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Lapicque's introduction of the integrate-and-fire model neuron (1907)

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In 1907, long before the mechanisms responsible for the generation of neuronal action potentials were known, Lapicque developed a neuron model that is still widely used today [3,7]. This remarkable achievement stresses that, in neural modeling, studies of function do not necessarily require an understanding of mechanism. Significant progress is possible if a phenomenon is adequately described, even if its biophysical basis cannot be modeled.

Lapicque modeled the neuron using an electric circuit consisting of a parallel capacitor and resistor (Fig. 1A). These represent the capacitance and leakage resistance of the cell membrane. Of course, such a simple circuit cannot generate action potentials, but Lapicque postulated that when the membrane capacitor was charged to certain threshold potential, an action potential would be generated and the capacitor would discharge, resetting the membrane potential (Fig. 1B). Lapicque used the model to compute the firing frequency of a nerve fiber resistively coupled to a stimulating electrode held at fixed voltage. Fig. 1C presents an analogous simulation showing the response of the model to a time-varying injected current. Due to the work of Hodgkin and Huxley [2], we can now construct models that include the dynamics of the voltage-dependent membrane conductances responsible for action potential generation. Nevertheless, for many modeling purposes, the simple model of Lapicque is adequate and extremely useful.

As interpreted today, integrate-and-fire models are not restricted to the linear membrane properties of a simple capacitor-resistor circuit. It is possible to include accurately modeled synaptic and subthreshold conductances in such a model (e.g., see [8]). The utility of the integrate-and-fire model lies in the separation of time scales between the extremely rapid action potential and slower process that affect synaptic integration, bursting, and adaptation. While Lapicque, because of the limited knowledge of his time, had no choice but to model the action potential in a simple manner, the stereotypical character of action potentials allows us, even today, to use the same approximation to avoid computation of the voltage trajectory during an action potential. This allows us to focus both intellectual and computation resources on the issues likely to be most relevant in neural computation, without expending time and energy on modeling a phenomenon, the generation of action potentials, that is already well understood.

Integrate-and-fire models have been used in a wide variety of studies ranging from investigations of synaptic integration by single neurons to simulations of networks containing hundreds of thousands of neurons. The integrate-and-fire model has proven particularly useful in elucidating the properties of large neural networks and the implications of large numbers of synaptic connections in such networks. For example, integrate-and-fire models

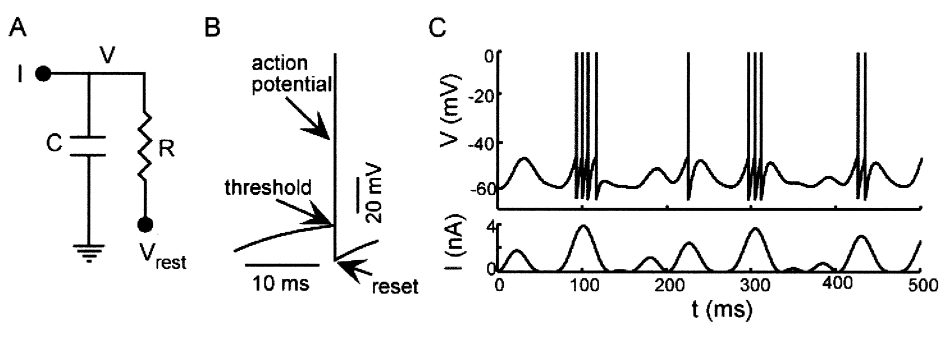

FIG. 1. The integrate-and-fire model of Lapicque. (A) The equivalent circuit with membrane capacitance C and membrane resistance R. V is the membrane potential, V_{rest} is the resting membrane potential, and I is an injected current. (B) The voltage trajectory of the model. When V reaches a threshold value, an action potential is generated and V is reset to a subthreshold value. (C) An integrate-and-fire model neuron driven by a time varying current. The upper trace is the membrane potential and the bottom trace is the input current.

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have played an important role in recent debates about the origin and nature of response variability in cortical neurons [1,4–6]. The utility of this model, devised early in the 20th century, is likely to last well into the 21st.

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