the weak input signal and the response of the system. We also demonstrate that the average degree of neurons within the hybrid scale-free network significantly influences the optimal amount of noise for the occurrence of stochastic resonance, indicating that there also exists an optimal topology for the amplification of the response to the weak input signal. Lastly, we verify that the presented results are robust to variations of the system size.

1. Introduction

Stochastic Resonance (SR) is an important finding that occurs in many fields of science ranging from classical and quantum physics to chemistry, engineering, and, in recent decades, also in biology and medicine [1–7]. SR refers to a phenomenon that a suitable level of noise evokes the best correlation between feeble input information (such as a weak signal) and the response of the nonlinear system. More precisely, when the noise level is small, the system is not able to detect the signal due to its small amplitude, but as the noise rises, the temporal output becomes highly correlated with the input resulting in an increase in a measure of the quality of signal transmission or detection performance. Finally, for very large noise intensities, the system output is dominated by the noise and the signal cannot be processed. During the several past decades, in parallel with the growing attention in the literature on the influence of noise on isolated and spatially extended nonlinear dynamical systems, the SR phenomenon became one of the most popular subjects in the field

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of neuroscience. Many findings obtained from experimental and theoretical studies at both single neuron and network level have uncovered that neurons can easily detect and process the weak input signal through the SR mechanism [8–13]. SR has also been observed in the central nervous system of mammalians that can utilize the neuronal noise for higher brain functions such as human tactile sensation [14,15], visual perception [16], and the animal feeding behavior [17,18]. Moreover, the subject has been investigated in detail by using various mathematical neuronal models of varying degrees of complexity and biological plausibility [19–22].

As is well known, neurons communicate by means of stereotyped pulses, called action potentials or spikes, and process the information by exchanging the spikes via synaptic contacts. There are two broad categories of synapses within the nervous system, electrical and chemical synapses. An electrical synapse consists of gap junctions bridging the plasma membrane of two neurons and permitting direct transfer of electrical signals between neurons. For this reason electrical synapses are local connections. The coupling strength of this type of synapse is linearly proportional to the membrane potential difference of the two coupled neurons. On the other hand, for the chemical synapse, signal transmission from pre- to post-synaptic neuron is achieved by neurotransmitters released from the pre-synaptic side in response to a received action potential. Chemical synapses mostly occur between axon terminals and dendrites; thus they are responsible for non-local long range connections. Since the transmission is more complex than that of electrical synapses, the time evolution of synaptic conductance at chemical synapses is a nonlinear process.

Thus far, many theoretical and experimental studies have investigated the influence of electrical and chemical synapses on various phenomena in the nervous system, such as synchronization [23,24], pattern formation [25], coherence and stochastic resonance [26,27], as well as vibrational resonance [28,29]. However, all of these works have considered the subjects in purely electrically or chemically coupled neuron populations. Indeed, these two types of synapses frequently coexist within the same neuronal population, which results in a hybrid coupling scheme [30,31]. For instance, it was shown that some interneuronal networks, such as networks of fast-spiking interneurons, are extensively connected by both chemical and electrical coupling [32–34]. In this context, Kopell and Ermentrout reported that an addition of a small amount of electrically coupled synapses to the network of chemically coupled inhibitory neurons can increase the degree of synchronization far more than a much larger increase in chemical coupling strength [35]. Baptista et al. studied the combined effects of both synapse types on the rate of information and the synchronization processes, and showed that larger chemical coupling strength needs to smaller electrical coupling strength for achieving complete synchronization, and also found a coupling strength range in which rate of information produced by the network is large [36]. Recently, vibrational resonance has been considered in a hybrid coupled small-world network of neurons, and it has been demonstrated that the chemical synapses are more efficient than the gap junctions for the transmission of the local input signal by the assistance of high frequency driving [37].

On the other hand, there is no record on SR in a hybrid coupled network in the literature. Thus, it is unclear how the interaction of these two coupling modes affects the weak signal detection performance of a noisy network. In this paper, we extend the previous studies by examining the stochastic resonance in a system of coupled neurons that are globally excited by a weak periodic input signal. By considering a hybrid coupling scheme of electrical and chemical synapses, we investigate how the joint contributions of these two coupling modes influence the SR performance of a complex network of neurons. We also analyze the impacts of different characteristic network parameters, i.e., average degree, coupling strength and system size.

2. Model and methods

Due to the better reflection of the topological properties of the real-world networks [38–43], a scale-free network topology is considered as the underlying interactions within the neurons. We construct a scale-free network with average degree of $k_{\text{avg}} = 4$ by following the procedure in Ref. [38]. Each neuron in the considered network is modeled by using the FHN neuron model because it has low complexity and has shown many characteristic behaviors of real biological neurons. In a scale-free network, the FHN model coupled through slow recovery variables is described by the following equations [44,45]:

$$\frac{dx_i}{dt} = a - y_i + \xi_i + I_i^{\text{syn}} + I_{\text{ext}}, \tag{1}$$

$$\varepsilon \frac{dy_i}{dt} = x_i - \frac{y_i^3}{3} + y_i. \tag{2}$$

Here, $y(t)$ is the activator variable representing the fast variables and can be considered as the membrane potential of the neuron and $x(t)$ is the inhibitory variable denoting slow recovery dynamics and can be thought of as the time dependent conductivity of the potassium channels embedded in the membrane [46]. ε is the time scale ratio between fast and slow variables of the model neuron. Here, we fix $\varepsilon = 0.001$ so that the activator variable $y(t)$ evolves much faster than the inhibitory variable $x(t)$, and this type of stiff excitation can help fast jumping between attractor's states. $i = 1, 2, \ldots, N$ is the neuron index and N is the total number of neurons in the network. N equals 200 unless otherwise indicated. The parameter a determines the system's behavior. If $a > 1$, the FHN model is excitable and has a stable fixed point; for $a < 1.0$ it loses stability and a stable limit cycle generating periodic spiking behavior appears through a supercritical Hopf bifurcation.

We fix $a = 1.03$ close to the bifurcation with the intent of using small noise intensity to excite oscillation. $I_{\text{ext}} = A_s \sin(\frac{2\pi}{T_s} t)$ is the subthreshold input signal, where $A_s = 0.01$ and $T_s = 3.6$ are the amplitude and the period of the input signal, respectively. $\xi(t)$ represents the Gaussian white noise with zero mean and the variance σ^2, $\langle \xi(t)\xi(t') \rangle = \sigma^2 \delta(t - t^2)$. I_i^{syn} is the synaptic current. By applying the procedure used in Ref. [37], we initially construct a scale-free network occurring only electrical synapses. Then, we change the synapses from electrical to chemical with the rate of f which denotes the fraction of chemical synapses in the network. Thereby, we obtain a hybrid scale-free network consisting of electrical and chemical synapses. The synaptic current in the network can be calculated for electrical synapses as below:

$$I_i^{\text{syn}} = g_e \sum_{j, j \neq i} C_e(i, j)(x_j - x_i), \tag{3}$$

where g_e is the synaptic coupling strength for the electrical synapses. $C_e(i, j)$ is the connectivity matrix with the dimension of $N \times N$. If the neurons i and j are connected, $C_e(i, j) = C_e(j, i) = 1$, otherwise $C_e(i, j) = 0$.
On the other hand, the synaptic current for the chemical synapses in the network can be calculated as below:

$$I_i^{\text{syn}} = g_c \sum_{j, j \neq i} C_c(i, j) s_j (x_{\text{syn}} - x_i) \tag{4}$$

where g_c is the synaptic coupling strength for the chemical synapses. $C_c(i, j)$ is the connectivity matrix with the dimension of $N \times N$. If the neurons i and j are connected, $C_c(i, j) = 1$, otherwise $C_c(i, j) = 0$. x_{syn} is the synaptic reversal potential which defines the character of the synapse. Here, we consider excitatory synapses and take $x_{\text{syn}} = 0$. Additionally, the connectivity matrix, $C_c(i, j)$, is not symmetric for chemical coupling because the signal transmission in chemical synapses is unidirectional. The synaptic dynamics of the jth neuron, s_j, is described by Ref. [37]:

$$\dot{s}_j = \frac{\alpha(x_j)(1 - s_j)}{\varepsilon} - \frac{s_j}{\tau_{\text{syn}}} \tag{5}$$

$$\alpha(x_j) = \frac{\alpha_0}{1 + \exp(-x_j / x_{\text{shp}})} \tag{6}$$

where τ_{syn} is the synaptic decay time constant. $\alpha(x_j)$ denotes the recovery variable and can be considered as the Heaviside function. If the pre-synaptic neuron is not active, that is $x_j < 0$, the synaptic dynamics of the jth neuron, s_j, is slowly changing variable and can be taken into account as $\dot{s}_j = -s_j / \tau_{\text{syn}}$. The constant parameters involved in the chemical synaptic coupling are chosen as in Ref. [37]: $\alpha_0 = 2.0$, $x_{\text{shp}} = 0.05$, $\tau_{\text{syn}} = 0.83$ and $g_e = g_c = 0.01$.

In the network, we consider the global stimulus case; thus, we add a subthreshold input signal to all neurons. Then, to quantitatively determine how the input information encoded in the frequency of input signal transported with the average activity of the network, we calculated the Fourier coefficients as the linear response at the input frequency, $\omega = 2\pi / T_s$ [1,20,21]:

$$Q_{\text{sin}} = \frac{\omega}{2n\pi} \int_0^{2n\pi/\omega} 2 y_{\text{avg}}(t) \sin(\omega t) \mathrm{d}t \tag{7}$$

$$Q_{\text{cos}} = \frac{\omega}{2n\pi} \int_0^{2n\pi/\omega} 2 y_{\text{avg}}(t) \cos(\omega t) \mathrm{d}t \tag{8}$$

$$Q = \sqrt{Q_{\text{sin}}^2 + Q_{\text{cos}}^2} \tag{9}$$

where $y_{\text{avg}}(t)$ is the average membrane potential or the mean field of the scale-free network. $y_{\text{avg}}(t) = 1/N \sum_{i=1}^{N} y_i(t)$ is calculated using individual membrane potentials y_i of the neurons, and n is the number of periods T_s covered by the integration time. To ensure statistical consistency, the Q values in all the figures below are obtained by averaging over 20 different network realizations for the given parameter sets.

3. Results

In what follows, we systematically analyze the factors that may have effects on the stochastic resonance in the hybrid scale-free networks. First, we investigated how the proportion of the chemical synapses in the network influences the stochastic resonance. To do so, for f values ranging from 0 to 1, where $f = 0$ represents the network consisting purely electrical synapses and $f = 1$ represents the counterpart occurring only chemical synapses, we calculated Fourier coefficients. Fig. 1 shows the dependence of Q on noise intensity as the ratio of the chemical synapses f changes. As seen in Fig. 1(a), regardless of the f values the Q curves exhibit bell shaped dependence on the noise intensity, indicating the clear signature of the SR in hybrid scale-free networks. Moreover, Q values increases and slightly moves smaller noise intensities as the ratio of the electrical synapses increases in the network (decreasing f). Notably, the Q values of purely electrically coupled networks ($f = 0$) are more pronounced than that of purely chemically coupled ones ($f = 1$). As shown in Fig. 1(b),

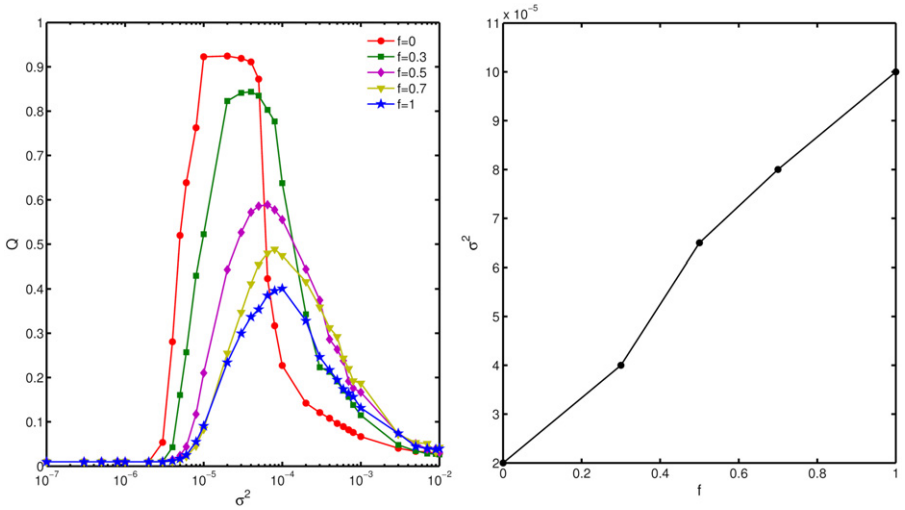

Fig. 1. The dependence of Q on the noise intensity σ^2. (Left panel) For different proportions of the chemical synapses f in the network. (Right panel) The dependence of the resonant noise intensity ensuring maximal Q on the proportion of chemical synapse f ($g_e = g_c = 0.01$).

the noise intensity providing the maximum Q decreases monotonously with the increasing rate of the electrical synapses (decreasing f); these results indicate that in the case of global stimulus, electrical coupling is more efficient than chemical coupling for the SR in a scale-free network. The efficiency of electrical coupling in the transmission of global stimulus was also demonstrated in Deng et al. (their Fig. 5) for the vibrational resonance of three coupled FHN neurons. However, recent studies have shown that nonlinear chemical coupling is more efficient than linear electrical coupling for promoting vibrational resonance in hybrid small-world neuronal networks for the case of local stimulus [37]. The superiority of the electrical coupling in promoting the SR in an SF network is due to the continuous interactions among the electrically connected neurons that give the opportunity of high synchronization and can enable to better control the firing rate compared to the selective interactions among the chemically coupled neurons.

Coupling strength is an important network parameter having effects on the spatiotemporal dynamics of the neuronal networks. In order to explore the influences of coupling strength on SR in a fully hybrid scale-free network ($f = 0.5$), we considered the homogeneous coupling scheme, that is $g_e = g_c = g$, and then computed Q for different values of coupling strength. Fig. 2(a) features the obtained results. It is seen that although the optimal noise intensity for the occurrence of maximum input–output relation does not change very much with the increase in g, the Q values gradually decrease. To show which type of synapse is more prominent in determining this behavior, we varied the coupling strength of one synapse type while keeping the other equal to $g = 0.01$, then again computed Q as a function of σ^2. The obtained results are depicted in Fig. 2(b) and (c) for varying values of g_e and g_c, respectively. With the increasing values of g_e the homogeneity in coupling tends to disappear and heterogeneity increases in favor of electrical coupling, and consequently, the network begins to act as if purely electrically coupled one. The optimal noise intensity required for the resonance moves to smaller values, and the Q increases first and then saturates due to the occurrence of complete synchronization in the network for intermediate values of g. In this context, the efficiency of electrical coupling in leading to synchronization was demonstrated in Ref. [35]. On the other hand, in the case of varying values of g_c, we show in Fig. 2(c) that Q decreases with the increase in g_c and the optimal noise intensity for maximal Q slightly moves to the larger values. The individual contributions of chemical and electrical synapses observed in Fig. 2(b) and (c) indicate that these two types of coupling schemes influence the SR performance oppositely as g increases. However, in the case of hybrid coupled network, although chemical and electrical synapses are present in the network with the same ratio and equal coupling strength ($g_e = g_c = g$), one can easily understand that the decrease in SR performance with the increase in g is mostly due to the chemical synapses (see Fig. 2(a)). The underlying influence of chemical synapses on such a decrease in SR arises from the fact that they allow neurons to be independent from each other and provide more chance to fire independently. It means that each transmitted action potential via chemical synapses may provide fluctuations in target neuron's membrane potential causing asynchronous firings in the whole network [37]. Moreover, an increase in coupling strength of chemical synapses will result in more asynchronous activity even though the presence of electrical synapses. Thus, the wave form of the mean field potential, that we consider to calculate the Q values, will exhibit subthreshold fluctuations, and consequently the maximums in Q decrease as the coupling strength increases.

So far, we have investigated the SR in a hybrid coupled scale-free topology with a fixed average degree, equaling $k_{\text{avg}} = 4$. Since $k_{\text{avg}} = 4$ determines the density of the links in the network, it is an important attribute of a population having significant effects on many phenomena emerging in complex networks. Thus, it is relevant to address its influence on SR in hybrid scale-free networks. To do so, we computed the input–output correlation measure Q as a function of the noise intensity for different values of k_{avg}, by fixed values of coupling strength $g_e = g_c = g = 0.01$ and synapse homogeneity

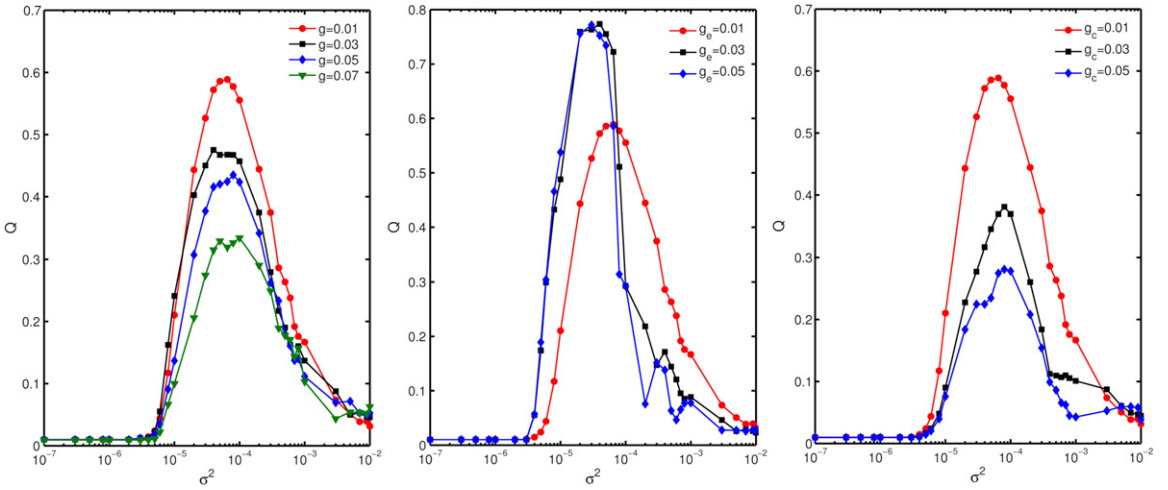

Fig. 2. The cooperative and individual influences of electrical and chemical coupling strengths on SR in a fully hybrid coupled scale-free network ($f = 0.5$). (Left panel) Q versus σ^2 with the variation in coupling strengths of both chemical and electrical synapses ($g = g_e = g_c$). (Middle panel) Q versus σ^2 for different levels of electrical coupling strength g_e by a fixed chemical coupling strength $g_c = 0.01$. (Right panel) Q versus σ^2 for different levels of chemical coupling strength g_c by a fixed electrical coupling strength $g_e = 0.01$.

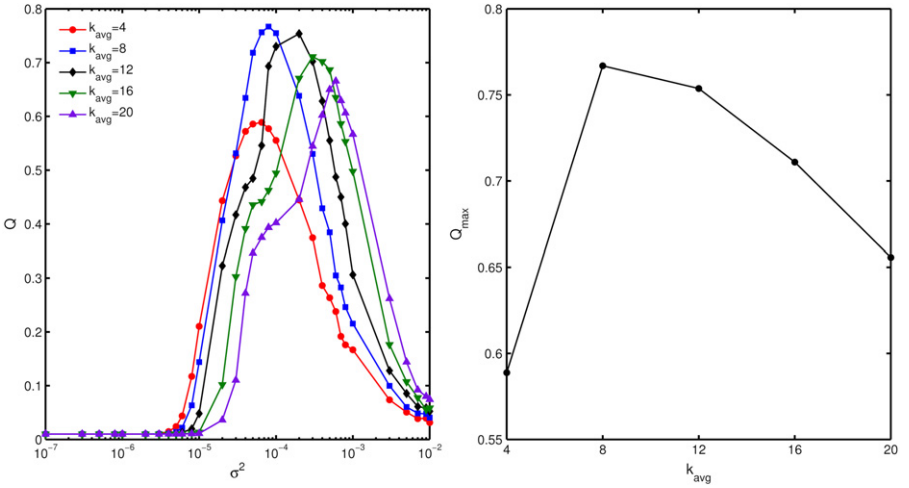

Fig. 3. The effect of average degree of neurons on SR in a fully hybrid scale-free network. (Left panel) Q versus σ^2 for different values of k_{avg}. (Right panel) Dependence of Q_{max} on the average degree k_{avg} ($g = g_e = g_c, f = 0.5$).

$f = 0.5$. Fig. 3(a) features the obtained results. It is seen that, irrespective of the value of the k_{avg}, amplification of the weak input signal can be feasible in a particular range of the noise intensity, indicating the robustness of the phenomenon against the changes of k_{avg} in a hybrid scale-free network.

It is also evident that the optimum noise intensities are required for the occurrence of maximal Q as the density of links in the network increases. On the other hand, SR peaks first slightly increase and then start to decrease with the increase in k_{avg}. To gain more insights into the relationship between average degree and SR, we demonstrated the dependency of Q_{max} on k_{avg} in Fig. 3(b). We obtained an optimal average degree $k_{avg} = 8$, that is the optimum network structure ensuring the best transmission of a weak input signal over the hybrid scale-free networks. In this context, the existence of an optimal average degree warranting the best collective firing regularity of a scale-free network has been recently reported in Ref. [47]. Moreover, Yu et al. also mentioned an optimal network structure for a small-world topology for the best transmission of a weak signal with the assistance of a high frequency driving [37].

Finally, in order to further test the generality of our findings, we examine the impact of system size on the SR in a hybrid scale-free network. To do this, we set $f = 0.5$, $k_{avg} = 4$ and $g_e = g_c = g = 0.01$, and computed Q as a function of noise intensity for different number of neurons in the network. The obtained results are presented in Fig. 4. It is clearly seen that variations of the system size do not have any effect on the weak signal detection performance of the population. In the light of this result, we can say that SR is largely robust in a hybrid coupled scale-free network to variations of the system size. Although the similar system size robustness has also been observed for various emerging phenomena in complex neuronal

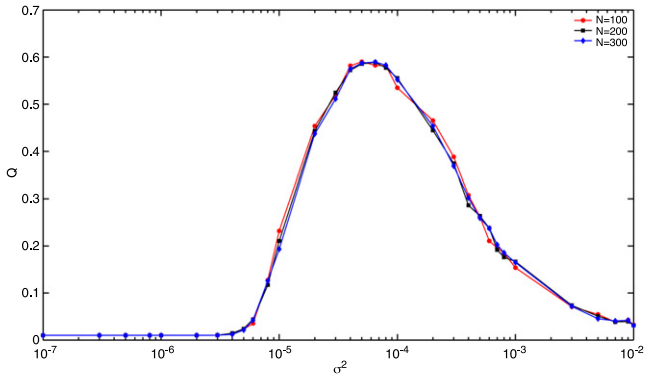

Fig. 4. The dependence of Q on the noise intensity, σ^2, for different network sizes N ($g = g_e = g_c, f = 0.5$).

networks with purely electrical or chemical synapses [48], to the best of our knowledge, our finding is the first demonstration of this robust behavior in a hybrid scale-free network.

4. Discussion

In summary, we have numerically studied the occurrence of the SR phenomenon in a hybrid scale-free network of FHN neurons coupled through inhibitory variables. Initially, we built a purely electrically coupled neuron population, and then investigated the influence of adding chemical synapses to this network on SR. The evidence presented in this paper has revealed that irrespective of the proportion of the chemical synapses in the network, an optimal intensity of the noise evokes the best correlation between the weak input signal and the system's response. In addition, although it was previously reported that the chemical synapse is more efficient than gap junctions in enhancing SR in an array of coupled neurons [26], we have indicated that electrical synapses are more efficient than chemical synapses in a more complex network of neurons, i.e. scale-free networks.

Besides, by considering a fully hybrid coupled neuron population ($f = 0.5$), we have analyzed the effect of coupling strength and network structure on the SR phenomenon. It is shown that increasing the coupling strength in a hybrid scale-free network degrades the correlation between input signal and system's response, thus the resonance weakens. This behavior is mainly due to the nature of chemical synapses which give more chance to the neurons to fire independently from each other. This independent firing results in an asynchronous firing regime in the network reducing the amplitude of SR due to the subthreshold average membrane potential oscillations of the system output as stated in the *Results* section. On the other hand, the average connection degree of neurons within the scale-free topology significantly influences the required noise in the system for the occurrence of SR, i.e. increasing the k_{avg} shifts the optimal noise intensity to the larger values. Moreover, we have found an optimal network structure specified by the average degree k_{avg}, ensuring the best system response to the weak input signal. Finally, the effects of network size on the SR phenomenon in fully hybrid scale-free networks have been analyzed, and it is obtained that the network size has no effect on the SR performance, indicating the robustness of the phenomenon against the variations of system size. We hope that the results presented in this paper may be helpful for deeper understanding of information processing in complex neuronal systems.

Throughout this paper, we have considered only excitatory neurons in the network, but in fact, excitatory and inhibitory neurons can coexist within the same neural population. Therefore, an interesting issue to be considered in future studies may be investigating the SR performance of a hybrid network with excitatory and inhibitory neurons. More realistic neuron models may be considered as well, for example entailing information transmission delays, which are known to be a key ingredient of neuronal dynamics that affects the SR phenomenon [49,50]. Furthermore, since we have assumed that the synaptic transmission is reliable within the neurons, it should also be interesting to investigate the SR performance of our setup with unreliable synaptic transmission.

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