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Network Models of Excitable Media

— Nonequilibrium Phase Transitions (Dynamics & Structure)

with **Samuel Johnson, Joaquín J. Torres, Miguel Angel Muñoz, Jorge Mejias, Sebastiano de Franciscis**:

- *Euro Physics Letters* **83**, 46006 (2008)
- *Physical Review E* **79**, 050104R (2009)
- *Physical Review Letters* **104**, 108702 (2010)
- *J. of Statistical Mechanics* P03003 (2010)
- *Physical Review E* **82**, 041105 (2010)
- & some work to be published in 2011

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The observation

Networked systems of *“excitable”* units (*excitable media*)

in which signals propagate without damping, e.g.,

forest fires (waves regenerate every time a tree ignites); electrical activity in cardiac muscle; waves in retina of eye; ill-condensed matter, and reaction-diffusion systems; the nervous system; genetic networks;…

“excitability”: a unit change of state causes its neighbors to move over threshold; unit then relaxes remaining silent for some time

often exhibit wandering among their dynam. *“attractors”*

overall activity changes autonomously to converge with t towards one case (pattern of activity), and it stays around but, eventually, goes to others;

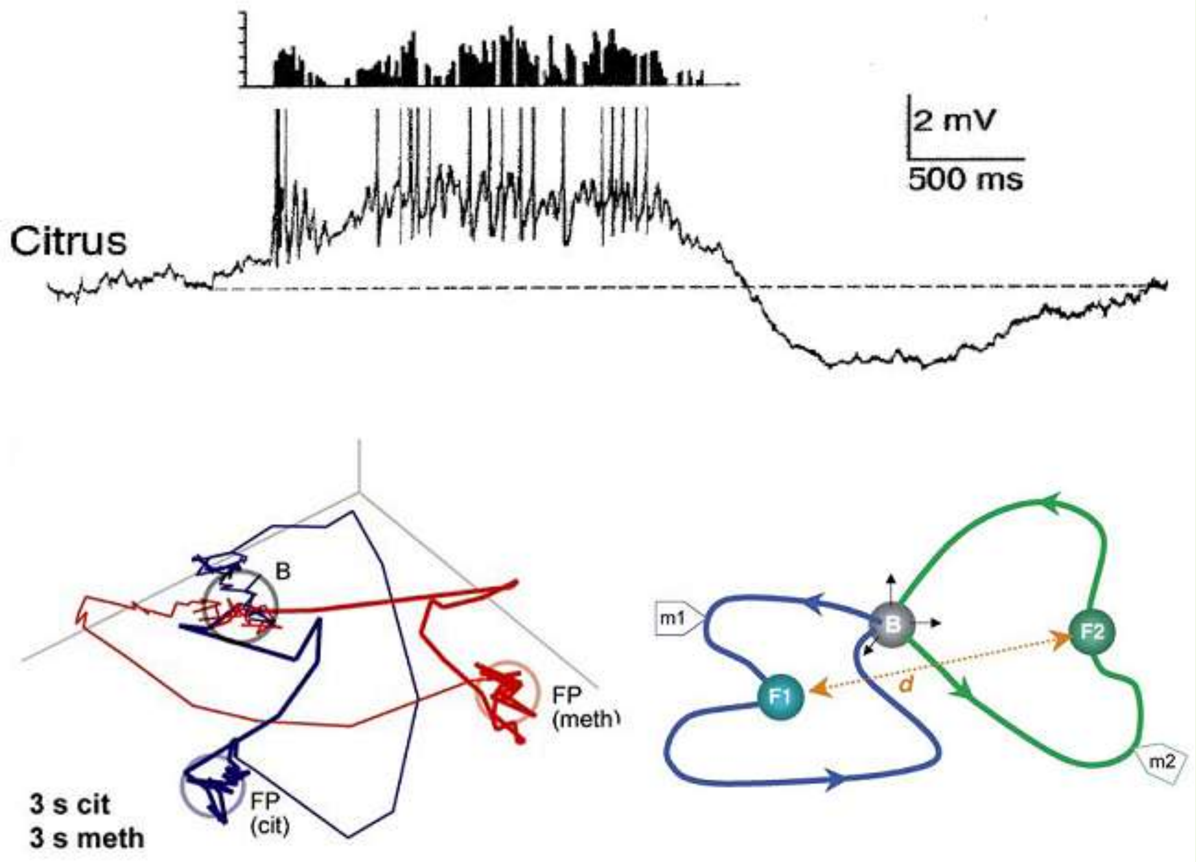
it may even keep constantly switching quite irregularly in a way that visits all or part of the different possible attractors

The observation

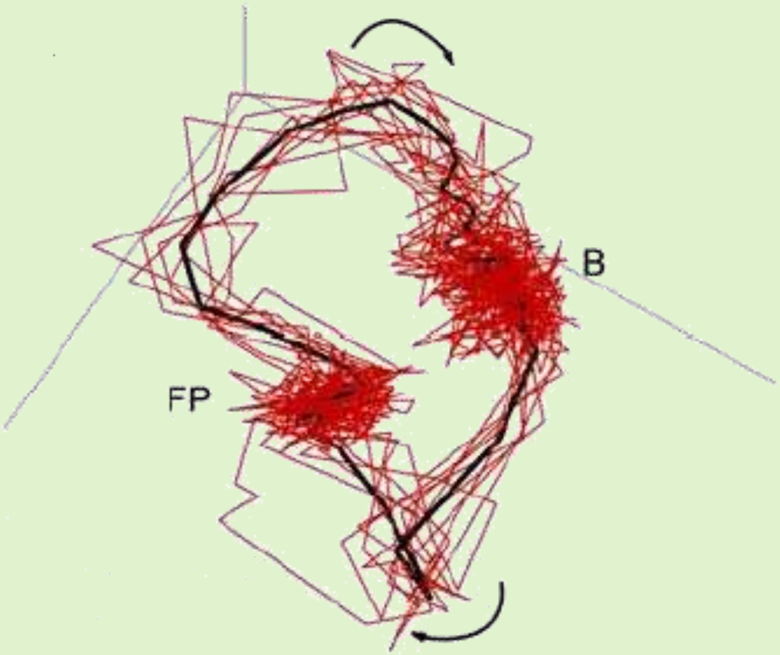
Experiment by Mazor & Laurent, *Neuron* **48**, 661 (2005):

Response to odor stimuli of certain neurons in the locust antennal lobe.

"animals brain is exploring a sequence of states generating a specific pattern of activity that represents one specific odor"



The observation



Kind of ***state of attention***: "instability inherent to chaotic motions facilitates system ability to move to any pattern at any time"

The model

- A processor unit (*neuron*) at each node
- Global activity $\boldsymbol{\sigma} \equiv \{\sigma_i\}$ (enough to assume: $\sigma_i = \pm 1$)
- Commun. line (*synapses*) weights $\mathbf{w} \equiv \{w_{ij} \in \mathbb{R}\}$ ($i,j = 1,\ldots,N$)
- Field on i due to weighted action of the other nodes:

$$h_i(\boldsymbol{\sigma},\mathbf{w}) = \sum_{j\neq i} w_{ij}\,\sigma_j$$

- Choice of weights, a feature of model, e.g., Hebbian + noise:

$$\acute{\omega}_{ij} = N^{-1}\sum_{\mu} \xi_i^{\mu}\,\xi_j^{\mu}$$ $\{\xi_i^{\mu} = \pm 1\}$, $\mu = 1,\ldots,P$ attractor patterns

and $w_{ij} = \acute{\omega}_{ij}\,x_j$, where x_j = stochastic variable with some $p(x)$

The model

$$h_i(\boldsymbol{\sigma},\mathbf{w}) \;=\; \sum_{j\neq i} w_{ij}\,\sigma_j$$

$w_{ij} = \acute{\omega}_{ij}\, x_j$ $\quad$ $\acute{\omega}_{ij}$ = Hebbian; x fast fluctuations with steady distribution:

$$p(x) \;=\; \zeta\,\delta(x-\phi) + (1-\zeta)\,\delta(x-1)$$

mimics, e.g., either synaptic fatigue / *depression* ($\phi < 1$) or facilitation ($\phi > 1$); $\phi = 1 \;\rightarrow$ standard model

$\zeta = f(\text{order})$ not essential what OP, even whether local or global order, e.g.,

ζ proportional to $\sum_\mu [m^\mu(\sigma)]^2$

$m^\mu(\sigma) = N^{-1}\sum_i \sigma_i\,\xi_i^\mu$ is overlap (current state / each stored pattern)

The model

Furthermore, we only update a fraction $\rho = n/N$ of the nodes at each unit of time, e.g., the Monte Carlo step:

- $\rho \to 1$: parallel (or Little) updating
- $\rho \to 0$: sequential (or Glauber) updating

The model

Parameters:

- T : «*temperature*», controls the stochasticity of dynamics
- ϕ : «*noise*», modulates the degree of fatigue or facilitation in communication lines (which depends on the current order)
- ρ : fraction of *silent* or non-synchronized (excitable) *units* in the system (e.g., chosen at random at each time)

One may also study influence of network topology

(but for simplicity let us assume first a fully connected net)

Results

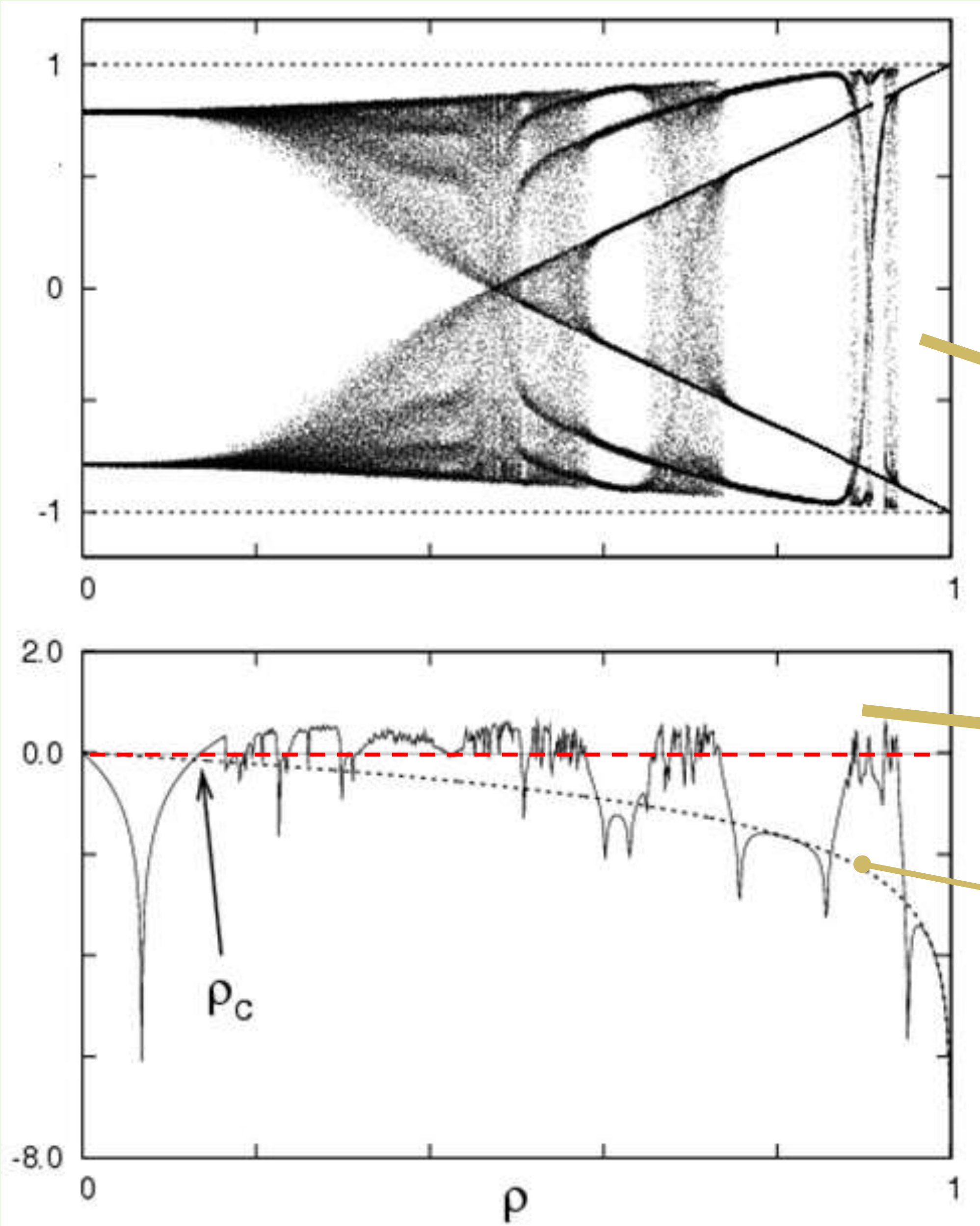
<u>Nonequilibrium steady states</u> due to competition between several processes:

- units (*neurons*) evolve at some characteristic time scale
- efficiency of connections (*synapses*) depends on:

  current activity **+** fast noise

- possibility of “silent” neurons, which thus conserve information, e.g., some correlations from previous state

<u>Bizarre</u> **<u>dynamics</u>**: irregular/chaotic, phase transitions, roaming among attractors,…



MC simulation:

Evidence of destabilization of attractors, and of transitions from regular to chaotic, as *ρ* is varied.

Overlap (versus ρ) between activity and a (randomly generated) pattern, for Φ = 0.5, *N* = 3600 and *β* = 20.

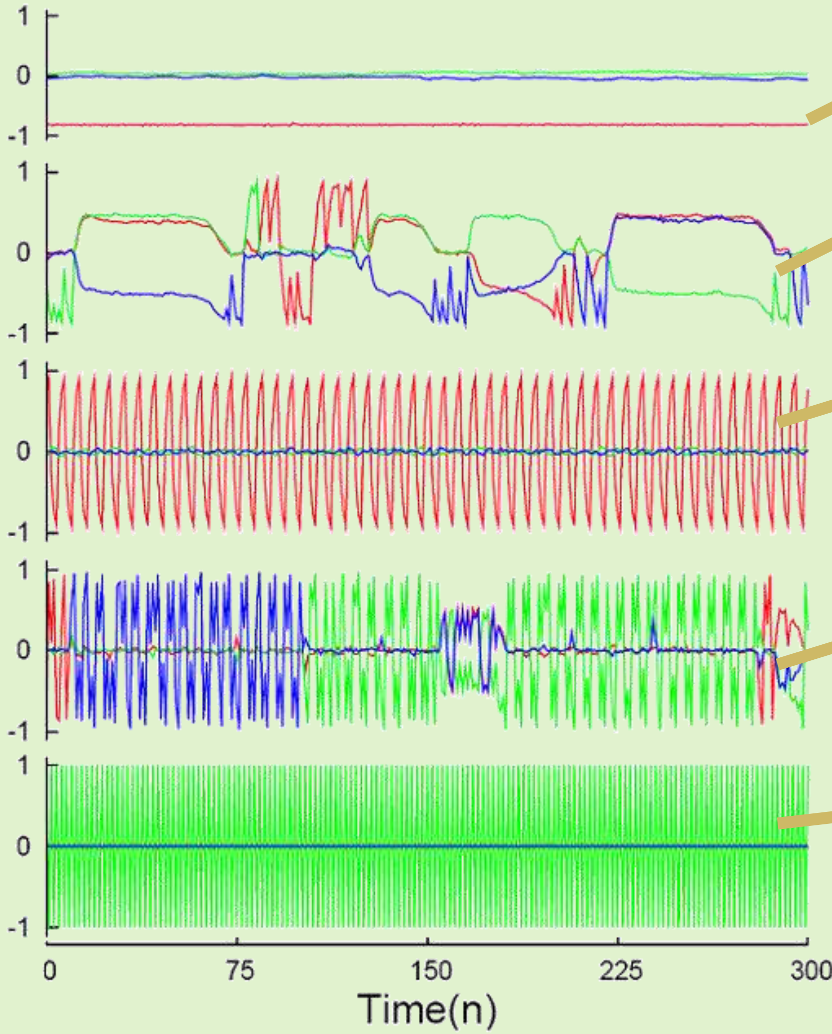
Lyapunov exponent (same case) with positive value in some (random) ranges

standard, Hopfield–Hebb case (namely, Φ = 1).

TYPICAL (MC) RUNS (after eventual transients)

overlap versus time

(N = 1600, P = 3 uncorrelated patterns, Φ = 0.4, T = 1/20)



After convergence, stability of one of the attractors — In fact, an *anti-pattern* (and practically zero overlap with the others) — for $\rho = 0.08 < \rho_c = 0.085$

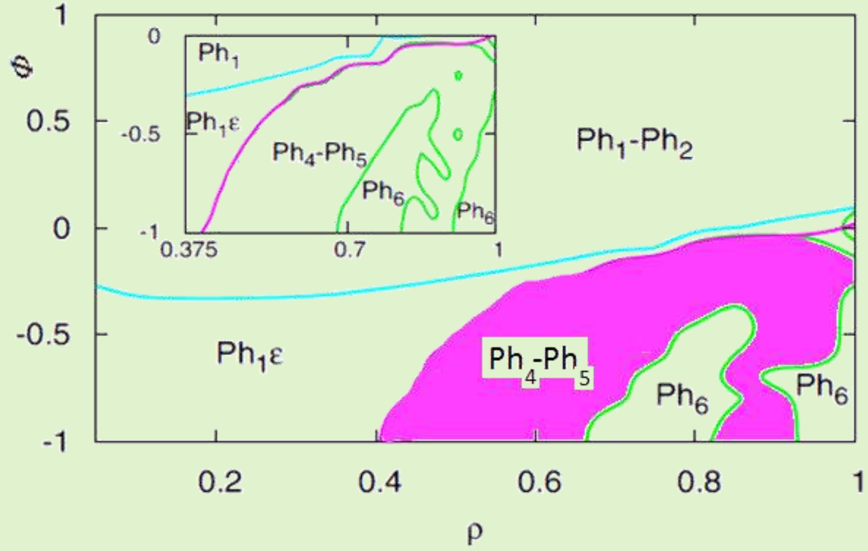
Fully irregular (positive Lyapunov exponent) behavior for $\rho = 0.50 > \rho_c$

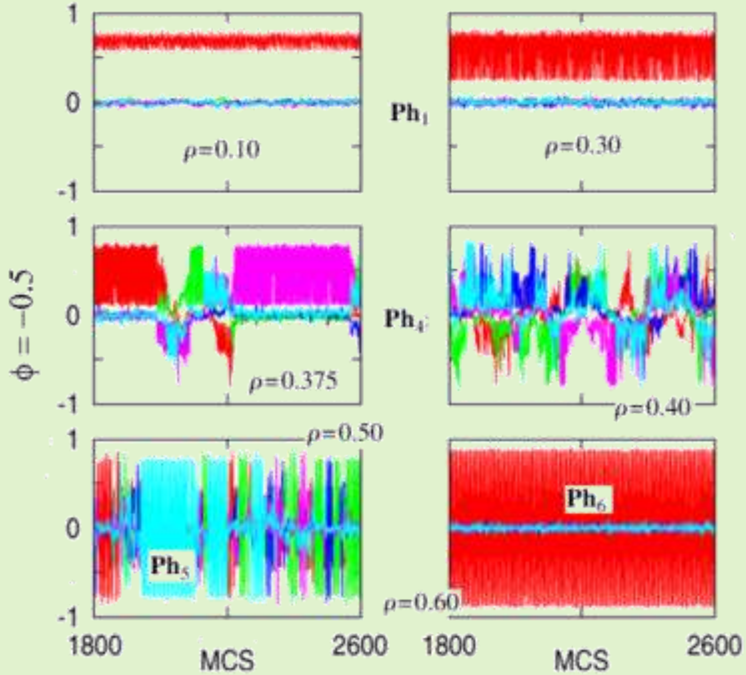
Regular oscillation between one attractor and its anti-pattern for $\rho = 0.65 > \rho_c$

Onset of chaos (again) as ρ is incresed somewhat; $\rho = 0.92$ in this case

Rapid and ordered periodic oscillations between one pattern and its antipattern (all nodes synchronized, $\rho = 1$)

Phase diagram for $N = 1600$, $P = 5$ and $T = 0.1$ (low)





Equilibrium

- **Ph_1 :** memory phase
- **Ph_2 :** mixture phase
- **Ph_3 :** disordered phase

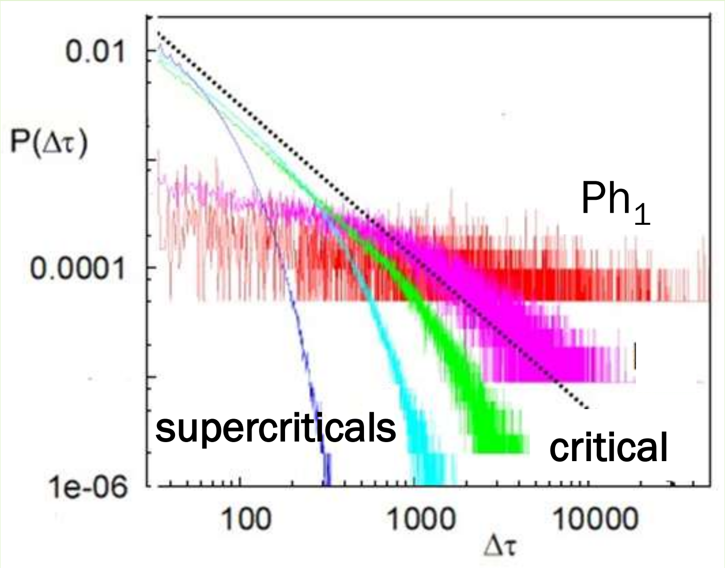
Nonequilibrium

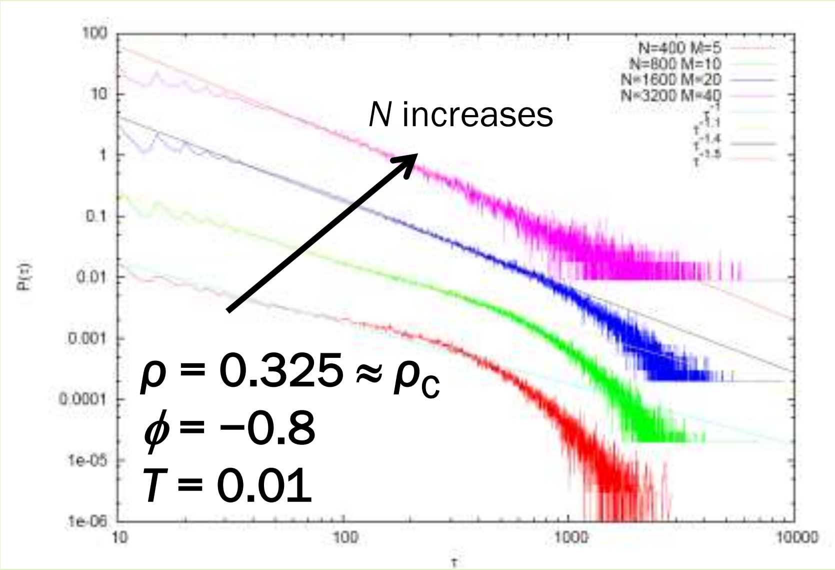
- **Ph_4 :** irregular roaming
- **Ph_5 :** irregular roaming randomly interr. by oscill.
- **Ph_6 :** pure pattern–antipattern oscillations

Critical behavior as irregular dynamics is approached

(memory phase Ph_1 → Irregular roaming Ph_4 or Ph_5; at very low *T* **)**

Distribution of times of permanence around a value of the local field *h* ($\Delta h = 0.1$)



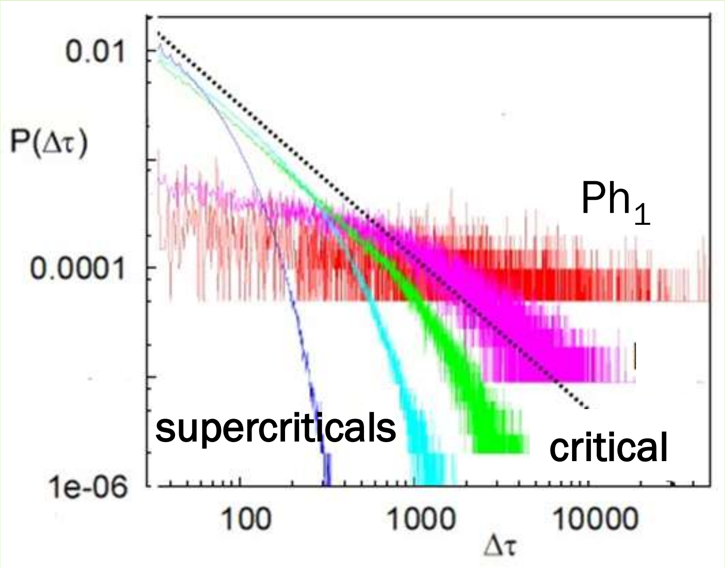


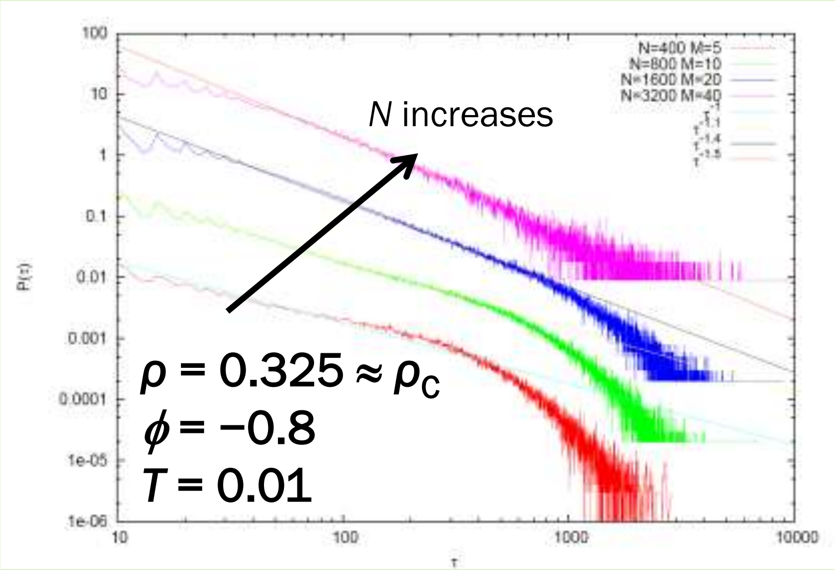
<u>Conclusion</u>: for large *N* (and *P*) (e.g., *N*=6400, *P*=40), one has **criticality** $\sim \Delta\tau^{-\beta}$, $\beta \approx 1 \longrightarrow 2$ (same from Fourier spectra, where one observes non-Gaussian 1/*f* noise in transition $Ph_1 \longrightarrow Ph_4$)

Critical behavior as irregular dynamics is approached

(memory phase Ph_1 → Irregular roaming Ph_4 or Ph_5; at very low T)

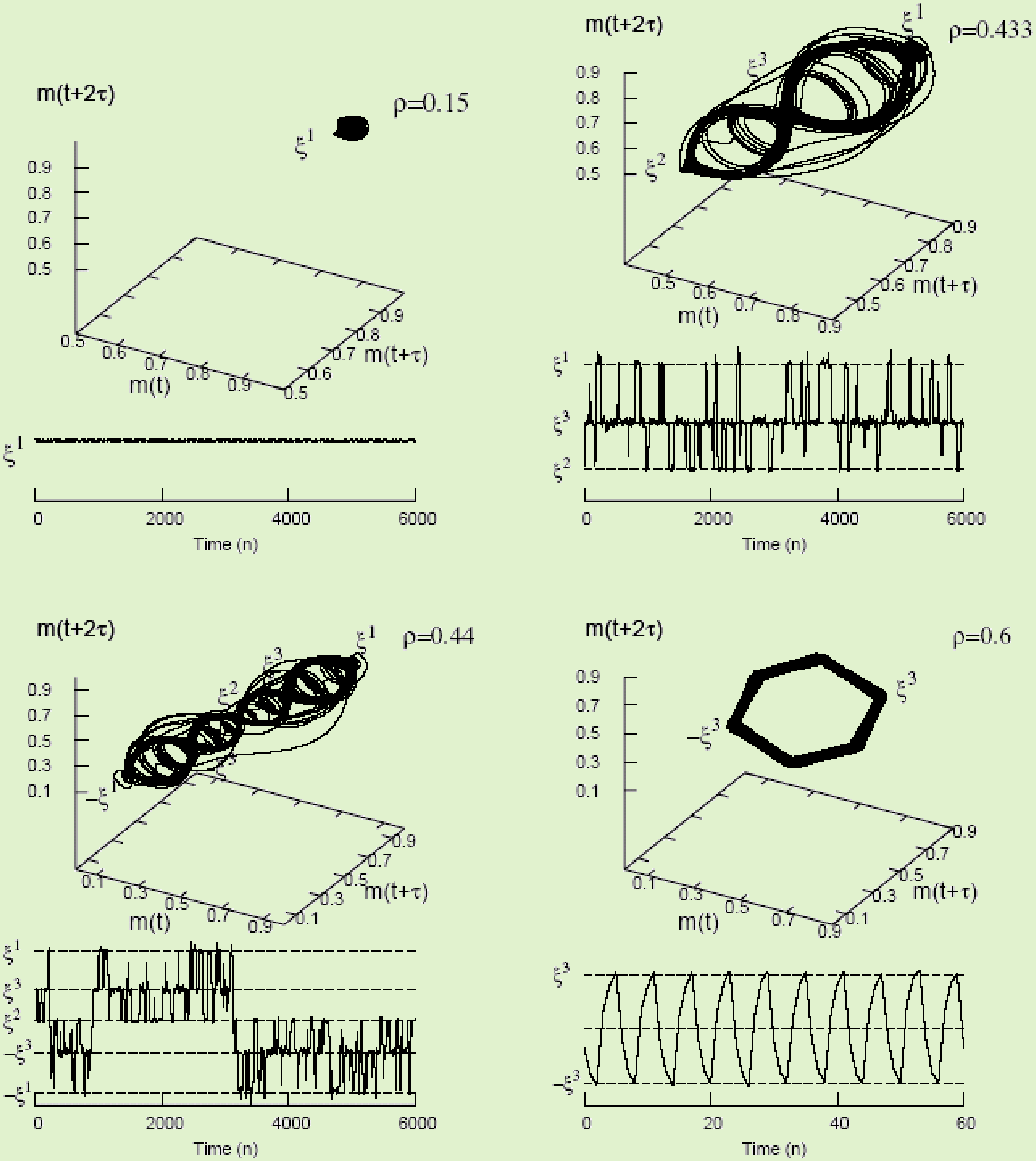
Distribution of times of permanence around a value of the local field h (Δh = 0.1)





Qualitatively similar behavior observed experimentally during heavy brain activity, e.g.,

- Eguiluz *et al*., *Phys. Rev. Lett*. 94, 018102 (2005)
- Freemen *et al*., *Clin. Neurophysiol*. 117, 1228 (2006)
- Magnasco *et al*., *Phys, Rev. Lett*. 102, 258102 (2009)
- Petermann *et al*., *PNAS* 106, 15921 (2009)



Chaotic switching among attractors

— simulates states of attention in the brain, and illustrates possible role of chaos in complex systems

number of attractors visited increases with ρ

— until activity settles down to a periodic jumping between one of the patterns and its anti-pattern.

mean firing rate

$$m = (2N)^{-1} \sum_i (1 + \sigma_i)$$

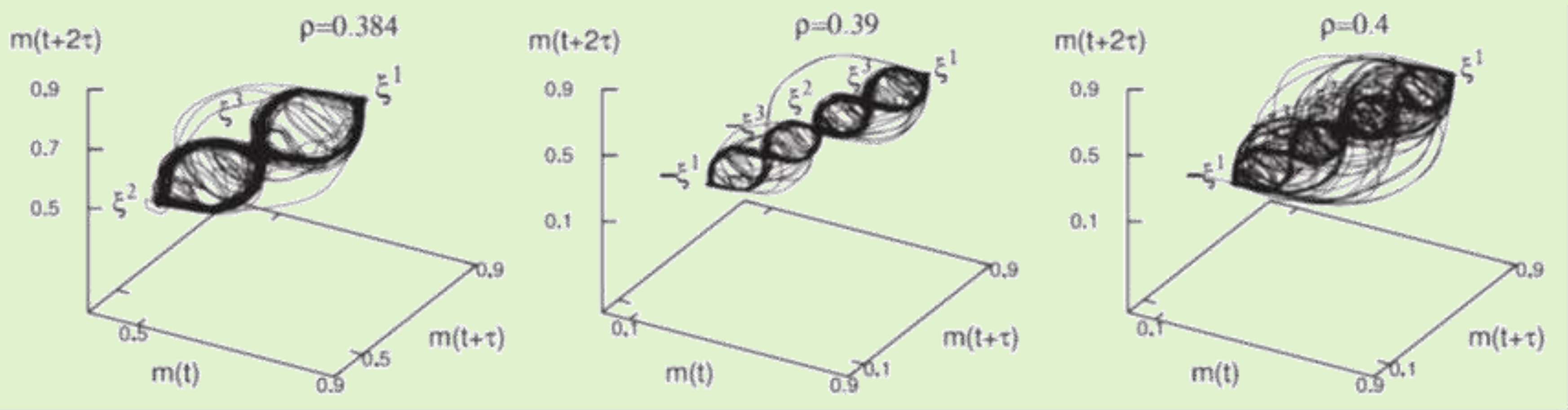
versus time, and phase space trajectories

$\Phi = ½$, $N = 1600$, $\beta = 167$, $\rho_C = 0.38$, and three patterns, namely, ξ^{μ} $\mu = 1,2,3$.

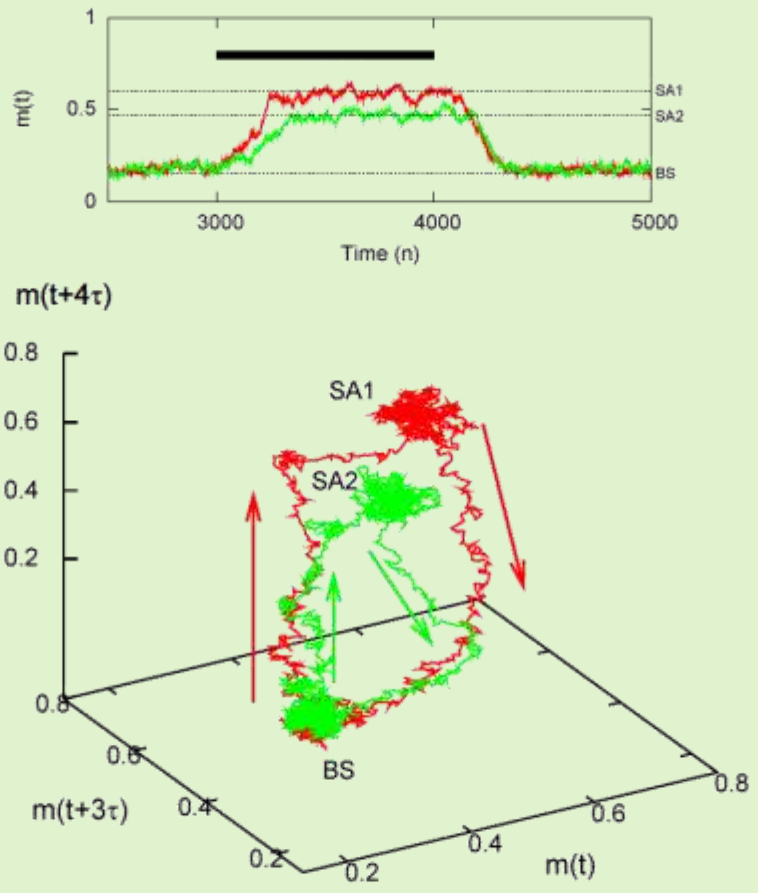
number of attractors visited increases with ρ

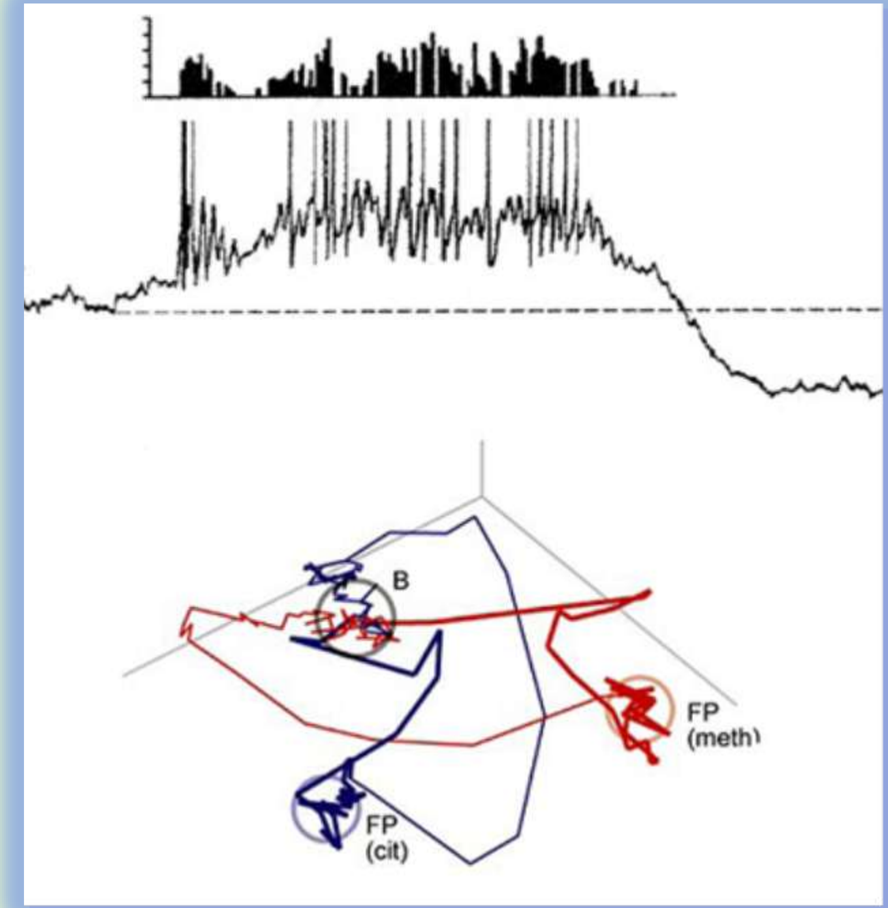
this shows phase space trajectories of mean firing rate : $m = (2N)^{-1} \sum_i (1 + \sigma_i)$

(as in previous slide, for $\Phi = ½$, $N = 1600$, $\beta = 167$, and three patterns).



Chaos, and roaming (induced by external stimuli) **as an state of attention***





Mazor & Laurent, *Neuron* 48, 661 (2005)

*Torres, Marro, Cortes & Wemmenhove, *Neural Networks* 21, 1272 (2008)

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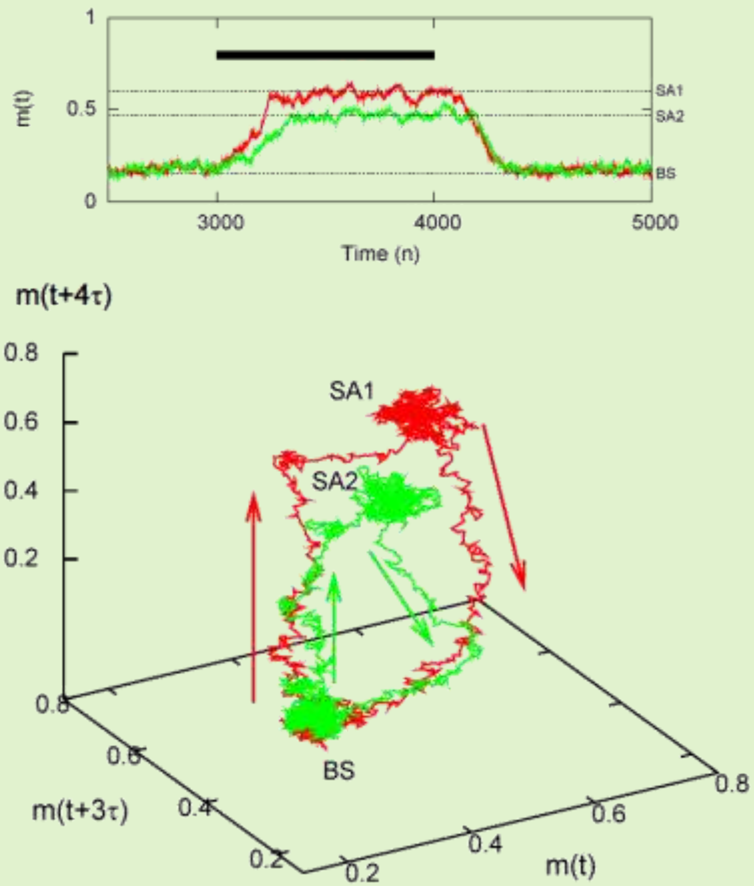
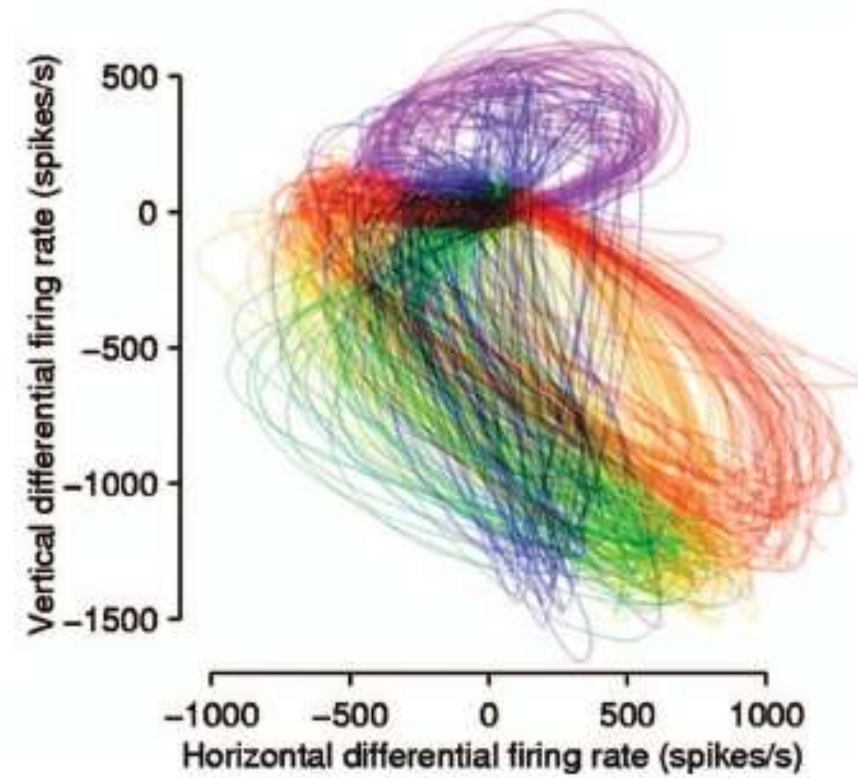


Firing rate with time in cultured neural nets; Wagenaar *et al*. (2006)



*Torres, Marro, Cortes & Wemmenhove, *Neural Networks* 21, 1272 (2008)

What about network structure?

- Linear preferential attachment can probably explain almost ubiquitously observed scale-free degree k (# node neighbors) distributions
- What if rule for a fixed-size network to evolve is nonlinear? → One has topological phase transitions and scale free solutions*

Model: prob. for attachment/detachment fact. in two parts:

- local term (on node degree)

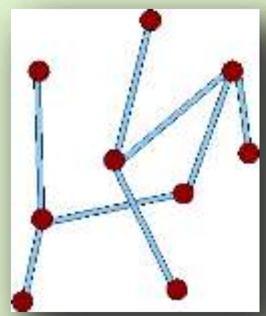
  e.g., enhanced electric activity induces synaptic growth and arborization, and activity of a neuron depends on current from neighbors, higher the more, so that k is a proxy

- global term (on mean network degree)

  e.g., synaptic growth and death depend on concentration of various molecules diffusing through large areas of tissue

* Johnson, Marro & Torres, *Phys. Rev. E* **79**, 050104R (2009); *J. Stat. Mech*. P03003 (2010)

Evolution of network structure



- N nodes of degree $k_i = \sum_j a_{ij}$ (adjacency matrix), $p(k,t=0)$ with mean $\kappa(t)$
- At every step, each node gains an edge (to a random node) and loses (a randomly chosen) edge with probabilities which factorize:

$$P_i^{\text{gain}} = u(\kappa)\,\pi(k_i) \qquad\qquad P_i^{\text{lose}} = d(\kappa)\,\sigma(k_i)$$

where $u, d = f(\kappa)$ as well as π, σ are arbitrary (but normalized).

- It follows (approximately, large N) the master equation:

$$\frac{dp(k)}{dt} = u\pi(k-1)\,p(k-1) + d\sigma(k+1)\,p(k+1) - \left[u\pi(k) + d\sigma(k)\right]p(k)$$

- From this, one may systematically work out most details, including the ones of the stationary state…

Evolution of network structure

Synaptic pruning (e.g., Chechik *et al.*): eliminating certain synapses improves brain energy consumption (¼ of humans at rest) while maintains optimal performance.

mean degree k = mean *synaptic density*, so that κ reflects energy consumption
→ use model with simple choice for global probabilities, e.g.:

$$u(\kappa_t) = \frac{n}{N}\left(1 - \frac{\kappa_t}{\kappa_{\max}}\right), \qquad d(\kappa_t) = \frac{n}{N}\left(\frac{\kappa_t}{\kappa_{\max}}\right)$$

n = expected value of # add-deleted edges / time step
$\kappa_{\max}$ = max. value the mean degree can have

higher synaptic density → less likely new synapses are to sprout / more likely existing ones are to atrophy, as expected e.g. for finite quantity of nutrients— and find (detailed bal.):

$$\frac{d\kappa_t}{dt} = 2\frac{n}{N}\left(1 - \frac{2\kappa_t}{\kappa_{\max}}\right): \quad \text{independ. of local probs.}$$

1. network then evolves towards heterogeneous (some times scale free) in quantitative agreement with synaptic pruning experiments; and
2. degree-degree correlations (*“disassortative nets”*) emerge naturally (as tends to be the case in biology); and
3. evolution leads to realistic small-world parameters.

Evolution of network structure

Synaptic pruning:

$$\frac{d\kappa_t}{dt} = 2\frac{n}{N}\left(1 - \frac{2\kappa_t}{\kappa_{\max}}\right)$$

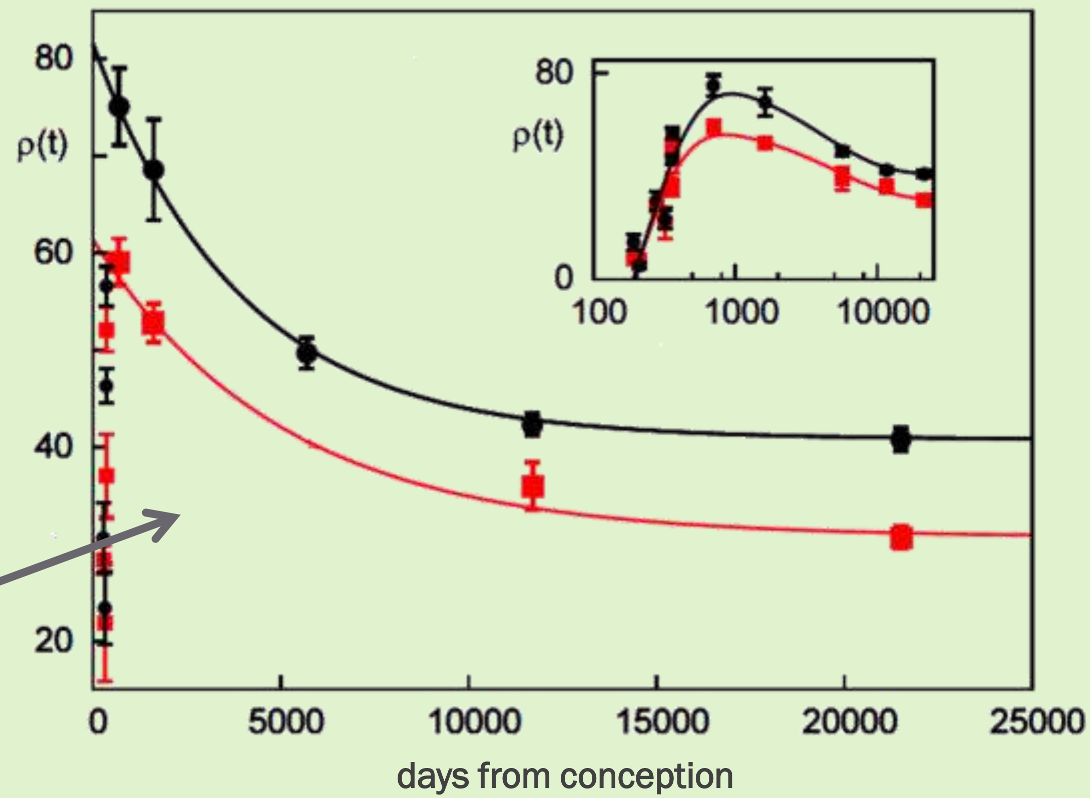
synaptic density $\rho_t = \kappa_t\, N/(2V)$

$\kappa_0 = \kappa_{\max}$

$\tau_{\text{pruning}} = (N/n)\, \rho_{t\to\infty}$

one has for data and model

(this includes transient growth $+ a\exp(-t/\tau_{\text{groth}})$ for inset; τ's are the only parameters to fit)



- Data — corresponding to layers 1 (red) and 2 (black) of human auditory cortex, from autopsies: Huttenlocher & Dabholkar, *J. Comparative Neurology* **387**, 167 (1997)
- Model: Johnson, Marro & Torres, *J. Statistical Mechanics: Theor. & Exper.* P03003 (2010)

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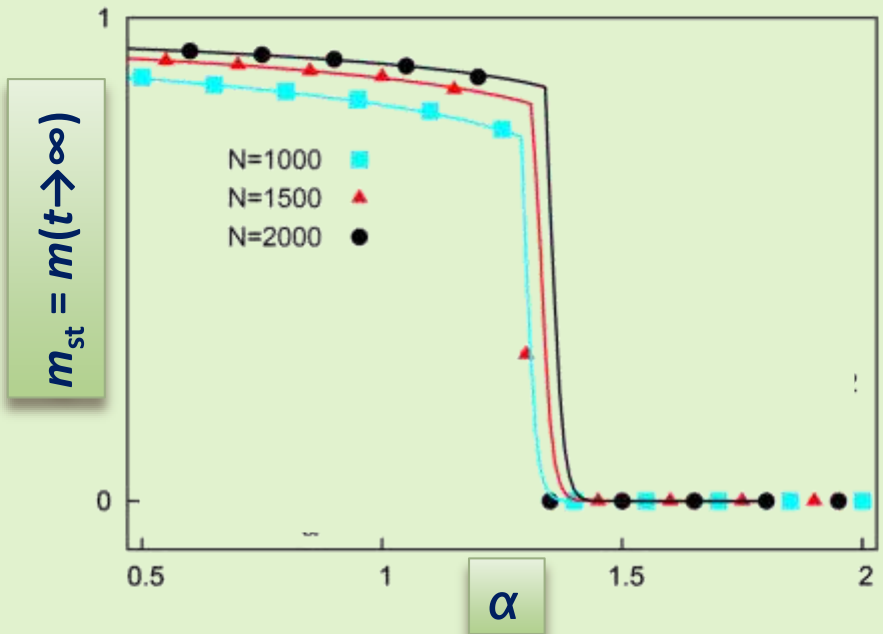
Network structure

Local probabilities: no effect on pruning but on diffusive behavior, which leads either to homogeneous or to heterogeneous states.

Let a **degree distribution** of mean κ and variance γ^2

Define $m \equiv \exp(-\gamma^2/\kappa^2)$: $m(\mathrm{t}) \rightarrow 1$ for regular network;

$m(\mathrm{t}) \rightarrow 0$ for highly heterogeneous



$$\sigma(k) = k$$

$$\pi(k) = k^{\alpha}$$

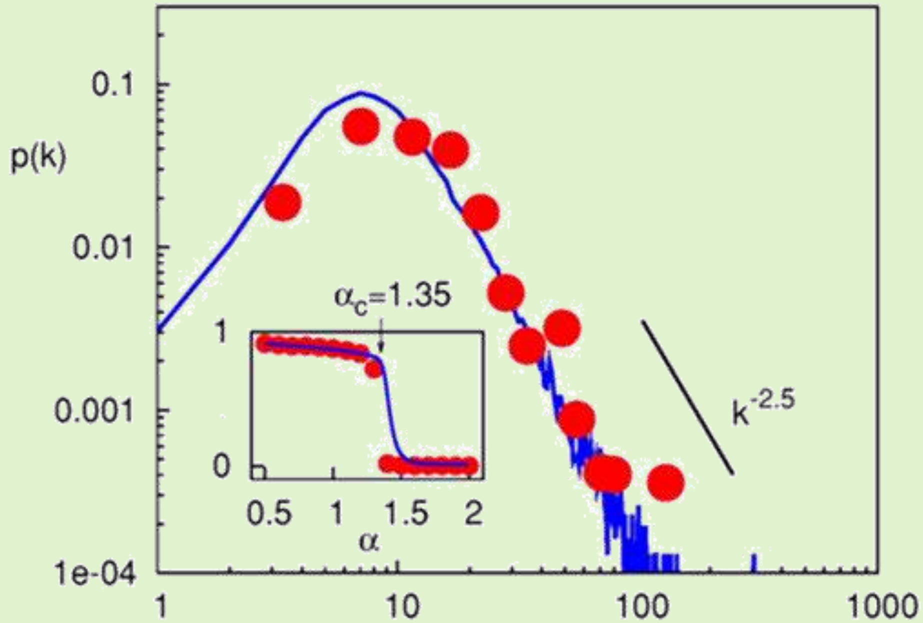
Network structure (applications)

Model also allows studying *mean minimum path*, *degree-degree correlations*, *clustering*, *synchronizability*,..., and makes contact with other experiments:

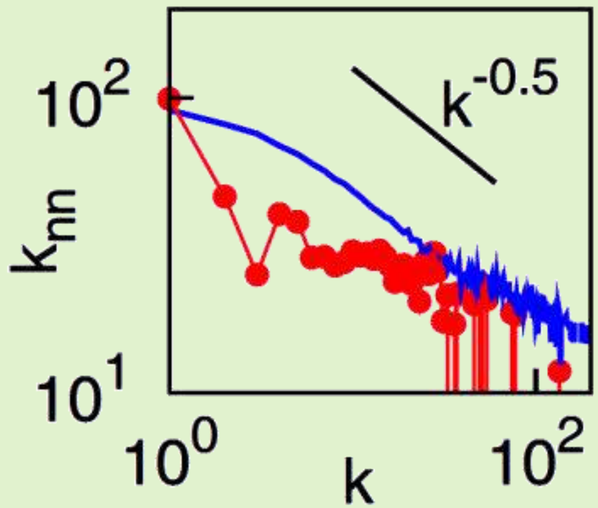
¿Can the neural network of worm *C. Elegans*

arise via stochastic rules as in our model?

For above global and local probs., $\sigma = k$ and $\pi = k^{\alpha}$, remarkable similarities:



Mean nearest-neighbor degree function for worm (red) and model (blue):



Comparison of parameter in both cases: C = clustering; ℓ = mean shortest path length; r = Pearson's correlation coefficient («Theory», from other models in the literature)

	Experiment	Simulation	Theory
C	0.28	0.28	0.23
l	2.46	2.19	1.86
r	−0.163	−0.207	−0.305

Summing up…

- A few versions of a network model with well defined familiar limits was worked out both analytically and computationally.
- Full connected case with rapid fluctuating (depressing/enhancing) edges and silent units (molecules, agents, neurons,…): equilibrium (disordered, memory and mixture) and nonequilibrium phases, one showing irregular roaming dynamics and $1/f$ noise as observed for some brain functions.
- Assuming evolving topologies with general local and global microscopic rules leads to a simple scenario producing either homogeneous, scale-free (at the critical point) or highly heterogeneous structures.
- This almost perfectly fits data from two experiments on nervous systems:
  - Synaptic pruning in humans: nonlinear global probs. reproduce initial increase and subsequent depletion (only two parameters for whole set)
  - Structure of *C. Elegans* neural net: assuming random deletion of edges and power-law prob. of growth, model reproduces at critical point worm's non-trivial features (small-world parameters, degree distribution, and even level of disassortativity).
- We also explain microscopic causes of stochastic multi-resonance, i.e., signal enhancement during transmission trough different levels of noise.

¡Gracias!

☺

Questions and comments: jmarro@ugr.es