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Linear response in neuronal networks: from neurons dynamics to collective response

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Linear response in neuronal networks: from neurons dynamics to collective response

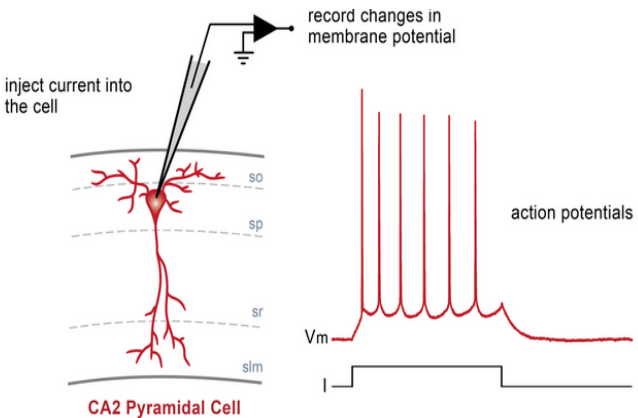
Bruno Cessac

Biovision Team, INRIA Sophia Antipolis, France.

14/15-01-2019

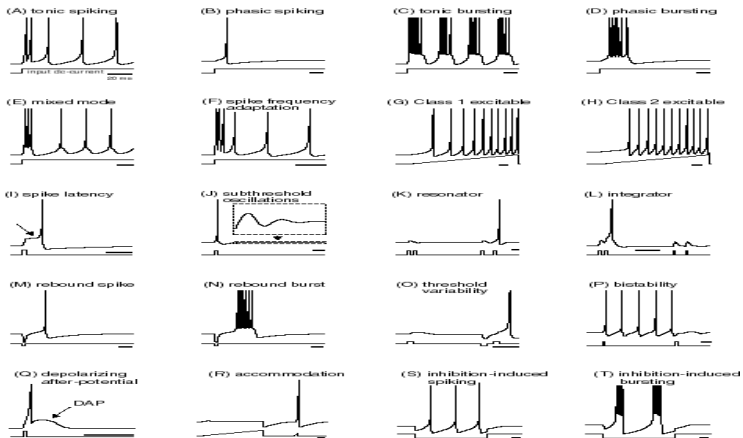
LACONEU summer school 2019.

Neuron response to a stimulus



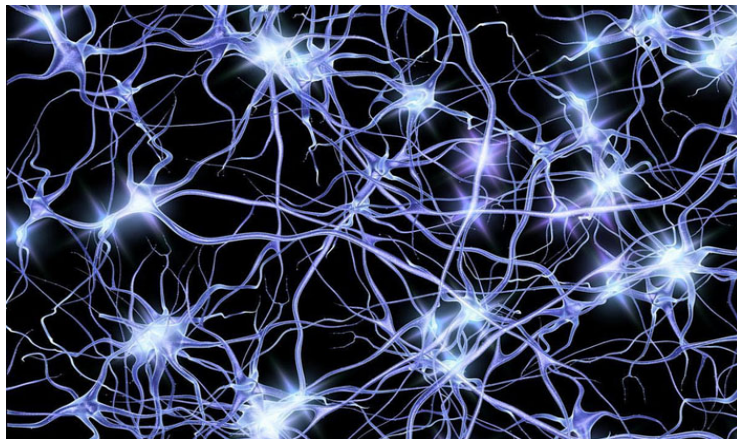
<https://www.plasticitylab.com/methods/>

Neuron response to a stimulus

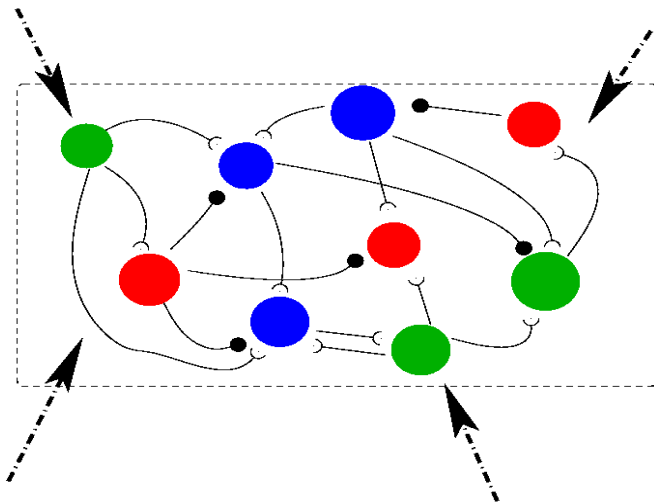


Izhikevich, E., IEEE Trans Neural Netw , 15 (5), 10631070, (2004).

Network response to a stimulus



Network response to a stimulus



Network response to a stimulus

- 1 How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?

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Network response to a stimulus

- ① How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?
- ② How to measure the influence of a stimulated neuron on another neuron ?
- ③ How does this "effective connectivity" relates to :
 - (a) Synaptic connectivity;
 - (b) Pairwise correlations;
 - (c) "Information" transport.

- 1 From firing rate neurons dynamics to linear response.
- 2 From spiking neurons dynamics to linear response.
- 3 General conclusions
- 4 Appendix: Linear response theory in physics vs linear response in neuronal networks

From firing rate neurons dynamics to linear response.

Amari-Wilson-Cowan model

Amari, 1971; Wilson-Cowan, 1972; Cohen-Grossberg, 1983; Sompolinsky et al, 1988; ...

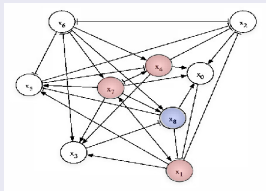
$$\frac{dV_i}{dt} = -\mu V_i + \sum_{j=1}^N J_{ij} f(V_j(t)) + S_i(t); \quad i = 1 \dots N. \quad (1)$$

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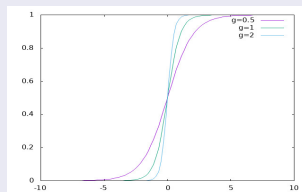
Network



Ex: $J_{ij} \sim \mathcal{N}\left(0, \frac{J^2}{N}\right)$

(Sompolinsky et al, 1988)

Non linearity



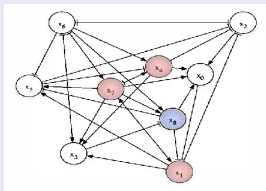
Ex: $f(x) = \frac{1}{2} (1 + \tanh(gx))$,
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$$\frac{d\vec{V}}{dt} = -\mu\vec{V} + \mathcal{J}.f(\vec{V}) + \vec{S}(t); \quad i = 1 \dots N. \quad (1)$$

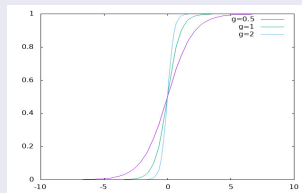
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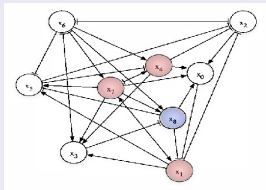
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$$\frac{d\vec{V}}{dt} = \underbrace{-\mu\vec{V} + \mathcal{J} \cdot f(\vec{V})}_{\vec{G}(\vec{V})} + \vec{S}(t); \quad i = 1 \dots N. \quad (1)$$

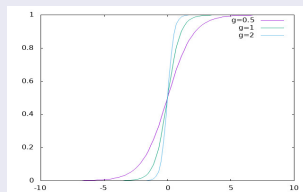
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Low gain g dynamics

Theorem. If g is small enough \vec{G} is contractive.

$$\forall \vec{V}, \vec{V}' \in \mathcal{M}, \quad \|\vec{G}(\vec{V}') - \vec{G}(\vec{V})\| \leq \eta \|\vec{V}' - \vec{V}\|, \quad 0 < \eta < 1$$

\Rightarrow

For $\vec{S} = 0$, there is a unique stable fixed point \vec{V}^* , $\vec{G}(\vec{V}^*) = \vec{0}$.

Low gain g dynamics

Small perturbation of the fixed point. $\vec{V} = \vec{V}^* + \vec{\xi}$.

$$\frac{d\vec{\xi}}{dt} = DG_{\vec{V}^*} \cdot \vec{\xi} + \vec{S}(t) + O(\|\vec{\xi}\|^2)$$

$$\vec{\xi}(t) = \int_{-\infty}^t e^{DG_{\vec{V}^*}(t-s)} \cdot \vec{S}(s) ds$$

$$\Lambda = P^{-1} \cdot DG_{\vec{V}^*} \cdot P; \quad \vec{\xi} = P\vec{\xi}'; \quad \vec{S} = P\vec{S}' \Rightarrow \vec{\xi}'(t) = \int_{-\infty}^t e^{\Lambda(t-s)} \cdot \vec{S}'(s) ds$$

$$\xi'_k(t) = \int_{-\infty}^t e^{\lambda_k(t-s)} \cdot S'_k(s) ds$$

Low gain g dynamics

Harmonic perturbation. $S'_k(t) = A'_k e^{i\omega t}$.

$$\lambda_k = \lambda_{k,r} + i\lambda_{k,i} \quad \omega = \omega_r + i\omega_i.$$

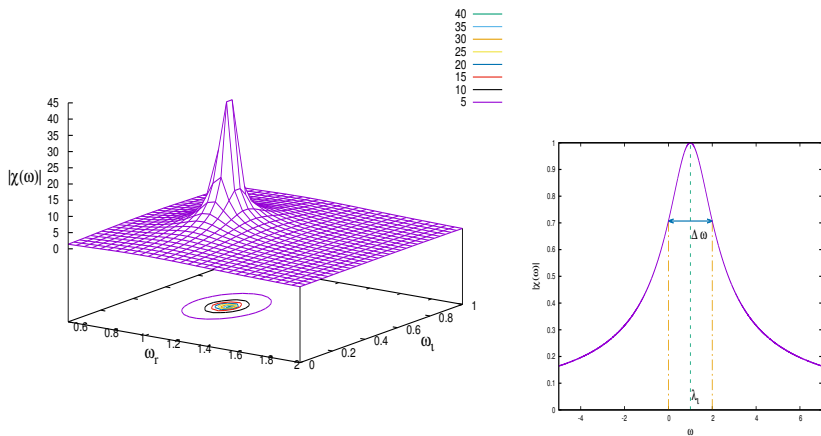
The integral is finite if $\omega_i < -\lambda_{k,r}$.

$$\xi'_k(t) = \hat{\chi}'_k(\omega) e^{i\omega t}.$$

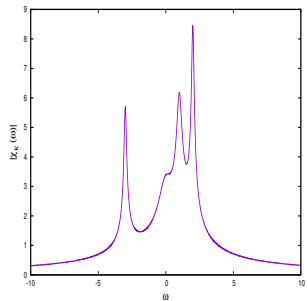
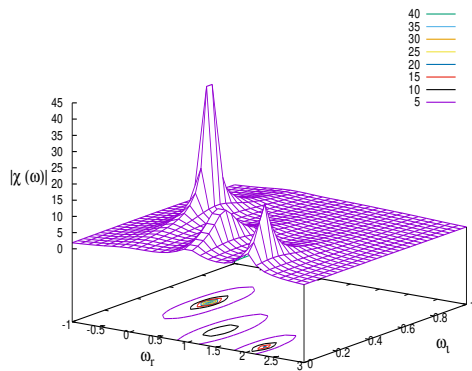
Complex susceptibility matrix.

$$\vec{\xi}(t) = \hat{\chi}(\omega) \cdot \vec{S} e^{i\omega t}. \quad (2)$$

Low gain g dynamics



Low gain g dynamics



Low gain g dynamics

Example 1. $f(x) = \tanh(gx) \Rightarrow$

$$\vec{V}^* = \vec{0}; \quad DG_{\vec{V}^*} = -\mu\mathcal{I} + g\mathcal{J}$$

Let $s_k \equiv s_{k,r} + is_{k,i}$ eigenvalues of \mathcal{J} .

$$\lambda_k = \underbrace{-\mu + g s_{k,r}}_{\lambda_{k,r}} \pm i \underbrace{g s_{k,i}}_{\lambda_{k,i}}$$

When \mathcal{J} is random, $J_{ij} \sim \mathcal{N}(0, \frac{J^2}{N})$ the probability distribution of eigenvalues is known.

(Girko, V. L., Theory Probab. Appl. 29, 694-706, 1984.).

Low gain g dynamics

Example 2. $f(x) = \frac{1+\tanh(gx)}{2} \Rightarrow$

$$\vec{V}^* \equiv \vec{V}^*(\mathcal{J}); \quad DG_{\vec{V}^*} = -\mu\mathcal{I} + gD(\vec{V}^*)\mathcal{J}$$

where $D(\vec{V}^*) = \text{diag}\left(\frac{1-\tanh^2(gV_i^*)}{2}\right)$.

The eigenvalues of $D(\vec{V}^*)\mathcal{J}$ cannot be determined from the eigenvalues of \mathcal{J} . However, when \mathcal{J} is random, $J_{ij} \sim \mathcal{N}(0, \frac{J^2}{N})$ the probability distribution of eigenvalues can be determined.

(Girko, V. L. Theory of Random Determinants. Boston, MA: Kluwer, 1990).

Low gain g dynamics

Summary:

- The linear response to a signal of weak amplitude is controlled by the Jacobian matrix $DG_{\vec{v}^*}$.
- Eigenvalues of $DG_{\vec{v}^*} \Rightarrow$ Poles of the complex susceptibility \Rightarrow Resonances.
- What is the phenomenological/neuronal interpretation of $DG_{\vec{v}^*}$?

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$$DG_{\vec{V}^*} = - \underbrace{\mu \mathcal{I}}_{\text{Leak}} + \underbrace{g}_{\text{Gain}} \underbrace{D(\vec{V}^*)}_{f'} \underbrace{\mathcal{J}}_{\text{Synapses}}$$

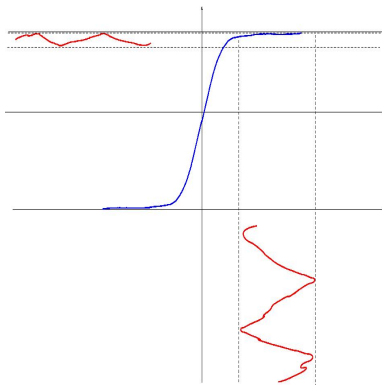
Low gain g dynamics

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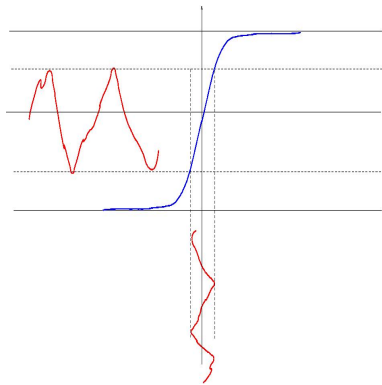
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Expansion/Contraction

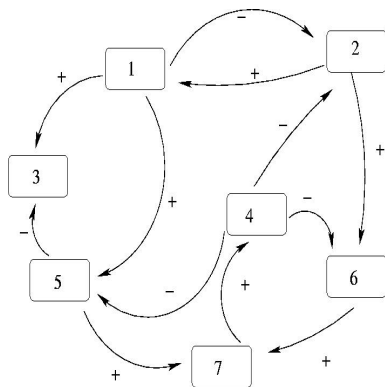


Saturation

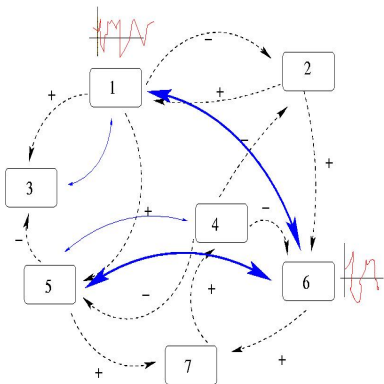


Amplification

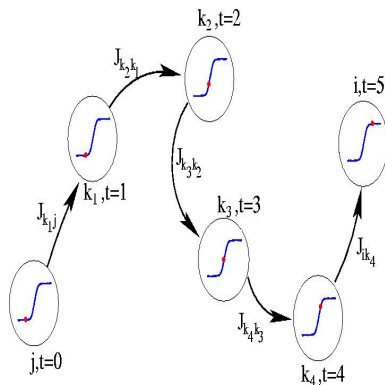
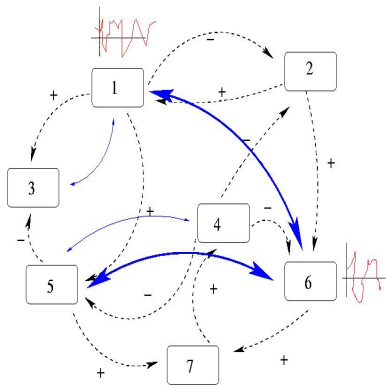
Expansion/Contraction



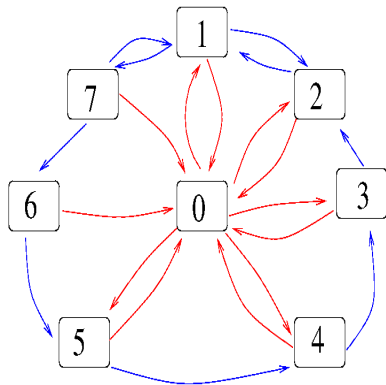
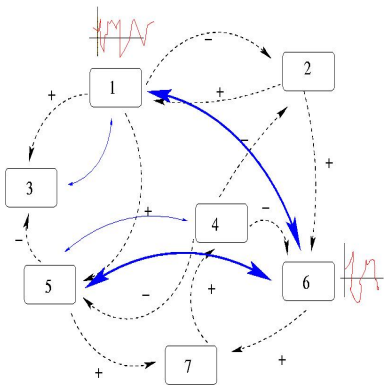
Expansion/Contraction



Expansion/Contraction



Expansion/Contraction



Linear response in a dynamical regime

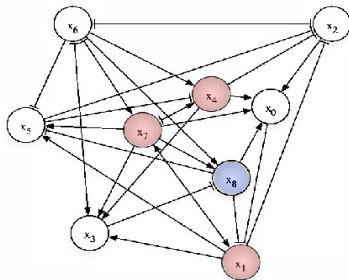
$$\frac{dV_i}{dt} = -\mu V_i + \sum_{j=1}^N J_{ij} f(V_j(t)) + I_i(t); \quad i = 1 \dots N.$$

$$V_i(t + dt) = V_i(t)(1 - \mu dt) + \sum_{j=1}^N J_{ij} f(V_j(t)) dt + S_i(t) dt$$

$$V_i(t + 1) = \sum_{j=1}^N J_{ij} f(V_j(t)) + S_i(t). \quad (3)$$

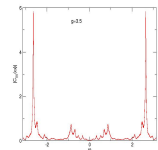
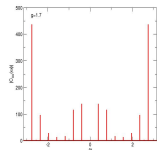
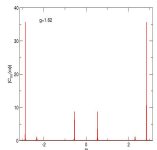
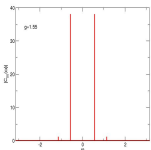
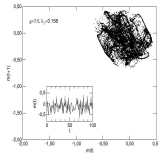
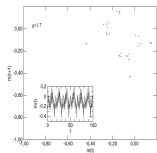
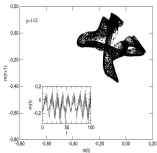
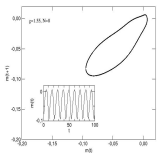
Linear response in the chaotic regime

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



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

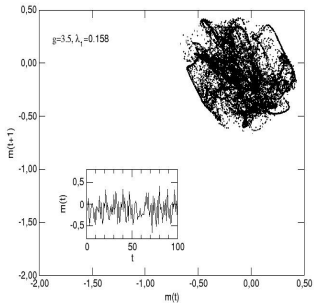
$$f(x) = \tanh(gx)$$

Transition to chaos by quasi periodicity as g increases g 

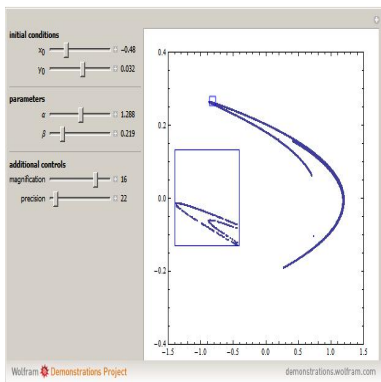
Doyon B. et al, International Journal Of Bifurcation and Chaos, Vol. 3, Num. 2, 279-291 (1993)

Cessac B. et al, Physica D, 74, 24-44 (1994)

Chaotic dynamics and strange attractors



Chaotic dynamics and strange attractors



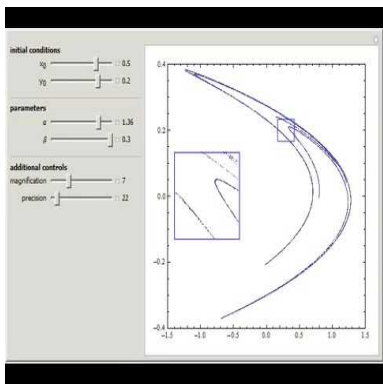
Hénon map

$$\begin{cases} x(t+1) = 1 - ax^2(t) + y(t) \\ y(t+1) = bx(t) \end{cases}$$

$$a = 1.4; b = 0.3$$

<https://upload.wikimedia.org/wikipedia/commons/a/ac/>

Chaotic dynamics and strange attractors



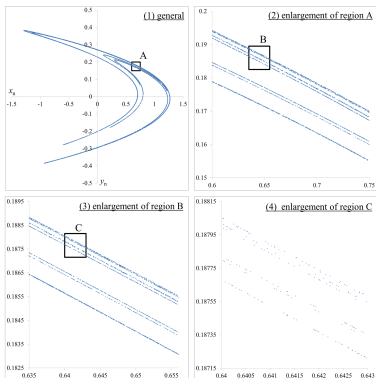
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<http://www.demonstrations.wolfram.com/OrbitDiagramOfTheHenonMap/>

Chaotic dynamics and strange attractors

Decomposition of Hénon's Transformation

The gridded square in the upper left is transformed in three steps: a non-linear bending (upper right) in the y -direction, the contraction towards the y -axis (lower left) and a reflection at the diagonal (lower right). The region shown is $-2.2 \leq x \leq 2.2$ and $-2.2 \leq y \leq 2.2$.

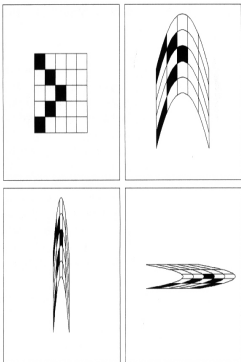


Figure 12.3

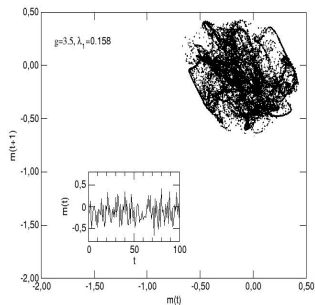
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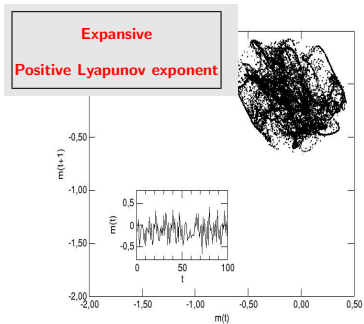
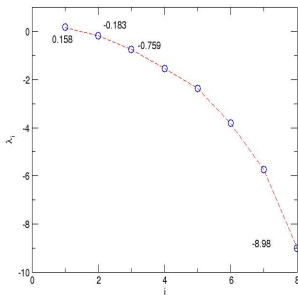
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<http://www.sfu.ca/~rpyke/335/W00/>

Chaotic dynamics and strange attractors



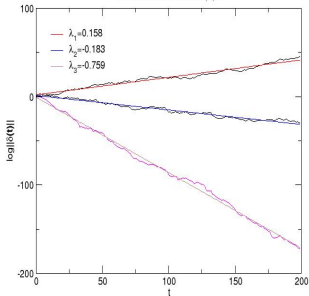
Chaotic dynamics and strange attractors

Lyapunov spectrum, $g=3.5$ 

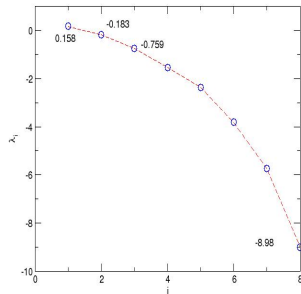
Chaotic dynamics and strange attractors

Evolution d'une perturbation:

Directions d'Oseledec 1,2,3



Lyapunov spectrum, $g=3.5$



Time dependent perturbation

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

Time dependent perturbation

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Switch the stimulus on at time t_0 ; $\vec{V}(t_0) = \vec{V}'(t_0)$.

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Switch the stimulus on at time t_0 ; $\vec{V}(t_0) = \vec{V}'(t_0)$.

$$\vec{\delta}(t) = \vec{V}'(t) - \vec{V}(t) \Rightarrow \vec{\delta}(t_0+1) = \vec{V}'(t_0+1) - \vec{V}(t_0+1) = \epsilon \vec{S}(t_0)$$

Time dependent perturbation

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

Time dependent perturbation

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

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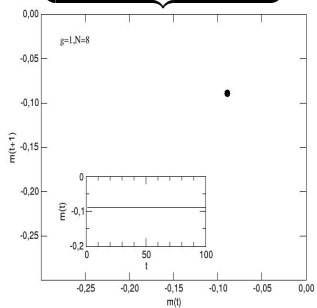
$$\vec{\delta}(t_0+2) = \vec{G}(\vec{V}(t_0+1) + \epsilon \vec{S}(t_0)) + \epsilon \vec{S}(t_0+1) - \vec{G}(\vec{V}(t_0+1))$$

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

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

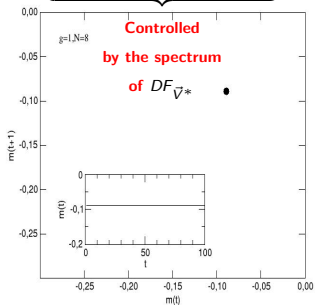
Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \underbrace{\sum_{\tau=t_0}^{t-1} (DF_{\vec{v}})^{t-\tau+1} \cdot \vec{S}(\tau)}_{\text{perturbation}} + \epsilon^2 \vec{R}(t)$$



Time dependent perturbation

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



Linear stability analysis

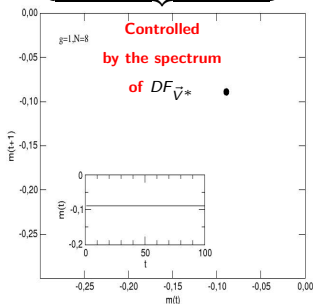
$$\vec{G}(\vec{V}) = \mathcal{J}f(g \vec{V})$$

$$DF_{\vec{V}} = g \mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g u_j) \delta_{ij}$$

Time dependent perturbation

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

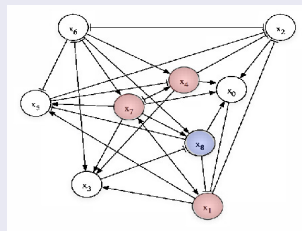


Linear stability analysis

$$\vec{G}(\vec{V}) = \mathcal{J}f(g \vec{V})$$

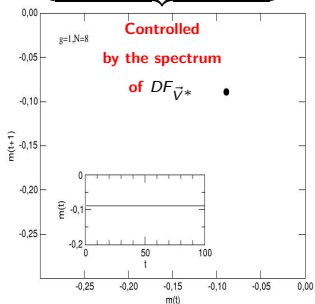
$$DF_{\vec{V}} = g \mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g u_j) \delta_{ij}$$



Time dependent perturbation

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

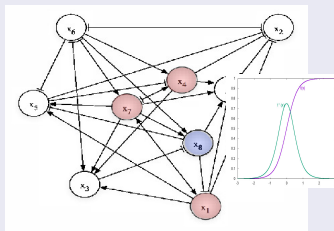


Linear stability analysis

$$\vec{G}(\vec{V}) = \mathcal{J}f(g \vec{V})$$

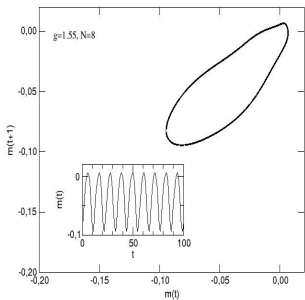
$$DF_{\vec{V}} = g \mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g u_j) \delta_{ij}$$



Time dependent perturbation

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



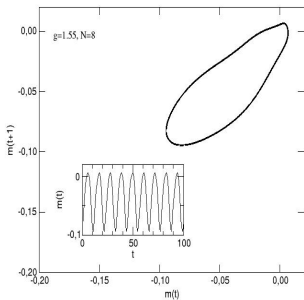
$$\vec{G}(\vec{V}) = \mathcal{J}f(g \vec{V}) + \theta$$

$$DF_{\vec{V}} = g \mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g u_j) \delta_{ij}$$

Time dependent perturbation

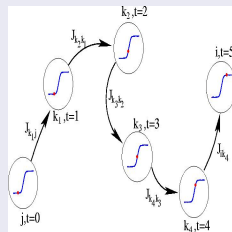
$$\vec{\delta}(t) = \epsilon \sum_{\tau=t_0}^{t-1} DF_{\vec{V}(t+1)}^{t-\tau+1} \cdot \vec{S}(\tau) + \epsilon^2 \vec{R}(t)$$



$$\vec{G}(\vec{V}) = \mathcal{J}f(g \vec{V}) + \theta$$

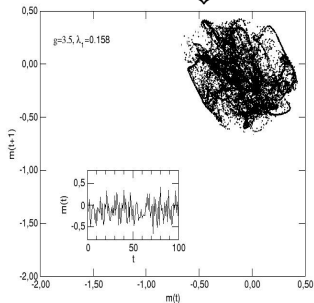
$$DF_{\vec{V}} = g \mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g u_j) \delta_{ij}$$



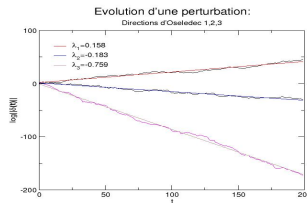
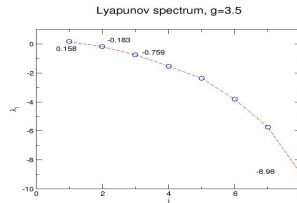
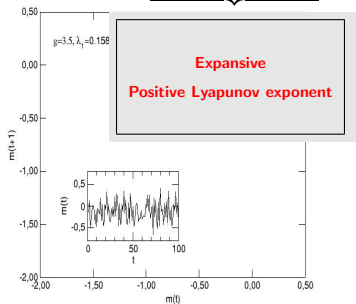
Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \underbrace{\sum_{\tau=t_0}^{t-1} DF_{\vec{v}(t+1)}^{t-\tau+1} \cdot \vec{S}(\tau)} + \epsilon^2 \vec{R}(t)$$



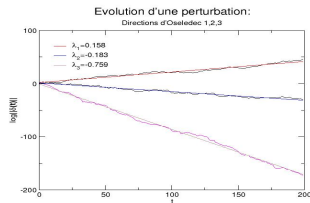
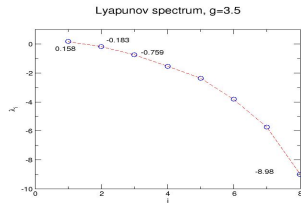
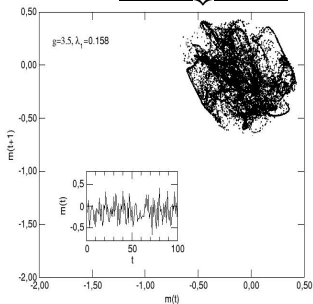
Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \underbrace{\sum_{\tau=t_0}^{t-1} DF_{\vec{v}(t+1)}^{t-\tau+1} \cdot \vec{S}(\tau)} + \epsilon^2 \vec{R}(t)$$



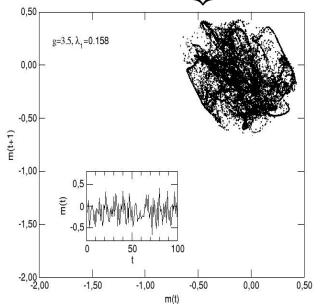
Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \underbrace{\sum_{\tau=t_0}^{t-1} DF_{\vec{v}(t+1)}^{t-\tau+1} \cdot \vec{S}(\tau)} + \epsilon^2 \vec{R}(t)$$



Time dependent perturbation

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



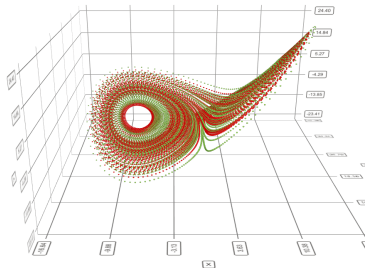
Linear response vs chaotic

Butterfly effect

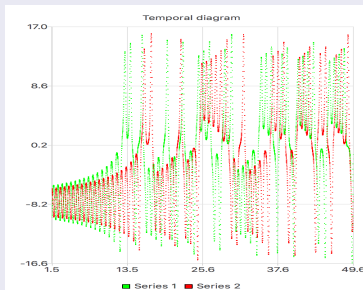
Van Kampen objection

The linear expansion provided by the positive Lyapunov exponent prevents linear response theory.

Time dependent perturbation



Linear response vs chaotic



The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

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

μ_L Lebesgue measure on the phase-space.

$$\mu \stackrel{w}{=} \lim_{t \rightarrow +\infty} \vec{G}^{*t} \mu_L, \quad \text{SRB measure}$$

$$\lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \Phi[\vec{G}^t(\vec{V})] \stackrel{\mu_L \text{ a.s.}}{=} \int_{\Omega} \Phi(\vec{V}) \mu(d\mathbf{X})$$

Natural notion of averaging "on" the attractor.

The Sinai-Ruelle-Bowen measure

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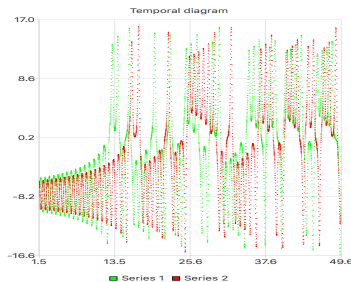
$$\lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \Phi(\vec{G}^t(\vec{V})) = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \Phi(\vec{G}^t(\vec{V} + \vec{\delta}))$$

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Natural notion of averaging "on" the attractor.

Decomposition of Hénon's Transformation

The gridded square in the upper left is transformed in three steps: a non-linear bending (upper right) in the y -direction, the contraction towards the y -axis (lower left) and a reflection at the diagonal (lower right). The region shown is $-2.2 \leq x \leq 2.2$ and $-2.2 \leq y \leq 2.2$.

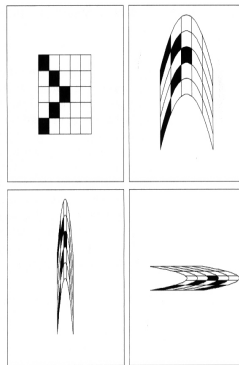


Figure 12.3

Out of equilibrium SRB state

D. Ruelle, J. Stat. Phys., 1998

$$\mu_t = \mu + \delta_t \mu = \lim_{n \rightarrow +\infty} \vec{G}'_t \dots \vec{G}'_{t-n} \mu$$

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

$$\delta_t \mu[\Phi] = \epsilon \sum_{\sigma} \left\langle \kappa_{\sigma} \vec{S}_{t-\sigma-1} \circ \vec{G}^{-1} | \Phi \right\rangle_{\text{eq}}$$

Linear response in the firing rate neural network

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

Convolution

$$\delta_t \rho[u_j] = \epsilon [\chi * S]_j(t)$$

$$= \epsilon \sum_{j=1}^N \sum_{\sigma=-\infty}^t \chi_{i,j}(\sigma) S_j(t - \sigma - 1)$$

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Linear response in the firing rate neural network

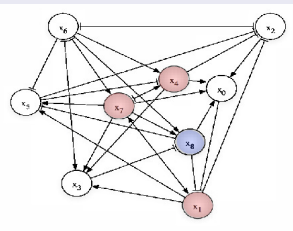
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Linear response in the firing rate neural network

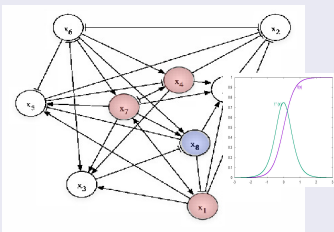
B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006)

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Linear response



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Linear response in the firing rate neural network

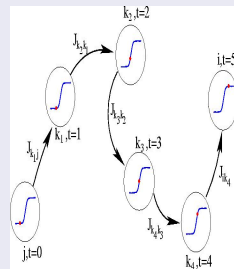
B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006)

Convolution

$$\delta_t \rho[u_i] = \epsilon [\chi * S]_i(t)$$

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Linear response



$$\chi_{i,j}(\sigma) = \sum \gamma_{ij}(\sigma) \prod_{l=1}^{\sigma} J_{k_l, k_{l-1}} \langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l-1)) \rangle_{eq}$$

Linear response in the firing rate neural network

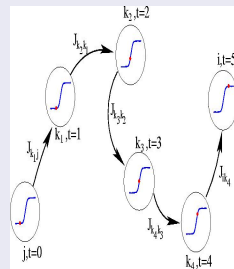
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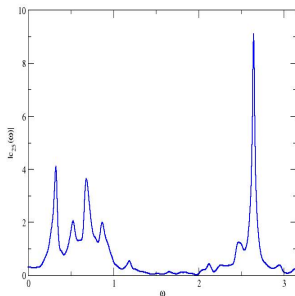
Linear response



$$\chi_{i,j}(\sigma) = \sum \gamma_{ij}(\sigma) \prod_{l=1}^{\sigma} J_{k_l, k_{l-1}} \langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l-1)) \rangle_{\text{eq}}$$

Resonances

Power spectrum

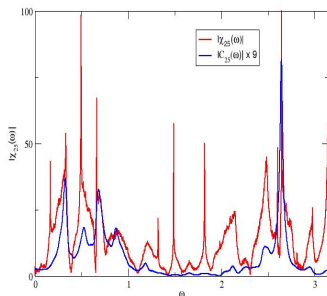


Ruelle resonances

- Ruelle-Pollicott resonances: In the power spectrum. Absolutely continuous part of the SRB measure.

Resonances

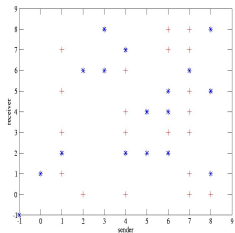
Complex susceptibility



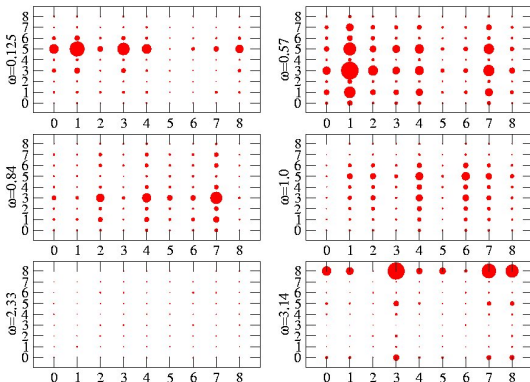
Ruelle resonances

- Ruelle-Pollicott resonances: In the power spectrum. Absolutely continuous part of the SRB measure.
- Exotic resonances. Not in the power spectrum. Singular part of the SRB measure.
- Predicted by D. Ruelle (J. Stat. Phys, 1999)
- Exhibited in B. Cessac, J.A. Sepulchre, PRE, 2004.

Response to a time-dependent stimulus



Connectivity matrix

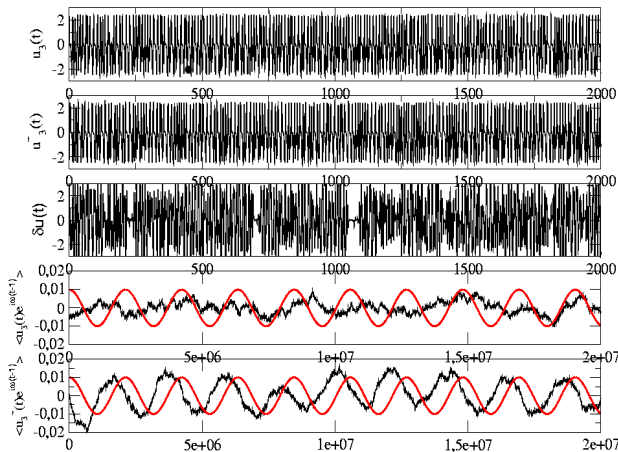


Response matrix

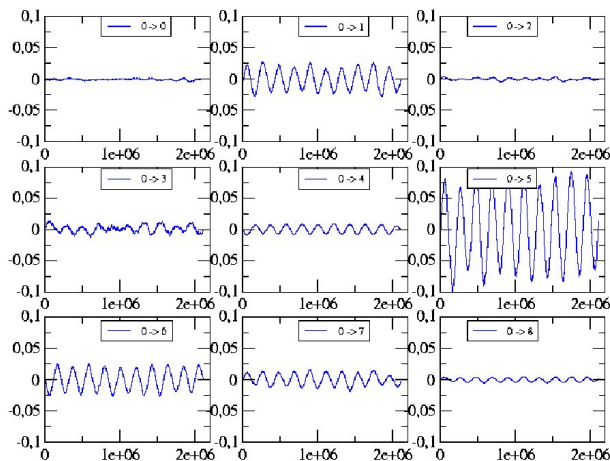
Response to a time-dependent stimulus

$$7 \rightarrow 3, \omega = 0,57$$

$$\omega_0 = 2.97 \cdot 10^6, \varepsilon = 10^{-3}, T = 10^6$$

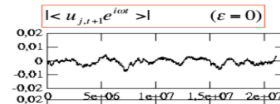
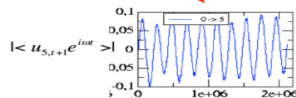
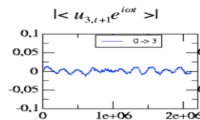
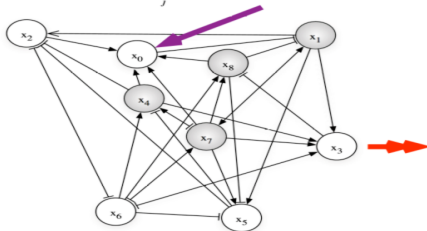


Response to a time-dependent stimulus



Response to a time-dependent stimulus

$$u_{0,t+1} = \sum_j^N J_{0,j} f(u_{j,t}) + \varepsilon \cos(\omega_M t) \sin(\omega t) \quad (\varepsilon \sim 10^{-3})$$



$$\langle u_{5,t+1} \rangle = \varepsilon \chi_{50}(\omega) \cos(\omega_M t) \sin(\omega t + \phi_{50}(\omega)) + O(\varepsilon^2)$$

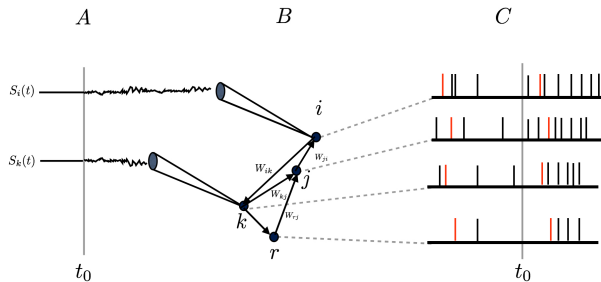
Main conclusions

- Linear response is possible in a chaotic neural network.
- Convolution kernel depending on synaptic graph and dynamics built on equilibrium (SRB) correlations.
- The response graph is different from the synaptic weights graph and depends on the stimulus.

From spiking neurons dynamics to linear response.

Linear response in spiking neuronal networks with unbounded memory

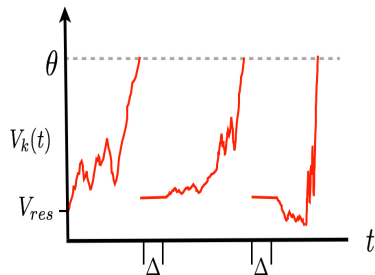
B. Cessac, R.Cofré, J. Math. Neuro. submitted, 2018



How are spike correlations modified by a time-dependent stimulus ?

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

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

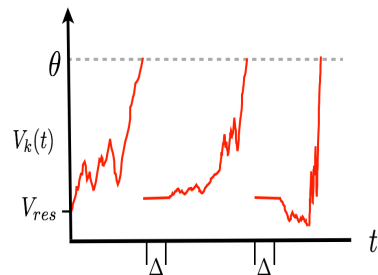


$\omega_k(n)$

0	0	1	0	0	0	0	1	0	0	1	0
---	---	---	---	---	---	---	---	---	---	---	---

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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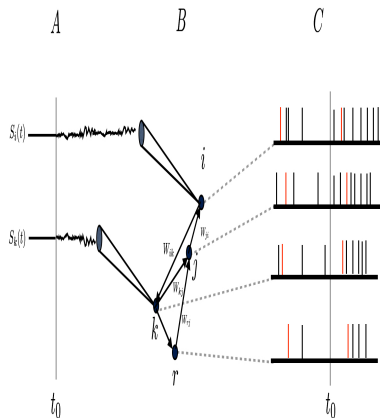
Spikes

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

$$t_k^{(l)} \in [n\delta, (n+1)\delta[\\ \Rightarrow \\ \omega_k(n) = 1$$

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

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

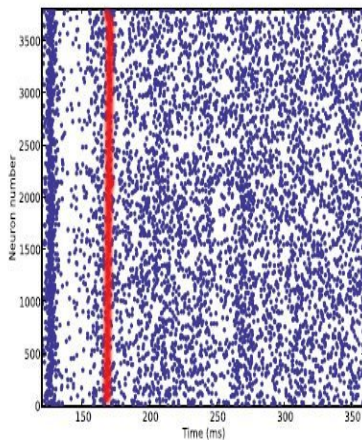


Spikes

- Voltage dynamics is time-continuous.
- Spikes are time-discrete events (time resolution $\delta > 0$).
- Spike state $\omega_k(n) \in \{0, 1\}$.

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

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

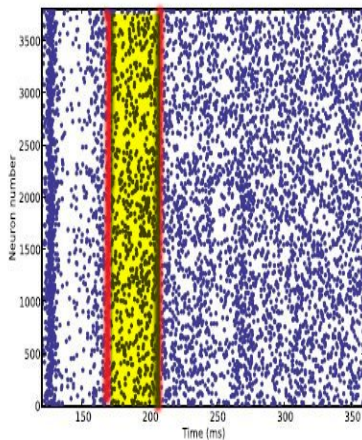


Spikes

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- Spike pattern $\omega(n)$.

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

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



Spikes

- Voltage dynamics is time-continuous.
- Spikes are time-discrete events (time resolution $\delta > 0$).
- Spike state $\omega_k(n) \in \{0, 1\}$.
- Spike pattern $\omega(n)$.
- Spike block ω_m^n .

A conductance-based Integrate and Fire model

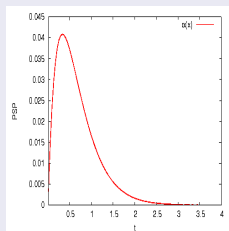
M. Rudolph, A. Destexhe, Neural Comput. 2006, (GIF model)

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

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L) - \sum_j g_{kj}(t, \omega)(V_k - E_j)$$

Synapses



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

A conductance-based Integrate and Fire model

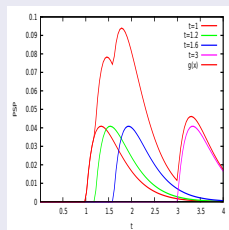
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$$t > t_j$$

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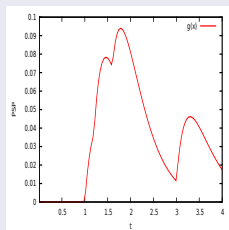
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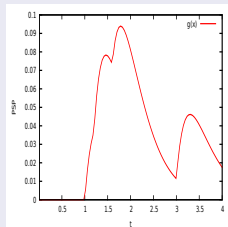
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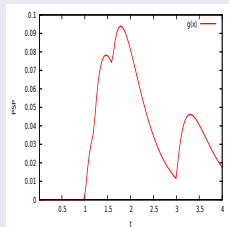
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$$W_{kj} \stackrel{\text{def}}{=} G_{kj} E_j$$

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

$$i_k(t, \omega) = g_{L,k} E_L + \sum_j W_{kj} \alpha_{kj}(t, \omega) + S_k(t) + \sigma_B \xi_k(t)$$

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- Linear in V .
- Spike history-dependent.

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$$\Gamma_k(t_1, t, \omega) = e^{-\frac{1}{C_k} \int_{t_1}^t V \tau_k(t, \omega) g_k(u, \omega) du}$$

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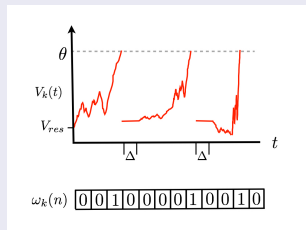
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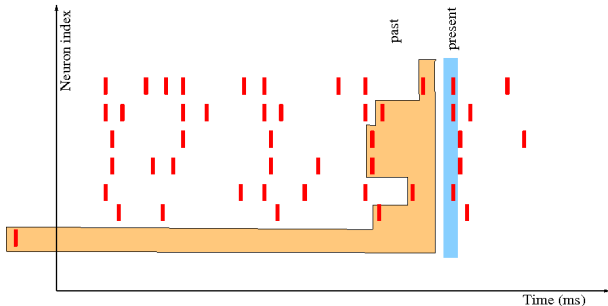
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Variable length Markov chain

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



Response to stimuli

How is the average of an observable $f(\omega, t)$ affected by the stimulus ?

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History dependence, observable

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History dependence, observable, network dynamics

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

Response to stimuli in a mean-field limit

Characteristic time

$$\tau_{d,k} = \frac{C_k}{g_L + \sum_{j=1}^N G_{kj} \nu_j \tau_{kj}}$$

Approximations

- (i) Replace $\tau_k(r-1, \cdot)$ by $-\infty$;
- (ii) Replace $\Gamma_k(t_1, r-1, \omega) = e^{-\frac{1}{C_k} \int_{t_1}^{r-1} g_k(u, \omega) du}$ by $e^{-\frac{(r-1-t_1)}{\tau_{d,k}}}$.

Response to stimuli in a mean-field limit

$$\delta^{(1)}\mu[f(t)] =$$

$$-\frac{2}{\sigma_B} \sum_{k=1}^N \frac{1}{\sqrt{\tau_{d,k}}} \sum_{r=-\infty}^{n=[t]} \left[\quad \right] (S_k * e_{d,k})(r-1)$$

$$e_{d,k}(u) = e^{-\frac{u}{\tau_{d,k}}}$$

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Markov approximation with memory depth 1

$$\left[\begin{array}{l} \gamma_k^{(1)} \mathcal{C}^{(sp)} [f(t, \cdot), \omega_k(r)] \\ + \sum_{i=1}^N \gamma_{k;i}^{(2)} \mathcal{C}^{(sp)} [f(t, \cdot), \omega_k(r) \omega_i(r-1)] \\ + \sum_{i,j=1}^N \gamma_{k;ij}^{(3)} \mathcal{C}^{(sp)} [f(t, \cdot), \omega_k(r) \omega_i(r-1) \omega_j(r-1)] \\ + \dots \end{array} \right]$$

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Response to stimuli in a mean-field limit

Ex: Firing rate of neuron m

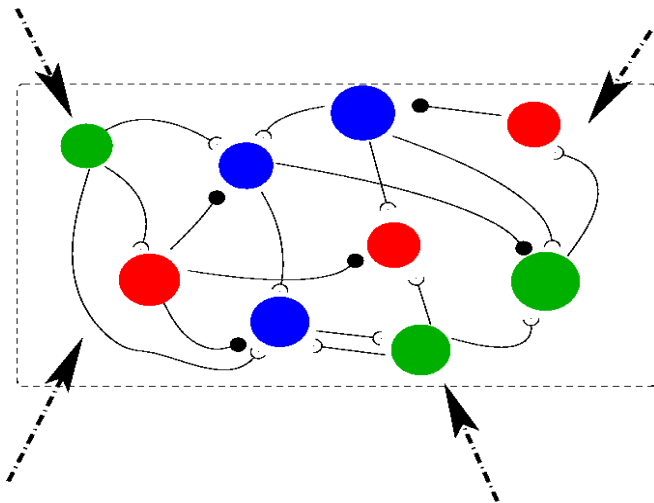
$$\delta^{(1)\mu} [\omega_m(t)] = -\frac{2}{\sigma_B} \sum_{k=1}^N \frac{1}{\sqrt{\tau_{d,k}}} \sum_{r=-\infty}^{n=[t]} \left[\begin{array}{l} + \sum_{i=1}^N \gamma_k^{(1)} \mathcal{C}^{(sp)} [\omega_m(t), \omega_k(r)] \\ + \sum_{i,j=1}^N \gamma_{k;i}^{(2)} \mathcal{C}^{(sp)} [\omega_m(t), \omega_k(r) \omega_i(r-1)] \\ + \gamma_{k;ij}^{(3)} \mathcal{C}^{(sp)} [\omega_m(t), \omega_k(r) \omega_i(r-1) \omega_j(r-1)] \\ + \dots \end{array} \right] (S_k * e_{d,k})(r-1)$$

Conclusions

- Linear response in a spiking neural network.
- Convolution kernel depending on synaptic graph and dynamics built on equilibrium correlations.
- Link with receptive fields for sensory neurons ?
- Further steps. Handle this equation ... in a simple numerical example.

General conclusions

Network response to a stimulus



Network response to a stimulus

- ① How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?
- ② How to measure the influence of a stimulated neuron on another neuron ?
- ③ How does this "effective connectivity" relates to :
 - (a) Synaptic connectivity;
 - (b) Pairwise correlations;
 - (c) "Information" transport.

Network response to a stimulus

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Information transport ? Requires a suitable probabilistic characterization (entropy transport, Granger causality, ...).

Linear response theory in physics

- Equilibrium stat. phys.
(Max. Entropy Principle).

$$P[S] = \frac{1}{Z} e^{-\beta H\{S\}}$$

$$H\{S\} = \sum_{\alpha} \lambda_{\alpha} X_{\alpha}\{S\}$$

$$\lambda_{\alpha} X_{\alpha} \sim E, P \times V, \mu \times N, h \times M, \dots$$

$$PV = nRT, \dots$$

- Equilibrium stat. phys. (Max. Entropy Principle).
- Non equilibrium stat. phys. Onsager theory.

$$\vec{j}_\alpha = \vec{\mathcal{F}}_\alpha(\vec{\nabla}\lambda_1, \dots, \vec{\nabla}\lambda_\beta, \dots)$$

$$\vec{j}_\alpha \sim \sum_{\beta} L_{\alpha\beta} \vec{\nabla}\lambda_\beta + \dots$$

$$\vec{j}_{el} = -\sigma_E \vec{\nabla}V; \quad \vec{j}_Q = -\lambda \vec{\nabla}T, \dots$$

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Linear transport coefficients



equilibrium correlations of currents.

Linear response theory in physics

Onsager theory in non equilibrium statistical mechanics.

gradients \Rightarrow fluxes

Linear relation between "small" gradients and fluxes.

Linear response theory in physics

Onsager-Ruelle - ... theory in dynamical systems.

Perturbation \Rightarrow response

Linear relation between "small" perturbations and response.

- Equilibrium stat. phys. (Max. Entropy Principle).
- Non equ. stat. phys. Onsager theory.
- Ergodic theory, chaotic systems.

The Sinai-Ruelle-Bowen measure is a Gibbs measure

$$H = -\log \det \Pi^u DF_X$$

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- Markov chains - finite memory.

$$P[\omega] = \frac{1}{Z} e^{-\beta H(\omega)}$$

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$X_{\alpha}(\omega)$ = Product of spike events

Hammersley, Clifford, unpublished, 1971

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- Non equ. stat. phys. Onsager theory.
- Ergodic theory.
- Markov chains - finite memory.
- Chains with complete connections - infinite memory (Left Interval Specification).

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O. Onicescu and G. Mihoc. CRAS Paris, 1935

R. Fernandez, G. Maillard, A. Le Ny, J.R. Chazottes, ...

Thanks !!