Synchronization Patterns in Firing Rate Models with Synaptic Delay

Ernest Montbrió

Center for Brain and Cognition, Pompeu Fabra University

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Introduction

- Brain oscillations, Hans Berger 1929 (EEG)
- Display a broad range of frequencies
- Correlated with sleep stages & tasks
- The reflect some coordination of spike discharges in large ensembles of neurons
- Inhibition largely involved, particularly in “fast oscillations” (>30Hz)
- Mathematical models:
  - **Inhibition + Synaptic Delays**

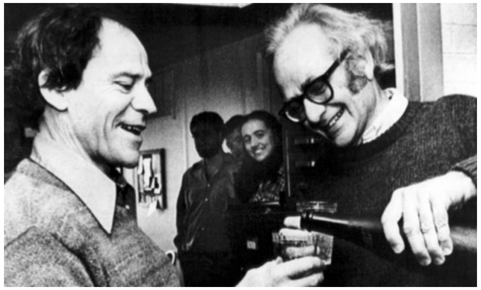
Modeling populations of neurons

- **Microscopic modeling:** Networks of spiking neurons

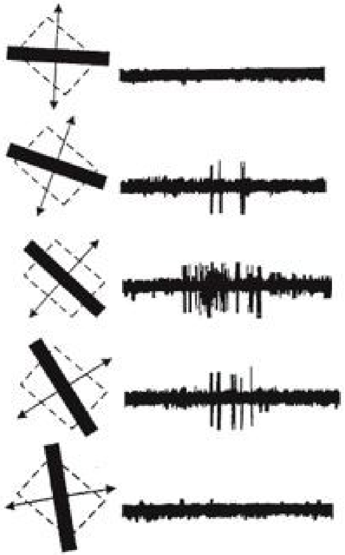
  Describe the activity of a population of N neurons by a set of O(N) ordinary differential equations, coupled via a given connectivity matrix

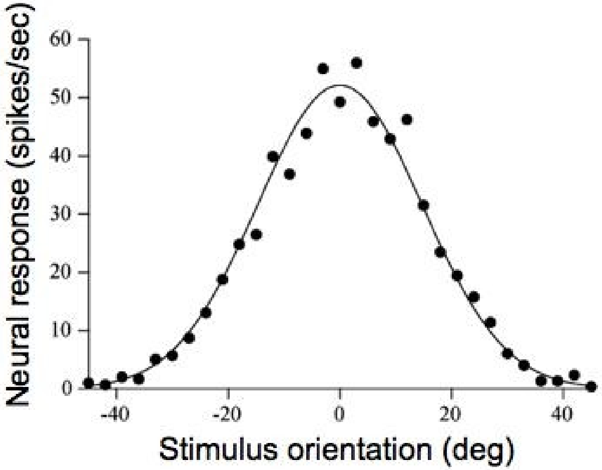
- **Macroscopic modeling:** Firing rate models *Wilson-Cowan, 1972*
  - Activity of a neuronal **population**, single “averaged” firing rate $r(t)$
  - **Heuristic** (not derived from spiking neuron networks)
  - Fail to describe **Synchronization**
  - **Analytically and numerically convenient, also from the point of view of experimental neuroscience**

Orientation selectivity in V1



Hubel and Wiesel 1981

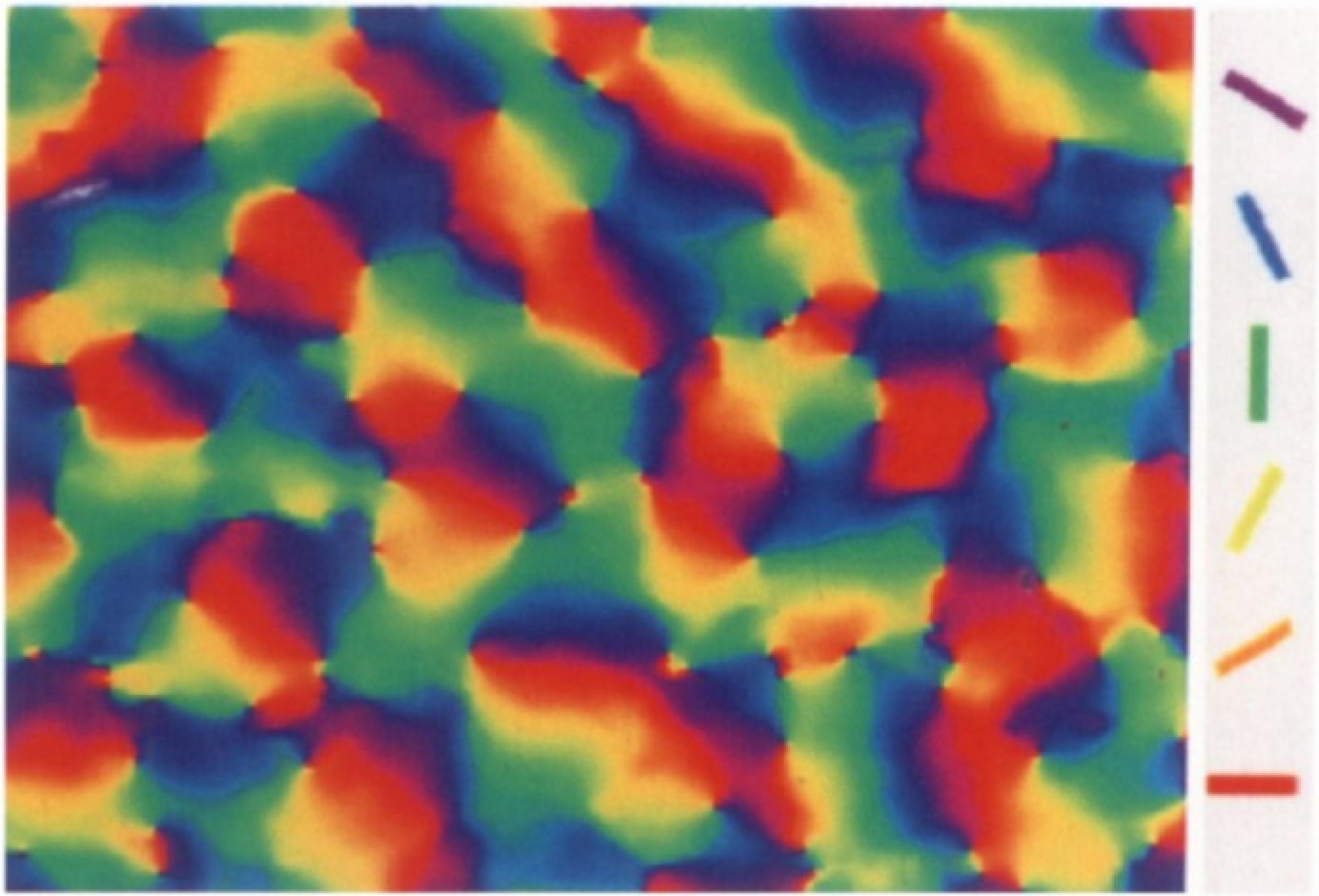




Hubel & Wiesel, 1968

- **Firing rate** codes for features of visual stimuli
- Selectivity also: Frequency: A1, Direction of the arm: M1; Spatial location: PFC...
- *Redundancy:* Nearby neurons have similar response properties: **Population Firing Rate**

Nearby neurons display similar response properties

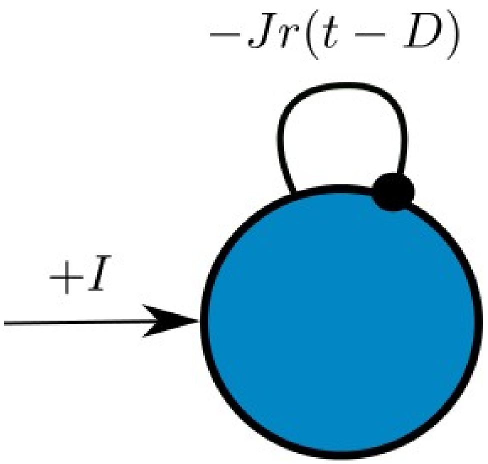


Blasdel, *J. Neuroscience* (1992)

Fast oscillations in Heuristic Firing Rate Models

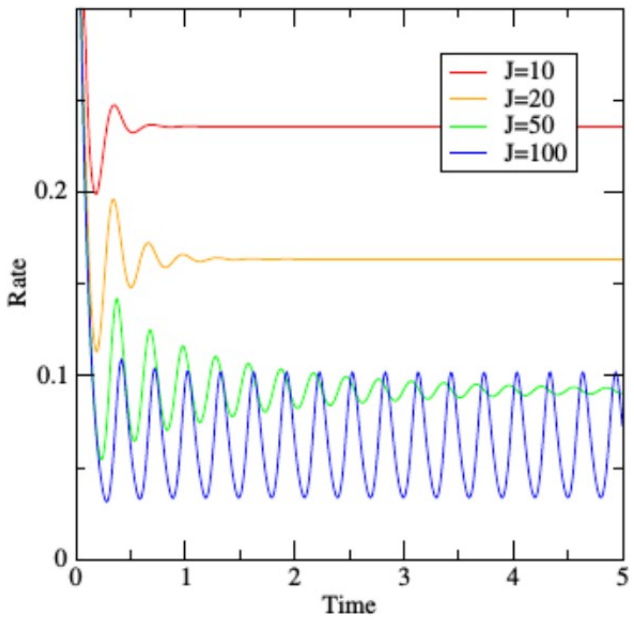
$$\tau\dot{r} = -r + \Phi(-Jr(t-D) + I)$$

- $r(t)$: Firing rate (at time t)
- $\Phi(I)$: Transfer function (f-I curve)
- $-Jr(t-D)$: **Time delayed**, **inhibitory** synaptic current
- I: External currents



Linear Stability analysis

- Fixed point $r^* = \Phi(Jr^* + I)$
- Characteristic equation $\tau\lambda = -1 + Je^{-\lambda D}$
- Hopf (supercritical): $\tan(\Omega_c D) = -(\tau/D)\Omega_c D$
- $T_c = \frac{2\pi}{\Omega_c} \in (2D, 4D)$
- $D \sim 5\text{ms} \to T_c \in (10, 20)\text{ms}$: **Fast Oscillations**



Roxin, Brunel, Hansel, *PRL* (2005); Brunel, Hakim, *Chaos* (2008)

Fast oscillations in *spiking neuron models*

- Often, neurons do not fire at the freq. of the mean field

Dichotomy between Macroscopic & Microscopic dynamics

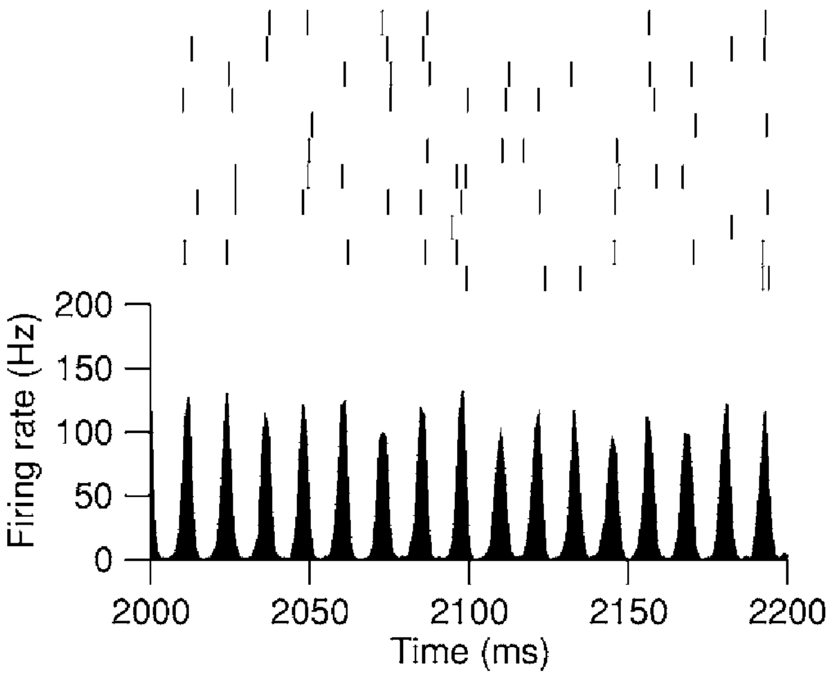
- In contrast w. **Collective Synchronization** Winfree *J. Theor Biol.* 1967, Kuramoto 1975, 1984.

- Interesting macroscopic, oscillatory state, in spiking neuron networks:

Sparse Synchronization Brunel & Hakim 1999

Microscopic analog of fast oscillations
Sparse Synchronization

- Networks of **non-oscillatory,** spiking neurons
- Strongly driven by **noise**
- **Inhibition**
- **Synaptic delays** (fixed and/or synaptic kinetics)



- Individual neurons
  Sparse, low firing rates

- Population Firing rate (Mean field)
  Fast Oscillations

Brunel, Hakim, *Neural Comp.* (1999);
Brunel, Hansel, *Neural Comp.* (2006);
Brunel, Wang, *J. Neurophys* (2003);
Brunel, Hakim, *Chaos* (2008)

Micro. description: ***Sparse Sync***

Macro. description: ***Fast Osc. in FRM***

} Same state?

FRM are heuristic: not *exact* derivations from spiking neuron networks

Can we find an **exact** correspondence between:

Fast Oscillations at the macroscopic level

↕

Some different state at the microscopic level

?

Derivation of Exact Firing Rate Equations

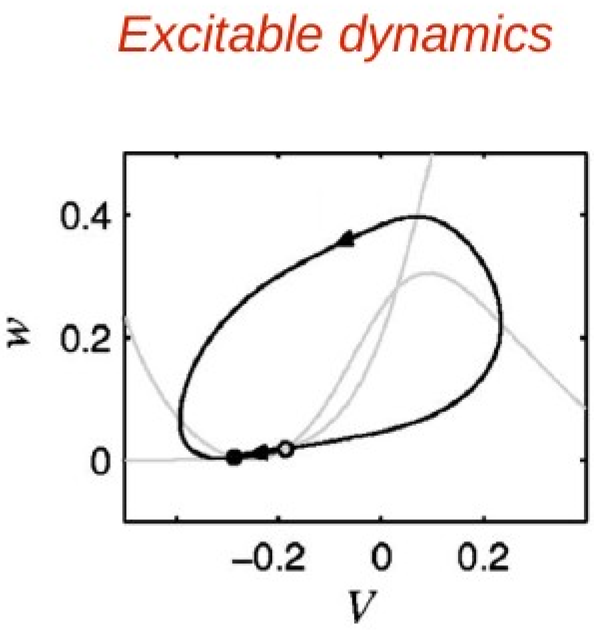
from a network of Spiking Neurons

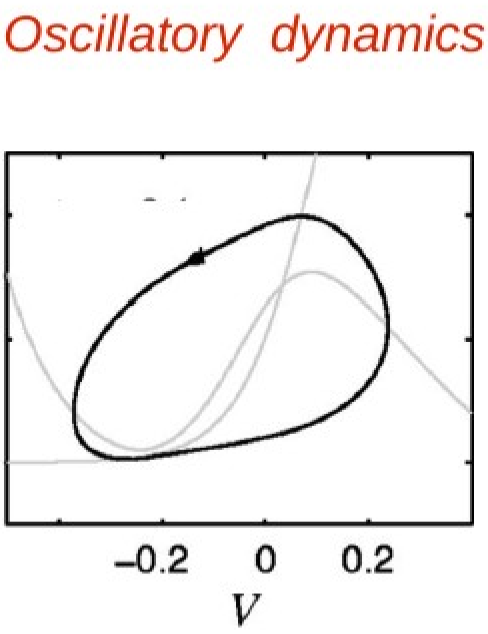
(with quenched noise, only!)

Montbrió, Pazó and Roxin, Physical Review X 2015

Spiking neurons
Quadratic Integrate & Fire model (QIF)

The QIF model is the normal form of a SNIC bifurcation



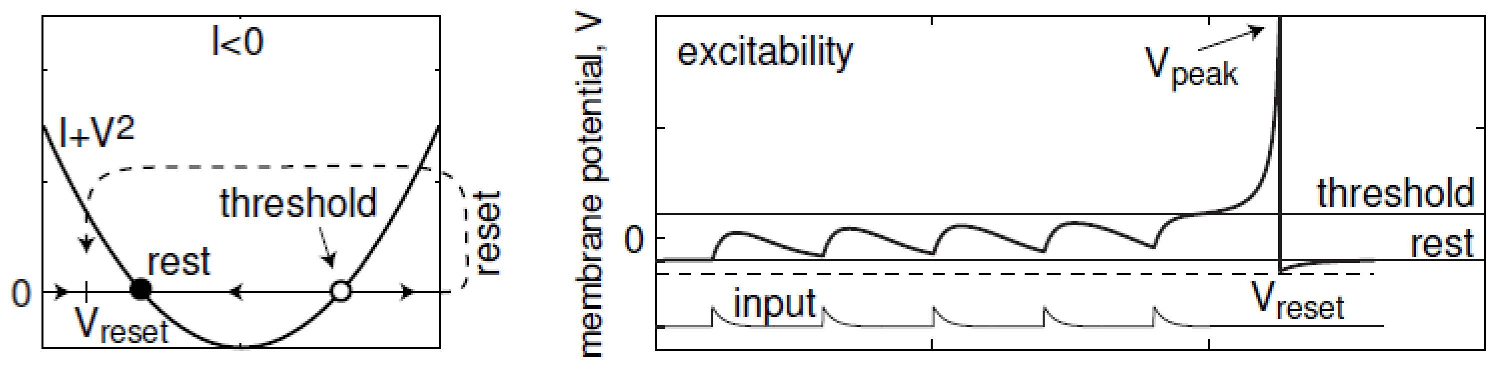


Ermentrout, Kopell, SIAM 1986

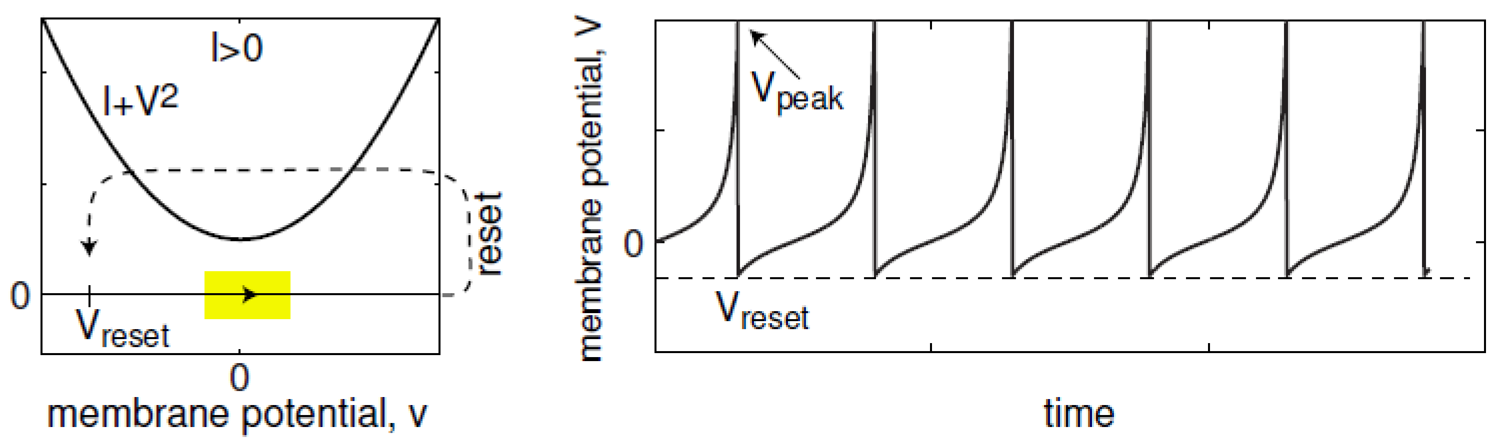
Dynamics of the QIF model

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

Excitable dynamics:



Oscillatory dynamics:



E. Izhikevich, "Dynamical Systems in Neuroscience", 2007

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): $s_D = \tau r_D$

Time delayed, Population-Averaged Firing Rate

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

$$\partial_t \rho + \partial_V \left[(V^2 + \eta + Js + I)\rho \right] = 0$$

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

Stationary solutions

$$-\partial_t \rho = \partial_V \left(\rho[V^2 + \eta]\right)$$

- If $\eta > 0$: $\rho(V|\eta) = \frac{C(\eta)}{V^2+\eta}$
- If $\eta \leq 0$: $\rho(V|\eta) = \delta(V - \tilde{C}(\eta))$

Lorentzian Ansatz

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

Center **Width**

General solutions?

- Lorentzian Ansatz: $\rho = \frac{1}{\pi}\frac{1}{(V-y)^2+x^2}$
- Continuity Eq: $-\partial_t \rho = \partial_V \left(\rho[V^2+\eta]\right)$

We substitute the LA into the continuity eq

- $\partial_t \rho = \frac{1}{\pi}\frac{1}{((V-y)^2+x^2)^2}\left(\dot{x}[(V-y)^2+x^2] - x[2x\dot{x} - 2\dot{y}(V-y)]\right)$
- $\partial_V \left(\rho[V^2+\eta]\right) = \frac{-2(V-y)x}{\pi((V-y)^2+x^2)^2}[V^2+\eta] + \frac{2Vx}{\pi((V-y)^2+x^2)}$

Equating the expressions

$$-\dot{x}\left((V-y)^2+x^2\right)+2x\left(\dot{x}-\dot{y}(V-y)\right) = -2(V-y)x[V^2+\eta]+2Vx\left[(V-y)^2+x^2\right]$$

The identity must hold at all orders!!

- $O(V^2)$: $\dot{x} = 2xy$
- $O(V)$: $\dot{y} = y^2 - x^2 + \eta$
- $O(1)$: Linear combination of previous equations

Dynamics in the Lorentzian manifold

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

Lorentzian ansatz

$$\partial_t \rho + \partial_V \left[(V^2 + \eta + Js + I)\rho\right] = 0$$

Continuity equation

$$w(\eta,t) \equiv x(\eta,t) + iy(\eta,t)$$

$$\partial_t w(\eta,t) = i\left[\eta + Js(t) - w(\eta,t)^2 + I(t)\right]$$

$s(t) = r(t)$: Fast Synapses

Closing this equation requires to express w as a function of r and some other meaningful macroscopic observables

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

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

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

Firing Rate Model for QIF neurons

Lorentzian distribution of currents

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

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

Cauchy Residue's theorem to solve

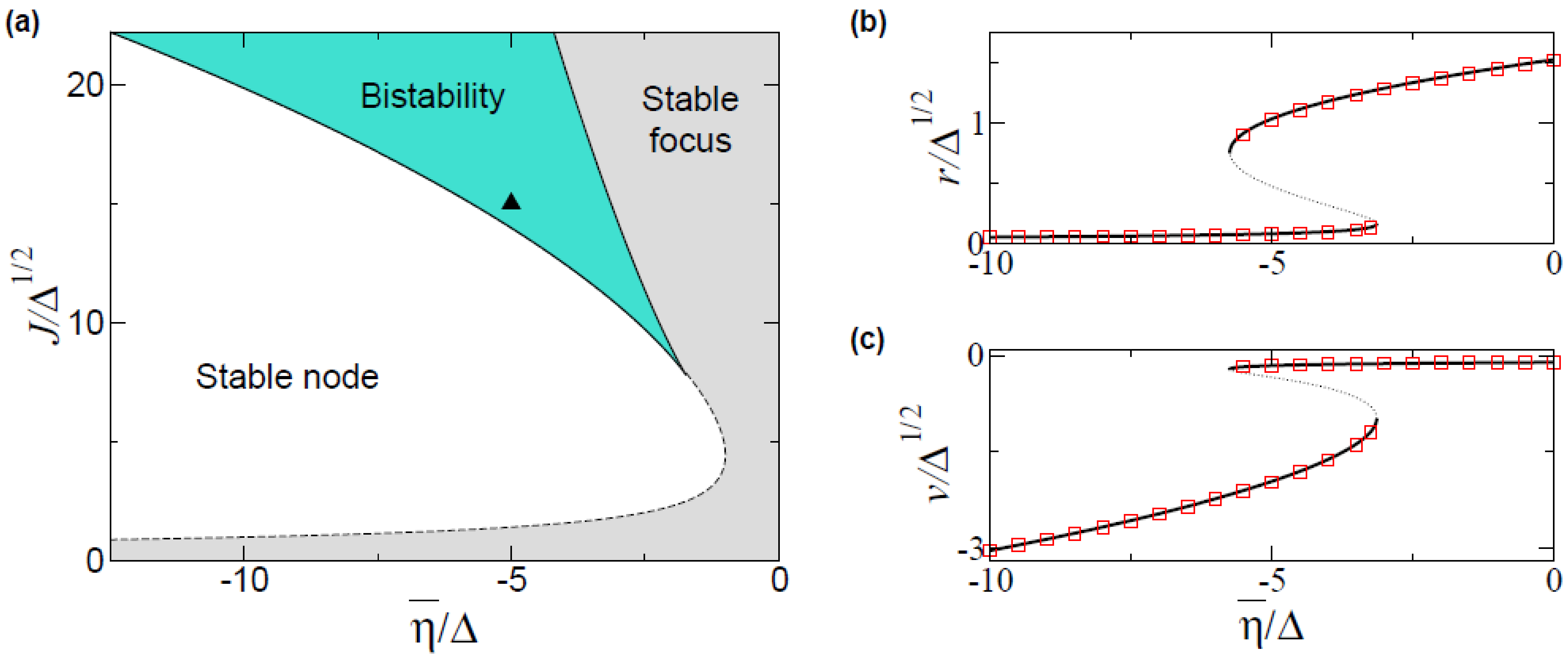
Ott & Antonsen, *Chaos*, 2008

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

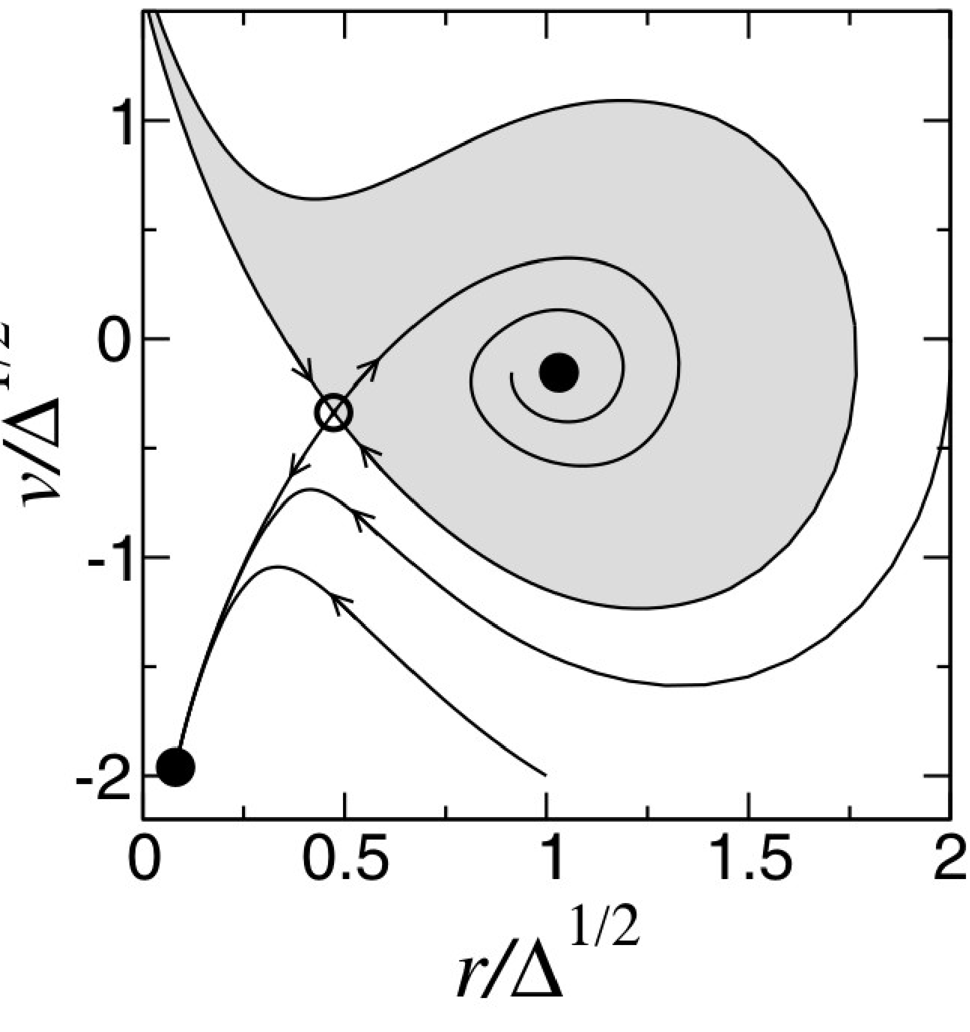
$$\tau \dot{r} = \frac{\Delta}{\pi \tau} + 2rv,$$

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

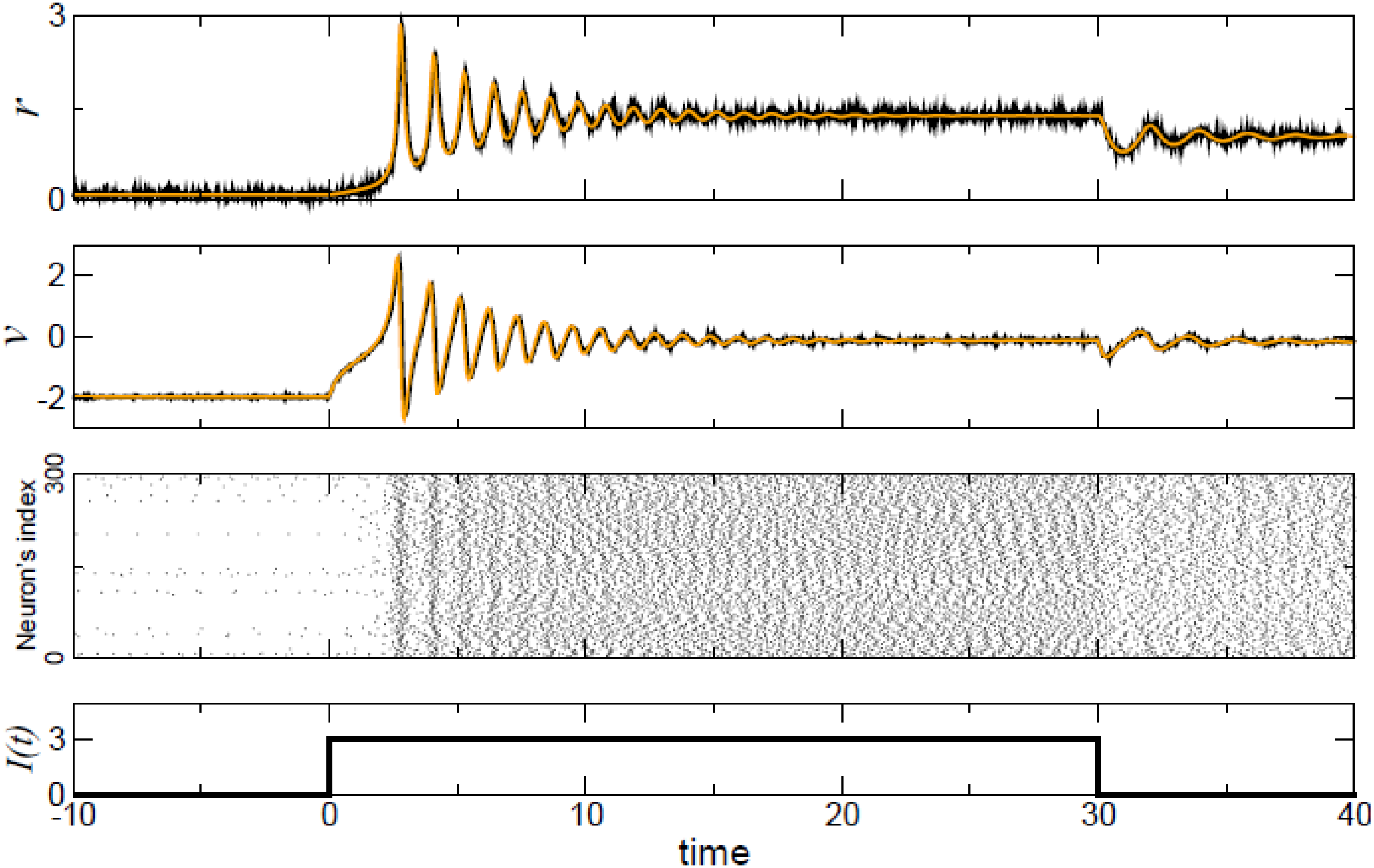
Analysis of the FRE *without delay*



Phase portrait: Movie!



Comparison
Spiking Neurons vs. Firing Rate Eqs.



Firing Rate Equations with time delays

Pazó & Montbrió, Physical Review Letters 2016

Linear Stability Analysis of Incoherence

$$\tau \dot{r} = \frac{\Delta}{\pi\tau} + 2rv,$$

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

For identical neurons, the only fixed point is:

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

Incoherent state (splay state)

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

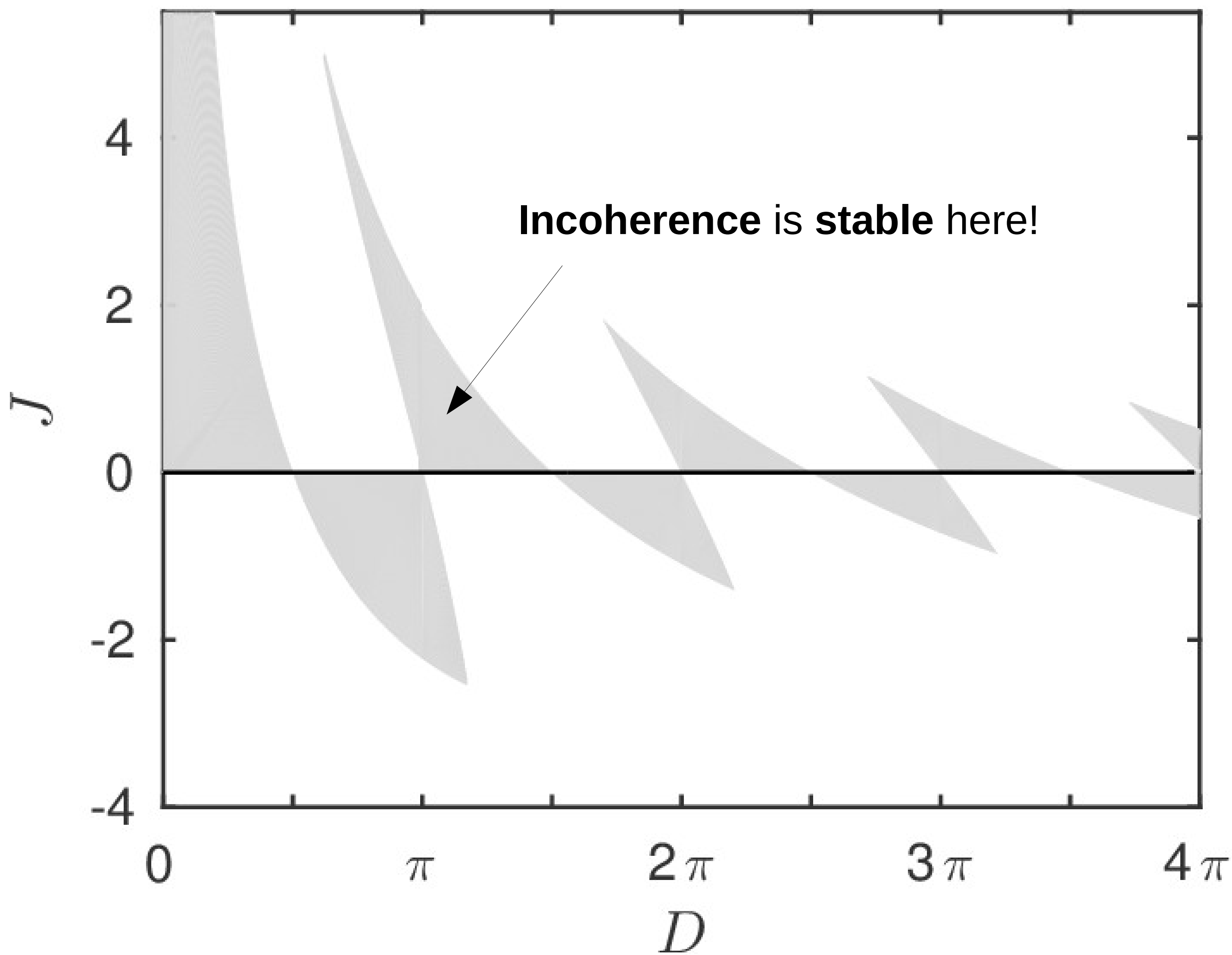
Linearizing around the f.p. and imposing the cond. of marginal stab: $\lambda = i\,\Omega$

Hopf boundaries:

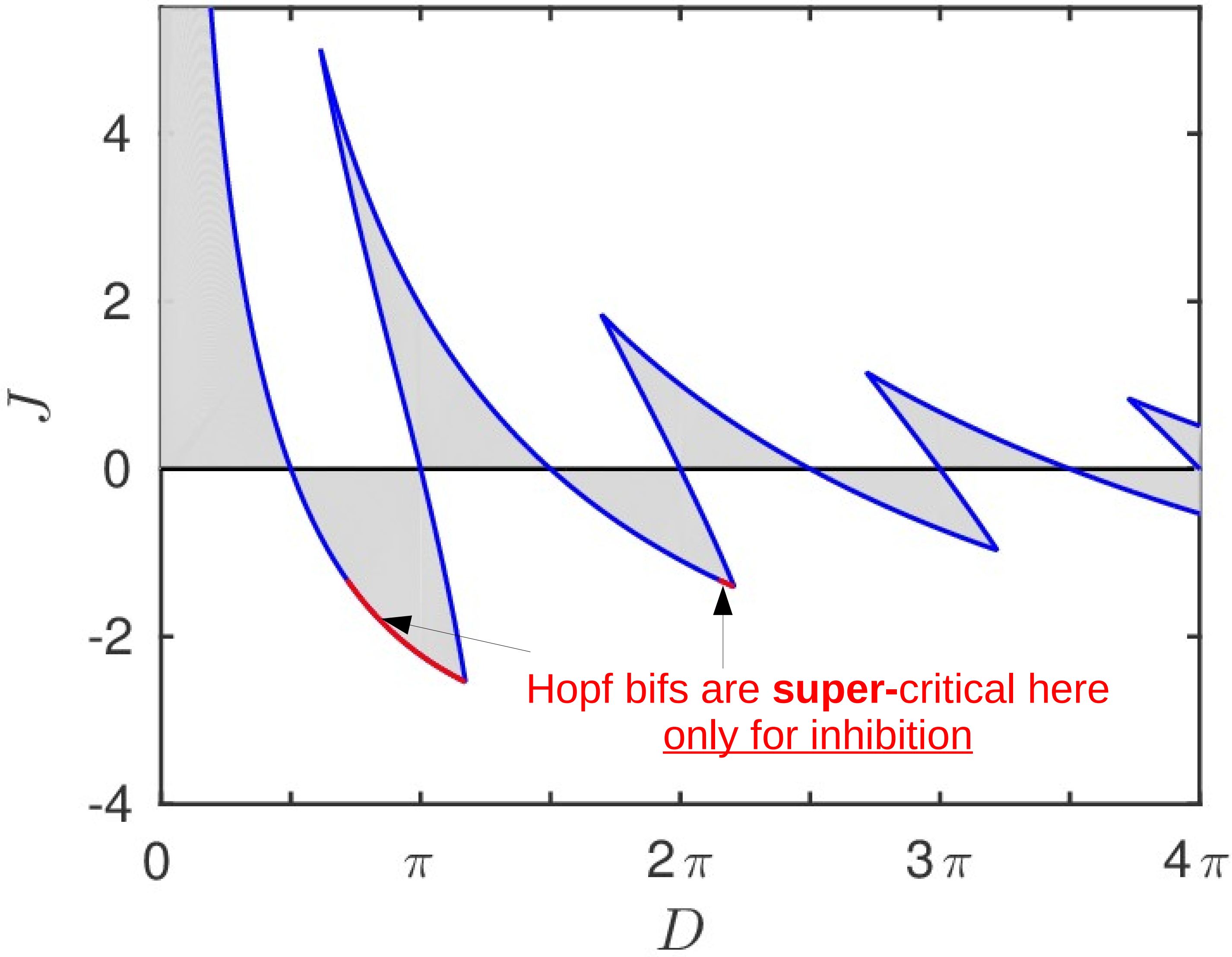
$$\Omega_n = n\pi/D.$$

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

Incoherence (Hopf) boundaries

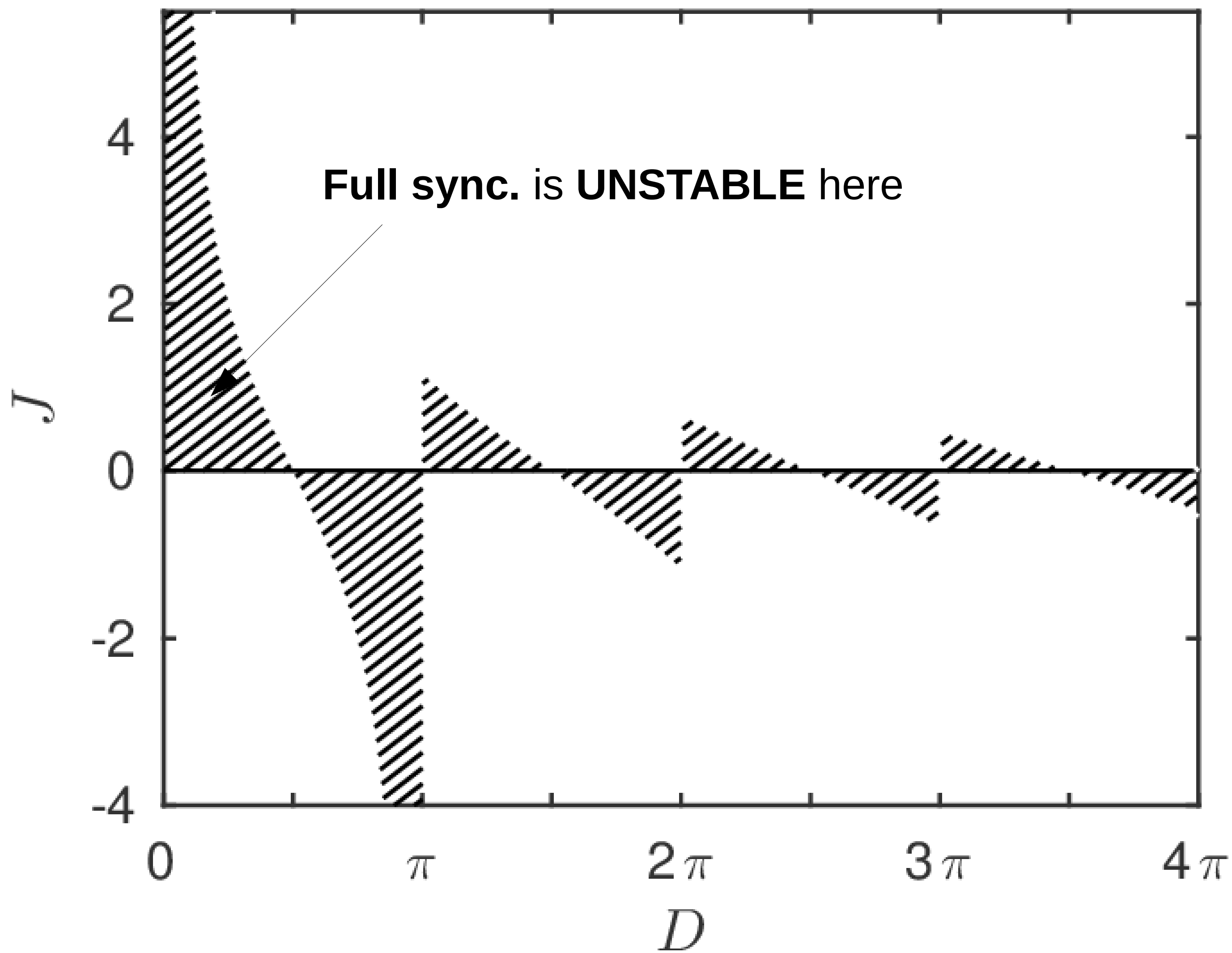


Weakly nonlinear analysis (two timing)

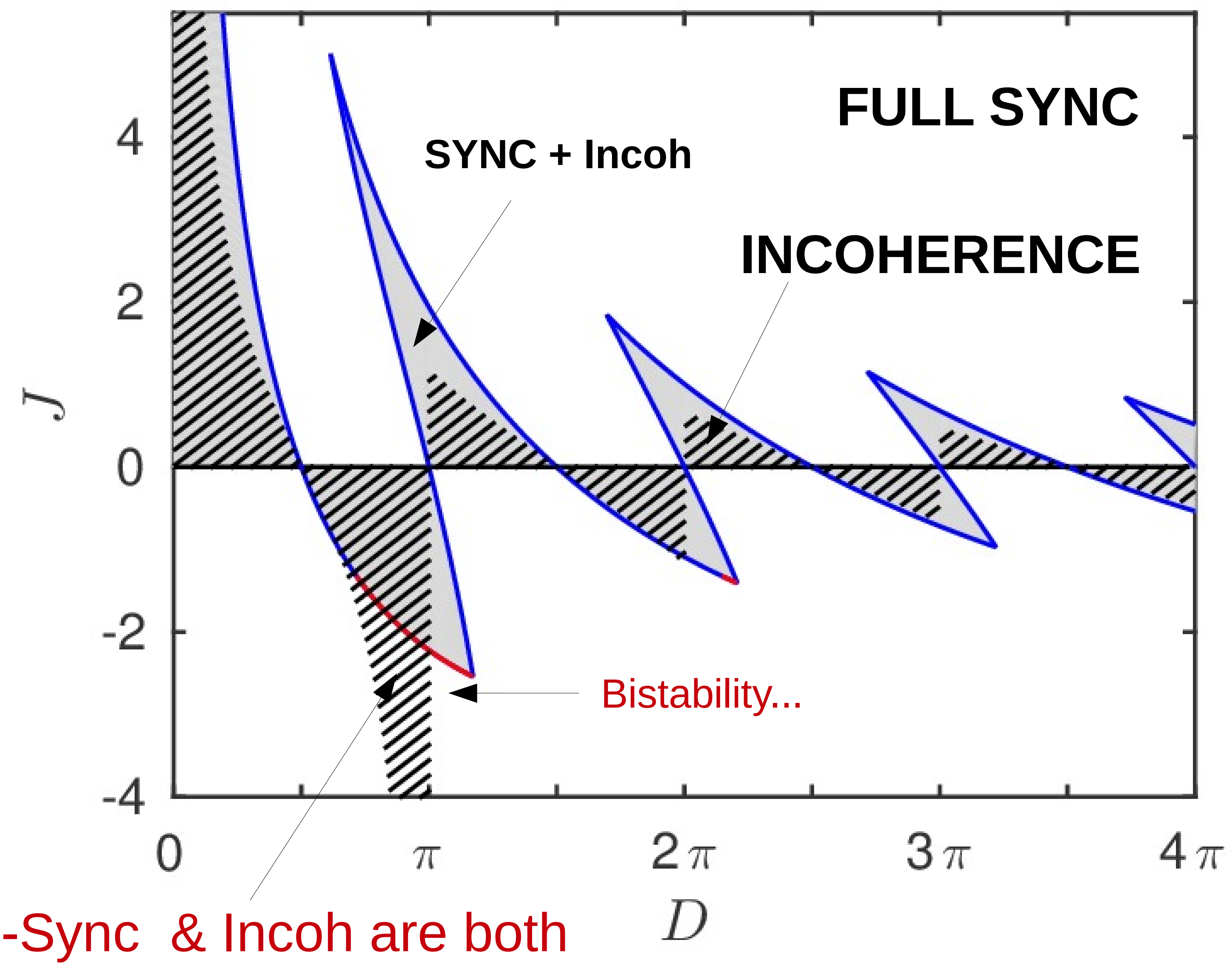


Synchronization boundaries

(obtained analytically via linear stability analysis of sync)

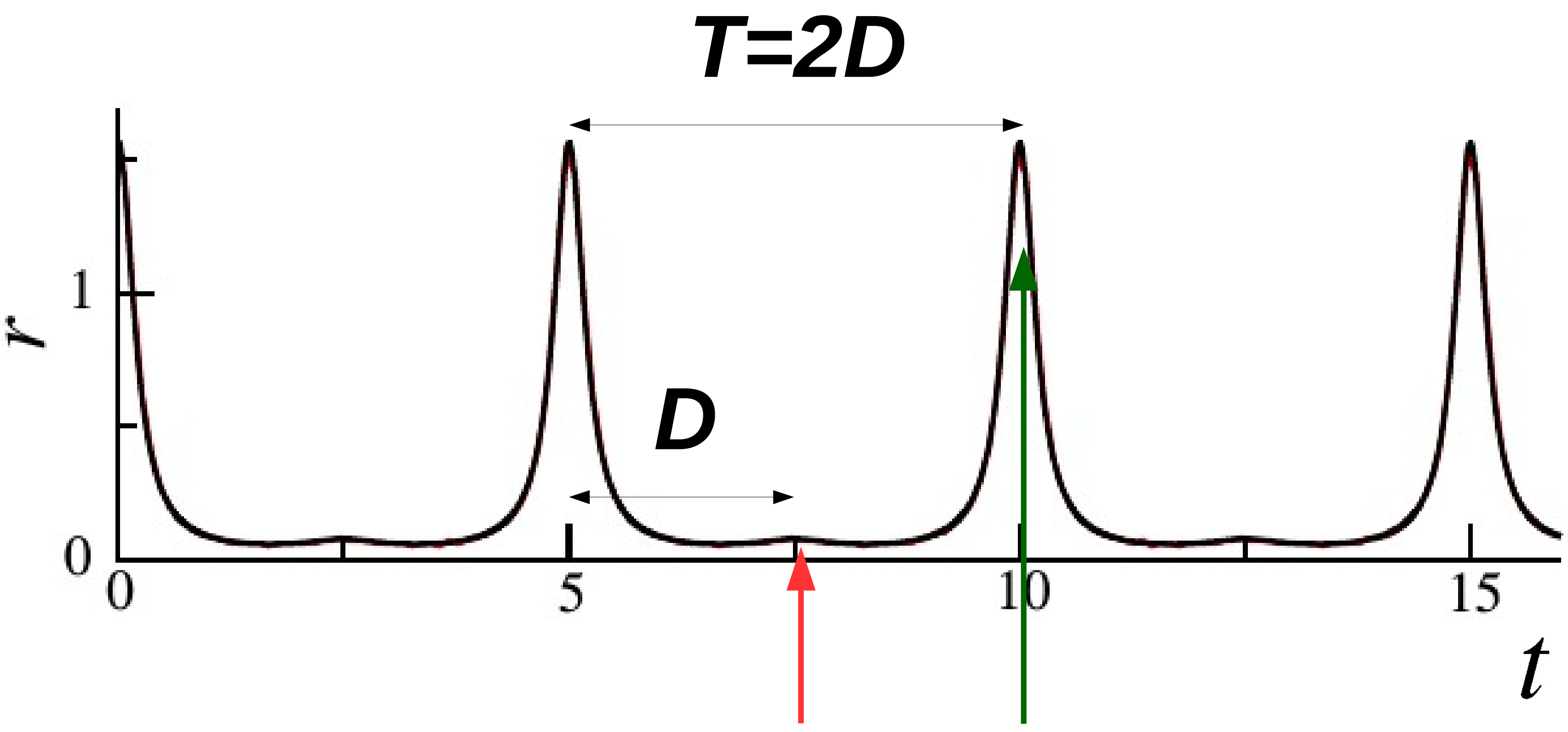


Phase diagram



Full-Sync & Incoh are both UNSTABLE here!

Fast oscillations in FRM

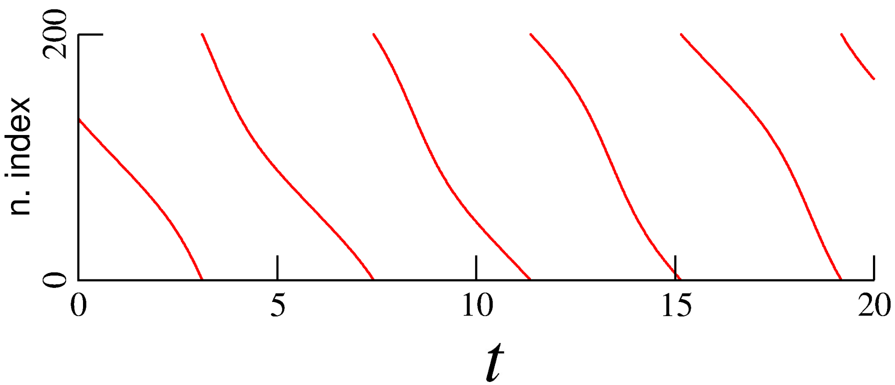


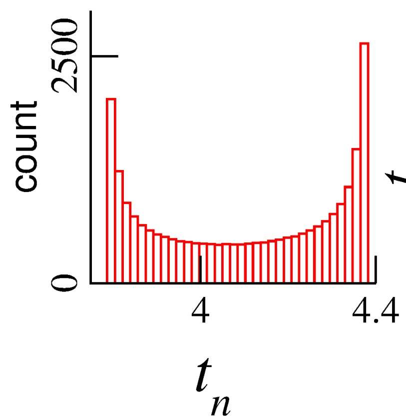
Delayed Inhibition (D)
prevents an increase of activity

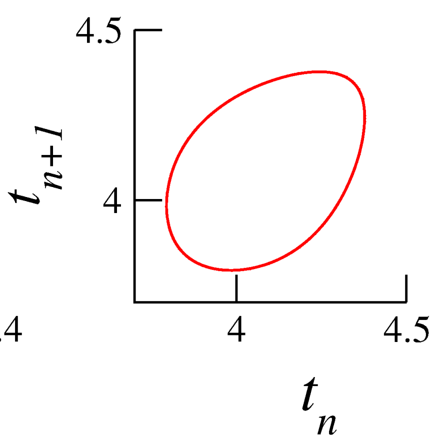
After a new time D
there is no inhibition...
Firing is possible again!

Micro vs. Macro dynamics

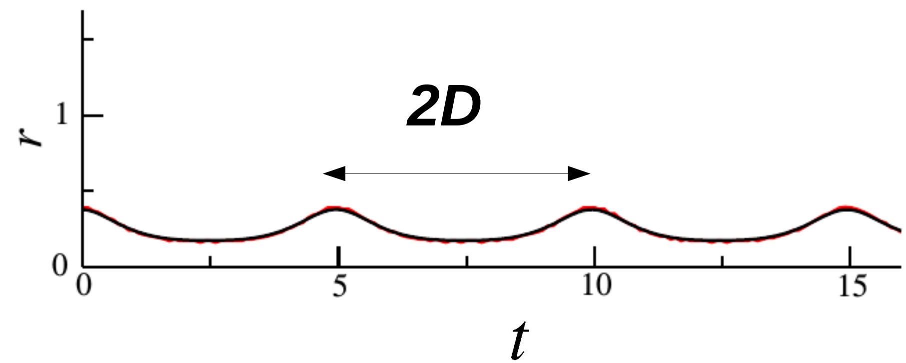
Microscopic dynamics (QIF network)

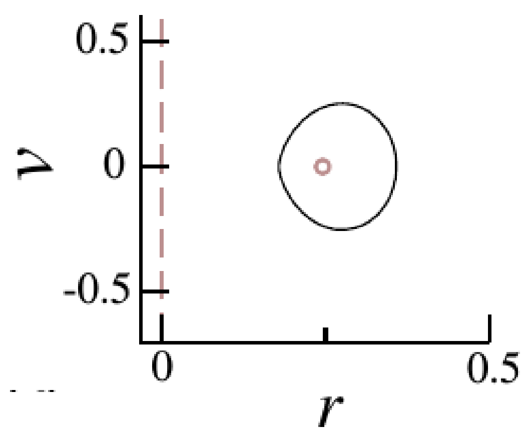






Macroscopic dynamics (FREs)





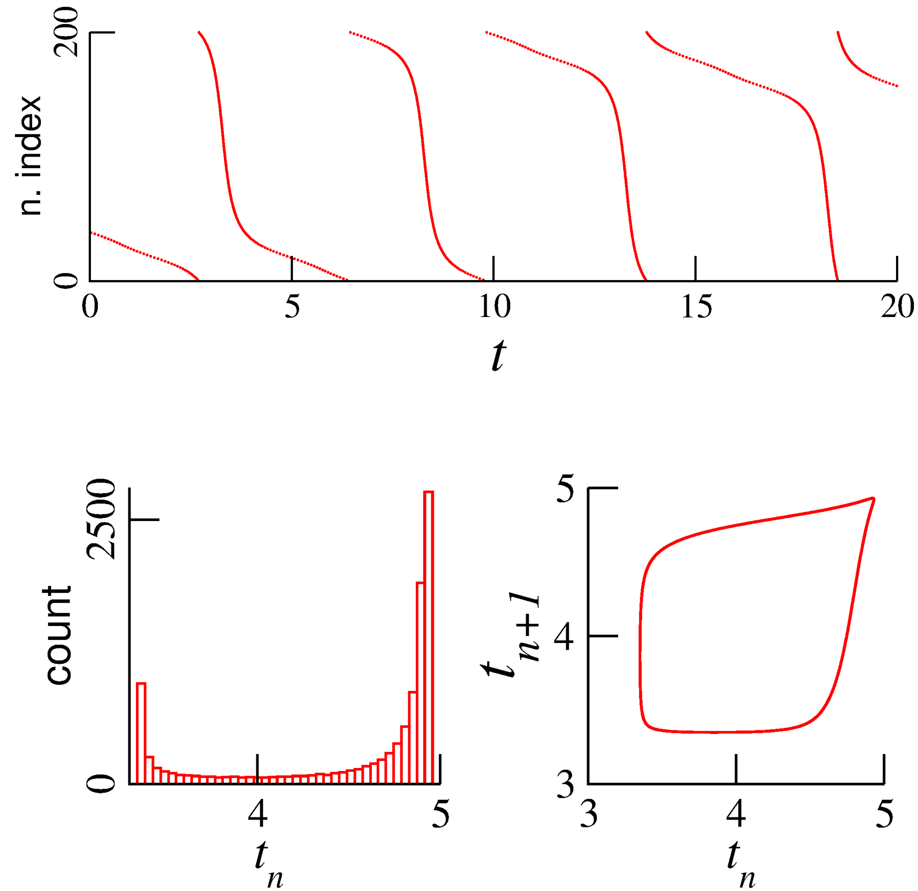
QUASIPERIODIC PARTIAL SYNCHRONIZATION in inhibitory networks

Van Vresswijk, *Phys Rev E* (1996)

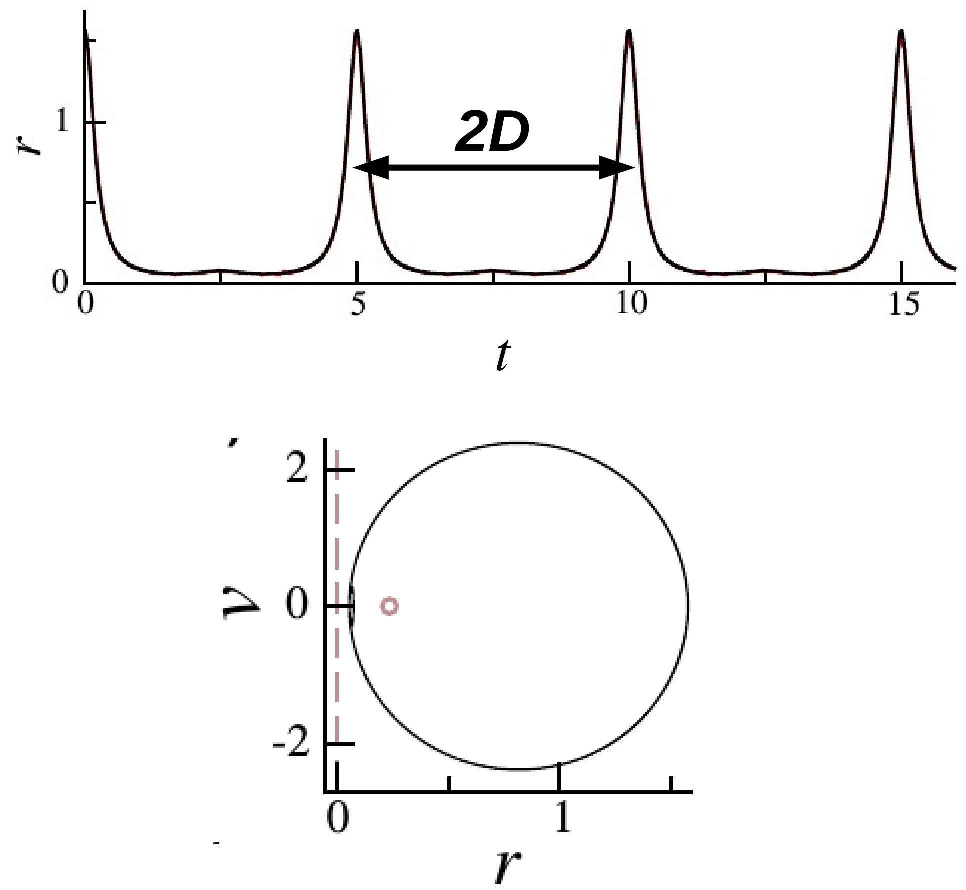
Mohanti, Politi, *J. Phys A* (2006); Rosenblum, Pikovsky, *PRL* 2007; Pikovsky, Rosenblum, *Physica D* (2009); Olmi, Politi, Torcini, EPL (2010); Luccioli et al, *Phys Rev Lett* (2012); Politi, Rosenblum, *PRE* (2015)...

period of QPS is always 2D

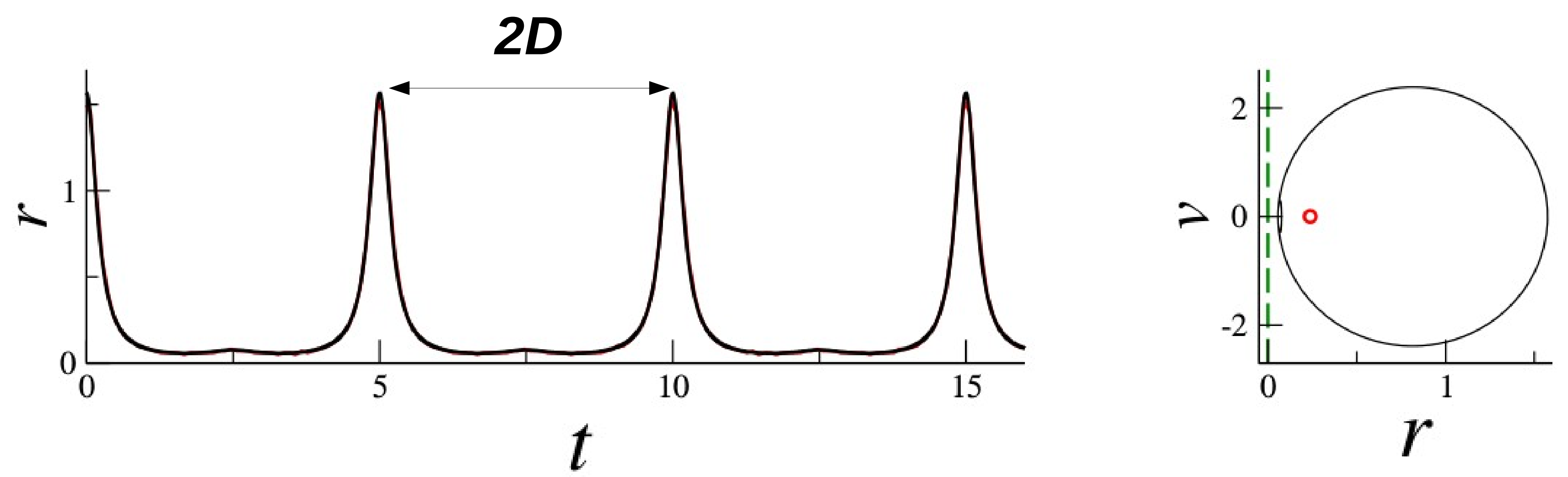
Microscopic dynamics (QIF network)



Macroscopic dynamics (FREs)



Symmetry of limit cycle implies *T=2D*



Period of oscillations remains constant

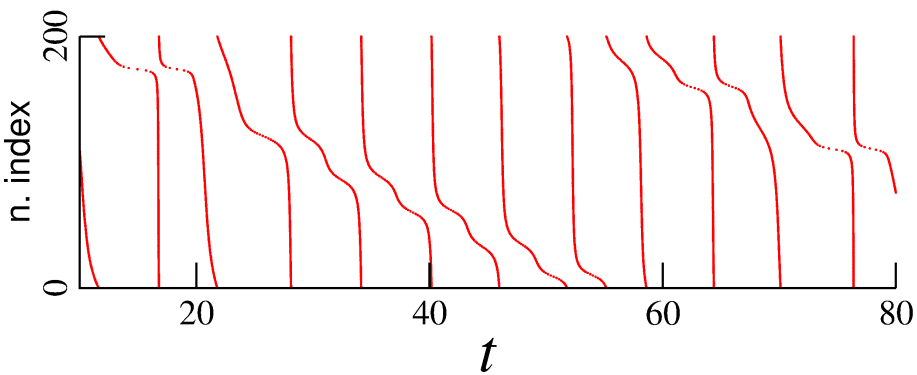
Limit cycle is symmetric *v* → *-v*

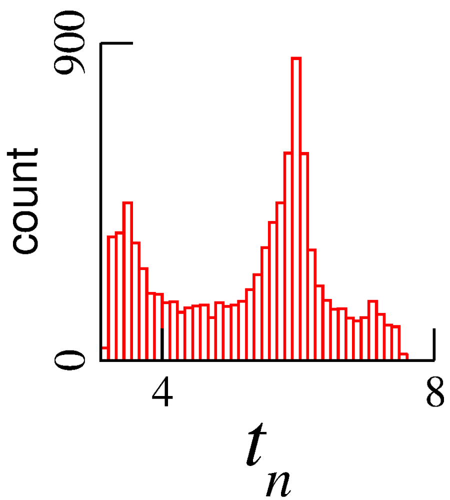
Using FRE for Δ=0, this symmetry implies that: $T_m = \frac{2D}{m}, \quad \text{with} \quad m = 1, 3, \ldots$

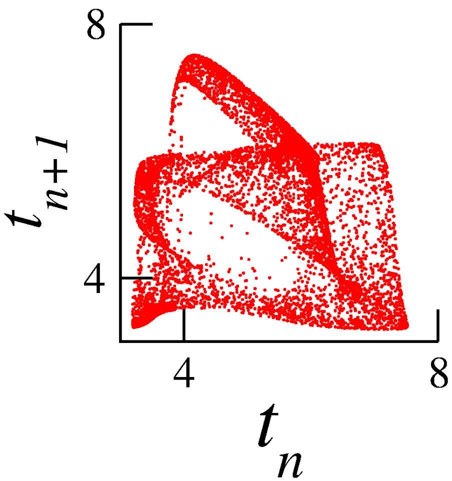
The symmetry is broken at period doubling bif...

Transition from QPS to Macroscopic Chaos

Microscopic dynamics (QIF network)

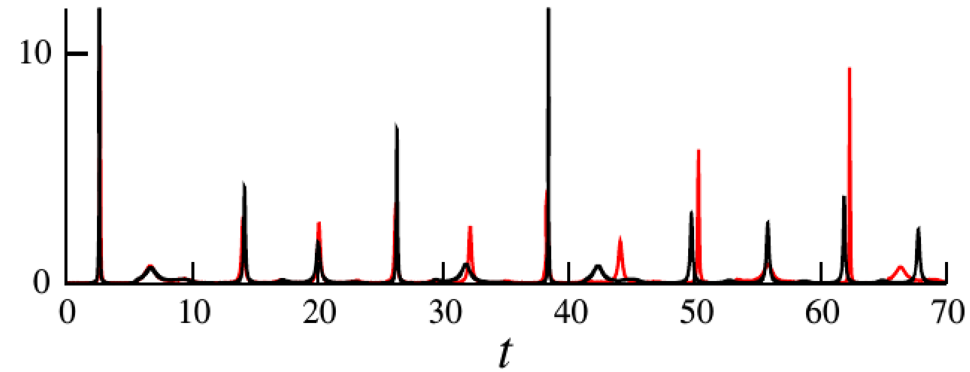


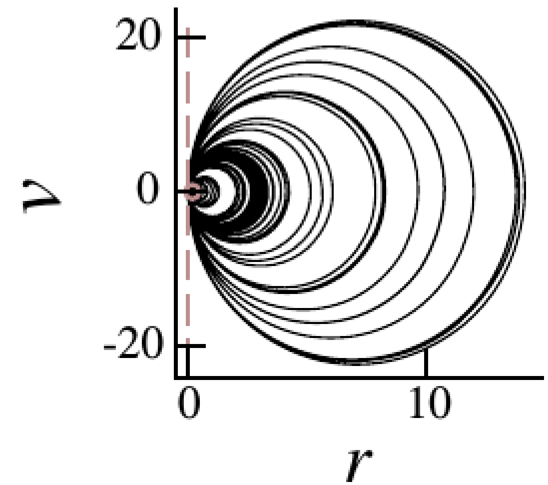




Neurons are not chaotic, though...

Macroscopic dynamics (FREs)

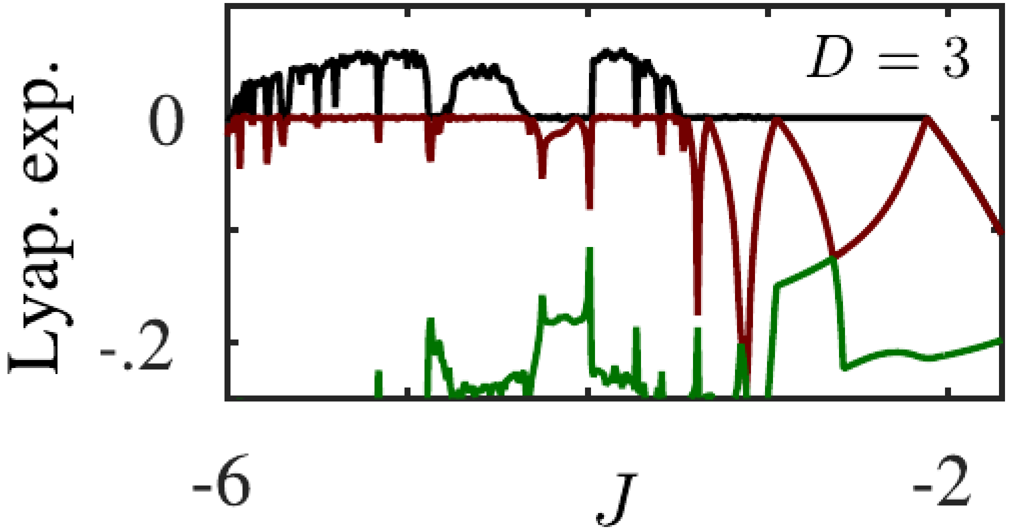


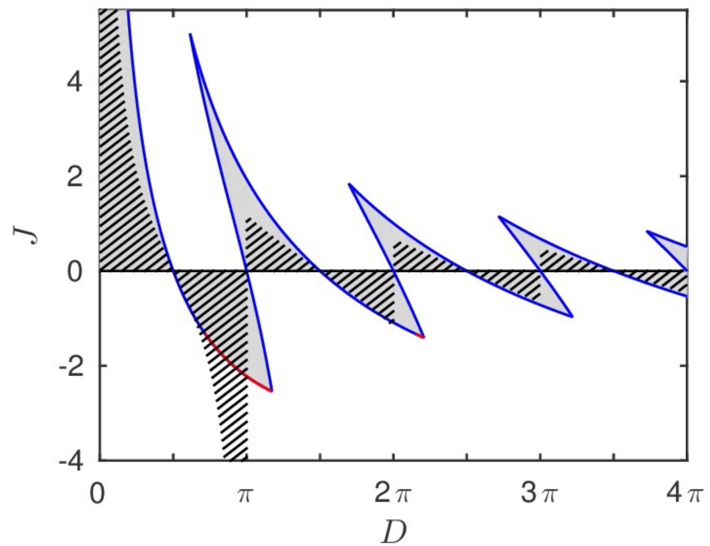


Collective chaos

Transition from QPS to Collective Chaos
period-doubling cascade

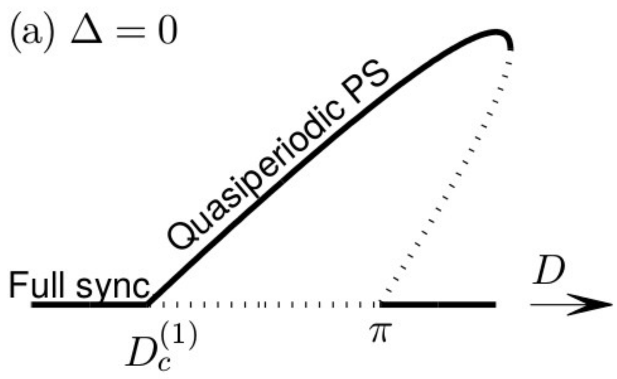
Using the FREs we find:

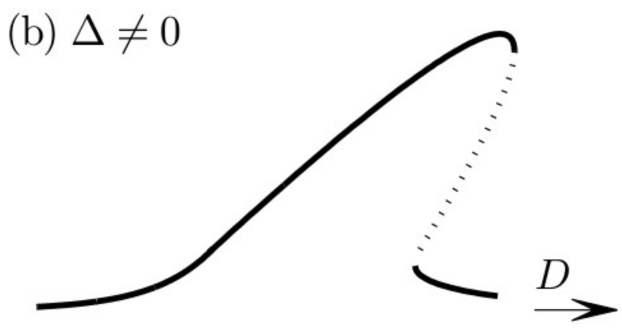


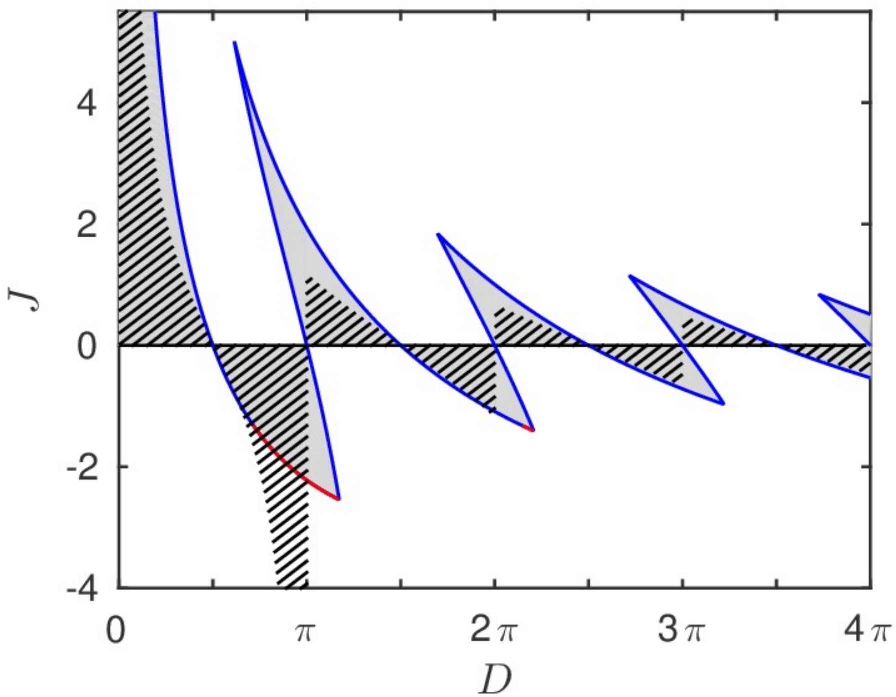


In the thermodynamic limit the system shows **genuine Collective Chaos**

Onset of QPS and (weak) heterogeneity



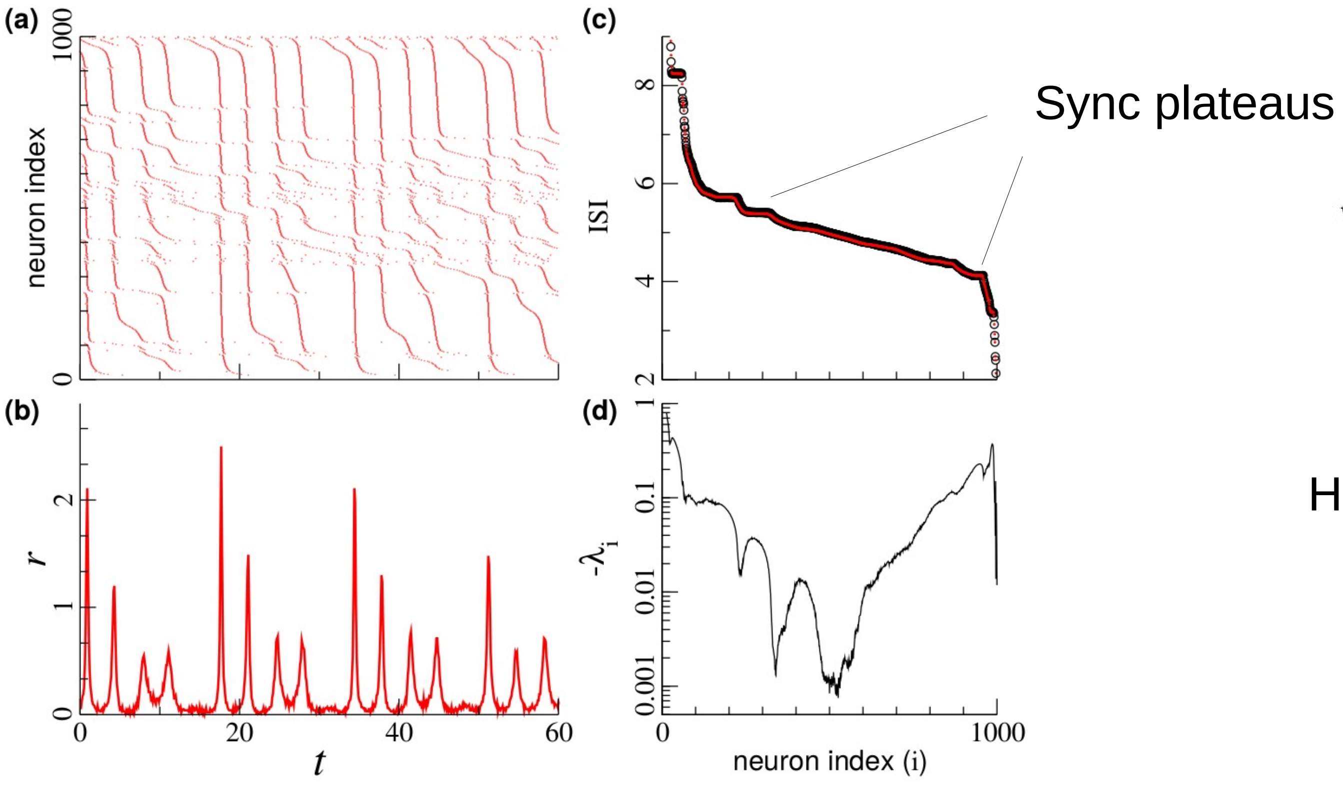


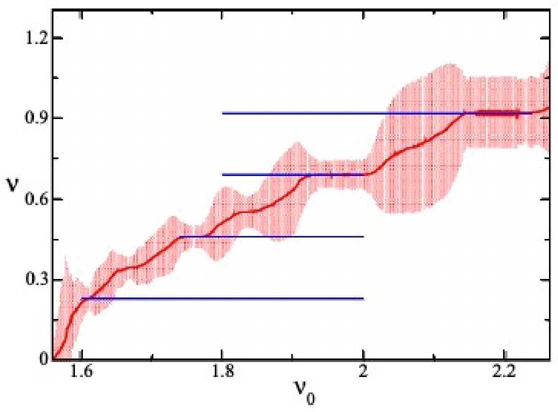


TC bifs. are not robust

bistability remains though!

Macroscopic chaos in heterogeneous networks





Heterogeneous Inhibitory LIF + Delay

Luccioli, Politi, *PRL* 2010

No chaos at microscopic level!

Summary

- Exact derivation of FRE for networks of QIF neurons

- Using the FRE we related
  - Quasiperiodic Partial Synchronization
  - Collective Chaos

  with (non-trivial) Fast Oscillations in Inhibitory Networks

- Transition from QPS to CC via period doubling cascade

- **Fast Oscillations in Inhibitory networks** may correspond to **Many possible Micro-states**

Thanks!

<u>*Collaborators:*</u>

Diego Pazó
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Bellaterra (Barcelona)

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