

# Neural Networks and Biological Modeling

Professor Wulfram Gerstner  
Laboratory of Computational Neuroscience

## ANSWERS TO QUESTION SET 12

### **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)

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

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  $\theta$  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

$$u(t) = u_{rest} + \frac{R}{\tau} \int_{t_0}^t e^{-\frac{t-s}{\tau}} I_{eff}(s) ds \quad (2)$$

$$= u_{rest} + \int_{t_0}^t \frac{R}{\tau} e^{-\frac{t-s}{\tau}} I(s) ds + \int_{t_0}^t (u_{rest} - \theta) e^{-\frac{t-s}{\tau}} S(s) ds \quad (3)$$

$$= u_{rest} + \int_0^{t-t_0} \frac{R}{\tau} e^{-\frac{s}{\tau}} I(t-s) ds + \int_0^{t-t_0} (u_{rest} - \theta) e^{-\frac{s}{\tau}} S(t-s) ds \quad (4)$$

$$\stackrel{t_0 \rightarrow -\infty}{=} u_{rest} + \int_0^{\infty} \underbrace{\frac{R}{\tau} e^{-\frac{s}{\tau}} I(t-s) ds}_{\epsilon(s)} + \int_0^{\infty} \underbrace{(u_{rest} - \theta) e^{-\frac{s}{\tau}} S(t-s) ds}_{\eta(s)}. \quad (5)$$

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  $\infty$ -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  $\infty$ .

**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

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

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

$$= \frac{R\beta}{\tau} e^{-\frac{t}{\tau}} \int_0^t e^{s(\frac{1}{\tau} - \frac{1}{\tau_w})} ds \Theta(t) \quad (8)$$

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

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

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  $\frac{du(t)}{dt} \propto -\alpha R w$ )

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

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  $\tau_m \rightarrow \infty$ , 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

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

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

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

**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:

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

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

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

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

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

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

where we define  $t^{(0)} = 0$  and  $t^{(5)} = T$ . Note that the product in front contains 4 terms, whereas the sum in the exponential contains 5 terms. This is due to there being 4 spikes that were emitted, and 5 periods without spikes where the neuron needs to survive.

## 4.2

$$\mathcal{L} = P(t^{(1)}|0) P(t^{(2)}|t^{(1)}) P(t^{(3)}|t^{(2)}) P(t^{(4)}|t^{(3)}) \frac{P(T|t^{(4)})}{\rho(T|t^{(4)})}$$

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