

# Soft Matter On Manifolds

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These notes<sup>1</sup> cover the four lectures delivered by Ronojoy Adhikari in the 2020 Lent term as part of the Part III course *Theoretical Physics of Soft Condensed Matter*. They present an introduction to the study of soft matter on manifolds.

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## 1 Outline and Motivation

In the preceding part of this course, a framework for a field theoretic description of soft matter was established: a system is characterised by an order parameter  $\Psi(\mathbf{x}, t)$  and obeys dynamical equations of the form

$$\partial_t \Psi(\mathbf{x}, t) = \Gamma \frac{\delta F}{\delta \Psi} + \mathbf{v} + \xi \quad (1.1)$$

The three terms capture, respectively, evolution to minimise the free energy functional, an *active* component which breaks time reversal symmetry, and noise. A remarkably large variety of phenomena are well described within this framework.

The order parameter  $\Psi$  is most generally a vector (or tensor) function of space and time. In particular, it has been implicit that  $\mathbf{x}$  is a coordinate in real space  $\mathbb{R}^d$ , be it in 1, 2 or 3 dimensions. We look to generalise this to describe situations where  $\Psi$  may be defined on a *non-Euclidean* manifold. Unlike in the Euclidean case, where geometry takes a backseat and is largely separate of the dynamics, on a general manifold the order parameter can both influence and be influenced by geometry; that is, there is a reciprocal coupling between the field and the manifold.

A program for this generalisation has the following components:

- i) Describe the manifold (differential geometry) *and* its mechanics (reduction theory)
- ii) Describe fields on this manifold (fibre bundles)
- iii) Describe the coupling between the field and the manifold

In particular, in **iii)** only certain types on couplings, namely *differential invariants*, are permitted (this is similar to a gauge principle).

This scheme is very general and in this short series of lectures we develop it in the simplest case: a one-dimensional manifold in  $\mathbb{R}^3$  i.e. a *curve*.

### 1.1 Morphogenesis

Our motivation for a scheme that realises the geometric aspects of soft matter comes from the field of developmental biology or *morphogenesis*. This concerns the interplay of chemicals, mechanics and geometry that facilitates *structurally stable* growth in organisms. The ingredients are

- i) An input of energy, to both create and maintain structure
- ii) Physical constraints arising from fundamental conservation laws and constitutive equations

So an appropriate abstraction would involve an active field theory on a manifold with certain physical constraints. The specific case we develop (a curve) has application to the *cilia* and *flagella* that protrude from certain cells.

## 2 A One-dimensional Manifold

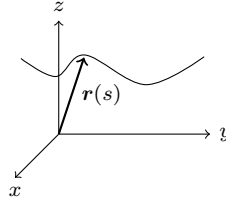
In this section we introduce the geometry and mechanics of a uniform, flexible rod. We begin with a summary of the fundamental differential geometry of curves in 3-space.

## 2.1 Frenet-Serret Apparatus

A curve in  $\mathbb{R}^3$  may be regarded as the image of a vector valued function  $\mathbf{r}(t)$  of a single variable or parameter  $t \in [t_0, t_f]$ . The form of  $\mathbf{r}$  and the choice of parameter is not unique. A natural one is the *arc-length* parametrisation  $\mathbf{r} = \mathbf{r}(s)$ . The arc length  $s$  is such that<sup>2</sup>

$$ds = \left| \frac{d\mathbf{r}}{dt} \right| dt = |\mathbf{v}(t)| dt \quad (2.2)$$

$\mathbf{v}(t)$  is identified as the velocity thus a curve parametrised in terms of  $s$  is traced at *unit* speed. We take  $\mathbf{r}$  to be smooth (at least piecewise) in the sense that it has a continuously turning tangent line, which translates to the existence of a continuous, nonvanishing derivative.



At any point on a curve there exists a right-handed triad of mutually perpendicular unit vectors that form a basis at that point called the *Frenet frame*. The first of these vectors is the unit tangent,

$$\mathbf{t}(s) = \frac{d\mathbf{r}}{ds} \left( = \frac{\mathbf{v}(s)}{|\mathbf{v}(s)|} \right) \quad (2.3)$$

Next the unit normal,<sup>3</sup>

$$\mathbf{n}(s) = \frac{1}{\kappa(s)} \frac{d\mathbf{t}}{ds} \quad (2.4)$$

where  $\kappa(s) = |d\mathbf{t}/ds|$  is the *curvature* ( $1/\kappa(s)$  the radius of curvature).

Finally, the unit binormal,

$$\mathbf{b} = \mathbf{t} \wedge \mathbf{n} \quad (2.5)$$

which satisfies<sup>4</sup>

$$\frac{d\mathbf{b}}{ds} = -\tau(s)\mathbf{n}(s) \quad (2.6)$$

where  $\tau(s)$  defines the torsion, a measure of the extent to which the curve fails to be planar at  $s$  i.e. the degree of twisting ( $\tau > 0$  in a right-handed twist). Since  $\mathbf{n} = \mathbf{b} \wedge \mathbf{t}$ , we also have

$$\frac{d\mathbf{n}}{ds} = -\tau\mathbf{n} \wedge \mathbf{t} + \kappa\mathbf{b} \wedge \mathbf{n} = -\kappa\mathbf{t} + \tau\mathbf{b} \quad (2.7)$$

<sup>2</sup>Given a curve specified by an arbitrary parameter  $t$ , if the arc length over any interval  $[t_0, t]$

$$s = s(t) = \int_{t_0}^t \left| \frac{d\mathbf{r}(\tau)}{d\tau} \right| d\tau \quad (2.1)$$

can be evaluated, and  $s = s(t)$  solved for  $t$  as a function of  $s$ , then  $\mathbf{r} = \mathbf{r}(t(s))$  is the arc length parametrisation.

<sup>3</sup>Differentiating  $\mathbf{t}(s) \cdot \mathbf{t}(s) = 1$  we get  $\mathbf{t} \cdot \mathbf{n} = 0 \leftrightarrow \mathbf{t} \perp \mathbf{n}$ .

<sup>4</sup>Differentiate  $\mathbf{b}(s) \cdot \mathbf{b}(s) = 1$  and (2.5) to find  $d\mathbf{b}/ds$  perpendicular to both  $\mathbf{b}$  and  $\mathbf{t}$ , hence parallel to  $\mathbf{n}$ .

Expressions (2.4), (2.6) and (2.7) are known as the Frenet-Serret formulas. In matrix form,

$$\frac{d}{ds} \begin{pmatrix} \mathbf{t} \\ \mathbf{n} \\ \mathbf{b} \end{pmatrix} = \begin{pmatrix} 0 & \kappa & 0 \\ -\kappa & 0 & \tau \\ 0 & -\tau & 0 \end{pmatrix} \begin{pmatrix} \mathbf{t} \\ \mathbf{n} \\ \mathbf{b} \end{pmatrix} \quad (2.8)$$

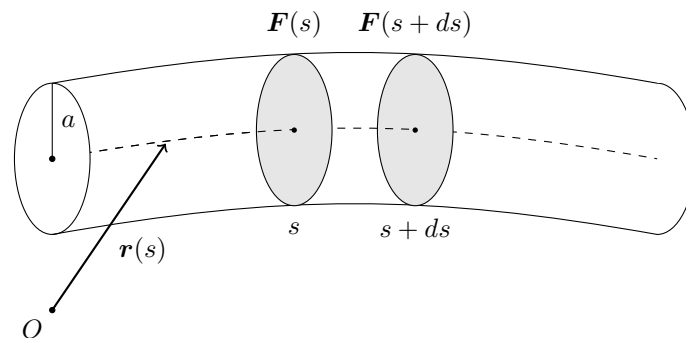
The parameters  $\kappa$  and  $\tau$  have the important property of being invariant under rigid body or Euclidean motions (problem sheet Q1); that is, following an arbitrary translation  $\mathbf{r} \rightarrow \mathbf{r} + \mathbf{a}$  and rotation  $\mathbf{r} \rightarrow \Omega \mathbf{r}$  the equations (2.8) hold for the transformed vectors with the *same*  $\kappa$  and  $\tau$ . The pair are said to be *differential invariants* (unchanged by the action of the Special Euclidean Lie group).

A theorem due to Cartan is that any differential invariant is a function of  $\kappa$  and  $\tau$ . The physical significance is that elastic deformations of a manifold should be invariant under Euclidean motions (rigid body motions should not affect he a rod bends, for example), so all deformations must be functions of  $\kappa$  and  $\tau$  alone; no other combinations of  $\mathbf{r}'(s)$  feature.

The second important result is that a curve with non-vanishing curvature is determined, up to Euclidean motions,<sup>5</sup> by  $\kappa(s)$  and  $\tau(s)$ . Consequently, the differential geometry of a curve is also completely determined by these two functions.

## 2.2 Rod Physics

Consider a long, thin rod with centreline  $\mathbf{r} = \mathbf{r}(s)$ :



If the rod's length is much greater than its diameter, bulk quantities are functions of a single variable – the arc-length,  $s$  – with negligible variation over the cross section.

The net force acting on the volume of the rod comprises internal forces,  $\mathbf{F}$ , and external forces, which in general include body forces such as gravity as well as surface forces transmitted across the boundary of the volume. The former has components

$$F_i(s) = \int \sigma_{ij} n_j dS \quad (2.9)$$

where  $\sigma_{ij}$  is the Cauchy stress tensor and the integral is taken over the cross section with normal  $n_j$ .

At equilibrium, force balance between cross sections at  $s$  and  $s + ds$  requires

$$d\mathbf{F} + \mathbf{f}ds = 0 \quad (2.10)$$

<sup>5</sup>This freedom can be eliminated by specifying two points on the curve.

where  $\mathbf{f}$  is the external force per unit length. Written as a differential equation,

$$\frac{d\mathbf{F}}{ds} + \mathbf{f} = 0 \quad (2.11)$$

we see that this is just conservation of linear momentum when the inertia is zero. A second ODE comes from the analogous conservation of angular momentum

$$d\mathbf{M} + (\mathbf{t}ds) \wedge \mathbf{F} + \mathbf{m}ds = 0 \quad (2.12)$$

$$\frac{d\mathbf{M}}{ds} + \mathbf{t} \wedge \mathbf{F} + \mathbf{m} = 0 \quad (2.13)$$

where  $\mathbf{M}$  is the (internal) cross-sectional moment and  $\mathbf{m}$  the external moment per unit length. The additional term  $\mathbf{t}ds \wedge \mathbf{F}$  is the torque on the cross-section at  $s$  due to internal forces  $\mathbf{F}(s+ds)$  acting on the cross-section at  $s+ds$ .

The general problem is as follows:  $\mathbf{F}(s) = \mathbf{F}(\kappa, \tau)$  and  $\mathbf{M}(s) = \mathbf{M}(\kappa, \tau)$  are unknowns to be found using the above equations and given external forces, moments and boundary conditions. These functions can there be resolved for  $\kappa, \tau$  along  $s$  and from which (integrating the Frenet-Serret equations)  $\mathbf{t}$ , and finally  $\mathbf{r}(s) = \int_0^s \mathbf{t}ds$  can be obtained.

Now that we have set out the basic geometry (Frenet-Serret frame) and mechanics (force and torque balance) of our manifold (rod), we need to couple the two. To do so, we introduce *frictional forces* associated with moving the rod through a viscous fluid. Clearly the geometry of any section the rod will affect the frictional forces there, but also frictional forces will influence the geometry i.e. shape of the rod.

Later, in order to actually do dynamics, we will have to introduce time dependence. For now note that when  $\mathbf{f}$ ,  $\mathbf{m}$  depend on time (2.11) and (2.13) become PDEs.

### 3 Friction on a Slender Rod

Aim: evaluate the frictional force  $\mathbf{f}$  on the rod in terms of its velocity

$$\mathbf{u}(t) = \frac{d\mathbf{r}(t)}{dt} \quad (3.1)$$

Stokes' law relates the frictional force on spherical objects with small Reynolds numbers (inf.) in a viscous fluid to the velocity of that object. To determine a corresponding expression for  $\mathbf{f}$  on the rod (section 3.3), we follow a derivation of Stokes' law that is readily generalised. We firstly recall the description of an incompressible ( $\partial_t \rho = 0$ ) Newtonian fluid.

#### 3.1 Stokes' Equations for a Newtonian Fluid

Conservation of mass requires

$$\nabla \cdot \mathbf{u} = 0 \quad (3.2)$$

and conservation of momentum

$$\rho \frac{D\mathbf{u}}{Dt} - \nabla \cdot \boldsymbol{\sigma} = 0 \quad (3.3)$$

where  $D/Dt$  denotes the material derivative. Expanding this derivative, (3.3) may be written

$$\partial_t (\rho \mathbf{u}) + \nabla \cdot \boldsymbol{\pi} = 0 \quad (3.4)$$

where

$$\boldsymbol{\pi} = (\rho \mathbf{v}) \mathbf{v} - \boldsymbol{\sigma} \quad \text{i.e.} \quad \pi_{ij} = \rho u_i u_j - \sigma_{ij} \quad (3.5)$$

is identified as the momentum flux.

On the basis that, on small scales, inertia in soft matter is unimportant, we neglect the term  $\partial_t (\rho \mathbf{u})$  leaving

$$\nabla \cdot \boldsymbol{\pi} = 0 \quad (3.6)$$

That the fluid is Newtonian means

$$\sigma_{ij} = - \overbrace{p \delta_{ij}}^{\text{pressure stress}} + \underbrace{\eta (\nabla_i u_j + \nabla_j u_i)}_{\substack{\text{viscous stresses} \\ \text{(non-uniform flow)}}} \quad (3.7)$$

i.e. viscous stresses are linear in velocity gradients.<sup>6</sup> The Reynold's number is defined as

$$R = \frac{\rho u L}{\eta} \quad (3.8)$$

where  $u$  is the magnitude of the velocity and  $L$  a typical linear dimension.  $R$  characterises the importance of advective and viscous effects in the flow through the radio

$$R \sim \frac{\rho u u}{\eta u / L} \sim \frac{\text{advective flux}}{\text{viscous stress}} \quad (3.9)$$

For the soft matter systems we consider,  $R \ll 1$  meaning viscous effects dominate. Under these conditions, the advective terms can be dropped giving

$$\nabla \cdot \boldsymbol{\pi} = -\nabla \cdot \boldsymbol{\sigma} = 0 \quad (3.10)$$

Using expression (3.7) for a Newtonian fluid,

$$-\nabla p + \eta \nabla^2 \mathbf{u} = 0 \quad (3.11)$$

We have arrived at Stokes' equations

$$\boxed{\begin{aligned} \eta \nabla^2 \mathbf{u} &= \nabla p \\ \nabla \cdot \mathbf{u} &= 0 \end{aligned}} \quad (3.12)$$

An immediate consequence is that the pressure in the fluid is harmonic:

$$\nabla^2 p = \nabla \cdot \nabla p = \eta \nabla^2 (\nabla \cdot \mathbf{u}) = 0 \quad (3.13)$$

and the velocity biharmonic:

$$\eta \nabla^4 \mathbf{u} = \eta \nabla^2 \nabla^2 \mathbf{u} = \nabla (\nabla^2 p) = \mathbf{0} \quad (3.14)$$

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<sup>6</sup> $\eta$  is the dynamic viscosity or simply the viscosity. A 'kinematic' velocity  $\nu = \eta/\rho$  may also be defined.

### 3.1.1 Boundary Conditions

Now consider a sphere of radius  $a$  and velocity  $\mathbf{V}$  in the flow. Frictional effects (drag) are imparted over the surface  $S$  of the sphere. We look to determine the net force  $\mathbf{F}$  in terms of  $\mathbf{V}$ .

For a viscous fluid, experiments indicate that no-slip boundary conditions are appropriate. These stipulate that the sphere and fluid velocities match on contact. Thus the net force on the sphere,

$$\mathbf{F} = \int_S \boldsymbol{\sigma} \cdot \mathbf{n} dS = \int_S \overbrace{\mathbf{f}(\mathbf{x})}^{\text{force density}} dS \quad (3.15)$$

must have force density  $f$  compatible with

$$\mathbf{u}(\mathbf{x}) = \mathbf{V} \quad \text{on } S \quad (3.16)$$

### 3.1.2 Integral Representation

Recall Green's functions provide a solution to Laplace's equation (Appendix A.1):

$$\nabla^2 \varphi = 0 \rightarrow \varphi(\mathbf{x}) = \int_S \varphi(\mathbf{x}') \partial_n G(\mathbf{x}, \mathbf{x}') - G(\mathbf{x}, \mathbf{x}') \partial_n \varphi(\mathbf{x}) dS' \quad (3.17)$$

where  $\partial_n$  denotes the normal derivative, and  $\mathbf{x}'$  is evaluated on the bounding surface  $S$ . Often  $\varphi$  is a constant here, without loss of generality zero, leaving

$$\varphi(\mathbf{x}) = - \int_S \overbrace{G(\mathbf{x}, \mathbf{x}') \partial_n \varphi(\mathbf{x})}^{\text{Green's function}} \underbrace{dS'}_{\text{charge density on } S} \quad (3.18)$$

The problem has effectively been moved to the boundary. There exists a similar integral representation for Stokes' equations:

$$u_i(\mathbf{x}) = \int_S K_{jik}(\mathbf{x}, \mathbf{x}') n_k(\mathbf{x}') u_j(\mathbf{x}') dS' - \int_S G_{ij}(\mathbf{x}, \mathbf{x}') f_j(\mathbf{x}') dS' \quad (3.19)$$

where  $f_j$  is the force density on  $S$  and  $K_{jik} n_k$  is associated with the normal derivative of  $G$ . Hence  $\mathbf{f}$  is determined as the gradient of the velocity. The Green's function  $G$  is now a tensor, reflecting the fact that the resolved function (velocity) is a vector instead of a scalar. Its components satisfy

$$-\nabla_i p_j + \eta \nabla^2 G_{ij} = -\delta(\mathbf{x} - \mathbf{x}') \delta_{ij} \quad (3.20)$$

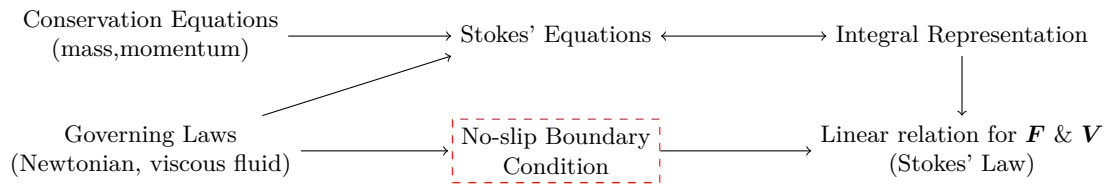
which differs from the scalar case by a new term arising from the gradient of the pressure (cf. (3.12)), while  $K_{jik}$  is given by

$$K_{jik} = -\delta_{jk} p_i + \eta (\nabla_k G_{ij} + \nabla_i G_{jk}) \quad (3.21)$$

The appropriate Green's function turns out to be (problem sheet Q3)

$$G_{ij}(\mathbf{x}, \mathbf{x}') = -\frac{1}{8\pi\eta} (\nabla_i \nabla_j - \delta_{ij} \nabla^2) |\mathbf{x} - \mathbf{x}'| \quad (3.22)$$

$$= \frac{1}{8\pi\eta} \left( \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right) \quad (r = |\mathbf{x} - \mathbf{x}'|) \quad (3.23)$$



**Figure 1:** Derivation of Stokes' law for drag on a sphere. The ingredient missing in the analogous derivation for the rod is the boundary condition. We take  $\dot{\mathbf{r}}$  for this purpose.

An important result for rigid body motion is that the  $K$  integral in (3.19) vanishes. So for a sphere the result reduces to

$$u_i(\mathbf{x}) = - \int_S \overbrace{G_{ij}(\mathbf{x}, \mathbf{x}')}^{\text{Green's Function}} \underbrace{f_j(\mathbf{x}')}_{\substack{\text{force density} \\ \text{on } S}} dS' \quad (3.24)$$

with  $G_{ij}$  as in (3.23). This can be viewed as an integral equation for  $\mathbf{f}$  that is linear in velocity.

### 3.2 Stokes' Law

Applying the boundary conditions (3.16) to (3.24) we have, for  $\mathbf{x} \in S$ ,

$$V_i = - \int_S G_{ij}(\mathbf{x}, \mathbf{x}') f_j(\mathbf{x}') dS' \quad (3.25)$$

To obtain  $\mathbf{F}$ , integrate over the surface (again):

$$4\pi a^2 V_i = - \iint G_{ij}(\mathbf{x}, \mathbf{x}') f_j(\mathbf{x}') dS' dS \quad (3.26)$$

$$= - \int_{S'} \left[ \int_S G_{ij}(\mathbf{x}, \mathbf{x}') dS \right] f_j(\mathbf{x}') dS' \quad (3.27)$$

Inserting the Green's function (3.23) yields, after a bit of work (Appendix A.2),

$$4\pi a^2 \mathbf{V} = - \frac{2a}{3\eta} \int_{S'} \mathbf{f}(\mathbf{x}') dS' \quad (3.28)$$

and so Stokes' law

$$\boxed{\mathbf{F} = -6\pi\eta a \mathbf{V}} \quad (3.29)$$

### 3.3 Rod Friction

Figure 1 summarises the steps leading to Stokes' law for a sphere. The only piece missing in the derivation of an analogous relation for the friction on a rod is a suitable boundary condition. We make the approximation that the velocity of the rod is given by the velocity of the centreline,  $\dot{\mathbf{r}}(s)$  (here a dot denotes a derivative with respect to time, not  $s$ ). This is valid provided, in



addition to being slender, the rod does not rotate i.e. spin around the axis of the rod can be neglected.

Then  $u_i = \dot{r}_i$  on  $S$  ( $S$  once again the surface of the rod), and (3.24) provides

$$\dot{r}_i(s) = - \int_S G_{ij}(\mathbf{r}(s), \mathbf{r}(s')) f_j(s') dS' \quad (3.30)$$

where all quantities vary with  $s$  only. This linear integral equation can be inverted for the general solution

$$f_i(s) = \int_S K_{ij}(s, s') \dot{r}_j(s') dS' \quad (3.31)$$

where  $K_{ij}$  is the inverse linear operator or kernel. Computing this quantity requires integrating  $G_{ij}$  in (3.23) over a small cylindrical patch. The final result for  $\mathbf{f}$  is

$$\mathbf{f}(s) = -\boldsymbol{\gamma} \cdot \dot{\mathbf{r}}(s) \quad (3.32)$$

where  $\boldsymbol{\gamma}$  is the second-rank tensor

$$\boldsymbol{\gamma} = \gamma_n \mathbf{n}\mathbf{n} + \gamma_t \mathbf{t}\mathbf{t} \quad (3.33)$$

So the friction is planar with components arising from motion along  $\mathbf{t}$  and  $\mathbf{n}$

$$\mathbf{f}(s) = - \underbrace{\gamma_n (\dot{\mathbf{r}} \cdot \mathbf{n})}_{\text{normal friction}} \mathbf{n} - \underbrace{\gamma_t (\dot{\mathbf{r}} \cdot \mathbf{t})}_{\text{tangential friction}} \mathbf{t} = f_n \mathbf{n} + f_t \mathbf{t} \quad (3.34)$$

The only combinations of the parameters  $\eta$ ,  $a$  of the system with dimensions of force density multiplied by time is  $\eta a$ , indicating that the coefficients  $\gamma_n$ ,  $\gamma_t$  are proportional to this product. So

$$\gamma_n = c_n \eta a, \quad \gamma_t = c_t \eta a \quad (3.35)$$

for dimensionless constants  $c_n$ ,  $c_t$ .

### 3.4 Constitutive Equations

The frictional law (3.32) allows us to close the system of equations (2.11), (2.13) in the sense that

$$\frac{d\mathbf{F}}{ds} - \boldsymbol{\gamma} \cdot \dot{\mathbf{r}}(s) = 0 \quad (3.36)$$

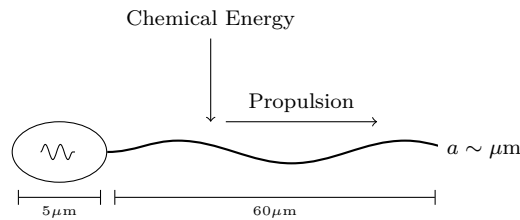
$$\frac{d\mathbf{M}}{ds} + \mathbf{t} \wedge \mathbf{F} + \mathbf{m} = 0 \quad (3.37)$$

makes no reference to our envisioned fluid.<sup>7</sup> Loosely, (3.36) tells us how the rod stretches and (3.37) how it bends. The most relevant cases involve no stretching, in which case the rod is said to be *inextensible*. Then the first equation is really just a constraint, providing  $\mathbf{F}$  for the second.

One way to proceed is to differentiate (3.37) with respect to  $s$ :

$$\frac{d^2 \mathbf{M}}{ds^2} + \frac{d\mathbf{t}}{ds} \wedge \mathbf{F} + \mathbf{t} \wedge \frac{d\mathbf{F}}{ds} + \frac{d\mathbf{m}}{ds} = 0 \quad (3.38)$$

<sup>7</sup>In other words, the sole role of the fluid was to impart  $\mathbf{f}$ . An extension would have it contributing noise also.



**Figure 2:** Sperm cell length scales. The tail (flagellum) is capable of propelling the head forward at  $\sim 100\mu\text{m} \cdot \text{s}^{-1}$ .

and use the Frenet-Serret formulae to obtain

$$\frac{d^2\mathbf{M}}{ds^2} + \kappa\mathbf{n} \wedge \mathbf{F} + \mathbf{t} \wedge \boldsymbol{\gamma} \cdot \dot{\mathbf{r}}(s) + \frac{d\mathbf{m}}{ds} = 0 \quad (3.39)$$

This is dynamical equation for a rod in a viscous fluid in which geometry and mechanics are coupled.

In section 5 we take the more direct approach of integrating the first equation for  $\mathbf{F}$

$$\mathbf{F}(s) - \mathbf{F}(s_0) = \int_{s_0}^s \boldsymbol{\gamma} \cdot \dot{\mathbf{r}}(s') ds' \quad (3.40)$$

and substituting this into the second equation. However, it is often far nicer to work with the second-order (3.39) rather than the first-order differential equation involving an integral that results from this approach ( $\mathbf{F}$  drops out of (3.39) – see problem sheet Q2).

## 4 Motility Engines

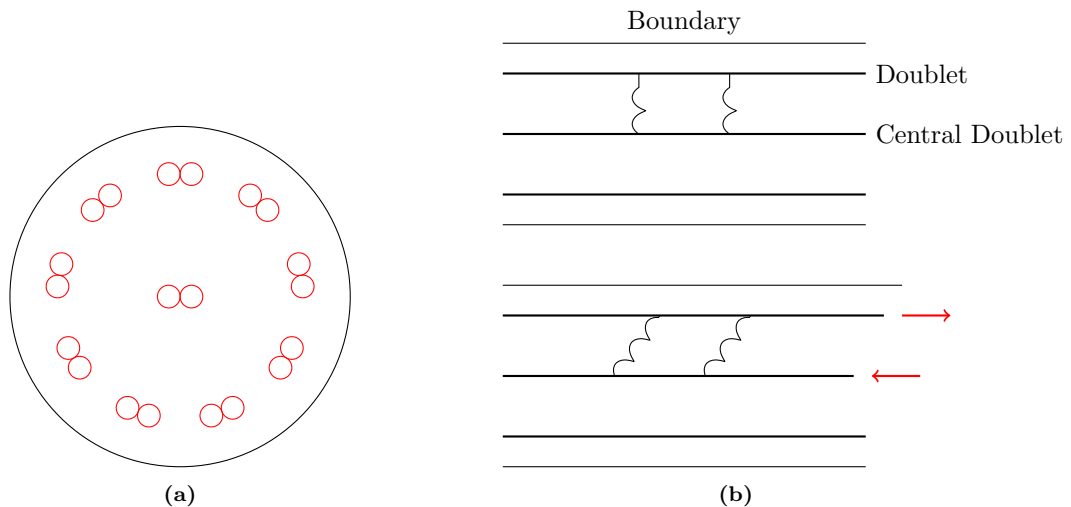
Before taking the equation for rod dynamics further, we discuss the biological systems we intend to model. These are ‘motility engines’ of cellular life in the form of flagella: appendages that consume ATP to produce mechanical motion and operate quite independently of the attached cell. The example we focus on is sperm cell which have a single flagellum (Figure 2).

### 4.1 Sperm Tail Structure and Function

Figure 3a shows the internal structure of the flagella. Nine pairs of filaments (doublets) surround a single inner doublet. This 9 + 2 system of rod is called an axoneme. Motor proteins linking the rods act to slide the doublets against each other, producing motion. Exactly how this sliding is related to the bending of the filaments is not fully understood, but we at least see the applicability of slender ( $L \gg a$ ) inextensible rods subject to shear. Interestingly, there is evidence that the tails operate entirely independently of the head: provided a supply of energy (ATP), severed tails continue to beat (wave). This is opposed to most oscillatory behaviour in the body (e.g. heart beats) that has biological regulation.

Two further observations of sperm motion are:

- i) The filaments beat in a plane
- ii) Speeds are of the order of  $100\mu\text{m} \cdot \text{s}^{-1}$



**Figure 3:** (a) Cross-section and (b) side view of a sperm flagellum. The mechanism of propulsion is not completely established, but involves motor proteins sliding the doublets against one another. For further observation and theory of sperm motility, consult the review by Gaffney et al. ([Annu. Rev. Fluid Mech. 2011. 43:501–28](#)).

The first of these simplifies the kinematics a great deal: we only need to consider planar curves. The second suggests that external fluid dissipation is negligible. Instead, internal sources of dissipation must be present. These should be included in a final model.

## 5 Flagella Dynamics

### 5.1 Planar Motion of a Curve

#### 5.1.1 Darboux Vector

The Darboux vector is the angular velocity  $\boldsymbol{\omega}$  of the Frenet frame such that

$$\frac{d}{ds} \begin{pmatrix} \mathbf{t} \\ \mathbf{n} \\ \mathbf{b} \end{pmatrix} = \boldsymbol{\omega} \wedge \begin{pmatrix} \mathbf{t} \\ \mathbf{n} \\ \mathbf{b} \end{pmatrix} \quad (5.1)$$

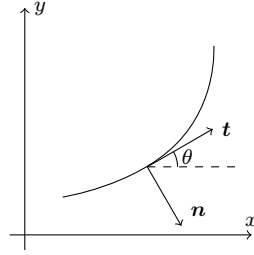
This can be expressed as

$$\boldsymbol{\omega} = \tau \mathbf{t} + \kappa \mathbf{b} \quad (5.2)$$

as may be verified using the Frenet-serret formulae. Note that  $\boldsymbol{\omega}$  is the angular velocity of the frame relative to the origin as you move along the curve i.e. vary  $s$  *not*  $t$  (contrast a rigid body rotating about its centre of mass or a particle rotating about  $O$  with time). We see that  $\kappa$  is a measure of rotation about the unit binormal and  $\tau$  a measure of rotation about the unit tangent. For a planar curve,  $\tau = 0$  and  $\boldsymbol{\omega}$  is normal to the  $\mathbf{t}$ - $\mathbf{b}$  frame:

$$\boldsymbol{\omega} = \frac{d\theta}{ds} \mathbf{b} \quad (5.3)$$

where  $\theta$  is the angle  $\mathbf{t}$  makes with the  $x$ -axis (say) of some fixed frame  $(x, y)$ .



Knowledge of  $\theta$  then specifies the curve up to rigid body motion: if  $\mathbf{t} = \cos\theta\hat{\mathbf{x}} + \sin\theta\hat{\mathbf{y}}$  then

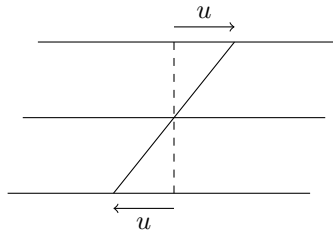
$$\mathbf{r}(s) = \mathbf{r}(0) + \int_0^s \mathbf{t}(s') ds' \quad (5.4)$$

### 5.1.2 Kinematics of Shear

The displacement of the continuum  $u(s)$  at  $s$  associated with the bending  $\theta(s)$  is

$$u(s) = a[\theta(s) - \theta(0)] = a\Delta\theta \quad (5.5)$$

where  $a$  is the radius of the flagella and  $u(0) = 0$  reflects the fact that the filaments are clamped at their base (the head of the sperm).



Since

$$\kappa = \left| \frac{d\mathbf{t}}{ds} \right| = \underbrace{\left| \frac{d\mathbf{t}}{d\theta} \right|}_{=1} \left| \frac{d\theta}{ds} \right| = \left| \frac{d\theta}{ds} \right| \quad (5.6)$$

we have

$$\kappa = \frac{1}{a} \left| \frac{du}{ds} \right| \quad (5.7)$$

So by observing the curvature of the tail we can infer the shear.

## 5.2 Dynamics in the Local Frame

For motion to remain planar internal forces must lie in the plane (as  $\mathbf{f}$  is planar)

$$\mathbf{F}(s) = F_t \mathbf{t} + F_n \mathbf{n} \quad (\mathbf{f}(s) = f_n \mathbf{n} + f_t \mathbf{t}) \quad (5.8)$$

and moments perpendicular to the plane

$$\mathbf{M} = M\mathbf{b}, \quad \mathbf{m} = m\mathbf{b} \quad (5.9)$$

The first constitutive equation (3.36) (force balance) becomes

$$\frac{d}{ds} (F_t \mathbf{t} + F_n \mathbf{n}) + f_n \mathbf{n} + f_t \mathbf{t} = 0 \quad (5.10)$$

Using the Frenet-Serret equations we have, upon resolving components

$$F_t' - \kappa F_n + f_t = 0 \quad (5.11)$$

$$F_n' + \kappa F_t + f_n = 0 \quad (5.12)$$

where prime denotes a derivative with respect to  $s$ . Similarly, from (3.37),

$$M' + F_n + m = 0 \quad (5.13)$$

which we note does not feature  $F_t$ , whilst  $F_n$  should be determined from (5.11) & (5.12) given  $f_t$  and  $f_n$ .

A possible model for the magnitude of the cross-sectional moment is

$$M = EI\kappa \quad (5.14)$$

where  $E$  is the Young's modulus and  $I$  the moment of inertia. As for the external moment per unit length, we posit

$$m = -aku + m^A \quad (5.15)$$

with the first term capturing the passive elastic response to the shear (Hooke's law) and the second an active component.

Taking the direct approach of integrating the force balance equation,

$$F_n = \mathbf{n} \cdot \int_s^L \overbrace{\boldsymbol{\gamma} \cdot \dot{\mathbf{r}}(s')}^{-\mathbf{f}(s')} ds' \quad (5.16)$$

$$= -\gamma_n \int_s^L \mathbf{n} \cdot \dot{\mathbf{r}} ds' \quad (\text{cf. (3.34)}) \quad (5.17)$$

$$\equiv -\gamma_n g_n(s) \quad (5.18)$$

and the moment equation (5.13) becomes

$$EI\partial_s \kappa - \gamma_n g_n - aku + m^A = 0 \quad (5.19)$$

Using  $u = a\Delta\theta(s)$ ,  $\kappa = \partial_s \Delta\theta(s)$ ,

$$\partial_s^2 \Delta\theta - \frac{a^2 k}{EI} \Delta\theta - \frac{\gamma_n}{EI} g_n + m^A = 0 \quad (5.20)$$

Introducing length and time scales  $\ell_k$ ,  $1/\nu_n$ , and rescaling  $m^A$ ,

$$\partial_s^2 \Delta\theta - \ell_k^2 \frac{a^2 k}{EI} \Delta\theta - \frac{\gamma_n \ell_k^2 \nu_n}{a^2 k} g_n + m^A = 0 \quad (\partial_s \rightarrow \partial_s / \ell_k, g_n \rightarrow \ell_k^2 \nu_n g_n) \quad (5.21)$$

so the choice

$$\ell_k = \sqrt{\frac{EI}{a^2 k}}, \quad \nu_n = \frac{EI}{\gamma_n \ell_k^4} \quad (5.22)$$

gives

$$\partial_s^2 \Delta\theta - \Delta\theta - g_n + m^A = 0 \quad (5.23)$$

In fact, order of magnitude estimates reveal that the viscous term  $g_n$  is negligible, with the prediction that any driven motion is unstable, a contradiction. We return to the idea that additional sources of damping must exist, internal to the filament. Indeed, since the filaments are made of soft matter they are susceptible to flow and dissipate energy. To take this into account, we introduce linear damping in each of  $M$ ,  $m$  as

$$M = EI\kappa + \Gamma_\kappa \dot{\kappa} \quad (5.24)$$

and

$$m = -aku - \Gamma_u \dot{u} + m^A \quad (5.25)$$

with  $\Gamma_\kappa$ ,  $\Gamma_u$  phenomenological constants. The resulting equation of motion

$$EI\partial_s^2 \Delta\theta + \Gamma_\kappa \partial_s^2 \partial_t \Delta\theta - a^2 k \Delta\theta - a\Gamma_u \partial_t \Delta\theta + m^A = 0 \quad (5.26)$$

now has two timescales: one for curvature relaxation

$$\nu_\kappa = \frac{EI}{\Gamma_\kappa} \quad (5.27)$$

and a second for shear relaxation

$$\nu_u = \frac{ak}{\Gamma_u} \quad (5.28)$$

In dimensionless form,

$$\partial_s^2 \Delta\theta + \partial_s^2 \partial_t \Delta\theta - \Delta\theta - \frac{\nu_\kappa}{\nu_u} \partial_t \Delta\theta + m^A = 0 \quad (5.29)$$

We complement this with a constitutive model for the active moment  $m^A$

$$\partial_t m^A + b_1 m^A = b_3 \Delta\theta \quad (5.30)$$

which couples activity and geometry. These two equations may be written in matrix form

$$\partial_t \begin{bmatrix} \left( \partial_s^2 - \frac{\nu_\kappa}{\nu_u} \right) \Delta\theta \\ m^A \end{bmatrix} = \begin{bmatrix} 1 - \partial_s^2 & -1 \\ b_3 & -b_1 \end{bmatrix} \begin{bmatrix} \Delta\theta \\ m^A \end{bmatrix} \quad (5.31)$$

These have the form of coupled reaction-diffusion equations with an anomalous  $\partial_t \partial_s^2$  term. Their linearity means linear stability analysis can be performed, assuming a travelling wave solution

$$\Delta\theta, m^A \sim e^{iq_n s - i\omega t} \quad (5.32)$$

where  $q_n$  is the wavenumber of an allowed mode, giving

$$\begin{bmatrix} (1 + q_n)^2 - i\omega \left( q_n^2 + \frac{\nu_\kappa}{\nu_u} \right) & -1 \\ b_3 & i\omega - b_1 \end{bmatrix} \begin{bmatrix} \Delta\theta \\ m^A \end{bmatrix} = 0 \quad (5.33)$$

Setting  $\det = 0$ , we get the eigenmodes

$$\omega_{1,2} = \alpha(q) + i\beta(q) \quad (5.34)$$

with oscillatory unstable motion present when  $\beta(q) > 0$ ,  $\alpha(q) \neq 0$ . Careful analysis shows<sup>8</sup> that this is a possibility and indeed non-linear terms must be considered in order to obtain stable oscillations.

<sup>8</sup>See the recent preprint [arXiv:1904.07783](https://arxiv.org/abs/1904.07783) for the details and further discussion.

## A Green's Functions

### A.1 Green's Second Identity

Green's second identity for twice differentiable functions  $f(\mathbf{x})$ ,  $g(\mathbf{x})$  on a domain  $D \subseteq \mathbb{R}^n$  with boundary  $\partial D$  is

$$\int_D (f\nabla^2 g - g\nabla^2 f) d\xi = \int_{\partial D} (f\nabla g - g\nabla f) \cdot \mathbf{n} dS \quad (\text{A.1})$$

Given a Green's function  $G(\mathbf{x}, \xi)$  satisfying

$$\nabla^2 G = \delta(\mathbf{x} - \xi) \quad \xi \in D \quad (\text{A.2})$$

the solution to

$$\nabla^2 \varphi(\mathbf{x}) = u(\mathbf{x}) \quad \mathbf{x} \in D \quad (\text{A.3})$$

$$\varphi(\mathbf{x}) = v(\mathbf{x}) \quad \mathbf{x} \in \partial D \quad (\text{A.4})$$

is, using (A.1),

$$\varphi(\mathbf{x}) = \int_D G(\mathbf{x}, \xi) u(\xi) d\xi + \int_{\partial D} (v(\xi) \partial_n G(\mathbf{x}, \xi) - G(\mathbf{x}, \xi) \partial_n \varphi(\mathbf{x})) dS \quad (\text{A.5})$$

where  $\partial_n = \mathbf{n} \cdot \nabla$  is the normal derivative. Often  $G$  is chosen to vanish on the boundary, in which case the second term of (A.5) is zero. The case considered in lectures corresponds to  $S = \partial D$  and  $u$  (and then  $v$ ) identically zero.

### A.2 Integrating the Stokes' Flow Green's Function

We look to evaluate

$$\int_S G_{ij}(\mathbf{x}, \mathbf{x}') dS \quad (\text{A.6})$$

where  $S$  is a spherical surface (radius  $a$ ) and

$$G_{ij}(\mathbf{x}, \mathbf{x}') = \frac{1}{8\pi\eta} \left( \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right) \quad (\text{A.7})$$

with positions  $r = |\mathbf{x} - \mathbf{x}'|$  measured relative to  $\mathbf{x}'$ .

Firstly, the  $\delta_{ij}$  term is trivial:  $r = a$  on the sphere so

$$\int_S \frac{\delta_{ij}}{r} dS = \frac{\delta_{ij}}{a} \int_S dS = 4\pi a \delta_{ij} \quad (\text{A.8})$$

By symmetry, the diagonal components of the second term must all be equal. For example,  $i = j = 1$  gives

$$\int_S \frac{x^2}{r^3} dS = \frac{1}{a^3} \int_0^\pi \int_0^{2\pi} (a \sin \theta \cos \phi)^2 (a^2 \sin \theta) d\theta d\phi \quad (\text{A.9})$$

$$= a \int_0^\pi \sin^3 \theta d\theta \int_0^{2\pi} \cos^2 \phi d\phi \quad (\text{A.10})$$

$$= a \cdot \frac{4}{3} \cdot \pi \quad (\text{A.11})$$

$$= \frac{4\pi a}{3} \quad (\text{A.12})$$

Similarly, the off-diagonal components are all equal and in fact vanish as seen from

$$\int_S xy dS = 0 \quad (\text{A.13})$$

by symmetry.

In total then,

$$\int_S G_{ij}(\mathbf{x}, \mathbf{x}') dS = \frac{1}{8\pi\eta} \left( 4\pi a + \frac{4\pi}{3} a \right) \delta_{ij} = \frac{2a}{3\eta} \delta_{ij} \quad (\text{A.14})$$

Contracting the second index with  $f_j$ , we indeed obtain (3.28).