Efficiency of swimming of micro-organism and singularity in shape space

Masako KAWAMURA

Department of Physics, Faculty of Science, Ochanomizu University
1-1, Otsuka 2, Bunkyou-ku, Tokyo, 112, JAPAN

Abstract

Micro-organisms can be classified into three different types according to their size. We study the efficiency of the swimming of micro-organism in two dimensional fluid as a device for helping the explanation of this hierarchy in the size. We show that the efficiency of flagellate becomes unboundedly large, whereas that of ciliate has the upper bound. The unboundedness is related to the curious feature of the shape space, that is, a singularity at the basic shape of flagellate.

1E-mail: masako@phys.ocha.ac.jp
1 Introduction

One thing that micro-organism attracts us is its specificity: The environment in which they live is so sticky that an ordinary Newtonian mechanics does not apply to their motions. Surprisingly, however, the exploration of the mathematical structure which lies behind the swimming of micro-organism has led to the gauge theory and the string theory. Shapere and Wilczek discussed the problem of the swimming of micro-organism in the light of the gauge field theory[1]. They took up the motion of ciliate in two and three dimensional fluid. Inspired by their works, not only the velocity of ciliate, but also that of flagellate in two dimensional fluid were obtained and their motions were studied from the point of view of string in Ref.[3]. It is known that micro-organisms can be grouped into three different types according to their size or the way of swimming, *i.e.*, ciliate, flagellate and bacterium with bacterial flagella[5]. In particular, such a kind of bacterium can exist only in three dimensional fluid, whereas ciliate and flagellate can exist even in two dimensional fluid. The difference in their *shape* in two dimensional fluid was discussed with the help of representation of \(W_{1+\infty}\) algebra in Ref.[4]. We now turn our attention to the *size* of micro-organism. The length scale of ciliate, such as paramecium, is \(20 \sim 2 \times 10^4 \mu m\). The size of flagellate, such as sperm, is smaller than ciliate, \(1 \sim 50 \mu m\). Bacterium with bacterial flagella is even smaller, \(0.2 \sim 5 \mu m\). Thus, we can find a hierarchy of the size of micro-organism and this is the prime focus in this paper.

Here, we shall discuss the problems in the efficiency of swimming of micro-organism in two dimensional fluid. In particular, we would like to investigate whether the calculation of the efficiency is useful as a tool for facilitating the explanation of the problem on the hierarchy of the size. In order to discuss the swimming of micro-organism, we need to know fluid mechanics at low Reynolds number. In the next section, we will give a brief review of the fluid mechanics at low Reynolds number and some useful results. We also need to know the power expenditure of micro-organism to define the efficiency of the swimming of micro-organism. In section 3, following [2], we shall show that we can define the metric tensor on shape space from the power expenditure. In section 4, we will formulate the efficiency of the swimming of micro-organism in the limit of Reynolds number zero and find that the efficiency of flagellate becomes unboundedly large, whereas that of ciliate has the upper bound. The result we obtain sheds some light on the question of the hierarchy of the size of micro-organism. It is thus natural to ask whether there is a relationship between the structure of the shape space and the problem of the efficiency. This is briefly explored in section 5, where it is shown that the considerations of the metric tensor in
shape space lead to an appealing result, that is, a singularity arises at the basic shape of flagellate. The singularity makes it possible to decrease the power expenditure and to increase the efficiency infinitely. The last section is devoted to summary.

2 Fluid Mechanics at low Reynolds number

In order to discuss the motion of micro-organism, we need to consider the fluid mechanics of low Reynolds number. Reynolds number $Re$ is defined as the ratio of the inertial force to the viscous force,

$$Re = \frac{\rho V L}{\mu},$$

where $\rho$, $V$, $L$ and $\mu$ denote the density of the fluid, the typical velocity, the typical length scale and the coefficient of viscosity of the fluid, respectively. Since for given $\rho$ and $\mu$, the size and the velocity of micro-organism are exceedingly small, Reynolds number becomes small. Requirement of imcompressible flow and low Reynolds number lead to the following equations of motion for the fluid velocity $v$ and the pressure $p$:

$$\nabla \cdot v = 0$$

$$-\frac{1}{\mu} \nabla p + \Delta v = 0$$

Notice that these equations are linear and do not include time-dependent terms. Therefore, if the swimmer changes its shape periodically, the net motion due to one cycle of the deformation is invariant under the arbitrary time rescaling. It only depends on the geometry of the sequence of the deformation. Therefore, the time $t$ is just a parameter that labels the sequence of the deformation. A micro-organism appears through a boundary condition. If we denote the surface of micro-organisms as

$$S = S(\sigma, t),$$

where $\sigma_i$'s ($i = 1, 2, \cdots, D-1$) parametrize the surface of $D$-dimensional micro-organism, then the boundary condition becomes

$$v(S) = \frac{\partial S(\sigma, t)}{\partial t}.$$ 

This is the no-slip boundary condition. We assume that $S$ is a periodic function of $t$ with period $T$,

$$S(\sigma, t) = S(\sigma, t + T),$$
and the swimmer changes its shape infinitesimally from the basic shape $S_0$,

$$S(t) = S_0 + \alpha(t), \quad |\alpha(t)| \ll |S_0|$$

$$\alpha(t) = \sum_n \alpha_n w_n,$$

where $w_n$ is a complete set of the functions describing the deformation of the shape. In computing a velocity of the swimmer, we can exploit the infinitesimalness of $\alpha$ by using perturbation theory. Then we expand the net motion due to one cycle of the deformation up to the second order of $\alpha$ and obtain,

$$\frac{1}{2} \int_0^T \sum_{n,m} F_{mn} \alpha_m \dot{\alpha}_n dt,$$

where

$$F_{mn} = T^i F_{mn}^{T^i} + M^{ij} F_{mn}^{M^{ij}},$$

and $T^i$, $M^{ij}$ are translation and rotation operator acting on the shape space, respectively. The first-order term does not contribute to the net motion because the term is a total derivative. $F_{mn}$ is interpreted as field strength tensor, evaluated at a shape $S_0$ (See [1]).

3 Metric tensor on shape space

A shape space is a set of all possible shapes $S_0$. It is convenient to consider the metric tensor on shape space, which was proposed by Shapere and Wilczek [2], before moving on to the problem of the efficiency of swimming of micro-organisms. The power expenditure required to deform the body of micro-organism is given by

$$P = -\int_{S_0} v_i \sigma_{ij} dS_j,$$

where $\sigma_{ij}$ is the stress tensor,

$$\sigma_{ij} = -p \delta_{ij} + \mu \left( \frac{\partial v_i}{\partial x_j} + \frac{\partial v_j}{\partial x_i} \right),$$

and we performed the integration over the surface of micro-organism $S_0$. It can be represented as

$$P = 4\pi \mu \sum_{m,n} P_{mn} \dot{\alpha}_m \dot{\alpha}_n$$

Note that this formulation is only applicable to the case of Reynolds number zero. Moreover, $P$ is non-negative quantity, since we can rewrite $P$ as

$$\frac{1}{2} \mu \int_{\text{exterior of } S_0} (\partial_j v_i + \partial_i v_j)^2 dV$$
by using Gauss' theorem and the equations of motion. \( P \) is also invariant under the transformation of reference axes for \( \alpha \to \tilde{\alpha}(\alpha) \). Thus we can express \( P \) in terms of the invariant line element \( ds \) in shape space:

\[
\left( \frac{ds}{dt} \right)^2 = P
\]

Therefore, \( P_{mn} \) can be interpreted as the metric tensor evaluated at \( S_0 \).

4 The efficiency of swimming of micro-organism

Let us define the efficiency of the swimming of micro-organism as the ratio of the absolute value of the average velocity to the average power expenditure.

\[
\eta \equiv \frac{|\bar{U}|}{\bar{P}}, \quad (10)
\]

where

\[
\bar{U} = \frac{1}{T} \int_0^T U(t) dt = \frac{1}{2T} \int_0^T \sum_{mn} F_{mn} \alpha_m \dot{\alpha}_n dt, \quad (11)
\]

\[
\bar{P} = \frac{1}{T} \int_0^T P dt = \frac{1}{T} \int_0^T \sum_{mn} P_{mn} \dot{\alpha}_m \dot{\alpha}_n dt, \quad (12)
\]

and \( U(t) \) is the velocity of micro-organism at time \( t \). We shall assume that the motion of micro-organism does not include rotational one which decreases the efficiency, since the shortest distance between two points is a straight line and our interest is in the maximum value of the efficiency.

We now employ variational method to calculate the maximum value of the efficiency \( \eta \):

\[
\frac{\delta \eta}{\delta \alpha_m} = 0 \quad (13)
\]

Henceforth, we shall concentrate on micro-organism in two dimensional fluid, i.e., ciliate and flagellate, and compare the efficiency of ciliate with that of flagellate.

4.1 Ciliated motion

We can take advantage of the two-dimensionality by using the complex coordinate. We regard the shape of ciliate as infinitesimal deformation of a circle:

\[
S(t, \theta) = e^{i\theta} + \sum_n \alpha_n(t) e^{i n \theta} \quad \mid \alpha_n \mid \ll 1
\]
Suppose that the direction of the translation is along the real axis of the complex plane, then the average velocity and the average power expenditure are given by

\[
\bar{U}_z = \frac{1}{2T} \int_0^T dt \sum_{mn} \left\{ F_{mn} \alpha_m \dot{\alpha}_n + F_{m\bar{n}} \alpha_m \bar{\alpha}_n + F_{m\bar{m}} \dot{\alpha}_m \bar{\alpha}_n + F_{\bar{m}\bar{n}} \bar{\alpha}_m \dot{\alpha}_n \right\}
\]

\[
\bar{P} = \frac{4\pi \mu}{T} \int_0^T dt \sum_{mn} P_{mn} \dot{\alpha}_m \bar{\alpha}_n
\]

where the field strength tensor are

\[
F_{mn} = \{(n + 1)\theta_{-n} - (m + 1)\theta_{-m}\} \delta_{m+n,-1} + O(\alpha)
\]

\[
F_{m\bar{n}} = \{-(n + 1)\theta_{-n} + (m + 1)\theta_{m}\} \delta_{m-n,1} + O(\alpha)
\]

\[
F_{m\bar{m}} = \{-(n + 1)\theta_n + (m + 1)\theta_{-m}\} \delta_{m-n,-1} + O(\alpha)
\]

\[
F_{\bar{m}\bar{n}} = \{-(n + 1)\theta_{-n} + (m + 1)\theta_{-m}\} \delta_{m+n,1} + O(\alpha),
\]

and

\[
\theta_n = \begin{cases} 
1 & (n \geq 0) \\
0 & (n < 0)
\end{cases}
\]

The metric tensor is

\[
P_{mn} = |n + 1| \delta_{m,n} + O(\alpha)
\]

From (13), we obtain

\[
\frac{\delta \eta}{\delta \alpha_m} \propto \sum_n (F_{mn} \dot{\alpha}_n - \lambda P_{mn} \bar{\alpha}_n) = 0
\]

where \( \lambda = | - 8\pi \mu \eta | \). If we take the limit of large mode number (\(|m| \to \infty\)), we obtain linear differential equations for \( \alpha \) in the leading order

\[
\begin{pmatrix} 2B & B \\ B & -2B \end{pmatrix} \begin{pmatrix} \dot{V}^- \\ \dot{V}^+ \end{pmatrix} = \lambda \begin{pmatrix} \ddot{V}^- \\ \ddot{V}^+ \end{pmatrix},
\]

where the eigenvector is

\[
V^- = \begin{pmatrix} \alpha_{-1} \\ \alpha_{-2} \\ \alpha_{-3} \\ \cdot \\ \cdot \\ \cdot \end{pmatrix}, \quad V^+ = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \cdot \\ \cdot \\ \cdot \end{pmatrix}
\]
and the matrix $B$ is

$$B = \begin{pmatrix}
\vdots & \ldots & 0 \\
\vdots & \ldots & 1 \\
-1 & 0 & 1 \\
-1 & 0 & 1 \\
\vdots & \ldots & 1 \\
0 & \ldots & \vdots
\end{pmatrix}.$$  

When we regard the index $n$ of $\alpha_n$ as the $n$-th lattice point, the matrix $B$ acts as a difference operator. The eigenvector of this difference operator is always given by a plane wave. By solving the eigenvalue equation $\|17\$, we obtain the value of the efficiency

$$\lambda = \frac{\sqrt{5}T}{\pi} |\sin \beta|,$$

where $\beta$ is an arbitrary real number. This gives an upper bound on $\lambda$. The eigenvector corresponding to the above eigenvalue is

$$\alpha_m(t) = \begin{cases} 
e^{-i(m\beta + m\frac{T}{2}t)} & m > 0 \\
(\pm \sqrt{5} - 2)e^{i(m\beta - m\frac{T}{2}t)} & m < 0 \end{cases}$$

Though our calculation has been limited to large mode number, it can be shown that including the finite mode number does not bring about more efficient stroke of micro-organism in two dimensional fluid (See Appendix in $\|2\$). In fact, a real ciliate is covered with thousands of short cilia, and this means that the mode number of the surface of the ciliate is extremely high.

### 4.2 Flagellated motion

We regard the shape of a flagellate as an infinitesimal deformation of a segment of a line. A convenient choice is a parametrization of the shape such that

$$S(t, \theta) = 2\{\cos \theta + i \sin \theta \alpha(t, \theta)\},$$

$^2$Though the result from Shapere and Wilczek is correct qualitatively, they made a few mistakes in solving the eigenvalue equation.
where

\[
\alpha(t, \theta) = \sum_{n=1}^{\infty} \alpha_n(t) \sin n\theta, \quad |\alpha(t, \theta)| \ll 1, \quad -\pi \leq \theta \leq \pi
\]

and suppose that \( \alpha_n \) is a real number so that the length of flagellate can be locally preserved at \( \mathcal{O}(\alpha) \). Fortunately, this requirement eliminates the possibility of rotational motion. In this case, by making use of the result from Ref. [3], the field strength tensor and the metric tensor evaluated at \( S_0 = 2 \cos \theta \) are

\[
F_{mn} = (2n + 1)\delta_{n-m,-1} - (2m + 1)\delta_{n-m,1} + \mathcal{O}(\alpha)
\]

\[
P_{mn} = 2n\delta_{n,m} - (n + 1)\delta_{n-m,-2} - (n - 1)\delta_{n-m,2} + \mathcal{O}(\alpha).
\]  

By calculating \((13)\) again, in the limit of large mode number, we obtain an eigenvalue equation of the following form:

\[
\begin{pmatrix}
0 & -B \\
B & 0
\end{pmatrix}
\begin{pmatrix}
\dot{V}_{\text{even}} \\
\dot{V}_{\text{odd}}
\end{pmatrix}
= \lambda
\begin{pmatrix}
-\frac{1}{2}B^2 & 0 \\
0 & -\frac{1}{2}B^2
\end{pmatrix}
\begin{pmatrix}
\ddot{V}_{\text{even}} \\
\ddot{V}_{\text{odd}}
\end{pmatrix},
\]  

where

\[
V_{\text{even}} = \begin{pmatrix}
\alpha_2 \\
\alpha_4 \\
\alpha_6 \\
\vdots
\end{pmatrix}, \quad V_{\text{odd}} = \begin{pmatrix}
\alpha_1 \\
\alpha_3 \\
\alpha_5 \\
\vdots
\end{pmatrix}
\]

By solving \((21)\), we obtain the eigenvectors

\[
\alpha_n(t) = \begin{cases}
\sin m\beta' \cos \frac{2\pi t}{T} & m: \text{even} \\
\pm \cos m\beta' \sin \frac{2\pi t}{T} & m: \text{odd}
\end{cases}
\]  

with the eigenvalues

\[
\lambda = \frac{T}{2\pi |\sin \beta'|}.
\]  

where \( \beta' \) is an arbitrary real number. Notice that this result gives no upper bound on \( \lambda \). This unboundedness is caused by the fact that the square of the difference operator \( B^2 \) appears in the right-hand side of \((21)\). It indicates naively that the efficiency of the swimming of flagellate can be much better than that of ciliate at Reynolds number zero. In other words, flagellates adjust themselves to the sticky world \((Re = 0)\) more efficiently than ciliates. This might be the reason why in general, the size of flagellate is smaller than that of ciliate.
5 Discussion

The reason why there is no upper bound on the efficiency of flagellate is intimately tied up with the structure of the shape space. From eq. (20), the matrix $P_{mn}$ is proportional to a non-local operator $B^2$, which has zero mode, in the limit of large mode number. This means that the shape space becomes singular at the basic shape of flagellate

$$S_0(\theta) = 2 \cos \theta,$$

where the dimensions of the shape space are reduced if we regard $P_{mn}$ as a metric tensor on the space. It turns out that the basic shape of the flagellate is a boundary of the shape space. Assuming that the time dependence of the eigenvector is, as we have done in previous sections, given by

$$\alpha_m(t) \propto e^{i \text{sign}(m) \frac{2\pi t}{T}}$$

for ciliate,

$$\alpha_n(t) \propto \cos \frac{2\pi t}{T}, \sin \frac{2\pi t}{T}$$

for flagellate,

the average power expenditure is expressed as

$$\bar{\mathcal{P}} = \frac{1}{T} \int_0^T \mathcal{P} dt$$

$$\propto \frac{1}{T^2} \left( \int_0^T \sqrt{\mathcal{P}} dt \right)^2$$

One cycle of the deformation of the shape corresponds to a closed path in the shape space. Since $\sqrt{\mathcal{P}} dt$ is the infinitesimal line element in the shape space, $\bar{\mathcal{P}}$ turns out to be proportional to the square of perimeter of the closed path in the shape space. On the other hand, the average velocity

$$\bar{U}^i = \frac{1}{T} \int_0^T F_{\omega_m \omega_n}^i \alpha_m \dot{\alpha}_n dt$$

is proportional to the area in the shape space enclosed by the closed path. Thus, roughly speaking, our definition of the efficiency of micro-organism (10) is provided by the ratio of the area in the shape space enclosed by the circular path to its perimeter squared. As the value of the efficiency is larger, the perimeter squared becomes much smaller than its area. Therefore, the shape space is sharpened like a needle around the basic shape of flagellate. Our study would be the first step towards understanding what the global structure of shape space is like.
6 Summary

The issue of the efficiency of the swimming of micro-organism has provided us various interesting results. The efficiency of the swimming of flagellate was of particular interest, because the value of the efficiency has no upper bound. While the metric tensor of the shape space seems to be locally flat around the basic shape of ciliate, a singularity is found at the basic shape of flagellate where the power expenditure becomes zero. This fascinating structure of the shape space reflects the unboundedness of the efficiency of flagellate.

By the same token, our treatment in this paper can be generalized to the case of micro-organism in three dimensional fluid. Shapere and Wilczek also found maximally swimming strokes for nearly spherical organism whose deformation is azimuthally symmetric. The organism corresponds to the ciliate in three dimensional fluid\cite{2}. Remarkably, the result for the sphere and cylinder in three dimensional fluid were identical in the limit of large mode number. The latter corresponds to ciliate in two dimensional fluid. Although the treatment of swimming motion of flagellate and bacterium with bacterial flagella in three dimensional fluid is likely to be more complicated, it would be interesting to explore the problem on the hierarchy of the size and the structure of the shape space.

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