Sequential synchronous activity in neural network

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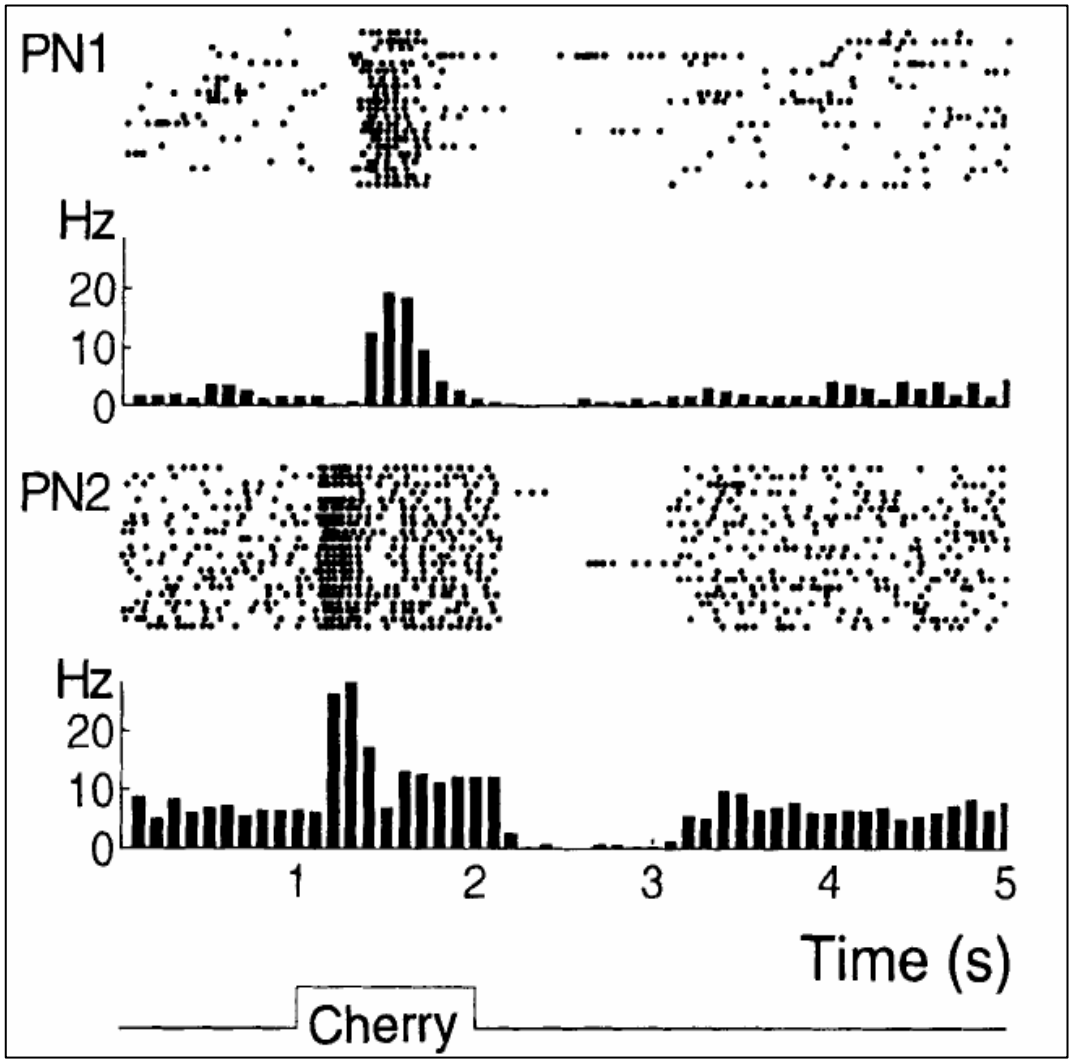
Contents

Introduction

- The responses of neural systems to different external stimuli can show different *transient dynamics* which is the sequential in time switching between different metastable states. (O. Mazor, G. Laurent, Neuron,2005)
- This dynamics *can be* associated with existence of stable heteroclinic channel (SHC) in the phase space of corresponding neural model (V.S. Afraimovich et al. Int. J. of Bifurcation and Chaos, 2004; T. Nowotny and M.I.Rabinovich, PRL, 2007; M.I. Rabinovich et al., Science 2008).

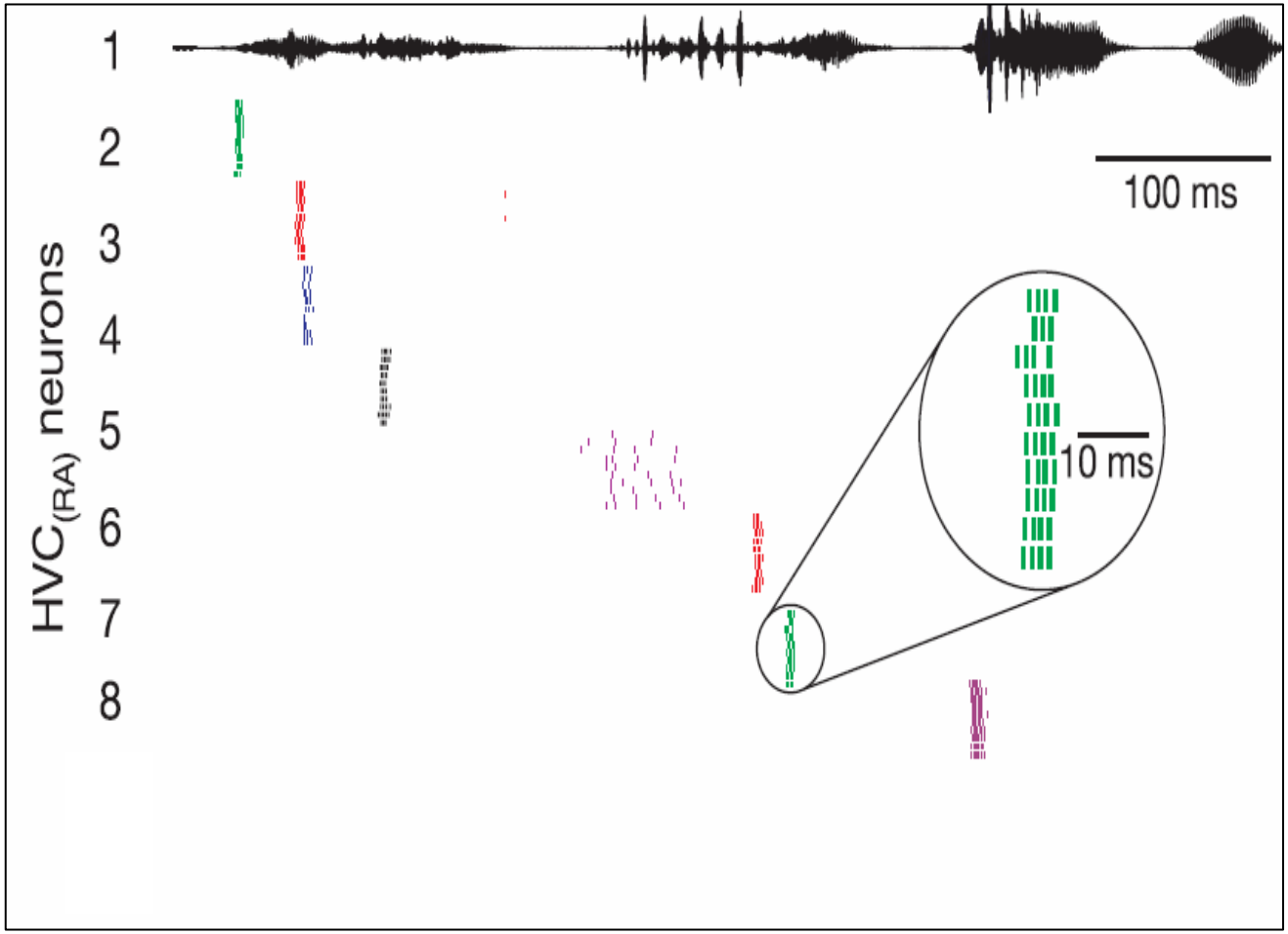
Sequential increasing of frequency of two projection neurons ($PN_{1,2}$) of locust antennal lobe



Odors evoke reliable temporal response patterns in projection neurons. Spike raster plots and histograms of the responses of two simultaneously recorded projection neurons in locust antennal lobe to the odour cherry (21 trials, one trial corresponds to one row).

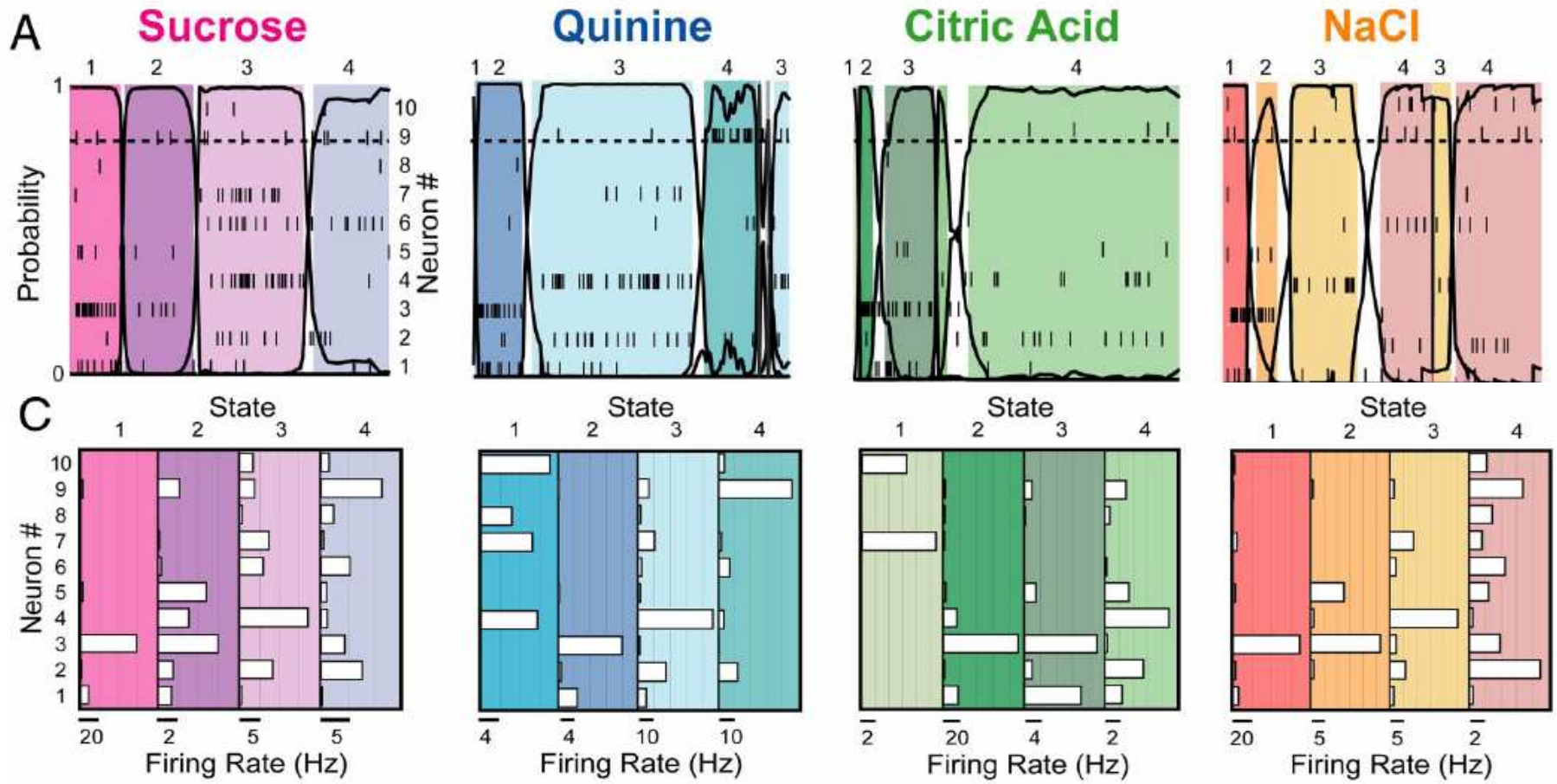
M.Wehr and G. Laurent, Nature, 1996

Sequential activation of neurons in HVC of birds



Spike raster plot of eight $HVC_{(RA)}$ neurons recorded in one bird during singing . Each row of tick marks shows spikes generated during one rendition of the song (ten renditions are shown for each neuron)

R.H.R. Hahnloser et. al. Nature, 2002



Neurons in the rat's gustatory cortex generate a taste-specific sequential pattern. The top row shows the sequential activity among 10 cortex neurons in response to four taste stimuli (the ticks denoting the action potentials). The translation of the four states into firing rates for each stimulus are given on the bottom row.

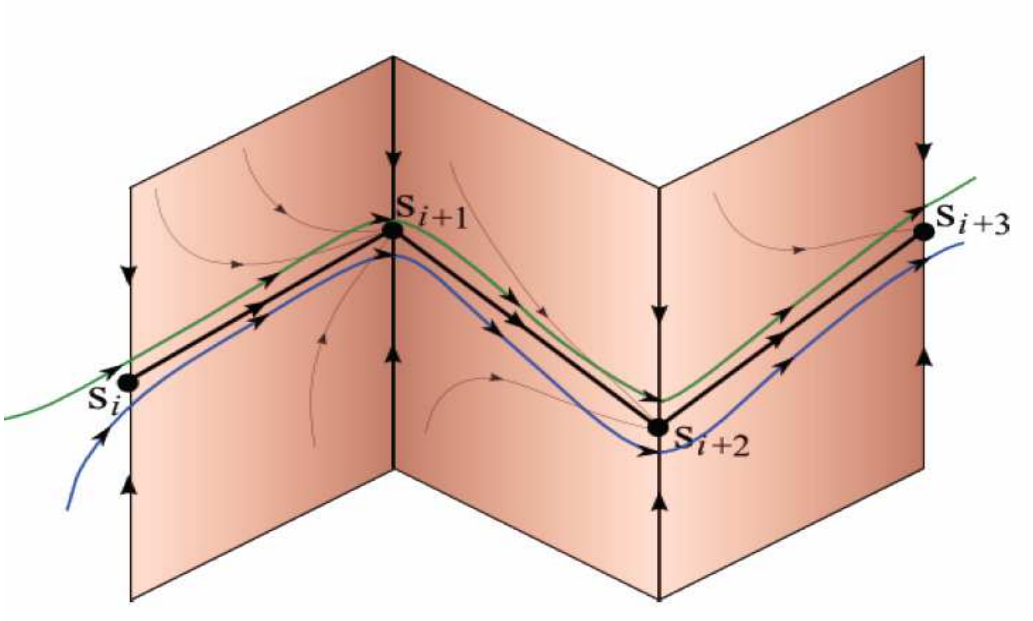
L.M. Jones et. al., PNAS, 2007

Nonlinear dynamics approach to neural system

- Neural activity can be modeled by the system of differential or difference equations. This fact allows to apply well-known methods and approaches of nonlinear dynamics and theory of oscillations to study the neural activity.
- From the point of view of dynamical systems theory we trying to understand various processes which take place in neuronal ensembles, to detect the role of different biological parameters and mechanisms in neural functions, and also to investigate the problems of storing and processing of information.
- One of the major modern hypothesis is the following: sequential dynamics can be modeled by the dynamical system which consist stable heteroclinic channel in the phase space. (M.I.Rabinovich)

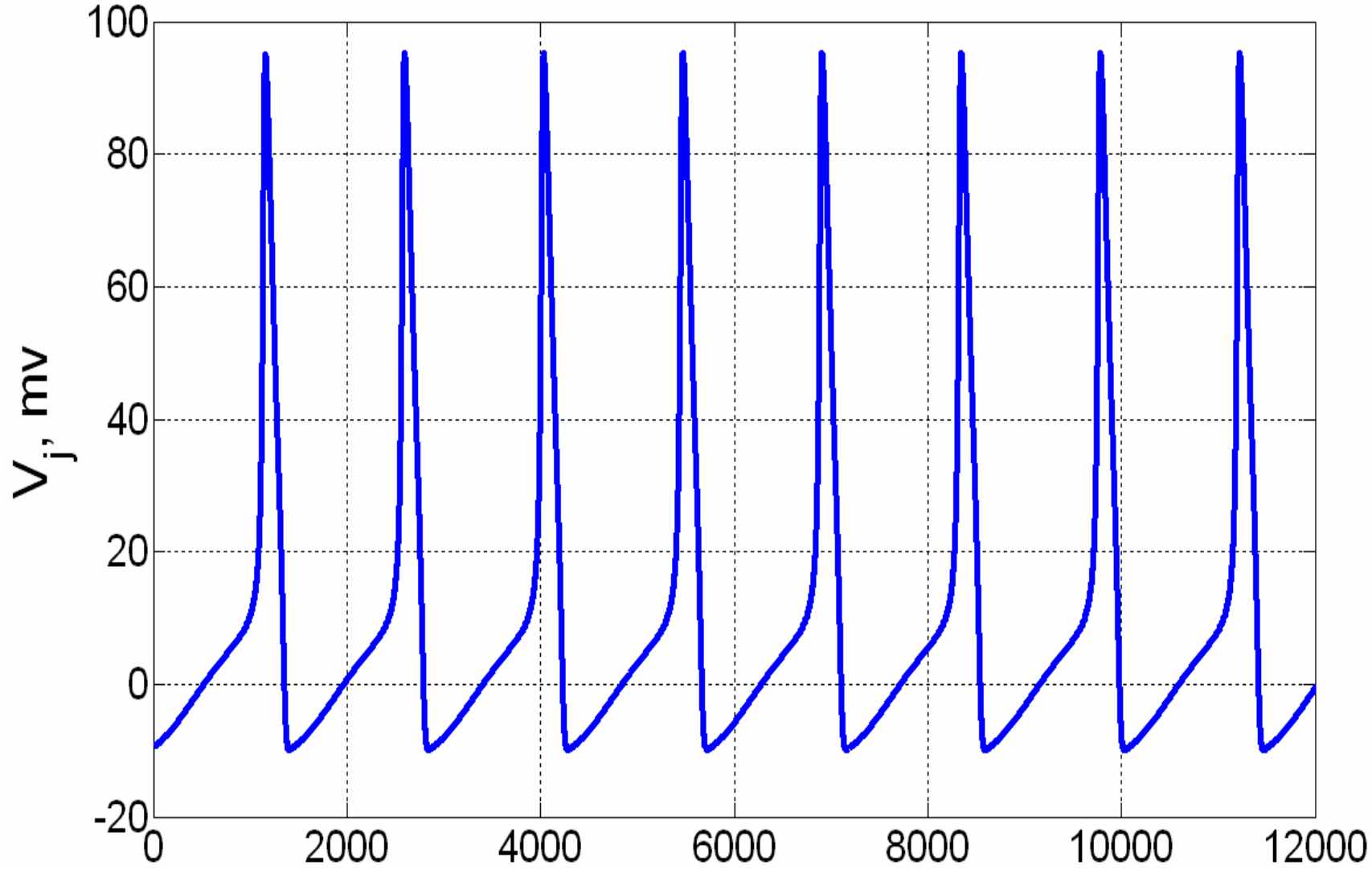
Stable heteroclinic channel (SHC) is a dynamical image of sequential behavior

- SHC is a set of trajectories in the vicinity of heteroclinic skeleton that consists of saddles and unstable separatreces that connect their surroundings (V.S. Afraimovich, 2008)



Mikhail I. Rabinovich, Ramon Huerta, Pablo Varona, Valentin S. Afraimovich
Transient Cognitive Dynamics, Metastability, and
Decision Making. PLOS computational biology, 2008.

Hodgkin-Huxley (H-H) model



Model of chemical synaptic coupling

$$\frac{dS_j}{dt} = \alpha[T](1 - S_j) - \beta S_j$$

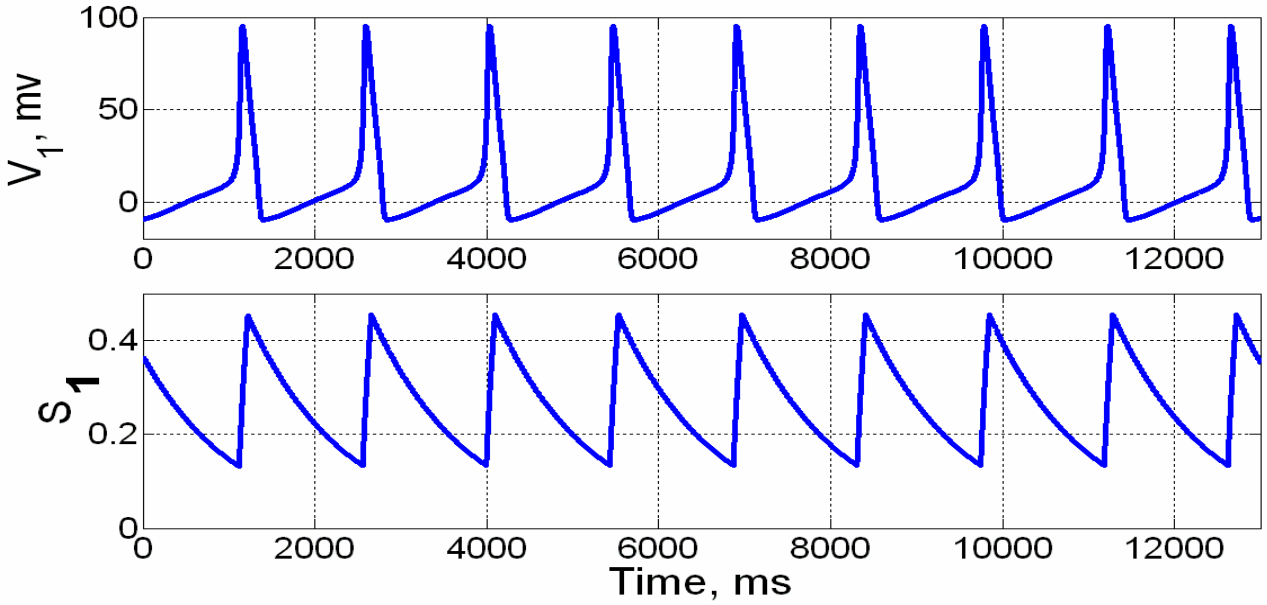
$$I_j^{syn} = \sum_{\substack{i=1 \\ i \neq j}}^{N} g_{ji} S_i(t)(E_{rev} - V_j);$$

[T] – concentration of transmitter

[T] = 1 during 1 ms after spike and [T]=0 otherwise,

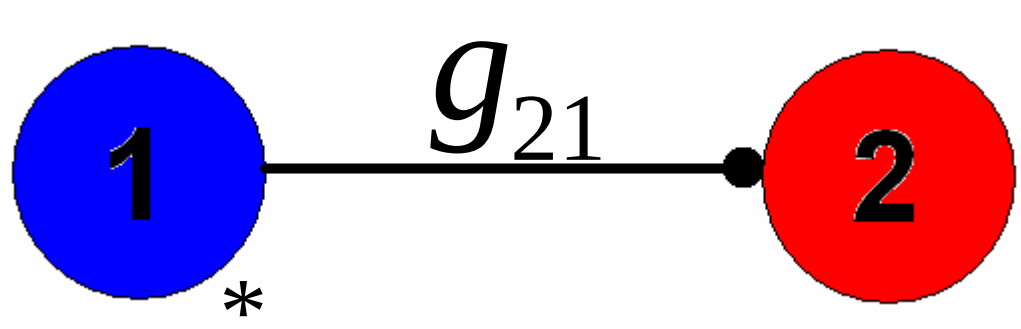
α, β - constants g_{ji} coupling

Time series of membrane potential V and a fraction of bind receptors S

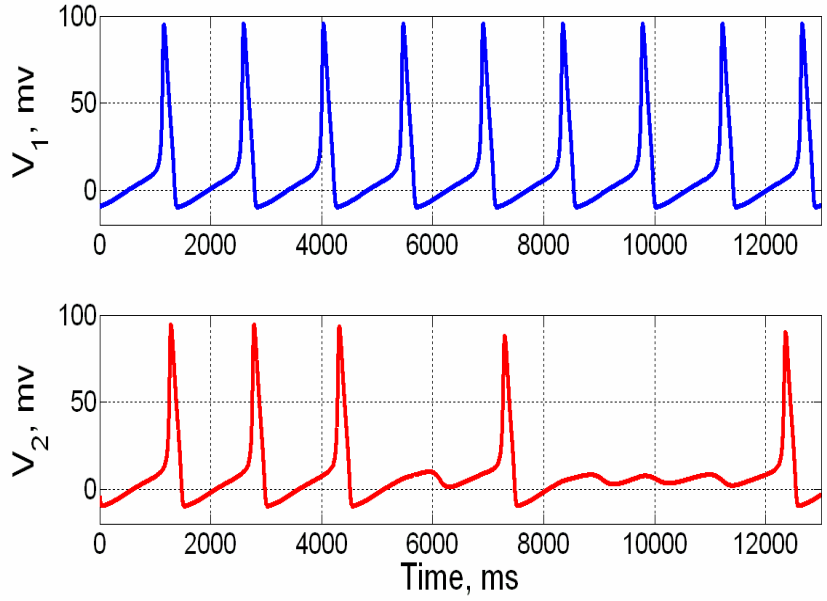


An efficient method for computing synaptic conductances based on a kinetic model of receptor binding
A. Destexhe et.al., Neural computation, 1994

Inhibitory coupling (E_{rev}=-10 mV)

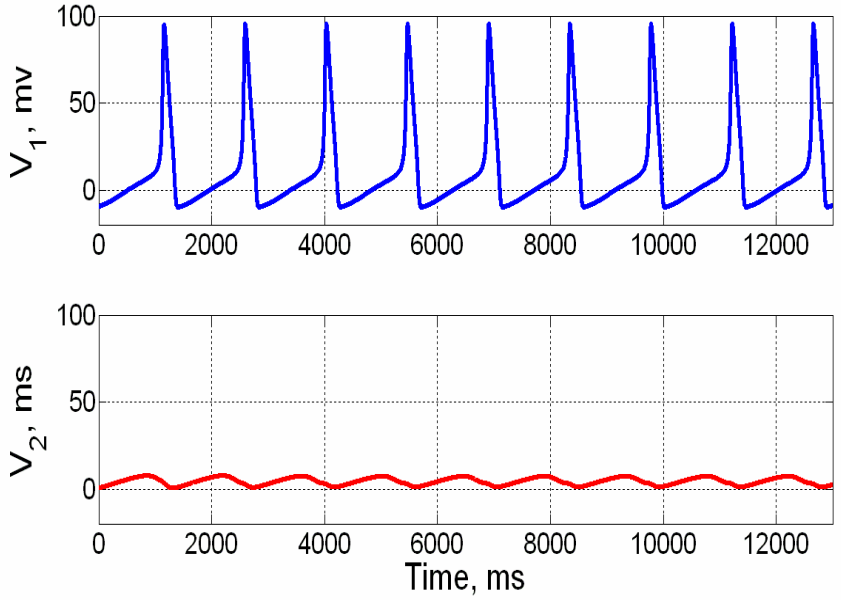


$g_{21} < g^*$



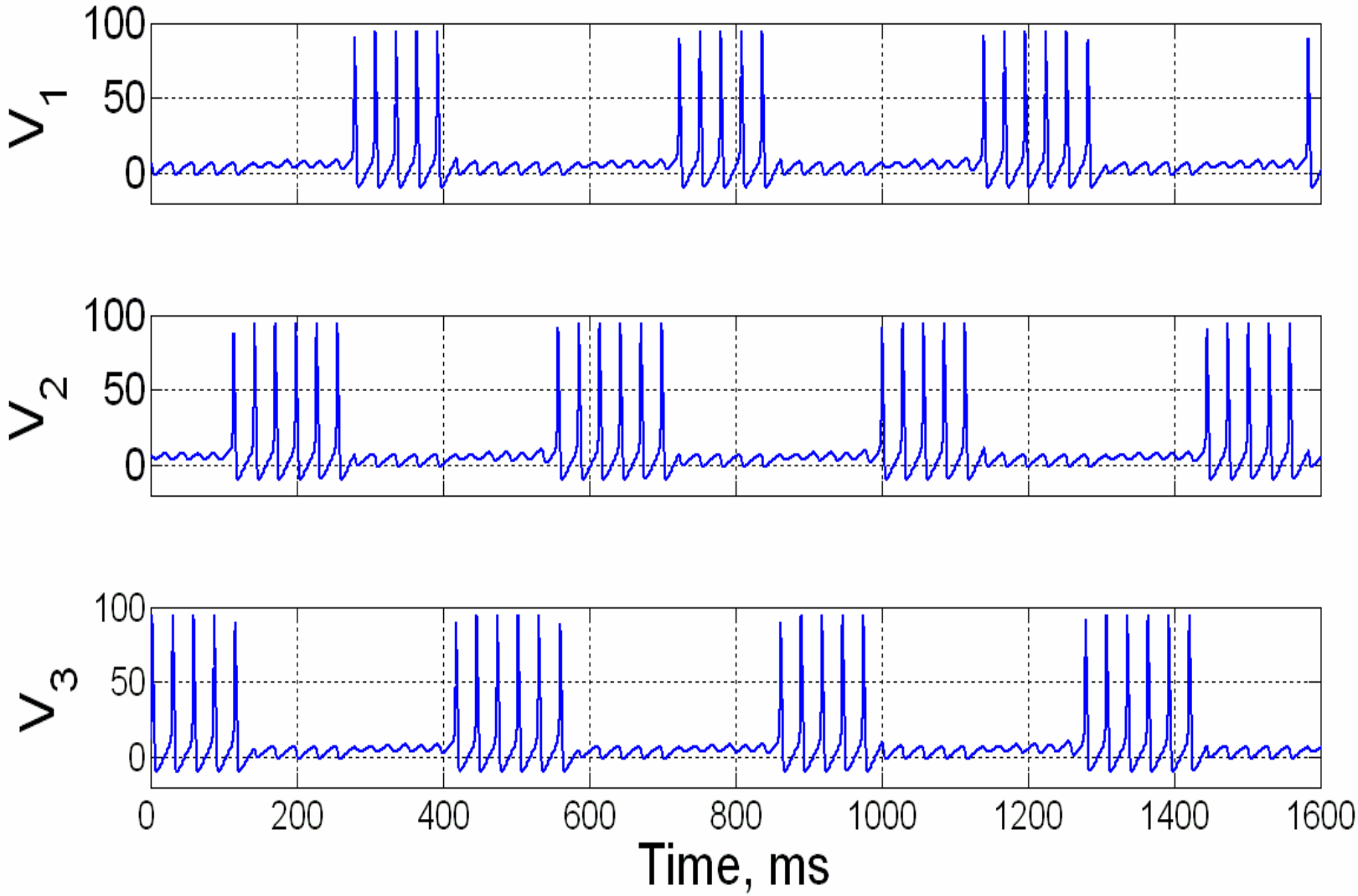
Not enough coupling strength to full suppression of postsynaptic neuron

$g_{21} > g^*$

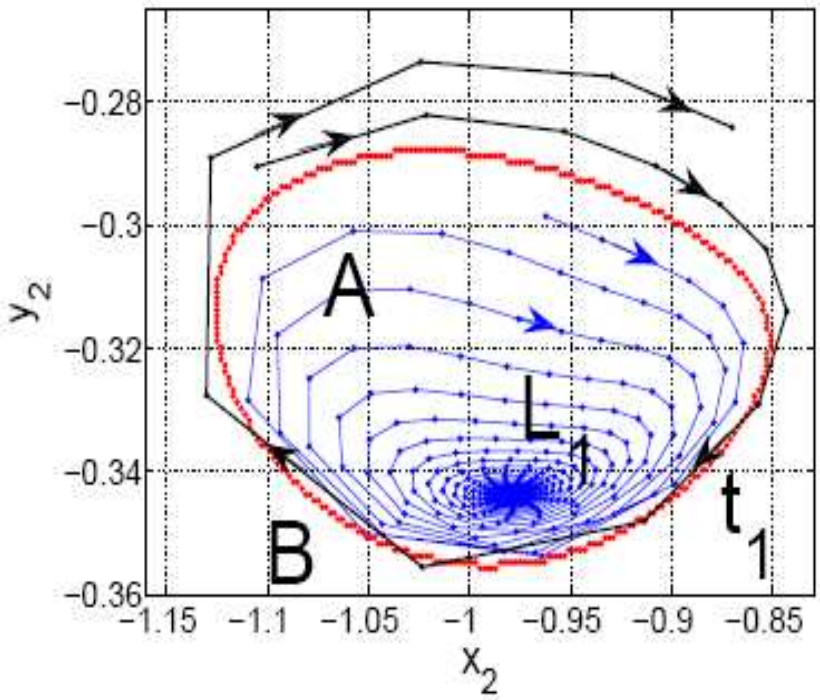


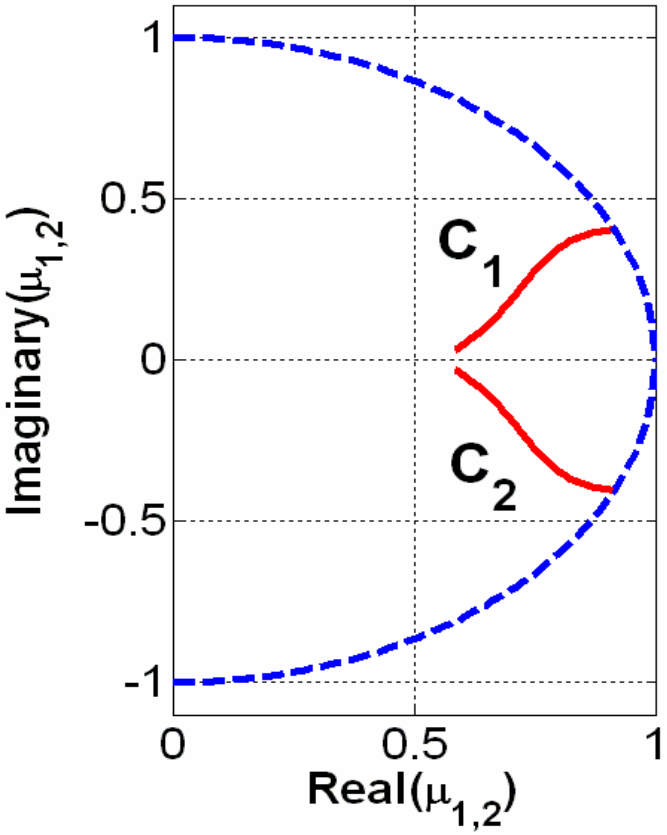
Full suppression (subthreshold oscillations in postsynaptic neuron)

Winnerless competition principle



Bifurcation in the models of the second type of excitability (H-H, *Bonhoeffer-Van der Pol*). We change a coupling.

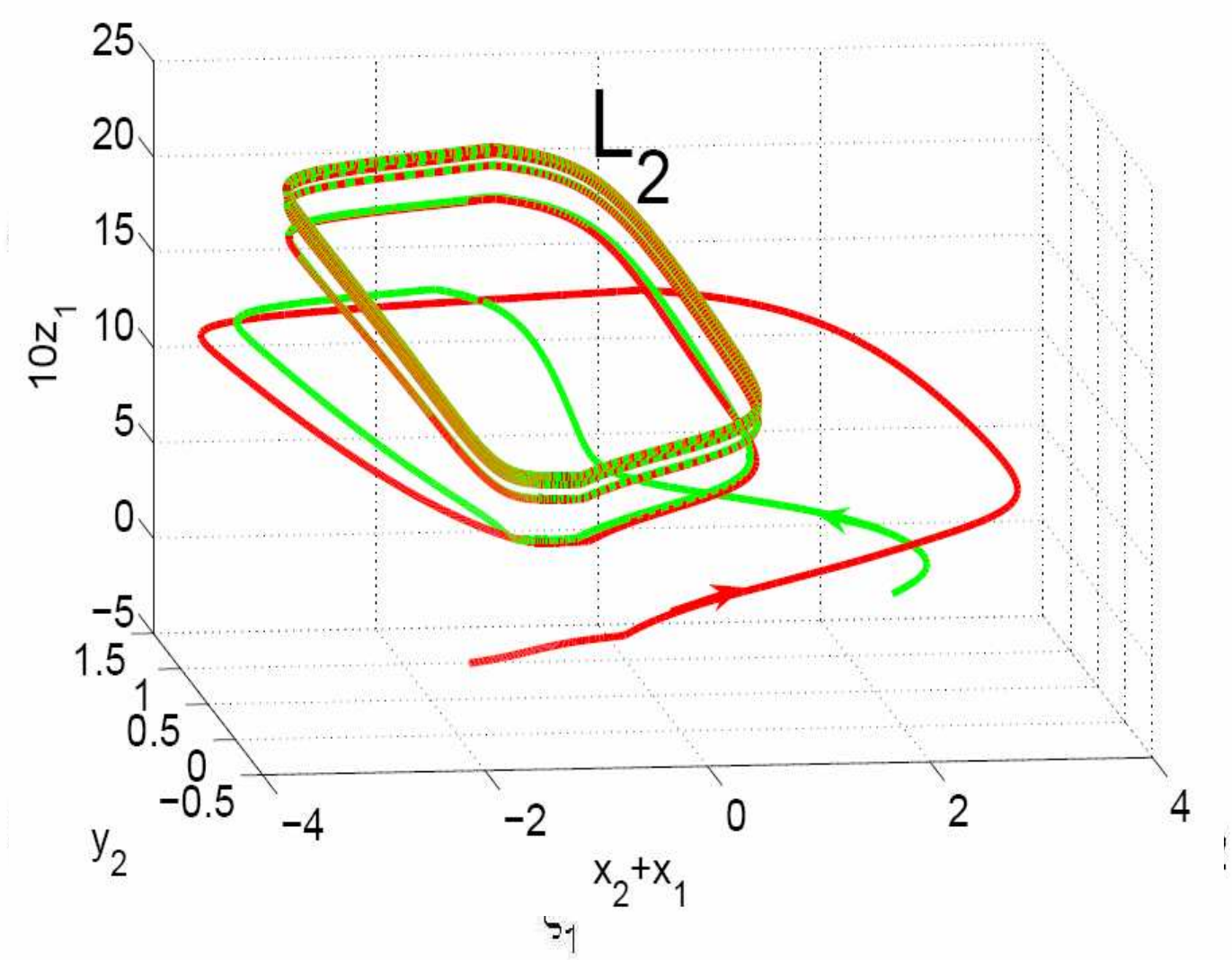




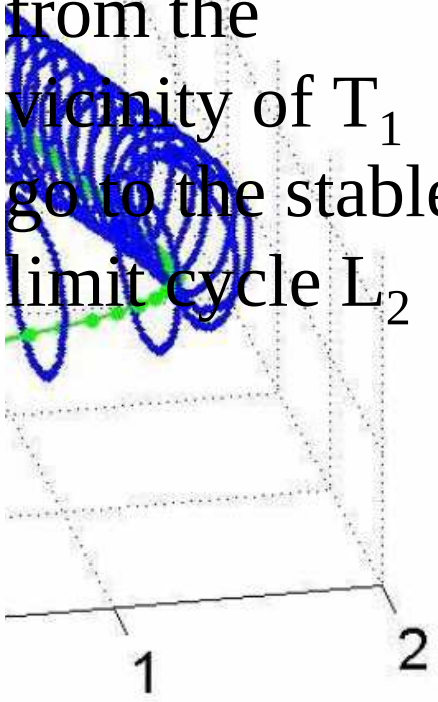
Red line – cross-section of saddle torus T_1 with the plane (x2,y2). Trajectories from the region B go to the stable limit cycle L_2, trajectories from the region A go the stable limit cycle L_1

$\mu_{1,2}$ – multipliers of the limit cycle L_1

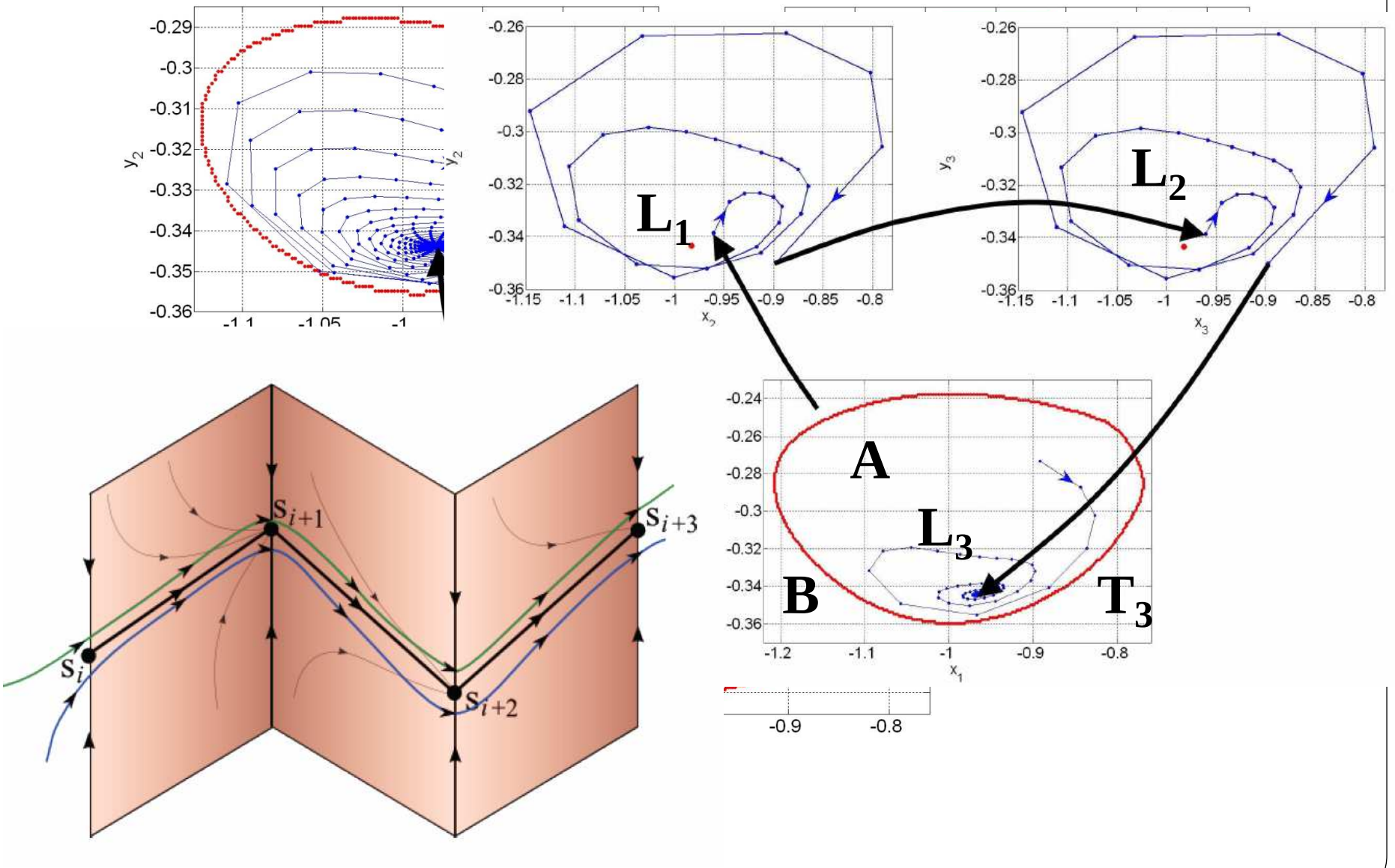
Unstable torus T1 and stable limit cycle L1.



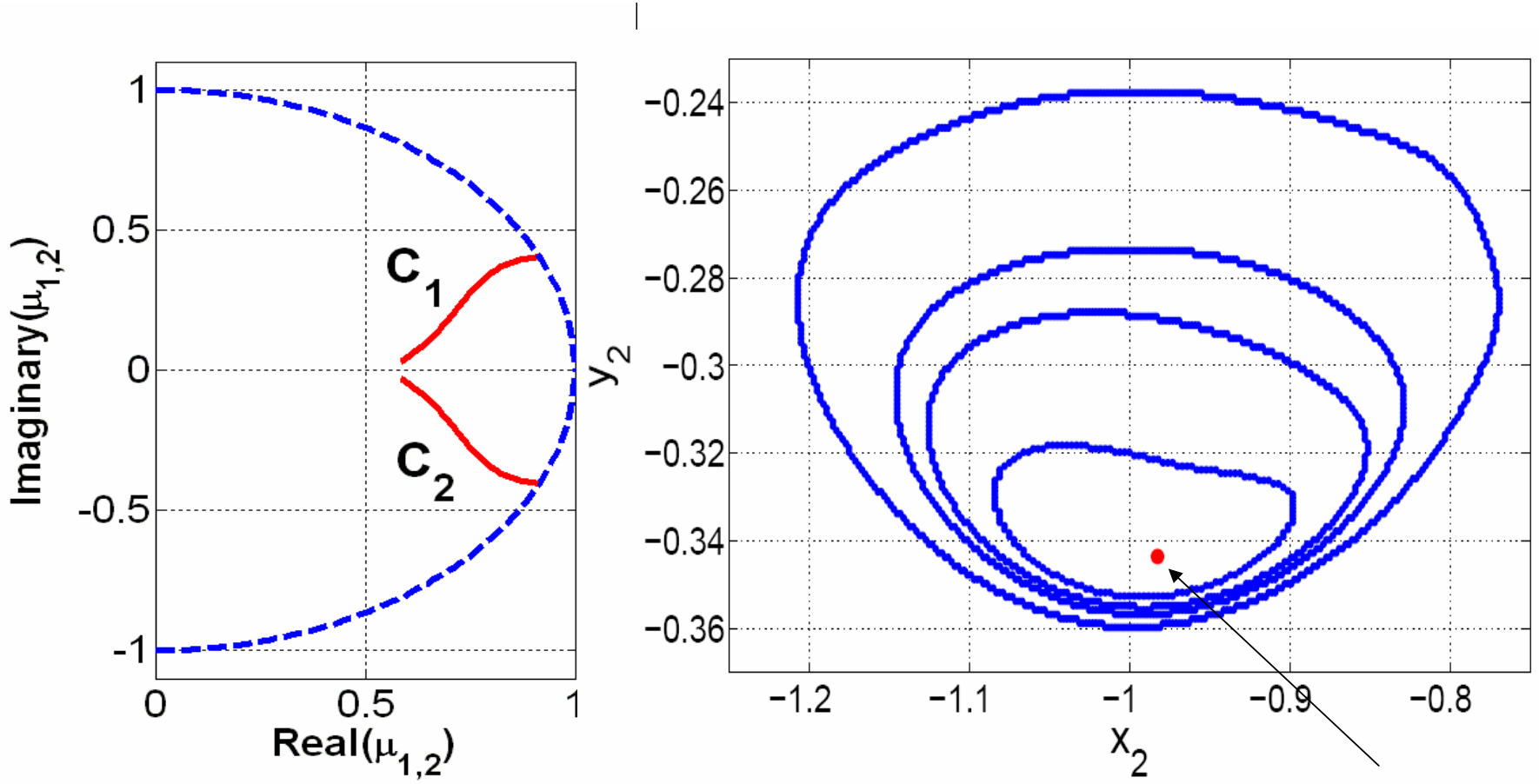
Trajectories (red and green) from the vicinity of T_1 go to the stable limit cycle L_2



Schematic illustration of trajectories



Saddle torus merges in the stable limit cycle – subcritical Neimark-Sacker bifurcation



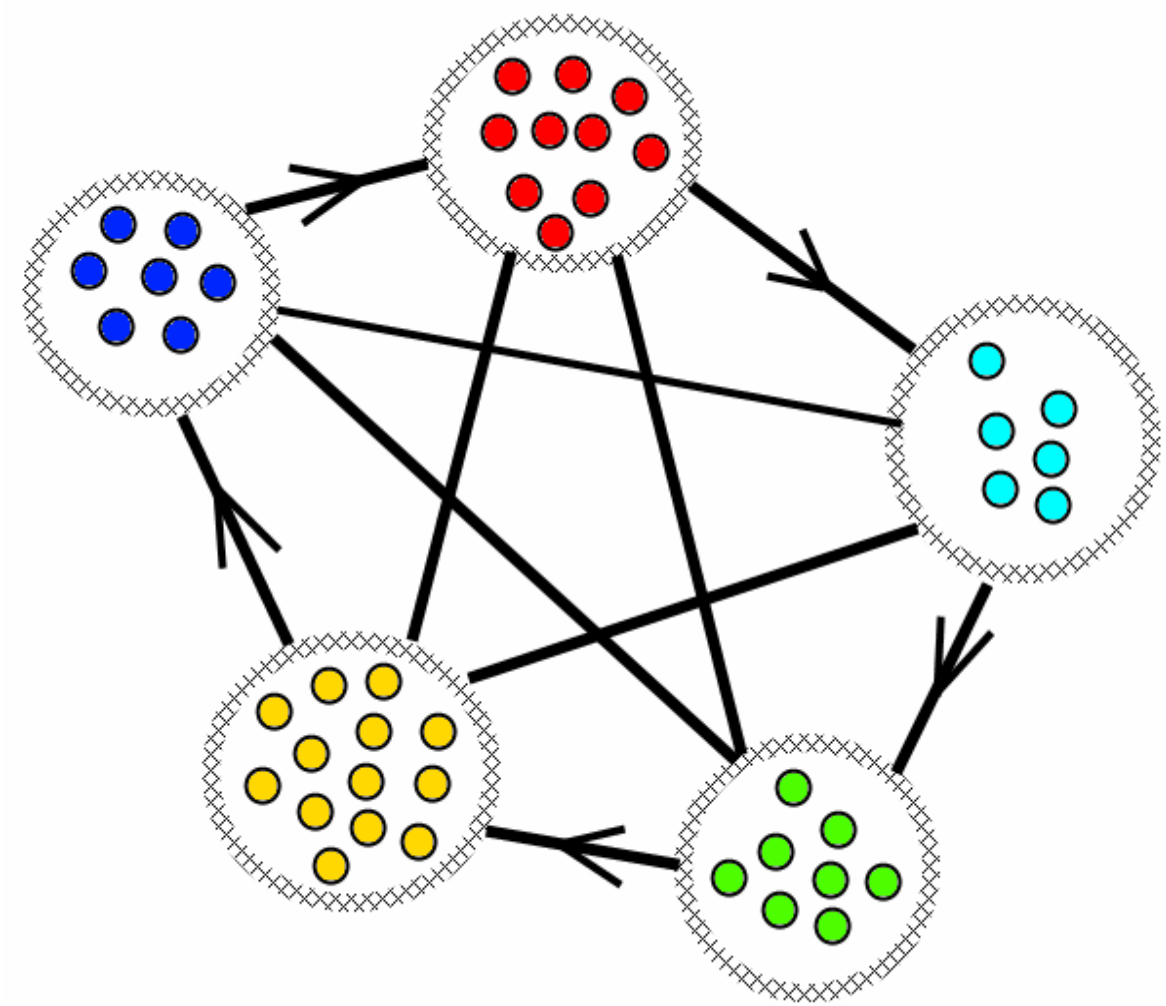
Change of coupling strength. Multipliers and torus cross-section

L_1

Sequential switching between **clusters** of neurons

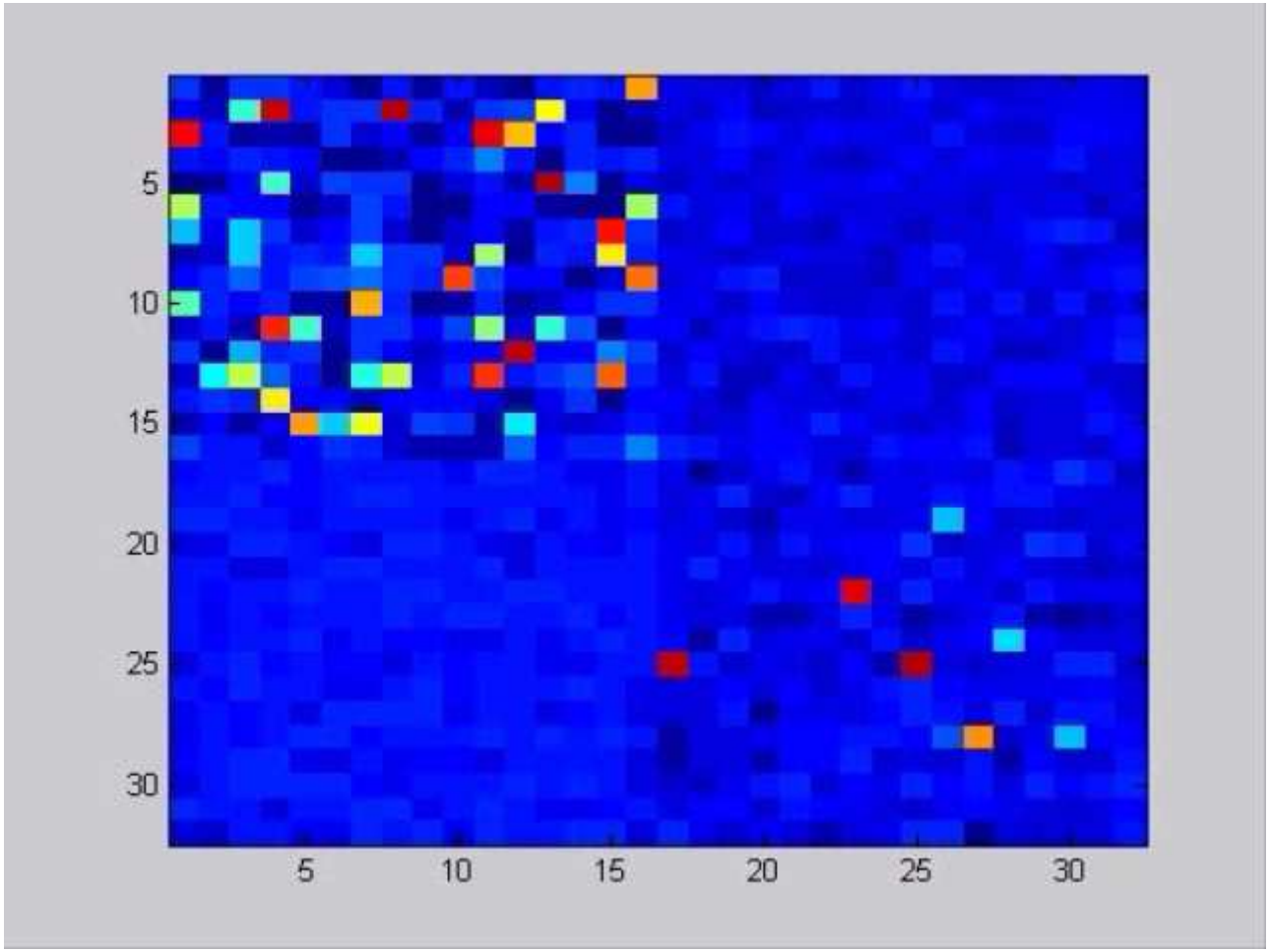
- Neural network – huge number of neurons and connections between them
- Is it possible to obtain sequential switching between groups (clusters) of neurons?
- What conditions for synaptic coupling provide sequential switching between clusters of neurons?
- Can we obtain a sequence larger than 3 states?

Conditions of occurrence of sequential switching between clusters



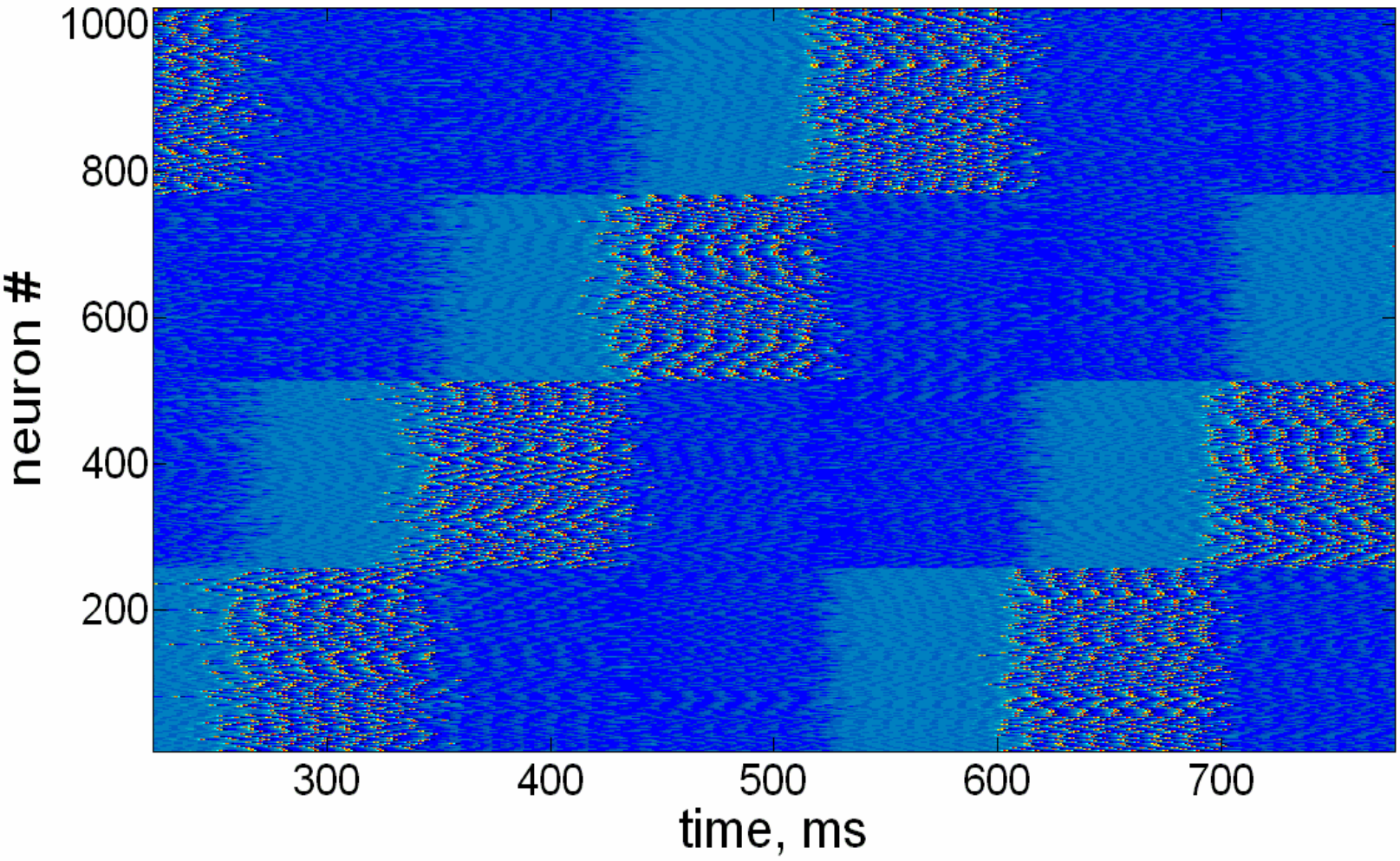
- *Non- inhibitory coupled* neurons form the clusters of simultaneous activity
- Clusters of neurons must be organized in graph with *all-to-all connections*
- *Asymmetry* of connections is necessary for origin of the sequential switching

EXAMPLE: Sequential switching of activity between clusters in network of N=1024 neurons. Each cluster consists of 256 neurons.

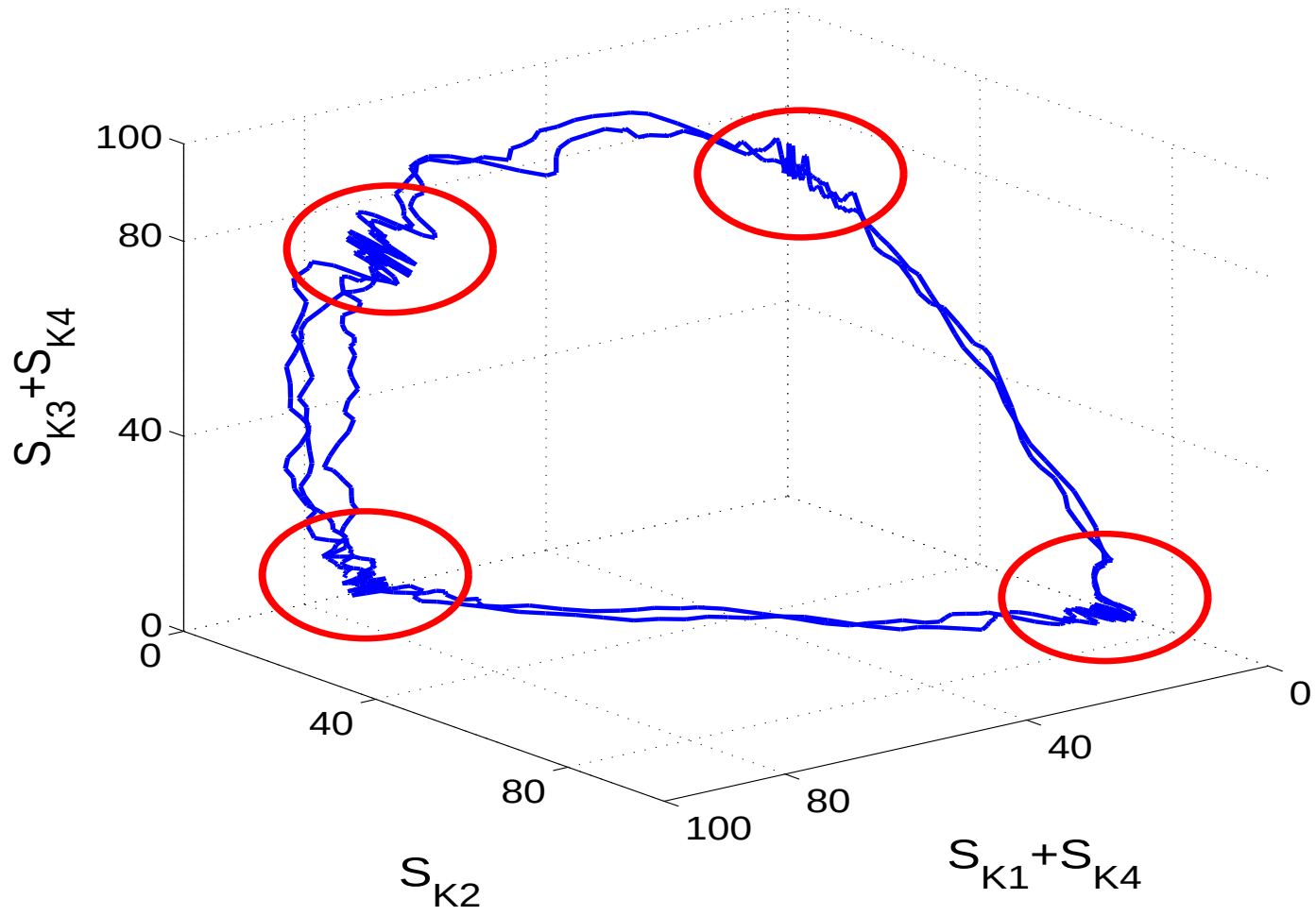


EXAMPLE: Synchronization of bursting activity

- Sequential dynamics leads to synchronization of bursting activity inside the clusters



Stable heteroclinic channel



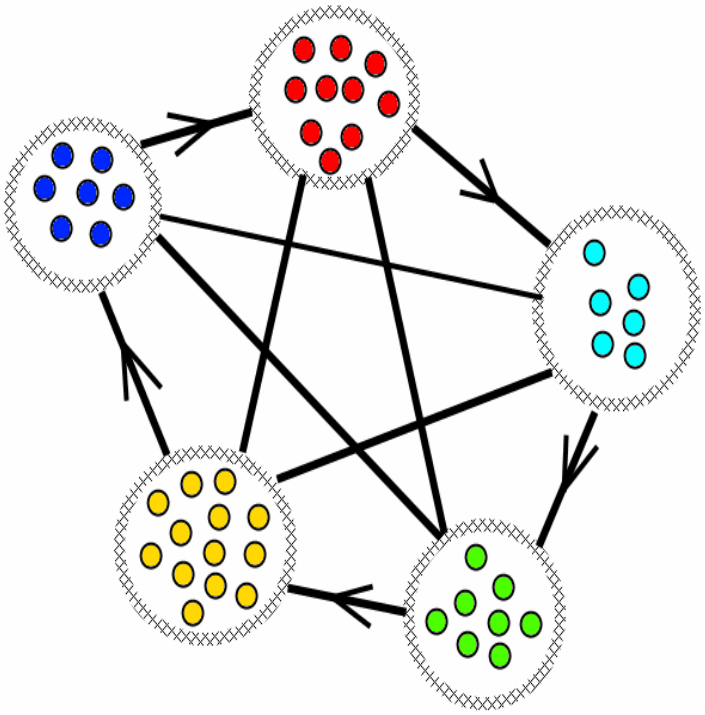
S_k1 = sum of all s_i from the cluster K1

Network with *random inhibitory* connections

- Is it possible to obtain constructions which are able to demonstrate sequential dynamics in network with random inhibitory connections?
- If yes, then how many such constructions - *functional subsystems* - can arise in random network?

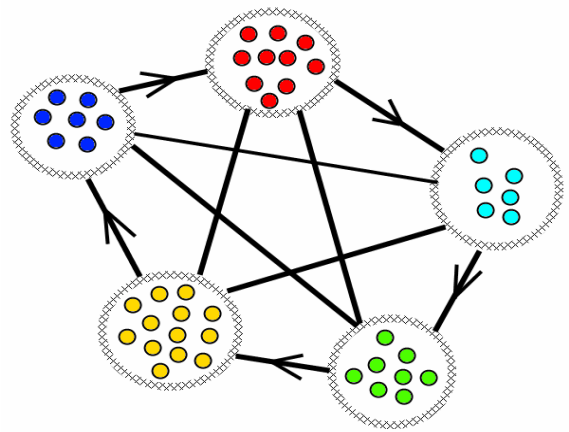
Functional subsystem

- a result of some external force



Network with random inhibitory connections

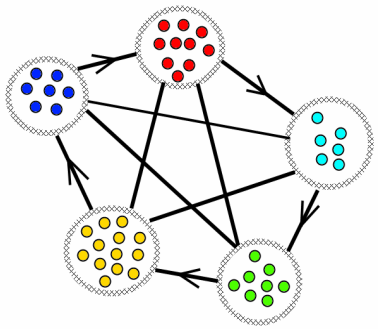
The mean value of number of *functional subsystems* **<K>** which are able to demonstrate sequential dynamics can be estimated as follows:

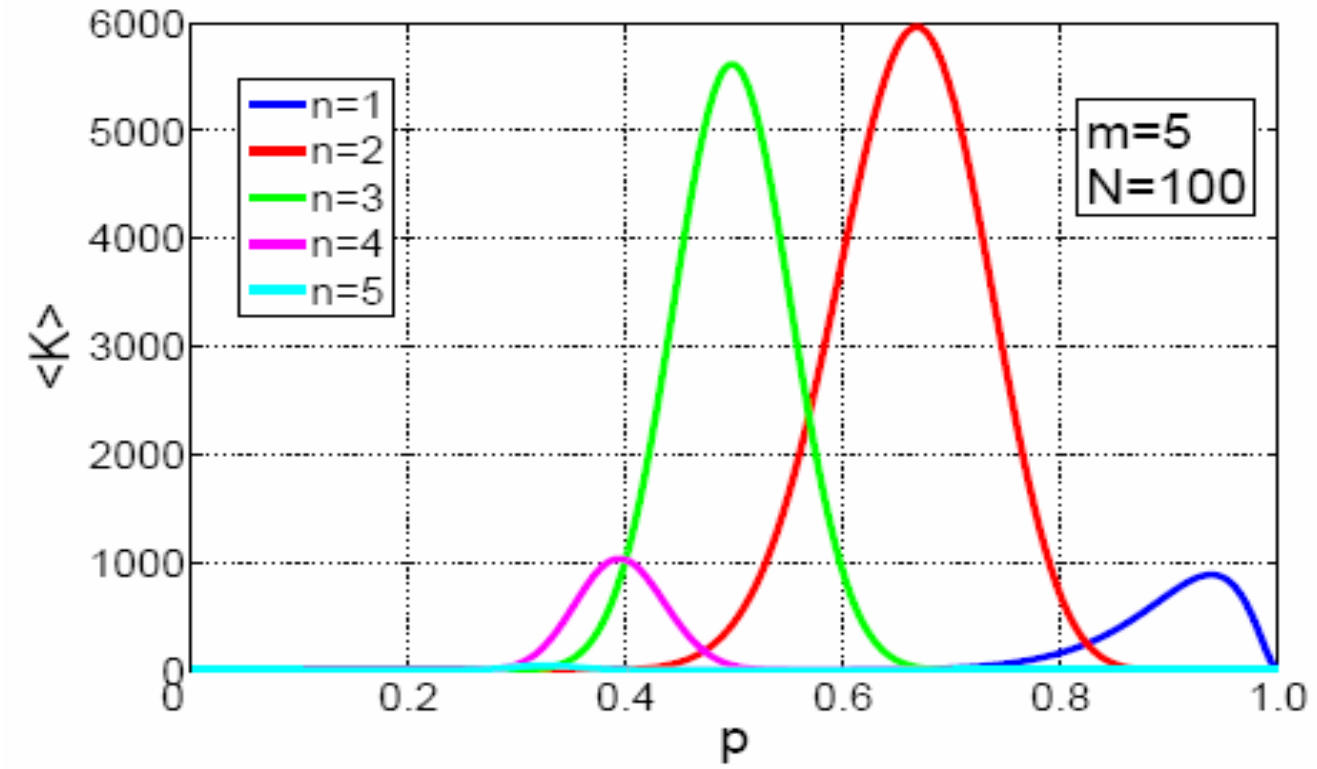


$$< K >= C_E^m \left(1 - \frac{\sum_{i=1}^{n} C_n^i C_{N-n}^{n-i}}{C_N^n}\right)^{C_m^2} \left((1-(1-p)^n)^n\right)^{\prod_m^{2-m}} (1-p)^{n^2 m}$$

m - number of clusters,
n - number of elements inside each cluster,
N - size of the network,
p – probability of unidirectional connection between any two neurons

The mean value of number of functional subsystems <K> which are able to demonstrate sequential dynamics

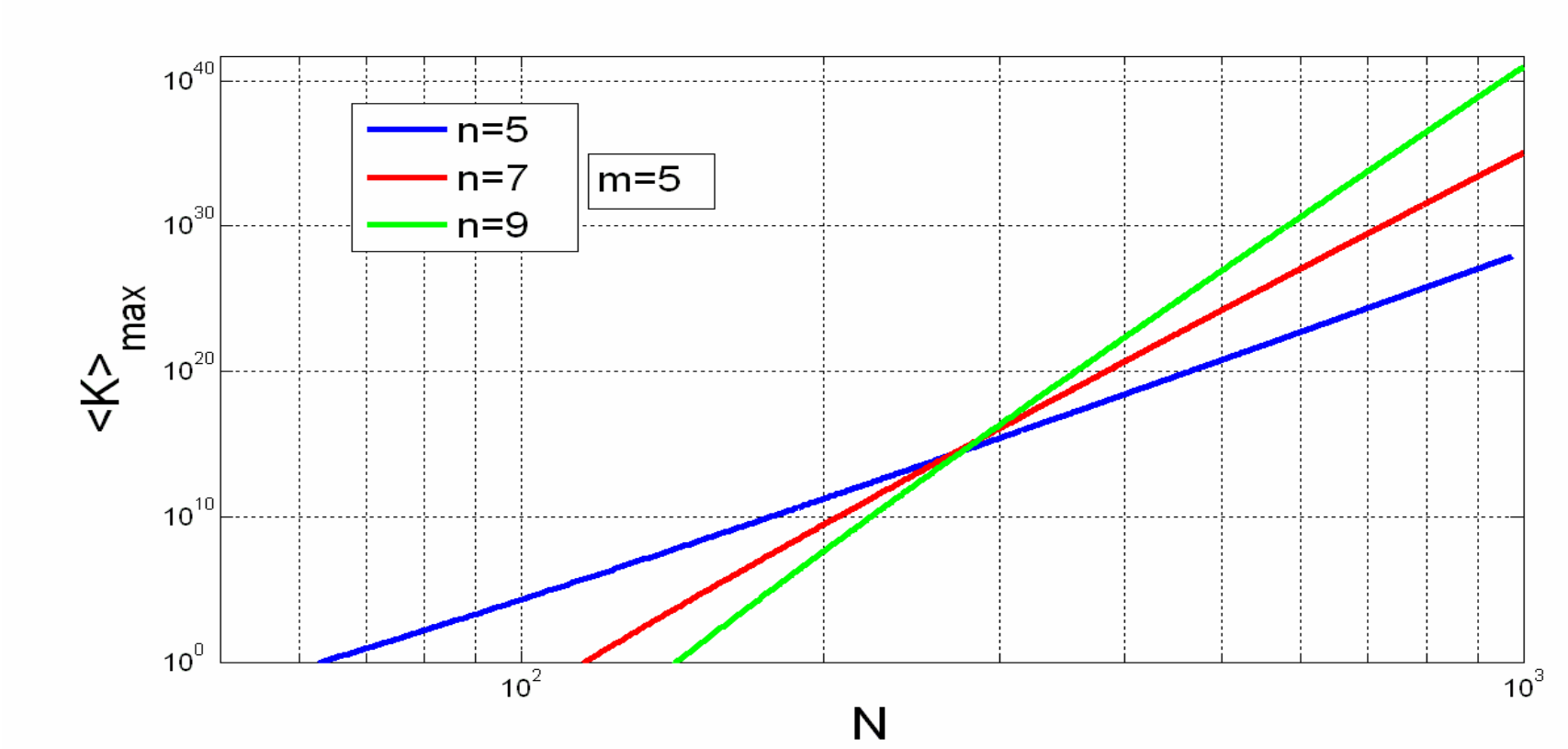




m-number of clusters, **n**-number of elements inside each cluster, **N**-size of the network, **p** – probability of connection between any two neurons

Example: N=100, p=0.7, m=5, n=2 <K> =6000

Power law dependence of maximum <K> on the size of network N



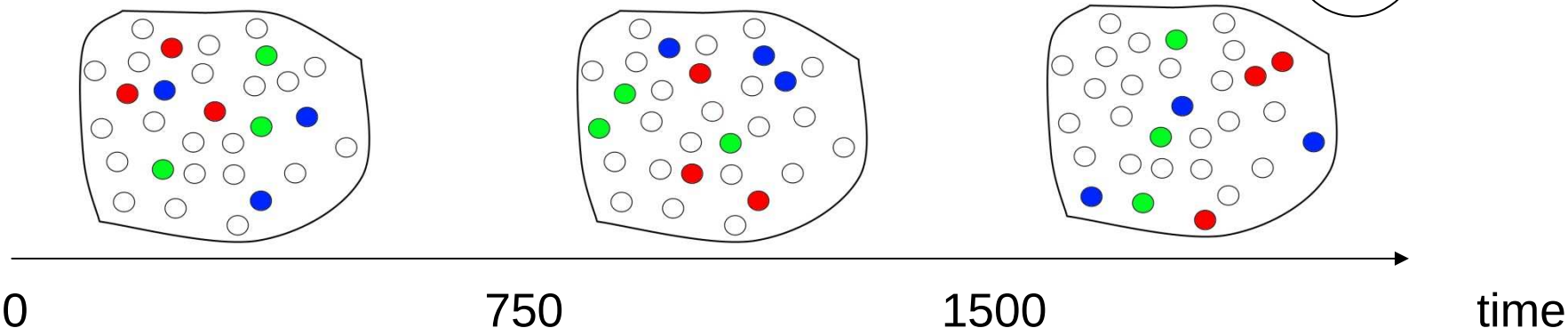
Huge network capacity:

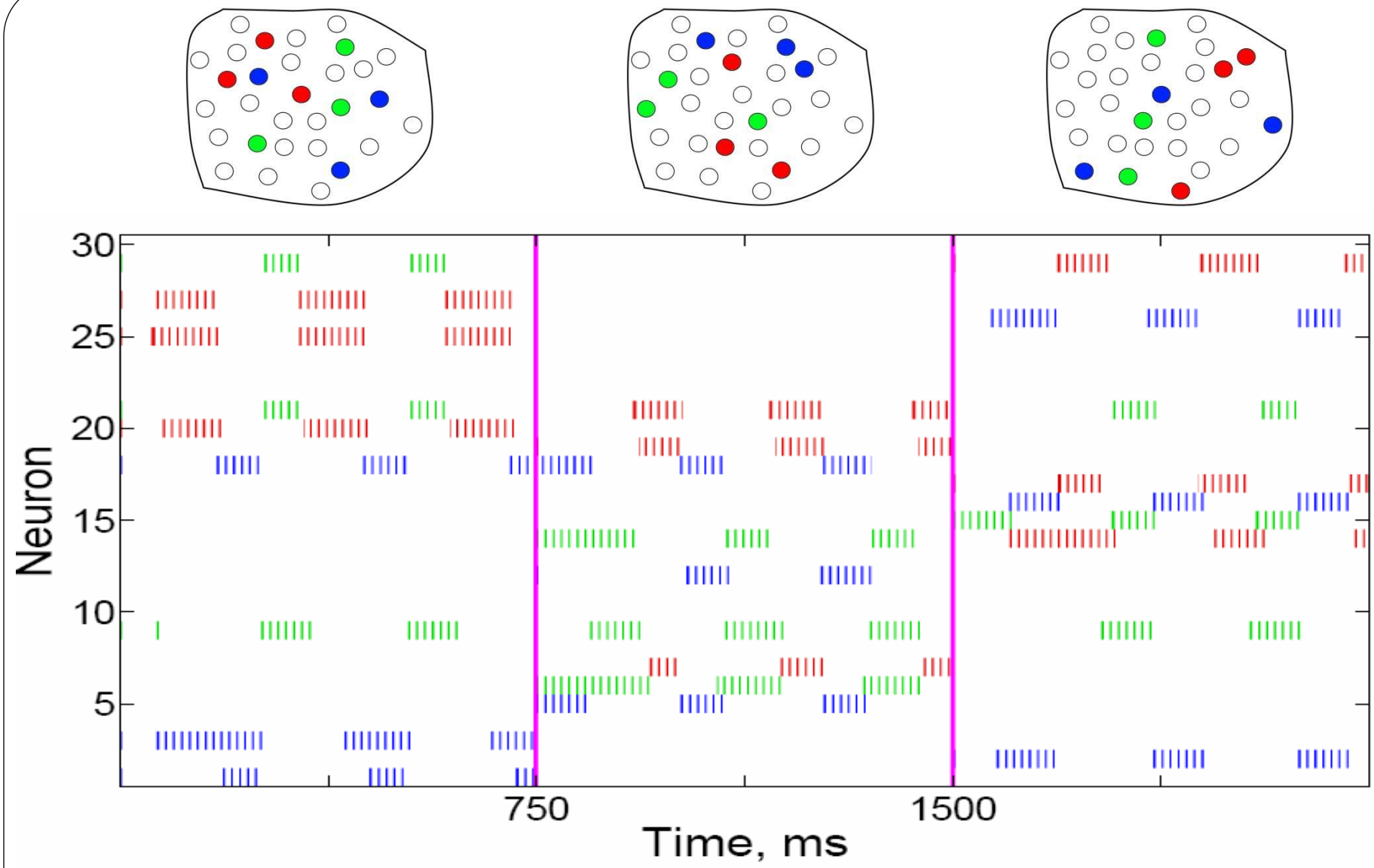
Example: N=1000, m=5,n=9 <K>=10 functional subsystems

EXAMPLE: 30 randomly coupled neurons. Probability p=0.28.
This network has 392 functional subsystems from m=3 clustres of n=3 neurons each.
We take only 3 functional subsystems.

We changed $I^{j}_{ext} + \Delta I$ .We added noise. We changed initial condtions

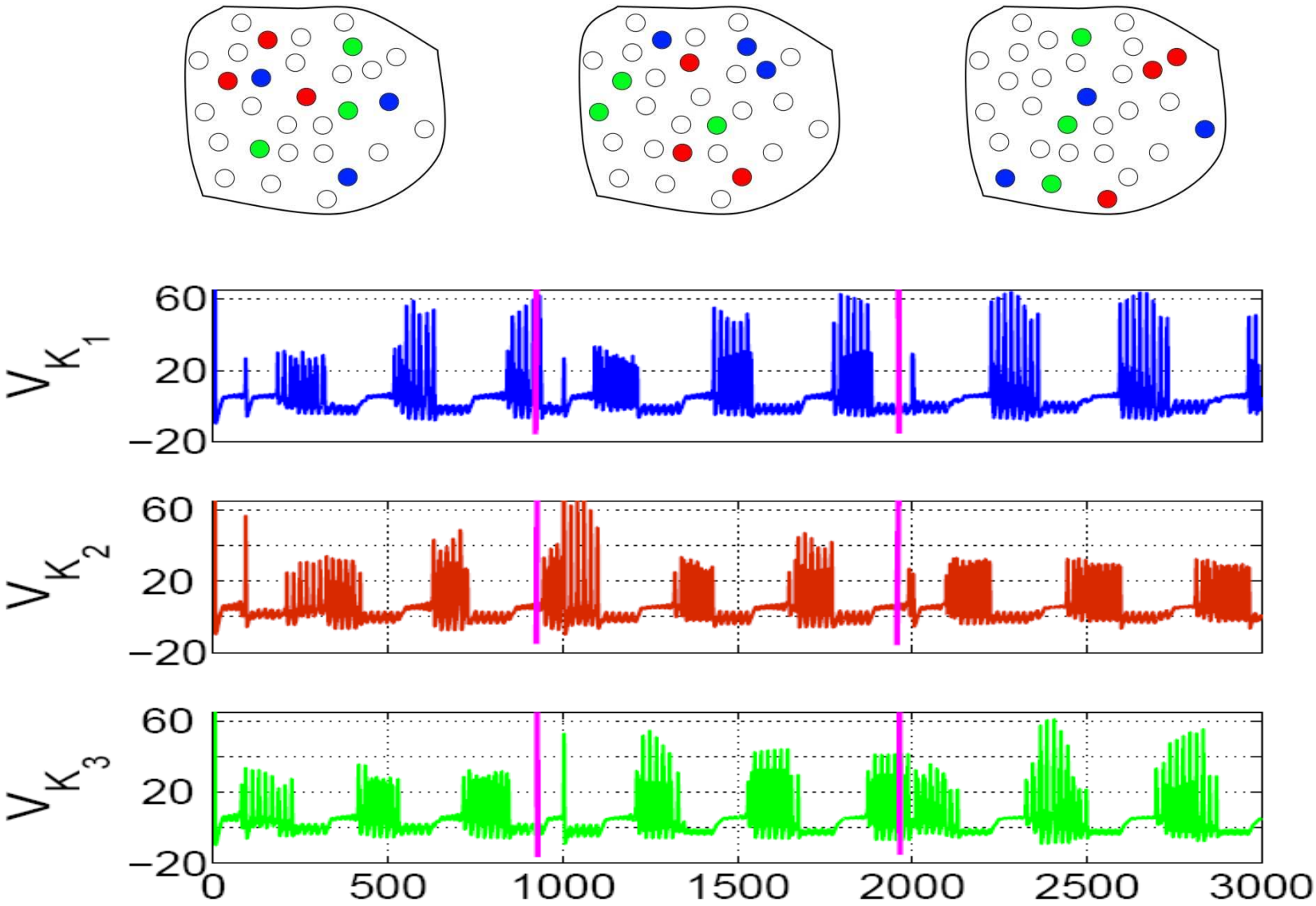
$$C_m \frac{dV_j}{dt} = g_l(V_l - V_j) + g_{Na} m^3 h(V_{Na} - V_j) + g_K n^4 (V_K - V_j) + I^{j}_{ext} + I^{syn}_{j}$$





Responses of the random network in the form of different active sequences of clusters to different sets of stimuli. In time (0:750) we force neurons from three clusters: K1=(1,3,18); K2=(20,25,27); K3=(9,21,29)…

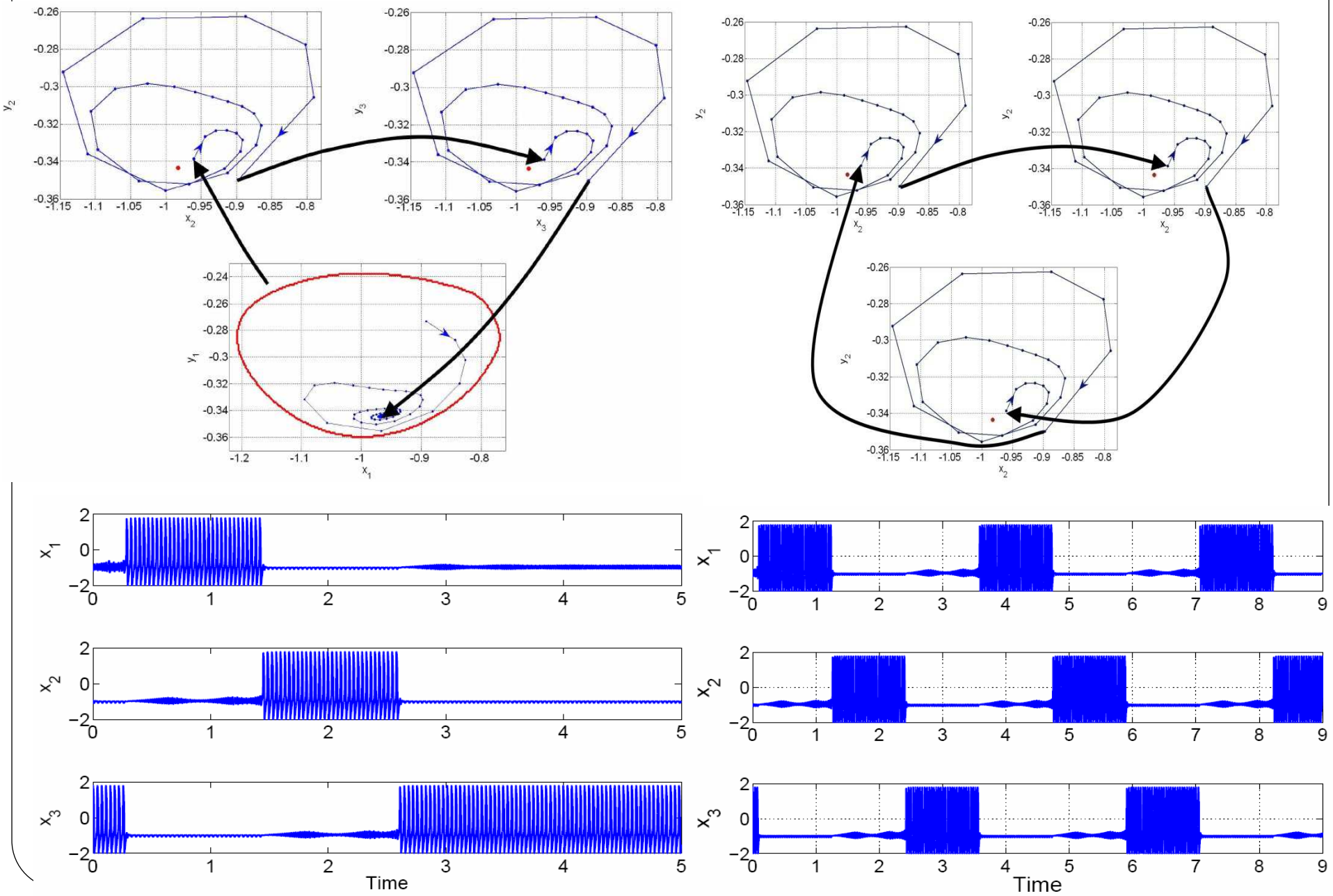
Switching and synchronization (Mean field voltage)



Conclusions

- Sequential dynamics in models of neuronal networks *can be* a result of arising of stable heteroclinic channels (SHC) in the phase space of the system. *Subcritical Neimark-Sacker bifurcation*.
- Even the networks with *random* inhibitory connections can contain *huge number of functional subsystems* - constructions which are able to demonstrate sequential dynamics
- *Certain set of external stimuli* on the network provides *certain sequence of firing clusters* of neurons
- Observed rhythmic behavior is *stable against noise* and *flexible* to the inputs to the sensory system

Heteroclinic channels



Bohnoeffer – Van der Pol eqs.

We consider the motif of three neurons (shown in Fig. 1), modeled by the Bonhoeffer-Van der Pol equations:

$$\begin{cases} \tau_1 \frac{dx_i(t)}{dt} = x_i - \frac{1}{3}x_i^3(t) - y_i(y) - z_i(t)(x_i(t) - v) + S_i, \\ \frac{dy_i(t)}{dt} = x_i(t) - by_i(t) + a, \quad i = 1, ..., 3 \end{cases} \tag{1}$$

synaptically inhibitory connected through the coupling $z_i(t)$ which is defined by

$$\tau_2 \frac{dz_i(t)}{dt} = \sum_j g_{ij} F(x_j) - z_i(t). \tag{2}$$

Here $x_i(t)$ denotes the membrane potential of the i-th neuron, $y_i(t)$ the variable corresponding to the action of all ionic currents, S_i the external stimuli to each neuron, v the reversal potential, g_{ij} the coupling coefficients between the i-th and j-th neuron and $F(x_j) = 1/(1 + \exp((0.5 - x_j)/20))$. The values of the parameters are fixed in all simulations to $a = 0.7$, $b = 0.8$, $\tau_1 = 0.08$, $\tau_2 = 3.1$, $v = -1.5$ and we chose the parameters $S_i > 0.35$ that corresponds to tonic spiking regime of individual uncoupled neurons. Depends on the level of nonsymmetry of inhibitory coupling this simple network demonstrates the variety of dynamical regimes:

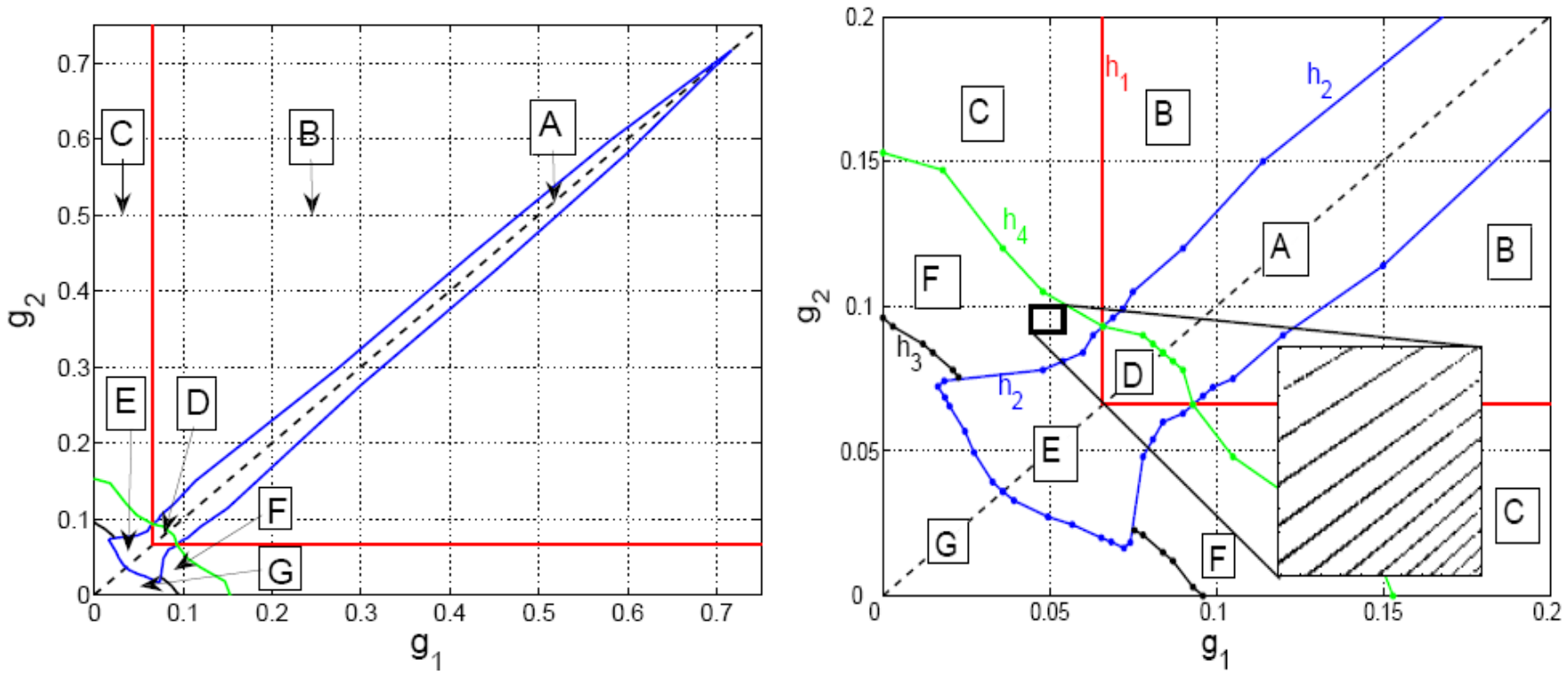


FIG. 3: (a) Bifurcation diagram of regimes in an ensemble of three inhibitory coupled neurons (see text for details); (b) Detailed area of the diagram.
Region **A**: Coexistence of three limit cycles $L^1_{1,2,3}$ (Fig.2(a)) and three limit cycles $L^2_{1,2,3}$ (Fig.2(b)).
Region **B**: Coexistence of three limit cycles $L^1_{1,2,3}$.
Region **C**: Periodic sequential switching of activity between all neurons (Fig.2(c)).
Region **D**: Coexistence of three limit cycles $L^1_{1,2,3}$, three limit cycles $L^2_{1,2,3}$, and limit cycle L^3 (Fig.2(d)).
Region **E**: Coexistence of three limit cycles $L^1_{1,2,3}$ and limit cycle L^3.
Region **F**: Region with complex structure. The black areas in the inserted figure correspond to coexistence of the three limit cycles $L^2_{1,2,3}$ with the limit cycle L^3. The white regions are the areas of coexistence of the sequential dynamics and the stable limit cycle L^3.
Region **G**: Existence of limit cycle L^3.

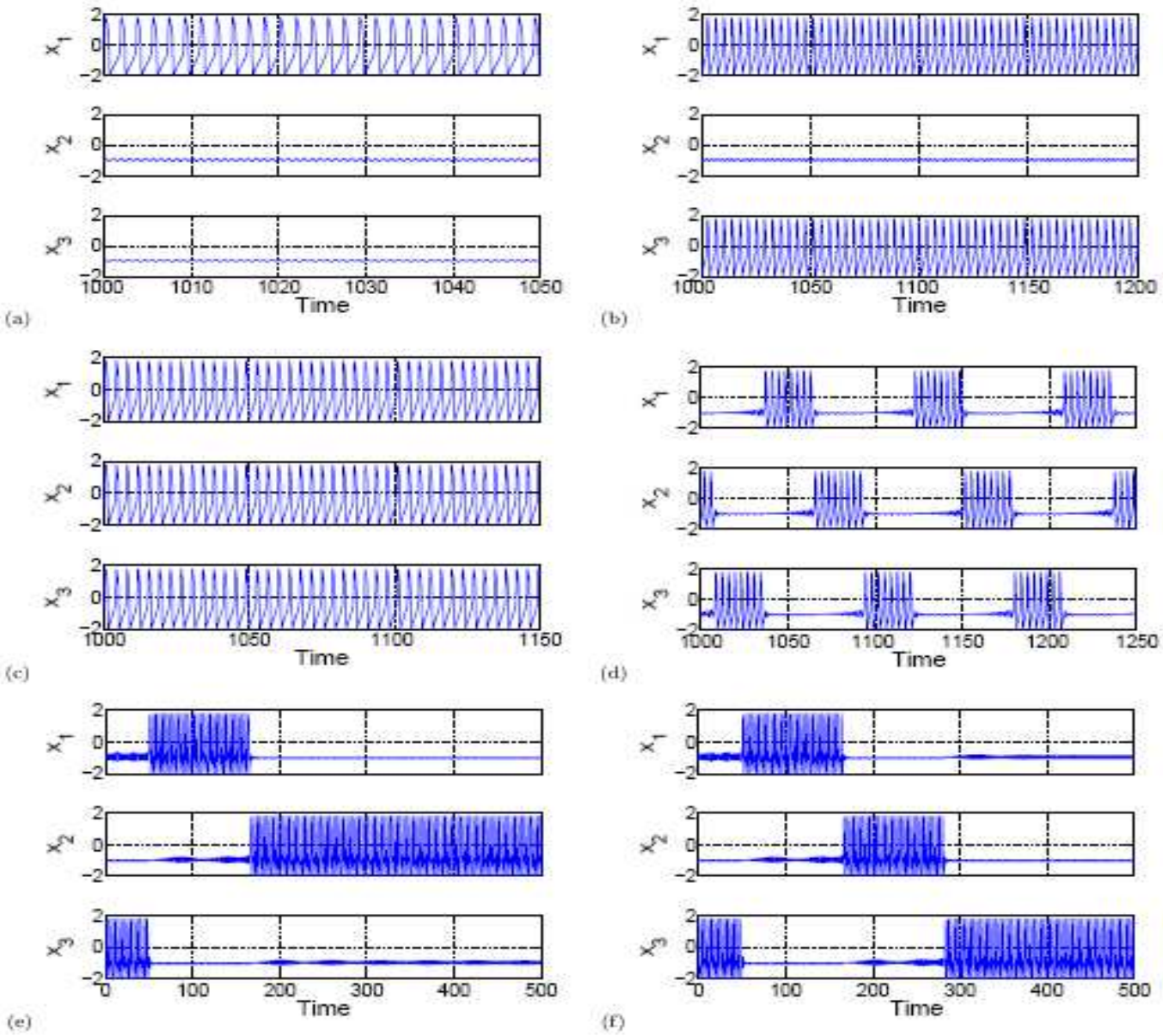


FIG. 2: (a) One neuron is active and suppresses the activity of the two other neurons; (b) Two neurons are active and suppress the activity of the other neuron; (c) Synchronous in-phase ($x_1 = x_2 = x_3$) spiking mode. (d)Periodical sequential activation of the neurons. (e),(f) Transient sequential activition of the neurons.

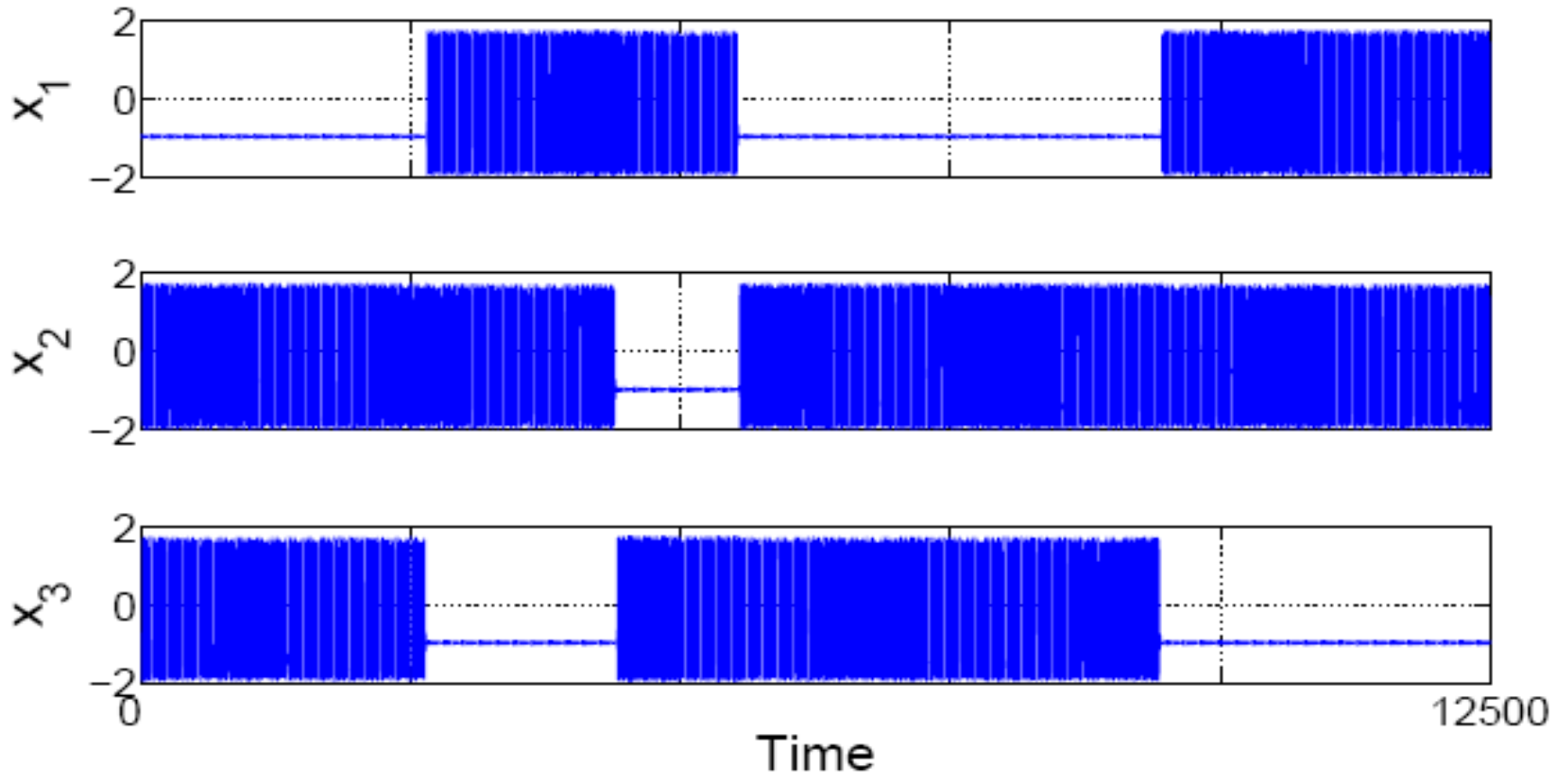
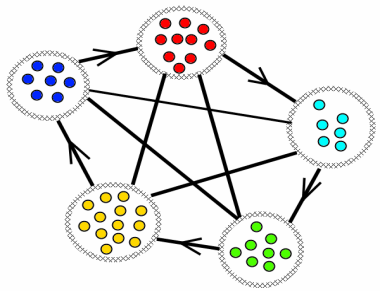


FIG. 12: Irregular sequential activation of neurons in the region **F**.



Let us suppose that the whole network can be divided into $m \geq 3$ subnetworks with clusters $\mathcal{K}_i$ consisting of *uncoupled* neurons:

$$\{1, \ldots, N\} = \mathcal{K}_1 \cup \ldots \cup \mathcal{K}_m. \tag{4}$$

Each cluster $\mathcal{K}_i$ consists of n_i neurons. To order these subsets we introduce a transformation of variables by the $N \times N$ permutation matrix P such that a new coupling matrix $E = P^{-1}GP$ may be introduced in block form:

$$E = \{\varepsilon^{kl}\}, \quad k, l = 1, \ldots, m. \tag{5}$$

An arbitrary partition of (4) under this permutation leads to the form

$$\begin{gathered}\{1, \ldots, N\} = \mathcal{K}_1 \cup \ldots \cup \mathcal{K}_m = \\ \{1, \ldots, n_1\} \cup \{1, \ldots, n_2\} \cup \ldots \cup \{1, \ldots, n_m\}\end{gathered} \tag{6}$$

with $N = \sum_{k=1}^{m} n_k$. Each block ε^{kl} of size $n_k \times n_l$ has entries

$$\varepsilon^{kl} = \{\varepsilon_{ij}^{kl}\}, \quad i = 1, \ldots, n_k, \quad j = 1, \ldots, n_l. \tag{7}$$

In the partition, we have

$$\varepsilon_{ij}^{kk} = 0, \quad i = 1, \ldots, n_k, \quad j = 1, \ldots, n_l. \tag{8}$$

To determine the conditions of sequential switching of the activity between clusters of neurons, we introduce the matrix $S = \{s_{lk}\}$ which defines a strong or weak coupling between any two clusters $\mathcal{K}_l$ and $\mathcal{K}_k$.

Definition 1. *The coefficients of the $m \times m$ matrix S are defined as*

$$s_{kl} = \frac{\sum\limits_{j=1}^{n_l} \theta(\sum\limits_{i=1}^{n_k} \varepsilon_{ij}^{kl})}{n_l} \tag{9}$$

where

$$\theta(x) = \begin{cases} 1, & \text{if } x \geq \tilde{g} \\ 0, & \text{if } x < \tilde{g}. \end{cases} \tag{10}$$

According to (9) all $s_{kl} \in [0, 1]$. The influence of the cluster $\mathcal{K}_k$ to the cluster $\mathcal{K}_l$ is strong if $s_{lk} = 1$, and the influence of the cluster $\mathcal{K}_k$ to the cluster $\mathcal{K}_l$ is weak if $s_{lk} = 0$. Strong unidirectional coupling between two clusters means that all neurons of the influenced cluster are suppressed (generating subthreshold oscillations). Despite weak coupling, all neurons of the inhibited cluster remain active. Note that $s_{kk} = 0$ for all k. The remaining values of s_{lk} that are within the range $(0, 1)$ are neither strong nor weak connections (i.e. the influenced clusters are not fully active or not fully suppressed).

Condition A. *The sequential switching between q clusters $\mathcal{K}_1$, $\mathcal{K}_2$, ..., $\mathcal{K}_q$ is possible if $s_{i,\ i+1(mod\ q)} = 0$ and all other $s_{jk} = 1$.*

For example, the matrix

$$\begin{pmatrix} 0 & 0 & 1 & 1 \\ 1 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 \\ 0 & 1 & 1 & 0 \end{pmatrix} \tag{11}$$

defines a sequential switching between clusters 1, 2, 3, 4.

Definition 2. *The sequence of switching of q clusters $\mathcal{K}_1, \mathcal{K}_2, ..., \mathcal{K}_q$ is defined as a Functional Structure (FS).*