Irregular behavior in neuronal networks

R. Zillmer
INFN, Sezione di Firenze

Collaborators:

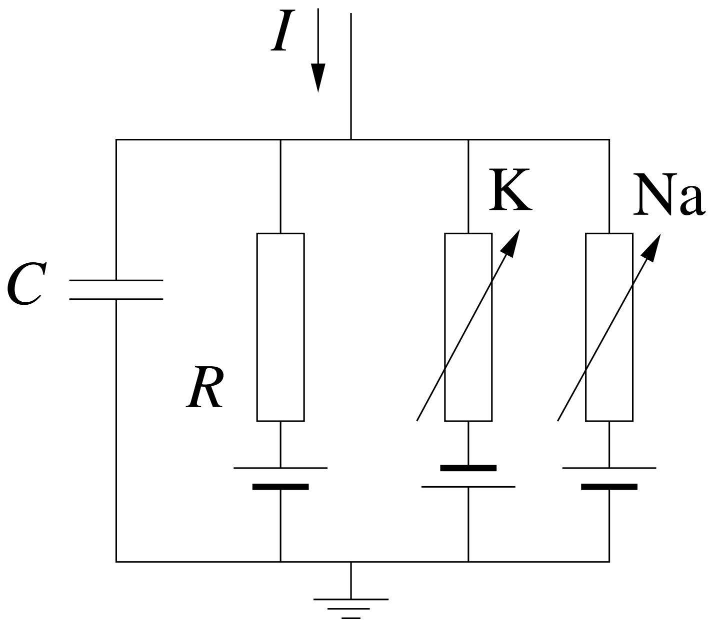
A. Torcini, R. Livi, A. Politi

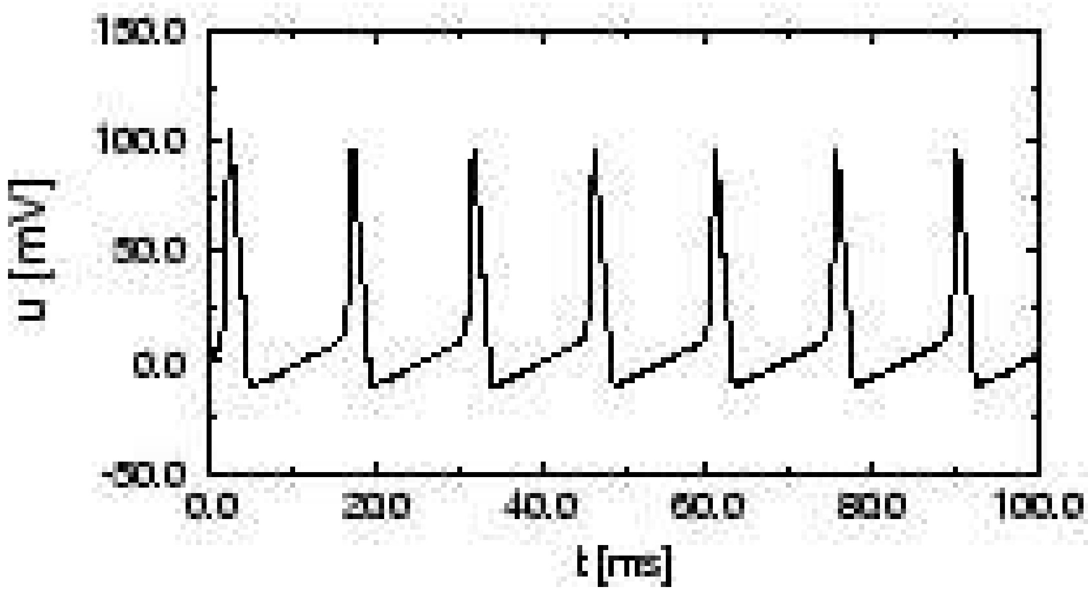
- introduction
- globally pulse coupled integrate-and-fire neurons
- dilution (broken links)$\rightarrow$ long irregular transients $\sim \exp(\alpha N)$
- properties of transients

Single neuron

- neuronal signals are short electrical pulses: **spikes** or **action potentials** resp.
- intracellular: incoming spike modifies **membran potential**

Hodgkin-Huxley (1952): Semirealistic model for the dynamics of the membran potential by taking into account Na+, K+, and a leak current. Dynamics of ion channels highly nonlinear.



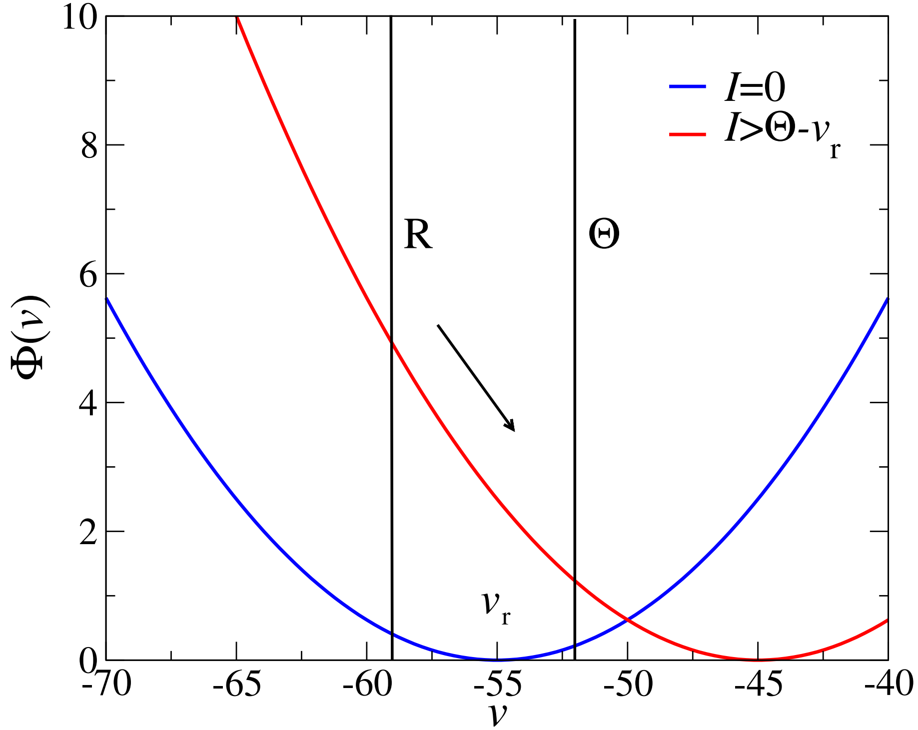


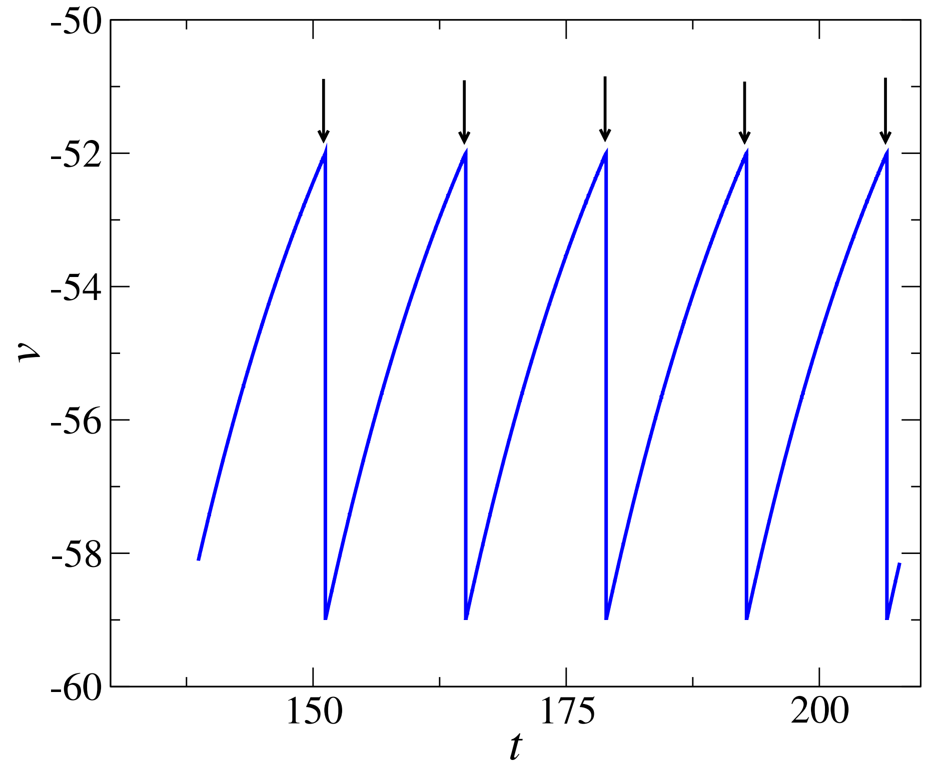
Leaky integrate-and-fire approximation

Linear integration combined with **reset** = formal spike event
In networks: at reset a delta-like pulse is sent to other neurons

Equation for membran potential v, with threshold Θ and reset R:

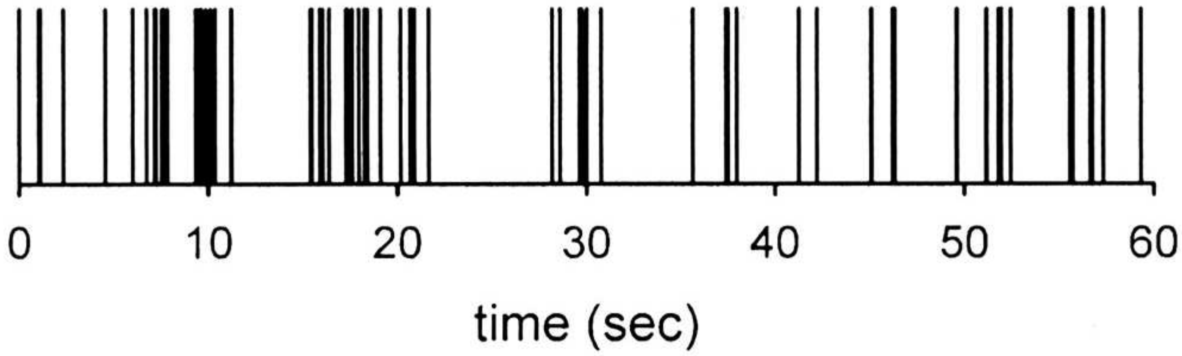
$$\tau \dot{v} = -(v - v_\mathrm{r}) + I = -\frac{\partial}{\partial v}\Phi(v) \ , \quad \Phi(v) = (v - v_\mathrm{r} - I)^2/2 \ , \quad v \in [R, \Theta]$$





Information coding

Real neurons have complex structure and behave not as reliable as the mathematical models
Typical spike train:



- single neuron in vitro: variability of response to constant input
- neurons in vivo ⇒ highly fluctuating input: neurons can produce very precise response (*Mainen, Sejnowsky, 1995*)

rate coding? **time coding**? mixing of both?

reliable more info, fast

Real neuronal networks

- density in cortex: $> 10^4$ neurons per mm^3
- layered structure (slices) of highly connected neurons
- single tasks or memories spread over wide areas (binding problem)
- connection between neurons via synapses:
  exciting (input rises potential), **inhibiting** (input lowers potential)
- neuromodulators change response to given input (drugs)
- plasticity: adaption (learning) by alterations of synaptic strength or connectivity
- high connectivity leads to very irregular activity of single neurons

Modelling neuronal networks

Networks of simple components which mimick real neurons
$\Rightarrow$ allow effective theoretical and numerical analysis
Different topologies: globally all to all coupling, small world, scale free network, layered structure

Hopfield network:

- neurons as interacting "spins" $\sigma_i = \pm 1$:

$$\sigma_i(t+1) = \text{sign}\left[\sum_j J_{ij}\sigma_j(t)\right]$$

- stored memory as stationary states
- for symmetric $J_{ij} = J_{ji}$ detailed balance $\Rightarrow$ point attractors
  e.g. $J_{ij} = S_i S_j \Rightarrow \sigma_i = S_i$ fixed point (memorized pattern)
- asymmetric J_{ij}: periodic states and long "chaotic" attractors

Networks of integrate-and-fire neurons

Equation for membran potential v_j:

$$\dot{v}_j = I - v_j - \sum_{i=1}^{N} \sum_{k=1}^{\infty} G_{ji} w(v_j) \alpha(t - t_i^{(k)}), \quad v \in [R, \Theta]$$

- more realistic behavior e.g. global oscillations, irregular firing, self sustained activity, effects of noise
- **mean-field** analysis of network **activity** in the limit of
  1. homogeneous global coupling (each neuron receives same input)
  2. sparse asymmetric coupling (inputs of different neurons uncorrelated)

Irregular activity induced by noise and/or asymmetric couplings (frozen disorder)

Pulse-coupled integrate-and-fire neurons

System of N identical all to all pulse-coupled neurons:

$$\dot{v}_j = I - v_j - \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{G_0}{N}(v_j + E)\,\delta(t - t_i^{(k)})\,, \quad v \in [R, \Theta]$$

- suprathreshold current I
- inhibitory coupling $\Rightarrow$ no simultaneous firings

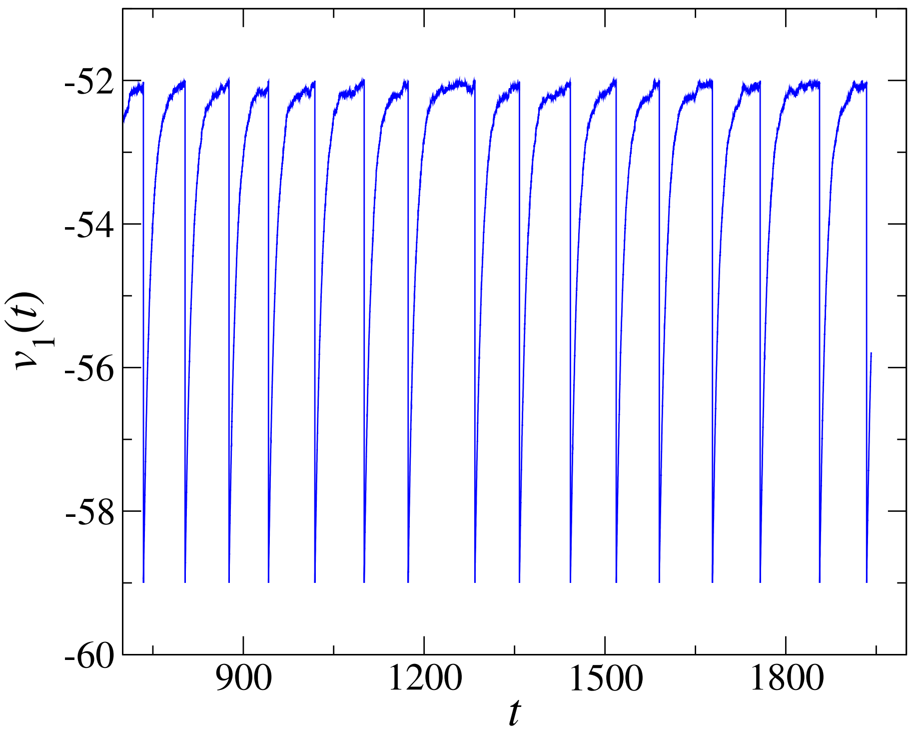
simple mean-field approach for the rate T_{mf}^{-1}:

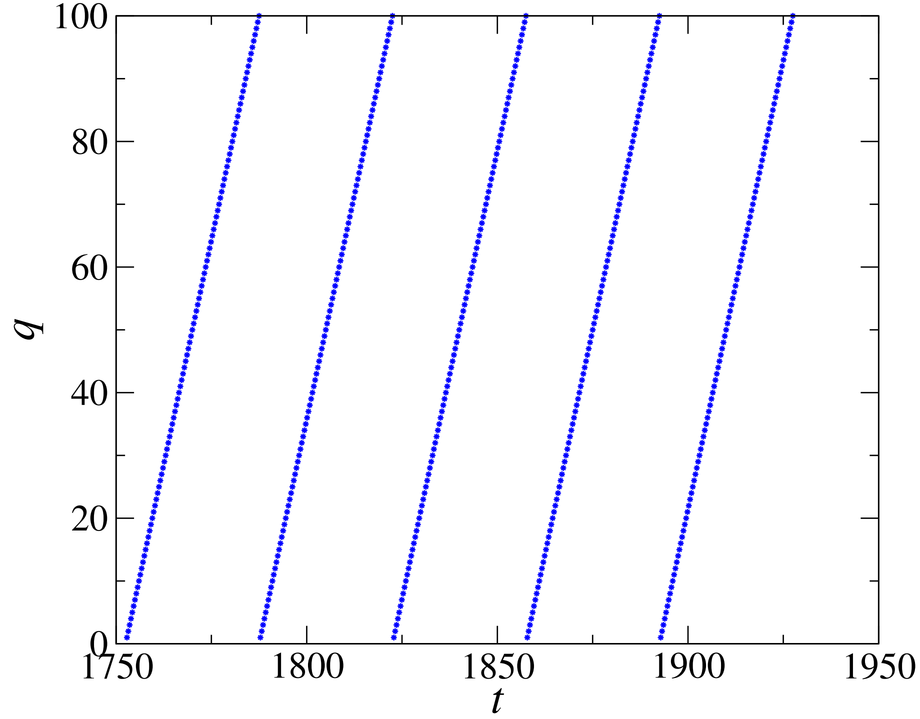
$$\dot{v}_j = I - v_j - G_0(v_j + E)T_{\mathrm{mf}}^{-1}$$

$\Rightarrow$ self-consistent solution for period T_{mf}

Dynamics of homogeneous system

$$\dot{v}_j = I - v_j - \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{G_0}{N}(v_j + E)\,\delta(t - t_i^{(k)})$$





Discrete time map for the pulse-coupled model

$$\dot{v}_j = I - v_j - \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{G_0}{N} (v_j + E)\, \delta(t - t_i^{(k)}) , \quad v \in [R, \Theta]$$

Explicit solution between firings, time-interval (isi) between two firings as discrete time step

$\Rightarrow$ map for residual time t_i of neuron i to reach threshold ($t_i \equiv \ln \Gamma_i$) :

neuron q closest to threshold: $\Gamma_q = \min_j \{\Gamma_j\}$, $\quad \mathrm{isi} = t_q = \ln \Gamma_q$

map for quiet neurons: $\Gamma_i(n+1) = e^{-G_0/N} \frac{\Gamma_i(n)}{\Gamma_q(n)} + \left(1 - e^{-G_0/N}\right) \frac{I+E}{I-\Theta}$

reset of firing neuron: $\Gamma_q(n+1) = \frac{I-R}{I-\Theta}$

time-step: $t = t + t_q$

Long irregular transients

Transients grow exponentially with system size $\Rightarrow$ relevant states for large systems

- long irregular transients $\sim \exp(\alpha N)$ in linearly stable CMLs (“stable chaos”, *Politi, Livi et al.*)
- long irregular transients in asymmetric Hopfield networks, spins - finite number of states (*Crisanti, Sompolinsky, 1988*)
- long chaotic transients (positive effective LE, riddled basin) in an excitatory pulse-coupled network (*Zumdieck, Timme, Geisel et al., 2004*)
- analytical results for short transients $\sim N$ to periodic state when coupling is size independent (*Jin, 2002*)

Information processing in brain should combine reliability (linear stability) with fast response and high information content (complex dynamics)

Diluted network

$$\dot{v}_j = I - v_j - \sum_{i=1,(\neq j)}^{N} \sum_{k=1}^{\infty} \frac{G_0}{N_{\text{eff}}} \varepsilon_{ji} (v_j + E)\, \delta(t - t_i^{(k)})\,, \quad v \in [R, \Theta]$$

Links are cut with given probability, $\varepsilon_{ji} = 1, 0$

Normalization of coupling strength with the number N_{eff} of active incoming links:

dilution indistinguishable for simple mean-field approach

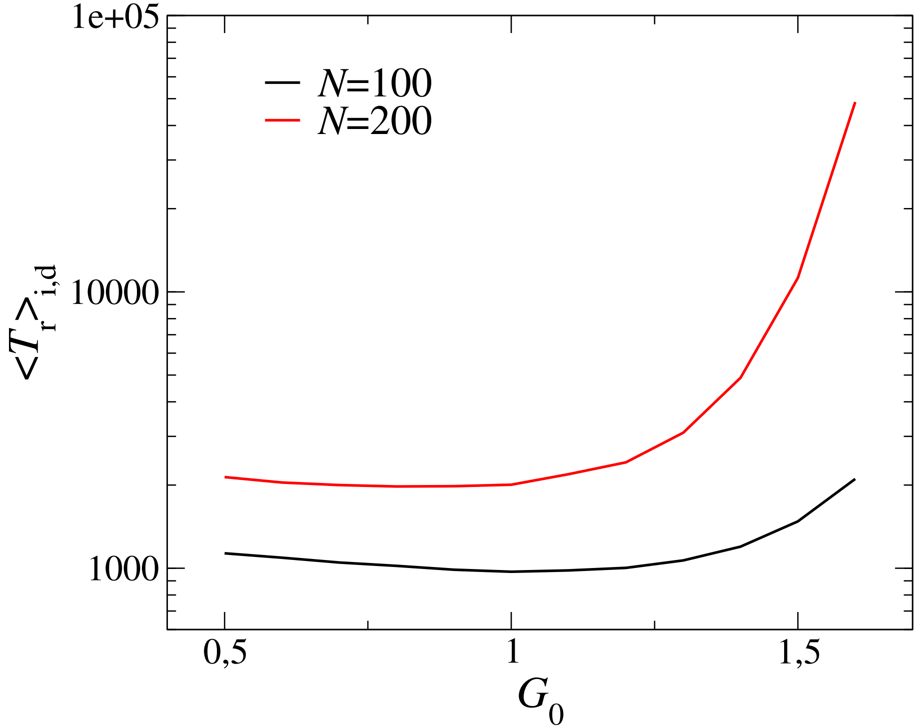
Negative Lyapunov exponent $\Rightarrow$ linear stability

For 5% cut links:

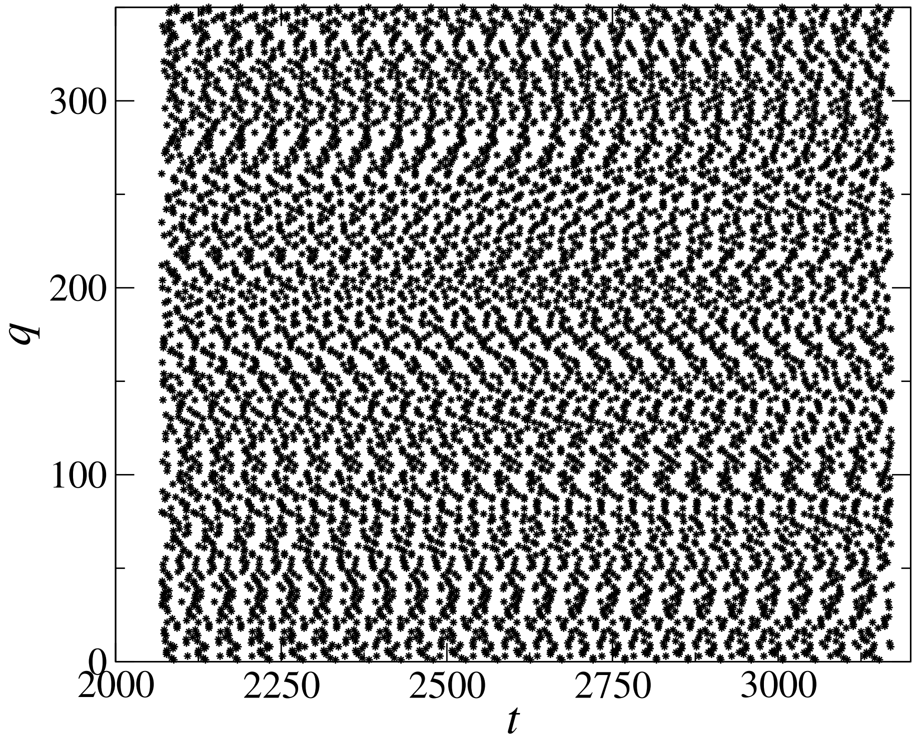
- multiple attractors (abolition of degeneracy with respect to exchange of neurons)
- for $G_0 < 1$ short transients $\sim N$ to periodic state
- for $G_0 > 1$ long stationary transients $\sim \exp(\alpha N)$
- irregular dynamics during transient (uncorrelated isi-times)

Long irregular transients to periodic state

length of transient



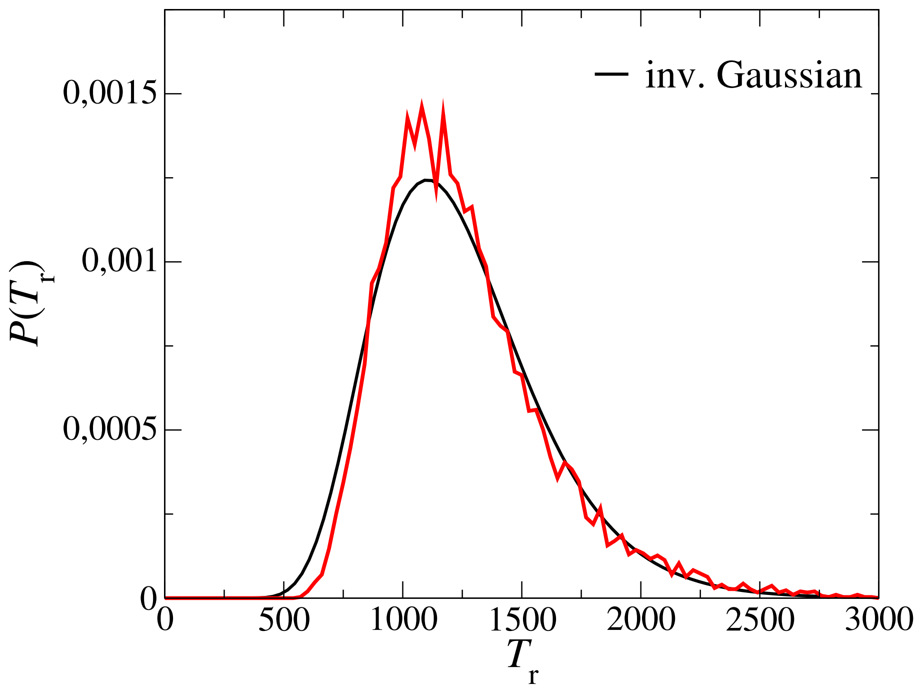
pattern for $G_0 = 1.5$



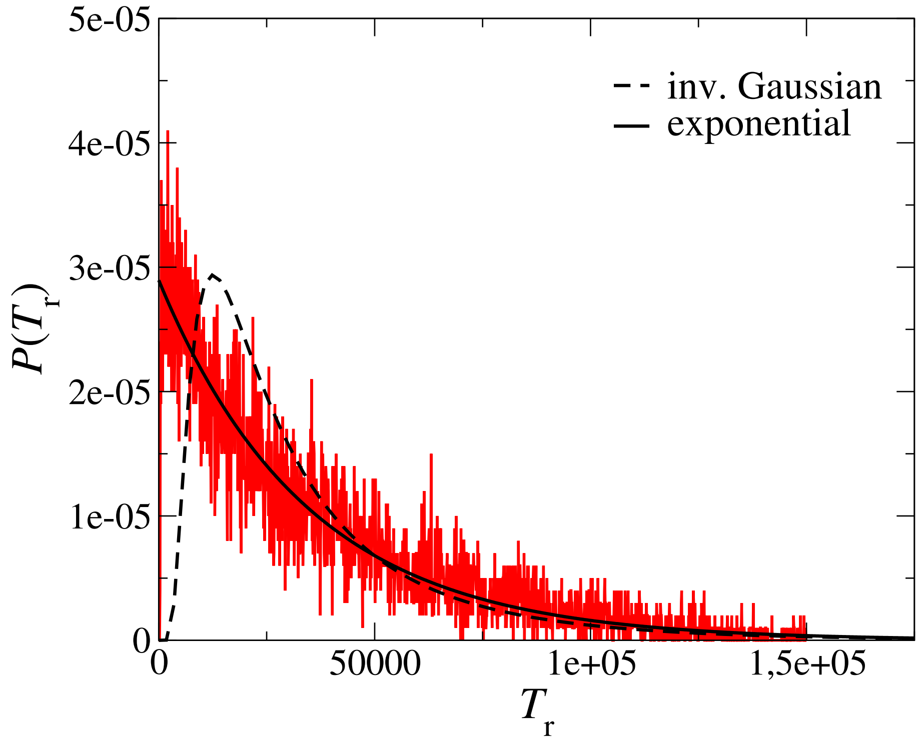
Statistics of the transient times

Normalized histogram (random initial conditions) of transient lengths for $N = 65$:

$G_0 = 1.0$



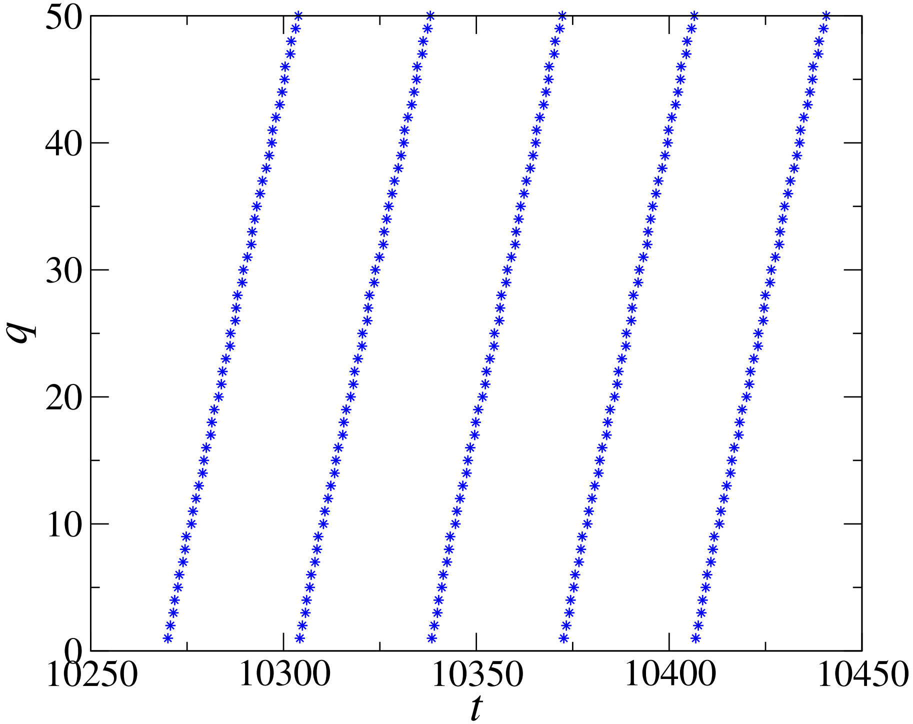
$G_0 = 2.1$



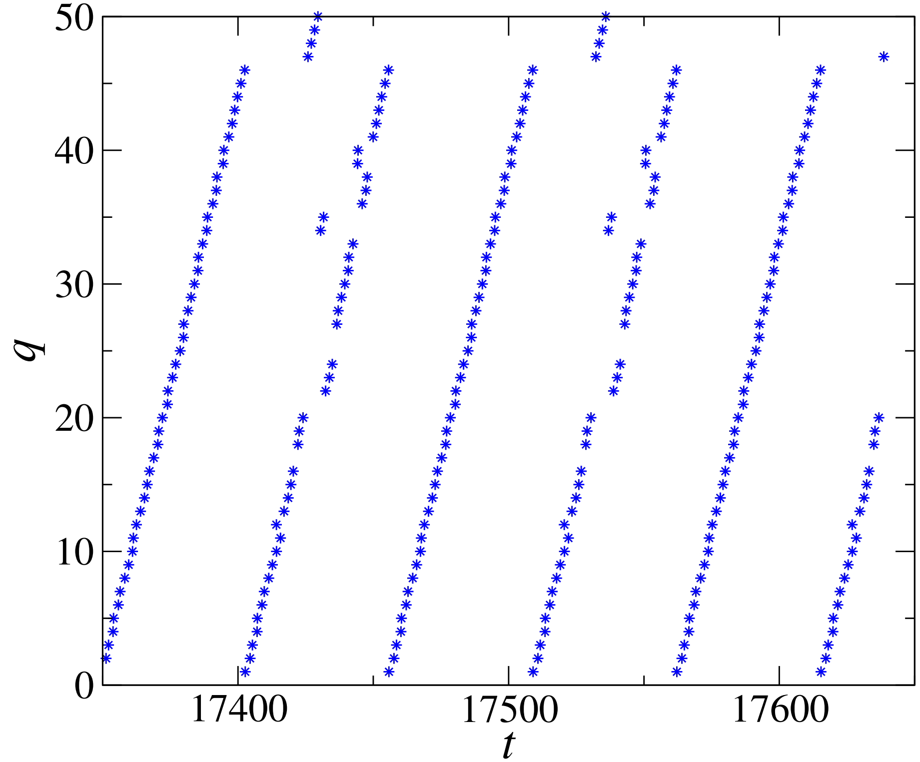
Bifurcation of the periodic state

For $G_0 \approx 1.5$ onset of double firing or suppression of neurons, resp.

$G_0 = 1.0$

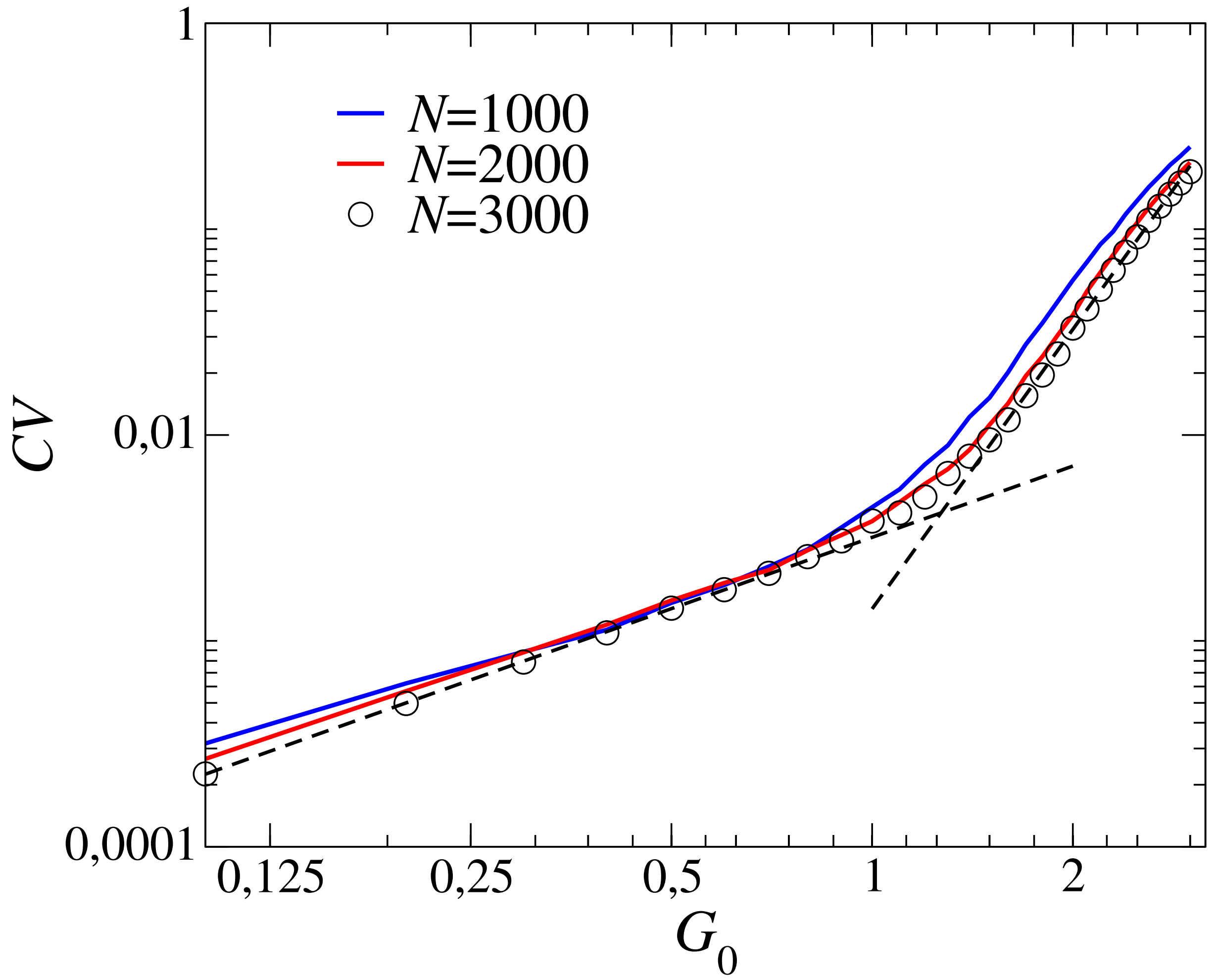


$G_0 = 2.0$



Variability of inter-spike-times

The **CV** (=variance/mean) of the neuron isi-times **during the transient** shows two scaling regimes, depending on the coupling strength G_0:



Finite perturbation growth

Consider evolution of small but finite perturbations of state:

$$\tilde{v}_i(t_0) = v_i(t_0) + \varepsilon\eta_i \quad , \quad \eta \in [-1, 1]$$

Hamming distance:

$$D_{\mathrm{H}}(t) = \frac{1}{N}\sum_{j=1}^{N} |\tilde{v}_j(t) - v_j(t)|$$

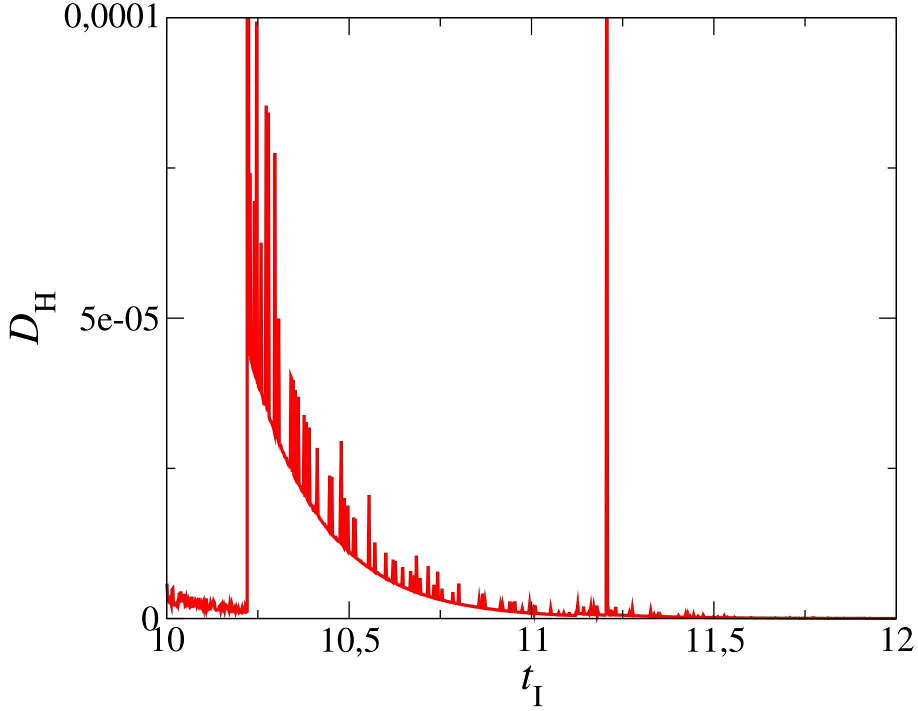
In both regimes ($G_0 < 1$ and $G_0 > 1$):

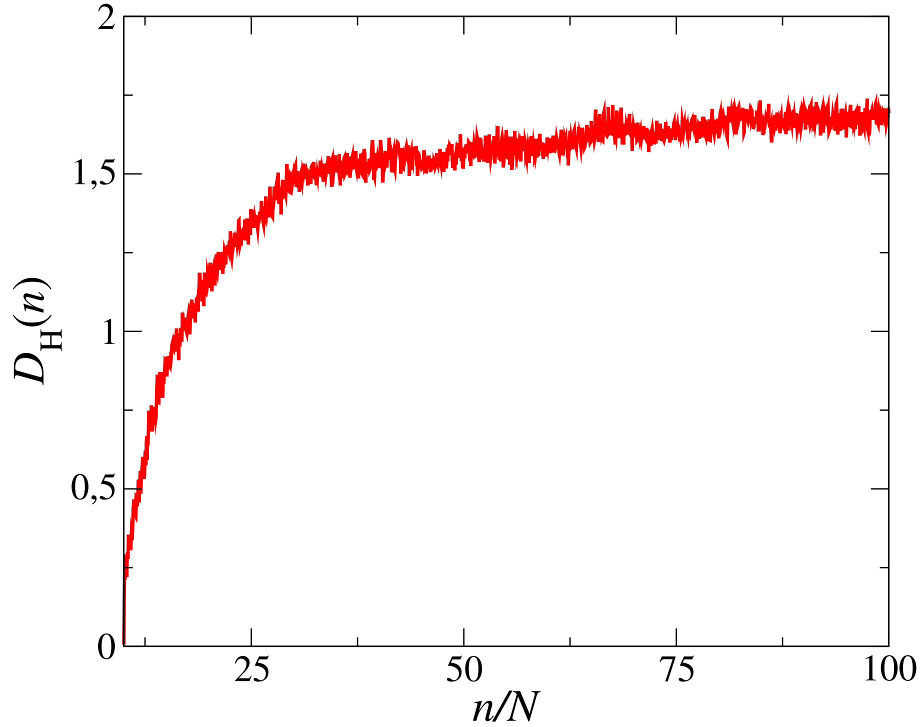
- for small enough $\varepsilon \sim 10^{-5}$ elimination of perturbation (up to a constant phase shift) in accordance with the negative Lyapunov exponent
- for $\varepsilon \sim 0.01$ amplification of perturbation, systems end up on different attractors

Finite perturbation growth

Evolution of the Hamming distance during transient ($N = 2000, G_0 = 2.1$):

perturbation amplitude: $\varepsilon = 10^{-5}$ $\varepsilon = 10^{-2}$





Finite perturbation: phase diffusion

Time intervals $t_j, \tilde{t}_j$ between two subsequent firings of the systems:

“Phase” difference:

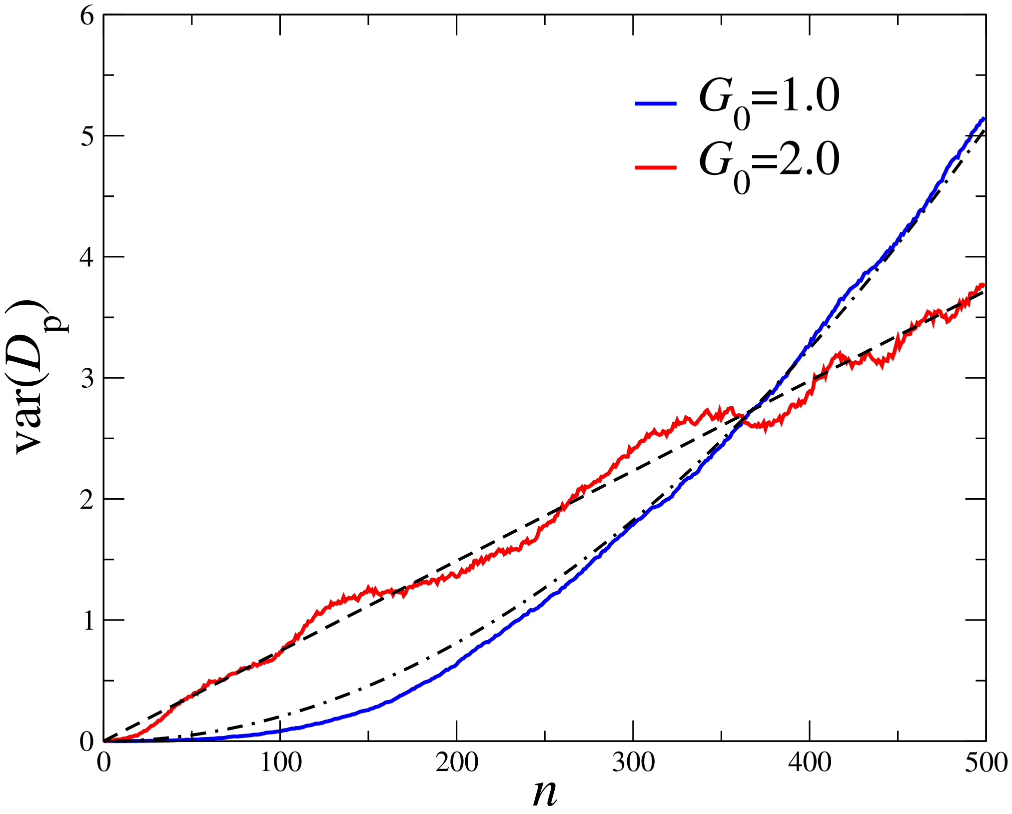
$$D_{\mathrm{p}}(n) = \sum_{1}^{n} \left[t_j(n) - \tilde{t}_j(n) \right]$$

Evolution of $D_{\mathrm{P}}(n)$ during transient ($\varepsilon \sim 0.01$):

- for $G_0 < 1$ **ballistic drift** (systems have different mean isi-time)
- for $G_0 > 1$ **normal diffusion** (mixing property of long stationary transient)

Finite perturbation: phase diffusion

Variance of “Phase” difference $D_{\rm P}(n)$ (average over different i.c.):



Summary and open work

- network of inhibitory pulse-coupled integrate-and-fire neurons
- negative Lyapunov exponent $\Rightarrow$ linear stability
- dilution: two regimes depending on the coupling strength G_0
  1. $G_0 < 1$: short transients, constant “drift” to periodic state
  2. $G_0 > 1$: long stationary transients $\sim \exp(\alpha N)$, irregular dynamics

     $\Rightarrow$ for large N irregular transients are the relevant stationary states

- other forms of frozen network disorder (e.g. varying G_{ij})
- comparison with excitatory networks (*Zumdieck, Timme, Geisel et al.*)
- relevance of stationary transient for information processing tasks