1. **An LIF Neuron with an 'autapse'.** An *autapse* is a synapse formed by a neuron connecting its own axon back to its own dendrites (i.e. a self (auto) synapse). In this problem, you will study the emergence of self-sustained spiking in an 'autaptically'-coupled neuron.

Current is applied to a neuron $u$ self-coupled by an autapse until it spikes at $u_{\text{th}} = 1\text{mV}$. After this, its voltage is reset to rest $u_{\text{rest}} = 0\text{mVs}$, the current is shut off, and a burst of neurotransmitter is released which rapidly initiates a synaptic current. Assuming membrane time constant is $\tau_m$ (ms), neurotransmitter decay time constant $\tau_x$ (ms), fast synaptic current time constant ($\tau_s \to 0\text{ms}$), membrane resistance $R = 1\Omega$, excitatory neurotransmitter release concentration $x_0$, and unit current conversion, the equations for neuron voltage $u$ and neurotransmitter $x$ after the first spike and prior to any other spikes are

$$\tau_m \frac{du}{dt} = -u + x, \qquad u(0) = 0,$$
$$\tau_x \frac{dx}{dt} = -x, \qquad x(0) = x_0.$$

(a) If $\tau_x > \tau_m$ and $x_0 = 2$, show it is possible for the neuron to spike a second time if $\tau_x$ is large enough as long as the spike threshold $u_{\text{th}} < 2\text{mV}$. To do this, solve for $x$ and then for $u$. Determine the maximum value of $u$ as a function of time $t$ (assuming first $u$ stays subthreshold). This formula should depend on $\tau_m$ and $\tau_x$. Argue the resulting formula can be made arbitrarily close to 2 by increasing $\tau_x$.

(b) Now, assume $\tau_x = \tau_m \equiv \tau$, so the membrane and synapse have the same timescale. Again, determine the maximum value $u_{\max}$ of $u(t)$ as a function of time $t$ when $x_0 = 2$. Is there any value of $\tau$ that will lead to $u$ reaching above a threshold value of $u_{\text{th}} = 1\text{mV}$? Hint: Determining the maximum of $u_{\max}$ as a function of $\tau$, optimize this, and compare this to 1mV. Does it go above?

(c) Lastly, determine the critical value of $x_0$ for the $\tau$-optimized $u_{\max}$ value to exactly reach 1.

a) $\tau_x \frac{dx}{dt} = -x \quad , \quad x(0) = x_0$

$x' + \frac{x}{\tau_x} = 0 \qquad \mu = e^{\frac{t}{\tau_x}}$

$e^{\frac{t}{\tau_x}} x = C \Rightarrow x = \frac{C}{e^{\frac{t}{\tau_x}}} \Rightarrow \boxed{x = x_0 e^{-\frac{t}{\tau_x}}}$

$\tau_m \frac{du}{dt} = -u + x \quad ; \quad u(0) = 0$

$u' + \frac{u}{\tau_m} = \frac{x_0 e^{-\frac{t}{\tau_x}}}{\tau_m} \qquad \mu = e^{\frac{t}{\tau_m}}$

$$\Rightarrow \boxed{u = \frac{X_0 \tau_x}{\tau_x - \tau_m}\left(e^{-\frac{t}{\tau_x}} - e^{-\frac{t}{\tau_m}}\right)}$$

Find maximum of $u$:

$$u' = \frac{X_0 \tau_x}{\tau_x - \tau_m}\left(\frac{e^{-\frac{t}{\tau_m}}}{\tau_m} - \frac{e^{-\frac{t}{\tau_x}}}{\tau_x}\right)$$

$$0 = \frac{X_0}{\tau_x - \tau_m}\left(\frac{\tau_x e^{-\frac{t}{\tau_m}}}{\tau_m} - e^{-\frac{t}{\tau_x}}\right)$$

$$0 = \frac{\tau_x}{\tau_m} e^{-\frac{t}{\tau_m}} - e^{-\frac{t}{\tau_x}}$$

$$0 = \tau_x e^{-\frac{t}{\tau_m}} - \tau_m e^{-\frac{t}{\tau_x}}$$

$$\ln\left(\tau_m e^{-\frac{t}{\tau_x}}\right) = \ln\left(\tau_x e^{-\frac{t}{\tau_m}}\right)$$

$$\ln(\tau_m) - \frac{t}{\tau_x} = \ln(\tau_x) - \frac{t}{\tau_m}$$

$$0 = \ln(\tau_x) - \ln(\tau_m) - \frac{t}{\tau_m} + \frac{t}{\tau_x}$$

$$= \ln(\tau_x) - \ln(\tau_m) - \left(\frac{1}{\tau_x} + \frac{1}{\tau_m}\right) t$$

$$t = \frac{\ln\left(\frac{\tau_x}{\tau_m}\right)}{\frac{1}{\tau_x} + \frac{1}{\tau_m}} = \frac{\ln\left(\frac{\tau_x}{\tau_m}\right) \tau_x \tau_m}{\tau_m + \tau_x}$$

The max value of $u$ is when $t = \frac{\ln\left(\frac{\tau_x}{\tau_m}\right)\tau_x \tau_m}{\tau_m + \tau_x}$

because $\tau_x > \tau_m$ we can see that as $\tau_x$ increase we can make the formula arbitrarly close to 2.

b) $\tau_x = \tau_m = \tau$ and $x_0 = 2$

$$\tau x' = -x \quad , \quad x(0) = x_0$$

$$x = x_0 e^{-\frac{t}{\tau}}$$

$$\tau u' = -u + x_0 e^{-\frac{t}{\tau}} \quad , \quad u(0) = 0$$

$$u = \frac{x_0 t e^{-\frac{t}{\tau}}}{\tau}$$

Find max:

$$\frac{du}{dt} = \frac{x_0}{\tau}\left(-\frac{(t-\tau)e^{-\frac{t}{\tau}}}{\tau}\right)$$

$$0 = \frac{-(t-\tau)e^{-\frac{t}{\tau}}}{\tau}$$

$$0 = -t + \tau$$

$$t = \tau$$

$$u_{max} = \frac{x_0}{e} = \frac{2}{e} < 2$$

c) Yes for $u$ to reach above threshold make $\tau = e^{-\frac{t}{\tau}}$ so:

$$u = \frac{x_0 t e^{-\frac{t}{\tau}}}{e^{-\frac{t}{\tau}}} = x_0 t = 2t > 1$$

for $t > 0$