Aging dynamics of d−dimensional locally activated random walks

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Locally activated random walks are defined as random processes, whose dynamical parameters are modified upon visits to given activation sites. Such dynamics naturally emerge in living systems as varied as immune and cancer cells interacting with spatial heterogeneities in tissues, or, at larger scales, animals encountering local resources. At the theoretical level, these random walks provide an explicit construction of strongly non-Markovian and aging dynamics. We propose a general analytical framework to determine various statistical properties characterizing the position and dynamical parameters of the random walker on d-dimensional lattices. Our analysis applies in particular to both passive (diffusive) and active (run and tumble) dynamics, and quantifies the aging dynamics and potential trapping of the random walker; it finally identifies clear signatures of activated dynamics for potential use in experimental data.

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I. INTRODUCTION

Locally activated random walks (LARWs) are defined as stochastic processes that undergo changes in their dynamic characteristics when they encounter specific sites, called hereafter activation sites [1–3]. Such locally activated dynamics, where activation sites either accelerate or slow down the process, can be typically observed in living systems, such as cells navigating through tissues [4,5], or on a larger scale, when animals exploit local resources, or, on the contrary, visit infected areas [6,7]. For example, it has been observed that immune (dendritic) cells, whose function is to collect chemical signals (antigens) left by pathogens, switch from a slow, nonpersistent state to a fast and persistent state, which eventually helps triggering the specific immune response [4]. This switch occurs when a threshold amount of chemical signals has been collected, after many visits to antigen concentrated spots; the switch can also occur in absence of infection signals, when the cells have been mechanically confined, as happens when they randomly migrate through tight pores distributed throughout tissues [8].

At the theoretical level, a minimal description of such dynamics suggests to endow the random walker (RWer) of interest, whose position at time t will be hereafter denoted by $x(t)$, with an internal scalar variable $a(t)$—called activation hereafter—, which is a random variable controlled by the history of successive visits of the RWer to given activation sites up to t. In turn it is posited that the parameters ruling the dynamics of the RWer, typically its instantaneous speed or persistence, depend on a. This minimal choice makes the dynamics of the position $x(t)$ of a LARWer genuinely non-Markovian, because it depends on the past trajectory $\{x(t')\}_{t'\leqslant t}$, and aging, because the statistics of the activation $a(t)$ is typically nonstationary, e.g., depends on the observation time. Beyond the applications mentioned above, the class of LARWs thus provides an explicit microscopic construction of non-Markovian, aging stochastic processes with a broad range of adjustable dynamic and geometric properties, which, as we show below, can be quantified analytically. Related examples of non-Markovian RWs, in which the memory of the complete past trajectory determines the future evolution, comprise self-avoiding walks [9], true self-avoiding walkers [10–12], self-interacting RWs [1,13–20], and RWs with reinforcement such as the elephant walks [21–23].

So far, the analysis of LARWs has been restricted to the example of 1d Brownian dynamics, with a single point like activation site [2]. Because a given point in space is almost surely never visited by a Brownian RWer for $d \geqslant 2$, this early analysis is not suitable to generalizations to higher space dimensions; it also left aside the case of multiple activation sites, which are of obvious importance for practical applications. In addition, this model was limited to Brownian motion and thus parametrized by a single parameter—the diffusion coefficient $D(a)$. It thus does not cover the case of persistent RWs—typically parametrized by both their instantaneous speed and persistence, which are paradigmatic models of active particles, required in particular in the description of living systems as exemplified above, be they cells or animals [24].

In what follows, we introduce a general d-dimensional lattice model of continuous time LARWs, which covers the case of both simple symmetric (Polya) and persistent RWs, with either accelerated or decelerated dynamics. We present a general framework to obtain exact, analytical determinations of the joint distribution $P(x, a, t)$ of the position and activation of the RWer at time t, which fully characterizes the process. Our analysis shows quantitatively that activation, even if localized at a single site, can deeply impact the dynamics at large scales. For generic accelerated processes, we show that the marginal distribution of the position of the RWer [denoted $P(x, t)$ for simplicity] is non-Gaussian for $d = 1, 2, 3$—thereby generalizing the result of [2] obtained for 1d Brownian LARW. In contrast to the 1d case, which leads to anomalous diffusion, we find for $d = 2, 3$ a diffusive scaling $x \sim t^{1/2}$ for all

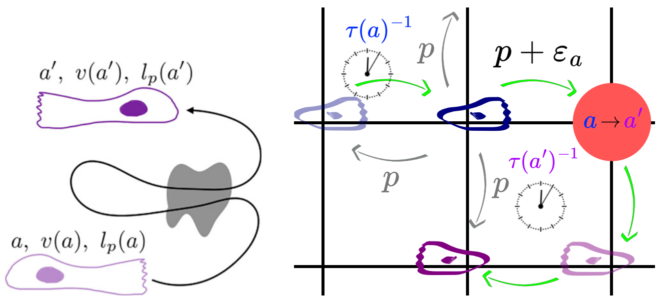

FIG. 1. Left: Sketch of a LARWer (e.g., immune cell), whose dynamic parameters (speed v and persistence length l_p) depend on the activation a, which increases upon each visit to the activation site (e.g., antigen carrying site). Right: A persistent LARW on a 2D square lattice, with persistence parameter ε_a ($p = \frac{1-\varepsilon_a}{4}$) and waiting time $\tau(a)$, which are the counterparts of the speed v and persistence length l_p for lattice models that we consider in this article. The trajectory of the RWer is represented by the green arrows, and the activation site is represented by the red disk. The activation increases from a to a' upon the visit of the activation site.

choices of activation dynamics. For decelerated processes, we identify and characterize quantitatively a transition between the diffusive regime and a phase where the RWer can be irreversibly trapped at the activation site. Last, we show that our approach can be generalized exactly to multiple activation sites in the one-dimensional case. In higher dimensions, we are able to provide quantitative large-scale asymptotics of the joint distribution.

II. LARW: GENERAL FRAMEWORK

We consider a RWer that performs a generic continuous time RW on a regular d-dimensional infinite lattice. More precisely, the RWer, if at site s with activation a, performs a jump with rate $1/\tau(a)$ to a site drawn from a given distribution, which does not need to be nearest neighbor (see explicit examples below and Fig. 1). The walk starts with activation $a = 0$ from the origin $x = 0$, which is assumed first to be the only activation site (called hereafter hotspot) of the lattice. In what follows, we assume that the activation a of the RWer is only increasing and given by the cumulative time spent on the hotspot up to time t, so that $a(t) = \int_0^t \mathbb{1}(x(t'))dt'$, where $\mathbb{1}(s) = 1$ if s is the hotspot and 0 otherwise; in turn, $\tau(a) > 0$ is a system dependent modeling choice, and can capture both accelerated [decreasing $\tau(a)$] and decelerated [increasing $\tau(a)$] processes. Importantly, the aging dynamics of a makes the position process $x(t)$ non-Markovian, because the jump rate of the RW depends explicitly on the activation a that is controlled by the full history of visits of the RWer to the hotspot. Nonetheless, the process $[x(t), a(t)]$ is Markovian, and the joint distribution $P(x, a, t)$ fully characterizes the process; we denote $\hat{P}(x, a, s) = \int_0^\infty e^{-st} P(x, a, t)dt$ its Laplace transform.

In what follows, we first show that even if $a(t)$ alone is not a Markovian process, an explicit evolution equation for $P(0, a, t)$ can be obtained. Writing $P(0, t + dt, a + dt)$ as a partition over the last time the hotspot was visited yields two different scenarii: (i) the walker was at 0 at time t with activation a and did not jump during dt, or (ii) the last visit at the hotspot before the visit at $t + dt$ ended at some earlier time $t' < t$ with activation $a + dt$. The key point is that between two consecutive visits to the hotspot, the activation a, and thus the jump rate $1/\tau(a)$ of the RWer remains constant. Thus, the probability of events involved in (ii) can be written in terms of the first-passage time (FPT) density to site 0 for a simple random walker with constant jump rate $1/\tau(a)$ starting from site 0 and jumping at time $t = 0^+$, which is denoted $F_a(0|0^+, t)$. This yields [see the Supplemental Material (SM) for details [25]]

$$\partial_t P(0, a, t) + \partial_a P(0, a, t) = -\frac{P(0, a, t)}{\tau(a)} + \int_0^t \frac{dt'}{\tau(a)} P(0, a, t') F_a(0|0^+, t - t'). \quad (1)$$

Next, we define $\xi_a(s) = (1 + s\tau(a))^{-1}$ and Laplace-transform (1) to obtain a first important result

$$\partial_a \hat{P}(0, a, s) = \frac{[\mathcal{F}(0|0, \xi_a(s)) - 1]\hat{P}(0, a, s)}{\tau(a)\xi_a(s)}, \quad (2)$$

where we introduced the discrete-time, nonactivated first-passage generating function $\mathcal{F}(0|0, \xi)$, related to its continuous-time, activated counterpart $\hat{F}_a(0|0^+, s)$ by $\hat{F}_a(0|0^+, s) = \mathcal{F}(0|0, \xi_a(s))/\xi_a(s)$ [9]. Integrating this equation is straightforward and yields an explicit expression for $\hat{P}(0, a, s)$, provided that $\mathcal{F}(0|0, \xi)$ is known.

We now show how to obtain the full joint distribution $P(x, a, t)$ from (2). For the walker to be on site x with activation a at t, it must jump away from 0 at an earlier time t' with activation a, and next reach site x without hitting 0 in the remaining time $t - t'$. This analysis yields the following renewal equation:

$$P(x, a, t) = \int_0^t \frac{dt'}{\tau(a)} P(0, a, t') P^a_{\text{surv}}(x|0^+, t - t'), \quad (3)$$

where we define $P^a_{\text{surv}}(x|0^+, t)$ to be the (survival) probability for a walker with activation a, starting from site 0 and jumping at time 0^+, to be at site x at time t, all this without visiting site 0 again. This quantity is related [9] to its nonactivated, discrete-time counterpart $\mathcal{P}_{\text{surv}}(x|0, \xi)$ by $\hat{P}^a_{\text{surv}}(x|0^+, s) = \tau(a)\xi_a(s)\frac{\mathcal{P}_{\text{surv}}(x|0, \xi_a(s))}{\xi_a(s)}$. The Laplace transform of (3) thus yields

$$\hat{P}(x, a, s) = \hat{P}(0, a, s)\mathcal{P}_{\text{surv}}(x|0, \xi_a(s)). \quad (4)$$

We now recall how all the quantities entering (2) and (4) can be deduced from the generating function $\mathcal{P}(x|y, \xi)$ of the propagator of the corresponding nonactivated RW. Standard results [9] yield the discrete-time generating function $\mathcal{P}_{\text{surv}}(x|0, \xi)$,

$$\mathcal{P}_{\text{surv}}(x|0, \xi) = \mathcal{F}(x|0, \xi) = \mathcal{P}(x|0, \xi)/\mathcal{P}(0|0, \xi) \quad (5)$$

as well as the first-return time to 0: $\mathcal{F}(0|0, \xi) = 1 - 1/\mathcal{P}(0|0, \xi)$. Using these results, one finally finds the exact expression of the Laplace transformed joint law:

$$\hat{P}(x, a, s) = \frac{\mathcal{P}(x|0, \xi_a)}{\mathcal{P}(0|0, \xi_a)} \exp\left(-\int_0^a \frac{db}{\tau(b)\xi_b \mathcal{P}(0|0, \xi_b)}\right). \quad (6)$$

We stress that this determination of the joint law is fully explicit for all processes for which the propagator of the underlying, non activated RW is known. We present explicit examples below.

III. d-DIMENSIONAL NEAREST NEIGHBOR LARWs

For the paradigmatic example of symmetric nearest neighbor RWs on the hypercubic lattice $\mathbb{Z}^d$, the generating function of the (nonactivated) propagator $\mathcal{P}(x|y,\xi)$ admits an explicit integral representation [9]. For $d=1$, making use of (6) yields an explicit, exact expression of the (Laplace transformed) joint law (see the SM). While this expression cannot, to the best of our knowledge, be Laplace inverted analytically for arbitrary $\tau(a)$, numerical inversion is straightforward and provides the joint law at all times. Under the condition that $\tau(a) \ll a$ for $a \to \infty$ (to be refined below), the following asymptotic expression of the joint law of x, a can be obtained in the regime $a \ll t, t \to \infty$,

$$P_{1D}(x,a,t) \sim \frac{Ze^{-\frac{Z^2}{2t}}}{\sqrt{2\pi}t^{3/2}}, \tag{7}$$

where $Z = \sqrt{\tau(a)}|x| + F_1(a)$, $F_1(a) = \int_0^a \frac{db}{\sqrt{\tau(b)}}$. In turn, considering the explicit example of $\tau(a) \sim a^{-\alpha}$ with $\alpha > -1$ [to ensure $\tau(a) \ll a$ for $a \to \infty$], integration over a using the saddle point method yields the asymptotics of the marginal distribution for large t,

$$P_{1D}(x,t) \sim \begin{cases} A\frac{x^{\frac{1}{1+\alpha}}}{t}\exp\left(-B\frac{x^{\frac{2+\alpha}{1+\alpha}}}{4t}\right), \alpha > 0, x \gg t^{\frac{1+\alpha}{2+\alpha}} \\ \sqrt{\frac{2}{\pi t}}\frac{e^{-\frac{x^2}{2t}}}{|\alpha|x}, -1 < \alpha < 0, x \gg \sqrt{t}, \end{cases} \tag{8}$$

where A, B are constants explicitly given in the SM. These asymptotic expressions are not normalized as they hold only in the given asymptotic regimes. Notice that the marginal distribution of accelerated $1D$ LARW is non-Gaussian, and even nonmonotonic as a function of x. These results generalize the earlier findings of [2] (recovered by taking the appropriate continuous limit, see the SM), where a similar $1d$ model of LARW for a Brownian particle in continuous space, with a pointlike hotspot was studied. Similarly, for $d=2$, (6) together with [9] provides an explicit expression of $\hat{P}_{2D}(x,a,s)$, which provides the joint law for all values of parameters by numerical inversion (see Fig 2). In addition, assuming $\tau(a) \ll a$, and in the regime $t \to \infty, a \ll t, x \gg \sqrt{t\tau(a)^{-1}}$, Laplace inversion can be performed analytically and yields

$$P_{2D}(x,a,t) \sim -\frac{\tau(a)}{\pi t}e^{-\frac{|x|^2\tau(a)}{t}}\partial_a e^{-\frac{\pi F_2(a)}{\log\frac{8t^2}{\tau(a)^2|x|^2}}}, \tag{9}$$

where $F_2(a) = \int_0^a \frac{db}{\tau(b)}$. This expression of the joint law is found to be in very good agreement with the numerical inversion (see Fig. 2). Of note, different behaviors are obtained according to the value of a relative to a threshold value $a_*(t)$, which can be determined from the analysis of (9), and turns out to scale as the typical value of a at time t (see the SM [25]) [26]. For $a < a_*$, trajectories with atypically low numbers of visits to the hotspot are selected. This leads to an effective repulsion from the hotspot, so that $P_{2D}(x,a,t)$ as a function of x displays a local minimum for $x=(0,0)$. Conversely, for $a > a_*$, trajectories with atypically large numbers of visits to the hotspot are selected, and $P_{2D}(x,a,t)$ shows a sharp maximum for $x=(0,0)$. We now turn to the determination of the marginal distribution of the position at time t. To be explicit, we consider the example $\tau(a) \sim \frac{1}{a^\alpha}$ with $\alpha > -1$ [to ensure $\tau(a) \ll a$ for $a \to \infty$]. Using again the saddle point method in the regime $x \gg \sqrt{t}, t \to \infty$, one finds, up to subleading log - log corrections, where log is the natural logarithm:

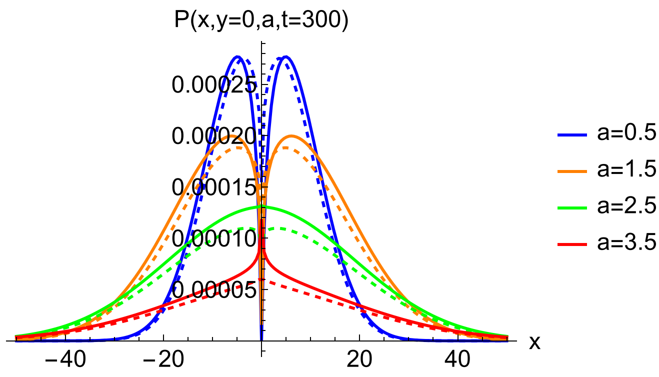

FIG. 2. Joint law of activation (colors) and position (abscissa, along a given axis, chosen here as $y=0$) of an accelerating 2D LARW with waiting time $\tau(a) = \frac{1}{a}$ at time $t=300$. Thick lines are obtained from numerical Laplace inversion of the exact joint law (in the SM), while dashed lines correspond to the asymptotics (9). The threshold activation is $a_*(t) \sim \sqrt{\log t} \sim 2.4$.

$$P_{2D}(x,t) \sim \begin{cases} \frac{A}{t}\left(\frac{x}{\sqrt{t}}\right)^{\frac{1-\alpha}{2\alpha+1}} e^{-\frac{B(x^2/t)^{\frac{1+\alpha}{1+2\alpha}}}{\log^{\frac{\alpha}{1+2\alpha}}(C(t^{1+\alpha}/x)^{\frac{1}{1+2\alpha}})}}, \alpha > 0 \\ \frac{\exp\left(-\frac{x^2}{t}\right)}{2|\alpha|x^2\log(t/x)}, -1 < \alpha < 0, \end{cases} \tag{10}$$

where A is a slowly varying function of x and t, and B, C are constants, explicitly given in the SM. This analytical expression of the distribution, confirmed by numerical simulations, is strongly non-Gaussian, similarly to the $1d$ case (see Fig. 3). In addition, for accelerated processes ($\alpha > 0$), this distribution is maximized for a nonvanishing, increasing in time displacement $r_*(t)$. We now turn to LARW on the $3d$ cubic lattice. As opposed to the above $d=1,2$ cases, the $3d$ nonactivated RW is known to be transient, so that $P(0|0,\xi_a)$ tends to the finite value $\frac{1}{1-R}$ as $as \ll 1$, where $R \simeq 0.34\ldots$, is the return probability on the cubic lattice [9]. This allows for an explicit Laplace inversion in the regime $x \to \infty, a \ll t, x^2\tau(a)/t$ fixed, which yields using (6) [assuming $\tau(a) \ll a$ for $a \to \infty$]:

$$P_{3D}(x,a,t) \sim (1-R)\sqrt{\tau(a)}\left(\frac{3}{2\pi t}\right)^{3/2} \times \exp\left(-\frac{3|x|^2\tau(a)}{2t} - (1-R)F_2(a)\right). \tag{11}$$

Noticeably, in contrast to the case of recurrent RWs for $d=1,2$, (11) is a Gaussian function of x (for a fixed), and is maximized at the origin, and this is regardless of $\tau(a)$, for

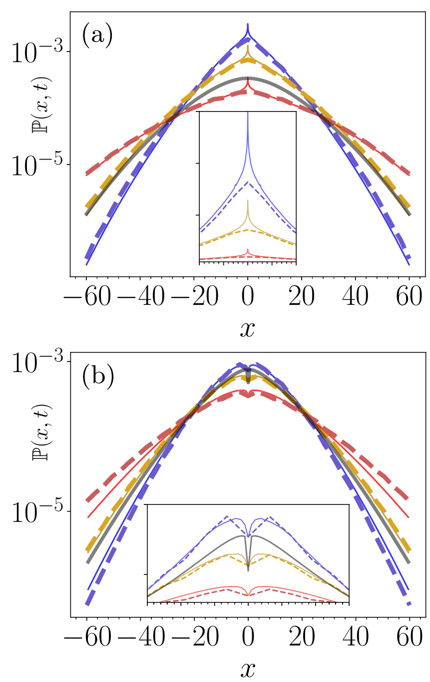

FIG. 3. Spatial distribution for a persistent 2D LARW with a single hotspot at the origin with persistence parameter ε, along a given axis x. Blue, yellow, and red curves correspond respectively to $\varepsilon = -0.3, 0, 0.4$. Black lines correspond to the saddle-point approximations (10) and are drawn for $\varepsilon = 0$. Thick lines are obtained from numerical integration over a of the asymptotic expression (9) with rescaled waiting time $\tilde{\tau}(a) = \frac{1-\varepsilon}{1+\varepsilon}\tau(a)$, while dashed lines correspond to numerical simulations. (a) Decelerating LARW, with $\tau(a) = \sqrt{1+a}$. Note the cusp at site $x = 0$. (b) Accelerating LARW, with $\tau(a) = \frac{1}{a}$. Note the nonzero typical displacement scaling logarithmically with time.

both accelerated and decelerated processes. Finally, taking the example of $\tau(a) \sim a^{-\alpha}$, the marginal distribution of the position is obtained by saddle-point integration of (11) in the regime $x \gg \sqrt{t}$,

$$P_{3D}(x,t) \sim \begin{cases} \frac{A}{t^{3/2}}\left(\frac{x}{\sqrt{t}}\right)^{\frac{1-2\alpha}{1+2\alpha}} e^{-B\left(\frac{x^2}{t}\right)^{\frac{1+\alpha}{1+2\alpha}}}, \alpha > 0 \\ \left(\frac{3}{2\pi t}\right)^{3/2} \frac{2t(1-R)}{3|\alpha|x^2} e^{-\frac{3x^2}{2t}}, -1 < \alpha < 0, \end{cases} \quad (12)$$

where A, B are constants and are given explicitly in the SM. Of note, this distribution shows a diffusive scaling $x^2 \propto t$, even if non-Gaussian. Therefore, a localized perturbation by a single hotspot, even for a transient RW that typically makes only a finite number of visits to this site, is sufficient to yield a non-Gaussian behavior.

IV. PERSISTENT (ACTIVE) LARWs

Last, we show that (2) can in fact be used beyond the case of symmetric nearest neighbor RWs. For the sake of simplicity, we consider a $1d$ RWer that performs a persistent RW on $\mathbb{Z}$ [27], which is the discrete space analog of the classical run and tumble model of active particle. Our results below can be generalized to d-dimensional persistent RWs as shown in the SM. In this model, after a jump $\sigma = \pm 1$, the walker performs an identical jump σ with probability $\frac{1+\varepsilon}{2}$, and $-\sigma$ with probability $\frac{1-\varepsilon}{2}$. Local activation is taken into account by allowing both the jump rate $1/\tau(a)$ and the persistence parameter $\varepsilon_a \in [-1, 1]$ to depend on activation a, whose definition is unchanged. Equation (4) remains valid for this process, and yields the exact Laplace transform of the joint distribution $\hat{P}(x \neq 0, a, s)$, given in Eq. (9) of the SM.

The $as \ll 1$ asymptotics of this equation show that at large scales the persistent LARW can be mapped exactly to a nonpersistent nearest neighbor LARW with rescaled waiting time $\tilde{\tau}(a) = \frac{1-\varepsilon(a)}{1+\varepsilon(a)}\tau(a)$, for which explicit expressions of the joint law have been obtained above. This result holds in any space dimension, and explicitly quantifies how the activation of either persistence $[\varepsilon(a)]$ or velocity $[1/\tau(a)]$ impacts on the large scale dynamics of the process.

V. ERGODICITY BREAKING AND TRAPPING

In the case of decelerated processes, the particle can eventually be trapped at the hotspot. Quantitatively, this trapping occurs if the particle asymptotically spends a finite fraction of time at 0, so that there is some $\gamma > 0$ such that $\lim_{t\to\infty} P(0, a = \gamma t, t) > 0$, and the joint law is nonsmooth (singular) at large times. The analysis of the joint law (6) shows (see the SM) that such ergodicity breaking occurs if and only if $S \equiv e^{-\int_0^\infty \frac{da}{\tau(a)}} > 0$. Of note, this condition holds in all space dimensions; in the example $\tau(a) \sim a^{-\alpha}$ discussed above this occurs for $\alpha < -1$. This condition of trapping is also realized if $\tau(a)$ diverges for a finite activation a_f. Importantly, explicit expressions (8), (9), (10), (12) have been obtained in the ergodic regime $S = 0$ [or more loosely $\tau(a) \ll a$], and thus remain smooth. In the case of nearest neighbor RWs, the trapping condition amounts to requiring that the probability S that the walker remains on the hotspot forever upon a given visit is nonvanishing. In turn, for persistent RWs this condition applies to the effective $\tilde{\tau}$, and reveals two possible mechanisms for trapping: either waiting times diverge $[\tau(a) \to \infty]$, as in the case of trapped nearest neighbor RWs, or the RW becomes infinitely antipersistent $[\varepsilon(a) \to -1]$. In addition, our analysis allows to quantify asymptotically in the large t regime the dynamics of trapping (see the SM); it shows in particular that for $d = 1, 2$, i.e., recurrent RWs, the RWer is eventually trapped with probability 1, while for $d = 3$ the RWer always has a nonvanishing probability to remain untrapped, which is quantified by our approach.

VI. LARW WITH MULTIPLE HOTSPOTS: EXACT FORMALISM

We now turn to the case of multiple hotspots, and start with the case of a one-dimensional nearest neighbor LARW with a periodic distribution of hotspots of period L. We consider $2N-1$ hotspots with positions $x_k = (-N+k)L$ for $k = 1, \dots, 2N-1$, keeping in mind that $N \to \infty$. Activation $a(t)$ is now the cumulative time spent on any of the hotspots x_i up to t. We extend the reasoning that led us to (2); we introduce a partition over the last visited hotspot, and observe that the RWer cannot cross a hotspot while keeping its activation a constant. Hence, writing $|P\rangle\,(a,s) =$

$|\hat{P}(x_1,a,s),\dots,\hat{P}(x_{2N-1},a,s)\rangle$, we can write

$$\partial_a |P\rangle = \frac{1}{\tau(a)}\left(\frac{1}{2}\hat{F}^D_{L-1}(\xi_a)A - \left(\frac{1}{\xi_a} - \hat{F}^G_{L-1}(\xi_a)\right)\mathbb{1}\right)|P\rangle, \tag{13}$$

where $A = (\delta_{|i-j|,1})_{1\leqslant i,j\leqslant 2N-1}$, and $\xi_a(s) = (1+s\tau(a))^{-1}$ still. We defined $\hat{F}^{G/D}_{L-1}(\xi) = \sum_{t=0}^{\infty}\xi^t F^{G/D}_{L-1}(t)$, where $F^{G/D}_{L-1}(t)$ is the distribution of the first-exit time t of a simple RWer through the left/right boundary of an interval of $L-1$ sites, starting from its left boundary. As found in, e.g., [9], these quantities write $\hat{F}^G_{L-1} = \frac{1}{\xi_a} - \frac{1}{\tanh L\mu_a}\frac{\sqrt{1-\xi_a^2}}{\xi_a}$, $\hat{F}^D_{L-1} = \frac{1}{\sinh L\mu_a}\frac{\sqrt{1-\xi_a{}^2}}{\xi_a}$ where $\mu_a = -\log(\frac{1-\sqrt{1-\xi_a^2}}{\xi_a})$. Because all the matrices in (13) commute, this equation can be solved by determining the common eigenvalues and eigenvectors of these matrices. The eigenvalues of the matrix A are $(2\cos(\frac{\pi j}{2N}))_{j=1,\dots,2N-1}$, while the corresponding eigenvectors are $|v_j\rangle = \frac{1}{\sqrt{N}}|(\sin(\frac{\pi jk}{2N}))_{k=1\dots 2N-1}\rangle$. Following standard steps, we take the $N\to\infty$ limit to find

$$\hat{P}(kL,a,s) = e^{-\beta(a,s)}I_k(\alpha(a,s))$$
$$\alpha = \int_0^a \frac{db}{\sinh L\mu_b}\frac{\sqrt{1-\xi_b^2}}{\xi_b\tau_b},$$
$$\beta = \int_0^a \frac{db}{\tanh L\mu_b}\frac{\sqrt{1-\xi_b^2}}{\xi_b\tau_b} \tag{14}$$

where $I_k(x)$ is a Bessel function. Similarly to the case of a single hotspot, we obtain from (14) the full joint distribution of position x and activation a (see the SM):

$$\hat{P}(x,a,s) = \frac{1}{\sinh L\mu_a}[\hat{P}(kL,a,s)\sinh(\mu_a[(k+1)L-x]) + \hat{P}((k+1)L,a,s)\sinh(\mu_a(x-kL))]. \tag{15}$$

VII. LARW WITH MULTIPLE HOTSPOTS: APPLICATIONS

Suppose now that $\tau(a)\gg a$, leading to eventual trapping of the RWer. Where is the RWer trapped? It must be on a hotspot. From a small-s expansion of (14), one finds that the last visited hotspot follows a Skellam law

$$P(\text{trapped at } kL) = e^{-K}I_k(K),\ K = \frac{\int_0^\infty \frac{da}{\tau(a)}}{L}. \tag{16}$$

This result has the following interpretation. Only the time spent on hotspots, i.e., the activation a, is relevant for determining the last hotspot visited. The RWer thus behaves as if it moved from hotspot to hotspot, ignoring the time spent on other sites. Due to local activation, this RWer thus performs a time-changed simple random walk between the hotspots. It is well known [9] that the distribution of the position of such a RWer is a Skellam law.

In the following, we assume that $\tau(a)\ll a$. We consider a LARW on $\mathbb{Z}^d$, with a periodic distribution of hotspots making up the sublattice H. One can then consider the periodized lattice $\Gamma = \mathbb{Z}^d/H$: it has a single hotspot at its origin. Let N be the number of sites in Γ and $x_\Gamma(t)$ be the position of the LARW at time t on Γ. We show in the SM that, at long times, position is uniform on Γ. The ergodic theorem thus implies that $a(t) \underset{t\to\infty}{\sim} t/N$. At long times, the dynamics of the walk on the whole lattice are thus effectively those of a walker with deterministic, time-dependent waiting time $\tau'(t) = \tau(\frac{t}{N})$. Hence, at large scales, the RWer behaves as Brownian motion with rescaled time $\tilde{t}(t) = \int_0^t \frac{dt'}{\tau(a(t'))} \underset{t\to\infty}{\sim} \int_0^t \frac{dt'}{\tau(t'/N)}$. The last equivalence holds since $\tau(a)\ll a$. Finally, the marginal distribution of the position is Gaussian in this limit, of variance $\tilde{t}(t)$, in strong contrast with the non-Gaussian behavior of the LARW with a single hotspot. This conclusion holds for any LARW with a finite density $\rho>0$ of hotspots, e.g., a Poissonian distribution of hotspots on $\mathbb{Z}^d$.

Finally, we have presented a comprehensive analytical framework for determining a range of statistical properties that describe the dynamics of both passive and active (run and tumble) LARWs on d-dimensional lattices. In the context of living systems, our analysis unveils notable and robust features of LARW [such as non-Gaussian behavior, diffusive or anomalous scaling, nonmonotonicity of $P(x,t)$, and trapping]. These features offer clear signatures of activated dynamics that can be potentially useful in the analysis of experimental data.

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