Handling spatio-temporal correlations in neuronal systems

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18-01-2017
Handling spatio-temporal correlations in neuronal systems

1. Introduction
2. Mathematical setting
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Introduction

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Handling spatio-temporal correlations in neuronal systems
Spike trains

Spike activity results from neurons dynamics under stimulation.
Spike trains

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Handling spatio-temporal correlations in neuronal systems
Spike trains

Local dynamics

Network interactions

Stimulus

\[ \Rightarrow \text{specific spatio-temporal correlations} \]
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\[ \text{specific spatio-temporal correlations} \]
A challenge: "Reading" "the" neural "code"
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- **Fundamental challenge:** Understanding how the nervous system "encodes"/"decodes" "information"
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Mathematical setting
This spike train has been generated by an hidden dynamics / stochastic process. Can we infer this process from the spike train's analysis?
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Can we infer this process from the spike train’s analysis?
What do we learn about:

- the stimulus;
- the underlying network;
- the response of that network to a stimulus.
Handling temporality and memory
Handling temporality and memory
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Models considering successive times as independent
Handling temporality and memory

The probability of a spike pattern depends on the network history (transition probabilities).
Handling temporality and memory

Probability of characteristic spatio-temporal patterns

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Probability of characteristic spatio-temporal patterns

Given a set of hypotheses on transition probabilities there exists a mathematical framework to solve the problem.
Handling temporality and memory

Estimate:

\[ P_n \left[ \omega(n) \mid \omega_{n-D}^{n-1} \right] \]

where \( D \) can be

- Finite and constant (Markov chain).
- Finite and variable (Variable length Markov chain).
- Infinite (Chain with complete connection).
1. Conjecture the form of the transition probability as a function of network parameters and stimulus (Poisson, Hawkes, GLM).
Estimating a probability in the spatio-temporal domain

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2. Extract the form of the transition probability from spatio-temporal correlations (Maximum entropy).
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2. Extract the form of the transition probability from spatio-temporal correlations (Maximum entropy).
3. Compute its form in simplified neural network models and extrapolate.
Example 1: The Generalized-Linear Model (GLM)

Paradigms of rates and receptive fields.

\[
\lambda_k(t|H_t) = f(b_k + (K_k \ast x)(t) + \sum_j (h_{kj} \ast y_j)(t)) \\
\theta = \{ \begin{array}{c} k \\ h_{kj} \\ \vdots \end{array} \}
\]

**Figure:** Generalized Linear Models.
Example 2: Maximum Entropy models

- Assume data is **stationary**.
- Choose a set of characteristic spike events.
- Compute their empirical mean.
  \( \pi_l \): emp. prob. of spike event \( l \).
- Find a probability distribution \( \mu \) which *reproduces the empirical averages*:

  \[
  \mu \left[ \text{Spike event } l \right] = \pi_l \quad (C)
  \]

  without any further assumption.

  \[\Leftrightarrow\]

  *Maximize the entropy under constraints \( C \).*

- In good cases this probability exists and is unique. It is called a **Gibbs distribution**.
Example 2: Maximum Entropy models

\[ H = \sum_l h_l m_l \]

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Extension to spatio-temporal events (memory) can be achieved to the price of a bit more mathematical complexity (Vasquez et al, 2012; Nasser-Cessac, 2014)
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Gibbs distribution extends to (i) non stationarity; (ii) infinite memory.
Example 3: An Integrate and Fire neural network model with chemical and electric synapses

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Sub-threshold dynamics:

\[ C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L) \]
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\[- \sum_j \bar{g}_{kj}(V_k - V_j)\]
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\[ - \sum_j \tilde{g}_{kj}(V_k - V_j) \]

\[ + i_k^{(ext)}(t) + \sigma_B \xi_k(t) \]
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**Spike generation process**

- In this example, the hidden process is *non Markovian*: it has an *infinite memory*, although it can be well approximated by a Markov process.
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- With gap-junctions the *conditional independence breaks down*. The explicit form of the transition probabilities has (not yet) been computed.
- The statistics of spike is described by a *Gibbs distribution* (even in the non stationary case). In the stationary case, it obeys a Maximum Entropy Principle.
Maximum entropy potentials with spatio-temporal constraints are generic


Given a set of transition probabilities $P \left[ \omega(D) \right| \omega_0^{D-1}] > 0$ there is a unique, up to a constant, equivalent MaxEnt potential, written as a linear combination of constraints (average of spike events) with a minimal number of terms. This potential can be explicitly and algorithmically computed.
Combinatorial Explosion of constraints
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$\Rightarrow$

- Intractable determination of parameters;
- Stimulus dependent parameters;
- Overfitting.
Response to stimuli

B. Cessac, R. Cofré, Linear Response of Gibbs measures from Spiking Neuronal Network Models, in preparation
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GIF model without stimulus ⇒ 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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If $S$ is weak enough: $\delta_{\mu} [ f(t) ] = [ \kappa f * S ](t)$, (linear response).
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$$\kappa_{k,f}(t - t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{t-t_1} C^{sp} \left[ f(t - t_1, \cdot), \frac{\mathcal{H}_k^{(1)}(r, \cdot)}{\sigma_k(r - 1, \cdot)} \Gamma_k(0, r - 1, \cdot) \right]$$
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History dependence.
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History dependence, observable
Response to stimuli

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*History dependence, observable, network dynamics*
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History dependence, (spontaneous) correlation between observable and network dynamics.
Handling data
The Enas software


https://enas.inria.fr/
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[https://enas.inria.fr/](https://enas.inria.fr/)

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Parameters estimation and information geometry
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\[ \chi_{ll}' = \frac{\partial^2 d_{KL}(\pi, \mu)}{\partial h_l \partial h_l'} \]

\[ \chi_{ll} = \frac{\partial^2 \mathcal{P}}{\partial h_l \partial h_l'}; \]

\[ \mathcal{P} = \sup_{\mu \in M_{inv}} h(\mu) + \mu(\mathcal{H}) \]

\[ \chi_{ll}' = C_{ll}'(0) + \sum_{n=0}^{+\infty} C_{ll}'(n) \]

\[ \delta \mu[m] = \chi \delta h \Rightarrow \delta h = \chi^{-1} \delta \mu[m] \]
Parameters estimation and information geometry
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\[ \chi_{\Pi'} = \frac{\partial^2 d_{KL}(\pi, \mu)}{\partial h_i' \partial h_j'} \]

\[ \chi_{\Pi'} = \frac{\partial^2 P}{\partial h_i' \partial h_j'}; \]

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Dimension reduction

Dimensionality Reduction and Reliable Observations on Maximum Entropy Models on Spiking Networks, R. Herzog, B. Cessac, M.J. Escobar, A. Palacios, In preparation
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Binning

Does binning affect the statistics?

B. Cessac, A. LeNy, E. Loecherbach, On the mathematical consequences of binning spike trains, Neural Computation, 2017
Does binning affect the statistics?

- Consider a (stationary) Markov process generating spike trains, with transition probabilities $P \left[ \omega(D) \Big| \omega_0^{D-1} \right]$. 

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Does binning affect the statistics ?

- Consider a (stationary) Markov process generating spike trains, with transition probabilities $P \left[ \omega(D) \mid \omega_0^{D-1} \right]$.
- Consider the process generated by binning. Is it still Markovian ?
Does binning affect the statistics?

- Consider a (stationary) Markov process generating spike trains, with transition probabilities $P\left[\omega(D) \mid \omega_0^{D-1}\right]$.
- Consider the process generated by binning. Is it still Markovian?

NO!
**Example.** Take 1 neuron, $D = 1$, and bin with 2 time steps. Call $\omega$ the initial process and $\varpi$ the binned process. Let $\mathbb{P}^{(b)}$ the probabilities in the binned process.

$$\varpi = 0 \quad \Rightarrow \quad (0, 0)$$

$$\varpi = 1 \quad \Rightarrow \quad (0, 1), (1, 0), (1, 1)$$
**Example.** Take 1 neuron, $D = 1$, and bin with 2 time steps. Call $\omega$ the initial process and $\varpi$ the binned process. Let $\mathbb{P}^{(b)}$ the probabilities in the binned process.

$$\varpi = 0 \Rightarrow (0, 0)$$

$$\varpi = 1 \Rightarrow (0, 1), (1, 0), (1, 1)$$

Let us first show that:

$$\mathbb{P}^{(b)}[\varpi(2) = 0 | \varpi(1) = 1, \varpi(0) = 1] \neq \mathbb{P}^{(b)}[\varpi(2) = 0 | \varpi(1) = 1].$$
Binning

\[ P^{(b)}[\varpi(2) = 0 | \varpi(1) = 1] = \frac{P^{(b)}[\varpi(2) = 0, \varpi(1) = 1]}{P^{(b)}[\varpi(1) = 1]} \]

\[ P^{(b)}[0|1] = \frac{P[0|0]P[0|0]P[0|1]+P[0|0]P[0|1]P[1|1]}{P[0|1]P[1|1]+P[1|1]P[1|0]} \]
\[ P(b)[0|11] = \frac{P(b)[011]}{P(b)[11]} \]
Binning

But:

\[ P^{(b)}[0|101] = P^{(b)}[0|10] \]
In general, the conditional probability

\[ P^{(b)}[\bar{\omega}(s + 1)|\bar{\omega}^s_l] = P^{(b)}[\bar{\omega}(s + 1)|\bar{\omega}^s_r], \]

where \( l \) is the first occurrence of the symbol 0 when going from \( s \) to \( r \) (we set \( l = r \), if \( \bar{\omega} \) does not contain the symbol 0).

⇒

The binned process is a Variable Length Markov Chain (VLMC) with unbounded memory.
Consequences:

1. Binning generate fallacious long-range time correlations.
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2. This can lead to wrong causal interpretation and fallacious long range space correlations.
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Proposition (Theorem 3.1 of chazottes-ugalde, 2011)

The transition kernel $P^{(b)}$ of the binned chain is continuous with an exponential rate $\alpha(N) > 0$, depending on $N$, the number of neurons.
Binning

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Theorem

The law \( \mathbb{P}^{(b)} \) of the binned chain is a Gibbs measure.
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The law $\mathbb{P}^{(b)}$ of the binned chain is a Gibbs measure.

3. Nice measure when conditioning upon past, but also upon future (anticipation).
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Theorem

The law $\mathbb{P}^{(b)}$ of the binned chain is a Gibbs measure.

3. Nice measure when conditioning upon past, but also upon future (anticipation).

4. **Open question:** behaviour of the binned process when the number of neurons tends to $\infty$ (fallacious phase transitions ?)
Conclusion
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Potential flaws

Part of these challenges relies on:

Reliable estimations of spike trains statistics (finite samples, induced biases, finding the right model, estimating its parameters...),
Generate proper synthetic data to calibrate/tests methods,
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- Inferring/guessing/extrapolating hidden relations (laws ?) relating a stimulus to the collective response of neurons.
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- *Inferring/guessing/extrapolating hidden relations (laws ?) relating a stimulus to the collective response of neurons.*
To fit

Extract a probabilistic model of $P[R \mid S]$, $P[S \mid R]$ from data.

To predict

Apply the probabilistic model to predict the behaviour of test samples.

To explain

How does a neural network "encode" a stimulus.

To predict is not to explain. (René Thom)
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Acknowledgment

**Neuromathcomp-Biovision team**
- Rodrigo Cofré
- Dora Karvouniari
- Pierre Kornprobst
- Sélim Kraria
- Hassan Nasser
- Daniela Pamplona
- Geoffrey Portelli
- Vivien Robinet
- Horacio Rostro
- Selma Souihel
- Wahiba Taouali
- Juan-Carlos Vasquez

**ANR KEOPS**
- Maria-José Escobar (CN Valparaiso)
- Adrian Palacios (CN Valparaiso)
- Ruben Herzog (CN Valparaiso)
- Cesar Ravelo (CN Valparaiso)
- Thierry Viéville (INRIA Mnemosyne)

**Renvision FP7 project**
- Luca Bernondini (IIT Genova)
- Matthias Hennig (Edinburgh)
- Alessandro Maccionne (IIT Genova)
- Evelyne Sernagor (Newcastle)

**Institut de la Vision**
- Olivier Marre
- Serge Picaud

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