Collective oscillations in disordered neural networks

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Summary

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

Investigation of the role played by the excitatory or inhibitory nature of the synapses (couplings among neurons) present in the network

- **Excitatory synapses**
  - Fully coupled networks: non trivial collective solutions (Partial Synchronization (PS))
  - Diluted networks: PS is robust to dilution, but becomes weakly chaotic

- **Inhibitory synapses**
  - Fully coupled networks: the dynamics converges rapidly to periodic patterns
  - Diluted networks: erratic (but non chaotic) long transients
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
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

\[ F(t) = \alpha^2 t e^{-\alpha t} \]
Pulse coupled network

A system of \( N \) identical \textit{all to all} pulse-coupled neurons:

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

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

More formally we can rewrite the dynamics as

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

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

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:

\[ E(n+1) = E(n)e^{-\alpha \tau(n)} + N Q(n) \tau(n)e^{-\alpha \tau(n)} \]

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

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 the comoving 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 potential $v$ displays only regular solutions: periodic or quasi-periodic.

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.
Links are cut with a certain probability $P \rightarrow \epsilon_{ji} = 1, 0$ – Erdös-Renyi Networks

\[
\dot{v}_i = I - v_i + \frac{g}{N} E_i(t)
\]

\[
\ddot{E}_i(t) + 2\alpha \dot{E}_i(t) + \alpha^2 E_i(t) = \alpha^2 \sum_{n \mid t_n < t} \epsilon_{ji} \delta(t - t_n).
\]

- To each neuron $i$ is associated a different field $E_i(t)$
- Excitatory Coupling $g > 0$ and Finite Pulse Width

Two strategies are chosen to introduce disorder in the network

- quenched $\rightarrow$ the coupling matrix $\epsilon_{ji}$ is fixed
- annealed $\rightarrow$ the coupling matrix $\epsilon_{ji}$ is dynamically generated
Phase I: the average field $\bar{E}(t)$ covers a small cloud of points

Phase II: the average field $\bar{E}(t)$ is almost periodic

- Perturbed Splay and Partially Synchronized States are still observable
- For finite $N$ these states exhibit fluctuations around the unperturbed (fully coupled) attractors: the attractors are structurally stable
- These states are weakly chaotic

\[
\bar{E}(t) = \frac{1}{N} \sum_{k=1}^{N} E_k(t)
\]
\[
\bar{Q}(t) = \frac{1}{N} \sum_{k=1}^{N} Q_k(t)
\]

where $Q = E + \alpha \dot{E}$
Quenched as well as annealed attractors converge to an asymptotic shape in the limit $N \to \infty$.

A random network behaves like a homogeneous globally coupled system with a rescaled value of the coupling constant

$$g_{\text{eff}} = g \ast P$$

to account for the different fraction of active links.

[S. Olmi, R. Livi, A. Politi, A. Torcini, PRE 81, 046119 (2010)]
Finite Size Effects

In order to measure the finite-size corrections, we consider \( \Delta \bar{Q} = \langle \bar{Q} \rangle(N) - \langle \bar{Q} \rangle(\infty) \), where \( \langle \cdot \rangle \) is the (time) average of the \( \bar{Q} \)-value of all the configurations falling in a certain window \( (0.36 \leq g \bar{E}(n) \leq 0.44) \).

To measure the degree of synchronization among the various fields we have computed the STD \( \sigma(n) \) of the instantaneous fields

\[
\sigma(n) = \left( \frac{\sum_{i=1}^{N} E_i^2(n)}{N} - \bar{E}^2(n) \right)^{1/2}.
\]

The fields tend to synchronize for increasing \( N \).
Lyapunov Spectra

**Fully Coupled Case**

- A vanishing of the first band as $\lambda_k \propto 1/N^2$ for the splay and the partially synchronized states.
- A constant second band $\lambda_k = -\alpha$ due to the $2N$ identical fields.

**Diluted Case**

- The shape of the first band depends on the random network realization in the quenched case.
- The second band is no more constant, the fields are no more identical.
By removing a small amount of links the system (at finite $N$) becomes chaotic.

Chaos disappears in the $N \to \infty$ limit and regular solutions are recovered.

The scaling of the maximal Lyapunov exponent $\lambda_1$ with $N$ depends on the disorder:

- **Quenched** – $\lambda_1 \sim 1/\sqrt{N}$
- **Annealed** – $\lambda_1 \sim 1/N$

A similar form of weak chaos has been observed in a model of coupled oscillators (Kuramoto model) with quenched disorder.

[O.V. Popovych at al., PRE 71 065201(R) (2005)]
Recent experimental analysis of the developing rodent neocortex have revealed that the (functional) connectivity has a power-law distribution with a large number of hubs

\[ P(C) = C^{-\gamma} \]

\[ \gamma = 1.1 - 1.3 \]

where \( C \) is the number of outgoing connections.


Will CPOs survive also for different topologies?

Preliminary results indicate that CPOs are still present for

- Scale-free networks with \( 1 < \gamma < 2 \)
- Erdös-Renyi networks with \( < C > \propto N^{2-\gamma} \) for \( 1 < \gamma < 2 \)
Which are the key ingredients making these Partially Synchronized States robust to topological modifications?

[in collaboration with A. Torcini, L. Tattini]

Pikovsky and Rosenblum have revealed the existence of quasi-periodic collective states by considering two coupled families of phase oscillators. Can more complicated regular or even chaotic collective dynamics emerge in pulse coupled networks?

[in collaboration with A. Torcini, A. Politi]

For more information on the Computational Neuroscience Group in Firenze:

http://neuro.fi.isc.cnr.it/