School of Mathematical Sciences

G14TNS Theoretical Neuroscience

Nonlinear integrate-and-fire models

Although conductance-based models like that of Hodgkin and Huxley provide a level of detail that helps us to understand how the kinetics of channels (with averaged activation and inactivation variables) can underly action-potential generation their high dimensionality precludes them from studies at the network level. Here the goal would be to predict emergent computational properties in populations and recurrent networks of neurons from the properties of their component cells. Thus simpler (lower dimensional and hopefully mathematically tractable) models are more appealing - especially if they can be fit to single neuron data. It is now known that extensions of the basic linear (leaky) integrate-and-fire (IF) model can accurately fit intracellular voltage recordings.[1]

A one-dimensional nonlinear IF model takes the form

$$\frac{dv}{dt} = f(v) + I(t),$$

such that v is reset to v_R just after reaching the value v_{th}. Firing times are defined iteratively according to

$$T_n = \inf\{t \,|v(t) \geq v_{th} \ ; \ t \geq T_{n-1}\}.$$

Leaky IF model

The linear (leaky) IF model (LIF) is attributed to Lapicque in 1907 (on frog nerve stimulation) and is defined with

$$f(v) = -\frac{v}{\tau}.$$

The term "integrate-and-fire" was first coined by Bruce Knight in the 60s. Because of its linear nature we may solve the sub-threshold dynamics of the model exactly (using an integrating factor, variation of parameters solution or Green's function):

$$v(t) = v_R e^{-(t-T_n)/\tau} + \int_{T_n}^{t} e^{-(s-t)/\tau} I(s) ds, \qquad T_n < t < T_{n+1}.$$

For a constant input oscillations will occur if $I\tau > h$ (so that the steady state value is above threshold). The period of oscillation $\Delta = T_{n+1} - T_n$ is determined by setting $v(T_{n+1}) = v_{th}$, giving

$$\Delta = \tau \ln \left(\frac{I\tau - v_R}{I\tau - v_{th}} \right) H(I\tau - v_{th}),$$

where H is a Heaviside function and we assume $v_{th} > v_R$.

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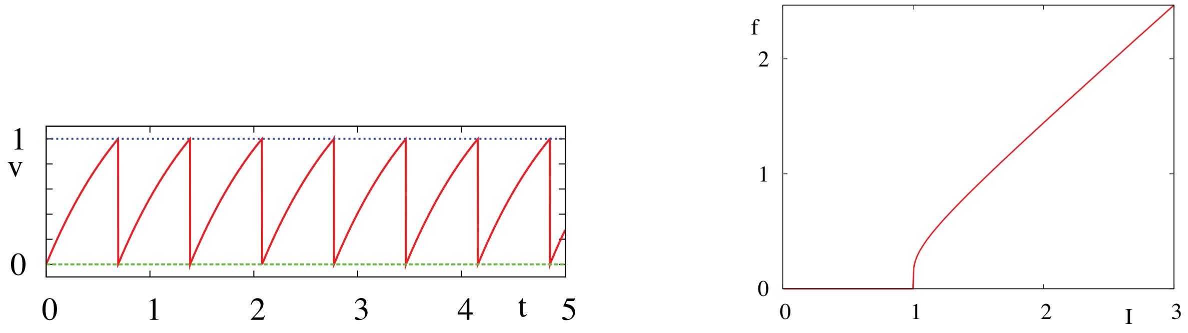
[1] Extracting nonlinear integrate-and-fire models from experimental data using dynamic I-V curves. Badel L, Lefort S, Berger TK, Petersen CCH, Gerstner W and Richardson MJE Biological Cybernetics 99: 361-370 (2008): http://www2.warwick.ac.uk/fac/sci/systemsbiology/staff/richardson/publications/badel2008BC.pdf

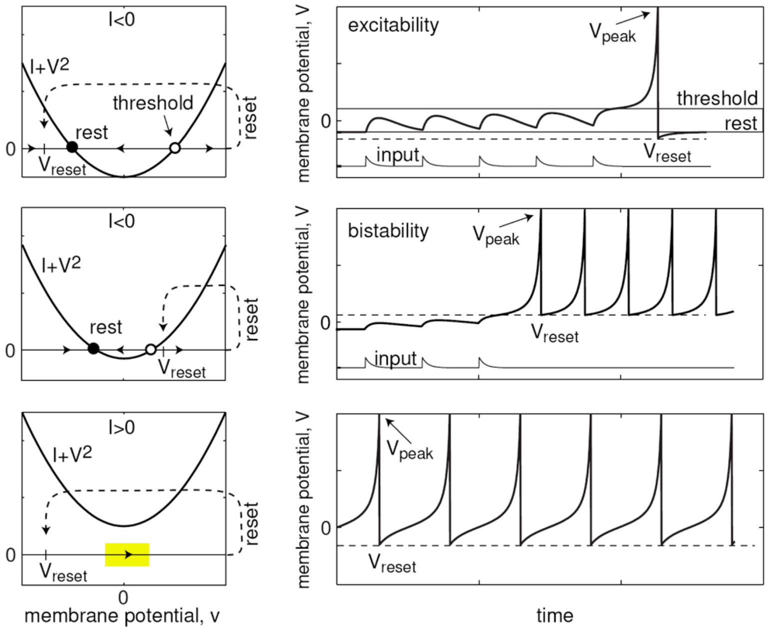


Left: LIF oscillator ($\tau = 1$, $v_{th} = 1$, $v_R = 0$). Right: Frequency of oscillation $f = \Delta^{-1}$ as a function of I.

The quadratic IF model

The quadratic IF (QIF) neuron is the simplest generalisation of the LIF model that captures qualitatively the behavior of the f-I curve of a large family of more realistic models. Interestingly, this model was apparently already known to Alan Hodgkin, and used to fit some of his data (and also subsequently analysed by Bruce Knight). It is defined by

$$f(v) = v^2.$$



QIF model with time-dependent input - redrawn from Izhikevich, E (2007) Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting,The MIT Press.

Unlike the LIF model the QIF does allow a representation of an action potential shape.

The neuron is an integrator; each input pulse shown in the figure (top), pushes v closer to threshold; the higher the frequency of the input, the sooner v reaches the threshold and starts the upstroke of a spike. The neuron is monostable when $v_R \leq 0$ and can be bistable otherwise. Indeed, the first spike in the middle figure is evoked by the input, but the subsequent spikes occur because the reset value is superthreshold.

Suppose the injected current I slowly ramps up from a negative to a positive value. The membrane potential follows the resting state $-\sqrt{|I|}$ in a quasi-static fashion until the bifurcation point $I = 0$ is reached. At this moment, the neuron starts to fire tonic spikes. In the monostable case $v_R < 0$

(bottom figure), the membrane potential is reset to the left of the ghost of the saddle-node point, thereby producing spiking with an arbitrary small frequency, and hence Type 1 firing - via a SNIC. In contrast, in the bistable case $v_R > 0$ (not shown in figure), the membrane potential is reset to the right of the ghost, no slow transition is involved, and the tonic spiking starts with a nonzero frequency (Type II firing).

The model has much in common with the θ-neuron model (and is effectively equivalent in the limit $v_{th} \to \infty$ and $v_R \to -\infty$).

In the oscillatory regime ($I > 0$) the trajectory (for constant drive) can be integrated:

$$\int_{v_R}^{v(t)} \frac{dv}{I + v^2} = \int_{T_n}^{t} ds, \qquad T_n < t < T_{n+1},$$

with solution

$$v(t) = \sqrt{I} \tan\left(\tan^{-1}\left(\frac{v_R}{\sqrt{I}} \right) + \sqrt{I} t \right).$$

The period of oscillation is calculated by setting $v(T_{n+1}) = v_{th}$ giving

$$\Delta = \frac{1}{\sqrt{I}} \left(\tan^{-1}\left(\frac{v_{th}}{\sqrt{I}} \right) - \tan^{-1}\left(\frac{v_R}{\sqrt{I}} \right) \right).$$

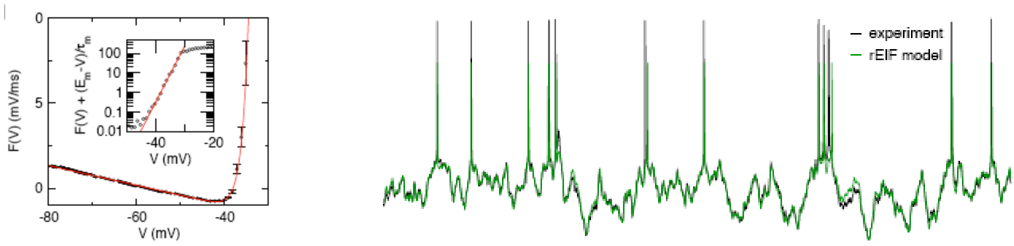
In the limit $v_{th} \to \infty$ and $v_R \to -\infty$ we see that $\Delta = \pi/\sqrt{I}$, and so the frequency of oscillation scales as $\sqrt{I}$ (as expected for a system with a SNIC).

The linear-exponential IF model

Real cortical data can be very accurately fit with the following choice:

$$f(v) = -\frac{1}{\tau}(v - v_L) + \frac{\kappa}{\tau} e^{(v - v_\kappa)/\kappa},$$

with $v_L = -68.5$ mV, $\tau = 3.3$ ms, $v_\kappa = -61.5$ mV and $\kappa = 4$ mV.



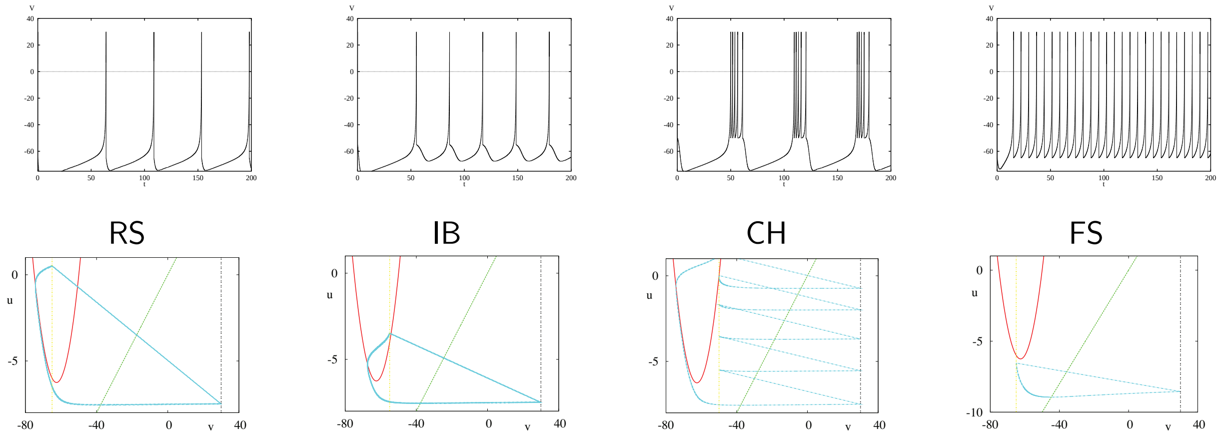
Left: fit of $f(v)$ to data from layer-5 pyramidal cells. Right: model vs. data.

The Izhikevich model

This is a two-dimensional nonlinear IF model - possessing two variables v and u, which we may interpret as a voltage and a recovery variable:

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I,$$
$$\frac{du}{dt} = a(bv - u),$$

where upon reaching threshold $v_R = 30$ mV the voltage is reset as in the IF model to a value $v_R = c$, and u is reset as $u \to u + d$. Two further parameters describe the sensitivity (b) and decay rate (a). It can capture a number of neuronal firing patterns including i) regular spiking (RS: $a = 0.02$, $b = 0.2$, $c = -65$, $d = 8$), ii) intrinsically bursting (IB: $a = 0.02$, $b = 0.2$, $c = -55$, $d = 4$), iii) chattering (CH: $a = 0.02$, $b = 0.2$, $c = -50$, $d = 2$), and iv) fast spiking (FS: $a = 0.1$, $b = 0.2$, $c = -65$, $d = 2$).

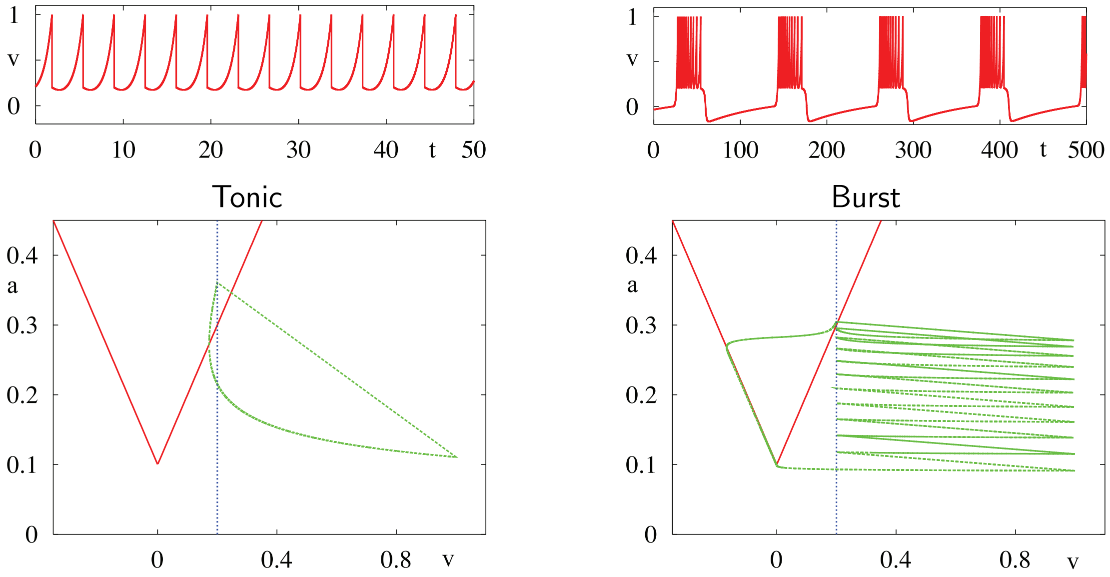


The absolute IF model

This may be regarded as a piecewise linear caricature of the Izhikevich model. In its simplest form it is given by:

$$\dot{v} = |v| + I - a, \qquad \dot{a} = -a/\tau_a, \qquad \tau_a > 0,$$

subject to the usual IF reset mechanism as well as the adaptive step $a(T_m) \to a(T_m) + g_a/\tau_a$, for some $g_a > 0$. For sufficiently small g_a the model fires tonically. For larger values of g_a the model can also fire in a burst mode.



Unlike the Izhikevich model this model is analytically tractable - as it is piecewise linear.