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PART ONE

FOUNDATIONS OF NEURONAL DYNAMICS

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Introduction: neurons and mathematics

The primary aim of this chapter is to introduce several elementary notions of neuroscience, in particular the concepts of action potentials, postsynaptic potentials, firing thresholds, refractoriness, and adaptation. Based on these notions a preliminary model of neuronal dynamics is built and this simple model (the leaky integrate-and-fire model) will be used as a starting point and reference for the generalized integrate-and-fire models, which are the main topic of the book, to be discussed in Parts II and III. Since the mathematics used for the simple model is essentially that of a one-dimensional linear differential equation, we take this first chapter as an opportunity to introduce some of the mathematical notation that will be used throughout the rest of the book.

Owing to the limitations of space, we cannot – and do not want to – give a comprehensive introduction to such a complex field as neurobiology. The presentation of the biological background in this chapter is therefore highly selective and focuses on those aspects needed to appreciate the biological background of the theoretical work presented in this book. For an in-depth discussion of neurobiology we refer the reader to the literature mentioned at the end of this chapter.

After the review of neuronal properties in Sections 1.1 and 1.2 we will turn, in Section 1.3, to our first mathematical neuron model. The last two sections are devoted to a discussion of the strengths and limitations of simplified models.

1.1 Elements of neuronal systems

Over the past hundred years, biological research has accumulated an enormous amount of detailed knowledge about the structure and function of the brain. The elementary processing units in the central nervous system are neurons, which are connected to each other in an intricate pattern. A tiny portion of such a network of neurons is sketched in Fig. 1.1, which shows a drawing by Ramón y Cajal, one of the pioneers of neuroscience around 1900. We can distinguish several neurons with triangular or circular cell bodies and long wire-like extensions. This picture can only give a glimpse of the network of neurons in the cortex. In reality, cortical neurons and their connections are packed into a dense network with more than 10^4 cell bodies and several kilometers of “wires” per cubic millimeter. Across areas of

Fig. 1.1 This reproduction of a drawing of Ramón y Cajal shows a few neurons in the mammalian cortex that he observed under the microscope. Only a small portion of the neurons contained in the sample of cortical tissue have been made visible by the staining procedure; the density of neurons is in reality much higher. Cell b is a typical example of a pyramidal cell with a triangularly shaped cell body. Dendrites, which leave the cell laterally and upwards, can be recognized by their rough surface. The axons are recognizable as thin, smooth lines which extend downwards with a few branches to the left and right. From Ramòn y Cajal (1909).

the brain the wiring pattern may look different. In all areas, however, neurons of different sizes and shapes form the basic elements.

Still, the cortex does not consist exclusively of neurons. Beside the various types of neuron, there are a large number of “supporter” cells, so-called glia cells, that are required for energy supply and structural stabilization of brain tissue. Since glia cells are not directly involved in information processing, we will not discuss them any further. We will also neglect a few rare subtypes of neuron, such as non-spiking neurons in the mammalian retina. Throughout this book we concentrate on spiking neurons only.

1.1.1 The ideal spiking neuron

A typical neuron can be divided into three functionally distinct parts, called *dendrites*, the *soma*, and the *axon*; see Fig. 1.2. Roughly speaking, the dendrites play the role of the “input device” that collects signals from other neurons and transmits them to the soma. The soma is the “central processing unit” that performs an important nonlinear processing step: if the total input arriving at the soma exceeds a certain threshold, then an output signal is generated. The output signal is taken over by the “output device,” the axon, which delivers the signal to other neurons.

The junction between two neurons is called a *synapse*. Let us suppose that a neuron sends a signal across a synapse. It is common to refer to the sending neuron as the *presynaptic cell* and to the receiving neuron as the *postsynaptic cell*. A single neuron in vertebrate

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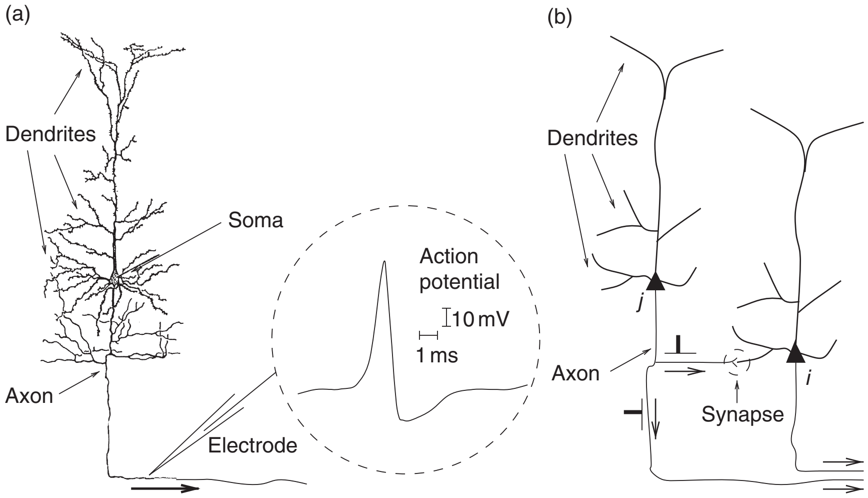

Fig. 1.2 (a) Single neuron in a drawing by Ramón y Cajal. Dendrites, soma, and axon can be clearly distinguished. The inset shows an example of a neuronal action potential (schematic). The action potential is a short voltage pulse of 1–2 ms duration and an amplitude of about 100 mV. (b) Signal transmission from a presynaptic neuron j to a postsynaptic neuron i. The synapse is marked by the dashed circle. The axons at the lower right end lead to other neurons. (Schematic figure.)

cortex often connects to more than 10^4 postsynaptic neurons. Many of its axonal branches end in the direct neighborhood of the neuron, but the axon can also stretch over several centimeters so as to reach neurons in other areas of the brain.

1.1.2 Spike trains

The neuronal signals consist of short electrical pulses and can be observed by placing a fine electrode either on the soma or close to the soma or axon of a neuron; see Fig. 1.2. The pulses, so-called action potentials or *spikes*, have an amplitude of about 100 mV and typically a duration of 1–2 ms. The form of the pulse does not change as the action potential propagates along the axon. A chain of action potentials emitted by a single neuron is called a *spike train* – a sequence of stereotyped events which occur at regular or irregular intervals; see Fig. 1.3. Since isolated spikes of a given neuron look alike, the form of the action potential does not carry any information. Rather, it is the number and the timing of spikes which matter. The action potential is the elementary unit of signal transmission.

Action potentials in a spike train are usually well separated. Even with very strong input, it is impossible to excite a second spike during or immediately after a first one. The minimal distance between two spikes defines the absolute refractory period of the neuron. The absolute refractory period is followed by a phase of relative refractoriness where it is difficult, but not impossible, to excite an action potential.

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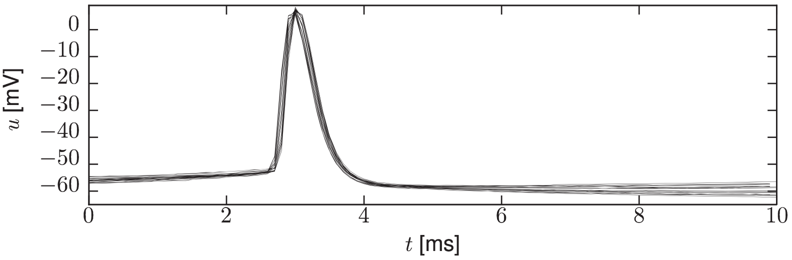

Fig. 1.3 Action potentials are stereotypical events. Membrane potential recordings aligned on the time of maximum voltage show little variability of the action potential shape. Data is courtesy of Maria Toledo-Rodriguez and Henry Markram (Toledo-Rodriguez *et al*., 2004).

1.1.3 Synapses

The site where the axon of a presynaptic neuron makes contact with the dendrite (or soma) of a postsynaptic cell is the synapse. The most common type of synapse in the vertebrate brain is a chemical synapse. At a chemical synapse, the axon terminal comes very close to the postsynaptic neuron, leaving only a tiny gap between pre- and postsynaptic cell membrane. This is called the *synaptic cleft*. When an action potential arrives at a synapse, it triggers a complex chain of biochemical processing steps that lead to a release of neurotransmitter from the presynaptic terminal into the synaptic cleft. As soon as transmitter molecules have reached the postsynaptic side, they will be detected by specialized receptors in the postsynaptic cell membrane and lead (either directly or via a biochemical signaling chain) to an opening of specific channels causing ions from the extracellular fluid to flow into the cell. The ion influx, in turn, changes the membrane potential at the postsynaptic site so that, in the end, the chemical signal is translated into an electrical response. The voltage response of the postsynaptic neuron to a presynaptic spike is called the *postsynaptic potential*.

Apart from chemical synapses neurons can also be coupled by electrical synapses, sometimes called gap junctions. Specialized membrane proteins make a direct electrical connection between the two neurons. Not much is known about the functional aspects of gap junctions, but they are thought to be involved in the synchronization of neurons.

1.1.4 Neurons are part of a big system

Neurons are embedded in a network of billions of other neurons and glial cells that make up the brain tissue. The brain is organized into different regions and areas. The cortex can be thought of as a thin but extended sheet of neurons, folded over other brain structures. Some cortical areas are mainly involved in processing sensory input, other areas are involved in working memory or motor control.

Neurons in sensory cortices can be experimentally characterized by the stimuli to which they exhibit a strong response. For example, neurons in the primary visual cortex respond

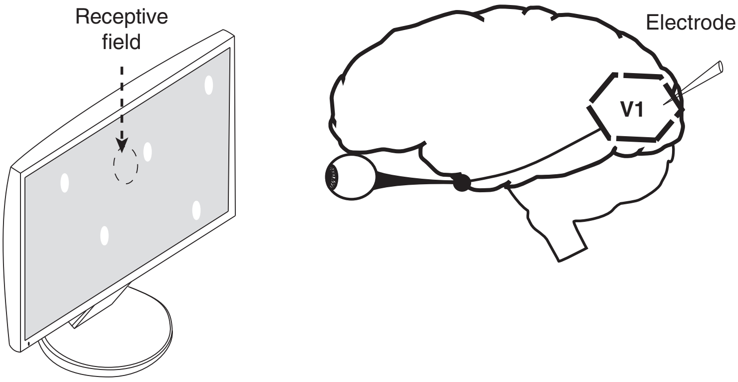

Fig. 1.4 Receptive fields in the visual cortex. An electrode probes the activity of a neuron while light dots are presented on a gray screen. The neuron responds whenever the stimulus falls into its receptive field, schematically indicated as an oval.

to dots of lights only within a small region of the visual space. The limited zone where a neuron is sensitive to stimuli is called the neuron's receptive field (Fig. 1.4).

The receptive field of so-called simple cells in the visual cortex is not homogeneous, but has typically two or three elongated subfields. When a light dot falls into one of the positive subfields, the neuron increases its activity, i.e., it emits more spikes than in the absence of a stimulus. When a light dot falls into a negative subfield, it decreases the activity compared to its spontaneous activity in the presence of a gray screen. A spot of light is in fact not the best stimulus. The neuron responds maximally to a moving light bar with an orientation aligned with the elongation of the positive subfield (Hubel and Wiesel, 1968).

A large body of the neuroscience literature consists in determining the receptive fields of neurons in sensory cortices. While neurons in the visual cortex respond to appropriate visual stimuli, neurons in the auditory cortex or somatosensory cortex respond to auditory or tactile stimuli. The concept of receptive field becomes less well defined if one moves away from the sensory cortex. For example, in the inferotemporal cortex, neurons respond to objects independently of their size and location; in working memory tasks, frontal cortex neurons are active during periods where no stimulus is present at all. In Parts II, III, and IV of this book we touch on aspects of receptive fields and memory of neuronal networks embedded in a big system. For the moment, we return to a simple, idealized neuron.

1.2 Elements of neuronal dynamics

The effect of a spike on the postsynaptic neuron can be recorded with an intracellular electrode which measures the potential difference $u(t)$ between the interior of the cell and its surroundings. This potential difference is called the *membrane potential*. Without any input, the neuron is at rest corresponding to a constant membrane potential u_{rest}. After the arrival of a spike, the potential changes and finally decays back to the resting potential; see Fig. 1.5a. If the change is positive, the synapse is said to be *excitatory*. If the change is negative, the synapse is *inhibitory*.

At rest, the cell membrane has already a strongly negative polarization of about –65 mV. An input at an excitatory synapse reduces the negative polarization of the membrane and is therefore called depolarizing. An input that increases the negative polarization of the membrane even further is called *hyperpolarizing*.

1.2.1 Postsynaptic potentials

Let us formalize the above observation. We study the time course $u_i(t)$ of the membrane potential of neuron i. Before the input spike has arrived, we have $u_i(t) = u_{\text{rest}}$. At $t = 0$ the presynaptic neuron j fires its spike. For $t > 0$, we see at the electrode a response of neuron i

$$u_i(t) - u_{\text{rest}} =: \varepsilon_{ij}(t)\,. \tag{1.1}$$

The right-hand side of Eq. (1.1) defines the postsynaptic potential (PSP). If the voltage difference $u_i(t) - u_{\text{rest}}$ is positive (negative) we have an excitatory (inhibitory) postsynaptic potential or short EPSP (IPSP). In Fig. 1.5a we have sketched the EPSP caused by the arrival of a spike from neuron j at an excitatory synapse of neuron i.

1.2.2 Firing threshold and action potential

Consider two presynaptic neurons $j = 1, 2$, which both send spikes to the postsynaptic neuron i. Neuron $j = 1$ fires spikes at $t_1^{(1)}, t_1^{(2)}, \ldots$, similarly neuron $j = 2$ fires at $t_2^{(1)}, t_2^{(2)}, \ldots$. Each spike evokes a postsynaptic potential ε_{i1} or ε_{i2}, respectively. As long as there are only few input spikes, the total change of the potential is approximately the sum of the individual PSPs,

$$u_i(t) = \sum_j \sum_f \varepsilon_{ij}(t - t_j^f) + u_{\text{rest}}\,, \tag{1.2}$$

i.e., the membrane potential responds linearly to input spikes; see Fig. 1.5b.

On the other hand, linearity breaks down if too many input spikes arrive during a short interval. As soon as the membrane potential reaches a critical value ϑ, its trajectory shows a behavior that is quite different from a simple summation of PSPs: the membrane potential exhibits a pulse-like excursion with an amplitude of about 100 mV. This short voltage pulse will propagate along the axon of neuron i to the synapses with other neurons. After the pulse the membrane potential does not directly return to the resting potential, but passes, for many neuron types, through a phase of hyperpolarization below the resting value. This hyperpolarization is called “spike-afterpotential.”

Single EPSPs have amplitudes in the range of 1 mV. The critical value for spike initiation is about 20 to 30 mV above the resting potential. In most neurons, four spikes – as shown

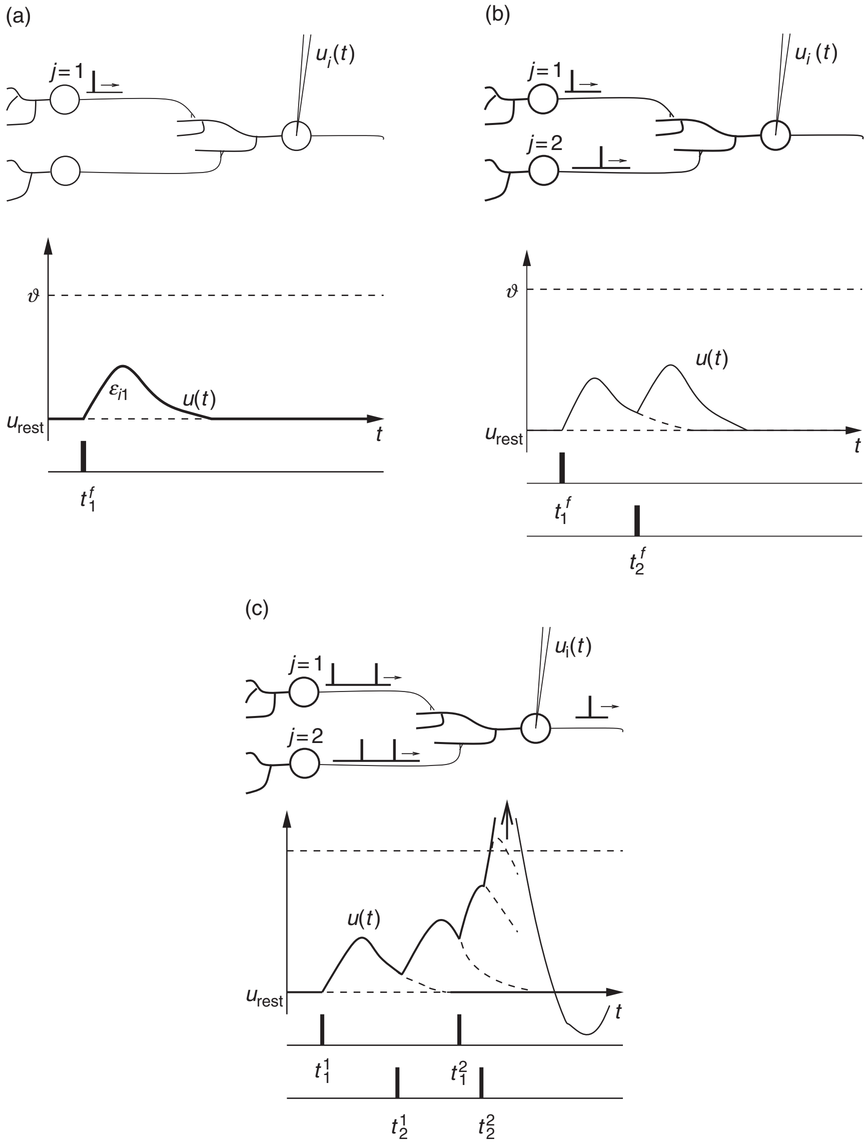

Fig. 1.5 A postsynaptic neuron i receives input from two presynaptic neurons $j = 1,2$. (a) Each presynaptic spike evokes an excitatory postsynaptic potential (EPSP) that can be measured with an electrode as a potential difference $u_i(t) - u_{\text{rest}}$. The time course of the EPSP caused by the spike of neuron $j = 1$ is $\varepsilon_{i1}(t - t_1^f)$. (b) An input spike from a second presynaptic neuron $j = 2$ that arrives shortly after the spike from neuron $j = 1$ causes a second postsynaptic potential that adds to the first one. (c) If $u_i(t)$ reaches the threshold ϑ, an action potential is triggered. As a consequence, the membrane potential starts a large positive pulse-like excursion (arrow). On the voltage scale of the graph, the peak of the pulse is out of bounds. After the pulse the voltage returns to a value below the resting potential u_{rest}.

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schematically in Fig. 1.5c – are thus not sufficient to trigger an action potential. Instead, about 20–50 presynaptic spikes have to arrive within a short time window to trigger a postsynaptic action potential.

1.3 Integrate-and-fire models

We have seen in the previous section that, to a first and rough approximation, neuronal dynamics can be conceived as a summation process (sometimes also called "integration" process) combined with a mechanism that triggers action potentials above some critical voltage. Indeed in experiments firing times are often defined as the moment when the membrane potential reaches some threshold value from below. In order to build a phenomenological model of neuronal dynamics, we describe the critical voltage for spike initiation by a formal threshold ϑ. If the voltage $u_i(t)$ (that contains the summed effect of all inputs) reaches ϑ from below, we say that neuron i fires a spike. The moment of threshold crossing defines the firing time t_i^f.

The model makes use of the fact that neuronal action potentials of a given neuron always have roughly the same form. If the shape of an action potential is always the same, then the shape cannot be used to transmit information: rather information is contained in the presence or absence of a spike. Therefore action potentials are reduced to "events" that happen at a precise moment in time.

Neuron models where action potentials are described as events are called "integrate-and-fire" models. No attempt is made to describe the shape of an action potential. Integrate-and-fire models have two separate components that are both necessary to define their dynamics: first, an equation that describes the evolution of the membrane potential $u_i(t)$; and second, a mechanism to generate spikes.

In the following we introduce the simplest model in the class of integrate-and-fire models using the following two ingredients: (i) a *linear* differential equation to describe the evolution of the membrane potential; (ii) a threshold for spike firing. This model is called the "leaky integrate-and-fire" model. Generalized integrate-and-fire models, which will be discussed in Part II of the book, can be seen as variations of this basic model.

1.3.1 Integration of inputs

The variable u_i describes the momentary value of the membrane potential of neuron i. In the absence of any input, the potential is at its resting value u_{rest}. If an experimenter injects a current $I(t)$ into the neuron, or if the neuron receives synaptic input from other neurons, the potential u_i will be deflected from its resting value.

In order to arrive at an equation that links the momentary voltage $u_i(t) - u_{\text{rest}}$ to the input current $I(t)$, we use elementary laws from the theory of electricity. A neuron is surrounded by a cell membrane, which is a rather good insulator. If a short current pulse $I(t)$ is injected into the neuron, the additional electrical charge $q = \int I(t')\mathrm{d}t'$ has to go somewhere: it will