



Optimal spatial synchronization on scale-free networks via noisy chemical synapses

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ABSTRACT

We show that the spatial synchronization of noise-induced excitations on scale-free networks, mediated through nonlinear chemical coupling, depends vitally on the intensity of additive noise and the coupling strength. In particular, a twofold optimization is needed for achieving maximal spatial synchrony, thus indicating the existence of an optimal noise intensity as well as an optimal coupling strength. On the other hand, the traditional linear coupling via gap junctions, while still requiring a fine-tuning of the noise intensity, does not postulate the existence of an optimal coupling strength since the synchronization increases monotonously with the increasing coupling strength. Presented results reveal inherent differences in optimal spatial synchronization evoked by chemical and electrical coupling, and could hence help to pinpoint their specific roles in networked systems.

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1. Introduction

Synchronization is key in numerous situations that constitute everyday life, and it is only natural that it has become an important paradigm throughout natural as well as social sciences. Whether it is the synchrony among group dancers or excitations of neurons, the joint execution of a seemingly simple task adds value to the final output that is often beyond expectations. Especially by nonlinear dynamical systems [1] synchronization is recurrently in the focus of attention, and most recently, insightful findings regarding the synchronization on complex networks have been presented [2–7] and reviewed [8]. More specifically, universalities in the synchronization of weighted random networks were reported in [6] and paths to synchronization on complex networks have been investigated in [7]. Moreover, it was shown that synchronization could reveal topological scales of complex networks [9]. Since neurons are known to be linked through complex networks [10–14], extending these findings to specific models of neuronal dynamics [15–19] seems justified and currently of substantial interest [20–22].

Another important ingredient of neuronal dynamics is noise, in particular since neurons are known to be noisy analog units, which if coupled can carry out highly complex and advanced computations with cognition and reliability [23]. After the realization of the fact that noise can play a constructive role in nonlinear dynamical systems [24]; a phenomenon that is most frequently celebrated as stochastic [25,26] or coherence resonance [27,28], noisy ingredients quickly became an inseparable part of studies examining excitable neuronal

dynamics [29,30], as comprehensively reviewed in [31]. Furthermore, effects of noise in general were studied for spatially extended systems [32,33], whereby relevant for the present work are studies examining array enhanced stochastic [34] and coherence resonance [35], as well as phase synchronization of excitable units [36,37].

Here we focus on the spatial synchronization of excitable Morris–Lecar neurons [17], whereby we use the scale-free network [38] as the underlying interaction topology. Moreover, we specifically examine the role of nonlinear coupling via chemical synapses and the standard linear diffusive coupling via gap junctions [39]. Thereby we conceptually follow an interesting study by Balenzuela and García-Ojalvo [40], reporting that indeed chemical synapses may be beneficial for the temporal coherence of a coupled neuronal system. As the main parameters we consider the intensity of additive noise and the coupling strength, and determine which conditions constitute an optimal environment for spatial synchronization of noise-induced excitations on the scale-free network. We show that the coupling via chemical synapses requires fine-tuning of the noise intensity as well as the coupling strength for optimal spatial synchrony, whereas by gap junctional interactions increasing coupling strengths do not evoke a resonance-like dependence. We thus reveal conditions under which optimal spatial synchronization of noise-induced excitations on scale-free networks can be achieved, thereby particularly focusing on the type of interactions among coupled neurons. Presented results could prove useful in further clarifying the specific importance of chemical and electrical coupling between neurons on complex interaction networks.

The remainder of this paper is organized as follows. In the next section we describe the Morris–Lecar model [17] with the two considered coupling schemes, as well as the scale-free network and other mathematical methods presently in use. Results are presented in

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Table 1
Parameter values of the Morris–Lecar model used throughout this work.

Parameter	Value
C_m	5.0 $\mu\text{F}/\text{cm}^2$
ϕ	1/15 s^{-1}
g_{Ca}	4.0 $\mu\text{S}/\text{cm}^2$
g_{K}	8.0 $\mu\text{S}/\text{cm}^2$
g_{L}	2.0 $\mu\text{S}/\text{cm}^2$
V_{Ca}	120 mV
V_{K}	−80.0 mV
V_{L}	−60.0 mV
V_{M1}	−1.2 mV
V_{M2}	18.0 mV
V_{W1}	2.0 mV
V_{W2}	17.4 mV
E_s	0.0 mV
α	2.0 $\text{ms}^{-1} \text{mM}^{-1}$
β	1.0 ms^{-1}
T_{max}	1.0 mM
τ_{syn}	1.5 ms
D	0.32–8.0 mV/ms (to be varied)
g^{syn}	0.1–10.0 nS (to be varied)

Section 3, whereas in the last Section we summarize and discuss our findings.

2. Mathematical model and setup

The networked model to be used presently consists of noisy Morris–Lecar neurons [17] that are governed by the differential equations of the form

$$\frac{dV_i}{dt} = \frac{1}{C_m} (I_i^{\text{app}} - I_i^{\text{ion}} - I_i^{\text{syn}}) + D\xi_i(t), \quad (1)$$

$$\frac{dW_i}{dt} = \phi\Lambda(V_i)[W_\infty(V_i) - W_i], \quad (2)$$

where V_i and W_i are the membrane potential and the fraction of open potassium channels of neurons $i=1, \dots, N$ respectively. Additive Gaussian noise with zero mean, intensity D , and autocorrelation $\langle \xi_i(t)\xi_j(t') \rangle = \delta_{ij}\delta(t-t')$ accounts for the stochastic components of neuronal dynamics, especially the synaptic current I_i^{syn} , whereas the externally applied current I_i^{app} is the main bifurcation parameter determining the deterministic dynamics of each neuron. Throughout this work we set $I_i^{\text{app}} = 46$ mA placing each neuron in an excitable steady state prior to a subcritical Hopf bifurcation (note that this depends also on the values of other parameters) [41]. Moreover, the ionic current is given by

$$I_i^{\text{ion}} = g_{\text{Ca}}M_\infty(V_i)(V_i - V_{\text{Ca}}^0) - g_{\text{K}}W_i(V_i - V_{\text{K}}^0) - g_{\text{L}}(V_i - V_{\text{L}}^0), \quad (3)$$

whereas the membrane potentials are described by the functions

$$M_\infty(V_i) = \frac{1}{2} \left[1 + \tanh\left(\frac{V_i - V_{\text{M1}}}{V_{\text{M2}}}\right) \right] \quad (4)$$

$$W_\infty(V_i) = \frac{1}{2} \left[1 + \tanh\left(\frac{V_i - V_{\text{W1}}}{V_{\text{W2}}}\right) \right], \quad (5)$$

$$\Lambda(V_i) = \cosh\left(\frac{V_i - V_{\text{W1}}}{2V_{\text{W2}}}\right). \quad (6)$$

The mathematical form of the synaptic current I_i^{syn} depends on the considered coupling scheme. In case of linear diffusive coupling via gap junctions I_i^{syn} takes the form

$$I_i^{\text{syn}} = \sum_{j \in \text{neigh}(i)} g_{ij}^{\text{syn}} (V_i - V_j), \quad (7)$$

whereas by nonlinear coupling via chemical synapses, based on [42], the form is

$$I_i^{\text{syn}} = \sum_{j \in \text{neigh}(i)} g_{ij}^{\text{syn}} r_j (V_i - E_s), \quad (8)$$

where r_j is the fraction of bond receptors given by

$$\frac{dr_j}{dt} = \alpha[T]_j(1 - r_j) - \beta r_j. \quad (9)$$

Eqs. (7) and (8) both feature g_{ij}^{syn} , which is the conductance of the synapse linking neuron i with neuron j , as well as the sum running over all the neighbors of neuron i on the scale-free network. In addition, Eq. (8) introduces an additional parameter E_s determining the synapse type, as well as the variable r_j , which is further determined by the concentration of neurotransmitters released into the synaptic cleft $[T]_j = T_{\text{max}}\Theta(T_b^j - \tau_{\text{syn}} - t)\Theta(t - T_b^j)$. Here T_b^j is the time at which neuron j fires and τ_{syn} is the time during which the synaptic connections are active. Parameter values used throughout this work are given in Table 1. For their meaning the reader is referred to the original works [17,42] as well as to Ref. [40].

As the underlying interaction network we use the scale-free network generated via growth and preferential attachment as proposed by Barabási and Albert [38], comprising $N=200$ vertices. If neurons i and j on the network are connected then $g_{ij}^{\text{syn}} = g_{ji}^{\text{syn}} = g^{\text{syn}}$, but otherwise $g_{ij}^{\text{syn}} = g_{ji}^{\text{syn}} = 0$ and $g_{ii}^{\text{syn}} = 0$. Using the notation of [38], we start with $m_0 = 2$ connected vertices, and subsequently every new vertex is attached to $m = 2$ old vertices already present in the network, whereby the probability Π that a new vertex will be connected to vertex i depends on its degree k_i in accordance with $\Pi = k_i/N^{-1}\sum_j k_j$. This growth and preferential attachment scheme yields a network with an average degree $k_{\text{avg}} = N^{-1}\sum_j k_j$ equaling 4, and a power-law degree distribution with the slope of the line equaling -2.9 on a double logarithmic graph. In order to warrant statistical accuracy, all below presented results were obtained as averages over 100 different realizations of the scale-free network for each pair of D and g^{syn} .

Finally, as a compact measure for the degree of spatial synchronization of noise-induced excitatory fronts we use

$$S = \frac{1}{T} \int_{t=0}^T [\langle V_i^2(t) \rangle - \langle V_i(t) \rangle^2] dt, \quad (10)$$

where $\langle \dots \rangle$ denotes averages over all $i=1, \dots, N$ coupled neurons. Low values of S characterize highly synchronous excitatory fronts ($S=0$ if

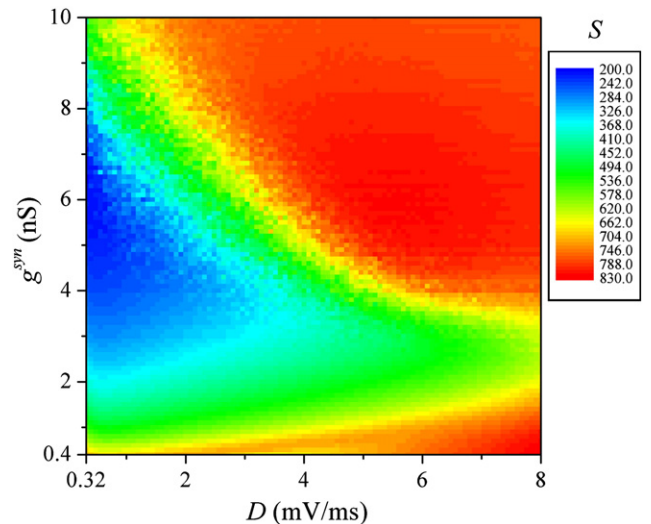


Fig. 1. Color map of spatial synchronization S in dependence on the noise intensity D and the coupling strength g^{syn} for the nonlinear coupling via chemical synapses.

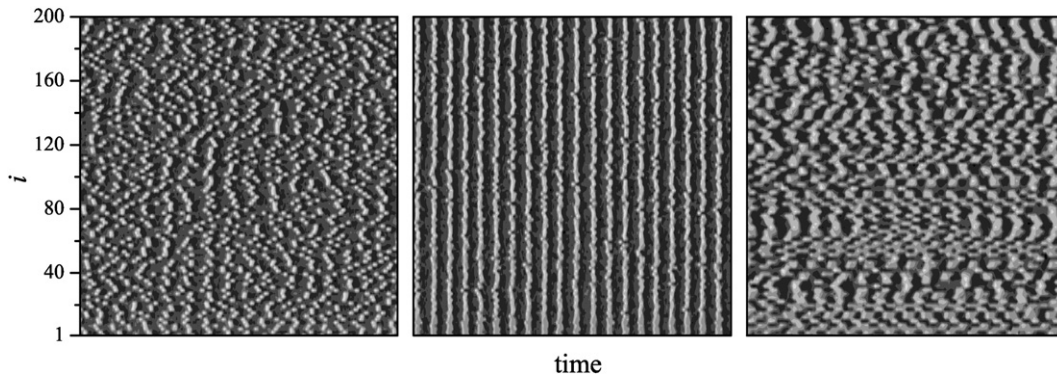


Fig. 2. Space–time plots of neuronal activity for the nonlinear coupling via chemical synapses, obtained for $D = 5.0$ mV/ms and $g^{\text{syn}} = 0.6$ nS (left panel), $g^{\text{syn}} = 3.0$ nS (middle panel), $g^{\text{syn}} = 10.0$ nS (right panel). The color profile is linear, white depicting $V_i = -80.0$ mV and black $V_i = 60.0$ mV.

the synchronization would be perfect), whereas large S arise when the spatial synchronization deteriorates.

3. Results

We start by presenting a color map displaying S in dependence D and g^{syn} in Fig. 1, which was obtained by using the nonlinear coupling via chemical synapses. It can be observed that the spatial synchrony depends crucially on the coupling strength. In particular, S exhibits well-expressed minima throughout the whole span of D . On the other hand, D evokes a resonant response as well, but the latter is only weakly expressed for small values of g^{syn} while at larger coupling strengths synchronization solely deteriorates as D increases. These features will be presented more accurately in what follows.

The impact of g^{syn} on spatial synchronization via chemical synapses can be visualized nicely by space–time plots, as presented in Fig. 2. While for small (left panel) and large (right panel) coupling strengths the excitatory fronts are very inconsistent and barely inferable, the spatial synchrony of the fronts is substantially improved by the optimal value of g^{syn} (middle panel) for the considered value of D . Conversely, the minima of S evoked by optimal values of D are not expressed enough so that the difference in spatial synchrony could be appreciated from visually inspecting the space–time plots (not shown).

These observations can be made quantitatively more precise by plotting cross-sections of the color map presented in Fig. 1. The top panel of Fig. 3 shows S in dependence on the coupling strength for different values of D . Indeed, it can be observed that the minima are well expressed for all noise intensities since the difference between S obtained for the optimal g^{syn} and limiting values of the considered interval ($g^{\text{syn}} = 0.4$ nS and $g^{\text{syn}} = 10$ nS) differ at least by 300 on both ends. The noise intensity D may also affect the spatial synchronization substantially, as shown in the bottom panel of Fig. 3, yet the minima can be observed only by small g^{syn} , whereas larger coupling strengths on scale-free networks don't support the phenomenon of noise-enhanced spatial synchronization. Note that for $g^{\text{syn}} \geq 6.4$ nS the spatial synchronization deteriorates fast as D increases. This can be linked to the fact that scale-free networks introduce an inherent level of diversity to the system, which if appropriately tuned, may evoke a resonant response on its own [43–45]. By higher coupling strengths the diversity, due to the scale-free interaction network, is sufficient to evoke optimally synchronized excitatory fronts, and thus the addition of dynamic Gaussian noise is unable to act constructively irrespective of D . Another noteworthy phenomenon can be observed by small values of $g^{\text{syn}} = 0.4$ nS, namely the so-called locally optimal response of the scale-free network that is responsible for the first minimum of S occurring at $D = 0.72$ mV/ms. By small coupling strengths neurons that are directly linked to the main hub of the scale-free network can form a quasi-isolated entity, which can be influenced by substantially

lower noise intensities than the whole network, as recently demonstrated for the phenomenon of stochastic resonance in Ref. [46].

It remains of interest to compare above results with those obtained with the linear coupling via gap junctions. The bottom panel of Fig. 4 shows a rather familiar dependence of S on D . In particular, there exists an optimal noise intensity by which the spatial synchronization of noise-induced excitations is best expressed. Similarly as by nonlinear coupling, this feature becomes weaker expressed as g^{syn} increases, until it eventually vanished completely for $g^{\text{syn}} \geq 3.2$ nS. Moreover, compared to the bottom panel of Fig. 3, the minima are

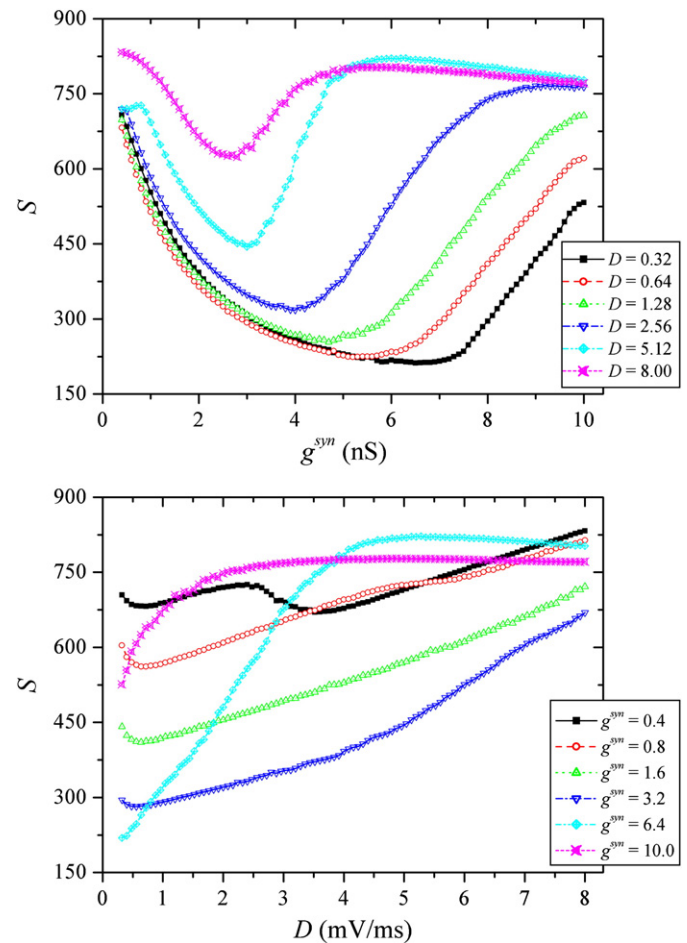


Fig. 3. Spatial synchronization S in dependence on the noise intensity D (bottom panel) and the coupling strength g^{syn} (top panel) for the nonlinear coupling via chemical synapses.

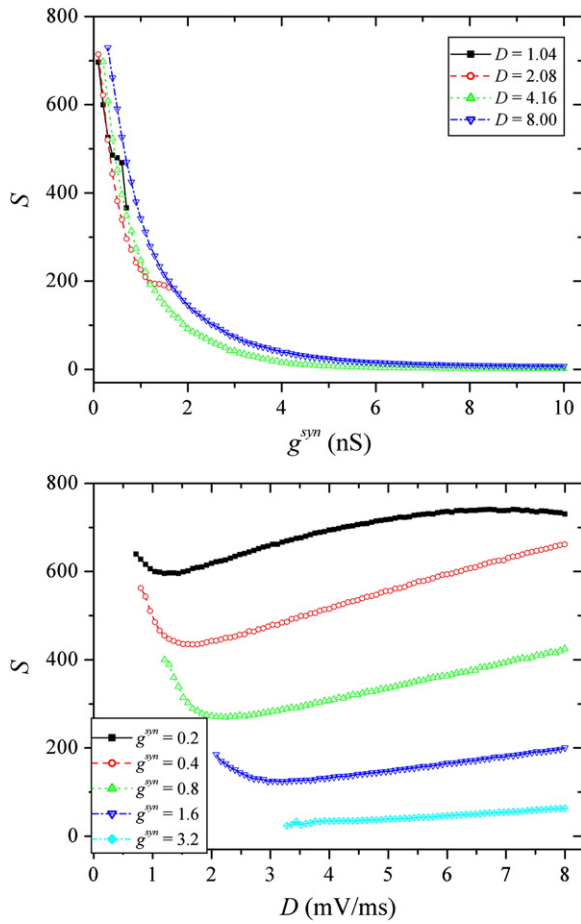


Fig. 4. Spatial synchronization S in dependence on the noise intensity D (bottom panel) and the coupling strength g^{syn} (top panel) for the linear diffusive coupling via gap junctions. Note that combinations of D and g^{syn} which failed to evoke excitations are not depicted.

somewhat better expressed. The top panel of Fig. 4, on the other hand, shows significantly different results than are presented in the top panel of Fig. 3 in that there is no resonant dependence of S on g^{syn} irrespective of D . In particular, as the coupling strength increases the synchronization becomes better pronounced (S decreases) during the whole span of D or noise becomes unable to induce excitations (note that for $D = 1.04$ mV/ms and $D = 2.08$ mV/ms curves don't extend to $g^{\text{syn}} = 10.0$ nS). However, since the linear coupling is active the whole time, not just during the spiking phase as by the nonlinear coupling via chemical synapses, the maximal level of spatial synchrony is higher in this case. Note that phase slips may occur also during the quiescent phase of neuronal dynamics, and the nonlinear coupling therefore has a disadvantage in terms of warranting spatially synchronous noise-induced excitatory fronts if compared to the linear diffusive coupling via gap junctions. Aside from these quantitative differences, the most significant qualitative difference is that by linear coupling the resonant response of S on g^{syn} is absent, while by nonlinear coupling it constitutes the most significant fine-tuning leading to the optimal spatial synchrony of neuronal excitations on scale-free networks.

4. Summary

In sum, we reveal inherent differences in spatial synchronization of noise-induced neuronal activity on scale-free networks that are brought about by different coupling schemes. While nonlinear coupling via chemical synapses requires a twofold optimization for warranting maximal spatial synchrony, the traditional linear coupling via gap junctions demands only the intensity of additive noise to be

fine-tuned. Furthermore, while the nonlinear coupling enables the observation of the locally optimal response by small coupling strengths, the linear coupling constitutes, by a given coupling strength and noise intensity, a substantially better environment for spatially synchronous excitatory fronts. Both coupling schemes, however, fail to enable noise-induced enhancement of spatial synchronization by high coupling strengths, which is arguably due to the inherent diversity of the scale-free structure that on its own constitutes an optimal environment by strong enough inter-neuronal interactions. The study thus supplements nicely recent findings on synchronization and noise-induced coherence [47–52], and also confirms that chemical synapses deserve separate treatment, as recently argued in [40]. In future studies, it remains of interest to investigate more thoroughly the impact of the average degree of scale-free networks on the phenomenon of synchronization via different types of coupling. Interestingly, Acebrón *et al.* [53] have shown that the amplification of weak signals on scale-free networks, which arguably plays a crucial role also in warranting synchronization through neuron-to-neuron communication, depends significantly on the average degree and the coupling strength, yet vanishes by all-to-all coupling. It is thus reasonable to assume that quantitatively different behaviors may be observed as the average degree of scale-free networks will increase, but significant qualitative changes will set in only when the scale-free topology is overruled by all-to-all coupling. Furthermore, it may also be instructive to examine the impact of diversity of constitutive units of scale-free networks, which for example has recently been found beneficial for intercellular calcium wave propagation [54]. We hope this work will be useful for further unveiling the importance of information transmission through chemical synapses on complex networks.

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