

# THEORETICAL NEUROSCIENCE I

## Lecture 3: Leaky-integrate-and-fire model

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# Content

1. Single-compartment model recap.
2. Arbitrary input currents.
3. Spike mechanism of LIF model.
4. Rate response to constant input current.
5. Spike-frequency adaptation.

# 1 Single-compartment model (recap)

If a neuron is “electrotonically compact”, it may be treated as a single “compartment”. Such a compartment is characterized by a single membrane potential, membrane capacity, and membrane resistance.

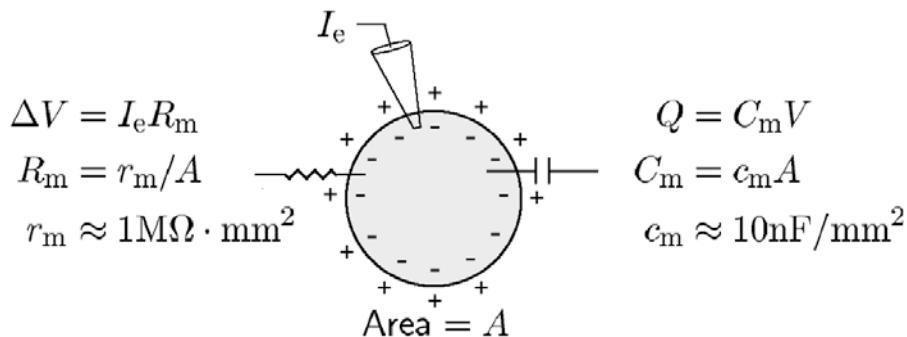


Figure 1: Single-compartment model. [1]

## Basic equation (recap)

With the help of Ohm’s Law and the Capacitor Equation for (outward) resistance and capacitance currents

$$I_R = \frac{V_m - E_L}{R_m} \qquad I_C = C_m \frac{dV_m}{dt}$$

we can relate an (inward) input current  $I_e(t)$  to the membrane potential  $V_m(t)$ :

$$I_e = \frac{V_m - E_L}{R_m} + C_m \frac{dV_m}{dt}$$

The reversal potential  $E_L$  takes into account the ion-specific nature of the membrane resistance. The inverse of the membrane resistance is sometimes called “leak conductance”:

$$g_L = \frac{1}{R_m}$$

## Time-constant and equilibrium potential (recap)

The resulting linear differential equation describes the voltage response to a current input:

$$R_m C_m \frac{d}{dt} V_m(t) = -V_m(t) + E_L + R_m I_e(t)$$

or

$$\tau_m \frac{d}{dt} V_m(t) = -V_m(t) + V_\infty(t)$$

where membrane time-constant  $\tau_m$  and equilibrium potential  $V_\infty(t)$  are defined as

$$\tau_m = R_m C_m \quad V_\infty(t) = E_L + R_m I_e(t)$$

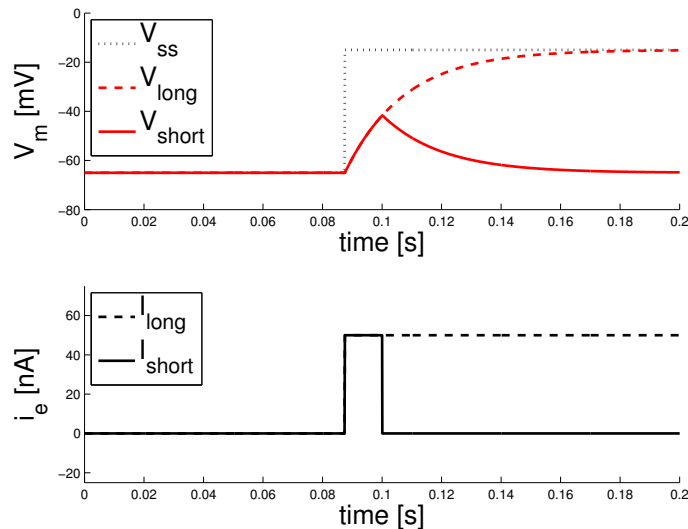


Figure 2: Time-constant and equilibrium potential.

## Membrane resistance and equilibrium potential (recap)

- The (instantaneous) input current determines the (instantaneous) equilibrium potential.

- The equilibrium potential is the potential needed to drive an (outward) resistance current equal to the (inward) input current.
- It therefore depends on the membrane resistance.
- The membrane potential moves *towards* the equilibrium potential.
- The membrane potential may not reach the equilibrium potential, because the input current may not remain constant for long enough.
- If reached, the membrane potential is ‘at equilibrium’.

## Membrane capacitance and membrane time-constant (recap)

- The membrane capacitance determines how much current is needed to change the membrane potential.
- If large, a given input current changes the membrane potential only slowly.
- If small, a given input current changes the membrane potential quickly.
- The membrane time-constant is the time it takes the membrane to move approximately 1/3 (precisely 1/e) of the way towards the equilibrium potential.
- The membrane time-constant is proportional to membrane resistance and membrane capacitance

$$\tau_m = R_m C_m$$

## Solution for constant input current (recap)

For a constant input current  $I_e(t) = I_0$ , the solution of the dynamic equation is

$$V_m(t) = V_\infty + (V_0 - V_\infty) \exp\left(-\frac{t}{\tau}\right)$$

where  $V_0$  is the initial value of the membrane potential

$$V_0 = V_m(t = 0)$$

and  $V_\infty$  is the equilibrium potential

$$V_\infty = E_L + R_m$$

## Summary of SCM recap

- The response of the membrane potential to an input current is described by a linear differential equation.
- The leak conductance (inverse membrane resistance) determines how far the membrane potential is driven by an input current.
- The membrane capacitance determines how much current has to flow to change the membrane potential.
- Together, membrane resistance and capacitance determine how slowly (or quickly) the membrane voltage responds to changes in input current.

## Explain!

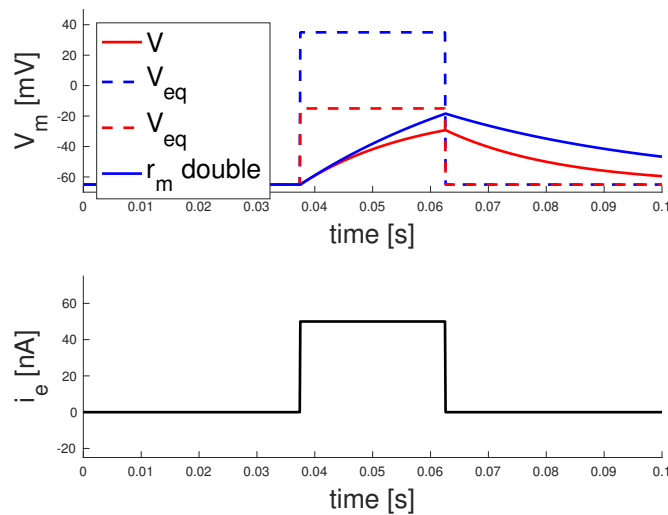


Figure 3: Responses to membrane potential.

Explain!

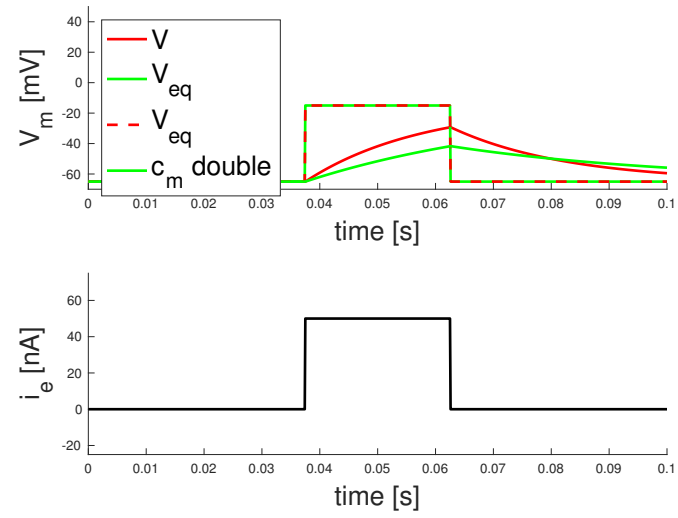


Figure 4: Responses to membrane potential.

## 2 Arbitrary input currents

We would like to solve the basic equation of the SCM

$$\tau_m \frac{dV_m}{dt} = -V_m(t) + E_L + r_m I_e(t)$$

for arbitrary, time-varying input currents  $I_e(t)$ .

To accomplish this, we introduce a common computational technique: *iterative integration*.

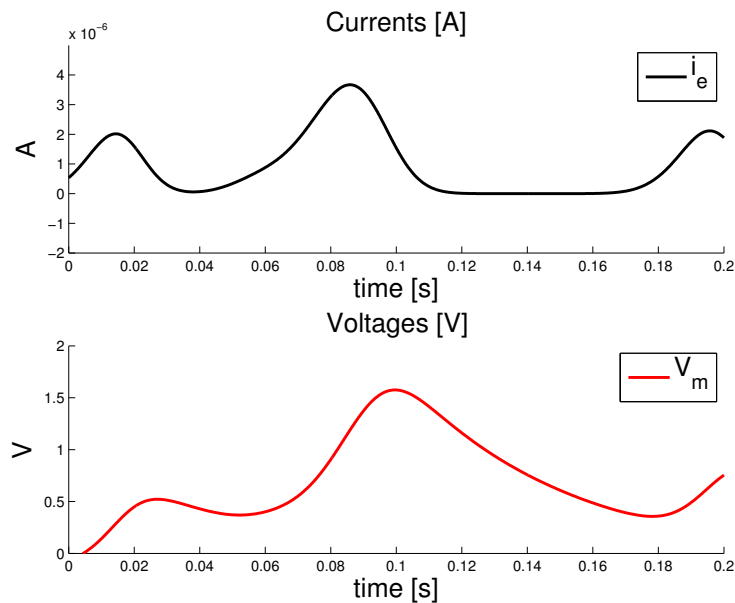


Figure 5: Iterative integration.

### Discretize time

We divide the time axis into intervals  $i$  from  $t_i$

$$t_i \leq t \leq t_{i+1}, \quad t_{i+1} = t_i + \Delta t$$

If  $\Delta t$  is chosen sufficiently small, the input current can be considered constant during each interval  $i$ .



$$I_e(t) \approx I_i \quad t_i \leq t \leq t_{i+1}$$

Thus, the equilibrium potential is constant as well

$$V_\infty(t) \approx V_i^\infty = E_L + r_m I_i$$

### Solve for time interval

Given the membrane potential at the beginning of an interval,  $V_i = V_m(t_i)$ , we wish to solve for the potential at the end of the interval,  $V_{i+1} = V_m(t_i + \Delta t)$ ,

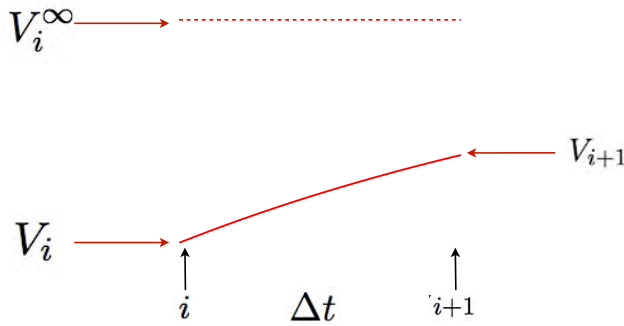


Figure 6: Solved for time interval.

### Solve for time interval

The general solution for times  $t \geq t_i$  is

$$V_m(t) = V_i^\infty + [V_i - V_i^\infty] \exp(-t-t_i/\tau_m)$$

and the particular solution for  $t_{i+1} = t_i + \Delta t$  is

$$V_{i+1} = V_i^\infty + [V_i - V_i^\infty] \exp(-\Delta t/\tau_m)$$

where

$$V_i^\infty = E_L + r_m I_i$$

Repeating the procedure for each interval, we iteratively obtain the time-varying membrane potential:

$$V_1 \rightarrow V_2 \rightarrow V_3 \rightarrow \dots \rightarrow V_i \rightarrow V_{i+1}$$

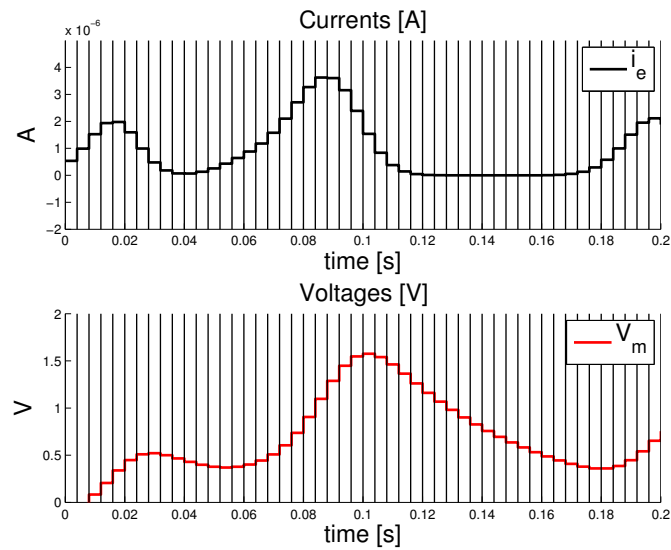


Figure 7: Divided in intervals.

**Smaller  $\Delta t$**

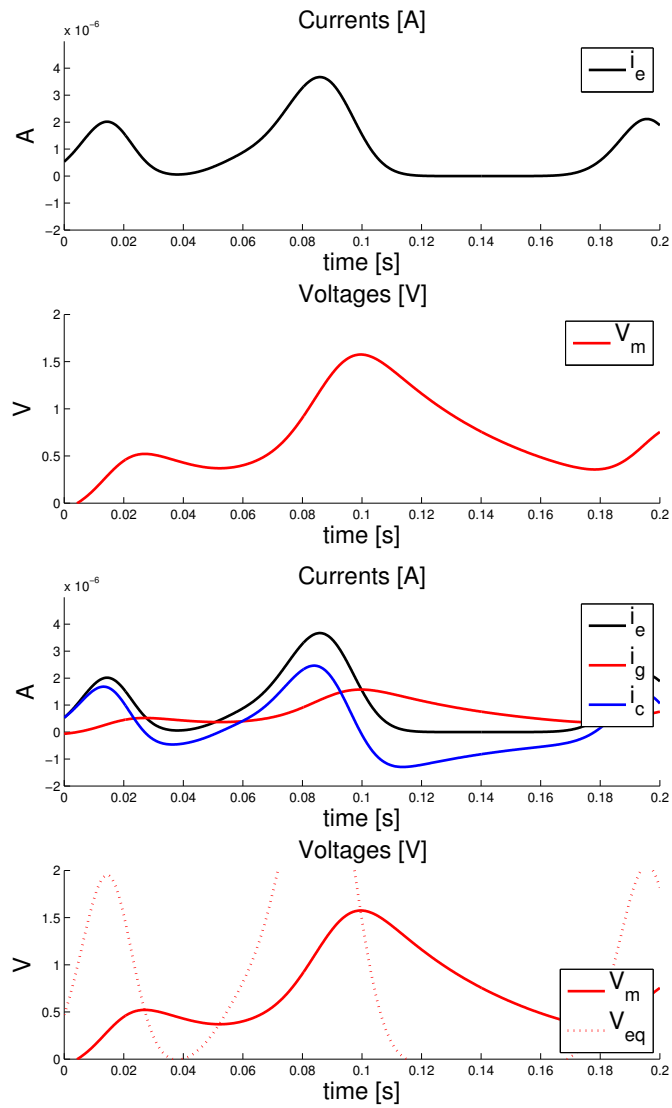


Figure 8: Smaller  $\Delta t$ .

## Piece-wise constant current

Consider this piece-wise constant input current  $I_e(t)$ :

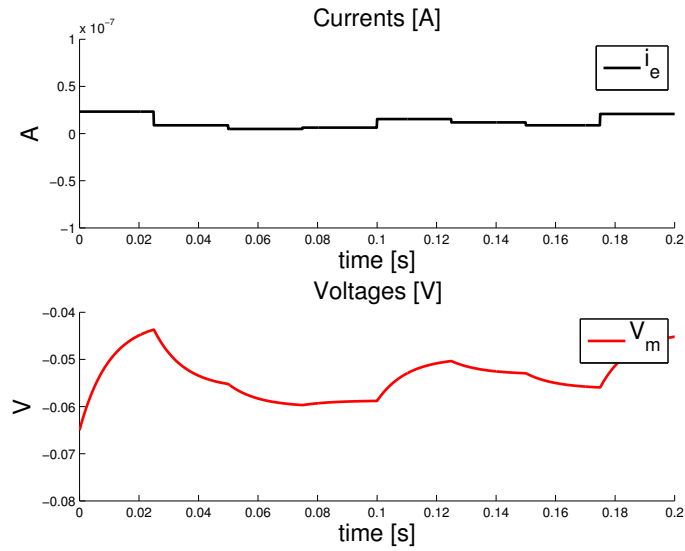


Figure 9: Piece-wise constant current

Compare equilibrium potential  $V_i^\infty = E_L + r_m I_i$

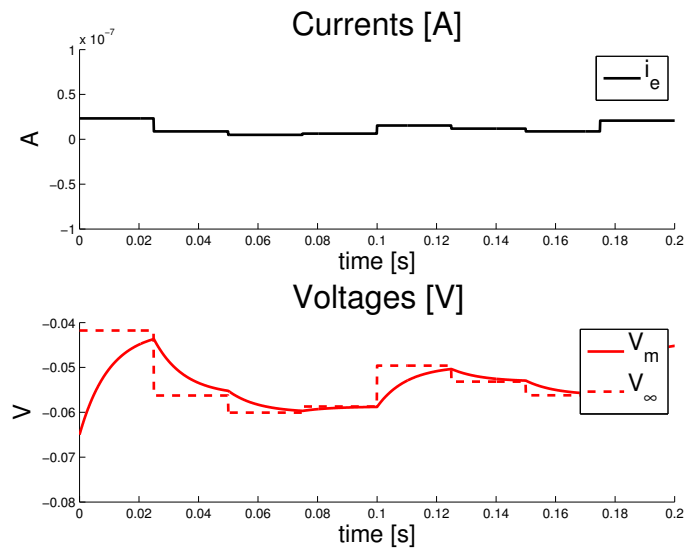


Figure 10: Now, compared with equilibrium potential.

Compare resistive and capacitive currents  $I_g(t) = \frac{1}{r_m} (V_m(t) - E_L)$   
and  $I_c(t) = c_m \frac{d}{dt} V_m(t)$

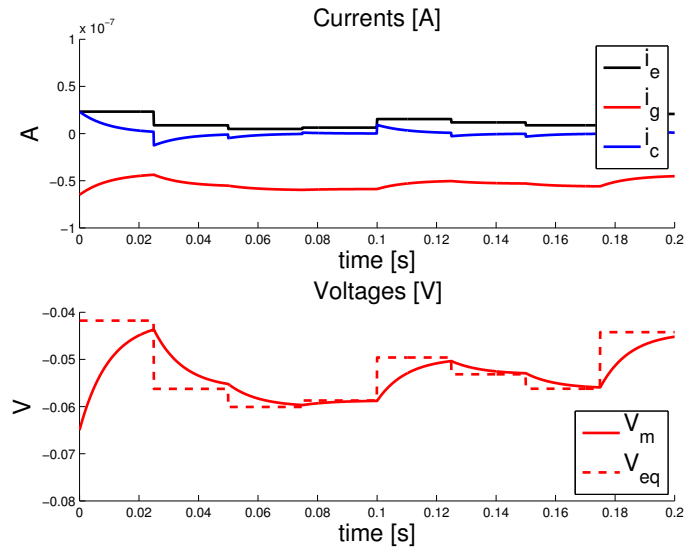


Figure 11: Comparison with resistive and capacitive currents.

## Summary of SCM generalization

- The single-compartment model (SCM) can be solved iteratively for arbitrary input currents (*e.g.*, electrode or synaptic currents).
- To do so, we divide time into short intervals, so that the input current may be considered piecewise constant.
- We can now understand the “leaky” and the “integrator” parts of the **leak-integrate and fire** model:
- It **integrates** because the membrane voltage sums (integrates) over input currents.
- It’s **leaky** because of leak conductance  $g_L = \frac{1}{r_m}$  dissipates the membrane potential over time.

### 3 Spike mechanism of LIF model

To complete the transition from SCM to LIF model, we add a mechanism for generating *spikes* or *action potentials*. This mechanism is artificial and ignores the biophysical basis of action potentials. It still offers a useful approximation of neuronal activity.

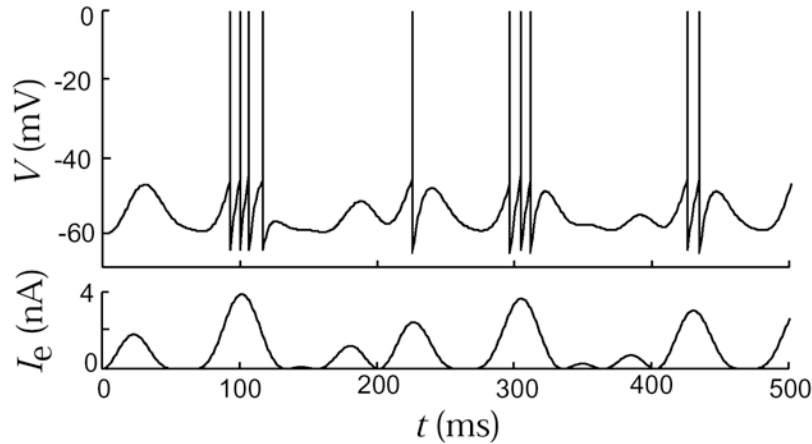


Figure 12: Spike mechanism. [2]

#### Threshold and reset potential

- *threshold potential*  $V_{th} > E_L$
- *reset potential*  $V_{reset} \ll E_L$
- When  $V_m(t) > V_{th}$ , set  $V_m(t + \Delta t) = V_{reset}$

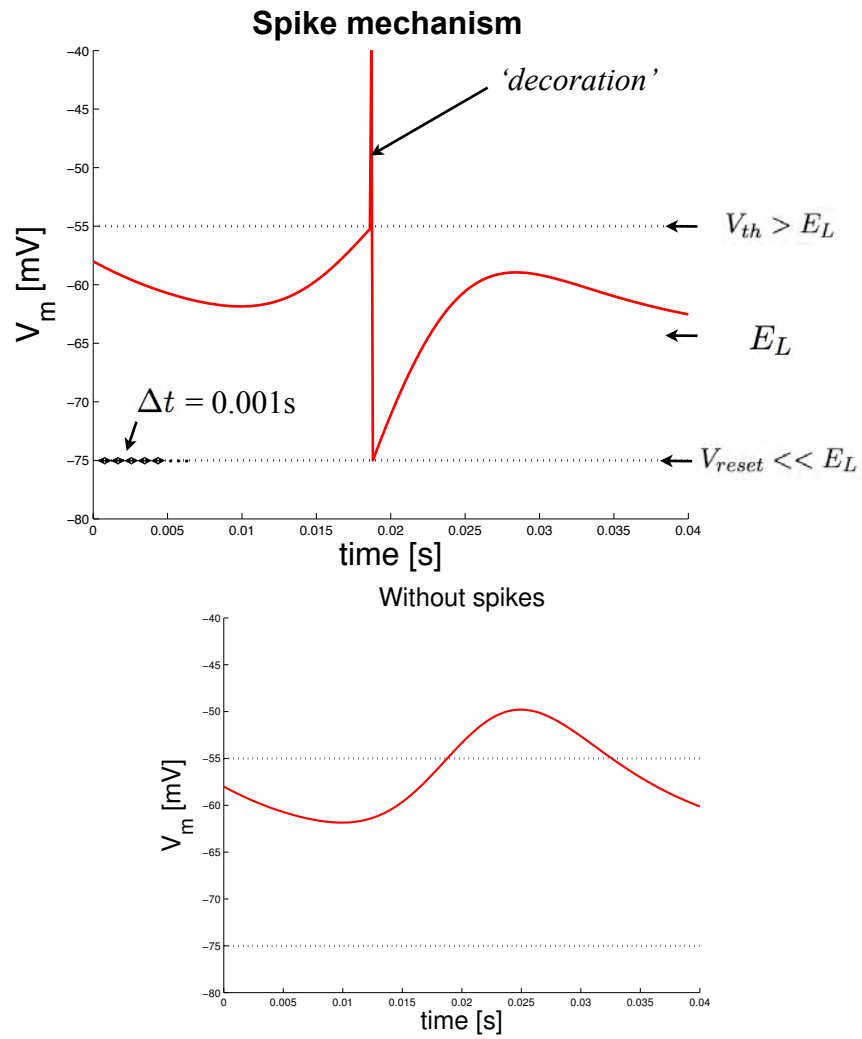


Figure 13: Top: Potential with spike. Bottom: Potential without spike.

$V_m(t)$  is changed continuously by input currents.

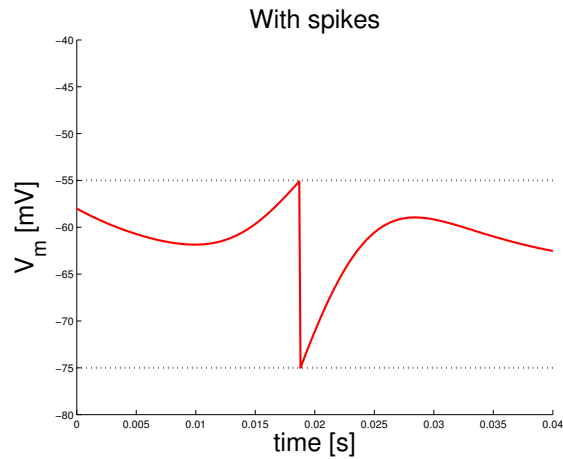


Figure 14: Taking off the spike above the threshold.

$V_m(t) < V_{th}$  is changed continuously by input currents.  $V_m(t) > V_{th}$  is changed discontinuously to  $V_{reset}$ .

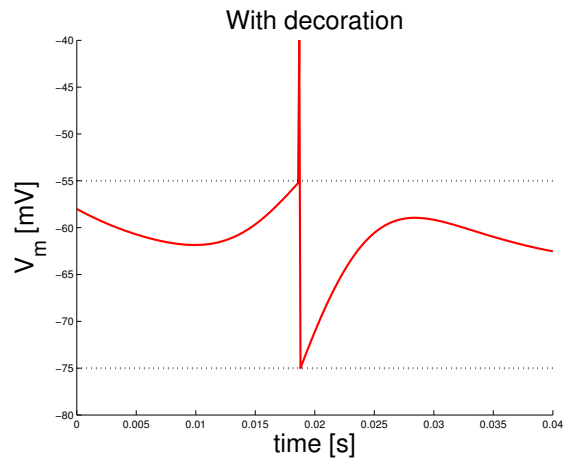


Figure 15: Spike merely used for decoration.

To give the discontinuity a more realistic appearance, the voltage trace is sometimes ‘decorated’ with a vertical line. This is for illustration only and is not part of the model!

### **Realistic and non-so-realistic aspects**

The realistic aspects of our firing mechanism are:



- $V$  changes continuously as long as it remains below a threshold value  $V_{th}$ .
- $V$  changes discontinuously whenever  $V_{th}$  is reached.
- After the discontinuity,  $V$  assumes a much lower value.

Of course, many other aspects are non-so-realistic:

- Instantaneous time-course.
- No depolarization during spike.
- No refractory period.
- No effect on membrane conductances.

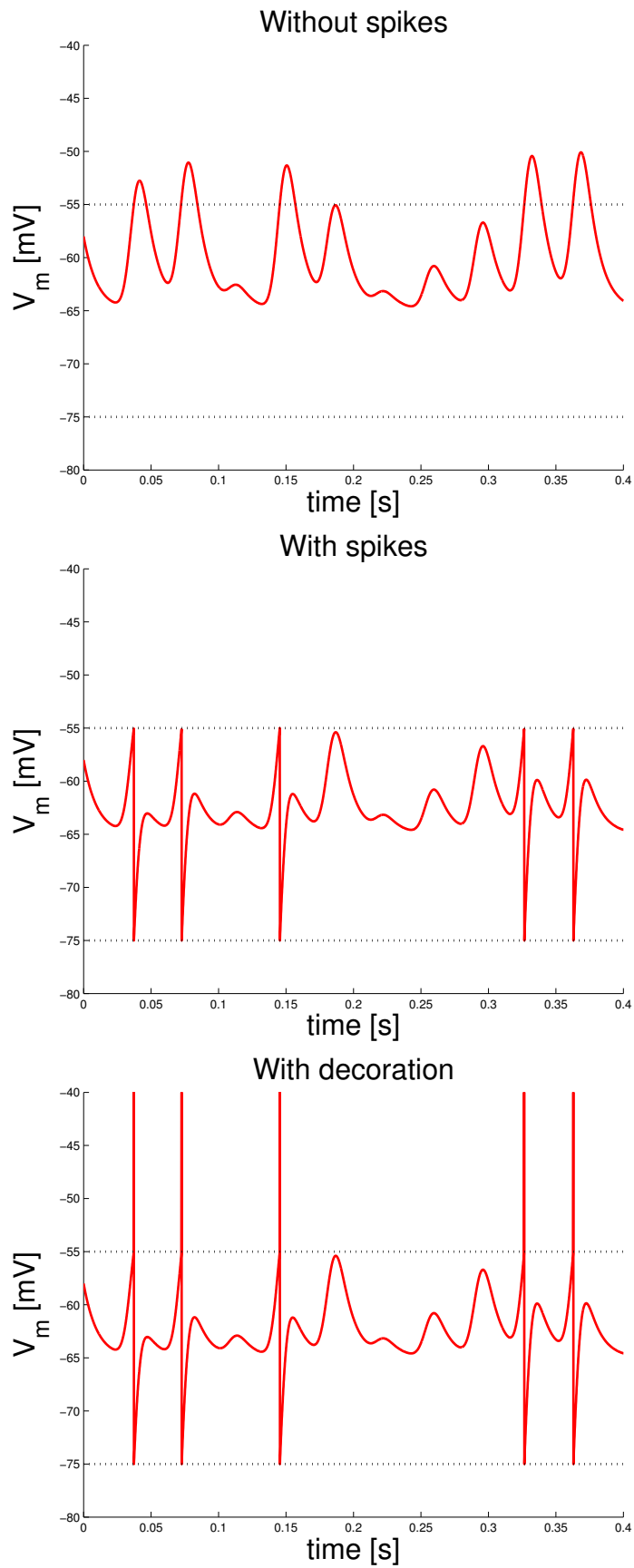


Figure 16: Difference of the potential with and without spikes.

## Summary LIF model

- Input currents are **integrated** by the membrane potential.
- Some of this current **leaks** out through the leak conductance.
- A threshold mechanism **fires** spikes, which are idealized action potentials.
- This is the **leaky-integrate-and-fire model**.

$$V_{i+1} = V_i^\infty + [V_i - V_i^\infty] \exp(-\Delta t / \tau_m) \quad V_{i+1} < V_{th}$$

$$V_{i+1} = V_{reset} \quad V_{i+1} > V_{th}$$

## 4 Rate response to constant input current (advanced)

When the input current  $I_e$  is constant, we can calculate the inter-spike interval  $t_{isi}$  exactly. The subthreshold potential always follows the same trajectory, beginning with  $V(0) = V_{reset}$  and ending at  $V(t_{isi}) = V_{th}$ .

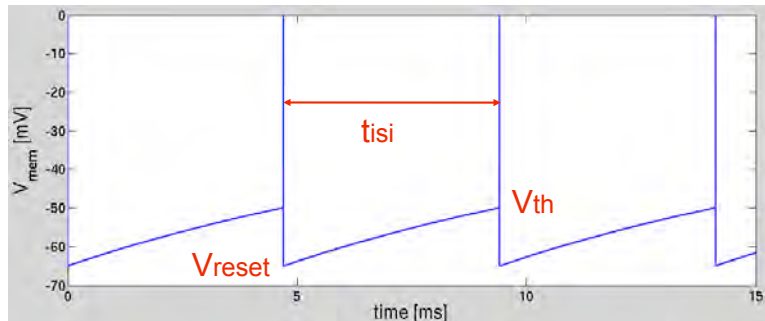


Figure 17: Inter-spike interval  $t_{isi}$

### Voltage between spikes

Solution of the basic equation

$$V_{th} = V_{\infty} + [V_{reset} - V_{\infty}] \exp\left(-\frac{t_{isi}}{\tau_m}\right), \quad V_{\infty} = E_L + r_m I_e$$

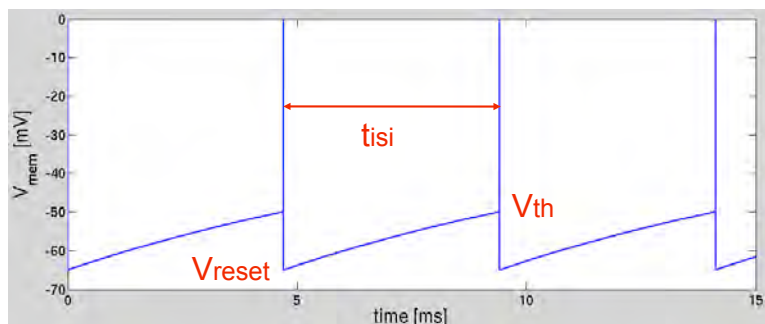


Figure 18: Voltage between spikes.

## Current-to-rate transfer function

We are now in a position to compute the response of a LIF neuron to input current.

Electrode current  $I_e$  represents the *input* to a LIF neuron. In a network model, this may be replaced by synaptic currents.

Spike rate  $r$  represents the *output* of a LIF neuron.

$$r \text{ [Hz]} = \frac{1}{t_{isi} \text{ [s]}}$$

We are interested in the ‘transfer function’

$$r = F(I_e)$$

## Solving for $t_{isi}$

$$V_{th} = V_{\infty} + [V_{reset} - V_{\infty}] \exp\left(-\frac{t_{isi}}{\tau_m}\right), \quad V_{\infty} = E_L + r_m I_e$$

$$\Leftrightarrow$$

$$\frac{V_{th} - V_{\infty}}{V_{reset} - V_{\infty}} = \exp\left(-\frac{t_{isi}}{\tau_m}\right)$$

$$\Leftrightarrow$$

$$t_{isi} = \tau_m \ln\left(\frac{V_{\infty} - V_{reset}}{V_{\infty} - V_{th}}\right) = \tau_m \ln\left(\frac{r_m I_e + E_L - V_{reset}}{r_m I_e + E_L - V_{th}}\right)$$

## Current threshold

A finite value for  $t_{isi}$  is obtained only if

$$r_m I_e + E_L - V_{th} \geq 0$$

The reason is that  $I_e$  must raise  $V_\infty = E_L + r_m I_e$  above  $V_{th}$ .

Only currents

$$I_e \geq \frac{V_{th} - E_L}{r_m}$$

produce spikes.

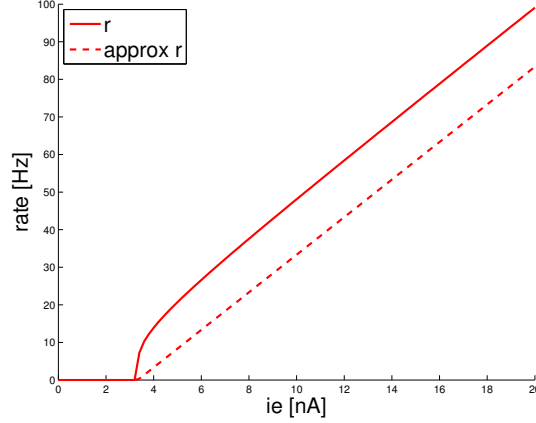


Figure 19: Comparison between "r" and "approximation r".

$$r \approx -16.6s^{-1} + 5s^{-1} \frac{I_e}{nA mm^{-2}} \quad I_e \geq 3.3 nA mm^{-2}$$

## Approximate formula

Seeking an approximate formula, we write

$$\begin{aligned} t_{isi} &= \tau_m \ln \left( \frac{r_m I_e + E_L - V_{reset}}{r_m I_e + E_L - V_{th}} \right) = \tau_m \ln \left( \frac{r_m I_e + E_L - V_{th} + V_{th} - V_{reset}}{r_m I_e + E_L - V_{th}} \right) = \\ &= \tau_m \ln \left( 1 + \frac{V_{th} - V_{reset}}{r_m I_e + E_L - V_{th}} \right) \end{aligned}$$

Approximating  $\ln(1 + z) \approx z$ , we obtain

$$t_{isi} \approx \frac{\tau_m (V_{th} - V_{reset})}{r_m I_e + E_L - V_{th}}$$

or

$$r = \frac{1}{t_{isi}} \approx -\frac{V_{th} - E_L}{\tau_m (V_{th} - V_{reset})} + \frac{1}{c_m (V_{th} - V_{reset})} I_e$$

## Summary constant input current

- For constant input currents, we can compute the inter-spike-interval,  $t_{isi}$ , exactly.
- This relates the output spike frequency  $r = 1/t_{isi}$  to the input current.
- Our model predicts an threshold input current, below which no spikes are fired.
- Above this threshold, it predicts an approximately linear increase of output spike frequency.

## 5 Spike-frequency adaptation (advanced)

The **leaky-integrate-and-fire model** may appear simplistic and unbiological.

However, it can be made as realistic as desired (as long as the details of the action potential are not important).

We illustrate this with a heuristic model of *spike-frequency adaptation*.

### **Spike-frequency adaptation**

Response rate to constant input declines over time. It *adapts* to a constant input current.

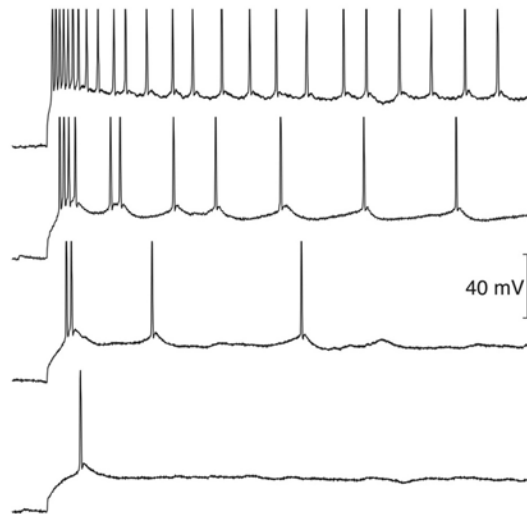


Figure 20: Spike frequency adaptation. [3]

### **$Ca^{2+}$ -gated $K^+$ -conductance**

A  $Ca^{2+}$ -gated  $K^+$ -conductance is thought to contribute to *spike-frequency adaptation*.

- During each spike, some  $Ca^{2+}$  enters the neuron. Repeated spikes elevate the  $Ca^{2+}$ -concentration.



- In response to elevated  $Ca^{2+}$ , certain  $K^+$ -conductances are opened.
- Due to the high negative reversal potential of  $K^+$ , this lowers the membrane potential and makes it more difficult to reach the firing threshold.
- In short, each spike makes it more difficult for another spike to occur.

## Heuristic model

We introduce a time-varying  $K^+$ -conductance  $g_{sfa}(t)$ .

Each spike increases the conductance by an amount  $\Delta g_{sfa}$ .

Between spikes,  $g_{sfa}$  relaxes exponentially to zero, with time-constant  $\tau_{sfa}$ .

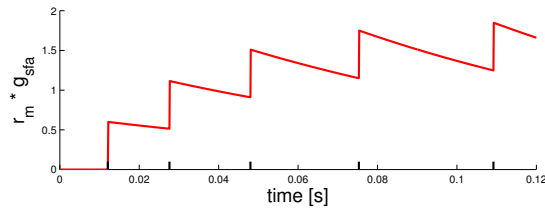


Figure 21: Each spike increases the conductance by an amount  $\Delta g_{sfa}$ .

## Dynamic equation of $g_{sfa}$

$$\tau_{sfa} \frac{dg_{sfa}}{dt} = -g_{sfa} \quad \text{if} \quad V(t) < V_{th}$$

$$g_{sfa}(t + dt) = g_{sfa} + \Delta g_{sfa} \quad \text{if} \quad V(t) \geq V_{th}$$

## Two dynamic equations

The dynamic equation takes into account a *constant* leak conductance  $g_L = \frac{1}{r_m}$  and a *time-varying* adaptation conductance  $g_{sfa}$ :

$$V(t) < V_{th} :$$

$$c_m \frac{dV}{dt} = -g_L (V - E_L) - g_{sfa} (V - E_K) + \frac{I_e}{A}$$

$$\tau_{sfa} \frac{dg_{sfa}}{dt} = -g_{sfa}$$

$$V(t) \geq V_{th} :$$

$$V(t + dt) = V_{reset}$$

$$g_{sfa}(t+dt) = g_{sfa} + \Delta g_{sfa}$$

## Membrane potential and SFA conductance

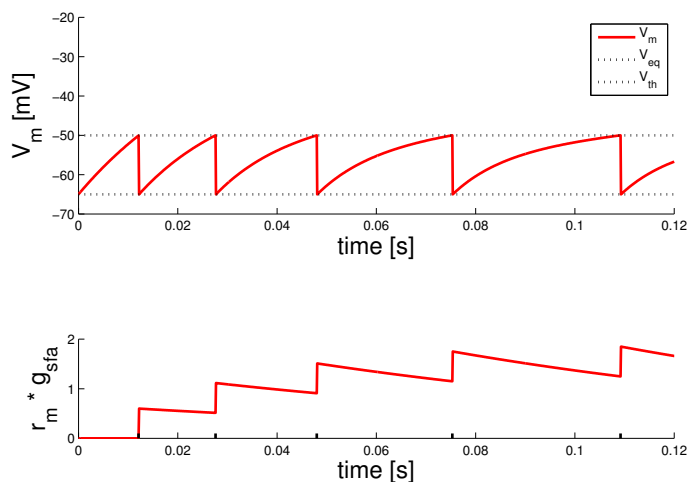


Figure 22: Membrane potential and SFA conductance.

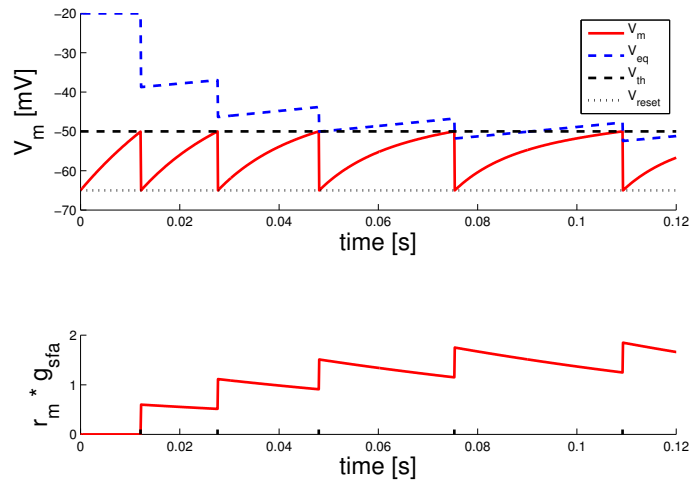


Figure 23: Inter-spike-intervals become progressively longer.

Note that  $g_{sfa}$  lowers the equilibrium potential  $V_{eq}$ , making it more difficult to reach the spiking threshold  $V_{th}$ .

### Graphical summary

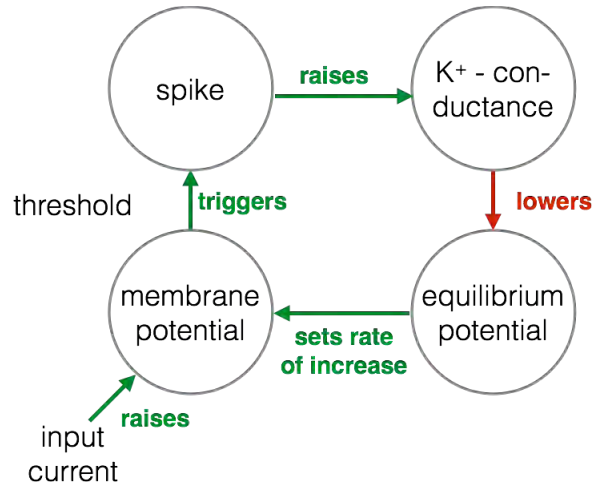


Figure 24: Summary.

### Hint for iterative solution

To solve this equation iteratively, we rearrange to determine the

effective values of  $\tau_{eff}$  and  $V_\infty$ :

$$\frac{\tau_m}{1 + r_m g_{sfa}} \frac{dV}{dt} = -V + \frac{E_L + r_m g_{sfa} E_K + r_m I_e/A}{1 + r_m g_{sfa}}$$

$$\tau_{eff} \frac{dV}{dt} = -V + V_\infty$$

$$\tau_{eff}(t) = \frac{\tau_m}{1 + r_m g_{sfa}(t)} \quad V_\infty(t) = \frac{E_L + r_m g_{sfa}(t) E_K + r_m I_e/A}{1 + r_m g_{sfa}(t)}$$

Note that both  $\tau_{eff}(t)$  and  $V_\infty(t)$  change with  $g_{sfa}(t)$ .

### **Summary of spike-frequency adaptation**

1. The LIF model can be refined by including additional conductances.
2. As an example, we have added a  $K+$  conductance that is increased by spikes.
3. The addition of time-varying conductances requires further dynamical equations.
4. In general, we need one dynamical equation for every independently time-varying quantity.

## 6 Bibliography

1. Model Neurons I: Neuroelectronics 5.1 Introduction 5.2 Electrical Properties of Neurons. Anonymous. Figure 5.3 Ref: <https://www.semanticscholar.org/paper/Model-Neurons-I%3A-Neuroelectronics-5.1-Introduction/0e259937bb89cd3ede50063ac32b98e56086c1b6>
2. Model Neurons I: Neuroelectronics 5.1 Introduction 5.2 Electrical Properties of Neurons. Anonymous. Figure 5.5 Ref: <https://www.semanticscholar.org/paper/Model-Neurons-I%3A-Neuroelectronics-5.1-Introduction/0e259937bb89cd3ede50063ac32b98e56086c1b6>
3. Dayan & Abbott (2001), Theoretical Neuroscience, MIT Press. Ref: <http://www.gatsby.ucl.ac.uk/~imate/biblio/dayanabbott.pdf>