

quantum field theories, and directly measure the entanglement in a many-body system. The Mott insulating state for bosons or fermions remains also currently relevant, as it serves as a starting point for probing quantum magnetism, potentially helping unravel the enormous puzzles associated with high- T_c superconductivity.

Today, realizing these kinds of strongly correlated system has become a major research direction for almost all experiments trying to build quantum

simulators in a variety of platforms. The work of Jaksch et al. can therefore truly be seen as the visionary work that laid out the path for the field of experimental quantum simulations.

Immanuel Bloch^{1,2}

¹Fakultät für Physik at Ludwig-Maximilians-Universität, München, Germany. ²Max-Planck-Institut für Quantenoptik, Garching bei München, Germany.

e-mail: immanuel.bloch@mpq.mpg.de

Published online: 4 December 2018

<https://doi.org/10.1038/s41567-018-0371-x>

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CELL MOTILITY

Peculiar polygonal paths

Many microorganisms use light-sensitive receptors to migrate. A case in point is the microalga *Euglena gracilis*, which avoids light intensity increases by swimming in polygonal trajectories — providing an elegant solution to navigational challenges.

Nicolas Waisbord and Jeffrey S. Guasto

The ability of single swimming cells to identify and bias their motion toward favourable conditions and away from predators and harmful toxins is a fundamental survival mechanism. Without it, bacteria would go without nutrients, photosynthetic microalgae without light, and chemical attractant signals from eggs would be lost to spermatozoa. Bacterial motility has been well characterized within the ‘run-and-tumble’ paradigm, but higher organisms move with more complexity. Writing in *Nature Physics*, Alan Cheng Hou Tsang and co-workers¹ have exposed a novel behaviour in one such microswimmer — the photosynthetic microalga *Euglena gracilis* — showing that these cells swim in polygonal trajectories (Fig. 1) that may hold importance for avoiding strong light sources and optimizing navigation.

Pioneering work by Howard Berg, beginning in the 1970s², established the run-and-tumble paradigm for bacterial motility, whereby cells swim in random walks consisting of straight paths (‘runs’) interspersed by sudden flagellar-actuated, random reorientations (‘tumbles’). In the presence of a chemoattractant gradient, bacteria bias their random walks towards favourable conditions by modulating the rate of stochastic reorientation, regulated by temporal sensing of the local chemical concentration^{3,4}. Recently, a more complex picture of chemo- and phototaxis has emerged for eukaryotic microorganisms, including

sperm and phytoplankton, illustrating a deterministic response^{5,6}. *E. gracilis* was known to swim with a combination of helical trajectories and localized spinning in the plane of ambient light propagation, considered sufficient to navigate light gradients. Through a methodology originally established by Berg, and since perfected by others, Tsang et al. used direct microscope imaging of cell motility combined with control theory to reveal polygonal trajectories of various orders when cells were subjected to a change in ambient light intensity.

For small intensity changes, the flagellar beating of *E. gracilis* both propels the cell forward and rolls the cell around its swimming axis, resulting in a helical trajectory. The latter behaviour serves to sweep the cell’s lateral eyespot, a photosensory organelle, around the body to search for light sources. Strong changes in light intensity modify the three-dimensional beating of the flagellum and result in in-plane cell spinning. Strikingly, for moderate step-changes in light intensity, Tsang and co-workers observed a periodic switching between these two behaviours, which resulted in polygonal trajectories.

Through direct imaging of the flagellar beating, they demonstrated that the polygonal trajectories result from the coupled swimming speed and the rolling frequency of the cell body, which feed back on the periodically shaded eyespot. Accounting for swimming kinematics and

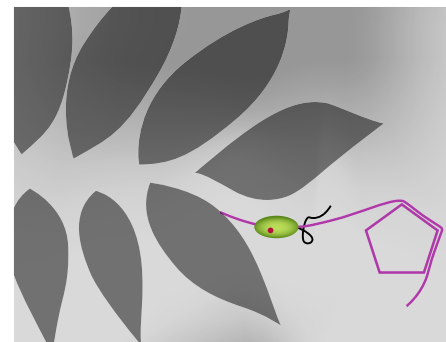


Fig. 1 | The single-celled, phototactic microalga *Euglena gracilis* swims in striking polygonal patterns in response to a sharp change in light intensity. Such patterns confer potentially important transport properties and behaviours to these cells for survival.

adaptation of photosensitivity enabled the development of a simple model that accurately reproduces a number of complex cell behaviours. Although aspects of the study could seem statistically fragile with relatively small sample sizes, the deterministic nature of the effect makes the results robust. The outcome is a holistic viewpoint linking the photosensory system, flagellar waveform, cell body kinematics and cell transport, which spans from sub-micrometre to millimetre scales.

In contrast to the universal characteristics of stochastic navigation in bacteria^{2,7}, the

more deterministic nature of eukaryotic microswimmers' taxes, combined with diverse cell morphologies and swimming styles, presents a cornucopia of species-specific navigation mechanisms. At least one common behaviour for eukaryotic swimmers, including *E. gracilis*, are the helical klinotactic swimming trajectories that often tie swimming kinematics to sensing. For example, the phototactic *Chlamydomonas reinhardtii* swims in helical patterns to sweep its eyespot perpendicular to the swimming direction, similar to *E. gracilis*, but uses two flagella for propulsion⁸. A temporal change in the light stimulus due to procession of the eyespot induces a differential beat amplitude of the two flagella, causing the cell to turn toward the light⁶.

Although marine invertebrate sperm cells lack a directional receptor, some swim in helical trajectories, enabling them to sample local chemoattractant concentrations azimuthally to the mean swimming direction. Changes in the perceived attractant concentration, sensed on two different timescales, induce either gradual or sharp changes in the path curvature for steering⁵, which are achieved through changes in flagellar curvature or beat harmonics⁹, similar to the work of Tsang and co-workers. In these examples, observations of cell kinematic responses to stimuli at both the flagellar and cell-trajectory scales provide the key to developing robust models of cell behaviour, without ever venturing into the molecular transduction pathways inside of the cell. Despite the drastic morphological, kinematic, and behavioural differences between swimming cells, the robust approach outlined above, combining microscopy and control theory,

gives us confidence that this generalized framework can explain even the most complex sensory and response behaviours of single swimming cells.

For *E. gracilis*, the authors' modelling of polygonal swimming and photoadaptation captures key, mid-range search behaviours. Near sharp light gradients, cells exhibit edge avoidance to prevent photodamage. This manoeuvre includes polygonal trajectories of increasing order and search radius due to photoadaptation, which in turn give way to spiral patterns to locate escape routes. Over large scales in spatially structured light gradients, polygonal, spinning and helical swimming behaviours combine into complex trajectories that are reminiscent of bacterial run-and-tumble behaviour. This broad range of swimming patterns is explained by the model, and results in transport ranging from sub-diffusive to ballistic motion to find suitable growth conditions. For bacterial motility and chemotaxis, random reorientations fit into a rather universal and appealing framework, especially for physicists. For instance, the run-and-tumble model has enabled numerous theoretical breakthroughs in active matter¹⁰. In contrast, the authors have demonstrated through *E. gracilis* that the eukaryotic world is not necessarily beholden to such simple, universal behaviours.

From an ecological viewpoint, the novel observations and comprehensive modelling presented in this study will pave new inroads for understanding the fundamental sensing and control mechanisms used by *Euglena* and other phototactic microorganisms for survival. However, natural habitats, including brackish water and wet soil, can be turbid and particle-laden, causing diffuse

optical landscapes having a range of length scales. It will be crucial to determine how *E. gracilis* interprets and responds to such complex, three-dimensional environments. The capability of this study to capture complex cell trajectories suggests that the model may be able to predict novel physical regimes and give new insights into the optimality of search and foraging behaviours. On larger scales, swimming microorganisms regulate the rates and spatial distributions of a host of macroscopic phenomena, including the food web and ecosystem dynamics. Our understanding of microscopic cell behaviours and our ability to accurately model the interactions of microorganisms with physical and chemical landscapes, illustrated here, are necessary for large-scale models of biogeochemical processes. □

Nicolas Waisbord and Jeffrey S. Guasto*

Department of Mechanical Engineering, Tufts University, Medford, MA, USA.

*e-mail: jeffrey.guasto@tufts.edu

Published online: 24 September 2018
<https://doi.org/10.1038/s41567-018-0320-8>

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