

SYDE 556/750
Simulating Neurobiological Systems
Lecture 2: Neurons

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Based on lecture notes by
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Accompanying Readings: Chapter 4.1 and Chapter 2.1 of Neural Engineering

Contents

1 Overview	1
2 Spiking Neurons	1
2.1 Qualitative neural behaviour	2
2.2 The Leaky Integrate and Fire Neuron	3
2.3 Characterizing the LIF Neuron	4
2.4 Limitations of the LIF neuron model	4
3 Artificial Neurons	4

1 Overview

As we discussed in the last lecture, we consider neurons to be the fundamental computational unit in the nervous system. Neurons compute by receiving action potentials (spikes) from pre-synaptic neurons. Then, under certain conditions, they may themselves emit an action potential that is propagated along the neuron's axon and in turn received by post-synaptic neurons.

From an engineering perspective, we could say that individual neurons exchange coded information. An important part of understanding nervous systems is thus to understand the “code” that is being used for neural communication.

Unfortunately, there is no scientific consensus as for what exactly this “neural code” is. Most evidence points at a combination of population coding (i.e., information is encoded in the relative activities of a group of neurons) and time coding (i.e., the timing of individual spikes matters) [1].



Note: There isn't a single neural code; different coding strategies are employed in different parts of the nervous system. Codes differ significantly between the peripheral nervous system (i.e., the sensory and motor neurons distributed throughout the body; especially the latter are clearly using a rate code) and the central nervous system.

What we do have however, are detailed models that describe how individual neurons generate spikes, i.e., what the conditions are under which incoming spikes are translated into a corresponding output spike. Thus, we will approach the problem of trying to decipher neural codes in two stages. First, in this lecture, we will have a look at single neurons and try to get an understanding of how neurons generate action potentials. We discuss a single model, the so called “Leaky Integrate-and-Fire” neuron, and summarize its behaviour in a simple analytical expression. Second, in the next two lectures, we think about the neural code in terms of *representation*, which will lead us to a theory predicting what the neural code may be.

2 Spiking Neurons



Note: We're going to have a slightly closer look at biologically detailed spiking neuron models towards the end of the class. For now, we're skimming over the details. Have a look at [2] (particularly Chapter 7 and 8) if you want to learn more about basic neurobiology.

Neurons are cells that specialise in the integration and transmission of electrical signals. Cells in general are separated from the environment by a thick, impermeable “barrier”, the *cell membrane*, consisting of a bi-layer of lipid molecules. The cell membrane establishes an “intracellular” space that is isolated from the “extracellular” space. Both spaces are filled with a watery liquid, called the *intracellular fluid* and *extracellular fluid*, respectively (fig. 1).

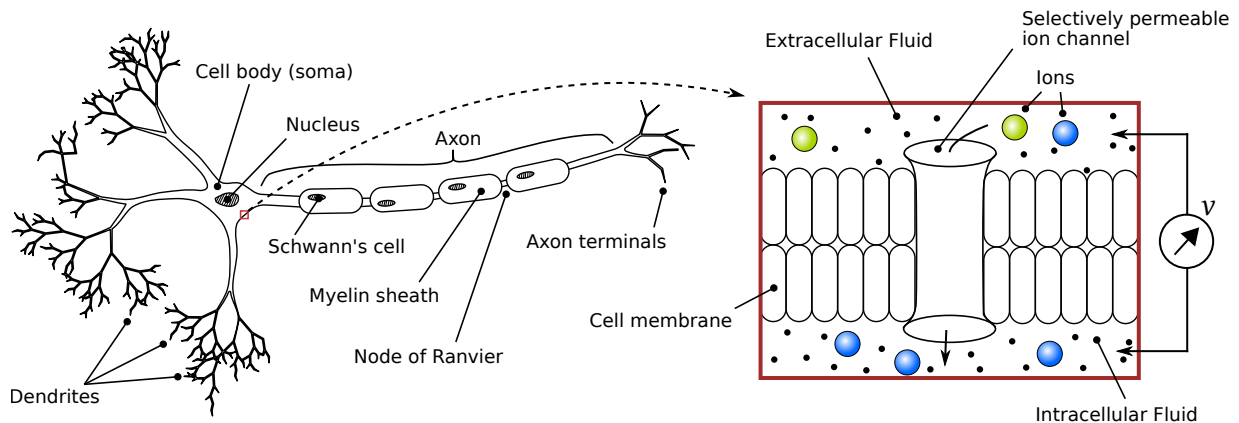


Figure 1: Illustration showing a text-book neuron, as well as a schematic cross-section through the cell membrane. Left part of the illustration from [3], adapted from [2]

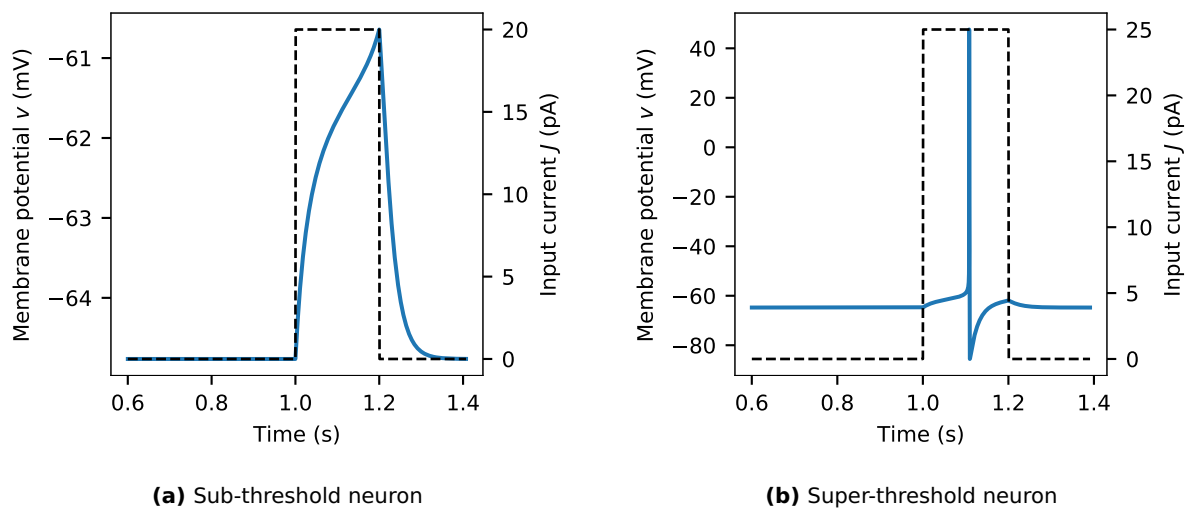


Figure 2: Computer simulation of a Hodgkin Huxley model neuron [4, 5]. The blue line corresponds to the membrane potential v , the dashed line to the current J that is being injected into the neuron.

2.1 Qualitative neural behaviour

When we insert a sharp electrode into a resting neuron (akin to the “single electrode recording” we saw in the last lecture), we can measure a difference in electrical potential, i.e., a voltage v , between the intra- and extracellular space (fig. 1). We call this voltage the *resting potential* E_L .¹

Instead of just measuring this potential we may also inject an external current into the neuron by hooking it up to a current source (i.e. a power supply that regulates current instead of voltage). When doing this, we find four things:

1. The cell acts like a *capacitor*, i.e., the voltage increases while we’re injecting a current

¹ The weird symbol “ E_L ” stems from the alternative name of this potential, the “**L**eak channel **E**quilibrium potential”.

(fig. 2a).

2. The capacitor is *leaky*. As soon as we stop injecting a current, the voltage collapses back to the resting potential v_{rest} injecting a current (fig. 2a).
3. As soon as the voltage surpasses a certain value, the *threshold potential* v_{th} , the cell will generate a spike.
4. Shortly after the spike has been produced, the voltage drops below the resting potential. During this period, the *refractory period* of length τ_{ref} we cannot get the neuron to spike again, even if we apply large input current J .



Note: Importantly, neurons in biology are *dynamical systems*, i.e., they possess a behaviour that evolves over time. *Artificial neurons* (see below) are time-independent. They are mathematical functions that take an input and “immediately” map it onto an output.

2.2 The Leaky Integrate and Fire Neuron

We can qualitatively summarize this behaviour in a very simple model, the so called “Leaky Integrate and Fire” neuron model. This model was first proposed by the French scientist Louis Lapicque in 1907 [6, 7].

Sub-threshold behaviour First, we have the *sub-threshold* behaviour, a so called leaky integrator.

$$\frac{d}{dt}v(t) = \frac{1}{C_m}(g_L(E_L - v(t)) + J), \quad \text{if } v(t) < v_{\text{th}}. \quad (1)$$

This differential equation corresponds to a capacitor with capacity C_m that is charged with a current J and that slowly discharges to a potential v_{reset} over a resistor with conductance (the inverse of the resistance) $g_L = \frac{1}{R}$ (the *leak conductance*).

Super-threshold behaviour Second, we have the *super-threshold behaviour*, the spike production and refractory period. Assume $v(t) = v_{\text{th}}$ at $t = t_{\text{th}}$. Then

$$\begin{aligned} v(t) &= \delta(t - t_{\text{th}}), & \text{if } t = t_{\text{th}}, \\ v(t) &= v_{\text{reset}}, & \text{if } t > t_{\text{th}} \text{ and } t \geq t_{\text{th}} + \tau_{\text{ref}}, \end{aligned} \quad (2)$$

where $\delta(t)$ is the Dirac delta function, i.e., the function defined as

$$\delta(t) = \begin{cases} \infty & \text{if } t = 0 \\ 0 & \text{if } t \neq 0, \end{cases} \quad \text{and} \quad \int_{-\infty}^{\infty} \delta(t) dt = 1.$$

Normalized equations For our modelling purposes, we don't really care about the exact values of v_{th} , v_{reset} and E_L . We can just normalise these voltages, i.e., assume that $v_{th} = 1$, and $v_{reset} = E_L = 0$.

We can rewrite eqs. (1) and (2) as

$$\begin{aligned} \frac{d}{dt}v(t) &= -\frac{1}{\tau_{RC}}(v(t) - Rf), & \text{if } v(t) < v_{th}, \\ v(t) &= \delta(t - t_{th}), & \text{if } t = t_{th}, \\ v(t) &= 0, & \text{if } t > t_{th} \text{ and } t \geq t_{th} + \tau_{ref}, \end{aligned} \quad (3)$$

where, $\tau_{RC} = C_m R$ and $R = \frac{1}{g_L}$.

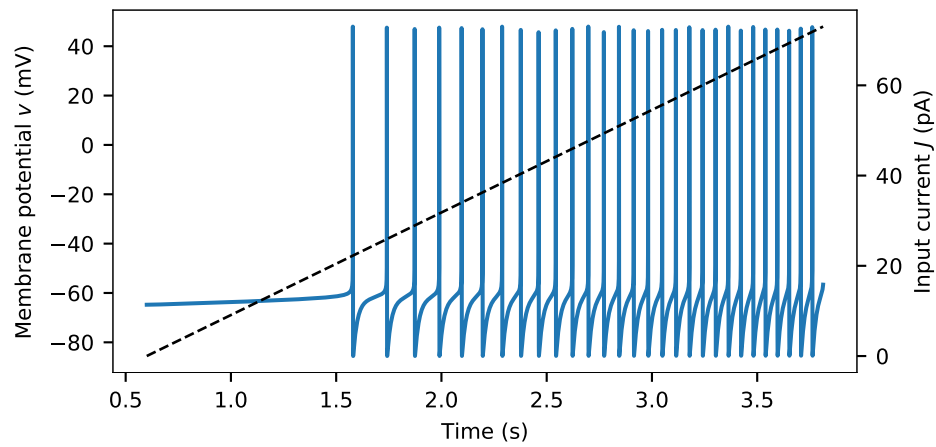
2.3 Characterizing the LIF Neuron

2.4 Limitations of the LIF neuron model

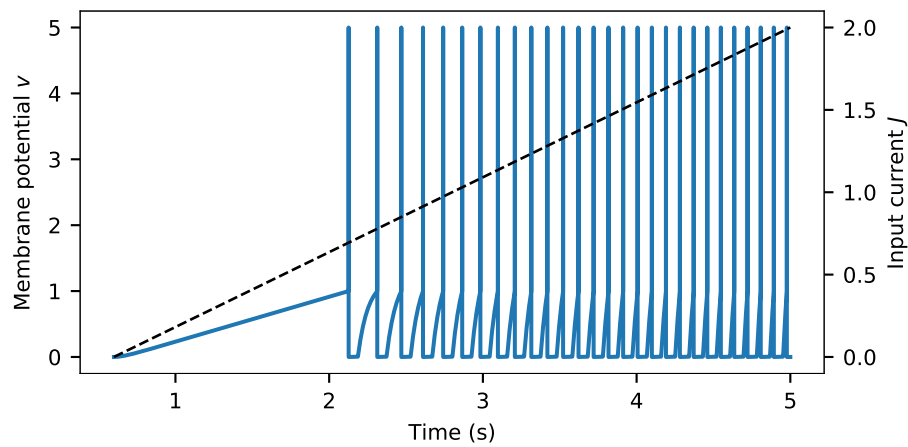
3 Artificial Neurons

References

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(a) Hodgkin-Huxley model neuron



(b) Normalized Leaky Integrate-and-Fire neuron

Figure 3: Effects of a current ramp on an Hodgkin-Huxley type model neuron and a (normalized) LIF neuron. As above, the blue line is the membrane potential, the dashed line is the input current.