

# Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting

Eugene M. Izhikevich



The MIT Press

*From The MIT Press*



**MITCogNet**

© 2007 Massachusetts Institute of Technology

All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher.

MIT Press books may be purchased at special quantity discounts for business or sales promotional use. For information, please email [special\\_sales@mitpress.mit.edu](mailto:special_sales@mitpress.mit.edu) or write to Special Sales Department, The MIT Press, 55 Hayward Street, Cambridge, MA 02142

This book was set in L<sup>A</sup>T<sub>E</sub>X by the author. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

Izhikevich, Eugene M., 1967–

Dynamical systems in neuroscience: the geometry of excitability and bursting / Eugene M. Izhikevich.

p. cm. — (Computational neuroscience)

Includes bibliographical references and index.

ISBN 978-0-262-09043-8 (hc. : alk. paper)

1. Neural networks (Neurobiology) 2. Neurons - computer simulation. 3. Dynamical systems. 4. Computational neuroscience. I. Izhikevich, E. M. II Title. III. Series.

QP363.3.I94 2007

573.8'01'13—DC21

2006040349

10 9 8 7 6 5 4 3 2 1

# Chapter 8

## Simple Models

The advantage of using conductance-based models, such as the  $I_{\text{Na}}+I_{\text{K}}$ -model, is that each variable and parameter has a well-defined biophysical meaning. In particular, they can be measured experimentally. The drawback is that the measurement procedures may not be accurate: the parameters are usually measured in different neurons, averaged, and then fine-tuned (a fancy term meaning “to make arbitrary choices”). As a result, the model does not have the behavior that one sees in experiments. And even if it “looks” right, there is no guarantee that the model is accurate from the dynamical systems point of view, that is, it exhibits the same kind of bifurcations as the type of neuron under consideration.

Sometimes we do not need or cannot afford to have a biophysically detailed conductance-based model. Instead, we want a simple model that faithfully reproduces all the neurocomputational features of the neuron. In this chapter we review salient features of cortical, thalamic, hippocampal, and other neurons, and we present simple models that capture the essence of their behavior from the dynamical systems point of view.

### 8.1 Simplest Models

Let us start with reviewing the simplest possible models of neurons. As one can guess from their names, the integrate-and-fire and resonate-and-fire neurons capture the essence of integrators and resonators, respectively. The models are similar in many respects: both are described by linear differential equations, both have a hard firing threshold and a reset, and both have a unique stable equilibrium at rest. The only difference is that the equilibrium is a node in the integrate-and-fire case, but a focus in the resonate-and-fire case. One can model the former using only one equation, and the latter using only two equations, though multi-dimensional extensions are straightforward. Both models are useful from the analytical point of view, that is, to prove theorems.

Many scientists, including myself, refer to these neural models as “spiking models”. The models have a threshold, but they lack any spike generation mechanism, that is, they cannot produce a brief regenerative depolarization of membrane potential corre-

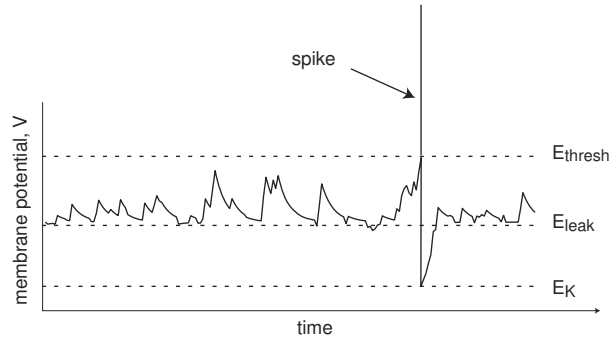


Figure 8.1: Leaky integrate-and-fire neuron with noisy input. The spike is added manually for aesthetic purposes and to fool the reader into believing that this is a spiking neuron.

sponding to the spike upstroke. Therefore, they are not *spiking models*; the spikes in figures 8.1 and 8.2, as well as in hundreds of scientific papers devoted to these models, are drawn by hand. The quadratic integrate-and-fire model is the simplest truly spiking model.

### 8.1.1 Integrate-and-Fire

The leaky integrate-and-fire model (Lapicque 1907; Stein 1967; Tuckwell 1988) is an idealization of a neuron having Ohmic leakage current and a number of voltage-gated currents that are completely deactivated at rest. Subthreshold behavior of such a neuron can be described by the linear differential equation

$$C\dot{V} = I - \overbrace{g_{\text{leak}}(V - E_{\text{leak}})}^{\text{Ohmic leakage}},$$

where all parameters have the same biophysical meanings as in the previous chapters. When the membrane potential  $V$  reaches the threshold value  $E_{\text{thresh}}$ , the voltage-sensitive currents instantaneously activate, the neuron is said to fire an action potential, and  $V$  is reset to  $E_K$ , as in Fig.8.1. After appropriate rescaling, the leaky integrate-and-fire model can be written in the form

$$\dot{v} = b - v, \quad \text{if } v = 1, \text{ then } v \leftarrow 0, \quad (8.1)$$

where the resting state is  $v = b$ , the threshold value is  $v = 1$ , and the reset value is  $v = 0$ . Apparently the neuron is excitable when  $b < 1$  and fires a periodic spike train when  $b > 1$  with period  $T = -\ln(1 - 1/b)$ . (The reader should verify this.)

The integrate-and-fire neuron illustrates a number of important neurocomputational properties:

- *All-or-none spikes.* Since the shape of the spike is not simulated, all spikes are implicitly assumed to be identical in size and duration.
- *Well-defined threshold.* A stereotypical spike is fired as soon as  $V = E_{\text{thresh}}$ , leaving no room for any ambiguity (see, however, exercise 1).

- *Relative refractory period.* When  $E_K < E_{\text{leak}}$ , the neuron is less excitable immediately after the spike.
- *Distinction between excitation and inhibition.* Excitatory inputs ( $I > 0$ ) bring the membrane potential closer to the threshold, and hence facilitate firing, while inhibitory inputs ( $I < 0$ ) do the opposite.
- *Class 1 excitability.* The neuron can continuously encode the strength of an input into the frequency of spiking.

In summary, the neuron seems to be a good model for an integrator.

However, a closer look reveals that the integrate-and-fire neuron has flaws. The transition from resting to repetitive spiking occurs neither via saddle-node nor via Andronov-Hopf bifurcation, but via some other weird type of bifurcation that can be observed only in piecewise continuous systems. As a result, the F-I curve has logarithmic scaling and not the expected square-root scaling of a typical Class 1 excitable system (see, however, exercise 19 in chapter 6). The integrate-and-fire model cannot have spike latency to a transient input because superthreshold stimuli evoke immediate spikes without any delays (compare with Fig.8.8(I)). In addition, the model has some weird mathematical properties, such as non-uniqueness of solutions, as we show in exercise 1. Finally, the integrate-and-fire model is not a spiking model. Technically, it did not fire a spike in Fig.8.1, it was only “said to fire a spike”, which was manually added afterward to fool the reader.

Despite all these drawbacks, the integrate-and-fire model is an acceptable sacrifice for a mathematician who wants to prove theorems and derive analytical expressions. However, using this model might be a waste of time for a computational neuroscientist who wants to simulate large-scale networks. At the end of this section we present alternative models that are as computationally efficient as the integrate-and-fire neuron, yet as biophysically plausible as Hodgkin-Huxley-type models.

### 8.1.2 Resonate-and-Fire

The resonate-and-fire model is a two-dimensional extension of the integrate-and-fire model that incorporates an additional low-threshold persistent  $K^+$  current or h-current, or any other resonant current that is partially activated at rest. Let  $W$  denote the magnitude of such a current. In the linear approximation, the conductance-based equations describing neuronal dynamics can be written in the form

$$\begin{aligned} C\dot{V} &= I - g_{\text{leak}}(V - E_{\text{leak}}) - W, \\ \dot{W} &= (V - V_{1/2})/k - W. \end{aligned}$$

known as the Young (1937) model (see also equation 2-1 in FitzHugh 1969). Whenever the membrane potential reaches the threshold value,  $V_{\text{thresh}}$ , the neuron is said to fire a spike. Young did not specify what happens after the spike. The resonate-and-fire