Lecture 5: Equations of motion: swimming, friction, Reynolds number (TB)

1. Friction in fluids
   - Pulling a sphere through a fluid typically leads to a friction force that is opposed to the direction of motion.
   - Stokes’ law for the frictional (or drag) force of a sphere in a viscous fluid: \( v = \mu F \), with \( \frac{1}{\mu} = 6\pi \eta R \) for a sphere of radius \( R \); \( \eta \) is the fluid viscosity, \( \mu \) the mobility.
   - Example: vesicle pulled along filament in a cell by a molecular motor; compare drag force and force the motor can exert:
     - Results in \( F \approx 1 \) nN. A typical force exerted by a molecular motor is 5 pN
     - This implies that it is no problem for a molecular motor to pull vesicles through the cytosol, even if the vesicle is larger or the velocity higher than in this example.
   - The energy ‘lost’ due to friction forces is dissipated into the heat bath.
   - Dissipation and fluctuations are related:
     - Einstein relation: \( D = \mu k_B T \)
     - The same random forces that cause the diffusion of the sphere underlie the friction force that occurs when we pull the sphere. These random forces are due to molecules of the surrounding fluid that constantly hit the sphere due to random thermal motion.
     - The Einstein relation is an example of the fluctuation dissipation theorem (FDT), a fundamental result of statistical physics.
     - Note: the FDT is very useful, but only valid for systems in thermodynamic equilibrium and only for small perturbations of a system.

2. Navier-Stokes equations
   - The Navier-Stokes equations describe the dynamics of fluids such as water or air.
   - In these equations, fluids are described as a continuum, i.e. not as individual particles.
   - Navier-Stokes equations for an incompressible Newtonian fluid (this is a special case but applicable to most real world situations):
     - \( \rho \left( \frac{\partial \vec{v}}{\partial t} + \vec{v} \cdot \nabla \vec{v} \right) = -\nabla p + \eta \nabla^2 \vec{v} + \vec{f} \),
     - \( \rho = \) fluid mass density, \( \vec{v} = \) flow velocity, \( p = \) pressure, \( \eta = \) viscosity
     - (constant for Newtonian fluid), \( \vec{f} = \) external force field (e.g. gravity)
   - These equations reflect Newton’s law: the terms on the left are essentially mass times acceleration, the terms on the right are forces. The second term on the right is due to viscosity ('internal friction') of the fluid.
   - Apart from the term \( \frac{\partial \vec{v}}{\partial t} \) that captures fluid acceleration due to temporal changes of the velocity field at a fixed location, there is a convective acceleration term \( \vec{v} \cdot \nabla \vec{v} \) that is due to fluid moving between regions in the flow field with different velocities, e.g. from a region with lower velocity to a region with higher velocity.
   - Additional assumptions are needed to solve the Navier-Stokes equations:
- Mass conservation: \( \frac{\partial \rho}{\partial t} + \nabla \cdot (\rho \mathbf{v}) = 0 \). This simply means that more mass needs to flow into a volume than flows out for the mass density there to increase. For incompressible fluids, this equation simplifies to \( \nabla \cdot \mathbf{v} = 0 \).
- Boundary conditions, e.g. \( \mathbf{v} = 0 \) at a surface boundary.
  - Note: The Navier-Stokes equations are generally hard to solve. In particular, the resulting flows may be non-stationary and turbulent in which case the solutions can sensitively depend on small details.
  - A relatively simple case is given by laminar flow. Here, there is no turbulence, the fluid flows in ‘layers’ and there are no currents perpendicular to the flow direction.
  - Simple example: for laminar flow, it is possible to calculate the fluid flow rate (fluid volume per time) through a long cylindrical pipe of radius \( R \) and length \( L \) with a pressure difference \( \Delta P \) between the ends:
    \[
    \Phi = \frac{dV}{dt} = \frac{\pi R^4 \Delta P}{8\eta L} \text{ (Hagen-Poiseuille law)}
    \]
    - The Hagen-Poiseuille law is biologically relevant, e.g. for blood flow through the cardiovascular system.

3. Reynolds number
   - Non-dimensionalization of the Navier-Stokes equations shows that there is a single dimensionless ratio that largely determines the flow properties, the Reynolds number \( Re = \rho v L / \eta \), where \( L \) is a characteristic length scale of the system, \( v \) a typical velocity, and \( \rho \) a typical mass density of the system.
   - The Reynolds number quantifies the relative importance of inertial and frictional forces.
   - Critical Reynolds numbers separate laminar from turbulent flow regimes (e.g. the flow through a cylindrical pipe becomes turbulent for \( Re > 2040 \)).
   - It is possible to study flows changing length scales etc. as long as the Reynolds number is kept constant. This is heavily used in practice, e.g. to design aircraft, buildings etc. using smaller models in wind tunnels.
   - Examples for Reynolds numbers:
     - Honeybee in air: \( Re \approx 10^4 \)
     - \( \rho = 1.225 \text{ kg/m}^3, v = 7 \text{ m/s}, L = 2.6 \text{ cm}, \eta = 1.78 \times 10^{-5} \text{ kg/m s} \)
     - A380 flying in air: \( Re = 2 \times 10^9 \)
     - Large fish swimming in water: \( Re = 5 \times 10^4 \)
     - Sperm cell in water: \( Re = 0.0035 \)
     - Bacterium in water: \( Re = 10^{-5} \)

4. Low Reynolds number world: microscopic swimmers
   - Cells are typically so small that the Reynolds number is very small. Hence, bacteria, sperm cells, etc. live in a friction dominated world. This implies that cells cannot coast but stop immediately when their propulsion is stopped.
   - The Navier-Stokes equations become much simpler in this limit because the inertial terms can be neglected (“Stokes equations”):
     - \( 0 = -\nabla p + \eta \nabla^2 \mathbf{v} + \mathbf{f} \)
     - \( \nabla \cdot \mathbf{v} = 0 \)
   - Note: There is no time dependence of the flow in these equations. Changes in the flow field occur only via the boundary conditions. The equations are time-reversible:
reversing the direction of time for a solution of these equations ("playing the tape backwards") also solves the equations.

- Fundamental question: How can directed motion ('swimming') be achieved at a microscopic scale?
  - Time reversal symmetry must be broken, i.e. the motion of a microscopic swimmer must look different if time is reversed. E.g. a simple back and forth beating (scallop opening and closing) cannot result in motion ('scallop theorem').
  - For other aspects of microscopic swimming, see Lauga and Purcell references below.
- Examples for microscopic swimmers:
  - Bacteria: use a flagellum, a hollow tube made out of protein, attached to a rotary motor which can rotate at ~1000rpm. Time reversal symmetry is broken by a helical wave.
  - Sperm cells: a sophisticated structure of microtubules connected with molecular motors (9+2 axoneme, see schematic below) generates travelling waves to propel the cell.

![Diagram of a sperm cell showing microtubules and molecular motors.]

**References / further reading:**

- Chapter 12 in Rob Philips book: Physical biology of the cell
- EM Purcell, American Journal of Physics 45 (1977)