Numerical Analysis of Small Deformation of Flexible Helical Flagellum of Swimming Bacteria*

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Formulations are conducted to numerically analyze the effect of flexible flagellum of swimming bacteria. In the present model, a single-flagellate bacterium is assumed to consist of a rigid cell body of the prolate spheroidal shape and a flexible flagellum of the helical form. The resistive force theory is applied to estimate the force exerted on the flagellum. The torsional as well as the bending moments determine the curvature and the torsion of the deformed flagellum according to the Kirchhoff model for an elastic rod. The unit tangential vector along the deformed flagellum is calculated by applying evolution equations for space curves, and also a deformed shape of the flagellum is obtained.

Key Words: Swimming Bacterium, Flexible Flagellum, Flagellar Hydrodynamics, Kirchhoff Rod Theory, Resistive Force Theory

1. Introduction

Motile bacteria swim in aqueous environments rotating helical flagella by use of rotary motors embedded in the cell surface and tumble rotating the flagella in the opposite direction⁽¹⁾. By modulating the frequency of tumbling, the bacteria move to a better environment. There are several review articles on the mechanism of bacterial movement and the structure of flagellar motor which are of interest for some fields^{(2),(3)}.

Recently, Magariyama et al. observed the motion of *Vibrio alginolyticus*, single-flagellate bacteria, and found that there is a difference in speed between the forward and backward swimming. It was shown that

the backward swimming speed is 1.5 times greater than the forward swimming speed on average⁽⁴⁾. They considered such conceivable causes of the difference in speed as asymmetric torque characteristics of a flagellar motor relating to the rotational direction and deformation of a flagellum due to viscous force exerted in the opposite direction of movement.

We have so far conducted analyses concerning the motion of bacteria applying the resistive force theory⁽⁵⁾, the boundary element method⁽⁶⁾ and the slender body theory⁽⁷⁾ of the Stokes flow. In addition, we carried out measurements for the bacterial motions of *Vibrio alginolyticus* and demonstrated that the measurement results of the propulsive speed of the bacteria are in good agreement with the results of analyses based on the boundary element method⁽⁸⁾. In these analyses, the bacterial flagella are assumed to be so rigid that the shape of the flagella does not change during swimming.

Recently, a numerical algorithm for the Kirchhoff rod model has been developed and applied to calculate the behavior of writhing instability of bacterial filaments⁽⁹⁾. In the present investigation, we conduct numerical analysis for the small deformation of a helical flagellum of bacteria which is caused by resistive force exerted on the flagellum rotating in an

* Received 29th August, 2003 (No. 02-0172). Japanese Original: Trans. Jpn. Soc. Mech. Eng., Vol. 69, No. 677, A (2003), pp.8-13 (Received 19th February, 2002)

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aqueous medium. First, resistive force on the surface of the rotating flagellum is evaluated assuming a rigid flagellum, then the deformation of the flagellum caused by the resistive force is estimated employing the Kirchhoff rod model. The effect of the deformation of the flagellum is examined by comparing the swimming speed between the deformed and the rigid flagellum. In addition, it is discussed whether the difference in the forward and backward swimming speeds of *Vibrio alginolyticus* can be derived from the deformation of the flagellum.

2. Formulation of Motion of a Bacterium

2.1 Motion of a cell body and a flagellum

As shown in Fig. 1, a bacterium moves in an aqueous medium rotating a flagellum. Resistive force exerted on the surface of a moving flagellum is estimated assuming a rigid flagellum. It is assumed that the bacterium consists of a prolate spheroidal cell body and a helical flagellum. In order to estimate the velocity and the force exerted on a segment of the flagellum, we introduce a coordinate system $O_f \xi_1 \xi_2 \xi_3$ fixed with the flagellum and put the origin O_f at a flagellar motor at the root of the flagellum. As the diameter of the flagellar filament is much smaller than the radius of the flagellar helix, the flagellum can be considered to be a space curve and is expressed as follows,

$$\mathbf{r}_f(s, t) = \xi_1(s) \mathbf{e}_1(t) + \xi_2(s) \mathbf{e}_2(t) + \xi_3(s) \mathbf{e}_3(t), \quad (1)$$

where s is the arc length along the flagellum and t is the time. Also $\mathbf{e}_i(t) (i=1, 2, 3)$ indicates the unit vector of the coordinate. The velocity $\mathbf{v}$ of an element of the flagellum at the position $\mathbf{r}_f$ can be expressed in terms of the velocity $\mathbf{V}_f$ and the angular velocity $\boldsymbol{\Omega}_f$ of the origin O_f of the coordinate fixed with the flagellum as follows,

$$\mathbf{v} = \mathbf{V}_f + \boldsymbol{\Omega}_f \times \mathbf{r}_f. \quad (2)$$

There is a relationship between the velocity $\mathbf{V}_b$ and the angular velocity $\boldsymbol{\Omega}_b$ of the center of the cell body O_b and $\mathbf{V}_f$ and $\boldsymbol{\Omega}_f$ of the origin O_f :

$$\mathbf{V}_b = \mathbf{V}_f - \boldsymbol{\Omega}_f \times \mathbf{r}_a, \quad (3)$$

$$\boldsymbol{\Omega}_b = \boldsymbol{\Omega}_f - \boldsymbol{\omega}_m, \quad (4)$$

where $\mathbf{r}_a$ is the displacement vector from O_b to O_f and $\boldsymbol{\omega}_m$ is the angular velocity of the flagellar motor.

Fig. 1 Schematic of a bacterium model

2.2 Estimation of resistive force exerted on a flagellum

The resistive force theory is applied to estimate the force exerted on each element of a flagellum moving at the velocity $\mathbf{v}$ relative to fluid at rest. The force per unit length of the flagellum can be evaluated as follows,

$$\mathbf{f} = -C_t \mathbf{v}_{||} - C_n \mathbf{v}_{\perp}, \quad (5)$$

where $\mathbf{v}_{||}$ and $\mathbf{v}_{\perp}$ are the tangential and perpendicular components of $\mathbf{v} (= \mathbf{v}_{||} + \mathbf{v}_{\perp})$. C_t and C_n are the tangential and the normal coefficient of resistance, respectively, which are written as follows,

$$C_t = \frac{2\pi\mu}{\ln(4\lambda/d) - 0.5}, \quad (6)$$

$$C_n = \frac{4\pi\mu}{\ln(4\lambda/d) + 0.5}, \quad (7)$$

where μ is the viscosity of the fluid. λ is the pitch of the flagellar helix and d is the diameter of the flagellar filament.

Introducing an orthogonal triad $\mathbf{t}, \mathbf{p}, \mathbf{q}$ to each element of the flagellum to which $\mathbf{t}$ is tangential, Eq. (5) can be written as follows,

$$\mathbf{f} = -C_t v_t \mathbf{t} - C_n (v_p \mathbf{p} + v_q \mathbf{q}), \quad (8)$$

where

$$v_t = \mathbf{v} \cdot \mathbf{t}, v_p = \mathbf{v} \cdot \mathbf{p}, v_q = \mathbf{v} \cdot \mathbf{q}. \quad (9)$$

The orthogonal triad satisfies such differential equations along the space curve of the flagellum as,

$$\frac{d\mathbf{t}}{ds} = \kappa_1 \mathbf{p} + \kappa_2 \mathbf{q}, \quad (10)$$

$$\frac{d\mathbf{p}}{ds} = -\kappa_1 \mathbf{t} + \omega \mathbf{q}, \quad (11)$$

$$\frac{d\mathbf{q}}{ds} = -\omega \mathbf{p} - \kappa_2 \mathbf{t}, \quad (12)$$

where s denotes the arc length of the space curve. There exist such relationships between κ_1, κ_2 and ω and the curvature κ and the torsion τ as,

$$\kappa = \sqrt{\kappa_1^2 + \kappa_2^2}, \quad (13)$$

$$\tau = \omega + \frac{\kappa_2 \kappa_{1s} - \kappa_1 \kappa_{2s}}{\kappa}. \quad (14)$$

Here, κ_{1s} and κ_{2s} denote partial derivatives with respect to s .

If we choose $\mathbf{p}$ and $\mathbf{q}$ to be identical to the normal vector $\mathbf{n}$ and the binormal vector $\mathbf{b}$ of the space curve, we obtain the relationships,

$$\kappa_1 = \kappa, \kappa_2 = 0, \omega = \tau. \quad (15)$$

Then, Eqs. (10)–(12) become the Frenet-Serret equations.

In the present analysis, we introduce the Frenet triad fixed with the flagellum before deformation, and consider the triad fixed with the deformed flagellum based on the orthogonal triad of $\mathbf{t}, \mathbf{p}, \mathbf{q}$.

Integrating $\mathbf{f}$ defined in Eq. (8) and $\mathbf{r}_f \times \mathbf{f}$ along the flagellum, we have the force and the moment of force acting on the root of the flagellum as follows,

$$\mathbf{F}_{f0} = A \mathbf{V}_f + B \boldsymbol{\Omega}_f, \quad (16)$$

$$\mathbf{M}_{f0} = C\mathbf{V}_f + D\boldsymbol{\Omega}_f, \quad (17)$$

where A, B, C, D are 3×3 resistance matrices which correspond to Eqs. (13), (14), (16), (17) of our previous paper⁽⁵⁾.

The force and the moment of force exerted on the cell body of the prolate spheroid, which moves at the velocity of $\mathbf{V}_b$ and rotates at the angular velocity of $\boldsymbol{\Omega}_b$, can be expressed as follows,

$$\mathbf{F}_b = E\mathbf{V}_b, \quad (18)$$

$$\mathbf{M}_b = F\boldsymbol{\Omega}_b, \quad (19)$$

where E and F are 3×3 diagonal matrices which are given by the singular method⁽¹⁰⁾ as follows,

$$E = -6\pi\mu a \begin{bmatrix} C_{F3}, & 0, & 0 \\ 0, & C_{F3}, & 0 \\ 0, & 0, & C_{F1} \end{bmatrix} \quad (20)$$

$$F = -8\pi\mu ab^2 \begin{bmatrix} C_{MR}, & 0, & 0 \\ 0, & C_{MR}, & 0 \\ 0, & 0, & C_{M0} \end{bmatrix} \quad (21)$$

$$C_{F1} = \frac{8e^3/3}{-2e + (1+e^2)\ln(1+e)/(1-e)} \quad (22)$$

$$C_{F3} = \frac{16e^3/3}{2e + (-1+3e^2)\ln(1+e)/(1-e)} \quad (23)$$

$$C_{M0} = \frac{4e^3/3}{2e - (1-e^2)\ln(1+e)/(1-e)} \quad (24)$$

$$C_{MR} = \frac{(4e^3/3) \times [(2-e^2)/(1-e^2)]}{-2e + (1+e^2)\ln(1+e)/(1-e)} \quad (25)$$

where a and b are the major and the minor radius of the ellipse, respectively, and $e (= \sqrt{a^2 - b^2}/a)$ is its eccentricity. It should be mentioned that the coefficients (22)–(25) become 1 for a spherical body when the spheroid becomes a sphere, namely, $a = b$.

2.3 Balance for force and moment of force in a bacterium

Because the size of a bacteria is very small and its density is almost the same as that of the surrounding fluid, the inertial force can be neglected and the propulsive force generated by the flagellum must balance the drag force of the cell body. Also, the torque produced by the flagellar motion must balance that exerted on the cell body. Hence the motion of the bacterium is described as follows,

$$\mathbf{F}_{f0} + \mathbf{F}_b = 0, \quad (26)$$

$$\mathbf{M}_{f0} + \mathbf{r}_a \times \mathbf{F}_{f0} + \mathbf{M}_b = 0. \quad (27)$$

Substituting Eqs. (16)–(19) into Eqs. (26) and (27), we have

$$\begin{bmatrix} A+E, & B+ER \\ C+RA, & D+RB+F \end{bmatrix} \begin{bmatrix} \mathbf{V}_f \\ \boldsymbol{\Omega}_f \end{bmatrix} = \begin{bmatrix} 0 \\ F\boldsymbol{\omega}_m \end{bmatrix}, \quad (28)$$

$$R = \begin{bmatrix} 0, & -r_{a3}, & r_{a2} \\ r_{a3}, & 0, & -r_{a1} \\ -r_{a2}, & r_{a1}, & 0 \end{bmatrix}. \quad (29)$$

Here, R is a matrix which is determined to satisfy $\mathbf{r}_a \times \mathbf{F}_{f0} = R\mathbf{F}_{f0}$ and then $r_{a1} = r_{a2} = 0, r_{a3} = a$. Thus, the

velocity and the angular velocity of the flagellum, $\mathbf{V}_f$ and $\boldsymbol{\Omega}_f$, are determined as a function of the angular velocity of $\boldsymbol{\omega}_m$.

3. Formulation for Deformation of a Flagellum

3.1 Force and the moment of force in a flagellum

When the flagellum moves in the fluid, the resistive force exerted on the surface of the flagellum generates the resultant force and the resultant moment of force in the cross section of the flagellum. As is shown in Fig. 2, the balance of the force $\mathbf{F}_f(s)$ and the moment of force $\mathbf{M}_f(s)$ in a segment of a slender rod can be written as,

$$\frac{d\mathbf{F}_f}{ds} + \mathbf{f} = 0, \quad (30)$$

$$\frac{d\mathbf{M}_f}{ds} = \mathbf{F}_f \times \mathbf{t} + \mathbf{g}. \quad (31)$$

Here, $\mathbf{t}$ is the tangential vector along the flagellum. Also, $\mathbf{f}$ is the force per unit length of the flagellum, which is given by Eq. (5), and $\mathbf{g}$ is the torque per unit length of the flagellum, which is negligible because the diameter of the flagellar filament is much smaller than the radius of the flagellar helix: $d \ll \rho$.

Decomposing $\mathbf{F}_f$ and $\mathbf{M}_f$ according to the triad along the flagellum as follows,

$$\mathbf{F}_f = F_t \mathbf{t} + F_p \mathbf{p} + F_q \mathbf{q}, \quad (32)$$

$$\mathbf{M}_f = M_t \mathbf{t} + M_p \mathbf{p} + M_q \mathbf{q}, \quad (33)$$

and substituting Eqs. (32) and (33) for Eqs. (30) and (31), we obtain

$$\frac{dF_t}{ds} - \kappa_1 F_p - \kappa_2 F_q = C_t v_t, \quad (34)$$

$$\frac{dF_p}{ds} + \kappa_1 F_t - \omega F_q = C_n v_p, \quad (35)$$

$$\frac{dF_q}{ds} + \kappa_2 F_t + \omega F_p = C_n v_q, \quad (36)$$

$$\frac{dM_t}{ds} - \kappa_1 M_p - \kappa_2 M_q = g, \quad (37)$$

$$\frac{dM_p}{ds} + \kappa_1 M_t - \omega M_q = F_q, \quad (38)$$

$$\frac{dM_q}{ds} + \kappa_2 M_t + \omega M_p = -F_p, \quad (39)$$

taking account of Eqs. (10)–(12). By integrating these equations with the boundary conditions at the tip of the flagellum: $F_t = F_p = F_q = 0, M_t = M_p = M_q = 0$, we

Fig. 2 Balance of force and torque on a segment of a rod

obtain M_t , M_p and M_q .

3.2 Deformation of a flagellum

The deformation of a flagellum is mainly produced by the bending and the torsion due to the moment of force acting on the cross section. Assuming that the flagellum is an isotropic elastic body, we apply the Kirchhoff rod model⁽¹¹⁾ to obtain the constitutive relation for the moment of force as follows

$$\mathbf{M}_f = EI(\kappa_1 - \kappa_0)\mathbf{q} + EI\kappa_2\mathbf{p} + GJ(\omega - \tau_0)\mathbf{t}. \quad (40)$$

Here, E is the Young's modulus and G is the modulus of rigidity; I and J are the moment of inertia of cross section. For a circular rod of diameter d , the moment of inertia can be written as $I = J/2 = \pi d^4/64$. κ_0 and τ_0 denote the curvature and the torsion of the flagellum before deformation. From Eq.(40), we obtain κ_1 , κ_2 and ω of the deformed flagellum due to the moment of force $\mathbf{M}_f$. Thus, we have not only the tangential vector $\mathbf{t}(s)$ of the deformed flagellum integrating Eqs. (10)–(12), but also the shape of the deformed flagellum integrating $\mathbf{t}(s)$.

3.3 Computational algorithm

In the numerical computations for the force and the moment of force in the cross section of the flagellum, the Frenet triad $\mathbf{t}$, $\mathbf{n}$, $\mathbf{b}$ consisting of the tangential, the normal and the binormal vector is adopted as the orthogonal triad along the flagellum without deformation. Then, Eq.(15) holds.

In the numerical computations, we divide a space curve for the flagellum of the length L into N segments with the same interval. Figure 3 shows a typical segment used in the numerical computations. The force and the moment of force as well as the position vector of the flagellum are evaluated in the cross sections on both sides. The curvature and the torsion as well as the orthogonal triad are evaluated at the center of the segments.

Numerical integrations of Eqs.(34)–(36) are conducted applying such a backward scheme as,

$$F_{ti} = F_{ti+1} - \Delta s(C_{ti+1} + \kappa_{i+1}F_{ni+1}), \quad (41)$$

from the tip of the flagellum where the boundary conditions can be written as $F_{tN} = F_{nN} = F_{bN} = 0$. Hence, F_{ti} , F_{ni} and F_{bi} are obtained from $i = N$ to 0.

Numerical integrations of Eqs.(37)–(39) are car-

ried out employing such a backward scheme as,

$$M_{ni} = M_{ni+1} - \Delta s(F_{bi+1} - \kappa_{i+1}M_{ti+1} + \tau_{i+1}M_{bi+1}), \quad (42)$$

and using the boundary conditions at the tip such as $M_{tN} = M_{nN} = M_{bN} = 0$. Hence M_{ti} , M_{ni} and M_{bi} are obtained from $i = N$ to 0.

The curvature κ_1 , κ_2 and the torsion ω of the deformed flagellum are estimated from Eq.(40) as follows,

$$\kappa_{1i} = \kappa_{0i} + (M_{bi} + M_{bi-1})/2EI, \quad (43)$$

Numerical integrations of Eq.(10)–(12) are performed employing such a forward scheme as,

$$\mathbf{t}_i = \mathbf{t}_{i-2} + 2\Delta s(\kappa_{1i-1}\mathbf{p}_{i-1} + \kappa_{2i-1}\mathbf{q}_{i-1}), \quad (44)$$

and using the boundary conditions at the root of the flagellum. Hence, $\mathbf{t}_i$, $\mathbf{p}_i$, $\mathbf{q}_i$ are obtained from $i = 0$ to N .

The position vector $\mathbf{r}_f$ of the deformed flagellum is evaluated numerically integrating $\mathbf{t}_i$ from $i = 0$ to N as follows,

$$\mathbf{r}_{fi} = \mathbf{r}_{fi-1} + \Delta s\mathbf{t}_i, \quad (45)$$

In the present numerical computations, the number of the segments of the flagellum is taken as $N = 1000$. If we take 100 segments of the flagellum, we will obtain exact results for the force and the moment of force in the cross section of the flagellum but will obtain inexact results for the deformed shape of the flagellum. In order to calculate Eqs.(10)–(12) correctly, it is necessary to take the number of segments of the flagellum as at least $N = 1000$.

4. Results and Discussion

Table 1 shows the size of *Vibrio alginolyticus* which is used in a numerical example of the present analysis. A helical shape of the flagellum is assumed as follows

$$\begin{aligned} \xi_1 &= r \cos 2\pi\xi_3/\lambda, \quad \xi_2 = -r \sin 2\pi\xi_3/\lambda, \\ r &= \rho[1 - \exp[-(\xi_3/c\lambda)^2]], \quad c = 1/2. \end{aligned}$$

Figure 3 shows the shape of the flagellum before deformation. We choose the Frenet triad $\mathbf{t}$, $\mathbf{n}$ and $\mathbf{b}$ as an orthogonal triad fixed with each segment of the flagellum before deformation. Figure 4 shows the curvature and the torsion of the flagellum without deformation.

As the Young's modulus of the flagellum was reported to have the same order of magnitude as

Fig. 3 Shape of flagellum before deformation

Table 1 Parameters of a bacterium

Symbol	Parameter	μm
l (2a)	Cell length	2
w (2b)	Cell width	1
d	Diameter flagellar filament	0.02
L	Length of flagellar filament	7.3
λ	Pitch of flagellar helix	1.4
ρ	Radius of flagellar helix	0.2

Fig. 4 Distributions of curvature and torsion of a flagellum

polystyrene⁽³⁾, we adopt Young's modulus $E=0.35 \times 10^{10}$ Pa and Poisson's ratio $\nu=0.34$ of polystyrene for the flagellum, and use $EI=2.75 \times 10^{-23}$ Nm² and $GJ=2.0 \times 10^{-23}$ Nm².

In the analysis of motion of a bacterium, assuming a flagellum to be so rigid that its shape does not change, we calculate the velocity and the angular velocity of each segment of the flagellum, and estimate the force and the moment of force exerted on the segment. We consider water as the aqueous medium in which bacteria swim.

4.1 Results of CCW rotation of a flagellum

Results are shown for the case of the rotation rate 1000 rps of a flagellar motor which rotates in the counterclockwise direction as observed from the outside of the cell body. The bacterium moves forward at the velocity of $V=136$ μm/s. The cell body of the bacterium rotates at 76 rps relative to stationary fluid in the opposite direction to the flagellum, and consequently the flagellum rotates at 924 rps relative to the fluid.

Figure 5 shows distributions of velocity components along the flagellum, where v_t , v_n and v_b denote the tangential, the normal and the binormal components, respectively. We apply the resistive force theory to estimate the force exerted on the flagellum from the velocity components using the resistance coefficients.

Figure 6 shows distributions of the force along the flagellum, where F_t , F_n and F_b denote the tangential, the normal and the binormal components, respectively. Considering the directions of $\mathbf{t}$ and $\mathbf{b}$, we understand that F_t and F_b are the components of the force which drive the bacterium forward. The driving force is shown to come to concentrate in F_t at the root of the flagellum.

Figure 7 shows the distributions of the moment of force in the cross section of the flagellum, where M_t denotes the torque around the flagellum and M_b and M_n denote the bending moments. It is shown that M_t at the root of the flagellum becomes approximately 3 pN μm which is comparable to the torque of the

Fig. 5 Velocity distributions along the flagellum in case of CCW rotation

Fig. 6 Distributions of force along the flagellum in case of CCW rotation

Fig. 7 Distributions of moment of force along the flagellum in case of CCW rotation

Fig. 8 Variations of curvature and torsion along the flagellum in case of CCW rotation

flagellar motor which was predicted by the boundary element method as 2 pN μm⁽⁷⁾.

Figure 8 shows variations of the curvature $\kappa_1 - \kappa_0$, κ_2 and the torsion $\omega - \tau_0$ as a result of deformation of the flagellum. The variations are obtained from the moment of force acting on the cross section of the

Fig. 9 Deformed shape of flagellum in case of CCW rotation

flagellum, where κ_0 and τ_0 are the curvature and the torsion of the flagellum before deformation, respectively, as shown in Fig. 4. It is observed that the curvature of the helical flagellum becomes larger and the absolute value of the torsion which is negative becomes larger due to the deformation.

Figure 9 shows the shape of the deformed flagellum which is calculated using the curvature and the torsion, $\kappa_1, \kappa_2, \omega$. It is observed that the radius of the flagellar helix becomes slightly smaller although the number of turns of the flagellar helix increases due to deformation.

4.2 Results of CW rotation of a flagellum

Results are shown for the case of clockwise rotation of the flagellum at the rotation rate of 1000 rps, which is the direction opposite to that of CCW rotation. The velocity at each segment of the flagellum points in the direction opposite to that in the case of CCW rotation, as does the force exerted on the flagellum. Consequently, distributions of the moment of force in the cross section become identical to that of the case of CCW multiplied by -1 . Figure 10 shows variations of the curvature and the torsion which are also identical with those for the case of CCW multiplied by -1 . It is shown that the curvature of the flagellum becomes smaller and the absolute value of the torsion which is negative becomes smaller due to the deformation. Figure 11 shows the shape of the flagellum deformed due to CW rotation. It is observed that the radius of the flagellar helix becomes slightly larger and the number of turns decreases due to the deformation.

4.3 Comparison of propulsive speed between CCW and CW rotation of a flagellum

We estimate the speed of forward movement at the rotation rate of 1000 rps in the CCW direction taking account of deformation of the flagellum and obtain the forward speed of $V(\text{CCW}) = 134 \mu\text{m/s}$. Additionally, we have the backward speed of $V(\text{CW}) = 139 \mu\text{m/s}$ at the rotation of 1000 rps in the CW direction. The comparison between the forward and the backward speed shows that the backward

Fig. 10 Variations of curvature and torsion along the flagellum in case of CW rotation

Fig. 11 Deformed shape of flagellum in case of CW rotation

speed is slightly faster than the forward speed. However, the results of observation that the backward swimming speed is 1.5 times greater than the forward swimming speed cannot be explained by the present results. The cause of the difference of the forward and the backward swimming speeds may reveal the characteristic of the flagellar motor which depends on rotational direction.

In the present results of numerical computation for flagellar deformation, the deformation is so small that it does not influence the force and the moment of force exerted on the flagellum. It should be mentioned that the present formulation cannot be directly applied to flagellar deformation in the case the deformation is sufficiently large to influence the force exerted on the flagellum.

A recent review of the detailed structure of a flagellum has shown that a flagellum is a hollow cylinder consisting of several protofilaments lined up side by side⁽¹²⁾. Hence a flagellum cannot be considered to be an isotropic elastic body. A future investigation of flagellar deformation should be conducted taking account of the detailed structure of the flagellum.

5. Conclusions

In the present investigation, formulations were conducted to numerically analyze the deformation of flagella of swimming bacteria. The resistive force theory was employed to analyze the movement of

single-flagellate bacteria and to evaluate the resistive force exerted on a flagellum. Applying the Kirchhoff rod model, the moment of force in the cross section of the flagellum was obtained and variations of the curvature and the torsion of the deformed flagellum were calculated. The shape of the deformed flagellum was obtained from the evolution equations of the space curves. Furthermore, the propulsive speed of the bacteria was analyzed taking account of the deformation and the effect of deformation of the flagella was discussed. It is possible to develop a formulation for peritrichate bacteria which swim rotating several flagella in a bundle from the present formulation for the single-flagellate bacteria.

Acknowledgments

We thank Dr. Yukio Magariyama, National Food Research Institute, for his advice. The present study was partly supported by a Grant-in-Aid for Scientific Research No. 12650168 from the Japan Society for the Promotion of Science.

References

- (1) Magariyama, Y. et al., Simultaneous Measurement of Bacterial Flagellar Rotation Rate and Swimming Speed, *BioPhys. J.*, Vol. 69 (1995), pp. 2154-2162.
- (2) Berg, H.C., Motile Behavior of Bacteria, *Phys. Today*, Vol. 53, No.1 (2000), pp. 24-29.
- (3) Magariyama, Y. and Kudo, S., Bacterial Motility as Nano-Micro Machine System, *Journal of JSME*, (in Japanese), Vol. 103, No. 984 (2001), pp. 752-755.
- (4) Magariyama, Y., Masuda, S., Takano, Y., Ohtani, T. and Kudo, S., Difference between Forward and Backward Swimming Speeds of the Single-Polar-Flagellated Bacterium, *FEMS Microbiology Letters*, Vol. 205 (2001), pp. 343-347.
- (5) Takano, Y., Goto, T. and Usui, Y., Analyses on Propulsion Mechanism of Micro-Organism with a Helical Flagellum, *Trans. Jpn. Soc. Mech. Eng.*, (in Japanese), Vol. 62, No. 593, B (1996), pp. 211-217.
- (6) Goto, T., Taga, Y. and Takano, Y., Study on Resistive Force Theory for Flagella with Boundary Element Method, *Trans. Jpn. Soc. Mech. Eng.*, (in Japanese), Vol. 63, No. 605, B (1997), pp. 188-193.
- (7) Goto, T., Inaoka, R. and Takano, Y., Numerical Analysis of Bacterium Motion Based on the Slender Body Theory, *JSME Int. J., Ser. C*, Vol. 43 (2000), pp. 875-881.
- (8) Goto, T., Masuda, S., Terada, K. and Takano, Y., Comparison between Observation and Boundary Element Analysis for Bacterium Swimming Motion, *JSME Int. J., Ser. C*, Vol. 44 (2001), pp. 953-963.
- (9) Klapper, I., Biological Applications of the Dynamics of Twisted Elastic Rods, *J. Comput. Phys.*, Vol. 125 (1996), pp. 325-337.
- (10) Chwang, A.T. and Wu, T.Y., Hydrodynamics of Low-Reynolds-Number Flow. Part 2. Singularity Method for Stokes Flows, *J. Fluid Mech.*, Vol. 67, Pt. 4 (1975), pp. 787-815.
- (11) Love, A.E.H., *A Treatise on the Mathematical Theory of Elasticity*, Dover, (1944), pp. 396-398.
- (12) Macnab, R.M., Protein Crystal Mimics Reality, *Nature*, Vol. 404 (2001), pp. 321-322.