



Linear Response in Neuronal Network Models

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Linear Response in Neuronal Network Models

Bruno Cessac

Université Côte d'Azur, INRIA, France, Biovision team and Neuromod Institute

06-12-2021

- 1 Introduction
- 2 From firing rate neurons dynamics to linear response.
- 3 From spiking neurons dynamics to linear response.
- 4 Conclusions

Neuronal networks



Neurons

Neurons are electrically active cells where electric currents are produced by ions transfer.

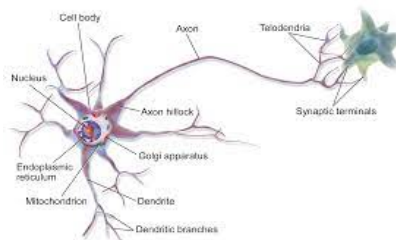


Figure: Neuron. From <https://en.wikipedia.org/wiki/Neuron>

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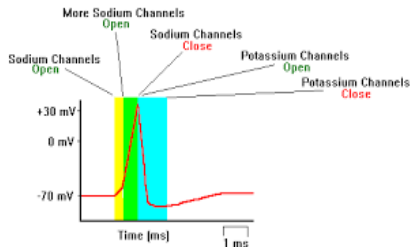


Figure: Spike. From <http://faculty.washington.edu/chudler/ap.html>

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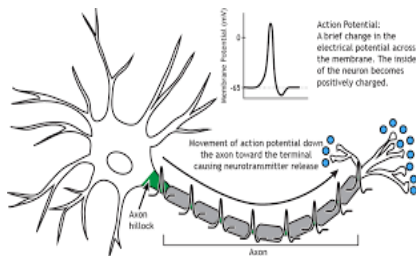


Figure: Spike propagation. From

<https://openbooks.lib.msu.edu/neuroscience/back-matter/images-of-animations/>

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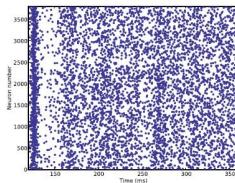


Figure: Spike train.

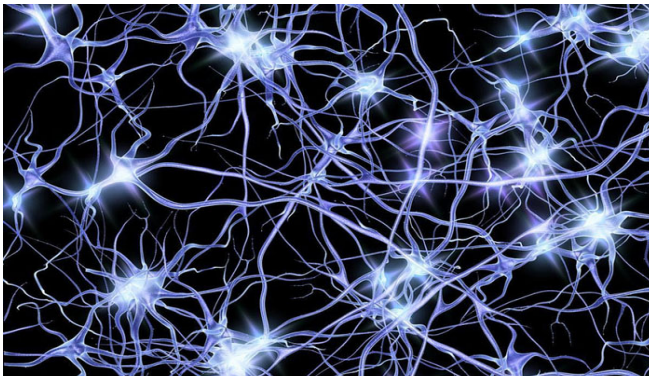
Neurons

Neurons are electrically active cells where electric currents are produced by ions transfer.

Most neurons (but not all of them) communicate by action potentials ("spikes").
Spike trains contain "a" "neural code".

Two main descriptions:

- 1 Firing rates (frequency of spikes within a small time interval) \Rightarrow first part of the talk.
- 2 Individual spikes \Rightarrow second part of the talk.

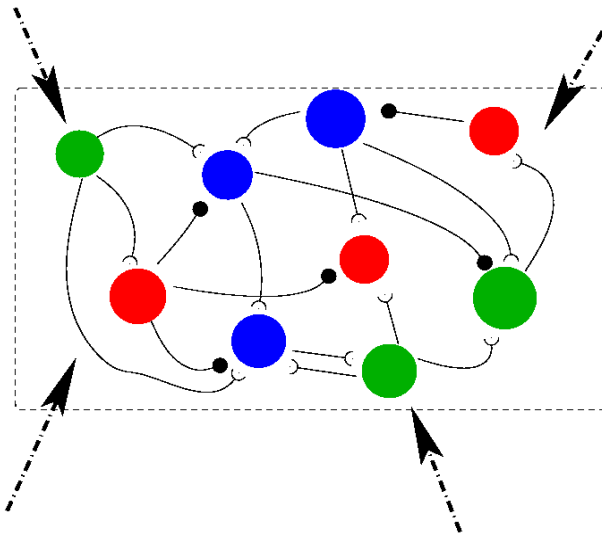




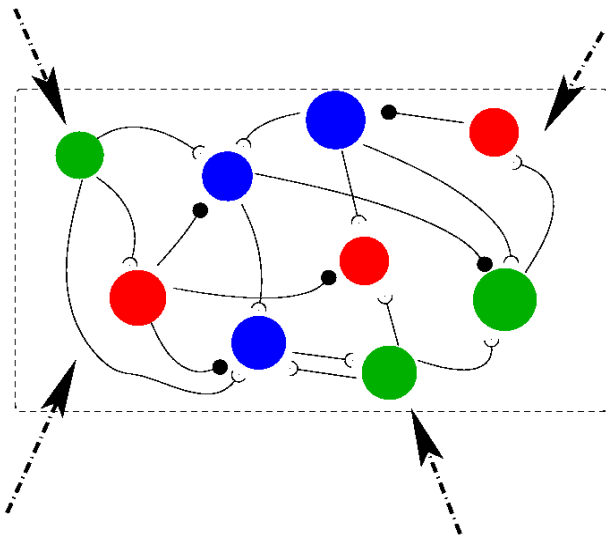
Neuronal networks are usually submitted to external, non stationary, entries (sensory stimuli, interactions between brain areas, ...)

How to compute the response of a neuronal network to a time dependent stimulus ?

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How to compute the response of a neuronal network dynamical system to a time dependent stimulus perturbation ?



From firing rate neurons dynamics to linear response.

Amari-Wilson-Cowan Model

Amari, 1972; Wilson-Cowan, 1972

Continuous time.

$$\frac{dV_i}{dt} = -V_i + \sum_{j=1}^N J_{ij} f(V_j(t)) + \varepsilon S_i(t); \quad i = 1 \dots N.$$

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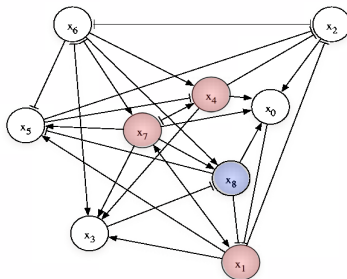
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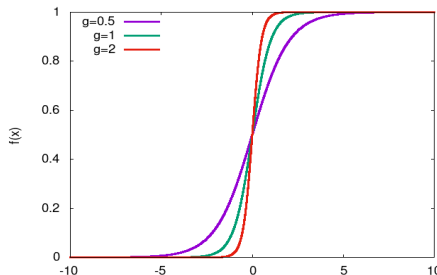
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- $\varepsilon > 0$, small parameter.

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Discrete time.

$$V_i(t+1) = \sum_{j=1}^N J_{ij} f(V_j(t)) + \varepsilon S_i(t); \quad i = 1 \dots N.$$

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Vector form.

- $\vec{V} = (V_i)_{i=1}^N$, state vector;
- $\vec{S} = (S_i)_{i=1}^N$, stimulus vector;
- $\mathcal{J} = (J_{ij})_{i,j=1}^N$, matrix of synaptic weights
- $f(\vec{V})$, vector $(f(V_i))_{i=1}^N$.

Continuous time.

$$\frac{d\vec{V}}{dt} = \underbrace{-\vec{V} + \mathcal{J} \cdot f(\vec{V})}_{\vec{F}(\vec{V})} + \varepsilon \vec{S}(t),$$

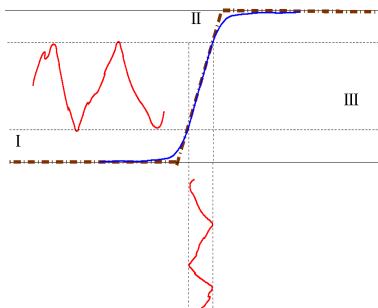
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The 3 "regions" of the sigmoid transfer function

Effect of $f(x) = \frac{1+\tanh(gx)}{2}$, $g > 1$, on a time varying signal.

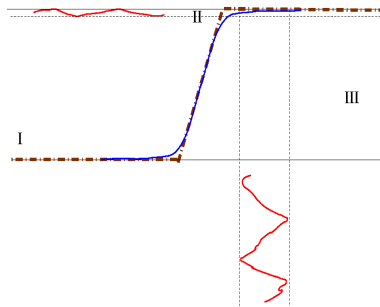
Amplification/Expansion



The 3 "regions" of the sigmoid transfer function

Effect of $f(x) = \frac{1+\tanh(gx)}{2}$, $g > 1$, on a time varying signal.

Saturation/Contraction



Contractive regime

Spontaneous dynamics. If g is small enough, spontaneous dynamics is contractive \Rightarrow there exists a unique stable fixed point \vec{V}^* attracting all trajectories.

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Time dependent perturbation $\vec{V} = \vec{V}^* + \vec{\delta} V$.

Continuous time.

$$\frac{d\vec{V}}{dt} = \vec{F}(\vec{V}) + \varepsilon \vec{S}(t) \Rightarrow \frac{d\vec{\delta} V}{dt} = D\vec{F}_{\vec{V}^*} \cdot \vec{\delta} V + \varepsilon \vec{S}(t) + O(\varepsilon^2),$$

$$\vec{\delta} V(t) = e^{D\vec{F}_{\vec{V}^*}(t-t_0)} \cdot \vec{\delta} V(t_0) + \varepsilon \int_{t_0}^t e^{D\vec{F}_{\vec{V}^*}(t-s)} \cdot \vec{S}(s) ds + O(\varepsilon^2),$$

$$\vec{\delta} V(t) \sim \varepsilon \int_{-\infty}^t e^{D\vec{F}_{\vec{V}^*}(t-s)} \cdot \vec{S}(s) ds = \varepsilon [\chi * S](t)$$

$$\chi(t) = e^{D\vec{F}_{\vec{V}^*} t}$$

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Discrete time.

$$\vec{\delta}V(t) \sim \varepsilon \sum_{\tau=-\infty}^{t-1} DG_{\vec{V}^*}^{t-\tau-1} \cdot \vec{S}(\tau) = \varepsilon [\chi * S](t)$$

$$\chi(t) = DG_{\vec{V}^*}^t$$

Susceptibility and resonances

Linear response

$$\vec{V} = \vec{V}^* + \vec{\delta} V \Rightarrow$$

$$\vec{\delta} V(t) \sim \varepsilon [\chi * S](t)$$

Fourier transform.

$$\delta \hat{V}(\omega) = \varepsilon \hat{\chi}(\omega) \cdot \hat{S}(\omega)$$

Complex susceptibility

Susceptibility and resonances

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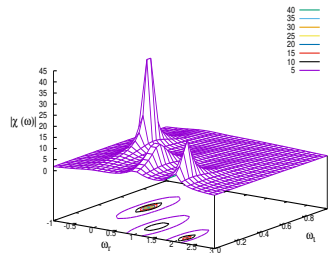
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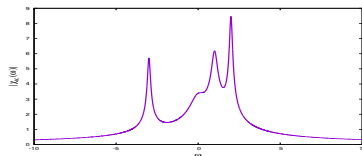
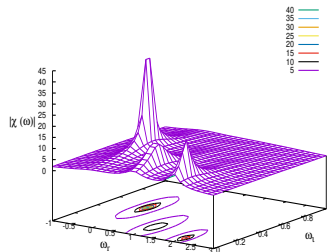
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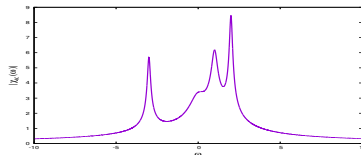
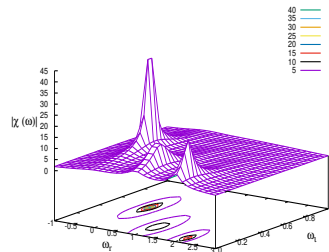
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Complex susceptibility

Complex poles of the susceptibility give resonances in the real frequency domain

- 1 Real part of the pole \Rightarrow maximum of the resonance.
- 2 Imaginary part of the pole \Rightarrow width of the resonance.

Resonances



The "neural" interpretation of resonances

Discrete time model

$$\vec{V}(t+1) = \underbrace{\mathcal{J} \cdot f(\vec{V}(t))}_{\vec{G}(\vec{V}(t))} + \varepsilon \vec{S}(t).$$

$$\chi(t) = D\vec{G}_{\vec{V}^*}^t$$

$$f(x) = \frac{1 + \tanh(gx)}{2}; \quad f'(x) = \frac{g}{2} (1 - \tanh^2(gx))$$

$$D\vec{G}_{\vec{V}^*} = g \mathcal{J} \cdot \Lambda(\vec{V}^*); \quad \Lambda_{ij}(\vec{V}^*) = f'(V_i^*) \delta_{ij}$$

$$\chi_{ij}(t) = \sum_{\gamma_{ij}(t)} \prod_{l=1}^t J_{k_l k_{l-1}} \prod_{l=1}^t f'(V_{k_{l-1}}^*),$$

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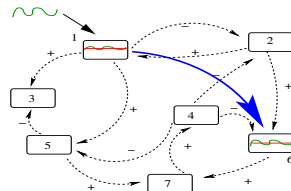
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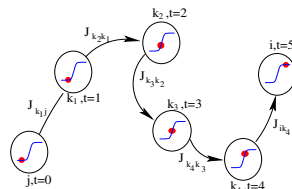
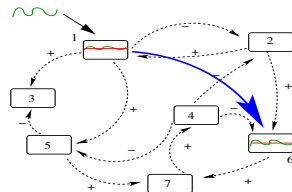
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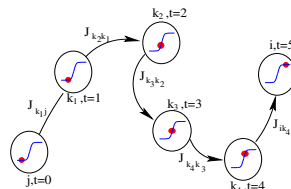
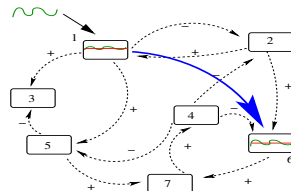
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Resonances are constructed via interactions of **state dependent** neural pathways.



Beyond the contractive regime

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Circular law

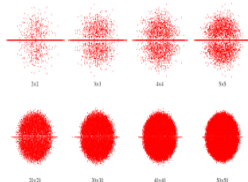


Figure: From <https://mathworld.wolfram.com/GirkosCircularLaw.htm>

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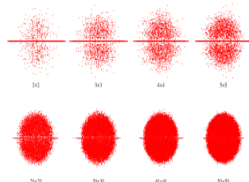


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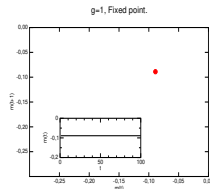
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Transition to chaos

$$m(t) = \frac{1}{N} \sum_{j=1}^N V_j(t)$$



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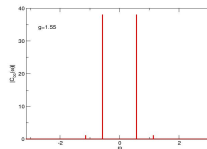
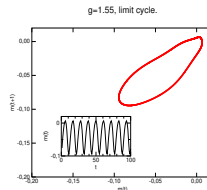
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Transition to chaos

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Beyond the contractive regime

Discrete time model

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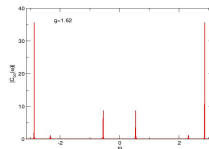
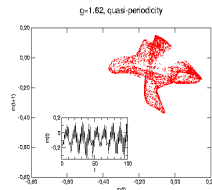
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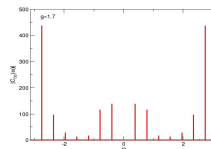
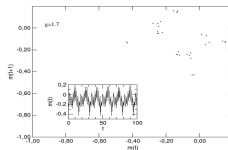
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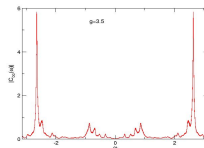
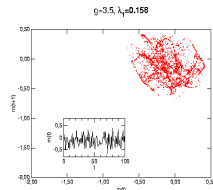
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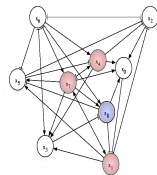
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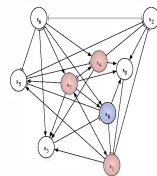
Geometric representation



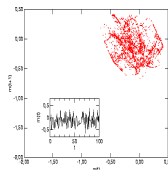
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$$g=3.5, k_1=0.158$$



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Time dependent perturbation

$$\vec{V}(t+1) = \vec{G}(\vec{V}(t)), \quad \vec{V}'(t+1) = \vec{G}(\vec{V}'(t)) + \varepsilon \vec{S}(t)$$

$$\vec{V}(t_0) = \vec{V}'(t_0); \quad \vec{\delta}V(t) = \vec{V}'(t) - \vec{V}(t), t \geq t_0$$

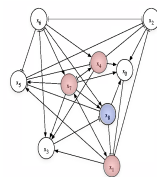
$$\vec{\delta}V(t_0+1) = \vec{V}'(t_0+1) - \vec{V}(t_0+1) = \varepsilon \vec{S}(t_0)$$

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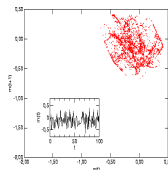
$$\vec{\delta}V(t_0+2) = \varepsilon \left[DG_{\vec{V}(t_0+1)} \cdot \vec{S}(t_0) + \vec{S}(t_0+1) \right] + \varepsilon^2 \vec{\eta}(t_0+1)$$

$$\vec{\delta}V(t) = \varepsilon \sum_{\tau=t_0}^{t-1} DG_{\vec{V}(t_0+\tau)}^{t-\tau-1} \cdot \vec{S}(\tau) + \varepsilon^2 \vec{R}(t)$$

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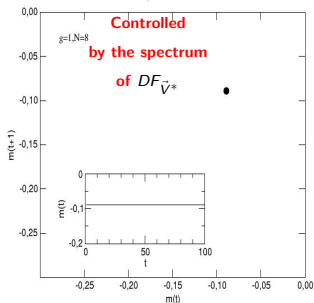
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Time dependent perturbation

Contractive case

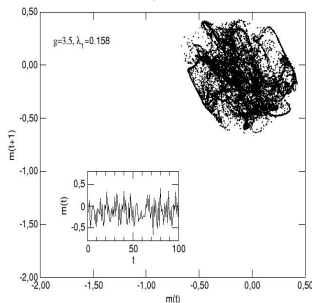
$$\delta \vec{V}(t) = \varepsilon \underbrace{\sum_{\tau=t_0}^{t-1} (DF_{\vec{V}^*})^{t-\tau+1}}_{\text{Controlled by the spectrum of } DF_{\vec{V}^*}} \cdot \mathbf{S}(\tau) + \varepsilon^2 \mathbf{R}(t)$$



Time dependent perturbation

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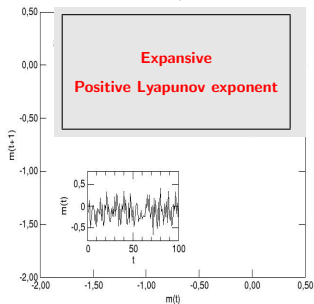
$$\vec{\delta V}(t) = \varepsilon \underbrace{\sum_{\tau=t_0}^{t-1} DG_{\vec{V}(\tau+1)}^{t-\tau-1}} \cdot \vec{S}(\tau) + \varepsilon^2 \mathbf{R}(t)$$



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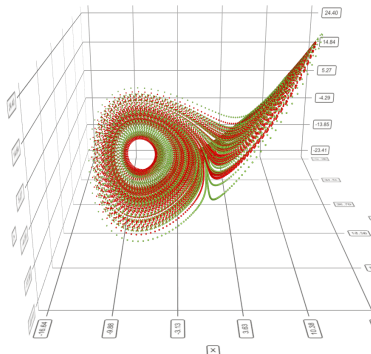


Linear response vs chaotic

Butterfly effect
Van Kampen objection

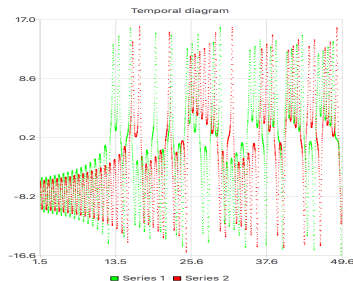
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The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

$$\lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \Phi(\vec{G}^t(\vec{V})) = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \Phi(\vec{G}^t(\vec{V} + \vec{\delta} V))$$

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Natural notion of averaging "on" the attractor.

Gibbs distributions

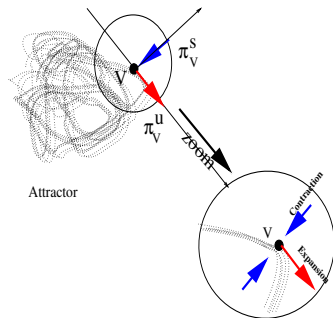
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The Sinai-Ruelle-Bowen measure is a Gibbs measure

$$H(\vec{V}) = -\log \det \pi_V^u D\vec{G}_{\vec{V}}$$

where π_V^u is the local projection on the unstable manifold.



Out of equilibrium SRB state

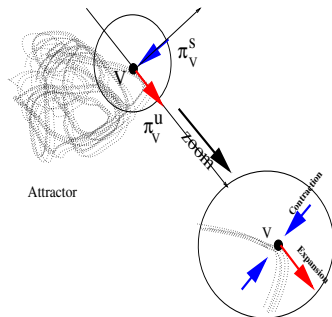
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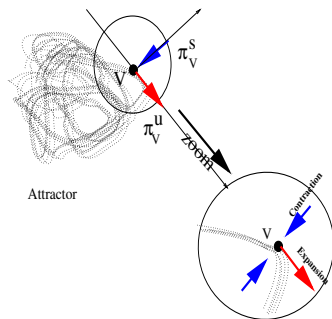
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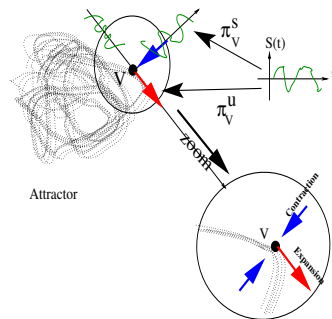
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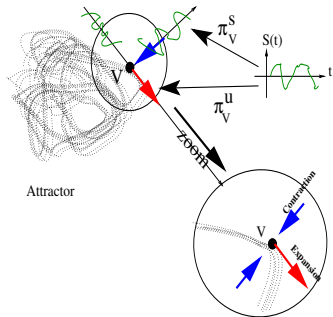
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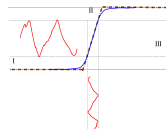
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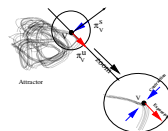
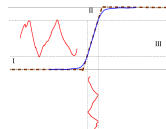
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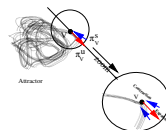
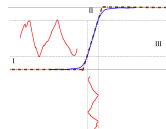
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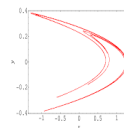
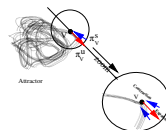
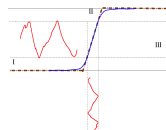
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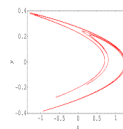
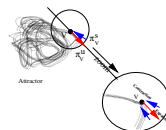
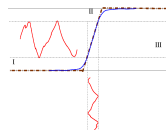
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$$D\vec{G}_{\vec{V}} = g \mathcal{J} \cdot \Lambda(\vec{V}); \quad \Lambda_{ij}(\vec{V}) = f(V_i) \delta_{ij}$$



Don't know.
Let's try and see.

Linear response in the firing rate neural network

B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006); B. Cessac Chaos (2019)

Convolution

$$\delta_t \mu[\Phi] = \varepsilon \sum_{\tau=-\infty}^{t-1} \int \mu(d\vec{V}) D\vec{G}_{\vec{V}}^{t-\tau-1} \vec{S}(\tau) \cdot \vec{V}_{(t-\tau-1)} \Phi$$

$$\Phi(\vec{V}) = \vec{V}$$

$$\delta_t \mu[\vec{V}] = \varepsilon \sum_{\tau=-\infty}^{t-1} \chi(t-\tau-1) \cdot \vec{S}(\tau) + O(\varepsilon^2) \equiv \varepsilon [\chi * S]_i(t)$$

$$\chi(t-\tau-1) = \left\langle D\vec{G}_{\vec{V}}^{t-\tau-1} \right\rangle_{eq}$$

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$$\chi_{ij}(t) = \Sigma \gamma_{ij}(t) \Pi_{l=1}^t J_{k_l k_{l-1}} \left\langle \Pi_{l=1}^t f'(V_{k_{l-1}}(l-1)) \right\rangle_{eq}$$

Linear response in the firing rate neural network

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Convolution

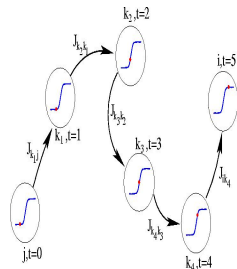
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$$\chi(t) = D\vec{G}_{\vec{V}^*}^t$$

Linear response



$$\chi_{i,j}(t) = \sum \gamma_{ij}(t) \prod_{l=1}^t J_{k_l k_{l-1}} \prod_{l=1}^t f'(V_{k_{l-1}}^*)$$

Linear response in the firing rate neural network

B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006); B. Cessac Chaos (2019)

Convolution

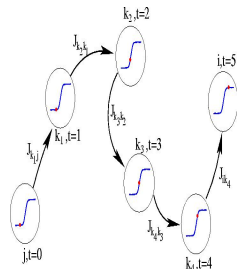
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Numerical computation

Complex susceptibility

$$\hat{\chi}_{ij}(\omega) = \sum_{t=-\infty}^{+\infty} e^{i\omega t} \chi_{ij}(t)$$

Consider two perturbations, $\varepsilon \cos(\omega t) \vec{e}_j$ and $-\varepsilon \sin(\omega t) \vec{e}_j$ where \vec{e}_j is the canonical basis vector in direction j and denote $\vec{V}^{(1)}, \vec{V}^{(2)}$ the corresponding perturbed dynamics.

Ergodic average

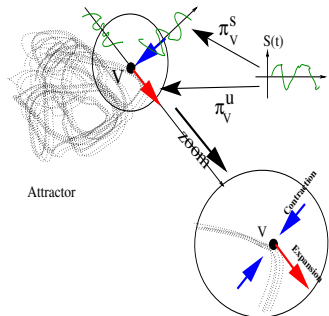
$$\hat{\chi}_{ij}(\omega) = \lim_{T \rightarrow +\infty} \frac{1}{T\varepsilon} \sum_{t=0}^{T-1} e^{i\omega(t-1)} \left[V_i^{(1)}(t) + i V_i^{(2)}(t) \right]$$

Resonances

Ruelle resonances

- The *tangent part* of the response is a correlation function \Rightarrow Green-Kubo relation.

Perturbations effect



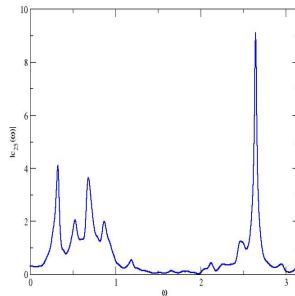
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- **Ruelle-Pollicott resonances:** In the power spectrum. Absolutely continuous part of the SRB measure. Do not depend on the observable (spectrum of the Ruelle-Perron-Frobenius operator).

Perturbations effect

Power spectrum

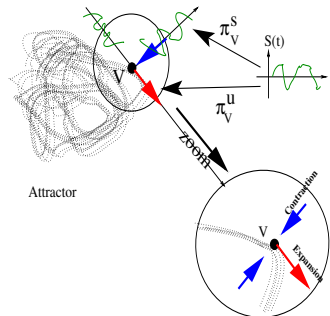


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Perturbations effect



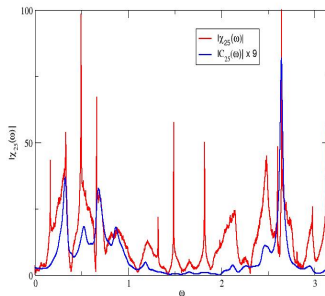
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Complex susceptibility



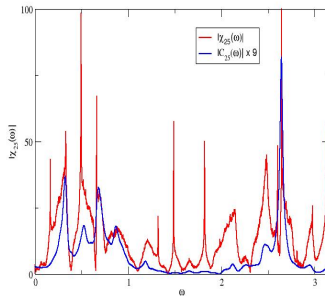
Resonances

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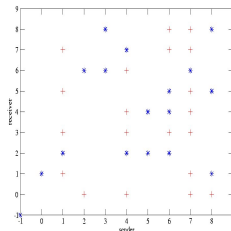
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- The *transverse part* (which does not exist in conservative systems) is not a correlation function.
- Exotic resonances. Not in the power spectrum. Singular part of the SRB measure.
- Predicted by D. Ruelle (J. Stat. Phys, 1999)
- Exhibited (numerically) in B. Cessac, J.A. Sepulchre, PRE, 2004.

Perturbations effect

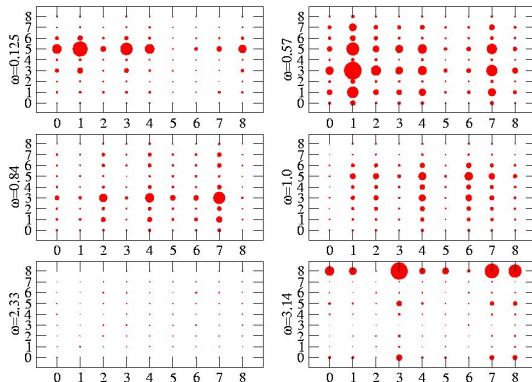
Complex susceptibility



Response to a time-dependent stimulus



Connectivity matrix



Response matrix

Signal propagation by amplitude modulation

B. Cessac, J.A. Sepulchre, Chaos (2006);

Amplitude modulation

- Fix a resonant frequency ω_0 .
- Define a slow amplitude modulation signal

$$S_i(t) = \cos(\omega_M t) \sin(\omega_0 t)$$

where ω_M corresponds to a very long period.

$$\hat{\chi}_{ij}(\omega) = \lim_{T \rightarrow +\infty} \frac{1}{T\varepsilon} \sum_{t=0}^{T-1} e^{i\omega(t-1)} \left[V_i^{(1)}(t) + i V_i^{(2)}(t) \right]$$

Can we recover the signal "hidden" in the chaotic background ?

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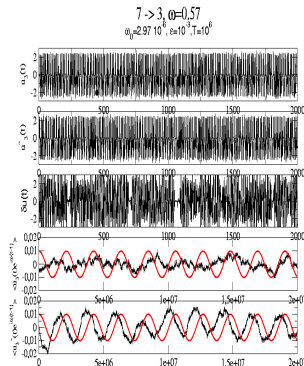
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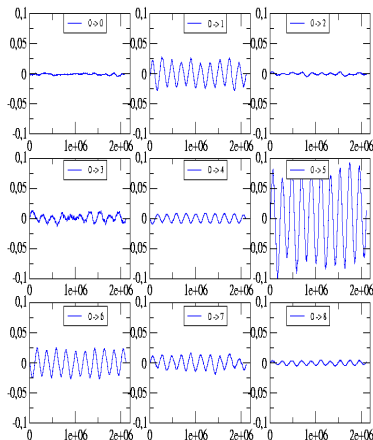
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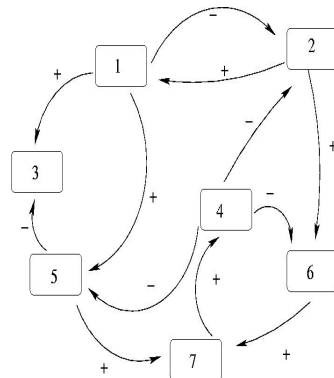
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Can we recover the signal "hidden" in the chaotic background ?

Effective connectivity

Structural connectivity



Signal propagation by amplitude modulation

B. Cessac, J.A. Sepulchre, Chaos (2006);

Amplitude modulation

- Fix a resonant frequency ω_0 .
- Define a slow amplitude modulation signal

$$S_i(t) = \cos(\omega_M t) \sin(\omega_0 t)$$

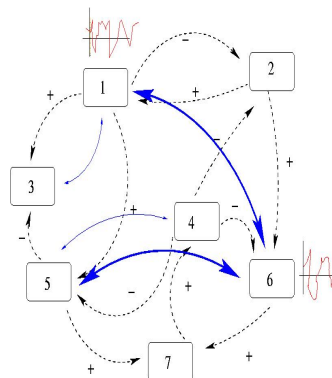
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$$\hat{\chi}_{ij}(\omega) = \lim_{T \rightarrow +\infty} \frac{1}{T\varepsilon} \sum_{t=0}^{T-1} e^{i\omega(t-1)} \left[V_i^{(1)}(t) + i V_i^{(2)}(t) \right]$$

Can we recover the signal "hidden" in the chaotic background ?

Effective connectivity

Correlation connectivity



Signal propagation by amplitude modulation

B. Cessac, J.A. Sepulchre, Chaos (2006);

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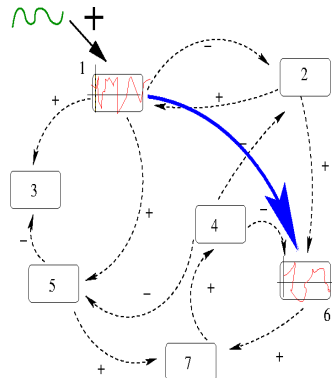
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Can we recover the signal "hidden" in the chaotic background ?

We have 3 different notions of connectivity which do not coincide.

Effective connectivity

Causal connectivity



Linear response theory

Gibbs like distributions

- Equilibrium stat. phys.
- Non equilibrium stat. phys. Onsager theory.
- Green-Kubo relations.
- Ergodic theory for "chaotic" systems. SRB measure.
- Non equilibrium SRB state.

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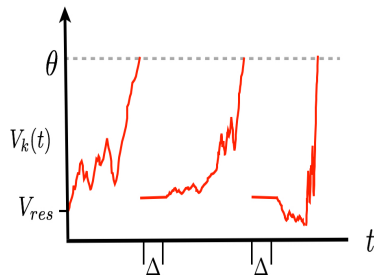
Firing rate model

- Linear response is possible in a chaotic neural network.
- Convolution kernel depending on synaptic graph and dynamics.
- The response graph is different from the synaptic weights graph and depends on the stimulus.
- Further steps in Onsager theory ? Transport of entropy ? Information current ?

From spiking neurons dynamics to linear response.

An Integrate and Fire neural network model with chemical and electric synapses

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013

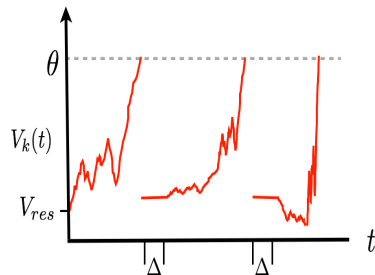


$\omega_k(n)$

0	0	1	0	0	0	0	1	0	0	1	0
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$\omega_k(n)$

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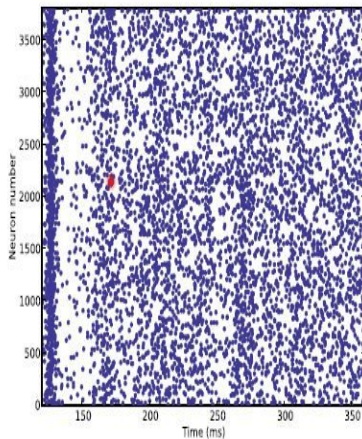
Spikes

- Voltage dynamics is time-continuous.
- Spikes are time-discrete events (time resolution $\Delta > 0$).

$$\begin{aligned} t_k^{(l)} &\in [n\Delta, (n+1)\Delta[\\ &\Rightarrow \\ \omega_k(n) &= 1 \end{aligned}$$

An Integrate and Fire neural network model with chemical and electric synapses

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013

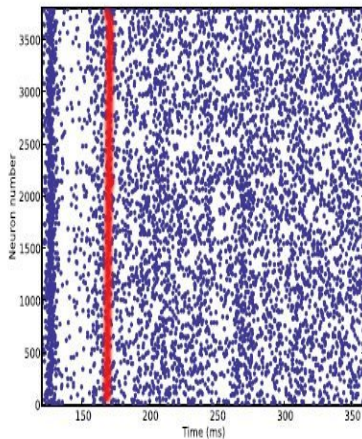


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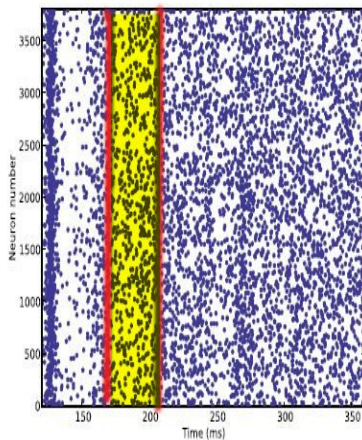


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- Spike block ω_m^n .

A conductance-based Integrate and Fire model

M. Rudolph, A. Destexhe, Neural Comput. 2006, (GIF model)
R. Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013

Model

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} = - \underbrace{g_{L,k}(V_k - E_L)}_{Leak}$$

A conductance-based Integrate and Fire model

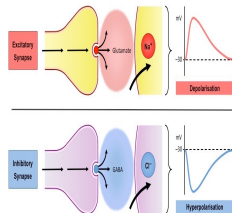
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<https://ib.bioninja.com.au/options/option-a-neurobiology-and/a5-neuropharmacology/synaptic-transmission.html>

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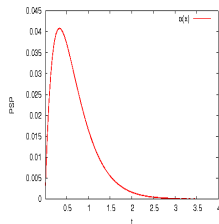
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Synapses



$$\alpha_{kj}(t) = \frac{t}{\tau} e^{-\frac{t}{\tau_{kj}}} H(t),$$

A conductance-based Integrate and Fire model

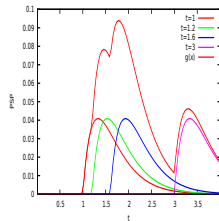
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Synapses



$$g_{kj}(t) = g_{kj}(t_j) + G_{kj} \alpha_{kj}(t - t_j)$$

$$t > t_j$$

A conductance-based Integrate and Fire model

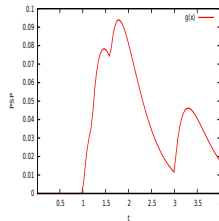
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A conductance-based Integrate and Fire model

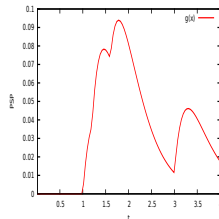
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$$g_{kj}(t, \omega) = G_{kj} \sum_{n \geq 0} \alpha_{kj}(t - n\Delta) \omega_j(n)$$

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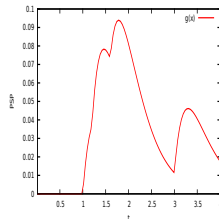
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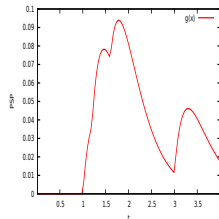
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Synapses



$$g_{kj}(t, \omega) = G_{kj} \sum_{n \geq 0} \alpha_{kj}(t - n\Delta) \omega_j(n)$$

A conductance-based Integrate and Fire model

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} + g_k(t, \omega) V_k = i_k(t, \omega)$$

$$W_{kj} \stackrel{\text{def}}{=} G_{kj} E_j$$

$$\alpha_{kj}(t, \omega) = \sum_{n \geq 0} \alpha_{kj}(t - n\delta) \omega_j(n)$$

$$i_k(t, \omega) = \underbrace{g_{L,k} E_L}_{\text{Leak}} + \underbrace{\sum_j W_{kj} \alpha_{kj}(t, \omega)}_{\text{Synapses}} + \underbrace{S_k(t)}_{\text{Stimulus}} + \underbrace{\sigma_B \xi_k(t)}_{\text{Noise}}$$

A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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- Linear in V .
- Spike history-dependent.

A conductance-based Integrate and Fire model

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$$\Gamma_k(t_1, t, \omega) = \begin{cases} e^{-\frac{1}{C_k} \int_{t_1}^t g_k(u, \omega) du} & \text{if } t \in [t_1, \tau_k(t, \omega)]; \\ 0, & \text{otherwise.} \end{cases}$$

A conductance-based Integrate and Fire model

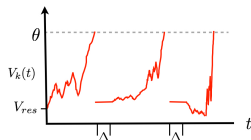
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$$\omega_k(n) \quad \boxed{0} \boxed{0} \boxed{1} \boxed{0} \boxed{0} \boxed{0} \boxed{0} \boxed{0} \boxed{1} \boxed{0} \boxed{0} \boxed{1} \boxed{0}$$

A conductance-based Integrate and Fire model

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} + g_k(t, \omega) V_k = i_k(t, \omega)$$

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Dynamics integration

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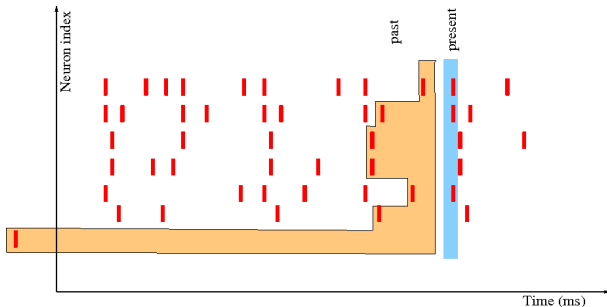
Variable length Markov chain

$$P_n \left[\omega(n) \mid \omega_{-\infty}^{n-1} \right] \equiv \Pi \left(\omega(n), \frac{V_{th} - V_k^{(det)}(n-1, \omega)}{\sigma_k(n-1, \omega)} \right)$$

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Markov chain: $P\left[\omega(n) \mid \omega_{n-D}^{n-1}\right] > 0$

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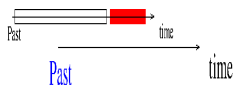
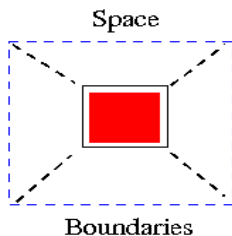
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Infinite memory depth $D \rightarrow +\infty$.

$$\phi \left(\omega_{-\infty}^l \right) = \log P \left[\omega(l) \mid \omega_{-\infty}^{l-1} \right]$$

O. Onicescu and G. Mihoc. CRAS Paris, 1935
R. Fernandez, G. Maillard, A. Le Ny, ...

Response to stimuli

B. Cessac, A. Ampuero, R. Cofré, Linear response for spiking neuronal networks with unbounded memory, Entropy, 2021

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History dependence, observable, network dynamics

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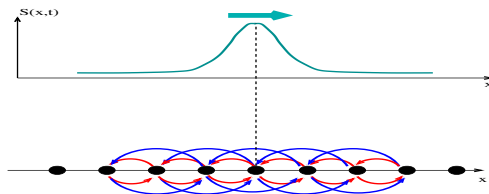
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History dependence, (spontaneous) correlation between observable and network dynamics

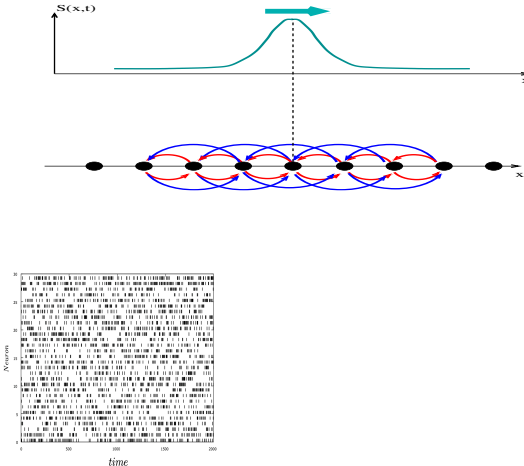
Collective spike response to stimuli

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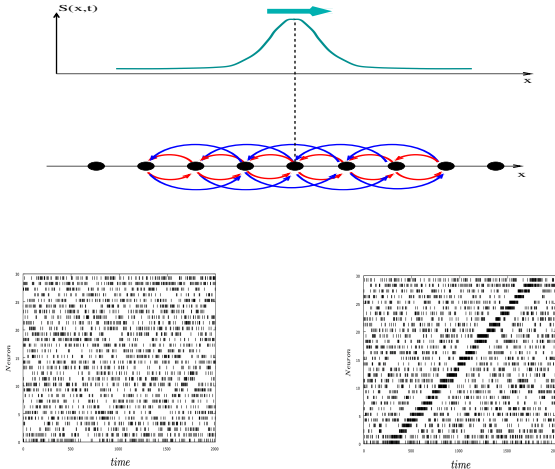
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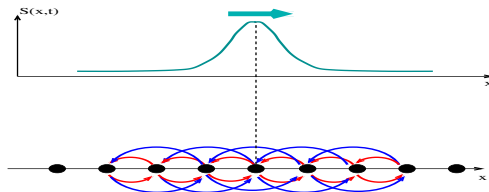
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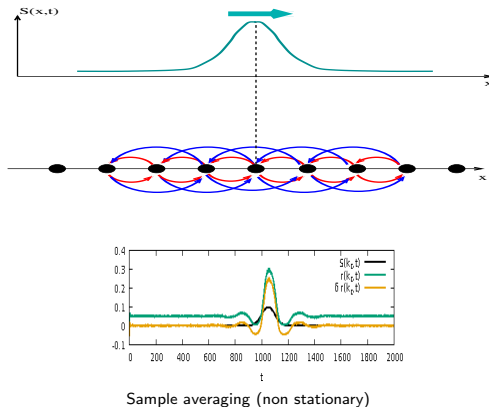
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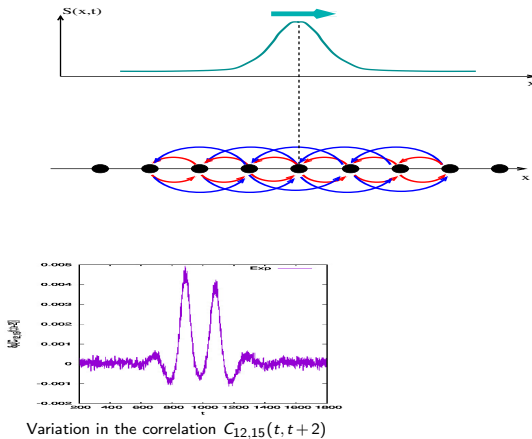
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Correlation variations are triggered by the stimulus, but they are constrained by the network dynamics.

Firing rates

Computations have been done using the INRIA Pranas software, B. Cessac et al, Frontiers in Neuroinformatics, 2017.

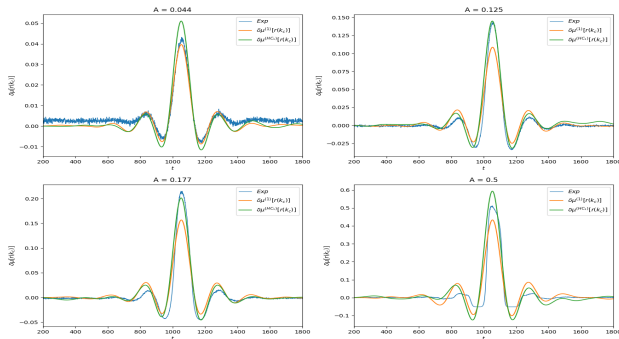


Figure: Linear response of $f(\omega, n) = \omega_{k_C}(n)$ for different values of stimulus amplitude A .

Higher order observable

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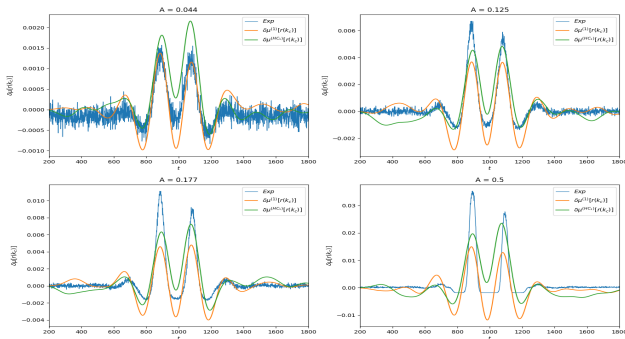


Figure: Linear response of the observable $f(n, \omega) = \omega_{k-2}(n-3)\omega_k(n)$.

Range of validity

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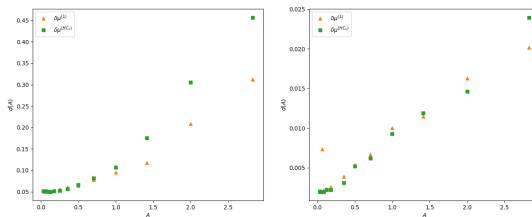


Figure: L^2 distance between the curves $\delta\mu^{(1)}[f(n)]$, $\delta\mu^{(HC1)}[f(n)]$ and the empirical curve, as a function of the stimulus amplitude A . Left panel show distance between rate curves and right panel distance between pairwise observable with delay.

Main conclusions

- Linear response in a spiking neural network.
- Convolution kernel depending on synaptic graph and dynamics.
- Link with receptive fields for sensory neurons ?

General conclusion

Gibbs like distributions

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- Non equilibrium stat. phys. Onsager theory.
- Green-Kubo relations.
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- Extend the Gallavotti-Ruelle idea of currents associated to entropy production to information fluxes in neuronal networks.