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First-passage-time statistics of a Brownian particle driven by an arbitrary unidimensional potential with a superimposed exponential time-dependent drift

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Abstract

In one-dimensional systems, the dynamics of a Brownian particle are governed by the force derived from a potential as well as by diffusion properties. In this work, we obtain the first-passage-time statistics of a Brownian particle driven by an arbitrary potential with an exponential temporally decaying superimposed field up to a prescribed threshold. The general system analyzed here describes the sub-threshold signal integration of integrate-and-fire neuron models, of any kind, supplemented by an adaptation-like current, whereas the first-passage-time corresponds to the declaration of a spike. Following our previous studies, we base our analysis on the backward Fokker–Planck equation and study the survival probability and the first-passage-time density function in the space of the initial condition. By proposing a series solution we obtain a system of recurrence equations, which given the specific structure of the exponential time-dependent drift, easily admit a simpler Laplace representation. Naturally, the present general derivation agrees with the explicit solution we found previously for the Wiener process in (2012 *J. Phys. A: Math. Theor.* **45** 185001). However, to demonstrate the generality of the approach, we further explicitly evaluate the first-passage-time statistics of the underlying Ornstein–Uhlenbeck process. To test the validity of the series solution, we extensively compare theoretical expressions with the data obtained from numerical simulations in different regimes. As shown, agreement is precise whenever the series is truncated at an appropriate order. Beyond the fact that both the Wiener and Ornstein–Uhlenbeck processes have a direct interpretation in the context of neuronal models, given their ubiquity in different fields, our present results will be of interest in other settings where an additive state-independent temporal relaxation process is being developed as the particle diffuses.

Keywords: first-passage-time, diffusion, neuron models, time-dependent drift

(Some figures may appear in colour only in the online journal)

1. Introduction

From the first attempts in the nineteenth century to account for the effects of randomness in nature, fluctuations have been recognized as a fundamental component in the description of several physical, chemical and biological systems [1–3]. A stochastic description can be formulated in continuous or discrete time for systems whose phase space is continuous, or embedded in a lattice. For many of these systems, Brownian motion and diffusion models have proven to be key conceptualizations, mathematically accessible and useful for characterizing their statistical behavior [1–6].

Random walks and diffusion processes evolve in certain regions of their phase space according to the equations or rules governing their dynamics. Complementary to dynamics, boundary conditions shape the probability distribution of the system being in a given state at a certain time. In this sense, different scenarios are prescribed by different combinations of boundary conditions [1, 3, 4]. Among these scenarios, first-passage-time (FPT) problems—also referred to as exit or escape times—represent a wide class of situations [7], where the random variable of interest is the time at which certain state conditions are met first. The statistics of this and other related variables, such as survival probability, are relevant in many fields and contexts [7–10]. Examples abound in different disciplines: diffusion-influenced reactions [11–16], the channel-assisted membrane transport of metabolites, ions, or polymers [17–20] and, in general, the variety of processes orchestrating intracellular transport [21], force-induced unbinding processes and the reconstruction of potential functions in experiments of single-molecule force spectroscopy [22–26], the random search and first encounters of mobile or immobile targets by a variety of agents, from foraging animals to proteins [27], including transport-limited reactions in active media [28], the absorption of particles in restricted geometries [29, 30] and, generically, geometry-controlled kinetics [31], escape from confined domains through narrow pores [32–34] as well as through large windows [35], the granular segregation of binary mixtures [36], the formation of loops in nucleic acids and the cyclization of polymers [37, 38], and finally, the nucleation and stochastic self-assembly of monomers [39], to name a few.

A particularly interesting FPT problem arises in the context of spiking neurons. In general, a neuron accumulates input currents up to a point at which its dynamics become independent of the inputs, and then generates a large excursion in its phase space in a relatively short period of time, producing a kind of stereotyped event called an *action potential* or a *spike* [40, 41]. To a large extent, these spikes form the basis of neuronal communication. Simplified models of spike generation take advantage of the large reproducibility of action potentials by splitting the dynamics into two phases: the phase where inputs and internal processes drive the neuron, i.e. the regime of sub-threshold integration, and the phase where the spike is manifested itself, which is not represented in detail but prescribed by a fire-and-reset rule [40, 41]. These *integrate-and-fire* (IF) models have different versions according to the processes included during sub-threshold integration [40–42].

However, all of them produce spikes by declaration once the voltage reaches a certain threshold for the first time. Then, the voltage is reset to a lower potential, which is the initial condition for the sub-threshold integration of the following spike. Because of how spikes are defined in these models, their relationship to FPT problems is straightforward. On the other hand, the reproducibility of *spike times* is not as precise as expected from deterministic systems [40, 41]. This randomness is accounted for by different stochastic phenomena (ionic gating, neuro-transmitter release, etc), which are normally incorporated in these models by adding noise—in general, Gaussian white or colored noise. Overall, the stochastic dynamics of the sub-threshold integration of IF models is equivalent to the motion of a Brownian particle (where different versions correspond to different potentials), whereas the presence of the threshold for declaring spikes sets the definition of the FPT [5, 40, 41, 43–46].

One of the processes that greatly affects spike production is the presence of adaptation currents. They are putatively responsible for the widespread observed phenomenon of spike frequency adaptation, where a neuron's discharge rate decreases in response to a step stimulus [40, 41]. The simplest version of adaptive IF models incorporates an additive current that decreases exponentially in time during sub-threshold evolution, and enables history-dependent behavior in the spike-and-reset rule [47–50]. Therefore, the first step towards developing a full understanding of the effect of spike-triggered adaptation currents on interspike interval statistics is to analyze the FPT problem of a Brownian motion—given by the associated IF model under analysis—with a superimposed exponentially decaying additive drift. This problem was partially covered by Lindner in 2004, in which he derived general expressions for the corrections to the moments of FPT distribution in a general time-dependent case, and assessed some particular explicit solutions for the first order moments in the case of exponential temporal driving [51]. To address the full FPT statistics of the temporally inhomogeneous problems that exponential time-dependent drift poses, we previously analyzed the survival probability and the FPT distribution based on the backward Fokker–Planck (FP) equation, and inductively solved the system of infinite recurrence equations that results from the proposal of a series solution. This approach was derived for the simple case of a Wiener process, corresponding to the *perfect* IF model in the spiking neurons framework [52, 53]. Here, we aim to extend these results to a system where the main driving force derives from an arbitrary potential. Furthermore, we were able to obtain the explicit solution to the Ornstein–Uhlenbeck process, which corresponds to the *leaky* IF model in the context of spiking neurons. Traditionally, this is considered to be the minimal biologically realistic IF model [44], obtained as a diffusion approximation of the Stein model [54].

2. First-passage-time in an arbitrary potential: theoretical framework

2.1. The homogeneous system

First, the methodology we use later to study the first-passage-time problem in a time-inhomogeneous setup is reviewed in a classical context: a particle driven exclusively by an arbitrary unidimensional potential [1, 4]. Even when different approaches can be taken, we focus on the analysis of the survival probability via the backward Fokker–Planck equation. Under this framework, the posterior analysis of a superimposed exponential time-dependent drift has proven to be mathematically tractable [52, 53].

We consider a continuous-time random walk representing the movement of an overdamped particle, whose position $x(t)$ evolves according to the following equation:

$$\frac{dx}{dt} = -\frac{dU(x)}{dx} + \sqrt{2D}\,\xi(t). \tag{1}$$

In equation (1), the conservative force driving the particle is written as the negative of the derivative of a generic position-dependent potential $U(x)$, whereas random forces are represented by an additive Gaussian white noise $\xi(t)$, defined by $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle = \delta(t - t')$. The particle is initially set at position x_0 and the first time it reaches the level $x_{\rm thr} > x_0$, the dynamics are no longer analyzed (or reset) and a first-passage-time (FPT) event is declared.

For this system, the evolution of the transition probability density function of a particle being at position x at time t—given that it will be at position t' at a posterior time t' ($t' > t$)—is governed by the backward Fokker–Planck (FP) equation [1, 4, 52], which reads

$$\frac{\partial P\left(x', t' \middle| x, t\right)}{\partial t} = U'(x)\,\frac{\partial P\left(x', t' \middle| x, t\right)}{\partial x} - D\frac{\partial^2 P\left(x', t' \middle| x, t\right)}{\partial x^2}, \tag{2}$$

where $U'(x)$ indicates the derivative of the potential with respect to x. Supplementing equation (2), initial and boundary conditions are set in accordance to the survival domain, $x' < x_{\rm thr}$. Explicitly,

$$P\left(x', t' \middle| x, t = t'\right) = \begin{cases} 1 & \text{for } x < x_{\rm thr}, \\ 0 & \text{for } x \geqslant x_{\rm thr}, \end{cases} \tag{3}$$

$$P\left(x', t' \middle| x = x_{\rm thr}, t\right) = 0. \tag{4}$$

Within the backward FP formalism, the survival probability at time t' for a particle released at position x and at time t,

$$F\left(t' \middle| x, t\right) = \int_{-\infty}^{x_{\rm thr}} P\left(x', t' \middle| x, t\right) dx', \tag{5}$$

is obtained simply by integrating both sides of equation (2) in x' from $-\infty$ to $x_{\rm thr}$. In terms of the auxiliary variable $\tau = t' - t$, the corresponding equation results

$$\frac{\partial F(x, \tau)}{\partial \tau} = -U'(x)\,\frac{\partial F(x, \tau)}{\partial x} + D\frac{\partial^2 F(x, \tau)}{\partial x^2}, \tag{6}$$

whereas initial and boundary conditions read

$$F(x, \tau = 0) = \begin{cases} 1 & \text{for } x < x_{\rm thr}, \\ 0 & \text{for } x \geqslant x_{\rm thr}, \end{cases} \tag{7}$$

$$F(x = x_{\rm thr}, \tau) = 0. \tag{8}$$

Once the survival probability, whose evolution is given by equations (6)–(8), is known, the FPT density function can be immediately evaluated. By construction, $F(x, \tau)$ is the probability that—given that the particle was released at position x—it remains alive or not absorbed at time τ within the survival domain. Equivalently, $F(x, \tau)$ represents the probability that the FPT is posterior to τ: $\mathrm{Prob}(T > \tau) = F(x, \tau)$, where T is the FPT random variable. Since we are focusing on the potentials that warranty level crossing (which can be set, for example, with a small positive drift), then $F(x, \tau)$ can be directly related to the cumulative distribution function of the FPT, $\Phi(\tau)$, through the relationship: $\Phi(\tau) = \mathrm{Prob}(T \leqslant \tau) = 1 - F(x, \tau)$. Therefore, the density function of the FPT, $\phi(\tau)$, is given by

$$\phi(\tau) = \frac{\mathrm{d}\Phi(\tau)}{\mathrm{d}\tau} = -\frac{\partial F(x, \tau)}{\partial \tau}, \tag{9}$$

where it should be noted that once the system defined by equations (6)–(8) has been solved, the initial backward position of the particle x remains as a parameter and can be removed from the notation.

2.2. An additive time-dependent exponential drift

In this work, we study the influence on survival probability and FPT statistics of a superimposed exponential time-dependent drift driven by the potential $U(x)$. This system is described by the Langevin equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = -U'(x) + \frac{\epsilon}{\tau_{\mathrm{d}}}\,\mathrm{e}^{-(t-t_0)/\tau_{\mathrm{d}}} + \sqrt{2D}\;\xi(t), \tag{10}$$

where ϵ and τ_{d} characterize the strength and time constant of the exponential driving, and t_0 refers to the initial time of the experimental setting.

The backward FP equation is similar to equation (2), except for an additional term in the drift coefficient

$$\frac{\partial P\left(x', t' \middle| x, t\right)}{\partial t} = \left[U'(x) - \frac{\epsilon}{\tau_{\mathrm{d}}}\,\mathrm{e}^{-(t-t_0)/\tau_{\mathrm{d}}}\right] \frac{\partial P\left(x', t' \middle| x, t\right)}{\partial x} - D\frac{\partial^2 P\left(x', t' \middle| x, t\right)}{\partial x^2}. \tag{11}$$

Proceeding as in the previous subsection, the survival probability $F(x, \tau; t')$, in terms of the auxiliary variable $\tau = t' - t$, reads

$$\frac{\partial F\left(x, \tau; t'\right)}{\partial \tau} = \left[-U'(x) + \frac{\epsilon}{\tau_{\mathrm{d}}}\,\mathrm{e}^{-\left(t'-t_0\right)/\tau_{\mathrm{d}}}\,\mathrm{e}^{\tau/\tau_{\mathrm{d}}}\right] \frac{\partial F\left(x, \tau; t'\right)}{\partial x} + D\frac{\partial^2 F\left(x, \tau; t'\right)}{\partial x^2}, \tag{12}$$

whereas the initial and boundary conditions are similar to those given by equations (7) and (8). Note that here the term 'initial' refers to the situation $\tau = 0$, and not to the initial time of the experimental setting, t_0.

Following our previous studies [52, 53], we propose a series expansion in powers of ϵ for $F(x, \tau; t')$,

$$F\left(x, \tau; t'\right) = F_0\left(x, \tau; t'\right) + \epsilon\, F_1\left(x, \tau; t'\right) + \epsilon^2\, F_2\left(x, \tau; t'\right) + \ldots = \sum_{n=0}^{\infty} \epsilon^n\, F_n\left(x, \tau; t'\right). \tag{13}$$

With this assumption, equation (12) reads

$$\left[\frac{\partial F_0}{\partial \tau} + U'(x)\frac{\partial F_0}{\partial x} - D\frac{\partial^2 F_0}{\partial x^2}\right] + \sum_{n=1}^{\infty} \epsilon^n \left[\frac{\partial F_n}{\partial \tau} + U'(x)\frac{\partial F_n}{\partial x} - \frac{1}{\tau_{\mathrm{d}}}\,\mathrm{e}^{-\left(t'-t_0\right)/\tau_{\mathrm{d}}}\,\mathrm{e}^{\tau/\tau_{\mathrm{d}}}\,\frac{\partial F_{n-1}}{\partial x} - D\frac{\partial^2 F_n}{\partial x^2}\right] = 0. \tag{14}$$

Given the arbitrariness of ϵ, each term between brackets should be identically 0, splitting equation (14) into an infinite system of coupled equations with a recursive structure,

$$\frac{\partial F_0}{\partial \tau} + U'(x)\,\frac{\partial F_0}{\partial x} - D\,\frac{\partial^2 F_0}{\partial x^2} = 0, \tag{15}$$

$$\frac{\partial F_n}{\partial \tau} + U'(x)\,\frac{\partial F_n}{\partial x} - D\,\frac{\partial^2 F_n}{\partial x^2} = \frac{1}{\tau_d}\,e^{-\left(t'-t_0\right)/\tau_d}\,e^{\tau/\tau_d}\,\frac{\partial F_{n-1}}{\partial x}, \quad \text{for } n \geqslant 1. \tag{16}$$

For the same reason, the non-homogeneous initial condition, $F(x, \tau = 0; t') = 1$ for $x < x_{\rm thr}$, has to be imposed on the zeroth-order function $F_0(x, \tau = 0; t')$, yielding

$$F_0\left(x,\,\tau = 0;\,t'\right) = \begin{cases} 1 & \text{if } x < x_{\rm thr}, \\ 0 & \text{if } x \geqslant x_{\rm thr}, \end{cases} \tag{17}$$

$$F_n\left(x,\,\tau = 0;\,t'\right) = 0 \quad \text{for } n \geqslant 1. \tag{18}$$

Without specificity of the order, the boundary condition reads $F_n(x = x_{\rm thr}, \tau; t') = 0$ for all n.

The preceding system of recursive *partial* equations, equations (15) and (16), can be Laplace-transformed to an equivalent system of *ordinary* equations,

$$s\,\tilde{F}_0^L(x) + U'(x)\,\frac{d\tilde{F}_0^L(x)}{dx} - D\,\frac{d^2\tilde{F}_0^L(x)}{dx^2} = 1, \tag{19}$$

$$s\,\tilde{F}_n^L(x) + U'(x)\,\frac{d\tilde{F}_n^L(x)}{dx} - D\,\frac{d^2\tilde{F}_n^L(x)}{dx^2} = \frac{1}{\tau_d}\,e^{-\left(t'-t_0\right)/\tau_d}\,\frac{d}{dx}\left[\left.\tilde{F}_{n-1}^L(x)\right]_{s-1/\tau_d}\right]. \tag{20}$$

The Laplace transform of each term of the survival probability, $\mathcal{L}[F_n(x, \tau; t')]$, is represented by $\tilde{F}_n^L(x)$, omitting the parametric dependence on s and tentatively on t'. In equations (19) and (20), the initial condition required by the Laplace transform of the temporal derivative, $\mathcal{L}[\partial F_n(x, \tau; t')/\partial\tau] = s\tilde{F}_n^L(x) - F_n(x, \tau = 0; t')$, has been assigned to an internal point, $x < x_{\rm thr}$, according to equations (17) and (18). This system of recursive equations has to be solved together with the Laplace-transformed boundary condition, $\tilde{F}_n^L(x = x_{\rm thr}) = 0$ for all n.

Up to now, we have addressed the evolution of survival probability from the backward state, x at time t, to the current position, x' at time t'. Since the experimental setup—and in particular the temporally inhomogeneous exponential time-dependent drift—refers to the time t_0, when the particle is at position x_0, we need to link this survival probability to the real initial state. According to the inverse Laplace transform, the zeroth-order function of this probability

$$F_0(x,\,\tau) = \frac{1}{2\pi j}\int_{\sigma-j\infty}^{\sigma+j\infty} e^{s\tau}\,\tilde{F}_0^L(x;\,s)\,ds, \tag{21}$$

can be directly evaluated at the initial setting, $x = x_0$ at time difference $\tau = t' - t_0$. In virtue of equation (19), its Laplace transform satisfies

$$\frac{d^2\tilde{F}_0^L(x_0)}{dx_0^2} - \frac{U'(x_0)}{D}\,\frac{d\tilde{F}_0^L(x_0)}{dx_0} - \frac{s}{D}\,\tilde{F}_0^L(x_0) = -\frac{1}{D} \tag{22}$$

and $\tilde{F}_0^L(x_0 = x_{\rm thr}) = 0$.

From equation (20), it is easy to show that higher order functions can be written as

$$\tilde{F}_n^L(x) = e^{-n\left(t'-t_0\right)/\tau_d}\,\tilde{\mathbb{F}}_n^L(x), \tag{23}$$

where the time-inhomogeneous part of the solution is restricted to the exponential factor. The time-homogeneous function $\tilde{\mathbb{F}}_n^L(x)$ satisfies

$$\frac{d^2\tilde{\mathbb{F}}_n^L(x)}{dx^2} - \frac{U'(x)}{D}\frac{d\tilde{\mathbb{F}}_n^L(x)}{dx} - \frac{s}{D}\tilde{\mathbb{F}}_n^L(x) = -\frac{1}{\tau_d D}\frac{d}{dx}\tilde{\mathbb{F}}_{n-1}^L(x)\bigg]_{s-1/\tau_d}. \tag{24}$$

To impose the real initial condition we need to obtain each term in the temporal domain. According to the inverse Laplace transform and equation (23), these functions read

$$F_n\left(x,\, \tau;\, t'\right) = e^{-n\left(t'-t_0\right)/\tau_d}\,\frac{1}{2\pi j}\int_{\sigma-j\infty}^{\sigma+j\infty} e^{s\tau}\,\tilde{\mathbb{F}}_n^L(x;\, s)\, ds. \tag{25}$$

However, this integral cannot be done directly and certain considerations have to be taken into account. Since we focus on systems in which there are appropriate solutions to the FPT problem in the unperturbed situation, the region of convergence of $\tilde{F}_0^L(x)$, bounded by the path of integration in equation (21), is assumed to be defined by $\sigma > 0$. Consequently, because of the shift in s in the forcing term, the equation for the first-order function $\tilde{\mathbb{F}}_1^L(x)$, equation (24) for $n = 1$, is valid in the region $\sigma > 1/\tau_d$. The argument is recursive and, therefore, the region of convergence of the nth-order function is $\sigma > n/\tau_d$. Accordingly, to evaluate the integral in equation (25) we make the substitution $z = s - n/\tau_d$,

$$F_n\left(x,\, \tau;\, t'\right) = e^{-n\left(t'-t_0\right)/\tau_d}\, e^{n\tau/\tau_d}\,\frac{1}{2\pi j}\int_{\sigma_z-j\infty}^{\sigma_z+j\infty} e^{z\tau}\,\tilde{\mathbb{F}}_n^L(x;\, z + n/\tau_d)\, dz, \tag{26}$$

where now $\sigma_z > 0$. Once we evaluate the initial setting, x_0 at time $t = t_0$ (or, equivalently, $\tau = t' - t_0$), the exponential time-dependent factors cancel out and the remaining contribution to the survival probability does not depend on t',

$$F_n(x_0,\, \tau) = \frac{1}{2\pi j}\int_{\sigma_z-j\infty}^{\sigma_z+j\infty} e^{z\tau}\,\tilde{\mathbb{F}}_n^L(x_0;\, z + n/\tau_d)\, dz. \tag{27}$$

Moreover, the region of convergence of its Laplace transform is the semi-plane defined by $\mathrm{Re}(s) > 0$. To obtain $\tilde{\mathbb{F}}_n^L(x_0;\, z + n/\tau_d)$ we take the inverse Laplace transform on both sides of equation (24),

$$\begin{aligned}&\frac{1}{2\pi j}\int_{\sigma-j\infty}^{\sigma+j\infty} e^{s\tau}\left[\frac{d^2\tilde{\mathbb{F}}_n^L(x_0;\, s)}{dx_0^2} - \frac{U'(x_0)}{D}\frac{d\tilde{\mathbb{F}}_n^L(x_0;\, s)}{dx_0} - \frac{s}{D}\tilde{\mathbb{F}}_n^L(x_0;\, s)\right] ds\\ &= -\frac{1}{\tau_d D}\,\frac{1}{2\pi j}\int_{\sigma-j\infty}^{\sigma+j\infty} e^{s\tau}\,\frac{d}{dx_0}\tilde{\mathbb{F}}_{n-1}^L\left(x_0;\, s - 1/\tau_d\right)\, ds,\end{aligned} \tag{28}$$

and apply the same substitution as before, $z = s - n/\tau_d$,

$$\begin{aligned}&\frac{1}{2\pi j}\int_{\sigma_z-j\infty}^{\sigma_z+j\infty} e^{z\tau}\left[\frac{d^2\tilde{\mathbb{F}}_n^L}{dx_0^2} - \frac{U'(x_0)}{D}\frac{d\tilde{\mathbb{F}}_n^L}{dx_0} - \frac{(z + n/\tau_d)}{D}\tilde{\mathbb{F}}_n^L\right] dz\\ &= -\frac{1}{\tau_d D}\,\frac{1}{2\pi j}\int_{\sigma_z-j\infty}^{\sigma_z+j\infty} e^{z\tau}\,\frac{d}{dx_0}\tilde{\mathbb{F}}_{n-1}^L\, dz,\end{aligned} \tag{29}$$

where we have simplified the notation to $\tilde{\mathbb{F}}_n^L = \tilde{\mathbb{F}}_n^L(x_0;\, z + n/\tau_d)$. From equation (29), it is straightforward to show that each function $\tilde{\mathbb{F}}_n^L(x_0;\, z + n/\tau_d)$ appearing in the integrand of equation (27) satisfies

$$\frac{d^2\tilde{\mathbb{F}}_n^L(x_0)}{dx_0^2} - \frac{U'(x_0)}{D}\frac{d\tilde{\mathbb{F}}_n^L(x_0)}{dx_0} - \frac{(s + n/\tau_d)}{D}\tilde{\mathbb{F}}_n^L(x_0) = -\frac{1}{\tau_d D}\frac{d}{dx_0}\tilde{\mathbb{F}}_{n-1}^L(x_0), \tag{30}$$

with $\tilde{\mathbb{F}}_n^L(x_0 = x_{thr}) = 0$.

To summarize, the survival probability from the initial state (x_0, t_0) to the current state $(x, t_0 + \tau)$ is given by

$$F(x_0, \tau) = F_0(x_0, \tau) + \epsilon\, F_1(x_0, \tau) + \epsilon^2\, F_2(x_0, \tau) + \dots = \sum_{n=0}^{\infty} \epsilon^n\, F_n(x_0, \tau), \tag{31}$$

where all functions are obtained from the corresponding inverse Laplace transforms, either given by equation (21) or equation (27). In turn, the Laplace transform of the unperturbed system, $\tilde{F}_0^L(x_0)$, satisfies equation (22), whereas all time-homogeneous higher order terms, $\tilde{\mathbb{F}}_n^L(x_0)$, are recursively obtained from equation (30). For any order, the boundary condition is zero, $\tilde{F}_0^L(x_{\rm thr}) = \tilde{\mathbb{F}}_n^L(x_{\rm thr}) = 0$.

As shown in section 2.1, FPT density function can be directly obtained once the survival probability from the initial state to the current state is known, see equation (9). Therefore, the series structure in equation (31) is inherited by the FPT density function [52, 53],

$$\phi(x_0, \tau) = \sum_{n=0}^{\infty} \epsilon^n\, \phi_n(x_0, \tau), \tag{32}$$

where each order function, $\phi_n(x_0, \tau)$, satisfies

$$\phi_n(x_0, \tau) = -\frac{\partial F_n(x_0, \tau)}{\partial \tau}. \tag{33}$$

In terms of the Laplace transform, this set of equations reads

$$\tilde{\phi}_0^L(x_0; s) = 1 - s\, \tilde{F}_0^L(x_0; s) \tag{34}$$

$$\tilde{\phi}_n^L(x_0; s) = -s\, \tilde{\mathbb{F}}_n^L(x_0; s), \quad n \geqslant 1, \tag{35}$$

where we have taken into account the conditions given by equations (17) and (18) at the real initial state. With these relationships, and based on equations (22) and (30), it is straightforward to derive the system of equations governing each term in the series solution for the FPT density function, equation (32),

$$\frac{\mathrm{d}^2\tilde{\phi}_0^L(x_0)}{\mathrm{d}x_0^2} - \frac{U'(x_0)}{D}\frac{\mathrm{d}\tilde{\phi}_0^L(x_0)}{\mathrm{d}x_0} - \frac{s}{D}\,\tilde{\phi}_0^L(x_0) = 0, \tag{36}$$

$$\frac{\mathrm{d}^2\tilde{\phi}_n^L(x_0)}{\mathrm{d}x_0^2} - \frac{U'(x_0)}{D}\frac{\mathrm{d}\tilde{\phi}_n^L(x_0)}{\mathrm{d}x_0} - \frac{(s + n/\tau_{\rm d})}{D}\,\tilde{\phi}_n^L(x_0) = -\frac{1}{\tau_{\rm d} D}\frac{\mathrm{d}}{\mathrm{d}x_0}\tilde{\phi}_{n-1}^L(x_0), \; n \geqslant 1, \tag{37}$$

with boundary conditions $\tilde{\phi}_0^L(x_{\rm thr}) = 1$ and $\tilde{\phi}_n^L(x_{\rm thr}) = 0$ for n $\geqslant 1$. In all cases, a second boundary condition is necessary for these second order ordinary differential equations; as usual, bounded solutions at $x_0 \to -\infty$ are required.

3. Explicit solutions

3.1. FPT statistics for the Wiener process

The Wiener process is defined by the potential $U(x) = -\mu x$, where $\mu > 0$ guarantees threshold crossing. The associated Langevin equation with additive time-dependent exponential drift is

$$\frac{dx}{dt} = \mu + \frac{\epsilon}{\tau_d} e^{-(t-t_0)/\tau_d} + \sqrt{2D}\, \xi(t). \tag{38}$$

This is the simplest system for the kinds of diffusion processes we are considering and it has already been solved in [52, 53]. The formulation of the FPT problem in these works is equivalent to the derivation presented here, although in this article we have managed to extend it to a general context, without explicit knowledge of the survival probability.

The solution to equations (36) and (37) for this particular potential read

$$\tilde{\phi}_0^L(x_0; s) = \exp\left\{\frac{(x_{thr} - x_0)}{2D}\left[\mu - \sqrt{\mu^2 + 4Ds}\right]\right\}, \tag{39}$$

$$\tilde{\phi}_n^L(x_0; s) = -\frac{\left[\mu - \sqrt{\mu^2 + 4Ds}\right]}{2D} \times \sum_{k=0}^{n} b_{n,k}(s) \exp\left\{\frac{(x_{thr} - x_0)}{2D}\left[\mu - \sqrt{\mu^2 + 4D(s + k/\tau_d)}\right]\right\}, \quad \text{for } n \geqslant 1, \tag{40}$$

where the coefficients are given by the recursive scheme,

$$b_{n,k}(s) = -\frac{b_{n-1,k}(s)}{n-k} \frac{\left[\mu - \sqrt{\mu^2 + 4D(s + k/\tau_d)}\right]}{2D}, \quad \text{for } k = 0, \ldots, n-1, \tag{41}$$

$$b_{n,n}(s) = -\sum_{k=0}^{n-1} b_{n,k}(s), \tag{42}$$

starting from $b_{1,0}(s) = 1$ and $b_{1,1}(s) = -1$. As shown in [53], it can be shown by mathematical induction that these expressions satisfy equations (36) and (37), for $U'(x_0) = -\mu$.

3.2. FPT statistics for the Ornstein–Uhlenbeck process

The potential for the Ornstein–Uhlenbeck process is given by $U(x) = -\mu x + \frac{1}{2} x^2/\tau_m$, where the time constant τ_m characterizes the relaxation process towards the equilibrium point, $x_{eq} = \mu\, \tau_m$, for noise-free dynamics without a threshold. Alternatively, τ_m sets the time constant of the exponential autocorrelation function of this process. The presence of the threshold divides the behavior of the system according to the driving force μ. In the supra-threshold regime (also denoted stimulus-driven), $\mu > x_{thr}/\tau_m$, whenever the particle is released at $x_0 < x_{thr}$, it reaches the threshold in a finite time. In contrast, in the sub-threshold regime (or noise-driven), $\mu < x_{thr}/\tau_m$, the particle cannot reach the threshold unless assisted by noise. In the special case $\mu = x_{thr}/\tau_m$, the particle hits the threshold in an infinite time. When supplemented by the time-dependent exponential drift, the associated Langevin equation reads

$$\frac{dx}{dt} = \mu - \frac{x}{\tau_m} + \frac{\epsilon}{\tau_d} e^{-(t-t_0)/\tau_d} + \sqrt{2D}\, \xi(t). \tag{43}$$

3.2.1. Zeroth-order density function. The density function of the FPT for the unperturbed system, $\phi_0(x_0; \tau)$, can be obtained from the inverse Laplace transform of the solution to equation (36) for this particular potential; in detail,

$$\frac{d^2\tilde{\phi}_0^L}{dx_0^2} + \left(\frac{\mu}{D} - \frac{x_0}{\tau_m D}\right)\frac{d\tilde{\phi}_0^L}{dx_0} - \frac{s}{D}\,\tilde{\phi}_0^L = 0. \quad (44)$$

It can be shown that, with the change of variable

$$z = \sqrt{\frac{\tau_m}{D}}\left(\mu - \frac{x_0}{\tau_m}\right), \quad (45)$$

the solution can be expressed as [55–57]

$$\tilde{\phi}_0^L(x_0; s) = e^{z^2/4}\, u_0(z; s), \quad (46)$$

where $u_0(z; s)$ satisfies

$$\frac{d^2u_0}{dz^2} + \left(-\tau_m\, s + \frac{1}{2} - \frac{1}{4}z^2\right)u_0 = 0. \quad (47)$$

The general solution to this homogeneous equation reads

$$u_0(z; s) = c_1\, \mathcal{D}_{-\tau_m s}(z) + c_2\, \mathcal{D}_{-\tau_m s}(-z), \quad (48)$$

where $\mathcal{D}_\nu(z)$ are the parabolic cylinder functions according to Whittaker's notation [58]. Given that $\mathcal{D}_{-\tau_m s}(-z)$ diverges at $z \to \infty$, well-behaved solutions require that $c_2 = 0$. Note that because of the transformation, the new domain is from z_{thr} to ∞, where $z_{thr} = \sqrt{\tau_m/D}\,(\mu - x_{thr}/\tau_m)$. In virtue of the boundary condition at the threshold, $\tilde{\phi}_0^L(x_{thr}) = 1$, it is straightforward to show that

$$u_0(z; s) = \frac{e^{-z_{thr}^2/4}}{\mathcal{D}_{-\tau_m s}(z_{thr})}\,\mathcal{D}_{-\tau_m s}(z). \quad (49)$$

Equivalently,

$$\tilde{\phi}_0^L(x_0; s) = e^{-\frac{\tau_m}{4D}\left[\left(\mu - \frac{x_{thr}}{\tau_m}\right)^2 - \left(\mu - \frac{x_0}{\tau_m}\right)^2\right]}\,\frac{\mathcal{D}_{-\tau_m s}\left[\sqrt{\frac{\tau_m}{D}}\left(\mu - \frac{x_0}{\tau_m}\right)\right]}{\mathcal{D}_{-\tau_m s}\left[\sqrt{\frac{\tau_m}{D}}\left(\mu - \frac{x_{thr}}{\tau_m}\right)\right]}. \quad (50)$$

3.2.2. Higher-order density functions. According to equation (37), the Laplace transform of higher-order density functions, $\tilde{\phi}_n^L(x_0; s)$, for the Ornstein–Uhlenbeck process satisfies

$$\frac{d^2\tilde{\phi}_n^L}{dx_0^2} + \left(\frac{\mu}{D} - \frac{x_0}{\tau_m D}\right)\frac{d\tilde{\phi}_n^L}{dx_0} - \frac{(s + n/\tau_d)}{D}\,\tilde{\phi}_n^L = -\frac{1}{\tau_d D}\frac{d\tilde{\phi}_{n-1}^L}{dx_0}, \quad n \geqslant 1. \quad (51)$$

In terms of the variable z, defined by equation (45), it is easy to show that all functions can be written as

$$\tilde{\phi}_n^L(x_0; s) = e^{z^2/4}\, u_n(z; s), \quad (52)$$

where $u_n(z; s)$, for $n \geqslant 1$, is governed by

$$\frac{d^2u_n}{dz^2} + \left[-\tau_m\left(s + \frac{n}{\tau_d}\right) + \frac{1}{2} - \frac{1}{4}z^2\right]u_n = \frac{1}{\tau_d}\sqrt{\frac{\tau_m}{D}}\left(\frac{1}{2}\, z\, u_{n-1} + \frac{du_{n-1}}{dz}\right), \quad (53)$$

and the boundary condition at the transformed threshold is $u_n(z_{thr}; s) = 0$.

Next, we prove by mathematical induction that for $\tau_\mathrm{m} \neq \tau_\mathrm{d}$, the solution to equation (53) reads

$$u_n(z;\, s) = \sum_{k=0}^{n} b_{n,k}(s)\, \mathcal{D}_{-\tau_\mathrm{m}[s+(n-k)/\tau_\mathrm{m}+k/\tau_\mathrm{d}]}(z), \tag{54}$$

where the coefficients are given by the recursive structure,

$$b_{n,k}(s) = \frac{\left[s + (n-1-k)/\tau_\mathrm{m} + k/\tau_\mathrm{d}\right]}{(n-k)} \frac{\sqrt{\tau_\mathrm{m}/D}}{\left(1 - \tau_\mathrm{d}/\tau_\mathrm{m}\right)}\, b_{n-1,k}(s), \quad \text{for } k = 0,\ldots, n-1, \tag{55}$$

$$b_{n,n}(s) = -\frac{1}{\mathcal{D}_{-\tau_\mathrm{m}(s+n/\tau_\mathrm{d})}(z_\mathrm{thr})} \sum_{k=0}^{n-1} b_{n,k}(s)\, \mathcal{D}_{-\tau_\mathrm{m}[s+(n-k)/\tau_\mathrm{m}+k/\tau_\mathrm{d}]}(z_\mathrm{thr}), \tag{56}$$

starting from

$$b_{1,0}(s) = \frac{\sqrt{\tau_\mathrm{m}/D}}{\left(1 - \tau_\mathrm{d}/\tau_\mathrm{m}\right)} \frac{\mathrm{e}^{-z_\mathrm{thr}^2/4}}{\mathcal{D}_{-\tau_\mathrm{m}s}(z_\mathrm{thr})}\, s \tag{57}$$

$$b_{1,1}(s) = -\frac{\sqrt{\tau_\mathrm{m}/D}}{\left(1 - \tau_\mathrm{d}/\tau_\mathrm{m}\right)} \frac{\mathrm{e}^{-z_\mathrm{thr}^2/4}}{\mathcal{D}_{-\tau_\mathrm{m}s}(z_\mathrm{thr})} \frac{\mathcal{D}_{-\tau_\mathrm{m}(s+1/\tau_\mathrm{m})}(z_\mathrm{thr})}{\mathcal{D}_{-\tau_\mathrm{m}(s+1/\tau_\mathrm{d})}(z_\mathrm{thr})}\, s. \tag{58}$$

Assuming that the nth-order function is given by equation (54), according to equation (53) the $(n+1)$ th-order function should satisfy

$$\frac{\mathrm{d}^2 u_{n+1}}{\mathrm{d}z^2} + \left\{-\tau_\mathrm{m}\left[s + \frac{(n+1)}{\tau_\mathrm{d}}\right] + \frac{1}{2} - \frac{1}{4}z^2\right\} u_{n+1} = \frac{1}{\tau_\mathrm{d}} \sqrt{\frac{\tau_\mathrm{m}}{D}} \times \sum_{k=0}^{n} b_{n,k}(s) \left\{\frac{1}{2}\, z\, \mathcal{D}_{-\tau_\mathrm{m}[s+(n-k)/\tau_\mathrm{m}+k/\tau_\mathrm{d}]}(z) + \frac{\mathrm{d}\mathcal{D}_{-\tau_\mathrm{m}[s+(n-k)/\tau_\mathrm{m}+k/\tau_\mathrm{d}]}(z)}{\mathrm{d}z}\right\}. \tag{59}$$

From the recurrence relationships that Weber parabolic cylinder functions satisfy [58], it is easy to show that

$$\frac{\mathrm{d}\mathcal{D}_\nu(z)}{\mathrm{d}z} + \frac{1}{2}\, z\, \mathcal{D}_\nu(z) = \nu\, \mathcal{D}_{\nu-1}(z), \tag{60}$$

and, therefore, the forcing term in equation (59) simplifies to

$$\frac{\mathrm{d}^2 u_{n+1}}{\mathrm{d}z^2} + \left\{-\tau_\mathrm{m}\left[s + \frac{(n+1)}{\tau_\mathrm{d}}\right] + \frac{1}{2} - \frac{1}{4}z^2\right\} u_{n+1} = -\frac{\tau_\mathrm{m}}{\tau_\mathrm{d}} \sqrt{\frac{\tau_\mathrm{m}}{D}} \times \sum_{k=0}^{n} b_{n,k}(s) \left[s + \frac{(n-k)}{\tau_\mathrm{m}} + \frac{k}{\tau_\mathrm{d}}\right] \mathcal{D}_{-\tau_\mathrm{m}[s+(n+1-k)/\tau_\mathrm{m}+k/\tau_\mathrm{d}]}(z). \tag{61}$$

The solution to the homogeneous part of this equation is given by an analogous expression to equation (48),

$$u_{n+1}^{\mathrm{hom.}}(z;\, s) = c_1\, \mathcal{D}_{-\tau_\mathrm{m}[s+(n+1)/\tau_\mathrm{d}]}(z) + c_2\, \mathcal{D}_{-\tau_\mathrm{m}[s+(n+1)/\tau_\mathrm{d}]}(-z), \tag{62}$$

whereas a particular solution is

$$u_{n+1}^{\text{part.}}(z;\, s) = \frac{\sqrt{\tau_{\rm m}/D}}{\left(1 - \tau_{\rm d}/\tau_{\rm m}\right)} \sum_{k=0}^{n} \frac{\left[s + (n-k)/\tau_{\rm m} + k/\tau_{\rm d}\right]}{(n+1-k)}\; b_{n,k}(s) \times \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1-k)/\tau_{\rm m}+k/\tau_{\rm d}\right]}(z). \tag{63}$$

The recursive structure of the coefficients is implicitly defined in equation (63) and agrees to equation (55). Therefore, the general solution $u_{n+1}(z;\, s) = u_{n+1}^{\text{hom.}}(z;\, s) + u_{n+1}^{\text{part.}}(z;\, s)$ can be expressed as

$$u_{n+1}(z;\, s) = \sum_{k=0}^{n} b_{n+1,k}(s)\, \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1-k)/\tau_{\rm m}+k/\tau_{\rm d}\right]}(z) + c_1\; \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1)/\tau_{\rm d}\right]}(z) + c_2\; \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1)/\tau_{\rm d}\right]}(-z). \tag{64}$$

As before, an appropriate behavior at $z \to -\infty$ implies that $c_2 = 0$, and the evaluation of the boundary condition, $u_{n+1}(z_{\rm thr};\, s) = 0$, determines c_1. Taking into account the definition given in equation (56), the $(n+1)$ th-order function reads

$$\begin{aligned} u_{n+1}(z;\, s) &= \sum_{k=0}^{n} b_{n+1,k}(s)\, \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1-k)/\tau_{\rm m}+k/\tau_{\rm d}\right]}(z) \\ &\quad + b_{n+1,n+1}(s)\; \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1)/\tau_{\rm d}\right]}(z), \\ &= \sum_{k=0}^{n+1} b_{n+1,k}(s)\; \mathcal{D}_{-\tau_{\rm m}\left[s+(n+1-k)/\tau_{\rm m}+k/\tau_{\rm d}\right]}(z), \end{aligned} \tag{65}$$

which clearly satisfies equation (54) for $(n+1)$. Therefore, as far as equation (54) is true for the nth-order function, it holds for the following order, where coefficients are related by equations (55) and (56).

The proof is completed by observing that the first-order function $u_1(z;\, s)$ belongs to the family described by equation (54). According to equation (53) and taking into account the solution for the zeroth-order function, equation (49), this function satisfies

$$\frac{{\rm d}^2 u_1}{{\rm d}z^2} + \left[-\tau_{\rm m}\left(s + \frac{1}{\tau_{\rm d}}\right) + \frac{1}{2} - \frac{1}{4}z^2\right] u_1 = -\frac{\tau_{\rm m}}{\tau_{\rm d}} \sqrt{\frac{\tau_{\rm m}}{D}}\, \frac{{\rm e}^{-z_{\rm thr}^2/4}}{\mathcal{D}_{-\tau_{\rm m} s}(z_{\rm thr})}\, s\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm m})}(z), \tag{66}$$

where we have used the recurrence relationship given by equation (60). The general solution to this equation is

$$u_1(z;\, s) = c_1\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm d})}(z) + c_2\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm d})}(-z) + \frac{\sqrt{\tau_{\rm m}/D}}{\left(1 - \tau_{\rm d}/\tau_{\rm m}\right)}\, \frac{{\rm e}^{-z_{\rm thr}^2/4}}{\mathcal{D}_{-\tau_{\rm m} s}(z_{\rm thr})}\, s\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm m})}(z). \tag{67}$$

Since $c_2 = 0$ for bounded solutions and c_1 is determined from the evaluation of the boundary condition, $u_1(z_{\rm thr};\, s) = 0$, the first-order function is explicitly given by

$$u_1(z;\, s) = \frac{\sqrt{\tau_{\rm m}/D}}{\left(1 - \tau_{\rm d}/\tau_{\rm m}\right)} \frac{{\rm e}^{-z_{\rm thr}^2/4}}{\mathcal{D}_{-\tau_{\rm m}s}(z_{\rm thr})}\, s\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm m})}(z) - \frac{\sqrt{\tau_{\rm m}/D}}{\left(1 - \tau_{\rm d}/\tau_{\rm m}\right)} \frac{{\rm e}^{-z_{\rm thr}^2/4}}{\mathcal{D}_{-\tau_{\rm m}s}(z_{\rm thr})} \frac{\mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm m})}(z_{\rm thr})}{\mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm d})}(z_{\rm thr})}\, s\, \mathcal{D}_{-\tau_{\rm m}(s+1/\tau_{\rm d})}(z), \tag{68}$$

which can be expressed according to equation (54), with coefficients given by equations (57) and (58). This step ends the demonstration by mathematical induction of the series solution to the FPT density function, given by equations (52) and (54) in the transformed variable z with coefficients defined by equations (55)–(58).

For completeness, the recursive solution for the special case of the Ornstein–Uhlenbeck process with $\tau_{\rm m} = \tau_{\rm d}$ is given in the Appendix.

3.3. Other potentials

The survival probability and FPT statistics for a system driven by an exponential time-dependent drift with an arbitrary potential can be formally obtained in a recursive scheme, whenever the Green's function of equation (37) exists. This function is practically the same as that of the unperturbed system, equation (36), so essentially the FPT problem for the time-inhomogeneous setup is as analytically tractable as for the unperturbed case. The procedure is exemplified in the Appendix, for the case of the Ornstein–Uhlenbeck process with $\tau_{\rm m} = \tau_{\rm d}$.

4. Comparison to numerical simulations

As the solution we have found for the present FPT problem is given in terms of a series, we need to confirm its convergence or resort to numerical simulations to test its validity. We did not come to any general conclusions about the domain of convergence in the parameter space, and so here we have exemplified the usefulness of our approach by taking several cases spanning different regimes, for those systems for which we have found explicit solutions. For the Wiener process, we refer the reader to [53], where we have shown that the series solution is valid in the prototypical case corresponding to the supra-threshold regime, as it provides an excellent description far beyond the linear perturbative scenario. For the Ornstein–Uhlenbeck process, a number of parameters is available: $\tau_{\rm m}$, $x_{\rm thr}$, x_0, μ, D, $\tau_{\rm d}$, and ϵ. However, the exact values of $x_{\rm thr}$ and x_0 do not add any complexity to the model, and $\tau_{\rm m}$ sets the timescale of the dynamics. Therefore, there are three main parameters to explore: μ, D, and $\tau_{\rm d}$, whereas ϵ controls the intensity of the superimposed time-dependent drift.

Given our interest in neuronal adaptation (see section 1), we focus on the correspondence between the Ornstein–Uhlenbeck process and the leaky integrate-and-fire neuron model to define the typical parameters. In this model, x is the transmembrane voltage; the input derived from the potential, $-U'(x)$, represents external driving as well as currents flowing through specific (leaky) membrane channels, and the superimposed exponential temporal drift corresponds to an adaptation current. Without stimulation, voltage decays to the resting potential, x_0, whereas when inputs drive the neuron across the threshold, $x_{\rm thr}$, a spike is declared and the voltage is reset to a starting point, here assumed to be equal to x_0. The specific problem of neuronal adaptation also includes a history-dependent process (see section 5 for further discussion), not included here. By redefining $(x - x_0)/x_{\rm thr} \to x$, the new dimensionless voltage x starts at $x_0 = 0$ and the FTP problem corresponds to reach the threshold $x_{\rm thr} = 1$. On the other hand, the temporal scale is set by $\tau_{\rm m}$, here assumed to be $\tau_{\rm m} = 10$ time units (ms), in agreement with the experimental values [40, 41]. All parameter values explored here have to be compared to this particular τ_m; otherwise, an adimensionalization procedure can be used. The remaining parameters are used to explore the convergence of the series solution in different cases. As mentioned in section 3.2, different dynamical regimes can be defined according to the intensity of the constant drift, μ. In turn, the intensity of the noise, D, essentially modulates the dispersion of the FPT distribution. Once the set of parameters to examine has been defined, numerical FPT distributions are obtained from the first-hitting times of the system evolving according to the Langevin equation that governs its dynamics, equation (43).

Explicit analytical results are given in the Laplace domain—the zeroth-order by equation (50) and higher order terms by equations (52) and (54); then numerical inversion is required to transform them into the temporal domain. In detail, we performed a standard numerical integration (function NIntegrate in the Mathematica package) between proper limits in the imaginary axis, according to the definition of the inverse Laplace transform with a real integration variable,

$$f(\tau) = \frac{1}{2\pi} \int_{-j\omega}^{+j\omega} \tilde{f}^{L}(j\omega)\, e^{j\omega\tau}\, d\omega, \tag{69}$$

with ω properly chosen to represent infinity. According to the integration parameters and the function being inverse transformed, numerical instabilities not associated with the validity of the series method itself may arise. However, in all the cases presented here, the analytical results in the temporal domain were consistent for different large ω limits and numerical parameters. In figure 1, the FPT statistics in the sub/supra-threshold regimes, with low/high noise intensities, and different strengths of time-dependent drift are shown. In all cases, the time constant of the exponential drift τ_d is set to 100 time units (ms). As observed, the series solution up to a certain order N, represented by the thin yellow lines, properly describes the FPT distributions obtained from the numerical simulations (stair-like colored histograms). However, different parameter combinations require a different N to converge. In general, when noise intensity is reduced, the FPT distribution becomes more sharply peaked (or distorted) in comparison to the unperturbed case, and the order of convergence increases concomitantly. This can be noticed in figures 1(a) and 1(c), where the noise intensity has been manipulated in a generic sub-threshold regime, or in figures 1(b) and 1(d) in a general supra-threshold condition. Naturally, larger amplitudes of time-dependent drift require more terms to be considered in the series expansion to converge to a final distribution, supposing the parameters are within the radius of convergence. This increase in the number of terms may affect convergence in the temporal domain—regardless of the radius of convergence of the series itself—because of the amplification of numerical errors and/or instabilities when a specific procedure with a given set of numerical parameters is used to inverse Laplace transform functions.

As the time constant of the time-dependent exponential drift decreases, the series solution requires more higher order terms in order to become accurate. This general behavior is depicted in figure 2, where the theoretical series solution (thin yellow lines) correctly represents the FPT distributions obtained from numerical simulations (stair-like colored histograms), for positive as well as negative intensities ϵ (figure 2(a) and 2(b), respectively) for different time constants τ_d. According to the general expression for the higher order terms in the series solution, equations (52) and (54), the coefficients weighting individual contributions for a given term, equations (55) and (56), are extremely sensitive to the ratio between extrinsic and intrinsic timescales, τ_d/τ_m. Given this dependence (and assuming that convergence exists), the order of convergence of the series solution should increase as $\tau_d/\tau_m \to 1$. In the examples analyzed here, convergent behavior was observed for

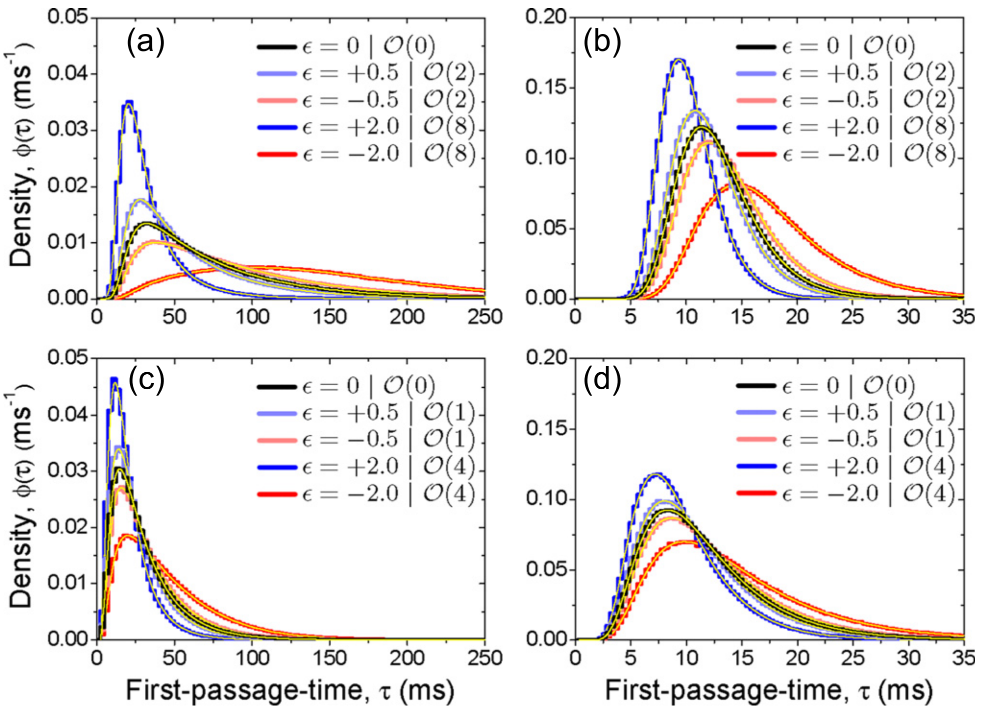

Figure 1. Comparison between the series solution for the FPT density function and numerical results for different cases of the Ornstein–Uhlenbeck process. (a) Low noise sub-threshold regime. (b) Low noise supra-threshold regime. (c) High noise sub-threshold regime. (d) High noise supra-threshold regime. In all cases, $x_0 = 0$, $x_{\mathrm{thr}} = 1$, $\tau_{\mathrm{m}} = 10$ ms, and $\tau_{\mathrm{d}} = 100$ ms. Different regimes are defined by $\mu = 0.075\ \mathrm{ms}^{-1}$ (sub-threshold), $\mu = 0.1333\ \mathrm{ms}^{-1}$ (supra-threshold), $D = 0.0025\ \mathrm{ms}^{-1}$ (low noise), and $D = 0.01\ \mathrm{ms}^{-1}$ (high noise). FPT distributions obtained from the numerical simulation of equation (43) for different intensities of the time-dependent exponential drift are shown by thick stair-like colored lines, labeled in the upper-right hand part of each panel: blue, light blue, black, light red, and red correspond to $\epsilon = +2.0, +0.5, 0, -0.5, -2.0$, respectively. The analytical expression, equation (32), obtained from the numerical inverse Laplace transform of the explicit solution, equation (50) for the unperturbed density, and equations (52) and (54) for higher order terms, up to the order N indicated for each intensity, $\mathcal{O}(N)$, is represented as a thin yellow line. In all cases, the analytical results excellently describe the FPT statistics obtained from numerical simulations.

consecutive terms in the series solution as this limit was reached. The special case $\tau_{\mathrm{m}} = \tau_{\mathrm{d}}$ cannot be described by the previous formulae, and a Green's function approach has been taken (see Appendix). On the other hand, as the time constant approaches zero, $\tau_{\mathrm{d}} \to 0$, the superimposed time-dependent exponential drift diverges and the system effectively corresponds to an unperturbed case with a shift in the initial condition [52]. In this limit, according to the value of ϵ, the FTP problem will be well-posed only when this initial condition is below the threshold.

The series solution for the FPT density function, equation (32), is explicitly given in terms of its Laplace transform: the zeroth-order by equation (50), and higher order terms by equations (52) and (54). Without performing any inverse transformation (and, therefore,

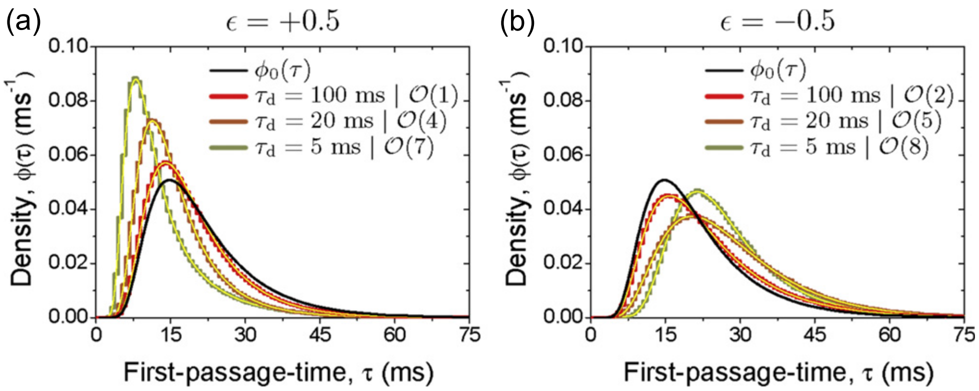

Figure 2. Comparison between the analytical and numerical results of the FPT statistics for different timescales defining time-dependent drift. Relatively moderate positive, $\epsilon = +0.5$, and negative, $\epsilon = -0.5$, intensities are considered in (a) and (b), respectively. FPT distributions for different time constants τ_d, obtained from numerical simulations are shown by different stair-like colored lines. Analytical results up to the order N indicated in the upper-right hand part of each panel, $\mathcal{O}(N)$, are represented by thin yellow lines. As observed, the agreement between the numerical results and theoretical expressions is excellent in all cases, but the order of convergence may differ substantially. Parameters governing the dynamics are $x_0 = 0$, $x_{\text{thr}} = 1$, $\tau_m = 10$ ms, $\mu = 0.100$ ms^{-1}, and $D = 0.005$ ms^{-1}.

avoiding all the numerical artifacts of numerical implementation), this result can be used to obtain important properties of the FPT distribution. In particular, its moments are given by [52, 53]

$$\langle \tau^k \rangle = \int_0^\infty \phi(\tau)\, \tau^k \, \mathrm{d}\tau = (-1)^k \left. \frac{\mathrm{d}^k \tilde{\phi}^L(s)}{\mathrm{d}s^k} \right|_{s=0}. \tag{70}$$

Since the series solution for $\phi(\tau)$ is a linear combination of different functions, the preceding relationship can be written as

$$\langle \tau^k \rangle = \sum_{n=0}^{\infty} \epsilon^n \, \langle \tau^k \rangle_{\phi_n}, \tag{71}$$

where

$$\langle \tau^k \rangle_{\phi_n} = (-1)^k \left. \frac{\mathrm{d}^k \tilde{\phi}_n^L(s)}{\mathrm{d}s^k} \right|_{s=0}. \tag{72}$$

According to equations (71) and (72), the evaluation of the moments is straightforward in the Laplace domain. In figure 3 we show the behavior of the first two moments for the intermediate case analyzed in figure 2, as a function of a wide range of the intensity ϵ. As observed, as the absolute value of ϵ increases, the order N considered in the series has to increase as well to account for the numerical results.

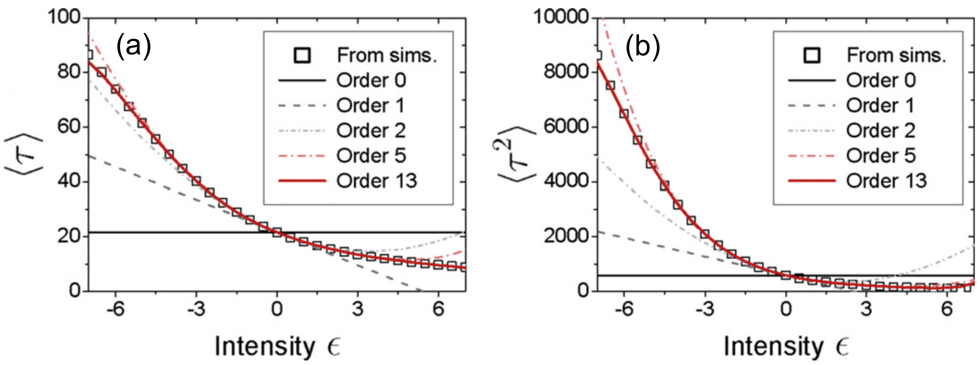

Figure 3. Comparison between analytical and numerical results for (a) the first and (b) the second moment of the FPT distribution, as a function of the intensity of time-dependent drift ϵ. The symbols represent the average of the numerical results, whereas the lines correspond to the series expression for the kth moment truncated at the order N indicated in the inset, $\langle \tau^k \rangle = \sum_{n=0}^{N} \epsilon^n \langle \tau^k \rangle_{\phi_n}$. The remaining parameters are $x_0 = 0$, $x_{\mathrm{thr}} = 1$, $\tau_{\mathrm{m}} = 10$ ms, $\tau_{\mathrm{d}} = 100$ ms,, $\mu = 0.100$ ms^{-1}, and $D = 0.005$ ms^{-1}.

5. Final remarks and discussion

In this work, we have studied the survival probability and the FPT statistics of a Brownian particle whose dynamics are governed by a generic unidimensional potential and a superimposed exponential time-dependent drift, equation (10), with a fixed threshold setting the limit where the FPT is defined. Based on the backward FP description, we first derived the diffusion equation of the survival probability from the backward state, equation (12), and then proposed a series solution in powers of the intensity of the time-dependent drift contribution, equation (13). With this procedure, the preceding diffusion equation translates into a system of infinite simpler equations, where each one defines the behavior of each term in the proposed series in a recursive scheme, equations (15) and (16). The particular mathematical structure of the forcing term in these equations—defined by the time-dependent exponential drift— enables a simpler representation in the Laplace domain, equations (22) and (30). From the survival probability, the FPT statistics are readily obtained, which naturally inherit the series structure, equation (32), where each term is governed by equations (36) or (37). The general derivation of this series solution agrees with the explicit solution we found previously for the Wiener process [53]. However, since the present approach is applicable to any unidimensional potential, we explicitly solved the series solution for the FPT statistics of an Ornstein–Uhlenbeck process (with the superimposed exponential time-dependent field), which is mathematically much more challenging than the Wiener process. Given that the convergence properties of the proposed series solution remained unknown, several cases were defined to numerically test the usefulness of the approach and the solution found. In all cases, the analytical and numerical results are in good agreement as long as the number of terms included in the series is large enough.

As discussed in section 1, different neuron models have a direct correspondence to different drift-diffusion Brownian motions. In particular, the Wiener and the Ornstein–Uhlenbeck processes correspond to the perfect and leaky IF neuron models, respectively. In all IF models, variable x is the transmembrane voltage of a spiking neuron; the drift derived from the potential, $-U'(x)$, corresponds to the external as well as the internal sub-threshold signals integrated by Langevin dynamics, equation (1), which model the capacitance properties of the cellular membrane. Additive Gaussian white noise is included in order to model randomness arising from different sources (random channel opening and closing, stochastic synaptic transmission, etc), with minimal mathematical complexity. The FPT problem results from the procedure used to declare a spike. Whenever the voltage reaches the threshold $x_{\rm thr}$, the voltage dynamics are no longer governed by the simple Langevin equation, equation (1), and a largely stereotyped waveform is generated by other mechanisms (not included in IF models). Therefore, to a great extent, the exact time at which this event was produced for the first time is the only meaningful information to be transmitted to downstream neurons. Once this event happens, there are mechanisms that restore the membrane potential to a reset potential x_0 (here also coincident to the resting potential), and a new sub-threshold integration cycle is launched. The superimposed time-dependent exponential drift considered here mimics the temporal evolution of a separate process of neuronal adaptation, which naturally also influences spike time statistics. This adaptation current not only modifies the FPT statistics of the homogeneous case (for example, the pure Wiener or Ornstein–Uhlenbeck processes or, equivalently, the adaptation-free perfect and leaky IF models), but also couples subsequent events, creating negative correlations [49, 50]. The analysis of successive interspike intervals and the emergence of these correlations can be described by a hidden Markov model [49], in which correlations arise from the fire-and-reset rule coupling the subsequent initial state of the adaptation current with the preceding interspike interval. In this description, the FPT statistics of the temporally inhomogeneous process considered here provide the relationship between the hidden variable (the initial state of the adaptation current) and the observable (the interspike intervals).

Since both Wiener and Ornstein–Uhlenbeck processes as well as generic drift-diffusion models are ubiquitous in describing different phenomena, the results obtained here on survival probability and FPT distribution will be of interest in other settings where an additive state-independent temporal relaxation process is being developed as the particle diffuses.

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Appendix

FPT statistics for the Ornstein–Uhlenbeck process, with $\tau_{\rm m} = \tau_{\rm d}$

Naturally, the equation governing the behavior of the unperturbed system, equation (36), does not depend on the timescale of the exponential time-dependent drift, $\tau_{\rm d}$. On the other hand, when $\tau_{\rm m} = \tau_{\rm d}$, equation (37) applied to the Ornstein–Uhlenbeck case, equation (51), reads

$$\frac{{\rm d}^2\tilde{\phi}_n^L}{{\rm d}x_0^2} + \left(\frac{\mu}{D} - \frac{x_0}{\tau_{\rm m} D}\right)\frac{{\rm d}\tilde{\phi}_n^L}{{\rm d}x_0} - \frac{(s + n/\tau_{\rm m})}{D}\,\tilde{\phi}_n^L = -\frac{1}{\tau_{\rm m} D}\,\frac{{\rm d}\tilde{\phi}_{n-1}^L}{{\rm d}x_0},\quad n \geqslant 1. \tag{73}$$

Again, with the substitution $z = \sqrt{\tau_{\rm m}/D}\,(\mu - x_0/\tau_{\rm m})$ and proposing the functional structure given by equation (52), the preceding equation transforms to

$$\frac{{\rm d}^2 u_n}{{\rm d}z^2} + \left[-\tau_{\rm m}\left(s + \frac{n}{\tau_{\rm m}}\right) + \frac{1}{2} - \frac{1}{4}z^2\right]u_n = \frac{1}{\sqrt{\tau_{\rm m} D}}\left(\frac{1}{2}\,z\,u_{n-1} + \frac{{\rm d}u_{n-1}}{{\rm d}z}\right). \tag{74}$$

As before, the boundary conditions are $u_n(z_{\rm thr}) = 0$ and $u_n(z \to \infty)$ bounded, where dependence on the parameter s has been omitted for simplicity. The solution to this infinite set of equations can be recursively found as

$$u_n(z) = \int_{z_{\rm thr}}^{\infty} g_n\left(z, z'\right) \frac{1}{\sqrt{\tau_{\rm m} D}} \left[\frac{1}{2} z' \, u_{n-1}\left(z'\right) + \frac{{\rm d}u_{n-1}\left(z'\right)}{{\rm d}z'} \right] {\rm d}z', \qquad (75)$$

where $g_n(z, z')$ is the Green's function of equation (74), which is obtained as the solution to

$$\frac{\partial^2 g_n\left(z, z'\right)}{\partial z^2} + \left[-\tau_{\rm m} \left(s + \frac{n}{\tau_{\rm m}} \right) + \frac{1}{2} - \frac{1}{4} z^2 \right] g_n\left(z, z'\right) = \delta\left(z - z'\right), \qquad (76)$$

with the boundary conditions defined above. Explicitly, this function reads

$$g_n\left(z, z'\right) = \frac{1}{{\rm Den}\left(z'\right)} \begin{cases} \left[\mathcal{D}_\nu(z_{\rm thr})\, \mathcal{D}_\nu(-z) - \mathcal{D}_\nu(-z_{\rm thr})\, \mathcal{D}_\nu(z) \right] \mathcal{D}_\nu\left(z'\right), & \text{for } z < z', \\ \left[\mathcal{D}_\nu(z_{\rm thr})\, \mathcal{D}_\nu\left(-z'\right) - \mathcal{D}_\nu(-z_{\rm thr})\, \mathcal{D}_\nu\left(z'\right) \right] \mathcal{D}_\nu(z), & \text{for } z > z', \end{cases} \qquad (77)$$

where

$$\text{Den}\left(z'\right) = \frac{1}{\nu\, \mathcal{D}_\nu(z_{\rm thr}) \left[\mathcal{D}_\nu\left(-z'\right) \mathcal{D}_{\nu-1}\left(z'\right) + \mathcal{D}_\nu\left(z'\right) \mathcal{D}_{\nu-1}\left(-z'\right) \right]}, \qquad (78)$$

and the order n of the function $g_n(z, z')$ comes into the index $\nu = -\tau_{\rm m}(s + n/\tau_{\rm m})$ exclusively.

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