From quasiperiodic partial synchronization to collective chaos in networks of inhibitory neurons

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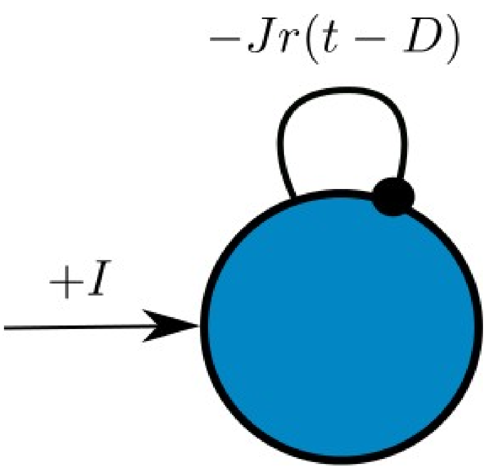
Introduction

- 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)
- Computational models:
  - **Inhibition + Synaptic Delays**

Fast oscillations in *Mean Field models*
Heuristic Firing Rate Models

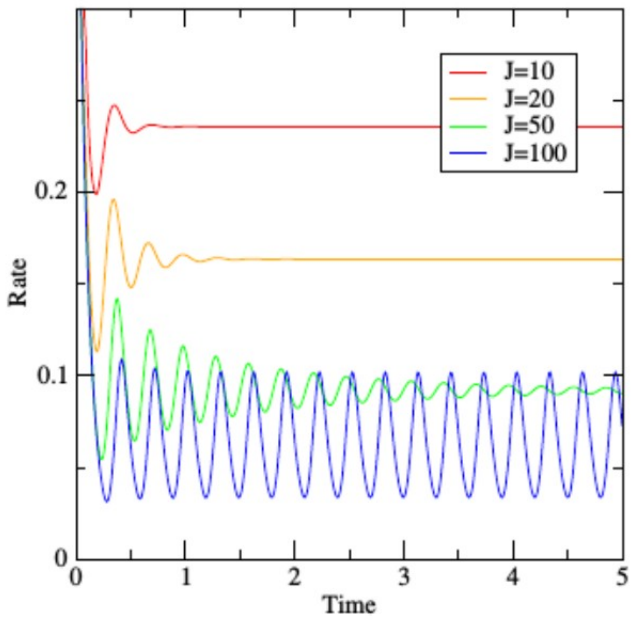
$$\tau \dot{r} = -r + \Phi(-Jr(t-D) + I)$$

- $r(t)$: 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); Roxin, Montbrió, *Phys D* (2011)

Fast oscillations in *spiking neuron models*

- In many cases, neurons do not fire at the freq. of the mean field.

  Dichotomy btw . Macroscopic & Microscopic dynamics

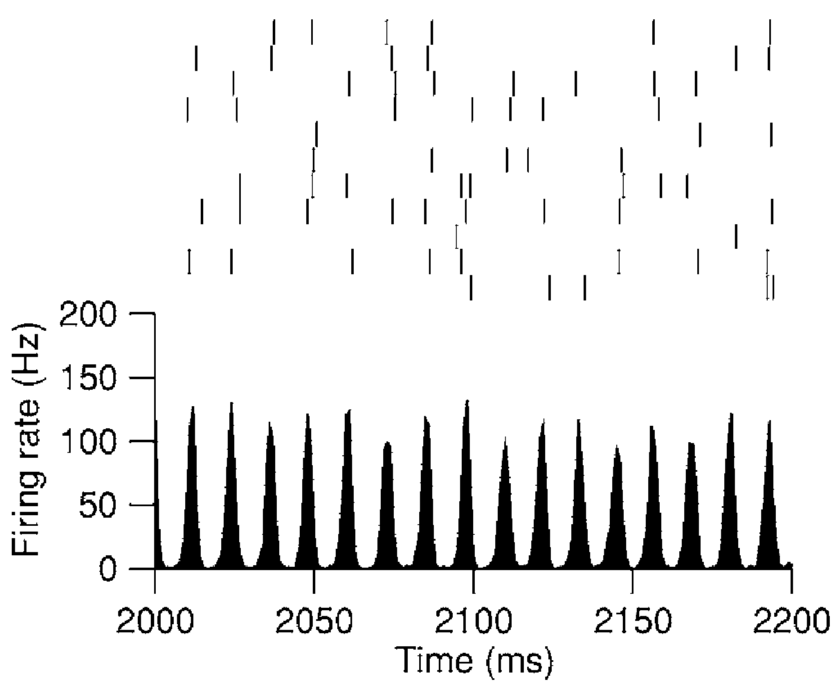
- Sharp contrast w. **Collective Synchronization** Winfree *J. Theor Biol.* 1967, Kuramoto 1975, 1984.

- Different macroscopic, self-organized state:

  Sparse Synchronization Brunel & Hakim 1999

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)

- *Sparse Sync* and *Fast osc. in Heuristic FRM* are assumed to be “the same state”
- HFRM are not derived from networks of spiking neurons though...
- Is there an exact link btw. Fast Oscillations in FRM (Inhib+Delay) and some state (not collective sync) in networks of oscillators?
- Let's look at the Kuramoto model with delay...

Kuramoto model with time delay

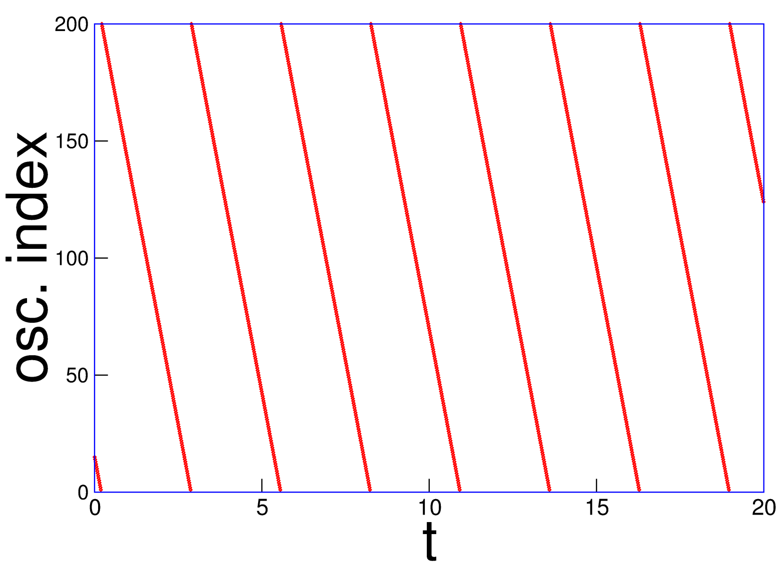
Coupling Strength

Time delay

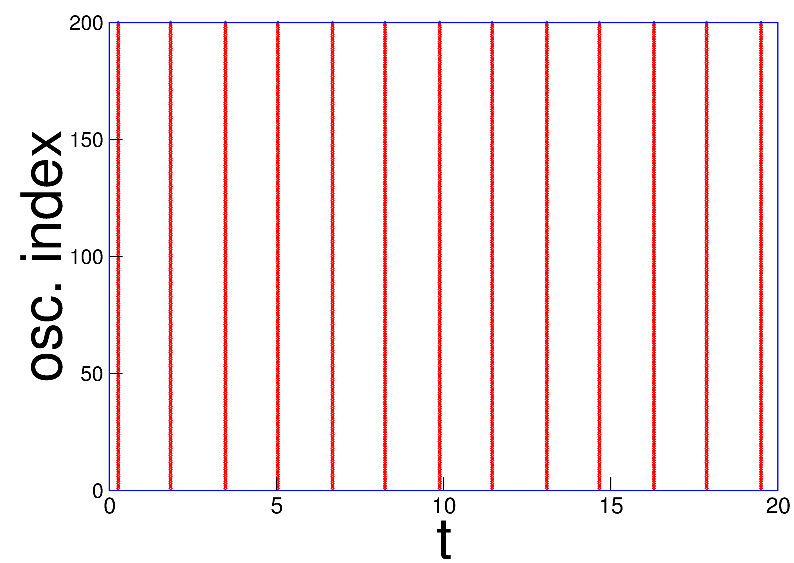
Natural frequencies

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

Incoherence
Asynchronous (splay) state

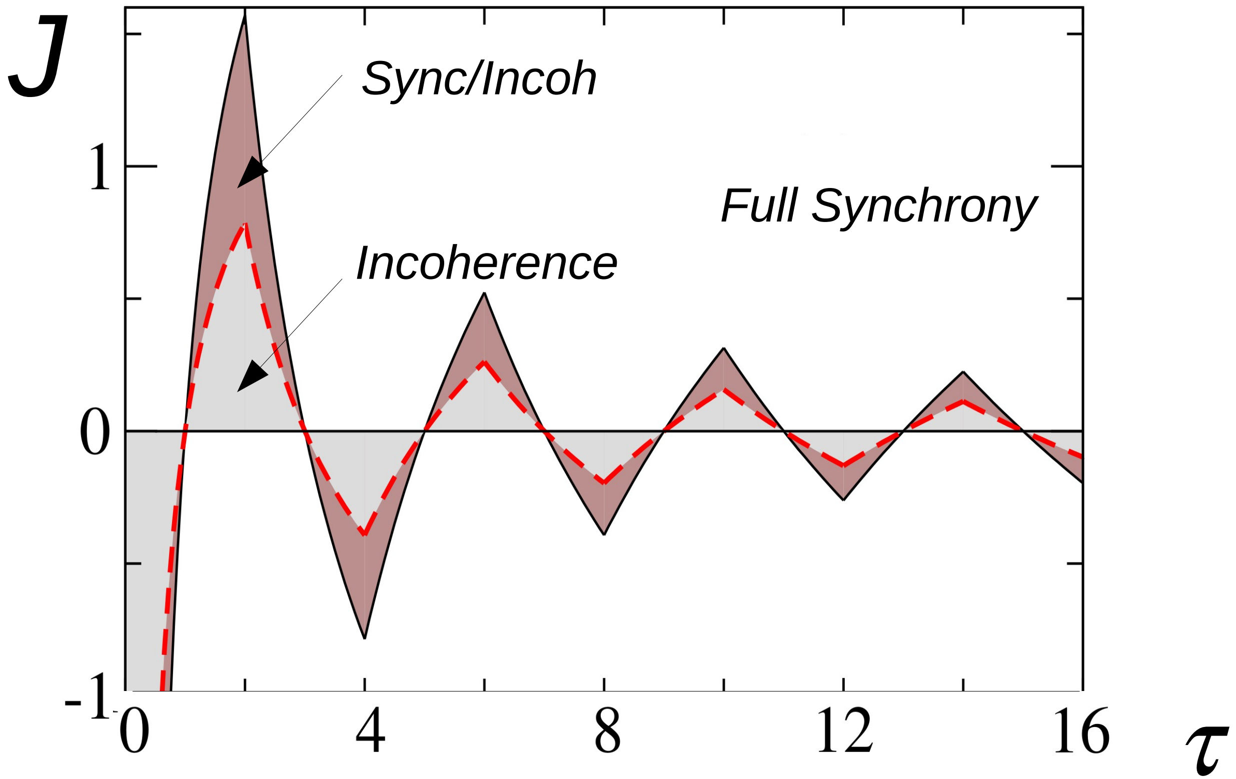


Full synchronization



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

Phase Diagram of the KM with delay



Not OK for modeling Fast Osc. in inhibitory networks:

- Only collective sync (also clustering)
- Same dynamics for **Excitation** and **Inhibition**

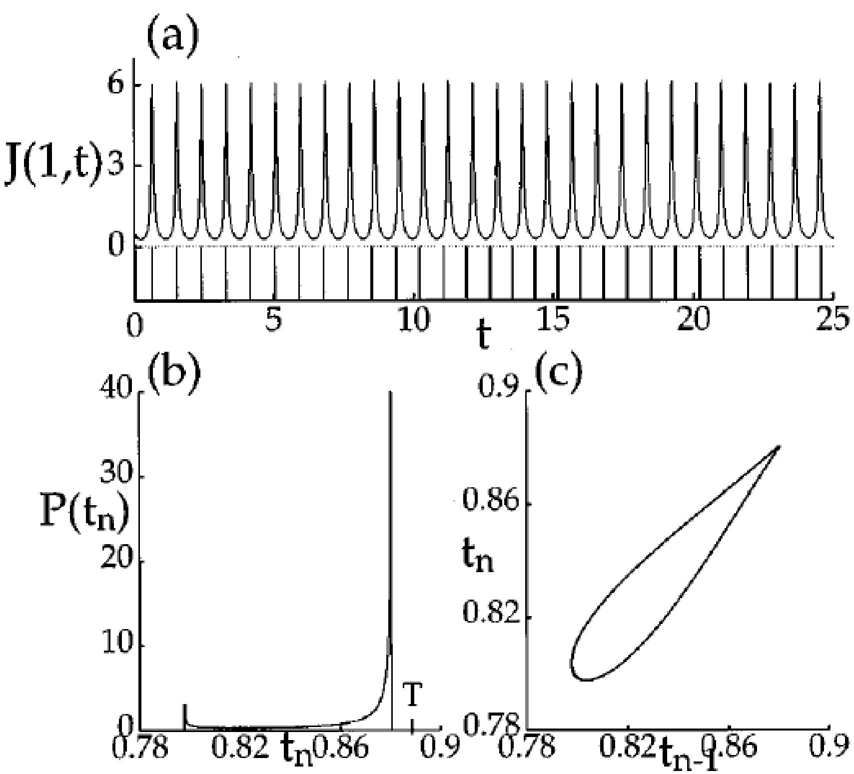
Yeung, Strogatz, *Phys Rev Lett* (1999)

Potential candidates in oscillatory networks...

- Quasiperiodic Partial Synchronization
- Collective Chaos

Quasiperiodic Partial Synchronization (QPS)

- Networks of **Identical + Oscillatory** + **Excitatory** LIF neurons
- Global coupling w. **synaptic kinetics** (alpha synapses)



Van Vresswijk, *Phys Rev E* (1996)

Mean Field:
Population Firing Rate
(Arbitrarily low-amplitude oscillations)

Neurons:
Quasiperiodic Dynamics
w. different mean freq

QPS in LIF and Phase-Osc. (NLC) networks
no inhibition:

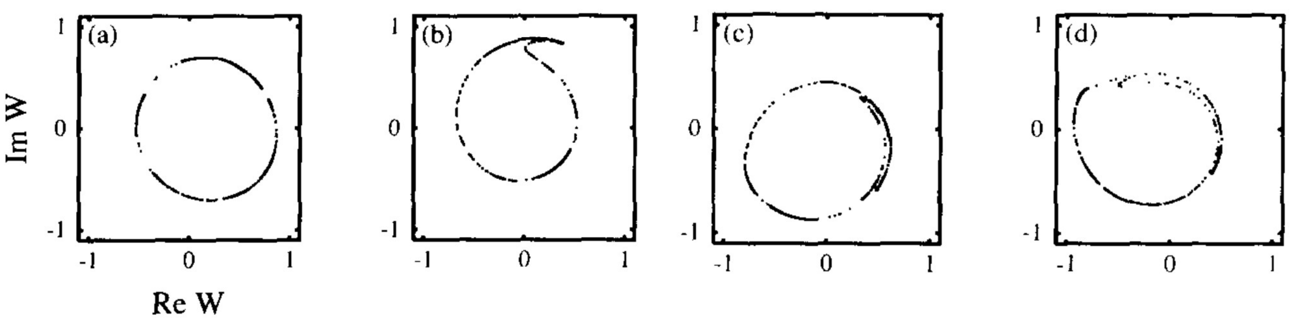
Mohanti, Politi, *J. Phys A* (2006);
Rosenblum, Pikovsky, *PRL* 2007;
Pikovsky, Rosenblum, *Physica D* (2009);
Olmi, Politi, Torcini, EPL (2010);
Luccioli et al, *Phys Rev Lett* (2012);
Politi, Rosenblum, *PRE* (2015)

Collective Chaos

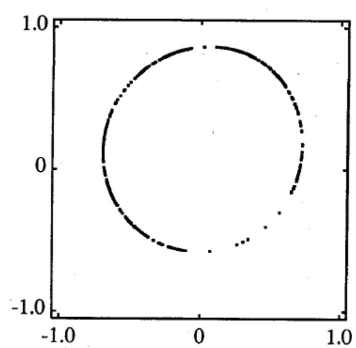
Globally-coupled, **Identical** Limit-Cycle Oscillators (Landau-Stuart)

Microscopic dynamics:

Chaos



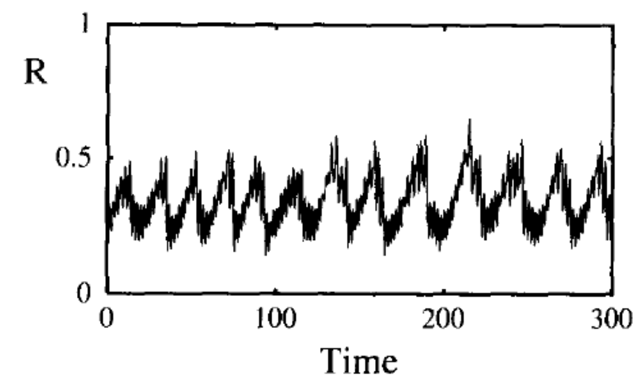
Or... No chaos at the microscopic level!



...Collective chaos in Populations of Oscillators with a single Phase-like variable?

Collective dynamics

Collective chaos



Nakagawa & Kuramoto, *Prog Theor Phys* (1993),Nakagawa & Kuramoto, *Phys D* (1994)

Hakim, Rappel *PRA* (1992); Takeuchi et al. *PRL* (2009,2011), Olmi, Politi, Torcini, *EPL* (2010); Ku, Girvan, Ott, *Chaos* 2015, Rosenblum, Pikovsky *PRE* (2015)

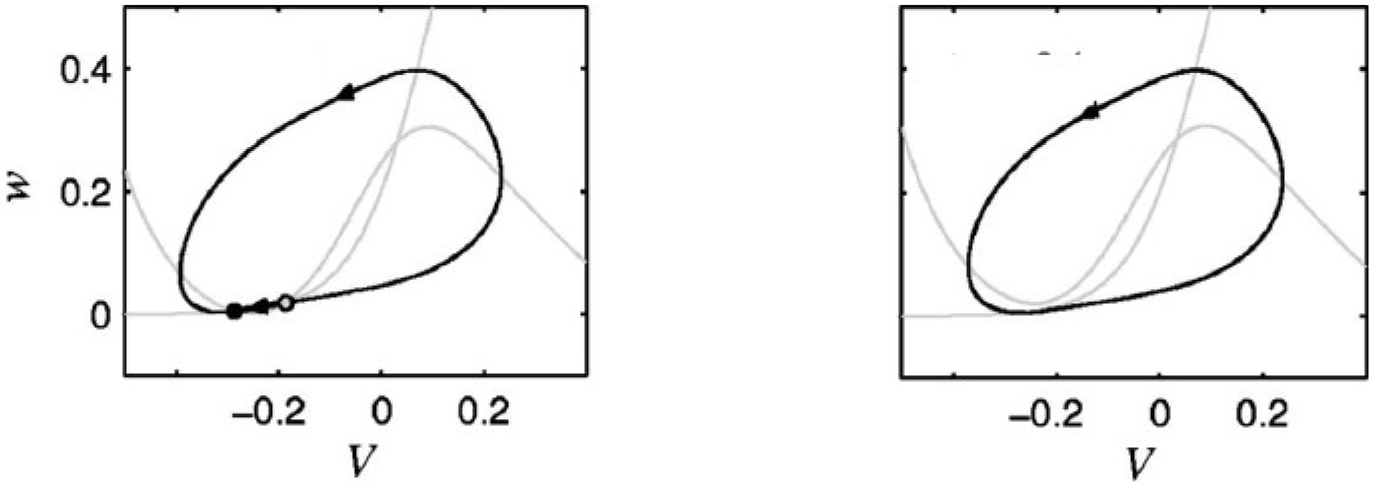
Derivation of a FRM with Inhibition + Delays (Not Heuristic)

Montbrió, Pazó and Roxin, PRX 2015
Pazó, Montbrió PRL 2016

Spiking neurons
Quadratic Integrate & Fire model (QIF)

The QIF model is the normal form of a SNIC bifurcation

Excitable dynamics *Oscillatory dynamics*

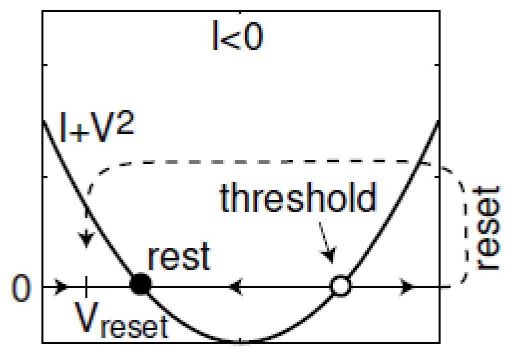


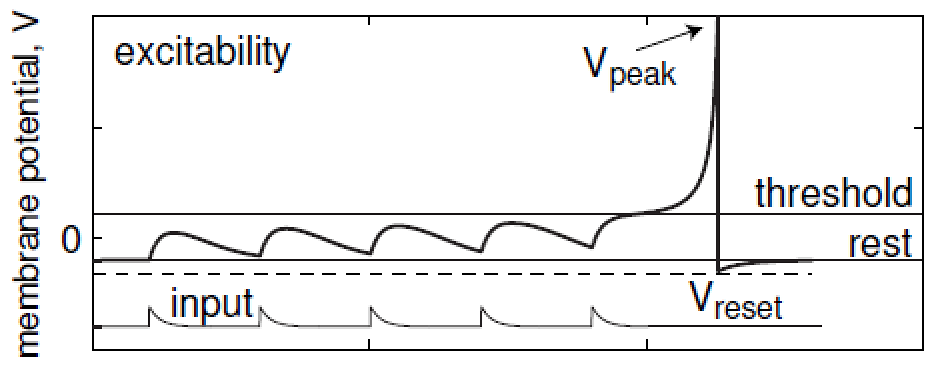
Ermentrout, Kopell, SIAM 1986;
Latham et al. J Neurophys. 2000;
Izhikevich, 2007

Dynamics of the QIF model

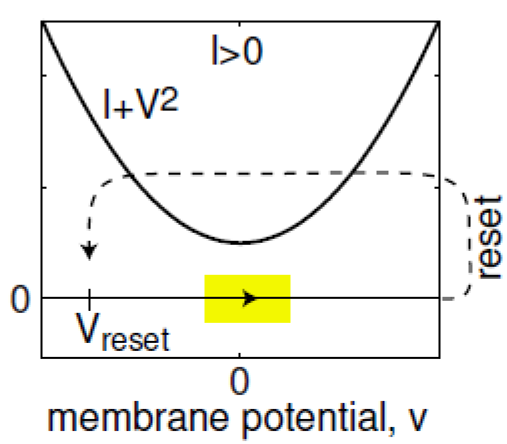
$$\dot{V} = I + V^2 \,, \qquad \text{if } V \geq V_{\text{peak}}, \quad \text{then } V \leftarrow V_{\text{reset}}$$

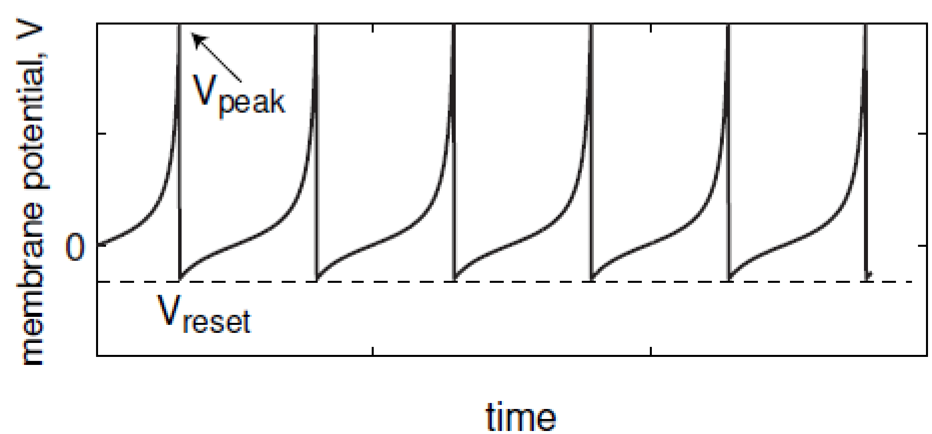
Excitable dynamics:





Oscillatory dynamics:





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

Ensemble of recurrently coupled QIF neurons with synaptic time delay

$$\boxed{\begin{aligned} \tau \dot{V}_j &= V_j^2 + I_j \,, \\ I_j &= \eta_j + J\, s_D \,, \end{aligned}}$$

- 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

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

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

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

- 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

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

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

Lorentzian ansatz

Continuity equation

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

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

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

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

Mean Membrane potential

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

Firing Rate Model

Lorentzian distribution of currents

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

Cauchy Residue's theorem to solve

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

$$\boxed{\begin{aligned} \tau \dot{r} &= \frac{\Delta}{\pi \tau} + 2rv, \\ \tau \dot{v} &= v^2 + \bar{\eta} + J\tau r_D - \tau^2 \pi^2 r^2, \end{aligned}}$$

Montbrió, Pazó and Roxin, *PRX 2015*
Pazó, Montbrió *PRL 2016*
Ott, Antonsen, *Chaos 2008*

Linear Stability Analysis of Incoherence

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

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

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

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)

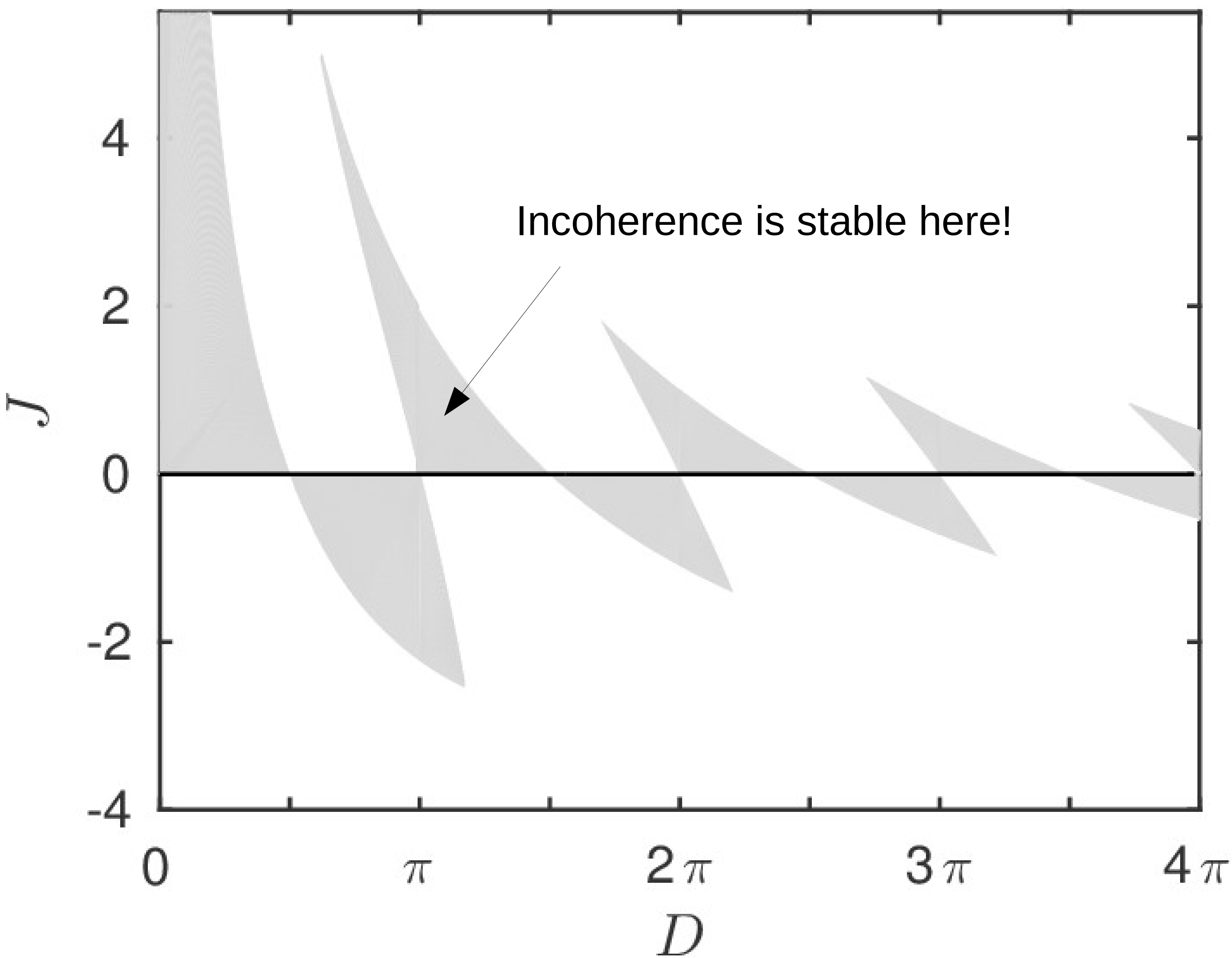
Linearizing around the f.p. and imposing the cond. of marginal stab: $\lambda = i\,\Omega$

Hopf boundaries:

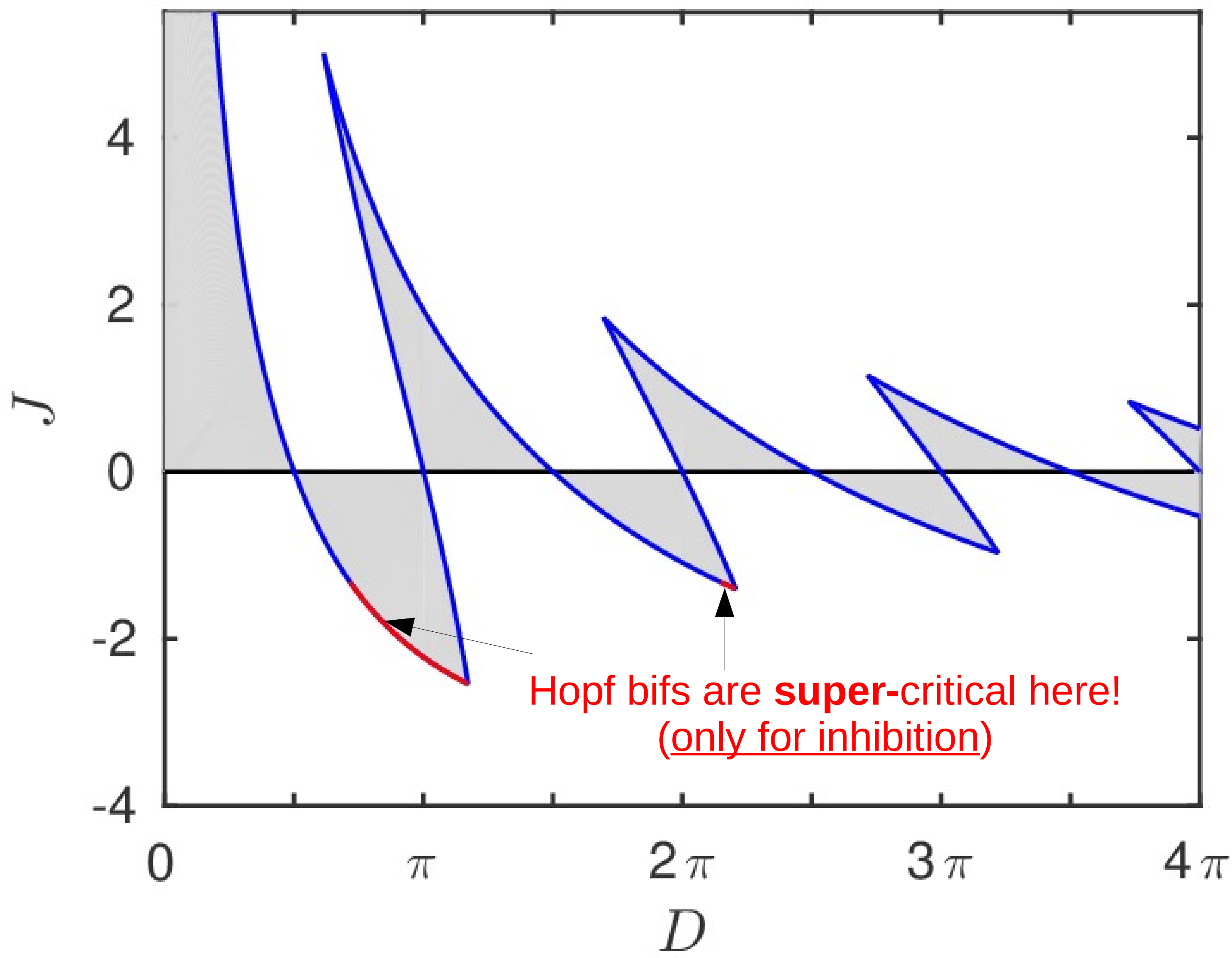
$$\Omega_n = n\pi/D.$$

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

Incoherence (Hopf) boundaries



Weakly nonlinear analysis (two timing)



Stability of Sync
QIF ↔ Phase models

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

When: V_{peak}=-$V_{reset} \rightarrow$ infty :

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

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

- **Theta-Neurons**: $V_j = \tan(\theta_j/2)$ *Ermentrout and Kopell,SIAM J Appl Math 1986*

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

Linear stability analysis of Sync

Winfree (QIF) model:

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

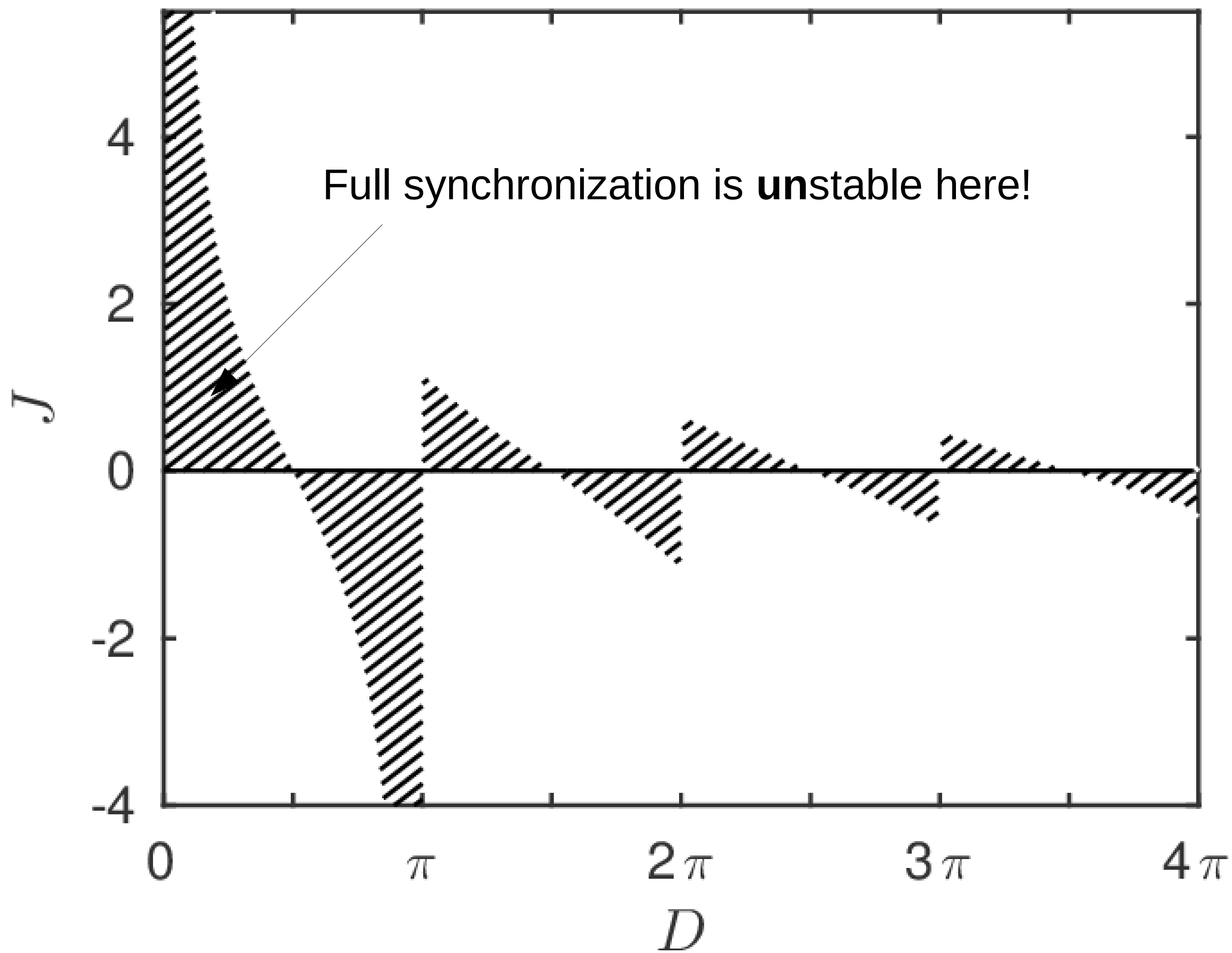
We find the boundaries:

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

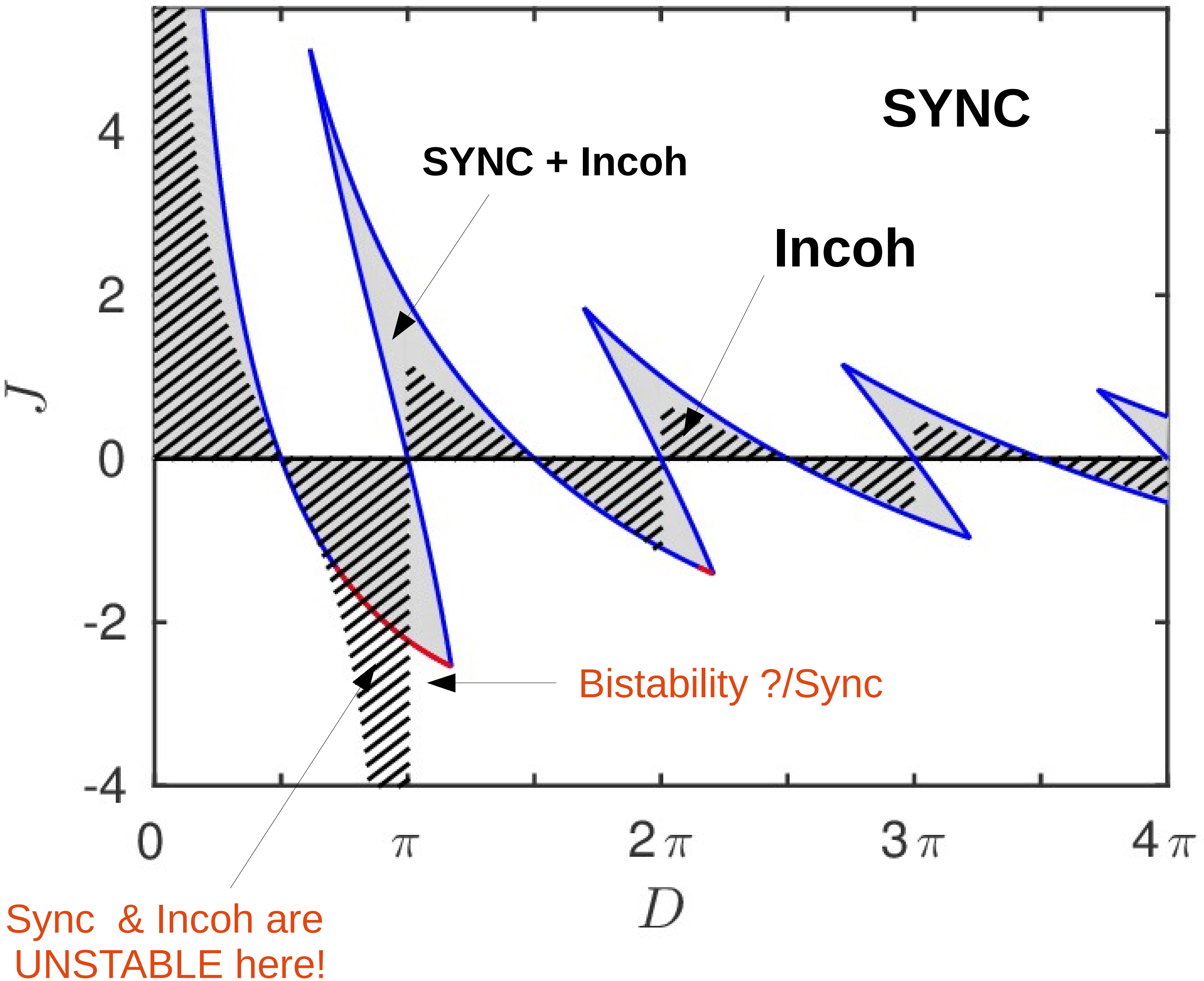
And:

$$\boxed{D = n\pi\ (n = 1, 2\ldots).}$$

Synchronization boundaries

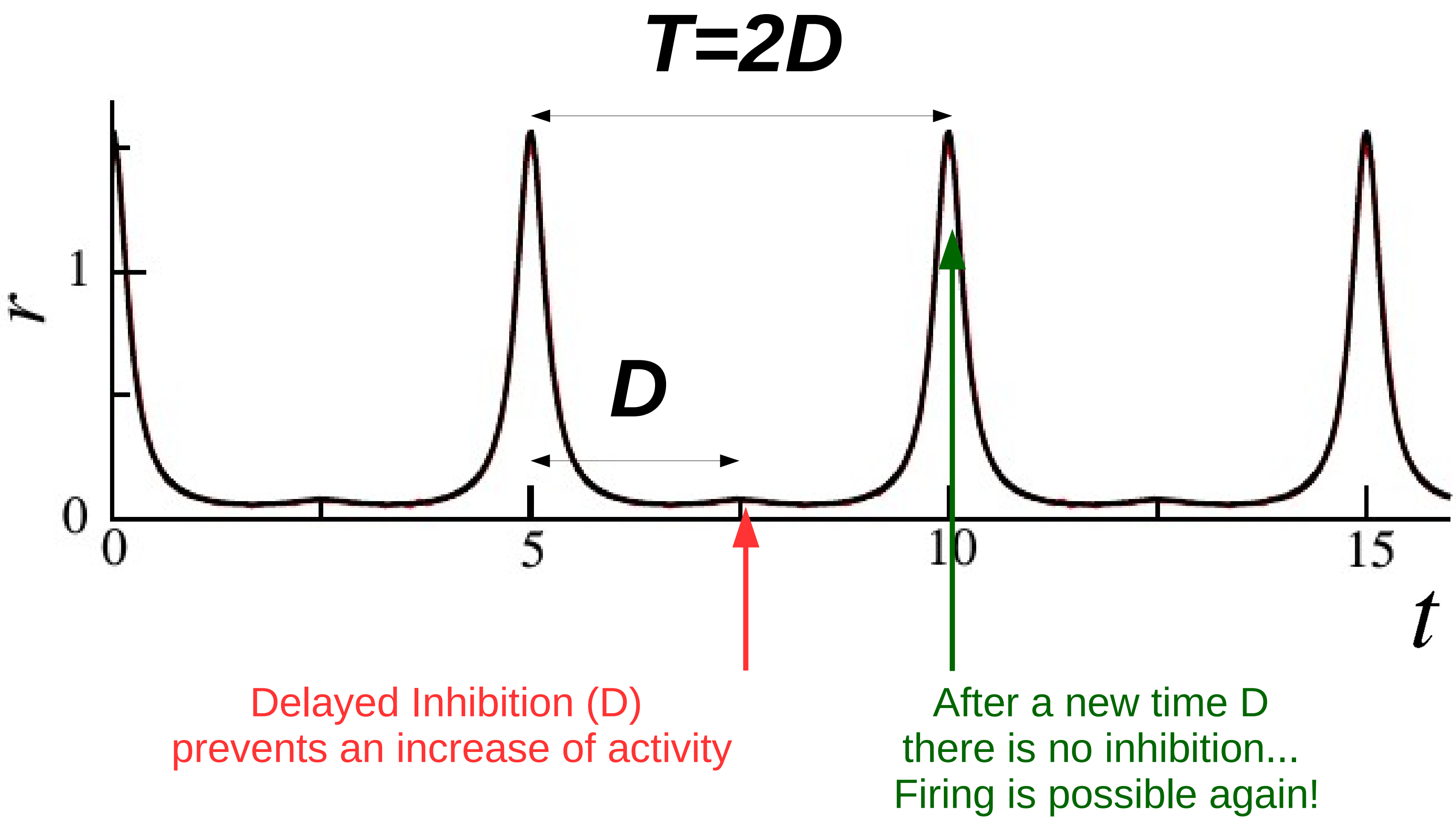


Phase diagram



Pazó, Montbrió, PRL (2016)

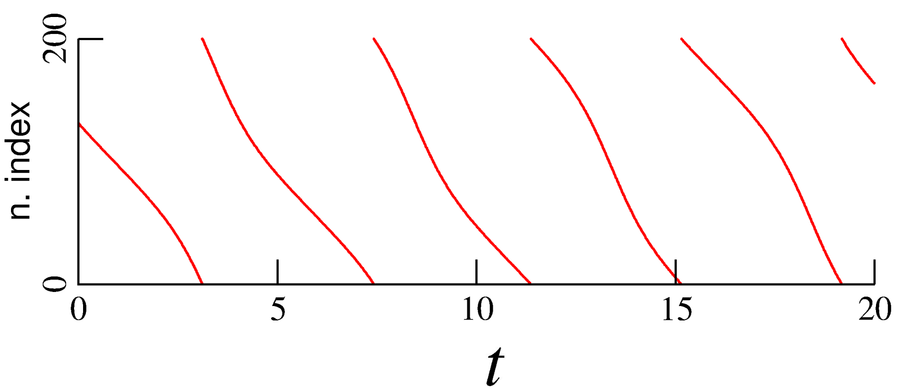
Fast oscillations as in Heuristic FRM

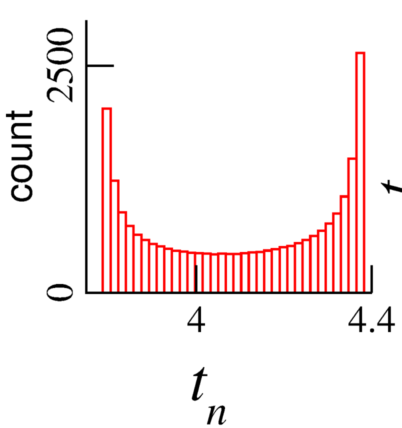


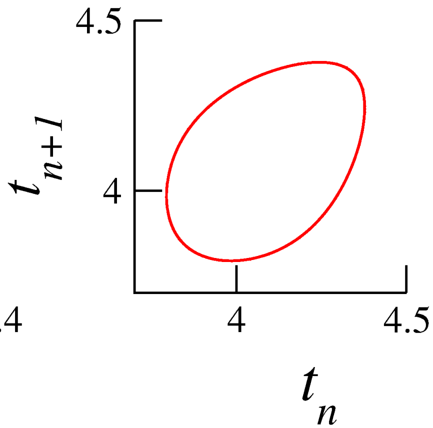
Micro vs. Macro dynamics: Fast osc. in Inhibitory networks & Quasiperiodic Partial Sync

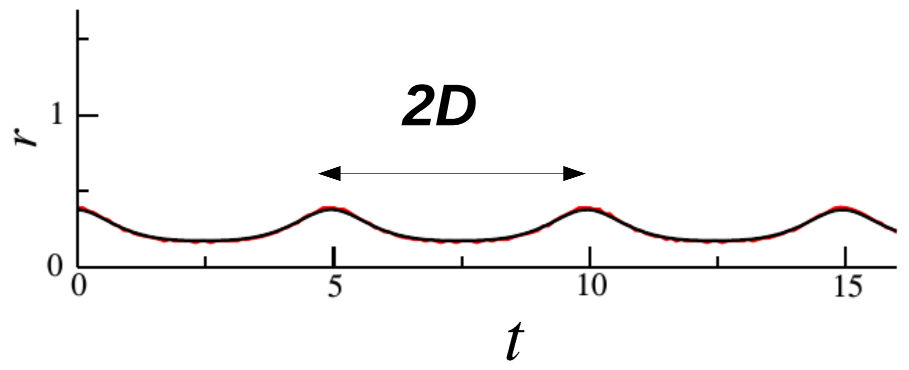
Microscopic dynamics (QIF network)

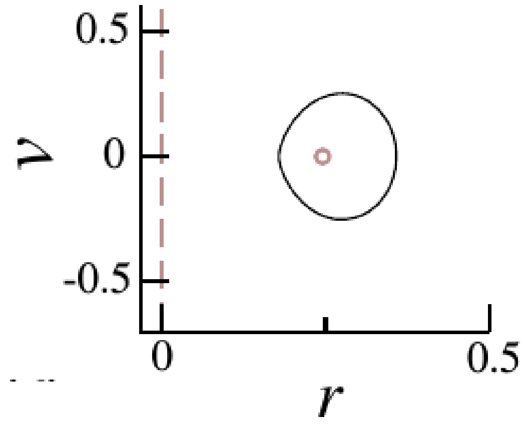
Macroscopic dynamics (FREs)





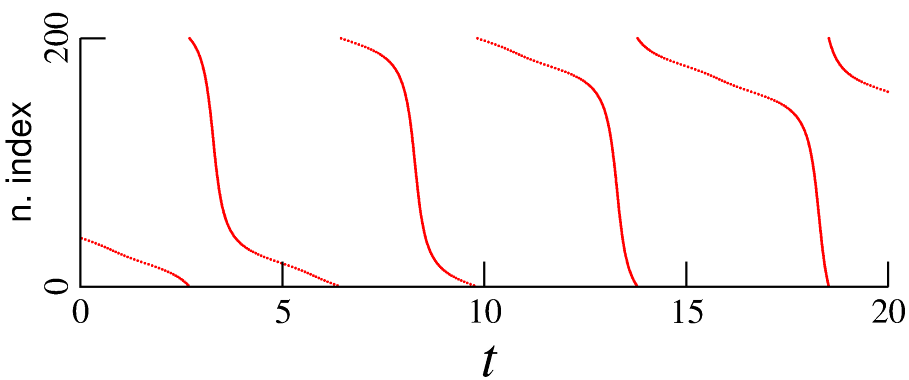


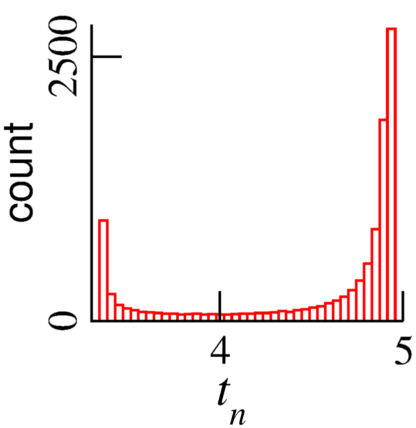


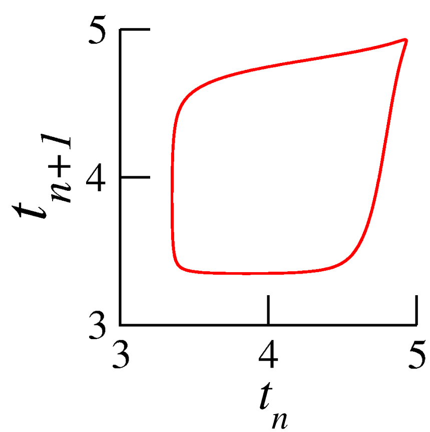


Decreasing J, **period of QPS remains constant** (symmetry of l.c. $v \to -v$)

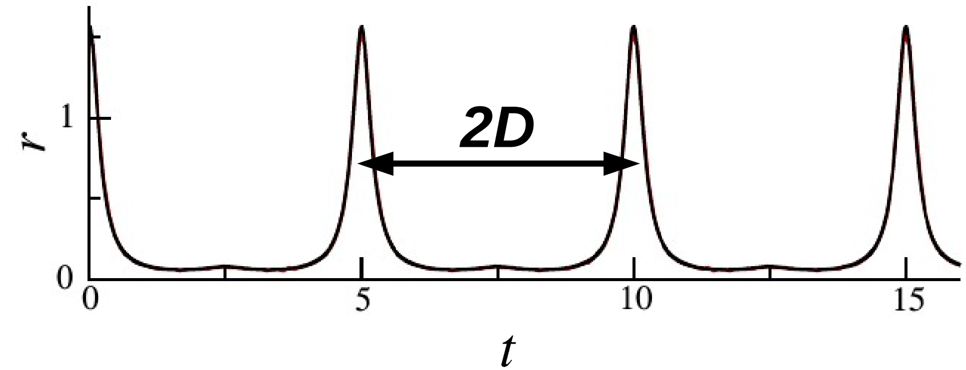
Microscopic dynamics (QIF network)

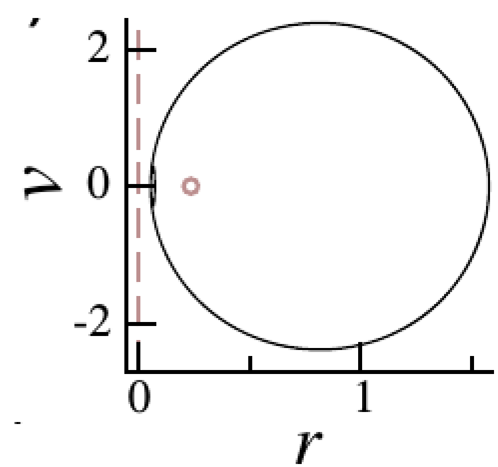






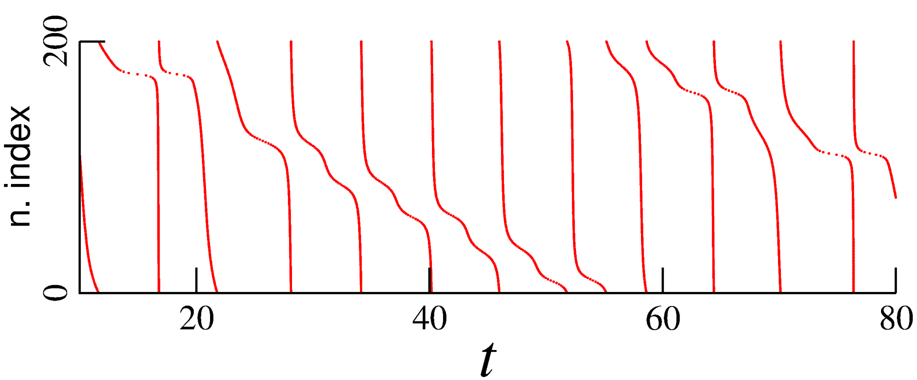
Macroscopic dynamics (FREs)

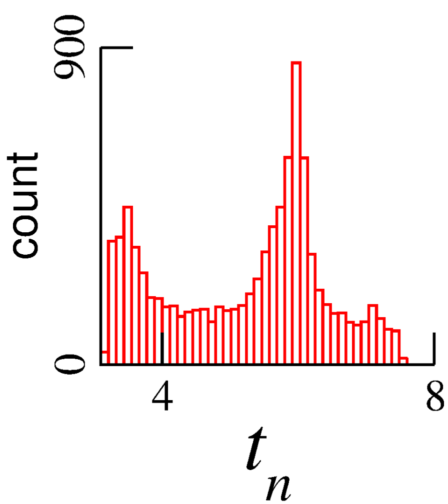


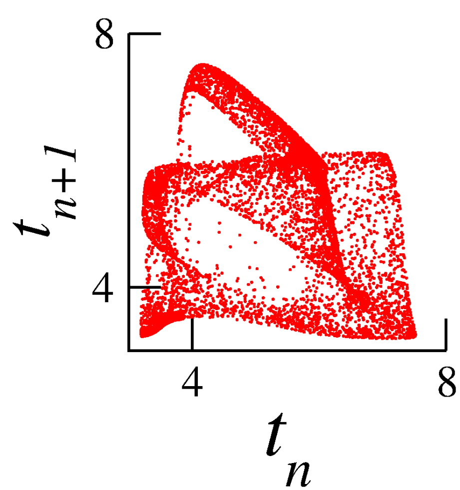


Decreasing *J,D:* Macroscopic Chaos

Microscopic dynamics (QIF network)

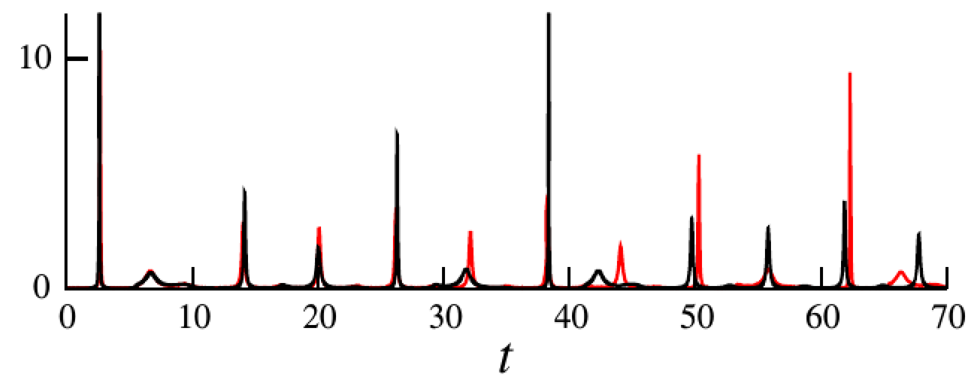


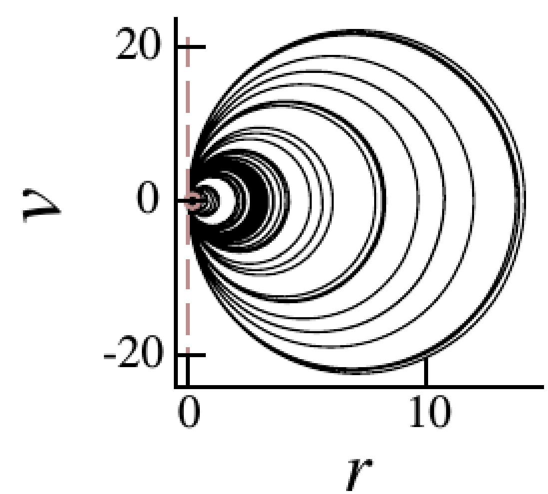




Neurons are not chaotic!

Macroscopic dynamics (FREs)

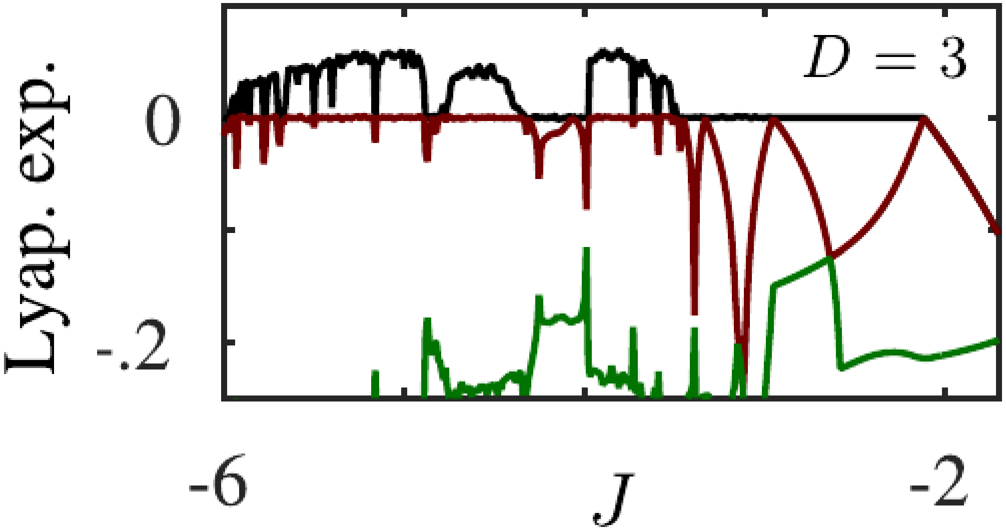


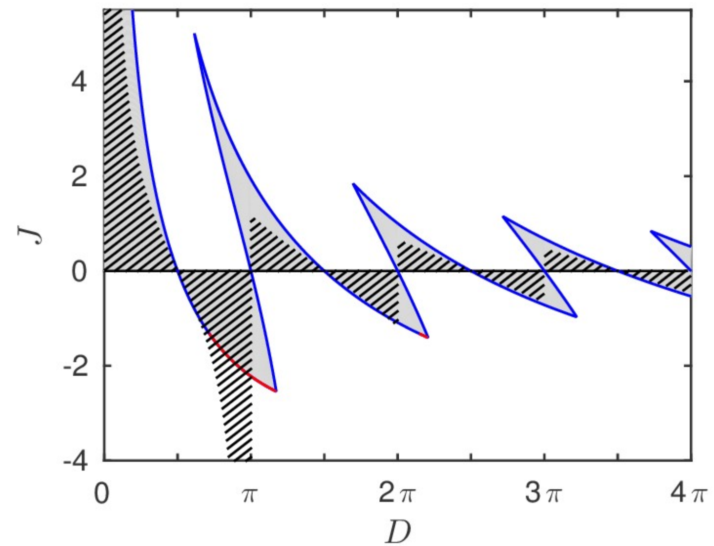


Collective chaos

Transition from QPS to Collective Chaos
period-doubling cascade

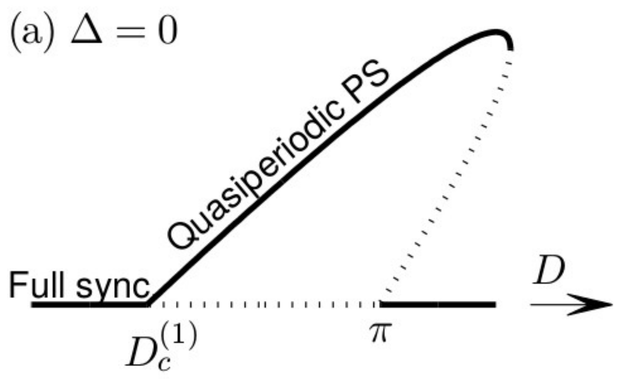
Using the FREs we find:

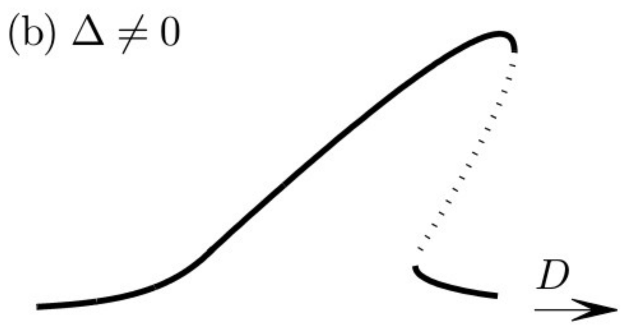


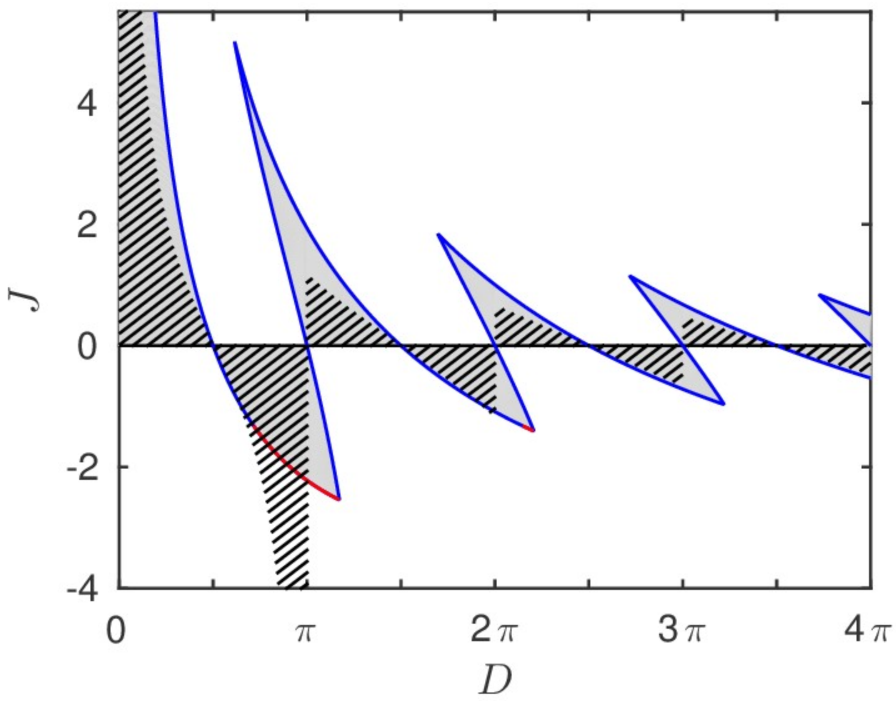


In the thermodynamic limit the system shows **genuine Collective Chaos**

Onset of QPS and (weak) heterogeneity



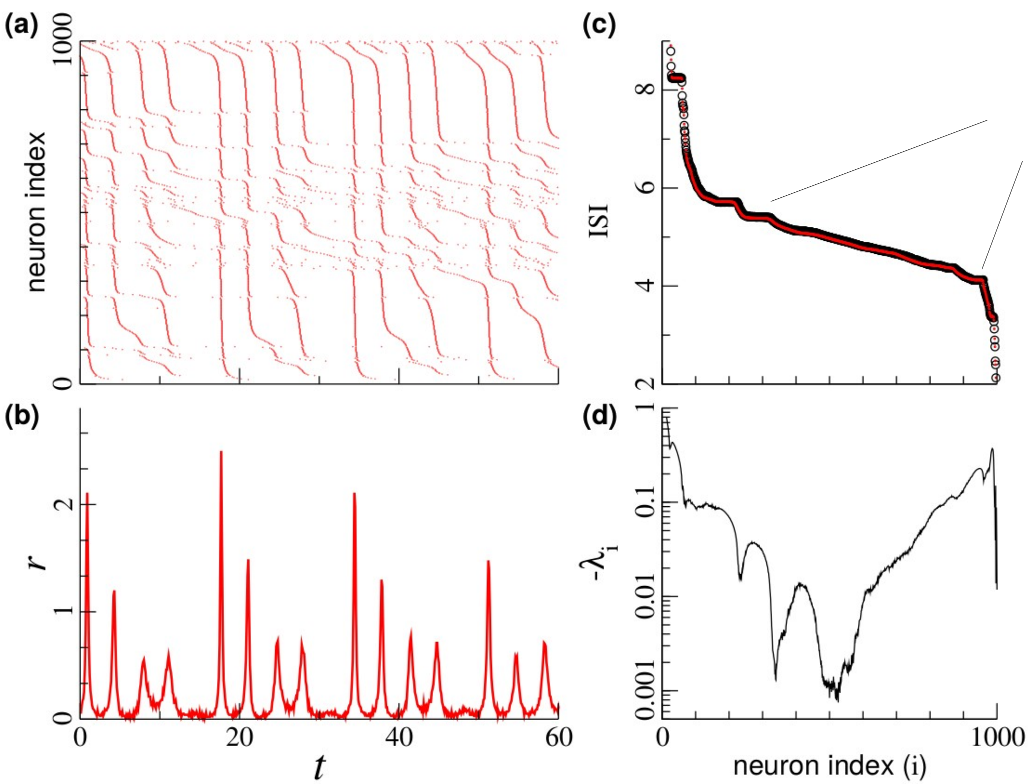




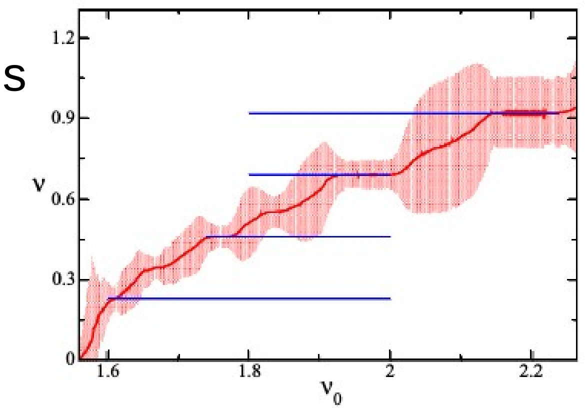
TC bifs. are not robust

bistability remains though!

Macroscopic chaos in heterogeneous networks



Sync plateaus



Heterogeneous Inhibitory LIF + Delay

Luccioli, Politi, *PRL* 2010

No chaos at microscopic level!

Summary

- Using an exact FRM we related QPS and CC to Fast Oscillations in Inhibitory Networks
- Same Collective Oscillations arise due to distinct Microscopic dynamics: sparse sync, QPS, CC...
- Transition from QPS to CC via period doubling cascade
- CC and QPS are also present in (weakly) Heterogeneous networks

Thanks!

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Modeling and Analysis