TD 5 – Balanced Networks

1 Poissonian spike trains

1.1 Poisson Process

① *Interpretation of RT*

This product represents the mean number of spikes in an interval of duration T.

Indeed, let N be the random variable of 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 the value 0 otherwise (because by assumption, at most 1 spike can occur during a elementary time bin). All those Bernoulli variables have the same expectancy, which is proportional to the rate R and the length of the elementary time interval ΔT.

By linearity of the mean :

$$\mathbb{E}(N) = \mathbb{E}\left(\sum_{i=1}^{M} N_i\right) = \sum_{i=1}^{M} \underbrace{\mathbb{E}(N_i)}_{R\Delta T} = M \times R\Delta T = RT$$

② *Probability of observing n spikes*

Since the number of spikes occurring in any bin is independent of the number of spikes occurring in the other bins, the probability of observing n spikes follows a Binomial law $\mathcal{B}(M, R\Delta T)$, which is the probability distribution of the counts of successes during a series of independent Bernoulli tests. Indeed :

- The total time interval is divided in M time bins, which correspond to the number of independent Bernoulli tests.
- The probability that one spike occurs during one time bin is $R\Delta T$, which corresponds to the probability of success in one Bernoulli test. The probability of no spike occurs is that of the opposite event : $1 - R\Delta T$.
- The probability of one specific pattern containing n spikes (i.e. a particular ordering of the spikes' occurrences) is the product of the probability of n successes and $M - n$ failures.
- The number of pattern containing n spikes (i.e. the number of orderings of n successes in M tests) is $\binom{M}{n} = \frac{M!}{n!(M-n)!}$, all with the same probability (and disjoint events).

Conclusion The probability to observe n spikes during a time T follows :

$$\forall\, n \in [\![0, N]\!], \quad \mathbb{P}_T(n) = \frac{M!}{n!(M-n)!}(R\Delta T)^n (1 - R\Delta T)^{M-n}$$

③ *Spike count Poisson distribution*

The Poisson distribution is obtained by taking the limit $\Delta T \to 0$, equivalently $M \to +\infty$. Let us keep only one variable which tends towards a limit, by expressing ΔT as a function of M :

$$\begin{aligned}
\mathbb{P}_T(n) &= \frac{M!}{n!(M-n)!}\left(R\frac{T}{M}\right)^n \left(1 - R\frac{T}{M}\right)^{M-n} \\
&= \frac{M(M-1)...(M-n+1)}{n!}\frac{(RT)^n}{M^n}\left(1 - \frac{RT}{M}\right)^{M-n} \\
&= \frac{(RT)^n}{n!}\frac{M(M-1)...(M-n+1)}{M^n}\, e^{(M-n)\ln\left(1-\frac{RT}{M}\right)} \\
&\sim \frac{(RT)^n}{n!}\frac{MM...M}{M^n}\, e^{(M-n)\left(-\frac{RT}{M}\right)} \\
&= \frac{(RT)^n}{n!} e^{-RT + \frac{nRT}{M}} \\
&\xrightarrow[M\to+\infty]{} \frac{(RT)^n}{n!} e^{-RT}
\end{aligned}$$

Poisson distribution

The Poisson distribution $\mathcal{P}(\lambda)$ can be seen as the limit of the binomial distribution $\mathcal{B}(N,p)$ for $N \to \infty$, $p \to 0$ and $\lambda = Np$ constant.
Here : $M \to \infty$, $R\Delta T \to 0$ and $MR\Delta T = RT$ constant.

Continuous random variables - Probability density

⚠ Contrary to discrete variables, a continuous random variable $X : \Omega \mapsto \mathbb{R}$ can take on values within an uncountable set. Therefore, the probability that it takes on an *exact* value is null.

$$\forall x \in X(\Omega),\ \mathbb{P}(X = x) = 0$$

Non-vanishing probabilities can only be ascribed to *intervals*.

$$\forall x, y \in X(\Omega),\ \mathbb{P}(X \in [x, y]) \geq 0$$

Therefore, the probability distribution associated with a continuous random variable is described by the **probability density function** p_X, which gives the *local* probability that the value of the random variable falls *within a range of values* :

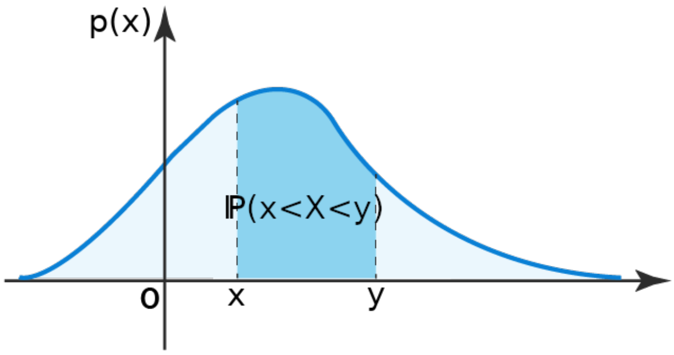
$$\lim_{dx \to 0} \mathbb{P}(X \in [x, x + \mathrm{d}x]) = p_X(x)dx$$

The probability that the random variable falls into an interval is obtained by *integration* :

$$\forall x, y \in X(\Omega),\ \mathbb{P}(X \in [x, y]) = \int_x^y p_X(x)\,\mathrm{d}x$$

Determining the probability density of a continuous random variable

It can be done by expressing the probability that the random variable falls within an interval $[x, x + \mathrm{d}x]$, and then taking the limit $\mathrm{d}x \to 0$ to find the limit probability $p_X(x)$.



④ *Distribution of inter-spike intervals*

The goal is to express the probability that an inter-spike interval lasts between t and $t + \delta t$:

$$\forall t \geq 0,\ \lim_{\delta t \to 0} \mathbb{P}(ISI \in [t, t + \delta t]) = p_{ISI}(t)\,\delta t$$

The event "$ISI \in [t, t + \delta t]$" requires that :

- No spikes occur during t, which has a probability given by a Poisson distribution :

$$\mathbb{P}_t(0) = \frac{(Rt)^0}{0!} e^{-Rt} = e^{-Rt}$$

- One spike occurs between t and $t + \delta t$, i.e. during a duration δt, which has a probability :

$$\mathbb{P}_{\delta t}(1) = \frac{(R\delta t)^1}{1!} e^{-R\delta t} = R\ \delta t\ e^{-R\delta t}$$

Those events are independent, because the time intervals $[0, t[$ and $[t, t + \delta t[$ are disjoint (assumption of the Poisson distribution). Therefore, the probability for the inter-spike-interval is obtained by the product :

$$\lim_{\delta t \to 0} \mathbb{P}(ISI \in [t, t + \delta t]) = p_{ISI}(t) \cancel{\delta t} = \lim_{\delta t \to 0} e^{-Rt} R \cancel{\delta t} e^{-R\delta t}$$

Taking the limit $\delta t \to 0$ yields the probability density of inter-spike intervals :

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

1.2 Mean and Variance

5 *Interpretation of the moment generating function*

With the *transfer theorem*, the expression can be seen as the mean of the random variable $Y = e^{\alpha X}$:

$$G_X(\alpha) = \int_\Omega e^{\alpha x} p_X(x) \, \mathrm{d}x = \mathbb{E}_X(e^{\alpha X})$$

6 *Derivation of the moment generating function*

- For $n = 0$, evaluating directly the moment generating function in $\alpha = 0$ yields 1 :

$$G_X(0) = \int_\Omega e^0 p_X(x) \, \mathrm{d}x = \int_\Omega p_X(x) \, \mathrm{d}x = 1$$

- For $n = 1$, evaluating the first derivative of moment generating function in $\alpha = 0$ yields the mean of the random variable X :

$$\begin{aligned} \frac{\mathrm{d}G_X}{\mathrm{d}\alpha} &= \frac{\mathrm{d}}{\mathrm{d}\alpha} \int_\Omega e^{\alpha x} p_X(x) \, \mathrm{d}x = \int_\Omega \frac{\mathrm{d}}{\mathrm{d}\alpha} e^{\alpha x} p_X(x) \, \mathrm{d}x = \int_\Omega x e^{\alpha x} p_X(x) \, \mathrm{d}x = \mathbb{E}(X e^{\alpha X}) \\ \left. \frac{\mathrm{d}^n G_X}{\mathrm{d}\alpha^n} \right|_{\alpha=0} &= \int_\Omega x p_X(x) \, \mathrm{d}x = \mathbb{E}(X) \end{aligned}$$

- For $n \in \mathbb{N}$, generalizing this computation by recurrence gives (thanks to the property of the exponential) :

$$\begin{aligned} \frac{\mathrm{d}^n G_X}{\mathrm{d}\alpha^n} &= \int_\Omega x^n e^{\alpha x} p_X(x) \, \mathrm{d}x = \mathbb{E}(X^n e^{\alpha X}) \\ \left. \frac{\mathrm{d}^n G_X}{\mathrm{d}\alpha^n} \right|_{\alpha=0} &= \int_\Omega x^n p_X(x) \, \mathrm{d}x = \mathbb{E}(X^n) \end{aligned}$$

7 *Generalization to discrete random variables*

For a discrete random variable X, the moment generating function G_X can be defined by replacing integrals by sums :

$$G_X(\alpha) = \sum_{x \in X(\Omega)} e^{\alpha x} \mathbb{P}(X = x) \tag{1}$$

8 *Moment generating function for a Poisson process*

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

9 *Mean and variance of the Poisson process*

- The mean can be computed with the first derivative of the moment generating function evaluated in $\alpha = 0$:

$$\begin{aligned} \frac{\mathrm{d}G_N}{\mathrm{d}\alpha} &= \frac{\mathrm{d}}{\mathrm{d}\alpha} e^{RT(e^\alpha - 1)} = e^{RT(e^\alpha - 1)} RTe^\alpha \\ \mathbb{E}(N) = \left. \frac{\mathrm{d}G_N}{\mathrm{d}\alpha} \right|_{\alpha=0} &= e^{RT(1-1)} RT \times 1 = RT \end{aligned}$$

- The variance can be computed similarly with the second derivative :

$$\frac{\mathrm{d}^2 G_N}{\mathrm{d}\alpha^2} = \frac{\mathrm{d}}{\mathrm{d}\alpha} \underbrace{e^{RT(e^\alpha - 1)}}_{u} \underbrace{RTe^\alpha}_{v} = \underbrace{e^{RT(e^\alpha-1)} RTe^\alpha}_{u'} \underbrace{RTe^\alpha}_{v} + \underbrace{e^{RT(e^\alpha-1)} RTe^\alpha}_{u} \underbrace{RTe^\alpha}_{v'} = RTe^\alpha e^{RT(e^\alpha-1)} (1 + RTe^\alpha)$$

$$\mathbb{E}(N^2) = \left.\frac{\mathrm{d}G_N}{\mathrm{d}\alpha}\right|_{\alpha=0} = RT \times 1 \times e^{RT(1-1)}(1 + RT \times 1) = RT(1+RT) = RT + (RT)^2$$

Using Koenig-Huygens formula :

$$\mathbb{V}(N) = \mathbb{E}(N^2) - \mathbb{E}(N)^2 = RT$$

10 *Fano factor*

For the Poisson process, the mean and the variance are equal : $\dfrac{\mathbb{V}(N)}{\mathbb{E}(N)} = 1$

2 Poisson inputs in a balanced network

(11) *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 :

$$I = \sum_{k=1}^{C_E} \tau_m J N_k - \sum_{k=1}^{\gamma C_E} \tau_m g J N_k = \tau_m J \sum_{k=1}^{C_E} N_k - \tau_m g J \sum_{k=1}^{\gamma C_E} N_k = \tau_m J \left(\sum_{k=1}^{C_E} N_k - g \sum_{k=1}^{\gamma C_E} N_k \right)$$

• By linearity, the mean of the sum is the sum of the means. In the Poisson process, the mean spike count for an individual neuron during a unit time is r :

$$\mathbb{E}(I) = \tau_m J \left(\sum_{k=1}^{C_E} \mathbb{E}(N_k) - g \sum_{k=1}^{\gamma C_E} \mathbb{E}(N_k) \right) = \tau_m J \left(\sum_{k=1}^{C_E} r - g \sum_{k=1}^{\gamma C_E} r \right) = \tau_m J \left(C_E r - g \gamma C_E r \right) = \tau_m J C_E r (1 - \gamma g)$$

(12) *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 :

$$\mathbb{V}(I) = (\tau_m J)^2 \left(\sum_{k=1}^{C_E} \mathbb{V}(N_k) + g^2 \sum_{k=1}^{\gamma C_E} \mathbb{V}(N_k) \right) = (\tau_m J)^2 \left(\sum_{k=1}^{C_E} r + g^2 \sum_{k=1}^{\gamma C_E} r \right) = (\tau_m J)^2 \left(C_E r + g^2 \gamma C_E r \right) = (\tau_m J)^2 C_E r (1 - \gamma g^2)$$

(13) *Comparison with a white noise process of mean μ and variance $\tau_m \sigma^2$*

The total input to a 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, whose mean and variance are the ones we just computed.

3 Stochastic integration of synaptic inputs

14 *Stochastic evolution of the membrane potential*

The function $f(V_t, t) = V(t)e^{t/\tau_m}$ is a function of two variables, V and t. Thus, its differential is the *plane* of best approximation :

$$\begin{aligned} \mathrm{d}f &= \frac{\partial f}{\partial V}\,\mathrm{d}V + \frac{\partial f}{\partial t}\,\mathrm{d}t \\ &= e^{t/\tau_m}\,\mathrm{d}V + \frac{V}{\tau_m}e^{t/\tau_m}\,\mathrm{d}t \end{aligned}$$

The differential $\mathrm{d}V$ rewrites in terms of $\mathrm{d}t$ by the differential equation :

$$\tau_m \frac{\mathrm{d}V}{\mathrm{d}t} = -V + I(t) \implies \mathrm{d}V = \frac{1}{\tau_m}(-V + I)\,\mathrm{d}t$$

Thus, a simplification occurs (which is the interest of the method of the variation of the constants) :

$$\begin{aligned} \mathrm{d}f &= e^{t/\tau_m}\left(\frac{1}{\tau_m}(-V + I)\,\mathrm{d}t\right) + \frac{V}{\tau_m}e^{t/\tau_m}\,\mathrm{d}t \\ &= \cancel{-\frac{1}{\tau_m}e^{t/\tau_m}V\,\mathrm{d}t} + \frac{1}{\tau_m}e^{t/\tau_m}I\,\mathrm{d}t + \cancel{\frac{1}{\tau_m}e^{t/\tau_m}V\,\mathrm{d}t} \end{aligned}$$

Replacing I by its expression :

$$\begin{aligned} \mathrm{d}f &= \frac{1}{\tau_m}e^{t/\tau_m}\left(\mu + \sqrt{\tau_m}\sigma \cdot \eta(t)\right)\mathrm{d}t \\ &= \frac{1}{\tau_m}e^{t/\tau_m}\mu\,\mathrm{d}t + \frac{1}{\tau_m}e^{t/\tau_m}\sqrt{\tau_m}\sigma \cdot \underbrace{\eta(t)\,\mathrm{d}t}_{\mathrm{d}\omega_t} \\ &= \frac{\mu}{\tau_m}e^{t/\tau_m}\,\mathrm{d}t + \frac{\sigma}{\sqrt{\tau_m}}e^{t/\tau_m}\,\mathrm{d}\omega_t \end{aligned}$$

Now, the expression of $\mathrm{d}f$ can be integrated with respects to time, until time t :

$$\begin{aligned} \text{On the one hand,} \quad \int_0^t \mathrm{d}f &= f(t) - f(0) = V(t)e^{t/\tau_m} - V_0 \\ \text{On the other hand,} \quad \int_0^t \mathrm{d}f &= \int_0^t \frac{\mu}{\tau_m}e^{s/\tau_m}\,\mathrm{d}t + \int_0^t \frac{\sigma}{\sqrt{\tau_m}}e^{s/\tau_m}\,\mathrm{d}\omega_s \\ &= \frac{\mu}{\cancel{\tau_m}}\cancel{\tau_m}\left(e^{t/\tau_m} - 1\right) + \frac{\sigma}{\sqrt{\tau_m}}\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s \end{aligned}$$

Equating both equations leads to express $V(t)$:

$$\begin{aligned} V(t)e^{t/\tau_m} - V_0 &= \mu\left(e^{t/\tau_m} - 1\right) + \frac{\sigma}{\sqrt{\tau_m}}\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s \\ V(t) &= V_0 e^{-t/\tau_m} + \mu\left(e^{t/\tau_m} - 1\right)e^{-t/\tau_m} + \frac{\sigma}{\sqrt{\tau_m}}e^{-t/\tau_m}\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s \\ V(t) &= V_0 e^{-t/\tau_m} + \mu(1 - e^{-t/\tau_m}) + \frac{\sigma}{\sqrt{\tau_m}}\int_0^t e^{(s-t)/\tau_m}\,\mathrm{d}\omega_s \end{aligned}$$

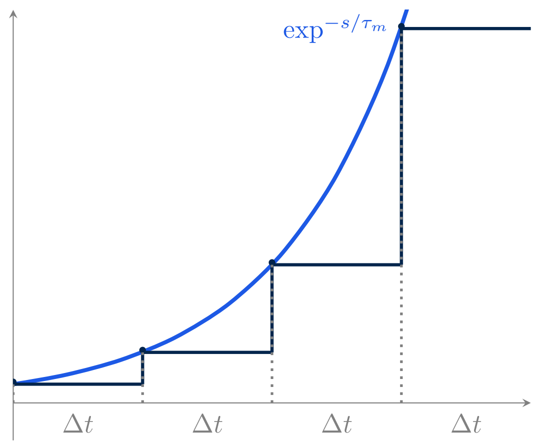
15 *Expectancy of the membrane potential over trials*

The membrane potential is composed of one deterministic term and one stochastic term. By linearity, the expectancy *over realizations of the noise* is given by :

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

The expectancy of the second term can be obtained by approximating the function $s \mapsto e^{s/\tau_m}$ as a limit of step functions on the interval $[0,t]$, so as to apply the linearity of the expectancy combined with the Wiener's property. To do so, the interval $[0,t]$ is divided in N sub-intervals of length Δt, such that the linear approximation is :

$$\forall s \in [0,t],\ e^{s/\tau_m} \approx \sum_{k=0}^{N} e^{k\Delta t/\tau_m} \mathbb{1}_{s\in[k\Delta t,(k+1)\Delta t[}$$



Then, the integral and the sum can be inverted, such that integrals are computed over segments :

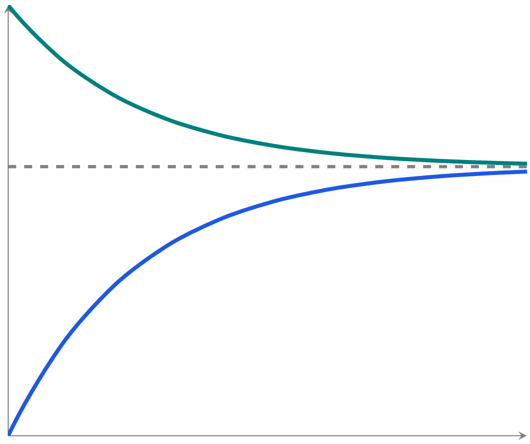
$$\begin{aligned}
\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s &\approx \int_0^t \sum_{k=0}^{N} e^{k\Delta t/\tau_m} \mathbb{1}_{s\in[k\Delta t,(k+1)\Delta t[}\,\mathrm{d}\omega_s \\
&= \sum_{k=0}^{N} \int_0^t e^{k\Delta t/\tau_m} \mathbb{1}_{s\in[k\Delta t,(k+1)\Delta t[}\,\mathrm{d}\omega_s \\
&= \sum_{k=0}^{N} \int_{k\Delta t}^{(k+1)\Delta t} e^{k\Delta t/\tau_m}\,\mathrm{d}\omega_s \\
&= \sum_{k=0}^{N} e^{k\Delta t/\tau_m} \int_{k\Delta t}^{(k+1)\Delta t} \mathrm{d}\omega_s \\
&= \sum_{k=0}^{N} e^{k\Delta t/\tau_m} \underbrace{(\omega_{(k+1)\Delta t} - \omega_{k\Delta t})}_{\sim\mathcal{N}(0,\Delta t)}
\end{aligned}$$

The expectancy is obtained by linearity, and the only random variable in the formula is the term $\omega_{(k+1)\Delta t} - \omega_{k\Delta t}$. It follows a Wiener process, which is a normal law $\mathcal{N}(0,\Delta t)$, therefore :

$$\begin{aligned}
\mathbb{E}\left(\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s\right) &\approx \mathbb{E}\left(\sum_{k=0}^{N} e^{k\Delta t/\tau_m}(\omega_{(k+1)\Delta t} - \omega_{k\Delta t})\right) \\
&= \sum_{k=0}^{N} e^{k\Delta t/\tau_m} \underbrace{\mathbb{E}\left(\omega_{(k+1)\Delta t} - \omega_{k\Delta t}\right)}_{0} \\
&= 0
\end{aligned}$$

The approximation becomes an equality when taking the limit $\Delta t \to 0$ (i.e. $N \to +\infty$). Therefore, the expectancy of the membrane potential reduces to its deterministic term :

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



16 *Variance of the membrane potential over trials*

- Applying the same reasoning as above (question 15), the function f can be approximated by a step function :

$$\forall s \in [0,t],\ f(s) \approx \sum_{k=0}^{N} f(k\Delta t)\mathbb{1}_{s\in[k\Delta t,(k+1)\Delta t[}$$

Integrating leads to :

$$\int_0^t f(s)\,\mathrm{d}\omega_s \approx \sum_{k=0}^{N} f(k\Delta t)(\omega_{(k+1)\Delta t} - \omega_{k\Delta t})$$

By independence of the random variables $(\omega_{(k+1)\Delta t} - \omega_{k\Delta t})$ for different values of k (disjoint intervals), the variance of the sum is the sum of the variances :

$$\begin{aligned}
V\left(\int_0^t f(s)\,\mathrm{d}\omega_s\right) &\approx \mathbb{V}\left(\sum_{k=0}^{N} f(k\Delta t)(\omega_{(k+1)\Delta t} - \omega_{k\Delta t})\right)\\
&= \sum_{k=0}^{N} f(k\Delta t)^2\,\mathbb{V}\left(\omega_{(k+1)\Delta t} - \omega_{k\Delta t}\right)\\
&= \sum_{k=0}^{N} f(k\Delta t)^2\Delta t\\
&\xrightarrow[N\to+\infty]{} \int_0^t f(s)^2\,\mathrm{d}s
\end{aligned}$$

- Application to compute the variance of $V(t)$:

The first two terms are deterministic, so their variance is null. The variance of the third term is obtained by applying the formula above :

$$\begin{aligned}
\mathbb{V}(V(t)) &= \mathbb{V}\left(V_0 e^{-t/\tau_m}) + \mu(1-e^{-t/\tau_m})\right) + \mathbb{V}\left(\frac{\sigma}{\sqrt{\tau_m}}\int_0^t e^{(s-t)/\tau_m}\,\mathrm{d}\omega_s\right)\\
&= 0 + \frac{\sigma^2}{\tau_m}\left(e^{-t/\tau_m}\right)^2\mathbb{V}\left(\int_0^t e^{s/\tau_m}\,\mathrm{d}\omega_s\right)\\
&= \frac{\sigma^2}{\tau_m}e^{-2t/\tau_m}\int_0^t e^{2s/\tau_m}\,\mathrm{d}s\\
&= \frac{\sigma^2}{\cancel{\tau_m}}e^{-2t/\tau_m}\frac{\cancel{\tau_m}}{2}(e^{2t/\tau_m}-1)\\
&= \frac{\sigma^2}{2}(1-e^{-2t/\tau_m})
\end{aligned}$$