Emergence of collective behaviours in neuronal networks

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Consiglio Nazionale Ricerche

La recherche va a mourir

Area della Ricerca CNR - Polo Scientifico - Sesto Fiorentino - Firenze

Istituto dei Sistemi Complessi

- ISC has been recently created (2004-2005) within the CNR in Rome and Firenze, the actual director is prof. Luciano Pietronero.
- The staff is composed by 60 permanent employees and 40 students, PhD and post-doc researchers.
- The main part of researchers are physicists.

Dynamical System Group in Firenze

- Nonlinear dynamics of complex systems (e.g. models of proteins, heat conduction, computational neuroscience) (modelization)
- Micromanipulation of biomolecules, cellular membranes, etc (Atomic Force Microscope) (experiments)
- Nonlinear data analysis of experimental data (EEG and in vitro measurements)
- Synchronization of chaotic systems composed by many elements (theory)
- Nonlinear optics of coupled lasers (experiments)

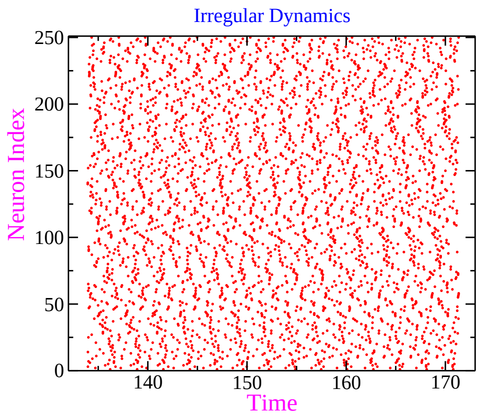
Comp. Neuroscience at ISC

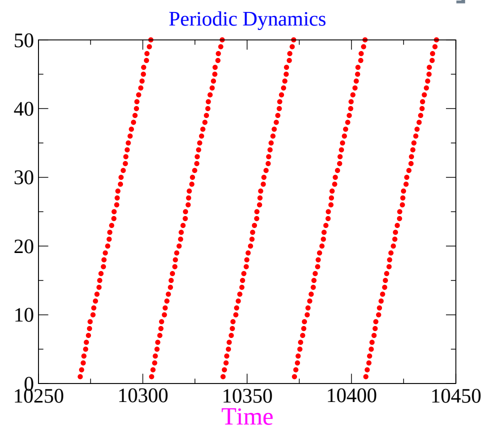
- Response of simple neuronal models subject to trains of uncorrelated and correlated post-synaptic potentials [T. Kreuz - S. Luccioli]
  - Hodgkin-Huxley Model – Phys. Rev. E 73 (2006) 041902
  - FitzHugh-Nagumo Model – Phys. Rev. Lett. 97 (2006) 238101
- Hindmarsh-Rose Model: from bursting to spiking chaos – Chaos 17 (2007) 043128 [G. Innocenti - A. Morelli - R. Genesio]
- Response of a rat stellate cell *in vitro* subject to periodic and irregular spike trains [J. Haas - T. Kreuz - DHI Abarbanel - A. Politi]
  - Recordings from single cells (Enthorinal Cortex layer II neurons) in cortical slices subject to a constant DC current plus excitatory conductance inputs delivered via dynamic clamp;
  - Nonlinear data analysis of the stellate cell response – a new distance to assess similarity between input and output spike trains – [T. Kreuz et al., Journal of Neuroscience Methods (2007)];
  - Once sorted the output spikes in forced, delayed and natural, a simple probabilistic model (without memory of the past emitted spike) is able to reproduce the response of the stellate cell in these conditions.

Comp. Neuroscience at ISC

Dynamics of Neuronal Networks

[M. Calamai, S. Luccioli, S. Olmi, A. Politi, R. Livi, R. Zillmer]

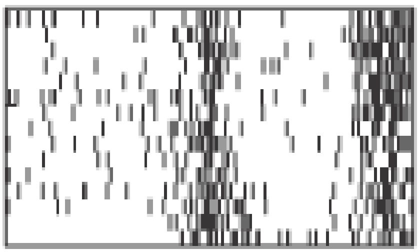


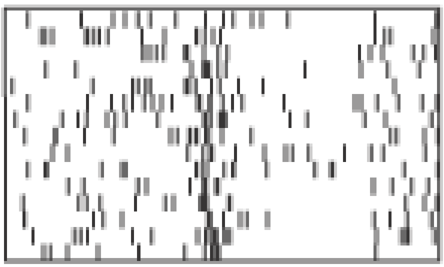


- Single neuronal model: leaky integrate-and-fire (LIF)
- Globally pulse coupled networks
  - Stability of splay states for LIF – Phys. Rev. E 76 (2007) 046102
  - Stability of splay states for generic neuronal model – arXiv:0903.1867 - 2009
- Diluted (broken connections) inhibitory networks
  - Long irregular transients ($\sim \exp^{\alpha N}$) – Phys. Rev. E 74 (2006) 036203
  - Networks with time delays
    [M. Timme (Göttingen)] – Frontiers in Comp. Neuroscience (2009)
    [N. Brunel - D. Hansel (Paris)] – PRE 79, 031909 (2009)

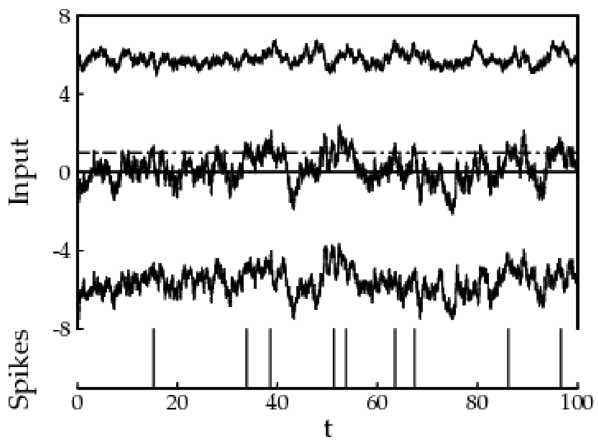
A possible paradox

- Cortical neurons in vivo emit spike trains that are highly irregular during spontaneous as well as evoked periods of activity;
- Neurons in vitro stimulated with weakly noisy current emit nearly periodic spike trains;
- Anatomy suggests a possible paradox : cortical neurons are connected to thousands of afferent synapses
  - By supposing a large number of uncorrelated (or weakly correlated) presynaptic inputs K.
  - The total postsynaptic current I will be proportional to $\propto K$;
  - The fluctuations in the current should be $\propto I/\sqrt{K}$;
  - This seems to be in contradiction with the emergence of irregular dynamics.
- How to solve this paradox ?





The Balanced State



A possible explanation of the mechanism leading to large variability in the cortical networks is to assume that excitatory and inhibitory inputs nearly balance: their fluctuations are small compared to the mean excitatory (resp. inhibitory) current, but are large with respect to the net postsynaptic current.

The neural firing is therefore driven by fluctuations instead than by the average input and is quite irregular.

The question if this behaviour is chaotic or not has not been adressed in details, some indication suggests that indeed is chaotic.

C. van Vreeswijk - H. Sompolinsky - Science 274 (1996) 1724 - 1726

Questions to address

Chaos in a Nutshell

Chaos implies that, even in absence of noise, two initial configurations that differ even for an infinitesimal amount will become first or late completely different:

this means that the effect of a minimal fluctuation will be to modify completetely the firing pattern

- Is it chaos really needed to explain irregular spiking in the brain ?
- Is it really necessary to have a dynamical balance of excitatory and inhibitory inputs to observe erratic discharges ?

We propose a different mechanism for erratic behaviours:

- In neuronal networks with predominant inhibition
- Not chaotic
- Robust to noise

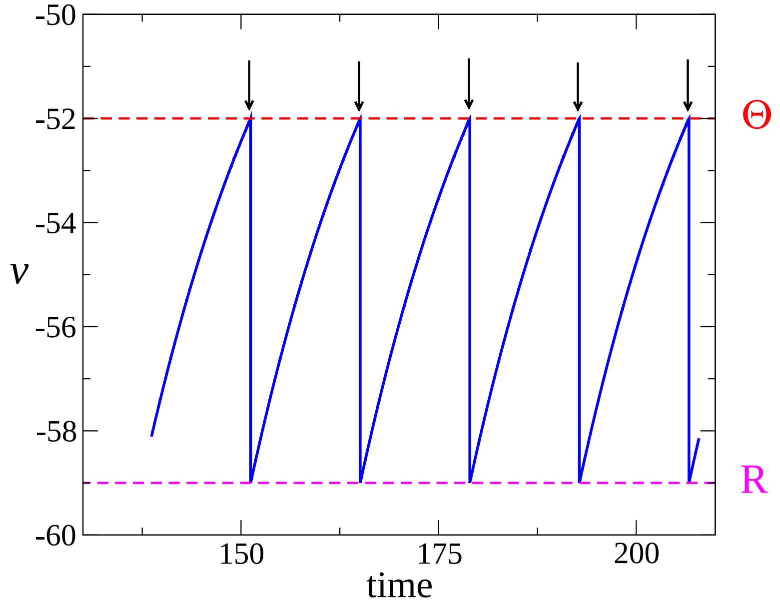
Leaky integrate-and-fire model

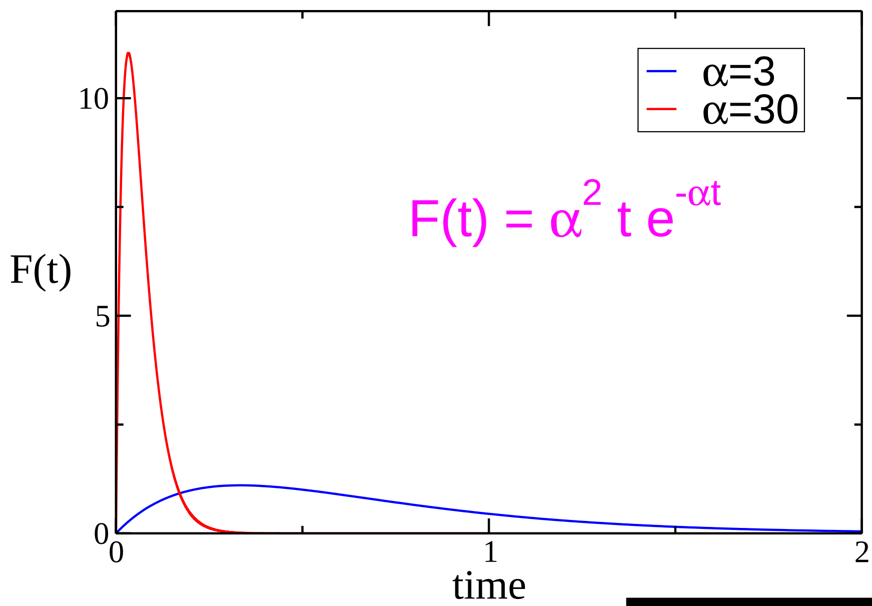
- Linear integration combined with **reset** = formal spike event
- Equation for the membrane potential v , with threshold Θ and reset R :

$$\tau\,\dot{v} \;=\; -(v - v_{\rm r}) + I$$

  - If $I + v_r > \Theta$ Repetitive Firing
  - If $I + v_r < \Theta$ Silent Neuron

- In networks: at reset a pulse is sent to other neurons





Pulse coupled network

System of N identical all to all pulse-coupled neurons:

$$\dot{v}_j = I - v_j + \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{g}{N} (v_j + E)\, \delta(t - t_i^{(k)})\,, \quad v \in [R, \Theta]$$

- the membrane potentials displays only regular solutions: periodic or quasi-periodic

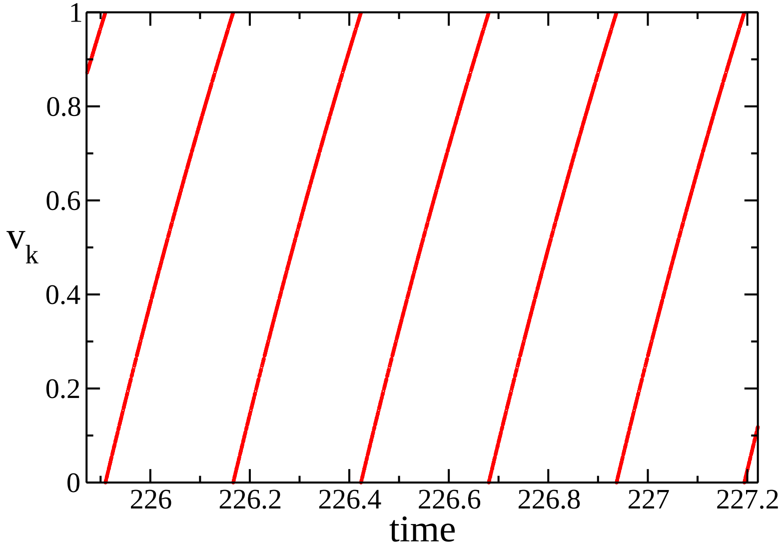
Depending on the shape of the pulse (value of α) :

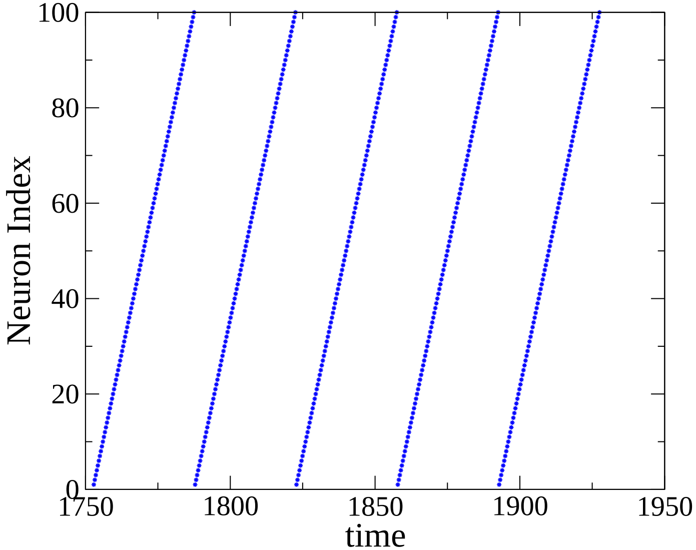
- Excitatory Coupling - $g > 0$
  - Low α – Splay State
  - Larger α – Partially Synchronized State
  - $\alpha \to \infty$ – Fully Synchronized State
- Inhibitory Coupling - $g < 0$
  - Low α – Fully Synchronized State
  - Larger α – Several Synchronized Clusters
  - $\alpha \to \infty$ – Splay State

Splay State

Splay States are collective solutions emerging in Homogeneous Networks of N neurons

- the dynamics of each neuron is periodic
- the interspike time interval (ISI) of each neuron is T
- the ISI of the newtork is T/N - constant firing rate
- the dynamics of the network is Asynchronous



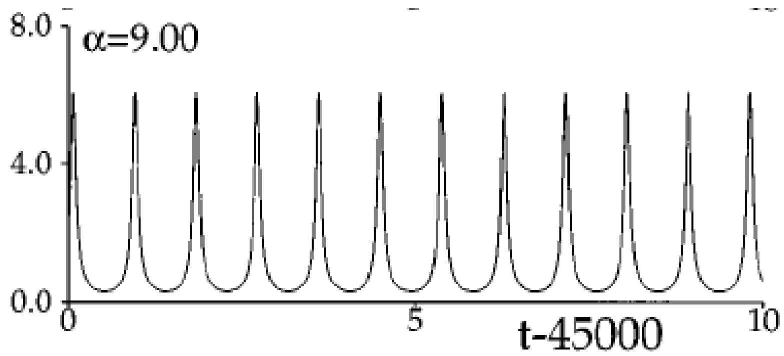


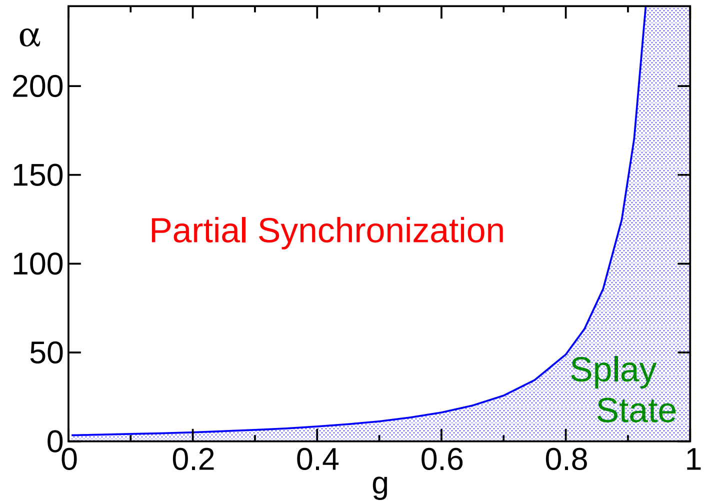
Abbott - van Vreeswiijk, PRE (1993) -- Zillmer et al. PRE (2007)

Partially Synchronized State

Partial Synchronization is a collective dynamics emerging in Excitatory Homogeneous Networks for sufficiently narrow pulses

- the dynamics of each neuron is quasi periodic - two frequencies
- the firing rate of the network is periodic





van Vreeswiijk, PRE (1996) - Mohanty Politi Europhys. Lett (2006)

Diluted Networks

$$\dot{v}_j = I - v_j + \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{g}{N} \epsilon_{ji} (v_j + E)\, \delta(t - t_i^{(k)}) \,, \quad v \in [R, \Theta]$$

Links are cut with given probability $P \rightarrow \epsilon_{ji} = 1, 0$

- Excitatory Coupling and Finite Pulse Width - $g > 0$
- Splay States and Partial Synchronization are still observable
- For finite N they show some fluctuation and they are chaotic
- For infinite N they converge to the states observed for fully coupled systems, but with reduced coupling $g_{eff} = g * P$.

Simona Olmi - Master Thesis (2009)

Diluted Inhibitory Networks I

For 5% cut links:

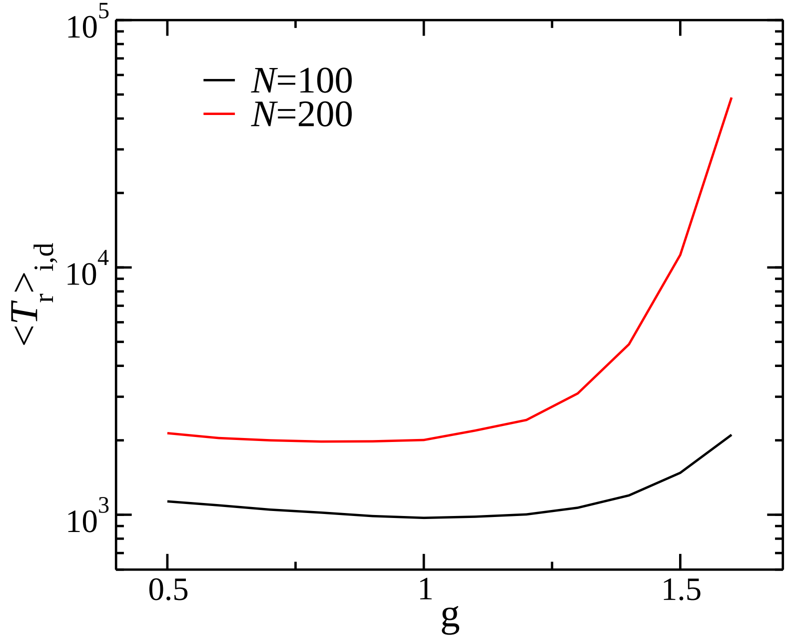
- **Negative Lyapunov exponent** $\longrightarrow$ No Chaos
- multiple attractors (abolition of degeneracy with respect to exchange of neurons)
- for $g < 1$ short transients $\sim N$ to periodic state
- for $g > 1$ long stationary transients $\sim \exp(\beta N)$
- irregular dynamics during transient (uncorrelated isi-times)

Information processing in brain should combine reliability (no chaos) with fast response and high information content (complex dynamics)

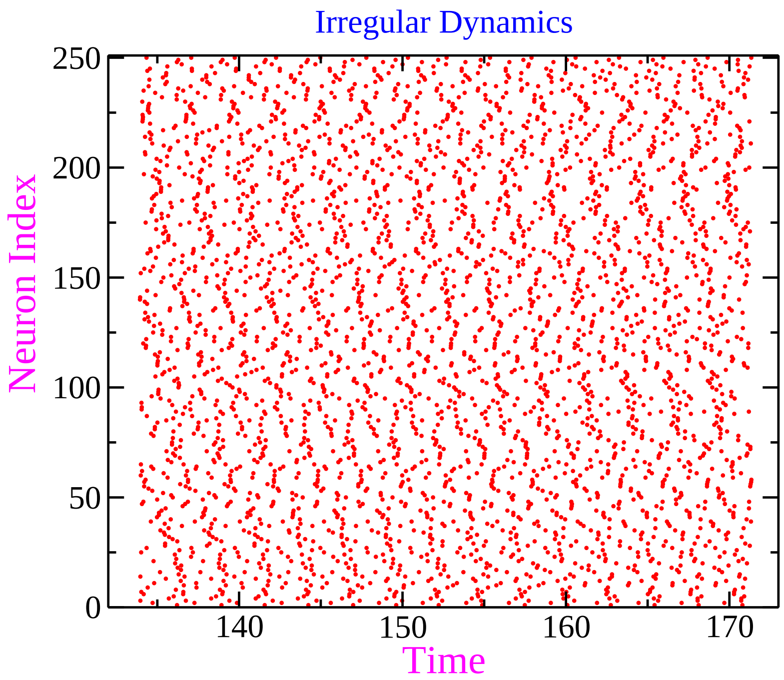
Diluted Inhibitory Networks II

Long irregular transients to periodic state

Length of Transients



Pattern for $g = 1.5$

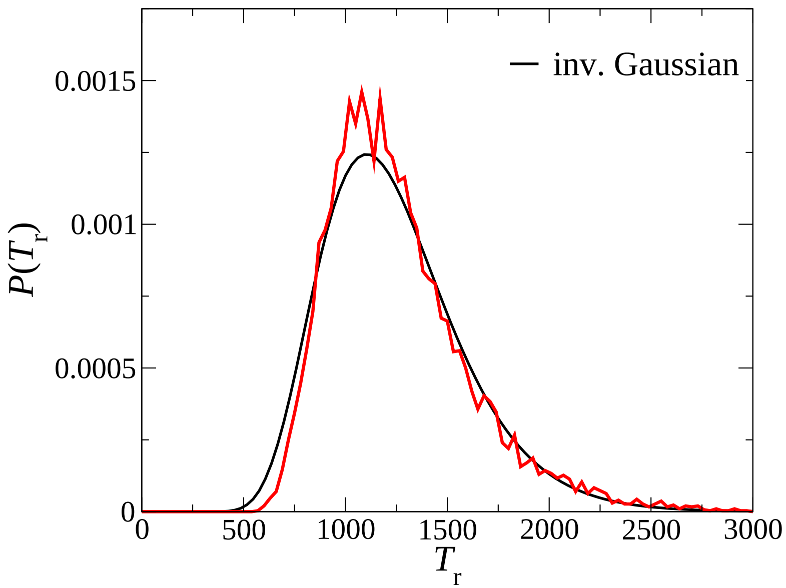


Diluted Inhibitory Networks III

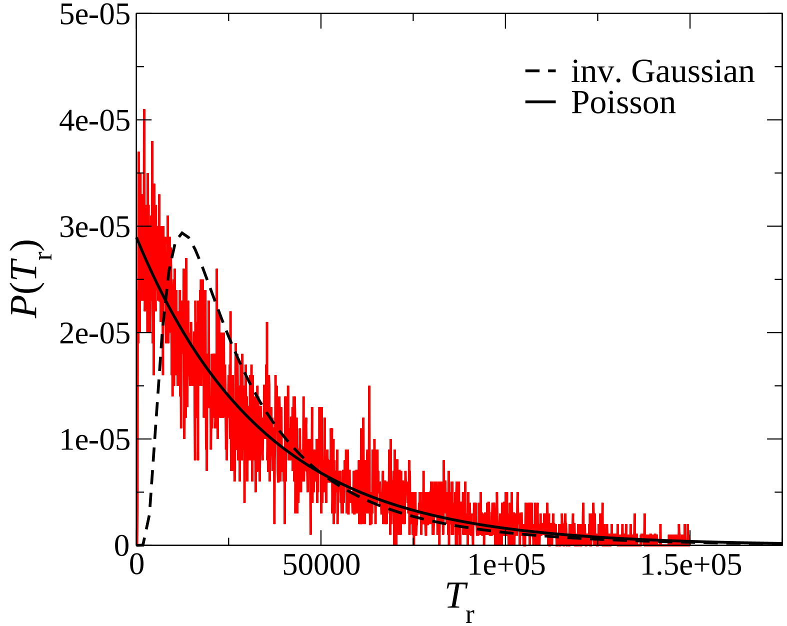
Statistics of the transient times

Normalized histogram (random initial conditions) of transient times for $N = 65$:

$g = 1.0$



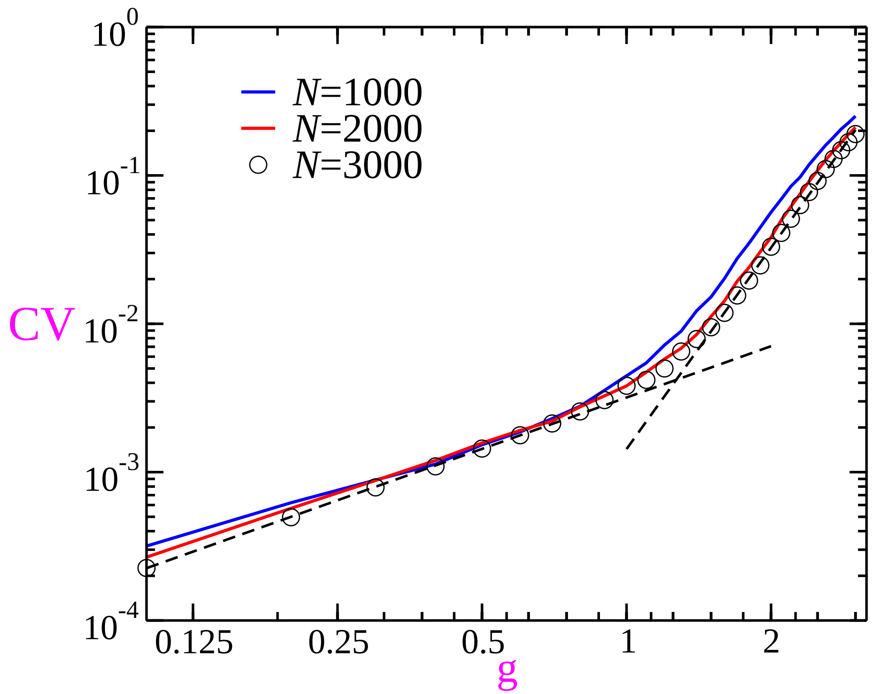
$g = 2.1$



Diluted Inhibitory Networks IV

Variability of inter-spike intervals

The coefficient of variation $CV = STD/mean$ of the neuron ISI-times during the transient shows two scaling regimes, depending on the coupling strength g :

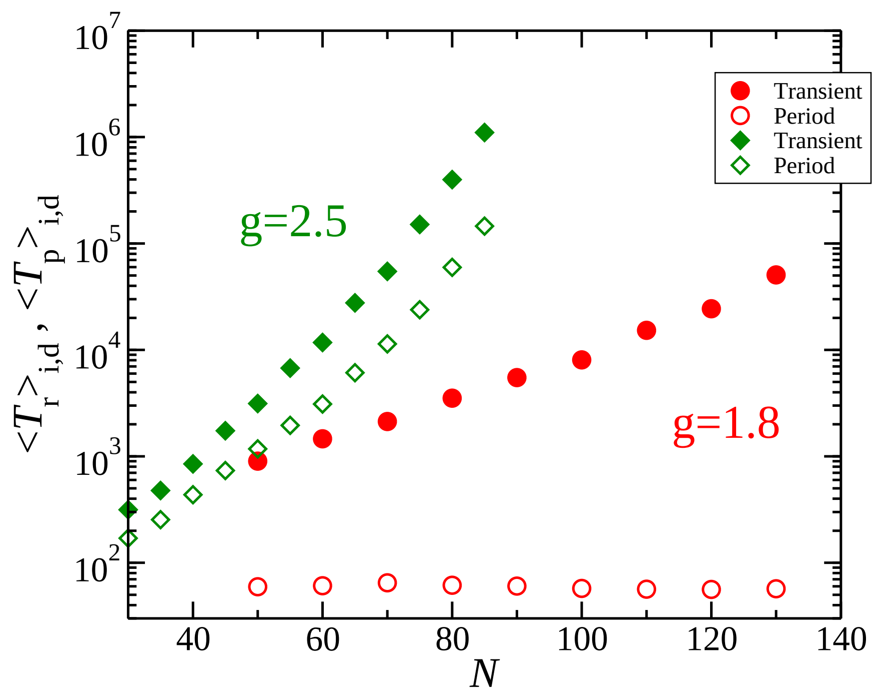


Diluted Inhibitory Networks V

Period of the Final (Stable) State

For large coupling g

- not only the average transients diverge exponentially with N, but also the average period of the final state.
- the final periodic orbit can be associated to large $CV \sim 0.8$



Stable Chaos

How is possible to have irregular dynamics without chaos and noise ?

- Stable Chaos can be observed whenever an Infinitesimal Perturbation (Fluctuation) is damped, while a Finite Perturbation is amplified.
- This phenomenon occurs when there is the possibility of istantaneous large amplification of the perturbation to a dynamical system, like e.g. local discontinuities of the flux (evolution map).
- In the context of neuronal networks the necessary conditions to have this phenomenon are
  - Predominant Inhibitory Coupling $\longrightarrow$ No Usual Chaos
  - Asymmetric Coupling (Diluted network) $\longrightarrow$ The Firing Order of the neurons is not preserved
- In fully coupled inhibitory networks the firing order cannot change: in this case only rapid transients to final periodic state are observed `[Jin, PRL, 89 (2002) 208102]`.

`For a review see A. Politi & AT -- arXiv: 0902.2545`

Non Chaotic Transients

- Transients are reliable:
  small fluctuations due to noise will not influence the firing order
  (Linear Stability)
- Transients contains high level of information:
  the firing rate is not simply periodic, but quite irregular (high CV)
  (Exponentially Long Transients)
- Transients respond fast:
  a modification of the external condition (not due to noise) leads to completely different firing patterns
  (Stable Chaos)

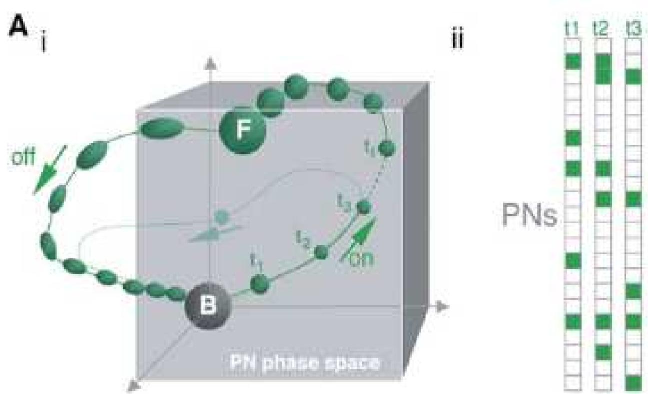
This mechanism can be a valid alternative to the Balanced State invoked to explain high irregularity of the firing patterns observed in vivo.

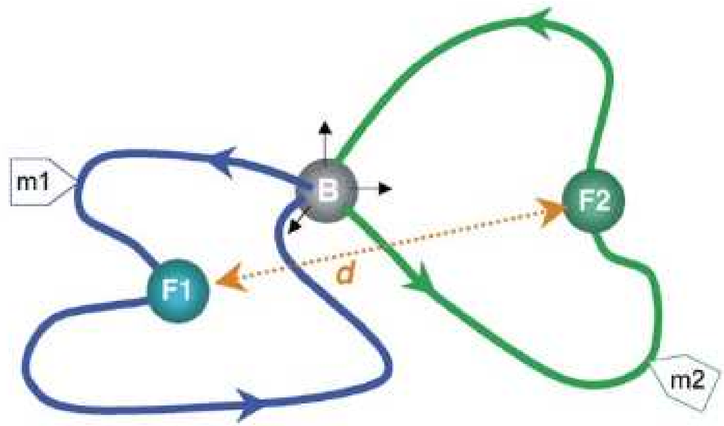
Since Balanced States are extremely sensible to noise fluctuations: driven by fluctuations

Are transients relevant ?

O. Mazor & G. Laurent, Neuron 48 (2005) 661-673

- Odor Representations by Projection Neurons (PNs) of the Locust Antennal Lobe;
- In the Odor Representations 3 phases can be identified: transient on, fixed point phase and return phase (transient off);
- During transients on the PNs are more active than during the other phases, they exhibit some sort of synchronized activity;
- Odor trajectories have their maximal distance during the transients : optimal phase to distinguish different stimuli (odors);





Recent Developments

- Long irregular (non chaotic) transients have been recently identified also in delayed neural networks with excitatory synapses and for pulses of finite duration
  `Timme et al., Frontiers in Comp. Neuroscience (2009)`
  `Zillmer, Brunel, Hansel PRE 79, 031909 (2009)`

- A dynamical mechanism somehow similar to Stable Chaos has been discussed in the last years in the context of neuroscience combining reliability with input specific response : Winnerless Competition
  `G. Laurent et al. Ann. Rev. Neuroscience 24 (2001) 263-297`
  `Ashwin & Timme, Nature 436, 36-37 (2005)`

For more information on the Computational Neuroscience Group in Firenze:

http://www.fi.isc.cnr.it/users/alessandro.torcini/neurores.html