Chimera States and Collective Chaos in neural networks

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Study of the dynamical regimes emerging in pulse coupled networks composed by very simple neuronal models (Leaky Integrate-and-Fire (LIF) neurons).

- Collective solutions in fully coupled excitatory LIF networks
  - Splay States
  - Partial Synchronization
- Collective solutions in two symmetrically coupled neural networks
  - Chimera States - First evidence in neural networks
  - Collective (high-dimensional) chaos
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 hippocampus 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
Collective Periodic Oscillations

Theoretical studies of fully coupled excitatory networks of LIF neurons have revealed the onset of macroscopic collective periodic oscillations (CPOs):

- the collective oscillations are a manifestation of a Partial synchronization
- the macroscopic period of the oscillations does not coincide with the average interspike-interval ISI (T) of the single neurons and the two quantities are irrationally related

Since real neural circuits are not fully connected, it is important to investigate the role of dilution for the stability of CPO
Leaky integrate-and-fire model

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

$$\tau \dot{v} = -(v - v_r) + I$$

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

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

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

More formally we can rewrite the dynamics as

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

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

The above set of $N + 2$ continuous ODEs can be reduced to a time discrete $N + 1$-d event driven map describing the evolution of the system between a spike emission and the next one.
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

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

with $\tau(n) = \ln \left[ \frac{v_q(n)-a}{1-gF(n)-a} \right]$ where $F(n) = F[E(n), Q(n), \tau(n)]$ and the index $q$ labels the neuron closest to threshold at time $n$. 
In a network 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 $j(n) = i - n \text{ Mod } N$;
- 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:

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

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.
For **fully coupled networks** the membrane potentials $v$ displays only **regular solutions**: periodic or quasi-periodic

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

Depending on the shape of the pulse (**value of $\alpha$**):

- **Excitatory Coupling** - $g > 0$
  - Low $\alpha$ – Splay State
  - Larger $\alpha$ – Partially Synchronized State
  - $\alpha \to \infty$ – Fully Synchronized State

- **Inhibitory Coupling** - $g < 0$
  - Low $\alpha$ – Fully Synchronized State
  - Larger $\alpha$ – Several Synchronized Clusters
  - $\alpha \to \infty$ – Splay State
Splay States are collective solutions emerging in Homogeneous Networks of $N$ neurons

- the dynamics of each neuron is periodic
- the field $E(t)$ is constant (fixed point)
- 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

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 $E(t)$


This peculiar collective behaviour has been recently discovered by Rosenblum and Pikovsky PRL (2007) in a system of nonlinearly coupled oscillators
Two fully coupled networks, each made of \( N \) LIF oscillators

\[
\dot{v}_j^{(k)}(t) = a - v_j^{(k)}(t) + g_s E^{(k)}(t) + g_c E^{(1-k)}(t)
\]

\[
\ddot{E}^{(k)}(t) + 2\alpha \dot{E}^{(k)}(t) + \alpha^2 E^{(k)}(t) = \frac{\alpha^2}{N} \sum_{j,n} \delta(t - t_{j,n}^{(k)}), \quad (k = 0, 1)
\]

- \( g_s > 0 \) self-coupling strength of the excitatory interaction
- \( g_c > 0 \) cross-coupling strength of the excitatory interaction
Macroscopic Attractors

- $g_s \equiv g_c$ Partial Synchronization (PS)
- $g_s < g_c$ Fully Synchronized (FS)
- $g_s > g_c$ Spontaneous Symmetry Breaking
  - Breathing Chimera: FS + PS
  - Generalized Chimera: PS1 + PS2

Symmetric States
- AntiPhase Partial Synchronization
- Torus
- Collective Chaos

Kuramoto parameter

$$r^{(k)}(t) = \left| \langle e^{i\theta_j^{(k)}(t)} \rangle \right|$$

$$\theta_j^{(k)}(t) = 2\pi \frac{t - t_{j,n}^{(k)}}{t_{q,n}^{(k)} - t_{q,n-1}^{(k)}}$$ phase of the $j$–th oscillator
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.

\[
\frac{d\theta^a_i}{dt} = \omega + \frac{\mu}{N} \sum_{j=1}^{N} \sin(\theta^a_j - \theta^a_i - \alpha) + \frac{\nu}{N} \sum_{j=1}^{N} \sin(\theta^b_j - \theta^a_i - \alpha) \quad \mu > \nu
\]

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.

Chimera States

\[ A = \eta - \nu \quad \beta = \frac{\pi}{2} - \nu \]

By increasing \( A \) one observes:

- the chimera stays stationary
- the stationary state loses stability and the chimera starts to breathe
- at a critical \( A_c \) the breathing period becomes infinite,
- beyond \( A_c \) the chimera disappears and the synchronized state becomes a global attractor
Collective Chaos

Collective chaos, meant as irregular dynamics of coarse-grained observables, has been found in ensembles of fully coupled one-dimensional maps as well as in two-dimensional continuous-time oscillators (Stuart-Landau oscillators).

What happens to one-dimensional phase oscillators’ ensembles which cannot become chaotic under external forcing?

The oscillator with sinusoidal force fields (Kuramoto-like) have at maximum 3 degree of freedoms, no space for high-dimensional chaotic behaviour, few numerical evidences of collective irregular dynamics.

LIF neural networks have no this kind of limitations.

The Finite Amplitude Lyapunov exponent $\lambda_F$ can be determined from the growth rate of a small finite perturbation for different amplitudes $\Delta$ of the perturbation itself (after averaging over different trajectories).

[E. Aurell et al. PRL (1996)]
High-Dimensional Chaos

- Large part of the spectrum vanishes for $N \to \infty$

- In the thermodynamic limit, the dynamics of globally coupled identical oscillators can be viewed as that of single oscillators forced by the same field

- The numerically computed conditional Lyapunov exponent $\lambda_c \leq 0$ of a LIF forced by the self-consistent field is zero

- Few Lyapunov exponents remains positive:
  - $\lambda_1 \to 0.0195(3)$
  - $\lambda_2$ and $\lambda_3$ grow with $N$ and become positive for $N > 200$ (no evident saturation)

- High-dimensional chaos however, we cannot tell whether the number of positive exponents is extensive (proportional to $N$) or sub-extensive
PS have been indentified in Kuramoto models only assuming nonlinear coupling 
[Pikovsky & Rosenblum, PRL (2007)]

Breathing Chimera have been identified also in the two-population setup of 
Kuramoto-like oscillators 
[Abrams, Mirollo, Strogatz, Wiley, PRL (2008)]

Some preliminar indication of low dimensional chaos at a macroscopic level have 
been reported in Kuramoto-like models 
[Golomb, Hansel, Shraiman, Sompolinsky PRA (1992) 
Marvel, Mirollo, Strogatz, Chaos (2009) ]

In the context of LIF symmetrically coupled populations :

- New collective stationary states have been identified (APS and PS1-PS2)
- As well as high-dimensional collective chaos

To what extent are pulse-coupled oscillators equivalent to Kuramoto-like models?

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