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Reverse and flick: Hybrid locomotion in bacteria

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Many bacteria are motile. They use one or more helical flagella as propellers, rotating them like the corkscrew on a wine bottle opener. Despite the limited morphological repertoire of the propulsive system, radically different movement strategies have evolved, likely reflecting the diversity of physicochemical conditions among bacterial habitats. In PNAS, Xie et al. (1) report on a newly discovered mechanism for turning used by *Vibrio alginolyticus*, an inhabitant of the coastal ocean: These monotrichous (“single-haired”) bacteria change direction with a “flick” of their flagellum. Intriguingly, Xie et al. (1) show that less can be more when it comes to bacterial flagella: With its single flagellum, *V. alginolyticus* outperforms the multiflagellated *Escherichia coli* in climbing nutrient gradients (“chemotaxis”), suggesting that the flick is part of an advanced chemotaxis system.

Our understanding of bacterial locomotion has long been driven and biased by the wealth of knowledge on *E. coli*, commonly found in animal intestines. *E. coli* is peritrichous, having four to eight flagella emerging from random points on its 2×1 μm hotdog-shaped body (2). Each flagellum is powered by a reversible rotary motor. When all motors spin counterclockwise (as seen from behind), hydrodynamic interactions cause the flagella to form a bundle that propels *E. coli* forward in a nearly straight “run” at ~ 30 $\mu\text{m}/\text{s}$. When one or more motors switch direction, the bundle comes apart, causing a change in direction (“tumble”) before a new run begins. The angle of reorientation during a tumble is nearly random, with the new run only slightly biased in the direction of the old one. This “run-and-tumble” movement pattern is common among peritrichous bacteria, including the pathogen *Salmonella typhimurium* and the soil-dwelling *Bacillus subtilis*.

Other bacteria, like *V. alginolyticus*, have a single flagellum and thus lack *E. coli*'s tumbling mechanism. When this flagellum rotates counterclockwise, it pushes the cell forward; clockwise, it pulls it backward. This “run-and-reverse” swimming is prevalent in the ocean: *Shewanella putrefaciens*, *Pseudoalteromonas haloplanktis*, and *Deleya marina*—all monotrichous—exhibit 180° reversals (3), as do $\sim 70\%$ of marine isolates (4). At least one of these run-and-reversers, *P. haloplanktis*, outperforms *E. coli* in responding to nutrient patches, climbing gra-

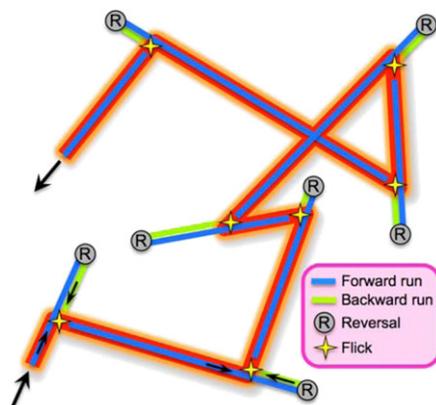


Fig. 1. Schematic of the hybrid movement pattern of *Vibrio alginolyticus*, which alternates reversals and flicks. Reversals are 180° reorientations, whereas flicks result in a broad distribution of reorientation angles with a mean of $\sim 90^\circ$. The effective trajectory is a random walk (red path) with some dead-end forays (after reversals and before flicks).

dients more rapidly and thus enhancing its exposure to high nutrient concentrations (5).

How can a simple back-and-forth movement result in high-performance chemotaxis, rather than causing the bacterium to endlessly retrace its steps? The answer might lie in a previously undetected component of the run-and-reverse motion: the flick. Xie et al. (1) show that *V. alginolyticus* executes a cyclic, three-step motion: forward, reverse, and flick (Fig. 1). As expected, motor reversal after the forward segment induces an $\sim 180^\circ$ reorientation. However, motor reversal after the backward segment is followed by a flick of the flagellum. Fluorescent labeling revealed that the flexible base of the flagellum develops a small kink whose angle is rapidly amplified by flagellar rotation. Although not a steering mechanism (which would imply active control over the change in direction), the flick induces a fast (< 0.1 s) reorientation and the flagellum thus acts as a rudder, not just as a propeller. The change in cell orientation induced by a flick has a broad Gaussian distribution centered at 90° , and hence is very effective at randomizing swimming direction. This, then, is a hybrid swimming mode: partly run-and-reverse, partly random tumble.

The resulting movement pattern is a random walk (red in Fig. 1) with dead-end forays, as can be seen by considering each step in the walk as a forward-backward-flick sequence (Fig. 1). Retracing its steps in the dead ends, after reversing and before flicking, reduces *V. alginolyticus*'s ef-

fectiveness in exploring its environment. Its diffusivity [$210 \mu\text{m}^2/\text{s}$, considering its $45 \mu\text{m}/\text{s}$ swimming speed and 0.31 s net run length (1)] is less than half that of *E. coli* [$450 \mu\text{m}^2/\text{s}$, assuming a $30 \mu\text{m}/\text{s}$ speed and 1 s run length (2)]. This comes at over twice the energetic cost for *V. alginolyticus*, because energy scales quadratically with swimming speed. If exploration were the main goal of the hybrid strategy, *V. alginolyticus* would be wasting its time and energy in the dead ends. It is possible that these drawbacks are outweighed by the savings of having just one flagellum, particularly in resource-poor environments such as the ocean. However, the fact that *V. alginolyticus* outperforms *E. coli* in terms of chemotaxis (1) implies otherwise. A similar observation for *P. haloplanktis* (5), along with evidence that this species also uses flicks (1), suggests that hybrid movement kinematics are more favorable for chemotaxis than run-and-tumble kinematics. Alternatively, these monotrichous marine bacteria possess considerably faster chemosensory responses than *E. coli*. Here I briefly explore these two hypotheses.

Mathematical modeling has shown that the distribution of reorientation angles can markedly affect the quest for nutrients, as measured by the chemotactic velocity—the speed at which bacteria climb nutrient gradients (6). Different movement patterns can be modeled in terms of the persistence parameter, α , the mean of the cosine of the reorientation angle between runs. For positive persistence, the new direction is more likely to lie in the forward hemisphere: For example, *E. coli*'s tumbles are biased forward, with a mean angle of 68° and $\alpha = 0.33$ (2). Entirely random tumbling results in $\alpha = 0$ (no persistence), whereas a perfect reverser has $\alpha = \cos(180^\circ) = -1$ (maximum negative persistence). In a linear nutrient gradient, the chemotactic velocity is predicted to increase with α (except near $\alpha \sim 1$) (6): Reversers should perform worse than *E. coli*. *V. alginolyticus*'s hybrid strategy increases persistence, because $\alpha = 0$ for flicks [mean reorientation $\sim 90^\circ$ (1)]. The alternation of reversals and flicks then suggests that $\alpha \sim -0.5$ for *V. alginolyticus*

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overall, for which the predicted chemotactic velocity is less than 60% of *E. coli*'s (6). However, Xie et al. (1) find that *V. alginolyticus* has a threefold larger chemotactic velocity than *E. coli*.

The secret of the impressive chemotaxis performance of *V. alginolyticus* and *P. haloplanktis* might lie in a signaling pathway that responds swiftly to changes in nutrient concentration. Altindal et al. (7) predict that the hybrid strategy can lead to a rich set of behaviors, depending on how the cell processes chemical signals ("response function"), and Xie et al. (1) find evidence that *V. alginolyticus* can rapidly modulate backward and forward run times. When a flick directs the cell up a nutrient gradient, forward and backward times are comparable, whereas a flick that directs the cell down the gradient is followed by a very short forward run: *V. alginolyticus* quickly (<0.2 s) corrects the effect of an erroneous flick. In the hybrid strategy, flicks would then be used to randomize direction and reversals to correct mistakes. This short reaction time would confer a prodigious advantage over bacteria relying on concentration comparisons made over seconds [~ 4 s for *E. coli* (2)]. Such a rapid chemosensory response has been reported for marine bacteria tracking swimming algae (8), where up to 12 consecutive correct turns enabled bacteria to remain in the alga's wake. Although this "steering" behavior might be a passive hydrodynamic effect whereby the wake's velocity gradients reorient a pursuing bacterium into the wake (9), the fact that both pursuers—*P. haloplanktis* and *S. putrefaciens*—were monotrichous and *P. haloplanktis* might flick (1) supports the possibility that turning was actively controlled by the cells. If proven, the pathways of these high-performance sensing systems and how they operate in the face of challenging physical constraints (e.g., noise due to short integration times) would represent fertile ground for chemotaxis research.

Fluid flow could be an additional factor promoting reversals. Velocity gradients

("shear") generate torques that reorient bacteria, hampering chemotaxis. Modeling shows that bacteria with smaller persistence are less susceptible to shear, with reversers performing better than *E. coli* for shear rates $>1/s$ (10), common in the sea.

Xie et al. find that *V. alginolyticus* has a threefold larger chemotactic velocity than *E. coli*.

Hence, reversals could be advantageous in flow and *V. alginolyticus*'s hybrid strategy might be a tradeoff between chemotaxis in quiescent and moving fluids. On the other hand, the advantage might be flow-dependent: Reversers are predicted to uptake significantly more nutrients than *E. coli* within the nutrient cloud exuded by a small alga in sheared flow (11), whereas no difference is expected in the wake of sinking marine snow particles (12).

Hybrid locomotion could be commonplace among monotrichous bacteria. Reports of run-and-reverse motility have focused on demonstrating the existence of reversals and may have overlooked flicks. For example, *P. haloplanktis* had been described as a run-and-reverser (13), yet it appears to exhibit a hybrid strategy (1). The prevalence of reversals (3, 4) and flicks (1) among marine bacteria could be a consequence of the ubiquity of shear and the often oligotrophic conditions favoring single over multiple flagella. On the other hand, monotrichous bacteria occur in many environments—the best-known example being the opportunistic pathogen *Pseudomonas aeruginosa*—and there is evidence for flicks in the soil-dwelling, hydrocarbon-degrading *Pseudomonas oryzaehabitans*, which alternates sudden, short backward motions with forward

motions along a new orientation (14), again with a single flagellum.

A full understanding of bacterial locomotion will hinge on integrating the biomechanics of the propulsion apparatus (e.g., how the flagellum deforms during a flick), the ecological drivers of motility (e.g., the shape and magnitude of nutrient gradients), the physical constraints on movement (e.g., hydrodynamic forces), and the effectiveness of the signaling network in translating concentration measurements into motion (e.g., how rapidly a wrong turn is corrected). Much remains to be discovered even for the model organism par excellence, *E. coli*. For example, recent microfluidic experiments showed *E. coli* capable of chemotactic velocities as large as 35% of swimming speed when exposed to suitable gradients, markedly higher than the 5–15% traditionally observed (15). Even *E. coli*'s gradient navigation mechanism, long accepted to result only from modulation of run lengths, could hold new surprises, with recent predictions suggesting that the degree of reorientation during a tumble—and thus persistence—depends on swimming direction relative to the gradient, because the latter affects the number of motors that switch direction during a tumble (16).

On the other hand, it is time to diversify our portfolio of model organisms for bacterial chemotactic motility. Xie et al.'s discovery of hybrid movement patterns in monotrichous bacteria (1) and evidence that this hybrid strategy correlates with high-performance chemotaxis in marine species (1, 5) makes monotrichous marine bacteria an appealing model system to expand our knowledge of motility among the smallest life forms on our planet.

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