Introduction to Cognitive Neuroscience

Neural Dynamics

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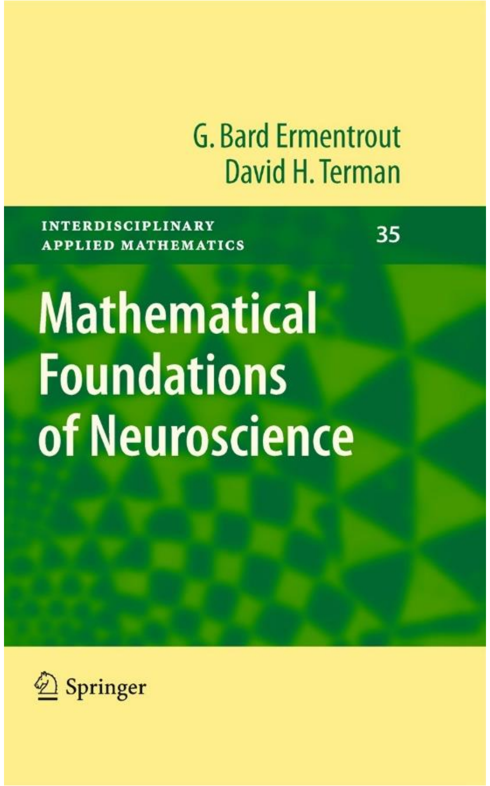
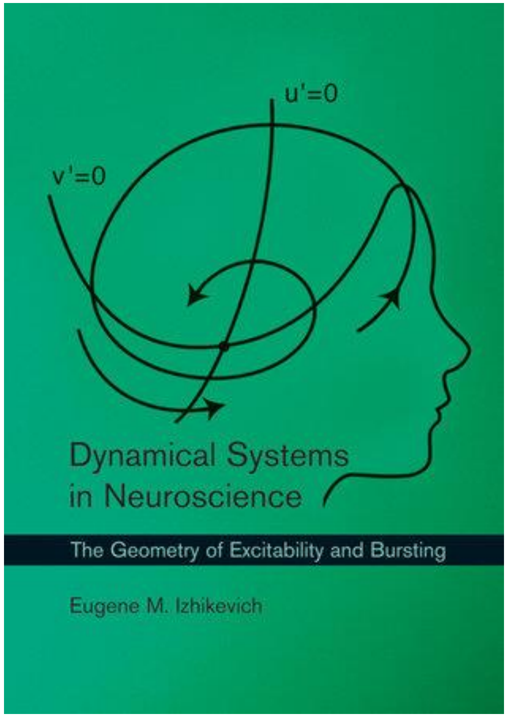
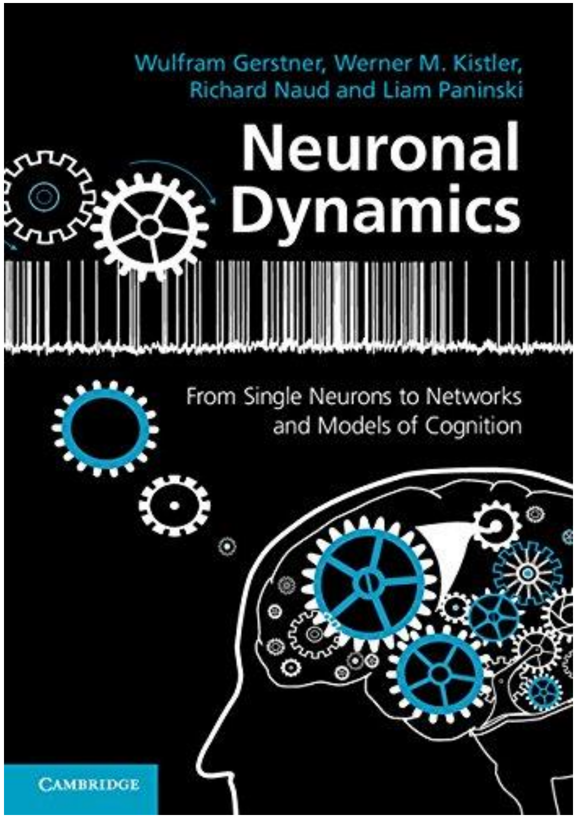
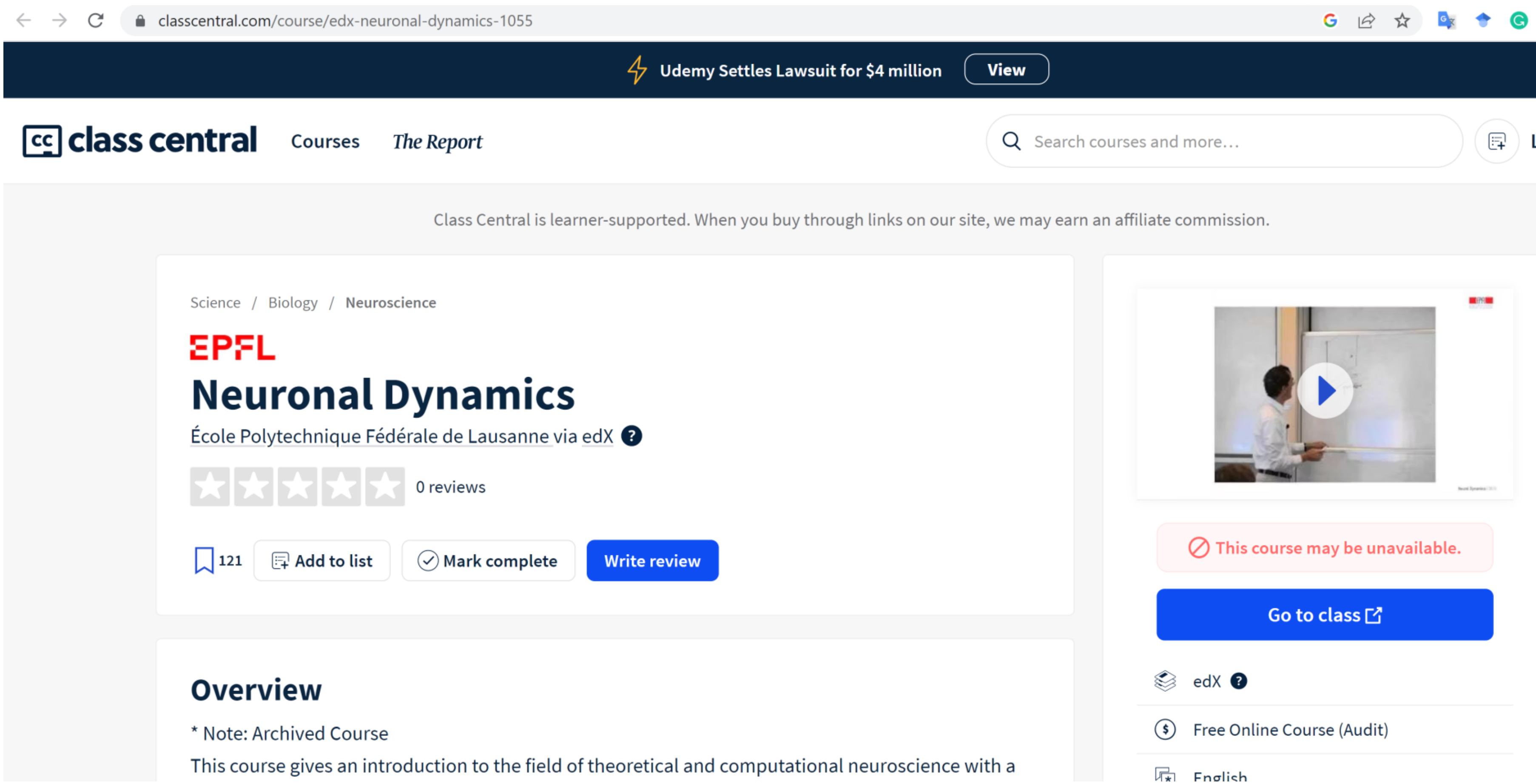
Some related books







Online course Gerstner



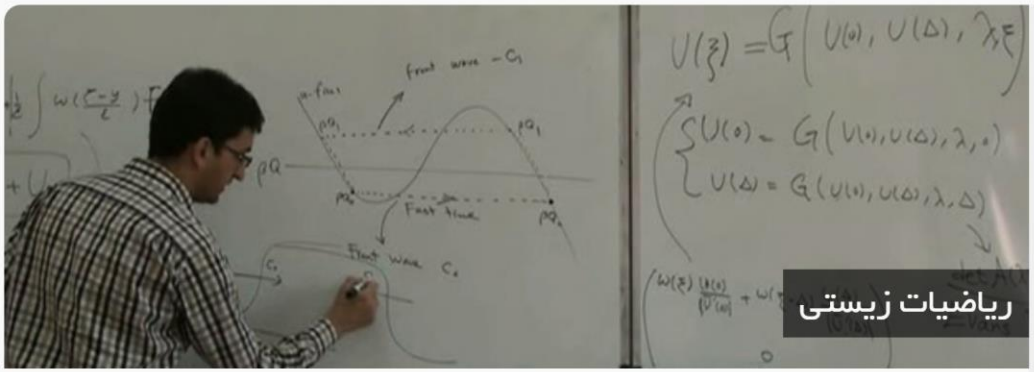
Online course Razvan and Abbasian

videos.math.sharif.ir/courses.php?course=biological_math-spring91

open courseware

Mathsci Dept, Sharif University of Technology

صفحه اصلی   درس ها   درباره ما   ارتباط با ما



مشخصات درس

ترم ارائه : بهار ۱۳۹۱

مقطع : کارشناسی

استاد درس

مرتضی فتوحی

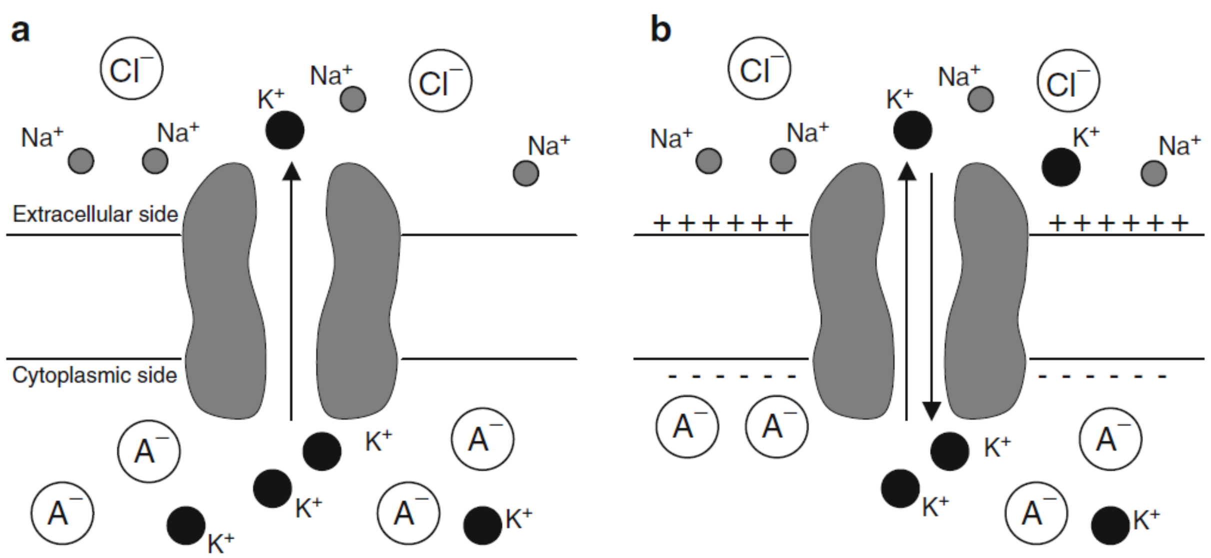
محتوای جلسات و ویدئوها

شماره	بخش	ویدئوی جلسه	جزوه ی درس
جلسه ۲	---	دانلود (فیلم)	---
جلسه ۳	---	دانلود (فیلم)	---
جلسه ۴	---	دانلود (فیلم)	---
جلسه ۵	---	دانلود (فیلم)	---
جلسه ۶	---	دانلود (فیلم)	---
جلسه ۷	---	دانلود (فیلم)	---

The Resting Potential

$$V_{\mathrm{M}} = V_{\mathrm{in}} - V_{\mathrm{out}},$$

$$E_{\mathrm{K}} = -\frac{RT}{zF} \ln \frac{[K^+]_{\mathrm{in}}}{[K^+]_{\mathrm{out}}}. \qquad (1.1)$$



The Goldman–Hodgkin–Katz Equation

- Currents flow according to:
  - The permeabilities of ion channels
  - Concentration gradients across the cell membrane

$$V_{\mathrm{M}} = \frac{RT}{F} \ln \frac{P_{\mathrm{K}}[\mathrm{K}^+]_{\mathrm{out}} + \mathrm{P}_{\mathrm{Na}}[\mathrm{Na}^+]_{\mathrm{out}} + \mathrm{P}_{\mathrm{Cl}}[\mathrm{Cl}^-]_{\mathrm{in}}}{P_{\mathrm{K}}[\mathrm{K}^+]_{\mathrm{in}} + \mathrm{P}_{\mathrm{Na}}[\mathrm{Na}^+]_{\mathrm{in}} + \mathrm{P}_{\mathrm{Cl}}[\mathrm{Cl}^-]_{\mathrm{out}}},$$

Different channels

- Non gated (leaky)
- Gated → changes in the permeabilities → action potentials

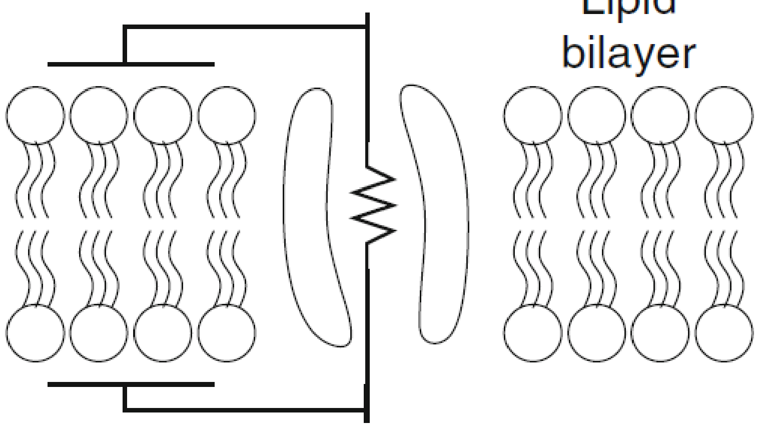
Equivalent circuit model

- (1) **Conductors** or resistors, representing the **ion channels**;
- (2) **Batteries**, representing the **concentration gradients** of the ions;
- (3) **Capacitors**, representing the ability of the membrane to **store charge.**
- **Lipid bilayer** has dielectric properties
  - Recall that capacitors store charge and then release it in the **form of currents**.

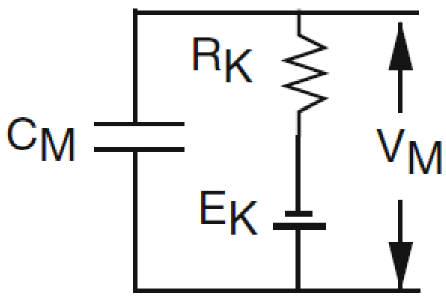
$$q = C_M V_M;$$

- c_M *:specific membrane capacitance:* **capacitance per square centimeter** (*~1F/cm2*);
  - The **bigger** cell, the **bigger** $\mathbf{C_M}$

Simple model



$$i_{\mathrm{cap}} = c_{\mathrm{M}} \frac{\mathrm{d}V_{\mathrm{M}}}{\mathrm{d}t}.$$



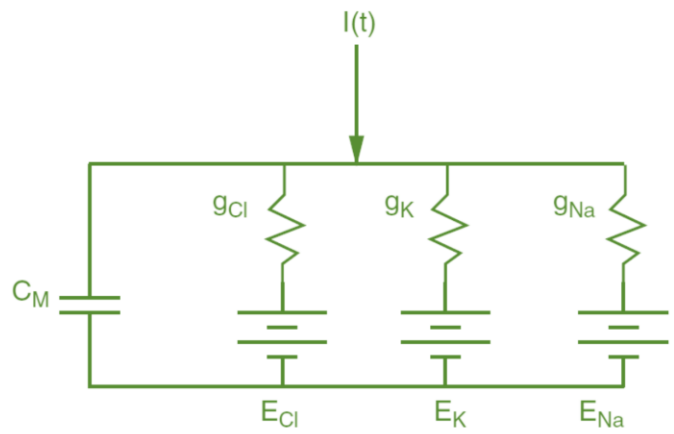
$$\hat{I}_{\mathrm{K}} = \hat{g}_{\mathrm{K}}(V_{\mathrm{M}} - E_{\mathrm{K}}).$$

g_K : conductance per unit area

$$I_{\mathrm{K}} = g_{\mathrm{K}}(V_{\mathrm{M}} - E_{\mathrm{K}}) = \frac{V_{\mathrm{M}} - E_{\mathrm{K}}}{r_{\mathrm{K}}}.$$

$$0 = i_{\text{cap}} + I_{\text{K}} = c_{\text{M}} \frac{\mathrm{d}V_{\text{M}}}{\mathrm{d}t} + \frac{V_{\text{M}} - E_{\text{K}}}{r_{\text{K}}}$$

$$c_{\text{M}} \frac{\mathrm{d}V_{\text{M}}}{\mathrm{d}t} = -\frac{V_{\text{M}} - E_{\text{K}}}{r_{\text{K}}} = -g_{\text{K}}(V_{\text{M}} - E_{\text{K}}).$$



$$i_{\text{ion}} = -g_{\text{Cl}}(V_{\text{M}} - E_{\text{Cl}}) - g_{\text{K}}(V_{\text{M}} - E_{\text{K}}) - g_{\text{Na}}(V_{\text{M}} - E_{\text{Na}}).$$

current source is not typically expressed as current per unit area:

total surface area of the neuron

$$c_M \frac{dV_M}{dt} = -g_{Cl}(V_M - E_{Cl}) - g_K(V_M - E_K) - g_{Na}(V_M - E_{Na}) + I(t)/A.$$

$$c_M \frac{dV_M}{dt} = -\frac{(V_M - E_R)}{r_M} + I(t)/A,$$

where

$$E_R = (g_{Cl}E_{Cl} + g_K E_K + g_{Na}E_{Na})r_M$$

cell's resting potential

Specific membrane resistance

$$r_M = \frac{1}{g_{Cl} + g_K + g_{Na}}$$

For a **passive membrane**:

$$\underset{\textit{steady state}}{V_{\mathrm{ss}}} = \frac{g_{\mathrm{Cl}} E_{\mathrm{Cl}} + g_{\mathrm{K}} E_{\mathrm{K}} + g_{\mathrm{Na}} E_{\mathrm{Na}} + I/A}{g_{\mathrm{Cl}} + g_{\mathrm{k}} + g_{\mathrm{Na}}}.$$

Weighted sum of the equilibrium potentials of the three currents

Similar to the GHK contribution to the resting potential by each ion is **weighted** in **proportion to the permeability**

Conductance and permeability are related concepts:

- Permeability depends on the state of the membrane (number of **open channels**)
- Conductance depends on both the state of the membrane and the **concentration** of the ions

The Membrane Time Constant:

How a passive, isopotential cell responds to an **applied current**.

Passive:

If its electrical properties **do not change** during signaling. Such a cell cannot generat an action potential;

Isopotential

If the membrane potential is **uniform** at all points of the cell

We will consider a spherical cell with radius r

$$I_{\mathrm{M}}(t) = \frac{I(t)}{4\pi\rho^2} = \begin{cases} \frac{I_0}{4\pi\rho^2} & \text{if } 0 < t < T \\ 0 & \text{otherwise.} \end{cases}$$

$$c_M \frac{dV_M}{dt} = -\frac{(V_M - E_R)}{r_M} + I(t)/A,$$

To simplify things, we take $E_R = 0$ so that V_M measures the deviation of the membrane potential from rest

$$E_R = 0 \quad \Longrightarrow \quad c_M \frac{dV_M}{dt} = -\frac{V_M}{r_M} + I_M(t).$$

If the cell starts at rest

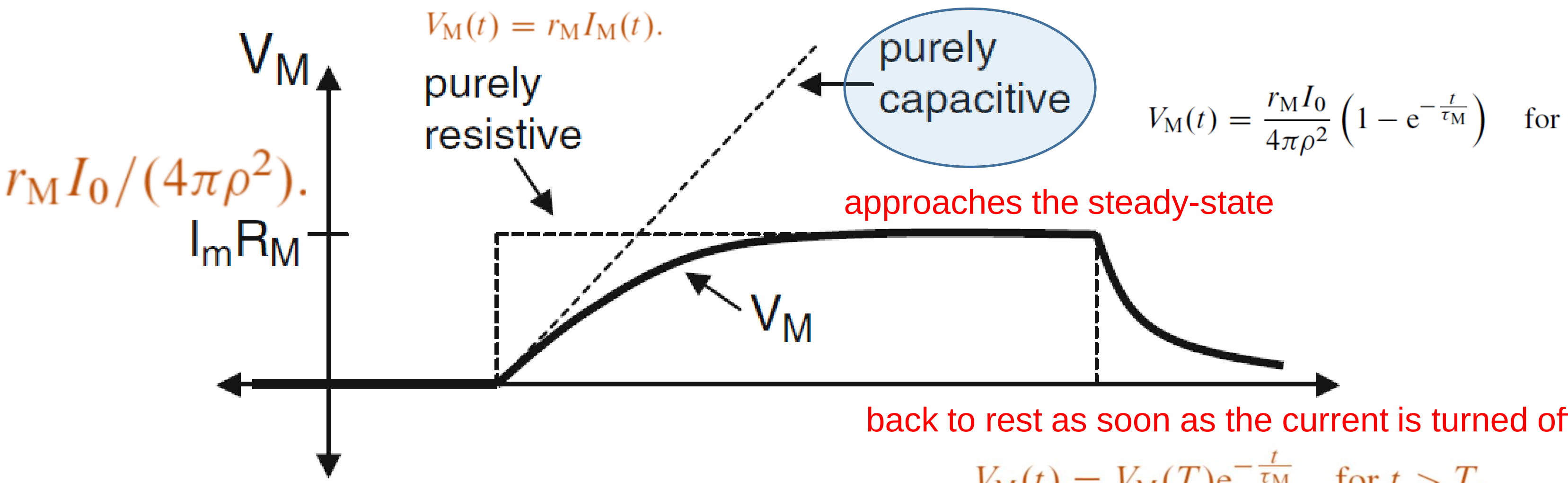
$$V_M(t) = \frac{r_M I_0}{4\pi\rho^2}\left(1 - e^{-\frac{t}{\tau_M}}\right) \quad \text{for } 0 < t < T,$$

$\tau_M \equiv c_M r_M$ Membrane time constant

$$c_M \frac{dV_M}{dt} = -\frac{V_M}{r_M} + \overset{0}{I_M(t)}.$$

$$V_M(t) = V_M(T)e^{-\frac{t}{\tau_M}} \quad \text{for } t > T.$$

The change of membrane potential in response to a step of current.



$$V_M(t) = \frac{r_M I_0}{4\pi\rho^2}\left(1 - e^{-\frac{t}{\tau_M}}\right) \quad \text{for } 0 < t < T,$$

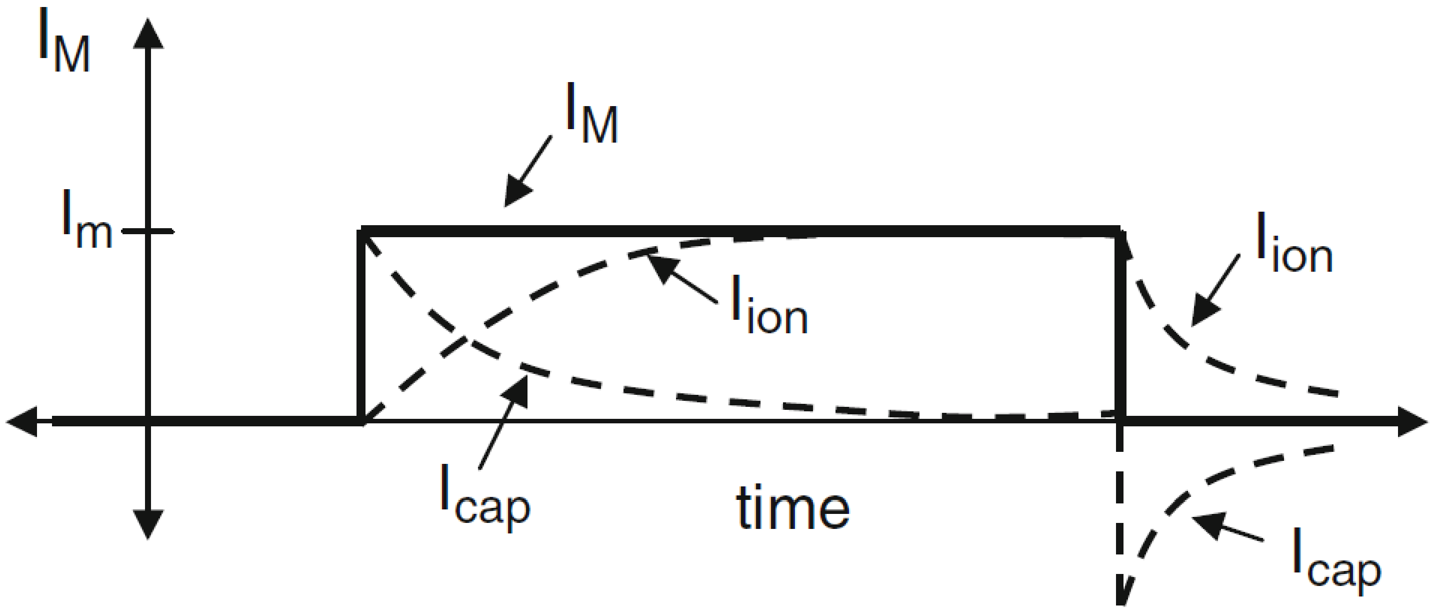
$$V_M(t) = V_M(T)e^{-\frac{t}{\tau_M}} \quad \text{for } t > T.$$

The steady-state membrane potential

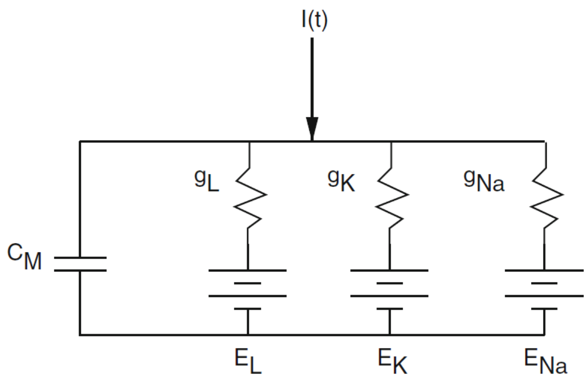
$$I_0 \frac{r_M}{4\pi\rho^2} \equiv I_0 R_{INP},$$

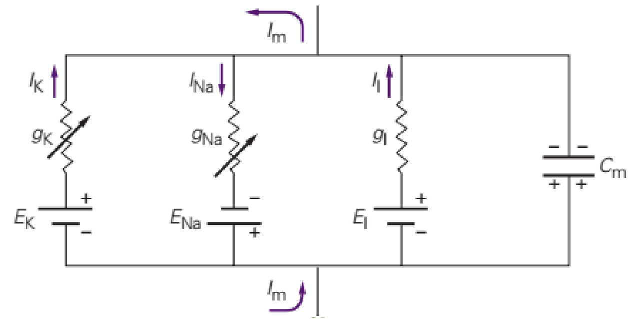
input resistance

The time course of the total membrane current, the ionic current, and the capacitive current



Equivalent circuit underlying the **Hodgkin–Huxley equations**

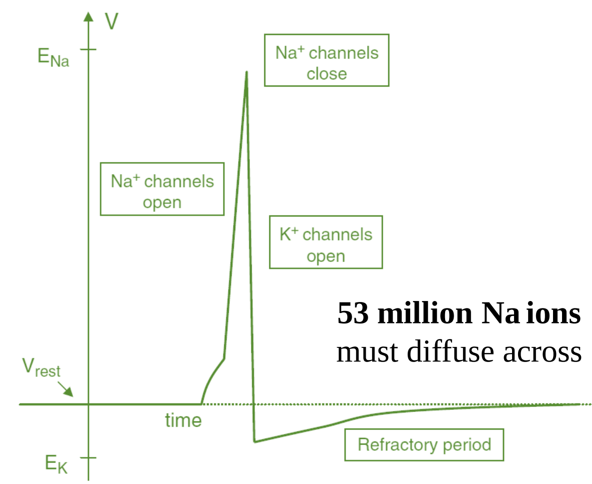




$$c_M \frac{dV}{dt} = -g_{Na}(V - E_{Na}) - g_K(V - E_K) - g_L(V - E_L).$$

$I_L \equiv g_L(V - E_L)$ is called the *leak current.*

Since most **nongated** channels are permeable to K ions, **E_L is close to E_K**.



53 million Na ions must diffuse across

AP: changes in the **relative conductances** of the dominant ionic species.

Voltage-Gated Channels

The **pores** have gates that can be either **open or closed**

The **probability** that a gate is open or closed depends on the membrane potential

$$C \underset{\beta(V)}{\overset{\alpha(V)}{\rightleftharpoons}} O,$$

α and β voltage-dependent **rate** constants

If we let **m** be **the fraction of open gates**, then **1-m** is the fraction of closed gates

Law of mass action: the principle that the **rate of a chemical** reaction is proportional to the **concentrations of the reacting substances**.

$$\frac{\mathrm{d}m}{\mathrm{d}t} = \alpha(V)(1-m) - \beta(V)m = (m_\infty(V) - m)/\tau(V),$$

where

$$m_\infty(V) = \frac{\alpha(V)}{\alpha(V)+\beta(V)} \quad \text{and} \quad \tau(V) = \frac{1}{\alpha(V)+\beta(V)}.$$

It is easy to solve this equation if V is constant. The solution starting at $m(0)$ is

$$m(t) = m_\infty(V) + (m(0) - m_\infty(V))\mathrm{e}^{-t/\tau(V)}.$$

voltage-dependent rate constants α and β.

Based on **thermodynamics**: the probability of opening or closing a channel depends **exponentially on the potential**

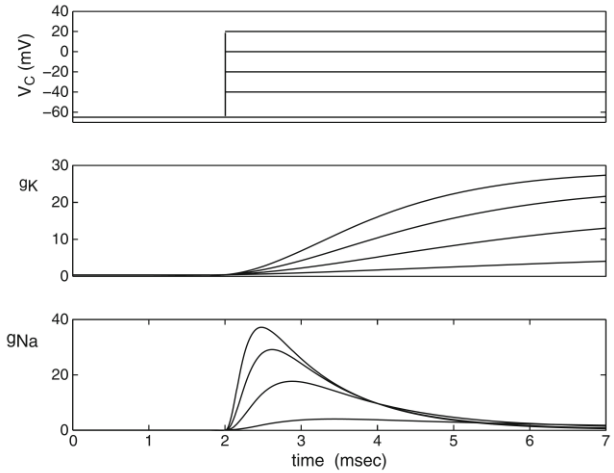
$$\alpha(V) = A_\alpha \exp(-B_\alpha V) \quad \text{and} \quad \beta(V) = A_\beta \exp(-B_\beta V).$$

$$m_\infty(V) = \frac{1}{1 + \exp(-(V - V_\mathrm{h})/V_\mathrm{s})},$$

Hodgkin and Huxley were able to isolate the K current by replacing Na ions in the external bathing solution with a larger, impermeant cation. This ***eliminated the inward Na current***

Now we can use TTX

$$g_K(t) = \frac{I_K(t)}{(V_M - E_K)} \quad \text{and} \quad g_{Na}(t) = \frac{I_{Na}(t)}{(V_M - E_{Na})}.$$



inactivated

Using the voltage-clamp data, Hodgkin and Huxley derived expressions for the K^+ and Na^+ conductances. They proposed that

$$g_K = \bar{g}_K n^4 \quad \text{and} \quad g_{Na} = \bar{g}_{Na} m^3 h,$$

where $\bar{g}_K$ and $\bar{g}_{Na}$ are maximum conductances and n, m, and h are gating variables

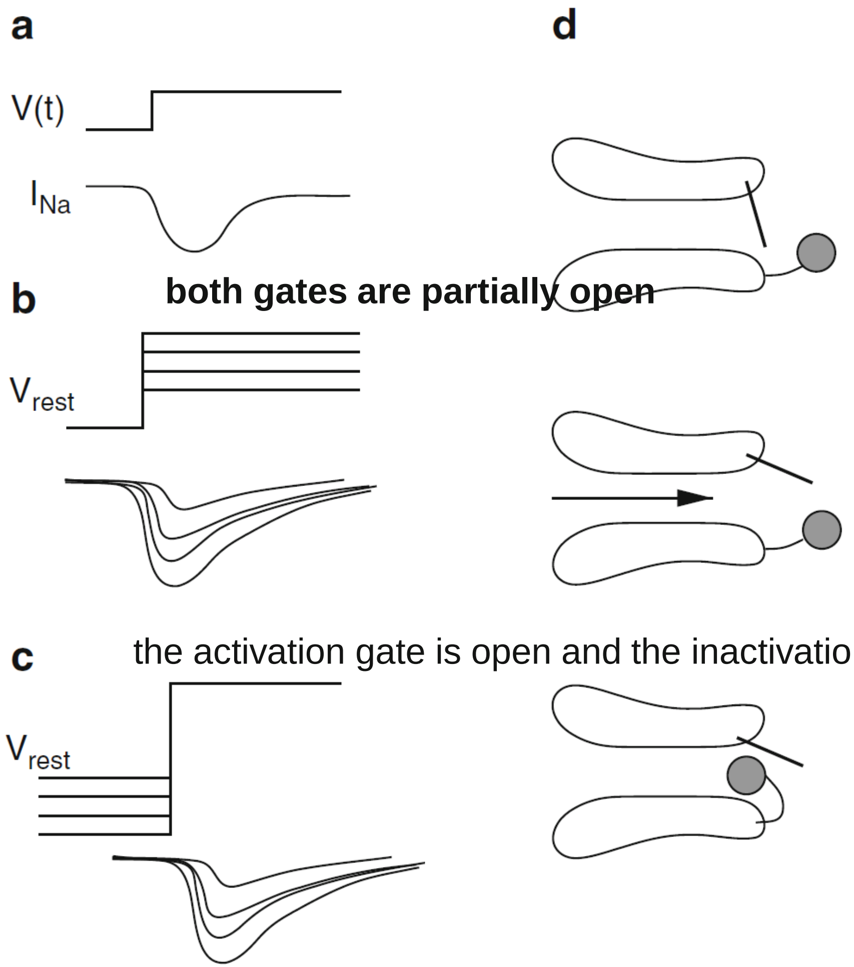
Values between 0 and 1.

probability that the sodium activation gate is open is m^3

probability that the sodium inactivation gate is open is h

n^4 represents the probability that a K^+

Na channel’s activation gate (***line***) is closed but the inactivation gate (***ball***) is open.



both gates are partially open

the activation gate is open and the inactivation gate is closed

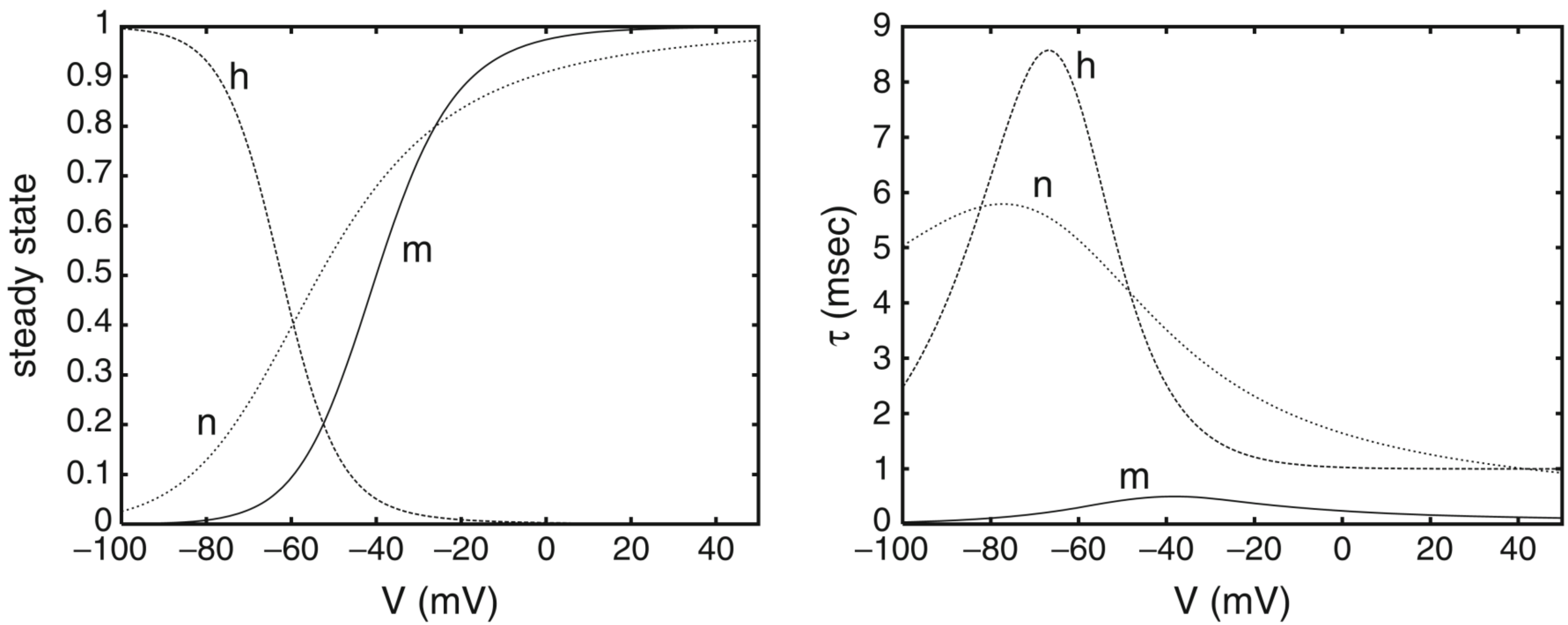
$$
\begin{aligned}
\frac{\mathrm{d}n}{\mathrm{d}t} &= \alpha_n(V)(1-n) - \beta_n(V)n = (n_\infty(V) - n)/\tau_n(V),\\
\frac{\mathrm{d}m}{\mathrm{d}t} &= \alpha_m(V)(1-m) - \beta_m(V)m = (m_\infty(V) - m)/\tau_m(V),\\
\frac{\mathrm{d}h}{\mathrm{d}t} &= \alpha_h(V)(1-h) - \beta_h(V)h = (h_\infty(V) - h)/\tau_h(V).
\end{aligned}
$$

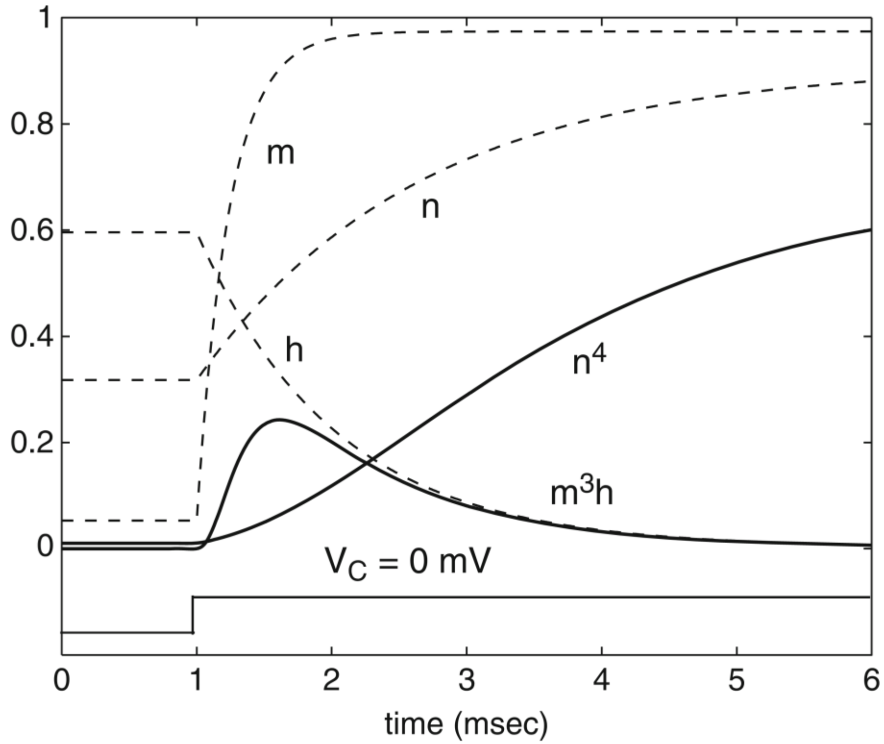
If $X = n$, m, or h, then

$$
X_\infty(V) = \frac{\alpha_X(V)}{\alpha_X(V) + \beta_X(V)} \quad \text{and} \quad \tau_X(V) = \frac{1}{\alpha_X(V) + \beta_X(V)}.
$$

Hodgkin–Huxley functions:

Left: the steady-state opening of the gates and
Right: the time constants





Response of the activation and inactivation variables m, h, and n to a step in voltage

Hodgkin–Huxley model is a system of four differential equations;
there is **one equation for the membrane potential** and **three equations for channel gating variables**.

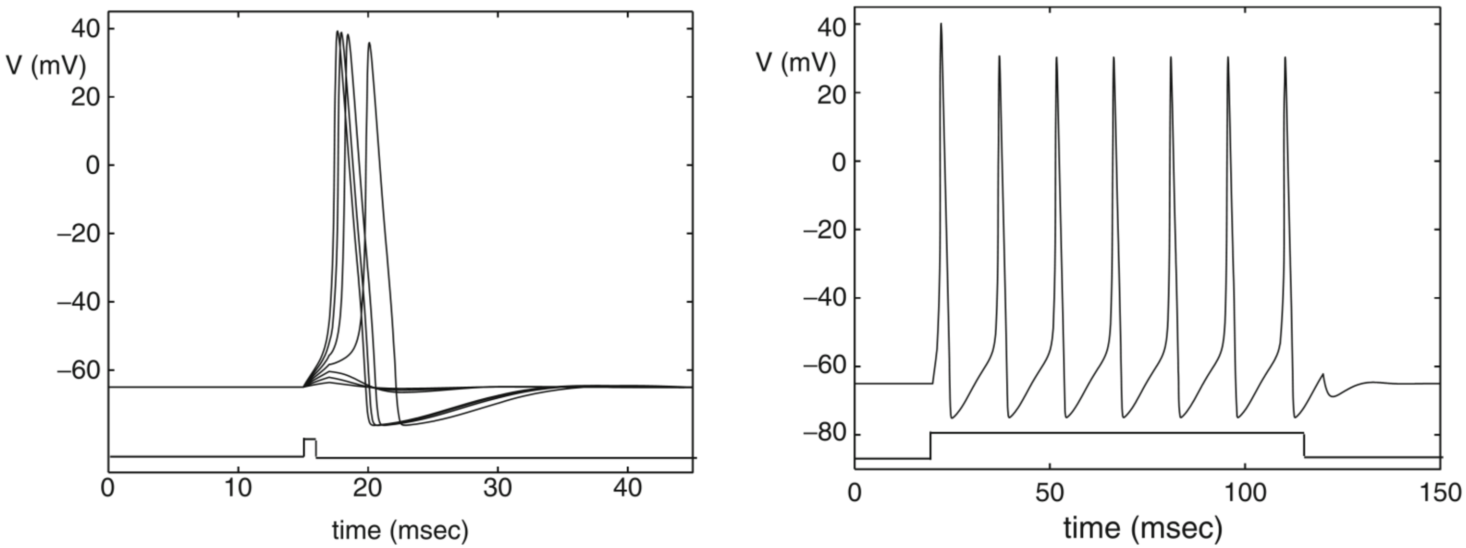
$$
\begin{aligned}
c_{\mathrm{M}}\frac{\mathrm{d}V}{\mathrm{d}t} &= -\bar{g}_{\mathrm{Na}}m^3h(V-E_{\mathrm{Na}}) - \bar{g}_{\mathrm{K}}n^4(V-E_{\mathrm{K}}) - \bar{g}_{\mathrm{L}}(V-E_{\mathrm{L}}),\\
\frac{\mathrm{d}n}{\mathrm{d}t} &= \phi[\alpha_n(V)(1-n) - \beta_n(V)n],\\
\frac{\mathrm{d}m}{\mathrm{d}t} &= \phi[\alpha_m(V)(1-m) - \beta_m(V)m],\\
\frac{\mathrm{d}h}{\mathrm{d}t} &= \phi[\alpha_h(V)(1-h) - \beta_h(V)h].
\end{aligned}
$$

Temperature factor:

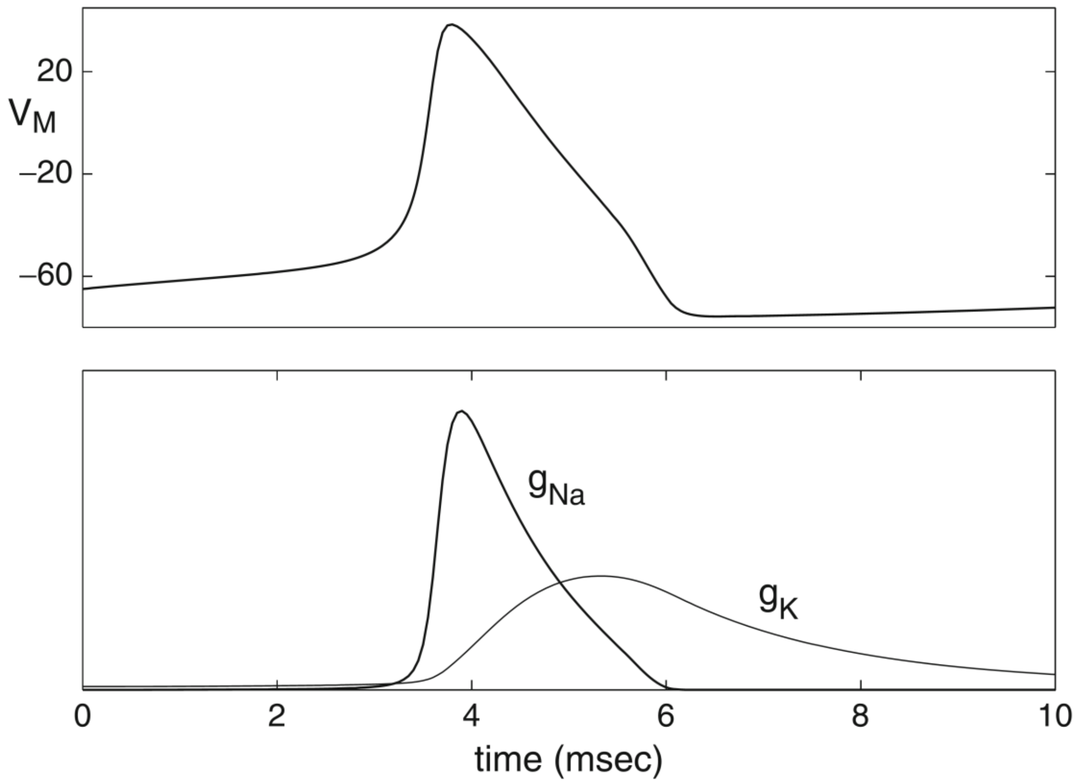
$$\phi = Q_{10}^{(T-T_{\mathrm{base}})/10}.$$

Q_{10} is the ratio of the rates for an increase in temperature of 10°C. For the squid giant axon, $T_{\mathrm{base}} = 6.3$°C and $Q_{10} = 3$.

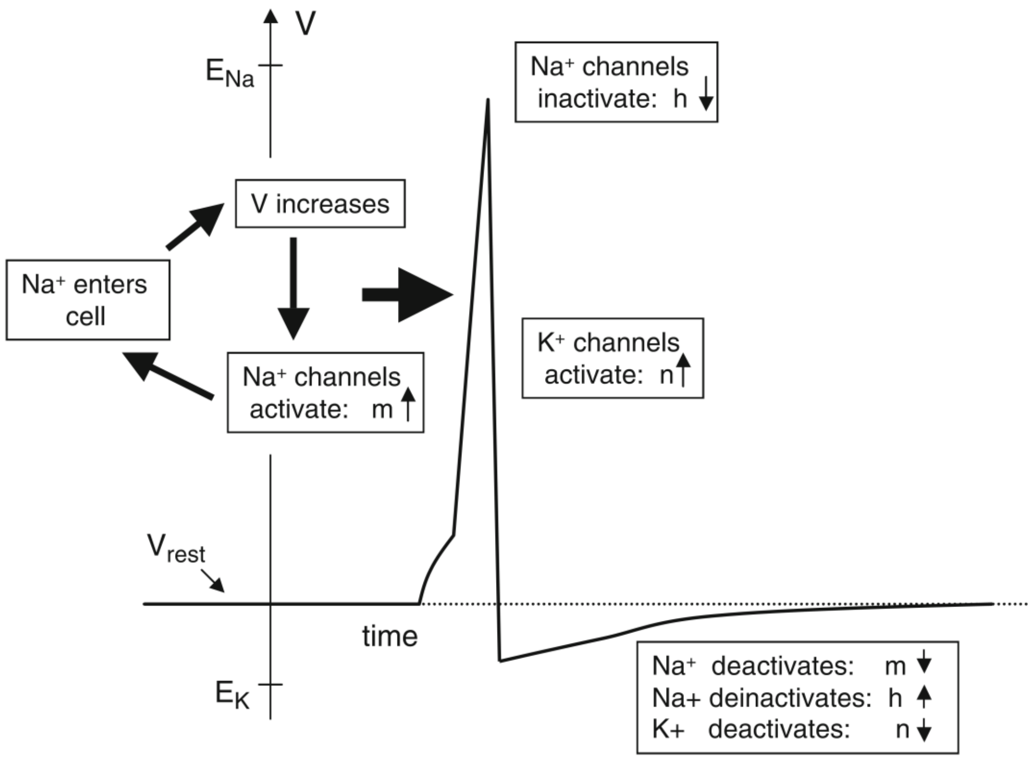
Responses of the Hodgkin–Huxley model to applied currents. *Left* transient responses showing "all-or-none" behavior and *right* sustained periodic response



Solution of the Hodgkin–Huxley equations showing an action potential. Also shown are the Na^+ and K^+ conductances



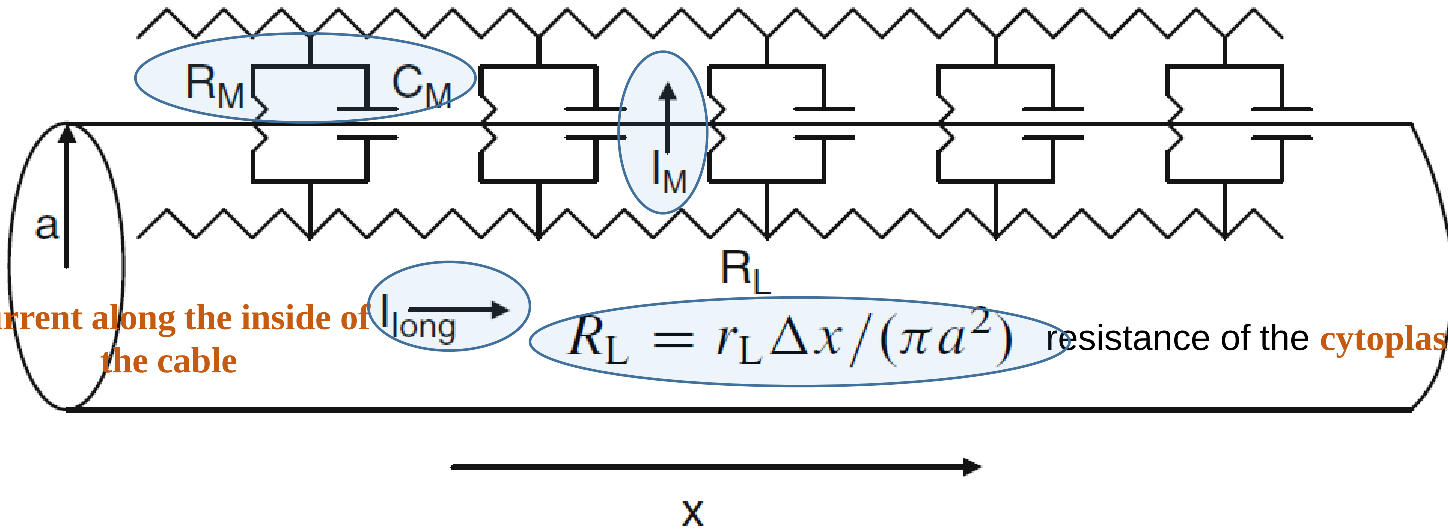
Mechanisms underlying the action potential



The Cable Equation

It is important to understand how the **geometry of the cell** affects the spread of the signal. Axon approximated by **cylinders**

I_M is the current across the membrane, $R_e = 0$, extracellular space is **isopotential**



current along the inside of the cable

$R_L = r_L \Delta x / (\pi a^2)$ resistance of the **cytoplasm**,

R_M is the membrane resistance, and C_M is the membrane capacitance

$$V_M(x + \Delta x, t) - V_M(x, t) = -I_{\text{long}}(x, t) R_L = -I_{\text{long}}(x, t) \frac{\Delta x}{\pi a^2} r_L .$$

$$V_M(x+\Delta x,t) - V_M(x,t) = -I_{\mathrm{long}}(x,t)R_L = -I_{\mathrm{long}}(x,t)\frac{\Delta x}{\pi a^2}r_L.$$

In the limit $\Delta x \to 0$

$$I_{\mathrm{long}}(x,t) = -\frac{\pi a^2}{r_L}\frac{\partial V_M}{\partial x}(x,t).$$

i_{ion} be the current per unit area

$$I_{\mathrm{ion}} = (2\pi a \Delta x) i_{\mathrm{ion}}.$$

$$C_M = (2\pi a \Delta x) c_M$$

$$I_{\mathrm{cap}}(x,t) = (2\pi a \Delta x) c_M \frac{\partial V_M}{\partial t}.$$

$$I_{\mathrm{cap}}(x,t) + I_{\mathrm{ion}}(x,t) = -I_{\mathrm{long}}(x+\Delta x,t) + I_{\mathrm{long}}(x,t),$$

$$(2\pi a\Delta x)c_{\mathrm{M}}\frac{\partial V_{\mathrm{M}}}{\partial t} + (2\pi a\Delta x)i_{\mathrm{ion}} = \frac{\pi a^2}{r_{\mathrm{L}}}\frac{\partial V_{\mathrm{M}}}{\partial x}(x+\Delta x,t) - \frac{\pi a^2}{r_{\mathrm{L}}}\frac{\partial V_{\mathrm{M}}}{\partial x}(x,t).$$

We divide both sides of this equation by $2\pi a\Delta x$ and let $\Delta x \to 0$

$$c_{\mathrm{M}}\frac{\partial V_{\mathrm{M}}}{\partial t} = \frac{a}{2r_{\mathrm{L}}}\frac{\partial^2 V_{\mathrm{M}}}{\partial x^2} - i_{\mathrm{ion}}.$$

$i_{\mathrm{ion}} = V_{\mathrm{M}}(x,t)/r_{\mathrm{M}}$, **specific membrane resistance**

$$c_{\mathrm{M}}\frac{\partial V_{\mathrm{M}}}{\partial t} = \frac{a}{2r_{\mathrm{L}}}\frac{\partial^2 V_{\mathrm{M}}}{\partial x^2} - \frac{V_{\mathrm{M}}}{r_{\mathrm{M}}}.$$

$$c_M \frac{\partial V_M}{\partial t} = \frac{a}{2r_L} \frac{\partial^2 V_M}{\partial x^2} - \frac{V_M}{r_M}.$$

We can rewrite this equation as

$$\tau_M \frac{\partial V_M}{\partial t} = \lambda^2 \frac{\partial^2 V_M}{\partial x^2} - V_M,$$

where

$$\lambda = \sqrt{\frac{a\,r_M}{2r_L}} \quad \text{and} \quad \tau_M = c_M r_M$$

space* or *length constant and the *membrane time constant*

steady-state solutions

$$\tau_M \overset{0}{\cancel{\frac{\partial V_M}{\partial t}}} = \lambda^2 \frac{\partial^2 V_M}{\partial x^2} - V_M,$$

we inject a step of current, I_0, at $x = 0$. As $t \to \infty$,

$$\lambda^2 \frac{d^2 V_{ss}}{dx^2} - V_{ss} = 0.$$

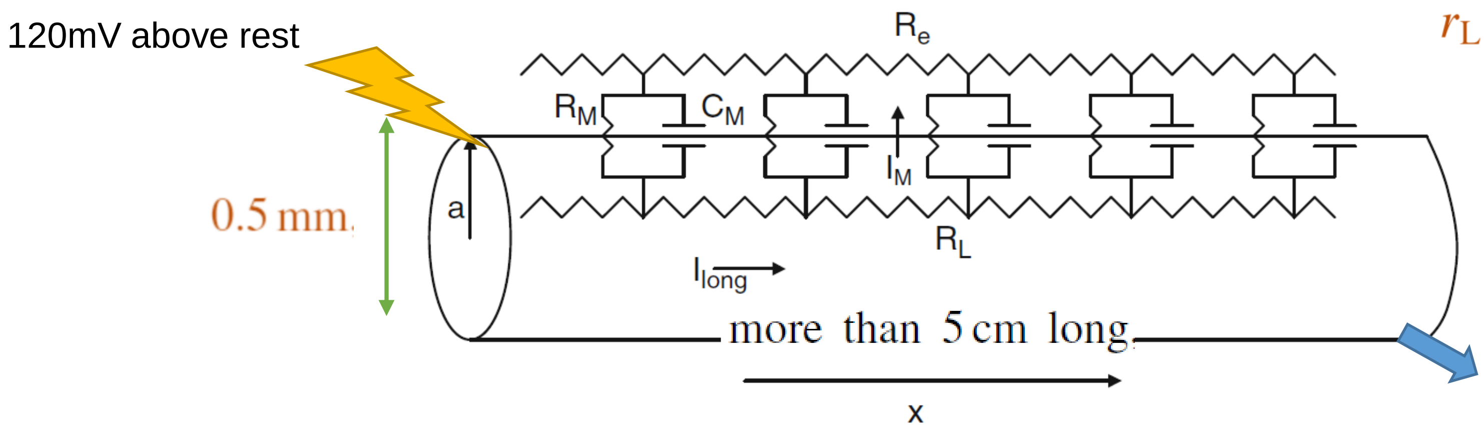
we need boundary conditions

$$I_{long}(x,t) = -\frac{\pi a^2}{r_L} \frac{\partial V_M}{\partial x}(x,t). \Rightarrow I_0 = -\frac{\pi a^2}{r_L} \frac{\partial V_M}{\partial x}. \Rightarrow \frac{dV_{ss}}{dx}(0) = -\frac{r_L}{\pi a^2} I_0.$$

$$\Rightarrow V_{ss}(x) = \frac{\lambda r_L}{\pi a^2} I_0 e^{-x/\lambda}.$$

The Squid Action Potential

$r_M = 700\ \Omega\ cm^2$
$r_L = 30\ \Omega\ cm$



10 μV above the rest, a 10,000-fold decrement

$$\lambda = \sqrt{\frac{a r_M}{2 r_L}} \Rightarrow \lambda = 5.4\ \text{mm}.$$

order of magnitude **smaller than the length**

$$c_M \frac{\partial V_M}{\partial t} = \frac{a}{2r_L}\frac{\partial^2 V_M}{\partial x^2} - \frac{V_M}{r_M}. \qquad i_{cap} = c_M \frac{dV_M}{dt}.$$

$$I_L = I_{cap} + I_{ion}$$

$$\frac{a}{2r_L}\frac{\partial^2 V_M}{\partial x^2} = c_M \frac{\partial V_M}{\partial t} + I_K + I_{Na} + I_L.$$

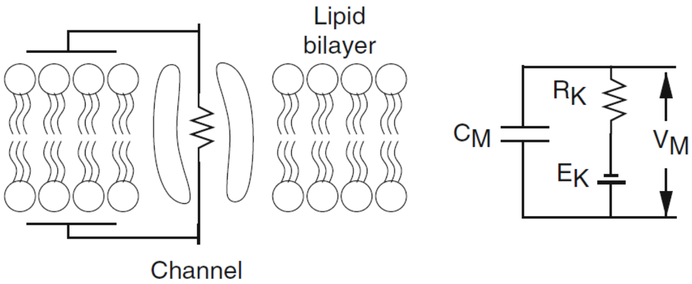
$$c_M \frac{\partial V_M}{\partial t} = \frac{a}{2r_L}\frac{\partial^2 V_M}{\partial x^2} - g_K(V_M - E_K) - g_{Na}(V_M - E_{Na}) - g_L(V_M - E_L).$$

Voltage clamp: capacitive could be zero in constant voltage $I_{cap} = C_M dV_M/dt = 0.$

Space-clamped: inserting a highly conductive axial wire inside the fiber $\frac{\partial^2 V_M}{\partial x^2} = 0.$

The leaky integrate-and-fire (LIF)

$$c_{\mathrm{M}} \frac{\mathrm{d}V_{\mathrm{M}}}{\mathrm{d}t} = -\frac{(V_{\mathrm{M}} - E_{\mathrm{R}})}{r_{\mathrm{M}}} + I(t)/A,$$



$$\tau_m \frac{dv}{dt} = -v(t) + RI(t)$$

τ_m is the membrane time constant

R is the membrane resistance.

simple resistor-capacitor (RC) circuit

Leakage term is due to the **resistor** and the **integration** of **I(t)** is due to the **capacitor**

Spiking events are not explicitly modeled in the LIF model.

When the membrane potential **v(t)** reaches a certain threshold $\mathbf{v_{th}}$ (**spiking threshold**), it is instantaneously reset to a lower value $\mathbf{v_r}$ (**reset potential**)

absolute refractory period Δ_{abs} immediately after $v(t)$ hits v_{th}.

Stimulation by a constant input current

$I(t) = I.$
assume $v_r = 0.$

The solution of Equation 1 is then given by:

$$v(t) = RI[1 - \exp(-\frac{t}{\tau_m})]$$

Asymptotic value of the membrane potential is RI.

If this value is less than the spiking threshold, v_{th},

Time of the first spike

Assuming $v(0) = v_r = 0$,

$t^{(1)}$, can be found by solving:

$$v_{th} = RI[1 - \exp(-\frac{t^{(1)}}{\tau_m})]$$

This yields:

$$t^{(1)} = \tau_m \ln \frac{RI}{RI - v_{th}}$$

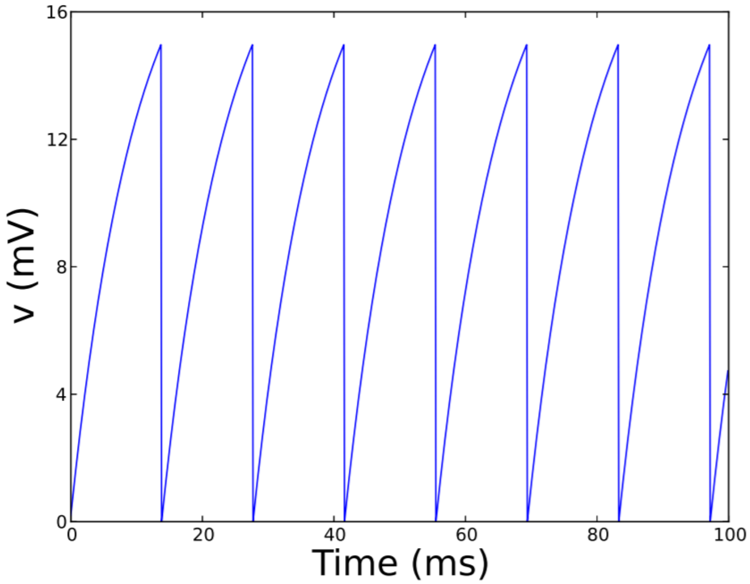
Firing rate of the neuron

$$T = \Delta_{abs} + \tau_m \ln \frac{RI}{RI - v_{th}}$$

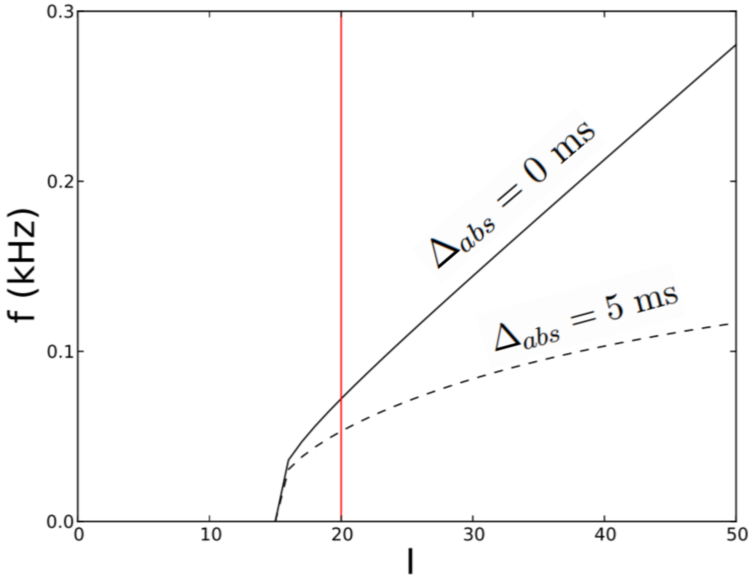
$$f = [\Delta_{abs} + \tau_m \ln \frac{RI}{RI - v_{th}}]^{-1}$$

Stimulation of a LIF neuron by a constant input current

the time-course of the membrane potential, *v(t)*



f-I curve for a LIF neuron

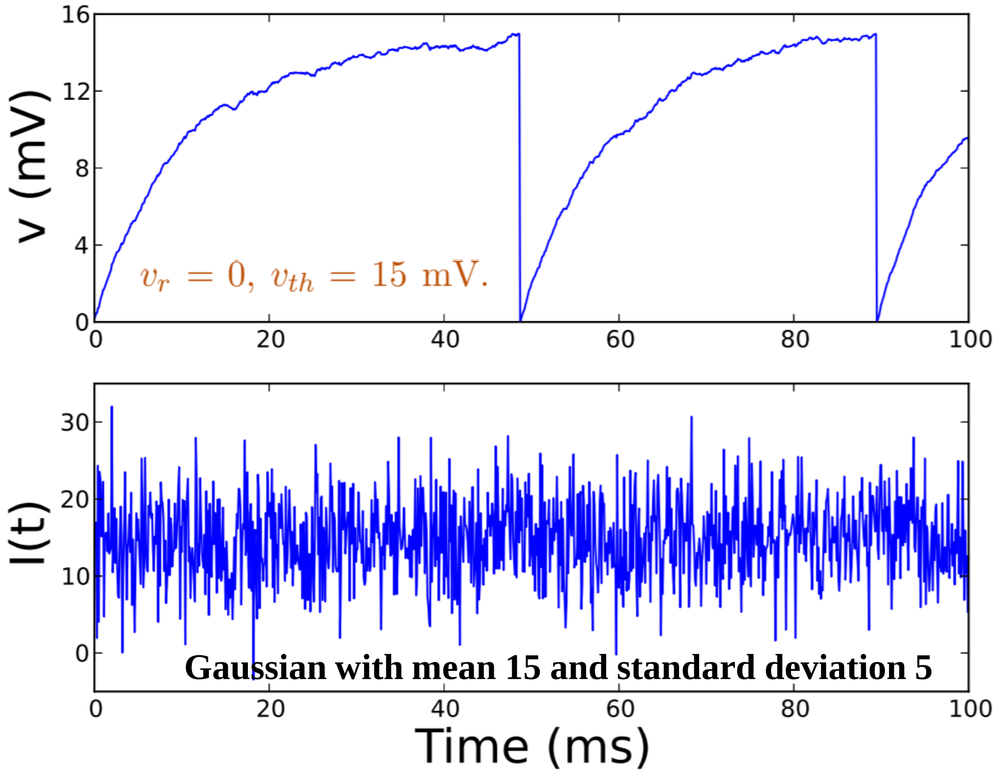


Stimulation by a time-varying input current

For a general time-varying input current ***I(t)***, the solution LIF neuron Equation, with the initial condition $v(t_0) = v_r$, is given by:

$$v(t) = v_r \exp(-\frac{t - t_0}{\tau_m}) + \frac{R}{\tau_m} \int_0^{t-t_0} \exp(-\frac{s}{\tau_m}) I(t-s) ds$$

Stimulation of a LIF neuron by a time-varying input current



Stimulation by synaptic currents

Each **pre-synaptic spike** makes a stereotyped contribution, described by a function ***α(t),*** to the post-synaptic current and contributions of different pre-synaptic spikes are linearly summed to obtain the total post-synaptic current.

Total post-synaptic current to the i-th neuron:

$$I_i(t) = \sum_j w_{ij} \sum_f \alpha(t - t_j^{(f)})$$

where $t_j^{(f)}$ represents the time of the f-th spike of the j-th pre-synaptic neuron;

w_{ij} is the **strength of synaptic efficacy**

Common choice for a

Dirac δ-pulse:

$$\alpha(t) = q\delta(t)$$

the alpha synapse

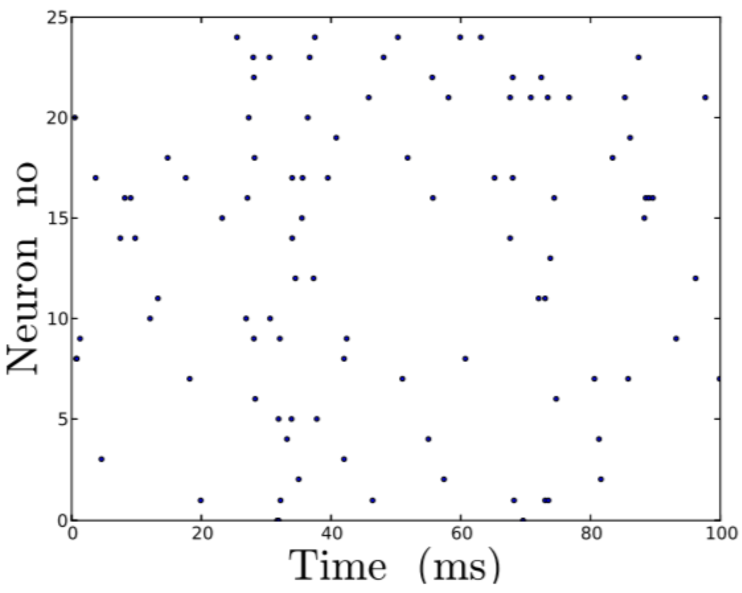
$$\alpha(t) = \alpha\frac{t}{\tau}\exp(1 - \frac{t}{\tau})$$

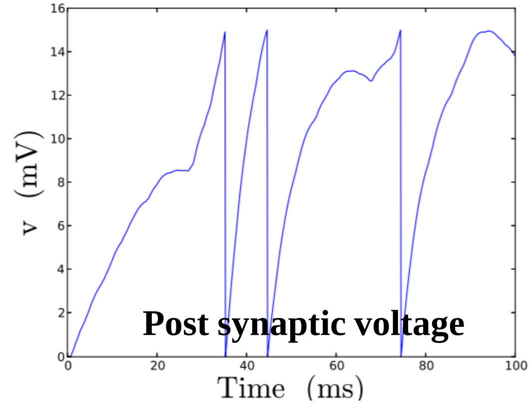
the bi-exponential synapse:

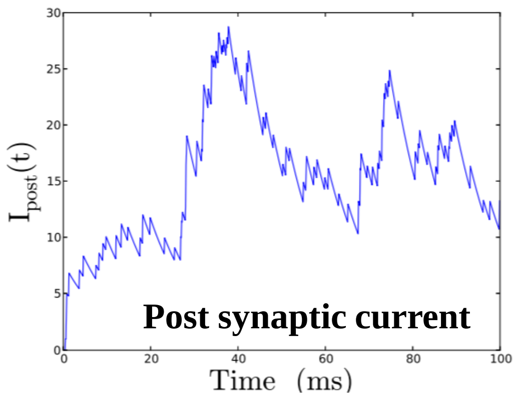
$$\alpha(t) = \beta\frac{\tau_2}{\tau_2 - \tau_1}[\exp(-\frac{t}{\tau_1}) - \exp(-\frac{t}{\tau_2})]$$

where α and β are normalizing constants and τ, τ_1 and τ_2 are the time constants of the synapses.

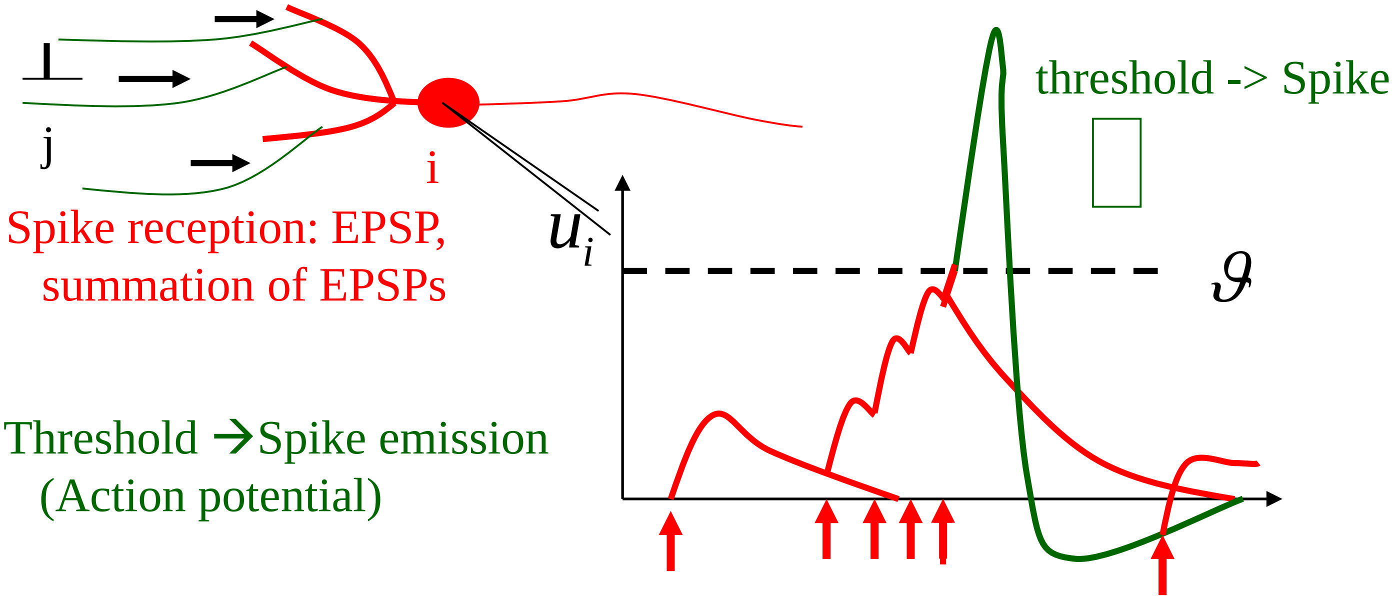
Stimulation of a LIF neuron by synaptic current







Phenomenology of spike generation

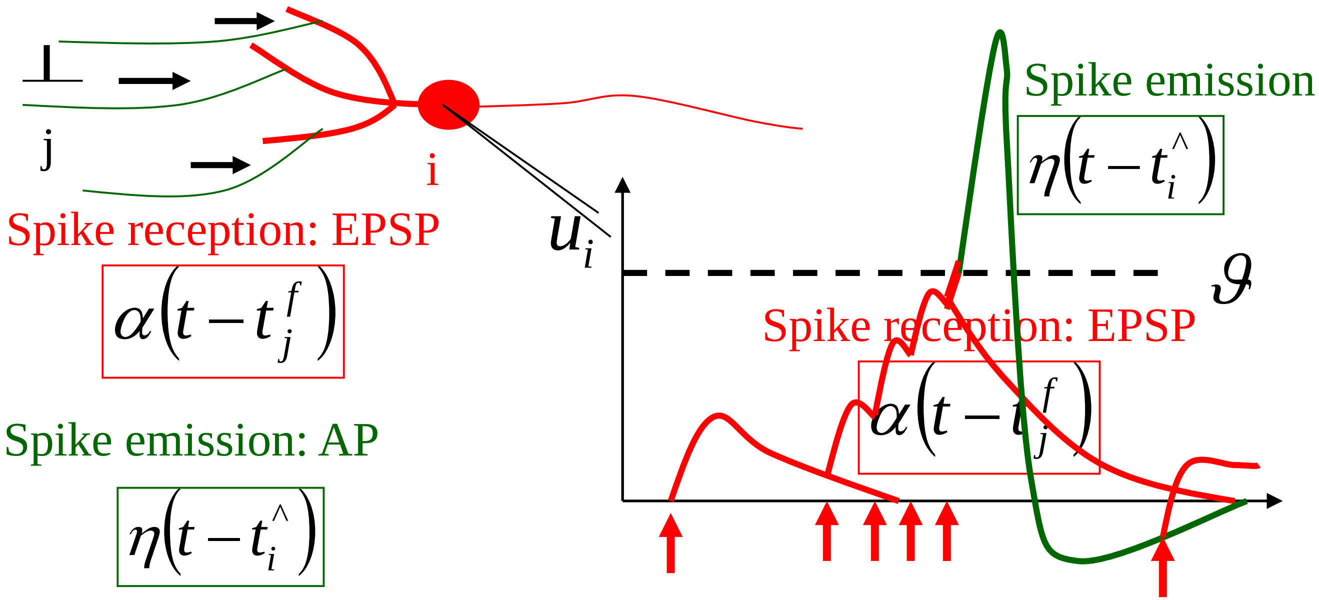


Spike reception: EPSP,
summation of EPSPs

Threshold → Spike emission
(Action potential)

Spike reception: EPSP

Spike Response Model



Last spike of i

All spikes, all neurons

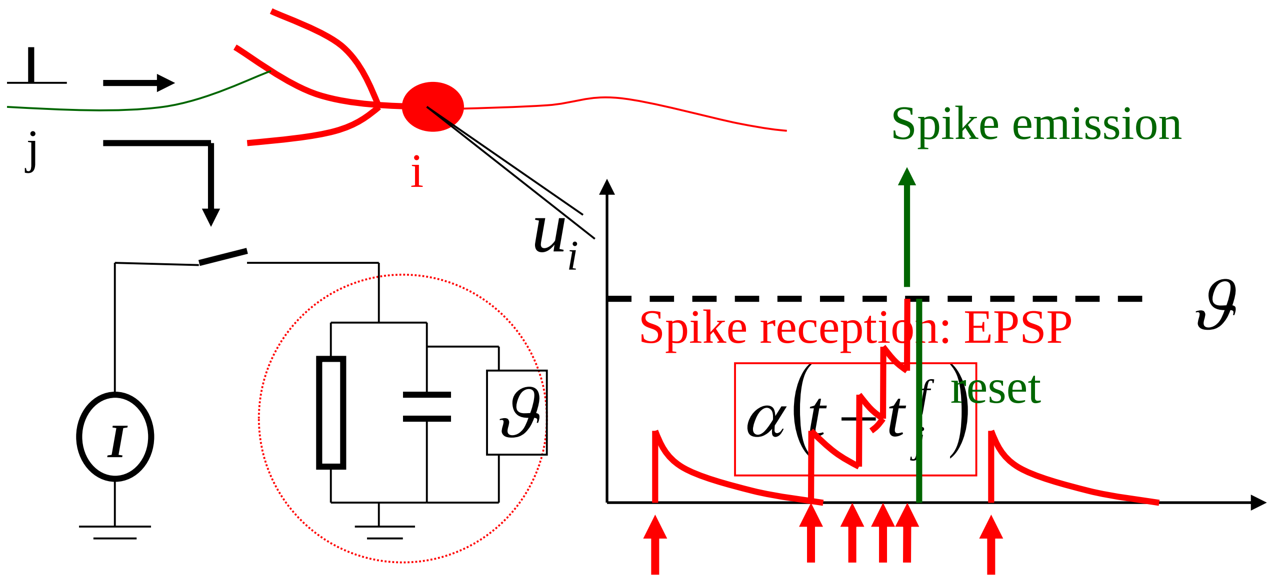
$$u_i(t) = \underbrace{\eta\left(t - t_i^\wedge\right)} + \sum_j \sum_f w_{ij}\, \underbrace{\alpha\left(t - t_j^f\right)}$$

linear

$$u_i(t) = \vartheta \Rightarrow \text{Firing:} \quad t_i^\wedge = t$$

threshold

Integrate-and-fire Model



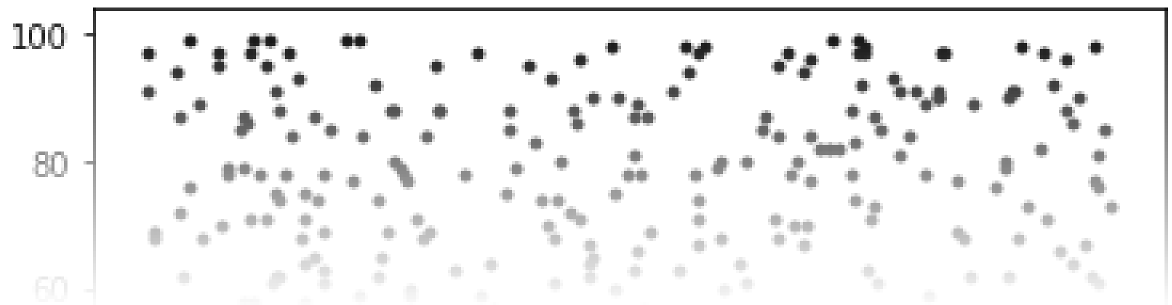
$$\tau \cdot \frac{d}{dt} u_i = -u_i + RI(t)$$ linear

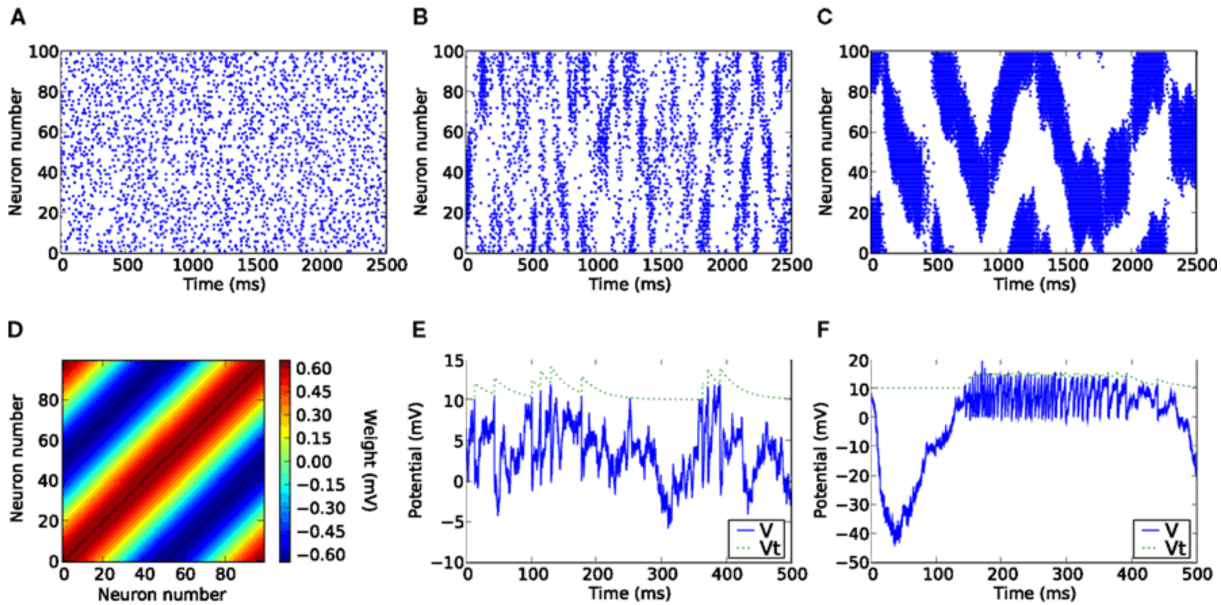
$$u_i(t) = \vartheta \Rightarrow$$ Fire+reset threshold

Lets try real program with Brian . . .

In [6]:

```
from brian2 import *
G = PoissonGroup(100, rates=50*Hz)
M = SpikeMonitor(G)
run(100*ms)
plot(M.t/ms, M.i, '.k');
```






```
from brian import *
w = .5*mV
def adaptive_threshold_reset(P, spikes):
    P.V[spikes] = 0*mV
    P.Vt[spikes] = clip(P.Vt[spikes]+2*mV, 10*mV, 15*mV)
eqs = ''' dV/dt  = (5*mV-V)/(10*ms) + 4*mV*xi/(10*ms)**.5 : volt
          dVt/dt = (10*mV-Vt)/(30*ms)                    : volt '''
group=NeuronGroup(100, model=eqs,
                       threshold=lambda V,Vt:V>=Vt,
                       reset=adaptive_threshold_reset)
C = Connection(group, group, 'V', delay=2*ms)
S = SpikeMonitor(group)
C.connect_full(group, group, weight=lambda i,j:w*cos(2.*pi*(i-j)*1./100))
group.V = rand(100)*5*mV+5*mV
group.Vt = 10*mV
run(2.5*second)
raster_plot(S)
show()
```