# DOING PHYSICS WITH PYTHON

## SPIKING NEURONS

## LEAKY INTEGRATE-AND-FIRE MODEL

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**Google drive** **GitHub**

## mns004.py

## INTRODUCTION

Body fluids are good electrical conductors because salts and other molecules dissociate into positive and negative ions. The inside of an axon is filled with an ionic fluid that is separated from the surrounding body fluid by a thin membrane that is from about 5 nm to 10 nm thick. The ionic solutes in the extracellular fluid are mainly $Na^+$ and $Cl^-$ ions. In the intracellular fluid, the positive ions are mainly $K^+$ and the negative ions are mainly large negatively charged organic ions. Hence, there is a large concentration of $Na^+$ ions outside the axon and a large concentration of $K^+$ ions inside the axon. The concentration of the different ion species does not equalize by diffusion because of the special properties of the cell membrane. In the resting state when the axon is non-conducting, the axon membrane is highly permeable to $K^+$ ions, slightly permeable to $Na^+$ ions and impermeable to large negative organic ions. More $K^+$ ions leak out of the cell than $Na^+$ ions that leak into the cell. This leaves the inside of the cell more negative than the outside. A potential difference therefore exists across the cell membrane because of the difference in the concentration of ions in the extracellular and intracellular fluids. This potential difference is called the **membrane potential** $v_m(t)$. The outside of the cell is taken as the reference potential 0 V. The resting membrane potential has a strong negative polarization and is constant at about -65 mV. This negative membrane potential restricts the further diffusion of the $K^+$ to the outside of the cell so that equilibrium is established where the electrical forces balance the chemical forces. Thus, the membrane acts as a capacitor in parallel with a resistor.

The mechanism for the generation of an electrical signal by a neuron is conceptually simple. When a neuron receives a sufficient stimulus from another neuron, the permeability of the cell membrane changes. As a result of the changes in membrane permeability, the sodium ions first rush into the cell while the potassium ions flow out of it. The movement of the ions across the membrane constitutes an electric current signal which propagates along the axon to its terminations. These membrane currents depolarize the cell so that the interior of the cell becomes positive and a neuronal voltage signal is generated. These short voltage pulses are called **spikes** or **action potentials** and have a duration of less than a few milliseconds and have a peak about +40 mV. The action potential propagates along an axon without a change in shape. We can model the membrane of a neuron as a *RC* circuit as shown in figure 1.

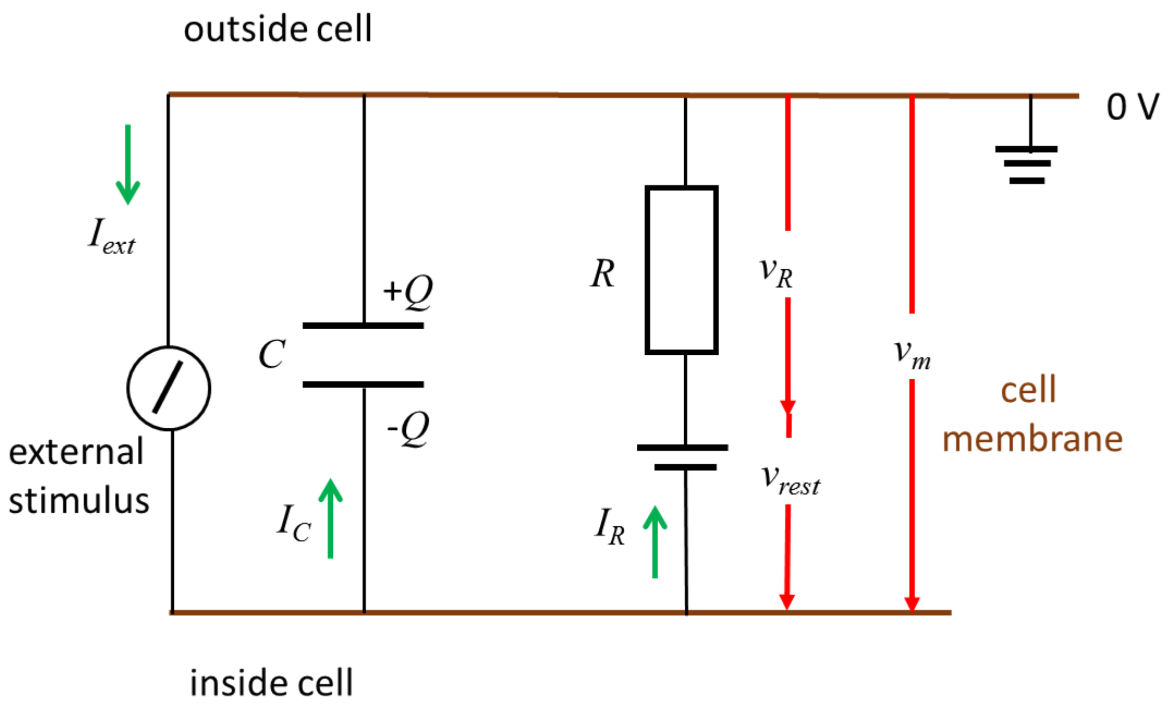



Fig. 1. *RC* circuit model of the nerve cell membrane used in the LIF model.

Capacitor current

$$Q = C\,v_m \qquad I_C = \frac{dQ}{dt} = C\,\frac{dv_m}{dt}$$

Leakage current through resistor

$$I_R = \frac{v_m - v_{rest}}{R}$$

Kirchhoff's current law

$$I_{ext} = I_C + I_R \qquad \tau = RC$$

$$(1) \qquad \tau \frac{dv_m}{dt} = -\left(v_m - v_{rest}\right) + R\,I_{ext}$$

Equation 1 is the **leaky integrate-and-fire** (LIF) differential equation for the membrane potential $v_m$ where $\tau = RC$ is the membrane time constant and $v_{rest}$ is the resting potential of the membrane

$$\left( \frac{dv_m}{dt} = 0 \qquad I_{ext} = 0 \qquad v_m(t) = v_{rest} \right).$$

We can solve equation 1 using the **fourth order Runge-Kutta method** to compute the membrane potential at a series of time steps of duration $\Delta t$ .

The spiking events are not explicitly modelled in the LIF model. Instead, when the membrane potential $v_m(t)$ reaches a certain threshold $v_{TH}$ (**spiking threshold**), it is instantaneously reset to a lower value $v_{reset}$ (**reset potential**) and the leaky integration process described by equation 1 continues with the membrane potential set at $v_{reset}$. However, we can artificially produce a spike when $v_m(t) > v_{TH}$ by setting $v_m(t) = v_{spike}$ then $v_m(t + \Delta t) = v_{reset}$ .

To add just a little bit of realism to the dynamics of the LIF model, it is possible to add an **absolute refractory period** $t_{ARP}$ immediately after a spike is generated when $v_m(t) = v_{spike}$. During the absolute refractory period, $v_m$ can be clamped to $v_{reset}$ and the leaky integration process re-initiated following a delay of $t_{ARP}$ after the spike.

## SIMULATIONS

The Python Code **mns004.py** is used to solve the system equation (equation 1) using the Runge-Kutta method. The variable flag is used to select the function for the external stimulus current.

Typical parameters used in the modelling are:

$$N = 5000 \quad R = 10^7\ \Omega \quad \tau = 10\ \text{ms}$$

$$v_{rest} = -60\ \text{mV} \quad v_{TH} = -30\ \text{mV} \quad v_{reset} = -80\ \text{mV}$$

$$v_{spike} = +20\ \text{mV} \quad t_{ARP} = 5\ \text{ms}$$

### Simulation 1 (flag = 0)

#### $I_{ext} = 0$ Exponential relaxation to resting potential

The membrane potential if disturbed from its resting potential and no spike is fired then the membrane potential will relax back to the resting potential. The relaxation time is determined by the time constant $(\tau = RC)$, the larger the time constant, the more slowly the membrane potential flows appraoches the resting value as shown in figure 1.1.

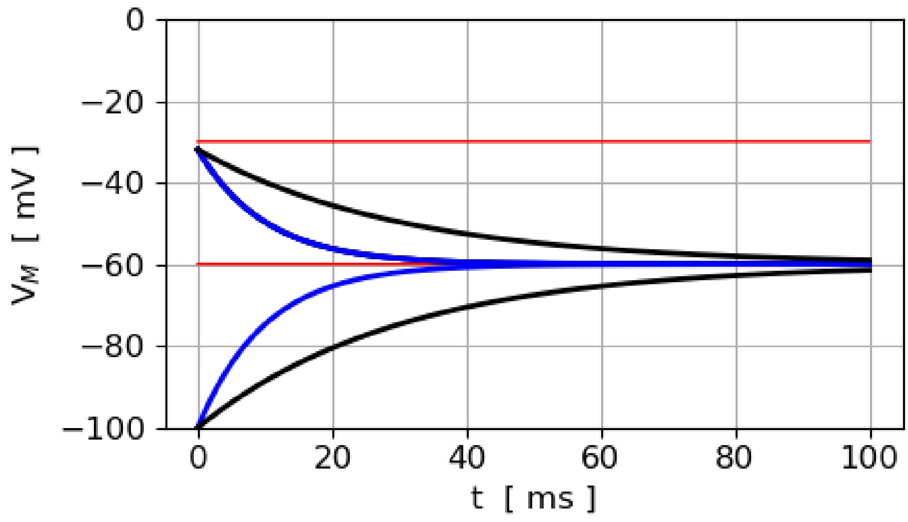



Fig. 1.1. Time evolution of the membrane potential for initial conditions $V_0$ = -32 mV and $V_0$ = -100 mV. The membrane potential $v_m$ relaxes to the resting membrane potential $v_{rest}$ = -60 mV. The rate of relaxation is determined by the time constant $\tau$. The larger the value of the time constant, the slower the relaxation. Blue curves $\tau = 10 \text{ ms}$ and black curves $\tau = 30 \text{ ms}$.

## Simulation 2 (flag = 1)

### Single pulse external current stimulus

The system is described by the ODE

(1) $$\tau \frac{dv_m}{dt} = -\left(v_m - v_{rest}\right) + R\, I_{ext}$$

When a short pulse acts as the external stimulus most of the charge $Q$ is deposited onto the capacitor and very little charge passes through the resistor. Initially the capacitor is charged and then discharges through the resistor as the input stimulus value goes to zero. For a short external current pulse with duration $\Delta t$ where $\Delta t \ll \tau$ and height $I_{max}$ then

$$v(t+\Delta t) = \left(1 - \frac{\Delta t}{\tau}\right) v(t) + \left(\frac{R}{RC}\right) \Delta t\, I_{ext} \qquad v(t) = v_m(t) - v_{rest}$$

and the charge $Q = \Delta t\, I_{\max}$ then we get

(2) $$v(t+\Delta) = v(t) + Q / C$$

So, the charge $Q$ must have a threshold value $Q_{TH}$ if the membrane potential is to exceed the threshold potential.

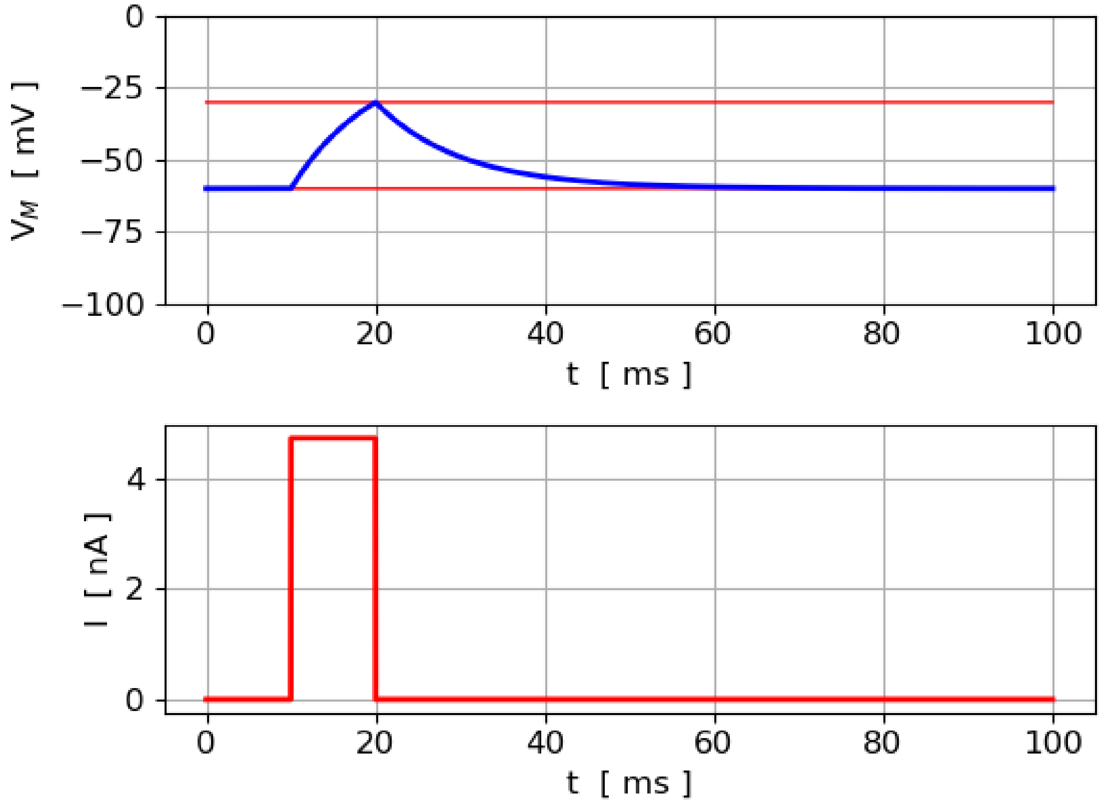



Fig 2.1. Short pulse: $\Delta t =$ 10 ms, $I_{\max} = 4.74\,\text{nA}$, **$Q$ = 47.4 pC**

$Q < Q_{TH}$ since no spike is fired, $\max(v_m) < v_{TH}$.

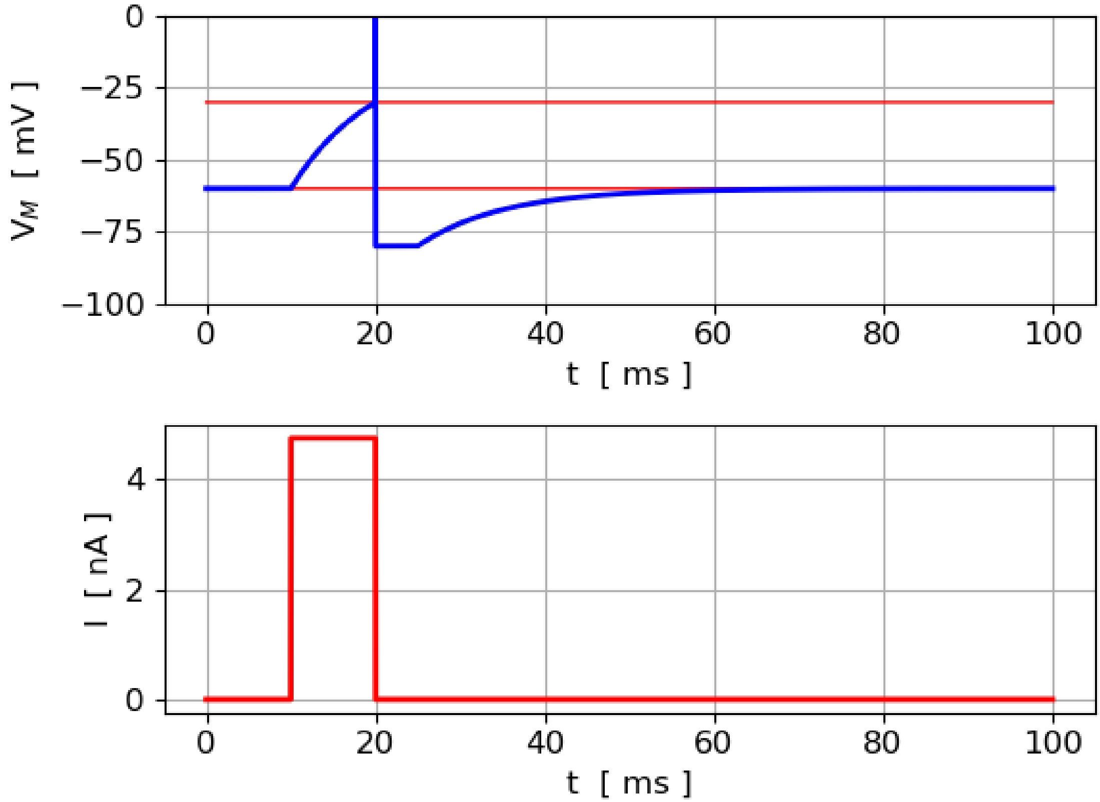
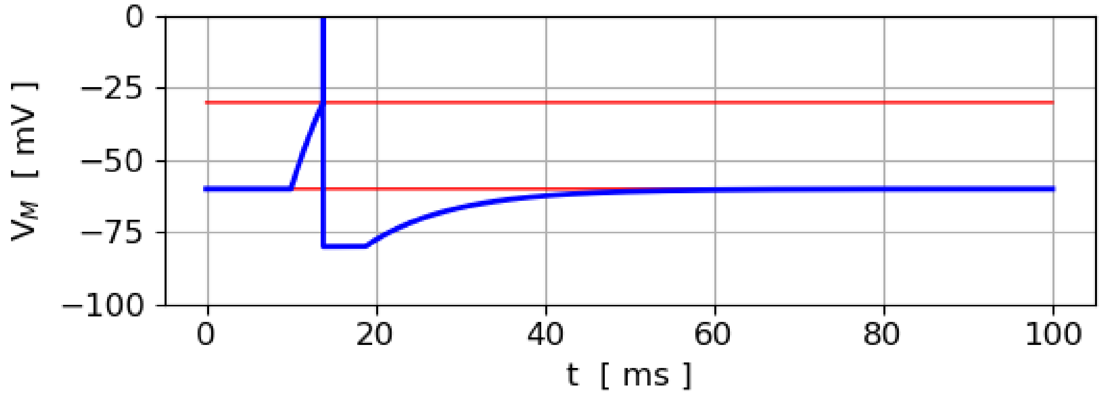



Fig 2.2. Short pulse: $\Delta t =$ 10 ms, $I_{max}$ = 4.75A, ***Q* = 47.5 pC**
$Q > Q_{TH}$ since a spike is fired, $\max(v_m) > v_{TH}$.

From figures 2.1 and 2.2 the threshold value of the charge can be approximated to be $Q_{TH} = 47.45\ \text{pC}$. Figure 2.3 shows a shorter pulse with a greater amplitude but with the same area under the $t$ vs $I_{ext}$ plot, so the same charge $Q$ is deposited and this results in an identical spiking of the neuron.



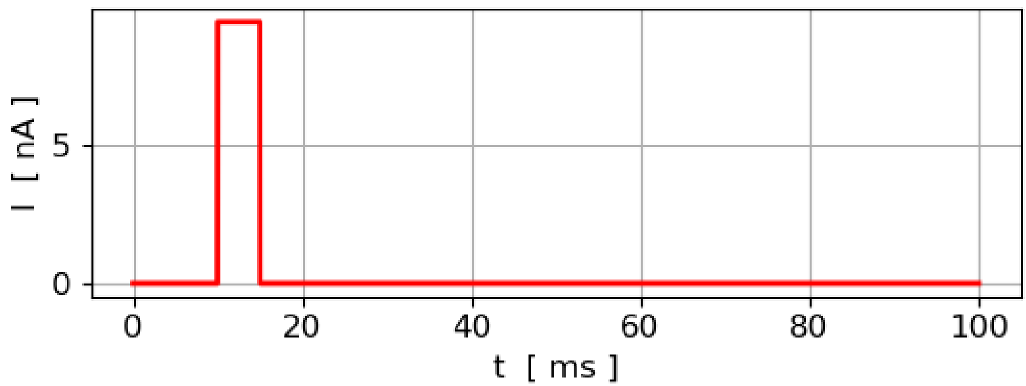




Fig 2.3. Short pulse: $\Delta t =$ 5 ms, $I_{max}$ = 9.50A, $\boldsymbol{Q}$ **= 47.5 pC**
$Q > Q_{TH}$ since a spike is fired, $\max(v_m) > v_{TH}$.

### Simulation 3 (flag = 2)

### Double pulse external current stimulus

Assume the first pulse results in the neuron spiking as shown in figure 3. We can ask the question; will a second pulse also produce a spike?

Pulse 1:

$$\Delta t = 10\ ms \quad I_{\max} = 4.80 \text{ nA} \quad Q = 48.00 \text{ pC}$$

Pulse 2 (figure 3.1):

$\Delta t = 10\ ms \quad I_{\max} = 4.80\ \text{nA} \quad Q = 48.00\ \text{pC}$

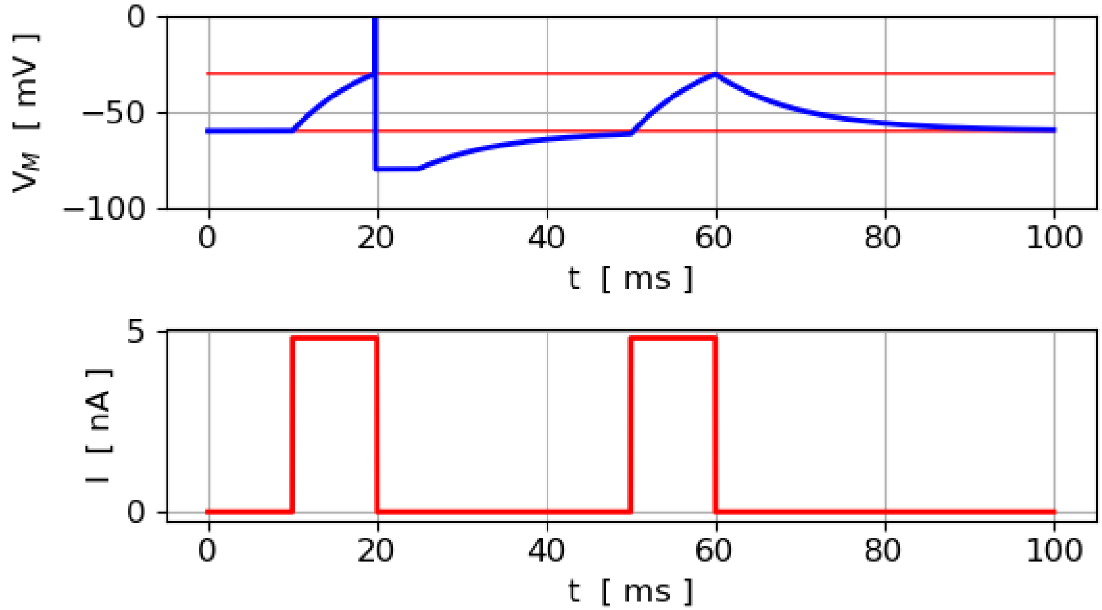



Fig. 3.1. The first pulse (pulse 1) produces a spike, but the second identical pulse (pulse 2) does not.

The second pulse occurs in a relative refractory period where the membrane potential has not as yet relaxed back to its resting potential.

Pulse 2 (figure 3.2):

$\Delta t = 10\ ms \quad I_{\max} = 5.00\ \text{nA} \quad Q = 50.00\ \text{pC}$

By increasing $I_{max}$, sufficient charge is now delivered to produce the second spike.

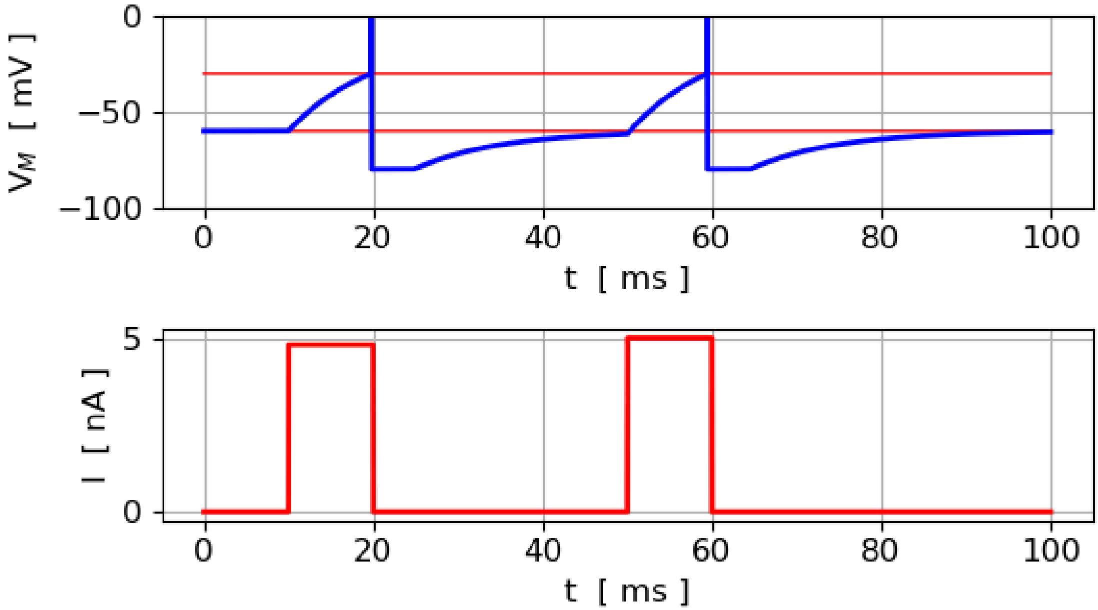



Fig. 3.2. Both pulses now cause an action potential.

If the second pulse arrives in the absolute refractory period after the first spike, then it is unlikely that the neuron will fire and produce a second spike.

Pulse 2 (figure 3.3):

$\Delta t = 10\ ms \quad I_{\max} = 7.00\ \text{nA} \quad Q = 70.00\ \text{pC}$

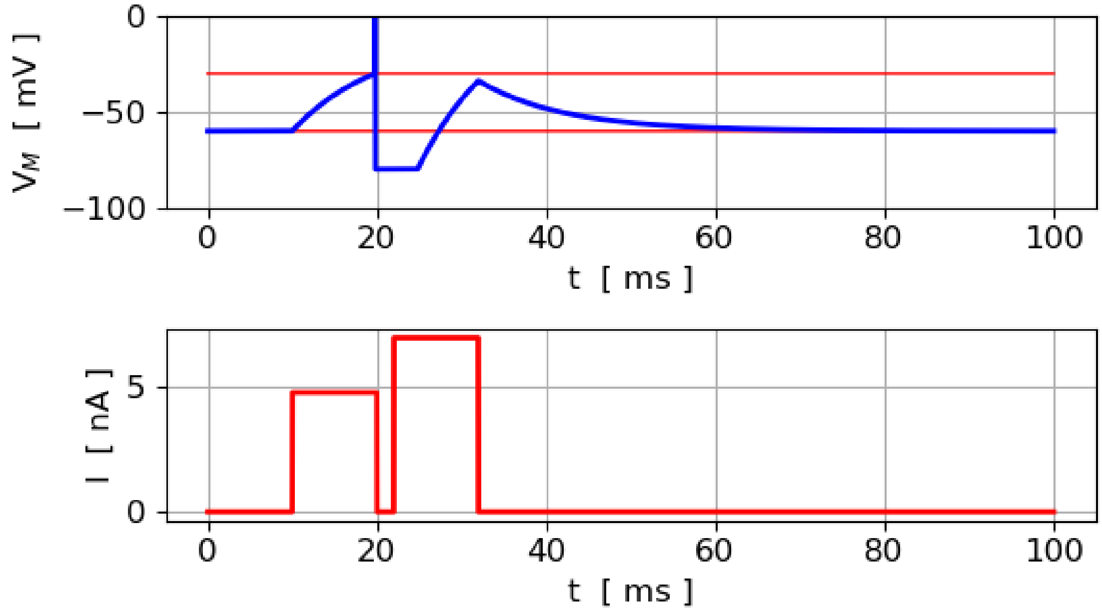



Fig. 3.3. Generally, a spike will not be fired if the second pulse occurs in the absolute refractory period.

## Simulation 4 (flag 3)

### Series of input pulses for the external current stimulus

A series of input pulses results in a linear summation of the membrane response to each pulse. If the membrane potential remains at a value less than the threshold potential then no spikes are generated. Only when the summation of the input pulses causes the membrane potential to reach the threshold potential does a spike occur as shown in figure 4.

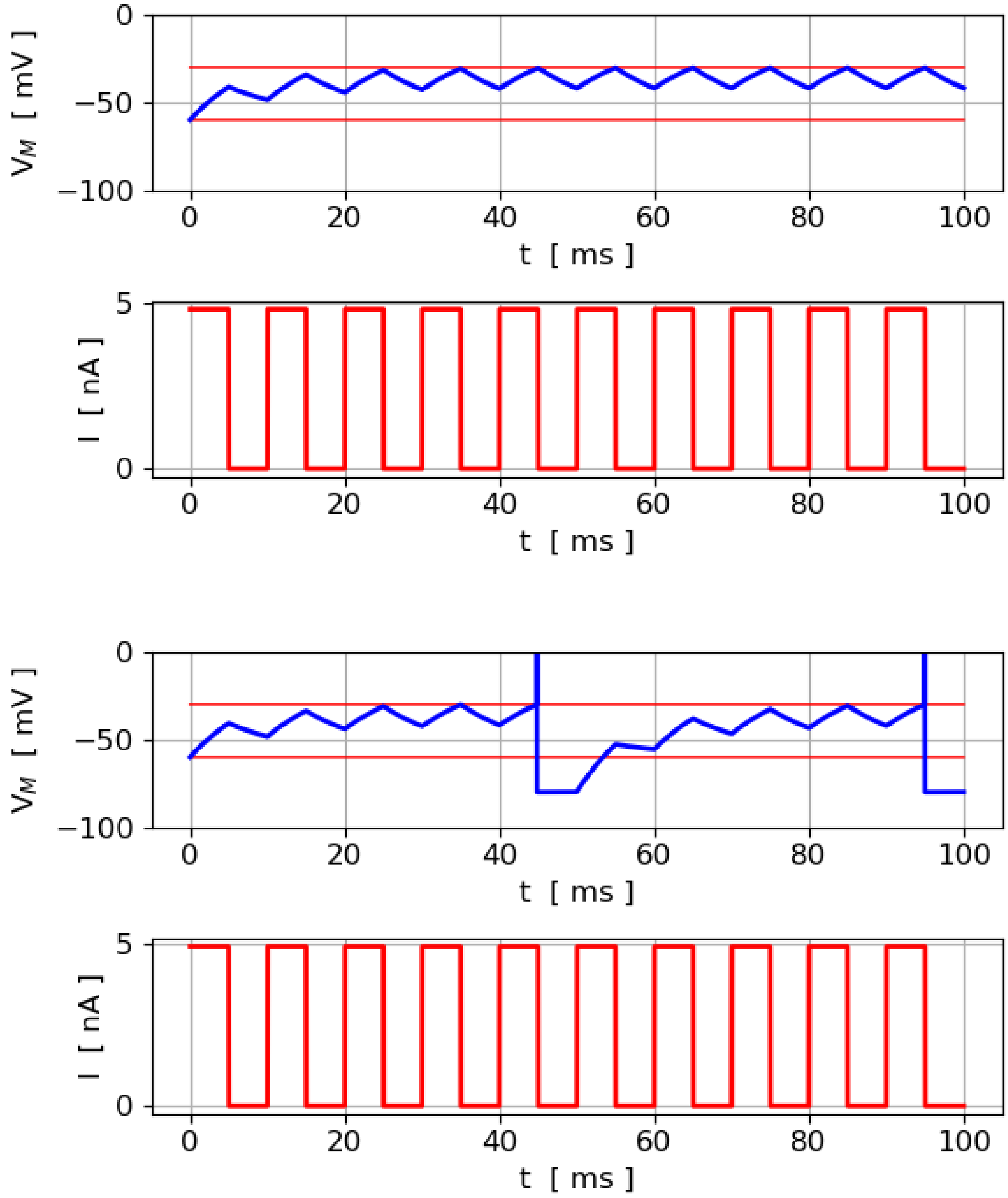


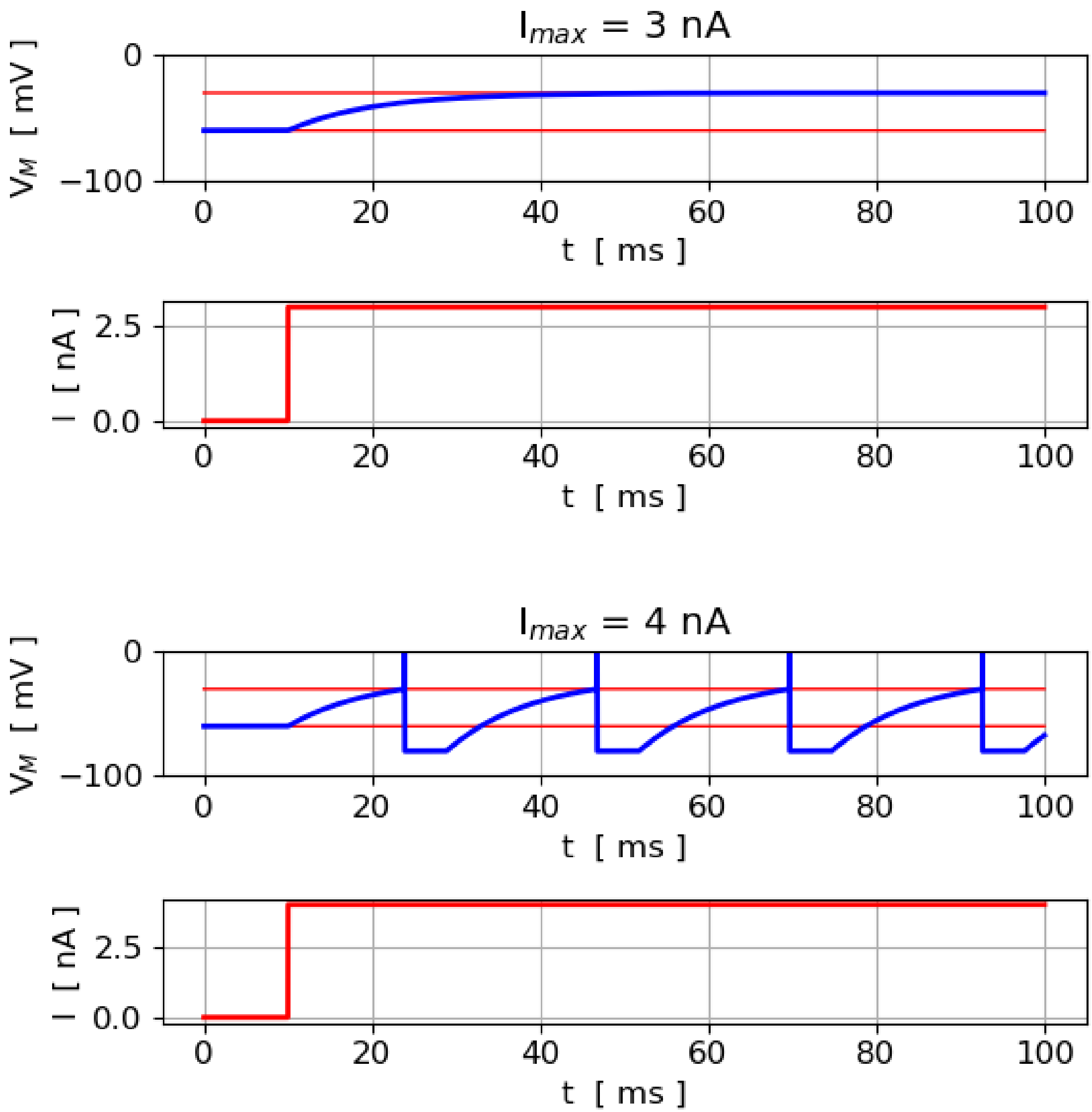

Fig. 4. Top input pulse $I_{max}$ = 4.8 nA and bottom pulse $I_{max}$ = 4.9 nA.

This in some sense is a realistic situation where the neuron is stimulated by pre-synaptic spikes arriving at its synapses. The pre-synaptic spikes are linearly summed to give the input current and when the threshold voltage is reached, a spike is generated.

## Simulation 5 (flag 4)

### Step external current stimulus

A step input stimulus of sufficient strength may result in a continual firing of the neuron at **regular intervals** as shown in figure 5. Provided the neuron fires then the firing rate increases with the strength of the external current step.



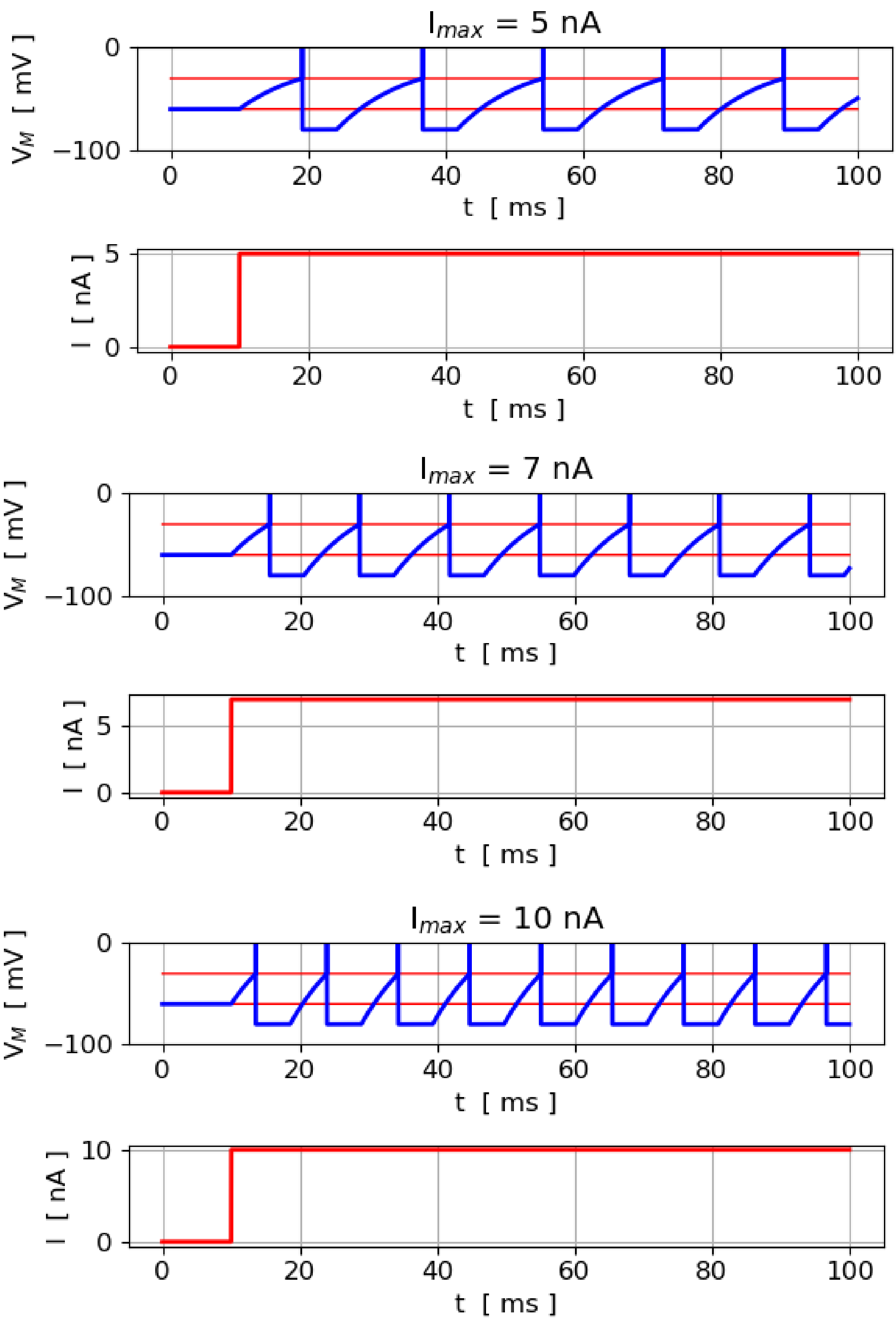



Fig. 5. Membrane potential response to a step external current stimulus. If the neuron fires, the frequency of the spiking increases with the height of the step.

## Simulation 6 (flag = 5)
### Ramp input

A ramp input stimulus produces action potentials with an increasing firing rate as the input strength increases (figure 6)

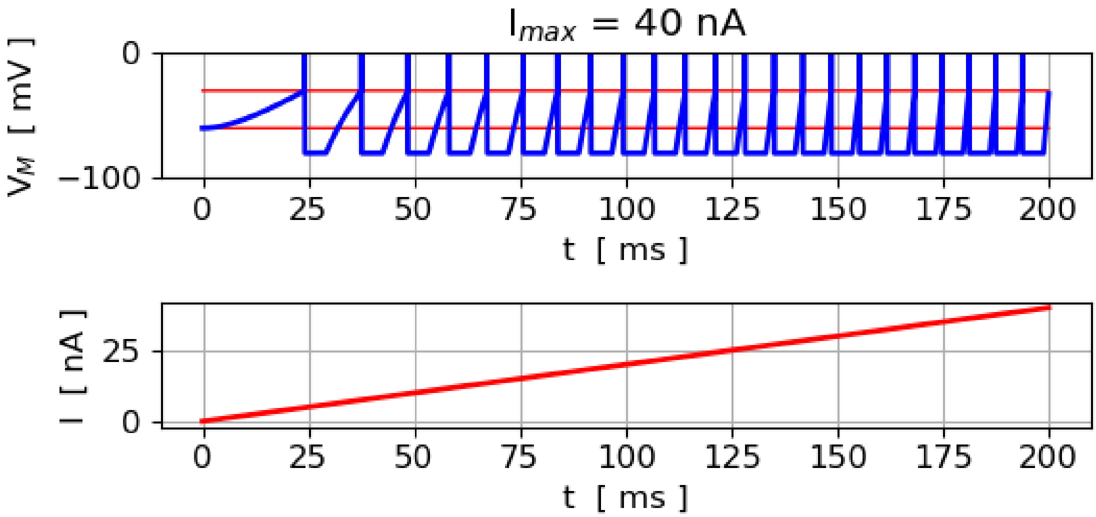



Fig. 6.1. Firing rate of neuron increases as strength of the input stimulus increases.

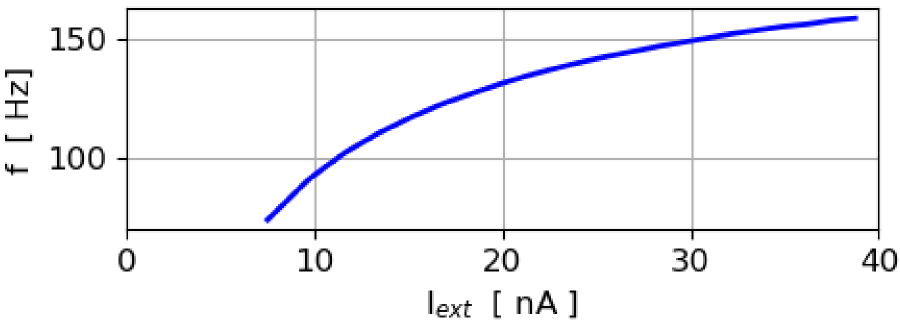



Fig. 6.2. An action potential is not produced until the external current exceeds a critical value which has a value of about 7.5 nA.

# REFERENCES

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