The physics of flagellar motion of *E. coli* during chemotaxis

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Abstract Flagellar motion has been an active area of study right from the discovery of bacterial chemotaxis in 1882. During chemotaxis, *E. coli* moves with the help of helical flagella in an aquatic environment. Helical flagella are rotated in clockwise or counterclockwise direction using reversible flagellar motors situated at the base of each flagellum. The swimming of *E. coli* is characterized by a low Reynolds number that is unique and time reversible. The random motion of *E. coli* is influenced by the viscosity of the fluid and the Brownian motion of molecules of fluid, chemoattractants, and chemorepellants. This paper reviews the literature about the physics involved in the propulsion mechanism of *E. coli*. Starting from the resistive-force theory, various theories on flagellar hydrodynamics are critically reviewed. Expressions for drag force, elastic force and velocity of flagellar elements are derived. By taking the elastic nature of flagella into account, linear and nonlinear equations of motions are derived and their solutions are presented.

Keywords Bacterial chemotaxis ·
Flagellar hydrodynamics · Equations of flagellar motion ·
Low Reynolds number flow

Introduction

Escherichia coli has existed from very early times and is one of the simplest and best understood living things. Despite the complexity of molecular interaction networks, reactions, and cellular pathways involved in the chemotaxis of *E. coli*, one can observe the interplay of various basic principles of physics for efficient swimming.

E. coli swims in an aquatic environment using its helical shaped flagella. The motion of *E. coli* is characterized by the fluid's viscosity, low Reynolds number flow, and diffusion. Observation of an *E. coli* swimming through a fluid brings the following questions to mind:

1. How does *E. coli* see the surrounding fluid?
2. How do the elastic filaments in flagella behave in viscous fluid?
3. What are the physics involved in flagellar bundling?
4. What are the hydrodynamic forces involved in the propulsion?

This paper critically reviews the current literature in the context of the physics involved in answering the above questions.

E. coli and chemotaxis

Chemotaxis refers to cell movement towards and away from a chemical source. During positive chemotaxis, the cell is attracted by the chemoattractant, and during negative chemotaxis the cell is repelled by the chemorepellant. Bacterial chemotaxis was first noted by Engelmann (1882). He demonstrated the accumulation of *Bacterium thermo* in oxygen-rich regions. Pfeffer also showed that bacteria can be attracted towards some chemoattractants (Pfeffer 1888).

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In 1959, Baracchini and Sherris demonstrated chemotaxis of *Pseudomonas viscas* towards oxygen. It was Adler (1966) who shifted chemotaxis research into the study of molecular mechanics. Since then many papers have been published on this topic.

One of the earlier definitions of chemotaxis defines it as a change in the direction of movement due to chemical gradient (Dunn 1981) (for a review of earlier works of chemotaxis, see Berg 1975). Later, chemoreception came to be defined using phobic response in which the velocity of the cell body decreases and then a change in the direction of motion occurs (Diehn et al. 1977). The most suitable definition in the context of *E. coli* is given by Ewer and Bursell (1950). According to them, chemotaxis is a change in the frequency of spontaneous directional changes due to chemical stimulus.

During chemotaxis, bacteria swim by using flagellar rotation (Berg and Anderson 1973; Silverman and Simon 1974). The flagellum is the fundamental organelle for bacterial motion. It protrudes behind the cell body and is a semi-rigid passive appendage that rotates about the flagellar axis (Berg and Brown 1972). The flagellum contains three parts: a basal body, a hook, and a filament (Doetsch and Sjoblad 1980). There is a reversible motor in the basal body that causes flagellar rotation (DeRosier 1998). The motor can rotate with a frequency in the range of 15–300 Hz during swimming (Jones and Aizawa 1991). When the flagella rotate in one direction, the cell body rotates more slowly in the opposite direction to balance the torque produced (Berg 1975). The swimming speed of *E. coli* is in the range 10–35 $\mu\text{m/s}$ (Vaituzis and Doetsch 1969). From the motor to the helical filament, there is a hook of length about 45 nm (Jones and Aizawa 1991). The flagellar filaments consist of 11 protofilaments that are comprised of flaggellin (protein monomers). The appendage grows like a whip up to 10–15 μm in length. Namba (2004) has studied the atomic structure of flagella using X-ray crystallography and electron cryomicroscopy and proved that reversal of the bacterial motor causes a change in the configuration of the 11 protofilaments and in turn a change in flagellar handedness, amplitude and pitch.

Description of *E. coli*'s flagellar motion

E. coli has two modes of motion, namely forward motion called “run” and rotational motion called “tumble” (Fig. 1). During run mode, the flagellar motor rotates counterclockwise (as viewed from outside the cell) and the left-handed helical filaments bundle together (Macnab and Koshland 1972). As the flagellum is left-handed helical, counterclockwise rotation produces a force on the cell body. Since the flagella are not distributed symmetrically and they are

Fig. 1 The swimming motions of *E. coli*. **a** “Run” mode where flagella are bundled due to counterclockwise rotation. **b** “Tumble” mode causes spinning of the cell body due to clockwise rotation of flagella

of different lengths, due to viscous drag, flagella are swept to the rear end of the cell body. This amplifies the net force along the direction of motion and gets aligned with the long axis of the cell by forming a left-hand bundle (Anderson 1975).

At regular intervals, one or more of the flagella motors switch their direction of rotation. This creates the tumble motion (Larsen and Adler 1974). Therefore *E. coli* always move through a series of runs interrupted by tumbles (Berg and Brown 1972). During the tumble, due to a complex process, the left-handed helix is transformed into a right-handed helix (Macnab and Ornston 1977). The tumble is due to flagellar clockwise rotations (Larsen and Adler 1974) and pauses (Eisenbach et al. 1990).

Therefore, the run mode makes *E. coli* swim in a straight line and the tumble mode—which is a brief, abrupt turning motion—rotates the bacteria in a random direction (Berg and Brown 1972). Due to runs and tumbles, *E. coli* executes a random walk without any net displacement. Depending on the strain and the growth phase, *E. coli* tumbles every 1–10 s in the absence of a stimulus (Staropoli and Alon 2000). Unlike counterclockwise rotation, which forms a left-handed flagellar bundle, clockwise rotation destabilizes the left-handed bundle and tries to form a right-handed bundle. This becomes incomplete due to the fact that tumbling takes place over a short time interval and with pauses (Eisenbach et al. 1990). Therefore a few flagella will have segments with both right and left handedness, which causes a large angle between segments (Macnab and Ornston 1977). Such a large angle produces angular motion to the cell body and forces each flagellum to act independently, which causes tumbling.

Ishihara et al. (1983) and Macnab and Han (1983) also proved through experiments that different flagella in a given cell reverse and pause asynchronously, which causes flagella to act independently. Turner et al. (2000) estimated that tumbling can occur only when one-fourth of the total flagella reverse to clockwise rotation. Therefore the larger the fluctuation of clockwise rotation, the more change that occurs in the swimming direction. The tumble mode was first photographed in *E. coli* by Ramsey and Adler (Berg and Brown 1972).

The swimming pattern changes due to the presence of chemoattractants or chemorepellents. Increased attractant gradient (or decreased repellent gradient) reduces the probability of clockwise rotation, hence tumbling is reduced. A decreasing attractant gradient (or increasing repellent) increases the clockwise rotation and tumbling is increased (Larsen and Adler 1974). This property ensures that during positive chemotaxis, runs in the right direction are longer and runs towards the wrong direction are shorter. The random walk thus takes the bacteria towards attractants or away from repellents.

The physics in *E. coli*'s world

Organisms that live in water face many physical limitations. *E. coli* should see water as a fine-grained substance of inexhaustible extent (Berg 1993). While swimming, *E. coli* drags some molecules with it and causes surrounding fluid to shear. Due to this, there is an efficient momentum transfer between adjacent layers of fluid. The behavior of the surrounding liquid environment is decided by viscous forces.

As *E. coli* is very light, it has less inertia and therefore it cannot coast. Thermal agitation and Brownian motion of water molecules assist *E. coli* to be always in random motion (Brown 1828). Due to random motion, it keeps rotating and drifting.

Viscosity

E. coli should make use of the viscous force produced by its flagellar rotation for both forward and rotational motion of the cell body. To travel at constant speed, the thrust generated by the rotational helix should be equal to the viscous drag experienced by the *E. coli* body. There will be more thrust if the surrounding fluid is more viscous. Therefore the swimming characteristics of *E. coli* are highly influenced by viscosity. Schneider and Doetsh (1974) established that velocity of the bacteria increases with increasing viscosity of the surrounding fluid but after reaching a particular value it starts decreasing. They also found that maximum velocity occurs at higher ranges of

viscosity for peritrichously flagellated bacteria than polarly flagellated bacteria.

Low Reynolds number

The Reynolds number is defined as a ratio of inertial force and viscous force. It can be written as

$$\text{Re} = \frac{Lu}{\mu/\rho} = \frac{Lu}{\nu} \quad (1)$$

where L is the length of the bacteria, u is the velocity, μ is the fluid viscosity, ρ is the density of the fluid, and ν is the kinematic viscosity (μ/ρ). By substituting the typical values for *E. coli*, one gets $\text{Re}=10^{-5}$. For comparison, a man paddling slowly in a swimming pool has a Reynolds number of 10^5 . Due to high inertia, it is easier for the swimmer to push off and coast from one point to another. As *E. coli* experiences high viscosity and almost no inertia, when *E. coli* stops its motion, it is stopped immediately without any coasting or displacement.

Based on the work of Ludwig (1930), Taylor (1952) pointed out some major differences in the world of low Reynolds numbers. Independent of the rate, reversing the displacement makes all elements of the system return to their initial positions. This means that during a rapid power stroke, the cell body moves forward but during the recovery stroke, however slow, the cell body returns to its initial position. This does not happen at a high Reynolds number. Therefore low Reynolds number fields are unique and time-reversible flows. To overcome this problem, *E. coli* move their flagella differently during power and recovery strokes, similar to the human breast stroke. *E. coli* moves flagella far from the cell body for the power stroke and closer for the recovery stroke. As this motion is cyclic but not reciprocal, it is not reversed in time.

Purcell has demonstrated three possible swimming mechanisms in low Reynolds number environments. They are “corkscrew swimmer,” “three-link swimmer,” and the “flexible oar.” The swimming model proposed by Taylor (1952) explained the self-propulsion through cylindrical tails propagating helical waves. Purcell’s three-linked swimmer had three rigid links that could move independently to generate a nonreciprocal motion. This was analyzed by Becker et al. (2003), and an expression for swimming velocity was given as a function of the angular amplitude between links. Recently Tam and Hosoi (2007) examined the coordinated motion of the links to determine what constitutes an optimal swimmer. The flexible oar swimming mechanism involved an elastic rod/tail, which was free at one end and fixed at the other end. The oscillations produced in the tail generated propulsive force. The type of oscillation of these rods was either transverse or angular, or a combination of both (for complete discussion

on the modes of oscillation, see Camalet and Julicher 2000; Wolgemuth and Goldstein 2000).

Diffusion

It is easy to study the motion mechanism in low Reynolds number conditions by scaling up the motion of a macroscopic object in a highly viscous media, but it is difficult to study diffusion where random motion due to thermal agitation is involved (Berg 1993). As we have seen, *E. coli* swims by picking up direction at random; it also diffuses.

The mean square displacement $\langle x^2 \rangle$ increases linearly with the number of steps taken by *E. coli* (Berg 1993). If t is the running time for the experiment, τ is the time taken to displace a distance δ , then in one dimension,

$$\langle x^2 \rangle = \left(\frac{t}{\tau} \right) \delta^2 = \left(\frac{\delta^2}{2\tau} \right) 2t = 2Dt \quad (2)$$

where $D = \delta^2/2\tau$ is the diffusion constant. The diffusion constant depends on the size of the particle, viscosity of the medium, and temperature. Berg calculated the translational diffusion constant for a motile cell as $4 \times 10^{-10} \text{ m}^2/\text{s}$, which is higher than nonmotile cells ($2 \times 10^{-13} \text{ m}^2/\text{s}$).

Berg extended this to 2D and 3D by considering motions along the x , y and z axes by taking them as statistically independent.

In 2D:

$$\langle x^2 + y^2 \rangle = 4Dt \quad (3)$$

In 3D:

$$\langle x^2 + y^2 + z^2 \rangle = 6Dt \quad (4)$$

Berg also calculated that a molecule will take 0.5 ms to diffuse the entire length of the *E. coli*.

Diffusion of attractants or repellents also affects the distance and time to overcome diffusion, and thus affects the precision of chemosensing. Berg and Purcell (1977) focused on the diffusion of attracting particles interacting with the receptors on the surface of bacteria. They have observed that a stationary cell can obtain the required information to detect concentration differences by counting molecules for a long time (temporal comparison). This can be done only if the molecule binds to a receptor. Actually a molecule diffuses around until it can find an empty binding site. After sticking for a short time, the molecule has to diffuse away. Though a molecule may take longer time to reach a specific binding site, once it reaches that site, it tends to collide several times before it diffuses away. This increases the chance of reaching a specific binding site.

Berg and Purcell (1977) showed that the movement of *E. coli* gets affected during the uptake of attractants. They also demonstrated that the local stirring caused by flagella

during swimming is highly useful in nonuniform environments. Strong et al. (1998) determined the optimal bacterial strategy for *E. coli* when the signal to noise ratio (SNR) is low or high. High SNR allows for detection of the chemotactic gradient in shorter time. During low SNR, due to the presence of noise, *E. coli* needs a threshold level of attractants to respond.

Bialek and Satyeshgar (2005) derived accurate limits at which bacterial receptors are able to respond to changes in the concentration of attractants. They identified that the efficiency of detection of attractant is independent of the size of the receptor cluster. They also showed that diffusive noise level is independent of kinetic parameters. They established that there is a minimum noise that exists due to diffusion of attractant molecules and proved experimentally that bacteria operate near this theoretically derived noise limit.

Flagellar hydrodynamics

There are various factors affecting the swimming of *E. coli*. Density, viscosity, and temperature of the surrounding fluid, physiological conditions of the bacteria, and conditions such as chemical substrates and fluid particles affect the flagellar motion.

The modern study of the hydrodynamics of bacteria started with Gray (1928). Taylor (1952) studied the motion of microorganisms in low Reynolds number conditions and the interaction of tails with the surrounding fluid. The resistive-force theory was provided by Gray and Hancock (1955); it estimated the normal and tangential resistance coefficient for a segment of a moving flagellum.

The slender-body theory was originated by Burgers and extended further by Cox (1970). Batchelor (1970) applied it to a long, noncircular cross-sectioned slender solid body. The flow passing a slender body and the twisting mechanism were studied by Keller and Rubinow (1976a, 1976b) using matched asymptotic expansions. Lighthill redefined slender-body theory and modified resistance coefficients using improved analysis of flagellar hydrodynamics (Lighthill 1976). It was Hidgon (1979a, b) who used stokeslets, dipoles, and rotlets to represent the cell body and applied them to the slender-body theorem. By using an imaging system, he represented fluid velocity as a singular integral equation. Ramia et al. (1993) extended this by studying the spherical body using the boundary-element method. Kim and Powers (2004) studied the flow surrounding a helical filament using the slender-body theory (Kim and Powers 2004).

All these works considered helical filaments as rigid structures that rotate as a whole and did not take the elastic nature of the flagellum into account. Kirchhoff's rod theory

was developed to calculate stable and unstable equilibrium configurations of a thin elastic rod. This was extended to study and analyze the mechanism of super-coiled structures such as flagella (Koehler and Powers 2000). The bending and torsional moments are obtained using Kirchhoff's rod model, and the force experienced by rotating flagella in a viscous fluid is calculated using resistive-force theory (Yoshida and Takano 2002). Gray and Hancock (1955) argued that the radius of curvature of the flagellum during undulation is large compared to its diameter. At this situation, normal and tangential force can be approximately given by the local flagellum velocity and resistance coefficients as discussed in the Lighthill model. By considering uniform distribution of stokeslets on the z -axis from $-b$ to c , with the radius of the cylinder a , such that $a \ll b, c$, Lighthill (1996) calculated tangential (K_T) and normal (K_N) resistance coefficients using the following equations:

$$K_T = \frac{4\pi\mu}{-1 + \log \frac{4bc}{c^2}} \quad (5)$$

$$K_N = \frac{8\pi\mu}{1 + \log \frac{4bc}{c^2}} \quad (6)$$

Therefore the approximate force exerted by a flagellar segment is

$$\mathbf{F} \approx K_N \mathbf{u}_N + K_T \mathbf{u}_T \quad (7)$$

where $\mathbf{u}_N$ and $\mathbf{u}_T$ are the normal and tangential components of the velocity. The total force can be thus calculated by integrating Eq. 7 over the entire flagellum. It is clear from Eqs. 5 and 6 that resistance to the normal motion is approximately twice that of tangential motion. The above equations also confirm that the resistance coefficients and hence force are weak logarithmic functions of the tail radius.

Lighthill extended this method to the oblique direction by considering the sum of normal and horizontal flows. This resistive-force theory, though easy to use, does not give any prediction about the flow induced by the flagella.

In all the above-mentioned methods, the structural details of the flagella are not taken into account. It was Srigiriragu and Powers (2005) who proposed a coarse-grained continuum model of flagella that incorporated their structural organization. Flores et al. (2005) also incorporated the structural details by considering the flagellum as a helical hollow tube with material points connected to each other through elastic springs. This method incorporates both the elastic and hydrodynamic behavior of flagellar propulsion. The main drawback of this model is that it does not explain what the material points are and fails to link them to any strands of protofilaments.

Gebremichael et al. (2006) have included the details of protofilaments constituting the flagellum in their computational model. They have represented flagellin proteins as a collection of material points at a coarse-grained level. They have incorporated elastic network model and smooth-particle hydrodynamics to explain the flagellar propulsion. In their model, the deformation of flagella and their influence on the hydrodynamics of propulsion were also investigated.

Flagellar bundling

During the forward motion of *E. coli*, we can see that the flagella are concentrated at the rear end of the cell body and form a single helix. One of the earliest works on this flagella bundling came from Lighthill (1976). He combined analytical and numerical methods using slender-body theory, but focused on a single flagellum. Macnab (1977) explained the flagellar bundling using helical geometry. He proved that during counterclockwise rotation, all helices are progressively brought into phase. He used hydrodynamic calculations to prove wrapping occurs in a right-handed sense.

Goto et al. (1999) combined three flagella using the boundary element method without addressing the dynamics of flagellar bundling. Powers (2002) mentioned the possibility of bundling based on rotational simulation. Kim et al. (2003) used a laboratory model with flexible helical filaments to prove that flagella wrap around one another during synchronization and also proved that no such synchronization occurs with the rigid flagella. Floresa et al. (2005) proved flagellar bundling using a computational model with hydrodynamic interaction based on Stokes flow. By considering three flagella, they explained the bundling phenomenon during counterclockwise rotation of the motor. They also proved that if one of the flagellar motors changes rotational direction, the bundling gets disturbed leading to tumbling.

Flagellar forces

Lighthill (1996) analyzed bacterial motion through distribution of stokeslets along a helical flagellum. A stokeslet represents the flow due to a concentrated force $\mathbf{f}$ acting at a point of fluid and is governed by Stokes equation:

$$-\Delta p + \mu \Delta \mathbf{u} + \mathbf{f} \delta(\mathbf{r}) = 0 \quad (8)$$

and the equation of the continuity:

$$\Delta \cdot \mathbf{u} = 0 \quad (9)$$

here δ indicates the Dirac delta function.

The divergence of the Stokes equation gives the Poisson equation in an unbounded domain:

$$\Delta^2 p = \Delta \cdot \mathbf{f} \delta(\mathbf{r}) \quad (10)$$

By substituting the pressure as a dipole field, $p = \Delta \cdot (-\frac{\mathbf{f}}{4\pi r})$, where $\mathbf{r}$ is the displacement vector with $r = \|\mathbf{r}\|$.

The velocity field $\mathbf{u}$ can be represented by

$$\mathbf{u} = \frac{r^2 \mathbf{f} + (\mathbf{f} \cdot \mathbf{r}) \mathbf{r}}{8\pi\mu r^3} \quad (11)$$

Assuming the ratio of flagellar radius a to the flagellum length L is small (Childress 1977), the flagellar velocity $\mathbf{w}$ is given by

$$\mathbf{w}(s_0) = \frac{\mathbf{f}_n(s_0)}{4\pi\mu} + \int_{r_0 > \rho} \frac{r_0^2 \mathbf{f} + (\mathbf{f} \cdot \mathbf{r}_0) \mathbf{r}_0}{8\pi\mu r_0^3} ds \quad (12)$$

where s is the distance along the centerline of the flagellum, $\mathbf{f}(s_0)$ is the velocity of the flagella when the cross-section of the flagellum at $s=s_0$, $\mathbf{r}_0$ is the position vector of s_0 , $\mathbf{f}_n(s_0)$ is the vector normal to the centerline at $s=s_0$.

The equation of the rotation of a spiral with constant radius and constant pitch is given by

$$x(s) = \alpha s, y(s) = b \cos(ks - \omega t), z(s) = b \sin(ks - \omega t) \quad (13)$$

where b is the radius, k is the period, and ω is the angular velocity at time t . The wave length of the equation is given by $\Lambda = 2\pi/k$ and the pitch is given by λ . And $\alpha = \lambda/\Lambda$ is the contraction of the spiral.

According to periodicity, we get

$$x(s + \Lambda) = x(s), y(s + \Lambda) = y(s), z(s + \Lambda) = z(s) \quad (14)$$

The wave velocity along the x -axis is written as

$$\mathbf{v} = \alpha \mathbf{c} \quad (15)$$

where c is the velocity of the wave travelling along the spiral.

The force $\mathbf{f}(s)$ per unit length therefore can be written as

$$\mathbf{f}_n(s_0) = (\hat{g}, \hat{h} \sin(ks), -\hat{h} \cos(ks)) \quad (16)$$

Based on Lighthill's idea, Dillion et al. (1995) built a bacterial swimming model in 2D and derived an equation of force as the combination of force produced by body, rotational motion, and swimming motion, i.e.,

$$\mathbf{f}(s) = \mathbf{f}_{body} + \mathbf{f}_{rotate} + \mathbf{f}_{swim} \quad (17)$$

The drag force per unit length of the rod can be written in vector form from Eq. 7,

$$\mathbf{f}_d = -[K_N \hat{\mathbf{n}} \hat{\mathbf{n}} + K_T \hat{\mathbf{t}} \hat{\mathbf{t}}] \cdot (\mathbf{r}_t - \mathbf{u}) \quad (18)$$

where $\hat{\mathbf{n}}$ and $\hat{\mathbf{t}}$ are unit normal and tangent to the flagellar filament, $\mathbf{r}_t$ is the relative velocity of the fluid (the subscript denotes time derivative), and $\mathbf{u}$ is the velocity of the fluid in the fixed frame.

Since flagella exhibit elastic properties, the propulsion mechanism should be an interplay of elasticity and

hydrodynamics (Schreiner 1971). In order to calculate elastic force, consider an elastic tail of arc length s , position vector $r(s)$, local angle $\psi(s)$. The elastic force experienced by such an element is a function of bending energy and inextensibility constraint

$$\varepsilon = \int_0^L \left[\frac{A}{2} k^2 + \frac{\Lambda}{2} \mathbf{r}_s^2 \right] ds \quad (19)$$

where the subscript s denotes a derivative. Here A is the bending stiffness, k is the curvature of the tail, and Λ is the Lagrange multiplier enforcing inextensibility.

The elastic force per unit length (Wolgemuth and Goldstein 2000; Camalet and Julicher 2000) is given by

$$\mathbf{f}_\varepsilon = -\frac{\delta \varepsilon}{\delta \mathbf{r}} \quad (20)$$

$$\mathbf{f}_\varepsilon = -(A \psi_{sss} - \psi_s \tau) \hat{\mathbf{n}} + (A \psi_{ss} \psi_s + \tau_s) \hat{\mathbf{t}} \quad (21)$$

where the local tension is given by $\tau = -\Lambda + Ak^2$.

Equations of motion and propulsive force

Camalet and Julicher (2000) have derived nonlinear equations of motion for an elastic tail with torque generating units along the tail. But in the case of *E. coli* the torque generators are only in the base of the flagella. Therefore the tail is to be considered as passive.

For local mechanical equilibrium along the flagella, the sum of drag force and elastic force should be zero:

$$\mathbf{f}_d + \mathbf{f}_\varepsilon = 0 \quad (22)$$

Substituting the values of f_d, f_ε from Eqs. 18 and 21 and rearranging we get

$$\psi_t = -\frac{1}{K_N} (A \psi_{ssss} - \tau \psi_{ss} - \tau_s \psi_s) + \frac{1}{K_T} (A \psi_s^2 \psi_{ss} + \tau_s \psi_s) \quad (23)$$

$$\tau_{ss} - \beta \tau \psi_s^2 = -A(1 + \beta)(\psi_s \psi_{sss}) - A \psi_{ss}^2. \quad (24)$$

Wriggins and Goldstein (1998) simplified the above two equations to linear form by assuming the slope of the tail is small, i.e., $\psi \approx y_x \ll 1$,

Therefore we get a linear equation

$$y_t \approx -\frac{A}{K_N} y_{xxxx} \quad (25)$$

Considering the case of harmonic angular actuation with the boundary condition $\psi = a_0 \sin(\omega t)$ at the base and substituting $x = L\tilde{x}, y = a_0 L \tilde{y}, t = \tilde{t}/\omega$, we get

$$\tilde{y}_{\tilde{t}} = -\frac{A/\omega K_N}{L^4} \tilde{y}_{\tilde{x}\tilde{x}\tilde{x}\tilde{x}} = -\left(\frac{l_\omega}{L}\right)^4 \tilde{y}_{\tilde{x}\tilde{x}\tilde{x}\tilde{x}}, \quad (26)$$

where $l_\omega = \left(\frac{A}{\omega K_N}\right)^{1/4}$ is the penetration length that decays exponentially.

This allows us to calculate the dimensionless length

$$\mathcal{L} = \frac{L}{l_\omega} = L \left(\frac{\omega K_N}{A} \right)^{\frac{1}{4}} \quad (27)$$

The above equation is the key parameter of the problem that represents “floppiness” of the flagellum and thus the overall effectiveness of the swimmer.

Solving Eq. 25 using the variable separation method (Wiggins et al. 1998), we get

$$y(x, t) = a_0 l_\omega \Re \{ e^{i\omega t} h(\eta) \} \quad (28)$$

where $\eta = \frac{x}{l_\omega}$ and $h(\eta) = \sum_{j=1}^4 c_j e^{jz_0 \eta}$

The propulsive force can be calculated from the negative of the total hydrodynamic drag force along the direction of the swimming. i.e.,

$$F = - \int_0^L \mathbf{f} \cdot \hat{\mathbf{e}}_x ds, \quad (29)$$

where $\mathbf{f}$ is the local force and $\hat{\mathbf{e}}_x$ is the unit vector in the direction of propulsion. Wiggins and Goldstein (1998) solved the above equation using local elastic force from Eq. 21

$$F = -\hat{\mathbf{e}}_x \cdot [Ak_s \hat{\mathbf{n}} - Ak^2 \hat{\mathbf{t}} + \hat{\Lambda} \hat{\mathbf{t}}]_0^L \quad (30)$$

$$F \approx A \left(y_{xxx} - \frac{1}{2} y_{xx}^2 \right)_{x=0} \quad (31)$$

The above force is independent of the difference in drag coefficients, K_T and K_N . But during isotropic drag, i.e., $K_T = K_N$ means no net propulsion. Integrating the x-component of the local drag force, we can get average propulsive force over a period of oscillation. Using small slope approximation, the propulsive force is therefore

$$\langle F \rangle \approx A \frac{K_N - K_T}{K_N} \left\langle y_x y_{xxx} - \frac{1}{2} y_{xx}^2 \right\rangle_{x=0}, \quad (32)$$

Substituting $x = l_\omega \tilde{x}$, $y = a_0 l_\omega \tilde{y}$, $t = T \tilde{t}$ and rearranging, we get

$$\langle F \rangle = a_0^2 l_\omega^2 (K_N - K_T) |\omega| \langle \mathcal{F} \rangle \quad (33)$$

Therefore the nondimensional force can be calculated as

$$\langle \mathcal{F} \rangle = \frac{\langle F \rangle}{a_0^2 l_\omega^2 (K_N - K_T) |\omega|} \quad (34)$$

The above equation is valid for both linear and nonlinear cases of motion.

Conclusion

The description of flagellar motion involves the application of modern fluid hydrodynamics. The behavior of elastic flagella in the aquatic environment is characterized by viscous drag and elastic force. It is clear from the linearity of Stokes equations that the rotational motion of a left-handed helix causes translational motion of *E. coli*. The linear and nonlinear equations of motion describe the propulsive force generated during chemotaxis of *E. coli*.

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