Active Matter and Collective Behavior

Carine Douarche — M2ICFP — 2021-2022
Active matter is observed in Nature

- Collective behavior is all around us: microtubules, swarm of bacteria, bird flocks, fish school, animal herds, ...
- How do we define these systems where there is no global orchestrating power?
- The individual unit are locally communicating with each other and yet remarkably through this type of communication we get animal group being able to synchronize their motion and respond to predators
- Fascinating collective dynamics with emerging properties that are not a priori expected
Active matter is observed in Nature

- New class of out of equilibrium systems:
  - What is the physics behind?
  - Need to build up new paradigm?
  - Statistical physics? Thermodynamics? New phenomena?
- How the behavior of an individual will influence the behavior of the group?
Active matter at all scales

Microtubule filaments ~ 7 nm

Fish ~ 20 cm

Escherichia coli ~ 2 µm

Land animal ~ 2 m

Keber et al. Science 2014

Douarche and coworkers. 2017
A need to build up artificial swimmers

Tunable model systems:
- microscopic to macroscopic scales
- self-propelled entities doted with motility
- minimal set of requirements to move?
- minimal set of requirements to perform collective motion (≠ behavior)?
Outline of this lecture

- Prerequisite of motility at low Reynolds’s number: **the scallop theorem**

- How do **artificial micro swimmers swim** (minimal set of requirements to move)?
  - Vibrating disks
  - Janus particles
  - Quincke rollers

- Nothing better than **biological micro swimmers**:  
  - introducing bacteria (as a model tunable system)  
  - how do they swim: breaking of symmetry, run and tumble  
  - translation and rotational diffusion  
  - a short introduction to multicellular swimmers
Prerequisite of motility at low Reynolds’s number: the scallop theorem
A little bit of hydrodynamics

A spherical particule of size $a$ that moves at the velocity $u$ in a newtoinian, viscous and incompressible fluid is subjected to the Navier-Stokes equation:

$$\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla)\mathbf{u} = -\frac{1}{\rho} \nabla p + \nu \Delta \mathbf{u} + \mathbf{g}$$
A little bit of hydrodynamics

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$$\frac{\partial u}{\partial t} + (u \cdot \nabla)u = - \frac{1}{\rho} \nabla p + \nu \Delta u + g$$

$U$ the characteristic velocity of the system
$L$ the characteristic length of the system
$T = \frac{L}{U}$ the characteristic time of the system

Adimensionalized equation:

$$\frac{\partial u^*}{\partial t^*} + (u^* \cdot \nabla^*)u^* = - \nabla^* p^* + \nu \frac{L}{L} \Delta^* u^* + \frac{L}{U^2} g$$
A little bit of hydrodynamics

A spherical particule of size $a$ that moves at the velocity $\mathbf{u}$ in a newtoinian, viscous and incompressible fluid is subjected to the Navier-Stokes equation:

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Adimensionalized equation:

$$\frac{\partial \mathbf{u}^*}{\partial t^*} + (\mathbf{u}^* \cdot \nabla^*) \mathbf{u}^* = -\nabla^* p^* + \frac{\nu}{LU} \Delta^* \mathbf{u}^* + \frac{L}{U^2} \mathbf{g}$$

Reynolds’s number: $Re = \frac{LU}{\nu} = \frac{\text{inertial forces}}{\text{viscous forces}}$
A few examples

When $Re << 1$ viscous forces dominate.

In which situation is it the case?

$$Re = \frac{aU}{\nu}$$

Kinematic viscosity of water $\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$

For Michael Phelps (2 m)
swim 100 m in 60 s

_Purcell, Life at low Reynolds’ number, 1976_
A few examples

When $Re \ll 1$ viscous forces dominate. In which situation is it the case?

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$$Re = \frac{aU}{\nu}$$

Kinematic viscosity of water

$$\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$$

$Re = 3 \times 10^6$

*Purcell, Life at low Reynolds’ number, 1976*
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For a fish (1 cm) swim 0.01 m s$^{-1}$

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A few examples

When $\text{Re} << 1$ viscous forces dominate. In which situation is it the case?

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Kinematic viscosity of water $\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$

For Michael Phelps (2 m)
swim 100 m in 60 s

$\text{Re} = 3 \cdot 10^6$

For a fish (1 cm)
swim 0.01 m s$^{-1}$

$\text{Re} = 10^2$

For a bacteria (3 $\cdot$ 10$^{-6}$ m)
swims at 30 $\mu$m s$^{-1}$

_Purcell, Life at low Reynolds’ number, 1976_
A few examples

When $Re << 1$ viscous forces dominate. In which situation is it the case?

$Re = \frac{aU}{\nu}$

Kinematic viscosity of water $\nu = 10^{-6}$ m$^2$ s$^{-1}$

For Michael Phelps (2 m) swim 100 m in 60 s

$Re = 3.10^6$

For a fish (1 cm) swim 0.01 m s$^{-1}$

$Re = 10^2$

For a bacteria (3.10$^{-6}$ m) swims at 30 µm s$^{-1}$

$Re = 10^{-4}$

Purcell, Life at low Reynolds’ number, 1976
A few examples

When $Re < 1$ viscous forces dominate.
In which situation is it the case?

\[ Re = \frac{aU}{\nu} \]

Kinematic viscosity of water
\[ \nu = 10^{-6} \text{ m}^2 \text{ s}^{-1} \]

For Michael Phelps (2 m) swim 100 m in 60 s
\[ Re = 3 \times 10^6 \]

For a fish (1 cm) swim 0.01 m s\(^{-1}\)
\[ Re = 10^2 \]

For a bacteria (3 \times 10^{-6} m) swims at 30 µm s\(^{-1}\)
\[ Re = 10^{-4} \]

*Viscosity dominates !!!*

*Purcell, Life at low Reynolds’ number, 1976*
How far run a bacteria when it stops swimming?

Drag force \(6\pi \eta au\)

Velocity \(u\)
How far run a bacteria when it stops swimming?

Drag force $6\pi \eta au$

Newtons’s second law of motion: $m \left( -\frac{du}{dt} \right) = 6\pi \eta au$

$m$ is the sphere’s mass

$m = \frac{4}{3} \pi a^3 \rho$ with $\rho$ the density of the sphere
How far run a bacteria when it stops swimming?

Newton's second law of motion: \( m \left( -\frac{du}{dt} \right) = 6\pi \eta au \)

- \( m \) is the sphere's mass
- \( m = \frac{4}{3} \pi a^3 \rho \) with \( \rho \) the density of the sphere

\[
\frac{du}{dt} = -\frac{6\pi \eta a}{m} dt \Rightarrow u(t) = u(0)e^{-t/\tau} \quad \text{with} \quad \tau = \frac{m}{6\pi \eta} = \frac{2a^2 \rho}{9\eta} = 2.10^{-7} \text{ s}
\]
How far run a bacteria when it stops swimming?

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\( d = \int_0^\infty u(t) dt = u(0)\tau = 0.04 \) Å
The scallop theorem

\[ \rho \frac{\partial \mathbf{u}}{\partial t} + \rho (\mathbf{u} \cdot \nabla) \mathbf{u} = -\nabla p + \eta \Delta \mathbf{u} + \rho \mathbf{g} \]

*Purcell, Life at low Reynolds number, 1976*
The scallop theorem

\[ \rho \frac{\partial \mathbf{u}}{\partial t} + \rho (\mathbf{u} \cdot \nabla) \mathbf{u} = - \nabla p + \eta \Delta \mathbf{u} + \rho \mathbf{g} \]

At low Reynolds’s number, inertial terms of the Navier-Stokes equation are negligible. The equation can thus be written:

\[ \nabla p = \eta \Delta \mathbf{u} \]

Purcell, *Life at low Reynolds number*, 1976
The scallop theorem

At low Reynolds’s number, inertial therms of the Navier-Stokes equation are negligible. The equation can thus be written:

$$\rho \frac{\partial u}{\partial t} + \rho (u \cdot \nabla) u = - \nabla p + \eta \Delta u + \rho g$$

For a same pressure field, the fields velocity $u$ and $-u$ are both solution of this equation. Time-symetric motion cannot achieve net displacement. **Time does not play any role**: rapid or slow motion lead to the same displacement pattern. Reciprocal motion doesn’t generate displacement.

At low Reynolds’s number motion are reversible.

*Purcell, Life at low Reynolds number, 1976*

Need to brake the symmetry !!!
How do artificial micro swimmers swim (minimal set of requirements to move)?
Artificial swimmers

- Mechanical Propulsion (Vibrating disks, robots)
- Electrical Propulsion (Quincke effect, Janus)
- Light activated Propulsion (Janus)
- Chemical Propulsion (Camphor boats, Janus)
Artificial swimmers

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Mechanical propulsion

**Vibrated polar disks**
4 mm in diameter and 2 mm in height
no thermal agitation

*Deseigne et al. PRL 2010*
*Deseigne et al. Soft Matter 2012*
Mechanical propulsion
Mechanical propulsion

Roach-like Robots

30 cm plate
60 roach-bots $\rightarrow$ gas phase
120 roach-bots $\rightarrow$ coexistence of two phases
Mechanical propulsion

**Roach-like Robots**

- 30 cm plate
- 60 roach-bots $\rightarrow$ gas phase
- 120 roach-bots $\rightarrow$ coexistence of two phases

*Deblais et al. PRL 2018*
Artificial swimmers

- Mechanical Propulsion (Vibrating disks)
- Electrical Propulsion (Quincke effect, Janus)
- Light activated Propulsion (Janus)
- Chemical Propulsion (Camphor boats, Janus)
Electrical propulsion

Driven by an external field: **Quincke Rollers**

insulating spheres of PMMA in a conducting fluid

5 µm in diameter at 1 mm s\(^{-1}\)

Spontaneous charge symmetry breaking resulting in a net electrostatic torque

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**Bricard, Nature 2013**
Electrical propulsion

Local energy conversion: Movement of striped **Nanorods**

**Self-electrophoresis.**
The cylindrical particles were 2 μm long and 200 nm in diameter and consisted of two connected metal segments.

Light activated swimmers

- Mechanical Propulsion (Vibrating disks)
- Electrical Propulsion (Quincke effect, Janus)
- Light activated Propulsion (Janus)
- Chemical Propulsion (Camphor boats, Janus)
Light activated propulsion

Local energy conversion: *Self-thermophoretic* particles.
Janus particles
Micrometric scale

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Light activated propulsion

Local energy conversion: **Light activated** particles.
Janus particles in a mixture close to a critical point
Micrometric scale

(a) Schematic explaining the self-propulsion mechanism: a Janus particle is illuminated and the cap is heated above $T_c$ inducing a local demixing that eventually propels the particle.
(b) A schematic phase diagram for water–2,6-lutidine. The insets are bright-field microscopy pictures of the mixed (i) and the demixed (ii) phase at the critical concentration.

Light activated propulsion

Local energy conversion: **Light activated** particles.

Janus particles in a mixture close to a critical point
Micrometric scale

Demixed regions around illuminated Janus particles. (a) Distribution of the lutidine-rich phase (yellow), labeled with a hydrophobic dye (Rhodamine 6G), around a Janus particle with a hydrophilic gold cap (bright half-moon shape) under illumination.

(b) Same as (a) for a Janus particle with a hydrophobic gold cap. Since the size of the demixed regions depends on the illumination intensity, the latter is set significantly higher than in the other experiments we present (10 \( \mu \text{W} \mu\text{m}^{-2} \)) in order to better visualize the gradient.

Artificial swimmers

- Mechanical Propulsion (Vibrating disks)
- Electrical Propulsion (Quincke effect, Janus)
- Light activated Propulsion (Janus)
- Chemical Propulsion (Camphor boats, Janus)
Chemical propulsion


Rome’s Vatican Museums
Chemical propulsion

Δ\(t\ll\tau_R\) \(\rightarrow\) \(\Delta L^2 = 4D\Delta t + V^2\Delta t^2\)

\(\Delta t \gg \tau_R\) \(\rightarrow\) \(\Delta L^2 = (4D + V^2\tau_R)\Delta t\)

Nothing better than biological micro swimmers
What is a bacteria?

Definition: nom féminin (from scientific latin bacterium, and from great baktēria, rod)
A bacteria is a living **unicellular and autonomous** organism and replicate by sissiparity.

- **Size:**
  - between 0.5 and 5 µm in length for the biggest majority of species
  - 500 µm for the biggest and 0.3 µm for the smallest

- **Morphology:**
  - Spherical
  - Rods
  - Curved
  - Helical

- **Arrangements:**
  - Isolated
  - Paired
  - Chain
  - Aggregate
They colonize all ecosystems

- we find their traces 3.8 billion years ago (appearance of water: 4.36 Gy)
- thanks to photosynthesis, cyanobacteria brought molecular oxygen into our atmosphere (2.2 Gy)
- able to adapt to extreme conditions of pH, temperature, pressure, amount of water, etc.

- 100 to 1000 billion microbial species currently live on earth
- in total, more than 14,000 species of bacteria have been cultured so far in the laboratory
- including approximately 2,300 species cultured from human samples
They colonize all ecosystems

- $4 \times 10^{30}$ to $6 \times 10^{30}$ bacteria on earth
- 40 million bacteria per gram of soil
- 1 million bacteria per milliliter of fresh water
- $10^{12}$ bacteria on the skin
- $10^{10}$ bacteria in the mouth
- $10^{14}$ bacteria in the gut
How are they observed?

In the 17th century with glass marbles:

• Observed around 1680 by Antoine Van Leeuwenhoek. He called them "animals".
• The word "bacteria" appeared in 1828.
• Louis Pasteur: work on fermentation process, role of these micro-organisms in infections, pasteurization, autoclave (1920).

... today with optical microscopes
Escherichia coli as a model for motility studies

- *Escherichia coli* has been a model for studying the motility of microorganisms
- It SWIMS
- It changes its way of swimming to reach regions that are more favorable to her
- It has flagella: long protein filaments (between 5 and 10) 10 µm long and 50 nm in diameter
- Each flagellum is driven at its base by a reversible rotary motor which rotates thanks to a flow of protons
- This motor consists of a self-assembly of proteins
The flagellar motor

Bacteria are propelled in their medium by protein filaments

http://www.fbs.osaka-u.ac.jp/labs/namba/npn/cont.html
Run and tumble

Swim: run at 20 µm/s for 1 s
tumble for 0.1 s
The flagellar motor: a self-assembly of proteins

Berg 2003
**Principal constituents**

**Filament** (Length: 10 μm, Diameter: 20 nm):
- Helical structure
- Center hole
- Rigid
- 98% of flagellar mass
- Helical arrangement of flagellin subunits

**Hook**
- Flexible and hollow
- 80 nm curved structure
- 1% of the flagellar mass
- Helical arrangement of a protein subunit
- Junction filament - basal body allows transmission of movement

**Basal body**
Basal Body:
- Complex structure: rod and rings
- 1% of the flagellar mass
- Energy of the flagellum: driving proton force
- Regulation of flagellar movements
- Type III export system

Basal Body Elements:
- Different proteins
- M and S rings (above and inside the cytoplasmic membrane)
- C rings (cytoplasm)
- P (peptidoglycan) and L (outer membrane) rings
- Sticks

The elements of the basal body in detail:
- M and S rings: engine parts
  - side by side
  - made of the same FliF protein
  - constitute the mobile part together with the rod
- C rings: switch
  - role in mobility (torsion and direction) and switch
- P and L rings: guides
  - P at peptidoglycan
  - L at the outer membrane (LPS)
  - Fixed and serve as guides for the sticks
Figure 1  Morphogenetic pathway for the flagellum of Salinivirga. The brackets indicate substructures that are assembled prior to the utilization of the type III export pathway. The Mot proteins constitute the stator element of the motor and are integral membrane proteins surrounding the MS ring, while FtsG and the C ring (FtsM and FtsN) constitute the motor/switch element of the motor and are peripheral membrane proteins anchored on the MS ring. Genes (italics) or proteins necessary at each stage are indicated. Modified from Reference 53, with permission.

Macnab, 2003
The flagellar motor: a self-assembly of proteins

Sequential assembly:
- Basal Body, Hook, Filament
- In the basal body, the MS ring appears first
- Flagellin passes through the central hole
- Self-assembly

Complex genetic control

50nm diameter motor capable of rotating in either direction

It can rotate at a speed of 200 Hz.

It works thanks to a gradient of protons from the outside to the inside of the cell
How does a bacterium breaks the symmetry?

**Fig. 6.3.** Analysis of viscous drag on two segments of a flagellar filament moving slowly to the right and turning rapidly counterclockwise. The velocity of each segment, $v$, is decomposed into velocities normal and parallel to the segment, $v_n$ and $v_p$, respectively. The segment shown on the left is moving upward in front of the plane of the paper; the one shown on the right (denoted by primes) is moving downward behind the plane of the paper. The frictional drags normal and parallel to each segment, $F_n$ and $F_p$, act in directions opposite to $v_n$ and $v_p$, respectively. Note that their magnitudes are in the ratios $F_n/F_p = 2v_n/v_p$. $F_n$ and $F_p$ are decomposed into components normal and parallel to the helical axis, $F_{n}$ and $F_{p}$, respectively. $F_{n}$ and $F_{n'}$ act in opposite directions and form a couple that contributes to the torque. $F_{p}$ and $F_{p'}$ act in the same direction and contribute to the thrust.

Low Reynolds number
Geometric configuration of flagella: asymmetry
Bacteria screw themselves in the middle
Random walk

At 1 dimension

\[ -4\delta \quad -3\delta \quad -2\delta \quad -\delta \quad 0 \quad \delta \quad 2\delta \quad 3\delta \quad 4\delta \]

The particle starts at \( x = 0 \) at time \( t = 0 \) and undergoes a random walk:
1. Each particle takes a step to the right or to the left every \( \tau \) seconds, advancing at a speed \( \pm v_x \) and traveling a distance \( \delta = \pm v_x \tau \). For reasons of simplicity, we consider \( \tau \) and \( \delta \) as constants.

2. At each step, the probability of going left is \( \frac{1}{2} \) and of going right is \( \frac{1}{2} \).
   The particles forget the path they traveled before the previous step.
   The successive steps are statistically independent.
   The spread is not biased.

3. The particles move independently of each other and do not interact with each other.
   In practice this is true provided the solution is reasonably diluted.
Random walk

At 1 dimension

\[-4\delta \quad -3\delta \quad -2\delta \quad -\delta \quad 0 \quad \delta \quad 2\delta \quad 3\delta \quad 4\delta\]

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2. At each step, the probability of going left is \(\frac{1}{2}\) and of going right is \(\frac{1}{2}\).
   The particles forget the path they traveled before the previous step.
   The successive steps are statistically independent.
   The spread is not biased.

3. The particles move independently of each other and do not interact with each other.
   In practice this is true provided the solution is reasonably diluted.

These rules imply two striking consequences:
- on average the particles go nowhere
- the root mean square displacement is not proportional to time but rather to the root of time.
Random walk

To prove this, we use a recurrence.

We consider a set of $N$ particles. Let $x_i(n)$ be the position of the $i$th particle after $n$ steps. According to rule 1, the position of a particle after the $n$th step differs from the position of the particle after the $(n-1)$th step by $\pm \delta$.

$$x_i(n) = x_i(n - 1) \pm \delta$$

According to rule 2 and 3, the + sign applies to half of the particles and the – sign to the other half. The average displacement can be found by summing over all particles $i$ and dividing by $N$.

$$\langle x(n) \rangle = \frac{1}{N} \sum_{i=1}^{N} x_i(n)$$
Random walk

By expressing $x_i(n)$ as a function of $x_i(n - 1)$ we find:

$$\langle x(n) \rangle = \frac{1}{N} \sum_{i=1}^{N} (x_i(n - 1) \pm \delta)$$

$$\langle x(n) \rangle = \frac{1}{N} \sum_{i=1}^{N} x_i(n - 1)$$

$$\langle x(n) \rangle = \langle x(n - 1) \rangle$$

One can conclude that the **average position of the particles does not change** from one step to another. As all particles start at the origin, where the average position is zero, then the average position remains zero. The spreading of all the particles is symmetrical with respect to the origin.
Random walk

How much do the particles spread out? An effective way to measure particle spreading is to calculate the root mean square displacement.

\[ \langle x^2(n) \rangle^{1/2} \]

We average the square of the distance rather than the displacement itself. Since the square is always positive, the result must be strictly positive. To calculate it we start from:

\[ x_i^2(n) = x_i^2(n - 1) \pm 2\delta x_i(n - 1) + \delta^2 \]

And we then calculate the average:

\[ \langle x^2(n) \rangle = \frac{1}{N} \sum_{i=1}^{N} x_i^2(n) \]

\[ \langle x^2(n) \rangle = \frac{1}{N} \sum_{i=1}^{N} (x_i^2(n - 1) \pm 2\delta x_i(n - 1) + \delta^2) \]

\[ \langle x^2(n) \rangle = \langle x^2(n - 1) \rangle + \delta^2 \]
Random walk

\[ \langle x^2(n) \rangle = \langle x^2(n - 1) \rangle + \delta^2 \]

As \( x_i(0) = 0 \) for all particles, then \( \langle x^2(0) = 0 \rangle \) and it comes:

\[ \langle x^2(1) \rangle = \delta^2, \quad \langle x^2(2) \rangle = 2\delta^2, \quad \langle x^2(3) \rangle = 3\delta^2, \ldots, \langle x^2(n) \rangle = n\delta^2 \]

We conclude that the mean square displacement increases with the number of steps \( n \) and therefore that the root of the mean square displacement increases in \( \sqrt{n} \). According to rule 1, the particles execute \( n \) steps in a time \( t = n\tau \). \( n \) is therefore proportional to time \( n = t/\tau \). This implies that the root of the mean square displacement is proportional to the root of time.

\[ \langle x^2(t) \rangle^{1/2} = \sqrt{\frac{\delta^2}{\tau}} t \]
The translational diffusion coefficient

\[ \langle x^2(t) \rangle^{1/2} = \sqrt{\frac{\delta^2}{\tau} t} \]

One can introduce a diffusion coefficient: \( D = \frac{\delta^2}{2\tau} \)

It is a length squared par second: the explored area mer unit of time

\[ \langle x^2(t) \rangle^{1/2} = \sqrt{2Dt} \]
\[ \langle x^2(t) \rangle = 2Dt \]

The diffusion coefficient characterizes the migration of a certain type of particle, in a given medium and at a given temperature. In general, it depends on the particle size, the structure of the medium and the absolute temperature. For a small water molecule at \( T_{amb} \), \( D = 10^{-9} \text{ m}^2 \text{ s}^{-1} \).
Random walk in 2 and 3D

Rules 1 and 3 apply in all dimensions of space. It is further asserted that the movements in the $x$, $y$ and $z$ directions are statistically independent.

Thus, if $\langle x^2(t) \rangle = 2Dt$

then $\langle y^2(t) \rangle = 2Dt$ and $\langle z^2(t) \rangle = 2Dt$.

Then in 2D the square of the distance between the origin and any point of coordinates $(x, y)$ is $r^2(t) = x^2(t) + y^2(t)$, that yields $\langle r^2(t) \rangle = 4Dt$

And in 3D, the square of the distance between the origin and any point of coordinates $(x, y)$ is $r^2(t) = x^2(t) + y^2(t) + z^2(t)$, that yields $\langle r^2(t) \rangle = 6Dt$
During the diffusion process, the particles have a non-zero velocity. In an incompressible viscous fluid, this gives rise to a frictional force. We always have: \( \delta \) the length of a step and \( \tau \) the time between two steps.

To study friction, we consider a Brownian particle pushed by a constant external force \( f_{\text{ext}} \) along the \( x \) axis (we restrict ourselves here to one dimension).

Between two steps, according to Newton's second law: \( \frac{dv_x}{dt} = \frac{f_{\text{ext}}}{m} \) where \( m \) is the mass of the particle.

The velocity then varies as: \( v_x(t) = v_{0,x} + \frac{f_{\text{ext}}}{m} t \) where \( v_{0,x} \) is the value of the velocity right after one step.

The resultant of the motion of the particle is therefore: \( \delta = v_{0,x} \tau + \frac{1}{2} \frac{f_{\text{ext}}}{m} \tau^2 \)
Friction is related to diffusion

\[ \delta = v_{0,x} \tau + \frac{1}{2} \frac{f_{\text{ext}}}{m} \tau^2 \]

As with each step, the particle forgets the trajectory it had previously, after each step, \( v_{0,x} \) points randomly to the right or to the left, so on average, the value of \( v_{0,x} \) is zero.

By replacing the previous expression, one get \( \langle \delta \rangle = \frac{f_{\text{ext}}}{2m} \tau^2 \).

Thus, even if the particle is shaken by random collisions, it drifts noticeably with a speed equal to:

\[ \langle v_{\text{drift}} \rangle = \frac{\delta}{\tau} = \frac{f_{\text{ext}}}{\zeta} \quad \text{where} \quad \zeta = \frac{2m}{\tau}. \]

Multiplying both numerator and denominator by \( \left( \frac{\delta}{\tau} \right)^2 \), one gets:

\[ \zeta = \frac{2m}{\tau^2} \frac{\delta^2}{\tau} = \frac{2m}{\tau^2} \langle v_{\text{drift}} \rangle^2 = \frac{m}{D} \langle v_{\text{drift}} \rangle^2 \quad \text{with} \quad D = \frac{\delta^2}{2\tau} \quad \text{and} \quad \langle v_{\text{drift}} \rangle = \frac{\langle \delta \rangle}{\tau} \]
Friction is related to diffusion

According to the energy equipartition theorem, a particle at an absolute temperature $T$ has, on average, a kinetic energy associated with a movement on each axis of $\frac{1}{2} k_B T$ where $k_B$ is the Boltzmann constant.

$$\langle \frac{1}{2} mv_{\text{drift}}^2 \rangle = \frac{k_B T}{m} \Rightarrow \langle v_{\text{drift}}^2 \rangle = \frac{k_B T}{m}.$$

Thus $\zeta = \frac{mv_{\text{drift}}^2}{D} = \frac{k_B T}{D} \Rightarrow D = \frac{k_B T}{\zeta}$

Einstein-Smoluchowski's Formula

For a viscous friction force, the first Stokes law gives: $\vec{f}_{\text{ext}} = 6\pi \eta a \vec{v}_{\text{drift}} = \zeta \vec{v}_{\text{drift}}$ which gives $\zeta = 6\pi \eta a$ where $a$ is the particle size.

We thus obtain the Stokes-Einstein relation: $D = \frac{k_B T}{6\pi \eta a}$
Bacterial diffusion

During the swimming of a bacterium, the time $\tau$ between two steps is not constant but is distributed exponentially (in fact, Poisson process with very large $n$). In fact, the diffusion coefficient of a bacterium can be written:

$$D = \frac{v^2 \tau}{3(1 - \alpha)}$$

where $\alpha$ is the mean value of the cosine of the angle between 2 successive runs. If the direction change is completely random, then $\alpha = 0$.

To solve this, we need to consider again the equation: $\langle x(n)^2 \rangle = n\delta^2$

where $\delta$ is now the component on $x$ of the length of a run $l$.

Geometrically, one can write that $\langle \delta^2 \rangle = \frac{\langle l^2 \rangle}{3}$.
As the length of the runs follows a Poisson law, we can write that:

$$\langle l^k \rangle = \int_0^\infty \lambda^k e^{-\lambda l} dl = \frac{k!}{\lambda^k}$$

where $\lambda$ is the probability that a run takes place per unit length.

In the case $k = 2$, we get:

$$\langle l^2 \rangle = \frac{2!}{\lambda^2} \text{ et } \langle l \rangle = \frac{1!}{\lambda^1} = \frac{1}{\lambda} \Rightarrow \langle l^2 \rangle = 2 \langle l \rangle^2 \Rightarrow \langle \delta^2 \rangle = \frac{2 \langle l \rangle^2}{3}$$

As $\langle l \rangle = v \tau$ and $n = \frac{t}{\tau}$ we get that $\langle \delta^2 \rangle = \frac{2v^2 \tau^2}{3}$ and $\langle x^2(t) \rangle = 2 \left( \frac{v^2 \tau}{3} \right) t$

Thus, $D = \frac{v^2 \tau}{3}$.

The mean cosine is positive if there is a forward directional bias and vice versa. In *E. coli* $\alpha \sim 0.33$. What is its diffusion coefficient? What is it comparable to? What then is the effective temperature?
Rotational diffusion

In the same way that there is translational diffusion, there is also rotational diffusion. Instead of walking one step $\pm \delta$ along the $x$ axis every $\tau$ seconds, the bacterium rotates with a step of $\pm \varphi$ around the $x$ axis.

As before, we get: $D_r = \frac{\varphi^2}{2\tau}$

where $D_r$ is the rotational diffusion coefficient in rad$^2$ sec$^{-1}$.

The assumption that runs have ballistic trajectories is limited by rotational diffusion.
To understand this, we decompose the trajectory into a series of runs of exponentially distributed duration $\tau$. If $\tau$ is small, the angle $\theta$ between 2 successive runs is small and:

$$\cos \theta \sim 1 - \frac{\theta^2}{2} \Rightarrow \alpha = \langle \cos \theta \rangle \sim 1 - \frac{\langle \theta^2 \rangle}{2} \Rightarrow \langle \theta^2 \rangle = 2(1 - \alpha).$$

By analogy, we also have: $\langle \theta^2 \rangle = 4D_r \tau$

(a bacterium that moves along the $x$ axis can rotate around $y$ and $z$, so it is a 2-dimensional random walk).

One obtain, $4D_r \tau = 2(1 - \alpha) \Rightarrow \frac{1}{1 - \alpha} = \frac{1}{2D_r \tau}$ and as $D = \frac{v^2 \tau}{3(1 - \alpha)}$, we finally obtain $D = \frac{v^2}{6D_r}$.

For a speed of 30 $\mu$m/s and one we obtain:
rotational diffusion: $D_r \sim 0.062$ rad$^2$ s$^{-1}$
translational diffusion coefficient: $D \sim 2 \times 10^{-9}$ m$^2$ s$^{-1}$

So why does the bacterium need to tumble?
Bacterial diffusion

$E. \ coli$

YFP DNA plasmid

$50 \mu m$
Bacterial diffusion

Fick’s law

\[ \langle r^2(t) \rangle = 2dDt \]
Different types of motility

Kearns, 2010 Nature Reviews
Swarming is the multicellular movement of bacteria across a surface and is powered by rotating helical flagella.

Swimming is the movement of individual bacteria in liquid, also powered by rotating flagella.

Twitching is surface movement of bacteria that is powered by the extension of pili, which then attach to the surface and subsequently retract, pulling the cell closer to the site of attachment.

Gliding is active surface movement that does not require flagella or pili and involves focal-adhesion complexes.

Sliding is passive surface translocation that is powered by growth and facilitated by a surfactant.
Swarming

An *E. coli* swarm by H. Berg
Surfactant secretion

Kearns 2010
Swarming direction is not biased

- When swimming over a glass surface in a layer of fluid much thicker than the bacteria, cells spiral to the right, because the cell bodies, which are in front, roll clockwise over the surface, whereas the flagellar bundles, which push from behind, roll counterclockwise.

- The torque resulting from this couple causes cells to veer to the right.

- When tracking cells in *E. coli* swarms, Berg and coworkers found that cells prefer to swim straight ahead, curving to the left approximately as much as to the right.
Swarming direction is not biased

The majority of cells’ paths had no appreciable left- or right-ward curvature (Fig. D). Of all the 0.17-s-long trajectories that were measured, ~50% had a curvature of <0.01 µm\(^{-1}\) or, equivalently, a radius >100 µm.

Trajectories were broadly distributed between leftward and rightward curvature. Although, in most locations (and especially averaging over all locations, the mean curvature was 0.003 µm\(^{-1}\). This small curvature contrasts with the behavior of cells swimming close to a glass surface.
Swarming direction is not biased

There are two possible explanations for the loss of clockwise bias in the swarm:

1. frequent collisions between tightly packed cells in the swarm might prevent them from curving;
2. the upper (swarm/air) interface might exert an opposite torque on the cell from the lower (swarm/agar) interface, offsetting most or all of its effect. The upper interface appears to be stationary, covered by a surfactant monolayer pinned at its edges.

Zhang, 2010
Different swarming patterns

- **Featureless mat**
- **Bull's eye** (Also known as zones of consolidation or terraces)
- **Dendrites** (Also known as deep branches or tendrils)
- **Vortex** (Also known as wandering colonies)
- **Non-swarming cells**
- **Suppressor mutants** (Also known as sectors or flares)
Gliding involves the presence of adhesion proteins on the membrane of the bacteria. There are adhesion focal points distributed periodically along the bacterial cell body.

Fig. 5. Schematic illustration of three subcellular regions and four patterns of protein localization of M. mobile. The direction of gliding is indicated by an open arrow. The proteins are located at the subcellular region indicated. The neck region is specialized for gliding and contains the spike structure which has been observed by rapid-freeze-fracture electron microscopy (Miyata & Petersen, 2004).

Kusomoto, 2004
Chemical into mechanical energy

Hiratsuka, 2006
Hiratsuka, 2006