Lecture 4:
Models of the Antennal Lobe

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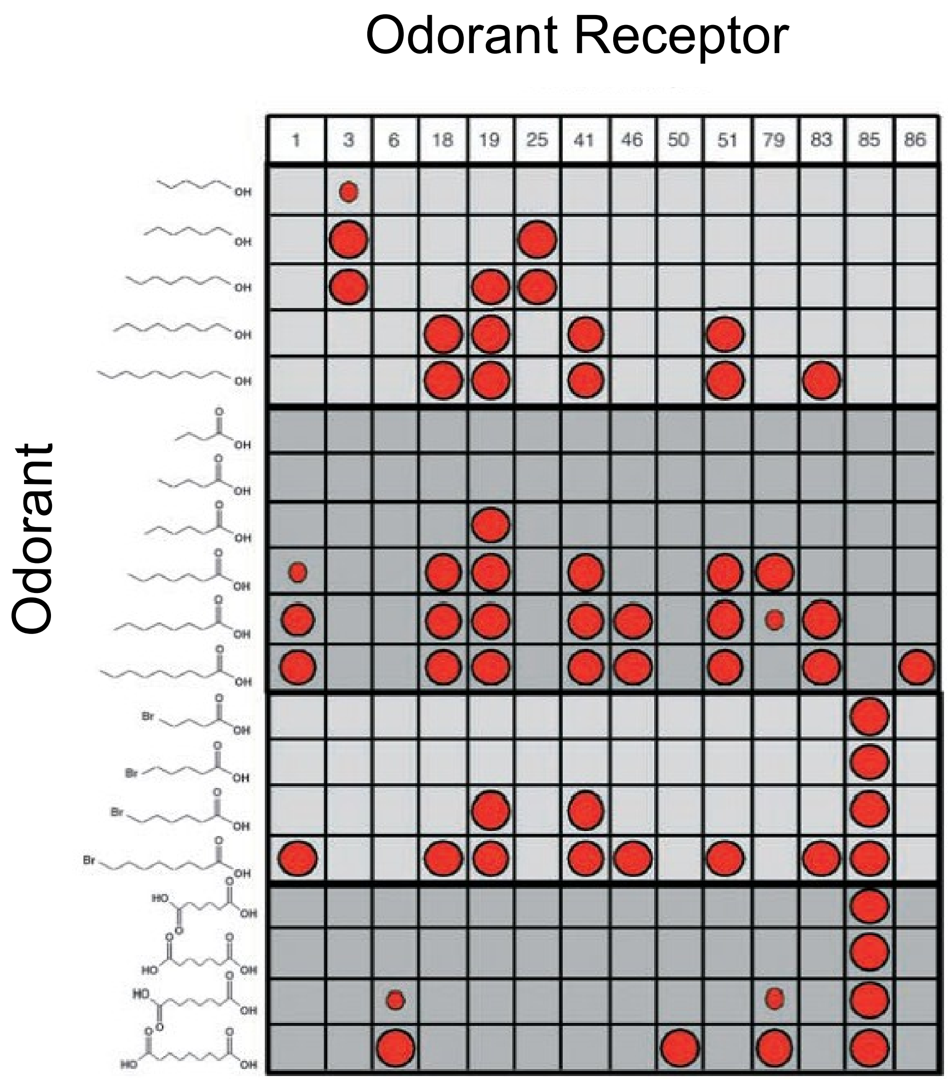
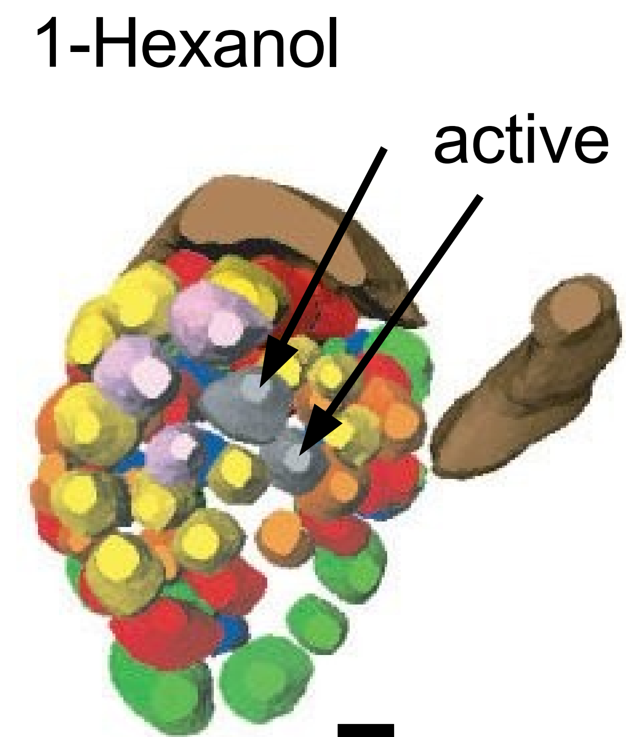
Links

- Lectures:
  http://www.informatics.sussex.ac.uk/users/tn41/Lecturex.pdf
- Exercises
  http://www.informatics.sussex.ac.uk/users/tn41/labs.tar.gz
- NeurAnim
  http://sourceforge.net/projects/neuranim

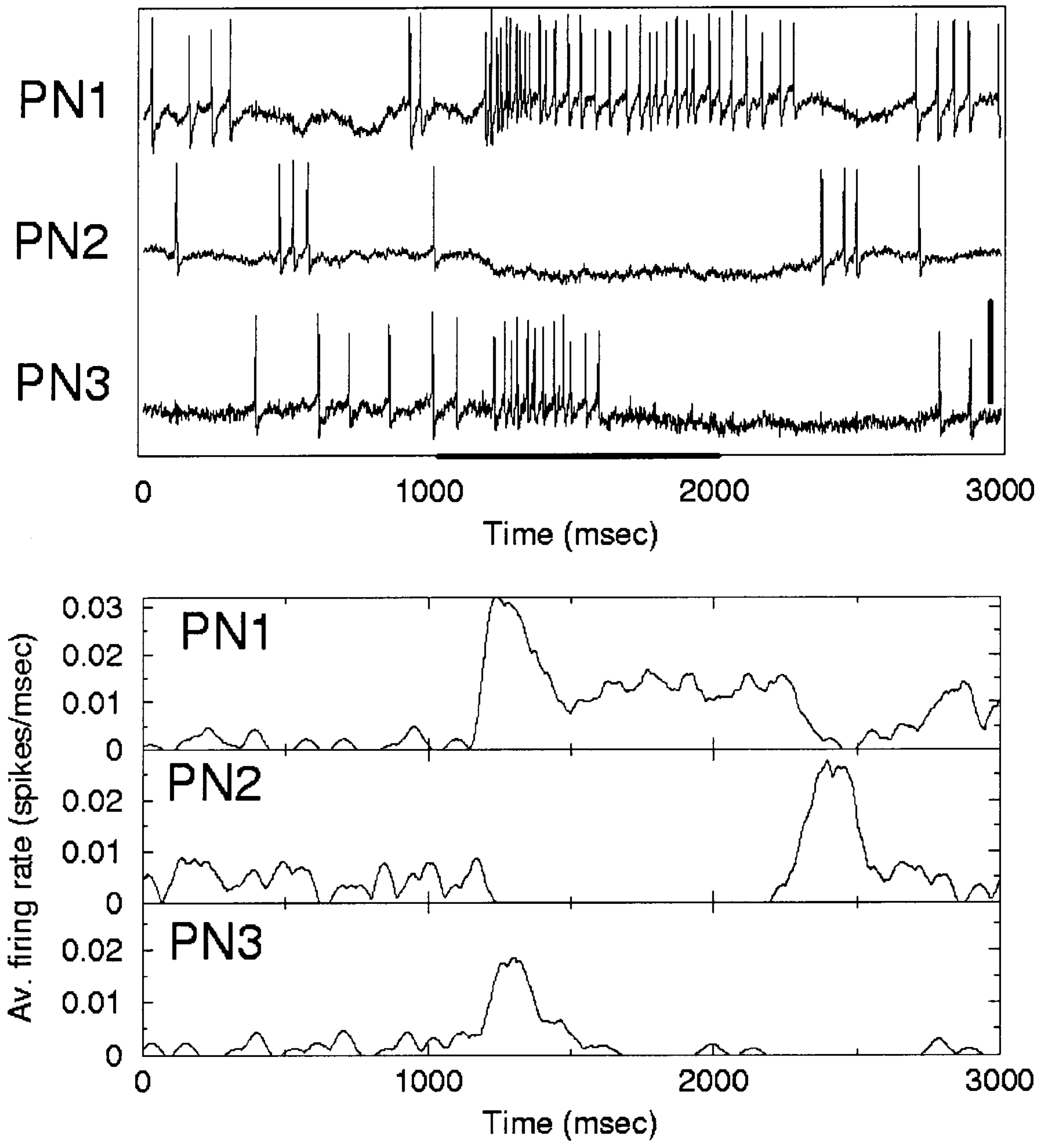
Last time ...





Pattern classification of **static** patterns

The truth is more complicated ...

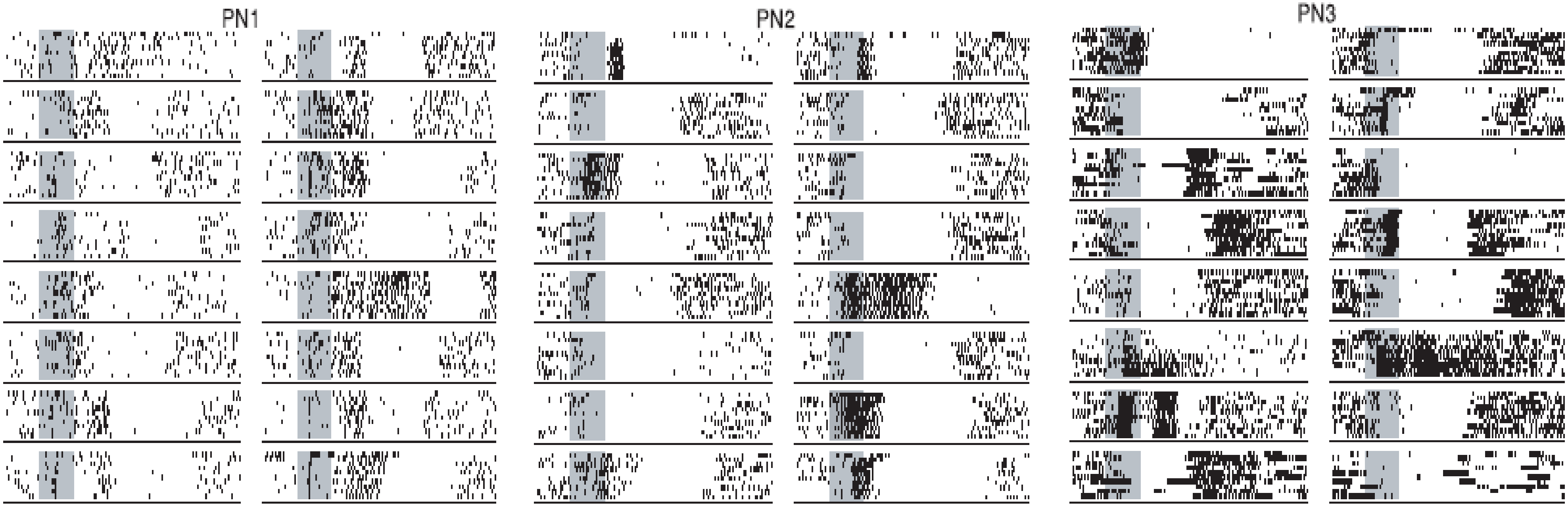


The activity of projection neurons in the locust shows a slow temporal patterning.

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



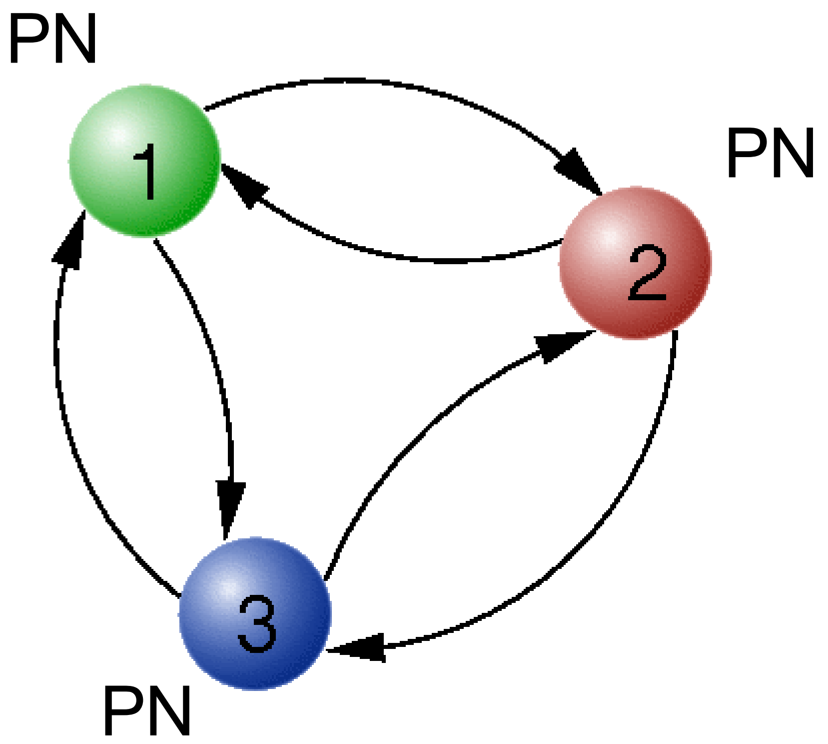
Javier Perez-Orive, et al., Oscillations and Sparsening of Odor Representations in the Mushroom Body,
Science 297: 359 (2002)

Winnerless competition

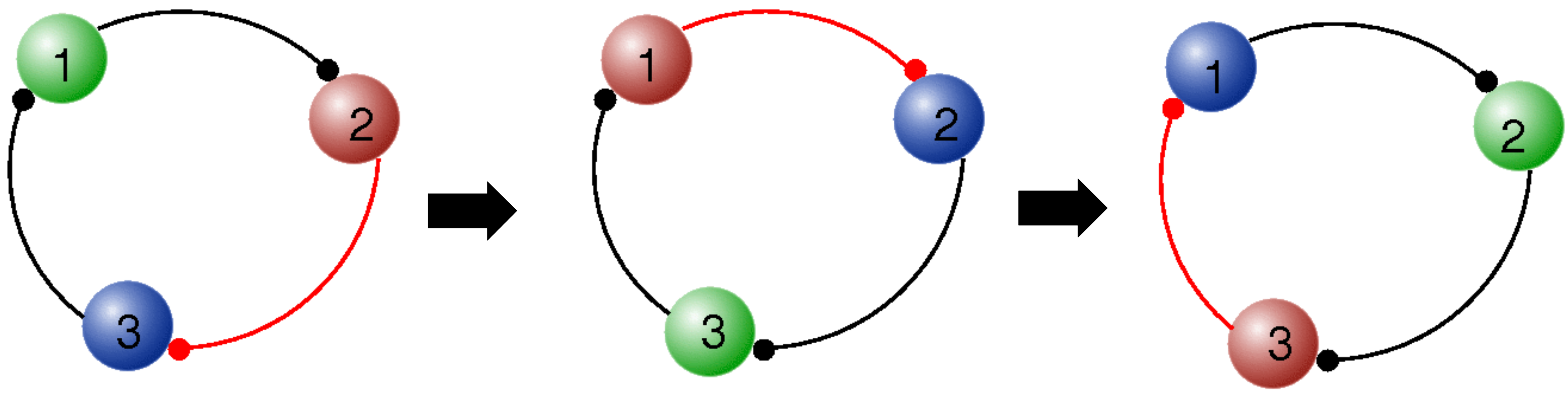
Projection neurons (PN) compete with each other for being active.

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



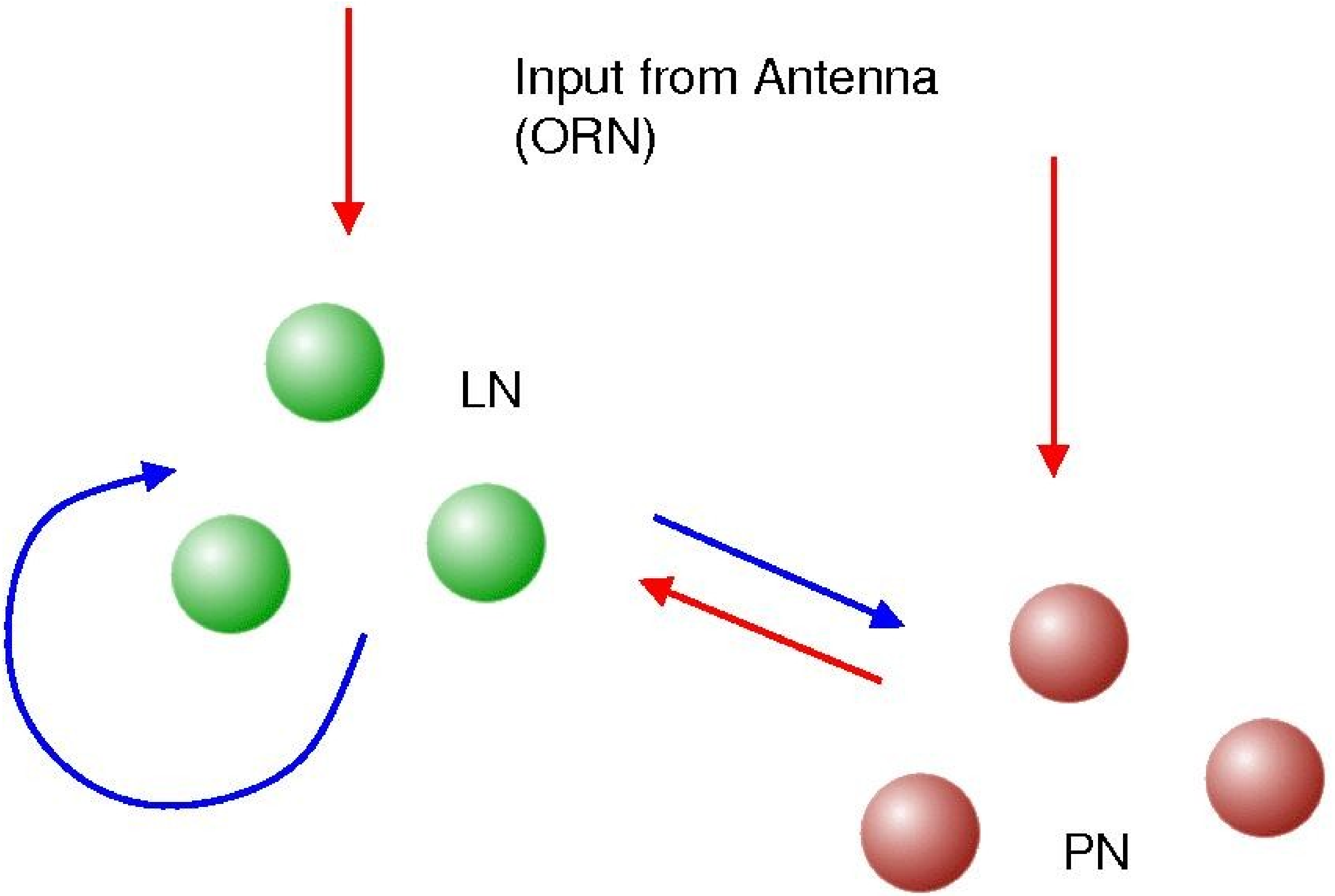
active recovering inhibited

active synapse inactive synapse

No neuron can stay active indefinitely.

“Infrastructure” in the AL

In the locust:



Excitatory:

ORN – PN

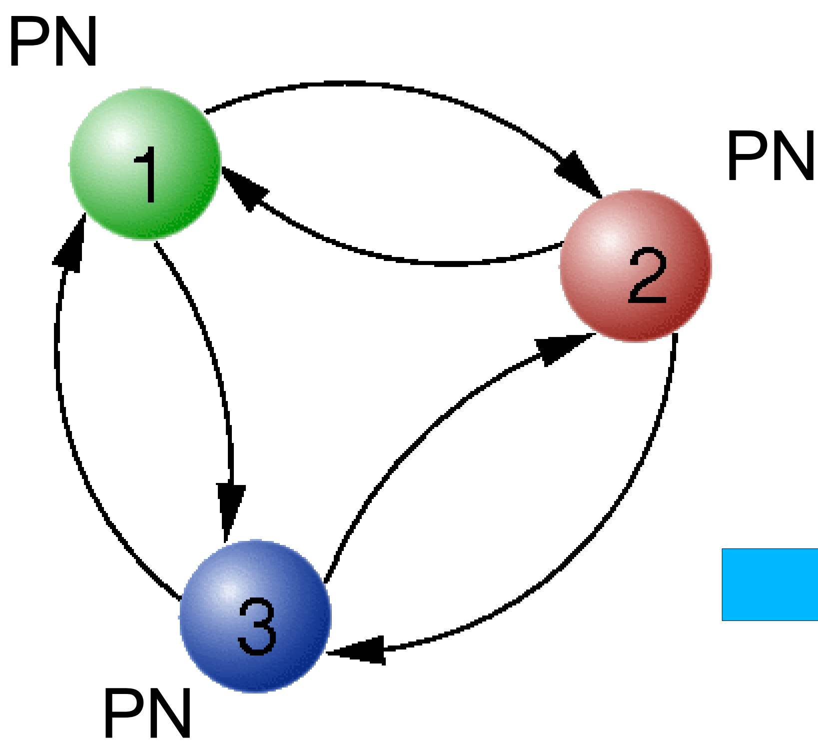
PN – LN

Inhibitory:

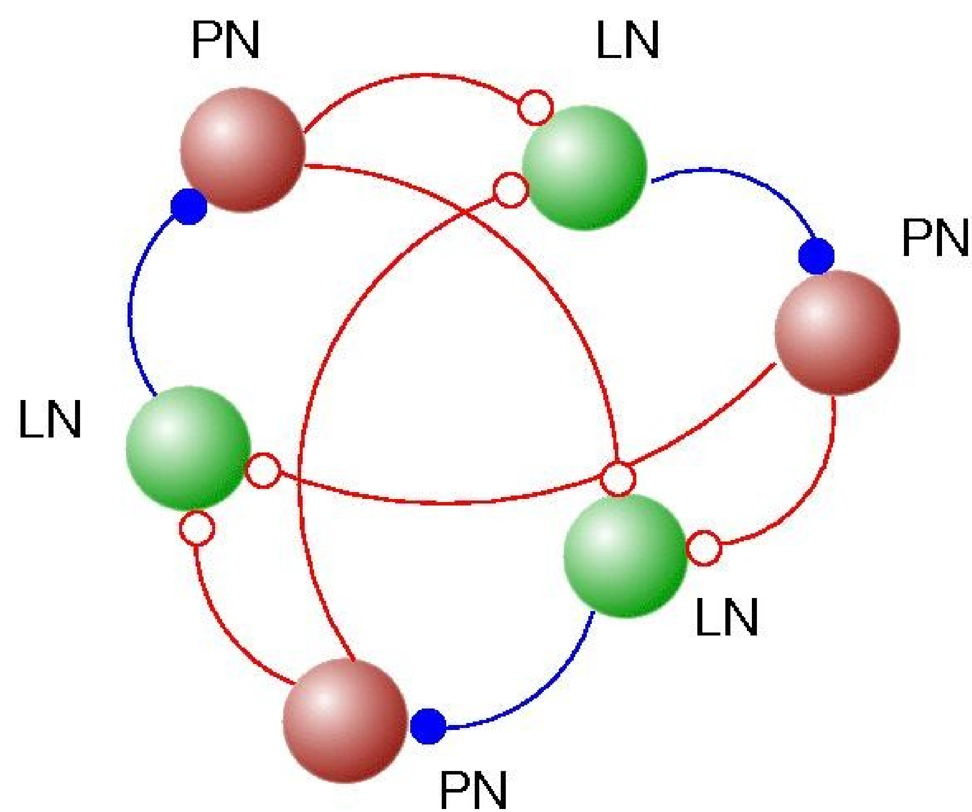
LN – PN

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)

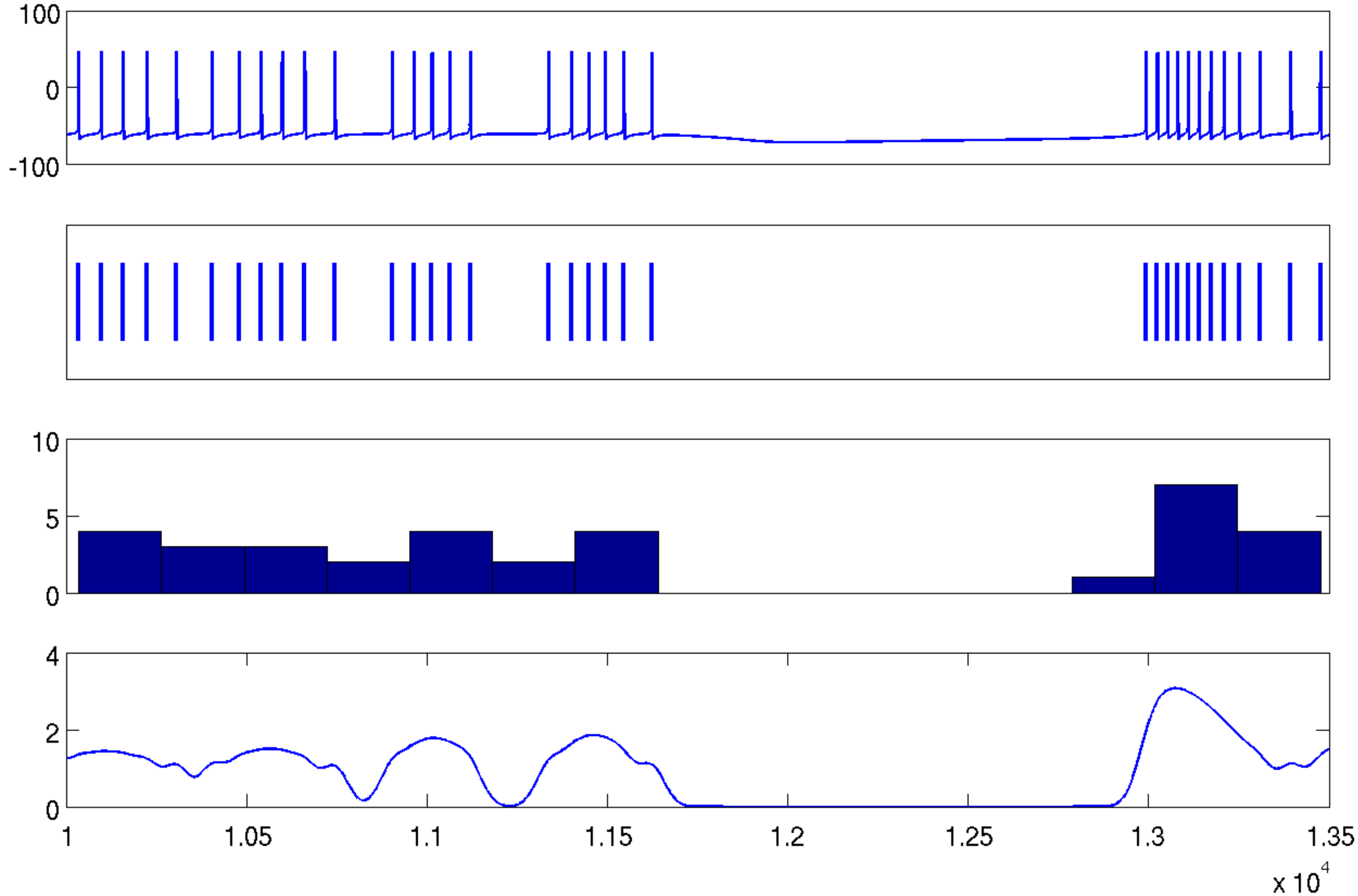
Example of obtaining a rate

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

$$r_i : \mathbb{R} \to \mathbb{R}$$
$$t \mapsto r_i(t)$$

- 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)

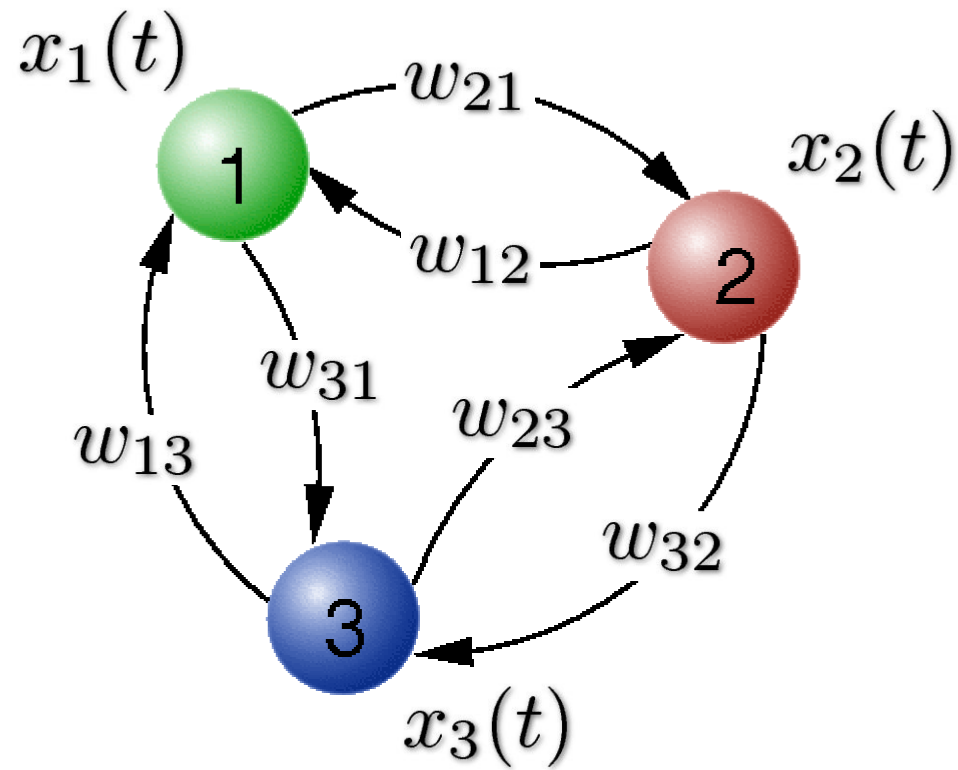
Lotka-Volterra model

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

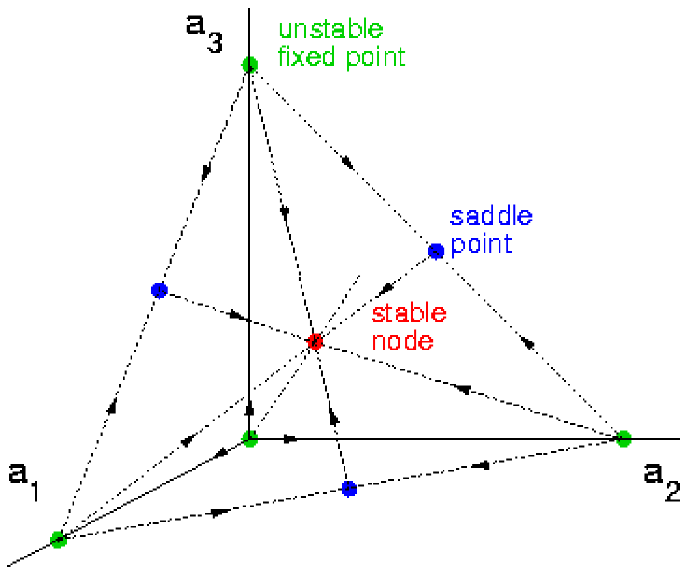
$$\frac{dx_i}{dt} = x_i\Big(\sigma(\vec{h},\vec{s}) - \sum_{j=1}^{N} w_{ij}x_j + h_i(t) + s_i(t)\Big)$$

$\sigma(\vec{h},\vec{s})$	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)

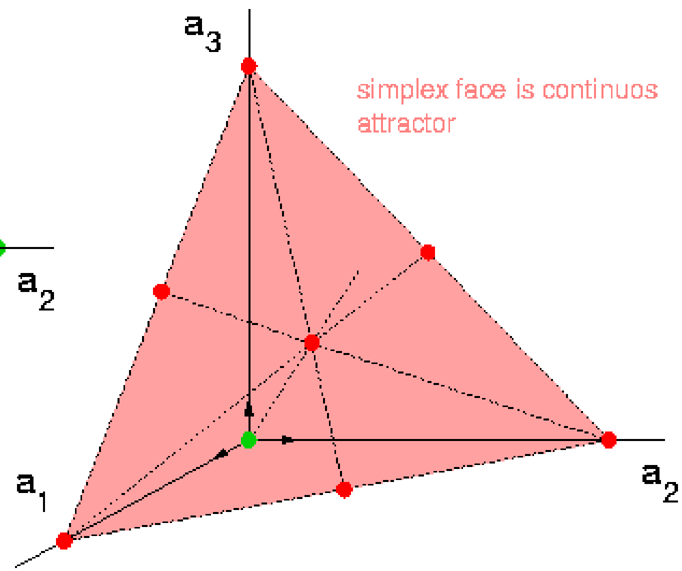
V. Afraimovich, M. I. Rabinovich, P.Varona, Heteroclinic contours in neural ensembles and the winnerless competition principle, Int. J. Bifurc. Chaos 14(4): 1195-1208, (2004).

Phase space structure of the Lvm: Symmetric connections

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

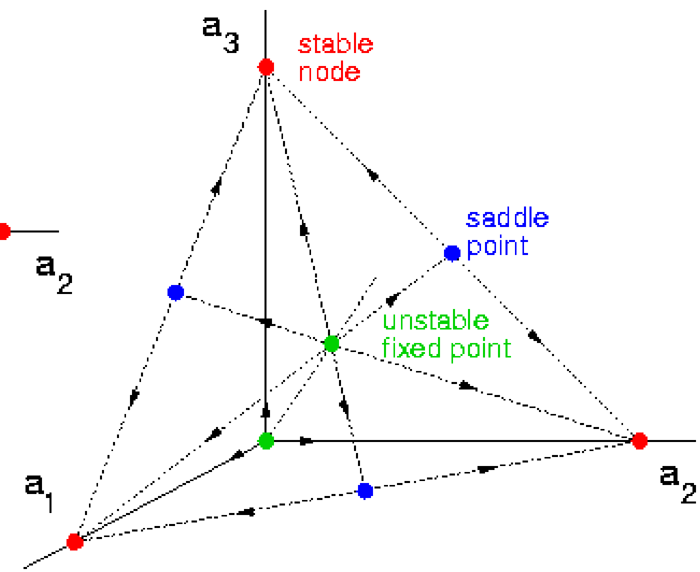


small w_{ij}



critical w_{ij}

large w_{ij}



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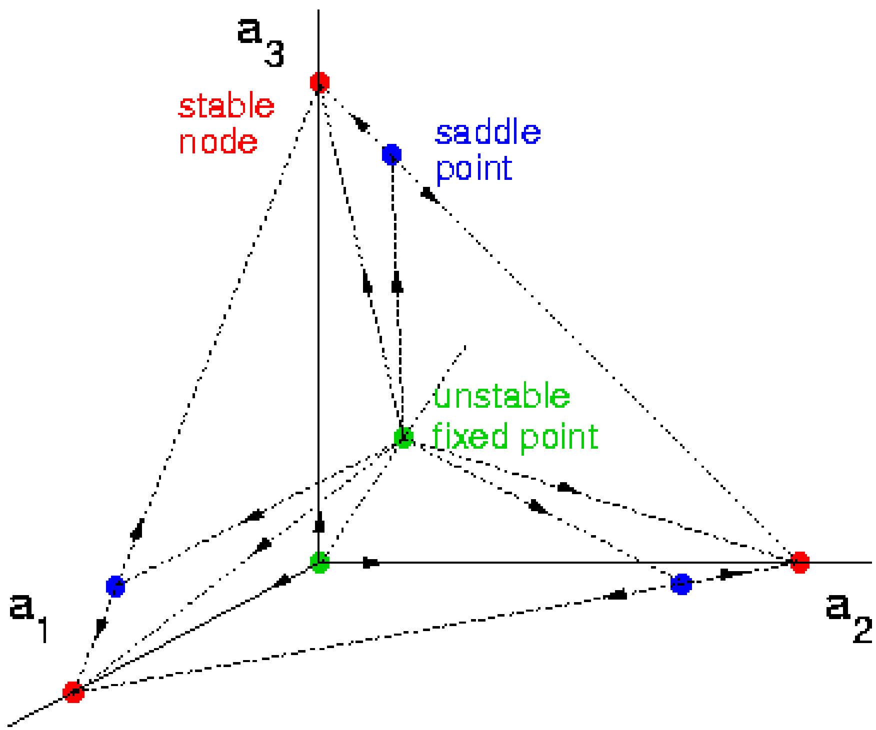
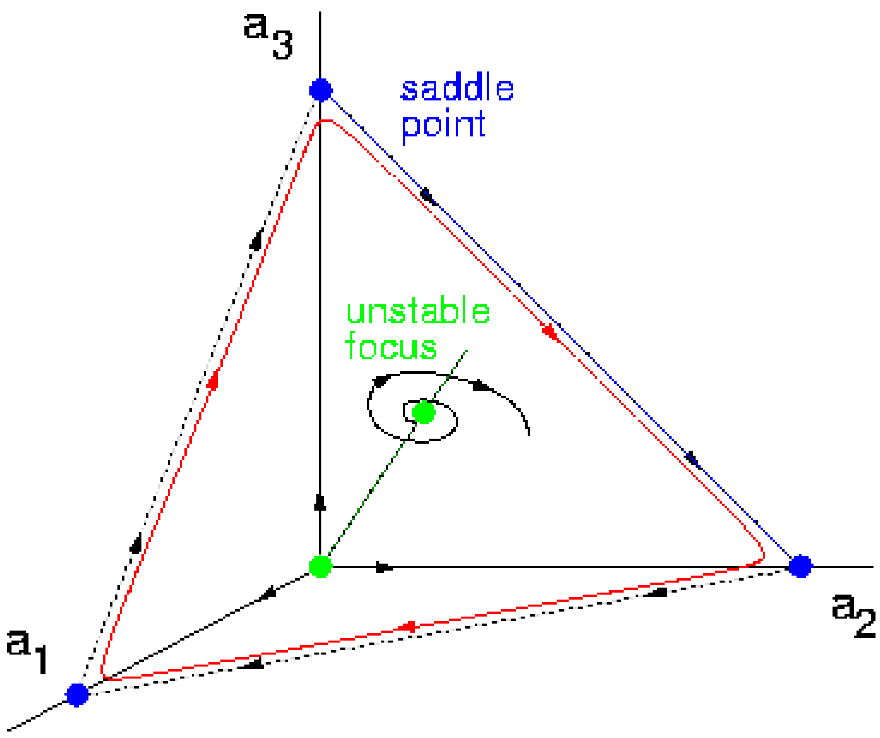
Asymmetric connections: Winnerless competition



small w_{ij}

large w_{ij}



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 $\rightarrow$ w_{ij} 1 $\rightarrow$ sequence 1
    odor 2 $\rightarrow$ w_{ij} 2 $\rightarrow$ 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)

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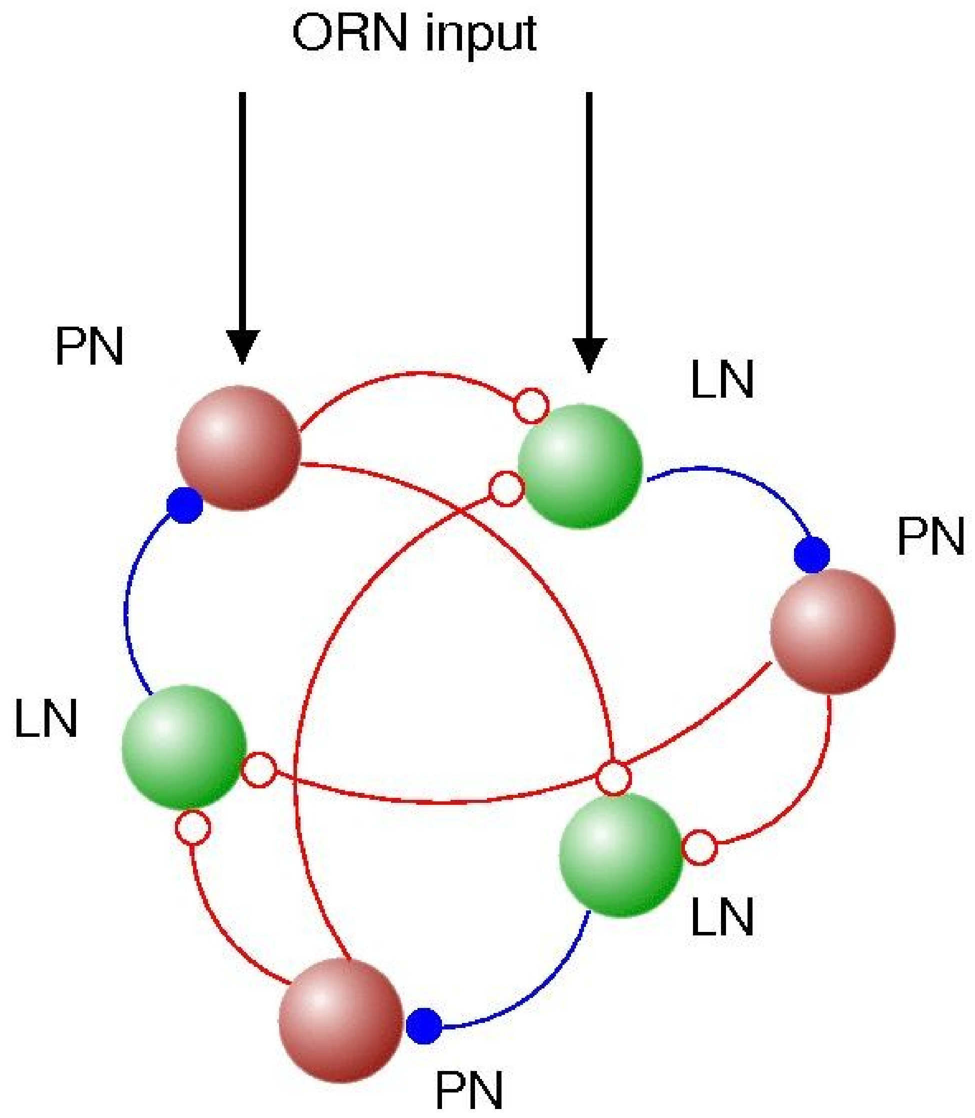
More Interpretation



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

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

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

  } 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)

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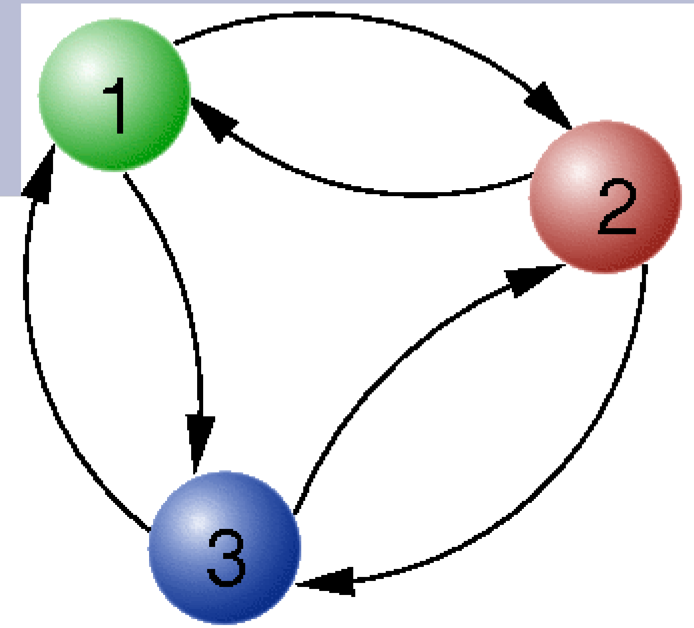
WLC with HH neurons



- The following describes work in
  T. Nowotny and M. I. Rabinovich, Dynamical origin of independent spiking and bursting activity in neural microcircuits, Phys Rev Lett **101**(7):079901
- Describe 3 neuron circuit with HH neurons (Traub and Miles 1991) (HH on white board?)
- Use modified synapses (based on Rall 1961):

Modified synapses

$$I_{\mathrm{syn},ji} = g_{ji}\, S_i\, (V_j - V_{\mathrm{rev}})$$

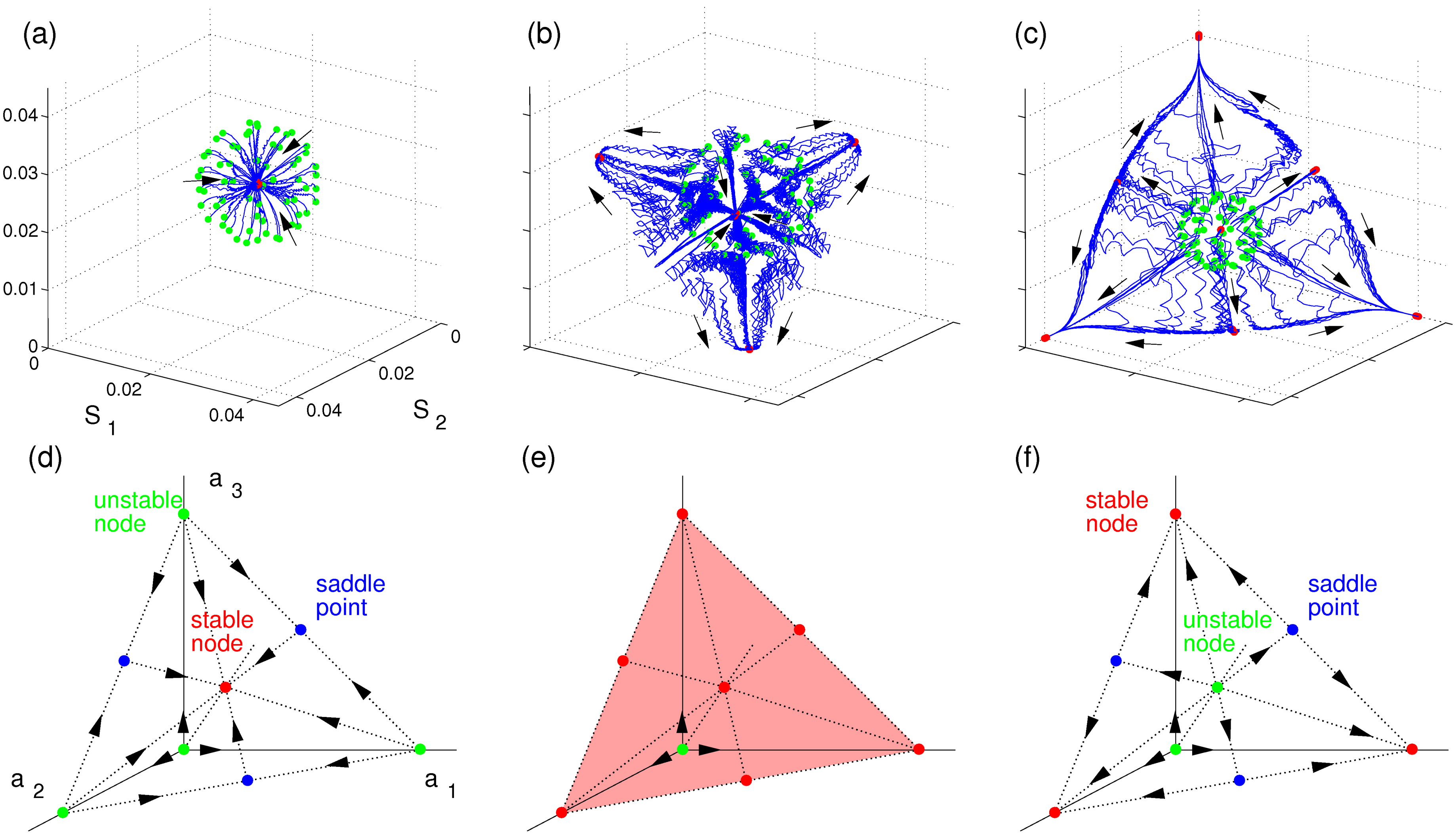
$$\tau \frac{dS_i}{dt} = (\kappa R_i - S_i) \frac{S_{\max} - S_i}{S_{\max}}$$

$$\tau \frac{dR_i}{dt} = \Theta(V_i - V_{\mathrm{th}}) - R_i,$$

“Sticky term” $\dfrac{S_{\max} - S_i}{S_{\max}}$

We use the synapse activation variables S as rate variables.

Compared to LTV: Symmetric connections



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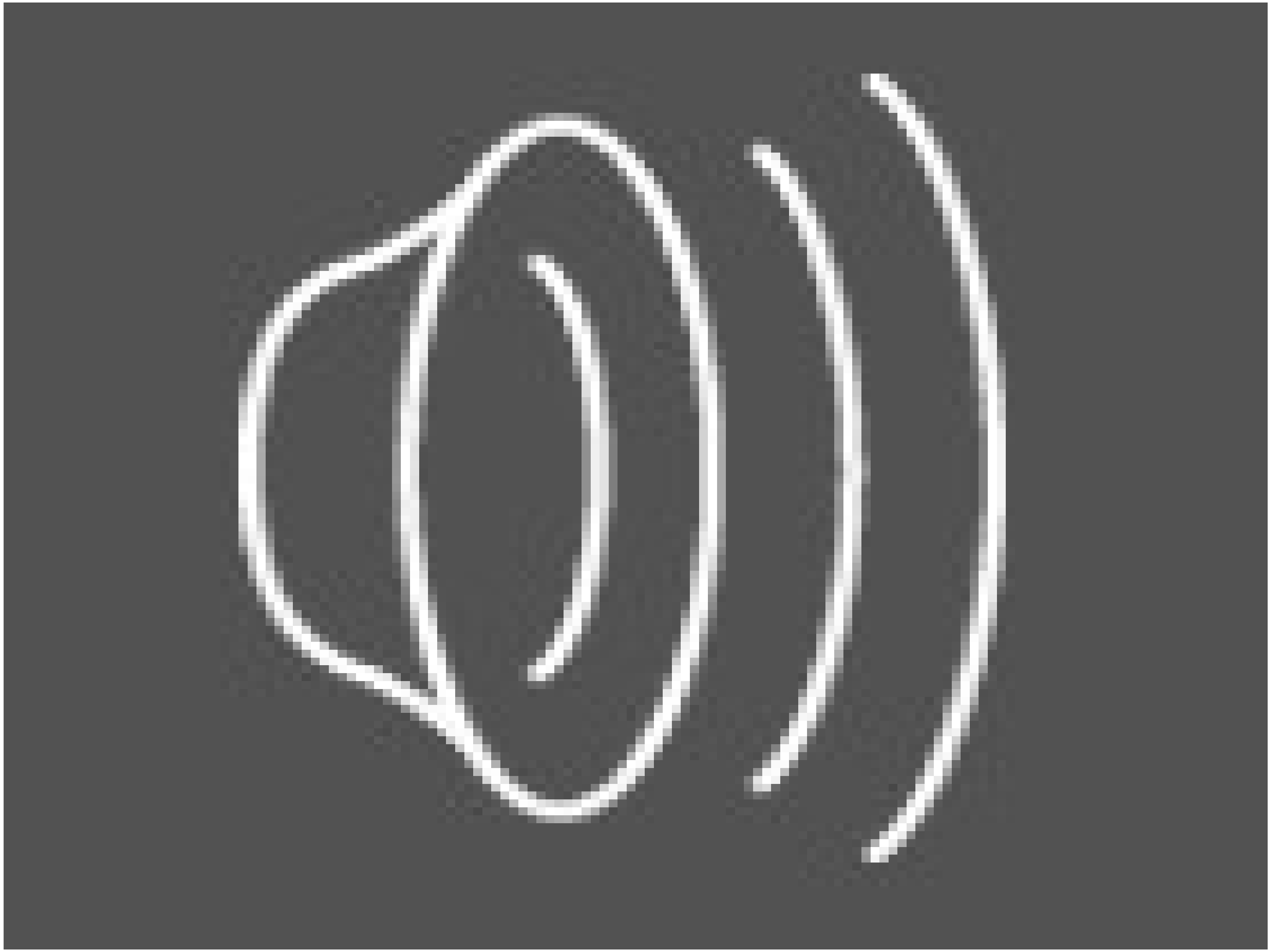
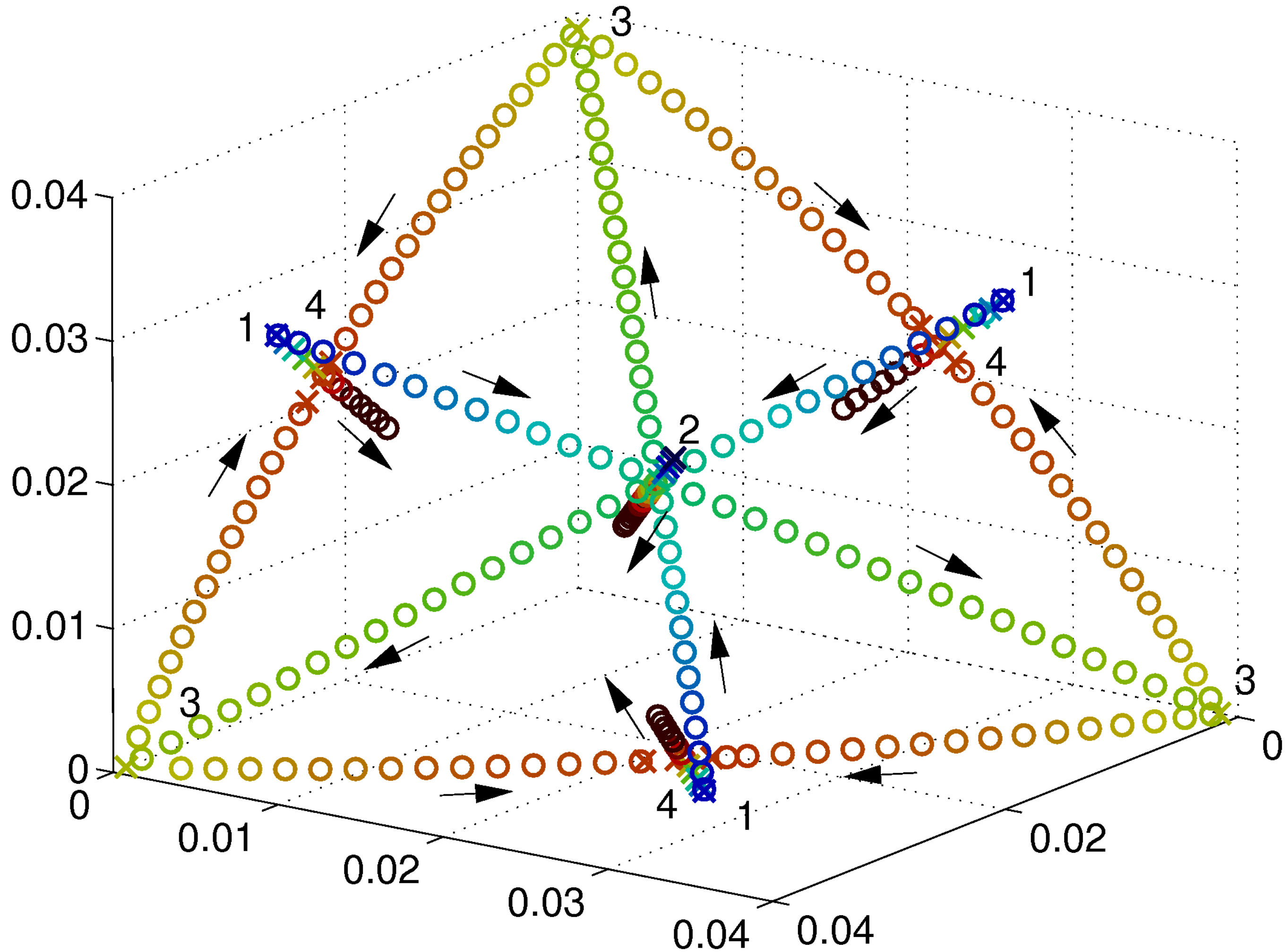
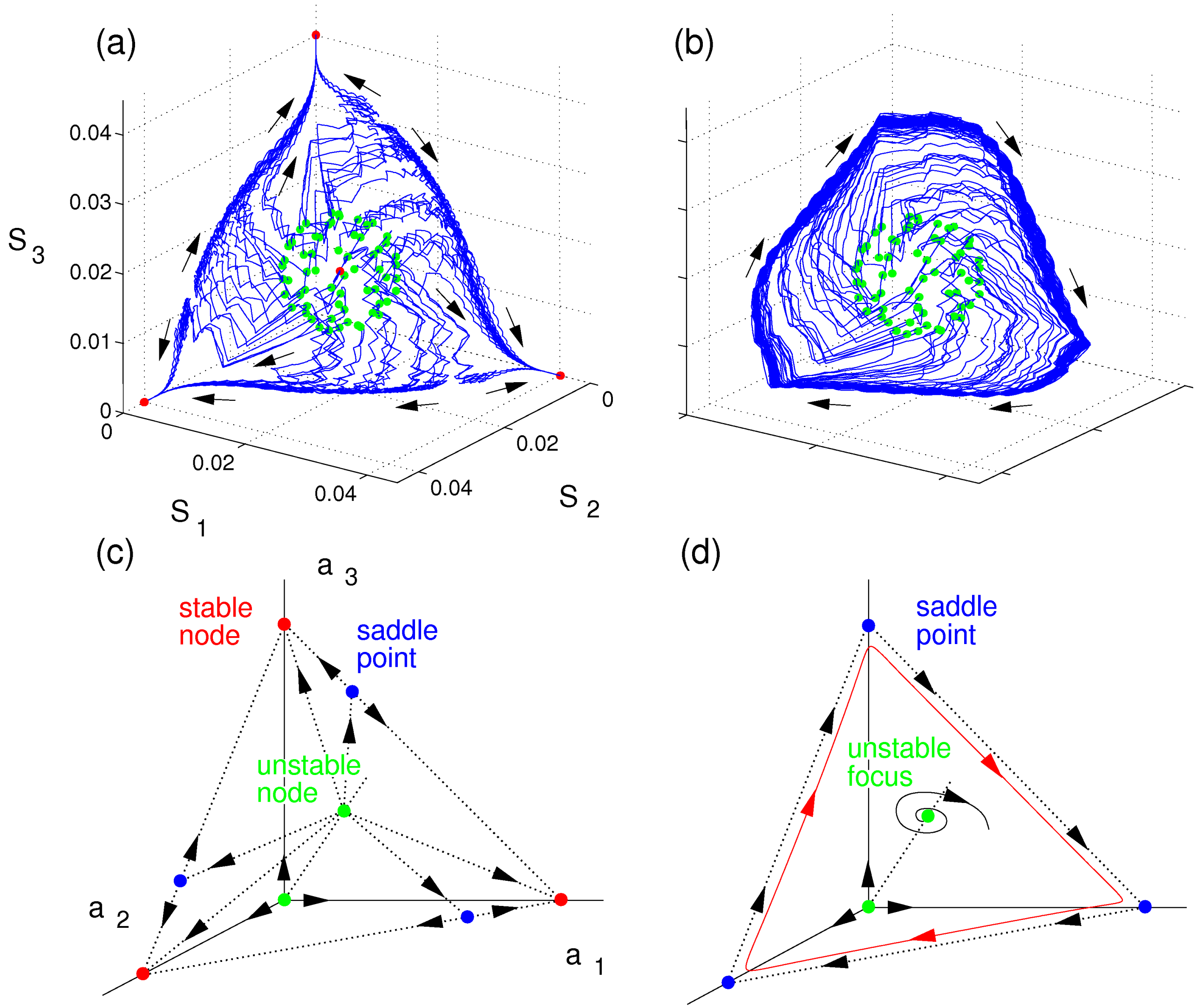
Bifurcation Analysis



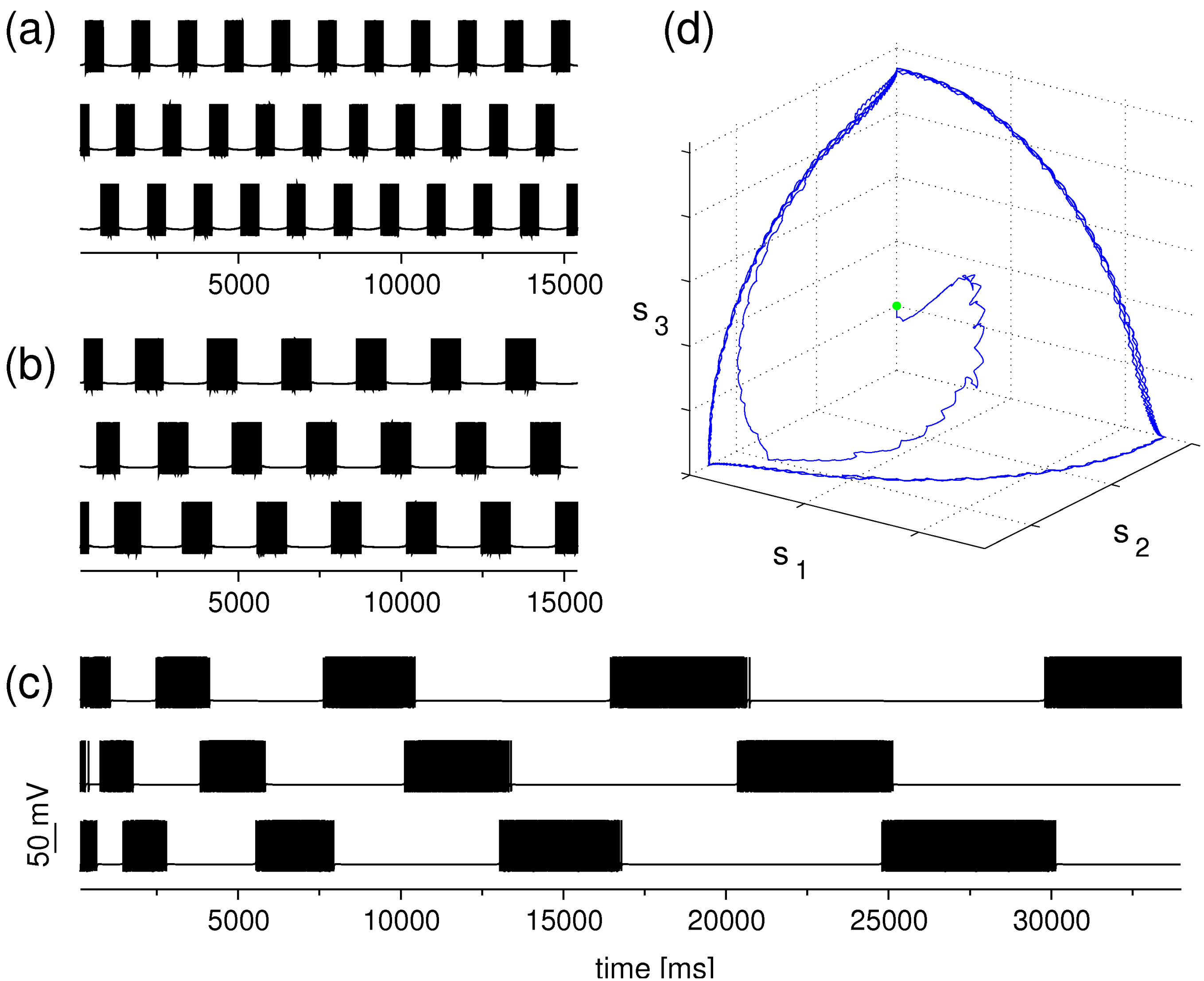
Bifurcation Analysis



Asymmetric connections



Heteroclinic exists and can be attracting



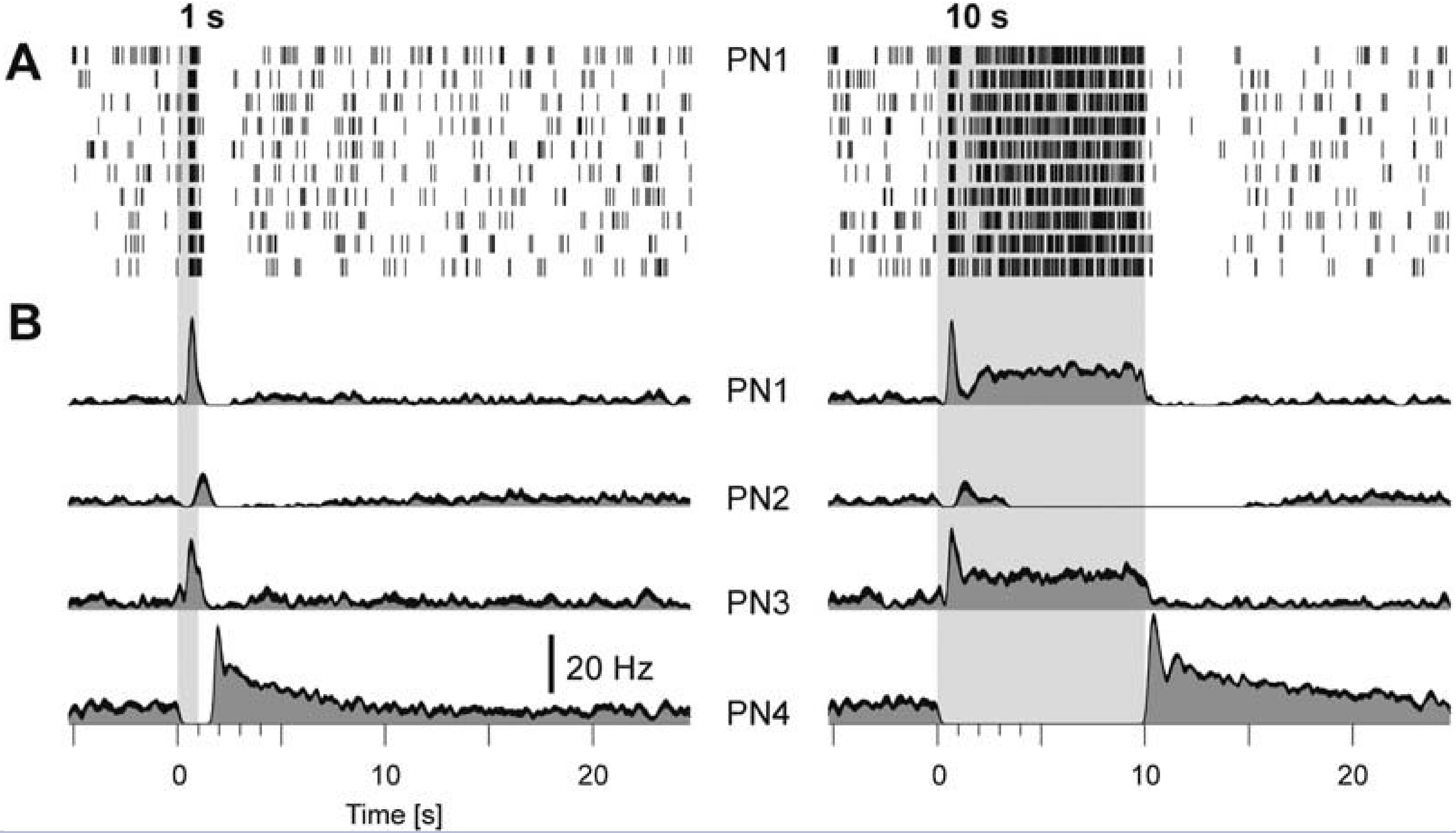
Increasing intrinsic spiking frequency

Discussion: Does this prove heteroclinic structure in a realistic model (in biology)?

- The model elements are all standard except the "sticky term"
- Biological interpretation of this term?
- If the term is removed, the existence & stability of a heteroclinic structure is unproven
- Does this mean we were cheating? Does it matter?

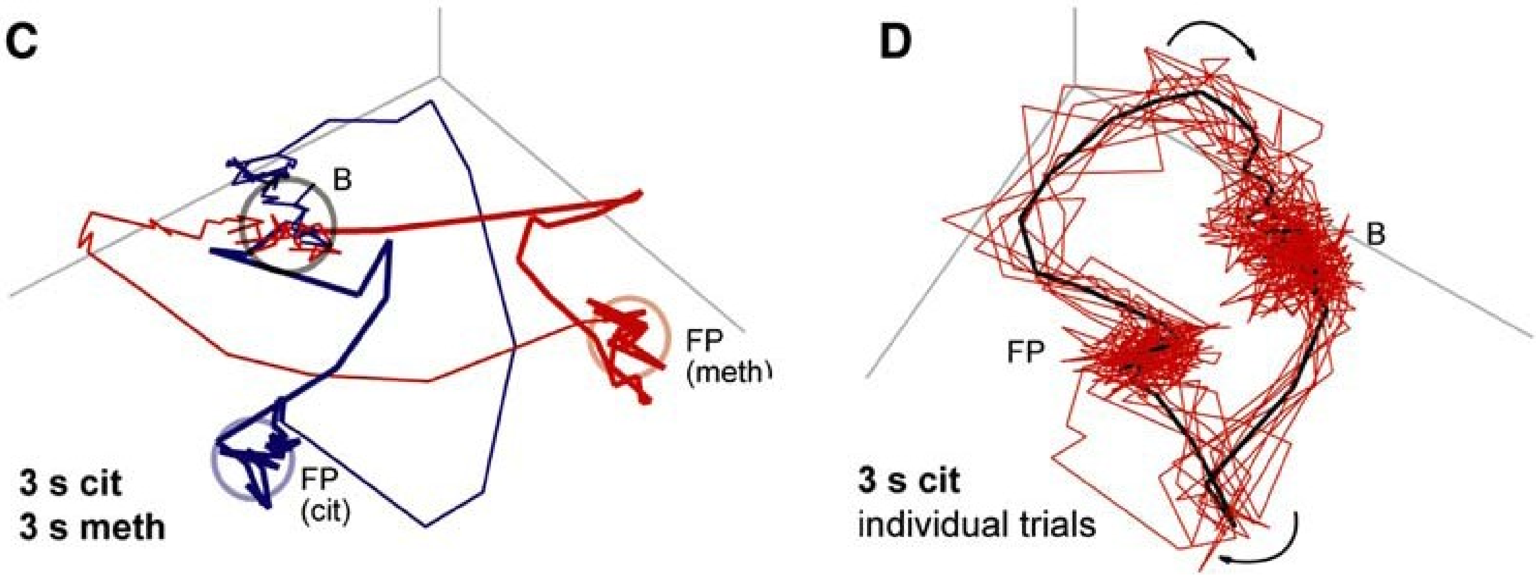
Experimental evidence

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



More evidence ...

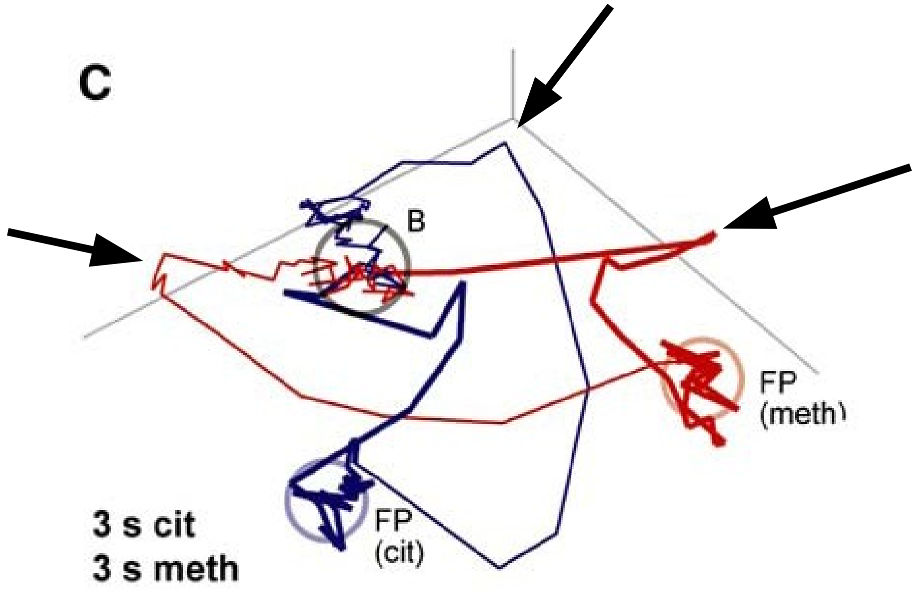
PCA analysis seems to suggest that the dynamics settles to fixed points!



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)



?

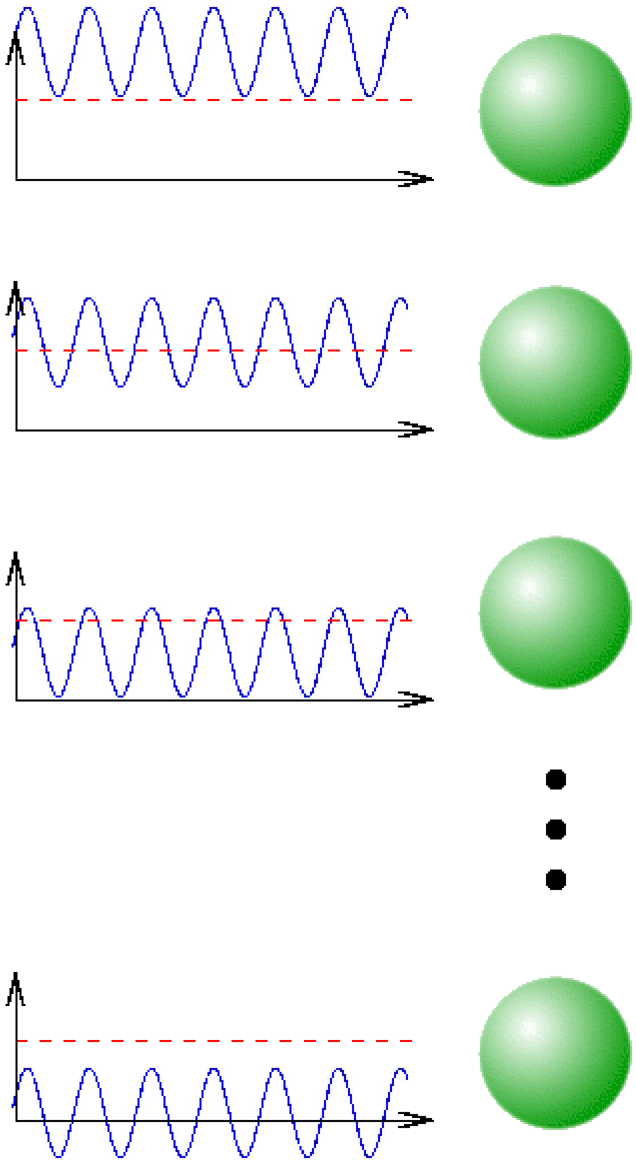
Brody & Hopfield

Model of olfactory processing

Hopfield's model of olfaction

- This is not **the** Hopfield model
- This model is based on what Brody and Hopfield call “Many Are Equal”
- ... which is based on a fundamental mechanism of synchronization by sub-threshold oscillations

Synchronziation by sub-threshold oscillations



$$I_1 = I_{\text{offset},1} + I \sin \omega t + \text{noise}$$

$$I_2 = I_{\text{offset},2} + I \sin \omega t + \text{noise}$$

$$I_n = I_{\text{offset},n} + I \sin \omega t + \text{noise}$$

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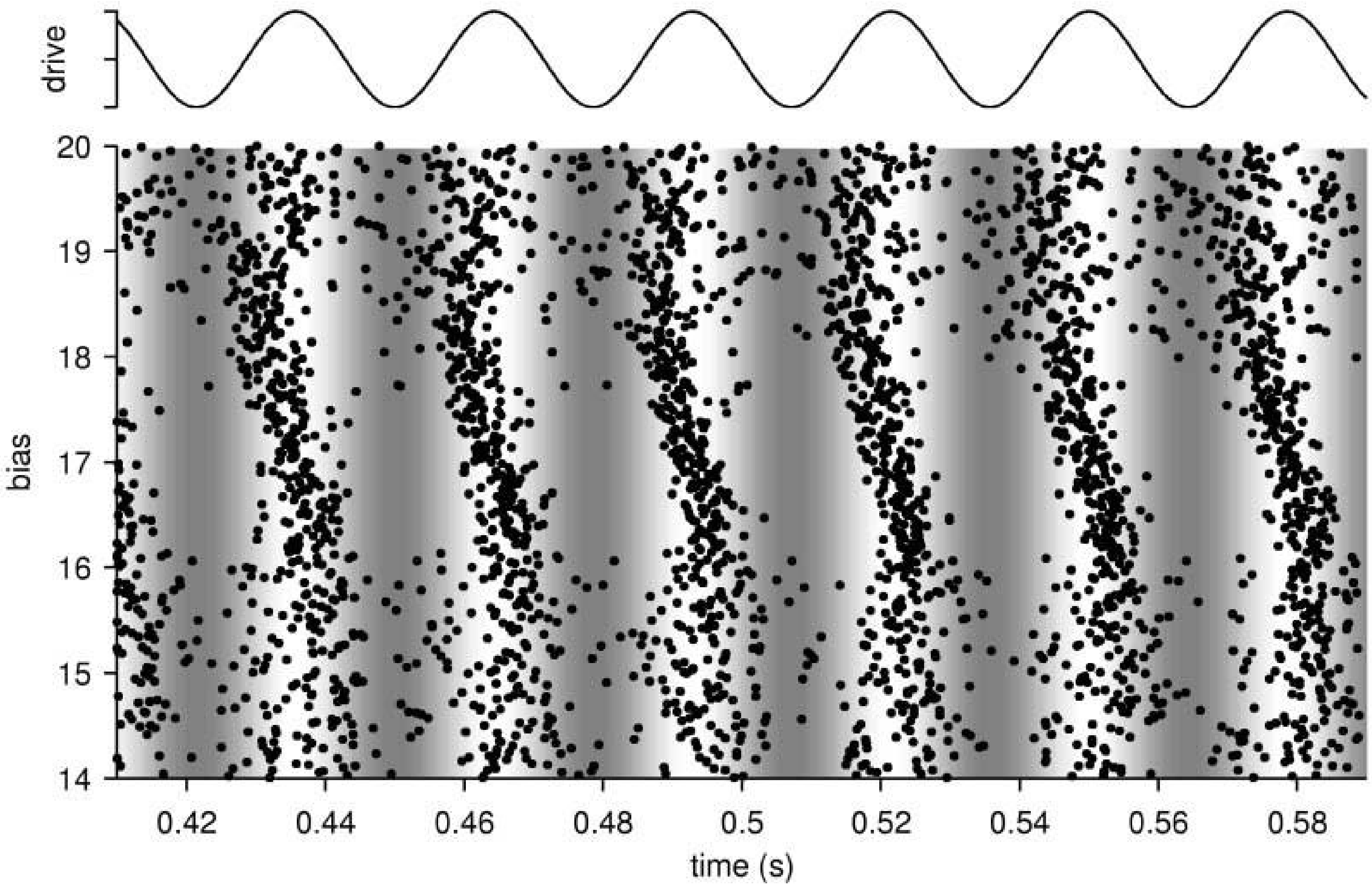
Synchronization by sub-thresold oscillations

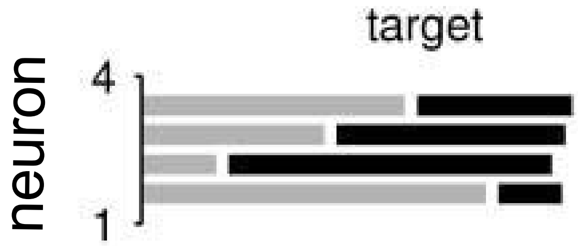


Brody & Hopfield, Simple Networks for Spike-Timing-Based Computation, with Application to Olfactory Processing, Neuron **37:** 843-852 (2003)

Recognition by coincidence detection

- This implies that neurons that receive the same constant input current fire at the same time
- Coincidence of spikes implies identical input.

Key – lock principle



- Grey – constant bias current in each “mitral cell”
- Black – input current evoked by an odor input
- If the input “is right”, all neurons receive the same input current and thus spike synchronously

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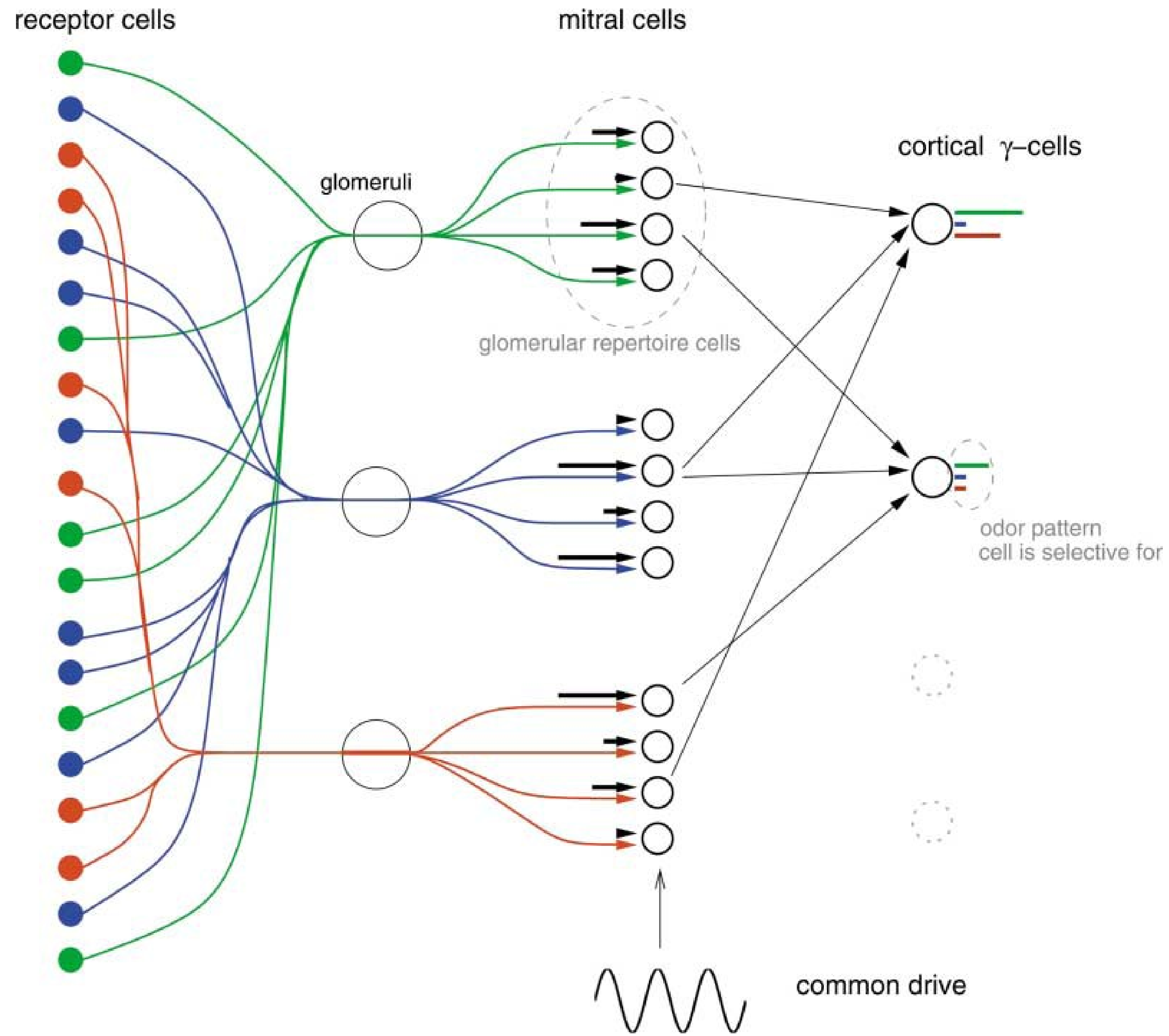
Hopfield's olfaction model



- The cortical cells connect to the mitral cell with the “correct bias”
- Odors are detected when the cortical cell gets synchronized input
- 400 ORN types, each odor excites 200

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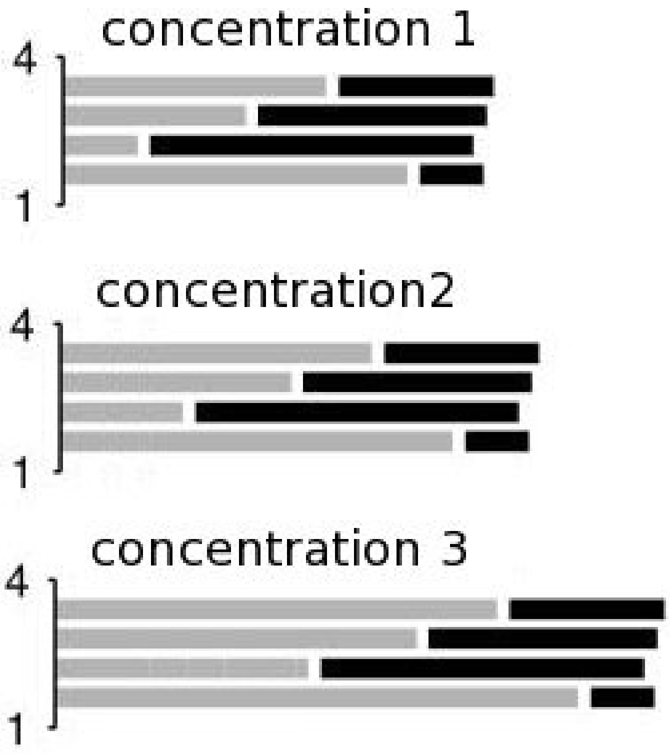
Discussion

- Odors are recognized reliably across a large range of concentrations



Discussion

- Odors are recognized against a stronger background odor
- Odors in a mixture can be recognized separately (if the set of active glomeruli does not have too much overlap)
- Odors in a binary mixture with fully overlapping glomerulus set can sometimes be recognized as well (?)

You can look at these points more with the Exercises.