Answers to question set 10

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

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

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 $\Delta t \to 0$, this probability vanishes; however, the probability density, defined by $p(t)dt = P(t,t + dt)$, has finite value,

$$p(\text{fire at } t) = \lim_{\Delta t \to 0} \frac{P(t,t + \Delta t)}{\Delta t} = \rho e^{-\rho t}.$$  \hspace{1cm} (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

$$P(\text{ISI} < 20\text{ms}) = \int_0^{20\text{ms}} \rho e^{-\rho s} ds = [\rho e^{-\rho s}]_{s=0}^{20\text{ms}} = 1 - e^{-20\rho}.$$  \hspace{1cm} (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:

$$P = \frac{\langle N_{\text{coinc}} \rangle}{N}.$$  \hspace{1cm} (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 $S_1$:

$$P \approx \frac{2\nu \Delta N}{N} = 2\nu \Delta = 8\%.$$  \hspace{1cm} (12)

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

Exercise 2: Stochastic spike arrival

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 $\alpha(t - t') = q\delta(t - t')$.

We need to solve the linear equation

$$\tau \frac{du}{dt} = -(u - u_{\text{rest}}) + R \sum_f \alpha(t - t').$$  \hspace{1cm} (13)

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

$$u(t) = u_{\text{rest}} + R \int_0^t dt' e^{-(t-t')/\tau} \sum_f \alpha(t' - t').$$  \hspace{1cm} (14)

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

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \sum_f \delta(s - (t' - t')).$$  \hspace{1cm} (15)
Taking the average over all possible spike trains,
\[ \langle u(t) \rangle = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \left( \sum f \delta(s - (t' - t)) \right) \] (16)
because all the deterministic quantities can be pulled out of the average.

Now since \( \sum f \delta(s - (t' - t)) = \nu \),
\[ \langle u(t) \rangle = u_{\text{rest}} + R \nu \int_{-\infty}^{t} \frac{e^{-(t-t')/\tau}}{\tau} \int_{-\infty}^{\infty} ds \alpha(s) \] (17)

2.1 With \( \alpha(t - t') = q \delta(t - t') \), we obtain:
\[ \langle u(t) \rangle = u_{\text{rest}} + R \nu q. \] (18)

2.2 The general solution is given by Eq. (17).

Exercise 3: Homework

3.1 We take the limit and use Stirling’s approximation and \( \lim_{n \to \infty} (1 - x/n)^n = e^{-x} \):
\[ P_N(T) = \lim_{N \to \infty} \frac{N!}{k!(N-k)!} \left( 1 - \frac{\nu T}{N} \right)^{N-k} \left( \frac{\nu T}{N} \right)^k \] (19)
\[ = \frac{\nu T)^k}{k!} \lim_{N \to \infty} \frac{N^N e^{-N}}{(N-k)^{N-k} e^{-N+k}} \left( 1 - \frac{\nu T}{N} \right)^{N-k} \left( \frac{1}{N} \right)^k \] (20)
\[ = \frac{(\nu T)^k e^{-k}}{k!} \lim_{N \to \infty} \frac{1 - \frac{\nu T}{N}}{(1 - k/N)^{N-k}} \] (21)
\[ = \frac{(\nu T)^k e^{-\nu T}}{k!} \] (22)
\[ = \frac{(\nu T)^k}{k!} e^{-\nu T} \] (23)

The expected number of spikes in an interval of duration \( T \) can be calculated from the definition of expectation,
\[ \langle N \rangle = \sum_{N=0}^{\infty} NP_N(T) \] (24)
\[ = e^{-\nu T} \sum_{N=1}^{\infty} \frac{(\nu T)^N}{(N-1)!} \] (25)
\[ = e^{-\nu T} \frac{(\nu T)^0}{0!} \sum_{N=0}^{\infty} \frac{(\nu T)^N}{N!} \] (26)
\[ = \nu T. \] (27)

\[ ^{1} \text{this can be seen by remarking that } \int \delta(s) ds = 1 \text{ so that } \int \int_0^T \delta(s - t') ds = \text{# of spikes in } (0,T) = \nu. \]