

Spike train statistics: from mathematical models to software to experiments

Bruno Cessac

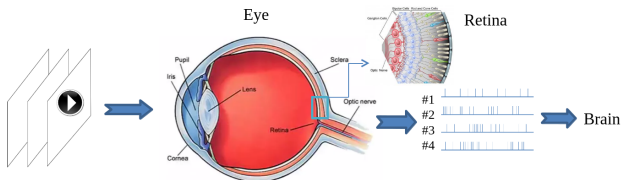
NeuroMathComp Team, INRIA Sophia Antipolis, France.

Marseille, 27-03-14

- 1 Context
- 2 Mathematics
- 3 Numerics
- 4 Experiments

Context

Spike coding



Stimulus

What is the response given a stimulus?

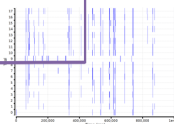
Encoding

Response

Decoding

Can we guess the stimulus given the response?

Rate coding, spike count, population coding ...



Response variability

Multi Electrodes Array

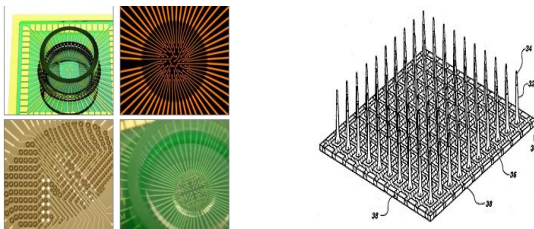


Figure: Multi-Electrodes Array.

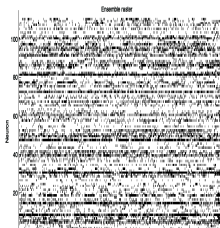


Figure: Spike train.

- Stimulus S \rightarrow spike response R .
- Try to infer $P[S | R]$.
- Bayesian inference \Rightarrow needs to know $P[R | S]$.

Can we have a reasonable idea of what $P[R | S]$ could be ?

To fit

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

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To predict

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

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To explain

How does a neural network "encode" a stimulus.

To fit

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



To predict

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

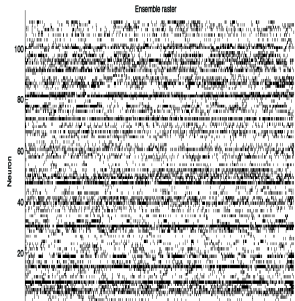


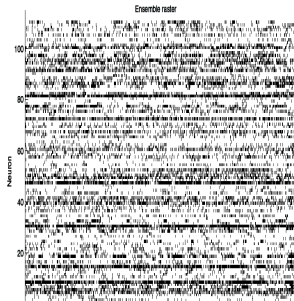
To explain

How does a neural network "encode" a stimulus.

To predict is not to explain.

(René Thom)





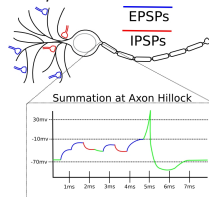
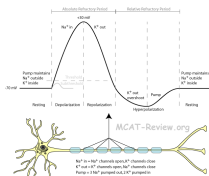
This spike train has been generated by an hidden *dynamics / stochastic process.*

Can we infer this process from the spike train's analysis ?

Some features of the hidden dynamics

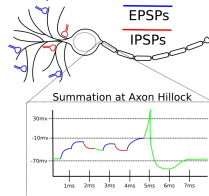
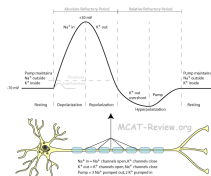
Some features of the hidden dynamics

1 Nonlinear and multiscale dynamics;



Some features of the hidden dynamics

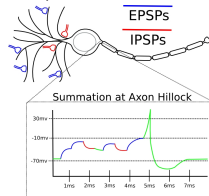
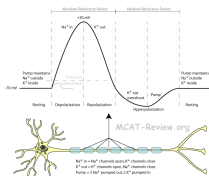
1 Nonlinear and multiscale dynamics;



2 Long memory tail (conductance, plasticity, adaptation).

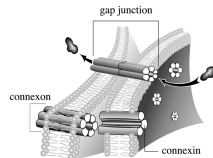
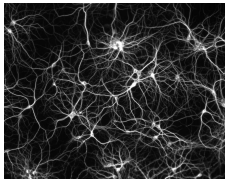
Some features of the hidden dynamics

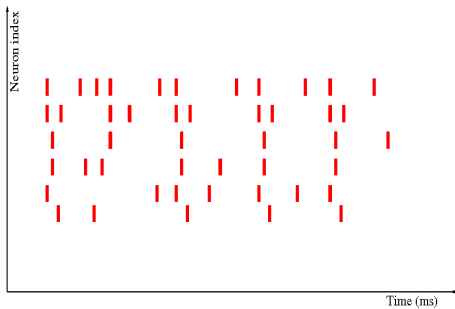
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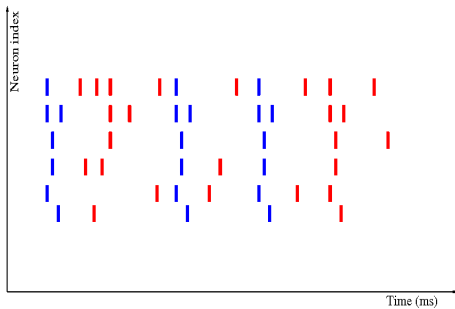


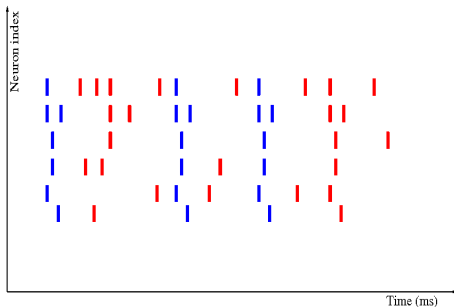
2 Long memory tail (conductance, plasticity, adaptation).

3 Collective dynamics



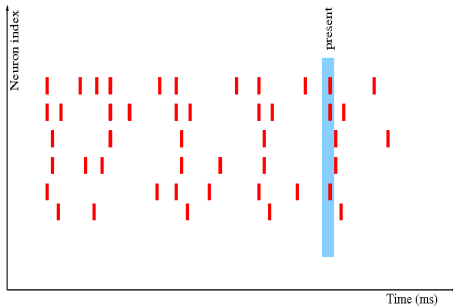






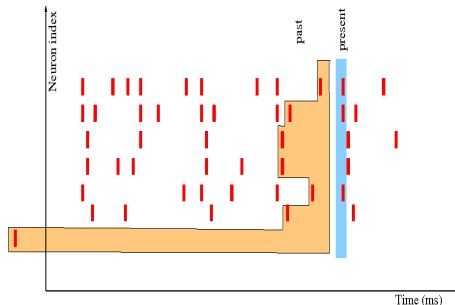
Probability of characteristic spatio-temporal patterns

- 1 Empirical probability (experiments).
- 2 Theoretical probability (**statistical model**).



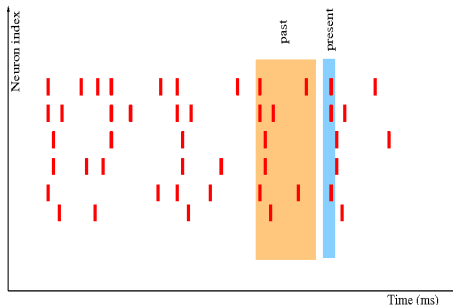
Probability of characteristic spatio-temporal patterns

- 1 The probability of a spike pattern



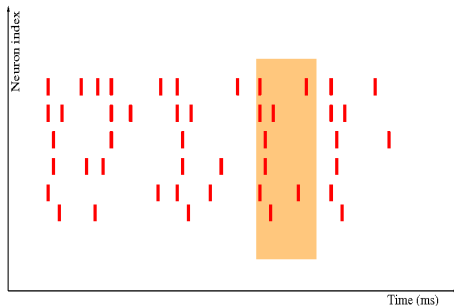
Probability of characteristic spatio-temporal patterns

- 1 The probability of a spike pattern
- 2 depends on the **network history** (transition probabilities).



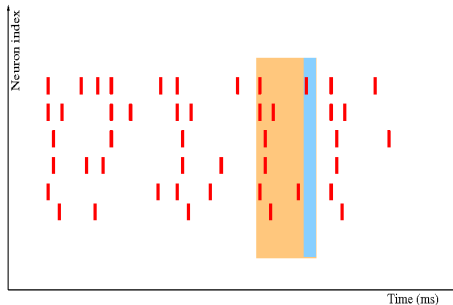
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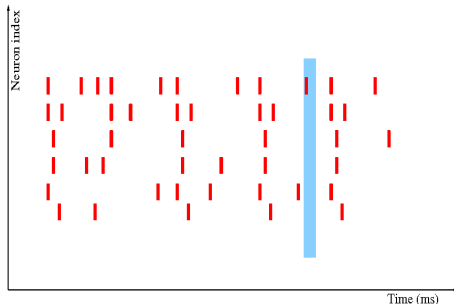
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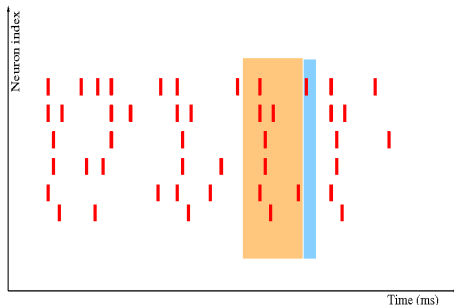
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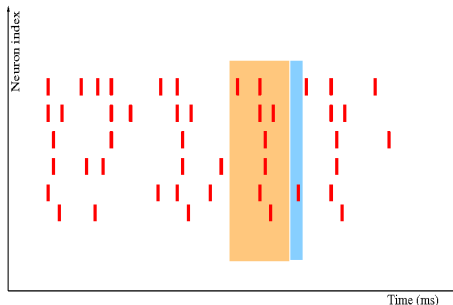
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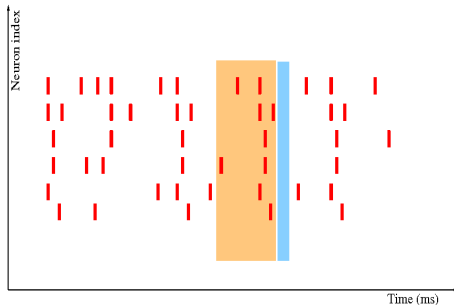
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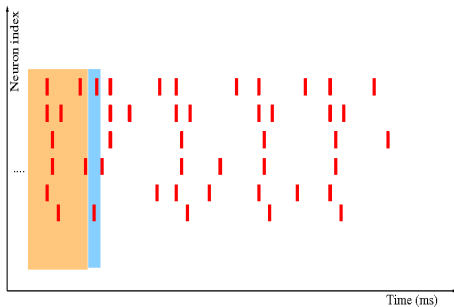
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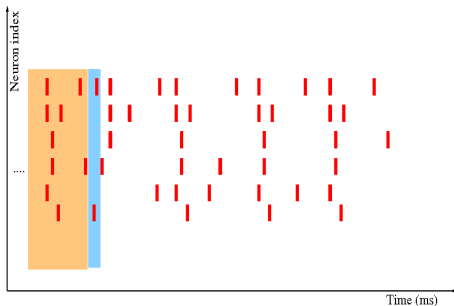


Probability of characteristic spatio-temporal patterns

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- 2 depends on the **network history** (transition probabilities).



Probability of characteristic spatio-temporal patterns



Probability of characteristic spatio-temporal patterns

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

Mathematics

Spike events

Spike events

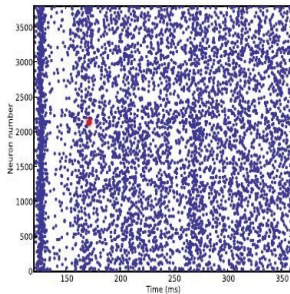


Figure: Spike state.

Spike state

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

Spike events

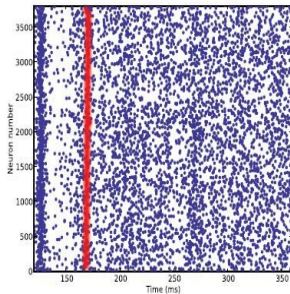


Figure: Spike pattern.

Spike state

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

Spike pattern

$$\omega(n) = (\omega_k(n))_{k=1}^N$$

Spike events

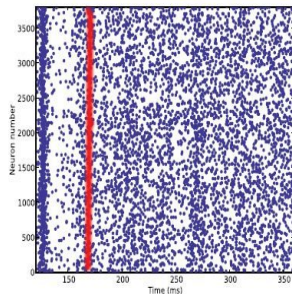


Figure: Spike pattern.

Spike state

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

Spike pattern

$$\omega(n) = (\omega_k(n))_{k=1}^N \quad \begin{pmatrix} 1 \\ 0 \\ 0 \\ 1 \end{pmatrix}$$

Spike events

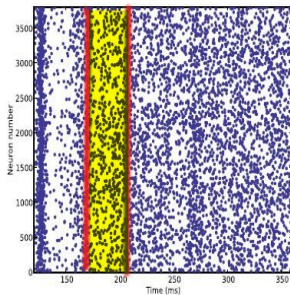


Figure: Spike block.

Spike state

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

Spike pattern

$$\omega(n) = (\omega_k(n))_{k=1}^N$$

Spike block

$$\omega_m^n = \{\omega(m)\omega(m+1)\dots\omega(n)\}$$

Spike events

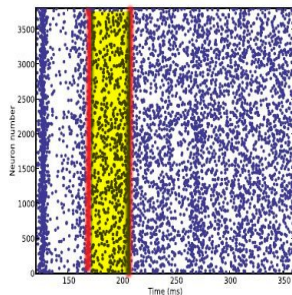


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$$\omega_m^n = \{\omega(m)\omega(m+1)\dots\omega(n)\}$$
$$\begin{pmatrix} 1 & 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{pmatrix}$$

Spike events

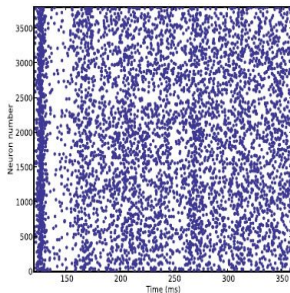


Figure: Raster plot/Spike train.

Spike state

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

Spike pattern

$$\omega(n) = (\omega_k(n))_{k=1}^N$$

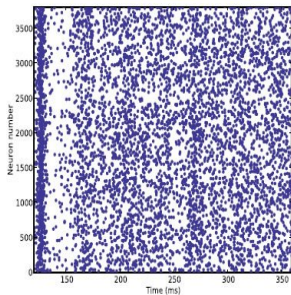
Spike block

$$\omega_m^n = \{\omega(m)\omega(m+1)\dots\omega(n)\}$$

Raster plot

$$\omega \stackrel{\text{def}}{=} \omega_0^T$$

Main idea



Construct:

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

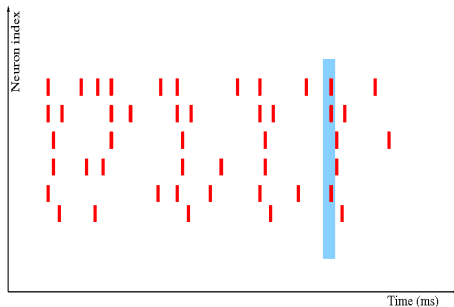
from data.

Spatial models ... let's forget about the past

Spatial models ... let's forget about the past

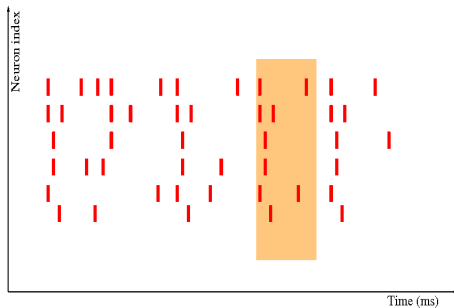
To remove time correlations, bin data at a time scale larger than the typical correlation time between cells.

Spatial models ... let's forget about the past



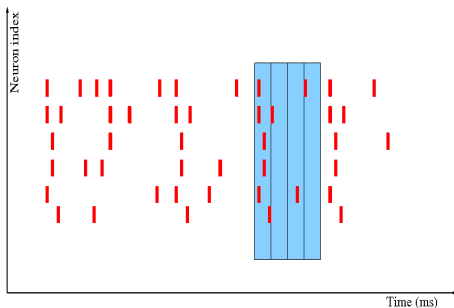
$$P_n [\omega(n) \mid \omega_{n-D}^{n-1}] = P_n [\omega(n)]$$

Spatial models ... let's forget about the past



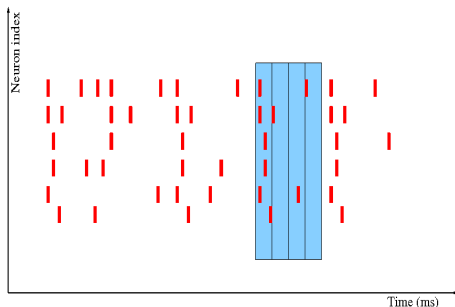
$$P[\omega_n^{n+3}]$$

Spatial models ... let's forget about the past



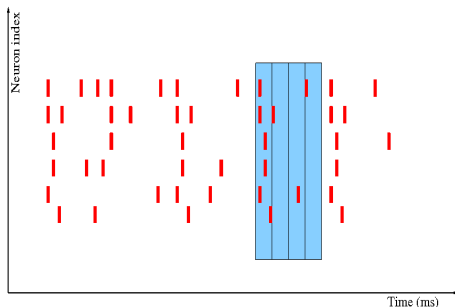
$$P[\omega_n^{n+3}] = P[\omega(n)]P[\omega(n+1)]P[\omega(n+2)]P[\omega(n+3)]$$

Spatial models ... let's forget about the past



Useful to estimate the *spatial* distribution of patterns.

Spatial models ... let's forget about the past



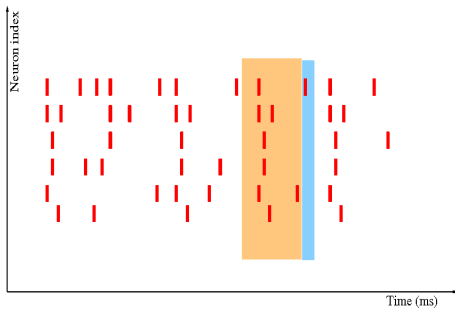
Useful to estimate the *spatial* distribution of patterns.
Most statistical models of Maximum Entropy are of this type

Markov chains

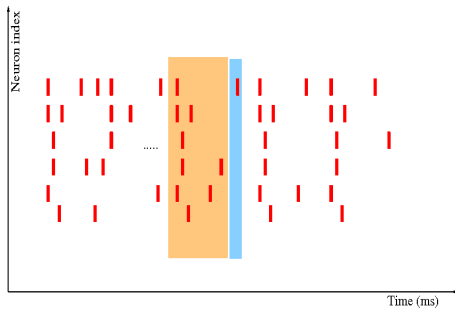
Markov chains

The actual state is influenced by a past with a fixed depth.

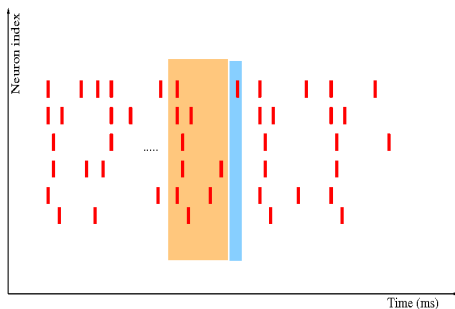
Markov chains ... fixed past depth



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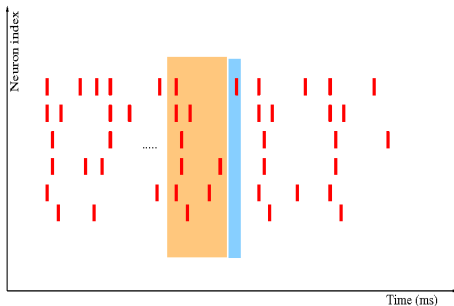


Markov chains ... fixed past depth



- Maximum entropy with memory (Marre et al, 2009; Vasquez et al, 2012; Nasser-Cessac, 2014).
- Conditional intensities models (GLM, LN,).

Markov chains ... fixed past depth



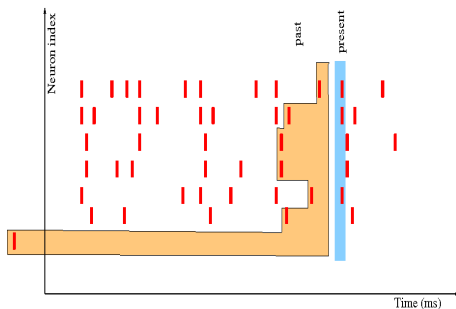
- Mathematics: Perron-Frobenius theorem, general theory of Markov chains.
- Numerics: Statistical inference of Markov chain, Monte-Carlo.

Variable Length Markov chains

Variable Length Markov chains

The actual state is influenced by a past with a variable but *bounded* depth.

Variable Length Markov chains



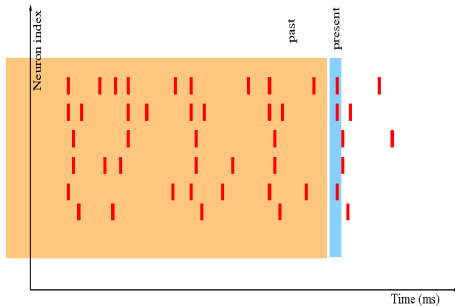
- Conditional intensities models.
- Integrate and Fire models (Cessac, 2010, 2012; Cofré-Cessac, 2013; Loecherbach-Galves, 2013).

Chains with complete connections ... unbounded memory

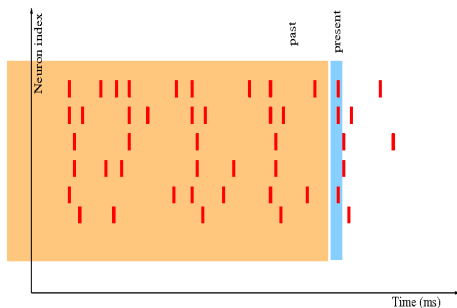
Chains with complete connections ... unbounded memory

The actual state is influenced by a past with an *unbounded* depth.

Chains with complete connections ... unbounded memory



Chains with complete connections ... unbounded memory



- Integrate and Fire models (Cessac, 2010, 2012; Cofré-Cessac, 2013; Loecherbach-Galves, 2013).
- Chains with complete connections \sim *Gibbs distributions*.

Examples

Example 1: The Generalized-Linear Model (GLM)

Paradigms of rates and receptive fields.

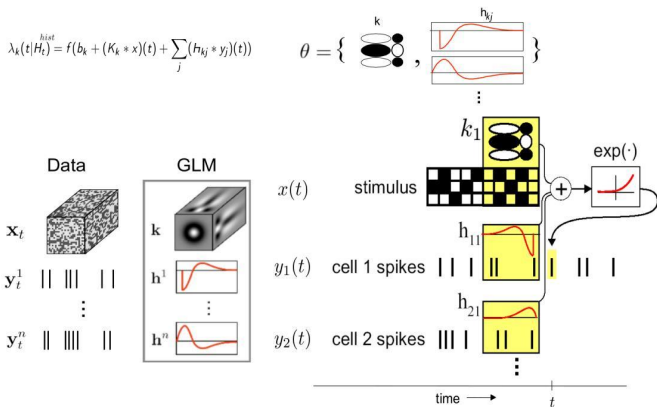
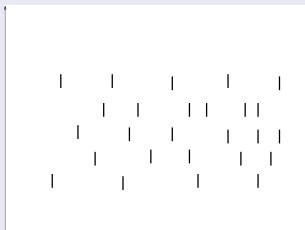


Figure: Generalized Linear Models.

Example 2: Maximum Entropy models

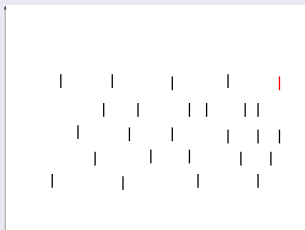
Measuring the statistics of **characteristic spike events**



Example 2: Maximum Entropy models

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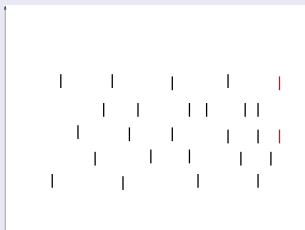
single spikes,



Example 2: Maximum Entropy models

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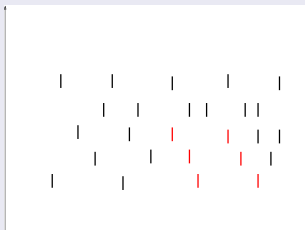
single spikes, pairs,



Example 2: Maximum Entropy models

Measuring the statistics of **characteristic spike events**

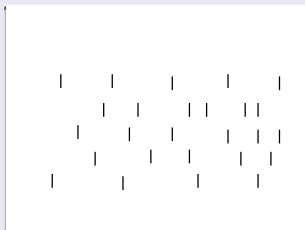
single spikes, pairs, triplets,



Example 2: Maximum Entropy models

Measuring the statistics of **characteristic spike events**

single spikes, pairs, triplets, ..., **what else ?**.



Example 2: Maximum Entropy models

- Assume data is **stationary**.

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Maximize the entropy under constraints C .

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Maximize the entropy under constraints C .

- In good cases this probability exists and is unique. It is called a *Gibbs distribution*.

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Most authors consider spatial events (no memory) because it fits with the usual definition of Gibbs distributions $\frac{e^{\beta H}}{Z}$.

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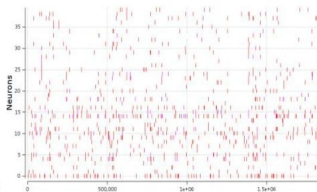
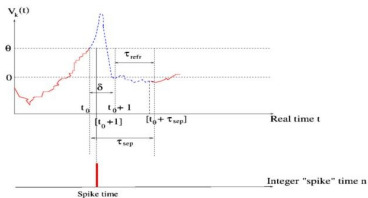
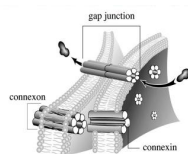
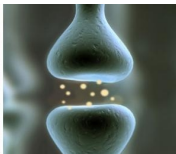
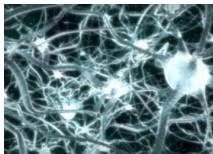
Extension to spatio-temporal events (memory) can be achieved to the price of a bit more mathematical complexity
(Marre et al, 2009; Vasquez et al, 2012; Nasser-Cessac, 2014)

Example 3

Can we have a *reasonable idea* of what could be the spike statistics by studying a *neural network model* ?

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

R.Cofré, B. Cessac: "Dynamics and spike trains statistics in conductance-based Integrate-and-Fire neural networks with chemical and electric synapses", *Chaos, Solitons and Fractals*, 2013.



What could be the hidden process ?

Sub-threshold dynamics:

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

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Sub-threshold dynamics:

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

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



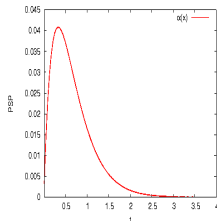
www.shutterstock.com - 154156187

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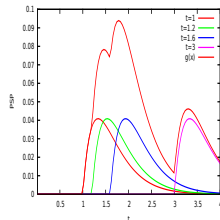


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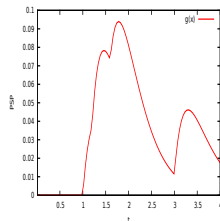


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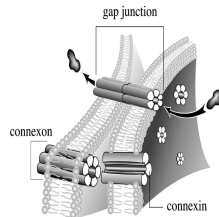
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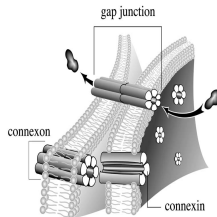
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Mathematical answers

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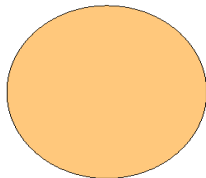
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- With gap-junctions the *conditional independence breaks down*. The explicit form of the transition probabilities has (not yet) been computed.
- The statistics of spike is described by a *Gibbs distribution* (even in the non stationary case). In the stationary case, it obeys a Maximum Entropy Principle.

What could be the hidden process ?

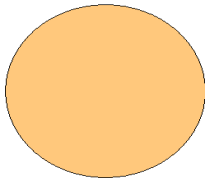
- We have now a *reasonable model* where we can have a mathematical characterization of spike statistics given a stimulus.
- *Gap junctions* might play a crucial role in shaping statistics.
- Possible *new paradigm* to fit data (beyond GLM and MaxEnt).

Relations between models (with R. Cofré).

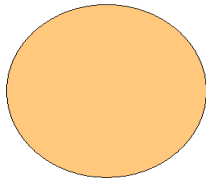
Neuromimetic models



Conditional intensities Models



Maximum Entropy Models



Relations between models (with R. Cofré).

Neuromimetic models

$O(N^2)$ parameters
Non stationary

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$O(N^{D+1})$ parameters
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Analytical results limited
to IF models.

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$O(N^2)$ parameters
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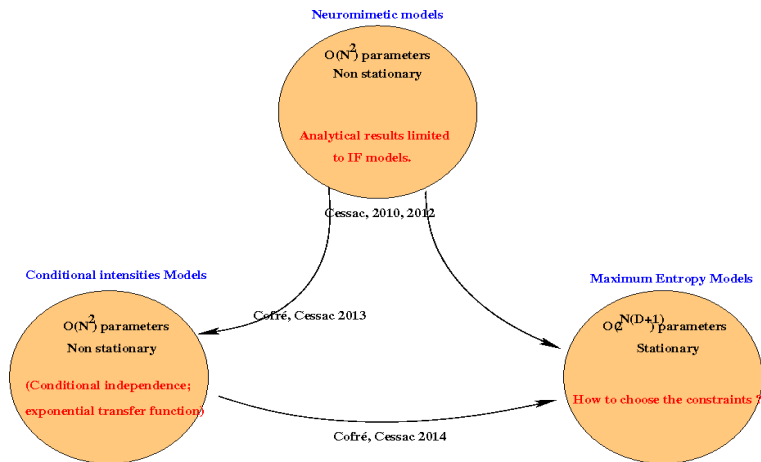
(Conditional independence;
exponential transfer function)

Maximum Entropy Models

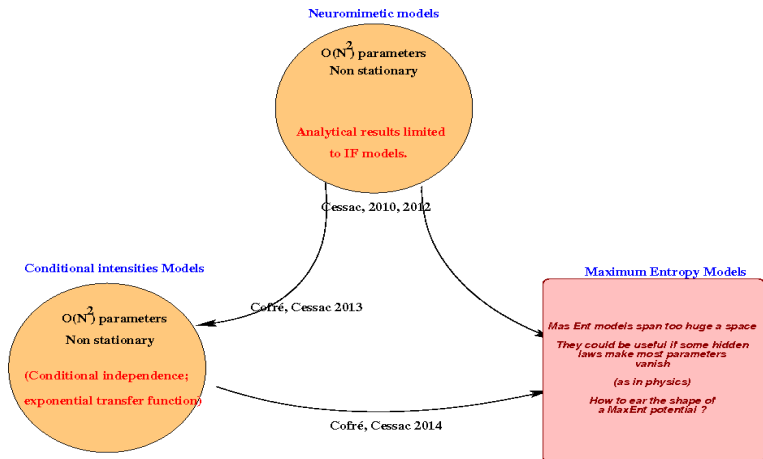
$O(N^{D+1})$ parameters
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How to choose the constraints ?

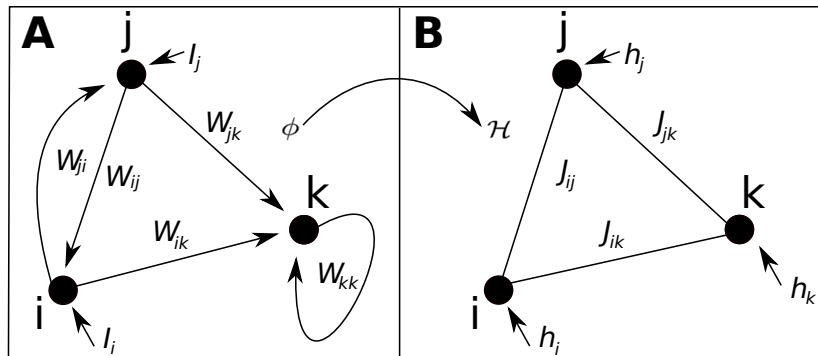
Relations between models (with R. Cofré).



Relations between models (with R. Cofré).



Real versus "functional" connectivity (with R. Cofré).



Numerics

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<http://enas.gforge.inria.fr/v3/>

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- Interface with the Virtual Retina simulator (INRIA Neuromathcomp).

Experiments

Gibbs distributions for retina ganglion cells

(with U. Princeton, U. Valaparaíso, Institut de la Vision)

- Comparing Spatial Max Ent models to Spatio-temporal in the retina.
- Small number of neurons (~ 5).
- The new version of Enas allows (~ 50) neurons.

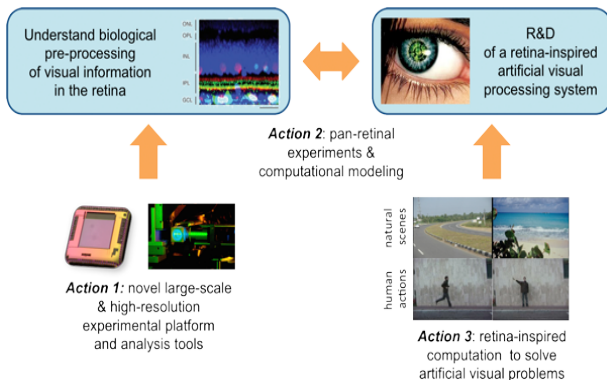
The KEOPS project (ANR)

(with U. Valparaiso, U. Santiago and INRIA Mnemosyne)

- Analyse of non-standard retinal cell behaviour
- Natural image scenarios
- Designing innovative visual operators.

The Renvision project (FP7)

(with I.I.T Genova, U. Newcastle, U. Edinburgh)



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- Pierre Kornprobst
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- Geoffrey Portelli
- Vivien Robinet (Kourou)
- Horacio Rostro (Mexico)
- Wahiba Taouali (INT)
- Juan-Carlos Vasquez (Bogota)

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- Serge Picaud

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