Integrate and Fire Model of Spike Generation

Professor David Heeger

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The integrate-and-fire model has a long and distinguished history dating back to Lapicque (1907, 1926), before anything specific was known about the biophysics of excitable membranes. More recent versions of this model have been analyzed by a number of people (Stein, 1967; 1968; Knight, 1972; Softky and Koch, 1993).

The integrate-and-fire model assumes that spike initiation is governed by a voltage threshold. When the somatic membrane potential exceeds that threshold, a spike is fired, and the membrane potential is reset back to V_{rest}.

In its simplest form, the membrane potential is assumed to literally integrate the input current:

$$C\frac{dV}{dt} = I(t).$$

When V achieves a criterion level V_{th}, a nerve impulse is fired, V is reset to 0, and the process starts again.

A much more palatable version, often called a *leaky* or *forgetful* integrate-and-fire model, assumes that the neuron is a single passive compartment. Then the membrane potential charges and discharges exponentially in response to injected current:

$$C\frac{dV}{dt} + g_l V - I(t) = 0,$$

where g_l is the leak conductance and V is the membrane potential with respect to rest. Again, when V achieves a criterion level V_{th}, a nerve impulse is fired, V is reset to 0, and the process starts again. The leaky integrate-and-fire model has been applied to model the firing behavior of many cells, such as neurons in the limulus eye (Knight, 1972) and cortical cells (Wehmeier *et al.*, 1989; Softky and Koch, 1993; Somers *et al.*, 1995).

For either model, the injected current $I(t)$ could of course be replaced with synaptic currents, e.g.,

$$C\frac{dV}{dt} + g_l V + g_{syn}(V - V_{syn}) = 0,$$

but I will ignore that complication for the purposes of this handout.

Because the model makes no pretense of mimicing the currents involved in shaping the action potentials, the pulse generation is not part of the model but is simply added on. Because of this lack of any spiking currents, the model also displays no afterhyperpolarization following a spike. We can remedy this by postulating that following the triggering of a pulse, the membrane potential is set to zero for a certain fixed refractory period T_{ref}. Or we can let the membrane evolve naturally following each spike but simply prevent spikes from occurring until the refractory period T_{ref} has passed. A somewhat more sophisticated model (e.g., Wehmeier *et al.*, 1989) activates a calcium conductance following each spike that pulls down the potential, e.g., through calcium-dependent potassium channels. This imitates both the absolute as well as the relative refractory period following spike initiation. This also has the advantage that spike frequency adaptation can easily be incorporated into the model. Another way to mimic a relative refractory period is to not keep the threshold for spike initiation constant but to increase V_{th} following each spike, for instance using the rule $V_{th} = k(1 - \tau t)$, where t is the time from the last spike (e.g., Somers *et al.*, 1995).

In the following, I will discuss only the leaky integrate-and-fire model with four parameters: a voltage threshold, a capacitance, a resistance, and an absolute refractory period. The refractory period is typically split, for convenience, into two parts: the duration of the spike (e.g., 1 msec) and the minimum interval between spikes (e.g., 3 msec) for a total of $T_{ref} = 4$ msec.

To characterize the discharge curve (firing rate vs. current or F-I curve) of the leaky integrate-and-fire model, recall that the passive neural membrane charges and discharges with an exponential time-course. The passive membrane response to a step of constant current I, switched on at $t = 0$ and remaining on indefinitely is given by:

$$V(t) = u(t)\,(I/g_l)\,\left(1 - e^{(-t/\tau)}\right),$$

where $u(t) = 0$ for $t < 0$ is the unit step signal, and we have assumed that $V(0) = V_{\text{rest}} = E_l = 0$.

However, the leaky integrate-and-fire neuron will only follow this equation as long as the voltage remains below V_{th}, since upon reaching the threshold a spike is initiate and the voltage is reset.

The minimal sustained current necessary to trigger an action potential is $I_{th} = V_{th}\,g_l$. For any current larger than I_{th}, an output impulse will be generated at time T, such that:

$$V_{th} = (I/g_l)\,\left(1 - e^{(-T/\tau)}\right).$$

Inverting this relationship gives the time to spike as:

$$T = -\tau ln\left(1 - \tfrac{g_l V_{th}}{I}\right).$$

When the current is greater than I_{th}, then the firing rate is given by:

$$F(I) = \frac{1}{T_{ref} + T}$$

An example is shown in Fig. 1. This behavior is remarkably similar to that of cortical cells.

In slice prepartion, neurons can ofter fire very regularly. And some neurons *in vivo* fire regularly. But in the cortex, the timing of successive action potentials is highly irregular (see the *Poisson Spike Model* handout). One of the main problems with the leaky integrate-and-fire model is that it is too deterministic, hence inconsistent with the behavior of *in vivo* cortical neurons. This problem can be partially overcome by adding lots of noisy inputs. For pointers to the literature on these issues, see the Poisson handout.

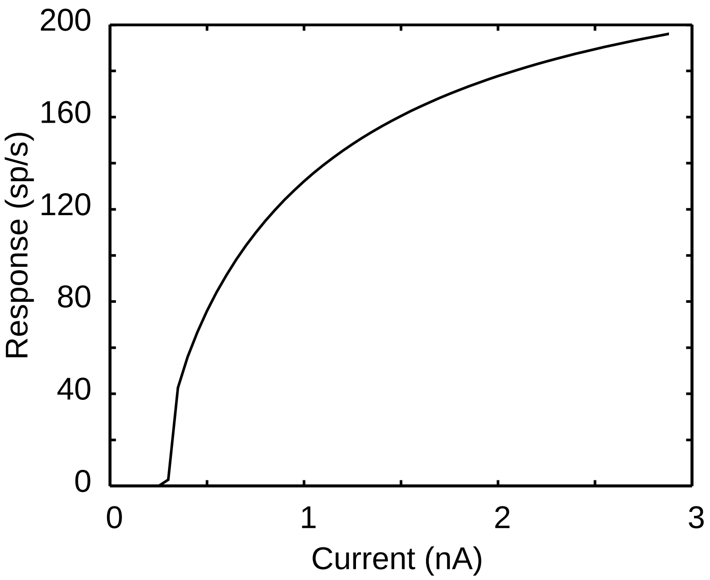

Figure 1: F-I curve a leaky integrate-and-fire neuron, that is, firing rate as a function function of injected current for current steps of various amplitudes. Parameters: $C = 0.2$ nF, $g = 0.02$ uS, $V_l = -70$ mV, $V_{th} = -55$ mV, $T_{ref} = 4$ msec, $E_l = V_{\text{rest}} = 0$ mV. Hence, $I_{th} = g_l V_{th} = 0.3$ nA.

References

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