LEARNING AS A PHENOMENON OCCURRING IN A CRITICAL STATE

Gan W. et al., 2000, Neuron
High magnification image of cortical

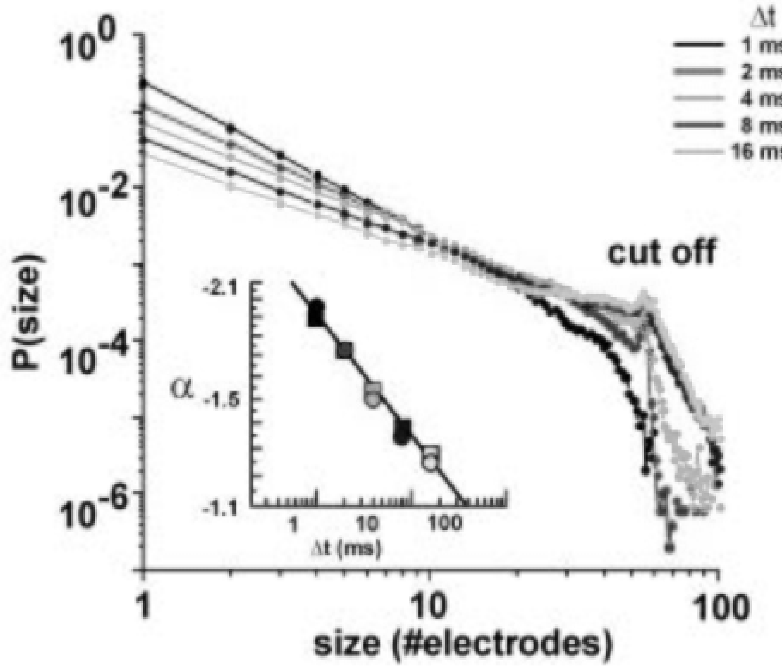
Neuronal avalanches

Beggs & Plenz (J. Neuroscience 2003, 2004) have measured spontaneous local field potentials continuously using a 60 channel multielectrode array in mature organotypic cultures of rat cortex *in vitro* and *in vivo* (PNAS 2008, 2009)

They have shown that spontaneous activity has an avalanche mode:

- Several avalanches (active electrodes) of all size per hour
- Activity initiated at one electrode may spread later to other electrodes in a not necessarily contiguous manner
- Avalanche size distribution is a power law with an exponent close to -3/2
- Avalanche duration distribution is a power law with an exponent close to -2.0

⇨ Critical state optimizes information transmission

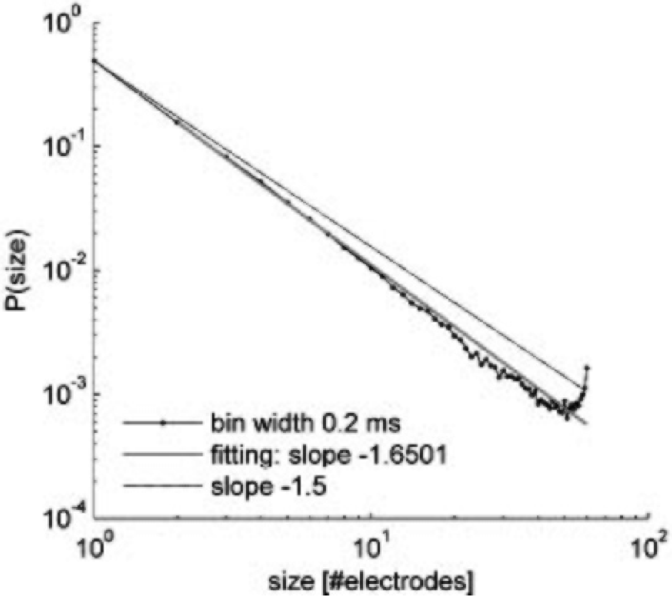


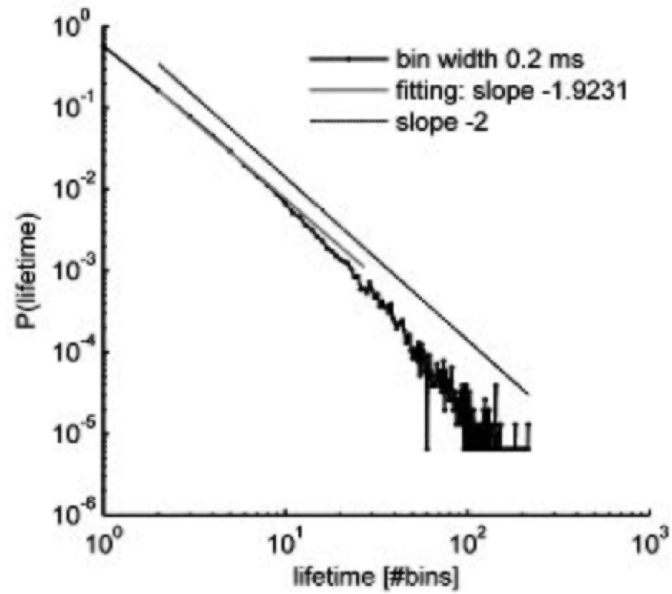
Dt temporal resolution of binnin

Avalanche activity found also in dissociated rat cortical neurons

(V. Pasquale et al, Neuroscience 2008)

- Neuronal avalanche behavior depends on time scale of observation
- Neuronal cultures developing in vitro organize differently and exhibit different dynamic state (critical, subcritical, supercritical)
- Critical behaviour depends on the interplay between spiking and bursting activity



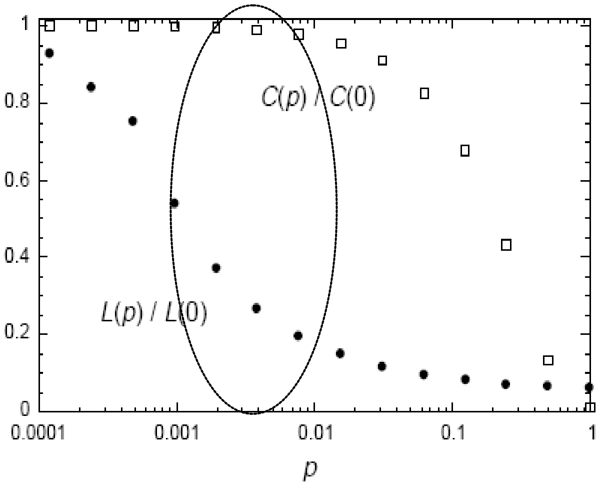


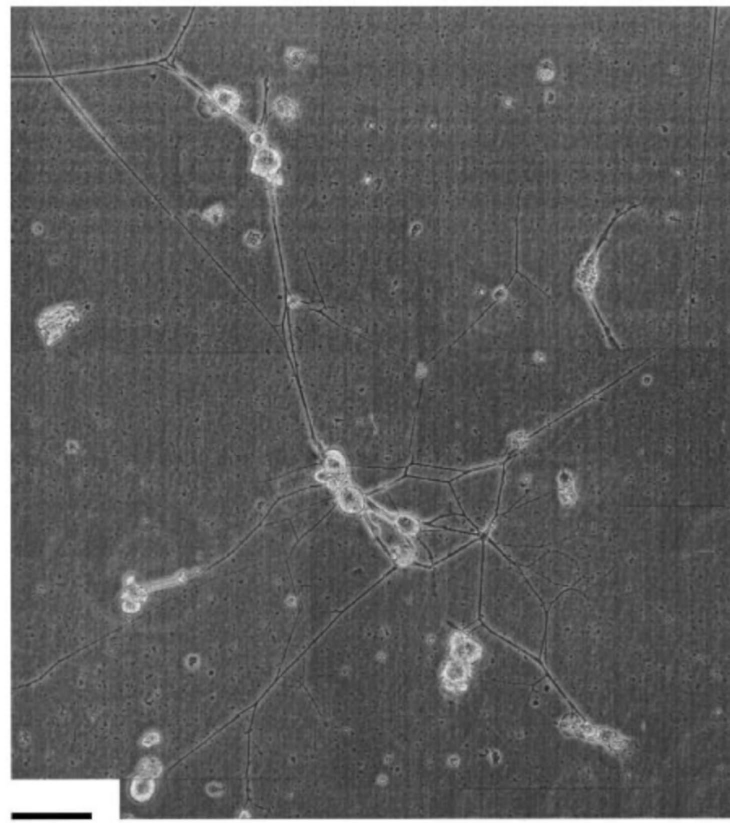
- Similar scaling behavior found for dissociated rat hippocampal neurons and leech ganglia (A. Mazzoni et al PLoS ONE 2007)

Morphology of neuronal networks

- The morphology of networks of living neurons has been studied *in vitro* (Shefi et al, PRE2002) → development of neurites in an ensemble of few hundreds neurons from the frontal ganglion of adult locusts.
- After few days the cultured neurons have developed an elaborated network with hundreds of connections

By a mapping onto a connected graph, the hort path length and the high clustering oefficient → network is small-world





fficient information transmission with a mall number of long range connections.

Degree distribution → broad scale

n vitro only 240 neurons)

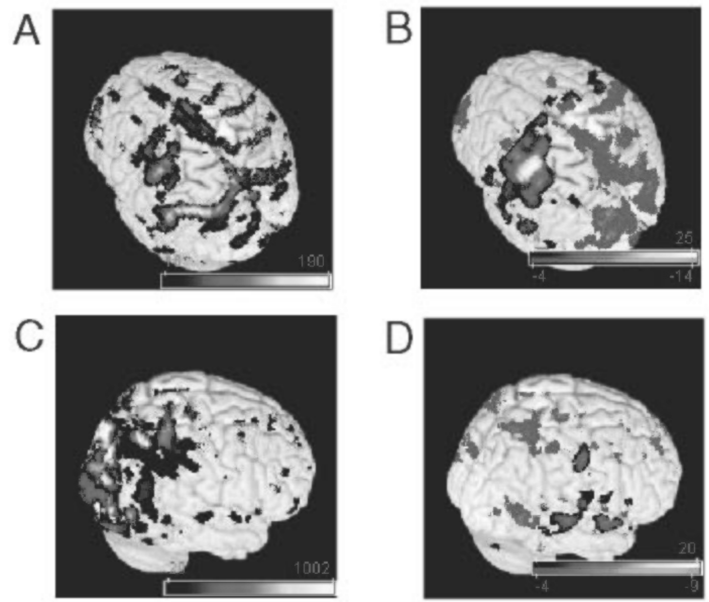
Scale-free Brain Functional Network

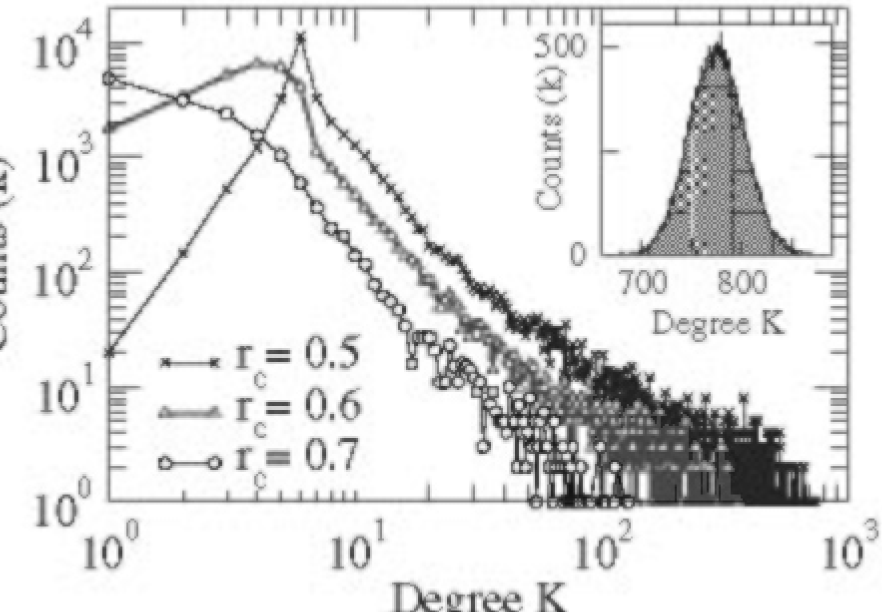
guiluz, Chialvo, Cecchi, Baliki, and Apkarian (PRL 005) measured by MRI the functionality etwork in humans performing different tasks

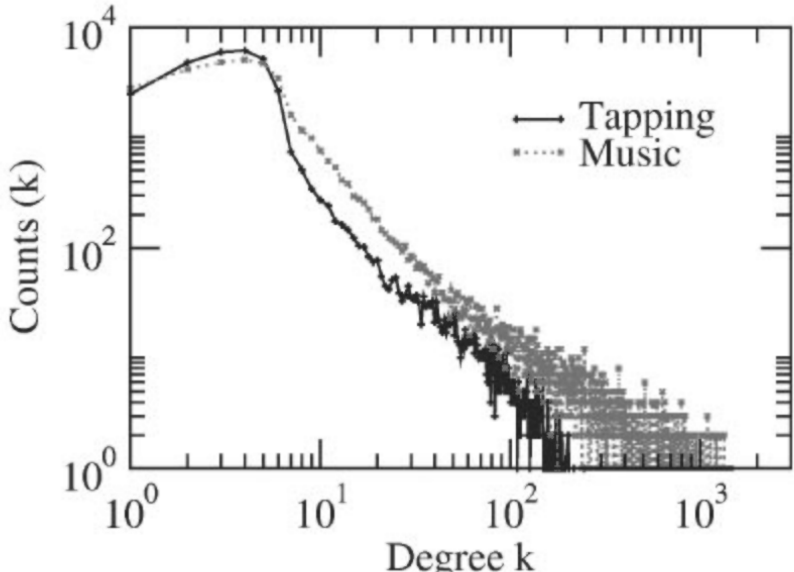
- Correlation coefficient between magnetic esonance activity in any pair of voxels, $r(x_1, x_2)$ veraged over time

- Two voxels are functionally correlated if

$$r(x_1, x_2) > r_c$$





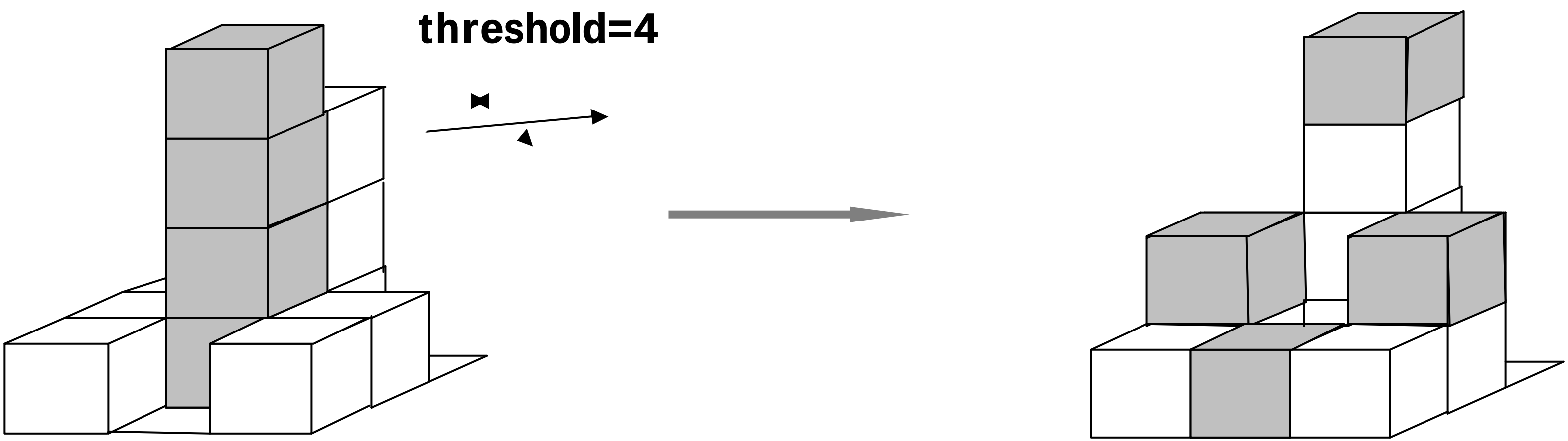


SELF-ORGANIZED CRITICALITY

Bak, Tang, Wiesenfeld, PRL 1987

Dynamical systems spontaneously evolving toward a critical state without parameter tuning → <u>no characteristic event size</u>

Sand pile **...by adding at random one grain...**



Size and duration distributions behave as power laws

$$P(s) \sim s^{-1}$$

$$P(T) \sim T^{-0.5}$$

Fundamental ingredient: separation of time scales

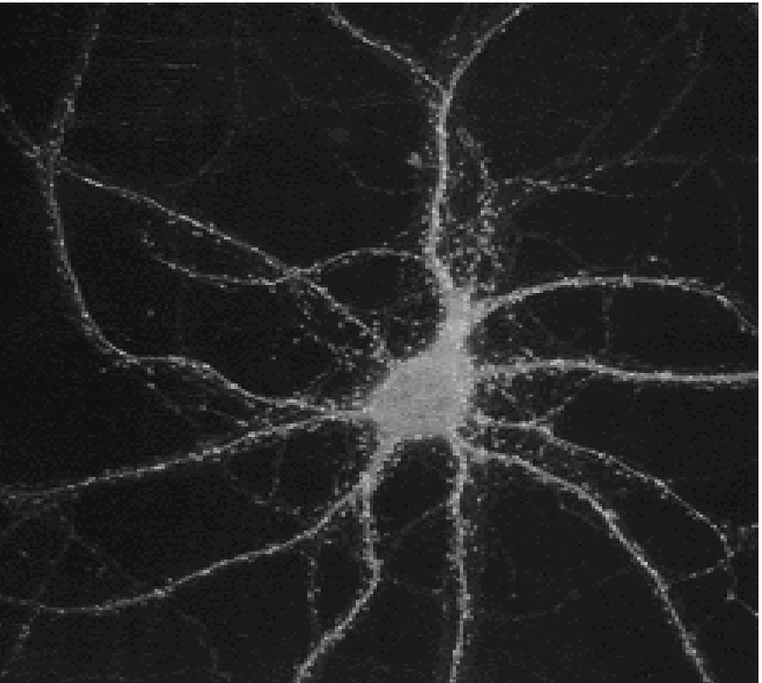
- Slow scale: adding a grain
- Fast scale: propagation of an avalanche

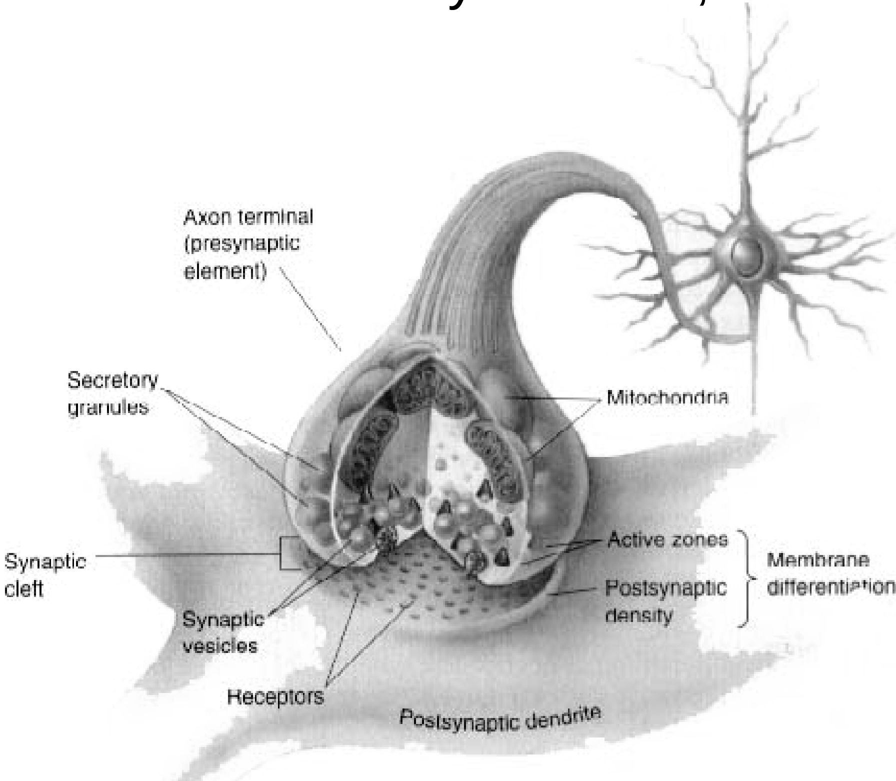
SOC applied to many natural phenomena

- Slides and avalanches
- Earthquakes
- Solar flares
- Fluctuations in confined plasma
- Biological evolution

Physiological ingredients

- A neuron is characterized by a membrane potential and is connected to other neurons via excitatory or inhibitory synapses
- A neuron fires when the membrane potential reaches a given threshold (-55mV), then goes back to rest potential (-70mV)
- Connected neurons receive charge and change their membrane potential according to the presynaptic neuron potential change
- After firing a neuron goes through the refractory period, time during which the neuron is unable to answer to any stimulus, regardless its intensity



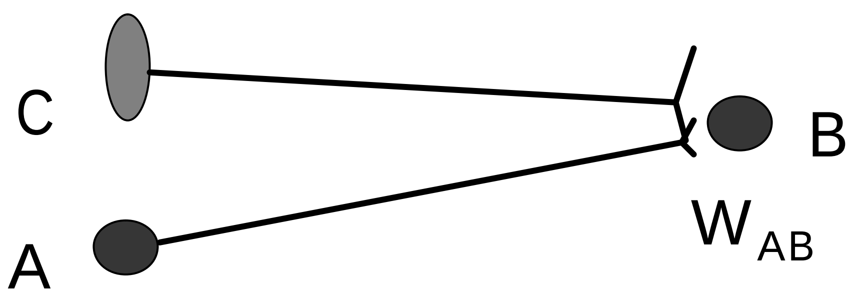


Donald Hebb (1904-1985) and "Hebbian synaptic plasticity"

Let us assume that the persistence or repetition of a reverberatory activity (or "trace") tends to induce lasting cellular changes that add to its stability…

When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cell firing B, is increased"

From: Hebb DO, The organization of behavior : a neuropsychological theory; New York, Wiley,1949.



The conjuction of activity at the presynaptic and postsynaptic neuron leads to increased synaptic activity: neurons that fire together wire together

MODEL FOR BRAIN PLASTICITY

LdA,CPC, HJH, PRL 2006, PRE 20

We introduce within SOC the main ingredients of neural activity:

Threshold firing, Neuron refractory period, Activity dependent synaptic plasticit

- We assign to each neuron a potential v_i and to each synapse a strength g_{ij}

$$\boxed{g_{ij} \neq g_{ji}}$$

- A neuron fires when the potential is at or above hreshold $\mathbf{v_{max}}$ (-55mV) distributing charge to the onnected neurons proportionally to the strength f each synapse

$$\boxed{v_j(t+1) = v_j(t) \pm \frac{q_i(t)}{k_{in_j}} \frac{g_{ij}(t)}{\sum_k g_{ik}(t)}}$$

- Synapses can be <u>excitatory</u> or <u>inhibitory</u> (i.e. at the postsynaptic neuron the potential can be added or subtracted)

- After firing a neuron is set to <u>zero resting potential</u> (-70mV) and remains uiescent for one time step (<u>refractory period</u>), the action potential is not allowed o reverberate back to the cell body

PLASTICITY RULES

- The active synapses connecting neurons not at resting potential have their strength increased proportionally to the current

$$\boxed{g_{ij}(t+1) = g_{ij}(t) + a i_{ij}(t)}$$

- The avalanche goes on and at the end all inactive synapses have their strength reduced by the average strength increase per bond

a is the parameter controlling synaptic plasticity

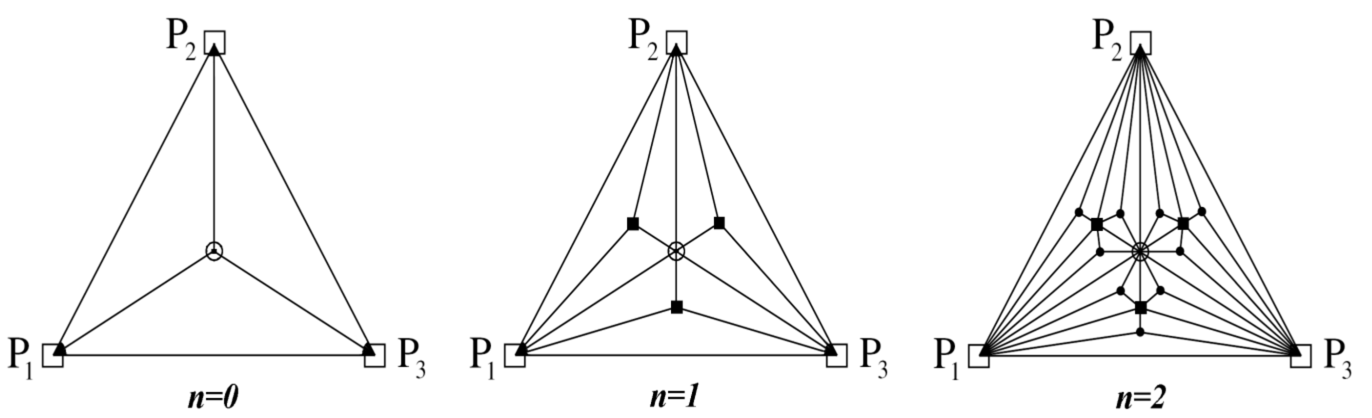
(represents the ensemble of all physiological factors influencing synaptic plasticity)

Network memorizes the most used paths, less used synapses atrophy

$\longrightarrow$ PRUNING

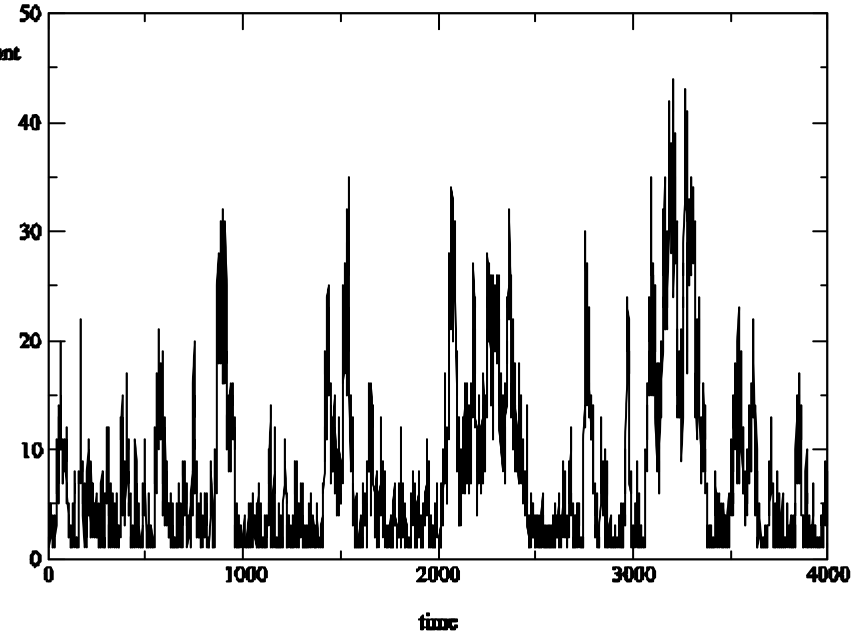
Morphology of the network

- Regular square lattice (no longer regular after pruning!)
- Small world lattice (rewiring 1% bonds)
- Eguiluz et al scale free network
- Scale free Apollonian network JS Andrade et al PRL 2005



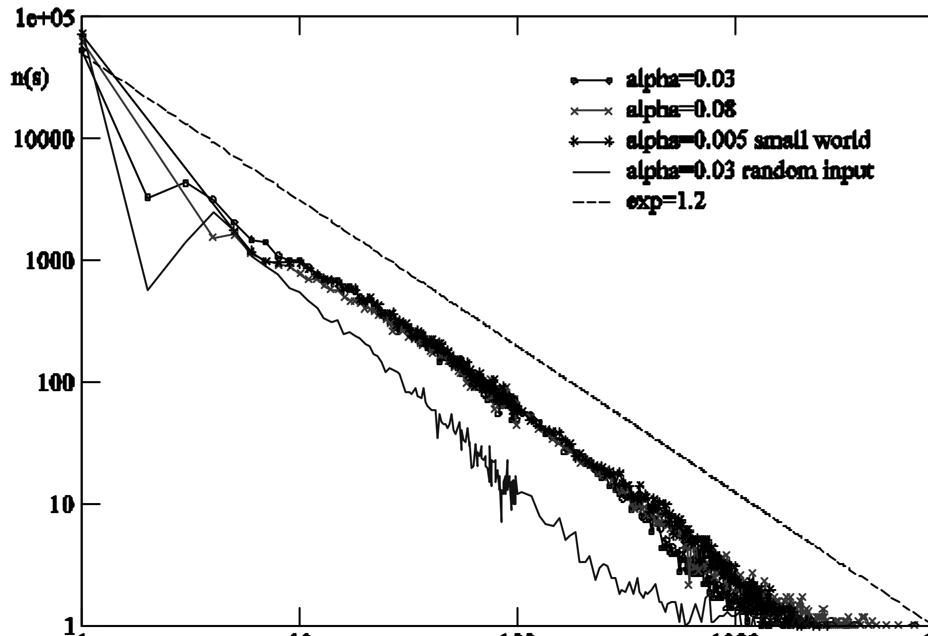
TIME SIGNAL AND NEURAL AVALANCHES

On a “trained” brain we monitor the total current flowing and the number of firin
neurons as function of (microscopic) time ⟶ avalanches of all size



We measure the avalanche size distribution for:

- different a
- different external stimuli
- regular, small world, scale free networ
- excitatory and inhibitory synapses



or external stimulus <u>at random site</u>

ecomes 1.5±0.1 ⟶ **Beggs & Plenz**

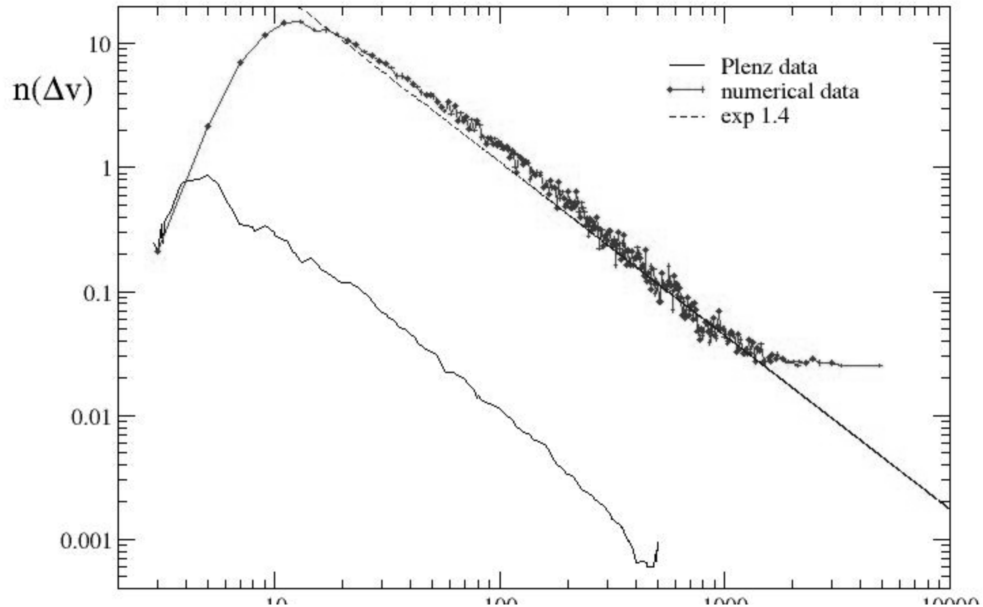
table with respect to parameters
nd lattice type

he exponent is 1.2±0.1 **for external**
timulus at <u>fixed input site</u>

Distribution of overall neuronal voltage variation during an avalanche

16000 neurons and 5% inhibitory synapses

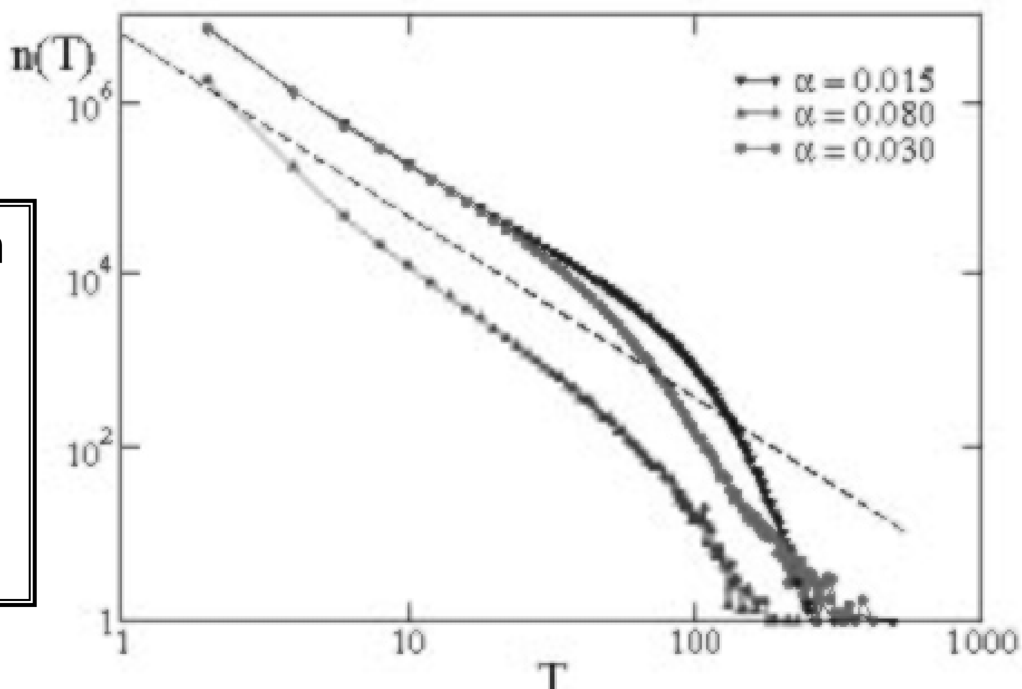
Eguiluz et al network



The avalanche duration distribution has a power law behaviour with an exponent -2.1±0.1

Apollonian network

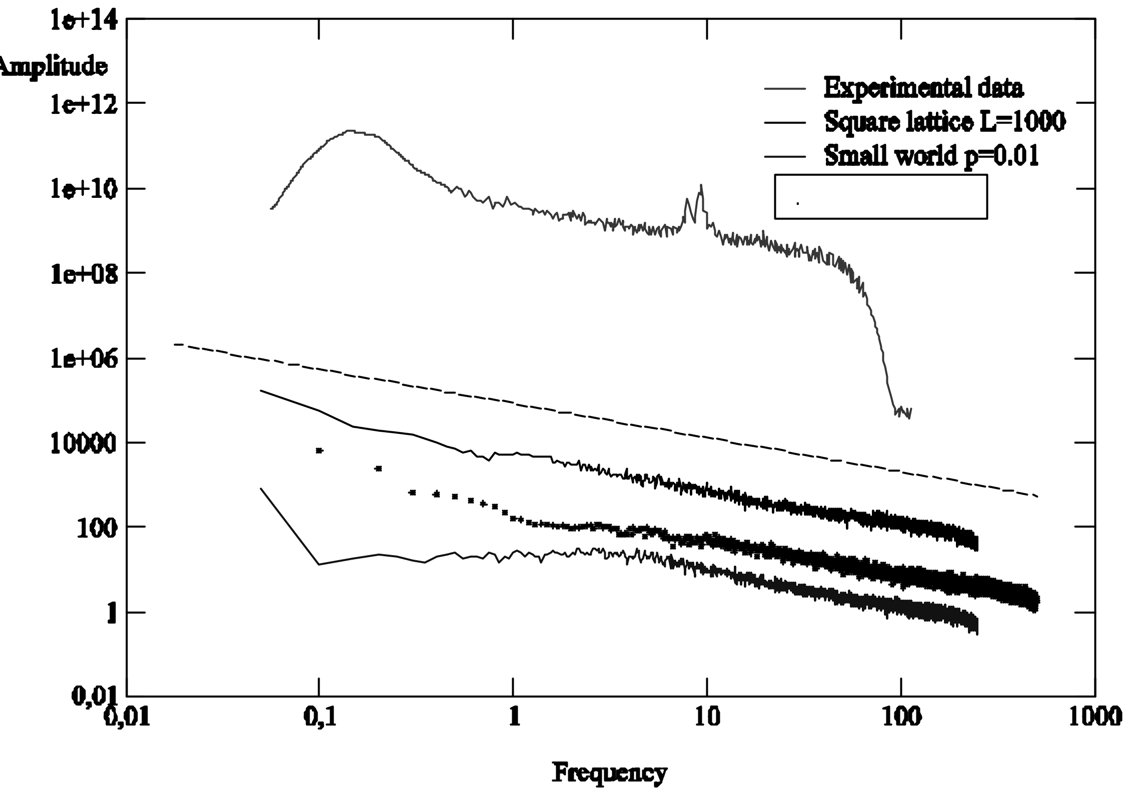
Beggs & Plenz



POWER SPECTRA AND EEG

In order to compare with numerical data, we calculate the power spectrum, i.e. amplitude squared of the Fourier transform as function of the frequency, and compare with experimental data from EEG of subject male resting with eyes closed (Novikov et al, PRER 1997, power law exponent 0.795)

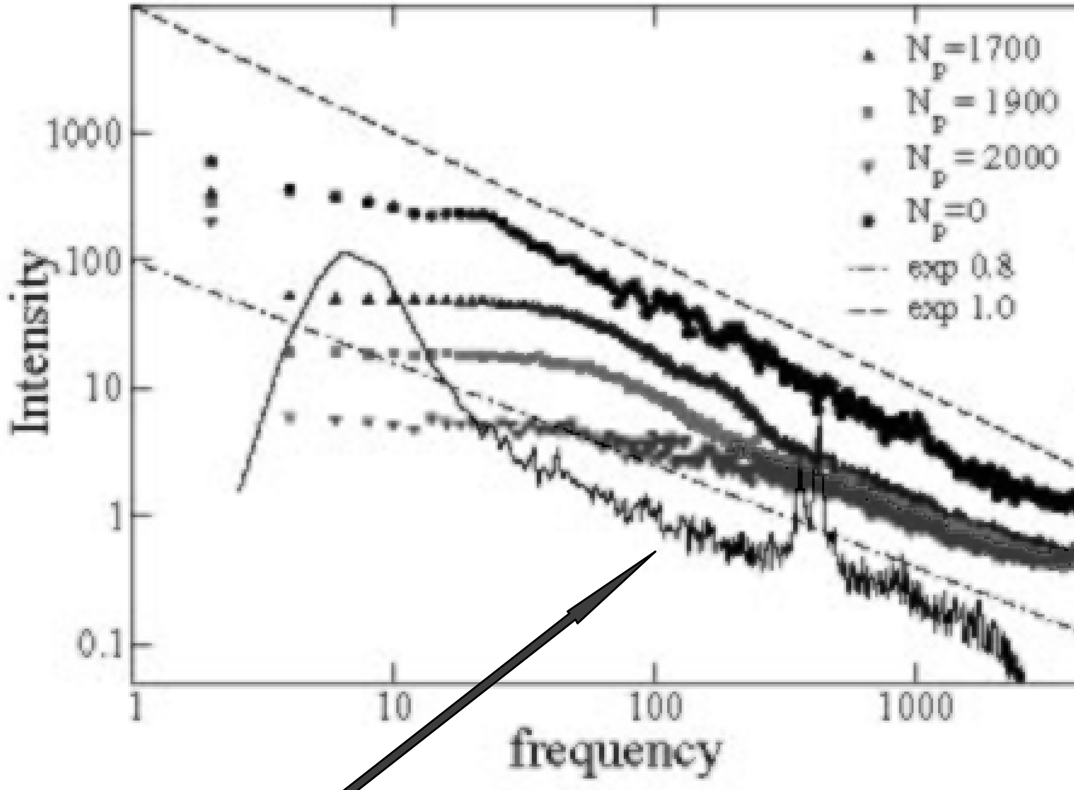
<u>We find universal scaling with slope 0.8±0.1</u>



Does not depend on:

- Parameter a
- Type of lattice
- Initial conditions

Apollonian network



For zero plastic training the

spectrum ⟶ 1/f noise

•No characteristic time scale

•Superposition of signals with different relaxation times and same amplitude

Experimental data by Novikov et al

Slope < 1 ⟶ high frequency signals more relevant

also human gait (Ashkenazy et al Physica A 2002)

LEARNING

- Many theoretical models proposed for learning →
  from perceptron to attractor neural networks

- Two-state neurons, fully connected networks

- Several algorithms for neuronal learning

- Extremal dynamics and uniform negative feedback

→ the system learns by mistakes

no cooperative effects

operating in a critical state optimizes information transmission

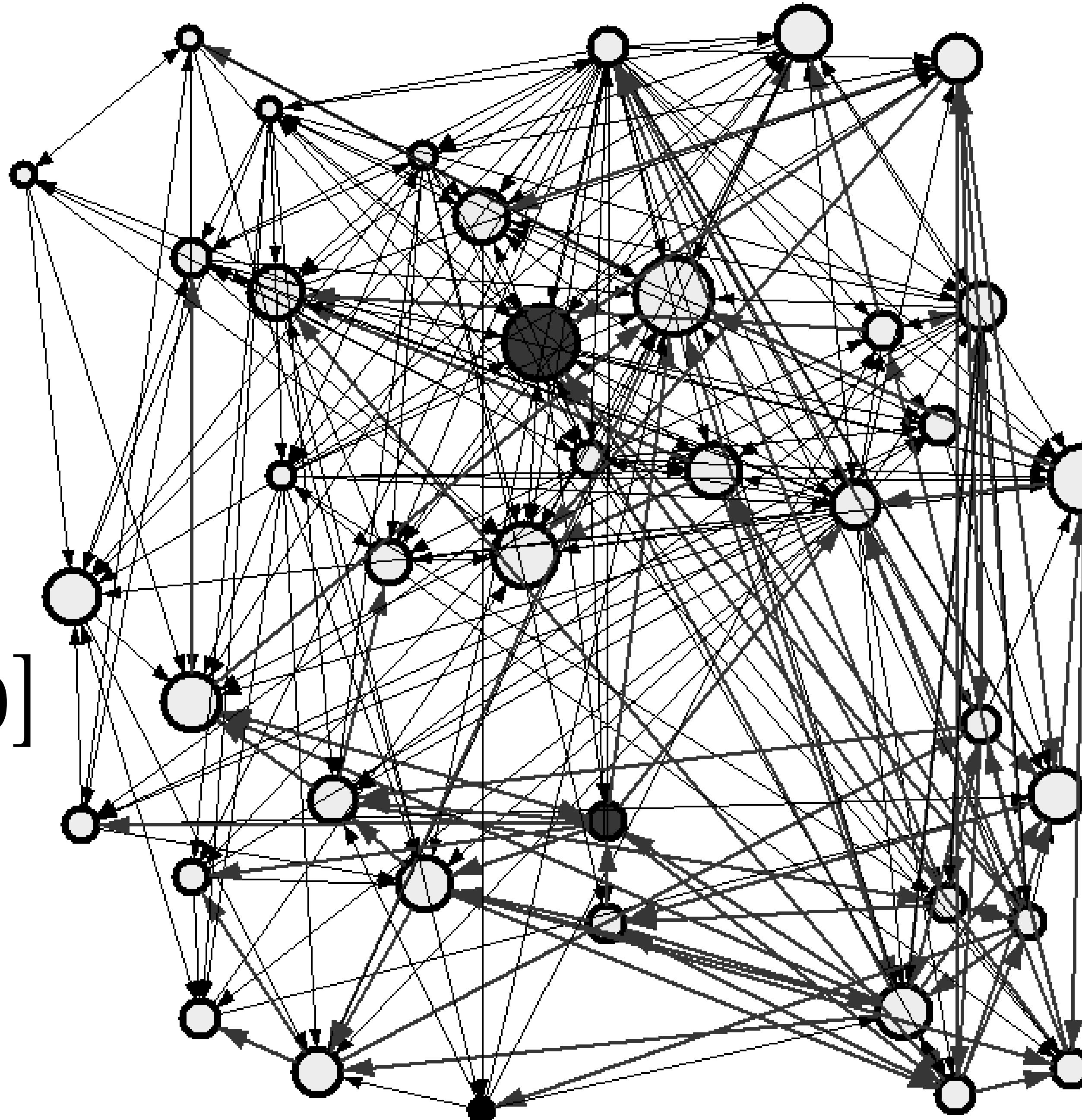
learning changes functional connectivity and sculpts spontaneous activity (Lewis et al PNAS 2010)

LdA, Herrmann, PNAS 201

➢We choose 2 input (red) and 1 output (black) neurons at fixed distance k_d on a scale free network where

$$k_{out} \in \left[k_{\min}, 100\right]$$

Soma size is proportional to k_{in}



- We test OR, AND, XOR and random rule with 3 inputs:
  - Set 1/0 at the input sites → firing/not firing
  - Let the avalanche propagate
  - Check state of output neuron (1 firing, 0 not firing)

- Non uniform negative feedback, <u>plasticity parameter a</u>:
  - If the answer is right, do nothing
  - If the answer is wrong, adjust the strength of synaptic connections involved in the avalanche propagation by

+ false negative

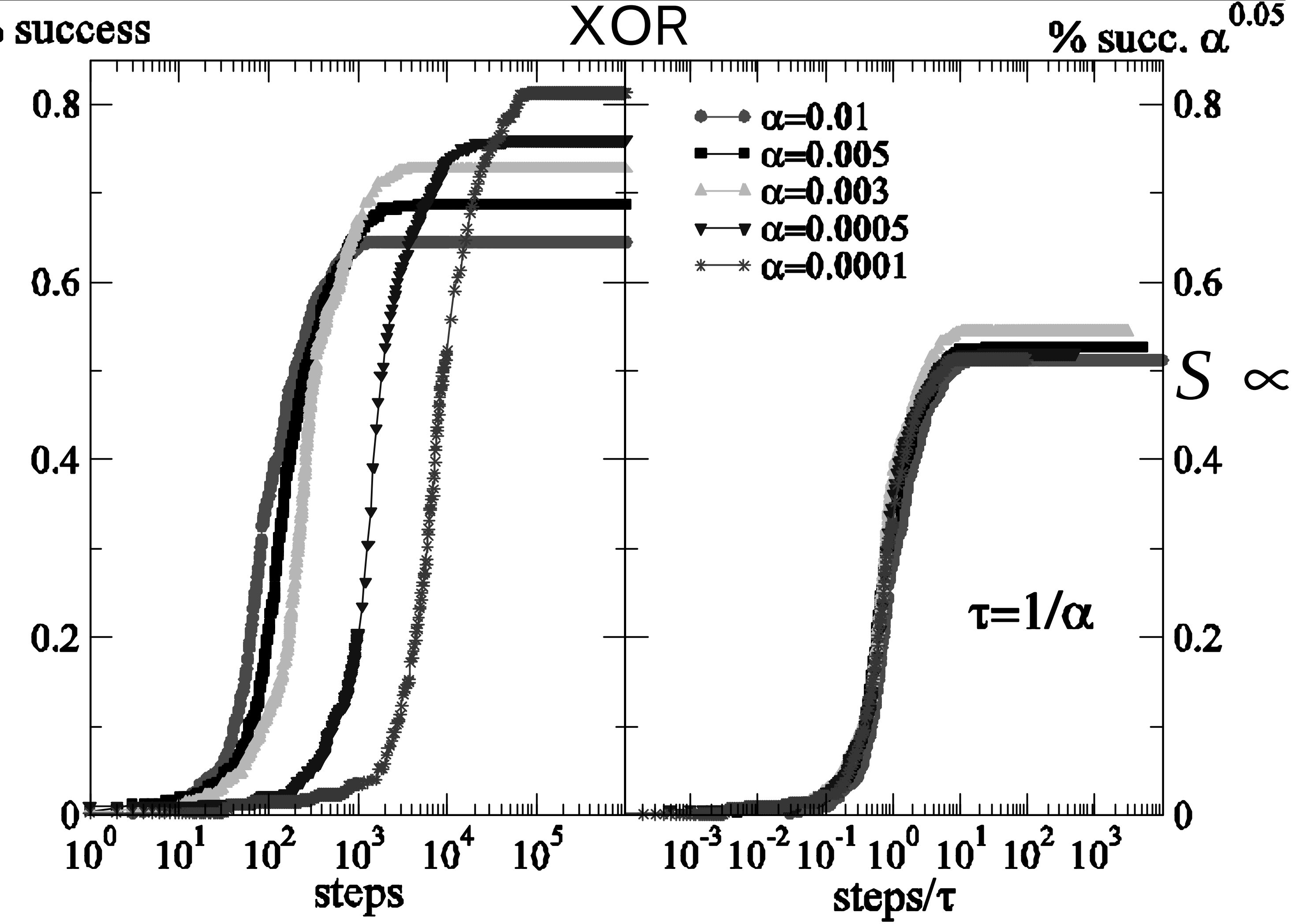
- false positive

$$\pm \frac{a}{d}$$

distance from the output neuron

Stick or carrot? → Good critic

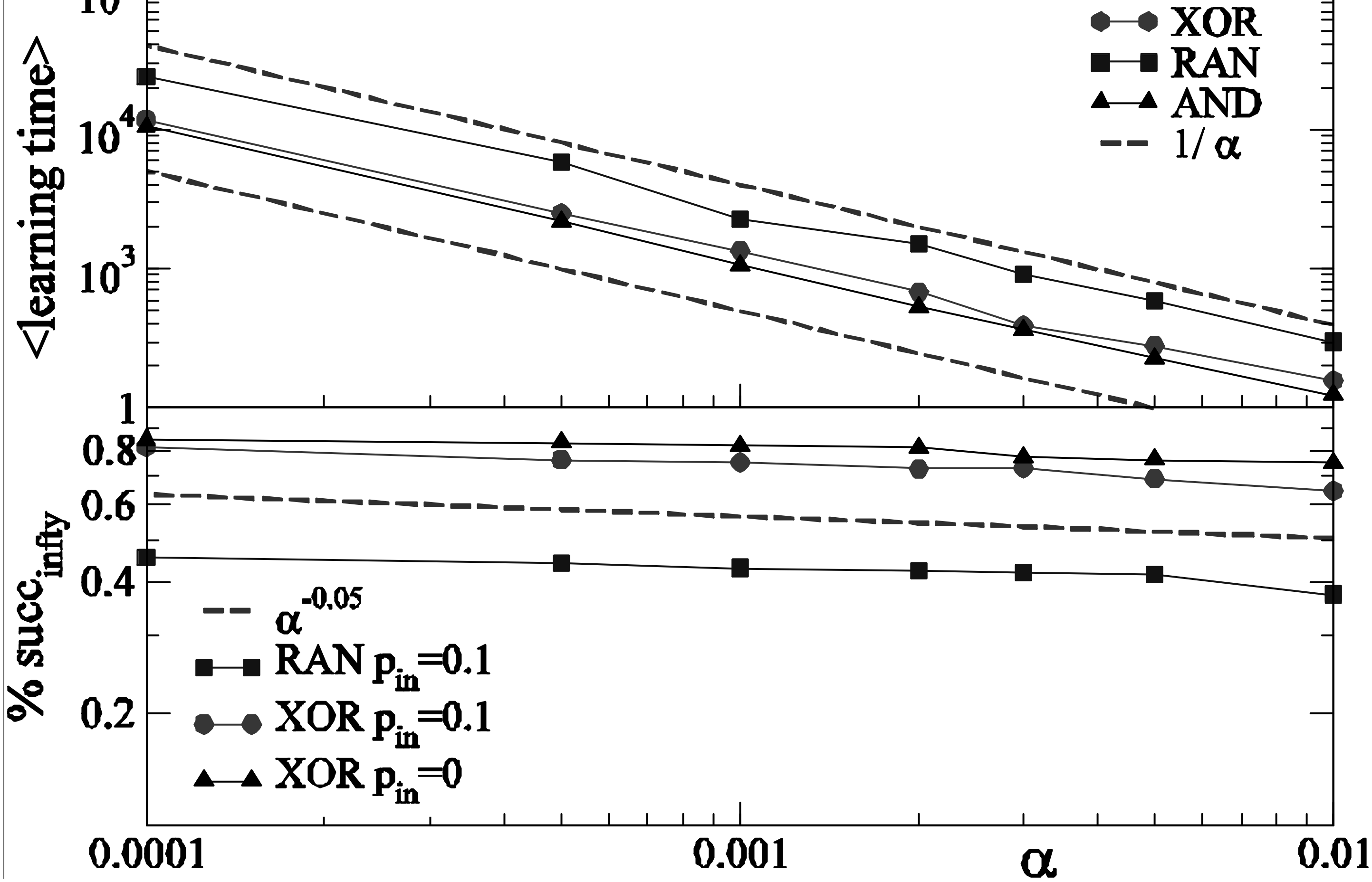
XOR



$S \propto a^{-b} f(t/t$

The percentage of success is higher for slower plastic adaptation

Lewis et al PNAS 2009

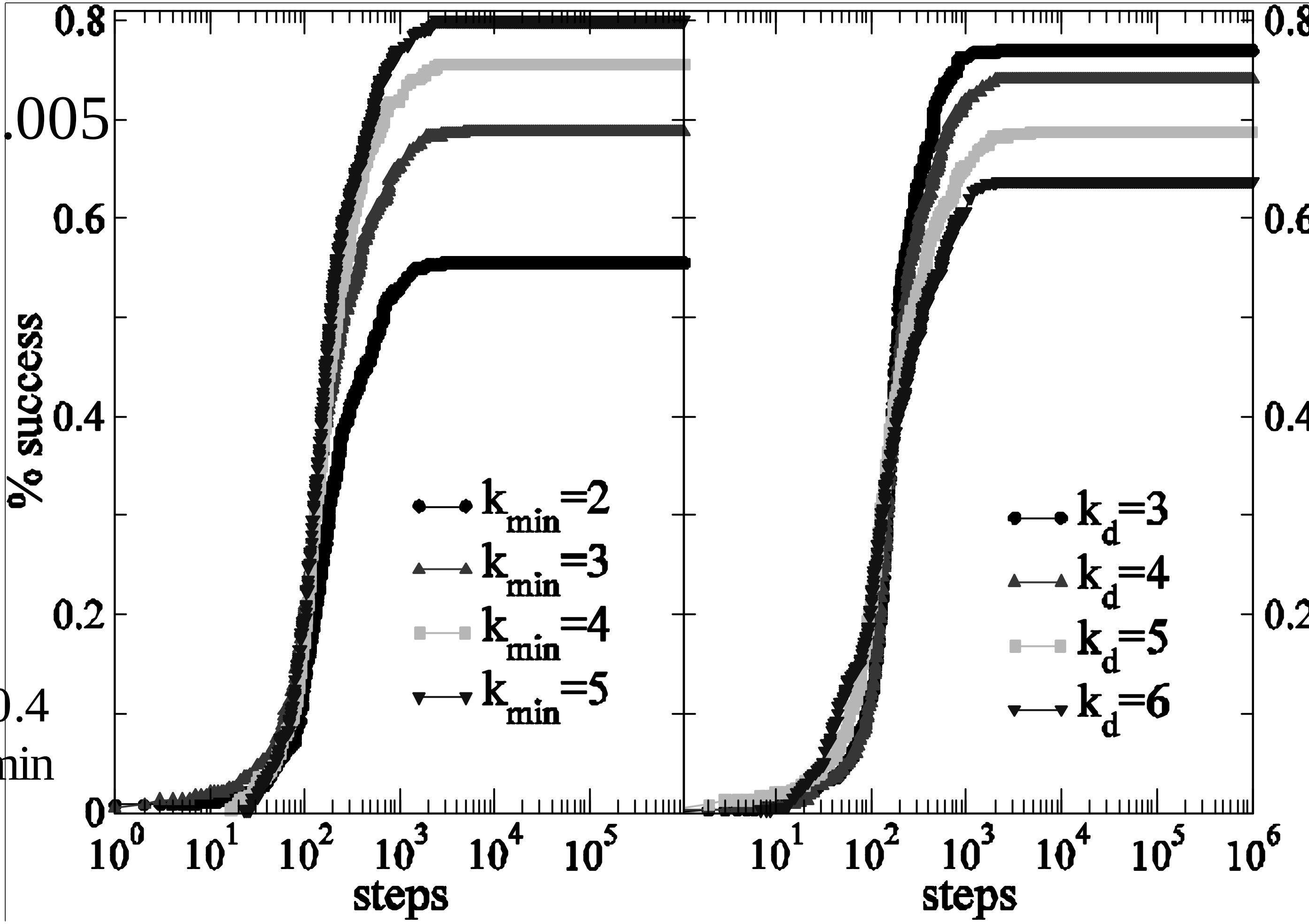


The average and median learning times scale as $t \approx 1/a$

The asymptotic percentage of success scales as $S_\infty \approx a^{-0.05}$

XOR

$a = 0.005$



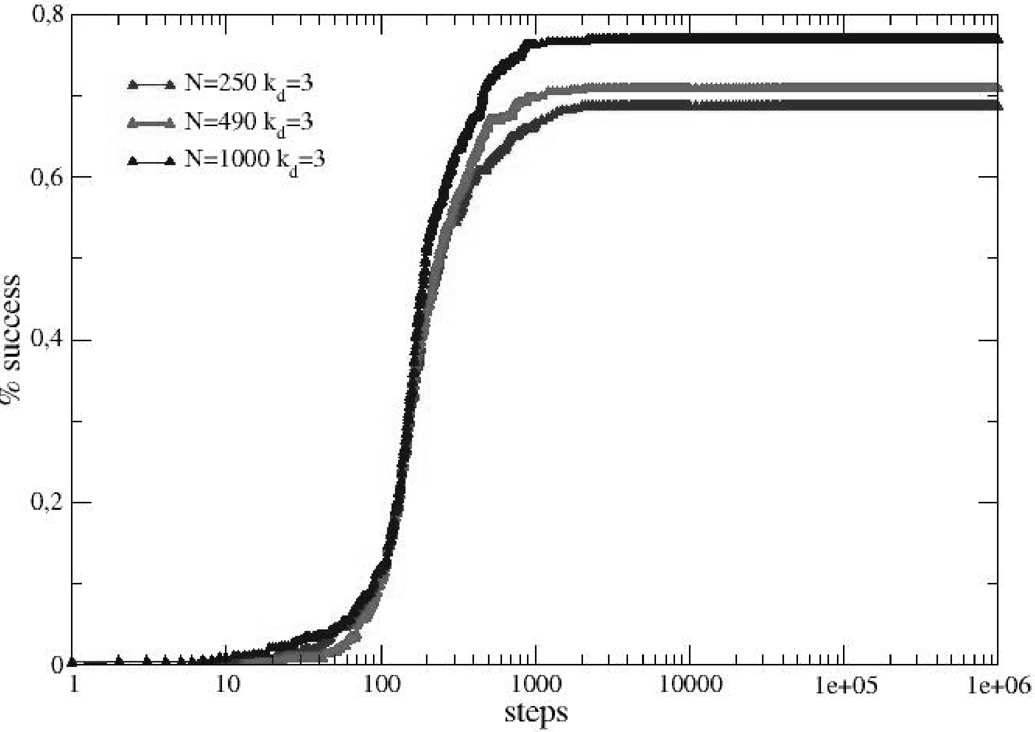
$\approx k_{\min}^{0.4}$

$\approx k_d^{-0.3}$

Learning performance increases with the level of connectivity of the system

Learning performance decreases with the input-output distance

Size Effects



Larger systems learn more efficiently

- Second chance → dependence on the initial state
- Dumb systems have less hubs than smart ones
- Memory depends on the rule and the intensity of perturbation

CONCLUSIONS

- Power law behaviour for avalanche size and duration distribution

  → experimental data for spontaneous activity

- Universal scaling behaviour of spectra as $1/f^{\beta}$ in agreement with EEG
- Learning is a truly collective process
- Better learning performances for slower plastic adaptation

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