THE MOTILITY OF THE TRYPANOSOME

Abstract. This document describes a simple model for the simulation of the movement of a certain kind of parasite called trypanosome.

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3. Introduction

3.1. Geometry. A Trypanosome consists of an ellipsoidal cell body and a slender cylindrical flagellum of length L and diameter d. We are only considering planar beating patterns, which means all the movement of the flagellum is contained in a flat plane. This means that we can describe the position of the centre line of the flagellum at any time as $\mathbf{X}$ (s,t) = (X (s,t),Y (s,t)) where s is the arclength along the centre line of the flagellum. Here, s = 0 corresponds to the connection point between

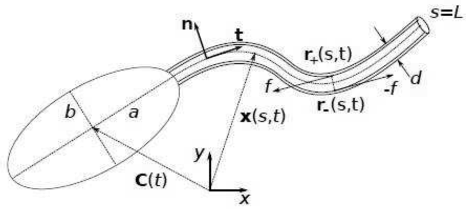


FIGURE 1. Geometry of the problem.

the flagellum and the cell body, and s = L to the end of the flagellum. We denote the normal and tangential vector on the centre line with $\mathbf{n}$ and $\mathbf{t}$, respectively, and they are equal to

$$\mathbf{t} = \frac{\partial \mathbf{X}}{\partial \mathbf{s}} = (\cos(\theta(\mathbf{s},\mathbf{t})), \sin(\theta(\mathbf{s},\mathbf{t}))), \qquad \mathbf{n} = (-\sin(\theta(\mathbf{s},\mathbf{t})), \cos(\theta(\mathbf{s},\mathbf{t}))) \tag{1}$$

where $\theta(s,t)$ is the angle between the centre line of the flagellum and the x-axis. From these expressions, we can then write $\mathbf{X}$ (s,t) in terms of $\theta(s,t)$ according to

$$\mathbf{X}(\mathbf{s},\mathbf{t}) = \mathbf{X}(\mathbf{0},\mathbf{t}) + \int_{\mathbf{0}}^{\mathbf{s}} \mathbf{t}\mathbf{ds} = \mathbf{X}(\mathbf{0},\mathbf{t}) + \int_{\mathbf{0}}^{\mathbf{s}} (\cos(\theta(\mathbf{s},\mathbf{t})), \sin(\theta(\mathbf{s},\mathbf{t},)))\mathbf{ds} \tag{2}$$

The axoneme, which is responsible for the bending of the flagellum, is modelled as two parallel fibres at distance b in the interior of the flagellum. The position of these fibres is then equal to $r_{\pm} = \mathbf{X}(s,t) \pm \mathbf{n}$. The bending is caused by a sliding force f working between these two fibres as in 1.

3.2. Full problem. The main assumption in the derivation of the problem is that at any time t there is a force balance between the forces working on the interior and the exterior of the flagellum and the cell body. On the exterior of the flagellum, there is a drag force due to the viscosity of the surrounding fluid. On the interior, we have bending forces due to the bending stiffness of the flagellum, and sliding forces. The force balance then becomes

$$\mathbf{f_{drag}} + \mathbf{f_{sliding}} + \mathbf{f_{bending}}(\mathbf{s},\mathbf{t}) = \mathbf{0} \tag{3}$$

To calculate the position of the centre line of the flagellum we use the principle of minimal potential energy which means that we can find the position of the centre line by calculating the minimum of a suitable enthalpy functional. This leads to the follow differential equation for the position of the centre line of the flagellum

$$\mathbf{f_{drag}} = (\mathbf{E}\theta_{\mathbf{sss}} - \mathbf{f_s b} - \mathbf{T}\theta_{\mathbf{s}})\mathbf{n} + (\theta_{\mathbf{s}}(-\mathbf{E}\theta_{\mathbf{ss}} + \mathbf{fb}) - \mathbf{T_s})\mathbf{t} \tag{4}$$

where T is the axial tension which is caused by the inextensibility of the flagellum.

3.2.1. Drag forces. Since $d \ll L$, we can use the so called resistive force theory to find an expression for the drag forces working on the exterior of the flagellum. This theory says that the drag force on a section of the flagellum with width ds can be approximated by

$$\mathbf{f_{drag}} = -\xi_{\parallel}(\dot{\mathbf{X}}(\mathbf{s},\mathbf{t}) \cdot \mathbf{t})\mathbf{t} - \xi_{\perp}((\dot{\mathbf{X}})(\mathbf{s},\mathbf{t}) \cdot \mathbf{n})\mathbf{n}, (\mathbf{4}) \tag{5}$$

where $\xi_{\parallel}$ and $\xi_{\perp}$ depend on the viscosity of the fluid and the diameter and the length of the flagellum, $\xi_{\perp} \approx 2\xi_{\parallel}$.

3.2.2. Boundary conditions. The boundary conditions for 4 are given as follows
•At $s = 0$:

$$\mathbf{F_{ext}} = (\mathbf{E}\theta_{\mathbf{s}}\mathbf{s} - \mathbf{fb})\mathbf{n} - \mathbf{Tt} \tag{6}$$

$$M_{ext} = -E\theta_s - b\int_0^L f(s,t)ds \tag{7}$$

•At $s = L$:

$$\mathbf{F_{ext}} = (-\mathbf{E}\theta_{\mathbf{s}}\mathbf{s} + \mathbf{fb})\mathbf{n} - \mathbf{Tt} \tag{8}$$

$$M_{ext} = E\theta_s \tag{9}$$

where $\mathbf{F_{ext}}$ and M_{ext} are the external force and angular momentum, respectively, working at the ends of the flagellum. At $s = L$ we assume that $\mathbf{F_{ext}} = \mathbf{0} = \mathbf{M_{ext}}$. At $s = 0$, the cell body is exerting a force and momentum on the flagellum due to drag forces working on the cell body. For a spherical cell body of radius a, velocity $\mathbf{U}$, and angular velocity Ω, the drag force and angular momentum working on the cell body are equal to

$$\mathbf{F_{ext}} = -\mathbf{6}\pi\mu\mathbf{aU}, \quad \mathbf{M_{ext}} = -\mathbf{8}\pi\mu\mathbf{a^3}\boldsymbol{\Omega} \tag{10}$$

Since the cell body is clamped to the flagellum, we have $\mathbf{U} = \dot{\mathbf{X}}(\mathbf{0}, \mathbf{t})$, and $\Omega = \dot{\theta}(0, t)$.

3.2.3. Full model. If we combine the various results from the previous sections, we find the following model:

•Equation in the $\mathbf{n}$ -direction for $0 < s < L$

$$\mathbf{f_{drag}} = -\xi_\perp \dot{\mathbf{X}}(\mathbf{s}, \mathbf{t}) \times \mathbf{n} = -\mathbf{E}\theta_{\mathbf{sss}} + \mathbf{f_s b} + \mathbf{T}\theta_{\mathbf{s}} \tag{11}$$

with boundary conditions

–At s = 0:

$$6\mu\pi a \dot{\mathbf{X}}(\mathbf{0}, \mathbf{t}) \cdot \mathbf{n} = -\mathbf{E}\theta_{\mathbf{s}}\mathbf{s} + \mathbf{fb} \tag{12}$$

$$8\mu\pi a^3 \dot{\theta}(0, t) = E\theta_s + b\int_0^L f(s, t)ds \tag{13}$$

–At $s = L$:

$$-E\theta_{ss} + fb = 0 \tag{14}$$

$$\theta_s = 0 \tag{15}$$

•Equation in the $(\mathbf{t})$-direction

$$\xi_{\|}\dot{\mathbf{X}}(\mathbf{s}, \mathbf{t}) \cdot (\mathbf{t}) = \theta_{\mathbf{s}}(\mathbf{E}\theta_{\mathbf{s}}\mathbf{s} - \mathbf{fb}) + \mathbf{T_s} \tag{16}$$

with boundary conditions

–At s = 0

$$6\mu\pi a(\dot{\mathbf{X}} \cdot \mathbf{t}) = \mathbf{T} \tag{17}$$

–At $s = L$

$$T = 0. \tag{18}$$

3.3. Scaling and linearization. Before we derive the linearized problem, we will derive a non-dimensional set of equations by chosing a scaling as follows

$$a, X, Y, s \sim L, T, fb \sim \frac{E}{L^2}, t \sim \frac{L^4 \xi_\perp}{E} \tag{19}$$

which gives us the following set of non-dimensional equations (* indicates the non-dimensional parameters):

•Equation in the $\mathbf{n}$-direction

$$\dot{\mathbf{X}}^*(\mathbf{s}^*, \mathbf{t}^*) \cdot (\mathbf{n}) = -\theta^*_{\mathbf{s^* s^* s^*}} + \mathbf{f}^*_{\mathbf{s}^*} + \mathbf{T}^*\theta^*_{\mathbf{s}^*} \tag{20}$$

with boundary conditions

–At $s = 0$:

$$F\dot{\mathbf{X}}^*(\mathbf{0}, \mathbf{t}^*) \cdot (\mathbf{n}) = -\theta_{\mathbf{s^* s^*}} + \mathbf{f}^*, (\mathbf{20}) \tag{21}$$

$$M\dot{\theta}^*(\mathbf{0}, \mathbf{t}^*) = \theta^*_{\mathbf{s}^*} + \int_{\mathbf{0}}^{\mathbf{1}} \mathbf{f}^*(\mathbf{s}^*, \mathbf{t}^*)\mathbf{ds}^* \tag{22}$$

–At $s = 1$:

$$-\theta^*_{s^*s^*} + f = 0 \tag{23}$$

$$\theta^*_{s^*} = 0 \tag{24}$$

•Equation in the **t**-direction

$$\dot{\mathbf{X}}^*(\mathbf{s}^*, \mathbf{t}^*) \cdot (\mathbf{t}) = \gamma(\theta^*_{\mathbf{s}^*}(\theta^*_{\mathbf{s}^*\mathbf{s}^*} - \mathbf{f}) + \mathbf{T}^*_{\mathbf{s}^*}) \tag{25}$$

with boundary conditions –At $s = 0$:

$$F\dot{\mathbf{X}}^* \cdot (\mathbf{t}) = \mathbf{T}^* \tag{26}$$

$$F\dot{\mathbf{X}}^* \cdot (\mathbf{t}) = \mathbf{T}^* \tag{27}$$

–At $s = 1$:

$$T^* = 0, \tag{28}$$

The non-dimensional constanst F, M and γ are equal to

$$F = \frac{6\pi\mu a}{L\xi_\perp}, \qquad M = \frac{8\pi\mu a^3}{L^3\xi_\perp}, \qquad \gamma = \frac{\xi_\perp}{\xi_\parallel} \approx 2. \tag{29}$$

To linearize these equations, we are going to assume that $|f^*| \ll 1$, and $|\theta^*| \ll 1$, hence we rescale f^* and θ^* as $f^* = \epsilon f_1$, and $\theta^* = \epsilon\theta_1$, where $0 < \epsilon \ll 1$. For the tangential and normal vectors, we then find

$$\mathbf{t} = (\cos(\epsilon\theta_1), \sin(\epsilon\theta_1)) \approx (1 - \frac{1}{2}\epsilon^2\theta_1^2, \epsilon\theta_1) \tag{30}$$

$$\mathbf{n} = (-\sin(\epsilon\theta_1)), \sin(\epsilon\theta_1)) \approx (-\epsilon\theta_1, 1) \tag{31}$$

The leading order terms for $\mathbf{X}^* = (\mathbf{X}^*, \mathbf{Y}^*)$ then become

$$\mathbf{X}^*(\mathbf{s}, \mathbf{t}) = \mathbf{X}^*(\mathbf{0}, \mathbf{t}) + \int_\mathbf{0}^\mathbf{s} \mathbf{t}\mathbf{ds}' = (\mathbf{s}, \mathbf{0}) + \mathbf{X}^*(\mathbf{0}, \mathbf{t}) + \int_\mathbf{0}^\mathbf{s} (-\frac{\mathbf{1}}{\mathbf{2}}\epsilon^\mathbf{2}\theta_\mathbf{1}^\mathbf{2}(\mathbf{s}', \mathbf{t}), \epsilon\theta_\mathbf{1}(\mathbf{s}', \mathbf{t}))\mathbf{ds}' \tag{32}$$

where

$$\mathbf{X}^*(\mathbf{0}, \mathbf{t}) = \epsilon^\mathbf{2}\mathbf{X}_\mathbf{2}(\mathbf{0}, \mathbf{t}), \epsilon\mathbf{Y}_\mathbf{1}(\mathbf{0}, \mathbf{t})) \tag{33}$$

hence

$$\mathbf{X}^*(\mathbf{s}, \mathbf{t}) = \mathbf{s} + \epsilon^\mathbf{2}\mathbf{X}_\mathbf{2}(\mathbf{s}, \mathbf{t}), \mathbf{Y}^*(\mathbf{s}, \mathbf{t}) = \epsilon\mathbf{Y}_\mathbf{1}(\mathbf{s}, \mathbf{t})) \tag{34}$$

with

$$X_2(s,t) = X^2(0,t) - \frac{1}{2}\int_0^s \theta_1^2(s', t)ds' \tag{35}$$

$$Y_1(s,t) = Y_1(0,t) + \int_0^s \theta_1(s', t)ds' \tag{36}$$

The leading order approximation for T^* becomes $T^* \approx \epsilon^2 T_2$.

If we substitute these approximations into the set of non-dimensional equations, we find for the leading order terms (dropping the $*'s$)

•Equation in the **n**-direction for

$$\dot{\theta}_1(s,t) = -\theta_{1ssss}(s,t) + f_{1ss}(s,t) \tag{37}$$

$$\dot{Y}_1(0,t) = -\theta_{1ssss}(0,t) + f_1 s(0,t) \tag{38}$$

with boundary conditions
–At $s = 0$:

$$F\dot{Y}_1 = -\theta_{1ss} + f_1 \tag{39}$$

$$M\dot{\theta}_1(0,t) = \theta_{1s} + \int_0^1 f_1(s,t)ds \tag{40}$$

–At $s = 1$:

$$-\theta_{1ss} + f = 0 \tag{41}$$

$$\theta_1 s = 0 \tag{42}$$

•Equation in the **t**-direction

$$\dot{X}_2(s,t) + \theta_1(s,t)\dot{Y}_1(s,t) = \gamma(\theta_1 s(\theta_{1ss} - f_1) + T_2 s) \tag{43}$$

with boundary conditions
–At $s = 0$

$$\mathcal{F}\dot{X}_2(0,t) + \theta_1(0,t)\dot{Y}_1(0,t) = T_2(0,t) \tag{44}$$

–At $s = 1$

$$T_2(1,t) = 0. \tag{45}$$

4. Geometry

A trypanosome consists of an ellipsoidal cell body and a slender cylindrical flagellum of length L and diameter d. We are only considering planar beating patterns, which means all the movement of the flagellum is contained in a flat plane. This means that we can describe the position of teh centre line of the flagellum at any time as $\mathbf{X(s,t)} = (\mathbf{X(s,t)}, \mathbf{Y(s,t)})$ where s is the arclength along the centre line of the flagellum. Here, $s = 0$ corresponds to the connection point between the flagellum and the cell body, and$s = L$ to the end of the flagellum. We denote the normal and tangential vector on the centre line with **n** and **t**, respectively, and they are equal to:

$$\begin{aligned} f_1(s,t) &= \mathrm{Re}\left(\exp(ikx + i\omega t)\right), \\ \theta_1(s,t) &= \mathrm{Re}\left(\hat{\theta}(s)\exp(i\omega t)\right), \\ Y_1(s,t) &= \mathrm{Re}\left(\hat{Y}(s)\exp(i\omega t)\right), \end{aligned}$$

5. Analysis and results

5.1. Traveling waves.

5.1.1. Traveling wave solution. The problem's nature suggests we look for traveling wave solutions of the form:

$$f_1(s,t) = \mathrm{Re}\left(\exp(ikx + i\omega t)\right) \tag{46}$$

$$\theta_1(s,t) = \mathrm{Re}\left(\hat{\theta}(s)\exp(i\omega t)\right) \tag{47}$$

$$Y_1(s,t) = \mathrm{Re}\left(\hat{Y}(s)\exp(i\omega t)\right) \tag{48}$$

where $\hat{\theta}(s)$ and $\hat{Y}(s)$ are complex-valued functions that can be obtained by substitution into the linearized equation for the normal direction:

$$\hat{\theta}'''' + i\omega\hat{\theta} = -k^2 e^{iks},$$
$$\hat{Y}(s) = \hat{Y}(0) + \int_0^s \hat{\theta}(s',t)\mathrm{d}s',$$

where $\hat{Y}(0)$ satisfies:

$$i\omega\hat{Y}(0) = -\hat{\theta}'''(0) + ik.$$

5.1.2. Boundary conditions. Under these assumptions, the boundary conditions of the linearized system become:

- At $s = 0$:

$$i\omega\mathcal{F}\hat{Y}(0) = -\hat{\theta}''(0) + 1,$$
$$i\omega\mathcal{M}\hat{\theta}(0) = \hat{\theta}'(0) + \frac{1}{ik}\left(e^{ik} - 1\right).$$

- At $s = 1$:

$$-\hat{\theta}''(1) + e^{ik} = 0,$$
$$\hat{\theta}'(1) = 0.$$

5.1.3. Equations for $\hat{\theta}(s)$. The equation for $\hat{\theta}(s)$ is a linear ordinary differential equation with constant coefficients. Consequently, we can write its solution as: $\hat{\theta} = \hat{\theta}_P + \hat{\theta}_H$ where the homogeneous ($\hat{\theta}_H$) and particular ($\hat{\theta}_P$) solutions satisfy:

$$\hat{\theta}_H'''' + i\omega\hat{\theta}_H = 0,$$
$$\hat{\theta}_P'''' + i\omega\hat{\theta}_P = -k^2.$$

The general solution is given by:

$$\hat{\theta}_H(s) = \alpha_1 e^{\lambda s} + \alpha_2 e^{i\lambda s} + \alpha_3 e^{-\lambda s} + \alpha_3 e^{-i\lambda s},$$
$$\hat{\theta}_P(s) = De^{iks},$$

where $D = -\frac{k^2}{k^4 + i\omega}$ and α_1, α_2, α_3, α_4 are the solutions of a linear system stemming from the boundary conditions (See Listing 1).

5.2. Vertical position. At this point it is possible to compute the vertical position $Y_1(s,t)$. This can be calculated from $\theta_1(s,t)$:

$$Y_1(s,t) = Y_1(0,t) + \int_0^s \theta_1(s',t)\mathrm{d}s' = Y_1(0,t) + \mathrm{Re}\left(e^{i\omega t}\int_0^s \hat{\theta}(s')\mathrm{d}s'\right).$$

Recalling from 5.1.3 that $\hat{\theta}(s)$ is a linear combination of exponential functions, then the integral on the right hand side of the previous equation is equal to

$$\frac{\alpha_1}{\lambda}\left(e^{\lambda s} - 1\right) - i\frac{\alpha_2}{\lambda}\left(e^{i\lambda s} - 1\right) - \frac{\alpha_3}{\lambda}\left(e^{-\lambda s} - 1\right) + i\frac{\alpha_4}{\lambda}\left(e^{-i\lambda s} - 1\right) - i\frac{D}{k}\left(e^{iks} - 1\right).$$

5.2.1. Position at the boundary $s = 0$. Combining

$$\dot{Y}_1(0,t) = -\theta_{1sss}(0,t) + f_{1s}(0,t) = -\operatorname{Re}\left(\hat{\theta}'''(0)e^{i\omega t}\right) + \operatorname{Re}\left(ike^{i\omega t}\right),$$

with our assumption that $Y_1(s,t) = \operatorname{Re}\left(\hat{Y}(s)e^{i\omega t}\right)$, we arrive at

$$\dot{Y}_1(0,t) = \operatorname{Re}\left(i\omega\hat{Y}(0)e^{i\omega t}\right) = \operatorname{Re}\left(\left(ik - \hat{\theta}'''(0)\right)e^{i\omega t}\right).$$

Thus,

$$Y_1(0,t) = \operatorname{Re}\left(\frac{1}{i\omega}\left(ik - \hat{\theta}'''(0)\right)e^{i\omega t}\right).$$

Figures 2 and 3 display some scenarios for the vertical position at the instants $t = 0, 10^{-3}, 20^{-3}, 40^{-3}$.

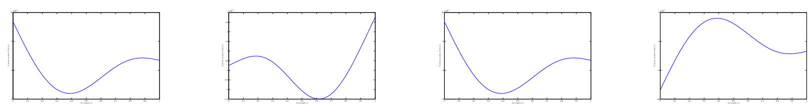


FIGURE 2. Snapshots of $Y_1(0,t)$ for $\omega = (2\pi)^4, k = 2\pi, \mathcal{F} = \mathcal{M} = 0, \gamma = 2$.

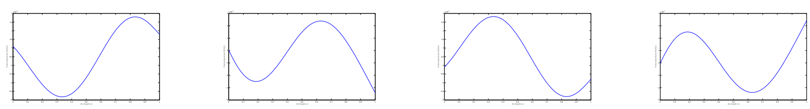


FIGURE 3. Snapshots of $Y_1(0,t)$ for $\omega = (2\pi)^4, k = 2\pi, \mathcal{F} = 6, \mathcal{M} = 2, \gamma = 2$.

5.3. Horizontal position. In a manner analogous to the one we used for obtaining the vertical position, we arrive at the following expression for the horizontal position:

$$X_2(s,t) = X_2(0,t) - \frac{1}{2}\int_0^s \theta_1^2(s',t)\mathrm{d}s'.$$

By taking partial derivatives in s on both sides of the equation, we can turn it into an ODE that can be numerically solved (e.g.: using `MATLAB`'s `ode45` function) once $X_2(0,t)$ is known.

5.4. Horizontal velocity. Using the equations in the tangential direction, we arrive at:

$$\dot{X}_2(0,t) = \frac{1}{1+\gamma\mathcal{F}}\int_0^1 \left(\frac{1}{2}\int_0^s \left(\theta_1^2(s',t)\right)_t \mathrm{d}s' + (\gamma-1)\theta_1(s,t)\dot{Y}_1(s,t)\right)\mathrm{d}s.$$

Integration by parts allows us reduce the double integral to a single integral

$$\dot{X}_2(0,t) = \frac{1}{1+\gamma\mathcal{F}}\int_0^1 \left(\frac{1}{2}(1-s)\left(\theta_1^2(s,t)\right)_t + (\gamma-1)\theta_1(s,t)\dot{Y}_1(s,t)\right)\mathrm{d}s,$$

and this greatly improves the computational cost of calculating these quadratures.

Figure 5.4 shows the dependency of the horizontal velocity on time for different periods and forces.

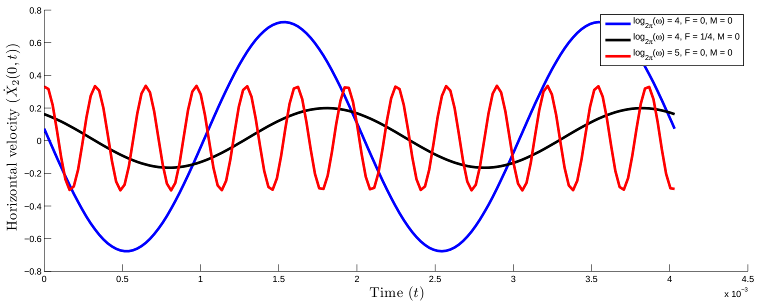
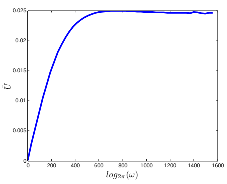


FIGURE 4. Graph of $\dot{X}_2(0,t)$

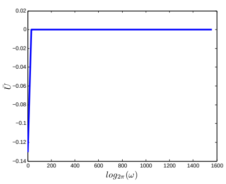
Finally, integrating $\dot{X}_2$ over the period of the traveling wave, we can calculate the average horizontal velocity $\bar{U}$ as follows:

$$\bar{U} = \frac{\omega}{2\pi}\int_0^{\frac{2\pi}{\omega}} \dot{X}_2(0,t)\,\mathrm{d}t = \frac{\omega}{2\pi}\frac{\gamma-1}{1+\gamma\mathcal{F}}\int_0^{2\pi/\omega}\int_0^1 Y_{1s}(s,t)\dot{Y}_1(s,t)\,\mathrm{d}s\,\mathrm{d}t.$$

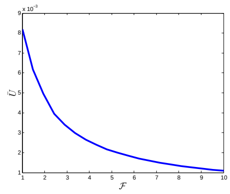
In Figure 5 we can see how the average horizontal velocity varies with regard to ω, k, $\mathcal{F}$, and $\mathcal{M}$. The most interesting factor is the dependency on the force exerted on the flagellum (the higher the force, the slower the parasite).



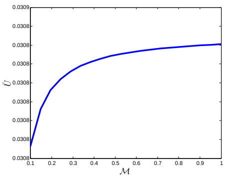
(a) $\bar{U}(\cdot,k,\mathcal{F},\mathcal{M},\gamma)$



(b) $\bar{U}(\omega,\cdot,\mathcal{F},\mathcal{M},\gamma)$



(c) $\bar{U}(\omega,k,\cdot,\mathcal{M},\gamma)$



(d) $\bar{U}(\omega,k,\mathcal{F},\cdot,\gamma)$

FIGURE 5. Average horizontal velocity in terms of different variables

5.5. Optimization. It is reasonable to assume that evolution has favored parasites that swim optimally in a given medium and, consequently, we want to find the parameters that maximize $\bar{U}$ in the hope that they would accurately reflect the true behavior of the parasite.

Consider the graph of $\bar{U}(\omega,k)$ for fixed $\mathcal{F},\mathcal{M}$ (two of these surfaces are displayed in figures 5.5 and 5.5), we would expect the real parasites to be modelled by the parameters where the graph of $\bar{U}$ achieves the highest peaks. In order to find those values we:

1. Picked a subset of values of $\mathcal{F}\in[1,10]$ and $\mathcal{M}\in[1,5]$ and ran unconstrained deterministic searches using `MATLAB`'s `fminsearch`, and

2. Ran a Genetic Algorithm to try to find global optima for $\bar{U}(\omega, k, \mathcal{F}, \mathcal{M})$ first in terms of $\mathcal{F}$, then in terms of $\mathcal{M}$, and finally for both $\mathcal{F}$ and $\mathcal{M}$). The results were, respectively:

$$\{\omega = 2.9287, k = 0.8714, \mathcal{F} = 1.0000 \text{ for } \mathcal{M} = 0\},$$

$$\{\omega = 2.6806, k = 0.4687, \mathcal{M} = 2.3348 \text{ for } \mathcal{F} = 1\}, \text{ and}$$

$$\{\omega = 2.7355, k = 0.4798, \mathcal{F} = 1.0009, \mathcal{M} = 4.3114\}.$$

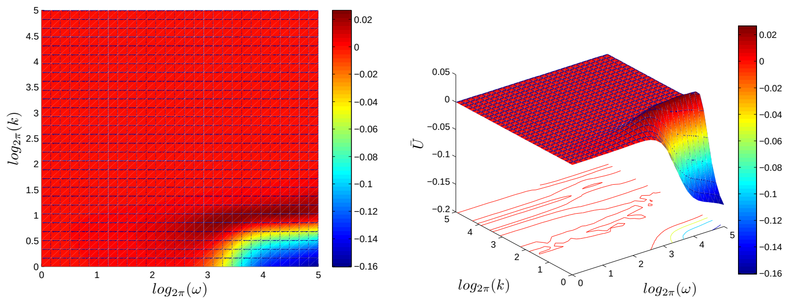


FIGURE 6. $\bar{U}(\omega, k)$ for $\mathcal{F} = 0, \mathcal{M} = 0$

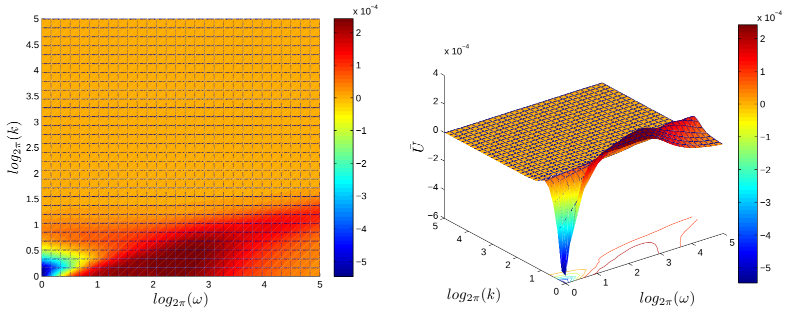


FIGURE 7. $\bar{U}(\omega, k)$ for $\mathcal{F} = 6, \mathcal{M} = 2$

6. Conclusions and future work

We have numerically solved the linearized model of the motility of the trypanosome. Some of the highlights of what we have done are:

- Studied the dependency of the trypanosome's mobility on the shape of its flagellum.
- Studied the dependency of the parasite's swimming ability on the forces exerted on it.
- Located possible values for modelling real life trypanosomes according to an optimization procedure.

However, there are some points we would have liked to investigate further had we been given more time such as:

- Solve the non-linear problem.
- Incorporating the fluid into our model.
- Redimensionalize the results.

Appendix A. Source code

Listing 1. Computation of the coefficients for the general solution of the ODE associated to the travelling wave

```
function v = compute_coeffs(l, w, k, F, M, gamma)

Maux1 = -l^3*F*[1 -i -1 i; 0 0 0 0; 0 0 0 0; 0 0 0 0];
Maux2 = -i*w*l*M*[0 0 0 0; 1 i -1 -i; 0 0 0 0; 0 0 0 0];

A = [l^2, -l^2, l^2, -l^2;
     l, i*l, -l, -i*l;
     l^2*exp(l), -l^2*exp(i*l), l^2*exp(-l), -l^2*exp(-i*l);
     l*exp(l), i*l*exp(i*l), -l*exp(-l), -i*l*exp(-i*l)] + ...
    Maux1 + Maux2;

b = [i*w*(1 - i*k*F)/(k^4 + i*w),
     i*exp(i*k)/k + w*(1 - i*M*k^3)/(k*(k^4 + i*w)),
     i*w*exp(i*k)/(k^4 + i*w),
     i*k^3*exp(i*k)/(k^4 + i*w)];

v = A\b;
```

Listing 2. Computation of the horizontal velocity

```
function Xdot20 = compute_Xdot20(w, k, F, M, gamma)

l = (-i*w)^(1/4);

a = compute_coeffs(l, w, k, F, M, gamma);

D = -k.^2/(k.^4 + i.*w);

thetahat = @(s, t) ...
    (a(1).*exp(l.*s) ...
     + a(2).*exp(i.*l.*s) ...
     + a(3).*exp(-l.*s) ...
     + a(4).*exp(-i.*l.*s)) ...
    + (D.*exp(i.*k.*s));

theta1 = @(s, t) ...
         real(thetahat(s, t).*exp(i.*w.*t));

theta1_sss = @(s, t) ...
    real((exp(i.*t.*w).*(l.^3.*(a(1).*exp(s.*l) ...
                            -i.*a(2).*exp(i.*s.*l) ...
                            - a(3).*exp(-(s.*l))) ...
                            + i.*a(4).*exp(-(i.*s.*l)) ...
                     + i.*k.^5.*exp(i.*k.*s)/(i.*w+k.^4))));

theta1_squared_t = @(s, t) ...
    real((2.*i.*w.*exp(2.*i.*t.*w) .* ...
          (a(1).*exp(s.*l) ...
           + a(2).*exp(i.*s.*l) ...
           + a(3).*exp(-(s.*l)) ...
           + a(4).*exp(-(i.*s.*l)) ...
           - k.^2.*exp(i.*k.*s)/(i.*w+k.^4)) .^2));
```

```
f1_s = @(s, t) ...
       real(i.*k.*exp(i.*(k.*s + w.*t)));

Ydot1 = @(s, t) -theta1_sss(s, t) + f1_s(s, t);

Xdot20tmp = @(t) 1/(1 + gamma*F) * ...
    (quad(@(s) -1/2*(s-1).*theta1_squared_t(s, t), 0, 1) ...
     + real(quad(@(s) ((gamma - 1).*theta1(s, t).*Ydot1(s, t)), 0, 1)));

Xdot20 = @(t) arrayfun(Xdot20tmp, t);
```

Listing 3. Computation of the average horizontal velocity

```
function [val Xdot20] = Ubar(w, k, F, M, gamma)

Xdot20 = compute_Xdot20(w, k, F, M, gamma);

val = w/(2*pi)*quad(Xdot20, 0, 2*pi/w);
```