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)

$$u(t) = u_{\text{rest}} + \frac{R}{\tau} \int_{t_0}^{t} e^{-\frac{t-s}{\tau}} I(s) ds$$  \hspace{1cm} (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 $u_{\text{rest}}$. This yields the effective input $I_{\text{eff}}(t) = I(t) - \frac{R}{\tau}(\theta - u_{\text{rest}}) \sum_f \delta(t - t_f) = I(t) - \frac{R}{\tau}(\theta - u_{\text{rest}}) S(t)$. In turn, we get the membrane potential

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

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

$$= u_{\text{rest}} + \int_{0}^{t-t_0} \frac{R}{\tau} e^{-\frac{q}{\tau}} I(q) dq + \int_{0}^{t-t_0} (u_{\text{rest}} - \theta) e^{-\frac{q}{\tau}} S(q) dq$$

$$t_0 \rightarrow -\infty \quad u_{\text{rest}} + \int_{0}^{\infty} \frac{R}{\tau} e^{-\frac{q}{\tau}} I(q) dq + \int_{0}^{\infty} (u_{\text{rest}} - \theta) e^{-\frac{q}{\tau}} S(q) dq.$$

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 $t = 0$

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

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

\[ = \frac{R}{\tau} \int_{-\infty}^{t} e^{-\frac{t-s}{\tau}} \beta e^{-\frac{s}{\tau w}} \Theta(s) ds \Theta(t) \] (7)

\[ = \frac{R \beta}{\tau} e^{-\frac{t}{\tau w}} \int_{0}^{t} e^{\left(-\frac{s}{\tau w}\right)} ds \Theta(t) \] (8)

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

\[ = \frac{R \beta}{\tau} \left( 1 - \frac{\tau}{\tau w} \right)^{-1} \left[ e^{-\frac{t}{\tau w}} - e^{-\frac{t}{\tau}} \right] \Theta(t). \] (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 \( \frac{du(t)}{dt} \propto -\alpha R w \))

\[ u(t) = u_{rest} + \int_{0}^{\infty} \epsilon(s) I(t-s) ds + \int_{0}^{\infty} \left[ \eta(s) - \kappa(s) \right] S(t-s) ds \] (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

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

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

\[ \rho_f(t|\hat{t}) = \alpha_0 [s - \Delta_{abs}]_+ \]

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

\[ P_f(s) = \rho_f(t|\hat{t}) \exp \left(-\int_{\hat{t}}^{t} \rho_f(t'|\hat{t}) dt' \right) \]

\[ = \alpha_0 [s - \Delta_{abs}]_+ \exp \left(-\frac{1}{2} \alpha_0 [s - \Delta_{abs}]_+^2 \right) \]

2.2 For a leaky integrate-and-fire neuron with constant input \( I_0 \), the membrane potential is
\[ u(t|\hat{t}) = R I_0 \left[ 1 - e^{-\frac{t-\hat{t}}{\tau_m}} \right], \]

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 \( \gamma = \beta R I_0 \) and \( \lambda = \tau_m^{-1} \).

The interval distribution for this hazard function is then equal to

\[ P_0(s) = \rho_0(t|\hat{t}) \exp \left( -\int_{\hat{t}}^t \rho_0(t'|\hat{t}) dt' \right) \]

\[ = \gamma \left[ 1 - e^{-\lambda(t - \hat{t})} \right] \exp \left( -\gamma s - \gamma \lambda^{-1} (e^{-\lambda s} - 1) \right) \]

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:

\[ \frac{\partial E}{\partial R} = 2 \sum_n \left[ u_n^{\text{data}} - R I_n \right] (-I_n) = 0. \]

(13)

\[ = 2 \left[ -\sum_n u_n^{\text{data}} I_n + R \sum_n I_n^2 \right] = 0. \]

(14)

Solving this for \( R \) yields

\[ R = \frac{\sum_n u_n^{\text{data}} I_n}{\sum_n I_n^2} \]

3.2 For \( I_n = I_0 \) the previous expression reduces to

\[ R = \frac{I_0}{I_0^2} \sum_n u_n^{\text{data}} \sum_n 1 = \frac{1}{I_0 n} \sum_n u_n^{\text{data}} = \frac{\bar{u}_n^{\text{data}}}{I_0}, \]

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
\[ L = \exp \left( -\int_0^{t_1(1)} \rho(t) dt \right) \rho(t_1(0) | t_1(1)) \exp \left( -\int_{t_1(2)}^{t_2(1)} \rho(t) dt \right) \rho(t_2(1) | t_1(1)) \exp \left( -\int_{t_2(2)}^{t_1(3)} \rho(t) dt \right) \rho(t_1(3) | t_1(2)) \exp \left( -\int_{t_1(4)}^{t_2(3)} \rho(t) dt \right) \rho(t_2(3) | t_1(3)) \exp \left( -\int_{t_2(4)}^{T} \rho(t) dt \right) \rho(T | t_1(4)) \]

\[= \rho(t_1(0)) \rho(t_2(1) | t_1(1)) \rho(t_3(2) | t_1(3)) \rho(t_4(3) | t_1(4)) \exp \left( -\int_0^T \rho(t) dt \right) \rho(T)\]

\[= \gamma^4 \left[ 1 - e^{-\lambda t_1(1)} \right] \left[ 1 - e^{-\lambda(t_2(2) - t_1(1))} \right] \left[ 1 - e^{-\lambda(t_3(3) - t_2(2))} \right] \left[ 1 - e^{-\lambda(t_4(4) - t_3(3))} \right] \exp \left( -\gamma T - \gamma \lambda^{-1}(e^{-\lambda T} - 1) \right) \]

**4.2**

\[ L = \rho(t_1(1)) \rho(t_2(2) - t_1(1)) \rho(t_3(3) - t_2(2)) \rho(t_4(4) - t_3(3)) \frac{P(T)}{\rho(T)} \]

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