Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

Integrate and Fire Models, Deterministic

Nicolas Fourcaud-Trocmé*
Center for Research in Neuroscience of Lyon, CNRS UMR5292 - INSERM U1028, Université Lyon 1, Lyon, Cedex, France

Synonyms

Exponential integrate-and-fire model, Izhikevich model, Leaky integrate-and-fire model, Quadratic integrate-and-fire model

Definition

The integrate-and-fire (IF) model is a single-compartment model describing the subthreshold dynamics of the neuron membrane potential V. The spiking dynamics is marked by a spiking threshold, potential at which the neuron emits a spike. After spike emission, V is set at the neuron's reset potential. Subthreshold dynamics was initially designed to capture neuron's passive membrane properties, and its dynamics was given by a single first-order linear differential equation.

Variations around this model have been introduced to describe either spike-activated currents, more complex subthreshold dynamics, or more realistic spike initiation dynamics. These models can be two or three dimensional or include nonlinear terms. However, they are always designed to describe the relevant mechanisms with a minimal set of variables and parameters which make them suitable for large-scale simulations or detailed mathematical analysis.

Detailed Description

Leaky Integrate-and-Fire Model

The leaky integrate-and-fire (LIF) model was first introduced by Lapicque (1907) to describe mathematically neuron firing times. It is based on the idea that neuron activity can be captured by the dynamics of its membrane potential which evolves according to neuron inputs (synaptic or current injection) and passive membrane properties (see, e.g., Eccles 1957). The main hypothesis of the LIF model is that action potential threshold and shape are invariant from spike to spike, and thus a precise description of the spike can be omitted and simply sketched by a spiking threshold. When V reaches this threshold, a spike is emitted, after which V is set at the neuron's resting membrane potential. This simple spiking dynamics captures the nonlinear input–output relationship of neurons and has been the subject of detailed mathematical analysis (Knight 1972; Tuckwell 1988).

Below spiking threshold, the membrane potential dynamics is described by the membrane passive dynamics. The equivalent electrical circuit is sketched in Fig. 1a and its main parameters are the following:

- C_m: the membrane capacitance

*Email: nfourcau@olfac.univ-lyon1.fr

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

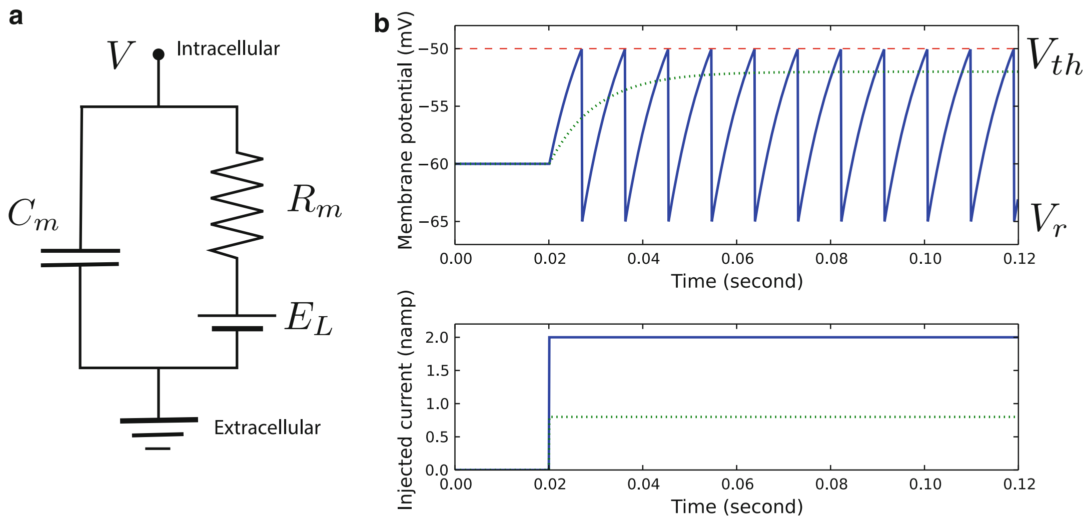

Fig. 1 Basis of the leaky integrate-and-fire (LIF) model. (**a**) Electrical RC circuit equivalent to the LIF model. (**b**) Subthreshold (*dashed line*) and suprathreshold (*full line*) activation of a LIF model. LIF parameters: $E_L = -65\ mV$, $\tau_m = 10$ ms, $V_r = -70$ mV, $V_{th} = -50$ mV

- g_L: the leak conductance (or equivalently its membrane resistance $R_m = 1/g_L$)
- E_L: the resting membrane potential, which is the neuron membrane potential in the absence of external stimulation

The standard equation describing the LIF model below threshold is then given by

$$C_m \frac{dV}{dt} = -g_L(V - E_T) + I(t) \tag{1}$$

where $I(t)$ represents any external input (electrode, synaptic, etc.) to the neuron. Another common form of Eq. 1 is

$$\tau_m \frac{dV}{dt} = -(V - E_L) + R_m I(t) \tag{2}$$

where τ_m is the membrane time constant:

$$\tau_m = \frac{C_m}{g_L} = R_m C_m \tag{3}$$

The first term on the right-hand side in Eqs. 1 or 2 is called the leak current. It pulls V toward its resting membrane potential. With this term, the LIF model is the original leaky integrate-and-fire model (also called forgetful IF). This term is sometimes neglected in which case the model is a perfect integrator (simple integrate-and-fire model, SIF). The previous equations only describe the subthreshold membrane potential dynamics. To capture neuron spiking mechanisms, the LIF model is completed by a constant spiking threshold V_{th}, potential at which the LIF model is considered to have emitted a spike. There is no detailed description of the actual spike shape. Following a spike, the potential V is reset to a reset potential V_r. See Fig. 1b for an example of LIF membrane potential trace.

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

To take into account the finite width of real spikes and the neuron absolute refractory period, we can add to the LIF model a refractory period τ_{ref}. It is a period following each spike during which the model is insensitive to external inputs. At the end of this period, V is reset at V_r.

Thanks to the simple form of its equation, assuming a constant input current $I(t) = I$, the LIF model trace can be exactly computed between spikes:

$$V(t) = V_r + (R_m I + E_L - V_r)\left(1 - e^{-\frac{t}{\tau_m}}\right) \tag{4}$$

This shows that if the input current is large enough, $R_m I \geq V_{th} - E_L$, then the LIF model emits a spike after a time T such that

$$V_{th} = V_r + (R_m I + E_L - V_r)\left(1 - e^{-\frac{T}{\tau_m}}\right) \tag{5}$$

Finally we obtain the LIF f-I curve, given by

$$f(I) = \frac{1}{\tau_{\text{ref}} + \tau_m \ln\left(\frac{R_m I + E_L - V_r}{R_m I + E_L - V_{th}}\right)} \tag{6}$$

Note that the logarithmic shape of the f-I curve, close to rheobase (current threshold), is not typical of f-I curves found with more detailed neuron model. Besides, this simple calculation in presence of a constant external input should not mask the strong nonlinearity introduced in the model by its hard spiking threshold making analytical computations more difficult as soon as more complex dynamics are considered. However, the simplicity of the LIF model makes it useful in large-scale simulations of neuronal networks.

Extensions of the LIF Model

The LIF model captures only subthreshold dynamics governed by passive membrane dynamics and has an oversimplified spiking mechanisms which can sometimes generate rather unphysiological behavior. Thus, many extensions of the model have been proposed to allow a description of additional features found in real neurons. We will describe here three major classes of extension:

- Currents activated during spiking, like afterhyperpolarization currents leading to spike rate adaptation
- Currents active below threshold which can generate resonant membrane properties
- More realistic spiking mechanisms allowing to better capture fast neuronal dynamics

As we will see, the common basis of all the extensions proposed for the LIF model is that they were intended to use the smallest number of parameters and the simplest equation possible to capture additional neuronal dynamics. The model proposed by Izhikevich (2003), gathering many of these extensions, can thus describe most of known neuronal spiking pattern with a very small set of parameters and first-order differential equations. It will be presented at the end of this section.

Spike-Activated Currents

In real neurons, spiking is induced by the strong activation of intrinsic sodium and potassium currents. This leads to a large fluctuation of neuron membrane potential and transient changes of ion

DOI 10.1007/978-1-4614-7320-6_148-1

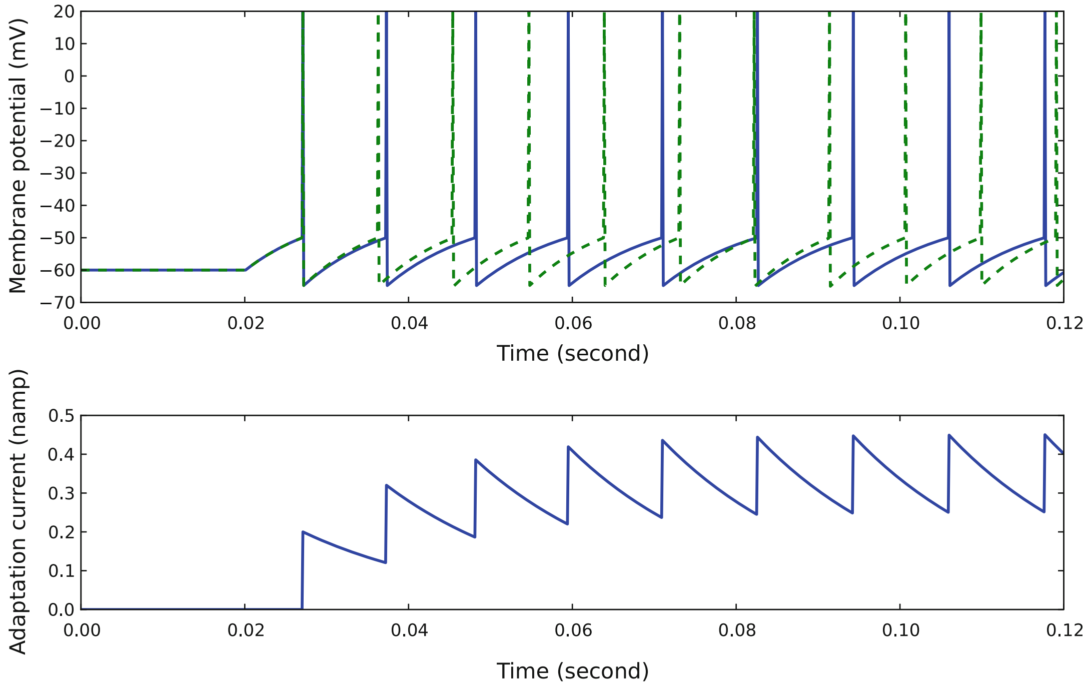

Fig. 2 Adaptation in a LIF model. *Top*: potential traces of a LIF model with (*full line*) and without (*dashed line*) adaptation current. *Bottom*: buildup of the adaptation current during spiking. Note that after a transient increase at the beginning of neuron firing, adaptation stabilizes. Adaptation parameters: $\tau_a = 20$ ms, $r_a = 0.2$ nA

intracellular concentration. These effects can cause other voltage-activated or ion-activated (like potassium-dependent) channels to be modulated during spiking. A common example is the activation during a spike of currents leading to spike rate adaptation. These types of currents are transiently activated during a spike but are then slowly inactivated between spikes and tend to hyperpolarize the neuron. The first version of such a current in a LIF model has been introduced by Treves (1993), and its simplest mathematical description is given by

$$\tau_m \frac{dV}{dt} = -(V - E_L) + R_m(-I_a + I(t)) \tag{7}$$

$$\tau_a \frac{dI_a}{dt} = -I_a \tag{8}$$

where the adapting current I_a is incremented by a positive constant r_a at each spike. An example of trace of an adapting LIF model is shown in Fig. 2. Note that the same formalism could be used to describe facilitating currents, leading to afterdepolarization (ADP), by changing to positive sign in front of I_a in Eq. 7. Other versions of the adapting current use a slowly decaying conductance g_a and then define $I_a = g_a(V - E\text{a})$ where E_a is the reversal potential of the adapting current and has to be lower than V_{th} in order to describe an hyperpolarizing current.

Subthreshold Voltage-Dependent Currents

In the previous section, the spike-activated current (or conductance) was not voltage-dependent between spikes. However, most of real neurons express currents which are activated in a voltage-dependent manner below the spike threshold and affect the neuron dynamics. An accurate description of this type of voltage-dependent currents generally requires to use the Hodgkin-Huxley

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

formalism. However, it is still possible to capture the most salient effects of such currents on the neuron dynamics by restraining their analysis in a narrow voltage band (Izhikevich 2001; Richardson et al. 2003). For example, Richardson et al. (2003) showed that it is possible to linearize the full conductance equation of voltage-dependent conductances around the neuron equilibrium potential to obtain a linear system able to capture membrane potential subthreshold resonance. Adding a standard LIF spiking threshold to the linearized model gives the generalized integrate-and-fire (GIF) model. The standard equation of a GIF model is given by

$$\tau_m \frac{dV}{dt} = -(V - E_L) + R_m(-g_x W_x + I(t)) \tag{9}$$

$$\tau_x \frac{dW_x}{dt} = -W_x + (V - E_x) \tag{10}$$

We emphasize that contrary to the current used to describe spike rate adaptation, here W_x depends on V. Depending on the parameters g_x and τ_x, this allows the system to have fixed points with complex basis solutions like for the simple or damped harmonic oscillator. Such solutions can capture resonant properties found in real neurons (Hutcheon and Yarom 2000). In Eq. 9 we had only one additional conductance to the original LIF model, but some neuron with low and high resonant frequencies may require two or more currents in order to capture their dynamics. Details on the derivation of additional current parameters from the standard Hodgkin-Huxley equations can be found in Richardson et al. (2003).

Spike Initiation Dynamics

In the standard LIF model, the spiking mechanism is sketched by a constant spiking threshold. However, in real neurons, the action potential is initiated by a strong sodium current with a fast, but not instantaneous, activation. Both mechanisms are similar when we are only interested in slow neuron dynamics, but discrepancies can appear when looking at the response to fast-fluctuating input, for example. Thus, extensions of the LIF model including a nonlinear term to model the non-instantaneous activation of sodium current have been proposed. The general form of these nonlinear integrate-and-fire (NLIF) models is given by

$$C_m \frac{dV}{dt} = g_L \psi(V) + I(t) \tag{11}$$

where $\psi(V)$ is a function which increases fast enough such that when V grows, it can diverge to infinity in a finite time. In this case, the spike time is given by the time of divergence of V, and it is then reset at potential V_r. It is no longer necessary to choose an arbitrary spike threshold, but for numerical simulation, a spike cutoff has to be defined assuming infinity has been reached.

Using this equation, we can define two important quantities:

- The voltage threshold V_T which is the highest steady-state voltage the neuron can sustain without emitting a spike. If ψ is convex, it is defined by $\psi'(V_T) = 0$.
- The spike shape factor Δ_T which is proportional to the curvature radius of the neuron current–voltage curve at its voltage threshold V_T. It is defined by $\Delta_T = 1/\psi''(V_T)$.

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

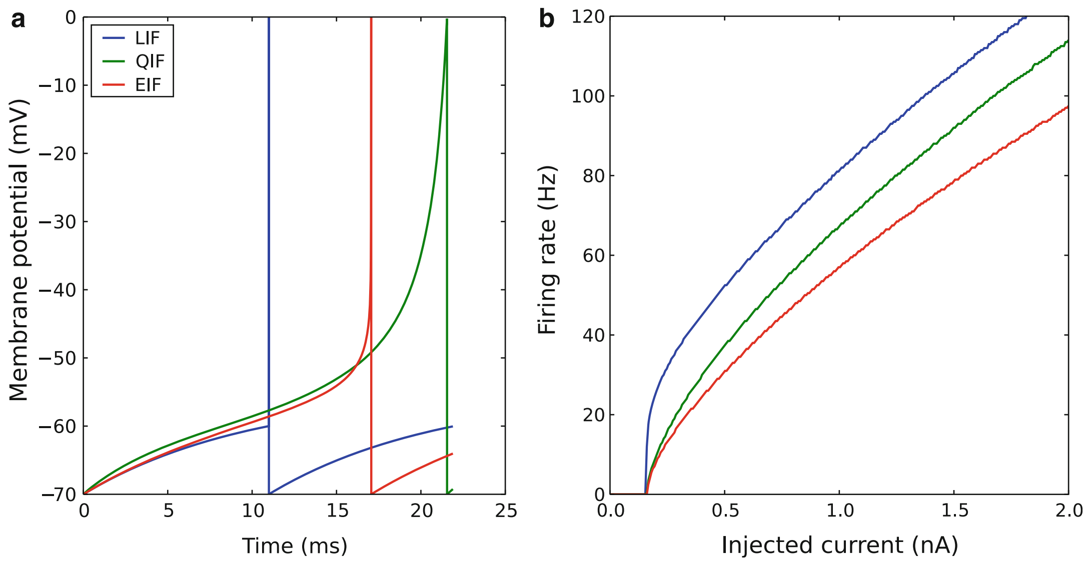

Fig. 3 Comparison of nonlinear IF models. *Left*: comparison of LIF, QIF, and EIF spiking initiation in response to the same constant current input. We observe that the LIF neuron is very reactive and spikes as soon as it reaches the spiking threshold V_{th}. The EIF model has a smooth but sharp spike, while the QIF model has the slowest spike. *Right*: comparison of LIF, QIF, and EIF f-I curves. We observe that LIF f-I curve has a logarithmic initial portion which is a consequence of its instantaneous spiking mechanism. QIF and EIF f-I curve initial portion have a square root shape, which depends only on V_T and Δ_T. This shape is classically observed in type I neurons. Parameters: for all models, $C_m = 1$ nF, $g_L = 0.1\mu$S, $E_L = -65$ mV; **LIF**, *left*, $V_{th} = -60$ mV, $V_r = -70$ mV; **LIF**, *right*, $V_{th} = -63.4$ mV, $V_r = -80$ mV, $\tau_{\text{ref}} = 1.35$ ms; **QIF**, $V_T = -59.9$ mV, $\Delta_T = 3.48$ mV, $V_{th} = -30$ mV, $V_r = -62.235$ mV, $I_0 = -0.16$ nA, $\tau_{\text{ref}} = 0$ ms; **EIF**, $V_T = -59.9$ mV, $\Delta_T = 3.48$ mV, $V_{th} = -30$ mV, $V_r = -68$ mV, $\tau_{\text{ref}} = 1.7$ ms

Two major classes of NLIF neurons have been used in the literature. The first one historically is the quadratic integrate-and-fire (QIF) (Ermentrout and Kopell 1986; Ermentrout 1996), also known as the theta model:

$$C_m \frac{dV}{dt} = \frac{g_L}{2\Delta_T}(V - V_T)^2 - I_0 + I(t) \tag{12}$$

For an input current below I_0, the model exhibits two fixed points: one stable and one unstable. When the input current increases and reaches I_0, the two fixed points merge and the neuron membrane potential is destabilized through a Hopf bifurcation which is the classical type I dynamics observed in many neuron models.

The second type of well-known NLIF neuron is the exponential integrate-and-fire model (EIF):

$$C_m \frac{dV}{dt} = -g_L(V - V_T) + g_L \Delta_T e^{\frac{V - V_T}{\Delta_T}} + I(t) \tag{13}$$

Here the divergence function is exponential which leads to a spike initiation speed intermediate between the instantaneous LIF spike and the rather slow QIF spike (see Fig. 3a). Fourcaud-Trocmé et al. (2003) have shown that this model captures best the fast dynamics of standard Hodgkin-Huxley-type models for cortical neurons, like the Wang-Buzsáki model (Wang and Buzśaki 1996).

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

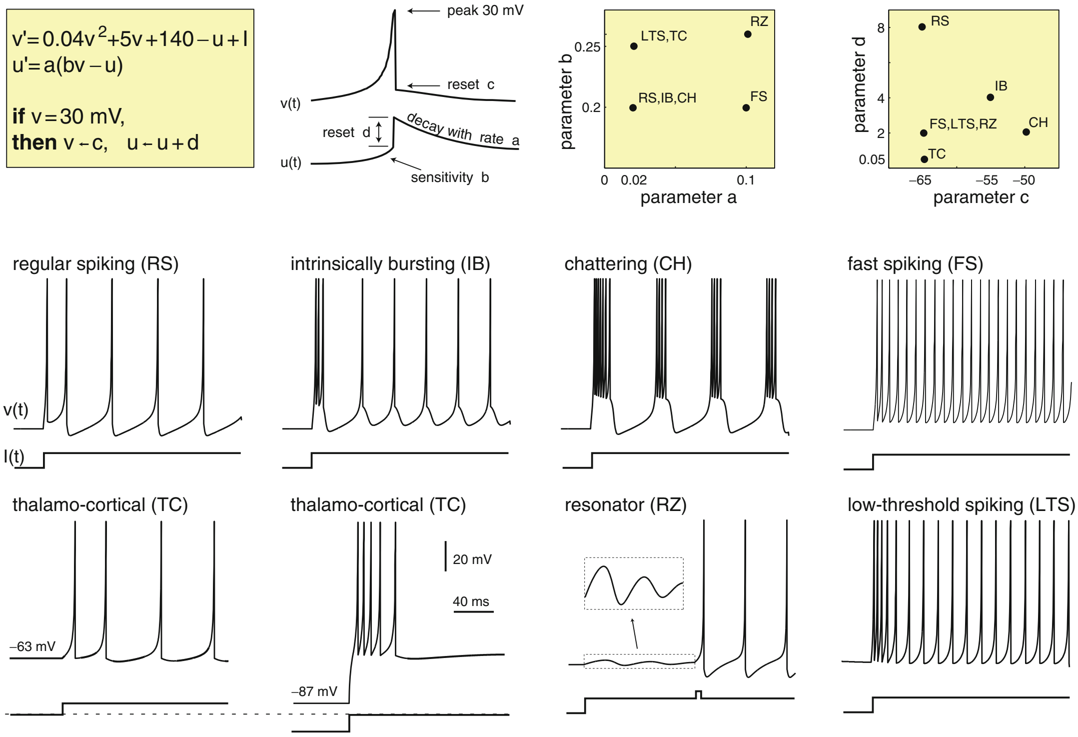

Fig. 4 Example of a comprehensive IF model. The model depicted in the upper equations includes subthreshold dynamics, a spiking mechanisms inspired by the QIF model, and spike-dependent adaptation. All these dynamical aspects depend only on two variables and four parameters. Careful choices of the parameters can lead to a great variety of neuronal dynamics reminiscent of actual neuronal recordings (Electronic version of the figure and reproduction permissions are freely available at www.izhikevich.com)

Comprehensive IF Models

The three types of extensions presented previously describe distinct aspects of neuron dynamics but are not exclusive. Some studies proposed to combine them in order to produce simple but realistic neuron models. One of the simplest has been proposed by Izhikevich (2003). It is defined by

$$\frac{dV}{dt} = 0.04V^2 + 5V + 140 - U + I(t) \tag{14}$$

$$\frac{dU}{dt} = a(bV - U) \tag{15}$$

Two additional parameters are the reset $V_r = \text{c}$ and the increase d of variable U after each spike. Note that depending on the set of parameters a, b, c, d, it can include all LIF extensions previously described. Using this model, Izhikevich has shown that most of the common recorded discharge patterns could be reproduced (see Fig. 4).

A second comprehensive model is the adaptive integrate-and-fire model (Brette and Gerstner 2005). It is described by

Encyclopedia of Computational Neuroscience
DOI 10.1007/978-1-4614-7320-6_148-1

$$C_m \frac{dV}{dt} = -g_L(V - V_T) + g_L \Delta_T e^{\frac{V - V_T}{\Delta_T}} - w + I(t) \tag{16}$$

$$\tau_w \frac{dw}{dt} = a(V - E_L) - w$$

Again, the model must be completed by a reset V_r and the increment b of the adaptive current w at each spike. This model is very similar to the model proposed by Izhikevich (2003) but its subthreshold dynamics and spike initiation dynamics are closer to standard Hodgkin-Huxley models. This facilitates the choice of the model parameters based on simple experimental measurements (injection of current pulses, steps, and ramps; see Brette and Gerstner 2005 for details).

Cross-References

- ► Capacitance, Membrane
- ► Excitability: Types I, II, and III
- ► Hodgkin-Huxley Model
- ► Theta Neuron Model
- ► Time Constant, Tau, in Neuronal Signaling

References

Brette R, Gerstner W (2005) Adaptive exponential integrate-and-fire model as an effective description of neuronal activity. J Neuro-physiol 94(5):3637–3642

Eccles JC (1957) The physiology of nerve cells. John Hopkins University Press, Baltimore

Ermentrout GB (1996) Type I membranes, phase resetting curves, and synchrony. Neural Comput 8:979–1001

Ermentrout GB, Kopell N (1986) Parabolic bursting in an excitable system coupled with a slow oscillation. SIAM J Appl Math 46:233–253

Fourcaud-Trocmé N, Hansel D, van Vreeswijk C, Brunel N (2003) How spike generation mechanisms determine the neuronal response to fluctuating inputs. J Neurosci 23(37):11628–11640

Hutcheon B, Yarom Y (2000) Resonance, oscillation and the intrinsic frequency preferences of neurons. Trends Neurosci 23:216–222

Izhikevich EM (2001) Resonate-and-fire neurons. Neural Netw 14(6–7):883–894

Izhikevich EM (2003) Simple model of spiking neurons. IEEE Trans Neural Netw 14(6):1569–1572

Knight BW (1972) The relationship between the firing rate of a single neuron and the level of activity in a population of neurons. J Gen Physiol 59:767–778

Lapicque L (1907) Recherches quantitatives sur l'excitation électrique des nerfs traitée comme une polarisation. J Physiol Paris 9:620–635

Richardson M, Brunel N, Hakim V (2003) From subthreshold to firing-rate resonance. J Neurophysiol 89:2538–2554

DOI 10.1007/978-1-4614-7320-6_148-1

Treves A (1993) Mean-field analysis of neuronal spike dynamics. Network 4:259–284

Tuckwell HC (1988) Introduction to theoretical neurobiology. Cambridge University Press, Cambridge

Wang XJ, Buzśaki G (1996) Gamma oscillation by synaptic inhibition in a hippocampal interneuronal network model. J Neurosci 16:6402–6413

External Links

http://www.scholarpedia.org/article/Adaptive_exponential_integrate-and-fire_model

http://www.izhikevich.org/publications/spikes.htm