Neural Networks and Biological Modeling

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Answers to question set 11

Exercise 1: Stochastic input

1.1 The expression for $u(t)$ was given by

$$u(t) = u_{rest} + \frac{R}{\tau_m} \int_0^t e^{-s/\tau_m} I(t-s) ds. \tag{1}$$

Taking the average of Eq.(1) over multiple repetitions or over a population of neurons, we obtain

$$\begin{aligned} \langle\, u(t)\,\rangle &= u_{\text{rest}} + \frac{R}{\tau_m} \int_0^t e^{-s/\tau_m} \underbrace{\langle\, I(t)\,\rangle}_{=I_0} ds \\ &= u_{\text{rest}} + R I_0 [1 - e^{-t/\tau_m}]\,. \end{aligned}$$

1.2 Using $(RI(t) - R\,\langle\, I(t)\,\rangle) = \xi(t)$ and $\langle\, \xi(t)\xi(t')\,\rangle = \tau_m a^2 \delta(t-t')$.

$$\begin{aligned} \left\langle\, [u(t) - \langle\, u(t)\,\rangle]^2 \,\right\rangle &= \left\langle \left[\frac{1}{\tau_m} \int_0^t e^{-s/\tau_m} \xi(s) ds \right]^2 \right\rangle \\ &= \frac{1}{\tau_m^2} \int_0^t \int_0^t e^{-(s+s')/\tau_m} \langle\, \xi(s)\xi(s')\,\rangle\, ds ds' \\ &= \frac{a^2}{\tau_m} \int_0^t \int_0^t e^{-(s+s')/\tau_m} \delta(s-s') ds ds' \\ &= \frac{a^2}{\tau_m} \int_0^t e^{-2s/\tau_m} ds \\ &= \frac{a^2}{2} \left(1 - e^{-2t/\tau_m}\right). \end{aligned}$$

Exercise 2: Diffusive noise (stochastic spike arrival)

2.1 The expression for $u(t)$ was given by

$$u(t) = u_{rest} + \frac{qR}{\tau} \int_0^t e^{-s/\tau} S(t-s) ds. \tag{2}$$

Taking the average of Eq.(2) over multiple repetitions or over a population of neurons, we obtain

$$\langle\, u(t)\,\rangle = u_{\text{rest}} + \frac{q}{C} \int_0^t e^{-s/\tau} \underbrace{\langle\, S(t-s)\,\rangle}_{=\nu} ds \tag{3}$$

$$= u_{\text{rest}} + \frac{q\tau\nu}{C} [1 - e^{-t/\tau}]\,. \tag{4}$$

2.2 Using $\langle\, S(t)\,\rangle = \nu$, $\tau = RC$ and $\langle\, S(t)S(t')\,\rangle = \nu\delta(t-t') + \nu^2$.

$$
\begin{aligned}
\langle\, u(t)u(t)\,\rangle &= u_{\text{rest}}^2 + \frac{2qu_{\text{rest}}}{C}\int_0^t e^{-s/\tau}\,\langle\, S(t-s)\,\rangle\, ds \;+\frac{q^2}{C^2}\iint_0^t\!\!\int_0^t e^{-s/\tau}e^{-s'/\tau}\,\langle\, S(t-s)S(t-s')\,\rangle\, ds\, ds' \\
&= u_{\text{rest}}^2 + \frac{2u_{\text{rest}}q\tau\nu}{C}[1-e^{-t/\tau}] + \frac{q^2\tau\nu}{2C^2}[1-e^{-2t/\tau}] + \frac{q^2\tau^2\nu^2}{C^2}[1-e^{-t/\tau}]^2. \\
&= \left(u_{rest} + \frac{q\tau\nu}{C}\left[1-e^{-t/\tau}\right]\right)^2 + \frac{q^2\tau\nu}{2C^2}\left[1-e^{-2t/\tau}\right]
\end{aligned}
$$

note that the units are consistent since q/C have units of voltage and $\tau\nu$ has no units.

2.3 It is easy to obtain the variance from the previous two questions:

$$
\langle\, u(t)^2\,\rangle - \langle\, u(t)\,\rangle^2 = \frac{\nu q^2 R^2}{2\tau}[1-e^{-2t/\tau}].
$$

2.4 Same technique as previous problem, but we replace the upper bound of the integral by ∞.

$$
\begin{aligned}
\langle\, u(t)u(t')\,\rangle &= u_{\text{rest}}^2 + \frac{2qu_{\text{rest}}}{C}\int_0^\infty e^{-s/\tau}\,\langle\, S(t-s)\,\rangle\, ds \;+\frac{q^2}{C^2}\int_0^\infty\!\!\int_0^\infty e^{-s/\tau}e^{-s'/\tau}\,\langle\, S(t-s)S(t'-s')\,\rangle\, ds\, ds' \\
&= u_{\text{rest}}^2 + \frac{2u_{\text{rest}}q\tau\nu}{C} + \frac{q^2\tau\nu}{2C^2}e^{(t-t')/\tau} + \frac{q^2\tau^2\nu^2}{C^2}. \\
&= \left(u_{rest} + \frac{q\tau\nu}{C}\right)^2 + \frac{\tau\nu q^2}{2C^2}e^{(t-t')/\tau} \qquad \text{, for } t' > t\ .
\end{aligned}
$$

For the general case the autocorrelation is:

$$
\langle\, u(t)u(t')\,\rangle = \left(u_{rest} + \frac{q\tau\nu}{C}\right)^2 + \frac{\tau\nu q^2}{2C^2}e^{|t-t'|/\tau}.
$$

2.5 We have $S(t) = w_1S_1(t) + w_2S_2(t)$, $\langle\, S_1\,\rangle = \nu_1$, $\langle\, S_2\,\rangle = \nu_2$, $\langle\, S_1(t)S_2(t')\,\rangle = \nu_1\nu_2$,$\langle\, S_1(t)S_1(t')\,\rangle = \nu_1\delta(t-t') + \nu_1^2$ and $\langle\, S_2(t)S_2(t')\,\rangle = \nu_2\delta(t-t') + \nu_2^2$.
The mean and the autocorrelation in the steady state regime ($t \to \infty$) will respectively be

$$
\begin{aligned}
\langle\, u(t)\,\rangle &= u_{\text{rest}} + \frac{q}{C}\int_0^\infty e^{-s/\tau}\,\underbrace{\langle\, w_1S_1(t-s) + w_2S_2(t-s)\,\rangle}_{=\nu_1+\nu_2}\, ds \\
&= u_{\text{rest}} + \frac{q\tau}{C}(w_1\nu_1 + w_2\nu_2)\,,
\end{aligned}
$$

and

$$
\langle\, u(t)u(t')\,\rangle = u_{\text{rest}}^2 + 2u_{\text{rest}}\frac{q\tau}{C}(w_1\nu_1 + w_2\nu_2) + \frac{q^2\tau^2}{C^2}(w_1\nu_1 + w_2\nu_2)^2 + \frac{q^2\tau}{2C^2}(w_1^2\nu_1 + w_2^2\nu_2)e^{-|(t-t')|/\tau}.
$$

2.6 In this case, we have $\nu_1 = \nu_2 = \nu$ and $\langle\, S_1(t)S_1(t')\,\rangle = \langle\, S_2(t)S_2(t')\,\rangle = \langle\, S_1(t)S_2(t')\,\rangle = \nu\delta(t-t') + \nu^2$.
We find

$$
\langle\, u(t)\,\rangle = u_{\text{rest}} + \frac{q\tau}{C}(w_1 + w_2)\nu\,,
$$

and

$$\langle\, u(t)u(t')\,\rangle = u_{\text{rest}}^2 + 2u_{\text{rest}}\frac{q\tau}{C}(w_1+w_2)\nu + \frac{q^2\tau^2}{C^2}(w_1+w_2)^2\nu^2 + \frac{q^2\tau}{2C^2}(w_1+w_2)^2\nu e^{-|(t-t')|/\tau}.$$

Note that the correlations between the two spike trains increase the autocorrelation of u since $(w_1+w_2)^2 > w_1^2 + w_2^2$.

Exercise 3: Firing Statistics

Defining $p(t,t')$ as the probability density of observing a spike a t and a spike at t', and $p(t|t')$ the conditional probability intensity (it is not really a prob. density because it does not integrate to one) of observing a spike at t given a spike at t', we have:

$$\langle\, S(t)S(t')\,\rangle = p(t,t') = p(t|t')p(t') \tag{5}$$

The first equality comes from the definition of the expected value as the sum of all possible results weighted by their probability to happen. The second equality is simply the expansion of the joint probability.

If $t \neq t'$, we know that $p(t|t') = p(t)$ and therefore:

$$\langle\, S(t)S(t')\,\rangle = \lim_{\Delta t\to 0}\frac{P_{\Delta t}(t)P_{\Delta t}(t')}{\Delta t^2} = \nu^2.$$

Otherwise, when $t = t'$, we have:

$$\langle\, S(t)S(t)\,\rangle = \lim_{\Delta t\to 0}\frac{P_{\Delta t}(t|t)P_{\Delta t}(t)}{\Delta t^2}$$

$P_{\Delta t}(t|t)$ is the probability of spiking between $t - \frac{\Delta t}{2}$ and $t + \frac{\Delta t}{2}$ given a spike at t. $P_{\Delta t}(t|t) = 1$:

$$\langle\, S(t)S(t)\,\rangle = \lim_{\Delta t\to 0}\frac{\nu}{\Delta t} \to \infty.$$

We can summarize the two cases by writing

$$\langle\, S(t)S(t')\,\rangle = \nu^2 + \nu\delta(t-t'). \tag{6}$$

Exercise 4: Renewal process

Given an output spike at $t = \hat{t}$, the survivor function $S(t-\hat{t})$ is given by

$$S(t-\hat{t}) = \exp\Big[-\int_{\hat{t}}^{t}\rho(t'|\hat{t})dt'\Big] = \exp\Big[-\int_{\hat{t}}^{t}\rho(t'-\hat{t})dt'\Big] = \exp\Big[-\int_{0}^{t-\hat{t}}\rho(s)ds\Big].$$

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

$$\int_0^{t-\hat{t}}\rho(s)ds = \begin{cases} \displaystyle\int_0^{t_{\text{abs}}}\rho(s)ds = 0 & \text{for } s < t_{\text{abs}} \\ \displaystyle\int_0^{t_{\text{abs}}}\rho(s)ds + \int_{t_{\text{abs}}}^{t-\hat{t}}\rho(s)ds = \frac{\rho_0}{4}\left(t-\hat{t}-t_{\text{abs}}\right)^2 & \text{for } t_{\text{abs}} < s < t_{\text{abs}}+2 \\ \displaystyle\int_0^{t_{\text{abs}}}\rho(s)ds + \int_{t_{\text{abs}}}^{t_{\text{abs}}+2}\rho(s)ds + \int_{t_{\text{abs}}+2}^{t-\hat{t}}\rho(s)ds = \rho_0\left(-1+t-\hat{t}-t_{\text{abs}}\right) & \text{for } t_{\text{abs}}+2 < s\,. \end{cases}$$