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Single neuron dynamics and computation

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At the single neuron level, information processing involves the transformation of input spike trains into an appropriate output spike train. Building upon the classical view of a neuron as a threshold device, models have been developed in recent years that take into account the diverse electrophysiological make-up of neurons and accurately describe their input-output relations. Here, we review these recent advances and survey the computational roles that they have uncovered for various electrophysiological properties, for dendritic arbor anatomy as well as for short-term synaptic plasticity.

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Introduction

The computation performed by single neurons can be defined as a mapping from afferent spike trains to the output spike train which is communicated to their post-synaptic targets. This mapping is stochastic, because of various sources of noise that include channel and synaptic noise; and plastic, because of various sources of plasticity, both intrinsic and synaptic.

For many years, the dominant conceptual model for single neuron computation was the binary Mc-Culloch-Pitts neuron [45]. In this model, the input vector is multiplied by a weight vector, and then passed through a threshold (see Fig. 1a). Adjusting synaptic weights and thresholds lead to neurons being able to learn arbitrary linearly separable dichotomies of the space of inputs [63].

This model has been conceptually tremendously useful, but it ignores fundamental temporal and spatial properties of neurons: the complex dynamics generated by a panoply of voltage-gated ionic currents; and the fact that synaptic inputs are stochastic, history-dependent and spread over a large dendritic tree. In this paper, we will review recent advances in our understanding of how these properties affect computation in single neurons.

Computation and dynamics: LNP/GL models and their relationship to neuronal biophysics

Electrophysiological data in various sensory systems have been successfully fitted by linear-non-linear-Poisson (LNP) or generalized linear models (GLM) [65]. In the LNP model, the inputs are first convolved linearly with a temporal filter (also called a kernel - the L operation). This convolution is then passed through a static non-linearity (the N operation), yielding an instantaneous firing rate. Finally, an inhomogeneous Poisson process is generated from the instantaneous firing rate (the P operation). This model is sketched in Figure 1b. In a GLM, spikes emitted by the neuron are convolved by another filter, and added to the input to the static non-linearity, to account for post-spike effects such as firing rate adaptation.

Recently, a procedure for approximating arbitrary spiking neuron models to LNPs has been developed ([54[•]] — see [31] for an alternative strategy). The idea is that the static non-linearity corresponds to the average firing rate of the neuron, with a stationary input and background noise with a given statistics. The temporal filter corresponds to the linearized firing rate (or impulse) response - how the instantaneous firing rate responds to a small sharp pulse of input current. Both quantities can be computed analytically (either exactly or approximately) in several popular 1 or 2 variable simplified spiking neuron models: the leaky integrate-and-fire (LIF) model [22,59]; the exponential integrate-and-fire (EIF) and quadratic integrate-and-fire (QIF) models [23,60]; generalized two-variable integrate-and-fire (GIF) models [57]; and generalized exponential models (GEM) [58]. The interest in such simplified integrate-and-fire-type models has been boosted by two observations: (i) 2 variable IF models can reproduce a wide diversity of firing patterns of real neurons [33,51,71]; (ii) they accurately fit electrophyiological recordings of real neurons [56,5[•],26,46].

The static non-linearities and temporal filters of such models are summarized in Figure 1c-e. In IF-type models, the static non-linearity is a monotonically increasing, sigmoid-shaped, function of the inputs (Fig. 1c1-e1) - note however that non-monotonic f-I curves can be observed in a specific class of model neurons [40] as well as in specific types of real neurons [30]. In the sub-threshold range,

Figure 1
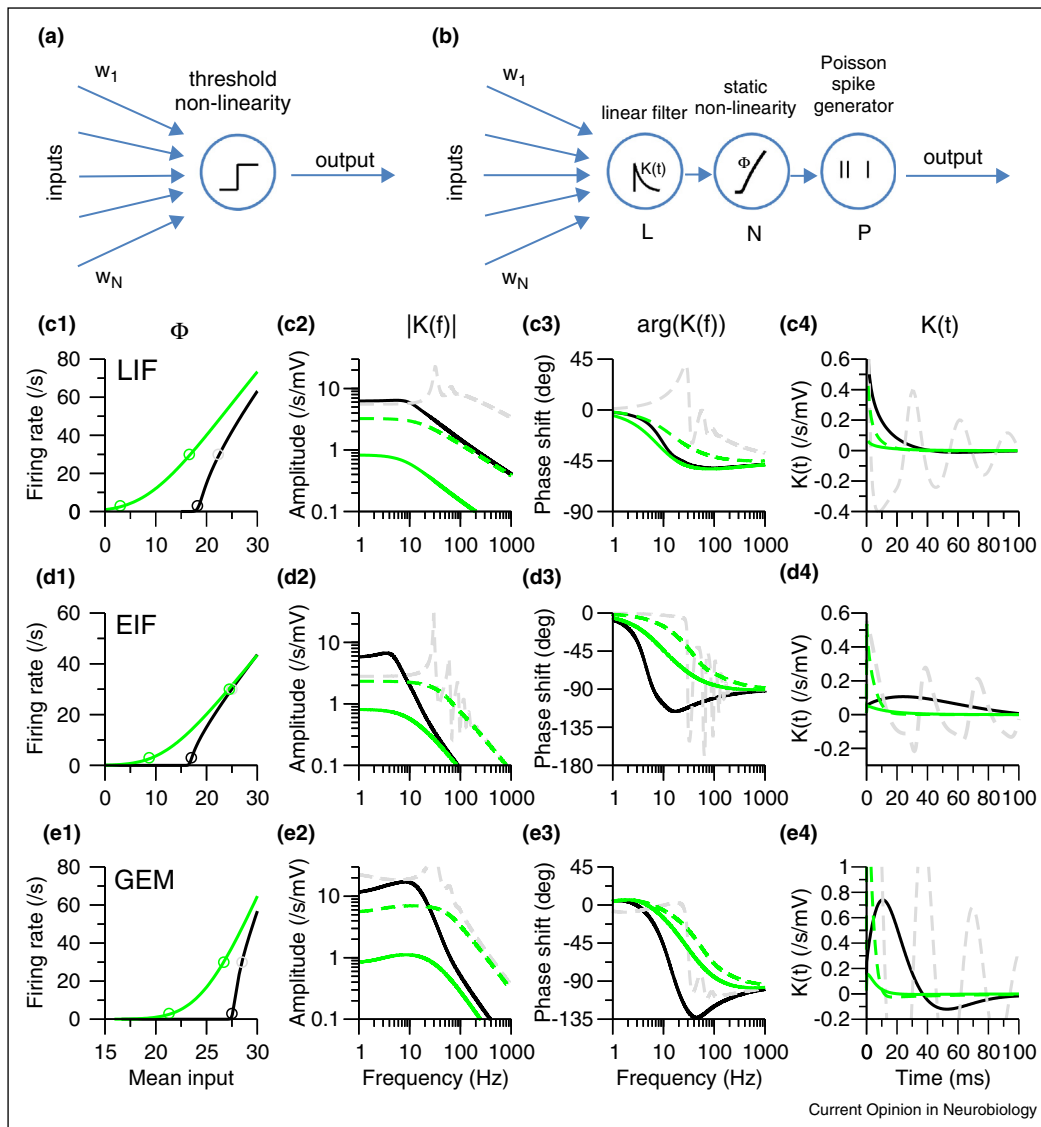
Computational properties of single-compartment neurons. a. The classic McCulloch-Pitts neuron performs a weighted sum of its synaptic inputs (each input i is multiplied by a synaptic weight w_i), and then a thresholding operation. b. The LNP neuron replaces the threshold by the LNP cascade: (L) convolution with a temporal filter $K(t)$, (N) application of a static non-linearity Φ, (P) generation of a Poisson process, with an instantaneous firing rate given by $\Phi(K \cdot$ input). c-d. Static non-linearities and temporal filters of selected simplified spiking neuron models. c: Leaky integrate-and-fire neuron (LIF). d: Exponential integrate-and-fire neuron (EIF). e: Generalized exponential model (GEM). In this series of panels, the first column shows the static non-linearity, for two different levels of noise (black, 1mV; green, 10mV). Circles indicate the points at which the temporal filters are computed in the other columns. The second and third columns show the amplitude and phase of the temporal filter in the Fourier domain (color indicates level of noise as in first column; full lines, firing rate of 3Hz; dashed line, firing rate of 30Hz). The fourth column shows the temporal filter (or impulse response) for the same parameters as in the 2nd and 3rd columns.

where firing is induced by fluctuations around the mean inputs, the gain of the transfer function strongly depends on the amplitude of the noise. The temporal filter also strongly depends on the noise (Fig. 1c2-e4). For strong noise, neurons fire in a highly irregular fashion. In this regime, one-variable IF-type models behave as low-pass filters, with a cut-off frequency that depends on membrane time constant, background firing rate, and spike generation dynamics (Fig. 1c2, c3, d2, d3). Two-variable models in which the second variable represents the dynamics of ionic currents providing negative feedback on the membrane potential (IH, IKs, etc) behave as band-pass filters, in a frequency range determined by the time scales of these intrinsic currents (Fig. 1e2, e3). For low noise, neurons are