Optimization of Flagellar Locomotion in the low Reynolds Number Regime

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Contents

1 Abstract

This report investigates the computational and theoretical techniques - modeled by E. Lauga and C. Eloy - used to optimize the shape of an activated flagellum for enhanced cell motility. Cell motility is ubiquitous and has a large affect on biological systems such as marine life ecosystems, reproduction, and infection. The physical principles governing flagellar propulsion are explored using computational fluid dynamics simulations, mathematical modeling, and the sequential quadratic programming (SQP) optimization algorithm. Through iterative refinement, we can identify optimized flagellar shapes that would minimize the energetic cost dependent on a single dimensionless sperm numbers (Sp). The computation of the optimum shapes are discretized into a series of Fourier modes that are parameterized by Sp. This research provides valuable insights into the design principles underlying efficient flagellar locomotion, with potential applications in biophysics.

2 Introduction

Flagellum locomotion in low Reynolds number environments is a captivating phenomenon that plays a significant role in various biological processes. The fluid dynamics at low Reynolds numbers - referring to a flow regime where the viscous forces dominate over inertial forces - presents a challenge for the mechanics of locomotion of a biological swimmer. At this scale using work to impart momentum to the surrounding particles as a mechanism of propulsion within the liquid will not work because the resistance of the liquid is too high. Uncovering this challenge necessiates a deep understanding of fluid dynamics, so first I will illuminate the relevant physical principles.

To clarify, a flagellum is a slender appendage found in many microorganisms and some specialized cells of larger organisms where the primary function of a flagellum is locomotion, allowing the organism, or cell, to move through fluid. The figure below shows various microscopic swimmers whereby the locomotion is governed by flagellar motion.

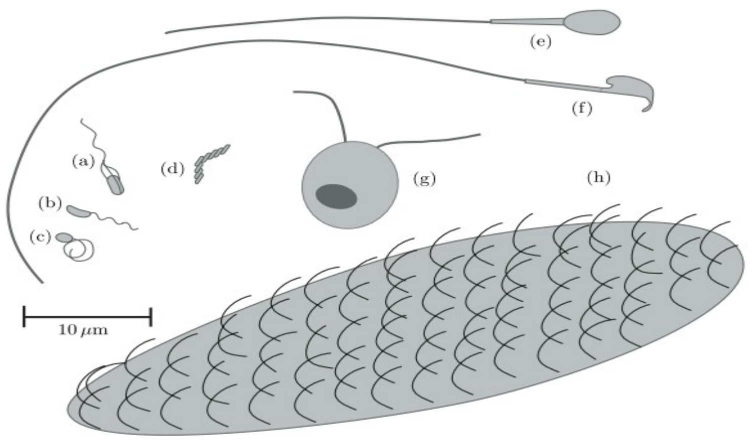

Figure 1. Sketches of microscopic swimmers, to scale. (a) *E. coli*. (b) *C. crescentus*. (c) *R. sphaeroides*, with flagellar filament in the coiled state. (d) *Spiroplasma*, with a single kink separating regions of right-handed and left-handed coiling. (e) Human spermatozoon. (f) Mouse spermatozoon. (g) *Chlamydomonas*. (h) A smallish *Paramecium*.

Figure 1

E. Lauga and T. Powers The hydrodynamics of swimming microorganism [2]

Flagellar kinematics involves the response to external forces and the hydrodynamic environment. Because low Reynolds numbers ensure an absence of inertial forces, the Stokes equations are time-reversible and thus any reversible flagellar deformation would result in no average locomotion. In reality, flagella are capable of achieving directed motion and generating propulsion, despite the absence of inertial forces. The key factors that break the time-reversibility and allows for net locomotion in flagella is the presence of internal molecular motors and the fluid-structure interactions that occur at a microscopic scale. Lauga E. (2011) [2] shows that the deformation of the flagellum is represented as a travelling wave and point out the dominant forces governing locomotion as the viscous drag and the elastic-structure force.

The optimization criterion is to compute a deformation or waveform of the flagellum that is constrained at a constant Sp so that the swimming efficiency is maximized. The Sp represents the ratio between the curvilinear wavelength of the flagellum and the elasto-viscous persistence length. The elasto-viscous persistence length represents the length scale over which the flagellum's elasticity and the surrounding fluid's viscosity interact. In short, the Sp is a measure of the flagellum's flexibility and the resistance to bending due to the viscous forces of the surrounding fluid, which characterizes the balance between the flagellum's ability to deform elastically and the resistance to this deformation by the surrounding fluid's viscosity.

The swimming efficiency is a ratio that measures the amount of locomotive work to the total energy that the flagellum uses. The locomotive work is defined as the mechanical work done by the flagellum to generate propulsion through the fluid. This mechanical work is associated with the interaction between the flagellum and the surrounding fluid as the flagellum moves in a wave-like pattern, it creates hydrodynamic forces that act on the fluid. These forces, in turn, generate thrust or propulsion, allowing the flagellum to move through the medium. Whereas the total energy expended by the flagellum includes not only the locomotive work but also other energy components associated with its motion. It encompasses the energy required for the flagellum to deform and generate the wave-like motion, as well as the energy dissipated due to fluid viscosity and internal resistive forces in the flagellum itself.

To computationally optimize the shape of an activated flagellum, the SQP algorithm is employed. SQP is a numerical optimization method that iteratively searches for the optimal shape of the flagellum deformation by minimizing a cost function where the optimum is found to be the global maximum of the swimming efficiency. In this case, the cost function is the energetic cost, which is inversely proportional locomotive efficiency. The energetic cost is the work produced by the power of activated internal motors of the flagellum. This energy is irreversible as it dissipates into the surrounding fluid. So by integrating the SQP algorithm with computational simulations, we can explore and refine time-varying flagellar shapes to achieve enhanced locomotion performance.

Altogether, the principles of hydrodynamic interactions between the flagellum and the surrounding fluid, the influence of flagellar geometry on propulsive forces, and the effect of fluid viscosity guide the modeling procedures outlined in Mathematical Models below. By taking these principles into account, we can guide the optimization process at constant Sp, which will be expressed in terms of Λ, the curvilinear length over one wavelength of deformation, see fig. (3). To visualize the propulsive mechanisms of flagellar locomotion the diagram below shows the driving force: the drag-based thrust along the length of the flagellum dependent on the angle, θ, that subtends between fluid velocity along any point on the flagellum and the tangential vector along the length of the flagellum.

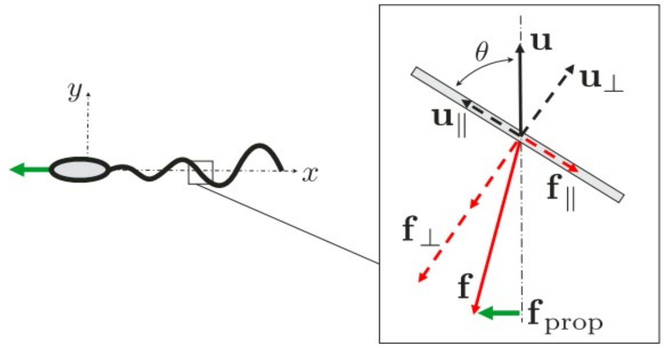

Figure 2. Physics of drag-based thrust: the drag anisotropy for slender filaments provides a means to generate forces perpendicular to the direction of the local actuation (see text for notation).

Figure 2

E. Lauga and T. Powers The hydrodynamics of swimming microorganism [4]

3 Mathematical Models

Quantifying the mechanics of locomotion relies on the application of resistive force theory and the elastohydrodynamic model. Resistive force theory considers the flagellum as a slender, flexible structure subjected to viscous drag forces. The resistive force incorporates the hydrodynamic interactions between the flagellum and the surrounding fluid taking into account the fluid flow around the flagellum during locomotion. The latter model combines the elasticity of the flagellum with hydrodynamic interactions and considers the flagellum as an elastic structure capable of bending and deforming in response to the fluid forces.

3.1 Kinematics of locomotion: Resistive Force Theory

The deformation is quantified into components of curvilinear coordinate unit-vector $\hat{\mathbf{s}}$, the curvilienar wavelength Λ, the swimming speed (U) and wavespeed (V).

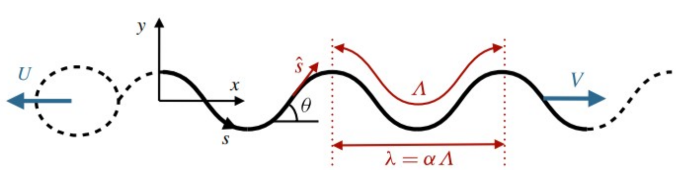

FIGURE 1. Mathematical model and notation. We consider an infinite planar flagellum of wavelength λ along x, with curvilinear coordinate s and tangent unit vectors $\hat{s}$. The wavespeed is denoted V in the $+x$ direction and the flagellum is assumed to be swimming with speed $-U$. The wavelength measured along the curvilinear direction is $\Lambda \equiv \lambda/\alpha$ $(\alpha \leqslant 1)$.

Figure 3

E. Lauga and C. Eloy Shape of optimal active flagella [3]

To compute fluid velocity with repsect to the flagellum the no-slip boundary condition is imposed so that the fluid velocity at the boundary of the flagellum is zero, meaning that the fluid particles adjacent to the surface do not slip along the surface of the flagellum but move with the same velocity as the surface itself.

$$\mathbf{u} = (V - U)\hat{\mathbf{x}} - c\hat{\mathbf{s}} \tag{1}$$

Eqn. 1 specifies the velocity of the fluid and the flagellum in the lab frame that is attached to the fluid at infinity at any given point along the backbone of the flagellum. With this, we can set up the general expression for the viscous forces acting locally along the flagellum as an approximation of the leading order term of the slender-body theory (Cox 1970) [1].

$$\mathbf{F} = \xi_{\perp}\mathbf{u} + (\xi_{\|} - \xi_{\perp})\hat{\mathbf{s}}\hat{\mathbf{s}} \cdot \hat{\mathbf{u}} \tag{2}$$

Here $\xi_{\perp}$ and $\xi_{\|}$ represent the resistance coefficients of the fluid. Substituting $\mathbf{u}$, we can obtain the viscous force per unit length (along the backbone of the flagellum) in terms of U and V. Following the model of E. Lauga and C. Eloy (2013), the free-swimming condition, as it is described in Lighthill (1975), enforces that the net force in both the x and y directions are zero as result of the low Reynold's number approximation.

3.2 Energetics: Elastohydordynamics

Elastodynamics plays a crucial role in understanding the bending and deformation of the flagellum during its undulatory motion. The flagellum is considered as a flexible rod that undergoes complex bending and shape changes as it propels. We will use Kirchhoff's equations to provide the mathematical framework to analyze the mechanics of deformation. These equations provide a static equilibrium condition for the forces and torques applied to the center of mass of an elastic rod. One approach to derive these equations is to consider the forces and torques applied to a solid rod of infinitesimal length ds, (see figure 4 below).

3.2.1 Interpretation of Kirchhoff's equations for small an elastic rod

Interpreting Kirchhoff's equations involves recognizing the roles of forces and torques applied to a solid rod. In static equilibrium both the net force and net torque applied to the center of mass of the rod must be zero. Kirchhoff's equations seek to balance the external and internal forces and torques. In this case the external force refers to the hydrodynamic force per unit length applied to the flagellum and the internal force refers to the response upon deformation from the external force and external torque. This "response" is characterized in twofold: (1) bending and (2) stretching of the flagellum. The bending torque is responsible for maintaining the curvature of the flagellum and resisting any changes in its shape. The magnitude of the bending force depends on the curvature of the flagellum, its flexural rigidity (related to the material properties and cross-sectional geometry), and the rate of change of curvature along the flagellum. The stretching force is present when the flagellum experiences stretching or extension and arises due to the resistance of the flagellum's material to deformation which is held together by molecular bonds. The stretching forces depend on the elongation or compression of the flagellum and the material properties, such as its Young's modulus.

I will use the notation $\mathbf{F}$, $\mathbf{T}$, $\mathbf{M}$ for the external force, internal tension (force due to internal stress), bending moment (torque due to internal forces); see figure below. Below displays the mechanics of the forces and bending moments acting upon an elastic rod of infinitesimal length ds.

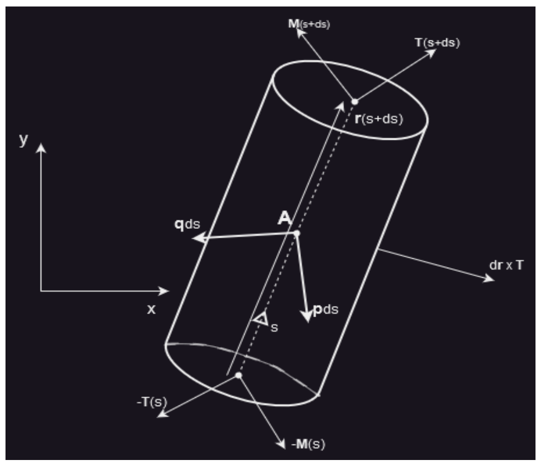

Figure 4: Forces and torques acting on a small cylindrical element length ds sketch created by author

So considering this small segment of a solid rod the forces and torques are evaluated along the curvilinear central line, on $\mathbf{r}(s)$. This small segment is subject to internal forces that react upon deformation and are applied at the boundaries on the segment. At the top cross-section, $\mathbf{r}(s+ds)$, the internal tension applied is denoted as $\mathbf{T}(s+ds)$, and the torque associated to the internal force at this point is denoted as $\mathbf{M}(s+ds)$. Now examining the bottom cross-section the bending moment from a neighboring element, ds', is $-\mathbf{M}(s)$ and likewise the internal tension is $-\mathbf{T}(s)$. Both the bending moment and internal tension at the bottom are opposing quantities that react to an external force applied to an adjacent chunk, ds'. The external force at the segment ds is applied to all points of matter that constitute this rod, so, therefore, this force denoted as $\boldsymbol{\rho} ds$ – where $\boldsymbol{\rho}$ is the external force per unit length – that acts on the center of mass of segment ds. The sum of internal forces from both ends of this chunk can take the form:

$$\frac{d\mathbf{T}}{ds} = \mathbf{T}(s+ds) - \mathbf{T}(s) \tag{3}$$

Here we can interpret the total internal tension as a sum of all internal-force-pairs for every segment ds along the flagellum. Referring to the internal force of the chunk as the ‘‘internal tension'' is misleading because the internal force really includes a linear superposition of two modes of deformation of a solid rod.[1] This means that the internal force is a sum of different types of forces that exist upon deformation: these are forces due to curvature about the x and y axis of the rod. Thus, we can conceptualize ‘‘tension'' as the stretching or bending in two dimension of molecular bonds that bind the solid rod together. Kirchhoff's equations state that the sum of the internal forces and the sum of the external forces must balance each other to maintain static equilibrium. The equilibrium condition involves considering the forces acting in only two directions as the rod is considerably thin compared to its length, resulting in a slender rod or filament-like geometry.

A. Forces in the x-direction:

The sum of the internal forces and the external forces in the x-direction should be zero. This condition arises from the conservation of momentum upon deformation and the viscous response, resulting in no net force in the x-direction.

B. Forces in the y-direction:

The sum of the internal forces and the external forces in the y-direction should also be zero. This condition ensures the balance of forces perpendicular to the flagellum's motion.

Writing out these sums yields a differential equation that says the total internal tension per unit length ds must balance with the external force acting upon the small chunk.

$$\mathbf{T}'ds + \boldsymbol{\rho} ds = 0 \tag{4}$$

Upon integration this equation says the magnitude of total internal tension must equal the magnitude of the total external force upon equilibrium.

Now consider the net torque on the rod. The torque due to the internal forces applied on the top cross-section $\mathbf{M}(s + ds)$ is calculated with respect to the center of mass of that cross-section. However, when calculating the torque with respect to point A, there is a difference due to the non-zero resultant of the internal force over this face given by: (1) $\mathbf{M}(s + ds) + (d\mathbf{r}/2) \times \mathbf{T}(s + ds)$. Similarly, considering the contribution of the bottom cross-section, this part ‘‘feels'' the external force applied onto the neighboring element ds', so we are left with: (2) $-\mathbf{M}(s) + (-d\mathbf{r}/2) \times -\mathbf{T}(s)$. These internal torques in the flagellum arise from the bending

[1] B. Audoly Y. Pomeau Elasticity and Geometry : From Hair Curls to the Non-linear Response of Shells pg.85-86

or curvature of a small chunk and are a consequence of the elastic properties of the flagellum. The external torque is being applied to the segment's center of mass, point A, (the same argument applied to the external force), and is denoted as $\mathbf{q}(s)ds$. The external torque acting on the chunk ds originate from the external force applied to the center of mass of ds. In static equilibrium sum of the internal torques and the sum of the external torques acting on the flagellum must balance each other. This condition ensures rotational equilibrium in the plane of motion – the two-dimensional plane in which the flagellum moves or oscillates – thus preventing the flagellum from rotating out of that plane. Combining (1) and (2) above gives a first-order equilibrium condition:

$$\frac{d\mathbf{M}}{ds} + \hat{\mathbf{s}} \times \mathbf{T} + \mathbf{q}(s) = 0 \tag{5}$$

This equation says that the sum of the internal torques – the bending moments applied to a small chunk, ds, $\mathbf{M}'$, and the torque associated with the internal tension of a small segment, $d\mathbf{r} \times \mathbf{T}(s)$, must equal the external torque applied at the segment. These derivations, eqns. (3) and (4), directly yields the Kirchhoff equations, which express the balance of force and torque on a small element of a solid rod. Note the external force and torque expressed above are force/torque densities or "volumic" quantities. The volumic external force represents the force per unit volume applied externally to the flagellum and accounts for the distributed external forces acting throughout the entire volume of the structure. Here $\boldsymbol{\rho}$ can be interpreted as the hydrodynamic force defined in eqn. (2). The volumic torque, $\mathbf{q}$, represents the torque per unit volume applied externally to the flagellum. Similar to the volumic external force, $\mathbf{q}$ considers the distribution of external torques throughout the volume of the structure. So arriving at eqns. (4) and (5), Kirchoff's equilibrium conditions for a perturbed solid rod of infinitesimal length are derived schematically by considering the forces and torques applied at the ends and about the center of mass, A.

3.2.2 Computing average power

In terms of an actuated flagella, the equilibrium conditions found above gives the necessary constraints to compute actuated power of flagellar motion and therefore also swimming efficiency. Eqn. 4 gives a template to compute power, which is dependent on the external torque, $\mathbf{q}$, of the flagellum. In the context of flagellar motion the external torque per unit length originate from the work produced by the molecular motors along the length of the flagellum. Using eqn. 4 we can show that

$$\mathbf{q} = \mathbf{M}'(s) + \hat{\mathbf{s}} \times \int_s^L \mathbf{F}(s)ds$$

where the integral bound L denotes the end or any point with the same phase, $(s+\Lambda)$, along the flagellum. The average power to deform deformation is taken to be the scalar product of the internal torque and local angular velocity:

$$P = \int_0^\Lambda [\mathbf{q} \cdot \dot{\theta}\hat{\mathbf{z}}]^+ ds \tag{6}$$

The radial velocity, $\dot{\theta}$, of a flagellum refers to the rate at which the flagellum rotates or twists at a specific point, s, along its length about the longitudinal axis of the flagellum; the $\hat{\mathbf{z}}$-direction points transverse (in and out of the page) to the plane of the deformed rod; the external torque, $\mathbf{q}$, is a vector that points orthogonal to the longitudinal axis (see figure 3) because the external torques act to rotate or twist the flagellum around its axis, which induces a torque that contributes to the flagellum's deformation. The power expended by the flagellum represents the rate at which work is being done through the molecular motors to sustain its motion. By integrating the product of the external torque and the z-component of the radial velocity over one curvilinear wavelength, we account for the contributions of all sections along the flagellum. The plus notation $[]^+$ in the integral refers to only positive work included in the "energy budget" of the flagellum. This means that elastic energy is not conserved and the work by the internal torques is not totally transferred to the fluid, rather some of it is wasted internally due to the "irreversibility of internal motors".[2] The power needed to actuate the flagellum through its environment indeed comes out to a scalar value that is dependent on actuations all along the flagellum.

3.2.3 Swimming efficiency

The efficiency of flagellar propulsion is governed by the deformation along the flagellum. We can express this as a ratio between the power needed to "drag" one period of the flagellum in the fluid and the actuation power.

$$\eta = \frac{\xi_{\parallel} \Lambda U^2}{P} \tag{7}$$

The efficiency is a dimensionless number and similar to thermodynamic efficiency, swimming efficiency measures how well the actuation power is being transferred to work or propulsion through the liquid. The efficiency is thus contrainted by the Sperm number, Sp, which measures the ratio of the curviliinear wavelength Λ, over an elasto-viscous perisistence length, l. This perisistence length characterizes the flexibility of the flagellum and is defined as

$$l = \left(\frac{TB}{\xi_{\perp}}\right)$$

[2]E. Lauga and C. Eloy Shape of Optimal active flagella

Here T is the internal tension, B is the bending rigidity (constant over Λ), and $\xi_\perp$ is fluid resistance coefficient in the perpendicular direction.

4 The optimization procedure

So far, we have found the two equilibrium conditions for the flagellum locomotion - eqns. (4) and (5) above - which led to the computation of actuation power of the idealized molecular motors and ultimately swimming efficiency, eqns. (6) and (7). Now the efficiency will be treated as the objective function to maximize for the optimization. This optimization procedure consists of numerically computing a deformation at a given Sp that would maximize efficiency. The computation of the shape is decomposed into discrete Fourier modes whereby the deformation is given by the local angle θ

$$\theta(s-ct) = \sum_{n=1}^{N} A_n cos[2\pi(s-ct)/\Lambda] \tag{8}$$

In this computation we took $t = 0$ and truncated the Fourier series with $N = 100$, and discretized the curvilienar coordinates of the flagellum, s, into 1000 elements. The optimization is carried out on MATLAB and employs the sequential quadratic programming algorithm. The SQP algorithm is an optimization technique used to solve constrained nonlinear optimization problems and will iteratively seek to find solutions for $\theta(s)$ that will maximize η. This computation is tricky to carry out because the alrgorithm is seeking out optimal values of the Fourier coefficients A_n for a deformation that would result in a globally maximized efficiency at a given Sp. Computing η at a given Sp leaves the computation with 100 variables to optimize, $\{A_1, A_2, A_3, ...A_{100}\}$. So the computation must keep the Fourier coefficients of all leading terms - material velocity, hydrodynamic force, internal tension, internal moments, internal torque, swimming power – in terms of variables for SQP optimization. To start, we must evaluate the swimming speed and wavespeed:

$$V = \alpha c$$

$$U = \frac{1-\beta}{2-\beta}\alpha c$$

Here the variables β and α describe the curvature of deformation as an integral of $\cos(\theta)$ over Λ and c is the speed such that a material point travels one Λ over one period of deformation, T.

4.1 Optimization psuedocode


```
%%%Psuedocode to set up the optimization

c= 1; %speed to travel alongbackbone
Lambda= 1; %curvilinear wavelength
syms s %%%define symbolic variable of curvilinear coordinate s
N = 10; %%% Number of fourier modes

% Define the Fourier coefficients 'a' as symbolic variables
a = sym('a', [N 1]);  %%% These are the coefficients that will computed
                      %%% by the SQP algorithm for an optimzed deformation

theta_fun = @(s,n) a(n)*cos(2*pi*n*s/Lambda);  %%%define shape

% Initialize the sum
theta = 0;

for n = 1:N %%%set up shape function to optimize
    theta = theta+theta_fun(s,n);
end

s_val=linspace(0,Lambda,1000);

alpha_func = @(a) 0;%initialize alpha and beta
beta_func = @(a) 0;

for i = 1:length(s_val)  %%% this loop computed alpha and beta as functions
                         %%% of theta
    theta_val = subs(theta, s, s_val(i));

    alpha_func = @(a) alpha_func(a) + (1/Lambda) * cos(theta_val);
    beta_func = @(a) beta_func(a) + (1/Lambda) * cos(theta_val).^2;
end

alpha=alpha_func(a);%%%redefine symbolic function as a function handle
beta=beta_func(a);

U=(1-beta)./(2-beta).*alpha*c;  %%% define swimming velocity
%%
%%% Viscous Force components
ksee_perp=1;%%%define perpendicular fluid resistance coeff

%%% Set up hydrodynamic/external force function for x & y directions
fx=@(s) ksee_perp*(alpha*c-U)*(1-1/2*cos(theta(s)).^2)-1/2*c*cos(theta(s));
fy= @(s) ksee_perp*-1/2*(alpha*c-U)*sin(theta(s))*cos(theta(s))-1/4*(3+cos(2* ↙
(theta(s)))*sin(theta(s)));

s_hat=[cos(theta),sin(theta),0];  %%%define s-hat vector

s = linspace(0, 1, 1000);
F_func = @(a) zeros(length(s), 3);  % Initialize empty matrix
```

```
% Assign function handles to the cells
for i = 1:length(s)
    F_func(i, 1) = @(a) fx(s(i)) * cos(theta(s(i)));
    F_func(i, 2) = @(a) fy(s(i)) * sin(theta(s(i)));
    F_func(i, 3) = @(a) 0;
end

F_integrated = zeros(1, 3); % Initialize the vector to store the integrated ↙
values

for col = 1:3
    integrand = zeros(size(s)); % Initialize the array to store the integrand ↙
values
    % Evaluate the integrand at each integration point
    for i = 1:length(s)
        integrand(i) = F_func(i, col); % Evaluate the function handle with the ↙
symbolic variable 'a'
    end
    % Perform numerical integration using trapz function
    F_integrated(col) = trapz(s, integrand);
end

syms s; %%% re-declare symbolic variable
B=1; %%%Defining bending moment
Diff2=diff(theta(s),2); %%%second deerivative of theta wrt s for bending moment
q=-B*Diff2*cross(s_hat,Internal_Tension); %%%define external torque
Diff1=[0;0;-c*diff(theta(s),1)]; %%%this is a an array of first-derivative of ↙
theta
% multiplied by the material speed to set up computation of power

f= -c*q*Diff1; %%%define integrand
func=matlabFunction(f); %%%re-define as function handle to integrate wrt s
P=integral(@(s) func(s),0,Lambda); %%%Avg power of deformation energy ↙
dissipated in fluid
eta=1/2*ksee_perp*Lambda*U.^2/P %%%define efficiency of flagellum deformation

l=(Internal_Tension*B/ksee_perp).^1/4; %%%elasto-viscous persistence length
Sp=Lambda./l;%%%Sperm number will be constraint for SQP
% Define options for the SQP algorithm where options set the find a
% globally minimized objective (inverse of eta); an initial guess (where to
% look); algorithm option; display on command; iteration count to 1000
options = optimoptions('fmincon', 'Algorithm', 'sqp', 'Display', 'iter');

% Run the SQP optimization
optimizedShape = fmincon(1./eta, initialGuess, [], Sp, options);
```

The figure below provides a forecast of an optimized deformation.

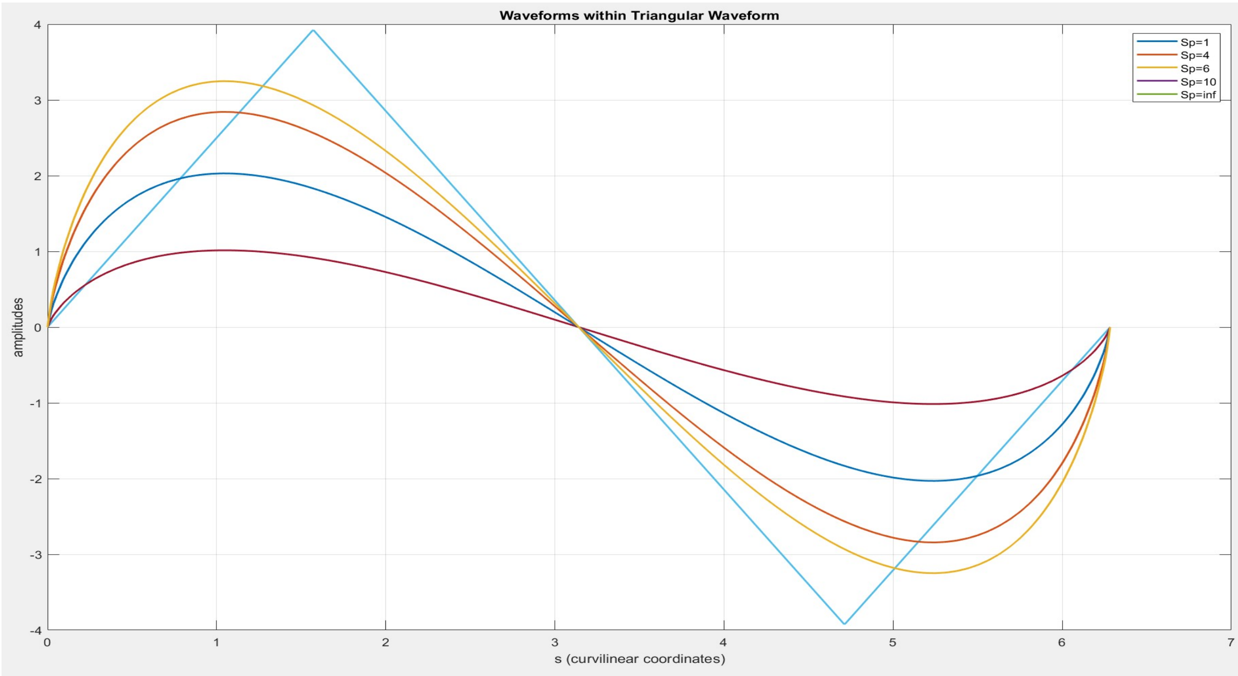

Figure 5: Waveforms of deformation parameterized by Sp, code found on page 17-18 generated by author

5 Conclusion

Thus far this report has explored computational and theoretical techniques for the shape optimization of activated flagella to enhance swimming efficiency. Through the utilization of mathematical models, kinematic analysis, and the consideration of Kirchoff's equilibrium conditions, we have gained insights into the intricate dynamics and mechanics of flagellar locomotion. The use of optimization algorithms, such as the SQP algorithm, has allowed us to explore the parameter space of Fourier coefficients A_n that dictate relative deformation.

Though the computation of the SQP optimization was never really finished, we have gained a comprehensive understanding of the various factors that govern this procedure such as the paramaterization of the sperm number; the energetics of elastic mechanics and their subsequent equilibrium conditions; localizing independent variables of the Fourier coefficients. Accounting for these factors we have gained a solid understanding of the interplay between flagellum morphology, fluid dynamics, and swimming efficiency.

6 References

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7 Code for waveforms and elastic force

7.1 Waveforms


```
% Define the triangular waveform parameters
T = 2*pi; % Period
N = 100; % Number of harmonics

% Define the time vector
t = linspace(0, T, 1000);

% Generate the triangular waveform
triangular_waveform = 2.5*(abs(mod(t-T/4, T)-T/2)-T/4);

% Initialize the sinusoidal waveforms
waveform_2 = zeros(size(t));
waveform_3 = zeros(size(t));
waveform_4 = zeros(size(t));
waveform_5 = zeros(size(t));

% Apply decreasing curvature to the sinusoidal waveforms
for k = 1:N
    curvature_factor = 1/(k)^2; % Adjust this factor for different curvature

    waveform_2 = waveform_2 + curvature_factor * sin(k*t);
    waveform_3 = waveform_3 + 2*curvature_factor * sin(k*t);
    waveform_4 = waveform_4 + 2.8*curvature_factor * sin(k*t);
    waveform_5 = waveform_5 + 3.2*curvature_factor * sin(k*t);
end

% Calculate the scaling factors and offsets
max_triangular = max(triangular_waveform);
min_triangular = min(triangular_waveform);

max_additional = max([max(waveform_2), max(waveform_3), max(waveform_4), max ↙
(waveform_5)]);
min_additional = min([min(waveform_2), min(waveform_3), min(waveform_4), min ↙
(waveform_5)]);

%scale_factor = (max_triangular - min_triangular) / (max_additional - ↙
min_additional);

% Apply the scaling factors and offsets to align the waveforms within the ↙
triangular waveform
waveform_2 = waveform_2  ;
waveform_3 = waveform_3  ;
waveform_4 = waveform_4  ;
waveform_5 = waveform_5  ;

% Plot the waveforms
plot(t, triangular_waveform, 'LineWidth', 1.5)
hold on
plot(t, waveform_2, 'LineWidth', 1.5)
plot(t, waveform_3, 'LineWidth', 1.5)
```

```
plot(t, waveform_4, 'LineWidth', 1.5)
plot(t, waveform_5, 'LineWidth', 1.5)

% Set the plot properties
xlabel('s (curvilinear coordinates)');
ylabel('amplitudes');
title('Waveforms within Triangular Waveform');
legend('Sp=1', 'Sp=4', 'Sp=6', 'Sp=10', 'Sp=inf');
grid on;
```

7.2 Elastic force


```
%%function [L,R,k] = circumcenter(X)
% x = linspace(0,pi,100);
% y = sin(x).^3;
% X = [x;y].'; %trasnpose function such that it is a 100x2 matrix,
%%%with arrays of x & y

%Fourier Series expanded to the nth degree
f=@(x)x.*(x>0 & x<-pi)-2*(x/pi+1).*(x>=-pi & x<=-pi/2);
n=3;
k=0:n;
a=1/pi*(integral(@(x)f(x).*cos(k*x),-pi,-pi/2, 'ArrayValued',true)+integral(@(x) ↙
f(x).*cos(k*x),0,pi/2,'ArrayValued',true));
k=1:n;
b=1/pi*(integral(@(x)f(x).*sin(k*x),-pi,-pi/2, 'ArrayValued',true)+integral(@(x) ↙
f(x).*sin(k*x),0,pi/2,'ArrayValued',true));
ffun=@(x)a(1)/2+sum(a(2:n+1).*cos((1:n)*x)+b(1:n).*sin((1:n)*x));
x=linspace(0,pi,100);
y=arrayfun(@(x)ffun(x),x);
figure(1)
plot(x,y)
X=[x;y].';

%cc=circumcenter()
% Radius of curvature and curvature vector for 2D or 3D curve
%  [L,R,k] = curvature(X)
%   X:   2 or 3 column array of x, y (and possibly z) coordiates
%   L:   Cumulative arc length
%   R:   Radius of curvature
%   k:   Curvature vector in cartesian coordinates x-vector + y-vector
% The scalar curvature value is 1./R
% Version 2.6: Calculates end point values for closed curve

 N = size(X,1);
 R = NaN(N,1);
  if size(X,2) == 2
    X = [X,zeros(N,1)];  % Use 3D expressions for 2D as well
  end
  L = zeros(N,1);
  R = NaN(N,1);
  k = NaN(N,3);
  for x = 2:N-1

    [R(x),~,k(x,:)] = circumcenter(X(x,:)',X(x-1,:)',X(x+1,:)');
    L(x) = L(x-1)+norm(X(x,:)-X(x-1,:));
  end
  if norm(X(1,:)-X(end,:)) < 1e-10 % Closed curve.
    [R(1),~,k(1,:)] = circumcenter(X(end-1,:)',X(1,:)',X(2,:)');
    R(end) = R(1);
    k(end,:) = k(1,:);
```

```
    L(end) = L(end-1) + norm(X(end,:)-X(end-1,:));
  end
  x = N;
  L(x) = L(x-1)+norm(X(x,:)-X(x-1,:));
  if size(X,2) == 2
    k = k(:,1:2);
  end

T=table(L,R,k);
  T.Properties.VariableNames={'Arclength', 'Radius', 'curvature'}

x_1=X(:,1);
y_1=X(:,2);
figure(2)

plot(x_1,y_1,'.');
hold on
quiver(x_1,y_1,k(:,1),k(:,2),'red');
daspect([1,1,1])
 hold on
size(k);

m=(k(1:100,1).^2+k(1:100,2).^2).^.5;

unit_k=k(:,1:2).*(m.^-1);
size(unit_k);
((unit_k(:,1)).^2+(unit_k(:,2)).^2).^.5; %check if k-vector is a unit

quiver(x_1,y_1,unit_k(:,1),unit_k(:,2),.3,'blue');
hold off

%% ALT: OBJ to obtain plot of curvature as a function of arclength

y=sign(k(:,2)).*m; %gives 'location' of curvature magnitude due to radius
figure()
subplot(4,1,1)
plot(L,y,'-')
legend('Curvature plot')
xlabel('arclength distance')
ylabel('curvature vector')
grid on

%%% Finite Differences
x=linspace(1,pi,100);
delx=diff(x(1,1:2)).';%interval between points
yderiv_cen = (y(3:end)-2*y(2:end-1)+y(1:end-2))./delx^2;

%%%%Use Central Diff to compute value of yderiv numerically
subplot(4,1,2)
plot(L(2:end-1),yderiv_cen(1:end),'red-','LineWidth',2)
```

```
legend('Central K_s_s')
grid on

%%%% Use Foward Diff to compute value of yderiv numerically
yderiv_for= (2*y(1:end-3)-5*y(2:end-2)+4*y(3:end-1)-y(4:end))./delx^2;
subplot(4,1,3)
plot(L(1:end-3),yderiv_for,'blue-','LineWidth',2)
legend('Forward K_s_s')
grid on
%%% Use Backward Diff to compute value of yderiv numerically
yderiv_back= (2*y(4:end)-5*y(3:end-1)+4*y(2:end-2)-y(1:end-3))./delx^2;
subplot(4,1,4)
plot(L(4:end),yderiv_back,'green-','LineWidth',2)
grid on
legend('Backward K_s_s')
%Try to create arrays that are the same size
A=y(1:end-4);
A1=y(2:end-3);
A2=y(3:end-2);
A3=y(4:end-1);
```