The design of bacterial flagella—part 3: motility behaviour and gear change mechanisms

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When it comes to flagella-mediated bacterial motility, flagella are more than just propellers. In part 2 of this 7-part review series, the design of bacterial flagella is discussed, including the diverse flagellar arrangements in various bacteria. These arrangements greatly influence motility behaviours of these species, as discussed here. Bacterial species use flagella in many ways (termed 'swimming modes') to move and change direction. Consideration is also given to the various gear-change mechanisms crucial for efficient motility. Flagellar motors use various gear-change mechanisms to change the motor's rotation direction, rotation speed, torque, operating range, and fuel type (for hybrid motors). Just as the design features of man-made gears point to human designers, so the design features of the gears in bacterial flagellar motors point to a divine designer.

As quoted in part 1, nothing pleased biblical creationist and father of microbiology Antony van Leeuwenhoek more than "these many thousands of living creatures, seen all alive in a little drop of water, moving among one another, each several creature having its own proper motion."[1,2] The diverse motility methods of bacteria continue to fascinate microbiologists. This paper discusses the diverse ways bacteria use flagella for motility and the various gear-change mechanisms used to regulate motor output. This paper will also highlight how the differences in the number and arrangement of flagella between species (discussed in part 2 of this 7-part series) has profound effects on their swimming behaviours. The motility mechanisms and gear mechanisms discussed in this review paper are much more advanced than the current best human-designed micro- and nanotechnology, implying these mechanisms are designed (as will be discussed in much more detail in part 7).

In the first half of this review, explanations are given concerning the diverse ways that bacteria use flagella to swim[3] and move across surfaces. In the second half, gear change mechanisms are considered that underlie how bacteria change swimming direction and maintain energy efficiency.

Swimming motility

Swimming speed varies greatly between bacterial species (e.g., 20–40 μm/s in *E. coli* and *Salmonella* vs 1 mm/s in *Ovobacter propellens*).[4]

Diverse bacterial species use flagella for at least eight different swimming modes: run, tumble, pull, wrap, over-whirl, flick, flex, and U-turn. These modes are discussed below.

Run and tumble

The two most studied swimming modes are the locomotive mode 'run' and the turning mode 'tumble' (figure 1a).[5,6] These two modes are used by bacteria with peritrichous flagella (located all over the cell body) such as *Escherichia coli, Salmonella enterica* and *Bacillus subtilis*.[7–9] When all peritrichous flagella are rotating counterclockwise (CCW), they each form a left-handed helix and come together to form a bundle that propels the cell forward in what is called a 'run' (lasting about 1 second).[10] When one or more flagella are rotated clockwise (CW), they become right-handed, typically causing the bundle to fall apart, and the cell reorients in what is called a 'tumble' (lasting about 0.1 seconds).[7,10] When all flagella resume CCW rotation, they reform a bundle at one end of the cell (can be either) and push the cell on a new run.[11]

There are rare cases of the run and tumble swimming method being used by monotrichous species (which have one flagellum).[12] In the purple bacterium *Rhodobacter sphaeroides*, tumbles are caused by the stopping of its single medial/subpolar flagellum, using a break, rather than rotation reversals (as in *E. coli*).[13–15] Stopping of motor rotation causes the filament to tightly coil and the cell to change orientation.[16]

In the plant symbionts *Sinorhizobium meliloti* and *Agrobacterium fabacearum* (formally *Bradyrhizobium lupini*), tumbling is caused by the asynchronous rotation (or stopping) of its speed-variable flagella (which always rotate CW).[17–21] These tumbles are much less vigorous than those in *E. coli*.[18]

As well as the tumble mode, peritrichously flagellated bacteria can use two other mechanisms to back out of tight spaces (see box 1).

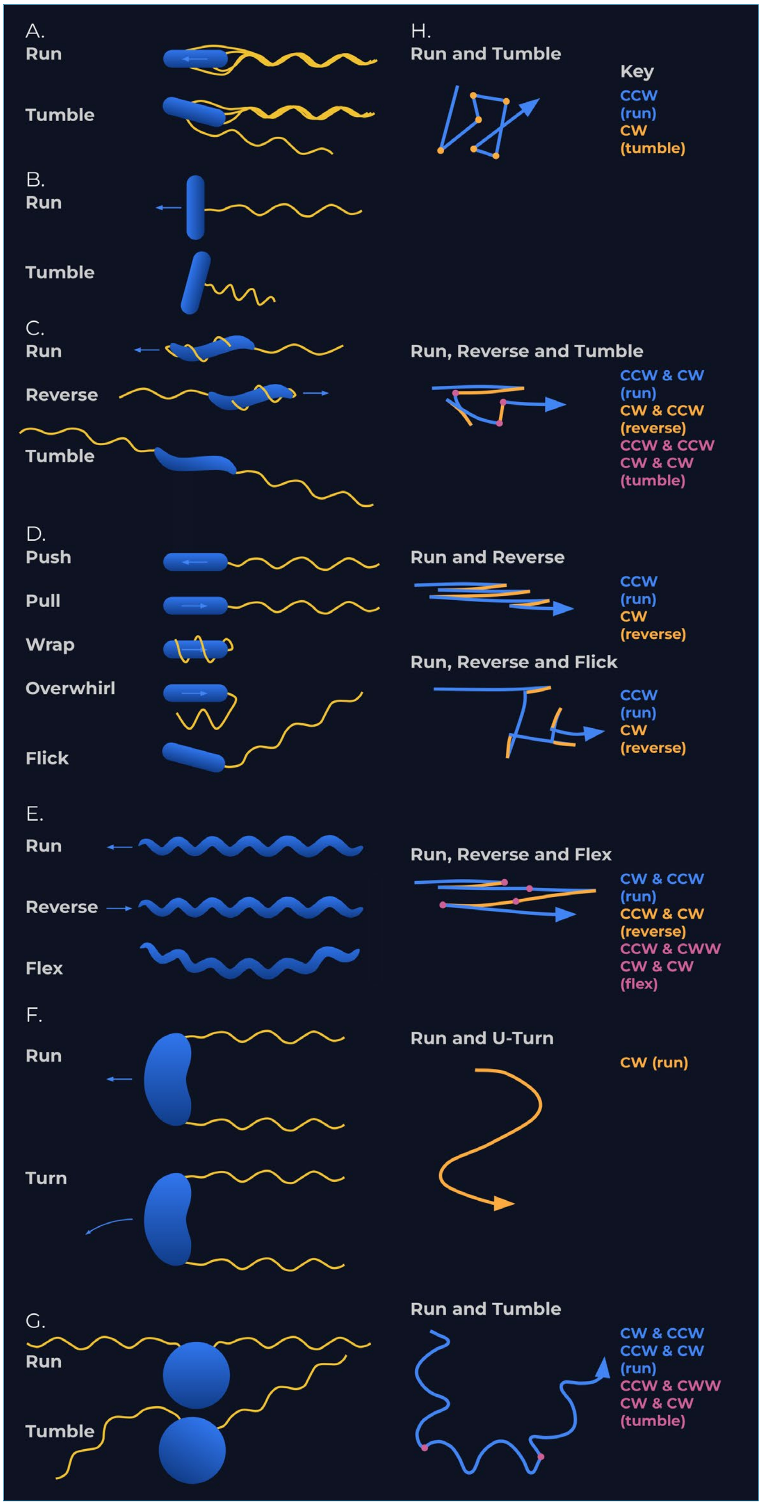

Figure 1. Swimming methods and modes. On the left are the swimming modes of various species. (A) Peritrichously flagellated species. (B) *Rhodobacter sphaeroides*. (C) *Magnetospirillum magneticum*. (D) Monotrichous species. (E) Spirochetes. (F) NivaVib1. (G) *Magnetococcus massalia* strain MO-1. (H) Examples of swimming methods that combine the modes displayed to their left. The key indicates colour coding and the rotation of the flagella. The notation 'CCW & CW' means the flagella at one pole are rotating CCW and at the other are rotating CW.

BOX 1

Getting out of tight spaces

In a tight space, *B. subtilis* and *E. coli* disassemble the flagellar bundle at the trailing end of the cell and reassemble it at the leading end to 'back out' of the tight space (figure 2a).[22,23] When *S. enterica* gets stuck in a dead end, the hook can switch to a locked state (under CW motor rotation) where it no longer functions as a universal joint and instead rotates as a fixed structure. This causes the filament to be rotated about the motor axis until it is facing the other way, at which point the hook switches back into the universal joint state and the rotation of the filaments can push the cell out of the dead-end (figure 2b).[24]

As discussed later in the main text, bacteria with one or more polar flagella can use the flagellum like a screw to back out of tight spaces (figure 2c).

Run-reverse

Bacteria with one or more polar flagella at one or both poles can use a run-reverse swimming method (figure 1d).[9,12,25,26] The run-reverse method is very effective at helping bacteria stay close to a nutrient source in high-shear environments (like the ocean).[27]

During a run, the rotation of the helical flagellum/flagellar bundle behind the cell pushes the cell forward. When the cell travels in reverse it uses one of three swimming modes: a fast pull mode in which the flagella pull the cell in a 'reverse-run', a slower wrap mode in which the flagella wrap around the cell body, and the over-whirling mode in which the bundle whirls adjacent to the cell (figure 1d).[28–31] The mode of the cells depends on the rotation direction of the flagella and the torque experienced by them (see table 1).[30]

The wrap mode helps bacteria traverse through structured environments.[32] Wrapping is thought to be caused by an instability of the flagellar filament(s), especially under increased load. This instability causes the filament(s) to be pulled backward and around the cell while it switches to a wider helical form that fits

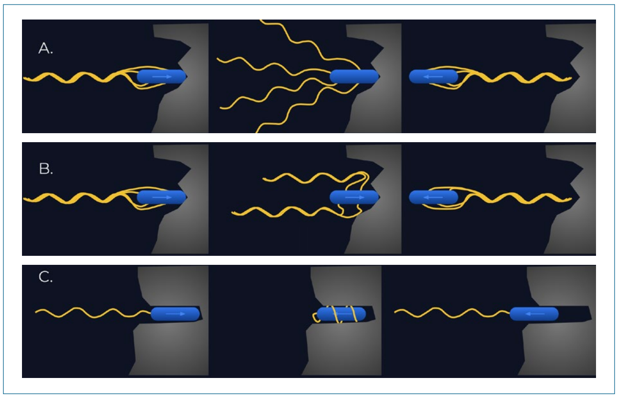

Figure 2. Various methods of backing out of tight spaces. (A) A peritrichously flagellated bacterium moving its bundle of flagella to the other end of the cell to back out of the tight space. (B) *S. enterica* hook locking. The hook rotating as a fixed structure causes the flagella to be pulled to the other end of the cell. (C) Screw thread motility by a bacterium with a polar flagellum.

Table 1. The key swimming modes of polar-flagellated bacteria

Rotation direction	Low torque	High torque
CW	Pull	Wrap (slow)
CCW	Push	Over-whirling (rare and very slow)

around the cell body.[28,33] Switching to and from the wrap mode can cause large changes in swimming direction.[28,31,33,34]

Polar-flagellated bacteria can also swim via screw thread motility. Screw thread motility uses the wrap mode to move across a surface and back out of narrow passages like a rotating screw (figure 2c).[26,28] Screw thread motility allows for more efficient movement of bacteria through structured and viscous environments, such as mucus, soil, marine sediment, and possibly biofilms.[26,35] Having segments along the length of the flagellar filament made of different flagellins (see part 2) fine-tunes the mechanical properties of the filament such that it forms a screw thread in structured environments (where it is beneficial), but not in bulk fluid (where it is not beneficial).[32,35,36]

Bacteria with lophtrichous flagella (multiple flagella on one or both poles) include a pause mode in their swimming.[31] The pause mode is thought to be related to pauses in motor rotation.[31] The pausing has been shown to allow for smooth and successful transition from the wrap to push mode.[31] Without pausing, cells fail at transitioning between modes, since the filament does not have time to relax and reposition correctly.

Multiple species have both a polar flagellum and lateral flagella.[37] The polar flagellum is always present, but the lateral flagella are induced to form under certain conditions, such as high viscosity or surface contact (see part 4).[37,38] Unlike the polar flagellum of *Shewanella putrefaciens*, its lateral flagella are not under the control of the cell's navigation system. Instead, their lateral flagella always push (rotating CCW) with their orientation flipping when the polar flagella switches between push and pull (thus always aiding the polar flagellum).[37] The lateral flagella of *S. putrefaciens* have been shown to decrease the turning angle between runs, resulting in cells moving across surfaces faster and more efficiently.[39]

Multicellular magnetotactic prokaryotes have flagella all over the cell, like cilia on ciliates. They use run-reverse motility (described as ping-ping motion), and swim in straight or helical trajectories.[40–42]

Run-reverse-tumble

In species with one or more flagella at both poles, the flagella at the leading pole typically wrap around the cell body, while the flagella at the lagging pole are extended.[25,28] In *Magnetospirillum magneticum*, the flagellum at the leading pole rotates CW, while the flagellum at the lagging pole rotates CCW.[43] When a cell reverses swimming direction, the pole that was leading is now lagging and vice versa, causing the wrapped flagella to unwrap and extend, while the extended flagella become wrapped.[28] Intermediate states have been observed where flagella at both poles are both wrapped or both extended.[28,44] These intermediate states have been described as a form of tumbling mode as they change cell orientation.[43]

Run-reverse-flick

Monotrichous (one polar flagellum) bacteria have a turning mode termed 'flick'.[9,45] Switching from push to pull results in an almost perfect reversal of direction with the cell retracing the path it just took. About 10 ms after switching from pull to push, the universal joint (hook) becomes weaker due to being untwisted, and is compressed beyond a finely tuned stability threshold, causing it to buckle.[46,47] This buckle results in a 'flick', where the flagellum pushes the cell at an angle, causing the cell to rapidly turn about 90° in less than 0.1 seconds.[45] Then, the universal joint straightens out again, causing the flagellum to align with the axis of the cell body and push the cell in the new direction. Dynamic instability of the filament also plays a role in flick initiation.[48] This dynamic instability of the hook and filament is a great example of mechanical instability (something engineers usually try to avoid) serving an important mechanical function.[49] During the post-flick run (push mode), the hook dynamically stiffens sixfold, likely through twisting of the hook, to prevent further buckling.[46]

It has been suggested that the flagellum hook may be redundant in monotrichous species.[50] However, discovery of the flick mechanism shows that the hook serves an important function in these species.

Flicking is more likely to occur the faster a cell is swimming (slow cells never flick and only swim by run-reverse).[46,51] Flicking increases cell chemotactic efficiency.

In *Vibrio alginolyticus*, the frequency of flicking can increase when acceleration of the swimming speed occurs in response to chemoattractant gradients.[52] This increase in swimming speed in response to chemoattractant gradients (called 'chemokinesis') has been observed in several bacterial species.[52,53]

Different flagellar arrangements can be combined to allow for the use of many swimming modes. For example, the soil bacterium *Bradyrhizobium diazoefficiens* has a polar flagellum that it uses to run, reverse, and flick, and lateral flagella that it sometimes uses to tumble.[54]

Run-reverse-flex

As mentioned in part 2, spirochetes are different from other flagellated bacteria because their flagella reside within the periplasmic space (and are thus termed 'periplasmic flagella' or 'endoflagella').[55–57] Spirochetes thus do not swim by the direct interaction between flagella and external fluid, as other bacteria do, and instead swim by the rolling or undulation of their cell body as driven by endoflagella.[58] One or more endoflagella wrap around the body, and their rotation is believed to cause the helical cell body to rotate in the opposite direction.[58]

Swimming behaviour differs between spirochete species. In *Borrelia* and *Brachyspira* species, rotation of endoflagella drives the propagation of waves in the helical cell body.[58] In *Leptospira* species, the leading end of the cell forms a large left-handed spiral, while the lagging end is curved like a question mark.[58] The rotation of the endoflagella causes the gyration of the spiral end and the rolling of the cell body.[58]

The endoflagella at the leading pole rotate CCW, while the endoflagella at the lagging pole rotate CW.[57] When both poles rotate in the same direction, the cell stops swimming and flexes or tumbles.[59] After a flex or tumble, the cell either continues in the direction it was swimming (stepping motion), or swims in the opposite direction (reversal motion) (figure 1h).[57] Spirochetes sometimes also coordinate the rotation reversals of the motors at either end of the cell to switch directly from a run to a reversal (or vice versa).

A crawling method is used by some spirochetes to move across surfaces. Crawling cells attach to the surface using mobile outer membrane adhesive components and then rotate their helical bodies to move across the surface like a screw.[60]

Run with U-turn

The sulfur bacterium *Thiovulum majus*, which localizes at oxic-anoxic boundaries (in or above ocean sediments), swims along helical paths without reversing or tumbling.[61] Instead, if swimming away from the oxic-anoxic boundary, they curve the path of their run to perform a 'U-turn' (figure 1h).[62] The mechanism behind this U-turn is unknown. One proposed mechanism is discussed in part 4.[62]

T. majus swims fast when far from the oxic-anoxic boundary (decreasing the time to find it) and slows down once the boundary is found.[62] *T. majus* cells often tether themselves to each other and use their flagella to pull sulfur-containing water towards themselves, rather than swimming to the sulfurous water.[63]

The large ovoid bacterium *Ovobacter propellens* and the large vibrioid bacterium NivaVib1 also swim using runs and U-turns.[12,63] Through some unknown mechanism, *O. propellens* cells can also turn abruptly between 110° and 270° without slowing down.[4] *O. propellens* can swim up to 1 mm per second (250 body lengths per second) in a helical path through CCW rotation of its large tuft of flagella.[4] NivaVib1 swims 'sideways' with its flagella pointing 90° to the axis of the cell body (figure 1f).[63,64]

Magnetotactic marine cocci

Magnetococcus marinus strain MC-1 and *Magnetococcus massalia* strain MO-1 are magnetotactic cocci that swim very fast: MC-1 can swim over 200 body lengths per second (over 500 μm/s),[65] while MO-1 can swim at 100 body lengths per second (350 μm/s).[66] Both swim in helical trajectories.[65–67]

It was thought previously that the forward and backward swimming motion of MO-1 cells was caused by runs and reversals. However, more recent evidence suggests that the reversal in swimming direction may be caused by the cell turning around (like the U-turns of *T. majus*), rather than from them reversing flagellar rotation.[68]

During a run, the two bundles of flagella on MO-1 cells are thought to both push.[68] In contrast one bundle of MC-1 pushes while the other pulls during a run.[66] MC-1 cells tumble rapidly when their flagellar bundles rotate in the same direction.[66]

Swimming across surfaces

When close to a surface, swimming cells are hydrodynamically attracted to the surface.[68,69] When swimming along a surface, pushing cells turn to the right, while pulling cells turn to the left, caused by a hydrodynamic effect termed 'wall-induced torque'.[33] This torque also occurs for peritrichously flagellated bacteria during a run, and previously it was assumed to hinder bacterial migration, since it caused cells to travel in circles on smooth surfaces.[69,70] However, some bacteria can periodically, and temporarily, attach to a surface between runs to travel in a series of semicircles rather than circles.[69] These bacteria are able to detect when they are on a surface and fine-tune the frequency of these attachment events to optimize surface exploration.[69,71] The systems behind this fine-tuning are unknown.[69] Natural surfaces (unlike man-made surfaces, such as glass) also often have obstacles which prevent peritrichously flagellated bacteria from getting trapped in a circular motion.[72]

It is worth noting that cells swimming in the wrap mode do not experience wall-induced torque, allowing for straight swimming near surfaces.[33] Polarly flagellated bacteria also can use the wrapping mode to escape from a surface.[31]

Fungal highways

One particularly interesting method of swimming across surfaces involves a type of symbiosis with fungi. Several soil bacteria (e.g., *Mycobacterium frederiksbergense* and *Pseudomonas putida*) use the wet surfaces of fungal hyphae as 'highways' to navigate through soil.[73–75] Bacteria do this even in non-saturated soil, which would normally inhibit their movement since they cannot swim through air pockets.[74–76]

Swarming across surfaces

Another motility method bacteria use to move across surfaces is called 'swarming'. Swarming is the collective movement of bacterial populations across solid or semi-solid surfaces, using flagella.[76,77] Bacteria use swarming to spread out on a surface. Swarmer cells differ from swimmer cells by synthesizing more flagella, secreting a surfactant that lowers the surface tension and sometimes they have longer, elongated cell bodies.[77–79] Swarming peritrichously flagellated bacteria synthesize more peritrichous flagella, while swarming polarly flagellated bacteria synthesize secondary lateral flagella.[35,80] It is worth noting that some polarly flagellated bacteria can swarm using only their polar flagella, or by synthesizing additional polar flagella.[28]

Gear-change mechanisms

Flagellar motors use various gear-change mechanisms to change the motor's rotation direction, rotation speed, torque, operating range, and fuel type (for hybrid motors).

Changing motor rotation direction

As shown above, changing the rotation direction of bacterial flagella is key to the motility behaviour of flagellated bacteria. However, the mechanism underlying this rotational switching long remained a mystery, before being solved in 2020 by four independent research groups.[81–84]

As mentioned in part 1, flagellar motors have a large central gear (C-ring), which is rotated by smaller powered gears (MotA ring of stators). Recent research has shown that the cogs of these gears interlock, something that was unknown at the time of the publication of part 1 (figure 3).[85] The smaller powered gears always rotate CW when viewed from outside the cell. The larger central gear has two different conformations: the CCW state and the CW state (figure 3b and figure 4).[82] In the CCW state, powered gears are positioned outside of the central gear, resulting in the CW rotation of the powered gears driving the central gear CCW. In the CW state, the powered gears are positioned inside the central gear, resulting in the CW rotation of the powered gears driving the central gear CW.[82,83,86] In mechanical terms, switching from the CCW state to the CW state causes the central gear to switch from functioning as an external gear to an internal gear.[87] This shift in the positions of the powered gears is caused by a conformational change in the cogs of the central gear (FliG C domain) in which they each rotate 180° (figure 3b).[86,88,89]

In bacteria with polar or periplasmic flagella, the stators have a greater positional stability than in peritrichously flagellated bacteria. Because of this, the stators cannot move

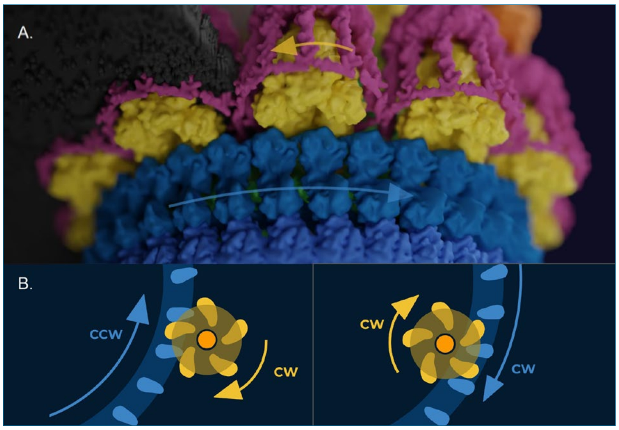

Figure 3. Flagellar gears. A) Computer model showing the MotA rings (a.k.a powered gears, shown in yellow) interlocking with the central gear (a.k.a. C-ring, shown in blue). B) Diagram of the motor rotation reversal gear mechanism, viewed from outside the cell ('above' for the orientation shown in A). Each of the cogs of the central gear (FliG C domain, shown in light blue) rotate 180°, causing the MotA ring to move to the inside of the central gear. Because the MotA ring always rotates CW, this causes the central gear to switch rotation direction.

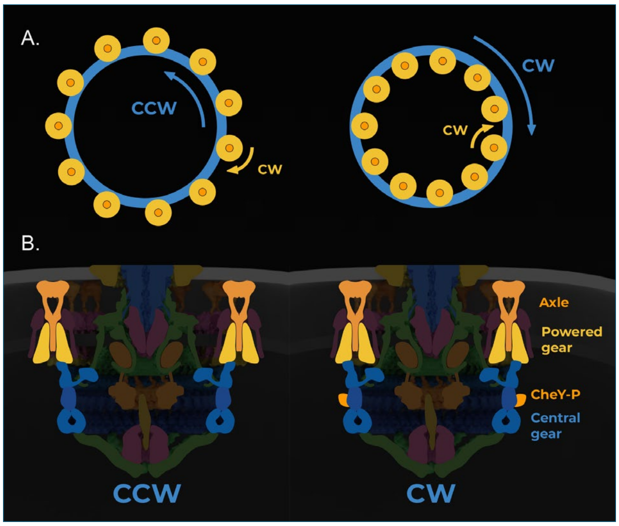

Figure 4. A diagram of the motor rotation reversal gear mechanism in peritrichously flagellated bacteria. The conformational change in the cogs of the central gear causes the stators (shown in yellow and orange) to move inside the central gear (shown in blue). (A) Top view. (B) Side cross-section view.

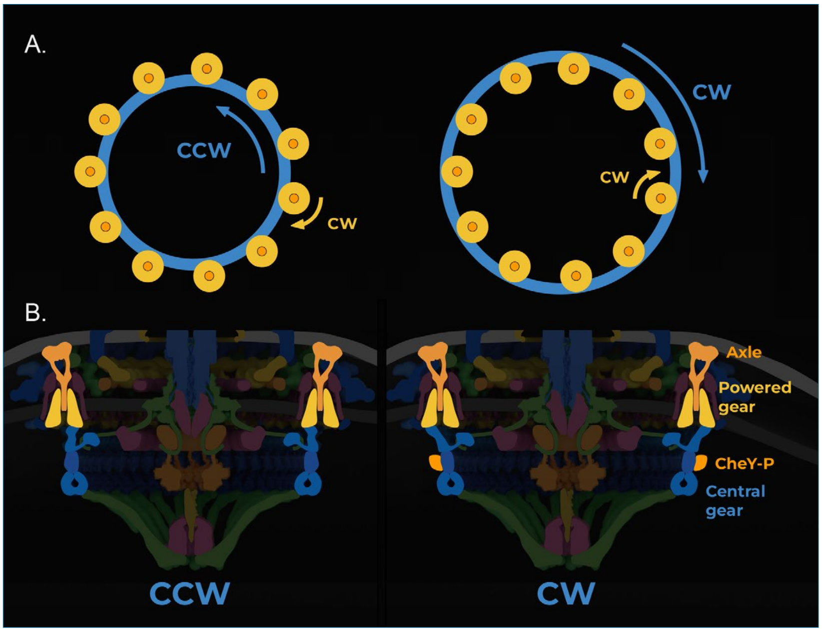

Figure 5. A diagram of the motor rotation reversal gear mechanism in spirochetes. Note that the diameter of the central gear increases, rather than the stators moving. (A) Top view. (B) Side cross-section view.

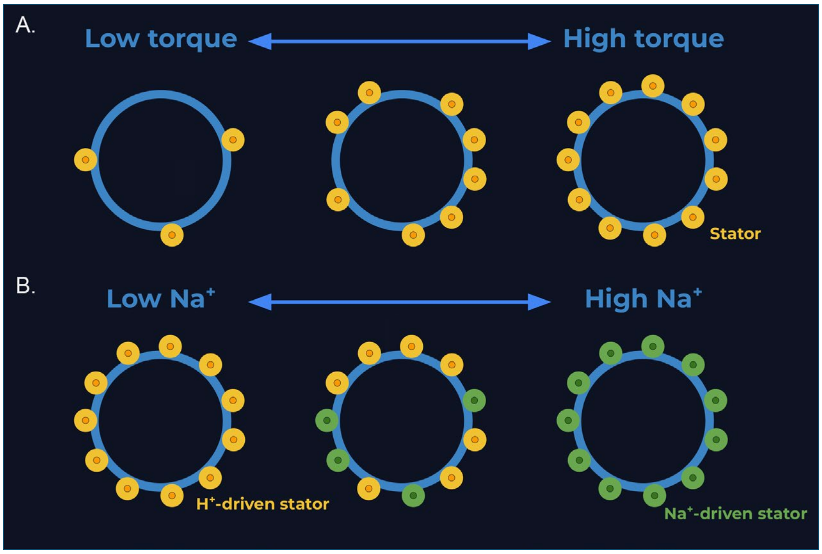

Figure 6. Gear mechanisms to vary motor torque (A) and fuel type (B).

during rotational switching of the motor. Thus, in bacteria with polar or periplasmic flagella, the diameter of the central gear increases when switching from the CCW to the CW state (figure 5).[83]

From an engineering perspective, the mechanical changes needed for rotational switching of flagellar motors are quite complex (this review glosses over most of the details—see the references of this section if interested). Mechanical gear-shifting mechanisms like this do not arise by chance. They require a lot of forethought and design to create. It is only reasonable to conclude that the same is true for this gear mechanism in flagellar motors.

Around the outside of the central gear, on and below each cog, is a binding site for a signalling protein called 'CheY-P' (i.e., phosphorylated CheY). Bacterial navigation systems influence the concentration of CheY-P inside the cell to regulate motor rotation reversals. The binding of CheY-P to the central gear affects the favourability of the two states (CCW vs CW) and the favourability of switching between these states. The specifics appear to differ between peritrichously and polarly flagellated bacteria, as will be discussed in part 4.

Changing power output

Some flagellar motors can regulate the torque produced by regulating the number of stators engaged.[90–96] If the cell swims into thicker fluid, it becomes harder to rotate flagella. Therefore, the number of stators engaged increases automatically, increasing the rotational force produced by the motor (figure 6a).[97] The opposite occurs if the cell swims into thinner fluid.

This gear mechanism likely is regulated by the stator units themselves. Stators continually engage and disengage with the central gear, being engaged for an average of 30 seconds (see box 2).[98,99] In *E. coli*, about 300 disengaged stators reside in the inner membrane per cell.[99] When engaged, each stator measures the torque exerted on it by the central gear, using a catch-bond mechanical sensor (the bond between the MotB anchor domain and cell wall increases in strength under load, likely due to a conformational change of the MotB anchor domain).[91,100–102] If the central gear is hard to turn, the stators stay engaged longer, resulting in more stators being engaged over time (this occurs over a few minutes). If the central gear is easy to turn, the stators are engaged only for a short time, resulting in fewer stators engaged over time. In this way, the number of stators engaged in the motor is fine-tuned continually to match the required power output. This makes the motor extremely energy efficient, since it does not use any more power than needed.

How the stators engage and disengage from the central gear is explained in box 2.

The proteins FliL and MotF can play a critical role in flagellar rotation in selected bacteria. They bind around the outside of stators, likely to help keep the proton channels unplugged when the stators are engaged.[17,103–105] The proteins can interact with each other and with MotA and MotB (refer to box 2). Another protein, called 'SwrD', has been shown to increase the torque produced by *B. subtilis* flagellar motors during swarming. This is possibly due to additional stators being recruited to the motors.[106] SwrD (or similar proteins, such as FlbD) may serve this function in firmicutes, clostridia, spirochaetes, and the deltaproteobacteria.[107]

Changing fuel type

As mentioned in part 2, some species have stators that use H^+ ions to power rotation, some have stators that use Na^+, and some have both H^+-driven and Na^+-driven stators.[111,112] In these hybrid motors, the ratio of H^+-driven to Na^+-driven stators varies depending on the availability of sodium ions.[112–115] Sodium ions bind to a Na^+-sensor on the peptidoglycan-binding domains of the Na^+-driven stators, promoting extended stator engagement.[112] When sodium ions are plentiful, the motor is mostly composed of Na^+-driven stators, but when the sodium ions become less plentiful, the number of engaged H^+-driven stators increases (figure 5b).[98,114]

Changing motor speed

How motors regulate rotation speed (for chemokinesis) is poorly understood. The navigation system may regulate stator engagement, via stator-binding proteins, since increasing the number of engaged stators increases motor rotation speed.[98] Species can also regulate motor rotation speed over longer timescales, using clutches and brakes (see part 4).

Changing motor operating range

Many studies have reported that the number of proteins in the central gear (especially FliM and FliN) can change over time.[116–121] Motors that only rotate counterclockwise have more FliM than motors that only rotate clockwise.[118,122] Flagellar motors are very sensitive to CheY-P and only have a small operating range of CheY-P concentrations.[119,123] The motors of a cell that are consistently low in CheY-P will spend a higher proportion of time in the CCW state, which causes the number of FliM in the central gear to increase over a few minutes.[119] The greater the number

BOX 2

How stators engage and disengage with the central gear

When a stator unit is disengaged, the MotB anchor domains are disconnected from the cell wall and sit on top of the powered gear (figure 7).[107] Part of the MotB tethers (called the 'plug region') plug the proton channels through the powered gear, effectively turning it off, and the MotB plugs also slot between MotA subunits, preventing rotation.[82,104] This ensures the stators do not use energy when disengaged. Removal of the plug region results in massive leakage of protons into the cytoplasm, inhibiting growth.[82]

When a stator unit engages with the motor, the stator unit is thought to detect the cogs of the central gear and trigger the unplugging of the plug region.[85,108] It is possible that the rotating central gear pushes on the power gear (MotA-ring) of the stator, inducing a conformational change in the stator, triggering the plugs to release.[96] This conformational change unlocks the rotation of the powered gears and opens the ion channels through the stator. As this happens, the MotB 'tethers' extend and unwind.[108–110] This causes the anchor section of MotB to change confirmation to expose the peptidoglycan-binding site, which then attaches to the cell wall, holding the stator unit in place.[109,110] The stator unit is thus turned on and starts spinning. A ratchet-like mechanism prevents the stator from rotating in the wrong direction.[104]

This process occurs in reverse when the stator unit disengages.

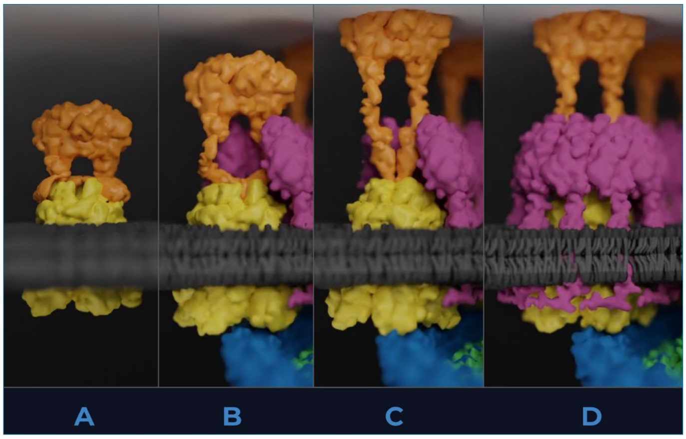

Figure 7. How stators engage with the central gear. (A) Stator units drift around in the membrane with their ion-channels plugged with the plug domains of MotB (MotB shown in orange). (B) When a stator engages with the central gear (shown in blue), it triggers the release of the MotB plugs, allowing for rotation of the powered gear (shown in yellow). Ions begin flowing through the channels, powering rotation. C) The peptidoglycan-binding domain of MotB binds to the peptidoglycan layer (shown in grey), holding the stator in place. D) A FliL ring (shown in pink) forms around the stator, further stabilizing the stator. These steps occur in reverse when the stator disengages.

of FliM in the central gear, the more sensitive the central gear is (i.e., the motor has adapted by shifting its operating range to lower levels of CheY-P).[118,119] It is worth noting that cryo-electron microscopy studies suggest that rotation direction does not affect the number of proteins in the central gear, in contrast to the results discussed above.[83,84]

Conclusion

Flagella are used not just as propellers, but also as rudders to change the orientation of cells and as screw threads to move through tight spaces or over surfaces. Flagella can propel movement in a diverse range of environments. In contrast, human-designed vehicles that go in a range of environments typically require different mechanisms to move through each environment (e.g., wheels for surfaces, propellers for water). Professor Charles Wolgemuth (physics, molecular and cell biology) said that, "bacteria have out-engineered us by figuring out how to make a single motility mechanism work in multiple environments."[124] In reality, it is not bacteria that have out-engineered us; it is God, in designing the bacteria. Just as the design features of man-made motility mechanisms and gears point to human designers, so do the design features of bacterial flagella and their gears point to a divine designer.

In the next paper in this series, part 4, discussion will focus on the sophisticated navigation systems that control bacterial swimming to navigate bacteria towards more favourable conditions.

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