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ON THE ROTATIONAL BROWNIAN MOTION OF A BACTERIAL IDLE MOTOR

I. THEORY OF TIME-DEPENDENT FLUORESCENCE DEPOLARIZATION

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A rotational diffusion equation and its Green's function for a spheroidal particle such as a bacterial body, to which an actively driving but idle motor is attached, are presented. As an application of the theory, general expressions for the time-dependent fluorescence depolarization caused by such a particle have been obtained. Measurement of such depolarization should provide a useful tool for determination of the rate of revolution of the rotating motor attached to cell bodies such as bacteria under various solution conditions, if a fluorescent (or phosphorescent) label is attached to the motor shaft.

1. Introduction

Recently, Silverman and Simon [1] found that the bacterial cell body can rotate even when the end of the flagellar filament is fixed to a slide glass. However, the direction of rotation of the body is opposite to that of the unfixed flagellar filament in solution. The structural features of the bacterial motor, which is embedded in the cell membrane, have been investigated by electron microscopic observation [2]. Furthermore, biochemical research has revealed that the bacterial motor is driven by the proton-motive force [3]. However, further studies are necessary for a better understanding of the driving mechanism of the bacterial motor.

One important point to be elucidated is the relationship between the rate of revolution of the motor and the proton-motive force in a load-free state. Since the bacterial flagellar filaments are visible under a dark-field optical microscope [4,5], measurement of the revolution of the motor in a loaded state is easy. However, since the motor shaft itself cannot be observed by optical microscopy, direct measurement of the rate of revolution in the load-free state is impossible. Therefore, we must consider indirect methods. One of the possible methods would be the measurement of time-dependent fluorescence depolarization. This technique is theoretically and experimentally well established [6,7] and is commonly used for observation of the rotational Brownian motion of polymer molecules in solution. Thus, one can estimate the size and shape of molecules through measurement of the rotational diffusion coefficient. However, no-one has previously dealt with the theory of the rotational Brownian motion of a particle coupled with an actively driving motor. In this paper, we develop such a theory and apply it to calculate the time-dependent fluorescence depolarization.

2. Rotational diffusion equation

Microorganisms such as bacteria exhibit rotational Brownian motion in suspension. Thus, if a fluorescent (or phosphorescent) label is attached

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to the bacterial motor shaft, the time-dependent fluorescence (or phosphorescence) depolarization observed will be affected by the Brownian motion of the bacterial cell body. Thus, we must consider not only the orientation and revolution of the motor shaft in solution but also the Brownian motion of the cell body to which the motor shaft is fixed. An appropriate hydrodynamical model of a bacterial cell body is a spheroid. Let x_i ($i = 1, 2, 3$) be the Cartesian coordinate system fixed to the three principal axes of the spheroid. Let x_3 be the longer axis. ζ_i ($i = 1, 2, 3$) is the angle around x_i, and D_i ($i = 1, 2, 3$) is the corresponding rotational diffusion coefficient. D_1 is equal to D_2.

We start from the following rotational diffusion equation,

$$\frac{\partial f}{\partial t} = \sum_{i=1}^{3} D_i \frac{\partial^2 f}{\partial \zeta_i^2}. \tag{1}$$

which describes the distribution of orientation of the fluorescent molecules in the case that the bacterial motor does not revolve [8]. Eq. 1 can be rewritten as follows:

$$\frac{\partial f}{\partial t} = -\mathrm{div}_\zeta \vec{j}f. \tag{2}$$

where $\vec{j}$ is given, by using the diffusion tensor $\vec{D}$, as follows,

$$\vec{j} = -\vec{D}(\mathrm{grad}_\zeta f)/f. \tag{3}$$

Eq. 3 is the so-called Fick's equation and its physical meaning is that $\vec{j}f$ is the probability flow due to the diffusion. Now, let us consider the case that the bacterial motor attached to the spheroidal cell body revolves idly. We assume that the angular velocity of the motor $\vec{\Omega}$ is constant. The probability flow due to the rotation of the motor is $\vec{\Omega}f$. Then, the total probability flow is

$$\vec{j}f = \vec{\Omega}f - \vec{D}\mathrm{grad}_\zeta f. \tag{4}$$

Consequently, the rotational diffusion equation for the fluorescent label attached to the motor shaft becomes

$$\frac{\partial f}{\partial t} = -\mathrm{div}_\zeta(\vec{\Omega}f - \vec{D}\mathrm{grad}_\zeta f). \tag{5}$$

Here we assume that the bacterial cell body has only one motor and that the motor shaft coincides with the x_3 axis. Then $\vec{\Omega}$ can be expressed as

$$\vec{\Omega} = \begin{pmatrix} 0 \\ 0 \\ \Omega \end{pmatrix} \tag{6}$$

Eq. 5 is expressed in the coordinate system fixed to the bacterial cell body. In order to calculate the time-dependent orientation of the fluorescent molecule, we introduce the Euler angles (θ, ϕ, ψ) which designate the relationship between the laboratory Cartesian coordinate system (X, Y, Z) and the coordinate system fixed to the cell body [9]. Thus, we obtain the following equation,

$$\frac{\partial f}{\partial t} = D_1\left(\frac{\partial^2 f}{\partial \theta^2} + \mathrm{cosec}^2\theta \frac{\partial^2 f}{\partial \phi^2} + \cot^2\theta \frac{\partial^2 f}{\partial \psi^2} - 2\,\mathrm{cosec}\,\theta \cot\theta \frac{\partial^2 f}{\partial \phi \partial \psi} + \cot\theta \frac{\partial f}{\partial \theta}\right) + D_3 \frac{\partial^2 f}{\partial \psi^2} - \Omega \frac{\partial f}{\partial \psi}. \tag{7}$$

The last term in the above equation, $-\Omega(\partial f/\partial \psi)$, appears because the fluorescent molecule rotates actively with respect to the cell body, superimposed on the random orientation of the cell body.

3. Green's function

In this section we calculate the Green's function $G(\theta, \phi, \psi;\ t|\theta', \phi', \psi';\ t')$ of eq. 7 which has the physical meaning of the conditional probability density that a particle which has been found at the Euler angles (θ', ϕ', ψ') at time t' will be located at the Euler angles (θ, ϕ, ψ) at time t. The Green's function can be readily expressed as

$$G(\theta, \phi, \psi;\ t|\theta', \phi', \psi';\ t') = \frac{1}{(2\pi)^2} \sum_l \sum_m \sum_n A_{lmn}(t - t')\Phi_{lm}^n(\theta)\Phi_{lm}^n(\theta') \times \exp\{il(\phi - \phi') + im(\psi - \psi')\}, \tag{8}$$

where Φ_{lm}^n is the eigenfunction which obeys the following eigenvalue equation;

$$L\Phi_{lm}^n = -(\lambda_{lm}^n - m^2)\Phi_{lm}^n, \tag{9}$$

where the operator L is

$$L = \frac{\partial^2}{\partial \theta^2} + \cot\theta \frac{\partial}{\partial \theta} - (l\,\mathrm{cosec}\,\theta - m\cot\theta)^2. \tag{10}$$

The eigenvalue equation (eq. 9) has already been

solved by Favro [10] as follows:
Eigenvalues:

$$\lambda_{lm}^{n}=n(n+1),\ n=0,1,2,\ldots$$
$$m=-n,\ -n+1,\ldots,\ 0,1,2,\ldots,n$$
$$l=-n,\ -n+1,\ldots,\ 0,1,2,\ldots,n \tag{11}$$

Eigenfunction:

$$\Phi_{lm}^{n}(\theta)=\begin{cases} N_{lm}^{n}(1+\cos\theta)^{(m+l)/2}(1-\cos\theta)^{(m-l)/2} \\ \times F\left(m+n+1, m-n, m-l+1; \dfrac{l-\cos\theta}{2}\right), \\ (m\geqq l) \\ N_{lm}^{n}(1+\cos\theta)^{(m+l)/2}(1-\cos\theta)^{(l-m)/2} \\ \times F\left(l+n+1, l-n, l-m+1; \dfrac{1-\cos\theta}{2}\right), \\ (m<l) \end{cases} \tag{12}$$

In eq. 12 $F(\alpha, \beta, \gamma; x)$ is the hypergeometric function which satisfies the hypergeometric equation

$$x(x-1)\frac{\partial^2 F}{\partial x^2}+\{(\alpha+\beta+1)x-\gamma\}\frac{\partial F}{\partial x}+\alpha\beta F=0, \tag{13}$$

and N_{lm}^{n} is the normalization constant which is given by

$$N_{lm}^{n}=\begin{cases} \left(\dfrac{2n+1}{2^{2m+1}}\right)^{1/2}\dfrac{1}{(m-l)!}\left\{\dfrac{(n-l)!(n+m)!}{(n+l)!(n-m)!}\right\}^{1/2}, \\ (m\geqq l) \\ \left(\dfrac{2n+1}{2^{2l+1}}\right)^{1/2}\dfrac{1}{(l-m)!}\left\{\dfrac{(n-m)!(n+l)!}{(n+m)!(n-l)!}\right\}^{1/2}, \\ (m<l) \end{cases} \tag{14}$$

The summation in eq. 8 has to be carried out under the condition of restriction for the eigenvalues given in eq. 11. The expansion coefficient, $A_{lmn}(t-t')$, is then obtained by solving the equation,

$$\frac{\mathrm{d}A_{lmn}}{\mathrm{d}t}+\{D_1(\lambda_{lm}^{n}-m^2)+m^2D_3+im\Omega\}A_{lmn}=\delta(t), \tag{15}$$

with the initial condition of $A_{lmn}(0)=1$. Then the solution of eq. 15 becomes

$$A_{lmn}(t)=\exp\left[-\{D_1(\lambda_{lm}^{n}-m^2)+m^2D_3+im\Omega\}t\right]. \tag{16}$$

Thus, by substituting eq. 16 into eq. 8, we can explicitly express the Green's function (eq. 8) as a function of the Euler angles.

4. Fluorescence polarization anisotropy

Let incident light which has polarization parallel to the Z axis be radiated along the X axis. We observe the intensity of the fluorescence which has polarization parallel to the Z axis, $I_P(t)$, and parallel to the X axis, $I_T(t)$. Then the fluorescence polarization anisotropy [11], $r(t)$, is defined as

$$r(t)=\{I_P(t)-I_T(t)\}/\{I_P(t)+2I_T(t)\}. \tag{17}$$

Following the expression of Aragon and Pecora [12], $I_P(t)$ and $I_T(t)$ are given as

$$I_P(t)=C\frac{1}{\tau_f}\exp(-t/\tau_f)\langle(\bar{\mu}_t\cdot\bar{k})^2(\bar{\mu}_0\cdot\bar{k})^2\rangle, \tag{18a}$$

$$I_T(t)=C\frac{1}{\tau_f}\exp(-t/\tau_f)\langle(\bar{\mu}_t\cdot\bar{i})^2(\bar{\mu}_0\cdot\bar{k})^2\rangle, \tag{18b}$$

where $\bar{\mu}_t$ and $\bar{\mu}_0$ are the vectors of the transition moment of the fluorescent molecule at time t and time 0, respectively, τ_f the fluorescence lifetime, and $\bar{i}$, $\bar{j}$ and $\bar{k}$ unit vectors along the X, Y and Z axes, respectively. The coefficient C implicitly includes several physical parameters. However, C is independent of the direction of the fluorescent molecules, and cancels out in eq. 17. $I_P(t)$ and $I_T(t)$ in eqs. 18a and 18b are calculated by assessing the terms in the angular brackets in these equations by using the joint probability density $G(\theta, \phi, \psi; t|\theta_0, \phi_0, \psi_0; 0)f(\theta_0, \phi_0, \psi_0)$, where $f(\theta_0, \phi_0, \psi_0)$ is the initial distribution, which should be $1/8\pi^2$.

Let $(\pi/2-p)$ be the angle between the transition moment of the fluorescent molecule and the motor shaft. Then, the orientation of $\bar{\mu}_t$ in XYZ space can be expressed using the Euler angles, as

$$\begin{aligned}\bar{\mu}_t=&\{\cos p(-\cos\theta\sin\phi\sin\psi+\cos\phi\cos\psi)\\&+\sin p\sin\theta\sin\phi\}\bar{i}\\&+\{\cos p(\cos\theta\cos\phi\sin\psi+\sin\phi\cos\psi)\\&+\sin p\sin\theta\cos\phi\}\bar{j}\\&+\{\cos p\sin\theta\sin\psi+\sin p\cos\theta\}\bar{k}.\end{aligned} \tag{19}$$

The $\bar{\mu}_0$ is obtained by replacing (θ, ϕ, ψ) by $(\theta_0, \phi_0, \psi_0)$. The averages which appear in eqs. 18 are the integrals about six variables, θ, ϕ, ψ, θ_0, ϕ_0 and ψ_0. Leaving the integrals about θ and θ_0, the averages are easily calculated to be

$$
\begin{aligned}
&\langle(\vec{\mu}_t\cdot\vec{k})^2(\vec{\mu}_0\cdot\vec{k})^2\rangle \\
&\quad= \tfrac{1}{32}\cos^4 p\sum_n \sum_{m=\pm 2} \exp\big[-\{D_1(\lambda^n_{0m}-m^2) \\
&\qquad + m^2 D_3 + im\Omega\}t\big] \\
&\qquad \times \int_0^\pi\int_0^\pi \sin^2\theta\,\sin^2\theta_0\,\Phi^n_{0m}(\theta)\,\Phi^n_{0m}(\theta_0)\sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{2}\sin^2 p\cos^2 p\sum_n \sum_{m=\pm 1} \exp\big[-\{D_1(\lambda^n_{0m}-m^2) \\
&\qquad + m^2 D_3 + im\Omega\}t\big] \\
&\qquad \times \int_0^\pi\int_0^\pi \sin\theta\cos\theta\sin\theta_0\cos\theta_0\,\Phi^n_{0m}(\theta)\,\Phi^n_{0m}(\theta_0)\sin\theta \\
&\qquad \times \sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \sum_n \exp(-D_1\lambda^n_{00}t)\Big\{\tfrac{1}{8}\cos^4 p\int_0^\pi\int_0^\pi \sin^2\theta\,\sin^2\theta_0\,\Phi^n_{00}(\theta) \\
&\qquad \times \Phi^n_{00}(\theta_0)\sin\theta\sin\theta_0\,d\theta\,d\theta_0 \\
&\qquad + \tfrac{1}{2}\sin^2 p\cos^2 p\int_0^\pi\int_0^\pi \sin^2\theta\cos^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0) \\
&\qquad \times \sin\theta\sin\theta_0\,d\theta\,d\theta_0 \\
&\qquad + \tfrac{1}{2}\sin^4 p\int_0^\pi\int_0^\pi \cos^2\theta\cos^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0) \\
&\qquad \times \sin\theta\sin\theta_0\,d\theta\,d\theta_0\Big\}.
\end{aligned}
\tag{20a}
$$

$$
\begin{aligned}
&\langle(\vec{\mu}_t\cdot\vec{i})^2(\vec{\mu}_0\cdot\vec{k})^2\rangle \\
&\quad= -\tfrac{1}{64}\cos^4 p\sum_n \sum_{m=\pm 2} \exp\big[-\{D_1(\lambda^n_{0m}-m^2) \\
&\qquad + m^2 D_3 + im\Omega\}t\big] \\
&\qquad \times \int_0^\pi\int_0^\pi \sin^2\theta\,\sin^2\theta_0\,\Phi^n_{0m}(\theta)\,\Phi^n_{0m}(\theta_0)\sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad - \tfrac{1}{4}\sin^2 p\cos^2 p\sum_n \sum_{m=\pm 1} \exp\big[-\{D_1(\lambda^n_{0m}-m^2) \\
&\qquad + m^2 D_3 + im\Omega\}t\big] \\
&\qquad \times \int_0^\pi\int_0^\pi \sin\theta\cos\theta\sin\theta_0\cos\theta_0\,\Phi^n_{0m}(\theta)\,\Phi^n_{0m}(\theta_0)\sin\theta \\
&\qquad \times \sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \sum_n \exp(-D_1\lambda^n_{00}t)\Big\{\tfrac{1}{16}\cos^4 p\int_0^\pi\int_0^\pi \cos^2\theta\,\sin^2\theta_0\,\Phi^n_{00}(\theta) \\
&\qquad \times \Phi^n_{00}(\theta_0)\sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{16}\cos^4 p\int_0^\pi\int_0^\pi \sin^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0)\sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{8}\sin^2 p\cos^2 p\int_0^\pi\int_0^\pi \cos^2\theta\cos^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0) \\
&\qquad \times \sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{8}\sin^2 p\cos^2 p\int_0^\pi\int_0^\pi \cos^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0) \\
&\qquad \times \sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{8}\sin^2 p\cos^2 p\int_0^\pi\int_0^\pi \sin^2\theta\,\sin^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0)\sin\theta \\
&\qquad \times \sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{4}\sin^3 p\cos p\int_0^\pi\int_0^\pi \sin^2\theta\sin\theta_0\cos\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0) \\
&\qquad \times \sin\theta\sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0 \\
&\qquad + \tfrac{1}{4}\sin^4 p\int_0^\pi\int_0^\pi \sin^2\theta\cos^2\theta_0\,\Phi^n_{00}(\theta)\,\Phi^n_{00}(\theta_0)\sin\theta \\
&\qquad \times \sin\theta_0\,\mathrm{d}\theta\,\mathrm{d}\theta_0\}.
\end{aligned}
\tag{20b}
$$

The integrals about θ and θ_0 can be calculated by using the series expansion form of $F(\alpha, \beta, \gamma; x)$,

$$
F(\alpha,\beta,\gamma;x) = \sum_{k=0}^{\infty} \frac{\alpha(\alpha+1)\ldots(\alpha+k-1)\beta(\beta+1)\ldots(\beta+k-1)}{k!\gamma(\gamma+1)\ldots(\gamma+k-1)}x^k.
\tag{21}
$$

The integrals necessary for calculation are as follows:

$$\int_0^\pi \Phi^0_{00}(\theta)\sin\theta\mathrm{d}\theta = 2N^0_{00}. \tag{22a}$$

$$\int_0^\pi \sin^2\theta\,\Phi^0_{00}(\theta)\sin\theta\mathrm{d}\theta = \tfrac{4}{3}N^0_{00}, \tag{22b}$$

$$\int_0^\pi \sin^2\theta\,\Phi^2_{00}(\theta)\sin\theta\mathrm{d}\theta = -\tfrac{4}{15}N^2_{00}. \tag{22c}$$

$$\int_0^\pi \sin^2\theta\,\Phi^2_{02}(\theta)\sin\theta\mathrm{d}\theta = \tfrac{16}{15}N^2_{02}. \tag{22d}$$

$$\int_0^\pi \sin\theta\cos\theta\,\Phi^2_{01}(\theta)\sin\theta\mathrm{d}\theta = \tfrac{4}{15}N^2_{01}. \tag{22e}$$

Thus, we obtain the fluorescence polarization anisotropy $r(t)$ as

$$
\begin{aligned}
r(t) &= \tfrac{1}{10}(\cos^2 p - 2\sin^2 p)^2\exp(-6D_1 t) \\
&\quad + \tfrac{6}{5}\sin^2 p\cos^2 p\cos\Omega t\exp\{-(5D_1+D_3)t\} \\
&\quad + \tfrac{3}{10}\cos^4 p\cos 2\Omega t\exp\{-(2D_1+4D_3)t\}.
\end{aligned}
\tag{23}
$$

When $\Omega = 0$, the above equation simplifies as follows:

$$
\begin{aligned}
r(t) &= \tfrac{1}{10}(\cos^2 p - 2\sin^2 p)^2\exp(-6D_1 t) \\
&\quad + \tfrac{6}{5}\sin^2 p\cos^2 p\exp\{-(5D_1+D_3)t\} \\
&\quad + \tfrac{3}{10}\cos^4 p\exp\{-(2D_1+4D_3)t\}.
\end{aligned}
\tag{24}
$$

Eq. 24 coincides with the time-dependent fluorescence depolarization of a spheroidal particle without a motor [6].

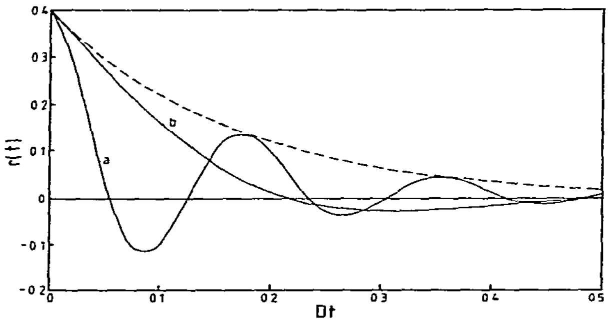

Fig. 1. The function of fluorescence polarization anisotropy $r(t)$ is plotted vs. Dt, where D_1 and D_3 are kept equal to D. The transition moment of the fluorescent molecule is assumed to be perpendicular to the motor shaft. Solid line a represents the case $\Omega/D = 1\times10^3$; and solid line b, $\Omega/D = 2.5\times10^2$.

In fig. 1, the functions of fluorescence polarization anisotropy $r(t)$ are plotted vs. Dt for several values of Ω/D, where D_1 and D_3 are kept equal as D for simplicity. If $\Omega = 0$, $r(t)$ simply decays with increasing time t, as shown by the broken line in fig. 1. If Ω/D takes a large value, a sinusoidal function is superimposed on the decay function, as shown by the solid line a in fig. 1. If Ω is comparatively small, $r(t)$ overshoots to a slightly negative value, as shown by the solid line b in fig. 1. The value $\Omega/D = 10^3$ is thought to be an appropriate one for the bacterial motor [13].

5. Discussion

We have obtained the exact solution, eq. 23, for the time-dependent fluorescence depolarization of a fluorescent molecule attached to the bacterial motor shaft. This solution is a natural extension of the well known theory [6,7] for a spheroidal particle which does not contain a motor but orients randomly. Thus, if the time-dependent fluorescence depolarization is measured, the rate of revolution of the bacterial motor, even in the load-free state, can be obtained by the use of eq. 23.

Eq. 23 contains up to the second order of the Fourier series with respect to the angular velocity Ω. Namely, the first, second and third terms on the right-hand side of eq. 23 correspond, respectively, to the zeroth-, first- and second-order components of the Fourier series. There the three relaxation times appear as $(2D_1 + 4D_3)^{-1}$, $(5D_1 + D_3)^{-1}$ and $(6D_1)^{-1}$. Since the magnitude of each relaxation time varies with D_1 and D_3, we cannot generally predict which relaxation time is the largest.

Note that if the transition moment is perpendicular to the motor shaft (i.e., $p = 0$), the first-order component of the Fourier series vanishes. This condition for labeling the fluorescent molecule is favorable for analyzing the revolution of the motor. On the other hand, if the transition moment is parallel to the motor shaft, the revolution of the bacterial motor is not observed by the time-dependent fluorescence depolarization, which then reflects only the random orientation of the cell body.

In the theory of the rotational Brownian motion developed in this paper, the Green's function is exactly obtained. This is a major advantage for application of the theory to other problems such as fluorescence correlation spectroscopy.

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