

A Stochastic Approach to the Study of Large Biological Neural Networks' Dynamics

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Microscopic point of view – A continuous-time Markov chain

We consider a network of N neurons, whose states evolve stochastically according to a Markov process. The state of a neuron j at time t is a random variable X_j^t with possible values:

- 0, representing the *sensitive* state,
- 1, representing the *active* state, and
- i , representing the *refractory* state.

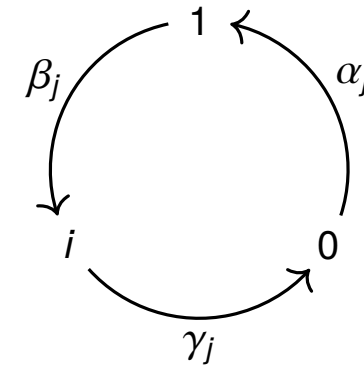


Fig. 1: States and transitions for neuron j .

The allowed transitions and their associated rates are described in Fig. 1. The transition rates β_j and γ_j are both constant, but the activation rate is a nonlinear function of the network's state:

Neuron j activates at a constant rate α_j only if its input exceeds its threshold θ_j .

The evolution of the network's state is ruled by a system of $3^N - 1$ differential equations. Our goal is to reduce this system, but to go beyond the mean-field approximation.

Splitting in populations

We split the network into n populations sharing similar properties, as described in Fig. 2. For each population J , we introduce analogs to the state of a neuron:

- S_J , the sensitive fraction of the population,
- A_J , the active fraction of the population,
- R_J , the refractory fraction of the population.

Since $S_J + A_J + R_J = 1$, only two fractions of each population, A_J and R_J , are needed.

We then see the expected values of the A_J 's and R_J 's as dynamical variables. As expectations of products appear naturally when developing equations for mean population behaviors, we also see covariances (including variances) of the A_J 's and R_J 's as dynamical variables, and obtain a reduced system of $n(2n + 3)$ differential equations.

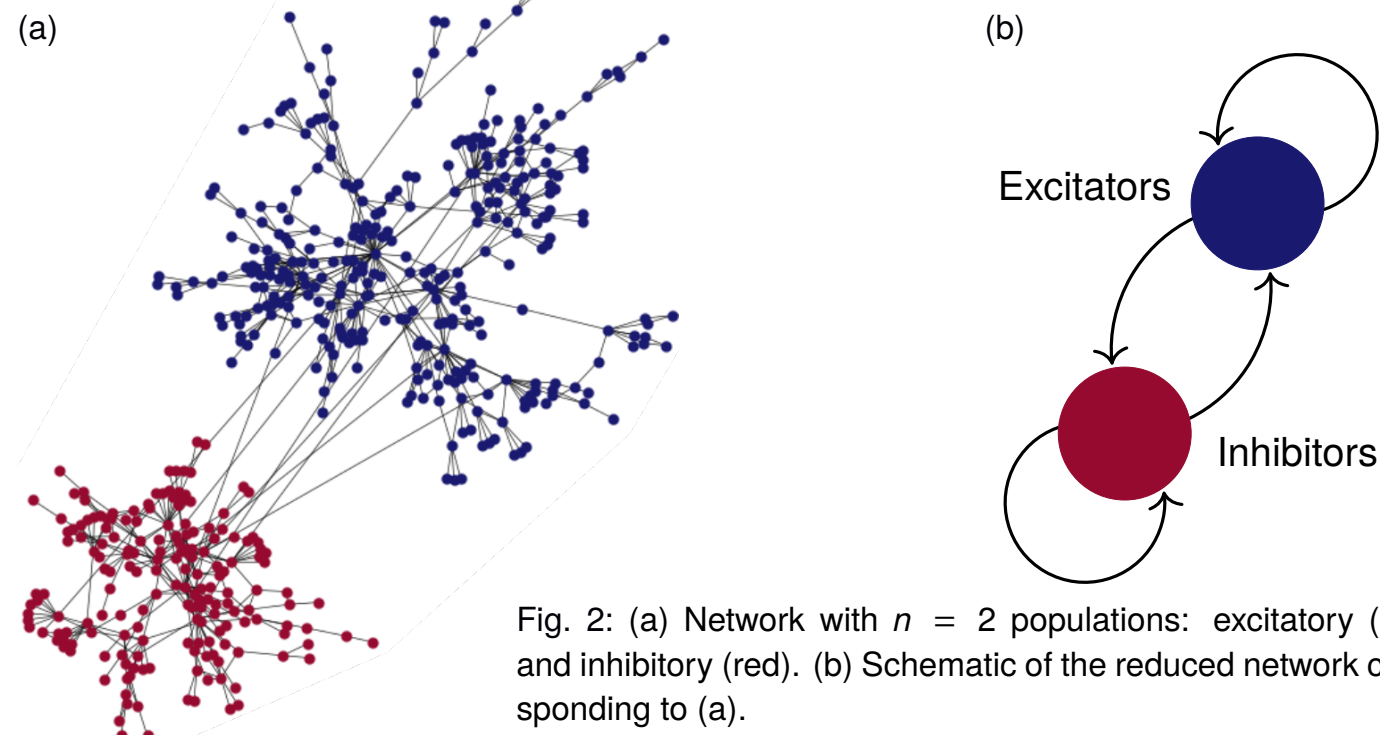


Fig. 2: (a) Network with $n = 2$ populations: excitatory (blue) and inhibitory (red). (b) Schematic of the reduced network corresponding to (a).

Macroscopic point of view – An ODE

Let B_J be the input in population J and F_{θ_j} be the cumulative distribution function of the thresholds in J , assumed to be three times differentiable. We denote by α_J the mean value of the α_j 's in J , and follow the same pattern for other transition rates.

To simplify notation, let

$$\mathcal{A}_J := \mathbb{E}[A_J], \quad \mathcal{R}_J := \mathbb{E}[R_J], \quad \mathcal{S}_J := \mathbb{E}[S_J], \quad \text{and} \quad \mathcal{B}_J := \mathbb{E}[B_J],$$

and let $C_{XY}^{JK} := \text{Cov}[X_J, Y_K]$ with X and Y standing for either A , R , S or B . For any populations J and K (which can be the same), we have

$$\dot{\mathcal{A}}_J = -\beta_J \mathcal{A}_J + \alpha_J F_{\theta_j}(\mathcal{B}_J) \mathcal{S}_J + \alpha_J \text{Cov}[\mathcal{S}_J, F_{\theta_j}(\mathcal{B}_J)] \quad (1a)$$

$$\dot{\mathcal{R}}_J = -\gamma_J \mathcal{R}_J + \beta_J \mathcal{A}_J \quad (1b)$$

$$\dot{C}_{AA}^{JK} = -(\beta_J + \beta_K) C_{AA}^{JK} + \alpha_K \text{Cov}[A_J, S_K F_{\theta_k}(B_K)] + \alpha_J \text{Cov}[A_K, S_J F_{\theta_j}(B_J)], \quad (1c)$$

$$\dot{C}_{RR}^{JK} = -(\gamma_J + \gamma_K) C_{RR}^{JK} + \beta_J C_{AR}^{JK} + \beta_K C_{AR}^{KJ} \quad (1d)$$

$$\dot{C}_{AR}^{JK} = -(\beta_J + \gamma_K) C_{AR}^{JK} + \beta_K C_{AA}^{JK} + \alpha_J \text{Cov}[R_K, S_J F_{\theta_j}(B_J)] \quad (1e)$$

where the dot denotes time derivative.

- System (1) generalizes Wilson–Cowan's model [2], which assumes that the A_J 's and R_J 's are all independent, and sets the \mathcal{R}_J 's to their equilibrium solutions.
- System (1) is not closed. More approximations must be made in (1a), (1c) and (1e).

Moment closure – The naive approach

The simplest approach is to approximate $F_{\theta_j}(B_J)$ with a second-order Taylor expansion around \mathcal{B}_J , and neglecting all centered moments of order 3 or higher. This yields

$$\text{Cov}[S_J, F_{\theta_j}(B_J)] \approx F'_{\theta_j}(\mathcal{B}_J) C_{SB}^{JJ} + \frac{1}{2} F''_{\theta_j}(\mathcal{B}_J) C_{BB}^{JJ}, \quad (2a)$$

$$\text{Cov}[X_J, S_K F_{\theta_k}(B_K)] \approx F_{\theta_k}(\mathcal{B}_K) C_{XS}^{JK} + F'_{\theta_k}(\mathcal{B}_K) S_K C_{XS}^{JK}, \quad (2b)$$

where X stands for A or R . Then (1)–(2) define a dynamical system in $\mathbb{R}^{n(2n+3)}$, but physiologically speaking, its solutions only make sense in a bounded subset of $\mathbb{R}^{n(2n+3)}$.

The naive approach is not enough

The naive approach will give rise to the following problems.

- Numerical integrations show that, in many cases, the system (1)–(2) has solutions which are meaningless, physiologically speaking.
- In system (1)–(2), the long-term behavior of solutions can change if covariances are considered. However, the behavior predicted with covariances may not be consistent with the microscopic model. An example is given on Fig. 3.

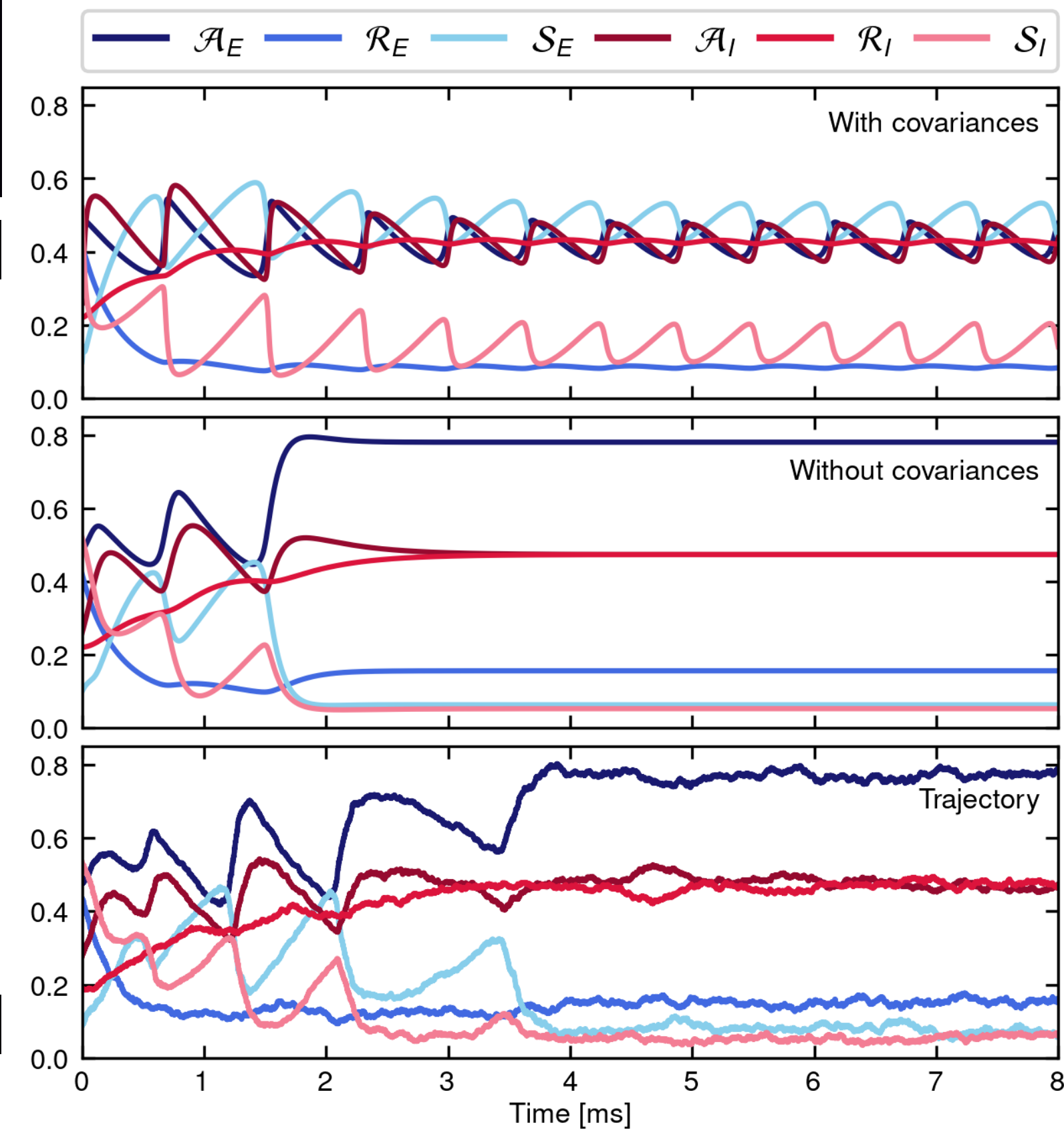


Fig. 3: On top, a solution of the dynamical system (1)–(2). In the middle, a solution of (1)–(2) from the same initial expectations as on top, but neglecting covariances from the start. On bottom, a sample trajectory of the underlying Markov process. The same network parameters were used in all cases. The labels E and I mean “excitatory” and “inhibitory”, respectively.

Moment closure – Other possible method

System (1) could also be closed by finding other approximations to the expectations $\mathbb{E}[S_J F_{\theta_j}(B_J)]$ and $\mathbb{E}[X_J S_K F_{\theta_k}(B_K)]$, where X stands for A or R , in such a way that they stay bounded between 0 and 1. We are currently studying this avenue.

References

- [1] C.C. Chow and Y. Karimipanih, *Journal of Neurophysiology*, **123**, 5 (2020).
- [2] H.R. Wilson and J.D. Cowan, *Biophysical journal*, **12**, 1 (1972).