Quasiperiodic partial synchronization and macroscopic chaos in populations of inhibitory neurons with delay

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Introduction

- Inhibitory networks are responsible for the generation of **fast neuronal oscillations** (> 50 Hz)
- Oscillations due to **inhibition** and **synaptic delays**
- Individual neurons do not fire at the freq of the fast, mean field oscillations
- Challenge for canonical, analytically tractable, phase oscillator models (Kuramoto model)
- Increasing interest for more complex forms of synchronization (*quasiperiodic partial synchronization, chimera states*...)

Kuramoto model with time delay

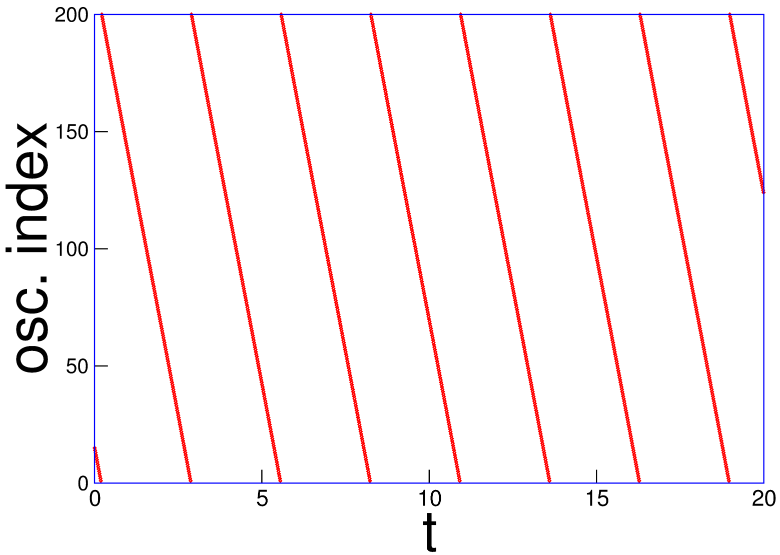
Coupling Strength

Natural frequencies

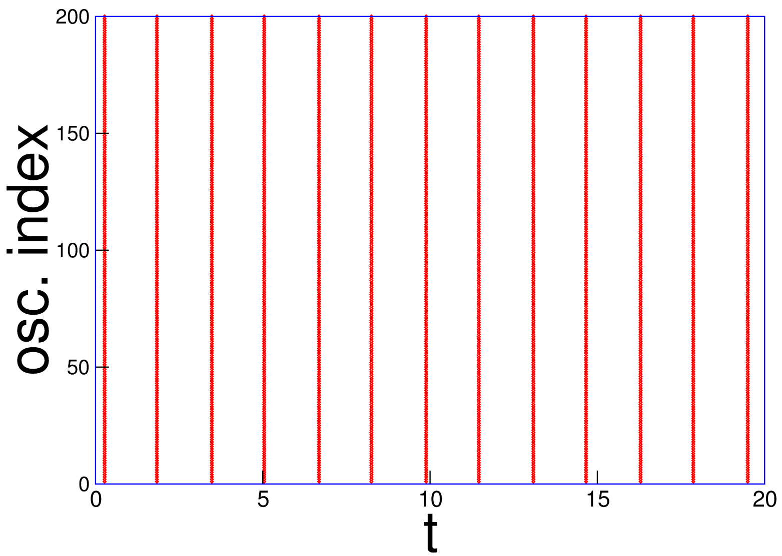
Time delay

$$\dot{\theta}_i(t) = \omega_i - \frac{K}{N}\sum_{j=1}^{N} \sin[\theta_i(t) - \theta_j(t-\tau)]$$

Incoherence
Asynchronous state

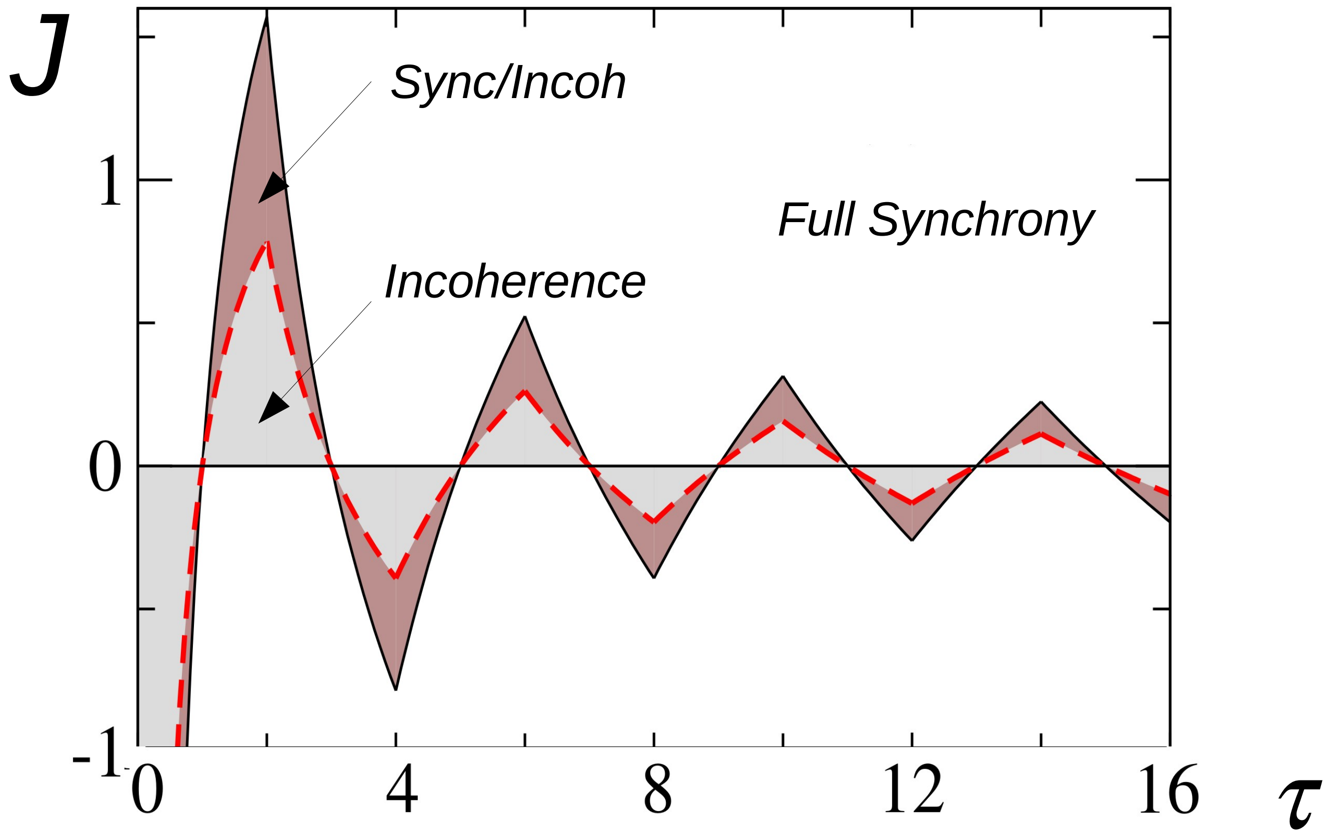


Full synchronization



Yeung, Strogatz, *Phys Rev Lett* (1999)

Kuramoto model with time delay phase diagram

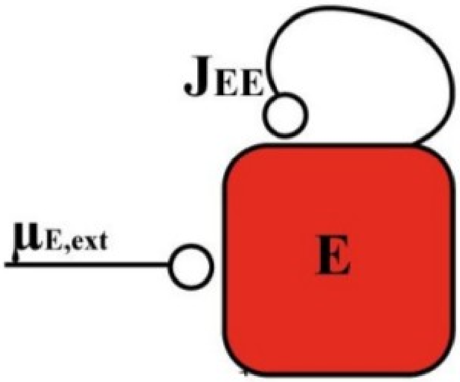


Same dynamics for Excitation and for Inhibition

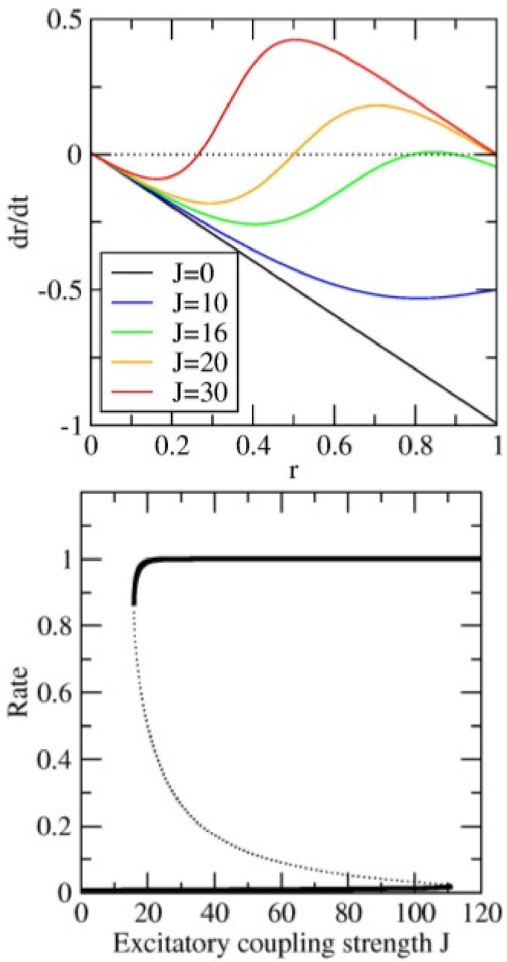
Yeung, Strogatz, *Phys Rev Lett* (1999)

Neuronal Mean field models
Heuristic Firing Rate Equations

Single excitatory population:

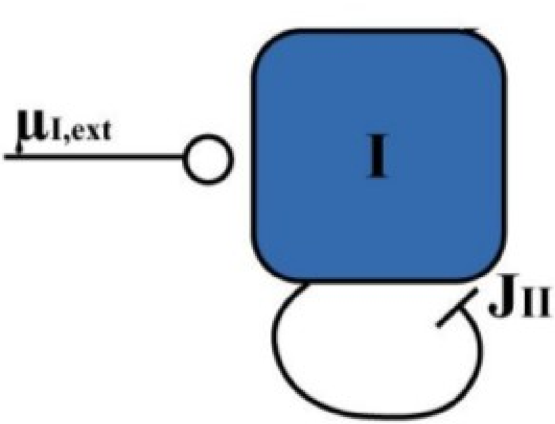


$$\tau \frac{dr}{dt} = -r + \Phi\left(I + Jr\right)$$



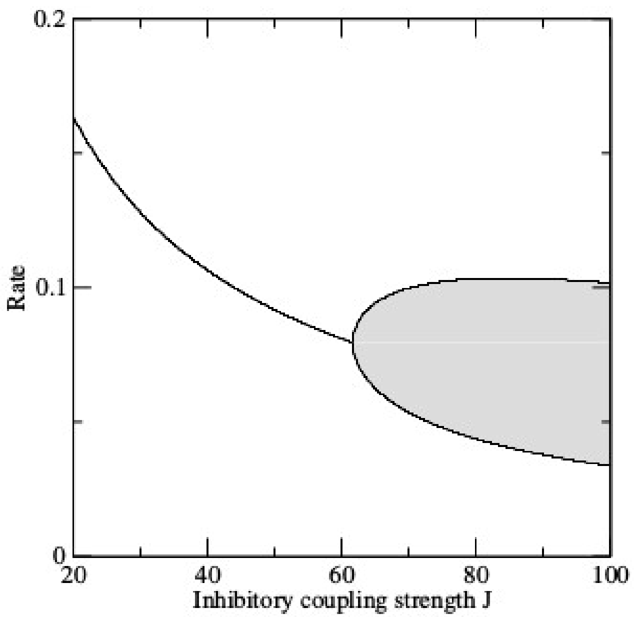
Wilson and Cowan, 1972; Amari 1974

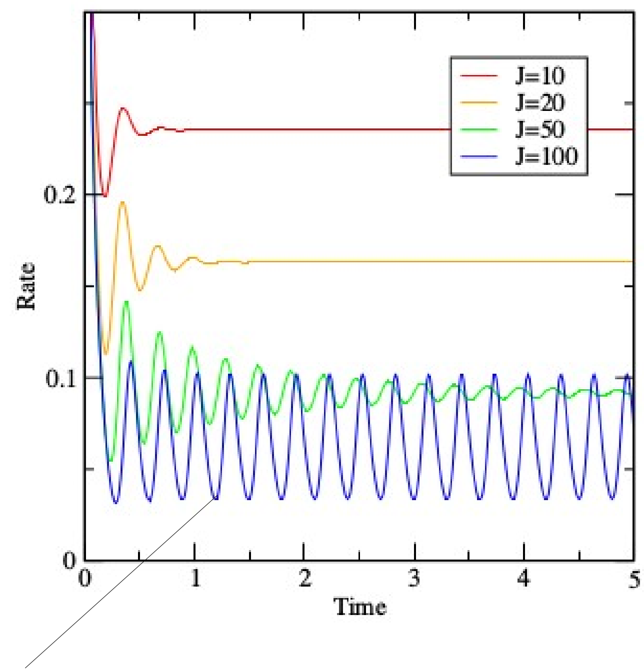
Fast oscillations in HFRE
Inhibitory population with delay



$$\tau \frac{dr_I}{dt} = -r_I + \Phi_I \left(I_{IX} - J_{II} r_I(t-D) \right)$$

- Oscillations at a frequency f_c appear when $\tilde{J}_{II} > J_c$
- For $D \ll \tau$, $J_c \sim \pi\tau/(2D)$, $f_c \sim 1/(4D)$





If D = 5 ms, freqs. between 50 and 100 Hz

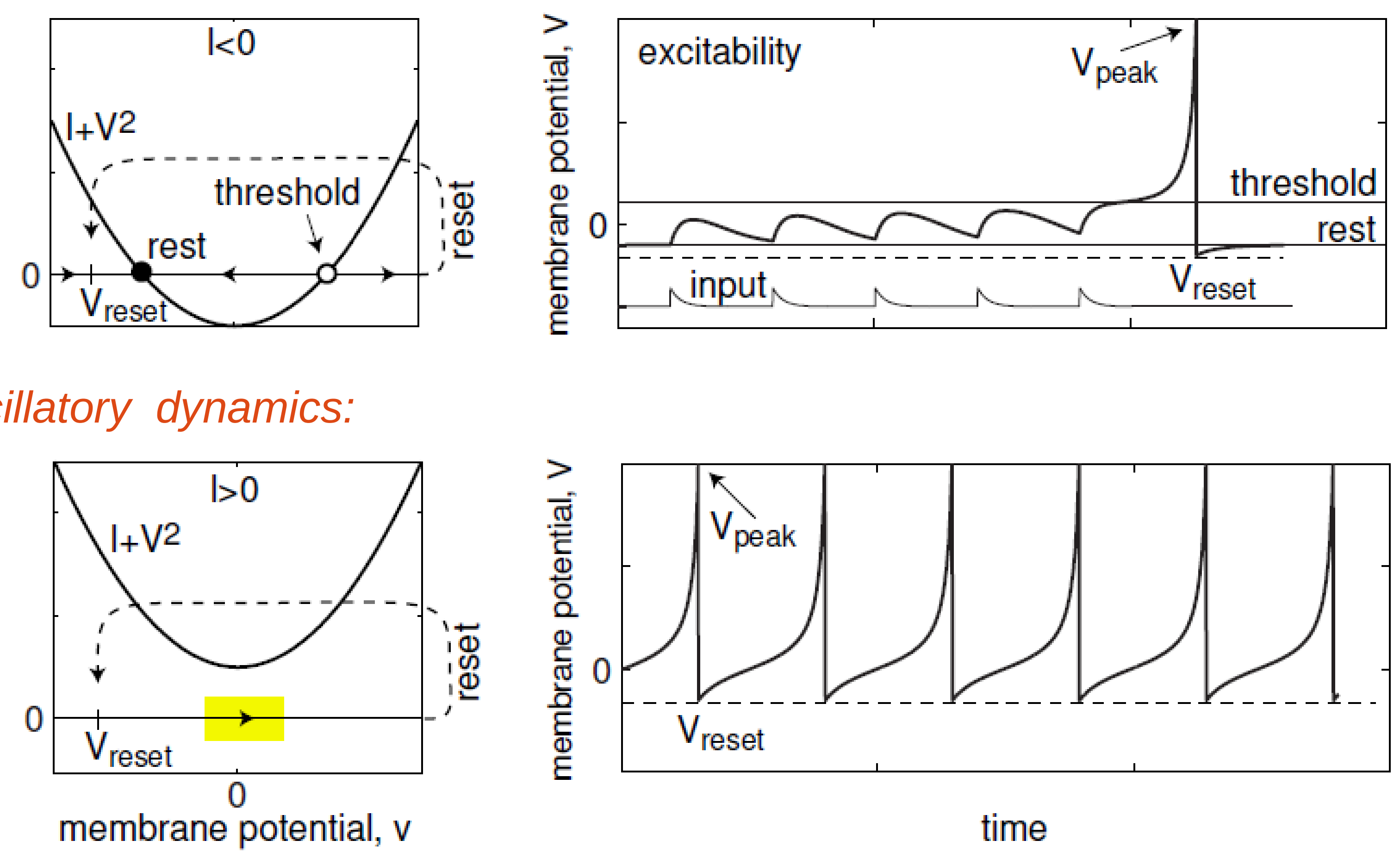
Roxin, Brunel, Hansel, *PRL* (2005)
Roxin, Montbrió, *Phys D* (2011)

Quadratic Integrate-and-fire neuron

$$\dot{V} = I + V^2\ , \qquad \text{if } V \geq V_{\text{peak}}, \quad \text{then } V \leftarrow V_{\text{reset}}$$

Excitable dynamics:

Oscillatory dynamics:



Ensemble of recurrently coupled QIF neurons with synaptic time delay

$$\tau \dot{V}_j = V_j^2 + I_j\,,$$

$$I_j = \eta_j + J\, s_D\,,$$

- Coupling: *J*>0: Excitation; *J*<0: Inhibition
- Mean synaptic activity ($s_D = s(t-D)$): $$s_D = \frac{\tau}{N\tau_s} \sum_{j=1}^{N} \sum_k \int_{t-D-\tau_s}^{t-D} \delta(t' - t_j^k)\, dt'.$$
- Fast synapses (τ_s->0): $s_D = \tau r_D$

Population-Averaged Firing Rate

Correspondence of QIF, Winfree and Theta models

$$\tau \dot{V}_j = V_j^2 + \eta_j + J\tau r_D$$

When: V_{peak}=-V_{reset} → infty :

- Inter-spike Interval self-oscillatory neurons (*η>0,J=0)*: $\mathrm{ISI} = \pi\tau/\sqrt{\eta_j}$.
- **Winfree Model** (identical, self-oscillatory neurons): $V_j = \sqrt{\eta}\tan\left(\frac{\psi_j}{2}\right)$,

$$\tau\dot{\psi}_j = 2\sqrt{\eta} + (1+\cos\psi_j)\frac{J}{\sqrt{\eta}}\tau r_D.$$

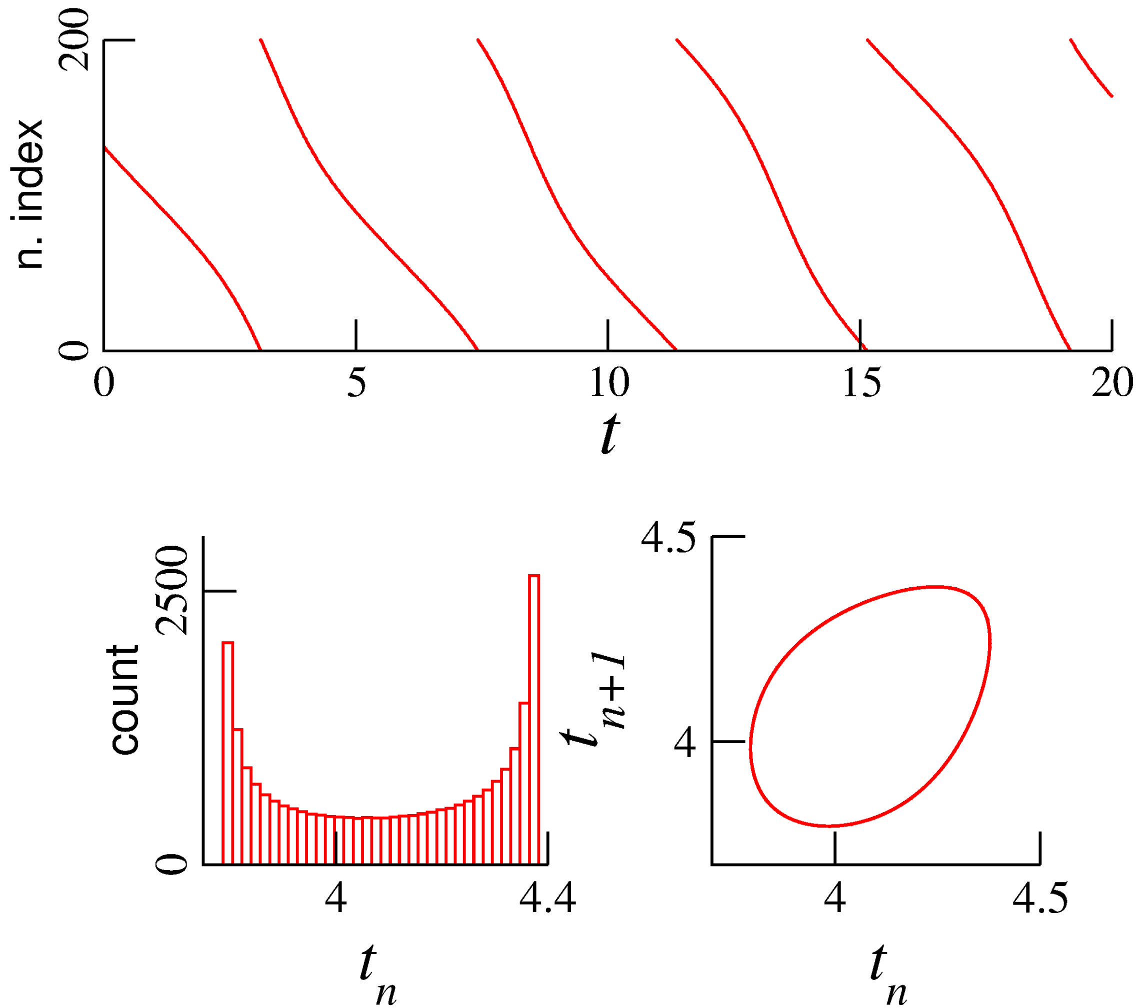
- **Theta-Neurons** (τ=1): $V_j = \tan(\theta_j/2)$

$$\tau\dot{\theta}_j = (1-\cos\theta_j) + (1+\cos\theta_j)\left[J\tau r_D + \eta_j\right]$$

Ermentrout and Kopell,SIAM J Appl Math 1986

Numerical simulations, QIF neurons

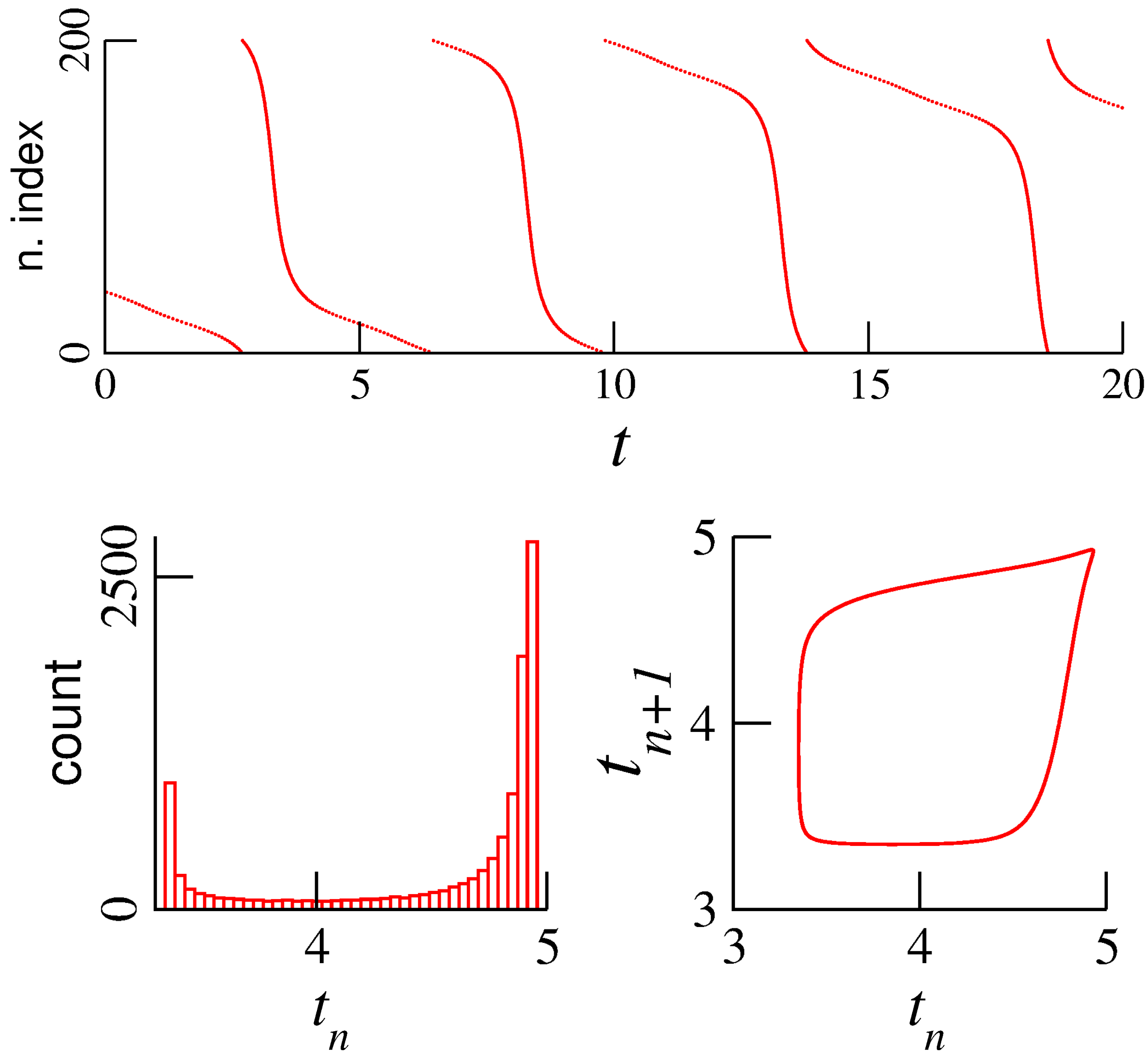
J=-1.65, D=2.5 ($\eta=\tau=1$)



Neurons display quasiperiodic dynamics **for inhibbitory (*J*<0) coupling only**

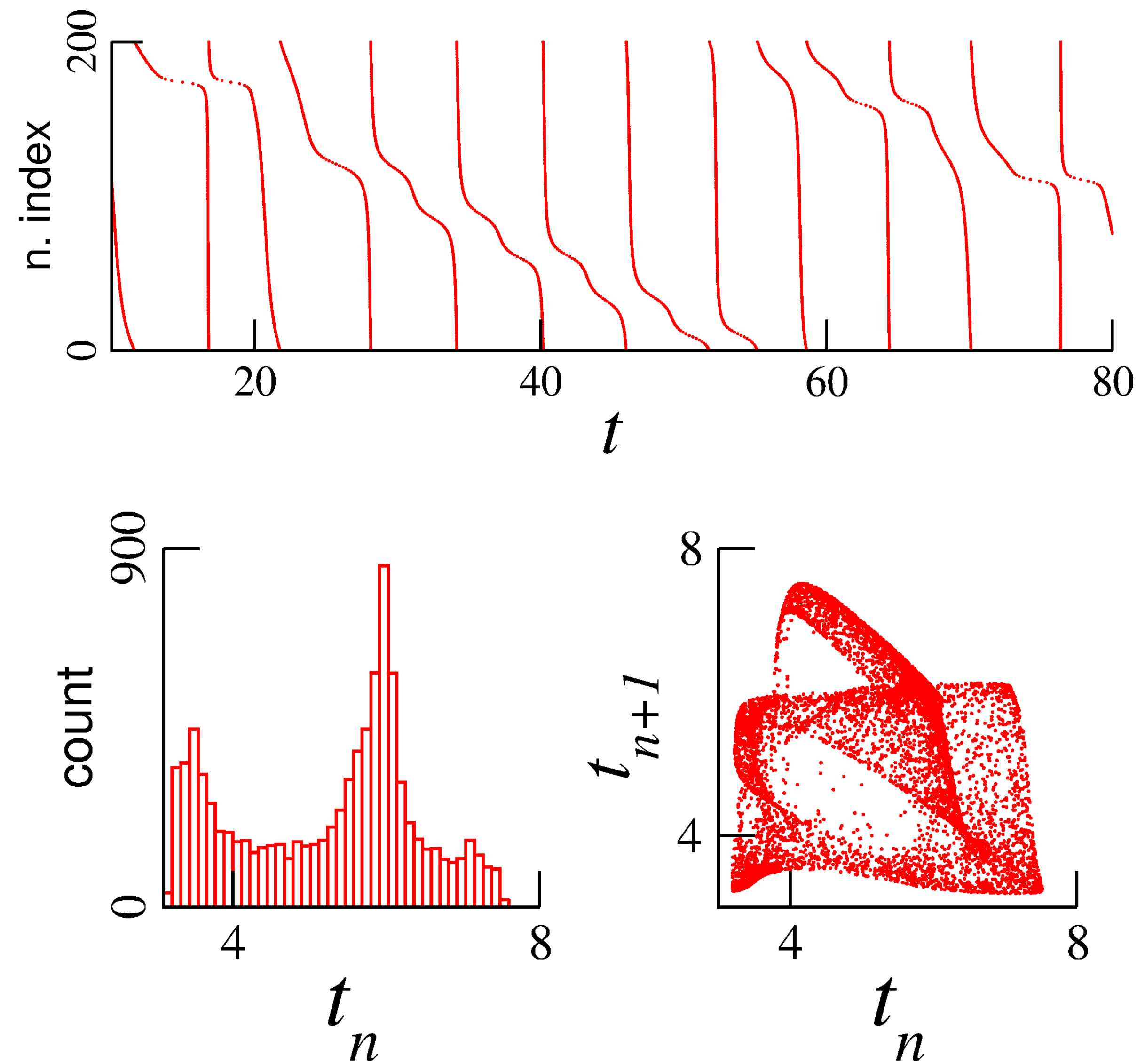
Numerical simulations (II)

J=-1.85, D=2.5 (η=τ=1)



Numerical simulations (III)
Macroscopic chaos?

J=-3.8, D=3 ($\eta = \tau = 1$)



Derivation of exact Firing Rate Equations

- Spiking neurons: QIF
- All-to-all coupling
- Quenched heterogeneity (no noise)
- Exact in the thermodynamic limit

Montbrió, Pazó and Roxin, *PRX* 2015; Pazó and Montbrió, *Submitted*

Thermodynamic limit
Continuous formulation

$\rho(V|\eta, t)dV$ Fraction of neurons with *V* between *V* and *V*+*dV* and parameter η at time *t*

$g(\eta)$ PDF of the currents η

The **Continuity Equation** is

$$\tau\partial_t\rho + \partial_V\left[(V^2 + \eta + J\tau r_D)\rho\right] = 0.$$

For each value of η!! Then the total density at time *t* is given by: $\int_{-\infty}^{\infty}\rho(V|\eta, t)g(\eta)d\eta$

Lorentzian Ansatz

$$\rho(V|\eta,t) = \frac{1}{\pi}\frac{x(\eta,t)}{[V - y(\eta,t)]^2 + x(\eta,t)^2}$$

Center — $y(\eta,t)$

Width — $x(\eta,t)$

Equivalence btw the LA and the Ott-Antonsen ansatz

- The LA is the Poisson Kernel in the **positive semi-plane** (*x>0*)
- The OA ansatz is Poisson Kernel in the **unit disk** (R<=1).

Ott and Antonsen, *Chaos*, 2008

Lorentzian Ansatz
Firing Rate & **Mean Membrane potential**

Firing Rate: Prob flux at threshold: $r(\eta,t) = \rho(V \to \infty|\eta,t)\dot{V}(V \to \infty|\eta,t)$

Firing Rate

$$x(\eta,t) = \pi r(\eta,t)$$

$$r(t) = \frac{1}{\pi}\int_{-\infty}^{\infty} x(\eta,t)g(\eta)d\eta$$

Mean Membrane potential

$$y(\eta,t) = \mathrm{P.V.}\int_{-\infty}^{\infty} \rho(V|\eta,t)V\,dV.$$

$$v(t) = \int_{-\infty}^{\infty} y(\eta,t)g(\eta)d\eta$$

2D Firing Rate equations (FRE)

Lorentzian distribution of currents

$$g(\eta) = \frac{1}{\pi} \frac{\Delta}{(\eta - \bar{\eta})^2 + \Delta^2}$$

Cauchy Residue's theorem to solve

$$r(t) = \frac{1}{\pi} \int_{-\infty}^{\infty} x(\eta, t) g(\eta) d\eta$$

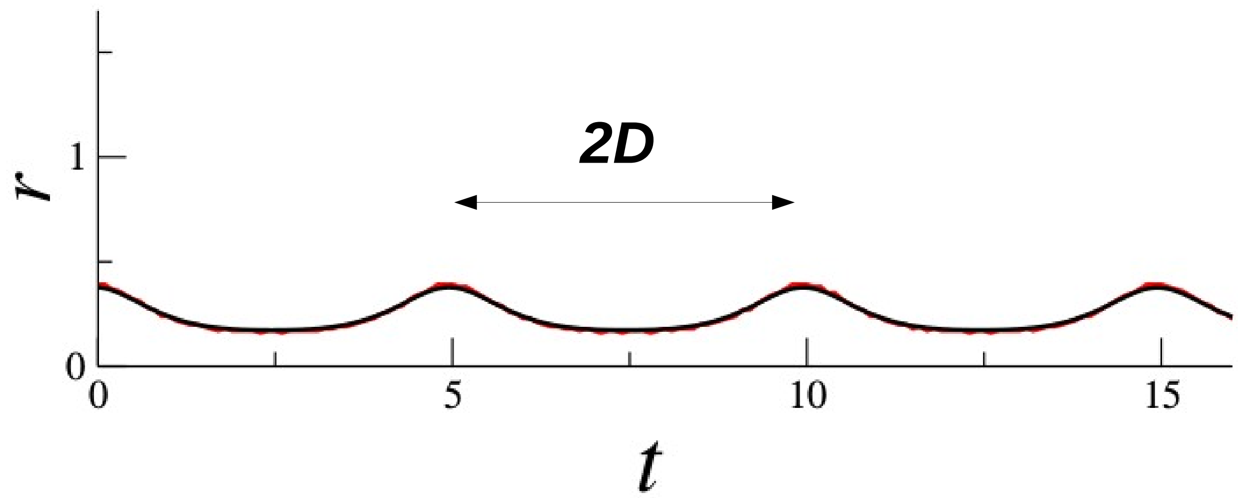
Substituting the LA in the continuity equation:

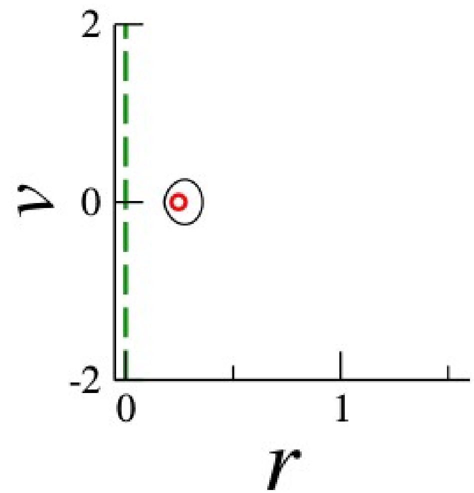
$$\tau \dot{r} = \frac{\Delta}{\pi \tau} + 2rv,$$
$$\tau \dot{v} = v^2 + \bar{\eta} + J\tau r_D - \tau^2 \pi^2 r^2.$$

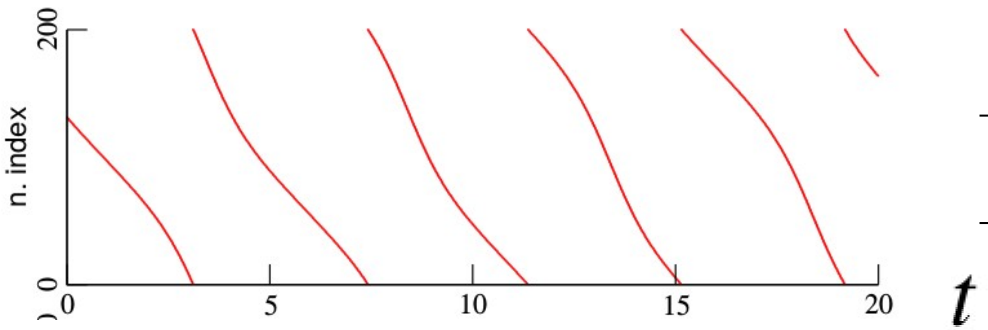
$\tau = \eta = 1$, without loss of generality

Numerical simulations using FRE

($J=-1.65$, $D=2.5$, $\Delta=0$)







→ Periodic activity of **collective variables**

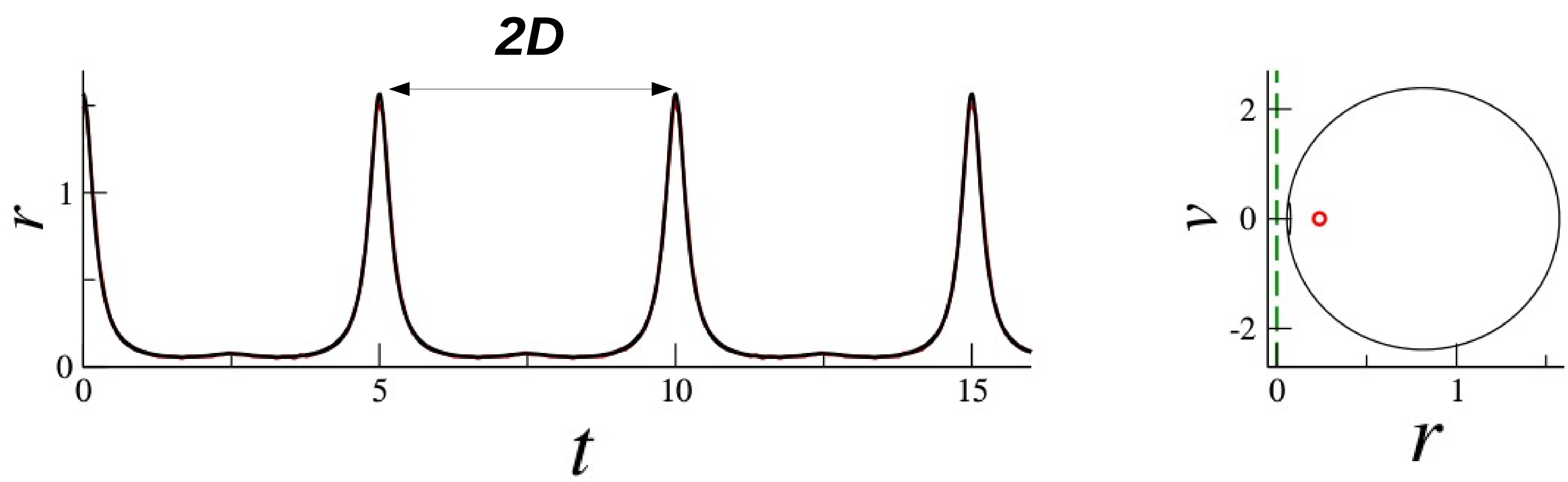
→ Quasiperiodic dynamics at **microscopic** level

Quasiperiodic partial synchronization in inhibitory networks

Van Vresswijk, *PRE* (1996); Mohanti, Politi, *J. Phys A* (2006);
Rosenblum, Pikovsky, *PRL* 2007; Pikovsky, Rosenblum *Physica D* (2009);
Politi, Rosenblum, *PRE* (2015)

Increasing inhibition...

(J=–1.65, D=2.5, Δ=0)



Period of oscillations remains constant

Limit cycle is symmetric $v \rightarrow -v$

Using FRE for Δ=0, this symmetry implies that:

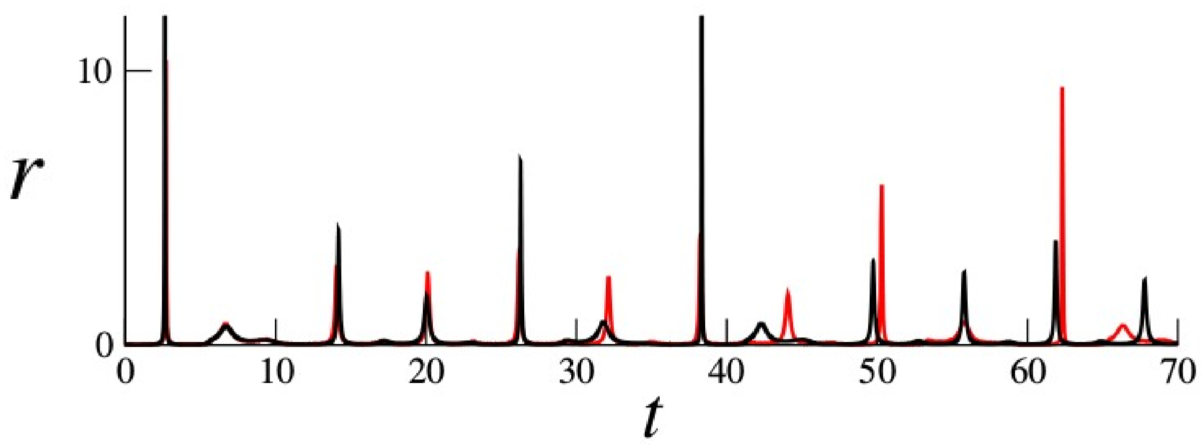
$$T_m = \frac{2D}{m}, \qquad \text{with} \quad m = 1, 3, \ldots$$

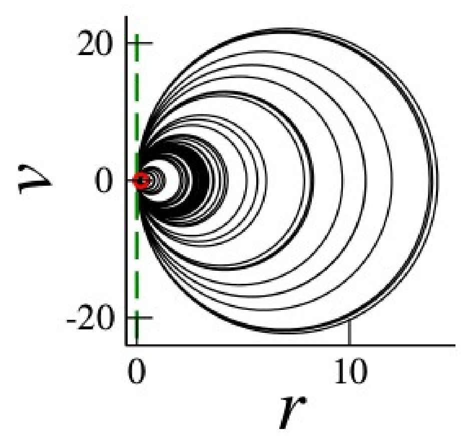
The symmetry is broken at period doubling bif...

Macroscopic chaos through quasiperiodic partial sync

(J=−3.8, D=3, Δ=0)

The QPS undergoes a succession of period doubling bifs leading to macroscopic chaos
(using the FRE: Largest Lyapunov exp. 0.055)





Analysis of FRE

$$\tau \dot{r} = \frac{\Delta}{\pi \tau} + 2rv,$$
$$\tau \dot{v} = v^2 + \bar{\eta} + J\tau r_D - \tau^2 \pi^2 r^2.$$

For identical neurons, the only fixed point is:

$$\left((J + \sqrt{J^2 + 4\pi^2})/(2\pi^2), 0\right)$$

Linearizing around the f.p. and imposing the cond. of marginal stab: $\lambda = i\,\Omega$

Hopf boundaries:

$$\Omega_n = n\pi/D.$$

$$J_H^{(n)} = \pi(\Omega_n^2 - 4) \times \begin{cases} (6\Omega_n^2 + 12)^{-1/2} & \text{for odd } n \\ (2\Omega_n^2 - 4)^{-1/2} & \text{for even } n \end{cases}$$

Analysis of the fully synchronized state Winfree model

Stability of the fully sync state in the the Winfree model:

$$\tau\dot{\psi}_j = 2\sqrt{\eta} + (1 + \cos\psi_j)\frac{J}{\sqrt{\eta}}\tau r_D.$$

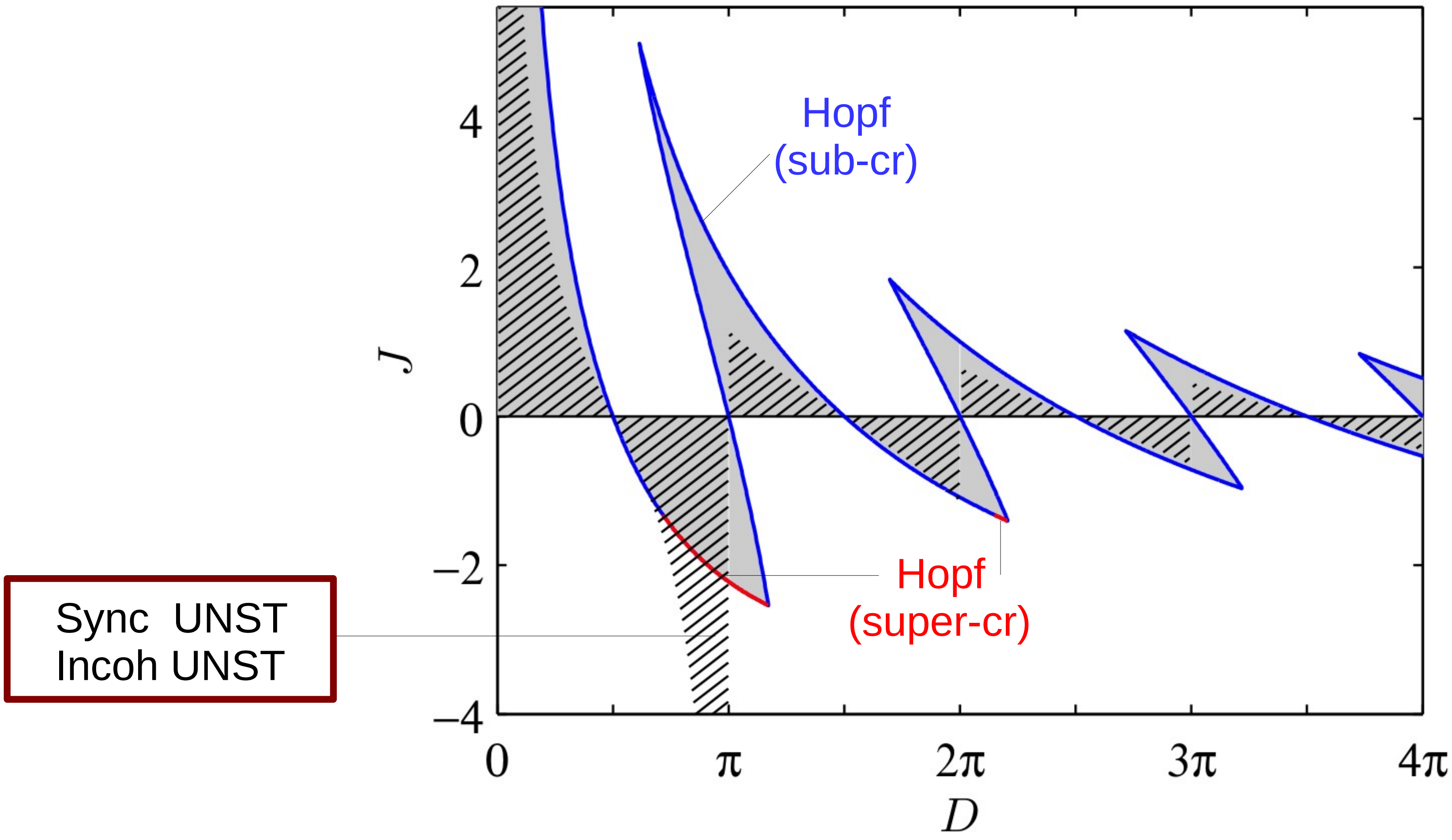
We find the boundaries:

$$J_c^{(m)} = 2\cot\left(\frac{D}{m}\right), \qquad \text{with } m = 1, 3, 5, \ldots$$

And by the evently spaced lines:

$$D = n\pi \; (n = 1, 2 \ldots).$$

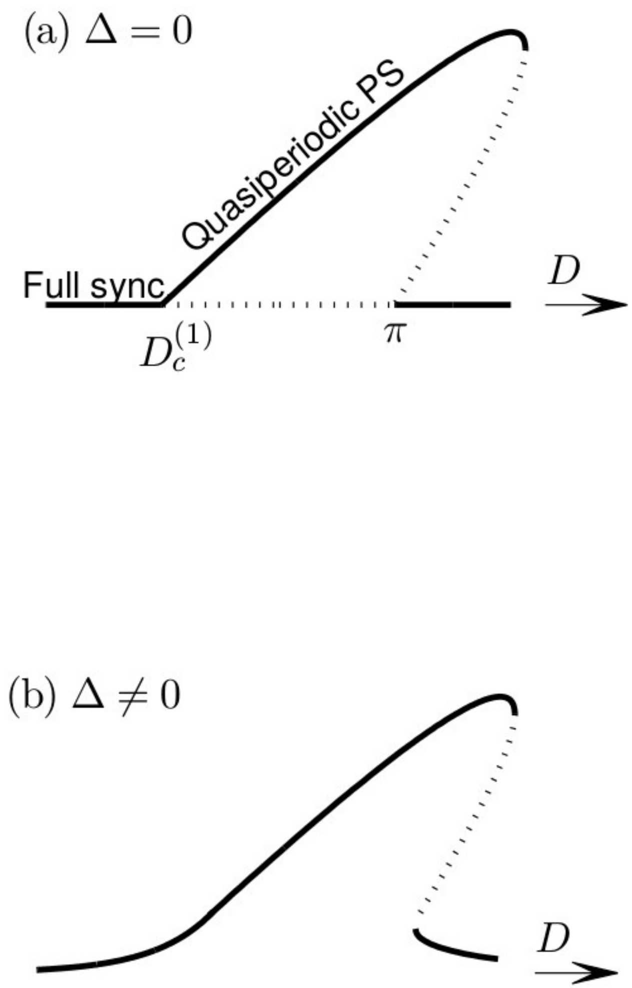
Phase diagram for identical neurons

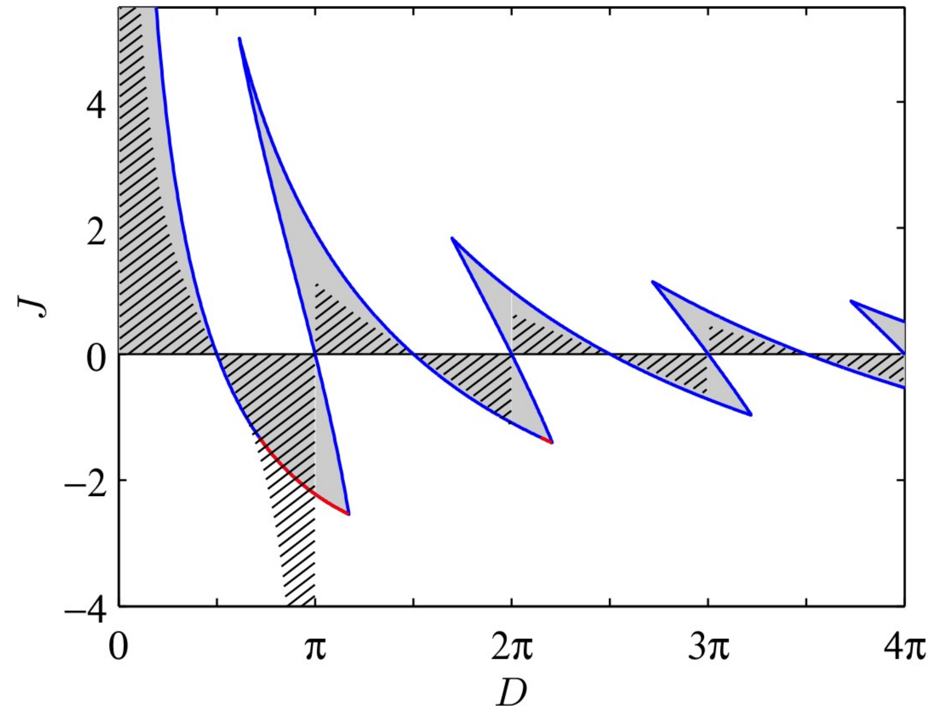


Shaded regions: Asynch/Incoherent state **STABLE**

Dashed regions: Full sync **UNSTABLE**

Onset of QPS and heterogeneity

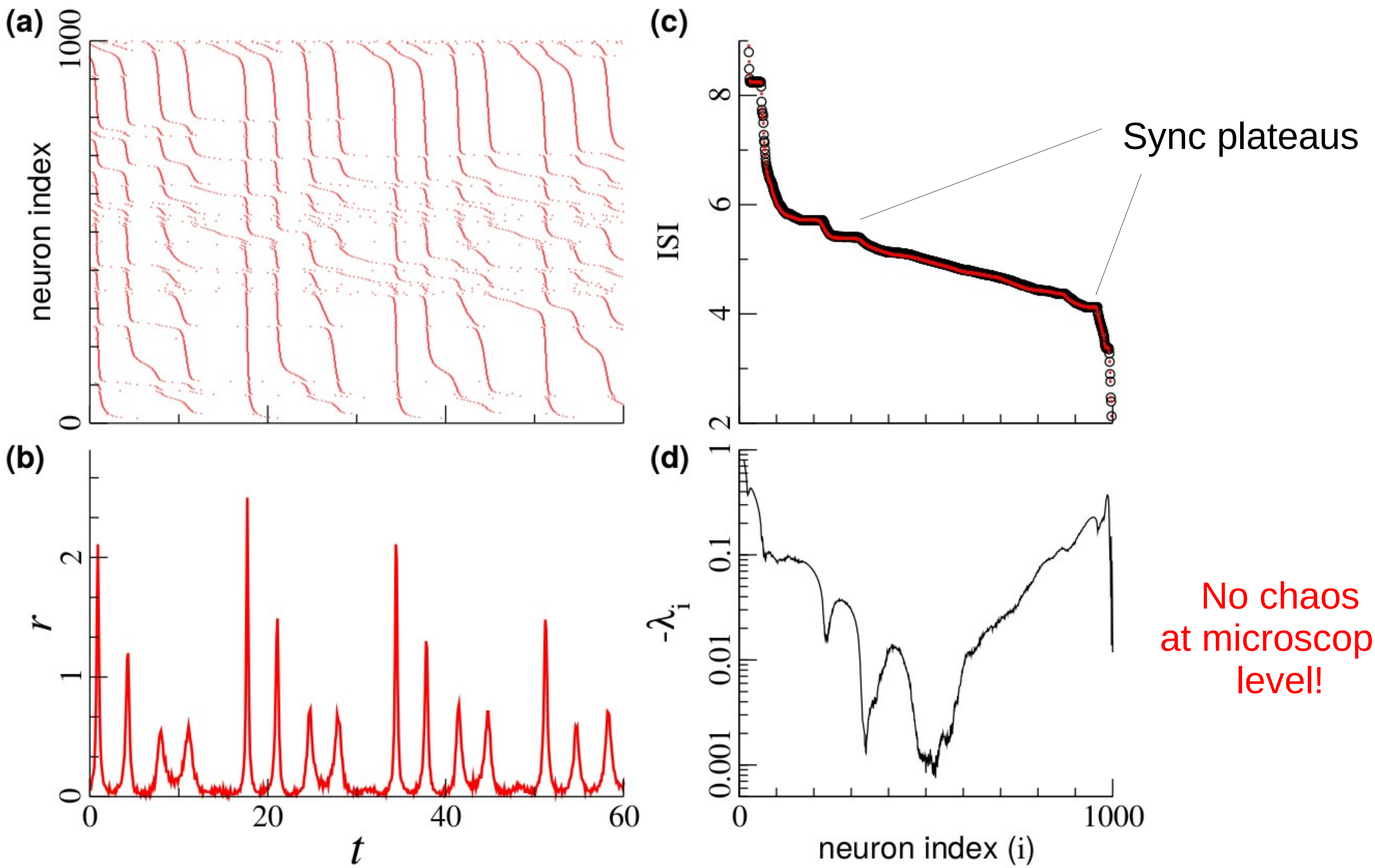




TC bifs. are not robust

bistability btw two partially sync states remains, though

Macroscopic chaos in heterogeneous networks



No chaos
at microscopic
level!

Thanks!

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ITN project: Complex Oscillatory Systems: Modeling and Analysis

Fedrico Devalle

Poster: *Solvable model for a network of spiking neurons with delays*