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

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LACONEU summer school 2019.
Neuron response to a stimulus

[Diagram showing a CA2 Pyramidal Cell with electrodes injecting current and recording membrane potential changes.]

https://www.plasticitylab.com/methods/
From firing rate neurons dynamics to linear response. From spiking neurons dynamics to linear response. General conclusions

Appendix: Linear response theory in physics vs linear response in neuronal networks

Neuron response to a stimulus


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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?
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?
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; …

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

Network
Ex: \( J_{ij} \sim N(0, J^2 N) \) (Sompolinsky et al, 1988)

Non linearity
Ex: \( f(x) = \frac{1}{2} (1 + \tanh(gx)) \), \( f(x) = \tanh(gx) \).
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(Network)

Ex: \( J_{ij} \sim \mathcal{N}\left(0, \frac{J^2}{N}\right) \)  
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Ex: \( f(x) = \frac{1}{2} \left(1 + \text{tanh}(gx)\right) \),  
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Amari-Wilson-Cowan model

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

\[
\frac{d \vec{V}}{dt} = -\mu \vec{V} + \mathcal{J} \cdot f(\vec{V}) + \vec{S}(t); \quad i = 1 \ldots N. \tag{1}
\]

**Network**

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

(Sompolinsky et al, 1988)

**Non linearity**

Ex: \( f(x) = \frac{1}{2} \left( 1 + \tanh(gx) \right), \quad f(x) = \tanh(gx). \)
From firing rate neurons dynamics to linear response. From spiking neurons dynamics to linear response. General conclusions

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\[
\frac{d \vec{V}}{dt} = -\mu \vec{V} + J \cdot f(\vec{V}) + \vec{S}(t); \quad i = 1 \ldots N. \quad (1)
\]

Network

Ex: \( J_{ij} \sim \mathcal{N}\left(0, \frac{J^2}{N}\right) \)  
(Sompolinsky et al., 1988)

Non linearity

Ex: \( f(x) = \frac{1}{2} \left(1 + \tanh(gx)\right) \), \( f(x) = \tanh(gx) \).
Low gain $g$ dynamics

**Theorem.** If $g$ is small enough $	ilde{G}$ is contractive.

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

$\Rightarrow$

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

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

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

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

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

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

\[
\bar{\xi}(t) = \hat{\chi}(\omega).\bar{S}e^{i\omega t}. \tag{2}
\]
Low gain $g$ dynamics
Low gain $g$ dynamics
Low gain $g$ dynamics

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

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

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

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

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

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.

Summary:

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

\[
DG_{\vec{V}^*} = -\mu I + g \begin{array}{c} \text{Leak} \\ \text{Gain} \end{array} D(\vec{V}^*) + \mathcal{J}
\]

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Linear response in neuronal networks: from neurons dynamics
Low gain $g$ dynamics

Summary:

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

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

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Linear response in neuronal networks: from neurons dynamics
Expansion/Contraction

Saturation

Amplification
Expansion/Contraction
Expansion/Contraction

[Diagram with labeled nodes 1 to 7 and arrows indicating connections with plus and minus signs]

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Expansion/Contraction
From firing rate neurons dynamics to linear response. From spiking neurons dynamics to linear response. General conclusions

Appendix: Linear response theory in physics vs linear response in neuronal networks

Expansion/Contraction

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Linear response in neuronal networks: from neurons dynamics
Linear response in a dynamical regime

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

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

\[
V_i(t + 1) = \sum_{j=1}^{N} J_{ij} f(V_j(t)) + S_i(t).
\]
Linear response in the chaotic regime

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

\[ \vec{V}(t+1) = J \cdot f(\vec{V}(t)) + \epsilon \vec{S}(t) \]

\[ f(x) = \tanh(g \cdot x) \]
From firing rate neurons dynamics to linear response. From spiking neurons dynamics to linear response. General conclusions

Appendix: Linear response theory in physics vs linear response in neuronal networks

Transition to chaos by quasi periodicity as $g$ increases

$g$


Cessac B. et al, Physica D, 74, 24-44 (1994)
Chaotic dynamics and strange attractors

$\gamma=3.5, \lambda=0.158$
Chaotic dynamics and strange attractors

\[
\begin{align*}
    x(t+1) &= 1 - ax^2(t) + y(t) \\
    y(t+1) &= bx(t)
\end{align*}
\]

\[a = 1.4; b = 0.3\]

https://upload.wikimedia.org/wikipedia/commons/a/ac/
Chaotic dynamics and strange attractors

Hénon map

\[
\begin{align*}
    x(t+1) &= 1 - ax^2(t) + y(t) \\
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\(a = 1.4; b = 0.3\)

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 $-2.2 \leq y \leq 2.2$.

Hénon map

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\begin{align*}
    x(t+1) &= 1 - ax^2(t) + y(t) \\
    y(t+1) &= bx(t)
\end{align*}
\]

$a = 1.4; b = 0.3$

http://www.sfu.ca/~rpyke/335/W00/
Chaotic dynamics and strange attractors
Chaotic dynamics and strange attractors

Expansive
Positive Lyapunov exponent

Lyapunov spectrum, g=3.5

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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

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

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

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

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

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

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

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

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

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

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

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

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

\[ \delta(t) = \epsilon \sum_{\tau = t_0}^{t-1} DG_{\vec{V}(t_0 + 1)}^{t-\tau+1} \cdot \vec{S}(\tau) + \epsilon^2 \vec{S}(t) \]
Time dependent perturbation

\[ \vec{\delta}(t) = \epsilon \sum_{\tau = t_0}^{t-1} (DF_{\vec{V}})^{t-\tau+1} \cdot \vec{S}(\tau) + \epsilon^2 \vec{R}(t) \]
Time dependent perturbation

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

Controlled by the spectrum of \( DF_{\vec{V}}^* \)

Linear stability analysis

\[ \tilde{G}(\vec{V}) = J f(g \vec{V}) \]

\[ DF_{\vec{V}} = g J \Lambda(\vec{V}) \]

\[ \Lambda_{ij} = f'(g u_j) \delta_{ij} \]
Time dependent perturbation

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

Controlled by the spectrum of \( DF_{\vec{V}} \)

Linear stability analysis

\[ \tilde{G}(\vec{V}) = \mathcal{J} f(g \cdot \vec{V}) \]

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

\[ \Lambda_{ij} = f'(g \cdot u_j) \delta_{ij} \]
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Time dependent perturbation

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

Controlled by the spectrum of \( DF_{\vec{V}} \)

Linear stability analysis

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Time dependent perturbation

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

\[ \vec{G}(\vec{V}) = J f(g \vec{V}) + \theta \]
\[ DF_{\vec{V}} = g J \Lambda(\vec{V}) \]
\[ \Lambda_{ij} = f'(g u_j) \delta_{ij} \]
Time dependent perturbation

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

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\[ \vec{\delta}(t) = \epsilon \sum_{\tau=t_0}^{t-1} DF^{t-\tau+1} \vec{V}(t+1) \cdot \vec{S}(\tau) + \epsilon^2 \vec{R}(t) \]
Time dependent perturbation

\[ \mathbf{\delta}(t) = \epsilon \sum_{\tau = t_0}^{t-1} DF_{t-\tau + 1} \mathbf{\tilde{V}}(t+1) \cdot \mathbf{\tilde{S}}(\tau) + \epsilon^2 \mathbf{\tilde{R}}(t) \]

Expansive positive Lyapunov exponent

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**Time dependent perturbation**

\[ \delta(t) = \epsilon \sum_{\tau = t_0}^{t-1} DF^{t-\tau+1} \cdot \vec{S}(\tau) + \epsilon^2 \vec{R}(t) \]

Lyapunov spectrum, \( g = 3.5 \)

Evolution d’une perturbation:

Directions d’Oscillog 1,2,3
Time dependent perturbation

\[ \delta(t) = \epsilon \sum_{\tau = t_0}^{t-1} DF_{\bar{V}(t+1)}^{t-\tau+1} \bar{S}(\tau) + \epsilon^2 \bar{R}(t) \]

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
The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

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

\(\mu_L\) Lebesgue measure on the phase-space.

\[
\mu \overset{w}{=} \lim_{t \to +\infty} \vec{G}^* t \mu_L, \quad \text{SRB measure}
\]

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

Natural notion of averaging ”on” the attractor.
The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

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

$\mu_L$ Lebesgue measure on the phase-space.

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

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi \left[ \vec{G}^t(\vec{V}) \right] = \int_{\Omega} \Phi(\vec{V}) \mu(d\vec{X})$$

Natural notion of averaging "on" the attractor.
From firing rate neurons dynamics to linear response. From spiking neurons dynamics to linear response. General conclusions

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\]

\(\mu_L\) Lebesgue measure on the phase-space.

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\mu = \lim_{t \to +\infty} \mathbf{G}^t \mu_L, \quad \text{SRB measure}
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\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi \left[ \mathbf{G}^t(\mathbf{V}) \right] \mu_L = \int_{\Omega} \Phi(\mathbf{V}) \mu(d\mathbf{X})
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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


\[ \mu_t = \mu + \delta_t \mu = \lim_{n \to +\infty} \tilde{G}_t \cdots \tilde{G}_{t-n} \mu \]

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

\[ \delta_t \mu [\Phi] = \epsilon \sum_{\sigma} \left\langle \kappa_{\sigma} \tilde{S}_{t-\sigma-1} \circ \tilde{G}^{-1} | \Phi \right\rangle_{eq} \]
Linear response in the firing rate neural network

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

Convolution

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

\[ = \epsilon \sum_{j=1}^{N} \sum_{\sigma=-\infty}^{t} \chi_{i,j}(\sigma)S_j(t - \sigma - 1) \]
Linear response in the firing rate neural network

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

\[ \chi_{i,j}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_l k_{l-1}} \langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l - 1)) \rangle_{eq} \]
Linear response in the firing rate neural network

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Convolution

\begin{align*}
\delta_t \rho[u_i] &= \varepsilon \left[ \chi * S \right]_i(t) \\
&= \varepsilon \sum_{j=1}^{N} \sum_{\sigma=-\infty}^{t} \chi_{i,j}(\sigma) S_j(t - \sigma - 1)
\end{align*}

Linear response

\[
\chi_{i,j}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_l k_{l-1}} \left\langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l - 1)) \right\rangle_{eq}
\]
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\delta_t \rho[u_i] = \epsilon [\chi * S]_i(t)
\]

\[
= \epsilon \sum_{j=1}^{N} \sum_{\sigma=-\infty}^{t} \chi_{ij}(\sigma) S_j(t - \sigma - 1)
\]

Linear response

\[
\chi_{ij}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_lk_{l-1}} \left\langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l - 1)) \right\rangle_{\text{eq}}
\]
Linear response in the firing rate neural network

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**Convolution**

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

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

**Linear response**

\[
\chi_{i,j}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_l k_{l-1}} \left\langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l - 1)) \right\rangle_{eq}
\]
Linear response in the firing rate neural network

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

Convolution

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

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

Linear response

\[ \chi_{i,j}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_lk_{l-1}} \left\langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}} (l-1)) \right\rangle_{eq} \]
Resonances

Ruelle resonances

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

Complex susceptibility

- 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)
Response to a time-dependent stimulus

Connectivity matrix

Response matrix
Response to a time-dependent stimulus

\[ 7 \rightarrow 3, \omega = 0.57 \]
\[ \omega_0 = 2.97 \times 10^6, \varepsilon = 10^{-3}, T = 10^6 \]
Response to a time-dependent stimulus

Bruno Cessac

Linear response in neuronal networks: from neurons dynamics
Response to a time-dependent stimulus

\[ u_{0,t+1} = \sum_{j} J_{0,j} f(u_{j,t}) + \varepsilon \cos(\omega_M t) \sin(\omega t) \]  
\( (\varepsilon \sim 10^{-3}) \)

\[ \langle u_{3,t+1} e^{i\omega t} \rangle \]

\[ \langle u_{5,t+1} e^{i\omega t} \rangle \]  
\( (\varepsilon = 0) \)

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

Spikes are time-discrete events (time resolution $\delta > 0$).

Spike state $\omega_k(n) \in \{0, 1\}$.

Spike pattern $\omega_k(n)$.

Spike block $\omega_k(n_m)$.

The figure shows a plot of $V_k(t)$ and $V_{res}$ against time $t$, with spikes occurring at discrete times indicated by $\Delta$. The spike pattern $\omega_k(n)$ is also shown as a sequence of 0s and 1s.
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 $\delta > 0$).

$t_k^{(l)} \in [n\delta, (n + 1)\delta[ \Rightarrow \omega_k(n) = 1$
An Integrate and Fire neural network model with chemical and electric synapses

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

Spikes

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

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Spikes

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- Spike pattern $\omega(n)$.
- Spike block $\omega_m^n$. 

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

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013
Sub-threshold dynamics:

\[ C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L) \]

\[ - \sum_j g_{kj}(t, \omega)(V_k - E_j) \]

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

\[ C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L) \]

\[- \sum_j g_{kj}(t, \omega)(V_k - E_j)\]

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

\[ t > t_j \]
A conductance-based Integrate and Fire model

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\[ g_{kj}(t) = G_{kj} \sum_{n \geq 0} \alpha_{kj}(t - t_j^{(n)}) \]
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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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Sub-threshold dynamics:

\[
C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L) - \sum_j g_{kj}(t, \omega)(V_k - E_j) + S_k(t) + \sigma_B \xi_k(t)
\]

\[
g_{kj}(t, \omega) = G_{kj} \sum_{n \geq 0} \alpha_{kj}(t - n\delta) \omega_j(n)
\]
A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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

\[ W_{kj} \overset{\text{def}}{=} G_{kj} E_j \]

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

\[ i_k(t, \omega) = g_{L,k} E_L + \sum_j W_{kj} \alpha_{kj}(t, \omega) + S_k(t) + \sigma_B \xi_k(t) \]
A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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

- Linear in \( V \).
- Spike history-dependent.

Dynamics integration

\[ \Gamma_k(t_1, t, \omega) = e^{-\frac{1}{C_k} \int_{t_1 \vee \tau_k(t, \omega)}^t g_k(u, \omega) \, du} \]
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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A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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

- Linear in $V$.
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Dynamics integration

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

$$V_k(t, \omega) = V_k^{(sp)}(t, \omega) + V_k^{(S)}(t, \omega) + V_k^{(noise)}(t, \omega)$$
A conductance-based Integrate and Fire model

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\[ V_k^{(det)}(t, \omega) \]
Sub-threshold dynamics:

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\[ V_k^{(det)}(t, \omega) \]

\[ V_k^{(sp)}(t, \omega) = V_k^{(syn)}(t, \omega) + V_k^{(L)}(t, \omega), \]
A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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

- Linear in \( V \).
- Spike history-dependent.

\[ V_k^{(syn)}(t, \omega) = \frac{1}{C_k} \sum_{j=1}^{N} W_{kj} \int_{\tau_k(t, \omega)}^{t} \Gamma_k(t_1, t, \omega) \alpha_{kj}(t_1, \omega) dt_1 \]
A conductance-based Integrate and Fire model

Sub-threshold dynamics:

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

- Linear in \( V \).
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\[ V_k^{(\text{syn})}(t, \omega) = \frac{1}{C_k} \sum_{j=1}^{N} W_{kj} \int_{\tau_k(t, \omega)}^{t} \Gamma_k(t_1, t, \omega) \alpha_{kj}(t_1, \omega) dt_1 \]

Dynamics integration

\[ \Gamma_k(t_1, t, \omega) = e^{-\frac{1}{C_k} \int_{t_1}^{t} \nu_k(t, \omega) g_k(u, \omega) du} \]

\[ V_k(t, \omega) = V_k^{(\text{sp})}(t, \omega) + V_k^{(S)}(t, \omega) + V_k^{(\text{noise})}(t, \omega) \]

\[ V_k^{(\text{det})}(t, \omega) \]
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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\[ \Gamma_k(t_1, t, \omega) = e^{-\frac{1}{C_k} \int_{t_1}^{t} \tau_k(t, \omega) g_k(u, \omega) du} \]

\[ V_k(t, \omega) = V_k^{(sp)}(t, \omega) + V_k^{(S)}(t, \omega) + V_k^{(noise)}(t, \omega) \]

\[ V_k^{(sp)}(t, \omega) = V_k^{(syn)}(t, \omega) + V_k^{(L)}(t, \omega), \]

\[ V_k^{(syn)}(t, \omega) = \frac{1}{C_k} \sum_{j=1}^{N} W_{kj} \int_{\tau_k(t, \omega)}^{t} \Gamma_k(t_1, t, \omega) \alpha_{kj}(t_1, \omega) dt_1 \]
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

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

$$V_k(t, \omega) = V_k^{(sp)}(t, \omega) + V_k^{(S)}(t, \omega) + V_k^{(\text{noise})}(t, \omega)$$

$$V_k^{(det)}(t, \omega)$$

$$V_k^{(sp)}(t, \omega) = V_k^{(syn)}(t, \omega) + V_k^{(L)}(t, \omega),$$

$$V_k^{(syn)}(t, \omega) = \frac{1}{C_k} \sum_{j=1}^{N} W_{kj} \int_{\tau_k(t, \omega)}^{t} \Gamma_k(t_1, t, \omega) \alpha_{kj}(t_1, \omega) dt_1$$
A conductance-based Integrate and Fire model

**Variable length Markov chain**

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

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

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

If \( S \) is weak enough: \( \delta \mu [ f(t) ] = [ \kappa_f * S ](t) \), (linear response).
Response to stimuli

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

If $S$ is weak enough: $\delta \mu [f(t)] = [\kappa_f * S](t)$, (linear response).

$$\kappa_{k,f}(t - t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{t-t_1} C^{(sp)} \left[ f(t - t_1, .), \frac{\mathcal{H}_{k(1)}(r, .)}{\sigma_k(r - 1, .)} \Gamma_k(0, r - 1, .) \right]$$
Response to stimuli

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

If $S$ is weak enough:  

$$\delta \mu \left[ f(t) \right] = \left[ \kappa_f * S \right](t),$$  
(linear response).

$$\kappa_{k,f}(t-t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{t-t_1} C^{sp} \left[ f(t-t_1, \cdot), \frac{\mathcal{H}^{(1)}_k(r, \cdot)}{\sigma_k(r-1, \cdot)} \Gamma_k(0, r-1, \cdot) \right]$$

**History dependence.**
Response to stimuli

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

If $S$ is weak enough: $\delta \mu [f(t)] = [\kappa_f * S](t)$, (linear response).

$$\kappa_{k,f}(t - t_1) = \frac{1}{C_k} \sum_{r = -\infty}^{t - t_1} C^{(sp)} \left[ f(t - t_1, .), \frac{H_k^{(1)}(r, .)}{\sigma_k(r - 1, .)} \Gamma_k(0, r - 1, .) \right]$$

History dependence, observable
Response to stimuli

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

If $S$ is weak enough: $\delta \mu [ f(t) ] = [ \kappa_f * S](t)$, (linear response).

$$\kappa_{k,f} (t - t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{t - t_1} C^{(sp)} \left[ f(t - t_1, .), \frac{\mathcal{H}^{(1)}_k(r, .)}{\sigma_k(r-1, .)} \Gamma_k(0, r - 1, .) \right]$$

History dependence, observable, network dynamics
Response to stimuli

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

If \( S \) is weak enough:

\[
\delta \mu [ f(t) ] = [ \kappa_f \ast S ](t), \quad \text{(linear response)}.
\]

\[
\kappa_{k,f}(t - t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{t-t_1} C^{(sp)} \left[ f(t - t_1, \cdot), \frac{\mathcal{H}_k^{(1)}(r, \cdot)}{\sigma_k(r - 1, \cdot)} \Gamma_k(0, r - 1, \cdot) \right]
\]

*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 \( \tau_k(r-1,) \) 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

\[ \delta^{(1)} \mu [ f(t) ] = - \frac{2}{\sigma_B} \sum_{k=1}^{N} \frac{1}{\sqrt{\tau_{d,k}}} \sum_{n=[t]}^{n=[t]} \left( S_k \ast e_{d,k} \right)(r - 1) \]

\[ e_{d,k}(u) = e^{-\frac{u}{\tau_{d,k}}} \]
Response to stimuli in a mean-field limit

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

Markov approximation with memory depth 1

\[ + \sum_{i=1}^{N} \gamma^{(2)}_{k;i} C^{(sp)} [ f(t, \cdot), \omega_k(r) \omega_i(r - 1) ] \]
\[ + \sum_{i,j=1}^{N} \gamma^{(3)}_{k;ij} C^{(sp)} [ f(t, \cdot), \omega_k(r) \omega_i(r - 1) \omega_j(r - 1) ] + \ldots \]
Response to stimuli in a mean-field limit

Markov approximation with memory depth 1

\[
\begin{bmatrix}
\gamma_{k}^{(1)} C^{(sp)} [ f(t, \cdot), \omega_{k}(r) ] \\
+ \sum_{i=1}^{N} \gamma_{k;i}^{(2)} C^{(sp)} [ f(t, \cdot), \omega_{k}(r) \omega_{i}(r-1) ] \\
+ \sum_{i,j=1}^{N} \gamma_{k;ij}^{(3)} C^{(sp)} [ f(t, \cdot), \omega_{k}(r) \omega_{i}(r-1) \omega_{j}(r-1) ] \\
+ \ldots \\
\end{bmatrix}
\]
Response to stimuli in a mean-field limit

Markov approximation with memory depth 1

\[
\begin{bmatrix}
\gamma_k^{(1)} C^{(sp)} [f(t, \cdot), \omega_k(r)] \\
\gamma_{k;i}^{(2)} C^{(sp)} [f(t, \cdot), \omega_k(r) \omega_i(r-1)] \\
\gamma_{k;ij}^{(3)} C^{(sp)} [f(t, \cdot), \omega_k(r) \omega_i(r-1) \omega_j(r-1)] \\
\end{bmatrix} + \sum_{i=1}^{N} \gamma_k^{(1)} C^{(sp)} [f(t, \cdot), \omega_k(r)] + \sum_{i,j=1}^{N} \gamma_{k;ij}^{(3)} C^{(sp)} [f(t, \cdot), \omega_k(r) \omega_i(r-1) \omega_j(r-1)] + \ldots
\]
Response to stimuli in a mean-field limit

Ex: Firing rate of neuron $m$

$$\delta^{(1)} \mu \left[ \omega_m(t) \right] =$$

$$- \frac{2}{\sigma_B} \sum_{k=1}^{N} \frac{1}{\sqrt{\tau d, k}} \sum_{r=-\infty}^{n=[t]} \left[ + \sum_{i=1}^{N} \gamma_{k,i}^{(1)} C^{(sp)} \left[ \omega_m(t), \omega_k(r) \right] + \sum_{i,j=1}^{N} \gamma_{k,ij}^{(2)} C^{(sp)} \left[ \omega_m(t), \omega_k(r) \omega_i(r-1) \omega_j(r-1) \right] + \ldots \right] \left( S_k \ast e_{d,k} \right)(r-1)$$
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

Spontaneous dynamics $\Rightarrow$ complex, noise, chaos, non linear.
Network response to a stimulus

Spontaneous dynamics $\Rightarrow$ complex, noise, chaos, non linear.

Stimulus effect $\Rightarrow$ requires to filter the spontaneous part $\Rightarrow$ suitable averaging.
Network response to a stimulus

Spontaneous dynamics $\Rightarrow$ complex, noise, chaos, non linear.

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Linear response. The response to the stimulus is obtained in terms of correlations computed with respect to spontaneous activity (Kubo like relations).
Network response to a stimulus

Spontaneous dynamics $\Rightarrow$ complex, noise, chaos, non linear.

Stimulus effect $\Rightarrow$ requires to filter the spontaneous part $\Rightarrow$ suitable averaging.

Linear response. The response to the stimulus is obtained in terms of correlations computed with respect to spontaneous activity (Kubo like relations).

Information transport ? Requires a suitable probabilistic characterization (entropy transport, Granger causality, ...).
Linear response theory in physics
Linear response theory in physics


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

\[ H\{S\} = \sum_\alpha \lambda_\alpha X_\alpha \{S\} \]

\[ \lambda_\alpha X_\alpha \sim E, P \times V, \mu \times N, h \times M, \ldots \]

\[ PV = nRT, \ldots \]
Linear response theory in physics

- Non equilibrium stat. phys. Onsager theory.

\[ \vec{j}_\alpha = \vec{F}_\alpha(\vec{\nabla}\lambda_1, \ldots, \vec{\nabla}\lambda_\beta, \ldots) \]

\[ \vec{j}_\alpha \sim \sum_\beta L_{\alpha\beta} \vec{\nabla}\lambda_\beta + \ldots \]

\[ \vec{j}_{el} = -\sigma_E \vec{\nabla}V; \quad \vec{j}_Q = -\lambda \vec{\nabla}T, \ldots \]
Linear response theory in physics

- Non equilibrium stat. phys. Onsager theory.
- Green-Kubo relations.

\[ \vec{j}_\alpha = \vec{F}_\alpha(\vec{\nabla}\lambda_1, \ldots, \vec{\nabla}\lambda_\beta, \ldots) \]

\[ \vec{j}_\alpha \sim \sum_\beta L_{\alpha\beta} \vec{\nabla}\lambda_\beta + \ldots \]

\[ \vec{j}_{el} = -\sigma_E \vec{\nabla} V; \quad \vec{j}_Q = -\lambda \vec{\nabla} T, \ldots \]

Linear transport coefficients ← equilibrium correlations of currents.
Linear response theory in physics

Onsager theory in non equilibrium statistical mechanics.

\[ \text{gradients} \Rightarrow \text{fluxes} \]

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.
Gibbs distribution

- Non equ. stat. phys. Onsager theory.
- Ergodic theory, chaotic systems.

The Sinai-Ruelle-Bowen measure is a Gibbs measure

\[ H = - \log \det \Pi^u D F_x \]
Gibbs distribution

- Non equ. stat. phys. Onsager theory.
- Ergodic theory.
- Markov chains - finite memory.

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

\[ H(\omega) = \sum_{\alpha} \lambda_\alpha X_\alpha(\omega) \]

\[ X_\alpha(\omega) = \text{Product of spike events} \]

Hammersley, Clifford, unpublished, 1971
Gibbs distribution

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

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

\[ H(\omega) = \sum_{\alpha} \lambda_{\alpha} X_{\alpha}(\omega) \]

\[ X_{\alpha}(\omega) = \text{Product of spike events} \]

Hammersley, Clifford, unpublished, 1971

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

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