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Lapicque's 1907 paper: from frogs to integrate-and-fire

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Abstract Exactly 100 years ago, Louis Lapicque published a paper on the excitability of nerves that is often cited in the context of integrate-and-fire neurons. We discuss Lapicque's contributions along with a translation of the original publication.

1 Introduction

Louis Lapicque (1866–1952) was a French physiologist and a pioneer in the field of neural excitability (Fulton 1953; Barbara 2005). Since Galvani it was know that nerves could be excited electrically. But the stimuli used to excite nerves, derived from batteries and capacitors, were hard to control. Therefore a central question at the time of Lapicque was: How much and how long a stimulation is required to excite a nerve? And furthermore, how could the relation between the stimulus and excitability be explained by the underlying biophysics. In his 1907 study Lapicque introduces a model of the nerve that he compares to data he obtained from frog nerve stimulation. This model, based on a simple capacitor circuit, would form the basis for later models of the membrane (Blair 1932).

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2 Electrophysiological methods used by Lapicque

As single neurons were hard to isolate, Lapicque stimulated nerve fibers extracellularly. The nerve typically used was the sciatic nerve of the frog that excites the leg muscle. (Lapicque gives no information what happened to the frogs afterward, but we have our suspicion...)

The stimulus that Lapicque used was a brief electrical pulse, which was delivered via two electrodes, that he designed and fabricated especially for this purpose (see Fig. 3). Ideally, one would use a current pulse in such stimulation experiments, but ideal current sources were not easy to construct. Instead, Lapicque used a voltage source, a battery. Arbitrary voltages between the battery voltage and zero were obtained by a voltage divider, created from a long wire with a slider, much like a modern potentiometer. This slider is the reason why the voltages in the paper are reported in centimeters of the slider. Furthermore, to mimic a current source, Lapicque put a large resistor (labeled R in the paper) in series with the electrode, resulting in an almost constant current during the stimulation.

To get accurate pulses of just a few milliseconds duration was not easy either. The instrument to do this was called a *rheotome* (literally current-cutter). There was a variety of ingenious rheotomes in use, for instance using pendulums or rotating discs (Geddes 1984). Lapicque used a more exotic one, namely, a ballistic rheotome. This is a gun-like contraption that first shoots a bullet through a first wire, making the contact, and a bit later the same bullet cuts a second wire in its path, breaking the contact. [Lapicque complains about the foul smell of the explosive!]. By varying the distance between the wires, the pulse duration was precisely adjusted, and consequently the durations are reported in centimeters as well. For each duration examined, Lapicque varied the voltage to determine how much was required to reach threshold. We do not know how the exact threshold was determined, but presumably, Lapicque simply observed whether there was enough stimulation to make the frog leg move.

3 Outcome of the study

Lapicque starts his paper by arguing that nerve membranes are nothing but semipermeable, polarizable membranes. Polarizable membranes can in first approximation be modeled as a capacitor with leak. The paper then compares his data to both an RC model of the membrane and a heuristic law of excitability obtained by Weiss (Irnich 2002). Interestingly, Weiss formula corresponds to a model with constant (voltage-independent) leak. By plotting Vt versus. t, Weiss' law would predict a straight line. However, the data does not exactly lie on a straight line, but is slightly convex, in agreement with Lapicque's model. Curiously, Lapicque's equation does not fit the data very well either! (see Figs. 2, 4, 5, 6). Lapicque is not put off by this, arguing that there are of course corrections. Indeed, given that a nerve bundle is stimulated extracellularly with rather coarse equipment, we should not be surprised either.

It is important, however, that Lapicque expresses the time constant in the excitation relation in fundamental quantities of the system. In particular, he observes that because of the inverse scaling of capacitance and resistance with area, the time constant (RC) is independent of the stimulation area. The contribution of the study is therefore not so much a more accurate description of the data, but a more fundamental relation between the membrane parameters and the excitability. The membrane time-constant and its relation to excitability would prove to be a very fruitful subject for Lapicque. He continued working on excitability in his career and introduced so called chronaxie, the time to threshold for a current twice the rheobase current, and researched how this time depended on species and nerve diameter. The chronaxie concept is still relevant today for the design of heart and muscle stimulators.

4 Integrate and fire neurons, from Lapicque to now

It is important to note that Lapicque's study is actually not about integrate-and-fire models. The relation between exciting a nerve and spike generation was still obscure and Lapicque does not hypothesize on this, nor on how the membrane resets after a spike. This raises the question who actually introduced the integrate-and-fire model. Though similar models appear in earlier papers (Hill 1936), the first papers in which the integrate-and-fire model as we know it was defined and analyzed appeared in the 1960s. At that time, several theorists (Richard Stein, Bruce Knight among others) started to analyze mathematically in detail the properties of the model. Richard Stein introduced in 1965 a leaky integrate-and-fire model with random Poisson excitatory and inhibitory inputs (Stein 1965). However, it was Bruce Knight that introduced the term 'integrate-and-fire' neuron in the sixties, and the first paper where the name appears seems to be his seminal 1972 paper on the dynamics of the firing rate of this model neuron (Knight 1972a), together with a companion experimental paper on visual cells of the *Limulus* (Knight 1972b). Bruce Knight introduced the term 'forgetful integrate-and-fire' neuron, but the term 'leaky integrate-and-fire' (LIF) neuron, coined by Rick Purple (a student of Hartline) soon became more popular. The integrate-and-fire neuron with no leak had been analyzed earlier by Gerstein and Mandelbrot (Gerstein and Mandelbrot 1964).

Even though the LIF model has several drawbacks, some of those can be cured by simple generalizations of the model. For example, the logarithmic behavior of the firing frequency close to the current threshold is non-generic, and changes qualitatively as soon as a more realistic spiking generation mechanism is introduced. The 'quadratic integrate-and-fire neuron' is the simplest generalization of the LIF model that captures qualitatively the behavior of the f–I curve of a large family of more realistic models (see e.g.Izhikevich 2006). Interestingly, this model was apparently already known to Alan Hodgkin, that used it to fit some of his data, and analyzed by Bruce Knight following discussions with Hodgkin (unpublished).

From the nineties onwards the leaky integrate-and-fire model and its variants became very popular when theorists started to study the dynamics of networks of spiking neurons. The LIF is easy and efficient to implement, and its behavior can in some cases be analyzed mathematically (Burkitt 2006a,b). The LIF has therefore become a tool of choice for theorists for understanding mechanisms at the network level. We hope that the accompanying translation will demonstrate to a wider audience the persistence and insight of Lapicque.

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