TD 5 – Balanced Networks

Practical Information

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TD Material
https://github.com/esther-poniatowski/2223_UlmM2_ThNeuro

Goals of the TD

In vivo, experimental recordings of single neurons display a wide variability : repeated stimulations do not result in strictly similar spikes sequences, and the number of spikes is not even conserved. On the contrary, *in vitro*, membrane potential dynamics turn out to be very predictable. One source of variability stems from the numerous inputs that each neuron receives when it is embedded in a network.

This TD aims to study neuronal responses properties in the context of balanced noisy inputs. This involves switching from deterministic to probabilistic mathematical descriptions.

Part 1 Poissonian spike trains.

Part 2 Poisson inputs in a balanced network.

Part 3 Stochatic integration of synaptic inputs.

1 Poissonian spike trains

1.1 Poisson Process

Random Processes

Stochastic descriptions of spike trains aims to express a probability distribution $\mathbb{P}(n, T)$ of the number of spikes n in any arbitrary time interval T.

The appropriate mathematical tool is **random processes**. A random process is a *family* of random variables indexed by *time*.

$$\{X(t),\ t \in [0, t_{max}]\}$$

In other words, each time t is associated with a random variable $X(t)$, whose possible values correspond to the states that the system can reach at this time.

Poisson Process

The Poisson process is one of the simplest random processes used to reproduce the firing statistics of single neurons subject to stochastic input.

This model takes the following assumptions :
- All spikes are produced independently.
- The number of spikes occurring in any time interval is independent of the number of spikes in any other disjoint interval.

Under those assumptions, the probability of observing n spikes during a duration T follows :

$$\mathbb{P}(n, T) = \frac{(RT)^n}{n!} e^{-RT} \quad \text{with } R \text{ the mean rate of spike occurrences} \tag{1}$$

To derive the probability distribution of the number of spikes over a duration T, the first step is to discretize the time interval T into M bins of length $\Delta T = \dfrac{T}{M} \ll 1/R$, such that (by assumption) **at most one spike occurs per bin** (for instance ΔT might correspond to the absolute refractory period of the neuron).
Then, the second step is to obtain the Poisson distribution as the limit distribution when $\Delta T \to 0$.

1. What is the probability that one spike occurs during an elementary time bin ΔT ? Deduce what the quantity RT represents.

2. Express the probability of observing n spikes in the total discretized interval T, as a function of n, M, T, R.

3. Take the limit $\Delta T \to 0$ to obtain the Poisson distribution of parameter RT.

4. Compute the distribution of inter-spike intervals.

1.2 Mean and Variance

Moment generating function

The moment generating function is a useful tool to compute the summary statistics of a random variable at different orders.

For a continuous random variable X with probability density p_X over a set Ω, the moment generating function G_X is defined as :

$$G_X(\alpha) = \int_\Omega e^{\alpha x} p_X(x)\,\mathrm{d}x, \quad \alpha \in I \subseteq \mathbb{R} \tag{2}$$

5. Interpret the moment generating function as an mean.

6. Show that, for all $n \in \mathbb{N}$:

$$\left.\frac{\mathrm{d}^n G_X}{\mathrm{d}\alpha^n}\right|_{\alpha=0} = \mathbb{E}(X^n) \tag{3}$$

7. How would the moment generating function generalize to discrete random variables ?

8. Express the moment generating function for the random variable N corresponding to the number of spikes generated by a homogeneous Poisson process of rate R in a window of size T.

9. Use the moment-generating function to compute the mean $\mathbb{E}(N)$ and variance $\mathbb{V}(N)$ of the variable N.

Fano factor

When experimentally measuring the firing statistics of a neuron, the **Fano factor** is useful to characterize the behavior of the neuron as either Poissonian, sub-Poissonian or supra-Poissonian.

10. Compute the Fano factor $\dfrac{\mathbb{V}(N)}{\mathbb{E}(N)}$.

2 Poisson inputs in a balanced network

Balanced network model

In a balanced network model, a neuron possesses C_E excitatory synapses and $C_I = \gamma C_E$ inhibitory synapses.

This neuron receives input synaptic currents by delta pulses : a spike in the pre-synaptic neuron k at time t_0 elicits a postsynaptic current $i_k(t)$ given by :

$$i_k(t) = \tau_m J_k \delta(t - t_0) \tag{4}$$

where τ_m is the membrane time-scale and J_k is the strength of synapse.

As a first approximation, all excitatory synapses are assumed to have the same strength J and all inhibitory synapses have the same strength $-gJ$.

Pre-synaptic spike trains follow a Poisson process of rate r. All pre-synaptic spike trains are independent across different synapses.

11 Compute the mean of the total synaptic current received during a unit time.

12 Compute the variance of the total synaptic input received during a unit time.

13 Compare with a white noise process of mean μ and variance $\tau_m \sigma^2$.

3 Stochastic integration of synaptic inputs

Ornstein-Uhlenbeck process

In line with deterministic models, the membrane potential dynamics of an integrate-and-fire neuron is modeled by the following differential equation :

$$\tau_m \frac{\mathrm{d}V}{\mathrm{d}t} = -V + I(t) \tag{5}$$

with :

- τ_m : membrane time constant,
- $I(t)$: arbitrary input current.

Under a stochastic description, the current $I(t)$ becomes a *random variable*.
It can be modeled as a **white noise** input :

$$I(t) = \mu + \sqrt{\tau_m}\sigma \cdot \eta(t) \tag{6}$$

with $\eta(t)$ a *reduced centered white noise*, such that :

- at each time step, $\eta(t)$ follows a gaussian law with mean $\mathbb{E}(\eta(t)) = 0$
- for any pair of two time steps t and t', $\mathbb{E}(\eta(t)\eta(t')) = \delta(t - t')$.

Consequently, the membrane potential value $V(t)$ at each time t (below the threshold) is also a *random variable*.
Its differential equation its that of an **Ornstein-Uhlenbeck process**, whose solution is :

$$V(t) = V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \,\mathrm{d}\omega_s \tag{7}$$

with ω_t a *Wiener process*, such that :

- $\mathrm{d}\omega_t = \eta(t)\,\mathrm{d}t$ represents the integral of the white noise over the interval $\mathrm{d}t$
- its increments over dijoint time intervals are independent,
- its increment between two time points follows a normal law :

$$\omega_t - \omega_s \sim \mathcal{N}(0, t - s) \quad (t > s) \tag{8}$$

14 *Proving the solution of the Ornstein-Uhlenbeck process*

By analogy with the method of the variation of the constants, the idea is to consider a function which is easier to integrate :

$$f(V_t, t) = V(t)e^{t/\tau_m}$$

(or equivalently, to look for the solution $V(t)$ under the form $V(t) = f(V_t, t)e^{-t/\tau_m}$).

Express the differential of the function f of two variables as a function of $\mathrm{d}V$ and $\mathrm{d}t$, and use then equations (5) and (6) to rewrite this differential as a function of $\mathrm{d}t$ only.
Integrate with respects to time in order to express the stochastic evolution of the membrane potential (7).

15 Compute the mean $\mathbb{E}(V(t))$, by expressing the function $s \mapsto e^{s/\tau_m}$ as a limit of step functions.

16 Show that for any function f, $\mathbb{V}\left[\int_0^t f(s)\,\mathrm{d}\omega_s\right] = \int_0^t f(s)^2\,\mathrm{d}s$.
Use this formula to compute the variance $\mathbb{V}(V(t))$.