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ELASTIC PROPERTIES OF BACTERIAL FLAGELLAR FILAMENTS

II. DETERMINATION OF THE MODULUS OF RIGIDITY

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Elongation of a helical bacterial flagellar filament subjected to fluid flow was calculated on the assumption that one end of the filament is firmly attached to a substratum. It was found that the quantity $[E(d/2\pi r)^2 + 2\mu]$ could be determined by measuring the elongation at various flow rates, where E is Young's modulus, μ the modulus of rigidity, r the radius of the helix, and d the helical pitch. Experiments were carried out to determine the above quantity for *Salmonella* flagellar filaments assuming a close-coil form. Because the above quantity is almost equal to 2μ for a helical form with a large radius/pitch ratio, we were able to determine the modulus of rigidity for this kind of flagellar filament from plots of elongation vs. flow rates. The modulus of rigidity was determined to be about 1×10^{11} dyn/cm^2, i.e., 2 orders of magnitude larger than the previously estimated value.

1. Introduction

Bacteria swim by rotating helical flagellar filaments, which are thin (diameter about 20 nm), long (up to 10–20 μm) tubular structures composed of a single kind of protein subunit [1]. It is now established that each flagellar filament is rotated by a structure (the basal body) buried in the membrane [2–4]. Therefore, the flagellar filament is essentially a solid propeller.

The flagellar filaments must have appropriate elasticity and rigidity to function as an efficient propeller. To provide a basis for measuring these values by experiments, we calculated the elongation of a bacterial flagellar filament subjected to a flow of the medium [5] (hereafter referred to as Part I). According to that theory, the quantity $[E(d/2\pi r)^2 + 2\mu]$ could be obtained by measuring the elongation, where E is the Young's modulus, μ the modulus of rigidity, r the radius of the helix and d the helical pitch. In that calculation, we assumed that the flagellar filament is attached to a substratum by one end and can freely rotate around its helical axis. In actual experiments, however, we found that one end of the flagellar filaments did stick to the glass surface but the filament rarely rotated around its axis. Therefore, we consider in this paper a more realistic situation where the flagellar filament is attached to the glass surface in such a way that free rotation around the helical axis is not allowed. In section 2, we present theoretical considerations of the filament elongation in the above situation. In section 3, we present results of application of the theory to the measurement of the modulus of rigidity of *Salmonella* flagellar filament. The result indicates that the flagellar filament has a larger torsional rigidity than that estimated before.

2. Theory

We consider here the elongation of a helical flagellar filament attached to the substratum by one end. The filament is assumed to be attached to the glass slide in such a way that rotation of the filament is allowed only in the plane parallel to the glass slide. In contrast to the situation considered in Part I, where the flagellar filament was assumed to be free to rotate around its helical axis, the filament in the present situation receives torque from the fluid flow. Therefore, the twisting as well as the stretching of the filament must be taken into consideration. As in Part I, the flagellar filament is assumed to be a chain of N identical beads each being in contact with the neighbors and the N-th bead being attached to the glass slide. The number of the beads N, is expressed by

$$N = \frac{\lambda}{2b}\left\{d^2 + (2\pi r)^2\right\}^{1/2}, \tag{1}$$

where b is the radius of the flagellar filament and λ the number of pitches.

We consider first the stretching of the filament. Let the partial helix of the filament be the chain of the beads which are numbered from the i-th to the N-th bead. We denote the number of pitches and the elongation of that helix by λ_i and d_i, respectively, λ_0 and d_0 being the number of pitches and the pitch length of the whole helix before the deformation. Then, Hooke's law for that helix is given by eq. 3 of Part I:

$$k_0\left(\lambda_i, \sum_{j=0}^{i-1} d_j\right)\lambda_i d_i = F_{zi} \quad (i \geqslant 1), \tag{2}$$

where we regard the filament as a coil spring and $k_0(\lambda, d)$ is the spring constant of the coil spring [6,7]:

$$k_0(\lambda, d) = \frac{b^4}{8\lambda}\left\{r^2 + (d/2\pi)^2\right\}^{-3/2} \times\left[E(d/2\pi r)^2 + 2\mu\right]. \tag{3}$$

In the present case, however, the translational force acting on the i-th bead becomes

$$F_{zi} = \sum_{j=0}^{i-1} \Xi_z\left(\sum_{k=0}^{j} d_k\right)v, \tag{4}$$

where v is the velocity of the fluid flow and $\Xi_z(d)$ the translational friction coefficient which is given as [8]

$$\Xi_z(d) = \frac{8\pi\eta b\left\{d^2 + (2\pi r)^2\right\}^{1/2}}{d\ \ln\left[(1/2b)\left\{d^2 + (2\pi r)^2\right\}^{1/2}\right]}. \tag{5}$$

Hooke's law is then written as

$$K\left(\sum_{j=0}^{i-1} d_j\right)d_i = \sum_{j=0}^{i-1} \Xi_z\left(\sum_{k=0}^{j} d_k\right)v \tag{6}$$

with

$$K(d) = \lambda k_0(\lambda, d). \tag{7}$$

Using the same procedure as in Part I, the approximate solution is obtained as

$$d_i = (d_2 - d_1)\left[(i-2) - \frac{\alpha}{6}i(i-1)(i-2)\right] + d_2 \quad (i \geqslant 3), \tag{8}$$

where

$$d_1 = \Xi_z(d_0)v/K(d_0), \tag{9a}$$

$$d_2 = 2(1-\alpha)d_1, \tag{9b}$$

and α is defined by

$$\alpha = \Xi_z(d_0)K'(d_0)v/K^2(d_0), \tag{9c}$$

the prime representing the derivative with respect to d_0.

Next, we consider the twisting of the filament. Let θ_0 be the angle of the first bead before deformation. If the first bead rotates by an angle θ_1, the angle of the second bead before the deformation is

$$\theta_0 + \theta_1 - (\theta_0 + \theta_1)/N.$$

If the second bead rotates by an angle θ_2, the angle of the third bead before the deformation is

$$\theta_0 + \theta_1 - (\theta_0 + \theta_1)/N + \theta_2 - \left\{\theta_0\left(1 - \frac{1}{N}\right) + \theta_1\left(1 - \frac{1}{N}\right) + \theta_2\right\}/(N-1).$$

Thus, the angle of the i-th bead before the deformation can be written as

$$\theta_0 p_i + \sum_{k=1}^{i-1} \theta_k q_{i,k} \quad (i \geqslant 2),$$

where we have defined p_i and $q_{i,k}$ as

$$p_i = \prod_{j=0}^{i-2}\left(1-\frac{1}{N-j}\right), \tag{10a}$$

$$q_{i,k} = \prod_{j=k-1}^{i-2}\left(1-\frac{1}{N-j}\right). \tag{10b}$$

Let the spring constant for the twisting of the helical filament be $k_T(d, \theta)$ which is obtained from the configurational energy of the elastic flagellar filament [6,7]. The explicit expression of $k_T(d, \theta)$ is given in appendix A. Hooke's law for the twisting of the filament is then

$$k_T\left(\sum_{j=0}^{i-1} d_j,\ \theta_0 p_i + \sum_{k=1}^{i-1} \theta_k q_{i,k}\right)\theta_i r = F_{\theta i} \quad (i \geqslant 2), \tag{11}$$

where $F_{\theta i}$ is the tangential force acting on the i-th bead. The tangential frictional force of the flow acting on one bead in the filament is given by [8]

$$F_\theta = \Xi_I v, \tag{12}$$

where Ξ_I is the interaction coefficient between the translational and the rotational movement of the flagellar filament and is given by

$$\Xi_I(d) = -(16\pi^2\eta b r)\left(\left\{d^2+(2\pi r)^2\right\}^{1/2} \times \ln\left[(1/2b)\left\{d^2+(2\pi r)^2\right\}^{1/2}\right]\right)^{-1}. \tag{13}$$

The tangential force acting on the i-th bead $F_{\theta i}$ is the sum of the tangential frictional force on the i-th bead and the torsional force from the $(i-1)$-th, the $(i-2)$-th,..., and the first bead. Therefore, the force $F_{\theta i}$ is

$$F_{\theta i} = \sum_{j=0}^{i-1} \Xi_I\left(\sum_{k=0}^{j} d_k\right) v. \tag{14}$$

Hereafter, we will confine ourselves to the case in which the twisting of the filament is small. Then the spring constant k_T can be approximated as follows:

$$\begin{aligned} k_T&\left(\sum_{j=0}^{i-1} d_j,\ \theta_0 p_i + \sum_{k=1}^{i-1} \theta_k q_{i,k}\right) \\ &\sim k_T(d_0, \theta_0 p_i) + (k_T)_d \sum_{j=1}^{i-1} d_j \\ &\quad + (k_T)_\theta \sum_{k=1}^{i-1} \theta_k q_{i,k}, \end{aligned} \tag{15}$$

where $(k_T)_d$ and $(k_T)_\theta$ represent, respectively

$$(k_T)_d = \partial k_T(d_0, \theta_0 p_i)/\partial d_0, \tag{16a}$$

$$(k_T)_\theta = \partial k_T(d_0, \theta_0 p_i)/\partial(\theta_0 p_i). \tag{16b}$$

Since we are interested mainly in the elastic properties of a flagellar filament, we assume, as in Part I, that the hydrodynamical interaction varies little with respect to the form of the flagellar helix. Thus, the variation of the angle θ_i can be written using eq. 11 along with eq. 15 as follows:

$$\theta_i = iQ_i - iR\sum_{j=1}^{i-1} d_j - iS_i\sum_{k=1}^{i-1} \theta_k q_{i,k}, \tag{17}$$

where we have defined Q_i, R and S_i as

$$Q_i = \left\{\Xi_I(d_0)(\theta_0 p_i)^2 v\right\}/K_T(d_0) r, \tag{18a}$$

$$R = \left\{\Xi_I(d_0)K'_T(d_0)(\theta_0 p_i)^2 v\right\}/K_T^2(d_0) r, \tag{18b}$$

$$S_i = -\left\{2\Xi_I(d_0)\theta_0 p_i v\right\}/K_T(d_0) r, \tag{18c}$$

$K_T(d_0)$ being defined by

$$k_T(d_0, \theta) = K_T(d_0)/\theta^2, \tag{19}$$

and $K'_T(d_0)$ being the derivative with respect to d_0. If we change the variable i to $i \pm 1$, we have $\theta_{i\pm1}$ in which the coefficients $Q_{i\pm1}$, $S_{i\pm1}$ and $q_{i\pm1,k}$ appear. These coefficients can be approximated as Q_i, S_i and $q_{i,k}$ respectively, since if N is large, the variations of p_i and $q_{i,k}$ are small provided i does not tend to N (see eqs. 10). With these approximations the following second-order difference equation is obtained:

$$\begin{aligned} &\theta_{i+1} - \left\{2-(i+1)\nu_i\right\}\theta_i \\ &\quad + \left\{1-(i-1)\nu_i\right\}\theta_{i-1} = \Lambda_i \quad (i \geqslant 2), \end{aligned} \tag{20}$$

with the initial conditions

$$\theta_1 = \Xi_I(d_0)v/k_{\mathrm{T}}(d_0, \theta_0)r, \tag{21a}$$

$$\theta_2 = 2Q_2 - 2Rd_1 - 2S_2 q_{2,1}\theta_1. \tag{21b}$$

In eq. 20, we have defined ν_i and Λ_i as

$$\nu_i = S_i q_{i,i-1}, \tag{22a}$$

$$\Lambda_i = \begin{cases} -R\{(i+1)d_i - (i-1)d_{i-1}\} & (i \geqslant 2), \\ \theta_2 - \theta_1 & (i = 1). \end{cases} \tag{22b}$$

By using the same procedure as in Part I, i.e., replacing the terms $(i \pm 1)\nu_i$ on the left-hand side of eq. 20 by $i\nu_i$, eq. 20 is reduced to a first-order difference equation by the transformation

$$\zeta_i = \theta_{i+1} - \theta_i:$$

$$\zeta_i - (1 - i\nu_i)\zeta_{i-1} = \Lambda_i \; (i \geqslant 2). \tag{23}$$

The solution of eq. 23 is easily obtained and θ_i becomes

$$\theta_i = \sum_{l=2}^{i-1} \left\{ \sum_{k=2}^{l} \prod_{j=k}^{l} (1 - j\nu_j)\Lambda_{k-1} + \Lambda_l \right\} + \theta_2$$
$$(i \geqslant 3). \tag{24}$$

Neglecting terms of order v^3 and higher, θ_i is approximated to be

$$\begin{aligned} \theta_i = {} & \{2Q_2 - 2Rd_1 - (2S_2 q_{2,1} + 1)\theta_1\}\,(i-1) + \theta_1 \\ & - (Rd_1/2)(i+2)(i-1)(i-2) \\ & - (S_2/p_2)(2Q_2 - \theta_1)H_i \; (i \geqslant 3), \end{aligned} \tag{25}$$

where

$$H_i = \sum_{l=2}^{i-1} \sum_{j=2}^{l} j p_j q_{j,j-1}. \tag{26}$$

Since we have assumed that N is large, p_2 and $q_{2,1}$ can be replaced by 1. Then θ_i becomes further

$$\begin{aligned} \theta_i = \frac{\Xi_I(d_0)v}{K_{\mathrm{T}}(d_0)r} \Bigg[& \theta_0^2 i - \frac{K'_{\mathrm{T}}(d_0)}{2K_{\mathrm{T}}(d_0)} \cdot \frac{\Xi_z(d_0)v}{K(d_0)} i^2(i-1) \\ & + \frac{2\Xi_I(d_0)v}{K_{\mathrm{T}}(d_0)r}\theta_0^3\{2(i-1) + H_i\} \Bigg] \; (i \geqslant 3). \end{aligned} \tag{27}$$

From eq. 27 we can calculate the total twisting angle θ_{T}, which is given in appendix B. Now we will calculate the total elongation of the flagellum d_{T}, which can be expressed as

$$d_{\mathrm{T}} = \sum_{i=1}^{N-1} \frac{d_i}{\rho_i}. \tag{28}$$

ρ_i is the number of beads per pitch of the i-th partial helix and is related to λ_i by

$$\frac{1}{\rho_i} = \frac{\lambda_i}{N - i + 1}. \tag{29}$$

In contrast to the situation considered in Part I, ρ_i is no longer a constant, but changes during twisting. If we denote the angle of a bead by θ, then the pitch number λ of the bead is expressed by $\lambda = \theta/2\pi$. Therefore eq. 29 is rewritten as

$$\frac{1}{\rho_i} = \begin{cases} \dfrac{1}{2\pi N}(\theta_0 + \theta_1) & (i = 1), \\ \dfrac{1}{2\pi(N - i + 1)}\left(\theta_0 p_i + \displaystyle\sum_{k=1}^{i-1} \theta_k q_{i,k} + \theta_i\right) \\ \qquad (i \geqslant 2). \end{cases} \tag{30}$$

Substituting eqs. 8, 9 and 30 into eq. 28, d_{T} becomes

$$\begin{aligned} d_{\mathrm{T}} = {} & \frac{d_1}{2\pi}\left[\frac{1}{N}(\theta_0 + \theta_1) + \frac{2}{N-1} \right. \\ & \left. \times (\theta_0 p_2 + \theta_1 q_{2,1} + \theta_2)(1 - \alpha)\right] \\ & + \frac{1}{2\pi} \sum_{i=3}^{N-1} \frac{1}{N - i + 1} \Bigg[\theta_o p_i (d_2 - d_1) \\ & \times \left\{(i-2) - \frac{\alpha}{6} i(i-1)(i-2)\right\} + \theta_0 p_i d_2 \\ & + \sum_{k=1}^{i-1} \theta_k q_{i,k}(d_2 - d_1)\Big\{(i-2) \\ & - \frac{\alpha}{6} i(i-1)(i-2)\Big\} + \sum_{k=1}^{i-1} \theta_k q_{i,k} d_2 \\ & + \theta_i(d_2 - d_1)\left\{(i-2) - \frac{\alpha}{6} i(i-1)(i-2)\right\} \\ & + \theta_i d_2 \Bigg]. \end{aligned} \tag{31}$$

As mentioned before, since we are dealing with large N, we should abandon the terms of lower order of N. Neglecting terms of order υ^3 and higher, we obtain the following expression for d_T:

$$d_\mathrm{T} = \frac{\theta_o d_1 N}{4\pi} - \frac{\theta_0 d_1}{\pi}\left[\frac{\alpha N^3}{48} - \frac{5\theta_0}{24}\cdot\frac{\Xi_\mathrm{I}(d_0)\upsilon N^3}{K_\mathrm{T}(d_0)r}\right]. \tag{32}$$

The first term on the right-hand side of eq. 32 is of the order of υ, and the second term of the order of υ^2. As mentioned in section 3, the experimental results show that d_T is expressed well by a linear curve with respect to υ. Therefore, we shall rewrite the first term (denoted by d_T^1) in a more convenient form so that we can easily compare the theoretical with the experimental result:

$$d_\mathrm{T}^1 = \frac{\Xi_z(d_0)\upsilon\lambda_0^2}{4K(d_0)b}\left\{d_0^2 + (2\pi r)^2\right\}^{1/2}. \tag{33}$$

Using eqs. 3 and 7, we obtain another expression:

$$E(d_0/2\pi r)^2 + 2\mu = \frac{2\eta\upsilon}{d_\mathrm{T}^1\pi^2}\cdot\frac{\lambda_0^2\left\{d_0^2 + (2\pi r)^2\right\}^{5/2}}{d_0 b^4 \ln\left[(1/2b)\left\{d_0^2 + (2\pi r)^2\right\}^{1/2}\right]} \tag{34}$$

which we shall use for the analysis of our experiment.

3. Experimental

Flagellar filaments with average lengths greater than 10 μm were prepared from *Salmonella* SJ670 flagellin by an in vitro reconstruction method [1]. The flagellar filaments of this species assume a left-handed helical form (normal type) having a pitch of 2.3 μm and a diameter of 0.4 μm at neutral pH values. At pH about 4.5, however, they take on a left-handed close-coil form with a pitch of about 0.5 μm and a diameter of 1.2 μm [9]. We took advantage of the fact that the close-coil form is easily elongated when subjected to a mechnical perturbation and the elongation can be directly observed by dark-field light microscopy. A solution of flagellar filaments was made in 10 mM acetic acid/sodium acetate buffer, pH 4.5, to give a protein concentration of about 0.02 mg/ml. A drop of this sample was placed on a glass slide and covered with a cover-slip: to provide enough space for the medium to flow, a small amount of Vaselin was placed on two opposite edges of the cover-slip before it was positioned on the specimen. Flow of the medium was produced by placing a drop of the buffer solution and a filter paper tip at two opposite sides of the cover-slip that had not been sealed with Vaselin. The specimen was observed with a dark-field microscope as descibed previously [9]. The images were recorded with an SIT TV camera (Ikegami Tsushinki Co., Tokyo) and a Sony V05850 video recorder (Sony Co., Tokyo), and analyzed frame-by-frame on the TV monitor. The velocity of the flow was estimated from the displacement of fine dust particles, which were inevitably contained in the flagellar specimen, passing by the flagellar filaments being analyzed.

Flagellar filaments have a natural tendency to stick to a glass surface by one of the two ends, the end corresponding to the proximal one in living bacteria [10]. Most of the filaments can pivot around the attachment site in the plane parallel to the glass surface, but cannot rotate around their helical axis. When flow is present in the medium, the flagellar filaments tend to be aligned in the direction of the flow and extended elastically in that direction. Fig. 1 shows images of a flagellar filament of the close-coil type extended in the

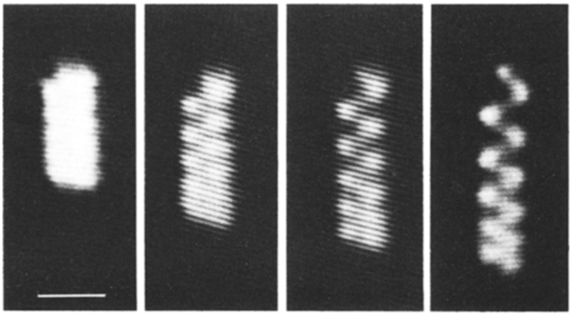

Fig. 1. Elongation of a close-coiled flagellar filament under flow. TV recording of dark-field microscope images. The upper end of this filament is attached to the glass surface. Scale bar: 2μm.

presence of different magnitudes of flow. This particular filament had about 5.3 helical turns and an end-to-end length of about 3 μm when flow was absent. When the medium was made to flow, however, the end-to-end length of this helix was increased up to 6 μm. Apparently, this elongation did not accompany the unwinding of the helix.

We recorded about 50 filaments elongated under flow. For analysis of the image, we chose two recordings that allowed us to measure both the filament length and the flow rate over a wide range. Fig. 2 shows the length-flow rate relation for these fibers. The data have large scatter, mainly owing to the difficulty in accurately measuring the flow rate near the specimen, but suggest a linear relationship between the length increase and the flow rate under these conditions. At higher flow rates, the flagellar filaments underwent a structural transition into another helical form (normal type) with a larger pitch, making the measurement of elastic elongation impossible. That structural transition can be induced by mechanical force has been reported previously [11].

We calculated the value of $[E(d_0/2\pi r)^2 + 2\mu]$ using eq. 34 and assuming b to be 10 nm [12]. The value of d_0 was obtained by extrapolating the data to $v = 0$, and the number of helical turns λ and the radius of the helix r by visual inspection of the image (fig. 1). These values must have errors up to ± 0.1 μm (d_0), ± 0.5 (λ) and ± 0.1 μm (r). The two sets of data in fig. 2 both yielded the value of $[E(d_0/2\pi r)^2 + 2\mu]$ to be about 10^{11} dyn/cm^2. For a helical form with a large helical diameter/pitch ratio, such as that examined here, we could regard $[E(d_0/2\pi r)^2 + 2\mu]$ as being almost equal to 2μ, because the orders of magnitude of E and μ are probably similar and $(d_0/2\pi r)^2/2$ is much smaller than unity (in the present case, $(d_0/2\pi r)^2/2 = 0.02$). Thus, the modulus of rigidity μ was practically determined. Among possible sources of errors in the above calculation, the most critical one is the estimation of b, which is contained in the form of b^4 in eq. 34. We must pay attention to the fact that a flagellar filament actually has a complex internal structure with a hollow core at its center [12]. In such a case, the b value used for the calculation of elastic properties must be smaller than the outermost radius of a flagellar filament, while b should be equal to the outermost radius for the calculation of the force caused by the fluid flow (see Part I). In practice, we may choose an 'effective' b value: it must be smaller than the outermost radius, which has been estimated to be close to 0.01 μm [12,13]. If we assume b to be 0.008 and 0.007 μm, μ would become about 5×10^{11} and 9×10^{11} dyn/cm^2, respectively. Therefore, it would be safe to conclude that the modulus of rigidity of the flagellar filament is of the order of 10^{11} or 10^{12} dyn/cm^2.

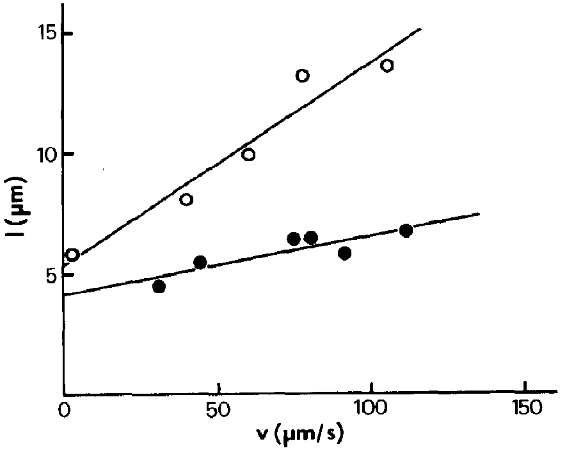

Fig. 2. Dependence of the end-to-end length l on the flow rate v. (○ and ●) Data on flagellar filaments with helical turn numbers of 11.5 and 6.5, respectively.

4. Discussion

We have determined the modulus of rigidity of bacterial flagellar filaments, applying a new theory to microscopic observation of single filaments of the close-coil type extended under flow. This is the first direct determination of the modulus of rigidity of a flagellar filament.

By analysing quasi-elastic light scattering spectra of flagellar solutions, Fujime et al. [14] measured the flexural rigidity of the flagellar filaments to be $2\text{–}4 \times 10^{-15}$ dyn cm^2. From this value and the assumption that a flagellar filament is a tube having an inner and outer diameter of 110 and 120

Å, respectively, they have estimated Young's modulus E to be of the order of 10^{11} dyn/cm^2. However, recent structural studies have indicated that the inner diameter of a flagellar fiber is much smaller and the outer diameter much larger than they assumed: less than 30 and about 200 Å, respectively [15]. If we use these values for the estimation, E becomes of the order of 10^{10} dyn/cm^2. Therefore, the order of magnitude of E appears to be similar to or smaller than that of μ. This estimation supports the view that what we measured in this experiment, $[E(d_0/2\pi r)^2 + 2\mu]$, is almost equal to 2μ.

Berg [16] found that a bacterial cell that was tethered to the glass surface by a single flagellum and rendered nonmotile by depletion of energy displayed a fluctuation in the angular orientation. The magnitude of the fluctuation was a few degrees. He attributed this to the thermal fluctuation in the twist of the flagellar filament and estimated the torsional constant B to be of the order of 10^{-11} dyn cm for a filament 1 μm long. In that calculation he used the flexural rigidity measured by Fujime et al. and assumed that Young's modulus is close to 2μ. Since $B = \pi b^4 \mu / 2L$ (L, length of the filament), the above value indicated that μ is of the order of 10^9 dyn/cm^2, i.e. 2 or 3 orders of mangitude smaller than what we measured in this study. There are several possible reasons for this discrepancy. For example, the basal hook or the basal body of a flagellum may have a much smaller modulus of rigidity than the filament and the angular deviation observed in the tethered bacterium could be due mainly to the twist in these parts.

The torque generated by the flagellar basal body has been estimated to be of the order of 10^{-11} dyn cm [16], which is the same as that of the torsional constant estimated by Berg. These estimated values lead to the prediction that a flagellar filament 1 μm long must be twisted by the order of 1 rad (or 57°) by the rotating basal body. A twist of 1 rad/μm would bring about a considerable deformation of the flagellar helical structure which normally has a structural twist of 2π rad/2.3 μm or 2.7 rad/μm. If, however, we adopt the modulus of rigidity obtained in this study, we could expect that the twist of the flagellar filament would be of the order of 0.01 rad.

In conclusion, our present study indicates that the bacterial flagellar filament has a large modulus of rigidity that is sufficient to keep the torsional deformation negligible under natural conditions. We could regard the flagellar filament as a solid propeller.

Appendix A

Bugl and Fujita [6] showed that the configurational energy of the helical cylinder U can be written as

$$U = \tfrac{1}{8}\pi b^4 \int_0^l ds \left\{ E(\kappa - \kappa_0)^2 + 2\mu(\tau - \tau_0)^2 \right\}, \tag{A1}$$

where l is the contour length, and κ and τ the curvature and the torsion, respectively; κ_0 and τ_0 are expressed by r and d as follows:

$$\kappa_0 = r / \left\{ r^2 + (d/2\pi)^2 \right\}, \tag{A2a}$$

$$\tau_0 = d/2\pi \left\{ r^2 + (d/2\pi)^2 \right\}. \tag{A2b}$$

Suppose the deformation of the helix is such that

$$\begin{array}{lcl} x = r\cos\theta & & x = r'\cos\theta' \\ y = r\sin\theta & \rightarrow & y = r'\sin\theta' \\ z = d\theta/2\pi & & z = d\theta/2\pi \end{array} \tag{A3}$$

In this case the variation of the configurational energy ΔU becomes

$$\Delta U = \tfrac{1}{8}\pi b^4 (d/2\pi\theta)^2 \left\{ r^2 + (d/2\pi)^2 \right\}^{-2} \times \left[E(d/2\pi r)^2 + 2\mu \right] (\Delta\theta)^2, \tag{A4}$$

where we have defined $\Delta\theta$ as

$$\Delta\theta = \theta' - \theta. \tag{A5}$$

On the other hand, if we regard the helix as a coil spring with the torsional spring constant k_T, the variation of the energy through the deformation $r\Delta\theta$ is $k_T(r\Delta\theta)^2/2$. Therefore, comparing the coefficients of $(\Delta\theta)^2$, we obtain the following expression for k_T

$$k_T = \tfrac{1}{4}\pi b^4 (d/2\pi r\theta)^2 \left\{ r^2 + (d/2\pi)^2 \right\}^{-2} \times \left[E(d/2\pi r)^2 + 2\mu \right]. \tag{A6}$$

Appendix B

We can calculate the total twisting angle θ_T from eq. 28:

$$\begin{aligned}\theta_T &= \sum_{i=1}^{N-1} \theta_i \\ &= \frac{\Xi_I(d_0)v}{K_T(d_0)r}\left[\frac{\theta_0^2}{2}N(N-1) - \frac{1}{24}\cdot\frac{K_T'(d_0)}{K_T(d_0)}\right. \\ &\quad \cdot\frac{\Xi_z(d_0)v}{K(d_0)}N(N-1)(N-2)(3N-1) \\ &\quad \left. + \frac{\Xi_I(d_0)v\theta_0^3}{K_T(d_0)r}\{2N(N-3)+2H+4\}\right], \end{aligned} \tag{B1}$$

where H is defined as

$$\begin{aligned} H = &\sum_{i=3}^{N-1}\sum_{l=2}^{i-1}\sum_{j=2}^{l} j\left\{1-\frac{1}{N-(j-2)}\right\} \\ &\times \prod_{k=0}^{j-2}\left(1-\frac{1}{N-k}\right). \end{aligned} \tag{B2}$$

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