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THEORETICAL NEUROSCIENCE

TD3: BALANCED NETWORKS

All TD materials will be made available at https://github.com/helene-todd/TheoNeuro2425.

In vivo, experimental recordings of single neurons display a wide variability: repeated stimulation do not result in strictly similar spikes sequences, and the number of spikes is not 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. In this tutorial, we will study neuronal responses properties in the context of balanced noisy inputs. This involves switching from deterministic to probabilistic mathematical descriptions.

1 Poissonian spike trains

A random process is a collection of random variables $\{X(t) \mid t \in \mathbb{R}_+\}$ indexed by time. 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.

The Poisson process $\{N(t) \mid t \in \mathbb{R}_+\}$ is one of the simplest random processes used to reproduce the firing statistics of single neurons subject to stochastic input. Note that this model takes the definitions (1) all spikes are produced independently, and (2) the number of spikes occurring in any time interval is independent of the number of spikes in any other disjoint interval.

Under those definitions, the probability of observing n spikes during a duration T is

$$\mathbb{P}(N(T) = n) = \frac{(\lambda T)^n}{n!} e^{-\lambda T}, \text{ with } \lambda \text{ the rate of spike occurrences.}$$

In order to derive this probability distribution, the first step will be to discretise the time interval T into M bins of length $\Delta T \ll 1/\lambda$, such that (by assumption) at most one spike occurs per M bin (for instance ΔT might correspond to the absolute refractory period of the neuron). Then, the second step will be to obtain the Poisson distribution as the limit distribution when $\Delta T \to 0$.

We start with the following definition: the probability of one spike occurring during a small time bin ΔT is $\lambda \Delta T$.

1. Justify why λT represents the mean number of spikes in an interval of duration T.

> Let N represent the number of spikes during an interval of duration T. It is the sum of M Bernoulli variables $N_i,\ i \in [\![1, M]\!]$, which take the value 1 if a spike occurs at the i^{th} time bin and 0 otherwise.

> We have that N_i are identically distributed, and their expectancy is proportional to the rate λ and the length of the elementary time interval ΔT, such that $N_i \sim \mathcal{B}(\lambda \Delta T)$.
>
> By linearity of the expectancy, we have
>
> $$\mathbb{E}(N) = \mathbb{E}\left(\sum_{k=1}^{M} N_i\right) = \sum_{k=1}^{M} (\mathbb{E}(N_i)) = \sum_{k=1}^{M} \lambda \Delta T = M\lambda\Delta T = \lambda T.$$

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

> Since the number of spikes occurring in any bin is independent of the number of spikes occurring in the other bins, the probability of a given pattern with n spikes is the product of the probability that there was a spike in n bins and that there was no spike in $M - n$ bins. The number of such patters is
>
> $$\binom{M}{n} = \frac{M!}{n!(M-n)!}.$$
>
> The probability to have n spikes is therefore a binomial, i.e. $N(T) \sim \mathcal{B}(M, \lambda\Delta T)$, and
>
> $$\begin{aligned} \mathbb{P}(N(T) = n) &= \frac{M!}{n!(M-n)!}(\lambda\Delta T)^n(1-\lambda\Delta T)^{M-n} \\ &= \frac{M!}{n!(M-n)!}\left(\lambda\frac{T}{M}\right)^n\left(1-\lambda\frac{T}{M}\right)^{M-n} \\ &= \frac{(\lambda T)^n}{n!}\frac{M(M-1)\dots(M-n+1)}{M^n}\exp\left((M-n)\log\left(1-\lambda\frac{T}{M}\right)\right). \end{aligned}$$

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

> Taking the limit $\Delta T \to 0$ or equivalently $M \to \infty$ in the previously obtained expression for $\mathbb{P}(N(T) = n)$, we get the Poisson distribution of parameter λT
>
> $$\mathbb{P}(N(T) = n) = \frac{(\lambda T)^n}{n!}\exp(-\lambda T),$$
>
> using
>
> $$\frac{M(M-1)\dots(M-n+1)}{M^n} \underset{M\to\infty}{\sim} 1,$$
>
> and
>
> $$\log\left(1-\lambda\frac{T}{M}\right) \underset{M\to\infty}{\sim} -\lambda\frac{T}{M}.$$

4. Compute the distribution of inter-spike intervals (ISIs).

> Let T denote the time of first arrival of a spike, in other words T represents the ISI.

Noting that for $t \geq 0$, the events $\{N(t) = 0\}$ and $\{T > t\}$ are strictly equivalent,

$$\mathbb{P}(T > t) = \mathbb{P}(N(t) = 0) = \frac{(\lambda t)^0}{0!} e^{-\lambda t} = e^{-\lambda t}.$$

Since

$$\mathbb{P}(T \leq t) = 1 - \mathbb{P}(T > t) = 1 - e^{-\lambda t},$$

we recognise the cumulative distribution function (CDF) of an exponential distribution of parameter λ, therefore $T \sim \mathcal{E}(\lambda)$.

5. Compute the mean and variance of the number of spikes generated by a Poisson process of rate λ in a window of size T. Deduce the Fano factor.

Reminder:

$$\sum_{n=0}^{\infty} \frac{x^n}{n!} = e^x.$$

The mean (or expectancy) is the following

$$\begin{aligned}
\mathbb{E}(N(T)) = \sum_{k=0}^{\infty} k \frac{(\lambda T)^k}{k!} e^{-\lambda T} &= e^{-\lambda T} \sum_{k=0}^{\infty} k \frac{(\lambda T)^k}{k!} = e^{-\lambda T} \sum_{k=1}^{\infty} k \frac{(\lambda T)^k}{k!} \\
&= e^{-\lambda T} \sum_{k=1}^{\infty} \frac{(\lambda T)^k}{(k-1)!} = e^{-\lambda T} \sum_{k=0}^{\infty} \frac{(\lambda T)^{k+1}}{k!} = e^{-\lambda T} \lambda T \sum_{k=0}^{\infty} \frac{(\lambda T)^k}{k!} \\
&= e^{-\lambda T} \lambda T e^{\lambda T} = \lambda T.
\end{aligned}$$

We begin by computing $\mathbb{E}(N(t)^2)$

$$\begin{aligned}
\mathbb{E}(N(T)^2) = \sum_{k=0}^{\infty} k^2 \frac{(\lambda T)^k}{k!} e^{-\lambda T} &= e^{-\lambda T} \sum_{k=1}^{\infty} k^2 \frac{(\lambda T)^k}{k!} = e^{-\lambda T} \sum_{k=1}^{\infty} k \frac{(\lambda T)^k}{(k-1)!} \\
&= e^{-\lambda T} \sum_{k=0}^{\infty} (k+1) \frac{(\lambda T)^{k+1}}{k!} = e^{-\lambda T} \lambda T \left(\sum_{k=0}^{\infty} k \frac{(\lambda T)^k}{k!} + \sum_{k=0}^{\infty} \frac{(\lambda T)^k}{k!} \right) \\
&= e^{-\lambda T} \lambda T \left(\lambda T e^{\lambda T} + e^{\lambda T} \right) = (\lambda T)^2 + \lambda T.
\end{aligned}$$

Therefore, the variance is the following

$$\mathbb{V}(N(T)) = \mathbb{E}(N(T)^2) - \mathbb{E}(N(T))^2 = (\lambda T)^2 + \lambda T - (\lambda T)^2 = \lambda T.$$

The Fano factor is therefore

$$\frac{\mathbb{V}(N(T))}{\mathbb{E}(N(T))} = 1.$$

2 Poisson inputs in a balanced network

Consider a neuron that receives C_E excitatory synapses and C_I inhibitory synapses. We will represent incoming synaptic currents by delta pulses: a pre-synaptic spike in neuron k at time t_0 elicits a postsynaptic current $i_k(t)$ given by

$$i_k(t) = \tau_m J_k \delta(t - t_0), \tag{1}$$

where τ_m is the membrane timescale and J_k is the strength of the 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.

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

> The total current I received by the post-synaptic neuron during a unit time is the sum of all the individual currents i_k arriving at its input synapses, which split between C_E excitatory and $C_I = \gamma C_E$ inhibitory currents. Let N_k by the random variable counting the number of spikes emitted by the neuron k during a unit time, following a Poisson process. Then
>
> $$I = \sum_{k=1}^{C_E} \tau_m J N_k - \sum_{k=1}^{\gamma C_E} \tau_m g J N_k = \tau_m J \sum_{k=1}^{C_E} N_k - \tau_m g J \sum_{k=1}^{\gamma C_E} N_k = \tau_m J \left(\sum_{k=1}^{C_E} Nk - g \sum_{k=1}^{\gamma C_E} N_k \right).$$
>
> In the Poisson process, the mean spike count for an individual neuron during a unit time is r, therefore by linearity of the expectancy
>
> $$\begin{aligned} \mathbb{E}(I) &= \tau_m J \left(\sum_{k=1}^{C_E} \mathbb{E}(N_k) - g \sum_{k=1}^{\gamma C_E} \mathbb{E}(N_k) \right) = \tau_m J \left(\sum_{k=1}^{C_E} r - g \sum_{k=1}^{\gamma C_E} r \right) \\ &= \tau_m J (C_E r - g\gamma C_E r) = \tau_m J C_E r (1 - \gamma g). \end{aligned}$$

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

> By independence of the different synapses, the variance can be obtained similarly, except that multiplying a random variable with a scalar requires to multiply the variance by the square of this scalar. In the Poisson process, the variance of the spike count for an individual neuron during a unit time is also r, and therefore
>
> $$\begin{aligned} \mathbb{V}(I) &= (\tau_m J)^2 \left(\sum_{k=1}^{C_E} \mathbb{V}(N_k) - g^2 \sum_{k=1}^{\gamma C_E} \mathbb{V}(N_k) \right) = (\tau_m J)^2 \left(\sum_{k=1}^{C_E} r + g^2 \sum_{k=1}^{\gamma C_E} r \right) \\ &= (\tau_m J)^2 (C_E r + g^2 \gamma C_E r) = (\tau_m J)^2 C_E r (1 - \gamma g^2). \end{aligned}$$

3 Noisy leaky integrate-and-fire neurons

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

$$\tau_m \frac{dV(t)}{dt} = E_l - V(t) + I(t). \tag{2}$$

In reality, neurons are connected to a multitude of other neurons through synapses: the input current $I(t)$, previously considered a constant, therefore becomes a random variable. It can be modelled as a white noise input of mean μ and variance $\tau_m \sigma^2$

$$I(t) = \mu + \sqrt{\tau_m}\sigma\eta(t),$$

where $\eta(t)$ is a white noise such that (1) $\mathbb{E}(\eta(t)) = 0$ and (2) 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 is an Ornstein-Uhlenbeck process, whose solution is

$$V(t) = V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} dW(s), \tag{3}$$

with $W(t)$ a Wiener process (also called Brownian motion), such that

- $dW(t) = \eta(t)dt$ represents the integral of the white noise over the interval dt,
- its increments over disjoint intervals are independent,
- its increments between two time points follows a normal law

$$W(t) - W(t') \sim \mathcal{N}(0, t - t'). \tag{4}$$

8. Propose a numerical implementation to simulate this stochastic system.

> To simulate such a stochastic system, one can pick a small step Δt as in the deterministic case. Increments ΔV in the membrane potential are therefore
>
> $$\Delta V(t) = \frac{E_l - V(t) + \mu}{\tau_m}\Delta t + \frac{\sigma}{\sqrt{\tau_m}}\Delta W(t), \text{ since } \eta(t)\Delta t = \Delta W(t).$$
>
> Note that $\Delta W(t)$ represents the increments of a Wiener process in a short time Δt. Using the property (4) of Wiener processes, we have that
>
> $$W(\Delta t) - W(0) \sim \mathcal{N}(0, \Delta t),$$
>
> and therefore
>
> $$\Delta W(t) \sim \mathcal{N}(0, \Delta t) = \sqrt{\Delta t}\mathcal{N}(0, 1).$$
>
> We can simulate the stochastic LIF by numerically generating a random variable that follows a normal distribution and using the Euler method, such that
>
> $$\Delta V(t) = \frac{E_l - V(t) + \mu}{\tau_m}\Delta t + \frac{\sigma\sqrt{\Delta t}}{\sqrt{\tau_m}}\mathcal{N}(0, 1).$$
>
> Finally, we have
>
> $$V(t + \Delta t) = V(t) + \Delta V(t).$$

9. Compute the mean $\mathbb{E}(V(t))$ and variance $\mathbb{V}(V(t))$.

We begin by rewriting equation (3) in terms of white noise

$$V(t) = V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \eta(s) ds.$$

Recalling that $\mathbb{E}(\eta(t)) = 0$, the expectancy of $V(t)$ is

$$\begin{aligned}
\mathbb{E}(V(t)) &= \mathbb{E}\left(V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \eta(s) ds \right) \\
&= \mathbb{E}\left(V_0 e^{-t/\tau_m} \right) + \mathbb{E}\left(\mu(1 - e^{-t/\tau_m}) \right) + \mathbb{E}\left(\frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \eta(s) ds \right) \\
&= V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \mathbb{E}\left(\eta(s)\right) ds \\
&= V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}).
\end{aligned}$$

Recalling that $\mathbb{V}(\eta(t)) = 1$ and that $\mathbb{V}(X + a) = \mathbb{V}(X)$ for a constant, the variance of $V(t)$ is

$$\begin{aligned}
\mathbb{V}(V(t)) &= \mathbb{V}\left(V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \eta(s) ds \right) \\
&= \mathbb{V}\left(\frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} \eta(s) ds \right) = \frac{\sigma^2}{\tau_m} \int_0^t \mathbb{V}\left(e^{(s-t)/\tau_m} \eta(s) \right) ds \\
&= \frac{\sigma^2}{\tau_m} \int_0^t e^{2(s-t)/\tau_m} \mathbb{V}\left(\eta(s)\right) ds = \frac{\sigma^2}{\tau_m} \int_0^t e^{2(s-t)/\tau_m} ds \\
&= \frac{\sigma^2}{\tau_m} \left[\frac{\tau_m}{2} e^{2(s-t)/\tau_m} \right]_{s=0}^{s=t} = \frac{\sigma^2}{\tau_m} \left(\frac{\tau_m}{2} - \frac{\tau_m}{2} e^{-2t/\tau_m} \right) \\
&= \frac{\sigma^2}{2} \left(1 - e^{-2t/\tau_m} \right).
\end{aligned}$$