Storage of spatial maps in an attractor neural network model of the hippocampus

R. Monasson, LPT-ENS, Paris

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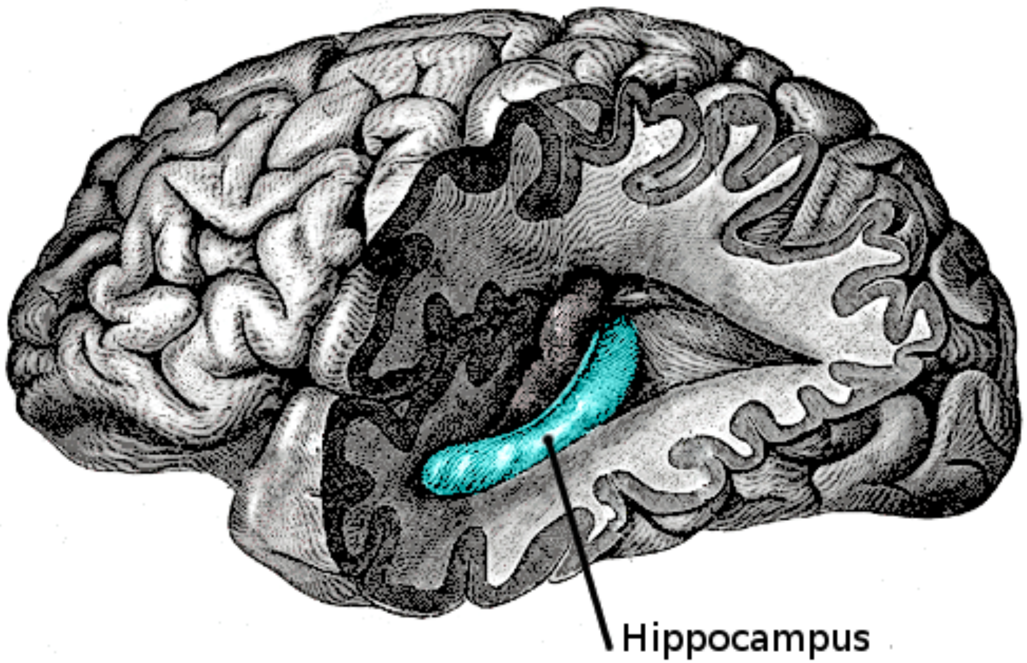
Plan

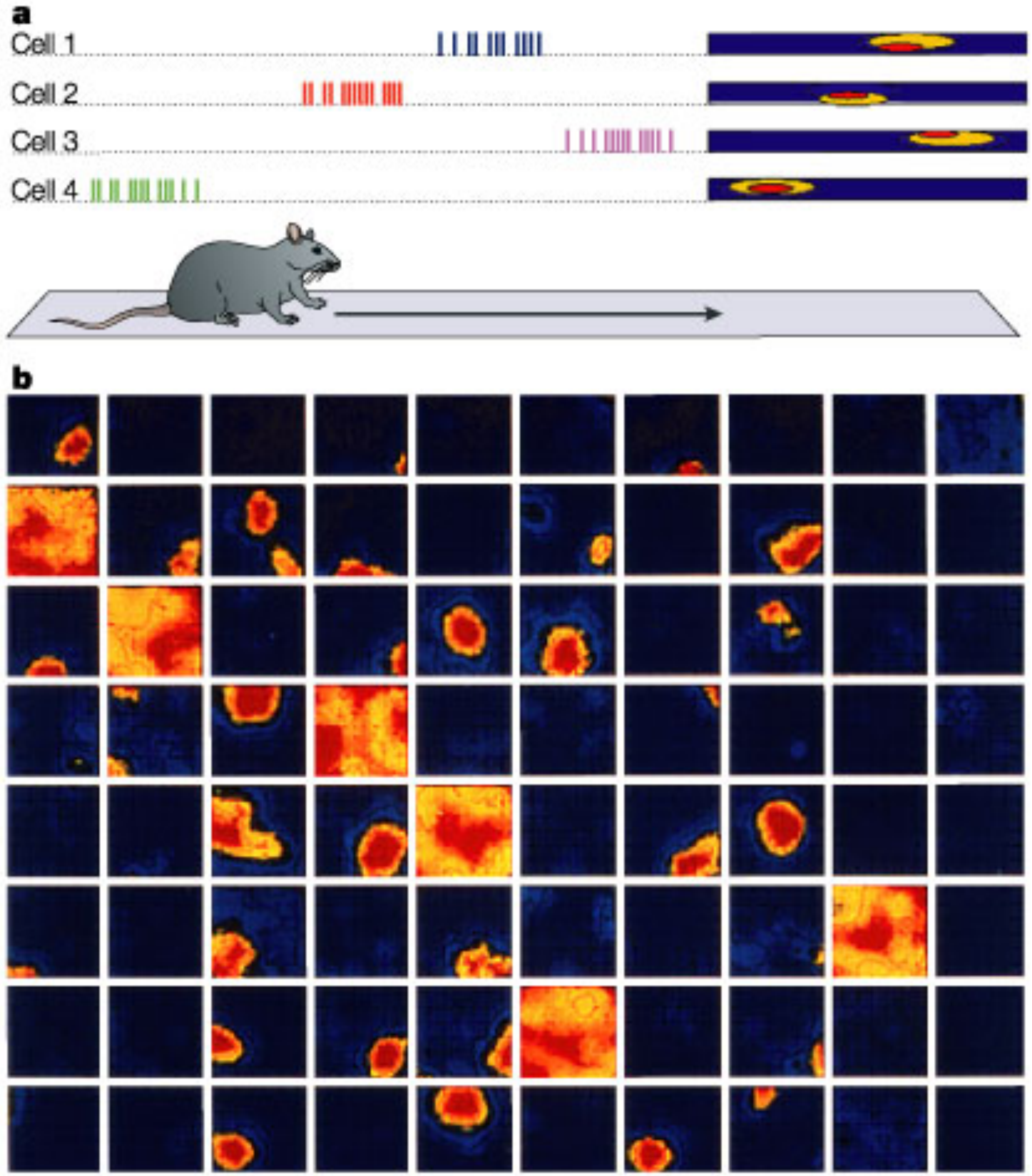
- Biological facts and motivations
- Model and statistical mechanics framework
- Storage of environments (spatial charts)
- Dynamics within one chart
- Transitions between charts
- Conclusion & Perspectives

Representation of Space in the Brain



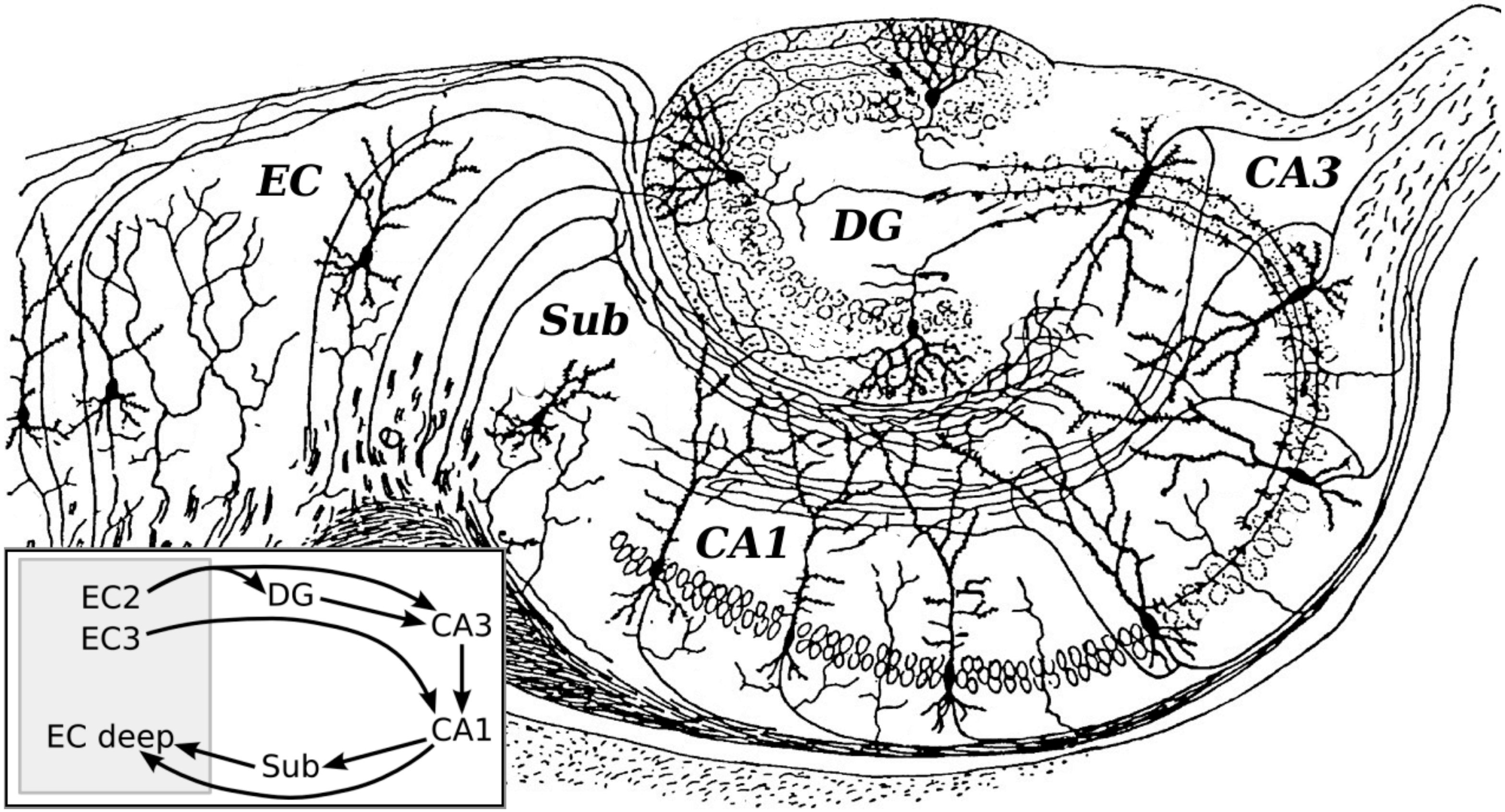
Electrode recordings: O'Keefe & Dostrovsky (1971)
Cells in the Hippocampus respond to position in space in a specific way (called place cells)

Place cells



Kazu Nakazawa, Thomas J. McHugh, Matthew A. Wilson & Susumu Tonegawa
Nature Reviews Neuroscience **5**, 361-372 (May 2004)

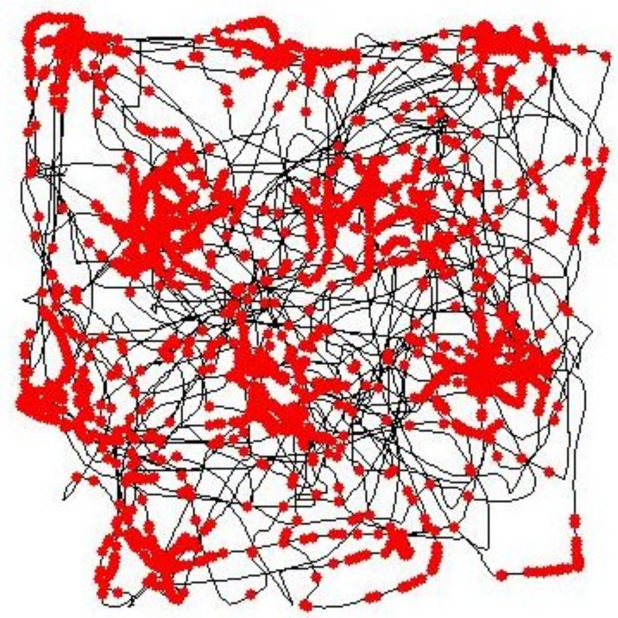
Where do place fields come from?



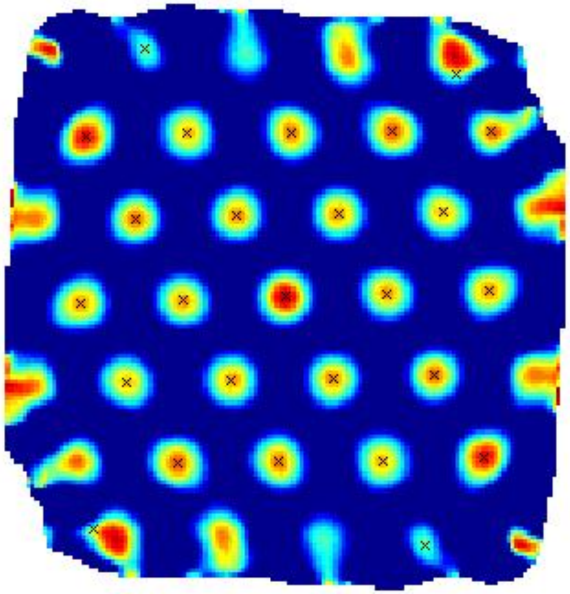
Medio-enthorinal cortex ➔ Hippocampus

Grid cells

Hafting, Fyhn, Molden, Moser & Moser, Nature 436, 801-806 (2005)

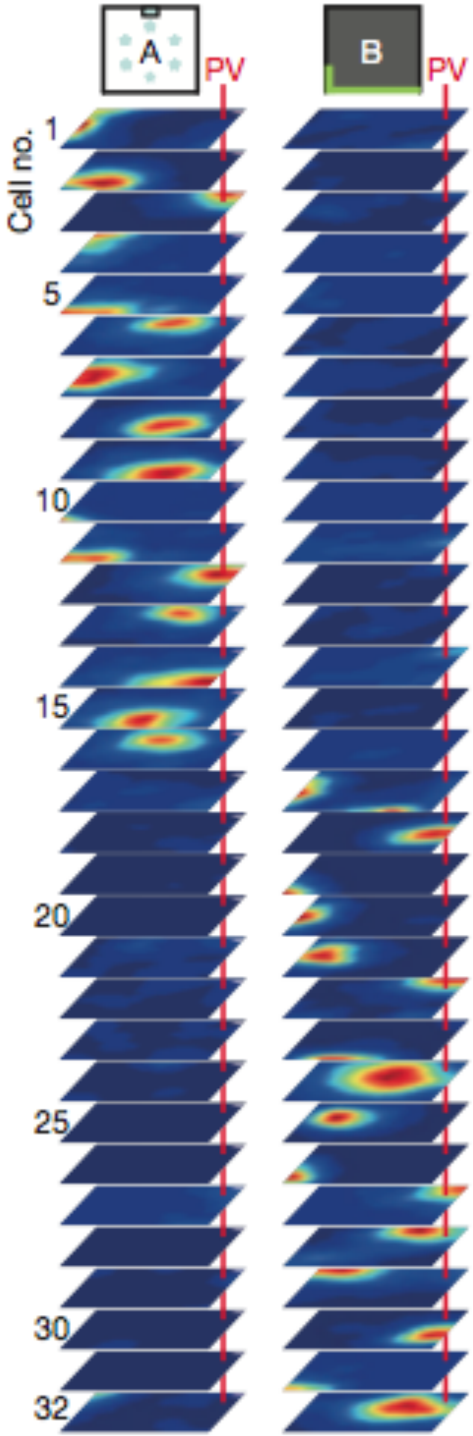


Trajectory of a rat through a square environment is shown in black. Red dots indicate locations at which a particular entorhinal grid cell fired.



Spatial autocorrelogram of the neuronal activity of the grid cell from the left figure.

- weighted sums of grid cell activities may produce localized activity (place fields)
- changes in weights results in ‘random’ remappings

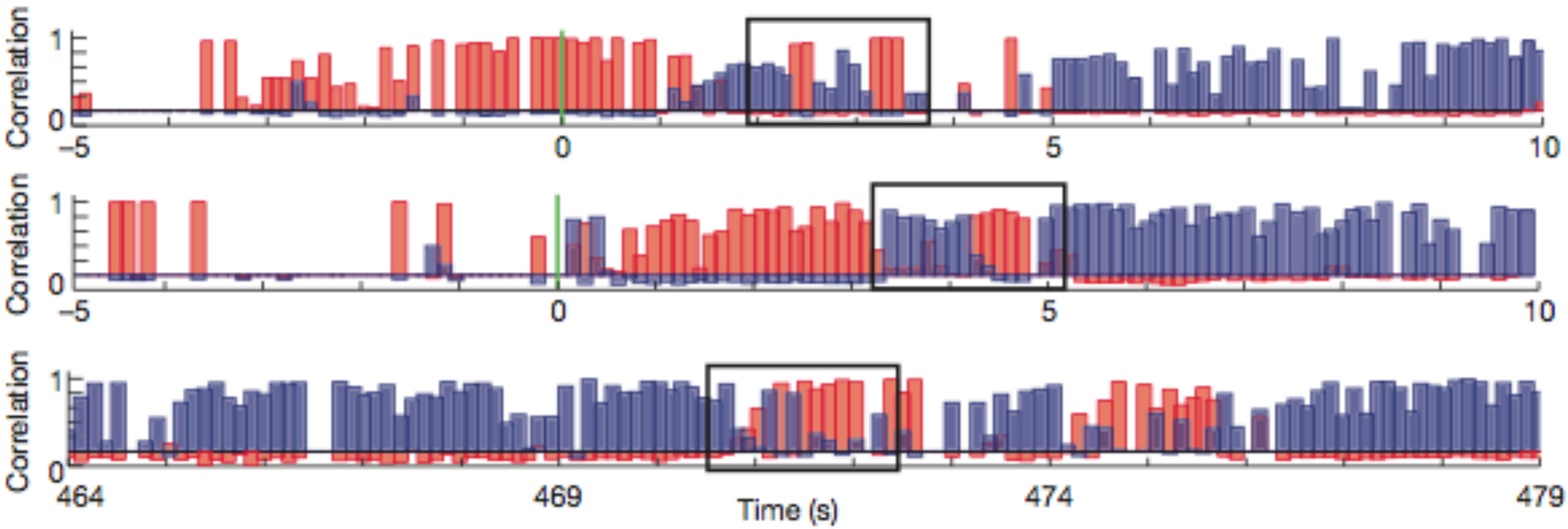


Teleportation (1)

- Rat in 2 different environments
- Place fields are specific to each environment
- Population vectors (average activity) specific to each environment
- Sudden changes of environment?

Jezek, Henriksen, Treves, Moser & Moser, Nature 478, 246 (2011)

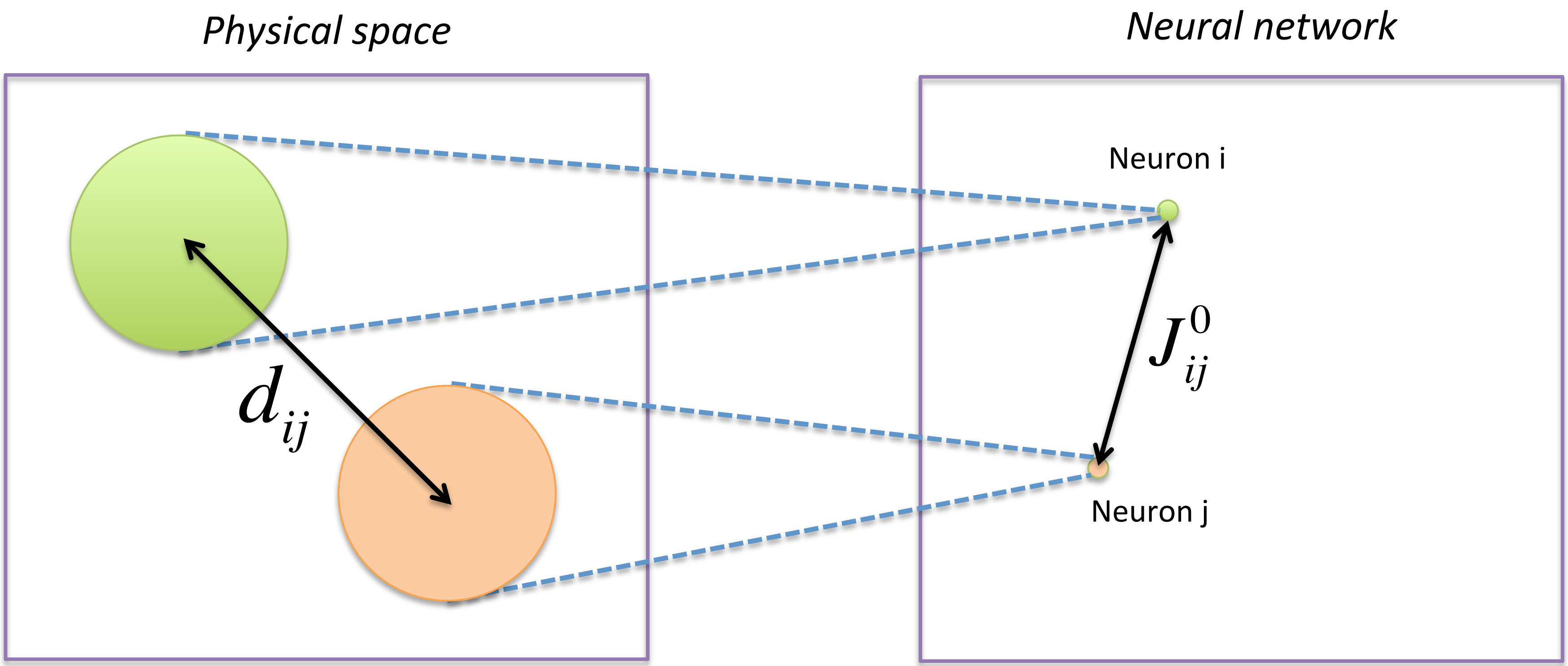
Teleportation (2)



How are different environments ‘stored’ in the hippocampus?
What is the dynamics of the neural activity within one environment?
In between two environments?

Model: one environment (1)

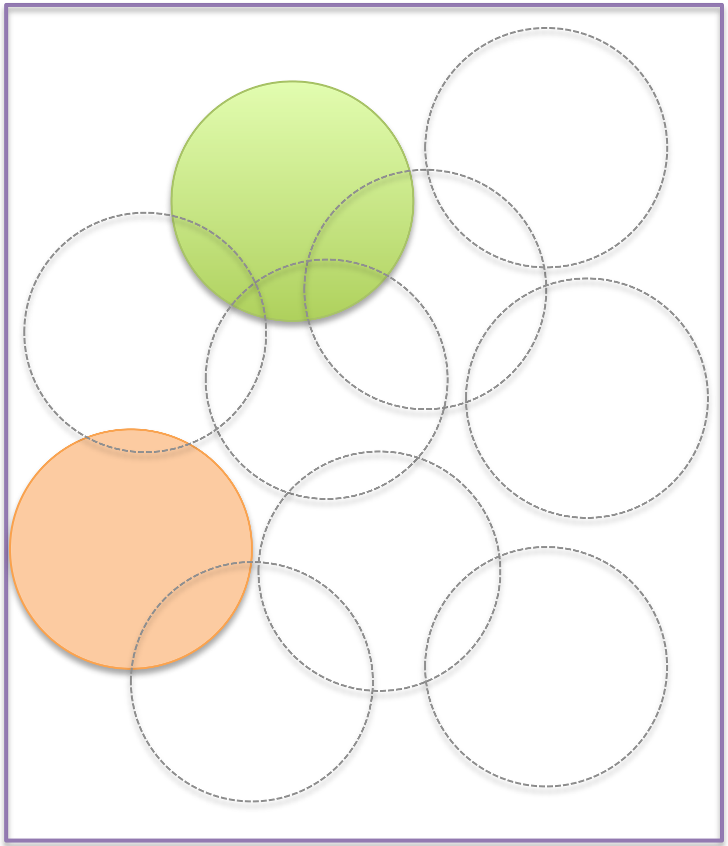
Neuron = binary state, silent or active : $\sigma_i = 0,1$



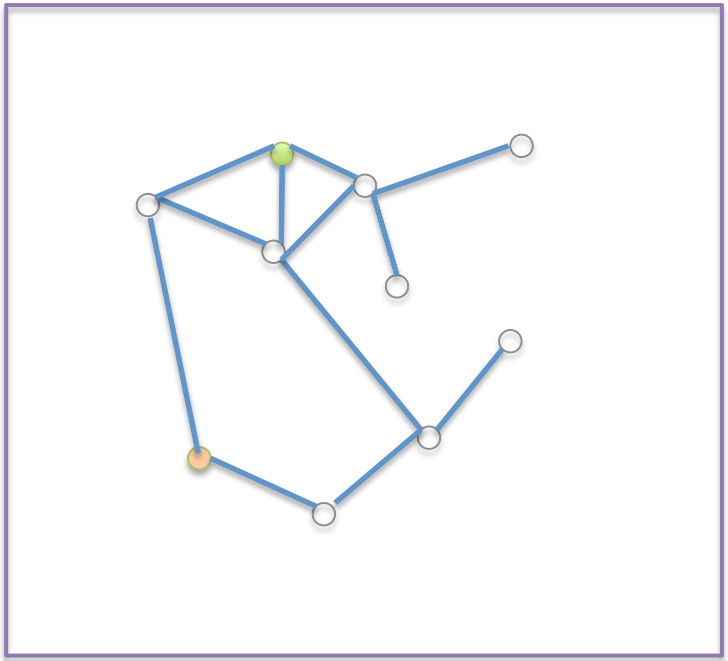
$$J_{ij}^0 = \begin{cases} \frac{1}{N} & \text{if } \; d_{ij} \leq d_c \;, \\ 0 & \text{if } \; d_{ij} > d_c \end{cases}$$

Model: one environment (2)

Physical space



Neural network



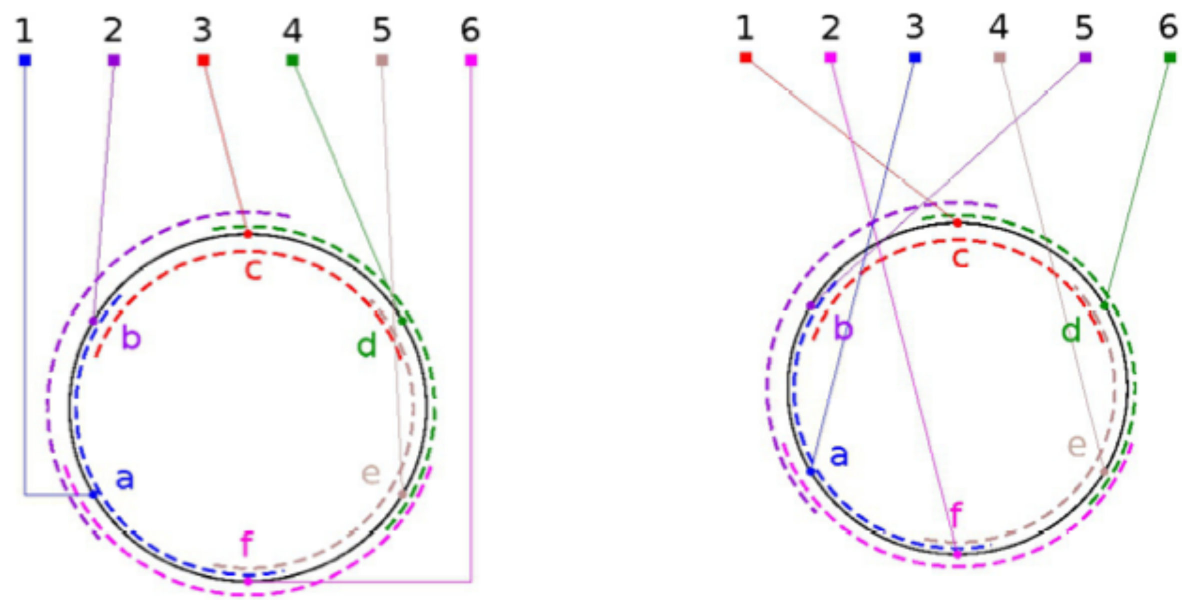
$$J^0_{ij} = \begin{cases} \frac{1}{N} & \text{if} \;\; d_{ij} \le d_c \;, \\ 0 & \text{if} \;\; d_{ij} > d_c \end{cases}$$

- we choose d_c so that each neuron is connected to *wN* other neurons (*w*<<1, but long range interactions)
- Interaction matrix invariant under translations (not necessary)

Model: random remappings

Hypothesis: place fields are randomly remapped onto neurons

Example in dimension D=1:



New environment = random permutation π

Battaglia, Treves (1998);
Tsodyks (1999); Hopfield (2010)

Model: statistical mechanics formulation

Interaction matrix for L+1 environments:

$$J_{ij} = \sum_{\ell=0}^{L} J_{ij}^{\ell} = J_{ij}^{0} + \sum_{\ell=1}^{L} J_{\pi^\ell(i)\pi^\ell(j)}^{0}$$

Probability of activity configuration:

$$P_J(\boldsymbol{\sigma}) = \frac{1}{Z_J(T)} \exp\big(-E_J[\boldsymbol{\sigma}]/T\big)$$

'Energy' :
(=-log likelihood)

$$E_J[\boldsymbol{\sigma}] = -\sum_{i<j} J_{ij}\,\sigma_i\,\sigma_j$$

Partition function:

$$Z_J(T) = \sum_{\boldsymbol{\sigma} \text{ with constraint } \sum_{i=1}^{N} \sigma_i = f\,N} \exp\big(-E_J[\boldsymbol{\sigma}]/T\big)$$

(inhibition)

Case of a single environment (1)

Translation-invariant and long-range interactions: exactly solvable model
(J.L. Lebowitz and O. Penrose, Journal of Mathematical Physics 7, 98 (1966))

Order parameter = Coarse-grained activity:

$$\rho(x) \equiv \lim_{\epsilon\to 0} \lim_{N\to\infty} \frac{1}{\epsilon N} \sum_{(x-\frac{\epsilon}{2})N \le i < (x+\frac{\epsilon}{2})N} \langle \sigma_i \rangle_J$$

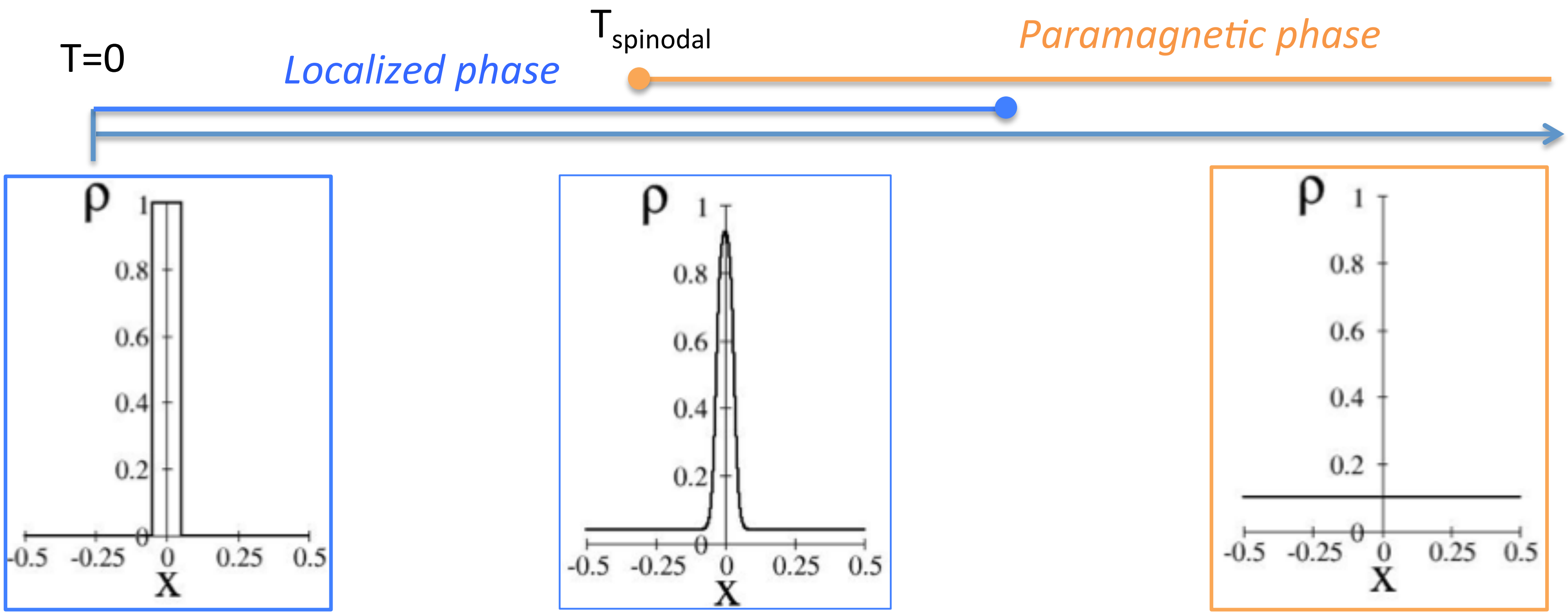
Single neuron self-consistent equations:

$$\begin{aligned} \rho(x) &= \frac{1}{1+e^{-\mu(x)/T}}\,, \\ \mu(x) &= \int \mathrm{d}y\, J_w(x-y)\rho(y) + \lambda \end{aligned}$$

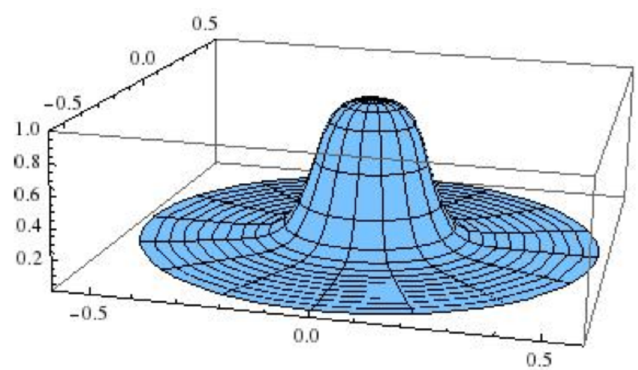
(imposes global activity)

(Similar to rate model for neurons)

Case of a single environment (2)



True also in D=2:

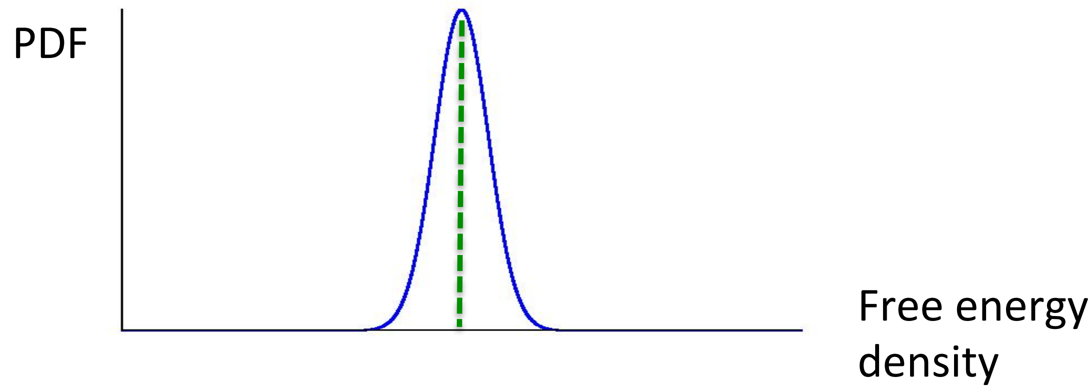


Multi-environment case: averaging over remappings

Free energy depends on realization of random interactions J

= permutations $\pi_1, \pi_2, \ldots, \pi_L$

Hypothesis: concentration when N→ ∞



Replica method: $\overline{Z_J(T)^n} = \int df \mu_N(f) e^{N(-n\beta f)} = e^{N(-n\beta f_{av} + \frac{n^2}{2}\Gamma + O(n^3)) + o(N)}$

Average free energy

Fluctuations

Multi-environment case: averaging over remappings

$$\overline{Z_J(T)^n} = \overline{\sum_{\vec{\sigma}} \exp\left[\beta \sum_{a=1}^{n} \sum_{i<j} \left(J_{ij}^0 + \sum_{\ell=1}^{L} J_{ij}^\ell \right) \sigma_i^a \sigma_j^a \right]}$$

$$= \sum_{\vec{\sigma}} \exp\left[\beta \sum_{a=1}^{n} \sum_{i<j} J_{ij}^0\, \sigma_i^a \sigma_j^a \right] \Xi(\vec{\sigma})^L \,, \quad \text{where}$$

$$\Xi(\vec{\sigma}) = \frac{1}{N!} \sum_{\pi^\ell} \exp\left[\beta \sum_{i<j} J_{ij}^0 \sum_{a=1}^{n} \sigma_{\pi^\ell(i)}^a \sigma_{\pi^\ell(j)}^a \right]$$

Average over permutations is not immediate … but can be done when N➔∞
(some similarity with Itzykson-Zuber integral, but discrete group here)

$$\log \Xi(\vec{\sigma}) = -\frac{\beta}{2} n f(1-f) + N \frac{\beta}{2} n w f^2 - \sum_{\lambda \neq 0} \text{Trace} \log \left[\mathbf{Id}_n - \beta\lambda(\mathbf{q} - f^2\, \mathbf{1}_n) \right]$$

$$q^{ab} \equiv \frac{1}{N} \sum_j \sigma_j^a \sigma_j^b$$

Multi-environment case: order parameters

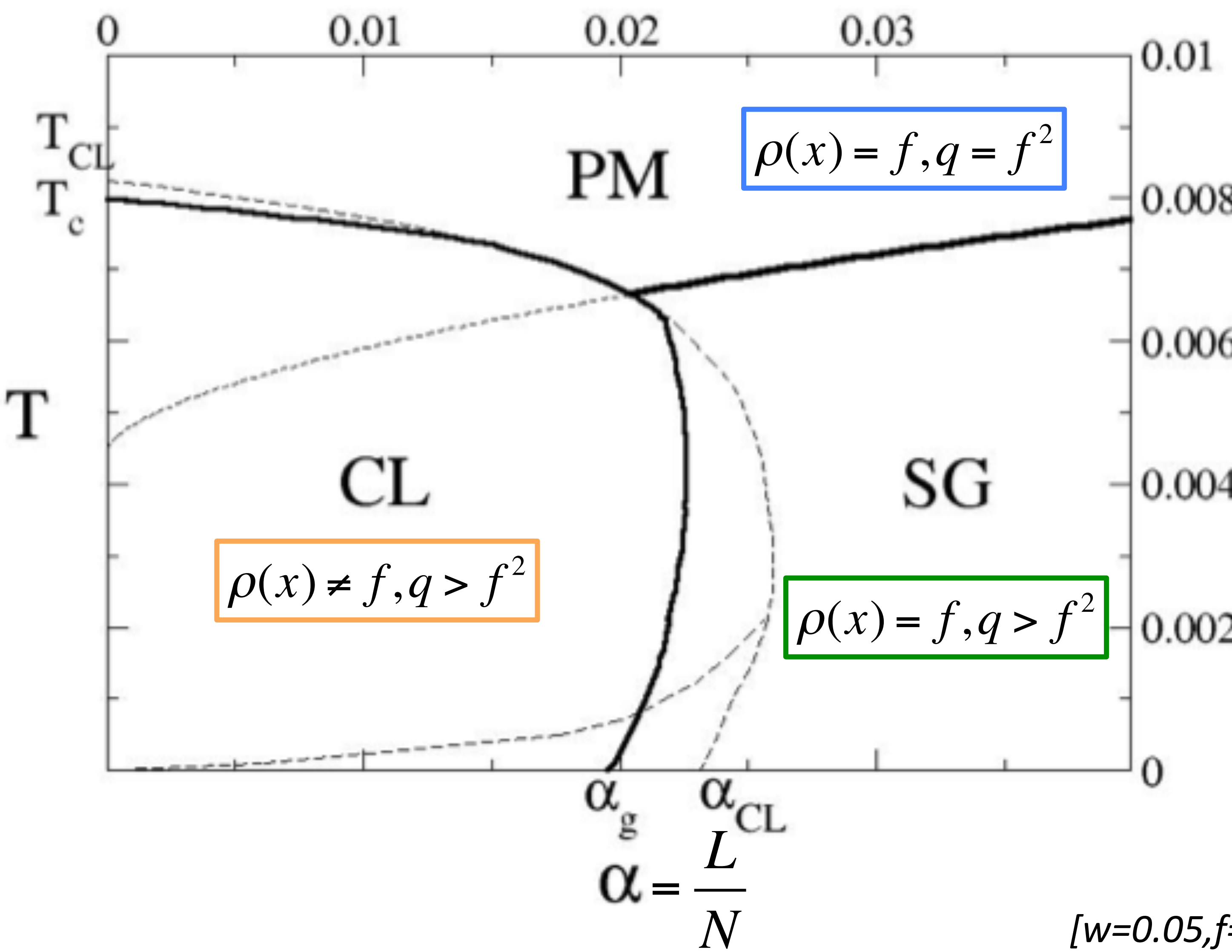
Local density of activity averaged over environments:

$$\rho(x) \equiv \lim_{\epsilon\to 0} \lim_{N\to\infty} \frac{1}{\epsilon N} \sum_{(x-\frac{\epsilon}{2})N \le i < (x+\frac{\epsilon}{2})N} \overline{\langle \sigma_i \rangle_J}$$

Edwards-Anderson overlap (measures spatial heterogeneities in the activity):

$$q \equiv \frac{1}{N} \sum_{i=1}^{N} \overline{\langle \sigma_i \rangle_J^2}$$

Phases and Transition Lines



[w=0.05,f=1,D=1]

Simulations and Dynamics

Monte Carlo Dynamics:

- Pick up one silent (index i) and one active spin (index j)
- Compute variation of energy when spins are swapped
- Accept with Metropolis rule

Observe:

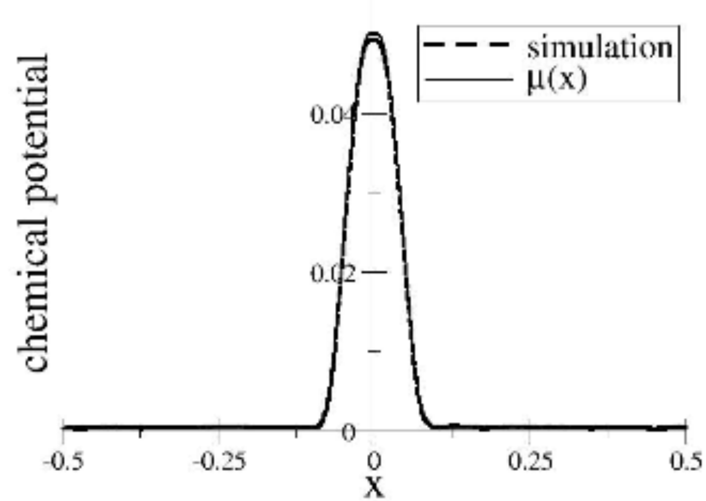
- Static properties …
- Stability and fluctuations of clump (=quasi-particle?)
- Motion of clump within one environment
- Transitions between environments

Check of equilibrium properties

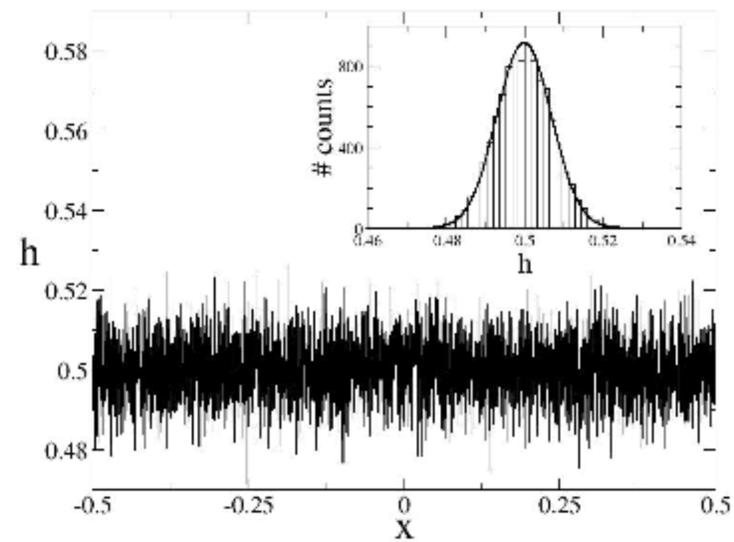
Local field acting on spin i:

$$h_i = \sum_j J_{ij}^0 \sigma_j + \sum_{l,j} J_{ij}^l \sigma_j$$

μ(x)



Gaussian random variable
of variance α r,
(r = conjugated parameter to q)



(D=1, N=10000, T=0.004, α=0.01)

The clump is a quasi-particle …

Master equation for spin dynamics (case of a single chart) ➔

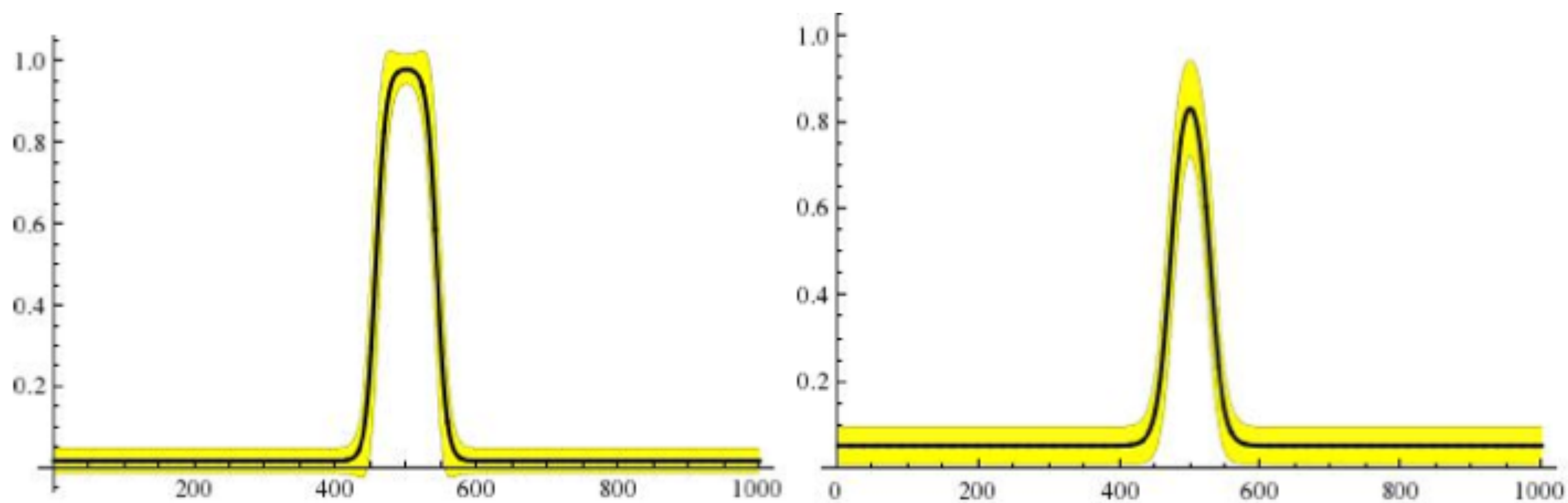
$$\frac{\partial \rho}{\partial t}(x,t) = -A[\{\rho\}]\frac{\delta F[\{\rho\}]}{\delta \rho(x,t)} + z(x,t)$$

- F = free energy functional used to determine equilibrium
- z = Gaussian random field, uncorrelated in time, correlated in space, of the order of $N^{-1/2}$

➔ Relaxation towards equilibrium density for all modes, with thermalization at ‘temperature’ of the order of N^{-1} <u>except</u> for zero mode (translation of clump), which diffuses with d=O(N^{-1})

…with weak fluctuations across environment

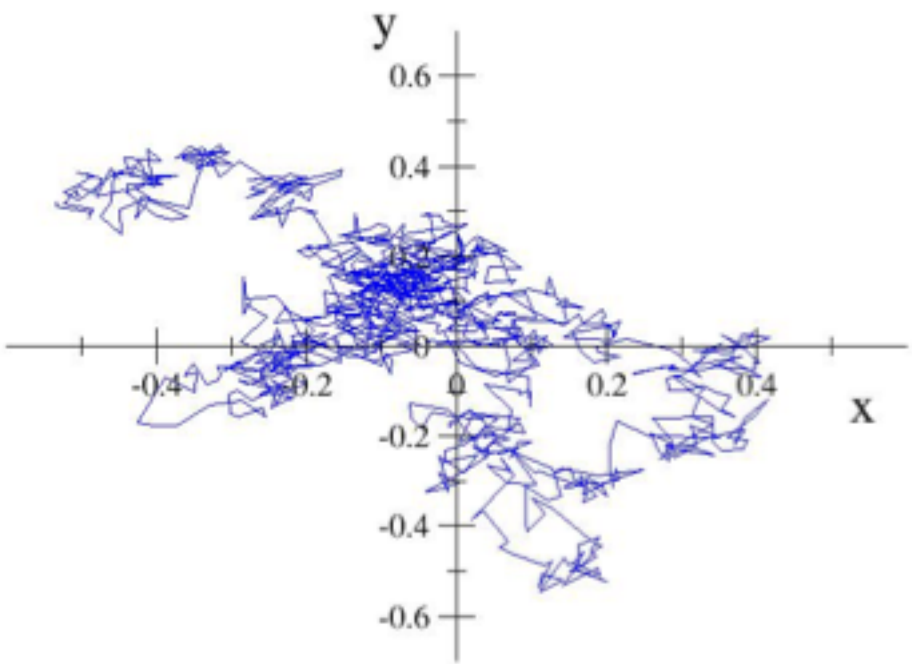
Calculation of $\delta\sigma_i^2 = \overline{(<\sigma_i> - \overline{<\sigma_i>})^2} = q(x) - \rho^2(x)$



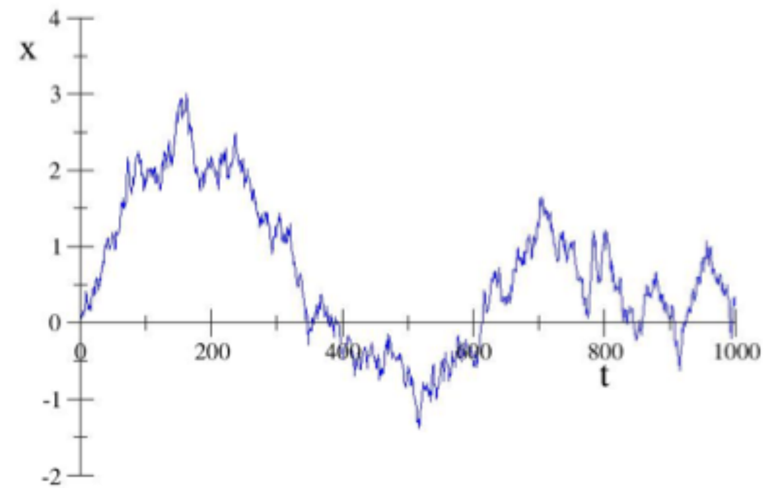
(D=1, f=0.1, w=0.05, left: T=0.005, right: T=0.007)

Dynamics within one environment (1)

Trajectory of clump center in D=2
(N=45x45 spins, α=0.001, T=0.004)



Position of clump center in D=1 as a function of time (MC rounds= t x 20)
(N=2000 spins, α=0.003, T=0.006)

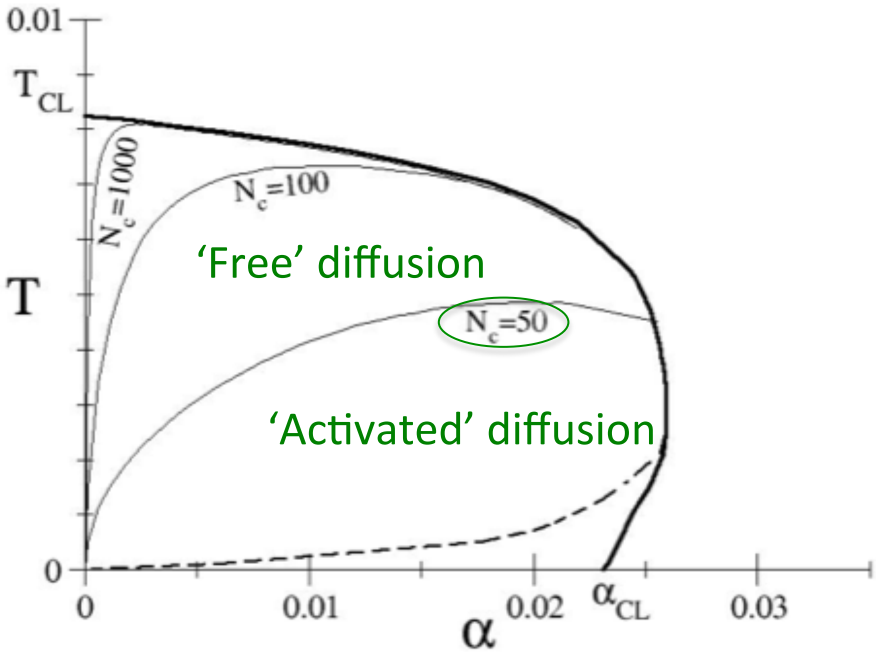


Dynamics within one environment (2)

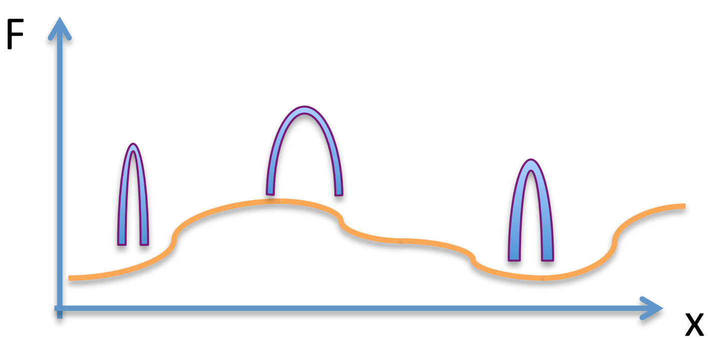
$$\overline{Z_J(T)^n} = \int df \mu_N(f) e^{N(-n\beta f)} = e^{N(-n\beta f_{av} + \frac{n^2}{2}\Gamma + O(n^3)) + o(N)}$$

Fluctuations

$$(\overline{\Delta F^2})^{1/2} = T\sqrt{\Gamma}\sqrt{N}$$



We can go further …



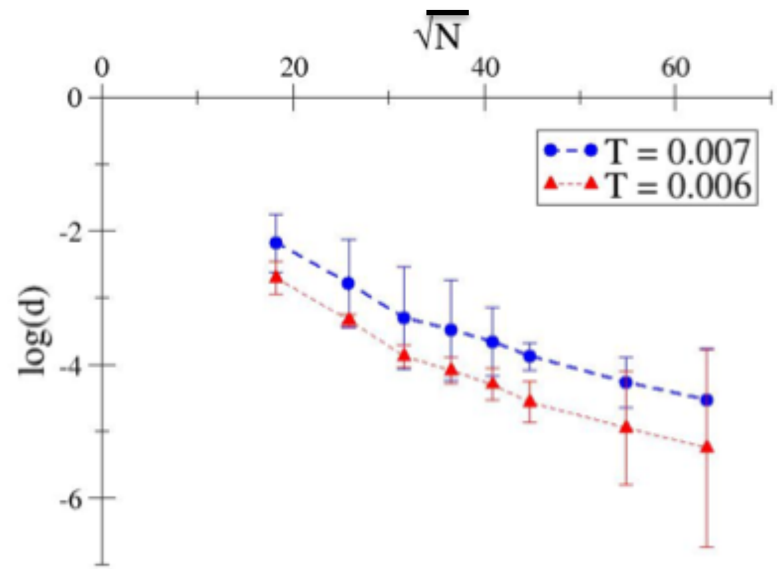
Compute $(\overline{\Delta F(x)\Delta F(y)})^{1/2} = T\sqrt{\Gamma(x-y)}\sqrt{N}$

Technically: two sets of n/2 replicas, n→0

Dynamics within one environment (3)

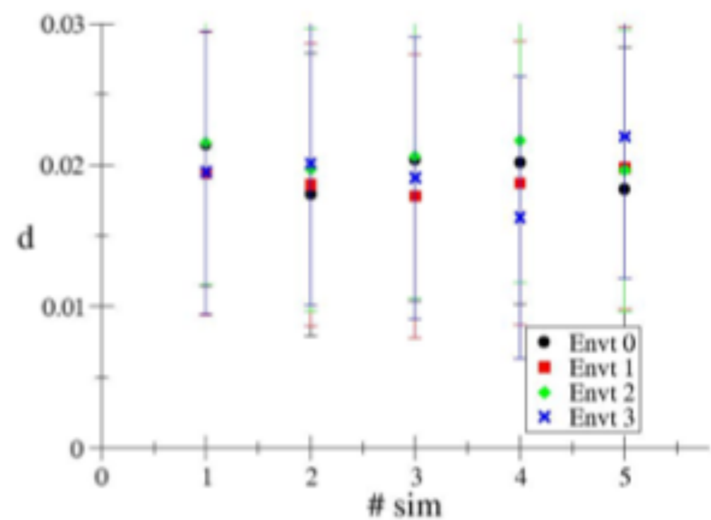
We expect $d \approx \frac{1}{N} e^{-\sqrt{N} G(\alpha,T)}$

Diffusion coefficient
(log. scale)

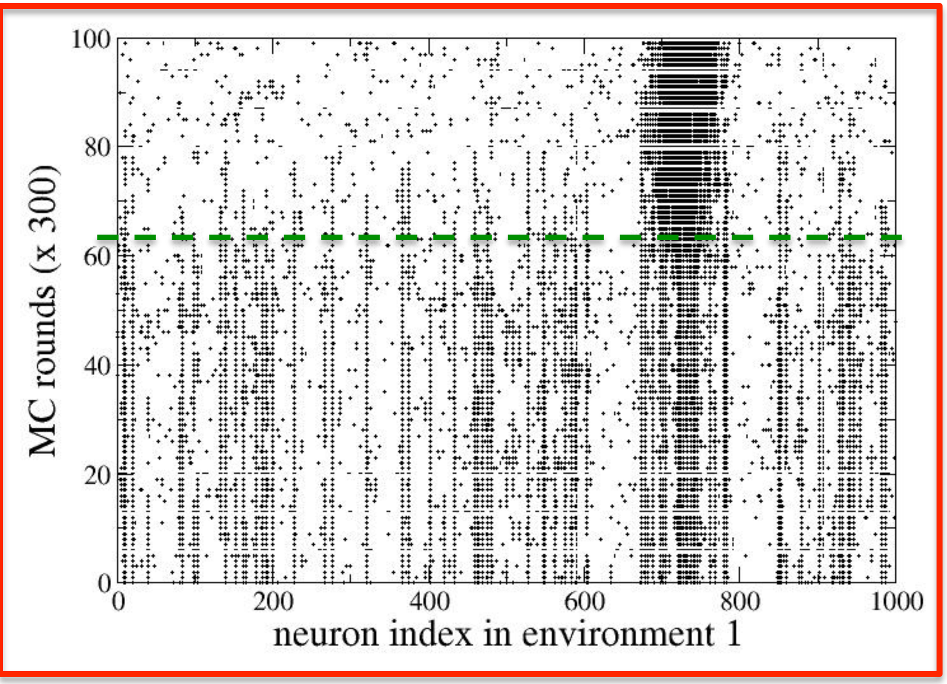


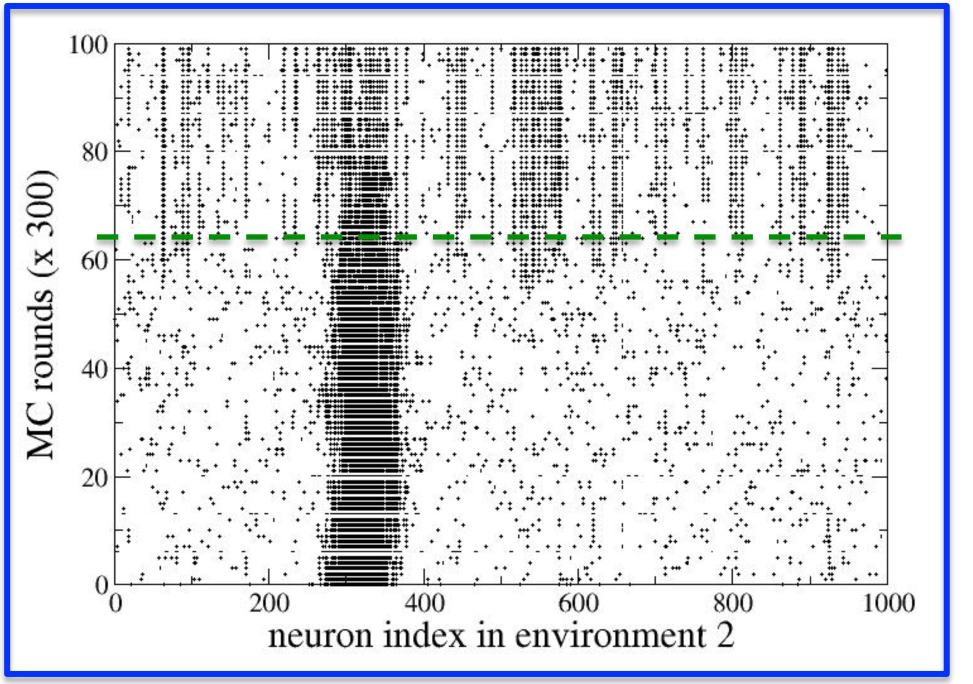
[D=1,
N=1000,
T=0.006,
α=0.003,
10000 rounds]

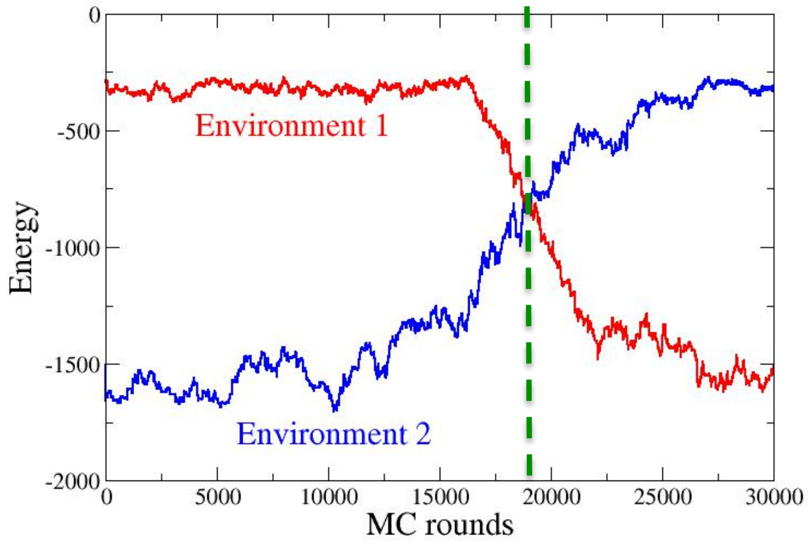
Chart-to-chart
fluctuations



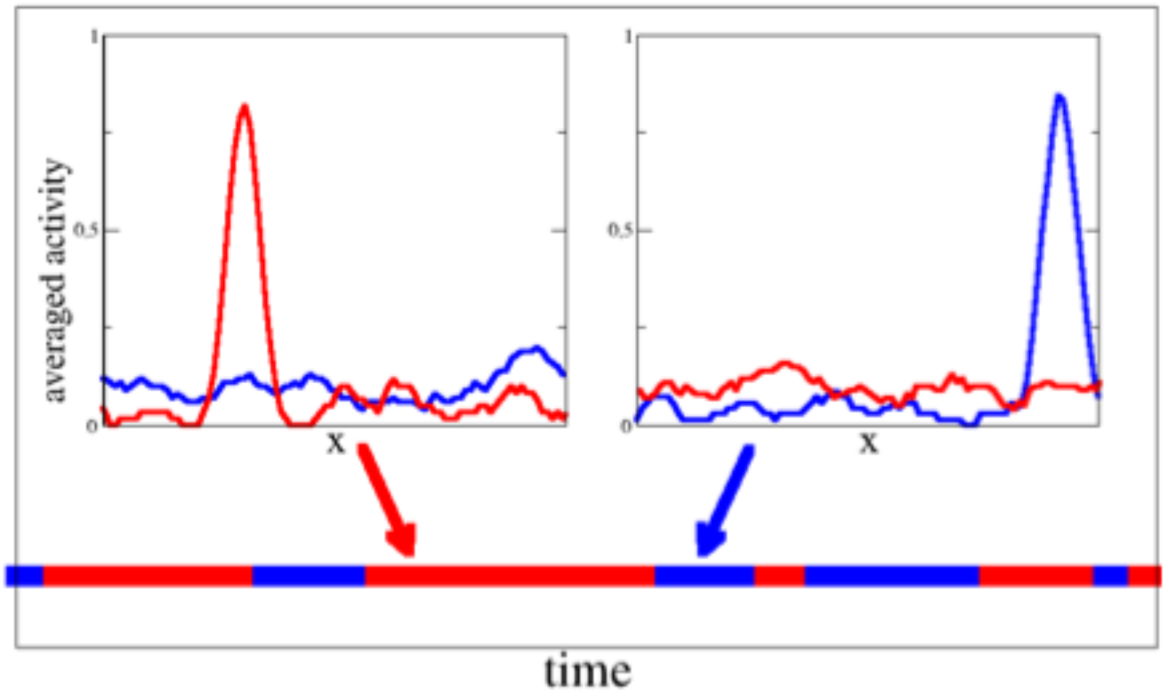
Dynamics: transitions between environments







Dynamics: transitions between environments



- Repeated transitions allow us to determine effective barrier heights and transition times:

$$\tau \approx e^{Nb(1 \to 2)}$$

- Transitions take place at preferred locations in space(s)

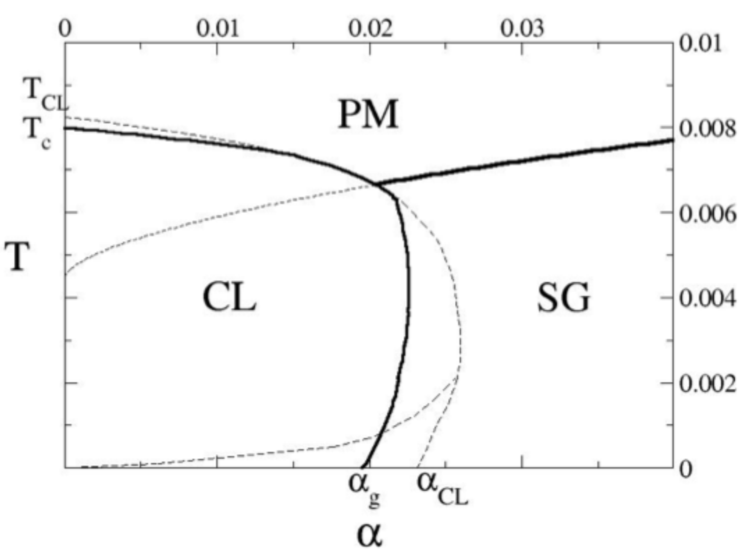
Conclusion & Perspectives

Storage of an extensive number of spatial charts in an attractor neural network…

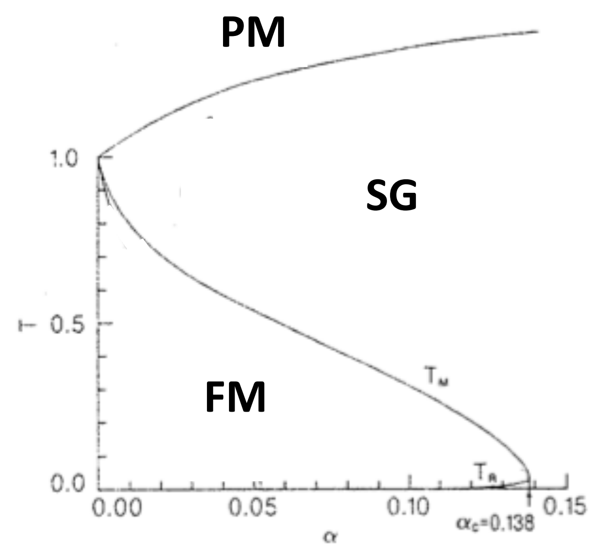
… very robust to neural noise (temperature) !

$$H = -\sum_{i<j}\sum_{l} J^0_{\pi^l(i),\pi^l(j)}\sigma_i\sigma_j$$

$$H = -\sum_{i<j}\left(\sum_{\mu}\xi_i^\mu\xi_j^\mu\right)\sigma_i\sigma_j$$



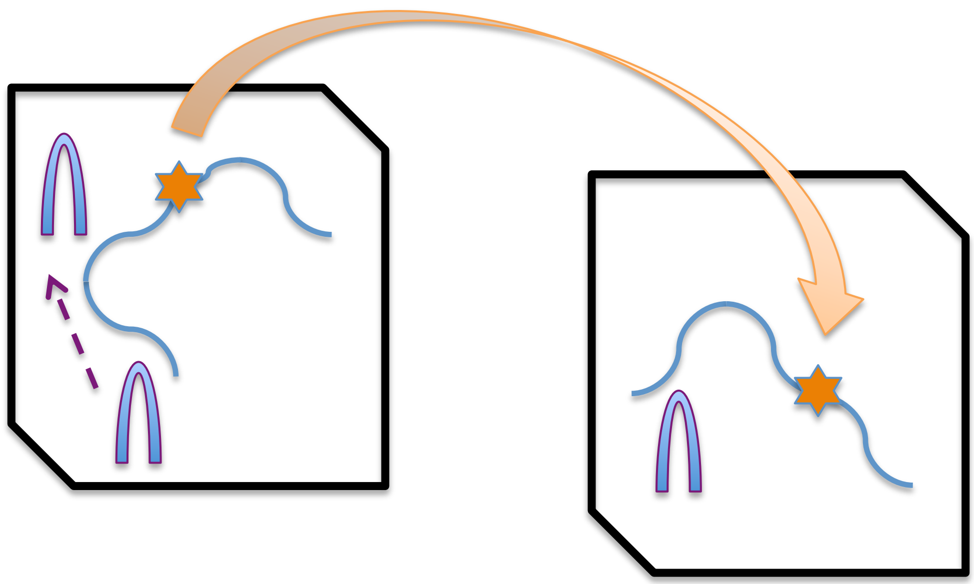
vs.



Amit, Gutfreund, Sompolinsky (1984)

Conclusion & Perspectives

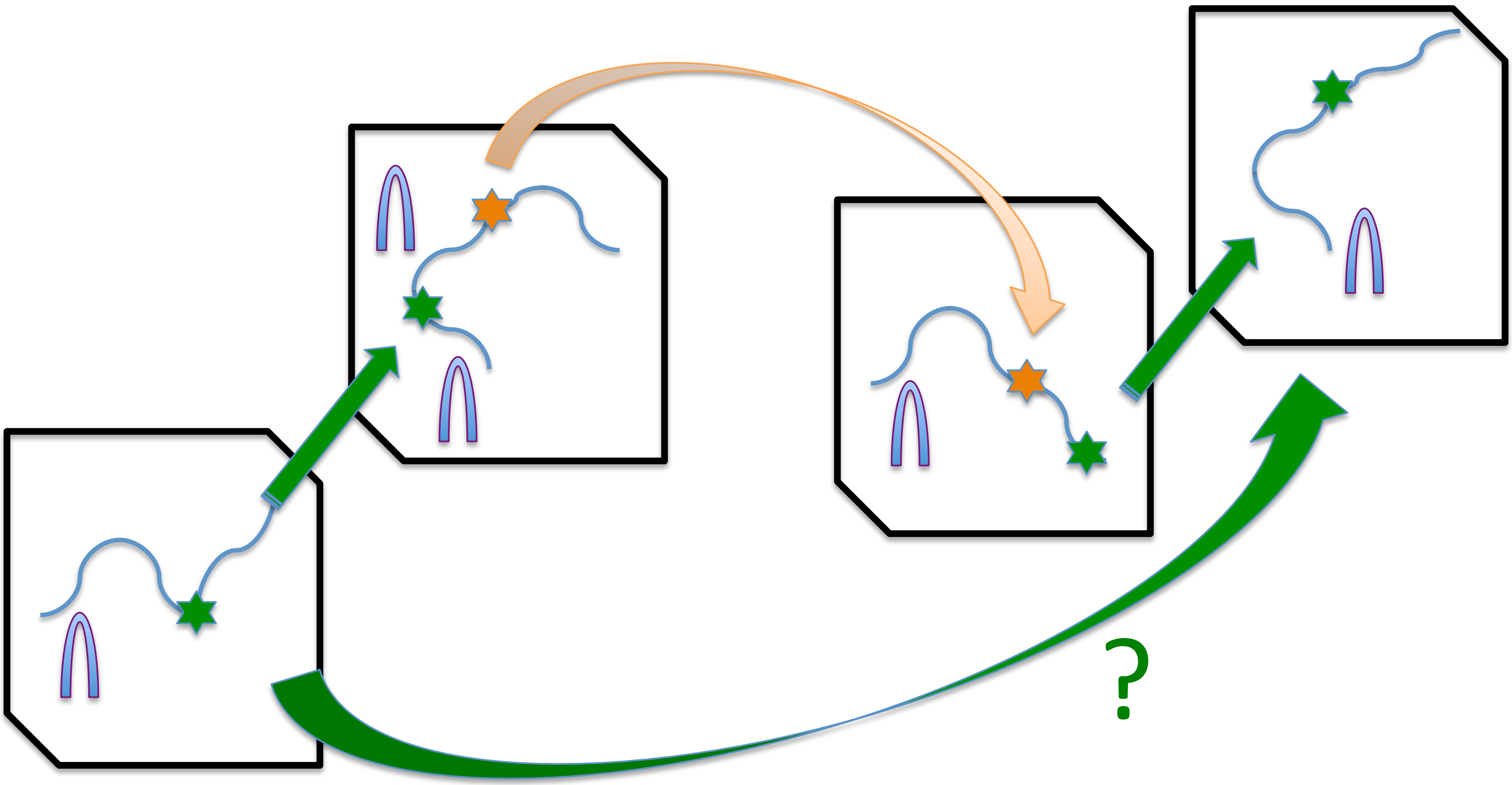
Complete picture of the dynamics within and between charts?



Competition between (activated) diffusion and transitions …
Depends on N (or effective N)
How to enhance diffusion in disordered landscape?
(modulation of activity, orthogonalization of maps, adaptation, …)

Conclusion & Perspectives

Complete picture of the dynamics within and between charts?



Conclusion & Perspectives

Comparison/relationship with experiments:

- quantitative estimates of parameters in the model?
- specific locations for transitions?
- differences between D=1,2,3?
- dynamical behavior of clump under external forcing (visual clues)?
- extension to other spaces, context-dependent place fields?

To go further

Some references:

F.P. Battaglia and A. Treves, Physical Review E 58, 7738 (1998).
M. Tsodyks, Hippocampus 9, 481 (1999).
J.J. Hopfield, Proceedings of the National Academy of Sciences 107, 1648 (2010).

Our paper: R.M., S. Rosay, Physical Review E 87, 062813 (2013) *(equilibrium only)*

and **Synopsis in Physics**, Knowing your Place, by D. Voss (http://physics.aps.org/)

Experiments: A Sense of Where You Are, New York Times, April 30th, 2013