

A Mathematical Explanation of an Increase in Bacterial Swimming Speed with Viscosity in Linear-Polymer Solutions

Yukio Magariyama* and Seishi Kudo†

*National Food Research Institute, Tsukuba 305-8642, Japan; and †Faculty of Engineering, Toin University of Yokohama, Aoba, Yokohama 225-8502, Japan

ABSTRACT Bacterial swimming speed is sometimes known to increase with viscosity. This phenomenon is peculiar to bacterial motion. Berg and Turner (*Nature*, 278:349–351, 1979) indicated that the phenomenon was caused by a loose, quasi-rigid network formed by polymer molecules that were added to increase viscosity. We mathematically developed their concept by introducing two apparent viscosities and obtained results similar to the experimental data reported before. Addition of polymer improved the propulsion efficiency, which surpasses the decline in flagellar rotation rate, and the swimming speed increased with viscosity.

INTRODUCTION

Many bacteria swim by rotating their helical flagellar filaments and/or helical cell bodies. It has been reported that some bacteria swim well in viscous media (Shoosmith, 1960; Schneider and Doetsch, 1974; Kaiser and Doetsch, 1975; Strength et al., 1976; Greenberg and Canale-Parola, 1977a,b). For example, the swimming speed of *Pseudomonas aeruginosa* (single polar flagellation) in polyvinylpyrrolidone (PVP) solutions increases with viscosity up to a characteristic point and thereafter decreases, as shown in Fig. 1 *a* (Schneider and Doetsch, 1974). The swimming speed of *Leptospira interrogans* (helical cell body without any external flagella) monotonically increases with viscosity in medium supplemented with methylcellulose until the viscosity exceeds 300 mPa · s (Kaiser and Doetsch, 1975). Other flagellation types of bacteria (*Bacillus megaterium*, peritrichous; *Escherichia coli*, peritrichous; *Sarcina ureae*, one flagellum/cell; *Serratia marcescens*, peritrichous; *Spirillum serpens*, bipolar; and *Thiospirillum jenense*, polar) also exhibit an increase in swimming speed in more viscous solutions (Schneider and Doetsch, 1974). No effect of temperature or buffer composition on the phenomenon was detected and different viscous agents, PVP and methylcellulose, produced a similar phenomenon (Schneider and Doetsch, 1974).

No such phenomena have been reported in larger organisms, and the traditional theories for bacterial motion predict that the swimming speed monotonically decreases with viscosity (Holwill and Burge, 1963; Chwang and Wu, 1971; Azuma, 1992; Ramia et al., 1993) (see Fig. 1 *b*).

Berg and Turner (1979) suggested that the above-mentioned phenomenon is caused by loose and quasi-rigid networks consisting of long, linear polymer molecules such as

PVP and methylcellulose (e.g., see the textbook by Strobl, 1997), and recommended Ficoll, which is a highly branched polymer, as a simple means of increasing the viscosity. This suggestion has guided many researchers in the experimental analysis of bacterial motion. However, they did not express it mathematically, and no quantitative analysis based on the suggestion has been made.

In this study we interpreted the suggestion by Berg and Turner and mathematically developed it with regard to the motion of a single-polar-flagellated bacterium such as *P. aeruginosa* and *Vibrio alginolyticus*. In addition, we showed that the obtained equations quantitatively explained the peculiar phenomenon of bacterial motion in polymer solutions.

RESULTS

Introduction of two apparent viscosities

Our purpose is to mathematically develop the suggestion by Berg and Turner (1979). Their suggestions are as follows: 1) solutions of long linear polymers are highly structured (gel-like); 2) the solute forms a loose, quasi-rigid network easily penetrated by particles of microscopic size; 3) the network can exert forces normal to a segment of a slender body; and 4) therefore, traditional hydrodynamic treatments do not apply to the motion of microorganisms (or of cilia and flagella) in solutions containing viscous agents.

Fig. 2 *a* is a schematic drawing expressing their suggestion. It is assumed that the length of a slender body such as a bacterial flagellar filament is much larger than the mesh size of a polymer network, and that the motion of the slender body is faster than the polymer network. Consequently, the network exerts force on an element of the slender body mainly in the normal direction. In other words, the network forms a virtual tube around the slender body, and the body moves easily in the tube, but with difficulty outside the tube. This idea is almost the

Submitted January 3, 2002, and accepted for publication April 16, 2002.

Address reprint requests to Dr. Yukio Magariyama, National Food Research Institute, Tsukuba 305-8642, Japan. Tel.: 81-298-38-8054; Fax: 81-298-38-7181; E-mail: maga@affrc.go.jp.

© 2002 by the Biophysical Society

0006-3495/02/08/733/07 \$2.00

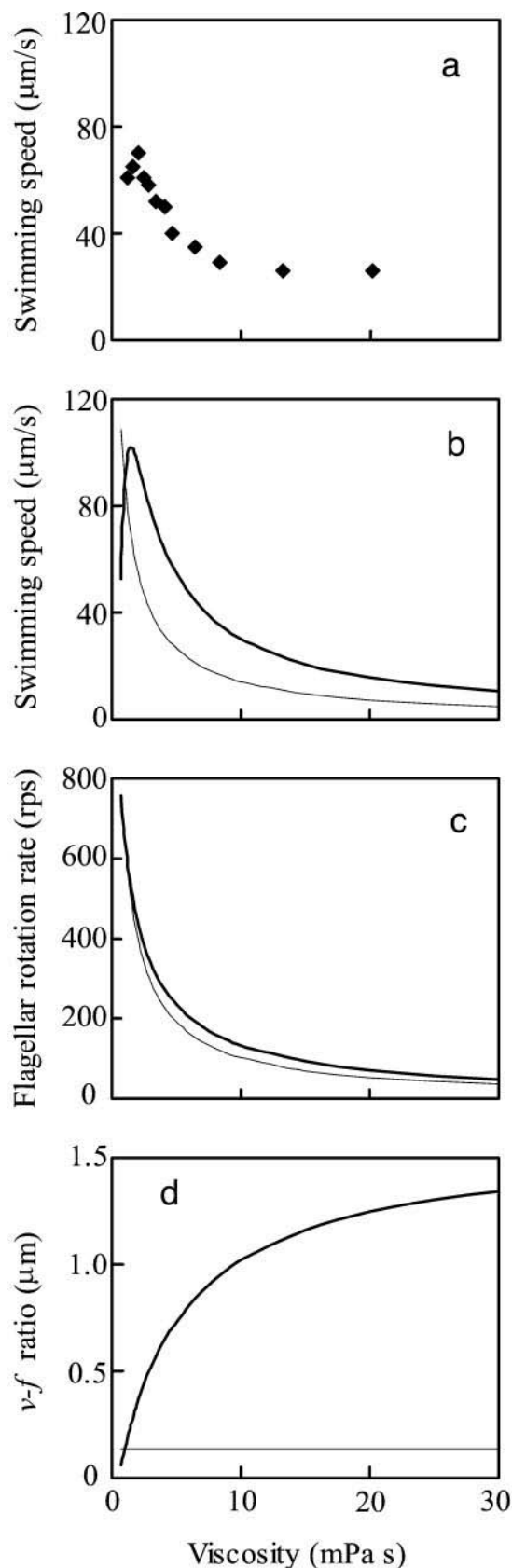


FIGURE 1 Bacterial swimming speeds, flagellar rotation rates, and v - f ratios as a function of viscosity. (a) Experimental data of bacterial swim-

ming speed. Bacterial species is *Pseudomonas aeruginosa* and viscous agent is polyvinylpyrrolidone. The data by Schneider and Doetsch (1974) are redrawn.

(b) Calculated swimming speeds as a function of viscosity. (c) Calculated flagellar rotation rates. (d) Calculated v - f ratios. In b, c, and d, thick (thin) lines refer to the modified (traditional) RFT. Values in Table 1 were used in the calculation.

The simplest way to express the idea mathematically is to introduce two apparent viscosities, μ_T^* and μ_N^* , referring to the motions of a microscopic body in the tangential and normal directions to the surface of the body. When a microscopic body moves in the virtual space that is surrounded with the polymer network, μ_T^* is assumed. Conversely, μ_N^* is assumed when the body goes outside the virtual space; in other words, when the polymer network must be reconstructed as the virtual space is moving. For example, when a microscopic sphere with radius a moves at a speed of v in a polymer solution, the drag force is assumed to be $-6\pi\mu_N^*av$ because the sphere moves to the outside of the original virtual space (see Fig. 2 b). In contrast, when the same sphere rotates at a rate of ω , the drag torque is assumed to be $-8\pi\mu_T^*a^3\omega$ because the motion is in the virtual space. When a solution does not contain any polymer molecules, μ_N^* equals μ_T^* and traditional hydrodynamics is valid. As the polymer concentration increases, the network becomes denser and the ratio of μ_N^* to μ_T^* becomes larger.

Mathematical expression of a modified resistive force theory

The following simple idea has often been adopted to obtain hydrodynamic force acting on a moving helix (Fig. 2 c). 1) The hydrodynamic force and torque acting on the whole helix can be obtained by integrating the force acting on a small element of the helix; 2) the force acting on the element is a composition of forces in the directions parallel and perpendicular to the element.

The original idea was adopted mainly for analyzing the motion of spermatozoa (Hancock, 1953; Gray and Hancock, 1955). Holwill and Burge (1963) applied it to the motion of flagellated bacteria, and the method is presently called resistive force theory (RFT). To derive a new theory of bacterial motion in a polymer solution, we modify the traditional RFT using apparent viscosities μ_T^* and μ_N^* .

The mathematical expression of the traditional RFT is summarized as follows (Magariyama et al., 1995). Here, the object is a bacterial cell that has a single-polar flagellum such as *P. aeruginosa* and *V. alginolyticus*, and the symbols are summarized in Table 1 (see also Fig. 2 d).

ming speed. Bacterial species is *Pseudomonas aeruginosa* and viscous agent is polyvinylpyrrolidone. The data by Schneider and Doetsch (1974) are redrawn. (b) Calculated swimming speeds as a function of viscosity. (c) Calculated flagellar rotation rates. (d) Calculated v - f ratios. In b, c, and d, thick (thin) lines refer to the modified (traditional) RFT. Values in Table 1 were used in the calculation.

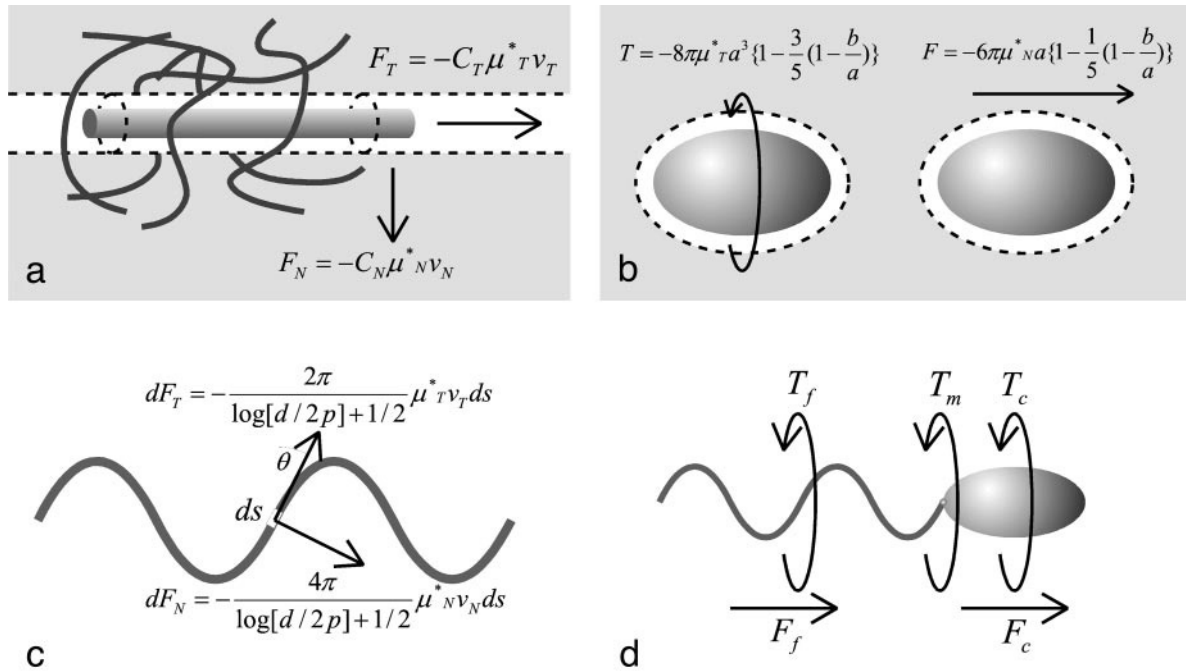


FIGURE 2 Motion model of free-swimming bacterial cell based on the modified RFT proposed in this study. (a) Schematic drawing expressing the concept of apparent viscosity for a slender body. (b) Schematic drawing expressing the concept of apparent viscosity for a spheroid body. (c) The force acting on a flagellar element ds . dF_T and dF_N are tangential and normal components of force acting on ds . θ is the pitch angle of the flagellar helix. (d) The forces acting on a cell body and a flagellar filament. The symbols used here are defined in Table 1.

Equations of motion

$$F_c + F_f = 0 \quad (1)$$

$$T_c - T_m = 0 \quad (2)$$

$$T_f + T_m = 0 \quad (3)$$

Drag force and torque acting on a cell body

$$F_c = \alpha_c \nu \quad (4)$$

$$T_c = \beta_c \omega_c \quad (5)$$

Drag force and torque acting on a flagellar filament

$$F_f = \alpha_f \nu + \gamma_f \omega_f \quad (6)$$

$$T_f = \gamma_f \nu + \beta_f \omega_f \quad (7)$$

Torque generated by a flagellar motor

$$T_m = T_0 \left(1 - \frac{\omega_f - \omega_c}{\omega_0} \right) \quad (8)$$

The actual motor torque has been reported to be approximately constant up to a knee rotation rate, and then monotonically decrease with rotation rate (Berg, 2000; Ryu et al., 2000; Chen and Berg, 2000). To simplify the analysis, we

assumed that the motor torque decreased linearly with the motor rotation rate because the motor of a free-swimming cell is considered to rotate faster than the knee rate. Under the assumption of a constant motor torque, the following argument and the result were also valid except for slight numerical differences.

Simultaneous equations 1–8 were analytically solved as follows.

$$\nu = K_0 \beta_c \gamma_f \quad (9)$$

$$\omega_f = -K_0 (\alpha_c \beta_c + \alpha_f \beta_c) \quad (10)$$

$$\omega_c = K_0 (\alpha_c \beta_f + \alpha_f \beta_f - \gamma_f^2) \quad (11)$$

$$K_0 = 1 / \left[\frac{\beta_c (\alpha_c \beta_f + \alpha_f \beta_f - \gamma_f^2)}{T_0} - \frac{\alpha_c \beta_c + \alpha_c \beta_f + \alpha_f \beta_c + \alpha_f \beta_f - \gamma_f^2}{\omega_0} \right] \quad (12)$$

Assuming that the shape of a cell body is a spheroid, the drag coefficients, α_c and β_c , are formulated by viscosity and cell shape in traditional low-Reynolds-number hydrodynamics (Happel and Brenner, 1973). In a polymer solution (Fig. 2 b) the viscosity, μ , in α_c should be modified to μ_N^* because a virtual space around the cell body moves as the cell body moves translationally, i.e., the polymer network

TABLE 1 Parameters necessary for calculating bacterial motion

| Symbol | Parameter | Value* |
|--------------------------------|--|--|
| ν | Swimming speed | |
| $\omega_c, \omega_f, \omega_m$ | Rotation rates of cell body, flagellar filament, and flagellar motor | |
| F_c, T_c | Hydrodynamic force and torque acting on cell body | |
| F_f, T_f | Hydrodynamic force and torque acting on flagellar filament | |
| T_m | Torque generated by flagellar motor | |
| μ | Viscosity | |
| μ_N^*, μ_T^* | Apparent viscosities in the normal and tangential directions | |
| α_c, β_c | Drag coefficients of cell body | |
| $\alpha_f, \beta_f, \gamma_f$ | Drag coefficients of flagellar filament | |
| $2a$ | Cell width | $0.80 \mu\text{m}$ |
| $2b$ | Cell length | $1.92 \mu\text{m}$ |
| $2d$ | Diameter of flagellar filament | $0.032 \mu\text{m}$ |
| L | Length of flagellar filament | $5.02 \mu\text{m}$ |
| p | Pitch of flagellar helix | $1.58 \mu\text{m}$ |
| r | Radius of flagellar helix | $0.14 \mu\text{m}$ |
| T_0 | Motor torque at rotation rate of 0 | $1.5 \times 10^{-18} \text{ N} \cdot \text{m}$ |
| ω_0 | Rotation rate at motor torque of 0 | 1700 rps |
| μ_0 | Viscosity of water at 25°C | $0.89 \times 10^{-3} \text{ N} \cdot \text{s} \cdot \text{m}^{-2}$ |
| ds | Small element of flagellar filament | |
| v_N, v_T | Velocities in the normal and tangential directions | |
| dF_N, dF_T | Hydrodynamic forces acting on ds in the normal and tangential directions | |
| θ | Helical angle of flagellar helix | |

*The values used to analyze the motion of *Vibrio alginolyticus* (Magariyama et al., 1995) were adopted in this study.

produces large resistive force. However, μ_T^* should be used as the viscosity in β_c because the virtual space does not move when the cell body rotates. Therefore, α_c and β_c were rewritten as follows.

$$\alpha_c = -6\pi\mu_N^*a \left\{ 1 - \frac{1}{5} \left(1 - \frac{b}{a} \right) \right\} \quad (13)$$

$$\beta_c = -8\pi\mu_T^*a^3 \left\{ 1 - \frac{3}{5} \left(1 - \frac{b}{a} \right) \right\} \quad (14)$$

Assuming that the shape of a flagellum is a helical thin filament, the drag coefficients, α_f , β_f , and γ_f , are given as follows in the traditional RFT (Holwill and Burge, 1963; Magariyama et al., 1995).

$$\alpha_f = \frac{2\pi\mu L}{(\log[d/2p] + 1/2)(4\pi^2 r^2 + p^2)} \times (8\pi^2 r^2 + p^2) \quad (15)$$

$$\beta_f = \frac{2\pi\mu L}{(\log[d/2p] + 1/2)(4\pi^2 r^2 + p^2)} \times (4\pi^2 r^2 + 2p^2)r^2 \quad (16)$$

$$\gamma_f = \frac{2\pi\mu L}{(\log[d/2p] + 1/2)(4\pi^2 r^2 + p^2)} \times (-2\pi r^2 p) \quad (17)$$

To modify the drag coefficients of the flagellar helix, we must first calculate the drag force acting on a small element of the flagellar filament, ds . The forces tangential and

normal to the element by the traditional RFT (Holwill and Burge, 1963) were modified as follows based on the definition of μ_T^* and μ_N^* .

$$dF_T = \frac{-2\pi}{\log\left[\frac{d}{2p}\right] + \frac{1}{2}} \mu_T^* v_T ds \quad (18)$$

$$dF_N = \frac{-4\pi}{\log\left[\frac{d}{2p}\right] + \frac{1}{2}} \mu_N^* v_N ds \quad (19)$$

The speeds of the element, v_T and v_N , can be expressed by using ν and ω_f as shown below.

$$v_N = \nu \cos[\theta] - r\omega_f \sin[\theta] \quad (20)$$

$$v_T = \nu \sin[\theta] + r\omega_f \cos[\theta] \quad (21)$$

$$\tan[\theta] = \frac{p}{2\pi r} \quad (22)$$

The total force and torque acting on a flagellar helix, F and T , can be obtained by integrating the force and torque acting on an element of the flagellar filament (Fig. 2 c).

$$F = \int_0^L (dF_N \cos[\theta] + dF_T \sin[\theta]) \quad (23)$$

$$T = \int_0^L (-dF_N \sin[\theta] + dF_T \cos[\theta])r \quad (24)$$

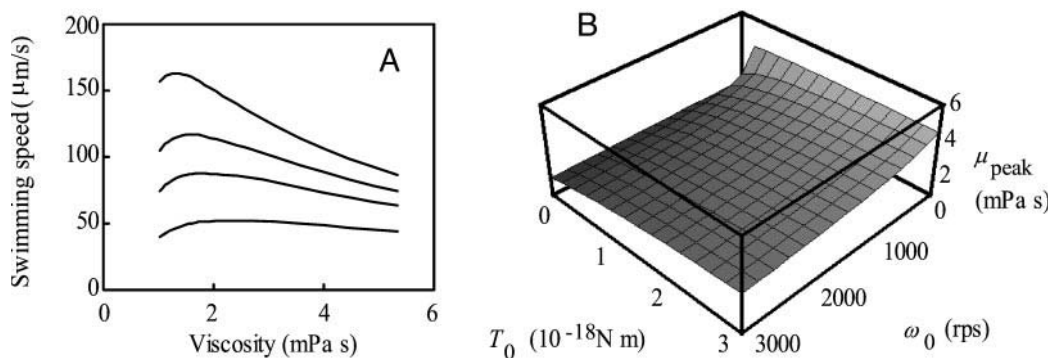


FIGURE 3 Peak positions of swimming speed calculated based on the modified RFT. (a) Swimming speeds as a function of viscosity. The swimming speeds were calculated for four different values of ω_0 , 8500, 1700, 850, and 340 rpm. The values of the other parameters are in Table 1. The upper curve was calculated for larger values of ω_0 . (b) Peak position of swimming speed as a function of T_0 and ω_0 .

The drag coefficients of the flagellar helix, α_f , β_f , and γ_f , were obtained from Eqs. 23 and 24 as follows.

$$\alpha_f = \frac{2\pi\mu_N^*L}{(\log[d/2p] + 1/2)(4\pi^2r^2 + p^2)} \left(8\pi^2r^2 + \frac{\mu_T^*}{\mu_N^*}p^2 \right) \quad (25)$$

$$\beta_f = \frac{2\pi\mu_N^*L}{(\log[d/2p] + 1/2)(4\pi^2r^2 + p^2)} \left(2p^2 + \frac{\mu_T^*}{\mu_N^*}4\pi^2r^2 \right) r^2 \quad (26)$$

$$\gamma_f = \frac{2\pi\mu_N^*L}{(\log[d/2p] + 1/2)(4\pi^2r^2 + p^2)} \left(2 - \frac{\mu_T^*}{\mu_N^*} \right) (-2\pi r^2 p) \quad (27)$$

Consequently, Eqs. 9–14 and 25–27 express the bacterial motion in a polymer solution.

A prediction based on an approximation

To calculate the bacterial swimming speed in polymer solutions, we assumed an extreme case in which the polymer network does not affect the tangential motion of a microscopic slender body but does affect the normal motion in the same way as the motion of a macroscopic body. In this extreme approximation, μ_T^* equals the viscosity of the solution without polymer, μ_0 , and is independent of the polymer concentration. Furthermore, μ_N^* is the same as the macroscopic viscosity of the polymer solution, μ , and increases with the polymer concentration. The values of the other parameters used in the calculation are summarized in Table 1.

The calculated swimming speed based on this approximation increased up to a characteristic viscosity and then decreased with viscosity, but the decrease was less than that predicted by the traditional RFT, as shown in Fig. 1 b. This result is similar to the experimental one. The calculated flagellar rotation rate monotonically decreased

with viscosity in a way similar to the prediction based on the traditional RFT, as shown in Fig. 1 c.

The ratio of swimming speed to flagellar rotation rate (v - f ratio) refers to the distance progressed per flagellar revolution, namely a kind of propulsion efficiency of the bacterial flagellar system. The v - f ratio calculated by the modified RFT increased with viscosity, although that by the traditional RFT was constant independent of viscosity, as shown in Fig. 1 d. This means that the improvement of the propulsion efficiency of the bacterial motion made up for a decline in flagellar rotation rate due to polymer addition and caused an increase in swimming speed with viscosity.

Peak position of swimming speed

The polar flagellum of *Vibrio alginolyticus* is driven by sodium ions, and the motor activity decreases with decreasing sodium concentration below 20 mM (Liu et al., 1990; Kawagishi et al., 1995). Atsumi et al. (1996) reported that the peak position of swimming speed of *V. alginolyticus* shifts toward high viscosity in PVP solutions as the sodium concentration is lowered, and that the difference between the swimming speeds in different sodium concentrations becomes smaller at higher viscosity. The modified RFT could also explain this experimental result, supposing that the decrease of sodium concentration reduces ω_0 . Fig. 3 a shows calculated swimming speeds as a function of viscosity with four different values of ω_0 , where the same values as Table 1 were used except ω_0 . As ω_0 decreased, 1) the curve of swimming speed moved downward; 2) the peak position shifted toward the higher viscosity, and 3) the peak became broader.

To further examine the peak shift caused by changes in the characteristics of motor torque, T_0 and ω_0 , we calculated μ_{peak} , which satisfies $\partial v / \partial \mu = 0$, with the values of bacte-

rial parameters and water viscosity fixed to those in Table 1. The obtained equation is

$$\begin{aligned} \mu_{\text{peak}} = & \{1.5 \times 10^{190} T_0 + 3.8 \times 10^{169} \omega_0 + 7.6 \times 10^{172} \\ & \times (2.7 \times 10^{36} T_0^2 + 7.5 \times 10^{15} T_0 \omega_0 \\ & + 7.9 \times 10^{-7} \omega_0^2)^{1/2}\} \\ & \times (3.3 \times 10^{193} T_0 + 8.7 \times 10^{172} \omega_0)^{-1} \end{aligned} \quad (28)$$

and μ_{peak} as a function of T_0 and ω_0 is shown in Fig. 3 *b*. With decreasing T_0 or increasing ω_0 , μ_{peak} decreased; that is, the peak position shifted toward the low viscosity, suggesting it become harder to detect the peak of swimming speed experimentally because the peak position becomes near or below the water viscosity. The exact torque characteristics of the *V. alginolyticus* motor, however, have not been measured, especially the change with sodium concentration. To confirm the validity of the present model further, it is desired to obtain such information.

DISCUSSION

The suggestion by Berg and Turner (1979) was mathematically expressed by introducing two apparent viscosities into the traditional RFT, and the peculiar phenomenon was successfully interpreted. The peak-position shift in swimming speed of *V. alginolyticus* with the sodium concentration was also explained, assuming that ω_0 decreased with the concentration.

The following observations have been reported about the motions of microscopic bodies in polymer solutions.

- The diffusion and sedimentation of microspheres in polymer solutions generally follow “Stokes-Einstein behavior,” i.e., $f = -6\pi\mu_{\text{trans}}^*a$, where f is a modified Stokes friction factor, a is the radius of the sphere, and μ_{trans}^* is the effective viscosity that is dependent on the concentration, molecular weight and morphology of the polymer, the sphere size, and so on (Kluijtmans, et al., 2000; Turner and Hallett, 1976; Yang and Jamieson, 1988; Brown and Rymden, 1988; Phillis et al., 1989; Onyemezu et al., 1993; Bu and Russo, 1994);
- The rotations of bacterial tethered cell in methylcellulose solutions are faster than those in Ficoll solutions at the same viscosities (Berg and Turner, 1979). The measurement of the rotational Brownian motion of globular proteins in dextran solutions indicates that the effective viscosity is expressed as $\mu_{\text{rot}}^* = \mu_0(\mu/\mu_0)^q$, where μ and μ_0 are the macroviscosities of polymer solution and water as mentioned above, and q is smaller than unity and is distinctly polymer- and protein-dependent (Lavallette et al., 1999).

Generally, μ_{trans}^* and μ_{rot}^* have different values in polymer solutions. In other words, these observations indicate that a

motion of a microscopic body in a polymer solution can be decomposed into two kinds of motions to which the Stokes-Einstein expression applies using the respective apparent viscosities. Of course, our assumption and/or deduced results should be experimentally verified in the next stage because the above reports are not direct evidence of two effective viscosities.

The modified RFT predicted an increase in the ν - f ratio (improvement of propulsion efficiency) with viscosity (polymer concentration) while the calculated ν - f ratio based on the traditional RFT was constant. To examine the validity of the modified RFT, we can simultaneously measure flagellar rotation rates and swimming speeds in polymer solutions. Such experiments in solutions containing no viscous agents have been carried out by using laser dark-field microscopy (LDM) (Kudo et al., 1990; Magariyama et al., 1995, 2001). We are planning to measure the ν - f ratio in polymer solutions by LDM.

The apparent viscosities depend on the characteristics of the polymer network, which are affected by the properties of the polymer such as the length (molecular weight), the morphology (linear or spherical), and the interaction between the molecules. Although the motion of a microscopic slender body in the tangential direction was not assumed to be affected by the polymer network in this study, the actual motion must be affected by the network because it moves to some degree. In addition, although we assumed that the change in sodium concentration altered only the motor torque, it may affect the characteristics of the polymer network as well. It is necessary to determine theoretically and/or experimentally how the hydrodynamic force acting on a flagellar element depends on the properties of a polymer in addition to the concentration.

To determine the values of apparent viscosities, we must estimate the hydrodynamic forces acting on a microscopic slender body in the normal and tangential directions. A conceivable experimental way is to measure the Brownian motion of a microscopic slender body in polymer solutions and determine its diffusion constants in the normal and tangential directions. We are planning to measure the Brownian motion of straight flagellar filaments or particles of tobacco mosaic virus (TMV) in polymer solutions and estimate the two apparent viscosities.

Most bacterial cells live in sticky conditions, e.g., surfaces of other organisms and biofilm, rather than in mobile liquids, e.g., marine water. In other words, they are usually living in various polymer solutions. The modified RFT indicates that a long, thin, helical shape is suitable for maintaining its swimming speed in viscous conditions containing polymer molecules because of the improved propulsion efficiency. The propulsion system of spirochetes, in which a helical or flat-sine wave of the cell body moves backward, may be an ultimate mechanism for swimming in highly viscous conditions.

We thank S. Sugiyama, T. Ohtani, S. Sunada, and T. Goto for helpful discussions.

This work was supported in part by the SCT-JST Program, Japan Science and Technology Corporation, and a grant-in-aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

REFERENCES

- Atsumi, T., Y. Maekawa, T. Yamada, I. Kawagishi, Y. Imae, and M. Homma. 1996. Effect of viscosity on swimming by the lateral and polar flagella of *Vibrio alginolyticus*. *J. Bacteriol.* 178:5024–5026.
- Azuma, A. 1992. The Biokinetics of Flying and Swimming. Springer-Verlag, Tokyo.
- Berg, H. C. 2000. Constraints on models for flagellar rotary motor. *Phil. Trans. R. Soc. Lond. B.* 355:491–501.
- Berg, H. C., and L. Turner. 1979. Movement of microorganisms in viscous environments. *Nature.* 278:349–351.
- Brown, W., and R. Rymden. 1988. Comparison of the translational diffusion of large spheres and high molecular weight coils in polymer solutions. *Macromolecules.* 21:840–846.
- Bu, Z., and P. S. Russo. 1994. Diffusion of dextran in aqueous (hydroxypropyl) cellulose. *Macromolecules.* 27:1187–1194.
- Chen, X., and H. C. Berg. 2000. Torque-speed relationship of the flagellar rotary motor of *Escherichia coli*. *Biophys. J.* 78:1036–1041.
- Chwang, A. T., and T. Y. Wu. 1971. A note on the helical movement of micro-organisms. *Proc. R. Soc. Lond. B.* 178:327–346.
- Gray, J., and G. J. Hancock. 1955. The propulsion of sea-urchin spermatozoa. *J. Exp. Biol.* 32:802–814.
- Greenberg, E. P., and E. Canale-Parola. 1977a. Relationship between cell coiling and motility of spirochetes in viscous environments. *J. Bacteriol.* 131:960–969.
- Greenberg, E. P., and E. Canale-Parola. 1977b. Motility of flagellated bacteria in viscous environments. *J. Bacteriol.* 132:356–358.
- Hancock, G. J. 1953. The self-propulsion of microscopic organisms through liquids. *Proc. R. Soc. Lond. A.* 217:96–121.
- Happel, J., and H. Brenner. 1973. Low Reynolds Number Hydrodynamics. Kluwer Academic Publishers, Dordrecht.
- Holwill, M. E. J., and R. E. Burge. 1963. A hydrodynamic study of the motility of flagellated bacteria. *Arch. Biochem. Biophys.* 101:249–260.
- Kaiser, G. E., and R. N. Doetsch. 1975. Enhanced translational motion of *Leptospira* in viscous environments. *Nature.* 255:656–657.
- Kawagishi, I., Y. Maekawa, T. Atsumi, M. Homma, and Y. Imae. 1995. Isolation of the polar and lateral flagellum-defective mutants in *Vibrio alginolyticus* and identification of their flagellar driving energy sources. *J. Bacteriol.* 177:5158–5160.
- Kluijtmans, S. G. J. M., G. H. Koenderink, and A. P. Philipse. 2000. Self-diffusion and sedimentation of tracer spheres in (semi)dilute dispersions of rigid colloidal rods. *Phys. Rev. E.* 61:626–636.
- Kudo, S., Y. Magariyama, and S.-I. Aizawa. 1990. Abrupt changes in flagellar rotation observed by laser dark-field microscopy. *Nature.* 346:677–680.
- Lavalette, D., C. Tétreau, M. Tourbez, and Y. Blouquit. 1999. Microscopic viscosity and rotational diffusion of proteins in a macromolecular environment. *Biophys. J.* 76:2744–2751.
- Liu, J. Z., M. Dapice, and S. Khan. 1990. Ion selectivity of the *Vibrio alginolyticus* flagellar motor. *J. Bacteriol.* 172:5236–5244.
- Magariyama, Y., S. Sugiyama, and S. Kudo. 2001. Bacterial swimming speed and rotation rate of bundled flagella. *FEMS Microbiol. Lett.* 199:125–129.
- Magariyama, Y., S. Sugiyama, K. Muramoto, I. Kawagishi, Y. Imae, and S. Kudo. 1995. Simultaneous measurement of bacterial flagellar rotation rate and swimming speed. *Biophys. J.* 69:2154–2162.
- Onyenemezu, C. N., D. Gold, M. Roman, and W. G. Miller. 1993. Diffusion of polystyrene latex spheres in linear polystyrene nonaqueous solutions. *Macromolecules.* 26:3833–3837.
- Phillies, G. D. J., J. Gong, L. Li, A. Rau, K. Zhang, L.-P. Yu, and J. Rollings. 1989. Macroparticle diffusion in dextran solutions. *J. Phys. Chem.* 93:6219–6223.
- Ramia, M., D. L. Tullock, and N. Phan-Thien. 1993. The role of hydrodynamic interaction in the locomotion of microorganisms. *Biophys. J.* 65:755–778.
- Ryu, W. S., R. M. Berry, and H. C. Berg. 2000. Torque-generating units of the flagellar motor of *Escherichia coli* have a high duty ratio. *Nature.* 403:444–447.
- Schneider, W. R., and R. N. Doetsch. 1974. Effect of viscosity on bacterial motility. *J. Bacteriol.* 117:696–701.
- Shoesmith, J. G. 1960. The measurement of bacterial motility. *J. Gen. Microbiol.* 22:528–535.
- Strength, W. J., B. Isani, D. M. Linn, F. D. Williams, G. E. Vandermolen, B. E. Laughon, and N. R. Krieg. 1976. Isolation and characterization of *Aquaspirillum fasciculus* sp. nov., a rod-shaped, nitrogen-fixing bacterium having unusual flagella. *Int. J. Sys. Bacteriol.* 26:253–268.
- Strobl, G. R. 1997. The Physics of Polymers, 2nd Ed. Springer-Verlag; Berlin, Heidelberg.
- Turner, D. N., and F. R. Hallett. 1976. A study of the diffusion of compact particles in polymer solutions using quasi-elastic light scattering. *Biochim. Biophys. Acta.* 451:305–312.
- Yang, T., and A. M. Jamieson. 1988. Diffusion of latex spheres through solutions of hydroxypropylcellulose in water. *J. Colloid Interface Sci.* 126:220–230.