



leakage conductance  
 $= \frac{1}{\text{resistance}}$

reset voltage (constant);  
 can be thought of as extracellular voltage.

$$I_{exc}(t) = \sum_i a_{E_i} \delta(t - \tau_i^E)$$

strength of excitatory input

At each reception of an excitatory spike, the voltage increases suddenly by an amount  $a_E / C$

$$I_{inh}(t) = - \sum_i a_{I_i} \delta(t - \tau_i^I)$$

amplitude of inhibition

times of inhibitory input spikes

Every time an inhibitory spike is received, the voltage is suddenly decreased by an amount  $a_I / C$

If one were simulating an entire network, then the times of excitation and inhibition would come from the solution of the dynamics of the other neurons whose axons are connected synaptically with the dendrites of the neuron under consideration. However, it's often useful to consider a single neuron or a piece of a network that is receiving input signals from "outside" (another part of neural network or from the sensory organs).

Unless one has a good reason to the contrary, a widely used and applicable statistical model for the times of the spikes arising from outside the network is through a **Poisson point process**

- the number of spikes in nonoverlapping intervals are independent
- the number of spikes in a time interval of length  $t$  is given by a Poisson distribution with mean  $\lambda t$
- where  $\lambda$  is the intensity (or rate) of the spikes
- More precisely, we define a **Poisson counting process**  $N(t)$  which is defined as the number of spikes received in the time interval  $[0, t]$ . The number of spikes received in a time interval  $(s, t]$  is then just  $N(t) - N(s)$ .

$$P(N(t) - N(s) = j) = e^{-\lambda t} \frac{(\lambda t)^j}{j!}$$

So in our neuron model we can take the input spike times as independent Poisson point processes for excitation and inhibition, with intensities (rates)

$$\lambda_E, \lambda_I$$

and we associate to these spike times the Poisson counting processes

$$N_E(t), N_I(t)$$

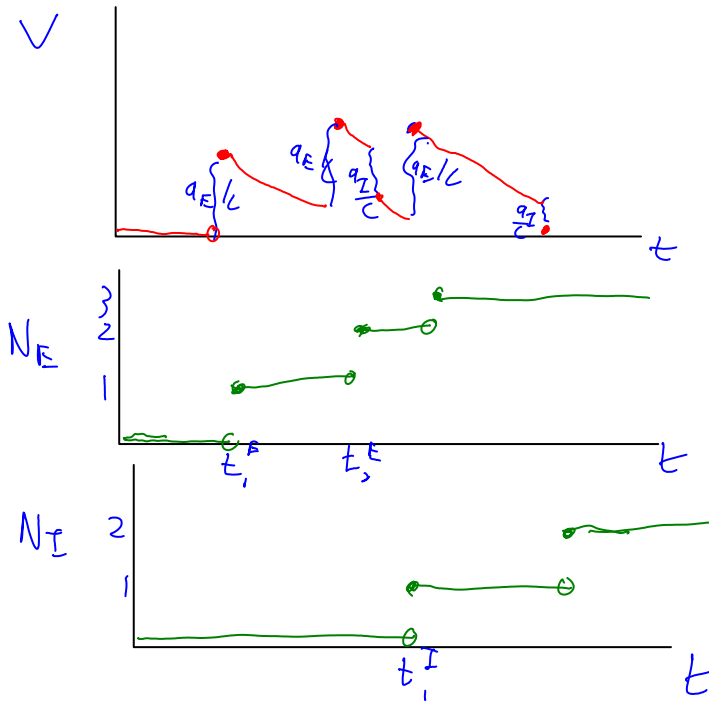
We can write the governing (**current-driven**) model for the neuron in physical form:

$$C \frac{dV(t)}{dt} = -g_L (V(t) - V_R) + \sum_i a_{E_i} \delta(t - \tau_i^E) - \sum_i a_{I_i} \delta(t - \tau_i^I)$$

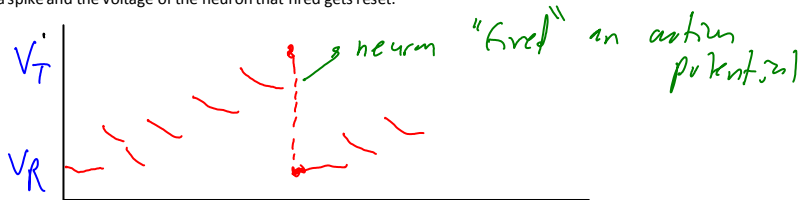
$$- \sum_j a_I \delta(t - T_j^I)$$

Mathematical form that avoids delta functions:

$$C \, dV(t) = -g_L (V(t) - V_R) \, dt + a_E \, dN_E(t) - a_I \, dN_I(t)$$



One couples this stochastic "subthreshold dynamics" to the firing events when the voltage crosses threshold. So when the voltage crosses threshold, then it sends a spike and the voltage of the neuron that fired gets reset.



A fundamental question of interest is what are the properties of the times at which the neuron fires as a function of the input parameters (i.e., the currents arising from the input spikes.) In particular, how fast on average does the neuron fire as a function of design parameters?

Firing rate  $\lim_{t \rightarrow \infty} \frac{N_o(t)}{t}$

$N_o(t) = \# \text{ spikes fired up to time } t$

Determining these properties relates to first-passage time calculations for the underlying stochastic dynamics. The calculations for this discontinuous spike model are rather complicated and unwieldy. Consequently, one often uses a diffusion approximation to approximate the stochastic dynamics of the neuron voltage.

Start with Kolmogorov forward equation for the probability density for the neuron voltage under the subthreshold dynamics -- this is the analogue to the Fokker-

Planck equation for white noise forcing:

$$\frac{\partial p_V(v, t)}{\partial t} = \frac{\partial}{\partial v} \left( \frac{g_L}{c} (v - V_R) p_V(v, t) \right) + \lambda_E \left( p_V\left(v - \frac{q_E}{c}, t\right) - p_V(v, t) \right) + \lambda_I \left( p_V\left(v + \frac{q_I}{c}, t\right) - p_V(v, t) \right)$$

Under conditions in which the jumps are small (in some certain nondimensional sense), one can Taylor expand the right hand side to second order in the spike amplitudes to get:

$$\frac{\partial p_V(v, t)}{\partial t} = \frac{\partial}{\partial v} \left( \left( \frac{g_L}{c} (v - V_R) - \lambda_E \frac{q_E}{c} + \lambda_I \frac{q_I}{c} \right) p_V(v, t) \right) + \frac{1}{2} \frac{\partial^2}{\partial v^2} \left( \left( \lambda_E \frac{q_E^2}{c^2} + \lambda_I \frac{q_I^2}{c^2} \right) p_V(v, t) \right) + \text{higher order terms}$$

$\leftarrow \overline{I}_{ext}$

This is the Fokker-Planck equation for

$$dV = \left( \overline{I}_{ext} - g_L (V - V_R) \right) dt + \sigma dW(t)$$