Colloidal Active Matter Mimics the Behavior of Biological Microorganisms—An Overview

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This article provides a review of the recent development of biomimicking behaviors in active colloids. While the behavior of biological microswimmers is undoubtedly influenced by physics, it is frequently guided and manipulated by active sensing processes. Understanding the respective influences of the surrounding environment can help to engineering the desired response also in artificial swimmers. More often than not, the achievement of biomimicking behavior requires the understanding of both biological and artificial microswimmers swimming mechanisms and the parameters inducing mechanosensory responses. The comparison of both classes of microswimmers provides with analogies in their dependence on fuels, interaction with boundaries and stimuli induced motion, or taxis.

1. Introduction

Life is a non-equilibrium state of matter which requires constant energy throughput for its maintenance. Living matter achieves complex structures and functions through the assembly of materials and dissipative processes. Looking at nature, we discover an incredible variety of different material properties, colors, shapes, and functions. To deduce general rules about the working principles of life, active matter physics investigates and classifies analogies between living and non-living objects.

Hanczyc defines life as a conjunction between a body that distinguishes the "self" from the environment, the ability to keep a metabolism, which is the process that converts resources from the environment into building blocks and provides energy, and the capacity to pass on some form of inheritable information to the next generation.[1] The creation of artificial life—able to replicate these behaviors—is extensively studied with droplets, vesicles,[2] and DNA nanotechnology.[3] However, these exciting approaches belong to synthetic biology and are reviewed in detail in other excellent reviews.[4]

While bio-inspiration has long been a driver for game-changing developments such as airplanes, submarines, radar, and water-repelling surfaces, on the small scale we see yet relatively few such developments.[5] There are fascinating micro-organisms that have evolved over billions of years, and over the course of this process they managed to adapt in different environments. The integration of living beings into their environment is a dynamic process that requires reaction and adaptation to external conditions and stimuli; it is all the more impressive, therefore, that some bacteria have adapted to water and land, but so-called thermo- and extremophiles have even adapted to survive the harshest conditions. Potential uses for smart small scale devices are plentiful, and range from drug delivery to sensing and environmental remediation, with specific literature available on all of these.[6–8] The first step is often assumed to be the ability to sense certain physical or chemical changes in the surroundings, and then evaluate which condition is more favorable and adapt accordingly. Artificial micromotors mimic biological microswimmers (**Figure 1**) in a fully synthetic way, giving microdevices motility, previously the attribute of living systems. Due to the small scale of these devices, their sensing and signal processing capabilities are very limited; yet still, several resemblances with living microswimmers have been observed and studied, and often impressive similarities or even additional understanding can be found. The goal of this review paper is to summarize recent progress in this area, and to give insight into the physical backgrounds of such biomimetic behaviors.

2. Comparison of Biological and Synthetic Active Matter

Biological microorganisms, often referred to as "microbes," are a highly diversified collection of living entities from all three branches of the tree of life: Bacteria and Archaea, which are

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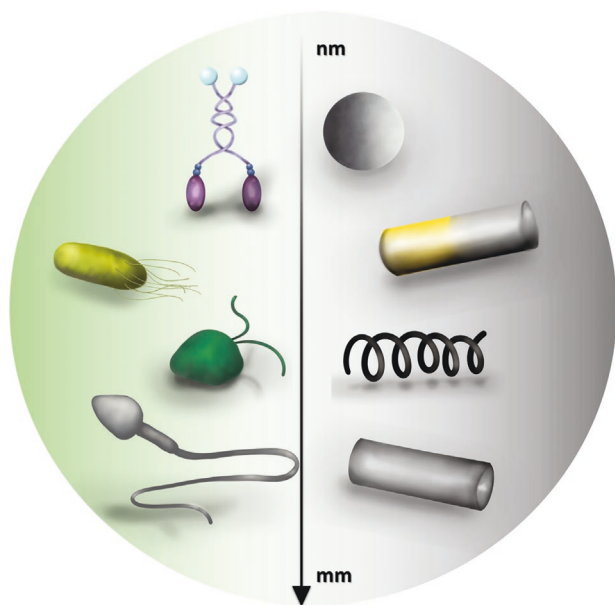Edgbaston, Birmingham B15 2TT, UK

Figure 1. Different biological (left side: protein motor, bacterium, algae, and sperm) and artificial (right side: Janus colloid, bimetallic rod, helical swimmer, and catalytic microtube) microswimmers that can be found from the nano to the microscale.

only found on the microscale, as well as many species from the third domain Eukaryota. Although viruses are in most definitions not alive, they are sometimes classified as microbes, but there is more specified literature available to explore this terminology.

In this micro-universe, many of the individual entities have the ability to displace themselves in liquid environments, and can therefore be referred to as *microswimmers*. This incredible variety of entities with different materials, colors, shapes, and functions, makes a generalization intricate. The probably most commonly-studied biological microswimmers include the male parts of reproductive cells, or spermatozoa, often many tens of micrometers in size. Different animal species present distinct shapes and properties, but most share the flagellated nature of their gametes.

Algae can exist as individual or multicellular colonies, ranging from fractions of micrometers to meters. Many of the unicellular microorganisms are motile, to optimize their position respective to sunlight, but even some algae colonies also have motile properties.[9] Smaller microswimmers are often bacteria, which rely on a flagella or cilia mediated swimming mechanism.[10]

On the other side, a variety of artificially moving systems have been developed over time, which are becoming more and more sophisticated and new functionalities and capabilities are being incorporated. To keep this review succinct, we will limit this review to phenomena observed on individual swimmers, while collective interactions and communication will be briefly mentioned in the outlook.

2.1. Physics of Microswimmer Flows

When considering biomimicry in colloidal active matter, it can be helpful to examine the fluid flows that biological and arti-

ficial microswimmers generate. When doing so, it is instructive to think about simple representations of the swimmers in terms of point forces, torques, and stresses, driving the flow. Since microswimmers are very small, inertia in the fluid is negligible. As such, the equations governing fluid flow are linear, and we can simply add up the flows generated by these forces, torques, and stresses, to get a good representation of the overall microswimmer flow.

Consider a neutrally-buoyant body of a microswimmer, comprising an inactive body (one sympathizes) being propelled forward by a beating flagellum. The flagellum exerts a backward force on the fluid, and the body is moved forward at a velocity such that the drag force on the body equals the propulsive force. Far away, the microswimmer's body looks like a point force driving flow forward (given by the Stokeslet tensor), while the flagellum looks like an equal force pointing in the opposite direction, at roughly the same location. The resulting fluid flow far from the swimmer is effectively that driven by a force dipole (given by the Stresslet tensor).

If the propulsive flagellum is behind the inactive body, flow is drawn in radially toward the microswimmer, and pushed out at either pole. This is known as a "Pusher" flow field, as shown in (**Figure 2**, top left). If the propulsive element (flagellum) is instead in front of the dragging body, the far-field flow is reversed, and the swimmer is a "Puller" (Figure 2, top right). Because of the direction of this flow, pushers, such as mammalian sperm, will be attracted to walls and follow boundaries closely, whereas pullers will not. Similar considerations apply to colloidal active matter (Figure 2, bottom). A Janus particle may have its dominant propulsion at the back, and drag at the front, resulting in a pusher flow, and would thus tend to interact with the environment more like a sperm—for instance being attracted to boundaries. A Janus particle with dominant propulsion on the front hemisphere would act as a puller—so that somewhere between pusher and puller lie neutral designs that have even more rapidly decaying flow fields.

While this fluid flow is a powerful tool for understanding a range of biomimetic behaviors in active colloids, there are two complexifying factors that are worth noting (**Figure 3**). First, biological microswimmers are typically powered by beating filaments, so that interactions between the filament and the environment deform the filament, changing dynamics (for instance in scattering off surfaces). Furthermore, the microswimmer can actively control this elastic deformation and modulate its beating, for instance to swim in a new direction. With a few notable exceptions, the majority of experimentally-realized active colloids are rigid particles. Second, active colloids are dependent on harnessing fuel in their surroundings in order to self-propel. The fluid dynamics of this fuel then becomes intrinsically linked to the propulsion generated, which can change for instance in the presence of boundaries in a passive manner. Incorporating elastic deformations, on the other hand, into the study of active particles, is a relatively new but exciting area of research.[11–13] The emergent behavior of active colloids is thus a complex interaction of solute, flow, and environmental interactions (Figure 3), where solute dynamics act in a way as a proxy for tail beating, which allows for the wealth of complex biomimicking behaviors we will now describe.
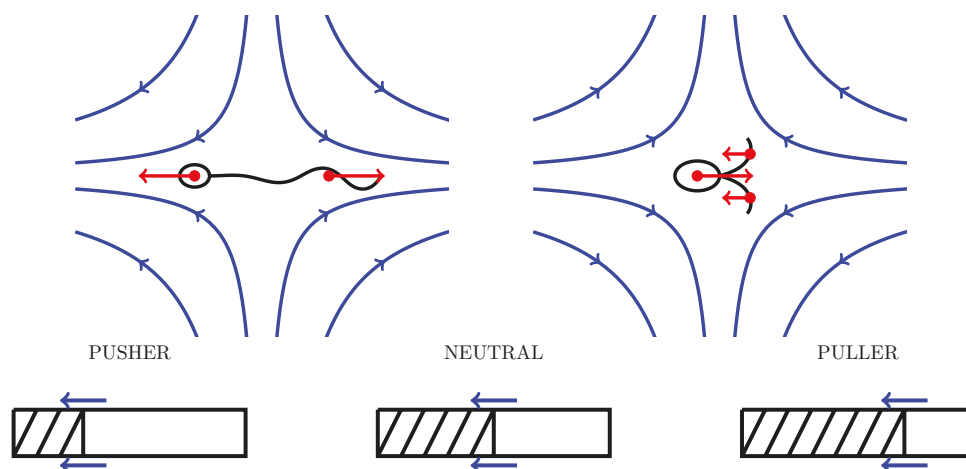
Figure 2. Top left: Human sperm acts as a pusher, generating extensional flow fields that are drawn in radially and pushed out at either pole. Top right: Puller swimmers, such as Chlamydomonas Reinhardtii, generate the opposite flow. Flow fields shown in blue, swimmers in back, point force representations in red. Bottom, active colloids, too generate their main propulsive flows at different portions of their bodies, and may be pushers, pullers, or neutral (force quadrupole) microswimmers, depending on their geometry and chemical patterning.

2.2. Fuel Dependence

For biological microorganisms, a lack of nutrients can be equated to running out of fuel. Despite the complex dependencies on a variety of factors (e.g., different micronutrients and a balanced composition of the medium), a general lack of individual nutrients has negative effects on well-being, and deprivation of nutrients is known to cause starvation (:-/) for many species (**Figure 4**).[14] To prevent such effects, organisms move either toward food sources or forage for prey, resulting in intricate behaviors that will be discussed in Section 2.4.4. These observations get even more complicated for mixotrophic organisms, that is, cells that can derive a certain part of their metabolic needs from a photosynthetic route.

In artificial microsystems, the connection between fuel availability and resulting speed is much more immediate. This connection has been well understood for a long time,[15] and confirmed for many different systems.[16,17] The correlations between fuel concentration and swimming speed in catalytic systems were found to frequently follow Michaelis–Menten dynamics, which are widely known from enzyme kinetics. Since a dependence on the saturation of catalytic spots with increasing fuel concentration is observed and limits the maximal velocity after a critical concentration, this model often fits the observed fuel-speed dependencies.[18] This behavior originates from the (enzymatic) reaction kinetics and is also observed in molecular motors.[19] However, not all of the systems where a fuel concentration dependence was imminent were of catalytic nature. For example in galvanophoretic micromotors, the peak speeds correlate with noble ion concentration,[20] while in hydrogen forming micromotors, where no clear "fuel" can be identified, a dependence on the medium is recorded, but not directly correlated.[21,22]
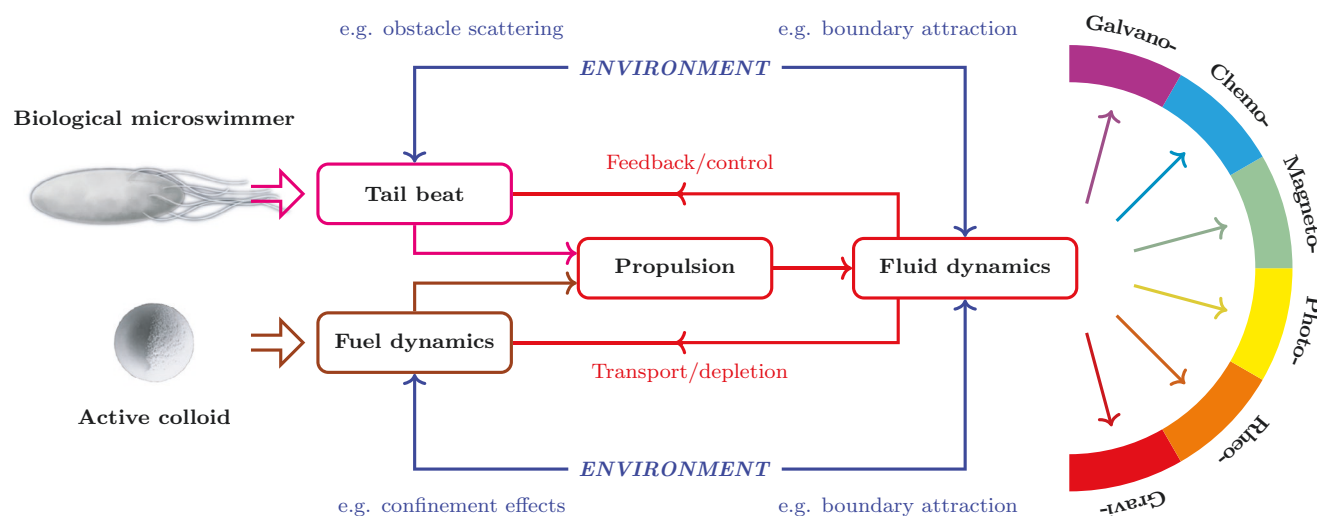

Figure 3. The multiphysical interactions of active colloids are remarkably similar to that of biological microswimmers, providing a means to examine biomimicking behaviors. These interactions give rise to a panoply of emergent behavior, such as the taxis in the right of the figure, which are described in this paper.
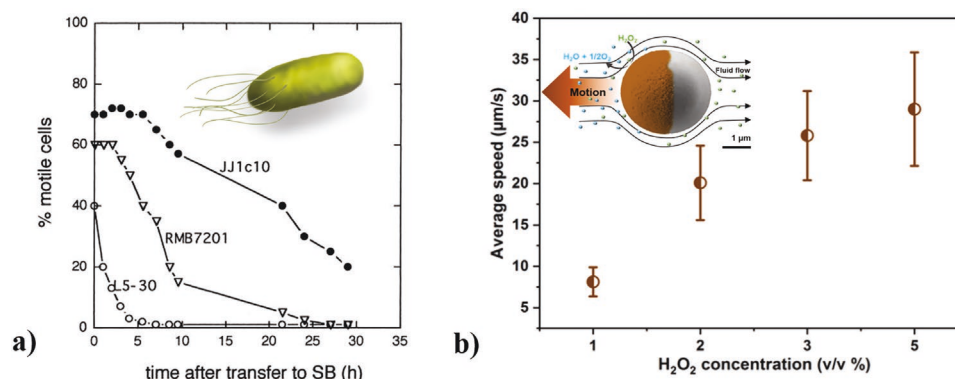
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Figure 4. a) Motility changes in different strands of *Rhizobium meliloti*, after transferring them in a media deprived of available nutrients. Reproduced with permission.[14] Copyright 1998, American Society of Microbiology. A similar response by b) Cu@SiO$_2$ Janus microswimmers which decrease in speed at low H$_2$O$_2$ concentration. Reproduced with permission.[17] Copyright 2022, American Chemical Society.

An additional remark concerning the efficiencies of these entities: While for entire organisms, the energy efficiency is rarely considered because it is an immensely complex construction, for active colloids the nominal efficiency can be calculated by relating the power input and output. This calculation was established by the Mallouk group early on,[23] but it is implemented scarcely. Even though the interest in such values is high and the power output can be obtained readily from velocity measurements, the power input is difficult to quantify. Generally, the efficiency values obtained for artificial systems is very low,[17,20,23] while biological nanomotors such as protein motors typically show very low energy consumptions.

2.3. Behavior in Complex Environments

Since the real environments of biological entities are rarely as sterile and simple as in lab settings, the observation of behaviors in more complex environments is important. The separation of individual components of such natural environments facilitates both experimental observation and the isolation of factors impacting microswimmer behavior. This separation benefits physical understanding and modeling of these systems. Individual factors influencing the environment include, for example, the presence of surface modifications, polymer content in the medium changing the viscosity, local temperatures or osmotic pressures changes, among several others.

2.3.1. Interactions with Walls

An observation that got much attention from biologists and physicists alike, is the fact that the random-walk trajectories of motile microswimmers are strongly modified by the presence of a substrate.[24,25] This interest originates partly because of the fascinating hydrodynamic phenomena leading to this behavior as well as the biological relevance associated with boundary interactions[26] and because wall interactions can pave the way toward biofilm formation.[27,28] It was first observed by Rothschild in 1963 that bull sperm aggregated near boundaries.[29] This observation inspired devices to control the trajectories of sperm for

potential in-vitro fertilization applications over a decade ago,[24] but looking further at applicability, the behavior close to boundaries is relevant for migration of pathogenic bacteria on surfaces and biofilm growth. An early study on this behavior numerically modeled the flow field via distributions of fundamental Stokes flow singularities along the surface of the microorganism,[30] and obtained circular trajectories with diameters around 10 μm. Later, Lauga et al., proposed a simple analytical model based on modeling the bacterium as a combination of a force dipole and a torque dipole, adding fundamental understanding. In general, bacteria are propelled by one ~O or multiple ≈O rotating flagella, which is causing a forward drift and a constant rotation along its swimming axis. Compared to a bacterium swimming in a bulk fluid, in the vicinity of a wall both the cell body and the helical bundle contribute to a rotation of the bacterium around the *z*-axis (see **Figure 5**a). The cell body near the surface experiences a net viscous force in *x*-direction when rotating. The wall induces a net force in *x*-direction on the flagellum, and its helical shape causes the local drag coefficient to be larger for parts of the helix that are closer to the substrate, rotating the entire cell clockwise (around the *z*-axis). The observation that the swimming direction of Escherichia coli (*E. coli*) cells is always clockwise, near planar glass surfaces[31] explains because the flagellar bundle rotates counter-clockwise and consequently, the cell rotation is clockwise.

The analogue of the modified swimming trajectories known for stresslet-like swimmers, like sperm cells[24,39] and also bacteria,[33] was found to be a stable swimming orientation for active colloids.[36] The orientation parallel to the motion vector of the particles results from complex interactions of the chemical and hydrodynamic fields, produced by the active swimmer.[40] This behavior and even the swimming angle were found to be surprisingly constant, even using different materials and different sources of propulsion.[20] Inspired by this reproducible behavior, the interactions with *side walls* were tested and found to follow the same patterns,[36] enabling the reliable guidance of particles along predefined pathways.[41] This principle is not unknown in nature, even nano-scale protein motors use microtubuli as guiding pathways to overcome Brownian motion.[42] Bacteria were found to swim faster when confined between two side walls[43] and completely crowded environments were shown to affect their scattering behavior and overall trajectories.[44,45] Reproducing such an
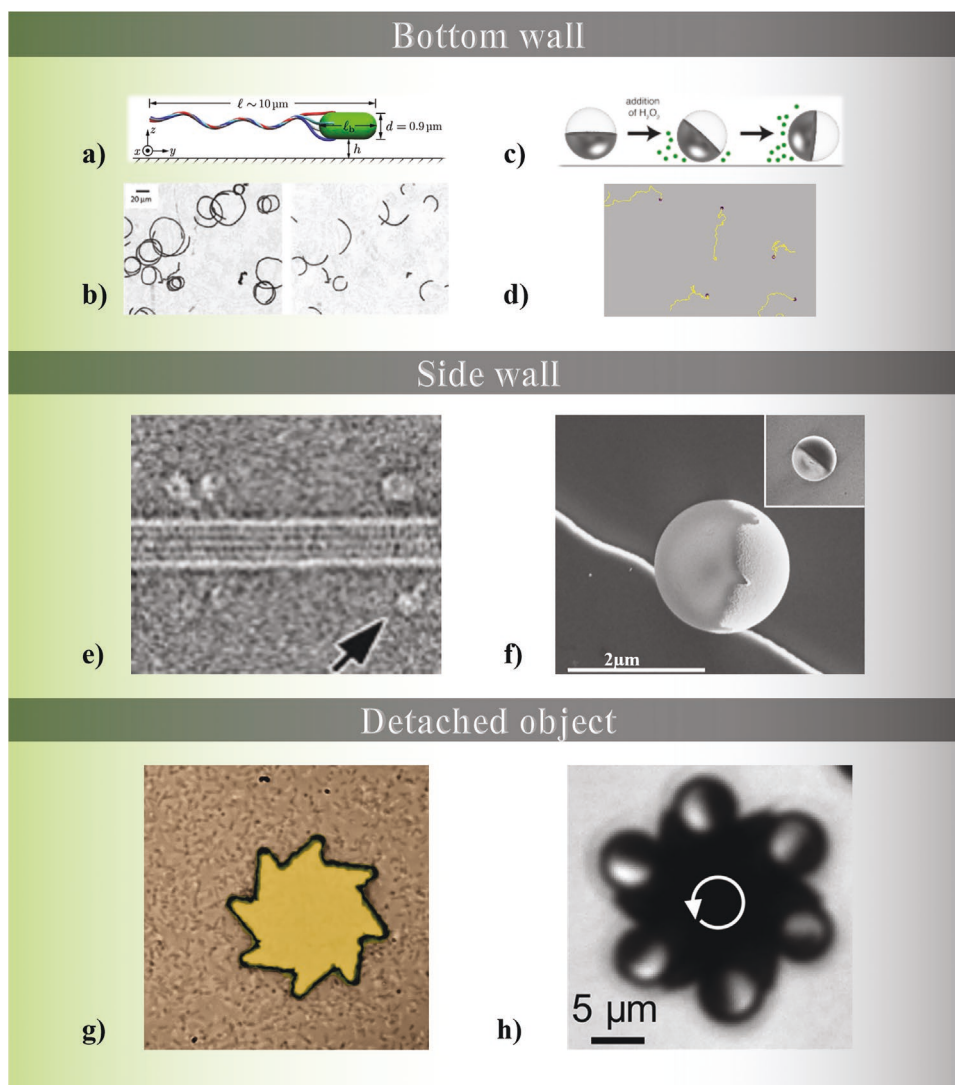
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Figure 5. Biological and artificial microswimmer present similar interactions with surfaces or walls. a) A model of the bacteria *E. coli* near a bottom surface, where b) it tends to swim in a circular trajectory. a) Reproduced with permission.[32] Copyright 2005, Nature publishing group. b) Reproduced with permission.[33] Copyright 2015, Nature publishing group. c,d) Pt@SiO$_2$ Janus particles orientation when swimming near a bottom surface. Reproduced with permission.[34] Copyright 2006, Cell press. As an example of a biological microswimmer interaction with a side wall case, e) a motor protein walk from the plus to minus end of a microtubule, is observed in a Cryo-electron micrograph. Reproduced with permission.[35] Copyright 2016, Nature publishing group. Artificial microswimmers present a similar response, f) a scanning electron micrograph shows a Pt@SiO$_2$ Janus particle adapting a walking orientation parallel to the side wall. Reproduced with permission.[36] Copyright 2016, Nature publishing group. Microswimmers can interact with a detached object, an example of this is when a micro-gear is present. g) Different gear shapes can rotate clockwise due to a bacterial driven movement (courtesy of Prof. Roberto Di Leonardo).[37] Copyright R. Di Leonardo. h) A stable rotating motor can also be achieved when a gear is surrounded by self-assembled Janus particles. Reproduced with permission.[38] Copyright 2015, Wiley.

experimental setup for artificial active matter is complicated by several factors, so there is no equivalent report yet, but pathways toward such observations have been reviewed by Xiao et al.[46]

These observed interactions between active matter and side walls have been proposed[48] and adapted to propel larger structures using living active matter.[49–51] DiLeonardo et al. engineered gear structures to self-assemble motile bacteria and initiate the rotational motion of the structure.[38] To increase the reproducibility and lower the associated randomness, a similar approach using Pt@SiO$_2$ Janus particles led to steady unidirectional rotation when a well-defined number of micromotors

self-organized in the gear in highly ordered configurations.[39] Both approaches show that manipulation and transport of micro-objects can be achieved with surprising precision using biological and artificial active matter and we envision more frequent combinations with micro-engineering.

2.3.2. Swimming in Highly Viscous Environments

Starting this discussion, we should explicitly define the term "viscous," or dominated by viscosity, which is ambiguous on

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the microscale. It is widely known, that the motion at small Reynolds number is dominated by viscous forces, even in water. This section is specifically considering fluids in which the magnitude of internal friction is increased compared to water, frequently by addition of polymers or macromolecules. Among different microorganisms, different probabilities to encounter environments with increased viscosities prevail: algae for example live mostly in aqueous environments, which rarely contain thickening agents like polymers. However, it is straightforward to imagine that the viscosity of a solution affects the flagellar beating patterns of small cells or organisms, as Woolley and Vernon demonstrated for sea urchin sperm[51] and was later observed for *Chlamydomonas reinhardtii* algae by the Arratia group.[52] The impact is likely to be affected by mechano-sensory responses of the cell as well as responding to the increased drag the swimmer experiences. This combination seems to cause a repulsive effect on Chlamydomonas, which leads to the occurrence of scattering patterns when in contact with a medium of higher viscosity.[53] From the theoretical side, there are several models that can be used to explain propulsion in high-viscosity media.[54,55] Two specific works can be related to these findings, for example, Liebchen et al. investigated the influence of body shapes. They found that an imbalance of the viscous forces can lead to effects that resemble the above-described behavior.[56] Interestingly, the size factor that separates algae from bacteria, has an immense impact on the interaction with polymeric, or viscous media. For several types of bacteria, the swimming speed was counter-intuitively reported to increase with viscosity in increased shear viscosity.[57–63] A first attempt to interpret this behavior by Berg and Turner ascribed this to the gel-like behavior of the network formed by the polymer chains.[58] However, depending on the specific polymer, its behaviors, and effects on the biological entities, this behavior can be weak[64] or even absent as experienced for specific smooth-swimming *E. coli*.[60,63] A recent work looked in very much detail at the interactions between *E. coli* and colloidal obstacles, concluding that it might actually be path-straightening, instead of polymer dynamics that cause the speed enhancement.[65] Additionally, the variety of experienced viscosities, such as different Newtonian fluids, shear-thinning, and viscoelastic media can also lead to many specific behaviors, with one example being *Heliobacter pylori*, a sometimes pathogenic bacterium that causes gastritis, ulcers, and possibly stomach cancer. Its spiral shape has evolved to penetrate the mucus linen that covers the stomach. To increase its motility, it makes use of an enzyme that locally lower the viscosity by degrading the mucus, leading to enhanced propulsion. The Fischer group also presented a fully synthetic bio-mimicking strategy, where magnetically driven nano-helices are coated with urease to locally degrade the gel-like environment.[66]

Since bacteria are very small, the length scale of this flow dynamics is comparable to the length scales of some polymers, which is very interesting from a theoretical standpoint. Since the mathematical representation of a polymer network around a bacterium has to be drastically simplified, different approaches defined two areas with specific viscosities in a tubular vicinity of the swimmer and the bulk, which resulted in an explanation of the observed behavior.[60,68] A different Ansatz was followed by Zöttl et al., who assumed that the increase of swimming speed in a viscous polymer solution is mainly due to an apparent slip caused by a non-uniform distribution of polymers in the vicinity of the bacteria, resulting in a reduction of flow resistance.[63]

Larger microorganisms, for example, *Caenorhabditis elegans* and trypanosomes also frequently encounter high-viscosity environments. As a typical soil organism, *C. elegans* shows improved propulsion properties in wet granular systems.[68,69] Trypanosomes evolved to switch between body fluids (blood, lymph, and spinal fluid in humans, insect guts, etc.) and were found to adapt their mode of motility to the physical properties of their environment.[70–72] A biohybrid microswimmer consisting of a flexible polydimethylsiloxane (PDMS) filament driven by cardiomyocites exploits viscous effects to create a non-reciprocal motion for propulsion.[73] On the other side, most synthetic microswimmers are mechanistically too simple to benefit from such intricate effects. It was found that micrometer-sized Janus particles and tubular swimmers experience drag-related speed reductions when swimming in viscous media.[64,74,75] An interesting effect, that is frequently overlooked in physical considerations, is the influence of polymers on the catalysts that create flows for propulsion, which has no direct counterpart in biological systems, but the toxicity that the polymer molecules might have on cells shows certain similarities.[64]

2.4. Taxis

Stemming from the Greek $\tau\alpha\xi\iota\sigma$, which means order or arrangement, the term taxis is used in general to describe a movement in response to a stimulus, directed toward or away from the source of the stimulus. A related term is "kinesis" (Greek $\kappa\iota\nu\eta\sigma\iota\sigma$ = motion), where the positional change upon exposure of a stimulus is non-directional, and the term "tropism"(Greek $\tau\rho\sigma\pi\sigma\sigma$ = a turn, way) where the response could be growth or reorientation, but does not include displacement. Tactic behavior is emerging as one of the most exciting features in artificial active matter;[77] when swimming in different environmental conditions, artificial microswimmers presents similar behavioral response than the ones found in nature (Figure 3).

Subclasses of tactic behavior are typically indicated by prefixing the stimulus causing the motion. Here, we only limit to these that have been attempted or achieved in a biomimetic fashion. To continue the thoughts on viscosity, we start by discussing viscotaxis, or the movement directed by viscosity.

2.4.1. Driven by Viscosity Gradients: Viscotaxis

Liebchen et al., theoretically predicted the response to viscosity gradients.[57] Similarly, Datt and Elfring demonstrated via hydrodynamic considerations that the response of a microswimmer to a viscosity gradient depends on its swimming gait, and that different gaits can lead to negative or positive taxis in viscosity gradients, that is viscotaxis.[78]

Due to the experimental difficulty of establishing precise viscosity gradients, the experimental results here are limited.

Nonetheless, this phenomenon is extraordinarily relevant to applications, since biological fluids such as physiological mucus, synovial fluid, and saliva are not only highly viscous but also have viscoelastic properties and environments are often characterized by in- or decreasing viscosity.[79] For spermatozoa, it is well known that a combination of different factors, such as the flow and (to a lesser extent) viscosity, in the female genital tract (see also Section 2.4.2) guide and select the best, "fittest" sperms toward the egg. Other possibly contributing guiding mechanisms are considered to be boundary following behavior and possibly also chemotaxis in the vicinity of the egg. In isolated experiments, both characteristic parameters, the curvilinear velocity, and straight-line velocity decrease when the sperm swim in highly viscous fluids, regardless of their viscoelastic characteristics. At equivalent viscosities, non-Newtonian behavior of a fluid seems to enhance the swimming speed compared to Newtonian one.[80–82] In comparison, biohybrid microswimmers like spermbots, that is, sperm cells loaded with artificial components, behave similarly in viscoelastic fluids, which implies the load does not change the swimming pattern significantly.[82] Even though sophisticated microfluidic setups are being used to study viscosity and flow-related phenomena,[83] the development of suitable technologies to establish controlled viscosity gradients with adjustable stiffness remains a challenge.

2.4.2. Response to Flowing Media: Rheotaxis

Rheotaxis or movement with respect to a fluid flow is a well-known phenomenon in several fish species, with salmon being probably the most famous example.[84] Biologists assume that this behavior is caused by sensorial responses, including visual, tactile, and position stimuli. While sensory information has to be internally processed in fish and this is hardly possible in single cellular entities, such as spermatozoa, a purely physical origin is assumed.[85,86] In sperm navigation, it is known that many physicochemical cues guide these biological microswimmers and fluid flow from the oviduct, leading to rheotactic navigation is crucial (**Figure 6**).[86] The rheotactic response was known to be consistent with fluid mechanics modeling for

some time, but there was no direct proof that the dominant mechanism was not mechanosensoric. In 2014, Kantsler et al. used microfluidics to study and model the response of spermatozoa to different flows and shear rates in two geometries, concluding that rheotaxis is a passive and shape-dependent mechanism.[87] This hypothesis was later reinforced by measuring the bending of the sperm flagella and the Ca_2^+ levels, which confirm a purely physical phenomenon. Also, bacteria, such as *E. coli* can exploit hydrodynamic interactions to cause upstream motion.[87,88] The hydrodynamic phenomenon is now assumed to be caused by anisotropy in shape, giving rise to the so-called weather-vane-mechanism.[16] Close to the surface the swimmer body experiences an attraction to the substrate, while the tail extends away from the surface, into the faster fluid flow, resulting in a downstream viscous drag. The resulting torque aligns the swimmer upstream.

Until recently, this was assumed to be a general rule, guiding the interaction with the flow, since for artificial microswimmers upstream motion had been confirmed for not fully axisymmetric systems: Palacci et al., investigated light-activated hematite cubes embedded in a polymeric sphere in externally imposed flow and found upstream motion,[90] which was also confirmed for bimetallic rods[91–93] and active droplets.[94,95] Theoretically, positive rheotaxis of a spherical microswimmer exposed to Poiseuille flow was predicted to have an oscillatory nature in a capillary,[96] while Uspal et al. found steady upstream swimming near a planar surface. The simple microfluidic implementation and control of externally applied flows enabled the experimental verification of the response of spherical microswimmers.[98] Since these Janus particles do not fit the weather-vane-geometry, the occurrence of "cross-stream-migration" instead of positive rheotaxis was not too surprising. When exchanging the catalytic material to Cu, the behavior changed drastically: The swimming direction inverted and the rheotactic behavior changed to the positive rheotaxis.

2.4.3. Magnetotaxis

Magnetotaxis is defined as the orientation and movement of living entities in a magnetic field, which is most frequently
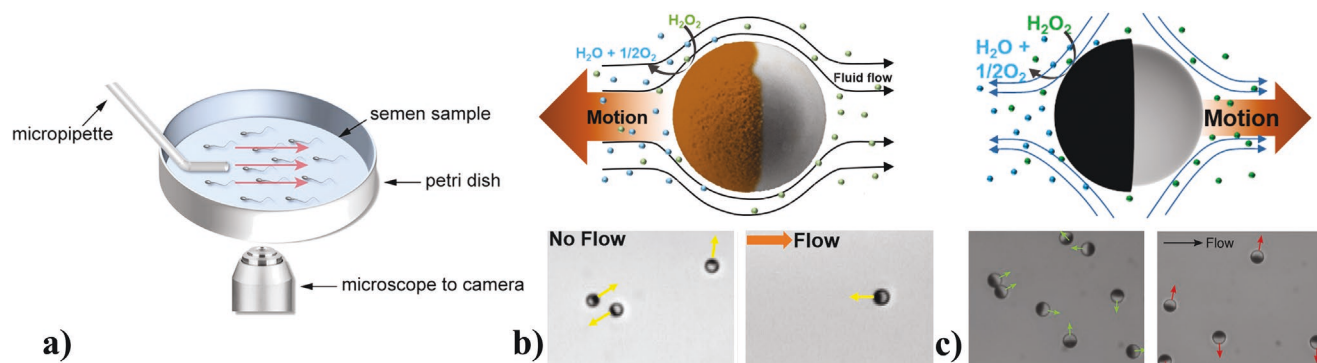

Figure 6. Biological and artificial micromotors frequently respond to flow. a) Schematic representation of experimental setup to evaluate sperm rheotaxis, the fluid flow direction inside the petri-dish is indicated by arrows. Reproduced with permission.[86] Copyright 2016, Springer Nature. b) In artificial microswimmers different behaviors have been observed: Cu@SiO$_2$ Reproduced with permission.[17] Copyright 2022, American Chemical Society, and c) Pt@SiO$_2$ Janus particles without and with flow. Reproduced with permission.[90] Copyright 2018, AAAS.

encountered in magnetotactic bacteria and used to navigate along geo-magnetic lines.[99] Mechanistically, a specialized organelle is used to detect the fields, which consists of a membrane intracellularly enclosing magnetic particles (mostly magnetite Fe_3O_4, but also iron sulfide has been reported[100]), the so-called magnetosome. The ancient process that is required to form such constructs is named "biomineralization" and the required coordination is at the focus of many ongoing research programs. Contrary to the evolutionary origin of the magnetosome, the physical mechanism of magnetotaxis has been understood rather quickly: the microorganism contains a linear organelle, which acts as a dipole within the cell and orients it when placed in a magnetic field, following the field lines. Motility itself is caused mostly by a flagellar mechanism, and Lins de Barros et al., found that the swimming speed first increases and then plateaus with increasing magnetic field strength. Whether the magnetization is parallel or anti-parallel to the swimming direction, depends on the sampling hemisphere of the species.[99]

Concerning artificial micromotors as synthetic analogues, magnetic properties have been used more frequently than any other guidance mechanism. One of the earliest and more sophisticated approaches was presented by Baraban et al., in 2013: they introduced a magnetic multilayer below the catalytic cap leading to an out-of-plane magnetization that enables high fidelity guiding.[101] Many different strategies followed over the years, starting from tubular microrockets,[102] magnetic particles attached to flexible biotemplates,[103] and inherently magnetic iron oxide microparticles[104] to assembled chains performing tasks.[105]

2.4.4. Chemotaxis

Migration in search of nutrients or food is one of the common survival strategies for most creatures on earth and one of the frequently encountered foraging strategies in chemotaxis, or the ordered, directed motion in response to a signaling molecule.

A first review on the early developments of bacterial chemotaxis was written by Berg in 1975, summarizing all the early migration of bacteria toward chemical cues like oxygen, light, and CO_2 and other chemicals like meat extract or asparagine.[108] In this work, he also discussed the literature that identified reasons for chemotactic behavior, being either specific receptors, a motor reflex, or the motion of the flagellum. Even though there is no clear evidence for a single specific mechanism, Berg concludes that swimming is caused by rotation of flagella; abruptly changing the direction of rotation affects the swimming path of the bacterium. This is influenced by the chemical cues the bacterium detects, but the specific coupling between receptors and flagella is yet not fully understood. More recent developments have shown that for bacteria, the underlying mechanism is based on transduction of sensed signals,[109,110] but also be a purely physical contribution might play a role.[111]

The opposite case where microorganisms migrate away from a potentially harmful chemical is termed negative chemotaxis and is just as important (**Figure 7**). While chemotaxis is generally believed to be an active sensing processes the explanations are as diverse and complex as are the various types of microorganisms. In sperm, for example, the active reorientation where sperm adjust their flagellar beating patterns has been shown for several species[110,111] and modeled.[112]

The artificial branch of the field of micro- and nanomotors, too, experienced a pronounced interest in the influence of chemical concentration fields on active motility. Chemotaxis was one of the earliest studied principles for self-propelled Janus particles and tubular micromotors,[115] but since the creation of stable gradients is intricate on the microscale, Baraban et al. used a microfluidic setup and thereby neglected the possible influence of the flow when demonstrating the migration toward the higher H_2O_2 concentration. To understand how an attraction to fuelling components is realized in artificial systems despite them lacking any complex receptors, and to disentangle and model the separate physical contributions, different chemotaxis assays have been created.[116–118] The experimental challenges on how to create a controlled and stable gradient in the vicinity of the microswimmers,[119,120] avoiding overlaying flows or capillarity has been solved recently by Xiao et al., by developing a technically refined strategy for gradient generation. Microfluidics combined with a stopped-flow technique was used to perform a chemotaxis assay with artificial Janus microswimmers.[114] The flow-based gradient generation using a pressure controller allows for more control over the linear gradient profile, its slope, and the position of the interface. Removing flows and capillary forces as a variable in the chemotactic setup ensures an unbiased observation of the purely physical contributions[121,122] to chemotactic behavior, resulting in both, positive and negative chemotaxis for $Cu@SiO_2$ swimmers in H_2O_2. Mechanistic insights were gained from COMSOL simulations, using an electrocatalytic model of the system.[17] Shortly, when the particles are aligned with the gradient, they experience equal
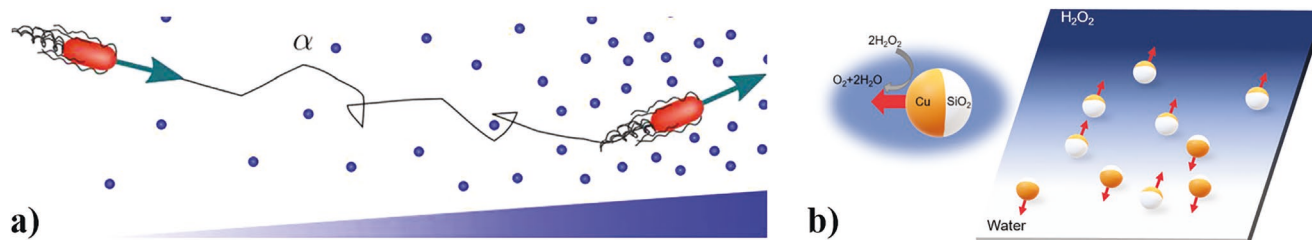

Figure 7. In a biological microswimmer, such as bacteria, a) chemotaxis can be observed by the decrease in tumbling rate and increase in the length of runs in direction of a favorable chemical gradient. Reproduced with permission.[114] Copyright 2007, Unites States National Academy of Science. A positive and negative chemotaxis can be observable in (b), where $Cu@SiO_2$ Janus particles present a biased movement up a higher H_2O_2 concentration, which is indispensable for its function as micromotors. Reproduced with permission.[115] Copyright 2022, Wiley.

propulsive forces and no torques on both sides and maintain their swimming direction. As soon as the particles experience Brownian motion and get slightly misaligned, the particles will experience uneven drag forces, inducing a torque that will reorient the particles' cap. These assumptions are not in contrast with the particle including the thin liquid layer around being force- and torque-free. Recently, similar chemotactic behavior was observed and modeled for ZnO micromotors.[123] A fuel independent influence of pH-taxis was demonstrated using a soaked cord, that locally released ions and establishes a pH gradient, but not completely excludes capillary effects.[124] A biological example where the chemoattractant is not a nutrient is *aerotaxis*, where individual organisms, such as *Chlamydomonas reinhardtii*[125] migrate in response of oxygen.

2.4.5. Phototaxis

In his treatment of the evolution of phototaxis, Jekely defines the phenomenon as "positive or negative displacement along a light gradient or vector."[126] It is especially frequent in phototrophic microorganisms, that is, bacteria or algae converting water and carbon dioxide to carbohydrates and oxygen because they require light to perform photosynthesis. Due to the different levels of complexity of the phenomenon and mechanistic details, Jekely also distinguishes between the phototaxis observed in different species. *Prokaryotes*, are typically smaller and simpler organisms and are mostly unable to sense the direction of light, for which the observed phenomenon frequently resembles the run-and-tumble-based chemotaxis. Even though bacteria are considered too small to sense gradients across their bodies and have to rely on detecting variations over time,[127] some cyanobacteria are capable of distinguishing between different wavelengths and directions of light.[128] A recent study concerning *Gonium*, a spinning algae species found intricate details how this differentiated colonial organism achieves phototaxis despite its simplicity.[129] Schuergers et al., were able to prove that the unicellular cyanobacterium *Synechocystis* can directly sense light by using their bodies as tiny microlenses,[130] a physical mechanism that is used by volvox algae, which frequently form colonies of about 500 μm size.[131] For the extremophile *Halobacter Salinarum*, living in the dead sea requires operational protection from solar UV light and relies on rhodopsin based sensors, which can cause swimming direction reversal when exposed to intense sunlight, which shows that even limiting the considerations to prokaryotes, biological variability makes understanding the mechanism of phototaxis cumbersome. For eukaryotes, even though different photoreceptors and signaling pathways are found, most organisms have a polarized body and use cilia to achieve a spiraling swimming motion. The occurrence of photo-signals modifies the beating pattern of the cilia, and thereby the swimming mode.[132]

In more recent years, a large variety of photo-driven micromotors have been presented,[90,133,134] opening the possibility to observe also light guided or directed motion, which was first shown for droplets.[135,136] Liquid crystal droplets driven helically by molecular motors were shown to respond to irradiation with re-orientation.[137] Approaches using colloidal particles were pioneered in the Bechinger group, exposing them to an inhomogeneous laser field[138] and almost contemporarily, a UV-induced interfacial tension gradient directed spiropyran terminated polymer particles toward the light source.[139] Instead of looking at static light gradients, the Bechinger group later also considered travelling light pulses, finding that their effect depends strongly on their relative speed, compared to the reorientation time of the active particles. When the particles reorient fast enough, travelling light pulses can be used to steer particle motion.[140] Photocatalytic micromotors based on hybrid structures containing carbo-nitrides were able to follow the path indicated by a light source[141] and also respond collectively.[142] TiO_2-based microswimmers are typically assumed to be self-electrophoretic, which was recently confirmed mechanistically for Janus particles but also holds for silicon nanotrees with nanowire heads. This geometry was shown to enable steering through the self-shading effect[143] which has also been treated theoretically.[144] Niese et al., studied a curious behavior that resembled "scotophobicity" or the fear of darkness using TiO_2-based particles that were covered with a magnetic layer to stabilize their position in x–y by an external magnetic field.[145] The interplay between activity stabilizing the swimming angle and Brownian motion taking over once the irradiated zone is left, led to this remarkable behavior, caused completely without sensing capabilities of the colloids. The phototactic behavior of self-thermophoretic Janus particles was studied theoretically, using mesoscale dynamics simulations.[146]

2.4.6. Thermotaxis

This case is a behavioral response to unfavorable environments with the goal of avoiding stressful conditions. It has been observed for most living organisms from bacteria[147] to sperm[148,149] and algae.[150] From a mechanistic point, there are few doubts that it is an active phenomenon, induced by sensorial signals. However, thermophoresis based on purely physical interactions has been predicted theoretically[151] and while thermophoretic micromotors have been demonstrated for a while now,[152,153] the existence of its tactic occurrence was confirmed just recently.[154]

2.4.7. Gravitaxis: The Movement in Response to Gravity

A less well-known type of stimulus, even though it is constantly present, is the gravitational field. Its ubiquity is responsible for the frequent occurrence of specific receptors, called statocysts that allow several multi-cellular, but also micro-organisms to sense the gravitational field and adapt their swimming direction accordingly.[155,156] However, a study performed on artificial systems showed, that a decentered balance point or center of mass can be sufficient to cause a gravitactic response,[157] which can also be confirmed in simple biological organisms.[158]

In conclusion, we can say that the catalogue of behaviors occurring in natural systems is extremely rich, and what we can achieve in artificial active matter yet lags behind. However, more frequently, the synthetic realization of behaviors that are observed, but not yet fully disentangled in nature, can help

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to identify important factors and contributions.[142,147] Smart task-oriented micromachines will require emulating biological behaviors, such as taxis or performance in a complex environment. A potential route to achieving more complex behaviors in micromachines is simply to add more physics into the swimmer design (Figure 3), for instance including multiple propulsion mechanisms, elastic materials, or even targeted shape-changes via responsive materials.[161] We also envision that these behaviors on the individual micromotor level will be pivotal when the collective answer of a group should be targeted. First examples of collective biomimicking behaviors have already been presented. We will introduce them briefly in the final outlook section of this manuscript.

3. Outlook - Collective Phenomena

Collective behaviors across species and scales are assumed to arise from underlying fundamental physical principles; this justified the search for common principles in organisms and active matter. Collective motion and interactions often arise spontaneously, without any external principle guiding the process. Perhaps the most prominent example where a physical model could be used to frame biological herding behavior is the Vicsek model,[160] inspired by magnetic moments depicted in an Ising model, it represents the simplest off-lattice model capable of describing a flocking state.[161] Therein, particles tend to align with their direct neighbors, leading to a transition to ordered collective motion. There are excellent specialized reviews treating various aspects of collective systems,[162] so here we will only mention a few specific behaviors that strongly resemble biological behaviors. Concerning biological macroscale systems, everybody remembers a flock of birds patterning the sky in summer, or a school of fish swimming toward bread crumbs in a pond. There have been impressive observations of related phenomena on the microscale[163] and large projects are constructed studying the transferability among species and scales and possibly, we can abstract general rules looking at synthetic systems.[164] Even if these processes are assumed to happen largely without explicit communication, or intended exchange of information among the members of a collective, information transfer and dissemination often happens through unexpected means: An impressive example is *Quorum sensing* a self-regulating mechanism in bacteria,[165,166] plants, archae and even in bacteriophages a similar process has been discovered.[167]

With the help of external computation, the Bechinger group was able to show a synthetic analogon of quorum sensing[168] which does not rely on biochemical principles, but instead on external fields. Communication between individual micromotors or groups of them, will become an increasing focus of active colloid research. Smart interaction will also require their mutual and coordinated response to external stimuli and collectively released cues. One of these responses in the biological world are *predator–prey interactions*. While the biological part includes the consumption of one species, resulting in well-predictable dynamics, with the well-known "Lotka–Volterra model" from ecological mathematics, the synthetic analogon mostly relies on chemicals released from one species, causing a phoretic response in the other. Examples include materials such as

ZnO,[123,169] TiO$_2$,[133,134,170] Ag$_3$PO$_4$,[171] and AgCl,[164] mostly photocorrosive materials that leave behind chemical cues, which can be sensed and reacted to by the other partners. There can be little doubt that, in order for artificial microswimmers to realize their full applications potential, controlling the collective behavior of swarms of active colloids to perform useful tasks will be a next critical step.

Conflict of Interest

The authors declare no conflict of interest.

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2202685 (11 of 13)

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