Self-Propulsion at Low Reynolds Number

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We formulate the problem of self-propulsion at low Reynolds number in terms of a gauge field over the space of shapes. The computation of this field is discussed, and carried out in some examples. We apply our results to determine maximally efficient infinitesimal swimming motions of spheres and circular cylinders.

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Swimming microorganisms live in a world without inertia.[1-3] In the limit of zero Reynolds number, the swimmer's path through a fluid is determined solely by the geometry of the sequence of shapes that it assumes, and not by the rate at which it changes shape. In this paper, we shall describe how, as a consequence of its intrinsically geometric nature, the problem of self-propulsion at low Reynolds number naturally resolves itself into the computation of a gauge field over the space of shapes which the swimmer may assume. This gauge field A, which takes its values in the Lie algebra of the group of rigid motions, determines the overall motion of the swimmer induced by a given infinitesimal change of shape. The net rotation and translation of a swimmer may be expressed as an integral of A along the path in shape space corresponding to the swimming stroke.

If the swimming stroke is composed of small deformations of a shape S, the problem reduces to computing the derivative of A, the "field strength" F at S. We compute F at two points in shape space, the sphere and the circular cylinder. The result describes all possible infinitesimal swimming motions of these shapes, and allows a determination of the strokes of maximal efficiency. Infinitesimal swimming motions are relevant to the study of ciliated protozoa, which swim by waving a layer of short, densely packed cilia, in synchronous waving motions. In an approximation known as the envelope model, the effects of the individual cilia are ignored and the shape is taken to be a smooth surface covering the entire ciliary layer.[4-6] The qualitative features of observed ciliary beating patterns are consistent with our analysis of efficient swimming strokes.

The gauge potential.— Generally, gauge structures are associated with redundancy in the description of a physical system. In electrodynamics, the simplest gauge theory, we are forced to make an arbitrary choice in order to eliminate a redundancy in the gauge potential, which is determined by Maxwell's equations only up to the addition of a gradient. A similar redundancy, depicted in Fig. 1, occurs in the context of the kinematics of deformable bodies. Namely, in order to discuss the motion of changing shapes, we must choose a point of reference and an orientation for each possible shape, relative to which the motion may be measured. In ordinary Newtonian mechanics, the natural reference point to choose is the center of mass. However, at zero Reynolds number, in the absence of inertia, this choice is as arbitrary as any other. Nor is there a canonical choice of orientation for a given shape. For each shape, the set of reference frames we may choose from is isomorphic to the Euclidean group E_3, since each frame is related to any other frame by a rigid motion. Thus, the choice of frames admits a gauge freedom with gauge group E_3.

Let us suppose we have now made a choice of a reference frame, or equivalently of a standard location in space, for each shape. We determine the location of any shape relative to its standard location. That is, if $S(\sigma)$ is a shape with boundary parameterized by σ, then there is a rigid motion R relating S to its associated standard shape S_0

$$S(\sigma) = R S_0(\sigma). \tag{1}$$

A body is self-propelling if it exerts no net force or torque on itself. A swimming stroke is therefore completely specified by a time-dependent sequence of standard shapes $S_0(\sigma,t)$; the overall rigid motion will be determined by the conditions of vanishing force and torque. By solving the fluid mechanical equations of

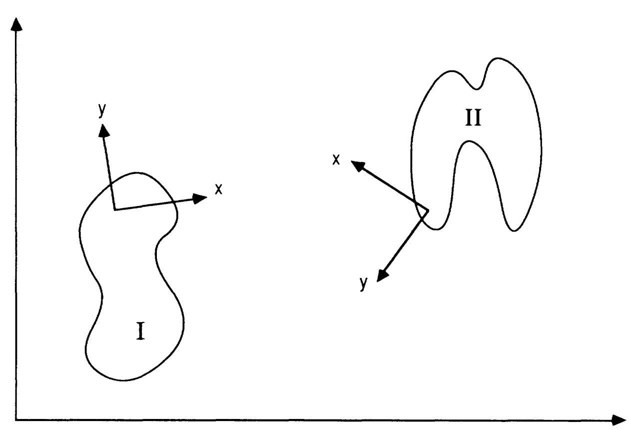

FIG. 1. In order to measure distances between different shapes, an arbitrary choice of reference frames must be made.

motion, we can uniquely determine the actual path of the swimmer through space as

$$S(\sigma,t)=R(t)S_0(\sigma,t), \tag{2}$$

where $R(t)$ is a sequence of rigid motions. The dynamical problem of self-propulsion at low Reynolds number thus resolves itself into the computation of $R(t)$, given $S_0(t)$.

We now define

$$\frac{dR}{dt}=R\left(R^{-1}\frac{dR}{dt}\right)\equiv RA. \tag{3}$$

A is defined on the tangent space to the space of standard shapes and takes its values in the Lie algebra of E_3. It is a linear map which gives the overall displacement of the shape S_0 resulting from an infinitesimal deformation $\dot{S}_0$. Integrating Eq. (3), we find the net translation and rotation from time t_1 to t_2 as a (reverse) path-ordered exponential

$$R(t_2)=R(t_1)\bar{P}\exp\int_{t_1}^{t_2}A(t)dt. \tag{4}$$

It should come as no surprise to readers familiar with gauge theory that, under a change in our choice of standard shapes $\tilde{S}_0=\Omega[S_0]S_0$, A transforms as a gauge potential should:

$$\tilde{A}=\Omega A\Omega^{-1}-(d\Omega/dt)\Omega^{-1}. \tag{5}$$

We now describe how to compute $A(t)$, given a sequence of forms $S_0(t)$. In general, this sequence of forms is not itself an allowed motion, for it will lead to net forces and torques on the swimmer. The correct motion, involving the same sequence of forms, will include additional time-dependent rigid displacements, which cancel the net forces and torques. These displacements tell us the net velocity of the shape relative to the fluid at infinity. In order to find $A(t)$, given $S_0(t)$ and its time derivative $\dot{S}_0(t)$, we must solve Stokes' equations for the response of the fluid to the deformation:

$$\nabla\cdot v=0,\ \ \nabla^2(\nabla\times v)=0\ , \tag{6}$$

$$v\,|_{S_0}=\delta S_0/\delta t. \tag{7}$$

Note the invariance of these equations under time reparametrizations, to which we alluded above. As they stand, Eqs. (6) and (7) determine the motion of the fluid only up to the addition of flows which rigidly translate or rotate the shape, and which thus do not affect the no-slip boundary condition (7). Hence, we are free to add such flows as are necessary in order to cancel any net forces or torques produced by our "trial motion" $S_0(t)$. The result, which can be shown to be uniquely determined, is the actual fluid motion.

As an example of the computation of A, we consider the case of a cylinder which swims by deforming its cross section. We can exploit the two dimensionality of this problem by defining a complex coordinate $z=x+iy$. Then the general solution of Eq. (6) may be written in terms of two functions ϕ_1 and ϕ_2 analytic outside of the shape as[1]

$$v(z)=\phi_1(z)-z\bar{\phi}_1'(z)+\bar{\phi}_2(z). \tag{8}$$

To determine v, we need only match $v(\sigma)$ to $\partial S_0/\partial t$ on the boundary of $S_0(\sigma)$ and then analytically extend $\phi_1(\sigma)$ and $\phi_2(\sigma)$ to the full complex plane. A may then be determined from the leading behavior of the trial motion v at infinity as the rigid motion of the shape necessary to cancel all net forces and torques. In fact, if we have the expansions

$$\phi_1(z)=\sum_{n<0}a_nz^{n+1},\ \ \phi_2(z)=\sum_{n<-1}b_nz^{n+1}, \tag{9}$$

then A is given directly in terms of the leading coefficients of ϕ_1 and ϕ_2 as

$$A^{\rm tr}=-a_{-1},\ \ A^{\rm rot}={\rm Im}\,b_{-2}. \tag{10}$$

Here $A^{\rm tr}$ and $A^{\rm rot}$ are the shape's net translational and rotational velocities. The boundary-value problem (7) is most easily solved when $S(\sigma)$ is a conformal mapping from the unit circle $\sigma=e^{i\theta}$ into the z plane. The use of S to conformally pull Eq. (8) back to the unit circle then reduces the problem to equating Fourier coefficients. If S is a conformal map of degree N, then in general $N+2$ simultaneous linear equations must be solved in order to determine a_{-1} and b_{-2}, and hence A. For conformal maps of degree less than 2, such as

$$S_0(\sigma,t)=\alpha_0(t)\sigma+\alpha_{-2}(t)\sigma^{-1}+\alpha_{-3}(t)\sigma^{-2}, \tag{11}$$

we find that

$$A^{\rm tr}=\alpha_{-2}\dot{\bar{\alpha}}_{-3},$$
$$A^{\rm rot}={\rm Im}\frac{\alpha_{-2}\dot{\bar{\alpha}}_{-2}+\alpha_{-3}\dot{\bar{\alpha}}_{-3}}{|\alpha_0|+|\alpha_{-2}|+|\alpha_{-3}|}. \tag{12}$$

Infinitesimal deformations: the field strength.—Cyclic swimming strokes composed of infinitesimal deformations may be treated as follows. Suppose we have a sequence of standard shapes

$$S_0(\sigma,t)=S_0(\sigma)+s(\sigma,t), \tag{13}$$

where $s(t)$ is infinitesimal, of order ϵ. We expand $s(t)$ and $A(t)$ in terms of a fixed basis of vector fields $w_n(\sigma)$ on S_0:

$$s(\sigma,t)=\textstyle\sum_n\alpha_n(t)w_n(\sigma), \tag{14}$$

$$A_{\dot{S}_0(t)}[S_0(t)]=\textstyle\sum_i\dot{\alpha}_i(t)A_{w_i}[S_0(t)]. \tag{15}$$

Then the path-ordered-exponential integral of Eq. (4) may be written

$$\bar{P}\exp\oint\textstyle\sum_nA_{w_n}[S_0(t)]\dot{\alpha}_n(t)dt. \tag{16}$$

We now expand Eq. (16) in powers of ϵ. The first-order term is the integral of a total derivative, and vanishes around a cycle. The second-order term is found to be

$$\oint \frac{1}{2}\sum_{m,n}\left(\frac{\partial A_{\omega_n}}{\partial w_m}-\frac{\partial A_{w_m}}{\partial w_n}-[A_{w_m},A_{w_n}]\right)\alpha_m\dot{\alpha}_n\,dt \equiv \oint \sum_{m,n} F_{mn}[S_0]\alpha_m\dot{\alpha}_n\,dt. \tag{17}$$

$F_{mn}[S_0]$, which we call the field strength, encodes all information on cyclic swimming motions due to arbitrary infinitesimal deformations of S_0.

To compute F_{mn}, we examine the following sequence of deformations:

$$S_0(\sigma)\rightarrow S_0(\sigma)+\epsilon w_m(\sigma)\rightarrow S_0(\sigma)+\epsilon w_m(\sigma)+\eta w_n(\sigma)\rightarrow S_0(\sigma)+\eta w_n(\sigma)\rightarrow S_0(\sigma). \tag{18}$$

The resulting net rotation and translation will be

$$(R,d)=1+\epsilon\eta F_{mn}. \tag{19}$$

We now apply this procedure to evaluate f_{mn} at the circular cylinder. In this case, we take as a basis for the vector fields on the circle

$$w_n(\sigma)=\sigma^{n+1}=e^{i(n+1)\theta} \tag{20}$$

and allow the infinitesimal parameters ϵ and η to be complex. Then for each m and n, F_{mn} will have four components, corresponding to the real and imaginary parts of ϵ and η, which we define by rewriting Eq. (19):

$$(R,d)=1+\epsilon\eta F_{mn}+\bar{\epsilon}\eta F_{\bar{m}n}+\epsilon\bar{\eta}F_{m\bar{n}}+\bar{\epsilon}\bar{\eta}F_{\bar{m}\bar{n}}. \tag{21}$$

The result of a straightforward calculation is

$$F^{\rm tr}_{mn}=[-(m+1)\theta_{-m}+(n+1)\theta_{-n}]\delta_{m+n,-1},$$
$$F^{\rm tr}_{\bar{m}n}=[(m+1)\theta_{-m}-(n+1)\theta_n]\delta_{m-n,1}=-F^{\rm tr}_{m\bar{n}}, \tag{22}$$
$$F^{\rm tr}_{\bar{m}\bar{n}}=[(m+1)\theta_{-m}-(n+1)\theta_{-n}]\delta_{m+n,1},$$
$$F^{\rm rot}_{mn}=-F^{\rm rot}_{\bar{m}\bar{n}}=[(m+1)\theta_{-m}-(n+1)\theta_{-n}]\delta_{m+n,0}, \tag{23}$$
$$F^{\rm rot}_{\bar{m}n}=-F^{\rm rot}_{n\bar{m}}=|m+1|\,\delta_{m-n,0},$$

where θ_n is 0 for negative n and 1 otherwise. Most of the components of F are zero, due to the symmetry of the circular cylinder. This means that only certain swimming motions, which couple modes m and $m\pm 1$ or $-m\pm 1$, lead to a net translation.

A similar calculation may be performed for small deformations of the sphere.[1] Expanding the deformation modes in vector spherical harmonics, one again finds that most of the components of F vanish, and that the non-vanishing components increase roughly linearly with the total angular momentum J.

Efficiencies.—Now that we have effectively found all the infinitesimal swimming motions of the circular cylinder and the sphere, it is natural to ask which of these motions are the most efficient. We define the efficiency to be proportional to the ratio of the shape's average net velocity to its energy output per cycle[2]:

$$\eta\sim\frac{\text{average velocity}}{\text{energy output per cycle}}=\frac{\bar{U}}{\mathcal{E}}\ . \tag{24}$$

We assume that the only work done by the organism is done against the fluid, so that

$$\mathcal{E}=\int_0^T dt\int_{S_0} dS_j\,v_i\sigma_{ij}, \tag{25}$$

where σ_{ij} is the fluid stress tensor.[5]

For the circular cylinder, the power output at time t is found to be

$$\mathcal{P}=2\pi\mu\epsilon^2\sum_n|n+1|\,|\dot{\alpha}_n|^2\equiv\sum_{m,n}P_{mn}\dot{\alpha}_m\dot{\alpha}_n \tag{26}$$

for the stroke

$$S_0(\sigma,t)=\sigma+\epsilon\sum_{n\neq-1}\alpha_n(t)\sigma^{n+1}. \tag{27}$$

Hence the efficiency of this stroke is

$$\eta\sim\frac{\int_0^T dt\,\sum_{m,n}F_{mn}\alpha_m\dot{\alpha}_n}{T\int_0^T\sum_{m,n}P_{mn}\dot{\alpha}_m\dot{\alpha}_n}. \tag{28}$$

To determine which strokes are maximally efficient, we set the variation of η with respect to each of the α_n equal to zero. This leads to an infinite set of equations of the form

$$\frac{\delta\eta}{\delta\alpha_m}\sim\sum_n F_{mn}\dot{\alpha}_n-\eta P_{mn}\ddot{\alpha}_n=0 \tag{29}$$

or, in a more succinct notation,

$$P^{-1}F\dot{\alpha}=\eta\ddot{\alpha}. \tag{30}$$

If V is an eigenvector of $P^{-1}F$ with eigenvalue η, then $\alpha(t)=\mathrm{Re}\exp(-2\pi it/T)V$ is a stroke of extremal efficiency. Our problem thus reduces to finding the eigenvectors of $P^{-1}F$ with maximum eigenvalue. This program may be carried through completely in the case of the circular cylinder, to find maximally efficient strokes coupling modes $k,k+1,\ldots,k+p$ and $-k,-(k+1),\ldots,-(k+p)$. The maximum attainable efficiency is found to be[2]

$$\eta_{\max}\sim\cos[\pi/(p+2)]<1. \tag{31}$$

Strokes of maximal efficiency are symmetric about the axis of propulsion, and irrotational. They are composed of traveling waves moving from the leading end of the shape (relative to the direction of the net motion) to the rear, attaining a maximum amplitude near the middle. A stroke with $k=10$, $\epsilon=0.1$, and $p=9$ is plotted in Fig.

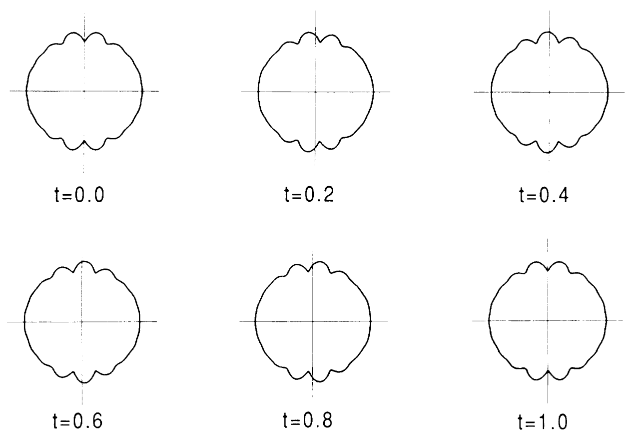

FIG. 2. A cylindrical swimming stroke of efficiency $\eta = 0.94$, coupling modes $10, 11, \ldots, 19$ and $-10, -11, \ldots, -19$.

2. Its efficiency is approximately 0.94 and the net (leftward) translation per cycle is $0.51\epsilon^2$ in units where the average radius is 1.

Similar results are obtained for the sphere, for large minimum mode number J, but we have not analyzed the case of deformations with finite mode numbers completely.

It would be worthwhile to extend our analysis to other shapes, such as prolate spheres and elliptical cylinders. It should be possible, by using conformal mapping techniques, to compute F for cylinders with a wide variety of cross-sectional shapes. It may also be possible to approximate the high-frequency components of F_{mn} for arbitrary shapes: Since the flows generated by high-frequency disturbances on the boundary of a shape tend to die rapidly with distance, it seems reasonable to treat them approximately, by replacing the shape locally with its tangent plane. Such an approximation has been discussed in the context of the envelope model (see Ref. 4 and references therein), although, to our knowledge, a firm mathematical justification is lacking.

We would also like to suggest the applicability of our ideas to other linear partial differential equations and other types of boundary conditions. For example, one might consider *unparametrized* shapes, appropriate to describing the motion of air bubbles. In this case, one would impose "slip" boundary conditions, and divide the shape space further by the group of reparametrizations. The gauge group would then be infinite dimensional.

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