Noise induces synchronous and phase-locked oscillations in a cortical model

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Abstract

We analyze effects of noise on the dynamics of a excitatory-inhibitory (EI) cortical model with finite range connections. The dynamics is studied both analytically and with numerical simulations. Both the case of periodic boundary conditions and the more plausible case of open boundary conditions are considered. In a proper parameter regime, noise induces synchronous and phase-locked oscillations.

Key words: Network dynamics, Phase-locked and Synchronous Oscillations, Noise

1 Introduction

The emergence of synchronous and phase-locked oscillations in neural systems have attracted a lot of attention in recent years. Many authors have shown the emergence of spatio-temporal patterns in the dynamics of neural systems, both experimentally and with numerical simulations of models. Here we analyze the dynamics of a model analytically tractable and focus on the effects of noise and boundary conditions. Our starting point in modeling are the stochastic Cowan-Wilson-like EI equations [1,2] governing the excitatory **u** and inhibitory **v** membrane potential dynamics:

$$\dot{u}_i = -\alpha u_i - \sum_j H_{ij} g_v(v_j) + \sum_j J_{ij} g_u(u_j) + \bar{F}_i(t), \tag{1}$$

$$\dot{v}_i = -\alpha v_i + \sum_j W_{ij} g_u(u_j) + F_i(t). \tag{2}$$

where $g(u_i(t))$ is the activation function of the i^{th} neuron at time t, $i = 1 \dots N$, α^{-1} is a time constant, J_{ij}, W_{ij} and H_{ij} are the synaptic connection strengths, and $\bar{F}_i(t)$ and $F_i(t)$ model the intrinsic noise, respectively on the excitatory

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and inhibitory units. We take the noise $\bar{F}_i(t), F_i(t)$ to be uncorrelated white noise, such that $\langle\ F_i(t)\ \rangle = \langle\ \bar{F}_i(t)\ \rangle = 0$ and $\langle\ F_i(t)\ F_j(t')\ \rangle = \Gamma\delta_{ij}\delta_{(t-t')}$, $\langle\ \bar{F}_i(t)\ \bar{F}_j(t')\ \rangle = \ \bar{\Gamma}\delta_{ij}\delta_{(t-t')}$. Since the connectivity formation of the cultured system we want to model has grown randomly and spontaneously, we can reasonably assume that strength of each connection is a function only of the type of pre-synaptic and post-synaptic neurons (Excitatory or Inhibitory), and of the distance between them. We put one excitatory and one inhibitory unit on each site of a square lattice with M rows and M columns, so that there will be N=M^2 excitatory units and N inhibitory units. Each inhibitory unit is connected to the excitatory unit that is on the same site. Each excitatory unit is connected to its four nearest neighbors and to its four next-nearest neighbors, with equal strength. We will consider two cases: Topliz periodic boundary conditions (tpbc) and open boundary conditions (obc). Numbering the unit in a type-writer way, from 0 to N-1, in the tpbc

$$J_{ij} = \begin{cases} j_0/8 & \text{if}(i-j) \text{ mod } N = \pm 1, \pm M, \text{ or } \pm M \pm 1 \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

Analogously excitatory-to-inhibitory connection $W_{ij} = w_0/8$ if $(i-j)$ mod $N = \pm 1$ or $\pm M$ or $\pm M \pm 1$, and is zero otherwise. H_{ij} is h_0 if $i = j$ and is zero otherwise. Notice that, apart from the units on the boundary, each unit is connected to its four nearest neighbors and to its four next-nearest neighbors. Furthermore the connection matrices J and W are Toplitz matrices so that eigenvectors are the Fourier basis $\xi_n(j) = \frac{1}{\sqrt{N}} e^{i2\pi nj/N}$ and eigenvalues, given the notation $J_{ij} = J(|i-j|) = J(x)$, can be easily calculated: $j_n = 2\sum_{x=0}^{N-1} J(x) cos(\frac{2\pi}{N} nx)$, and analogously for $\mathbf{W}$. The highest eigenvalue of $\mathbf{J}$ is j_0 (and w_0 for $\mathbf{W}$), corresponding to the eigenvector with n=0. H is diagonal and have all eigenvalues equal to h_0. In the obc case, we connect each excitatory unit to its nearest-neighbors and next-nearest neighbors sites, so units on the boundary are connected to less then 8 sites. In the next section the model dynamics is analyzed in terms of the eigenvectors and eigenvalues of the connection matrices. Note that in both tpbc and obc each matrix $\mathbf{J}, \mathbf{H}, \mathbf{W}$ is symmetric, but the resultant connectivity is highly asymmetric.

2 Model Dynamics

The model dynamics is analyzed in terms of the eigenvectors and eigenvalues of the connection matrices $\mathbf{J}, \mathbf{H}, \mathbf{W}$. Linearizing the equations (1,2) around the fixed point $\{\bar{\mathbf{u}}, \bar{\mathbf{v}}\}$, and assuming noise to be only on the $\mathbf{v}$ units ($\bar{\Gamma} = 0$), we get

$$\ddot{\mathbf{u}} + (2\alpha - \mathsf{J})\dot{\mathbf{u}} + [\alpha^2 - \alpha\mathsf{J} + \mathsf{HW})]\mathbf{u} = -\mathbf{HF}(t) \tag{4}$$

In absence of noise, following [2], we find that the solutions are $\mathbf{u} = \sum_n (m_n(t)\boldsymbol{\xi}_n + c.c.)$ where $m_n = c_+ e^{\lambda_n^+ t} + c_- e^{\lambda_n^- t}$ and

$$2\lambda_n^{\pm} = -2\alpha - j_n \pm \sqrt{{j_n}^2 - 4h_n W_n} \tag{5}$$

In presence of noise $\mathbf{F}$, solutions becomes $\mathbf{u} = \sum_n (m_n(t)\boldsymbol{\xi}_n + c.c.)$ where

$$m_n = c_+ e^{\lambda_n^+ t} + c_- e^{\lambda_n^- t} + \int_0^t ds \left\{ \frac{e^{\lambda_n^+(t-s)} - e^{\lambda_n^-(t-s)}}{\lambda_n^- - \lambda_n^+} \right\} h_n F_n(s). \tag{6}$$

F_n is the projection of the vector $\mathbf{F}$ along the eigenvector $\boldsymbol{\xi}_n$. If all the n modes have $\Re[\lambda_n] < 0$, the activity $\mathbf{u}$ decays toward the fixed point in the absence of noise. If all the n modes have $\Re[\lambda_n] < 0$ and also $\Im[\lambda_n] = 0$, then the effects of noise are trivial (regime A). If the mode with the greatest real part, call it n=a, has $\Re[\lambda_a] < 0$ but $\Im[\lambda_a] \neq 0$ (regime B) then, interestingly, spontaneous collective aperiodic oscillations are induced by noise. When there's a mode with $\Re[\lambda_n] > 0$ and $\Im[\lambda_n] \neq 0$, then spontaneously growing oscillations arises also without noise (regime C). In that case non-linearity beyond our linear approximation constrains the growing oscillations to a finite amplitude. Let's compute analytically the Power Spectrum Density (PSD), i.e. the Fourier transform of the correlation function $C(t-t') = \sum_i C_i(t-t') = \sum_i \langle u_i(t) u_i(t') \rangle - \langle u_i(t) \rangle \langle u_i(t) \rangle$. The contribution of mode n when $\lambda_n = \Re[\lambda_n] < 0$, to the PSD, is simply $\tilde{C}^n(\omega) \propto \frac{h_0^2 \Gamma \tau_n^4}{(1+\omega^2 \tau_n^2)^2}$, clearly peaked in $\omega = 0$. On the contrary, the contribution of a mode with $\lambda_a = -1/\tau_a + \imath\omega_a$ ($\tau_a > 0$) to the PSD is $\tilde{C}^a(\omega) = \frac{h_a^2 \Gamma \tau_a^4}{4(1+\omega_a^2 \tau_a^2)} [\frac{2+\omega/\omega_a}{1+\tau_a^2(\omega+\omega_a)^2} + \frac{2-\omega/\omega_a}{1+\tau_a^2(\omega-\omega_a)^2}]$. This is peaked at ω close to ω_a (when $\tau_a \omega_a < 1$). So noise induces, in the regime B, a collective oscillatory behavior, that correspond to a broad peak in the power-spectrum of neurons activity near the characteristic frequency ω_a.

The spatio-temporal pattern of activity is governed by the eigenvector $\boldsymbol{\xi}_a$ corresponding to the sustained mode. A phase locked oscillation arises when the dominant eigenvector is complex (indeed $u_i(t) = \xi_{ai} e^{-\imath\omega_a t}$+c.c. $\propto |\xi_{ai}| \cos(\omega_a t - \phi_{ai})$, with $\xi_{ai} = |\xi_{ai}| e^{\imath\phi_{ai}}$), and a synchronous oscillation arises when the dominant eigenvector has positive real elements. In the tpbc case, we know analytically the eigenvalues and eigenvectors of the connection matrices. In such a case, given the connectivity structure in eq. 3, oscillations needs ${j_n}^2 - 4h_n W_n < 0$, and

$$\Re[\lambda_n] = \frac{1}{2}(j_n - 2\alpha) \quad \text{and} \quad \Im[\lambda_n] = \frac{1}{2}\sqrt{|{j_n}^2 - 4h_n W_n|} \tag{7}$$

Therefore the dominant mode is the one with larger j_n, $i.e.$n=0 (since elements of $\mathbf{J}$ are non-negative numbers). Therefore, in the tpbc case, the winning eigenvector is real and positive, given by $\boldsymbol{\xi}_0 = (\frac{1}{\sqrt{N}}, \frac{1}{\sqrt{N}}, ..., \frac{1}{\sqrt{N}})$, and oscillations are synchronous. In the obc case, we don't know apriori the eigenvalues and eigenvectors of matrices $\mathbf{J}, \mathbf{W}$. So we will investigate now the boundary effects. In the obc case, the connection matrix $\mathbf{J}$ (and analogously for $\mathbf{W}$) differs from the tpbc matrix $\mathbf{J}$ since some elements J_{ij} are zero instead of being $j_0/8$. We can write the obc matrix as the tpbc matrix $\mathbf{J}$ minus a perturbation $\mathbf{G}$. The NxN matrix $\mathbf{G}$ has $6M-2$ elements different from zero. Let's consider the connection matrix

$$\mathbf{J}' = \mathbf{J} - \epsilon \mathbf{G} \tag{8}$$

then we get the tpbc matrix when $\epsilon = 0$ and the obc matrix when $\epsilon = 1$. The larger seven eigenvalues of matrix $\mathbf{J}'$ are plotted as a function of ϵ in figure 3, for two different network sizes. Unperturbated eigenvalue $n \neq 0$ is always coincident with the eigenvalue $N-n$. The perturbation $\mathbf{G}$ removes this degeneracy for some couples. The network dynamics is governed by the mode with larger eigenvalue j_n (see eq.7). As the size of the network grows, the unperturbated eigenvalues becomes closer to each others, however the effect of the perturbation becomes smaller and smaller, so that the larger eigenvalues is always the one corresponding to the synchronous mode n=0.

We perform numerical simulations of the network model with the short-range connectivity (see eq. 3) in the tpbc and obc cases, with $N = 100$ excitatory and N inhibitory units. Results are shown in fig. 1 (parameter regime B). As we expect, in both tpbc and obc cases noise induces synchronous oscillatory activity. In the obc case, the amplitude of oscillations changes among neurons, indeed the dominant eigenvector $\boldsymbol{\xi}_0$, shown in fig.3.b, is real and positive but not constant. Eigenvector is such that amplitude of oscillations is smaller near the boundary of the square (i.e. sites with index $i < 10, i.leq.90$ or $i \bmod M = 0, M-1$). As we expect, since in this parameter regime $\Re[\lambda_n] < 0$ for all n, when noise is zero then there's no oscillations at all in the network. Numerical simulations of the nonlinear model, with tpbc and obc, in the parameter regime C, where the dominant mode has $\Re[\lambda_0] > 0$ and $\Im[\lambda_0] \neq 0$, are shown in fig.2. As we expect, even without noise there are spontaneous oscillations and they are synchronous, independently from the boundary conditions.

2.1 Asymmetry of the connection matrices and phase-locked oscillations

Let's introduce an asymmetry in the connection matrices. For example let's consider the case where H_{ij} is h_0 if $(i-j) = 0$, is $0.3h_0$ if $(i-j) = -1$ and zero otherwise. It means that the inhibitory unit on the site j is connected to the excitatory unit on the same site j and to the excitatory unit $j-1$ on the left, (but not to the excitatory unit $j+1$ on the right). The asymmetry of the matrix implies that eigenvalues are not real, but complex numbers. Since matrix element ij depends from $i-j$ then we have still a Toplitz matrix, with complex eigenvalues and eigenvectors $\boldsymbol{\xi}$ given by the Fourier basis. When eigenvalues of $\mathbf{J}, \mathbf{W}$ or $\mathbf{H}$ are not real but complex, then clearly eqs. 7 doesn't hold, and it may happen that the dominant eigenvector (i.e. the one with the largest $\Re(\lambda)$) is complex, then a phase locked oscillation arises. If the dominant phase-locked mode has $\Re[\lambda] < 0$ then the phase-locked oscillations are sustained by noise, while if $\Re[\lambda] > 0$ then the phase-locked oscillations arises spontaneously even in absence of noise. This is confirmed by numerical simulations of the obc system shown in fig.3.c.

3 Conclusion

We consider an intrinsic white noise term in a spiking rate cortical model and analyze effects of noise on the spontaneous activity of the system. We compare the system with particular periodic boundary conditions (tpbc) with the more realistic case of open boundary conditions. As we expect the boundary effects are negligible, when the size of the network is enough large. Linear analysis predicts that, in a proper range of parameters (depending from eigenvalues of the connections matrices), noise induces a collective oscillatory behavior in the neurons activity. When connections strength depends only from distance $|i-j|$ and the type of pre- and post-synaptic unit, the oscillation is synchronous among units. We show here that this holds both in the tpbc and obc cases. When connections strength depends also from the sign of $i-j$, so that $\mathbf{J}, \mathbf{W}, \mathbf{H}$ are Topliz but not symmetric matrices, then phase-locked oscillations may arise.

References

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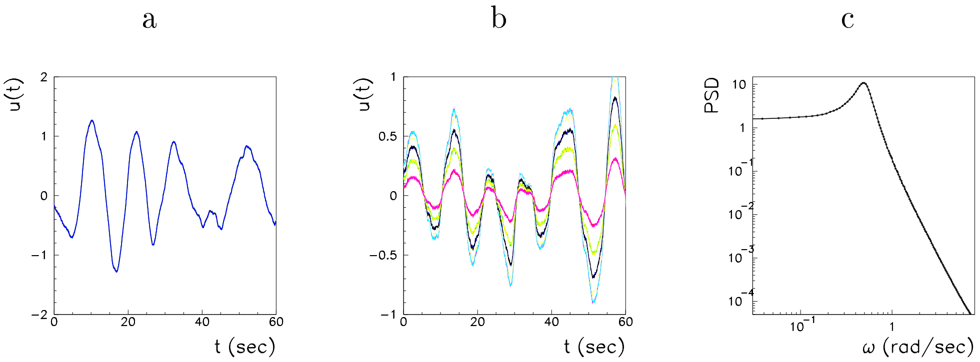

Fig. 1. Simulations of the 10 x 10 system in regime B, using tpbc (a) and open boundary condition (b & c). The values of parameters has been chosen in such a way to satisfy the conditions for the regime B (specifically, $\alpha = 50sec^{-1}$, $N = 100$, $W_0 = h_0 = \sqrt{0.25j_0^2 + 0.25}$, $j_0 = 2(\alpha - 0.1)$, so that $\omega_0 = 0.5rad/sec$). a: Excitatory activity $u_i(t), i = 1, \ldots, 10$ in the tpbc case. Activity of all the excitatory units overlap each other. $\Gamma = 0.001$. b: $u_i(t), i = 1, \ldots, 8$ in the model with obc. Activity is synchronous, but with different amplitudes. Non zero elements of J_{ij} and W_{ij} have been renormalized to $j_0/7.75$ and $W_0/7.75$, $\Gamma = 0.04$. c: PSD of the activity shown in b.

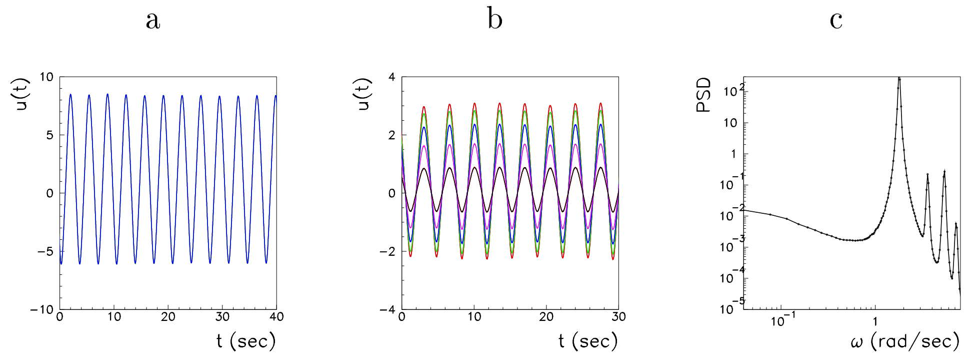

Fig. 2. Simulations of the model in regime C, using tpbc condition (a) and obc (b & c). (Parameters are as in fig.1 apart from $j_0 = 2(\alpha + 0.07)$, $W_0 = h_0 = \sqrt{0.25j_0^2 + 0.25}$). a: $u_i(t)$, $i = 1 \ldots 10$, in the tpbc case. b: $u_i(t)$ for $i = 1 \ldots 10$ in the obc case. Activities of all the units are synchronous but with different amplitudes. c: PSD of the activity shown in b.

a b c

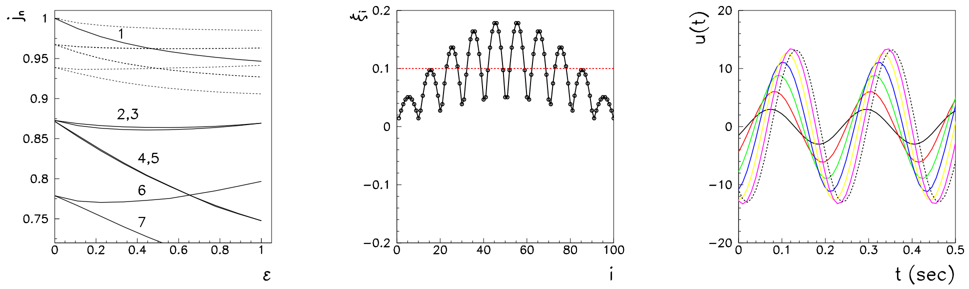

Fig. 3. a. The first 7 eigenvalues of matrix $\mathbf{J}' = \mathbf{J} + \epsilon \mathbf{G}$ are shown as a function of ϵ, for $M = 10$ (solid line) and $M = 20$ (dashed line). $\epsilon = 0$ corresponds to tpbc while $\epsilon = 1$ corresponds to the obc connectivity case. The larger eigenvalue is always the mode n=0, for all $0 < \epsilon < 1$. b. Eigenvector of the principal mode $n = 0$ in a MxM lattice with M=10. ξ_i is shown as a function of $i = 1 \ldots N$ in the obc (solid line with circles) and in the tpbc (dashed line) case. c. Simulation of the nonlinear model with obc. Parameters are the same as in fig. 1.bc, except for the matrix $\mathbf{H}$ that is asymmetric ($H_{i,i} = h_0$ and $H_{i,i+1} = 0.3 * h_0$).