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BROWNIAN MOTION OF HELICAL FLAGELLA

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We develope a theory of the Brownian motion of a rigid helical object such as bacterial flagella. The statistical properties of the random forces acting on the helical object are discussed and the coefficients of the correlations of the random forces are determined. The averages $\langle z^2(t)\rangle$, $\langle \theta^2(t)\rangle$ and $\langle z(t)\theta(t)\rangle$ are also calculated where z and θ are the position along and the angle around the helix axis respectively. Although the theory is limited to short time interval, direct comparison with experiment is possible by using the recently developed cinematography technique.

1. Introduction

It was about a hundred years ago that Pfeffer and Englemann found the so-called chemotaxis of bacteria; the active motion of bacteria toward attractant or away from repellent. However, since the quantitative treatment of bacterial chemotaxis was difficult at that time, there was long interruption before the research of the chemotaxis was resumed by Adler [1]. Since then, many studies about the subject were carried out [2]. At the same time, the researches of the structure and the function of flagella started. In the study of the structure of flagella the first discovery was the construction of flagella from flagellin monomers [3] and the second was the polymorphism of flagellar shape [4,5]. These phenomena are interesting in connection with the self-organization or self-assembly of proteins. The way how a flagellum rotates was revealed by the beautiful experiments by Silverman and Simon [6] and by Berg [7]. But the mechanism of rotation and the structure of basal body – flagella motor – are not yet known. The propelling force of flagellar rotation was first discussed theoretically by Taylor [8,9] followed by the more complete theories [10,11,12,13]. The accuracy of the theory is now almost sufficient regarding to the experimental errors.

The actual motion of bacteria seems at first sight Brownian motion. However, this motion is the active stochastic behavior of bacteria to run after or to run away from certain chemicals. On the other hand, considering their size, they surely undergo the Brownian motion in its original meaning, although it is hidden during the actual motion; in the actual motion of bacteria, the Brownian motion is superposed on the active stochastic behavior. A flagellum cut off from the bacterial body, on the contrary, does not have active motility. Consequently, the Brownian motion is observed without any additional effect. Since in the recent experiment, more precise measurements are needed, there must be some cases that one should take into account the Brownian motion of flagella. For instance, it needs long time interval to take a photograph of a single flagellum. Since this time interval is long as compared with that for a flagellar bundle, even by the use of a high-speed film, the effect of the Brownian motion can not be avoided. In addition, from the purely physical point of view, this subject is interesting in the sense that the rotation around and the translation along the flagellar axis couples. Nevertheless at present, no theory of the Brownian motion of flagella seems to exist.

In this paper, we consider the Brownian motion of a rigid helical flagellum, because the flagellum is in most cases supposed rigid if the condition of the suspension is kept constant. In general, it is somewhat complicated to get the time-dependent solution of the motion of the rigid body in three dimensions. In the present case of a helical flagellum the coupling between the rotation and the translation makes the problem more difficult. We will consider as the first step of the theory a simpler case in which only two variables are taken into account: The angle around the flagellar axis and the displacement along the axis. Details are described in the following sections.

2. Langevin equations

The position of a rigid body in three dimensions is described by six variables; three for the position of the center of mass and the remaining three for the angles between the laboratory system and the system fixed to the body. Usually the equation of motion can be decoupled to two equations governing two sets of variables mentioned above. Even in this case, to solve the equation of motion is difficult for arbitrary external forces. In the case of helical flagella, since there exists the coupling between the rotation around the helix axis and the translation along this axis, the equation of motion can no longer be decoupled. And the equation of motion becomes more complicated. We will avoid this difficulty by reducing the number of variables. Let us first turn our attention to the three rotational friction coefficients (as the flagellum is axially symmetric, two of them are the same): The friction coefficient around the helix axis Ξ_θ and the friction coefficients around the axis perpendicular to the helix axis Ξ_R. Suppose the friction coefficient Ξ_R are larger than Ξ_θ, then the rotational motion around the helix axis is faster than the rotation perpendicular to that axis, which can be neglected for suitable time interval. As for the motion of the center of mass, the motion perpendicular to the axis can be neglected if the friction coefficient for the perpendicular movement to the axis Ξ_P are larger than that for the parallel movement Ξ_z. The remaining variables are therefore the angle around the helix axis and the position along the axis. The Langevin equations becomes as follows:

$$\begin{pmatrix} L_{11} & L_{12} \\ L_{21} & L_{22} \end{pmatrix}\begin{pmatrix} v \\ \omega \end{pmatrix} = \begin{pmatrix} \mathscr{A}_z \\ \mathscr{A}_\theta \end{pmatrix} \quad \text{or} \quad \mathbf{L}\cdot\mathbf{V}=\mathbf{A}, \tag{2.1a}$$

$$L_{11} = M\mathrm{d}/\mathrm{d}t + \Xi_z, \qquad L_{12} = \Xi_\mathrm{I} r, \qquad L_{21} = \Xi_\mathrm{I}, \qquad L_{22} = Mr\mathrm{d}/\mathrm{d}t + \Xi_\theta/r, \tag{2.1b}$$

where v is the velocity of the flagellum parallel to and ω is the angular velocity around the axis, $\mathscr{A}_z$ and $\mathscr{A}_\theta$ are respectively the translational and the tangential components of random force, M and r are the mass and the radius of the helical flagellum, Ξ_z and Ξ_θ are respectively the translational and the rotational friction coefficients parallel and around the helix axis and Ξ_I is the interaction coefficient between the translational and the rotational movements.

3. Properties of the random force

We will write the special solutions of eq. (2.1a), $\mathbf{V}_s(t)$ in the form

$$\mathbf{V}_s(t) = \int_{t_0}^{t} \mathbf{G}(t-t')\cdot\mathbf{A}(t')\mathrm{d}t', \tag{3.1}$$

where $\mathbf{G}$ is the Green's function of eq. (2.1a) in the form of the tensor of order 2, the components of which are written as $G_{ij}(t)$. The equations for the Green's functions are

$$\left.\begin{aligned} L_{11}G_{11}(t) + L_{12}G_{21}(t) &= \delta(t), \\ L_{21}G_{11}(t) + L_{22}G_{21}(t) &= 0, \end{aligned}\right\} \quad (3.2a) \qquad \left.\begin{aligned} L_{11}G_{12}(t) + L_{12}G_{22}(t) &= 0, \\ L_{21}G_{12}(t) + L_{22}G_{22}(t) &= \delta(t). \end{aligned}\right\} \quad (3.2b)$$

Let the Fourier transformation of $G_{ij}(t)$ be $\widetilde{G}_{ij}(\lambda)$:

$$G_{ij}(t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \widetilde{G}_{ij}(\lambda) e^{i\lambda t} d\lambda. \tag{3.3}$$

By substituting eq. (3.3) into eqs. (3.2), $\widetilde{G}_{ij}(\lambda)$ can be solved as follows:

$$\widetilde{G}_{11}(\lambda) = \frac{1}{M^2 r} \frac{i\lambda M r + \Xi_\theta / r}{Q(\lambda)}, \qquad \widetilde{G}_{12}(\lambda) = -\frac{1}{M^2 r} \frac{\Xi_I r}{Q(\lambda)}, \qquad \widetilde{G}_{21}(\lambda) = -\frac{1}{M^2 r} \frac{\Xi_I}{Q(\lambda)},$$
$$\widetilde{G}_{22}(\lambda) = \frac{1}{M^2 r} \frac{i\lambda M + \Xi_z}{Q(\lambda)}, \tag{3.4}$$

where $Q(\lambda)$ is

$$Q(\lambda) = -\lambda^2 + (i/M)(\Xi_z + \Xi_\theta/r^2)\lambda - (1/M^2)(\Xi_I^2 - \Xi_z \Xi_\theta / r^2). \tag{3.5}$$

Now the integral in eq. (3.3) can be carried out using the complex integral. The solutions of the equation $Q(\lambda) = 0$, $\lambda_\pm$ are

$$\lambda_\pm = -(i/2M)[-(\Xi_z + \Xi_\theta/r^2) \pm \{(\Xi_z - \Xi_\theta/r^2)^2 + 4\Xi_I^2\}^{1/2}]. \tag{3.6}$$

In the case of the cylinder limit of the bead model of helical flagella, following relation is shown

$$\Xi_z + \Xi_\theta / r^2 > \{(\Xi_z - \Xi_\theta/r^2)^2 + 4\Xi_I^2\}^{1/2}. \tag{3.7}$$

Therefore $\lambda_\pm$ are located on the upper half-plane of the complex plane. The results of integration are

$$G_{ij}(t) = \Omega(g_{ij}^+ e^{-\eta_+ t} + g_{ij}^- e^{-\eta_- t}), \tag{3.8}$$

where

$$\eta_\pm = -i\lambda_\mp, \qquad g_{11}^\pm = \eta_\pm M r - \Xi_\theta / r, \qquad g_{12}^\pm = \Xi_I r, \qquad g_{21}^\pm = \Xi_I, \qquad g_{22}^\pm = \eta_\pm M - \Xi_z,$$
$$\Omega = \frac{-1}{M^2 r} \frac{1}{\eta_+ - \eta_-}. \tag{3.9}$$

Next we will consider the solution $\mathbf{V}_0(t)$ of the homogeneous equation of eq. (2.1a). They can be easily obtained as follows:

$$v_0(t) = C_1^+ e^{-\eta_+ t} + C_1^- e^{-\eta_- t}, \qquad \omega_0(t) = C_2^+ e^{-\eta_+ t} + C_2^- e^{-\eta_- t}. \tag{3.10}$$

Let the initial conditions be $v(t_0) = v^0$, $\omega(t_0) = \omega^0$. As the form of the special solution is given by eq. (3.1), $\mathbf{V}_s(t_0) = 0$. Therefore $\mathbf{V}_0(t)$ must satisfy the initial conditions. This can be done by taking the integration constants as

$$C_1^+ = (\omega^0 - \Gamma_- v^0)/e^{-\eta_+ t_0}(\Gamma_+ - \Gamma_-), \qquad C_1^- = (\Gamma_+ v^0 - \omega^0)/e^{-\eta_- t_0}(\Gamma_+ - \Gamma_-), \qquad C_2^\pm = \Gamma_\pm C_1^\pm, \tag{3.11}$$

where $\Gamma_\pm$ is given by

$$\Gamma_\pm = -(1/2\Xi_I r)[(\Xi_z - \Xi_\theta/r^2) \pm \{(\Xi_z - \Xi_\theta/r^2) + 4\Xi_I^2\}^{1/2}]. \tag{3.12}$$

Notice that as $t_0 \to -\infty$, the solution satisfying the initial condition is the special solution, eq. (3.1).

Now we are ready to examine the properties of the random force. In the presence case of a helical flagellum, since the coupling between the translation and rotation exists, the correlation between $\mathcal{A}_z$ and $\mathcal{A}_\theta$ becomes finite. Taking notice to this respect we assume the correlations of the random force as

$$\langle \mathcal{A}_z(t)\mathcal{A}_z(t')\rangle = \kappa_z\delta(t-t'), \qquad \langle \mathcal{A}_\theta(t)\mathcal{A}_\theta(t')\rangle = \kappa_\theta\delta(t-t'), \qquad \langle \mathcal{A}_z(t)\mathcal{A}_\theta(t')\rangle = \kappa_I\delta(t-t'). \tag{3.13}$$

The coefficients κ_z, κ_θ and κ_I are determined making use of the law of equipartition of energy. As for the first moment, we put as usual $\langle \mathcal{A}_z\rangle = \langle \mathcal{A}_\theta\rangle = 0$.

We will now calculate the average values $\langle v^2\rangle$, $\langle \omega^2\rangle$ and $\langle v\omega\rangle$. According to eq. (3.1),

$$\langle v^2\rangle = \int_{-\infty}^{t}\int_{-\infty}^{t} \{G_{11}(t-t')G_{11}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{11}(t-t')G_{12}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_\theta(t'')\rangle + G_{12}(t-t')G_{11}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{12}(t-t')G_{12}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_\theta(t'')\rangle\}\,\mathrm{d}t'\mathrm{d}t'', \tag{3.14a}$$

$$\langle \omega^2\rangle = \int_{-\infty}^{t}\int_{-\infty}^{t} \{G_{21}(t-t')G_{21}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{21}(t-t')G_{22}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_\theta(t'')\rangle + G_{22}(t-t')G_{21}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{22}(t-t')G_{22}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_\theta(t'')\rangle\}\,\mathrm{d}t'\mathrm{d}t'', \tag{3.14b}$$

$$\langle v\omega\rangle = \int_{-\infty}^{t}\int_{-\infty}^{t} \{G_{11}(t-t')G_{21}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{11}(t-t')G_{22}(t-t'')\langle \mathcal{A}_z(t')\mathcal{A}_\theta(t'')\rangle + G_{12}(t-t')G_{21}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_z(t'')\rangle$$
$$+ G_{12}(t-t')G_{22}(t-t'')\langle \mathcal{A}_\theta(t')\mathcal{A}_\theta(t'')\rangle\}\,\mathrm{d}t'\mathrm{d}t''. \tag{3.14c}$$

Using eq. (3.9) along with eqs. (3.13), eqs. (3.14) become

$$\langle v^2\rangle = \frac{-\Omega^2}{2\eta_+\eta_-(\eta_+ + \eta_-)}\,[\kappa_z\{\eta_+(\eta_+ + \eta_-)(g_{11}^-)^2 - 4\eta_+\eta_- g_{11}^+ g_{11}^-$$
$$+ \eta_-(\eta_+ + \eta_-)(g_{11}^+)^2\} + g_{12}^+\kappa_I\{2\eta_+(\eta_+ + \eta_-)g_{11}^- - 4\eta_+\eta_-(g_{11}^+ + g_{11}^-)$$
$$+ 2\eta_-(\eta_+ + \eta_-)g_{11}^+\} + (g_{12}^+)^2\kappa_\theta(\eta_+ - \eta_-)^2], \tag{3.15a}$$

$$\langle \omega^2\rangle = \frac{-\Omega^2}{2\eta_+\eta_-(\eta_+ + \eta_-)}\,[(g_{21}^+)^2\kappa_z(\eta_+ - \eta_-)^2 - g_{21}^+\kappa_I\{2\eta_+(\eta_+ + \eta_-)g_{22}^-$$
$$- 4\eta_+\eta_-(g_{22}^+ + g_{22}^-) + 2\eta_-(\eta_+ + \eta_-)g_{22}^+\} + \kappa_\theta\{\eta_+(\eta_+ + \eta_-)(g_{22}^-)^2$$
$$- 4\eta_+\eta_- g_{22}^+ g_{22}^- + \eta_-(\eta_+ + \eta_-)(g_{22}^+)^2\}], \tag{3.15b}$$

$$\langle v\omega\rangle = \frac{-\Omega^2}{2\eta_+\eta_-(\eta_+ + \eta_-)}[-g_{21}^+\kappa_z\{\eta_+(\eta_+ + \eta_-)g_{11}^- - 2\eta_+\eta_-(g_{11}^- + g_{11}^+)$$

$$+\eta_-(\eta_+ + \eta_-)g_{11}^+\} + \kappa_{\rm I}\{\eta_-(\eta_+ + \eta_-)g_{11}^+g_{22}^+ - 2\eta_+\eta_-(g_{11}^-g_{22}^+ + g_{11}^+g_{22}^-)$$

$$+\eta_+(\eta_+ + \eta_-)g_{11}^-g_{22}^- + \eta_+(\eta_+ + \eta_-)g_{12}^+g_{21}^+ - 4\eta_+\eta_-g_{12}^+g_{21}^+ + \eta_-(\eta_+ + \eta_-)g_{12}^+g_{21}^+$$

$$-g_{12}^+\kappa_\theta\{\eta_+(\eta_+ + \eta_-)g_{22}^- - 2\eta_+\eta_-(g_{22}^+ + g_{22}^-) + \eta_-(\eta_+ + \eta_-)g_{22}^+\}]. \tag{3.15c}$$

The averages $\langle v^2\rangle$, $\langle\omega^2\rangle$ and $\langle v\omega\rangle$ are, on the other hand, given by the law of equipartition of energy as

$$\langle v^2\rangle = kT/M, \qquad \langle\omega^2\rangle = kT/Mr^2, \qquad \langle v\omega\rangle = 0, \tag{3.16}$$

where k is the Boltzmann constant and T is temperature. By equating eqs. (3.15) and eqs. (3.16), we can calculate after elementary but tedious calculation, the values of κ_z etc. and we get

$$\kappa_z = 2\Xi_z kT, \qquad \kappa_\theta = 2(\Xi_\theta/r^2)kT, \qquad \kappa_{\rm I} = 2\Xi_{\rm I}kT. \tag{3.17}$$

4. Averages of position and angle

In the preceding section we have got the solution of the Langevin eq. (2.1). The position $z(t)$ and the angle $\theta(t)$ of the helical flagellum are therefore easily obtained by integrating $\mathbf{V}(t)$:

$$z(t) = \int_{t_0}^{t} dt'\left[\int_{t_0}^{t} G_{11}(t'-t'')\mathcal{A}_z(t'') + G_{12}(t'-t'')\mathcal{A}_\theta(t'')\}dt'' + C_1^+e^{-\eta_+t'} + C_1^-e^{-\eta_-t'}\right] + z^0, \tag{4.1a}$$

$$\theta(t) = \int_{t_0}^{t} dt'\left[\int_{t_0}^{t} \{G_{21}(t'-t'')\mathcal{A}_z(t'') + G_{22}(t'-t'')\mathcal{A}_\theta(t'')\}dt'' + C_2^+e^{-\eta_+t'} + C_2^-e^{-\eta_-t'}\right] + \theta^0, \tag{4.1b}$$

where z^0 and θ^0 are the initial condition $z(t_0) = z^0$, $\theta(t_0) = \theta^0$. Among the integrals in eqs. (4.1), the integrals which do not contain random force (denoted $D_z(t)$ and $D_\theta(t)$ respectively) can be easily integrated as

$$D_z(t) = \frac{\omega^0 - \Gamma_- v^0}{\eta_+ e^{-\eta_+t_0}(\Gamma_+ - \Gamma_-)}(e^{-\eta_+t} - e^{-\eta_-t_0}) + \frac{\Gamma_+v^0 - \omega^0}{\eta_- e^{-\eta_-t_0}(\Gamma_+ - \Gamma_-)}(e^{-\eta_-t} - e^{-\eta_-t_0}), \tag{4.2a}$$

$$D_\theta(t) = \frac{\Gamma_+(\omega^0 - \Gamma - v^0)}{\eta_+ e^{-\eta_+t_0}(\Gamma_+ - \Gamma_-)}(e^{-\eta_+t} - e^{-\eta_-t_0}) + \frac{\Gamma_-(\Gamma_+v^0 - \omega^0)}{\eta_- e^{-\eta_-t_0}(\Gamma_+ - \Gamma_-)}(e^{-\eta_-t} - e^{-\eta_-t_0}). \tag{4.2b}$$

The integrals containing random force are of the form

$$I = \int_{t_0}^{t} dt' \int_{t_0}^{t} e^{-\eta(t'-t'')}\mathcal{A}(t'')dt''. \tag{4.3}$$

Integrating by parts, I becomes

$$I = \frac{1}{\eta} \int_{t_0}^{t} \{1 - \mathrm{e}^{-\eta(t-t')}\} \mathcal{A}(t')\,\mathrm{d}t'. \tag{4.4}$$

onsequently $z(t)$ and $\theta(t)$ become

$$z(t) = \Omega \int_{t_0}^{t} [\{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\mathcal{A}_z(t') + \{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\mathcal{A}_\theta(t')]\,\mathrm{d}t' + D_z(t), \tag{4.5a}$$

$$\theta(t) = \Omega \int_{t_0}^{t} [\{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\mathcal{A}_z(t') + \{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\mathcal{A}_\theta(t')]\,\mathrm{d}t' + D_\theta(t), \tag{4.5b}$$

where $\mathcal{G}_{ij}(t)$ is defined by

$$\mathcal{G}_{ij}(t) = -(g_{ij}^{+}/\eta_{+})\mathrm{e}^{-\eta_{+}t} - (g_{ij}^{-}/\eta_{-})\mathrm{e}^{-\eta_{-}t}. \tag{4.6}$$

n eqs. (4.5), we have put $t_0 = 0$ and $z^0 = \theta^0 = 0$. Using eqs. (4.5) the averages $\langle z^2(t)\rangle$, $\langle\theta^2(t)\rangle$ and $\langle z(t)\theta(t)\rangle$ are de-cribed as

$$\begin{aligned}\langle z^2(t)\rangle - D_z^2(t) = \Omega^2\Big[\kappa_z &\int_0^t \{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\,\mathrm{d}t' \\ + \kappa_\mathrm{I} &\int_0^t \{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\,\mathrm{d}t' \\ + \kappa_\mathrm{I} &\int_0^t \{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\,\mathrm{d}t' \\ + \kappa_\theta &\int_0^t \{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\,\mathrm{d}t'\Big],\end{aligned} \tag{4.7a}$$

$$\begin{aligned}\langle \theta^2(t)\rangle - D_\theta^2(t) = \Omega^2\Big[\kappa_z &\int_0^t \{\mathcal{G}_{21}(t-t') - \mathcal{G}_{12}(0)\}\{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\,\mathrm{d}t' \\ + \kappa_\mathrm{I} &\int_0^t \{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\,\mathrm{d}t' \\ + \kappa_\mathrm{I} &\int_0^t \{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\,\mathrm{d}t' \\ + \kappa_\theta &\int_0^t \{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\,\mathrm{d}t'\Big],\end{aligned} \tag{4.7b}$$

$$\langle z(t)\theta(t)\rangle - D_z(t)D_\theta(t) = \Omega^2\Big[\kappa_z \int_0^t \{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\,\mathrm{d}t'$$

$$+\kappa_1 \int_0^t \{\mathcal{G}_{11}(t-t') - \mathcal{G}_{11}(0)\}\{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\,\mathrm{d}t'$$

$$+\kappa_1 \int_0^t \{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\{\mathcal{G}_{21}(t-t') - \mathcal{G}_{21}(0)\}\,\mathrm{d}t'$$

$$+\kappa_\theta \int_0^t \{\mathcal{G}_{12}(t-t') - \mathcal{G}_{12}(0)\}\{\mathcal{G}_{22}(t-t') - \mathcal{G}_{22}(0)\}\,\mathrm{d}t'\Big], \tag{4.7c}$$

where use is made of eqs. (3.13). By elementary integration $\langle z^2(t)\rangle$, $\langle\theta^2(t)\rangle$ and $\langle z(t)\theta(t)\rangle$ are calculated to be

$$\langle z^2(t)\rangle - D_z^2(t) = \Omega^2\{\kappa_z\Lambda_{11,11} + \kappa_1(\Lambda_{11,12} + \Lambda_{12,11}) + \kappa_\theta\Lambda_{12,12}\}, \tag{4.8a}$$

$$\langle\theta^2(t)\rangle - D_\theta^2(t) = \Omega^2\{\kappa_z\Lambda_{21,21} + \kappa_1(\Lambda_{21,22} + \Lambda_{22,21}) + \kappa_\theta\Lambda_{22,22}\}, \tag{4.8b}$$

$$\langle z(t)\theta(t)\rangle - D_z(t)D_\theta(t) = \Omega^2\{\kappa_z\Lambda_{11,21} + \kappa_1(\Lambda_{11,22} + \Lambda_{12,21}) + \kappa_\theta\Lambda_{12,22}\}, \tag{4.8c}$$

where

$$\Lambda_{ij,kl} = -\frac{g_{ij}^+ g_{kl}^+}{2\eta_+^3} S_2^+ - \frac{g_{ij}^- g_{kl}^-}{2\eta_-^3} S_2^- - \frac{1}{\eta_+\eta_-(\eta_+ + \eta_-)}(g_{ij}^+ g_{kl}^- + g_{ij}^- g_{kl}^+) S_0$$

$$- \mathcal{G}_{ij}(0)\left(\frac{g_{kl}^+}{\eta_+^2} S_1^+ + \frac{g_{kl}^-}{\eta_-^2} S_1^-\right) - \mathcal{G}_{kl}(0)\left(\frac{g_{ij}^+}{\eta_+^2} S_1^+ + \frac{g_{ij}^-}{\eta_-^2} S_1^-\right) + \mathcal{G}_{ij}(0)\mathcal{G}_{kl}(0)t, \tag{4.9}$$

$$S_0 = \mathrm{e}^{-(\eta_+ + \eta_-)t} - 1, \qquad S_1^\pm = \mathrm{e}^{-\eta_\pm t} - 1, \qquad S_2^\pm = \mathrm{e}^{-2\eta_\pm t} - 1. \tag{4.10}$$

We will examine the limiting behavior of eqs. (4.8) for both $t \gg 1/\eta_\pm$ and $t \ll 1/\eta_\pm$. First in the case of $t \gg 1/\eta_\pm$, $D_z(t), D_\theta(t), S_0, S_1^\pm$ and $S_2^\pm$ are of order o(t). Therefore

$$\langle z^2(t)\rangle \to \Omega^2\{\kappa_z\mathcal{G}_{11}(0)\mathcal{G}_{11}(0) + \kappa_1(\mathcal{G}_{11}(0)\mathcal{G}_{12}(0) + \mathcal{G}_{12}(0)\mathcal{G}_{11}(0)) + \kappa_\theta\mathcal{G}_{12}(0)\mathcal{G}_{12}(0)\}t, \tag{4.11a}$$

$$\langle\theta^2(t)\rangle \to \Omega^2\{\kappa_z\mathcal{G}_{21}(0)\mathcal{G}_{21}(0) + \kappa_1(\mathcal{G}_{21}(0)\mathcal{G}_{22}(0) + \mathcal{G}_{22}(0)\mathcal{G}_{21}(0)) + \kappa_\theta\mathcal{G}_{22}(0)\mathcal{G}_{22}(0)\}t, \tag{4.11b}$$

$$\langle z(t)\theta(t)\rangle \to \Omega^2\{\kappa_z\mathcal{G}_{11}(0)\mathcal{G}_{21}(0) + \kappa_1(\mathcal{G}_{11}(0)\mathcal{G}_{22}(0) + \mathcal{G}_{12}(0)\mathcal{G}_{21}(0)) + \kappa_\theta\mathcal{G}_{22}(0)\mathcal{G}_{22}(0)\}t. \tag{4.11c}$$

On the other hand in the case of $t \ll 1/\eta_\pm$, since $\Lambda_{ij,kl}$ is of order o(t^2),

$$\langle z^2(t)\rangle \to \{(\omega^0 - \Gamma_- v^0)/(\Gamma_+ - \Gamma_-) + (\Gamma_+ v^0 - \omega^0)/(\Gamma_+ - \Gamma_-)\}^2 t^2, \tag{4.12a}$$

$$\langle\theta^2(t)\rangle \to [\Gamma_+(\omega^0 - \Gamma_- v^0)/(\Gamma_+ - \Gamma_-) + \Gamma_-(\Gamma_+ v^0 - \omega^0)/(\Gamma_+ - \Gamma_-)\}^2 t^2, \tag{4.12b}$$

$$\langle z(t)\theta(t)\rangle \to \{(\omega^0 - \Gamma_- v^0)/(\Gamma_+ - \Gamma_-) + (\Gamma_+ v^0 - \omega^0)/(\Gamma_+ - \Gamma_-)\}$$

$$\times\{\Gamma_+(\omega^0 - \Gamma_- v^0)/(\Gamma_+ - \Gamma_-) + \Gamma_-(\Gamma_+ v^0 - \omega^0)/(\Gamma_+ - \Gamma_-)\}\, t^2, \tag{4.12c}$$

which are reduced to

$$\langle z^2(t)\rangle \to (v^0 t)^2, \qquad \langle\theta^2(t)\rangle \to (\omega^0 t)^2, \qquad \langle z(t)\theta(t)\rangle \to v^0\omega^0 t^2. \tag{4.13}$$

Eqs. (4.13) represent simply that the motion of a flagellum for $t \ll 1/\eta_\pm$ is determined by the initial conditions,

$v(t_0) = v^0$ and $\omega(t_0) = \omega^0$. Let us rewrite eqs. (4.11) using the physical quantities, i.e. Ξ_z, Ξ_θ etc. The results are

$$\langle z^2(t)\rangle \to 2\,kT \frac{\Xi_\theta}{\Xi_z\Xi_\theta - r^2\Xi_\mathrm{I}^2}\,t, \qquad \langle \theta^2(t)\rangle \to 2\,kT \frac{\Xi_z}{\Xi_z\Xi_\theta - r^2\Xi_\mathrm{I}^2}\,t, \qquad \langle z(t)\theta(t)\rangle \to -2\,kT \frac{r\Xi_\mathrm{I}}{\Xi_z\Xi_\theta - r^2\Xi_\mathrm{I}^2}\,t. \tag{4.14}$$

Eqs. (4.14) are the relations that determine the three coefficients, Ξ_z, Ξ_θ and Ξ_I, from the measured values $\langle z^2(t)\rangle$, $\langle \theta^2(t)\rangle$ and $\langle z(t)\theta(t)\rangle$. However, these three coefficients have been calculated theoretically as the function of flagellar shape [12]:

$$\Xi_z = \{1 + (2\pi r/d)^2\}\psi_1, \qquad \Xi_\theta = 2r^2\psi_1, \qquad \Xi_\mathrm{I} = -(2\pi r/d)\psi_1, \tag{4.15}$$

where

$$\psi_1 = \frac{4\pi\eta_s\lambda d}{\{2 + (2\pi r/d)^2\}\ln[(d/2b)\{1 + (2\pi r/d)^2\}]}, \tag{4.16}$$

b is the radius of the flagellar filament, d is the length of the pitch, λ is the number of the pitch and η_s is the viscosity of suspension. Although eqs. (4.15) are the expressions for $b \ll d$, more general expressions could be used if one would not mind complexities. Therefore we will rewrite eqs. (4.14) by means of these parameters. Before that, we will estimate the order of $\eta_\pm$. The values of above parameters are almost as follows; $d = 2.3\ \mu$m, $b = d/100$, $r = 0.2\ \mu$m, $\lambda = 10$ for normal type flagella. Mass of a flagellum is 9.9×10^7 molecular weight/μm, viscosity of suspension η_s is 10^{-2} poise for water. Substituting these values into eqs. (3.6) and (3.9), the order of $\eta_\pm$ is calculated to be $10^9\ \mathrm{s}^{-1}$. Consequently, eqs. (4.14) are sufficiently good approximation for $t \gg 10^{-9}$ s. The expressions of eq. (4.14) by means of flagellar parameters are easily calculated as follows:

$$\langle z^2(t)\rangle \to 4\,kTt\frac{1}{\psi}, \qquad \langle \theta^2(t)\rangle \to 2\,kTt\left\{1 + \left(\frac{2\pi r}{d}\right)^2\right\}\frac{1}{r^2\psi}, \qquad \langle z(t)\theta(t)\rangle \to 2\,kTt\,\frac{2\pi r}{d}\,\frac{1}{r\psi}, \tag{4.17}$$

where $\psi = \{2 + (2\pi r/d)^2\}\psi_1$.

5. Discussion

We have considered the Brownian motion of helical flagella, and obtained the coefficients of the correlations of the random force. Also we have obtained the average values of $z^2(t)$, $\theta^2(t)$ and $z(t)\theta(t)$ as the function of Ξ_z, Ξ_θ and Ξ_I. Contrary to the cases of rod and cylinder, $\langle z(t)\theta(t)\rangle$ is shown to be finite which is due to the fact that the coupling between $\mathcal{A}_z$ and $\mathcal{A}_\theta$ exists. Eqs. (4.14) tell us that, by measuring $\langle z^2(t)\rangle$, $\langle \theta^2(t)\rangle$ and $\langle z(t)\theta(t)\rangle$ one could obtain these three coefficients. We further obtained the expressions for $\langle z^2(t)\rangle$ etc. as the function of flagellar shape using theoretically calculated values of Ξ_z, Ξ_θ and Ξ_I.

In this paper, flagella are considered to be rigid. However, the oscillation along the helix axis may exist in the actual flagellar motion. End effect is also neglected. To take into account these effects, the three coefficients Ξ_z, Ξ_θ and Ξ_I must be reconsidered. Although the theory is limited to small time interval, recent technical development in cinematography would make us possible to compare the theory with the experiment directly by choosing suitable time scale through controlling the replaying speed.

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References

[1] J. Adler, Science 166 (1969) 1588.
[2] J. Adler, Ann. Rev. Biochem. 44 (1975) 341.
[3] E.J. O'Brien and P.M. Bennett, J. Mol. Biol. 70 (1972) 133.
[4] R. Kamiya and S. Asakura, J. Mol. Biol. 106 (1976) 167.
[5] R. Kamiya and S. Asakura, J. Mol. Biol. 108 (1977) 513.
[6] M. Silverman and M. Simon, Nature 249 (1974) 73.
[7] H.C. Berg, Nature 249 (1974) 77.
[8] G.I. Taylor, Proc. Roy. Soc. (GB) A209 (1951) 447.
[9] G.I. Taylor, Proc. Roy. Soc. (GB) A211 (1952) 225.
[10] M.E.J. Holwill and R.E. Burge, Arch. Biochim. Biophys. 101 (1963) 249.
[11] A.T. Chwang and T.Y. Wu, Proc. Roy. Soc. (GB) B178 (1971) 327.
[12] H. Hoshikawa and N. Saito, J. Phys. Soc. Japan 40 (1976) 877.
[13] M.J. Lighthill, SIAM Rev. 18 (1976) 161.