A geometric theory of swimming: Purcell’s swimmer and its symmetrized cousin

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Abstract. We develop a qualitative geometric approach to swimming at low Reynolds numbers which avoids solving differential equations and uses instead landscape figures describing the swimming and dissipation. This approach gives complete information about swimmers that swim on a line without rotations and gives the main qualitative features of general swimmers that can also rotate. We illustrate this approach for a symmetric version of Purcell’s swimmer, which we solve by elementary analytical means within slender body theory. We then apply the theory to derive the basic qualitative properties of Purcell’s swimmer.
1. Introduction

Micro-swimmers have been of general interest lately, motivated by both engineering and biological problems [1–10]. They can be remarkably subtle as was illustrated by E M Purcell in his famous talk on ‘Life at low Reynolds numbers’ [11] where he introduced a deceptively simple swimmer, shown in figure 1. Purcell asked ‘What will determine the direction this swimmer will swim?’ This simple-looking question was left as an open question for almost 15 years, until Becker et al [4] found that the direction of swimming depends, among other things, on the stroke’s amplitude: increasing the amplitudes of certain small strokes that propagate the swimmer to the right results in propagation to the left\(^2\). This shows that even simple qualitative aspects of low-Reynolds-number swimming can be quite un-intuitive.

Purcell’s swimmer, made of three slender rods, can be readily analyzed numerically by solving three coupled, non-linear, first-order, differential equations [3]. However, at present, there appears to be no general method that can be used to gain direct qualitative insights into the properties of the solutions of these differential equations.

\(^2\) Two movies of this swimmer moving to the left (right) by doing small (large) amplitude strokes can be found at http://stacks.iop.org/NJP/10/063016/mmedia. Note the non-trivial behavior of this swimmer due to both its rotation and translation.

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Figure 1. Purcell’s swimmer. The swimmer controls the angles $|\theta_{1,2}| < \pi$. The angles increase in the direction of the arrows. The location of the swimmer in the plane is determined by two position coordinates $x^{1,2}$ and one orientation $x^0 = \phi$. The length of each arm is $\ell$ and the length of the body is $\ell_0$.

Figure 2. The swimming curvature (measured in the dissipation metric) on the surface of controls for the symmetric Purcell swimmer. The closed curve shows the optimal stroke. The swimmer pictures are representative of the swimmer shape along the stroke (the black dots): each shape corresponds to the minimal/maximal $\theta_1/\theta_2$ point of the stroke near it. A bona fide optimizer exists since the swimming curvature vanishes on the boundary $\theta_j = \pi, 0$.

Our first aim here is to describe a geometric approach which allows one to describe the qualitative features of the solution of the swimming differential equations without actually solving them. Our tools are geometric. The first tool is the notion of curvature borrowed from non-Abelian gauge theory [12]. This curvature can be represented graphically by landscape diagrams such as figures 2–4 and it gives precise information about infinitesimal closed
Figure 3. The curvature for rotation for Purcell’s three-linked swimmer with \( \lambda = 2 \), plotted with the flat measure on \((\theta_1, \theta_2)\).

Figure 4. The landscape of the \( x \)-curvature for Purcell’s swimmer with \( \lambda = 0.75 \) shown with the Tam and Hosoi optimal distance stroke [3]. The curvature is given relative to the flat measure in \((\theta_1, \theta_2)\).

(i.e. full) strokes. We have taken care not to assume any pre-existing knowledge about the gauge theory on the part of the reader. Rather, we have attempted to use swimming as a natural setting where one can build and develop a picture of the notions of non-Abelian gauge fields in terms of infinitesimal strokes. Purcell’s original question, ‘What will determine the direction in...
which this swimmer will swim?’ can often be answered by simply looking at such landscape pictures.

Our second tool is the notion of metric and curvature associated with the dissipation. The ‘dissipation curvature’ can also be described as a landscape diagram and it gives information on the energy cost of strokes. This gives us a second useful geometric tool that gives qualitative information on the solutions of rather complicated differential equations.

We begin by illustrating these geometric methods for the symmetric version of Purcell’s swimmer, shown in figure 5. This is a much simpler swimmer than Purcell’s original swimmer, because symmetry protects the swimmer against rotations, so it can only swim on a straight line. This makes it simple to analyze by elementary analytical means. In particular, it is possible to determine, using the landscape portraits in figure 2, which way it will swim. In this (Abelian) case, a single landscape portrait gives full quantitative information on the distance covered in any given stroke\(^3\). We then turn to the non-Abelian case of the original Purcell’s swimmer which can also rotate. This now requires three landscape portraits (curvatures) to describe any closed infinitesimal stroke: one representing infinitesimal rotation and two representing the two possible translations in the plane. Since translations and rotations do not commute, these curvatures represent non-Abelian gauge fields. Although the landscape portraits (curvatures) give precise information on small strokes, this information cannot be integrated to learn about large strokes in general. This can be viewed as a failure of Stokes’ integration theorem. Nevertheless, as we shall explain, the curvatures do give considerable qualitative information about large strokes as well.

2. The symmetric Purcell’s swimmer

Purcell’s swimmer, which was invented as ‘The simplest animal that can swim that way’ [11], is not simple to analyze at all. A variant of it that is simple to analyze is shown in figure 5. The swimmer has four arms, each of length \(\ell > 0\) and one body arm of length \(\ell_0\) (possibly of zero length). The swimmer can control the angles \(\theta_j\), and the arms are not allowed to touch. Both angles increase in the counterclockwise direction, \(0 < \theta_j < \pi\).

\(^3\) A movie of this swimmer can be found at http://stacks.iop.org/NJP/10/063016/mmedia.
Being symmetric, this swimmer cannot rotate and can swim only in the ‘body’ direction. It falls into the class of ‘simple swimmers’, which includes the ‘three linked spheres’ of Glolestanian and Najafi [1] and the Pushmepullyou [8], whose hydrodynamics is elementary because they cannot turn.

Let us first address Purcell’s question, ‘What will determine the direction this swimmer will swim?’ for the stroke shown in figure 2. In the stroke, the fore and aft pairs of arms each move symmetrically, so that the swimmer shape has two degrees of freedom. First, both pairs sweep backwards together, pushing the swimmer forward. Then each pair sweeps forward, one by one, pulling the swimmer back. Which half of the cycle wins?

To answer that, one needs to remember that swimming at low Reynolds numbers relies more on effective anchors than on good propellers. Since one needs twice the force to drag a rod transversally than to drag it along its axis [13], an open pair of arms \( \theta_j \approx \pi / 2 \) acts like an anchor. This has the consequence that rowing with both pairs, in the same direction and in phase, is less effective than bringing them back out of phase. The stroke actually swims backwards. This reasoning also shows that the swimmer is Sisyphian: it performs a lot of forward and backward movements for little net gain\(^4\).

2.1. The swimming equation

The swimming equation at low Reynolds numbers is the requirement that the total force (and torque) on the swimmer is zero. The total force (and torque) is the sum of the forces (and torques) on the four arms and body. For the symmetric swimmer, the torque and force in the transversal direction vanish by symmetry. The swimming equation is the condition that the force in the body direction vanishes. This force depends linearly on the known rate of change of the controls, \( \dot{\theta}_i \), and unknown velocity \( \dot{X} \) of the ‘body rod’. It gives a linear equation for the velocity.

For slender arms and body, the forces are given by Cox’s [14] slender body theory: the element of force, \( dF(s) \), acting on a segment of length \( ds \) located at the point \( s \) on the slender body is given by

\[
dF(s) = k(t(t \cdot v) - 2v) \, ds, \quad k = \frac{2\pi \mu}{\ln \kappa},
\]

where \( t(s) \) is a unit tangent vector to the slender body at \( s \) and \( v(s) \) is its velocity there. \( \mu \) is the viscosity and \( \kappa \) is the slenderness (the ratio of length to diameter).

The force on the \( a \)th arm depends linearly on the velocities of the controls \( \dot{\theta}_j \) and swimming velocity \( \dot{X} \). (We will use \( a \) as the index for the arm on which the force is calculated, and \( j \) as a running index indicating the control.) For example, the force component in the \( x \)-direction on the \( a \)th arm takes the form

\[
F_a = f_{ax} \dot{X} + f_{aj} \dot{\theta}_j,
\]

where \( f_{ax} \) are functions of the controls \( \theta_j \), given by elementary integrals

\[
f_{ax} = k(\cos^2 \theta_a - 2) \int_0^\ell ds, \quad f_{aj} = 2k \sin \theta_j \int_0^\ell s \, ds.
\]

\(^4\) Multimedia simulations can be viewed at http://physics.technion.ac.il/~avron.
Similar equations hold for the left arm and the body. The requirement that the total force on the swimmer vanishes gives a linear relation between the variation of the controls and the displacement:

\[
dx = \frac{dX}{\ell} = -a(\xi, \lambda) (d\xi_1 + d\xi_2), \quad \xi_j = \cos \theta_j,
\]

where

\[
a(\xi, \lambda) = \frac{1}{4 + \lambda - \xi_1^2 - \xi_2^2}, \quad \lambda = \frac{\ell_0}{2\ell}.
\]

As one expects, the body, \(\lambda\), is just a ‘dead weight’ and a trim swimmer with \(\lambda = 0\) is best.

### 2.2. Infinitesimal strokes

The notation \(dx\) stresses that the differential displacement does not integrate to a function of the controls, that is, \(x\) depends on the path and not just on the instantaneous values of the controls \(\xi_i\) (or alternatively \(\theta_i\)). This is the essence of swimming: \(x\) fails to return to its original value even though the controls \(\xi_i\) do.

Swimming is best captured not by the infinitesimal displacement change, \(dx\), due to infinitesimal changes in the controls, \(d\xi\), given in equation (2.4), but rather by the infinitesimal displacement due to an infinitesimal (closed) stroke. These are given by:

\[
F = dF = 2a^2(\xi, \lambda)(\xi_2 - \xi_1) d\xi_1 \wedge d\xi_2,
\]

\(a(\xi)\) is given in equation (2.5). \(d\xi_1 \wedge d\xi_2\) designates the infinitesimal area associated with a closed (full) stroke. Reversing the stroke reverses the area form. There are two reasons why \(F\) captures swimming better than \(dx\):

1. The displacement associated with a stroke is given by integrating \(dx\). Since a full stroke is a closed path, there are mutual cancellations when the integral is evaluated. \(F\), as the derivative of \(dx\), measures only the leftover from the mutual cancellations in an infinitesimal stroke.
2. Incomplete strokes are represented by open paths in shape space. In this case \(dx\) of equation (2.4) measures the displacement of points on the body arm. The displacement of points on other arms will be different, due to the changing angles. Thus \(dx\) is generally different for different points on a swimmer. In contrast, \(F\), which measures the displacement after a full stroke, is the same for all points of the swimmer.

The mathematical structure described here is that of an (Abelian) gauge theory [12]. The infinitesimal \(A \cdot d\ell\) with \(A\), the magnetic vector-potential, is the analogue of \(dx\) in equation (2.4). The magnetic flux though an infinitesimal loop is the analogue of \(F\) in equation (2.6).

In gauge theories, \(F\) is also known as the curvature. The reason for the name comes from the observation, originally due to Levi Civita, that the curvature of manifolds is expressed in the failure of parallel transport of tangent vectors to return to themselves upon completing a full cycle.

We introduced \(F\) as the infinitesimal displacement associated with an infinitesimal loop in the control space. However, in the Abelian case of the symmetric Purcell swimmer, it contains all the information necessary to compute the displacement for arbitrarily large full strokes.
The displacement is given by the surface integral for a region enclosed by a curve \( \gamma \). Indeed, by Stokes’ theorem, the distance covered in one stroke:

\[
\oint_{\gamma} dx = \int_{S(\gamma)} dF,
\]

where \( S(\gamma) \) is the area enclosed by \( \gamma \). As we shall see, this result fails for general swimmers that can also rotate.

The total curvature associated with the full square of shape space, \(|\xi_j| \leq 1\), is 0 by symmetry. The total positive curvature associated with the triangular half of the square, \(\xi_1 \leq \xi_2\), is 0.274. This means that the swimmer can swim, at most, about a quarter of the length of its arms in a single stroke.

Since \( F \) was defined as the displacement change due to an infinitesimal stroke, it has no numerical value—just like an infinitesimal flux in the magnetic field case. One can write \( F = F(\xi) \, d\xi_1 \wedge d\xi_2 \), and assign to \( F \) a numerical value, provided one has a recipe for computing the infinitesimal area \( d\xi \wedge d\xi_2 \). \( F \) is then the analogue of the magnetic field. In the magnetic field case there is a natural notion of area that comes from the Euclidean geometry of space. However, in the case of swimming the coordinates \( d\xi_j \) describe controls and it is not a priori obvious how should one measure distances in control or shape space. For example, \( d\theta_1 \) and \( d\xi_1 \), which are both natural coordinates, would give different notions of area. In the next section, we shall describe a natural way to introduce a metric in control or shape space. This allows us to assign a numerical value to the analogue of the magnetic field. This metric is induced by the energy dissipation.

### 2.3. The metric in shape space

The power of swimming at low Reynolds numbers is quadratic in the driving: \( g_{jk}(\theta) \dot{\theta}_j \dot{\theta}_k \), where \( g_{jk}(\theta) \) is a function on shape space and we use the summation convention where repeated indices appear. This suggests that the natural metric in shape space is, in either coordinate system,

\[
g_{jk}(\xi) d\xi_j d\xi_k = g_{jk}(\theta) d\theta_j d\theta_k.
\]

In particular, the associated area form is

\[
\sqrt{\det g(\theta)} d\theta_1 \wedge d\theta_2 = \sqrt{\det g(\xi)} d\xi_1 \wedge d\xi_2.
\]

The curvature can now be assigned a natural numerical value

\[
2a^2(\xi, \lambda) \frac{\xi_1 - \xi_2}{\sqrt{\det g(\xi)}} = 2a^2(\xi, \lambda) \frac{\xi_1 - \xi_2}{\sqrt{\det g(\theta)}} \sin \theta_1 \sin \theta_2.
\]

Each arm of the symmetric Purcell swimmer dissipates energy at the rate

\[
- \int_0^\ell dF(s) \cdot v ds = -k \int_0^\ell ( (t \cdot v)^2 - 2v \cdot v ) ds
\]

\[
= -k \int_0^\ell ( \dot{X}^2 - 2s^2 \dot{\theta}_j^2 \cos^2 \theta_j - 2(s \dot{\theta}_j \sin \theta_j - \dot{X})^2 ) ds
\]

\[
= \frac{k \ell^3}{3} (3x^2 + 2\dot{\theta}_j^2 + 6\dot{\theta}_j x^0).
\]
And the total energy dissipation by the arms is evidently
\[ \frac{2k\ell^3}{3} \left( 6\dot{x}^2 + 2(\dot{\theta}_1^2 + \dot{\theta}_2^2) + 6(\ddot{\xi}_1 + \ddot{\xi}_2)\dot{x} \right). \]  
(2.12)

In a body-less swimmer, \( \lambda = 0 \); this is also the total dissipation, and we consider this case from now on. Since we are interested in the metric up to units, we shall henceforth set \( 4k\ell^3 = 3 \).

Using the swimming equation, equation (2.4), gives \( g : \)

\[ g(\theta) = a(\xi, 0) \left( \frac{5 - 2\xi_2^2 + \xi_1^2}{\sin \theta_1 \sin \theta_2} \sin \theta_1 \sin \theta_2 \right), \quad \xi_j = \cos \theta_j, \]  
(2.13)

and \( a(\xi, 0) \) is given in equation (2.5). In particular, \( g(\theta) \) is a smooth function on shape space, while \( g(\xi) \) is singular at the boundaries. One can now meaningfully plot the curvature (normalized by the determinant of the metric), which is shown in figure 2.

2.4. The optimal stroke

Efficient swimming covers the largest distance for a given energy resource and at a given speed\(^6\). Alternatively, it minimizes the energy needed for covering a given distance at a given speed\(^7\).

Fixing the speed for a given distance is equivalent to fixing the time \( \tau \) it takes to complete a stroke. In this formulation, the variational problem of finding the most efficient stroke takes the form of a problem in Lagrangian mechanics of minimizing the action

\[ \int_0^\tau g_{jk}(\theta) \dot{\theta}_j \dot{\theta}_k \, dt + q \int dx, \]  
(2.14)

where \( q \) is a Lagrange multiplier. \( dx \) is given in equation (2.4). This can be interpreted as the motion of a charged particle on a curved surface in an external magnetic field [15]. Conservation of energy then says that the solution has constant speed (in the metric \( g \)). For a closed path, the kinetic term is then proportional to the length of the path and the constraint is the flux enclosed by it. Thus, the variational problem can be rephrased geometrically as the ‘isoperimetric problem’: find the shortest path that encloses the most flux.

The charged particle moves on a curved surface. What does this surface look like? From the dissipation metric, we can calculate, using the Brioschi formula [16], the Gaussian curvature \( K \) (not to be confused with \( \mathcal{F} \)) of the surface. A plot of it is given in figure 6. Though \( K \) and \( \mathcal{F} \) are both ‘curvatures’, they represent different physics: \( K \) teaches us about the energy dissipation but not about the swimmer’s locomotion. \( \mathcal{F} \), in contrast, teaches us about the distance traveled but not about the energy dissipation.

Inspection of figure 2 suggests that pretty good strokes are those that enclose only one sign of the curvature \( \mathcal{F} \). The actual optimal stroke can only be found numerically. It is plotted in figure 2. The efficiency of this stroke is about the same as the efficiency of the Purcell’s swimmer for rectangular strokes of [4], but less than the optimally efficient strokes found in [3].

\(^5\) An alternate natural normalization is one that preserves the area \( 4\pi^2 \).

\(^6\) One needs to constrain the average speed since one can always make the dissipation arbitrarily small by swimming more slowly.

\(^7\) The distance is assumed to be large compared with a single stroke distance. The number of strokes is not given \textit{a priori}. New Journal of Physics 10 (2008) 063016 (http://www.njp.org/)
Figure 6. The Gaussian curvature on the surface of controls induced by the dissipation metric.

Slender body theory does not allow the arms to get too close. How close they are allowed to get depends on the slenderness $\kappa$. The smallest angle allowed $\delta \theta$ must be such that $(2\delta \theta) \log \kappa \gg 1$. As the optimal stroke gets quite close to the boundary, with $\delta \theta \sim 0.1$ radian, it can be taken seriously only for sufficiently slender bodies with $\log \kappa \gg 5$, which is huge. The optimal stroke is therefore more of mathematical than physical interest. One can use a refined slender body approximation by taking higher orders in Cox’s expansion for the force. This will leave the structure without changes, but will make equations (2.6) and (2.13) much more complicated.

From a mathematical point of view, it is actually quite remarkable that a minimizer exists. By this we mean that the optimal stroke does not hit the boundary of shape space $|\xi_j| = 1$ where slender body theory is squeezed out of existence. This can be seen from the following argument. Inspection of equations (2.10) and (2.13) shows that the curvature vanishes linearly near the boundary of shape space (this is most easily seen in the $\theta$ coordinates). Suppose now that the optimal path runs along the boundary. Shifting the path a distance $\varepsilon$ away from the boundary would shorten it linearly in $\varepsilon$, while the change in the flux integral will be only quadratic. This shows that the path that hits the boundary cannot be a minimizer.

### 3. Purcell’s swimmer

Purcell’s swimmer can move in either direction in the plane and can also rotate. Since the Euclidean group is not Abelian (rotations and translations do not commute), the notion of ‘swimming curvature’ that proved to be so useful in the Abelian case needs to be modified. As we shall explain, landscape figures can be used to give a qualitative geometric understanding of the swimming and, in particular, can be used to answer Purcell’s question ‘What will determine
the direction this swimmer will swim?’. However, unlike the Abelian case, the swimming curvature does not give full quantitative information on the swimming, and one cannot avoid solving a system of differential equations in this case if one is interested in quantitative details.

The location and orientation of the swimmer (in the lab frame) shall be denoted by the triplet $x^\alpha$, where $x^0 = \phi$ is the orientation of the swimmer, see figure 1, and $x^{1,2}$ are Cartesian coordinates of the center of the ‘body’. We use super-indices and Greek letters to designate the response, while lower indices and Roman characters designate the controls $|\theta_j| < \pi$.

3.1. Linear response versus a gauge theory

The common approach to low-Reynolds-number swimming is to write the equations of motion in a fixed, lab frame. We first review this and then describe an alternate approach where the equations of motions are written in a frame that instantaneously coincides with the swimmer.

By the general principles of low-Reynolds-number hydrodynamics, there is a linear relation between the change in the controls $\theta_j$ and the response $d x^\alpha$:

$$d x^\alpha = A^\alpha_j \, d \theta_j , \quad (3.1)$$

(summation over repeated indices implied). Note that $j = 1$ and 2, since there are two controls, while $\alpha = 0$, 1 and 2 for the three responses.

The response coefficients $A$ are functions of both the control coordinates $\theta_k$ and the location coordinates $x^\beta$ of the swimmer in the lab. However, in a homogeneous medium it is clear that $A^\alpha_j$ can only be a function of the orientation $x^0 = \phi$. Moreover, in an isotropic medium it can only depend on the orientation $\phi$ through

$$A^\alpha_j (\phi, \theta) = R^{\alpha\beta}(\phi) A^\beta_j (\theta) ; \quad R^{\alpha\beta}(\phi) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \cos \phi & -\sin \phi \\ 0 & \sin \phi & \cos \phi \end{pmatrix} . \quad (3.2)$$

In the lab frame, the nature of the solution of the differential equations is obscured by the fact that one cannot determine $d x$ independently for different points on the stroke (because of the dependence on $\phi = x^0$). This is a crucial difference from the simple case of the symmetric swimmer which cannot rotate. As a consequence, for the Purcell swimmer $A^\alpha_j$ does not define a function of the control parameters alone. In particular, for a given stroke, a closed path in shape space, this function is only defined on the curve, but does not have a unique extension into the interior of the curve. This has the consequence that Stokes’ theorem cannot be applied in this context.

Since, as in the case of the symmetric swimmer (see the discussion under equation (2.6)), the values of $d x^\alpha$ do not teach us much about the swimmer, we will look for an analogue of $\mathcal{F}$ for Purcell’s swimmer. This can be done in a different coordinate system: the coefficients $A^\alpha_j$ (defined in equation (3.2)) may be viewed as the transport coefficients in a rest frame that instantaneously coincides with the swimmer. They play a key role in the geometric picture that we shall now describe. In the frame of the swimmer one has

$$d y^\alpha = A^\alpha_j \, d \theta_j , \quad (3.3)$$

which is an equation that is fully determined by the controls. The price one pays is that the $d y$ coordinates cannot be simply added to calculate the total change in a stroke $\gamma$, since one has to

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8 All distances are dimensionless being measured in units of arm length $\ell$.

9 In this section, we use the convention the $\theta_1$ increases counterclockwise and $\theta_2$ clockwise.
consider the changes in the reference frame as well. In order to do that, $dy$ must be viewed as (infinitesimal) elements of the Euclidean group

$$E(y^\alpha) = \begin{pmatrix} \cos y^0 & \sin y^0 & y^1 \\ -\sin y^0 & \cos y^0 & y^2 \\ 0 & 0 & 1 \end{pmatrix}. \quad (3.4)$$

The composition of $dy$ along a stroke $\gamma$ is a matrix multiplication

$$E(\gamma) = \prod_{\theta \in \gamma} E(dy^\alpha(\theta)). \quad (3.5)$$

The product is, of course, non-commutative. We denote generators of translations and rotations by

$$e^0 = \begin{pmatrix} 0 & 1 & 0 \\ -1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad e^1 = \begin{pmatrix} 0 & 0 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad e^2 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}. \quad (3.6)$$

They satisfy the Lie algebra

$$[e^0, e^\alpha] = -\varepsilon^{0\alpha\beta} e^\beta, \quad [e^1, e^2] = 0, \quad (3.7)$$

where $\varepsilon^{\alpha\beta\gamma}$ is the completely anti-symmetric tensor. One can write equation (3.3) concisely as a matrix equation

$$dy = A_j d\theta_j, \quad dy = y^\alpha e^\alpha, \quad A_j = A_j^\alpha e^\alpha, \quad (3.8)$$

where $dy$ and $A_j$ are $3 \times 3$ matrices (summation over repeated indices implied).

### 3.2. The swimming curvatures

Once the (six) transport coefficients $A_j^\alpha$ are known, one can, in principle, simply integrate the system of three, first-order, non-linear ordinary differential equations, equation (3.1). This can normally be done only numerically. Numerical integration is practical and useful, but not directly insightful. We want to describe tools that allow for a qualitative understating of swimming in the plane without actually solving any differential equation.

Low-Reynolds-number swimmers perform many mutually canceling maneuvers with a small net effect. The swimming curvature measures only what fails to cancel for infinitesimal strokes. Since reversing a loop reverses the response, it is natural to expect that $\delta y^\alpha$ for a closed (square) loop is proportional to the area form. Integrating equation (3.8) around a closed infinitesimal loop gives

$$\delta y = F d\theta_1 \wedge d\theta_2, \quad (3.9)$$

where

$$F = \partial_1 A_2 - \partial_2 A_1 - [A_1, A_2], \quad F = F^\alpha e^\alpha, \quad \partial_j = \frac{\partial}{\partial \theta_j}. \quad (3.10)$$

$F$ and $\delta y$ are $3 \times 3$ matrices. $F$ has the structure of curvature of a non-Abelian gauge field [17]. In coordinates, this reads

$$F^\alpha = \partial_1 A_2^\alpha - \partial_2 A_1^\alpha + \varepsilon^{0\alpha\beta} \left( A_1^0 A_2^\beta - A_2^0 A_1^\beta \right). \quad (3.11)$$
Figure 7. The failure of Stokes’ theorem in the non-commutative case: the integration on the adjacent segments traversed in opposite senses do not cancel in the non-commutative case.

In the lab coordinates one has, of course,
\[
\delta x^\alpha = \tilde{F}^\alpha d\theta_1 \wedge d\theta_2, \quad \tilde{F}^\alpha = R^{\alpha\beta}(\phi) \mathcal{F}^\beta(\theta),
\]
(3.12)
The curvature is Abelian when the commutator vanishes. This is the case in equation (2.10) and it is also the case for the rotational curvature. The Abelian curvature gives full information on the swimming of finite stroke by a simple application of Stokes’ formula. This is, unfortunately, not the case in the non-Abelian case. One cannot reconstruct the translational motion of a large stroke from the infinitesimal closed strokes \(\delta y\) because Stokes’ theorem only works for commutative coordinates and \(\delta y\) are not. This failure is illustrated in figure 7. (In the \(\delta x\)-coordinates, one cannot reconstruct the displacement by surface integrating equation (3.12), since \(\tilde{F}^\alpha\) depends on \(\phi\), and the knowledge of \(\phi\) along the curve does not determine \(\phi\) in the interior.)

For the Purcell swimmer, \(\mathcal{F}\), although explicit, is rather complicated. Since the dissipation metric is complicated too, we give two plots of \(\mathcal{F}\): figures 3, 4 and 8 give the curvature relative to the flat measure on \((\theta_1, \theta_2)\), and describe how far the swimmer swims for small strokes. In figures 9–11, the curvature is plotted relative to the dissipation measure and it displays the efficiency of small strokes.

3.3. The equations of motion

Using slender body theory, in a manner analogous to what was done for the symmetric swimmer, one can calculate explicitly the force (and torque) on the \(a\)th rod in the form
\[
F_a^\alpha = f_{aj}^\alpha \dot{\theta}_j + f_a^{\beta\alpha} \dot{x}^\beta,
\]
(3.13)
where \(f_{aj}^\alpha\) are explicit and relatively simple functions of the controls (compare with equation (2.3)). The swimming equation is then given by
\[
\sum_a F_a^\alpha = \left( \sum_a f_{aj}^\alpha \right) \dot{\theta}_j + \left( \sum_a f_a^{\alpha\beta} \right) \dot{x}^\beta = 0.
\]
(3.14)
Figure 8. The landscape of the $y$-curvature for Purcell's swimmer with $\lambda = 0.75$. The curvature is given relative to the flat measure in $(\theta_1, \theta_2)$.

Figure 9. The rotation curvature for Purcell's three-linked swimmer with $\lambda = 2$, plotted using the measure induced by dissipation.

This reduces the problem of finding the connections $A$ to a problem in linear algebra. Formally

$$A^\beta_j = \left( \sum_a f^\beta_a \right)^{-1} \left( \sum_a f^\alpha_j \right),$$

(3.15)
Figure 10. The $x$-curvature relative to the dissipation metric and the optimal efficient stroke found by Tam and Hosoi [3].

where the bracket on the left is interpreted as a $3 \times 3$ matrix, with entries $\alpha, \beta$, and the inverse means an inverse in the sense of matrices. Although this is an inverse of only a $3 \times 3$ matrix, the resulting expressions are not very insightful. We spare the reader this ugliness which is best done using a computer program.

3.4. Symmetries

Picking the center point of the body as the reference fiducial point is, in the terminology of Wilczek and Shapere [12], a choice of gauge. This particular choice is nice because it implies symmetries of the connection $A$ [3, 4]. Observe first that the interchange $(\theta_1, \theta_2) \rightarrow (-\theta_2, -\theta_1)$ corresponds to a rotation of the swimmer by $\pi$. Using this in equation (3.2), one finds

$$A^\beta_1(\theta_1, \theta_2) = \begin{cases} + A^\beta_2(-\theta_2, -\theta_1), & \beta = 0; \\ - A^\beta_2(-\theta_2, -\theta_1), & \text{otherwise}. \end{cases}$$

(3.16)

This relates the two halves of the square divided by the diagonal $\theta_1 + \theta_2 = 0$.

A second symmetry comes from the interchange $(\theta_1, \theta_2) \rightarrow (\theta_2, \theta_1)$ corresponding to the reflection of the swimmer around the central vertical of the middle link. Some reflection shows then that

$$A^\beta_1(\theta_1, \theta_2) = \begin{cases} + A^\beta_2(\theta_2, \theta_1), & \beta = 2; \\ - A^\beta_2(\theta_2, \theta_1), & \text{otherwise}. \end{cases}$$

(3.17)

This relates the two halves of the square divided by the diagonal $\theta_1 = \theta_2$.

The symmetries can be combined to yield the result that $A^0$ and $A^2$ are anti-symmetric and $A^1$ is symmetric under inversion

$$A^\beta_j(\theta) = - A^\beta_j(-\theta), \quad A^1_j(\theta) = A^1_j(-\theta), \quad A^2_j(\theta) = - A^2_j(-\theta).$$

(3.18)
3.5. Rotations

The rotational motion of Purcell’s swimmer, in any finite stroke, is fully captured by the Abelian curvature

$$F^0 = \mathcal{F}^0 = \partial_1 A^0_2 - \partial_2 A^0_1.$$  \hfill (3.19)

This reflects the fact that rotations in the plane are commutative.

The symmetry of equation (3.16) implies

$$(\partial_2 A^0_1)(\theta_1, \theta_2) = (\partial_1 A^0_2)(-\theta_2, -\theta_1),$$  \hfill (3.20)

and this says that $\mathcal{F}^0$ is anti-symmetric under reflection in the diagonal $\theta_1 + \theta_2 = 0$. Similarly, equation (3.21) implies

$$(\partial_2 A^0_1)(\theta_1, \theta_2) = -(\partial_1 A^0_2)(\theta_2, \theta_1),$$  \hfill (3.21)

and this says that $\mathcal{F}^0$ is symmetric about the line $\theta_1 = \theta_2$. Figure 5 is a plot of the curvature and it clearly has the requisite symmetries.

The total curvature associated with the full square of shape space vanishes (by symmetry). For $\lambda = 2$, one can see in figure 3 three positive islands surrounded by three negative lakes. The total curvature associated with the three islands is quite small, about $0.1$. This means that the Purcell swimmer with $\lambda = 2$ turns only a small fraction of a circle in any full stroke.

3.6. Translation

The curvatures corresponding to the two translations of a swimmer with $\lambda = 0.75$ are shown in figures 4, 8, 10 and 11 (here, we use $\lambda = 0.75$ for comparison with [3]). The symmetries of the figures are a consequence of equations (3.16) and (3.21). From the first we have

$$(\partial_2 A^\beta_1)(\theta_1, \theta_2) = -(\partial_1 A^\beta_2)(-\theta_2, -\theta_1), \quad \beta = 1, 2,$$  \hfill (3.22)
which implies that $\mathcal{F}^{1,2}$ are symmetric under reflection in the diagonal $\theta_1 + \theta_2 = 0$. Similarly, from equation (3.21), we have

\[
(\partial_2 A^\beta_1)(\theta_1, \theta_2) = \begin{cases} 
+ (\partial_1 A^2_2)(\theta_2, \theta_1), & \beta = 2; \\
- (\partial_1 A^1_2)(\theta_2, \theta_1), & \beta = 1.
\end{cases}
\]

(3.23)

This says that $\mathcal{F}^1$ is symmetric and $\mathcal{F}^2$ is anti-symmetric under reflection in the diagonal $\theta_1 = \theta_2$.

The curvatures for the translations are non-Abelian and cannot be used to calculate the swimming distances for finite strokes because Stokes’ theorem fails.

4. Qualitative analysis of swimming

4.1. When is a stroke small?

The landscape figures for the translational curvatures provide precise information on the swimming distance for infinitesimal strokes. They are then also useful for characterizing small strokes. The question is how small is small? For a stroke of size $\epsilon$, the controls are of size $\delta \theta = O(\epsilon)$ and the swimming distance measured by the curvature is $O(\mathcal{F}\epsilon^2)$. The error in this has terms of the form $O(A\mathcal{F}\epsilon^3)$. This suggests that the relative error in the swimming distance as measured in a finite stroke is of the order of $O(A\epsilon)$. Hence, a stroke is small provided $|A\epsilon| \ll 1$. Clearly, a Purcell swimmer swims substantially less than an arm length as the arm moves. This shows that $|A| \ll 1$ and so strokes of the order of a radian can be viewed as small strokes.

A radian is the scale of the structures in the landscape of the figures of the curvature. This means that the landscape carries qualitative information about the swimming of moderate strokes.

4.2. $x$ versus $y$

The $x$-curvature is symmetric under inversion

\[
\mathcal{F}^1(\theta) = \mathcal{F}^1(-\theta).
\]

(4.1)

Since both $A^0$ and $A^2$ are anti-symmetric under inversion, one sees that the non-Abelian part of the $x$-curvature is of the order of $O(\theta^2)$ near the origin. The $x$-translational curvature, which is non-zero near the origin, is almost Abelian for small strokes.

The $y$-curvature, in contrast, is anti-symmetric under inversion

\[
\mathcal{F}^{1,2}(\theta) = - \mathcal{F}^{2,1}(-\theta)
\]

(4.2)

and so vanishes linearly at the origin. The non-Abelian part is also anti-symmetric under inversion, and it too vanishes linearly. The $y$-curvature is therefore not approximately Abelian for small strokes, but is small.

4.3. Which way does a swimmer swim?

The swimming direction can be easily determined for those strokes that are in a region where the translational curvature has a fixed sign. This answers Purcell’s question for many strokes. Strokes that enclose both signs of the curvature are subtle.

There are also terms of the form $O(A^3 \epsilon^3)$.
4.4. Subtle swimmers

Purcell’s swimmer can reverse its direction of propagation by increasing the stroke amplitude [4]. This can be seen from the landscape diagram, figure 4: small square strokes near the origin sample only slightly negative curvature. As the stroke amplitude increases, the square gets larger and begins to sample regions where the curvature has the opposite sign, eventually sampling regions with substantial positive curvature.

4.5. Optimal distance strokes

The curvature landscapes are useful when one wants to search for optimal strokes as they provide an initial guess for the stroke. (This initial guess can then be improved by standard optimization numerical methods.)

For example, Tam and Hosi [3] looked for strokes that cover the largest possible distance. For strokes near the origin, a local optimizer is the stroke that bounds the approximate square blue region in figure 4 (in this case $\lambda = 0.75$).

4.6. Efficient strokes

The curvature normalized by dissipation, figure 10 gives a guide for finding efficient small strokes. Care must be taken, since while the displacement can be approximated from the surface area, the energy dissipation is proportional to the stroke’s length and not the stroke’s area. In regimes where the Gaussian curvature of the dissipation (figure 12) is positive, it is possible to have strokes with small length which bound a large area. In the case of Purcell’s swimmer, this suggests two possible regimes: around the origin and the positive curvature island in the

**Figure 12.** The Gaussian curvature induced by the dissipation metric of Purcell’s swimmer.
upper left (lower right) corner of figure 12. The optimizer near the origin is the optimal stroke found in [3], while the optimizer in the upper left corner [18]—although more efficient (note the values of $\frac{\sqrt{\det g(\theta)}}{\sqrt{\det g(\theta)}}$ in figure 11)—is of mathematical interest only, since it is near the boundary, where the first-order slender body approximation, equation (2.1), is relevant only for extremely slender bodies.

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