Which Model to Use for Cortical Spiking Neurons?

Eugene M. Izhikevich

***Abstract*— We review the biological plausibility and computational efficiency of eleven most useful and widely used models of spiking and bursting neurons. Our goal is to identify a model that is most applicable to large-scale simulations of cortical neural networks. We discuss why the integrate-and-fire neuron, being the simplest and the most efficient spiking model, is not appropriate for simulations and should be avoided by all means. Finally, we discuss some reasonable alternatives.**

***Index Terms*— Hodgkin-Huxley, quadratic integrate-and-fire, PCNN, spike-timing**

I. Extended Abstract

IN any study of network dynamics, there are two crucial issues: (1) what model describes spiking dynamics of each neuron, and (2) how the neurons are connected. Inappropriate choice of the spiking model or the connectivity may lead to results having nothing to do with the information processing by the brain. Here we consider the first issue, i.e., we compare and contrast various models of spiking neurons.

First, we review 20 most important neuro-computational features of real neurons, see Fig. 1, and their possible contribution to temporal coding and spike-timing information processing. We emphasize the richness and complexity of spiking behavior of individual neurons in response to simple pulses of dc-current.

Though not all features in Fig. 1 are relevant to cortical pyramidal neurons, some are believed to play an important role in cortical information processing. For example, the regular spiking (RS) pyramidal neurons (Connors and Gutnick 1990) exhibit tonic activity (A) with spike frequency adaptation (F), class 1 excitability (G) with variable threshold (O); They also show spike latency (I) and some accommodation (R). In contrast, the fast spiking (FS) inhibitory interneurons show no frequency adaptation, but have class 2 excitability (H), subthreshold oscillations (J), resonance (K) and rebound responses (M). As a result, the RS and FS neurons have drastically different behavior and play quite different roles *in vivo*.

We also review other types of neurons, such as thalamo-cortical neurons, low-threshold-spiking (LTS), intrinsically-bursting (IB) and chattering neurons (Gray and McCormick 1996, Gibson et al. 1999), and discuss their most important dynamic features.

Of course, no model should exhibit all the 20 neuro-computational properties in Fig. 1 simultaneously simply because some of the properties are mutually exclusive. For example, a neuron cannot be an integrator and a resonator at the same time. Yet, there are properties that cannot be sacrificed if one wants to have an accurate neuronal model.

The Neurosciences Institute, 10640 John Jay Hopkins Drive, San Diego, CA, 92121, http://www.nsi.edu/users/izhikevich, Eugene.Izhikevich@nsi.edu

In Fig. 2 we review some widely used models of spiking and bursting neurons that can be expressed in the form of ordinary differential equations, and rank them according to (1) the number of neuro-computational features they can reproduce, and (2) their implementation efficiency, i.e., the number of floating point operations (addition, multiplication, etc.) needed to simulate the model during a 1 ms time span. The results of our comparison are summarized in Fig. 2, top.

As the reader can see in the figure, many models of spiking neurons have been proposed. Which one to choose? The answer depends on the type of the problem. If the goal is to study how the neuronal behavior depends on measurable physiological parameters, such as the maximal conductances, steady-state (in)activation functions and time constants, then the Hodgkin-Huxley-type model is the best. Of course, you could simulate only tens of coupled spiking neurons in real time.

In contrast, if you want to simulate thousands of spiking neurons in real time with 1 ms resolution, then there are plenty of models to choose from. The most efficient is the integrate-and-fire model. However, the model cannot exhibit even the most fundamental properties of cortical spiking neurons, and for this reason it should be avoided. The only advantage of the integrate-and-fire model is that it is linear, and hence amenable to mathematical analysis. If no attempts to derive analytical results are made, then there is no excuse for using this model in simulations.

The quadratic integrate-and-fire model, which is equivalent to the Ermentrout-Kopell theta-neuron (Ermentrout 1996, Hoppensteadt and Izhikevich 1997), is practically as efficient as the linear one, and it exhibits many important properties of real neurons, such as spikes with latencies, activity-dependent threshold and bistability of resting and tonic spiking modes. However, it is one-dimensional and hence it cannot burst and cannot exhibit spike frequency adaptation.

An extension of the quadratic integrate-and-fire model is presented in Fig. 3, top. It consists of only two differential equations, one non-linear term v^2, and 4 parameters, yet it can exhibit all neuro-computational features in Fig. 1. (In fact, all voltage traces in Fig. 1 were obtained using this model). We show that this simple model is canonical in the sense that a large class of Hodgkin-Huxley-type models can be reduced to the form in Fig. 3 by an appropriate change of variables. As a result, the model describes dynamics of biological neurons not only qualitatively, but also quantitatively, as one can see in Fig. 4.

In this review, I will stay away from mathematical details of the models, but rather illustrate their behavior, advantages and drawbacks qualitatively. This review talk should be understandable to an undergraduate student in neuroscience.

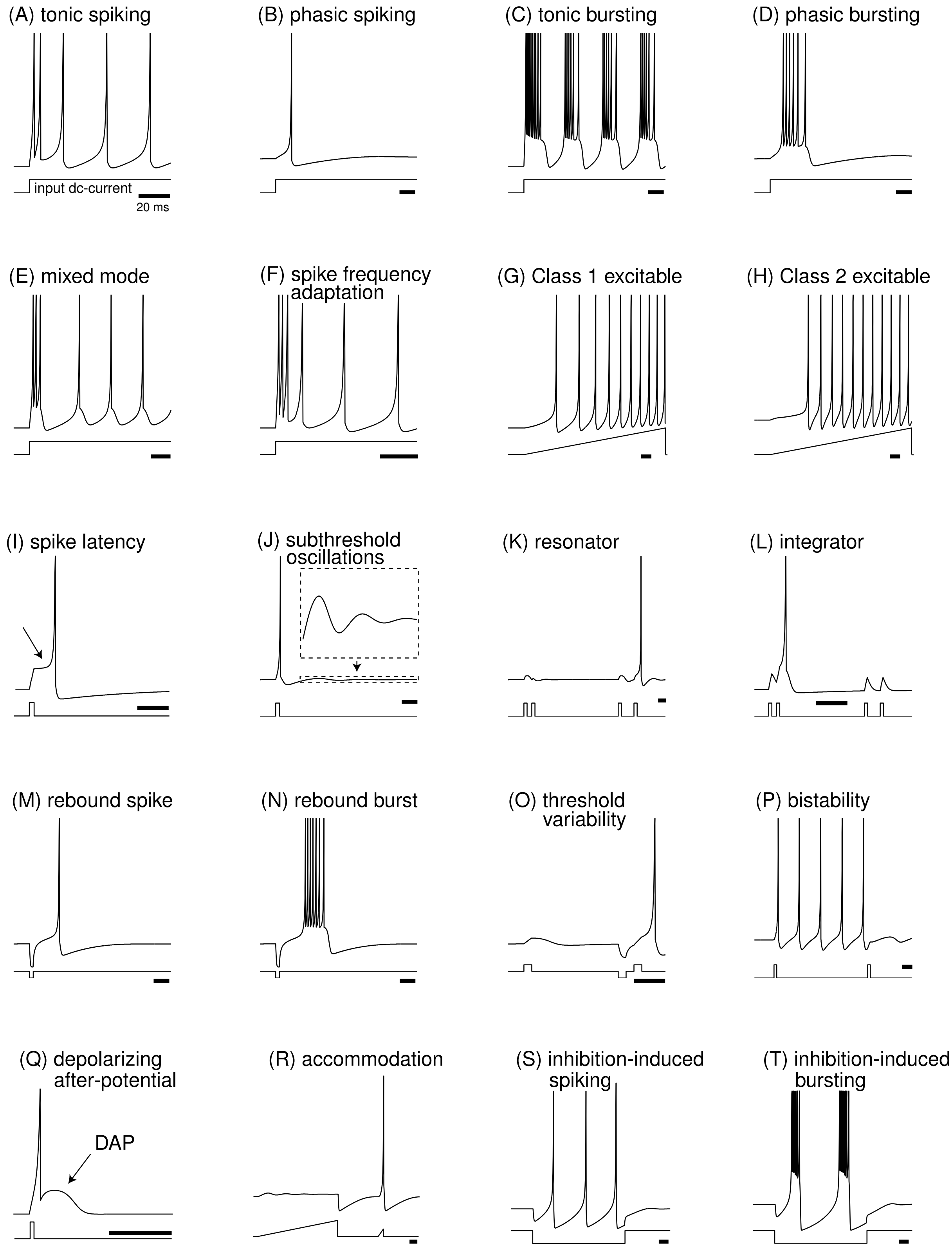
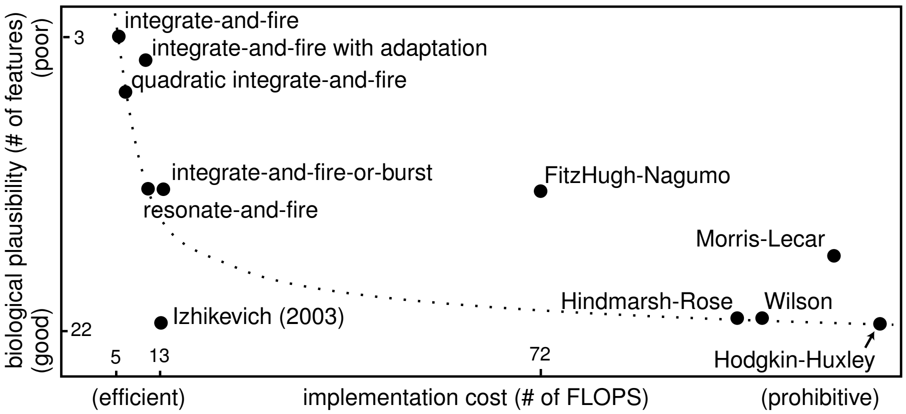


Fig. 1. Summary of the neuro-computational properties of biological spiking neurons. Shown are simulations of the model from Fig. 3, with different choices of parameters. Each horizontal bar denotes 20 ms time interval. The MATLAB file generating the figure and containing all the parameters can be downloaded from the author's website.



Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	inhibition-induced spiking	inhibition-induced bursting	chaos	# of FLOPS
integrate-and-fire	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	5
integrate-and-fire with adapt.	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	10
integrate-and-fire-or-burst	-	+	+		+	-	+	+	-	-	-	-	+	+	+	-	+	+	-	-	-		13
resonate-and-fire	-	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+	-	-	+	10
quadratic integrate-and-fire	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	+	-	-	-	-	-	7
Izhikevich (2003)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
FitzHugh-Nagumo	-	+	+	-		-	-	+	-	+	+	+	-	+	-	+	+	-	+	+	-	-	72
Hindmarsh-Rose	-	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	120
Morris-Lecar	+	+	+	-		-	-	+	+	+	+	+	+	+		+	+	-	+	+	-	-	600
Wilson	-	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+				180
Hodgkin-Huxley	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	1200

Fig. 2. Comparison of the neuro-computational properties of spiking and bursting models; see Fig. 1. "# of FLOPS" is an approximate number of floating point operations (addition, multiplication, etc.) needed to simulate the model during a 1 ms time span. Each empty square indicates the property that the model should exhibit in principle (in theory) if the parameters are chosen appropriately, but the author failed to find the parameters within a reasonable period of time.

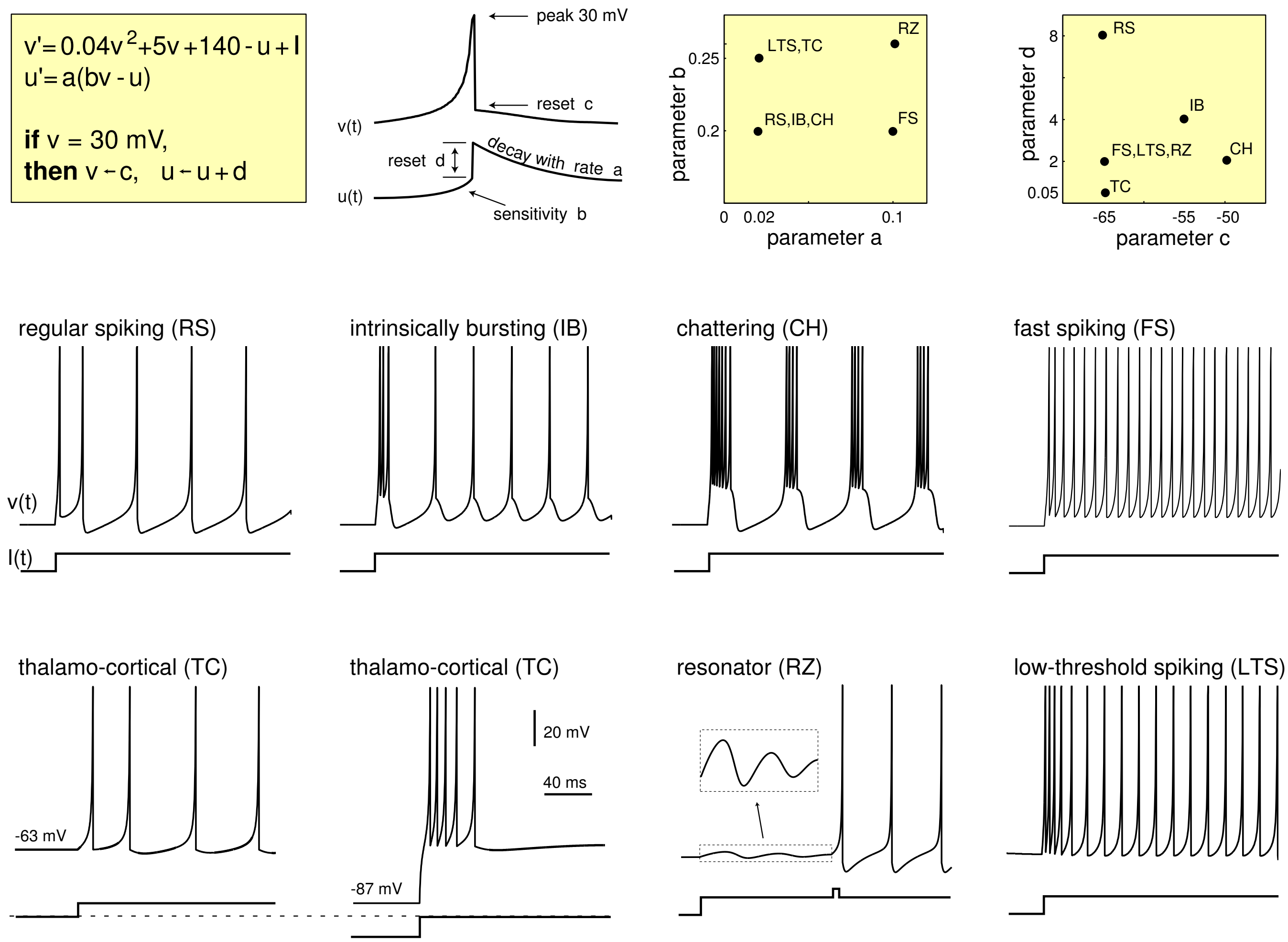


Fig. 3. Known types of neurons correspond to different values of the parameters a, b, c, d in this simple model. RS, IB and CH are cortical excitatory neurons. FS and LTS are cortical inhibitory interneurons. Each inset shows a voltage response of the model neuron to a step of dc-current $I = 10$ (bottom). Time resolution is 0.1 ms (Izhikevich 2003).

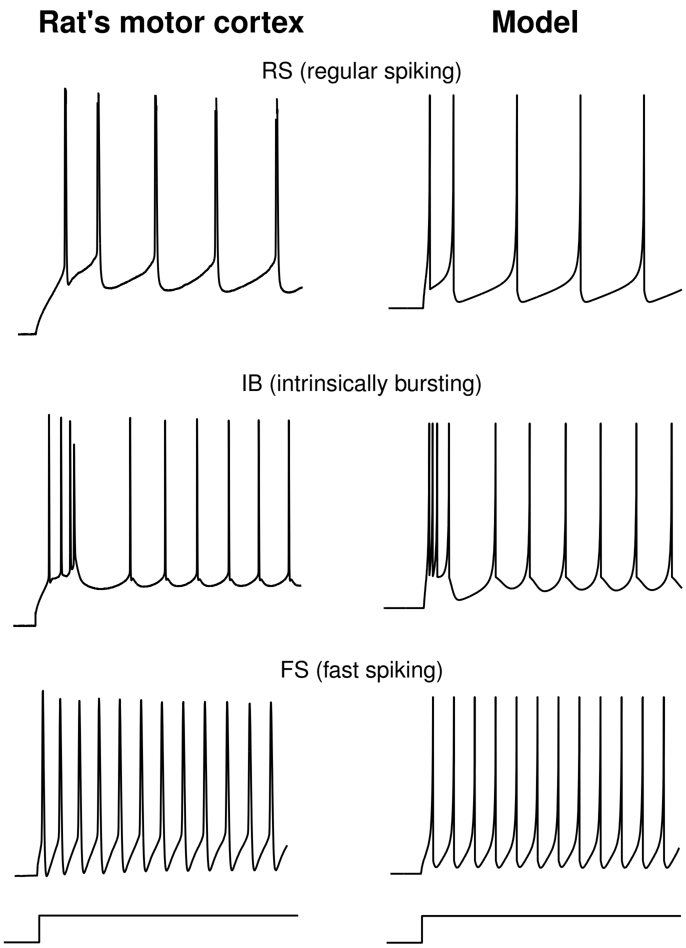


Fig. 4. The simple model in Fig. 3 can reproduce firing patters of neurons recorded from the rat's motor cortex. Data are kindly shared by Niraj Desai, model parameters as in Fig. 3.

REFERENCES

[1] B.W. Connors and M.J. Gutnick *Intrinsic firing patterns of diverse neocortical neurons*, Trends in Neuroscience, 13:99–104, 1990

[2] G. B. Ermentrout, *Type I membranes, phase resetting curves, and synchrony.* Neural Comput., 8:979-1001, 1996

[3] R. FitzHugh *Impulses and physiological states in models of nerve membrane*, Biophysical Journal, 1, pp. 445-466, 1961

[4] J.R. Gibson, M. Belerlein and B.W. Connors *Two networks of electrically coupled inhibitory neurons in neocortex*, Nature, 402:75-79, 1999

[5] C.M. Gray and D.A. McCormick *Chattering cells: superficial pyramidal neurons contributing to the generation of synchronous oscillations in the visual cortex.* Science. 274 (5284): 109-113, 1996

[6] A. L. Hodgkin and A. F. Huxley *A quantitative description of membrane current and application to conduction and excitation in nerve*, Journal Physiol., 117, pp. 500-544, 1954.

[7] F.C. Hoppensteadt and E.M. Izhikevich *Weakly Connected Neural Networks*, Springer-Verlag, 1997

[8] E.M. Izhikevich, N.S. Desai, E.C. Walcott, F.C. Hoppensteadt *Bursts as a unit of neural information: selective communication via resonance*. Trends in Neuroscience, 26:161-167, 2003

[9] E.M. Izhikevich *Simple Model of Spiking Neurons*, IEEE Transactions on Neural Networks, 2003, in press.

[10] E.M. Izhikevich *Resonate-and-fire Neurons*, Neural Networks, 14:883-894, 2001

[11] C. Morris and H. Lecar, *Voltage oscillations in the barnacle giant muscle fiber*, Biophys. J., vol. 35, pp. 193-213, 1981.

[12] R.M. Rose and J.L. Hindmarsh, *The assembly of ionic currents in a thalamic neuron. I The three-dimensional model*, Proc. R. Soc. Lond. B, 237, 267-288, 1989

[13] G. D. Smith, C. L. Cox, S. M. Sherman, and J. Rinzel *Fourier Analysis of Sinusoidally Driven Thalamocortical Relay Neurons and a Minimal Integrate-and-Fire-or-Burst Model*, J. Neurophysiol. 83: 588-610, 2000.

[14] H.R. Wilson, *Simplified Dynamics of Human and Mammalian Neocortical Neurons*, J. Theor. Biol. 200: 375-388, 1999.