



More than propellers: how flagella shape bacterial motility behaviors

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Bacteria use a wide variety of flagellar architectures to navigate their environment. While the iconic run-tumble motility strategy of the peritrichously flagellated *Escherichia coli* has been well studied, recent work has revealed a variety of new motility behaviors that can be achieved with different flagellar architectures, such as single, bundled, or opposing polar flagella. The recent discovery of various flagellar gymnastics such as flicking and flagellar wrapping is increasingly shifting the view from flagella as passive propellers to versatile appendages that can be used in a wide range of conformations. Here, we review recent observations of how flagella shape motility behaviors and summarize the nascent structure-function map linking flagellation and behavior.

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Current Opinion in Microbiology 2021, 61:73–81

This review comes from a themed issue on **Cell regulation**

Edited by **Sean Crosson** and **Aretha Fiebig**

For complete overview of the section, please refer to the article collection, “**Cell regulation**”

Available online 9th April 2021

<https://doi.org/10.1016/j.mib.2021.02.005>

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Introduction

While most bacteria swim by rotating flagella, helical appendages driven by a rotary motor (Figure 1a), species differ vastly in their flagellar architectures, that is, the number, position, and shape of flagella [1] (Figure 1b). The growth cost incurred by flagellar expression [2–4] indicates that flagellation is likely subject to strong natural selection, yet an understanding of the motility behaviors that are enabled by specific flagellar architectures and their possible adaptive values is only beginning to take shape.

Pioneering work on the peritrichously flagellated *Escherichia coli* revealed that its trajectories consist of near-straight segments called runs and brief turning events called tumbles [5]. Runs are driven by all flagella rotating counterclockwise (CCW) in a bundle, and tumbles occur

when one or more flagella transiently rotate clockwise (CW). Other species achieve turns by pausing flagellar rotation [6] or desynchronizing flagellar rotation by varying rotation speeds [7] (Figure 1c). In many non-peritrichous species, however, either direction of flagellar rotation results in locomotion, and turns result from a change in rotation direction. Polar monotrichous species, which include the majority of marine bacteria, were long thought to be constrained to a run-reverse motility pattern [8] (Figure 1d). In 2011, careful observations surprisingly revealed that *Vibrio alginolyticus* actually performs a multi-step pattern where turning events alternate between reversals and turns by a much smaller angle, so-called ‘flicks’ [9••] (Figure 1e). This unexpected discovery of a novel behavior in a well-studied organism with the simplest flagellar architecture evoked a fresh look at the possible range of flagellar motility behaviors and sparked a new era of discovery.

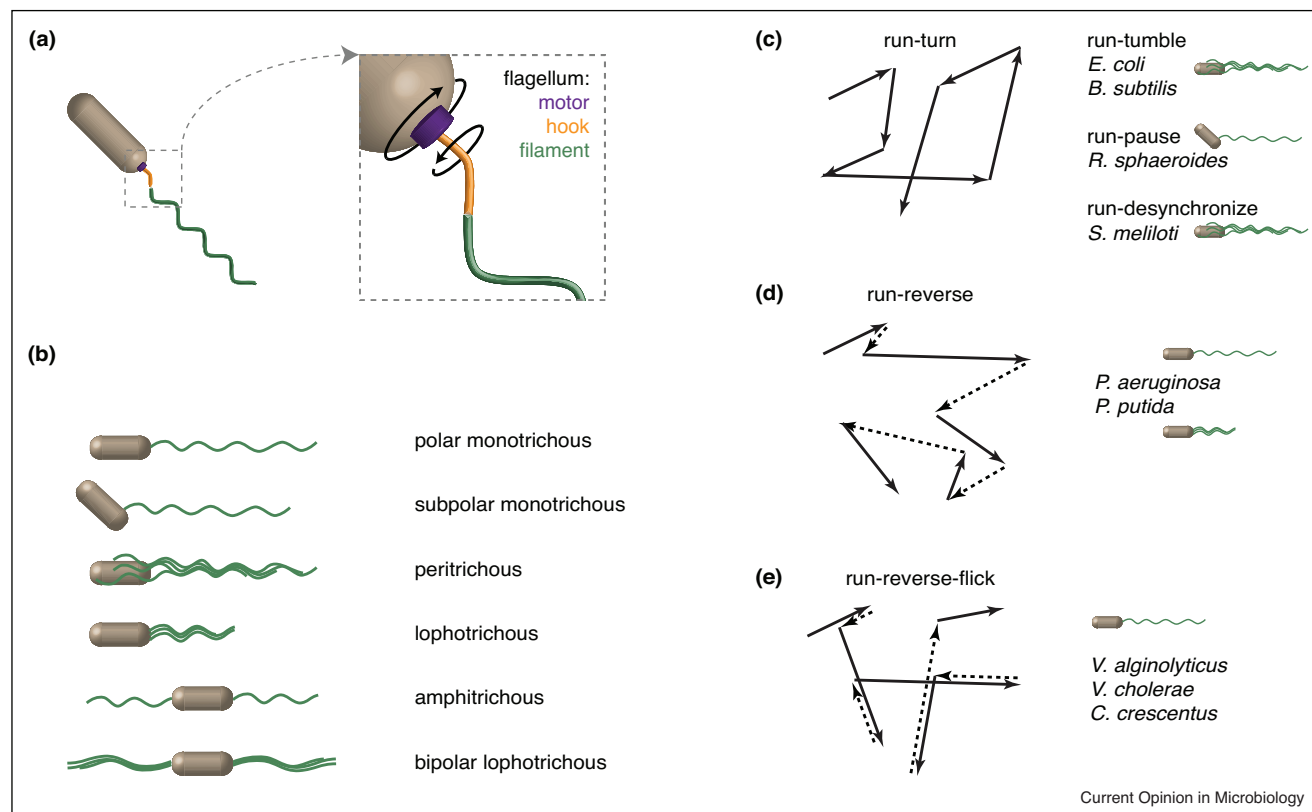
Here, we review the emerging understanding of how flagellar architectures and gymnastics shape bacterial swimming motility behaviors since the discovery of the ‘flick’ in 2011. We highlight flagellar ‘wrapping’ reported in 2017, and other recent reports of novel behaviors. We limit ourselves to motility driven by external flagella as recent reviews [10,11] cover spirochete motility driven by internal, periplasmic flagella.

Focus on the hook

Flicking has since been observed in a wide range of species with single polar flagella, including the freshwater bacterium *Caulobacter crescentus* [12], the saprophyte *Shewanella putrefaciens* [13], the human pathogen *Vibrio cholerae* (Grognot *et al.*, unpublished) and many marine bacteria [14••]. Compared to a run-reverse scenario, flicks enable the bacteria to explore new directions much more rapidly, and the strategy has been argued to enable rapid exploitation of transient resources that are typical of pelagic environments [15,16].

The discovery turned the focus to a mechanical element that had received little attention so far: the flagellar hook. The flagellar hook is a short, flexible segment of the flagellum that connects the rigid flagellar filament to the rotary motor. It is thought to act as a universal joint [17] that enables the rotary motor to transmit torque to the filament, even when their axes of rotation are not aligned. The flick revealed another role for the hook: Son *et al.* showed that flicks result from a mechanical buckling instability in the flagellar hook [14••]. When the cells

Figure 1



Basics of flagellar motility. **(a)** Flagellar motility is driven by a flagellar motor (purple), embedded in the cell envelope, rotating the helical flagellar filament (green) and the cell body against each other. The flagellar hook (yellow) functions as a universal joint that can transmit torque from the motor to the filament even when their axes of rotation are not aligned. CCW rotation (viewed from the flagellum looking towards the cell body) of a left-handed flagellum results in the flagellum pushing the cell. **(b)** Common flagellar architectures and their nomenclature. Some species can express more than one set of flagella. **(c–e)** Examples of common bacterial motility patterns and species that exhibit them. The flagellated pole is lagging during solid and leading during dashed trajectory segments.

swim backward, the hook is stretched out, but when the cell reverses direction, the hook is compressed until it buckles. The resulting misalignment of cell body and flagellum leads to the cell being pushed off course and swimming off sideways in a new direction (Figure 2a).

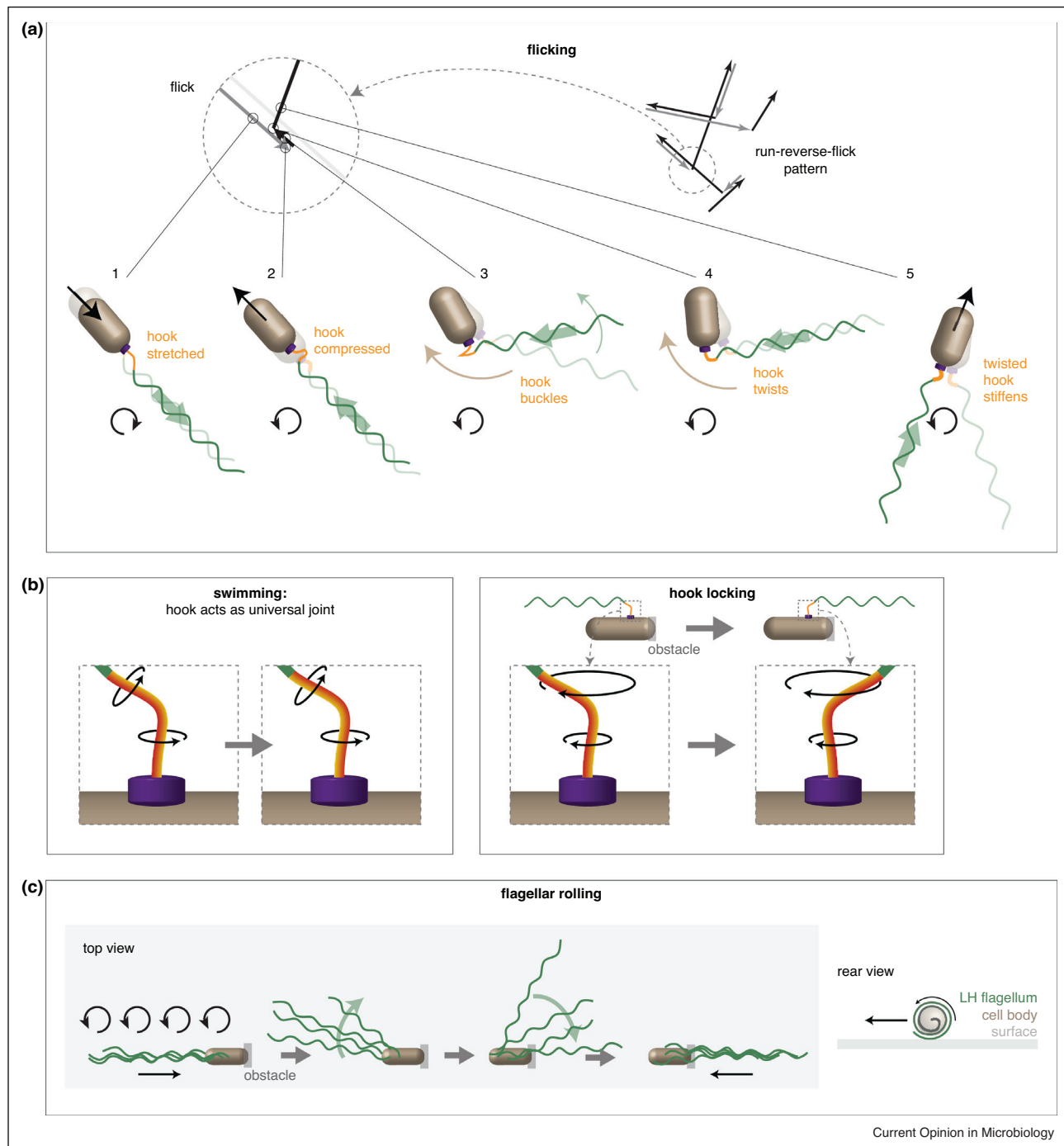
Simulations indicate that hook flexibility has opposite effects on the stability of swimming in monotrichous and peritrichous species [18,19], and recent experimental work shows that the length of the hook is likely optimized for maximal bundle stability in the peritrichously flagellated *Salmonella typhimurium* [20]. When acting as a universal joint, the elements of the hook undergo conformation changes during rotation to accommodate the orientation of the filament. By contrast, Duchesne *et al.* inferred that the hook of confined *Salmonella* cells can lock into a fixed conformation when switching to CW rotation and swing a filament around the cell [21] (Figure 2b). The observed motion looks similar to the rolling of flagellar filaments to the opposite pole of an *E.*

coli cell sandwiched to 2D as reported by Wu *et al.*, but the latter occurs via hydrodynamic interactions with one of the surfaces during continuous CCW rotation and does not require any unusual action of the hook [22] (Figure 2c). Both mechanisms enable the cell to reverse direction and escape a dead end.

Flagellar wrapping

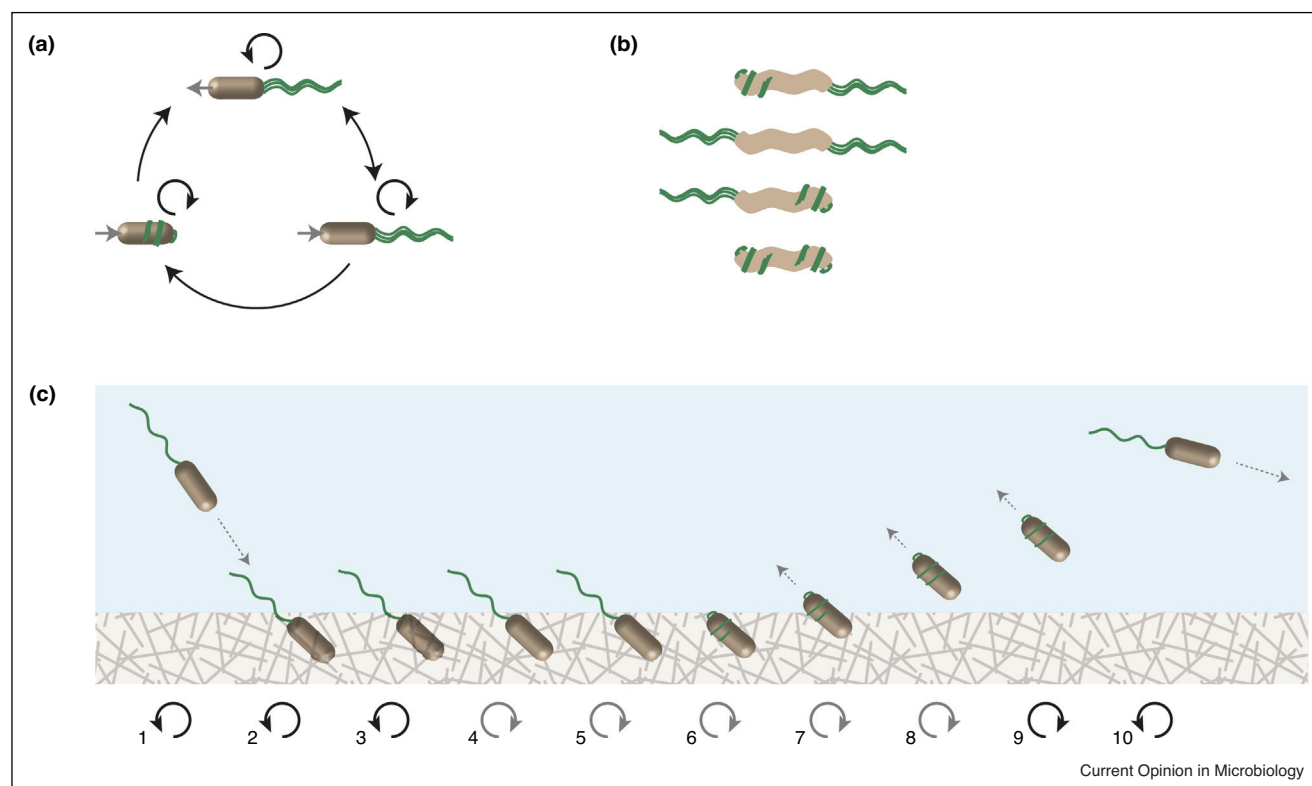
In 2017, multiple groups independently reported a new mode of motility whereby the flagellum wraps around the cell body, like threading on a screw, during locomotion with the flagellated pole leading. Kühn *et al.* observed that the polar monotrichous species *S. putrefaciens*, which normally performs run-reverse-flick motility in liquid medium [13], can wrap its filament around the cell when mechanically trapped or placed in high viscosity environments [23]. Hintsche *et al.* observed flagella pushing, pulling, and wrapping around the cell in the lophotrichously flagellated *Pseudomonas putida* [24] (Figure 3a).

Figure 2



Novel reorientation mechanisms. **(a)** The flick observed in polar monotrichous species such as *V. alginolyticus* [9[•],14^{••}]. The flagellar hook is stretched out during pulling (1), but is compressed when the flagellum changes rotation direction and pushes the cell (2). The hook buckles, producing a kink between the flagellum and the cell body (3). The flagellum keeps pushing the cell body sideways, turning it, while gaining rigidity as it is being twisted (4). The stiffened hook can then support swimming in pushing mode (5). The time between the motor switching rotation direction and the reorientation is only approximately 10 ms [14^{••}]. **(b)** Reorientation of stuck bacteria by the hook locking mechanism proposed by Duchesne *et al.* [21]. During swimming, rotation of the flagellar filament about its axis is achieved by conformational changes of the elements of the rotating hook (compression on the inner and extension on the outer side of the bend). By contrast, during the proposed reorientation mechanism, each element of the hook retains its compressed or extended conformation during rotation so that the hook's bend rotates around, swinging the filament to the other side of the cell. Elements of the hook are assigned fixed colors (yellow to red). **(c)** On a surface, *E. coli* mutants that can only rotate their left-handed flagella CCW and cannot turn during free swimming can nevertheless re-orient when encountering an obstacle by rolling their flagella along the surface to the opposite pole of the cell [22].

Figure 3



Flagellar wrapping. **(a)** Transitions between flagellar conformations observed in *P. putida* [24^{••}]. When the flagella bundle switches from CCW to CW rotation, it can pull the cell or transition onward into a wrapped state. In both cases, the cell moves with the flagellated pole leading. The wrapped state differs in polymorphic conformation from the pushing and pulling states. The flagella are left-handed in all three states but may partially change handedness transiently during the transition from pulling to wrapped [23^{••},25^{••}]. **(b)** Flagellar conformations observed in the bipolar lophotrichous *H. suis* [26]. **(c)** Wrapping may aid bacteria escape from traps. When a swimming bacterium (1) becomes trapped (2), for example, by a polymer network, such that neither pushing (2–3) or pulling (4–5) is sufficient for freeing it, escape may be facilitated by the flagellum transitioning into the wrapped state (6), removing the cell from the trap by a screw-like motion (7–9) [23^{••},30,32^{••}].

Kinosita *et al.* observed the wrapping behavior in two other lophotrichous species, *Burkholderia* sp. RPE64 and *Vibrio fischeri* [25^{••}]. Flagellar wrapping has since also been observed in the bipolar lophotrichous *Helicobacter suis* [26] (Figure 3b) as well as the amphitrichous *Campylobacter jejuni* [27]. Previous observations of a ‘parachute’ arrangement of flagella in the amphitrichous *Magnetospirillum magneticum* [28] likely also represent wrapping.

In the wrapped state, the flagellar handedness, direction of motor rotation, and direction of travel are identical to that observed for an extended, pulling flagellum [23^{••},25^{••}]. Intriguingly, wrapping decreases the free-swimming speed in aquatic environments compared to the pulling mode [23^{••},24^{••},29], but the probability of flagellar wrapping increases with the viscosity of the surrounding medium [23^{••},25^{••},26]. Cells that are trapped between two surfaces, such as glass and an agar pad, however, can free themselves by rotating the wrapped flagellum around themselves and moving without slip like

a screw [23^{••}]. Kühn *et al.* thus propose that wrapping might present a mechanism for escaping traps (Figure 3c) [23^{••},30].

The wrapped configuration is driven by polymorphic transitions of the flagellar filament [23^{••},25^{••}]. While such polymorphism also exists in flagella of uniform composition [31], wrapping requires a specific composition of different flagellins in *S. putrefaciens* [32^{••}] and *C. jejuni* [27], and many of the above species seem to encode multiple flagellins [33].

Flagellar architectures

The contrasting patterns of run-tumble motility for peritrichous species and run-reverse-flick motility for many polar monotrichous species set the stage for a more systematic analysis of the relationship between flagellar architecture and the resulting motility pattern. In particular, lophotrichous bacteria, driven by the rotation of tufts

of flagella, have received more attention in recent years. Theves *et al.* found that *P. putida* shows run-reverse motility with runs alternating between two different swimming speeds [34]. The slower speed was later attributed to the wrapped mode by Hintsche *et al.* who observed pushing, pulling, and wrapping behavior [24**]. Pulling by a flagellar bundle had also been observed in *Helicobacter pylori* [35]. The configuration had been thought to be mechanically unstable [36,37], and more recent work indicates that this may be a short-lived state in *P. putida* [29]. Lophotrichous flagella can support extremely high swimming speeds. Speeds of hundreds of $\mu\text{m/s}$ were observed in the magnetotactic species *Magnetococcus massalia* and *Magnetococcus marinus* which are propelled by two sheathed tufts [38,39], and for *Ovobacter propellens*, propelled by a bundle of hundreds of

flagella, speeds of 1 mm/s have been reported [40]. The rich space of states and transitions available to species with two sets of flagella at different positions is only beginning to be explored [26,28,38] (Figure 3b).

Some species even modify their flagellar architectures on demand. Ferreira *et al.* discovered that a range of γ -proteobacteria, including *V. cholerae*, *V. fischeri*, *S. putrefaciens*, and *Pseudomonas aeruginosa*, eject flagella under nutrient depletion [41]. Species like *Vibrio parahaemolyticus*, in turn, express additional peritrichous lateral flagella under conditions that impede the rotation of its single polar flagellum [42]. Lateral flagella can facilitate surface swarming [43], but can also increase swimming speeds in polymer solutions [44]. Bubendorfer *et al.* reported an additional role of lateral flagella in *Shewanella putrefaciens*,

Table 1

A summary of reported bacterial motility patterns and behaviors, ordered by flagellar architectures. References in the second column refer to pertinent reviews.

Flagellar architecture	Species	Motility pattern	Notes
Peritrichous	<i>Escherichia coli</i> [63]	Run-tumble [5]	Hook locking [21]
	<i>Salmonella enterica</i> serovar typhimurium [63]	Run-tumble [64]	Roll [22]
	<i>Bacillus subtilis</i>	Run-tumble [65]	Hook locking [21]
	<i>Serratia marcescens</i>	Run-tumble [66]	
	<i>Sinorhizobium meliloti</i> [67]	Run-desynchronize [7]	
	<i>Bradyrhizobium lupini</i>	Run-pause [68]	
	<i>Thiovulum majus</i>	Fast helical runs with U-turns [46]	Large cells with many flagella [46]
Subpolar monotrichous	<i>Rhodobacter sphaeroides</i> [67]	Run-pause [6]	Flagella coil during pause [6]
Polar monotrichous	<i>Vibrio alginolyticus</i>	Run-reverse-flick [9**]	Flicking [9**,14**]
	<i>Vibrio cholerae</i>	Run-reverse-flick	Fluctuating swimming speed
	<i>Shewanella putrefaciens</i>	(Grognot <i>et al.</i> , unpublished)	(Grognot <i>et al.</i> , unpublished)
	<i>Pseudomonas aeruginosa</i>	Run-reverse-flick [13]	Flagellar wrapping [23**,32**]
		Run-reverse [52]	Pauses during runs [52,55]
	<i>Azospirillum brasilense</i>	Run-reverse [53]	Pauses during runs [53].
	<i>Caulobacter crescentus</i>	Run-reverse-flick [12]	Flicks? [53]
Amphitrichous (one at each pole)	<i>Pseudomonas fluorescens</i>	Run-reverse [69]	Pauses during runs, 'flips' [69]
	<i>Campylobacter jejuni</i> [70]	Run-reverse [71]	Flagellar wrapping [27]
	<i>Magnetospirillum magneticum</i> [72]	Run-reverse [28]	Pauses during runs. Wrapping? [28]
Lophotrichous (flagellar tuft)	<i>Pseudomonas putida</i>	Run-reverse [34]	Pauses during runs [34]
	<i>Helicobacter pylori</i> [70]	Run-reverse [35]	Wrapping [24**]
	<i>Burkholderia</i> sp. RPE64		Wrapping [25**]
	<i>Vibrio fischeri</i>		Wrapping [25**]
	<i>Candidatus Ovobacter propellens</i>	Run-reverse? [40]	Tuft contains hundreds of flagella [40]
Sheathed bilophotrichous (two sheathed tufts)	<i>Magnetococcus marinus</i> [72]	Fast helical runs with sudden turns [38]	
	<i>Magnetococcus massalia</i> [72]	Straight swimming northward [73]	
Bipolar lophotrichous (one tuft at each pole)	<i>Helicobacter suis</i>		Wrapping [26]
Dual flagellar architecture: single polar + lateral	<i>Shewanella putrefaciens</i>	Run-reverse-flick [13]	Lateral flagella modify flick angle [13]
	<i>Bradyrhizobium diazoefficiens</i>	Run-reverse-flick [74]	
Magnetoglobules	isolates from the Mediterranean [72]	Run-reverse [47]	Aligned with magnetic north-south axis [47]

which performs run-reverse-flick motility powered by its polar flagellum, the additional presence of lateral flagella increases drag which decreases flick angles, resulting in a higher chemotactic speed [13].

An open question is whether and how flagella interact with each other. How lophotrichous bacteria synchronize the rotation direction of their bundled flagella is unknown. Although several studies have proposed that flagella at the opposite ends of amphitrichous cells coordinate their behavior [27,28,38,45], that notion has not been supported by a statistical analysis so far. It is also unknown how the many flagella on the large *Thiovulum majus* cells orchestrate their U-turns [46], or how the thousands of flagella that line multicellular magnetotactic bacteria, so-called magnetoglobules, coordinate their run-reverse motility [47].

Table 1 summarizes bacterial motility behaviors observed for specific flagellar architectures. Future work will reveal whether this nascent structure-function map linking bacterial flagellar architectures to the resulting motility behaviors also translates to archaea. Archaeal flagella, also called archaeella, are mechanically similar to bacterial flagella, but consist of unrelated proteins [48,49]. Initial studies of archaeal swimming behavior indicate run-reverse motility at speeds that vary from only a few $\mu\text{m/s}$ to hundreds of $\mu\text{m/s}$ [50,51]. Archaea present an intriguing opportunity to determine whether the mechanical principles that govern bacterial swimming behaviors are conserved across domains of life. Public databases collating observations such the recently established collection of physical parameters of microscopic swimmers (BOSO-Micro, <https://osf.io/4tyx6/>) could contribute to systematic investigations.

Flagellar pausing and speed variations

Pauses in swimming [34,52,53] or flagellar rotation [6,54,55] are being reported for an increasing number of species. In *Rhodobacter sphaeroides*, pauses in the rotation of its unidirectional motor drive turning events by allowing flagellar polymorphic transitions that enable a larger degree of rotational reorientation than is possible during locomotion [6,56]. The function of pausing is less clear in other species. Because bacteria infer spatial gradients from temporal gradients, a pause in locomotion should result in a decrease in information whose adaptive value is hard to fathom.

In addition, flagellar rotation speeds are variable and can even be controlled by the chemotaxis system in some species, such as *Sinorhizobium meliloti* [7] and *V. alginolyticus* [57]. Future work will need to address whether and how speed variations, pausing, and direction switching of the flagellar motor are related to each other and how they contribute to chemotaxis.

Conclusions

The recent discoveries of new motility behaviors particularly in polarly flagellated and lophotrichous bacteria complement the large body of work on peritrichously flagellated species like *E. coli*. Novel, label-free, high-throughput 3D tracking techniques [58–60] are opening up the possibility of routine characterization full 3D swimming behaviors in large bacterial populations that will enable us to increasingly fill in the map between flagellar architectures and the resulting repertoire of motility behaviors.

The last decade has revealed a versatility in flagellar functions that extends well beyond acting as simple propellers: During a flick, the alignment of flagellum and cell body is modified to facilitate a cellular reorientation — the propeller becomes a steering device. During the flagellar wrapping, the shape of the flagellar filament changes drastically and the propeller reshapes itself from a corkscrew to a threaded-screw geometry.

Some of the newly discovered behaviors only become apparent or beneficial in complex environments, such as near surfaces, in confinement, or in viscous or structured environments. While much bacterial motility work has focused on swimming behavior in aquatic environments, it is increasingly appreciated that such behavior may both vary with the environment and be adapted to specific types of habitats.

A crucial open question is whether and how many of the newly discovered behaviors contribute to chemotaxis or maybe even are controlled by the chemotaxis system. Novel high-throughput motility and chemotaxis assays [61] (Grognot *et al.*, doi:10.21203/rs.3.rs-61942/v1) may be able to help shed light on this question. In *E. coli*, information on the temporal evolution of the extracellular chemical concentration is integrated by the chemosensory system into the concentration of phosphorylated CheY ([CheY-P]), the chemotaxis response regulator. [CheY-P] binding to the motor then determines the probability of tumble-inducing CW rotation, the so-called CW bias. *E. coli*'s chemotactic strategy is widely assumed to translate to other species. Pioneering work in *V. alginolyticus* [62], however, has revealed a different strategy: instead of biasing the rotation direction, chemosensory input modifies the duration of the current rotation interval regardless of its direction. Different hardware may require different software. In *V. alginolyticus*, and likely in most species aside from peritrichous ones, both flagellar rotation directions produce locomotion. Recent work has found similar behavior also in other polar monotrichous species, *Pseudomonas aeruginosa* [52] and *Caulobacter crescentus* (Grognot *et al.*, doi:10.21203/rs.3.rs-61942/v1).

We suggest that this strategy may even be more widespread. In particular, it would resolve a conundrum in

the chemotactic behavior of amphitrichous species that have flagella at both cell poles. For these cells to move effectively, the flagella on opposite ends of the cells have to rotate in opposite directions. In the *E. coli* paradigm, however, chemotactic signals would bias the rotation direction of both flagella to favor the same state, resulting in their actions opposing each other. To explain how the two flagella instead appear to coordinate their rotation directions, it has been proposed that motors on opposite ends of the cell may be different from each other [11,27]. The conundrum is resolved, however, if we assume that *V. alginolyticus*'s chemotactic strategy applies: both flagella would be biased to retain or change their state, irrespective of its identity. Finally, we propose a unified behavioral strategy that encompasses both of the above schemes: whatever works, keep doing it!

Funding

This work was supported by the Rowland Institute at Harvard.

Conflict of interest statement

Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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