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ELASTIC PROPERTIES OF BACTERIAL FLAGELLAR FILAMENTS

I. FREE ROTATION CASE

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Elongation of a helical bacterial flagellar filament in a fluid flow with one end attached to a slide glass is calculated. The flagellar filament is regarded as a coil spring. In this case, the spring constant is a function of the elastic constants of the flagellar filament. Relations between the elongation and the elastic constants are discussed.

1. Introduction

A bacterial flagellar filament has in a sense a very simple construction; a protein called flagellin is the only component. It may be the reason why the bacterial flagellar filament is one of the first biological organisms reconstructed in vitro from the component monomers. However, until recently, our knowledge was poor about how flagellin monomers are packed to make a flagellar filament of a helical shape [1–3]. The bacterial flagellar filament exhibits polymorphism; i.e., the filament makes reversible transitions among different helical shapes [4]. Although its biological significance remains unexplained, the polymorphism must reflect the specific character of the inner structure of a flagellar filament.

Recently, a cinematography technique coupled with a dark-field microscope has been developed to observe directly the behavior of flagella on bacteria and also the flagellar filament isolated [4,5]. Under the microscope we can observe the isolated flagellar filament in a solution the ends of which are attached to the slide glass. If a flow exists in the solution, the filament is oriented in parallel to the direction of the flow and elongated by the frictional force due to the flow. Sometimes, the force induces the transition into the helical shape [5].

In this paper we calculate the elongation of a flagellar filament in a fluid flow. The elongation is determined by the spring constant of the flagellar filament or the rigidity and Young's modulus of the filament. The measurement of elongation will give information about the elastic properties of the filament which must be related to its inner structure.

The attached end sometimes rotates freely on the slide glass or else it is fixed rigidly to the slide glass. The condition under which state appears is not known. In this paper, free rotation is assumed. The other case where the end is rigidity fixed is treated in the following paper.

2. Model and equation for elongation of the flagellar filament

In considering the elongation of a helical flagellar filament, the filament is regarded as a coil

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spring. The spring constant is expressed in terms of Young's modulus, E, and the modulus of rigidity, μ, of the flagellar filament as [6,7].

$$k_0(\lambda, d) = \frac{b_0^4}{8\lambda}\left\{r^2 + \left(\frac{d}{2\pi}\right)^2\right\}^{-3/2}\left[E\left(\frac{d}{2\pi r}\right)^2 + 2\mu\right], \qquad (1)$$

where λ is the number of pitches, d the pitch length, r the radius of the flagellar helix and b_0 the radius of the flagellar filament. However, if the flagellar filament has a complex structure, e.g., suppose that it is made up of the inner part and the outer part, and that the stiffness of the flagellar filament is mainly due to the inner part, then b_0 in eq. 1 should be the radius of the inner part. Thus, b_0 may not be equal to the radius of the flagellar filament which is observed microscopically.

When is subjected to a flagellar filament attached to the slide glass a fluid flow, a frictional force acts equally on each part of the filament. Then, the force to elongate the filament is larger near the attached end. A part of the filament near the attached end is more elongated than the part far from this end. Such a situation must be taken into consideration in our calculation. For this purpose, we employ the following model.

Let us assume that the flagellar filament is constructed from N identical beads each being in contact with the neighbors, and that the Nth bead is attached to the slide glass. The number of the beads, N, is expressed by

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

where b is the radius of the flagellar filament, and need not be equal to b_0.

If we consider the partial helix in the fluid flow which is constructed from the ith to the Nth beads and denote the number of the pitches of that helix by λ_i, then the pitch length of that helix can be written as

$$\sum_{j=0}^{i-1} d_j$$

where d_0 is the pitch length before the deformation and d_j ($j = 1, 2, \ldots, N-1$) is the elongation of the partial helix which is constructed from the

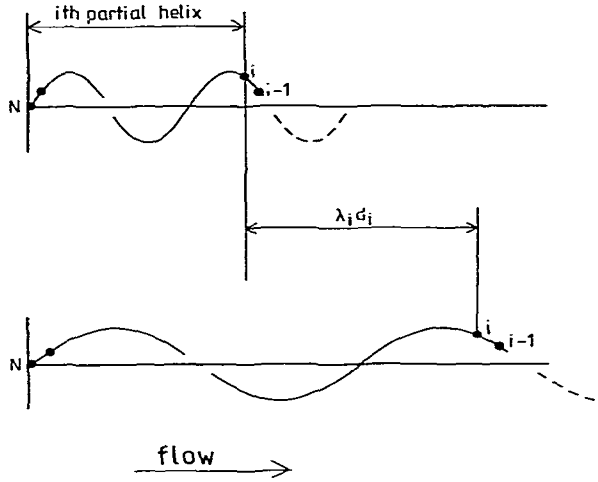

Fig. 1. A partial helix is defined as a part of the flagellar helix which is constructed from the ith to the Nth bead. Let this partial helix be called the ith partial helix. The elongation of this partial helix is denoted by $\lambda_i d_i$, where λ_i is the corresponding pitch number. In considering the elongation of this partial helix, the pitch length is $\sum_{j=0}^{i-1} d_j$, since the elongations of the $(i-1)$th, $(i-2)$th, ..., and first partial helix must be taken into account.

jth to the Nth beads divided by the corresponding pitch number λ_j (see fig. 1). Then Hooke's law, which describes the elongation of that partial helix, can be written as follows:

$$k_0\left(\lambda_i, \sum_{j=0}^{i-1} d_j\right)\lambda_i d_i = F_i, \qquad i \geqq 1, \qquad (3)$$

where F_i is the force acting on the ith bead. The force F_i is the sum of the frictional force exerted by the fluid flow on the ith bead and the tension from the $(i-1)$th bead. This tension is also due to the frictional forces exerted by the fluid flow on the $(i-1)$th, $(i-2)$th, ..., and first bead. Since the frictional force varies with the deformation of the flagellar helix due to the hydrodynamical interaction between the beads, the exact calculation of the frictional force is difficult. However, an approximate calculation which is thought to be sufficient in our case was done by Hoshikawa and Saito [8]. They calculated the force exerted by the fluid flow on one bead in the flagellar filament:

$$F = -\frac{\Xi_\theta}{r}\omega + \Xi_I v, \tag{4a}$$

$$F_z = -\Xi_I r\omega + \Xi_z v, \tag{4b}$$

where F_θ and F_z are, respectively, the tangential and translational components of the force, Ξ_θ and Ξ_z the rotational and translational friction coefficients, respectively, and Ξ_I the interaction coefficient between the translational and the rotational movements, and v and θ the translational velocity and angular velocity of the fluid, respectively. Ξ_θ, Ξ_z and Ξ_I are given as functions of the structural parameters of the flagellar filament (see ref. 8).

As mentioned in section 1, the attached end exhibits two different states; the freely rotating state and the rigidly fixed state. In this paper, as the attached end is considered to rotate freely, the tangential component of the force F_θ vanishes. Under this condition the translational component F_z is

$$F_z = \left\{ -\frac{\Xi_I^2}{\Xi_\theta} r^2 + \Xi_z \right\} v \equiv \Xi v. \tag{5}$$

The coefficient Ξ becomes

$$\Xi(d) = \frac{8\pi\eta b}{\{d^2 + (2\pi r)^2\}^{1/2} \ln\left[(1/2b)\{d^2 + (2\pi r)^2\}^{1/2}\right]} \cdot \frac{d^2 + 2(\pi r)^2}{d}, \tag{6}$$

where η is the viscosity of the fluid. Hooke's law can be written using eqs. 3, 5 and 6 as

$$k\left(\sum_{j=0}^{i-1} d_j\right) d_i = \sum_{j=0}^{i-1} \Xi\left(\sum_{k=0}^{j} d_k\right) v \tag{7a}$$

with

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

3. The elongation of the flagellar filament

As long as one is considering elongation of a certain type, it is reasonable to limit oneself to the case when the elongation is small as compared with the natural length of the flagellar filament. In this case, the inverse of the spring constant and the friction coefficient can be approximated as follows:

$$\frac{1}{k\left(\sum_{j=0}^{i-1} d_j\right)} \approx \frac{1}{k(d_0)} - \frac{k'(d_0)}{k^2(d_0)} \sum_{j=1}^{i-1} d_j, \tag{8a}$$

$$\Xi\left(\sum_{k=0}^{j} d_k\right) \approx \Xi(d_0) + \Xi'(d_0) \sum_{k=1}^{j} d_k. \tag{8b}$$

where the prime represents the derivative with respect to d_0. Note that the differentiation $k'(d_0)$ and $\Xi'(d_0)$ must be carried out under the condition that the contour length of the flagellar filament is constant. The derivatives are usually positive. The spring constant, $k_0(\lambda, d)$ of eq. 1 or $k(d)$ of eq. 7b, which is the coefficient of the second order of the deformation of the helix in the configurational energy, is derived in the case where the deformation is small. In this case the coefficient of the third order of the deformation becomes equal to $k'(d_0)$.

Substituting eqs. 8 into eq. 7, Hooke's law becomes

$$d_i = \frac{i}{k(d_0)} \Xi(d_0) v - \frac{ik'(d_0)}{k^2(d_0)} \Xi(d_0) v \sum_{j=1}^{i-1} d_j + \frac{\Xi'(d_0)}{k(d_0)} v \sum_{j=1}^{i-1} \sum_{k=1}^{j} d_k, \tag{9}$$

from which the following second-order difference equation is derived:

$$d_{i+2} = \left\{ \frac{\Xi'(d_0) v}{k(d_0)} - \frac{(i+2)\Xi(d_0) k'(d_0) v}{k^2(d_0)} + 2 \right\} d_{i+1} + \left\{ \frac{i\Xi(d_0) k'(d_0) v}{k^2(d_0)} - 1 \right\} d_i. \tag{10}$$

Since we are interested mainly in the elastic properties of a flagellar filament, we assume that the hydrodynamic interaction varies little with respect to the form of the flagellar helix and expand d_i in a Taylor's series around $\Xi'(d_0) = 0$. As is easily examined, the coefficients of every power of $\Xi'(d_0)$ except of the zeroth power are of the order of $O(v^2)$. Even in the lowest order term of this series, the essential information about the elastic properties of a flagellar filament ought to be included. Therefore, in the following part of this paper, we neglect terms of order $\Xi'(d_0)O(v^2)$ and higher, and limit ourselves to the lowest order term. Then eq. 10 can be written as

$$d_{i+2} = (2 - i\alpha)d_{i+1} + (i\alpha - 1)d_i, \tag{11}$$

where α is defined by

$$\alpha = \frac{\Xi(d_0)k'(d_0)v}{k^2(d_0)}. \tag{12}$$

In deriving eq. 11, use is made of the approximation $(i+2)v \approx iv$. This approximation is inadequate for small i. Fortunately, the number of beads N for the bacterial flagellar filament is considered to be large even for one pitch, then the approximation in appropriate. The initial conditions are

$$d_1 = \frac{\Xi(d_0)v}{k(d_0)}. \tag{13a}$$

$$d_2 = 2(1-\alpha)d_1. \tag{13b}$$

Eq. 11 is reducible to a first-order difference equation by the transformation $\delta_i = d_{i+1} - d_i$, and is easily solved to be

$$\delta_i = (d_2 - d_1)\prod_{j=1}^{i-1}(1 - j\alpha), \qquad i \geqq 2. \tag{14}$$

Again solving the first-order difference equation (eq. 14), the solution of eq. 11 becomes

$$d_i = (d_2 - d_1)\sum_{k=3}^{i}\prod_{j=1}^{k-2}(1 - j\alpha) + d_2, \qquad i \geqq 3. \tag{15}$$

Neglecting terms of order v^3 and higher, eq. 15 is approximated to be

$$d_i = (d_2 - d_1)\left[(i-2) - \frac{\alpha}{6}i(i-1)(i-2)\right] + d_2. \tag{16}$$

The total elongation of the flagellar filament d_T is given as

$$d_T = \sum_{i=1}^{N-1}\frac{d_i}{p}. \tag{17}$$

where p is the number of the beads included in one pitch. Substituting eq. 16 into eq. 17, d_T becomes

$$d_T = \frac{d_1}{p}\left[\tfrac{1}{2}(N^2 - N - 4) - \frac{\alpha}{24}(N^4 - 6N^3 + 35N^2 - 78N - 96)\right]. \tag{18}$$

In deriving eq. 18, we neglect terms of order v^3 and higher as we have done in deriving eq. 16. The N dependence of eq. 18 is at first sight exact, however, we have used the approximation which is adequate only when N is large. Therefore, we should abandon the terms of lower order of N, then d_T becomes finally

$$d_T = \frac{1}{4}\frac{\Xi(d_0)v\lambda_1^2}{k(d_0)b}\{d_0^2 + (2\pi r)^2\}^{1/2} \times\left[1 - \frac{1}{48}\frac{\Xi(d_0)k'(d_0)v\lambda_1^2}{k^2(d_0)b^2}\{d_0^2 + (2\pi r)^2\}\right]. \tag{19}$$

4. Discussion

We employed the 'bead' model for calculation of the elongation of a flagellar filament. In the last equation (eq. 19), however, the total elongation of the flagellar filament was expressed in terms of elastic moduli and the structural parameters of the helix. The hypothetical beads disappeared in the final result. The first term of the right-hand side of eq. 19 is proportional to the second power of the number of pitches or the total length of the flagellar filament. The second term arising from the change of the elastic property with elongation of the flagellar filament is negative and proportional to the fourth power of the number of pitches or the total length. In the experiment, it is important to investigate the relation between the total elongation and the initial length of the flagellar filament. After confirmation of the relation expected from the present theoretical result, we can estimate the elastic moduli by quantitative comparison of the data with the eq. 19.

The theory is limited to a small deformation of the flagellar filament. The approximation $\Xi'(d_0) \equiv 0$ is consistent with this case, since the variation of $\Xi(d)$ may be negligible if the deformation is small. To neglect the terms of order v^3 and higher is also compatible with this situation. Therefore, this theory is applicable as long as the elongation of the flagellar filament is small.

The spring constant given by Bugl and Fujita [6] is derived for the continuous-wire model. On the other hand, the calculations in this paper are carried out on the basis of the discrete-bead model.

This would seem at first sight to be inconsistent. However, our problem can be reconsidered to be the problem in which the helical wire is elongated not by the fluid flow but by many weights each being attached at a different sites on the wire. Our treatment is in this sense consistent and is thought to reflect the essential feature of the problem.

In this paper we have considered the case when the attached end of the flagellar filament is assumed to be freely rotating. Unfortunately, under the usual experimental conditions the attached end of the flagellar filament tends to become fixed rigidly to the slide glass. This case will be treated in the following paper in which comparison with the experiment will made.

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