PHYS 4xx Forces and torques

Transport and movement

We have described in the previous lecture several mechanisms for generating movement in the cell through the polymerization of filaments, or the crawling of molecular motors. Let's summarize some of the observed speeds:

motion	*typical speed* (μm/s)	*example*
actin filament growth	10^{-2} - 1	0.3 μm/s at [*M*] = 10 μM
actin-based cell crawling	10^{-2} - 1	fibroblasts move at ~10^{-2} μm/s
myosin on actin	10^{-2} - 1	0.1 - 0.5 μm/s common in muscles
microtubule growth	up to 0.3	0.03 μm/s at [*M*] = 10 μM
microtubule shrinkage	0.4 - 0.6	0.5 μm/s
fast axonal transport	1-4	
slow axonal transport	10^{-3} - 10^{-1}	

[*M*] = monomer concentration. Fast axonal transport involves kinesin or dynein moving along microtubules.

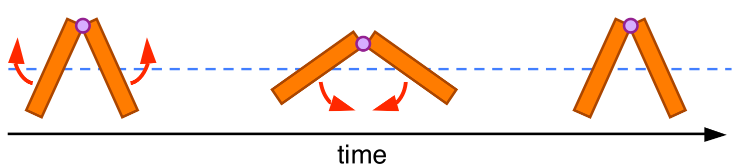
The cell uses motors and other mechanisms to overcome viscous drag and accommodate these speeds. For spherical objects at low speeds, Stokes' Law provides an accurate estimate of the applicable drag force

$$F_{\text{drag}} = c_1 v \qquad \text{with} \qquad c_1 = 6\pi\eta R.$$

Typical drag force on a small vesicle is 0.05 pN.

Swimming

Purcell (1977) provided a nice overview of swimming in a viscous environment. At low Reynolds number, inertial effects are unimportant: in the absence of a driving force, everything stops instantly. How does a cell swim in such an environment? The simplest cycle for swimming that does work at the macroscopic scale doesn't work for cells:



Here, the opening movement is slow, and then the plates (or shells) snap shut rapidly.

The reason why there is no net movement lies in the absence of inertia. Each plate in the drawing experiences a torque due to drag that is proportional to its angular velocity, $d\theta/dt$. This pair of torques generates a force F to propel the object, but because of drag, the velocity dx/dt that can be achieved by the object is linearly proportional to F and does not grow with time as it would under drag-free conditions. In other words,

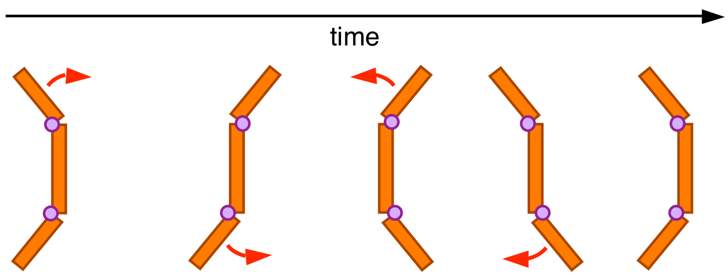
$$dx/dt = [constant] \cdot d\theta/dt, \qquad (1)$$

where the magnitude of the proportionality constant need not concern us. The sign of the motion is also accounted for in Eq. (1): if $d\theta/dt > 0$, then dx/dt and the object moves forward, but if $d\theta/dt < 0$ the motion is reversed. Now, to find the overall movement between t_1 and t_2, all we need to do is integrate Eq. (1) to obtain

$$x(t_2) - x(t_1) = [constant] \cdot [\theta(t_2) - \theta(t_1)]. \qquad (2)$$

Thus, for this object, over one complete cycle of the motion when θ returns to its original value, $\theta(t_2) = \theta(t_1)$ and consequently $x(t_2) = x(t_1)$: the object hasn't moved.

The problem is that the forces are equal and opposite in each half of the cycle: the motion is reciprocating. To create translational motion in a viscous environment, the cycle must be non-reciprocating:



Cilia and flagella both undergo non-reciprocating motion:
•cilia bend away from the direction of motion, so their shape is different in each half of their wave-like motion
•flagella rotate around an axis without reversing (except to change direction).

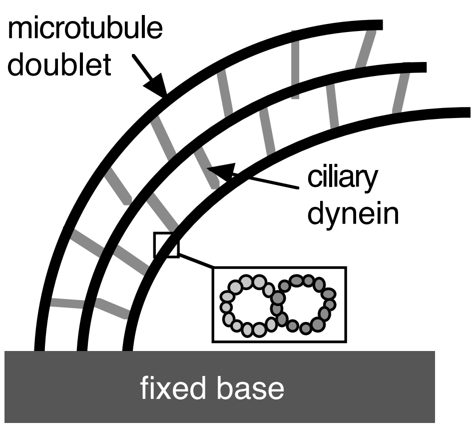
Cilia and flagella

Swimming movement of the cell (as opposed to the gliding of a cell on a substrate) can be accomplished by the motion of *flagella*. A cell uses *cilia* to beat synchronously and move water across its surface. Cilia and flagella are whip-like structures extending from cells

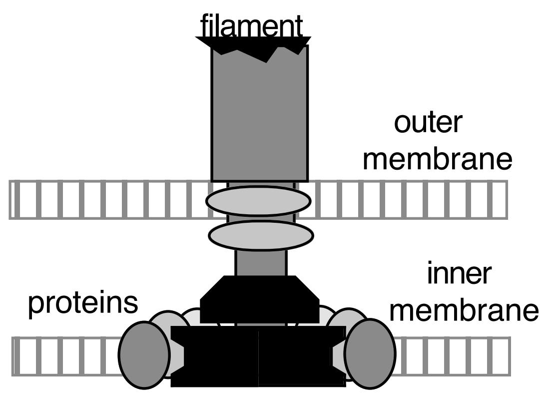
TEM of a platinum-shadowed replica of *Aquaspirillum metamorphum*
(bar = 500 nm; from Terry Beveridge)

Architecture:

- core is the axoneme, a bundle of MTs about 225 nm in diameter, consisting of 2 MTs in its center, surrounded by 9 MT doublets (11 + 13 tubulins like CO)
- in cilia, microtubules are cross-linked by (ciliary) dynein motors which cause the MTs to bend when the motors attempt to walk along the filaments



cilium

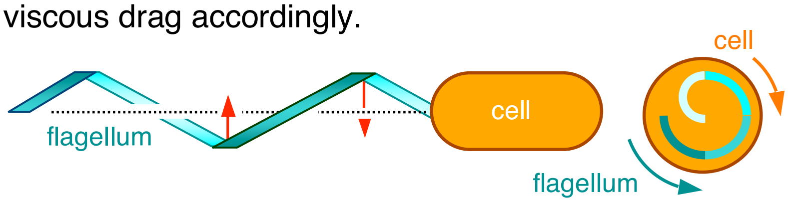


flagellum

- base of filament may also be driven to rotate by molecular motors (Gram-negative bacterium is shown at right)

Rotational motion with drag

A bacterium will be driven to rotate in opposition to the rotation of its flagella, and will experience viscous drag accordingly.



(a) (b)

The drag torque τ experienced by an object rotating with a frequency ω is given by

$\tau = f_{drag}\ \omega$ with $f_{drag} = 8\pi\eta R^3$

where f_{drag} is the rotational drag coefficient.
Typical magnitude of this torque for a bacterium is 1.6×10^{-18} N•m