1. Introduction

Cell motility is a major achievement of biological evolution and is essential for a wide spectrum of cellular activities. Microorganisms, such as spermatozoa, bacteria, protozoa, and algae, use flagella—whip-like structures protruding from their bodies—for their propulsion. Swimming of uni- and multicellular organisms is essential for their search for food (chemotaxis), the reaction to light (phototaxis), and the orientation in the gravitation field (gravitaxis). Furthermore, flagellar motion plays a major role in higher organisms, where they transport fluid in the respiratory system in form of cilia, are involved in cellular communications, and even determine the morphological left–right asymmetry in the embryo.

Unicellular swimmers, e.g. bacteria like *Escherichia coli*, spermatozoa, and *Paramecia* are typically of a few to several tens of micrometers in size. The physics ruling the swimming on this micrometer scale is very different from that applying to...
swimming in the macro-world. Swimming at the micrometer scale is swimming at low Reynolds numbers (Purcell 1977a), where viscous damping by far dominates over inertia. Hence, swimming concepts of the high Reynolds number macro-world are ineffective on small scales. In the evolutionary process, microorganisms acquired propulsion strategies, which successfully overcome and even exploit viscous drag.

The design of artificial nano- and microswimmers is highly desirable to perform a multitude of tasks in technical and medical applications. Two general design strategies are currently followed, each posing particular challenges. First, successful concepts realized in nature can be adopted or underlying principles and mechanisms can be exploited. Second, novel construction principles can be invented, which are simpler but potentially more efficient, or plainly more practical from an engineering perspective. Major obstacles in such an endeavor are the availability of sustainable energy sources for artificial microswimmers, and physical concepts for efficient energy conversion into a propulsive force. Another issue is the active control of artificial microswimmers, such that they perform tasks or respond to external stimuli. The design and fabrication of a synthetic swimmer with such features would be extremely valuable in a diversity of fields like medicine, biology, material science, and environmental science. Such machines might transport cargo, e.g. in medicine or microfluidic chips, conduct operations in cells, remove toxic materials from human bodies or toxic water streams, or actively control material behavior as, e.g. viscoelastic properties.

Microswimmers hardly ever swim alone. Sperm cells are released by the millions to compete in the run for the egg. Bacteria grow by dividing and invading their surroundings together. Artificial microswimmers will only be able to deliver useful quantities of pharmaceuticals or modify material properties when present in large numbers. Indeed, in assemblies of motile microorganisms, cooperativity reaches a new level of complexity as they exhibit highly organized movements with remarkable large-scale patterns such as networks, complex vortices, or swarms.

In this article, we review the physics of locomotion of biological and synthetic microswimmers, and the emergent collective behavior of their assemblies. Several previous articles concerning microswimmers have addressed different aspects of their motility and collective behavior. Generic aspects of the emergent large-scale behavior of self-propelled particles and active soft matter have been reviewed by Toner et al (2005), Ramaswamy (2010), Vicsek and Zafeiris (2012), Marchetti et al (2013), and Saintillan and Shelley (2013). The hydrodynamics of swimming has been reviewed by Lauga and Powers (2009), Ishikawa (2009), Koch and Subramanian (2011), and Golestanian et al (2011). Aspects of bacterial motility have been discussed by Harshey (2003) and Cates (2012). Sperm motility and chemotaxis has been reviewed by Alvarez et al (2014). The dynamical properties of active Brownian particles have been discussed by Romanczuk et al (2012), with emphasize on the stochastic dynamics in the framework of statistical physics. The propulsion of synthetic swimmer on the nanoscale and the development of nanomachines have been addressed by Ozin et al (2005), Sengupta et al (2012) and Ebbens and Howse (2010).

Figure 1. Salmonella swim by a bundle of rotating helical flagella. From Brennen and Winet (1977). © Copyright 1977 Annual Reviews.

1.1. Biological microswimmers

1.1.1. Flagellated bacteria. A wide variety of bacteria exploit helical filaments, called flagella, for their propulsion. Different species possess various numbers and different arrangements of flagella. According to the arrangement, flagellated bacteria are classified as monotrichous bacteria which possess a single flagellum only, lophotrichous, bacteria with multiple flagella located at a particular spot on their surface, amphitrichous bacteria which grow a single flagellum on each of the two opposite ends, and peritrichious bacteria which are covered by multiple flagella pointing in all directions (Janssen and Graham 2011). Prominent examples of peritrichious bacteria are Escherichia coli (Berg 2004), Salmonella typhimurium, see figure 1, Rhizobium lupini, or Proteus mirabilis bacteria to name just a few. A flagellum is rotated by a motor complex, which consists of several proteins, and is anchored in the bacterial cell wall (Berg 2003, Berg 2004, Brennen and Winet 1977), see figure 2. The motor itself is connected to the flagellum by a flexible hook.

Bacteria like E. coli and Salmonella swim in a ‘run-and-tumble’ motion illustrated in figure 3 (Macnab 1977, Turner et al 2000, Berg 2004, Hyon et al 2012). In the ‘run’ phase (stage 1 in figure 3), the helical winding of all flagella is left-handed, and they rotate counterclockwise. The flagella form a bundle (see also figure 1), and the bacterium moves forward in a direction determined by its long axis. At the beginning of the ‘tumble’ phase, one flagellum reverses its rotational direction to clockwise (stage 2 in figure 3). The flagellum leaves the bundle which implies a random reorientation of the bacterium (stage 3 and 4). The reversal of the rotational direction is accompanied by a change of the helical handedness from left-handed to right-handed and the flagellum undergoes a polymeric transition (Calladine 1975, Macnab 1977, Armitage and Macnab 1987, Shah et al 2000, Darnton and Berg 2007, Darnton et al 2007, Vogel and Stark 2010, Vogel and Stark 2013, Calladine et al 2013). At the end of the tumbling phase, all flagella start to rotate again in the same counterclockwise direction (stage 5), the bundle reforms (stage 6), and the bacterium returns to a directional motion (stage 7 and 8).

The flagella of bacteria like Rhizobium meliloti or Rhizobium lupini are only capable of limited polymorphic transitions and their motors are unidirectional (Platzer et al 1997, Scharf 2002, Schmitt 2002). These bacteria modulate the rotation speed of individual motors to induce tumbling (Platzer et al 1997, Scharf 2002).
Uni-flagellated bacteria, e.g. *Vibrio alginolyticus*, tumble by motion reversal and by exploitation of a buckling instability of their hook (Son et al. 2013). This mechanism represents an example of one of the smallest engines in nature where a biological function arises from controlled mechanical failure, and reveals a new role of flexibility in biological materials.

The purpose of the run-and-tumble motion is to detect gradients in the concentration of chemicals (e.g. food) or temperature (to avoid regions of too high or too low temperature). This is achieved by extending the ‘run’ phase in case of improving environmental conditions, and by shortening it in case of worsening conditions.

Bacteria not only swim as individuals, but exhibit collective behavior at a moist surface or in a thin liquid film in form of swarming (Copeland and Weibel 2009, Darnton et al. 2010, Kearns 2010, Partridge and Harshey 2013b). Swarming was distinguished from other forms of surface translation (Heinrichsen 1972, Darnton et al. 2010, Kearns 2010), e.g. swimming, due to particular shape changes which swarming bacteria undergo. During the transition from swimming to swarming cells, the number of flagella increase and the cells become often more elongated by suppression of cell division (Stahl et al. 1983, Jones et al. 2004, Darnton et al. 2010, Kearns 2010). This points toward the significance of flagella and flagella interactions between adjacent cells (Stahl et al. 1983, Jones et al. 2004) for swarming, aside from possible shape induced physical interactions.

1.1.2. *Listeria*. *Listeria* is a facultative anaerobic bacterium, capable of surviving in the presence or absence of oxygen. It can grow and reproduce inside the host cell. Outside the...
body, *Listeria* use flagella for swimming, but at body temperature flagellin production is turned off, and *Listeria* hijack the actin cytoskeleton of the cell for its mobility. By expressing actin promotors on their surface, a thick actin gel develops on the surface. The gel forms a comet and pushes the bacterium through the cell.

In vitro, this mechanism can be mimicked by micrometer-size colloid beads coated with nucleation promotion factors. The gel initially forms isotropically, but due to tension in the growing gel layer, the symmetry is broken spontaneously, and an actin comet forms (Kawska et al 2012). The physics of *Listeria* motility has been reviewed recently by Prost et al (2008).

1.1.3. Eukaryotic cells. Eucaryotic swimmers are usually propelled by cilia or (eukaryotic-)flagella. These motile hair-like extensions of the cell consist of a bundle of microtubules, which are connected by motor proteins and other connecting proteins, see figure 4. The underlying structure is called the axoneme. It consists of two central microtubules, which are surrounded by nine double microtubules (rather stiff filaments with a persistence length of about 1 mm). The microtubules are connected by many proteins (nexin links, central spokes, ...), which stabilize the structure. Motor proteins (dynein) connecting neighboring double microtubules cause a local active bending force by sliding the microtubules relative to each other. Thus, motor activity is spread out over the whole length of the eukaryotic flagellum. The axoneme structure is well conserved across all eukaryotes. Hence, it seems very likely that it has evolutionary already been present in the very first eukaryotic cells.

![Figure 4.](http://en.wikipedia.org/wiki/Cilium)

The main structural difference between cilia and flagella is their length. A typical cilium is 10 $\mu$m long, while sperm flagella are about 50 $\mu$m long. The second large difference concerns their beat patterns. While flagella beat with an almost perfect propagating sinusoidal bending wave, the ciliar beat has two distinct phases. During the power stroke, the cilium is stretched out straight and moves rather fast in one direction (frames 1–11), while during the recovery stroke, it bends and slowly retracts (frames 13–27). Adapted from Brumley et al (2014) under the Creative Commons 4.0 license.

![Figure 5.](http://en.wikipedia.org/wiki/Cilium)

![Figure 6.](http://en.wikipedia.org/wiki/Cilium)
molecular motors results in a negative force-velocity relation at zero velocity. The system is thus intrinsically unstable, and starts moving in one direction. As the filaments move relative to each other and deform, elastic forces build up, eventually causing stalling and motion reversal. The system thus starts to oscillate in time. This oscillation explains how the axoneme’s internal machinery self-organizes to generate the flagella beat (Jülicher and Prost 1997, Camalet et al 1999, Riedel-Kruse et al 2007, Hilfinger et al 2009).

The domain of eukaryotes is home to an extraordinary number of different microswimmers. While all employ axonemes as motors, they use them in all kinds of ways and arrangements to propel themselves. In the following, we present a few examples of eukaryotic microswimmers, which have received particular attention in the biophysical community.

1.1.4. Sperm. Many sperm cells consist of a (roughly spherical) head, which comprises the genetic material, a midpiece, which contains many mitochondria for energy production, and the eukaryotic flagellum, see figure 7. A sperm cell is propelled though a fluid by a snake-like wiggling of its flagellum, as shown in figure 8. The flagellar beat is a propagating bending wave, with wave lengths smaller than the flagellar length. The beat can either be planar, as in figure 8, in particular for sperm swimming near surfaces (Friedrich et al 2010), or be 3D with a conical envelope (Cosson et al 2003, Woolley 2003). The purpose of sperm motility is of course the transport of the genetic material to the egg. Here, chemotaxis is important to guide...
the spermatozoa to find their target (Kaupp et al. 2003, Kaupp et al. 2008, Eisenbach and Giojalas 2006, Friedrich and Jülicher 2007, Alvarez et al. 2014).

1.1.5. Trypanosomes. Trypanosomes (T. brucei) are motile parasites responsible for sleeping sickness. Their motility is mediated by a single flagellum. However, unlike in sperm the flagellum of a trypanosome emerges from the flagellar pocket near the base of the cell and runs along the length of the entire body, as illustrated in figure 9. The cell surface hydrodynamic drag is used by trypanosomes to sweep antibodies to the flagellar pocket, the ‘cell mouth’, for host immune evasion. Trypanosomes are pulled forward by the planar beat of the flagellum, while the asymmetrically shaped body induces also a rotational motion (Uppaluri et al. 2011, Babu and Stark 2012, Heddergott et al. 2012).

1.1.6. Ciliates. Ciliates are a phylum of microorganisms characterized by motile cilia on their surface. Among them, Paramecia and Opalina have received significant attention in the biophysics community as model systems. Paramecia is a group of unicellular ciliate protozoa, which range from about 50–350 µm in length and move with a speed of approximately 10³ µm s⁻¹ (ten body lengths per second). They generally feed on bacteria and other small cells. Opalina is a genus of protozoa found in the intestines of frogs and toads. It is without a mouth or contractile vacuole. The surface of Opalina is covered uniformly with cilia. Both in Paramecia and Opalina, cilia beat neither independently nor completely synchronously, but instead (as explained above) in the form of metachronal waves (Tamm and Horridge 1970, Machemer 1972, Okamoto and Nakaoka 1994), see figures 5 and 6.

1.1.7. Chlamydomonas reinhardtii. Chlamydomonas reinhardtii is a single-celled green algae of about 10 µm in diameter, which swims with two flagella, see figure 10. Chlamydomonas are equipped with a light-sensing ‘eyespot’. Widely distributed worldwide in soil and fresh water, C. reinhardtii is used as a model organism in biology in a wide range of subfields. The swimming motion of Chlamydomonas resembles the human breast-stroke: the flagella are pulled back in a nearly straight shape, and are then bend over and pushed forward again. The oscillatory velocity field induced by swimming C. reinhardtii has been observed in time-resolved measurements recently (Drescher et al. 2010, Guasto et al. 2010).

1.1.8. Volvox. Volvox is another green algae. It forms spherical colonies of up to 50000 cells. Each mature Volvox colony is composed of numerous flagellate cells similar to Chlamydomonas, embedded in the surface of a hollow sphere. The cells move their flagella in a coordinated fashion, with distinct anterior and posterior poles of the colony. Each individual cell has an eye-spot, more developed near the anterior, which enable the colony to swim towards light (Solar et al. 2011). Recently, the flow field around freely swimming Volvox has been measured directly (Drescher et al. 2010, Drescher et al. 2009). The order of Volvocales contains many more microswimmers, in particular spherical swimmers of many different sizes.
1.19. Gliding motility of cells. Another form of cellular motility is gliding or crawling. In this case, cells do not swim in a fluid, but move on a substrate or through a gel or porous material. Because this form of locomotion on a substrate is not swimming, it goes somewhat beyond the scope of this review. However, the investigation of crawling eukaryotic cells and gliding bacteria can be a way to separate hydrodynamic contributions from generic self-propulsion effects, and provides new insights into the collective behavior of many self-propelled particles.

Crawling eukaryotic cells propel themselves with the help of their actin cytoskeleton. Velocities are of the order of a few tens of microns per hour, two to four orders of magnitude slower than swimming cells. Model organisms studied experimentally include Madin–Darby Canine Kidney (MDCK) cells, which display intriguing collective behavior (Poujade et al. 2007, Trepat et al. 2009, Basan et al. 2013), and lymphocytes, keratocytes (Kim et al. 2012) and keratinocytes for single-cell motility.

Also many bacteria can move actively by gliding on a substrate. A particularly well studied example is myxobacteria, which typically travel in swarms. Myxococcus xanthus has a signaling system that requires cell-to-cell contact, coordinates cell movements and gives rise to rippling patterns (Kaiser 2003). It has an elongated, spherocylinder-like body with an aspect ratio of about 10. After collisions, the bacteria acquire nearly identical nematic orientation. This makes myxobacteria a very interesting model system to study the collective behavior of self-propelled rod-like particles (Harvey et al. 2011, 2013, Gejji et al. 2012, Peruani et al. 2012).

1.2. Synthetic microswimmers

Locomotion on the nanoscale through a fluid environment is one of the grand challenges confronting nanoscience today (Ozin et al. 2005). The vision is to synthesize, probe, understand, and utilize a new class of motors made from nanoscale building blocks that derive on-board or off-board power from in situ chemical reactions. The generated mechanical work allows these motors to move through a fluid phase while simultaneously or sequentially performing a series of tasks. A large variety of such swimmers have been constructed recently, from bimetallic nanorods (Paxton et al. 2004, Fournier-Bidoz et al. 2005, Ozin et al. 2005), to rotating (Manghi et al. 2006) and deforming filaments (Belovs and Cébers 2009), and artificial sperm (Dreyfus et al. 2005, Williams et al. 2014). Some examples are given below.

1.2.1. Bimetallic nanorods and microspheres. A simple class of synthetic nanoscale motors are made from bimetallic Pt–Au nanorods immersed in a H₂O₂ solution (Paxton et al. 2004, 2006, Fournier-Bidoz et al. 2005). The catalytic reaction 2 H₂O₂ → 2 H₂O + O₂ occurs at the Pt end of the rod and is the power source for the motion. One plausible mechanism for motion involves the surface tension gradient due to O₂ adsorption on the nonreactive Au end. The molecular-level details of how O₂ generated at the Pt end of the nanorod leads to the propulsive force remain to be elucidated.

1.2.2. Catalytic Janus colloids. Similarly, spherical particles (like polystyrene or silica beads with metallic caps), which catalyze a chemical reaction inside the fluid, display self-propulsion (Howsie et al. 2007, Erbe et al. 2008). The catalytic reaction implies an asymmetric, non-equilibrium distribution of reaction products around the colloid, which generates osmotic or other phoretic forces (Golestanian et al. 2005, Rücker and Kapral 2007, Golestanian 2009, Popescu et al. 2009, 2010, 2011, Thakur and Kapral 2011, Sabass and Seifert 2012, Baraban et al. 2013, Upsal et al. 2015). These objects are denoted ‘diffusio-phoretic swimmers’.

The concept of diffusio-phoretic swimmers can be taken one step further by constructing self-assembled, photoactivated colloidal microswimmers. An example is a polymer sphere, which includes a smaller hematite cube in dilute H₂O₂ solution. The decomposition reaction is catalyzed by the hematite cubes, but only under illumination. Pairs of spheres and cubes then self-assemble into self-propelled microswimmers at a surface (Palacci et al. 2013). The dynamic assembly results from a competition between self-propulsion of particles and an attractive interaction induced respectively by osmotic and phoretic effects activated by light.

1.2.3. Thermophoretic Janus colloids. Janus colloids with a metallic cap can also display self-propulsion due to self-thermophoresis. In this case, the cap is heated by a laser beam, which generates a temperature difference between the two sides of the Janus particle; the colloid then diffuses in this temperature gradient (Jiang et al. 2010, Rings et al. 2010, Yang and Ripoll 2011, Bickel et al. 2013, Braun and Cichos 2013, De Buyl and Kapral 2013). This approach has been extended to thermophoretic Janus colloids in binary fluid mixtures (with an upper miscibility gap) near the demixing critical point (Volpe et al. 2011, Buttinoni et al. 2012). In this case, heating by the laser beam leads to the formation of a droplet of one phase which adheres to the cap. This approach has the advantage that a small laser power suffices to induce self-propulsion.

1.2.4. Bubble jets. Another type of catalytic microswimmer consists of a hollow microtube with functionalized surface. Such a microswimmer has been developed and fabricated by templated electrodeposition on a pre-stressed thin polymer film, which generates strain and leads to detachment from the substrate and roll-up into a tube. The catalytic reaction decomposes H₂O₂ into O₂ and water inside the tube, which leads to the formation of nano- and microbubbles. By spontaneous symmetry breaking, the bubbles leave the tube on one side; this implies a jet-like propulsion. Such tubular micro-engines offer several advantages, like easy motion control, integration of various functions, scalable size in diameter and length, and straight trajectories (Sanchez and Pumera 2009, Mei et al. 2011, Sanchez et al. 2011).

1.2.5. Rotators. Rotating discs (Grzybowski et al. 2000, Llopis and Pagonabarraga 2008), rotating spheres or dumbbells (Tierno et al. 2008) are another important class of swimmers. These rotors can be autonomous swimmers, like the Volvox algae mentioned above, or actuated synthetic particles,
like super-paramagnetic particles rotated by an external magnetic field (Bleil et al. 2006). Rotators show an interesting collective behavior, like a circling motion of Volvox around each other (Drescher et al. 2009), or a lane formation of rotating magnetic discs in microfluidic channels (Götze and Gompper 2010a, 2011).

1.2.6. Self-propelled droplets. Aqueous droplets suspended in an oil phase containing surfactants can also be made to swim. Propulsion arises for example due to the spontaneous bromination of mono-olein as the surfactant. The droplet surface is covered by a dense surfactant monolayer, which reacts with the bromine fuel that is supplied from inside the droplet, such that bromination proceeds mainly at the droplet surface, and reduces the amphiphilicity of the surfactant. This results in a self-sustained bromination gradient along the drop surface, which propels the droplet due to Marangoni stresses (Thutupalli et al. 2011).

1.2.7. Biomimetic microswimmers. Artificial microswimmers can be constructed by using similar design principles as those found in biological systems. A by now classical example is a swimmer which mimics the propulsion mechanism of a sperm cell (Dreyfus et al. 2005). The flagellum is constructed from a chain of magnetic colloid particles and is attached to a red blood cell, which mimics the sperm head. This artificial swimmer is set into motion by an altering magnetic field, which generates a sidewise oscillatory deflection of the flagellum. However, the swimming motion is not the same as for a real sperm cell; the wiggling motion is more a wagging than a travelling sine wave, and generates a swimming motion toward the tail end, opposite to the swimming direction of sperm.

A more recent example of a biohybrid swimmer which mimics the motion of sperm has been presented by Williams et al. (2014). In this case, the microswimmer consists of a polydimethylsiloxane filament with a short, rigid head and a long, slender tail on which cardiomyocytes (heart-muscle cells) are selectively cultured. The cardiomyocytes contract periodically and deform the filament to propel the swimmer. This is a true microswimmer because it requires no external force fields. The swimmer is about 2 mm long and reaches a swimming velocity up to 10 μm s⁻¹.

Another interesting example is artificial cilia (Sanchez et al. 2011). The assembly of oscillatory active filament bundles requires three main components. The first two, kinesin motor clusters and microtubules, spontaneously organize into aster-like structures (Nédélec et al. 1997). Addition of a third component, a non-adsorbing polymer, induces attractive interactions between microtubules through the depletion mechanism, leading to their bundling. This greatly increases the probability of kinesin clusters to simultaneously bind and walk along neighboring microtubules, where the relative motion of microtubules in these bundles depends on their polarity. This generates a cilia-like beat pattern, which is, however, symmetric in its forward and backward motions (Sanchez et al. 2011), see figure 12.

Biomimetic systems of externally actuated semi-flexible strings, like chains of magnetic beads (Gauger et al. 2009, Kim and Netz 2006), filaments of segmented electro-active polymers

1.2.8. Motility assays. An in vitro system to study the interaction of motor proteins with biological polar filaments like actin and microtubules are motility assays. In these systems, motor proteins are grafted onto a planar substrate with their active heads pointing upwards. Polar filaments, which are lying on such a motor-protein carpet, attach to the motors and are pushed forward, see figure 13. The filaments in such a system are neither swimmers nor self-propelled particles, but it is nevertheless a interesting model system to study the collective behavior of many moving particles with self-organized directions of motion, which shows phenomena like density waves and vortices (Schaller et al. 2010, Sumino et al. 2012).

1.3. Theoretical model microswimmers

Several detailed theoretical models have been designed during the last decades to describe and understand the behavior of flagellated microswimmers, but also of diffusio-phoretic spheres and rods, etc. These models and their properties will be reviewed in detail in the remainder of this article. However, there are also some model swimmers, which serve as generic models to elucidate the physical principles of microswimmers. The latter models are briefly introduced here.
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) machine performs a directed motion (Purcell 1977a).

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Therefore, Purcell suggested a swimmer consisting of three

between two rigid segments is varied periodically in time.

numbers, see section 2 below—is not possible when the angle

ming of micromachines in viscous fluids—at low Reynolds

30 years ago by Purcell (1977a) that directed forward swim-

Figure 14. The Purcell swimmer consists of three rod-like

connected segments, which can be tilted with respect to each other.

When the two angles \( \theta_1 \) and \( \theta_2 \) are varied in the non-reciprocal temporal sequence shown at the bottom, this micro-machine moves forward. Reproduced with permission from Purcell (1977a) Life at low Reynolds numbers Am. J. Phys. 45 3. Copyright 1977, American Association of Physics Teachers.

1.3.1. Purcell swimmer. It was recognized already more than 30 years ago by Purcell (1977a) that directed forward swimming of micromachines in viscous fluids—at low Reynolds numbers, see section 2 below—is not possible when the angle between two rigid segments is varied periodically in time. Therefore, Purcell suggested a swimmer consisting of three rigid segments as shown in figure 14. When the two angles are varied periodically in time, but in a way which breaks time-reversal symmetry, as shown at the bottom of figure 14, this machine performs a directed motion (Purcell 1977a).

1.3.2. Three-bead swimmer. A very simple 1D swimmer can be constructed from three spheres that are linked by rigid rods, whose lengths can change between two values (Najafi and Golestanian 2004). With a periodic motion that breaks the time-reversal symmetry as well as the translational symmetry, the model device swims at low Reynolds numbers as shown in figure 15. This swimmer is similar in spirit to the Purcell swimmer, but has the advantage that it can be treated theoretically much more easily, so that many of its properties can be analyzed in detail or even calculated analytically (Najafi and Golestanian 2004, 2008, Alexander et al 2008).

1.3.3. Squirmers. A particular class of microswimmers are almost spherical organisms that are propelled by active hair-like organelles (cilia) covering the body. On a mesoscopic length scale, the synchronized beating of the cilia can be mapped onto a spherical envelope (Lighthill 1952, Blake 1971b), and its time average corresponds to a steady tangential surface velocity. These objects—called ‘squirmers’—may also serve as a simple generic model for other types of microswimmers, for example the self-propelled droplets mentioned above (Thutupalli et al 2011).

The squirmer is modeled as a hard sphere of radius \( R \) with a prescribed tangential surface velocity \( v_{sq} \), causing a propulsion in the direction of the squirmer’s instantaneous orientation \( \hat{e} \). The relative velocity at a surface point \( r_s \) (with respect to the squirmer’s center) is given by (Blake 1971b)

\[
v_{sq}(r_s, \hat{e}) = \sum_{n=1}^{\infty} B_n \frac{2}{n(n+1)} \left( \frac{\hat{e} \cdot r_s}{R} \frac{r_s}{R} - \hat{e} \right) P^n_{1}(\cos \theta)\]

where \( P^n_{1}(\cos \theta) \) is the derivative of the \( n \)th Legendre polynomial with respect to the argument and \( B_n \) is the amplitude of the \( n \)th mode of the surface velocity. The absolute local surface velocity of the squirmer is given by

\[
v(r - r_s, \hat{e}) = v_{s} + v_{sq}(r - r_s, \hat{e}) + \Omega \times (r - r_s),
\]

where \( r_s, \hat{e}, v_{s}, c, \) and \( \Omega \) are the sphere position, velocity, and angular velocity, respectively. The constant \( B_1 \) sets the average velocity of the squirmer, \( v = \langle \hat{e} \cdot v_{s} \rangle = 2B_1/3 \) (Ishikawa et al 2006). To cope with the biodiversity of real microswimmers, the characteristic surface velocity of the model can be varied by adjusting the coefficients \( B_n \) with \( n \geq 2 \). In most cases studied so far, only \( B_1 \) and \( B_2 \) are taken to be non-zero, so that \( B_n = 0 \) for \( n \geq 3 \).

This model was employed, for example, to study the hydrodynamic interaction of two squirmers without (Ishikawa et al 2007) and with (Götze and Gompper 2010b) thermal fluctuations, monolayers of squirmers without thermal fluctuations (Ishikawa and Pedley 2008), or their behavior in external flows (Zöttl and Stark 2012, 2013, Gachelin et al 2013, Pagonabarraga and Llopis 2013).
2. Life at low Reynolds numbers

2.1. Hydrodynamics

The dynamics of the incompressible fluid surrounding a microswimmer is described by the Navier–Stokes equations

\[ \nabla \cdot \mathbf{v} = 0, \]

\[ \rho \frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla)\mathbf{v} = -\nabla p + \mathbf{f}, \]

where \( \rho \) is the fluid density, \( \eta \) the fluid viscosity, \( \mathbf{v}(\mathbf{r}, t) \) the position- and time-dependent fluid velocity field, \( p(\mathbf{r}, t) \) the pressure field, and \( \mathbf{f}(\mathbf{r}, t) \) an applied body force. Scaling length, velocity, and time by characteristic values \( L, v_0, \) and \( T_0, \) respectively, yields

\[ \text{Re}_T \frac{\partial \mathbf{v}'}{\partial t} + \nabla (\mathbf{v}' \cdot \nabla)\mathbf{v}' = \nabla^2 \mathbf{v}' - \nabla p' + \mathbf{f}', \]

where the prime denotes dimensionless quantities. Here, the dimensionless number \( \text{Re} = \rho v_0 L / \eta \) is the classical Reynolds number, which is a measure of the importance of the non-linear advection term compared to the viscous forces. A second dimensionless number is the oscillatory Reynolds number \( \text{Re}_T = \rho L^2 / (\eta T_0). \) It indicates the importance of the linear unsteady term, which scales as \( \rho v_0 / T_0, \) compared to the viscous term (Dhont 1996, Lauga and Powers 2009, Lauga 2011). \( \text{Re}_T = \tau_0 / T_0 \) is the ratio of the viscous timescale \( \tau_0 = \rho L^2 / \eta \) for shear wave propagation over the distance \( L \) and the characteristic time \( T_0. \) Examples for \( T_0 \) could be the self-advection time \( L/v_0 \) (for which \( \text{Re}_T = \text{Re} \)), the rotational period of a bacterial flagellum, or the period of a beating cycle of a cilia. For a swimmer of length \( L = 10 \mu m \) and a velocity of \( v_0 = 50 \mu m \cdot s^{-1}, \) the Reynolds number in water (with the kinematic viscosity \( \nu = \eta / \rho = 10^{-6} \text{m}^2 \cdot \text{s}^{-1} \)) is \( \text{Re} \approx 10^{-3}. \) In this case, the non-linear contribution on the left-hand-side of equation (5) can be neglected, leading to the linearized Navier–Stokes equation

\[ \rho \frac{\partial \mathbf{v}}{\partial t} = -\nabla^2 \mathbf{v} - \nabla p + \mathbf{f}. \]

For \( \text{Re}_T \ll 1, \) i.e. \( \tau_0 \ll T_0, \) equation (6) turns into the Stokes equation (creeping flow),

\[ \nabla p - \nabla^2 \mathbf{v} = \mathbf{f}, \]

and all inertia terms are absent.

The Stokes equation (7) is linear and time-independent, and is thus symmetric under time reversal, an aspects with far reaching consequences for microswimmers undergoing periodic shape changes, as first realized by Purcell (1977a). This is expressed by the famous ‘scallopl theorem’, which can be stated as: if the shape changes displayed by a swimmer are identical when viewed in reverse order, it will generate an oscillatory, but no directed motion (Purcell 1977a, Lauga and Powers 2009, Lauga 2011). It means that just by opening and closing its two shells, a mussel (scallopl cannot move forward. Additional degrees of freedom are required to generate a sequence of moves, which are not time reversibele. This aspect is discussed in more detail in section 5 below.

2.2. Solution of Stokes equation

The linearized Navier–Stokes equations (3), (6), and (7), can be solved analytically for an unbounded system with an external force field \( \mathbf{f}(\mathbf{r}, t) \). In this case, the velocity field is given by

\[ \mathbf{v}(\mathbf{r}, t) = \int_0^t \int \mathbf{H}(\mathbf{r} - \mathbf{r}', t - t') \cdot \mathbf{f}(\mathbf{r}', t') \, d^3r' \, dt', \]

with the time- and position-dependent hydrodynamic tensor \( \mathbf{H}(\mathbf{r}, t) \) (Bedeaux and Mazur 1974, Espanol et al 1995). An explicit expression for the tensor \( \mathbf{H}(\mathbf{r}, t) \) has been provided by Espanol et al (1995), Huang et al (2012, 2013) and Theers and Winkler (2013). The creeping flow limit, i.e. the solution of equations (3) and (7), follows when \( \mathbf{f}(\mathbf{r}, t) \) change significantly slower with time than \( \mathbf{H}(\mathbf{r}, t). \) With time-independent \( \mathbf{f}(\mathbf{r}) \), integration over \( t' \) in equation (8) yields

\[ \mathbf{v}(\mathbf{r}) = \int \mathbf{H}(\mathbf{r} - \mathbf{r}') \mathbf{f}(\mathbf{r}') \, d^3r'. \]

\( \mathbf{H}(\mathbf{r}) \) is the well-known Oseen tensor, with the Cartesian components (Espanol et al 1995, Dhont 1996)

\[ H_{ij}(\mathbf{r}) = \frac{1}{8 \pi \eta r^2} \left[ \delta_{ij} r + \frac{r_i r_j}{r^2} \right]. \]

The presence of confining surfaces modifies the fluid flow field. At surfaces, the fluid velocity is typically very small, because the collisions of fluid particles with the surface imply that the molecules are scattered backwards and thereby transfer momentum parallel to the wall. Thus, no-slip boundary conditions, with \( \mathbf{v}(\mathbf{r}) = 0 \) at the surface, are usually employed. The solution of Stokes equations is still given by equation (9), however, the Oseen tensor has to be replaced by the Blake tensor (Blake 1971a), which satisfies the no-slip boundary condition.

2.3. Dipole swimmers

Most swimmers move autonomously, with no external force applied, and hence the total interaction force of the swimmer on the fluid, and vice versa, vanishes. In the simplest case, which actually applies to many microswimmers like bacteria, spermatozoa, or algae, the far-field hydrodynamics (at distances from the swimmer much larger than its size) can well be described by a force dipole (Ishikawa 2009, Lauga and Powers 2009). This has been confirmed experimentally for E. coli by Drescher et al (2011). Two classes of such dipole swimmers can be distinguished, as shown schematically in figure 16. If
the swimmer has its 'motor' in the back, and the passive body drags along the surrounding fluid in front, the characteristic flow field of a 'pusher' emerges, see figure 16(a). Similarly, if the swimmer has its motor in the front, and the passive body drags along the surrounding fluid behind, the characteristic flow field of a 'puller' develops, see figure 16(b). It is important to notice that the flow fields of pushers and pullers look similar, but with opposite flow directions. This has important consequences for the interactions between swimmers and of swimmers with walls, as will be explained below.

Mathematically, the flow field $u_d(r - r_0)$ of a hydrodynamic force dipole located at $r_0$ can be obtained very easily from the Oseen tensor (10) by considering two opposite forces $f_0 = \hat{d} \hat{e}$ of equal magnitude at $r = r_0 \pm d/2$ with $d = d \hat{e}$. An expansion to leading order in $d/|r - r_0|$ yields

$$u_d(r) = \frac{P}{8\pi \eta r^3} \left[ -1 + \frac{3(r \cdot \hat{e})^2}{r^2} \right] r,$$

where $P = f_0 d$ is the dipole strength. Note that the flow field of a force dipole decays as $1/r^3$ from the center of the dipole, faster than the force monopole or Stokeslet, see equation (10).

The flow lines of a hydrodynamic dipole oriented in the x-direction are shown in figure 17. There are two inflow and two outflow regions in the $xy$-projection, which are separated by the separatrices $y = \pm \sqrt{2} x$. In three dimensions, the outflow region is a cone.

The flow field of a hydrodynamic dipole in front of a surface can be obtained by the image method known from electrostatics. Considering, for simplicity, a planar wall with slip boundary conditions. The flow field is then given by

$$v_w(r - r_0) = u_d(r - r_0; \hat{e}) + u_d(r - r_0; \hat{e}')$$

for a wall at $z = 0$, with $r_0 = (x_0, y_0, z_0)$, $r_1 = (x_0, y_0, -z_0)$, where $z_0 > 0$, and $\hat{e}'$ the mirror image of $\hat{e}$ with respect to the $z = 0$ plane. This implies that at $z = 0$ the velocity field $v_w$ is perpendicular to the surface vanishes identically, i.e. $v_w(z = 0) \equiv 0$. The dipole experiences a force near the surface, which is determined by the hydrodynamic interactions between the dipole and its image. It is given by the $z$-component of the flow field of the image charge at the location of the dipole, thus

$$v_{w_z}(z_0) = -\frac{P}{32\pi \eta e_0^2} \left[ 1 - 3(\hat{e} \cdot \hat{e})^2 \right],$$

because $(\hat{e} \cdot \hat{e})^2 = (\hat{e} \cdot \hat{e})^2$. This result shows that the hydrodynamic force is attractive to the wall, and that it decays as the dipole flow field quadratic with the distance from the wall.

The exact solution for a no-slip wall (Berke et al 2008) yields the same functional dependence on the angle and the wall distance as equation (14), only the numerical prefactor in equation (14) is smaller by a factor 2/3.

2.4. Fluctuations and noise

Fluctuations and noise may strongly affect the motion of microswimmers. There are two major sources of noise in active systems. On the one hand, thermal fluctuations are present in both passive and active systems. On the other hand, active processes themselves can give rise to fluctuations. For example, in cilia beating, the motor proteins are sensitive to the availability of ATP molecules, their number attached to a filament varies in time, and different cilia will typically have different numbers of active motors. Furthermore, the smaller a system is, the more important fluctuations become.

The importance of noise for the dynamics of microswimmers can be estimated by the Péclet number $Pe$, which compares advective and diffusive time scales. The self-advection time scale is $L/v_0$, and $L$ are the typical swimmer velocity and length, respectively, and the diffusive time scale is $L^2/D_T$, with the translational diffusion coefficient $D_T$. Hence, a Péclet number can be defined by $Pe = v_0 L/D_T$. For motion in thermal equilibrium and under the assumption of the swimmer to be spherical, $D_T$ can be related to the rotational diffusion coefficient $D_R$ via $D_T = D_R L^2/3$. Thus, the Péclet number is equivalently given by

$$Pe = \frac{v_0}{LD_R}.$$
For the dynamics of a self-propelled sphere, we consider the persistent motion of a Brownian particle with independent stochastic processes for its velocity and acceleration. Hence, the equation of motion for translation is

\[ \dot{r} = v + \frac{1}{\gamma_T} \Gamma, \] (16)

which is coupled to changes of the velocity described by

\[ \dot{v} = -\gamma_R v + \xi. \] (17)

Strictly speaking, in this description the magnitude of the velocity is not preserved, only the relation \( \langle v^2 \rangle = v_0^2 \) applies. In equations (16) and (17), \( \gamma_T \) and \( \gamma_R \) are the translational and rotational friction coefficients, where the latter is related to the rotational relaxation time \( \tau_R \) by \( \gamma_R = 1/(d - 1)D_T \). \( \Gamma \) and \( \xi \) are Gaussian and Markovian stochastic processes, with zero mean and the moments

\[
\langle \Gamma(t)\Gamma(t') \rangle = 2d\gamma_T^2D_T\delta(t-t'),
\]
(18)

\[
\langle \xi(t)\xi(t') \rangle = 2(d-1)D_RD_R\delta(t-t'),
\]
(19)

in \( d \geq 1 \) dimensions. Equations (16)–(19) yield the mean square displacement of the sphere center (Uhlenbeck and Ornstein 1930, Risken 1989)

\[
\Delta r^2 = \langle (r(t) - r(0))^2 \rangle = 2dD_T t + 2v_0^2\sqrt{\tau_R}t \exp(-t/\tau_R) - 1,
\]
(20)

which implies \( \Delta r^2 = 2dD_T t + v_0^2 t^2/2 \) for \( t \ll \tau_R \) and \( \Delta r^2 = (2dD_T + 2v_0^2/[d(d - 1)D_R]) t^2 \) for \( t \gg \tau_R \). The latter defines the effective translational diffusion coefficient

\[ D_{T,\text{eff}} = D_T + \frac{v_0^2}{d(d - 1)D_R}, \] (21)

which is much larger than \( D_T \) for \( v_0 \gg \sqrt{D_T D_R} \). Note that for a sphere embedded in 3D space, but confined in its translational motion to two dimensions, e.g. to a surface, the effective diffusion coefficient still has the same effective diffusion constant (21) with \( d = 3 \), but \( \Delta r^2 = 4D_{T,\text{eff}} t^2 \). In particular, these results show that the Péclet number (15), which involves the rotational diffusion constant, remains appropriate to characterize the importance of noise for self-propelled particles.

The mean square displacement of self-propelled Janus colloids on a surface has been measured as a function of fuel concentration by Howse et al (2007) as well as by Volpe et al (2011) for various illumination intensities. The extracted effective diffusion coefficients are well described by \( D_{T,\text{eff}} \) of equation (21), indicating that diffusion is dominated by self-propulsion and rotational diffusion. The relevance of higher moments of the displacement distribution has been addressed by Zheng et al (2013). In particular, a non-Gaussian character of the diffusiophoretic motion of self-propelled Janus spheres is theoretically predicted and experimentally confirmed.

For active systems, in general, fluctuations have no reason to be thermal (see equations (18) and (19)). While a Gaussian distribution of the noise is still a reasonable first order approximation, the amplitude can be much larger than that due to thermal fluctuations. An instructive example is the \( E. coli \) rotary motor. A motor rotation is typically driven by protons that generate a torque by passing into the cell via the motor (Mora et al 2009). However, the flux of protons is not continuous, but rather determined by discrete events of proton translocation. The stochasticity of this process creates a ‘shot noise’. Modelling the motor in some detail, Mora et al (2009) derive an expression for the effective diffusion coefficient of the flagellar rotation. At high load, the effective diffusion coefficient is thermal, but at low loads, diffusion increases and becomes dominated by the shot noise.

Measurements of the rotational diffusion coefficient of \( Chlamydomonas \) yield \( D_R = 0.4 \text{ rad}^2 \text{ s}^{-1} \) (Drescher et al 2011). This value can be compared with that of a passive sphere of radius \( R = 5 \mu m \), which is \( D_R = k_B T/(8\pi R^3) = 3 \times 10^{-3} \text{ rad}^2 \text{ s}^{-1}, \) i.e. it is about two orders of magnitude smaller than the value of the active microorganism.

Similarly, for \( E. coli \) the values \( D_R = 0.057 \text{ rad}^2 \text{ s}^{-1} \) (Drescher et al 2011) and \( D_R = 2 \text{ rad}^2 \text{ s}^{-1} \) (Saragosti et al 2012) have been reported for non-tumbling and tumbling cells, respectively. A study of paralyzed \( E. coli \) (Tavaddod et al 2011) yields the rotational diffusion coefficient \( D_R = 0.032 \text{ rad}^2 \text{ s}^{-1}, \) which is only a factor two smaller than the value of swimming but non-tumbling cells. Thus, tumbling events evidently increase the rotational diffusion coefficient by more than an order of magnitude.

We conclude that noise and fluctuations in microswimmer motion can be much more pronounced compared to that of the dynamics of respective passive objects, and that activity-based noise can be the dominant contribution to observed phenomena.

3. Swimming due to flagellar motion

3.1. Anisotropic hydrodynamic friction of slender bodies

A microorganism is able to swim forward in a fluid by wiggling or rotating a flagellum, because the hydrodynamic friction of a long, slender body in a viscous environment is anisotropic. This can be demonstrated easily for a long and thin rod of radius \( a \) and length \( L \): it experiences less friction when pulled along its axis than perpendicular to it.

We approximate the rod as a sequence of touching beads of radius \( a \). In general, the equation of motion of the \( i \)th bead is given by (Bird et al 1987, Winkler 2007)

\[ \zeta(r_i - v(r_i)) = F_i, \] (22)

i.e. the frictional force is equal to the applied force. Here, \( \zeta = 6 \pi \eta a \) is Stokes friction coefficient for a sphere with no-slip boundary conditions moving in a viscous fluid. The fluid velocity \( v(r) \) is determined by the motion of all other beads \( i \neq j \) and follows from equation (9). The force density on the fluid originates from the forces of the various beads

\[ f(r) = \sum_i F_i \delta(r - r_i(t)). \] (23)

Thus, we obtain (Doi and Edwards 1986)

\[ \ddot{r}_i(t) = \frac{1}{\zeta} \frac{\dot{r}_i(t)}{\zeta} + \sum_{j \neq i} \mathbf{H}(r_i(t) - r_j(t)) \mathbf{F}_j, \] (24)
which turns into (Harnau et al 1996)
\[
\mathbf{r}(s, t) = \frac{1}{3\pi \eta} \int \mathbf{f}(s) + \int \mathbf{H}[\mathbf{r}(s, t) - \mathbf{r}(s', t)] \mathbf{f}(s') \, ds'
\] (25)
in the continuum limit, where \(s\) (with \(-L/2 < s < L/2\)) is the contour coordinate along the centerline of the rod, and \(f(s)\) the linear force density.

The anisotropic friction coefficients of a rod are defined by the force–velocity relation
\[
\mathbf{F} = \zeta_{||} \mathbf{v}_|| + \zeta_\perp \mathbf{v}_\perp
\] (26)
for the motion parallel (\(v_||\)) and perpendicular (\(v_\perp\)) to the rod axis. Calculations based on equation (26), with constant friction coefficients \(\zeta_{||}\) and \(\zeta_\perp\), are denoted ‘resistive-force theory’ (Gray and Hancock 1955, Lighthill 1976).

To calculate \(\zeta_{||}\) and \(\zeta_\perp\), it is easiest to consider the special cases of a rod aligned along the \(x\)-axis of the reference frame and pulled parallel and perpendicular to its long axis, respectively, with the constant force \(\mathbf{F} = F \hat{\mathbf{e}}\). Since, we consider a rigid body, the force density is \(f(s) = F \hat{\mathbf{e}} L\), and the average rod velocity \(v_{\text{rod}} = \int \mathbf{r}(s) ds / L\) becomes
\[
v_{\text{rod}} = F \left[ \frac{\hat{\mathbf{e}}}{3\pi \eta L} + \frac{\hat{\mathbf{e}} + (\hat{\mathbf{e}} \cdot \hat{\mathbf{r}}) \hat{\mathbf{r}}}{4\pi \eta L^2} \int_0^L \frac{L - s}{s} \, ds \right].
\] (27)
The lower cutoff of the integral excludes a region of the thickness of the rod and prevents self-interactions. Because \((\hat{\mathbf{e}} \cdot \hat{\mathbf{r}}) \hat{\mathbf{r}} = 1\) and 0 for parallel and perpendicular orientation of the force, respectively, evaluation of the integral yields
\[
\zeta_{||} = 2 \zeta_{\text{h}}, \quad \zeta_\perp = \frac{4\pi \eta L}{\ln(L/2a)}
\] (28)
in the asymptotic limit of a long rod (Doi and Edwards 1986). It is therefore easier to pull a long rod along its axis than perpendicular to it by a factor two. The logarithmic divergence is a result of the long-range nature of hydrodynamic interactions of different parts of the rod, which reduce the friction coefficient compared to that of a rod of non-interacting beads (~ \(L\)). Corrections of the friction coefficients for a more precise hydrodynamic calculation for a cylinder are provided in Tirado et al (1984) and Howard (2001).

3.2. Swimming velocity of beating flagella and sperm

The result (28) together with equation (26) can now be used to calculate the swimming velocity of a sinusoidally beating flagellum. In this case, the time-dependent shape is given by
\[
y(x, t) = A \sin (kx - \omega t),
\] (29)
where \(A\) is the beating amplitude, \(\omega\) the frequency, and \(k = 2\pi / \lambda\) the wave number with the wave length \(\lambda\). The velocity of a segment of the flagellum at \(x\) is then
\[
v_y(x, t) = \frac{\partial y}{\partial t} = -A \omega \cos (kx - \omega t),
\] (30)
where geometric nonlinearities are neglected. With the local tangent vector (not normalized)
\[
t(x, t) = (1, Ak \cos (kx - \omega t), 0)^T,
\] (31)
the velocity \(v(x, t) = (0, v_x(x, t), 0)\) can be decomposed into \(v_|| = (v \cdot t) t / ||t||^2\) and \(v_\perp = v - v_||\), with
\[
v_\perp = - \frac{A^2 \omega k \cos^2 (kx - \omega t)}{1 + A^2 k^2 \cos^2 (kx - \omega t)} l.
\] (32)
According to equation (26), this generates the force
\[
F_\perp = \frac{\zeta_{||} - \zeta_\perp}{L} \int \frac{A^2 \omega k \cos^2 (kx - \omega t)}{1 + A^2 k^2 \cos^2 (kx - \omega t)} \, dx
\] (33)
in the swimming direction, while the force in the perpendicular direction vanishes when averaged over the whole flagellum. For small beating amplitudes, equation (33) can easily be integrated, which yields the average propulsion force
\[
F_\perp = \frac{1}{2} \left( \zeta_{||} - \zeta_\perp \right) A^2 \omega k .
\] (34)
The swimming velocity then follows from \(v_\perp \approx F_\perp / \zeta_{||}\) as
\[
v_{\text{flag}} = -\frac{1}{2} \left( \frac{\zeta_\perp}{\zeta_{||}} - 1 \right) A^2 \omega k .
\] (35)
This simplified calculation shows several important aspects of flagellar propulsion. First, swimming is only possible due to the frictional anisotropy, i.e. \(\zeta_{||} \neq \zeta_\perp\). Second, for a travelling wave in the positive \(x\)-direction, the flagellum moves in the negative \(x\)-direction, i.e. movement is opposite to the direction of the travelling wave. Third, the swimming velocity increases linearly with the beating frequency \(\omega\) and the wave vector \(k\), but quadratically with the beating amplitude \(A\). And finally, the swimming velocity is independent of the fluid viscosity.

A more refined calculation has been performed by Gray and Hancock (1955), also employing resistive force theory, to determine the swimming velocity of sperm. For the sinusoidal beating pattern (29) and \(\zeta_\perp / \zeta_{||} = 2\), they find
\[
v_{\text{sperm}} = \frac{1}{2} A^2 \omega k \left[ 1 + A^2 k^2 \right.
\]
\[
+ \sqrt{1 + \frac{A^4 k^2 \omega^2}{2} \left( \ln \left( \frac{4L}{3a} \right) - \frac{4}{3} \right) \right]^{-1}.
\] (36)
Here, \(L\) is the length of the flagellum and \(R_0\) is the radius of the head. The general conclusions with respect to equation (35) remain valid, but additional effects appear. The second term in the brackets of equation (36)—its origin is already recognizable in equation (32)—arises from the finite beating amplitude and implies a saturation of the velocity for large beating amplitudes. The last term in the brackets describes the reduction of velocity due the drag of the passive head.

Friedrich et al (2010) employed a wave form with increasing amplitude of the flagellar beat with increasing distance from the head to describe the beat geometry of bull sperm, and use direct experimental input for the beat amplitude and frequency. In this way, experimental trajectories can be reproduced quite accurately by resistive force theory, when
the friction anisotropy is chosen appropriately. This yields the friction anisotropy \( \zeta_1/\zeta_4 = 1.81 \pm 0.07 \).

The swimming of sperm has also been analyzed by slender-body theory (Hancock 1953, Lighthill 1976, Johnson and Brokaw 1979) (taking into account the hydrodynamic interactions of different parts of the deformed flagellum as in section 3.1 for slender rods) by Higdon (1979a, b). Results agree with the resistive-force approach by Gray and Hancock (1955) within about 10%.

A higher order solution, taking into account the full hydrodynamics, is possible for an infinitely long flagellum in two spatial dimensions (where hydrodynamics is of longer range than in three dimensions)—corresponding to an infinite sheet—agree with the resistive-force approach by Gray and Hancock (1953, Lighthill 1976, Johnson and Brokaw 1979) as well as slender body theory (Hancock 1953, Lighthill 1976, Johnson 2013).

The sperm structure or beating pattern is typically not described as an infinite sheet. Here, the swimming velocity

\[
\nu_{\text{sperm}} = \frac{1}{2} A^2 \omega k \left( 1 - \frac{19}{16} A^2 k^2 \right)
\]

(37)

has already been obtained by Taylor (1951) in his pioneering work. This result confirms all qualitative features discussed above, but shows somewhat different numerical coefficients (which is in part due to the different dimensionality).

The sperm structure or beating pattern is typically not completely symmetric, but has some chirality. In this case, sperm swim on helical trajectories (Crenshaw 1989, Elgeti and Gompper 2008). In particular, the helicity of the swimming trajectories is very pronounced for sea urchin sperm (Crenshaw 1996, Kaupp et al 2003, Böhmer et al 2005).

3.3. Propulsion by helical flagella

Resistive force theory (Gray and Hancock 1955, Lighthill 1976) as well as slender body theory (Hancock 1953, Lighthill 1976, Johnson and Brokaw 1979) have been applied to describe propulsion of rotating helical flagella. Various aspects of the approaches have been summarized by Lauga and Powers (2009) in their review. Here, we briefly address slender-body results in the light of recent experiments on macroscopic helices at low Reynolds numbers (Rodenborn et al 2013).

As shown by Lighthill (1976), the velocity of a point at \( s \) along the contour of a flagellum of finite thickness can be described as

\[
\nu(s) = \frac{1}{4 \pi \eta} f_z(s) + \int H(r(s) - r(s')) f_z(s') \Theta(|r(s) - r(s')| - \delta) ds'.
\]

(38)

within the far-field approximation (as in equation (25)). Here, \( \delta = a \sqrt{\epsilon} / 2 \) is the cutoff to avoid self-interactions, \( \Theta(x) \) is Heaviside’s step function, and \( f_z \) is the normal component of the Stokeslet strength (equation (10)), i.e.

\[
f_z = (\mathbf{I} - \mathbf{t} \otimes \mathbf{t}) f,
\]

(39)

where \( \mathbf{t} \) is the local tangent vector to the filament and \( \mathbf{I} \) the unit matrix (Lauga and Powers 2009, Rodenborn et al 2013).

A helix oriented along the \( z \)-axis can be parameterized as

\[
r(s) = (R_h \cos \varphi, R_h \sin \varphi, sP/(2\pi))^T.
\]

(40)

Here, \( \varphi = 2 \pi s \cos \theta / P \) is the helical pitch, \( \theta \) the pitch angle, and \( R_h \) the helix radius. From equation (40), we obtain the tangent vector and the force (39). Assuming a very long helix \( L/P \approx 1 \), we can neglect end effects and approximate the local force density by

\[
f(s) = \left( -f_{\rho} \sin \varphi, f_{\varphi} \cos \varphi, f_z \right)^T.
\]

(41)

and the local velocity by

\[
v(s) = (-\Omega R_h \sin \varphi, \Omega R_h \cos \varphi, v_z)^T.
\]

(42)

Inserting equations (40)–(42) in equations (38) and (39), respectively, the translational velocity \( v_z \) and rotational frequency \( \Omega \) can be represented as

\[
\begin{pmatrix}
\frac{v_z}{\Omega} \\
\frac{A_{11} A_{12}}{A_{12} A_{22}} \left( \frac{f_z}{m_z} \right)
\end{pmatrix}
\]

(43)

by the pulling force density \( f_z \) and the moment density \( m_z = R \delta f_z \). Note that we assume the helix to remain aligned along the \( z \)-axis, i.e. other torques are compensated by additional external forces. Neglecting end effects, the matrix elements are given by

\[
A_{11} = \frac{1}{4 \pi \eta} \frac{\sin^2 \theta}{\sin \theta} + \frac{1}{\sin \theta} \int_{v_0}^{v_1} \left( \frac{1}{\Phi} + \frac{\varphi^2 \cos^2 \theta}{\Phi^3} \right) d\varphi.
\]

(44)

with the abbreviations \( v_0 = 2 \pi \delta \cos \theta / P \), \( v_1 = \pi L \cos \theta / P \), and \( \Phi(\varphi) = [4 \sin^2 (\varphi/2) + \varphi^2 \cos^2 \theta]^{1/2} \) (Rodenborn et al 2013). Inversion of equation (43) yields the thrust, torque, and drag as function of helix length and driving frequency \( \Omega \) or velocity \( v_z \). In the asymptotic limit \( L \rightarrow \infty \), the thrust \( F_T = L \cdot f \) obeys (Rodenborn et al 2013)

\[
F_T \sim = \frac{L}{\ln (L \cos \theta / R_h)} \Omega.
\]

(45)

i.e. shows a logarithmic dependence on the total helix height \( L \cos \theta \). The proportionality factors follow from equations (44). In particular, a logarithmic dependence is obtained for \( A_{11} \), since \( \Phi = \varphi \cos \theta \) as \( \varphi \rightarrow \varphi_L \rightarrow \infty (L \rightarrow \infty) \). The other terms converge to finite values. As before, the logarithm appears due to hydrodynamic interactions.

As an example, figure 19 shows experimental results for the thrust of helical flagella of various lengths obtained in experiments on macroscopic scale models at low Reynolds numbers by Rodenborn et al (2013). The data compare very well with the slender body theories by Lighthill (1976) and Johnson (1980), respectively, and the regularized Stokeslet
approach by Cortez et al (2005). The above asymptotic calculations apply for \( L/IP > 10^2 \). Over the range of ratios \( L/IP \) relevant for bacteria (\( 3 \leq L \cos(\theta)/P \leq 11 \)), there is a quantitative difference between the full theory and the asymptotic approximation. However, the qualitative length dependence is well captured. More results are presented by Rodenborn et al (2013).

In order to determine the swimming properties of a bacterium, we have to consider both, the flagellum bundle as well as the body. For simplicity, we adopt resistive force theory to illustrate the dependence of the swimming velocity on the motor torque rotating a single flagellum (Lauga and Powers 2009). Inversion of equation (43) yields the force and torque on a flagellum due to translation and rotation. Considering the limit of small pitch angles \( \theta \ll 1 \), elimination of rotation by external torques yields \( F_T = \zeta b v_z \). Preventing translation, rotation with the velocity \( \nu' = Rb \Omega \) yields the thrust force \( F_z = F_T = (\zeta_l - \zeta_b) \theta v_z = (\zeta_l - \zeta_b) \Omega R b \) (see figure 20) and the momentum \( M_z = \zeta_l R b v'_z = \zeta_l^b R b \Omega \) with the friction coefficients (28) (Lauga and Powers 2009). Hence, we obtain

\[
\left( \begin{array}{c} F_z \\ M_z \end{array} \right) = \left( \begin{array}{cc} (\zeta_l - \zeta_b) \Omega R b \\ (\zeta_l - \zeta_b) \Omega R b \end{array} \right) \left( \begin{array}{c} v_z \\ \Omega \end{array} \right) . \tag{46}
\]

More precise resistive force theory results have been presented by Chattopadhyay et al (2006), Magariyama et al (1995) and Purcell (1977b). Alternatively, the inverse matrix of equation (43), with the elements of equation (44), yields a more precise description within slender-body theory.

Approximating the cell body by a sphere of radius \( R_b \) and assuming \( R_b \ll L \), the frictional body force \( F_b \) and the body torque \( M_b \) are

\[
F_b = -\zeta_b M_b , \tag{47}
\]

\[
M_b = -\zeta^b \Omega b ,
\]

where \( \zeta_b = 6 \pi \eta R_b \) and \( \zeta^b = 8 \pi \eta R_b^3 \) are the translation and rotational friction coefficients. The helix is driven by a rotary motor with the frequency \( \Omega_m \) relative to the body. In response, the helix and body rotate with the frequencies \( \Omega \) and \( \Omega_b \). These frequencies are related by \( \Omega + \Omega_b = \Omega_m \). Since the whole bacterium is force and torque free, i.e. \( F_z + F_b = 0 \) and \( M_z + M_b = 0 \), its swimming velocity is given by (Lauga and Powers 2009)

\[
v_z \approx \frac{\theta (\zeta_l - \zeta_b) \nu'_z}{\zeta^b} \frac{\nu'_z}{\zeta_l R_b} \Omega_m . \tag{48}
\]

The friction coefficient \( \zeta_b \) does not appear, since we assume \( \zeta_l \gg \zeta_b (L \gg R_b) \). Evidently, swimming is again—as in the sperm case—only possible due to frictional anisotropy. Moreover, \( v_z \) depends linearly on the body rotational friction coefficient. Hence, without body, the bacterium could not swim. Due to the approximation \( \theta \ll 1 \), \( v_z \) depends linearly

\[
\frac{F_z}{(L \cos(\theta)/P)^2}
\]

**Figure 19.** Thrust of a helical flagellum as function of its length according to Rodenborn et al (2013). The experimental data (squares) agree well with the slender body theory by Lighthill (1976b) (blue), the regularized Stokeslet theory by Cortez et al (2005), and the slender body theory by Johnson (1980). The black and green lines are obtained by resistive force theory according to Lighthill (1976) and Gray and Hancock (1955), respectively.

**Figure 20.** Helical segment moving in a viscous fluid. Only half of a helical pitch is shown. The drag-based thrust force \( F_T \) appears by the motion of the red rodlike segment in the direction \( \nu' \) (see also Lauga and Powers 2009).

**Figure 21.** Contour plot of stable equilibrium pitching angles of ellipsoidal microswimmers (pusher), at fixed distance (equal to the long axis of the ellipsoid) from a wall, as a function of the inverse aspect ratio \( e \) and the asymmetry parameter \( f \) for the active part of the surface, as indicated by the swimmer shapes. Positive pitching angles are pointing away from the surface. The swimmers are driven by an active region of the rear end, as indicated by the arrows, where \((L + 1)/2\) is the active fraction of length. Used with permission from Spagnolie and Lauga (2012) Hydrodynamics of selfpropulsion near a boundary: predictions and accuracy of far-field approximations J. Fluid Mech. 700 105–4.

\[
\left( \begin{array}{c} F_z \\ F_T \end{array} \right) = \left( \begin{array}{cc} (\zeta_l - \zeta_b) \Omega R b \\ (\zeta_l - \zeta_b) \Omega R b \end{array} \right) \left( \begin{array}{c} v_z \\ \Omega \end{array} \right) . \tag{46}
\]

More precise resistive force theory results have been presented by Chattopadhyay et al (2006), Magariyama et al (1995) and Purcell (1977b). Alternatively, the inverse matrix of equation (43), with the elements of equation (44), yields a more precise description within slender-body theory.

Approximating the cell body by a sphere of radius \( R_b \) and assuming \( R_b \ll L \), the frictional body force \( F_b \) and the body torque \( M_b \) are

\[
F_b = -\zeta_b M_b , \tag{47}
\]

\[
M_b = -\zeta^b \Omega b ,
\]

where \( \zeta_b = 6 \pi \eta R_b \) and \( \zeta^b = 8 \pi \eta R_b^3 \) are the translation and rotational friction coefficients. The helix is driven by a rotary motor with the frequency \( \Omega_m \) relative to the body. In response, the helix and body rotate with the frequencies \( \Omega \) and \( \Omega_b \). These frequencies are related by \( \Omega + \Omega_b = \Omega_m \). Since the whole bacterium is force and torque free, i.e. \( F_z + F_b = 0 \) and \( M_z + M_b = 0 \), its swimming velocity is given by (Lauga and Powers 2009)

\[
v_z \approx \frac{\theta (\zeta_l - \zeta_b) \nu'_z}{\zeta^b} \frac{\nu'_z}{\zeta_l R_b} \Omega_m . \tag{48}
\]

The friction coefficient \( \zeta_b \) does not appear, since we assume \( \zeta_l \gg \zeta_b (L \gg R_b) \). Evidently, swimming is again—as in the sperm case—only possible due to frictional anisotropy. Moreover, \( v_z \) depends linearly on the body rotational friction coefficient. Hence, without body, the bacterium could not swim. Due to the approximation \( \theta \ll 1 \), \( v_z \) depends linearly
on the pitch angle. Changing the handedness of the helix leads to a change of the swimming direction.

We like to mention that a helix driven by an external torque also swims (Ghosh and Fischer 2009, Schamel et al. 2014). However, it is not torque free and therefore is not an autonomous swimmer. Under the same assumptions as above, the swimming velocity is \( v_h \approx \frac{8 M}{\rho} \left[ \left( \frac{\zeta_1 - \zeta_0}{C^3} \right) / \left[ \zeta_2 / R_h \right] \right] \), very similar to equation (48), but now with the helix frequency \( \Omega = M / \zeta_2 \), determined by the applied torque \( M \), and the overall helix rotational friction coefficient \( \zeta_2 \).

4. Swimming near surfaces

Surfaces, interfaces, and confinement are ubiquitous in the microswimmer world. Microswimmers being small, they might be expected to be typically far away from surfaces. There are three important points to remember, however. First, many biological microswimmers regularly encounter surfaces and confinement, from sperm cells in the reproductive tract to microorganisms in the soil (Foissner 1998, Or et al. 2007). Second, microorganisms often rely on the presence of surfaces for their function and survival; for example, bacteria form biofilms on surfaces for spreading, to enhance cell–cell exchange and nutrient uptake. And third, important points to remember, however. First, many biological microswimmers regularly encounter surfaces and confinement, from sperm cells in the reproductive tract to microorganisms in the soil (Foissner 1998, Or et al. 2007). Second, microorganisms often rely on the presence of surfaces for their function and survival; for example, bacteria form biofilms on surfaces for spreading, to enhance cell–cell exchange and nutrient uptake.

A generic phenomenon of microswimmers near surfaces is an effective surface accumulation. Already in 1963, Rothschild discovered and quantified an accumulation of sperm cells near a glass cover slide (Rothschild 1963). Other microswimmers like E. coli (Berke et al. 2008) or Chlamydomonas (Kantsler et al. 2013) also accumulate at walls. Two mechanisms have been suggested to explain this effect, hydrodynamic interactions and propulsion together with steric interactions. We will discuss these two mechanisms in the following sections.

Other surface induced phenomena include rectification of microswimmer motion by ratchets (Tailleur and Cates 2009, Berdakin et al. 2013, Kantsler et al. 2013), rotation of microgears in bacterial suspensions (Di Leonardo et al. 2010), collective surface adhesion in clusters (Wensink and Löwen 2008) or geometric traps for microswimmers (Kaiser et al. 2012).

4.1. Hydrodynamics of surface capturing

The far-field interactions of microswimmers can be understood in terms of a multipole expansion. For a force free swimmer, the dominant term in the dipole term, which distinguishes pushers from pullers, see section 2.3. A microswimmer at a distance \( z \) from a no-slip wall, with an orientation angle \( \theta \) between the swimming direction and the surface normal vector (pointing into the fluid), experiences a angular velocity (Berke et al. 2008)

\[
\Omega_r (\theta, z) = \frac{3 P \cos \theta \sin \theta}{64 \pi \eta z^3} \left[ 1 + \frac{\gamma^2 - 1}{2 (\gamma^2 + 1)} (1 + \cos^2 \theta) \right]
\]

(49)

and a drift velocity (Berke et al 2008)

\[
u_z (\theta, z) = -\frac{3 P}{64 \pi \eta z^2} (1 - 3 \cos^2 \theta).
\]

(50)

where \( P \) is the dipole strength and \( \gamma \) the aspect ratio of the swimmer shape.

Equation (50) allows several interesting predictions. First, the hydrodynamic interactions decay slowly as \( 1/z^2 \) with increasing distance from the surface, as already explained in section 2.3. Second, for pushers (like sperm), the hydrodynamic interaction is attractive for orientations nearly parallel to the wall (with \( \theta \) near 90°), but repulsive for orientations nearly perpendicular to the wall (with \( \theta \) near 0°); for pullers (like Chlamydomonas), the hydrodynamic interaction is repulsive when they are swimming parallel to the surface. However, in these considerations, the rotation of the swimmer orientation due to hydrodynamic interactions has not yet been taken into account. Equation (49) shows that for the pusher, swimming parallel to the surface and being slowly attracted to it is indeed the stable state. On the other hand, for pushers the parallel orientation is unstable, a reorientation toward the surface occurs, and the microswimmer moves to the surface head-on (Berke et al. 2008, Spagnolie and Lauga 2012).

As both pushers and pullers come closer to the surface, higher orders in the multipole expansion become important. For spherical or ellipsoidal squirmers, the importance of higher order terms has been studied (Spagnolie and Lauga 2012). The swimmers are driven by imposing a surface velocity on part of the particle, like in the squirmer model (see section 1.3). A boundary-integral formulation of the Stokes equation is used to generate numerically ‘exact’ results for comparison. In the multipole expansion, a general axisymmetric swimmer is described as a linear combination of fundamental solutions to the Stokes equations: a Stokeslet dipole, a source dipole, a Stokeslet quadrupole, and a rotlet dipole. For spherical and ellipsoidal microswimmers, the multipole expansion is found to be surprisingly accurate, sometimes down to surface distances of a tenth of the swimmer length.

Physically, the main result is—see figure 21—that microswimmers that are both slender and sufficiently active (but not completely active, \( \gamma \neq 1 \)) exhibit pitching equilibria with their noses down toward the wall, while microswimmers that are not sufficiently slender or not sufficiently active exhibit pitching equilibria with their noses turned up away from the wall (Spagnolie and Lauga 2012). This has important consequences, because a swimmer which points away from the wall will usually not remain at the wall, but escape due to is forward motion. Furthermore, hydrodynamically caused rotation rates for microswimmers approaching a wall are found to be typically small, and for large impact angles not large enough to avoid a collision between the swimmer and the wall (Spagnolie and Lauga 2012). Thus, eventually a more detailed, swimmer-specific modelling is required.

Ellipsoidal squirmers, with surface velocities given by a sum of Legendre polynomials (compare equation (1) for the spherical squirmer), were studied by Ishimoto and Gaffney (2013). A fixed-point analysis yields stable swimming...
positions for pushers and pullers over a wide range of aspect ratios and $B_2$- and $B_3$-amplitudes. However, when $B_2$ and $B_3$ are too small, no fixed point is found because hydrodynamic interactions are too weak. Pusher spheres show only unstable fixed points (unless $B_3$ is very strong), while puller spheres display stable fixed points with a swimmer orientation toward the wall. As the aspect ratio increases, puller trajectories at a fixed distance from the wall become more unstable, and conversely pushers become stable. Pushers at a fixed point have an orientation away from the wall. Some of the unstable fixed points are found to be surrounded by stable limit cycles, which correspond to swimmers which change their distance from the wall periodically. For an elongated puller with aspect ratio $a = 2$, the distance from the wall is predicted to vary between its size and three times its size (Ishimoto and Gaffney 2013). Furthermore, it is predicted that a change of boundary conditions from no-slip to slip significantly changes the location and characteristics of fixed points, and thereby of the swimming behavior near surfaces.

Another important aspect is the competition of hydrodynamic interactions with rotational diffusion (Elgeti and Gompper 2009, Drescher et al 2011). When a pusher is deviating by a (small) angle $\delta \phi$ from parallel alignment with the wall due to rotational diffusion, then—in the far-field approximation—it takes a time of order $t_r = \delta \phi \Omega_r$, (see equation (49)) to become aligned again due to hydrodynamic interactions. During this time, it can swim a distance $\Delta z = v_0 \sin(\delta \phi) t_r$ away from the wall due to self-propulsion, but drifts toward the wall by a distance $\Delta z = u t_r$, due to hydrodynamic interactions, see equation (50). This implies that for $\delta \phi \gtrsim (r_0 z)^2$, the effective swimmer velocity points away from the wall, where $r_0$ is the swimmer size and $z$ is the distance from the wall, and in the time interval $t_r$, travels a distance $\Delta z \sim r_0$. For distances $z$ a few times $r_0$, this implies $\Delta z \sim z$. Thus, for small swimming velocities and large angular fluctuations, a microswimmer is expected to exhibit also large fluctuations in its distance from a wall. Here, the importance of orientational fluctuations can be quantified by the orientational Peclet number $P_{\theta}(z) = \Omega_r(z)/D_r$. Of course, very close to a wall, hydrodynamic interactions become more important, but also the dipole approximation breaks down.

A similar conclusion was reached by Drescher et al (2011), who considered cell–cell scattering. By estimating the mean-square angular change of orientation in cell–cell encounters, both due to hydrodynamic interactions and to rotational diffusion, Drescher et al (2011) estimated a hydrodynamic horizon $r_H$, beyond which hydrodynamic interactions become irrelevant. For non-tumbling E. coli, $r_H$ is found to be comparable to the length of the cell body, about 3 µm. However, other effects like flagellar interactions would become important at such short distances. Of course, rotational diffusion becomes less important with increasing microswimmer size. 

4.2. Propulsion-induced surface accumulation

Hydrodynamics is not the only mechanism that can explain accumulation of swimmers at surfaces. Indeed, it has to be
realized that any self-propelled particle in confinement will eventually encounter a surface. Without a reorientation, the particle will just stay there. Therefore, rotational diffusion is required to induce a detachment from the wall. In order to elucidate this adhesion mechanism, and how noise drives a self-propelled particle away from a wall, it is interesting to consider the behavior of ‘Brownian’ rods—in the absence of any hydrodynamic interactions. In this case, excluded-volume interactions favor parallel orientation near the wall, while the noise leads to fluctuations of the rod orientation and thereby an effective repulsion from the wall. The competition of these two effects gives rise to an interesting adsorption behavior (Elgeti and Gompper 2009, Li and Tang 2009).

Results of Brownian dynamics simulations (Elgeti and Gompper 2009) are shown in figure 22. While passive rods are depleted from the surface (because their entropy is reduced near the surface due to restricted orientational fluctuations), active rods show an increased probability density near the surface, which grows with increasing propulsion force $f_z$, see figure 22(a). In addition, the surface accumulation of the rods strongly depends on the rod length $l$. The surface excess—the integrated probability density to find a rod near the surface relative to a uniform bulk density distribution—is shown in figure 22(b). The results show (i) that short rods show little or no surface aggregation for any propelling force, and (ii) that the surface excess initially increases with increasing $f_z$ and $l$, but then saturates and becomes nearly independent of $f_z$ and $l$ for large propulsion forces and rod lengths (Elgeti and Gompper 2009).

The physical mechanism behind this behavior is as follows. A rod hits the surface at some point in time, because swimming directions in the bulk are randomly distributed. After contact with the wall, it gets reoriented parallel to the wall. Then it moves parallel to the wall, slowly wiggling its trajectory from the wall again, until it is sufficiently far from the wall that frequent contacts no longer occur.

The surface accumulation of self-propelled rods can be understood more quantitatively by exploiting an analogy of the trajectories of rod-like microswimmers with the conformations of semi-flexible polymers. The self-propulsion of the rod, combined with rotational diffusion leads to a trajectory with a persistence length

$$\xi_p \sim v / D_R \sim \eta v l^3 / k_B T \quad (51)$$

similar to a fluctuating polymer. The key difference however, is that the path is directed, and thus not forward–backward symmetric like a polymer. The trajectory of a rod colliding with the wall displays a sharp kink, impossible for a semi-flexible polymer. Leaving the wall, on the other hand, happens at a shallow angle, similar to a semi-flexible polymer attached parallel to the wall at one end. This difference in possible conformations leads to an effective attraction of rod-trajectories to the wall, and a repulsion of polymers. In the end, the polymer analogy predicts very well the scaling of the surface excess (Elgeti and Gompper 2009). In particular, in the ballistic regime, with $\xi_p \gg d$, the scaling arguments predict the probability to find the rod near the wall

$$p = 1 / (l + a d), \quad (52)$$

Figure 24. Surface excess $s$ of active Brownian spheres as a function of Péclet number $Pe$ for various wall separations $d$, as indicated. Results from the analytic calculation for very narrow channels (dotted lines) match well the simulations for very narrow channels, but fail for wider channels. The approximation for small Péclet numbers (dashed lines) works well for large wall separations. It overestimates the surface excess for large $Pe$. All analytic expression have no adjustable parameters. From Elgeti and Gompper (2013b).

Wall accumulation or self-propelled spheres

Another, even simpler model microswimmer is a self-propelled Brownian sphere. The essential difference to the self-propelled rod is that the sphere has no geometric alignment interaction with the wall (Elgeti and Gompper 2013b). Again, self-propulsion leads to accumulation of particles near the wall. The simulation results shown in figure 23 demonstrate that the (normalized) probability density $\rho(\Delta z)$ to find a particle at a distance $\Delta z$ from the wall is strongly peaked close to the wall for $Pe \gtrsim 5$. Figure 24 shows the surface excess $s$ as a function of the Péclet number $Pe = v_0 / \sqrt{D_R D_T}$ for different channel widths. Note that $s$ does not saturate at a value $s_{\text{max}} < 1$ as is observed for self-propelled rods above, but approaches unity for large $Pe$ (complete adhesion).

The large degree of symmetry allows for an analytic treatment via the Fokker–Planck equation

$$\partial_t \rho(z, \theta, t) = D_R \frac{1}{\sin(\theta)} \partial_\theta [\sin(\theta) \partial_\theta \rho(z, \theta, t)] - v_0 \cos(\theta) \partial_z \rho(z, \theta, t) + D_T \partial^2_z \rho(z, \theta, t), \quad (53)$$

where the angle $\theta = 0$ corresponds to particles oriented in the positive $z$-direction. This equation already demonstrates the main origin of surface accumulation. The rotational diffusion is independent of the spatial position, but particles are driven to one of the chamber walls depending on their orientation.
Thus particles oriented toward the top, accumulate at the top, those pointing down, accumulate at the bottom wall. Less particles remain in the center. Solutions for small Peclet number and narrow channels are depicted in figure 24, and work well within their respective limits.

Within a concave confinement (i.e. a ring or an ellipse in two dimensions), slow rotational diffusion suppresses surface detachment; the particle moves along the confinement wall, until it reaches a location where its orientation is perpendicular to the wall. This leads to complete adsorption of self-propelled particles in small enough closed environments, and to accumulation in regions of largest wall curvature (because here the largest reorientation by rotational diffusion is required to remove the particle) (Fily et al 2014).

These approaches neglect interactions between several swimmers. However, in experiments, microswimmers often occur at finite concentration or even dense suspensions. In these cases, collective effects can play an important role. For example, in a system of many self-propelled Brownian rods between walls in two dimensions, the rods moving along the walls in opposite directions block each other and lead to the formation of ‘hedgehog-like’ clusters (Wensink and Löwen 2008). This effect can be exploited to capture active particles. As shown above, self-propelled rods accumulate already at walls at infinite dilution. However, combining the ‘hedgehog effect’ of swimmers blocking each other in a wedge-like geometry, very strong capture of swimmers can be achieved, up to the point of complete trapping. In complete trapping, the swimmers block each other in such a way that none can escape the trap, even at opening angles where single swimmers would escape again (Kaiser et al 2012) (see figure 25).

Capturing of many particles at interfaces can also be exploited to separate different particle species. Self-propelled discs or rods of different size or velocity in confinement at high densities separate with small and fast particles favored at the interface (Costanzo et al 2014, Yang et al 2014). For soft discs of different size and velocity, this segregation can be understood by considering the elastic-energy barrier for a particle to squeeze between two others (Yang et al 2014). For hard rods of different velocity, the faster particles push the slower ones away from the wall (Costanzo et al 2014). External flows in a channel can be used to subsequently separate the different particles into different compartments (Costanzo et al 2014).

4.3. Sperm hydrodynamics near surfaces

Sperm frequently encounter situations of swimming in confined geometry, for example in the female reproduction tract (Fauci and Dillon 2006). The swimming behavior of sperm near walls and surfaces has been studied for sperm of bull (Rothschild 1963, Friedrich et al 2010), human (Winet et al 1984), sea urchin (Böhmer et al 2005, Cosson et al 2003, Kaupp et al 2003), mouse, rat, and chinchilla (Woolley 2003). All experiments reveal circular or curvilinear trajectories close to the surface. Such trajectories are relevant for the movement of sperm on the epithelial layer that lines the oviduct, and when sperm reach the surface of the much larger
egg. For example, many fish eggs on their surface possess a small orifice, called pylum, that must be reached by the sperm for successful fertilization.

For sea urchin sperm, portions of the tail were observed to be outside of the focus plane of the microscope (Cosson et al. 2003), suggesting an out-of-plane component of the beating pattern. Mouse sperm, which are characterized by a strongly curved midpiece, adhere to the wall only when the ‘left’ side of the head faces the glass surface (Woolley 2003). Chinchilla sperm undergo a rolling motion as they move along the surface, thereby touching the wall with different parts of their head (Woolley 2003). Finally, the beating pattern of bull sperm seems to be nearly planar parallel to the wall (Friedrich et al. 2010).

Several explanations have been proposed to account for the capture of sperm near a surface (Rothschild 1963, Cosson et al. 2003, Woolley 2003). In his pioneering study of bull sperm near surfaces, Rothschild concluded that hydrodynamic interactions are the most likely origin of this effect (Rothschild 1963). For rodent sperm, two mechanisms have been proposed (Woolley 2003). For sperm that exhibit a 3D beating pattern and display a rolling motion as they progress (like chinchilla sperm), it was argued that the conical shape of the flagellar envelope establishes a thrust toward the surface. Alternatively, for sperm that exhibit a 2D beating pattern (like mouse sperm), the discoidal shape of the sperm head, which is slightly tilted with respect to the plane of the flagellar beat, may act as a hydrofoil (Woolley 2003).

Since sperm is a pusher, far-field hydrodynamics predicts a parallel orientation with the wall and an effective hydrodynamic attraction. When the microswimmer comes closer to the wall, so that the dipole approximation is no longer justified, mesoscale simulations (see, e.g. reviews by Kapral (2008) and Gompper et al. (2009)) can be employed to elucidate the physical mechanism of attraction to the wall (Elgeti et al. 2010). Alternatively, sperm motion near a wall can be studied by a numerical solution of the Navier–Stokes equations (Smith et al. 2009).

The sperm model used in the simulations of Elgeti et al. (2010) is shown in figure 26. The main qualitative result is that sperm swims very close to the wall. Figure 27 shows the flow field of a symmetric, non-chiral sperm near a surface, as obtained from the simulation. The influx of fluid in the midpiece region, which is characteristic for dipole swimmers in the bulk, becomes very asymmetric near the surface: the flow onto the midpiece from above relative to flow from below is greatly enhanced due to the presence of the wall (figure 27(a)). This imbalance of fluxes generates an attraction to the wall in the midpiece region, in qualitative agreement with the predictions by a force-dipole approximation for large distances from the wall (Berke et al. 2008). The flow field near the end of the tail also has a component toward the wall (figure 27(a)); this component is responsible for a hydrodynamic repulsion of the tail from the wall, which induces a tilt of the sperm axis toward the surface (figure 26). Furthermore, due to the no-slip boundary conditions, the flow in the plane parallel to the wall is screened (figure 27(b)). The far-field
approximation predicts the decay $r^{-3}$ for large distances (Drescher et al. 2011, Spagnolie and Lauga 2012).

Thus, the simulations (Elgeti et al. 2010) reveal that (i) the beating plane of sperm gets oriented parallel to the wall (in agreement with experimental observations (Friedrich et al. 2010)), (ii) the sperm develops a small tilt angle toward the wall (compare figure 26(a)), which enhances the attraction compared to the pure dipole force, and (iii) the elongated shape of sperm contributes to the adhesion effect.

In contrast, on the basis of the numerical solution of the Navier–Stokes equations, Smith et al. (2009) predict that sperm swims nearly parallel to the wall, but with a distance comparable to the sperm length, and with a small angle away from the wall.

The trend of microswimmers to follow boundaries can then be exploited to create traps and ‘one-way channels’ in micro-fabricated devices (Denissenko et al. 2012, Galajda et al. 2007, Guidobaldi et al. 2014 and Hulme et al. 2008). For the rectification of sperm motion in microchannels, the channels walls are given a ‘clover-leaf’ structure, where sperm following the walls are redirected by 180°, then leave the wall at a sharp corner (Denissenko et al. 2012), see figure 28. In the same experiments, it was found that sperm indeed seem to swim at interfaces with finite angle towards the surface confirming the predictions of Elgeti et al. (2010), but at variance with the results of Smith et al. (2009).

Chiral sperm also adhere to surfaces. In this case, sperm swim on helical trajectories in the bulk (Crenshaw 1989, Crenshaw 1996, Gray and Hancock 1955), and in circles at a wall, see figure 26(b), in good agreement with the experiments mentioned above. The radius of the swimming circles decreases with increasing chirality. Weakly chiral sperm display a rolling motion, while strongly chiral sperm do not roll.

Figure 27. Averaged flow field in the vicinity of a symmetric sperm cell adhering to a wall. (a) Plane perpendicular to the wall, and (b) plane parallel to the wall, with both planes containing the average sperm shape. A snapshot of a sperm is superimposed. The flow field generated by the beating tail is directed away from the sperm along their swimming direction and toward the sperm along its side. From Elgeti et al. (2010). Copyright 2010 Elsevier.

Figure 28. A microfluidic device, micro-fabricated in PDMS, which presents a ‘one-way street’ for swimming sperm. In this anisotropic channels sperm swim preferentially in a counter-clockwise fashion. Center: a magnification showing how sperm traveling in the wrong direction are forced to turn. The colors represent the time sequences red–green–blue. Used with permission from Denissenko et al. (2012) Human spermatozoa migration in microchannels reveals boundary-following navigation Proc. Natl. Acad. Sci. USA 109 (21) 8007–10. Copyright 2012 PNAS.

4.4. Bacteria swimming at surfaces

The swimming behavior of bacteria close to surfaces differs from the run-and-tumble motion in free solution. Experiments show that individual *E. coli* bacteria swim in clockwise, circular trajectories near planar glass surfaces (Berg and Turner 1990, Frymier et al. 1995, DiLuzio et al. 2005, Hill et al. 2007, Kaya and Koser 2012, Molaei et al. 2014). In the following, individual cells at surfaces are considered, which could be swimmer or swarmer cells.

The direction of circular motion at a wall depends on the boundary conditions. Since the cell is force and torque free, the body and flagella bundle rotation imply a clockwise rotational motion for a no-slip boundary condition (Lauga et al. 2006, Li et al. 2008, Lemelle et al. 2010, Lopez and Lauga 2014), see figure 29. Hydrodynamics gives rise to an increased drag of the fluid confined between the cell and the surface and a torque appears on the swimmer, which turns the cell in clockwise direction for no-slip boundaries. In contrast, as shown by Lemelle et al. (2010) and Lopez and Lauga (2014), slip boundary conditions allow for counter-clockwise circular motion. As a consequence of the preferred circular swimming direction for no-slip boundary conditions, *E. coli* swim preferentially on the right-hand side of a microchannel, when it is confined to the bottom surface (DiLuzio et al. 2005).

Recent experimental studies revealed the flow field near a swimming *E. coli* bacterium, in particular next to a surface (Drescher et al. 2011), see figure 30. In this case, the flow field can be well described by a simple force dipole model.
as discussed in section 2.3. Moreover, these studies support the argument that hydrodynamic effects contribute to the observed long residence times of bacteria close to no-slip surfaces (Berke et al. 2008).

In contrast, the experiments of Drescher et al. (2011) suggest that cell-surface collisions determine the cell behavior next to surfaces, as proposed by Li and Tang (2009), Elgeti and Gompper (2009) and Hernandez-Ortiz et al. (2009), rather than long-range hydrodynamic interactions (Berke et al. 2008). To arrive at the more complete picture of the cell–surface interactions, more precise measurements and more detailed theoretical considerations are necessary.

5. Synchronization

Synchronization of motion is a common phenomenon in nonlinear many-particle systems, and thus appears in a broad range of physical, biological, engineering, and social systems (Pikovsky et al. 2002, Strogatz 2004). The phenomenon appears at all length scales from atoms to macroscopic bodies. For microswimmers, synchronization is fundamental for coordinated cyclic motion of cilia and flagella. The synchronous beating of the two flagella of Chlamydomonas causes straight swimming, while asynchronous beating implies tumbling motion (Qian et al. 2009, Drescher et al. 2010, Guasto et al. 2010, Goldstein et al. 2011, Lauga and Goldstein 2012, Bennett and Golestanian 2013a). The helical flagella of bacteria, like E. coli, synchronize their rotational motion during bundling (Kim et al. 2003, Kim and Powers 2004, Reichert and Stark 2005, Reigh et al. 2012, Reigh et al. 2013). Multi-ciliated and multi-flagellated microorganisms such as unicellular Paramecia (Knight-Jones 1954) or Volvox (Brumley et al. 2012) exhibit metachronal waves (MCW) (Sleigh 1962). Here, synchronization is essential for microswimmer motility. Furthermore, coordinated flagellar motion plays a major role in eukaryotes (Polin et al. 2009, Stocker and Durham 2009), where they transport fluid in the respiratory system in form of cilia (Afzelius 1976), are involved in cellular communications (Wang et al. 2006), and even determine the morphological left–right asymmetry in the embryo (Cartwright et al. 2004).

As early as 1951, Taylor (1951) suggested that hydrodynamic interactions lead to synchronization of nearby swimming spermatozoa. Since then, the hydrodynamic interactions of active systems at low Reynolds numbers has become a subject of major interest. A recent review by Golestanian et al. (2011) addresses a number of important aspects of hydrodynamical induced synchronized motions. Here, we will present and discuss the most important aspects and address recent developments.

Synchronization is not easily achieved for systems governed by low Reynolds number hydrodynamics and thus described by the Stokes equation (7). The presence of kinematic reversibility of this equation combined with swimmer symmetries may prevent synchronization (Kim and Powers 2004, Reichert and Stark 2005, Elfring and Lauga 2009, Theers and Winkler 2013). To overcome this fundamental limitation of life at low Reynolds numbers and to generate a time-irreversible dynamics, various alternatives have been suggested. This comprises inclusion of additional degrees of freedom such as system flexibility (Kim and Powers 2004, Reichert and Stark 2005, Niedermayer et al. 2008, Qian et al. 2009, Reigh et al. 2012,
Reigh et al. 2013, Uchida and Golestanian 2012), or specific, non-reversible driving forces Bennett and Golestanian 2013a,b. Uchida and Golestanian 2011, 2012. In addition, specific system designs combined with hydrodynamic interactions lead to synchronization, as has been shown for models of undulating sheets (Elfring and Lauga 2009, 2011) and for the flagellar beat of Chlamydomonas (Bennett and Golestanian 2013a, 2013b, Geyer et al. 2013). For the latter, it has been shown that synchronization of flagella beating can be achieved even without hydrodynamic interactions (Friedrich and Jülicher 2012, Polotzek and Friedrich 2013). Alternatively, a more general linear unsteady Stokes equation can be adopted to describe the fluid properties (Lauga 2011, Theers and Winkler 2013). Here, the time-reversal symmetry of the fluid-dynamical equation is broken by inertial terms, see equation (6).

5.1. Basic concepts

Minimalistic models are useful to shed light on the mechanisms of hydrodynamic synchronization. An example is the rigid rotor model of Lenz and Ryskin (2006), where each rotor possesses a single degree of freedom only. Hence, it is particularly useful for analytical studies of fluid mediated interactions between several rotors. Adopting this model, we consider two beads of radius $a$ moving along circles of radius $R$. The circles are centered at $r_i^0 = (-1)^i d/2$ ($i = 1, 2$), where $d = d_{ci}$ and $d$ is the center-to-center distance; both beads are confined in the $xy$-plane. The trajectories of the bead centers can be expressed as

$$r_i(t) = r_i^0 + Re_i(t),$$

with the radial unit vectors $\hat{e}_i = \cos \phi_i(t), \sin \phi_i(t), 0)^T$, in terms of the phase angles $\phi_i(t)$. The driving forces

$$F_i^d(t) = F_i(q_i)\hat{t}_i(t)$$

point along the tangents $\hat{t}_i(t) = (-\sin \phi_i(t), \cos \phi_i(t), 0)^T$ of the trajectories. The equations of motion of the particles are given by

$$\ddot{r}_i = \frac{1}{\zeta_i} F_i + v(r_i) = \frac{1}{\zeta_i} F_i + \sum_{j \neq i} H_{ij} F_j$$

(56)

within the Stokes description (7) of the fluid, with the hydrodynamic tensor $H_{ij} = H r_i - r_j$ (10), and the total force $F_i$ on a particle. Since the flow field $v(r_i)$ at the position of particle $i$, induced by the motion of other particles, is typically not aligned with the tangent vector $\hat{t}_i$, a constraining force $F_i^c$ is necessary to enforce a circular trajectory ($F_i = F_i^d + F_i^c$). However, within the far-field approximation of the hydrodynamic tensor, the constraining force yields corrections of the order $O((ald)^2)$ to the flow field $v(r_i)$. Hence, for $ald \ll 1$, we can neglect such contributions and the equations of motion of the phase angles are ($F_i \hat{t}_i = F_i^d \hat{t}_i = F_i$)

$$\dot{\phi}_i(t) = \omega_i + \frac{1}{R} \sum_{j \neq i} F_j \hat{t}_j(t) \cdot H_{ij} \hat{t}_j(t),$$

(57)

with the frequencies $\omega_i = F_i/(6\pi \eta a R)$. As pointed out by Lenz and Ryskin (2006), Golestanian et al. (2011), Uchida and Golestanian (2011), and Theers and Winkler (2013), for constant forces $F_1 = F_2 = F$, the symmetry of the Oseen tensor $H(r) = H(-r)$ implies a constant phase difference $\Delta \phi = \phi_2 - \phi_1$, so no synchronization occurs.

The same conclusion has been reached by Kim and Powers (2004) and Reichert and Stark (2005) for rigid rotating helices. An extra degree of freedom can be introduced by adding some flexibility in the model. The flexibility can arise from different origins, such as intrinsic flexibility of a filament or flexibility of the anchoring point. Indeed, as shown by Flores et al. (2005), Reichert and Stark (2005), Janssens and Graham (2011) and Reigh et al. (2012), flexible filaments exhibit synchronized motion.

As far as rotors are concerned, various models for elastic deformation have been investigated. Niedermayer et al. (2008) allowed for radial fluctuations of a harmonically bound particle. Qian et al. (2009) considered a sphere attached to a rigid rod with its other end confined in a harmonic potential. Uchida and Golestanian (2012) investigated a bead driven by an optical tweezer, whose focus is dragged along a prescribed trajectory. We will adopt the latter approach to illustrate the consequences of elastic deformations on the synchronization of rotors. The position of the bead $i$ is given by $r_i(t) = r_i^0 + Re_i(t) + u_i(t)$ for a circular trajectory of the tweezer focus $Re_i(t)$ and the displacement $u_i(t)$ in the potential. With the approximation of the tweezer field by a harmonic potential, the equations of motion (56) again apply, with the force balance $F_i + k u_i = 0$, where $k$ is the trap stiffness. For an isolated rotor, i.e. in the absence of fluid flow due to other rotors, $v(r) = 0$, and in the stationary state the force $F_i$ obeys the relation

$$F_i = \zeta_i k R \frac{d F_i}{k R \cdot \omega_i}.$$

(58)

with $\omega_i = \frac{\omega_i}{\zeta}$, and for a constant driving force, this yields the relation $\omega_i = F_i/(\zeta R)$ between the force and intrinsic frequency $\omega_i$. Multiplication of equation (56) by $\hat{t}_i$ yields

$$u_i \hat{t}_i = \frac{\zeta}{k} \hat{t}_i v(r_i)$$

(59)

to $O(k^{-1})$. Similarly, multiplication of equation (56) by $\dot{t}_i$ yields the equation of motion for the angles $\phi_i$

$$\dot{\phi}_i = \omega_i \left(1 - \frac{\zeta}{k R} \sum_j \hat{t}_j \cdot H_{ij} \dot{t}_j + \zeta \sum_j \omega_j \hat{t}_j \cdot H_{ij} \dot{t}_j + \frac{F_i}{k R} \hat{t}_i \right)$$

(60)

to $O(k^{-1})$. By assuming circular trajectories, the far field approximation for the Oseen tensor, and equal forces $F_1 = F_2 = F$, we finally obtain the equation of motion for the phase difference $\Delta \phi = \phi_2 - \phi_1$

$$\frac{\Delta \phi}{\Delta t} = -\frac{9 a}{2 d} \frac{\omega F}{k R} \sin \Delta \phi.$$  

(61)

For $\Delta \phi \ll 1$, we find an exponentially decaying phase difference $\Delta \phi \sim \exp(-t/T_\phi)$, with the characteristic synchronization time (Qian et al. 2009, Uchida and Golestanian 2012)

$$T_\phi = \frac{k d R}{9 k a F}.$$  

(62)
The two beads synchronize their rotational motion on a time scale, which is proportional to the trap stiffness $k$. In the limit $k \to \infty$, i.e. the rotation on the circle discussed above, the synchronization time diverges. The same linear dependence on the constant of the harmonic potential has been obtained by Niedermayer et al. (2008).

In addition, Qian et al. (2009) considered dumbbell-like rotors with harmonically bound centers as models for symmetric paddles. Here, also a linear dependence of the synchronization time on $k$ is obtained, but with the much stronger dependence $\tau_s \sim kd^2/(a^3 RF)$ on the rotor distance.

Flexibility of rotors is not a necessary requirement for synchronization (Uchida and Golestanian 2011, 2012, Theers and Winkler 2013). Alternatively, synchronization can be achieved for rigid trajectories by a particular, phase-angle dependent driving forces and/or for trajectories of certain non-circular shapes (Uchida and Golestanian 2011, 2012). For cilia or the flagella of Chlamydomonas, significant force modulations can be expected due to the asymmetry between power and recovery strokes. Uchida and Golestanian (2011, 2012) analyzed the necessary conditions for in-phase synchronization for phase-dependent driving forces $F_i(t) = F(q_i(t))\hat{n}_i$, where now $\hat{n}_i = \hat{n}_{i \parallel} / \hat{n}_{i \perp}$ with the abbreviation $\hat{n}_{i \parallel} = d/r_i \hat{d}$. For circular trajectories, the equations of motion (56) yield

$$\frac{d\Delta \varphi}{dt} = \omega_2 - \omega_1 + \frac{1}{R} [F(q_1) - F(q_2)] \hat{t}_1 \cdot \hat{H}_1 \cdot \hat{t}_2$$

for the phase difference. For small phase differences $\Delta \varphi$, linearization leads to

$$\frac{d\Delta \varphi}{dt} = \left( \omega'(q_1) - \frac{1}{R} F'(q_1) \hat{t}(q_1) \cdot \hat{H}(d) \cdot \hat{t}(q_1) \right) \Delta \varphi.$$  (64)

Integration of the ratio $\Delta \varphi/\Delta \varphi$ over one time period $T$ yields the cycle-averaged characteristic time (Uchida and Golestanian 2011, 2012)

$$\tau_s^{-1} = \frac{2}{T} \int_0^{2\pi} d\varphi F(q) \cdot \hat{H}(d) \cdot \hat{t}(q) \, d\varphi$$

in the limit $ad \ll 1$. Uchida and Golestanian (2012) analyzed and identified force profiles which lead to synchronization. Here, we mention and consider the relation

$$F(q) = F[1 - A \sin(2\varphi)]$$

only, where $A$ $(0 < A < 1)$ is a constant. Up to $O(A^2)$, integration results in

$$\tau_s = \frac{2d}{3\alpha A^2} T.$$

i.e. a characteristic synchronization time which depends on the rotor distance $d$ and the bead diameter $a$ only as far as the rotor geometry is concerned.

It is interesting to note that in this description, synchronization is caused by the tensorial character of the hydrodynamic interactions. The contribution of the diagonal part of the Oseen vanishes by the integration (65) (Uchida and Golestanian 2011, 2012). In contrast, for the harmonically bound beads, all parts of the hydrodynamic tensor contribute to the time $\tau_s$.

More details of the phase-angle dependent driving forces and different trajectory shapes are discussed by Uchida and Golestanian (2012). In particular, the combined effect of harmonically bound beads, driven by phase-angle dependent forces are addressed. The characteristic decay rate $\tau_s^{-1}$ of the combined effects is the sum of the contributions of the individual contributions equation (62) and (67).

Kotar et al. (2013) recently presented experimental results for the synchronization of two colloids, which are driven by feedback-controlled optical tweezers. Both, the elasticity of the trajectory and a phase-angle dependent driving force was implemented, as discussed above. The colloids exhibit strong synchronization within a few cycles, even in the presence of noise, consistent with the considerations described above.

The relevance of the various contributions depends on the actual parameters, e.g. the stiffness of the radial (harmonic) potential and amplitude of the force modulations along the trajectory. These values have been chosen by Kotar et al. (2013) such that both contributions are important. As pointed out by Uchida and Golestanian (2012), however, for small disturbance of a trajectory by hydrodynamic interactions, compared to the size of a trajectory, flexibility has only a weak effect in establishing synchronization. Although this may apply to certain systems only, it reflects a shift in paradigm from a flexibility dominated synchronization mechanism to driving-force governed processes.

A different hydrodynamic route was adopted by Theers and Winkler (2013), who started from the linearized Navier–Stokes equation (6). In this case, the hydrodynamic tensor $t$ is time dependent. This leads to the equations of motion

$$\dot{\varphi}_i + \omega + \frac{F}{R} \sum_{\jmath \neq i} \int_0^t \dot{t}(t') \cdot \hat{H}(r(t) - r(j(t')), t - t') \cdot \hat{t}(t') dt'$$

for the phase angles of circular rotors driven by the constant force $F_i = F_2 = F$, with the intrinsic frequency $\omega = F(\zeta R)$. Here, the whole time history contributes to the dynamical behavior. In the limit $ad \ll 1$ and for times $t \gg \tau_s = d^2/\nu$, an approximate expression for the integral can be derived, which becomes

$$\frac{d\Delta \varphi}{dt} = -\frac{2\sqrt{\pi}}{d} \int_0^t \left( \frac{d}{dt'} \right)^{3/2} \sin(\omega t') \, dt' \Delta \varphi(t)$$

for small phase differences. In the long-time limit, the phase difference decays exponentially with the characteristic time (Theers and Winkler 2013)

$$\tau_s = \frac{d}{4\pi^{3/2} a} \sqrt{\frac{T}{\tau_s}}$$

Compared to the other mechanisms described above, $\tau_s$ depends on the square-root of the ratio $T/\tau_s$ of the rotation period $T$ and the shear-wave propagation time $\tau_s$. This ratio can be identified with the oscillatory Reynolds number $Re_T$ (5). Hence, the synchronization time (70) is determined by the oscillatory Reynolds number, but with a square-root dependence.
For typical parameters of *E. coli* bacteria, the time-dependent hydrodynamic correlations have a weak effect on synchronization only. Studies of the combined effect of phase-angle dependent driving forces and time-dependent hydrodynamic interactions yield a faster synchronization dynamics than the individual mechanisms only.

Various other concepts have been put forward to study synchronization of two rotors and, in particular, the appearance of a phase lag as a prerequisite for the formation of metachronal waves. For the latter, in addition, hydrodynamic interactions with a surface are taken into account by employing the Blake tensor (Blake 1971a) for hydrodynamic interactions near a no-slip wall. Among the first to study this phenomenon were Lenz and Ryskin (2006), Vilfan and Jülicher (2006) and Niedermayer et al (2008). As discussed above (equation (62)), synchronization is obtained for beads confined in radially harmonic potentials and equal driving forces. A phase-locked motion has been found for different driving forces by Niedermayer et al (2008). In contrast, Brumley et al (2012) found a stable phase lag even for equal driving forces. They considered the equation of motion of a bead

\[ \dot{\mathbf{r}} = \mathbf{\xi}^{-1} \mathbf{F}_i + \sum_{j \neq i} \hat{H}_{ij} \mathbf{F}_j, \]

(71)

where \( \mathbf{\xi} = \xi [\mathbf{I} + 9 \mathbf{a} (\mathbf{1} + \hat{\mathbf{e}}_i \hat{\mathbf{e}}_j)/(16 \pi)] \) is the friction tensor and \( \hat{H}_{ij} \) is Blake’s tensor, which take into account the no-slip boundary condition at the wall at \( z = 0 \). The force is given by \( \mathbf{F}_i = -k (|\mathbf{r}|-R) \hat{\mathbf{e}}_i + \hat{\mathbf{F}}_i \). As pointed out by Brumley et al (2012), a numerical solution of the equation yields a stable phase lag \( \Delta \varphi \neq 0 \). A numerical solution of equation (71) is shown in figure 31 for bead trajectories perpendicular to the surface. Due to the boundary condition, the flow properties are different for the motion toward and away from the surface. This shifts the phase difference from perfect synchronization to a finite phase lag (Brumley et al 2012). Interestingly, \( \Delta \varphi \) is independent of the initial condition and the strength \( k \) of the potential. Phase-locking seems to be a consequence of nonlinear interactions in the system, because Niedermayer et al (2008) found synchronization rather then phase-locking for their approximate description. As indicated in figure 31, the trajectory is ellipse-like, with the long axis along the \( x \)-axis and the short axis along the \( z \)-axis (perpendicular to the surface), with a somewhat smaller deviation \( |r - R|/R \) on the side further away from the surface than close to it.

5.2. Experimental results: microrotors and colloidal oscillators

As an experimental realization of driven rotors, chiral propellers have been designed, which are driven by radiation pressure (Di Leonardo et al 2012). In the light of the discussions of section 5.1, the symmetry-breaking mechanism is provided by the flexibility of the optical trap, which is used to provide stable alignment and the driving torque. As shown by Di Leonardo et al (2012), two such rotors synchronize their rotational dynamics by hydrodynamic interactions. However, the coupling is very weak, and requires a fine-tuning of the relative torque within a resolution of \( 10^{-3} \). Even then, phase slips occur, where one of the rotors moves faster than the other until a stable phase-locked state may appear again.

In contrast, strong static correlations are obtained through hydrodynamic interactions between colloidal particles in rotating energy landscapes (Koumakis and Di Leonardo 2013). Thereby, the particles are driven periodically around a circle by rotating energy landscapes with a variable number of minima. In the co-moving, rotating frame, a colloid experiences a tilted periodic potential due to the hydrodynamic interactions with the other colloids. This enhances the probability to overcome the barriers and allows the different colloids to synchronize their rotational motion.

Another strategy to synchronize the dynamics of beads has been proposed by Gueron et al (1997) and Gueron and Levit-Gurevich (1998). It is based on the difference between the power stroke and the recovery stroke of cilia, or, more generally, the presence of two phases with broken symmetry. The latter concept has been applied to colloidal systems by Lagomarsino et al (2003), Kotar et al (2010), Bruot et al (2011), Damet et al (2012) and Lhermerout et al (2012). Here, the periodic motion of colloids is controlled by a configuration-dependent external input. Thereby, various properties can be switched from one state to another upon a particular geometry being assumed by the colloids. Examples are different effective drag (Lagomarsino et al 2003), or harmonic potentials with different equilibrium positions (Kotar et al 2010). The latter can be realized by optical traps. These strategies lead to a synchronized motion by hydrodynamic interactions (Lagomarsino et al 2003, Kotar et al 2010, Bruot et al 2011, Wollin and Stark 2011, Damet et al 2012, Lhermerout et al 2012).
5.3. Synchronization of Chlamydomonas beating

Chlamydomonas with its two beating flagella (see section 1.1) has become a model system for experimental studies of synchronization (Polotzek and Friedrich 2013). When the flagella beat synchronously, the alga swims along a straight path, while dephasing leads to reorientation in a run-and-tumble-like manner (Goldstein et al. 2009, Polin et al. 2009, Lauga and Goldstein 2012).

The measured flow field of a swimming Chlamydomonas (Drescher et al. 2010, Guasto et al. 2010) is well described by three Stokeslets (see figure 32). This finding has stimulated a more detailed theoretical modeling of Chlamydomonas by three spheres—two spheres driven on circular orbits, which are mimicking the flagellar beat (see section 5.1), are linked by a frictionless scaffold to a third sphere representing the cell body Bennett and Golestanian 2013a,b, Friedrich and Jülicher 2012, and Polotzek and Friedrich 2013).

The extra translational and overall rotational degrees of freedom, compared to the two degrees of freedom of the rotors of the systems of section 5.1, combined with non-linearities, give rise to additional features. As shown by Bennett and Golestanian (2013b), Friedrich and Jülicher (2012), and Polotzek and Friedrich (2013), force and momentum balance predominantly couple the phases of the rotors via translation and rotation of the cell body. This coupling suggest the possibility of flagella synchronization by local hydrodynamic friction even in the absence of hydrodynamic interactions. The efficiency of synchronization naturally depends on the geometry. It is weaker than hydrodynamic coupling, when the cell body is much larger than the distance between the neighboring flagella or cilia (Uchida and Golestanian 2012).

The three-sphere model exhibits a very rich dynamical swimming behavior, when a phase-angle dependent driving force and noise are added. Without hydrodynamic interactions, the cell just moves forward and backward and there is no net motion. However, in the presence of hydrodynamic interactions, which vary in strength during a beating cycle, the broken symmetry between the power and recovery stroke leads to a net propulsion (Bennett and Golestanian 2013b). Interestingly, a run-and-tumbling motion is obtained in the presence of noise. The threshold-like run-and-tumble behavior displayed by bacteria like E. coli and believed to be controlled by a sophisticated biochemical feedback mechanism, emerges here naturally from nonlinearities in the propulsion mechanism and could be triggered even by white noise. Moreover, the same model could describe the experimentally observed antiphase beating pattern of a Chlamydomonas mutant (Bennett and Golestanian 2013b, Leptos et al. 2013).

An experimental and theoretical study of the effect of the hydrodynamic coupling on the synchronization of the flagella beating is presented by Geyer et al. (2013). The central mechanism of an efficient synchronization is the adaptation of the flagellar beat velocity to environmental conditions—the flagella beat speeds up or slows down in response to the exerted hydrodynamic friction forces. A perturbation of the synchronized beating leads to a yawing motion of the cell, which is reminiscent to rocking of the cell body (see figure 33) (Geyer et al. 2013). This rotational motion confers different hydrodynamic forces on the flagella, with the consequence that one of them beats faster and the other slows down. The coupling between cell-body rotation and flagellar beating speed leads to a rapid reestablishment of a synchronized motion.

The studies by Geyer et al. (2013) suggest that cell rocking is an important mechanism for flagella synchronization. However, synchronized beating was also observed for Chlamydomonas cells with their bodies restrained by a micro-pipette (Rüffer and Nultsch 1998, Goldstein et al. 2009, Polin et al. 2009). A rather fast synchronization has been obtained, faster than pure hydrodynamic interactions would suggest (Geyer et al. 2013). Rotational motion with a small amplitude of a few degrees only, which may result from either a residual rotational compliance of the clamped cell or an elastic anchorage of the flagellar pair, provides a possible mechanism for rapid synchronization, which is analogous to synchronization by cell-body rocking in free-swimming cells (see figure 33).

These results lead to the conclusion that hydrodynamic interactions are an integral part of the synchronization mechanism of flagella beating. However, additional degrees of freedom of a specific system may enhance synchronization. In this context, we like to point out that purely hydrodynamic synchronization of the motion of two flagella has recently been documented by Brumley et al. (2014).
5.4. Synchronization of rotating bacterial flagella and bundle formation

Synchronization of the rotational motion of helical flagella of bacteria is essential for bundle formation and hence their swimming motion. Theoretical (Reichert and Stark 2005) and simulation (Kim and Powers 2004) studies show that rigid helices rotated by stationary motors do not synchronize their rotational motion. However, addition of certain flexibility, e.g. for helices with their ends confined in harmonic traps, combined with hydrodynamic interactions lead to a synchronized rotation even for separated and mechanically not interacting helices (Reichert and Stark 2005) as already suggested by macroscopic-scale model experiments (Macnab 1977, Kim et al 2003).

A more detailed picture of bundle formation has been achieved by computer simulations of model flagella (Flores et al 2005, Janssen and Graham 2011, Reigh et al 2012, 2013). In particular, the role of fluid dynamics has been elucidated. Considering two parallel helices composed of mass points (see figure 34) with bending and torsional elastic energy, and using a mesoscale hydrodynamics simulation technique (Kapral 2008, Gompper et al 2009), Reigh et al (2012) calculated the hydrodynamic forces on each helix due to their rotation motion. The simulations reveal a zero force along the radial distance, consistent with the results for macroscopic helices of Kim and Powers (2004). However, there are large transverse forces in opposite directions. The rotation of a helix creates a flow field, which tries to drag the other helix in the transverse direction. A ‘ tipping’ momentum has been determined by Kim and Powers (2004), which expresses the same effect. Hence, there is no simple attraction between helices by hydrodynamic interactions, as has been speculated. Bundling is rather induced by the common flow field created by the rotation of the individual helices. This expresses the importance of the rotational flow field as suggested by Flores et al (2005).

Releasing the constraints on the orientation provides insight into the full bundling process (Janssen and Graham 2011, Reigh et al 2012), as illustrated in Figure 34. Starting from an aligned initial state, the tangential hydrodynamic forces cause a tilt of the individual helices, which brings them in closer contact near their fixed ends and

Figure 33. Flagella synchronization by cell-body yawing. (a) For a free-swimming cell, the cell body exhibits a yawing motion characterized by the angle $\alpha(t)$, when the two flagella beat initially asynchronously. The flagellar phase difference $\Delta \phi$ between the left and right phase (see section 5.1) decreases with time approximately exponentially, $\exp(-\lambda t / T)$, where $\lambda$ defines a dimensionless synchronization strength. Dots indicate the completion of a full beat cycle of the left flagellum. (b) Trapped cell body to prevent translation. Cell-body yawing is restricted by an elastic restoring torque that acts at the cell body center. The two flagella synchronize with a synchronization strength $\lambda$ that can become even larger than in the case of a free swimming cell. For very large clamping stiffness, the cell body cannot move and the synchronization strength attenuates to a basal value $\lambda = 0.03$, which arises solely from direct hydrodynamic interactions between the two flagella. Used with permission from Geyer et al (2013) Cell-body rocking is a dominant mechanism for flagellar synchronization in a swimming alga Proc. Natl. Acad. Sci. USA 110 18058. Copyright 2013 PNAS.

Figure 34. Snapshots, side views (top) and top views (bottom), of various stages of the bundling process for $d/R_0 = 3.5$. (i) Initial state, the red helix is out of phase. (ii) The helices synchronized their rotation and start to bundle. (iii) Parts of the helices are bundled. (iv) Final, bundled state. From Reigh et al (2012). Copyright 2012 RSC.
simultaneously separates their free ends. Such a spatial approach was already assumed to be necessary by Macnab (1977). The whole mechanism is quantitatively reflected in the time dependence of the helix separations shown in figure 35, where the mean distance at \( P_2 \) rapidly approaches its stationary-state value, while \( P_2 \) increases initially and only slowly reaches its stationary-state value. Naturally, the details depend on the separation \( d \) between the anchoring points (Reigh et al. 2012). In the stationary state, a compact bundle is formed, where the helices are wrapped around each other. The stationary-state distances are assumed in sequence from \( P_1 \) to \( P_3 \), which implies that bundling occurs from the anchoring plane to the tail. Figure 35 shows that, starting from an initial phase mismatch, the helices first synchronize their rotational motion and then subsequently form a bundle. Thereby, synchronization by hydrodynamic interactions is achieved within a few rotations. The simulations predict a synchronization time proportional to \( \Delta \phi_{12} = -\pi \) (black), \( \Delta \phi_{13} = 0 \) (red), and \( \Delta \phi_{12} = -\pi \) (green). From Reigh et al (2012). Copyright 2012 RSC.

This raises the question of the stability of a flagellar bundle. There are various sources, which give rise to fluctuations and variations in the torque of a flagellum, such as an intrinsic noise in the motor torque, or the inequality of motors (Chen and Berg 2000, Xing et al. 2006). Variations may even be induced on purpose, as for bacteria such as *R. lupini*, which control the motor torque to induce tumbling (Scharf 2002). Simulations of three flagella, in which one helix is driven by a different torque than the other two, yield the following qualitative classification of the bundling dynamics (see figure 36) (Reigh et al. 2013). At small torque differences, the bundle remains stable with a phase lag between the various flagella. For very large torque differences, the bundle disintegrates and the flagella rotate asynchronously and independently, i.e. the phase differences of neighboring helices are drifting. In between, there is an intermittent regime, where phase slippage occurs, i.e. the synchronized rotational motion is interrupted by events, where the flagellum with the larger torque leaves the bundle, rotates faster, and rejoins the bundle. The time interval between individual slippages decreases with increasing torque difference and ultimately drifting is obtained. This is quantitatively shown in figure 36. It is important to note that bundle formation is rather robust over a wide range of torques and separations, so that bundles are able to sustain considerable torque differences. Even for distances as large as \( d/R_h = 4 \), phase locking occurs for torque differences as large as \( \Delta M/M_1 = 1/3 \). Both, the high bundle stability and the asymmetry of the phase diagram with respect to the reference torque \( M_1 = 400 k_BT \), whereas the torque \( M_2 \) is varied (Reigh et al. 2013).

Bundling is a rich phenomenon, with a multitude of bundling states depending on the elastic properties of a flagellum. For example, it has been shown by Janssen and Graham (2011) that for certain flagellum flexibilities and depending on the initial condition, either rather tight bundles, with the flagella in mechanical contact, or loose bundles, with intertwined, non-touching flagella can be found.

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**Figure 35.** Phase angle difference \( \Delta \phi \) (bottom) and average distances \( \langle d \rangle \) (top) between equivalent points \( P_i = i \) along the helix contour as a function of time for the separation \( d/R_h = 2.5 \). The three helices have the initial phase differences \( \Delta \phi_{12} = -\pi \) (black), \( \Delta \phi_{13} = 0 \) (red), and \( \Delta \phi_{12} = -\pi \) (green). From Reigh et al (2012). Copyright 2012 RSC.

**Figure 36.** Phase diagram indicating stable bundles (green), intermittent slippage (yellow), and drifting states (red) of a system of three helices exposed to different torques and for various helix-base separations \( d \). Two helices \( (1, 3) \) experience the torque \( M_1 = M_3 = 400 k_BT \), whereas the torque \( M_2 \) is varied (Reigh et al. 2013).
5.5. Synchronization of sperm and flagella

When two sperm swim close to each other, at distances smaller than the sperm length, then the dipole approximation does not apply and the full hydrodynamic interactions between two time-dependent flagellar shapes have to be taken into account. An particularly interesting aspect of this interaction is that the flagellar beats of the two sperm can now affect each other. What typically happens is phase locking, i.e. the two flagella adjust such as to beat in synchrony.

This synchronization of the beat of swimming sperm has been studied by mesoscale simulations in two dimensions (Yang et al 2008). Two sperm, S1 and S2, are placed inside a fluid, initially with straight and parallel tails at a small distance with touching heads. They start to beat at $t = 0$ with fixed frequency $\omega_0$ but with different initial phases $\varphi_1$ and $\varphi_2$. Here, the beat is driven by the local time-dependent preferred curvature $c(t, x) = A \sin(\omega_0 t - k_0 x + \varphi)$ at position $x$ along the flagellum. The flagellar shapes and the relative positions can adjust due to hydrodynamic interactions.

In the dynamical behavior of these hydrodynamically interacting sperm, two effects can be distinguished, a short time ‘synchronization’ and a longer time ‘attraction’ (Yang et al 2008). If the initial phase difference $\Delta \varphi = \varphi_2 - \varphi_1$ is not too large, ‘synchronization’ is accomplished within a few beats. This process is illustrated by snapshots at different simulation times in figure 37. The synchronization time depends on the phase difference, and varies from about two beats for $\Delta \varphi = 0.5 \pi$ to about five beats for $\Delta \varphi = \pi$. A difference in swimming velocities adjusts the relative positions of the sperm. After a rapid transition, the velocities of two cells become identical once their flagella beat in phase.

The synchronization and attraction of sperm has also been observed experimentally (Yang et al 2008, Woolley et al 2009). Figure 38 shows two human sperm with synchronized beats, which swim together for a while, but then depart again due to somewhat different beat frequencies and thus different swimming velocities. On the other hand, for bull sperm, persistent synchrony of the flagellar beats has been observed only when the heads are tightly coupled mechanically (Woolley et al 2009).

Symmetry arguments show that synchronization is not possible for two co-swimming flagella with a prescribed, reflection-symmetric wave form (Elfring and Lauga 2009), described in the spirit of Taylor (1951) by two infinite parallel 2D sheets with propagating lateral waves with the same wave vector $k$ but a phase shift $\phi$, as illustrated in figure 39, and thus corresponding to the 2D system described above, except that the flagella are infinitely long. Suppose that the force $f_\phi$ between the swimmers acts to decrease the phase difference $\phi$, as shown in figure 39(a). This setup can be reflected at the vertical plane to obtain figure 39(b), or first at the horizontal plane and then by kinematic reversal to obtain figure 39(d). Obviously, figures 39(b) and (d) describe exactly the same physical situation. However, the force $f_\phi$ is reducing the phase difference in figure 39(b) while it is increasing $\phi$ in figure 39(d), indicating that $f_\phi \equiv 0$. Thus, flagella with pure sine waves cannot synchronize.

On the other hand, wave forms which are not front-back symmetric, such as wave forms of sperm with increasing amplitude of the flagellar beat with increasing distance from the head (Friedrich et al 2010), or flagella which can respond elastically to hydrodynamic forces (Yang et al 2008, Llopis et al 2013) (compare figure 37), this symmetry argument does not apply, and non-zero forces can appear. A more detailed calculation by Elfring and Lauga (2009)—based on the lubrication approximation valid for small distances between the oscillating sheets—shows that the time evolution of the phase difference between co-swimming cells depends on the nature of the geometrical asymmetry, and that microorganisms can phase-lock into conformations which either minimize (in-phase mode) or maximize (peristaltic mode) energy dissipation. However, the relative arrangement of the two sperm also plays an important role (Llopis et al 2013). For two sperm with parallel beating planes, even the sign of the interaction can change depending on whether the beating planes are coplanar or are stacked on top of each other.

5.6. Cilia synchronization

Motile cilia are abundant in eucaryotic microswimmers to generate propulsion. From Paramecium over Volvox, cilia are used from unicellular to multicellular organisms to propel fluid across their surface (Alfelsius 1976). In higher organisms and humans, cilia are not only involved in moving mucus in the lungs, but also in embryonic development, e.g. in breaking the left–right symmetry (Cartwright et al 2004), and in cell signaling (Wang et al 2006). Already in the 1960s (Sleigh 1962), it was observed that arrays of cilia beat neither randomly nor synchronously, but in a wave pattern called a metachronal wave (MCW).
Several theoretical models have been proposed to explain the hydrodynamic origin of this phenomenon. One approach is to focus on highly simplified systems similar to those presented in section 5.1. Either the rotating spheres are placed near a no-slip wall (Vilfan and Jülicher 2006, Niedermayer et al 2008, Uchida and Golestanian 2010, Golestanian et al 2011, Brumley et al 2012), or spheres oscillate on a line with different hydrodynamic radii in the two directions of motion (Lagomarsino et al 2003, Wollin and Stark 2011). One-dimensional chains of such simplified cilia, can show metachronal waves under special conditions (Lagomarsino et al 2003, Wollin and Stark 2011, Brumley et al 2012). For Volvox, such a rotating-sphere model has been compared in detail with the experimental situation (Brumley et al 2012). By choosing the right orbit parameters, the experimentally observed metachronal wave pattern can be reproduced (see figure 40). Hence, the simple theoretical approach can help to understand the origin of the nontrivial synchronization with finite phase lag. As it turns out, the presence of a surface already suffices to create a non-zero phase lag (see section 5.1).

A second approach uses efficiency arguments. The idea is that the cilia beat has been optimized during evolution to attain maximum efficiency (Osterman and Vilfan 2011, Eloy and Lauga 2012). Here, efficiency is defined as minimal power needed to actuate the cilium along a certain path to generate the fluid transport with a velocity \( v \). By simple dimensional analysis (Osterman and Vilfan 2011, Eloy and Lauga 2012), or by comparison with a reference flow driven by a constant force density parallel to a wall in a slab of thickness \( L \) (the cilium length) (Elgeti and Gompper 2013a), it has been shown that the efficiency should scale as

\[
e = \frac{Q^2}{P},
\]

where \( Q \) is the average volumetric flux and \( P \) the average power consumption. This approach yields a well defined cilia stroke (Osterman and Vilfan 2011, Eloy and Lauga 2012) that looks very similar to observed cilia strokes, see figure 5. This mechanism can be understood as follows. In the fast power stroke, the cilium is nearly fully extended, to reach as far out from the wall as possible, where the fluid flow is least restricted by the presence of the no-slip wall; in contrast, in the slow recovery stroke, the cilium curves and bends sideways to move closely to the wall to generate as little backflow as possible, and at the same time not to bend too much to avoid damage of the microtubule structure. This efficiency argument can be taken one step further to provide a potential explanation of metachronal waves. If all cilia beat synchronously, the whole fluid body flows back and forth with every stroke, which implies a high energy dissipation. Thus the synchronous beat is highly inefficient. By numerically calculating the dissipation for different wave vectors, Osterman and Vilfan (2011) predict anti-plectic metachronal waves, see figure 41. However, it is not obvious whether global efficiency optimization can be a criterion for the evolution of a collective cilia beat in a system, which should perform well under a variety of environmental conditions.

A third approach is to model cilia as semiflexible filaments with a pre-defined beating mode, and to allow for self-organized metachronal waves by hydrodynamic interactions. This approach has been followed for 1D chains of cilia (Gueron et al 1997, Gueron and Levit-Gurevich 1999), for small 2D patches of cilia (Gueron and Levit-Gurevich 2001), and in a mean-field approach (Guirao and Joanny 2007). Elgeti and Gompper (2013a) were able to extend this type of approach recently to much larger 2D arrays (up to 60 × 60 cilia) in a 3D fluid with noise. The beat pattern of a single cilium looks like that of a cilium of paramecium. The beat pattern of an individual cilium can react to the surrounding fluid flow, because the model only imposes time-dependent curvature forces, and employs geometric thresholds for the switch between power and recovery stroke, and vice versa (Lindemann and Lesich 2010). Here, metachronal waves emerge autonomously despite the presence of strong noise (see figure 42). Furthermore, this approach allows the study of the appearance of defects, transport efficiency, and wave vectors. In particular, it predicts a large increase in efficiency and propulsion velocity due to metachronal coordination, without the assumption that the system has evolved to optimal efficiency. This efficiency gain is due to the rectification of fluid flow across a ciliated surface, which avoids the oscillatory back-and-forth motion of a perfectly synchronized beat with large viscous energy loss.
This result indicates that the efficiency gain by metachronal coordination is a rather universal feature, and does not require an evolutionary optimization strategy. Elgeti and Gompper (2013a) could also demonstrate the presence of defects in the wave pattern of MCWs and characterize some of their properties. It seems that defects assume a form similar to dislocations in 2D crystals (see figure 43). However, the defects do not travel with the wave, but remain stationary while the wave passes over them. More detailed studies are needed to fully elucidate the defect dynamics in MCWs.

6. Collective and cooperative motion

Microswimmers hardly ever swim alone. In nature, the density of microswimmers can reach astonishing densities. Sperm cells are released by the millions to compete in the run for the egg. Coordinated motion is exploited, for example, by spermatozoa of the wood mouse *Apodemus sylvaticus*, which self-assemble into unique train-like aggregates of hundreds or thousands of cells and thereby significantly increased sperm motility (Sivinski 1984, Moore and Taggart 1995, Hayashi 1996, 1998, Moore et al 2002, Immler et al 2007). Bacteria grow by dividing and invading their surroundings together. Artificial microswimmers will only be able to deliver useful quantities of pharmaceuticals or modify material properties when present in large numbers.

In assemblies of motile microorganisms, cooperativity reaches a new level as they exhibit highly organized movements with remarkable large-scale patterns such as networks, complex vortices, or swarms (Heinrichsen 1972, Kearns 2010, Wensink et al 2012, Gachelin et al 2014). Such patterns are typically displayed by bacteria confined to two dimensions, e.g. *E. coli* or *Bacillus subtilis* involving hundreds to billions of cells (Harshey 1994, Liu et al 2000, Avron et al 2004, Darnton et al 2010). Flagella are an essential ingredient in swarming of biological cells, as is evident for, e.g. *E. coli*, which produce more flagella and, in addition, elongate and become multinucleate (Harshey 2003, Daniels et al 2004, Kaiser 2007, Copeland and Weinb 2009, Darnton et al 2010), which underlines the complexity of the interactions in such assemblies.

The full characterization of the complex dynamical behavior requires an understanding of the underlying (physical)
cooperative mechanism on various levels, starting from the interactions of individual cells, fluid-mediated interactions, up to the generic principles of the formation of large-scale patterns.

6.1. Hydrodynamic interactions between microswimmers

Similar as the interactions of microswimmers with a surface, the interaction of two microswimmers at long distances is determined by their dipole flow fields. The dipole approximation predicts that the interactions of microswimmers depends on their relative orientation, and that pushers and pullers in equivalent positions and orientations have interactions equal in magnitude and opposite in sign, because their dipole strengths \( P \) have opposite signs, see section 2.3. This behavior can be understood easily by considering the flow fields of two parallel-swimming pushers or pullers, where pushers attract and pullers repel each other. This effect is also present for shorter distances between the swimmers; the results of mesoscale hydrodynamics simulations of two squirmers (Götte and Gompper 2010b) shown in figure 44 demonstrate that for pushers, the fast backward flow velocity in the rear part extracts fluid from the gap between the swimmers, and thereby induces attraction (figure 44(a)); in contrast, for pullers, the fast backward flow velocity in the front part injects fluid into the gap, and thereby induces repulsion (figure 44(b)).

However, the hydrodynamic interaction between microswimmers is much more complex, because they will usually meet at different relative positions and orientations, and possibly different relative phases of their internal propulsion mechanisms. This gives rise to a rich behavior of attraction,
repulsion, or entrainment depending on these parameters (Ishikawa et al. 2006, Alexander et al. 2008, Götze and Gompper 2010b). An example is shown in figure 45, which shows the trajectories of two initially parallel oriented pushers, which have a small offset in the forward direction. As a result of this offset, the two squirmers do not attract each other, but rather change their direction of motion together toward the pusher in front. Pullers show the opposite trend and change their direction of motion toward the puller in the back.

6.2. Generic model of flocking

Collective behavior of active bodies is frequently found in microscopic systems such as bacteria (Ben-Jacob et al. 2000, Sokolov et al. 2007, Chen et al. 2012, Peruani et al. 2012, Gachelin et al. 2013) and synthetic microswimmers (Ibele et al. 2009, Theurkauff et al. 2012, Palacci et al. 2013, Buttinoni et al. 2013, Wang et al. 2013), but also in macroscopic systems such as flocks of birds and schools of fish (Cavagna et al. 2010, Vicsek and Zafeiris 2012). Despite the very different propulsion mechanisms and interactions in these systems, they all favor alignment of neighboring bodies, thus leading to similar forms of collective behavior.

Therefore, it is natural to look for a model, which is able to capture the generic collective properties of all the various systems of self-propelled particles and organisms. Such a model was proposed in a pioneering work by Vicsek et al. (1995a). In this model, now often called the ‘Vicsek model’, N polar point particles move in space with constant magnitude of velocity v0. The dynamics proceeds in two steps, a streaming step of duration Δt, in which particles move ballistically, and an interaction step, in which particles align their velocity direction with the average direction of motion of their neighbors. In two spatial dimensions, this implies the dynamics for the position r_i and velocity v_i of particle i,

\[ r_i(t + Δt) = r_i(t) + v_i(t) Δt, \]

\[ θ_i(t + Δt) = θ_i(t) + Δθ_i, \]

where \( θ_i \) is the angle between \( v_i \) and the x-axis of a Cartesian coordinate system, \( ⟨θ_i(t)⟩_ρ \) is the average orientation of all particles within a circle of diameter \( σ \), and \( Δθ_i \) is a random noise uniformly distributed in the interval \(-η/2, +η/2\). The essential control parameters of the Vicsek model are the particle density \( ρ \), the noise strength \( η \), and the propulsion velocity \( v_0 \) in units of \( σ/Δt \).

A numerical investigation of this model by Vicsek et al. (1995a) shows a phase transition with increasing density or decreasing noise strength from a random isotropic phase to an aligned phase, in which particles move collectively in a spontaneously selected direction. This observation of a
non-equilibrium phase transition in a system of self-propelled point particles has led to numerous analytical (Toner and Tu 1995, Sinha and Ramaswamy 2002, Ramaswamy et al 2003, Toner et al 2005, Peruani et al 2008, Baskaran and Marchetti 2009, Bertin et al 2009, Golestanian 2009) as well as computational (Grégoire and Chaté 2004, Huepe and Aldana 2004, D’Orsogna et al 2006, Szabó et al 2006, Aldana et al 2007, Chaté et al 2008, Ginelli et al 2010, Redner et al 2013) studies. A review is provided by Vicsek and Zafeiris (2012).

6.3. Self-propelled rods

When we consider a system of self-propelled particles beyond the phenomenological description of interactions as in the Vicsek model (Vicsek et al 1995a), the simplest physical interaction which leads to alignment is volume exclusion of rod-like microswimmers and self-propelled rods. Here polar interactions, with alignment in the swimming directions, have to be distinguished from nematic interactions, with alignment independent of the direction of motion. Of particular interest are experiments with elongated self-propelled particles on the microscopic scale in two dimensions, such as motility assays where actin filaments are propelled on a carpet of myosin motor proteins (Harada et al 1987, Schaller et al 2010), microtubules propelled by surface-bound dyneins (Sumino et al 2012), and microswimmers that are attracted to surfaces (as described in section 4).

Self-propelled rods in two dimensions are often modelled as linear chains of (overlapping) beads (Wensink and Löwen 2008, Yang et al 2010, Abkenar et al 2013). Both, models with strict excluded-volume interactions and with a finite overlap energy, which allows rods to cross, have been employed. In the latter case, rod crossing is included to mimic in a 2D simulation the possible escape of rods into the third dimension when two rods collide (like actin filaments or microtubules in a motility assay) (Abkenar et al 2013).

In such models, self-propulsion of rods leads to enhanced aggregation and cluster formation, as well as to various kinds of ordered phases in Brownian Dynamics simulations (Kraikivski et al 2006, Peruani et al 2006, Wensink and Löwen 2008, Yang et al 2010, McCandlish et al 2012, Wensink et al 2012, Abkenar et al 2013), as well as in theoretical approaches based on the Smoluchowski equation (Baskaran and Marchetti 2008a, 2008b, Peruani et al 2010) and on continuum models in the ‘hydrodynamic limit’ (Baskaran and Marchetti 2008a, 2008b).

A few simulation snapshots of a 2D system, with different rod number densities \( \rho \), propulsion velocities \( v_0 \), and noise levels are shown in figure 46, and a corresponding phase diagram in figure 47. Here, the importance of propulsion compared to noise is characterized by the Péclet number \( \text{Pe} = L_{\text{rod}} v_0 / D_B \), where \( L_{\text{rod}} \) is the rod length, \( v_0 \) the swimming velocity of an isolated swimmer, and \( D_B \) the diffusion coefficient in the direction of the instantaneous rod orientation. The phase diagram of figure 47 describes a system in which rods interact with a ‘soft’ interaction potential, so that the rods are penetrable at high Péclet numbers (Abkenar et al 2013). Disordered states, motile clusters, nematic phases, and lane formation are observed. In particular, figure 46 displays a phase with a single polar cluster, which is formed at intermediate rod density and not too large Péclet numbers, and a phase with both nematic order and a lane structure where rods moving in opposite directions self-organize in lanes at high rod density \( \rho L_{\text{rod}}^2 = 25.5 \) and Péclet number \( \text{Pe} = 75 \). Colors indicate rod orientation. From Abkenar et al (2013). Copyright 2013 American Physical Society.

Figure 46. Simulation snapshots of a system of self-propelled soft rods (with aspect ratio 18) display (left) a giant polar cluster coexisting with a very dilute phase of single swimmers at intermediate density \( \rho L_{\text{rod}}^2 = 10.2 \) and Péclet number \( \text{Pe} = 25 \), and (right) a phase of nematic alignment, in which rods moving in opposite directions self-organize in lanes at high rod density \( \rho L_{\text{rod}}^2 = 25.5 \) and Péclet number \( \text{Pe} = 75 \). Colors indicate rod orientation. From Abkenar et al (2013). Copyright 2013 American Physical Society.

Figure 47. Phase diagram for self-propelled rods (with aspect ratio 18) as a function of density \( \rho \) and Péclet number \( \text{Pe} \). The energy barrier is \( E = 1.5 k_B T \); the gray lines are guides to the eye. The region \( \text{Pe} < 0 \) has no physical meaning; it only indicates the presence of isotropic and nematic states for passive rods (with \( \text{Pe} = 0 \)). From Abkenar et al (2013). Copyright 2013 American Physical Society.
for nematic interactions, high-density bands with rods moving parallel to the band in both directions are expected (Peshkov et al. 2012). Because rods in the simulations are constructed as chains of beads, the dominant contribution of the interaction is nematic, but there is also a polar component (i.e. a somewhat larger probability for parallel than anti-parallel alignment after collisions) due to an effective friction resulting from the (weakly) corrugated interaction potential (Abkenar et al. 2013). However, neither with polar nor with nematic interactions do Vicsek and continuum hydrodynamic models predict the polar bands with rod orientation parallel to the band, as shown in figure 46(a). Thus, clearly more work is needed to elucidate the origin of the differences in the results of models of rod-like particles and with anisotropic interaction potentials and of effective continuum descriptions.

Self-propelled hard rods show also interesting structures in the absence of noise. A phase diagram as a function of aspect ratio $a$ and volume fraction $\phi$, as obtained from simulations (Wensink et al. 2012) is shown in figure 48. At small volume fractions, a dilute phase of single rods is observed for all aspect ratios. For higher volume fractions, several phases of densely packed rods are found, which differ in their internal structure. With increasing aspect ratio, this is a jammed phase of very short rods, a turbulent phase, and a swarming phase—which is reminiscent of the giant cluster of noisy rods in figures 46(a) and 47—and finally a laning phase for long rods with aspect ratio $a \geq 12$—again similar to the corresponding phase of noisy rods in figures 46(b) and 47.

A phase of particular interest is here the ‘turbulent’ phase. This phase is denoted turbulent, because its velocity field displays the typical random swirls and vortices, which are characteristic for high Reynolds number turbulence. Such a phase has indeed been observed in dense populations of Bacillus subtilis, both at surfaces and in 3D bulk suspensions (Mendelson et al. 1999, Sokolov et al. 2007, Cisneros et al. 2011, Wensink et al. 2012), see figure 49(a). This phase has also been studied in some detail theoretically and in simulations (Aranson et al. 2007, Wolgemuth 2008, Wensink et al. 2012, Dunkel et al. 2013). The structure and dynamics of the turbulent phase can be characterized by velocity distributions, velocity increment distributions, and spatial correlation functions (or equivalently structure functions). The results of such an analysis is a typical vortex size $R_v$, see figure 49(b), which in two dimensions is about three times the bacterial length $L$. A comparison with high Reynolds number turbulence can be made by calculating the energy spectrum $E(k)$ as a function of the wave vector $k$, which is closely related to the Fourier transform of the spatial velocity correlation function $\langle \psi(t, r) \psi(t, r + R) \rangle$. The main difference between classical and bacterial turbulence is that the energy input occurs in the former case on large length scales, but in the latter case on small scales of the bacterium size $L$. This has important consequences for the behavior of $E(k)$. In classical turbulence, the famous Kolmogorov–Kraichnan scaling (Kraichnan and Montgomery 1980) predicts in three dimensions an energy-inertial downward cascade with $E(k) \sim k^{-5/3}$. In 2D, there can be both an energy-inertial upward cascade with $E(k) \sim k^{5/3}$ and an enstrophy-transfer downward cascade with $E(k) \sim k^{-3}$. For bacterial turbulence, similar power-law regimes are found, but the exponents are different. Here, $E(k) \sim k^{5/3}$ for small $k$, and $E(k) \sim k^{-5/3}$ for large $k$ (Wensink et al. 2012). Thus, self-sustained bacterial turbulence shares some properties with classical turbulence on small scales, but differs on large scales (Wensink et al. 2012).

6.4. Active Brownian spheres

The collective phenomena of section 6.3 above and sections 6.5 and 6.7 below are affected by the anisotropic shape and specific interactions between individual cells. These specificities give rise to particular phenomena but may be masked by more general underlying organization principles of microswimmers. Indeed, studies of Brownian, spherical self-propelled colloidal particles without any alignment rule reveal a rich structural and dynamical collective behavior (Deseigne et al. 2010, Bialké et al. 2012, Buttinoni et al. 2012, 2013, Fily and Marchetti 2012, Theurkauff et al. 2012, Palacci et al. 2013, Redner et al. 2013, Fily et al. 2014, Stenhammar et al. 2014, Wysocki et al. 2014).

Experiments using either spherical gold/platinum Janus particles (Theurkauff et al. 2012) and polymer spheres with an encapsulated hematite cube (Palacci et al. 2013) in a hydrogen peroxide solution, or carbon-coated colloidal Janus particles dissolved in a near-critical mixture of water and lutidine (Buttinoni et al. 2013) and heated by laser light, yield well-ordered crystalline aggregates at low densities and a phase-transition into large clusters and a dilute gas phase at higher densities in two dimensions. Thereby, the clusters are highly dynamic. Colloids adsorb and evaporate from a cluster, and clusters continuously merge and dissociate (Theurkauff et al. 2012, Buttino et al. 2013). The mean cluster size itself depends linearly on the swimming speed (Buttinoni et al. 2013). Large clusters exhibit a well-ordered, crystalline...
internal structure, which dynamically changes mainly due to movements of dislocations.

In order to elucidate the mechanism governing the aggregation of the active colloids, computer simulations have been performed of a minimal model. Every colloid is described as a point-particle, which is propelled with constant velocity along a body-fixed direction. In addition, it is exposed to a random, white-noise force and the colloid-colloid interaction force, e.g. arising from a Yukawa-like potential. The orientation of the colloid performs a random walk with the respective rotational diffusion coefficient. Hence, no alignment forces or hydrodynamic interactions are taken into account (Bialké et al. 2012, 2013, Fily and Marchetti 2012, Buttinoni et al. 2013, Palacci et al. 2013, Redner et al. 2013, Fily et al. 2014, Stenhammar et al. 2014, Wysocki et al. 2014). These simulations indeed yield cluster formation and phase separation solely by propulsion and excluded-volume interactions.

For 2D systems, simulation results are in qualitative agreement with experiments. For monodisperse spheres, clusters are formed with pronounced crystalline order. For polydisperse spheres (Fily et al. 2014), the high-density phase remains fluid-like, with very little collective dynamics.

Simulations reveal a far richer behavior of self-propelled spheres in three-dimensions (Stenhammar et al. 2014, Wysocki et al. 2014). As for 2D systems, the system phase separates into a dilute gas-like and dense fluid-like phase above a critical density at a given swimming velocity, or more precisely, Pécellet number \( \text{Pe} = \frac{v_0}{\sigma D_b} \), where \( v_0 \) is the swimming velocity, \( \sigma \) the colloid diameter, and \( D_b \) the rotational diffusion coefficient. Figure 50 presents the probability distribution \( P(\phi) \) of the local packing fraction \( \phi_l \) as a function of the global packing fraction \( \phi \). Below a critical volume fraction \( \phi_c \approx 0.3375 \), the system is essentially homogeneous and \( P(\phi) \) is unimodal. While approaching \( \phi_c \) with increasing \( \phi \), \( P(\phi) \) broadens (by formation of transient clusters) and becomes bimodal above \( \phi_c \). The appearing structures are illustrated in figure 51. At low overall density, transient spherical clusters are formed, which turn into a bicontinuous structure, whose surface is reminiscent of the Schwarz P surface, and finally at high \( \Phi \), gas-phase droplets float in a dense matrix (Stenhammar et al. 2014, Wysocki et al. 2014).

The phase diagram for various Pécellet numbers and densities is displayed in figure 52 (Wysocki et al. 2014). The gray line indicates the spinodal line separating the two-phase region from the one-phase region. Similar results were obtained by Stenhammar et al. (2014), who also predicted binodal lines. The existence of the spinodal (and binodal) lines in the phase diagram are in analogy with equilibrium phase diagrams, despite the non-equilibrium character of the present phase separation (Stenhammar et al. 2014). Speck et al. (2014) derived an effective Cahn–Hilliard equation for repulsive active Brownian particles on large length and time scales, which underlines the similarities in the phase behavior between passive and active systems.

The phase separation at the higher densities can be understood as follows. The pressure of a hard sphere fluid increases with \( \phi \) and diverges at random close packing for the metastable branch as

\[
\rho_{HS} = -\frac{6k_B T}{\pi \sigma^3} \phi^2 \frac{d}{d\phi} \ln \left\{ \left( \frac{\phi_{RCP}}{\phi} \right)^{1/3} - 1 \right\}.
\] (77)
respectively. Redrawn from Wysocki et al. (2014) Cooperative motion of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett.

Figure 51. Snapshots of the gas–liquid interfaces of a system of active Brownian spheres (a), (b) just above the clustering transition ($\phi = 0.3375$ and $\phi = 0.4$) and (c) at a high density ($\phi = 0.6$). The red and green isodensity surfaces correspond to $\phi_l = 0.54$ and $\phi_i = 0.5$, respectively. Redrawn from Wysocki et al (2014) Cooperative motion of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett. 105 48004.

Figure 52. Phase diagram of an suspension of active Brownian spheres. Symbols denote the homogenous liquid phase (◦), the gas-liquid coexistence (□) and the crystal-gas coexistence (▲). The equilibrium transition points of hard-spheres for freezing ($\phi_G = 0.494$), melting ($\phi_m = 0.545$), glass-transition point ($\phi_G \approx 0.58$), and random close packing ($\phi_{RCP} \approx 0.64$), are indicated by F, M, G, RCP, respectively. The most probable $\phi_i$ is color-coded, i.e. in the two-phase region one can read off the density of the dense liquid phase $\phi_{liq}$. The solid line marks $\text{Pe},(\phi)$ which is proportional to equation (76). Redrawn from Wysocki et al (2014) Cooperative motion of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett. 105 48004.

According to free volume theory (Kamien and Liu 2007). Self-propelled particles at low $\phi$ easily overcome this pressure, coagulate due to their slow-down during collisions (overdamped dynamics) and hence form clusters. The density within the cluster, $\phi_{liq}$, adjusts such that $p_{HS}(\phi_{liq})$ balances the active pressure $p_a$. An initially homogenous system can only phase separate if the active pressure $p_a \sim \gamma_i V_0 / \sigma^2$ exceeds $p_{HS}(\phi)$, which leads to a critical line $\text{Pe},(\phi)$ (spinodal) between the liquid-gas coexistence and the homogenous liquid phase at high $\phi$, (see figure 52); a similar argument has been put forward by Fily et al (2014) in the context of soft disks.

Remarkably, the local packing fraction in the liquid phase can assume rather large values, deep within the glassy region ($\phi_G \approx 0.58 \leq \phi_{liq} \leq \phi_{RCP} \approx 0.64$) of passive hard spheres (Pusey and van Megen 1986, Kamien and Liu 2007, Brambilla et al 2009). Nevertheless, particles remain mobile and no long-range crystalline order is detected. This indicates a activity-induced shift of the glass-transition point toward higher concentrations, as also discussed by Ni et al (2013), Fily et al (2014b) and Berthier and Kurchan (2013).

Another remarkable aspect is the intriguing dynamics within the liquid phase of the phase-separated system (see figure 53). Large-scale coherent displacement patterns emerge, with amplitudes and directions strongly varying spatially. In addition, transient swirl- and jet-like structures appear frequently. This is in contrast to 2D systems, which exhibit far less coherent motions. Figure 53(a) shows a swirl spanning the whole cluster while figure 53(b) displays a large mobile region moving between the gas-phase regions of the system. Thereby, the fluid density is above the glass transition density $\phi_{liq} = 0.62 > \phi_G = 0.58$. Spatio-temporal correlation functions for the colloid displacements indicate the existence of a universal finite-size scaling function, which suggests that the system becomes scale invariant with large-scale correlated fluid flow pattern in the asymptotic limit of large systems (Wysocki et al 2014). A similar behavior has been discussed in other active systems, however, with a notable polar alignment mechanisms, such as startling flocks (Cavagna et al 2010) and motile bacteria colonies (Chen et al 2012).

Various analytical calculations have been performed to achieve a theoretical understanding of the generic principles underneath the propulsion-induced phase transitions (Tailleur and Cates 2008, Fily and Marchetti 2012, Bialké et al 2013, Cates and Tailleur 2013, Stenhammar et al 2013, 2014, Fily et al 2014, Wittkowski et al 2014, Farrell et al 2012). Adopting an effective continuum theory with a density-dependent effective propulsion speed, Bialké et al (2013) predicted an instability region in the density driving-speed diagram above a lower minimal velocity. A similar approach using the free energy, yields a dynamical equation for the colloid packing fraction. With suitable parameters, this equation qualitatively reproduces the colloid density distributions (see figure 51) found in simulations for two- and three-dimensional systems (Stenhammar et al 2014). Fily et al (2014) predicted the spinodal lines of their soft, polydisperse active colloids in two dimensions. The success of this approach suggest a remarkable analogy between non-equilibrium and equilibrium phase transitions (Stenhammar et al 2014).

Finally, we like to discuss the importance of hydrodynamic interactions for the phase behavior of spherical active
colloids (Matas-Navarro et al. 2014, Zöttl and Stark 2014). The study of 2D systems of active discs suggest that aggregation is strongly suppressed by hydrodynamic interactions. On the other hand, a simulation study of a quasi-2D system of squirmer suspensions confined between two parallel walls, separated by a distance comparable to the swimmer size, indicates that hydrodynamic near-field interactions determine the phase behavior of active particles (Zöttl and Stark 2014). Near-field hydrodynamics implies an increase of the rotational diffusion, a slow-down of translational motion during collisions, and thereby leads to an enhanced self-trapping and the formation of crystalline clusters, see figure 54. This indicates that dimensionality strongly affects the appearing structures in the presence of hydrodynamic interactions, as reflected by the significantly more ordered structures of active particles in a 2D system compared to a quasi-2D system. However, figure 54 suggests that hydrodynamic interactions enhance phase separation and structure formation compared to bare Brownian interactions, in particular for pullers.

6.5. Spermatozoa and flagella

Experiments in recent years (Moore and Taggart 1995, Hayashi 1996, 1998, Moore et al. 2002, Riedel et al. 2005, Immler et al. 2007) have revealed an interesting swarm behavior of sperm at high concentration, for example the distinctive aggregations or trains of hundreds of wood-mouse sperm (Moore et al. 2002, Immler et al. 2007) or the vortex arrays of swimming sea urchin sperm on a substrate (Riedel et al. 2005). Thus, it is interesting to study the clustering, aggregation, and vortex formation of many sperm cells or flagella.

The results of sections 6.1 and 5.5 show that when two sperm with the same beat frequency happen to get close together and swim in parallel, they synchronize and attract through hydrodynamic interactions. The collective behavior of sperm at finite concentrations has mainly been studied numerically so far (Yang et al. 2008). Mesoscale simulations were performed for a 2D system with a number density of about three sperm per squared sperm length. Considering that in real biological systems the beat frequency is not necessarily the same for all sperm, beat frequencies $\omega$ were selected from a Gaussian distribution with variance $\delta_\omega = \langle(\Delta \omega)^2\rangle / \langle\omega\rangle$, where $\langle(\Delta \omega)^2\rangle$ is the mean square deviation of the frequency distribution.

Figure 54 shows some snapshots of systems of symmetric sperm with different width $\delta_\omega$ of the Gaussian frequency

Figure 53. Collective motion of active Brownian spheres, in the steady state at Pe = 272. Snapshots (slices of thickness $\sigma$) of a system (a) just above the clustering transition ($\phi = 0.3375$) and (b) at a high concentration ($\phi = 0.6$). Arrows indicate the direction of the displacements over a short lag time. The magnitude is color-coded and is expressed by the effective Péclet number $Pe_{\text{eff}}$. Redrawn from Wysocki et al. (2014) Cooperative motion of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett. 105 48004.

Figure 54. Typical snapshots of the collective motion and aggregation of squirmers in a quasi-2D geometry, depending on the area fraction $\phi$ and the squirmer type ($\beta = B_2/B_1$, see equation (1)). Also shown are snapshots for active Brownian spheres moving in quasi-2D (BD Q-2D), and active Brownian disks moving in 2D (BD 2D). The colors indicate the local bond-orientational order. Used with permission from Zöttl and Stark (2014). Copyright 2014 American Physical Society.
Obviously, the average cluster size is smaller for large $\delta$, there is a balance between cluster formation and break-up. Nearby free sperm or by merging with other clusters. Thus, the cluster size can grow by collecting nearby free sperm or by merging with other clusters. Thus, there is a balance between cluster formation and break-up. Obviously, the average cluster size is smaller for large $\delta$ than for small $\delta$ (see figure 55).

For $\delta = 0$, the average cluster size continues to increase with time. Systems with $\delta > 0$ reach a stationary cluster size after about 50 beats. The stationary cluster size is plotted in figure 56 as a function of the width $\delta_f$ of the frequency distribution. We find a decay with a power law 

$$\langle n_c \rangle \sim \delta_f^{-\gamma},$$

where $\gamma = 0.20 \pm 0.01$. The negative exponent indicates that the cluster size diverges when $\delta_f \to 0$.

Similar power-law behaviors of the cluster size as a function of the noise level, or of the cluster-size distribution itself, have been found for many systems of interacting microswimmers, from self-propelled rods (see section 6.3) to swimming flagella (Yang et al 2010). Such power laws reflect an underlying universal behavior of self-propelled systems. Indeed, much simpler models with a majority rule to align the velocity of a particle with its neighbors predict such behavior (Vicsek et al 1995b).

6.6. Sperm vortices

Individual sperm cells of many species swim on helical trajectories in the bulk and on circular trajectories at surfaces, as described in section 4.3. When the surface number density $\rho_0$ of sperm increases beyond a value of about 2000 mm$^{-2}$, a new phenomenon is observed (Riedel et al 2005), which is the formation of sperm vortices, in which several sperm cells together form ring-like arrangements with a diameter $d_0$ of about 25 $\mu$m. These vortices are themselves forming a fluid structure with a local hexagonal order, see figure 57. The onset of this structure formation corresponds to a dimensionless surface density of $\rho_0 d_0^3 \approx 1$, which shows that this density is the overlap density of circular trajectories. With increasing surface density, the number of cells in each vortex increases.

The study of this intriguing phenomenon by an extension of the 3D simulations for single sperm described in section 4.3 is quite difficult due to the large number of involved microswimmers. Therefore, Yang et al (2014) have resorted to a 2D description, in which each flagellum is confined to the surface plane, and different flagella interact via excluded-volume interactions. Furthermore, hydrodynamics is either taken into account by resistive-force theory or by a 2D mesoscale hydrodynamics approach. Snapshots and averaged trajectories are shown in figure 58.

Both, in experiments and simulations, the correlation function $G_{r, r}(r)$ of the instantaneous centers of the circular trajectories and the variance $\Delta$ of the spatial distribution of these centers have been determined (Riedel et al 2005, Yang et al 2014). A comparison of the results leads to the following conclusions. First, the comparison of the simulation results with and without hydrodynamic interactions reveals much weaker correlations with hydrodynamic interactions, see figure 59(b). The origin of this behavior is that hydrodynamic interactions lead to the synchronization and attraction of sperm swimming together, as discussed in section 5.5, but also disrupt the circular paths of sperm belonging to neighboring vortices, which move in opposite directions. Second, since the agreement of the simulation results with anisotropic friction only with experimental data is quite reasonable, see figure 59(a), we conclude that hydrodynamic interactions play a minor role in the vortex formation. However, it should be noticed that both hydrodynamic and excluded-volume interactions are stronger.
in two or three spatial dimensions. Therefore, it is conceivable that when the fluid above the surface is taken into account, hydrodynamic interactions contribute significantly to the stabilization of vortex arrays. Third, the order parameter above the overlap concentration is found in simulations and experiments to increase linearly with increasing surface number density. This implies that the characteristic diameter of a vortex hardly changes, but that its mass increases by increasing the number of involved sperm or flagella.

A Vicsek-type model has been designed to capture the dynamics of structure formation of ensembles of circle microswimmers in two dimensions (Yang et al. 2014). Many properties are found to be very similar as for the explicit flagella model described above. Thus, we expect a similar behavior for other circle swimmers in two dimensions, such as the L-shapes colloidal microswimmers of Wensink et al. (2014), or of other chiral microswimmers aggregating at surfaces.

6.7. Swarming of bacteria

Flagellated microorganisms exhibit collective behavior at a moister surface or in a thin liquid film in form of swarming (Copeland and Weibel 2009, Darnton et al. 2010, Kearns 2010, Partridge and Harshey 2013b). Swarming bacteria show a distinctively different motile behavior than swimming cells (Heinrichsen 1972, Darnton et al. 2010, Kearns 2010). Thereby flagella are the most important requirement, but cell–cell interactions also play a major role. Chemotaxis is considered to be of minor importance for swarming compared to physical interactions (Kearns 2010, Partridge and Harshey 2013b). During the transition from swimming to swarming cells, the number of flagella increase and the cells become often more elongated by suppression of cell division, i.e. cells become multi- or even hyperflagellated (Stahl et al. 1983, Jones et al. 2004, Darnton et al. 2010, Kearns 2010). E. coli and Salmonella bacteria double their length and increase the number of flagella, but the flagellar density remains approximately constant (Copeland et al. 2010, Kearns 2010, Partridge and Harshey 2013a 2013b). The changes for P. mirabilis are even more dramatic; their length increases 10–50 times and an increase of their flagellum number from fewer than 10–5000 is reported (Copeland and Weibel 2009, McCarter 2010, Tuson et al. 2013). As stated by Kearns (2010), neither is the reason known why swarming requires multiple flagella on the cell surface nor is a significant cell elongation required for many bacteria. Aside from a possible amplification of swarming by shape-induced alignment of adjacent cells, elongation associated with the increase in the number of flagella may help to overcome surface friction (Partridge and Harshey 2013b).

The particular swarming behavior, specifically the role played by flagella, seems to depend on the bacteria density and/or the number of flagella as suggested by experiments on E. coli (Copeland et al. 2010, Darnton et al. 2010, Turner et al. 2010) and B. mirabilis cells (Stahl et al. 1983, Jones et al. 2004). Studies of systems of lower density E. coli bacteria reveal stable cohesive flagella bundles during frequent collisions between cells (Copeland et al. 2010). Thereby, the bundles do not need to be aligned with the body (Turner et al. 2010). Moreover, transient flagella bundles are formed with adjacent cells. For higher density B. mirabilis systems, strong bundles between adjacent cells are found.

Since the large-scale patterns in swarming bacteria colonies (Cisneros et al. 2007, Wensink et al. 2012) are determined by cell–cell interactions, it is of fundamental importance to unravel the interactions between flagellated bacteria on the level of individual cells.

7. Other forms of active matter

7.1. Mixtures of filaments and motor proteins: active gels

An active system, which shares many propeties with suspensions of microswimmers, are mixtures of polar biological filaments with motor proteins. The most prominent examples are actin-myosin and microtubule-kinesin or microtubule-dynein systems. In both cases, the filaments are polar, which means that the motor proteins are walking only in one direction along the filament. In the experiments (Nédélec et al. 1997, Surrey et al. 2001), clusters of at least two motorproteins are used, which can connect to two filaments simultaneously. The motor proteins move along both filaments until they reach the ends, where they either get stuck or drop off. This leads to many interesting structures like asters, nematic phases, swirls, and vortices.

On the theoretical side, mixtures of filaments and motor proteins have been modeled both on the molecular and on the continuum level. On the molecular level, semi-flexible polymers connected by motors with attachment, detachment, and forward-stepping rates have been considered Head et al. 2011a, 2011b, 2014, Kruse et al. 2001, Surrey et al. 2001, Gordon et al. 2012). On the continuum level, the starting point is the nearly parallel arrangement of long passive filaments in the nematic phase, for which a well-established liquid-crystal description exists (de Gennes and Prost 1995); additional contributions are then added to this liquid-crystal model to capture the motor activity. These hydrodynamic theories of active gels are equally suited to describe suspensions of microswimmers. Phenomena like swirls and vortices, arrays of vortices and spontaneous collective
orientation can all be interpreted in the framework of these continuum approaches (Kruse et al 2004, Voituriez et al 2006, Elgeti et al 2011, Giomi et al 2011, Fuerthauer et al 2013). For a comprehensice discussion, we refer to the review articles by Toner et al (2005), Ramaswamy 2010 and Marchetti et al (2013).

7.2. Cellular tissues

Another interesting form of active matter are migrating cellular tissues. A well-studied experimental model of such tissues are Madin–Darby canine kidney cells, as explained in section 1. Indeed, similar phenomena as in bacterial turbulence (see section 6.3) can be observed in collectively migrating cellular tissues, however qualitatively different phenomena also emerge. In particular, the adhesion between cells and their active orientation strategy can lead to novel behavior.

When plated on adhesive substrates, the cells move and grow. Similar to the vortices observed in self-propelled rods or bacteria, these cells display swirl structures even when already forming a closed monolayer. As the density increases, this ‘active liquid’ undergoes a glass-like transition, and eventually becomes fully dynamically arrested (Angelini et al 2010, Angelini et al 2011, Basan et al 2013).

A remarkable feature of growing cellular colonies is that they do not spread by a pressure pushing cells outward, but rather as closed monolayers under tension (Trepat et al 2009). This tensile state can only be understood if the motility forces against the substrate are considered. Indeed a simple mechanism of alignment of the motility force with the actual velocity can lead to tensile growing states (Basan et al 2013).

Another feature emerging from the adhesion between the ‘micro-crawlers’ is the formation of growth fingers. A classic experiment is a wound-healing assay. Here, cells are plated confluently around a rubber block. When the block is removed, cells start to migrate into the newly available space. This leads to a fingering instability with the formation of...
distinct leader cells (Poujade et al. 2007, Petitjean et al. 2010, Basan et al. 2013).

Thus, while not microswimmers, motile epithelial tissues are closely related in some aspects to swimming microorganisms. However, the adhesion among themselves and with the substrate also creates novel features not present in microswimmers.

8. Summary and conclusions

In this review article, we have illustrated various physical aspects of locomotion of microswimmers. After an overview of the basic propulsion concepts exploited by biological cells and applied in synthetic systems, we have addressed low Reynolds number hydrodynamics and its implication for the coordinated and concerted motion of individual flagellated cells, and the interaction between cells and colloidal microswimmers, respectively. Alterations in the dynamical behavior due to restricting surfaces have been illuminated along with physical mechanisms for surface-capturing. In addition, the complex collective behavior of assemblies of microswimmers has been addressed, which emerges from physical interactions such as hydrodynamics and volume-exclusion interactions due to shape anisotropies or even simply and foremost by their propulsion.

Active systems comprise an exciting and broad range of phenomena. Not all of the aspects could be addressed in this article. Some further characteristics are:

- Biological fluids are typically multicomponent systems containing polymers and other colloid-like objects, which renders them viscoelastic rather than Newtonian. The non-Newtonian environment strongly affects the behavior of the microswimmer and often leads to an enhanced swimming velocity (Chaudhury 1979, Furford et al. 1998, Fu et al. 2009, Lauga and Powers 2009, Elfring et al. 2010, Liu et al. 2011, Mino et al. 2011, Zhu et al. 2012, Spagnolie et al. 2013, Riley and Lauga 2014). By the presence of nonlinear constitutive equations, locomotion in complex fluids overcomes limitations expressed by the scallop theorem (Lauga and Powers 2009). This is achieved on the one hand by the rate (velocity) dependence by the nonlinear evolution equations, and on the other hand, by the nonlinear rheological properties of the fluid.

- Since microswimmers in the absence of external forces are force- and torque-free, their far-field flow profile is well described by a force-dipole. There are, however, some notable exceptions, for example when a microswimmer is not neutrally buoyant or when it is magnetically actuated. The far-field of such a swimmers is usually dominated by the Stokeslet. Examples include Volvox algae, which are heavier than water, and thus react to gravity. Their far field was indeed measured to be dominated by the Stokeslet (Drescher et al. 2010). Paramecium is diamagnetic, and thus can be manipulated with magnetic fields, causing external forces and torques (Guevorkian and Valles 2006a, 2006b).

- Sedimentation in a gravitational field is also strongly affected by active propulsion (Tailleur and Cates 2009, Enculescu and Stark 2011). While the density profile is still exponential, the effective temperature is much larger than the real temperature (Tailleur and Cates 2009), and the particles are polarized in the upwards direction (Enculescu and Stark 2011)—even in the absence of any hydrodynamic interactions. Theoretical and experimental studies of L-shaped active colloids, i.e. of particles with a chiral shape, demonstrate that the presence of a gravitational field leads to different classes of trajectories, from straight downward and upward motion (gravitaxis) to trochoid-like trajectories (ten Hagen et al. 2014). This suggests that gravitaxis of biological microswimmers opposite to the gravitational field can be entirely due to the interplay of self-propulsion and shape asymmetry, and requires no active steering.

- Exposure to an external flow and confinement, such as in microfluid channels, leads to particular, activity-induced effects (Zöttl and Stark 2012, 2013, Garcia et al. 2013). A paradigmatic example is E. coli bacteria, which exhibit positive rheotaxis in channel flow, i.e. a rapid and continuous upstream motility (Hill et al. 2007, Nash et al. 2010, Costanzo et al. 2012, Costanzo et al. 2014, Fu et al. 2012, Kaya and Koser 2012). Recent measurements for microalgae indicate that they even swim along the vorticity direction in shear flow (Chengala et al. 2013). Moreover, experiments indicate that flow gradients can lead to accumulation and layer formation of gyrotactic phytoplankton (Durham et al. 2009). Strong shear flow can produce large spatial heterogeneities, characterized by cell depletion from low-shear regions due to ‘trapping’ in high-shear regions (Rusconi et al. 2014). This impacts bacterial behavior by hampering chemotaxis and promoting surface attachment.

- The effective viscosity of suspensions of microswimmers in shear or extensional flow depends on the swimming activity, and is therefore different from that of suspensions of passive particles (Hatwalne et al. 2004, Sokolov and Aranson 2009, Rafai et al. 2010, Giomi et al. 2010, Saintillan 2010, Gyrya et al. 2011, Mussler et al. 2013). Typically, it is found that the effective viscosity increases for pullers and decreases for pushers.

Our understanding of the behavior of the ‘classical’ biological microswimmers (such as sperm, bacteria, and algae) dramatically advanced, and many novel microswimmers have been designed in recent years and decades. This opens a route for many new applications of microswimmers, e.g. as microgears (Di Leonardo et al. 2010). What is universal about the swimming behavior (and can thus be described by the hydrodynamic far-field approximation), and what is specific for a certain class of swimmers (like the synchronization of different wave forms of flagella)? How can synthetic microswimmers be designed to react to external stimuli and find their targets? How can the ‘biological complications’ be incorporated into theoretical models? The investigations of these and related questions are challenging and exciting research topics in the future.
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References

Abkenar M, Marx K, Auth T and Gompper G 2013 Collective behavior of penetrable self-propelled rods in two dimensions Phys. Rev. E 88 062314
Afzelius B A 1976 A human syndrome caused by immotile cilia Science 193 317
Aldana M, Dossetti V, Huec C, Kenkre V M and Larralde H 2007 Phase transitions in systems of self-propelled agents and related network models Phys. Rev. Lett. 98 095702
Alexander G P, Pooley C M and Yeomans J M 2008 Scattering of low Reynolds number swimmers Phys. Rev. E 78 045302
Angelini T E, Hannezo E, Trepat X, Fredberg J J and Weitz D A 2010 Cell migration driven by cooperative substrate deformation patterns Phys. Rev. Lett. 104 168104
Armitage J P and Macnab R M 1987 Unidirectional, intermittent swimming in Escherichia coli Nat. Rev. Microbiol. 106 15567–72
Brumley D R, Wan K Y, Polin M and Goldstein R E 2014 Flagellar synchronization through direct hydrodynamic interactions eLife 3 e02750

Bruot N, Damet L, Kotar J, Cicuta P and Lagomarsino M C 2011 Noise and synchronization of a single active colloid Phys. Rev. Lett. 107 094101

Buttinoni I, Bialké K, Kümmler F, Löwen H, Bechinger C and Speck T 2013 Dynamical clustering and phase separation in suspensions of self-propelled colloidal particles Phys. Rev. Lett. 110 238301

Buttinoni I, Volpe G, Kümmler F, Volpe G and Bechinger C 2012 Active Brownian motion tunable by light J. Phys.: Condens. Matter 24 284129

Calladine C R, Luis B F and Pratap J V 2013 A ‘mechanistic’ explanation of the multiple helical forms adopted by bacterial flagellar filaments J. Mol. Biol. 425 914

Calladine C R 1975 Construction of bacterial flagella Nature 255 121

Camalet S, Jülicher F and Prost J 1999 Self-organized beating and vorticity direction in a shear flow Phys. Rev. Lett. 82 1590–3

Cartwright J H E, Piro O and Tuval I 2004 Fluid-dynamical basis of the embryonic development of left-right asymmetry in vertebrates Proc. Natl Acad. Sci. USA 101 7234

Cates M E and Tailleur J 2013 When are active Brownian particles and run-and-tumble particles equivalent? Consequences for motility-induced phase separation Europhys. Lett. 101 20010

Cates M E 2012 Diffusive transport without detailed balance in motile does: microbiology need statistical physics? Rep. Prog. Phys. 75 042601

Casavera A, Cimarelli A, Giardina I, Parisi G, Santagati R, Stefanini A and Viale M 2010 Scale-free correlations in starling flocks Proc. Natl Acad. Sci. USA 107 11865–70

Chaté H, Ginelli F, Grégoire G and Raynaud F 2008 Collective motion of self-propelled particles interacting without cohesion Phys. Rev. E 77 046113

Chattopadhyay S, Moldovan R, Yeung C and Wu X L 2006 Swimming efficiency of bacterium Escherichia coli Proc. Natl Acad. Sci. USA 103 13712

Chaudhury T K 1979 On swimming in a visco-elastic liquid J. Fluid Mech. 95 189

Chengala A, Hondzo M and Sheng J 2013 Microalgae propels along with direct hydrodynamic interactions eLife 3 e02750

Crenshaw H C 1989 Kinematics of helical motion of microorganisms capable of motion with four degrees of freedom Biophys. J. 56 1029–35

Crenshaw H C 1996 A new look at locomotion in microorganisms: rotating and translating Am. Zool. 36 608–18

Darnton N, Cicuta G M, Kotar J, Lagomarsino M C and Cicuta P 2012 Hydrodynamically synchronized states in active colloidal arrays Soft Matter 8 8672

Dartnall H J and Stocker R 2009 Disruption of vertical motility by shear triggers formation of thin phytoplankton layers Science 323 1067

D’Orsogna M R, Chuang Y L, Bertozzi A L and Chayes L S 2006 The Theory of Polymer Dynamics Doi M and Edwards S F 1986 (Oxford: Clarendon)

Darnton N C, Turner L, Rojevsky S and Berg H C 2007 On torque and tumbling in swimming Escherichia coli J. Bacterial. 189 1756–64

Darnton N C, Turner L, Rojevsky S and Berg H C 2010 Dynamics of bacterial swimming Biophys. J. 98 2082

Deshegine J, Dauchot O and Chaté H 2010 Collective motion of vibrated polar disks Phys. Rev. Lett. 105 098001

d’Enfert P and Kapral R 2013 Phoretic self-propulsion: a mesoscopic description of reaction dynamics that powers Brownian motion Nanoscale 5 1337

d’Enfert P and Prost J 1995 The Physics of Liquid Crystals (Oxford: Clarendon)

Darnton N C, Turner L, Rojevsky S and Berg H C 2010 Dynamics of bacterial swimming Biophys. J. 98 2082

Di Leonardo R, Angelani L, Dell’arciprete D, Ruocco G, Lebba V, Schippa S, Conte M P, Mecarini F, De Angelis F and Di Fabrizio E 2010 Bacterial ratchet motors Proc. Natl Acad. Sci. USA 107 9541–5

Di Leonardo R, Buzás A, Kelemen L, Viznyüzicsz G, Oroszi L and Ormos P 2012 Hydrodynamic synchronization of light-driven microtubrorgs Phys. Rev. Lett. 109 034104

Di Lazzaro W R, Turner L, Mayer M, Garstecki P, Weibel D B, Berg H C and Whitesides G M 2005 Escherichia coli swim on the right-hand side Nature 435 1271

Di Leonardo R, Angelani L, Dell’arciprete D, Ruocco G, Lebba V, Schippa S, Conte M P, Mecarini F, De Angelis F and Di Fabrizio E 2010 Bacterial ratchet motors Proc. Natl Acad. Sci. USA 107 9541–5

Di Leonardo R, Buzás A, Kelemen L, Viznyüzicsz G, Oroszi L and Ormos P 2012 Hydrodynamic synchronization of light-driven microtubrorgs Phys. Rev. Lett. 109 034104

Di Leonardo R, Angelani L, Dell’arciprete D, Ruocco G, Lebba V, Schippa S, Conte M P, Mecarini F, De Angelis F and Di Fabrizio E 2010 Bacterial ratchet motors Proc. Natl Acad. Sci. USA 107 9541–5

Di Leonardo R, Buzás A, Kelemen L, Viznyüzicsz G, Oroszi L and Ormos P 2012 Hydrodynamic synchronization of light-driven microtubrorgs Phys. Rev. Lett. 109 034104

Di Leonardo R, Buzás A, Kelemen L, Viznyüzicsz G, Oroszi L and Ormos P 2012 Hydrodynamic synchronization of light-driven microtubrorgs Phys. Rev. Lett. 109 034104

Drescher K, Dinkel J, Cisneros L H, Ganguly S and Goldstein R E 2011 Fluid dynamics and noise in bacterial cell–cell and cell–surface scattering Proc. Natl Acad. Sci. USA 108 10940

Drescher K, Goldstein R E, Michel N, Polin M and Tuval I 2010 Direct measurement of the flow field around swimming microorganisms Phys. Rev. Lett. 105 168101

Drescher K, Leptos K C, Tuval I, Ishikawa T, Pedley T J and Goldstein R E 2009 Dancing volvox: hydrodynamic bound states of swimming algae Phys. Rev. Lett. 102 168101

Dreyfus R, Baudry J, Roper M L, Fermigier M, Stone H A and Bibette J 2005 Microscopic artificial swimmers Nature 437 862–5

Dunkel J, Heidenreich S, Drescher K, Wensink H H, Bär M and Goldstein R E 2013 Fluid dynamics of bacterial turbulence Phys. Rev. Lett. 110 228102

Durham W M, Kessler J O and Stocker R 2009 Disruption of vertical motility by shear triggers formation of thin phytoplankton layersScience 323 1067

Ebbens S J and Howse J R 2010 In pursuit of propulsion at the nanoscale Soft Matter 6 726–38

Eisenbach M and Gijovlas L C 2006 Sperm guidance in mammals: an unpaved road to the egg Nat. Rev. Mol. Cell. Biol. 7 276–85

Elfring G J and Lauga E 2009 Hydrodynamic phase locking of swimming microorganisms Phys. Rev. Lett. 103 088101
Elfring G J and Lauga E 2011 Passive hydrodynamic synchronization of 2D swimming cells Phys. Fluids 23 011902
Elfring G J, Pak S and Lauga E 2010 Two-dimensional flagellar synchronization in viscoelastic fluids J. Fluid Mech. 646 505–15
Elgeti J, Cates M E and Marenduzzo D 2011 Defect hydrodynamics in 2D polar active fluids Soft Matter 7 3177–85
Elgeti J and Gompper G 2008 Hydrodynamics of active mesoscopic systems N/C Symp. (N/C Series vol 39) ed G Münster (Jülich: Neumann Institute for Computing) p 53
Elgeti J and Gompper G 2009 Self-propelled rods near surfaces Europhys. Lett. 85 38002
Elgeti J and Gompper G 2013a Emergence of metachronal waves in cilia arrays Proc. Natl Acad. Sci. USA 110 4470–5
Elgeti J and Gompper G 2013b Wall accumulation of self-propelled spheres Europhys. Lett. 101 48003
Elgeti J, Kaupp U B and Gompper G 2010 Hydrodynamics of sperm cells near surfaces Biophys. J. 99 1018–26
Eloy C and Lauga E 2012 Kinematics of the most efficient cilium Soft Matter 8 108101
Enculescu M and Stark H 2011 Active colloidal suspensions exhibit polar order under gravity Phys. Rev. Lett. 107 058301
Erbe A, Zientara M, Baraban L, Kreidler C and Leiderer P 2008 Various driving mechanisms for generating motion of colloidal particles J. Phys.: Condens. Matter 20 404215
Español P, Rubio M A and Záñiga I 1995 Scaling of the time-dependent self-diffusion coefficient and the propagation of hydrodynamic interactions Phys. Rev. E 51 803
Farrell F D C, Marchetti M C, Marenduzzo D, Tailleur J 2012 Pattern formation in self-propelled particles with density-dependent motility Phys. Rev. Lett. 108 248101
Fauci L J and Dillon R 2006 Biofluidmechanics of reproduction Annu. Rev. Fluid Mech. 38 371–94
Fily Y, Baskaran A and Hagan M F 2014 Dynamics of self-propelled particles under strong confinement Soft Matter 10 5609
Fily Y, Henkes S and Marchetti M C 2014 Freezing and phase separation of self-propelled disks Soft Matter 10 2132
Fily Y and Marchetti M C 2012 Athermal phase separation of self-propelled Particles with no alignment Phys. Rev. Lett. 108 235702
Flores H, Lobaton E, Mendez-Diez S, Tlupova S and Cortez R 2005 A study of bacterial flagellar bundling Bull. Math. Biol. 67 137–68
Foissner W 1998 An updated compilation of world soil ciliates (protozoa, ciliophora), with ecological notes, new records, and descriptions of new species Eur. J. Protistol. 34 195–235
Fournier-Bidoz A,Arsenault A, Manners I and Ozin G A 2005 Synthetic self-propelled nanorotors Chem. Commun. 28 441–3
Friedrich B M and Jülicher F 2007 Chemotaxis of sperm cells Proc. Natl Acad. Sci. USA 104 13256–61
Friedrich B M and Jülicher F 2012 Flagellar synchronization independent of hydrodynamic interactions Phys Rev. Lett. 109 138102
Friedrich B M, Riedel-Kruse I H, Howard J and Jülicher F 2010 High-precision tracking of sperm swimming fine structure provides strong test of resistive force theory J. Exp. Biol. 213 1226–34
Frymier P D, Ford R M, Berg H C and Cummings P T 1995 Three-dimensional tracking of motile bacteria near a solid planar surface Proc. Natl Acad. Sci. USA 92 6195
Fürthauer S, Strempel M, Grill S W and Jülicher F 2013 Active chiral processes in thin films Phys. Rev. Lett. 110 048103
Fulford G R, Katz D F and Powell R L 1998 Swimming of spermatozoa in a linear viscoelastic fluid Biotherapy 35 295
Fu H C, Wolgemuth C W and Powers T R 2009 Swimming speeds of filaments in nonlinear viscoelastic fluids Phys. Fluids 21 033102
Fu H, Powers T and Stocker R 2012 Bacterial rheotaxis Proc. Natl Acad. Sci. USA 109 4780–5
Gachelin J, Miño G, Berthet H, Lindner A, Rousselet A and Clément É 2013 Non-Newtonian viscosity of Escherichia coli suspensions Phys. Rev. Lett. 110 268103
Gachelin J, Rousselet A, Lindner A and Clément E 2014 Collective motion in an active suspension of Escherichia coli bacteria New J. Phys. 16 025003
Galajda P, Keymer J, Chaikin P and Austin R 2007 A wall of funnels concentrates swimming bacteria J. Bacteriol. 189 8704–7
Garcia X, Rafai S and Pefia P 2013 Light control of the flow of Phototactic microswimmer suspensions Phys. Rev. Lett. 110 138106
Gauger E M, Downton M T and Stark H 2009 Fluid transport at low Reynolds number with magnetically actuated artificial cilia Eur. Phys. J. E 28 231–42
Gejji R, Lushnikov P M and Alber M 2012 Macroscopic model of self-propelled bacteria swimming with regular reversals Phys. Rev. E 85 021903
Geyer V F, Jülicher F, Howard J and Friedrich B M 2013 Cell-body rocking is a dominant mechanism for flagellar synchronization in a swimming alga Proc. Natl Acad. Sci. USA 110 18058–63
Ghosh A and Fischer P 2009 Controlled propulsion of artificial magnetic nanostructured propellers Nano Lett. 9 2243
Ginelli F, Peruani F, Bär M and Chaté H 2010 Large-scale collective properties of self-propelled rods Phys. Rev. Lett. 104 184502
Giomi L, Liverpool T B and Marchetti M C 2010 Sheared active fluids: thickening, thinning, and vanishing viscosity Phys. Rev. E 81 051908
Giomi L, Mahadevan L, Chakraborty B and Hagan M F 2011 Excitable patterns in active nematics Phys. Rev. Lett. 106 218101
Goldstein R E, Polin M and Tuvalu I 2009 Noise and synchronization in pairs of beating eukaryotic flagella Phys. Rev. Lett. 103 168103
Goldstein R E, Polin M and Tuvalu I 2011 Emergence of synchronized beating during the regrowth of eukaryotic flagella Phys. Rev. Lett. 107 148103
Golestanian R, Liverpool T B and Ajdari A 2005 Propulsion of a molecular machine by asymmetric distribution of reaction products Phys. Rev. Lett. 94 220801
Golestanian R, Yeomans J M and Uchida N 2011 Hydrodynamic synchronization at low Reynolds number Soft Matter 7 3074–82
Golestanian R 2008 Three-sphere low Reynolds number swimmer with a cargo container Eur. Phys. J. E 25 1
Golestanian R 2009 Anomalous diffusion of symmetric and asymmetric active colloids Phys. Rev. Lett. 102 188305
Gompper G, Ihle T, Kroll D M and Winkler R G 2009 Multi-particle collision dynamics: a particle-based mesoscale simulation approach to the hydrodynamics of complex fluids Adv. Polym. Sci. 221 1–87
Gordon D, Bernheim-Grosawaher A, Keasar C and Farago O 2012 Hierarchical self-organization of cytoskeletal active networks Phys. Biol. 9 026005
Götz I O and Gompper G 2010a Flow generation by rotating colloids in planar microchannels Europhys. Lett. 92 64003
Götz I O and Gompper G 2010b Mesoscopic simulations of hydrodynamic squirmer interactions Phys. Rev. E 82 041921
Götz I O and Gompper G 2011 Dynamic self-assembly and directed flow of rotating colloids in microchannels Phys. Rev. E 84 041921
Gray J and Hancock G J 1955 The propulsion of sea-urchin spermatozoa J. Exp. Biol. 32 802–14
Grégoire G and Chaté H 2004 Onset of collective and cohesive motion Phys. Rev. Lett. 92 025702
Grzybowsk B A, Stone H A and Whitesides G M 2000 Dynamic self-assembly of magnetized, millimetre-sizes objects rotating at a liquid-air interface Nature 405 1033–6
Guasto J S, Johnson K A and Golub J P 2010 Oscillatory flows induced by microorganisms swimming in two dimensions Phys. Rev. Lett. 105 168102
Gueron S, Levit-Gurevich K, Liron N and Blum J 1997 Cilia internal mechanism and metachronal coordination as the result of hydrodynamical coupling Proc. Natl Acad. Sci. USA 94 6001

Gueron S and Levit-Gurevich K 1998 Computation of the internal forces in cilia: application to ciliary motion, the effects of viscosity, and cilia interactions Biophys. J. 74 1658

Gueron S and Levit-Gurevich K 1999 Energetic considerations of ciliary beating and the advantage of metachronal coordination Proc. Natl Acad. Sci. USA 96 12240–5

Gueron S and Levit-Gurevich K 2001 A three-dimensional model for ciliary motion based on the internal 9 + 2 structure Proc. Biol. Sci. 268 599–607

Guevorkian K and Valles J M Jr 2006a Aligning Paramecium caudatum with static magnetic fields Biophys. J. 90 3004–11

Guevorkian K and Valles J M Jr 2006b Swimming paramecium in magnetically simulated enhanced, reduced, and inverted gravity environments Proc. Natl Acad. Sci. USA 103 13051–6

Guidobaldi A, Jeyaram Y, Berdakin I, Moshchalkov V V, Condat C A, Marconi V I, Giojalas L and Silhanek A V 2014 Geometrical guidance and trapping transition of human sperm cells Phys. Rev. E 89 032720

Guirao B and Joanny J 2007 Spontaneous creation of macroscopic flow and metachronal waves in an array of cilia Biophys. J. 92 1900–17

Gyongy V, Lipnikov K, Aranson I S and Berlyand L 2011 Effective shear viscosity and dynamics of suspensions of microswimmers from small to moderate concentrations J. Math. Biol. 62 707–40

Hancock G J 1953 The self-propulsion of microscopic organisms through liquids Proc. R. Soc. Lond. A 217 96

Harada Y, Noguchi A, Kishino A and Yanagida T 1987 Sliding movement of single actin filaments on one-headed myosin filaments Nature 326 805–8

Harnau L, Winkler R G and Reineker P 1996 Dynamic structure factor of semiflexible macromolecules in dilute solution J. Chem. Phys. 104 6355

Harshey R M 1994 Bees aren’t the only ones: swarming in gram-negative bacteria Mol. Microbiol. 13 389

Harshey R M 2003 Bacterial motility on a surface: many ways to a common goal Annu. Rev. Microbiol. 57 249

Harvey C W, Alber M, Tsimring L S and Aranson I S 2013 Continuum modeling of myxobacteria clustering New J. Phys. 15 035029

Harvey C W, Morcos F, Sweet C R, Kaiser D, Chatterjee S, Harvey C W, Alber M, Tsimring L S and Aranson I S 2013 Hydrodynamic correlations in multiparticle collision dynamics fluids Phys. Rev. E 86 056711

Howard J 2001 Mechanisms of Motor Proteins and the Cytoskeleton (Sunderland: Sinauer Associates)

Hosse J R, Jones R A L, Ryan A J, Gough T, Vafabakhsh R and Golestanian R 2007 Self-motile colloidal particles: from directed propulsion to random walk Phys. Rev. Lett. 99 048102

Huang C C, Gompper G and Winkler R G 2012 Hydrodynamic correlations in dilute solution J. Chem. Phys. 138 144902

Huang C C, Gompper G and Winkler R G 2013 Effect of hydrodynamic correlations on the dynamics of polymers in dilute solution Phys. Rev. Lett. 92 168701

Huepe C and Aldana M 2008 New tools for characterizing swarming systems: a comparison of minimal models Physica A 387 2809–22

Hulme S E, DiLuzio W R, Shevkoplyas S S, Turner L, Mayer M, Berg H C and Whitesides G M 2008 Using ratchets and sorters to fractionate motile cells of Escherichia coli by length Lab Chip 8 1888

Hyon Y, Powers T, Stocker R and Fu H 2012 The wiggling trajectories of bacteria J. Fluid Mech. 705 58–76

Ibele M, Mallouk T. E and Sen A 2009 Schooling behavior of light-powered autonomous micromotors in water Angew. Chem. Int. Edn Engl. 48 3308–12

Imler S, Moore H D M, Breed W G and Birkehead T R 2007 By hook or by crook? morphometry, competition and cooperation in rodent sperm PLoS One 2 e170

Ishikawa T and Pedley T J 2008 Coherent structures in monolayers of swimming particles Phys. Rev. Lett. 102 088103

Ishikawa T, Sekiya G, Imai Y and Yamaguchi T 2007 Hydrodynamic interactions between two swimming bacteria Biophys. J. 93 2217–25

Ishikawa T, Simmonds M P and Pedley T J 2006 Hydrodynamic interaction of two swimming model micro-organisms J. Fluid Mech. 568 119–60

Ishikawa T 2009 Suspension biomechanics of swimming microbes J. R. Soc. Interface 6 815–34

Ishimoto K and Gaffney E A 2013 Squirmers near a boundary Phys. Rev. E 88 062702

Janssen P J A and Graham M D 2011 Coexistence of tight and loose guarding by male fishflies J. Insect Physiol. 57 249–56

Jiang H R, Yoshinaga N and Sano M 2010 Active motion of Janus particles by self-thermophoresis in defocused laser beam Phys. Rev. Lett. 105 062702

Johnson R E 1980 An improved slender-body theory for Stokes flow J. Fluid Mech. 99 411

Jones B V, Young R, Mahenthiralingam E and Stickler D J 2004 Ultrastructure of Proteus mirabilis swarmer cell rafts and role of swimming in cather-associated urinary tract infection Infect. Immun. 72 3941
Matas-Navarro R, Golestanian R, Liverpool T B and Fielding S M 2014 Hydrodynamic suppression of phase separation in active suspensions Phys. Rev. E 90 032304

McCandlish S R, Baskaran A and Hagan M F 2012 Spontaneous segregation of self-propelled particles with different motilities Soft Matter 8 2527–34

McCart L L 2010 Bacterial acrobatics on a surface: swirling packs, collisions, and reversals during swarming J. Bacteriol. 192 3246

Meli V F, Solovev A A, Sanchez S and Schmidt O G 2011 Rolled-up nanotext on polymers: from basic perception to self-propelled catalytic microengines Chem. Soc. Rev. 40 2109

Mendelson N H, Bourque A, Wilkening K, Anderson K R and Watkins J C 1999 Organized cell swimming motions in Bacillus subtilis colonies: patterns of short-lived whirls and jets J. Bacteriol. 181 600–9

Miño G, Mallouk T E, Darnige T, Hoyos M, Dauchet J, Dunstan J, Mendelson N H, Bourque A, Wilkening K, Anderson K R and McCarter L L 2010 Bacterial acrobatics on a surface: swirling hydrodynamic interactions during swarming J. Bacteriol. 192 7174–84

Ni R, Cohen Stuart M A and Dijkstra M 2013 Pushing the glass effective viscosity of non-gravitactic Chlamydomonas reinhardtii microswimmer suspensions Europhys. Lett. 101 54004

Najafi A and Golestanian R 2004 Simple swimmer at low Reynolds number: three linked spheres J. Chem. Phys. 120 98102

Paxton W F, Kistler K C, Olmeda C C, Sen A, St Angelo S K, Cao Y, Mallouk T E, Lammert P E and Crespi V H 2004 Catalytic nanomotors: autonomous movement of striped nanorods J. Am. Chem. Soc. 126 13424

Paxton W, Sundararajan S, Mallouk T and Sen A 2006 Chemical locomotion Angew. Chem. Int. Edn 45 5420

Peruani F, Deutsch A and Bär M 2006 Nonequilibrium clustering of self-propelled rods Phys. Rev. E 74 030904

Peruani F, Deutsch A and Bär M 2008 A mean-field theory for self-propelled particles interacting by velocity alignment mechanisms Eur. Phys. J. Spec. Top. 157 111–22

Peruani F, Schimansky-Geier L and Bär M 2010 Cluster dynamics and cluster size distributions in systems of self-propelled particles Eur. Phys. J. Spec. Top. 191 173–85

Peshkov A, Aranson I S, Bertin E and Cinelli F 2012 Nonlinear field equations for aligning self-propelled rods Phys. Rev. Lett. 109 268701

Pettietjean L, Reffay M, Grassland-Mongrain E, Poujade M, Ladox B, Buguin A and Silberzan P 2010 Velocity fields in a collectively migrating epithelium Biophys. J. 98 1790–800

Pikovsky A, Rosenblum M and Kurths J 2002 Synchronization: a Universal Concept in Nonlinear Science (Cambridge: Cambridge University Press)

Platzter J, Sterr W, Hausmann M and Schmitt R 1997 Three genes of a motility operon and their role in flagellar rotary speed variation in Rhizobium meliloti J. Bacteriol. 179 6391–9

Polim M, Tuval I, Drescher K, Golub J P and Goldstein R E 2009 Chlamydomonas swims with two ‘gears’ in a eukaryotic version of run-and-tumble locomotion Science 325 487

Petrozek K and Friedrich B M 2013 A three-sphere swimmer for flagellar synchronization New. J. Phys. 15 045005

Popescu M N, Dietrich S and Oshanin G 2009 Confinement effects on diffusiophoretic self-propellers J. Chem. Phys. 130 194702

Popescu M N, Dietrich S, Tasinkevych M and Ralston J 2010 Phoretic motion of spheroidal particles due to self-generated solute gradients Eur. Phys. J. E 31 351–67

Popescu M N, Tasinkevych M and Dietrich S 2011 Pulling and pushing a cargo with a catalytically active carrier EPL 95 28004

Popescu M N, Golestanian R and Ritort F 2008 Nonequilibrium cluster formation in colonies of gliding bacteria Proc. Natl Acad. Sci. USA 105 173–85

Popescu M N, Dietrich S, Tasinkevych M and Ralston J 2011 Pulling and pushing a cargo with a catalytically active carrier EPL 95 28004

Portill J, Joanny J F, Lenz P and Sykes C 2008 The physics of Listeria propulsion Cell Motility (New York: Springer)

Purcell E M 1977a Life at low Reynolds numbers Am. J. Phys. 45 3

Pratt J D and Harshay R M 2013a More than motility: Salmonella flagella contribution to overriding friction and facilitating colony hydration during swarming J. Bacteriol. 195 919

Pratt J D and Harshay R M 2013b Swarming: flexible roaming plans J. Bacteriol. 195 909

Pusey W, Hagan M and Stark H 2005 Synchronization of rotating helices by hydrodynamic interactions Eur. Phys. J. E 17 493
Reigh S Y, Winkler R G and Gompper G 2012 Synchronization and bundling of anchored bacterial flagella Soft Matter 8 4363
Reigh S Y, Winkler R G and Gompper G 2013 Synchronization, slippage, and unbundling of driven helical flagella PLoS One 8 e70868
Riedel I H, Kruse K and Howard J 2005 A self-organized vortex array of hydrodynamically entrained sperm cells Science 309 300–3
Riedel-Kruse I, Hilfinger A and Jülicher F 2007 How molecular motors shape the flagellar beat HFSP J 1 192–208
Riley E E and Lauga E 2014 Enhanced active swimming in viscoelastic fluids Europhys. Lett. 108 34003
Rings D, Schachoff R, Selmeke M, Cichos F and Kroy K 2010 Hot Brownian motion Phys. Rev. Lett. 105 090604
Risken H 1989 The Fokker–Planck Equation (Berlin: Springer)
Rodénborn B, Chen C H, Swinney H L, Liu B and Zhang H P 2013 Propulsion of microorganisms by a helical flagellum Proc. Natl Acad. Sci. USA 110 E338
Romanczuk P, Bär M, Ebeling W, Lindner B and Schimansky-Geier L 2012 Active Brownian particles Eur. Phys. J. Spec. Top. 202 1
Rothschild I. 1963 Non-random distribution of bull spermatozoa in a drop of sperm suspension Nature 198 1221–2
Rucker G and Kapral R 2007 Chemically powered nanomotors Phys. Rev. Lett. 98 150603
Rüffer U and Nultsch W 1998 Flagellar coordination in Chlamydomonas cells held on micropipettes Cell Motil. Cytoskeleton 41 297
Rusconi R, Guasto J S and Stocker R 2014 Bacterial transport suppressed by fluid shear Nat. Phys. 10 212
Rycroft C H 2009 VORO ++ : a 3D voronoi cell library in C ++ Chaos 19 044111
Sabass B and Seifert U 2012 Dynamics and efficiency of a self-propelled, diffusiophoretic swimmer J. Chem. Phys. 136 064508
Saintillan D and Shelley M J 2013 Active suspensions and their nonlinear models C. R. Phys. 14 497–517
Saintillan D and Shelley M J 2010 Extensional rheology of active suspensions Phys. Rev. E 81 056307
Sanchez S and Lamparter M 2009 Nanorobots: the ultimate wireless self-propelled sensing and actuating devices Chem. Asian J. 4 1402–10
Sanchez S, Solovev A A, Harazim S M, Denecke C, Mei Y F and Schmidt O G 2011 The smallest man-made jet engine Chem. Rec. 11 367–70
Sanchez T, Welch D, Nicoastro D and Dogic Z 2011 Cilia-like beating of active microtubule bundles Science 333 456–9
Sanderson J M and Sleigh M A 1981 Ciliary activity of cultured rabbit tracheal epithelium: beat pattern and metachrony J. Cell Sci. 47 331–47
Saragosti J, Silberzan P and Buguin A 2012 Modeling E. coli tumbles by rotational diffusion. Implications for chemotaxis PLoS One 7 e35412
Sareh S, Rossiter J, Conn A, Drescher K and Goldstein R E 2012 Swimming like algae: biomimetic soft artificial cilia J. R. Soc. Interface 20120666
Schaller V , Weber C, Semmrich F, Frey E and Bausch A R 2010 Polar patterns of driven filaments Nature 467 73–7
Schamel D, Mark A G, Gibbs J G, Miksch C, Morozov K I, Leshansky A M and Fischer P 2014 Nanopropellers and their actuation in complex viscoelastic media ACS Nano 8 8794–8801
Scharf B 2002 Real-time imaging of fluorescent flagellar filaments of Rhizobium lupini H13-3: flagellar rotation and pH-induced polymorphic transitions J. Bacteriol. 184 5979–86
Schmitt R 2002 Sinorhizobial chemotaxis: a departure from the enterobacterial paradigm Microbiology 148 627–31
Sengupta S, Ibele M E and Sen A 2012 Fantastic voyage: designing self-powered nanorobots Angew. Chem. Int. Edn 51 8434–45
Shah D S H, Perehinec T, Stevens S M, Aizawa S I and Sackett R E 2000 The flagellar filament of Rhodobacter sphaeroides: ph-induced polymorphic transitions and analysis of the flic gene J. Bacteriol. 182 5218
Simha R A and Ramaswamy S 2002 Hydrodynamic fluctuations and instabilities in ordered suspensions of self-propelled particles Phys. Rev. Lett. 89 058101
Sivinski J 1984 Sperm Competition and the Evolution of Animal Mating Systems ed R L Smith (Orlando FL: Academic) pp 86–116
Sleigh M 1962 The structure of cilia The Biology of Cilia and Flagella (Oxford: Pergamon) pp 11–75
Smith D J, Gaffney E A, Blake J R and Kirkman-Brown J C 2009 Human sperm accumulation near surfaces: a simulation study J. Fluid Mech. 621 289–320
Sokolov A, Aranson I S, Kessler J O and Goldstein R E 2007 Concentration dependence of the collective dynamics of swimming bacteria Phys. Rev. Lett. 98 158102
Sokolov A and Aranson I S 2009 Reduction of viscosity in suspension of swimming bacteria Phys. Rev. Lett. 103 148101
Sole S, Beirne J, Crescitelli N, Dyer K, Drescher K and Goldstein R E 2013 The flagellar beat response in suspending voxx species J. Physiol. 47 580–3
Son K, Guasto J S and Stocker R 2013 Bacteria can exploit a flagellar buckling instability to change direction Nat. Phys. 9 494
Sparagnoti S E and Lauga E 2012 Hydrodynamics of self-propulsion near a boundary: predictions and accuracy of far-field approximations J. Fluid Mech. 700 105–47
Sparagnoti S E, Liu B and Powers T R 2013 locomotion of helical bodies in viscoelastic fluids: enhanced swimming at large helical amplitudes Phys. Rev. Lett. 111 068101
Speck T, Bialké J, Menzel A M and Löwen H 2014 Effective Cahn–Hilliard equation for the phase separation of active Brownian particles Phys. Rev. Lett. 112 218304
Stahl S J, Stewart K R and Williams F D 1983 Extracellular slime associated with Proteus mirabilis during swarming J. Bacteriol. 154 930
Stenhammar J, Marenduzzo D, Allen R J and Cates M E 2014 Phase behaviour of active Brownian particles: the role of dimensionality Soft Matter 10 14899–99
Stenhammar J, TGBocchi A, Allen R J, Marenduzzo D and Cates M E 2013 Continuum theory of phase separation kinetics for active Brownian particles Phys. Rev. Lett. 111 145702
Stocker R and Durham W M 2009 Tumbling for stealth Science 325 400
Strogatz S H 2004 Sync: How Order Emerges From Chaos in the Universe, Nature, and Daily Life (New York: Hyperion)
Sumino Y, Nagai K H, Shitaka Y, Tanaka D, Yoshikawa K, Chaté H and Oiwa K 2012 Large-scale vortex lattice emerging from collectively moving microtubules Nature 483 448–52
Surrey T, Nédélec F, Leibler S and Karsenti E 2001 Physical properties determining self-organization of motors and microtubules Science 292 1167–71
Szabó B, Szöllösi G J, Gönczi B, Jurányi Z, Selmeczi D and Vicsek T 2006 Phase transition in the collective migration of tissue cells: experiment and model Phys. Rev. E 74 061908
Tailleur J and Cates M E 2008 Statistical mechanics of interacting run-and-tumble bacteria Phys. Rev. Lett. 100 218103
Tailleur J and Cates M E 2009 Sedimentation, trapping, and rectification of dilute bacteria Europhys. Lett. 86 60002
Tamaš L and Horridge G A 1970 Relation between orientation of central fibrils and direction of beat in cilia of opalina Proc. R. Soc. Lond. B 175 219
Tavaddod S, Charsooghi M A, Abdi F, Khalesifard H R and Shah D S H, Perehinec T, Stevens S M, Aizawa S I and Sockett R E 2011, The flagellar filament of Rhodobacter sphaeroides: ph-induced polymorphic transitions and analysis of the flic gene J. Bacteriol. 182 5218
Taylor G I 1951 Analysis of the swimming of microscopic organisms Proc. R. Soc. Lond. A 209 447–61
Ten Hagen B, Kümmer F, Wittkowski R, Takagi D, Löwen H and Bechinger C 2014 Gravity of asymmetric self-propelled colloidal particles Nat. Commun. 5 4829
Thakur S and Kapral R 2011 Dynamics of self-propelled nanomotors in chemically active media J. Chem. Phys. 135 024509
Theers M and Winkler R G 2013 Synchronization of rigid microrotors by time-dependent hydrodynamic interactions Phys. Rev. E 88 023012
Theurkauff I, Cottin-Bizonne C, Palacci J, Ybert C and Bocquet L 2012 Dynamic clustering in active colloidal suspensions with chemical signaling Phys. Rev. Lett. 108 268303
Thutupalli S, Seemann L and Herminghaus S 2011 Swarming behavior of simple model squirmer New. J. Phys. 13 073021
Tierno P, Golestanian R, Pagonabarraga I and Sagues F 2008 Controlled swimming in confined fluids of magnetically actuated colloidal rotors Phys. Rev. Lett. 101 218103
Tirado M M, Martínez C L and de la Torre J G 1984 Comparison of theories for the translational and rotational diffusion coefficients of rod-like macromolecules. Application to short DNA fragments J. Chem. Phys. 81 2047
Toner J, Tu Y and Ramaswamy S 2005 Hydrodynamics and phases of flocks Ann. Phys. 318 170
Toner J and Tu Y 1995 Long-range order in a 2D dynamical XY model: How birds fly together Phys. Rev. Lett. 75 4326–9
Trepat X, Wasserman M R, Angelini T E, Millet E, Weitz D A, Butler J P and Fredberg J J 2009 Physical forces during collective cell migration Nat. Phys. 5 426–30
Turner L, Ryu W S and Berg H C 2006 Real-time imaging of fluorescent flagellar filaments J. Bacteriol. 182 2792
Turner L, Zhang R, Darnton N C and Berg H C 2010 Visualization of flagella during bacterial swarming J. Bacteriol. 192 3259
Tuson H H, Copeland M F, Carey S, Sacotte R and Weible D B 2013 Flagellum density regulates Proteus mirabilis swarmer cell motility in viscous environments J. Bacteriol. 195 3568
Uchida N and Golestanian R 2010 Synchronization and collective dynamics in a carpet of microfluidic rotors Phys. Rev. Lett. 104 178103
Uchida N and Golestanian R 2011 Generic conditions for hydrodynamic synchronization Phys. Rev. Lett. 106 058104
Uchida N and Golestanian R 2012 Hydrodynamic synchronization between objects with cyclic rigid trajectories Eur. Phys. J. E 35 1
Ulheinbeck G E and Ornstein L S 1930 On the theory of the Brownian motion Phys. Rev. 36 325
Uppaluri S, Nagler J, Stellamanns E, Heddegort N, Herminghaus S, Engstler M and Pfohl T 2011 Impact of microscopic motility on the swimming behavior of parasites: stricter trypanosomases are more directional PLoS Comput. Biol. 7 e1002058
Uspal W E, Popescu M N, Dietrich S and Tasinkevych M 2015 Self-assembly of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett. 105 48004
Xing J, Bai F, Berry R and Oster G 2006 Torque-speed relationship of the bacterial flagellar motor Proc. Natl Acad. Sci. USA 103 1260
Yang X, Manning M L and Marchetti M C 2014 Aggregation and segregation of confined active particles Soft Matter 10 6477
Yang Y, Elgeti J and Gompper G 2008 Cooperation of sperm in two dimensions: synchronization, attraction and aggregation through hydrodynamic interactions Phys. Rev. E 78 061903
Yang Y, Marceau V and Gompper G 2010 Swarm behavior of self-propelled rods and swimming flagella Phys. Rev. E 82 031904
Yang M and Ripoll M 2011 Simulations of thermophoretic nanoswimmers Phys. Rev. E 84 061401
Yang Y, Qiu F and Gompper G 2014 Self-organized vortices of circling self-propelled particles and curved active flagella Phys. Rev. E 89 012720
Zeng X, ten Hagen B, Kaiser A, Wu M, Cui H, Silber-Li Z and Löwen H 2013 Non-Gaussian statistics for the motion of self-propelled Janus particles: experiment versus theory Phys. Rev. E 88 032304
Zhu L, Lauga E and Brandt L 2012 Self-propulsion in viscoelastic fluids: pushers versus pullers Phys. Fluids 24 051902
Zöttl A and Stark H 2012 Nonlinear dynamics of a microswimmer in Poiseuille flow Phys. Rev. Lett. 108 218104
Zöttl A and Stark H 2013 Periodic and quasiperiodic motion of an elongated microswimmer in Poiseuille flow Eur. Phys. J. E 36 1
Zöttl A and Stark H 2014 Hydrodynamics determines collective motion and phase behavior of active colloids in quasi-2D confinement Phys. Rev. Lett. 112 118101

Volpe G, Buttini I, Vogt D, Kümmner H J and Bechinger C 2011 Microswimmers in patterned environments Soft Matter 7 8810
Wang Q, Pan J and Snell W J 2006 Intraflagellar transport particles participate directly in cilium-generated signaling in Chlamydomonas Cell 125 549
Wang W, Duan W, Sen A and Mallouk T E 2013 Catalytically powered dynamic assembly of rod-shaped nanomotors and passive tracer particles Proc. Natl Acad. Sci. USA 110 17744–9
Wensink H H, Dunkel J, Heidenreich S, Drescher K, Goldstein R E, Löwen H and Yeomans J M 2012 Meso-scale turbulence in living fluids Proc. Natl Acad. Sci. USA 109 14308
Wensink H H, Kantler V, Goldstein R E and Dunkel J 2014 Controlling active self-assembly through broken particle-shape symmetry Phys. Rev. E 89 010302
Wensink H H and Löwen H 2008 Aggregation of self-propelled colloidal rods near confining walls Phys. Rev. E 78 031409
Williams B J, Anand S V, Rajagopalan J and Saif M T A 2014 A self-propelled biohybrid swimmer at low Reynolds number Nat. Commun. 5 3081
Winet H, Bernstein G S and Head J 1984 Observations on the response of human spermatozoa to gravity, boundaries and fluid shear J. Reprod. Fert. 70 511–23
Winkler R G 2007 Diffusion and segmental dynamics of rodlike molecules by fluorescence correlation spectroscopy J. Chem. Phys. 127 054904
Wittkowski R, Tributsch A, Stenhammar J, Allen R J, Marenduzzo D and Cates M E 2014 Scalar field theory for active-particle phase separation Nat. Commun. 5 4351
Wolgemuth C W 2008 Collective swimming and the dynamics of bacterial turbulence Biophys. J. 95 1564–74
Wollin C and Stark H 2011 Metachronal waves in a chain of rowers with hydrodynamic interactions Eur. Phys. J. E 34 42
Woolley D M, Crockett R F, Groom W D I and Revell S G 2009 A study of synchronization between the flagella of bull spermatozoa, with related observations J. Exp. Biol. 212 2215–23
Woolley D M 2003 Motility of spermatozoa at surfaces Reproduction 126 259–70
Wysocki A, Winkler R G and Gompper G 2014 Cooperative motion of active Brownian spheres in three-dimensional dense suspensions Europhys. Lett. 105 48004
Zöttl A and Stark H 2013 Periodic and quasiperiodic motion of an elongated microswimmer in Poiseuille flow Eur. Phys. J. E 36 1
Zöttl A and Stark H 2014 Hydrodynamics determines collective motion and phase behavior of active colloids in quasi-2D confinement Phys. Rev. Lett. 112 118101