Identification of criticality in neuronal avalanches

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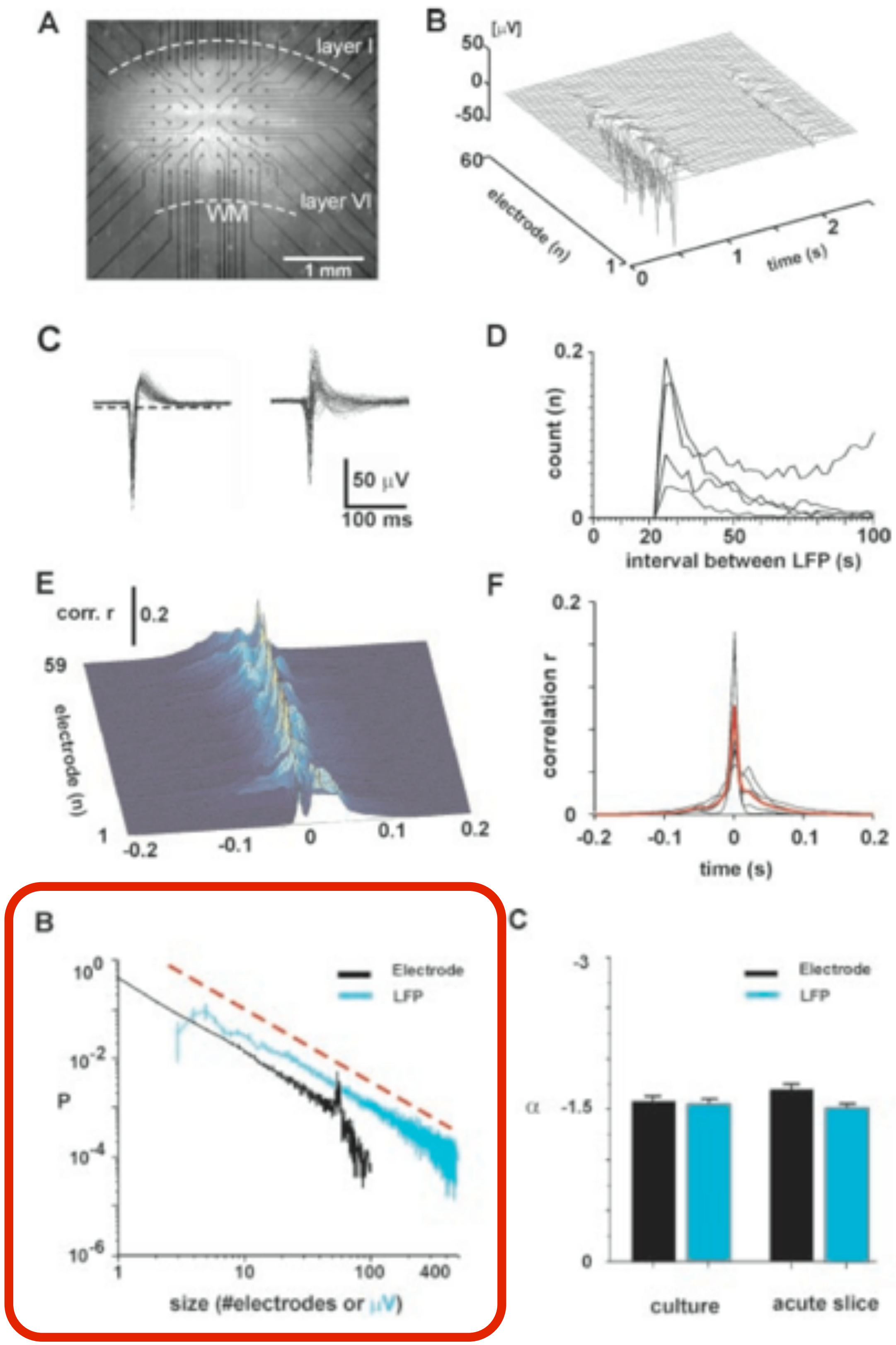
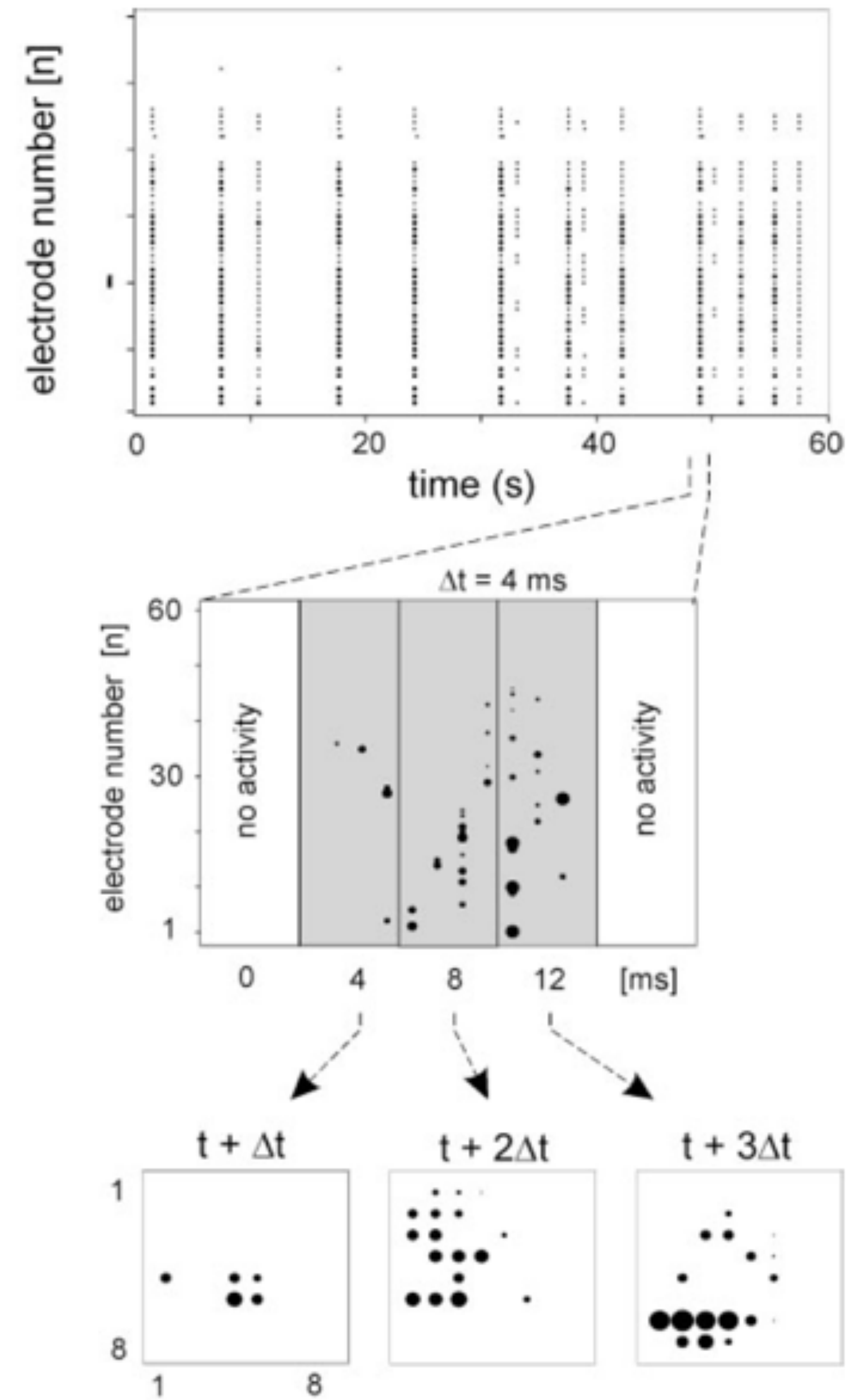
What are neuronal avalanches?





Beggs and Plenz (2003). *J Neurosci* 23(35):11167-77

"So you think you have a power law — Well isn't that special?"

Cosma Shalizi, Carnegie Mellon University

Three-Toed Sloth

Slow Takes from the Canopy (My Very Own Internet Tradition)

June 15, 2007

« Reformatting in Progress | Main | Books to Read While the Algae Grow in Your Fur, May 2007 »

So You Think You Have a Power Law — Well Isn't That Special?

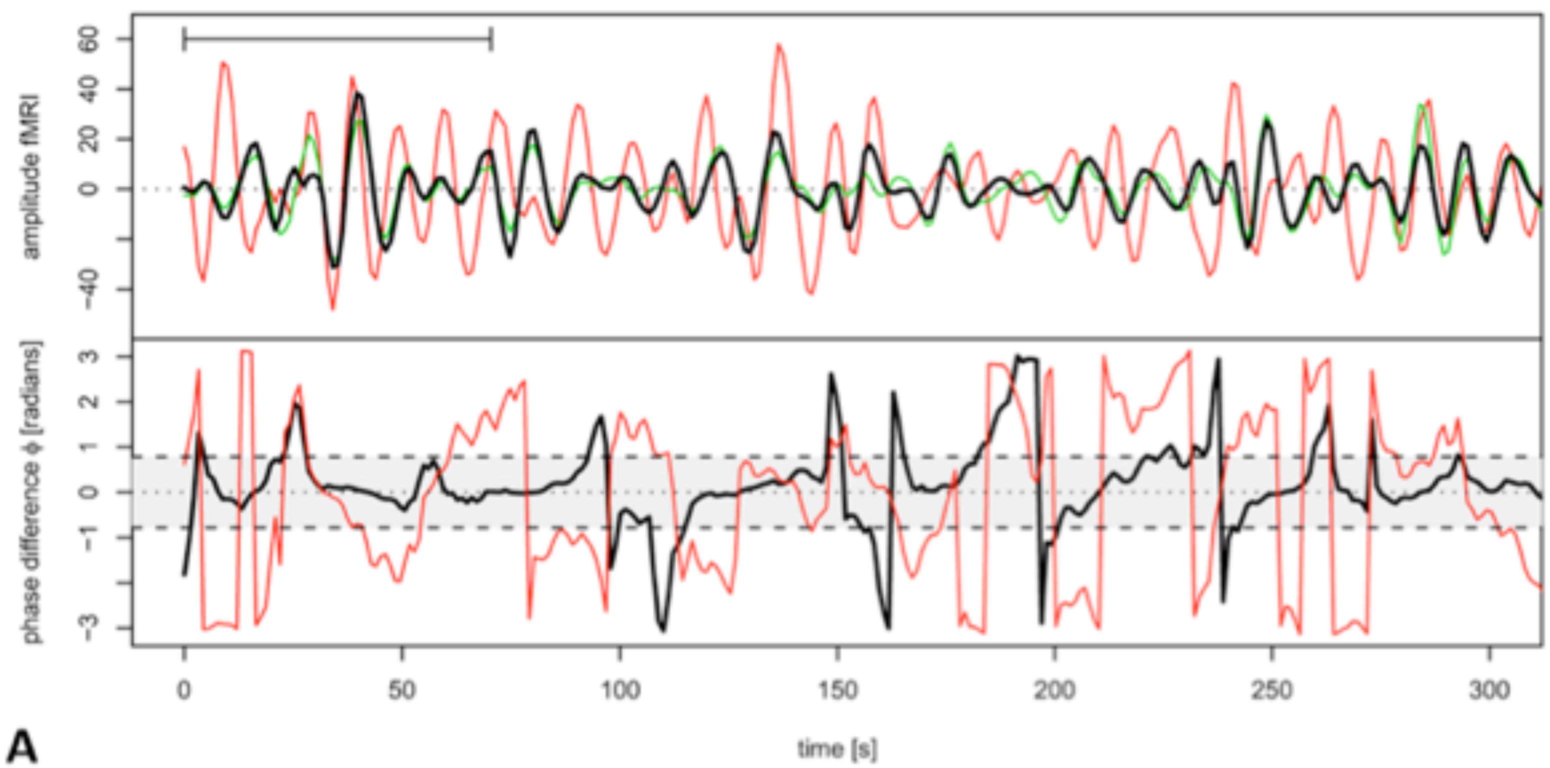
Regular readers who care about such things — I think there are about three of you — will recall that I have long had a thing about just how unsound many of the claims for the presence of power law distributions in real data are, especially those made by theoretical physicists, who, with some honorable exceptions, learn nothing about data analysis. (I certainly didn't.) I have even whined about how I should really be working on a paper about how to do all this right, rather than merely snarking in a weblog. As evidence that the age of wonders is not passed — and, more relevantly, that I have productive collaborators — this paper is now loosed upon the world:

Aaron Clauset, CRS and M. E. J. Newman, "Power-law distributions in empirical data", arxiv:0706.1062, with code available in Matlab and R; forthcoming (2009) in *SIAM Review*

> *Abstract*: Power-law distributions occur in many situations of scientific interest and have significant consequences for our understanding of natural and man-made phenomena. Unfortunately, the empirical detection and characterization of power laws is made difficult by the large fluctuations that occur in the tail of the distribution. In particular, standard methods such as least-squares fitting are known to produce systematically biased estimates of parameters for power-law distributions and should not be used in most circumstances. Here we describe statistical techniques for making accurate parameter estimates for power-law data, based on maximum likelihood methods and the Kolmogorov-Smirnov statistic. We also show how to tell whether the data follow a power-law distribution at all, defining quantitative measures that indicate when the power law is a reasonable fit to the data and when it is not. We demonstrate these methods by applying them to twenty-four real-world data sets from a range of different disciplines. Each of the data sets has been conjectured previously to follow a power-law distribution. In some cases we find these conjectures to be consistent with the data while in others the power law is ruled out.

Broadband Criticality of Human Brain Network Synchronization

Kitzbichler et al. (2009). *PLoS Comp Biol* 5:e1000314.



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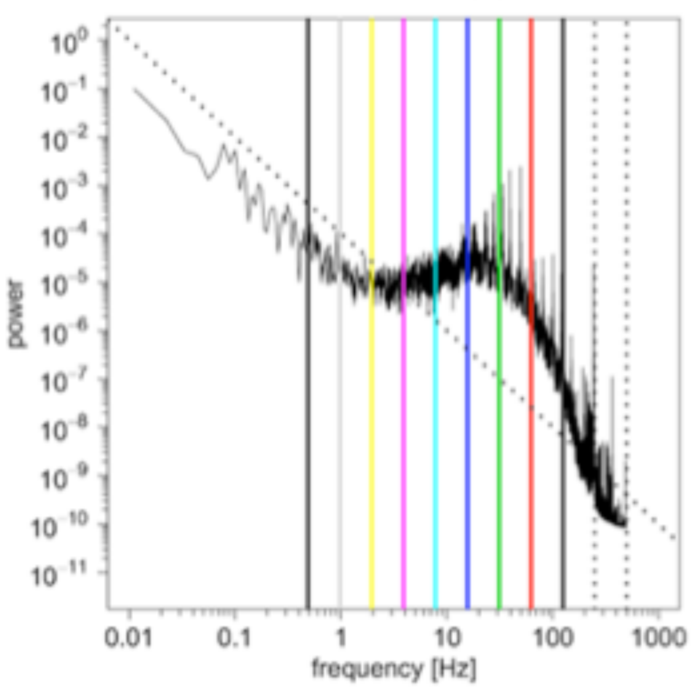
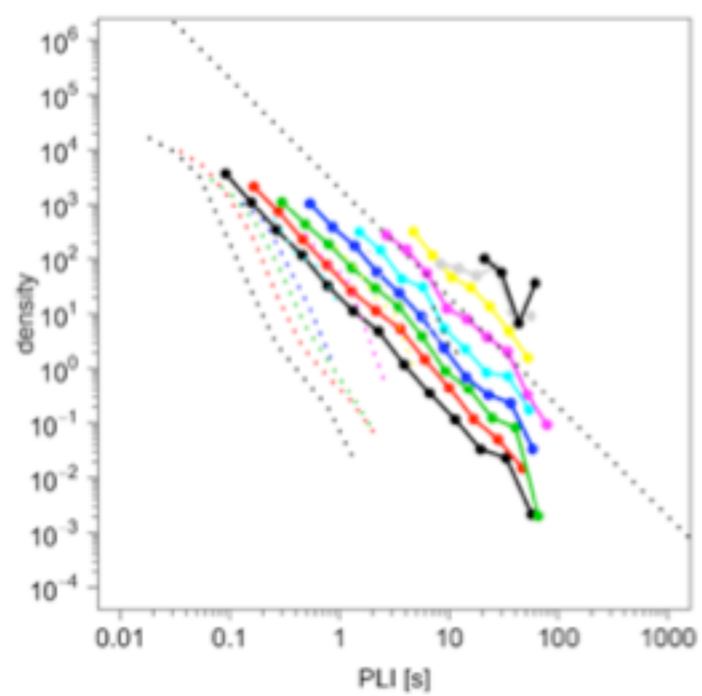
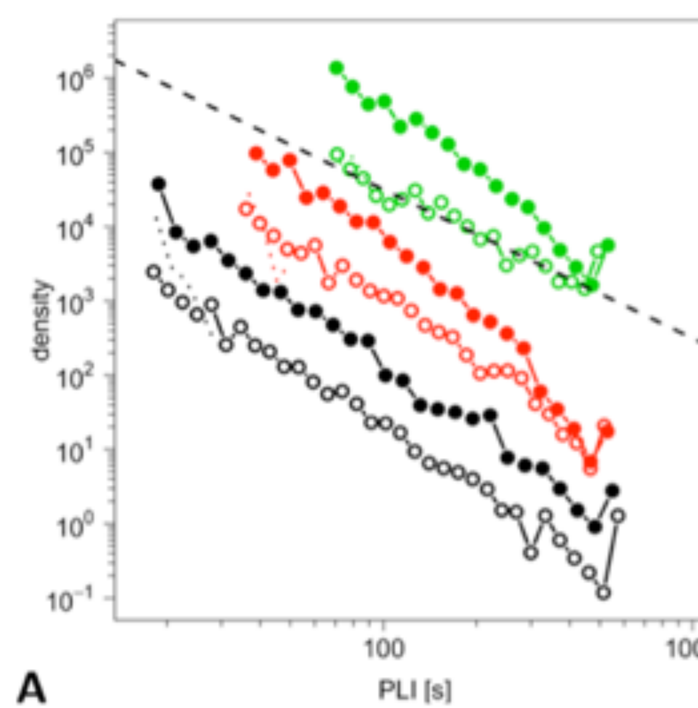






A

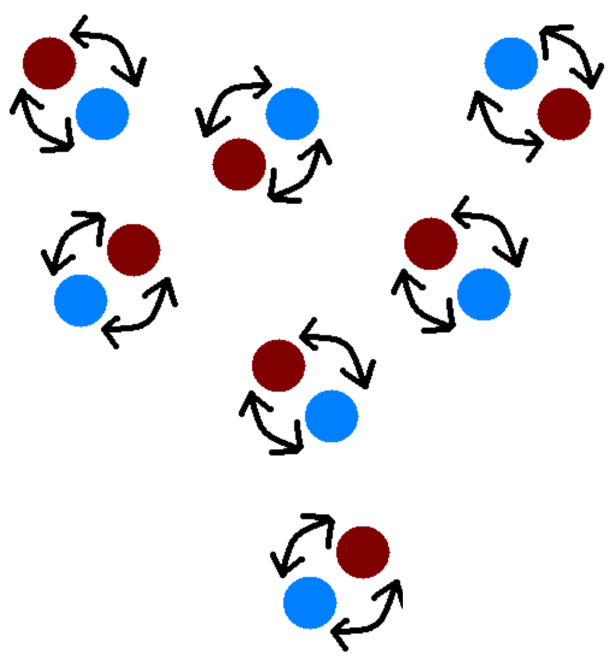
Kuramoto system at critical coupling show power laws of PLIs

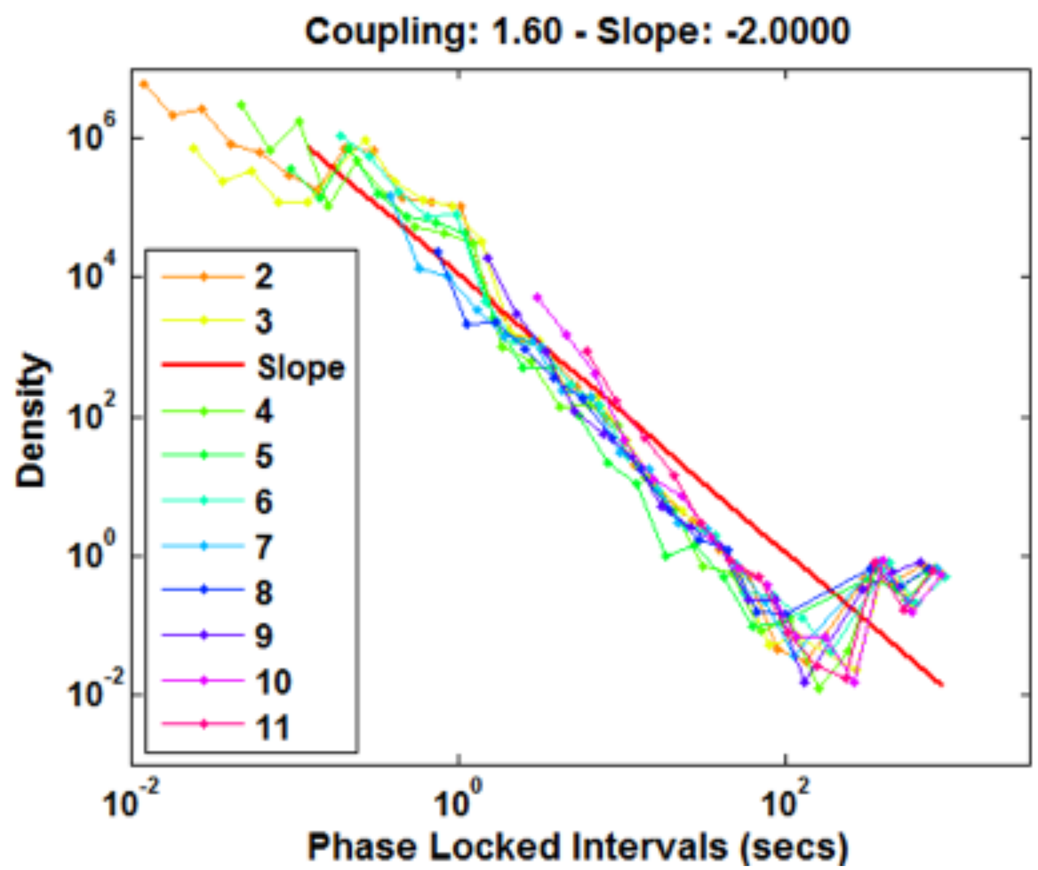
PLIs of fMRI show PL

Power laws of PLIs do not imply criticality

Botcharova, Farmer and Berthouze (2012). *Phys Rev E* 86:051920

We obtained exact derivation of phase evolution for **independent** pairs of Kuramoto oscillators.





$$\dot{\theta}_i = \omega_i + \frac{K}{N}\Sigma_{j=1}^{N}\sin(\theta_j - \theta_i)$$

A non-critical system can produce power laws in PLIs.

PHYSICAL REVIEW A VOLUME 38, NUMBER 1 JULY 1, 1988

Self-organized criticality

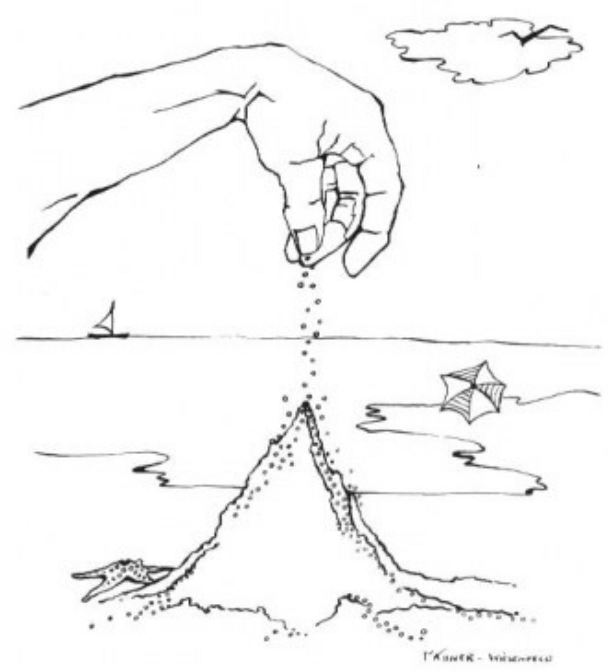
Per Bak, Chao Tang, and Kurt Wiesenfeld
Department of Physics, Brookhaven National Laboratory, Upton, New York 11973
(Received 28 August 1987)

We show that certain extended dissipative dynamical systems naturally evolve into a critical state, with no characteristic time or length scales. The temporal "fingerprint" of the self-organized critical state is the presence of flicker noise or $1/f$ noise; its spatial signature is the emergence of scale-invariant (fractal) structure.

Highly correlated brain dynamics produces synchronized states with no behavioral value, while weakly correlated dynamics prevents information flow.

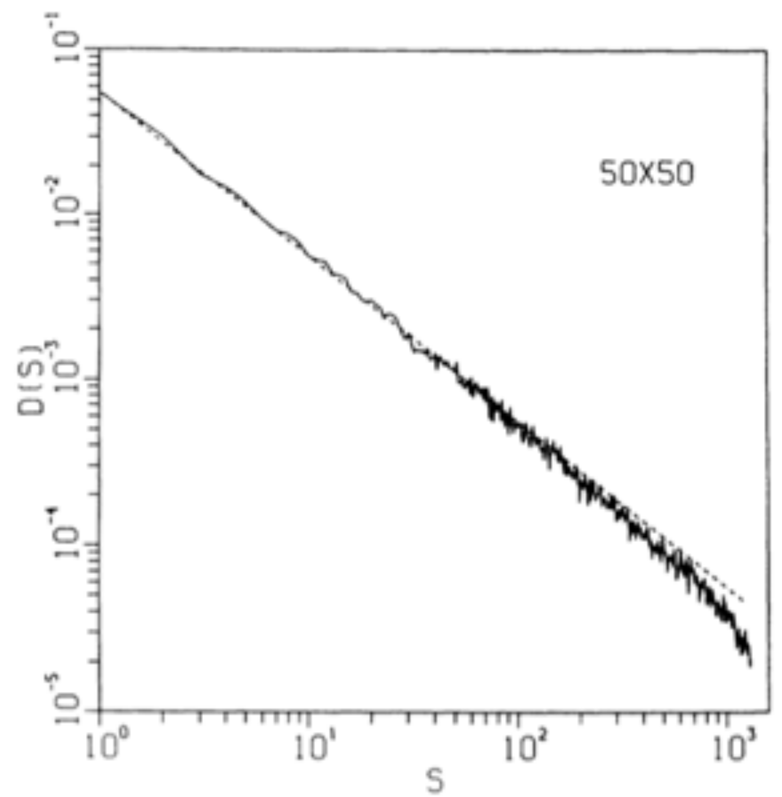
see also: edge of chaos / highly-optimised tolerance, etc…

The prototypical SOC model: the sandpile model



Building a sandpile

Avalanches

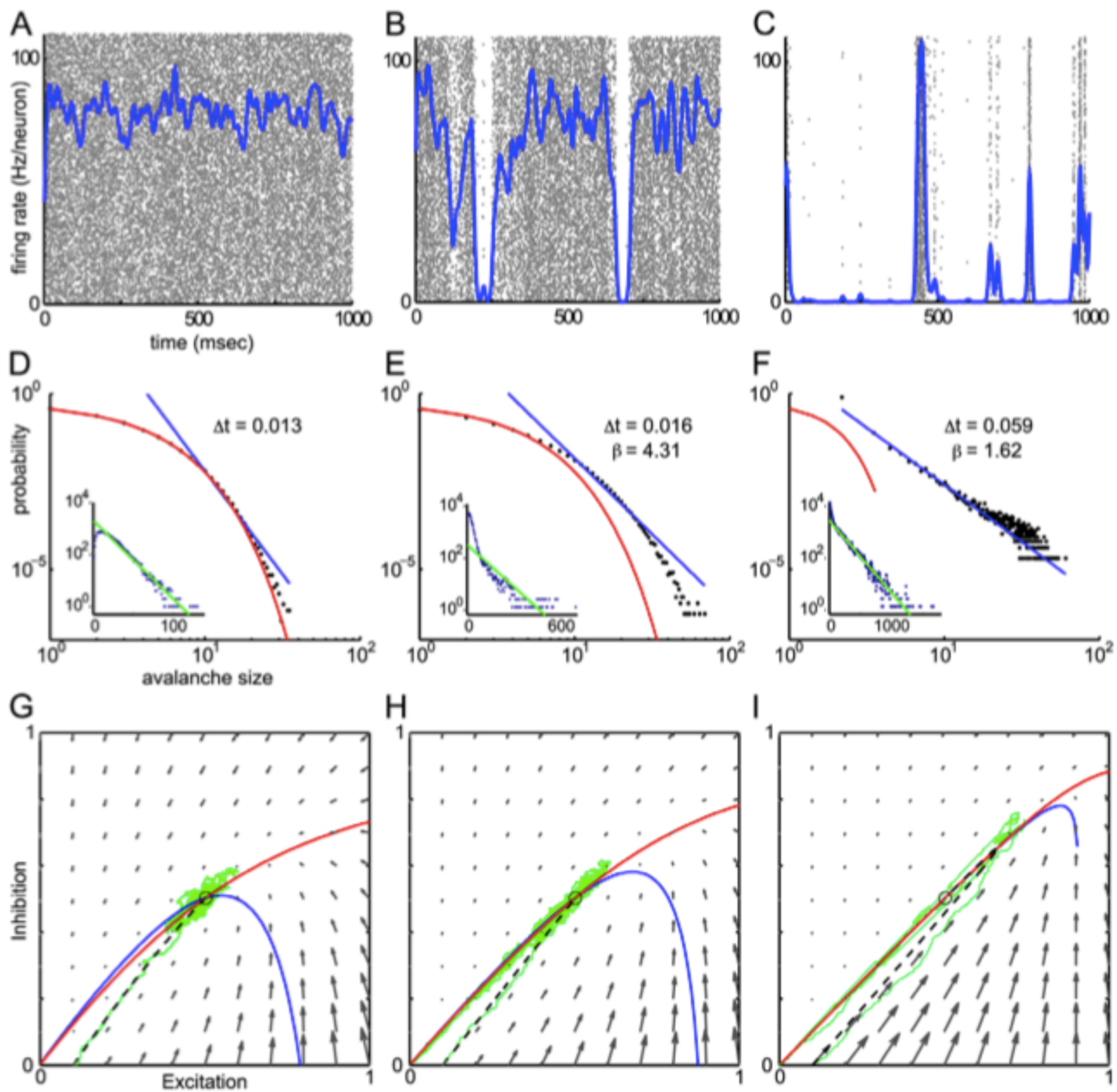


Power-law distribution of avalanches

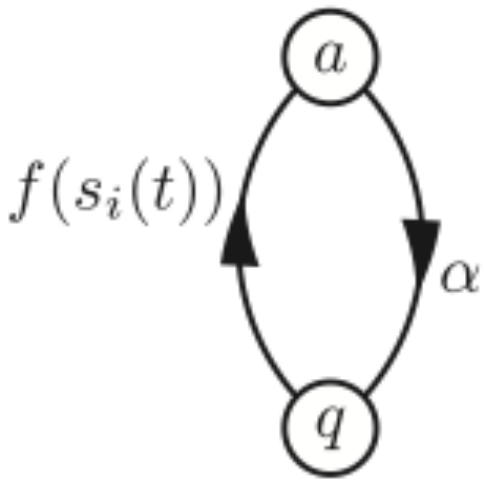
- System is far away from equilibrium
- System has infinite susceptibility
- Measured events follow power law

Avalanches in a Stochastic Model of Spiking Neurons

Benayoun et al. (2010). *PLoS Comp Biol* 6(7):e1000846



The model



$$P(Q \to A, \text{ in time } dt) = f\big(s_i(t)\big)\, dt,$$

$$P(A \to Q, \text{ in time } dt) = \alpha\, dt,$$

where $$s_i(t) = \sum_j \frac{w_{ij}}{N} a_j(t) + h_i$$

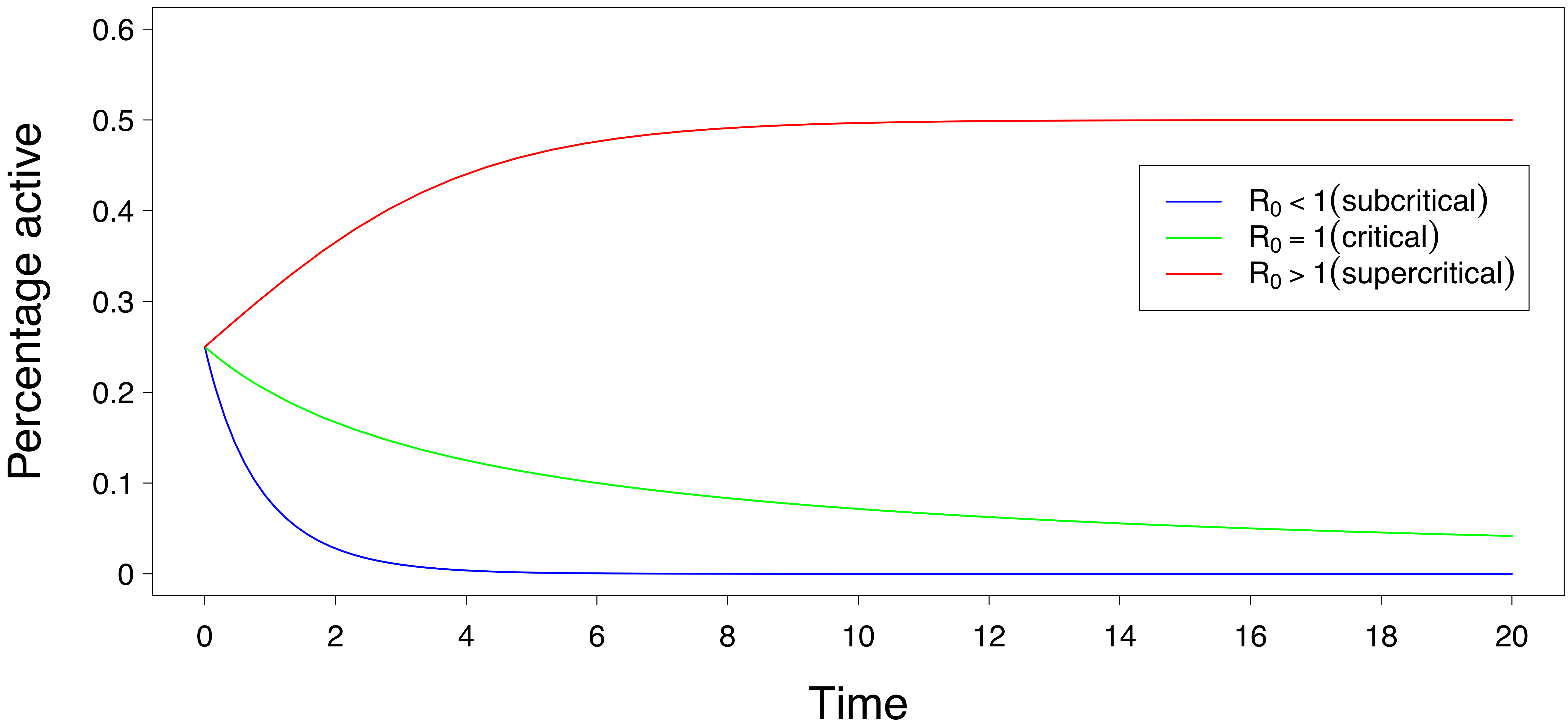
Assumptions: Fully connected unweighted network; no input; linear activation function

ODE: $$\frac{dA}{dt} = \frac{wA}{N} Q - \alpha A = \frac{wA}{N}(N - A) - \alpha A.$$

Stability analysis

Non-zero equilibrium: $A^* = N(1 - \alpha / w)$

Stability of equilibrium: $g'(A^*) = \alpha - w$ where $g(A) = \frac{dA}{dt}$

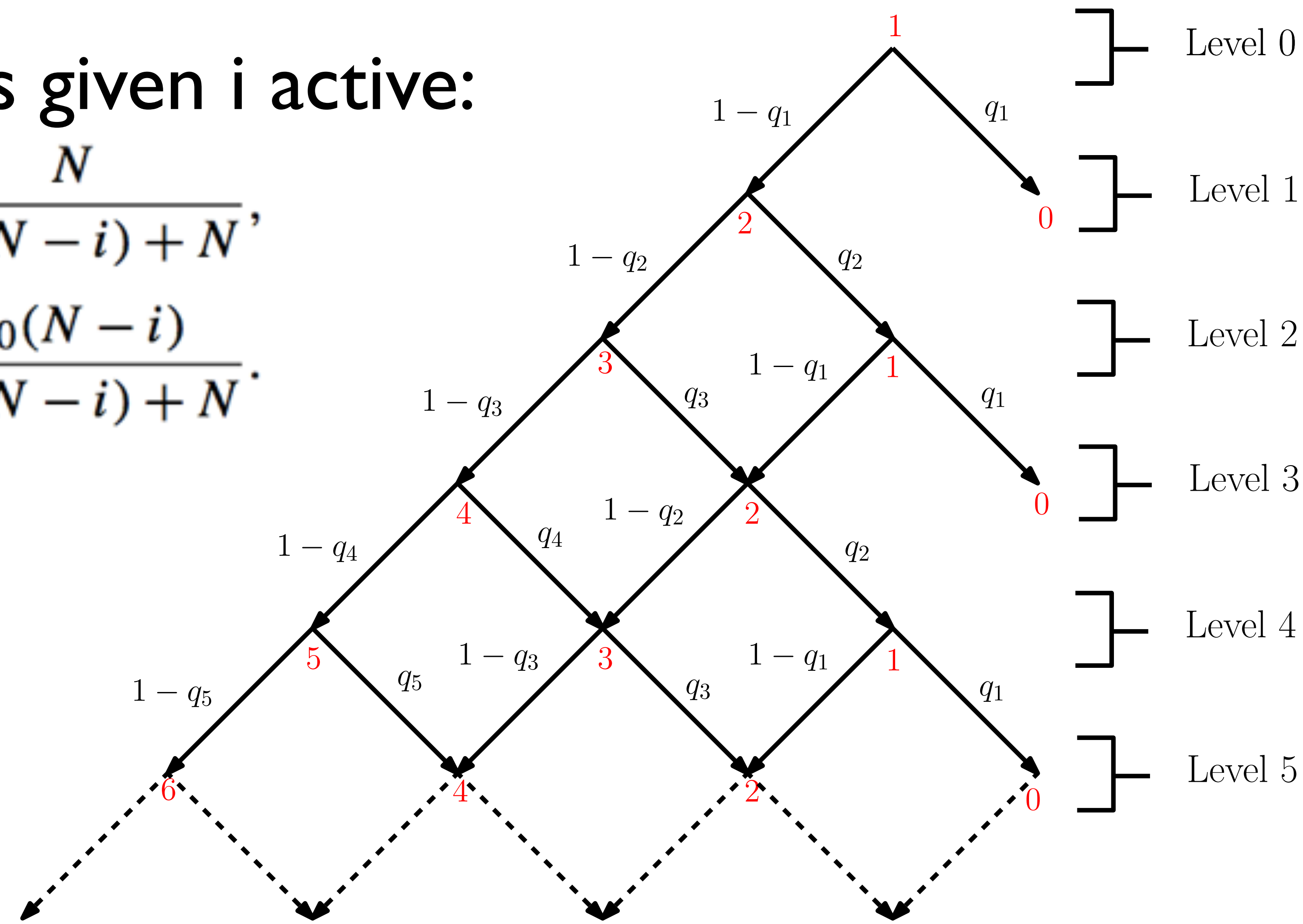


Recursive derivation of **exact** distribution of avalanche size (1)

Transition probabilities given i active:

$$q_i = \frac{\alpha N}{w(N-i)+\alpha N} = \frac{N}{R_0(N-i)+N},$$

$$1-q_i = \frac{w(N-i)}{w(N-i)+\alpha N} = \frac{R_0(N-i)}{R_0(N-i)+N}.$$



Between levels:

$$p_j^i = \begin{cases} p_{j-1}^2 q_2, & \text{if } i = 1, \\ p_{j-1}^{i-1}(1-q_{i-1}) + p_{j-1}^{i+1} q_{i+1}, & \text{for } 1 < i < N, \\ p_{j-1}^{N-1}(1-q_{N-1}), & \text{if } i = N. \end{cases}$$

where p_j^i is probability of having i active at level j

Recursive derivation of **exact** distribution of avalanche size (2)

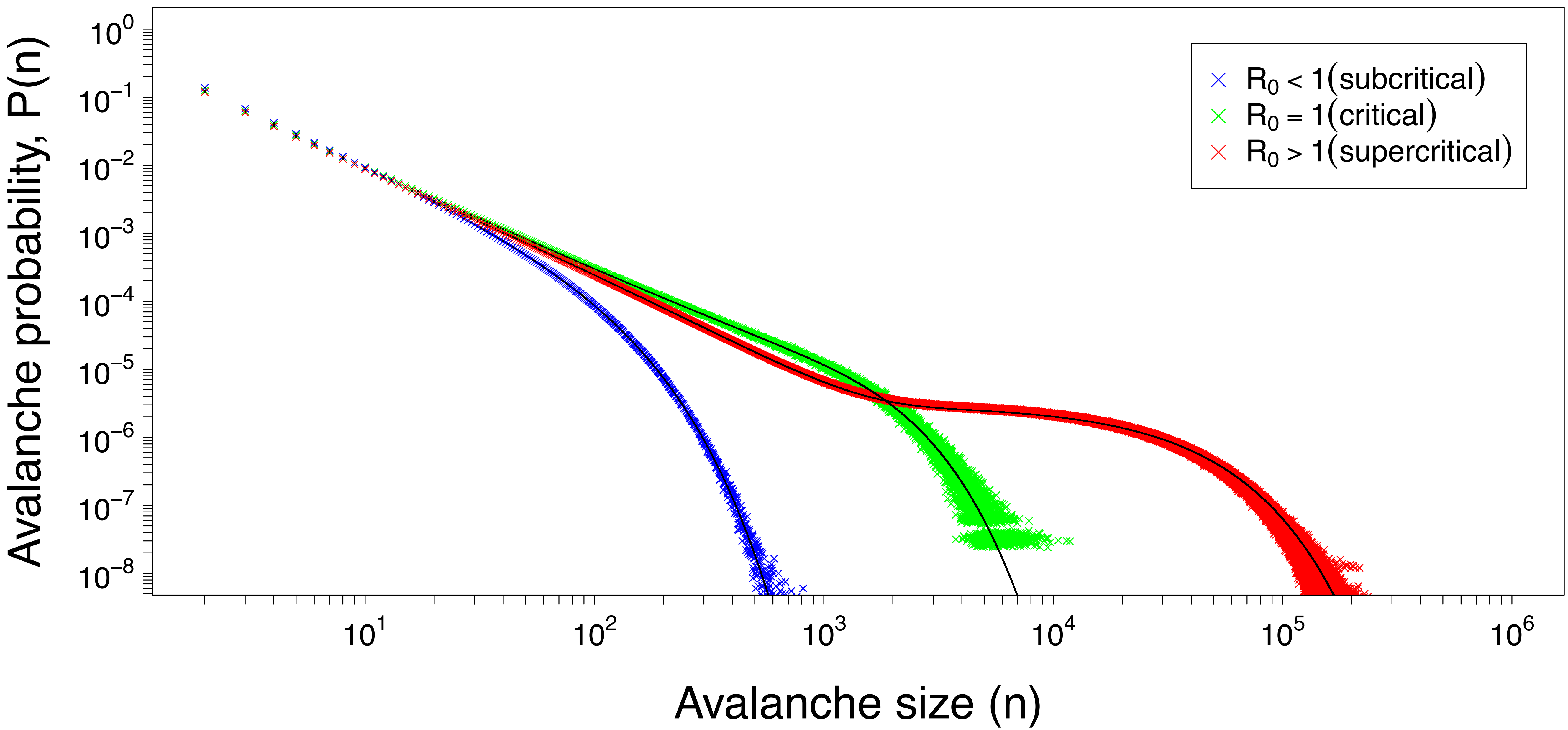
If $\mathbf{p}(l) = \begin{pmatrix} p_l^1 \\ \vdots \\ p_l^N \end{pmatrix}$ then $\mathbf{p}(l+1) = \mathbf{A} \cdot \mathbf{p}(l)$ where

$$\mathbf{A} = \begin{pmatrix} 0 & c_1 & & & & & \\ \ddots & \ddots & \ddots & & & & \\ & \ddots & \ddots & \ddots & & & \\ & & b_i & 0 & c_i & & \\ & & & \ddots & \ddots & \ddots & \\ & & & & \ddots & \ddots & \ddots \\ & & & & & b_N & 0 \end{pmatrix}$$

and $b_i = (1 - q_{i-1})$, $c_i = q_{i+1}$

Probability of avalanche having size (k+1) is $P(k+1) = q_1 e^T A^{2k} e$
where $e = (1, 0, 0, \ldots, 0)^T$

Exact vs Gillespie simulations



Also: very good agreement (for critical regime) with Kessler's closed-form formula based on random walks and Fokker-Planck approximation.

If $\lambda_1, \lambda_2, \ldots, \lambda_N$ are the eigenvalues of transition matrix then, we get:

$$P(n) = q_1 \sum_{i=1}^{N} d_i \lambda_i^{2n}$$

where d_i are specified by the eigenvectors.

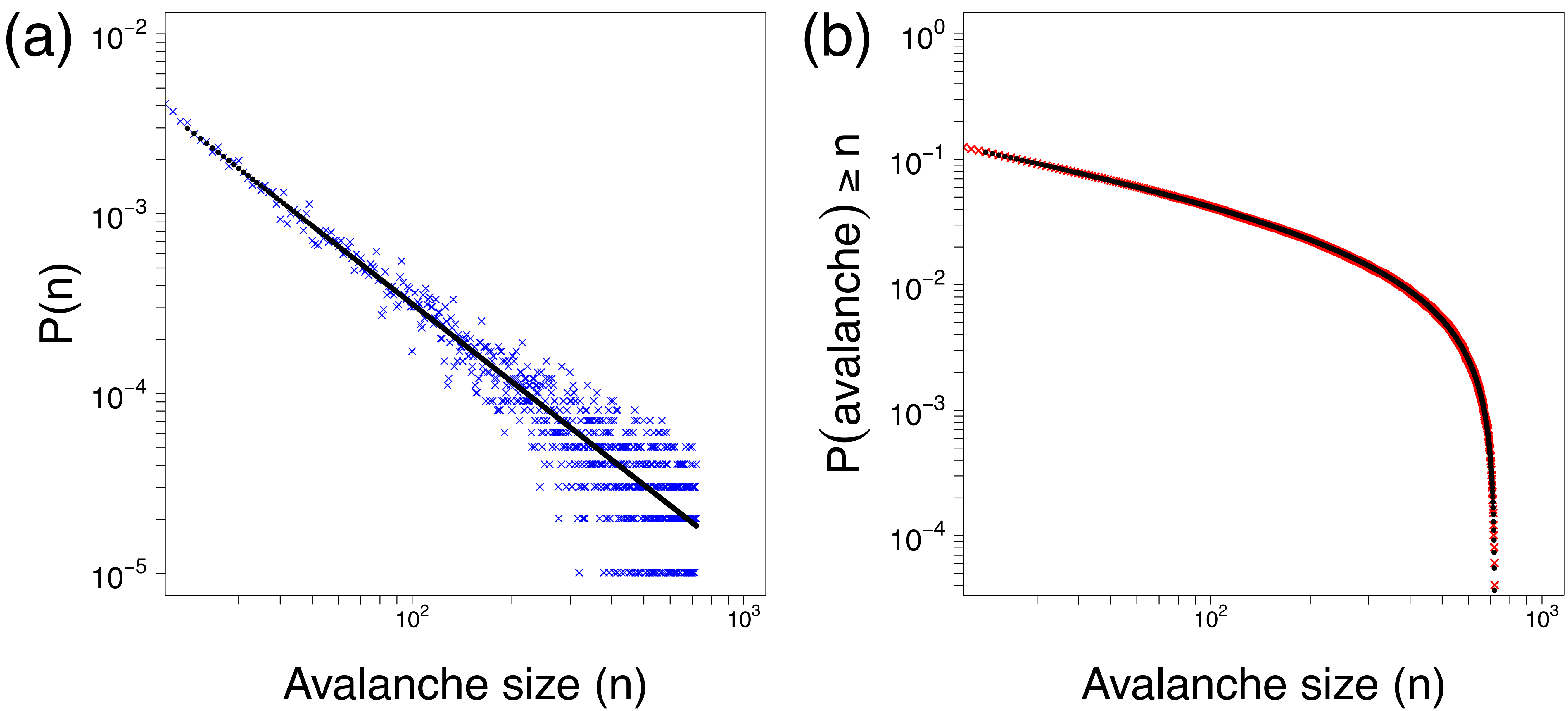
This can be further rewritten as:

$$P(n) = q_1 \sum_{i=1}^{\tilde{N}} e_i \lambda_i^{2n}$$

where: $e_i = d_i + d_{N-i+1}$

P(n) is a linear combination of exponentials

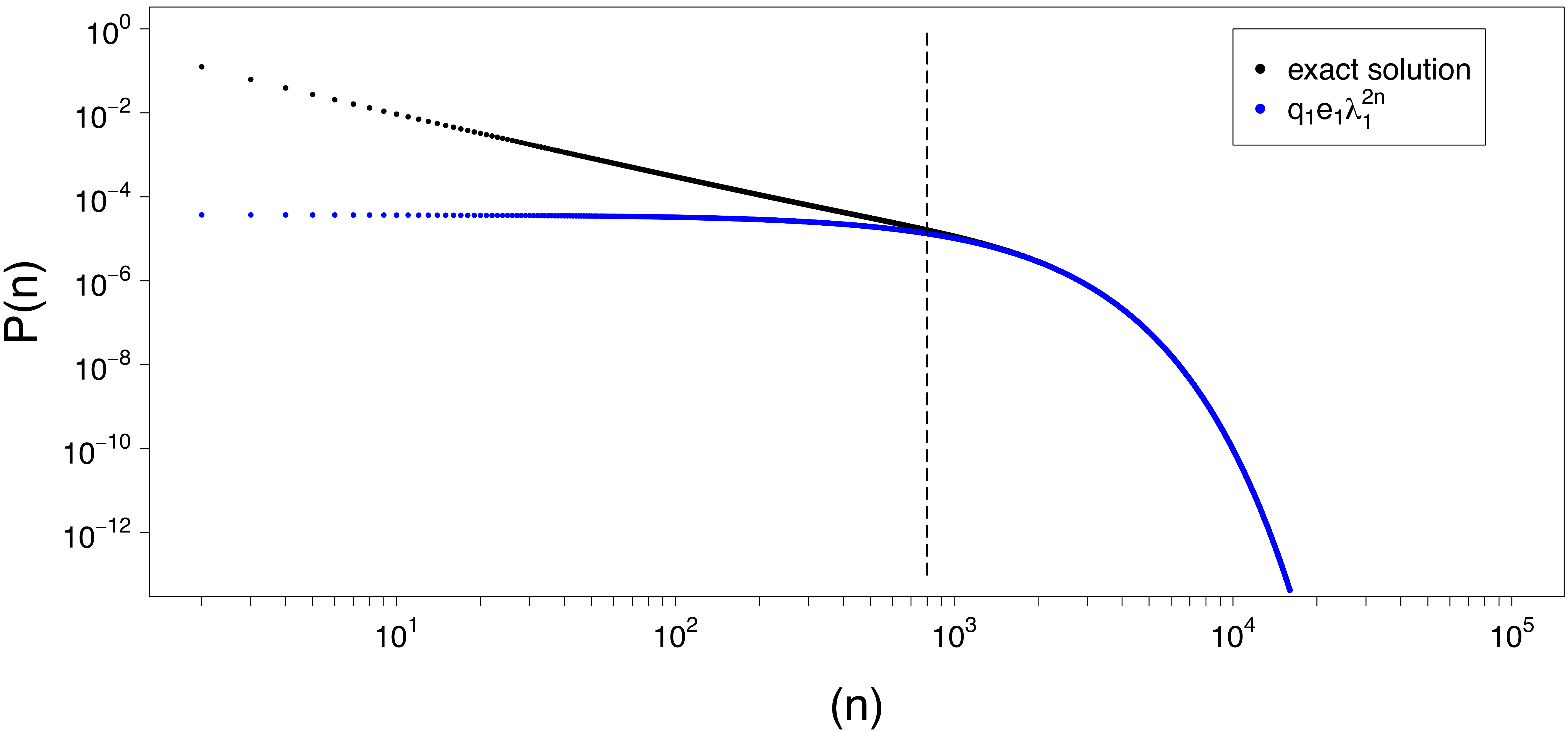
We know it's not a power law, but does it behave like one?



… provided **cut-off at (nearly) system size** and number of avalanches considered is not too large

Origin of the truncation: the role of the lead eigenvalue

$$\lim_{n\to\infty} \frac{P(n)}{q_1 e_1 \lambda_1^{2n}} = 1$$



Aside: Can it ever be a true power law?

Yes, under some conditions, in particular that the eigenvalues are well approximated by a geometric distribution.

Question to Alexander:
Is there such a system? How would it come about?

Alternative marker 1: Critical slowing

From the master equation: $\frac{\partial \mu}{\partial t} = -\alpha\mu + (1-\mu)w\mu$

If $\alpha \neq w$ then $\mu(t) = \frac{w-\alpha}{Ae^{(\alpha-w)t} + w}$ where $A = \frac{\mu_0}{w - w\mu_0 - \alpha}$

If $\alpha < w$, then as $t \to \infty$, $\mu \to \frac{w-\alpha}{w}$
If $\alpha > w$ then as $t \to \infty$, $\mu \to 0$.

Exponential convergence

If $\alpha = w$ (critical regime!) then $\mu(t) = \frac{1}{\alpha t + \mu_0^{-1}}$

as $t \to \infty$, $\mu(t) \to 0$ PL convergence

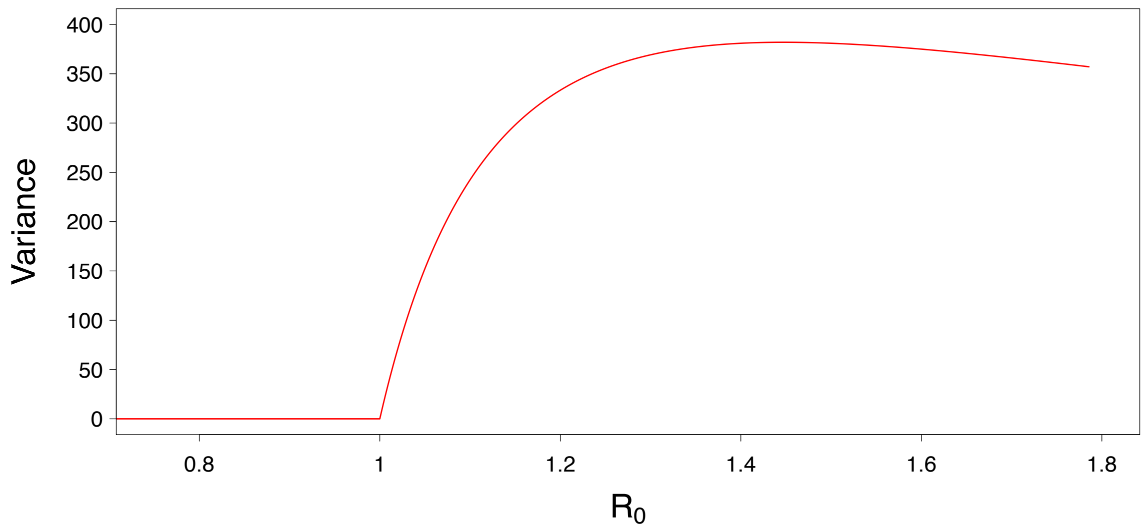
Alternative marker 2: Divergence of susceptibility

From the master equation:

$$\frac{\partial \sigma^2}{\partial t} = -2\big(\alpha + w\mu - w^2(1-\mu)\big)\sigma^2 + \big(\alpha\mu + (1-\mu)w\mu\big)$$

This gives: $$\sigma^2 = \frac{(\mu + (1-\mu)R_0\mu)}{2(1 + R_0\mu - R_0 w(1-\mu))}$$

$$\lim_{t\to\infty} \sigma^2(t) = \begin{cases} \alpha & \text{if } \alpha < 1 \ (R_0 > 1), \\ \frac{1}{2} & \text{if } \alpha = 1 \ (R_0 = 1), \\ 0 & \text{otherwise } (R_0 < 1). \end{cases}$$

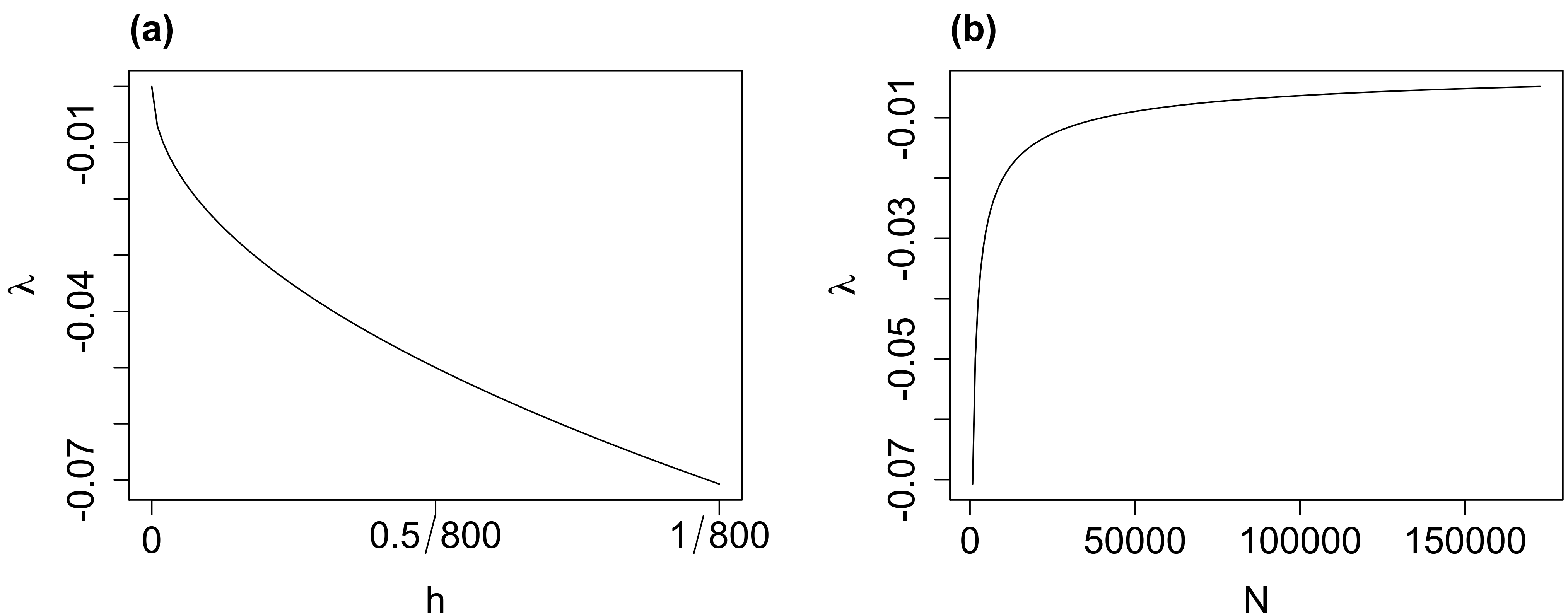


Part II: The driven case, 0<h<1/N

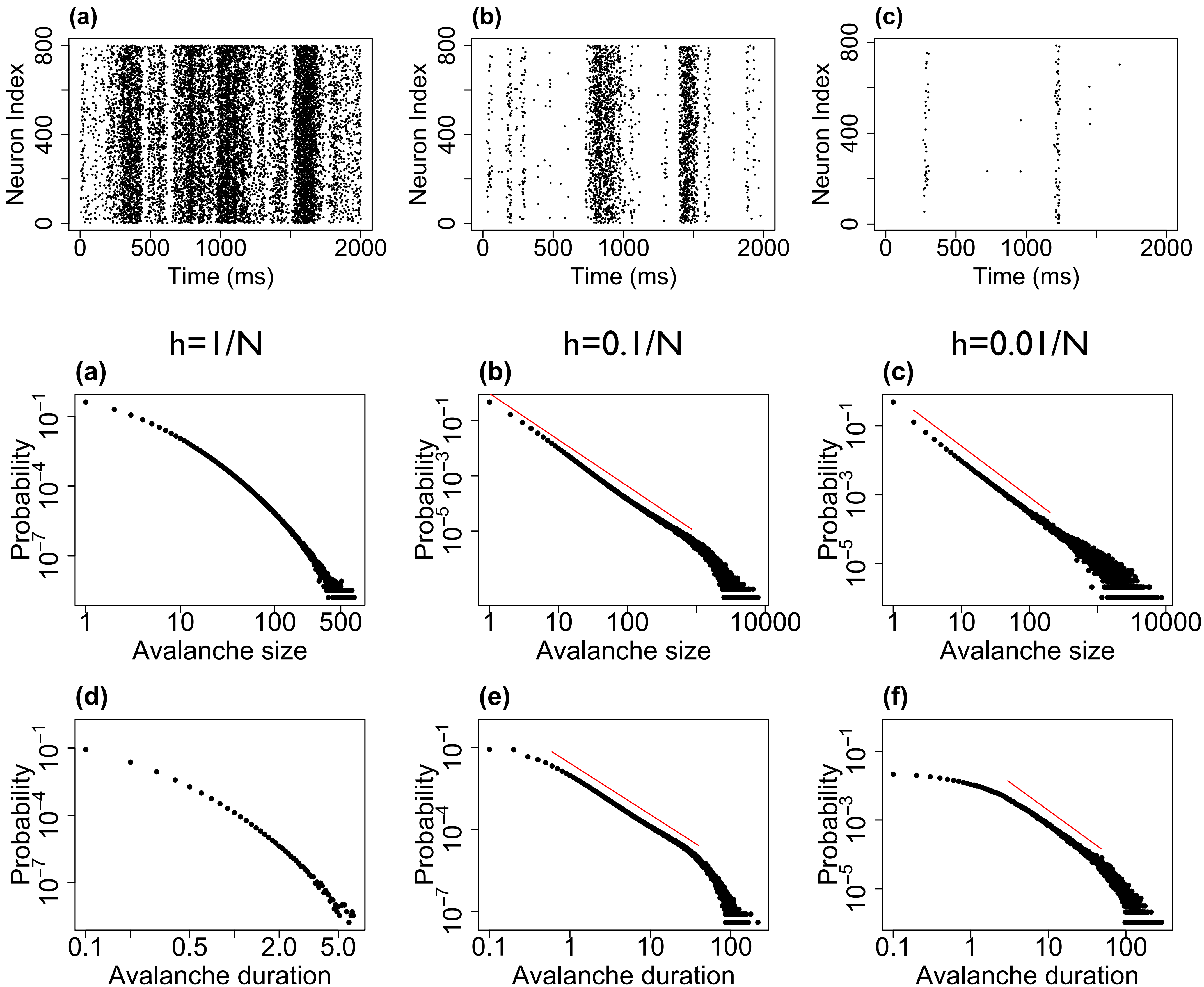
Fixed point: $$A = -\frac{hN}{2} \pm \sqrt{\frac{N^2h^2}{4} + N^2h}$$

Eigenvalue: $$\lambda = -\sqrt{h^2 + 4h}.$$

Two 'routes' to reaching the critical regime:



Bursting in the driven regime



Distribution of inter-avalanche intervals (1)

Adaptation of the tree approach previously described to describe those transitions that form a period of consecutive active to quiescent transitions

$$q_i = \frac{\alpha i N}{(wi + hN)(N - i) + \alpha i N}$$

Then $$P(IAI_k) = p(N_0, k) = (1 - q_{N_0-k}) \prod_{j=0}^{k-1} q_{N_0-j}$$

Since time steps used in Gillespie are taken from exponential distribution with rate r which depends on the number of active neurones,

$$f(x, N_0, k) = \sum_{j=0}^{k} r_{N_0-j} e^{-r_{N_0-j} x} \left(\prod_{i=0, i \neq j}^{k} \frac{r_{N_0-i}}{r_{N_0-i} - r_{N_0-j}} \right)$$

Distribution of inter-avalanche intervals (2)

Distribution of durations for a given number of active neurones:

$$F(x, N_0) = \sum_{k=1}^{N_0} f(x, N_0, k)\, p(N_0, k)$$

(weighted sum of hypoexponentials)

We can work out the distribution of initial states (by induction):

$$\begin{aligned} P(k+1) &= \frac{1}{q_{k+1}}\big(P(k) - (1 - q_{k-1})P(k-1)\big) \\ &= \frac{(1-q_1)(1-q_2)\cdots(1-q_k)}{q_2 q_3 \cdots q_{k+1}} P(1). \end{aligned}$$

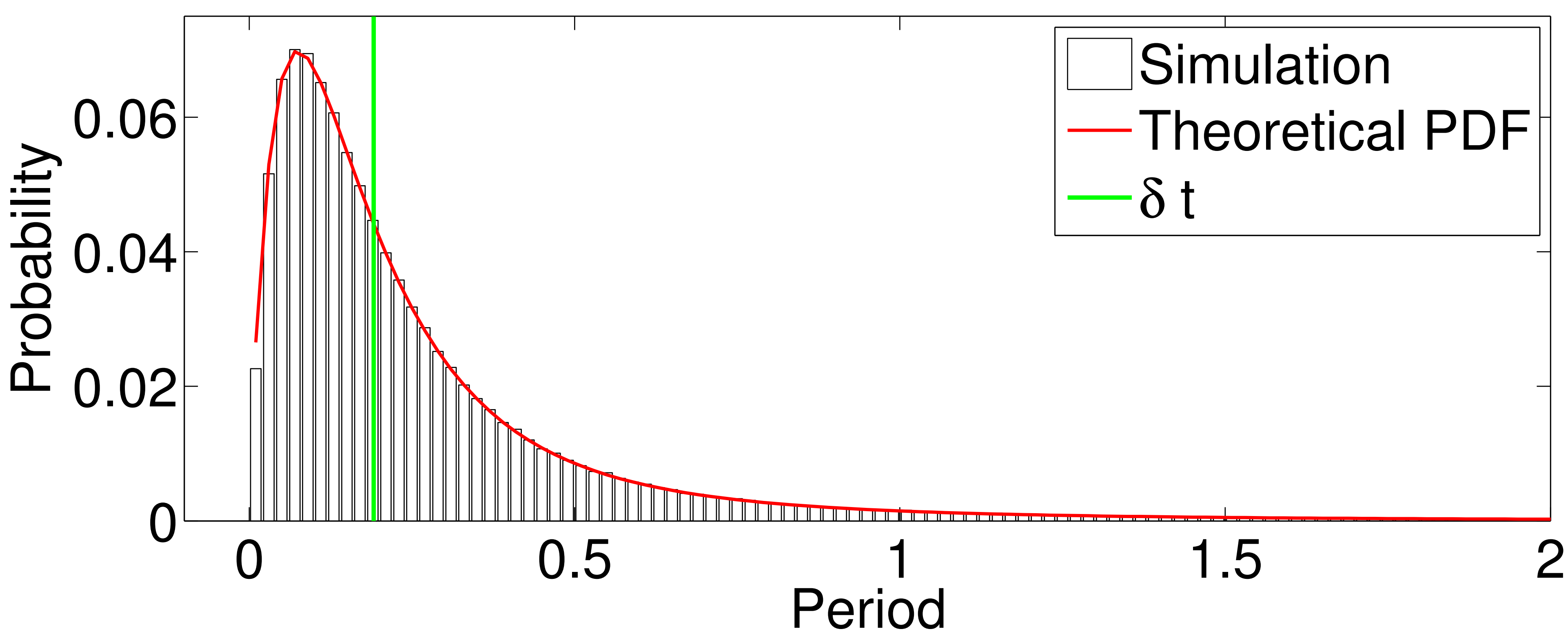
The probability $P_A(N_0)$ of having a given number of active neurones following a quiescent to active transition is:

$$P_A(N) = (1 - q_{N-1})P(N-1)$$

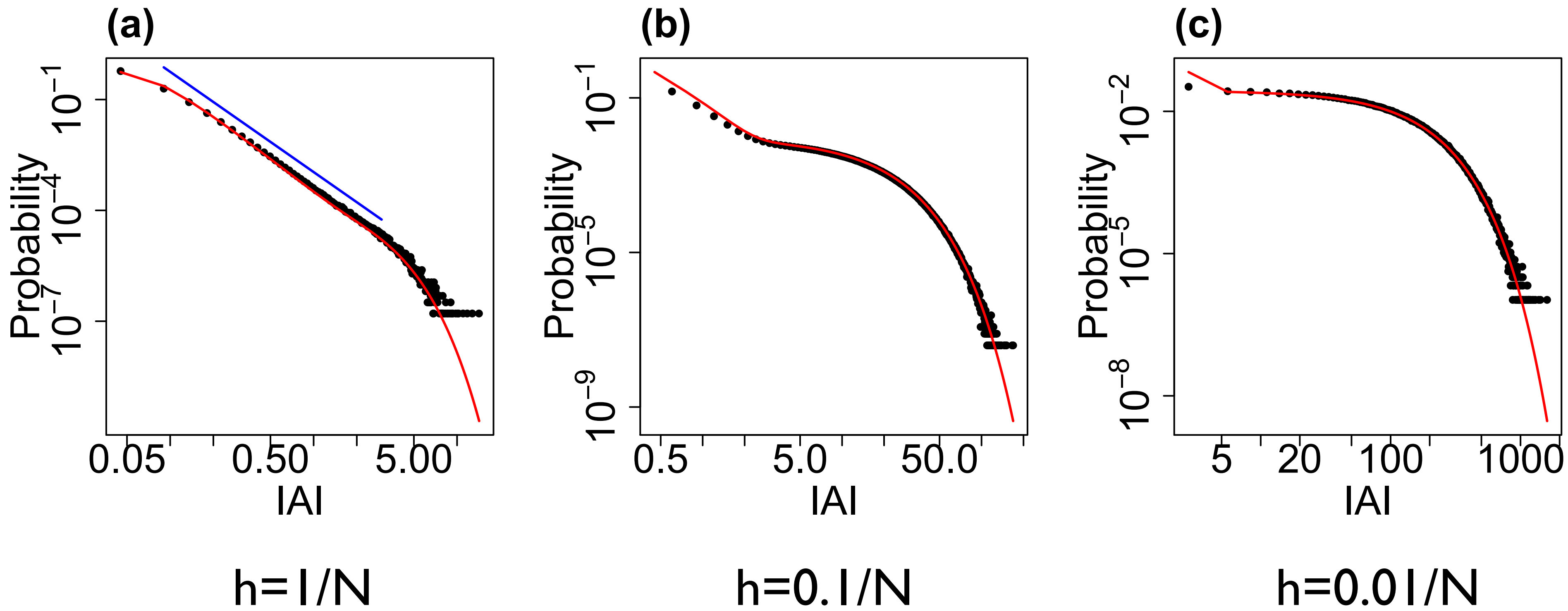
Distribution of inter-avalanche intervals (3)

So that: $$\wp(x) = \sum_{i=0}^{N} \left(P_A(i) \sum_{m=1}^{i} f(x,i,m)\, p(i,m) \right)$$

Theoretical vs Gillespie simulations



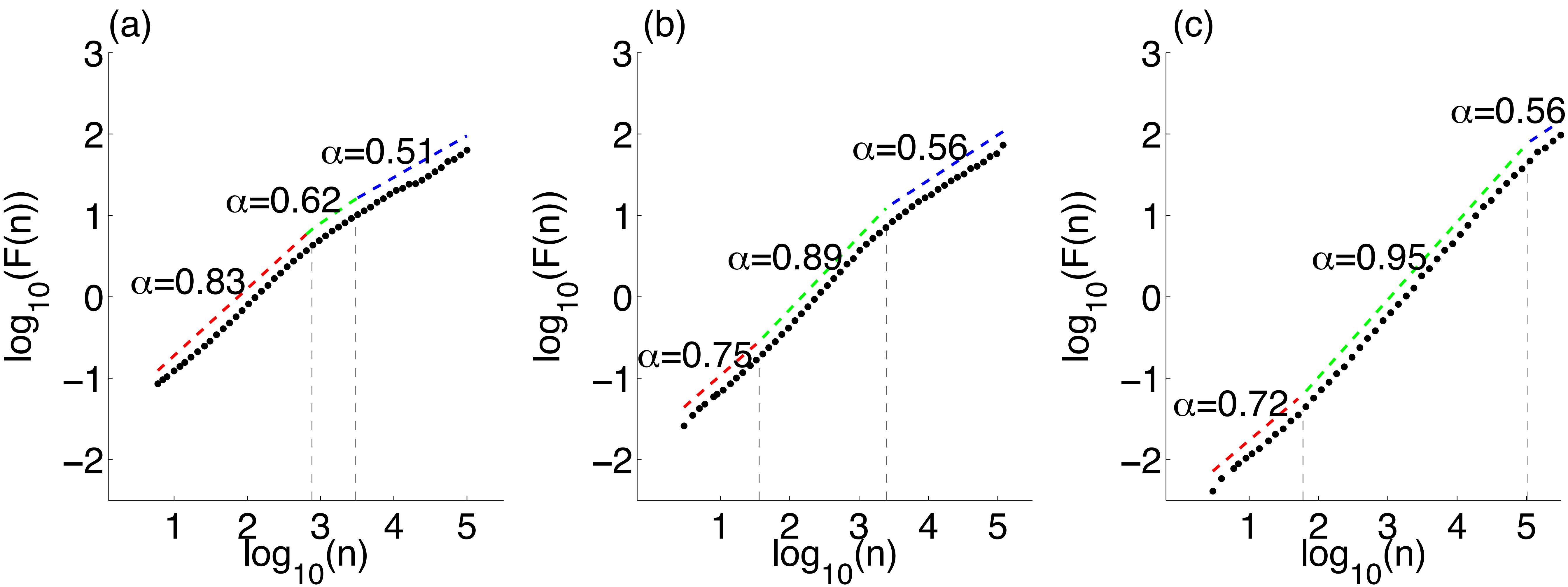
Assessment of PL in distribution of IAIs



For h=0.01/N, distribution is exponential.
For h=1/N, we find (partial) power laws.

Alternative marker: LRTCs in IAIs

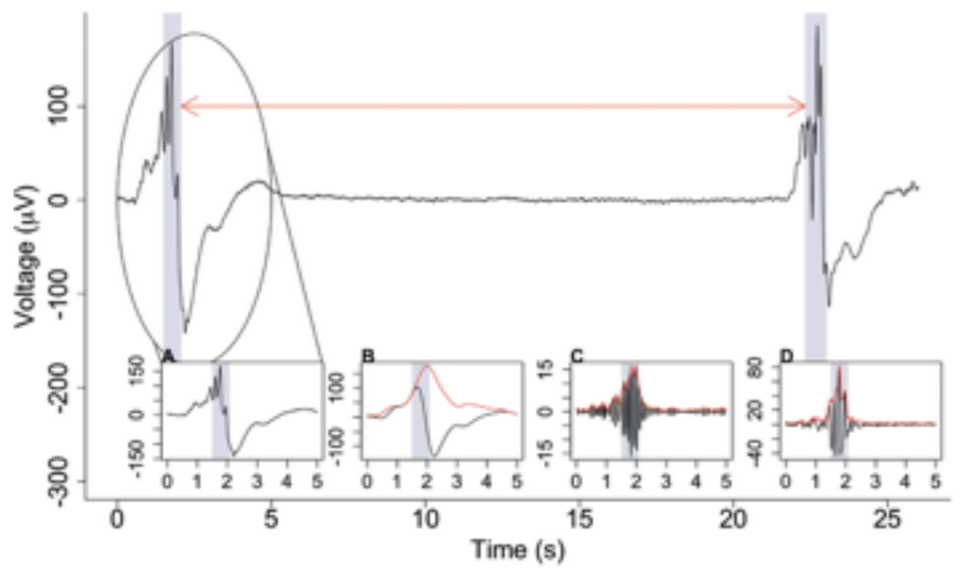
Presence of power law of auto-covariance function of the IAIs through estimation of the Hurst exponent by detrended fluctuation analysis (DFA).

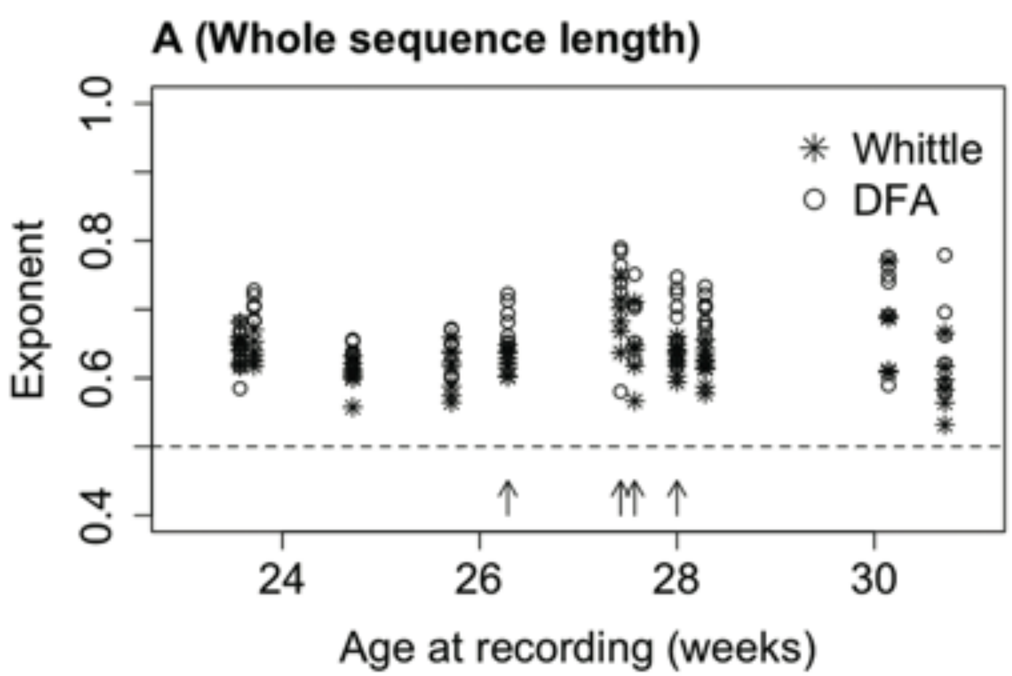


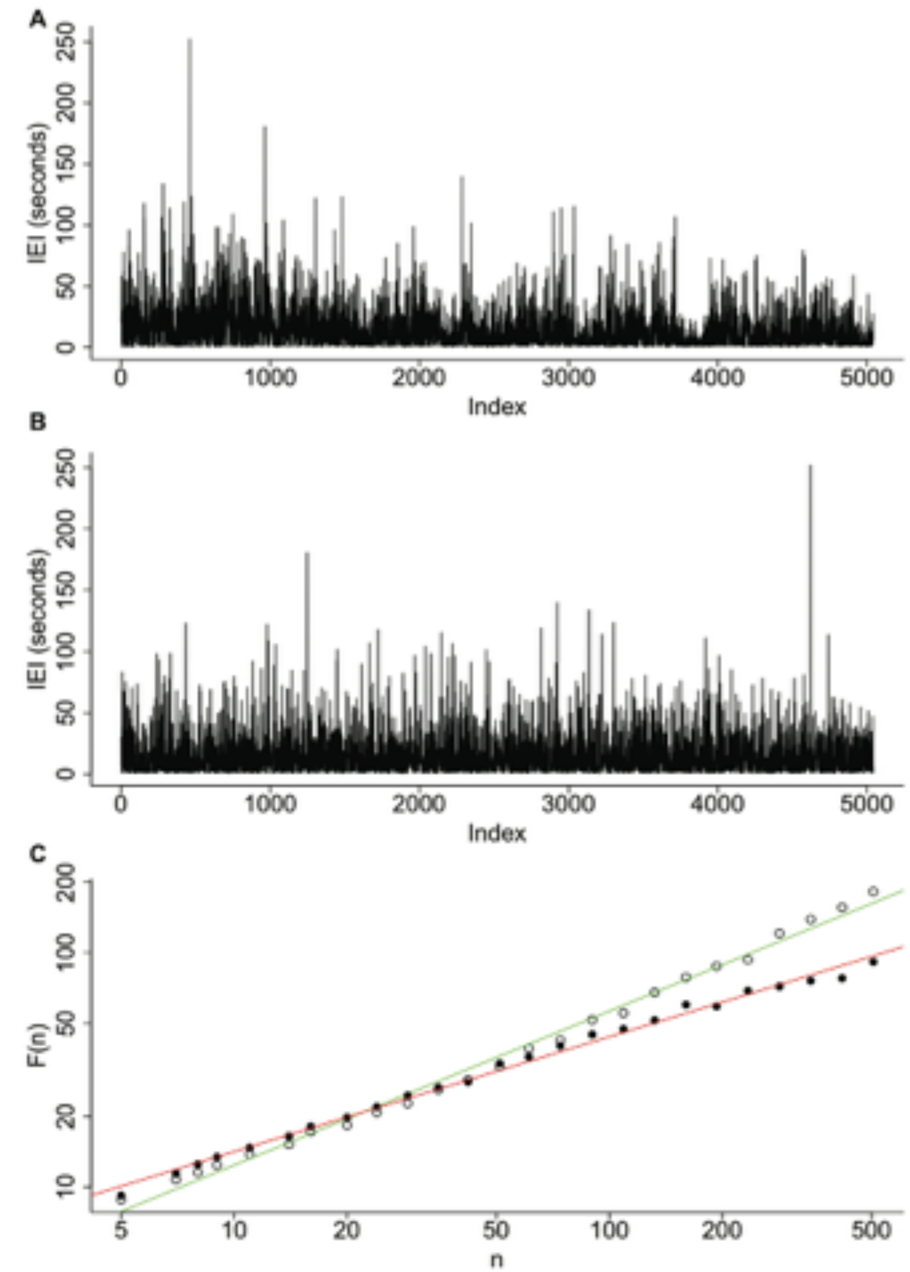
N=800 N=3200 N=172800

LRTCs in waiting times of human preterm EEG

Hartley, Berthouze et al. (2012). *PLoS One* 7(2):e31543







In summary: Two ‘routes’ to criticality

1. Approaching the critical regime through a reduction in the external input results in distribution of avalanche sizes displaying scale-free behaviour. Further, even though the distribution of IAIs was theoretically derived and was shown to be a weighted sum of hypoexponentials, the hypothesis that the IAI distribution follows a power law was not rejected by statistical testing.

2. Approaching the critical regime through increasing the system size results in lengthening of the long-range temporal correlations. These correlations are observed despite the fact that the distribution of avalanche sizes no longer exhibits scale-free behaviour and does not change with the increase in system size. These temporal correlations are lost if the critical regime is instead approached through reducing the external input.

Conclusions

New insights about origin and signature of criticality (in the sense of a system operating at a transcritical bifurcation) in a **finite size** system.

Identification of **alternative markers** of criticality (which may require behavioural or pharmacological manipulations).

Highlights that power-law statistics is not a necessary (or even sufficient) condition for a system to be critical and that more robust (critical?) assessment tools are required.

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Engineering and Physical Sciences Research Council

MRC Medical Research Council