

SOME GENERALIZATIONS OF INTEGRATE-AND-FIRE MODELS

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ABSTRACT.

We present a class of neuronal models that emits a spike (fires) if a scalar quantity, the membrane potential, satisfies a threshold condition. Equations use two generic functions ϵ and η that describe the subthreshold behavior and the spike process, respectively. Special cases include the leaky integrate-and-fire neuron and the piecewise linear FitzHugh-Nagumo model.

1 Introduction Neuronal activity is the result of a highly nonlinear dynamic process. A complete description of the underlying microscopic processes does not always provide a clear understanding of the behavior and its mathematical analysis is often not feasible. Hence a simplified description is highly desirable and has been attempted repeatedly [11], [5], [12], [14], [1], [9]. In this work we aim at a simplified model of neuronal activity with a single scalar variable $v(t)$, the membrane potential of the neuron. If a spike is triggered at a time t^f the membrane potential follows an invariant time course $\eta(t - t^f)$ and we call t^f the firing time of the neuron. We consider that the neuron performs a linear integration of the inputs weighted by a kernel $\epsilon(t)$. The temporal evolution is given by

$$(1) \quad v(t) = \sum_{t^f \in \mathcal{F}} \eta(t - t^f) + \int_0^t \epsilon(s)I(t - s)ds + u_{\text{rest}}$$

where $I(t)$ is the input current and u_{rest} the resting potential. Rescaling v we take $u_{\text{rest}} = 0$. The firing set \mathcal{F} is derived from a threshold process defined, in its general version, by $T(v)(t) = 0 \Rightarrow t \in \mathcal{F}$ where T has values in $C^0(R)$. The motivations of the integral formulation (1) come from the well-known experimental results of (i) the approximately-invariant shape of a spike and (ii) an approximately linear behavior of the neuron when no spike has been previously triggered. Expression (1) should be contrasted with differential formulations of the neuronal activity and is known as the spike-response-model (see [6] and references therein). An advantage of this expression is to provide an intuitive understanding of the neuronal activity while allowing a rigorous mathematical analysis. The non-trivial dynamics of (1) is the consequence of the nonlinearity of the model due to the threshold process which gives rise to an additional spike function η each time the threshold criterion is satisfied.

It has been shown that (1) allows a phenomenological and a numerical description of various types of neurons, in particular the Hodgkin-Huxley dynamics [10], [6]. In this paper, we present analytical derivations of (1) from simplified well-known neuronal models. At the same time, we give explicit expressions for the two kernels η , ϵ and the threshold function T .

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2 Derivation of the kernels and the threshold We will derive expressions for the two kernels η and ϵ . Basically we require $\eta(t)$ to be a pulse-shaped function that satisfies (i) $\eta(t) = 0$ for $t < 0$ and (ii) $\eta(t)$ has a decay to a low activity resting state that we take to be equal to 0. The impulse response ϵ satisfies (i) $\epsilon(t) = 0$ for $t < 0$ and (ii) has a decay to 0 (iii) ϵ reaches its maximum at the origin. Rescaling input $I(t)$ we choose $\epsilon(0) = 1$.

2.1 Integrate-and-fire models with explicit reset Expression (1) was first derived from the integral formulation of the leaky integrate-and-fire neuron [6]. The basic circuit of an integrate-and-fire model consists of a capacitor C in parallel with a resistor R driven by a current $I(t)$. When the membrane potential satisfies a threshold condition the model is reset to a value v_r . The kernels are given (for $C = 1$) by

$$(2) \quad \begin{aligned} \eta(t) &= -(\vartheta - v_r)e^{-\frac{t}{\tau}}, \\ \epsilon(t) &= e^{-\frac{t}{\tau}}, \end{aligned}$$

for $t > 0$ and 0 otherwise, where $\tau = RC$ is the membrane time constant. Parameter $\vartheta > v_r$ is the threshold that defines the firing set of the integrate-and-fire model

$$(3) \quad v(t) = \vartheta \Rightarrow t \in \mathcal{F}.$$

A completely analogous analysis can also be performed for the generalized integrate-and-fire models where the dynamics is described by n variables, the membrane potential $v(t)$ and auxiliary variables $w_i(t)$, $i = 1, \dots, n-1$ [13]. Let $X = (v(t), w_1(t), \dots, w_{n-1}(t))$ be the state variable, we consider the subthreshold linear evolution $\dot{X}(t) = AX(t) + I_v(t)$ where A is a square matrix and $I_v(t) = (1/C I(t), 0, \dots, 0)$. When $v(t) = \vartheta$ holds the potential is reset to a subthreshold value v_r . Since the subthreshold dynamics is linear, it is straightforward to derive the impulse response of this filter. To simply illustrate our purpose, we consider the two-dimensional model

$$(4) \quad \begin{aligned} \frac{dv(t)}{dt} &= -\frac{v(t)}{\tau} - \beta w(t) + \frac{1}{C}I(t), \\ \frac{dw(t)}{dt} &= v(t) - \gamma w(t). \end{aligned}$$

For $\gamma = 0$ and $\beta > 0$, one recognizes the damped oscillator $\ddot{v} + \gamma\dot{v} + \omega_0^2 v = 1/C\dot{I}$ where $\gamma = 1/\tau$ monitors the damping force and $\omega_0^2 = \beta$ is the frequency of the related harmonic oscillator. Note that (4) includes the standard IF model ($\beta = 0$) and the recently proposed resonate-and-fire model ($\gamma = 1/\tau$, $\beta = 1$) [8]. Basically, the kernel $\epsilon(t)$ presents two different expressions monitored by the sign of $\Delta = (\gamma - 1/\tau)^2 - 4\beta$. For $\Delta > 0$, the kernel ϵ is the linear combination of exponential functions $\epsilon(t) = \mu_1 \exp(\lambda_1 t) + \mu_2 \exp(\lambda_2 t)$ while for $\Delta < 0$ this kernel has an exponential decay with damped oscillations; $\epsilon(t) = \mu \exp(\lambda t) \sin(\omega t + \psi)$ (we do not consider the degenerated case $\Delta = 0$). The kernel η is directly obtained from $\epsilon(t)$ and stems from the reset process.

Neuronal models without superthreshold behavior such as integrate-and-fire models are expressed through an $\eta(t)$ function that describes a reset pulse rather than the entire form of the spike. In this case, we note $\eta(t) = -\eta_r(t)$ where $\eta_r(t)$ has a jump discontinuity at 0 (see FIG. 4 B). To account for the entire form of a spike, we have introduced a generalization of the integrate-and-fire neuron that incorporates a superthreshold behavior, namely the integrate-and-fire model with spikes (IFS) [16]. A simplified version derived from the piecewise linear idealization of a conductance based integrate-and-fire model is given by

$$(5) \quad \frac{dv}{dt} = -\frac{v}{\tau} + \mu h(v - \vartheta) + \frac{1}{C}I(t)$$

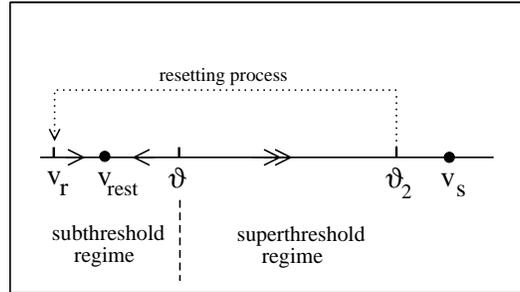


Figure 1: Schematic representation of the integrate-and-fire model with spikes in the phase space (without input currents). The direction of the arrows indicates the flow and the dashed arrow describes the reset process. Trajectories that start in the subthreshold regime return directly to the stable resting state v_{rest} . If ϑ is reached a spike-like excursion of the membrane potential driven by a (virtual) fixed point $v_s = \mu\tau$ (see (5)) occurs. The dynamics is stopped if v reaches a second threshold ϑ_2 and is reinitialized at a subthreshold value v_r . This model presents an interesting relation to phase models (e.g. the θ -model [4]).

where $\mu > 0$ and $h(x)$ is the Heaviside step function $h(x) = 1$ if $x > 1$ and 0 otherwise. This model incorporates a reset process if $v(t)$ reaches a second threshold ϑ_2 (FIG. 1), $v(t) = \vartheta_2 \Rightarrow v(t^+) = v_r$ where $\vartheta_2 > \vartheta$ monitors the amplitude of a spike. Thus we define the resetting set \mathcal{R} from $v(t) = \vartheta_2 \Rightarrow \tau = t^r \in \mathcal{R}$. It has been shown [16] that the spike is given by

$$(6) \quad \eta(t - t^f) = \eta_f(t - t^f) - \eta_r(t - t^r)$$

where $\eta_f(t) = \mu\tau(1 - \exp(-t/\tau))$ and $\eta_r = (\vartheta - v_r)\exp(-t/\tau) + \eta_f(t)$. The kernel ϵ is given by (2). In this formulation, the spike is split into two parts. A first term, η_f , describes the sharp part of the spike while η_r stands for the afterpotential. Note that we find a slightly different formulation than (1) since the reset time t^r is defined implicitly and hence the spike shape presents a small variability. This phenomenon does not appear to be relevant in the modeling of neuronal activity and a realistic approximation is to fix $t^r = t^f + \delta$ where δ stands for the spike duration. Hence the resetting set \mathcal{R} is simply derived from a translation of the firing set.

2.2 Smooth integrate-and-fire models Integrate-and-fire models yield a non-smooth reset pulse η_r related to the non-smooth recovery behavior. A more realistic modeling of neuronal activity that accounts for a smooth recovery process can be obtained from two (or higher) dimensional nonlinear differential models. Most of two-dimensional models have a dimensionless version given by

$$(7) \quad \begin{aligned} \frac{dv}{dt} &= f(v, w) + I(t) \\ \frac{dw}{dt} &= g(v, w) \end{aligned}$$

We address the following question : can we find an integral formulation as in equation (1) from the model (7) ?. In general it is not possible to obtain an explicit expression for $v(t)$

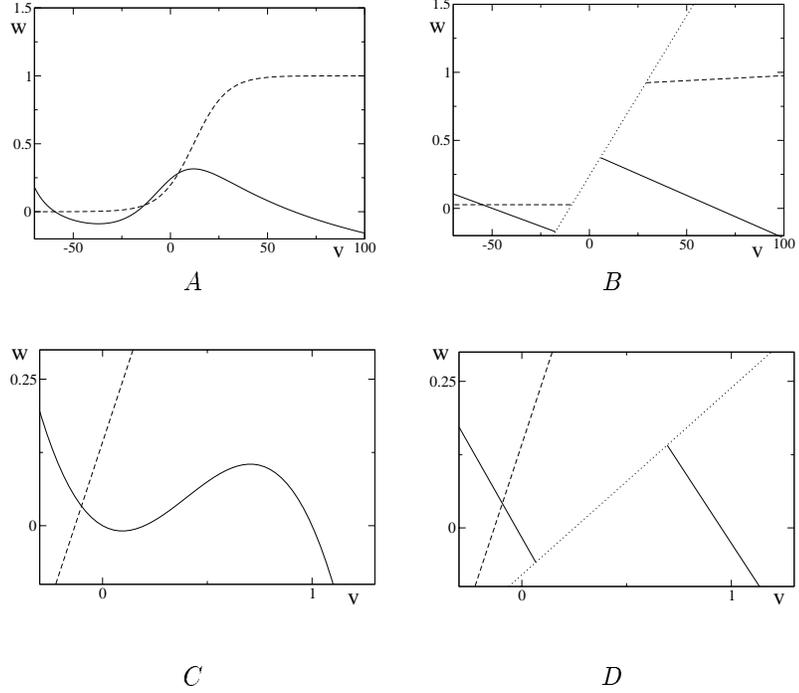


Figure 2: (A) Nullclines of the Morris-Lecar model and (B) their piecewise linear reductions. Panel (C) shows the nullclines of the FitzHugh-Nagumo model and (D) their piecewise linear reductions. The generic expression of these models is given by (7). We represent, in A and C, $f(v, w) = 0$ (solid lines) and $g(v, w) = 0$ (dashed lines). Figures (B) and (D) are obtained by considering a line of discontinuity (dotted lines) that acts as the threshold of the model and by defining a linear approximation of the two functions f and g in the subthreshold and suprathreshold regimes.

due to the nonlinearity of these models. The technique we propose uses a piecewise linear idealization of the nonlinear functions. This allows the splitting of the phase space into two different parts representing the different regimes of the neuron, i.e. the subthreshold and the suprathreshold regime. The transition between these two regimes defines the threshold condition just as in the IFS model.

Let us illustrate our treatment on two of the most popular simplified models that are the FitzHugh-Nagumo model [5] and the Morris-Lecar model [12]. In FIG. 2 we show in the phase plane the geometrical piecewise linear reduction of the Morris-Lecar model (FIG. 2A,B) and FitzHugh-Nagumo model (FIG. 2C,D). We introduce a linear partition of the phase space by defining a threshold line given by $v(t) - \alpha w(t) - \vartheta = 0$. Let us suppose that we stimulate the neuron by a constant suprathreshold current. In order to analyze the trajectory we have to introduce two different times corresponding to a crossing of the threshold line from left to right and conversely. Hence we introduce the two sets \mathcal{F} and \mathcal{R} . A firing time $t^f \in \mathcal{F}$ is defined when the neuron enters in the suprathreshold regime while a reset time $t^r \in \mathcal{R}$ is defined when the subthreshold regime is reached again. For example, if the recovery process is given by $dw/dt = -w/\tau_w + g(v)$ these two set are analytically

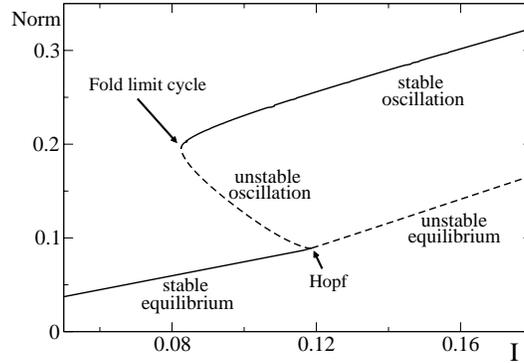


Figure 3: Bifurcation diagram of the piecewise linear FitzHugh-Nagumo model (9). The constant current I is the bifurcation parameter and we take $\tau = 1$, $\mu = 1$, $\alpha = 4$, $\vartheta = 0.2$, $b = 1$ and $\gamma = 0.5$. To avoid mathematical complications we consider a smooth version of the Heaviside function $h_\epsilon(x) = 0.5(1 + \tanh(x/\epsilon))$ and we take $\epsilon = 0.00125$. Computations were performed with AUTO [3].

defined from

$$(8) \quad v(t) - \alpha \int_0^t e^{-\frac{t-s}{\tau w}} g(v(s)) ds = \vartheta \Rightarrow t \in \mathcal{F} \cup \mathcal{R}$$

Just as in the case of the IFS model we approximate the resetting set \mathcal{R} by a translation of the firing set \mathcal{F} which imposes a nearly invariant shape of a spike. Hence the model (7) can be mapped onto (1). The spike is described by $\eta(t - t^f) = \eta_f(t - t^f) - \eta_r(t - t^r)$ with $t^r = t^f + \delta$ where η_f and η_r are two pulse shaped functions. In our qualitative analysis [16] these two functions are the same and present two distinct expressions that are well fitted by the two functions $\exp(-t) \sinh(\omega t)$ and $\exp(-t) \sin(\omega t)$. Just as for the generalized IF model, the kernel $\epsilon(t)$ presents two qualitatively different shapes depending on parameters, viz, resonator or integrator type.

3 Validity of the piecewise linear reduction Each simplification of a model is, of course, an approximation of the full behavior. We may therefore wonder if, as a minimal condition, the piecewise linear model reproduces at least qualitatively the behavior of the full model. In [2] a pulse-based model is derived from the Hodgkin-Huxley model using a piecewise linear approximation for the dynamics of the auxiliary variables. Then the validity of the model is tested using different input scenarios. Here, we address this question using the piecewise linear FitzHugh-Nagumo system under a constant current

$$(9) \quad \begin{aligned} \frac{dv}{dt} &= -\frac{v}{\tau} + \mu h(v - \alpha(w - I) - \vartheta) - w + I \\ \frac{dw}{dt} &= b(v - \gamma w) \end{aligned}$$

and considering I as a bifurcation parameter. Since we are interested in qualitative properties we consider identical parameters τ , b and γ in the subthreshold and superthreshold regime. An input current affects the v -nullcline of the original model and hence the threshold line of the reduced model. An accurate description is obtained by considering the

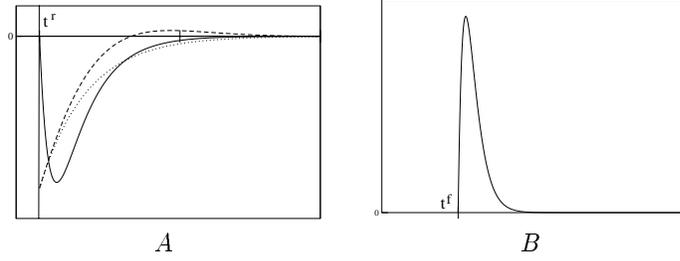


Figure 4: The action potential $\eta(t - t^f)$ is the response of the neuron to the threshold crossing at t^f . The kernel is split into $\eta(t - t^f) = \eta_f(t - t^f) - \eta_r(t - t^r)$ where $t^r = t^f + \delta$. A) Reset kernel $\eta_r(t)$. Standard integrate-and-fire models have a reset kernel with discontinuity (dotted line for the standard IF model and dashed solid line for the generalized IF model) while smooth two-dimensional models have a continuous reset (solid line). B) Two dimensional models with smooth recovery processes also have a continuous action potential. For IF models the action potential $\eta_f(t)$ vanishes.

contribution of the input into the definition of the line of discontinuity. This choice depends on the dependence between the original v -nullcline and the input. We show in FIG. 3 the bifurcation diagram of (9) where the constant current I is the bifurcation parameter. The piecewise linear model has a bifurcation structure similar to the original model and the two relevant bifurcations (the fold of limit cycle bifurcation and the subcritical Hopf bifurcation) are reproduced (see for example [7]).

4 Discussion The spike-response-model (1) has been proposed as a framework for various neuronal models. The advantage is the provision of a synthetic representation that allows mathematical analysis. In this paper we have addressed the question of how models can be mapped onto the spike-response-model. We find that the standard IF model and the generalized IF model have a direct mapping to the integral formulation. Other models that account for spike description or smooth recovery process can be written in this formalism provided that we define the kernel $\eta(t - t^f) = \eta_f(t - t^f) - \eta_r(t - t^r)$ and we consider the approximation $t^r = t^f + \delta$. We summarize in FIG. 4 some typical shapes of these two kernels. We distinguished between two kernels $\epsilon(t)$ that we report as integrator and resonator kernel. However the resonance properties of the full system are less trivial due to the interaction with the spike function. Basically, integrator kernels present an exponential decay whereas resonator exhibit damped oscillations. We consider $\epsilon_{\text{int}}(t) = \exp(-t/\tau)$ and $\epsilon_{\text{res}}(t) = \exp(-t/\tau) \cos \omega t$ as typical kernels of integrator and resonator neurons respectively (FIG. 5). The kernel ϵ_{int} can be derived from the leaky integrate-and-fire neuron while ϵ_{res} from the leaky resonate-and-fire neuron. More complicated kernels yielding new resonant effects can be derived from the generalized IF model [13].

We have obtained different kernels coming from differential equations for the simplified modeling of neuronal activity. The main drawbacks of this technique is to introduce a direct correlation (on the same time scale) between the two kernels η and ϵ which is not probably true for detailed models. For example the kernel η of IF models is not related to a relaxation in the dynamics but guarantees the reset of the past of the neuron, i.e. $\eta(t) = -C(\vartheta - v_r)\epsilon(t)$. However our study suggests interesting improvements of simplified neuronal models. First, from the expression (6) for η we can easily account for a natural

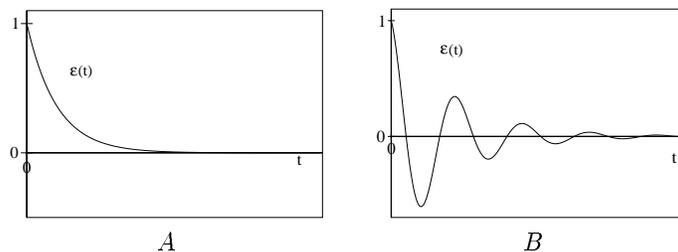


Figure 5: Kernels ϵ for the description of the subthreshold activity of neurons. We distinguish two different types. A) Kernel with an exponential decreasing to zero (integrator kernel). A popular example is given by the standard integrate-and-fire neuron where $\epsilon(t) = \exp(-t/\tau)$. Panel B shows an ϵ kernel with damped oscillations (resonator kernel). A generic example is the function $\epsilon(t) = \exp(-t/\tau) \cos \omega t$ that is obtained from the generalized integrate-and-fire model.

difference between the time scale of the two parts of a spike, η_f and η_r . Theoretical studies that will be reported elsewhere show that the kernel η_r and its interplay with ϵ has an important role in the behavior of the system. Secondly our linear partition between the subthreshold and the superthreshold regime suggests a non trivial threshold process that may improve the prediction of real data.

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