Numerical Analysis of Bacterium Motion Based on the Slender Body Theory*

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The swimming motion of a bacterium model consisting of a spherical cell body and a rotating helical flagellum is discussed. In order to calculate the speed and efficiency, we adopt the slender body theory (SBT) developed by Higdon. The effect of flagellar dimensions on the swimming motion is elucidated. The results are compared with those of the boundary element method (BEM), which is expected to provide more accurate results. The agreement is excellent, and the computational time of the SBT is about 1/400 of the time of the BEM. From the viewpoint of fluid dynamics, the optimal flagella for speed and efficiency are both illustrated. The difference between the two shapes is apparent in the radius of the flagellar helix. The reason for this is explained taking into account the roles of the force and torque produced by the flagellar motion. In addition, the two flagella are compared to the flagellum in the real world. The bacterial flagellum resembles in shape the most efficient flagellum rather than the fastest one.

Key Words: Propulsion, Bio-fluid Mechanics, Numerical Analysis, Swimming Motion, Bacterium, Flagellum, Slender Body Theory, Optimization

1. Introduction

We investigate the swimming motion of the bacterium. Most bacteria swim rotating their helically shaped flagella. Although the bacterium is the simplest organism, it has survived in a long competition. The motility assists them in moving toward nutrients and escaping from a harmful environment⁽¹⁾. We presume that the bacterium shape has been optimized in some way to accommodate the circumstances through the long history of evolution. The dimensions of a flagellar helix directly depend on the structure of a protein, flagellin, of which the flagellum is composed. The reason why this protein is selected from other various proteins is possibly due to the total efficiency.

The input is energy consumption for producing and transporting the protein, and for driving a motor that rotates the flagellum, and the output is swimming speed. Because a flagellum is an organ for swimming motion, we consider that the flagellum has dimensions optimized for its function. In this paper, from the viewpoint of fluid dynamics, we numerically analyze the swimming motion assuming that a bacterium consists of a spherical cell body and a rotating helical flagellum, and investigate the effects of the dimensions of the flagellum on the swimming speed and efficiency. We also calculate the optimum shapes for the fastest swimmer and the most efficient swimmer, and compare them to the flagellar shape in nature.

For our purpose, we apply a numerical method^{(2),(3)} based on the slender body theory, which is one of the singularity methods, instead of the resistive force theory, which is a simple, convenient theory to calculate the force produced by a flagellum, and has been widely applied to the analyses of bacterium motion⁽⁴⁾⁻⁽⁸⁾. In the resistive force theory, a flagellum is divided into short segments, and the force and the velocity of each segment are linearly connected by resistance coefficients. The resistive force theory has

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Fig. 1 Cells of *Vibrio alginolyticus*. This photograph was taken through a dark field microscope

Fig. 2 Schematic of a bacterium model and definitions of vectors

succeeded in estimating the swimming speed qualitatively. In most cases, however, the fluid dynamical interactions between short segments are not considered, and there is a degree of ambiguity surrounding the choice of resistance coefficients⁽⁹⁾. Therefore, we adopt the slender body theory, which is expected to give us quantitatively accurate results.

2. Analysis

2.1 Analytical model for a monotrichously flagellated bacterium

In this study, we analyze the swimming motion of monotrichously flagellated bacteria. Some bacteria are monotrichously flagellated like *Vibrio alginolyticus* though some of the others are peritrichously flagellated. Figure 1 is a photograph of *Vibrio alginolyticus*, which was taken through a dark field microscope by the authors. At one end of the cell body, each cell has one flagellum driven by a rotary motor.

For the sake of simplicity, we deal with a bacterium model that consists of a spherical cell body and a flagellum of helical shape. A schematic of the model is shown in Fig. 2. We assume that the cell body and the flagellum are both rigid. The center of the cell body of radius r_b is indicated as O_0 . A rotary motor at O_1 drives the flagellum with the angular velocity of ω . The velocity of the point O_0 and the angular velocity of the cell body are defined as $\mathbf{U}_0$ and $\mathbf{\Omega}_0$, respectively. Details of the flagellar shape will be explained in section 3.1.

2.2 The slender body theory

The flow induced by the motion of rigid objects in a highly viscous flow is described by using singularities, e.g. Stokeslets, stresslets, distributed in the field. For a simple object, such as a sphere, a prolate spheroid, an oblate spheroid, the singularity distribution that rigorously satisfies the non-slip boundary condition on the surface has been found⁽¹⁰⁾. For an object of arbitrary shape, however, it is difficult to write the singularity distribution in an explicit form. In the slender body theory^{(11)–(13)}, singularities are distributed along a needle-like body so as to approximately satisfy the boundary condition. Neglecting the effect of singularities that are at a relatively long distance from the point of interest makes it feasible to evaluate the strength of the singularities. Higdon^{(2),(3)} applied this theory to the analysis on the swimming motion of microorganisms with a flagellum, and he suggested a numerical scheme to calculate the singularity distribution on the flagellum. In the present study, we basically follow his scheme with the exception of a slight modification to deal with the case in which the axis of flagellar rotation does not penetrate the center of a spherical cell body.

2.3 Flow field induced by a flagellum

Let us think about Stokeslets and dipoles distributed on a flagellum. Green's functions expressing the flow field at $\mathbf{x}$ induced by a Stokeslet and a dipole at $\mathbf{X}$ are

$$S_{ij}(\mathbf{x}, \mathbf{X}) = \frac{\delta_{ij}}{r} + \frac{(x_i - X_i)(x_j - X_j)}{r^3} \quad (1)$$

$$D_{ij}(\mathbf{x}, \mathbf{X}) = -\frac{\delta_{ij}}{r^3} + 3\frac{(x_i - X_i)(x_j - X_j)}{r^5} \quad (2)$$

respectively. Here, δ_{ij} is Kronecker's delta, and $r = |\mathbf{x} - \mathbf{X}|$. The suffix j shows the direction of the Stokeslet and dipole. When Stokeslets and dipoles with a strength of f_j and d_j , respectively, are uniformly distributed along a short segment of length L , the fluid velocity induced at the position $\mathbf{x}$ is

$$u_i(\mathbf{x}) = \int_0^L \left\{ S_{ij}(\mathbf{x}, \mathbf{X}) \frac{f_j}{8\pi\mu} + D_{ij}(\mathbf{x}, \mathbf{X}) \frac{d_j}{4\pi} \right\} ds \quad (3)$$

Because a flagellum is usually very thin, the radius of the flagellum a is much smaller than the length of the short segment L . According to the original slender body theory, the line distribution of dipoles $\mathbf{d}$ is connected with that of Stokeslets $\mathbf{f}^{(14)}$,

$$\mathbf{d} = -\frac{a^2}{4\mu} \mathbf{f}_\perp \quad (4)$$

where $\mathbf{f}_\perp$ refers to a component perpendicular to the center line of the flagellum. This distribution approximately satisfies the boundary condition on the surface of the segment, excluding the regions close to the ends of the segment.

Dividing the flagellum into N segments of short length, and continuing to assume that the distributions of the Stokeslets and dipoles are constant on each segment, we may approximate Eq. (3) at

$$u_i(\mathbf{x}) = \sum_{n=1}^N [K_{ij}(\mathbf{x}, \mathbf{X}^n) f_j(\mathbf{X}^n)]. \quad (5)$$

Here, $\mathbf{X}^n$ is the positioning vector of the middle point of the n th segment, and K_{ij} is a matrix whose elements are analytically obtained through the integration in Eq. (3).

2.4 Effects of a cell body

Next, we consider a cell body, which provides two influences on a flow field. One of them is that the cell body becomes an additional boundary in the field for the singularities distributed on the flagellum. The other one is that the translation and rotation of the cell body induces fluid flow in exactly the same way as the flagellar motion does.

In order to take the former effect into account, we introduce mirror images of the singularities. Oseen⁽¹⁵⁾ founded an analytical solution of a mirror image of a Stokeslet about a sphere (referred by Higdon⁽²⁾). Numerically integrating the solution over every short segment, we may express the velocity induced by the mirror images as

$$u_i^*(\mathbf{x}) = \sum_{n=1}^N [K_{ij}^*(\mathbf{x}, \mathbf{X}^n) f_j(\mathbf{X}^n)]. \quad (6)$$

We applied Gauss's formula in which eight points are employed for the numerical integration in the calculation of K_{ij}^* .

The latter effect is directly incorporated. When a sphere translates and rotates with the velocity $\mathbf{U}_0$ and the angular velocity $\boldsymbol{\Omega}_0$, the velocity field around it is

$$u_{bi}(\mathbf{x}) = \frac{3}{4} r_b \left\{ S_{ij}(\mathbf{x}, 0) - \frac{r_b^2}{3} D_{ij}(\mathbf{x}, 0) \right\} U_{0j} + \frac{r_b^3}{|\mathbf{x}|^3} \varepsilon_{ijk} x_k \Omega_{0j}. \quad (7)$$

Here, ε_{ijk} is Eddington's denotation defined by

$$\varepsilon_{ijk} = \begin{cases} 1 & (i, j, k) \text{ is an even permutation} \\ & \text{of } (1, 2, 3) \\ -1 & (i, j, k) \text{ is an odd permutation} \\ & \text{of } (1, 2, 3) \\ 0 & \text{others} \end{cases} \quad (8)$$

2.5 Expression for the velocity field

Since the cell body and the flagellum are both assumed to be rigid, the velocity vector of a short flagellar segment at the positioning vector $\mathbf{x}$, whose origin is at the center of a spherical cell O_0 , is expressed by using the velocity of the cell $\mathbf{U}_0$, its angular velocity $\boldsymbol{\Omega}_0$, and the rotation rate of the motor $\boldsymbol{\omega}$:

$$u_{fi}(\mathbf{x}) = U_{0i} + \varepsilon_{ijk} \{ x_k \Omega_{0j} + (x_k - r_{bk}) \omega_j \}. \quad (9)$$

The vector $\mathbf{r}_b$, the origin of which is the center of the cell body O_0 , indicates the position of the root of the

flagellum O_1 , where a rotary motor exists. Introducing $\mathbf{r}_b$ we can deal with the case of an inclined flagellum whose axis is not aligned with the radial direction of a cell body although we do not show the results for the case in the paper.

Because of the non-slip condition on the surface of a bacterium model moving in a viscous fluid, at any points on a flagellum, the velocity of the flagellar kinetic motion coincides with the velocity of the flow induced by the motion of the bacterium model. Thus, if we focus on the exact center point of each segment $\mathbf{X}^m$ in Eqs. (5)–(7), the velocity is written in the form:

$$\mathbf{u}_f(\mathbf{X}^m) = \mathbf{u}(\mathbf{X}^m) + \mathbf{u}^*(\mathbf{X}^m) + \mathbf{u}_b(\mathbf{X}^m). \quad (10)$$

Substituting Eqs. (5)–(7) and Eq. (9) into Eq. (10), we rewrite it as

$$\begin{aligned} & \Gamma_{ij}^1(\mathbf{X}^m) U_{0j} + \Gamma_{ij}^2(\mathbf{X}^m) \Omega_{0j} \\ & - \sum_{n=1}^N [\{K_{ij}(\mathbf{X}^m, \mathbf{X}^n) + K_{ij}^*(\mathbf{X}^m, \mathbf{X}^n)\} f_j(\mathbf{X}^n)] \\ & - \varepsilon_{ijk} (x_k - r_{bk}) \omega_j = 0 \end{aligned} \quad (11)$$

where

$$\Gamma_{ij}^1(\mathbf{X}^m) = \delta_{ij} - \frac{3r_b}{4} \left\{ S_{ij}(\mathbf{X}^m, 0) - \frac{r_b^3}{3} D_{ij}(\mathbf{X}^m, 0) \right\} \quad (12)$$

$$\Gamma_{ij}^2(\mathbf{X}^m) = \left(1 - \frac{r_b^3}{|\mathbf{X}^m|^3} \right) \varepsilon_{ijk} X_k^m. \quad (13)$$

Supposing that the rotation rate of the rotary motor $\boldsymbol{\omega}$ is given, then unknown vectors in Eq. (11) are $\mathbf{f}(\mathbf{X}^n)$ ($n=1 \sim N$), $\mathbf{U}_0$, $\boldsymbol{\Omega}_0$. Since each of the unknown vectors has three components, the number of unknowns becomes $3(N+2)$. On the other hand, Eq. (11) is a set of linear algebraic equations of which number is $3N$ because $m=1 \sim N$, $i=1 \sim 3$. For the determination of all the unknowns, we need six other equations. The complements are equations for the balances of net force and net torque exerted on the bacterium model, and will be provided in the next section.

2.6 Balance in net force and net torque

Since a bacterium swims by itself without any external force and the inertial force is negligible in a highly viscous fluid, the force and torque exerted on the bacterium should be zero in both cases. In other words, the force and associated torque produced by a flagellum are cancelled by the drag and the counter rotation of the cell body.

The mirror image of a Stokeslet at position $\mathbf{X}$ produces the force and torque. Their components parallel to the vector $\mathbf{X}$ are

$$\mathbf{F}_R = \left(-\frac{3}{2} \frac{r_b}{|\mathbf{X}|} + \frac{r_b^3}{2|\mathbf{X}|^3} \right) \mathbf{f}_R \quad (14)$$

$$\mathbf{M}_R = 0. \quad (15)$$

Also, the components perpendicular to $\mathbf{X}$ are

$$\mathbf{F}_T = \left(-\frac{3}{4} \frac{r_b}{|\mathbf{X}|} - \frac{r_b^3}{4|\mathbf{X}|^3} \right) \mathbf{f}_T \quad (16)$$

$$\mathbf{M}_T = -\frac{r_b^3}{|\mathbf{X}|^3} \mathbf{X} \times \mathbf{f}_T. \quad (17)$$

Adding them to the force and torque produced by the Stokeslets distributed along the flagellum and at the center of the cell, we obtain the whole force and torque exerted on the bacterium model as

$$\sum_{n=1}^N \left[\left(\left(1 - \frac{3}{4} \frac{r_b}{|\mathbf{X}^n|} + \frac{r_b^3}{4|\mathbf{X}^n|^3} \right) \delta_{ij} + \left(-\frac{3}{4} \frac{r_b}{|\mathbf{X}^n|} + \frac{r_b^3}{4|\mathbf{X}^n|^3} \right) \frac{X_i^n X_j^n}{|\mathbf{X}^n|^2} \right) f_i^n \Delta s \right] + 6 \pi \mu r_b U_{0j} = 0, \quad (18)$$

$$\sum_{n=1}^N \left\{ \left(1 - \frac{r_b^3}{|\mathbf{X}|^3} \right) \varepsilon_{ijk} X_j f_k^n \Delta s \right\} + 8 \pi \mu r_b^3 \Omega_{0i} = 0. \quad (19)$$

Here, Δs refers to the length of each short segment.

If the rotation rate of the rotary motor ω is given, the velocities $\mathbf{U}_0$, $\mathbf{\Omega}_0$ and the singularity distribution $\mathbf{f}(\mathbf{X}^n)$ are calculated from Eqs.(11), (18), (19). Once these unknowns are determined, the velocity field around the bacterium model is calculated from Eq. (5)-(7).

3. Results and Discussions

3.1 Dimensions of the flagellum model

As shown in Fig. 2, the shape of the flagellum is assumed to be a helix. The helical radius of the part in the proximity of the cell body gradually diminishes so that the flagellum is smoothly connected to the cell body. The radius is described as a function of x , a distance from the root of the flagellum measured along the axis of the helix :

$$\alpha(x) = \alpha_0 \{1 - \exp[-(2.146 x/\lambda_a)^2]\}. \quad (20)$$

Here, α_0 is the maximum radius of the flagellar helix. λ_a refers to a parameter to define the length of the part whose radius diminishes in size. When x equals λ_a , α becomes 0.99 α_0 .

We obtained optimal flagellar shapes for efficiency and swimming speed changing the following dimensions of the flagellum: the number of waves in the helix n , the pitch angle of the helix β , the length of the flagellum L , the radius of the flagellum a , and λ_a/λ .

When the rotational axis of a flagellum coincides with a radius of a spherical cell body, the cell traces a helix^{(16),(17)}. We define the swimming speed U_m as the velocity component along the axis of the helical trajectory. We also define the efficiency η as the ratio between the power required to translate the cell body with the swimming speed U_m and the mechanical power consumption due to the swimming motion of the bacterium :

$$\eta = \frac{6 \pi \mu r_b U_m^2}{P}. \quad (21)$$

Here, μ is the viscosity. P is an integral over the whole surface on the bacterium whose integrand is an

inner product of fluid force exerted on a small surface and its velocity, and is equivalent to the power of the rotary motor.

The singularity distribution along the flagellum was examined in every calculation. The number of short segments was adjusted to avoid the oscillation in the distribution of the singularity strength. In the results shown here, the flagellum was divided into 40 or 60 segments.

3.2 Efficiency

Figures 3(a)-(e) show the relationships between the efficiency and the parameters described in the previous section. In every figure, all the parameters except the one shown on the abscissa are chosen as values of the most efficient shape.

Figure 3(a) shows the relation of the number of waves in a flagellar helix n and the efficiency η . Up to $n \approx 2$ the efficiency increases rapidly. In this range, especially when $n \leq 1$, even one wave is not formed in the flagellar helix, and the radius of the helix is smaller than the original value α_0 . Since the length L remains constant, the increase in the number of waves n causes the decrease in the helical radius α_0 . Thus, the efficiency slightly decreases in the range in which n is over 2. The efficiency reaches a peak when $n \approx 2.4$.

The effect of the pitch angle of a flagellar helix β on the efficiency is shown in Fig. 3(b). The efficiency attains the maximum value at $\beta \approx 42^\circ$.

As for the effect of the length of a flagellum L , at $L/r_b \approx 12$, the efficiency gets to maximum as shown in Fig. 3(c). To change the length means to shrink or to expand similarly keeping the figure because the number of waves n and the pitch angle β are held at constants. Thus, a flagellum of long length has a helix of a big radius. Because the velocity of a short segment of a flagellum is proportional to the radius, a longer flagellum produces a stronger propulsive force. On the other hand, the longer flagellum also generates a stronger torque, which should be balanced by cell body rotation in the opposite direction to the flagellar rotation. This counter rotation reduces the effective flagellar motion relative to the neighboring fluid. The tension between them settles the efficiency with a certain flagellar length.

Figure 3(d) shows the effect of λ_a , the length of an adjoining part of a flagellum to a cell body. The parameter λ_a hardly affects the efficiency. From the point of view of comparing an analytical result with an experimental one, this fact is fortunate for us because the halation from the cell body makes it difficult to observe the adjoining part (see Fig. 1).

The efficiency gradually decreases with the radius of a flagellum a as presented in Fig. 3(e). In the present study, we chose $a/r_b = 0.03$ as the optimum

Fig. 3 Efficiency as a function of the flagellar parameters, (a) number of waves, (b) pitch angle, (c) length, (d) length of the joining part, (e) radius. $\circ$, SBT; $\bullet$, BEM

referring to the observational data of *Vibrio alginolyticus*⁽⁶⁾.

In the Figs. 3(a)–(e), the results of the boundary element method are shown as well as the results of the slender body theory. The agreement between the results of the slender body theory and those of the boundary element method is excellent. The boundary element method does not require the assumption about slenderness and is expected to give us more reliable results compared with the slender body theory and the resistive force theory. In the slender body theory, the cell body is restricted to a spherical shape because it is generally difficult to find the mirror images of Stokeslets for the other shapes. In contrast, the boundary element method allows us to deal with an arbitrarily shaped cell body⁽¹⁸⁾. The advantage of

the slender body theory is, however, that it does not need many elements, and this leads to less memory and less computational time. In the present study, the CPU time of the slender body theory was about 1/400 of the CPU time of the boundary element method.

3.3 Swimming speed

Figures 4(a) and (b) respectively show the effects of the number of waves n and the pitch angle β on the swimming speed U_m . In every figure, the other parameters are fixed to the values of the fastest swimmer. Although the swimming speed shows a peak with both parameters just as the efficiency does, the optimal parameters for maximum swimming speed are apparently different from the parameters for maximum efficiency. For instance, at $n \approx 1.5$ and $\beta \approx 44^\circ$ the swimming speed reaches a peak, by

Fig. 4 Swimming speed as a function of the flagellar parameters, (a) number of waves, (b) pitch angle

Fig. 5 Optimum shapes of the bacterium model. They are optimized with respect to (a) efficiency, and (b) swimming speed

contrast, at $n \approx 2.4$ and $\beta \approx 42^\circ$ the efficiency achieves a maximum (see Figs. 3(a), (b)). We also see the differences in the other parameters though they are not shown in the paper.

3.4 Optimum shapes for swimming and a comparison with observational shape

The schematics of bacterium models which are optimized for the efficiency η and the swimming speed U_m are shown in Figs. 5(a) and (b), respectively. The difference is apparent in a radius of flagellar helix. As explained for Fig. 3(c), the effect of the helical radius is contradictory. A big radius leads to high swimming speed. At the same time, the big radius causes the counter rotation of the cell body, which reduces the efficiency. Table 1 indicates the dimensions of the two models shown in Fig. 5. Since

Table 1 Parameters of flagellar shapes

		n	β	L/r_b	λ_α/λ
Optimum	Efficiency	2.40	42.1°	12.3	3.03
	Speed	1.54	44.4°	15.4	1.58
<i>Vibrio alginolyticus</i>		2.76	29.1°	9.4	—
(Observed)

Fig. 6 Schematic of a bacterium, *Vibrio alginolyticus*, which is drawn according to the mean values of the observed data⁽⁶⁾

the lengths of the two flagella and their pitch angles are comparable, the difference in the radius is mainly due to the difference in the number of waves n .

Figure 6 is a schematic drawing based on an observational result of *Vibrio alginolyticus*⁽⁶⁾. The average dimensions of this bacterium are also shown in Table 1. The radius of the flagellar helix is comparable or smaller than the radius of the cell body. A similarity can be seen in the most effective swimmer shown in Fig. 5(a). In the observation, the standard deviation in the length of a flagellum is substantial. This is due to the difference between individual cells. Moreover, the shape of the bacterium cell is ellipsoid-like instead of spherical. Therefore, It may be inappropriate to compare the analytical result to the observed one. However, from the point of view of fluid dynamics, the bacterium seems to have a shape optimized to efficiency rather than swimming speed.

4. Conclusions

We analyzed the swimming motion of a monotrichously flagellated bacterium model by use of the slender body theory and calculated the swimming speed and the efficiency. The feature of the slender body theory applied for the bacterium motion is summarized as,

(1) The slender body theory is one of the appropriate methods to analyze the bacterium swimming motion. The results of the slender body theory agree well with the results of the boundary element method, which is more accurate and includes fewer assumptions. The computational time of the slender body theory is two decimals less than the time of the boundary element method.

(2) A hurdle is, however, a modification for a cell body of arbitrary shape. The slender body theory

requires an analytical solution for mirror images of Stokeslets. To seek such solutions is a mathematically complex problem.

We also optimized the shape of a flagellum for swimming speed and efficiency. Regarding the optimal shapes, we obtained the following results:

(1) The difference in the flagellar shape between the fastest swimmer and the most efficient swimmer is apparent in the radius of the flagellar helix. This is explained by the fact that the flagellar shape is prescribed by the contradictory nature of the force produced by a flagellum. One of them is acting as a propulsive force. The other is generating a torque cancelled by the counter rotation of the cell body, which reduces the effective rotation of the flagellum.

(2) The bacterium flagellum in nature resembles the flagellum of the most efficient swimmer rather than the flagellum of the fastest swimmer. From the perspective of fluid dynamics, the bacterium seems to have evolved in a manner that ensures efficient swimming.

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