Linear Response of General Observables in Spiking Neuronal Network Models.

Bruno Cessac

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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 to a time dependent stimulus.



1 Linear response theory in physics

2 From firing rate neurons dynamics to linear response.

3 From spiking neurons dynamics to linear response.



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• Equilibrium stat. phys. (Max. Entropy Principle). $P[S] = \frac{1}{Z}e^{-\beta H\{S\}}$ $H\{S\} = \sum_{\alpha} \lambda_{\alpha} X_{\alpha} \{S\}$ $\lambda_{\alpha} X_{\alpha} \sim E, P \times V, \mu \times N, h \times M, \dots$ $PV = nRT, \dots$

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- 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 response theory in physics

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

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

$$\vec{j}_{lpha} \sim \sum_{eta} \mathcal{L}_{lphaeta} \vec{
abla} \lambda_{eta} + \dots$$

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From firing rate neurons dynamics to linear response.

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



$$J_{i}(t+1) = \sum_{j} J_{ij}f(g \ u_{j}(t)) + \theta_{i}$$

$$f(x) = \frac{1}{2}(1 + \tanh(x))$$

 $\mathbf{u}(t+1) = \mathcal{J}f(g \mathbf{u}(t)) + \theta \equiv \mathbf{F}(\mathbf{u}(t))$

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

No mean-field, no "thermodynamic" limit.

Dynamics



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Time dependent perturbation

$$\begin{aligned} \mathbf{u}(t+1) &= \mathbf{F}(\mathbf{u}(t))\\ &\tilde{\mathbf{u}}(t+1) = \mathbf{F}(\tilde{\mathbf{u}}(t)) + \epsilon \mathbf{S}(t)\\ &\delta \mathbf{u}(t) = \tilde{\mathbf{u}}(t) - \mathbf{u}(t) \end{aligned}$$



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Time dependent perturbation

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$$\delta \mathbf{u}(t) = \tilde{\mathbf{u}}(t) - \mathbf{u}(t)$$



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The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi(\mathbf{F}^{t}(\mathbf{u})) = \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi(\mathbf{F}^{t}(\mathbf{u} + \delta))$$

 μ Lebesgue measure on the phase-space.

$$\boldsymbol{\rho} \stackrel{\mathrm{w}}{=} \lim_{t \to +\infty} \mathbf{F^{*t}} \boldsymbol{\mu}, \quad \mathrm{SRB} \text{ measure}$$

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi \left[\mathbf{F}^{\mathsf{t}}(\mathsf{u}) \right]^{\mu} \stackrel{a.s.}{=} \int_{\Omega} \Phi(\mathsf{u}) \rho(\mathsf{d}\mathsf{X})$$

Natural notion of averaging "on" the attractor.

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

The Sinai-Ruelle-Bowen measure is a Gibbs measure

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

Out of equilibrium SRB state

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

$$\rho_t = \rho + \delta_t \rho = \lim_{n \to +\infty} \tilde{\mathbf{F}}_t \dots \tilde{\mathbf{F}}_{t-n} \mu$$

$$\delta_{t}\rho\left[\Phi\right] = \epsilon \sum_{\tau=-\infty}^{t-1} \int \rho(d\mathbf{u}) D\mathbf{F}_{\mathbf{u}}^{\mathbf{t}-\tau-1} \mathbf{S}_{\tau} \left[\mathbf{F}^{-1}(\mathbf{u})\right] \cdot \nabla_{\mathbf{u}(\mathbf{t}-\tau-1)} \mathbf{\Phi} + \mathsf{NL}$$
$$\delta_{t}\rho[\Phi] = \epsilon \sum_{\sigma} \left\langle \kappa_{\sigma} \mathbf{S}_{\mathbf{t}-\sigma-1} \circ \mathbf{F}^{-1} | \mathbf{\Phi} \right\rangle_{eq}$$

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Linear response in the firing rate neural network

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Convolution

$$\frac{\delta_t \rho[u_i] = \epsilon [\chi * S]_i(t)}{\epsilon \sum_{j=1}^{N} \sum_{\sigma = -\infty}^{t} \chi_{i,j}(\sigma) S_j(t - \sigma - 1)}$$

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

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Resonances

Power spectrum



Ruelle resonances

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

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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)

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• Exhibited in B. Cessac, J.A. Sepulchre, PRE, 2004.

Response to a time-dependent stimulus





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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.
- Further steps in Onsager theory ? Transport of entropy ?

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From spiking neurons dynamics to linear response.

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



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

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



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

Spikes

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

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

$$\Rightarrow$$

$$\omega_k(n) = 1$$

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



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

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

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L)$$
$$-\sum_{k} g_{ki}(t, \omega)(V_k - E_i)$$



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Sub-threshold dynamics:

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



Sub-threshold dynamics:

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

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

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

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

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

- Linear in V.
- Spike history-dependent.

Dynamics integration

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

Sub-threshold dynamics:

$$\mathcal{C}_k \, rac{d \mathcal{V}_k}{d t} + \mathfrak{g}_k \, (\, t, \omega \,) \, \mathcal{V}_k = i_k(t, \omega).$$

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Dynamics integration

$$F_{k}(t_{1}, t, \omega) = e^{-\frac{1}{C_{k}} \int_{t_{1} \vee \tau_{k}(t,\omega)}^{t} g_{k}(u,\omega) du}$$

$$v_{k(t)}$$

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

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

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$$v_{k}(t,\omega) = \underbrace{V_{k}^{(sp)}(t,\omega) + V_{k}^{(S)}(t,\omega)}_{V_{k}^{(det)}(t,\omega)} + V_{k}^{(noise)}(t,\omega)$$

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$$V_k(t_1, t, \omega) = e^{-\frac{1}{C_k} \int_{t_1 \vee \tau_k(t, \omega)}^t g_k(u, \omega) \, du}$$
$$V_k(t, \omega) = \underbrace{V_k^{(sp)}(t, \omega) + V_k^{(S)}(t, \omega)}_{V_k^{(det)}(t, \omega)} + V_k^{(noise)}(t, \omega)$$
$$V_k^{(sp)}(t, \omega) = V_k^{(syn)}(t, \omega) + V_k^{(L)}(t, \omega),$$

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

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Dynamics integration

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

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

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Variable length Markov chain

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



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

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$$\mu\left[\omega_{m}^{n}\right] = \prod_{l=m+D}^{n} P\left[\omega(l) \mid \omega_{l-D}^{l-1}\right] \mu\left[\omega_{m}^{m+D-1}\right], \quad \forall m < n \in \mathbb{Z}$$

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

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

$$\mu\left[\omega_{m}^{n}\right] = \exp\sum_{l=m+D}^{n} \phi_{l}\left(\omega_{l-D}^{l}\right) \mu\left[\omega_{m}^{m+D-1}\right], \quad \forall m < n \in \mathbb{Z}$$

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

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- 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, 1971

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

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

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

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Response to stimuli

B. Cessac, R. Cofré, Linear Response of Gibbs measures from Spiking Neuronal Network Models, submitted

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

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$$\phi(n,\omega) = \log \Pi\left(\omega(n), \frac{V_{th} - V_k^{(sp)}(t,\omega) - V_k^{(S)}(t,\omega)}{\sigma_k(n-1,\omega)}\right)$$

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GIF model without stimulus \Rightarrow stationary Gibbs distribution.

time-dependent stimulus $S(t) \Rightarrow$ non stationary Gibbs distribution.

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

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

Response to stimuli

B. Cessac, R. Cofré, Linear Response of Gibbs measures from Spiking Neuronal Network Models, submitted

GIF model without stimulus \Rightarrow stationary Gibbs distribution.

time-dependent stimulus $S(t) \Rightarrow$ non stationary Gibbs distribution.

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

History dependence.

Bruno Cessac Linear Response of General Observables in Spiking Neuronal N

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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 and Bruno Cossegning Linear Response of General Observables in Spiking Neuronal N

Main conclusions

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

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Linear response in experiments

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Response to stimuli

Range R observable monomial decomposition (Hammersley-Clifford, 71)

$$f(t,\omega) = \sum_{l} f_{l}(t) m_{l}(\omega)$$

Range R Gibbs potential monomial decomposition

$$\phi(r,\omega)\sim \sum_{l}\phi_{l}(r)m_{l}(\omega_{r-D}^{r}).$$

Linear response

$$\delta^{(1)}\mu[f_{l}(t)] = \sum_{r=n_{0}+1}^{n=[t]} \sum_{l'} f_{l}(t) \,\delta\phi_{l'}(r) \,\mathcal{C}^{(sp)}\left[m_{l}(\omega_{n-D}^{n}), m_{l'}(\omega_{r-D}^{r})\right].$$

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Main conclusions

- The response to a time dependent stimulus is expressed in terms of correlations of unperturbed dynamics.
- Which correlations are relevant ?
- Problem of dimension reduction.

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- Equilibrium stat. phys. (Max. Entropy Principle).
- Non equ. stat. phys. Onsager theory.
- Ergodic theory.
- Markov chains finite memory.
- Chains with complete connections - infinite memory (Left Interval Specification).
- Information geometry.

S. Amari et al; G. Mastromatteo et al.

R. Herzog, M. J. Escobar, R. Cofré, A. Palacios, B. Cessac, submitted to PNAS.

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