DIFFUSION OF MAGNETOTACTIC BACTERIA IN ROTATING MAGNETIC FIELD

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Abstract: Various kinds of so-called circle swimmers that operate in low-Reynolds number environments garner a lot of interest and are being studied extensively. Magnetotactic bacteria are examples of such swimmers. When placed in a rotating magnetic field these bacteria move in circles if the field frequency is less than a critical value. Here an expression for diffusion coefficients of magnetotactic bacteria in rotating field with random switching of swimming direction are derived and compared to a numerical simulation.

1. Introduction

Various kinds of so-called circle swimmers have been studied by various groups of researchers [1,2,3,4,5]. Effective diffusion coefficients of circle swimmers subjected to thermal noise are calculated in [1,2]. A specific example of circle swimmers is magnetotactic bacteria. If these bacteria are subjected to a rotating magnetic field they move in circles provided that the field frequency is less than a critical value and that thermal noise can be neglected [6]. A random walk of the centers of circular trajectory is observed due to random switching of the direction of rotation of their flagella [6,7]. Here the properties of this random walk are studied using the Fokker-Planck equation for the position and the direction of swimming of the bacteria.

2. Diffusion of circle swimmers

When the field frequency ω is less than a critical value (synchronous regime) the magnetotactic bacteria rotate synchronously with the field. Suppose that the bacterium moves with speed v in direction $\vec{n}$ of it's magnetic moment and consider the probability density function $f(\vec{x},\vec{n},t)$ of the position of the bacterium $\vec{x}$ and the direction of motion $\vec{n}$. Using the operator of infinitesimal rotations $\vec{K}_{\vec{n}} = \vec{n} \times \partial/\partial\vec{n}$ the Fokker-Planck equation accounting for a random switching rate λ of the direction of a rotary motor rotation reads

$$\frac{\partial f}{\partial t} = -\frac{\partial(v\vec{n}f)}{\partial\vec{x}} - \vec{\omega}\vec{K}_{\vec{n}}f - \lambda f + \lambda\hat{f} + D_B\frac{\partial^2 f}{\partial\vec{x}^2} + D_R\vec{K}^2_{\vec{n}}f \ , \tag{1}$$

where $f = f(\vec{x},\vec{n},t)$, $\hat{f} = f(\vec{x},-\vec{n},t)$ and D_B and D_R are translational and rotational diffusion coefficients respectively.

A simple approach to analysis is based on calculation of time-evolution for several moments of the distribution from equation (1) [8]. The obtained set of equations is closed and reads

$$\begin{aligned}
\frac{d}{dt}\langle\vec{x}^2\rangle &= 2v\langle\vec{x}\vec{n}\rangle + 6D_B \ , \\
\frac{d}{dt}\langle x_z^2\rangle &= 2v\langle x_z n_z\rangle + 2D_B \ , \\
\frac{d}{dt}\langle\vec{x}\vec{n}\rangle &= v + \omega\langle(\vec{n}\times\vec{x})_z\rangle - 2(D_R+\lambda)\langle\vec{x}\vec{n}\rangle \ , \\
\frac{d}{dt}\langle(\vec{n}\times\vec{x})_z\rangle &= -2(D_R+\lambda)\langle(\vec{n}\times\vec{x})_z\rangle - \omega\langle\vec{x}\vec{n}\rangle + \omega\langle x_z n_z\rangle \ ,
\end{aligned} \tag{2}$$

$$
\begin{aligned}
\frac{d}{dt}\langle x_z n_z \rangle &= v\langle n_z^2 \rangle - 2(D_R+\lambda)\langle x_z n_z \rangle \ , \\
\frac{d}{dt}\langle n_z^2 \rangle &= 2D_R - 6D_R\langle n_z^2 \rangle \ .
\end{aligned}
$$

In order to derive the set of equations (2) the condition of normalization $\int f(\vec{x},\vec{n},t)d\vec{x}d^2\vec{n}=1$ and the anti-hermitian property of the operator $\vec{K}_{\vec{n}}$ are used. Since the set is closed it is possible to obtain an analytical solution for $\langle \vec{x}^2 \rangle$ and $\langle x_z^2 \rangle$which characterize the random process of the particle diffusion. In the stationary case where all other moments considered are constant the solution is

$$
\begin{aligned}
\frac{d}{dt}\langle x_z^2 \rangle &= 2D_B + \frac{v^2}{3(D_R+\lambda)} \ , \\
\frac{d}{dt}\langle \vec{x}^2 - x_z^2 \rangle &= 4D_B + \frac{2v^2}{3(D_R+\lambda)(1+[\frac{\omega}{2(D_R+\lambda)}]^2)} \ .
\end{aligned}
\tag{3}
$$

Therefore there are two distinct effective diffusion coefficients $D_{||}$ (along the angular velocity $\vec{\omega}=\omega\hat{e}_z$) and $D_\perp$ (in the plane of rotation) and they read

$$
\begin{aligned}
D_{||} &= D_B + \frac{v^2}{6(D_R+\lambda)} \ , \\
D_\perp &= D_B + \frac{v^2}{6(D_R+\lambda)(1+[\frac{\omega}{2(D_R+\lambda)}]^2)} \ .
\end{aligned}
\tag{4}
$$

In the limit $\lambda \to 0$ these expressions reduce to those found in [2] using correlation functions.

It is seen that in absence of rotating external field ($\omega=0$) the rate of swimming direction reversal λ plays the role of rotational diffusion coefficient and constricts motion of the bacterium. External field further restricts motion in the plane of rotation but there exists a maximum of the transversal diffusion coefficient $D_\perp$ at $\lambda_{max}=\omega/2-D_R$ if $\omega>2D_R$. Thus in this case a bacterium has a possibility to increase its diffusion coefficient for seeking more favorable conditions by adapting the switching rate of the rotary motor. If $\omega<2D_R$ it is not advantageous for the bacterium to employ the switching mechanism.

3. Numerical simulation algorithm

In the synchronous regime the tangent vector to the trajectory $\vec{n}$, which we choose along the magnetic moment of the bacterium, rotates with the angular velocity of the field:

$$
\frac{d\vec{n}}{dt} = \vec{\omega}\times\vec{n} \ . \tag{5}
$$

Using the fluctuation-dissipation theorem equations for the change of $\vec{x}$ and $\vec{n}$ in a time interval Δt can be obtained and read

$$
\begin{aligned}
\Delta\vec{x} &= v\vec{n}\Delta t + \sqrt{2D_B\Delta t}\ \vec{G}, \\
\Delta\vec{n} &= (\vec{\omega}\Delta t + \sqrt{2D_R\Delta t}\ \vec{H}\ )\times\vec{n},
\end{aligned}
\tag{6}
$$

where components of vectors $\vec{G}$ and $\vec{H}$ are standard normal random variables. A set of switching times τ_i $(i=1,...N)$ distributed according to the Poisson law $p_i=\exp{(-\lambda\tau_i)}$ are introduced and at time moments $T_i = \sum_{j=1}^{i-1} \tau_j + \tau_i$ the tangent vector $\vec{n}$ reverses it's direction.

The generated trajectory is used to calculate autocorrelation of the bacterium position $\vec{x}$, which in turn is used to obtain diffusion coefficients $D_{||}$ and $D_{\perp}$ using regression analysis in the region where the autocorrelation becomes linear. The estimated diffusion coefficients for a range of λ values and different field frequencies are shown in Fig.1. The results are in excellent agreement with (4) and shows the maximum in transversal diffusion at $\lambda_{max} = D_R/2$ when $\omega = 3D_R$.

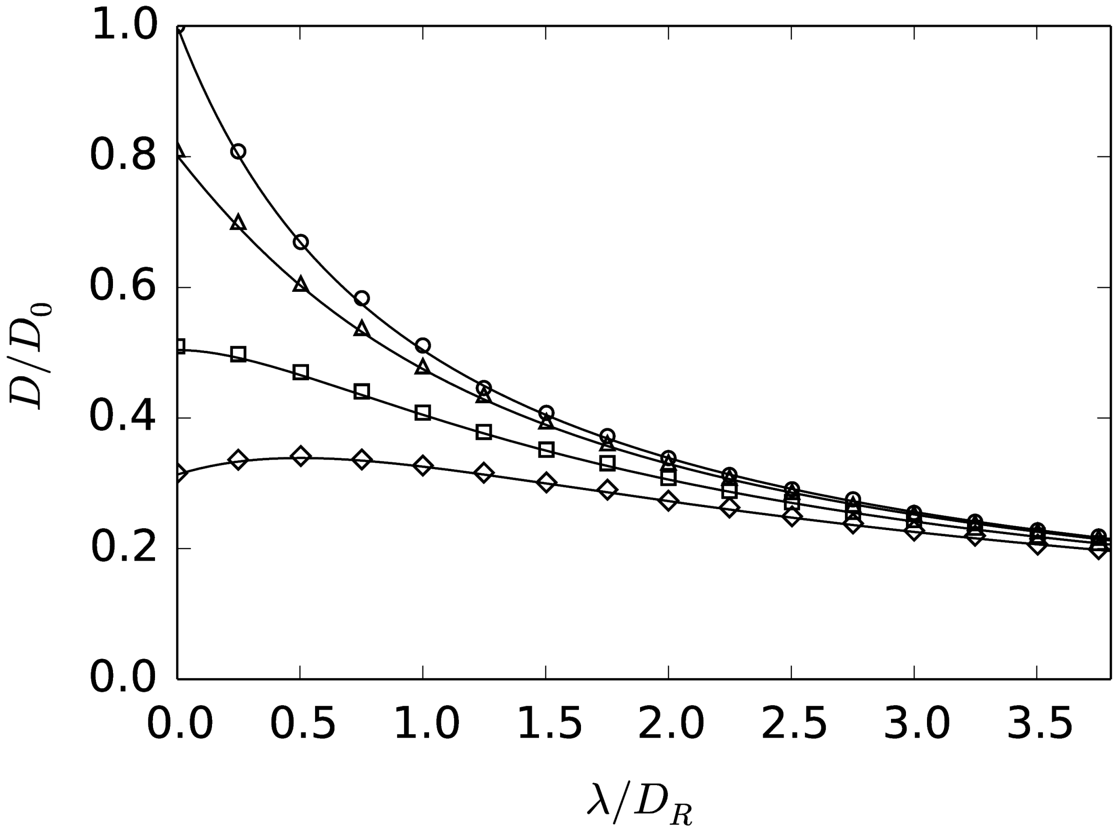

Figure 1: Diffusion coefficients as functions of switching rate λ. Here $D_0 = D_B + v^2/6D_R$. Numerically computed diffusion coefficients shown are $D_{||}$ (circles) and $D_{\perp}$ at $\omega = D_R$ (triangles), $\omega = 2D_R$ (squares) and at $\omega = 3D_R$ (diamonds). Respective theoretical curves according to equations (4) are shown. Common parameters of simulations: bacterium size $r = 1\mu m$, speed $v = 5\mu m/s$, $D_B = 0.214\mu m^2/s$, $D_R = 0.161 s^{-1}$ (assuming spherical bacteria in water at room temperature) and trajectory length $2.5 \times 10^6 s$.

4. Conclusion

In [8] it was noted that previous experimentally observed random trajectories of bacteria are caused by the switching of rotary motors and not due to thermal fluctuations. Here we provide a theory for the interaction between ordinary rotational diffusion and random reversal of swimming direction of bacteria. It is seen that maximum of the diffusion coefficient in the plane of the rotating field, already noted in [8], exists only when the field frequency is sufficiently large so the bacterium can increase it's diffusion by switching the swimming direction with an appropriate rate.

5. References

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