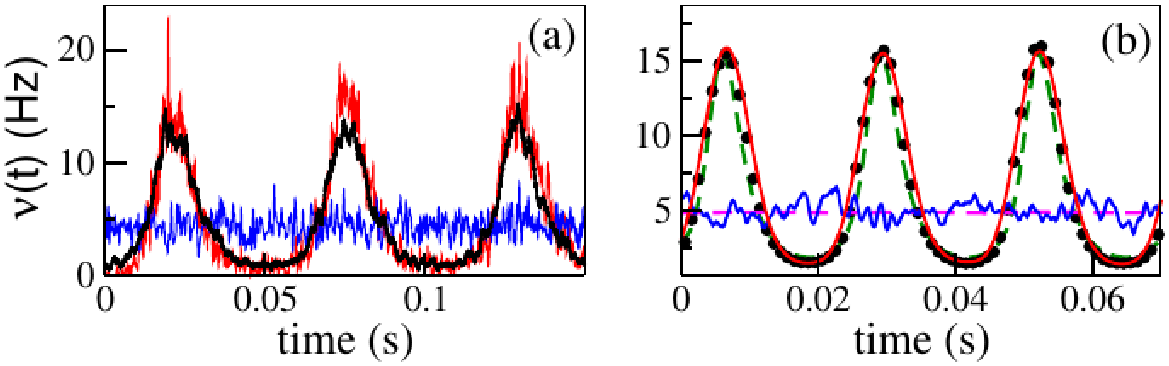
Discrete synaptic events induce global oscillations in balanced neural networks

Denis G. Goldobin, Matteo di Volo, Alessandro Torcini



Summary of the Talk

- Shot versus continuous noise : relevance for neural dynamics
- Inhibitory Random Network of Quadratic Integrate and Fire (QIF) Neurons
- Role of Endogenous Fluctuations
- Mean Field Analysis for a Network with constant in-degree K:
    - Langevin Formulation (shot-noise and diffusion approximation)
    - Complete Continuity Equation and Fokker Planck Equation
- Phase Diagram for Macroscopic Regimes (Asynchronous versus Oscillatory Regimes)
- Different Bifurcation Scenarions
- Two different kinds of Global Oscillations
- Summary

Discrete Stochastic Events

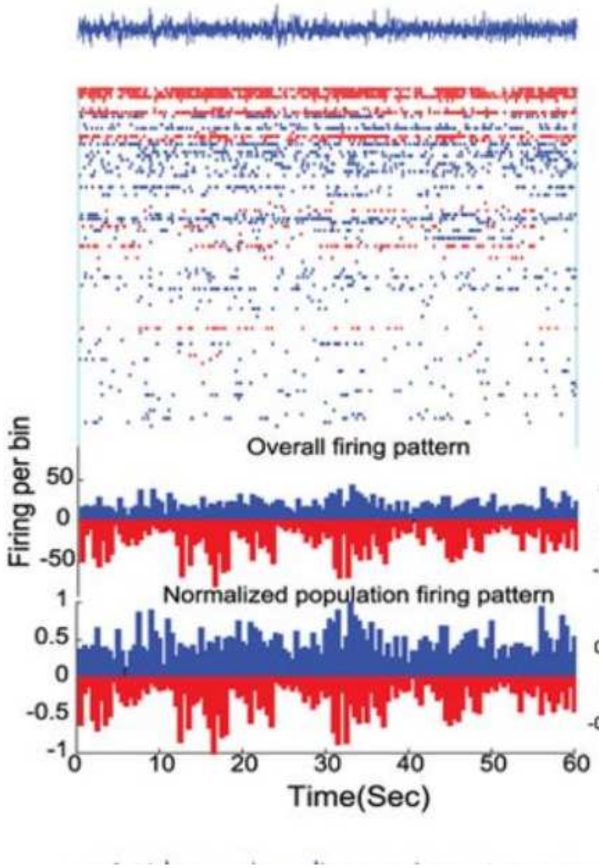
In several contexts the discrete nature of stochastic events should be taken into account to correctly predict the system dynamics

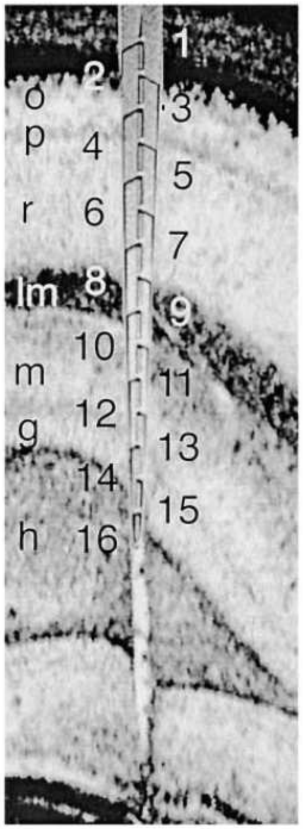
- Shot-noise: which is discontinous since it is conveyed by pulses (electric charges)
- White noise : which is associated to thermal fluctuations and is continuous

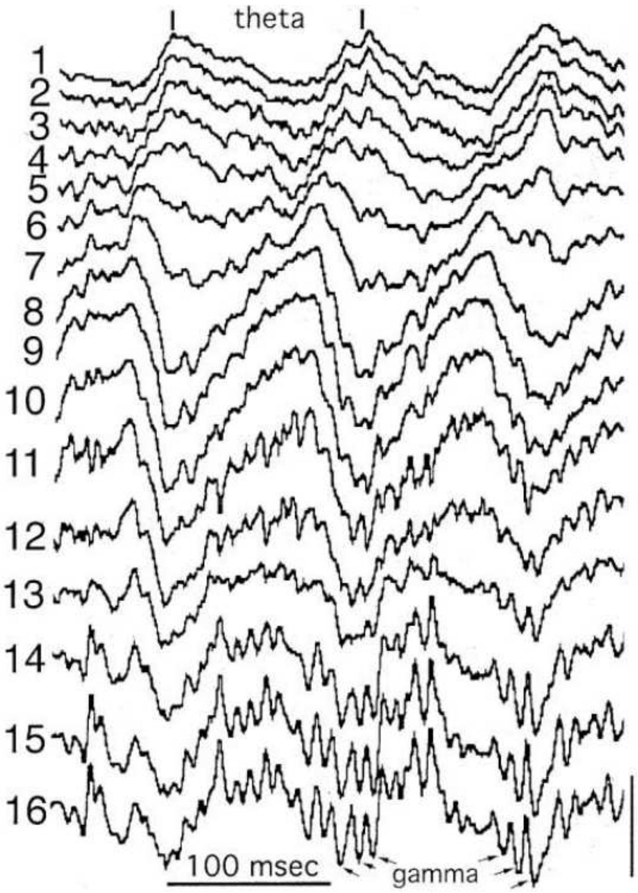
Neural Dynamics

- A neuron receives discrete inputs from other neurons via pulses: post-synaptic potentials (PSPs)
- The distribution of the PSPs displays long tails towards large amplitudes
  `B. Barbour, N. Brunel, V. Hakim, J.-P. Nadal, TRENDS in Neurosciences (2007); S. Song, et al. PLoS Biology (2005)`
- Networks of inhibitory neurons with low connectivity (in-degree $K = 30 - 80$) have been identified in the cat visual cortex and in the rat hippocampus, where they are believed to be at the origin of Global Oscillations (GOs) in the γ-band
  `G. Buzsáki, X.-J. Wang, Annual review of neuroscience (2012)`

Dynamical Regimes in the Brain







ASYNCHRONOUS STATE

GLOBAL OSCILLATIONS

Quadratic Integrate and Fire Neuron

This a very simple model, which can mimick realistic neural dynamics

$$\frac{dV}{dt} = V^2 + I$$

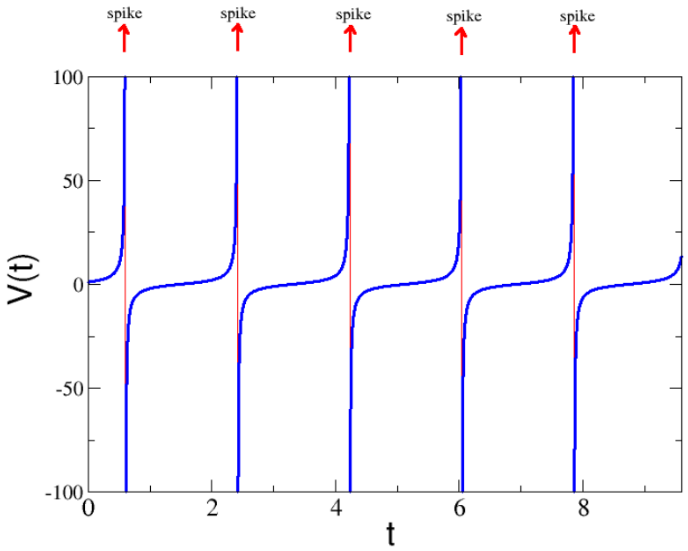
- V membrane potential with threshold $V_{th} = +\infty$ and reset $V_r = -\infty$
- I neural excitabilty
  - $I > 0$ Tonic Neuron
  - $I \leq 0$ Excitable Neuron
- Normal form for the saddle-node on a limit cycle (SNIC) bifurcation
- Hodgkin's Class I excitable membrane

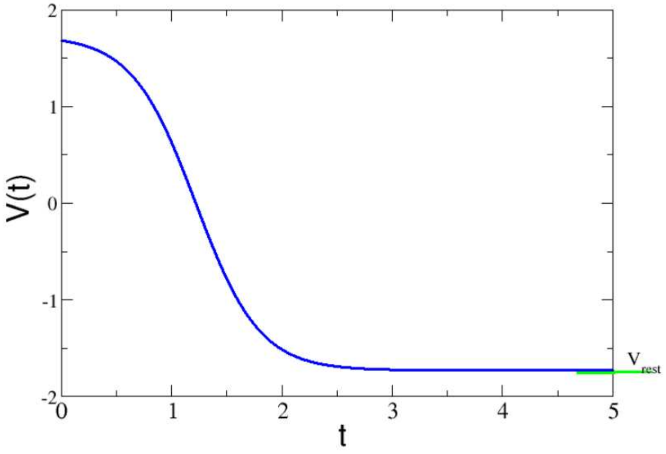
The model has been developed to reproduce parabolic bursting in neurons of the Aplysia abdominal ganglion (when sinusoidally forced) and low firing neurons (Class I).

`Ermentrout and Kopell, (1986) SIAM Journal on Applied Mathematics`

`Latham et al. (2000) Journal of Neurophysiology`

Quadratic Integrate and Fire Neuron





Tonic neuron $I > 0$

- The firing period is $T_{firing} = \frac{\pi}{\sqrt{I}}$

Excitable neuron $I \leq 0$

- If $V(t_0) \leq \sqrt{|I|}$ - Subthreshold Dynamics $V \to V_{rest} = -\sqrt{|I|}$
- If $V(t_0) > \sqrt{|I|}$ emission of a spike followed by relaxation to V_{rest}

Balanced Inhibitory QIF Network

The simplest model exhibiting the balanced regime is a purely inhibitory network with a constant excitatory drive, for simplicity we assume that

- the in-degree is K for all neurons
- all neurons receive exactly K inputs from randomly selected neighbours
- due to this random choice the endogenous fluctuations in the input current are still present

The evolution of the membrane potentials $\{V_i\}$ for a network of inhibitory Quadratic Integrate and Fire (QIF) neurons can be written as,

$$\dot{V}_i = I + V_i^2 - g \sum_{j \neq i}^{N} \sum_{n} \varepsilon_{ij} \delta(t - t_j^{(n)}) \quad i = 1, \dots, N$$

$$g = \frac{g_0}{\sqrt{K}} \quad \text{and} \quad I = \sqrt{K} i_0$$

`Monteforte & Wolf, PRL (2010); di Volo & AT PRL (2018)`

Mean-field : Langevin formulation

The evolution of the membrane potential of a generic neuron in the mean field approximation can be written as

$$\dot{V} = F(V) + I - gS(t) \quad ; \quad F(V) = V^2 \quad \text{for the QIF}$$

where

- $S(t)$ is assumed to be a Poissonian spike train
- since the inputs can be assumed as uncorrelated $K << N$:
  - $S(t)$ is a spike train with rate of arrival of the spikes $R(t) = K\nu(t)$
  - $\nu(t) = \frac{1}{N}\sum_{j=1}^{N}\sum_{n}\delta(t - t_j^{(n)})$ is the population firing rate

Diffusion Approximation (DA)

Usually the Diffusion Approximation (DA) is applied to approximate the spike trains as white continuous noise under the assumptions

- the PSPs have small amplitudes g
- the arrival rate is high ($K >> 1$)

The Poissonian spike train $S(t)$ can be approximated as

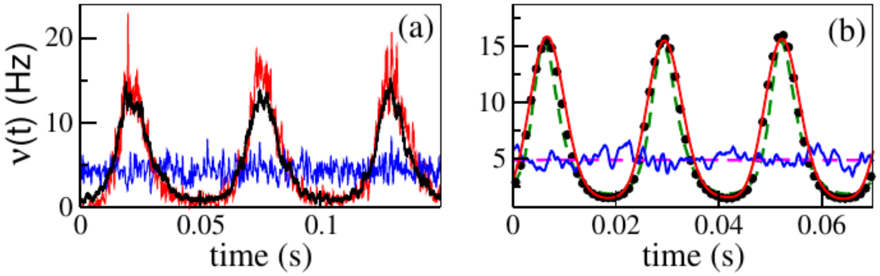
$$S(t) = K\nu(t) + \sqrt{K\nu(t)}\xi(t)$$

and the Langevin equation becomes

$$\dot{V} = F(V) + \sqrt{K}[i_0 - g_0\nu(t)] + \sigma(t)\xi(t)$$

- $\xi(t)$ is a random Gaussian variable
- the noise amplitude is $\sigma(t) = g_0\sqrt{\nu_0(t)}$ independent of K

Complete versus DA Approach



Small $K = 20 - 200$, large $g_0 = 1 - 4$

- Black - Network simulations
- Blue - DA
- Red - Complete Approach

- **(a)** Morris-Lecar Conductance Based model - Class II excitable membrane
- **(b)** QIF Neuron : Current-based model of Class I excitability

We simulated $N = 20000 - 80000$ uncoupled Langevin equations, where the firing rate population $\nu(t)$ is self-consistently determined

The DA does not capture the global oscillations

Complete Mean Field : Population Dynamics

In the MF framework the population dynamics is usually described in terms of

$P(V,t)$: distribution of the membrane potentials of the neurons at time t

The time evolution is given for the QIF by the complete continuity equation

$$\partial_t P(V,t) + \partial_V [(V^2 + I)P(V,t)] = R(t)\Delta P(V,T)$$

with

- boundary condition $\lim_{V\to\infty} V^2 P(V,t) = \nu(t)$
- $\Delta P(V,T) = [P(V^+,t) - P(V,t)]$ with $V^+ = V + g$.

The stationary solution $P_0(V,t)$ corrresponds to asynchronous dynamics, the study of the instabilities of this solution will determine the emergence of Global Oscillations

The Fokker Planck Equation

By assuming that g is sufficiently small we can expand the term

$$\Delta P(V,t) = \sum_{p=1}^{\infty} \frac{g^p}{p!} \partial_V^p P(V,t) \ ;$$

by limiting to the first two terms in this expansion we recover the Diffusion Approximation corresponding to the following Fokker-Planck Equation

$$\partial_t P(V,t) + \partial_V [(V^2 + A(t)] P(V,T)] = D(t) \partial^2_{V^2} P(V,t)$$

where

$$D(t) = \frac{g_0^2 \nu_0(t)}{2} \qquad A(t) = \sqrt{K}[i_0 - g_0 \nu(t)]$$

and with boundary condition

$$\lim_{V \to \infty} V^2 P(V,t) = \nu(t)$$

Complete Mean Field

The QIF model evolution can be transformed in that of a phase oscillator, by introducing the phase :

$$\psi = 2\arctan\left(V/\sqrt{I}\right) \in [-\pi, \pi]$$

which leads to a uniformly rotating phase in the absence of incoming pulses for supra-threshold neurons with $I > 0$
By considering the probability distribution of the phases this can be expanded in Fourier as follows

$$w(\psi,t) = P(V,t)\Big(I + V^2\Big)/(2\sqrt{I}) = (2\pi)^{-1}\sum_{n=-\infty}^{+\infty} z_n e^{-in\psi}$$

where z_n are the so-called Kuramoto-Daido order parameters, with $z_0 = 1$ and $z_{-n} = z_n^*$.

Complete Mean Field

After laborious but straightforward calculations, one obtains the following evolution equations

$$\dot{z}_n = i2n\sqrt{I} z_n + K\nu \left[\sum_{m=0}^{+\infty} I_{nm}(\alpha)\, z_m - z_n \right] \qquad n = 1, 2, 3, \ldots$$

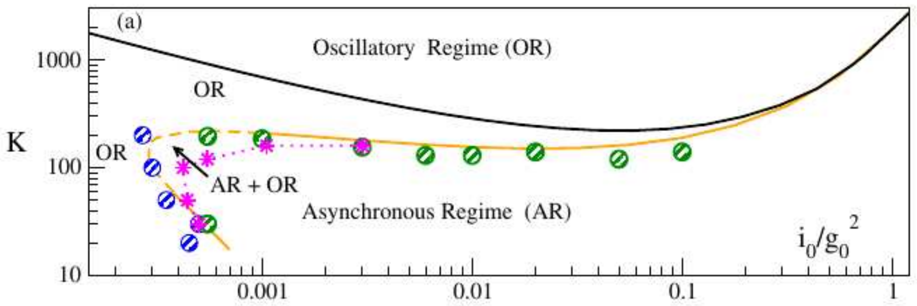
where $\alpha \equiv g/\sqrt{I} = g_0/(\sqrt{i_0} K^{3/4})$ and

$$I_{nm}(\alpha) \equiv \frac{1}{2\pi} \int_0^{2\pi} \frac{e^{in\psi} \left(e^{-i\psi_a}\right)^m \mathrm{d}\psi}{1 + \frac{\alpha^2}{2} + \alpha \sin\psi + \frac{\alpha^2}{2} \cos\psi} \quad .$$

The firing rate can be self-consistently determined by the flux at the firing threshold as follows

$$\nu = 2\sqrt{I} w(\pi, t) = \frac{\sqrt{I}}{\pi} \mathrm{Re} \left(1 + 2 \sum_{k=1}^{\infty} (-1)^k z_k \right)$$

Phase Diagram



Bifurcation Lines

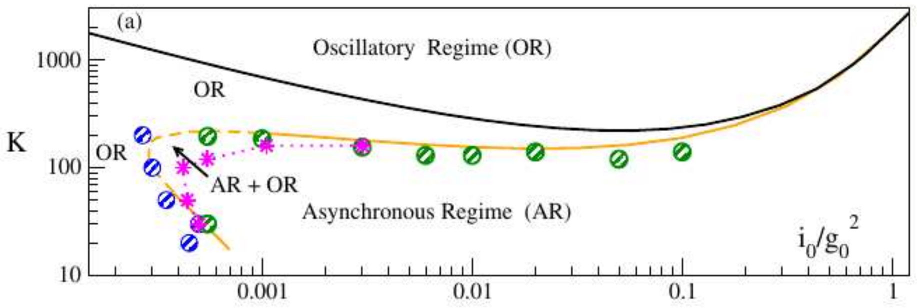
- Black - DA
- Orange - CMF
- Symbols - Network Simulations

The system is controlled by only two parameters: K and α. Therefore a bidimensional phase diagram in the plane $(i_0/g_0^2, K)$ is sufficient to cover all the macroscopic regimes observable in the network.

- The linear stability of the stationary solution by considering a truncation of the Fourier expansion to $M \geq 100$ modes in order to guarantee a numerical accuracy of $\mathcal{O}(10^{-12})$ has allowed us to find the Hopf Bifurcatione lines to the Oscillatory Regime
- A weakly nonlinear approach allowed us to obtain the amplitude equations and to determine the super- or sub-critical nature of the bifurcations

`DA analysis in Di Volo, Segneri, Goldobin, Politi, AT Chaos (2022)`

Phase Diagram



Bifurcation Lines

- Black - DA
- Orange - CMF
- Symbols - Network Simulations

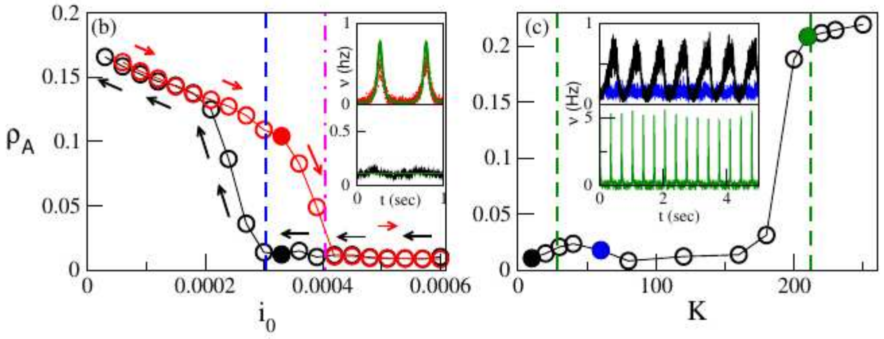
- DA disagrees with network simulations for $i_0/g_0^2 < 0.2$
- DA reports only super-critical Hopf bifs. and Oscillations ONLY for $K > 200$
- CMF agrees with network simulations in the whole phase diagram
- CMF report sub- and super-critical HBFs with a coexistence region of asynchronous and oscillatory solutions
- CMF tells that we can have oscillatory regimes even for $K = 10$

Bifurcations

A typical order parameter to measure the level of synchronization is

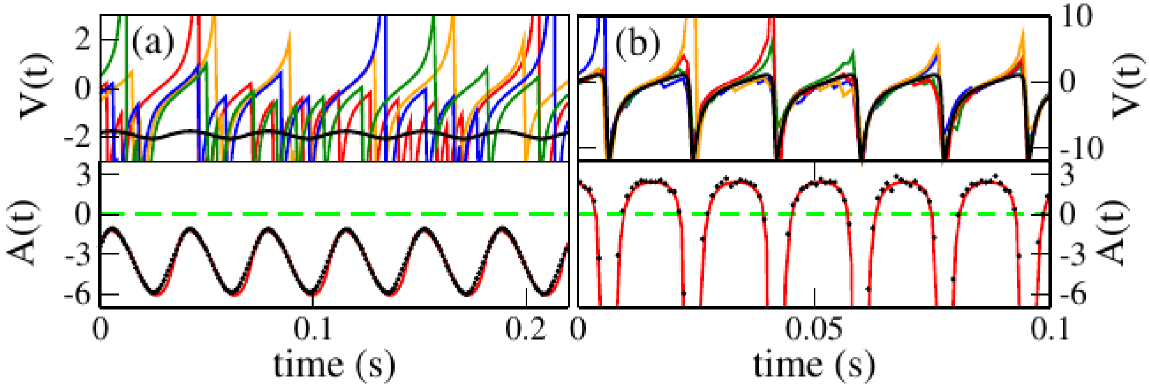
$$\rho^2 \equiv \frac{\sigma^2(V)}{\sum_{i=1}^{N} \sigma^2(v_i)/N} \qquad V = \sum_{i=1}^{N} \frac{v_i}{N} \ ,$$

- Perfect synchronization $\rho = 1$ — Asynchronous state (AS) $\rho = 1/\sqrt{N}$
- Quasi-adiabatic simulations by varying K (i_0)



- (b) $K = 100$ – Sub-critical Hopf (Hysteresis) : coexistence of AR and OR
- (c) $i_0 = 0.00055$ - Two kinds of GOs at small and large K

Two kinds of Global Oscillations



- The GOs are due to the neurons not receiving any inhibitory PSP from reset to threshold (free suprathreshold neurons);
- $(K = 10)$ Cluster Activation a neuron fires delivering large amplitude inhibitory PSPs inducing a transient synchronization in K neurons and a sub-group, not receiving further PSPs, can eventually reach threshold together
- $(K = 210)$ Drift-driven at each population burst, a non negligible part of the neurons can get synchronized by the discharge of small inhibitory PSPs, despite the fluctuations a sufficient percentage of neurons is able to fire together

Summary

- We have developed a Complete Mean Field formalism for a inhibitory random QIF neural network in the balanced regime by encompassing finite amplitude PSPs
- The Complete approach reproduces quite well the emergence of Global Oscillations via super- and sub-critical Hopf bifurcations at variance with the Diffusion Approximation
- Two different kinds of Global Oscillations are identified at low and large in-degree
- The results can be extended to non instantaneouns synapses, e.g. by considenting an exponential PSP profile
- Our theoretical results support the Buzsaki hypothesis that γ-oscillations in the hippocampus can be generated by sub-networks of interneurons with low in-degrees $K = 30 - 80$

`di Volo, Goldobin, and Torcini, ArXiv (2024)`

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THE PARIS SEINE INITIATIVE

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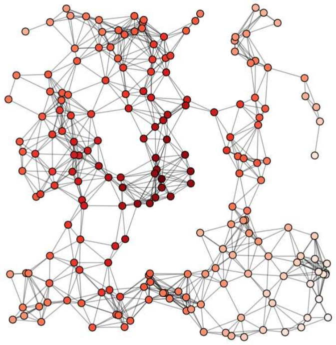
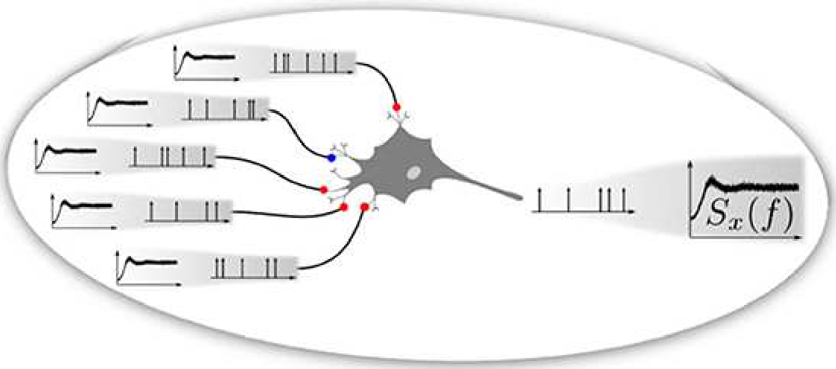
Nina

Cortical Dynamics

A cortical area can be seen as a recurrent random network made of a large number N of excitatory and inhibitory neurons, each one receiving many inputs ($K \simeq 10,000$):

- the output of a neuron is an input to another neuron of the same area, the input and output firing rate should be quite similar;
- the inputs are uncorrelated due to the high dilution in the connections $K/N << 1$;
- neurons emit spikes in an irregular fashion and not too frequently despite the many excitatory and inhibitory inputs. Why ?





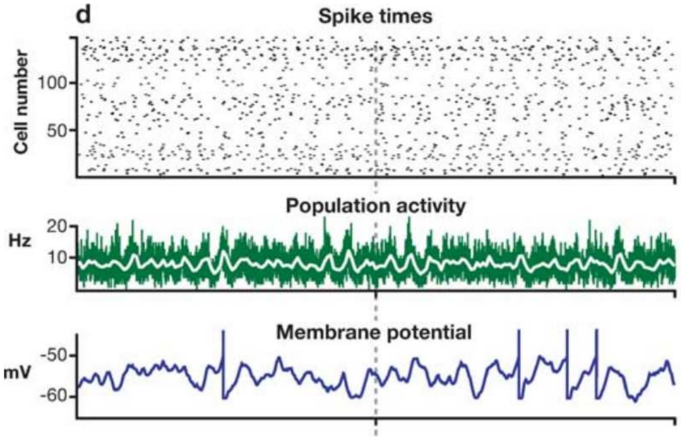
The Balanced Network

Each neuron in a random recurrent network receives independent Poissonian trains of spikes of amplitude J from K neurons firing with frequency ν_0. Therefore

- Average Excitatory and Inhibitory Synaptic Currents $I_e \simeq I_i \simeq JK\nu_0$
- Fluctuations of the total current $I = I_e + I_i \quad \sigma^2(I) \simeq J^2 K \nu_0$

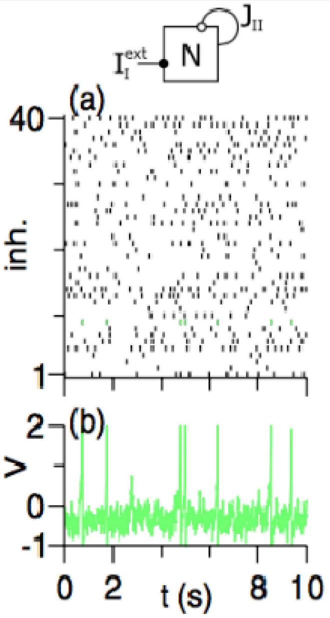
The neurons in the cortex fire quite irregularly with a finite frequency ($\simeq \nu_0$), therefore $I = I_e + I_i$ and $\sigma^2(I)$ should be both $\mathcal{O}(1)$, this is possible if

- Excitatory and Inhibitory Inputs cancel each other at leading order $\mathcal{O}(K)$:
  $I = I_e + I_i \simeq 0 — \sigma(I) = J\sqrt{K\nu_0}$
- The neurons fire due to current fluctuations
- Synaptic couplings scale as $J \propto \frac{1}{\sqrt{K}}$



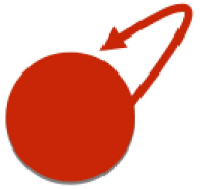
Vogels, Rajan, Abbott, Annu. Rev. Neurosci. (2005); van Vreeswijk Sompolinsky, Science (1996)

A Balanced Inhibitory Network



$dV_i/dt = F(V) + I_i(t)$

$$I_i(t) = \sqrt{K} I_i^{\text{ext}} + \sum_{j \in \text{pre}(i)} \sum_s \frac{J_{ij}}{\sqrt{K}} \delta(t - t_j^{(s)}).$$



Inhibitory network

$$\boxed{A = \sqrt{K}(I - JR)}$$

$I > JR$ → $R \to \infty$, $I < JR$

$I < JR$ → $R \to 0$, $I > JR$

Large K limit the only stable state is the balanced state

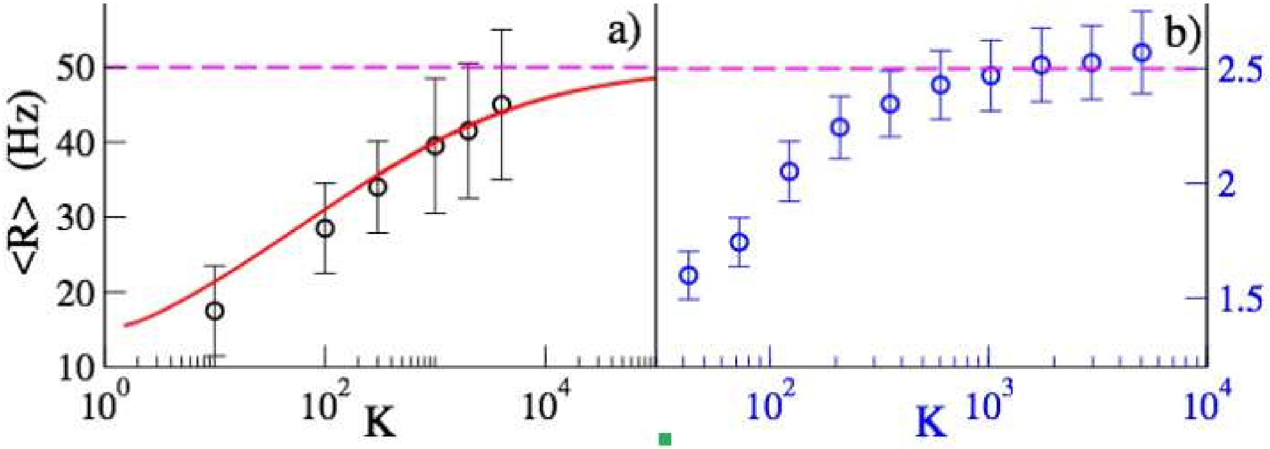
-> ***R=I/J***

Monteforte & Wolf PRL 2010

Asynchronous Dynamics

- If the dynamics is asynchronous the population firing rate is constant $\nu_0(t) = \nu_0$
- For sufficiently large in-degree $K >>> 1$
  - the total input $A(t) = \sqrt{K}[i_0 - g_0\nu_0]$ dynamically adjust
  - the system approaches the balanced state, where

$$\lim_{K \to \infty} \nu_0 = \frac{i_0}{g_0}$$



Quadratic Integrate and Fire

Morris-Lecar Model

Fokker-Planck derivation (DA)

In order to solve the FPE, we map the membrane potential onto a phase variable $V = \tan\left(\frac{\theta}{2}\right) \quad \theta \in [-\pi, \pi[$ the PDF now reads as

$$R_g(\theta) = P_g(V)\frac{dV}{d\theta} \quad , \qquad \text{where} \quad \frac{dV}{d\theta} = \frac{1}{2\cos^2(\theta/2)}$$

and the FPE can be rewritten as

$$\partial_t R_g(\theta, t) = -\partial_\theta \left[\psi_0(\theta) R_g(\theta, t) - Z_0(\theta)\partial_\theta R_g(\theta, t)\right]$$

where

$$\begin{aligned} \psi_0(\theta) &= (1 - \cos(\theta)) + (A_g + D_g \sin(\theta))(1 + \cos(\theta)) \quad , \\ Z_0(\theta) &= D_g (1 + \cos(\theta))^2 \end{aligned}$$

with boundary condition $2\int dg R_g(\pi, t) L(g) = \nu(t)$ and $L(g)$ is theLorentzian distribution of the synaptic couplings

Fokker-Planck derivation (DA)

Since we are now dealing with a phase variable, it is natural to express the PDF in Fourier space,

$$R_g(\theta,t) = \frac{1}{2\pi}\left[1 + \sum_{m=1}^{\infty}\left(a_m(g,t)\mathrm{e}^{-im\theta} + c.c.\right)\right] .$$

The associated Kuramoto-Daido order parameters for the population synchronization are given by

$$z_m(t) = \int dg\; a_m(g,t)\; L(g)$$

while the equations for the various modes are

$$\begin{aligned}
\dot{a}_m &= m\left[i(A_g+1)a_m + \frac{i}{2}(A_g-1)(a_{m-1}+a_{m+1})\right] \\
- \quad D_g & \left[\frac{3m^2}{2}a_m + (m^2 - \frac{m}{2})a_{m-1} + (m^2 + \frac{m}{2})a_{m+1}\right. \\
+ & \left.\frac{m(m-1)}{4}a_{m-2} + \frac{m(m+1)}{4}a_{m+2}\right]
\end{aligned}$$

Fokker-Planck derivation (DA)

Since g is distributed according to a Lorentzian distribution

$$L(g) = \frac{1}{2i}\left[\frac{1}{(g-g_0)-i\Delta_g} - \frac{1}{(g-g_0)+i\Delta_g}\right] ,$$

with two complex poles at $g = g_0 \pm i\Delta_g$. We can average over the heterogeneities by invoking the Cauchy's residue theorem and obtain the Kuramoto-Daido order parameters

$$z_m(t) = \int dg \;\; a_m(g,t) \;\; L(g) = a_m(g_0 - i\Delta_g, t)$$

Fokker-Planck derivation (DA)

By averaging the FPE over the g-distribution, one finds

$$\begin{aligned}
\dot{z}_m &= m\left[(iA_{g_0}+i-\nu\Gamma)z_m+\frac{1}{2}(iA_{g_0}-i-\nu\Gamma)(z_{m-1}+z_{m+1})\right]\\
&- D_{g_0}(1-\frac{i\Delta_g}{g_0})\left[\frac{3m^2}{2}z_m+(m^2-\frac{m}{2})z_{m-1}\right.\\
&+ \left.(m^2+\frac{m}{2})z_{m+1}+\frac{m(m-1)}{4}z_{m-2}+\frac{m(m+1)}{4}z_{m+2}\right]
\end{aligned}$$

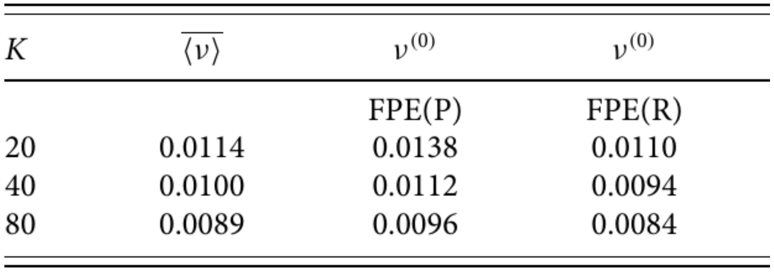
where $A_{g_0}=\sqrt{K}[i_0-g_0\nu(t)]$, $D_{g_0}=g_0^2\nu(t)/2$, $\Gamma=\Delta_0 g_0$

Self Consistent Solution for the Asynchronous Regime

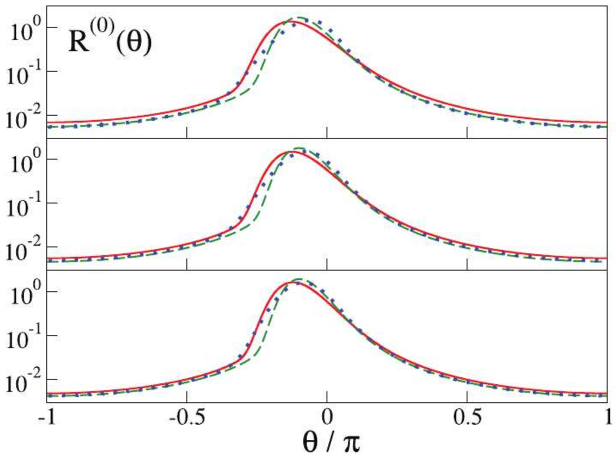
In the Asynchronous Case the firing rate ν is stationary and therefore identical to the flux for any V

$$\nu^{(0)} = [(V^2 + A_{g_0})P_0(V)] - \sigma^2 \partial_V P_0(V)$$

The solution of this self-consistent equation gives an analytic expression for $P_0(V)$ and its normalization ν



K	$\overline{\langle \nu \rangle}$	$\nu^{(0)}$	$\nu^{(0)}$
		FPE(P)	FPE(R)
20	0.0114	0.0138	0.0110
40	0.0100	0.0112	0.0094
80	0.0089	0.0096	0.0084



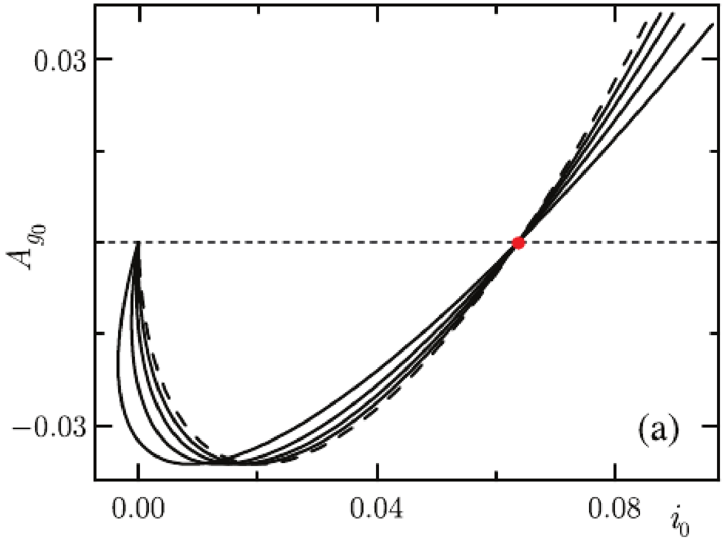
$$V = \tan\left(\frac{\theta}{2}\right) \qquad \theta \in [-\pi, \pi[\qquad 2\cos^2(\theta/2)R^{(0)}(\theta) = P_0(V)$$

Balanced Asynchronous State

The state is balanced if the total input current and the current fluctuations

$$A_{g_0} = \sqrt{K}[i_0 - g_0\nu_0] \qquad \sigma^2 = CV^2 g_0^2 \nu_0$$

remains finite in the limit $K \to \infty$.



For $K \to \infty$

- $\nu_0 = \frac{i_0}{g_0}$ and σ^2 is finite
- the total input stays also finite
  - $i_0 = i^*$ – $A_{g_0} \equiv 0$ – $\forall K$ perfectly balanced
  - $i_0 < i^*$ – $A_{g_0} < 0$ – fluctuation driven
  - $i_0 > i^*$ – $A_{g_0} > 0$ – mean driven

It is commonly believed that in the balanced state the dynamics is fluctuation driven: not true `A. Lerchner et al., Neural Comput (2006)`

Collective Oscillations in the Brain

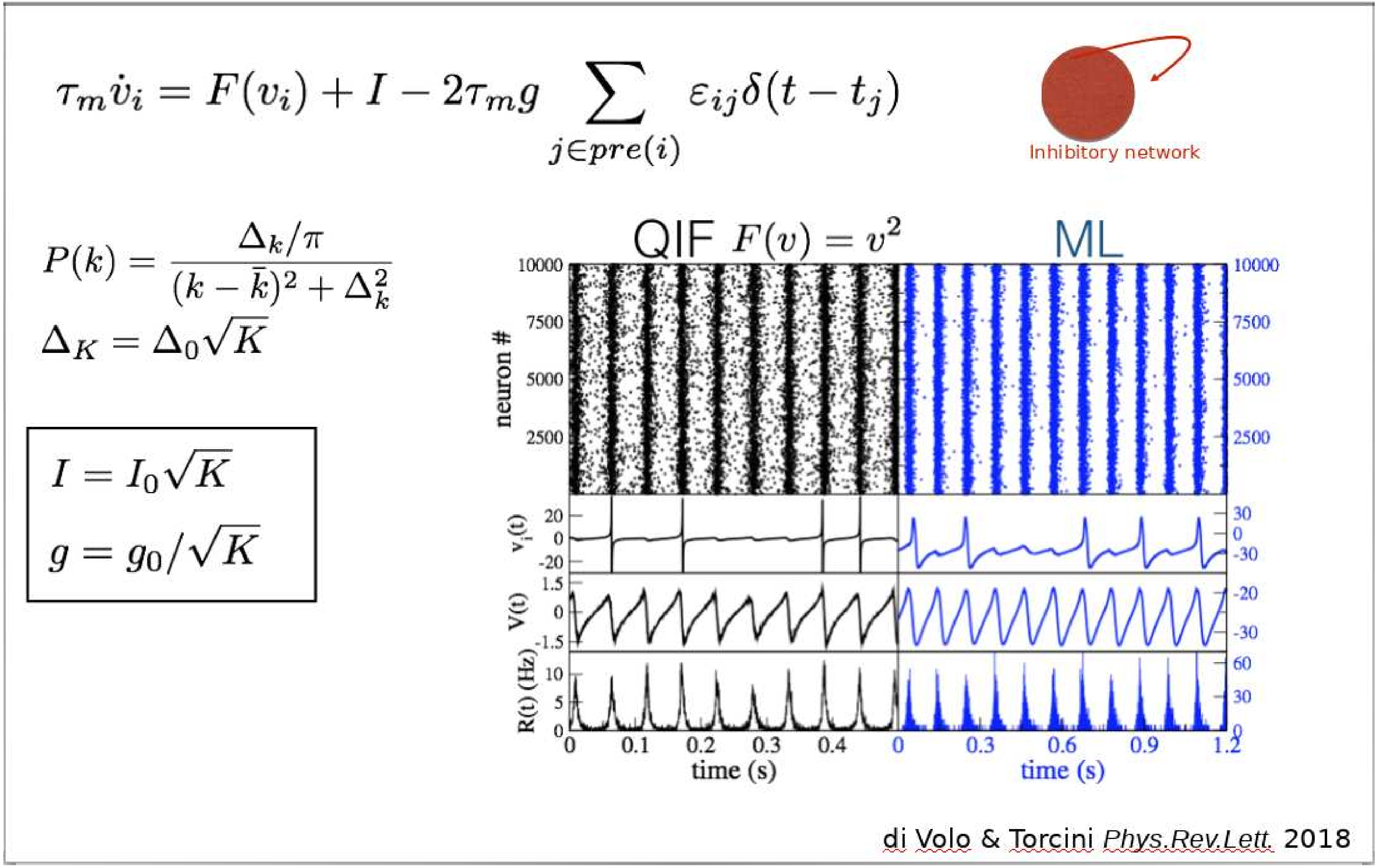
- Collective oscillations (COs) have been observed experimentally over a broad range of frequencies in the cortex
- The neurons fire irregularly with a firing rate ν_0 much lower than those of COs
- In theoretical studies
  - COs emerge in sparse networks due to endogeneous fluctuations via a Hopf bifurcation from an asynchronous state in presence of a synaptic time scale τ_e or transmission delay τ_e
- the COs' frequencies are related to the extra time scale $f_{CO} \simeq 1/(2\tau_e)$

`(Brunel, 2000; Brunel & Hakim, 1999; van Vreeswijk et al., 1994)`

Open Questions:

- How can be the broad range of observed COs' frequencies explained ?
- Which is the role of the neural fluctuations due to balance ?

COs in inhibitory balanced network without an extra time scale



$$\tau_m \dot{v}_i = F(v_i) + I - 2\tau_m g \sum_{j \in pre(i)} \varepsilon_{ij} \delta(t - t_j)$$

$$P(k) = \frac{\Delta_k/\pi}{(k-\bar{k})^2 + \Delta_k^2}$$

$$\Delta_K = \Delta_0 \sqrt{K}$$

$$\boxed{\begin{array}{l} I = I_0 \sqrt{K} \\ g = g_0/\sqrt{K} \end{array}}$$

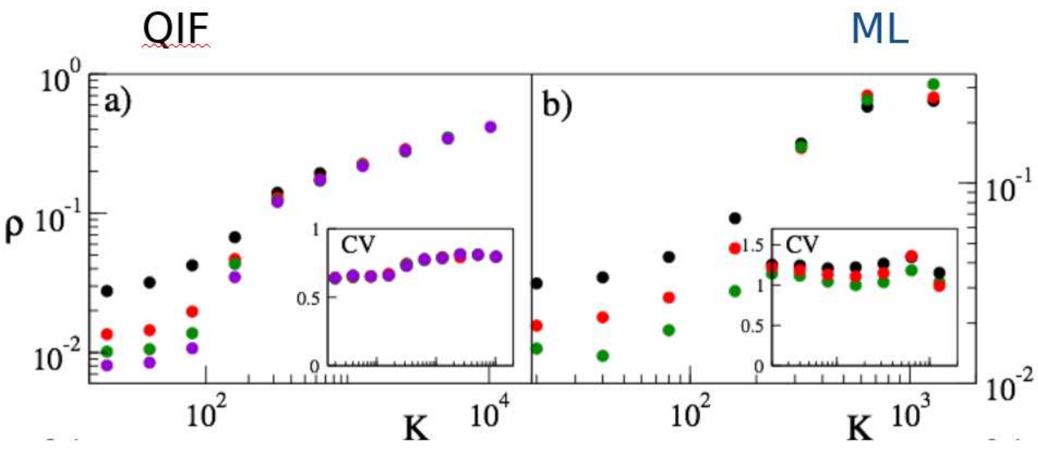
di Volo & Torcini *Phys.Rev.Lett.* 2018

Transition from AS to COs

A typical order parameter to measure the level of synchronization is

$$\rho^2 \equiv \frac{\sigma^2(V)}{\sum_{i=1}^N \sigma^2(v_i)/N} \qquad V = \sum_{i=1}^N \frac{v_i}{N} \ ,$$

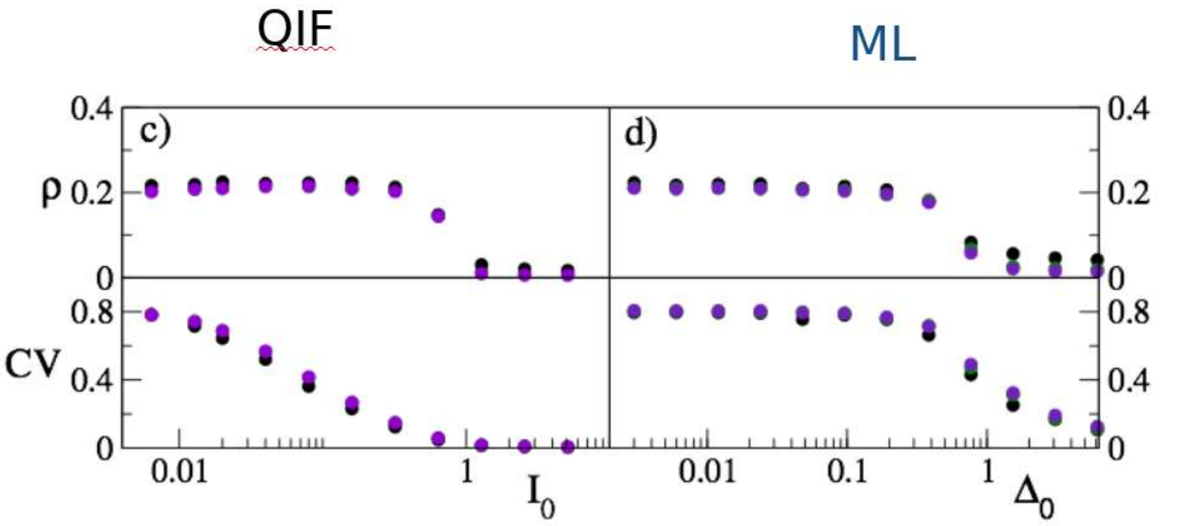
- Perfect synchronization $\rho = 1$ — Asynchronous state (AS) $\rho = 1/\sqrt{N}$



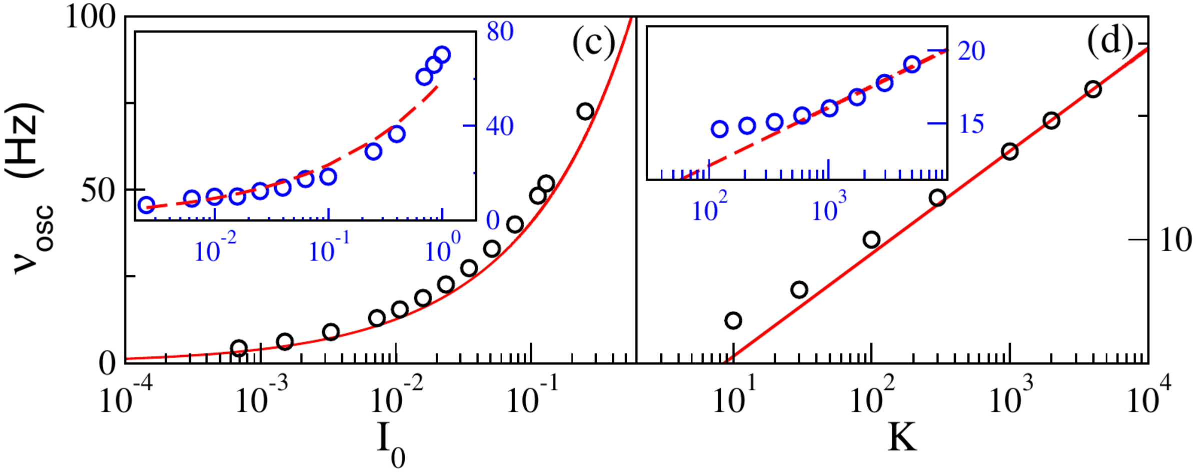
- By increasing K we have a clear transition from AS to COs
- The microscopic dynamics is always irregular $CV \simeq 0.8$

Role of neural fluctuations

Range of COs frequencies



Neural fluctuations, due to balance, are necessary to observe collective oscillations

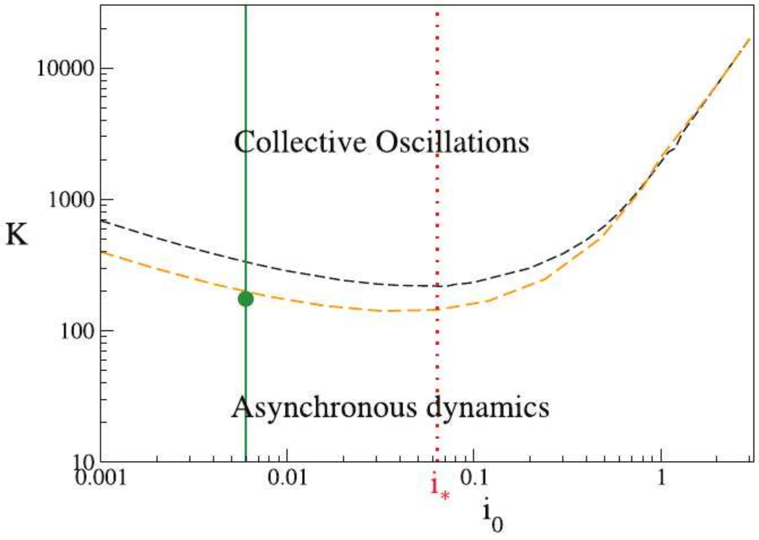


Frequencies of the COs can range over a wide interval $\nu_{osc} \propto (i_0)^{1/2} K^{1/4}$

Phase diagram of the homogeneous case

A phase diagram in the plane (i_0, K) for the homogeneous case can be obtained within the Fokker-Planck formulation:

- a super-critical Hopf bifurcation line leads from asynchronous dynamics to collective oscillations
- a reasonable good agreement with direct simulations is observable



- Black dashed line : Poisson approximation
- Orange dashed line : renewal approximation with $CV = 0.8$
- green dot : network simulations

Homogeneous Case

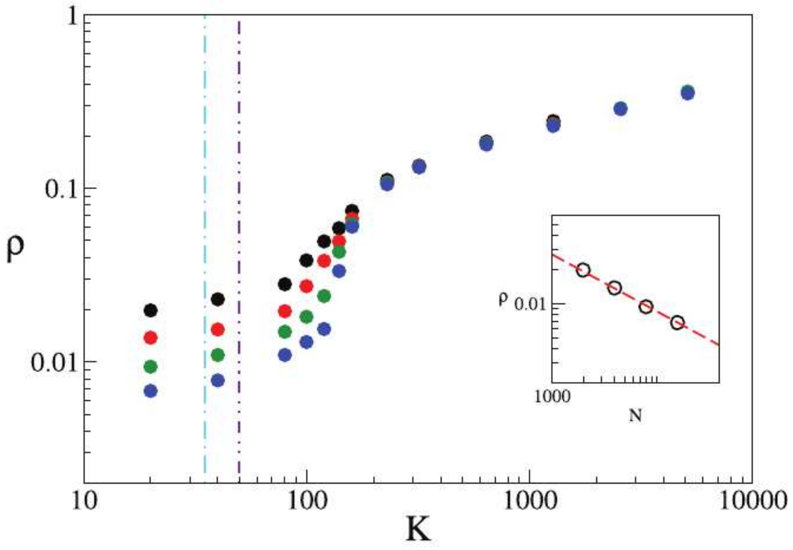


FIG. 10. Order parameter ρ vs the in-degree K for different network sizes: $N = 2000$ (black circles), 4000 (red circles), 8000 (green circles), and 16 000 (blue circles). The two-dotted–dashed vertical violet (dotted–dashed cyan) line indicates K^{HB} (K^{SN}) for the sub-critical Hopf (saddle node) bifurcation point obtained within the 2CC approximation. The inset reports the scaling of ρ vs N for $K = 20$, and the red dashed line corresponds to a power law $N^{-1/2}$. Parameters as in Fig. 7.

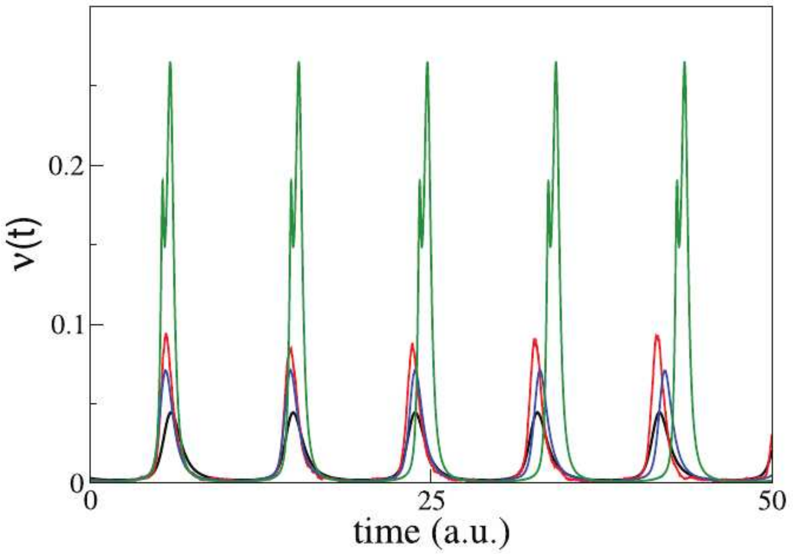


FIG. 11. Instantaneous firing rate $\nu(t)$ vs time. The data refer to network simulations with $N = 16\,000$ (red line), to MF solutions obtained by truncating the FPE to $M = 64$ modes for the Poissonian noise (black line) or the renewal approximation with $CV = 0.8$ (blue line), as well as to the 2CC approximation (green line). Parameters as in Fig. 7 and $K = 640$.

Nature of the Oscillatory Regime

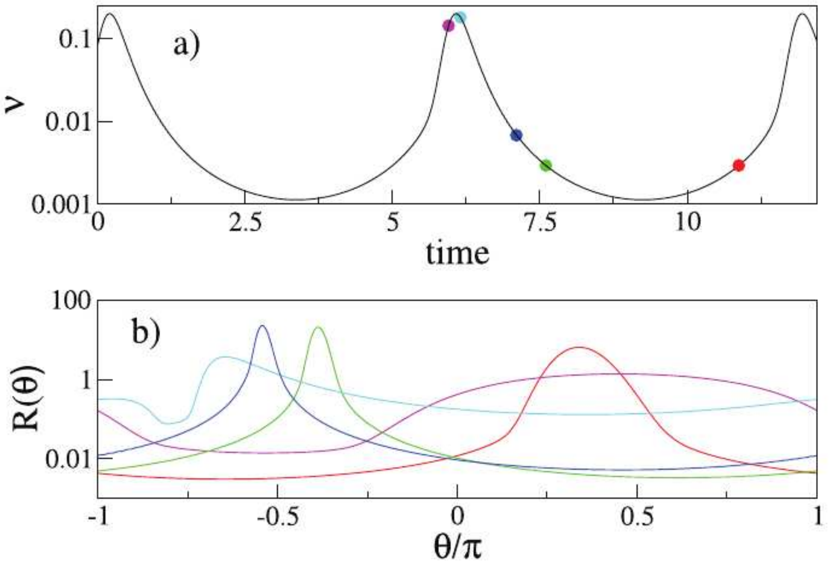
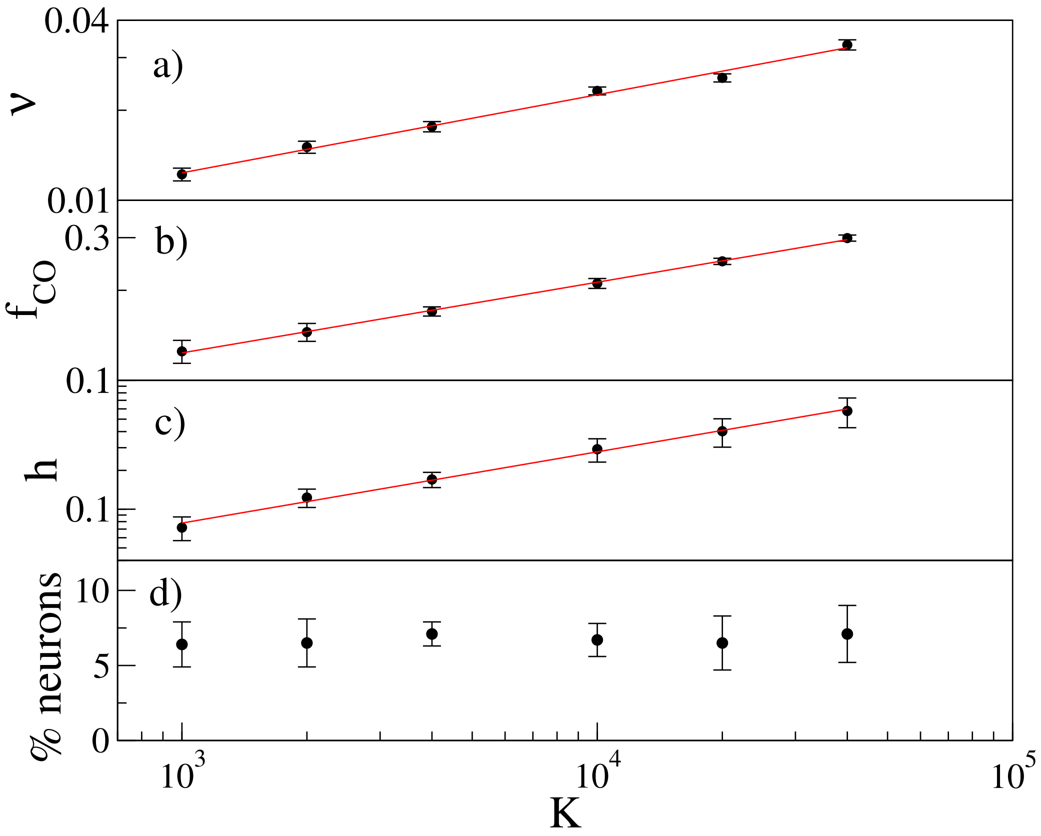


FIG. 13. In panel (a), we show the firing rate ν in time estimated from the FPE truncated at $M = 128$ by estimating the current fluctuations within the Poisson approximation [Eq. (10)]. In panel (b), we report the PDFs $R(\theta)$ vs the angle θ at different times (see the corresponding dots in the top panel). Parameters: $i_0 = 0.006$, $g_0 = 1$, $K = 4000$, and $\Delta_0 = 0$.

- Almost silent intervals alternate to short bursts of activity (log scale)
- The bursts are not related to a synchronous activity
- Just before the burst the PDF of the membrane potentials is very broad (magenta line) (log scale)
- The narrow peak is a consequence of an increasingly fast dynamics due to the fact that many membrane potentials (7 %) find themselves in a region where their “velocity” is very large just before the threshold

Nature of the Oscillatory Regime



The average firing rate $< \nu > \simeq N_p * f_{CO}$, where the number of neuron in the burst N_p is independent by K, therefore $< \nu >$ scales as $f_{CO} \propto K^{1/4}$

Mean field for a heterogeneous network

In the mean field hypothesis the synaptic currents can be approximated as

$$I_i^{syn} = \frac{g_0}{\sqrt{K}} \sum_{j \in pre(i)} \varepsilon_{ij} \delta(t - t^{(j)}) \simeq \frac{g_0}{\sqrt{K}} k_i R = g_i R$$

where the in-degrees k_i are Lorentzian distributed with median K and HWHM $\Delta_K = \Delta_0 \sqrt{K}$.

We can consider the neurons as fully coupled but but with random values of the coupling g_i distributed as a Lorentzian with

- Median $\bar{g} = -g_0 \sqrt{K}$ and HWHM $\Gamma = g_0 \Delta_0$

By employing the residues' theorem we can take into account exacly of the Lorentzian distribution of the heterogeneities and end up in a Fokker-Planck formulation analogous to that for the homogeneous case

See `I. Ratas and K. Pyragas, Phys. Rev. E (2019)` for an analogous approach for a globally coupled heterogeneous QIF network with additive Gaussian noise

Heterogeneous Network

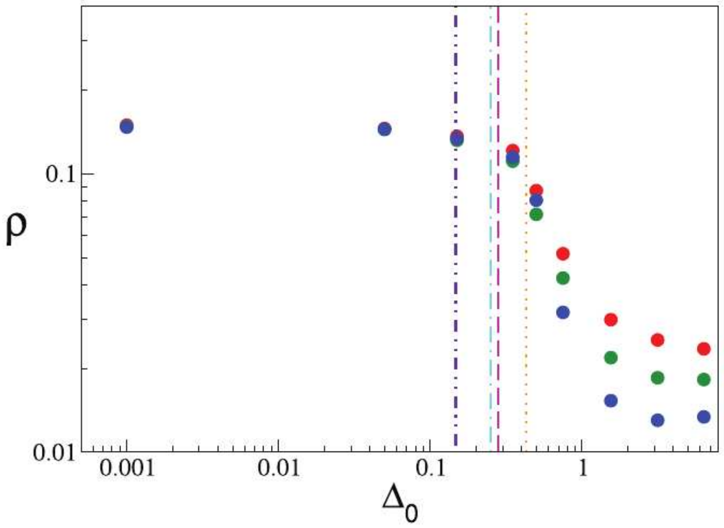


FIG. 14. Heterogeneous model: order parameter ρ vs Δ_0. Symbols refer to direct simulations of the network for different sizes: $N = 4000$ (red), 8000 (green), and 16 000 (blue). The vertical magenta dashed (orange dotted) line denotes Δ_0^{HB} corresponding to the super-critical Hopf bifurcation identified from the analysis of the FPE truncated to $M = 64$ within a Poissonian (renewal) approximation where the amplitude of the current fluctuations is given by Eq. (10) [Eq. (11) with $CV = 0.8$]. The vertical violet two-dotted–dashed (cyan dotted–dashed) line indicates Δ_0^{HB} (Δ_0^{SN}) for the sub-critical Hopf (saddle node) bifurcation point as obtained within the 2CC approximation. The data have also been averaged over 20 different network realizations. Other parameters: $K = 400$, $i_0 = 0.006$, $g_0 = 1$.

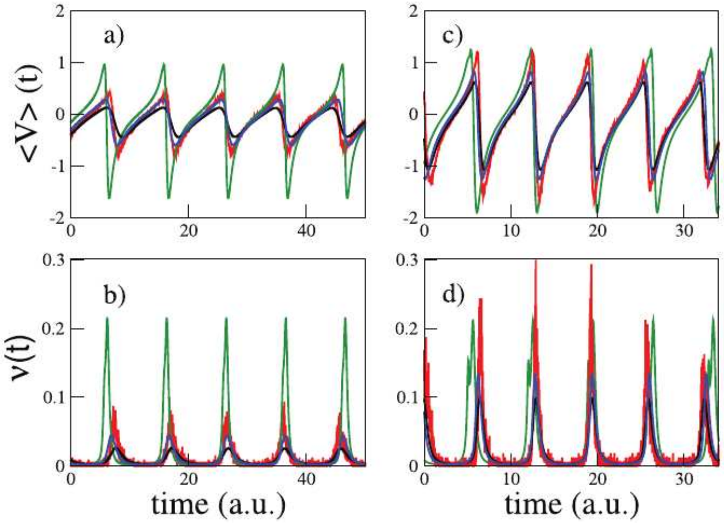


FIG. 16. Time traces of the mean membrane potential $v(t)$ [panels (a) and (c)] and of the firing rate ν [panels (b) and (d)]. The parameters (K, i_0) are $(500, 0.006)$ in (a) and (b) and $(1000, 0.01)$ in (c) and (d). The red lines always refer to direct simulations for $N = 16\,000$ (red line). Black (blue) lines correspond to the integration of the FPE, truncated after $M = 64$ Fourier modes for a Poissonian noise (renewal noise with $CV = 0.8$). Finally, green lines correspond to the 2CC approximation. The structural heterogeneity is $\Delta_0 = 0.1$.

Ott-Antonsen Approach

If one neglects fluctuations (i.e. setting $D_{g_0} = 0$), the Ott-Antonsen (OA) manifold $z_m = (z_1)^m$ is invariant and attractive, and the FPE reduces to

$$2\dot{z}_1 = (iA_{g_0} - \nu\Gamma)[1 + z_1]^2 - i[1 - z_1]^2$$

where

$$z_1 = \frac{1 - W^*}{1 + W^*} \quad \text{with} \quad W = \pi\nu + i\upsilon$$

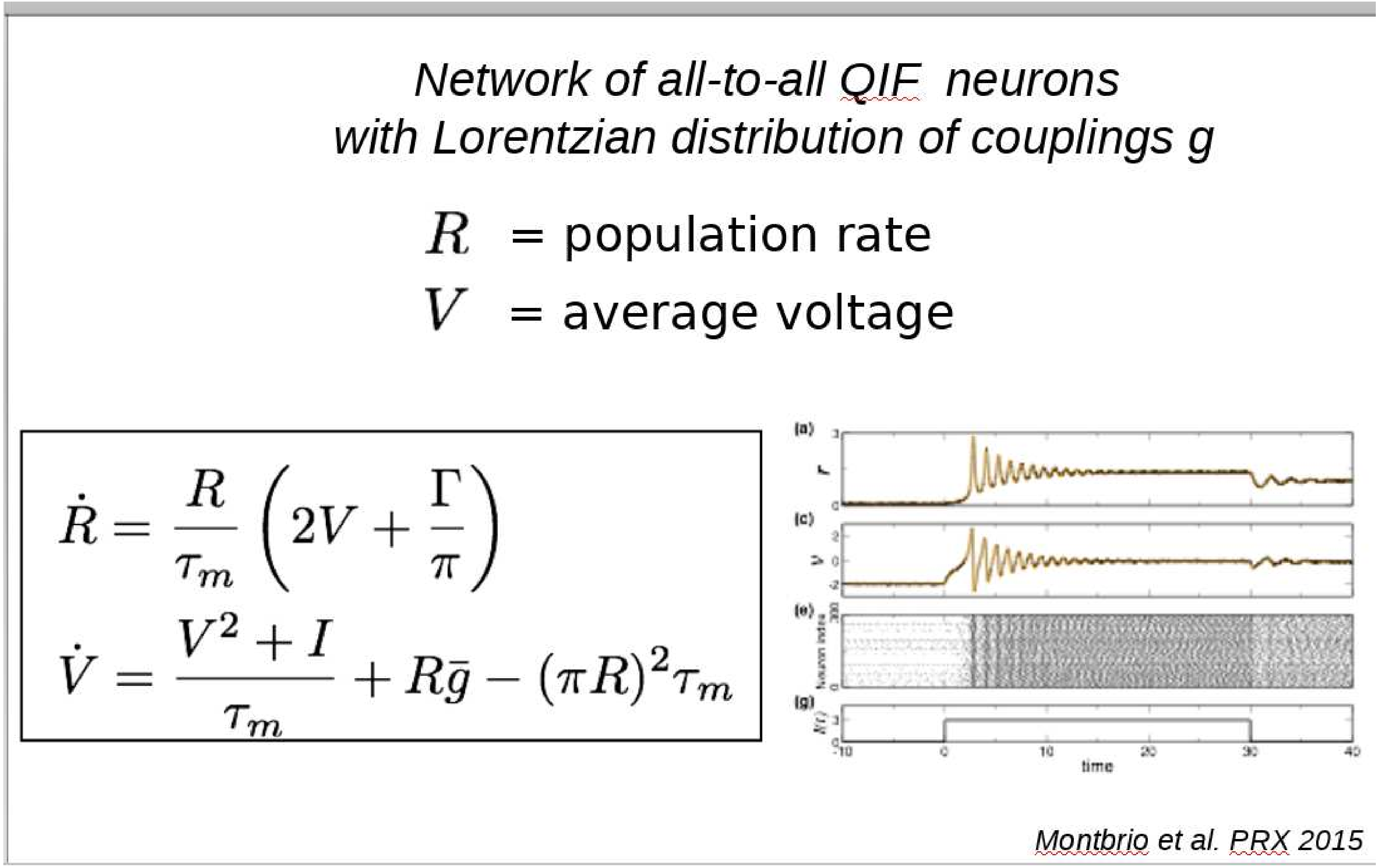
The application of this transformation leads to the two following ODEs for $\upsilon(t)$ and $\nu(t)$:

$$\dot{\nu} = \nu(2\upsilon + \Gamma/\pi) \;\; ; \;\; \dot{\upsilon} = \upsilon^2 + \sqrt{K}(i_0 - g_0\nu) - (\pi\nu)^2$$

This reduced mean field model has been studied in `diVolo, Torcini PRL (2018)` and it does not give rise to collective oscillations

`Ott, E., & Antonsen, T. M., Chaos (2009)`

Exact mean field model



Network of all-to-all QIF neurons
with Lorentzian distribution of couplings g

R = population rate
V = average voltage

$$\dot{R} = \frac{R}{\tau_m}\left(2V + \frac{\Gamma}{\pi}\right)$$
$$\dot{V} = \frac{V^2 + I}{\tau_m} + R\bar{g} - (\pi R)^2 \tau_m$$

Montbrio et al. PRX 2015

Mean field for a sparse network

In the mean field hypothesis the synaptic currents can be approximated as

$$I_i^{syn} = \frac{g_0}{\sqrt{K}} \sum_{j \in pre(i)} \varepsilon_{ij} \delta(t - t^{(j)}) \simeq \frac{g_0}{\sqrt{K}} k_i R = g_i R$$

where the in-degrees k_i are Lorentzian distributed with median K and HWHM $\Delta_K = \Delta_0 \sqrt{K}$.

We can consider the neurons as fully coupled but but with random values of the coupling g_i distributed as a Lorentzian with

- Median $\bar{g} = -g_0 \sqrt{K}$ and HWHM $\Gamma = g_0 \Delta_0$

Therefore the mean field (MF) for the random network can be written as

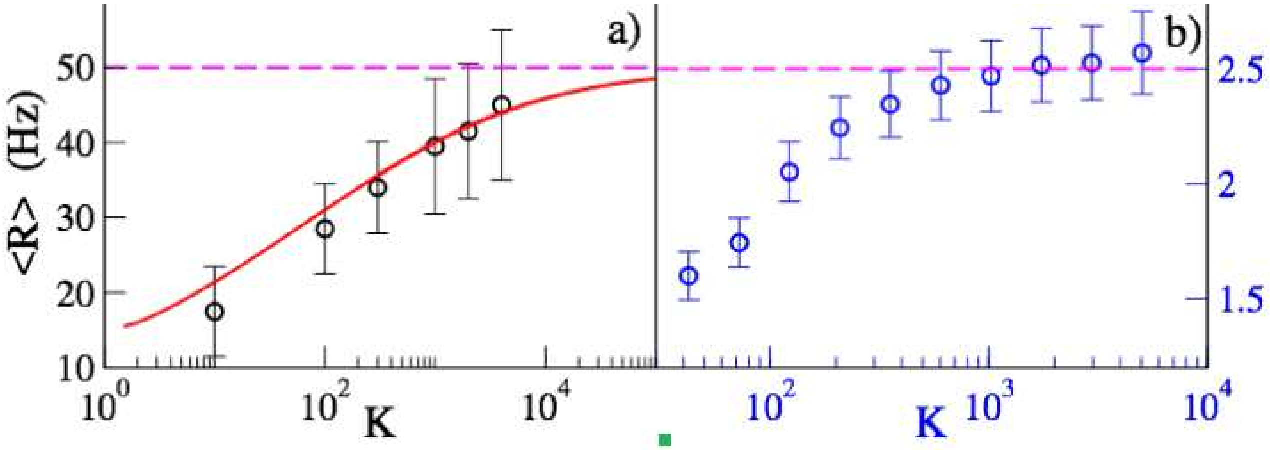
$$\tau_m \dot{R} = R(2V + \frac{g_0 \Delta_0}{\pi})$$

$$\tau_m \dot{V} = V^2 + \sqrt{K}(I_0 - \tau_m g_0 R) - (\pi R \tau_m)^2 \quad .$$

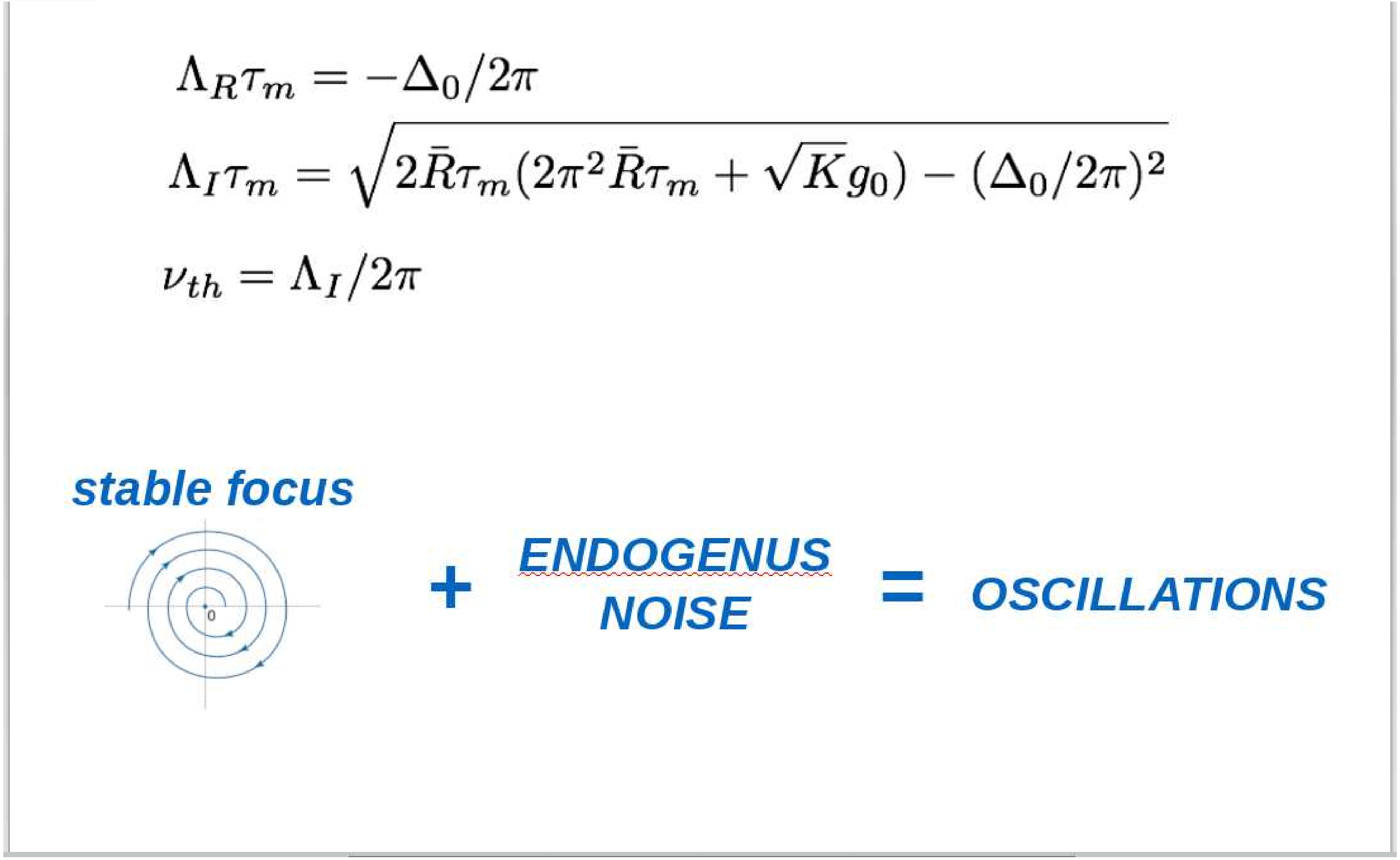
Asynchronous Dynamics

The MF dynamics has as stationary state a fixed point solution $(\bar{V}, \bar{R})$:

- $\bar{V} = (-g_0\Delta_0)/(2\pi)$
- $\bar{R}\tau_m = \frac{g_0\sqrt{K}}{2\pi^2}\left(\sqrt{1+\frac{4\pi^2}{\sqrt{K}}\frac{I_0}{g_0^2}+\frac{\Delta_0^2}{K}}-1\right) \to \frac{I_0}{g_0}$



Linear Stability Analysis



$$\Lambda_R \tau_m = -\Delta_0/2\pi$$

$$\Lambda_I \tau_m = \sqrt{2\bar{R}\tau_m(2\pi^2\bar{R}\tau_m + \sqrt{K}g_0) - (\Delta_0/2\pi)^2}$$

$$\nu_{th} = \Lambda_I/2\pi$$

stable focus

+ ENDOGENUS NOISE = OSCILLATIONS

Circular Cumulants

In presence of weak noise a possible approach to go beyond the Ott-Antonsen Ansatz consists in circular cumulants (CCs) $\{\kappa_m\}$.

- Transfom QIF model in θ-model via the nonlinear transformation $V_i = \tan\left(\frac{\theta_i}{2}\right)$ with $\theta_i \in [-\pi, \pi]$;
- Write the FPE in Fourier space for a network in presence of extrinsic or intrinsic noise fluctuations;
- The FPE in Fourier consists of evolution equations involving the moments $\{Z_n\}$ of the observable $\mathrm{e}^{i\theta}$ that are the Kuramoto-Daido order parameters.
- The CCs are the cumulants associated to the moments $\{Z_n\}$

I.V. Tyulkina, D.S. Goldobin, L.S. Klimenko, A. Pikovsky PRL (2018) have shown that a truncations in terms of few CCs is able to describe the system dynamics in presence of noise, the truncation in terms of CCs is much more effective that in terms of Kuramoto-Daido order parameters.

Circular Cumulants

We have applied the CCs approach to homogeneous and heterogeneous balanced sparse QIF networks : M. di Volo, M. Segneri, D.S. Goldobin, A. Politi, AT Chaos (2022)
We observed that

- even 2 CCs are sufficient to capture the emergence of COs via a Hopf bifurcation for homogeneous and heterogeneous cases;
- the 2 CCs are not able to well reproduce the mean field variables (r, v) and the nature of the bifurcation;
- The evolution equations of the CCs are quite complicated to treat because by increasing the order of the expansion (e.g. from 2 to 3 CCs):
  - all the evolution equations are modified ;
  - even the definitions of the firing rate and of the mean membrane potential are modified.

Circular Cumulants

The 2CC approximation for the FPE (27) [correct up to order $o(D_{g0})$] reads as

$$\dot{z}_1 = z_1(iA_{g_0} + i - \Gamma\nu) + H(1 + \kappa_2 + z_1^2) - \frac{D_{g_0}}{2}\left(1 - i\frac{\Delta_g}{g_0}\right)(1 + z_1)^3, \quad (38)$$

$$\dot{\kappa}_2 = 2(iA_{g_0} + i - \Gamma\nu)\kappa_2 + 4Hz_1\kappa_2 - D_{g_0}\left(1 - i\frac{\Delta_g}{g_0}\right) \times \left(\frac{1}{2}(1 + z_1)^4 + 6(1 + z_1)^2\kappa_2\right), \quad (39)$$

where

$$H = \frac{1}{2}\left[i(A_{g_0} - 1) - \Gamma\nu\right].$$

The firing rate ν and the mean membrane potential v can be obtained from Eq. (28) by restricting the sum to the first two CCs,

$$W^* = \pi\nu - iv = \frac{1 - z_1}{1 + z_1} + \frac{2\kappa_2}{(1 + z_1)^3}; \quad (40)$$

this is a generalization of the conformal transformation (30) to a situation where the OA ansatz is no longer valid.

Circular Cumulants: homogeneous

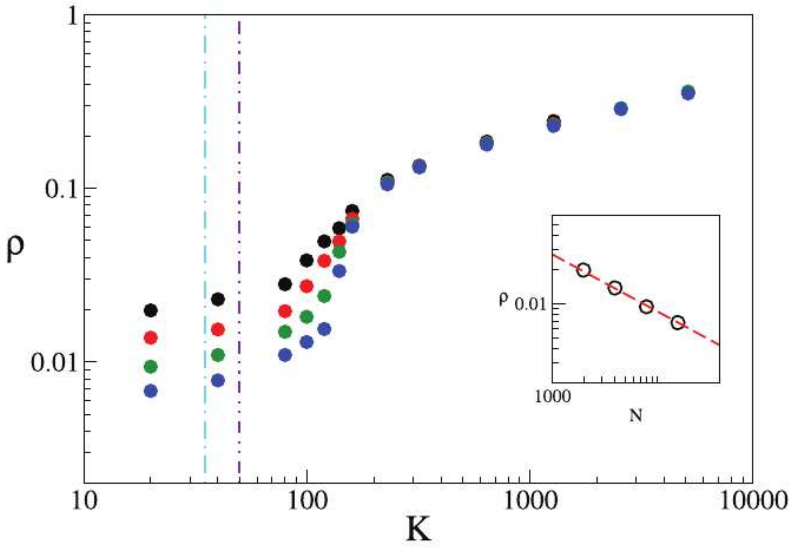
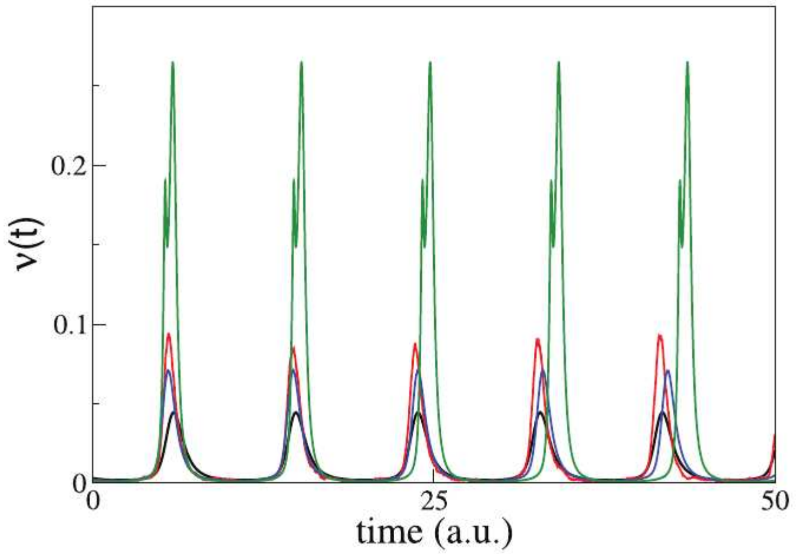


FIG. 10. Order parameter ρ vs the in-degree K for different network sizes: $N = 2000$ (black circles), 4000 (red circles), 8000 (green circles), and 16 000 (blue circles). The two-dotted–dashed vertical violet (dotted–dashed cyan) line indicates K^{HB} (K^{SN}) for the sub-critical Hopf (saddle node) bifurcation point obtained within the 2CC approximation. The inset reports the scaling of ρ vs N for $K = 20$, and the red dashed line corresponds to a power law $N^{-1/2}$. Parameters as in Fig. 7.



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Circular Cumulants: heterogeneous

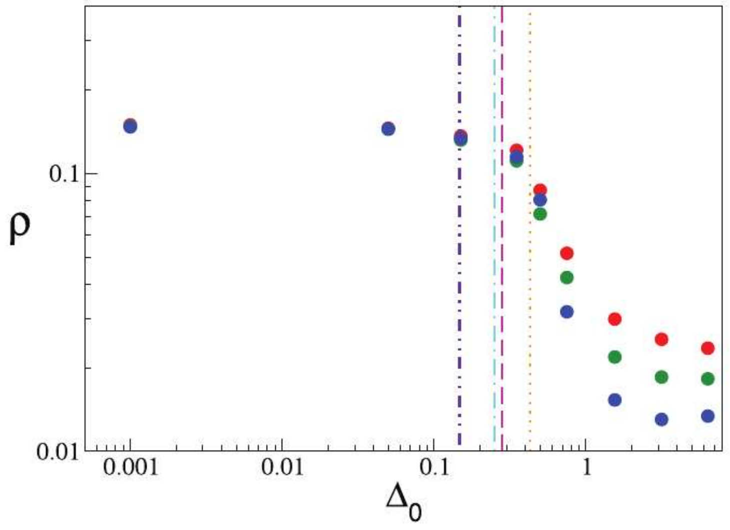


FIG. 14. Heterogeneous model: order parameter ρ vs Δ_0. Symbols refer to direct simulations of the network for different sizes: $N = 4000$ (red), 8000 (green), and 16 000 (blue). The vertical magenta dashed (orange dotted) line denotes Δ_0^{HB} corresponding to the super-critical Hopf bifurcation identified from the analysis of the FPE truncated to $M = 64$ within a Poissonian (renewal) approximation where the amplitude of the current fluctuations is given by Eq. (10) [Eq. (11) with $CV = 0.8$]. The vertical violet two-dotted–dashed (cyan dotted–dashed) line indicates Δ_0^{HB} (Δ_0^{SN}) for the sub-critical Hopf (saddle node) bifurcation point as obtained within the 2CC approximation. The data have also been averaged over 20 different network realizations. Other parameters: $K = 400$, $i_0 = 0.006$, $g_0 = 1$.

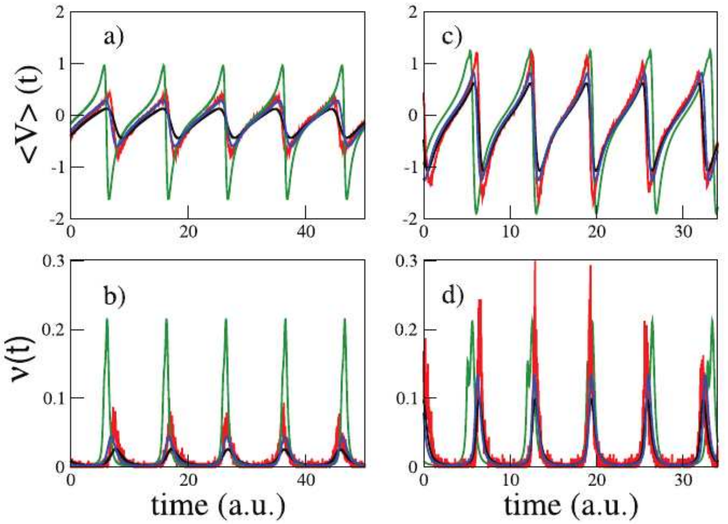
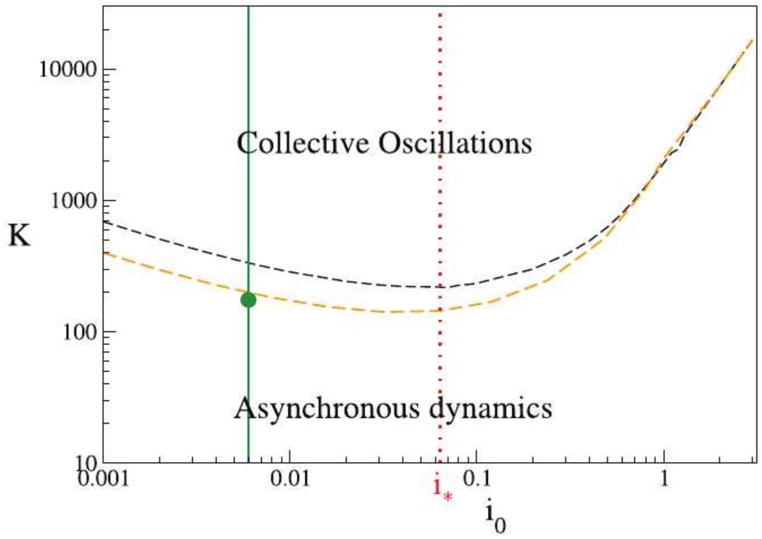
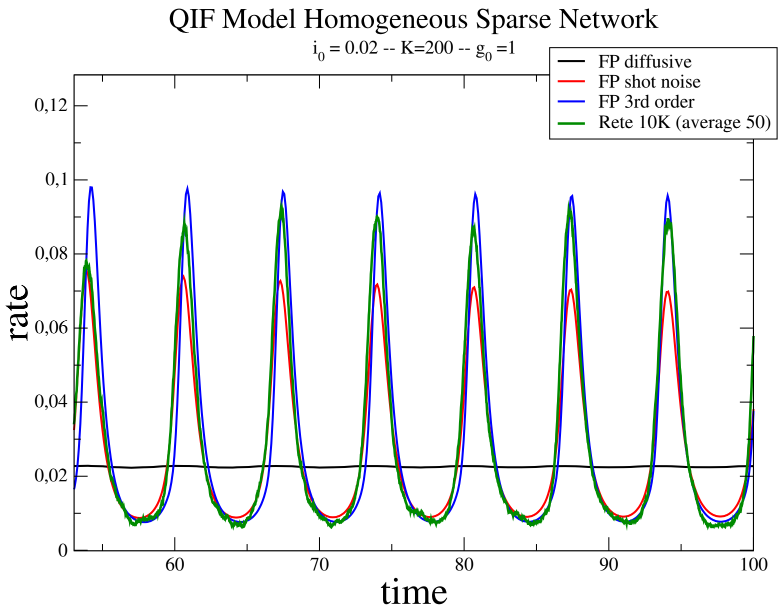


FIG. 16. Time traces of the mean membrane potential $v(t)$ [panels (a) and (c)] and of the firing rate ν [panels (b) and (d)]. The parameters (K, i_0) are $(500, 0.006)$ in (a) and (b) and $(1000, 0.01)$ in (c) and (d). The red lines always refer to direct simulations for $N = 16\,000$ (red line). Black (blue) lines correspond to the integration of the FPE, truncated after $M = 64$ Fourier modes for a Poissonian noise (renewal noise with $CV = 0.8$). Finally, green lines correspond to the 2CC approximation. The structural heterogeneity is $\Delta_0 = 0.1$.

Diffusive versus Shot Noise

The nature of the noise can change the collective dynamics of the network




QIF Model Homogeneous Sparse Network

i_0 = 0.02 -- K=200 -- g_0 =1

`Goldobin, di Volo & AT, in preparation`

Brunel-Hakim explanation for COs

- purely inhibitory spiking network
- a system with current fluctuations of amplitude σ
- the spikes are transmitted with a synaptic delay τ_e

The explanation if the following:

- 1) a fluctuation leads to an increase of the input current δI and of the the firing rate of the inhibitory neurons of δR
- 2) after a delay τ_e the input current is reduced by $-J\delta R$ and so the firing rate of the inhibitory neurons
- 3) after another delay τ_e the input current increases due to the reduction of the firing rate, and the process repeats

The period of COs $T_{CO} \simeq 2\tau_e$, to have a frequency $f_{CO} \simeq 50$ Hz, I should consider a delay of order $\tau_e \simeq 10$ ms