Neural Networks and Biological Modeling

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Answers to Question Set 13

Exercise 1: From adaptive integrate-and-fire to the SRM

1.1 The only difference to earlier exercises is the incorporation of the spike reset into the solution. Integrating the differential equation for u without the reset yields (see earlier sheets)

$$u(t) = u_{rest} + \frac{R}{\tau} \int_{t_0}^{t} e^{-\frac{t-s}{\tau}} I(s) ds \tag{1}$$

Now to reset the membrane potential at the spike times to the resting potential, we have to include an artificial pulse input at the spike times t^f , which effectively sets the membrane potential from θ to u_{rest}.
This yields the effective input $I_{eff}(t) = I(t) - \frac{\tau}{R}(\theta - u_{rest}) \sum_f \delta(t - t^f) = I(t) - \frac{\tau}{R}(\theta - u_{rest})S(t)$.
In turn, we get the membrane potential

$$\begin{aligned}
u(t) &= u_{rest} + \frac{R}{\tau} \int_{t_0}^{t} e^{-\frac{t-s}{\tau}} I_{eff}(s) ds & (2)\\
&= u_{rest} + \int_{t_0}^{t} \frac{R}{\tau} e^{-\frac{t-s}{\tau}} I(s) ds + \int_{t_0}^{t} (u_{rest} - \theta) e^{-\frac{t-s}{\tau}} S(s) ds & (3)\\
&= u_{rest} + \int_{0}^{t-t_0} \frac{R}{\tau} e^{-\frac{s}{\tau}} I(t-s) ds + \int_{0}^{t-t_0} (u_{rest} - \theta) e^{-\frac{s}{\tau}} S(t-s) ds & (4)\\
&\overset{t_0 \to -\infty}{=} u_{rest} + \int_{0}^{\infty} \underbrace{\frac{R}{\tau} e^{-\frac{s}{\tau}}}_{\epsilon(s)} I(t-s) ds + \int_{0}^{\infty} \underbrace{(u_{rest} - \theta) e^{-\frac{s}{\tau}}}_{\eta(s)} S(t-s) ds. & (5)
\end{aligned}$$

The second last equality is easily seen by substitution (substitute $q = t - s$ and later rename). The last equality comes from the fact that the initial time t_0 can be arbitrarily chosen and thus can be sent to $-\infty$.
A second way to obtain the ∞-bounds in the integrals is introducing the input current with a suitable Heaviside-function $\Theta(t - t_0)$. Then every input before t_0 is set to 0 and the integration (over s) can be extended until ∞.

1.2 Integrating the equation for w gives for a single spike at $t = 0$

$$w(t) = \beta e^{-\frac{t}{\tau_w}} \Theta(t),$$

where $\Theta(t)$ is the Heaviside step function.

Since the equation for $\frac{du(t)}{dt}$ is linear and $w(t)$ is independent of u, we can treat $w(t)$ as another external input. For a single spike at $t = 0$, the effect on the membrane potential only by the w input is then described by

$$\kappa(t) = \frac{R}{\tau} \int_{-\infty}^{t} e^{-\frac{t-s}{\tau}} w(s) ds \Theta(t) \tag{6}$$

$$= \frac{R}{\tau} \int_{-\infty}^{t} e^{-\frac{t-s}{\tau}} \beta e^{-\frac{s}{\tau_w}} \Theta(s) ds \Theta(t) \tag{7}$$

$$= \frac{R\beta}{\tau} e^{-\frac{t}{\tau}} \int_{0}^{t} e^{s(\frac{1}{\tau} - \frac{1}{\tau_w})} ds \Theta(t) \tag{8}$$

$$= \frac{R\beta}{\tau} \left(\frac{1}{\tau} - \frac{1}{\tau_w}\right)^{-1} \left[e^{-\frac{t}{\tau_w}} - e^{-\frac{t}{\tau}}\right] \Theta(t) \tag{9}$$

$$= R\beta \left(1 - \frac{\tau}{\tau_w}\right)^{-1} \left[e^{-\frac{t}{\tau_w}} - e^{-\frac{t}{\tau}}\right] \Theta(t). \tag{10}$$

Finally, the effect of multiple spikes is described by the convolution of this kernel with the spike train $S(t)$. With the results of the previous question, this gives an effective membrane potential (including the minus sign of $\frac{du(t)}{dt} \propto -\alpha R w$)

$$u(t) = u_{rest} + \int_0^\infty \epsilon(s) I(t-s) ds + \int_0^\infty \underbrace{[\eta(s) - \kappa(s)]}_{\eta_{eff}(s)} S(t-s) ds \tag{11}$$

where now $\eta_{eff}(s)$ is the effective kernel we are looking for.

Exercise 2: Integrate-and-fire model with linear escape rates

2.1 For a non-leaky integrate-and-fire model by considering the limit of $\tau_m \to \infty$, the membrane potential of the model is

$$u(t|\hat{t}) = u_r + \frac{1}{C} \int_{\hat{t}}^{t} I(t')\, dt'$$

Let us set $u_r = 0$ and consider a linear escape rate

$$\rho(t|\hat{t}) = \beta[u(t|\hat{t}) - \theta]_+ \tag{12}$$

For constant input I_0 we have $u(t|\hat{t}) = \frac{I_0}{C}(t - \hat{t})$ and so the hazard is

$$\rho_I(t|\hat{t}) = \alpha_0 [s - \Delta^{abs}]_+$$

where $\alpha_0 = \frac{\beta I_0}{C}$ and $\Delta^{abs} = \frac{\theta C}{I_0}$ is the absolute refractory time. $s = t - \hat{t}$ denotes the difference between the current time and timing of the last spike.

The interval distribution for this hazard function is then equal to

$$\begin{aligned} P_I(s) &= \rho_I(t|\hat{t}) \exp\left(-\int_{\hat{t}}^{t} \rho_I(t'|\hat{t}) dt'\right) \\ &= \alpha_0 [s - \Delta^{abs}]_+ \exp\left(-\frac{1}{2}\alpha_0 \left([s - \Delta^{abs}]_+\right)^2\right) \end{aligned}$$

2.2 For a leaky integrate-and-fire neuron with constant input I_0, the membrane potential is

$$u(t|\hat{t}) = RI_0 \left[1 - e^{-\frac{t-\hat{t}}{\tau_m}}\right],$$

where we have assumed $u_r = 0$. For a linear escape rate (Eq. 12), and the assumption $\theta = 0$ the hazard is then equal to

$$\rho_0(t - \hat{t}) = \gamma \left[1 - e^{-\lambda(t-\hat{t})}\right],$$

with $\gamma = \beta RI_0$ and $\lambda = \tau_m^{-1}$.

The interval distribution for this hazard function is then equal to

$$\begin{aligned}
P_0(s) &= \rho_0(t|\hat{t}) \exp\left(-\int_{\hat{t}}^{t} \rho_0(t'|\hat{t})dt'\right) \\
&= \gamma \left[1 - e^{-\lambda(t-\hat{t})}\right] \exp\left(-\int_{\hat{t}}^{t} \gamma \left[1 - e^{-\lambda(t-\hat{t})}\right] dt'\right) \\
&= \gamma \left[1 - e^{-\lambda(t-\hat{t})}\right] \exp\left(-\gamma s - \gamma\lambda^{-1}(e^{-\lambda s} - 1)\right)
\end{aligned}$$

where $s = t - \hat{t}$.

Exercise 3: Optimization of a free parameter

3.1 To find the minimum of the error function E with respect to the free parameter R, take the derivative and set it to zero:

$$\frac{\partial E}{\partial R} = 2 \sum_n \left[u_n^{data} - RI_n\right](-I_n) \tag{13}$$

$$= 2\left[-\sum_n u_n^{data} I_n + R \sum_n I_n^2\right] \stackrel{!}{=} 0. \tag{14}$$

Solving this for R yields

$$R = \frac{\sum_n u_n^{data} I_n}{\sum_n I_n^2}$$

3.2 For $I_n = I_0$ the previous expression reduces to

$$R = \frac{I_0}{I_0^2} \frac{\sum_n u_n^{data}}{\sum_n 1} = \frac{1}{I_0 n} \sum_n u_n^{data} = \frac{\bar{u}^{data}}{I_0},$$

which is clearly the resistance estimated from the mean voltage and given input current.

Exercise 4: Likelihood of a spike train

4.1 From the previous exercise we know that the hazard for a leaky integrate-and-fire neuron is equal to

$$\rho(t|\hat{t}) = \rho(t - \hat{t}) = \gamma \left[1 - e^{-\lambda(t-\hat{t})}\right],$$

So the likelihood that this spike train could have been generated by such a neuron is equal to

$$
\begin{aligned}
\mathcal{L} = &\exp\left(-\int_0^{t^{(1)}} \rho(t)dt\right) \rho(t^{(1)}|0) \exp\left(-\int_{t^{(1)}}^{t^{(2)}} \rho(t)dt\right) \rho(t^{(2)}|t^{(1)}) \exp\left(-\int_{t^{(2)}}^{t^{(3)}} \rho(t)dt\right) \\
&\rho(t^{(3)}|t^{(2)}) \exp\left(-\int_{t^{(3)}}^{t^{(4)}} \rho(t)dt\right) \rho(t^{(4)}|t^{(3)}) \exp\left(-\int_{t^{(4)}}^{T} \rho(t)dt\right) \\
= &\rho(t^{(1)}|0)\rho(t^{(2)}|t^{(1)})\rho(t^{(3)}|t^{(2)})\rho(t^{(4)}|t^{(3)}) \exp\left(-\int_0^T \rho(t)dt\right) \\
= &\gamma^4 \left[1 - e^{-\lambda t^{(1)}}\right] \left[1 - e^{-\lambda(t^{(2)} - t^{(1)})}\right] \left[1 - e^{-\lambda(t^{(3)} - t^{(2)})}\right] \left[1 - e^{-\lambda(t^{(4)} - t^{(3)})}\right] \exp\left(-\gamma T - \gamma\lambda^{-1}(e^{-\lambda T} - 1)\right)
\end{aligned}
$$

4.2

$$
\mathcal{L} = \rho(t^{(1)})\rho(t^{(2)} - t^{(1)})\rho(t^{(3)} - t^{(2)})\rho(t^{(4)} - t^{(3)})\frac{P(T)}{\rho(T)}
$$

where $P(.)$ is the interval distribution and $\rho(.)$ is the hazard function.