

TD4: Balanced Networks

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TD material is available at:

https://github.com/Elieoriol/2122_UlmM2_ThNeuro/tree/master/TD4

In this tutorial, we will try to model the stochasticity neurons are subject to and its consequences on balanced networks.

1 Noisy Leaky Integrate-and-Fire neurons

Neurons are connected to a multitude of other neurons through synapses. Therefore, the current which was supposed constant in our early LIF model, is in fact stochastic in biological networks. We propose to model this stochastic current with a white noise of mean μ and variance $\tau_m \sigma^2$:

$$\tau_m \frac{dV}{dt} = E_l - V + I(t)/g_l \quad I(t) = \mu + \sigma \sqrt{\tau_m} \eta(t) \quad (1)$$

with $\eta(t)$ a reduced centered white noise defined by $\langle \eta(t) \rangle = 0$ and $\langle \eta(t) \eta(t') \rangle = \delta(t - t')$.

To simulate such a stochastic system, one can pick a small step Δt as in the deterministic case. Increments ΔV in membrane potential therefore write:

$$\Delta V = \frac{E_l - V + \mu/g_l}{\tau_m} \Delta t + \frac{\sigma/g_l}{\sqrt{\tau_m}} \Delta \eta_t \quad (2)$$

where $\Delta \eta_t = \eta(t) \Delta t$ is called a Wiener process; it represents the integral of the white noise, in other words the white noise summed over the interval Δt . An important property to remember of a Wiener process W is the following:

$$W(t) - W(s) \sim \mathcal{N}(0, t - s) \quad (t > s) \quad (3)$$

Therefore, $\Delta \eta_t \sim \sqrt{\Delta t} \mathcal{N}(0, 1)$ and:

$$\Delta V = \frac{E_l - V + \mu/g_l}{\tau_m} \Delta t + \frac{\sigma}{g_l} \sqrt{\frac{\Delta t}{\tau_m}} \mathcal{N}(0, 1) \quad (4)$$

Note: One can see why the variance was defined as $\tau_m \sigma^2$ instead of just σ^2 ; as we have seen that $\eta(t)$ has the dimension of the inverse square root of a time, σ then has the dimension of a current.

1. **num** Can you describe the effect of the white noise term, particularly in the sub-threshold regime? What is the influence of σ on the f-I curve? Show numerically that the new f-I curve is given by:

$$\nu = \frac{1}{\tau_m \sqrt{\pi} \int_{\frac{V_T - m}{\sigma_0}}^{\frac{V_T h - m}{\sigma_0}} e^{s^2} (1 + \operatorname{erf}(s)) ds} \quad (5)$$

with $m = E_l + \mu/g_l$ and $\sigma_0 = \frac{\sigma}{g_l \sqrt{\tau_m}}$. The same parameters as in the first tutorial can be used.

Note: The analytical resolution for the equations with noise are much harder than the classical ones. For more information see Dynamics of the Firing Probability of Noisy Integrate-and-Fire Neurons, N. Fourcaud and N. Brunel, 2002 Neural Computation.

The white noise term adds fluctuations to the deterministic LIF evolution of the membrane potential, such that in the sub-threshold regime, the probability to fire a spike, due to fluctuations, becomes non-zero. The larger the amplitude of the noise is (its variance), the bigger this probability becomes and the more often the neuron spikes. Increasing σ , we should get a higher average firing rate as compared to the LIF model.

2. **num** Plot the histogram of interspike intervals under different conditions of noise in the sub-threshold and supra-threshold regimes. How does it look like in the sub-threshold regime?

In the LIF model, either the neuron spikes with a fixed ISI, either it does not spike at all. In the noisy variant, the distribution of the ISI broadens and becomes Poisson-like in the sub-threshold regime.

2 Poisson Process

An experimenter can record the times at which a neuron emits spikes in response to a given stimulus. However, repeating the same stimulus, one observes that the spikes don't occur at the same time; the number of spikes is not even conserved. One way to describe these spike trains is therefore to use a random process with a given rate of spike occurrence R .

The simplest random process is the Poisson process that describes well the statistics of firing of single neurons subject to stochastic inputs as seen in the previous exercise. In the Poisson process, all events (here spikes) are independent, such that the mean number of spikes in an interval of duration T is RT , and the actual number of spikes on a given trial in one interval is independent of the number of spikes in any other interval.

1. This property of independence is enough to obtain the full probability distribution of the number of spikes in any given interval. A way to obtain it is to divide the interval into M bins of length $\Delta T \ll 1/R$ such that there is at most one spike per bin (for instance ΔT can correspond to the absolute refractory period of the neuron). What is the probability of observing n spikes in the total interval?

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. There are $\binom{M}{n} = \frac{M!}{n!(M-n)!}$ such patterns.

The probability to have n spikes therefore is binomial, $n \sim \mathcal{B}(M, R\Delta T)$:

$$\begin{aligned} P(n) &= \frac{M!}{n!(M-n)!} (R\Delta T)^n (1 - R\Delta T)^{M-n} \\ &= \frac{M!}{n!(M-n)!} \left(R\frac{T}{M}\right)^n \left(1 - R\frac{T}{M}\right)^{M-n} \\ &= \frac{(RT)^n}{n!} \frac{M(M-1)\dots(M-n+1)}{M^n} e^{(M-n)\log(1-R\frac{T}{M})} \end{aligned}$$

Now take the $\Delta T \rightarrow 0$ limit, or equivalently $M \rightarrow \infty$, to get the Poisson distribution of parameter RT :

$$P(n) \approx \frac{(RT)^n}{n!} e^{-RT}$$

Note: This is an useful limit to remember. In the limit $N \rightarrow \infty$, $p \rightarrow 0$ and $\lambda = Np$ constant, the binomial distribution $\mathcal{B}(N, p)$ tends to the Poisson distribution $\mathcal{P}(\lambda)$. Here we had $M \rightarrow \infty$, $R\Delta T \rightarrow 0$ and $MR\Delta T = RT$ constant.

2. What is the distribution of interspike intervals?

The probability that an interspike interval lasts between t and $t + \delta t$ is the product of the probability that no spikes occur during t and one spike occurs between t and $t + \delta t$:

$$\mathbb{P}(ISI \in [t, t + \delta t]) = p_{ISI}(t) \delta t = e^{-Rt} \cdot R\delta t e^{-R\delta t}$$

Taking $\delta t \rightarrow 0$, we get the probability density of interspike intervals:

$$p_{ISI}(t) = Re^{-Rt}$$

3. Let X be a random variable with probability density $P(X)$. We define:

$$G_X(\alpha) = \int e^{\alpha X} P(x) dX = \langle e^{\alpha X} \rangle_X \quad (6)$$

Show that:

$$\left. \frac{d^n G_X}{d\alpha^n} \right|_{\alpha=0} = \langle X^n \rangle \quad (7)$$

G_X is called the **moment-generating function** of the random variable X . We have a similar definition with sums instead of integrals in the case of a discrete probability distribution.

$$\begin{aligned} \frac{d^n G_X}{d\alpha^n} &= \int X^n e^{\alpha X} P(X) dX \\ \left. \frac{d^n G_X}{d\alpha^n} \right|_{\alpha=0} &= \int X^n P(X) dX = \langle X^n \rangle \end{aligned}$$

4. Use the moment-generating function to compute the mean and variance of the number of spikes generated by a homogeneous Poisson process of rate R in a window of size T . Compute the Fano factor $\Delta n^2 / \langle n \rangle$.

We first express G_n :

$$G_n(\alpha) = \sum_{n=0}^{\infty} \frac{e^{\alpha n} (RT)^n e^{-RT}}{n!} = e^{-RT} \sum_{n=0}^{\infty} \frac{(RT e^{\alpha})^n}{n!} = e^{-RT} e^{RT e^{\alpha}} = e^{RT(e^{\alpha} - 1)}$$

We now compute its first and second derivatives to get the mean and variance of the distribution:

$$\begin{aligned} \frac{dG_n}{d\alpha} &= e^{RT(e^{\alpha} - 1)} RT e^{\alpha} &\Rightarrow \quad \langle n \rangle &= \left. \frac{dG_n}{d\alpha} \right|_{\alpha=0} = RT \\ \frac{d^2 G_n}{d\alpha^2} &= RT e^{\alpha} e^{RT(e^{\alpha} - 1)} [1 + RT e^{\alpha}] &\Rightarrow \quad \langle n^2 \rangle &= \left. \frac{d^2 G_n}{d\alpha^2} \right|_{\alpha=0} = (RT)^2 + RT \\ & &\Rightarrow \quad \Delta n^2 &= \langle n^2 \rangle - \langle n \rangle^2 = RT = \langle n \rangle \end{aligned}$$

The Fano factor is as such equal to 1. When experimentally measuring the firing statistics of a neuron, computing the Fano factor is useful to tell if the behavior of the neuron is either Poissonian, sub-Poissonian or supra-Poissonian.

See *The Variable Discharge of Cortical Neurons: Implications for Connectivity, Computation, and Information Coding*, M. N. Shadlen and W. T. Newsome, 1998 *The Journal of Neuroscience*, for an example of supra-Poissonian behavior in the MT area of an awake monkey.

3 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 presynaptic spike in neuron k at time t_0 elicits a postsynaptic current $i_k(t)$ given by:

$$i_k(t) = \tau_m J_k \delta(t - t_0) \quad (8)$$

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

1. Assuming that all excitatory synapses have the same strength J and all inhibitory synapses have the same strength $-gJ$, compute the mean and the auto-correlation function of the total synaptic input $I(t)$ for Poisson presynaptic spike trains of rate r . Compare with a white noise process of mean μ and variance $\tau_m \sigma^2$.

$I(t)$ is the sum of all the $i_k(t)$ currents. All presynaptic spikes are independants (for different connections). This means that we can just sum the mean and variance of each presynaptic spike train. We note $\gamma C_E = C_I$.

$$\langle I(t) \rangle = \langle \sum_k i_k(t) \rangle = \sum_k \langle i_k(t) \rangle = \tau_m r \sum_k J_k = \tau_m r J C_E (1 - g\gamma)$$

We do the same computations for the variance (using the variance of a Poisson process):

$$\Delta I(t)^2 = \sum_k \Delta i_k(t)^2 = \sum_{exc.} \Delta i_k(t)^2 + \sum_{inh.} \Delta i_k(t)^2 = C_E \tau_m^2 J^2 r (1 + g^2 \gamma)$$

The total input to the neuron is a large sum of identically distributed independent excitatory and inhibitory Poisson inputs. The central limit theorem applies such that the total input is equivalent to a white noise process of mean and variance the ones we just computed.

2. The membrane potential dynamics of an integrate-and-fire neuron is given by:

$$\tau_m \frac{dV}{dt} = -V + I(t) \quad (9)$$

where τ_m is the membrane time constant and $I(t)$ is an arbitrary input current.

Not considering the threshold, compute the mean $\langle V(t) \rangle$ and auto-correlation $\langle V(t)V(t+\tau) \rangle - \langle V(t) \rangle \langle V(t+\tau) \rangle$ for a white noise input $I(t) = \mu + \sqrt{\tau_m} \sigma \cdot \eta(t)$, with $\langle \eta(t) \rangle = 0$ and $\langle \eta(t)\eta(t') \rangle = \delta(t - t')$. $\langle \cdot \rangle$ indicates here an average across the realizations of the white noise.

Hint: Consider the function $f_t = V(t)e^{t/\tau_m}$ and apply Itô's lemma to it. This is the standard way to get the properties of the Ornstein-Uhlenbeck process that we are in fact studying here. We recall the Itô formula when working with 1-D stochastic variables X_t subject to a white noise of variance σ_t^2 and $f(X_t, t)$ a sufficiently regular function:

$$d[f(X_t, t)] = \frac{\partial f}{\partial t}(X_t, t) dt + \frac{\partial f}{\partial x}(X_t, t) dX_t + \frac{1}{2} \frac{\partial^2 f}{\partial x^2}(X_t, t) \sigma_t^2 dt \quad (10)$$

We apply Itô's lemma to the function $f_t = V(t)e^{t/\tau_m}$, for which the second derivative with respect to V is zero. Hence:

$$df_t = \frac{V(t)}{\tau_m} e^{t/\tau_m} dt + e^{t/\tau_m} dV$$

From (9) with $I(t)$ a white noise of mean μ and variance $\tau_m \sigma^2$ (such that we can write $I(t) dt = \mu dt + \sqrt{\tau_m} \sigma d\eta_t$ with $d\eta_t = \eta(t) dt$ the reduced Wiener process more often denoted dW_t), this equation can be rewritten:

$$df_t = \frac{V(t)}{\tau_m} e^{t/\tau_m} dt + e^{t/\tau_m} \left(-\frac{V(t)}{\tau_m} dt + \frac{\mu}{\tau_m} dt + \frac{\sigma}{\sqrt{\tau_m}} d\eta_t \right) = e^{t/\tau_m} \left(\frac{\mu}{\tau_m} dt + \frac{\sigma}{\sqrt{\tau_m}} d\eta_t \right)$$

We integrate from 0 to t :

$$V(t)e^{t/\tau_m} = V_0 + \frac{\mu}{\tau_m} \int_0^t e^{s/\tau_m} ds + \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{s/\tau_m} d\eta_s$$

Therefore:

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

We take the expectation over realizations of the noise:

$$\langle V(t) \rangle = V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m})$$

We compute the auto-correlation the same way:

$$\begin{aligned} C(\tau) &= \langle (V_t - \langle V_t \rangle)(V_{t+\tau} - \langle V_{t+\tau} \rangle) \rangle \\ &= \left\langle \frac{\sigma}{\sqrt{\tau_m}} \int_0^t e^{(s-t)/\tau_m} d\eta_s \cdot \frac{\sigma}{\sqrt{\tau_m}} \int_0^{t+\tau} e^{(s-t-\tau)/\tau_m} d\eta_s \right\rangle \\ &= \frac{\sigma^2}{\tau_m} e^{-(2t+\tau)/\tau_m} \left\langle \int_0^t e^{s/\tau_m} d\eta_s \int_0^{t+\tau} e^{s/\tau_m} d\eta_s \right\rangle \\ &= \frac{\sigma^2}{\tau_m} e^{-(2t+\tau)/\tau_m} \int_0^t \int_0^{t+\tau} e^{s/\tau_m} e^{s'/\tau_m} \langle d\eta_s d\eta_{s'} \rangle \\ &= \frac{\sigma^2}{\tau_m} e^{-(2t+\tau)/\tau_m} \int_0^t \int_0^{t+\tau} e^{s/\tau_m} e^{s'/\tau_m} \delta(s - s') ds ds' \\ &= \frac{\sigma^2}{\tau_m} e^{-(2t+\tau)/\tau_m} \int_0^t e^{2s/\tau_m} ds \\ &= \frac{\sigma^2}{2} e^{-(2t+\tau)/\tau_m} (e^{2t/\tau_m} - 1) = \frac{\sigma^2}{2} e^{-\tau/\tau_m} (1 - e^{-2t/\tau_m}) \end{aligned}$$

3. Suppose the integrate-and-fire neuron receives C_E excitatory synapses and C_I inhibitory synapse of respective strengths J and $-gJ$. What are the mean and auto-correlation function of the membrane-potential dynamics (forgetting the threshold) if presynaptic spike trains are Poisson with rate r ?

We use the central limit theorem such that the sum of Poisson processes is equivalent to a white noise process with the mean and variance computed in the first question. We insert their expressions in the results of the previous question.