How to steer a complex organism: Mechanism of Phototaxis in Marine Zooplankton

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It is a general rule of nature that larger organisms are more complex, particularly when measured by the number of distinct types of cells present. This undoubtedly reflects the fitness advantage conferred by a division of labor among specialized cells over a situation in which all cells are totipotent (able to do all the functions of life). Yet, increasing size has both costs and benefits, and the search for understanding the driving forces behind the evolutionary transition from single cell organisms to multicellular ones is becoming a very active area of research. Coupled with this is a desire to understand how multicellular organisms actually accomplish the tasks of life.

Unicellular organisms certainly have the ability to sense their environment and move accordingly, as is clear from the remarkable chemotactic behavior of bacteria. Peritrichously flagellated (cells with flagella evenly distributed over their surface) such as *E. coli* swim by means of multiple helical flagella turned by rotary motors. When those motors turn in the same direction the flagella bundle behind the cell and allow it to move forward in a straight line, but a stochastic process within the cell, with a time constant on the order of seconds, leads to one or more motors reversing and the disintegration of the flagellar bundle. The result is a "tumble" that reorients the cell, and then it swims off in a new direction when the motors resynchronize. The frequency of tumbling in this "run-and-tumble" locomotion can be modulated to allow cells to climb gradients of molecular concentration (chemotaxis).

Larger, more advanced eukaryotic organisms such as algae and zooplankton swim with a more deterministic motion, often by means of a different type of flagellum from the bacterial one. These cilia are not passive objects but active ones, with molecular motors distributed along their length producing waves of bending motion. They are among the most highly conserved structures in biology, responsible for innumerable functions in our bodies, from mucus clearing in the lungs to the breaking of left-right symmetry in development. Rather than bundling and unbundling flagella, eukaryotes tend to modulate the beat dynamics of their flagella in response to external stimuli, and one of the most well-studied (if not well-understood!) processes is phototaxis, motion toward light.

In a variety of aquatic eukaryotes phototaxis is achieved by means of a photosensor known as the eyespot, which has a fair degree of directionality in its response. Signals received by the photosensor trigger biochemical changes that can modulate the beating of the flagella, enabling the organisms to turn. Most intriguingly, many of these organisms tend to swim naturally in helical trajectories, even in the absence of phototactic cues. So, in the presence of a light signal the eyespot is constantly receiving a modulated light signal, and thus modulating the flagella periodically. Precisely how helical swimming, modulating of flagellar beating, and phototaxis are all linked is a fascinating problem. In the excellent recent article by Jékely, *et al.*, the link between these three phenomena is analyzed for the case of larvae of the annelid *Platynereis dumerilii*. These quasi-spherical larvae are some 100 μm in diameter, and are propelled by a band of cilia around a line of latitude. This particular arrangement leads to spiral swimming. The authors show that a neuron connects the eyespot to the multiciliated cells, and careful studies show that there is an asymmetry in the strength of the light-mediated response of cells on the two sides of the larvae. Thus, there are cilia used for steering, and others which do not steer.

One of the key results of this work comes from studies of a simple mathematical model that links the asymmetric cilia response to self-propulsion. They show that axial rotation of the larval body is essential for phototaxis, and that the helical swimming actually increases the fidelity of the phototaxis, apparently by allowing three-dimensional scanning of the environment. The authors mention the analogous processes in the unicellular organism *Chlamydomonas*, which also swims in a helical path, receiving periodic signals at its eyespot, and modulating the flagellar beating accordingly. With the authors' emphasis squarely on the evolutionary biology of the eye, their work is a very nice synthesis of cell biology, microscopic fluid dynamics, and control theory that goes a long way toward unravelling phototaxis. Looked at another way, though, these findings can help get to an even deeper issue: how much simpler multicellular organisms that *lack* any kind of nervous system are able to achieve accurate phototaxis. This is a crucial step in the evolutionary process. To paraphrase the algal biologist David Kirk: How does one coordinate thousands of oarsmen without a cox?

Stay tuned.