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# Efficient evaluation of neuron populations receiving colored-noise current based on a refractory density method

Anton V. Chizhov[1,2,*] and Lyle J. Graham[2]
[1]*A.F. Ioffe Physico-Technical Institute of RAS, 26 Politekhnicheskaya Street, 194021 St. Petersburg, Russia*
[2]*Laboratory of Neurophysics and Physiology, UMR 8119 CNRS, Université René Descartes,*
*45 rue des Saints Pères, 75006 Paris, France*

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The expected firing probability of a stochastic neuron is approximated by a function of the expected subthreshold membrane potential, for the case of colored noise. We propose this approximation in order to extend the recently proposed white noise model [A. V. Chizhov and L. J. Graham, Phys. Rev. E **75**, 011924 (2007)] to the case of colored noise, applying a refractory density approach to conductance-based neurons. The uncoupled neurons of a single population receive a common input and are dispersed by the noise. Within the framework of the model the effect of noise is expressed by the so-called hazard function, which is the probability density for a single neuron to fire given the average membrane potential in the presence of a noise term. To derive the hazard function we solve the Kolmogorov-Fokker-Planck equation for a mean voltage-driven neuron fluctuating due to colored noisy current. We show that a sum of both a self-similar solution for the case of slow changing mean voltage and a frozen stationary solution for fast changing mean voltage gives a satisfactory approximation for the hazard function in the arbitrary case. We demonstrate the quantitative effect of a temporal correlation of noisy input on the neuron dynamics in the case of leaky integrate-and-fire and detailed conductance-based neurons in response to an injected current step.

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## I. INTRODUCTION

Individual cortical neurons operate within the background activity of neuron populations. Relative to the single-cell activity this background activity is macroscopic, and therefore calls for independent approaches for its mathematical description. Computationally efficient approaches, which are alternatives to the Monte Carlo simulation of a great number of single neurons, include probability density methods (PDMs) [1–5], etc. A fundamental problem of the theory of these methods is how to reduce the dimension of the neuron's state variable space. Because of this problem, efficient application has been restricted to the consideration of simple integrate-and-fire-like neurons receiving a common input and a white noise term, resulting in one-dimensional (1D) PDMs. However, a more realistic model can consider the finite bandwidth of synaptic currents, i.e., synaptic noise has a nonzero correlation time and thus becomes colored noise. Considerations of more elaborate neurons or noninstantaneous synaptic kinetics generally lead to multidimensional PDMs, that reduces the efficiency of the solution. Known solutions of 2D PDMs [4,6,7], etc., are constrained by strict limitations on the ratios of characteristic time constants of the membrane and synapses, but still provide fruitful mathematical analysis of population response properties, neuronal synchronization, etc. We have recently proposed a method to reduce a multidimensional PDM approach for conductance-based neurons to a 1D PDM [8] in the case of white input noise. The question whether a similar approach could allow construction of a one-dimensional PDM in the case of colored noise is addressed in the present paper.

In our previous works we have proposed a macroscopic approach towards realistic simulations of the population activity of adaptive [8] or nonadaptive [9] neurons, based on the refractory density approach with a hazard function, applied to a conductance-based single neuron threshold model. The dynamics of a neural population continuum are described by a set of one-dimensional partial differential equations in terms of the distributions of the refractory density $\rho$ [2,10], where the refractory state is defined by the time elapsed since the last action potential $t^*$, the mean membrane potential $U$, and the gating variables of the voltage-dependent channels, across the entire population. The source term in the density equation is a probability density of firing, or a hazard function $H$, which was derived from the Kolmogorov-Fokker-Planck (KFP) equation, assuming that a single neuron is governed by a deterministic average-across-population input and a white noise term. Simulations showed that this model quite precisely and computationally efficiently reproduces the activity of a large number of discrete conductance-based neurons. The applicability of the RDA to biophysically detailed neuron models is the main reason why the hazard function is useful. Thus the hazard function describes the noise influence on the firing for any threshold model of a neuron independently on the intrinsic neuron properties, and therefore allows splitting of the problem. Together with the fact that the state variables of the threshold neuron can be parametrized by a single variable, especially the time elapsed since the last spike time moment, this approach leads to the reduction of the multidimensional probability density description of a neural population to a set of one-dimensional equations in partial derivatives [9,8]. Based on the fact that in the case of white noise [8] there was a close correspondence between the refractory density approach and individual neuron simulations for both integrate-

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[*] Anton.Chizhov@mail.ioffe.ru

and-fire neurons and generic conductance-based neurons, in the present paper we explicitly derive the colored-noise hazard function for integrate-and-fire neurons and then present simulations verifying this approach for conductance-based neurons.

*Refractory density approach for integrate-and-fire neurons*. A simple example of RDA for leaky integrate-and-fire neurons (LIF) is given below. The LIF neuron is given by the equation

$$C\frac{dV}{dt} = -g_L(V - V_{rest}) + I_a + \sigma\xi(t), \tag{1}$$

where $\xi(t)$ is a gaussian white noise process characterized by its mean value, $\langle\xi(t)\rangle = 0$, and autocorrelation $\langle\xi(t)\xi(t')\rangle = C/g_L\delta(t-t')$; $\sigma$ is the noise amplitude. The neuron fires when the potential $V$ crosses the threshold $U^T$. Immediately after, the spike $V$ is reset to $V_{reset}$.

As justified in [8], Eq. (1) is well approximated by the system of equations for the refractory density $\rho(t,t^*)$ and mean membrane potential $U(t,t^*)$, which are as follows:

$$\frac{\partial\rho}{\partial t} + \frac{\partial\rho}{\partial t^*} = -\rho H, \tag{2}$$

$$C\left(\frac{\partial U}{\partial t} + \frac{\partial U}{\partial t^*}\right) = -g_L(U - V_{rest}) + I_a, \tag{3}$$

where $I_a$ is the applied current; $g_L$ is the leak conductance and the membrane capacitance $C$. The boundary conditions are $\nu(t) \equiv \rho(t,0) = \int_{+0}^{\infty}\rho H dt^*$ and $U(t,0) = V_{reset}$, where $\nu(t)$ is the population firing rate. In the case of the white noise, the hazard function $H$ is approximated in [8] as a function of $U$ varying in time $t$ at a given $t^*$, depending as well on $\sigma$ and $U^T$. When calculating the dynamics of a neural population, the integration of Eq. (3) defines at each time moment $t$ the distribution of not-noisy voltage $U$ across $t^*$. Then, the effect of threshold crossing and diffusion by noise are taken into account by the $H$ function, and the result of the integration of Eq. (2) is expressed in the distribution of $\rho$ across $t^*$ and the firing rate $\nu$.

Here we generalize our approach to the case of colored noise. The effects of noise in the refractory density approach is contained in the hazard function $H$ which must evaluate the probability density of firing, given the mean membrane potential $U$ over all refractory states parametrized by $t^*$. The exact solution of this problem requires integration of the corresponding KFP equation. We show here that for colored noise, in the same way as was done for the white noise case, the hazard function can be well approximated by a sum of two particular solutions of the equation. Comparisons with numerical simulations reveal the quality of the approximation.

The effects of input correlations on the response of spiking neurons have been thoroughly analyzed in previous work (see, for example, [11–13,4,7]). The present work is mainly aimed at the extension of the refractory density formalism developed for conductance-based neurons in the case of input correlations, rather than the analysis of the effect of these correlations.

## II. DERIVATION OF THE HAZARD FUNCTION

The hazard function $H$ is defined as the probability for a neuron to release a spike during the infinitely small interval $[t, t+\Delta t]$ per $\Delta t$. Generally, to estimate this quantity for any considered group of neurons, one needs to calculate the rate of the decrease of the number of silent neurouns, divided by their number. If we consider only those neurons of the entire population which are characterized by the state $t^*$, their number is given by $\rho(t,t^*)$. Thus taking into account that $\partial/\partial t + \partial/\partial t^* = d/dt$. we rewrite Eq. (2) as

$$\frac{d\rho}{dt} = -\rho H(t), \tag{4}$$

which can be considered as a definition of the hazard function $H$. The spike-release probability density for a single neuron is equivalent to the firing rate of such population, scaled by the number of neurons, which follows from the boundary condition to Eq. (2), i.e., $H(t) = \nu(t)/\rho$.

In the framework of the threshold neuron approach, consideration of the hazard function depends on the membrane potential $U(t)$ and on the threshold $U^T$, specifically the comparison of $U$ with $U^T$. This dependence implies comparison of $U$ with the threshold potential $U^T$. As in our earlier work [9,8], we assume that $U^T$ depends only on $U$ and $dU/dt$, we can treat $H$ as a function of the function $U(t)$ only, i.e., $H = H[U(t)]$.

A formula to calculate the spike-release probability density $H$ should consider a model of noise and the variation of the cellular parameters and of the synaptic inputs over the entire neuron population. Here we assume that the functional impact of these factors may be expressed in an additive colored noise term affecting the potential of a given neuron. The other parameters governing the neuron are given by their average over all the neurons at the time elapsed since the last action potential $t^*$.

*Single neuron model*. When noise is not present, for the undisturbed potential $U(t)$ we write

$$C\frac{dU}{dt} = -I_{tot}(U,t), \tag{5}$$

where $I_{tot}$ is the total current; $C$ is the capacitance. We do not specify the explicit components of $I_{tot}$, in particular those due to various active conductances, instead we refer the reader to previous work [4] where we described how this term can include the conductances of an adaptive pyramidal neuron. Overall it seems that this approach is valid for a wide range of membrane conductances whose dynamics are either of the same time scale or slow compared to the duration of a single spike. However, the approach may be limited in the case of conductances of intermediate time scale such as the calcium currents postulated to underly bursting dynamics.

When noise is present, for the disturbed potential $V(t)$ we write the equations

$$C\frac{dV}{dt} = -I_{tot}(V,t) + h(t), \tag{6}$$

$$\tau\frac{dh}{dt} = -h + \sqrt{2\tau}\sigma\xi(t), \tag{7}$$

where $\xi(t)$ is the gaussian white noise characterized by its mean value, $\langle\xi(t)\rangle=0$, and autocorrelation $\langle\xi(t)\xi(t')\rangle=\tau\delta(t-t')$; $\tau$ is the time constant of noise correlations; $\sigma$ is the noise amplitude. The neuron fires when the potential $V$ crosses the threshold $U^T$. Importantly, we do not consider the reset of neuron states after firing, meaning we solve only the first passage problem. The justification for this simplification is as follows: We assume that the time scale of voltage diffusion is much faster than any interspike interval. This condition implies that voltage fluctuations in the vicinity of the reset state immediately after a spike will be forgotten by the time the subsequent near-threshold state is reached. Therefore the reset level associated with the preceding spike is unimportant and may be ignored.

We introduce the conductance as $g_{tot}(V,t)=\partial I_{tot}(V,t)/\partial V$, and the membrane time constant as $\tau_m(V,t)=C/g_{tot}(V,t)$. From the comparison of Eq. (5) with Eq. (6) we can conclude that at least if the noise amplitude $\sigma$ tends to 0 the expected value of $V(t)$ is equal to $U(t)$. Analogously, it holds for small noise that $g_{tot}(V,t)\approx g_{tot}(U,t)$. Thus we can linearize the current $I_{tot}(V,t)\approx I_{tot}(U,t)+g_{tot}(U,t)(V-U)$. After subtraction of Eq. (5) from Eq. (6) we obtain the equation for the voltage fluctuations,

$$C\frac{d(V-U)}{dt} = -g_{tot}(U,t)(V-U) + h(t). \tag{8}$$

We then neglect the dynamics of $g_{tot}(U,t)$, i.e., $dg_{tot}/dt\approx 0$, $d\tau_m/dt\approx 0$, under the assumption that just prior to crossing the threshold the voltage evolution depends only on the value of $g_{tot}(U,t)$ and not on its temporal derivative. Dividing Eq. (8) by $g_{tot}(U,t)/\sigma$ and introducing the dimensionless variable $u\equiv g_{tot}(U,t)(V-U)/\sigma$ reflecting the voltage fluctuations and $q(t)\equiv h(t)/\sigma$ as the noisy current scaled by the noise amplitude, we obtain the equations

$$\tau_m(U,t)\frac{du}{dt} = -u + q(t), \tag{9}$$

$$\tau\frac{dq}{dt} = -q + \sqrt{2\tau}\xi(t). \tag{10}$$

The neuron fires at the threshold $\tilde{T}(t)=g_{tot}(U,t)[U^T-U(t)]/\sigma$.

*Kolmogorov-Fokker-Planck equation*. We can find the expected firing probability for the neuron by considering the corresponding KFP equation [14] for the probability density of a neuron to be in the state $u$, $\tilde\rho(t,u,q)$, which is

$$\frac{\partial\tilde\rho}{\partial t} + \frac{\partial}{\partial u}\left[\frac{-u+q}{\tau_m}\tilde\rho\right] + \frac{\partial}{\partial q}\left[-\frac{q}{\tau}\tilde\rho\right] - \frac{1}{\tau}\frac{\partial^2\tilde\rho}{\partial q^2} = 0 \tag{11}$$

with the boundary conditions $\tilde\rho(t,-\infty,q)=\tilde\rho(t,u,-\infty)=\tilde\rho(t,u,+\infty)=\tilde\rho(t,\tilde{T}(t),q\leqslant\tilde{T}(t))=0$, where the inequality takes into account that the equation of transfer in the direction of coordinate $u$ requires the condition of an inflow boundary, i.e., when the factor $(-u+q)/\tau_m$ in the second term is nonpositive. The initial distribution corresponds to the stationary solution found below. This assumption holds because in practice the neuron trajectory always starts from its silent or reset state, rather than near threshold, i.e., the difference of the mean and threshold voltages is larger than any characteristic voltage dispersion. Taking also into account the fast voltage diffusion mentioned above, we conclude that during the evolution of the voltage towards threshold, the distribution of voltages would approach a gaussian distribution regardless of the initial distribution. Moreover, the large difference of the mean and threshold voltages compared to the voltage dispersion allows us to neglect the tail of the distribution at voltages above the threshold.

The expected firing rate of the population, scaled by the number of neurons, or the spike-release probability density for a single neuron $H(t)$, is given by the flux through the boundary at $u=\tilde{T}$, i.e.,

$$\tilde{H}[U(t)] \equiv \tau_m H[U(t)] = -\tau_m\frac{1}{\rho}\frac{d\rho}{dt} = \frac{1}{\rho}\int_{\tilde{T}}^{\infty}(q-\tilde{T})\tilde\rho(t,\tilde{T},q)dq, \tag{12}$$

where $\rho$ is the integral characterizing the probability for a neuron to remain in the inactive state,

$$\rho(t) = \int_{-\infty}^{\tilde{T}}\int_{-\infty}^{\infty}\tilde\rho(t,u,q)dqdu. \tag{13}$$

Note that $\rho(t,t^*)$ in Eq. (2) is the same quantity as $\rho(t)$ in Eq. (13), however, for the derivation presented in this section it is unimportant whether the neurons are discriminated by the parameter $t^*$ or not, and whether $\rho$ is scaled by the units of $t^*$ or not.

Introducing the ratio of membrane and noise time constants, $k(U,t)\equiv\tau_m(U,t)/\tau$, we rewrite Eq. (11) as follows:

$$\tau_m(U,t)\frac{\partial\tilde\rho}{\partial t} = \frac{\partial}{\partial u}(u-q)\tilde\rho + k(U,t)\left[\frac{\partial}{\partial q}q\tilde\rho + \frac{\partial^2\tilde\rho}{\partial q^2}\right]. \tag{14}$$

As mentioned above, in the case of white noise $(k=\infty)$ we have obtained a good approximation for $\tilde{H}$ as a sum of self-similar $A$ and frozen stationary $B$ solutions of the KFP equation for the firing probability density [8]. The physical interpretation of the these solutions is that the activity $B$ is due to the "movement" of the threshold boundary $u=\tilde{T}(t)$ towards the probability density function (pdf), whereas the activity $A$ results from "flow" through a threshold boundary $u=\tilde{T}$ because of transfer and diffusion processes changing the pdf. These processes, which provide "sources" of neuron leakage, are independent. Relying on this fact, we supposed and then verified that the activities are additive, i.e., the sum of the solutions $A+B$ gives a satisfactory approximation for $\tilde{H}$ in any arbitrary case of neuron stimulation. An approximation in the case of colored noise is constructed in the same way. The considered particular cases are limit cases in the sense that $B$ is zero in the unvarying $U(t)$ regime, and $A$ is negligible in the fast-varying $U(t)$ regime.

*Stationary solution*. The form of Eq. (14) in the stationary case, $d\rho/dt=0$, is as follows:

$$(1+k)\tilde{\rho}+(u-q)\frac{\partial\tilde{\rho}}{\partial u}+kq\frac{\partial\tilde{\rho}}{\partial q}+k\frac{\partial^2\tilde{\rho}}{\partial q^2}=0. \tag{15}$$

Its solution is

$$\tilde{\rho}(u,q)=\frac{1+k}{2\pi\sqrt{k}}\exp\left\{\frac{1+k}{2k}[-(1+k)u^2-q^2+2qu]\right\}. \tag{16}$$

The marginal distribution is

$$\tilde{\rho}(u)=\int_{-\infty}^{\infty}\tilde{\rho}(u,q)dq=\frac{1}{\sigma_u\sqrt{2\pi}}\exp\left(-\frac{1}{2}\frac{u^2}{\sigma_u^2}\right),\quad \sigma_u=\frac{1}{\sqrt{1+k}}. \tag{17}$$

The stationary voltage dispersion depends on $\sigma$ as follows: $\sigma_V=\sigma/(g_{tot}\sqrt{1+k})$.

For the sake of consistency between the following formulas and the results from [4] for the white noise case, we introduce the parameter $T(t)=\tilde{T}(t)/\sqrt{2}\sigma_u$.

*Frozen stationary distribution*. In the case when the threshold $\tilde{T}(t)$ is decreasing rapidly, the initial stationary distribution remains almost unchanged except for a cutting off at the threshold $u=\tilde{T}$. The hazard function in this particular case, $B\equiv\tilde{H}$, depends on $T(t)$ and its time derivative $dT/dt$, i.e., $B=B(T,dT/dt)$. We will find $B$ according to Eq. (12) where $\rho$ is governed by Eq. (13). For simplicity, we consider the case of a monotonically decreasing but otherwise arbitrary $T(t)$. Substituting the stationary distribution Eq. (16) into Eq. (13) we get

$$\rho(t)=\frac{1}{2}[\mathrm{erf}(T)+1]. \tag{18}$$

According to Eq. (12), $B$ is obtained as follows:

$$B\left(T,\frac{dT}{dt}\right)=-\frac{\tau_m}{\rho}\frac{d\rho}{dt}=-\sqrt{2}\tau_m\left[\frac{dT}{dt}\right]_+\tilde{F}(T), \tag{19}$$

where

$$\tilde{F}(T)=\sqrt{\frac{2}{\pi}}\frac{\exp(-T^2)}{1+\mathrm{erf}(T)}, \tag{20}$$

and $[x]_+=x$ for $x>0$ and zero otherwise, which annihilates the hazard function when $T$ increases.

*Self-similar solution*. We can explicitly describe the shape $p(t,u,q)$ and the amplitude $\rho(t)$ of the probability distribution $\tilde{\rho}(t,u)$ by the substitution

$$\tilde{\rho}(t,u,q)=\rho(t)p(t,u,q). \tag{21}$$

As seen from Eqs. (13) and (21) the shape $p$ is normalized as $\int\int p\,dq\,du=1$. The amplitude of the probability distribution $\rho(t)$ decreases due to crossing the threshold $T$ and is described by the equation

$$\tau_m\frac{d\rho}{dt}=-\rho\tilde{H}(t). \tag{22}$$

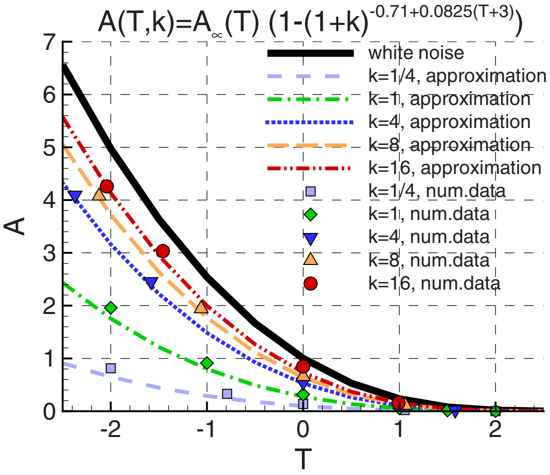

FIG. 1. (Color online) The function $A$ is the component of the approximate hazard function which characterizes the spike-release probability density for a neuron in the regime of constant $T$, the dimensionless distance between the membrane potential and threshold.

The shape $p(t,u,q)$ is renormalized, i.e., it is governed by Eq. (14), with the added source term proportional to $p(t,u,q)$ itself, i.e.,

$$\tau_m(U,t)\frac{\partial p}{\partial t}=\frac{\partial}{\partial u}(u-q)p+k(U,t)\left[\frac{\partial}{\partial q}qp+\frac{\partial^2 p}{\partial q^2}\right]+\tilde{H}(t)p, \tag{23}$$

$$\tilde{H}[U(t)]=\int_{\tilde{T}}^{\infty}(q-\tilde{T})p(t,\tilde{T},q)dq. \tag{24}$$

The boundary conditions are $\tilde{\rho}(t,-\infty,q)=\tilde{\rho}(t,u,-\infty)=\tilde{\rho}(t,u,+\infty)=\tilde{\rho}(t,\tilde{T}(t),q\leqslant\tilde{T}(t))=0$.

When the potential difference between the mean potential $U$ and the threshold $U^T$ is changing slowly, the diffusion process described by the KFP equation dominates the transfer between nonspiking and spiking neurons. The limit case is when $T$ is constant. The solution of Eq. (23) in this case is self-similar with decreasing amplitude $\rho(t)$ and constant shape $p(t,u)$, described by the stationary variant of Eq. (24),

$$\frac{\partial}{\partial u}(u-q)p+k(U,t)\left[\frac{\partial}{\partial q}qp+\frac{\partial^2 p}{\partial q^2}\right]+\tilde{H}(t)p=0, \tag{25}$$

with the same boundary conditions. Setting different values of $T$, the solution of the equation is obtained numerically. To get a convergent solution, we applied the total-variation-diminishing (TVD) scheme of the second order approximation [15]. Of particular interest is the resulting dependence of the activity $\tilde{H}$, denoted for the constant $T$ case as $A$, on $T$ and $k$, shown in Fig. 1. The dependence on $k$ can be approximated as

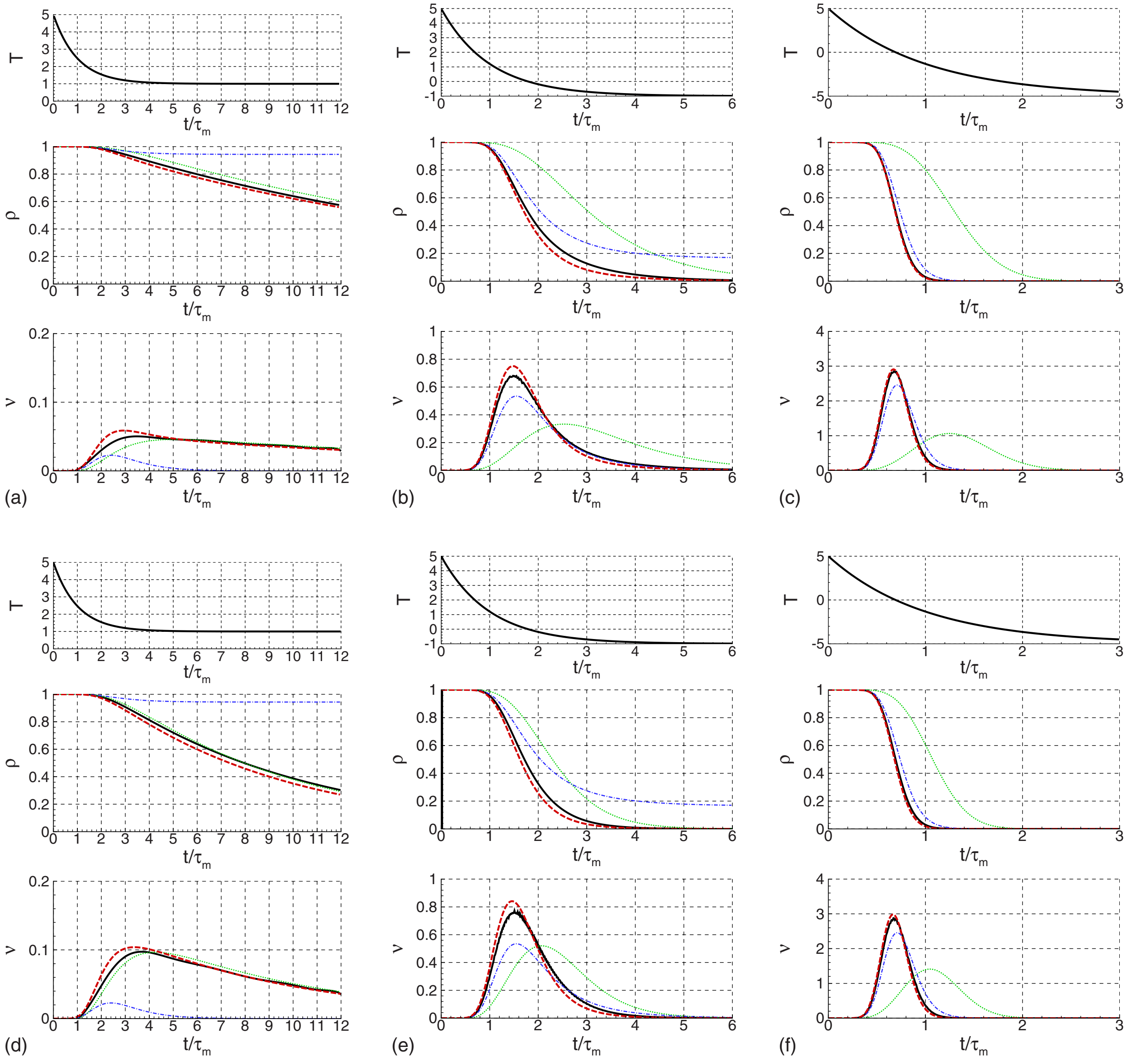

FIG. 2. (Color online) Comparison of the firing rate, $\nu(t)=\partial\rho/\partial t$, calculated by the full Fokker-Planck Eq. (14) (black solid lines) with the approximations by $\tau_m d\rho/dt=-\rho A(T,k)$ (green dotted line), $\tau_m d\rho/dt=-\rho B(T,dT/dt)$ (blue dot-dash line), and $\tau_m d\rho/dt=-\rho[A(T,k)+B(T,dT/dt)]$ (red long-dash line); $\nu$ is scaled by $\tau_m$. The evolution of $T(t)$ is defined by the input $U(t)=U_{max}[1-\exp(-t/\tau_m)]$, $U^T=5\sigma/g_{tot}$, correspondent to the current-step stimulation. The subthreshold (a,d), near-threshold (b,e), and supra-threshold (c,f) regimes were set by $U_{max}/(\sigma/g_{tot})=4$, 6, or 10, correspondingly, for the two values of $k$: $k=1$ for (a,b,c) and $k=8$ for (d,e,f).

$$A(T,k) = A_\infty(T)[1-(1+k)^{-0.71+0.0825(T+3)}],$$

$$A_\infty(T) = \exp(6.1\times 10^{-3} - 1.12T - 0.257T^2 - 0.072T^3 - 0.0117T^4). \qquad (26)$$

The term $A_\infty(T)$ is the solution for the hazard function in the self-similar case for white noise, i.e., $\lim_{k\to\infty} A(T,k)=A_\infty(T)$. The function $A_\infty(T)$ has been obtained as an approximate formula of the exact but complicated analytical solution of the Kolmogorov-Fokker-Planck equation in the self-similar case for white noise [8]. The approximation holds for the significant range of $T$, $[-2,3]$. The factor in the formula for $A(T,k)$ has been obtained as an approximation of the numerically calculated points shown in Fig. 1.

*Cumulative result: Approximation of hazard function in the arbitrary case.* The result is the following formula:

$$H[U(t)] = \frac{1}{\tau_m}[A(T(U),k) + B(U,dU/dt)], \qquad (27)$$

where $A(T,k)$ is given by Eq. (26) and shown in Fig. 1(a);

$$T = \sqrt{\frac{1+k}{2}}\,\frac{g_{tot}(U^T-U)}{\sigma}, \quad k=\tau_m/\tau,$$

and

$$B(U,dU/dt) = -\sqrt{2}\tau_m\left[\frac{dT}{dt}\right]_+ \tilde{F}(T), \quad \tilde{F}(T) = \sqrt{\frac{2}{\pi}\frac{\exp(-T^2)}{1+\mathrm{erf}(T)}}, \tag{28}$$

$[x]_+ = x$ for $x > 0$ and zero otherwise.

This approximation of $H$ for arbitrary conditions is then applied to the refractory density model describing a population of integrate-and-fire neurons by using Eqs. (2) and (3), or by using the equations developed in [8] for neurons with various active conductances.

## III. RESULTS

We now verify the approximation of the hazard function and its application in the refractory density approach for linear integrate-and-fire neurons with colored synaptic noise, i.e., when $I_{tot} = g_{tot}(V - V_{rest})$, $g_{tot} = g_L = \mathrm{const}$, $\tau_m = \mathrm{const}$. All the neurons receive the same current step input.

*RDA and full KFP for the first passage problem.* To check the approximation of the hazard function we consider the first passage problem. Because the full KFP equation (14) in this case is strictly equivalent to the initial statement of the problem based on Eqs. (6) and (7), we compare its solution with the solution using the approximated hazard function, based on Eqs. (4) and (26)–(28). Comparison of the numerical solutions of the full KFP equation (14) (black solid line) with the solutions of Eqs. (4) and (26)–(28) is shown in Fig. 2; all governing parameters are given in the figure caption. We simulated three cases of neuron stimulation, corresponding to injected current steps of three different amplitudes. As can be seen in the figure, the approximation by Eq. (27) works well in different regimes of neuron stimulation and with different ratios of noise and membrane time constants, thus corresponding to different spectrums of the colored noise. In fact, the approximation $\tilde{H} = A$ works well only in the subthreshold stimulation regime, and the approximation $\tilde{H} = B$ does well only in the superthreshold stimulation regime, whereas Eq. (27) gives a good approximation in all three regimes. Note that the sum of the "$A$" and "$B$" solutions do not give the "$A+B$" solution.

*RDA and individual neuron simulation for step current stimulation problem.* We demonstrate an effect of temporal noise correlations by consideration of the responses of a population to an injected current step in the cases of white and colored ($\tau_m/\tau = 4$) noise, as shown in Fig. 3. The direct simulation (DS) of individual neurons based on Eq. (1) and the population model based on Eqs. (2), (3), and (26)–(28) give similar qualitative results, and both show a quantitative change in the responses depending on the input noise spectrum.

*RDA and known analytical expressions for steady-state firing.* In the steady-state regime the RDA approach based on Eqs. (2) and (3) is reduced to the following ordinary differential equations:

$$\frac{d\rho}{dt^*} = -\rho H, \tag{29}$$

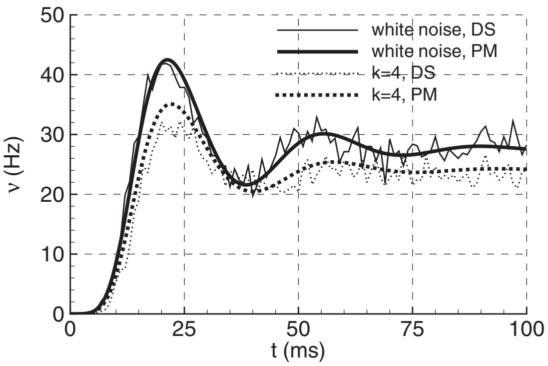

FIG. 3. The transient response of the firing rate of a population of LIF neurons after a step of injected current $I_a = 400$ pA. Responses were obtained by both direct simulation of 8000 of individual neurons (DS) and by evaluating the population model (PM). The parameters of the LIF neurons are $V_{rest} = -65.7$ mV, $V_{reset} = -75.1$ mV, $C = 1\ \mu\mathrm{F/cm}^2$, $\tau_m = 14.4$ ms, $U^T = V_{rest} + 10$ mV, the membrane area $S = 5.27 \times 10^{-4}\ \mathrm{cm}^2$. The amplitude of noise was such that the stationary voltage dispersion would be $\sigma_V = 2$ mV; the time parameter of the colored noise was such that $\tau_m/\tau = 4$. The initial conditions corresponded to steady-state gaussian distribution of $V$ and $h$.

$$C\frac{dU}{dt^*} = -g_L(U - V_{rest}) + I_a, \tag{30}$$

with the conditions $U(0) = V_{reset}$, $\int_0^\infty \rho dt^* = 1$, and the parameter $V_{reset} = V_{rest}$. The solution by the RDA for $\nu \equiv \rho(0)$ as a function of $I_a$ is expressed [8] by

$$\nu = \left[\tau_m \int_0^a \exp\left(-\int_0^{u'} \frac{\tau_m H(u)}{a-u} du\right) \Big/ (a - u')du'\right]^{-1}, \tag{31}$$

with $a = I_a / g_L(U^T - V_L)$.

We compare this solution given by the RDA and the new hazard function Eq. (27) to the steady-state firing rate computed by Moreno-Bote and Parga (MB) [13], by both direct simulations and approximate analytical expression. The parameters from the earlier work of [13] correspond to ours, $\tau_m = 10$ ms, $a = \tau_m \mu_{MB}$, $\sigma/(U^T g_L) = \tau_m\sqrt{\sigma_{MB}^2/(2\tau)}$, for three regimes with (i) $a = 0.8$, $\sigma_{MB}^2 = 4$ Hz (bottom); (ii) $a = 0.8$, $\sigma_{MB}^2 = 12$ Hz (middle); and (iii) $a = 1.05$, $\sigma_{MB}^2 = 1$ Hz (top). Figure 4 presents the firing rate vs the time scale of the noise $\tau$. The comparison of the solutions shows that the quality of the RDA approach with the new approximation of the hazard function is consistent with the previous analytical results. In particular, the residual errors are of the same scale as the errors of the hazard function approximation (26) and the errors of the numerical solution of the integral (31).

*RDA for full coductance-based model of cortical adaptive neurons.* We now demonstrate the approximation of the colored-noise hazard function into a full conductance-based model of a population of adaptive neurons. The full models for a single neuron and for a population have been introduced in [8], and here we substitute the white-noise approximation of the hazard function by its colored-noise generali-

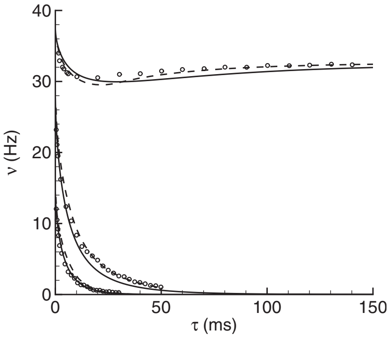

FIG. 4. The firing rate vs the time scale of the noise in the steady state. The solution by Eq. (31) (solid line) that incorporates the proposed hazard function approximation (26) is compared to the individual neuron simulations (dots) and the known analytical expression from [13]. The curves for superthreshold (top) and two subthreshold (middle and bottom) regimes are shown; the parameters are given in text.

zation given by Eqs. (27) and (28). The response of a population to an injected current step (400 pA) in the case of colored ($\tau_m/\tau=4$) noise, shown in Fig. 5, corresponds well to the direct simulation (DS) of individual neurons.

## IV. DISCUSSION

The results of our present and previous works show that a population of similar conductance-based neurons with first-order synaptic noise kinetics can be precisely described by a one-dimensional PDM. In particular, the present paper shows that in the case of noninstantaneous noise, instead of a 2D nonstationary KFP equation, the system can be evaluated by solving a set of 1D transport equations derived from the refractory density approach, with the hazard function parametrized by the ratio of membrane and noise time constant.

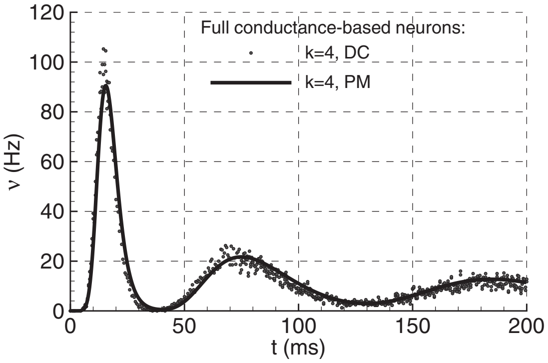

FIG. 5. The transient response of the firing rate of a population of conductance-based neurons after a step of injected current $I_a$ =400 pA. Responses were obtained by both direct simulation of 8000 of individual neurons (DS) and the evaluation of the population model (PM). The parameters of the models are given in [8]. The amplitude of noise was such that the stationary voltage dispersion would be $\sigma_V$=2 mV; the time parameter of the colored noise was such that $\tau_m/\tau$=4.

Simulations show only quantitative but not qualitative effect of noise correlations in time, and only for rather weak intensities of stimulation.

These results support the use of the proposed population model based on Eqs. (2) and (3) for either integrate-and-fire neurons or neurons described by the equations from [8] for conductance-based neurons, with the hazard function given by Eqs. (27) and (28). In particular, the model should simplify analyses such as that proposed in [4], or simplify network simulations such as described in [6].

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