From retina to statistical physics

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4ème journée de la physique niçoise, 20-06-14

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Multi Electrodes Array



Figure: Multi-Electrodes Array.

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Multi Electrodes Array



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Raster



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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.

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Figure: Spike state.

Spike state

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



Figure: Spike pattern.

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

Spike pattern

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



Figure: Spike pattern.

Spike state

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

Spike pattern

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

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

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Figure: Spike block.

Spike state

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

Spike pattern

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

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

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Figure: Spike block.

Spike state

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

Spike pattern

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

Spike block

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

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Figure: Raster plot/Spike train.

Spike state

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

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

$$\boldsymbol{\omega} \stackrel{\mathrm{def}}{=} \boldsymbol{\omega}_{\mathbf{0}}^{T}$$

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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:

$$\pi_{\omega}^{(\mathcal{T})}\left[\,\omega_{i}\,
ight]=\mu(\omega_{i});\pi_{\omega}^{(\mathcal{T})}\left[\,\omega_{i}\omega_{j}\,
ight]=\mu(\omega_{i}\omega_{j})$$

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

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End of the story ?



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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** !

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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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Spikes correlations seem to play a role in spike coding.

Although this statement depends on several assumption that could bias statistics

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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.

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Easy !

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

Easy !

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

$$+\sum_{i,j=1}^N J^{(1)}_{ij}\omega_i(0)\,\omega_j(1)$$

Easy !

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$$+\sum_{i,j,k=1}^{N}J_{ijk}^{(2)}\omega_{i}(0)\omega_{j}(1)\omega_{k}(2)$$
OK. So let us consider spatio-temporal constraints.

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

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

$$+\sum_{i,j=1}^N J^{(1)}_{ij}\omega_i(0)\,\omega_j(1)$$

+
$$\sum_{i,j,k=1}^{N} J_{ijk}^{(2)} \omega_i(0) \omega_j(1) \omega_k(2)$$

+????

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Ising model considers successive times as independent





The probability of a spike pattern



Probability of characteristic spatio-temporal patterns

The probability of a spike pattern



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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.

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

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• 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*: $P_n \left[\omega(n) \mid \omega_{n-D}^{n-1} \right].$

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

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$$\mu\left[\,\omega_{m}^{m+D}\,\right] =$$

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 - Generating arbitrary depth D blocks probabilities:

$$\mu\left[\omega_{m}^{m+D}\right] = P_{m+D}\left[\omega(m+D) \mid \omega_{m}^{m+D-1}\right] \mu\left[\omega_{m}^{m+D-1}\right]$$

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

Chapman-Kolmogorov relation

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

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

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

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

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

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

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

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

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







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



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

(normalized potential)

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

- *P*(*H*) is called "**topological pressure**" and is formaly 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**.

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

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This formalism allows to handle the spatio-temporal case

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

$$+\sum_{i,j=1}^{N}J_{ij}^{(1)}\omega_{i}(0)\omega_{j}(1)$$

+
$$\sum_{i,j,k=1}^{N} J_{ijk}^{(2)} \omega_i(0) \omega_j(1) \omega_k(2) + \ldots$$

even numerically.

J.C. Vasquez, A. Palacios, O. Marre, M.J. Berry II, B. Cessac, J. Physiol. Paris, Vol 106, Issues 3–4, (2012). H. Nasser, O. Marre, and B. Cessac, J. Stat. Mech. (2013) P03006. H. Nasser, B. Cessac, Entropy (2014), 16(4), 2244-2277.

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Gibbs distribution

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Exponential number of possible terms.



Exponential number of possible terms.

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

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

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



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$$-\sum_{j} \bar{g_{kj}} \left(V_k - V_j\right)$$



Sub-threshold dynamics:

$$egin{aligned} &C_k rac{dV_k}{dt} = -g_{L,k}(V_k - E_L) \ &-\sum_j g_{kj}(t,\omega)(V_k - E_j) \ &-\sum_j g_{kj}(V_k - V_j) \end{aligned}$$

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



Sub-threshold regime

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

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

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

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

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Sub-threshold regime

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

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

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

Homogeneous Cauchy problem

$$\left\{ egin{array}{cc} rac{dV(t,\omega)}{dt} &=& \Phi(t,\omega)V(t,\omega), \ V(t_0) &=& v, \end{array}
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Homogeneous Cauchy problem

$$\left[\begin{array}{cc} rac{dV(t,\omega)}{dt} &=& \Phi(t,\omega)V(t,\omega), \ V(t_0) &=& v, \end{array}
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Theorem

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

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

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

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converges uniformly in $[t_0, t_1]$.

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

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Flow

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

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

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

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This holds only in two cases :

•
$$\overline{G}=0;$$

 $\Gamma(t_0,t,\omega)=e^{-rac{1}{c}\int_{t_0}^t G(s,\omega)ds}$

B. Cessac, J. Math. Neuroscience, 2011.

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B. Cessac, J. Math. Neuroscience, 2011.

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

In general:

$$\Gamma(t_{0}, t, \omega) = \mathcal{I}_{N} + \sum_{n=1}^{+\infty} \sum_{\substack{X_{1} = (B, A(s_{1}, \omega)) \\ X_{2} = (B, A(s_{2}, \omega)) \\ \dots \\ X_{n} = (B, A(s_{n}, \omega))}} \int_{t_{0}}^{t} \cdots \int_{t_{0}}^{s_{n-1}} \prod_{k=1}^{n} X_{k} d_{s_{1}} \cdots d_{s_{n}}.$$

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

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Exponentially bounded flow

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

- $\Gamma(t_0, t_0, \omega) = \mathcal{I}_N$ and $\Gamma(t_0, t, \omega)\Gamma(t, s, \omega) = \Gamma(t_0, s, \omega)$ whenever $t_0 \le t \le s$;
- Our For each v ∈ ℝ^N and ω ∈ Ω, (t₀, t) → Γ(t₀, t, ω)v is continuous for t₀ ≤ t;
- There is M > 0 and m > 0 such that :

$$||\Gamma(s,t,\omega)|| \le M e^{-m(t-s)}, s \le t.$$
(1)

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Proposition

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

 $\sigma_1 < g_L,$

then the flow Γ in our model has the exponentially bounded flow property.

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then the flow Γ in our model has the exponentially bounded flow property.

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 $t \ge t_0$ given by:

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

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

$$V(t,\omega) = V^{(d)}(t,\omega) + V^{(\mathit{noise})}(t,\omega),$$

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$$V(t,\omega)=V^{(d)}(t,\omega)+V^{(\mathit{noise})}(t,\omega),$$

$$V^{(d)}(t,\omega) = V^{(cs)}(t,\omega) + V^{(ext)}(t,\omega),$$

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$$\mathcal{V}(t,\omega)=\mathcal{V}^{(d)}(t,\omega)+\mathcal{V}^{(extsf{noise})}(t,\omega),$$

$$V^{(d)}(t,\omega) = V^{(cs)}(t,\omega) + V^{(ext)}(t,\omega),$$

$$V^{(cs)}(t,\omega) = \frac{1}{c} \int_{-\infty}^{t} \Gamma(s,t,\omega) \,\chi(s,\omega) \,I^{(cs)}(s,\omega) ds,$$

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$$V^{(noise)}(t,\omega) = rac{\sigma_B}{c} \int_{ au_k(t,\omega)}^t \Gamma(s,t,\omega) \ dW(s).$$

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Transition probabilities

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



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Fix ω , *n* and t < n. Set:

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

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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:

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

with $P\left[\omega_{k}(n) \mid \omega_{-\infty}^{n-1}\right] =$
 $\omega_{k}(n) \pi \left(X_{k}(n-1,\omega)\right) + \left(1 - \omega_{k}(n)\right) \left(1 - \pi \left(X_{k}(n-1,\omega)\right)\right),$

where

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

and

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

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

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

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

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



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

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

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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.

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

They are therefore somewhat *redundant*.

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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 $P\left[\omega(D) \mid \omega_0^{D-1}\right] > 0$ 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.

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.



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• Neuromimetic models have typically $O(N^2)$ parameters where N is the number of neurons.

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- The equivalent MaxEnt potential has *generically* a number of parameters growing exponentially with *N*, non linear and redundant functions of the network parameters (synaptic weights, stimulus).

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

BUT

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

BUT Real neural networks are not generic

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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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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)):

$$\mathcal{H}^{(2)}\left(\omega_{0}^{D}\right) = \mathcal{H}^{(1)}\left(\omega_{0}^{D}\right) - f\left(\omega_{0}^{D-1}\right) + f\left(\omega_{1}^{D}\right) + \Delta, \quad (2)$$

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

Summing over periodic orbits we get rid of the function f

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

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We eliminate equivalent constraints.

Conclusion

Given a set of transition probabilities $P\left[\left.\omega(D) \mid \omega_0^{D-1}\right.\right] > 0$ 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.