

## Walks of molecular motors in two and three dimensions

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**Abstract.** – Molecular motors interacting with cytoskeletal filaments undergo peculiar random walks consisting of alternating sequences of directed movements along the filaments and diffusive motion in the surrounding solution. An ensemble of motors is studied which interacts with a single filament in two and three dimensions. The time evolution of the probability distribution for the bound and unbound motors is determined analytically. The diffusion of the motors is strongly enhanced parallel to the filament. The analytical expressions are in excellent agreement with the results of Monte Carlo simulations.

*Introduction.* – Small particles, dispersed in a liquid, constantly undergo random movements. This was first observed by the botanist Brown and later explained by Einstein and Smoluchowski in terms of thermally excited collisions. The corresponding diffusion coefficient depends on the temperature  $T$  and on the viscosity of the liquid which reflects the balance between thermal fluctuations and viscous dissipation. Such diffusive processes are also ubiquitous in biological systems [1] and, in particular, within biological cells [2].

When the diffusing particles are attracted towards a 2-dimensional surface or a 1-dimensional filament, they can attain a bound state in which their motion is restricted to this low-dimensional manifold. Even though the corresponding diffusion coefficient is expected to be small, the reduced dimensionality of the diffusion process can enhance the probability for two diffusing particles to collide and, thus, the rate of diffusion-controlled reactions [3].

Molecular motors can bind to filaments such as microtubules or DNA and then undergo 1-dimensional diffusion or “sliding” in the absence of adenosine triphosphate (ATP). This has been observed both for cytoskeletal motors at microtubules [4] and for RNA polymerase at DNA [5]. In addition, these motors are able to hydrolyse ATP and to use the released free energy in order to change their own conformation [6,7]. In this way, detailed balance is broken and the molecular motors can perform directed walks along the filaments as studied in the framework of ratchet models, see, *e.g.*, [8] and the extensive review in [9].

Since the binding energy,  $\Delta E$ , between the motor particle and the filament is necessarily finite, the motor particle will again unbind from the filament after a certain walking time,

$\Delta t_b$ , which is of the order of  $\exp[\Delta E/k_B T]$ . On time scales which are large compared to  $\Delta t_b$ , the motor particle undergoes peculiar random walks which consist of alternating sequences of directed movement and unbiased diffusion [10, 11]. Such walks can be studied in the context of lattice models which we have recently introduced and studied for open and closed compartments using scaling arguments and Monte Carlo (MC) simulations [11].

In the present work, we consider unbounded geometries, *i.e.*, systems without confining walls, for which we are able to obtain *analytical* solutions both in two and in three dimensions. Furthermore, we show that the *diffusion of both the bound and the unbound motors* is strongly enhanced parallel to the filament. For large times, the corresponding diffusion coefficients are found to attain anomalously large values in two dimensions and to exhibit large logarithmic correction terms in three dimensions. All analytical results are compared with and confirmed by extensive MC simulations as shown in figs. 1 and 2 below.

*2-dimensional case ( $d = 2$ ).* – Consider a discrete time random walk on a square lattice with lattice sites labeled by integer coordinates  $(n, m)$ . At each step, a motor “particle” has probability  $1/4$  to jump to any of its four nearest-neighbor sites. On the line with  $m = 0$  which corresponds to the filament, the motion is different: The particle jumps forward from  $(n, 0)$  to  $(n + 1, 0)$  with probability  $1 - \gamma - \frac{1}{2}\delta - \frac{1}{2}\epsilon$  and backward from  $(n, 0)$  to  $(n - 1, 0)$  with probability  $\frac{1}{2}\delta$ , where  $\gamma$  is the probability to make no jump at all. The latter parameter is included in order to incorporate the large difference between the diffusion coefficient in the solution and on the filament [11]. In addition, the particle leaves the filament and, thus, jumps from  $(n, 0)$  to  $(n, \pm 1)$  with probability  $\frac{1}{4}\epsilon$  where the parameter  $\epsilon$  is taken to be small.

As long as the motor is bound to the filament with  $m = 0$ , it has the average velocity  $v_b = 1 - \gamma - \delta - \frac{1}{2}\epsilon$ . It also has the probability  $\frac{1}{2}\epsilon$  to unbind per unit time. Thus, the probability that the motor is still bound after  $t$  time steps is  $(1 - \frac{1}{2}\epsilon)^t \approx \exp[-\frac{1}{2}\epsilon t]$ .

As the initial distribution, we take an ensemble of non-interacting particles at  $n = m = 0$ . The master equation for this dynamics can be solved using Fourier-Laplace (FL) transforms, see, *e.g.*, [12]. The FL transforms for the full probability  $P$  and for the probability  $P_b$  to be

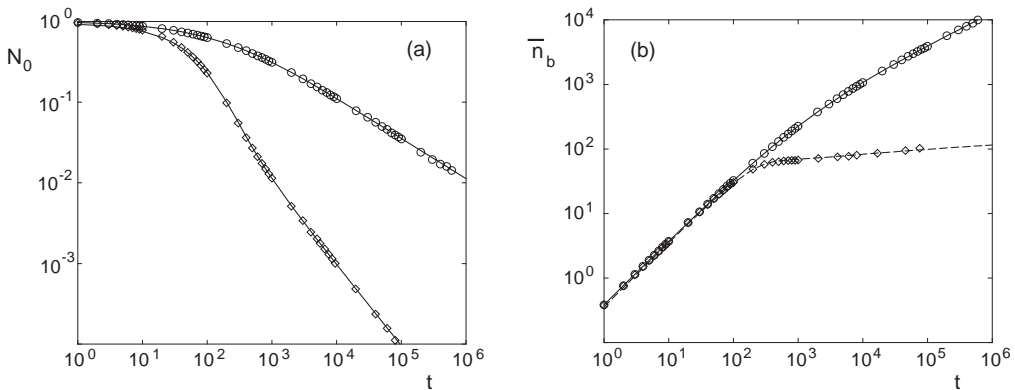


Fig. 1 – (a) Fraction  $N_0$  and (b) average position  $\bar{n}_b$  of motors bound to the filament as a function of time  $t$ . In both figures, the circles and diamonds are MC data for  $d = 2$  and  $d = 3$ , respectively, and the curves represent the analytical results, see text. For large  $t$ , the bound fraction  $N_0 \sim 1/\sqrt{t}$  in  $d = 2$  (circles) and  $N_0 \sim 1/t$  in  $d = 3$  (diamonds). The parameters, which determine the jump probabilities of the underlying random walks, have the values  $\gamma = 0$ ,  $\delta = 0.6$ , and  $\epsilon = 0.05$ .

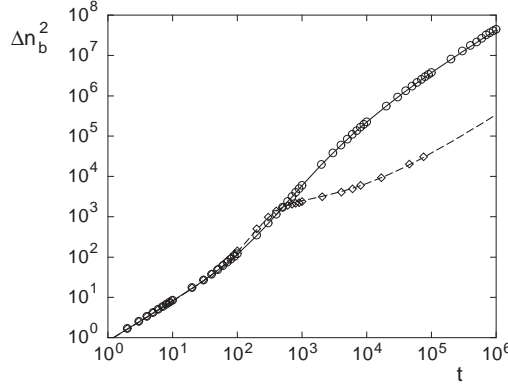


Fig. 2 – Positional variance  $\Delta n_b^2$  of bound motors as a function of time  $t$ . The MC data for  $d = 2$  (circles) and  $d = 3$  (diamonds) are again compared with the analytical results (full and dashed curve). For large  $t$ , the diffusion coefficient  $D_b(t) = \frac{1}{2} d\Delta n_b^2/dt$  attains the anomalously large value  $D_b(\infty) = \frac{v_b^2}{2\epsilon^2}(4 - \pi)$  in  $d = 2$  (circles), whereas  $D_b(t) \approx \frac{1}{6} + \frac{9v_b^2}{2\pi^2\epsilon^2} \frac{\ln t}{t}$  in  $d = 3$  (diamonds) with the usual diffusion constant  $D_b(\infty) = \frac{1}{6}$  but a large correction term  $\sim \ln t/t$ . The jump probabilities have the same values as in fig. 1.

bound to the filament are given by

$$P(q, r, s) = \sum_{t=0}^{\infty} \sum_{m, n=-\infty}^{\infty} \frac{e^{iqm+irn}}{(1+s)^{t+1}} P_{n,m}(t) \quad \text{and} \quad P_b(r, s) = \sum_{t=0}^{\infty} \sum_{n=-\infty}^{\infty} \frac{e^{irn}}{(1+s)^{t+1}} P_{n,0}(t) \quad (1)$$

and can be related to each other due to the translational invariance of the system parallel to the filament. By integration over  $q$ , one then obtains the explicit solution

$$P_b(r, s) = \frac{1}{s + (1 - \gamma)(1 - \cos r) + \frac{1}{2}\epsilon(\cos r - e^{-\mu}) - iv_b \sin r}, \quad (2)$$

where  $\cosh \mu = 2 + 2s - \cos r$ . This result is easily checked for  $\epsilon = 0$  (random walk in one dimension) and for  $\gamma = 0$ ,  $\delta = \frac{1}{2}$ , and  $\epsilon = 1$  (non-biased random walk in two dimensions). Likewise, one obtains a closed expression for  $P(q, r, s)$  and for the FL transformed distribution of the unbound motors which we define via  $P_{ub}(q, r, s) \equiv P(q, r, s) - P_b(r, s)$ .

*Fraction of bound motors.* – The fraction  $N_0(t) \equiv \sum_n P_{n,0}(t)$  of motors bound to the filament can be calculated in closed form which leads to

$$N_0(t) = \oint \frac{ds}{2\pi i} (1+s)^t P_b(r=0, s) = \int_0^{1/\epsilon^2} \frac{dy}{\pi\sqrt{y}} \frac{(1-\epsilon^2 y)^{t+1/2}}{1+(1-2\epsilon)y} \approx \int_0^{\infty} \frac{dy}{\pi\sqrt{y}} \frac{e^{-y\epsilon^2 t}}{1+y}, \quad (3)$$

where the asymptotic equality holds for small  $\epsilon$  and large  $t$ . For small  $t$ , the survival fraction  $N_0(t)$  can be expanded in powers of  $\epsilon\sqrt{t}$  which leads to  $N_0(t) \approx 1 - 2\frac{\epsilon\sqrt{t}}{\sqrt{\pi}} + \epsilon^2 t - \frac{4\epsilon^3 t^{3/2}}{3\sqrt{\pi}}$ . Thus, although the motors detach at times  $\sim 1/\epsilon$ , they stay close to the filament until times  $t \sim 1/\epsilon^2$ . For  $t \gg 1/\epsilon^2$ , on the other hand, the survival fraction decays to zero as  $N_0(t) \approx (1 - \frac{1}{2\epsilon^2 t} + \frac{3}{4\epsilon^4 t^2})/\sqrt{\pi\epsilon^2 t}$ . The complete time evolution of  $N_0(t)$ , as obtained by numerical evaluation of the exact integral in (3), is displayed in fig. 1(a). We have also determined this quantity in a completely different way using Monte Carlo (MC) simulations. Inspection of fig. 1(a) shows that the results of these two approaches agree very well.

*Average position on the filament.* – The first moment of the probability distribution  $P_{n,0}$  for the motors on the filament is given by

$$N_1(t) \equiv \sum_n n P_{n,0}(t) = \frac{2v_b}{\pi\epsilon^2} \int_0^\infty \frac{dy}{\sqrt{y}} \frac{1 - e^{-y\epsilon^2 t}}{(1+y)^2} \quad (4)$$

as follows from an expansion of (2) to first order in  $r$ . For small  $t$ , this leads to  $N_1(t) \approx v_b t [1 - (8/3\sqrt{\pi})\epsilon\sqrt{t} + \dots]$ . In the same limit, the average position  $\bar{n}_b \equiv N_1/N_0$  and the average velocity  $\bar{v}_b \equiv d\bar{n}_0/dt$  behave as  $\bar{n}_b \approx v_b t (1 - \frac{2}{3}\epsilon\sqrt{t}/\sqrt{\pi})$  and  $\bar{v}_b \approx v_b (1 - \frac{\epsilon\sqrt{t}}{\sqrt{\pi}})$ , respectively. For large  $t$ , the integral in (4) leads to  $N_1(t) \approx \frac{v_b}{\epsilon^2} (1 - \frac{2}{\epsilon\sqrt{\pi t}})$  and thus to

$$\bar{n}_b \approx \frac{v_b\sqrt{\pi t}}{\epsilon} \left(1 - \frac{2}{\epsilon\sqrt{\pi t}}\right) \quad \text{and} \quad \bar{v}_b \approx \frac{\pi}{2} N_0(t) v_b \approx \frac{\sqrt{\pi}}{2} \frac{v_b}{\epsilon\sqrt{t}}. \quad (5)$$

The complete time evolution of the average position  $\bar{n}_b$  is displayed in fig. 1(b). Again, we compare  $\bar{n}_b$  as obtained from the integrals in (3) and (4) with MC data and find very good agreement. Note that the average position  $\bar{n}_b$  of the bound motors behaves as  $\sim \sqrt{t}$  for large  $t$ . As shown below, the same time dependence applies to the average position of *all* motors as previously predicted by scaling arguments [10, 11].

*Variance and diffusion coefficient on the filament.* – The second moment of the probability distribution  $P_{n,0}$  for the bound motors is

$$N_2(t) \equiv \sum_n n^2 P_{n,0}(t) \approx \frac{1-\gamma}{v_b} N_1(t) + \frac{2v_b^2}{\pi\epsilon^4} \int_0^\infty dx \frac{(1 - e^{-x\epsilon^2 t})(1 - 3x)}{(1+x)^3 x^{3/2}} \quad (6)$$

as obtained from an expansion of (2) to second order in  $r$  and for small  $\epsilon$ . For small  $t$ , this leads to  $N_2(t) \approx (1-\gamma)t + v_b^2 t^2 (1 - \frac{16}{5} \frac{\epsilon\sqrt{t}}{\sqrt{\pi}})$ . The positional variance, defined via  $\Delta n_b^2 \equiv \frac{N_2(t)}{N_0(t)} - \frac{N_1^2(t)}{N_0^2(t)}$ , *i.e.*, with respect to the conditional probability  $P_{n,0}(t)/N_0(t)$ , then behaves as

$$\Delta n_b^2 \approx (1-\gamma)t + \frac{2v_b^2}{15} \frac{\epsilon t^{5/2}}{\sqrt{\pi}} \quad \text{for small } t. \quad (7)$$

The relative variance  $\Delta n_b^2/\bar{n}_b^2 \approx \frac{2}{15} \frac{\epsilon\sqrt{t}}{\sqrt{\pi}}$  is small since  $t \ll 1/\epsilon^2$ . We now define a *time-dependent* diffusion coefficient via  $D_b(t) \equiv \frac{1}{2} d\Delta n_b^2/dt$  which exhibits the small- $t$  behavior

$$D_b(t) \approx \frac{1}{2}(1-\gamma) + \frac{1}{6\sqrt{\pi}} v_b^2 \epsilon t^{3/2}. \quad (8)$$

In addition, the behavior for large  $t$  is found to be

$$\Delta n_b^2 \approx \frac{v_b^2}{\epsilon^2} \left(4 - \pi - \frac{2\sqrt{\pi}}{\epsilon\sqrt{t}}\right) t \quad \text{and} \quad D_b(t) \approx \frac{v_b^2}{2\epsilon^2} \left(4 - \pi - \frac{\sqrt{\pi}}{\epsilon\sqrt{t}}\right). \quad (9)$$

Note that the diffusion constant  $D_b(\infty) \sim v_b^2/2\epsilon^2$  is quite large compared to the value  $D_b(0) = \frac{1}{2}(1-\gamma)$  as appropriate for the 1-dimensional diffusion of a bound motor. In fact, one has  $D_b(t) \sim v_b^2/\epsilon^2$  as soon as  $t \gtrsim 1/\epsilon^2$ , see (8). This broadening occurs since the unbound motors lag behind the bound ones. The time-dependence of  $\Delta n_b^2$  is shown in fig. 2.

*Probability distribution on the filament.* – At large times,  $N_2/N_0 \sim (N_1/N_0)^2$  which indicates that the probability distribution attains a scaling form. It follows from (2) that  $P_b(r, s) \approx 1/(s - iv_b r + \epsilon\sqrt{s})$  for small  $r$  and  $s$ . The inverse Fourier transform gives  $P_{n,0}(s) = 0$  for  $n < 0$ . For  $n > 0$ , we close the contour along the negative real axis. After the substitution  $s = -u^2$ , the  $u$ -integral can be taken over the whole real axis, at the expense of a factor  $\frac{1}{2}$ . The integral is then Gaussian and leads to

$$P_{n,0}(t) \approx \frac{\epsilon n}{2\sqrt{\pi}v_b(v_b t - n)^{3/2}} \exp\left[-\frac{\epsilon^2 n^2}{4v_b(v_b t - n)}\right] \quad \text{for } 0 \leq n \leq v_b t, \quad (10)$$

which vanishes exponentially in  $1/(v_b t - n)$  as  $n$  approaches  $v_b t$  from below which shows that, for large  $t$ , all motors unbind before they reach the position  $n = v_b t$ .

*Properties of the unbound motors.* – Eventually all motors will become unbound and diffuse in the surrounding solution. We now discuss how this behavior is affected by the filament. The FL transformed distribution,  $P_{ub}(q, r, s)$ , of the unbound motors behaves as

$$P_{ub}(q, r, s) \approx \frac{4\epsilon\sqrt{s}}{(s - iv_b r + \epsilon\sqrt{s})(q^2 + 4s)} \quad (11)$$

for small  $q, r, s$  with  $q \sim \sqrt{s}$ . Using this asymptotic expression, we can calculate the moments  $N_a^{ub}(t) \equiv \sum_n \sum_{m \neq 0} n^a P_{n,m}$  for the distribution of the unbound motors. The fraction of unbound motors,  $N_0^{ub}$ , satisfies  $N_0^{ub}(t) = 1 - N_0(t)$ . The first moment  $N_1^{ub}$  determines the average displacement and velocity,  $\bar{n}_{ub}$  and  $\bar{v}_{ub}$ , of the unbound motors parallel to the filament via  $\bar{n}_{ub} \equiv N_1^{ub}/N_0^{ub}$  and  $\bar{v}_{ub} \equiv d\bar{n}_{ub}/dt$ . For small  $t$ ,  $\bar{n}_{ub} \approx \frac{2}{3}v_b t(1 - \frac{1}{4}\epsilon\sqrt{\pi t})$  and  $\bar{v}_{ub} \approx \frac{2}{3}v_b(1 - \frac{3}{8}\epsilon\sqrt{\pi t})$ , while for large  $t$ ,

$$\bar{n}_{ub} \approx \frac{2v_b\sqrt{t}}{\epsilon\sqrt{\pi}} \left[1 - \left(\frac{\pi}{2} - 1\right) \frac{1}{\epsilon\sqrt{\pi t}}\right] \quad \text{and} \quad \bar{v}_{ub} = \frac{v_b}{\epsilon\sqrt{\pi t}} \left[1 + \mathcal{O}\left(\frac{1}{t}\right)\right]. \quad (12)$$

Although each individual unbound motor has, on average, zero velocity, the velocity  $\bar{v}_{ub}$  is non-zero, since the cloud of unbound motors moves via repeated interactions with the filament. The average velocity of *both bound and unbound* motors is given by  $N_0\bar{v}_b + N_0^{ub}\bar{v}_{ub}$ . For large  $t$ , this latter quantity is dominated by the unbound term  $N_0^{ub}\bar{v}_{ub}$  which becomes asymptotically equal to  $N_0v_b$  in agreement with scaling arguments [11].

For small and large  $t$ , the positional variance  $\Delta n_{ub}^2$  behaves as

$$\Delta n_{ub}^2 \approx v_b^2 t^2 \frac{4}{45} \left(1 - \frac{1}{8} \frac{\epsilon\sqrt{t}}{\sqrt{\pi}}\right) \quad \text{and} \quad \Delta n_{ub}^2 \approx 2(\pi - 2)v_b^2 t/\pi\epsilon^2, \quad (13)$$

respectively. The corresponding diffusion constant is given by  $D_{\parallel}(\infty) = (\pi - 2)v_b^2/\pi\epsilon^2$ . The relation  $D_{\parallel}(\infty) \sim v_b^2/\epsilon^2$  implies that the parallel diffusion in the bulk is strongly enhanced by the presence of the filament.

The motor displacement perpendicular to the filament has the variance

$$\Delta m^2 = \frac{\epsilon}{2\pi} \int_0^\infty ds \frac{e^{-st} - 1 + st}{s^{3/2}(s + \epsilon^2)} \quad (14)$$

with the asymptotic behavior

$$\Delta m^2 \approx \frac{2\epsilon t^{3/2}}{3\sqrt{\pi}} \quad \text{and} \quad \Delta m^2 \approx \frac{1}{2}t \left(1 - 2\frac{1}{\epsilon\sqrt{\pi t}}\right) \quad (15)$$

for small and large  $t$ , respectively. Thus, the perpendicular diffusion is initially suppressed but the corresponding diffusion coefficient eventually attains its unperturbed value  $D_{\perp}(\infty) = \frac{1}{4}$ .

In real space, the probability distribution as given by (11) becomes

$$P_{n,m}(t) = \frac{\epsilon(\epsilon n + 2|m|v_b)}{2\sqrt{\pi v_b}(v_b t - n)^{3/2}} \exp\left[-\frac{(\epsilon n + 2|m|v_b)^2}{4v_b(v_b t - n)}\right] \quad \text{for } 0 \leq n \leq v_b t \quad (m \neq 0). \quad (16)$$

*3-dimensional case ( $d = 3$ ).* – Now consider the same kind of random walk but on a cubic lattice. The jump probabilities per time step are  $\frac{1}{6}$  away from the filament,  $1 - \gamma - \frac{1}{2}\delta - \frac{2}{3}\epsilon$  and  $\frac{1}{2}\delta$  in the forward and backward direction, respectively, on the filament, and  $\frac{1}{6}\epsilon$  for each of the four unbinding directions, where  $\gamma$  is again the probability to make no step at all. The average velocity within the bound state is  $v_b = 1 - \gamma - \delta - \frac{2}{3}\epsilon$ , and the probability to stay in such a bound state for  $t$  successive steps is  $\exp[-2\epsilon t/3]$ . We now denote the perpendicular coordinate by  $\mathbf{m} = (m_1, m_2)$  and the perpendicular momentum by  $\mathbf{q} = (q_1, q_2)$ . After integration over  $q_1$  and  $q_2$ , we obtain

$$P_b(r, s) = \frac{3I(r, s)}{\epsilon + [3(1 - \epsilon)s + \frac{1}{2}(\epsilon - 3\delta)(e^{-ir} - 1) - \frac{1}{2}(6 - 6\gamma - 3\delta - 5\epsilon)(e^{ir} - 1)]I(r, s)} \quad (17)$$

with

$$I(r, s) \equiv \int_0^{2\pi} \frac{dq_1 dq_2}{2\pi} \frac{1}{3 + 3s - \cos r - \cos q_1 - \cos q_2} = \frac{\sqrt{m}}{\pi} K(m), \quad (18)$$

where  $K(m) \equiv \int_0^{\pi/2} d\phi / \sqrt{1 - m \sin^2 \phi}$  is a complete elliptic integral at  $m = 4/(3 + 3s - \cos r)^2$ .

Using the explicit expressions for the FL transform of the probability distributions, one can now compute all quantities of interest for the 3-dimensional case. Since these computations are somewhat tedious, we will only present the results and describe the details elsewhere [13].

The statistical properties of the bound motors are displayed in figs. 1 and 2 where the fraction  $N_0$ , the average position  $\bar{n}_b$ , and the variance  $\Delta n_b^2$  are shown both for the 2- and the 3-dimensional case. For large  $t$ , the displacement of the unbound motors behaves as  $\bar{n}_{ub} \approx \frac{3v_b}{2\pi\epsilon}(\ln t + \gamma_E)$ . Again, this is equal to the asymptotic displacement averaged over both bound and unbound motors, and the corresponding velocity is given by  $v_b N_0(t) \approx 3v_b/(2\pi\epsilon t)$  as predicted by scaling arguments [11].

The parallel variances of the bound and unbound motor positions exhibit logarithmic corrections and behave as  $\Delta n_b^2(t) \approx \frac{t}{3} + \Psi(t)$  and  $\Delta n_{ub}^2(t) \approx \frac{t}{3} + \frac{1}{2}\Psi(t)$  for large  $t$  with  $\Psi(t) \equiv \frac{9v_b^2}{2\pi^2\epsilon^2}[(\ln t + \gamma_E)^2 - \frac{\pi^2}{3}]$ ,  $\tau_0 \equiv 3/16$ , and Euler's constant  $\gamma_E \simeq 0.5778$ . The corresponding time-dependent diffusion coefficients behave as  $D_b(t) \approx \frac{1}{6} + \frac{1}{2}\Psi'(t)$  and  $D_{\parallel}(t) \approx \frac{1}{6} + \frac{1}{4}\Psi'(t)$  with  $\Psi'(t) = \frac{9v_b^2}{\pi^2\epsilon^2 t}[\ln t + \gamma_E]$ . At the crossover time  $t \sim 1/\epsilon$ , the logarithmic terms are  $\sim \ln(1/\epsilon)/\epsilon$  and, thus, are large compared to the value  $\frac{1}{6}$  which is the diffusion coefficient of the motors in the absence of the filament. For displacements in the directions perpendicular to the filament, one finds the variances  $\Delta m_1^2(t) = \Delta m_2^2(t) \approx \frac{t}{3} - \frac{1}{2\pi\epsilon}(\ln t + \gamma_E)$  for large  $t$ .

*Filament with several protofilaments.* – Microtubules consist of 13 parallel protofilaments, on each of which motors can run. To incorporate this in our model, we assume that the pinning line at  $m = 0$  has  $k$  internal states, and  $k$  may be equal to 13. The average occupation of each of these states is denoted by  $p_{n,0}^j$ ,  $j = 1, \dots, k$ . There is a small probability,  $\frac{1}{2}\zeta$ , that a motor goes from protofilament  $j$  to  $j + 1$  in one time step, and similarly for going to protofilament  $j - 1$ . To take into account the cylindrical structure of the microtubule, we identify  $j = k$  with  $j = 0$ . We assume that, after unbinding, the motor may enter the surrounding solution at a randomly chosen neighboring site of our lattice.

In this model, the total fraction of motors at position  $n$  along the tubule is  $P_{n,\mathbf{0}} = \sum_{j=1}^k P_{n,\mathbf{0}}^j$ . The motion on the individual protofilaments can again be described by a master equation. To solve it, we introduce the Fourier transform  $P_{n,\mathbf{0}}^\omega = \sum_{j=1}^k P_{n,\mathbf{0}}^j e^{ij\omega}$  with  $\omega = 2\pi\ell/k$  with  $\ell = 0, \dots, k-1$ . At the initial time  $t = 0$ , all motors are taken to be on the filament position  $n = 0$ ,  $\mathbf{m} = \mathbf{0}$ , and on the protofilament  $j = 0$ . We then find for the asymmetric modes with  $\omega \neq 0$

$$P_b^\omega(r, s) = \frac{1}{s + 1 - (1 - \gamma - \frac{1}{2}\delta - \frac{3}{2}\epsilon)e^{ir} - \gamma - \frac{1}{2}\delta e^{-ir} + \zeta(1 - \cos \omega)}, \quad (19)$$

which, in this simple model, has decoupled from  $P_b^{\omega=0}(r, s)$ .

The bound fractions on the individual protofilaments are obtained from (19) with  $r = 0$  which leads to

$$N_0^j(t) \equiv \sum_n p_{n,\mathbf{0}}^j(t) = \frac{1}{k} N_0(t) + \frac{1}{k} \sum_{\omega \neq 0} e^{-ij\omega} e^{-\frac{3}{2}\epsilon t} e^{-\zeta(1 - \cos \omega)t}. \quad (20)$$

The first term describes the symmetric distribution of the motors over the  $k$  protofilaments and decays algebraically, see fig. 1(a). The second term represents the asymmetry arising from the initial distribution. There are two decay mechanisms of this asymmetry. The term  $\exp[-\frac{3}{2}\epsilon t]$  expresses that unbinding and subsequent rebinding to a randomly chosen protofilaments restores the symmetry. The factor  $\exp[-\zeta(1 - \cos \omega)t]$  expresses that hopping to neighboring protofilaments also restores the symmetry. The asymmetry between the average occupation of the various protofilaments thus disappears after some transient time.

In summary, we have studied the walks of molecular motors which arise from many diffusional encounters with a single filament. In the absence of confining walls or boundaries, we have been able to *analytically* calculate the statistical properties of these walks both for two and for three dimensions. The analytical expressions were found to be in excellent agreement with the results of MC simulations. The diffusion of both bound and unbound motors was shown to be strongly enhanced parallel to the filament. This enhanced diffusion could be used, *e.g.*, in order to increase the rate of diffusion-controlled chemical reactions.

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