Vibrational Resonance in a heterogeneous scale free network of neurons

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Abstract

Vibrational resonance (VR) is a phenomenon whereby the response of some dynamical systems to a weak low-frequency signal can be maximized with the assistance of an optimal intensity of another high-frequency signal. In this paper, we study the VR in a heterogeneous neural system having a complex network topology. We consider a scale-free network of neurons where the heterogeneity is in the intrinsic excitability of the individual neurons. It is shown that emergence of VR in heterogeneous neuron population requires less energy than a homogeneous population. We also find that electrical coupling strength among neurons plays a key role in determining the weak signal processing capacity of the heterogeneous population. Lastly, we investigate the influence of interneuronal link density on the VR and demonstrate that the energy needed to obtain the resonance grows with the increase in average degree.

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I. INTRODUCTION

The concept of resonance generally refers to an increase in the amplitude of the oscillations provoked by a particular external forcing or signal. In a nonlinear system when it is a highfrequency periodic signal that enhances the amplitude, the phenomenon is called vibrational resonance (VR) [1]. The role of resonances in different biological processes is capital, and recently attention has been paid to this phenomenon in biology [2–7].

Neural networks are biological units that process incoming sensorial or motor information, in form of electrical or chemical signals, with the purpose of taking a determinate action. The underlying dynamics of these signals can span over a variety of time scales: from milliseconds to days. One of the most significant example of existence of such bichromatic signals in the nervous system is the bursting neuron which operates in two widely different time scales [8]. Thus, it is not rare to have periodic signals with very different frequency at the input of a given neuronal network. As we will study in this article, the VR phenomenon is likely to occur in neuronal networks when two periodic signals with widely-separated frequency are present simultaneously at the input. In terms of information processing, the fast periodic forcing can help the network to detect and amplify a weak input signal. In this view, an interpretation of the VR is the optimization of the signal to noise ratio by the perturbation. In recent years, several works, though not many, have investigated the emergence of VR in neural systems both at the level of single neuron and networks with different topologies and coupling scheme [4, 9–15]. A common assumption in these modeling studies is that the neurons in the population have been considered as identical units forming a homogeneous system. However, actual neuronal populations, even cells within the same functional column, exhibits a prominent heterogeneity in their response properties, such as mean firing rate, receptive field location and size, and stimulus selectivity [16]. It has been demonstrated both experimentally and theoretically that the heterogeneity in neural systems is relevant in many contexts, such as in synchronization phenomenon [17, 18], coherence resonance [19], neural coding efficiency $[16]$, reliability $[20]$ or adaptation $[21]$.

Our prime interest here is to study the importance of the diversity among neurons as to the collective detection of a low frequency signal by the network. We understand diversity as the spread of the intrinsic excitability among a population of neurons, which we will call a *heterogeneous population*. It is a natural assumption if we consider a biological system, as no one is expecting uniformity in a real network. The excitability controls the reactions of a neuron to a given input signal. Consequently, the global behavior of a heterogeneous network will differ from the homogeneous case. We will see in section III B how the diversity in the excitability is a key parameter regarding the VR.

Obviously, there are many more parameters a↵ecting the possible occurrence of the VR in a neuronal network. Among others, the topology and coupling strength are particularly interesting since they dramatically affect the dynamics of the network. In Sec. IIIC the coupling strength is treated as a global parameter that varies for all neurons. We find that this global coupling can optimize the detection of the input signal of the network.

In the last part of the study, we investigate the influence of the network structure on the VR. The network is constructed following a scale-free law of degree distribution, which is a topology that has been found in many fields of science including neurosciences [22]. This topology is used as a universal model through the article. We will discuss its relevance and its significance for the VR in Sec. III D.

II. MODEL AND METHODS

We consider a population of non-identical FitzHugh-Nagumo (FHN) neurons that is governed by the following differential equations:

$$
\varepsilon \frac{dv_i}{dt} = v_i - \frac{v_i^3}{3} - w_i + \sum_j g_{ij}(v_j - v_i),\tag{1}
$$

$$
\frac{dw_i}{dt} = v_i + a_i + I_{ex},\tag{2}
$$

where v_i and w_i represent the fast activation variable (membrane potential) and the slow recovery variable of neuron *i*, respectively. $\varepsilon = 0.01$ is the inherent time scale that separate the fast and slow dynamics. In this work, we assume that all the neurons in the population are subject to two different periodic signals injected to the neuron through the external current

$$
I_{ex} = A\cos(\omega t) + B\cos(\Omega t + \varphi_i). \tag{3}
$$

The information to be processed is encoded in the weak signal $A \cos(\omega t)$ having a low frequency ω and amplitude *A*. The other external drive $B \cos(\Omega t + \varphi_i)$ indicates a high frequency signal with amplitude *B*, frequency $\Omega \gg \omega$ and phase $\varphi_i \in [-\pi, \pi]$. Unless stated otherwise, we set the external signals parameters as $A = 0.01$, $\omega = 0.1$ and $\Omega = 5$ (dimensionless parameters).

In Eq. 2, the parameter a_i affects the dynamics of individual neurons, hence allowing us to control the diversity of the neuron population. The FHN neuron model is excitable having a stable fixed point for $a_i > 1$, and it exhibits oscillatory behavior for $a_i < 1$. When $a_i = 1$, the stability of the fixed point is lost through a Hopf bifurcation. Presently in our modeling, we allow a_i to take numerical values from a Gaussian probability distribution, satisfying $\langle a_i \rangle = a_0$ and $\langle (a_i - a_0)(a_j - a_0) \rangle = \delta_{ij}\sigma^2$. σ will be referred from now on as the diversity strength. When the firing threshold is normally distributed ($\sigma > 0$) we call the network heterogeneous. The homogeneous case ($\sigma = 0$) occurs when all the neurons are identical in parameters.

Since we are interested in the weak signal detection performance of the neurons in their excitable regime in presence of a high-frequency driving, we set $a_0 = 1.05$ that keeps all the neurons far away from the bifurcation point over certain interval of σ . Finally, g_{ij} is the bidirectional electrical coupling strength between neuron *i* and *j*, beeing $g_{ij} = g_{syn}$ if the two are connected and $g_{ij} = 0$ otherwise.

As the underlying interaction network of the neuron population, we use a scale-free (SF) topology based on the preferential attachment algorithm [23]. The construction process of SF network starts with a set of *m* fully connected nodes, and at each time step every new node makes m links to m different nodes already present in the network. To incorporate the preferential attachments of these links, we assume that the probability Π that a new vertex will be connected to node *i* depends on its degree k_i , such that $\Pi = k_i / \sum_j k_j$. After a time evolution, this procedure builds a network with an average degree $\langle k \rangle = 2m$, and a power-law degree distribution $P(k) \simeq k^{-3}$. Without loss of generality, we set $m = 2$ and $N = 200$ nodes throughout this work, yielding a SF network with an average degree $\langle k \rangle = 4$.

To evaluate the effect of VR on the network, the collective temporal behavior is measured by calculating the average membrane potential

$$
V_{avg}(t) = \frac{1}{N} \sum_{i=1}^{N} v_i(t),
$$
\n(4)

where $v_i(t)$ is the time series of each FHN neuron simulated for $n = 300$ periods of the low-frequency signal $(T = 2\pi/\omega)$. The response of the network output to the low-frequency signal is usually defined by means of the *Q* factor [1]

$$
Q = \sqrt{Q_s^2 + Q_c^2},\tag{5}
$$

where Q_s and Q_c are computed via the Fourier coefficients after eliminating a sufficiently large transients, T_0 :

$$
Q_s = \frac{2}{nT} \int_{T_0}^{T_0 + nT} V_{avg} \sin(\omega t) dt,
$$
\n(6)

$$
Q_c = \frac{2}{nT} \int_{T_0}^{T_0 + nT} V_{avg} \cos(\omega t) dt.
$$
 (7)

Q is a measure of the Fourier spectrum of V_{avg} at the frequency ω . With this value we can test the response of the network to the low frequency signal. The described mathematical model is integrated numerically using the Forward Euler method with a time step $\Delta t = 0.005$. The simulations presented below have been averaged over 50 realizations of the network for any given set of the model parameters.

III. RESULTS AND DISCUSSION

A. Homogeneous population

For the purpose of comparison and simplicity, we first investigate the VR in a SF network by considering a homogeneous neuron population ($\sigma = 0$). To illustrate the response of the network we represent in Fig. 1 the spatiotemporal dynamics of the network in three typical situations: for small, intermediate and high values of the amplitude *B* of the high-frequency forcing.

For small values of *B* in Fig. 1 (a), it is seen that all the neurons in the network are in a quiescent state, and therefore, the system is not able to detect the external low-frequency signal for the given amplitude A. However, for an optimal value $B_{opt} = 0.06$, most neurons in the network fire in a strongly correlated manner with the input signal resulting in a high encoding performance of the network. Finally, with a further increase in the amplitude of the high-frequency driving, the correlation between neuronal activity and the input signal is destroyed. The neurons fire regardless of the periodic weak input signal.

To quantify the above-outlined spatiotemporal dynamics more precisely, we have computed the dependence of *Q* on *B* in Fig 1(b) for the same parameters. It can be observed

Figure 1: Response of the homogeneous neuron population. (a) the activity of the whole network is plotted as a function of time. The three panels have been simulated for three different values of amplitude *B* of the high-frequency forcing, illustrating a non-resonant case $(B = 0.02)$, an optimal case for $B = 0.06$, and another non-resonant situation where the network is busy. (b) the factor Q is represented as a function of *B*. The peak at $B = 0.06$ shows that the network resonates for this amplitude of the high-frequency forcing. ($\sigma = 0$, $g_{syn} = 0.005$, $N = 200$, $k_{avg} = 4$)

that there exists an optimal region of the high-frequency driving signal amplitude *B*, thus exhibiting a bell shaped dependence characteristic of the vibrational resonance. Although the phenomenon was previously reported on the level of single neuron and in some complex networks of homogeneous neurons [4, 10], to the best our knowledge, this is the first demonstration of emergence of vibrational resonance in a scale free network topology.

B. Heterogeneous population

Next, as the main goal of the current study, we now investigate how the intrinsic diversity among neurons affects the weak signal detection performance of the population having a SF topology. To obtain a heterogeneous SF neuronal network, we have increased the diversity strength σ from zero to some critical value σ_c , which guaranties that all the neurons in the population are in their excitable regime. A further increase in σ beyond this critical value σ_c causes the transition of some neurons from excitable to repetitive firing regime. Our results

Figure 2: B_{opt} as a function of σ . We show in (a) the results of the VR for different values of the diversity parameter σ . It is clear from that figure that the VR happens in all the cases. In (b) we represent the maximum of the curve as a function of σ . The optimum value shifts toward smaller values as σ increases, meaning that the signal can be detected with smaller amplitudes of *B*. $(g_{syn} = 0.005, N = 200, k_{avg} = 4)$

are summarized in Fig. 2.

As a first comment, it is seen in Fig. $2(a)$ that regardless of the value of diversity strength σ , an optimal amplitude of the high frequency signal can maximize the response of the heterogeneous SF network to a low frequency signal encoding the information. In addition, with the increase of the diversity strength, the optimal resonant amplitude of the high frequency signal *Bopt* shifts towards smaller values of *B* as seen in Fig. 2(b). This fact indicates that the weak signal detection in a heterogeneous network is a less-energy consuming process when compared with the homogeneous population. In the context of information theory, it has also been reported in a recent experimental study that the diverse neuronal populations are more efficient in encoding information than their homogeneous counterparts [24].

To account for this fact in our simulations, we will classify the population into two groups depending on the value of the excitability threshold *aⁱ* as the population diversity increases. The first group consists of the neurons with $a_i < a_0$, whereas the second group is formed by the neurons which have $a_i \ge a_0$. Since the neurons in the first group are more excitable than the neurons in the homogeneous case (all of which have $a_i = a_0$), smaller amplitudes *B*

Figure 3: Space-time plots of typical patterns of network activity for some different values of σ and *B* which provide the maximal *Q* values in Fig. 2 (a). Notice that one can easily follow the input signal by visual inspection of spatiotemporal patterns for each case. However, since the synchronization in the network worsens with the inclusion of diversity, tracking the periodic input is not easy as in the case of non-diverse network explaining the decrease in resonance peaks in Fig. 2 (a).

of the high frequency driving trigger the detection of the weak input signal for some of the neurons. Through the synaptic coupling, this small number of neurons are able to pull the other units in the same group which are almost ready to be excited and, hence, produce a partial collective behavior correlated with the input signal. This partial collective behavior acts as a strong basin of attraction for the whole system which forces the neurons in the second group to track the input signal.

An additional increase of σ increases the cleavage between the two groups of neurons. The first group become more excitable while the second group become less excitable. Moreover, some neurons in the first group have a_i values very close to the bifurcation point that occurs at $a_i = 1$. The behavior of these neurons can be easily switched from excitable state to oscillatory state by the synaptic noisy current resulting from the activity of the network. Therefore, these repetitively firing neurons are independent from the input signal. Since the number of neurons following the weak forcing decreases due to these autonomous neurons, the collective network response Q decays as σ increases.

To gain more insight about this type of behavior, we have obtained the spatiotemporal

pattern of the neurons in Fig. 3 for different values of σ and *B* providing the maximum of *Q* depicted in Fig. 2 (a). In the homogeneous case $\sigma = 0$, all the neurons are locked synchronously to the input signal exhibiting a burst-type behaviour. For intermediate values of σ , the number of spikes during the bursting period decreases. Finally, for very large values of σ , a combination of bursting and persistent firing neurons appears due to the mechanism discussed before (see bottom panel in Fig. 3). As a conclusion, the diversity strength augmentation has a two-fold effect on the sensing of the weak signal: on one hand the pool of sensitive neurons grows and ensures less energy requirement for the detection while on the other hand the emergence of incoherent spiking neurons decreases the signal to noise ratio.

C. Influence of the coupling strength

A parameter having important effects on network dynamics is the coupling strength among neurons. Therefore, it is likely that the parameter *gsyn* has an influence on the VR in our considered system. In order to demonstrate the effects of electrical coupling strength more clearly, we have performed simulations for both homogeneous and heterogeneous populations by considering different values of g_{syn} . Obtained results are depicted in Fig.4 (a)-(b) and in Fig.4 (c)-(d) for homogeneous and heterogeneous networks, respectively.

In a homogeneous network $(\sigma = 0)$, it is seen in Fig. 4 (a) that although the maximal *Q* values do not change very much, the optimal energy level for the emergence of resonance peaks increases steadily with *gsyn*. This finding is summarized in Fig. 4 (b) which shows that the dependence of *Bopt* on *gsyn* almost monotonically increases, indicating that the required energy for the detection rises with the coupling strength. A similar effect has also been shown previously for the small-world and the modular networks of neurons [12]. Thus, in homogeneous systems, it seems that the network topology does not have a significant influence on VR performance when the coupling strength among units varies.

On the other hand, for the case of the heterogeneous population, we observe an interesting effect of g_{syn} on the VR performance as depicted in Fig. 4 (c-d). When the coupling strength is small in a heterogenous network, although the required energy level is the same compared to the homogenous case, the resonance peak weakens (see $g_{syn} = 0.001$ curves in Fig. 4 (a)and (c)). However, with the increase in *gsyn* from small values, one can distinguish two

Figure 4: The influence of electrical coupling strength on the emergence of VR in homogeneous and heterogeneous neural networks. (a) Q versus *B* in homogeneous network ($\sigma = 0$) for different values of *gsyn*. (b) The corresponding high frequency driving amplitude *Bopt* in dependence on g_{syn} . (c) Q versus *B* in heterogeneous network ($\sigma = 0.01$) for different values of g_{syn} . (d) The corresponding high frequency driving amplitude *Bopt* in dependence on *gsyn*.

different modes for the weak signal detection capability of the heterogenous population. In the first mode, with the increase in *gsyn*, the optimal high frequency driving amplitude for the best response of the network decreases whereas the peak amplitudes of resonance curves (*Qmax*) increases. Further increase in *gsyn* starts the second mode in which the location of the resonance peaks on the *B*-axis gradually shifts to the right resulting in higher energy requirements for the emergence of VR. At the same time, *Qmax* remains almost constant as *gsyn* increases.

In view of these two regimes, it is evident that there exists an optimal value of the coupling strength at $g_{syn} = 0.01$, which guaranties the smallest *B* for an almost perfect signal detection performance. This can be inferred nicely from Fig. 4 (d) depicting the

resonance like dependence of *Bopt* on *gsyn*. Thus, we conclude that *gsyn* plays a key role in determining the capacity of the heterogeneous neuron population to have good signal detection performances with less energy.

D. Influence of the topology

So far, we have only considered the heterogeneous SF network with the average degree of $k_{avg} = 4$. However, the average degree determines the interneuronal link density in a SF network and has relevant effects on the dynamics. It is therefore crucial to investigate the effect of k_{avg} on the VR.

As clearly seen in Fig. 5 (a), with the increase in average degree *kavg*, while the optimal amplitude of high frequency signal, B_{opt} , slides towards higher B values, the weak signal detection performance of the system does not change distinctly. In the light of these results, we can say that the average degree has no prominent effect on Q_{max} for heterogeneous SF networks. But if we consider *Bopt* ensuring the best response, we deduce that the occurrence of VR in a SF network requires more energy as the network is more densely connected (meaning higher *kavg*).

These results are consistent with a recent study on stochastic resonance in a neuron network with heterogeneous synapses [25]. The authors have stated that a rise in the average degree also increases the optimal noise intensity conducting to the best coherence between the weak input signal and the system response.

To clarify the role played by the topology in the VR we also have performed computations for the following network configurations:

- Random Erdös-Renyi network,
- Small World network,
- Regular network.

For all these topologies the qualitive results of the resonance curves are similar to the SF network as shown in Figs. 5 (a-d). First, the weak signal detection quality for the considered topologies is nearly constant. Moreover, for all cases, the increase in *kavg* leads to a shift of

Figure 5: Effect of interneuronal link density on VR in heterogeneous neural networks obtained by fixed values of $g_{syn} = 0.01$ and $\sigma = 0.01$. The different networks topologies are: (a) Scale Free, (b) Random ER, (c) Regular, and (d) Small World networks. It is clear that although the signal detection performance does not change very much, heterogeneous system needs more energy with the increase in number of connections in the network.

the optimal amplitude of the high-frequency driving B_{opt} towards higher values of B . These results provide good evidence that the performance (measured with the maximum of *Q*) of VR in neuronal networks is independent from the topology whether it is highly or sparsely connected. Also, regardless of network topology, an increase in *kavg* causes the same trend in the resonance curves.

On the other hand, the required energy levels to obtain the same signal detection efficiency

Figure 6: Optimal forcing B_{opt} as a function of k_{avg} for different network topology.

do depend on the network type. In Fig. 6, we plot the optimal amplitude *Bopt* as a function of the average degree *kavg* for all network models. It can be seen that although the *Bopt* values are very similar at small k_{avg} for each cases, significant differences start to appear between the SF topology and the others as *kavg* increases. For instance, SF network always guarantees the smallest *Bopt* for the weak signal processing while small-world and regular networks need the highest *Bopt* values.

From the analysis of these two figures we have therefore concluded that the network topology has an impact on the energy efficiency of the VR, whereas the quality of the detection in terms of maximum of Q is not affected.

IV. CONCLUSIONS

In conclusion, we have investigated the VR performance of FHN neurons interacting through electrical coupling in a SF network. In contrast to previous works, where the VR was only considered in homogeneous networks, we have mainly examined the effects of diversity (heterogeneity) on the VR phenomenon. With the aid of our findings presented in the section III, we have shown that VR is a robust phenomenon occurring regardless of the value of the diversity strength.

Moreover, the diversity in the excitability of the neurons enhances the detection of the weak input signal at the cost of a lower amplification, that is, there is a tradeoff between *Bopt* and *Qmax*. When compared with homogeneous networks, the heterogeneous network gives the opportunity for the neurons to detect the weak input signal by consuming less energy.

In order to characterize what is the influence of the network on the previous results, we have analyzed the role of the coupling strength and the average degree of the connectivity on VR. For homogeneous networks, we have obtained that the value of *Bopt* increases with the coupling strength, while the maximum of *Q* remains almost constant. This result reveals that the stronger the coupling strength, the more the energy is required for the optimal sensing of weak input signal.

Meanwhile, for heterogeneous networks, there is a an optimal value of the coupling strength for which *Bopt* is minimal. It ensures the optimal detection of the weak input signal with a minimal energy consumption. Besides, increasing the coupling strength first enhances the peak of resonance until it reaches at saturation value.

Finally, we have analyzed the influences of the average degree on the VR in heterogeneous networks. We have found that although increasing link density does not significantly change the VR performance of the heterogeneous SF networks, it increases the high frequency signal level for the optimal detection of weak input signal. In the context of link density effects, our findings are consistent with the results in [10] and [25]. Moreover we have corroborated these results for different network topologies. The qualitative behavior ot the VR for the heterogeneous network is independent of the network topology.

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