

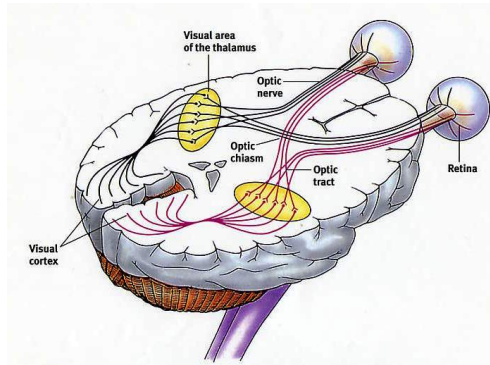
Statistical analysis of spike trains in neuronal networks

Bruno Cessac

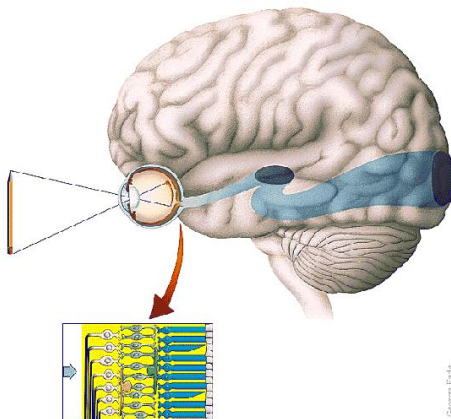
NeuroMathComp Team, INRIA Sophia Antipolis, France.

Mathematical Modeling and Statistical Analysis in
Neuroscience, 02-07-14

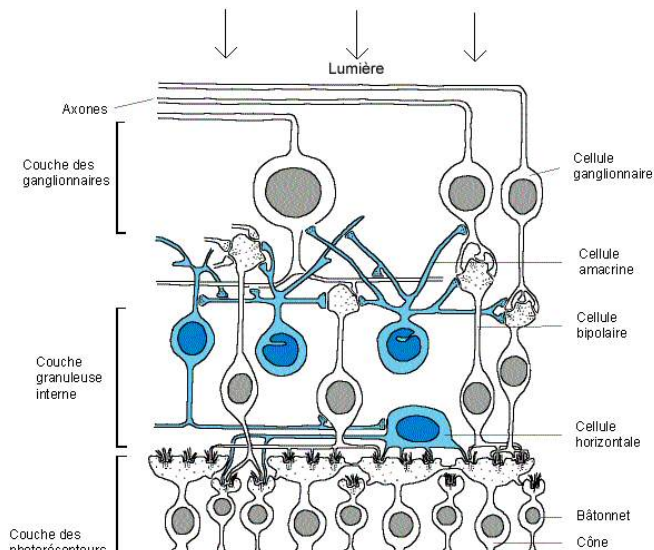
Visual system



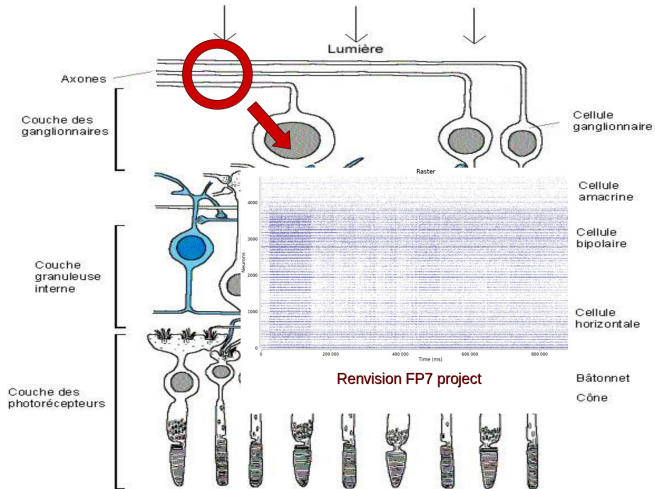
Visual system



Visual system



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Multi Electrodes Array

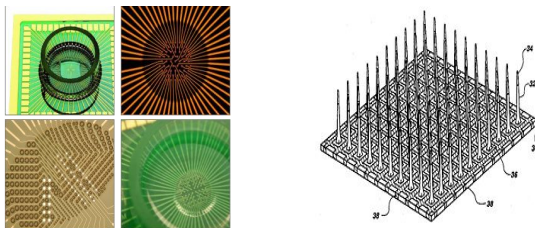
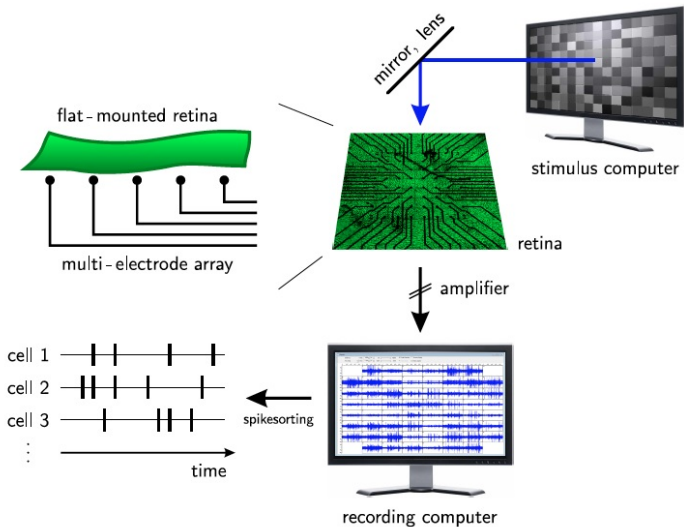
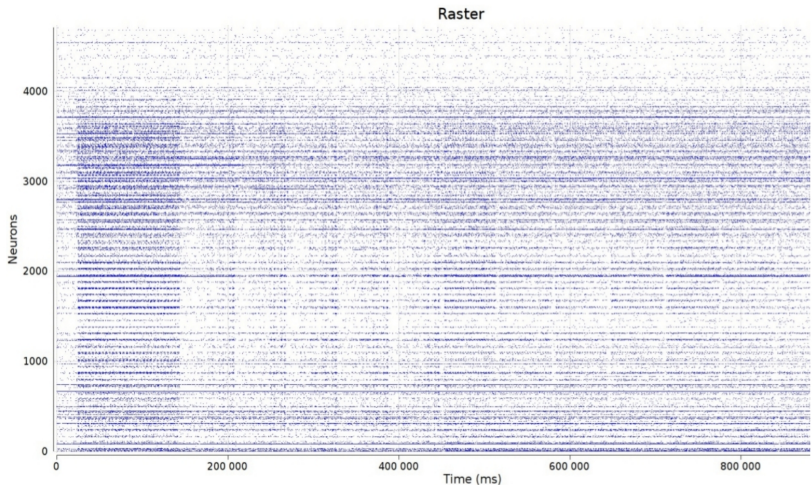


Figure : Multi-Electrodes Array.

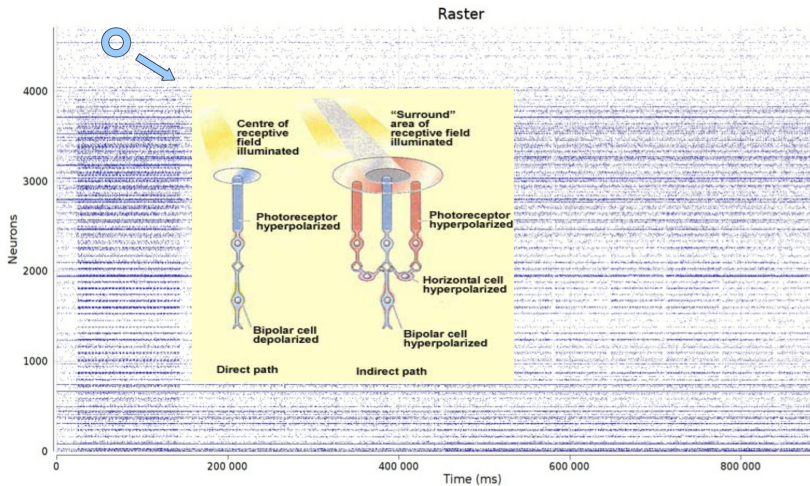
Multi Electrodes Array



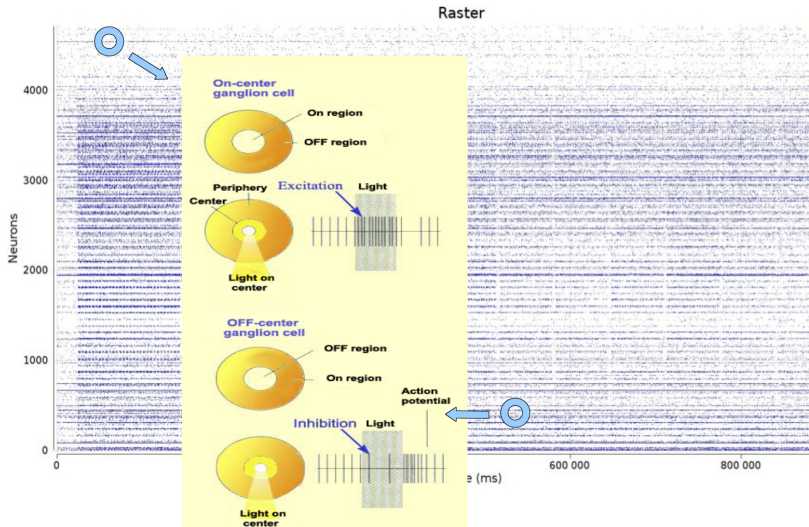
Encoding a visual scene



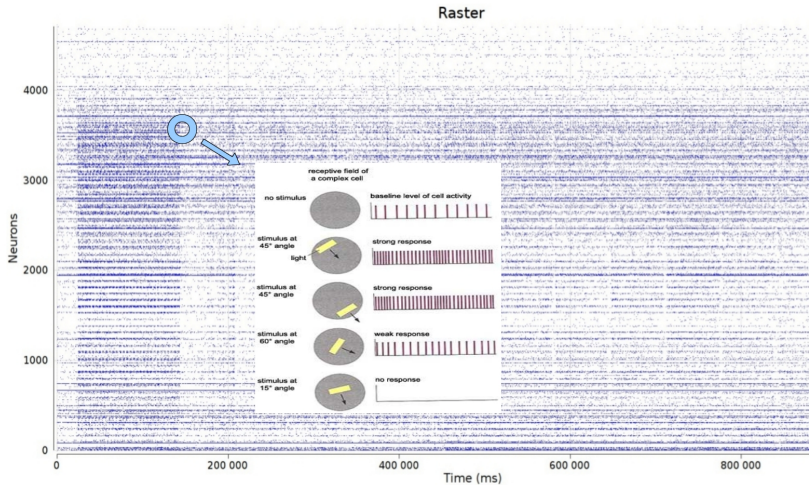
Encoding a visual scene



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Encoding a visual scene



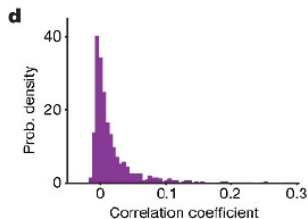
Do Ganglion cells act as **independent** encoders ?

Do Ganglion cells act as **independent** encoders ?

Or do their dynamical (spatio-temporal) **correlations** play a role in encoding a visual scene (*population coding*) ?

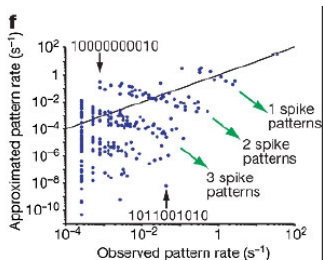
Let us measure (instantaneous pairwise) correlations

E. Schneidman, M.J. Berry, R. Segev, and W. Bialek. "Weak pairwise correlations imply strongly correlated network states in a neural population". Nature, 440(7087):1007-1012, 2006.



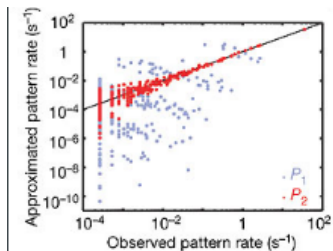
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Constructing a statistical model handling measured correlations

- Assume **stationarity**.
- Measure empirical correlations.
- Select **the** probability distribution which maximizes the entropy and reproduces these correlations.

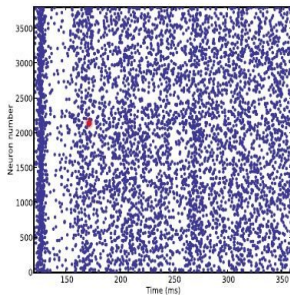


Figure : Spike state.

Spike state

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

Spike events

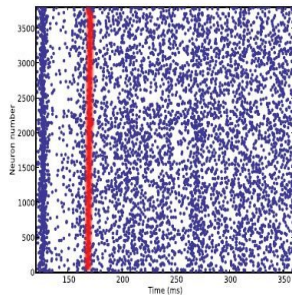


Figure : Spike pattern.

Spike state

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

Spike pattern

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

Spike events

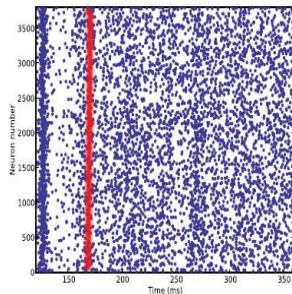


Figure : Spike pattern.

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

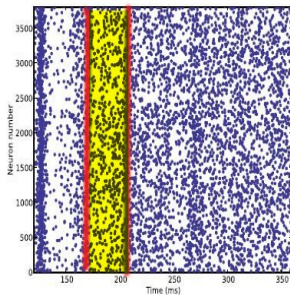


Figure : Spike block.

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

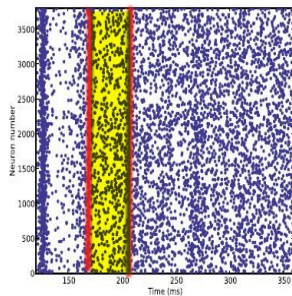


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$$\begin{pmatrix} 1 & 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{pmatrix}$$

Spike events

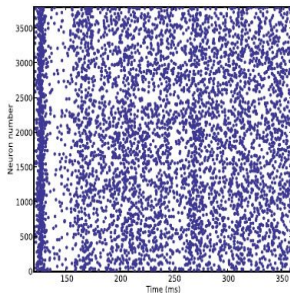


Figure : Raster plot/Spike train.

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

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

Constructing a statistical model handling measured correlations

- Let $\pi_\omega^{(T)}$ be the **empirical measure**:

$$\pi_\omega^{(T)} [f] = \frac{1}{T} \sum_{t=1}^T f \circ \sigma^t(\omega)$$

e.g. $\pi_\omega^{(T)} [\omega_i] = \frac{1}{T} \sum_{t=1}^T \omega_i(t)$: firing rate;

$$\pi_\omega^{(T)} [\omega_i \omega_j] = \frac{1}{T} \sum_{t=1}^T \omega_i(t) \omega_j(t).$$

- Find **the** (stationary) probability distribution μ that maximizes **statistical entropy** under the constraints:

$$\pi_\omega^{(T)} [\omega_i] = \mu(\omega_i); \pi_\omega^{(T)} [\omega_i \omega_j] = \mu(\omega_i \omega_j)$$

Constructing a statistical model handling measured correlations

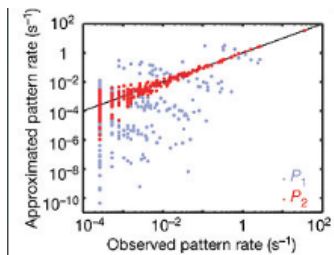
There is a **unique** probability distribution which satisfies these conditions.

This is the **Gibbs distribution** with potential:

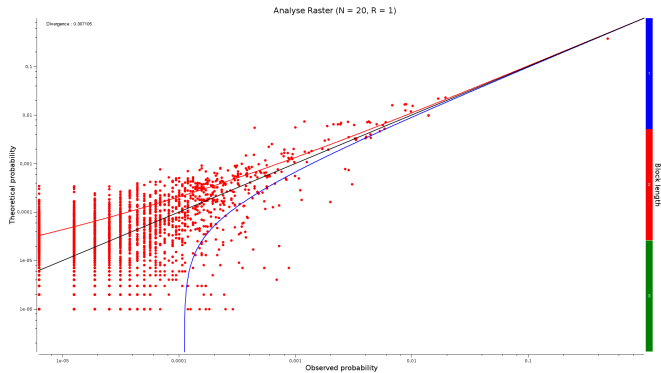
$$H(\omega(0)) = \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij} \omega_i(0) \omega_j(0)$$

Ising model

End of the story ?



End of the story ?



End of the story ?

The Ising potential:

$$H(\omega(0)) = \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij} \omega_i(0) \omega_j(0)$$

does not consider **time correlations** between neurons.
It is therefore bad at predicting **spatio-temporal patterns** !

Which correlations ?

Spikes correlations seem to play a role in spike coding.

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Although this statement depends on several assumption that could bias statistics

Stationarity;

Binning;

Stimulus dependence ?

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Modulo these remarks, Maximum entropy seems to be a relevant setting to study the role of spatio-temporal spike correlations in retina coding.

OK. So let us consider spatio-temporal constraints.

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Easy !

$$H(\omega_0^D) = \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij}^{(0)} \omega_i(0) \omega_j(0)$$

OK. So let us consider spatio-temporal constraints.

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$$\begin{aligned} H(\omega_0^D) &= \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij}^{(0)} \omega_i(0) \omega_j(0) \\ &\quad + \sum_{i,j=1}^N J_{ij}^{(1)} \omega_i(0) \omega_j(1) \\ &\quad + \sum_{i,j,k=1}^N J_{ijk}^{(2)} \omega_i(0) \omega_j(1) \omega_k(2) \end{aligned}$$

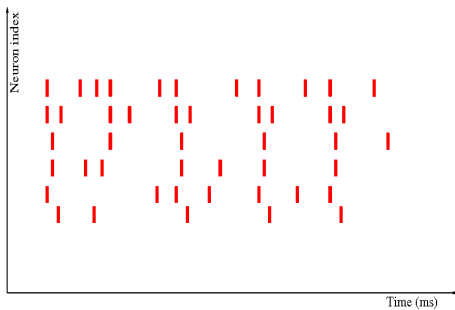
OK. So let us consider spatio-temporal constraints.

Easy ! **Euh... In fact not so easy.**

$$\begin{aligned} H(\omega_0^D) &= \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij}^{(0)} \omega_i(0) \omega_j(0) \\ &\quad + \sum_{i,j=1}^N J_{ij}^{(1)} \omega_i(0) \omega_j(1) \\ &\quad + \sum_{i,j,k=1}^N J_{ijk}^{(2)} \omega_i(0) \omega_j(1) \omega_k(2) \\ &\quad + \text{????} \end{aligned}$$

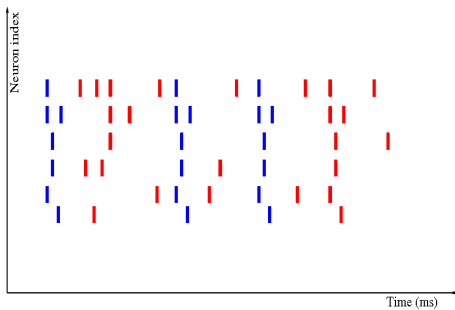
Two "small" problems.

Handling temporality and memory.



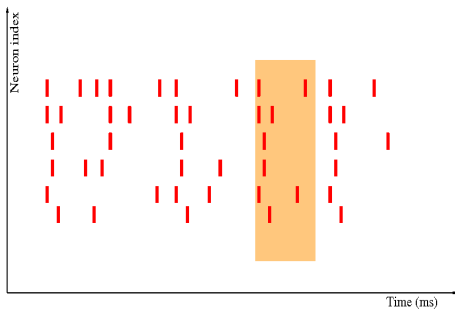
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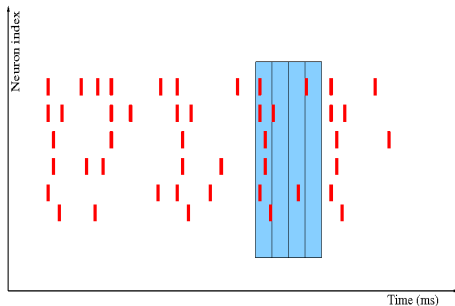
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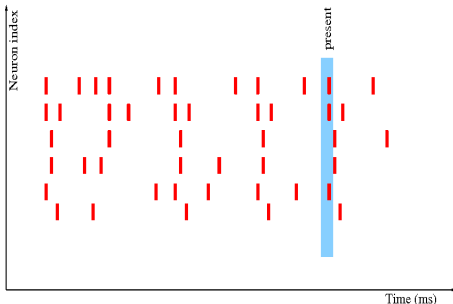
Handling temporality and memory.



Ising model considers successive times as **independent**

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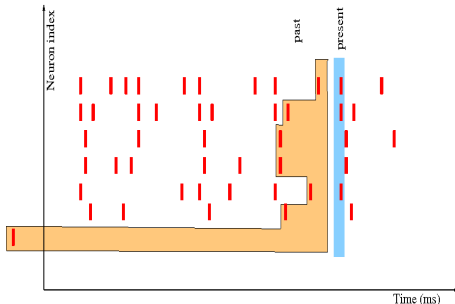


Probability of characteristic spatio-temporal patterns

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

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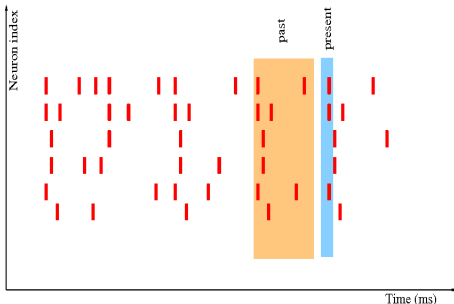


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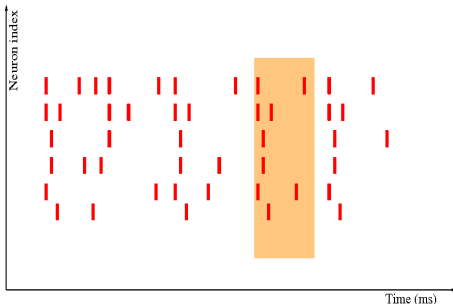


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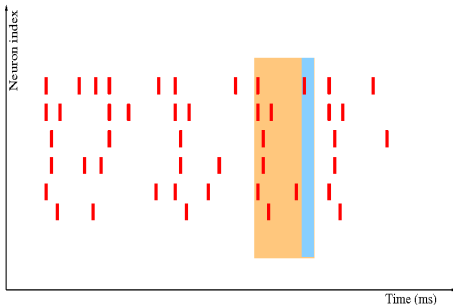


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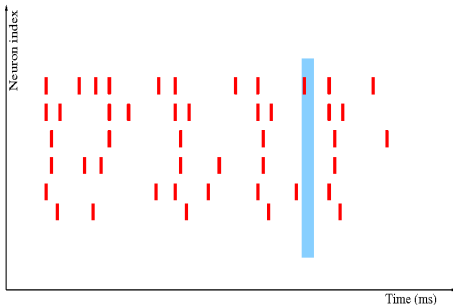


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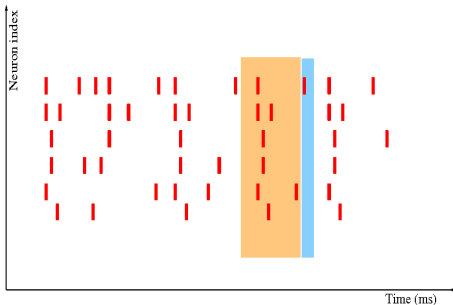


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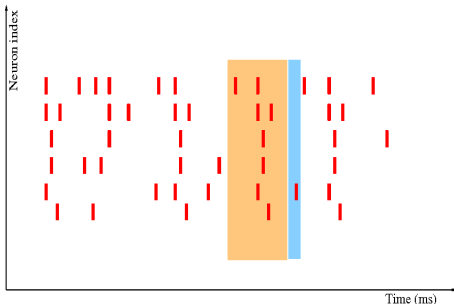


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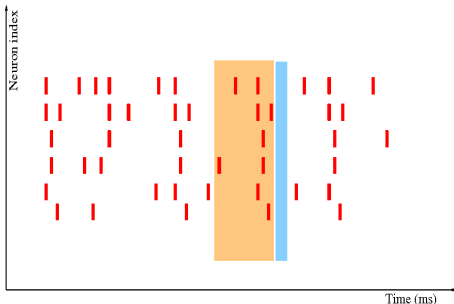


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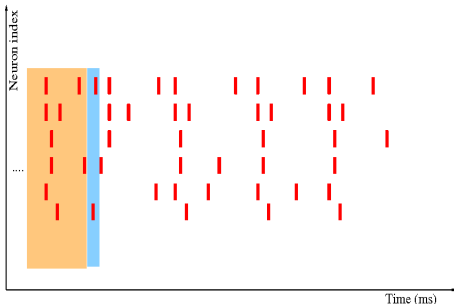


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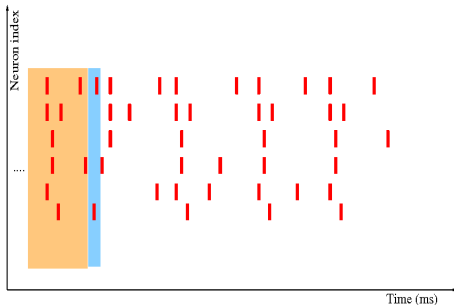


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depends on the **network history** (transition probabilities).

Two "small" problems.

Handling temporality and memory.



Probability of characteristic spatio-temporal patterns

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

Handling memory.

- Markov chains
- Variable length Markov chains
- Chains with complete connections

...

- **Gibbs distributions.**

- Probability distribution on (bi-infinite) rasters:
 $\mu[\omega_m^n], \forall m < n \in \mathbb{Z}$

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- Conditional probabilities with memory depth D :
 $P_n[\omega(n) \mid \omega_{n-D}^{n-1}]$.

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$$\left(\begin{array}{cccc|c} 1 & 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 & 1 \end{array} \right)$$

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- Generating arbitrary depth D blocks probabilities:

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$$\mu [\omega_m^{m+D}] =$$

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$\forall m < n \in \mathbb{Z}$

Chapman-Kolmogorov relation

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

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

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

$$\mu[\omega_m^n] = \exp \sum_{l=m+D}^n \phi_l \left(\omega_{l-D}^l \right) \mu \left[\omega_m^{m+D-1} \right]$$

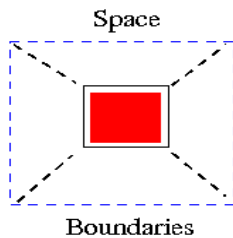
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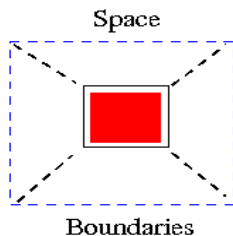
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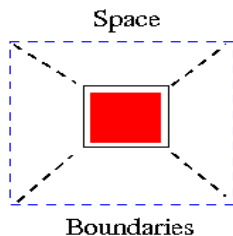
Gibbs distribution



Gibbs distribution



$$\forall \Lambda \subset \mathbb{Z}^d, \mu(\{S\} \mid \partial \Lambda) = \frac{1}{Z_{\Lambda, \partial \Lambda}} e^{-\beta H_{\Lambda, \partial \Lambda}(\{S\})}$$



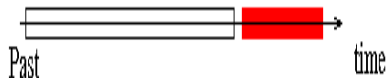
$$\forall \Lambda \subset \mathbb{Z}^d, \mu(\{S\} \mid \partial \Lambda) = \frac{1}{Z_{\Lambda, \partial \Lambda}} e^{-\beta H_{\Lambda, \partial \Lambda}(\{S\})}$$

$$f(\beta) = -\frac{1}{\beta} \lim_{\Lambda \uparrow \infty} \frac{1}{|\Lambda|} \log Z_{\Lambda, \partial \Lambda}$$

(*free energy density*)

Gibbs distribution

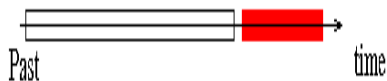




$$\forall m, n, \quad \mu \left[\omega_m^n \mid \omega_m^{m+D-1} \right] = \exp \sum_{l=m+D}^n \phi_l \left(\omega_{l-D}^l \right)$$

(*normalized potential*)

Gibbs distribution



$$\forall m < n, \quad A < \frac{\mu[\omega_m^n]}{\exp \sum_{l=m+D}^n H(\omega_{l-D}^l)} \exp-(n-m)P(H) < B$$

(non normalized potential)

- $P(H)$ is called "**topological pressure**" and is formally equivalent to free energy density.
- *Does not require time-translation invariance (stationarity).*
- In the stationary case (+ assumptions) a **Gibbs state** is also an **equilibrium state**.

$$\sup_{\nu \in M_{inv}} h(\nu) + \nu(H) = h(\mu) + \mu(H) = P(H)$$

.

This formalism allows to handle the spatio-temporal case

$$\begin{aligned} H(\omega_0^D) &= \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij}^{(0)} \omega_i(0) \omega_j(0) \\ &\quad + \sum_{i,j=1}^N J_{ij}^{(1)} \omega_i(0) \omega_j(1) \\ &\quad + \sum_{i,j,k=1}^N J_{ijk}^{(2)} \omega_i(0) \omega_j(1) \omega_k(2) + \dots \end{aligned}$$

even numerically.

J.C. Vasquez, A. Palacios, O. Marre, M.J. Berry II, B. Cessac, J. Physiol. Paris, , Vol 106, Issues 34, (2012).

H. Nasser, O. Marre, and B. Cessac, J. Stat. Mech. (2013) P03006.

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Two small problems.

Exponential number of possible terms.

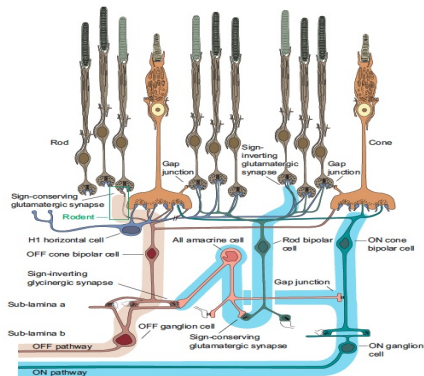
Two small problems.

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Contrarily to what happens usually in physics, we do not know
what should be
the **right potential**.

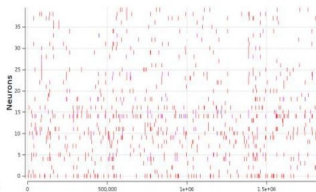
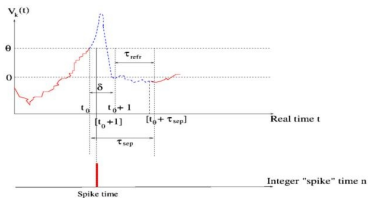
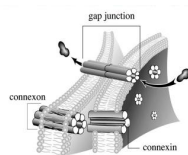
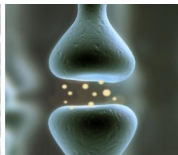
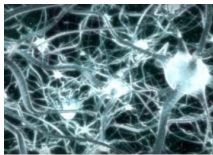
Can we have a *reasonable idea* of what could be the spike statistics by studying a *neural network model* ?

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



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.



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Sub-threshold dynamics:

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

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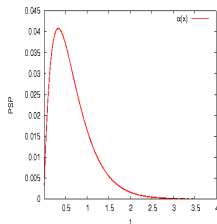


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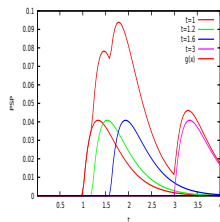


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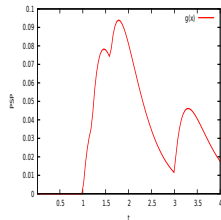


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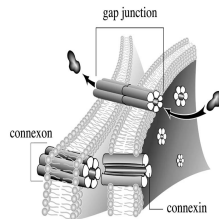
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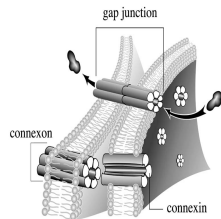
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$$+ i_k^{(ext)}(t) + \sigma_B \xi_k(t)$$



$$C \frac{dV}{dt} + [G(t, \omega) - \bar{G}] V = I(t, \omega),$$

$$G_{kl}(t, \omega) = \left[g_{L,k} + \sum_{j=1}^N g_{kj}(t, \omega) \right] \delta_{kl} \stackrel{\text{def}}{=} g_k(t, \omega) \delta_{kl}.$$

$$I(t, \omega) = I^{(cs)}(t, \omega) + I^{(\text{ext})}(t) + I^{(B)}(t)$$

$$I_k^{(cs)}(t, \omega) = \sum_j W_{kj} \alpha_{kj}(t, \omega), \quad W_{kj} \stackrel{\text{def}}{=} G_{kj} E_j.$$

$$\begin{cases} dV &= (\Phi(t, \omega)V + f(t, \omega))dt + \frac{\sigma_B}{c} \mathcal{I}_N dW(t), \\ V(t_0) &= v, \end{cases}$$

$$\Phi(t, \omega) = C^{-1} (\bar{G} - G(t, \omega))$$

$$f(t, \omega) = C^{-1} I^{(cs)}(t, \omega) + C^{-1} I^{(ext)}(t)$$

Homogeneous Cauchy problem

$$\begin{cases} \frac{dV(t,\omega)}{dt} = \Phi(t, \omega)V(t, \omega), \\ V(t_0) = v, \end{cases}$$

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Theorem

$\Phi(t, \omega)$ square matrix with bounded elements.

$$M_0(t_0, t, \omega) = \mathcal{I}_N$$

$$M_k(t_0, t, \omega) = \mathcal{I}_N + \int_{t_0}^t \Phi(s, \omega) M_{k-1}(s, t) ds, \quad t \leq t_1,$$

converges uniformly in $[t_0, t_1]$.

Brockett, R. W., "Finite Dimensional Linear Systems", John Wiley and Sons, 1970.

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Flow

$$\Gamma(t_0, t, \omega) \stackrel{\text{def}}{=} \lim_{k \rightarrow \infty} M_k(t_0, t, \omega)$$

Homogeneous Cauchy problem

If $\Phi(t, \omega)$ and $\Phi(s, \omega)$ commute

$$\Gamma(t_0, t, \omega) = \sum_{k=0}^{\infty} \frac{1}{k!} \left(\int_{t_0}^t \Phi(s, \omega) ds \right)^k = e^{\int_{t_0}^t \Phi(s, \omega) ds}$$

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This holds only in two cases :

- $\overline{G} = 0$;

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- $G(t, \omega) = \kappa(t, \omega) \mathcal{I}_N$

Homogeneous Cauchy problem

In general:

$$\Gamma(t_0, t, \omega) = \mathcal{I}_N + \sum_{n=1}^{+\infty} \sum_{\substack{X_1 = (B, A(s_1, \omega)) \\ X_2 = (B, A(s_2, \omega)) \\ \dots \\ X_n = (B, A(s_n, \omega))}} \int_{t_0}^t \cdots \int_{t_0}^{s_{n-1}} \prod_{k=1}^n X_k d_{s_1} \cdots d_{s_n}.$$

$$B = C^{-1}\overline{G}; \quad A(t, \omega) = -C^{-1}G(t, \omega)$$

Definition: An **exponentially bounded flow** is a two parameter (t_0, t) family $\{\Gamma(t_0, t, \omega)\}_{t \leq t_0}$ of flows such that, $\forall \omega \in \Omega$:

- 1 $\Gamma(t_0, t_0, \omega) = \mathcal{I}_N$ and $\Gamma(t_0, t, \omega)\Gamma(t, s, \omega) = \Gamma(t_0, s, \omega)$ whenever $t_0 \leq t \leq s$;
- 2 For each $v \in \mathbb{R}^N$ and $\omega \in \Omega$, $(t_0, t) \rightarrow \Gamma(t_0, t, \omega)v$ is continuous for $t_0 \leq t$;
- 3 There is $M > 0$ and $m > 0$ such that :

$$\|\Gamma(s, t, \omega)\| \leq Me^{-m(t-s)}, s \leq t. \quad (1)$$

Proposition

Let σ_1 be the largest eigenvalue of \bar{G} . If:

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Remark The typical electrical conductance values are of order 1 nano-Siemens, while the leak conductance of retinal ganglion cells is of order 50 micro-Siemens. *Therefore, this condition is compatible with the biophysical values of conductances in the retina.*

Theorem

If $\Gamma(t_0, t, \omega)$ is an exponentially bounded flow, there is a unique strong solution for $t \geq t_0$ given by:

$$V(t_0, t, \omega) = \Gamma(t_0, t, \omega)v + \int_{t_0}^t \Gamma(s, t, \omega)f(s, \omega)ds + \frac{\sigma_B}{c} \int_{t_0}^t \Gamma(s, t, \omega)dW(s)$$

R. Wooster, "Evolution systems of measures for non-autonomous stochastic differential equations with Levy noise", Communications on Stochastic Analysis, vol 5, 353-370, 2011

Membrane potential decomposition

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Transition probabilities

Pb: to determine $P [\omega(n) \mid \omega_{-\infty}^{n-1}]$

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Fix ω , n and $t < n$. Set:

$$\hat{\theta}_k(t, \omega) = \theta - V_k^{(d)}(t, \omega), \quad (1)$$

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Neuron k emits a spike at integer time n ($\omega_k(n) = 1$) if:

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"First passage" problem, in N dimension, with a time dependent boundary $\hat{\theta}_k(t, \omega)$. (general form unknown).

Conditional probability

Without electric synapses the probability of $\omega(n)$ conditionally to $\omega_{-\infty}^{n-1}$ can be approximated by:

$$P[\omega(n) \mid \omega_{-\infty}^{n-1}] = \prod_{k=1}^N P[\omega_k(n) \mid \omega_{-\infty}^{n-1}],$$

with $P[\omega_k(n) \mid \omega_{-\infty}^{n-1}] =$

$$\omega_k(n) \pi(X_k(n-1, \omega)) + (1 - \omega_k(n)) (1 - \pi(X_k(n-1, \omega))),$$

where

$$X_k(n-1, \omega) = \frac{\theta - V_k^{(det)}(n-1, \omega)}{\sigma_k(n-1, \omega)},$$

and

$$\pi(x) = \frac{1}{\sqrt{2\pi}} \int_x^{+\infty} e^{-\frac{u^2}{2}} du.$$

Conditional probability

- $\phi(\omega) = \log P [\omega(n) \mid \omega_{-\infty}^{n-1}]$ defines a (infinite range) normalized potential defining a *unique Gibbs distribution*.

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- The general form (with electric synapses) is *yet unknown*.

Back to our second "small" problem

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Is there a **Maximum Entropy potential** corresponding to ϕ (in the stationary case) ?

Back to our second "small" problem

One can make a Taylor expansion of $\phi(\omega)$.

Back to our second "small" problem

Using $\omega_i(n)^k = \omega_i(n)$, $k \geq 1$ one ends up with a potential of the form:

$$\phi(\omega) = \sum_{i=1}^N h_i \omega_i(0) + \sum_{i,j=1}^N J_{ij}^{(0)} \omega_i(0) \omega_j(0) + \dots$$

Back to our second "small" problem

The expansion is *infinite* although one can approximate the *infinite range potential* ϕ by a finite range approximation (*finite memory*), giving rise to a finite expansion.

Back to our second "small" problem

The coefficients of the expansion are *non linear functions* of the network parameters and stimulus.

They are therefore somewhat *redundant*.

Back to our second "small" problem

Rodrigo Cofré, Bruno Cessac, "Exact computation of the maximum-entropy potential of spiking neural-network models", *Phys. Rev. E* 89, 052117.

Given a set of *stationary* transition probabilities $P[\omega(D) | \omega_0^{D-1}] > 0$ there is a unique (up to a constant) *Maximum Entropy* potential, written as a linear combination of spike interactions terms with a minimal number of terms (*normal form*). This potential can be explicitly (and algorithmically) computed.

Hints: Using variable change one can eliminate terms in the potential ("normal" form).

The construction is based on equivalence between Gibbs potentials (*cohomology*) and *periodic orbits expansion*.

Back to our second "small" problem

However, there is still a number of terms **growing exponentially with the number of neurons and the memory depth.**

These terms are **generically** non zero.

Back to the retina

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- Intractable determination of parameters;
- Stimulus dependent parameters;
- Overfitting.

BUT

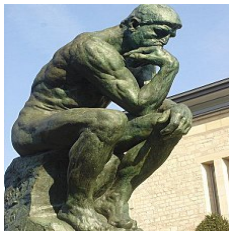
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- Stimulus dependent parameters;
- Overfitting.

BUT *Real neural networks are not generic*

MaxEnt approach might be useful if there is some hidden law of nature/ symmetry which cancels most terms in the expansion.



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- Vivien Robinet (Post Doc → MCF Kourou)
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- Wahiba Taouali (Post Doc → Post Doc INT Marseille)
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Can we hear the shape of a Maximum entropy potential

Two distinct potentials $\mathcal{H}^{(1)}, \mathcal{H}^{(2)}$ of range $R = D + 1$ correspond to the same Gibbs distribution (are “equivalent”), if and only if there exists a range D function f such that (Chazottes-Keller (2009)):

$$\mathcal{H}^{(2)}\left(\omega_0^D\right) = \mathcal{H}^{(1)}\left(\omega_0^D\right) - f\left(\omega_0^{D-1}\right) + f\left(\omega_1^D\right) + \Delta, \quad (2)$$

where $\Delta = \mathcal{P}(H^{(2)}) - \mathcal{P}(H^{(1)})$.

Can we hear the shape of a Maximum entropy potential

Summing over periodic orbits we get rid of the function f

$$\sum_{n=1}^R \phi(\omega \sigma^n l_1) = \sum_{n=1}^R \mathcal{H}^*(\omega \sigma^n l_1) - R\mathcal{P}(\mathcal{H}^*), \quad (3)$$

We eliminate equivalent constraints.

Can we hear the shape of a Maximum entropy potential

Conclusion

Given a set of transition probabilities $P \left[\omega(D) \mid \omega_0^{D-1} \right] > 0$ there is a unique, up to a constant, 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.