University *of Ljubljana*
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SEMINAR

Life at low Reynolds number

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May 20, 2009

Abstract

The aim of this seminar is to present the basic facts about life at low Reynolds number and the physics of group transport of sperm in the female reproductive tract. Thus, the seminar is divided into two parts. The first deals primarily with the mechanics of Stokes flow and with two postulates of swimming at low Reynolds number which bound microorganism to have evolved in a particular way to allow motion in that inertialess world. In the second part we are interested in sperm and their interaction, their interaction with surrounding walls and with each other. Also, we discuss how a sperm seeks its way to the egg by a process called chemotaxis. This is a physical treatment, mostly intuitive.

Contents

1 Introduction

The duty, shear responsibility of human male sperm cells* to swim from the lower parts of the female reproductive tract through the cervix and across the length of the uterus toward the ovum, is indeed noteworthy. Not one, but hundreds and thousands of sperm cells set on a voyage so unlikely to produce fertilization results, yet nature has arranged things so that even this small and weak creature in a non hospitable environment such as the acidic cervical mucus, may accomplish its task successfully. We should like to know what physical obstacles must sperm overcome. How do sperm cells swim [4, 5], how they interact with each other [3], how does the surrounding environment affect them [9]. To learn this we must first investigate the laws which govern their dynamics.

The reason microorganisms move is familiar. Bacteria such as E. coli† detect gradients of nutrients and move to regions of higher concentrations. Sperm cells of many organisms swim toward the ovum by a process called *chemotaxis*: detecting gradients of the substance released by the female egg and moving in that direction [6]. But what is not so familiar to most is the fact that the world of swimming sperm, the world of micrometers, is different from the macro-world. In this fluidic world microorganisms swim at low Reynolds number [1, 2]. In a world with this quality one cannot rely on inertial forces to move, since their effect is practically marginal. Any attempt to move by imparting momentum to the fluid, as what one usually does when paddling in water, would be foiled by the large force of viscous drag. Microorganism have evolved strategies that overcome this problem and exploit the drag force to their advantage. Bellow is a short pictorial overview of these microorganisms.

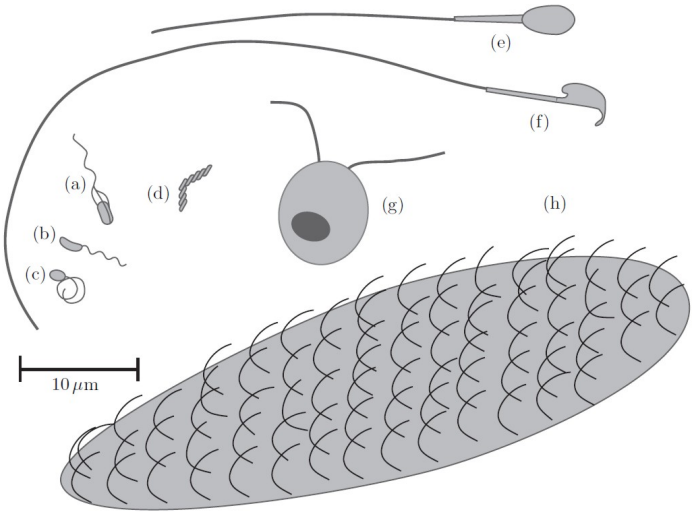


Figure 1: Microorganisms, sketched to scale. (a) E. coli. (b) C. crescentus. (c) R. sphaeroides, with filament in the coiled state. (d) Spiroplasma. (e) Human sperm cell. (f) Mouse sperm cell. (g) Chlamydomonas. (h) A smallish Paramecium. Source: [1].

*We shall adopt this expression even though in formal language a more appropriate term is *a spermatozoon*.

†Escherichia coli. A bacterium which is commonly found in the lower intestine of warm-blooded animals.

Let us define a swimming organism: *a swimming organism is a creature or an object that moves by varying its shape in a periodic manner.*

Many swimmers use their tails or appendages for propulsion. The appendage could be a relatively stiff helix that is rotated by a motor embedded in cell walls (E. coli), or it could be a flexible filament undergoing deformations due to the motors distributed along the length of the filament (Human and mouse sperm cells, for example). There are, of course, bacteria that swim with no external flagellar filaments, but we will be interested only in the swimming of sperm with whip-like flagella (Figure 1a, b, c, e, f). Figure 1 shows different swimmers drawn to scale so that we can compare them. The sperm of most mammals consist of a head, containing genetic material, propelled by a filament with planar or even helical beat pattern, depending on the species. The length of the flagellum is about 20 μm for hippos, 50 μm for humans, 80 μm for mice, and can even be 1 mm or several cm long in some fruit flies. Figure 2 displays a typical diagram of a human sperm.

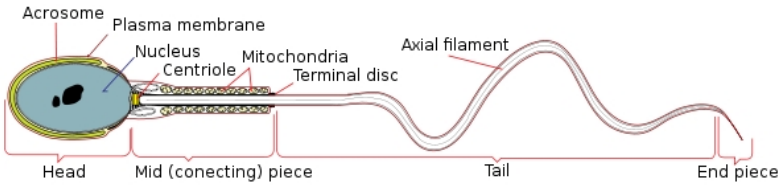


Figure 2: The human sperm cell.

2 Hydrodynamics at low Reynolds number

2.1 General properties

We briefly discuss, beforehand, the general hydrodynamic laws of flow at low Reynolds number. From the Cauchy equation of continuous media, ie. Newton's Law, the so called Navier-Stokes equation for an incompressible Newtonian fluid may be derived,

$$\rho\left(\frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v}\cdot\nabla)\,\mathbf{v}\right) = \rho\,\mathbf{f}^{\text{ext}} - \nabla p + \eta\nabla^2\mathbf{v}, \qquad \nabla\cdot\mathbf{v} = 0. \tag{1}$$

Where $\mathbf{v}$ is the fluid flow (velocity) field, ρ is the density of the fluid, p is the hydrostatic pressure and η the coefficient of viscosity. A Newtonian fluid is a fluid for which the relationship between the stress tensor and the shear stress tensor (v_{ik}) is linear:

$$p_{ik} = -p\delta_{ik} + 2\eta v_{ik} \tag{2}$$

Such is the fluid of human semen. It is necessary to add to equation (1) sufficient boundary conditions, usually that the velocity field on the boundary of a submerged body is zero, $\mathbf{v}\,|_{\partial B} = 0$. The condition for incompressibility, $\nabla\cdot\mathbf{v} = 0$, follows from the equation of continuity, and causes the relation between the shear stress tensor and stress tensor to drop a term proportional to $\delta_{ik}v_{ll}$. Also, if we were to solve a general Navier-Stokes equation, we would need an additional equation (since there

are five variables: $\mathbf{v}$, ρ, p), a thermodynamic relation $p = p(\rho)$. Once we have solved the problem for $\mathbf{v}$ and p, the stress tensor is given by equation (2), and the force $\mathbf{F}$ and torque $\mathbf{M}$ acting upon the organism submerged in fluid are found by integrating along its surface:

$$\mathbf{F} = \oint_{\partial V} P \cdot \mathbf{n}\, dS, \qquad \mathbf{M} = \oint_{\partial V} \mathbf{r} \times (P \cdot \mathbf{n})\, dS. \tag{3}$$

Note that P is the matrix representation of the tensor p_{ik}! If we put the Navier-Stokes equation in a non-dimensional form, we would discover that the solution is parametrized by three constants. The solutions of the Navier-Stokes equation are identical for the same three constants. One of them, and for us the most important one, is the Reynolds number, $\mathrm{Re} = \frac{VL\rho}{\eta}$, where V is a typical velocity of the flow and L is the characteristic size of the body. The Reynolds number has many interpretations. We offer three:

- Consider a body of characteristic size L placed in a steady flow with velocity V. The Reynolds number is the ratio between the inertial term in equation (1), $\rho\mathbf{v} \cdot \nabla\mathbf{u}$, and viscous term, $\eta\nabla^2\mathbf{u}$. Thus, $\mathrm{Re} = \rho LV/\eta$. A low-Reynolds-number flow is one for which viscous forces dominate in the fluid.

- The typical time scale for a velocity perturbation to be transported convectively (by inertial term) by the flow along the body is $t_{\mathrm{conv}} = L/U$. Whereas the typical time scale for this perturbation to diffuse away from the body due to viscosity is $t_{\mathrm{diff}} = \rho L^2/\eta$. Thus, $\mathrm{Re} = \frac{t_{\mathrm{diff}}}{t_{\mathrm{conv}}}$. So we see that in a low-Reynolds-number flow the fluid transport is dominated by viscous diffusion.

- A familiar interpretation is that the Reynolds number is the ratio of inertial and viscous forces acting upon the body. Inertial forces may be approximated from the Bernoulli equation, $f_{\mathrm{inert}} = \rho V^2 L^2$, whilst the viscous force is $f_{\mathrm{visc}} = \eta VL$. Again we see that the low Reynolds number, $\mathrm{Re} = \frac{f_{\mathrm{inert}}}{f_{\mathrm{visc}}}$, means that the effect of inertial forces on the body is marginal.

Why are these interpretations important? They helps us determine whether the sperm cells are swimming in fluids, mostly the semen and cervical mucus, at low Reynolds number. In water ($\rho = 1\,\mathrm{kg/dm^3}$, $\eta = 10^{-3}\,\mathrm{Pa\,s}$) a human sperm with $V \approx 200\,\mu\mathrm{m/s}$ and $L \approx 50\,\mu\mathrm{m}$ moves at $\mathrm{Re} = 10^{-2}$. A swimming bacterium such as E. Coli has a Reynolds number of $\mathrm{Re} = 10^{-5} - 10^{-4}$.

Since we have established that the swimmer swims in fluid at low Reynolds number, we can make a final simplification to the Navier-Stokes equation. We can assume that $\mathrm{Re} = 0$ and add to this the condition for stationarity: $\partial\mathbf{v}/\partial t = 0$. Equation (1) simplifies to the inhomogeneous Stokes equation

$$\eta\nabla^2\mathbf{v} = \nabla p - \mathbf{f}^{\mathrm{ext}}, \qquad \nabla \cdot \mathbf{v} = 0. \tag{4}$$

This equation has a few special features, the two most important one being: it is linear and independent of time.

Now we continue the discussion with the motion of solid bodies at low Reynolds number. This will be useful in understanding the drag force on the sperm cell.

2.2 Motion of solid bodies

When a solid physical body is submerged in a viscous fluid and moves at a low Reynolds number (theoretically $\mathrm{Re} = 0$), the trajectory of the body can be calculated in the following way. Since the Stokes equation governing the motion of the body is linear, we expect the relationships between forces, torques, velocities and angular velocities to be also linear. This is pretty clear from experience. We know that the force acting upon a moving sphere in a stationary fluid (equally, if the fluid moves and the sphere is stationary), moving with velocity $\mathbf{V}$, is linearly proportional to its speed ($\mathbf{F} = 6\pi a\eta\mathbf{V}$). The same holds for torque and angular velocity if the sphere's translational velocity is zero but rotates with the angular rate $\mathbf{\Omega}$ - then the torque is $\mathbf{M} = 8\pi a^3\eta\,\mathbf{\Omega}$, where a is the radius of the sphere. If the sphere rotates and moves forward, the principle of superposition would apply for both force and torque since the Stokes equation is linear, $\mathbf{F} = A\mathbf{V} + B\mathbf{\Omega}$ and $\mathbf{M} = C\mathbf{V} + D\mathbf{\Omega}$.

The head of the sperm cell is practically a sphere (in reality, it is a prolate spheroid), so we already know one part of the drag force which acts upon the cell while it swims in the fluid. The flagellum is its propulsion motor. So far the reader may be under the impression that the head of the sperm carries only the genetic material, it serves no other mechanical purpose, excluding the balancing of momentum. The reader is always right! In fact, it turns out, as we shall see in chapters ahead, that the crucial condition for successful flagellar motility is the so-called *drag anisotropy*: drag force and torque must not be isotropic. Without drag anisotropy biological locomotion would not be possible at low Reynolds number!

We move to mention the fundamental singular solutions of the Stokes equation, which are, for the most part, familiar from electrostatic analogs.

2.3 Fundamental solutions of the Stokes equation

Solutions of a linear equation may be sought in the form of the fundamental Green functions. The primary, or the first fundamental solution, is associated with a singular force acting in a point, say, the origin,

$$\mathbf{f}^{\mathrm{ext}} = \mathbf{F}\delta(\mathbf{r}),$$

$\mathbf{F}$ being a constant vector and $\delta(\mathbf{r})$ the three-dimensional Dirac delta. Flow under these conditions is called a *Stokeslet* and $\mathbf{F}$ characterizes its strength in magnitude and direction. Velocity $\mathbf{v}$ and pressure p of a Stokeslet are

$$\mathbf{v} = \frac{1}{8\pi\eta}\left(\frac{\mathbf{F}}{r} + \frac{(\mathbf{r}\cdot\mathbf{F})\,\mathbf{r}}{r^3}\right), \tag{5}$$

$$p = \frac{\mathbf{r}\cdot\mathbf{F}}{4\pi r^3}. \tag{6}$$

Again, physically this solution represents the flow field due to a point force, $\mathbf{F}$, acting on the fluid at the origin of the coordinate system.* The velocity field is similar to the electric field of an electric dipole. It decays in space as $1/r$, while the pressure decreases like $1/r^2$. The total force exerted by a Stokeslet on the fluid outside a control volume enclosing the Stokeslet is $8\pi\eta\mathbf{F}$.

*It should be noted that this solution can also be obtained by solving the force-free Stokes equations: $\nabla p = \eta\nabla^2\mathbf{v}$. In our further proceedings the external force will be identically equal to zero.

The Stokeslet solution exhibits the directional anisotropy mentioned before. If we evaluate equation (5) in the direction parallel and perpendicular to the applied force, we obtain

$$\begin{aligned} v_{\parallel} &= \left(\mathbf{v}\cdot\frac{\mathbf{F}}{F}\right)_{\mathbf{r}\cdot\mathbf{F}=rF} = \frac{F}{4\pi r\eta}, \\ v_{\perp} &= \left(\mathbf{v}\cdot\frac{\mathbf{F}}{F}\right)_{\mathbf{r}\cdot\mathbf{F}=0} = \frac{F}{8\pi r\eta}, \end{aligned}$$

which means that the velocity in the parallel direction to the force is twice as great than that in the perpendicular direction. In other words, one would need to apply a force in the perpendicular direction twice as large as in the parallel direction ($F_{\perp} = 2F_{\parallel}$) to obtain the same velocity. This is the kind of anisotropy we were taking about before.

Another thing should be said. There are many more fundamental solutions of the Stokes equation with singularly distributed force. In fact, a derivative of any order of the equations (5) and (6) is also a solution of the Stokes equation, where the corresponding $\mathbf{f}^{\text{ext}}$ is the derivative of the same order of $\mathbf{F}\delta(\mathbf{r})$. This fundamental solutions are needed when trying to solve the Stokes equations for a given geometry of the body by means of linear superposition.

When a flow is described by a number of different fundamental solutions, the one with the lowest spatial decay is the one that dominates in the far field. Since a cell swimming in a viscous fluid at low Reynolds number is force and torque free, the flow singularities that describe point-forces (Stokeslests) and point-torques (antisymmetric force-dipole or rotlets) cannot be included in the far field description. As a result, the flow field far from a swimming cell is in general well represented by a symmetric force-dipole, or stresslet. Such far-field behavior has important consequences on cell-cell hydrodynamic interactions (for further discussion see [10]).

3 Life at low Reynolds number

Now we focus on the swimmers self-propelled motion at low Reynolds number. We expand the definition of a swimmer: *an organism is a swimmer if by deforming its surface, it is able to sustain movement through fluid in the absence of external non-hydrodynamic forces and torques.* Body may, of course, include appendages, such as the flagella of a human sperm. But appendages are not necessary (drag anisotropy is crucial!).

3.1 A new meaning of Re

Consider a sperm cell of mass m and characteristic size L swimming with constant velocity V through a viscous Newtonian fluid of density ρ and viscosity η. Imagine sperm stops moving its flagella; it will then decelerate according to Newton's law and eventually stop. Let us calculate the length over which the sperm will coast during its deceleration. From $f_{\text{drag}} = ma$ and the fact that at low Reynolds number the drag force is purely viscous, $f_{\text{drag}} = VL\eta$, it follows $a = VL\eta/m$. Supposing constant deceleration and approximate swimmer's density $\rho_s = m/L^3$, the coasting distance is $d = V^2/2a = \rho_s VL^2/2\eta = L\text{Re}\,\rho_s/\rho$. By introducing dimensionless coasting distance d/L the Reynolds number gets a neat interpretation: since $\rho_s/\rho \approx 1$, the Reynolds

number becomes the non-dimensional cruising distance, $d/L = \mathrm{Re}$. For a human sperm cell the cruising distance is about $d/L = 10^{-2}$. This means that the swimmer will stop moving almost immediately after it stops swimming (only Newtonian fluids are considered so far; possible elasticity of the fluid and its anisotropy are neglected). The same calculation can be done for a swimmer at higher Reynolds number, possibly a human swimming in the river. In this case, the drag force has an inertial quality. The coasting distance in higher-Reynolds-number world is $d/L = \rho_s/\rho \approx 1$. A human swimmer in water can cruise for a meter or so.

We see from this analysis that the response of the fluid at low Reynolds number to the motion of boundaries is practically instantaneous. This conclusion was already anticipated by our second interpretation of the Reynolds number in section 2.1. The rate at which the momentum of a swimmer is changing is completely negligible when compared to the typical magnitude of the forces from the surrounding viscous fluid. We can, therefore, state that the external forces acting upon the swimmer (non-hydrodynamic) and the forces by which the fluid acts upon the body are in balance. The same should hold for torques.

$$\mathbf{F}^{\text{ext}} + \mathbf{F} = \mathbf{0}, \qquad \mathbf{M}^{\text{ext}} + \mathbf{M} = \mathbf{0} \tag{7}$$

Since, already we have assumed that no external forces act upon the swimmer when we were outlying the general theory of Stokes flow, and expecting the same to be true for torques, we can deduce from (9) that $\mathbf{F} = \mathbf{0}$ and $\mathbf{M} = \mathbf{0}$.

4 The problem of swimming

Although it has been said that the swimmer is by definition a deformable body, it may also be viewed at any instant as a solid body translating with a constant velocity $\mathbf{V}$, rotating with the constant rotation rate $\mathbf{\Omega}$. The velocity of a point $\mathbf{r}$ on the surface of the body is $\mathbf{v}_S$, relative to a coordinate system fixed to a point inside the body. With this definitions we can express the instantaneous velocity of a point on the surface like so:

$$\mathbf{v}(\mathbf{r}, t) = \mathbf{v}_S(\mathbf{r}, t) + \mathbf{V} + \mathbf{\Omega} \times \mathbf{r}.$$

This is the needed boundary condition for solving the Stokes equation for the flow around the body. It can be shown that the velocity $\mathbf{V}$ and $\mathbf{\Omega}$ are determined by the velocity of the surface points on the body $\mathbf{v}_S$ (for reference see [1]), given beforehand the solution to the dual problem of the flow induced by the motion of a rigid body with instantaneous shape $S(t)$, subject to force $\mathbf{F}$ and torque $\mathbf{M}$.

Sperm cells swim by waving their flagella, which we suppose are slender. This limit of slender bodies allows us to gain an intuitive insight into the problem of locomotion through drag. After all, the problem of swimming of arbitrarily shaped *creatures* is a difficult one.

Consider, if you will, the sperm's flagella being a thin filament, piece-wise stiff, immersed in a viscous fluid. The fluid is stationary except for the flows induced by the deformations of the filament. The shape of the filament will be described by the tangent vector $\mathbf{t}(\mathbf{s})$, depending on the parameter s - the length of the filament from the origin of the coordinate system placed in the sperm's head. The velocity of the filament is given by $\mathbf{v}(s, t)$, where t is time. The velocity always points upward because we have chosen a coordinate system in which sperm stands still. The local

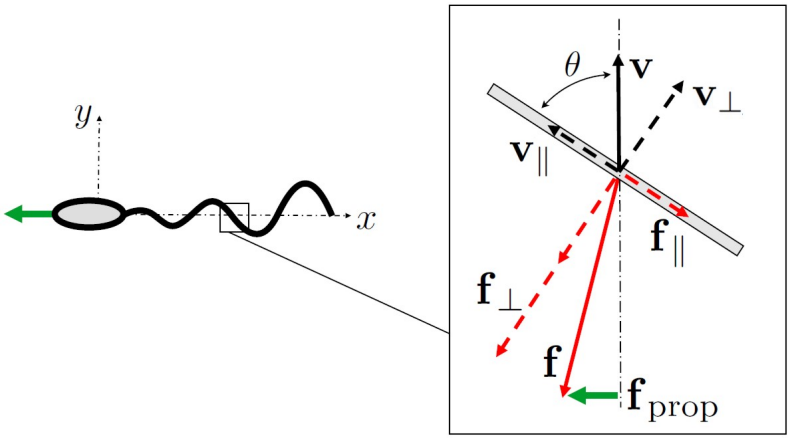


Figure 3: Physics of drag-based thrust: The drag anisotropy for slender filaments provides a means to generate forces perpendicular to the direction of the local actuation. Source: [1].

viscous force per unit length opposing the motion of the filament* is

$$\mathbf{f} = -\xi_{\parallel}\mathbf{v}_{\parallel} - \xi_{\perp}\mathbf{v}_{\perp}, \tag{8}$$

where $\mathbf{v}_{\parallel}$ and $\mathbf{v}_{\perp}$ are the projections of the local velocity of the filament onto the directions parallel and perpendicular to the filament (see figure 3). In other words: $\mathbf{v}_{\parallel} = (\mathbf{v}\cdot\mathbf{t})\mathbf{t}$ and $\mathbf{v}_{\perp} = \mathbf{v} - \mathbf{v}_{\parallel}$. Coefficients $\xi_{\perp}$ and $\xi_{\parallel}$ are the corresponding *drag coefficients*.

Now, we regard every short segment of the sperm's filament to be solid and reasonably straight, moving with velocity $\mathbf{v}$ at an angle θ with the local tangent (figure 3). Velocity parallel to the tangent has a magnitude of $v_{\parallel} = v\cos\theta$, similarly for the velocity perpendicular to the tangent: $v_{\perp} = v\sin\theta$. The propulsive force is therefore $\mathbf{f}_{\text{prop}} = (\mathbf{f}\cdot\mathbf{e_x})\mathbf{e_x}$, where $\mathbf{e_x} = (1,\,0)$ is the unit vector in the direction of x. Whereas, the force $\mathbf{f}$ is composed like so $\mathbf{f} = f_{\parallel}\mathbf{e}_{\parallel} + f_{\perp}\mathbf{e}_{\perp}$, where $\mathbf{e}_{\parallel} = -(\sin\theta,\,\cos\theta)$ and $\mathbf{e}_{\perp} = (\cos\theta,\,\sin\theta)$ are unit vectors in the directions of the filament and perpendicular to it. All this gives for the propulsion force

$$\mathbf{f}_{\text{prop}} = \left(\xi_{\parallel} - \xi_{\perp}\right) v\sin\theta\cos\theta\mathbf{e_x}. \tag{9}$$

This component of force is parallel to the sperm's velocity. In order to generate a net propulsion from a time-periodic movement of the filament, we see from equation (9) that v and θ must vary periodically in time. Thus we have decomposed the drag force acting on the filament into contributions by short cylinders, theoretically very thin and straight. The total propulsion force will then be the sum of all such contributions throughout the filament.

Two things should be repeated so not to loose the reader just before the most important *theorem* of swimming at low Reynolds number. First, drag anisotropy is absolutely vital and follows directly from the properties of the Stokes flow. If the

*We must stress that at all times the total force acting upon the body is still zero (equation 7). The total force is the sum of the drag force with which the fluid acts upon the sperm and opposes movement, and the force with which the filament propels the sperm. $\mathbf{F} + \mathbf{F}_{\text{prop}} = 0$.

coefficient $\xi_{\parallel}$ and $\xi_{\perp}$ of the linear drag on a cylinder were equal (indeed they are not, but look at equation (9)), the propulsion force would be zero. And second, and this will be the most important reasoning, almost a theorem so far: the periodic actuation of the filament must be sufficiently subtle in order to generate non-zero forces on average; it must obey the so-called ***scallop theorem***.

4.1 The scallop theorem and rate independence

We have stated that the Stokes equation is linear and independent of time. How does that influence the swimmer in a viscous liquid? If we scale swimmer's velocity and rotation rate by a factor, say α, $\mathbf{V} \to \alpha\mathbf{V}$ and $\mathbf{\Omega} \to \alpha\mathbf{\Omega}$, then by linearity, the flow around it will transform similarly as $\mathbf{v} \to \alpha\mathbf{v}$ and $p \to \alpha p$. The instantaneous flow streamlines will stay the same, and the force and torque on the swimmer will also change by the same factor, $\mathbf{F} \to \alpha\mathbf{F}$ and $\mathbf{M} \to \alpha\mathbf{M}$. If we were to set $\alpha = -1$, the force $\mathbf{F}$ and the flow $\mathbf{v}$ would change direction, while the flow patterns would remain identical. This, and the fact that the flow is defined at every moment by the kinematics of the swimmer because the relaxation of fluid is instantaneous, postulates **the rate independence** of the swimmer:
The distance travelled by the swimmer between two different surface configurations does not depend on the rate at which the surface deformation occurs, but only on the geometry of intermediate shapes.

To elucidate this theorem further consider a scallop depicted on figure 4. The scallop comprises of one hinge and two legs, waving like packman's mouth. The scallop is doomed, since the low-Re world is unaware of inertia, it will not help to close the valves quickly and reopen them slowly. The rate by which you change the shape of your body does not matter at all!

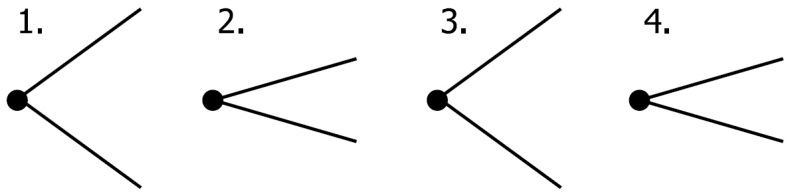
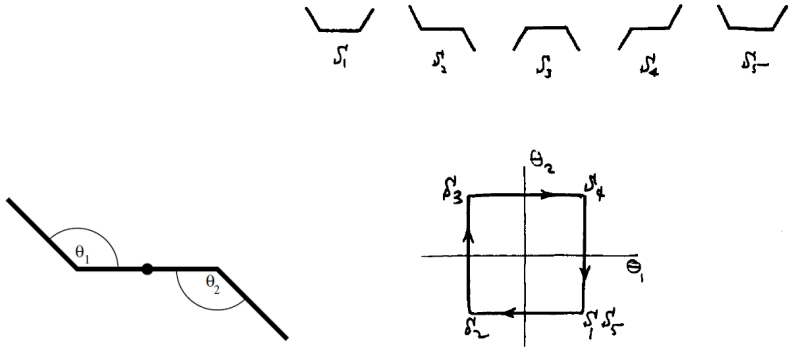


Figure 4: The swimming stroke of a scallop: This swimmer consists of two legs connected by a joint and is immersed in a viscous liquid. As the angle between the two legs changes periodically, the swimmer will move back and forth. Its net displacement, however, will be zero in the zero-Reynolds-number limit, since the swimming stroke is reciprocal. Opening the valves slowly and closing them fast is useless. Source: [8].

And now comes the famous *scallop theorem*, which has nothing to do with the culinary arts. First of all, a swimmer should always deform its body, its flagella, in a cyclic fashion. It does not do any good to use a motion that goes to zero asymptotically or if it stops in the middle. One has to keep moving - remember, there is no inertia at low Reynolds number. So let us take another look at the scallop on figure 4. A scallop lives in a world of higher Reynolds number and can move by slowly opening and closing fast its shell, hence squirting water and imparting momentum on the fluid. If the scallop was small enough to live in the world of sperm, it would not be able to move with this method. The problem is that it exactly repeats its move in every cycle causing to oscillate only. We say that it moves *reciprocally*: *The motion of a*

swimmer is called reciprocal if the sequence of shapes which the swimmer assumes is invariant under time-reversal. The story of the scallop would change if it had another hinge. Than it would not move reciprocally, since we introduce an additional degree of freedom. See figure 5. The swimmer in this case is called the *Purcell's swimmer*. If you were to draw a configuration-space diagram of angles θ_1 and θ_2 between the legs and the horizontal body-line, you would truly see that the swimmer follows a loop in that configuration space, enabling it to swim. Never does it repeat its move.



(a) (b)

Figure 5: a) The Purcell's swimmer (invented by E. M. Purcell). The swimmer consists of two hinges. As the angles θ_1 and θ_2 change cyclically, the swimmer moves back and forth with a non-zero net displacement. b) A drawing made by Purcell himself. The swimmer depicted moves to the right. Reversing the order of shapes changes the direction of the swimmer. Source: [2].

It should be said that it is not always intuitively clear which way these swimmers will move. Our experience from paddling on water are of no use and one must make some serious considerations or even calculations.

This was the essence of the **scallop theorem**:
If the sequence of shapes displayed by a swimmer deforming in a time-periodic way is identical when viewed after a time-reversal transformation, then the swimmer cannot move on average.

There is no point in proving the theorem mathematically, we would only loose space, even if the proof is simple. The rate independence and the scallop are valid even if the swimmer is confined within walls. It just so happens that the geometry of the fluid bears little importance when discussing the ability to swim. However, the walls do change the swimmers trajectories.

To conclude, we propose that the deformation of the spermatozoon flagella is wave-like, with amplitude $y(x,t)$. By assuming that the deformations are small, ie. $\left|\frac{\partial y}{\partial x}\right| \ll 1$, we can give the propulsive force generated along the filament by:

$$\mathbf{F}_{\text{prop}} \approx \left(\xi_\perp - \xi_\parallel\right) \int_0^L \frac{\partial y}{\partial t} \cdot \frac{\partial y}{\partial x}\, dx\, \mathbf{e}_\mathbf{x}, \tag{10}$$

which is obtained by integrating (9) throughout the length of the filament; L is its length. In addition, to satisfy the force balance, we need to obtain the drag force which opposes the motion of the swimmer. This drag force is composed of two parts: the drag force on the swimmer's spherical head and the drag force on the filament.

4.2 Calculating the speed of sperm

In this subsection we shall estimate the speed at which the sperm travels. We shall consider only the limit where propulsion is generated by the deformation of the sperm's slender filament. One could also imagine the filament to move, say in circles, which is not so unusual for animal sperm, not that much for human sperm. Although this limit is highly idealized, our approximation will capture the essential physical aspects of swimming speeds.

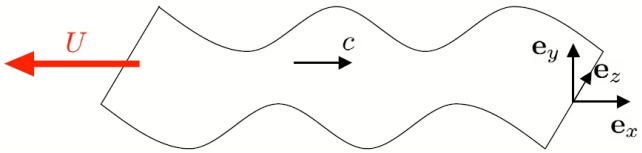


Figure 6: Taylor's swimming sheet. Here $\mathbf{U}$ is equal to $\mathbf{V}$ and $c = \omega/k$. Source: [11].

G. I. Taylor, in 1951, considered as a model for swimmer's flagella a sheet immersed in a viscous fluid on which transverse waves of small amplitude propagate (Figure 6). Here, $h(x,t) = b\sin(kx - \omega t)$, is the amplitude of the sheet over the plane $y = 0$, where the x direction is parallel to the direction of the wave, b being its amplitude, k wave number, and ω the frequency of oscillations. Note that we work in the reference frame in which material points of the sheet move up and down only. Supposing the amplitude is small compared to the wavelength and that the sheet is infinite, Taylor was able to solve the Stokes equation with the no-slip boundary condition, $\mathbf{v}(x, h(x,t)) = \frac{\partial h}{\partial t}\mathbf{e_y}$, and an unknown but steady flow far from the sheet, $\lim_{y\to\infty} \mathbf{v}(x,y) = -\mathbf{V}$. Since we work in the rest frame of the sheet, $\mathbf{V}$ is the swimming velocity of the sheet in the laboratory frame. He did his calculation by expanding the boundary conditions in bk, and solving the Stokes equation order by order. For the velocity of the sheet he got

$$\mathbf{V} = -\frac{1}{2}\omega b^2 \mathbf{k}.$$

For the rate at which the sheet does work he calculated $P = \omega^2 k b^2 \eta$. The power of the sheet depends on the viscosity of the fluid, whilst the speed does not. This is because we have imposed a waveform independent of load. If the beat frequency of human sperm's flagella is 50 Hz, the amplitude 5 μm and wavelength 20 μm, then its speed is approximately 1 mm/s which is of the proper order of magnitude, perhaps a bit too high. (Amplitude and wavelength can be obtained from figure 12.)

Taylor's calculations are valid when the amplitude of the deflection of the swimmer is small. However, this is hardly so, since real flagella undergo large-amplitude deformations. Fortunately, we are interested only in the order of magnitude of the swimmer's speed, so the small-amplitude approximation will be sufficient.

Now we must calculate the drag force on the filament which opposes the motion. The idea is to model the corresponding flow by replacing a real flagella with a line distribution of singular solutions of the Stokes equation of appropriate strength and then calculating the drag force exerted on it. If we were to do this calculation, and put into account that each sphere influences the other, the drag anisotropy would reveal itself in a familiar fashion:

$$\mathbf{f} = -\xi_{\parallel}\mathbf{v}_{\parallel} - \xi_{\perp}\mathbf{v}_{\perp}, \tag{11}$$

where the symbols $\parallel$ and $\perp$ signify parallel and perpendicular directions with respect to the rod (the rod is placed horizontally). The drag coefficients are:

$$\xi_\perp = 2\xi_\parallel = 4\pi\eta/\ln(L/a), \tag{12}$$

where L is the length of the rod and a its radius.

If we did not account for the interaction among spheres, we would loose the drag anisotropy, which is characteristic for Stokeslets but not for spheres (a sphere can be modeled with a Stokeslet and a source-dipole). If the deformation of a filament is small, it is reasonable to assume that the viscous force per unit length acting on a curved filament is the same as that on a straight rod of the same length. For this local drag theory to hold the filament must be *exponentially thin* (see [1]), that is, to make $1/\ln(L/a)$ of the order of $\varepsilon \ll 1$; in other words we need $a/L \approx \exp(-1/\varepsilon)$.

Finally, consider a sphere of radius a propelled by the beating flagella of equal thickness and with a planar sine stroke: $h(x,t) = b\sin(kx - \omega t)$, ie. sperm. Following Taylor, we too work in the rest frame of the swimmer. Suppose some external force and torque are applied to the swimmer's head preventing the swimmer to rotate or move in the y-direction. In real swimmers this transverse component of the velocity and rotation is usually always present and plays an important role in determining swimmer's trajectory and the shape of the flagella. Anyway, the balance of forces must hold: the sum of the drag force on the sperm's head and flagella balance the propulsion force. The drag force on the sphere is $6\pi\eta a\mathbf{V}$, the linear density of the drag force on the filament is according to (11) $-\xi_\parallel \mathbf{v}_\parallel - \xi_\perp \mathbf{v}\perp$, where $\mathbf{v}_\parallel$ and $\mathbf{v}_\perp$ are velocities parallel and perpendicular to the x-axis, and the propulsion force follows from equation (10). Integrating the density of the drag force on the filament throughout its length L and using the balance law, we get:

$$\left(-\xi_\parallel \mathbf{v}_\parallel L - \xi_\perp \mathbf{v}_\perp L - 6\pi\eta a\mathbf{V}\right) + \left(\xi_\perp - \xi_\parallel\right)\int_0^L \frac{\partial h}{\partial t}\cdot\frac{\partial h}{\partial x}\,dx\,\mathbf{e_x} = \mathbf{0}.$$

Since the sperm does not move in the y direction (that is $\mathbf{V} = \mathbf{v}_\parallel$), this simplifies to

$$\xi_\parallel V L + 6\pi\eta a V = \left(\xi_\perp - \xi_\parallel\right)\int_0^L \frac{\partial h}{\partial t}\cdot\frac{\partial h}{\partial x}\,dx.$$

Plugging in this equation the sine waveform $h(x,t)$ we get

$$V = -\frac{\xi_\perp - \xi_\parallel}{2\xi_\parallel}\frac{\left(kL + \sin kL\cos(kL - 2\omega t)\right)\omega b^2}{1 + \frac{6\pi\eta a}{\xi_\parallel L}}. \tag{13}$$

Averaging over one period of the oscillation yields

$$\langle V\rangle = -\frac{\xi_\perp - \xi_\parallel}{2\xi_\parallel}\frac{\omega b^2 k}{1 + \frac{6\pi\eta a}{\xi_\parallel L}}. \tag{14}$$

When $L \gg a$ and $\xi_\perp = 2\xi_\parallel$ this equation reduces to the speed of the Taylor's sheet. For $L \gg a$ the speed is also independent of the L for fixed k and b, since lengthening the flagella increases the drag forces and propulsion forces equally. For a typical sperm: $b = 5\,\mu$m, $a = 5\,\mu$m, $L = 50\,\mu$m, $\lambda = 20\,\mu$m, $\nu = 50\,$Hz, $\eta = 10^{-1}\,$Pas. This gives the average speed of 300 μm/s.

5 The transport of human sperm

Now we discuss the interesting part of the seminar: the difficult life* of human sperm cells, their group dynamics and interaction.

An average human ejaculate contains from 180 million sperm cells (60 million per ml) up to 400 million sperm cells. Both quantity and quality of the sperm are important determinants of fertility. (A man is considered *clinically* infertile if his sperm concentration falls below 20 million/ml of semen. But remember, it only takes one sperm to make a baby.) Figure 7 depicts the sperm's path in the female reproductive tract.

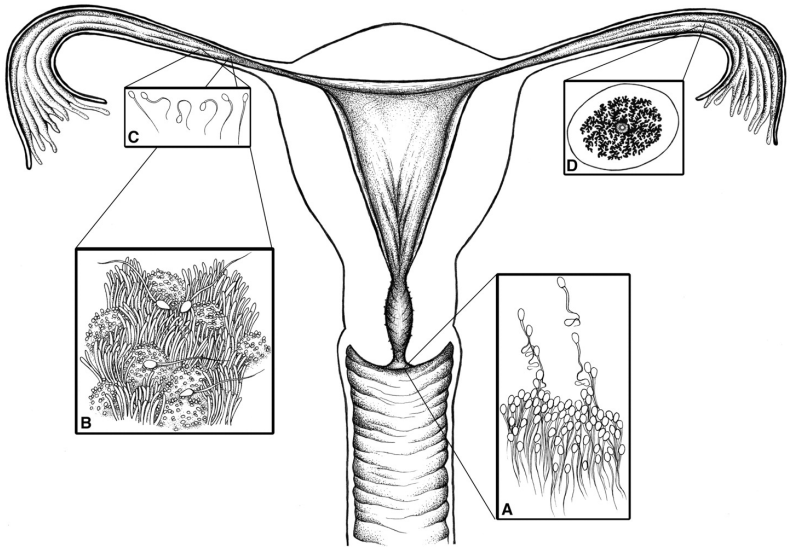


Figure 7: Human female reproductive tract illustrating stages of sperm transport. (A) Sperm entering cervical mucus at external orifice of the uterus of cervix. The mucus fills the upper half of the inset. (B) Sperm interacting with endosalpingeal epithelium in Fallopian tube. (C) Hyperactivated motility of sperm in Fallopian tube. (D) Oocyte in cumulus within a transverse section of the tubal ampulla. Source: [7].

At coitus, human sperm cells are deposited into the interior vagina, where, to avoid vaginal acid and immune responses, they quickly contact cervical mucus and enter the cervix. Cervical mucus filters out sperm with poor morphology and motility and as such only a minority of ejaculated sperm actually enter the cervix. In the uterus, muscular contractions may enhance passage of sperm through the uterine cavity. A few thousand sperm swim through the uterotubal junctions to reach the Fallopian tubes (uterine tubes, oviducts) where sperm are stored in a reservoir, or at least maintained in a fertile state, by interacting with endosalpingeal (oviductal) epithelium. As the time of ovulation approaches, sperm become capacitated and hyperactivated, which enables them to proceed towards the tubal ampulla. Sperm may be guided to the oocyte by a combination of thermotaxis and chemotaxis. Motility hyperactivation assists sperm in penetrating mucus in the tubes and the cumulus oophorus and zona pellucida of the oocyte, so that they may finally fuse with the oocyte plasma membrane.†

*But under no circumstances should a spermatozoon be considered a life form!

†Paragraph taken from [7].

A sperm moves its flagella by the aid of Dynein molecular motors distributed along the length of the filament. This motors in the flagellum of the sperm generate a regular bending wave with a frequency from 5 to 50 Hz; the flagellar beat propels the sperm cell in semen or cervical mucus at speeds of about $100 - 300\,\mu$m/s. The human sperm cell itself consist of three pieces (see figure 2):

- a head of length $\approx 5\,\mu$m which contains the genetic material,
- midpiece of length $\approx 7\,\mu$m which accommodates several mitochondria which serve as the power house of the sperm cell and generate the chemical fuel ATP which is required, for example, to power the flagellar beat,
- a flagellum of length $\approx 50\,\mu$m which propels the sperm in liquid.

5.1 Swimming in viscoelastic mucus

One may be fascinated to know that sperm actually swim in two different types of fluid. One is Newtonian (semen) and the other non-Newtonian (cervical mucus). The difference being that the cervical mucus contains polymers making it viscoelastic and therefore cannot be characterized by a simple universal constitutive relation such as that for a Newtonian fluid (stress proportional to strain rate), and exhibits phenomena such as elasticity and shear thinning. When a sperm moves through the viscoelastic mucus of the female reproductive tract, the theory of swimming in a purely viscous fluid discussed before is not applicable to its full extent; the Scallop theorem, for example, is invalid. The model of the flagella still stands, however, the calculations are different. We will not indulge in them, suffice it to say that in the mucus, flagella's beating is confined mostly to the distal tip. See figure 8. It shows how the beating patterns of sperm change when the viscosity increases. The head of the sperm is held still by a pipette. In figure 8 a), the beating patterns of a sperm in Hanks' medium with viscosity of 1 mPa s, 35 mPa s, 4000 mPa s, and cervical mucus with viscosity 4360 mPa s are shown. Hanks' medium is a Newtonian solution of salts and glucose in water. Figure 8 b) shows theoretical predictions based on the fading-memory model, the Oldroyd-B fluid.

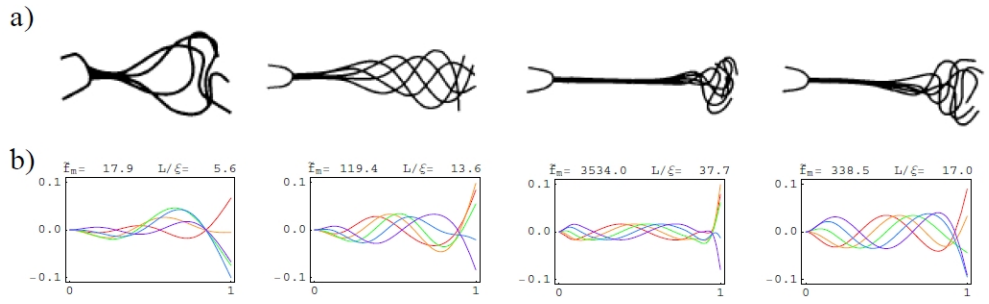


Figure 8: a) Beating patterns of human sperm observed by Ishijima et al. (for reference see [3]), in (from left to right) 1 mPa s Hanks' solution, 35 mPa s Hanks' solution, 4000 mPa s Hanks' solution, 4360 mPa s cervical mucus. b) Shapes of beating patterns of filaments with fixed head positions and clamped boundary conditions according to theory. Source: [3].

Sperm in cervical mucus also have a higher beat frequency, smaller amplitude, and shorter wavelength than in semen. The swimming speed is the same in both media, but sperm in cervical mucus swim along straighter paths.

5.2 Cooperation of sperm and influence of walls

A sperm itself (human or otherwise) is a remarkable result of natural evolution. Imagine having to travel at such great length only to fertilize the egg, facing dangers on your way such as acids and walls of conduits. Would it not be safer to swim in groups? Indeed, but not only safer, it is energetically better. It turns out that sperm cooperate so that their phases lock in. It can be shown with the aid of the Taylor's swimming sheet that when two swimmers with the same prescribed flagella-waveform are swimming in phase, they dissipate the least amount of mechanical energy, and the dissipation goes up monotonically with the phase difference. So, there are physical reasons why sperm should swim together. On the other hand, this interaction can never be neglected, since the average distance between sperm per ejaculate is on the scale of a few micrometers. Using numerical simulations through the multiparticle collision dynamic (MPC) this can be graphically shown. Firstly, see figure below. Two swimmers with the same waveform but different phases are seen to swim with slightly different velocities, until their phase difference $\Delta\phi$ dissolves, thereafter they are perfectly *synchronized* or perfectly out of phase, with both configurations being stable.

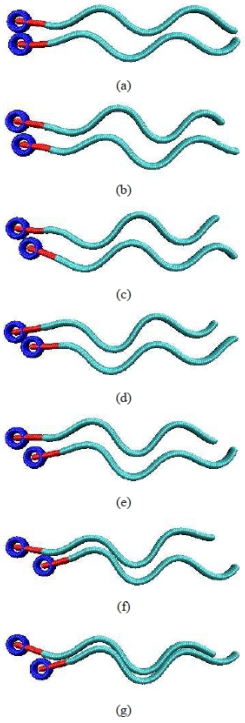
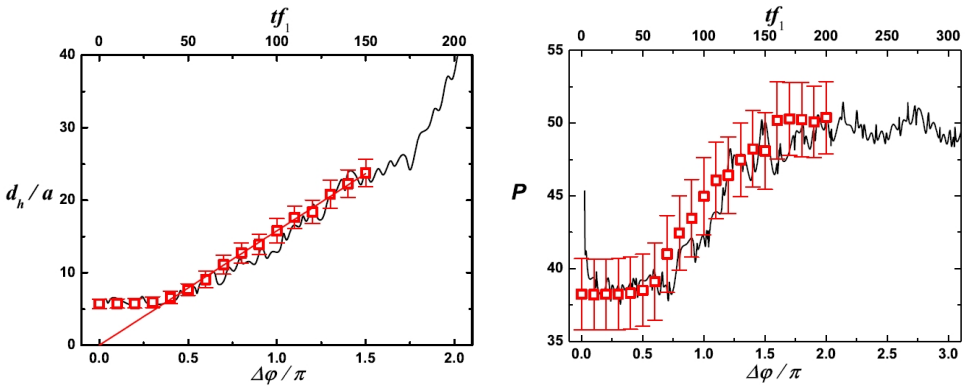


Figure 9: From (a) to (e), the synchronization takes place. From (e) to (g), two synchronized sperm form a tight cluster due to hydrodynamics attraction. The initial phase difference is $\Delta\phi = \pi/2$. Source: [3].

Synchronization is a fast process achieved in only a few beats of the filament. The process of *attraction* takes a little longer. Two sperm attract one another because of the interaction between their Stokes flows. This is similar to the attraction of two electrical charge configurations.

What happens if we put in a wall? When two parallel sperm are placed between two walls, there seems to be a critical initial distance between the sperm (let that be the distance between the heads), below which synchronization occurs, and above which swimming towards the wall occurs. Our understanding would be that the viscous drag towards the walls was competing with the viscous attraction between sperm. This is important for the balance in cluster formation which will be discussed later.

To analyze the cooperating pair further, let us choose the head-head distance d_h to characterize the attraction and synchronization, because it is easy experimentally to track the head's position. Figure 10a) shows the results of a simulation with two interacting sperm, first with the same beat frequencies and different phases, then with the same phases and different beat frequencies. There is a plateau at about $d_h = 5a$ for phase difference $\Delta\phi < 0.4\pi$, which corresponds to the sperm heads touching each other. After that head-head distance increases linearly with the phase difference. For $\Delta\phi > 1.5\pi$, the phase difference is so large that the attraction is not strong enough to overcome the thermal fluctuations and pull the sperm close together.



(a) (b)

Figure 10: a) Head-head distance of two cooperating sperm. Here $a = 1$ μm and $f_1 = 8$ Hz. Simulation data are shown for fixed phase difference (red, with squares), with error bars denoting the standard deviation. The distance d_h is also shown as a function of time t (top axis, f_1 is the constant frequency of the first sperm) in a simulation with 0.5% difference in the beat frequencies of the two sperm (solid black line). (b) The corresponding power of the two sperm. Here $f_1 = 8$ Hz and the unit of power is 10^{-16} W. Red symbols demonstrate data for fixed phase difference. Solid black line stands for energy consumption versus time in a simulation with 0.5% difference in beat frequencies of the two sperm. Source: [4].

So far, we have considered only sperm with a single beat frequency. This is rare in nature, it would be extraordinary if all the sperm had the same beating frequency. Let us see what happens to two sperm whose frequencies differ by 0.5% but have the same initial phase. We know that the phase difference should increase lineary with time ($\Delta\phi = 2\pi(f_2 - f_1)t$). The black curve on figure 10a) shows exactly this. Figure 10b) shows the energy consumption for the corresponding experiments. The energy consumptions is nearly constant at small phase differences. For $\Delta\phi > 0.5\pi$ it increases roughly linearly until it reaches another plateau. The second plateau corresponds to two sperm swimming separately, so that the energy consumptions is approximately twice the value of a single sperm! Although in the presence of walls

two synchronizations still occur at the beginning, the two sperm leave each other soon after (see figure 11).

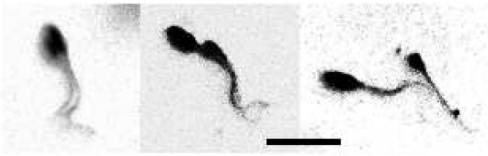
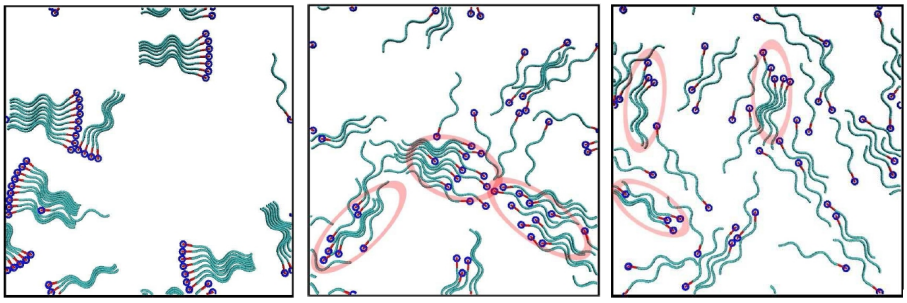


Figure 11: Snapshots of two synchronized human sperm. At first they have a small phase difference, after 4 second the phase difference has developed, and after 7 seconds they depart. The scale bar corresponds to a length of 25 μm. Source: [4].

Finally, we have come to the question of multi-sperm systems. Let us set the inital phases of all sperm to zero and suppose that sperm have beating frequencies distributed according to Gauss' curve with width δ_f. It turns out that the average cluster size will be smaller with bigger width δ_f. There is a balance between cluster formation and break-up. Swimming close to the walls makes some sperm to leave the group, but at the same time, other sperm join it. Also, bigger clusters have slightly lesser speeds. (see Figure 12).



(a) (b) (c)

Figure 12: a) Snapshots from simulations of 50 symmetric sperm with different width δ_f of a Gaussian distribution of beating frequencies. $\delta_f = 0$, 0.9%, 4.5%. Source: [4].

5.3 Sperm chemotaxis

We conclude this seminar by saying a few words about the mechanism which guides sperm to the female ovum in the Fallopian tube. Usually sperm cells of many species are guided to the egg by chemottractants, a process called chemotaxis. In the absence of a chemottractant sperm swim in circles. Chemottractants stimulate a signaling system in the flagellum, which regulates the motors to control sperm swimming. In the presence of a chemottractant, swimming paths are drifting circles in two dimensions and deformed helices in three dimensions. The rules the sperm are using are quite simple: If things are getting better, do not stop so soon. One could imagine sperm doing runs and every now and again a short stop to see where the gradient of the chemottractant is pointing. But closer they get to the egg, longer are the lengths of distances between stops.

6 Conclusion

We have reviewed the basic problems of swimming at low Reynolds number. This shed some light on the dynamics of human sperm cells in semen and cervical mucus and the difficulties of their voyage therein. Nature, through the process of evolution, has put things together so that there is a fine balance between the complexity of space and biological solutions possible under such strict conditions. In a viscous, even viscoelastic cervical fluid, where one can expect to be attacked by the immune system at any time, from the entering point to the distant Fallopian tube, the sperm has managed to organize its tactics and form groups so to reduce energy dissipation, it has increased its chances of survival. But still, only a few thousand out of millions of sperm come to the near vicinity of the egg, other die on the way. And only one or two individual sperm, if any at all, will complete their goal of fertilization. How glorious is their victory and noble their enterprise in that lasting world at low Reynolds number!

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