INTEGRATE-AND-FIRE MODELS

Integrate-and-fire models (IF models) date back to the work of Lapicque in 1907. Their importance comes from the fact that they are solvable, even in cases where the input is stochastic. More recently they have been used to analyse the emergent states in networks of neurons.

Theoretical Neuroscience, Dayan and Abbott. Chapter 5 p162-166. MIT Press
Spiking Neuron Models, Gerstner and Kistler. Chapter 4 p93-100. Cambridge University Press

• THE LEAKY INTEGRATE-AND-FIRE (LIF) MODEL
The model comprises a leaky, passive subthreshold dynamics characterised by a timescale τ_L,

$$\tau_L \frac{dV}{dt} = E_L - V + \frac{I}{g_L}. \tag{1}$$

If the voltage ever reaches the threshold V_{th} then a spike is registered, the voltage is instantly reset at V_{re} and the dynamics continue. It sometimes proves convenient to absorb the current into the effective fixed point or resting potential $E_0 = E_L + I/g_L$. If $E_0 < V_{th}$ there is stable fixed point but the model is excitable - a synaptic pulse that brings the voltage above V_{th} releases a spike. If $E_0 > V_{th}$ the neuron is spontaneously firing - it is a non-linear oscillator. The critical value of the resting potential is $E_0 = V_{th}$ which corresponds to a critical current $I^* = g_L(V_{th} - E_L)$.

• FIRING-RATE OF THE LIF NEURON
The firing-rate of the neuron for $E_0 > V_{th}$ can be calculated by remembering the form of the response of a passive neuron (Eq. 1) for a relaxation from an initial state at $t = 0$. Choosing the initial voltage to be V_{re} we have

$$V(t) = E_0 + (V_{re} - E_0)e^{-t/\tau_L}. \tag{2}$$

A single period of duration T takes the neuron from the reset V_{re} to the threshold V_{th} so that

$$V(T) = V_{th} = E_0 + (V_{re} - E_0)e^{-T/\tau_L} \quad \text{giving} \quad T = \tau_L \log\left(\frac{E_0 - V_{re}}{E_0 - V_{th}}\right). \tag{3}$$

The inverse of the period is the firing rate r; thus

$$r = \frac{1}{\tau_L \log\left(\frac{E_0 - V_{re}}{E_0 - V_{th}}\right)}. \tag{4}$$

We now consider the firing in various limits. First a case where the neuron is just starting to fire, which occurs when $E_0 = V_{th} + \epsilon$ where ϵ is small. In this case the rate is

$$r \simeq \frac{1}{\tau_L \log\left(\frac{V_{th} - V_{re}}{\epsilon}\right)} \tag{5}$$

which gives a zero firing rate as $\epsilon \to 0$ from above. Hence the LIF neuron can fire an arbitrarily low rate and is therefore a Type I model. We now consider the other extreme, the high-firing rate limit when E_0 is very large. Consider two variables $\theta = V_{th} - V_{re}$ and $\mathcal{E} = E_0 - (V_{th} + V_{re})/2$. In terms of these variables the firing rate can be written

$$r = \frac{1}{\tau_L \log\left(\frac{\mathcal{E}+\theta/2}{\mathcal{E}-\theta/2}\right)} \simeq \frac{1}{\tau_L \log\left(1 + \theta/\mathcal{E}\right)} \simeq \frac{\mathcal{E}}{\tau_L \theta} = \frac{E_0 - (V_{th} + V_{re})/2}{V_{th} - V_{re}}. \tag{6}$$

Hence for strong current the firing rate grows linearly with E. This is unrealistic as the firing rate in real neurons saturates. This feature can be dealt with by including a refactory time: after the spike the neuron stays at V_{re} for a time τ_r before the dynamics restarts. By considering the full period as $T_r = T + \tau_r$ we can write the firing rate for a refactory neuron as

$$r_r = \frac{r}{1 + r\tau_r}. \tag{7}$$

When $r\tau_r \ll 1$ the firing rates of the refactory and non-refactory neuron are similar $r_r \simeq r$. For $r\tau_r \gg 1$ the firing rate for the refactory neuron becomes $r_r = 1/\tau_r$ and hence a maximal firing rate has been enforced.

• Exponential IF (EIF) Model

An important recent improvement to the LIF is to include an exponential term that accounts for the near instantaneous activation of the sodium current's m variable. The voltage equation takes the form

$$\tau_L \frac{dV}{dt} = E_L - V + \Delta_T \exp^{(V - V_T)/\Delta_T} + \frac{I}{g_L} = F(V). \tag{8}$$

In this case the ultimate threshold is at $V_{th} = \infty$ (when the spike starts the voltage diverges in finite time) with a subsequent reset to V_{re}. The voltage range for spike initiation is Δ_T and the effective threshold is measured by V_T. There are two cases: if the current is below a critical value there are two fixed points, the lower one is stable and the upper unstable - the model is excitable; if the current is above the critical value there are no fixed points and the model is spontaneously oscillating. At the critical current the fixed points merge, the RHS of equation (8) is zero and so is its derivative with respect to voltage:

$$E_L - V^* + \Delta_T \exp^{(V^* - V_T)/\Delta_T} + \frac{I^*}{g_L} = 0 \quad \text{and} \quad -1 + \exp^{(V^* - V_T)/\Delta_T} = 0. \tag{9}$$

From the second equation the critical fixed-point voltage is at V_T and the critical current is

$$I^* = g_L \left(V_T - \Delta_T - E_L \right). \tag{10}$$

Above the critical point the firing rate $r = 1/T$ can be found from

$$\int_{V_{re}}^{V_{th}} \frac{dV}{F(V)} = \frac{T}{\tau_L} \tag{11}$$

where $F(V)$ is given in equation (8). This equation gives the firing rate of any IF type model as a function of $F(V)$. In general this integral must be calculated numerically. Finally, it can also be noted that in the limit $\Delta_T \to 0$ the EIF model becomes identical to the LIF model with V_T the threshold for the instantaneous spike.

• Non-Leaky IF (NLIF) Model

One other (drastic) approximation to neuronal dynamics worth mentioning is the NLIF model in which g_L is set to zero

$$C \frac{dV}{dt} = I \quad \text{where } I > 0 \tag{12}$$

with the threshold at a finite V_{th} and reset to V_{re}. The voltage dynamics are linear and the firing rate is given simply by $r = I/C(V_{th} - V_{re})$.

• Type I and Type II IF Neurons
The models treated above are of Type I: if the RHS of equation (8) is expanded to second order in voltage around its minimum the canonical Type I model can be found. Type II behaviour can be seen in IF type models, but a second variable is required that comes from a voltage-gated current with negative feedback. Such neurons also show bistability, in which a steady state or an oscillating case are possible.

• Spike-Frequency Adaptation
Many neurons have a type of voltage-gated current that activates at high voltage (i.e. it is triggered by spikes) and that gives rise to a hyperpolarising current that switches off slowly (a long time constant). This may be modelled by

$$\begin{aligned} \tau_L \frac{dV}{dt} &= E_0 - V - A \\ \tau_A \frac{dA}{dt} &= -A + \tau_A a \sum_{\{t_k\}} \delta(t - t_k) \end{aligned} \tag{13}$$

where A is the strength of the hyperpolarising current and where $\{t_k\}$ are the set of spike times that must be calculated self-consistently. Treating the equation for A, we can relate its value just before spike k to its value just before spike $(k+1)$

$$A_{k+1} = (A_k + a)e^{-(t_{k+1} - t_k)/\tau_A}. \tag{14}$$

For large times and constantly spaced pulses of period T we get the steady-state result

$$A^* = (A^* + a)e^{-T/\tau_A}. \tag{15}$$

where T still needs to be derived self-consistently.

For the general case this system is hard to solve analytically. However, in the limit where the firing rate is much higher than τ_A, i.e. $r\tau_A \gg 1$, some results may be extracted. In this limit the dynamics of V are much faster than that of A. In the voltage equation the A may be considered constant, and so the firing rate (for the LIF case) and the A equation become

$$r_A \simeq \frac{E_0 - A - (V_{th} + V_{re})/2}{\tau_L(V_{th} - V_{re})} \tag{16}$$

$$\tau_A \frac{dA}{dt} = -A + \tau_A a r_A \tag{17}$$

where in the last equation the sum of delta functions has been replaced by the firing rate r_A. The A equation has a fixed point $A^* = \tau_A a r_A^*$ which agrees with equation (15) in the limit $T/\tau_A \ll 1$. On combining equations (16-17) these we get

$$\frac{dA}{dt} = -A\left(\frac{1}{\tau_A} + \frac{a}{\tau_L(V_{th} - V_{re})}\right) + \frac{a(E_0 - (V_{th} + V_{re})/2)}{\tau_L(V_{th} - V_{re})} \tag{18}$$

which has a steady state

$$A^* = a\left(E_0 - (V_{th} + V_{re})/2\right) / \left(a + \frac{\tau_L}{\tau_A}(V_{th} - V_{re})\right). \tag{19}$$

On solving this with initial value $A = 0$ at $t = 0$ and substituting into the voltage equation, we get

$$r = r_A^* + (r_0 - r_A^*)e^{-t\left(\frac{1}{\tau_A} + \frac{a}{\tau_L(V_{th} - V_{re})}\right)} \tag{20}$$

where r_A^* is equation (16) with $A = A^*$ and r_0 is equation (16) with $A = 0$.