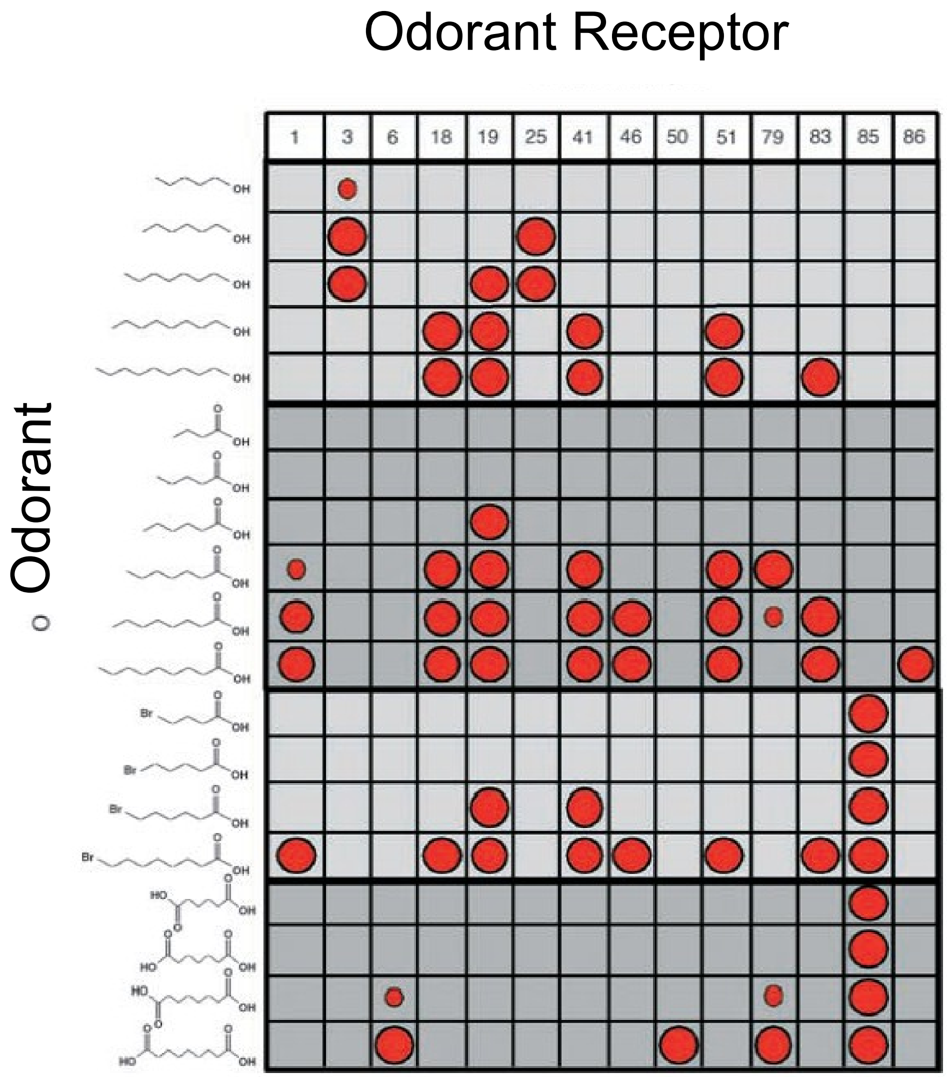
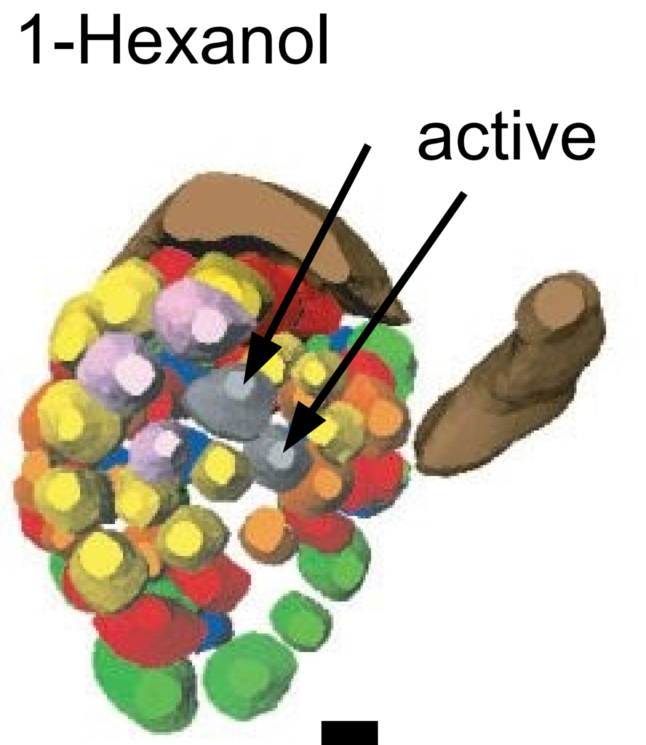
Lecture 4:

Models of the Antennal Lobe

Dr. Thomas Nowotny
University of Sussex

Last time ...

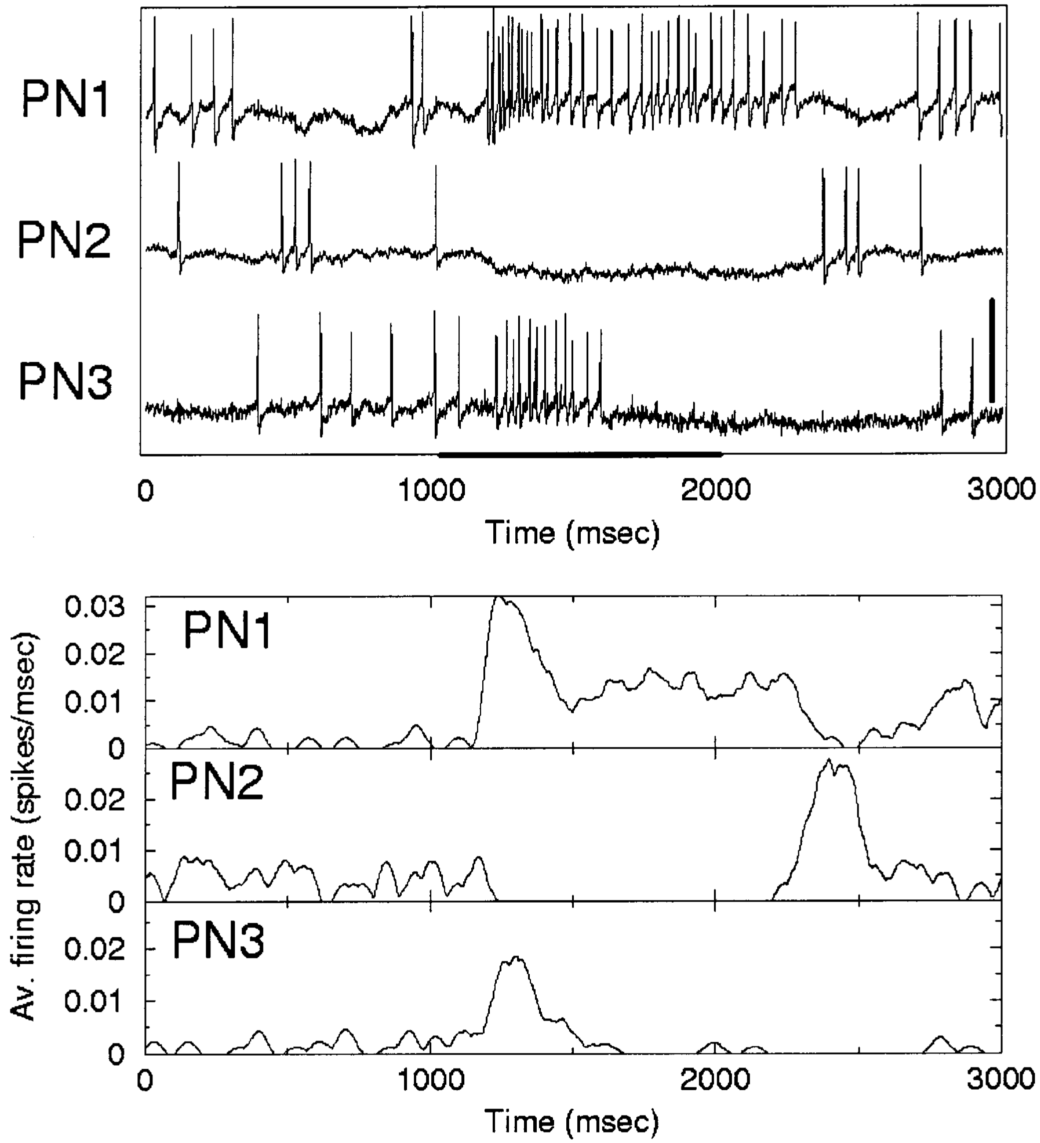




Pattern classification of **static** patterns

Dr. Thomas Nowotny,
Centre for Computational Neuroscience and Robotics
University of Sussex

The truth is more complicated ...

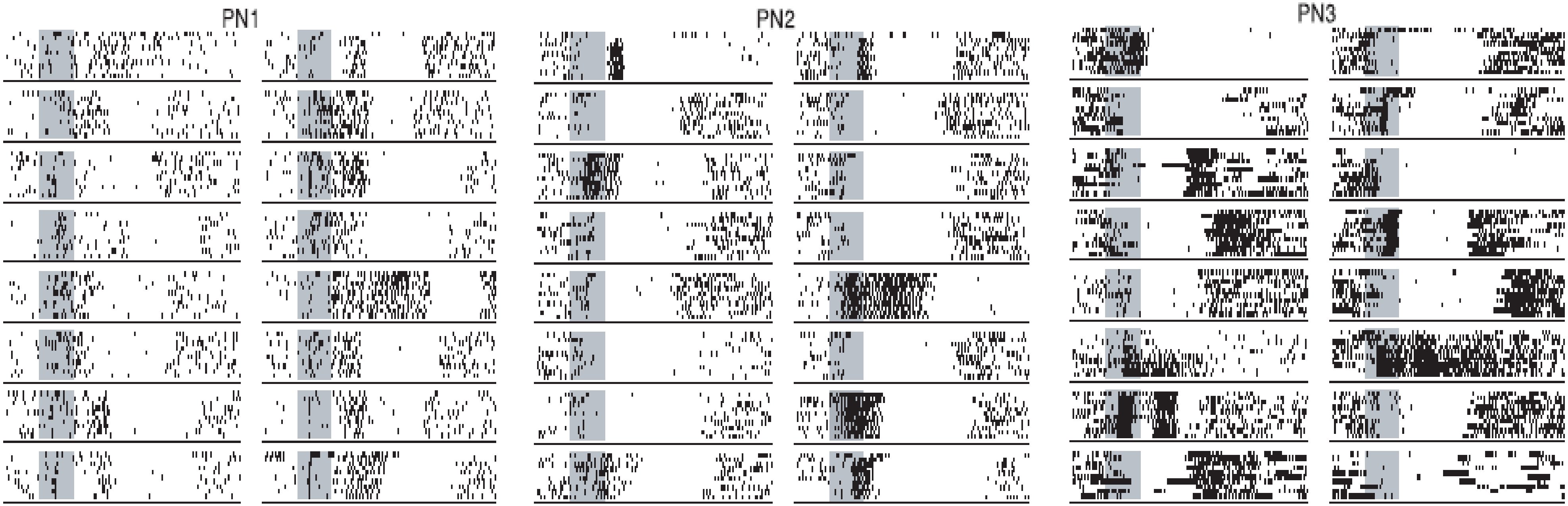


The activity of projection neurons in the locust shows a slow temporal patterning.

Neurons are not only not excited but possibly inhibited by odor input.

M. I. Rabinovich, R. Huerta, A. Volkovskii, H. D. I. Abarbanel, M. Stopfer and G. Laurent, Dynamical coding of sensory information with competitive networks, J Physiol – Paris 94: 465-471 (2000)

Complex slow patterning



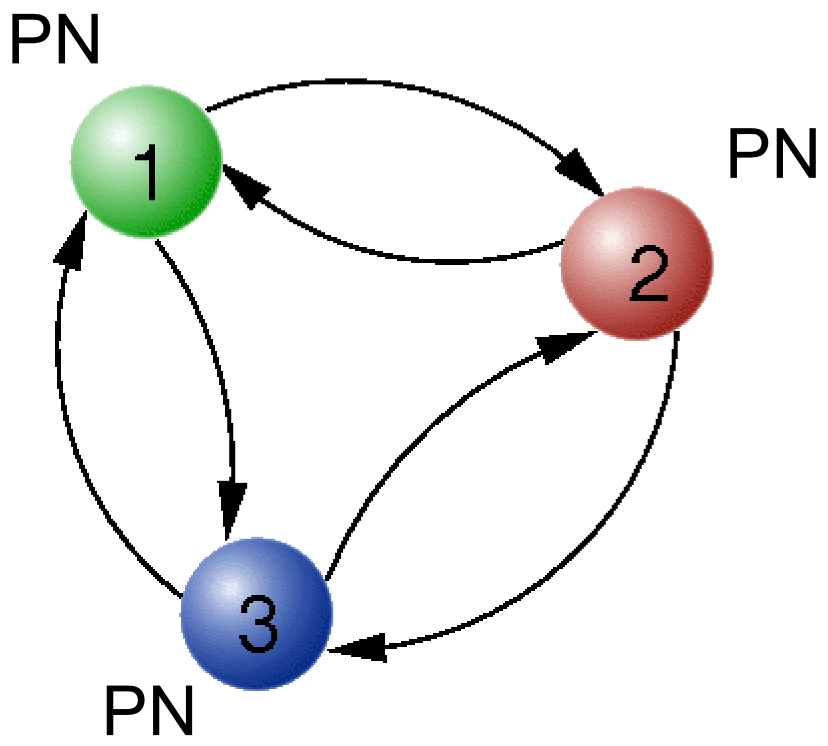
Javier Perez-Orive, et al., Oscillations and Sparsening of Odor
Representations in the Mushroom Body,
Science 297: 359 (2002)

Winnerless competition

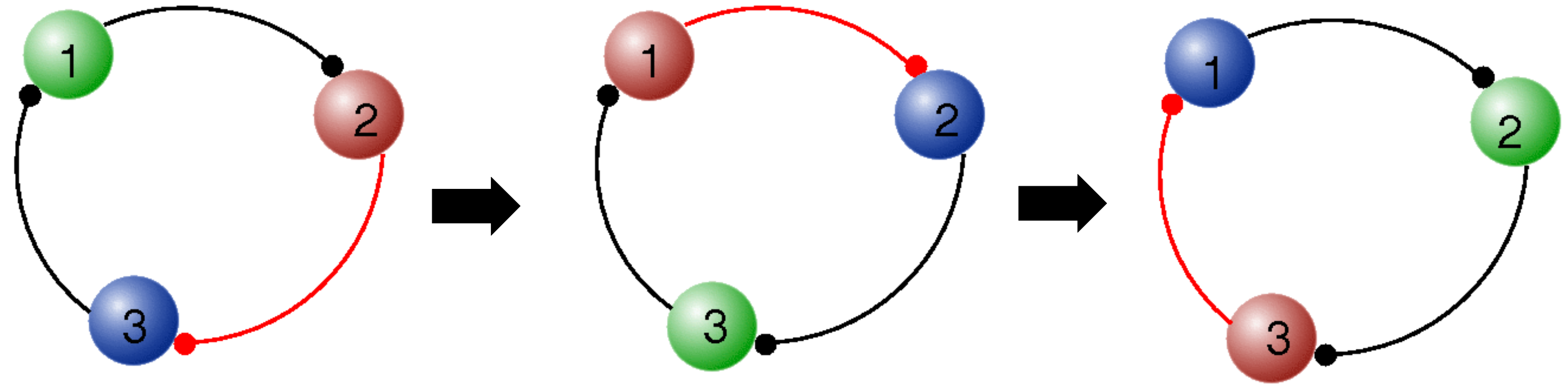
Projection neurons (PN) compete with each other for being active.

But the connections are such that none can become a “winner” for more than a short time.

The competition is likely mediated by local inter-neurons (LN).



Example of a WLC scenario



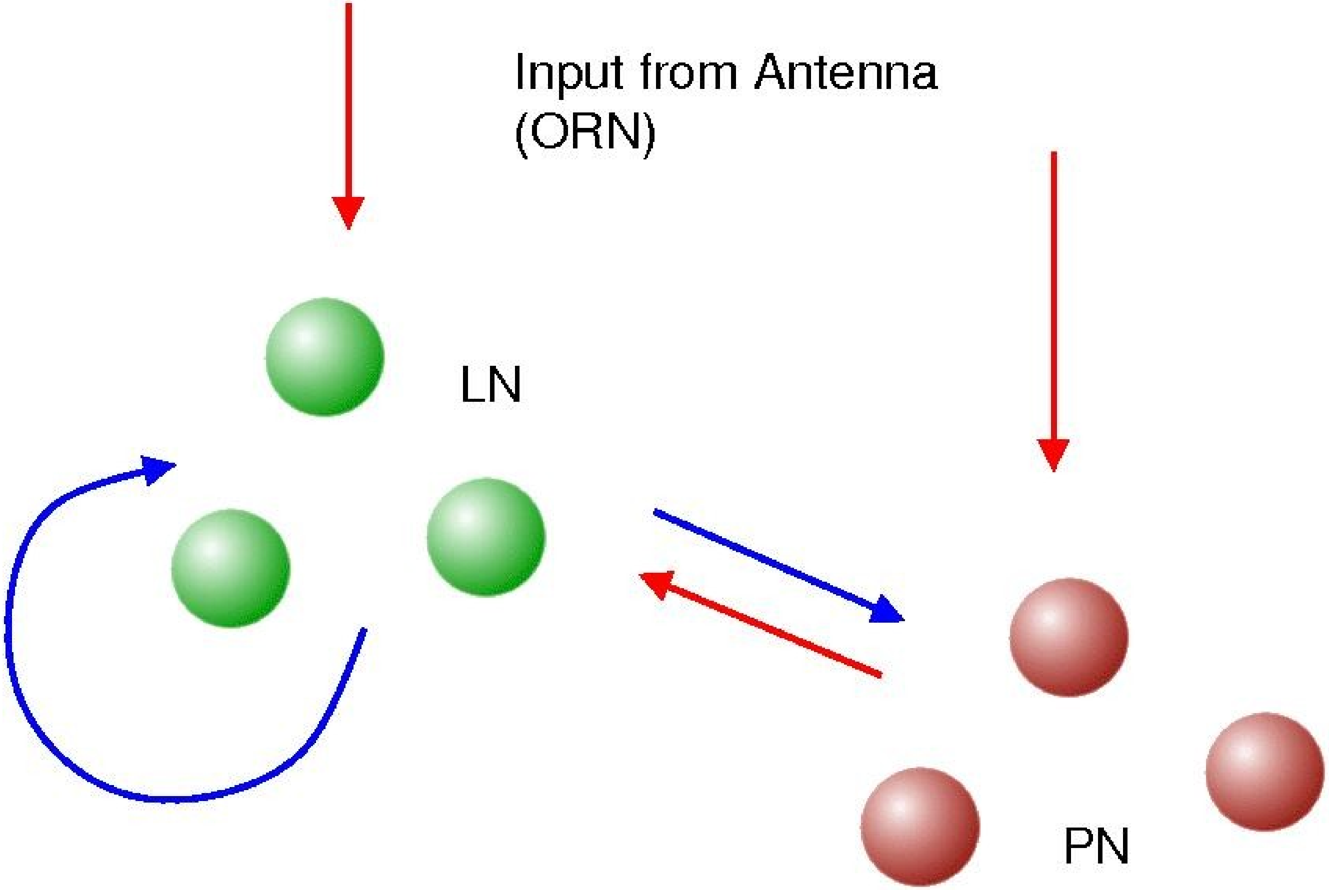
🟥 active
🟩 recovering
🟦 inhibited

— active synapse
— inactive synapse

No neuron can stay active indefinitely.

“Infrastructure” in the AL

In the locust:



Excitatory:

ORN – PN

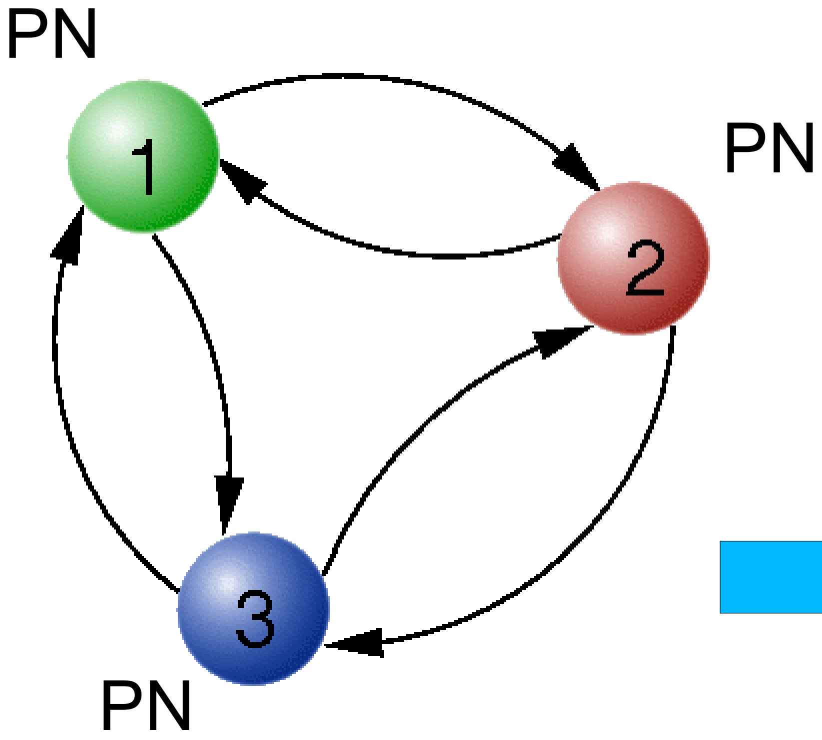
PN – LN

Inhibitory:

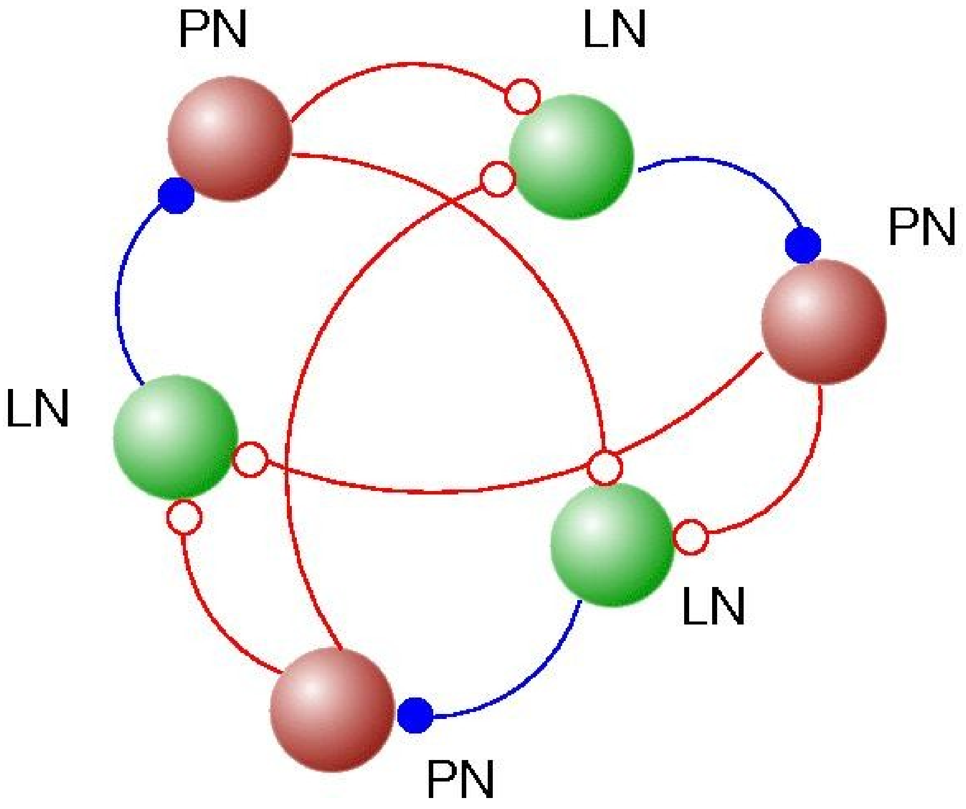
LN – PN

LN – LN

WLC scenario



Inhibition mediated by local interneurons



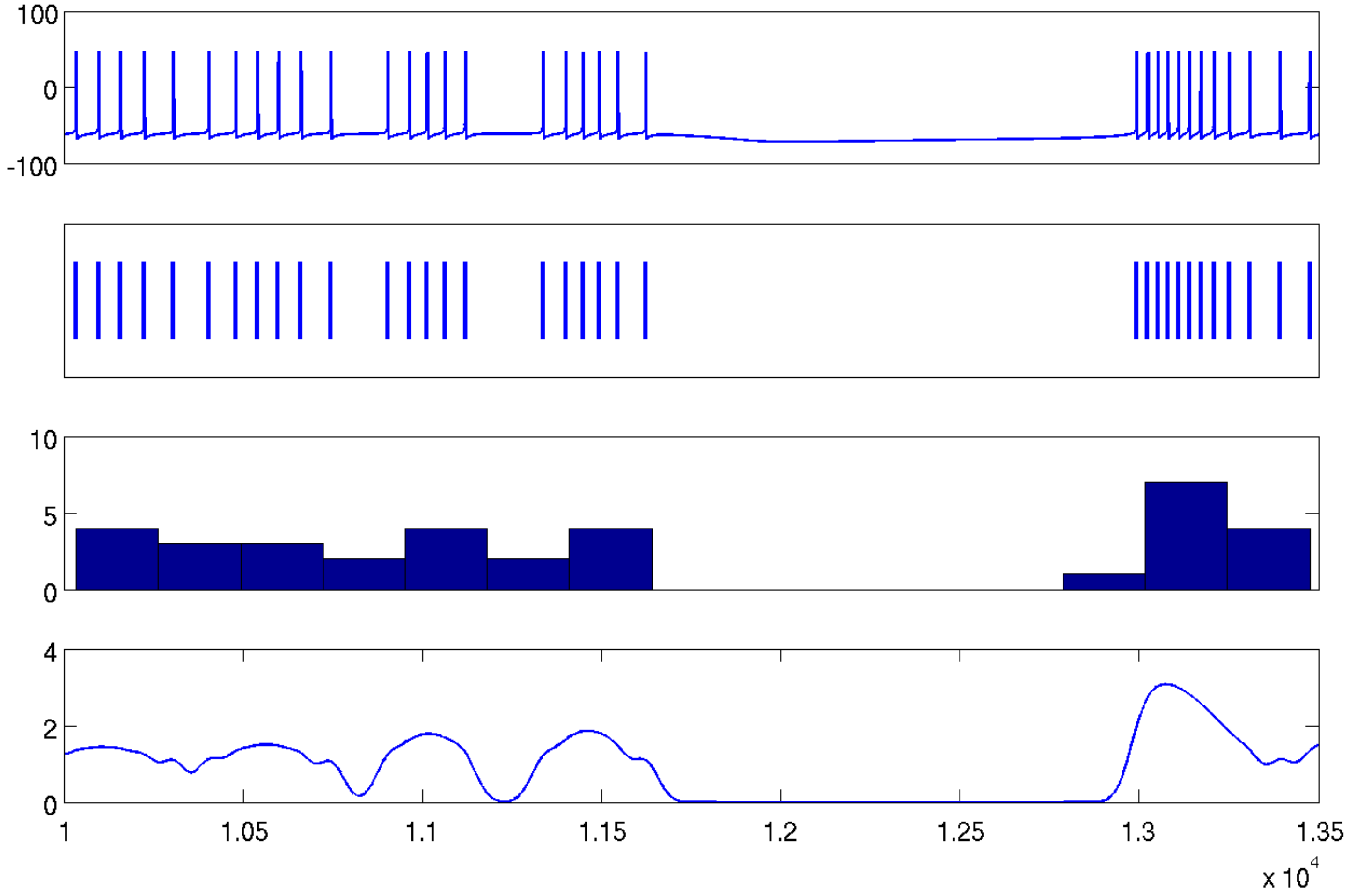
What may this be good for?

- Robustness – the overall spatio-temporal pattern may be less vulnerable to high frequency perturbations
- Sensitivity – similar patterns may become more different over time
- Augmenting the coding space – the space of all spatio-temporal patterns is much larger than of static activation patterns

Rate models

- Neural activity is described by more “coarse grained” rate variables
- What exactly “rate” represents is not generally agreed, typical methods to obtain a rate are
  - Binning spike counts (discrete rate)
  - Convolving with a kernel (SDF)

Example of obtaining a rate



Membrane potential

Detected spikes

Binned spike counts

Spike density function

Rate models

- In models it is tacitly assumed that activity of a neuron i is described by a function

$$\begin{aligned} r_i : \mathbb{R} &\to \mathbb{R} \\ t &\mapsto r_i(t) \end{aligned}$$

- The action of synapses is then described as a change in rate,

$$\frac{dr_i}{dt} = f(r_i, r_j, c_{ij}, t)$$ (description with ODE)

$$r_i(t + \Delta t) = f(r_i(t), r_j(t), c_{ij}, t)$$ (time discrete model)

A rate model is a Dynamical System

- The definitions of rate models I have given define a classical dynamical system
- They are typically analyzed in the language of Dynamical Systems Theory
- On the next couple of slides I'll give a high-speed refresher of the most basic concepts:

Fixed points

Fixed points are states of the system that do not change over time even though subject to the system dynamics.

If the system is given as an ODE,

$$\frac{d}{dt}\vec{r} = f(\vec{r}, c_{ij}, t)$$

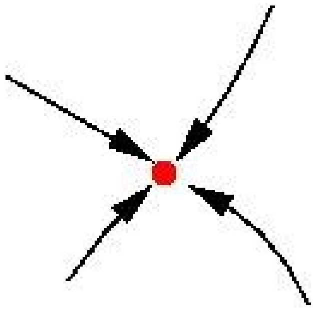
then this correspondsd to

$$f(\vec{r}_{FP}, c_{ij}, t) = 0$$

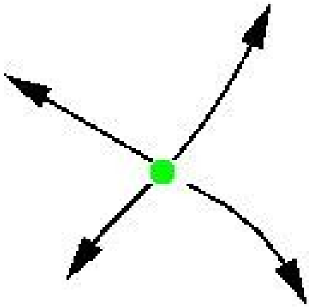
Fixed point can be ...

Character of fixed points

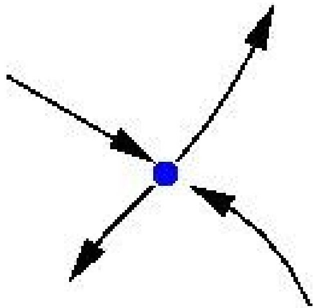
Stable fixed points:
Nearby points are attracted to them



Unstable fixed points:
Nearby points are repelled from them



Saddle points:
There are attractive and repelling directions

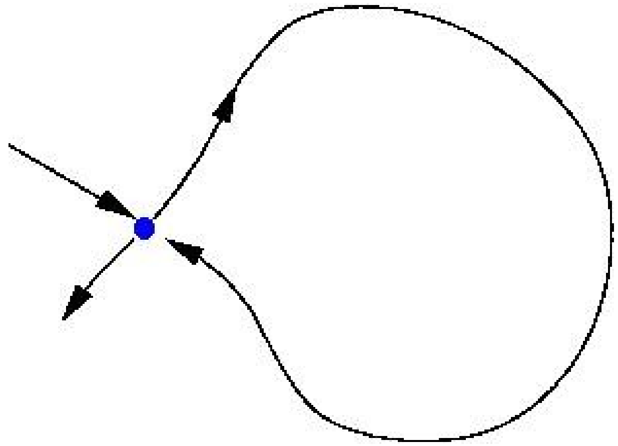


Orbits

An orbit, or trajectory, is a solution of the dynamical system as a function of time.

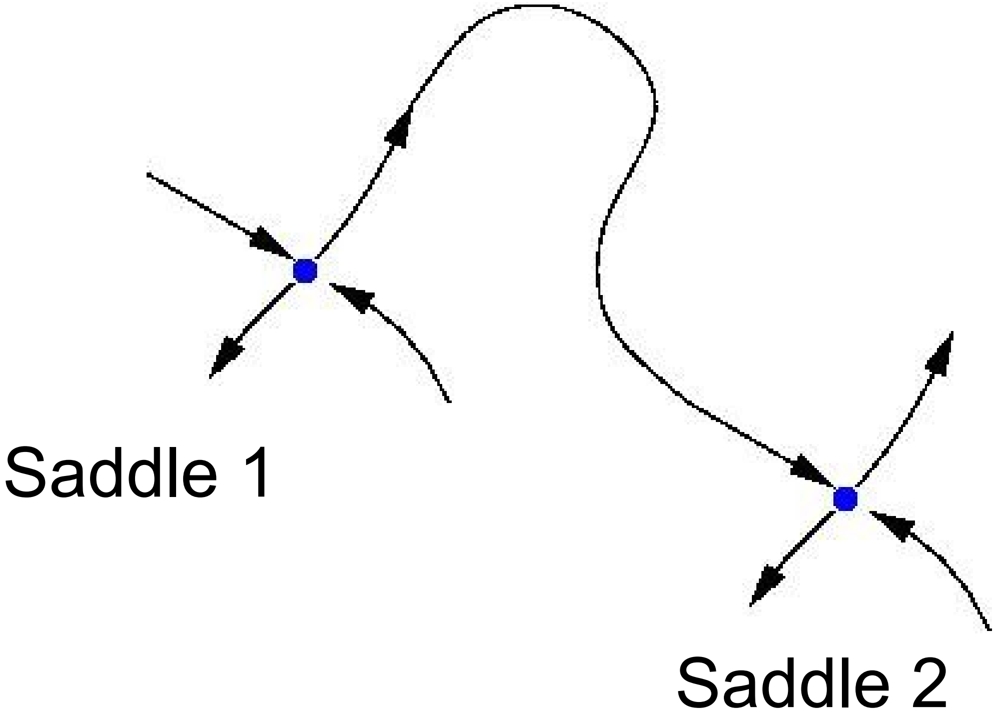
There are special orbits:

- Fixed points by themselves are orbits
- Orbits can end in a fixed point or start from one
- Periodic orbits “go in circles” not involving FP. They are called limit cycles
- Homoclinic orbits connect a FP with itself (saddle points only):



The heteroclinic cycle

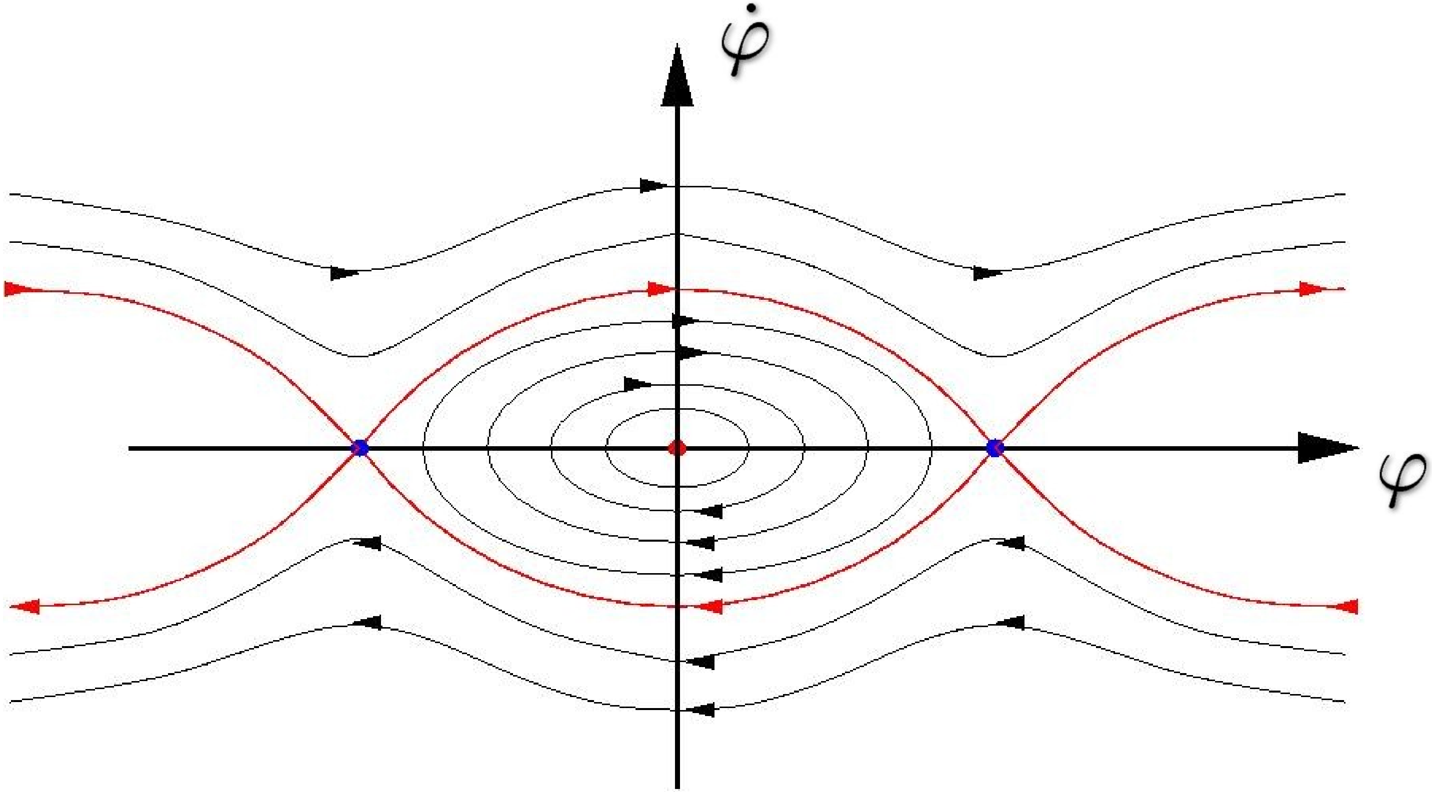
- Heteroclinic orbits connect the “unstable manifold” of one saddle point with the “stable manifold” of another:



Why are these orbits important?

The special orbits (separatrices) define ”what is going on overall” (the global dynamics) of the system:

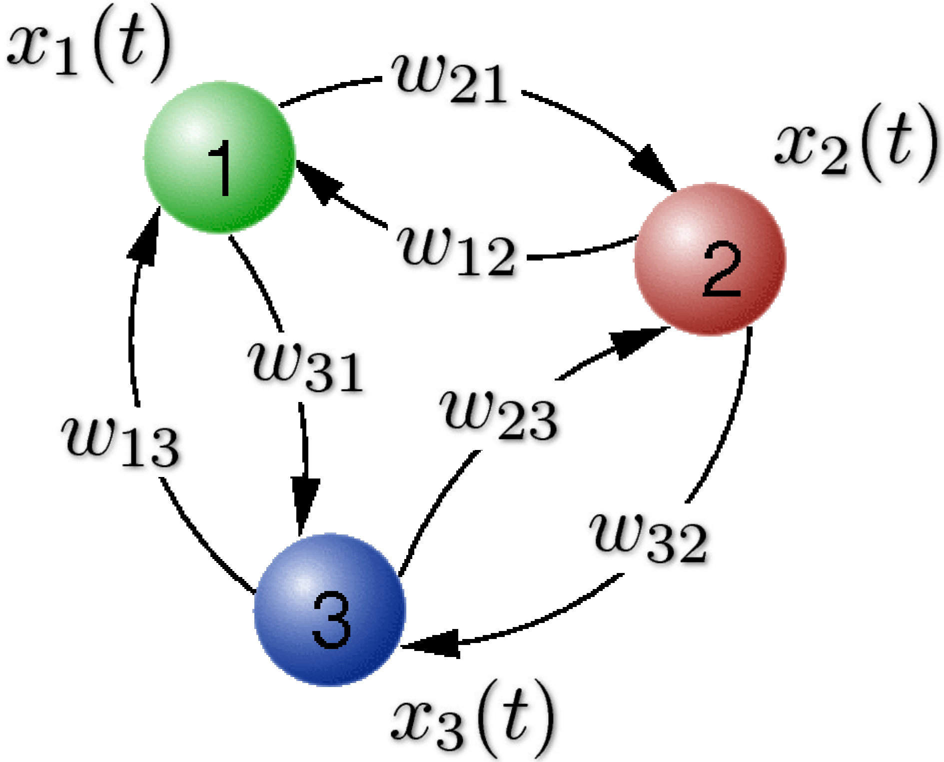
Example: phase space of the pendulum:



Back to neuroscience: Lotka-Volterra model

The Lotka-Volterra model was originally used to describe the interaction of competing species.

Now it is often used to describe circuits of neurons in a rate description.



$$\frac{dx_i}{dt} = x_i\left(1 - \sum_{j=1}^{3} w_{ij}x_j\right)$$

$$w_{ii} = 1$$

May, R. M. & Leonard, W. J. “Nonlinear aspects of competition between three species" SIAM J. Appl. Math. 29, 243-253 (1975)

Extended Lotka-Volterra model (LVm) for the AL

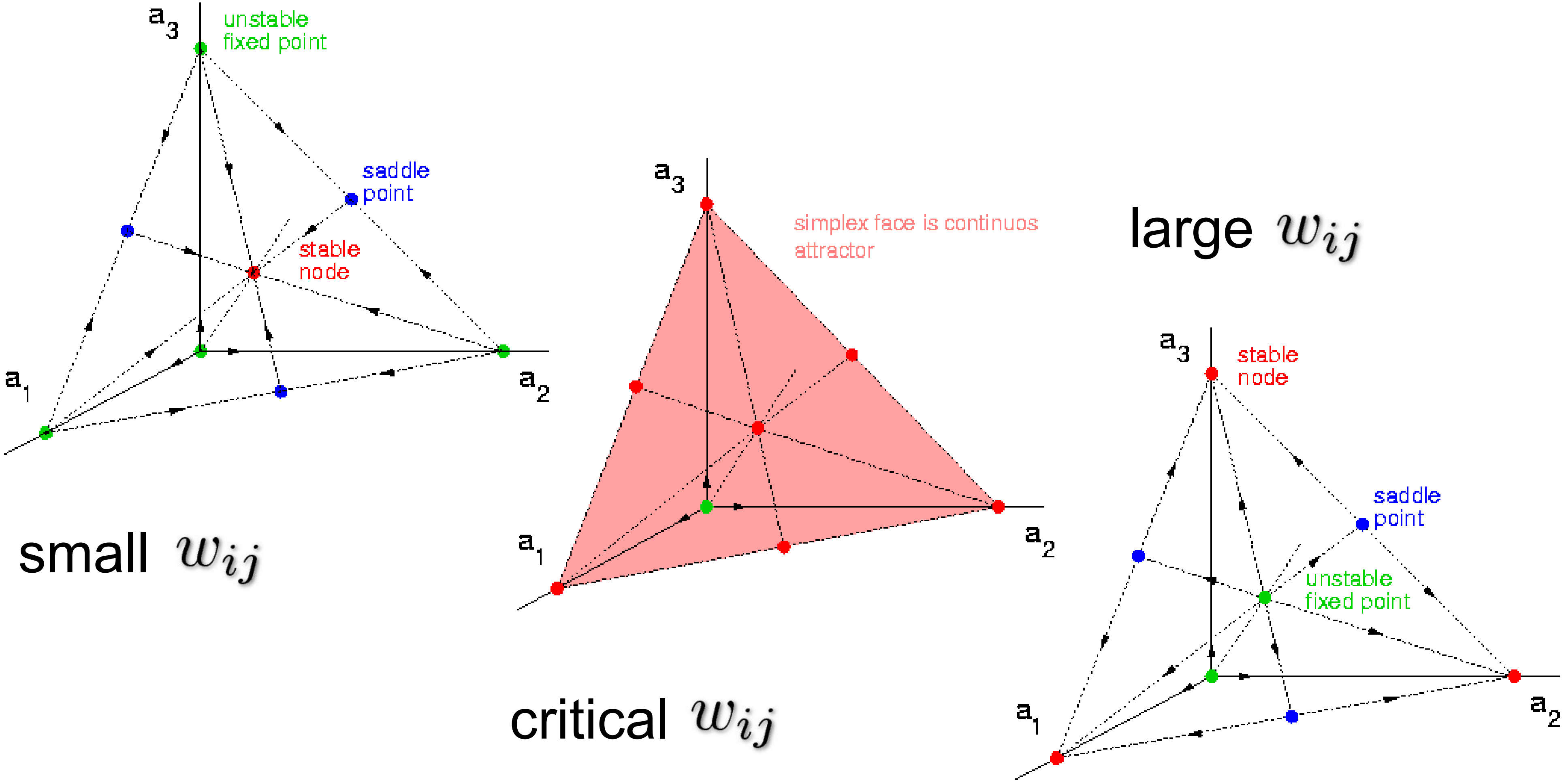
$$\frac{dx_i}{dt} = x_i\Big(\sigma(\vec{h},\vec{s}) - \sum_{j=1}^{N} w_{ij}x_j + h_i(t) + s_i(t)\Big)$$

$\sigma(\vec{h},\vec{s})$	General excitation of the neurons (can depend on inputs)
$s_i(t)$	Inputs from sensory neurons
$h_i(t)$	Inputs from other neurons (e.g. LNs)

V. Afraimovich, M. I. Rabinovich, P.Varona, Heteroclinic contours in neural ensembles and the winnerless competition principle, Int. J. Bifurc. Chaos 14(4): 1195-1208, (2004).

Phase space structure of the LVm: Symmetric connections

For symmetric weights $w_{ij} = w_{ji}$

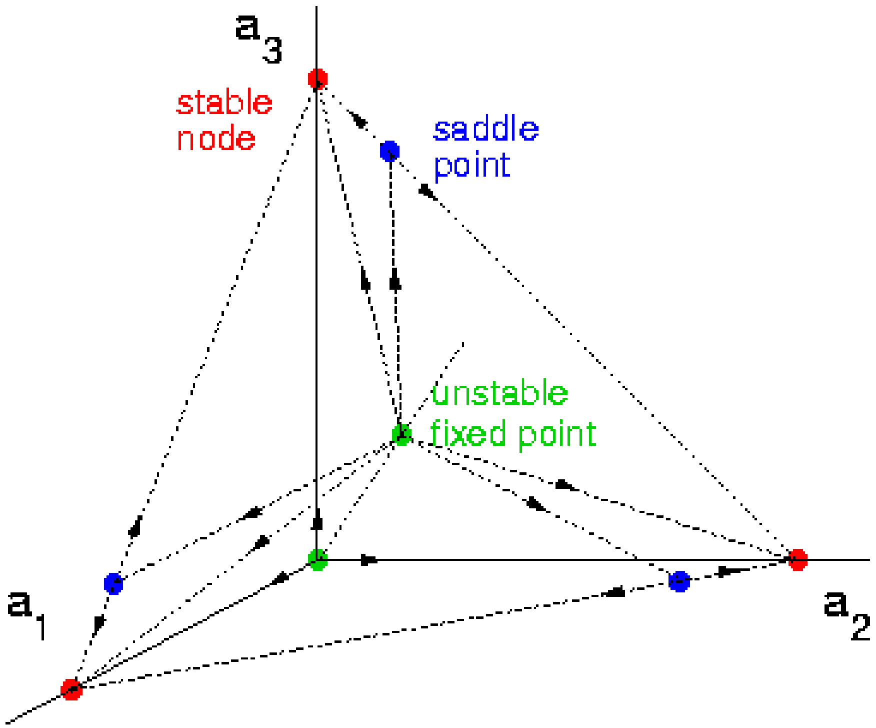


small w_{ij}

critical w_{ij}

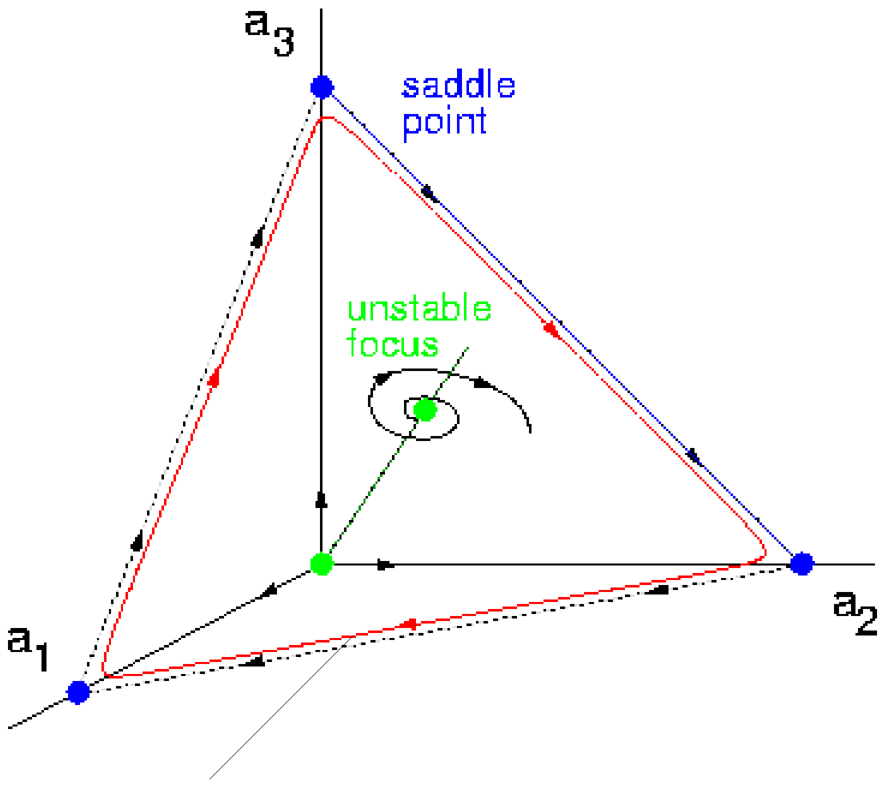
large w_{ij}

Asymmetric connections: Winnerless competition



small w_{ij}

large w_{ij}



Heteroclinic Orbit

Existence theorem

- If $w_{ij} > 1$ and $w_{ji} < 1$, then there exist a heteroclinic contour that consists of saddle points and one-dimensional separatrices connecting them

Chi, C. et al. “On the asymmetric May-Leonard model of three competing species" SIAM J. Appl. Math. 58, 211-226, 1998;

Afraimovich, et al. “Chaotic behavior of three competing species of May-Leonard model under small periodic perturbations”,Int. J. Bifurcation and Chaos 11, 435-447, 2001

Stability theorem

If

$$w_{ij} = \begin{pmatrix} 1 & \alpha_1 & \beta_1 \\ \beta_2 & 1 & \alpha_2 \\ \alpha_3 & \beta_3 & 1 \end{pmatrix} \qquad 0 < \alpha_i < 1 < \beta_i$$

$$\kappa_i = \frac{\beta_i - 1}{1 - \alpha_i}$$ and $$\kappa_1 \cdot \kappa_2 \cdot \kappa_3 > 1$$

➡ Heteroclinic is global attractor.

Afraimovich V, et al. “Heteroclinic contours in neural ensembles and the winnerless competition priniciple, Int J Bifurc and Chaos **14**(4) 1195-1208 (2004)

Taster of the proof

- $0 < \alpha_i < 1 < \beta_i$ ensures that the system has the saddle points.
- In a local neighborhood of the saddle i and in suitable coordinates on can find a map

$$\xi = c\,\eta^{\kappa_i} \qquad \kappa_i = \frac{\beta_i - 1}{1 - \alpha_i}$$ (saddle values)

(ξ - deviation from unstable manifold
η - deviation from stable manifold)

$\kappa > 1$: Local contraction

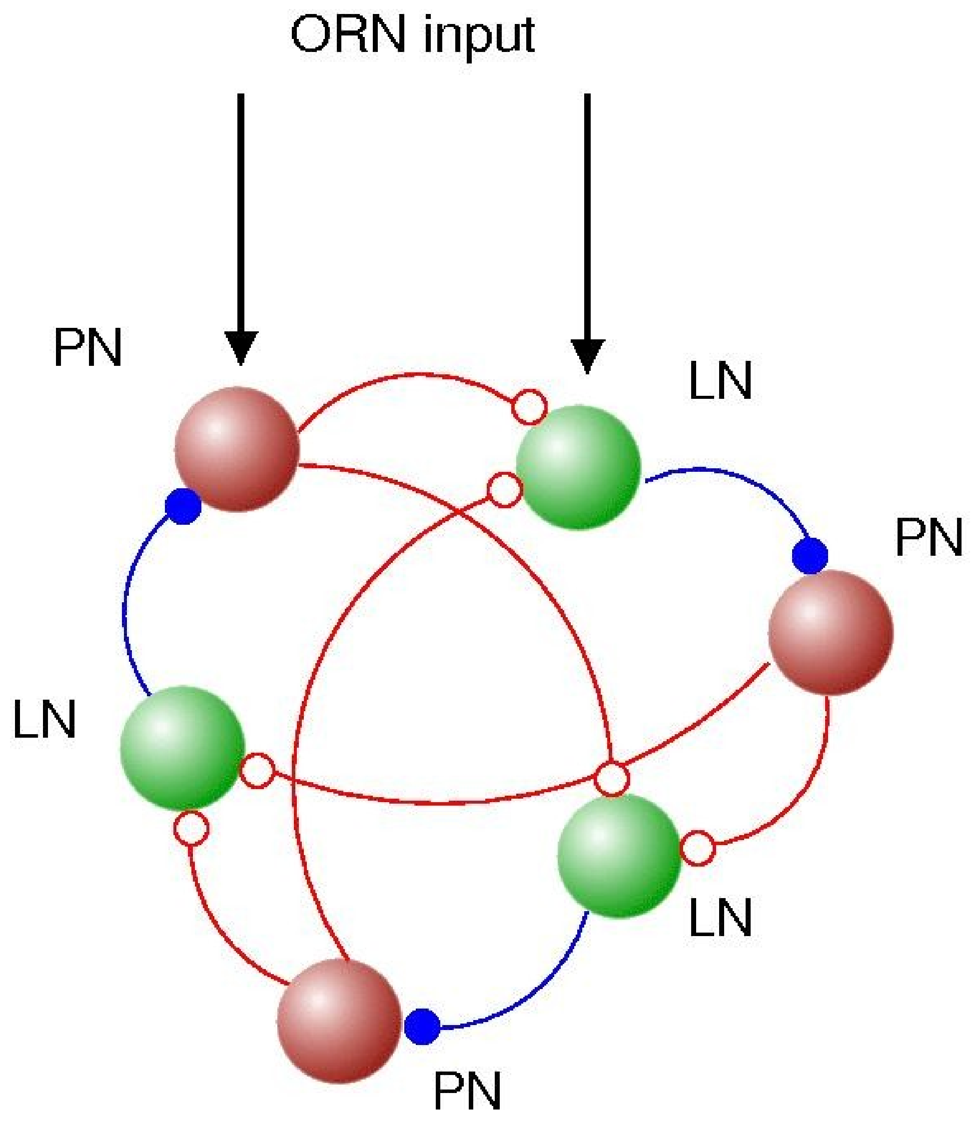
- $\kappa_1 \cdot \kappa_2 \cdot \kappa_3 > 1$: "Attraction on average"

Interpretation

- The weights w_{ij} determine the *sequence* of the neuronal activity
  - ➔ Odor input has to determine the weight matrix; This may be accomplished by input to the non-spiking interneurons in locust:

    odor 1 ➡ w_{ij} 1 ➡ sequence 1
    odor 2 ➡ w_{ij} 2 ➡ sequence 2
- Sensitivity vs stability
  - The structure of the heteroclinic (the sequence) is very sensitive to changes in w_{ij}
  - The structure is stable against noise in the variables (rates)

More Interpretation



ORN input to the (non-spiking) local neurons changes the effective coupling w_{ij} in an input-dependent manner!

(Some) critical discussion

- Lotka-Volterra model as a model of neurons

$$\frac{dx_i}{dt} = x_i\left(\sigma(\vec{h}, \vec{s}) - \sum_{j=1}^{N} w_{ij} x_j + h_i(t) + s_i(t)\right)$$

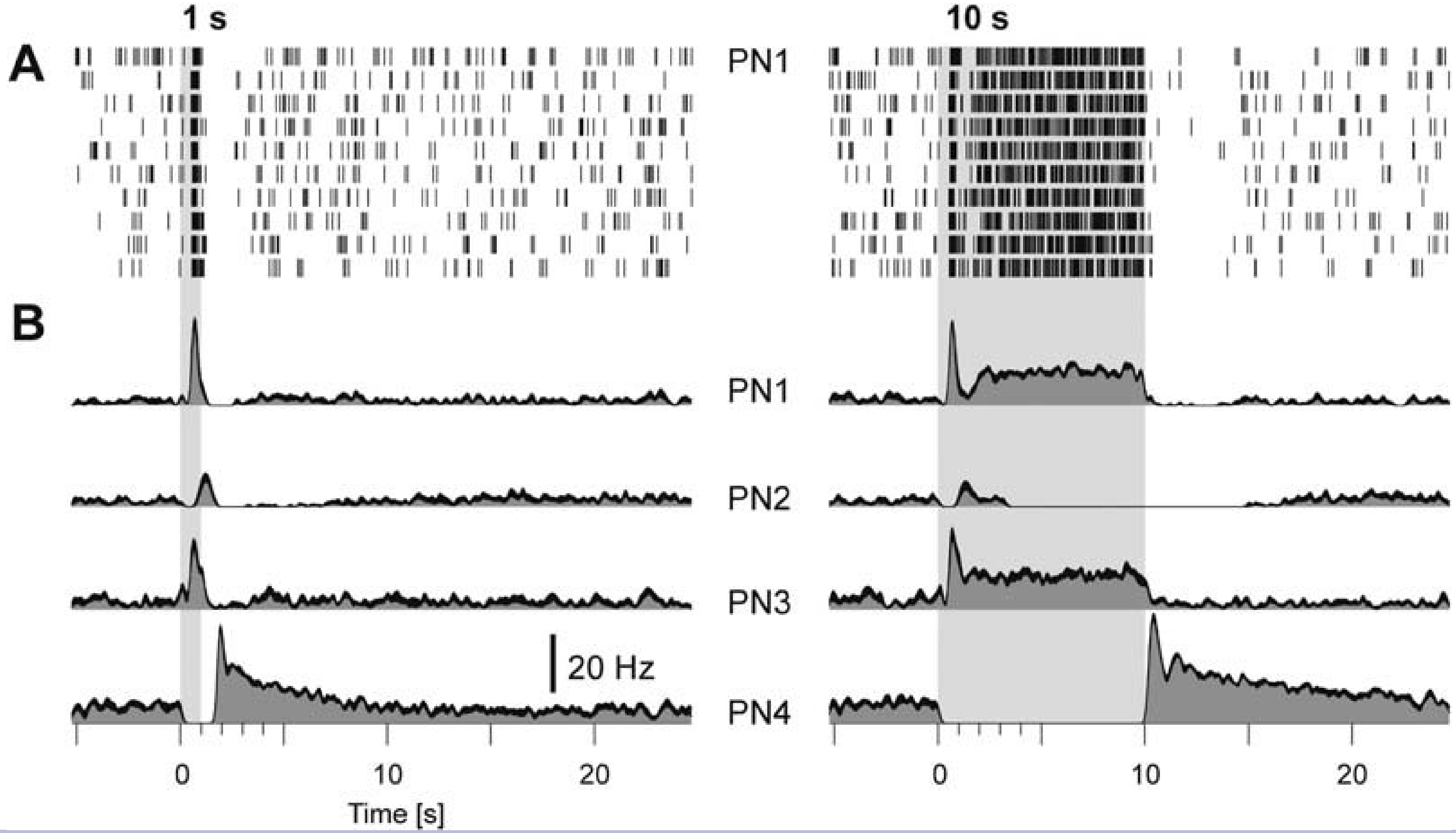
  - Neurons, if silent, remain silen
  - Even input can't excite them

$$\left.\begin{array}{l} \\ \\ \end{array}\right\}$$ Essential for existence of saddles

  - On the other hand: Not a problem as noise is always present?
    (but then, the heteroclinic cycle is not stable in presence of noise ... it will therefore be hard to find experimentally)

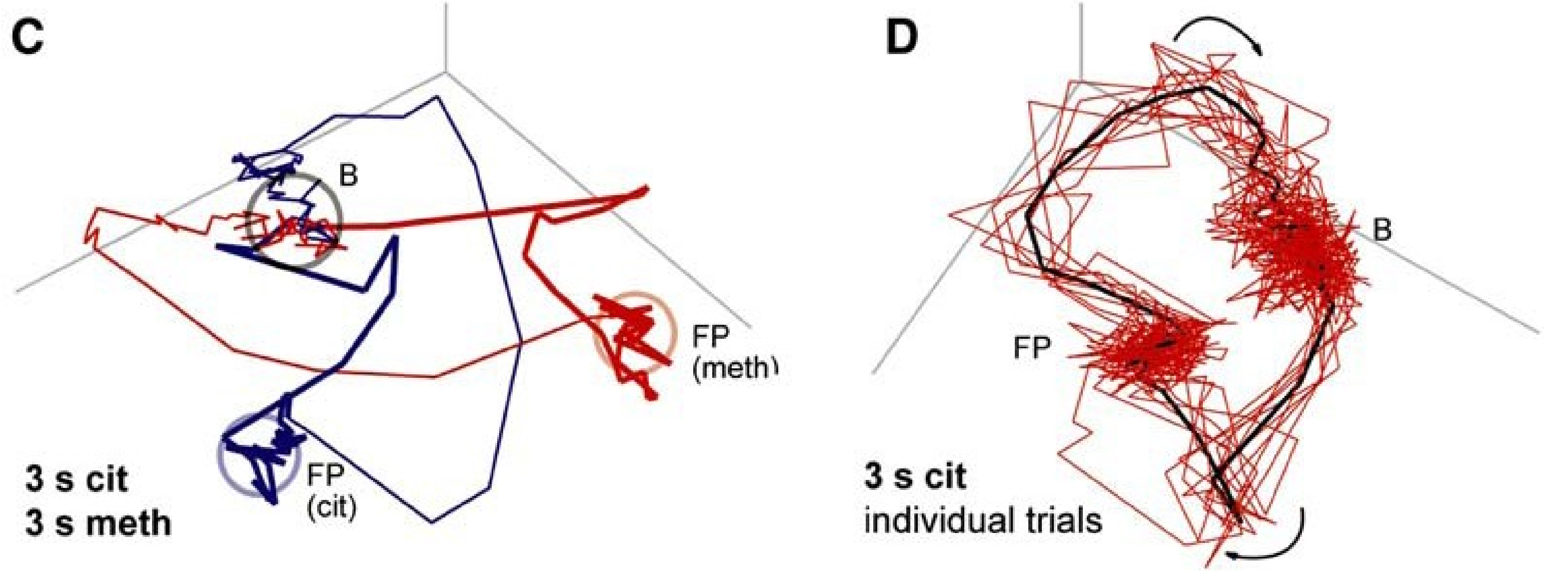
Experimental evidence

- Mazor and Laurent,Transient Dynamics versus Fixed Points in Odor Representations by Locust Antennal Lobe Projection Neurons, Neuron, **48:** 661–673, 2005



More evidence ...

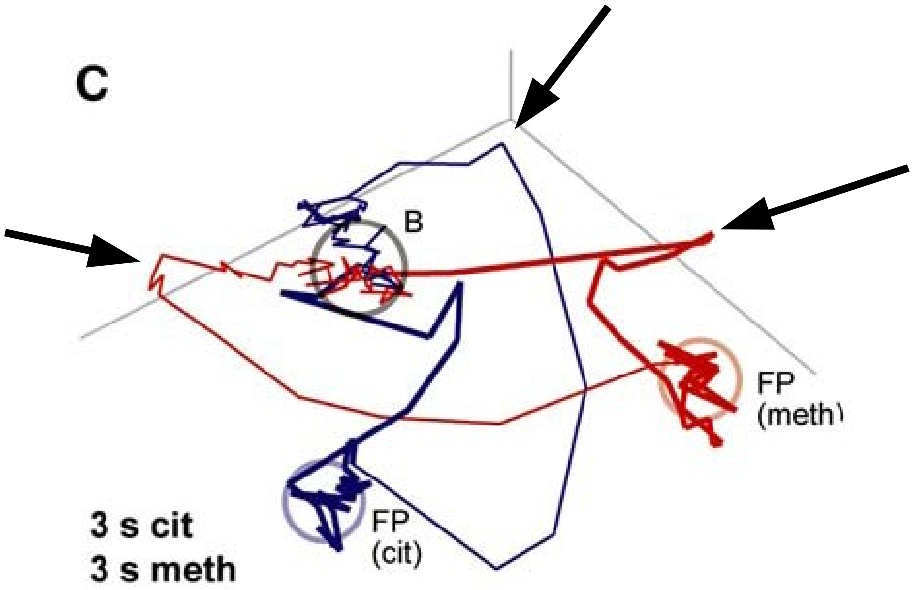
PCA analysis seems to suggest that the dynamics settles to fixed points!



Mazor and Laurent, Neuron **48:** 661–673, 2005

Heteroclinic channels?

- Open heteroclinic structure leading to a fixed point
- Still “switching” dynamics transiently (note the “elbows” in the trajectory)



?

Tomorrow ...

- Are heteroclinic dynamics observable in models with Hodgkin-Huxley neurons? (and, therefore, reasonable as a description of actual biological circuits?)
- Some interesting things about the pheromone subsystem
- General discussion