Neural Networks and Biological Modeling

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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 Δt 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.,

$$S(n\Delta t) = (1 - \rho\Delta t)^n \,. \tag{1}$$

Although this expression is correct for a discrete process, it has the drawback of being dependent on the discretization time step Δt. 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

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

Alternatively, one can use the identity

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

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

$$S(t) = \lim_{n\to\infty} \exp\left[-\sum_{i=1}^{n} \rho\Delta t\right] \to \exp\left[-\int_0^t \rho dt\right] = exp\left[-\rho t\right] \,. \tag{4}$$

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 Δt. Because of independence, we have

$$S(t + \Delta t) = S(t)S(\Delta t) \,, \tag{5}$$

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

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

which becomes as $\Delta t \to 0$

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

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

1.2 Again, due to independence, we have

$$\begin{aligned} P(t, t + \Delta t) \equiv P\left(\text{fire for the first time in } (t, t + \Delta t)\right) &= P\left(\text{not fire until } t\right) \times P\left(\text{fire in } (t, t + \Delta t)\right) \\ &= e^{-\rho t} \times \rho\Delta t \,. \end{aligned} \tag{8}$$

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

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

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

$$P(\text{ISI} < 20\text{ms}) = \int_0^{20\text{ms}} \rho e^{-\rho s} ds = \left[-e^{-\rho s}\right]_{s=0}^{20\text{ms}} = 1 - e^{-20\rho} \,. \tag{10}$$

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 $p_{\text{burst}} \simeq 0.0015$, whereas for $\rho = 20\text{Hz}$, $p_{\text{burst}} \simeq 0.109$.

(iii) Given knowledge of the interspike interval distribution and survivor function as a function of the firing rate ρ, 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_{coinc}, divided by the total number of spikes (N) in spike train one:

$$P = \frac{\langle N_{coinc} \rangle}{N} \,. \tag{11}$$

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

$$P \approx \frac{2\nu \Delta N}{N} = 2\nu\Delta = 8\% \,. \tag{12}$$

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 $\alpha(t - t^f)$. The case of problem 2.1 then corresponds to the choice $\alpha(t - t^f) = q\delta(t - t^f)$.

We need to solve the linear equation

$$\tau \frac{du}{dt} = -(u - u_{\text{rest}}) + R \sum_f \alpha(t - t^f) \,. \tag{13}$$

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

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \frac{e^{-(t-t')/\tau}}{\tau} \sum_f \alpha(t' - t^f) \,. \tag{14}$$

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

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \sum_f \delta(s - (t' - t^f)) \,. \tag{15}$$

Taking the average over all possible spike trains,

$$\langle u(t) \rangle = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \left\langle \sum_f \delta(s - (t' - t^f)) \right\rangle \tag{16}$$

because all the deterministic quantities can be pulled out of the average.
Now since[1] $\left\langle \sum_f \delta(s - (t' - t^f)) \right\rangle = \nu$,

$$\begin{aligned}
\langle u(t) \rangle = & \quad u_{\text{rest}} + R\nu \underbrace{\int_{-\infty}^{t} dt' \frac{e^{-(t-t')/\tau}}{\tau}}_{=1} \int_{-\infty}^{\infty} ds \alpha(s) \\
= & \quad u_{\text{rest}} + R\nu \int_{-\infty}^{\infty} \alpha(s) ds \,.
\end{aligned} \tag{17}$$

2.1 With $\alpha(t - t^f) = q\delta(t - t^f)$, we obtain:

$$\langle u(t) \rangle \quad = \quad u_{\text{rest}} + R\nu q. \tag{18}$$

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 $\lim_{n\to\infty}(1 - x/n)^n = e^{-x}$:

$$\begin{aligned}
P_N(T) &= \lim_{N\to\infty} \frac{N!}{k!(N-k)!} \left(1 - \frac{\nu T}{N}\right)^{N-k} \left(\frac{\nu T}{N}\right)^k & (19)\\
&= \frac{(\nu T)^k}{k!} \lim_{N\to\infty} \frac{N^N e^{-N}}{(N-k)^{N-k} e^{-N+k}} \left(1 - \frac{\nu T}{N}\right)^{N-k} \left(\frac{1}{N}\right)^k & (20)\\
&= \frac{(\nu T)^k e^{-k}}{k!} \lim_{N\to\infty} \frac{\left(1 - \frac{\nu T}{N}\right)^{N-k}}{(1 - k/N)^{N-k}} & (21)\\
&= \frac{(\nu T)^k e^{-k}}{k!} \frac{e^{-\nu T}}{e^{-k}} & (22)\\
&= \frac{(\nu T)^k}{k!} e^{-\nu T} & (23)
\end{aligned}$$

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

$$\begin{aligned}
\langle N \rangle &= \sum_{N=0}^{\infty} N P_N(T) & (24)\\
&= e^{-\nu T} \sum_{N=1}^{\infty} \frac{(\nu T)^N}{(N-1)!} & (25)\\
&= e^{-\nu T} (\nu T) \sum_{N=0}^{\infty} \frac{(\nu T)^N}{N!} & (26)\\
&= \nu T \,. & (27)
\end{aligned}$$

[1] this can be seen by remarking that $\int \delta(s) ds = 1$ so that $\frac{1}{T} \sum_f \int_0^T \delta(s - t^f) ds = \frac{\#\text{ of spikes in } (0,T)}{T} = \nu$.