

PAPER



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Langevin equations for the run-and-tumble of swimming bacteria

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The run and tumble motions of a swimming bacterium are well characterized by two stochastic variables: the speed $v(t)$ and the change of direction or deflection $x(t) = \cos \varphi(t)$, where $\varphi(t)$ is the turning angle at time t . Recently, we have introduced [G. Fier, D. Hansmann and R. C. Buceta, *A stochastic model for directional changes of swimming bacteria*, *Soft Matter*, 2017, **13**, 3385–3394.] a single stochastic model for the deflection $x(t)$ of an *E. coli* bacterium performing both types of movement in isotropic media without taxis, based on available experimental data. In this work we introduce Langevin equations for the variables (v, x) , which for particular values of a control parameter β correspond to run and tumble motions, respectively. These Langevin equations have analytical solutions, which make it possible to calculate the statistical properties of both movements in detail. Assuming that the stochastic processes x and v are not independent during the tumble, we show that there are small displacements of the center of mass along the normal direction to the axis of the bacterial body, a consequence of the flagellar unbundling during the run-to-tumble transition. Regarding the tumble we show, by means of the directional correlation, that the process is not stationary for tumble-times of the order of experimentally measured characteristic tumble-time. The mean square displacement is studied in detail for both movements even in the non-stationary regime. We determine the diffusion and ballistic coefficients for tumble- and run-times, establishing their properties and relationships.

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1 Introduction

Currently, self-propelled microorganisms (SPM) without taxis (or directed motion) are studied as systems capable of remaining out of equilibrium, transiting between two or more metastable states. SPM under taxis (chemical, thermal, or electromagnetic, among others) can retain this behaviour even by moving in the direction of the gradient of the guide field.¹ Flagellated SPM (bacteria, algae, protozoa, sperm, *etc.*) have developed efficient mechanisms to move in bulk fluids or thin fluid layers on moist surfaces.² The basic movements of flagellated bacteria include translational and rotational degrees of freedom which may be restricted by constraints that are imposed by the medium geometry or by neighbouring congeners. In turn, the required resources (nutrients, temperature, oxygen, or other) facilitate the development and movement to explore and colonize the environment.^{3–5}

The locomotion mode of the motile flagellated bacteria (MFB) is referred to as swimming when bacterium moves individually in bulk liquid, and is called swarming when the

bacteria move collectively in a liquid thin film over a moist surface. Low density populations of MFB immersed in fluid media without constraints and low Reynolds number show movement patterns which depend on their species and strain, *e.g.* run-tumble, run-reverse or run-reverse-flick. MFB move rotating their helical flagella (*e.g.* *Escherichia coli* or *Salmonella typhimurium*), which are jointed to a reversible rotary motor.⁶ A bacterium runs or turns when its flagellum or flagella (forming a bundle) spin with a fixed chirality. The *E. coli* motion is reduced to two consecutive steps called run and tumble. During the run, the flagella bundle of *E. coli* spins counterclockwise (CCW), viewed from behind. In contrast, during the slowdown (with reverse thrust) the flagella spin clockwise (CW).⁷ The change in the spinning direction (CCW to CW) unbundles the flagella⁸ rotating *E. coli* around its center of mass.⁹ It is widely accepted that, during the tumble, the bacterium only changes the direction, leaving the center of mass without movement. However, unbundling flagella slightly moves the center of mass of the bacterium;⁸ this little studied aspect will be dealt with in this paper. After tumbling, the motor reversal (CW to CCW) forms a new flagella bundle that spins generating a drive in the new run direction. *E. coli* is the most studied MFB, in both its genomic and its internal biochemical processes.^{1,10} Well-established experimental results concerning the run-and-tumble movement of *E. coli* allow further theoretical studies and conclusions can be extended to other MFB.

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The path of a swimming bacterium consists of quasi-straight sections called runs, which are connected by tumbles or abrupt turns. This path is characterized at a time t by its position $\mathbf{r}(t)$ in the three-dimensional reference frame. Each tumble motion is performed in the plane spanned by two consecutive runs (*i.e.* run-tumble-run), here called tumble-plane. Successive tumble-planes are connected to each other by a rotation. The velocity $\mathbf{v}(t)$ of the swimming bacterium on a tumble-plane can be specified by defining an intrinsic reference frame with two coordinate axes, where (v_x, v_y) are Cartesian coordinates or (v, φ) are polar coordinates. In the tumble-plane the velocity is

$$\mathbf{v}(t) = v(t)\mathbf{e}(t), \quad (1)$$

where $\mathbf{e}(t)$ is the heading unit vector, which sets the orientation (or polarity) of the bacterium, *e.g.* the *E. coli* orientation from the tail to the head. There is always a preferred direction of movement, which usually matches head–tail axis. However, the orientation does not always coincide with the direction of movement. The speed $v(t)$ can be positive or negative according to the bacteria moving forwards or backwards, respectively, *e.g.* running or tumbling *E. coli* have speeds which are greater than or equal to zero. The orientation, in terms of the deflection $x(t) = \cos[\varphi(t)]$, is

$$\mathbf{e}(t) = x(t)\mathbf{e}_0 + \sqrt{1 - [x(t)]^2}\mathbf{n}_0, \quad (2)$$

with $(\mathbf{e}_0, \mathbf{n}_0)$ the canonical basis on the tumble-plane and where $\mathbf{e}_0 = \mathbf{e}(t_0)$, taking $\varphi(t_0) = 0$ (see plot (a) of Fig. 1). The movement of the SPMs is frequently studied as a the stochastic process described by stochastic differential equations (called Langevin equations). The Langevin equations can include terms of external and self-propelling forces, and noise (due to random forces or torques). Particularly, Langevin equations have been used to model experimental observations on the cells' motion.^{11,12} In order to find the Langevin equation for the velocity \mathbf{v} it is useful to note that the acceleration, in terms of its tangential and normal components, is

$$\dot{\mathbf{v}}(t) = \dot{v}(t)\mathbf{e}(t) + \frac{v(t)\dot{x}(t)}{\sqrt{1 - [x(t)]^2}}\mathbf{n}(t), \quad (3)$$

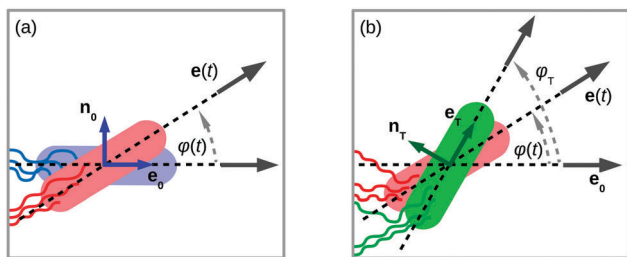


Fig. 1 Plot (a): shows the orientation of the bacterium at time t in terms of the unit vector $\mathbf{e}(t)$, with $\varphi(t)$ being the turning angle respect to the incoming direction $\mathbf{e}_0 = \mathbf{e}(t_0)$, for both tumble and run motions. Eqn (2) gives us the vector $\mathbf{e}(t)$ in terms of the canonical basis $(\mathbf{e}_0, \mathbf{n}_0)$ and its normal vector is $\mathbf{n}(t) = \sqrt{1 - x^2}\mathbf{e}_0 - x\mathbf{n}_0$. Plot (b): shows the orientation of the bacterium at time t in terms of the unit vector $\mathbf{e}(t)$, with $\varphi(t) - \varphi_T$ the angle respect to the outgoing direction $\mathbf{e}_T = \mathbf{e}(t_T)$, for the tumble motion. Eqn (22) gives us the vector $\mathbf{e}(t)$ in terms of the canonical basis $(\mathbf{e}_T, \mathbf{n}_T)$.

where $\mathbf{n}(t)$ is the normal vector to the trajectory (see Fig. 1 for details) and the overdot indicates derivative with respect to time. It is easy to show that the component of the normal acceleration is $a_n = -v\dot{\varphi}$ and the angular velocity is $\mathbf{e} \wedge \dot{\mathbf{e}} = \dot{\varphi}\mathbf{u}$, where $\mathbf{u} = \mathbf{e}_0 \wedge \mathbf{n}_0$ is the normal unit vector to the tumble-plane. In this work, we propose Langevin equations for the stochastic variables $x(t)$ and $v(t)$, which determine the velocity $\mathbf{v}(t)$ on a tumble-plane given by eqn (1). In such way, we can treat the run and tumble movements following two-dimensional classical approaches.¹³ The velocity $\mathbf{v}(t)$ of a bacterium is assumed to be a continuous-time stochastic process in 2-dimensions whose statistical properties will be studied in this paper. On this reference frame, in a lapse $[t_0, t]$ the displacement of the center of mass of a bacterium (for run or tumble motion) is $\mathbf{r}(t) - \mathbf{r}(t_0) = \int_{t_0}^t \mathbf{v}(t')dt'$. We show that the velocity correlation $\langle \mathbf{v}(t') \cdot \mathbf{v}(t'') \rangle$ and the mean-squared displacement (MSD) $\langle |\mathbf{r}(t) - \mathbf{r}(t_0)|^2 \rangle$ for the run and tumble movements can be conveniently described in this reference frame.

The noise includes the effects of the collisions of the SPM, or the internal processes responsible for locomotion (*e.g.* flagellar motor), among others. The noise takes into account all the fast variables of the system which have very small characteristic-times compared to the time-scale of tumble or run processes. During the run bacteria move steadily forwards with noise fluctuations in their orientation and speed. On the contrary, during the tumble, the bacteria stop moving forwards and perform turning movements that include noise fluctuations in their orientation and speed.

Throughout a century, great efforts have been made to develop a theoretical description that includes all the characteristics experimentally observed in the run and tumble movements. Initially, the movement of the SPMs was associated with the Brownian motion;¹⁴ subsequently, the tendency to maintain the run direction led to the idea of persistent random walks.¹⁵ Several works regarding run and tumble dynamics and chemotaxis are based on this, interpreting random re-orientations produced by active tumble motions analogously to collisions between diffusing molecules. Lovely and Dahlquist (LD)¹⁶ were the first who proposed that the behavior of *E. coli* could be approximated by straight runs interrupted by instantaneous turns where the microscopic parameters, speed and collision rates are constant. A general theoretical framework of run and tumble motions, which is based on an effective Smoluchowski equation, has been developed by Schnitzer.¹⁷ Here microscopic parameter depend on the direction of the bacterial movement. This allowed to carry out studies of *E. coli* in non-isotropic mediums where the tumble rate varies with position depending on the concentration of attractants (or repellents). Further generalizations of the LD model,¹⁶ which involve to non-Poissonian run and tumble dynamics¹⁸ or alternating different tumbles events,¹⁹ were developed recently. Additionally, the run and tumble dynamics have been recently be studied as curved runs interrupted by tumbles by Condat *et al.*²⁰ using the Langevin approach.

Most of the existing models which describe the run and tumble motion using a Langevin equation for the speed $v(t)$ include a drift term capable of describing both movements in a steady state. Fier, Hansmann and Buceta (FHB)²¹ have recently

derived Langevin equations for the orientation change $x(t)$ of the bacterium in the run and tumble movements which are able to describe completely the well-known experimental results of Berg and Brown (BB).²² Based on the same experimental data, six years ago Saragosti *et al.*²³ proposed a pure rotational diffusion process in order to model the tumble motion. In contrast, the FHB model assumes that the tumble motion is the result of a stochastic process governed by rotational thrust and complemented by noise. In addition, the same Langevin equation is able to model the orientation changes of the bacteria during the run motion, varying the parameters of the FHB model to reproduce a Ornstein–Uhlenbeck (OU) process. The tumble processes are usually negligible when it is assumed that the tumble-time is one order of magnitude less than the runtime. FHB model has shown that the ratio between mean runtime and mean tumble-time allows to establish a single model for both movements. The changes of orientation or deflections $x(t)$ of the bacteria are fully described by the following Langevin equation

$$\dot{x} = -\frac{dU}{dx} + \eta_x(t), \quad (4)$$

where $\eta_x(t)$ is Gaussian white noise with zero-mean and $U = U(x)$ is a phenomenological potential which has been derived by FHB from the measurements made by BB for the tumble-angle distribution $P(\varphi_T)$.²² Assuming that the probability density function (PDF) of tumble-angle deflection is $P(x_T) = \mathcal{N}e^{-U(x)}$, with $x_T = \cos \varphi_T$ and \mathcal{N} the normalization constant, we proposed the potential

$$U(x) = U_0 - \rho \left[x - \frac{\gamma}{\delta} \cosh(\delta x) \right] \quad (5)$$

in ref. 21, where U_0 is an adjustable constant and the constant parameters $\{\delta, \gamma, \rho\}$ are able to specify both movement states, *i.e.* the deflection in the run and tumble (see Fig. 2). The three parameters are linked together by the phenomenological relationship

$$\rho^2 \delta \sqrt{1 + \gamma^2} = C = \text{const.} \quad (6)$$

The values are $\rho(\delta_T, \gamma_T) = 1$ for the tumble and $\rho(\delta_R, \gamma_R) = r > 1$ for the run, where the sub-index $T(R)$ denotes the value that corresponds to the tumble (run) movement. The estimated values are $\delta_T = 9.062$ and $\gamma_T = 6.63 \times 10^{-3}$ for the tumble

motion, and $\delta_R = 4.71 \times 10^{-2}$ and $\gamma_R = 4.98$ for the run motion.²¹ With this data, using eqn (6), the constant is $C \approx \delta_T$ and the calculated ratio $r \approx \sqrt{\delta_T/(\delta_R \gamma_R)} \approx 6.21$ is very close to the experimental ratio for *E. coli* measured by Berg and Brown $r_{\text{exp}} \approx 6.14$.²²

Experimentally, it has been shown that the run- and tumble-times are random variables that follow an exponential distribution.²² Here, the run- or tumble-times correspond to the moments when the run or tumble movements stop, respectively. FHB have shown that the turning of the bacteria in the tumble motion is well characterized by a non-stationary stochastic process.²¹ Also, FHB have shown that the turning in the run motion is characterized by an Ornstein–Uhlenbeck process. The FHB model shows that different turn movements of swimming *E. coli* are characterized by a control parameter β that takes values $\beta_T \approx 1$ (for tumble) or $\beta_R \approx 0$ (for run). Both values of β are connected by a transition that passes through the critical value $\beta_c = 0$. The parameter β is related to the parameters $\{\delta, \gamma, \rho\}$ of Langevin eqn (15) by (see details in ref. 21)

$$\beta(\gamma, \delta) = -\frac{4}{\gamma^2} \left(\frac{\gamma e^{-\delta} + 1 - \sqrt{1 + \gamma^2}}{\gamma e^{-\delta} + 1 + \sqrt{1 + \gamma^2}} \right), \quad (7)$$

which is used to estimate values for *E. coli*: $\beta_T \approx 0.965$ and $\beta_R \approx -0.010$.

In the context of SPM modeling it is important to note that, besides minor similarities, there are big differences between colloidal systems and SPMs. Colloids are passive particles that perform Brownian motion in thermal equilibrium and whose mean velocity goes to zero for long times. In contrast, SPMs are particles that move actively in their environment and have a characteristic nonzero mean velocity for long times. Without additional external forces on the particle, the Langevin equation for the speed of the SPMs is

$$\dot{\mathbf{v}} = -\lambda(\mathbf{r}, \mathbf{v})\mathbf{v} + \eta_v(t), \quad (8)$$

where λ is an effective friction coefficient that depends on velocity \mathbf{v} in all cases. The noise $\eta_v(t)$ is Gaussian white with zero-mean. All models proposed for the coefficient of friction $\lambda(\mathbf{v})$ have in common that, at high speeds, energy is dissipated with $\lambda(\mathbf{v}) > 0$ and, for low speeds, the internal energy is converted into active motion with $\lambda(\mathbf{v}) < 0$ (active friction).²⁴

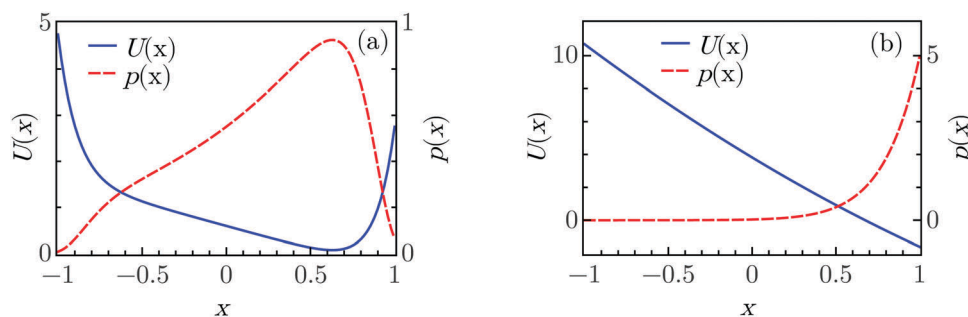


Fig. 2 Both plots show the potential $U(x)$ given by eqn (5) and the PDF $p(x) = \mathcal{N}e^{-U(x)}$ as a functions of the deflection x , where \mathcal{N} is the normalization constant. The chosen constants are: for the tumble motion (plot (a)) $\rho = 1$, $\gamma = 6.63 \times 10^{-3}$, and $\delta = 9.062$; for the run motion (plot (b)) $\rho = 6.15$, $\gamma = 4.980$, and $\delta = 4.71 \times 10^{-2}$.

A well-known example of a velocity-dependent friction function that vanishes at $v = v_s$, introduced by Schienbein and Gruler,¹³ is

$$\lambda(\mathbf{v}) = \lambda_0 \left(1 - \frac{v_s}{v}\right), \quad (9)$$

with $v > 0$, which allows to describe the active movement of different types of cells.²⁵ In this work we will give a very precise physical meaning at the steady speed v_s in terms of the values that β takes in both run and tumble movements.

Here, we investigate a single stochastic model for the run and tumble motions of a swimming flagellated bacterium, starting from the Langevin equations for the speed $v(t)$ and deflection $x(t)$, and we study statistical properties of both movements. In Section 2, we present the Langevin equations and their solutions *via* the Green function method. Statistical properties of the tumble motion are determined in Section 3. First, we show that there is a small normal component of the average velocity to the axis of the bacterium body, which is a consequence of flagellar unbundling in the transition from CCW to CW. Then, we show that the directional correlation is non-stationary at tumble-times. Finally, in the same section, we show that the mean square displacement (MSD) is a relevant quantity in the tumble motion, even though the translation speeds are negligible, since it can explain the diffusion and ballistic behaviours at tumble times. In Section 4, we determine the MSD of the run motion as a function of the initial conditions and the noise intensities for both the speed and the deflection, obtaining the properties of the diffusion and the ballistic movement at runtimes. Finally, we present the conclusions of this work and an outlook.

2 Langevin equations and its solutions for the run and tumble motions

The velocity \mathbf{v} of a flagellated bacterium that performs run and tumble movements can be completely characterized by its speed v and deflection x respecting a reference frame, both as a function of time t . We propose Langevin equations for the stochastic variables x and v . For deflection x we use eqn (15) in view of the fact that it reproduces the experimental results.²¹ For the speed v we use a slightly generalized version of eqn (8) referring to the results of previous studies.²⁴

Introducing the steady speed v_s as a function of the control parameter β on the friction function $\lambda(\mathbf{v})$ given by eqn (9), the Langevin eqn (8) for the dimensionless speed $v = v(\beta, t)$ is

$$\dot{v} = -\lambda_0(\beta)[v - v_s(\beta)] + \eta_v(t), \quad (10)$$

where

$$v_s(\beta) = \frac{\beta_T - \beta}{\beta_T - \beta_R}, \quad (11)$$

with $\beta_R \leq \beta \leq \beta_T$, and $\eta_v(t)$ being Gaussian white noise with zero-mean. Using eqn (11) the steady speeds are $v_s = 1$ for the run motion and $v_s = 0$ for the tumble motion. It is easy to

observe that the relaxation coefficient (or asymptotic value of the friction force $\lambda(\mathbf{v})$ when $v \gg v_s$) is

$$\lambda_0(\beta) = \frac{1}{\tau(\beta)} \quad (12)$$

where $\tau(\beta)$ is the characteristic time of the run or tumble processes. The complete solution of eqn (10) for speed, with initial condition $v(t_0) = v_0$, is

$$v(\beta, t) = v_s(\beta) + [v_0 - v_s(\beta)]G_v^{(\beta)}(t, t_0) + \int_{t_0}^t \eta_v(s)G_v^{(\beta)}(t, s)ds, \quad (13)$$

where the Green function, for both run and tumble motions, is

$$G_v^{(\beta)}(t, t') = e^{-|t-t'|/\tau(\beta)}. \quad (14)$$

The Langevin eqn (4) for the deflection $x = x(\beta, t)$ of a bacterium making run or tumble motions is

$$\dot{x} = \rho[1 - \gamma \sinh(\delta x)] + \eta_x(t), \quad (15)$$

and its complete solution (see details in ref. 21) is

$$x(\beta, t) = x_s(\beta) + [x_0 - x_s(\beta)]G_x^{(\beta)}(t, t_0) + \int_{t_0}^t \eta_x(s)G_x^{(\beta)}(t, s)ds, \quad (16)$$

where the Green function is

$$G_x^{(\beta)}(t, t') \simeq \begin{cases} \frac{\ln[1 - \beta e^{-\max(t,t')/\tau(\beta)}]}{\ln[1 - \beta e^{-\min(t,t')/\tau(\beta)}]} & \text{if } \beta = \beta_T \\ e^{-|t-t'|/\tau(\beta)} & \text{if } \beta = \beta_R \end{cases}, \quad (17)$$

and the steady state solution is

$$x_s(\beta) = \begin{cases} \frac{1}{\delta_T} \operatorname{arsinh}\left(\frac{1}{\gamma_T}\right) & \text{if } \beta = \beta_T \\ 1 & \text{if } \beta = \beta_R \end{cases}. \quad (18)$$

The characteristic time $\tau = \tau(\beta)$ of the run or tumble motions is²¹

$$\tau = \frac{1}{\rho\delta\sqrt{1+\gamma^2}}, \quad (19)$$

or using the phenomenological relationship given by eqn (6) we find $\rho = C\tau$, where the constant $C \cong \delta_T$. We assume that $\eta_u(t)$ (where $u = x, v$) are Gaussian white noises with zero-means, *i.e.* $\langle \eta_u(t) \rangle = 0$ and correlations

$$\langle \eta_u(t)\eta_u(t') \rangle = 2Q_{uu}\delta(t - t'). \quad (20)$$

Usually, it is assumed that the stochastic processes (x, v) are independent as a consequence of the noises (η_x, η_v) being uncorrelated. However, this hypothesis is unrealistic for the tumble because here speed and direction of motion are not totally decoupled. This can be concluded from the calculations of the average velocity shown in Section 3. Consequently, it is appropriate to assume the noises are cross-correlated

$$\langle \eta_x(t)\eta_v(t') \rangle = 2Q_{xv}\delta(t - t'), \quad (21)$$

where the noise intensity Q_{xv} is different from zero for the tumble motion and is equal to zero for the run motion, as we will show in this paper.

3 Statistical properties of the tumble motion

In order to describe the statistical properties of the tumble motion it is practical to use the heading unit vector in the canonical basis ($\mathbf{e}_T, \mathbf{n}_T$) of an intrinsic reference frame, which is defined by bacterial orientation at the end of the tumble movement (or outgoing direction), so that $\mathbf{e}_T = \mathbf{e}(t_T)$. The bacterial orientation at the outgoing direction and at the beginning (or incoming direction) of a tumble is related by $\mathbf{e}_T = x_T \mathbf{e}_0 + \sqrt{1 - x_T^2} \mathbf{n}_0$ and $\mathbf{n}_T = -\sqrt{1 - x_T^2} \mathbf{e}_0 + x_T \mathbf{n}_0$, where $x_T = \cos \varphi_T$ is the tumble deflection and $(\mathbf{e}_0, \mathbf{n}_0)$ is the canonical basis at the beginning of the tumble (see plot (b) of Fig. 1). Expanding the unit vector $\mathbf{e}(t)$ (given by eqn (2)) in the canonical basis ($\mathbf{e}_T, \mathbf{n}_T$) around $x = x_T$ up to second order, we obtain

$$\mathbf{e}(t) \simeq \left\{ 1 - \frac{[x(\beta_T, t) - x_T]^2}{2(1 - x_T^2)} \right\} \mathbf{e}_T - \frac{[x(\beta_T, t) - x_T]}{\sqrt{1 - x_T^2}} \left\{ 1 + \frac{x_T [x(\beta_T, t) - x_T]}{2(1 - x_T^2)} \right\} \mathbf{n}_T. \quad (22)$$

Taking eqn (1) into account, the lowest-order approximation of the average velocity, close to the tumble deflection, is

$$\langle \mathbf{v}(\beta_T, t) \rangle \simeq \langle v(\beta_T, t) \rangle \mathbf{e}_T - \frac{1}{\sqrt{1 - x_T^2}} \langle v(\beta_T, t) [x(\beta_T, t) - x_T] \rangle \mathbf{n}_T, \quad (23)$$

where (taking $v_s(\beta_T) = 0$)

$$\langle v(\beta_T, t) \rangle = v_0 G_v^{(\beta_T)}(t, t_0), \quad (24)$$

$$\langle x(\beta_T, t) \rangle = x_s(\beta_T) + [x_0 - x_s(\beta_T)] G_x^{(\beta_T)}(t, t_0), \quad (25)$$

and

$$\begin{aligned} \langle v(\beta_T, t) [x(\beta_T, t) - x_T] \rangle &= \langle v(\beta_T, t) \rangle [\langle x(\beta_T, t) \rangle - x_T] \\ &+ 2Q_{xv} \int_{t_0}^t G_x^{(\beta_T)}(t, s) G_v^{(\beta_T)}(t, s) ds. \end{aligned} \quad (26)$$

By introducing the function $w(t) = \beta e^{-t/\tau_T}$, taking $t_0 = 0$ and using eqn (23) it can be shown that the normal component of the average velocity at the end of the tumble is (see details in Section A of Appendix)

$$\begin{aligned} \langle \mathbf{v}(\beta_T, t) \rangle \cdot \mathbf{n}_T &= -\frac{1}{\sqrt{1 - x_T^2}} \left\{ \frac{1}{\beta_T} v_0 [x_s(\beta_T) - x_T] w \right. \\ &+ \frac{1}{\beta_T} \{ v_0 [x_s(\beta_T) - x_T] - 2Q_{xv} \tau_T \beta_T I_{xv}(\beta_T) \} w \ln(1 - w) \\ &+ 2Q_{xv} \tau_T w \ln(1 - w) I_{xv}(w) \}, \end{aligned} \quad (27)$$

where

$$I_{xv}(u) = -\frac{1}{2u^2} + \frac{1}{2u} - \frac{\ln u}{12} - \frac{u}{24} - \frac{19u^2}{1440} - \dots, \quad (28)$$

with $0 < u \leq \beta \lesssim 1$, is a Laurent series. The normal component is nonzero for all tumble-times $t_T > 0$. Particularly, taking into account that $w \ln(1 - w) I_{xv}(w) \rightarrow \frac{1}{2}$ when $w \rightarrow 0$ (or $t \rightarrow +\infty$), it is easy to see that the normal component reaches a steady value (sv) for sufficiently long times (*i.e.* $t \gg \tau_T$) given by

$$\langle \mathbf{v}(\beta_T, t) \rangle \cdot \mathbf{n}_T|_{sv} = -\frac{Q_{xv} \tau_T}{\sqrt{1 - x_T^2}}, \quad (29)$$

with $Q_{xv} \neq 0$. Eqn (27) shows that, during the tumble, there is a small displacement of the center of mass in the normal direction to the axis of the bacterium, which is a consequence of assuming that the stochastic processes x and v are not independent. This result can be explained by the displacement of the center of mass as a consequence of the flagellar unbundling during the transition from CCW to CW. This conclusion is also valid when using the initial condition $v_0 = 0$, since in this case the mean velocity has only a normal component, which depends exclusively on the noise intensity Q_{xv} .

Another statistic observable of interest is the directional correlation function which, making use of eqn (22), is

$$\begin{aligned} \langle \mathbf{e}(t) \cdot \mathbf{e}(t') \rangle &= \langle \cos[\theta(t, t')] \rangle \simeq 1 \\ &- \frac{1}{2(1 - x_T^2)} \langle [x(t) - x(t')]^2 \rangle + O(4), \end{aligned} \quad (30)$$

where $\theta(t, t') = \varphi(t) - \varphi(t')$ is the angle between the heading unit vectors at times t and t' , which are close to the tumble-time t_T . In the Appendix we show that the second-order term of the correlation given by eqn (30) is

$$\begin{aligned} \langle [x(t) - x(t')]^2 \rangle &= 2Q_{xx} \tau \left\{ \left[\frac{[x_0 - x_s(\beta_T)]^2}{2Q_{xx} \tau_T \ln^2(1 - \beta_T)} - I_{xx}(\beta_T) \right] \right. \\ &\times [\ln(1 - w) - \ln(1 - w')] \\ &+ [\ln^2(1 - w) I_{xx}(w) \\ &- 2 \ln(1 - w) \ln(1 - w') I_{xx}(w_>) \\ &+ \ln^2(1 - w') I_{xx}(w')] \}, \end{aligned} \quad (31)$$

where $w = w(t)$, $w' = w(t')$, $w_> = \max(w, w')$, and

$$I_{xx}(u) = \frac{1}{2u^2} - \frac{1}{u} - \frac{\ln u}{12} + \frac{u^2}{480} + \frac{u^3}{720} + \dots, \quad (32)$$

with $0 < u \leq \beta \lesssim 1$, is a Laurent series (see Section B of Appendix). Note that the poles of I_{xx} at $u = 0$ are removed from eqn (31) by the logarithmic functions. In particular, the term containing the second-order pole contributes to the stationary term (st) of eqn (31)

$$\langle [x(t) - x(t')]^2 \rangle_{st} = 2Q_{xx} \tau_T (1 - e^{-|t-t'|/\tau_T}). \quad (33)$$

It is easy to see that the remaining terms are non-stationary and dependent on w and w' . Then the directional correlation up to the second order is

$$\langle \mathbf{e}(t) \cdot \mathbf{e}(t') \rangle \simeq 1 - \frac{Q_{xx}\tau_T}{(1-x_T^2)} \left(1 - e^{-|t-t'|/\tau_T}\right) + \mathcal{R}(t, t'), \quad (34)$$

where \mathcal{R} includes non-stationary terms with the following properties: $\lim_{z, z' \rightarrow +\infty} \mathcal{R}(z, z') = 0$ and $\mathcal{R}(z, z) = 0$. The directional correlation shows that the process is non-stationary since $t = t_T \approx \tau_T$, which is in agreement with the conclusion drawn from the covariance.²¹ Our result is quite different from the result corresponding to the diffusion of $\mathbf{e}(t)$ on the surface of a d -dimensional sphere of unit radius ($d \geq 2$), where the directional correlation is $\langle \mathbf{e}(t) \cdot \mathbf{e}(t') \rangle = e^{-|t-t'|/\tau_T}$.²⁶ Even though the behaviours are similar, in our model the process is non-stationary and the correlation depends explicitly on the noise intensity Q_{xx} .

The mean square displacement (MSD) is defined by

$$F_{\text{MSD}}(t) \doteq \langle |\mathbf{r}(t) - \mathbf{r}(t_0)|^2 \rangle = \int_{t_0}^t \int_{t_0}^t \langle \mathbf{v}(t_1) \cdot \mathbf{v}(t_2) \rangle dt_1 dt_2, \quad (35)$$

where $\langle \mathbf{v}(t_1) \cdot \mathbf{v}(t_2) \rangle = \langle v(t_1)v(t_2) \cos[\theta(t_1, t_2)] \rangle$ is the velocity correlation function. If we assume that the stochastic processes (x, v) are independent, which is equivalent to taking $Q_{xv} = 0$, the velocity correlation is $\langle \mathbf{v}(t_1) \cdot \mathbf{v}(t_2) \rangle = \langle v(t_1)v(t_2) \rangle \langle \cos[\theta(t_1, t_2)] \rangle$. Otherwise, if the processes are not independent (*i.e.* $Q_{xv} \neq 0$), which is the case for the tumbling motion, the velocity correlation can be calculated from eqn (1) and (22) obtaining the following approximation

$$\begin{aligned} \langle \mathbf{v}(t_1) \cdot \mathbf{v}(t_2) \rangle &\simeq \langle v(t_1)v(t_2) \rangle \\ &- \frac{1}{2(1-x_T^2)} \langle v(t_1)v(t_2)[x(t_1) - x(t_2)]^2 \rangle. \end{aligned} \quad (36)$$

By a standard calculation we found that the lowest order contribution (*i.e.* the speed correlation function), with initial time $t_0 = 0$, is

$$\langle v(t_1)v(t_2) \rangle = Q_{vv}\tau_T [e^{-|t_1-t_2|/\tau_T} - (1-\sigma)e^{-(t_1+t_2)/\tau_T}], \quad (37)$$

where

$$\sigma = \frac{v_0^2}{Q_{vv}\tau_T}, \quad (38)$$

which shows that taking $\sigma = 1$ ensures the stationary behaviour,²⁷ and where the mean square speed is $\langle v^2 \rangle = v_0^2$. However, with this choice, the stationarity of the stochastic process v is a particular property of the system. A suitable choice for the initial condition is $0 \leq \sigma < 1$, so that it reproduces all possible non-stationarity situations. Then, for the tumble motion, the MSD contribution to lowest order is

$$T_{\text{MSD}}(t) = 2Q_{vv}\tau_T^3 \left[-\frac{3-\sigma}{2} + \frac{t}{\tau_T} + (2-\sigma)e^{-t/\tau_T} - \frac{1}{2}(1-\sigma)e^{-2t/\tau_T} \right]. \quad (39)$$

The usual asymptotic analysis to determine the diffusion constant is meaningless if the bacterium stops its turning motion at tumble-times which are of the order of the characteristic

tumble-time. For this reason, we calculate its Taylor series at times close to the tumble-time (*i.e.* $t \lesssim t_T$) to study the behaviour of the MSD

$$T_{\text{MSD}}(t) = T_{\text{MSD}}(t_T) + 2D(t_T)(t - t_T) + B(t_T)(t - t_T)^2 + \dots, \quad (40)$$

where

$$\begin{aligned} D(t_T) &= \frac{1}{2} \left[\frac{dT_{\text{MSD}}}{dt} \right]_{t=t_T} \\ &= Q_{vv}\tau_T^2 [1 - (2-\sigma)e^{-t_T/\tau_T} + (1-\sigma)e^{-2t_T/\tau_T}] \end{aligned} \quad (41)$$

is the diffusion coefficient at the tumble-time and

$$\begin{aligned} B(t_T) &= \frac{1}{2} \left[\frac{d^2T_{\text{MSD}}}{dt^2} \right]_{t=t_T} \\ &= Q_{vv}\tau_T [(2-\sigma) - 2(1-\sigma)e^{-t_T/\tau_T}]e^{-t_T/\tau_T} \end{aligned} \quad (42)$$

is the square ballistic coefficient at the tumble-time. The diffusion coefficient (eqn (41)) to lowest order is equal to zero for tumble-time zero and reaches a maximum asymptotic value $Q_{xv}\tau_T^2$ for very long tumble-times ($t_T \gg \tau_T$) as it is shown in Fig. 3. Besides, the square ballistic coefficient is equal to $v_0 = \sqrt{\sigma Q_{xv}\tau_T}$ at tumble-time zero and converges to zero for very long tumble-times as shown in Fig. 3. In addition, Fig. 3 shows that the ballistic behaviour is more important than the diffusion for $t_T \lesssim \tau_T$. Plot (a) of Fig. 3 shows a global maximum of ballistic contribution at $t^* = 0$ for $2/3 \leq \sigma \leq 1$. Plot (c) of Fig. 3 shows a local minimum at $t^* = 0$ and a global maximum at $0 < t^* \leq \tau_T \ln 2$ for $0 \leq \sigma < 2/3$. Considering eqn (41), (42) and (37), the mean square velocity (MSV) at tumble-times yields

$$\langle [v(t_T)]^2 \rangle = \frac{1}{\tau_T} D(t_T) + B(t_T). \quad (43)$$

Assuming an exponential distribution of tumble-times $P(t_T) = (\lambda_T/\tau_T)e^{-\lambda_T t_T/\tau_T}$, the average of the square ballistic coefficient is

$$\bar{B}_T = Q_{vv}\tau_T \frac{(2+\sigma\lambda_T)\lambda_T}{(\lambda_T+1)(\lambda_T+2)} \quad (44)$$

and the average of the diffusion coefficient is $\bar{D}_T = \bar{B}_T \bar{t}_T$, where $\bar{t}_T = \tau_T/\lambda_T$ is the mean tumble-time. Experiments show that $\lambda_T \approx 1$;²² then, taking $\lambda_T = 1$ we find that $\frac{1}{3} \leq \bar{B}_T / (Q_{vv}\tau_T) \leq \frac{1}{2}$ if $0 \leq \sigma \leq 1$.

4 Statistical properties of the run motion

One statistical observable of interest is the directional correlation function of the run motion. Making use of eqn (2) and noting that the angle between two directions is $\theta(t, t') = \varphi(t) - \varphi(t')$, it turns out for small deflections that

$$\langle \mathbf{e}(t) \cdot \mathbf{e}(t') \rangle = \langle \cos[\theta(t, t')] \rangle \approx \langle x(t) \cdot x(t') \rangle. \quad (45)$$

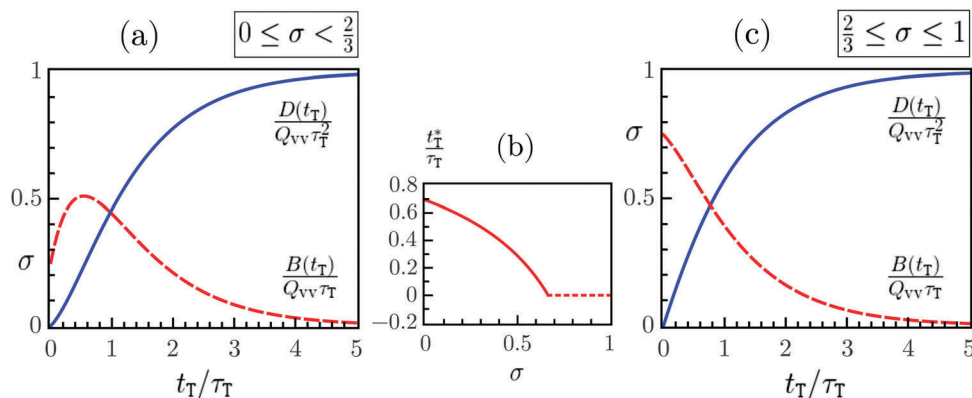


Fig. 3 Plots (a) and (c): show the diffusion coefficient $D(t_T)$ (blue continuous line) and square ballistic coefficient $B(t_T)$ (red dashed line) as a function of the tumble-time t_T for two values of the parameter σ (see eqn (38)) included in the intervals mentioned in each plot. Both functions and time are dimensionless. The ballistic contribution $B(t_T)$ reaches a maximum for tumble-times $t_T^* = \tau_T \ln[4(1 - \sigma)/(2 - \sigma)]$ if $0 \leq \sigma \leq 2/3$ or $t_T^* = 0$ if $2/3 \leq \sigma \leq 1$. Plot (b): shows the dimensionalized tumble-time t_T^* as a function of σ . Note that $t_T^*/\tau_T \leq \ln 2 \approx 0.693$, a value corresponding to the case $\sigma = 0$ (or zero initial velocity).

Taking into account that $x_s(\beta_R) = 1$ (eqn (18)), the deflection correlation function is

$$\langle x(t_1)x(t_2) \rangle = 1 + b_x(e^{-t_1/\tau_R} + e^{-t_2/\tau_R}) + b_x^2 e^{-(t_1+t_2)/\tau_R} + \varepsilon_x[e^{-|t_1-t_2|/\tau_R} - e^{-(t_1+t_2)/\tau_R}], \quad (46)$$

where $b_x = x_0 - 1$ and $\varepsilon_x = Q_{xx}\tau_R$, with $0 \lesssim |b_x| \leq \varepsilon_x$ and $b_x \lesssim 0$ considering the initial condition $x_0 \lesssim 1$. The directional correlation function satisfies $\langle \mathbf{e}(t_1) \cdot \mathbf{e}(t_2) \rangle \leq 1$. Consequently, the correlation function satisfies $\langle x(t_1)x(t_2) \rangle \lesssim 1$ for small deflections. If the initial condition is very close to the stable state solution, *i.e.* $|b_x| \ll 1$, using eqn (46) we find the inequality

$$g(t, T) = \frac{1 + e^{T/\tau_R}}{2 \sinh(t/\tau_R)} \approx \frac{\varepsilon_x}{|b_x|} = \frac{Q_{xx}\tau_R}{1 - x_0}, \quad (47)$$

where $t = \min(t_1, t_2)$ and $T = |t_1 - t_2|$. The plot of Fig. 4 shows g as a function of time t for several values of T . We observe that there is a minimum time $t_{\min} \leq \tau_R \operatorname{arcsinh}[|b_x|/(2\varepsilon_x)]$, defined by the autocorrelation ($T = 0$), time from which the bacterium stops its runs. In fact, the experimental observations confirm the existence of a minimum runtime,²² which based on eqn (47)

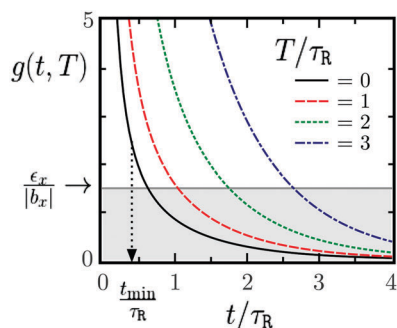


Fig. 4 Shows $g(t, T)$ as a function of time t for several values of T (see left-side of the inequality given by eqn (47)). In the non-shaded region $g \geq \varepsilon_x/|b_x|$. The minimum runtime is defined in the interval $0 < t_{\min} \leq \tau_R \operatorname{arcsinh}[|b_x|/(2\varepsilon_x)]$, as the plot shows.

can be related to the noise intensity and the initial condition of each run (Fig. 4). Taking into account that $v_s(\beta_R) = 1$ (eqn (11)), the speed correlation function is

$$\langle v(t_1)v(t_2) \rangle = 1 + b_v(e^{-t_1/\tau_R} + e^{-t_2/\tau_R}) + b_v^2 e^{-(t_1+t_2)/\tau_R} + \varepsilon_v[e^{-|t_1-t_2|/\tau_R} - e^{-(t_1+t_2)/\tau_R}], \quad (48)$$

where $b_v = v_0 - 1$ and $\varepsilon_v = Q_{vv}\tau_R$, with $0 \lesssim |b_v| \leq \varepsilon_v$. We assume the initial condition $v_0 = v_s(1 + b_v)$ with $|b_v| \ll 1$, so that $v_0 \approx 1$. Eqn (46) and (48) are useful in order to determine the MSD of the run motion assuming that the processes (x, v) are independent, which is equivalent to taking $Q_{xv} = 0$, or

$$\langle \mathbf{v}(t_1) \cdot \mathbf{v}(t_2) \rangle = \langle v(t_1)v(t_2) \rangle \langle \mathbf{e}(t_1) \cdot \mathbf{e}(t_2) \rangle, \quad (49)$$

where the directional correlation function can be approximated by eqn (45) assuming small deflections. The assumption that the processes (x, v) are independent is in agreement with the experimental fact that there is no flagellar unbundling during the run motion and, consequently, there is no reason for a net displacement perpendicular to the translation direction. The MSD for the run motion is

$$R_{\text{MSD}}(t) = \tau_R^2 \left\{ \left(\frac{t}{\tau_R} \right)^2 + 2(b_x + b_v) \left(\frac{t}{\tau_R} \right) (1 - e^{-t/\tau_R}) + (\varepsilon_x + \varepsilon_v) \left(-3 + 2 \frac{t}{\tau_R} + 4e^{-t/\tau_R} - e^{-2t/\tau_R} \right) + (\varepsilon_x b_v + \varepsilon_v b_x) \left[2 - \left(3 + 2 \frac{t}{\tau_R} \right) e^{-t/\tau_R} + 2e^{-2t/\tau_R} - e^{-3t/\tau_R} \right] + \varepsilon_x \varepsilon_v \left[-\frac{5}{4} + \frac{t}{\tau_R} + \left(1 + 2 \frac{t}{\tau_R} \right) e^{-2t/\tau_R} + \frac{1}{4} e^{-4t/\tau_R} \right] + O(b^2) \right\}, \quad (50)$$

where $O(b^2)$ contains terms whose order is greater than 1 in the parameters b_x and b_v . In analogy to the tumble-motion, the usual asymptotic analysis to determine the diffusion constant is meaningless if the bacterium stops its run motion at runtimes whose

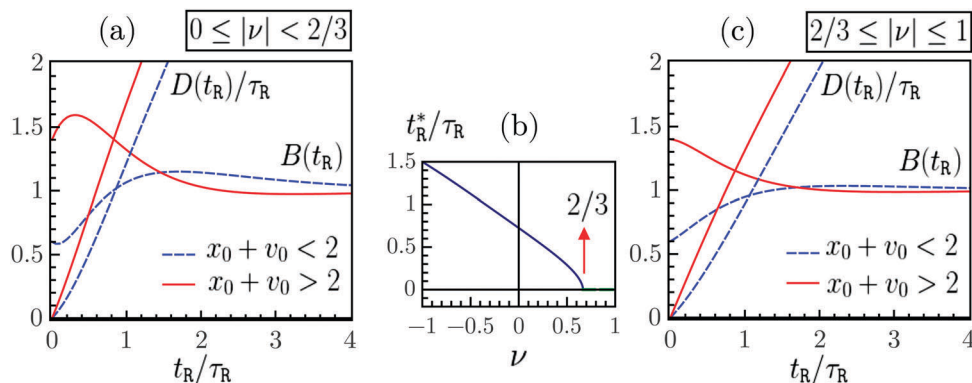


Fig. 5 Plots (a) and (c): show the diffusion coefficient $D(t_R)$ and square ballistic coefficient $B(t_R)$ as a function of the runtime t_R for two different intervals of the parameter ν (defined by eqn (54)). Both functions and time are dimensionless. These plots were made taking $x_0 + v_0 = 2 \pm 0.2$ (both plots), $\varepsilon_x = \varepsilon_v = 1/2$ (plot (a)) and $\varepsilon_x = \varepsilon_v = 1/8$ (plot (c)). Plot (b): shows the adimensionalized runtime t_R^* as a function of ν , where t_R^* is the time where $B(t_R)$ reaches a global maximum. This plot was made taking $\varepsilon_x = \varepsilon_v = 1/2$.

order is that of the characteristic runtime. In consequence, to study the MSD behaviour, we calculate its Taylor series at times close to the runtime (*i.e.* $t \approx t_R$)

$$R_{\text{MSD}}(t) = R_{\text{MSD}}(t_R) + 2D(t_R)(t - t_R) + B(t_R)(t - t_R)^2 + \dots, \quad (51)$$

where

$$\begin{aligned} D(t_R) &= \frac{1}{2} \left[\frac{dR_{\text{MSD}}}{dt} \right]_{t=t_R} \\ &= \tau_R \left\{ \frac{t_R}{\tau_R} + (b_x + b_v) \left[1 - \left(1 - \frac{t_R}{\tau_R} \right) e^{-t_R/\tau_R} \right] \right. \\ &\quad + (\varepsilon_x + \varepsilon_v) \left(1 - e^{-t_R/\tau_R} \right)^2 \\ &\quad + (\varepsilon_x b_v + \varepsilon_v b_x) \left(\frac{1}{2} + \frac{t_R}{\tau_R} - 2e^{-t_R/\tau_R} + \frac{3}{2}e^{-2t_R/\tau_R} \right) e^{-t_R/\tau_R} \\ &\quad \left. + \varepsilon_x \varepsilon_v \left(\frac{1}{2} - 2\frac{t_R}{\tau_R} e^{-2t_R/\tau_R} - \frac{1}{2}e^{-4t_R/\tau_R} \right) + O(b^2) \right\} \end{aligned} \quad (52)$$

is the diffusion coefficient at the runtime and

$$\begin{aligned} B(t_R) &= \frac{1}{2} \left[\frac{d^2R_{\text{MSD}}}{dt^2} \right]_{t=t_R} \\ &= 1 + (b_x + b_v) \left(2 - \frac{t_R}{\tau_R} \right) e^{-t_R/\tau_R} \\ &\quad + 2(\varepsilon_x + \varepsilon_v) \left(1 - e^{-t_R/\tau_R} \right) e^{-t_R/\tau_R} \\ &\quad + (\varepsilon_x b_v + \varepsilon_v b_x) \left(\frac{1}{2} - \frac{t_R}{\tau_R} + 4e^{-t_R/\tau_R} - \frac{9}{2}e^{-2t_R/\tau_R} \right) e^{-t_R/\tau_R} \\ &\quad + 2\varepsilon_x \varepsilon_v \left(-1 + 2\frac{t_R}{\tau_R} + e^{-2t_R/\tau_R} \right) e^{-2t_R/\tau_R} + O(b^2) \end{aligned} \quad (53)$$

is the square ballistic coefficient at the runtime. If the initial conditions satisfy $v_0 + x_0 \gtrsim 2$ or $b_v + b_x \gtrsim 0$ (see red-solid line

plots of Fig. 5) the ballistic contribution $B(t_R)$ reaches a global maximum for runtimes $t_R^* > 0$ if $0 \leq \nu \leq 2/3$ or $t_R^* = 0$ if $2/3 \leq \nu \leq 1$, where

$$\nu \approx \frac{b_x + b_v}{\varepsilon_x + \varepsilon_v} = \frac{x_0 + v_0 - 2}{(Q_{xx} + Q_{vv})\tau_R}. \quad (54)$$

This behaviour is similar to the one observed for the ballistic contribution in the tumble movement. In contrast, for $v_0 + x_0 \lesssim 2$ or $b_v + b_x \lesssim 0$ (see blue-dashed line plots of Fig. 5) the ballistic contribution $B(t_R)$ reaches a global minimum for runtimes $t_R^* \approx 0$ and reaches a global maximum for runtimes $t_R^* \approx \tau_R$. In both cases, $B(t_R) \approx 1$ for long runtimes $t_R \gg \tau_R$. The diffusion coefficient shows common features independently of the initial conditions, as can be seen from left and right plots of Fig. 5. In all cases, $D(t_R) \approx [1 + 2(b_x + b_v)]t_R$ for short runtimes $t_R \ll \tau_R$ and $D(t_R) \approx t_R$ for long runtimes $t_R \gg \tau_R$. The diffusion and square ballistic coefficients given by eqn (52) and (53), respectively, depend on 4 parameters; this fact makes their analysis difficult. However, Fig. 5 shows the behaviour of the two remaining parameters for the special case of equal noise intensities, *i.e.* $Q_{xx} = Q_{vv}$. Assuming an exponential distribution of runtimes $P(t_R) = (\lambda_R/\tau_R)e^{-\lambda_R t_R/\tau_R}$, the average of the square ballistic coefficient is

$$\begin{aligned} \bar{B}_R &= 1 + (b_x + b_v) \frac{(1 + 2\lambda_R)\lambda_R}{(\lambda_R + 1)^2} \\ &\quad + 2(\varepsilon_x + \varepsilon_v) \frac{\lambda_R}{(\lambda_R + 1)(\lambda_R + 2)} \\ &\quad + 8\varepsilon_x \varepsilon_v \frac{\lambda_R}{(\lambda_R + 2)^2(\lambda_R + 4)} \end{aligned} \quad (55)$$

and the average of the diffusion coefficient is $\bar{D}_R = \bar{B}_R \bar{t}_R$, where $\bar{t}_R = \tau_R/\lambda_R$ is the mean runtime.

5 Conclusions

Previous to this work, the movements of run and tumble have been studied separately or as sequences of both movements.

These studies have been primarily focused on a single run or sequence of runs abruptly interrupted by tumbles.²⁰ In contrast, in the present work we study both run and tumble movements, but as independent processes and not as a sequence of successive movements. Little attention has been paid to the theoretical modeling of the movement of the tumble, especially because of the limited availability of experimental data. Nevertheless, there are experimental data provided by the pioneering work of Berg and Brown.²² In their work statistical quantities for both movements were measured, such as the distributions of the tumble-angles and tumble-durations, and the ratio between the mean durations of the run and tumble. With these data, in a previous work,²¹ we were able to derive a single Langevin equation for the change of orientation or deflection $x(t)$ of the bacterium in the run and tumble movements. Additionally, to complete the theoretical model, in this paper we establish a unique Langevin equation for the speed $v(t)$ of the run and tumble movements. Each type of movement is characterized by values taken by a control parameter β . In particular, the steady state solutions as well as the characteristic times are functions of this parameter. Langevin equations are solved analytically, which makes it possible to calculate the statistical properties of each movement in detail. Assuming that the stochastic processes (x, v) are not independent during the tumble, we show that there are small displacements of the center of mass of the bacterium in normal direction to the body axis of the bacterium. This result is in agreement with the observation of the flagellar unbundling during the CCW to CW transition. In addition, we show that the directional correlation during the tumble has non-stationary terms at tumble-times close to the characteristic time of this movement. For the tumble movement, we also derive the mean square displacement (MSD) and, at times close to the tumble-time, we determine the diffusion coefficient and the square ballistic coefficient. At very small tumble-times compared to the characteristic time, we observe that the ballistic contribution is more important than the contribution of the diffusion, which can be concluded from the maximum it shows at initial times. On the contrary, at tumble-times much longer than the characteristic time the ballistic coefficient goes to zero and the diffusion coefficient saturates. The statistical properties of the run movement are studied following the same methodology. Furthermore, we focus on studies of the MSD. First, we establish the conditions that need to satisfy the parameters so that the directional correlation is well defined. Assuming that the stochastic processes (x, v) are independent, we calculate the MSD. We show that its behaviour depends on the initial conditions of speed and deflection as well as on the noise intensities linked to the variables. In general, it can be observed that the ballistic contribution to short runtimes is always more important than the diffusion. This behaviour seems to be trivial but depends on the initial conditions as well as on extrema values (maximum or minimum) of the ballistic coefficient at short runtimes. At long runtimes, it can be observed that the diffusion coefficient goes as time and the ballistic coefficient approaches a constant.

As a final conclusion and outlook, we believe that this work can serve as basis for research of other flagellated bacteria with

different movements to those analyzed here, such as the *Vibrio alginolyticus*, an uni-flagellate bacterium that resides in marine environment, showing sequences of forward-run, reverse, backward-run and flick motions.^{28,29}

Conflicts of interest

There are no conflicts to declare.

Appendix

A. The integral of second term of eqn (26) is

$$\int_{t_0}^t G_x^{[\beta_T]}(t, s) G_v^{[\beta_T]}(t, s) ds = \tau_T \beta_T e^{-t/\tau_T} \ln(1 - \beta_T e^{-t/\tau_T}) \times \left[I_{xv}(\beta_T e^{-t/\tau_T}) - I_{xv}(\beta_T e^{-t_0/\tau_T}) \right], \quad (56)$$

where

$$I_{xv}(u) = - \int^u \frac{dz}{z^2 \ln(1-z)}. \quad (57)$$

After integrating the series expansion of the function I_{xv} around $z = 0$ we obtain eqn (28).

B. We calculate the directional correlation (see eqn (31)) by means of the correlation

$$\begin{aligned} & \langle [x(t) - x_s(\beta_T)] [x(t') - x_s(\beta_T)] \rangle \\ &= \langle x(t) \rangle - x_s(\beta_T) \langle x(t') \rangle - x_s(\beta_T) \\ &+ 2Q_{xx} \int_{t_0}^{\min(t, t')} G_x^{[\beta_T]}(t, s) G_x^{[\beta_T]}(t', s) ds. \end{aligned} \quad (58)$$

The integral of the second term is (see ref. 21 for details)

$$\begin{aligned} & \int_{t_0}^{\min(t, t')} G_x^{[\beta_T]}(t, s) G_x^{[\beta_T]}(t', s) ds = \tau_T \ln(1 - \beta_T e^{-t/\tau_T}) \\ & \times \ln(1 - \beta_T e^{-t'/\tau_T}) \\ & \times \left[I_{xx}(\beta_T e^{-\min(t, t')/\tau_T}) - I_{xx}(\beta_T e^{-t_0/\tau_T}) \right], \end{aligned} \quad (59)$$

where

$$I_{xx}(u) = - \int^u \frac{dz}{z \ln^2(1-z)}. \quad (60)$$

After integrating the series expansion of the function I_{xx} around $z = 0$ we obtain eqn (32).

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