NOISE-INDUCED UP/DOWN DYNAMICS IN SCALE-FREE NEURONAL NETWORKS

JORDI GRAU-MOYA[*], ANTONIO J. PONS[†]
and JORDI GARCIA-OJALVO[‡]
*Departament de Física i Enginyeria Nuclear,
Universitat Politècnica de Catalunya, Edif. GAIA,
Rambla de Sant Nebridi s/n, 08222 Terrassa,
Barcelona, Spain*
*jordi.grau@tuebingen.mpg.de
†apons@upc.edu
‡jordi.g.ojalvo@upc.edu

Cortical neuronal networks are known to exhibit regimes of dynamical activity characterized by periods of elevated firing (up states) separated by silent phases (down states). Here, we show that up/down dynamics may emerge spontaneously in scale-free neuronal networks, provided an optimal amount of noise acts upon all network nodes. Our conclusions are drawn from numerical simulations of networks of subthreshold integrate-and-fire neurons, connected to each other according to a scale-free topology. We study the structure of the up/down regime both in time and in terms of the node degree. We also examine whether localized random perturbations applied to specific network nodes are able to generate up/down dynamics, showing that this regime arises when noisy inputs are applied to low-degree (nonhub) network nodes, but not when they act upon network hubs.

Keywords: Up/down states; neuronal noise; scale-free neuronal networks.

1. Introduction

Even though associated with a state of brain quiescence, slow-wave sleep is characterized by rich firing patterns at the level of single neurons. These firing patterns give rise to the low-frequency rhythms in brain activity (on the order of Hz) that define this sleep stage [Steriade *et al.*, 2001]. This activity takes the form of alternating phases of sustained firing (up states) and hyperpolarization leading to the complete absence of spikes (down states). The time scale of the switchings between the two states is of the order of tenths of seconds to seconds, much larger than the time between spikes in the up phase [Steriade & Timofeev, 2003]. Similar alternance between depolarized and hyperpolarized regimes has been observed beyond slow-wave sleep, specifically in the visual cortex of anesthesized cats [Lampl *et al.*, 1999], in the somatosensory cortex of resting (but awake) rats and mice [Petersen *et al.*, 2003], and in cortical slice preparations [Sanchez-Vives & McCormick, 2000; Cossart *et al.*, 2003; Cunningham *et al.*, 2006; Johnson & Buonomano, 2007]. Much effort has been devoted in recent years to understand the mechanisms leading to such striking dynamical behavior in cortical networks. For instance, spontaneous up/down dynamics has been reported in neuronal network models including either nonstandard currents in the

---

dynamics of individual neurons [Bazhenov *et al.*, 2002; Kang *et al.*, 2004; Parga & Abbott, 2007] or multilayered connectivity architectures [Destexhe, 2009], or both [Compte *et al.*, 2003; Hill & Tononi, 2005]. Those models make distinct assumptions on both the local neuronal dynamics and the connectivity architecture necessary to generate up/down activity. Therefore, it is still unclear what are the minimal mechanisms leading to that behavior. To address this issue, here we consider a very simple model consisting of a network of standard integrate-and-fire neurons. We show, on the basis of numerical simulations, that when the neurons operate below threshold, an optimal amount of noise is sufficient to generate alternating phases of up and down activity that qualitatively mimic the slow oscillations observed in cortical networks.

Following multiple lines of experimental evidence gathered in recent years [Sporns *et al.*, 2004], we assume our neuronal network to have a nontrivial coupling architecture (i.e. neurons are not simply connected to their spatial neighbors) [Boccaletti *et al.*, 2006]. From the *functional* point of view, different experimental studies have revealed that the connectivity of brain networks displays both small-world [Buldú *et al.*, 2011; Castellanos *et al.*, 2011] and scale-free [Eguíluz *et al.*, 2005; van den Heuvel *et al.*, 2008; Chialvo, 2010] properties. In the latter scenario, the distribution of degrees (number of connections) of the network nodes follows a power law, in such a way that a relatively small (but non-negligible) number of highly connected functional nodes coexists with a larger number of less connected brain regions. At the *anatomical* level, experimental evidence reveals the existence of structural hubs in the brain [Zamora-Lopez *et al.*, 2009; Gong *et al.*, 2009; Modha & Singh, 2010; Guye *et al.*, 2010]. Also, studies of the robustness of brain networks to localized lesions give results that are consistent with an inhomogeneous distribution of degrees, in the sense that cortical networks are more sensitive to lesions in certain nodes more than in others [Kaiser *et al.*, 2007]. On the other hand, physical constraints reduce the probability of existence of highly connected nodes, leading instead to truncated power-law degree distributions [Bullmore & Sporns, 2009]. The situation is complicated by the strong multiscale character of the brain's spatial organization [Zalesky *et al.*, 2010]. Accordingly, several studies have challenged the view that anatomical networks

in the brain are fully scale-free [Sporns & Zwi, 2004], usually in favor of less node-heterogeneous (but still complex) connectivity architectures such as that of small-world networks [Humphries *et al.*, 2006]. Thus, it seems reasonable to assume that neuronal networks exhibit a combination of small-world properties [Strogatz, 2001] and an inhomogeneous connectivity profile, in which certain neurons are more connected than others.

In this paper, we focus, similarly to other numerical studies in the literature [Wang *et al.*, 2009b; Gong *et al.*, 2010], on a scale-free neuronal network, in order to take into account the existence of network nodes with different connectivity. Part of the results presented below, specifically the emergence of up/down dynamics induced by global noise, also arise in small-world and random networks, as we also show. However, the results related to the influence of local noise, presented in the last part of the paper, are specific to the case of a scale-free coupling architecture.

Noise is known to have an important and nontrivial influence in excitable systems [Lindner *et al.*, 2004], and in particular, in neuronal networks [McDonnell & Ward, 2011]. A large body of literature exists on phenomena such as stochastic resonance and stochastic coherence (usually called coherence resonance) in neuronal lattices, both with nearest-neighbor coupling [Jung & Mayer-Kress, 1995; Zhou *et al.*, 2001; Busch & Kaiser, 2003; Perc, 2005; Balenzuela & García-Ojalvo, 2005] and with complex coupling architectures, including small-world [Hao *et al.*, 2011; Wu *et al.*, 2011], scale-free [Wang *et al.*, 2009a; Chun-Biao *et al.*, 2010], and arbitrary [Gosak *et al.*, 2010] connectivity profiles. In most of those works, noise was seen to optimize the temporal regularity of the dynamics of the network, in terms of an increase in the coherence of periodicity of neuronal firing, either intrinsic to the neurons (stochastic coherence) or coming from an external driving of the network (stochastic resonance). In this work, on the other hand, noise enhances the up/down character of the network's dynamical behavior without leading to an increase in its periodicity, neither at the single-neuron nor at the population level.

The paper is organized as follows. Section 2 describes the dynamical neuronal model and describes the topological properties of the network. Section 3 presents the effect of increasing network-wide noise on the dynamics of the system, and

quantifies this effect. The structure, both in time and in node space, of the up/down dynamics observed for the optimal noise level is studied in Sec. 4. Finally, Sec. 5 examines the response of the network to local noisy perturbations depending on the degree of the input node. The paper ends with a discussion in Sec. 6.

2. Neuronal Network Model

We assume that the nodes in our neuronal network are described by a standard integrate-and-fire model [Gerstner & Kistler, 2002]. According to this model, the dynamics of the membrane potential $V_i(t)$ is given by a simple RC circuit equation

$$\frac{dV_i}{dt} = -\frac{V_i}{\tau_m} + I_{\text{ext},i} + I_{\text{syn},i} + D\xi_i(t), \qquad (1)$$

provided $V_i(t)$ is below a threshold value V_{th}, with i denoting a given neuron in the network. The parameter τ_m represents the time constant of the membrane, $I_{\text{ext},i}$ is the external current per unit capacitance acting upon the neuron, $I_{\text{syn},i}$ is the synaptic current (also per unit capacitance) coming from other neurons in the network, and $\xi_i(t)$ is a Gaussian white noise with zero mean and correlation $\langle \xi_i(t)\xi_j(t') \rangle = 2\delta_{ij}\delta(t - t')$, with D representing the noise intensity. In the presence of external and synaptic current, the membrane potential grows in a more or less monotonic manner, balanced by the relaxation term and driven by the random fluctuations. When the potential reaches the threshold, it is reset to 0, and kept there during a refractory time τ_{ref}.

The synaptic current acting upon neuron i is given by

$$I_{\text{syn},i}(t) = g \sum_{j \neq i} \sum_{\text{spikes}} A_{ij} f(t - t_{\text{spike},j}), \qquad (2)$$

Table 1.   Parameter values.

Symbol	Meaning	Value
V_{th}	Threshold potential	$10\,\text{mV}$
τ_m	Membrane time constant	$5\,\text{msec}$
I_{ext}	External current	$1.7\,\text{nA/nF}$
D	Noise intensity	variable
τ_{ref}	Refractory time	$5\,\text{msec}$
τ_d	Post-synaptic current decay time	$3\,\text{msec}$
τ_r	Post-synaptic current rise time	$0.1\,\text{msec}$
g	Synaptic strength	$0.894\,\text{nA/nF}$

Table 2.   Network characteristics.

Number of neurons	300
Number of edges	596
Average degree (in-degree + out-degree)	3.973
Clustering coefficient	0.34
Characteristic path length	5.63
In-degree distribution exponent	1.691
Out-degree distribution exponent	1.682

where the first sum runs over all other neurons in the network, with A_{ij} representing the adjacency matrix that defines the connectivity of the network. The second sum runs over all spikes fired by these pre-synaptic neurons. The post-synaptic current is represented by the α-function $f(t)$:

$$f(t) = \exp\left(\frac{-t}{\tau_d}\right) - \exp\left(\frac{-t}{\tau_r}\right), \qquad (3)$$

where τ_d is the decay time of the post-synaptic current and τ_r is the corresponding rise time. The strength of the synaptic coupling is measured by the parameter g.

The values of the model parameters used in this study are given in Table 1. For these parameter values and in the absence of synaptic input, the critical current for spike generation is $I_{\text{ext}} = 2.0\,\text{nA/nF}$. Thus, for the value of I_{ext} chosen, the neuron is operating at 85% of its firing threshold in the absence of synaptic input. In the opposite scenario, i.e. in the absence of external current, the critical synaptic strength g_{crit} needed to reach the firing threshold with a single input spike is $g_{\text{crit}} = 7.45\,\text{nA/nF}$. The value of g chosen in our simulation is well below that critical level, and was chosen such that in the presence of both external and synaptic inputs, noise was necessary (and sufficient) to excite a spike in the post-synaptic neuron in response to a pre-synaptic spike. The model was integrated using the Heun method [García-Ojalvo & Sancho, 1999] with a time step $dt = 0.1\,\text{msec}$.

The neuronal network was created with the NetworkX package (http://networkx.lanl.gov), modified to make the links directed. The topological characteristics of the network used in this study are given in Table 2.

3. Up/Down Activity Induced by Network-Wide Noise

We first examine the behavior of the network described above (see Table 2) for increasing levels of
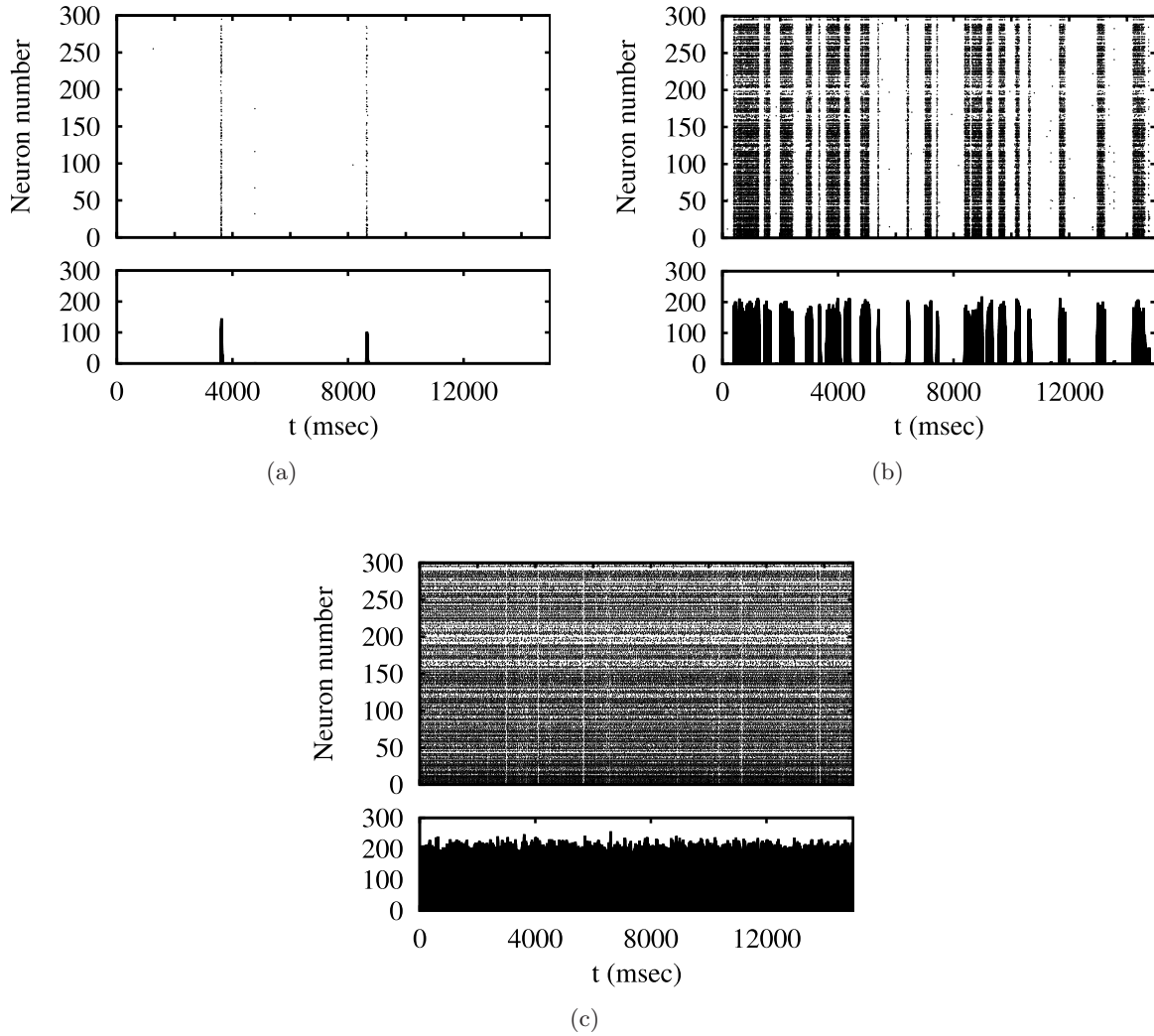
(a)

(b)

(c)

Fig. 1.   Dynamics of the scale-free network of leaky integrate-and-fire neurons for increasing noise intensity D. For each value of D, a raster plot showing the state of activity of all neurons with time (top panel) and a histogram of the number of neurons active as time progresses (bottom panel) are shown. Noise intensity values are (a) $D = 0.07$, (b) $D = 0.09$, and (c) $D = 0.14$. Other parameters are given in Table 1.

noise. The dynamics is depicted in Fig. 1 for three different values of the noise intensity D. For each noise level, a raster plot shows the state of activity of each of the 300 neurons in the network (with each black dot denoting a spike) as a function of time. A histogram of firings across the population (sliding bins with 1 msec time step and 25 msec size), corresponding to the multiple-unit activity (MUA) of the neuronal population, is shown in the bottom panel. For low noise intensity [Fig. 1(a)] spikes occur very sparsely, induced by noise in individual neurons. Usually these spikes cannot lead to firing in the downstream neurons (since the noise is weak), except in rare occasions in which the activity is able to propagate once throughout most of the network, before dying away.

As noise increases [Fig. 1(b)], however, it becomes more probable for spikes to activate the entire neuronal population, and even to reverberate in the network [Rué et al., 2010] leading to self-sustained activity, in which a given neuron might fire multiple times. These phases of activity, that qualitatively resemble the up states described above, end when the perturbation finds no way to continue propagating because none of the postsynaptic neurons reaches threshold.

Finally, for a large enough noise level [Fig. 1(c)] the up state does not self-terminate, since random fluctuations are high enough to always induce firing in any of the post-synaptic neurons receiving an input spike at any given time. In that situation, the network is always active. Therefore, we can see that
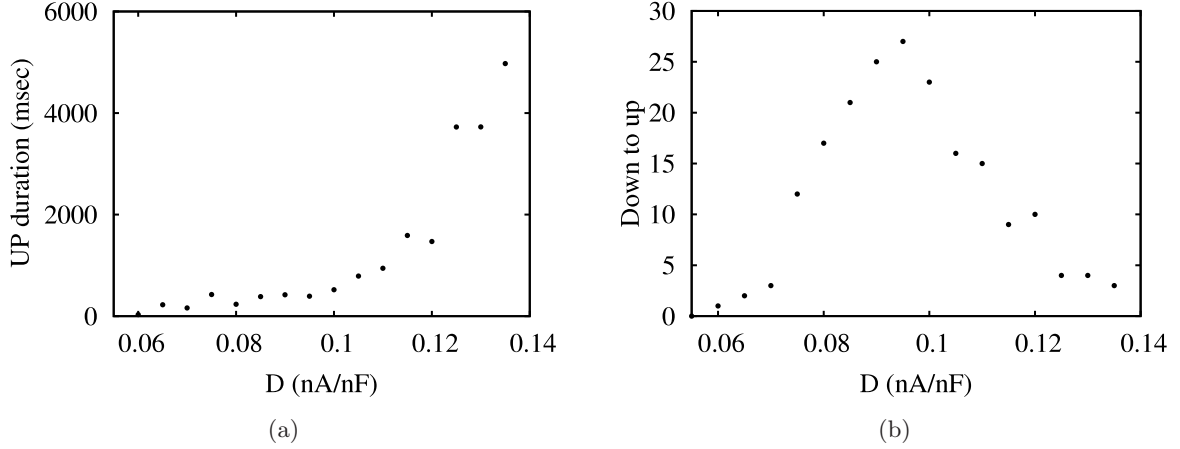
(a)

(b)

Fig. 2. Statistics of the up/down dynamics as a function of noise intensity. (a) Average duration of the up states and (b) number of down-to-up transitions in a fixed time window for increasing D.

an intermediate level of noise is able to generate a regime of up/down dynamics that is sustained as long as the random fluctuations and the (constant) external current persist.

In order to quantify this behavior, we now compute the average duration of the up states, defined in terms of the time that the MUA signal surpasses a certain threshold (here taken equal to 40 neurons). This quantity is shown in Fig. 2(a) for increasing noise levels, which reveals a monotonic increase with noise, which is very mild for intermediate noise levels, corresponding to a well-defined up/down regime such as the one shown in Fig. 1(b), followed by a sharp increase for large noise levels, for which it becomes very difficult for the activated phases to self-terminate, as mentioned above. We also quantify the amount of switchings between up and down state, by plotting in Fig. 2(b) the number

of up activations (for a fixed time window of 15 sec), again as the noise increases. The figure shows a nonmonotonic dependence on the noise intensity in this case, with a maximum number of up-state activations for an intermediate range of noise, as we already anticipated from Fig. 1.

4. Structure of the Noise-Induced Up/Down Oscillations

We now concentrate specifically on the noise-induced up/down regime depicted in Fig. 1(b). First we examine its temporal structure by computing the distribution of up-state and down-state durations, presented in Fig. 3. The two distributions agree with an exponential decrease, as confirmed in the inset plots, with approximately the same decay constant. These exponential distributions of
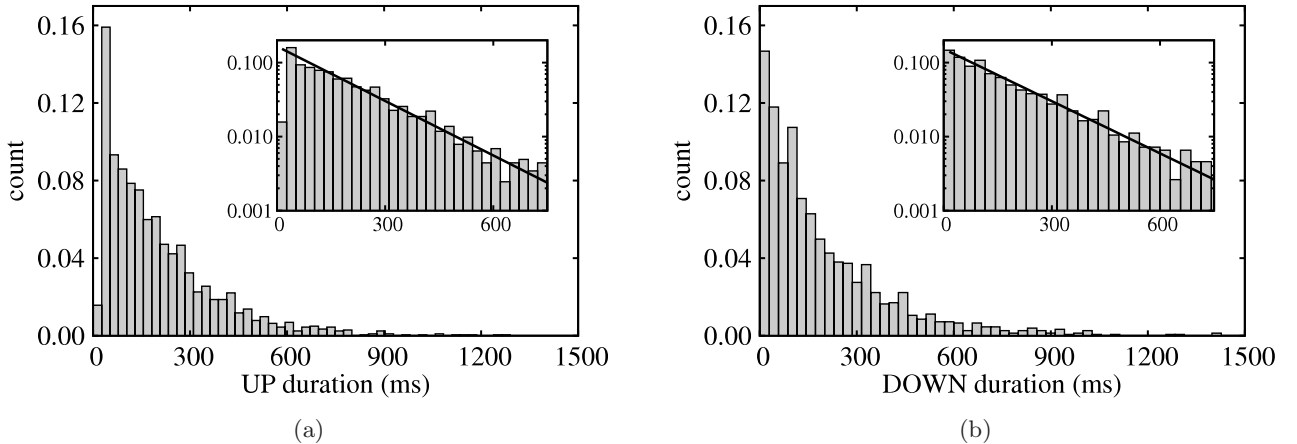

(a)

(b)

Fig. 3. Distribution of (a) up-state and (b) down-state durations for $D = 0.095\,\text{nA/nF}$, which corresponds to the maximum in Fig. 2(b). The decay rates for the two exponentials are $-5.6 \pm 0.3\,\text{sec}^{-1}$ and $-5.4 \pm 0.2\,\text{sec}^{-1}$, respectively.
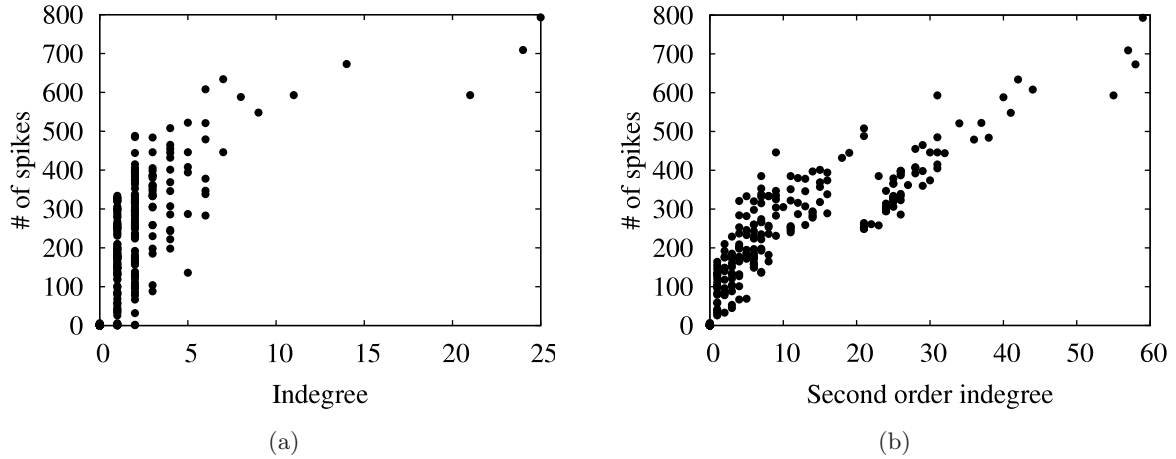
(a)

(b)

Fig. 4.   Number of spikes fired by every neuron in the network, in a fixed time window, as a function of the (a) first-order and (b) second-order in-degree of the node. Each neuron is represented by a black circle.

durations are consistent with a Poissonian statistics for the up-to-down and down-to-up transitions, which would indicate that the probability for an up state to initiate while the network is in the down state, and for the up state to terminate, would be constant in time.

Besides the obvious temporal structure of the up/down regime, the raster plot shown in Fig. 1(b) also reveals inhomogeneities in the firing response of the different neurons in the network, with certain neurons (for instance, those around the index 200) firing in the up phases much less than others. It is reasonable to think that such inhomogeneities in the firing rate should be associated with the topological differences between the nodes, typical of a scale-free network. To check this, we plot in Fig. 4 the relationship between the total number of spikes fired

by each neuron in a fixed time window (of width 15 msec) and the number of incoming connections that the neurons have, both direct [Fig. 4(a)] and in second order [Fig. 4(b)]. The two figures show a clear correlation between the firing rate and the (first- and second-order) in-degree, with the neurons with more incoming connections exhibiting a larger firing rate overall, and those with a very small number of connections exhibiting a firing rate almost negligible. Thus, the topology of the scale-free network determines the firing-rate pattern of the different neurons in the network.

The emergence of up/down dynamics induced by network-wide noise is not exclusive to scale-free networks. Figure 5 shows the activity of a ring lattice of neurons for increasing rewiring probability p, ranging from a purely regular lattice for $p = 0$
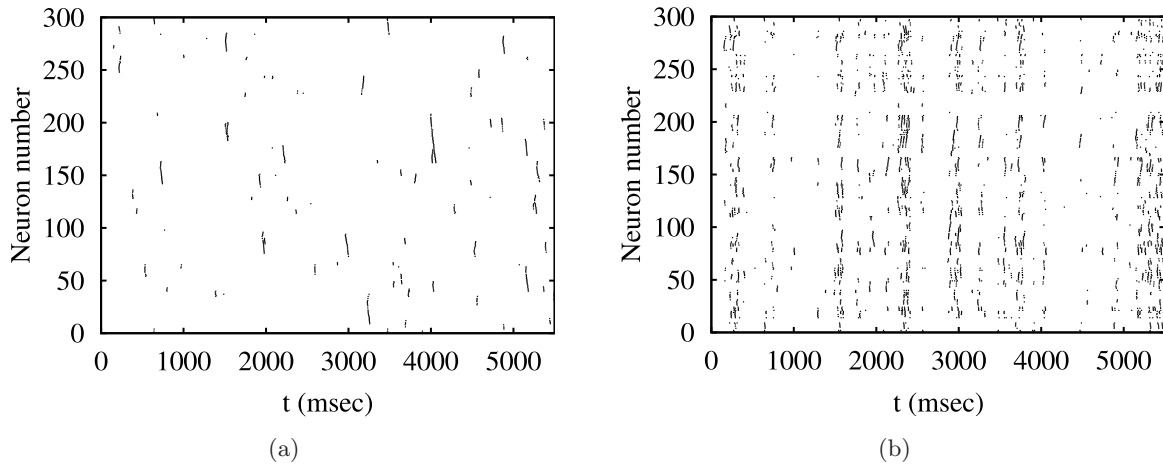

(a)

(b)

Fig. 5.   Raster plot showing the activity of a network with small world connectivity for increasing rewiring probability p and an intermediate level of noise, $D = 0.095 \, \text{nA/nF}$. (a) $p = 0.0$ (regular 1-d lattice), (b) $p = 0.2$, (c) $p = 0.6$, (d) $p = 1.0$ (random network). Here $g = 1 \, \text{nA/nF}$, corresponding to 90% of the critical value g_{crit}.
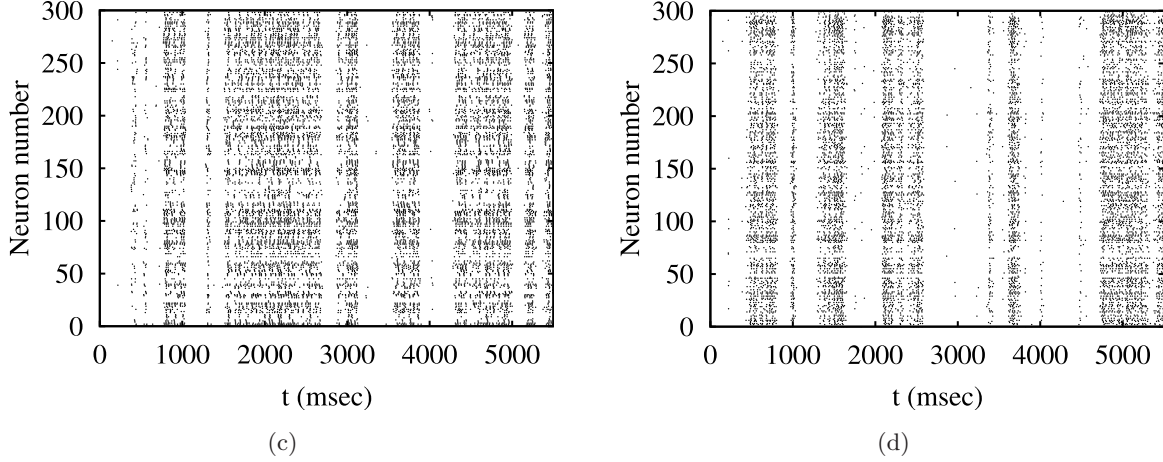
Fig. 5.   (*Continued*)

[Fig. 5(a)] to a random network for $p = 1$ [Fig. 5(c)], while an intermediate p leads to small-world connectivity [Fig. 5(c)]. The intensity of the network-wide noise is fixed to have an intermediate value, and the coupling strength is also chosen constant, slightly below the critical value beyond which firing is triggered by a single incoming spike. The results of Fig. 5 show that both small-world (c) and random networks (d) exhibit noise-induced up/down dynamics for the chosen parameters, which indicates that clustering is able to lead to this dynamical behavior (as shown by the small-world network case), but that neither clustering nor degree heterogeneity are *necessary* in that respect (as shown by the random-network case).

## 5. Effect of Local Noisy Perturbations

We now go back to the case of scale-free networks, and turn our attention to the situation in which a given neuron in the network receives a local random perturbation, in the form of a Poisson spike train with rate λ. The network-wide noise presented by $\xi_i(t)$ in Eq. (1) is kept at a low level, for which it does not generate a self-sustained up/down dynamics. We are interested in establishing whether a local synaptic noise, which could represent a localized (e.g. sensory) input in a certain area of a cortical network, would be enough to produce a regime of slow oscillations such as the one that has been described earlier in this paper. At this point, we have to take into account the intrinsic heterogeneity in connectivity topology characteristic of a scale-free network, and thus we will study the effect of synaptically perturbing two types of nodes: a hub

and a node with low connectivity. In the study presented in what follows, we consider a noise intensity $D = 0.03$ nA/nF, and a synaptic coupling strength $g = 1$ nA/nF, corresponding to 90% of the critical value g_{crit} described in Sec. 2. In this case, we also assume that the neuron that is being controlled is not affected by synaptic inputs coming from other neurons in the network, so that it exhibits a pure Poissonian firing rate.

We begin by analyzing the effect of local synaptic noise acting upon neuron #0 (according to the indexing used in the y axis of Fig. 1), whose out-degree is 22 and in-degree is 25, and thus it corresponds to a network hub. The effect of varying the rate λ of the Poisson spike train acting upon this neuron is shown in Fig. 6, for three different values of λ. At first glance, the behavior of the network with respect to λ follows the same trend shown by the network-wide noise controlled by D in Fig. 1: for small Poisson rate λ the spiking events are rare [Fig. 6(a)], while they become more frequent as λ increases [Fig. 6(b)], until for very large rates the whole network exhibits a regime of sustained activity [Fig. 6(c)] mimicking the behavior for large D shown in Fig. 1(c). In spite of this seeming overall similarity between the effects of local synaptic noise and network-wide membrane-potential noise, a closer analysis reveals substantial differences arising from the fact that we are acting upon a network hub. Indeed, all network activation events displayed for low and intermediate values of λ are directly triggered by the input spike train (shown in the panel above each raster plot), and therefore there are no regimes of self-sustained up states even for intermediate noise levels [Fig. 6(b)].
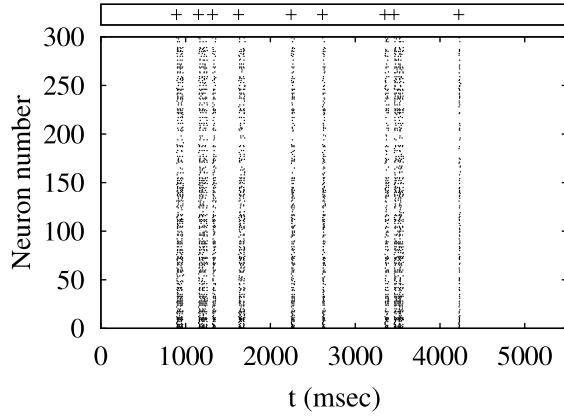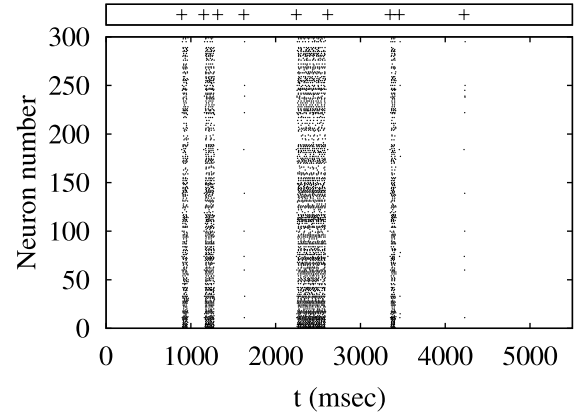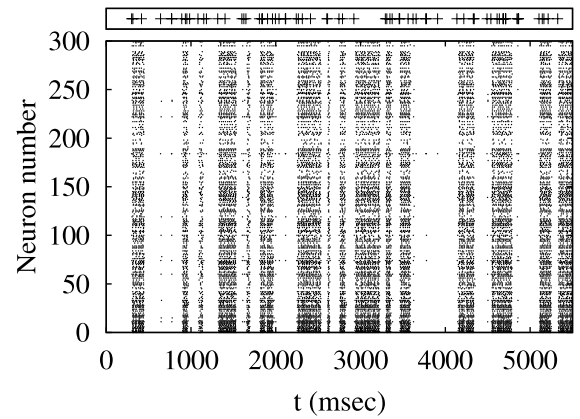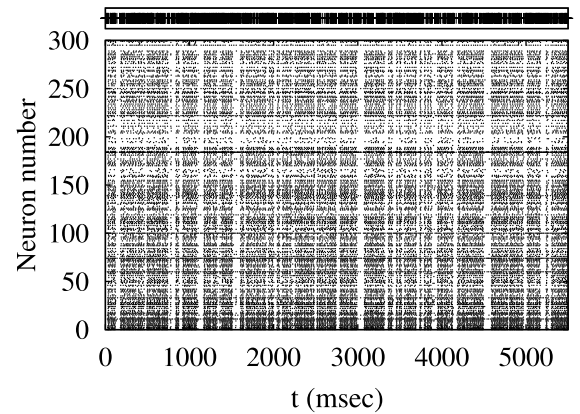
(a)
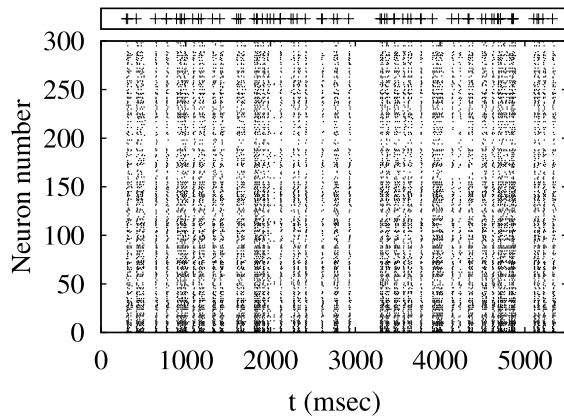
(b)
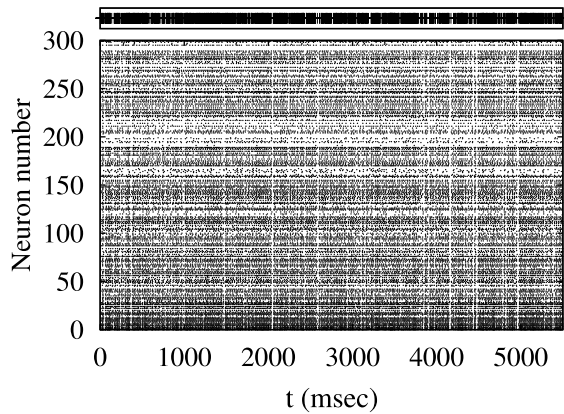
(c)

Fig. 6. Effect of local synaptic noise, in terms of a random train of incoming spikes, acting upon a network hub (neuron #0, following the indexing used in Fig. 1), for three different values of the Poisson rate: (a) $\lambda = 0.002$, (b) $\lambda = 0.01$, (c) $\lambda = 0.2$. Other parameters are given in Table 1 and in the text. On top of each raster plot, the sequence of input spikes acting on neuron #0 is shown.

(a)

(b)

(c)

Fig. 7. Effect of local synaptic noise, in terms of a random train of incoming spikes, acting upon a nonhub neuron (neuron #184, following the indexing used in Fig. 1), for three different values of the Poisson rate: (a) $\lambda = 0.002$, (b) $\lambda = 0.01$, (c) $\lambda = 0.2$. Other parameters are given in Table 1 and in the text. On top of each raster plot, the sequence of input spikes acting on neuron #184 is shown.

The situation is different when the local noise acts upon a nonhub neuron with low out-degree. The response of the network to this perturbation for three values of λ is shown in Fig. 7. In this case the perturbed neuron is #184, its out-degree is 2 and it has no incoming connection. In contrast with the case in which a hub is perturbed, some of the spikes acting on the neuron are able to elicit up-like states, even for small λ [Fig. 7(a)]. For larger Poisson rate [Fig. 7(b)] the dynamics resembles the up/down switching exhibited by the population under optimal neuron-wide membrane potential noise [Fig. 1(b)]. Finally, for large enough λ the network exhibits, as usual, a regime of sustained global firing. Therefore, an optimal amount of local noise (in the form of a Poissonian spike train) acting upon a nonhub neuron is able to generate up/down dynamics, similarly to the case of membrane-potential noise. On the other hand, we have seen above that when the local random perturbations are applied to a hub neuron no up/down dynamics emerges. These results contrast with previously reported results on stochastic resonance on a scale-free network of bistable elements, where a local perturbation (in that case, a periodic driving) was more effective in the presence of global noise (in terms of the collective network response) when applied to a hub than to a low-degree node [Perc, 2008].

6. Discussion

Recent evidence indicates that up/down dynamics arises from the interaction between network-based and neuron-mediated mechanisms [Cunningham *et al.*, 2006]. Here we have shown that relatively simple requirements need to be fulfilled at both these levels for this type of dynamics to exist. Specifically, a network architecture involving a nontrivial connectivity profile, plus a subthreshold neural dynamics, are sufficient to lead to an irregular pattern of up/down switchings.

The nontrivial coupling architecture of the network considered here allows that a sufficiently large amount of noise initiates an avalanche-like wave of activity [Levina *et al.*, 2007; Petermann *et al.*, 2009], which spontaneously terminates when the excitation can no longer propagate across the network, either because it reaches a terminal node or due to its inability to excite any of the postsynaptic

neurons at any given time. The resulting firing pattern has a nontrivial structure both in time, with an exponential distribution of up-state durations, and in node-space, with the in-degree of the different nodes determining the firing rate of each neuron in the up state. While these structural properties of the up/down dynamics are characteristic of scale-free networks, our study shows that this regime also arises in networks with homogeneous degree distributions, such as small-world networks and random networks.

Another specific characteristic of noise-induced up/down dynamics in scale-free networks arises when the behavior is caused by local random perturbations. In that case the response of the network depends on the degree of the node that is subject to local noise: when a hub is perturbed no up/down regime is produced; only noisy perturbations acting upon low-degree nodes generate this regime. This behavior suggests that the out-degree of different neurons in neuronal populations might be limited. In the case of small-world and random networks this dichotomy does not exist: local noise is able to induce up/down dynamics in all nodes, provided their degree is sufficiently smaller than the number of nodes in the network (in which case the local input would completely saturate the network) but not too small (in which case the local excitation would not be able to leave the local neighborhood of the input node). Taken together, the results presented here show that a combination of noise, subthreshold dynamics and coupling is enough to generate rich firing patterns, with physiological implications, in neuronal networks.

Acknowledgments

References

Balenzuela, P. & García-Ojalvo, J. [2005] "Role of chemical synapses in coupled neurons with noise," *Phys. Rev. E* **72**, 021901.

Bazhenov, M., Timofeev, I., Steriade, M. & Sejnowski, T. J. [2002] "Model of thalamocortical slow-wave

sleep oscillations and transitions to activated states," *J. Neurosci.* **22**, 8691–8704.

Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. & Hwang, D. U. [2006] "Complex networks: Structure and dynamics," *Phys. Rep.* **424**, 175–308.

Buldú, J. M., Bajo, R., Maestú, F., Castellanos, N., Leyva, I., Gil, P., Sendiña-Nadal, I., Almendral, J. A., Nevado, A., del Pozo, F. & Boccaletti, S. [2011] "Reorganization of functional networks in mild cognitive impairment," *PLoS One* **6**, e19584.

Bullmore, E. & Sporns, O. [2009] "Complex brain networks: Graph theoretical analysis of structural and functional systems," *Nat. Rev. Neurosci.* **10**, 186–198.

Busch, H. & Kaiser, F. [2003] "Influence of spatiotemporally correlated noise on structure formation in excitable media," *Phys. Rev. E* **67**, 041105.

Castellanos, N. P., Leyva, I., Buldú, J. M., Bajo, R., Paúl, N., Cuesta, P., Ordóñez, V. E., Pascua, C. L., Boccaletti, S., Maestú, F. & del Pozo, F. [2011] "Principles of recovery from traumatic brain injury: Reorganization of functional networks," *Neuroimage* **55**, 1189–1199.

Chialvo, D. R. [2010] "Emergent complex neural dynamics," *Nat. Phys.* **6**, 744–750.

Chun-Biao, G., Matjaz, P. & Qing-Yun, W. [2010] "Delay-aided stochastic multiresonances on scalefree FitzHugh–Nagumo neuronal networks," *Chinese Phys. B* **19**, 040508.

Compte, A., Sanchez-Vives, M. V., McCormick, D. A. & Wang, X.-J. [2003] "Cellular and network mechanisms of slow oscillatory activity and wave propagations in a cortical network model," *J. Neurophysiol.* **89**, 2707–2725.

Cossart, R., Aronov, D. & Yuste, R. [2003] "Attractor dynamics of network up states in the neocortex," *Nature* **423**, 283–288.

Cunningham, M. O., Pervouchine, D. D., Racca, C., Kopell, N. J., Davies, C. H., Jones, R. S. G., Traub, R. D. & Whittington, M. A. [2006] "Neuronal metabolism governs cortical network response state," *Proc. Natl. Acad. Sci. USA* **103**, 5597–5601.

Destexhe, A. [2009] "Self-sustained asynchronous irregular states and Up-Down states in thalamic, cortical and thalamocortical networks of nonlinear integrate-and-fire neurons," *J. Comput. Neurosci.* **27**, 493–506.

Eguíluz, V. M., Chialvo, D. R., Cecchi, G. A., Baliki, M. & Apkarian, A. V. [2005] "Scale-free brain functional networks," *Phys. Rev. Lett.* **94**, 018102.

García-Ojalvo, J. & Sancho, J. [1999] *Noise in Spatially Extended Systems* (Springer Verlag).

Gerstner, W. & Kistler, W. [2002] *Spiking Neuron Models*: *Single Neurons*, *Populations*, *Plasticity* (Cambridge University Press, Cambridge).

Gong, G., He, Y., Concha, L., Lebel, C., Gross, D. W., Evans, A. C. & Beaulieu, C. [2009] "Mapping anatomical connectivity patterns of human cerebral cortex using in vivo diffusion tensor imaging tractography," *Cereb. Cortex* **19**, 524–536.

Gong, Y., Xie, Y., Lin, X., Hao, Y. & Ma, X. [2010] "Ordering chaos and synchronization transitions by chemical delay and coupling on scale-free neuronal networks," *Chaos Solit. Fract.* **43**, 96–103.

Gosak, M., Korošak, D. & Marhl, M. [2010] "Optimal network configuration for maximal coherence resonance in excitable systems," *Phys. Rev. E* **81**, 056104.

Guye, M., Bettus, G., Bartolomei, F. & Cozzone, P. J. [2010] "Graph theoretical analysis of structural and functional connectivity MRI in normal and pathological brain networks," *Magn. Reson. Mater. Phys.* **23**, 409–421.

Hao, Y., Gong, Y. & Lin, X. [2011] "Multiple resonances with time delays and enhancement by non-gaussian noise in Newman–Watts networks of Hodgkin–Huxley neurons," *Neurocomputing* **74**, 1748–1753.

Hill, S. & Tononi, G. [2005] "Modeling sleep and wakefulness in the thalamocortical system," *J. Neurophysiol.* **93**, 1671–1698.

Humphries, M. D., Gurney, K. & Prescott, T. J. [2006] "The brainstem reticular formation is a small-world, not scale-free, network," *Proc. Roy. Soc. B* **273**, 503–511.

Johnson, H. A. & Buonomano, D. V. [2007] "Development and plasticity of spontaneous activity and Up states in cortical organotypic slices," *J. Neurosci.* **27**, 5915–5925.

Jung, P. & Mayer-Kress, G. [1995] "Spatiotemporal stochastic resonance in excitable media," *Phys. Rev. Lett.* **74**, 2130–2133.

Kaiser, M., Martin, R., Andras, P. & Young, M. P. [2007] "Simulation of robustness against lesions of cortical networks," *Eur. J. Neurosci.* **25**, 3185–3192.

Kang, S., Kitano, K. & Fukai, T. [2004] "Self-organized two-state membrane potential transitions in a network of realistically modeled cortical neurons," *Neur. Netw.* **17**, 307–312.

Lampl, I., Reichova, I. & Ferster, D. [1999] "Synchronous membrane potential fluctuations in neurons of the cat visual cortex," *Neuron.* **22**, 361–374.

Levina, A., Herrmann, J. M. & Geisel, T. [2007] "Dynamical synapses causing self-organized criticality in neural networks," *Nat. Phys.* **3**, 857–860.

Lindner, B., Garcia-Ojalvo, J., Neiman, A. & Schimansky-Geier, L. [2004] "Effects of noise in excitable systems," *Phys. Rep.* **392**, 321–424.

McDonnell, M. D. & Ward, L. M. [2011] "The benefits of noise in neural systems: Bridging theory and experiment," *Nat. Rev. Neurosci.* **12**, 415–426.

Modha, D. S. & Singh, R. [2010] "Network architecture of the long-distance pathways in the macaque brain," *Proc. Natl. Acad. Sci. USA* **107**, 13485–13490.

Parga, N. & Abbott, L. F. [2007] "Network model of spontaneous activity exhibiting synchronous transitions between up and down states," *Front Neurosci.* **1**, 57–66.

Perc, M. [2005] "Spatial coherence resonance in excitable media," *Phys. Rev. E* **72**, 016207.

Perc, M. [2008] "Stochastic resonance on weakly paced scale-free networks," *Phys. Rev. E* **78**, 036105.

Petermann, T., Thiagarajan, T. C., Lebedev, M. A., Nicolelis, M. A. L., Chialvo, D. R. & Plenz, D. [2009] "Spontaneous cortical activity in awake monkeys composed of neuronal avalanches," *Proc. Natl. Acad. Sci. USA* **106**, 15921–15926.

Petersen, C. C. H., Hahn, T. T. G., Mehta, M., Grinvald, A. & Sakmann, B. [2003] "Interaction of sensory responses with spontaneous depolarization in layer 2/3 barrel cortex," *Proc. Natl. Acad. Sci. USA* **100**, 13638–13643.

Rué, P., Pons, A. J., Domedel-Puig, N. & García-Ojalvo, J. [2010] "Relaxation dynamics and frequency response of a noisy cell signaling network," *Chaos* **20**, 045110.

Sanchez-Vives, M. V. & McCormick, D. A. [2000] "Cellular and network mechanisms of rhythmic recurrent activity in neocortex," *Nat. Neurosci.* **3**, 1027–1034.

Sporns, O., Chialvo, D. R., Kaiser, M. & Hilgetag, C. C. [2004] "Organization, development and function of complex brain networks," *Trends Cogn. Sci.* **8**, 418–425.

Sporns, O. & Zwi, J. D. [2004] "The small world of the cerebral cortex," *Neuroinformatics* **2**, 145–162.

Steriade, M., Timofeev, I. & Grenier, F. [2001] "Natural waking and sleep states: A view from inside neocortical neurons," *J. Neurophysiol.* **85**, 1969–1985.

Steriade, M. & Timofeev, I. [2003] "Neuronal plasticity in thalamocortical networks during sleep and waking oscillations," *Neuron* **37**, 563–576.

Strogatz, S. H. [2001] "Exploring complex networks," *Nature* **410**, 268–276.

van den Heuvel, M. P., Stam, C. J., Boersma, M. & Hulshoff Pol, H. E. [2008] "Small-world and scale-free organization of voxel-based resting-state functional connectivity in the human brain," *Neuroimag.* **43**, 528–539.

Wang, Q., Perc, M., Duan, Z. & Chen, G. [2009a] "Delay-induced multiple stochastic resonances on scale-free neuronal networks," *Chaos* **19**, 023112.

Wang, Q., Perc, M., Duan, Z. & Chen, G. [2009b] "Synchronization transitions on scale-free neuronal networks due to finite information transmission delays," *Phys. Rev. E* **80**, 026206.

Wu, H., Jiang, H. & Hou, Z. [2011] "Spatiotemporal dynamics on small-world neuronal networks: The roles of two types of time-delayed coupling," *Chaos Solit. Fract.* **44**, 836–844.

Zalesky, A., Fornito, A., Harding, I. H., Cocchi, L., Yücel, M., Pantelis, C. & Bullmore, E. T. [2010] "Whole-brain anatomical networks: Does the choice of nodes matter?" *Neuroimage* **50**, 970–983.

Zamora-Lopez, G., Zhou, C. & Kurths, J. [2009] "Graph analysis of cortical networks reveals complex anatomical communication substrate," *Chaos* **19**, 015117.

Zhou, C., Kurths, J. & Hu, B. [2001] "Array-enhanced coherence resonance: Nontrivial effects of heterogeneity and spatial independence of noise," *Phys. Rev. Lett.* **87**, 098101.