



ENHANCING NETWORK SYNCHRONIZATION BY SPARSE REPULSIVE COUPLINGS

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In a small-world network of mainly attractively coupled nonidentical neurons, we show that a small fraction of phase-repulsive couplings is able to strongly improve synchronization for certain values of the link strength, and long-range connection probability. By means of a spectral analysis we relate the observed dynamical behavior with the structural properties of the network.

Keywords: Small-world network; synchronization; phase-repulsive coupling.

1. Introduction

One of the most important mechanisms for information transmission and processing in large ensembles of oscillators is synchronization, specially in biological networks. Different experiments have pointed out this fact in the neural tissue, finding a relationship between the functioning of the system and the net structure [Sergev *et al.*, 2002; Eguíluz *et al.*, 2005]. The importance of the synchronous behavior in real collectives has given rise to the question of how to optimize the network topology for synchronization. Several strategies have been developed with the aim to find the best method to achieve synchronization in complex networks, mainly focusing on a weighting procedure of the links in networks with heterogeneous degree [Boccaletti *et al.*, 2006]. Most of the works are devoted to the study of synchronization in networks of attractively coupled identical units, but heterogeneity of dynamical units is naturally present in real networks, biological or social. Also, in real systems, heterogeneity in connections is also a common feature; it is known that biological networks combine different kinds of interactions to improve synchronization

and transmission performance, as in the case of excitatory and inhibitory synapses coexistence in the brain [Ravinovich *et al.*, 2006].

In a previous work [Leyva *et al.*, 2006] we explored both the heterogeneity of the units and couplings in a network of Hodgkin–Huxley neurons. There, we showed that a small percentage of repulsive links in a small-world structure can induce the emergence of a collective oscillatory state in cases where the equivalent network based on only attractive connections is unable to synchronize or even to activate the ensemble. In this work, we extend the previous study to a different neural model, to show that the only dynamical constraint for the phenomenon to appear is the neural excitability [Hodgkin & Huxley, 1952]. A structural analysis allows us to reveal the relationship between the dynamics and the topology.

2. Model and Numerical Results

We wish to study the onset of synchronous behavior in a heterogeneous population of excitable units, where initially a small part of the ensemble is

self-oscillatory while the remaining stay in a quiescent state. For this purpose, we study the dynamics of an ensemble of nonidentical coupled units using two well-known models for neural excitability: the Hodgkin–Huxley (HH) and the Fitz-Hugh–Nagumo (FHN). The HH model belongs to class 1 excitability spiking at arbitrarily low frequency, whereas the FHN is a class 2 excitability model with a certain firing frequency band [Izhikevich, 2005]. Both models have a different complexity level but the common feature is the existence of a transition from excitable to oscillatory dynamics by tuning only one control parameter, corresponding to the external current.

2.1. The HH network

Initially, we study a network of N Hodgkin–Huxley (HH) neurons considered as spatially isopotential cells. The model reads:

$$C\dot{V}_i = I_i - I_i^{\text{ion}}(V_i, x_i) + d \sum_j \ell_{ij} V_j$$

$$\dot{x}_i = \alpha_x(1 - x_i) - \beta_x x_i$$

The variables and parameters are the standards in literature [Hodgkin & Huxley, 1952]. $\mathbf{L} = (\ell_{ij}) = (c_{ij})/k_i$ is the Laplacian matrix, zero-row sum, with k_i normalizing the connection strength by the number of incoming links to node i , and $\mathbf{C} = (c_{ij})$ is the connectivity matrix, equal to ± 1 if nodes i and j are connected, and zero otherwise. The minus sign in the connection indicates that the neurons associated to those nodes are repulsively connected. The coefficient d stands for the global coupling strength.

The heterogeneity in the population is introduced by means of the external bias current I_i , which is uniformly distributed within the interval $I_0 \pm \Delta I$, with $I_0 = 9 \mu\text{A}/\text{cm}^2$ near the Hopf bifurcation according to class I excitability, in such a way that for the chosen $\Delta I = 0.2 \mu\text{A}/\text{cm}^2$, about 70% of the neurons stay at rest while the remaining will fire periodically.

In order to observe how unit heterogeneity and phase repulsive couplings influence a coherent behavior, initially we consider just a regular lattice (short-range links) topology with identical (all positive or all negative) connections for an ensemble of N neurons. As expected, the system reaches a phase synchronized state for a certain $d = d_+ \sim 0.2$ and, equivalently, for $d = d_- \sim 0.02$ it reaches an antiphase coherent state. Since $d_- < d_+$, phase-repulsive coupling results are more effective

to globally activate and entrain the whole network [Leyva *et al.*, 2006].

However, our main interest is to explore the influence of a complex topology (long-range links) in the activation and synchronization of the network. Taking into account the previous result, we consider the possibility of being repulsive at least for part of the long-range connections. Then, we fix $d = 0.1$ for the coupling strength, that is, within the unsynchronized regime for local positive coupling as explained above, \mathbf{C} is modeled by keeping the regular short-range connections positive $c_{i,i\pm 1} = +1$, and by randomly adding a fraction p of long-range couplings $c_{ij} = c_{ji} = \pm 1$ with a probability q of being negative.

Figure 1 shows space-time plots of the voltage variable through the whole network for different probabilities p and q . In the absence of long-range connections (not showed), for the chosen coupling strength d , only about the initial 30% of the neurons is firing and the array is not activated or synchronized, as said above. When long-range links are included, the first observation is that for any p , a minimum fraction of the newly added links needs to be repulsive in order to increase the activity of the network, as evident when comparing Fig. 1(a) with Figs. 1(b)–1(d). There, the activity generated by the initially active neurons is reduced or even annihilated when all the long-range connections are attractive ($q = 0$). However, the scenario completely changes when, for the same p , some of the shortcuts are repulsive ($q > 0$) like in Figs. 1(b)–1(d) where self-sustained electrical activity emerges for nonzero q .

In addition, we observe the existence of optimal values for p (let us call this value $p = p_c$) and q for which the collective oscillation becomes maximally phase-coherent. This fact can be observed by comparing Fig. 1(b) where $p = p_c$ and Fig. 1(d) for the same q but slightly higher p .

We now quantitatively study how the dynamics is affected by p and q , by measuring the mean firing rate (MF) of the network and the standard deviation of the global electrical voltage $V(t) = \sum_{i=1}^N V_i(t)$ obtained as $\sigma_V = \sqrt{\langle V^2(t) \rangle - \langle V(t) \rangle^2}$, where $\langle \dots \rangle$ denotes temporal average. While MF measures the network activation, a high σ_V indicates that this activity is coherent. When the network is fully activated MF approaches 70 Hz.

The effect of the topology in the dynamics as a function of p and q can be seen in the contour plots in the $p - q$ space shown in Fig. 2. We first

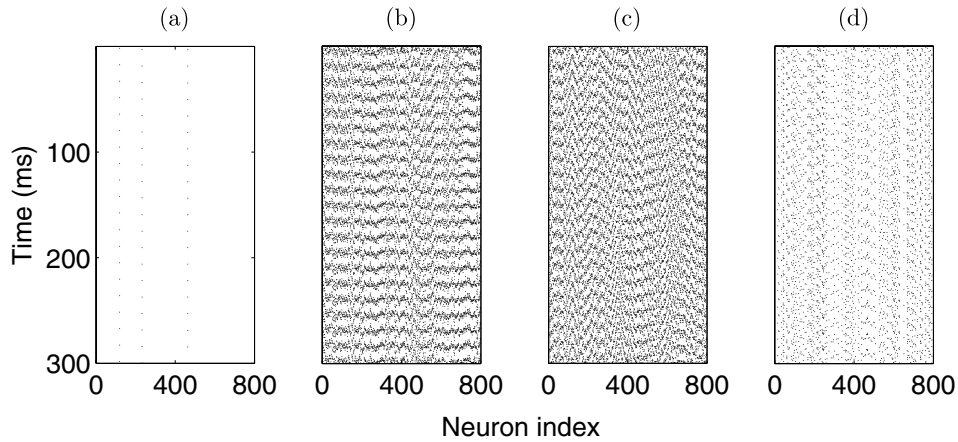


Fig. 1. Space-time plots of the neuron voltage for a $N = 800$ Hodgkin–Huxley units network, with $\Delta I = 0.2$, $d = 0.1$, and different coupling connectivities: (a) network with long range couplings, $p = p_c = 0.0055$, and $q = 0$; (b) same as (a) but $q = 0.3$; (c) same as (b) but $q = 0.45$; (d) same as (b) but $p = 0.015$.

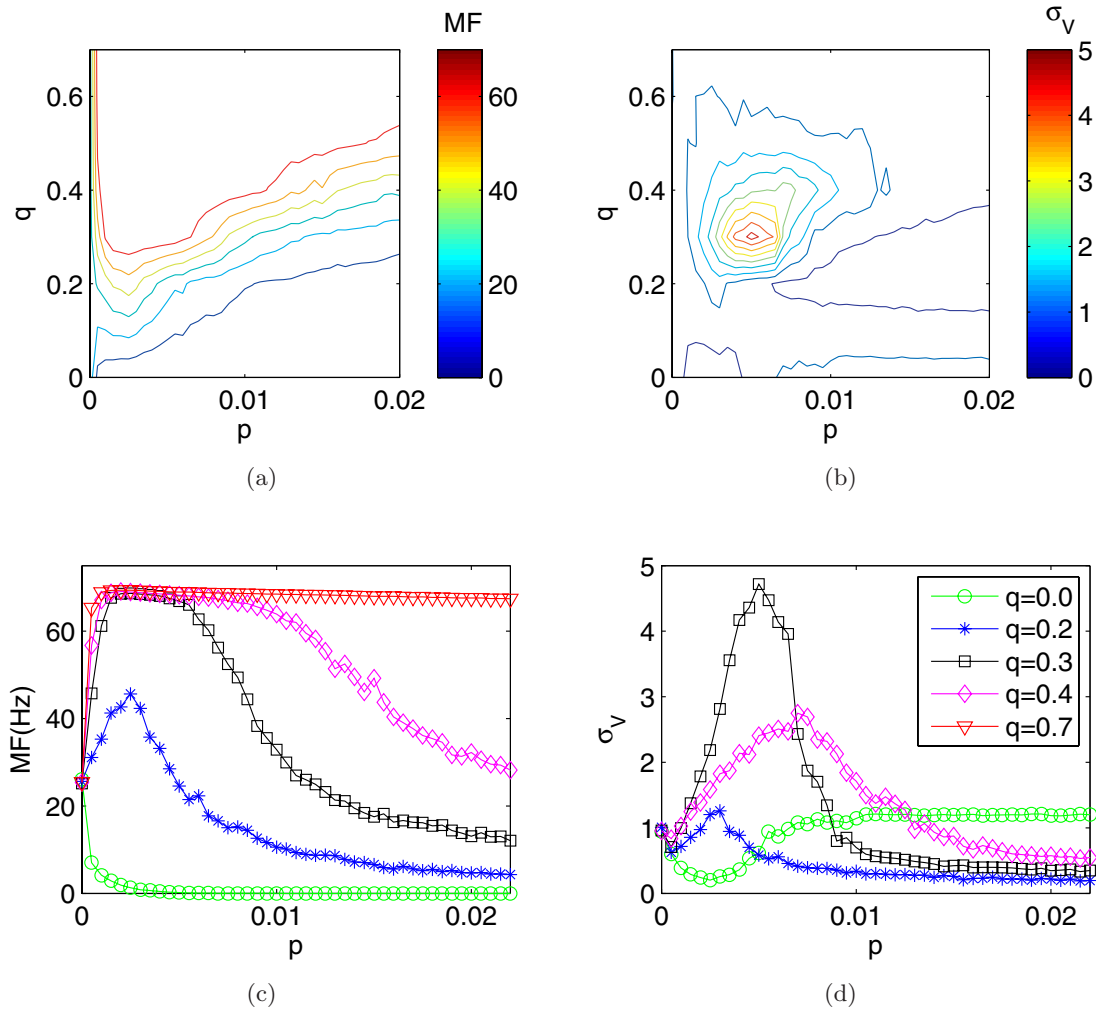


Fig. 2. (a)–(c) Mean frequency (MF) and (b)–(d) network coherence σ_V as a function of p and q in a $N = 800$ Hodgkin–Huxley network. Panels (a) and (b) are contour plots in the $p - q$ plane. It becomes evident from panel (b) that there exist values for p and q for which the coherence is maximum. Each point is averaged over 100 simulations, 1 s long (transients avoided), for different network and initial condition realizations. Panels (c) and (d) are cross-sections of the 3D representation of MF and σ_V for several values of q , respectively. Legend in panel (d) applies also to panel (c).

observe the different behavior of both the activity and coherence as a function of p . The effect of the activity (measured by the MF rate) is shown in the left panels (a) and (c), and the coherence is represented in the right panels (b) and (d) through σ_V . While for MF, there is a transition towards a fully activated system at certain p , the σ_V reaches a maximum at this point. In Figs. 2(b) and 2(d) the signature of a resonance is clear both in p and q , as observed in Fig. 1.

In Fig. 2, we also observe the importance of q in the response of the network. First, it is clear that a value $q \neq 0$ is needed to activate the network, which is related to the larger ability of a negative perturbation to move the system out from the stable point (quiescent state). The q value of maximal activity depends slightly on p . Additionally, this activity will be coherent for a (p, q) pair of values that shift to higher p as q increases.

2.2. The FHN network

In order to confirm the validity of our results we perform a similar study with a Fitz-Hugh–Nagumo neuron network, described by the equations:

$$\dot{V}_i = I_i + V_i - \frac{V_i^3}{3} - w_i + d \sum_j \ell_{ij} V_j$$

$$\dot{w}_i = 0.08(V_i - 0.8w_i + 0.7)$$

FHN is a simplified model based on the HH model, using a polynomial approximation to the ionic currents. However, it retains the main dynamical features regarding the excitability, which seems

central for the existence of the resonance described above for the HH network. To obtain an equivalent heterogeneity in the population, the external bias current I_i is now distributed within the interval $I_i = 0.323 \pm 0.003$. As in the previous case, this interval is chosen to assure that the ratio 70%/30% of silent and oscillating neuron is maintained.

First, we study the synchronization properties of a regular lattice of nodes with all positive or negative links. We observe that again the phase-repulsive lattice is much more effective in activating the network, with activation thresholds of $d_+ = 0.3$ and $d_- = 0.05$, respectively. This asymmetry is the key for the trade-off between activation and synchronization when long-range links are included.

In Fig. 3, the space-time plots of a network of $N = 600$ FHN neurons can be observed, for several situations dynamically equivalent to those in Fig. 1. As in the previous case, there exists a critical long-range link probability $p = p_c$ and an optimal fraction $q = q_c$ of negative long-range links to maximally activate and synchronize the network [Fig. 3(b)]. A smaller q fraction results in a mostly inactive ensemble [Fig. 3(a)], while a higher q yields an active but incoherent state [Fig. 3(c)]. Furthermore, when $p > p_c$, the activity decays even for $q = q_c$ [Fig. 3(d)].

Figure 4 is equivalent to Fig. 2. Here it can be seen that a strong resonance also appears in the coherence of the network for certain values of both probabilities p and q . If we compare these results with its counterpart in Fig. 2, we observe that the resonance is wider both in p and q than for the HH case. This fact is due to the higher asymmetry than

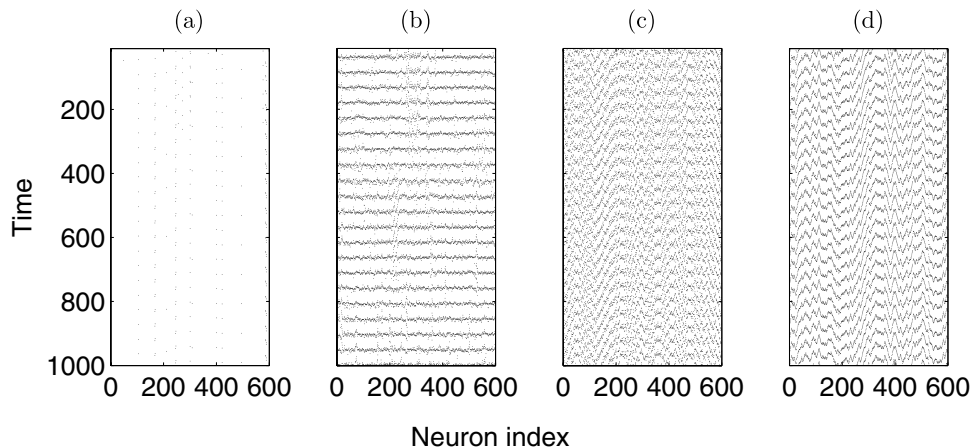


Fig. 3. Space-time plots of the neuron voltage V_i for a $N = 600$ FHN units network, with $d = 0.1$, and different coupling connectivities: (a) network with long-range couplings, $p = p_c = 0.01$, and $q = 0$; (b) same as (a) but $q = 0.2$; (c) same as (b) but $q = 0.4$; (d) same as (b) but $p = 0.001$.

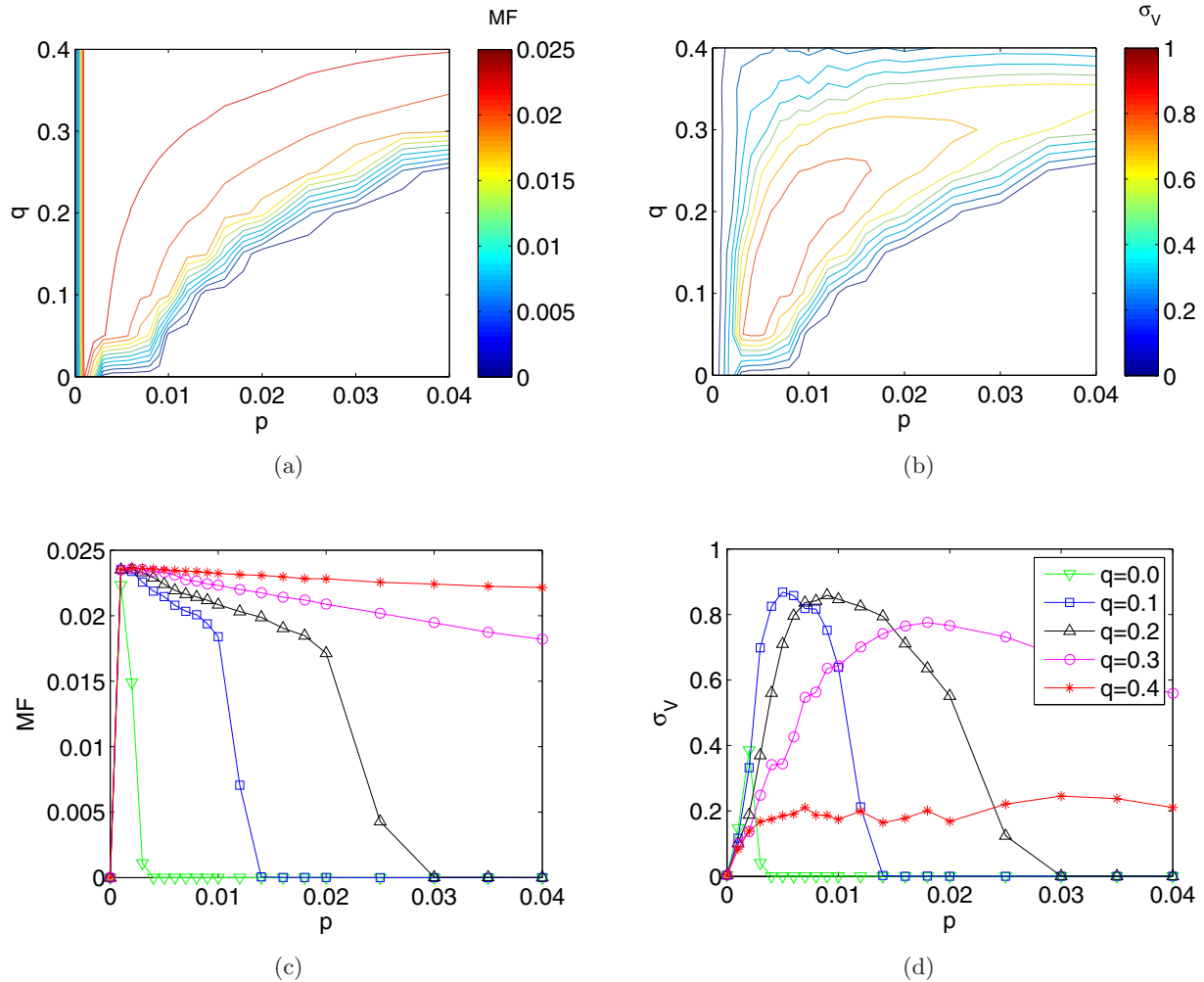


Fig. 4. Mean frequency (MF) and network coherence σ_V as a function of p and q in a $N = 600$ FHN network. Figure description is the same as in Fig. 2. It can be seen that the $p - q$ resonance is wider here than in the HH-network, due to the **higher asymmetry in the attractor**.

in the HH case in the activation efficiency for the positive and negative links.

3. Structural Analysis

Once we know the dynamical features of the phenomenon, the linkage with the network topology is pointed out from the observation that the critical link probability p_c depends strongly on the ensemble size as $\simeq \ln(N)/N$, that is, coincides with the birth of the giant connected component (GCC) of the Poisson random graph with N nodes, which is precisely the network we have when only the randomly added long-range connections are considered (i.e. when we neglected the local couplings) [Leyva *et al.*, 2006].

Therefore, we wish to analyze whether the network structure has some bearing on the dynamics.

Recently, the master stability function method has been successfully used for this goal in several situations [Boccaletti *et al.*, 2006]. However, this method requires the dynamical units to be identical in order to consider the stability of the perfectly synchronous state, which is not our case. Then, to perform our analysis we use a purely structural analysis, based on the properties of \mathbf{L} , ignoring the dynamics imposed on it, that is, we consider

$$\dot{\mathbf{V}} = d\mathbf{L}\mathbf{V} \quad (1)$$

where $\mathbf{V} = (V_1, \dots, V_N)$. Then, there is a basis in which $V_i \approx \exp(d\lambda_i t)$, where λ_i are the eigenvalues of \mathbf{L} .

It is well known that all the eigenvalues of the Laplacian associated to a network with only attractive couplings are negative. However, when we add some repulsive connections, \mathbf{L} has both positive and

negative eigenvalues. We find that any set of initial states rapidly evolves into the subspace S^+ , associated with the positive eigenvalues, within a time smaller than the characteristic temporal scale of the system dynamics ($\tau \approx 15$ ms for the HH unit).

To quantify the effect of S^+ , we note that, for a given positive λ_i^+ , $e^{d\lambda_i^+ t}$ is a measure of how much the system spreads into the subspace defined by the corresponding eigenvector. Then, the ratio

$$\frac{e^{d\lambda_i^+ t}}{e^{d\lambda_{\max}^+ t}} = e^{d(\lambda_i^+ - \lambda_{\max}^+)t} \quad (2)$$

measures how different is the evolution in that subspace with respect to that where the system develops faster. By defining the geometric average of this ratio,

$$g(t) = e^{d(\langle \lambda^+ \rangle - \lambda_{\max}^+)t} \quad (3)$$

we can estimate the homogeneity of the evolution in S^+ with a number in $(0, 1]$. Then, $g \rightarrow 1$ means similar evolution in all dimensions in S^+ , whereas $g < 1$ implies that the behavior is determined by those vectors with the largest associated eigenvalues.

We are now interested in the behavior of $g(t)$ as a function of p and q . As the shape of $g(t)$ with p is not very sensitive to time, we fix $t = d^{-1} \sim \tau$ to focus our study within the time scale of our dynamical unit. In Fig. 5 we observe that $g \equiv g(\tau)$ presents a minimum at p_c which is lower for higher values of q , and whose position shifts to higher p as q increases, as in the numerical simulations of

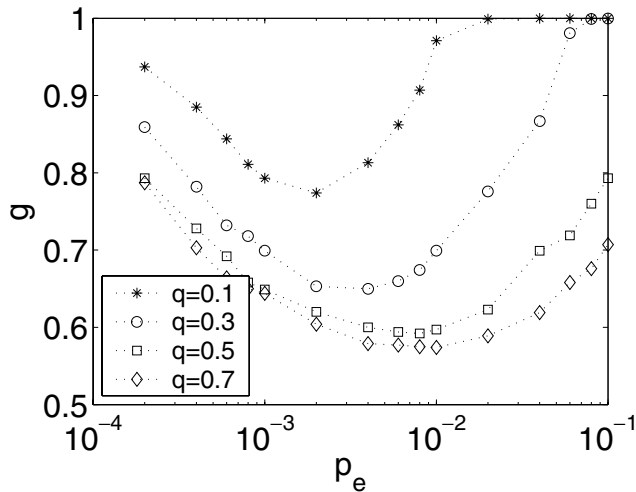


Fig. 5. Dependence of the structure parameter g with the adding link probability p , in a log-linear scale, for different probabilities q . Each point is an average over 100 different realizations of a $N = 800$ network.

the networks. In this last case, the system becomes more heterogeneous due to the connectivity, and therefore, the intrinsic dynamics is minimally constrained by the structure that arises around p_c due to the repulsive shortcuts.

The results reflect the fact that at p_c there is a transition from a $2 - k$ lattice to a network with an exponential degree distribution, indicating the presence of hubs. In this state, where the eigenvalues dispersion is large, the activity is enhanced, as observed in the numerical simulations, and the network is compatible with the diversity of the dynamical units, which are allowed to reach a partially coherent state. On the other hand, far from p_c the nodes are indistinguishable from a topology point of view and the dynamical units are constrained to evolve alike, when they have different intrinsic dynamics, failing to attain a coherent behavior.

In summary, we have shown numerically how a small fraction of phase-repulsive links can enhance activity and coherence in a complex network of nonidentical dynamical units, initially in different dynamical regimes. We have numerically proved this statement for complex ensembles of two different neuronal models. A spectral analysis allows us to obtain information about how the topology influences the dynamics.

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