Randomly curved runs interrupted by tumbling: A model for bacterial motion

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Small bacteria are strongly buffeted by Brownian forces that make completely straight runs impossible. A model for bacterial motion is formulated in which the effects of fluctuational forces and torques on the run phase are taken into account by using coupled Langevin equations. An integrated description of the motion, including runs and tumbles, is then obtained by the use of convolution and Laplace transforms. The properties of the velocity-velocity correlation function, of the mean displacement, and of the two relevant diffusion coefficients are examined in terms of the bacterial sizes and of the magnitude of the propelling forces. For bacteria smaller than *E. coli*, the integrated diffusion coefficient crosses over from a jump-dominated to a rotational-diffusion-dominated form.

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I. INTRODUCTION

Thirty years ago, Berg and Brown published a seminal paper on the motion of *Escherichia coli*, showing that chemotaxis towards aminoacids results from the suppression of spontaneous directional changes [1]. They presented a detailed analysis of the bacterium displacement, which has two phases: roughly straight stretches ("runs") are separated by "tumbles." During each tumble the bacterium stops for about 0.1 s and then starts a new run in a different direction. *E. coli* has several flagella spread over its surface; bacterial runs result from the synchronous counterclockwise rotation of all the flagella, while a tumble starts when one of the motors changes its direction of rotation to clockwise, changing the conformation of the corresponding filament and triggering a complex process that has only recently been understood [2,3]. In each run, *E. coli* swims at speeds of the order of 20 μm/s for about 1 s. Run durations exhibit a Poisson distribution, the Poisson rate constant being the tumble rate, whose reciprocal is the mean run duration [4]. This mechanism is used by *E. coli* and other enteric bacteria, such as *Salmonella typhimurium* to explore space and to migrate toward regions containing higher food concentrations. Despite its very different chemosensory mechanism [5], the photosynthetic bacterium *Rhodobacter sphaeroides* also exhibits chemotactic swimming similar to that of enteric bacteria. [6]

On the other hand, polarly flagellated particles reverse direction instead of tumbling [7]. In the case of marine bacteria, this seems to be an adaptive response to oceanic turbulence [8]. Berg and Brown also studied the effects of rotational diffusion, which makes completely straight runs impossible [1,9]. By assuming that the power available to an organism for swimming is proportional to its volume, Dusenbery estimated the effect of size on the ability of a free-swimming microbe to disperse in random directions or to follow external stimuli [10]. The effect of thermal noise on the motion of smaller bacteria (sizes $\lesssim 1$ μm) is stronger; in fact, marine bacteria need to swim very fast in order to cover significant distances before their direction of motion becomes randomized. Speeds of the order of 200 μm/s are common for the smallest bacteria [8,11]. As discussed by Mitchell [12,13], these high speeds put a heavy stress on the energetic resources of the smallest organisms, a problem which has been recently addressed from the point of view of the propulsion efficiency in a noisy medium [14]. From the preceding considerations, it is clear that, in addition to the stochastic changes of direction inherent to the tumbles, we must include stochastic elements in the description of the individual runs.

Various theoretical approaches have been used to investigate bacterial motion: Lovely and Dahlquist treated correlations between successive directions of motion when the tumble rate is constant [15], D'Orsogna, Suchard, and Chou developed a self-interacting random walk model for the interplay between chemotaxis and chemokinesis in one dimension [16], and Rosen analyzed bacterium mobility with a Navier–Stokes approach [17]. Schnitzer [4], on the other hand, used an effective Smoluchowski equation to describe the biased random walk of *E. coli* during chemotaxis. Later, Strong and coworkers found the optimal chemotactic strategy for *E. coli* in the high and low signal-to-noise limits [18] and Bearon and Pedley modeled chemotaxis in shear flow [19]. In this paper we adopt a different technique to model the combined effects of stochastic forces and tumbles on the bacterial motion: we use coupled Langevin equations to describe the individual runs and then we apply convolutions and Laplace transforms to integrate the runs. The results are expressed in terms of experimentally accessible parameters, such as the magnitude of the propelling force, the friction coefficient, the bacterium size, and the mean run length. For

simplicity, we will work in two dimensions. The generalization to three dimensions is algebraically involved, and does not yield relevant new physical or biological results.

II. SUPERPOSITION OF BROWNIAN AND PROPELLED MOTIONS: A MODEL FOR THE RUN

During a run, the translational motion of a bacterium can be described by a Langevin equation

$$\frac{d\vec{v}}{dt} = -\gamma\vec{v} + \vec{F}(t) + G\hat{n}, \tag{1}$$

where $\vec{v}$ is the bacterium velocity, γ is the friction coefficient, and G is the magnitude of the deterministic propelling force (per unit mass) due to flagellar motion, which we take to be directed along the bacterial axis. The direction of this axis is specified by the unit vector $\hat{n}$. The stochastic force $\vec{F}$, which is due to thermal fluctuations, is assumed to be of the white-noise type

$$\langle F_i(t)F_j(t')\rangle = A\,\delta(t-t')\,\delta_{ij}. \tag{2}$$

A stochastic torque $h(t)$ causes fluctuations in the direction $\hat{n}$ of the main axis, which makes an instantaneous angle $\theta(t)$ with the x axis. The overdamped rotational motion is described by

$$\Gamma\frac{d\theta}{dt} = h(t), \tag{3}$$

where Γ is a rotational friction coefficient. The stochastic torque is correlated as [20]

$$\langle h(t)h(t')\rangle = B\Gamma^2\delta(t-t'). \tag{4}$$

The set of stochastic equations [(1)–(4)] can be solved, yielding for the velocity components

$$v_x(t) = v_{0x}e^{-\gamma t} + e^{-\gamma t}\int_0^t d\tau e^{\gamma\tau}\{F_x(\tau) + G\cos[\theta(\tau)]\} \tag{5}$$

and

$$v_y(t) = v_{0y}e^{-\gamma t} + e^{-\gamma t}\int_0^t d\tau e^{\gamma\tau}\{F_y(\tau) + G\sin[\theta(\tau)]\}. \tag{6}$$

Here $\vec{v}_0$ is the velocity at time $t=0$.

We can now calculate the velocity-velocity correlation functions $\langle v_i(t_1)v_j(t_2)\rangle$, where the symbol $\langle\rangle$ indicates an average over the realizations of the random forces and torques. To do this, we write

$$\theta(\tau) = (1/\Gamma)\int_0^\tau dsh(s) + \theta(0) \tag{7}$$

and use the randomness of the initial conditions to compute the averages of the trigonometric functions. We further use the well-known formula for the average of an exponential [21]

$$\left\langle \exp\left[\frac{i}{\Gamma}\int_a^b dsh(s)\right]\right\rangle = \exp\left(-\frac{1}{2\Gamma^2}\int_a^b\int_a^b\langle h(s)h(s')\rangle dsds'\right). \tag{8}$$

For instance, the correlation for motion in one direction is given by

$$\langle v_x(t_1)v_x(t_2)\rangle = v_{0x}^2e^{-\gamma(t_1+t_2)} + \frac{A}{2\gamma}\varphi + \frac{2G^2}{[B^2-(2\gamma)^2]}\left[\frac{B}{2\gamma\Gamma^2}\varphi + \psi\right], \tag{9}$$

with

$$\varphi = e^{-\gamma|t_2-t_1|} - e^{-\gamma(t_1+t_2)} \tag{10}$$

and

$$\psi = e^{-(\gamma t_1+Bt_2/2)} + e^{-(\gamma t_2+Bt_1/2)} - e^{-\gamma(t_1+t_2)} - e^{-(B/2)|t_2-t_1|}. \tag{11}$$

The cross-correlation function, on the other hand, simply decays in time, $\langle v_x(t_1)v_y(t_2)\rangle = v_{0x}v_{0y}\exp[-\gamma(t_1+t_2)]$. When the average over the direction of the initial velocity is taken, the cross-correlation function vanishes.

If we use the fluctuation-dissipation theorem, $A = 2\gamma k_BT/m$ and $B = k_BT/(I\Gamma)$, where m and I are the bacterium mass and moment of inertia, respectively, and T is the temperature, we obtain for the steady state mean square speed

$$\langle v^2(t\to\infty)\rangle = 2\frac{k_BT}{m} + \frac{G^2}{\gamma^2 + \gamma k_BT/(2I\Gamma)}. \tag{12}$$

The first term results from the stochastic forces and has the usual form (of course, in a three-dimensional system it must be replaced by $3k_BT/m$). More interesting is the second term, which results from the action of the propelling forces; it is proportional to the square of the applied force, but it is reduced by friction and by rotational diffusion. At higher temperatures, the fluctuational torques decrease $\langle v^2\rangle$ by rapidly changing the direction of motion; on the other hand, an increase in either the moment of inertia or the rotational friction would slow down rotational fluctuations, contributing to increase the mean square speed. If we choose $v_0=0$, we obtain the short time approximation, $\langle v^2\rangle \sim (4\gamma k_BT/m)t$.

The orientational correlation of the bacterial axis is easy to calculate. In particular, we get

$$\langle\theta^2(t)\rangle = Bt, \tag{13}$$

i.e., the rotational diffusion coefficient is $D_r = k_BT/2I\Gamma$. We could, instead, calculate the mean speed. Assuming that the bacterium is initially at rest, with $\hat{n}\|\hat{x}$, then,

$$\langle v_x(t)\rangle = \frac{Ge^{-\gamma t}}{\gamma - D_r}[e^{(\gamma-D_r)t} - 1]. \tag{14}$$

Therefore, at short times, $\langle v_x(t)\rangle \sim Gt$. Under usual conditions, $\gamma > D_r$, and, at long times, $\langle v_x(t)\rangle \sim (G/\gamma)\exp(-t/t_1)$,

with the "randomization" time $t_1=D_r^{-1}$ being about 20 s for *E. coli* but of the order of 1/60 s for the smallest bacteria.

Additional information is provided by the average forward speed, i.e., the instantaneous speed in the direction of the bacterial axis. The result is surprisingly simple: assuming that $v_0=0$, we obtain

$$\langle \vec{v}(t)\bullet\hat{n}(t)\rangle = Gt_A[1-\exp(-t/t_A)], \tag{15}$$

where the characteristic alignment time is

$$t_A = \frac{1}{\gamma + D_r}. \tag{16}$$

To investigate size effects it is useful to approximate the bacterium by a sphere of radius R and to express our results in terms of R. If η and ρ are, respectively, the viscosity and the density, $\gamma=9\eta/(2\rho R^2)\approx(0.122/R^2)\ \mathrm{cm^2/s}$, $\Gamma=15\eta/(2\rho R^2)\approx(0.193/R^2)\ \mathrm{cm^2/s}$, and $D_r=k_BT/(8\pi\eta R^3)\approx(0.61\times10^{-13}/R^3)\ \mathrm{cm^3/s}$. Therefore, $\gamma\gg D_r$ for all bacterial sizes and $t_A\ll t_1$. By looking at the asymptotic form of $\langle v^2\rangle$, Eq. (12)

$$\langle v^2(t\to\infty)\rangle = 2\frac{k_BT}{m} + \frac{G^2}{\gamma(\gamma+D_r)} \tag{17}$$

We see that the contribution of the propelling forces is approximately $(G/\gamma)^2$, i.e., the power per unit mass $G\times(G/\gamma)$ generated by the propelling force divided by the friction coefficient, which agrees with Eq. (12) in Ref. [14]. The propelling force G depends on the microorganism state. In fact, it can be estimated from Eq. (1) by replacing v by its experimental steady-state value $\bar{v}$ and taking the time derivative and the fluctuational force equal to zero.

It is easy to apply our formulas to extract information from experimental data. For instance, we can estimate the power per unit mass, $P=G^2/\gamma$, required to propel real bacteria. The mean speed obtained by Berg and Brown for wild-type *E. coli* was $\langle v\rangle=14.2\ \mu\mathrm{m/s}$ [1]. Assuming $R=1\ \mu\mathrm{m}$, we get $P\approx25\ \mathrm{cm^2/s^3}$. This value may be compared with that corresponding to the fastest registered run for a small marine bacterium [11], for which $v=407\ \mu\mathrm{m/s}$. By taking $R=0.2\ \mu\mathrm{m}$, we obtain a remarkably high value for the power per unit mass generated by the bacterial motors: $P\approx5\times10^5\ \mathrm{cm^2/s^3}$.

The mean square speed is plotted in Fig. 1 as a function of time for representative values of the bacterial sizes and speeds. Here and in all numerical evaluations, we chose $v_0=0$ and $T=302$ K. After an initial linear increase, $\langle v^2(t)\rangle$ reaches the asymptotic value predicted by Eq. (12) in a very short time. The convergence to the asymptotic value is faster for the smaller bacteria.

An exact analytical expression can also be obtained for the mean square displacement during a run by integrating Eq. (9)

$$[\Delta x(t)]^2 = \int_0^t\int_0^t \langle v_x(t_1)v_x(t_2)\rangle dt_1dt_2. \tag{18}$$

A complicated expression follows, but at long times the motion becomes effectively diffusive

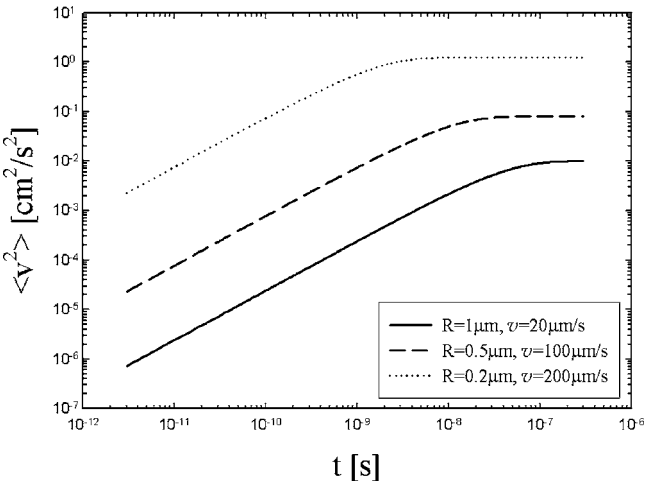

FIG. 1. Mean square speed as a function of time for three representative combinations of bacterial sizes and speeds. Starting from the top curve, these correspond to forces per unit mass equal to $6.1\times10^6\ \mathrm{cm/s^2}$, $4.9\times10^5\ \mathrm{cm/s^2}$, and $2.4\times10^4\ \mathrm{cm/s^2}$. Note the rapid evolution towards the steady-state speed given by Eq. (12).

$$Q_1 \equiv \langle(\Delta\vec{r})^2\rangle \sim 4D_1t. \tag{19}$$

The "intrarun" diffusion coefficient is

$$D_1 = \frac{k_BT}{m\gamma} + \frac{1}{2D_r}\left(\frac{G}{\gamma}\right)^2. \tag{20}$$

The diffusion coefficient contains the contributions of two different sources: to the usual Einstein term we must add the contribution of the flagellar motion, which is proportional to G^2. A strong propulsion system increases rapidly the size of the domain explored by the bacterium, even in the absence of interruptions. Note that in the absence of stochastic torques $(T\to0)$, the bacterium heading cannot change and Eq. (19) never applies. The absence of singularity in our result is confirmed by a careful evaluation of the limit.

For a bacterium of the *E. coli* size moving at 14.2 μm/s [1], $D_1\approx1.7\times10^{-5}\ \mathrm{cm^2/s}$ (of course, this cannot be directly measured unless tumbling is somehow inhibited). In the case of the extremely fast marine bacterium mentioned before, $D_1\approx1.1\times10^{-4}\ \mathrm{cm^2/s}$.

At short times, $\gamma t\ll1$,

$$Q_1 = v_0^2t^2 + \gamma\left(\frac{4k_BT}{3m} - v_0^2\right)t^3. \tag{21}$$

The propeller contribution is of order G^2t^4.

In Fig. 2 we show the mean square displacement as a function of time for various values of the propelling force G. The diffusive regime is reached after times of the order of the minute for bacteria of the size of *E. coli*, but much faster ($\sim$1 s) for the smallest bacteria. In terms of the bacterial size, the intrarun diffusion coefficient, given by Eq. (20), reads,

$$D_1 = \frac{k_BT}{6\pi\eta R} + \frac{16\pi\rho^2G^2R^7}{81\,\eta k_BT}. \tag{22}$$

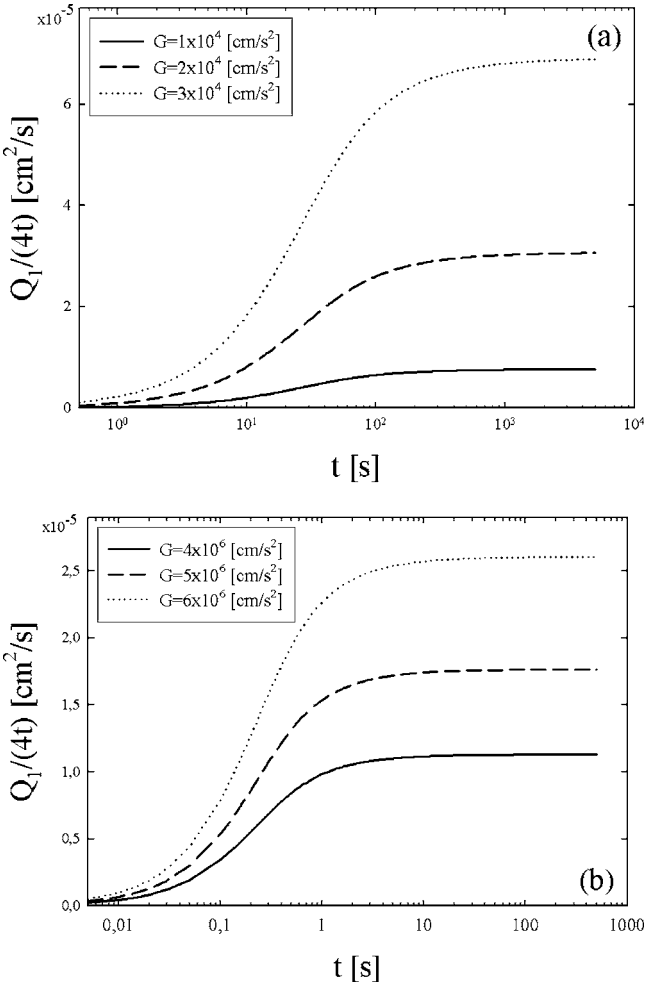

FIG. 2. Single run mean square displacements (divided by $4t$) as functions of time for the indicated values of the propelling force G for a bacterium of radius (a) $R=1$ μm and (b) $R=0.2$ μm. Steady state speeds are, starting from the bottom, $\bar{v}=8.2$, 16.4, and 24.6 μm/s in (a), and 130, 165, and 200 μm/s in (b). The diffusive regime becomes evident at long times.

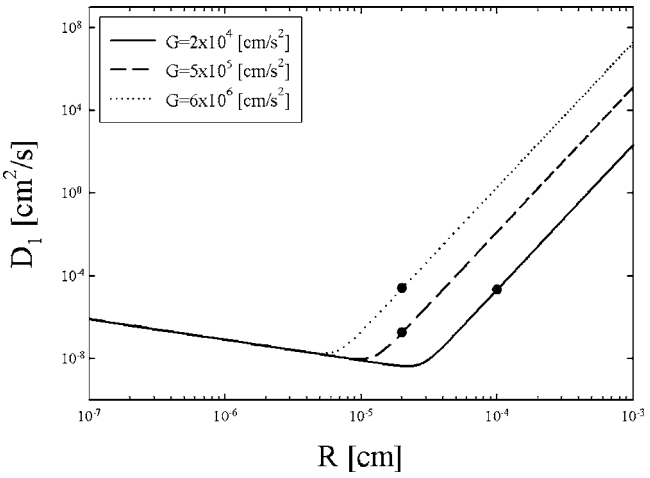

FIG. 3. Intrarun diffusion coefficient as a function of bacterial radius, for the indicated values of the propelling force. The dot on the extreme right curve corresponds to *E. coli* swimming at 16.4 μm/s, while those on the left correspond to a $R=0.2$ μm bacterium moving at 16.4 and 200 μm/s, respectively.

This function is plotted in Fig. 3 for representative values of the propelling force. Unless the bacterium is moving very slowly, the second term is dominant and the diffusion coefficient grows very fast with both G and R.

III. AN INTEGRATED DESCRIPTION OF RUNS AND TUMBLES: THE DIFFUSION COEFFICIENT

We will now integrate the description of the run and tumbles, by assuming that each run starts in an arbitrary direction and that its duration has a distribution $p_1(t)$. The probability that no interruption (tumble) has occurred in a period of length t is

$$c(t) = 1 - \int_0^t p_1(t')dt'. \tag{23}$$

The total mean square displacement is then

$$Q(t) = c(t)Q_1(t) + \int_0^t p_1(t')[Q_1(t') + Q(t-t')]dt'. \tag{24}$$

The first term on the right-hand side contains the contribution of uninterrupted runs. The second term is the contribution of the first run, interrupted at $t' < t$, while the last term contains the contribution of runs during the period $(t-t')$, following the first interruption at t'.

Defining

$$f(t) = c(t)Q_1(t) + \int_0^t p_1(t')Q_1(t')dt', \tag{25}$$

taking Laplace transforms, and solving for $\tilde{Q}(s)$ (s is Laplace's variable), we obtain,

$$\tilde{Q}(s) = \frac{\tilde{f}(s)}{1 - \tilde{p}_1(s)}. \tag{26}$$

We may further assume that the distribution of run durations is exponential, as suggested by experiments [22]; thus, $p_1(t) = (1/\tau_0)\exp(-t/\tau_0)$. In this case, upon antitransforming, we obtain an exact analytical form for $Q(t)$,

$$Q(t) = [b_1 e^{-2\gamma t} + b_2 e^{-\gamma t} + b_3 e^{-(\gamma+B)t} + b_4 e^{-(B/2)t} + b_5]e^{-t/\tau_0} + b_6 t + b_7, \tag{27}$$

where the coefficients b_i are algebraic functions of the physical parameters γ, Γ, $k_B T$, and G. At long times, Eq. (27) reduces to $Q(t) \sim 4Dt$. The complete expression for the overall diffusion coefficient is

$$D = \frac{\tau_0^2}{(1+\gamma\tau_0)(1+2\gamma\tau_0)}\left[2\frac{k_B T\gamma}{m} + \xi\frac{G^2\tau_0}{2}\right], \tag{28}$$

where

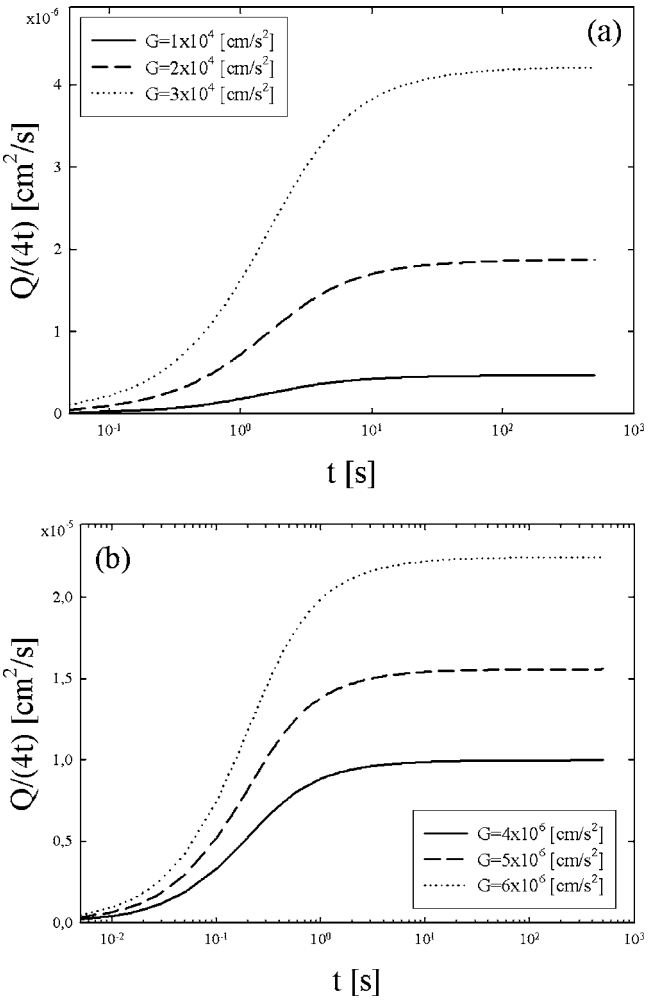

FIG. 4. Integrated mean square displacements (divided by $4t$) as functions of time for a bacterium of radius (a) $R=1$ μm and (b) $R=0.2$ μm as functions of time. Here $\tau_0=1$ s. Steady state speeds are, starting from the bottom, $\bar{v}=8.2$, 16.4, and 24.6 μm/s in (a), and 130, 165, and 200 μm/s in (b).

$$\xi = \frac{3 + 2\gamma\tau_0 + k_B T\tau_0/(I\Gamma)}{[1 + k_B T\tau_0/(2I\Gamma)][1 + \gamma\tau_0 + k_B T\tau_0/(2I\Gamma)]}. \quad (29)$$

The dependence of the mean square displacement on time is depicted in Fig. 4. Although the figure is qualitatively similar to Fig. 2, we see that for bacteria in the *E. coli* size range the diffusive regime is reached much faster (at times of the order of a few seconds): tumbles accelerate the onset of the diffusive regime. However, the diffusion coefficient turns out to be considerably smaller than that corresponding to the uninterrupted motion. On the other hand, the similarity between Figs. 2(b) and 4(b) is remarkable; moreover, if $\tau_0 \sim 1$ s, we observe that $D \approx D_1$ for small bacteria. Next we investigate the reason for this coincidence.

In general, the inequality $\gamma\tau_0 \gg 1$ is satisfied. Under these conditions, Eq. (28) can be simplified to read

$$D \simeq \frac{1}{2\gamma^2}\left[\frac{2\gamma k_B T}{m} + \frac{G^2\tau_0}{1 + D_r\tau_0}\right]. \quad (30)$$

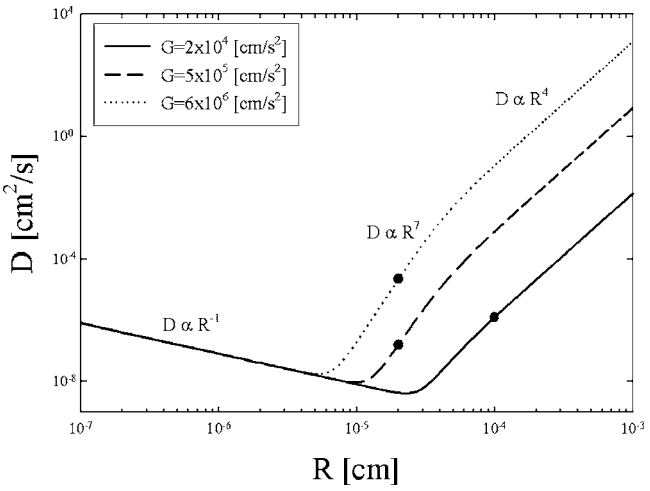

FIG. 5. Integrated diffusion coefficient as a function of bacterial radius, for the indicated values of the propelling force. The approximate dependence of D with R is also indicated. The dot on the extreme right curve corresponds to *E. coli* swimming at 16.4 μm/s, while those on the left correspond to the $R=0.2$ μm bacterium moving at 16.4 and 200 μm/s, respectively.

Unless the bacterium forward motion is very slow, the second term in this expression is dominant, and we can write, approximately,

$$D \approx \frac{\bar{v}^2\tau_0}{2(1 + D_r\tau_0)}, \quad (31)$$

where $\bar{v}=G/\gamma$. If $D_r\tau_0 \ll 1$, we are in the "jump dominated" regime and reobtain a well-known result [15]: $D \sim \bar{v}^2\tau_0/2$. If, on the contrary, we are dealing with a very small bacterium with long runs, $D_r\tau_0 \gg 1$, we are in the "rotational-diffusion dominated" regime, and $D \sim \bar{v}^2/2D_r$. By comparing with Eq. (20), we can see that $D \approx D_1$. Small bacteria can substantially reduce their diffusion coefficient by tumbling only if τ_0 is much shorter than 1 s.

The integrated diffusion coefficient is plotted in Fig. 5 as a function of bacterial size for representative values of G. As in the case of the intrarun diffusion coefficient, fast-moving bacteria are located on the upward branches of the curves (the "propulsion-dominated" regime). In this case, however, higher speeds are needed to move the bacterium out of the noise-dominated branch. As shown by the dots in the figure, the value of D corresponding to fast swimming small bacteria is about 20 times larger than that corresponding to fast swimming *E. coli*. This is in contrast with the case of D_1, for which the corresponding values differ by only 10%, approximately.

For large values of the force density, Fig. 5 exhibits three well defined regions depending on radius size. If the radius is very small, $D \sim R^{-1}$, for small bacterial sizes, $D \sim R^7$, and for large bacteria D_r becomes negligibly small and $D \sim R^4$. For small values of G, on the other hand, the R^7 regime disappears and D passes almost directly from the R^{-1} to the R^4 power law.

Let us go back to further examine Eq. (28). The diffusion coefficient is a monotonically increasing function of the run

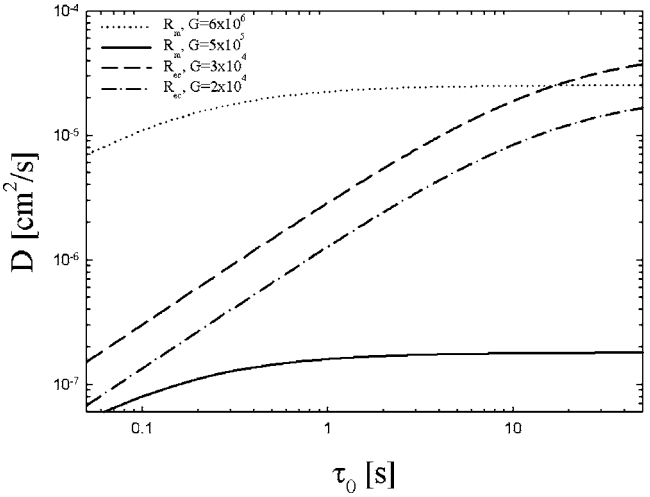

FIG. 6. Integrated diffusion coefficient as a function of mean run length for typical bacterial values, as indicated. $R_m=0.2$ μm and $R_{ec}=1$ μm are the radii corresponding to a small marine bacterium and to *E. coli*, respectively, and the units of G are cm/s^2.

duration τ_0. This was to be expected, because frequent interruptions make long-range displacement impossible. In the case of very long runs, $\tau_0\to\infty$, the diffusion coefficient approaches the single-run value: $D\to D_1$. If rotational diffusion is neglected ($I\to\infty$) and friction is high ($\gamma\tau_0\gg 1$), the diffusion coefficient corresponds to overdamped translational motion. In the small τ_0 limit all motion coherence is destroyed and the diffusion coefficient goes to zero: $D(\tau_0\to 0)\sim 24\gamma k_B\tau_0^2$. Figure 6 shows the dependence of the integrated diffusion coefficient on τ_0. For small values of τ_0, the frequent heading changes result in a sharp decrease in the mean square displacement of the particle, while for values of τ_0 longer than the times required for the onset of the intrarun diffusional regime, run interruptions become irrelevant and the integrated diffusion coefficient tends to the intrarun diffusion coefficient, $D\to D_1$: by the time a tumble occurs, all memory of the initial heading has been lost because of the thermal noise. The figure also shows that the asymptotic value is approached for run lengths τ_0 about 100 times shorter in the case of small bacteria.

Returning to Berg and Brown's wild-type *E. coli*, and using $v=14.2$ μm/s and $\tau_0=0.86$ s [1], we find from Eq. (30) that $D\approx 8.2\times 10^{-7}$ cm^2/s, a value much smaller than the one we predicted for D_1.

As already observed in Ref. [1], the bacterium optimizes its search for food by increasing the interval between interruptions when it records a positive food gradient. Brown and Berg studied bacteria moving in a homogeneous medium where the chemoattractant concentration was changing in time. They found that the characteristic run duration τ_0 depended on the chemoattractant concentration C and its time variation as [22,23],

$$\tau_0=\tau_{00}\exp\left[-\frac{a_1}{a_2+C}\Theta\left(\frac{dC}{dt}\right)\frac{dC}{dt}\right], \tag{32}$$

where a_2 is a constant concentration, τ_{00} and a_1 are constant times and $\Theta(x)$ is Heaviside's step function. In the quasistatic limit, $\tau_0|dC/dt|\ll C$, Eq. (32) can be inserted into Eqs. (28)–(31) to obtain the dependence of the diffusion coefficient with the chemoattractant concentration and its temporal variation.

IV. CONCLUSIONS

The model presented in this paper describes bacterial motion as consisting of several elements: the continuous random walk ("run"), which results from the superposition of ordinary Brownian motion and propelled motion with directional diffusion, is randomly interrupted and restarted in a different direction ("tumbling"). We have applied statistical techniques to describe the single runs of a small self-propelled object, and the integrated superposition of runs and tumbles. The main result is an expression for the long-time diffusion coefficient [Eqs. (28) and (29)] which shows that tumbling always leads to a reduction of the diffusion coefficient. If tumbles were inhibited, bacteria in the *E. coli* size range would reach the diffusive regime in times of the order of a few minutes, while the addition of the tumbles reduces this time to a few seconds. This reduction does not occur for a very small bacterium. Although, for a given bacterium, the functional forms of the mean square displacements $Q_1(t)$ and $Q(t)$ are very similar, the diffusion coefficient corresponding to an ideal tumbleless bacterium is usually one order of magnitude larger than that for tumbling bacteria in the *E. coli* size range. As a consequence, space exploration by these bacteria is made *less* efficient by tumbling. This indicates that the evolutionary reason for the existence of tumbling may have been the need to respond to chemotactic signals rather than a means to explore larger volumes.

ACKNOWLEDGMENTS

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