Coherent activity in excitatory neural networks'

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Effects of excitatory coupling

When Inhibition and not Excitation Synchronizes Neural Firing

In this paper of 1994 by Van Vreeswijk, Abbott, and Ermentrout the authors affirm:

- It is commonly believed that excitatory synaptic coupling tend to synchronize neural firing, while inhibitory coupling pushes the neurons toward anti-synchrony

- However, in the reticular nucleus of the thalamus, synchronized oscillations occur via purely inhibitory coupling [Wang and Rinzel (1992)]

- For two coupled neurons we will show that such reversed behaviour is the rule rather than the exception

Which is the situation for large populations of neurons ?

Collective Dynamics in the Brain

- Rhythmic coherent dynamical behaviours have been widely identified in different neuronal populations in the mammalian brain [G. Buszaki - Rhythms of the Brain]

- Collective oscillations are commonly associated with the inhibitory role of interneurons

- Pure excitatory interactions are believed to lead to abnormal synchronization of the neural population associated with epileptic seizures in the cerebral cortex

However, coherent activity patterns have been observed also in "in vivo" measurements of the developing rodent neocortex and hyppocampus for a short period after birth, despite the fact that at this early stage the nature of the involved synapses is essentially excitatory [C. Allene et al., The Journal of Neuroscience (2008)]
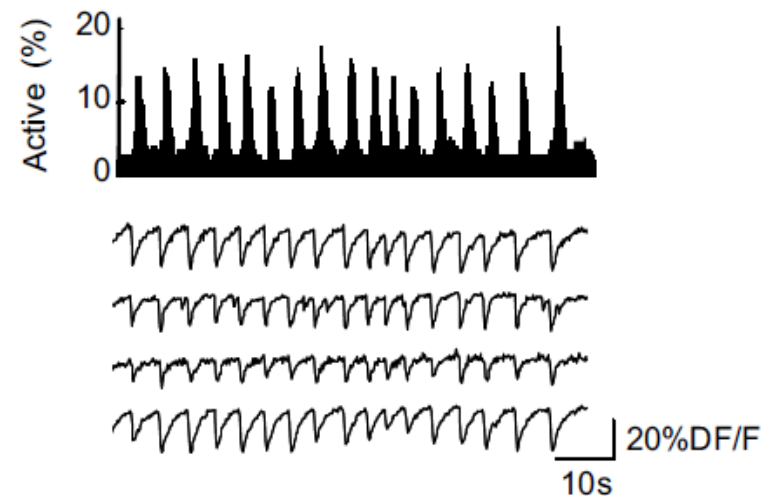
Calcium fluorescence traces
two-photon laser microscopy

Summary

We analyze pulse-coupled leaky integrate-and-fire (LIF) neurons

Analysis of the dynamics of two coupled neurons

- LIF neuronal models coupled
    - α pulses and exponential pulses
    - inhibitory and excitatory coupling
- Hodgkin-Huxley coupled neurons

Van Vreeswijk, Abbott, Ermentout, JCN (1994);
Hansel, Mato, Meunier, Neural computation (1995)

- Emergence of collective solution in fully coupled networks of LIF neurons
    - Splay states
    - Coherent collective solutions - Partial Synchronization

Abbott - van Vreeswijk, Physical Review E (1993)
Mohanty, Politi EurophysLett (2006)
Zillmer et al. Physical Review E (2007)

Leaky integrate-and-fire

- One of the simplest neuronal models : LIF neuron;

- LIF combines linear integration with reset **+** spike emission;

- Equation for the membrane potential v, with threshold Θ and reset R :

$$\dot{v}(t) = I - v(t) \qquad v(t) = R + I(1 - e^{-t}) \implies R + I$$

  - If $(R + I) > \Theta$ Repetitive Firing, Supra-Threshold - $T = \log \frac{I}{(R+I)-\Theta}$
  - If $(I + R) < \Theta$ Silent Neuron, Below Threshold - $v(t = \infty) = R + I$

- In networks: at threshold a pulse is sent to the connected neurons

$$F(t) = \alpha^2 \, t \, e^{-\alpha t}$$
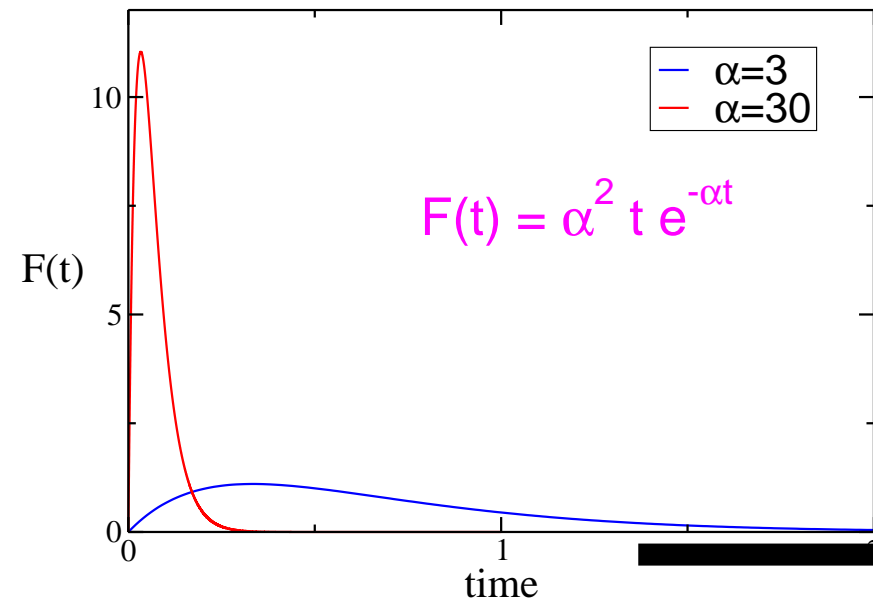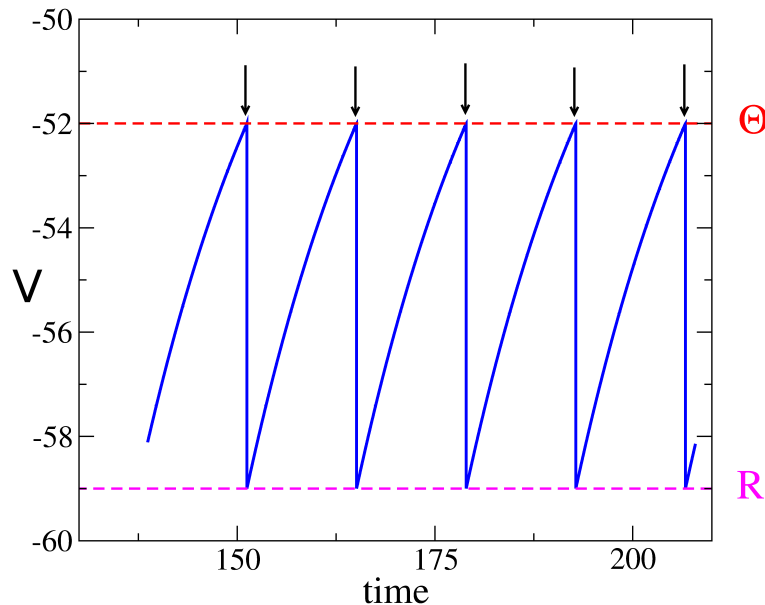
Two pulse coupled LIFs

We consider two simmetrically pulse coupled LIF neurons, where $R = 0$ and $\Theta = 1$, the equation for neuron 1 is (for neuron 2 is analogous)

$$\dot{v}_1(t) = I - v_1(t) + E_1(t) \qquad E_1(t) = \sum_{k \mid t_2^{(k)} < t} E_s(t - t_2^{(k)})$$
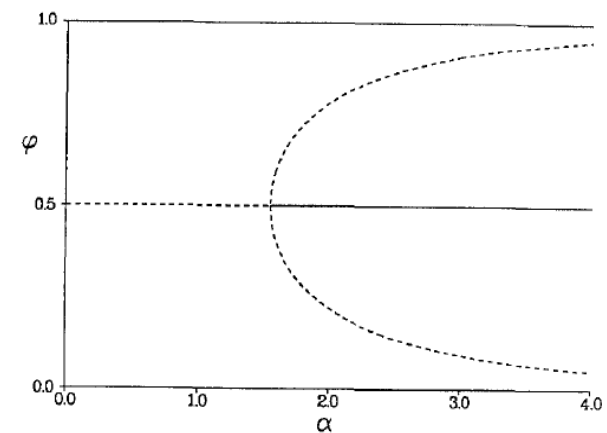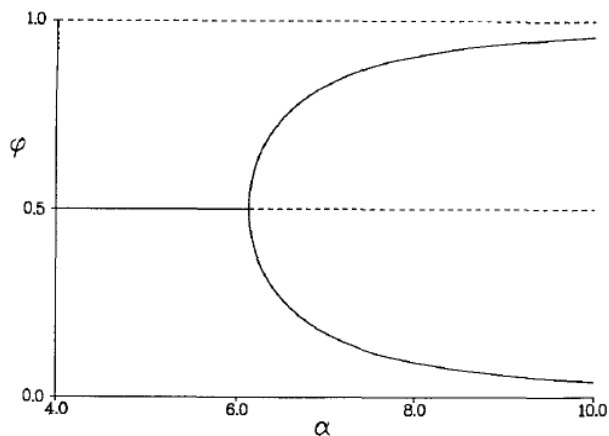
- E_1 is the synaptic input to neuron 1

- $t_2^{(k)}$ are the firing times of neuron 2 (no delay in the pulse trasmission)

- Pulses

  - α-function $E_s(t) = g\alpha^2 t e^{-\alpha t}$

  - Exponential pulses $E_s(t) = g\gamma e^{-\gamma t}$

  - Delta pulses $E_s(t) = g\delta(t)$

- The strenght g of the synapses is given by the normalization condition $\int_0^\infty E_s(t)dt \equiv g$

- The synapse speed is α for the α-function

$E_S(t)$

Neuron 1

Neuron 2

$E_S(t)$
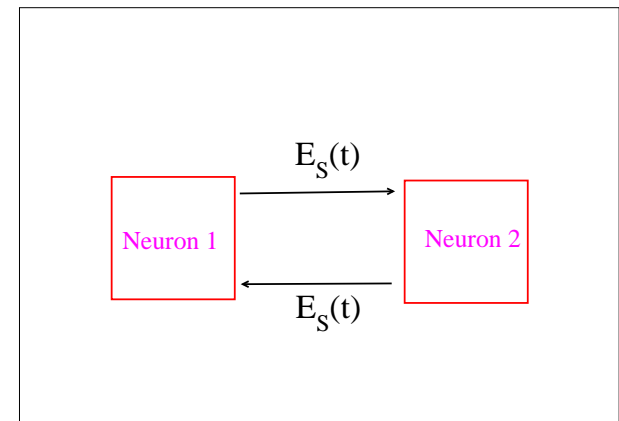
Two pulse coupled LIF

- Hp1) The two uncoupled $g = 0$ neurons are supratreshold $I > 1$ (periodic firing)

- Hp1) When coupled $g \neq 0$ they continue to fire periodically with period T

- The 2 neurons fire at times $t_1^{(n)} = nT$ and $t_2^{(n)} = (n - \phi)T$

- $0 < \phi < 1$ is the phase difference among the neurons

  - Complete Synchrony $\phi = 0$ (or $\phi = 1$) - Complete Anti-synchrony $\phi = 1/2$

- Excitatory case $g = 0.4$ – Inhibitory case $g = -0.4$ (DC current $I = 1.3$)

- Excitatory case - Never completely synchronized (only for $\alpha \to \infty$)

- Inhibitory case - The complete synchronization solution is always present

Theoretical explanation

- Neuron 1 fires at times $t_1^{(n)} = nT$ with $n = -\infty, \dots, -2, -1, 0$

- The synaptic input to neuron 2 at time $t = \theta T$ with $0 < \theta < 1$ is the sum of all the pulses received in the past

$$E_2(\theta T) = E_T(\theta) = \sum_{n=-\infty}^{0} E_S(\theta T - nT)$$

- For α-fuctions the sum gives

$$E_T(\theta) = \frac{g\alpha^2 T \mathrm{e}^{-\alpha\theta T} \left[\theta(1 - \mathrm{e}^{-\alpha T}) + \mathrm{e}^{-\alpha T}\right]}{(1 - \mathrm{e}^{-\alpha T})^2}$$

- E_T is periodic outside the interval $]0 : 1[$

- Neuron 2 fires at times $t_2^{(n)} = (n - \phi)T$ – The synaptic input to neuron 1 is

$$E_1(\theta T) = \sum_{n=-\infty}^{0} E_S(\theta T - nT + \phi) = E_T(\theta + \phi)$$

Theoretical explanation

- Neuron 1 fires at time $t = 0 \implies x_1(0^+) = 0$

- At time T the neuron 1 reaches again threshold therefore

$$x_1(T) = I(1 - \mathrm{e}^{-T}) + T\mathrm{e}^{-T} \int_0^1 d\theta \mathrm{e}^{\theta T} E_T(\theta + \phi) = 1$$

- Neuron 2 fires at time $t = -\phi T$ and after a period T it is again at threshold

$$x_2((1 - \phi)T) = I(1 - \mathrm{e}^{-T}) + T\mathrm{e}^{-T} \int_0^1 d\theta \mathrm{e}^{\theta T} E_T(\theta - \phi) = 1$$

- From the two above equations one can obtain the period T_0 and the phase ϕ_0

- By combining the two equations above

$$G(\phi) = \frac{x_1(T) - x_2[(1 - \phi)T]}{T} = \mathrm{e}^{-T} \int_0^1 d\theta \mathrm{e}^{\theta T} [E_T(\theta + \phi) - E_T(\theta - \phi)]$$

- If $\phi \equiv \phi_0$ and $T \equiv T_0$ then $G(\phi_0) \equiv 0$, possible solutions are

$$\phi_0 = 0 \quad \text{and} \quad \phi_0 = 1/2 \quad \text{since} \quad E_T(\theta + 1/2) = E_T(\theta - 1/2)$$

Stability of the solutions

- Any solution ϕ_0 is stable whenever $G'(\phi_0) > 0$

- One can notice that

$$x_2[(1-\phi)T] = 1 - TG(\phi)$$

- if $\phi \equiv \phi_0$ and $T \equiv T_0$ then $x_2[(1-\phi_0)T_0] \equiv 1$, since $G(\phi_0) = 0$

- If the phase is perturbed $\phi = \phi_0 + \delta\phi$ the neuron 2 will fire at time

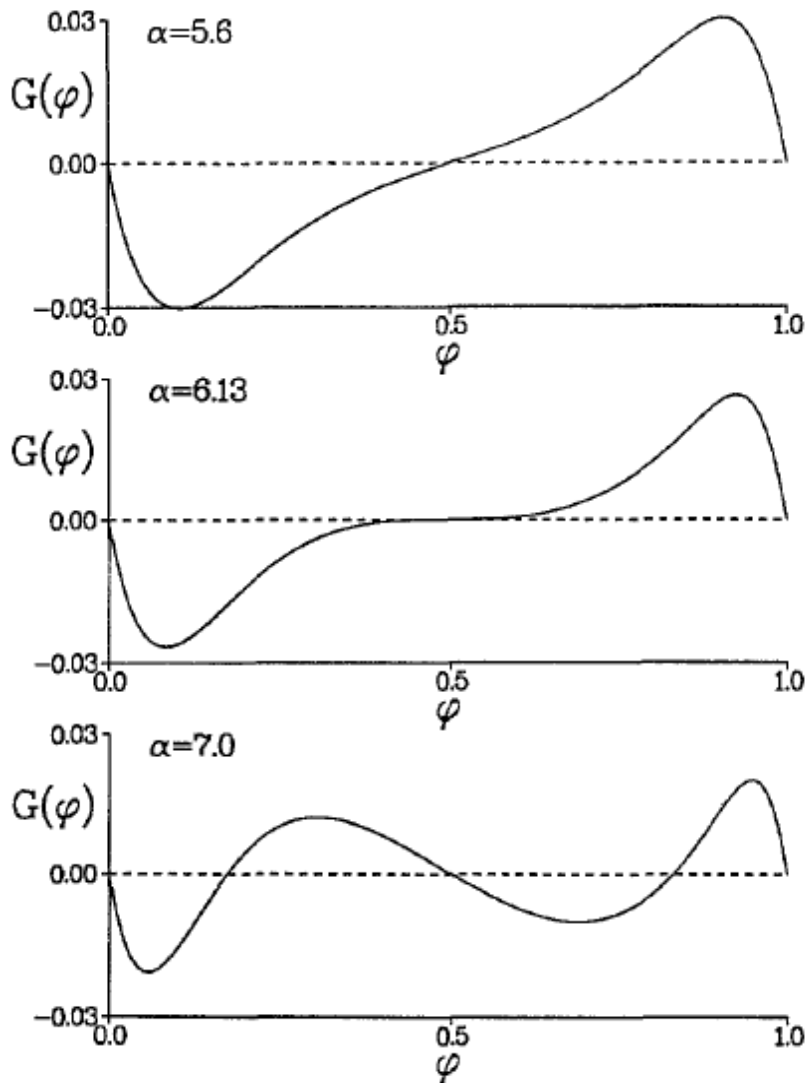$$t_2^{(n)} = (n-\phi)T_0 = (n-\phi_0)T_0 - (\delta\phi)T_0$$

- since the solution is stable, the neuron to maintain constant the period T_0 will fire next time at

$$t_2^{n+1} = (n+1-\phi_0)T_0 + (\delta\phi)T_0 = (n+1-\phi)T_0 + 2(\delta\phi)T_0$$

- Therefore at time $t = (1-\phi)T_0$ the neuron has not reach the threshold

$$x_2[(1-\phi)T] < 1 \implies G(\phi) \simeq G(\phi_0) + G'(\phi_0)\delta\phi > 0 \implies G'(\phi_0) > 0$$

Excitatory Coupling

- $g > 0$ - α-pulses

- $\alpha = 5.6 \implies \phi = 1/2$ Stable and $\phi = 0(1)$ Unstable

- $\alpha = 6.13 \implies$ Bifurcation - $\phi = 1/2$ becomes Unstable and two new solutions emerge

- $\alpha = 7.0 \implies \phi = 1/2$ and $\phi = 0(1)$ Unstable - 2 New stable solutions

- The completely synchronized state $[\phi = 0(1)]$ becomes stable only for $\alpha \to \infty$
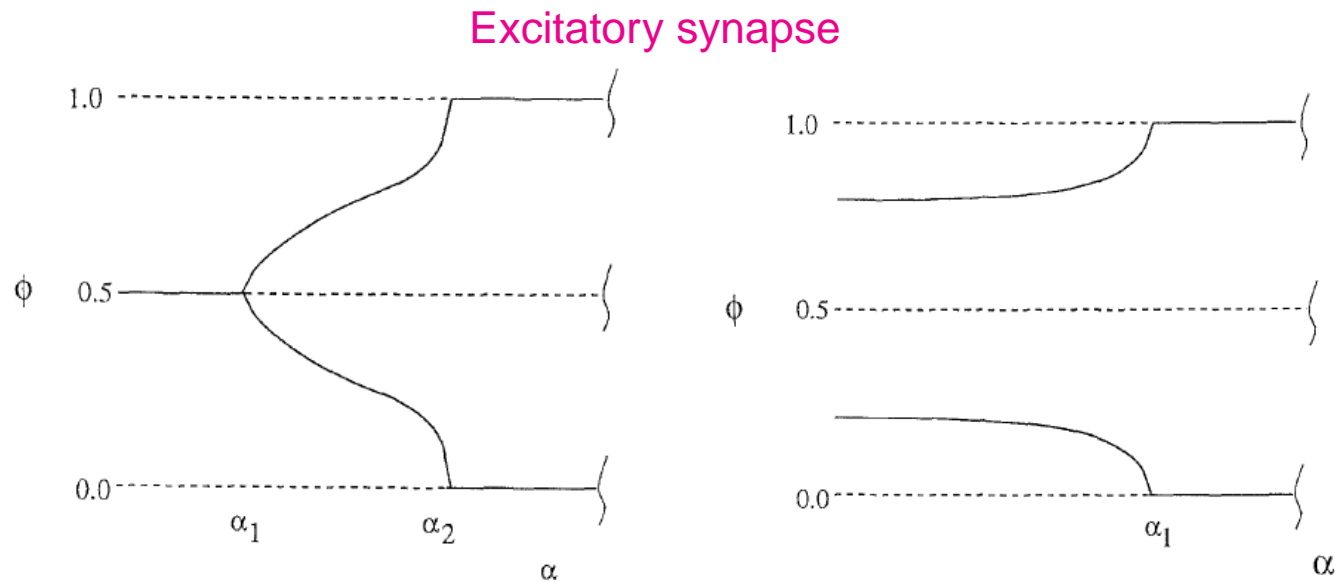 The synapse respond istantaneouslly (like exponential and delta-pulses)

Inhibitory Coupling

- $g < 0$ - α-pulses

- For inhibitory coupling the stability is reversed since $G(\phi) \propto g$

- The synchronous state is always stable

- The anti-synchronous state $\phi = 1/2$ becomes stable for sufficiently large $\alpha > 1.55$

Hodgkin-Huxley Model

Excitatory synapse
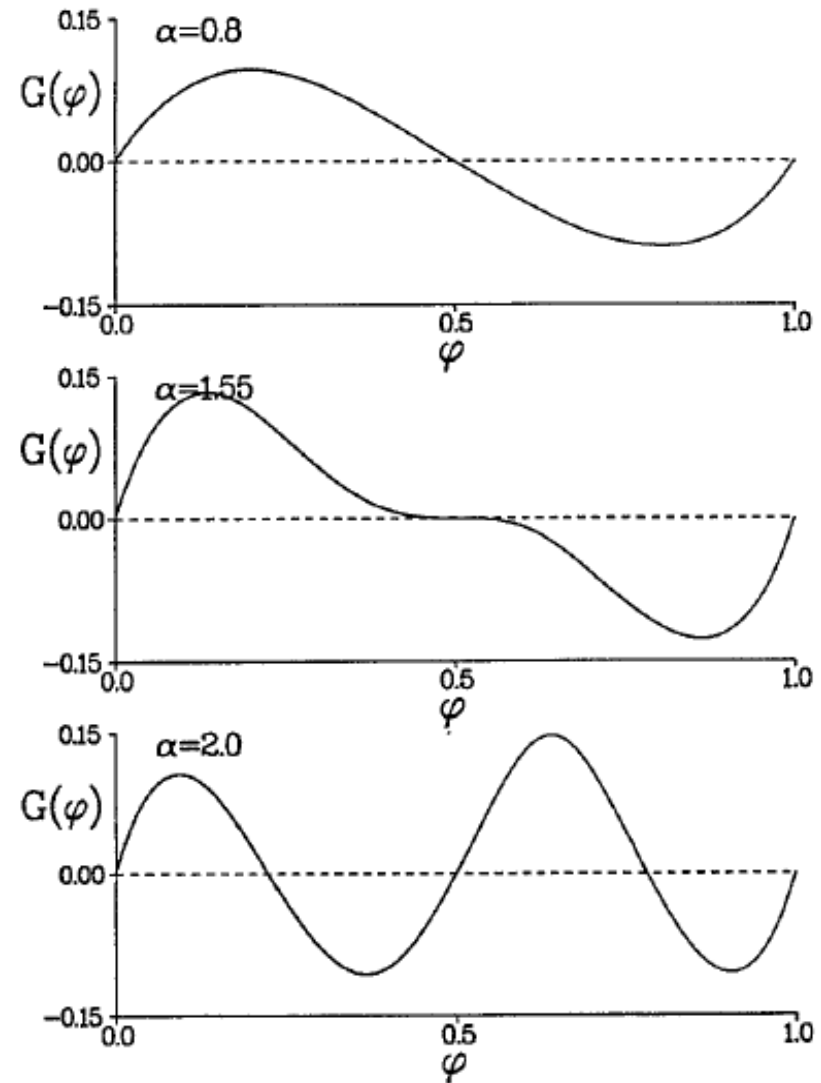
- ● α-pulses

  - ● For the Hodgkin-Huxley model one can have synchronization for finite $\alpha > \alpha_2 = 0.82/ms$, whenever the rise time is slower than the width of an action potential, nanely $1/\alpha < 1.2ms$

- ● exponential-pulses

  - ● For two coupled HH models for low decay constant one has stable asynchronous states at $\alpha < \alpha_1 \sim 0.3/ms$, while the synchronous states is always stable for faster decay rates.

Conclusions

To summarize the results presented so far for the LIF model

- $g > 0$

    - the synchronous state is stable only for extremely rapid synaptic response (namely, $\alpha = \infty$) : like exponential or delta functions
    - the anti-synchronous state is stable for slow synapses $\alpha < \alpha_c$

- $g < 0$

    - the synchronous state is always stable apart for extremely rapid synapses
    - the anti-synchronous state is stable for fast synapses $\alpha > 1.55$

In general excitation is desynchronizing for neurons with a response of Type I and for neuron of Type II (Hodgkin-Huxley) whenever the synaptic response is sufficiently slow

- Type I : the arrival of an EPSP always advances the next firing time

- Type II : the arrival of an EPSP just after the refractory period delays the next firing, while a EPSP received at a later time advances the next firing time

[Van Vreeswijk, Abbott, Ermentout, JCN (1994);
Hansel, Mato, Meunier, Neural computation (1995)]

Pulse coupled network

A system of N identical all to all pulse-coupled neurons:

$$\dot{v}_j = I - v_j + \frac{g}{N} \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} P(t - t_i^{(k)}), \quad j = 1, \ldots, N$$

with the pulse shape given by $P(t) = \alpha^2 t \exp(-\alpha t)$.

More formally we can rewrite the dynamics as

$$\dot{v}_j = I - v_j + gE(t), \quad j = 1, \ldots, N$$

the field $E(t)$ is due to the (linear) super-position of all the past pulses

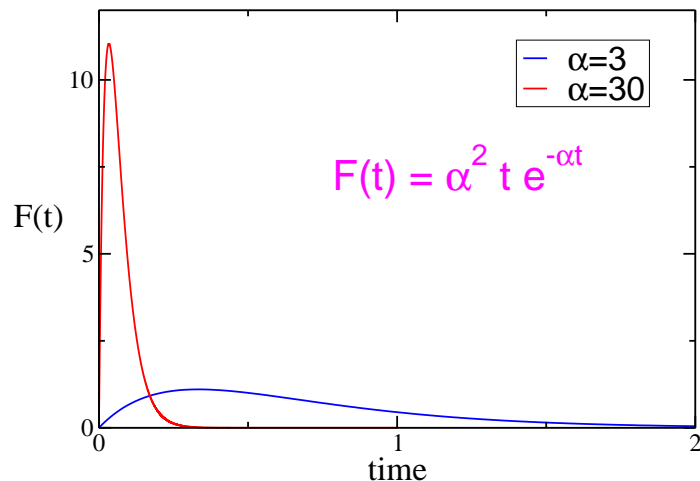- The field evolution (in between consecutive spikes) is given by

$$\ddot{E}(t) + 2\alpha \dot{E}(t) + \alpha^2 E(t) = 0$$

- the effect of a pulse emitted at time t_0 is

$$\dot{E}(t_0^+) = \dot{E}(t_0^-) + \alpha^2/N$$

Abbott - van Vreeswiijk, Physical Review E (1993)

Fully coupled network

$$F(t) = \alpha^2\, t\, e^{-\alpha t}$$

Legend: $\alpha=3$, $\alpha=30$

Only regular solutions for fully coupled networks:

- the membrane potentials v is periodic or quasi-periodic

- the field E is constant or periodic

van Vreeswiijk, Physical Review E 1996

Depending on the shape of the pulse (value of α) new collective solutions emerge:

- 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 States

These states are collective modes emerging in networks of fully coupled nonlinear oscillators.

- all the oscillations have the same wave-form X ;

- their phases are "splayed" apart over the unit circle

The state x_k of the single oscillator can be written as

$$x_k(t) = X(t + kT/N) = A\cos(\omega t + 2\pi k/N) \; ; \quad \omega = 2\pi/T \; ; \qquad k = 1, \ldots, N$$

- N = number of oscillators

- T = period of the collective oscillation

- X = common wave form

For pulse coupled neuronal networks the splay state corresponds to the N neurons firing one after the other at regular intervals T/N – Asynchronous State

Splay States

Splay states have been numerically and theoretically studied in

- Josephson junctions array (Strogatz-Mirollo, PRE , 1993)
- globally coupled Ginzburg-Landau equations (Hakim-Rappel, PRE, 1992)
- globally coupled laser model (Rappel, PRE, 1994)
- fully pulse-coupled neuronal networks (Abbott-van Vreesvijk, PRE, 1993)

Splay states have been observed experimentally in

- multimode laser systems (Wiesenfeld et al., PRL, 1990)
- electronic circuits (Ashwin et al., Nonlinearity, 1990)

Nowdays Relevance for Neural Networks

- LIF + Dynamic Synapses - Plasticity (Bressloff, PRE, 1999)
- More realistic neuronal models (Brunel-Hansel, Neural Comp., 2006)

Splay State – LIF

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

- the dynamics of each neuron is periodic – the field $E = 1/T$ is constant
- the interspike time interval (ISI) of each neuron is T
- the ISI of the network is T/N - constant firing rate
- the dynamics of the network is Asynchronous
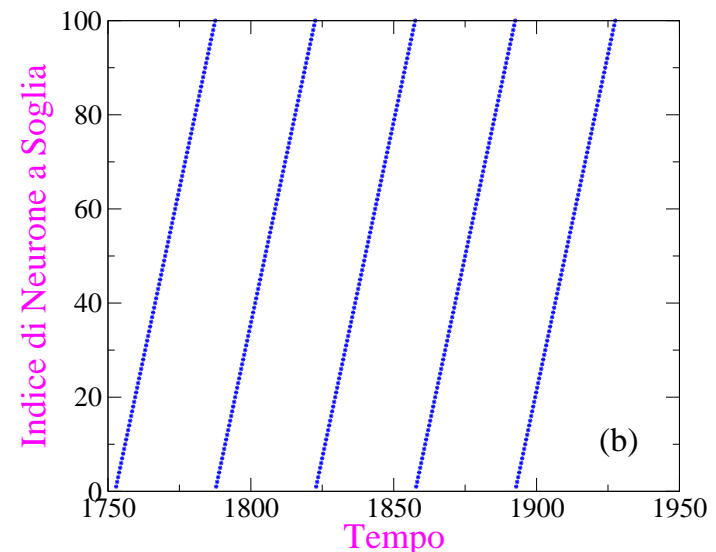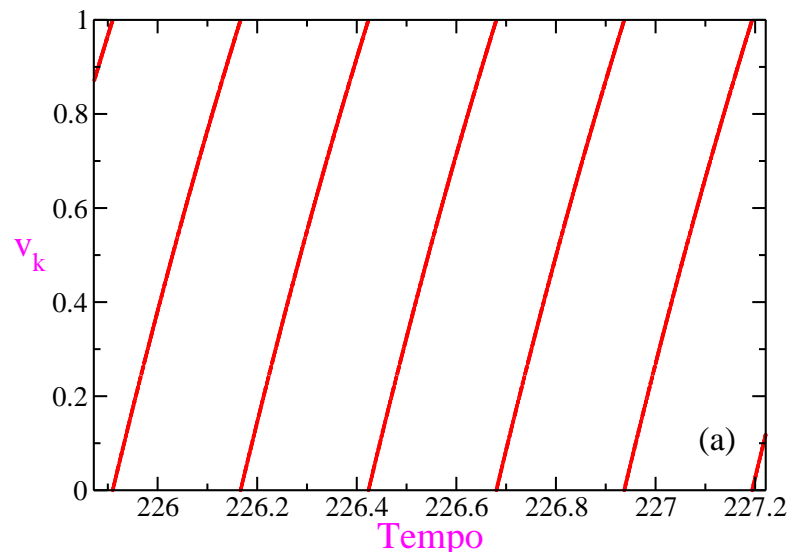
Abbott - van Vreeswijk, PRE (1993) -- Zillmer et al. PRE (2007)

Splay state - LIF

In this framework, the periodic splay state reduces to the following fixed point:

$$\tau(n) \equiv \frac{T}{N}$$

$$E(n) \equiv \tilde{E}, \; Q(n) \equiv \tilde{Q}$$

$$\tilde{x}_{j-1} = \tilde{x}_j e^{-T/N} + 1 - \tilde{x}_1 e^{-T/N}$$

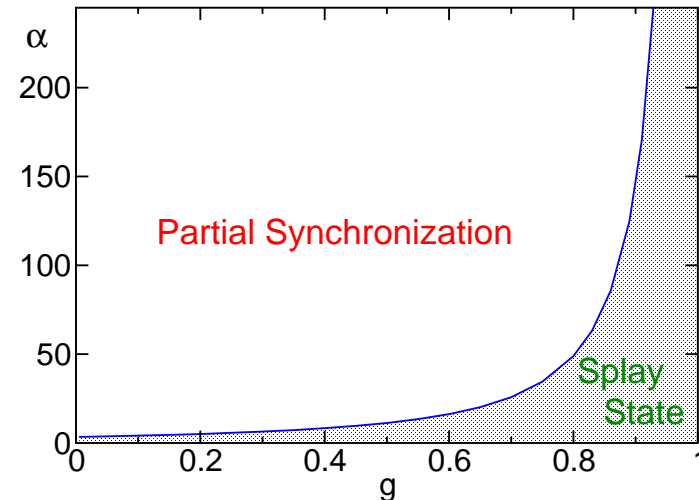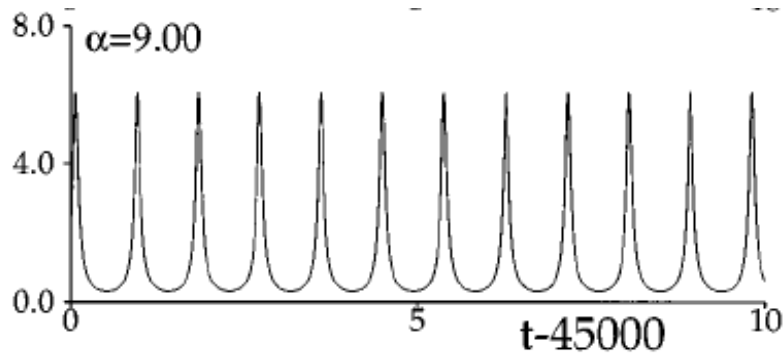where T is the time between two consecutive spike emissions of the same neuron.

A simple calculation yields,

$$\tilde{Q} = \frac{\alpha^2}{N^2} \left(1 - e^{-\alpha T/N}\right)^{-1}, \; \tilde{E} = T\tilde{Q} \left(e^{\alpha T/N} - 1\right)^{-1}.$$

and the period at the leading order ($N \gg 1$) is given by

$$T = \ln\left[\frac{aT + g}{(a-1)T + g}\right]$$

Partial Synchronization


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 and the field $E(t)$ are periodic

- the quasi-periodic motions of the single neurons are arranged (quasi-synchronized) in such a way to give rise to a collective periodic field $E(t)$

van Vreeswiijk, PRE (1996) - Mohanty, Politi EPL (2006)

# Quasi Periodic Motion
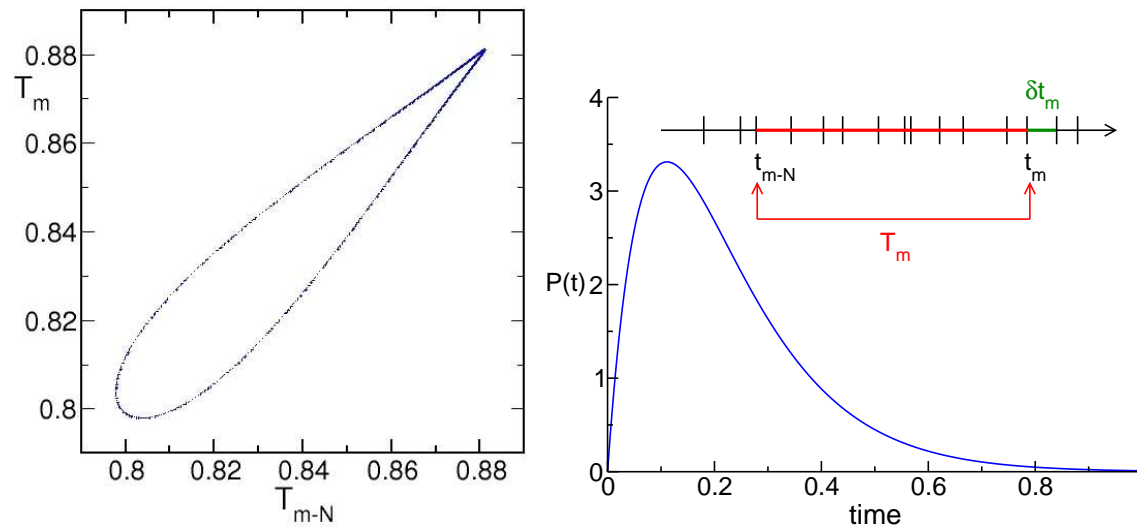
The dynamics of each neuron is quasiperiodic, this can be shown by reporting the Interspike Interval (ISI)of a single neuron $T_m = t_m - t_{m-N}$ versus the previous one T_{m-N} where $\{t_m\}$ is the sequence of the firing times.

The map $T_m = F(T_{m-N})$ represents a Poincaré section of the time evolution of the system, therefore a quasiperiodic motion is represented by a closed curve and T is periodic

Periodic Mean-Field

T(t)

Small α - Splay State

Large α -- Partial Synchronizaton
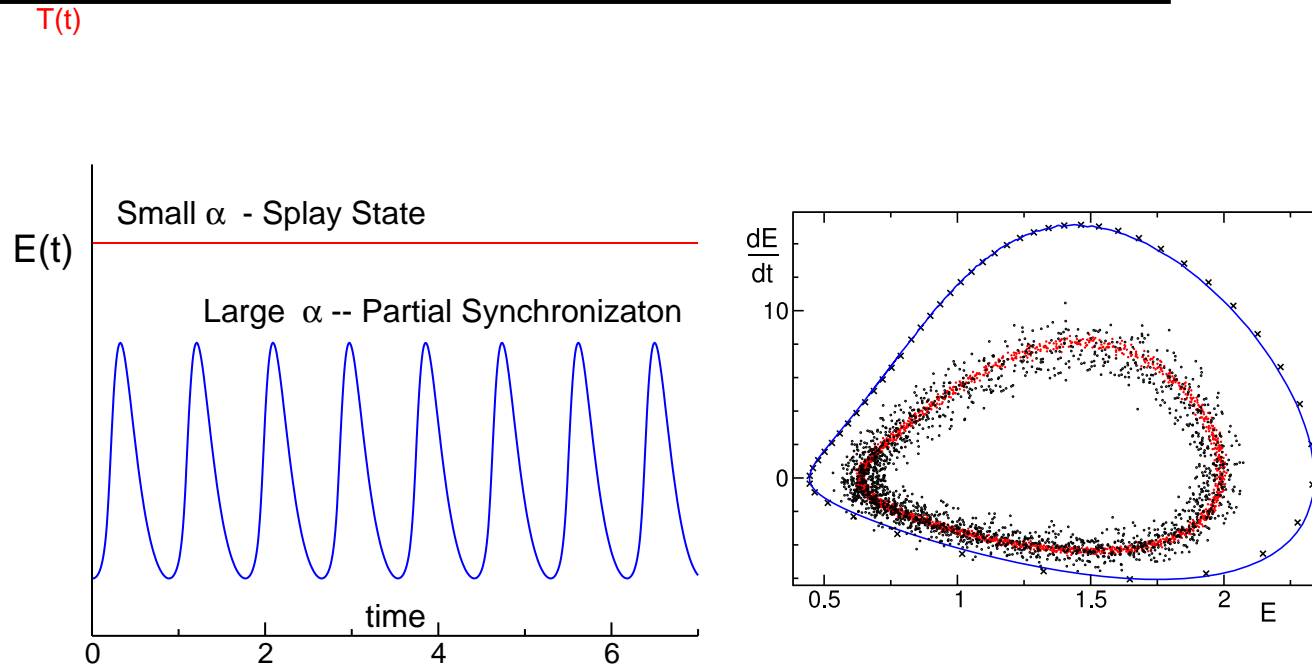
The ratio between the period of the field $E(t)$ and the average ISI of the single neurons is irrational

This peculiar collective behaviour has been recently discovered by `Rosenblum and Pikovsky PRL (2007)` in a system of nonlinearly coupled oscillators and studied also in the conntext of diluted neural networks by `Olmi, Livi, Politi, AT Physical Review E (2010)`
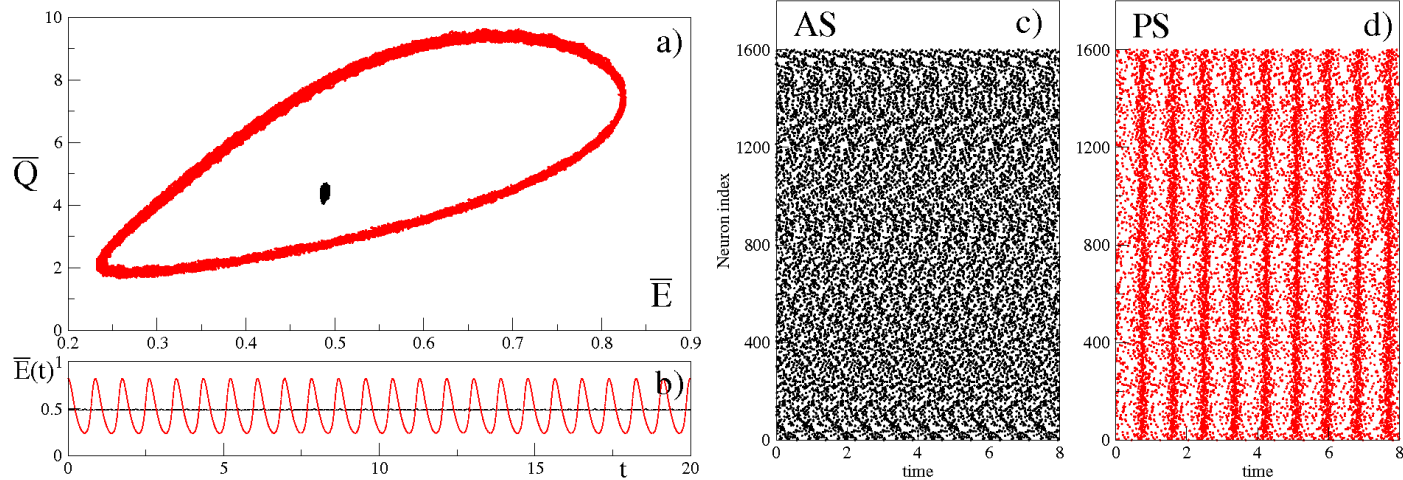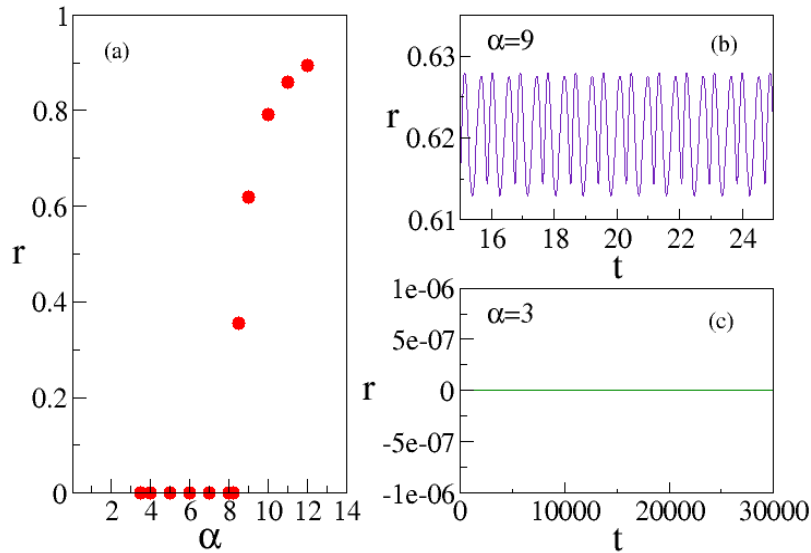
- The Splay State is Asynchronous

- Partially Synchronized exhibit collective dynamics
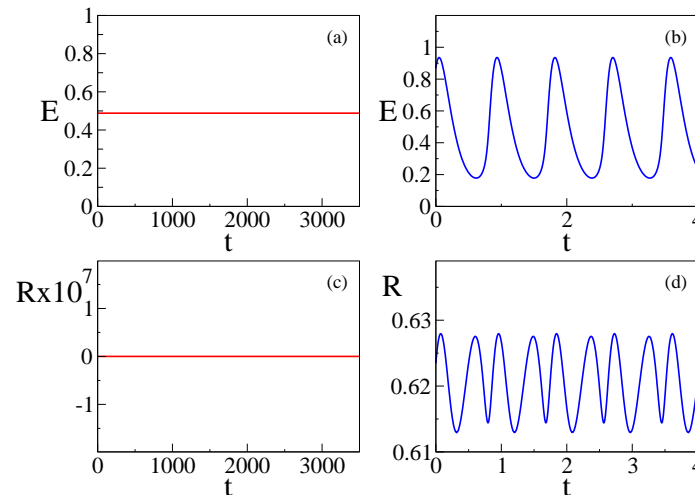
Bifurcation

The bifurcation is Hopf supercritical leading to the emergence of oscillatory state from a stationary fixed point

$$\Delta \propto \sqrt{\alpha - \alpha_c}$$