Single Neuron Dynamics for Retaining and Destroying Network Information?

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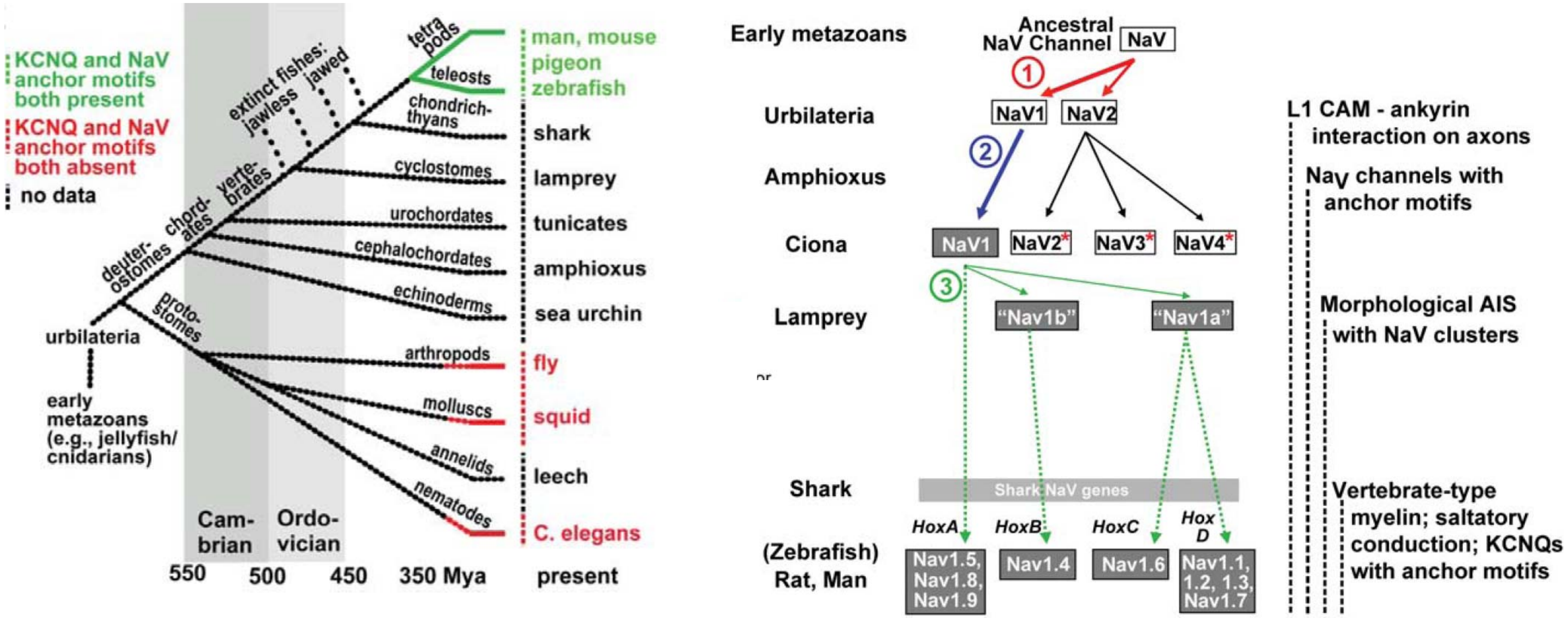
Why care about the micro-biophysics of AP initiation?

The axon initial segment and vertebrate self-respect



Hill et al. 2009,

Theoretical reasons to care?

How Spike Generation Mechanisms Determine the Neuronal Response to Fluctuating Inputs

Nicolas Fourcaud-Trocmé, David Hansel, Carl van Vreeswijk, and Nicolas Brunel
Centre National de la Recherche Scientifique Unité Mixte de Recherche 8119, Neurophysique et Physiologie du Système Moteur, Unité de Formation et de Recherche Biomédicale, Université Paris 5 René Descartes, 75270 Paris Cedex 06, France

Experimental implications

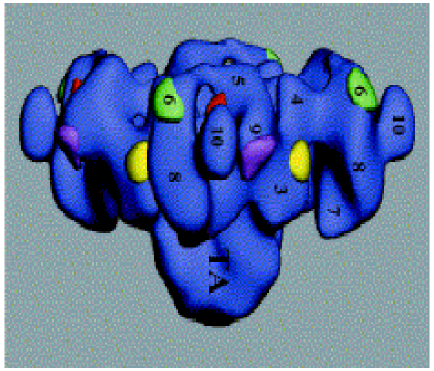
How sharp are spikes in cortical neurons?

Our work shows that the spike slope factor, Δ_T, is one of the main parameters on which the response of a neuron to fluctuating inputs depends. Activation curves of Na^+ channels have been measured in several preparations, including neocortical pyramidal cells (Fleidervish et al., 1996), hippocampal pyramidal cells, granule cells, and basket cells (Martina and Jonas, 1997; Fricker et al., 1999; Ellerkmann et al., 2001). These authors used Boltzmann functions to fit the observed data. Using their best-fit parameters, one finds Δ_T in the range of 3–6 mV for these types of cells. However, in all cases, there are few data points in the region of the threshold, leading to a considerable uncertainty in the estimate of this parameter. Therefore, more experiments are needed to determine the spike slope factor of cortical neurons.

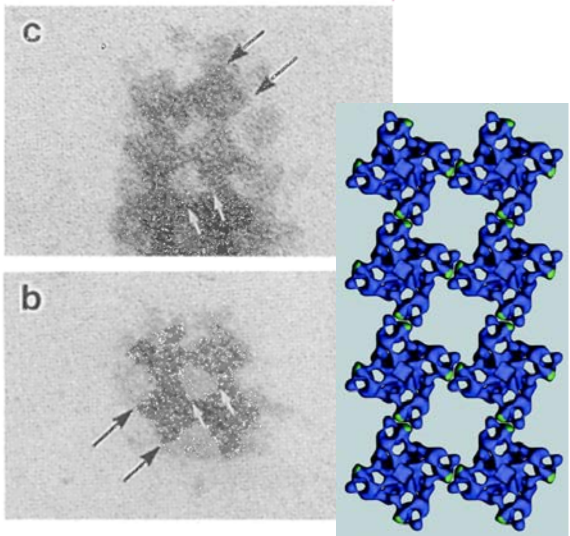
Fourcaud-Trocme et al. 2009,

Cooperative gating in clustered Ca2+ channels

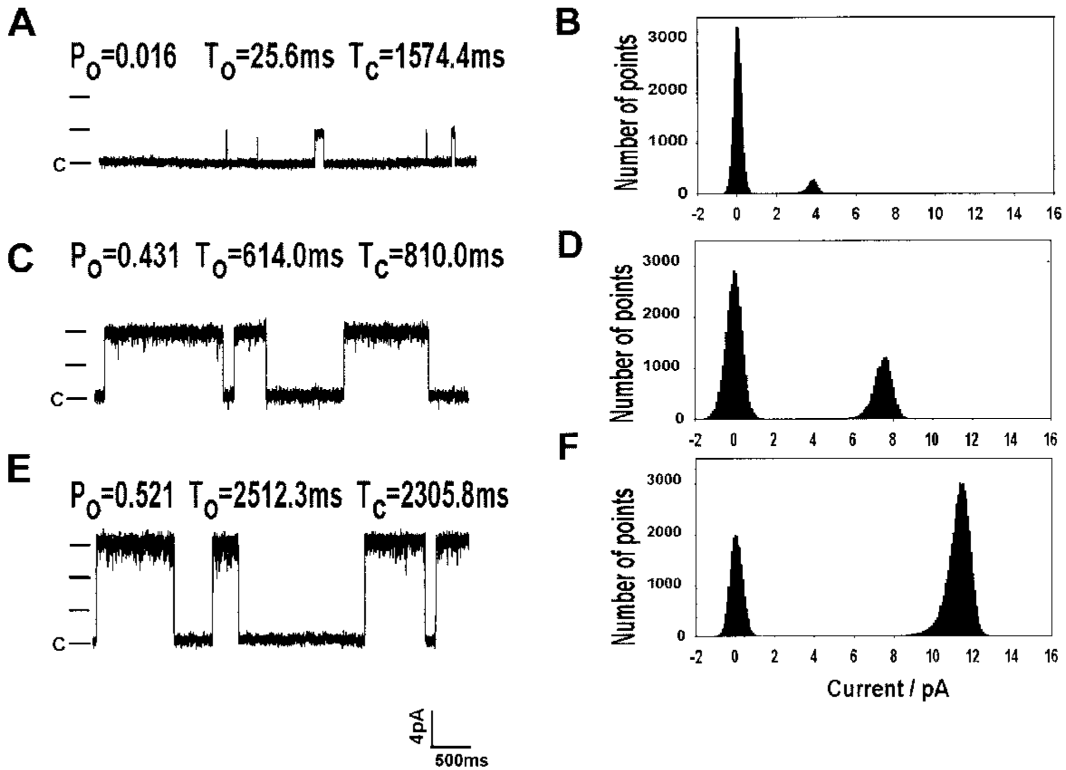
structure



clustering



cooperative activation

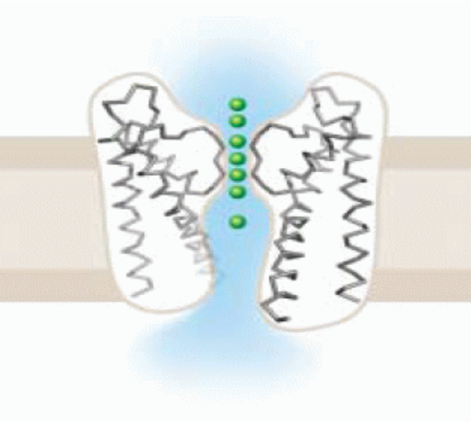


Marx et al. Science 1998,

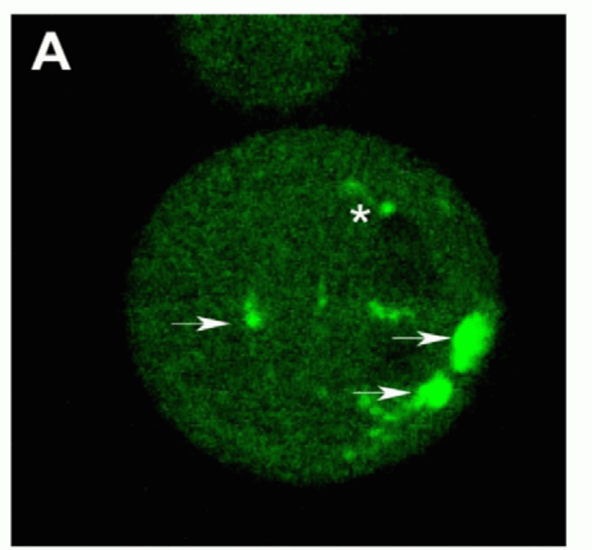
Marx et al. Circulation 2001

Cooperative gating in clustered K+ channels

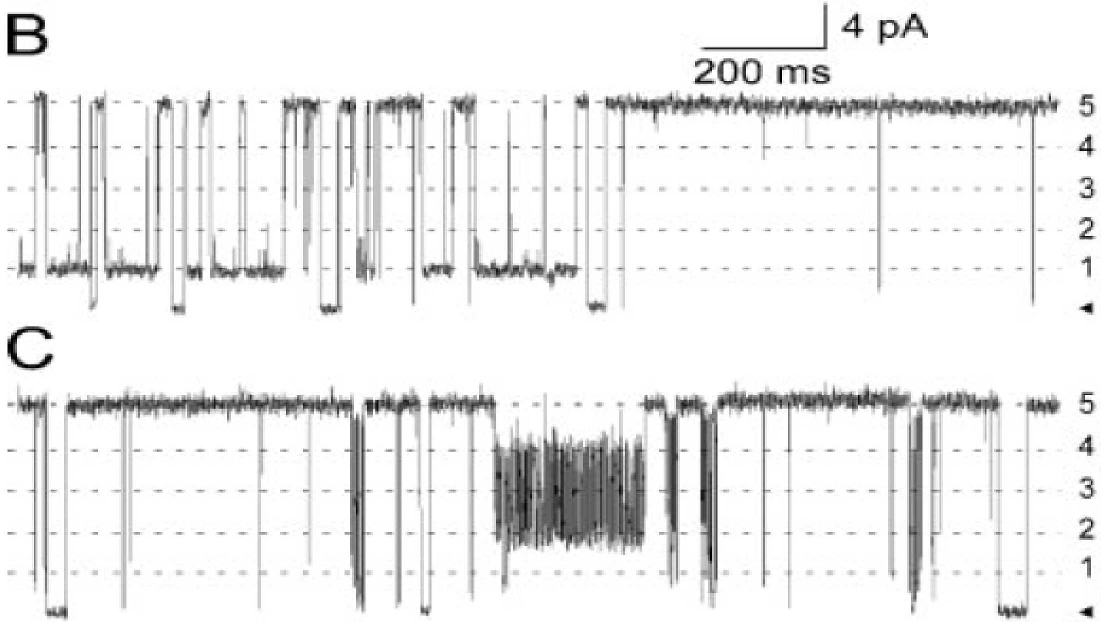
structure



clustering



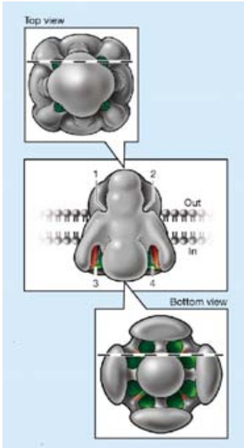
cooperative activation



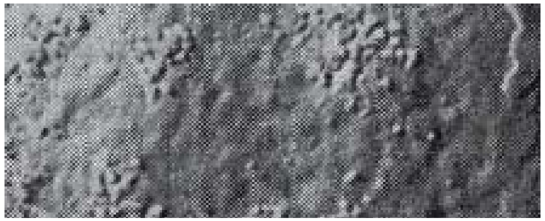
Molina et al. J Chemical Biology 2006

Cooperative gating in clustered Na+ channels

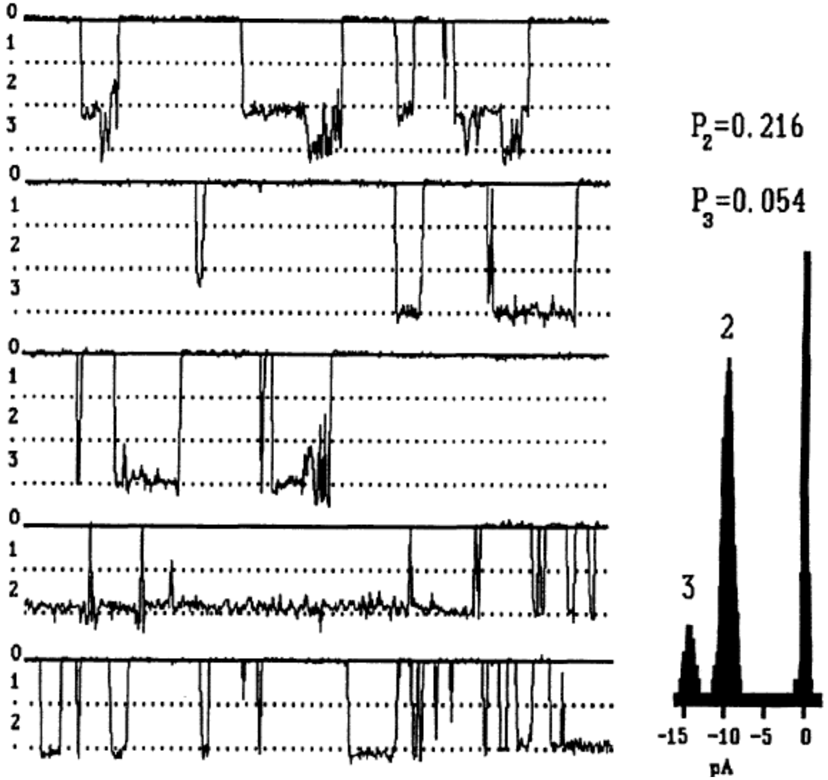
structure



clustering



cooperative activation



„To a true believer, there can be no plainer demonstration of … “ cooperative gating

D. Bray & Th. Duke (2004)

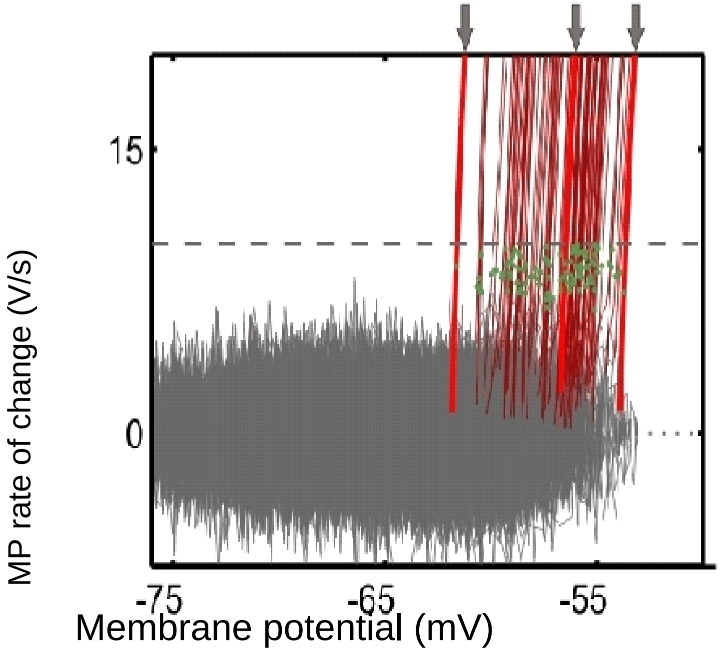
„Conformational spread: the propagation of allosteric states in large multiprotein complexes“.

Undrovinas, Fleidervish, Makielski, Circ. 1992

Post et al. Biochim. Biophys. Acta 1985

Cortical neurons have *really* rapid AP onsets

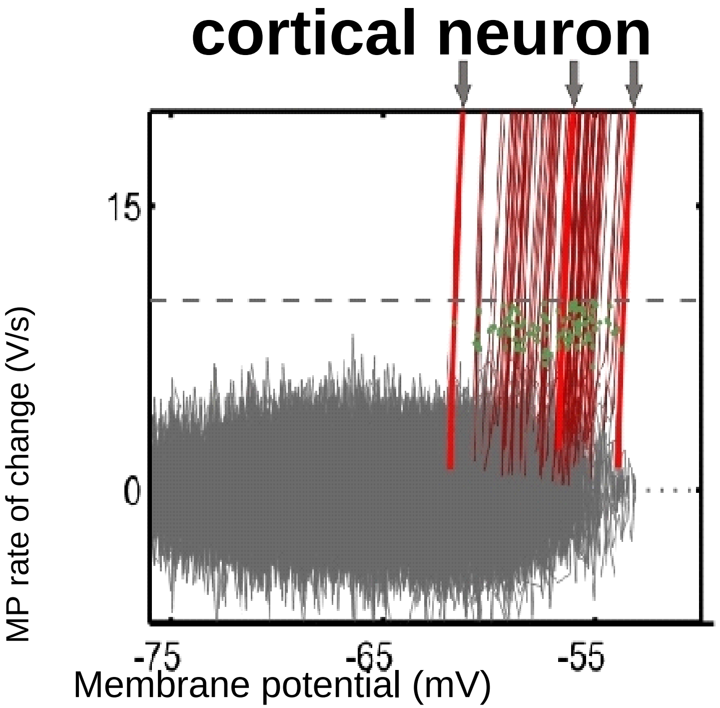
cortical neuron

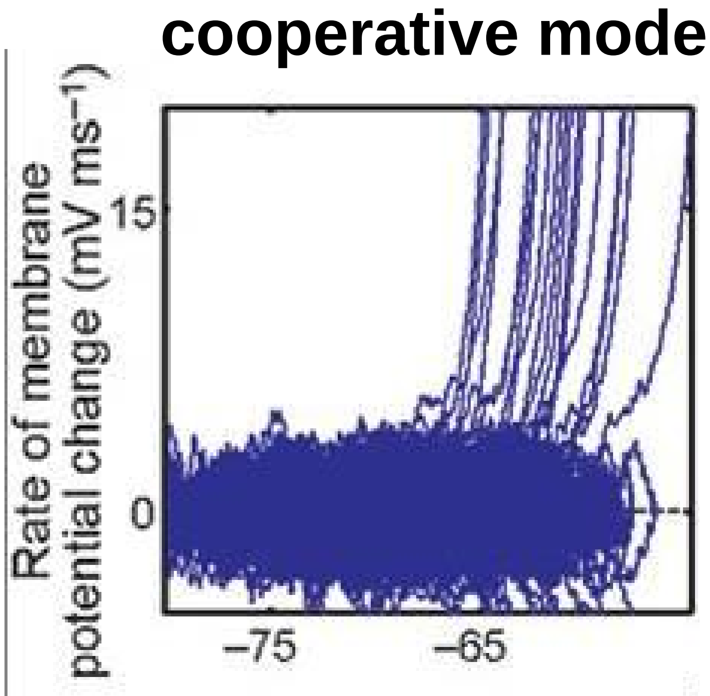


Naundorf, Wolf, Volgushev (2006, 2007)

See also Gerstner & Richardson's work on fitting adaptive EIF to cortical neurons.

Cortical neurons have *really* rapid AP onsets





Naundorf, Wolf, Volgushev (2006, 2007)

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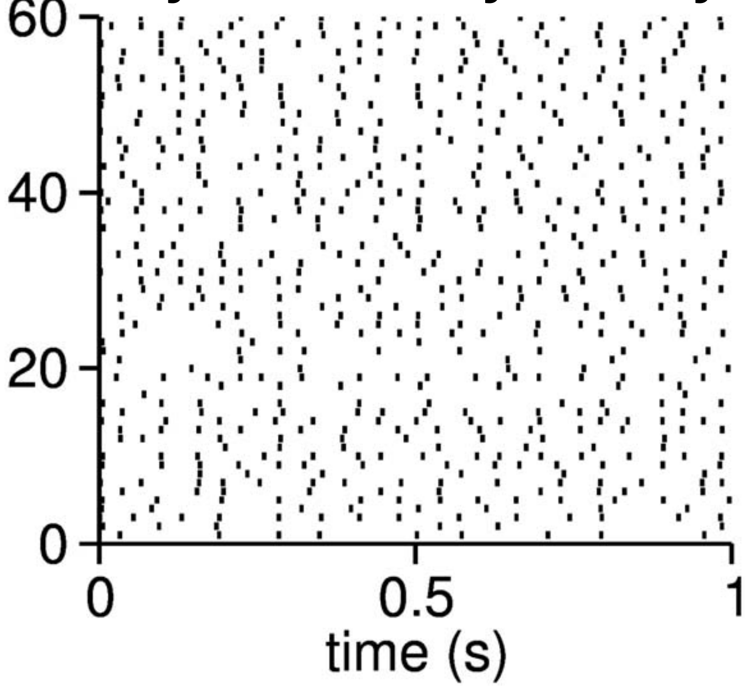
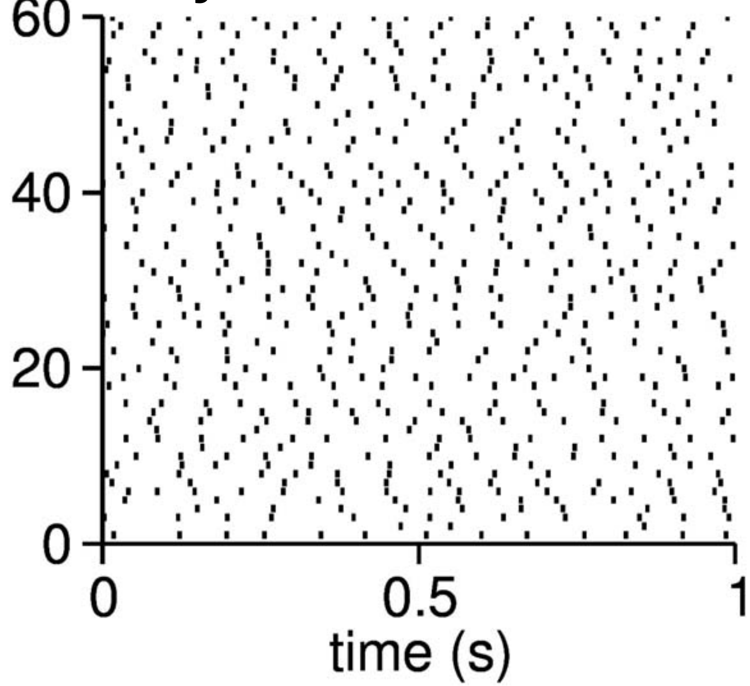
Single cell and network dynamics

Collective network states:

Rhythms and Synchrony



Asynchronouse states



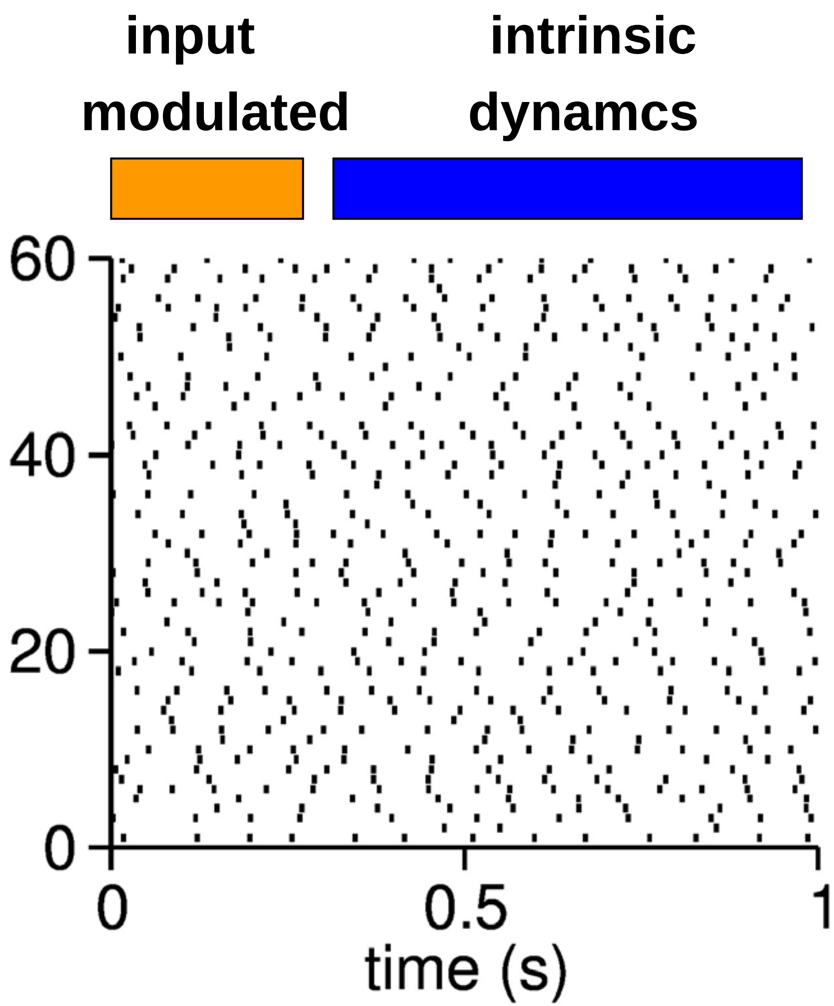
important single cell properties:

subthreshold oscilations, synaptic delays, phase response curves …

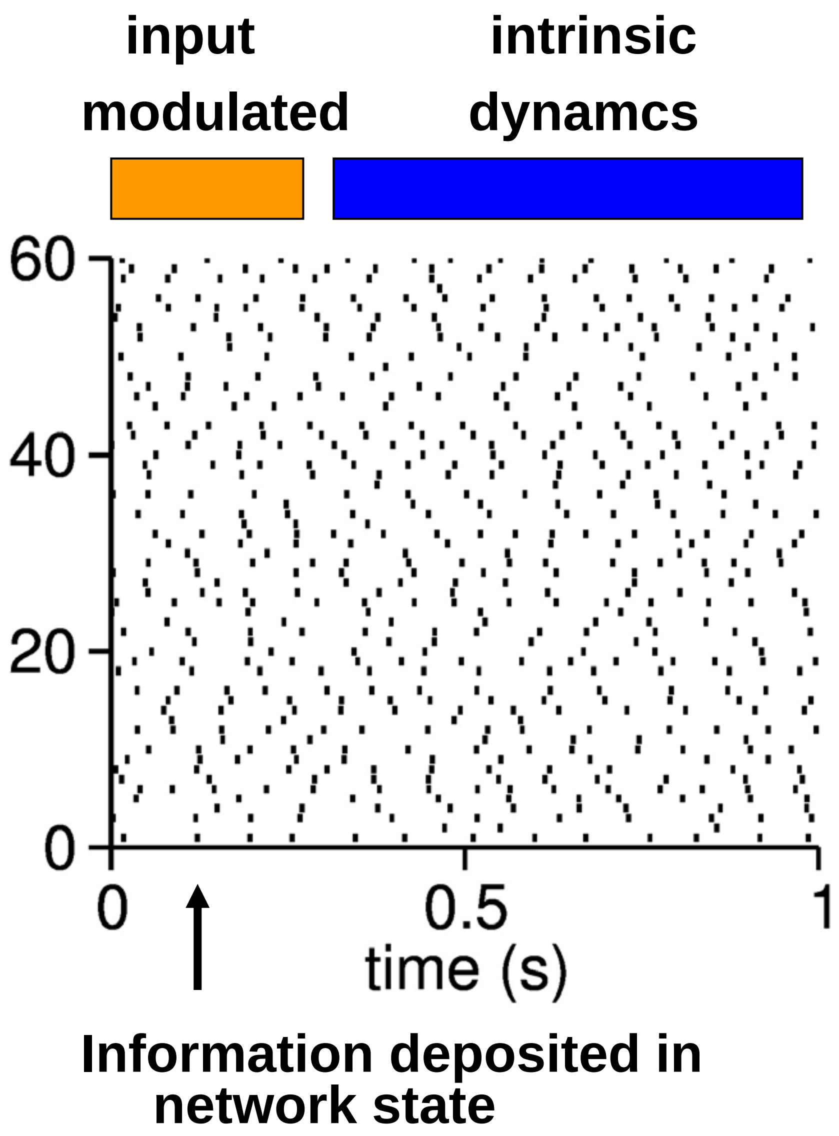
important single cell properties :

?

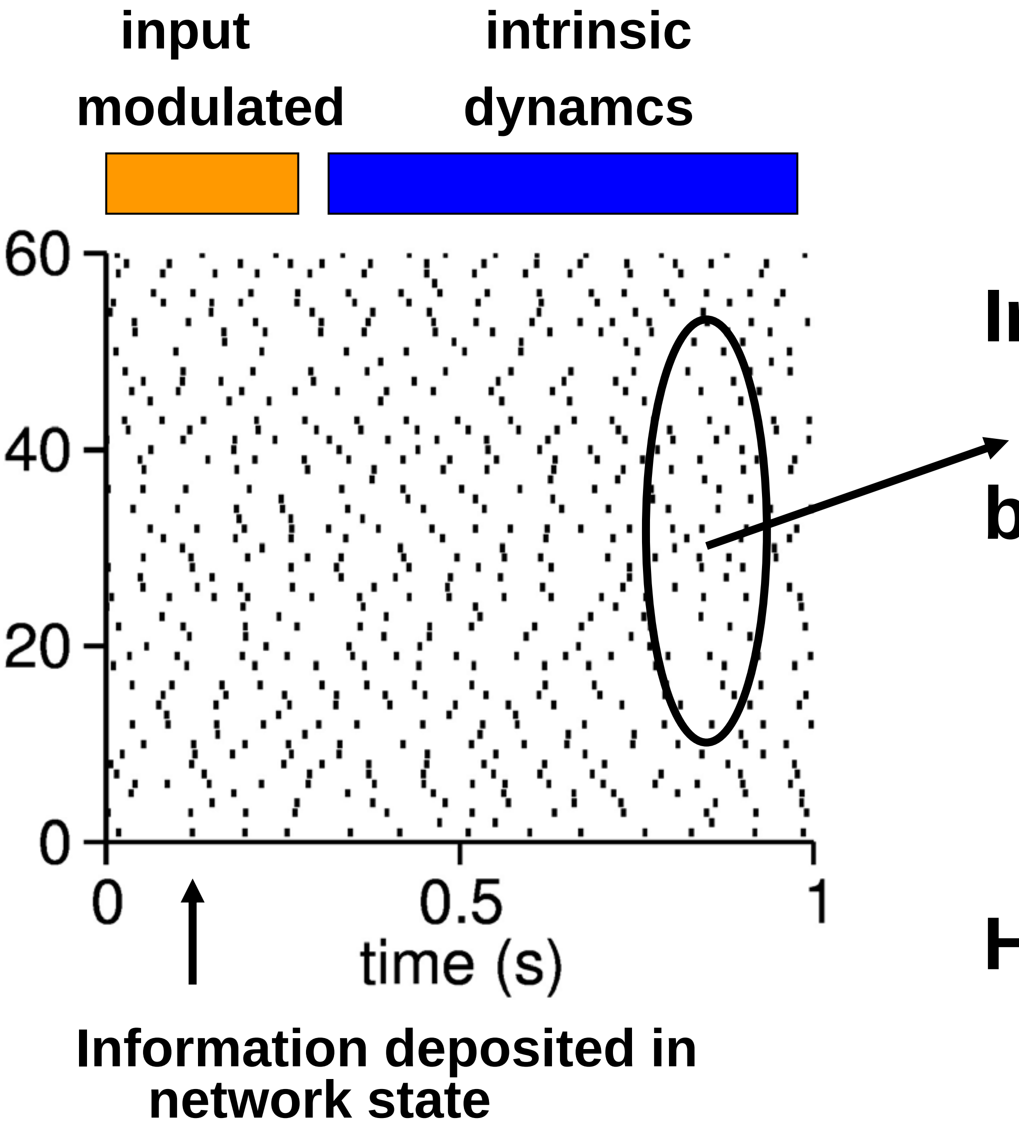
Information preservation in network dynamics



Information preservation in network dynamics



Information preservation in network dynamics



Information recoded, preserved, degraded, ..

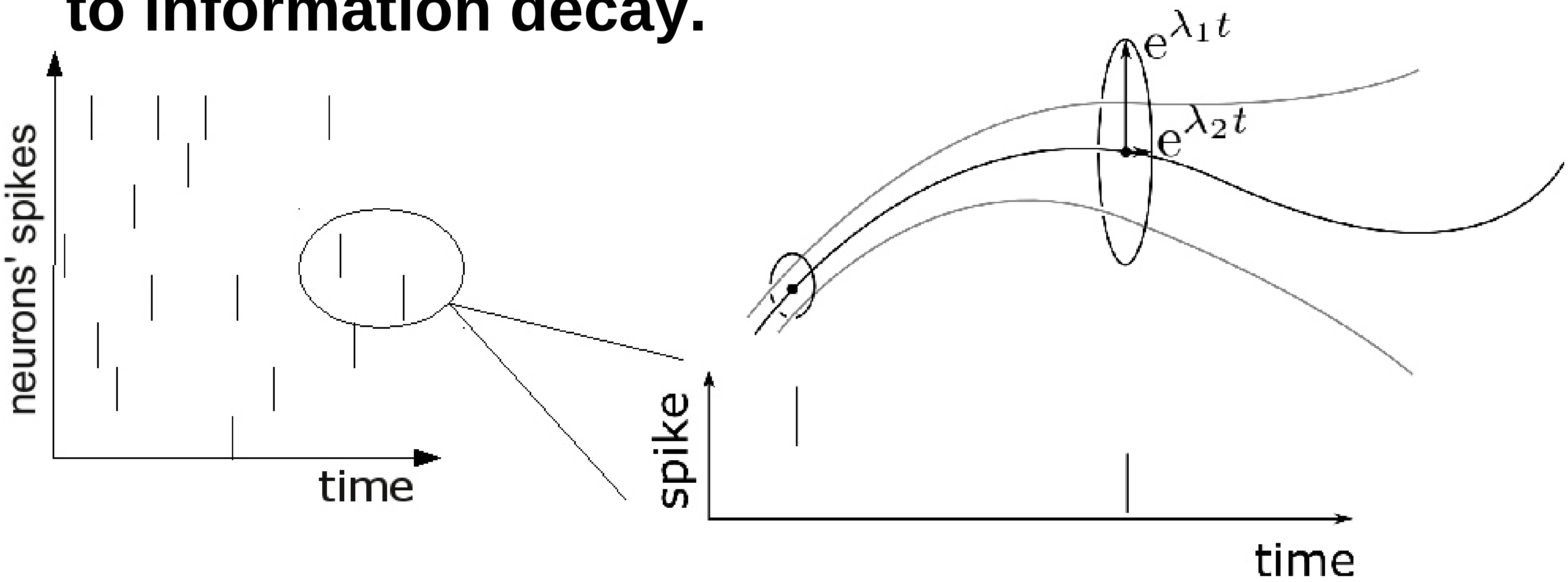
by

intrinsic network dynamics

How to quantify?

Degrading information by dynamics

Generic *chaotic* dynamics will in general lead to information decay.



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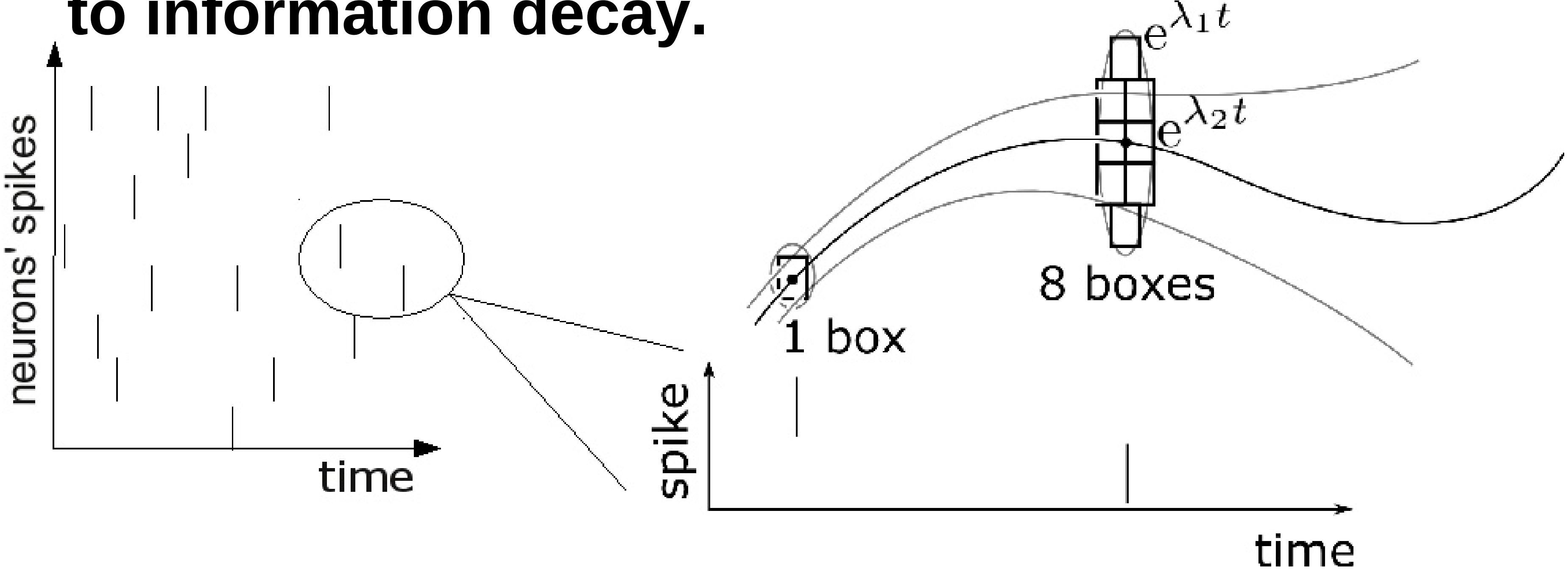

Stretching and folding of phase space characterized by Lyapunov exponents: $\lambda_i, \quad \lambda_1 > \lambda_2 > \ldots > \lambda_N$

Degrading information by dynamics

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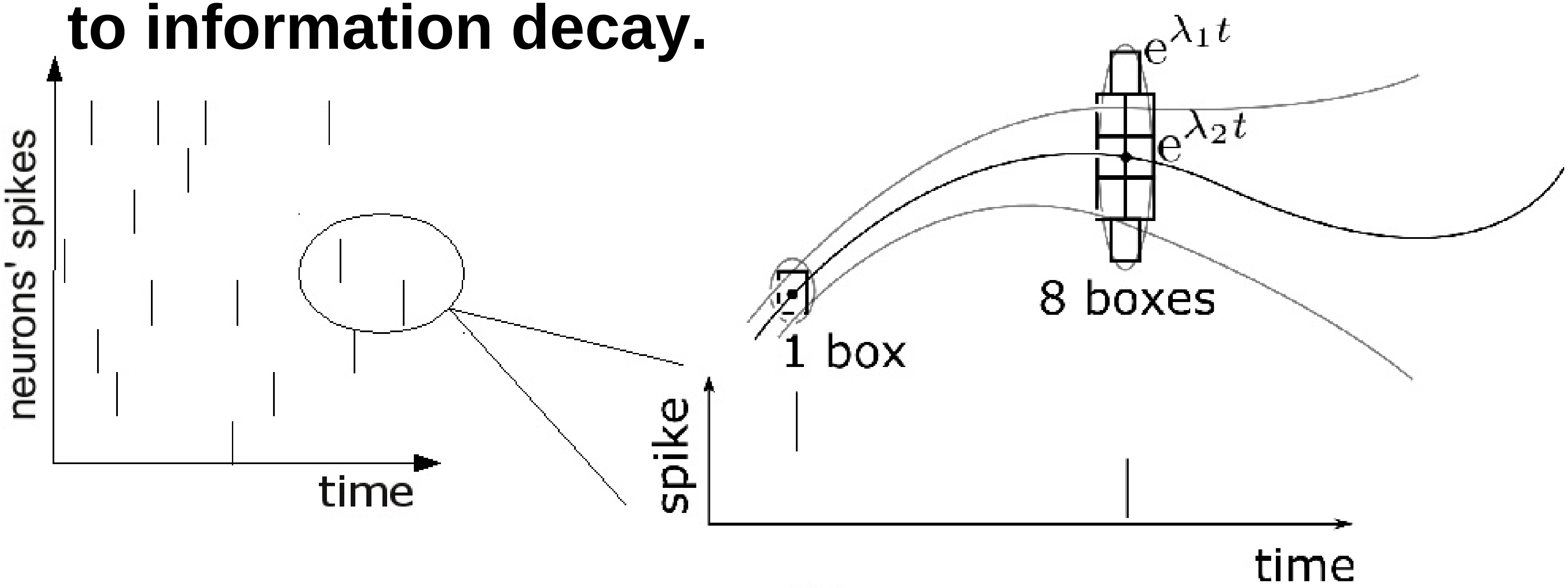
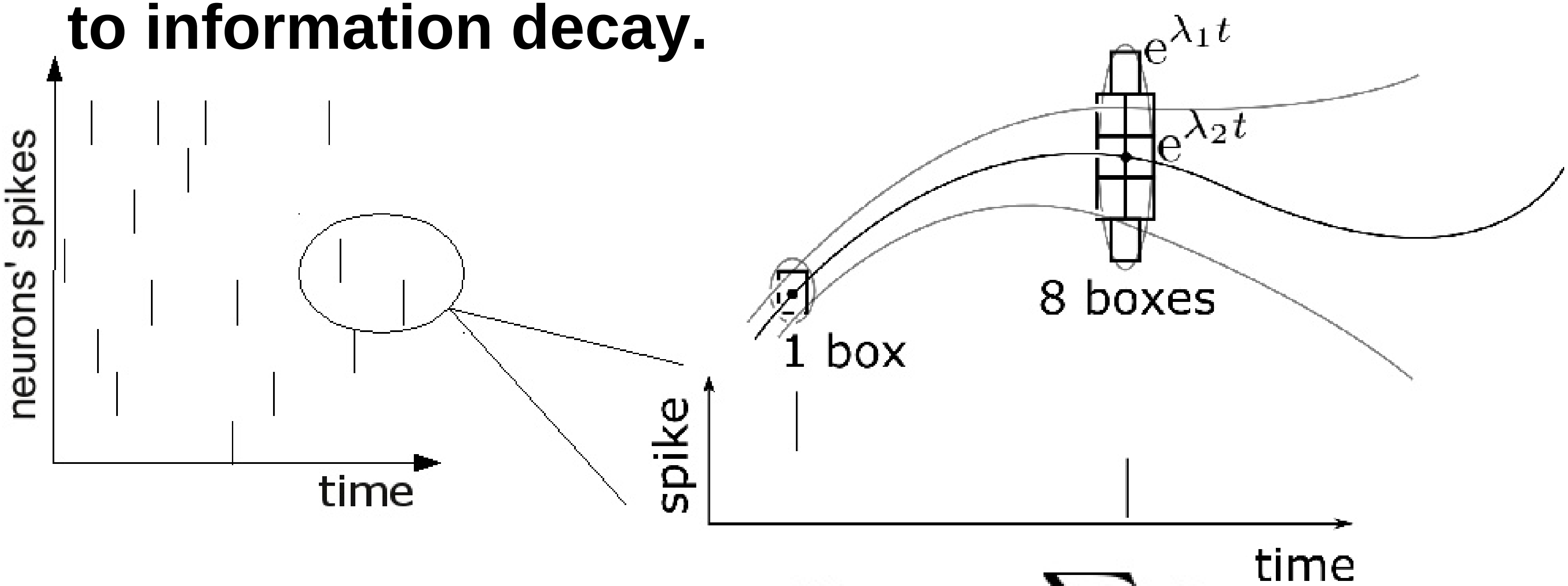


Kolgomorov-Sinai-Entropy : H_{KS}

Rate of information loss about initial condition

Degrading information by dynamics

Generic *chaotic* dynamics will in general lead to information decay.



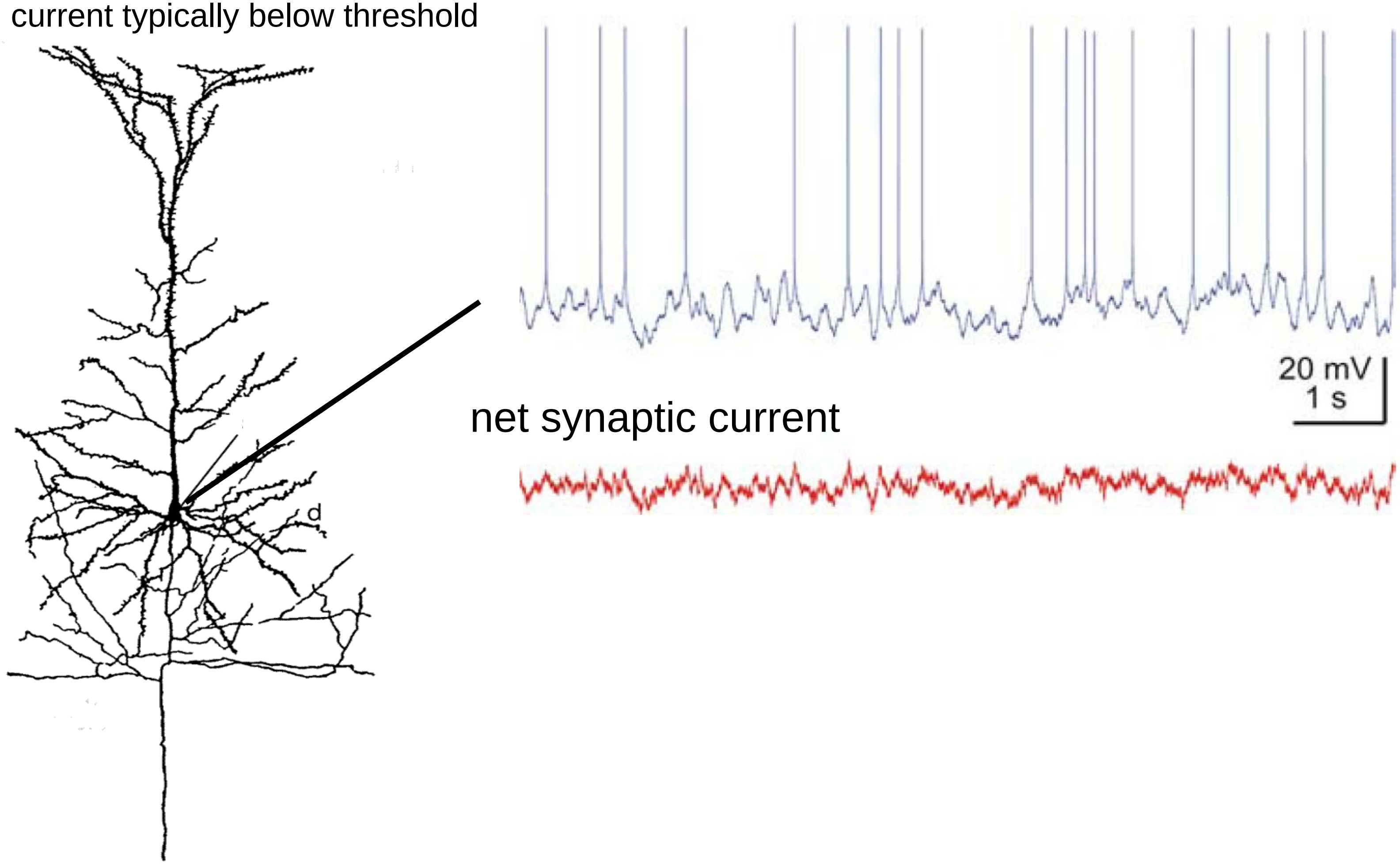
Kolgomorov-Sinai-Entropy : $H_{KS} = \sum_{\lambda_i > 0} \lambda_i$

Pesin (1977)

Pesin Theory: KS-Entropy from complete Lyapunov spectrum.

Irregular activity in cortical circuits

ca. 10 000 synaptic inputs
irregular firing
mean current typically below threshold



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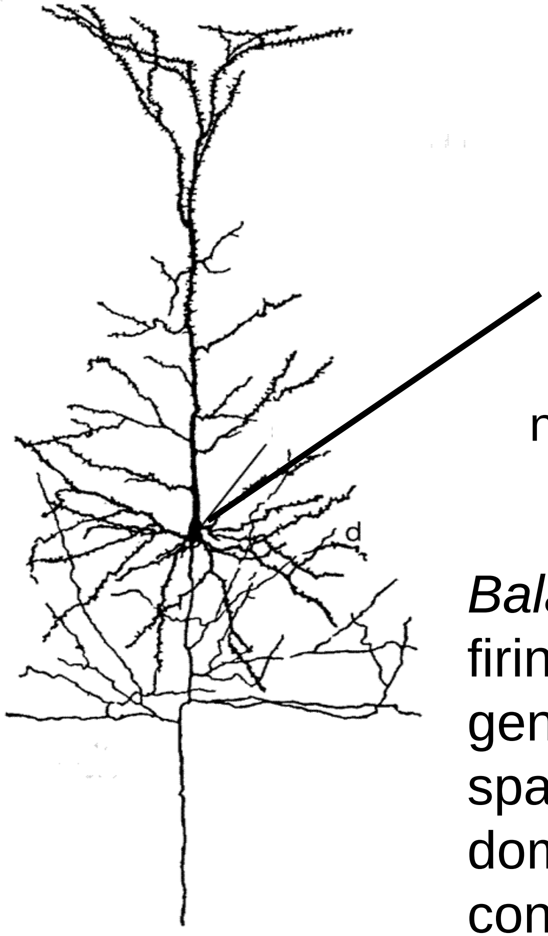
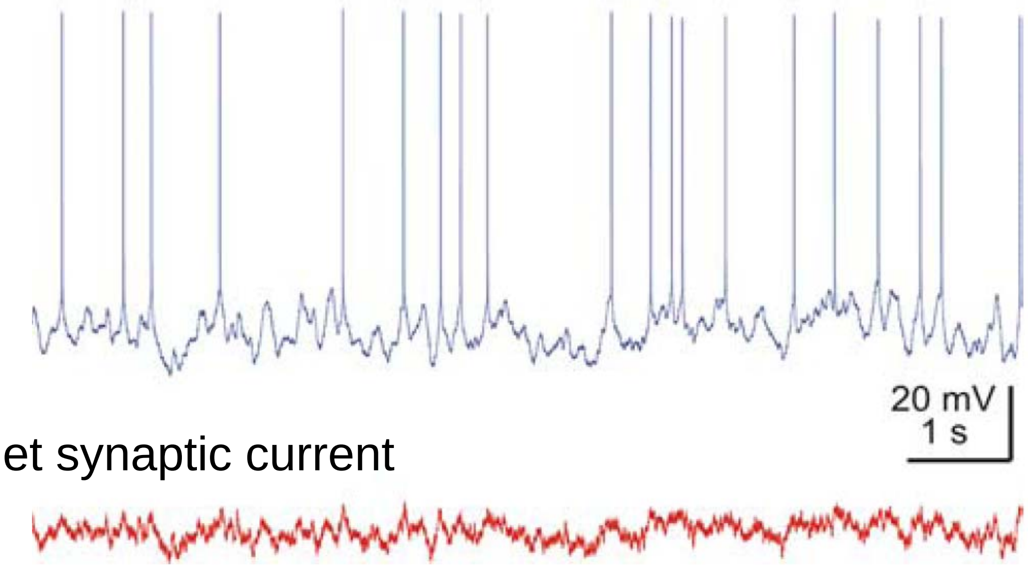
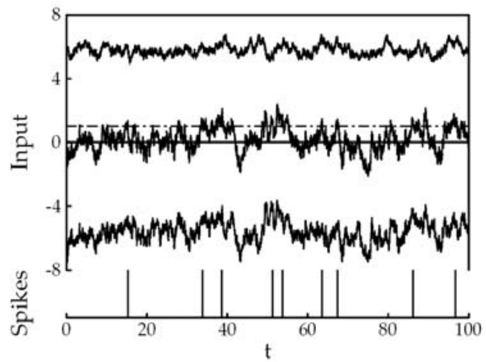




net synaptic current

Balanced State:
firing irregularity robustly generated by
sparse networks,
dominated by inhibition,
connected by strong synapses.



van Vreeswijk & Sompolinsky (1996)

Balanced chaos and single neuron dynamics

What is the nature of chaos in balanced states?

Binary neurons:

infinite largest Ly

van Vreeswijk and Sompolinsky (1996,

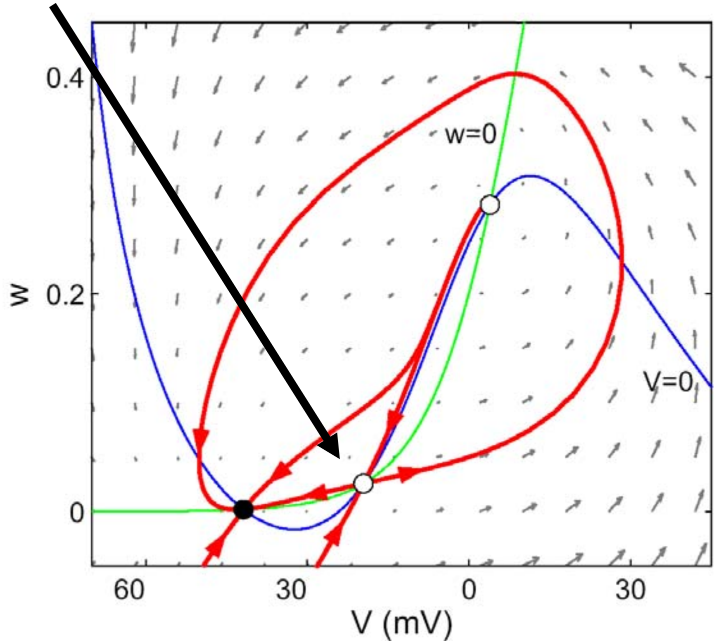
I&F neurons, all inhibitory

No positive Lyapunov e

Zillmer, et al. (2006)
Jahnke, Memmesheimer, Timme (2008
Zillmer, N. Brunel, D. (2009)
Jahnke, Memmesheimer, Timme (2009

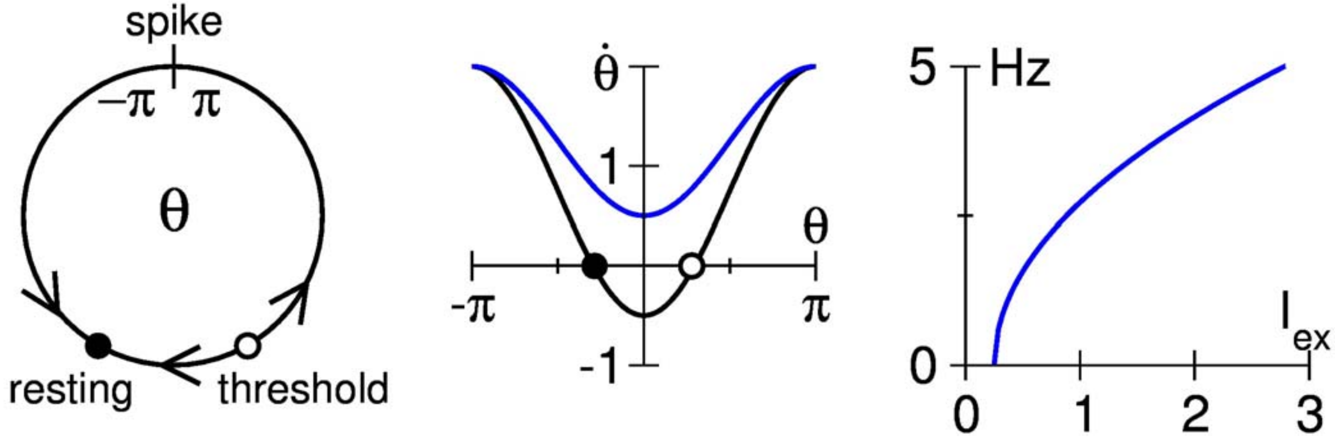
Note:

Elementary single neuron instability (AP threshold) not represented.



Balanced theta networks

theta neuron:



Balanced theta networks

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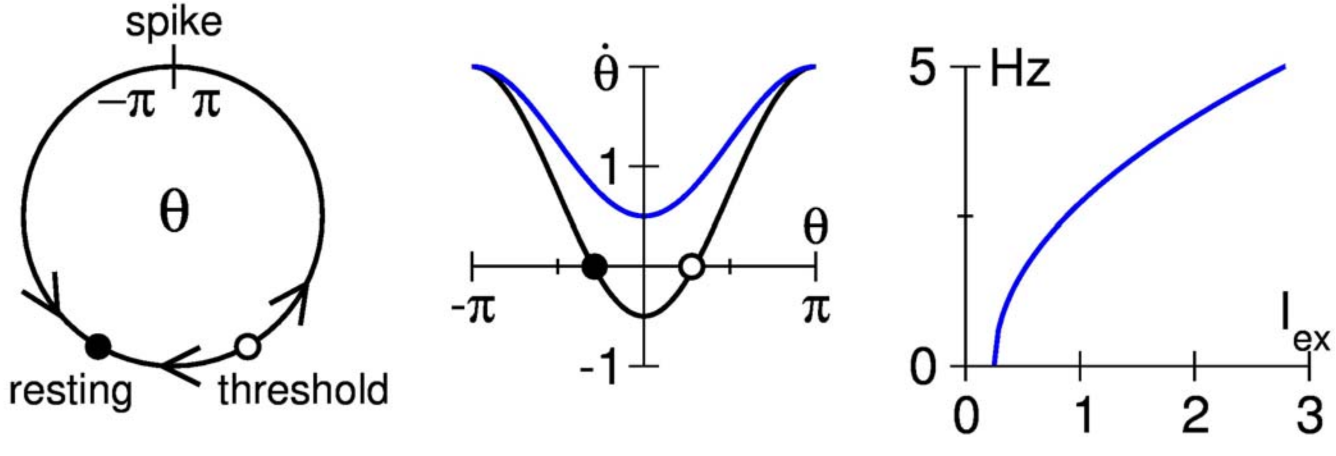
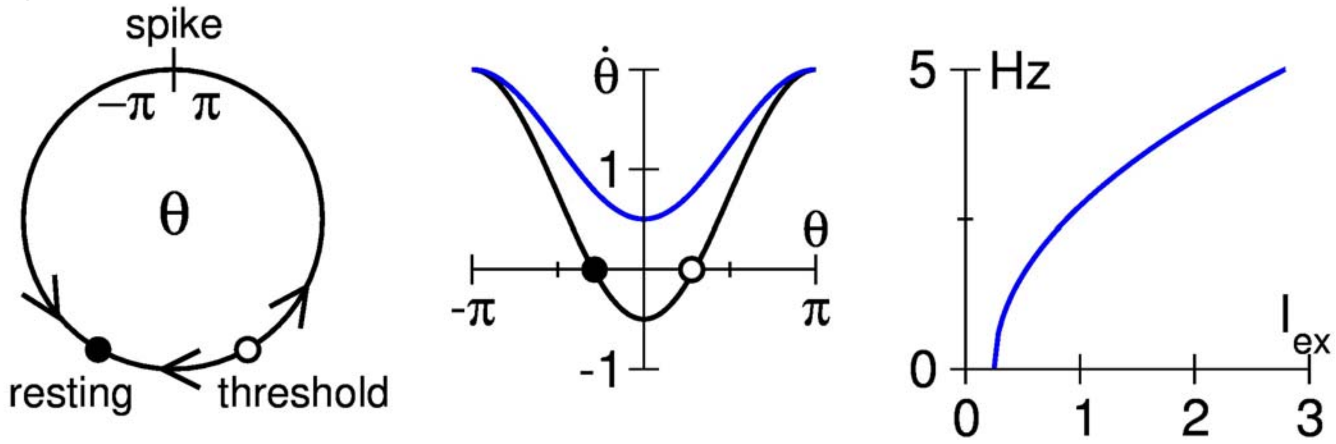


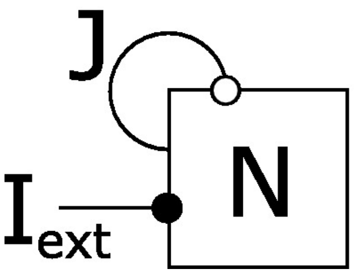
$$\tau_m \dot{\theta}_i = (1 - \cos\theta_i) + I_i(t)(1 + \cos\theta_i)$$

$$I_i(t) = I_{\text{ext}} + \sum_{j \in \text{pre}(i)} 2 J_{ij} \tau_m \delta(\theta_j(t) - \pi)$$

Balanced theta networks

theta neuron:





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N **neurons, connected with probability** K/N

synaptic strength: $J_{ij \in pre(i)} = -J/\sqrt{K}$

The Lyapunov spectrum

(i) Single theta neuron equation can be solved analytically.
(ii) Individual neurons follow autonomous dynamics between spikes.

Enables numerically exact calculation of the complete Lyapunov spectrum:

Explicit formula for time of next spike in the network.
Explicit map for all single neuron phases at next spike time.

Event based simulations numerically exact !

Exact single-spike Jacobian *D* of the phase map known: precise propagation of all possible network state perturbations.

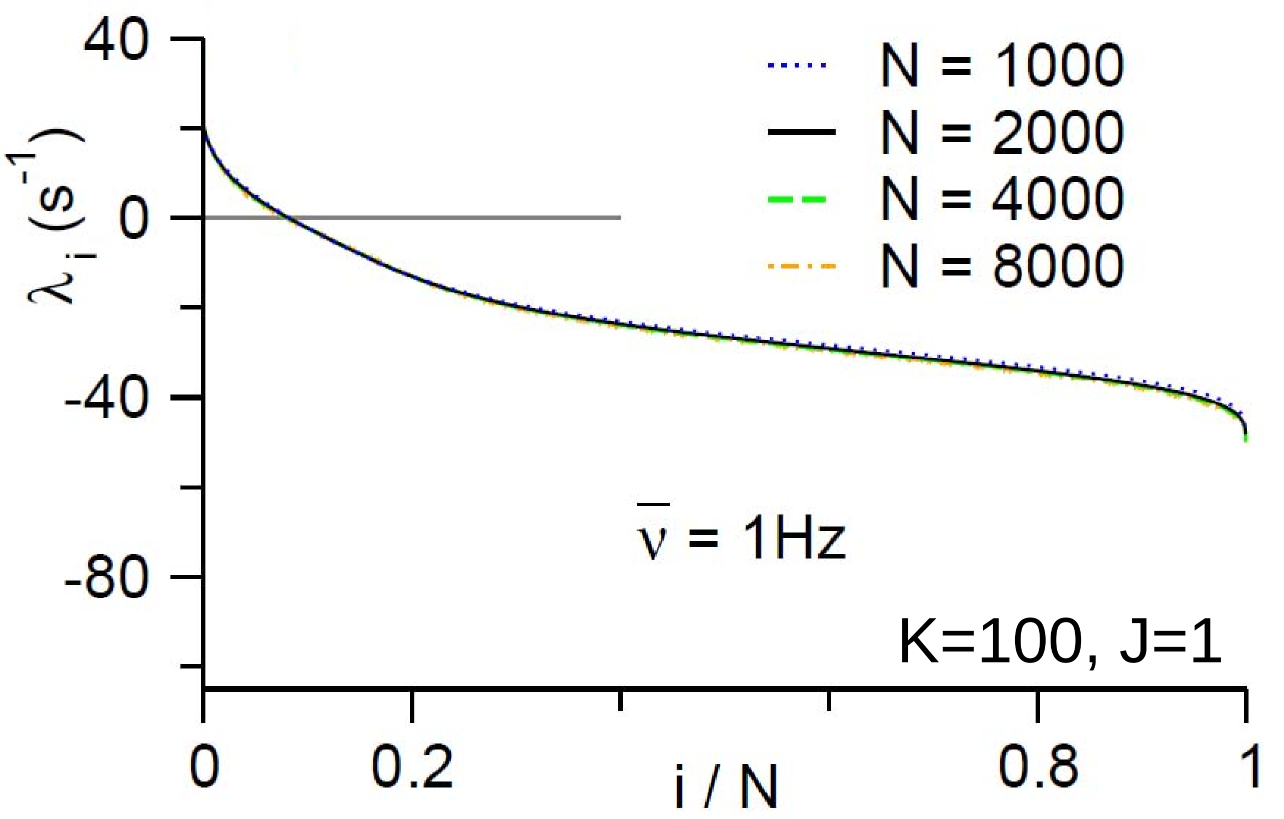
$$D(t_s) = \begin{pmatrix} 1 & 0 & \cdots & & & & \cdots & 0 \\ 0 & 1 & & & & & & \vdots \\ \vdots & & \ddots & & & & & \\ & & & 1 & & & & \\ & & & & \ddots & & & \\ & & & 1 - d_{i^*}(t_s) & & d_{i^*}(t_s) & & \\ & & & & & & \ddots & \vdots \\ \vdots & & & & & & 1 & 0 \\ 0 & \cdots & & & & \cdots & 0 & 1 \end{pmatrix} \leftarrow \text{rows } i^*$$

$\uparrow$ column j^*

$$d_{i^*}(t_s) = \frac{V_{i^*}(t_s^-)^2 + I_{\text{ext}}}{(V_{i^*}(t_s^-) + J_{i^*j^*})^2 + I_{\text{ext}}}$$

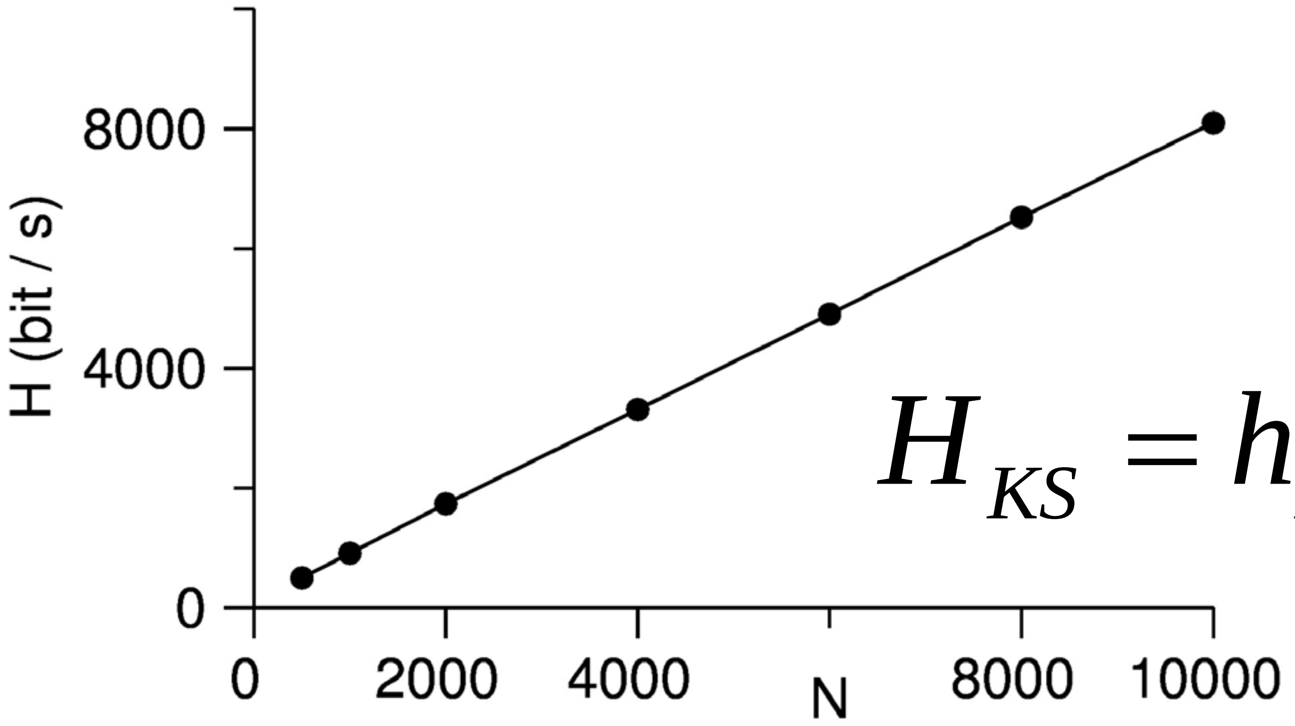
$$L(t_p) = \prod_{s=1}^{p} D(t_s)$$

Extensive Network Chaos



Maximum Lyapunov exponent positive and finite.
Size invariant Lyapunov spectrum.
Extensive number of unstable degrees of freedom.

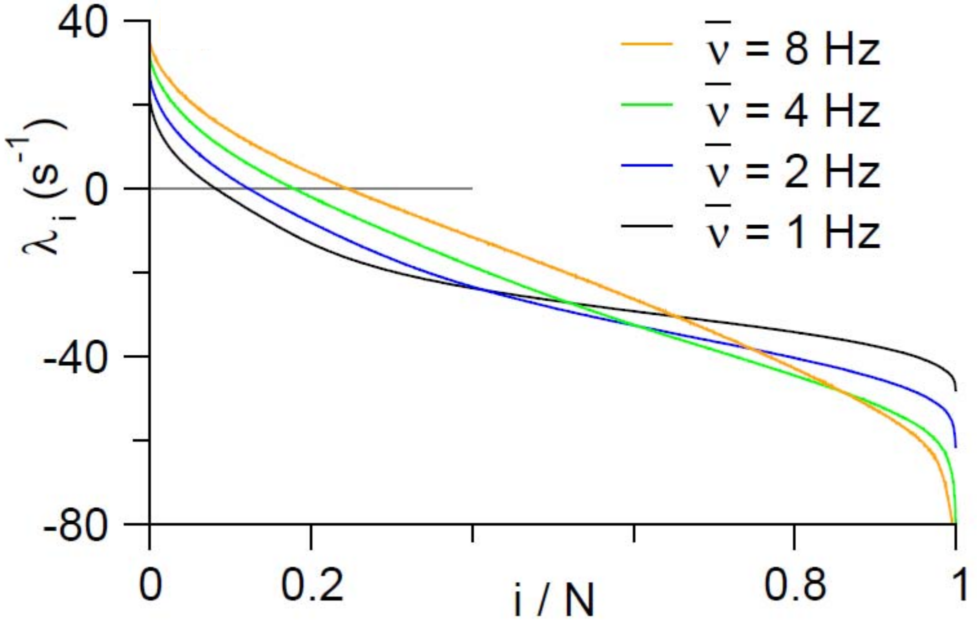
KS-Entropy density

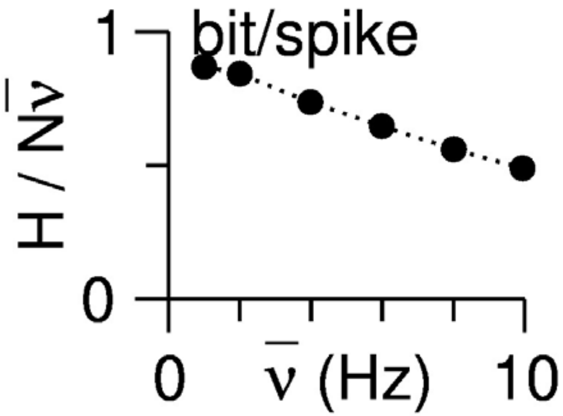


$$H_{KS} = h_{KS} N$$

h_{KS} : dynamical entropy production per neuron

Information degradation spike by spike





Maximal Lyapunov exponent, fraction of unstable directions and KS-Entropy increase with firing rate.

Information loss on the order of 1 bit / spike / neuron.

Sensory cortex activity codes up to 1/2 bit/spike of sensory information. e.g. Panzeri et al. Neuron (2001)

Varying the single neuron instability

Preserve all computational advantages of the theta neuron but make instability of spike threshold a free parameter.

Voltage representation:

„r-theta neuron"

AP onset rapidness : r

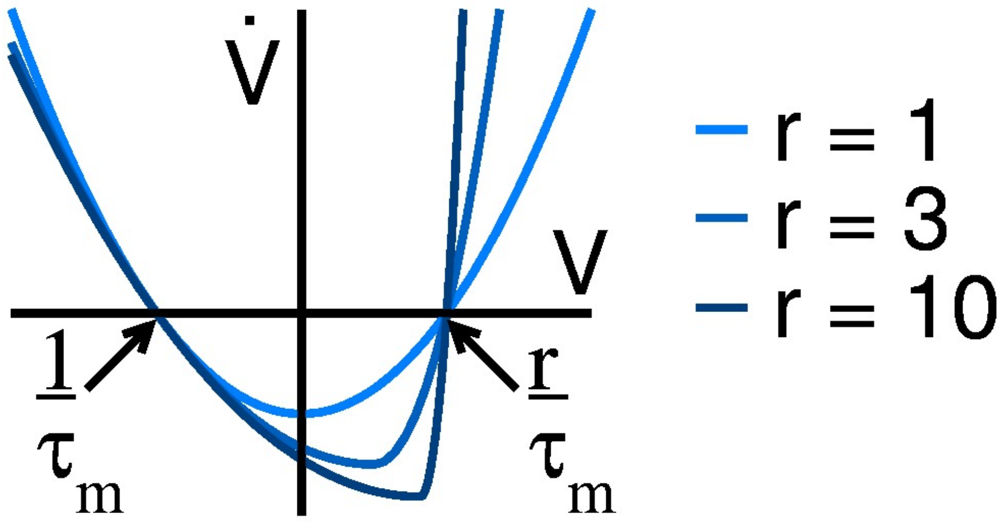
ratio of

membrane time constant

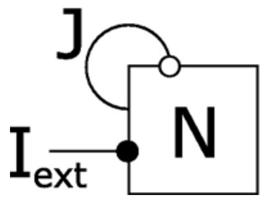
and

time scale of initial

AP upstroke



Same network structure as before:

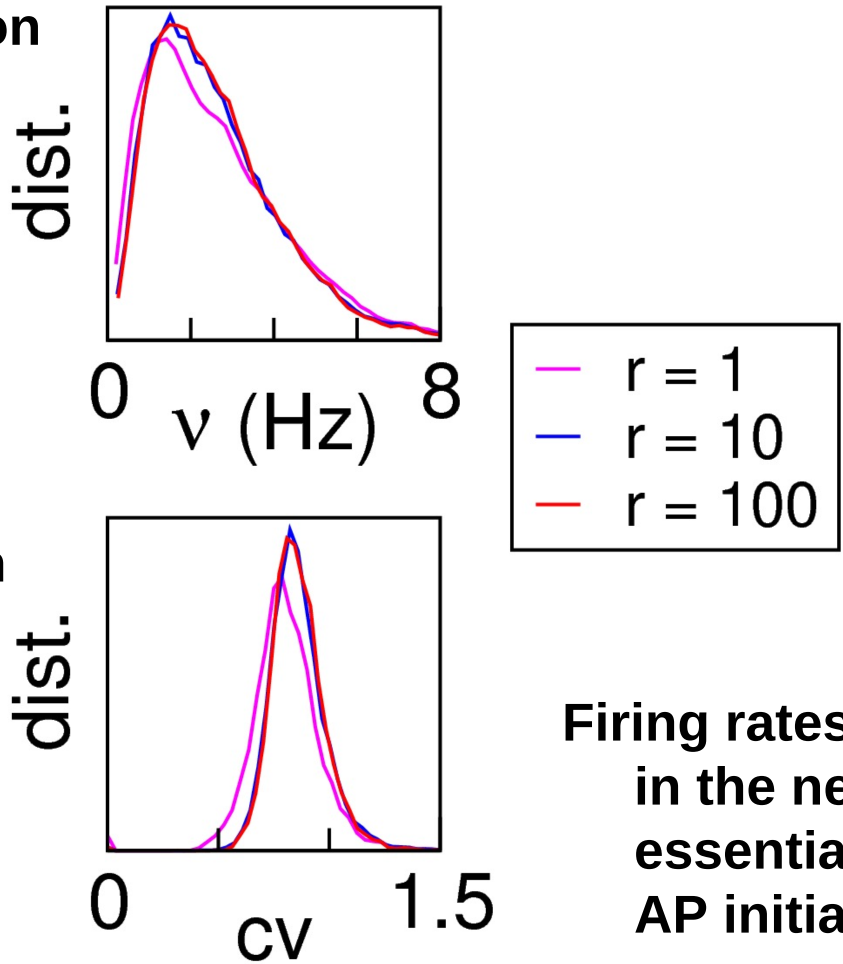


Impact on spike statistics?

Firing rate distribution

CV value distribution

Mean firing rate 2.4 Hz

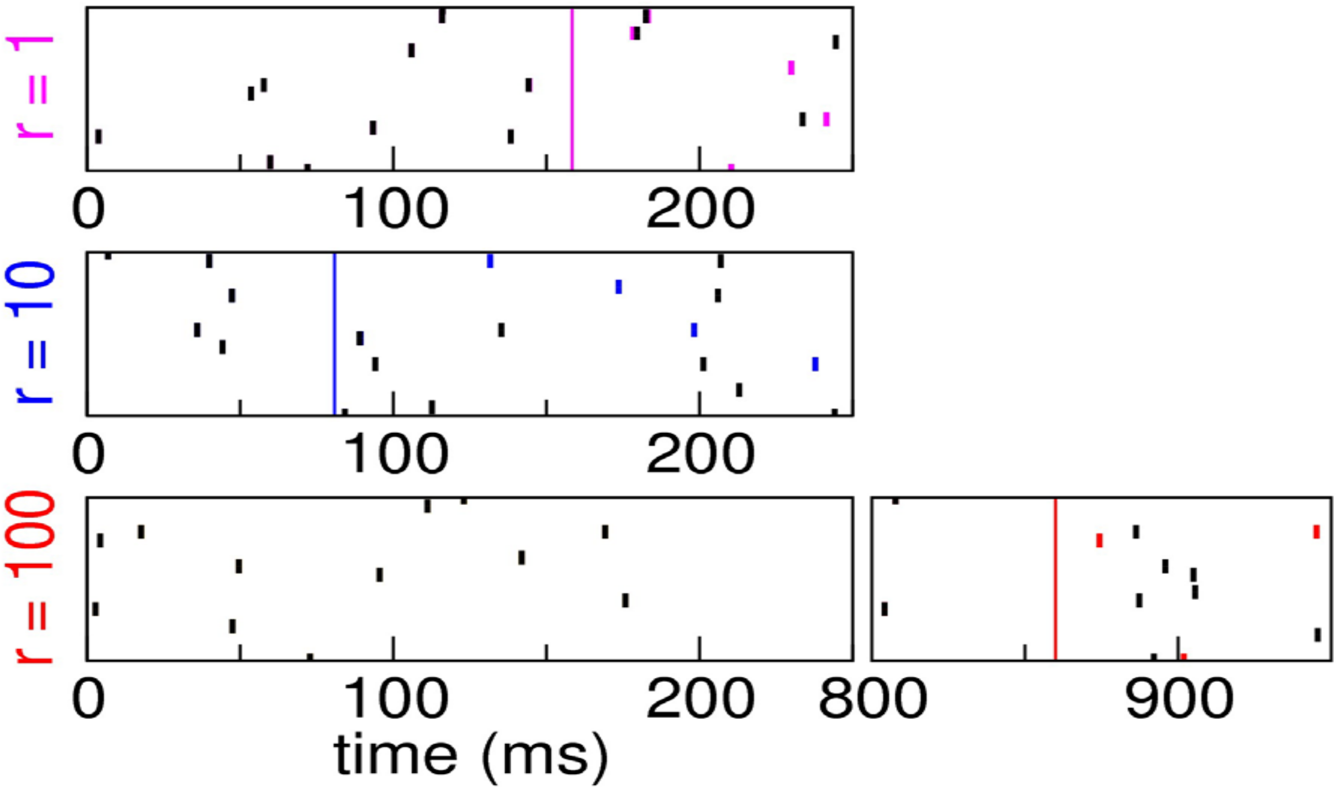


Firing rates and cv values in the network essentially insensitive to AP initiation dynamics.

Impact on collective dynamics?

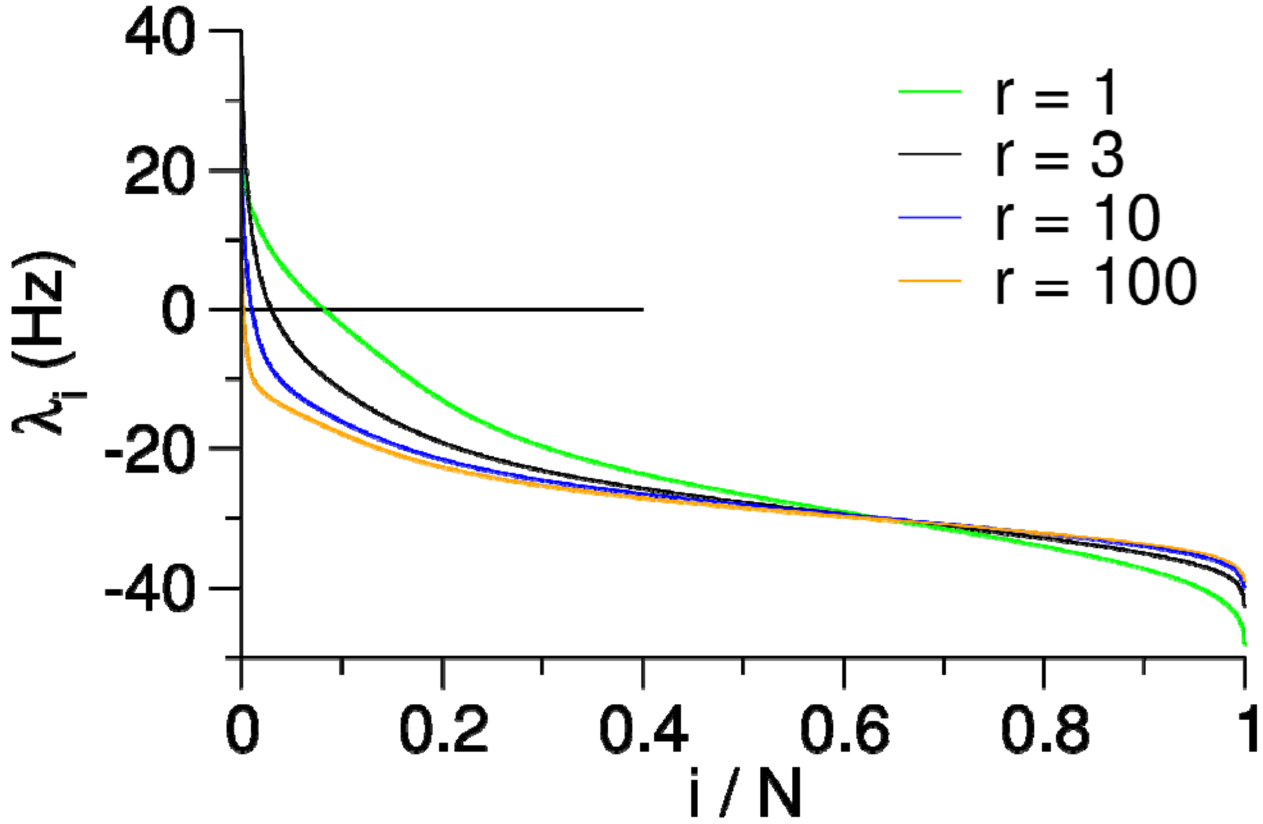
Two initial conditions.

Phases of all neurons slightly perturbed at t=0.



Divergence of network states after initial perturbation depends on single neuron instability?

Impact on collective dynamics?

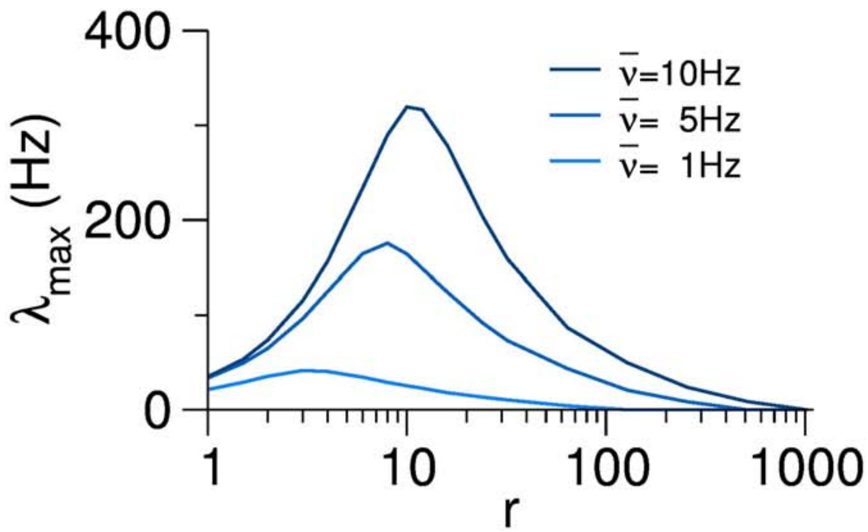


Extensive Chaos for all r.

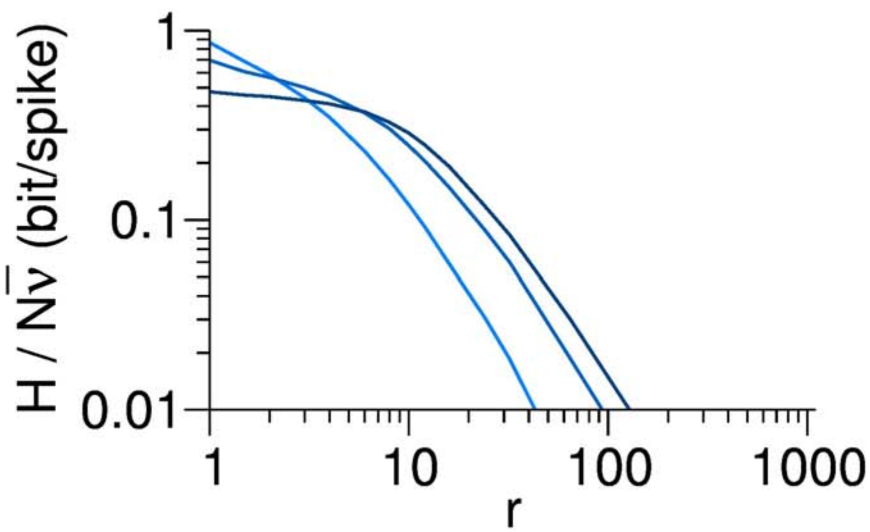
Fraction of unstable degrees of freedom decreases when increasing single neuron instability.

Fighting information loss by single neuron instability

Maximum Lyapunov exponent



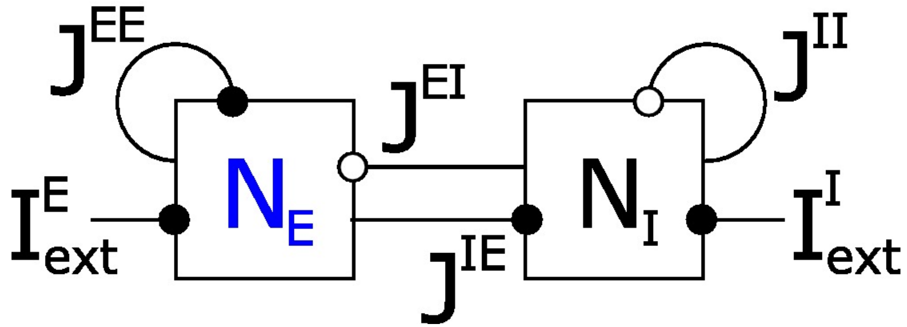
KS-Entropy per neuron and spike



Changing the time scale of action potential initiation can reduce maximum Lyapunov exponent and dynamical entropy production by orders of magnitude.

What about excitation??

Two population networks of r-theta neurons:

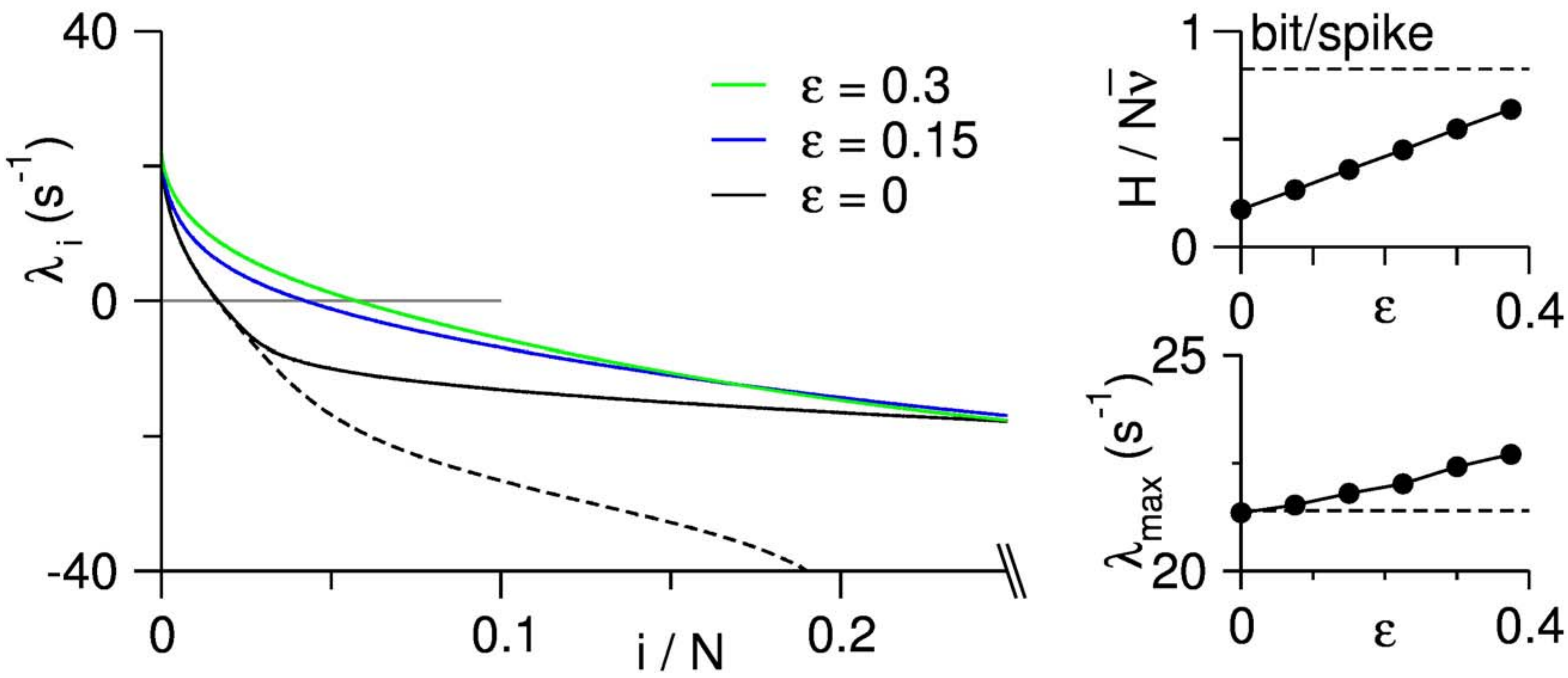


$$J = \frac{J_0}{\sqrt{K}} \begin{pmatrix} 0.9\varepsilon & -\sqrt{1-(0.9\varepsilon)^2} \\ \varepsilon & -\sqrt{1-\varepsilon^2} \end{pmatrix}$$

Activating excitatory interactions while preserving input current statistics.

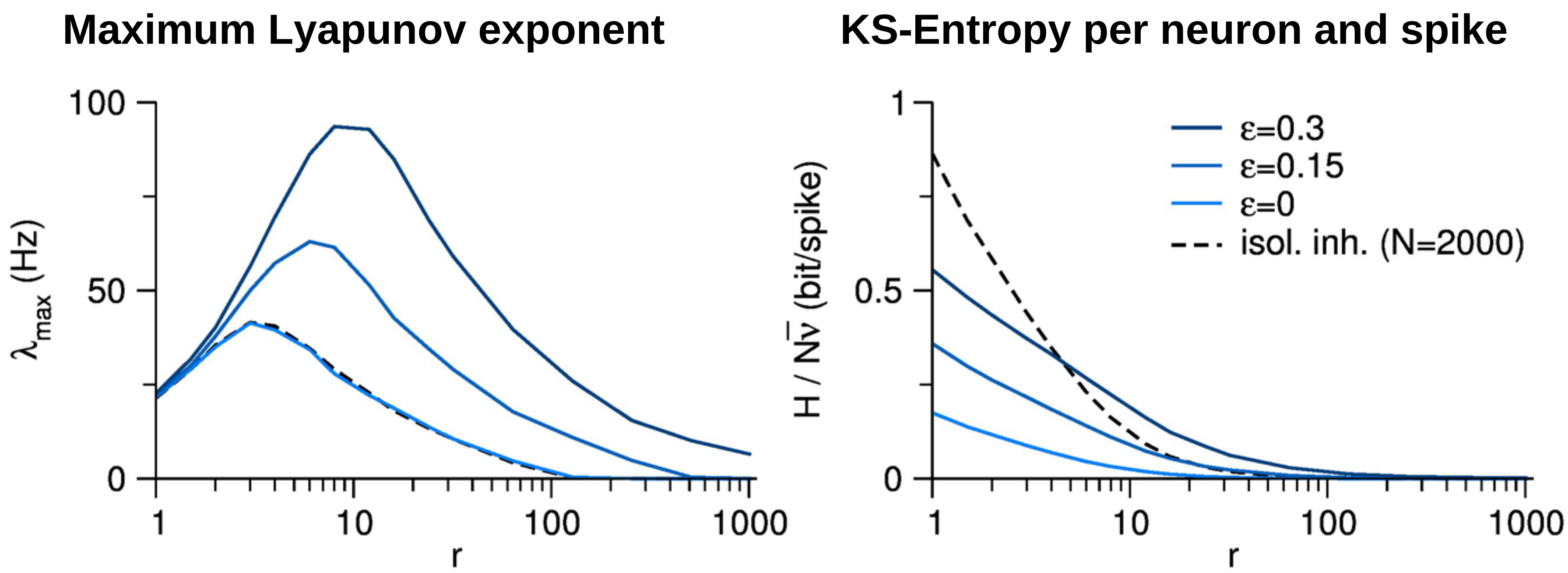
More chaos in mixed circuits

e.g. r=1



Activating excitatory connections inceases Lyapunov exponent and dynamical entropy production.

Taming chaos in mixed circuits



Changing the time scale of action potential initiation also reduces maximum Lyapunov exponent and dynamical entropy production as in inhibitory networks.

Conclusions

- **Balanced chaos extensive: KS-entropy per neuron and spike**
- **KS-entropy on the order of 1 bit / neuron and spike**
- **Excitatory circuits typically increase entropy production.**
- **Onset rapidness of APs is a key property setting the stength of chaos in balanced networks.**
- **Single neuron instability supresses entropy production by network dynamics.**
- **Cortical AP generators might be taylored to tune the network dynamics towards the *edge of chaos*.**

Perspectives – Open Questions

- **Extensive network chaos? Why?**
- **Impact of cellular parameters (synaptic dynamics)**
- **Entropy production by stochasticity of synaptic transmission.**

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