Extensive chaotic dynamics in neural networks in the balanced state

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Abstract

The irregular activity of neurons in the cortex [1] is thought to arise from strong input fluctuations [2], which result from a balance between excitatory and inhibitory synaptic inputs [3]. This is called the balanced state of cortical networks. However, recent studies of the underlying dynamics of the balanced state have led to contrary results, strongly depending on the used single neuron models [3, 4].

Here, we study the network dynamics of sparsely coupled theta neurons in the balanced state. The theta neuron model has an active spike generating mechanism and is the standard form of type I neurons [5]. In a random matrix approximation of the Jacobian, we derive an expression for the mean Lyapunov exponent. By analyzing the full set of Lyapunov exponents and the maximal Lyapunov vector in a numerically exact way, we reveal extensive spatio-temporal deterministic chaos.

The studied networks exhibit high-dimensional chaotic attractors, giving rise to many dynamical degrees of freedom to encode information. At the same time, the intrinsic entropy production is surprisingly high, limiting information processing to the immediate stimulus response.

Model & Methods

- N **theta-neurons** on a random graph, **average indegree** $K << N$:

$$\tau_m \dot{\theta}_i(t) = (1-\cos\theta_i(t)) + I_i(t)(1+\cos\theta_i(t))$$

- **Delta-pulse** coupling J_{ij}, **no delays**, constant external currents I_{ext}:

$$I_i(t) = I_{\text{ext}} + \sum_{j\in\text{pre}(i)} 2J_{ij}\tau_m\,\delta(\theta_j(t)-\pi)$$

- Numerically exact **event based simulations** of analytic map of phases $\vec{\theta}$ between successive spikes at times $\{t_s\}$
- **Analytic single spike Jacobian**:

$$[D(t_s)]_{ij} = \begin{cases} d_{i^*}(t_s) & \text{for } i=j=i^* \\ 1-d_{i^*}(t_s) & \text{for } i=i^* \text{ and } j=j^* \\ \delta_{ij} & \text{otherwise} \end{cases}$$

with $d_{i^*}(t_s) = \frac{V_{i^*}(t_s^-)^2+I_{\text{ext}}}{V_{i^*}(t_s^+)^2+I_{\text{ext}}}$, where $V(t) = tan\frac{\theta(t)}{2}$
j^* is the spiking neuron at time t_s and i^* its postsynaptic neurons

- Calculation of **Lyapunov exponents** in the standard procedure [6]:

$$\vec{\lambda} = \lim_{t_p\to\infty}\frac{1}{t_p}\ln\left(\text{Eig}\prod_{s=0}^{p} D(t_s)\right)$$

- **Entropy production** (Pesin's formula):

$$H_{KS} = \sum_i^{\lambda_i>0}\lambda_i$$

- **Attractor dimension** (Kaplan-Yorke conjecture):

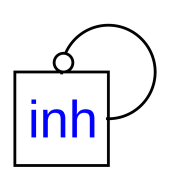
$$D_{KY} = n + \frac{S_n}{|\lambda_{n+1}|}$$

(for maximal n such that $S_n = \sum_i^n \lambda_i > 0$)

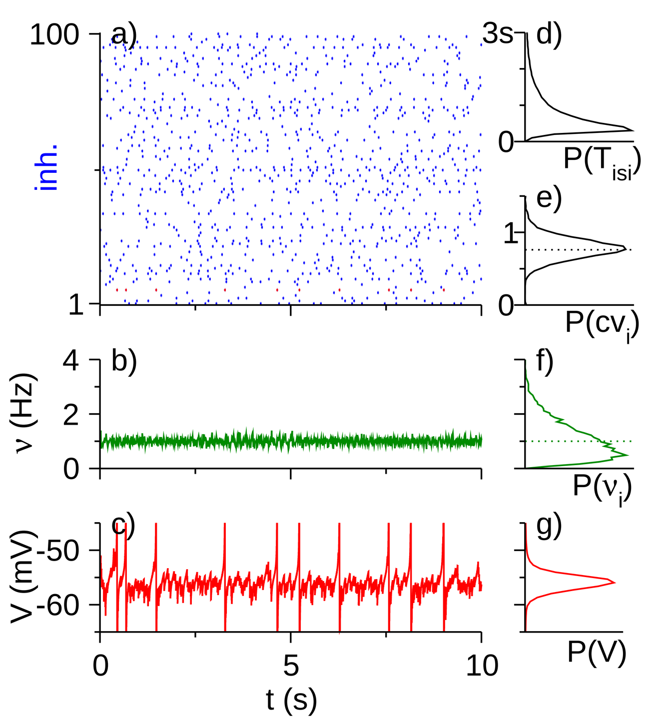
- **Mean Lyapunov exponent** from random matrix approximation:

$$\bar{\lambda} = K\bar{\nu}\int \ln\left[\frac{V^2+I_{\text{ext}}}{(V+J)^2+I_{\text{ext}}}\right]P(V)\text{d}V$$

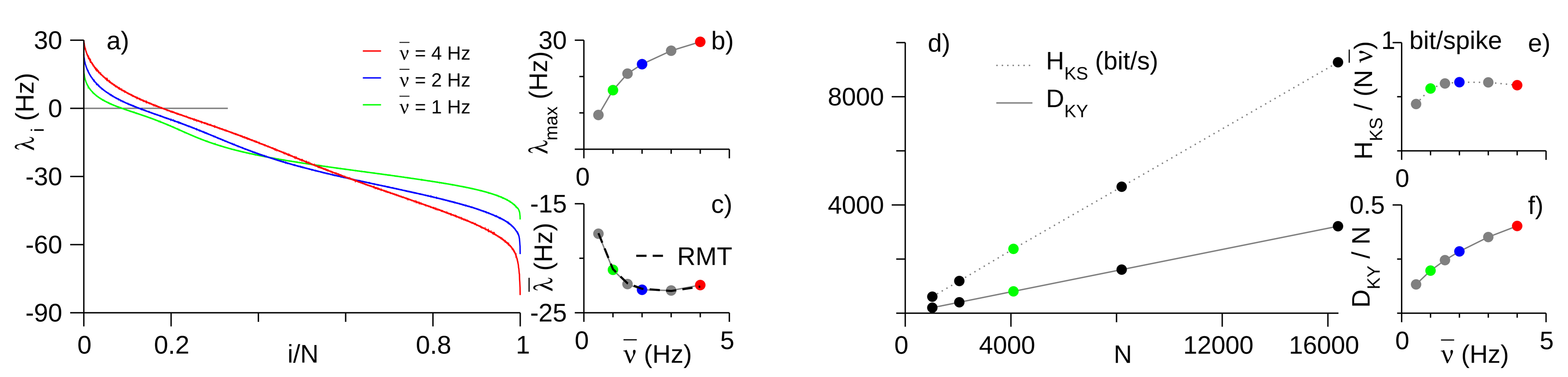
Purely inhibitorily coupled networks



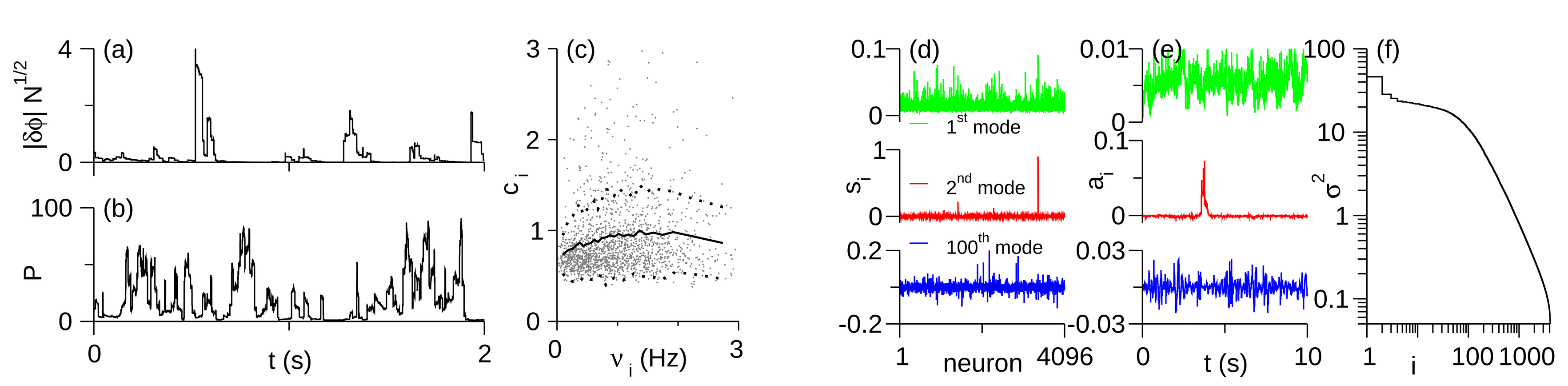
Inhibitory couplings $J_{ij} = -\frac{J_0}{\sqrt{K}}$ balance external currents $I_{\text{ext}} > 0$



Characteristics of the balanced state: a) Asynchronous and temporally irregular firing patterns, b) Constant average network firing rate (10 ms bins), c) Strongly fluctuating membrane potentials, d-g) Broad distributions of inter-spike intervals T_{isi}, coefficients of variations cv_i, firing rates ν_i and membrane potentials V (parameters: $N = 10000$, $K = 32$, $\bar{\nu} = 1$ Hz, $J_0 = 1$, $\tau_m = 10$ms)



Extensive deterministic chaos: a) Full Lyapunov spectra $\vec{\lambda}$ at different average network firing rates $\bar{\nu}$, b) Positive maximal Lyapunov exponents c) Negative mean Lyapunov exponents, d-f) Attractor dimension D_{KY} and entropy production H_{KS} vs. system size N and network firing rates (parameters as above but $N = 4096$)

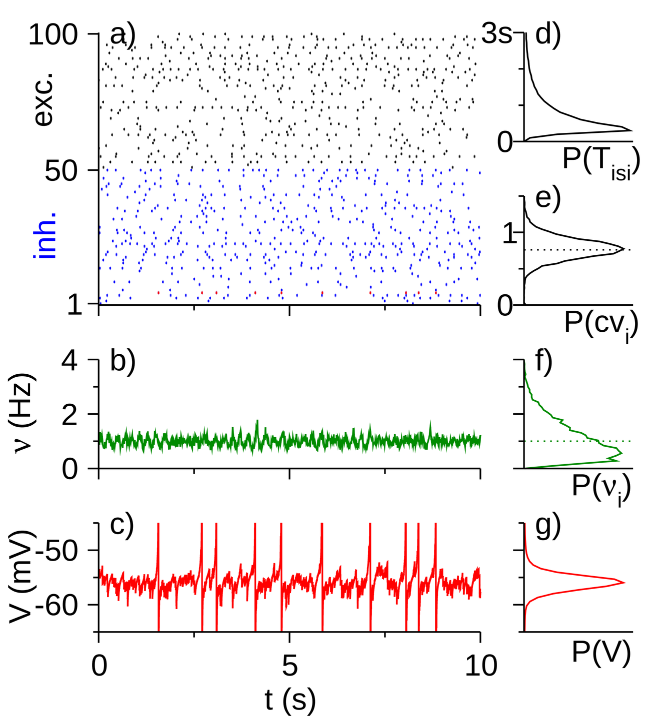


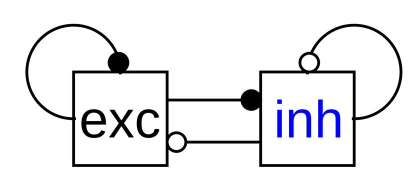
Spatio-temporal chaos: a) Maximal Lyapunov vector component $\delta\phi_i(t)$ for one neuron with chaos index $c_i = 1$, b) Participation number $P(t) = 1/\sum_i[\delta\phi(t)]^4$, c) Chaos indices $c_i^2 = N\text{var}[\delta\phi_i(t)]$ vs. firing rates ν_i Karhunen-Loève decomposition (a.k.a. PCA) of $\delta\vec{\phi}(t)$ for 10s: d) eigenmodes, e) amplitudes, f) eigenvalues

The balanced state exhibits:

- Deterministic chaos (positive and finite maximal Lyapunov exponent)
- Extensive chaos (linear scaling of attractor dimension and entropy production with system size)
- Spatio-temporal chaos (chaos patterns uncorrelated in space and time)
- High-dimensional chaotic attractor (tenths of whole phase space)
- Large entropy production 0.5 bits/spike (compared to estimated information of 0.6 to 3.2 bits/spike [7])

Networks with excitatory and inhibitory populations





Intra-population couplings:

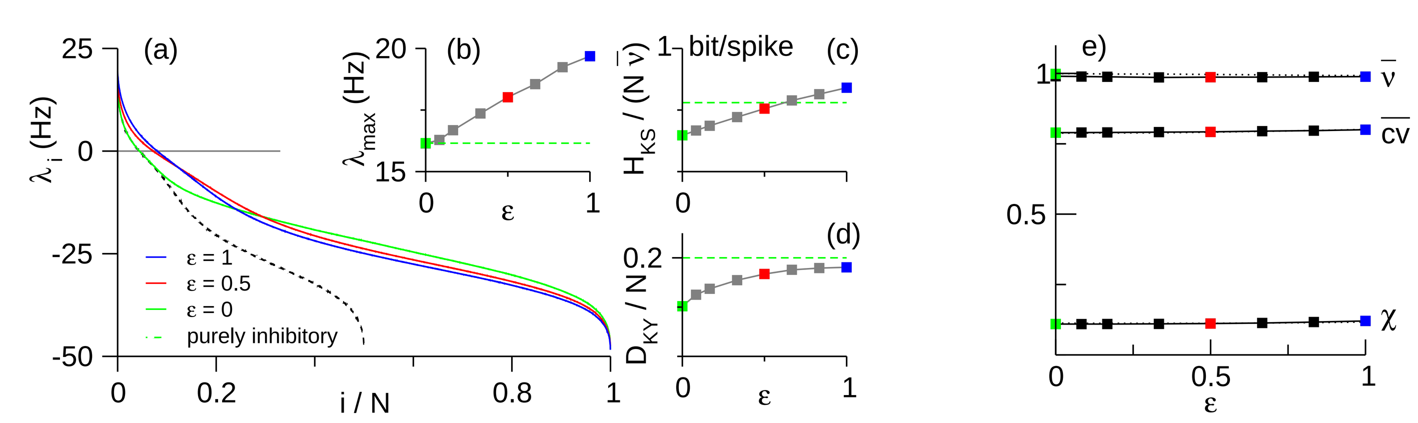
$$J_{EE} = \frac{J_0}{\sqrt{K}}0.27\varepsilon \qquad J_{II} = -\frac{J_0}{\sqrt{K}}\sqrt{1-(0.3\varepsilon)^2}$$

Inter-population couplings:

$$J_{IE} = \frac{J_0}{\sqrt{K}}0.3\varepsilon \qquad J_{EI} = -\frac{J_0}{\sqrt{K}}\sqrt{1-(0.27\varepsilon)^2}$$

Temporal variance of synaptic input currents are the same as in the purely inhibitory networks:

$$\sigma_I^2 = J_0^2\bar{\nu}$$



Excitatory-inhibitory loop activation ε: a) Full Lyapunov spectra, b) Maximal Lyapunov exponents, c) Attractor dimension density, d) Entropy production per spike (dashed lines from purely inhibitory networks), e) Average network firing rate $\bar{\nu}$, coefficient of variation $\bar{\text{cv}}$ and spatial order parameter $\chi^2 = \text{var}_{[\theta_i]}/[\text{var}_{\theta_i}]$

- Activation of excitatory-inhibitory loops leads to more chaotic dynamics while the network statistics remain unchanged, spatio-temporal and extensive character as in inhibitory networks (not shown)

Conclusion

- Deterministic extensive spatio-temporal chaos in balanced neural networks of type I neurons
- High dimensional chaotic attractors, providing many degrees of freedom to encode information
- High entropy production limits information processing to immediate stimulus response

Outlook: How does the brain use these chaotic balanced networks?

- Chaos control?
- Intrinsic noise generator?

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