Collective neuronal phenomena: the rise and fall of Directed Percolation in modeling neuronal avalanches

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ICTP-SAIFR - São Paulo - 2015-10

Outline:

Part I: The rise

- Neuronal avalanches in cortical slices, anesthetized or resting animals
- The critical brain hypothesis
- Directed percolation, branching processes etc
  - An example of a (theoretical) critical brain at work
- Summary of the pros

Part II: The fall

- Fingerprints of brain criticality in freely-behaving animals
- The undersampling issue
- Summary of the cons

What next then?

- Undersampling
- Long-range time correlations

Concluding remarks

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Outline:

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Acknowledgements

- Tiago L. Ribeiro (NIH, USA)
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FACEPE Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco

CNPq Conselho Nacional de Desenvolvimento Científico e Tecnológico

CAPES

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Outline:

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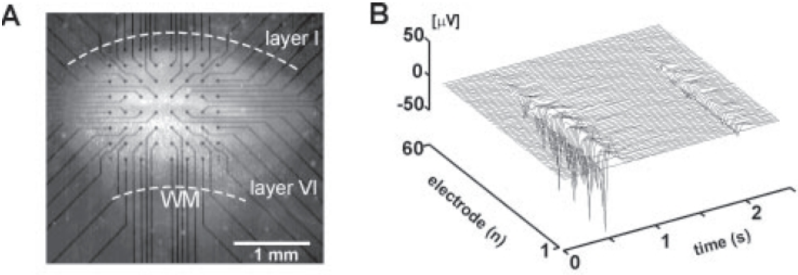
Multieletrode recording in slices of rat cortex

60 electrodes
(in vitro)

Local Field Potential (LFP)
= “average” electrical activity



Beggs and Plenz, *J. Neurosci.*, **23** 11167 (2003)

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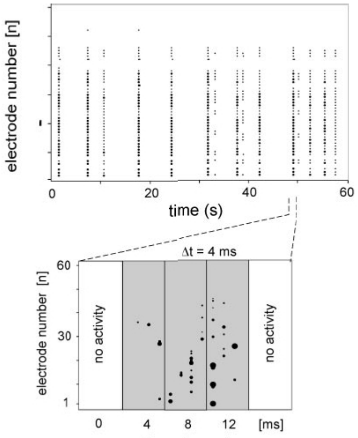

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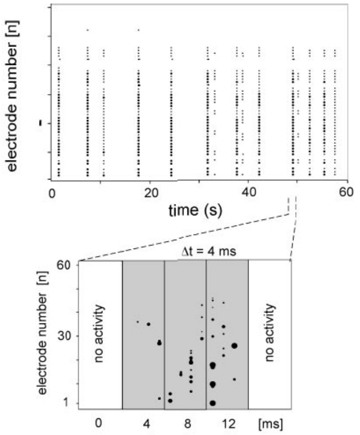

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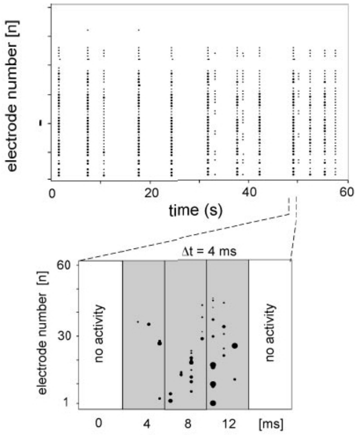

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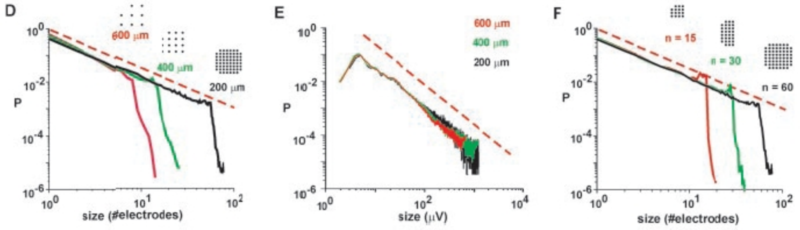
Neuronal avalanches:

Separation of Time Scales (STS)

(duration $\ll$ recurrence interval)

Multieletrode recording in slices of rat cortex

Distribution of avalanche sizes is a power law



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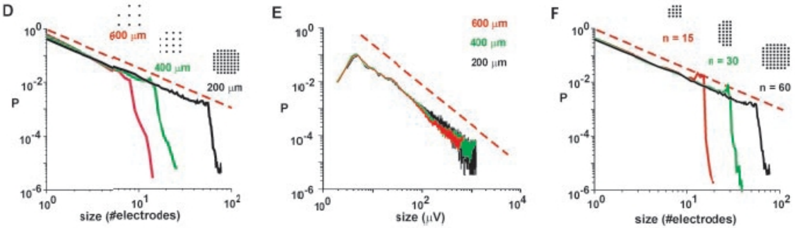

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$$P(s) \sim s^{-3/2}$$

Multieletrode recording in slices of rat cortex

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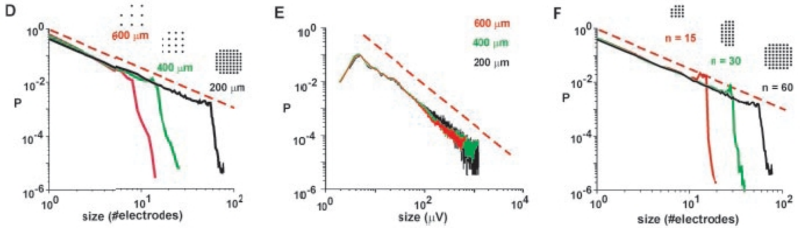

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$$\boxed{P(s) \sim s^{-3/2}}$$

fat tail $\Longrightarrow$ {
- mean size of an avalanche
- typical size of an avalanche
- "mean $\pm$ standard deviation"

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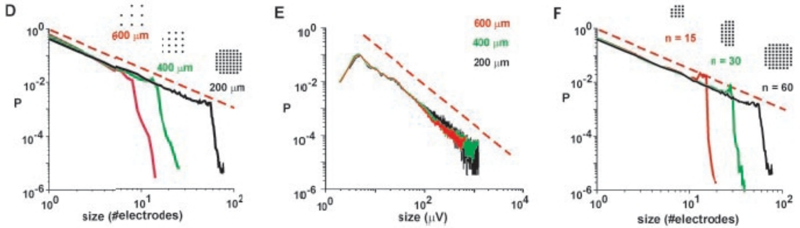

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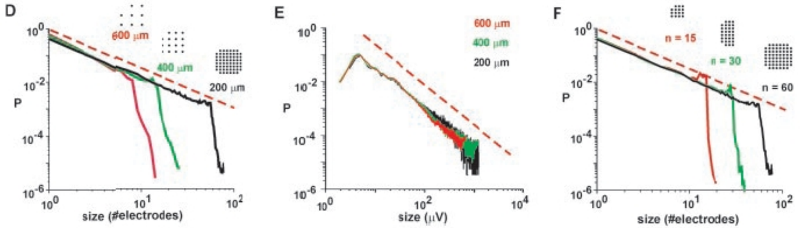

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(non-trivial) scale-invariant statistics

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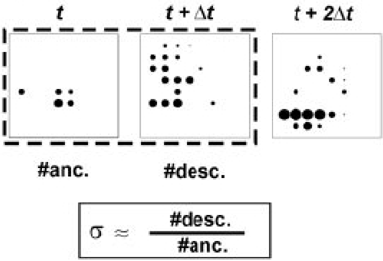
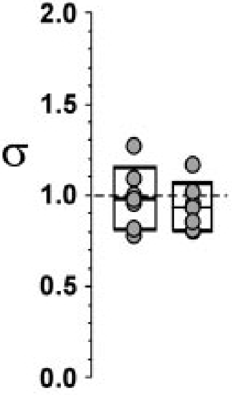
Multieletrode recording in slices of rat cortex

Branching ratio $\sigma \approx 1$





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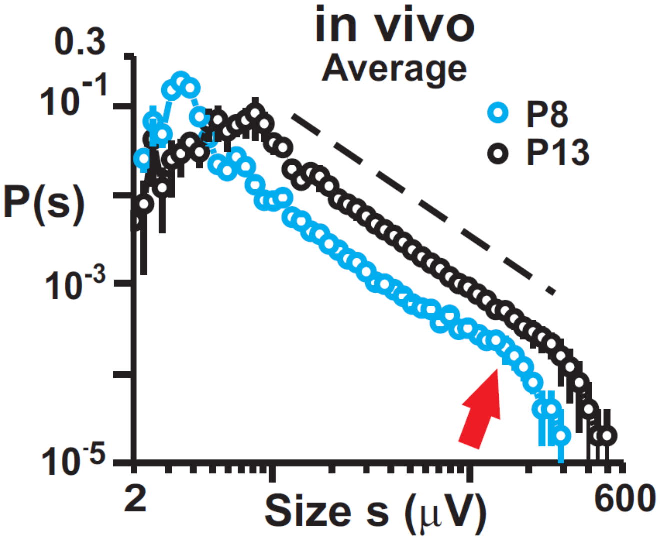
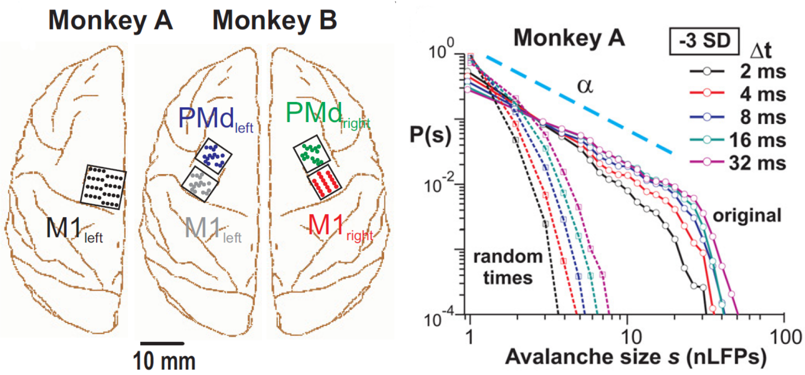
Anesthetized rats



Gireesh and Plenz, *PNAS*, **105** 7576 (2008)

Unanesthetized (but resting) monkeys



Petermann et al., *PNAS*, **106** 15921 (2009)

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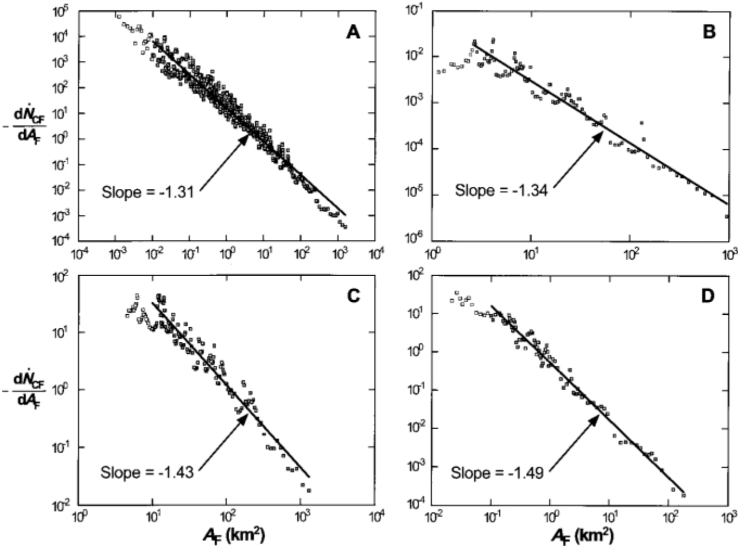
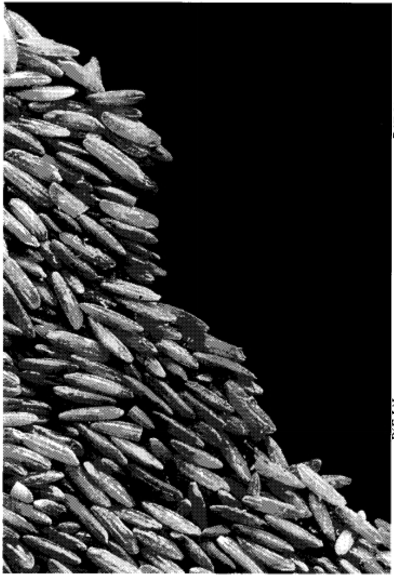
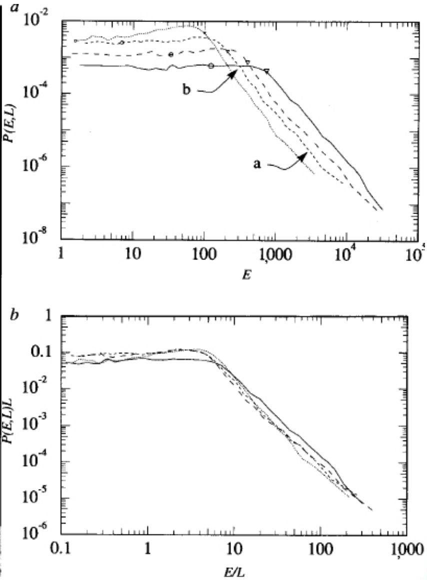
Forest fires



Malamud et al., *Science*, **281** 1840 (1998)

Rice piles





Frette el al., *Nature*, **379** 49 (1996)

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Solar flares

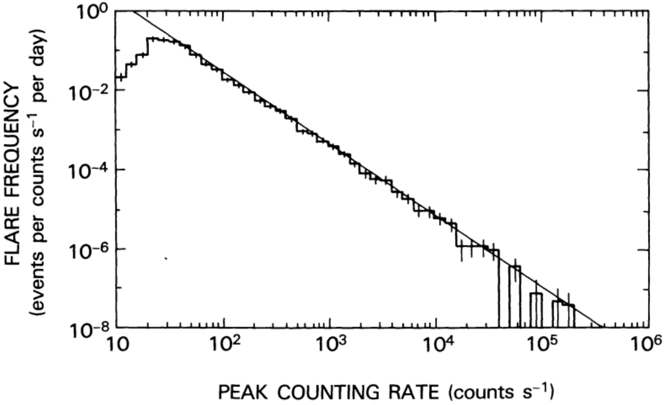

Fig. 3. Peak rate spectrum of all complete events detected with HXRBS from launch to February 1985. The straight line through the data corresponds to the power-law expression given in the text with a spectral index of -1.8.

Dennis, *Solar Phys.*, **100** 465 (1985)

Outline:

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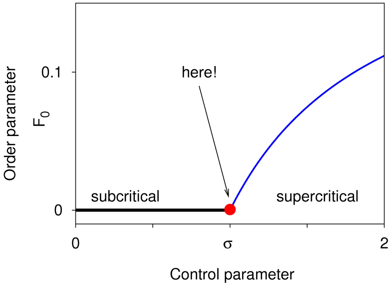
The critical brain hypothesis

The brain (as a dynamical system) operates near a critical point

Turing (50's)
Bak & Chialvo (90's)
Chialvo *Nat. Phys.* (2010)
Shew & Plenz *Neuroscientist* (2013)



Second order phase transition

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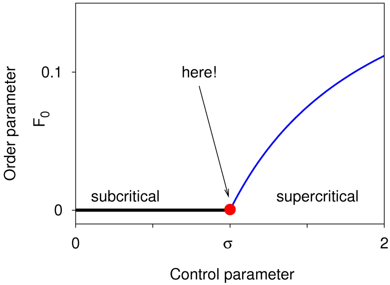

Second order phase transition

Control parameter(s)?

Order parameter(s)?

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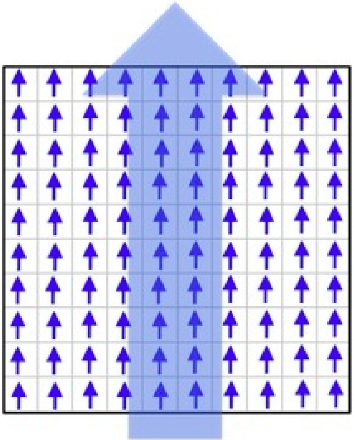
Example: ferromagnetism

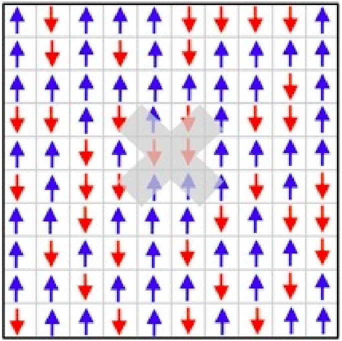
Iron atoms $\Longrightarrow$ **Magnet**

Low temperature

High temperature



magnetic



non-magnetic

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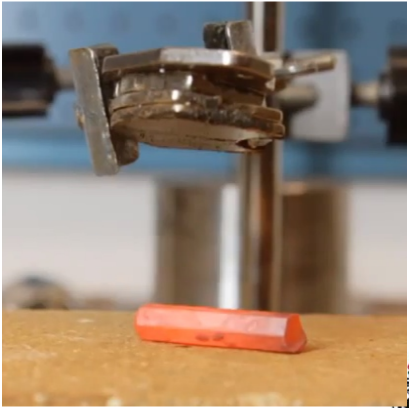

http://www.youtube.com/watch?v=haVX24hOwQI

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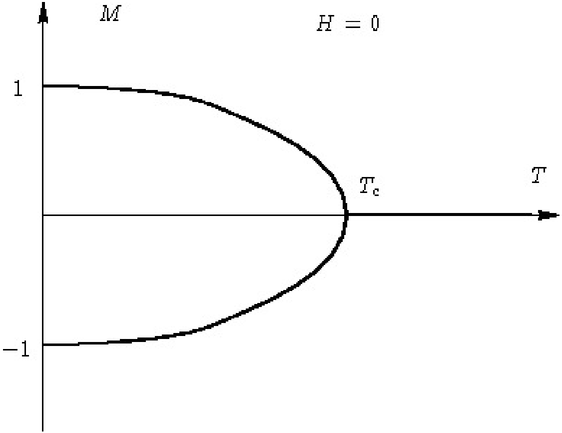

Phase transition at “critical temperature” T_c

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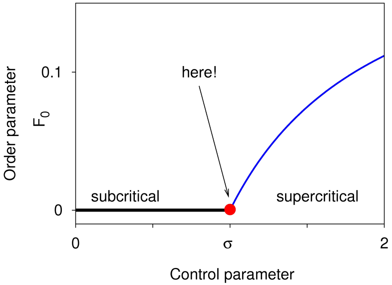


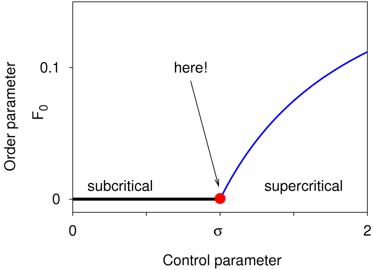
Second order phase transition

Control parameter(s)?

Order parameter(s)?

Two-slide course on phase transitions

Phase transition at a critical point (CP)



Nontrivial scale-invariant behavior near CP characterized by critical exponents:

- $F_0 \propto (\sigma - \sigma_c)^{\beta}$ (order parameter near CP)
- $F \overset{\sigma=\sigma_c}{\propto} h^{1/\delta_h}$ (response to stimulus h *at* CP)
- $C(\mathbf{x}) \propto e^{-|\mathbf{x}|/\xi}$, $\xi \propto |\sigma - \sigma_c|^{-\nu_\perp}$ (divergent correlation length)
- $P(s) \sim s^{-\tau}$ (no characteristic avalanche size)
- ...

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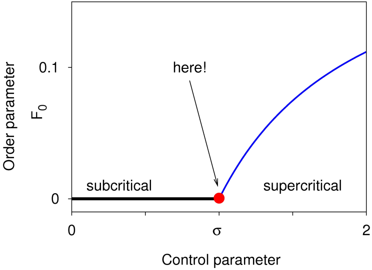
Phase transition at a critical point (CP)



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What is universality?

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Let us imagine two different models, A and B:

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Model A:

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What is universality?

Let us imagine two different models, A and B:

Model A: Model B:

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- $\dots$

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Model A:

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Model B:

- $F_0 \propto (\sigma - \sigma_c')^{\beta'}$
- $F \overset{\sigma=\sigma_c'}{\propto} h^{1/\delta_h'}$
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What is universality?

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Model A:

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- $P(s) \sim s^{-\tau}$
- …

Model B:

- $F_0 \propto (\sigma - \sigma'_c)^{\beta'}$
- $F \overset{\sigma=\sigma'_c}{\propto} h^{1/\delta'_h}$
- $\xi \propto |\sigma - \sigma'_c|^{-\nu'_\perp}$
- $P(s) \sim s^{-\tau'}$
- …

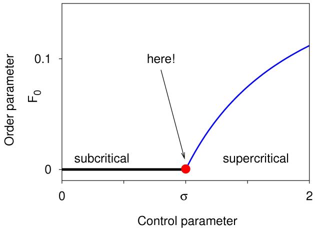
Models A and B belong to the same **universality class** if their critical exponents are the same:

$$\beta = \beta'$$
$$\delta_h = \delta'_h$$
$$\nu_\perp = \nu'_\perp$$
$$\tau = \tau'$$
$$\vdots$$

End of two-slide course on phase transitions

The critical brain hypothesis

The brain (as a dynamical system) operates near a critical point



Why would you expect the hypothesis to be true?

Theory predicts that scale-invariant dynamics provide

- optimal transmission capacity
- optimal information processing
- largest "repertoire" (e.g. for memory storage) etc.
- optimal sensitivity and dynamic range to incoming stimuli

All highly desirable for a brain! (evolutionary pressure)

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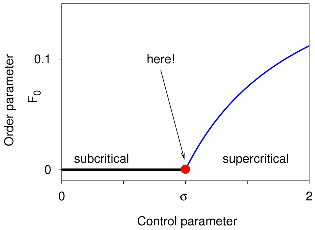

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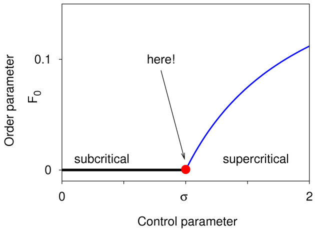

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  Bertschinger & Natschläger, Neural Comput. **16**, 1413, 2004

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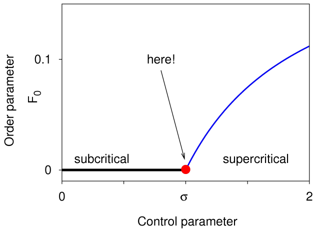

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  Haldeman & Beggs, Phys. Rev. Lett. **94**, 058101, 2005, Shew et al., J. Neurosci. **31**, 55, 2011

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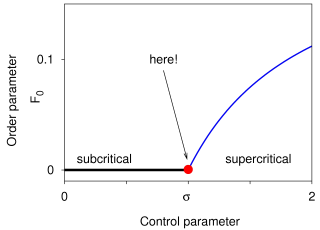

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  Kinouchi & Copelli, Nat. Phys. **2** 348, 2006, Shew et al., J. Neurosci. **29** 15595, 2009

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- **Directed percolation, branching processes etc**
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What next then?

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Concluding remarks

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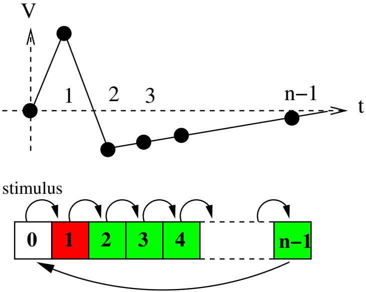
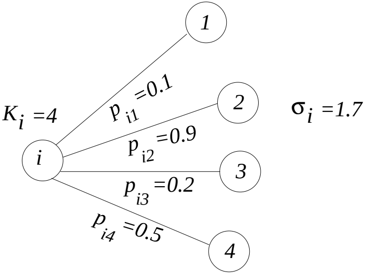
Example of criticality in a (very) simple model of the brain

Example of criticality in a (VERY VERY) SIMPLE model of the brain

A network of excitable cellular automata



Random graph: $\langle K_i \rangle = K$
(Erdős-Rényi)



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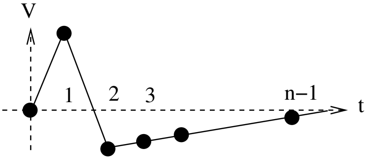

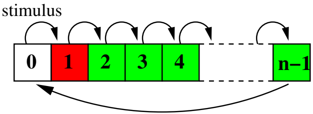

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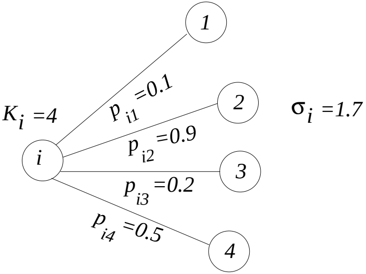

Control parameter:

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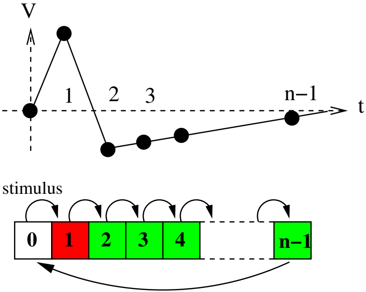

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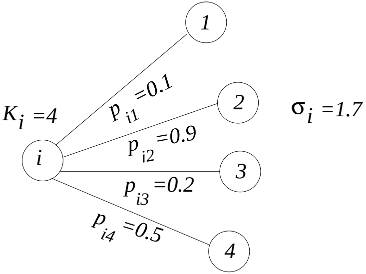

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Order parameter:

Firing rate

$\boxed{F = \langle \rho \rangle = \lim_{t \to \infty} P_t(1)}$:

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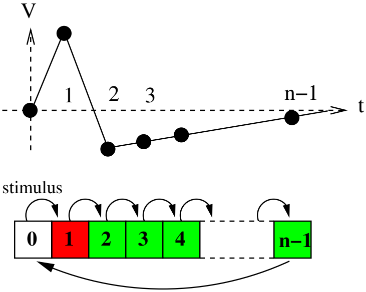

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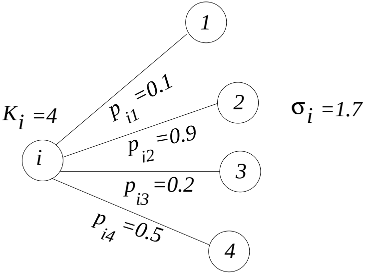

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Mean-field equation:

$$F = \overbrace{(1 - (n-1)F)}^{\text{P(quiet)}} \times \left[1 - \underbrace{(1 - \sigma F / K)^K}_{\text{P(! from neighbors)}} \times \underbrace{(1 - p_h)}_{\text{P(! external)}} \right]$$

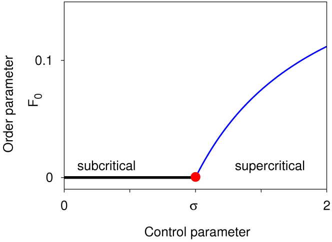
Without stimulus:

$F_0 = F(p_h = 0)$

UFPE

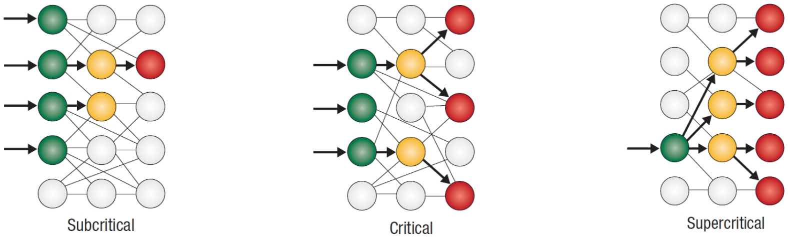
Branching process (Galton-Watson model, 1874)

Contact process (Harris, 1974), Directed percolation (DP) universality class



Connected excitable neurons:
phase transition at $\sigma = \sigma_c = 1$

$\sigma < 1$ $\sigma = \sigma_c = 1$ $\sigma > 1$



O. Kinouchi & M. Copelli, *Nat. Phys.* **2**, 348 (2006); D. Chialvo, *Nat. Phys.* **2**, 301 (2006)

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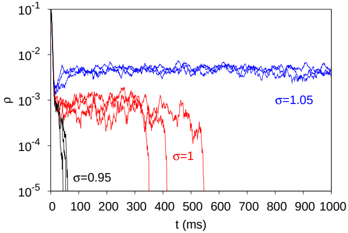
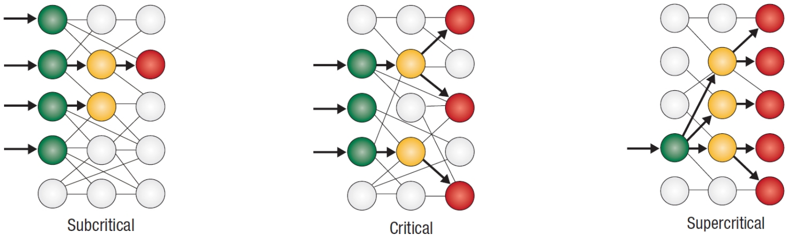


Control parameter: σ =branching ratio
Order parameter: $F = \langle \rho \rangle \sim$ firing rate

DP phase transition: between absorbing and active (but otherwise unstructured) phases

$\sigma < 1$ $\qquad$ $\sigma = \sigma_c = 1$ $\qquad$ $\sigma > 1$



O. Kinouchi & M. Copelli, *Nat. Phys.* **2**, 348 (2006); D. Chialvo, *Nat. Phys.* **2**, 301 (2006)

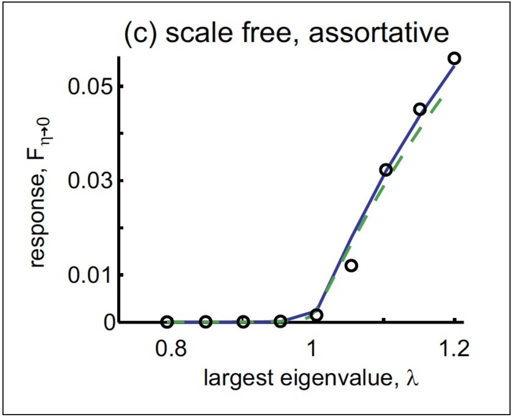
UFPE

More rigorous criterion for criticality:

E.g. Scale-free networks etc.

$$\boxed{\lambda = \text{largest eigenvalue of } \{p_{ij}\} = 1 \text{ at criticality}}$$

($\sigma_c = 1 = \lambda$ for uncorrelated random graphs!)



Larremore et al., *Phys. Rev. Lett.* **106** 058101 (2011)

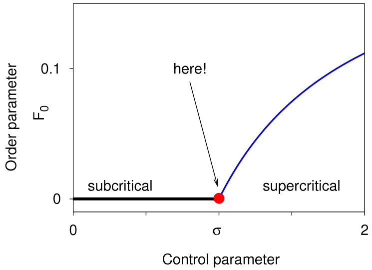
Larremore et al., *Phys. Rev. E* **85** 066131 (2012)

Theory vs. Experiments

(STS = Separation of Time Scales)

Theoretical prediction:

System at critical point +
STS *by hand*=



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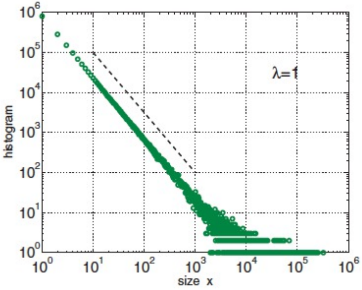

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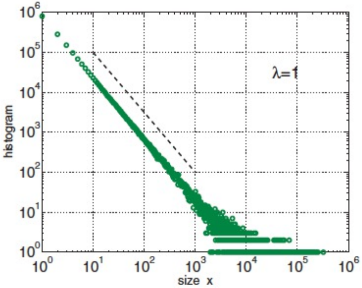

Larremore et al. (2012)

Experimental results:

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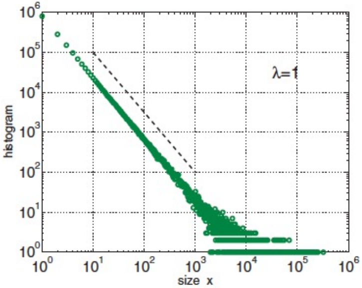

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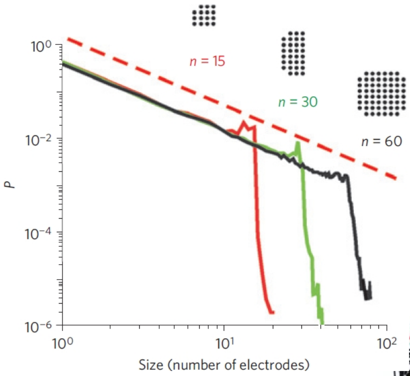
STS *emerges!*



Beggs & Plenz (2003)

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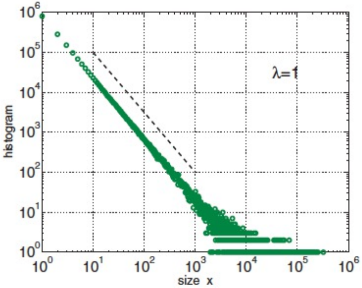

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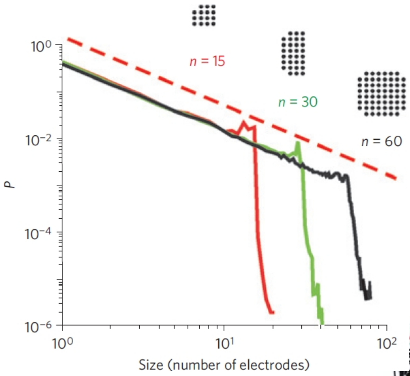

Beggs & Plenz (2003)

Neuronal avalanches are compatible with critical dynamics

UFPE

Critical exponents interdependent via scaling theory

Directed percolation (DP) universality class for $d = 4$: upper critical dimension

Exponent	$d=1$	$d=2$	$d=3$	$d=4$
$\beta=\beta'$	0.27649(4)[a]	0.583(4)[b]	0.805(10)[c]	1
$1/\delta_h$	0.111(3)[d]	0.285(35)[d]	0.45(2)[e]	1/2
γ'	0.54386(7)[a]	0.35	0.19	0
$\nu_{\parallel}$	1.73383(3)[a]	1.295(6)[f]	1.105(5)[c]	1
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$\nu_{\parallel}/\nu_{\perp}$	1.58074(4)	1.766(2)	1.901(5)	2
τ	1.108	1.268	1.395	3/2
σ	0.391	0.459	0.490	1/2
γ	2.277	1.593	1.232	1
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τ_t	1.159	1.450	1.730	2
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Muñoz et al, *Phys. Rev. E*, **59** 6175 (1999)

UFPE

Outline:

Part I: The rise

- Neuronal avalanches in cortical slices, anesthetized or resting animals
- The critical brain hypothesis
- Directed percolation, branching processes etc
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- Summary of the pros

Part II: The fall

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What next then?

- Undersampling
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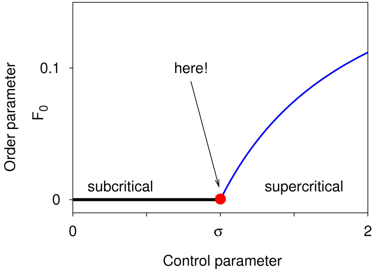
Concluding remarks

UFPE

Phase transition at a critical point (CP)



Nontrivial behavior near CP characterized by critical exponents:

- $F_0 \propto (\sigma - \sigma_c)^{\beta}$ (order parameter near CP)
- $F \overset{\sigma=\sigma_c}{\propto} h^{1/\delta_h}$ (response to stimulus h *at* CP)
- $C(t) \propto e^{-t/\tau}$, $\tau \propto |\sigma - \sigma_c|^{-\nu_\parallel}$ (divergent correlation time)
- $C(\mathbf{x}) \propto e^{-|\mathbf{x}|/\xi}$, $\xi \propto |\sigma - \sigma_c|^{-\nu_\perp}$ (divergent correlation length)
- …

UFPE

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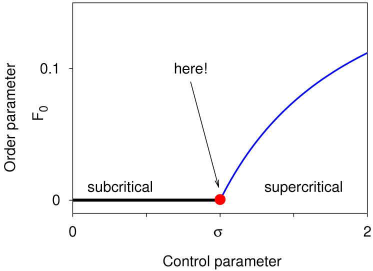

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- ...

UFPE

Psychophysics

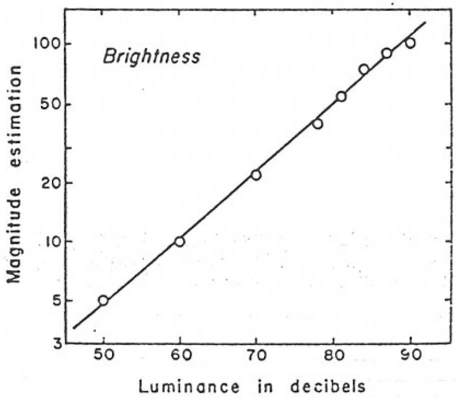
Psychophysics

Founded in 1860: first experimental area of neuropsychology

- What is the human perception of the intensity of a sensory stimulus?

Psychophysics: Nonlinear Response!

Stevens law: perception $\propto$ (stimulus intensity)^m



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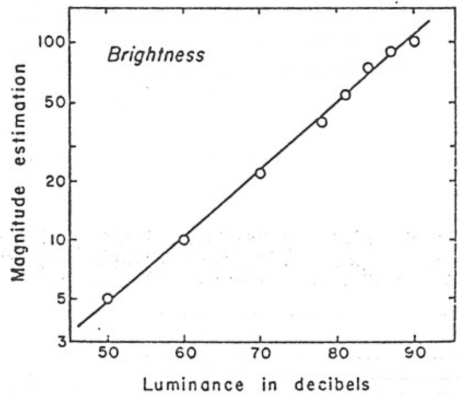
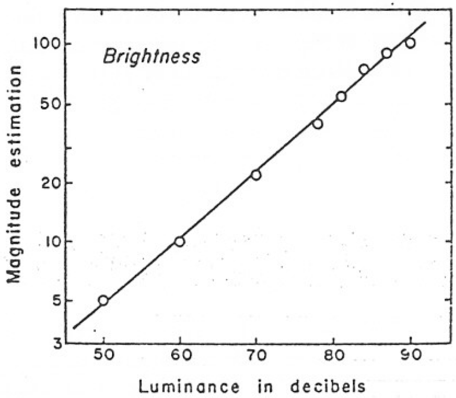


$\boxed{m < 1}$

Stevens law: perception $\propto$ (stimulus intensity)^m

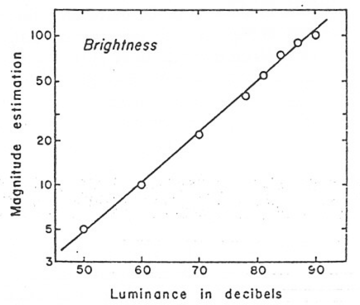


$\boxed{m < 1}$

HOW?

Stevens law: perception $\propto$ (stimulus intensity)^m

Psychophysics



Continuum	Measured Exponent	Stimulus condition
Brightness	0.5	Point source
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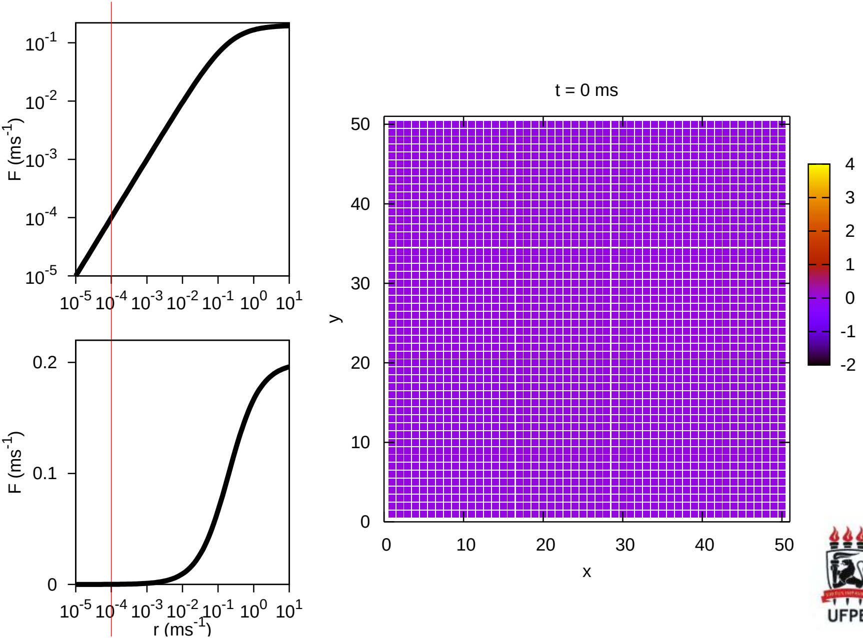
S. S. Stevens, “Psychophysics: Introduction to its Perceptual, Neural and Social Prospects” (1975)

Response to weak stimulus (no coupling, $\sigma = 0$)



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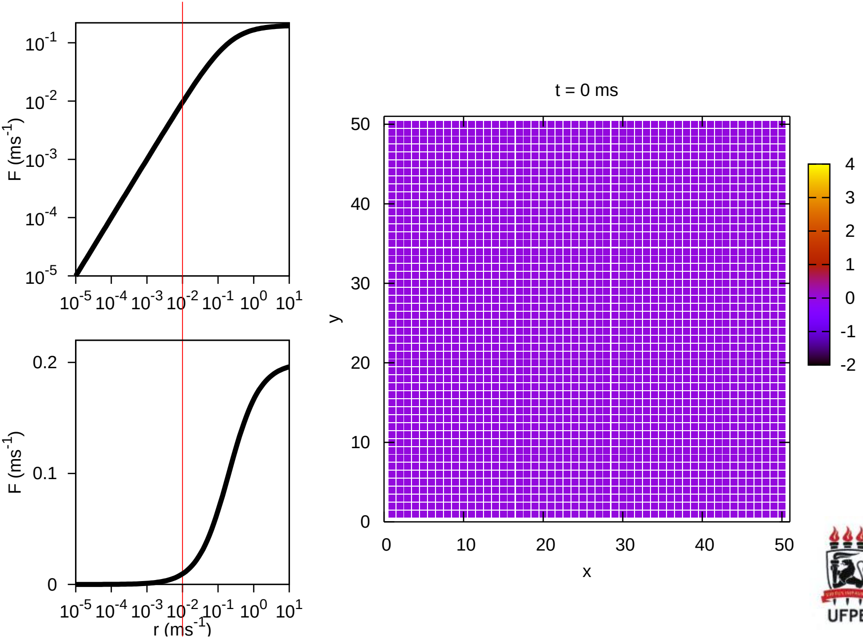
Response to stronger stimulus (no coupling, $\sigma = 0$)



UFPE

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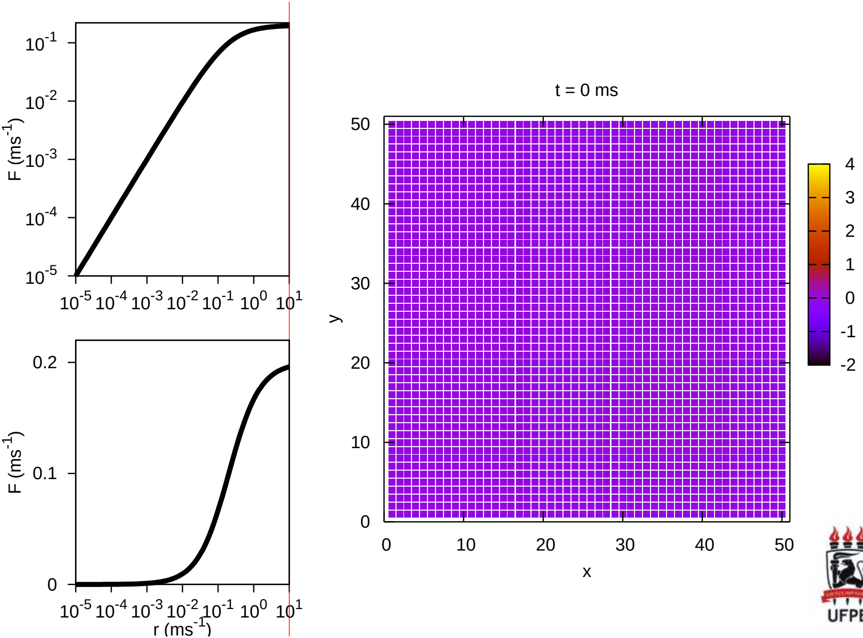
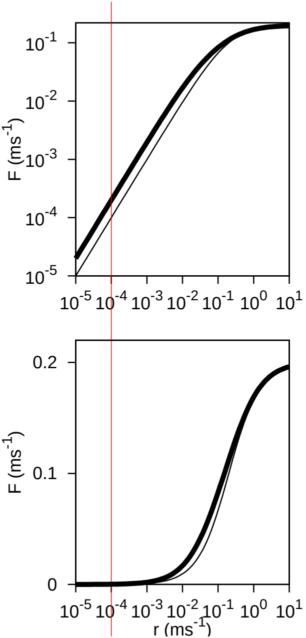
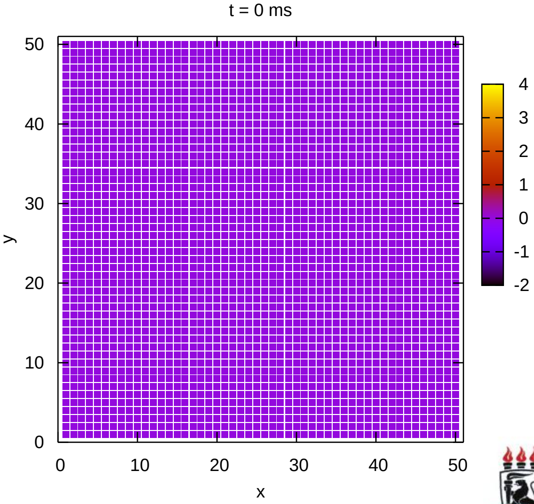
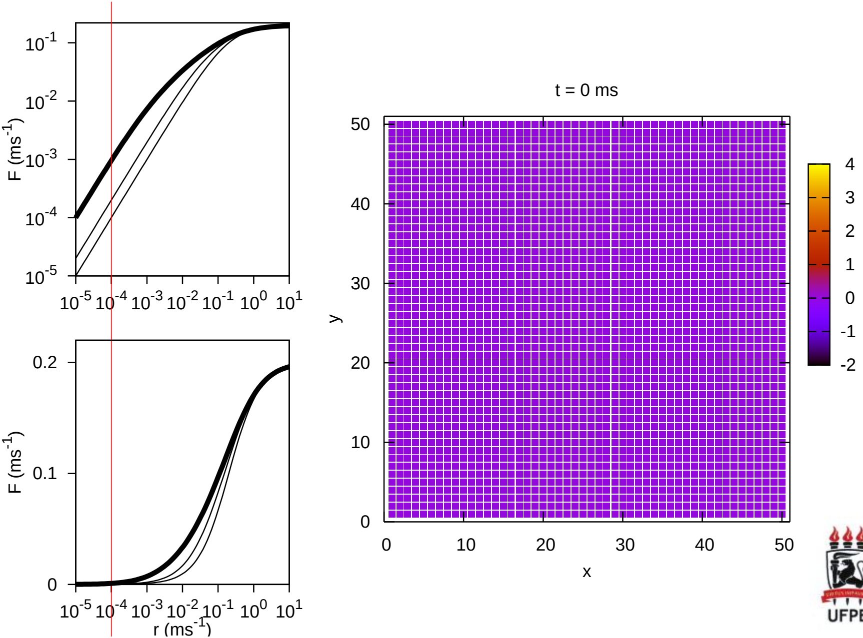


Response to stimulus (weak coupling, $\sigma \gtrsim 0$)

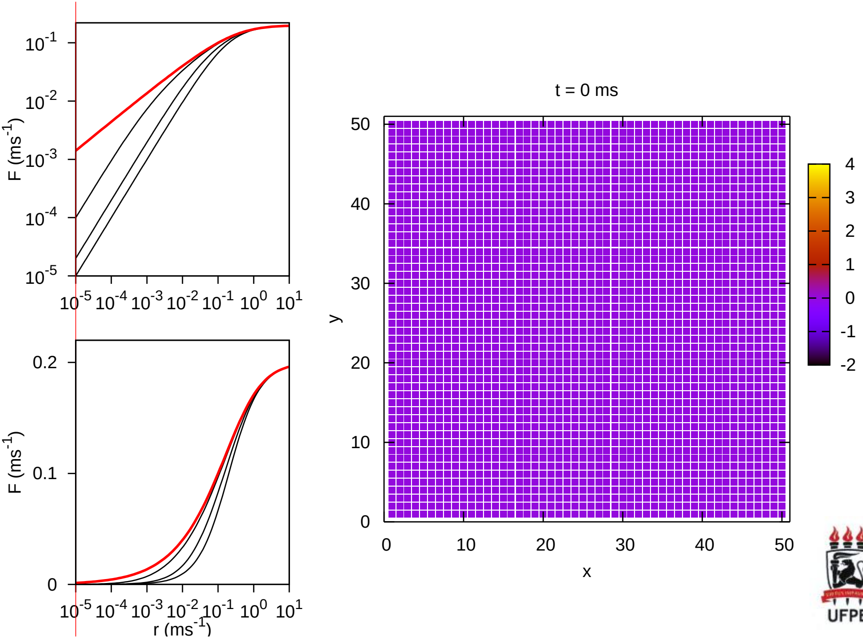




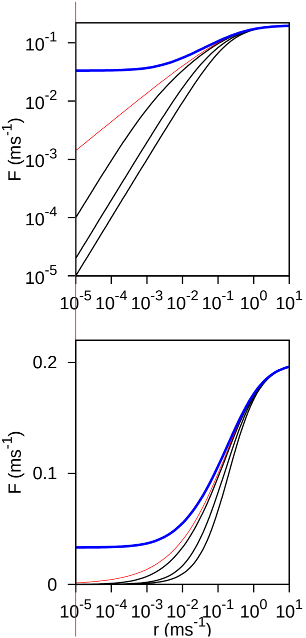
Response to stimulus (stronger coupling, $\sigma \lesssim 1$)

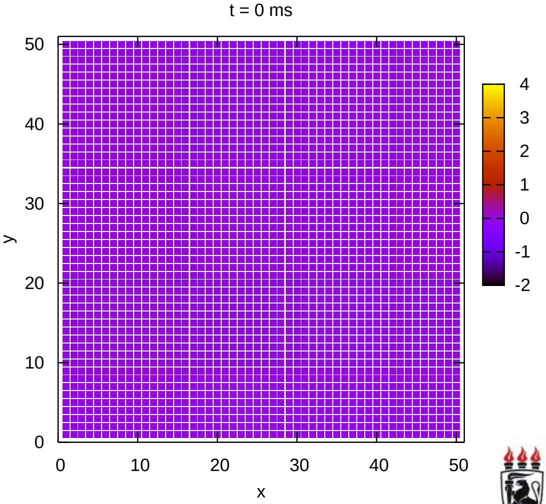


Response to stimulus (critical coupling, $\sigma \simeq 1$)



Response to stimulus (supercritical coupling, $\sigma > 1$)



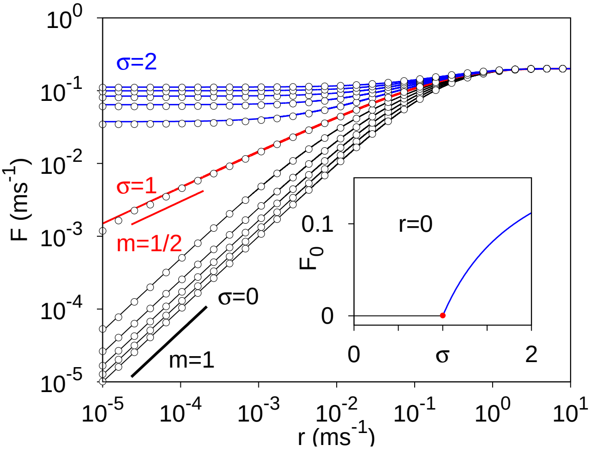


Family of response curves

Random graphs:

critical exponent $m = 1/\delta_h \leq 1/2$ agrees with:

- psychophysical exponents (Stevens law)
- olfactory glomerulus responses to odorants



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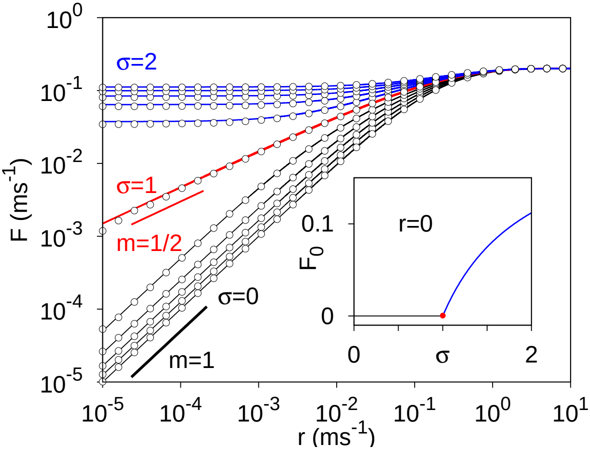

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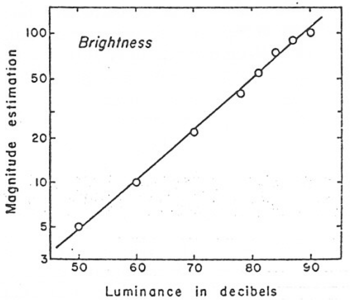

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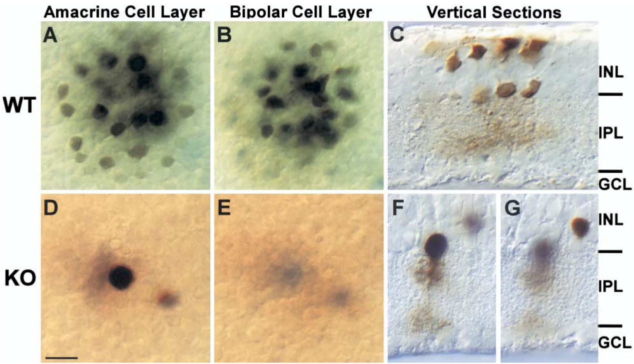
UFPE

Supported by experimental data

Gap Junctions in the mouse retina



Deans et al., *Neuron*, **36** 703 (2002)

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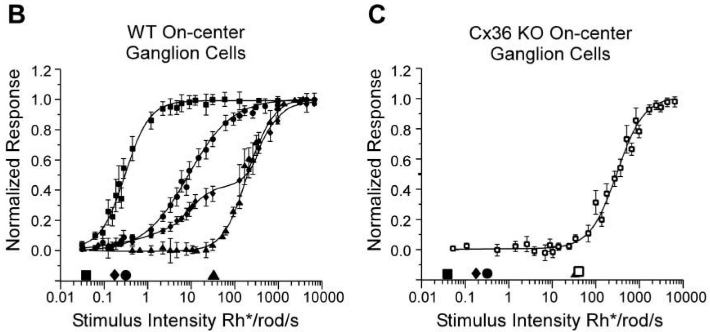
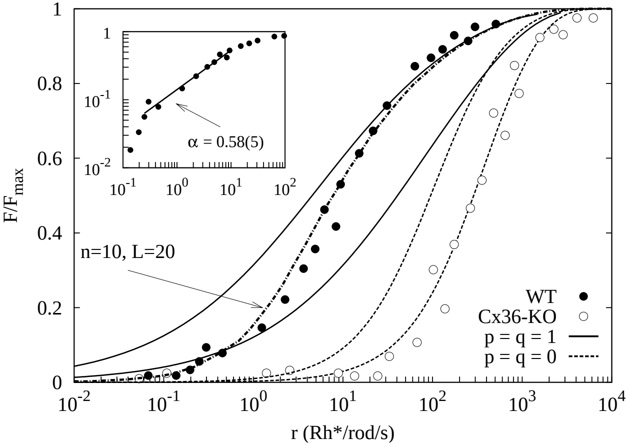


Deans et al., *Neuron*, **36** 703 (2002)

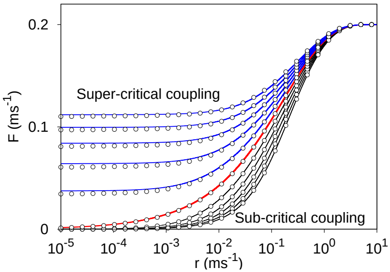
Ganglion cell response has exponent $m \simeq 0.58$!



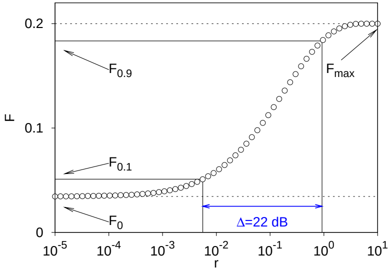
L. S. Furtado & M. Copelli, *Phys. Rev. E*, **73** 011907 (2006)

Family of response curves

Firing rate vs stimulus



Dynamic range definition:

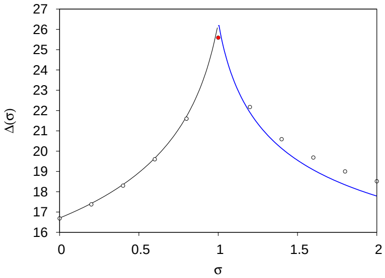


UFPE

Dynamic range is optimal at criticality

General property of excitable media

Theory



Kinouchi & Copelli
Nat. Phys. **2** 348 (2006)

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General property of excitable media

Supported by very different models:

- Probabilistic excitable models
  - random graphs: Kinouchi & MC (*Nat. Phys.* 06)
  - hypercubic lattices: Furtado & MC (*PRE* 06), Assis & MC (*PRE* 08)
  - scale-free networks: MC & Campos (*EPJB* 07), Wu et al. (*PRE* 07), Larremore et al. (*PRL* 11)
- Deterministic excitable models
  - cellular automata: MC et al (*PRE* 02), MC & Kinouchi (*Phys. A* 05), MC et al (*Neurocomput.* 05)
  - Morris-Lecar lattices: Ribeiro & MC (*PRE* 08)
- Detailed conductance-based retina model: Publio et al (*PLoS ONE* 10)
- Active dendritic trees: Gollo et al (*PLoS CB* 09, *PRE* 12)
- Disinhibition transition in the antennal lobe: Buckley & Nowotny (*PRL* 11)

UFPE

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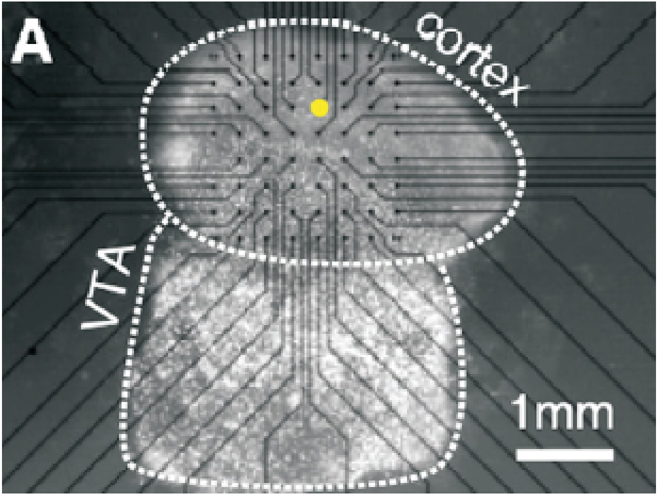
Is it true experimentally?

UFPE

Stimulated slices



Shew et al., *J. Neurosci.* **29** 15595 (2009)

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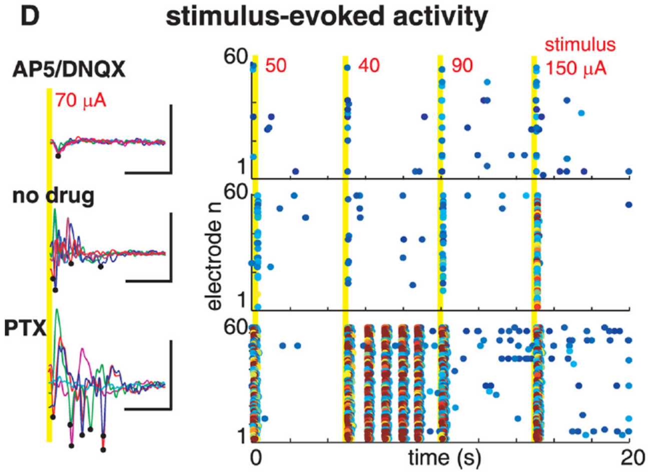

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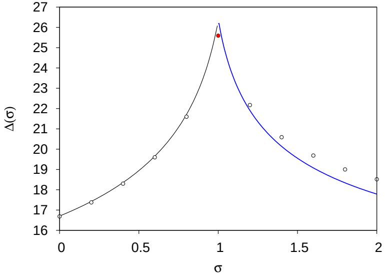

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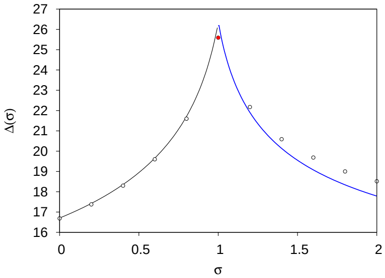
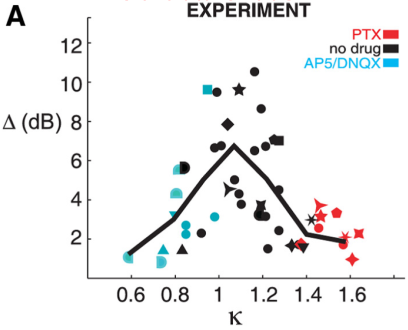


Kinouchi & Copelli
Nat. Phys. **2** 348 (2006)

Cortical slices



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Concluding remarks

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Are critical branching processes satisfactory models of neuronal avalanches?

Branching-process-like models (absorbing vs active phases):

- Pros:
  - Neuronal avalanche exponents ($\tau = 3/2$ and $\tau_t = 2$)
  - Response exponents ($1/\delta_h = 1/2$: psychophysics, sensory systems, ...) + optimal dynamic range at criticality
  - Theoretical workhorse (useful picture) for over a decade

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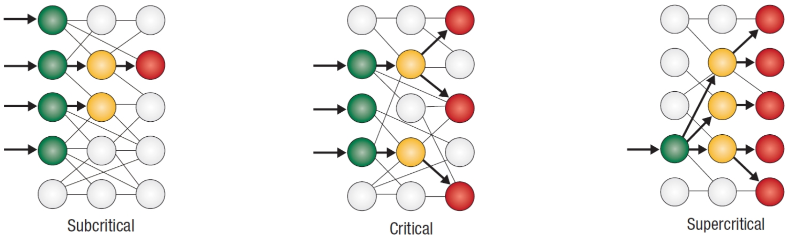
$\sigma < 1$ $\sigma = \sigma_c = 1$ $\sigma > 1$



Outline:

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Outline:

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Acknowledgements

- **Tiago L. Ribeiro** (NIH, USA)
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- CNPq & CAPES

FACEPE Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco

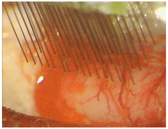
CNPq Conselho Nacional de Desenvolvimento Científico e Tecnológico

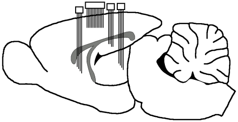
CAPES

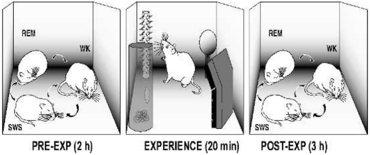
UFPE

Non-anesthetized and freely-behaving rats

In collaboration with Brain Institute UFRN (Natal)







Ribeiro et. al, *Frontiers Neurosci.* **1** 43 (2007)

Main differences:

- Freely-behaving (FB) rats, across the sleep-wake cycle (WK, SWS, REM)
- 3 brain regions (V1, S1 and HP)
- Exposure to novel objects (PRE, EXP, POST)
- Spikes (not LFPs)
- Anesthesia (AN) as well

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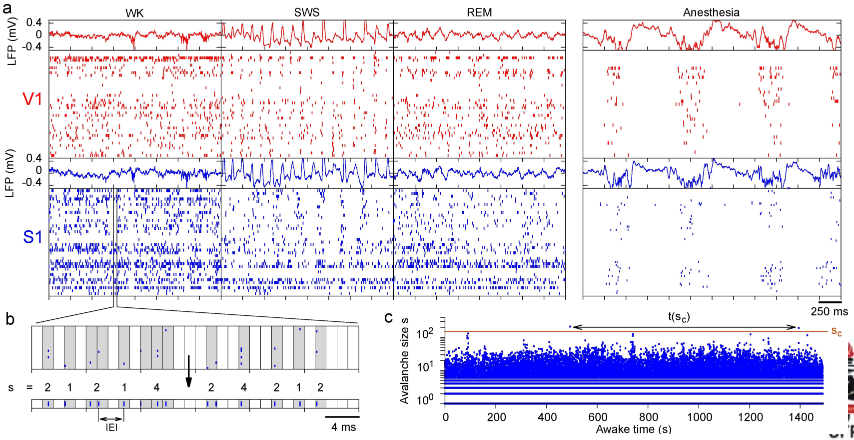
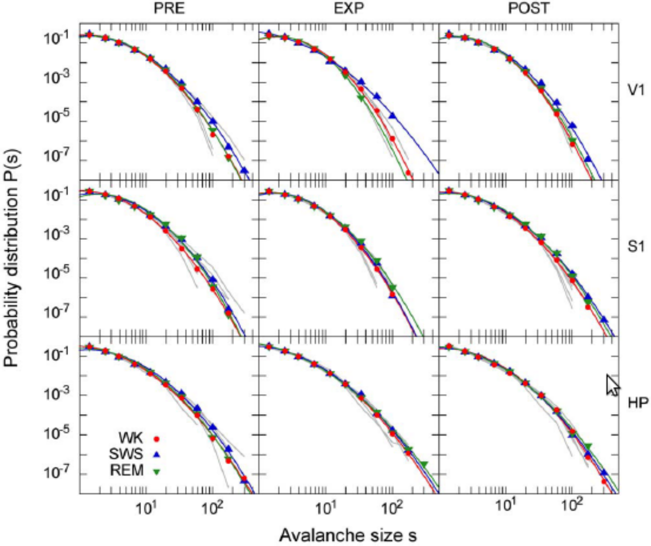
Spike avalanches in freely-behaving (FB) rats

- Separation of time scales in AN, but not in FB (avalanches?)
- time bin = $\langle \mathrm{ISI} \rangle$ (calculated for each situation)

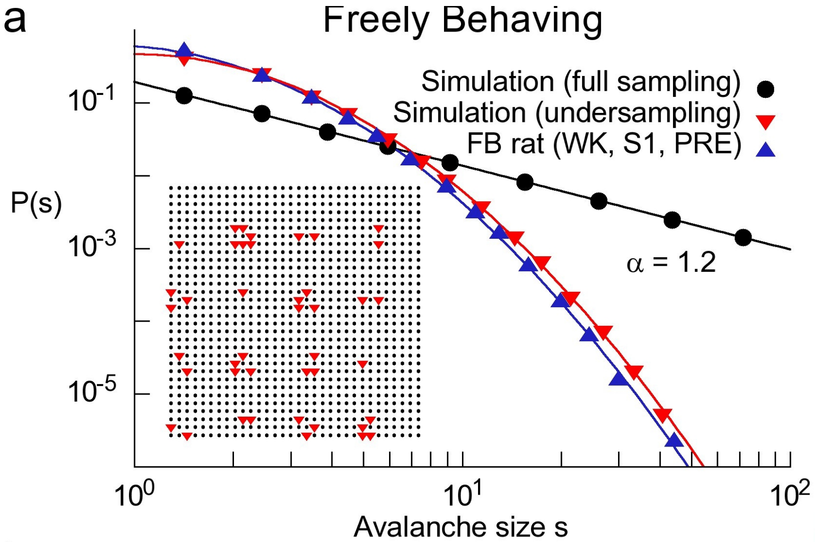


Size distribution of spike avalanches

Not power laws. Well fit by lognormals.
Very similar across the sleep-wake cycle and brain regions!



Critical model + undersampling = Lognormal-like size distributions

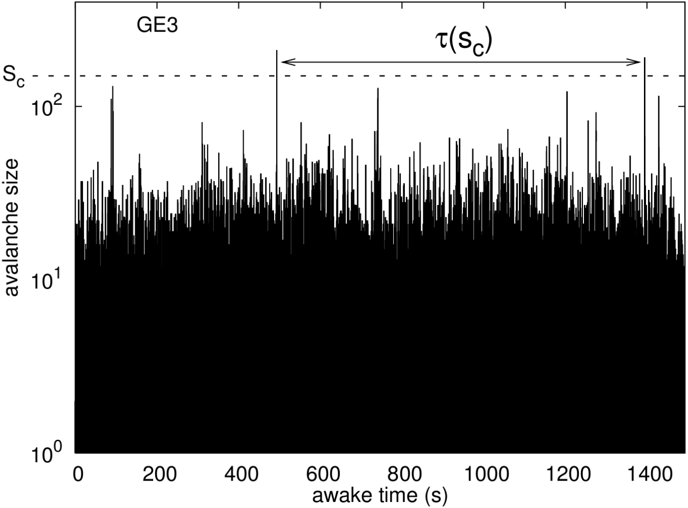


Ribeiro et al., PLoS One **5** e14129 (2010)

Avalanche size time series

Can we obtain fingerprints of criticality from the FB time series?

1) Fourier spectrum & DFA



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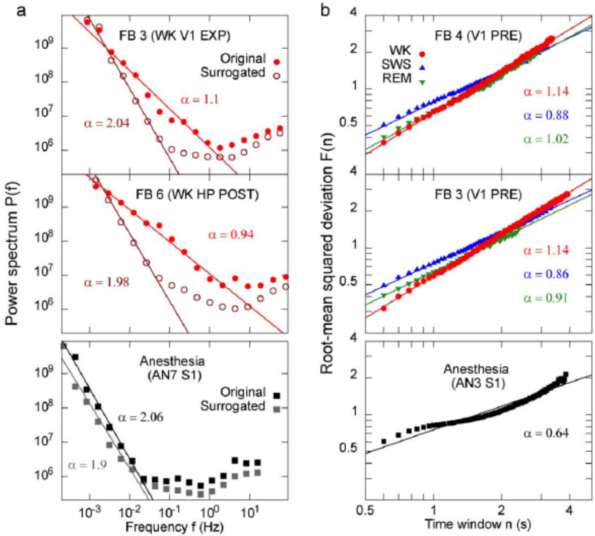
Long-range time correlations

$C(t) \sim t^{-\gamma} \Longrightarrow \gamma = 2 - 2\alpha$ and $S(f) \sim f^{-\beta} \Longrightarrow \beta = 1 - \gamma = 2\alpha - 1$

$1/f$ spectra — Detrended Fluctuation Analysis



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DFA = Detrended Fluctuation Analysis

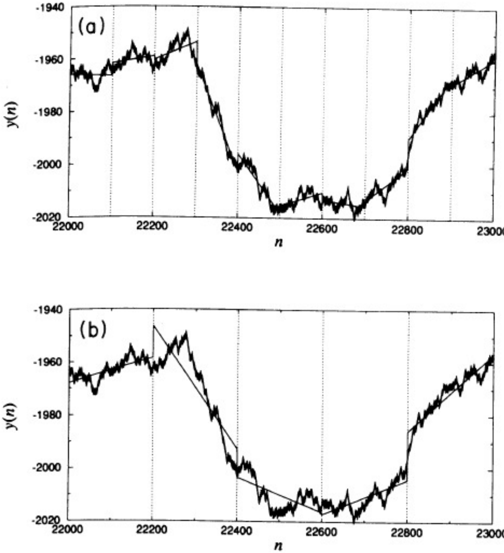
$$\boxed{F(n) = \sqrt{\frac{1}{N}\sum_{k=1}^{N}\left[y(k) - y_n(k)\right]}}$$

If $F(n) \sim n^{\alpha}$, then

$$\boxed{C(\tau) \sim \tau^{-\gamma}, \text{ with } \gamma = 2 - 2\alpha}$$

$$\boxed{S(f) \sim f^{\beta}, \text{ with } \beta = 1 - \gamma = 2\alpha - 1}$$

- $0 < \alpha < 0.5 \Rightarrow$ anticorrelations
- $\alpha = 0.5 \Rightarrow$ white noise
- $0.5 < \alpha < 1 \Rightarrow$ persistent long-range power-law correlations
- $\alpha = 1 \Rightarrow 1/f$ noise



Peng et al., *Phys. Rev. E* **49** 1685 (1994)

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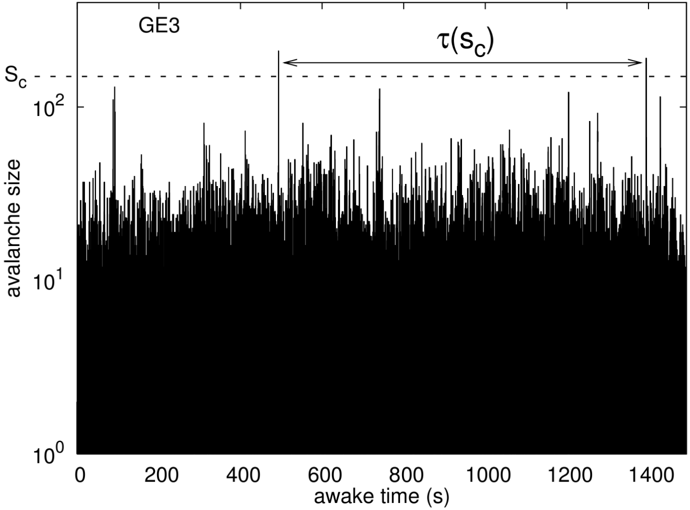
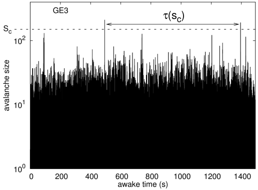
Can we obtain fingerprints of criticality from the FB time series?

2) Waiting-time distribution



Scaling in the distribution of waiting times

Waiting-time distribution



$D(\tau; s_c)$

Scaling in the distribution of waiting times

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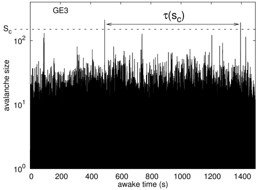

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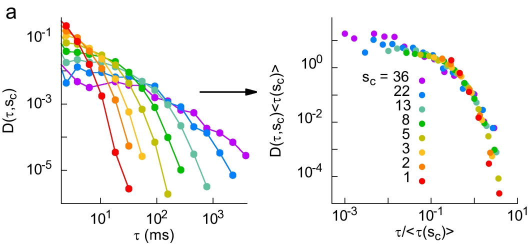

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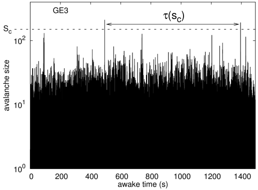
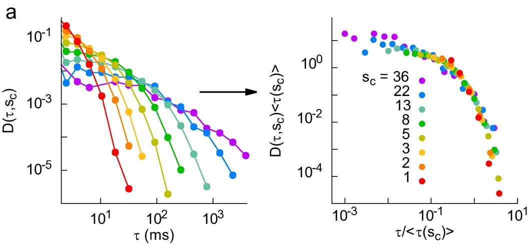


$D(\tau; s_c) =$
$\langle \tau(s_c) \rangle^{-1} F(\tau / \langle \tau(s_c) \rangle)$



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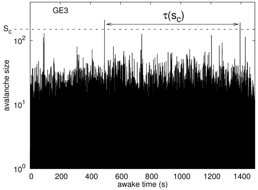

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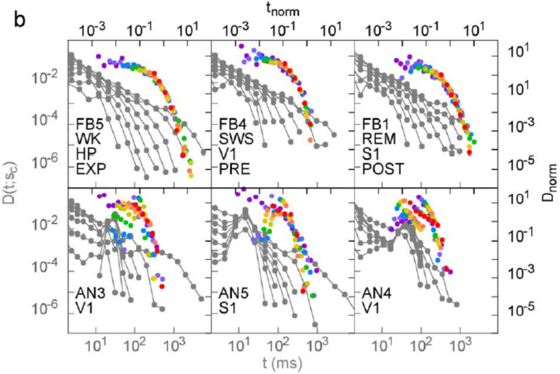

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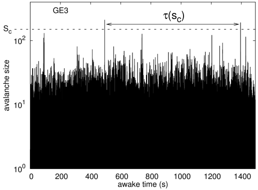
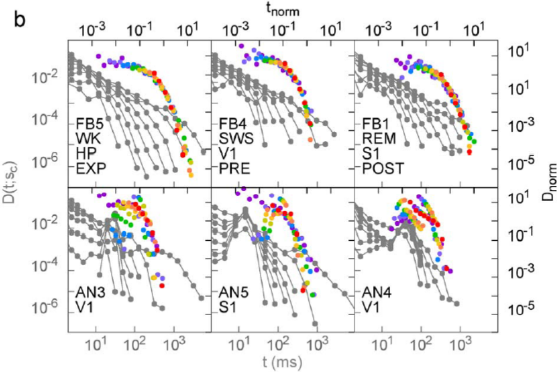
Waiting-time distribution



$$D(\tau; s_c) = \langle \tau(s_c) \rangle^{-1} F(\tau / \langle \tau(s_c) \rangle)$$

Scaling across brain regions and behavioral states!

(but not anesthesia...)



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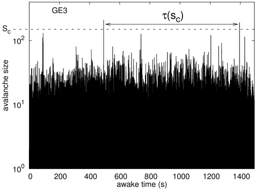
Scaling in the distribution of waiting times

Waiting-time distribution



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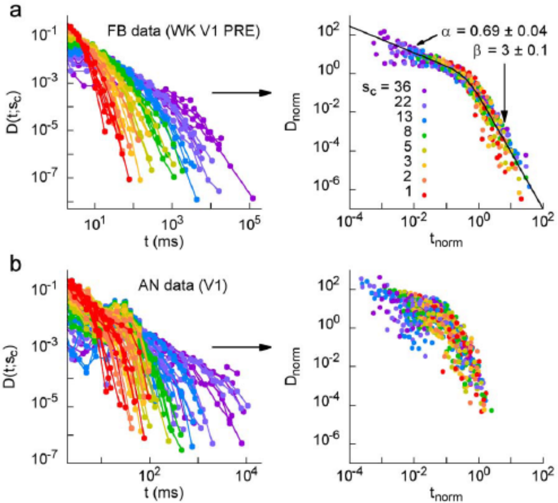

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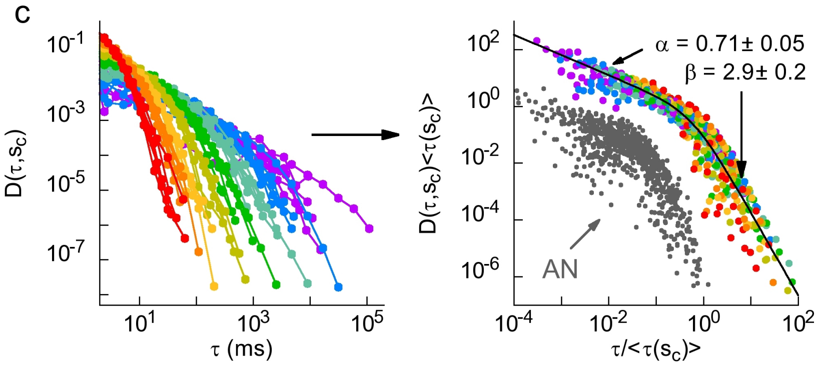
Scaling in the distribution of waiting times

Universality: Single scaling function for 7 rats and 6 decades...
Well fit by double power law (like earthquakes!)



What is universality?

Let us imagine two different models, A and B:

Model A:

- $F_0 \propto (\sigma - \sigma_c)^{\beta}$
- $F \overset{\sigma=\sigma_c}{\propto} h^{1/\delta_h}$
- $\xi \propto |\sigma - \sigma_c|^{-\nu_\perp}$
- $P(s) \sim s^{-\tau}$
- $\ldots$

Model B:

- $F_0 \propto (\sigma - \sigma_c')^{\beta'}$
- $F \overset{\sigma=\sigma_c'}{\propto} h^{1/\delta_h'}$
- $\xi \propto |\sigma - \sigma_c'|^{-\nu_\perp'}$
- $P(s) \sim s^{-\tau'}$
- $\ldots$

Models A and B belong to the same **universality class** if their critical exponents are the same:

$$\beta = \beta'$$

$$\delta_h = \delta_h'$$

$$\nu_\perp = \nu_\perp'$$

$$\tau = \tau'$$

$$\vdots$$

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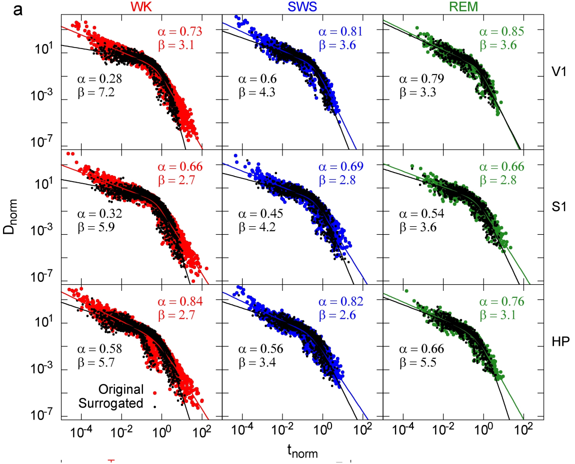
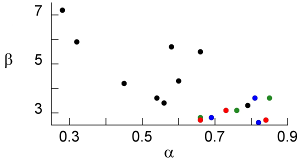
Scaling in the distribution of waiting times

Universality: very similar exponents across the sleep-wake cycle and brain regions (but not shuffled data)





Scaling in the distribution of waiting times

Universality + Long-range time correlations in experiments!

Scaling in the distribution of waiting times

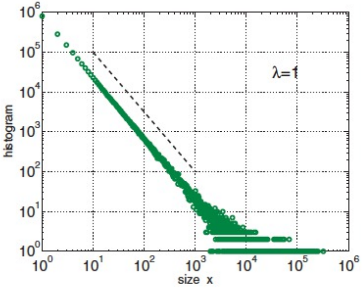
Universality + Long-range time correlations in experiments!
But what about models?

Scaling in the distribution of waiting times

STS = separation of time scales

Universality + Long-range time correlations in experiments!
But what about models?

Theoretical prediction:
System at critical point +
STS *by hand*=
power-law distributed
avalanches!



Larremore et al. (2012)

Scaling in the distribution of waiting times

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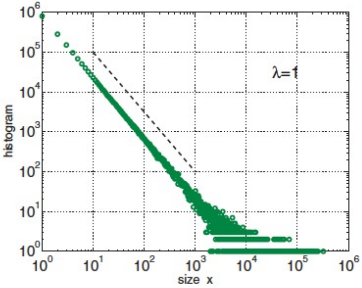

Larremore et al. (2012)

If STS has to be imposed by hand in a model, by construction it does not have long-range time correlations.

Waiting-time distributions are also arbitrarily chosen in the simulation...

Pros and cons so far...

Are critical branching processes satisfactory models of neuronal avalanches?

Branching-process-like models (absorbing vs active phases):

- Pros:
  - Neuronal avalanche exponents ($\tau = 3/2$ and $\tau_t = 2$)
  - Response exponents ($1/\delta_h = 1/2$: psychophysics, sensory systems, ...) + optimal dynamic range at criticality
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- Pros:
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  - Response exponents ($1/\delta_h = 1/2$: psychophysics, sensory systems, ...) + optimal dynamic range at criticality
  - Theoretical workhorse (useful picture) for over a decade
- Cons:
  - STS has to be imposed by hand
  - No time correlations between consecutive avalanches

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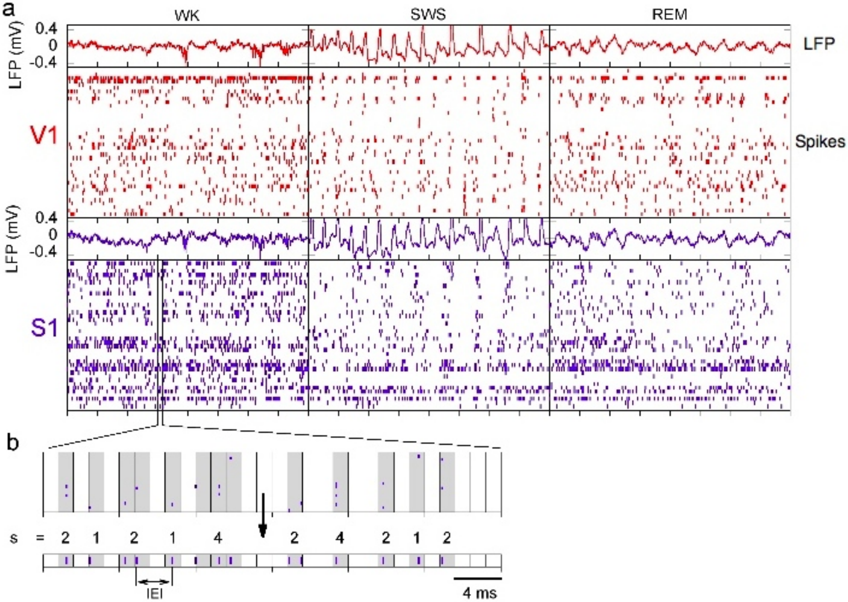
Outline:

Spike avalanches in freely-behaving rats



Ribeiro et al., PLoS One **5** e14129 (2010)

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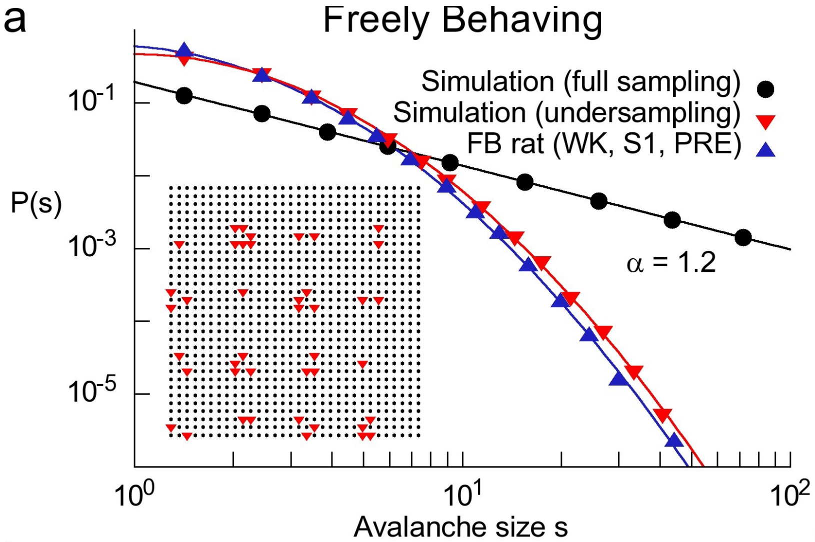
Critical model + undersampling = Lognormal-like size distributions



Ribeiro et al., PLoS One **5** e14129 (2010)

Undersampling changes avalanche statistics!

- Priesemann et al., BMC Neurosci. **10** 40 (2009)
- Ribeiro et al., PLoS One **5** e14129 (2010)
- Priesemann et al., PLoS Comput. Biol. **9** e1002985 (2013)
- Priesemann et al., Front. Syst. Neurosci. **8** 108 (2014)

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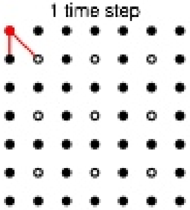
Undersampling changes avalanche statistics!

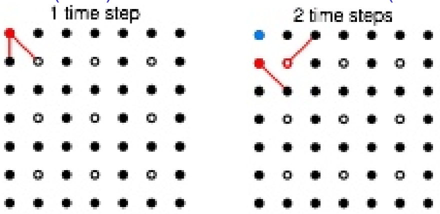
•=neurons (7×7)   ∘=measured neurons (3×3)   red=active



- • avalanche size measured with full sampling = 1
- ∘ avalanche size measured with undersampling = 0

Undersampling changes avalanche statistics!

•=neurons (7×7) ○=measured neurons (3×3) red=active



- avalanche size measured with full sampling = 3

○ avalanche size measured with undersampling = 1 (finished!)

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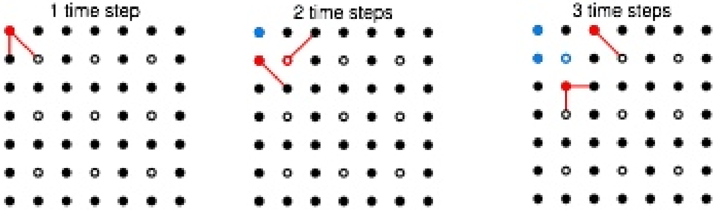
Undersampling changes avalanche statistics!

•=neurons (7×7) ○=measured neurons (3×3) red=active



• avalanche size measured with full sampling = 5
○ avalanche size measured with undersampling = 0 [1]

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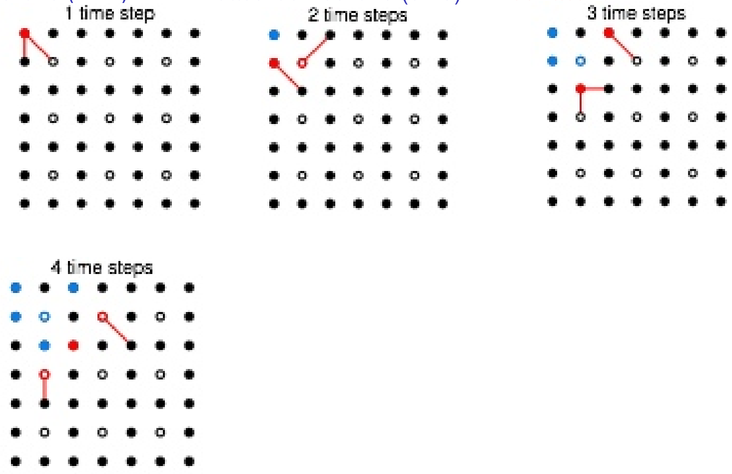
Undersampling changes avalanche statistics!

●=neurons (7×7) ○=measured neurons (3×3) red=active



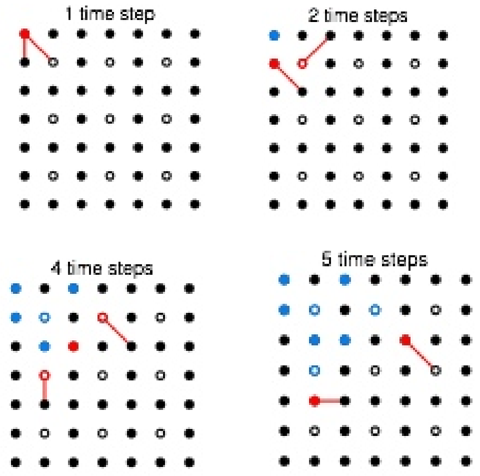
- avalanche size measured with full sampling = 8

○ avalanche size measured with undersampling = 2 (finished!)

[1]

Undersampling changes avalanche statistics!

•=neurons (7×7) ○=measured neurons (3×3) red=active



- avalanche size measured with full sampling = 10

○ avalanche size measured with undersampling = 0 [1, 2]

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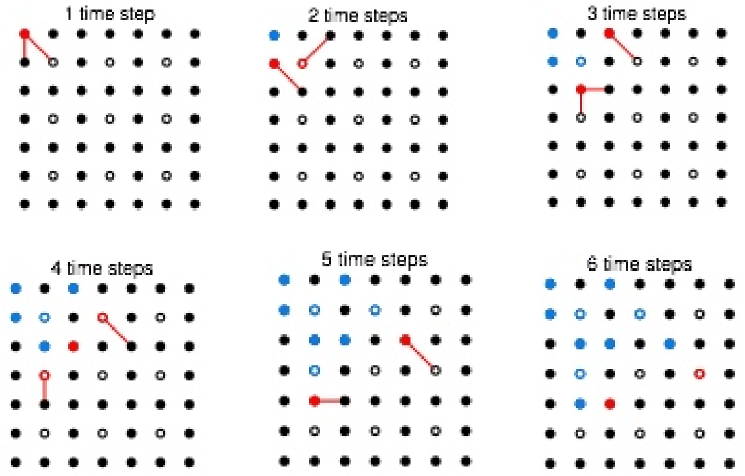
Undersampling changes avalanche statistics!

•=neurons (7×7) ○=measured neurons (3×3) red=active



• avalanche size measured with full sampling = 12

○ avalanche size measured with undersampling = 1 [1, 2]

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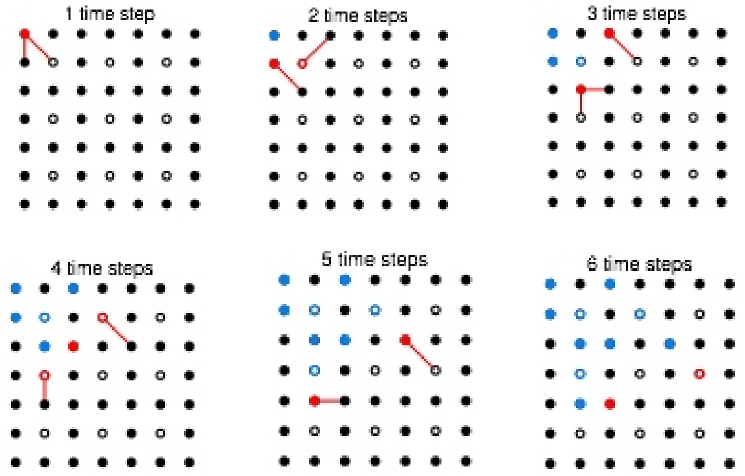
Undersampling changes avalanche statistics!

•=neurons (7×7)   ∘=measured neurons (3×3)   red=active



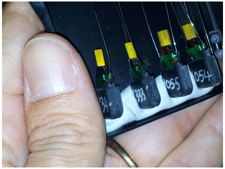
- • avalanche size measured with full sampling = 12
- ∘ avalanche sizes measured with undersampling = 1, 2, 1

Undersampling solves one problem, but creates another...

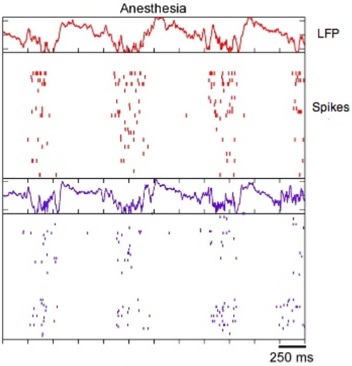
Undersampling solves one problem, but creates another...

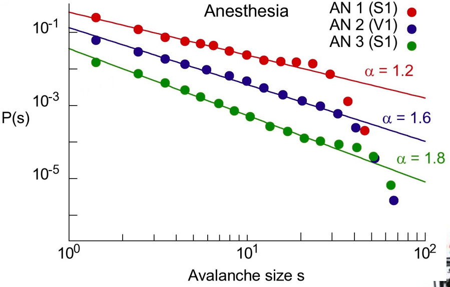
Anesthetized rats with the the same undersampling:
$\Longrightarrow$ power-law size distributions!

Spike avalanches in anesthetized rats



- 150 μm-500 μm electrode spacing
- Anesthesia: ketamine-xylazine (8 mg/kg)





Ribeiro et al., PLoS One **5** e14129 (2010)

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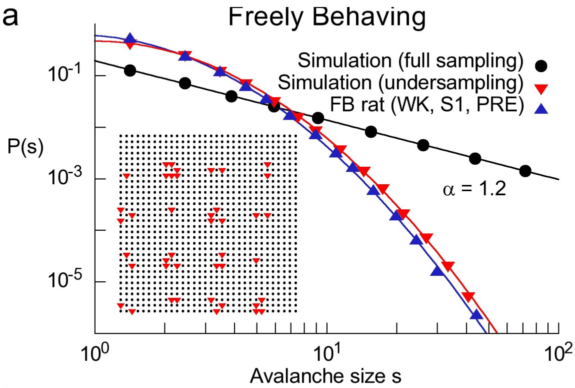
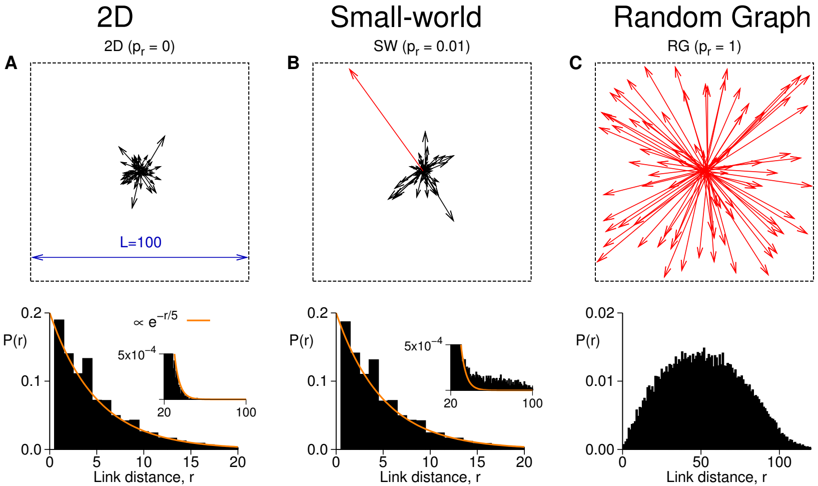


If the model is undersampled (LIKE THE DATA IS!), can it still yield power-law size distributions?

Investigating undersampling in 3 topologies

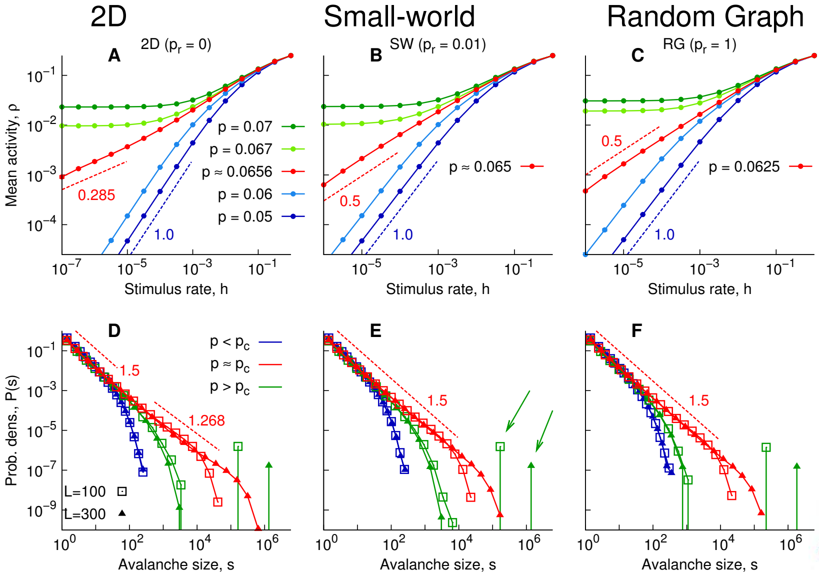
p_r=rewiring probability; $K_{out} = 16$



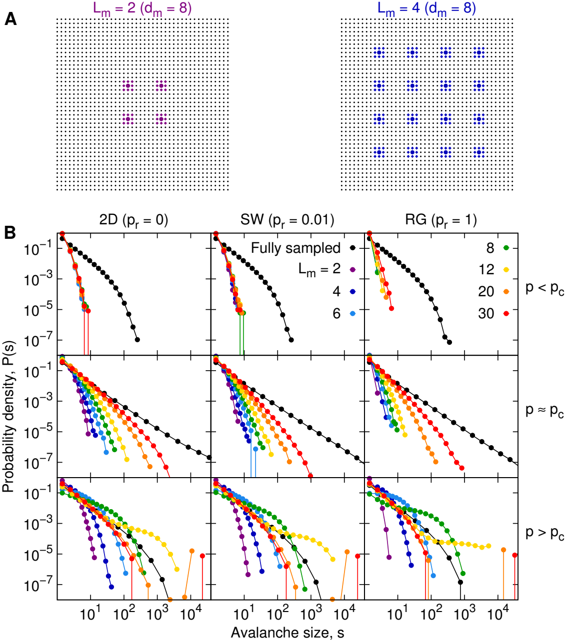
Ribeiro et al. PLoS ONE **9** e94992 (2014)

Determining the critical point

p=transmission probability per link



Varying the number of sampled sites (fixed spacing)



- $0 - 3$ neurons per electrode
- $d_m = 8 \Rightarrow$ $\sim 250\ \mu$m among electrodes
- $L_m = 8$ (64 electrodes): typical arrays
- $L_m = 30$ (900 electrodes): state of the art!
- Subcritical case: nothing changes
- Supercritical case: bumps for large enough matrices
- Critical case: power laws gone!

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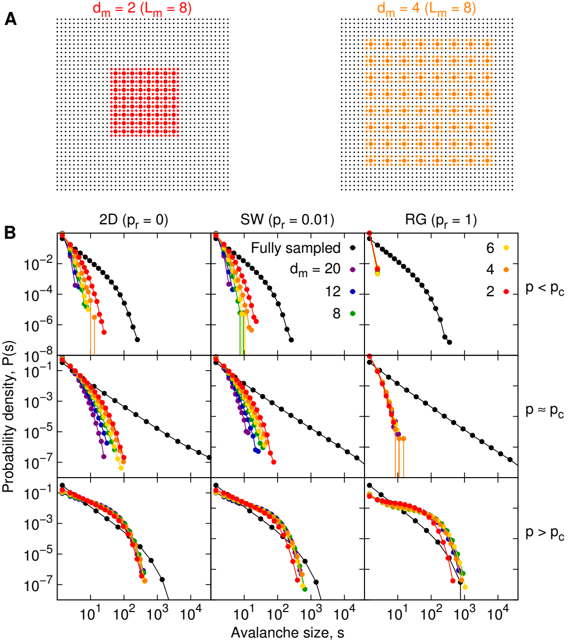
Varying the density of sampled sites (fixed number)



- 0 – 3 neurons per electrode
- $L_m = 8$: typical arrays
- All cases: little changes. Power laws gone!

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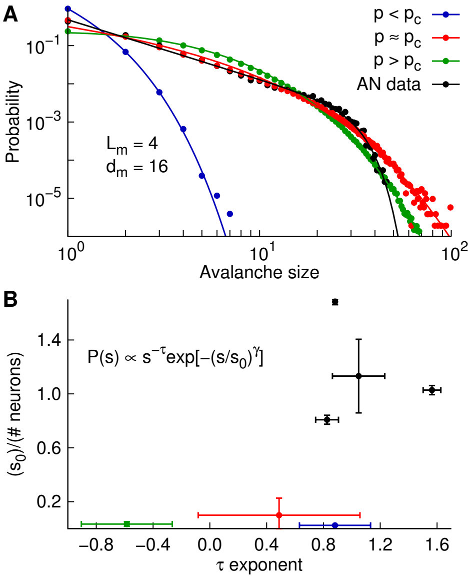
Last resort: choosing a rescaled time bin



Ribeiro et al. PLoS ONE **9** e94992 (2014)

- $\boxed{\Delta t^* = \langle ISI \rangle}$
- SW model and data (4 rats): $L_m = 4$ and $d_m = 16$ (500 μm)
- Fit is better, but not much (e.g. wrong cutoff)

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Outline:

UFPE

Are critical branching processes satisfactory models of neuronal avalanches?

Branching-process-like models (absorbing vs active phases):

- Pros:
  - Neuronal avalanche exponents ($\tau = 3/2$ and $\tau_t = 2$)
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UFPE

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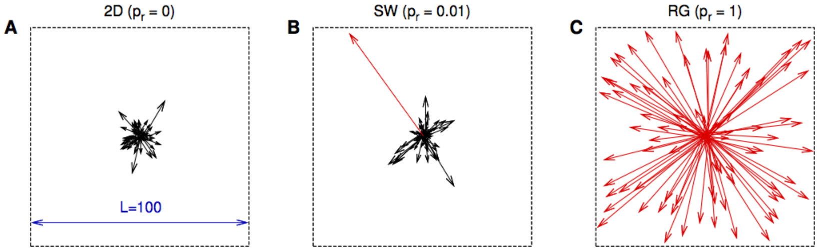
Undersampling: no power laws in 3 topologies



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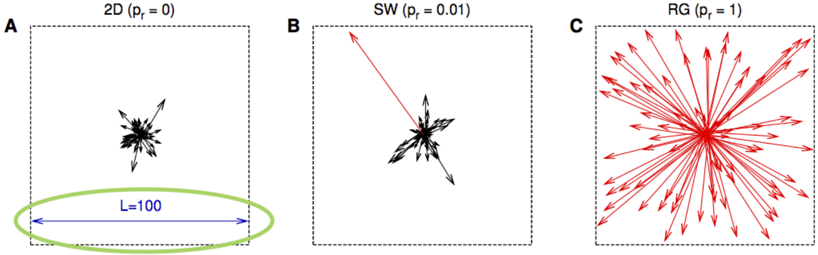

$$\boxed{\langle K \rangle = 16}$$

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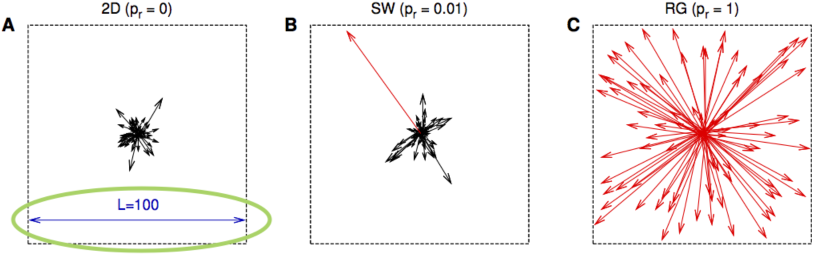

$\boxed{\langle K \rangle = 16}$

But if the brain has $\sim 10^9$ neurons, and
each cortical neuron receives $\sim 10^4$ synapses...

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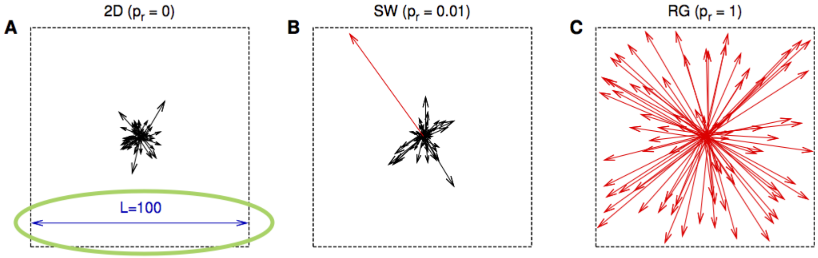

$\boxed{\langle K \rangle = 16}$

But if the brain has $\sim 10^9$ neurons, and
each cortical neuron receives $\sim 10^4$ synapses...
... then maybe a better model would have $\langle K \rangle = \sqrt{N}$

UFPE

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Is undersampling overcome with a different topology?

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Griffiths phases and the stretching of criticality in brain networks Paolo Moretti[1] & Miguel A. Muñoz[1] Nat. Commun. 4 2521 (2013)

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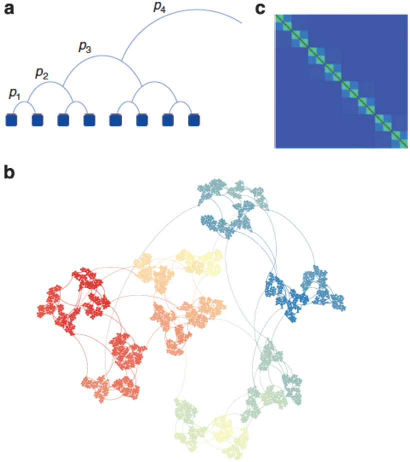

Hierarchical-modular networks

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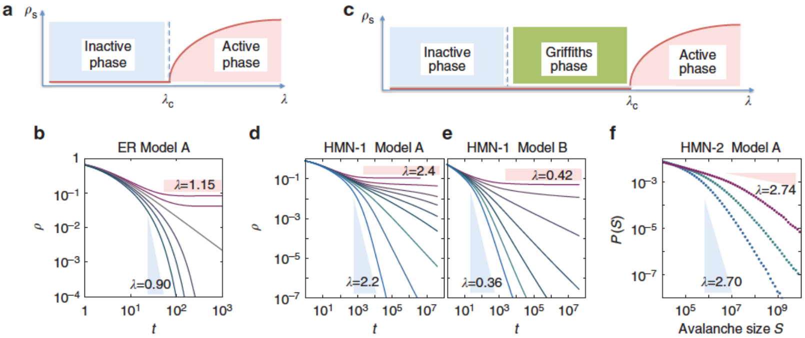
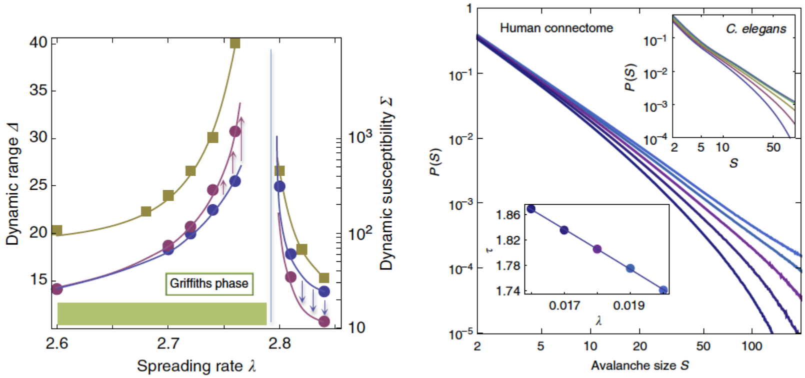


Disorder $\Rightarrow$ Rare active regions $\Rightarrow$ Generic power laws!

Moretti & Muñoz, Nat. Commun. **4** 2521 (2013)

Is undersampling overcome with a different topology?



Moretti & Muñoz, Nat. Commun. **4** 2521 (2013)

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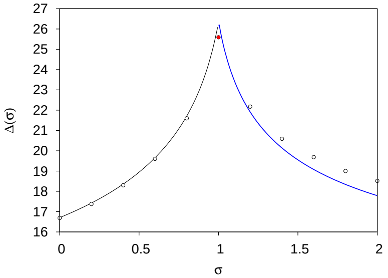
Outline:

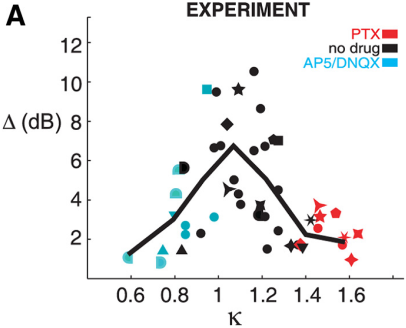
Dynamic range is optimal at criticality

Theory



Kinouchi & Copelli
Nat. Phys. **2** 348 (2006)

Cortical slices



Shew et al.
J. Neurosci., **29** 15595 (2009)

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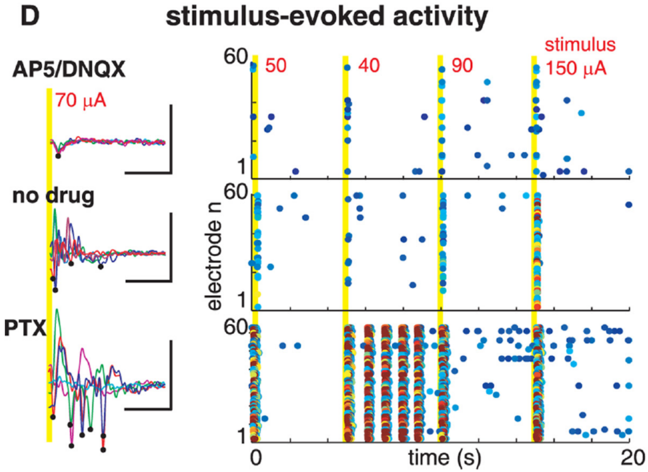
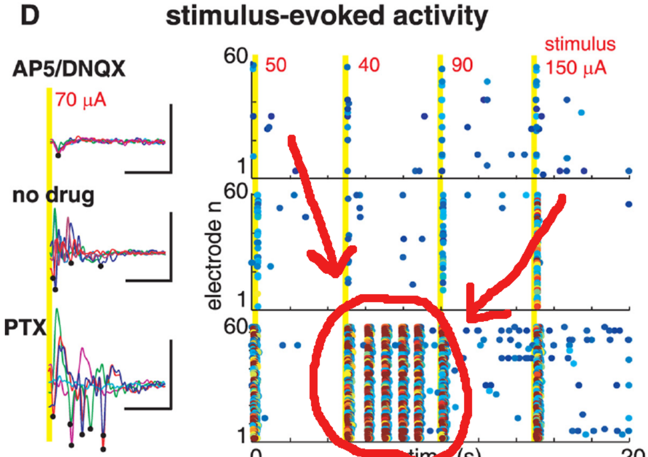
Supercritical slices



Shew et al., *J. Neurosci.* **29** 15595 (2009)

Supercritical slices: collective oscillations?

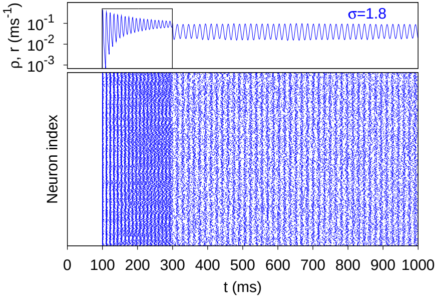
Directed percolation (DP) not fully compatible with "supercritical" collective oscillations (coexistence?) in experiment



Shew et al., *J. Neurosci.* **29** 15595 (2009)

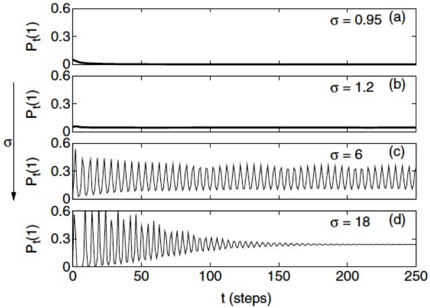
Oscillations in DP-like models, but avalanches?...

Increasing σ even more...



Kinouchi & Copelli
Nat. Phys. **2** 348 (2006)

Reentrance, coexistence etc

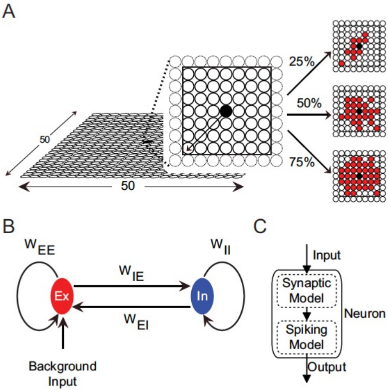


Rozenblit & Copelli
JSTAT **P01012** (2011)

A model with excitatory and inhibitory neurons

Spiking neurons, not excitable!

50×50 grid
(interaction square: 7×7)



Poil et al., *J. Neurosci.* **32** 9817 (2012)

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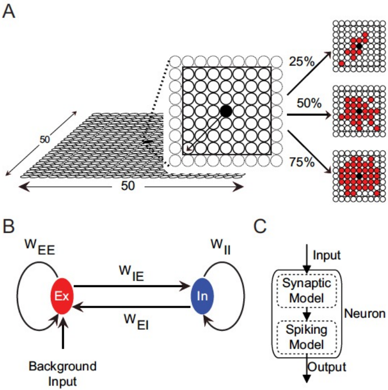
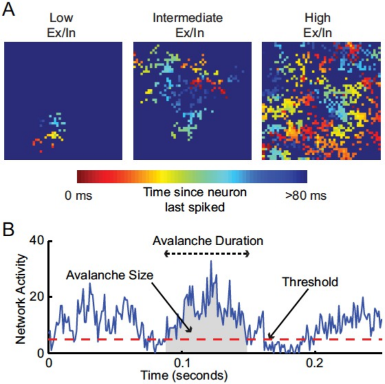


Avalanche: above threshold



Poil et al., *J. Neurosci.* **32** 9817 (2012)

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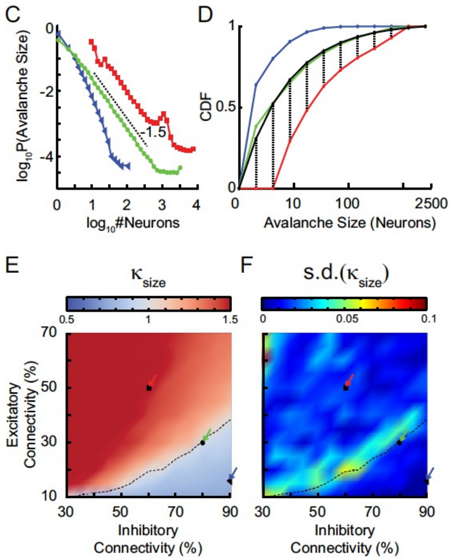
- Avalanches with power-law size distribution!
- But only along a transition line in parameter space
- What kind of transition is this?



Poil et al., *J. Neurosci.* **32** 9817 (2012)

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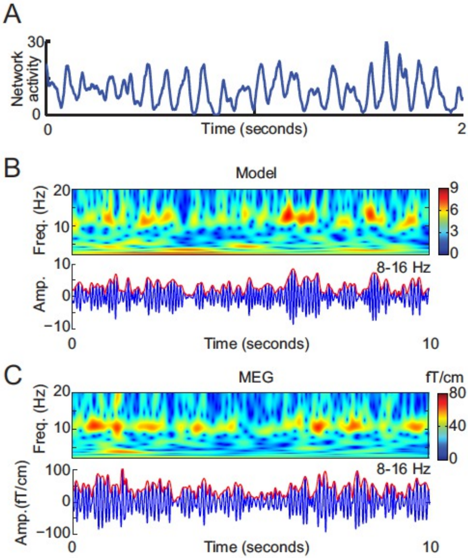
- Oscillations emerge! (8-16 Hz)
- Similar to MEG data



Poil et al., *J. Neurosci.* **32** 9817 (2012)

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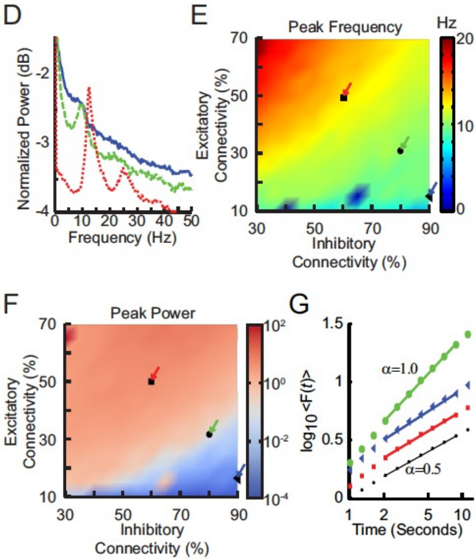
Spiking neurons, not excitable!

- Peak frequency increases with excitatory connectivity
- Transition from low to high peak power
- DFA exponent $\alpha \simeq 1$ at the transition



Poil et al., *J. Neurosci.* **32** 9817 (2012)

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DFA = Detrended Fluctuation Analysis

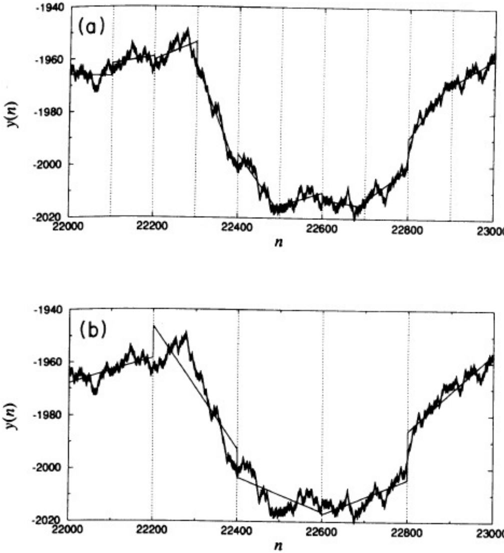
$$\boxed{F(n) = \sqrt{\frac{1}{N} \sum_{k=1}^{N} [y(k) - y_n(k)]}}$$

If $F(n) \sim n^{\alpha}$, then

$$\boxed{C(\tau) \sim \tau^{-\gamma}, \text{ with } \gamma = 2 - 2\alpha}$$

$$\boxed{S(f) \sim f^{\beta}, \text{ with } \beta = 1 - \gamma = 2\alpha - 1}$$

- $0 < \alpha < 0.5 \Rightarrow$ anticorrelations
- $\alpha = 0.5 \Rightarrow$ white noise
- $0.5 < \alpha < 1 \Rightarrow$ persistent long-range power-law correlations
- $\alpha = 1 \Rightarrow 1/f$ noise



Peng et al., *Phys. Rev. E* **49** 1685 (1994)

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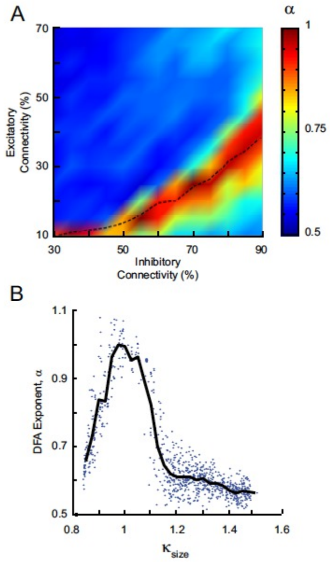

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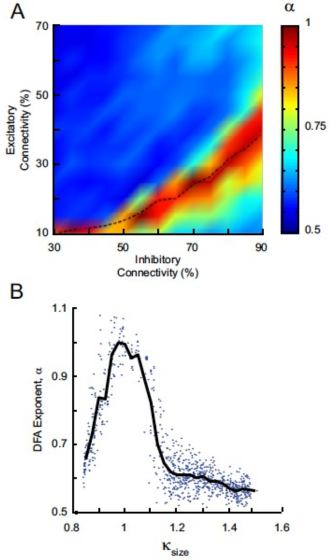
$\boxed{\alpha \simeq 1 \text{ at the transition}}$

$\Downarrow$



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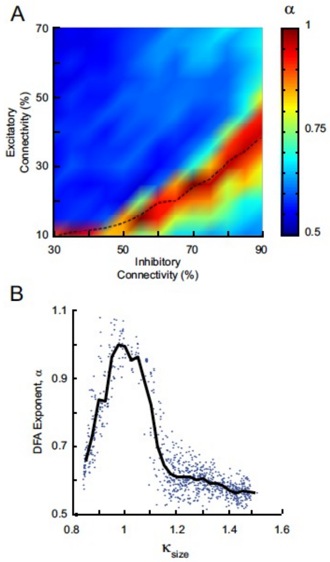

$\alpha \simeq 1$ at the transition

$\Downarrow$

neuronal avalanches + long-range power law correlations

Poil et al., *J. Neurosci.* **32** 9817 (2012)

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But ...

- How robust is the model if system size is increased (beyond 50×50...)?
- Should the "interaction square" be scaled up as well?
- If so, is the system really two-dimensional? (Remember, $\tau = 3/2$ is a mean-field exponent!)
- What would be an appropriate order parameter to characterize the transition?
- Does $P(s) \sim s^{-3/2}$ survive undersampling?

Poil et al., *J. Neurosci.* **32** 9817 (2012)

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  - Hierarchical networks (critical point or Griffiths phase??) [Moretti & Muñoz, Nat. Comm. (2013)]
- Avalanches as collective excitations near oscillatory behavior? [Poil et al, J. Neurosci. (2012)]

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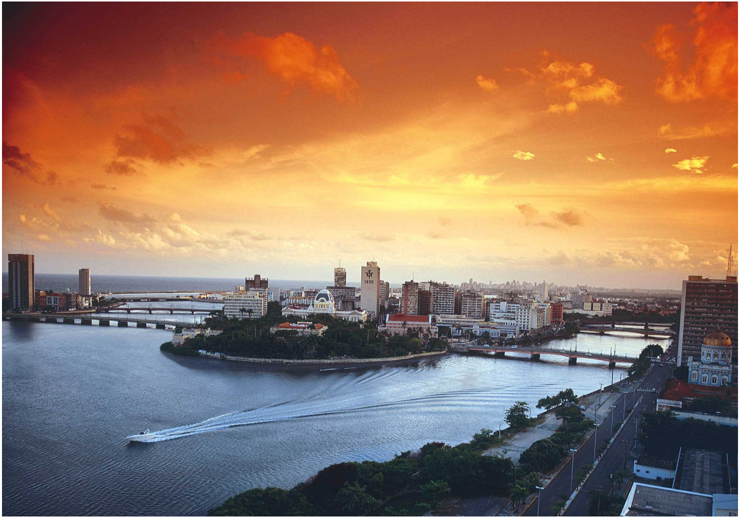
Thank you!






New neuroelectrophysiology lab: students and post-docs wanted!

Come visit us in Recife!



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