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# Dynamic properties of molecular motors in burnt-bridge models

**Maxim N Artyomov**[1]**, Alexander Yu Morozov**[2]**,
Ekaterina Pronina**[2] **and Anatoly B Kolomeisky**[2]

[1] Department of Chemistry, Massachusetts Institute of Technology, Cambridge, MA 02139, USA
[2] Department of Chemistry, Rice University, Houston, TX 77005, USA
E-mail: maxart@mit.edu, am4@rice.edu, pronina@rice.edu and tolya@rice.edu

**Abstract.** Dynamic properties of molecular motors that fuel their motion by actively interacting with underlying molecular tracks are studied theoretically via discrete-state stochastic 'burnt-bridge' models. The transport of the particles is viewed as an effective diffusion along one-dimensional lattices with periodically distributed weak links. When an unbiased random walker passes the weak link it can be destroyed ('burned') with probability $p$, providing a bias in the motion of the molecular motor. We present a theoretical approach that allows one to calculate exactly *all* dynamic properties of motor proteins, such as velocity and dispersion, under general conditions. It is found that dispersion is a decreasing function of the concentration of bridges, while the dependence of dispersion on the burning probability is more complex. Our calculations also show a gap in dispersion for very low concentrations of weak links or for very low burning probabilities which indicates a dynamic phase transition between unbiased and biased diffusion regimes. Theoretical findings are supported by Monte Carlo computer simulations.

## Contents

## 1. Introduction

Recently much attention has been devoted to experimental and theoretical studies of motor proteins, that are active enzyme molecules that move along linear molecular tracks by consuming a chemical energy and transforming it into mechanical work [1]. Motor proteins play important role in many biological processes [2]–[4]. While conventional molecular motors are powered by the hydrolysis of adenosine triphosphate (ATP) or related compounds, it was shown recently that a protein collagenase utilizes a different mechanism for the transport along the collagen fibrils [5, 6]. It fuels its motion by a proteolysis, i.e., the collagenase catalyses the cutting of a protein filament at some specific positions, and the enzyme molecule is always found on one side of the proteolysis site. Since the collagenase molecule cannot cross the broken site once the cleavage of the filament occurred, it leads to the biased diffusion of the motor protein along the fibril.

It was suggested that the unusual dynamics of collagenase can be described by the so-called 'burnt-bridge model' (BBM) [5]–[9]. In BBM the motor protein molecule is viewed as an unbiased random walker that hops along the one-dimensional lattice composed of strong and weak links. Strong links are not affected when crossed by the walker, whereas the weak links ('bridges') might be destroyed ('burnt') with a probability $0 < p \leq 1$ when the walker passes over them; and the burnt bridges cannot be crossed again. However, theoretical studies of dynamic properties of motor proteins in BBM are still very limited. Limiting cases of very low burning probabilities and $p \to 1$ case have been analysed earlier by using spatial continuum approximation [7], which is valid only for very low concentrations of bridges. But experimental studies [5, 6] suggest that the density of proteolysis sites on collagen is significant. A different approach was utilized by Antal and Krapivsky [8], who investigated discrete-time dynamics of motor proteins. They calculated the mean drift velocity of the particle $V$ for periodically distributed bridges for the entire range of parameters, while the dispersion $D$ has been determined only for the special simple case of $p = 1$ for both periodic and random bridge distributions. However, it was pointed out later [9] that the realistic description of motor protein dynamics requires a continuous-time description since motor proteins move following Poisson statistics. It
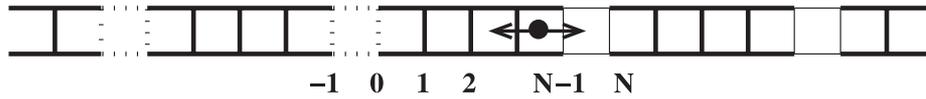
**Figure 1.** Schematic picture for the burnt-bridge model of the transport of single particles. Thick solid lines describe lattice cells with strong links that cannot be burned. Thin solid lines correspond to the weak links that can be burned with the probability $p$ when the particle crosses them from left to right. Already burned bridges are shown with dotted lines. The particle can hop with equal rates one step forward or backward unless the link is already destroyed.

is interesting to note that the behaviour similar to the burnt-bridge mechanism has also been observed in the dynamics of a classical particle in a one-dimensional randomly driven potential [10, 11].

Recently, we developed a theoretical approach to investigate continuous-time and discrete-time dynamics of collagen motor proteins in BBM [9] for the periodic distribution of weak links. First, it was shown that the special case of $p = 1$ corresponds to the motion of the single particle on infinite periodic lattices [12], for which all dynamic properties can be obtained exactly. For the general case of $p < 1$ we developed a simple method by considering a reduced chemical kinetic scheme, and some dynamic properties have been explicitly calculated. However, there is a deficiency with this method. In this approach the analytical expressions for the dispersion and correlation functions have not been obtained, although the simultaneous knowledge of the velocity and dispersion is crucial for understanding mechanisms of motor protein transport [1, 9]. The goal of the present work is to develop a comprehensive theoretical method that allows one to determine *all* dynamic properties of motor proteins in BBM for general sets of parameters.

## 2. Model

In our model the single motor protein is represented by a particle that jumps along an infinite one-dimensional lattice with transition rates in both directions assumed to be equal to one, as illustrated in figure 1. The size of the lattice spacing is also taken to be equal to one. The lattice consists of strong and weak bonds. Whereas the random walker has no effect on the strong links, it destroys the weak ones with the probability $p$ when crossing them. After the bridge is burnt, the particle is always assumed to be to the right of it. In addition, it is postulated that all bridges are intact at $t = 0$. Therefore, the trapping of the walker between two burnt bridges cannot occur, the particle continuously moves to the right.

The dynamic properties of the molecular motors in BBM strongly depend on the details of the bridge burning [9]. There are two possibilities of breaking weak links. In the first model, which we term a forward BBM, the bridge burns only when crossed from left to right, but it always stays intact if crossed in the opposite direction. In the second model, which describes a forward–backward BBM, the bridge is burnt when crossed in either direction. Both models are identical for the case of $p = 1$ because of irreversible burning. However, for the general case of $p < 1$ the walker's dynamics in two scenarios, although qualitatively similar, can show some difference [9]. For simplicity, in this paper

we will only analyse forward BBM, although our method can be easily extended for forward–backward BBM.

Two parameters specify the dynamics of the molecular motors in BBM: the burning probability $p$ and the concentration of bridges $c$. Another important factor that strongly influences the dynamic properties is the distribution of bridges [8]. Two possible distributions of weak links, periodic and random, have been considered so far [8]. In this paper we will investigate the periodic bridge distribution, in which the bridges are located at a constant distance $N = 1/c$ lattice spacings apart from each other. Thus weak links can be found at the lattice sites with the coordinates $kN$, where $k$ is integer (see figure 1). Periodic distribution of bridges is more realistic for the description of dynamics of collagenases [5, 6].

## 3. Computation of dynamic properties

Our theoretical approach is a generalization of the method proposed by Derrida for explicit calculation of dynamic properties of the random walker on infinite periodic one-dimensional lattices [12]–[14]. It was shown earlier that the original version of Derrida's method can be directly applied to the special case of BBM with $p = 1$ (with periodic bridge distribution) [9], and it leads to analytical computations of all dynamic properties of the system in this special case. However, the direct application of the method cannot be done for the case of the bridge burning with the probability $p < 1$, since it is unclear how the transition rates depend on $p$. We propose a method that explicitly takes into account the presence of the weak links, the feature that is not accounted for in the application of the original Derrida's method.

Let us define $P_{kN+i,y}(t)$ as the probability that at time $t$ the walker is at point $x = kN + i$ ($i = 0, 1, \ldots, N-1$) given that the right end of the last burnt bridge is at the point $yN$. We note that $y$ and $k \geq 0$ are some integers, and

$$R_{kN+i}(t) = \sum_{y=-\infty}^{+\infty} P_{(y+k)N+i,y}(t), \qquad (k \geq 0; i = 0, 1, \ldots, N-1), \qquad (1)$$

where $R_{kN+i}(t)$ is the probability to find the random walker $kN + i$ sites apart from the last burnt bridge at time $t$. It was found in [9] that in the stationary-state limit ($t \to \infty$) the explicit expressions for these functions are given by

$$R_{kN+i}(t \to \infty) = R_{kN+i} = R_0 x^k \Big[1 - \frac{i}{N}(1 - x)\Big], \qquad (2)$$

where

$$R_0 = \frac{2p}{\sqrt{p^2(N-1)^2 + 4pN}} = \frac{2pc}{\sqrt{p^2(1-c)^2 + 4pc}}, \qquad (3)$$

and

$$x = 1 + \tfrac{1}{2}p(N-1) - \tfrac{1}{2}\sqrt{p^2(N-1)^2 + 4pN}. \qquad (4)$$

Following the Derrida's method [12], we introduce additional auxiliary functions $S_{kN+i}(t)$,

$$S_{kN+i}(t) = \sum_{y=-\infty}^{+\infty} (yN + kN + i)P_{yN+kN+i,y}(t), \qquad (k \geq 0; i = 0, 1, \ldots, N-1). \tag{5}$$

The dynamics of the system is governed by a set of Master equations:

$$\frac{\mathrm{d}P_{yN,y}(t)}{\mathrm{d}t} = P_{yN+1,y}(t) - P_{yN,y}(t) + p\sum_{y'=-\infty}^{y-1} P_{yN-1,y'}(t), \tag{6}$$

for $k = i = 0$, and

$$\frac{\mathrm{d}P_{yN+kN,y}(t)}{\mathrm{d}t} = P_{yN+kN+1,y}(t) + (1-p)P_{yN+kN-1,y}(t) - 2P_{yN+kN,y}(t), \tag{7}$$

for $k \geq 1$ and $i = 0$. Also,

$$\frac{\mathrm{d}P_{yN+kN+i,y}(t)}{\mathrm{d}t} = P_{yN+kN+i+1,y}(t) + P_{yN+kN+i-1,y}(t) - 2P_{yN+kN+i,y}(t) \tag{8}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$. It should be noted that substituting the definition (1) into equations (6)–(8) leads to the equations for $R_{kN+i}$ that have been already obtained in [9], although through the different route,

$$\frac{\mathrm{d}R_0(t)}{\mathrm{d}t} = p\sum_{k=1}^{\infty} [R_{kN-1}(t)] + R_1(t) - R_0(t), \tag{9}$$

$$\frac{\mathrm{d}R_{kN}(t)}{\mathrm{d}t} = (1-p)R_{kN-1}(t) + R_{kN+1}(t) - 2R_{kN}(t), \tag{10}$$

for $k \geq 1$ and

$$\frac{\mathrm{d}R_{kN+i}(t)}{\mathrm{d}t} = R_{kN+i-1}(t) + R_{kN+i+1}(t) - 2R_{kN+i}(t), \tag{11}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$.

In a similar way, the time evolution of the functions $S_{kN+i}(t)$ can be obtained from equations (5) and (6)–(8). After some rearrangement it can be shown that

$$\frac{\mathrm{d}S_0(t)}{\mathrm{d}t} = S_1(t) - S_0(t) + p\sum_{\alpha=1}^{\infty} S_{\alpha N-1}(t) + p\sum_{\alpha=1}^{\infty} R_{\alpha N-1}(t) - R_1(t), \tag{12}$$

$$\frac{\mathrm{d}S_{kN}(t)}{\mathrm{d}t} = S_{kN+1}(t) + (1-p)S_{kN-1}(t) - 2S_{kN}(t) + (1-p)R_{kN-1}(t) - R_{kN+1}(t), \tag{13}$$

for $k \geq 1$ and

$$\frac{\mathrm{d}S_{kN+i}(t)}{\mathrm{d}t} = S_{kN+i+1}(t) + S_{kN+i-1}(t) - 2S_{kN+i}(t) + R_{kN+i-1}(t) - R_{kN+i+1}(t), \tag{14}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$.

At large times the solutions of equations (12)–(14) can be found assuming the following form,

$$S_j(t) = a_j t + T_j, \tag{15}$$

with time-independent coefficients $a_j$ and $T_j$. Substituting equation (15) into equations (12)–(14) yields,

$$a_1 - a_0 + p \sum_{\alpha=1}^{\infty} a_{\alpha N-1} = 0, \tag{16}$$

$$a_{kN+1} + (1-p)a_{kN-1} - 2a_{kN} = 0, \tag{17}$$

for $k \geq 1$ and

$$a_{kN+i+1} + a_{kN+i-1} - 2a_{kN+i} = 0, \tag{18}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$.

One can easily see that equations (16)–(18) are identical to the system of equations for the functions $R_j$ (equations (9)–(11)) in the stationary-state limit (with $\mathrm{d}R_j/\mathrm{d}t = 0$). Therefore their solutions are the same up to the multiplicative constant, i.e.,

$$a_{kN+i} = CR_{kN+i}, \tag{19}$$

where $R_{kN+i}$ is given by equation (2). Because of the normalization condition $\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} R_{kN+i} = 1$ [9], it follows that $C = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} a_{kN+i}$. To find it explicitly, it is convenient to write the equations for $T_j$ which result from the substitution of equation (15) into equations (12)–(14),

$$a_0 = T_1 - T_0 + p \sum_{\alpha=1}^{\infty} T_{\alpha N-1} + p \sum_{\alpha=1}^{\infty} R_{\alpha N-1} - R_1, \tag{20}$$

$$a_{kN} = T_{kN+1} + (1-p)T_{kN-1} - 2T_{kN} + (1-p)R_{kN-1} - R_{kN+1}, \tag{21}$$

for $k \geq 1$ and

$$a_{kN+i} = T_{kN+i+1} + T_{kN+i-1} - 2T_{kN+i} + R_{kN+i-1} - R_{kN+i+1}, \tag{22}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$. Summing over equations (20)–(22) produces

$$C = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} a_{kN+i} = R_0. \tag{23}$$

Therefore, according to equation (19)

$$a_{kN+i} = R_0 R_{kN+i}, \tag{24}$$

with $R_{kN+i}$ and $R_0$ given by equations (2) and (3).

Based on this analysis it is now possible to obtain the expression for the velocity of the particle. The mean position of the random walker is the following,

$$\langle x(t) \rangle = \sum_{y=-\infty}^{+\infty} \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} (yN + kN + i)P_{yN+kN+i,y}(t)$$

$$= \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} \left\{ \sum_{y=-\infty}^{+\infty} (yN + kN + i)P_{yN+kN+i,y}(t) \right\} = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} S_{kN+i}(t). \tag{25}$$

Therefore the mean velocity is given by

$$V = \frac{\mathrm{d}}{\mathrm{d}t}\langle x(t)\rangle = \sum_{k=0}^{\infty}\sum_{i=0}^{N-1}\frac{\mathrm{d}}{\mathrm{d}t}S_{kN+i}(t). \tag{26}$$

In the large-time limit it can be shown from equations (15) and (23) that

$$V(c,p) = \sum_{k=0}^{\infty}\sum_{i=0}^{N-1}a_{kN+i} = R_0, \tag{27}$$

with $R_0$ explicitly given in equation (3). Note that, as expected, this expression reproduces the result for $V(c,p)$ already obtained in [9] via the reduced chemical kinetic scheme method.

In order to calculate the diffusion coefficient $D(c,p)$, it is necessary to find functions $T_{kN+i}$ from equations (20)–(22). To this end, it is convenient to rewrite equations (20)–(22) by replacing $a_{kN+i}$ according to equations (24) and (2), and using the following relations,

$$p\sum_{\alpha=1}^{\infty}R_{\alpha N-1} - R_1 = \frac{2R_0}{N}(1-x) - R_0, \tag{28}$$

$$(1-p)R_{kN-1} - R_{kN+1} = R_{kN+i-1} - R_{kN+i+1} = \frac{2R_0}{N}(1-x)x^k, \tag{29}$$

that follow from equation (2) and equations (9)–(11) in the stationary-state limit. As a result, equations (20)–(22) are transformed into the following expressions,

$$T_1 - T_0 + p\sum_{\alpha=1}^{\infty}T_{\alpha N-1} + \Gamma - R_0 = 0, \tag{30}$$

$$T_{kN+1} + (1-p)T_{kN-1} - 2T_{kN} + \Gamma x^k = 0, \tag{31}$$

for $k \geq 1$ and

$$T_{kN+i+1} + T_{kN+i-1} - 2T_{kN+i} + \Gamma x^k + \frac{i}{N}(1-x)R_0^2 x^k = 0, \tag{32}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$. In equations (30)–(32) we defined a new function $\Gamma$,

$$\Gamma = \frac{2R_0}{N}(1-x) - R_0^2, \tag{33}$$

with $R_0$ and $x$ given by equations (3) and (4), correspondingly.

We are looking for the solution of the equations (30)–(32) in the following form,

$$T_{kN+i} = (Ak+B)x^k\left[1 - \frac{i}{N}(1-x)\right] - \frac{i(i+1)}{2}\Gamma x^k - \frac{i(i^2-1)}{6}\frac{(1-x)}{N}R_0^2 x^k - \Delta x^k. \tag{34}$$

There are three unknown variables in equation (34): $A$, $B$ and $\Delta$. It is easy to see that regardless of their values, equation (34) automatically solves equation (32). The $B$-term solves the homogeneous system (equations (30)–(32) without $\Gamma$- and $R_0$-terms) as follows from the comparison of equations (30)–(32) with equations (16)–(18) and equation (2). As we show below, the value of $B$ does not affect the result for the dispersion $D(c,p)$ and it

may remain undetermined. Therefore, there are two unknowns, $A$ and $\Delta$, that need to be determined from equations (30) and (31). Substituting equation (34) into equations (30) and (31) yields the system of equations for $A$ and $\Delta$:

$$\frac{A}{N}(1-p)[1+(N-1)x] + \Delta[-x+(1-p)] = -(1-p)\alpha, \tag{35}$$

$$A\frac{p}{N}[1+(N-1)x]\frac{x}{(1-x)^2} - \Delta\frac{p}{1-x} = \frac{p\alpha}{1-x} + R_0, \tag{36}$$

with

$$\alpha = \frac{N(N-1)}{2}\Gamma + \frac{(N-1)(N-2)}{6}(1-x)R_0^2, \tag{37}$$

while the parameters $\Gamma$, $R_0$, $x$ are given by equations (33), (3), and (4).

Solving the system of equations (35)–(36) results in the following expressions for $A$ and $\Delta$:

$$A = \frac{N(1-x)[\alpha px + R_0(1-x)(-1+p+x)]}{p[1+(N-1)x](-1+p+x^2)}, \tag{38}$$

$$\Delta = \frac{(1-p)[\alpha p + R_0(1-x)^2]}{p(-1+p+x^2)}. \tag{39}$$

Since $R_0$, $x$ (and hence $\Gamma$ and $\alpha$) are functions of $(c,p)$, equations (38) and (39) provide the expressions for $A(c,p)$ and $\Delta(c,p)$. Then substituting them into equation (34) yields the formula for $T_{kN+i}(c,p)$.

It should be pointed out that equation (34) is not the only possible form of $T_{kN+i}$ that solves the system of equations (30)–(32). As an alternative, one can use, for example, $\tilde{T}_{kN+i}$ which is the same as (34) except for the last term when $\Delta x^k$ in equation (34) is replaced by $i\tilde{\Delta}x^k$. As a result, corresponding expressions for $\tilde{A}(c,p)$ and $\tilde{\Delta}(c,p)$ can be obtained. However, these expressions are much more cumbersome than those given by equations (38) and (39), and the final resulting equation for the diffusion coefficient $D(c,p)$, as can be shown, does not depend on the specific choice of the functions $T_{kN+i}$.

In order to calculate the diffusion coefficient $D(c,p)$ additional auxiliary functions are introduced, following Derrida's method [12],

$$U_{kN+i}(t) = \sum_{y=-\infty}^{+\infty} (yN+kN+i)^2 P_{yN+kN+i,y}(t), \qquad k \geq 0, \quad i = 0, 1, \ldots, N-1. \tag{40}$$

The next step is to determine a set of equations that govern the time evolution of $U_j(t)$. Corresponding derivation is similar to that of the equations (12)–(14) for functions $S_{kN+i}$. Using the definitions of $U_{kN+i}$, $S_{kN+i}$ and $R_{kN+i}$, given by equations (40), (5) and (1) together with equations (6)–(8), leads to the following expressions,

$$\frac{\mathrm{d}U_0(t)}{\mathrm{d}t} = U_1(t) - U_0(t) - 2S_1(t) + R_1(t) + p\sum_{\alpha=1}^{\infty} U_{\alpha N-1}(t)$$

$$+ 2p\sum_{\alpha=1}^{\infty} S_{\alpha N-1}(t) + p\sum_{\alpha=1}^{\infty} R_{\alpha N-1}(t), \tag{41}$$

$$\frac{\mathrm{d}U_{kN}(t)}{\mathrm{d}t} = U_{kN+1}(t) + (1-p)U_{kN-1}(t) - 2U_{kN}(t) - 2S_{kN+1}(t)$$
$$+ 2(1-p)S_{kN-1}(t) + R_{kN+1}(t) + (1-p)R_{kN-1}(t), \tag{42}$$

for $k \geq 1$, and

$$\frac{\mathrm{d}U_{kN+i}(t)}{\mathrm{d}t} = U_{kN+i+1}(t) + U_{kN+i-1}(t) - 2U_{kN+i}(t) - 2S_{kN+i+1}(t)$$
$$+ 2S_{kN+i-1}(t) + R_{kN+i+1}(t) + R_{kN+i-1}(t), \tag{43}$$

for $k \geq 0$ and $i = 1, \ldots, N-1$.

The diffusion constant or dispersion is generally defined as

$$D = \frac{1}{2} \lim_{t \to \infty} \frac{\mathrm{d}}{\mathrm{d}t} [\langle x(t)^2 \rangle - \langle x(t) \rangle^2]. \tag{44}$$

From the definition (40) and the summation of equations (41)–(43) it follows that

$$\frac{\mathrm{d}}{\mathrm{d}t} \langle x(t)^2 \rangle = \frac{\mathrm{d}}{\mathrm{d}t} \sum_{y=-\infty}^{+\infty} \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} (yN + kN + i)^2 P_{yN+kN+i,y}(t)$$
$$= \frac{\mathrm{d}}{\mathrm{d}t} \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} U_{kN+i}(t) = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} \frac{\mathrm{d}U_{kN+i}(t)}{\mathrm{d}t} = 2S_0(t) + 2 - R_0(t), \tag{45}$$

which implies that we do not need to actually solve the system (41)–(43) to get the diffusion coefficient. In the derivation of equation (45) we also used the fact that the probabilities $R_{kN+i}(t)$ are normalized. In the stationary-state limit we have $S_0(t) \to a_0 t + T_0$, where $a_0 = R_0^2$ (from equation (24)) and $T_0 = B - \Delta$ (from equation (34)). Also, $R_0(t) \to R_0$ at steady-state conditions. Therefore,

$$\frac{\mathrm{d}}{\mathrm{d}t} \langle x(t)^2 \rangle = 2R_0^2 t + 2B - 2\Delta + 2 - R_0. \tag{46}$$

Taking into account that in the large-time limit $(\mathrm{d}/\mathrm{d}t)\langle x(t) \rangle = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} a_{kN+i} = R_0$ (see equation (27)) and $S_{kN+i}(t) \to a_{kN+i}t + T_{kN+i}$ and using the expression for $\langle x(t) \rangle$ (equation (25)), we obtain

$$\frac{\mathrm{d}}{\mathrm{d}t} \langle x(t) \rangle^2 = 2\langle x(t) \rangle \frac{\mathrm{d}}{\mathrm{d}t} \langle x(t) \rangle = 2R_0 \langle x(t) \rangle = 2R_0 \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} S_{kN+i}(t \to \infty)$$
$$= 2R_0 \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} \{a_{kN+i}t + T_{kN+i}\} = 2R_0^2 t + 2R_0 \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} T_{kN+i}. \tag{47}$$

Substituting the results (46) and (47) into equation (44) yields the diffusion constant,

$$D = \frac{1}{2} \left[ 2B - 2\Delta + 2 - R_0 - 2R_0 \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} T_{kN+i} \right]. \tag{48}$$

Note that in this expression all time-dependent terms disappear, as expected, confirming our initial assumptions.

To obtain the final expression for the dispersion in equation (48) we have to compute the term with $\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} T_{kN+i}$. It can be shown from equation (34) that

$$
\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} T_{kN+i} = \sum_{k=0}^{\infty} \sum_{i=0}^{N-1} x^k \left\{ (Ak + B) \left[ 1 - \frac{i}{N}(1-x) \right] - \frac{i(i+1)}{2} \Gamma \right.
$$
$$
\left. - \frac{i(i^2-1)}{6} \frac{(1-x)}{N} R_0^2 - \Delta \right\}. \tag{49}
$$

Utilizing the fact that

$$
\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} B x^k \left[ 1 - \frac{i}{N}(1-x) \right] = \frac{B}{2(1-x)} [N + 1 + (N-1)x] = \frac{B}{R_0}, \tag{50}
$$

(as follows from equations (3) and (4)) and

$$
\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} A k x^k \left[ 1 - \frac{i}{N}(1-x) \right] = \frac{Ax}{2(1-x)^2} [N + 1 + (N-1)x], \tag{51}
$$

yields equation (49) taking the form,

$$
\sum_{k=0}^{\infty} \sum_{i=0}^{N-1} T_{kN+i} = \frac{Ax}{2(1-x)^2} [N + 1 + (N-1)x] + \frac{B}{R_0} - \frac{N(N^2-1)}{6(1-x)} \Gamma
$$
$$
- \frac{(N-2)(N^2-1)}{24} R_0^2 - \frac{N}{1-x} \Delta, \tag{52}
$$

where we also took into account that $0 \leq x < 1$ (for $p \neq 0$) and used the following known results, $\sum_{i=0}^{N-1} i(i+1) = N(N^2-1)/3$ and $\sum_{i=0}^{N-1} i(i^2-1) = (N(N-2)(N^2-1))/4$.

Finally, substituting equation (52) into equation (48) leads to the following result for the diffusion coefficient $D$,

$$
D = \frac{1}{2} \left[ -2\Delta + 2 - R_0 - 2R_0 \left\{ \frac{Ax}{2(1-x)^2} [N + 1 + (N-1)x] - \frac{N(N^2-1)}{6(1-x)} \Gamma \right. \right.
$$
$$
\left. \left. - \frac{(N-2)(N^2-1)}{24} R_0^2 - \frac{N}{1-x} \Delta \right\} \right]. \tag{53}
$$

In this expression the undetermined parameter $B$ cancels out and does not affect the result for $D$, as was mentioned above. In the equation (53) parameters $A$, $\Delta$, $\Gamma$, $R_0$, $x$ are given explicitly by equations (38), (39), (33), (3), and (4), correspondingly; the parameter $\alpha$ in the expressions for $A$ and $\Delta$ is given by equation (37). Since all these parameters are functions of only the concentration of bridges $c$ and the burning probability $p$, equation (53) provides the exact and explicit expression for $D(c,p)$.

## 4. Illustrative examples

To illustrate our theoretical approach we compute dynamic properties of single motor protein in BBM for several sets of parameters. First, let us consider a simple case of $p = 1$, i.e., when any crossing of the bridge burns it. It can be easily shown that

$$
x = 0, \qquad R_0 = \frac{2}{N+1}, \qquad \Gamma = \frac{4}{N(N+1)^2}, \qquad \alpha = \frac{2}{3} \frac{(N-1)}{(N+1)}. \tag{54}
$$

Parameters $A$ and $\Delta$ have removable singularity at $p = 1$ (and therefore so does $D$). Thus we need to compute $\lim_{p \to 1} A$ and $\lim_{p \to 1} \Delta$. To do so we introduce a parameter $\varepsilon \ll 1$ so that $p = 1 - \varepsilon$. Then $x = \varepsilon/(N+1) + \mathrm{O}(\varepsilon^2)$ as $p \to 1$. Using this relation we obtain

$$\lim_{p \to 1} A = \frac{2}{3} \frac{N(2N+1)}{(N+1)^2}, \qquad \lim_{p \to 1} \Delta = -\frac{2}{3} \frac{(N+2)}{(N+1)}. \tag{55}$$

Then, according to equation (53) and equation (27), the dynamic properties of motor proteins are given by

$$V = \frac{2}{N+1} = \frac{2c}{c+1}, \tag{56}$$

and

$$D = \frac{2}{3} \frac{(N^2 + N + 1)}{(N+1)^2} = \frac{2}{3} \frac{(c^2 + c + 1)}{(c+1)^2}. \tag{57}$$

These expressions coincide with those obtained in [9] where the velocity and diffusion constant were computed for periodic bridge distribution with $p = 1$ from the original Derrida's method, confirming the validity of our theoretical method.

Another interesting example is $c = 1$, when every bond in the lattice is a potential bridge that can be burned. In this case all auxiliary functions can be easily obtained,

$$x = 1 - \sqrt{p}, \qquad R_0 = \sqrt{p}, \qquad \Gamma = p, \qquad \alpha = 0, \qquad A = \frac{\sqrt{p}}{2}, \qquad \Delta = -\frac{\sqrt{p}+1}{2}. \tag{58}$$

Substituting these results into equations (27) and (53), we obtain for the dynamic properties the following expressions,

$$V = \sqrt{p}, \qquad D = \tfrac{1}{2}. \tag{59}$$

It is interesting to note that in this case the mean velocity depends on the burning probability, while the dispersion is independent of $p$. When $p = 0$ the diffusion constant is equal to one because it corresponds to unbiased motion of the random walker. However, any non-zero probability of burning changes the dynamic behaviour at large times significantly by lowering fluctuations. Thus for any $p > 0$ the particle is always in the biased diffusion regime in the stationary-state limit.

Generally, in the case of very low burning probability, i.e., when $p \ll c$, we have the following expressions for the auxiliary functions (to the leading order in $p/c$),

$$x \simeq 1 - \sqrt{p/c}, \qquad R_0 \simeq \sqrt{pc}, \qquad \Gamma \simeq pc, \qquad \alpha \simeq \frac{(1-c)p}{2c},$$
$$A \simeq \tfrac{1}{2}\sqrt{p/c}, \qquad \Delta \simeq -\tfrac{1}{2}. \tag{60}$$

Then the dynamic properties are equal to

$$V \simeq \sqrt{pc}, \qquad D \simeq \tfrac{1}{2}. \tag{61}$$

In the opposite limiting case, when $c \ll p$, our calculations to the leading order in $c/p$ produce,

$$x \simeq c\left(\frac{1}{p} - 1\right), \qquad R_0 \simeq 2c, \qquad \Gamma \simeq \frac{4c^3}{p}, \qquad \alpha \simeq \frac{2}{3}, \qquad A \simeq \frac{4}{3}, \qquad \Delta \simeq -\frac{2}{3}. \tag{62}$$

The corresponding expressions for the mean velocity and dispersion are given by

$$V \simeq 2c, \qquad D \simeq \tfrac{2}{3}. \tag{63}$$

The value for the dispersion is rather unexpected since in the case of no bridges ($c = 0$) we have $D = 1$, as expected for the unbiased diffusion of the random walker.

## 5. Discussions

To test our theoretical approach, Monte Carlo computer simulations of dynamic properties of motor proteins in the burnt-bridge model have been developed. We performed computer simulations by using methods discussed in detail in [9]. Since the velocity of the motor protein in BBM has already been determined in analytical calculations and Monte Carlo simulations, we concentrated our efforts on computations of dispersion $D(c, p)$. Diffusion constants or dispersions have been calculated in simulations via the formula $D = (\langle x^2 \rangle - \langle x \rangle^2)/2t$. Since the results of computer simulations for dispersion indicate large fluctuations, especially for very low $c$ and $p$, typically $10^5$–$10^6$ simulation runs have been averaged over to decrease stochastic noise.

The results of Monte Carlo computer simulations for dispersions with different parameters are presented in figure 2. Comparison of numerical computations with analytical predictions indicates a very good agreement for all conditions, and it validates our theoretical method. As shown in figure 2(a), $D(c)$ is a monotonically decreasing function for any fixed value of $p \neq 0$ for $c > 0$, and it decreases more slowly for larger values of burning probability $p$. This behaviour is expected since the burning of the bridges limits the mobility of the hopping particle. At very low concentration of bridges ($c \ll p$) dispersion for all values of $p \neq 0$ approached a limiting value of $2/3$, in agreement with analytical predictions. However, this limiting value is less than $D = 1$ for the case of the diffusion on the lattice without bridges. In the limit of $c \to 0$ the computer simulations estimate the diffusion constant of the molecular motor as $D \approx 0.36$–$0.38$. This result can be understood in the following way. Since Monte Carlo simulations cannot run forever, the system does not reach the stationary state in this case. The particle feels the last burnt bridge as a hard wall, and the next bridge is not reached during the simulation run. Then we expect the effective dispersion of the particle obtained in simulations to approach that of a diffusing particle with reflecting boundary conditions on one side: $D = 1 - 2/\pi \approx 0.3634$. The Monte Carlo value of the diffusion constant agrees well with this result.

Dispersion as a function of the burning probability shows a more complex dependence, as illustrated in figure 2(b). For $p = 0$ the dispersion is equal to one, as expected, for any $c$. The increase in $p$ first significantly lowers the dispersion and then $D(p)$ starts to increase. This non-monotonic behaviour is rather unexpected because one can naively argue that the increase in the burning probability should limit fluctuations of the particle, leading to the decrease in the diffusion constant. One can understand the dynamics of the single particle in BBM in the following way. Irreversible burning of the bridges limits the motion of the particle in one direction, but it allows the particle to move further to the right until it crosses another bridge that will burn. It leads to larger effective hopping rates, resulting in the larger dispersions. Note that for $c = 1$ the dispersions is constant
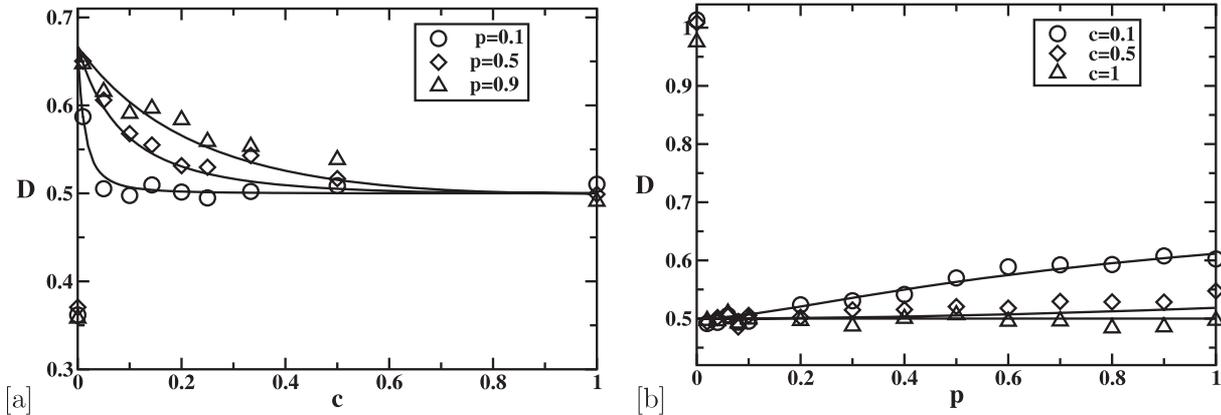
**Figure 2.** Diffusion constants of the particle in the burnt-bridge model with periodically distributed bridges: (a) as a function of concentration of bridges; and (b) as a function of burning probability. Solid lines are results of analytical calculations. Symbols are from Monte Carlo computer simulations.

and equal to $1/2$ for any $p > 0$, in agreement with theoretical predictions. In addition, $D(p) \rightarrow 1/2$ for very low probabilities of burning ($p \ll c$) and $c \neq 0$.

The presented theoretical analysis provides a full description of dynamics of motor protein in BBM. Most observed trends in the dynamic properties can be well understood, however there are several surprising observations. First, in the limit of very low concentration of bridges ($c \ll p$) our analytical calculations and computer simulations yield $D(c) = 2/3$ which is not equal to $D = 1$ expected for the case of $c = 0$. This jump in the dispersion is a signature of the dynamic phase transition [9], that separates unbiased diffusion regime ($c = 0$) from biased diffusion behaviour ($c > 0$). Similar dynamic phase transition is also taking place when $p \rightarrow 0$, with the dispersion jumping from $D(p \rightarrow 0) = 1/2$ to $D(p = 0) = 1$. Another interesting observation is the fact that $D = 1/2$ for $c = 1$ for *any* value of the burning probability $p$. This can be understood by analysing the trajectories of the particle. After the bridge is burned the random walker spends most of its time near the burning position that behaves like a hard wall and it rarely diffuses forward. This lowers significantly fluctuations in the system, and the dynamics of the particle become independent of the burning probability $p$.

## 6. Summary and conclusions

A comprehensive theoretical approach for describing the dynamics of motor protein particles in a one-dimensional burnt-bridge model with periodically distributed bridges is presented. Our theoretical method allows one to calculate exactly all dynamic properties of the system for any set of parameters, and specific calculations are given for the mean velocity and dispersion. It is found that dispersion is a monotonically decreasing function of the concentration of weak links $c$, while the dependence of $D$ on the burning probability $p$ is more complex. Trends in dispersions are discussed using simple physical arguments. Theoretical analysis also indicates that there is a gap in the dispersions in the limit of $c \rightarrow 0$, that can be associated with a dynamic phase transition between biased and

unbiased diffusion regimes. In addition, our calculations show that for any concentration of bridges the fluctuations of the particle are lowered. This is due to the fact that the particle spends most of the time near the last burned bridge that acts as a hard wall. Our theoretical findings are confirmed by extensive Monte Carlo simulations.

In this paper only periodic distribution of weak links have been considered. This situation is realistic for collagenases moving along collagen fibrils [5], although different distributions of weak links are also generally possible. It will be interesting to investigate BBM with random distribution of bridges, for which limited theoretical results are available [8]. It will also be important to generalize our theoretical approach for studying the dynamics of dimers moving on the parallel lattices in BBM. There are theoretical predictions that dimers are more effective molecular motors than monomers [6]. In addition, our theoretical method provides an explicit analysis of dynamic properties of random walkers in quasi-periodic lattice, and this results can be applied for investigation of motor protein dynamics in other systems [1].

## Acknowledgments

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