"Burnt-bridge" mechanism of molecular motor motion

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Motivated by a biased diffusion of molecular motors with the bias dependent on the state of the substrate, we investigate a random walk on a one-dimensional lattice that contains weak links (called "bridges") which are affected by the walker. Namely, a bridge is destroyed with probability p when the walker crosses it; the walker is not allowed to cross it again and this leads to a directed motion. The velocity of the walker is determined analytically for equidistant bridges. The special case of p=1 is more tractable—both the velocity and the diffusion constant are calculated for uncorrelated locations of bridges, including periodic and random distributions.

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I. INTRODUCTION

The motion of a particle depends on the medium in which it moves. Often the inverse is also true, that is, the particle motion changes the medium. Such problems are characterized by an infinite memory—not only the present position of the particle, but the entire past determines the future—and they are usually extremely difficult. Perhaps the most famous example is the self-avoiding walk, which is a random walk on a lattice with the restriction that hops to already visited sites are forbidden [1]. Similarly, in a path-avoiding walk, a random walker is not allowed to go over already visited links. A generalization of the path-avoiding walk assumes that the medium is a lattice with two kinds of links, strong and weak: strong links are unaffected by the walker while weak links, called bridges, "burn" when they are crossed by the walker. The random walker is not allowed to cross a burnt-bridge [2,3]. Obviously the burnt-bridge model reduces to the path-avoiding walk if all links are weak.

In this paper, we investigate a stochastic burnt-bridge model [4] in which the crossing of an intact bridge leads to burning only with a certain probability p, while with probability 1-p the bridge remains intact. The stochastic burntbridge model is a simplification of models proposed to mimic classical molecular motors [2,3] with energy coming from adenosine triphosphate (ATP) hydrolysis [5]. (There are, of course, various other models describing molecular motors; see, e.g., Refs. [6-12].) A more direct biological application of the stochastic burnt-bridge model has been recently suggested by Saffarian et al. [13], who shows that experimental results on the motion of the activated collagenase (MMP-1) along collagen fibrils are consistent with Monte Carlo simulations of a two-track stochastic burntbridge model with weakly coupled tracks (the hopping rate over the rungs between the tracks is small compared to the hopping rate along the tracks). The collagenase motor activity is of great interest since it affects various physiological and pathophysiological processes (e.g., to wound healing and tumor progression). This inspires theoretical work on the stochastic burnt-bridge model.

We shall focus on the one-track stochastic burnt-bridge model. Forbidding the crossing of the burnt-bridges essentially imposes a bias, and the goal is to compute the velocity v(c,p) and the diffusion coefficient D(c,p) as functions of the density of bridges c and the bridge-burning probability p. The velocity and the diffusion coefficient also depend on the positioning of the bridges. We shall tacitly assume that the bridges are placed without correlations, and we shall often specify our findings to two particularly interesting and natural positioning of the bridges—a regular equidistant spacing and a random distribution.

The rest of this paper is organized as follows. In the next section, we describe various versions of the burnt-bridge model and outline the major results. Section III is devoted to the derivation of the velocity and the diffusion coefficient for the burnt-bridge model and a modified burnt-bridge model. In Sec. IV, the stochastic burnt-bridge model is studied, and the velocity is computed for equidistant bridges. Finally, a few open questions are discussed (Sec. V). Various calculations are relegated to the Appendixes.

II. MODELS AND MAIN RESULTS

The definition of the burnt-bridge model is sketched in Fig. 1. The particle undergoes a discrete time nearest-neighbor random walk on a one-dimensional lattice that contains two kinds of links, strong and weak. The weak links are called bridges and, when the walker crosses a bridge, it gets burnt. A burnt-bridge cannot be crossed again: the walker next to a burnt-bridge always steps away from it. No bias is initially imposed as the hopping rates to the right and left are



FIG. 1. The random walker (filled triangle) hops to adjacent sites when it is away from the bridges. Strong links are shown by horizontal lines, intact bridges are depicted by arcs, and the absence of a link indicates a burnt-bridge.

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assumed to be equal. The first burning event, however, effectively generates the bias—if the first burning event has happened when the bridge was crossed from left to right, the walker will always be to the right of the last burnt-bridge. Trapping of the walker between two burnt-bridges is impossible since we assume that initially all bridges were intact. For concreteness we assume that the first bridge is crossed from the left. We set the time t and the position x of the walker to 0 at this instant.

The stochastic burnt-bridge model proposed by May *et al.* [4] posits that an intact bridge is burnt with a certain probability p < 1 when crossed by the walker. To avoid the trapping of the walker, it is additionally postulated that when the bridge burns while the walker attempts to cross it from the right, the walker remains at the same position [4]. Hence, trapping is impossible and the walker is drifting to the right. Without loss of generality, we can set the lattice spacing and the time step between successive hops to unity. Thus, if there were no bridges (c=0), the walker would undergo a random walk with v=0 and D=1/2. For c>0, the walker asymptotically behaves as a biased random walk, that is, the probability of finding the walker at position x is a Gaussian centered around $\langle x \rangle = vt$ with width $\langle x^2 \rangle - \langle x \rangle^2 = 2Dt$ as $t \to \infty$.

The model depends on two parameters—the burning probability p and the density of bridges c. The distribution of the bridges also affects the behavior of the random walker. We mainly discuss two extreme distributions, periodic (bridges are equidistant) and random (each link is a bridge with probability c). In the periodic case the density c attains only inverse integer values (1,1/2,1/3,...) while when bridges are placed at random the density can attain any value $0 < c \le 1$.

The burnt-bridge model (p=1) is much simpler than the stochastic burnt-bridge model. For the burnt-bridge model, the velocity has been computed in the realm of a continuum approximation by May *et al.* [4]. The same paper argues that for the stochastic burnt-bridge model with $p \le 1$ the velocity scales as \sqrt{p} .

The continuum approximation becomes asymptotically exact in the $c \rightarrow 0$ limit, yet in biological applications the density c can be rather large and therefore the discreteness is essential. Further, the burning probability p is usually notably smaller than 1, for instance p = 0.1 was used in Ref. [13] to fit the experimental data. Therefore, it is very desirable to compute the velocity v(c,p) and the diffusion coefficient D(c,p) over the entire range of c and p. (The diffusion coefficient has not been studied in the earlier work, even for p = 1.)

We computed v(c,p) for all $0 < c \le 1$, 0 and we determined the diffusion coefficient when <math>p=1. The final expressions for the velocity and the diffusion coefficient are simple but the derivations are tedious, so here we summarize our findings; the derivations are presented in the following sections.

We start with the burnt-bridge model (p=1). In this case, the velocity $v(c) \equiv v(c,p=1)$ exhibits a remarkably simple dependence on the bridge density (Fig. 2)

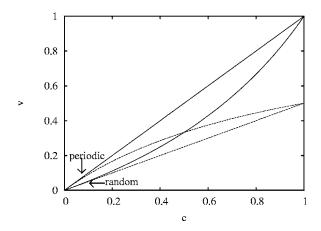


FIG. 2. Velocity of the walker in the original (solid) and in the modified (dashed) burnt-bridge model, for random and periodic bridge distributions.

$$v(c) = \begin{cases} c & \text{periodic} \\ c/(2-c) & \text{random.} \end{cases}$$
 (1)

In the $c \rightarrow 0$ limit we recover the expressions computed in Ref. [4] in the realm of continuum approximation. Unexpectedly, the continuum approximation is exact in the periodic case; for random locations, the continuum approximation gives v(c)=c/2, which is only asymptotically exact. [For c=1, that is, for the path-avoiding walk, one should get v=1, so the continuum approximation v(c)=c/2 could not be exact.]

The diffusion coefficient also depends simply on c for periodically and randomly positioned bridges

$$D(c) = \begin{cases} \frac{1}{3}(1 - c^2) & \text{periodic} \\ \frac{3}{2} \frac{1 - c}{(1 - c/2)^2} & \text{random.} \end{cases}$$
 (2)

The diffusion coefficient monotonously decreases as c increases (see Fig. 3) and D(1)=0, since on a lattice fully

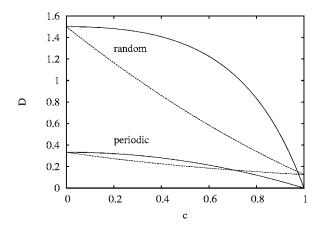


FIG. 3. Diffusion coefficient in the original (solid) and in the modified (dashed) burnt-bridge model, for random and periodic bridge distributions.

covered by bridges, the walker moves deterministically. The diminishing nature of D(c) has apparently been observed experimentally in Ref. [13]. Intriguingly, Eq. (2) gives $D_{\rm per}(+0)=1/3$ [$D_{\rm ran}(+0)=3/2$], which is smaller (larger) than the "bare" diffusion coefficient $D_{\rm bare}=1/2$ that characterizes diffusion on the one-dimensional lattice without bridges. This sudden jump of the diffusion coefficient occurs when the density becomes positive. The reason is that any positive c (irrespective of however small it is) makes a lasting influence on the fate of the walker, which is forced to remain to the right of the last burnt-bridge. Thus, the very rare burning events substantially affect the diffusion coefficient.

The details of the walker dynamics at the boundary of a burnt-bridge affect the velocity and the diffusion coefficient. To illustrate this assertion, recall that in the framework of the burnt-bridge model the walker at the boundary of a burnt-bridge always moves to the right. Another natural definition is to allow an attempt to cross the burnt-bridge—the attempt fails and the walker remains at its position. In other words, the walker next to a burnt-bridge either stays at the same position or moves to the right with the same probability 1/2 during the next time step. The velocity for this modified burnt-bridge model is

$$v(c) = \begin{cases} c/(1+c) & \text{periodic} \\ c/2 & \text{random.} \end{cases}$$
 (3)

The continuum approximation again manages to get one answer right—now it is exact in the random case and approximate in the periodic case.

The diffusion coefficient for the modified burnt-bridge model is

$$D(c) = \begin{cases} \frac{1}{3} \frac{1}{1+c} - \frac{1}{6} \frac{c^2}{(1+c)^2} & \text{periodic} \\ \frac{3}{8} c^2 - \frac{7}{4} c + \frac{3}{2} & \text{random.} \end{cases}$$
 (4)

Perhaps the largest difference between the two models is that in the realm of the modified burnt-bridge model the walker never moves deterministically—even when c=1 it moves diffusively although the diffusion coefficient is small, namely it is 4 times smaller than the bare diffusion coefficient. Not surprisingly, the quantitative predictions of the two models are substantially different when c is large (see Figs. 2 and 3)

For the stochastic burnt-bridge model, we succeeded in computing velocity for periodically located bridges. The velocity reads

$$v(c,p) = \frac{cp}{cp + 2 - p} \frac{2 - p + V}{p(1 - c) + V},$$
 (5)

where we used the shorthand notation

$$V = \frac{p(2-p)(1-c)}{2} \left\{ -1 + \sqrt{1 + \frac{4c}{p(2-p)(1-c)^2}} \right\}.$$

For p=1, Eq. (5) agrees with already known result v=c [see Eq. (1)]; for c=1 (the lattice fully covered by bridges), the

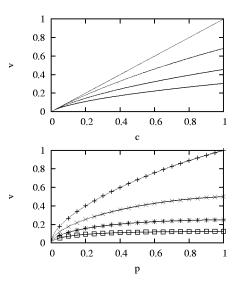


FIG. 4. The velocity v(c,p) vs c (for p=1,1/2,1/4,1/8, top to bottom) and p (for c=1,1/2,1/4,1/8, top to bottom) in the stochastic burnt-bridge model. The lattice is periodically covered by bridges. The symbols are the results of numerical simulations.

velocity is given by the following neat expression:

$$v(1,p) = \frac{p + \sqrt{p(2-p)}}{2}.$$
 (6)

From Eq. (5) (see also Fig. 4) one finds the asymptotics

$$v(c,p) \to \begin{cases} c & \text{when } c \leqslant p \\ \sqrt{cp/2} & \text{when } p \leqslant c. \end{cases}$$
 (7)

For $c \leqslant p$, the distance between neighboring bridges is large. Thus, the walker typically crosses the next bridge several times and hence almost all bridges get burnt. Therefore, the p=1 results ought to be recovered. Equation (7) shows that this is indeed correct in the periodic case; in the random case (where we do not know an exact solution) we similarly expect $v(c,p)\approx c/2$ when $c\leqslant p$. In the complimentary limit $p\leqslant c$, the walker on average makes many steps before the burning occurs, and it is intuitively obvious that we can renormalize $c\to 1$ and simultaneously $p\to cp$. Hence, $v(c,p)\to v(1,cp)$ when $p\leqslant c$, and therefore the asymptotics given in (7) can also be extracted from the simple solution (6).

Another interesting and experimentally accessible quantity is the fraction of bridges left intact by the walker. In the long time limit it is given by

$$I(c,p) = 1 - \frac{Vcp + 2 - p}{cV + 2 - p}.$$
 (8)

Figure 5 shows that the fraction of intact bridges is a decreasing function of p for fixed c (this is intuitively obvious) and an increasing function of c for fixed p. This latter feature is understood by noting that on average a bridge is visited more often when the density of bridges gets smaller.

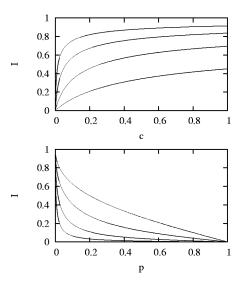


FIG. 5. The fraction of intact bridges, I(c,p) vs c (for p = 1/4, 1/16, 1/64, 1/256, from bottom to top), and vs p (for c = 1, 1/4, 1/16, 1/64, from top to bottom) in the periodic case of the stochastic burnt-bridge model.

III. BURNT-BRIDGE MODEL (p=1)

Here, we derive the results presented in the previous section for the burnt-bridge model (p=1). We consider periodically (equidistant locations) and randomly positioned bridges. These are the two most interesting cases, although the formalism can be straightforwardly extended to the general class of bridge positionings where the distances between neighboring bridges are uncorrelated.

A. Velocity and diffusion coefficient

At time t=0 the walker is at site x=0, the right end of the only burnt bridge, and all the other bridges are intact. The walker successively crosses the intact bridges, which immediately turn into burnt bridges. Instead of the original walker, it proves convenient to consider an equivalent walk whose position at time t is on the right end of the last burnt bridge. This walk is still discrete in space and time, but the step length is now equal to the distance between successive bridges, and the time between the steps is at least as large as the step length.

The following derivation is essentially the discrete time version of the so-called continuous time random walk (CTRW) [14,15]. This title refers to the continuous nature of the waiting time distribution, while in our model the discrete nature of time is essential, and therefore we present the complete derivation of the necessary results. Even though the equivalent walk always steps to the right, the derivation is the same as for a general walk which can step in both directions; hence, we present a general derivation. Note that the following derivation requires all the moments used below to be finite, which is indeed the case for the burnt-bridge model.

We denote by $\Psi(\xi, \tau)$ the probability that the equivalent walk makes a step of length ξ after waiting τ units of time. Let $\Psi_j(x,t)$ be the probability that the walk arrives at site x at

time t and at the jth step. Since the walk starts at site 0 at time 0, we have $\Psi_1(x,t) \equiv \Psi(x,t)$. The probability $\Psi_j(x,t)$ satisfies the recurrence formula

$$\Psi_j(x,t) = \sum_{x'=-\infty}^{\infty} \sum_{t'=0}^{t} \Psi_{j-1}(x-x',t-t')\Psi(x',t').$$
 (9)

Using the generating function (the discrete version of the Fourier-Laplace transform)

$$\Psi_j(q,u) = \sum_{x=-\infty}^{\infty} \sum_{t=0}^{\infty} \Psi_j(x,t) q^x u^t, \tag{10}$$

we transform the convolution (9) into the product

$$\Psi_{i}(q,u) = \Psi_{i-1}(q,u)\Psi(q,u) = [\Psi(q,u)]^{j}. \tag{11}$$

The probability Q(x,t) of arriving at site x at time t (after an arbitrary number of steps) is

$$Q(x,t) = \sum_{j=0}^{\infty} \Psi_j(x,t).$$
 (12)

The corresponding generating function can be written in a closed form

$$Q(q,u) = \sum_{i=0}^{\infty} [\Psi(q,u)]^{i} = \frac{1}{1 - \Psi(q,u)}.$$
 (13)

The probability P(x,t) that the walk is at site x at time t can be obtained by noting that, in order to be at site x at time t, the walk has to arrive at site x not later than at time t and has to stay there until t. Hence

$$P(x,t) = \sum_{t'=0}^{t} \phi(t-t')Q(x,t'), \tag{14}$$

where $\phi(t)$ is the probability that the walk does not move for a time interval t

$$\phi(t) = 1 - \sum_{t'=0}^{t} \Psi(t'). \tag{15}$$

The probability $\Psi(t)$ that the walk makes at least one step during the time interval t is obtained by summing over all possible step lengths

$$\Psi(t) = \sum_{x = -\infty}^{\infty} \Psi(x, t). \tag{16}$$

Using Eq. (15), we compute the generating function of $\phi(t)$

$$\phi(u) = \frac{1 - \Psi(u)}{1 - u} \tag{17}$$

The generating function of P(x,t) is now easily derived since Eq. (14) is a convolution

$$P(q,u) = \phi(u)Q(q,u) = \frac{1 - \Psi(u)}{(1 - u)[1 - \Psi(q,u)]}.$$
 (18)

In order to study the long-time behavior of the walk, we introduce the new variables γ and ϵ via $q=e^{i\gamma}$ and $u=e^{-\epsilon}$. The goal is to calculate $\Psi(\gamma,\epsilon)$ up to the second order in γ and ϵ , from which we will infer the asymptotic behavior. First, we note that even though the probability $\Psi(x,t)$ is not separable in general, it can always be written as the product

$$\Psi(x,t) = S(x)\Psi(t|x), \tag{19}$$

of the probability S(x) that the next step has length x (distance to the next bridge) times the conditional probability $\Psi(t|x)$ that the next step happens after t waiting time, given that the length of this step is x. Now, we calculate the generating function with respect to time in the $\epsilon \to 0$ limit. Plugging (19) into

$$\Psi(x, \epsilon) = \sum_{t \ge 0} \Psi(x, t) e^{-\epsilon t},$$

and expanding in ϵ up to the second order, we obtain

$$\Psi(x, \epsilon) = S(x) \left(1 - \epsilon [t]_x + \frac{\epsilon^2}{2} [t^2]_x \right),$$

where the moments of time are calculated at some fixed x length of interval

$$[t^n]_x = \sum_{t=0}^{\infty} t^n \Psi(t|x).$$
 (20)

Performing the Fourier transform of $\Psi(x,u)$ and taking the $\gamma \rightarrow 0$ limit, we arrive at

$$\Psi(\gamma, \epsilon) = 1 - \epsilon \langle [t]_x \rangle + i \gamma \langle x \rangle - i \epsilon \gamma \langle x[t]_x \rangle + \frac{\epsilon^2}{2} \langle [t^2]_x \rangle - \frac{\gamma^2}{2} \langle x^2 \rangle,$$

up to second order in γ and ϵ . We also need to calculate $\Psi(u)$, the generating function of $\Psi(t)$ defined by Eq. (16). It is sufficient to know it only up to first order in ϵ

$$\Psi(\epsilon) = 1 - \epsilon \langle [t]_{r} \rangle$$
.

Plugging the above results into Eq. (18), we find that up to first order in both γ and ϵ , the quantity $\Psi(\gamma, \epsilon)$ attains the form $P(\gamma, \epsilon) = (\epsilon - i\gamma v)^{-1}$ with the velocity

$$v = \frac{\langle x \rangle}{\langle [t], \rangle}.$$
 (21)

Calculating $P(\gamma, \epsilon)$ up to second order, and using the first-order expression for $\epsilon \approx -i \gamma v$ in the terms containing $\epsilon \gamma$ and ϵ^2 , we arrive at

$$P(\gamma, \epsilon) = \frac{1}{\epsilon - i\gamma v + \gamma^2 D},$$
 (22)

with the diffusion coefficient given by

$$D = \frac{\langle x^2 \rangle}{2\langle [t]_x \rangle} + \frac{\langle [t^2]_x \rangle \langle x \rangle^2}{2\langle [t]_x \rangle^3} - \frac{\langle x[t]_x \rangle \langle x \rangle}{\langle [t]_x \rangle^2}.$$
 (23)

Since Eq. (22) is the Laplace-Fourier transform of the Gaussian

$$P(x,t) = \frac{1}{\sqrt{4\pi Dt}} \exp\left\{-\frac{(x-vt)^2}{4Dt}\right\},$$
 (24)

we conclude that P(x,t) is indeed Gaussian in the long-time limit. It is centered around a mean value $\langle x \rangle = vt$ with a mean-square deviation $\langle x^2 \rangle - \langle x \rangle^2 = 2Dt$, with v being the velocity of the walk and D being the diffusion coefficient. Note that this result applies to any random walk—discrete or continuous—where the steps are uncorrelated and all of the moments used in Eq. (23) are finite. Specifically, it applies to the burnt-bridge model (p=1) if the distances between bridges are uncorrelated.

1. Special cases

Consider first equidistant bridges separated by distance ℓ . Then, $S(x) = \delta_{x,\ell}$, and therefore the first two moments are $\langle x \rangle = \ell$ and $\langle x^2 \rangle = \ell^2$. The velocity (21) and diffusion coefficient (23) simplify to

$$v = \frac{\ell}{[t]_{\ell}}, \quad D = \frac{\ell^2}{2} \frac{[t^2]_{\ell} - [t]_{\ell}^2}{[t]_{\ell}^3}.$$

Using the moments of time computed in Appendix A [Eqs. (A5) and (A9)], we arrive at Eqs. (1) and (2).

For randomly distributed bridges, the probability that the walk makes a step of length x, that is, the probability of having two neighboring bridges at distance x > 0, is

$$S(x) = c(1-c)^{x-1}. (25)$$

We again use Eqs. (A5) and (A9) for the moments of time, and we also need the first four moments of x

$$\langle x \rangle = \frac{1}{c},$$

$$\langle x^2 \rangle = \frac{2-c}{c^2},$$

$$\langle x^3 \rangle = \frac{6 - 6c + c^2}{c^3},$$

$$\langle x^4 \rangle = \frac{24 - 36c + 14c^2 - c^3}{c^4}.$$
 (26)

Using these expressions in Eqs. (21) and (23), we obtain the velocity and the diffusion coefficient given by Eqs. (1) and (2), respectively.

Finally, consider the bimodal distribution

$$S(x) = q_1 \delta_{x,\ell_1} + q_2 \delta_{x,\ell_2}, \tag{27}$$

with two possible separations between the bridges, ℓ_1 and ℓ_2 , occurring independently with respective probabilities q_1 and q_2 (of course, $q_1, q_2 \ge 0$ and $q_1 + q_2 = 1$). In this situation, the velocity (21) becomes

$$v = \frac{q_1 \ell_1 + q_2 \ell_2}{q_1 \ell_1^2 + q_2 \ell_2^2},$$

and the diffusion coefficient (23) turns into

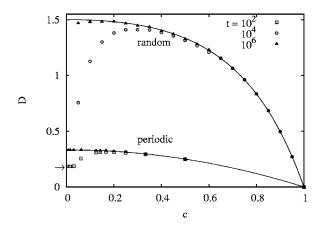


FIG. 6. The diffusion coefficient D(c) for the random and periodic bridge locations. Results of the simulations are also displayed for comparison. The arrow points to the theoretical value D=1/2 $-1/\pi$ corresponding to a random walk with a reflecting boundary.

$$D = \frac{1}{2} - \frac{(q_1\ell_1^3 + q_2\ell_2^3)(q_1\ell_1 + q_2\ell_2)}{(q_1\ell_1^2 + q_2\ell_2^2)^2} - \frac{1}{3} \frac{(q_1\ell_1 + q_2\ell_2)^2}{(q_1\ell_1^2 + q_2\ell_2^2)^2} + \frac{5}{6} \frac{(q_1\ell_1^4 + q_2\ell_2^4)(q_1\ell_1 + q_2\ell_2)^2}{6(q_1\ell_1^2 + q_2\ell_2^2)^3}.$$
 (28)

For the system with bimodal bridge distribution (27), and apparently for an arbitrary uncorrelated positioning of bridges, the diffusion coefficient exceeds that of the corresponding periodic system at the same bridge density. This general assertion is easy to verify in a particularly interesting case when the density of bridges vanishes. Taking the limit $\ell_1, \ell_2 \rightarrow \infty$, and keeping the ratio $\ell_1/\ell_2 = r(\le 1)$ constant, we recast Eq. (28) into

$$D = \frac{1}{2} + \left(\frac{q_1 r + q_2}{q_1 r^2 + q_2}\right)^2 \left[\frac{5}{6} \frac{q_1 r^4 + q_2}{q_1 r^2 + q_2} - \frac{q_1 r^3 + q_2}{q_1 r + q_2}\right]. \quad (29)$$

A straightforward analysis of Eq. (29) shows that the diffusion coefficient is larger than 1/3, which is the diffusion coefficient in the periodic case (q_1 =0 or q_2 =0). From Eq. (29) one finds that for $a \ll 1$, the maximal diffusion coefficient, approximately $D \approx \frac{10}{81} r^{-2}$, is achieved when the system is predominantly composed of shorter segments ℓ_1 , namely when $q_2 \approx r^2/2$. Therefore, a "superposition" of two equidistant distributions, each characterized by the diffusion coefficient 1/3, may have an arbitrarily large diffusion coefficient.

2. Simulations

The velocity and the diffusion coefficient of the walker are determined using the basic formulas $v = \langle x \rangle / t$ and $D = (\langle x^2 \rangle - \langle x \rangle^2)/2t$. Since the motion is self-averaging, simulating a single walker for a long time is sufficient to obtain the velocity. To measure the diffusion coefficient, however, one has to perform averages over several runs. In the case of randomly distributed bridges, one also has to average over the bridge distribution.

Figure 6 shows numerical results for the diffusion coefficient at various times. The convergence to the theoretical predictions is slow when the density of bridges is small.

During a short time interval the walker does not reach the second bridge, and actually behaves as a simple random walk with a reflecting boundary at the origin. Hence, the probability of finding the particle at position $x \ge 0$ is a Gaussian centered around the origin, and the formal definition of the diffusion coefficient yields $D=1/2-1/\pi$. For the time intervals large compared to the time (of the order of c^{-2}) between overtaking successive bridges, the coarse-grained motion becomes similar to a biased random walk with the diffusion coefficient approaching the theoretical predictions: D(+0)=1/3 in the periodic case and D(+0)=3/2 in the random case.

B. Correlation function

A correlation function measured experimentally in Ref. [13] is apparently proportional [16] to the probability C(t) that the walker at the site x_0 will be at the same position time t later

As a warm-up, consider the extreme cases of the lattice without bridges (c=0) and the lattice fully covered by bridges (c=1). In the former case, the correlation function obviously vanishes for odd t, while for even t it is given by the well-known expression

$$C(2t) = 2^{-2t} \binom{2t}{t}. \tag{30}$$

Note that the correlation function decays algebraically in the large time limit

$$C(2t) \to \frac{1}{\sqrt{\pi t}}$$
 as $t \to \infty$. (31)

For the lattice fully covered by bridges the walker can move only to the right, the probability of not making a step is 1/2, and therefore the correlation function

$$C(t) = 2^{-t} \tag{32}$$

is purely exponential.

In the general case 0 < c < 1, the walker cannot leave the "cage" formed by two neighboring bridges. As always, we consider the cage with sites $x=0,\ldots,\ell-1$. For simplicity, let us assume again that the initial position is $x_0=0$. Rather than considering the walker in the cage $(0, \ell-1)$ with a special behavior at x=0 and the absorbing boundary at $x=\ell$, one can analyze the ordinary random walker in the extended cage $(-\ell,\ell)$ with absorbing boundaries at $x=\ell$ and $x=-\ell$. The correlation function is merely the probability that this ordinary random walker will be at x=0 at time t and will remain inside the extended cage in intermediate times. This is a classic problem in probability theory whose solution is a cumbersome sum of expressions like (30) with alternating (positive and negative) signs. Therefore, we employ a continuum approximation which becomes asymptotically exact when $\ell \gg 1$ (and accordingly $c = \ell^{-1} \ll 1$). The solution is an infinite series of exponentially decaying terms. Keeping only the dominant term, we obtain

$$C(t) \to c \exp\left\{-\frac{\pi^2 c^2}{8}t\right\} \tag{33}$$

as $t \to \infty$. More precisely, the asymptotics (33) is valid when $t \ge c^{-2}$. In the regime $1 \le t \le c^{-2}$, the dominant asymptotics is the same as in the c=0 case, that is, $C(t) \sim t^{-1/2}$. It is therefore understandable that a formula

$$C(t) \approx (1+t)^{-1/2} \exp\left\{-\frac{\pi^2 c^2}{8}t\right\},$$
 (34)

fits experimental data well (and indeed it does [13]). Yet, the true asymptotic behavior, Eq. (33), is purely exponential without the power-law correction of Eq. (34).

C. Modified burnt-bridge model

The precise definition of the walker dynamics at the boundary of the burnt bridge affects the results. We assumed that the walker at the boundary of the burnt bridge always moves to the right. Recall, however, that in the stochastic version (p < 1), when the walker attempts to hop over the bridge from the left and the bridge burns, the walker actually remains at the same position. This suggests modifying the rule at the boundary of the burnt bridge—the walker either moves one step to the right or remains at the same position if it has tried the forbidden move across the burnt bridge. This defines the modified burnt-bridge model.

The calculation of v(c) and D(c) goes along the same lines as for the original burnt-bridge model (Sec. III A). The only change is that instead of Eqs. (A5) and (A9) one should use the moments of time [computed in Appendix A] which are given by Eqs. (A10) and (A13). This leads to the results presented in Sec. II and displayed in Figs. 2 and 3.

For c=1, the diffusion coefficient of Eq. (4) is the same D(1)=1/8 in both the periodic and the random case. This particular result also follows from an independent calculation which we present here as it provides a good check of self-consistency. The key simplifying feature of the lattice fully covered with bridges is that the walker never hops to the left. The position x_t of the walker after t time steps satisfies

$$x_{t+1} = \begin{cases} x_t & \text{probability } 1/2\\ x_t + 1 & \text{probability } 1/2, \end{cases}$$
 (35)

from which

$$\langle x_{t+1} \rangle = \langle x_t \rangle + \frac{1}{2},\tag{36}$$

and

$$\langle x_{t+1}^2 \rangle = \langle x_t^2 \rangle + \langle x_t \rangle + \frac{1}{2}.$$
 (37)

The variance $\sigma_t = \langle x_t^2 \rangle - \langle x_t \rangle^2$ satisfies a simple recurrence

$$\sigma_{t+1} = \sigma_t + \frac{1}{4},\tag{38}$$

which follows from Eqs. (36) and (37). The initial condition $x_0=0$ implies $\langle x_0 \rangle = \sigma_0=0$. Solving (36) and (38) subject to these initial values, we obtain

$$\langle x_t \rangle = \frac{1}{2}t, \quad \sigma_t = \frac{1}{4}t.$$
 (39)

The velocity and the diffusion coefficient can be read off the general relations $\langle x_t \rangle = vt$ and $\sigma_t = 2Dt$. Thus, we recover the already known value v(1) = 1/2 and obtain the diffusion coefficient D(1) = 1/8 (which happens to be 4 times smaller than the bare diffusion coefficient).

IV. STOCHASTIC BURNT-BRIDGE MODEL (p < 1)

Apart from randomness in hopping, the stochastic burnt-bridge model has an additional stochastic element—crossing the bridge leads to burning with probability p, while with probability 1-p the bridge remains intact. Recall that to avoid the possibility of trapping we additionally assume that if the particle attempts to cross the bridge from the right and the bridge burns, the attempt is a failure and the walker does not move. We have succeeded in computing v(c,p) in the situation when the bridges are equidistant. We again employ an approach involving auxiliary functions T(x) [see Appendix A] and L(x) defined below. Perhaps the entire problem can be treated by a direct approach discussed in Appendix B, but that approach is more lengthy and we have only succeeded in computing the velocity for c=1 that way.

We must determine the average position of the first bridge that burns, and the average time of that event. The walker starts at x=0, but it is again useful to consider a more general situation when the walker starts at an arbitrary position x. Denote by L(x) the average position of the walker at the moment when the first bridge burns. The walker hops $x \to x\pm 1$, and therefore

$$L(x) = \frac{1}{2} [L(x-1) + L(x+1)], \tag{40}$$

when $x \neq n\ell - 1$, $n\ell$ with n = 1, 2, 3, On the boundaries of the bridges, the governing equation (40) should be modified to account for possible burning events

$$L(n\ell - 1) = \frac{L(n\ell - 2) + (1 - p)L(n\ell) + pn\ell}{2}, \quad (41a)$$

$$L(n\ell) = \frac{L(n\ell+1) + (1-p)L(n\ell-1) + pn\ell}{2}.$$
 (41b)

Equation (40) shows that L(x) is a linear function of x on each interval between the neighboring bridges, i.e.,

$$L(x) = A_n + (x - n\ell)B_n, \tag{42}$$

for $n\ell \le x \le (n+1)\ell - 1$. Plugging (42) into (41a), we obtain

$$A_{n-1} + \ell B_{n-1} = (1-p)A_n + pn\ell. \tag{43}$$

Similarly, Eq. (41b) reduces to

$$A_n = B_n + (1 - p)[A_{n-1} + (\ell - 1)B_{n-1}] + pn\ell.$$
 (44)

Using (43), we get rid of the Bs in (44) and obtain

$$A_{n-1} - 2gA_n + A_{n+1} = -\frac{p\ell}{1-p} - pn\ell \frac{p + (2-p)\ell}{1-p}.$$
 (45)

Here, we used a shorthand notation

$$g = \frac{p(2-p)(\ell-1)+2}{2(1-p)}. (46)$$

The recurrence (45) admits a general solution

$$A_n = n\ell + \alpha + A_{\perp}\lambda_{\perp}^n + A_{\perp}\lambda_{\perp}^n, \tag{47}$$

where $A_n = n\ell + \alpha$ with $\alpha = \ell/[p + (2-p)\ell]$ is a particular solution of the inhomogeneous equation (45); the remaining contribution $A_+\lambda_+^n + A_-\lambda_-^n$ with

$$\lambda_{\pm} = g \pm \sqrt{g^2 - 1} \tag{48}$$

is the general solution of the homogeneous part of (45).

If the walker is initially located far away from the origin, $x \gg \ell$, the first bridge would burn somewhere in its proximity, that is $L(x) \sim x$. This in conjunction with (42) led to $A_n - n\ell = O(1)$ when $n \gg 1$. On the other hand, the general solution (47) grows exponentially since $\lambda_+ > 1$. This shows that the corresponding amplitude must vanish: $A_+ = 0$. Since L(x) is constant on the interval $0 \le x \le \ell - 1$, we have $B_0 = 0$, or [see (43)]

$$A_0 = (1 - p)A_1 + p\ell. (49)$$

By inserting $A_0 = \alpha + A_-$ and $A_1 = \ell + \alpha + A_-\lambda_-$ into (49) and solving for A_- , we get

$$A_{-} = \frac{\ell - p\alpha}{1 - (1 - p)\lambda_{-}}. (50)$$

Return now to the situation when the walker starts at the origin. The average displacement of the walker after the first burning event is $\langle x \rangle = L(0) = A_0 = \alpha + A_-$, or

$$\langle x \rangle = \frac{\ell}{p + (2 - p)\ell} \left[1 + \frac{(2 - p)\ell}{1 - (1 - p)\lambda_{-}} \right].$$
 (51)

In the limiting cases p=1 and $\ell=1$ we indeed recover $\langle x \rangle = \ell$ and (B9), respectively.

The second part of the program is to determine the average time when the first burning occurs. Again, we choose to investigate a more general quantity T(x). It satisfies Eq. (A2) when $x \neq n\ell - 1, n\ell$. On the boundaries of the bridges, the governing equations become

$$T(n\ell - 1) = \frac{T(n\ell - 2) + (1 - p)T(n\ell)}{2} + 1,$$
 (52a)

$$T(n\ell) = \frac{T(n\ell+1) + (1-p)T(n\ell-1)}{2} + 1.$$
 (52b)

We seek a solution of (A2), (52a), and (52b) which is invariant under the transformation $x \leftrightarrow -x$, and periodic in the large x limit. A solution to Eq. (A2) is quadratic in x, viz., $-x^2+Yx+Z$ with arbitrary Y,Z. The same holds in our situation except that solutions in different intervals between the neighboring bridges differ. Thus

$$T(x) = -(x - n\ell)^2 + (x - n\ell)Y_n + Z_n.$$
 (53)

Plugging (53) into (52a) and (52b), we obtain

$$\ell Y_{n-1} + Z_{n-1} = (1-p)Z_n + \ell^2,$$

$$\frac{Z_n - 1 - Y_n}{1 - p} = Z_{n-1} + (\ell - 1)Y_{n-1} - (\ell - 1)^2.$$

Using the first equation, we exclude the Ys from the second, which turns into a recurrence

$$Z_{n-1} - 2gZ_n + Z_{n+1} + \ell \frac{p + (2-p)\ell}{1-p} = 0,$$
 (54)

whose general solution read

$$Z_{n} = \frac{\ell}{p} + Z_{+} \lambda_{+}^{n} + Z_{-} \lambda_{-}^{n}.$$
 (55)

The symmetry $x \leftrightarrow -x$ leads to $Y_0 = 0$, or

$$Z_0 = (1 - p)Z_1 + \ell^2. (56)$$

The periodicity in the large-x limit implies that Z_n remains finite for large n. The exponentially growing part of the solution should therefore vanish, $Z_+=0$. Thus, $Z_0=Z_-+\ell/p$ and $Z_1=Z_-\lambda_-+\ell/p$. By inserting these relations into (56), we obtain

$$Z_{-} = \frac{\ell(\ell - 1)}{1 - (1 - p)\lambda_{-}}. (57)$$

Thus, the average time in the original problem is given by $\langle t \rangle = T(0) = Z_0$, or

$$\langle t \rangle = \frac{\ell}{p} + \frac{\ell(\ell - 1)}{1 - (1 - p)\lambda_{-}}.$$
 (58)

In the limiting cases p=1 and $\ell=1$ we indeed recover $\langle t \rangle = \ell^2$ and $\langle t \rangle = p^{-1}$ [Eqs. (A5) and (B2)], respectively. Finally, the velocity is

$$v = \frac{\langle x \rangle}{\langle t \rangle} = \frac{p}{p + (2 - p)\ell} \frac{1 - (1 - p)\lambda_{-} + (2 - p)\ell}{1 - (1 - p)\lambda_{-} + p(\ell - 1)}.$$
 (59)

Using (48), one can transform (59) into (5).

In the initial state all bridges are intact, and a fraction of them remains intact as the walker moves along. The walker passes on average $\langle x \rangle / \ell$ bridges per one burnt bridge. Hence, the fraction I of bridges which forever remains intact approaches

$$I = \frac{\langle x \rangle / \ell - 1}{\langle x \rangle / \ell} = 1 - \frac{\ell}{\langle x \rangle} \tag{60}$$

in the long-time limit. Using Eq. (51), one recasts (60) into Eq. (8).

The calculation of the diffusion coefficient seems to be very challenging. For a system full of bridges (c=1), however, the walk is somewhat analogous to the p=1 (and c < 1) case, and D might be possible to derive using the approach presented in Sec. III A. The complete analysis appears to be very cumbersome, but if $p \rightarrow 0$ in addition to c

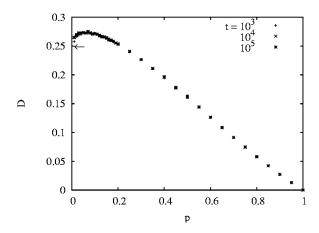


FIG. 7. Numerical results for the diffusion coefficient for a system full of bridges (c=1) as function of p for several times. The arrow points to the analytic result $D(p \rightarrow 0) = 1/4$.

=1, the successive burnt bridges are (on average) separated by large gaps and therefore one can employ a continuous treatment. Following the steps described in Sec. III A, we obtained D=1/4. This prediction agrees with simulations. Interestingly (see Fig. 7), D is a nonmonotonous function of p.

Solving the stochastic burnt-bridge model for randomly distributed bridges does not look possible in the realm of the above framework. Indeed, instead of working with ordinary *deterministic* recurrences like (45), one has to tackle *stochastic* recurrences (see Appendix C).

V. DISCUSSION

Our current understanding of the stochastic burnt-bridge model is certainly incomplete—only the periodic case is somewhat tractable, albeit even in this situation we do not know how to compute various interesting quantities like the diffusion coefficient or the probability that in the final state two nearest burnt bridges are separated by k intact bridges.

In many biological applications, molecular motors move along a homogeneous polymer filament (kinesin and myosin are classical examples [5]), while in other applications the track is inhomogeneous (this particularly happens when motors move along DNA). It would be interesting to study the burnt-bridge model when in addition to the disorder related to location of the bridges there is the disorder associated with hopping rates. Earlier work on random walkers under the influence of a random force (see Refs. [17,18] and references therein) and recent work motivated by single-molecule experiments on motors moving along a disordered track [19,20] may be useful in that regard.

Finally, we notice that the appealing simplicity of the burnt-bridge model suggests that in addition to mimicking molecular motors it may find various other applications. For instance, there is a connection between the stochastic burnt-bridge model and front propagation in autocatalytic reactions [4]. This connection inspires the analysis of the burnt-bridge model on higher dimensions, e.g., on two-dimensional lattices where a similar model [21] was utilized to mimic the

intracellular signaling mechanism by which extracellular signals are converted into cellular responses [22].

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APPENDIX A: CALCULATION OF $[t]_\ell$ AND $[t^2]_\ell$ FOR AN INTERVAL

Let t be the first passage time, namely, the time it takes for the simple random walk in an interval $[0,\ell]$ starting at site 0 to reach site ℓ for the first time, with a reflecting boundary at site 0. Here, we compute the first two moments, $[t]_{\ell}$ and $[t^2]_{\ell}$, of this random variable. We will present an elementary approach that does not require the calculation of the complete first passage probability [23]. (The calculations in Sec. IV can also be considered as a generalization of this method.)

The process can be understood in terms of a random variable t(x), which is the time it takes to reach site ℓ if the walker starts at site x. As the walker from site x steps equally probably to either side

$$t(x) = \begin{cases} t(x-1) + 1 & \text{probability } 1/2\\ t(x+1) + 1 & \text{probability } 1/2, \end{cases}$$
(A1)

and for the average time $T(x) = [t(x)]_{\ell}$, we arrive at the recursion formula

$$T(x) = \frac{1}{2} [T(x-1) + T(x+1)] + 1.$$
 (A2)

This master equation holds for $1 \le x \le \ell - 1$, while for x = 0 it should be replaced by

$$T(0) = T(1) + 1, (A3)$$

since when the walker is at site 0, it always makes a step to the right. The recurrence (A2) and (A3) is supplemented by the boundary condition $T(\ell)=0$.

Equation (A3) can be rewritten in the general form (A2) if T(-1)=T(1). Further, one finds that Eq. (A2) holds for x=-1 if T(-2)=T(2), and generally Eq. (A2) applies for all $|x| \le \ell - 1$. Hence, we seek a solution invariant under the transformation $x \leftrightarrow -x$; the absorbing boundary conditions are $T(\pm \ell)=0$. [Numerous examples of analyzing equations like (A2) with absorbing boundary conditions are described in Ref. [23].] The solution is very neat

$$T(x) = (\ell + x)(\ell - x), \tag{A4}$$

and in particular

$$[t]_{\ell} \equiv T(0) = \ell^2. \tag{A5}$$

For the derivation of the second moment, it is again convenient to consider $T_2(x) = [t^2(x)]_{\ell}$, which is the average

square time to reach site ℓ for the first time if the walker starts at position x. From Eq. (A1), one obtains the governing equation for $1 \le x \le \ell - 1$

$$0 = \frac{1}{2}D^2T_2(x) + T(x-1) + T(x+1) + 1,$$
 (A6)

where $D^2F(x)=F(x-1)-2F(x)+F(x+1)$ is the shorthand notation for the discrete derivative of the second order. For x=0 we have

$$T_2(0) = T_2(1) + 2T(1) + 1.$$
 (A7)

We can again seek a solution to Eq. (A6) satisfying the symmetry requirement $x \leftrightarrow -x$ and the absorbing boundary conditions are $T_2(\pm \ell) = 0$. Using Eq. (A4), we recast Eq. (A6) into

$$D^{2}T_{2}(x) = 4x(x+1) - 4x + 2 - 4\ell^{2},$$
 (A8)

which yields

$$T_2(x) = \frac{1}{3}x^2(x^2 + 2 - 6\ell^2) + [t^2]_{\ell},$$

with

$$[t^2]_{\ell} = \frac{1}{3}\ell^2(5\ell^2 - 2).$$
 (A9)

The derivation of the moments for the modified burnt-bridge model, where the hopping rule differs from the original model only from site 0, follows the same lines. The new rule affects only Eq. (A3), which now becomes $T(0) = \frac{1}{2}[T(0)+T(1)]+1$. This equation can be recast in the general form (A2) if T(-1)=T(0), and overall the symmetry T(x)=T(-x-1) allows us to reduce the problem to solving (A2) subject to $T(\ell)=0$ and $T(-\ell-1)=0$. The solution $T(x)=(\ell+1+x)(\ell-x)$ yields

$$[t]_{\ell} \equiv T(0) = \ell(\ell+1). \tag{A10}$$

For the second moment the governing equation is given by Eq. (A6) for $1 \le x \le \ell - 1$, and for x = 0 it is

$$T_2(0) = \frac{T_2(0) + T_2(1)}{2} + T(0) + T(1) + 1.$$
 (A11)

The boundary condition is $T_2(\ell)=0$.

A solution of Eq. (A8) invariant under the transformation $x \leftrightarrow -x-1$ and satisfying the absorbing boundary conditions $T_2(\ell) = T_2(-\ell-1) = 0$ is

$$D^2T_2(x) = 4x(x+1) + 2 - 4(\ell^2 + \ell),$$
 (A12)

which is solved to yield

$$T_2(x) = \frac{1}{3}(x-1)x(x+1)(x+2) + [1-2(\ell^2+\ell)]x(x+1) + [t^2]_{\ell},$$

with

$$[t^2]_{\ell} = \frac{1}{3}\ell(\ell+1)[5\ell(\ell+1) - 1]. \tag{A13}$$

APPENDIX B: DIRECT CALCULATION OF v(1,p)

Here, we present an alternative, direct calculation of the velocity for a lattice fully covered with bridges (c=1). At each time step, the walker makes a move, so after t time steps all bridges remain intact with probability $(1-p)^t$. Hence, the first burning event would happen at time (t+1) with probability

$$B(t) = p(1-p)^t$$
, (B1)

and thus the average time till the first burning event is

$$[t] = \sum_{t \ge 0} (t+1)p(1-p)^t = p^{-1}.$$
 (B2)

We also need the probability distribution P(x,t) of the position of the walker. As described earlier, we can consider the unconstrained random walk on the infinite line, and then "fold" it at the origin to give

$$P(x,t) = \begin{cases} P_0(x,t) + P_0(-x,t) & \text{for } x > 0 \\ P_0(0,t) & \text{for } x = 0, \end{cases}$$
(B3)

with $P_0(x,t)$ being the probability distribution of the unconstrained walker. When the walker starts from the origin at time t=0, this probability is

$$P_0(x,t) = \begin{cases} 2^{-t} \begin{pmatrix} t \\ \frac{t+x}{2} \end{pmatrix} & \text{for } t+x \text{ even} \\ 0 & \text{for } t+x \text{ odd.} \end{cases}$$
(B4)

The probability that a bridge burns at time (t+1) when the walker hops from site x is P(x,t)B(t), and the total probability is obtained after summing over all t

$$\mathcal{B}(x) = \sum_{t=0}^{\infty} P(x,t)B(t).$$
 (B5)

If the walker is hopping to the right when the burning occurs, the move is completed; otherwise, the walker remains in its position. Both of these alternatives occur equiprobably when x>0, while when x=0 the walker surely hops to the right. The average final position of the walker is therefore

$$\langle x \rangle = \mathcal{B}(0) + \sum_{r=1}^{\infty} \left(x + \frac{1}{2} \right) \mathcal{B}(x).$$
 (B6)

Using (B3) and (B5), and the identity $\Sigma_{x \ge 0} \mathcal{B}(x) = 1$, we transform (B6) into

$$\langle x \rangle = \frac{1}{2} + \frac{1}{2} \sum_{t=0}^{\infty} P_0(0, t) B(t) + \sum_{v=-\infty}^{\infty} |x| \sum_{t=0}^{\infty} P_0(x, t) B(t).$$

The first sum reduces to

$$\frac{p}{2} \sum_{k=0}^{\infty} a^{2k} \binom{2k}{k} = \frac{p}{2\sqrt{1 - 4a^2}},$$
 (B7)

where a=(1-p)/2. Next, we rewrite the second sum as

$$\sum_{t=0}^{\infty} B(t)V(t), \quad V(t) = \sum_{x=-t}^{t} |x| P_0(x,t),$$

and simplify V(t) by separately considering even and odd times

$$V(t) = \begin{cases} 2^{-2k+1} \sum_{m=-k}^{k} |m| \binom{2k}{k+m} & \text{for } t = 2k \\ 2^{-2k} \sum_{m=-k}^{k+1} |m| \binom{2k+1}{k+m} & \text{for } t = 2k+1. \end{cases}$$

Evaluating the sums (by hand or with the help of MAPLE), one obtains

$$V(t) = \begin{cases} 2^{-2k+1}(k+1) \binom{2k}{k+1} & \text{for } t = 2k\\ 2^{-2k}(k+1) \binom{2k+1}{k+1} & \text{for } t = 2k+1. \end{cases}$$

Putting this into $\Sigma_{t\geq 0}B(t)V(t)$, we find that the sum is equal to

$$2p\sum_{k=0}^{\infty} \left[a^{2k}(k+1) \binom{2k}{k+1} + a^{2k+1}(k+1) \binom{2k+1}{k+1} \right]$$
$$= 2p \left[\frac{2a^2 + a}{(1 - 4a^2)^{3/2}} \right]. \tag{B8}$$

Combining (B7) and (B8), we obtain the average displacement

$$\langle x \rangle = \frac{1}{2} + \frac{1}{2} \sqrt{\frac{2-p}{p}} \tag{B9}$$

and therefore $v = \langle x \rangle / [t] = p \langle x \rangle$ is indeed given by (6).

APPENDIX C: STOCHASTIC BURNT-BRIDGE MODEL IN THE CASE OF RANDOMLY POSITIONED BRIDGES

The formalism detailed in Sec. IV for the periodic location of bridges to the situation formally applies to the situa-

tion when bridges are arbitrarily distributed. Let (ℓ_1-1,ℓ_1) , $(\ell_1+\ell_2-1,\ell_1+\ell_2)$, etc. be bridge locations. Away from bridges the governing equation (40) is valid, while on the boundaries the modified equations are almost identical to (41a) and (41b); the only exception is that $n\ell$ should be replaced by $L_n \equiv \ell_1 + \dots + \ell_n$. The average position of the walker L(x) is again a linear function of x on each interval between neighboring bridges; for $L_n \leq x \leq L_n + \ell_{n+1} - 1$

$$L(x) = A_n + (x - L_n)B_n.$$
 (C1)

The analogs of Eqs. (43) and (44) are

$$B_{n-1} = [-A_{n-1} + (1-p)A_n + pL_n]/\ell_n,$$

$$A_n = B_n + (1-p)[A_{n-1} + (\ell_n - 1)B_{n-1}] + pL_n$$

Using the first equation, we exclude the Bs from the second and thereby recast it into a recurrence

$$\frac{A_{n+1}}{\ell_{n+1}} + \frac{A_{n-1}}{\ell_n} = \frac{A_n}{1-p} \left[p(2-p) + \frac{1}{\ell_{n+1}} + \frac{(1-p)^2}{\ell_n} \right] + p + pL_n \left[2-p + \frac{1}{\ell_{n+1}} - \frac{1-p}{\ell_n} \right].$$
(C2)

In the interesting case when the ℓ 's are independent, identically distributed random variables, one must solve the stochastic inhomogeneous recurrence (C2). Even a homogeneous version of Eq. (C2) is analytically intractable. The additional challenging feature of the inhomogeneous recurrence (C2) is infinite memory manifested by factor L_n ; as a result, it is not clear how to find a particular solution of Eq. (C2) which is required if one wants to reduce the problem to solving a homogeneous version of Eq. (C2).

The case of weak disorder is probably exceptional, e.g., it should be possible to compute the growth rates λ_{\pm} . One can, however, avoid such a lengthy analysis by noting that in the present context the condition of weak disorder implies that bridges are located almost periodically and their concentration is small ($c \le 1$). Assuming additionally that the bridge burning probability is not anomalously small, so that $c \le p$, an argument presented after Eq. (7) shows that in the leading order the burnt-bridge model must be recovered. Thus, $v \approx c$ and $D \approx (1-c^2)/3$.

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