TD 5 – Balanced Networks

Practical Information

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

Goals of the TD

Experimentally, in in vivo single neurons recordings, repeated stimulations do not result in strictly similar spikes sequences, on the contrary, the number of spikes is not even conserved. An yet, membrane potential dynamics turn out to be very predictable in votro. One source of variability stems from the numerous inputs 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.

1 Poissonian spike trains

1.1 Poisson Process

A stochastic description of spike trains aim 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**, with a given rate of spike occurrence R. A random process is a *family* of random variable indexed by *time*. More precisely, each time is associated with a random variable whose possible values correspond to the states that the system can reach at this time.

The simplest random process is the **Poisson process** which reproduces the statistics of firing of single neurons subject to stochastic inputs. In the Poisson process, all spikes are produced independently, and the actual number of spikes in one interval is independent of the number of spikes in any other interval.

To obtain the full probability distribution over any time interval T, the first step is to discretize time into M bins of length $\Delta T = \dfrac{T}{M} \ll 1/R$, such that at most one spike occurs per bin (for instance ΔT can correspond to the absolute refractory period of the neuron).

Under those assumbtions, the probability of observing n spikes during an interval T follows :

$$\mathbb{P}(n, T) = \frac{(RT)^n}{n!} e^{-RT} \tag{1}$$

① What does the quantity RT represent ?

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

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

The moment generating function G_X of a continuous random variable X with probability density $\mathbb{P}(X)$ is defined as :

$$G_X(\alpha) = \int_\Omega e^{\alpha x} \mathbb{P}(x) \, \mathrm{d}x \tag{2}$$

with Ω the set of the random variable X.

⑤ Interpret the moment generating function as an mean.

⑥ Show that :

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

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.

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

In a **balanced network model**, a neuron that receives C_E excitatory synapses and $C_I = \gamma C_E$ inhibitory synapses. Incoming 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 spikes are independent (for different connections).

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

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

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

where τ_m is the membrane time constant and $I(t)$ is an 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 defined by $\mathbb{E}(\eta(t)) = 0$ and $\mathbb{E}(\eta(t)\eta(t')) = \delta(t - t')$.
The mean is taken across all the possible realizations of the white noise.

Consequently, the membrane potential value 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 :

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

where $\mathrm{d}\eta_t = \eta(t)\,\mathrm{d}t$ is called a *Wiener process*, which represents the integral of the white noise over the interval $\mathrm{d}t$. An important property of a Wiener process is the following :

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

(14) By analogy with the method of the variation of the constants, consider the function of two variables :

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

Differentiate this function and use equations (5) and (6) to obtain the membrane potential stochastic evolution (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 $\mathbb{E}\left[\left(\int_0^t f(s)\,\mathrm{d}\eta_s\right)^2\right] = \int_0^t f(s)^2\,\mathrm{d}s$. Use this formula to compute the variance $\mathbb{V}(V(t))$.