DOING PHYSICS WITH MATLAB

THE NEURON MEMBRANE AS A CAPACITOR

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MATLAB

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simpson1d.m (function: integration using Simpson's rule)

RC01.m (RC circuit: charging a capacitor)

RC02.m (RC circuit: discharging a capacitor)

RC03.m (RC circuit: step or pulse current input)

INTRODUCTION

Many electronic circuits use combinations of resistors and capacitors for controlling the timing of events. For example, the flash unit in a camera: typically there is a delay before taking a flash picture because of the time required to charge the capacitor. In a nerve cell called a **neuron**, currents can pass through the cell membrane from inside to out or from outside to in. Inside and outside the neuron is an electrolytic fluid which is a good conductor and the membrane acts as a dielectric (insulator) separating the two electrolytes. Thus, the simplest model of a segment of the neuron membrane is a capacitor and resistor connecting the outside to the inside of the cell.

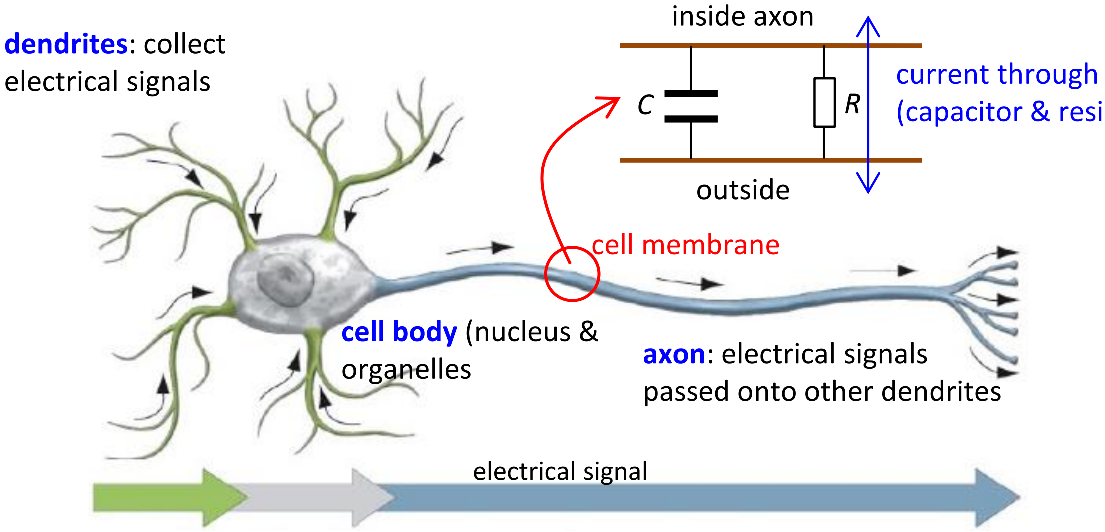


Fig. 1. The membrane of a neuron can be modeled as a combination of a resistor and a capacitor.

To understand the transient effects in RC circuits and to start thinking about how signals are propagated along nerve cells, models of RC circuits will be developed.

CHARGING A CAPACITOR RC01.m

Let a capacitor *C* and resistor *R* be connected in series to a battery of emf *E* via a switch. At time *t* = 0, the switch is closed and initially the capacitor is uncharged.

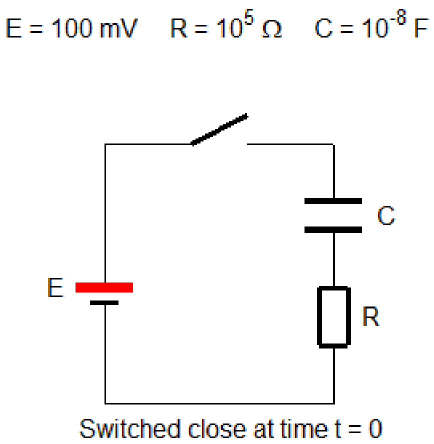


Fig. 2. *RC* circuit diagram used to charge the capacitor.

Variables and default values

E = 100 mV battery emf

$R = 10^3\ \Omega$ resistance (typical neuron membrane resistance value)

$C = 10^{-6}$ F capacitance (typical neuron membrane capacitance)

$\tau = RC = 10^{-3}$ s = 1.00 ms time constant (tau). For nerves: time constants ~ ms

V_C	potential across capacitor [V]
V_R	potential across resistor [V]
Q	charge on plates of capacitor [C]
$I = I_R = I_C$	current [A]
P_E	power supplied by battery [W]
P_C	power stored by capacitor [W]
P_R	power dissipated by resistor [W]
w_E	energy supplied by battery [J]
w_C	energy stored by capacitor [J]
w_R	energy dissipated by resistor [J]

Derivations

From Kirchhoff's voltage law, we can write the differential equation for V_C and solve it to find all the parameters that describe the RC circuit.

Kirchhoff's voltage law

$$E = V_C + V_R$$

Voltage and charge stored by capacitor

$$V_c = \frac{Q}{C} \qquad Q = C V_C$$

Current (series circuit)

$$I = I_R = I_C = \frac{dQ}{dt} = C\frac{dV_C}{dt}$$

ODE to solve (from Kirchhoff's voltage law)

$$V_R = I_R\, R = R\,C\,\frac{dV_C}{dt}$$

$$\frac{dV_C}{\left(E - V_C\right)} = \frac{1}{R\,C}\,dt$$

Solution of ODE with initial conditions t = 0 and V_C = 0

$$V_C = E\left(1 - e^{-t/RC}\right) = E\left(1 - e^{-t/\tau}\right)$$

From the solution V_C

$$V_R = E\, e^{-t/\tau}$$

Current

$$I = I_C = I_R = \left(\frac{E}{R}\right) e^{-t/\tau}$$

Charge

$$Q = C\,E\,\left(1 - e^{-t/\tau}\right)$$

Power

$$P_E = E\,I \qquad P_C = V_C\,I \qquad P_R = V_R\,I_R$$

Energy (integration by Simpson's rule)

$$w_E = \int_0^t P_E\, dt \qquad w_C = \int_0^t P_C\, dt \qquad w_R = \int_0^t P_R\, dt$$

The ODE for V_C can also be solved using the **finite difference method**.

ODE to be solved

$$\frac{dV_C}{dt} = \frac{1}{\tau}\left(E - V_C\right)$$

Finite differences approximate the derivative $\quad (\Delta t << \tau)$

$$\frac{V_C(t+\Delta t) - V_C(t)}{\Delta t} = \frac{1}{\tau}\left(E - V_C(t)\right)$$

Solve starting with $t = 0$ and $V_C(0) = 0$

$$V_C(t+\Delta t) = V_C(t) - \frac{\Delta t}{\tau}\left(E - V_C(t)\right)$$

Graphical Predictions RC01.m

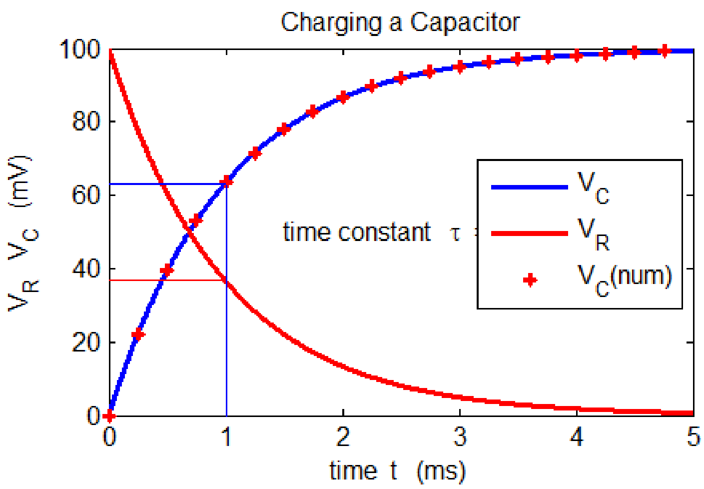


Fig. 3. When the switch is closed, **exponential** changes occur in the potential across the capacitor *C* and the resistor *R*. The applied potential difference *E* at all times is the sum of the potential difference across the capacitor V_C and resistor V_R ($E = V_C + V_R$). As soon as the switch is closed: $V_C = 0$ and $V_R = E$. In a time of one time constant $\tau = RC$ the capacitor potential V_C increases by 63% of its final value and the potential across the resistor V_R drops by 63% to 37% of its initial value.

If a membrane is suddenly allowed to charge passively to a new membrane potential, the time course of the voltage is exponential and undergoes 63% of the total change in about 1 ms.

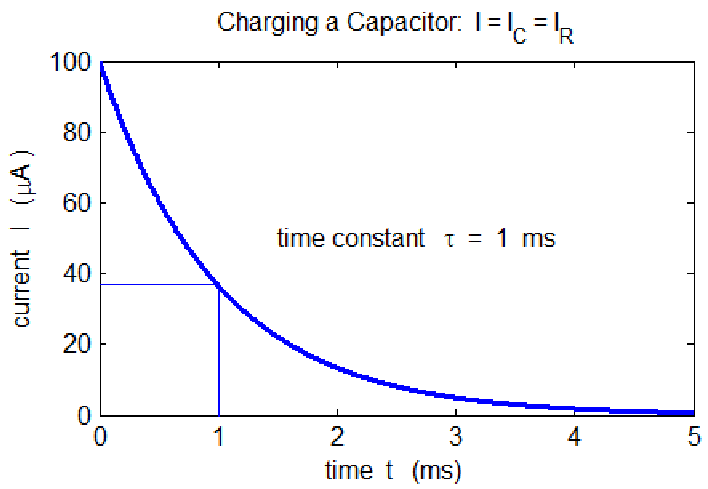


Fig. 4. When the switch is closed, the current decreases **exponentially**. In a time of one time constant $\tau = RC$ the current ($I = I_C = I_R$) in the circuit drops by 63% to 37% of its initial value.

Once fully charged, a capacitor in a DC circuit acts like an open switch in the branch in which it is placed. This property is used in many electronic circuits to remove a DC voltage component of a signal.

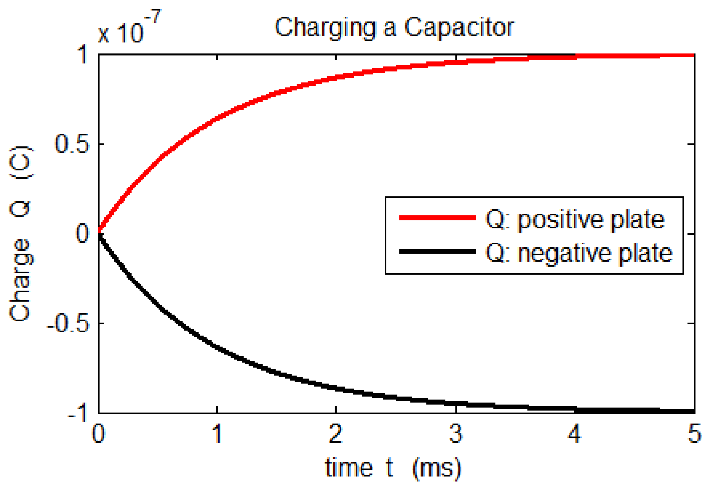


Fig. 4. When the switch is closed, the capacitor is

charged as the charged stored on the two plates increases as an exponential function. The curve for the charge is identical in shape to the potential difference across the capacitor as $Q \propto V_C$. For $t > 5\,\tau$, the capacitor can be considered fully charged.

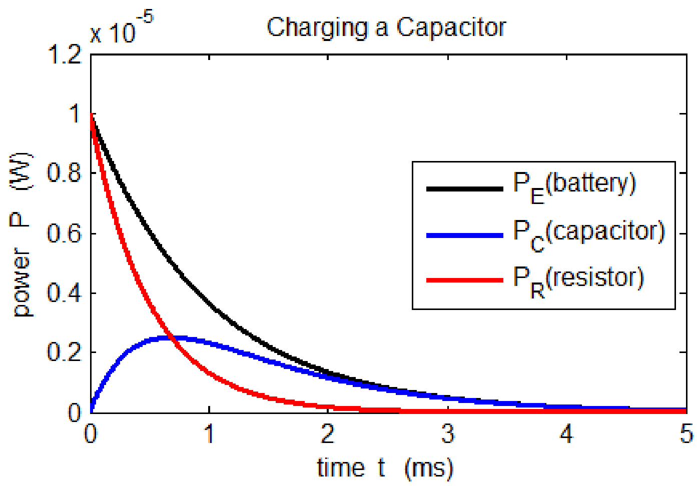


Fig. 5. The battery supplies the energy in the circuit. Some of this energy is stored by the capacitor and the remainder of the energy is dissipated as internal energy by the resistor's current (Ohmic losses).

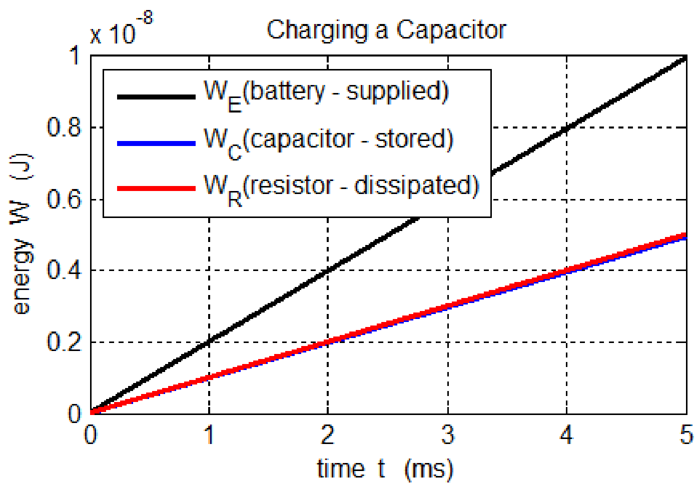


Fig. 6. The battery supplies the energy in the circuit.

Some of this energy is stored by the capacitor and the remainder of the energy is dissipated as internal energy by the resistor’s current (Ohmic losses). The energy stored by the capacitor at all times in equal to half the energy dissipated by the resistor (W_C = W_R).

The energy stored by the capacitor is given by

$$W_C = \tfrac{1}{2}CV^2 = (\tfrac{1}{2})(10^{-6})(10^{-1})^2 \text{ J} = 5.0 \times 10^{-9} \text{ J}$$

which agrees with the prediction of our model.

DISCHARGING A CAPACITOR RC02.m

Let a capacitor *C* and resistor *R* be connected in parallel to each other and with no connection to a source of emf. At time *t* = 0, the switch is closed and initially the capacitor is fully charged.

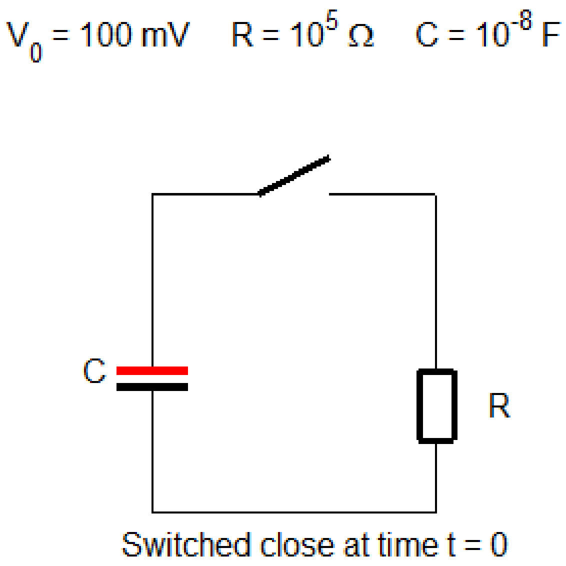


Fig. 7. *RC* circuit diagram used to discharge the capacitor.

Derivations

From Kirchhoff's voltage law, we can write the differential equation for V_C and solve it to find all the parameters that describe the RC circuit.

Kirchhoff's voltage law

$$V_C + V_R = 0$$

Voltage and charge stored by capacitor

$$V_c = \frac{Q}{C} \qquad Q = C V_C$$

Initial values $t = 0$ $V_0 = 100$ mV

$$V_{c0} = \frac{Q_0}{C} \qquad Q_0 = C V_{C_0}$$

Current (series circuit)

$$I = I_R = I_C = \frac{dQ}{dt}$$

ODE to solve (from Kirchhoff's voltage law)

$$V_R = I_R R = R \frac{dQ}{dt}$$

Solution of ODE with initial conditions $t = 0$ and $Q_0 = V_{C0}$

$$\frac{dQ}{dt} = -\frac{1}{RC} Q$$

$$Q = Q_0 \, e^{-t/RC} = Q_0 \, e^{-t/\tau}$$

From the solution Q

$$V_C = V_0 \, e^{-t/\tau} \qquad V_R = -V_0 \, e^{-t/\tau}$$

Current

$$I = I_C = I_R = -\frac{V_0}{R} e^{-t/\tau}$$

Power

$$P_E = E\,I \qquad P_C = V_C\,I \qquad P_R = V_R\,I_R$$

Energy (integration by Simpson's rule)

$$w_E = \int_0^t P_E\,dt \qquad w_C = \int_0^t P_C\,dt \qquad w_R = \int_0^t P_R\,dt$$

Graphical Predictions RC02.m

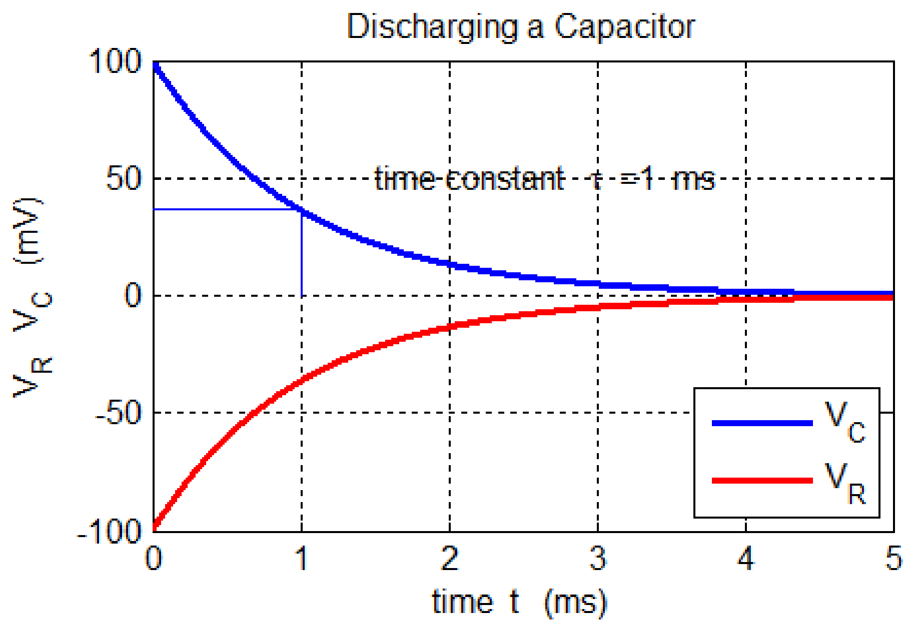


Fig. 8. When the switch is closed, **exponential** changes occur in the potential across the capacitor *C* and the resistor *R*. At all times is the sum of the potential difference across the capacitor V_C and resistor V_R is zero ($V_C + V_R = 0$). As soon as the switch is closed: V_C = +100 V and the voltage drop across the resistor is V_R = -100 mV. In a time of one time constant $\tau = RC$ the capacitor potential V_C and resistor potential V_R magnitudes decreases by 63% of their final values to a value of 37% of their initial values.

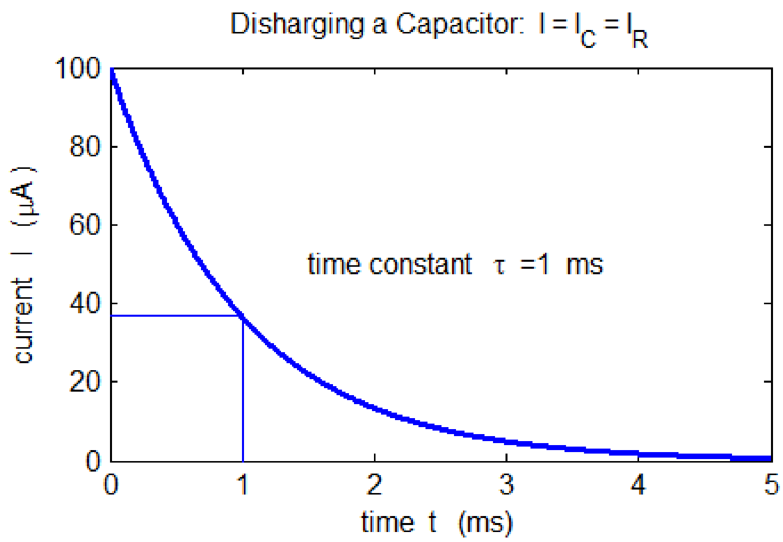


Fig. 9. When the switch is closed, the current decreases **exponentially**. In a time of one time constant $\tau = RC$ the current ($I = I_C = I_R$) in the circuit drops by 63% to 37% of its initial value.

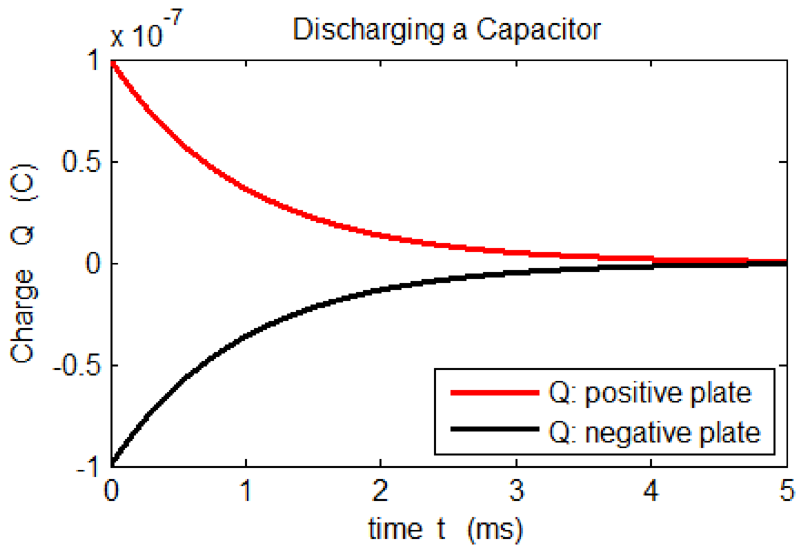


Fig. 10. When the switch is closed, the capacitor is fully charged as the charged stored on the two plates then decreases as an exponential function. The curve for the charge is identical in shape to the potential difference across the capacitor as $Q \propto V_C$. For $t > 5\,\tau$, the capacitor can be considered fully discharged.

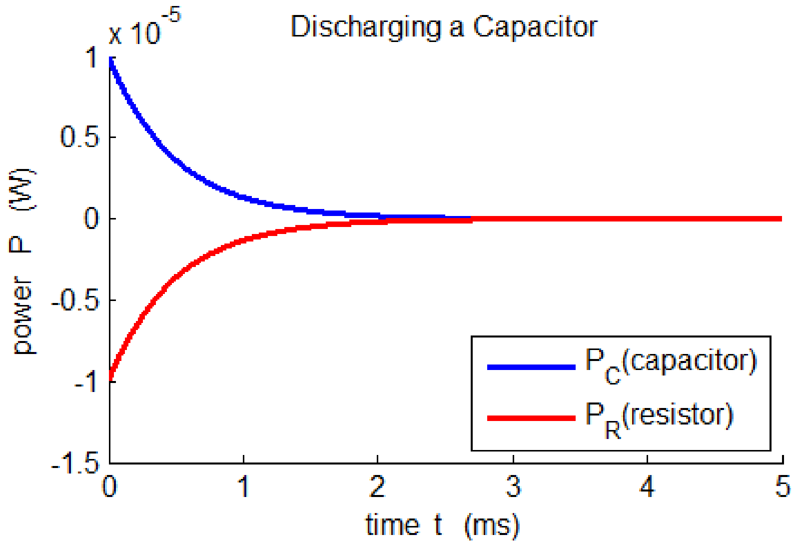


Fig. 11. The energy initially stored by the capacitor is dissipated as internal energy by the resistor’s current (Ohmic losses).

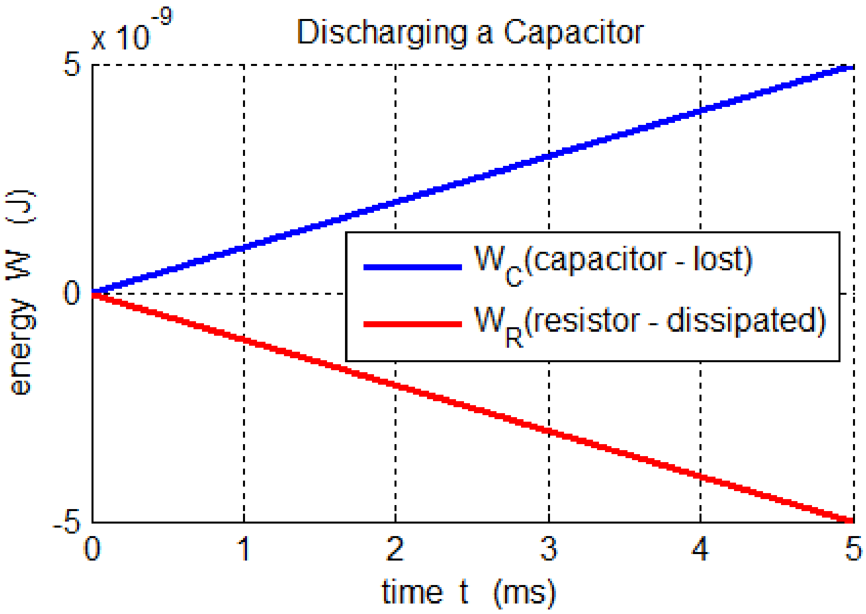


Fig. 12. The energy is stored by the capacitor is lost as internal energy by the current in the resistor.

TRANSIENT RESPONSE: STEP (PULSE) CURRENT INPUT **RC03.m**

The capacitor *C* and resistor *R* are connected in parallel and a current is injected into the circuit as shown in figure 13.

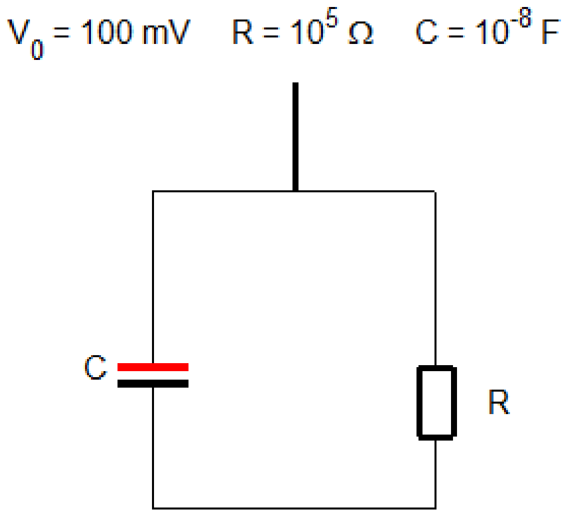


Fig. 13. *RC* circuit diagram for current injection.

Derivations

Capacitor and resistor connected in parallel

$$V = V_C = V_R$$

Kirchhoff's current law: *I* is the injected current

$$I - I_C - I_R = 0$$

Conservation of charge

$$I = I_C + I_R$$

Currents

$$I_R = \frac{V}{R} \qquad Q = CV \quad \Rightarrow \quad I_C = \frac{dQ}{dt} = C\frac{dV}{dt}$$

ODE to be solved for *V*

$$I\,\frac{dV}{dt} = \frac{I}{C} - \frac{V}{RC}$$

The easiest way to solve this ODE is to use the **finite difference method** where the derivative is replaced by a difference equation:

Good approximation provided *dt* << τ = *RC*

$$\frac{dV}{dt} = \frac{V_C(t+\Delta t) - V_C(t)}{\Delta t}$$

Can find successive values of *V* in time steps Δt

$$V(t+\Delta t) = V(t) + \frac{\Delta t\, I(t)}{C} - \left(\frac{\Delta t}{\tau}\right)V(t)$$

Charge at time *t*

$$Q(t) = CV(t)$$

Currents at time *t*

$$I_R(t) = \frac{V(t)}{R} \qquad I_C(t) = I(t) - I_R(t)$$

Graphical Predictions RC03.m

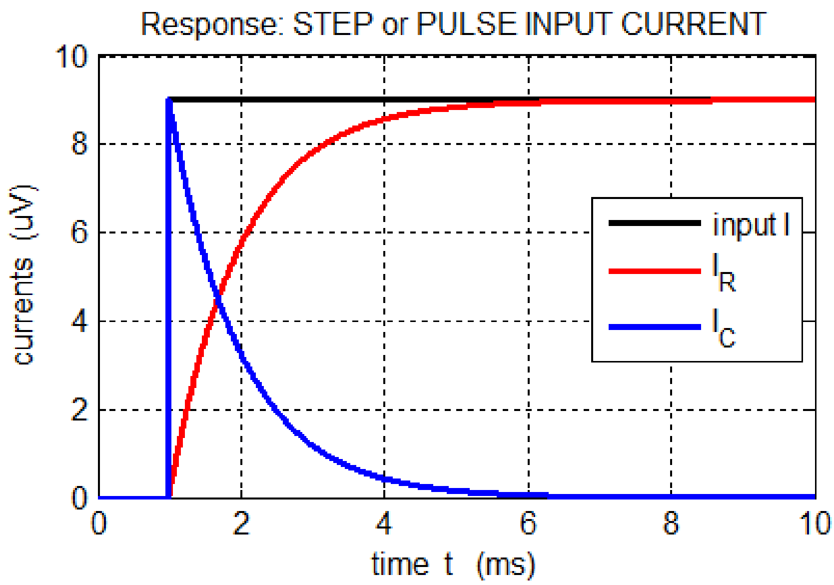


Fig. 14. Variation in the currents as functions of time. *I* is the external current injected into the circuit. The resistive current I_R and capacitive current I_C vary exponentially with a characteristic time constant $\tau = R\,C$ = 1 ms. When the input current *I* jumps, the capacitor charges almost immediately then discharges through the resistor *R*, while the capacitive current I_C decreasing exponentially. The resistive current increases exponentially to a maximum level after a time interval of about 5τ.

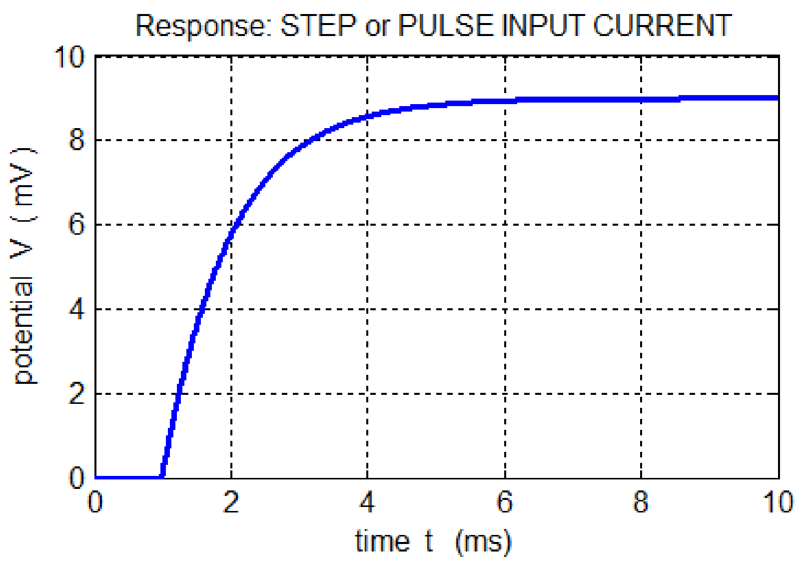


Fig. 15. The voltage across the parallel combination of *R* and *C* increases exponentially to a maximum level with a characteristic time constant
$\tau = R\,C = 1$ ms.

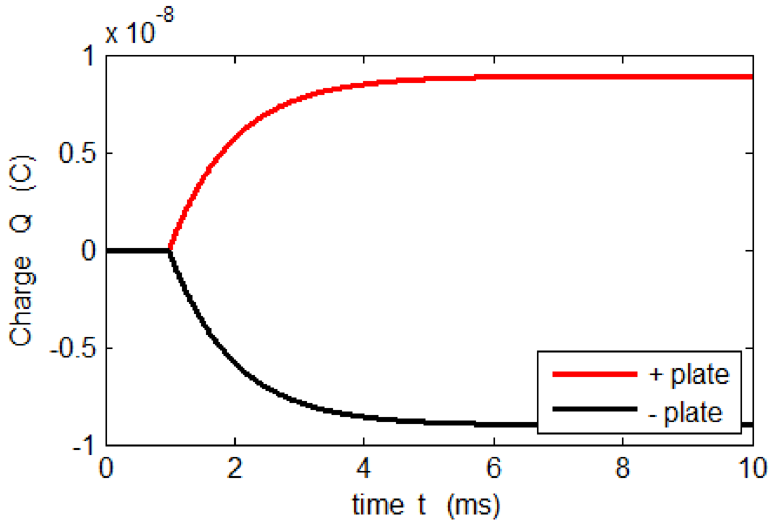


Fig. 16. The charge *Q* on the plates of the capacitor *C* increases exponentially to a maximum level with a characteristic time constant $\tau = R\,C = 1$ ms. The shape of the curve is the same as the variation in voltage

since $Q \propto V$.

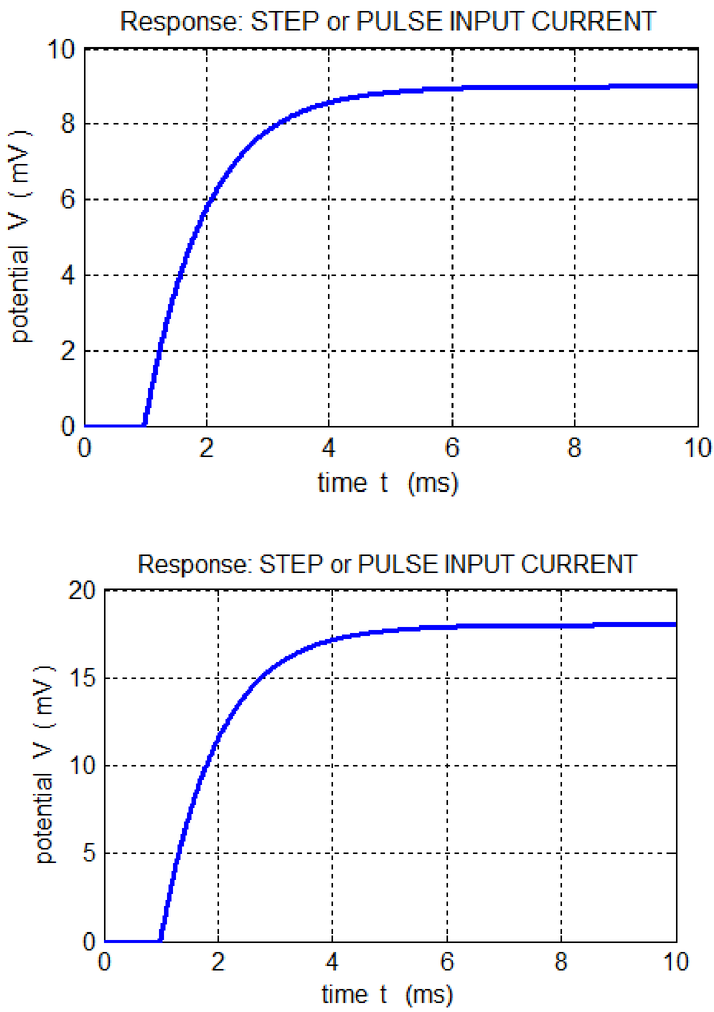


Fig. 17. When the magnitude of the step current increases by a factor of 2, then the change in the maximum potential difference also doubles.

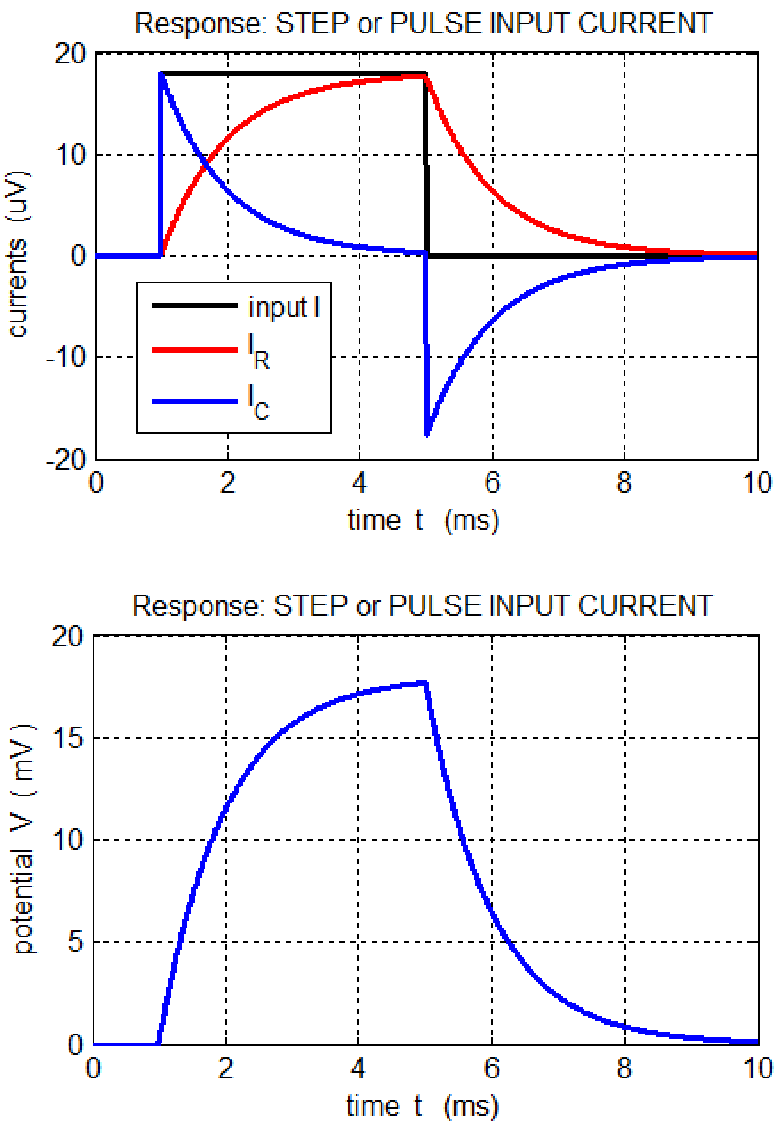
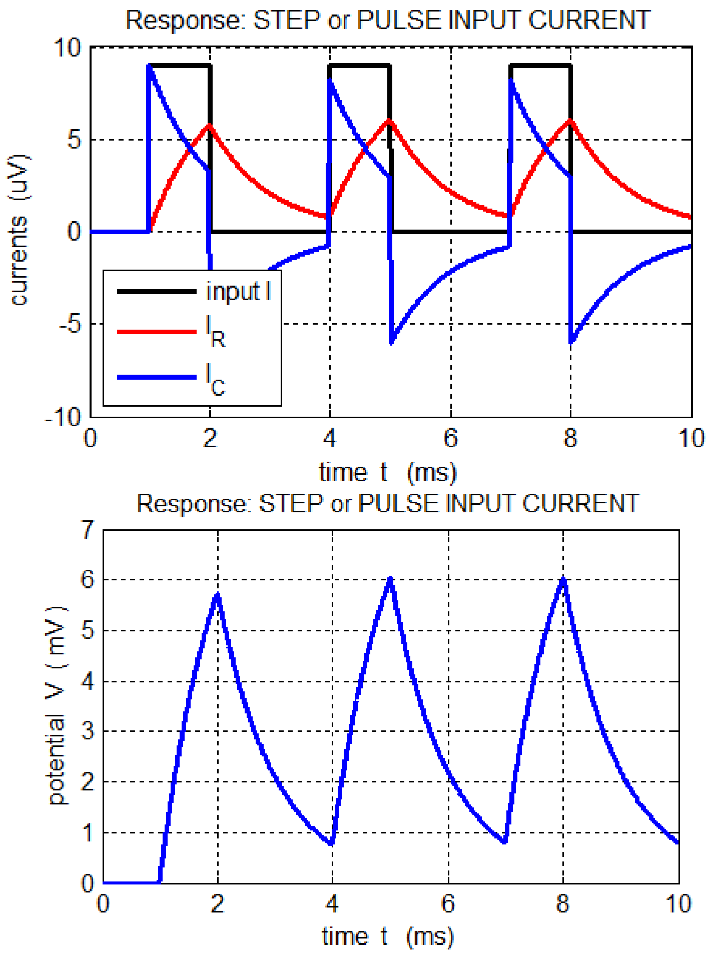


Fig. 18. Response for a pulse input. The capacitor charges then discharges. The potential difference V curve is the same shape as the curve for the resistive current I_R since $I_R \propto V$.

For a neuron, at any instant, the total current $I(t)$ is equal to the sum of the currents through the membrane: $I(t) = I_C(t) + I_R(t)$ where $I_R(t)$ is a **conducting current** and $I_C(t)$ is known as a **displacement current**. The current thus depends upon the voltage and the rate of change of the voltage and this parallel combination offers minimum opposition to current for rapidly changing voltages since there is not enough time for the capacitance to charge significantly.



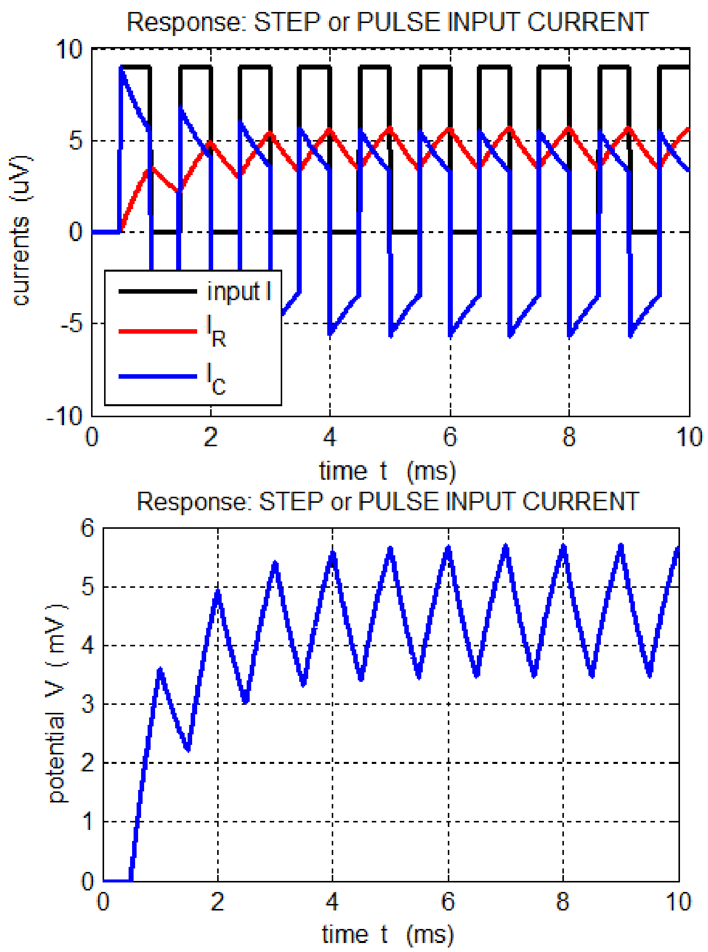


Fig. 19. Response for a series of pulses. For a rapid series of pulses the conductive current I_R has small fluctuations about an average value. The result of many pulses arriving at a neuron is that the voltage across the membrane can grow as the capacitor charges and discharging. This can result is a sufficient voltage across the membrane to produce an action potential (large voltage spike) then can initiate the propagation of a signal along the axon.