

Probability distributions for the run-and-tumble models with variable speed and tumbling rate

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Abstract In this paper we consider a telegraph equation with time-dependent coefficients, governing the persistent random walk of a particle moving on the line with a time-varying velocity $c(t)$ and changing direction at instants distributed according to a non-stationary Poisson distribution with rate $\lambda(t)$. We show that, under suitable assumptions, we are able to find the exact form of the probability distribution. We also consider the space-fractional counterpart of this model, finding the characteristic function of the related process. A conclusive discussion is devoted to the potential applications to run-and-tumble models.

Keywords Telegraph equation with time-dependent velocity, run-and-tumble models, exact marginal probability distribution

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1 Introduction

Many motile bacteria, such as the common *E.coli*, explore the environment performing run-and-tumble motion [5]. Helicoidal filaments, called flagella, powered by internal motors allow the cell to wander around: when flagella rotate counterclockwise

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(as seen from behind) the cell performs a straight line motion (*run*), while a clockwise flagellar rotation induces a random reorientation of the cell body (*tumble*). In the absence of external force fields or chemicals in the bacterial solution, the swim speed c and the rate λ at which swimmers change direction are assumed to be constant in time and space. In the idealized one-dimensional case the corresponding run-and-tumble equation of motion reduces to the usual telegrapher's equation [1–3, 22, 27, 32]

$$\frac{\partial^2 p}{\partial t^2} + 2\lambda \frac{\partial p}{\partial t} = c^2 \frac{\partial^2 p}{\partial x^2}. \quad (1)$$

However, in many interesting real situations swimmers' speed and tumbling rate can be spatial or time dependent quantities. Recent investigations have demonstrated that the speed of genetically engineered bacteria, expressing proteorhodopsin protein, can be tuned by modulating the intensity of an external light field [4, 12, 29–31]. In such a case one can have a direct control on the swimmers speed by simply applying a suitable external field. In particular, time-dependent external fields give rise to time variable swimmers speed. Recent investigations have also shown that, for some marine bacteria, there is a correlation between the speed and the reorientation frequency. More specifically one observe a linear relationship between the two quantities in the low-speed regime [28]. In such a case it is then appropriate to make the assumption of proportionality between λ and c .

Motivated by these interesting problems, in Section 2, we provide some general results regarding the telegraph equation with time-dependent parameters $c(t)$ and $\lambda(t)$. We then analyze the interesting case of proportionality between velocity and tumbling rate, reporting exact expressions for the probability distribution and the mean square displacement and discussing the long-time diffusive behavior for different choice of $c(t)$.

In Section 3 we generalize the above results to the case of the space-fractional telegraph equation with time-dependent velocity and rate. Indeed, in the recent literature space and time-fractional generalizations of the telegraph equations have attracted the interest of different authors, see for example [6, 10, 11, 15, 25, 26]. In [10] the relationship between space-time fractional telegraph equations and time-changed processes has been discussed. In the recent paper [23], Masoliver has introduced a fractional persistent random walk, whose probability law is governed by the space-time fractional telegraph equation. The physical motivation for this kind of generalization is strictly related to the analysis of sub- and super-diffusive processes, as well as the telegraph process leads to a ballistic process for short times (and a classical diffusive one for long times). We analyze here the space-fractional counterpart of the generalized telegraph equation studied in Section 2, finding the characteristic function of the non-homogeneous fractional telegraph process with varying velocity.

In a final section we interpret the obtained results in the context of run-and-tumble models with time-variable swimmers' speed. In particular, we consider genetically engineered *E.coli* bacteria whose dynamics is described by run-and-tumble models in which the value of the speed is controlled by an external field. We derive the equation of motion in some simple situations, such as the case of a sudden switch of external fields.

2 Non-homogeneous telegraph process with time-varying parameters

The telegraph process has attracted the interest of many researchers, starting from the seminal works of Goldstein [16] and Kac [19], being a relevant prototype of finite velocity random motion, whose probability law coincides with the fundamental solution of the telegraph equation. There is a wide literature about the applications and generalizations of the telegraph process, we refer to the recent monograph [21] for a complete review about this topic. We also observe that the telegraph equation, whose origin comes back to the classical equations of electromagnetism, has been also suggested by Davydov, Cattaneo and Vernotte as an alternative to the classical heat equation for diffusion processes with finite velocity of propagation, overcoming the so-called paradox of the infinite velocity of heat propagation (we refer to the classical review [18] and [15] about this topic).

A persistent random walk with a variable velocity is studied in [24], leading to a generalization of the telegraph process. As discussed in [24] and [32], in few special cases the explicit probability law of this generalized telegraph process can be found. Some results about telegraph process with space-varying velocity have been found in [14].

On the other hand, some recent studies have been devoted to a non-homogeneous version of the telegraph process, where the particle changes directions at times distributed according to a non-stationary Poisson distribution with rate $\lambda(t)$. An interesting case was considered by Iacus in [17] and more recently a special case related to the Euler–Poisson–Darboux equation has been considered in [13], see also [9]. Moreover, in [7], large deviations principles have been applied to the non-homogeneous telegraph process. More general and relevant models of finite velocity diffusion processes are the so-called Lévy walks, we refer for example to the recent review [33] about this topic.

Here we consider the persistent random walk of a particle moving on the line and switching from the time-varying velocity $c(t)$ to $-c(t)$ at times distributed according to a non-stationary Poisson distribution with rate $\lambda(t)$. Therefore, here we consider both the generalizations recently suggested in the literature and we show that, in a special case, this can help to find the explicit probability law. We assume that $c(t) \in L^1[0, t]$. According to the classical treatment of the two-direction persistent random walk given for example by Goldstein [16] (see also [24]), for the description of the position $X(t)$ of the particle at time $t > 0$, we use the probabilities

$$a(x, t)dx = P\{X(t) \in dx, V(t) = c(t)\}, \quad (2)$$

$$b(x, t)dx = P\{X(t) \in dx, V(t) = -c(t)\}, \quad (3)$$

satisfying the system of partial differential equations

$$\begin{cases} \frac{\partial a}{\partial t} = -c(t)\frac{\partial a}{\partial x} + \lambda(t)(b(x, t) - a(x, t)), \\ \frac{\partial b}{\partial t} = c(t)\frac{\partial b}{\partial x} + \lambda(t)(a(x, t) - b(x, t)), \end{cases} \quad (4)$$

subject to the initial conditions $a(x, 0) = b(x, 0) = \frac{1}{2}\delta(x - x_0)$. The functions $a(x, t)$ and $b(x, t)$ denote the probability density functions for the position of the

random walker at time $t > 0$ while moving respectively in the positive or negative x direction. These equations can be simply combined in a single equation for the total probability $p(x, t) = a(x, t) + b(x, t)$. Let us introduce the auxiliary function $w(x, t) = a(x, t) - b(x, t)$. By adding and subtracting the equations in (4), we obtain

$$\begin{cases} \frac{\partial p}{\partial t} = -c(t) \frac{\partial w}{\partial x}, \\ \frac{\partial w}{\partial t} = -c(t) \frac{\partial p}{\partial x} - 2\lambda(t)w, \end{cases} \quad (5)$$

and finally the following telegraph equation with time-varying coefficients

$$\frac{1}{c(t)} \frac{\partial}{\partial t} \frac{1}{c(t)} \frac{\partial p}{\partial t} + \frac{2\lambda(t)}{c^2(t)} \frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2}. \quad (6)$$

We observe that, from the physical point of view, in the context of the hyperbolic formulation of the heat wave propagation, equations (5) are formally equivalent to the heat balance equation with a time-dependent diffusivity coefficient coupled with a Cattaneo law with time-varying relaxation.

As pointed out by Masoliver and Weiss in [24], equations like (6) are generally difficult to be handled analytically. However, we observe that, taking $c(t) = c_0 w(t)$, by means of the change of variable (see also [32])

$$\tau = \int_0^t w(s) ds, \quad (7)$$

equation (6) is reduced to a simpler telegraph-type equation

$$\left[\frac{\partial^2}{\partial \tau^2} + 2\lambda_{\text{eff}}(\tau) \frac{\partial}{\partial \tau} \right] p(x, \tau) = c_0^2 \frac{\partial^2 p}{\partial x^2}, \quad (8)$$

where

$$\lambda_{\text{eff}}(\tau) = \frac{\lambda(t(\tau))}{w(t(\tau))}. \quad (9)$$

This is a general scheme that allows to find, in some cases, the explicit form of the probability law (see also the discussion in [32]).

We now consider in detail the case $\lambda_{\text{eff}} = \text{const.}$ (i.e. $\lambda(t) \sim \lambda_0 w(t)$) admitting an exact solution. This means that the rate of changes of directions follows the velocity-dependence in time. In this case we have that equation (6), by means of the change of variable (7), is reduced to

$$\left[\frac{\partial^2}{\partial \tau^2} + 2\lambda_0 \frac{\partial}{\partial \tau} \right] p(x, \tau) = c_0^2 \frac{\partial^2 p}{\partial x^2}, \quad (10)$$

corresponding to the classical telegraph equation with velocity c_0 and changing direction rate λ_0 .

Therefore, considering the initial conditions $p(x, 0) = \delta(x)$ and $\partial_\tau p(x, \tau)|_{\tau=0} = 0$ and going back to the variable t , we have that the absolutely continuous component

of the probability distribution of the non-homogeneous telegraph process, in this case is given by

$$P\{X(t) \in dx\} = dx \frac{e^{-\lambda_0 \int_0^t w(s)ds}}{2} \left[\frac{\lambda_0}{c_0} I_0 \left(\frac{\lambda_0}{c_0} \sqrt{\left(c_0 \int_0^t w(s)ds \right)^2 - x^2} \right) + \frac{1}{c_0 w(t)} \frac{\partial}{\partial t} I_0 \left(\frac{\lambda_0}{c_0} \sqrt{\left(c_0 \int_0^t w(s)ds \right)^2 - x^2} \right) \right], \quad |x| < \left(c_0 \int_0^t w(s)ds \right), \quad (11)$$

where

$$I_0(t) = \sum_{k=0}^{\infty} \left(\frac{t}{2} \right)^{2k} \frac{1}{k!^2}, \quad (12)$$

is a modified Bessel function. The component of the unconditional probability distribution that pertains to the probability of no-changes of direction according to the Poisson distribution with time-dependent rate $\lambda(t)$ is concentrated on the boundary $x = \pm \int_0^t c(s)ds$ and it is given by

$$P\left\{X(t) = \pm \int_0^t c(s)ds\right\} = \frac{e^{-\lambda_0 \int_0^t w(s)ds}}{2}. \quad (13)$$

Observe that, in the case $c(t) = c_0$ (i.e. $w(t) = 1$), we recover the probability distribution of the classical telegraph process with rate λ_0 .

An interesting quantity describing the spatial extent of the random motion is the mean square displacement r^2 , i.e. the second moment of the probability distribution (11):

$$r^2(t) = \frac{c_0^2}{2\lambda_0^2} \left[2\lambda_0 \int_0^t w(s)ds - 1 + e^{-2\lambda_0 \int_0^t w(s)ds} \right]. \quad (14)$$

The asymptotic behavior of r^2 , which is linear in t in the classical persistent random walk, now depends on the long time behavior of the velocity function $c(t) = c_0 w(t)$. We can distinguish different regimes. Assuming a power-law behavior of $w(t)$ at long time, $w(t) \sim t^{-\beta}$, we have the following cases:

– $\beta > 1$

The integral of w , i.e. $\tau(t)$, is finite for $t \rightarrow \infty$, resulting in a finite asymptotic mean square displacement, $r^2(t) \rightarrow \text{const}$. The motion is confined in a finite space domain whose boundaries are at $x_B = \pm \int_0^\infty c_0 w(t)dt$. A finite stationary probability distribution, given by (11) in the limit $t \rightarrow \infty$, exists.

– $\beta = 1$

In such a case we have logarithmic diffusion, $r^2(t) \sim \ln(t)$

– $0 < \beta < 1$

The mean square displacement grows as a power of time, $r^2(t) \sim t^\alpha$, with $\alpha = 1 - \beta < 1$. The random walk exhibits anomalous diffusion (subdiffusion).

– $\beta = 0$

In this case the asymptotic velocity is finite, resulting in a linear time dependence of the mean square displacement, $r^2(t) \sim t$ (normal diffusion).

– $\beta < 0$

The velocity grows with time and the random walk is superdiffusive, i.e. $r^2(t) \sim t^\alpha$, with $\alpha = 1 - \beta > 1$.

We can also observe that, assuming an exponential decay $w(t) \sim e^{-\nu t}$ a finite stationary probability distribution exists for $t \rightarrow +\infty$, while if $w(t)$ is a bounded function, the normal diffusive behaviour is recovered.

3 The space-fractional telegraph equation with time-varying coefficients

The space-fractional telegraph equation was firstly considered by Orsingher and Zhao in [26] and more recently studied by Masoliver in [23] in the context of the fractional generalization of the persistent random walk. The relationship between space-time fractional telegraph equations and time-changed processes have been obtained by D'Ovidio et al. [10]. We here consider the space-fractional telegraph equation with time-dependent rate and velocity

$$\frac{1}{c(t)} \frac{\partial}{\partial t} \frac{1}{c(t)} \frac{\partial p}{\partial t} + \frac{2\lambda(t)}{c^2(t)} \frac{\partial p}{\partial t} = \frac{\partial^{2\alpha} p}{\partial |x|^{2\alpha}}, \quad 0 < \alpha \leq 1. \quad (15)$$

The space-fractional derivative appearing in (15) is the Riesz derivative [20]

$$\frac{\partial^{2\alpha} f}{\partial |x|^{2\alpha}} = -\frac{1}{2 \cos \alpha \pi} \frac{1}{\Gamma(1 - 2\alpha)} \frac{d}{dx} \int_{-\infty}^{+\infty} \frac{f(z)}{|x - z|^{2\alpha}} dz, \quad \alpha \in (0, 1), \quad (16)$$

whose Fourier transform is given by (see e.g. [10] for details)

$$\mathcal{F} \left[\frac{\partial^{2\alpha} f}{\partial |x|^{2\alpha}} \right] (k) = -|k|^{2\alpha} \hat{f}(k), \quad (17)$$

where we denote by $\hat{f}(k)$ the Fourier transform of the function $f(x)$. We here consider in detail the space-fractional counterpart of the case considered in the previous section, i.e. by taking $c(t) = c_0 w(t)$ and the change of variable $\tau = \int_0^t w(s) ds$, we obtain the following equation

$$\frac{\partial^2 p}{\partial \tau^2} + 2\lambda_{\text{eff}}(\tau) \frac{\partial p}{\partial \tau} = c_0^2 \frac{\partial^{2\alpha} p}{\partial |x|^{2\alpha}}, \quad (18)$$

where $\lambda_{\text{eff}}(\tau) = \lambda(t(\tau))/w(t(\tau))$.

Considering the special case $\lambda(t) \sim \lambda_0 w(t)$, we can obtain the characteristic function of the non-homogeneous space-fractional telegraph process with time-varying velocity. Indeed, we obtain in the Fourier space

$$\frac{\partial^2 \hat{p}}{\partial \tau^2} + 2\lambda_0 \frac{\partial \hat{p}}{\partial \tau} = -c_0^2 |k|^{2\alpha} \hat{p}, \quad 0 < \alpha \leq 1. \quad (19)$$

Therefore, we obtain the characteristic function of the space-fractional telegraph process by means of simple calculations and going back to the original time variable,

$$\widehat{p}(k, t) = \frac{e^{-\lambda_0 \int_0^t w(s) ds}}{2} \left[\left(1 + \frac{\lambda_0}{\sqrt{\lambda_0^2 - c_0^2 |k|^{2\alpha}}} \right) e^{\sqrt{\lambda_0^2 - c_0^2 |k|^{2\alpha}} \left(\int_0^t w(s) ds \right)} + \left(1 - \frac{\lambda_0}{\sqrt{\lambda_0^2 - c_0^2 |k|^{2\alpha}}} \right) e^{-\sqrt{\lambda_0^2 - c_0^2 |k|^{2\alpha}} \left(\int_0^t w(s) ds \right)} \right]. \quad (20)$$

The problem to find the inverse Fourier transform of (20) seems to be solvable only in the case $\alpha = 1$ (that leads to the probability law of the classical telegraph process).

We can observe that the main features of the space-fractional telegraph process strongly differ from that of the classical telegraph process, since it has discontinuous sample paths and it does not preserve the finite velocity of propagation. Indeed, as it was shown by Orsingher and Zhao in [26], the random process related to the space-fractional telegraph equation describes the one-dimensional motion of a particle which moves forward and backward performing jumps of random amplitude. This is not surprising, since the appearance of the fractional Laplacian is related to non-locality and leads to almost surely discontinuous paths. On the other hand, this model is interesting in the context of the studies about fractional persistent random walk models, as fully discussed by Masoliver in [23].

4 Discussion: applications to run-and-tumble models

We now discuss how the obtained general results can be applied in the context of run-and-tumble models.

Let us first assume that the tumbling rate is constant, λ_0 . This is, for example, the case in which a time-dependent and spatially homogeneous external field induces a time-dependent speed $c(t)$ without changing tumbling processes in genetically engineered bacteria. In terms of the auxiliary variable τ the equation of motion turns out to be Eq. (8) with a time-dependent effective tumbling rate

$$\lambda_{\text{eff}}(\tau) = \frac{\lambda_0}{w(t(\tau))}. \quad (21)$$

A simple interesting case can be analyzed by considering a spatially uniform light field which is abruptly switched off at $t = 0$. One can assume that, due to finite time response of the internal processes inside the cell body, the swimmer speed exponentially relaxes towards zero

$$c(t) = c_0 \exp(-\gamma t), \quad (22)$$

where γ^{-1} is the relaxation time [4, 29]. In this case one has that

$$\lambda_{\text{eff}} = \frac{\lambda_0}{1 - \gamma \tau}, \quad (23)$$

leading to the partial differential equation

$$\left[\frac{\partial^2}{\partial \tau^2} + \frac{2\lambda_0}{1 - \gamma\tau} \frac{\partial}{\partial \tau} \right] p(x, \tau) = c_0^2 \frac{\partial^2 p}{\partial x^2}. \quad (24)$$

We observe that similar equations arise in the analysis of random flights in higher dimension, see for example [8].

As mentioned in the Introduction, for some bacteria it has been found that there is a proportionality between the speed and the reorientation frequency. The assumption $\lambda_{\text{eff}} = \text{const.}$, made in the second part of Section 2 and leading to the Eq. (10), is then appropriate for these systems and all the results found in this approximation apply to this case. It is still an open question to find, for other microorganisms, the relationship between tumbling rate and swim speed. For example, it would be interesting to investigate such a issue in the case of genetically engineered bacteria, for which one could control the bacterial speed by varying the external field and then measure the corresponding tumbling rate.

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