Exercise 1: Poisson neuron

1.1 We present two methods to solve this problem.

**Method 1:** The probability that the neuron does not fire during a small time interval $\Delta t$ is given by $S(\Delta t) = 1 - \rho \Delta t$. Since a Poisson process is independent of its past history, the probability that the neuron does not fire during $n$ such time intervals is the product of the probabilities for each time intervals, i.e.,

$$S(n\Delta t) = (1 - \rho \Delta t)^n. \quad (1)$$

Although this expression is correct for a discrete process, it has the drawback of being dependent on the discretization time step $\Delta t$. Thus it is desirable to take the limit as $\Delta t \to 0$. This can be done by setting $t = n\Delta t$ and taking the limit as $n \to \infty$ with $t$ fixed. Remembering the formula $\lim_{n \to \infty} (1 + \frac{a}{n})^n = e^a$, one concludes that

$$S(t) = \lim_{n \to \infty} \left(1 - \frac{\rho t}{n}\right)^n = e^{-\rho t}. \quad (2)$$

Alternatively, one can use the identity

$$(1 - \rho \Delta t)^n = \exp \left[ \sum_{i=1}^{n} \log (1 - \rho \Delta t) \right], \quad (3)$$

and expand the logarithm as $\log(1 + x) = x + \ldots$, which yields

$$S(t) = \lim_{n \to \infty} \exp \left[- \sum_{i=1}^{n} \rho \Delta t \right] \to \exp \left[- \int_{0}^{t} \rho dt \right] = \exp [-\rho t]. \quad (4)$$

The latter calculation has the advantage that it also works for time dependent rates $\rho = \rho(t)$, which is less obvious from Eq.(2).

**Method 2** A different way to obtain this result is to consider the variation of $S(t)$ during a small time interval $\Delta t$. Because of independence, we have

$$S(t + \Delta t) = S(t)S(\Delta t), \quad (5)$$

where $S(\Delta t) = 1 - \rho \Delta t$ by assumption. Rearranging, we obtain

$$\frac{S(t + \Delta t) - S(t)}{\Delta t} = -\rho S(t), \quad (6)$$

which becomes as $\Delta t \to 0$

$$\frac{d}{dt} S(t) = -\rho S(t), \quad (7)$$

the solution of which is indeed $S(t) = e^{-\rho t}$.

1.2 Again, due to independence, we have

$$P(t, t + \Delta t) \equiv P(\text{fire for the first time in } (t, t + \Delta t)) = P(\text{not fire until } t) \times P(\text{fire in } (t, t + \Delta t)) = e^{-\rho t} \times \rho \Delta t. \quad (8)$$
As $\Delta t \rightarrow 0$, this probability vanishes; however, the probability density, defined by $p(t)dt = P(t, t + dt)$, has finite value,

$$p(\text{fire at } t) = \lim_{\Delta t \rightarrow 0} \frac{P(t, t + \Delta t)}{\Delta t} = \rho e^{-\rho t}. \quad (9)$$

1.3

(i) The interval distribution was calculated earlier, $P(t) = \rho e^{-\rho t}$.

(ii) The probability to observe an interspike interval smaller than 20 ms is

$$P(\text{ISI} < 20 \text{ms}) = \int_{0}^{20 \text{ms}} \rho e^{-\rho s} ds = \left[ -e^{-\rho s} \right]_{s=0}^{20 \text{ms}} = 1 - e^{-20\rho}. \quad (10)$$

Due to independence, the probability of getting a burst of two such intervals is just the square of this probability. Thus, for $\rho = 2 \text{Hz} = 2 \cdot 10^{-3} \text{ms}^{-1}$, we get $p_{\text{burst}} \approx 0.0015$, whereas for $\rho = 20 \text{Hz}$, $p_{\text{burst}} \approx 0.109$.

(iii) Given knowledge of the interspike interval distribution and survivor function as a function of the firing rate $\rho$, the observer can determine the strength of the input with fair confidence after observing a few spikes.

1.4 Let us label the spike trains corresponding to each neuron $S_1$ and $S_2$. The percentage is the number of spikes in $S_1$ coincident with a spike in $S_2$, $N_{\text{coinc}}$, divided by the total number of spikes ($N$) in spike train one:

$$P = \frac{\langle N_{\text{coinc}} \rangle}{N}. \quad (11)$$

And $\langle N_{\text{coinc}} \rangle$ is just the probability to observe a spike in $S_2$ within a small observation window size $2\Delta = 4 \text{ms}$, times the number of spikes in $S_1$:

$$P \approx \frac{2\Delta \rho_0 N}{N} = 2\rho_0 \Delta = 8\%. \quad (12)$$

Here, we had to assume that the observation windows do not overlap, i. e. $\Delta \ll \rho_0$.

**Exercise 2: Stochastic spike arrival**

We first need to solve the linear equation

$$\tau \frac{du}{dt} = - (u - u_{\text{rest}}) + RI(t). \quad (13)$$

We know (c.f. exercise set 1) that the solution is given by

$$u(t) = u_{\text{rest}} + \frac{R}{\tau} \int_{t'}^{t} e^{-(t-t')/\tau} I(t') dt'. \quad (14)$$

Let us first solve the general problem with arbitrary presynaptic current shape $\alpha(t - t')$. The case of problem 2.1 then corresponds to the choice $\alpha(t - t') = q\delta(t - t')$.

So for $I(t) = \sum_f \alpha(t - t_f)$ we have:

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} e^{-(t-t')/\tau} \sum_f \alpha(t' - t_f) dt'. \quad (15)$$

Writing $\alpha(t' - t_f) = \int_{-\infty}^{\infty} \alpha(s) \delta(s - (t' - t_f)) ds$, we obtain

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \sum_f \delta(s - (t' - t_f)). \quad (16)$$
Taking the average over all possible spike trains,
\[
\langle u(t) \rangle = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \left\{ \sum_{f} \delta(s-(t'-t')) \right\}
\]
because all the deterministic quantities can be pulled out of the average.

Now since \( \langle \sum_{f} \delta(s-(t'-t')) \rangle = \nu \),
\[
\langle u(t) \rangle = u_{\text{rest}} + R \nu \int_{-\infty}^{\infty} \alpha(s) ds.
\]

2.1 With \( \alpha(t-t') = q \delta(t-t') \), we obtain:
\[
\langle u(t) \rangle = u_{\text{rest}} + R\nu q.
\]

2.2 The general solution is given by Eq. (18).

Exercise 3: Renewal process

Given an output spike at \( t = \hat{t} \), the survivor function \( S(t-\hat{t}) \) is given by
\[
S(t-\hat{t}) = \exp \left[ - \int_{\hat{t}}^{t} \rho(t'|\hat{t}) dt' \right] = \exp \left[ - \int_{\hat{t}}^{t} \rho(t'-\hat{t}) dt' \right] = \exp \left[ - \int_{0}^{t-\hat{t}} \rho(s) ds \right].
\]

where we made the variable change \( s = t' - \hat{t} \).

The interspike interval distribution is \( P(t-\hat{t}) = \rho(t-\hat{t})S(t-\hat{t}) \). Thus we only need to calculate the integral of the hazard function \( \rho(t-\hat{t}) \). This gives

\[
\int_{0}^{t-\hat{t}} \rho(s) ds = \begin{cases} 
\int_{0}^{\lambda_{\text{abs}}} \rho(s) ds = 0 & \text{for } s < \lambda_{\text{abs}} \\
\int_{0}^{\lambda_{\text{abs}}} \rho(s) ds + \int_{\lambda_{\text{abs}}}^{\lambda_{\text{abs}}+2} \rho(s) ds = \frac{\rho_0}{4} (t-\hat{t}-\lambda_{\text{abs}})^2 & \text{for } \lambda_{\text{abs}} < s < \lambda_{\text{abs}} + 2 \\
\int_{0}^{\lambda_{\text{abs}}} \rho(s) ds + \int_{\lambda_{\text{abs}}}^{\lambda_{\text{abs}}+2} \rho(s) ds + \int_{\lambda_{\text{abs}}+2}^{t-\hat{t}} \rho(s) ds = \rho_0 (-1 + t - \hat{t} - \lambda_{\text{abs}}) & \text{for } \lambda_{\text{abs}} + 2 < s .
\end{cases}
\]

\(^1\)this can be seen by remarking that \( \int \delta(s) ds = 1 \) so that \( \frac{1}{T} \sum_{f} \int_{0}^{T} \delta(s-t') ds = \text{# of spikes in } (0,T) = \nu. \)
Exercise 4: Homework

4.1 We take the limit and use Stirling’s approximation and \( \lim_{n \to \infty} (1 - x/n)^n = e^{-x} \):

\[
P_k(T) = \lim_{N \to \infty} \frac{N!}{k!(N-k)!} \left( 1 - \frac{\nu T}{N} \right)^{N-k} \left( \frac{\nu T}{N} \right)^k
\]

(20)

\[
= \frac{(\nu T)^k}{k!} \lim_{N \to \infty} \frac{N!}{(N-k)!} \frac{e^{-N}}{e^{-k}} \left( 1 - \frac{\nu T}{N} \right)^{N-k} \left( \frac{1}{N} \right)^k
\]

(21)

\[
= \frac{(\nu T)^k e^{-k}}{k!} \lim_{N \to \infty} \frac{1}{(N-k)!} \frac{N-N-k}{N-N-k} \left( \frac{\nu T}{N} \right)^{N-k}
\]

(22)

\[
= \frac{(\nu T)^k e^{-k}}{k!} e^{-\nu T}
\]

(23)

\[
= \frac{(\nu T)^k}{k!} e^{-\nu T}
\]

(24)

The expected number of spikes in an interval of duration \( T \) can be calculated from the definition of expectation,

\[
(k) = \sum_{k=0}^{\infty} k P_k(T)
\]

(25)

\[
= \sum_{k=0}^{\infty} \frac{(\nu T)^k}{(k)!} e^{-\nu T}
\]

(26)

\[
= e^{-\nu T} \sum_{k=1}^{\infty} \frac{(\nu T)^k}{(k-1)!}
\]

(27)

\[
= e^{-\nu T} \sum_{k=1}^{\infty} \frac{(\nu T)^k}{(k-1)!}
\]

(28)

\[
= e^{-\nu T} (\nu T) \sum_{k=0}^{\infty} \frac{(\nu T)^k}{k!}
\]

(29)

\[
= \nu T.
\]

(30)

For the third equality we considered that for \( k = 0 \) the sum is 0, so we can start with \( k = 1 \). For the fourth equality we performed a change of variables and for the last one we used the definition of the exponential function \( e^x = \sum_{n=0}^{\infty} \frac{x^n}{n!} \).