

## BIOMECHANICS

## How fish feel the flow

**Hair-like sensors are suspected to aid fish navigation in complex environments. Laboratory experiments and computational simulations reveal how these sensors can detect water flow to direct the swimming responses of fish.**

JOHN O. DABIRI

It's hard out there for a fish. Survival requires constant vigilance to avoid predators and obstacles, especially in near-shore environments. Although many fish exploit visual cues to escape harm, the greatest danger that lurks in the water is largely invisible: the persistent and unpredictable churning of currents, which can carry an unsuspecting fish far off course or cause it to crash into underwater objects. Moreover, some fish are naturally blind or live in light-poor regions where visual cues are minimal. Yet even under such circumstances, fish are remarkably effective at maintaining a constant position at the same location (a phenomenon known as station-keeping) and avoiding obstacles.

These feats have been attributed to the action of motion-sensitive hair cells that form a structure called the lateral line, which runs along the length of a fish's body<sup>1,2</sup>. But how does the lateral line sense local patterns of water motion, and how do fish use that information

to navigate? In a paper online in *Nature*, Oteiza *et al.*<sup>3</sup> propose an elegant mechanism based on a robust principle of fluid dynamics, which only requires the fish to respond to the flow by making a simple choice between either continuing to swim without changing direction or making a turning manoeuvre.

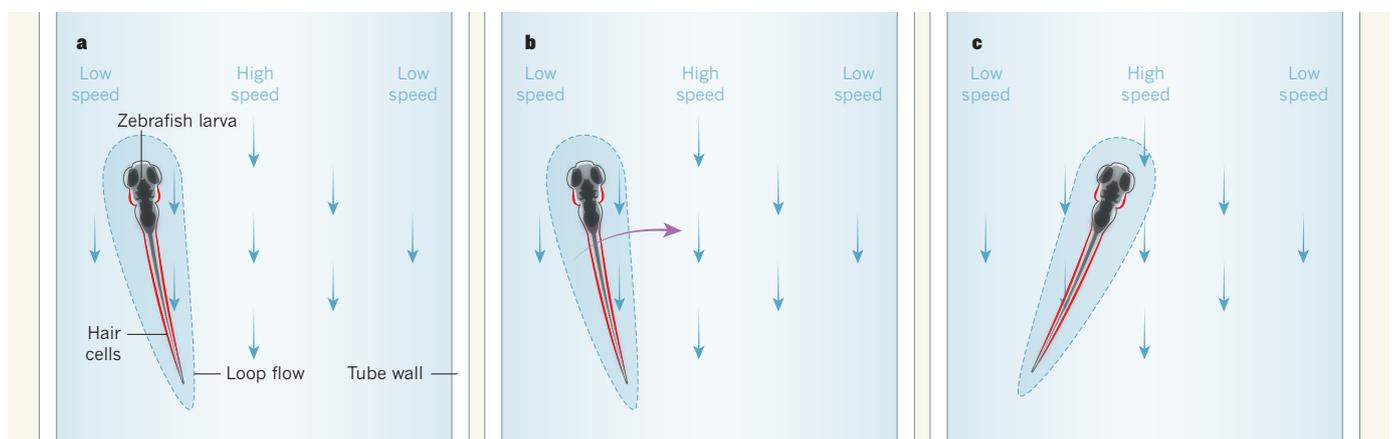
Oteiza and colleagues conducted laboratory experiments in which larval zebrafish (*Danio rerio*) swam in a transparent cylindrical tube through which water was pumped at a steady speed. Friction between the water and the walls of the tube slows the water at the sides, creating a spatial gradient in the speed of the flow from the centre of the cylinder, where the flow is fastest, to the stationary water that is in contact with the tube walls.

The authors confirmed that, consistent with previous studies<sup>4–6</sup>, the zebrafish could position themselves in the tube away from the walls and orient their bodies to swim against the direction of water flow (Fig. 1). Because both skills come in handy for station-keeping and obstacle avoidance in nature, the laboratory

experiments provide a useful system with which to mimic and investigate swimming processes that are relevant to life in the wild. By performing chemical ablations of the lateral line and conducting experiments in the dark to remove visual cues, the researchers demonstrated that the lateral-line system was necessary to achieve oriented movement in response to water flow (a process known as rheotaxis), and that this orientation could not be based on touch or sensing the uniform acceleration of the surrounding mass of water.

How does the lateral line help a fish to orient itself? Oteiza and colleagues' key insight is the application of a nineteenth-century mathematical theorem named after physicists William Thomson (Lord Kelvin) and George Stokes<sup>7</sup>. The Kelvin–Stokes theorem states that, in most cases, the local flow gradients in any region of a fluid will be uniquely associated with the velocity of the flow along a closed loop that surrounds the region. In other words, if a swimming fish can combine knowledge of the speed of the flow of water along different parts of its body — a task enabled by the machinery that the lateral-line system provides — then the information it gathers is sufficient to deduce local gradients in flow speed. The gradients relevant to the Kelvin–Stokes theorem in this context are related to the tendency of the local fluid to rotate, a property known as its vorticity.

One way to understand the connection between flow gradients and fluid rotation is to imagine a boat positioned with its bow



**Figure 1 | Flow-based navigation.** **a**, To understand how fish adjust their position when swimming, Oteiza *et al.*<sup>3</sup> studied the response of larval zebrafish (*Danio rerio*) in a tube in which water moves at high speed at the centre and at low speed near the walls. Blue arrows indicate the direction of the water flow. Zebrafish have a series of hair cells (location of cells shown in red) known as the lateral line, and the authors propose that this system can sense the flow of water in a loop (dashed blue line) that surrounds the fish. They demonstrate that the Kelvin–Stokes theorem<sup>7</sup> can be used to translate the sensed fluid flow into knowledge of the tendency of the fluid inside the loop to rotate (a phenomenon known as vorticity), as well as the magnitude

of the corresponding flow-speed gradients, and that sensing these aspects of fluid flow can help to guide fish navigation. **b**, Oteiza and colleagues observed that when a fish swims towards a region of increasing difference between the flow speeds on either side of its body, the fish turns (purple arrow) in the same direction as the local rotation of the water (not shown), which is also the direction that will carry the fish away from obstacles. **c**, Navigation that is based on the lateral-line sensing of flow-speed gradients enables the fish to swim at the centre of the tube and to avoid the walls. In the wild, this ability could enable fish to navigate complex underwater environments in which visual cues might be insufficient.

facing the direction of the water flow, with water flowing past the boat's right-hand side faster than on its left. If the boat were floating passively, when viewed from above, it would begin to rotate clockwise. The speed of this rotation would be proportional to the difference in the flow speeds on either side, which form a gradient across the boat. A similar information pathway — sensing the velocity around the fish's body through the lateral line, followed by deducing the corresponding direction of local vorticity and estimating the local flow-speed gradients, which are proportional to the vorticity — is at the heart of the proposed mechanism for flow-based navigation in zebrafish.

Successful navigation requires a way of using knowledge of local flow conditions to robustly guide a fish away from harm. The researchers made a striking observation in relation to this. Whenever a fish swam towards a region in which the difference between the flow speeds on either side of its body increased in comparison to the difference at the fish's previous location, the fish made a turn in the direction of the local flow vorticity (by veering either clockwise or anticlockwise). This action reliably steered the animal away from the region near the wall, and towards the centre

of the oncoming flow. Conversely, when the fish swam towards a region in which the flow gradients decreased in comparison to those it encountered previously, it continued to swim in the same direction without a turning bias. Because flow gradients usually decrease the farther away a fish is from a solid object, this navigation strategy should translate into the avoidance of real-world obstacles and the bodies of predators.

The authors took important first steps towards extending their results beyond the realm of controlled laboratory experiments by developing computer simulations that demonstrated the robustness of their observations when modelling the situation in quasi-turbulent flows. However, real aquatic environments present other challenges, such as 3D flow that cannot be navigated solely with turns in a horizontal plane. In addition, the Kelvin–Stokes theorem that underlies the proposed navigation strategy can fail if there are local sources or sinks of water in the vicinity, such as the suction flow that some predators use to ingest prey<sup>4</sup>. Paradoxically, the proposed mechanism for rheotaxis could also lead fish towards regions of flow that, although they exhibit small flow gradients, could simultaneously have large, uniform flow speeds

that overpower the fish's ability to escape such strong currents. Thus, the mechanism described by Oteiza and colleagues is probably paired with other sensing strategies — yet to be discovered, and perhaps also making use of the lateral line — that enable fish to navigate the full complexity of the underwater world. As the full repertoire of these sensing and control skills becomes apparent, we will not only learn more about fish ecology, but might also gain inspiration for new types of bio-robotic navigation in both water and air. ■

**John O. Dabiri** is in the School of Engineering, Stanford University, Stanford, California 94305, USA.

*e-mail:* jodabiri@stanford.edu

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