Swimming at Low Reynolds Number

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Abstract

The characteristic length of many microorganisms is such that the hydrodynamic interaction with their surroundings is governed by the equation for Stokes flow. In this paper, I present a computational model for calculating the flow generated by a simple microorganism utilizing a rotating motor and a number of connected, rigid rods to induce locomotion. The efficiency of several flagella combinations is presented.

Introduction

Since the introduction of the now famous Scallop Theorem [2], a number of interesting questions about low Reynolds number swimming have been asked. One of the more interesting questions is: what types of flagellar tail combinations induce locomotion? Let's start with the famous Naviér-Stokes equation for incompressible fluids ($\nabla \cdot u = 0$)

$$\nabla p = \mu \nabla^2 u - \rho \left(\frac{\partial u}{\partial t} + (u \cdot \nabla) u \right),$$

where p is the pressure, μ is the fluid viscosity, ρ the fluid density (inertial force multiplier) and u is the velocity of the flow. This equation can be made dimensionless through the introduction of the Reynolds number $R \equiv \frac{\rho L U}{\mu}$, where L and U represent the characteristic length and velocity, respectively, for a given problem. For microorganisms, the characteristic lengths and velocities are very small, meaning that the inertial term in the Naviér-Stokes equation becomes negligible. The resulting equation governing low Reynolds number flow becomes

$$\nabla p = \mu \nabla^2 u,$$

which is known as the Stokes equation.

Since the ∇^2 operator acting on u is linear, the viscous force exerted on a fluid by a low Reynolds number swimmer scales directly with the stroke velocity applied by the swimmer.

The consequence is that the rate at which a flagellar tail rotates does *not* enable it to move faster through a viscous fluid. Take, for example, a simple scallop. The scallop opens and closes via a spring mechanism connecting its upper and lower halves. This represents a one degree of freedom system. The scallop can either increase or decrease the rate at which it opens and closes and yet it will be unable to propel itself through a viscous fluid since the fluid will apply an equal and opposite force to balance. In order to move, a system must utilize multiple degrees of freedom. One simple organism to consider would be a rigid rod connected by two motors each capable of applying torques in any direction; see Figure 1.

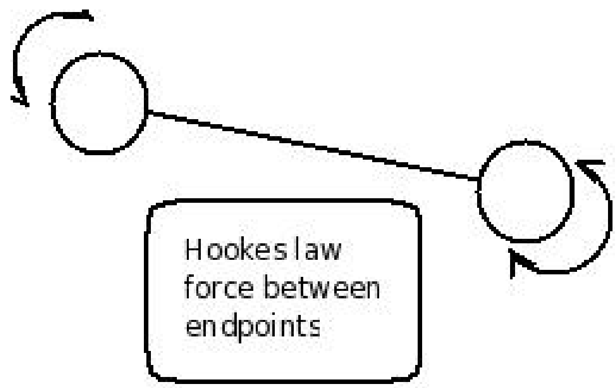

Figure 1: Example of a low Reynolds number swimmer

The fluid flow will arrange itself to balance viscous forces with those generated by torques applied at each endpoint. The resulting flow, since the organism has two degrees of freedom, will exert different forces at different points along the organism which, after integration, result in net displacement of the organism from its original position. To extend the argument further, it is possible to change the magnitudes and directions of the torque so that the organism can move in *any* desired direction. While this simple example illustrates an organism which can move in any direction, there may be more efficient combinations; i.e. organisms which can move farther in a shorter amount of time.

This paper focuses on the numerical simulation of different flagella that are composed of multiple rods interacting with one another and the surrounding fluid via Hooke's law forces and applied torques. Each rod introduces a new degree of freedom to the system, as does each applied torque. The focus is specifically on an organism with torque application at one point (the head of the flagella) and connected rods. This simple microorganism is simulated using different flagellar combinations. The output of this paper is the efficiency of each flagellar combination; quantified as the distance traveled as a function of the number of motor cycles underwent.

Theory

The dimensionless Stokes equation for incompressible flows is

$$0 = -\nabla P + \nabla^2 \mathbf{u} + \mathbf{f} \quad (1)$$

$$0 = \nabla \cdot \mathbf{u} \quad (2)$$

where P is the dimensionless pressure, $\mathbf{u}$ the dimensionless flow velocity, and $\mathbf{f}$ the dimensionless force.

The solution of (1),(2) comes in the form of Stokeslets and Rotlets [1], which assume point forces and torques,

$$\mathbf{U}_s(\mathbf{x}; \mathbf{x}_0, \mathbf{f}_0) = \frac{\mathbf{f}_0}{8\pi r} + \frac{[\mathbf{f}_0 \cdot (\mathbf{x} - \mathbf{x}_0)](\mathbf{x} - \mathbf{x}_0)}{8\pi r^3} \text{ (Stokeslet)} \quad (3)$$

$$\mathbf{U}_r(\mathbf{x}; \mathbf{x}_0, \mathbf{L}_0) = \frac{\mathbf{L}_0 \times (\mathbf{x} - \mathbf{x}_0)}{8\pi r^3} \text{ (Rotlet).} \quad (4)$$

In the above constructions, $r = ||\mathbf{x} - \mathbf{x}_0||_2$ and $\mathbf{f}_0$ and $\mathbf{L}_0$ represent force and torque, respectively, applied at point $\mathbf{x}_0$. Since it is desirable to evaluate the flow arbitrarily close to the points where the forces and torques are applied, it is clear that the above construction will lead to unacceptable singularities in the flow. In addition, real flagellar tails have non-zero cross-sectional area, which will lead to forces and torques that are not applied at a singular point. The way to remove these singularities is through the introduction of a "spread" to the forces and torques applied. This spread is chosen to match the cross-sectional area of a flagella.

First, we select a cutoff function that (*i*) is radially symmetric and (*ii*) defines a delta function in the limiting case as the spread goes to 0. A suitable such cutoff function is

$$\phi_\delta(\mathbf{x}) = \frac{15\delta^4}{8\pi(r^2 + \delta^2)^{7/2}}$$

It is clear that (*i*) is satisfied. By inspection, $\lim_{\delta \to 0} \phi_\delta(0) \to \infty$ and

$$\int_{\mathbb{R}^3} \phi_\delta(\mathbf{x}) d\mathbf{x} = 1$$

which shows (*ii*) holds. Convolving this cutoff function with (3) and (4) yields the *regularized* Stokeslet and Rotlet

$$\mathbf{U}_{\delta,s}(\mathbf{x}; \mathbf{x}_0, \mathbf{f}_0) = \frac{\mathbf{f}_0(r^2 + 2\delta^2)}{8\pi(r^2 + \delta^2)^{3/2}} + \frac{[\mathbf{f}_0 \cdot (\mathbf{x} - \mathbf{x}_0)](\mathbf{x} - \mathbf{x}_0)}{8\pi(r^2 + \delta^2)^{3/2}} \text{ (Stokeslet)} \quad (5)$$

$$\mathbf{U}_{\delta,r}(\mathbf{x}; \mathbf{x}_0, \mathbf{L}_0) = \frac{(2r^2 + 5\delta^2)}{16\pi(r^2 + \delta^2)^{5/2}}[\mathbf{L}_0 \times (\mathbf{x} - \mathbf{x}_0)] \text{ (Rotlet).} \quad (6)$$

For non-zero δ the regularized Stokeslet and Rotlet remove the singularities induced in the solution to (1), (2).

Numerical Setup

Since the Stokes equation is linear, its solution can be represented as a superposition of each solution for a given Stokeslet and/or Rotlet combination, that is

$$\mathbf{U}(\mathbf{x}) = \sum_{i=1}^{N_r} \mathbf{U}_{\delta,r}(\mathbf{x}; \mathbf{x}_i, \mathbf{L}_i) + \sum_{j=1}^{N_s} \mathbf{U}_{\delta,s}(\mathbf{x}; \mathbf{x}_j, \mathbf{f}_j).$$

N_r and N_s represent the number of Rotlets and Stokelets, respectively.

In this paper, I assume a system of rigid rods of constant unstretched lengths are connected together to form a flagellum; see Figure 2. Applying a constant motor torque at the head

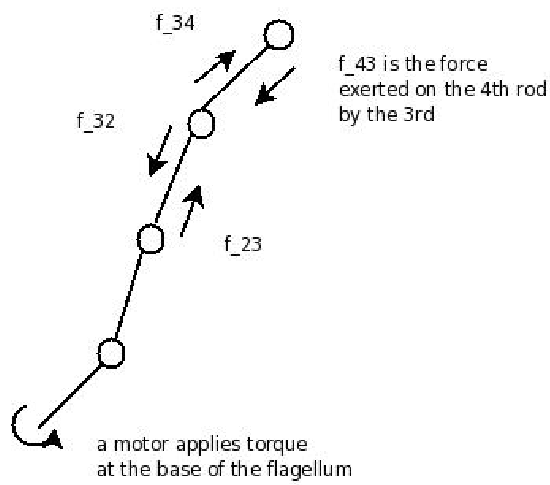

Figure 2: Example of simulated flagellum

of the first rod activates Hooke's law forces between each pair of points connected by rigid rods (high spring constant k) obeying

$$\begin{aligned} \mathbf{f}_{jk} &= \frac{k}{L_0^{jk}}(L^{jk} - L_0^{jk})\frac{(\mathbf{x} - \mathbf{x}_0)}{L^{jk}} \\ \mathbf{f}_{jk} &= -\mathbf{f}_{kj} \\ L^{jk} &= ||\mathbf{x}_k - \mathbf{x}_j||_2, \end{aligned}$$

where $\mathbf{f}_{jk}$ is interpreted as the force acting on the k^{th} particle as a result of the j^{th} particle's interaction, L^{jk} is the length of the rod connecting the k^{th} particle to the j^{th} particle and L_0^{jk} is the rest length of the rod connecting the k^{th} particle to the j^{th} particle. This paper is concerned with the case of one motor driving varying numbers of flagellar tails.

For the numerical implementation of a one-motor flagellum consisting of N_s rods, the flow field can be time-evolved for any point $\mathbf{x}_k$ by

$$\mathbf{U}(\mathbf{x}_k) = \frac{d\mathbf{x}_k}{dt} = \mathbf{U}_{\delta,r}(\mathbf{x}_k; \mathbf{x}_0, \mathbf{L}_0) + \sum_{j=1}^{N_s} \sum_{\text{nearest neighbors } (l)} \mathbf{U}_{\delta,s}(\mathbf{x}_k; \mathbf{x}_j, \boldsymbol{f}_{jl}).$$

The resulting ODE is solved using a Runge-Kutta 4^{th} order integrator. Since the rod endpoint positions will change at each timestep and a finite spatial mesh width must be assumed for numerical integration, a 3D interpolator needs is used evaluate the flow velocity at each rod endpoint. The specific interpolation scheme used is **Matlab**'s 3D spline interpolator.

From previous results [1], the error from regularization of the Stokeslet (the addition of the spread across spatial extent δ) is $\mathcal{O}(\delta) + \mathcal{O}(\Delta s^2/\delta^3)$ near the body, where Δs^2 is a discrete element of area on the body (flagellum). Away from the body, the error decreases to $\mathcal{O}(\delta^2) + \mathcal{O}(\Delta s^2/\delta^3)$. Previous papers have used small $\delta(\sim .01)$ and correspondingly small Δs^2 to ensure the force and torque applications are point-like and the regularization method converges.

Results

The simulation setup parameters are summarized in Table 1. All of the parameters are dimensionless.

Table 1: Simulation Parameters

Parameter	Value
δ	0.052
motor torque (L_0)	.01
spring constant (k)	1000
rod length	0.01
time step (dt)	0.01

I will begin with the simple case of a flagellum consisting of one rod. Once the motor starts turning, the flow field is dominated by the Rotlet generated by the motor torque applied. As such, it is expected that the streamlines of the flow will be circular. Figure 3 shows this behavior

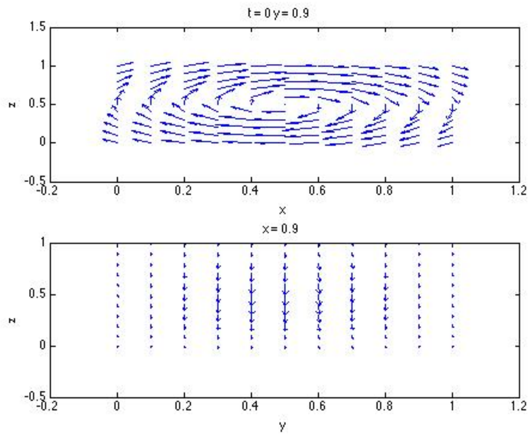

Figure 3: Streamlines at first time step

From Figure 3, we see that, if the only contribution to the flow is the Rotlet from the motor at the base of the flagellum, the flow is circular and the organism will not be capable of aperiodic motion. This is a direct consequence of the Scallop Theorem. However, for the case being studied, the motor torque activates a spring-like force in the rod it is stirring. This force then influences the flow via its Stokeslet interaction with the fluid. The time-evolved flow incorporating this force's interaction, coupled with the motor torque interaction, is shown in Figure 4.

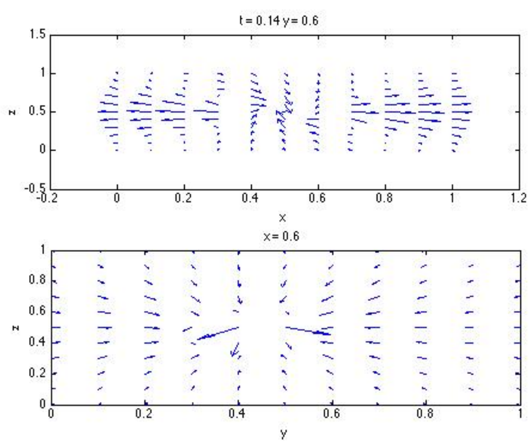

Figure 4: Streamlines at intermediate time step

From Figure 2, the flow is no longer circular. The streamlines now point forward, indicating that the flow induced by the flagellum propels the organism forward. By introducing the possibility of deformation of shape of the rod (i.e. bending the rod in spring-like manner), the organism is now able to propel itself forward in a highly-viscous fluid. The natural question that arises now is: How does the introduction of more rods affect the efficiency of the flagellum? Put another way: Do more rods lead to more forward motion?

The question of efficiency is most easily answered by setting up a numerical experiment. Let's consider the case of constant unstretched flagellar length (the same as is found in Table 1), but with different numbers of rods making up that length. In order to measure efficiency, the introduction of a dimensionless period, defined by

$$\text{number of cycles} = \frac{1}{2\pi}\frac{1}{2}L_0 t^2$$

is made. Figure 5 shows the efficiency of several configurations.

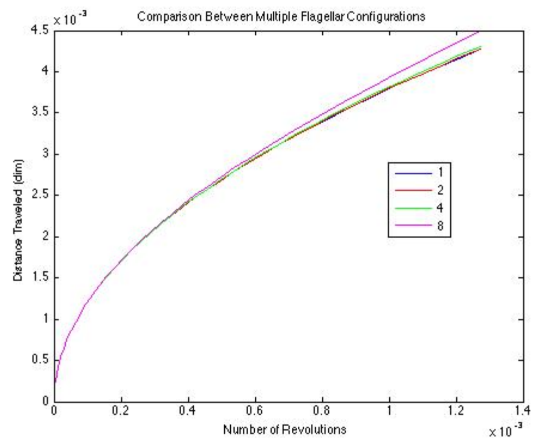

Figure 5: Efficiencies of 1,2,4 and 8 rod configurations

Intuitively, it makes sense that more rods, initiating more hydrodynamic force interactions, lead to greater forward motion.

Conclusion

The equation of motion for a low Reynolds number fluid is presented along with its closed form solutions in terms of Stokeslets and Rotlets. Numerical experiments were executed showing the Scallop Theorem and its consequences to low Reynolds number swimmers. It was shown that the incorporation of more rods in flagella of common length leads to greater forward motion.

References

[1] Flores, H., Lobaton, E., Méndez-Diez, S., Tlupova, S, Cortez, R., 2005. *A study of bacterial flagellar bundling*. Bulletin of Mathematical Biology. 67, 137-168.

[2] Purcell, E.M., 1977. *Life at Low Reynolds Number*. American Journal of Physics. 45, 3-11.