# Collective Dynamics in Neural Networks

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# Summary

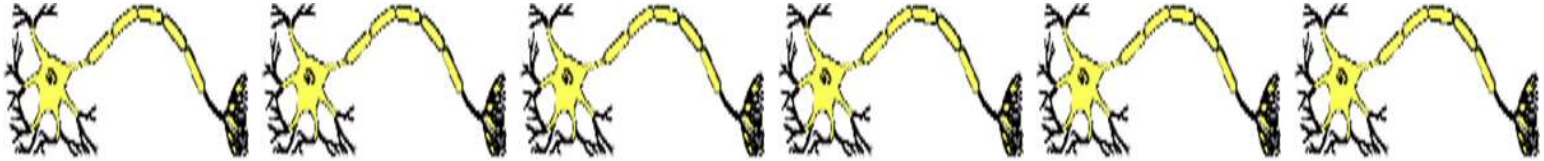
- Neurons in Brief
- Neurons as Oscillators
- Pulse-Coupled Neural Networks
- Collective Solutions
  - Splay-state
  - Partial Synchronization
- Chimera States

# Neurons in Brief

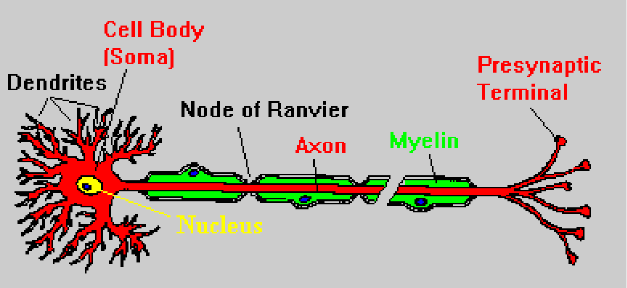
Cells of the nervous system, called neurons, are specialized in transporting and elaborating "messages" (information).

These functions are performed via the transmission of electric signals, associated to ionic currents, through the membrane of the neuronal cells

- The human brain contains 100 billions neurons
- One mm$^3$ of cerebral cortex contains 100.000 neurons .
- Neurons can have different forms and dimensions: the smallest have diameters of 4 $\mu$m, while the largest can have axons of 1 or 2 meters



# Neuron Morphology

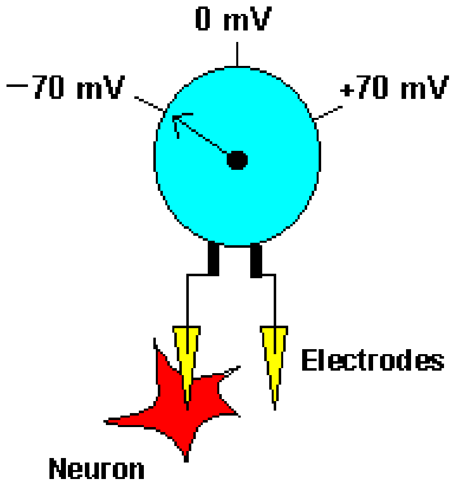


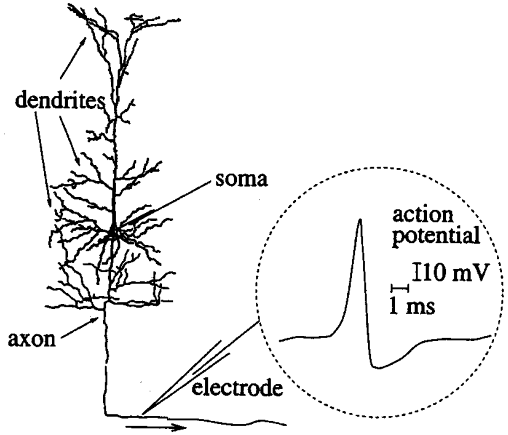
Despite their enourmous variety, neurons have some common morphological aspect:

- The soma is a compact almost sperical structure (diamter $\simeq 70\ \mu$m) it is the unity deputed to information elaboration (CPU )
- The dendrites collect information from other neurons and bring it to the soma, they are ramified nearby the cell body (lenght up to 1 mm) (Input )
- The axons bring information to other neurons, normally there is only 1 axon for cell, they can be as long as 1 meter (Output )
- The Synapses are the junctions among two neurons. these are the structures transmitting information from one nervous cell to the other. There are two types of synapses: chemical and electrical (gap junction), the most common among the vertebrates is the chemical one. The synapses can be inhibitory as well as excitatory.

# Neuronal Signals

The membrane potential $V_m$ represents the voltage difference between internal and external part of the neuronal cell, at rest (without any stimulation) $V_m \simeq$ -60mV / -75 mV . The neuron is in a dynamical equilibrium





The neuronal signal represents the temporal and spatial variation of $V_m$. The Action Potentials (AP) are voltage pulses emitted during the neuronal dynamics: they have a quite standard shape for pyramidal neurons

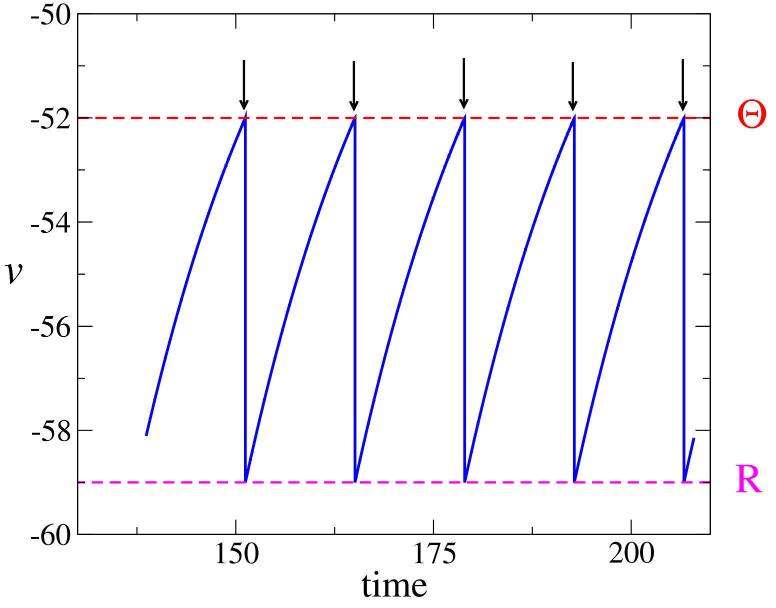
- The AP is generated each time a stimulus (depolarizing current) leads $V_m$ above a certain threshold $\Theta \sim -55$ mV ;
- The AP has duration of 1-2 ms and amplitude of 100-120 mV ; in the descending phase the pulse, before returnig to the rest state, passes through an iperpolarization stage, of $\sim 10$ ms (refractory period)
- The AP travels along the axon and it is transmitted to the other neurons, representing the elementary unit for neuronal signal transmission

# Leaky integrate-and-fire model

- Linear integration combined with a reset mechanism + formal spike event
- Equation for the membrane potential $v$ , with threshold $\Theta$ and reset $R$ :

$$\tau \dot{v} = -(v - v_{\mathrm{r}}) + I \qquad v(t) = v(0)\mathrm{e}^{-t/\tau} + (I + v_{\mathrm{r}})(1 - \mathrm{e}^{-t/\tau})$$

  - If $I + v_r > \Theta$ Repetitive Firing (Oscillator)
  - If $I + v_r < \Theta$ Silent Neuron (Fixed point)



# Leaky integrate-and-fire model

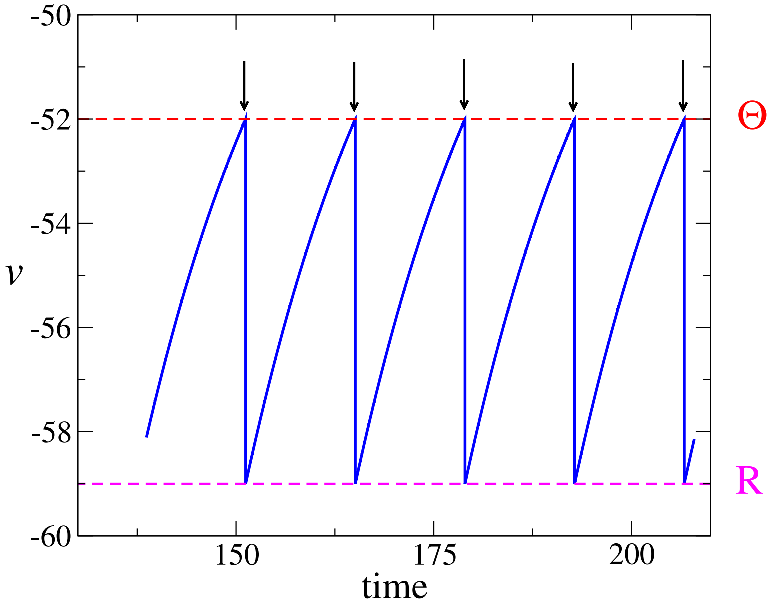
Periodic Behaviour

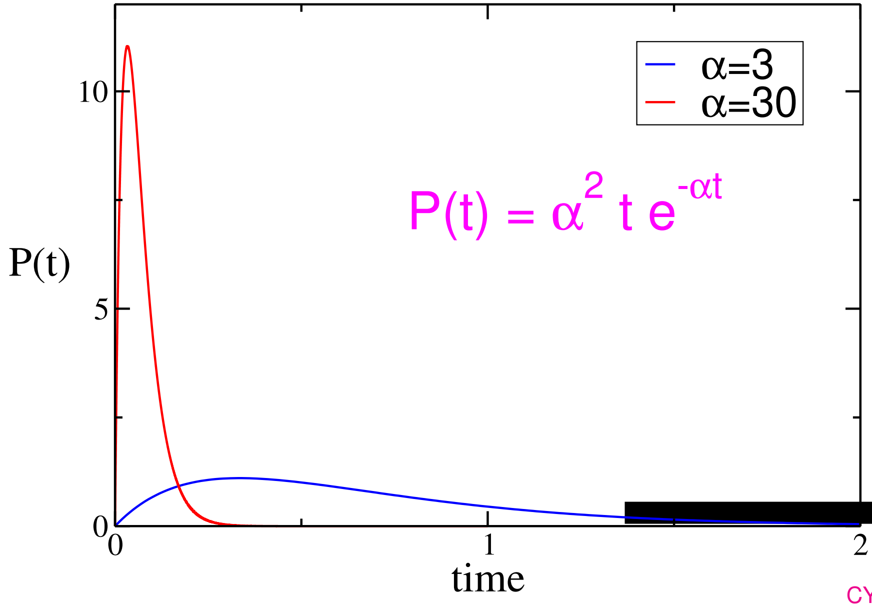
- If $I + v_r > \Theta$ Repetitive Firing (Oscillator)
- At $t = 0$ the neuron has been resetted to $V(0) = v_r$
- After one period $t = T$ the neuron is at threshold $V(T) = \Theta$

Since the solution is $v(t) = v(0)\mathrm{e}^{-t/\tau} + (I + v_\mathrm{r})(1 - \mathrm{e}^{-t/\tau})$ the period $T$ is given by

$$T = \tau \ln \frac{I}{\Theta - v_r - I}$$

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





# Pulse coupled network

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

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

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.

$\alpha$-function

If we choose the pulse shape given by $P(t) = \alpha^2 t \exp(-\alpha t)$, we can verify that it satisfies the following ODE :

- $\ddot{P}(t) + 2\alpha\dot{P}(t) + \alpha^2 P(t) = 0$
- Boundary condition $P(0) = 0$
- the effect of a pulse emitted at time $t = 0$ is $\dot{P}(0) = \alpha^2$

# Pulse coupled network

- 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

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

- $N$ is the normalization constant since each neurons receives $N$ spikes, as in the Kuramoto model , it allow the field $E$ to be an extensive quantity

Therefore we have $N$ ODEs for the membrane potentials $v_j$ and 2 ODEs for the field $E$, for a total of N+2 ODEs to integrate numerically

`Abbott - van Vreeswiijk, Physical Review E (1993)`

# Event-driven map(I)

Let us introduce

$$Q = \frac{\alpha E + \dot{E}}{N}$$

Therefore I can rewrite the 2 ODEs for the field $E$ as

$$\dot{E} = -\alpha E + NQ$$

$$\dot{Q} = -\alpha Q$$

If we integrate the field equations between successive spike emissions of any neuron, we can rewrite in an exact way the time evolution between successive spike emissions

This corresponds to perform a Poincaré section and to write a Poincaré map, whenever a neuron reach threshold !!!

# Event-driven map(II)

The set of $N+2$ continuous ODEs can be reduced to a time discrete event driven map

By integrating the field equations between successive pulses, one can rewrite the evolution of the field $E(t)$ as a discrete time map:

$$E(n+1) = E(n)e^{-\alpha\tau(n)} + NQ(n)\tau(n)e^{-\alpha\tau(n)}$$

$$Q(n+1) = Q(n)e^{-\alpha\tau(n)} + \frac{\alpha^2}{N^2}$$

where $\tau(n)$ is the interspike time interval (ISI) and $Q := (\alpha E + \dot{E})/N$ .

For the LIF model also the differential equations for the membrane potentials can be exactly integrated

$$v_i(n+1) = [v_i(n) - a]\mathrm{e}^{-\tau(n)} + a + gF(n) = [v_i(n) - v_q(n)]\mathrm{e}^{-\tau(n)} + 1 \quad i = 1, \dots, N$$

with

$$\tau(n) = \ln\left[\frac{v_q(n) - a}{1 - gF(n) - a}\right] \qquad q \text{ is the neuron next to threshold}$$

where $F(n) = F[E(n), Q(n), \tau(n)]$

# Event-driven map(III)

In a networks of identical neurons the order of the potentials $v_i$ is preserved, therefore it is convenient :

- to order the variables $v_i$;
- to introduce a comoving frame $j(n) = i - n$ Mod $N$;
- in this framework the label of the closest-to-threshold neuron is always $1$ and that of the firing neuron is $N$.

The dynamics of the membrane potentials for the LIF model becomes simply:

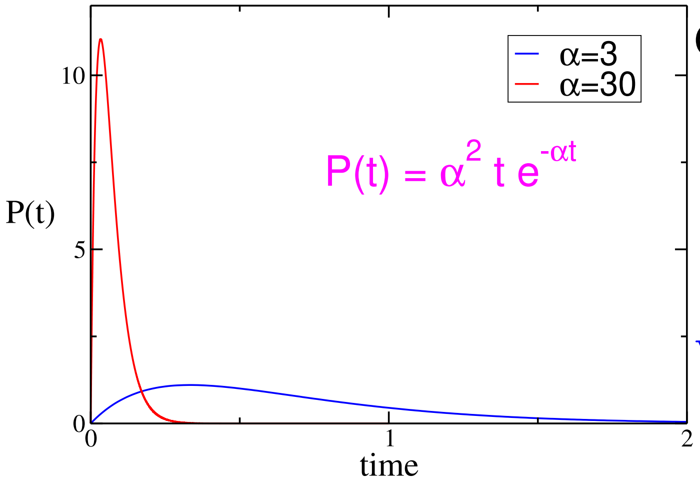
$$v_{j-1}(n+1) = [v_j(n) - v_1(n)]e^{-\tau(n)} + 1 \qquad j = 1, \dots, N-1 \ ,$$

with the boundary condition $v_N = 0$ and $\tau(n) = \ln\left[\frac{v_1(n)-a}{1-gF(n)-a}\right]$.

A network of $N$ identical neurons is described by $N+1$ equations

Zillmer et al. Physical Review E (2006)

# Fully coupled network



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 $\alpha$) new collective solutions emerge:

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

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

- $N$ = 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)

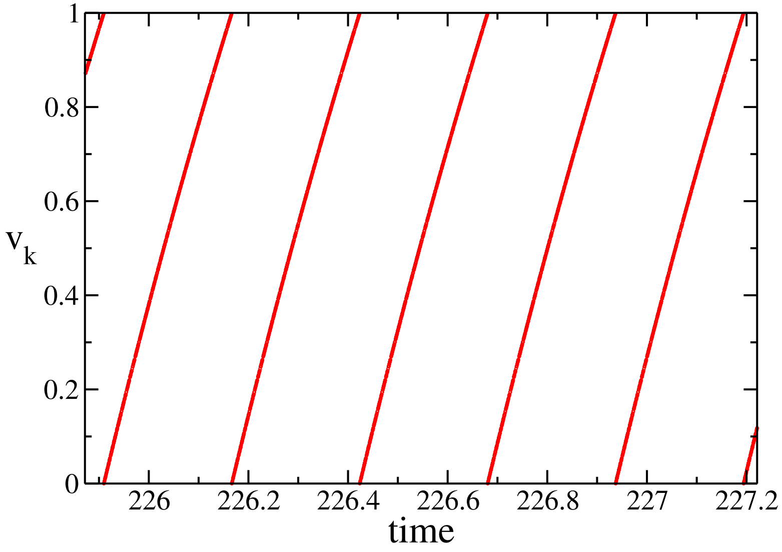
Nowdays Relevance for Neural Networks

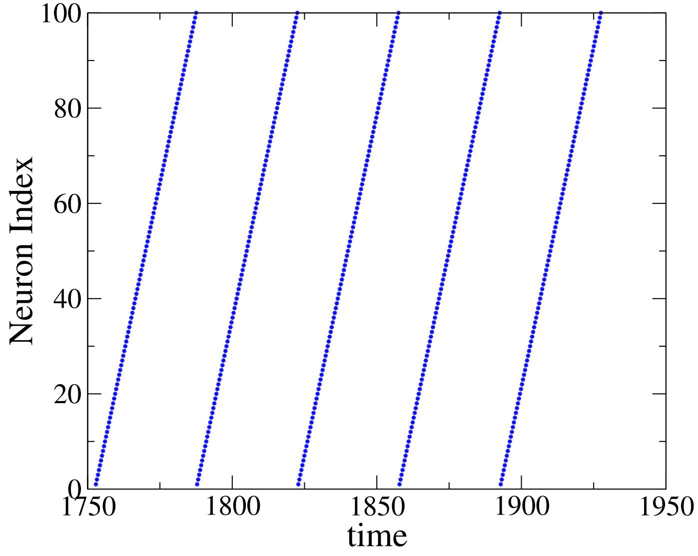
- LIF + Dynamic Synapses - Plasticity (Bressloff, PRE, 1999)
- More realistic neuronal models (Brunel-Hansel, Neural Comp., 2006)

# 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

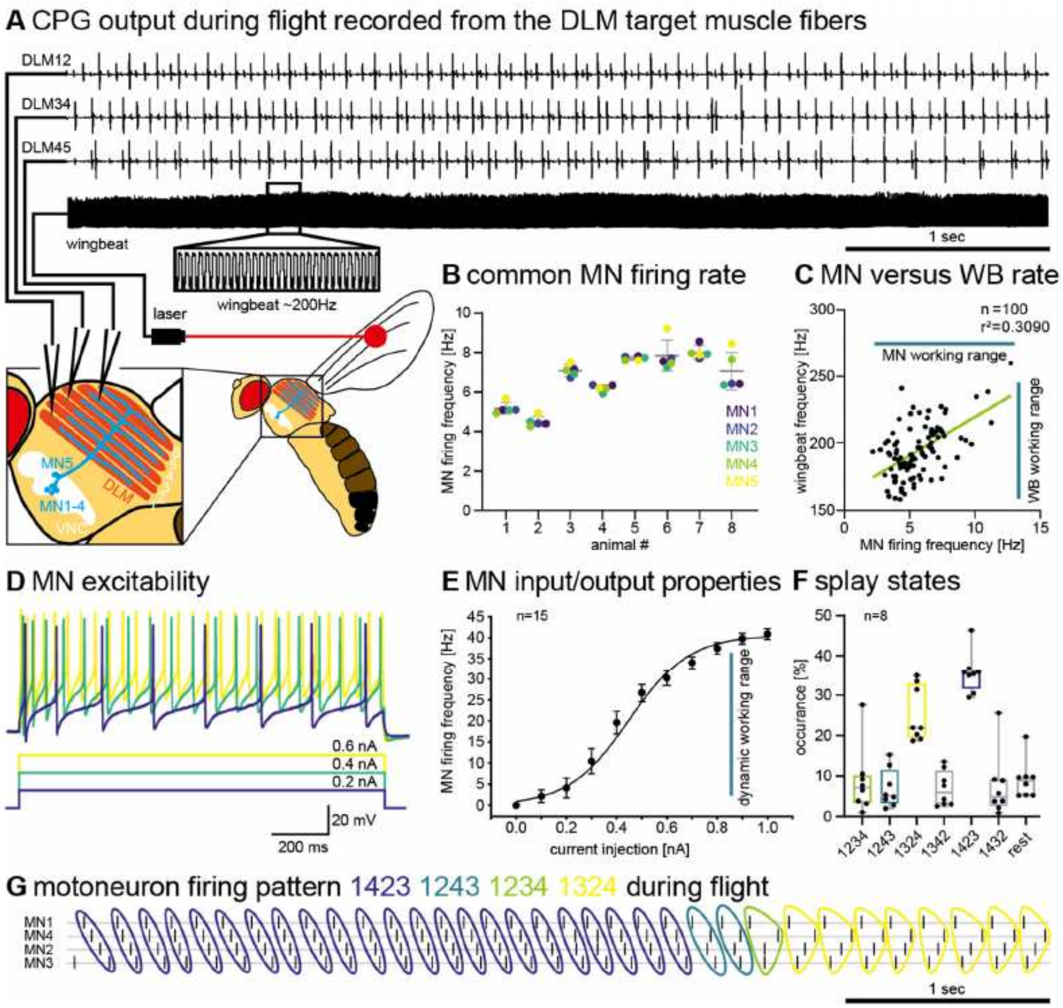




Abbott - van Vreeswiijk, PRE (1993) -- Zillmer et al. PRE (2007)

# Splay States for Drosophila Flight

Insect Asynchronous Flight is controlled by motoneurons connected by gap junctions in a Central Pattern Generator firing as in a splay state (2022)



# 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

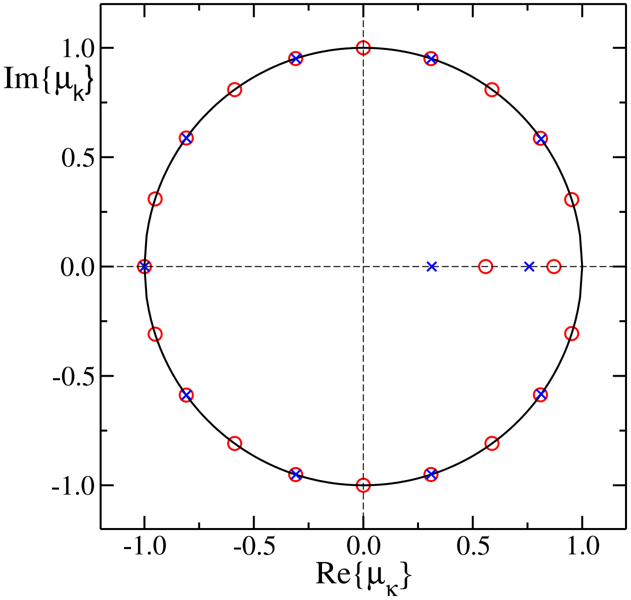
$$T = \ln\left[\frac{aT + g}{(a-1)T + g}\right]$$

# Stability of the splay state

- In the limit of vanishing coupling $g \equiv 0$ the Floquet (multipliers) spectrum is composed of two parts:
  - $\mu_k = \exp(i\varphi_k)$, where $\varphi_k = \frac{2\pi k}{N}$, $k = 1, \dots, N-1$
  - $\mu_N = \mu_{N+1} = \exp(-\alpha T/N)$ .

  The last two exponents concern the dynamics of the coupling field $E(t)$, whose decay is ruled by the time scale $\alpha^{-1}$
- As soon as the coupling is present the Floquet multipliers take the general form
  - $\mu_k = e^{i\varphi_k} e^{T(\lambda_k + i\omega_k)/N}$
    $\varphi_k = \frac{2\pi k}{N}$ , $k = 1, \dots, N-1$
  - $\mu_N = e^{T(\lambda_N + i\omega_N)/N}$
    $\mu_{N+1} = e^{T(\lambda_{N+1} + i\omega_{N+1})/N}$

  where, $\lambda_k$ and $\omega_k$ are the real and imaginary parts of the Floquet exponents.



# Analogy with extended systems

The “phase” $\varphi_k = \frac{2\pi k}{N}$ plays the same role as the wavenumber for the stability analysis of spatially extended systems: the Floquet exponent $\lambda_k$ characterizes the stability of the $k-$th mode

- If at least one $\lambda_k > 0$ the splay state is unstable
- If all the $\lambda_k < 0$ the splay state is stable
- If the maximal $\lambda_k = 0$ the state is marginally stable

We can identify two relevant limits for the stability analysis:

- the modes with $\varphi_k \sim 0$ mod$(2\pi)$ corresponding to $||\mu_k - 1|| \sim N^{-1}$
  Long Wavelengths (LWs)
- the modes with finite $\varphi_k$ corresponding to $||\mu_k - 1|| \sim \mathcal{O}(1)$
  Short Wavelengths (SWs)

For the LIF model the implicit expression of the Floquet spectrum is

$$A(\mathrm{e}^T - 1)\mu_k^{N-1} = -\left(A(\mathrm{e}^T - 1) + \mathrm{e}^\tau\right)\frac{\mathrm{e}^{\tau - T} - \mu_k^{N-1}}{1 - \mu_k \mathrm{e}^\tau} + \mathrm{e}^\tau \frac{1 - \mu_k^{N-1}}{1 - \mu_k}$$

where $A = A(\tau, \bar{x}_1, \bar{E}, \bar{E})$

# Infinite Network – LIF

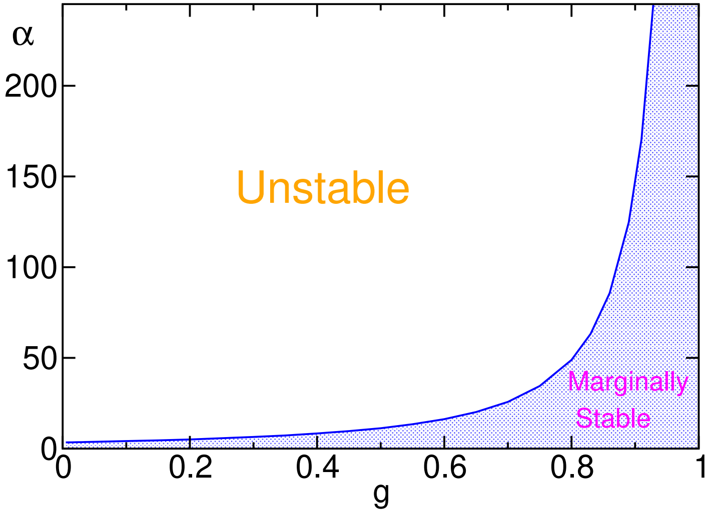
Post-synaptic potentials with finite pulse-width $1/\alpha$ and large network sizes ($N$)

$N \to \infty$ Limit

- The instabilities of the LW-modes determine the stability domain of the splay state, this corresponds to the Abbott-van Vreeswijk mean field analysis (PRE 1993)
- The spectrum associated to the SW-modes is fully degenerate

$$\omega_k \equiv 0 \qquad \lambda_k \equiv 0$$

- The splay state is always unstable for inhibitory coupling
- For excitatory coupling there is a critical line in the $(g, \alpha)$-plane dividing unstable from marginally stable regions

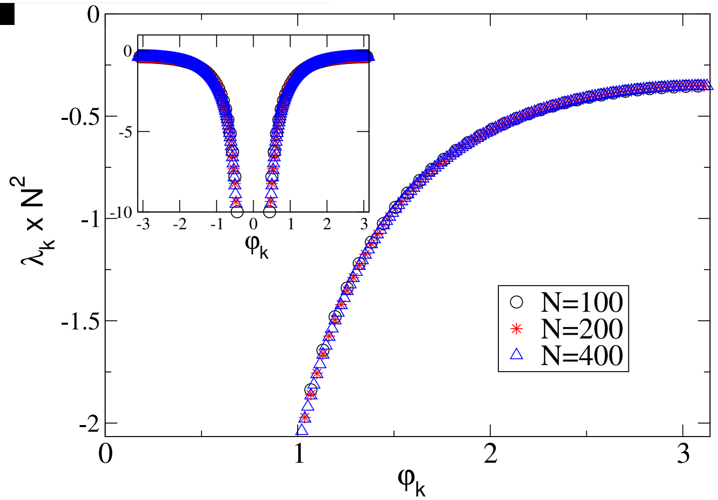


Zillmer, Livi, Politi, AT, Physical Review E (2007)

# Finite Network – LIF

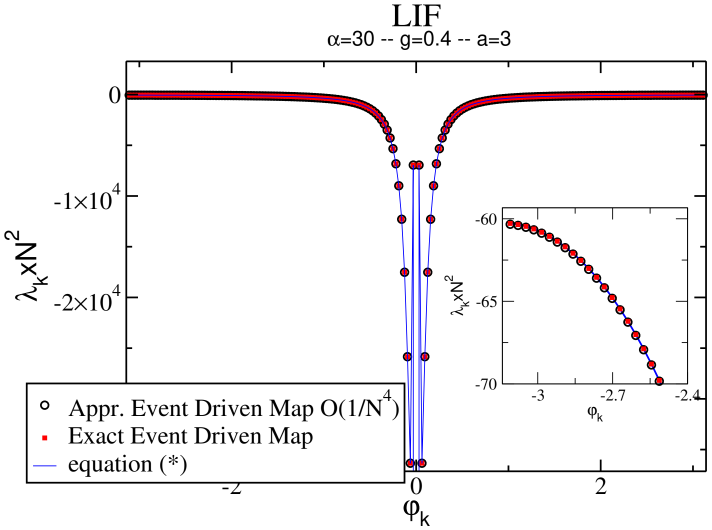
In finite networks,

- Splay state are strictly stable;
- the maximum Floquet exponent approaches zero from below as $1/N^2$



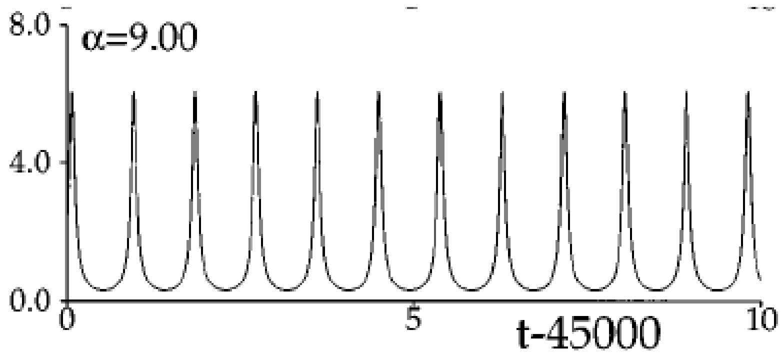
- A perturbative expansion $O(1/N^2)$ of the Floquet matrix is sufficient to well reproduce the Floquet spectrum

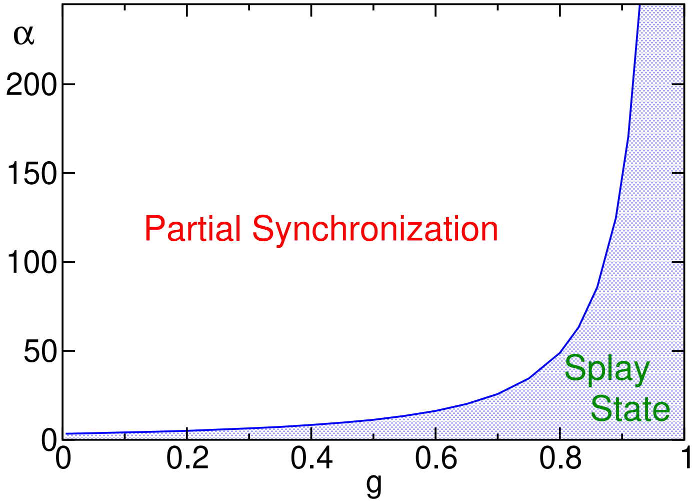
$$\lambda_k * N^2 = \frac{g\alpha^2}{12T^2}(\mathrm{e}^T - 2 + \mathrm{e}^{-T})\left[1 + \frac{6}{(\cos\phi_k - 1)}\right]$$



Calamai, Politi, AT, Physical Review E (2009)

# Partial Synchronization



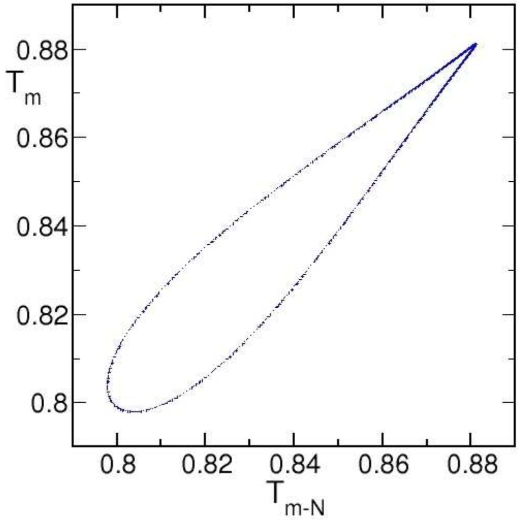


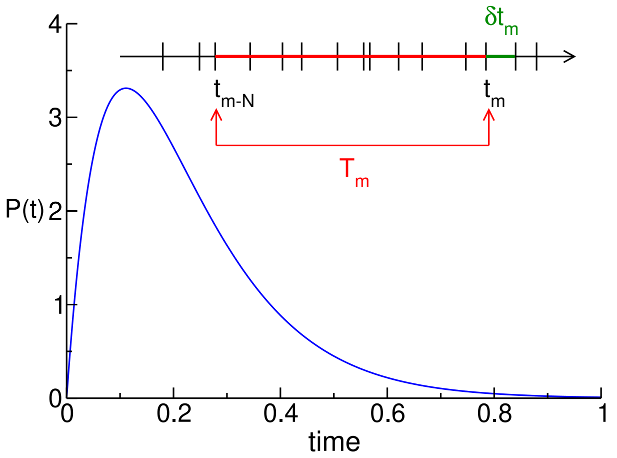
Partial Synchronization is a collective dynamics emerging in Excitatory Homogeneous Networks for sufficiently narrow pulses

- 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



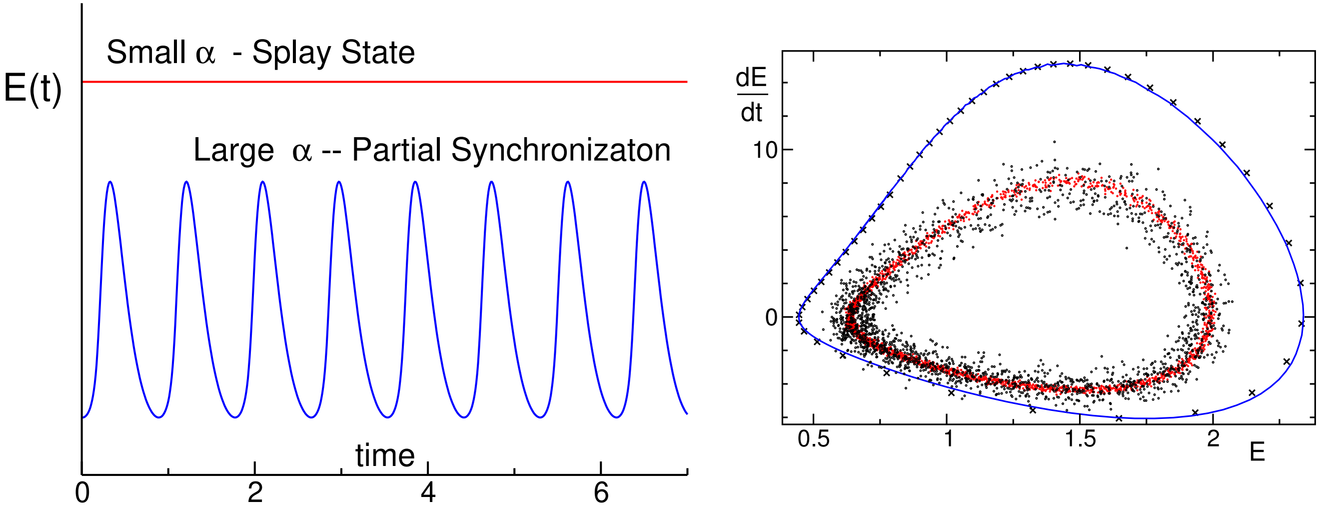


The dynamics of each neuron is quasiperiodic, this can be shown by reporting the Interspike Interval (ISI)of a single neuron $T_m = t_m - t_{m-N}$ versus the previous one $T_{m-N}$ where $\{t_m\}$ is the sequence of the firing times.

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

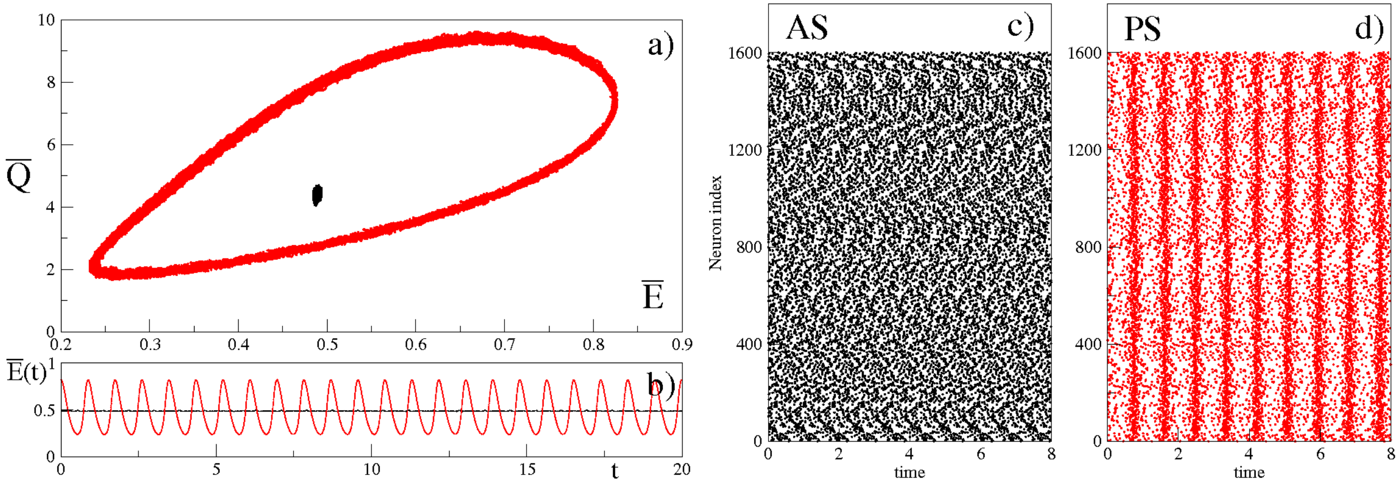
T(t)



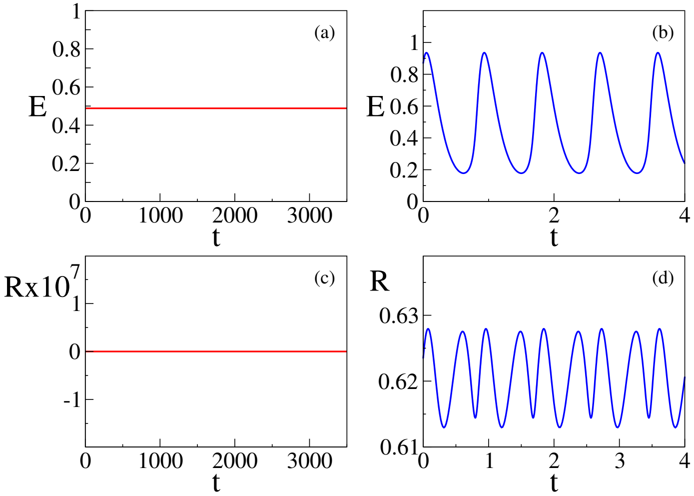
The ratio between the period of the field $E(t)$ and the average ISI of the single neurons is irrational

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)`

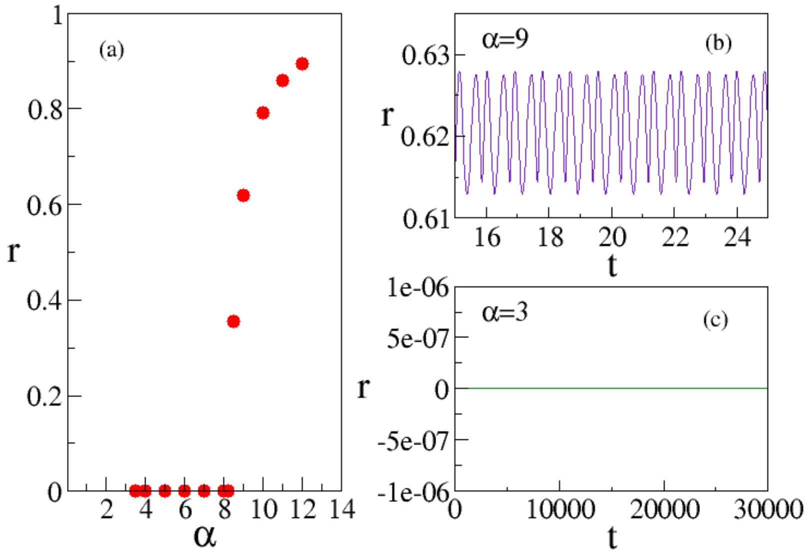
# Splay vs Partial Synchronization



- The Splay State is Asynchronous
- Partially Synchronized exhibit collective dynamics

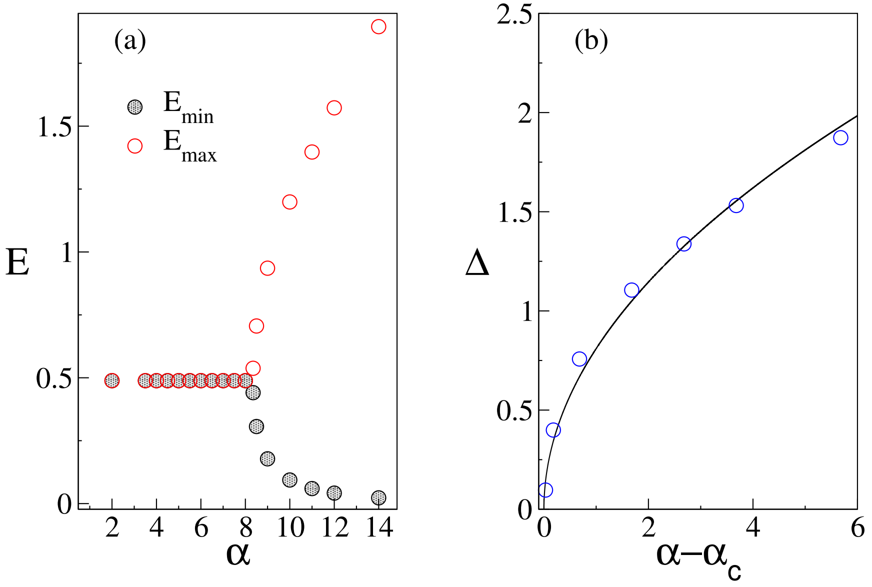


# Bifurcation



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

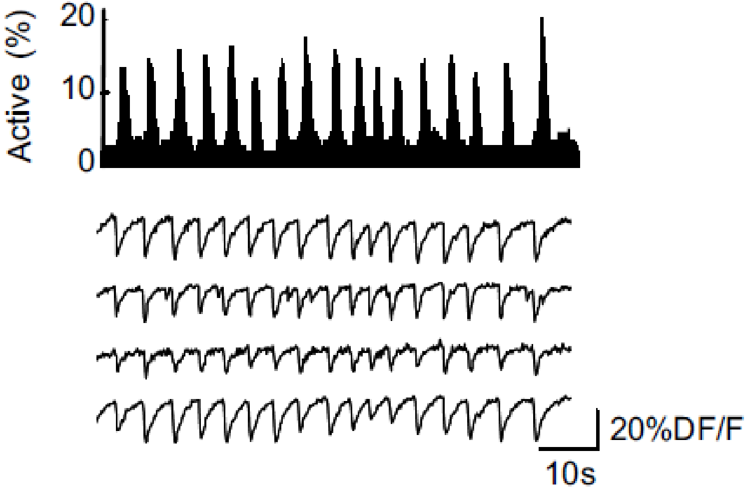
$$\Delta \propto \sqrt{\alpha - \alpha_c}$$



# 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

# Chimera

La Chimera d'Arezzo
Etruscan Art

In Greek mythology, Chimera was a monstrous fire-breathing female creature of Lycia in Asia Minor, composed of the parts of multiple animals: upon the body of a male lion with a tail that terminated in a snake's head, the head of a goat arose on her back at the center of her spine (Wikipedia)

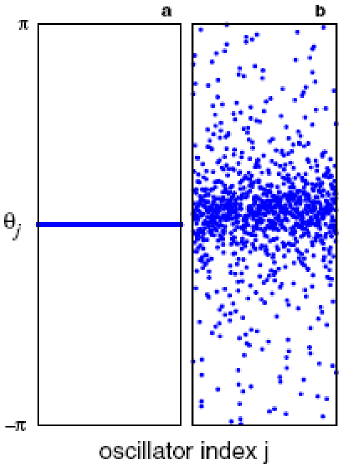
# Chimera in Oscillator Population

Let us consider two oscillator populations $\{\theta^a\}$ and $\{\theta^b\}$ made of identical oscillators, where each oscillator is coupled to equally to all the others in its group, and less strongly to those of the other group

$$\frac{d\theta_i^a}{dt} = \omega + \frac{\mu}{N}\sum_{j=1}^{N}\sin(\theta_j^a - \theta_i^a - \alpha) + \frac{\nu}{N}\sum_{j=1}^{N}\sin(\theta_j^b - \theta_i^a - \alpha) \qquad \mu > \nu$$

Simulations of the 2 populations reveals two different dynamical behaviours

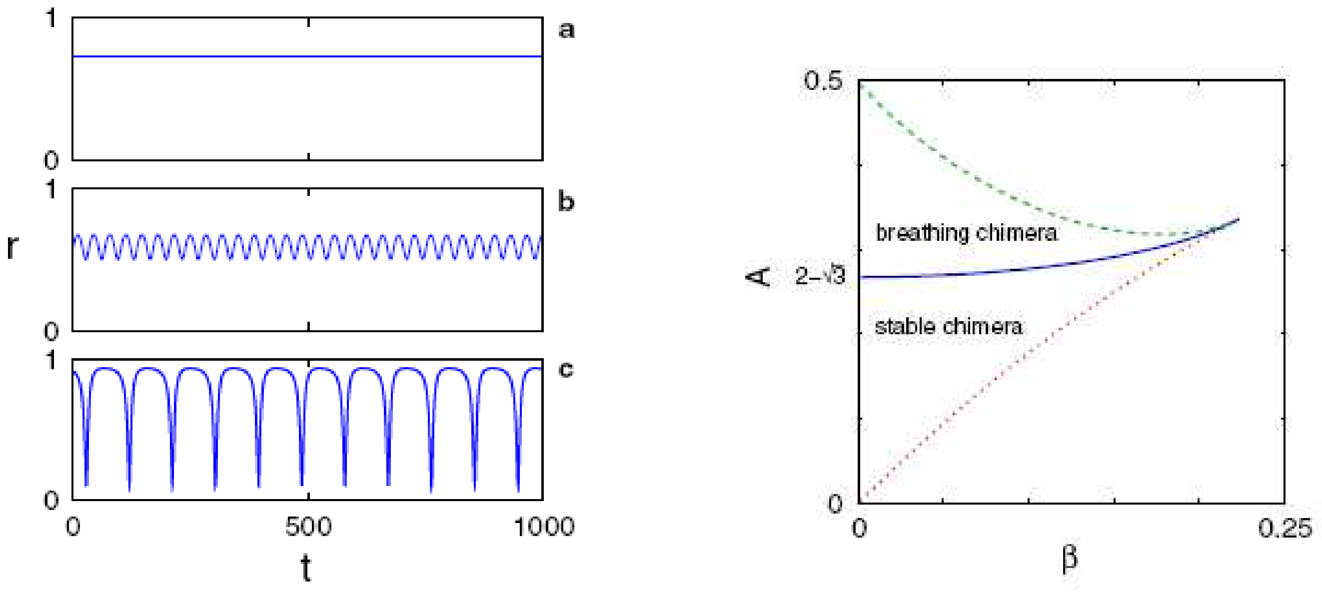
- Synchronized state $r = 1$
- A Chimera State: one population is synchronized and the other not



The oscillators are identical and symmetrically coupled : the Chimera State emerges from a spontaneous symmetry breaking

`Abrams, Mirollo, Strogatz, Wiley,`
`Phys. Rev. Lett 101 (2008) 084103`

# Chimera States

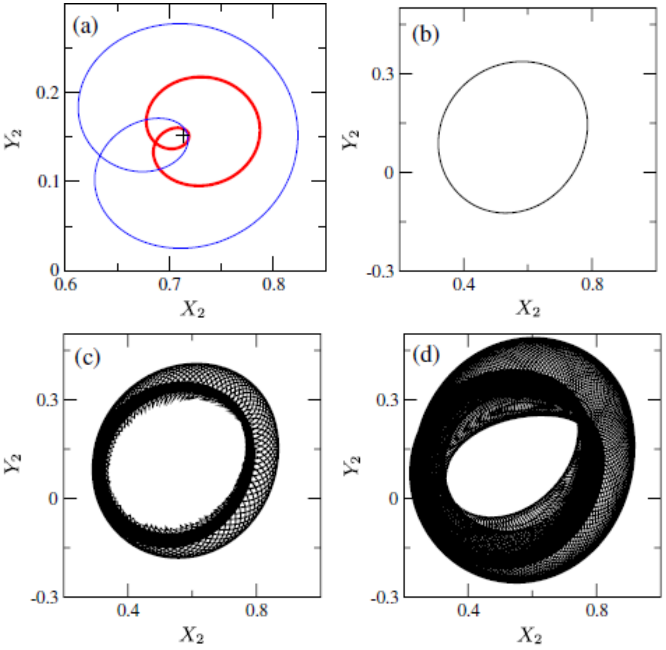


$$A = \mu - \nu \qquad \beta = \frac{\pi}{2} - \nu$$

By increasing $A$ one observes:

- the chimera stays stationary
- the stationary state looses stability and the chimera starts to breathe
- at a critical $A_c$ the breathing period become infinite,
- beyond $A_c$ the chimera disappears and the synchronized state becomes a global attractor

# Quasiperiodic Chimeras



Order parameter for the non-synchronized family of oscillators

$$X_2 + iY_2 = r_2 \mathrm{e}^{i\Theta_2} = \frac{1}{N}\sum_{j=1}^{N} \mathrm{e}^{i\theta_j}$$

A. Pikovsky and M. Rosenblum, Phys. Rev. Lett 101 (2008) 264103

Collective chaos can be observed in more complex models ...