than possible via the nervous system, and damped elastic elements can buffer perturbations. Both mechanisms may provide simplified control and enhanced stability, which reduce energetic requirements over the timescale of several strides or, indeed, a lifetime. The ability to store and return elastic strain energy may also provide metabolic savings over an evolutionary timescale by enabling advantageous changes to morphology and physiology, such as a reduction in limb mass or the use of slow but efficient muscle. Cycling of elastic strain energy might therefore have energetic benefits over a single movement cycle, multiple movements cycles, a lifetime, and evolutionary time. Fundamental questions of muscle energetics, the role of damping and resonance, and the effects of scale and body bauplans remain unanswered. Thus, the role of elastic energy in locomotion remains an exciting and relevant avenue for functional morphologists, physiologists, and biomechanists alike.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Primer

Fish swimming efficiency

James C. Liao

Every spring a 600 lb Atlantic bluefin tuna travels over 3000 miles from Newfoundland to its spawning grounds in the Gulf of Mexico. That it does so on a meal of a couple of bluefish is nothing short of remarkable. Humans will likely never engineer such an efficient swimming machine. Of course, that has not stopped us from trying. We have achieved remarkable progress by following a strategy of inspiration by nature. At the same time, our fish-like robots often fall short of matching fish performance by a considerable margin. Despite our advances, we are still left asking the question: How do fish swim so well?

First, some groundwork. Fish move in many ways, but this review will concentrate on how the majority of fish species swim, which is by bending the body. Axial undulation occurs by the sequential contraction of segmented muscles that pull on skin and skeleton to bend the body into a mechanical wave that travels tailward. Body undulation is the fundamental movement strategy for several key behaviors, from swimming continuously during long-distance migrations to accelerating in an eye-blink to escape from predators.

The study of fish locomotion has benefited tremendously from an engineering perspective. In our world of steel, plastic and fiberglass, we can define the efficiency of a boat as forward force (thrust) multiplied by speed, divided by the power required to move the propeller. Power out is always less than power in because the motor's power is inevitably wasted in unwanted swirls of water and the production of heat. This measurement of efficiency is only possible because the thrust of the propeller is separated from the drag of the hull. Not so in a swimming fish. Using bones, muscle and skin, thrust and drag are inseparable in fish: different sections of the body can produce either depending on how it is oriented and moving with respect to the flow.

What is efficiency but a measure of performance? The measure of efficiency for a Formula One racing car may be in miles per gallon of fuel, but for a largemouth bass it may simply be successfully catching the next bluegill sunfish, regardless of the precise energetics. What matters to a fish is survival. We need to be mindful of this mechanical *versus* ecological distinction in performance because mechanical advantages, when considered in isolation, cannot define efficient swimming. The danger lies in the assumption of all engineering analyses, *ceteris paribus* ('all other things being equal') which cannot be applied when comparing biological animals. With this perspective in mind, in this primer I will introduce the extraordinary solutions that fish have found to overcome the physics of swimming through water by covering four main topic areas: structure, movement, flow and sensing.

Structure

The drag force opposing a swimmer's forward motion comes from two main sources. One is friction drag and depends on the skin surface, and the other is pressure drag and depends on the body shape. Sharks, tunas and other fast fishes have bumpy skin to ease friction drag, reducing it about 10% (Figure 1A). Water hugs streamlined fish as a result of flow streamlines that obey the law of continuity. But water cannot hang onto even the most perfect fusiform (spindle-like) shapes. Sooner or later, water loses its grip and detaches from the body. When flow separates from a solid surface like this, it creates a wide wake and causes a lot of drag. Functionally, it is akin to opening a big parachute. What bumps give you, in the way golf balls with dimples travel longer paths compared to smooth ones, is the ability generate turbulence right next to the skin of the fish. This keeps the water hugging the body just a little longer to delay flow separation, which thins the wake, allowing fish to open comparatively smaller parachutes.

If we are talking about *any* geometric object gliding through water (cube, car or catfish), pressure drag is a much bigger deal than friction drag. That is because you can play all the physiological tricks you want, but if evolution hands you a box of a body, you won't go fast. We can ignore pressure drag as we are largely in the land of streamlined shapes when dealing

with fishes, but we will revisit it later when we discuss movement.

The tail is the business end of a swimming fish. Tail shapes matter enormously, and some fish cheat the drag game by having forked, high aspect ratio tails, where the ratio of the height to surface area is much greater compared to paddle-shaped, low aspect ratio tails (Figure 1B). What this does is create large thrust forces without having a lot of drag-producing surfaces. Drag is especially bad at the tail tip, where spinning eddies form and are shed. These tip vortices act as a trailing necklace of little parachutes that slows a tail down, and their effect is magnified in low aspect ratio tails. In a steady race across a reef, the forked tail of a King Mackerel gives it an efficiency edge over the broom-shaped tail of a Nassau Grouper.

As shapes matter, so does stiffness. Contracting muscle not only powers locomotion but can also actively stiffen the body in ways that increase swimming efficiency. Stiff bodies transmit muscle forces more effectively to the water, similar to how shifting bike gears enables more efficient climbing of a hill. Fish can make floppy muscles twice as stiff just by playing with the timing lag between contraction and bending. For example, muscles toward the tail can lengthen as they contract, which stiffens the body to push harder against the water, and allows anterior muscles to transfer energy, which can lead to higher tailbeat frequencies (Figure 1C).

Efficient swimming only happens within a sweet spot of stiffnesses, which hovers near the resonant frequency of the body. It also depends on the body size, shape and species, as well as the type of behavior and swimming speed. While muscles can provide active stiffening, the skeleton, skin and scales are a source of passive stiffening, and taken together can substantially tune the flexibility of the body to promote efficient swimming. But anatomy not only provides stiffness, it can also bring springiness. The connective tissue that surrounds muscle allows for elastic energy storage. This phenomenon is found from hopping kangaroos to gravity-driven robots, where kinetic energy can be passively recaptured during repetitive movements, like a child jumping on a trampoline. Springs are also found in fish scales and the integument that keeps them bound together, serving as an elastic sheath that recycles movement energy.

Movement

Jazz musician Duke Ellington got it right when he sang “it don’t mean a thing if it ain’t got that swing”. Swimming efficiently requires the right motions. Undulating fish are not boats; they cannot produce thrust without changing the shape of their ‘hull’. The paradox of swimming is that to generate thrust to move forward you need to wiggle. Wiggling turns a fusiform body into a non-streamlined shape for part of the swimming cycle, as when the head yaws to one side. This increases pressure drag and thus forfeits the advantages of drag reduction that come with a sleek form.

This line of reasoning suggests that eels, with their snake-like motions, limit their swimming efficiency because they wag their heads too much (Figure 2A). In contrast, efficient swimmers should keep their heads arrow-straight and only flap their tails, helping to separate thrust from drag along the body. Tunas, for instance, rapidly oscillate their tail by using special tendon anatomy, propelling themselves forward in a way that avoids bending the whole body into a sinuous wave. By presenting a streamlined shape in the front driven by a flapping motor in the back, tunas are thought to demonstrate the most efficient of the 4 exemplar fish swimming modes (anguilliform eels; sub-carangiform trout; carangiform jacks; and thunniform tunas). At the same time, new research is revealing surprising similarities between these classic movement modes that could redefine our understanding of swimming movements.

Other fish minimize drag not in space (along their body) but in time, adopting a burst-and-coast behavior (Figure 2B). The burst phase is the undulatory, muscle-powered part of swimming, which generates forward momentum. This acceleration comes at the cost of head and body wagging that can drag an otherwise streamlined shape backwards. Once momentum is underway, however, a fish can passively coast forward with the slim profile of an airfoil. This straight gliding behavior reduces drag about 50% compared to powered swimming. The amount of head-wag drag varies: some heads, like those of eels, are tubular, and not laterally compressed like those of a bluegill sunfish, and this minimizes the drag due to yawing. Burst and coast swimming can be combined with other mechanisms to enhance swimming. For example fish fins, like bird wings, have biomorphing capabilities: fish can rapidly expand the surface area of their fins and turn them into a broad paddle during the burst phase, only to collapse them to avoid drag during the coast phase.

What happens to the water as a result of tail movement holds an important secret to efficient swimming. When a tail flaps to one side and fluid moves across

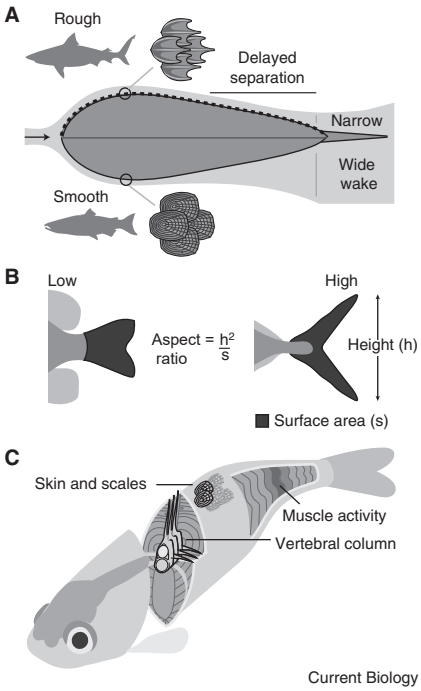

Figure 1. Structural modifications of the body enhance the ability to reduce drag and increase thrust.
Sharks and other fast-swimming fishes have rough scales (A) that create a bumpy surface compared to the smoother scales of other fishes. These bumps generate turbulence which keeps the water hugging the body longer to delay flow separation. A rough surface thins the wake, allowing fish to better slip through the water in a way similar to how dimples on a golf ball allow for longer flight paths. The tails of fast swimming fishes are forked rather than broom-shaped, a feature that minimizes the surface area to the height of the fin (C). Fish have passive mechanisms to increase thrust generation by stiffening the body, using their scales, skin and vertebral column. Fish also actively stiffen the body when they contract their axial muscles during swimming. Illustrations courtesy of Elias Lunsford.

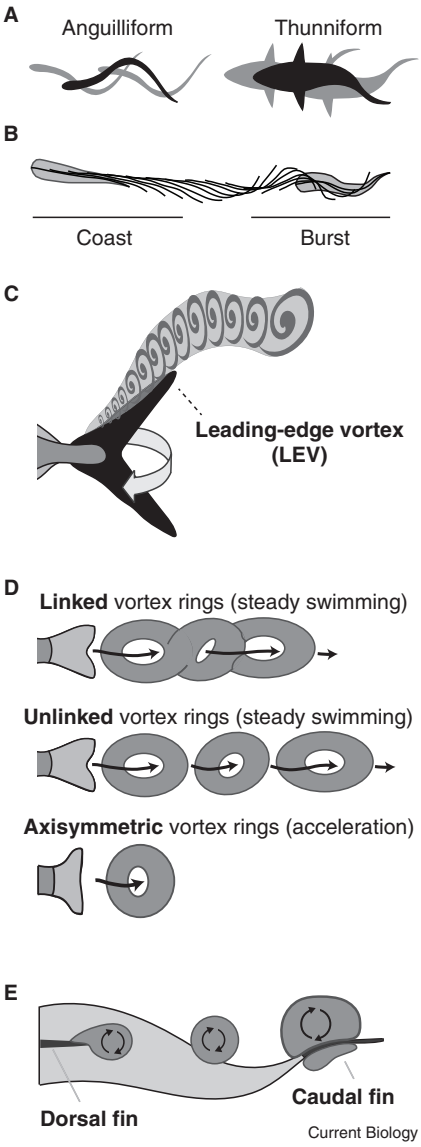

Figure 2. Moving the body in ways that increase hydrodynamic swimming efficiency. Some species like tunas are thought to swim efficiently by flapping their tails and keeping their heads straight, rather than wiggle their whole bodies like eels (A). Within a species, a burst-and-coast behavior serves to reduce drag by separating active, draggy propulsion and passive, streamlined gliding (B). The moving tail generates a leading-edge vortex (LEV), which substantially enhances the production of thrust temporarily (C). The wake of a steadily swimming fish can reveal its efficiency. Linked vortex rings, in the shape of interconnected, wide doughnuts, form behind species that have a certain stiffness and swim above a certain speed (D). Other species that are more flexible or swim more slowly can generate unlinked rings that can lead to inefficient, sloppy wakes. During acceleration, vortex rings become axisymmetric, adopting the most efficient shape required for forward thrust. Vortices generated by median fins, such as the dorsal fin, can be recycled by the proper timing of tail movement to boost locomotion (E). Illustrations courtesy of Elias Lunsford.

it, it creates a big swirl, called a leading-edge vortex. The leading-edge vortex forms and stays momentarily attached, producing a large, temporary force (Figure 2C). Holding onto a leading-edge vortex promotes efficient swimming; the longer the leading-edge vortex is attached, the more force it generates. How a tail moves determines how long this vortex stays attached. The right twist, combined with limiting the tail's high angle with respect to the oncoming flow (both are better with a flexible tail), promotes a vortex that stays attached longer, leading to more lift through favorable pressure distributions. Crook the tail too hard to one side and the potentially lift-producing vortex quickly becomes a parachute, reducing forward thrust. Indeed, it has been found that inefficient swimmers lack a leading-edge vortex. Though our example is at the tail, the leading-edge vortex and the circumstances of its separation can be found on parts of the body and other fins. In a vast ocean, movement is still a game of millimeters, where drag and thrust are interconverted based on slight tilts in three dimensions.

Breaking free from our bias of 'boat-propeller' thinking, studies show that substantial thrust in the form of negative pressure generated at the head sucks the fish forward, analogous to lift generated from an airplane wing. The head and undulating body itself can also pump out low pressure regions that create thrust along sections of the body. Historically, head movements have been interpreted as simply an unintended consequence of undulation, existing because of the recoil of an oscillating tail. It is worth mentioning that head movements coupled correctly with body undulation can optimize propulsion, flow sensing and respiration *simultaneously* without apparent tradeoffs. Doing many things well is itself a form of efficiency, and arguably one that matters more to the survival of a fish than being exceptional at any one particular behavior. Overall, a picture is emerging in which the whole body generates thrust by pulling and pushing itself forward.

You can tell how well a fish swims by the stability of its wake. Scientists have long sought a universal fluid dynamic parameter to encapsulate swimming efficiency across animal diversity. Our best attempt has been a dimensionless variable called the Strouhal number, which measures how often vortices are created and how close they are together. From a fish's perspective, the Strouhal number describes how far and fast the tail wags from side-to-side compared to its forward motion. Fish are most efficient when they come in at a Strouhal number of 0.2–0.4. This is because the Strouhal number is a major determinant of wake structure, which has the final say on what is or is not efficient, more so than body shape, Reynolds number (the ratio of inertial to viscous forces) or swimming mode. A Strouhal number of 0.2–0.4 reflects a wake that has distinct, minimal vortices that facilitate efficient forward swimming, with less energy lost in the wake than from more abundant chaotic vortices. A more chaotic, sloppy wake is often the signature of a floppy fish. This is because when a flexible fish swims, the fluid itself exerts a deforming force back upon the body. If the body deforms too much, it interferes with this momentum transfer and slows swimming, which is revealed in the messy footprints fish leave behind. Any jumble of swirls that adorns the main propulsive jet represents wasted energy since it does not contribute to moving forward.

A wake with a minimal amount of vortices would represent, in three-dimensions, continuously linked vortex rings, where one 'arm' of a doughnut-shaped ring is shared between two successive doughnuts (Figure 2D). These paired vortices, often from stiff-bodied swimmers, lead to higher swimming efficiencies because the energy is invested into water jets that are better directed to move the fish forward. Another situation arises where vortices are unlinked, indicating doughnuts being generated with each tail flick that do not touch each other. The Strouhal number is most useful when predicting the efficiency of stiffer fishes that swim with linked vortex rings. More flexible species can lie outside this range and could be considered less efficient swimmers by engineering standards. Yet some of these species undertake the longest migrations in the fish world. It is important to note that the Strouhal number is only a coarse approximation that works for continuously swimming

fishes and says nothing about efficiency during other transient, but equally important, behaviors, such as acceleration.

Our understanding of how fish swim is biased by studies of steady swimming at constant velocity, largely because of that workhorse for experimental fish biomechanics — the laboratory flow tank. Far less is known about how fish accelerate and decelerate, which are arguably more important in successfully catching prey and escaping danger. The tide is turning, with more researchers recognizing the potential of studying unsteady movements for revealing new hydrodynamic insights. For example, it has been found that accelerating fish can increase propulsive efficiency by enhancing thrust through the alteration of vortex ring geometry, specifically by making more symmetrical vortex rings (not bigger rings as previously thought) than are generated during steady swimming (Figure 2D). While fish exhibit many different ways to swim steadily, this behavioral diversity collapses into a single swimming pattern during acceleration, regardless of the body size, morphology, or ecology.

Vortices are generated not just at the tail, but also along the dorsal and anal fins. This sets up a situation where coordination among these median control surfaces allows fish to recapture their own vortices. A well-timed tail swish can recycle the energy of a vortex created previously by anteriorly located dorsal and anal fins, which can increase thrust and efficiency of the tail by almost 30% (Figure 2E). By actively moving and not simply acting as a passive extension of the body, median fins generate left-side and right-side vortices that do not cross the body midline, which results in increased propulsive efficiency. Taken together, fish summon favorable shapes, stiffnesses and movement patterns to enhance vortex generation and control. It should come as no surprise, then, that fish are masters at exploiting vortices that are already found in their environment.

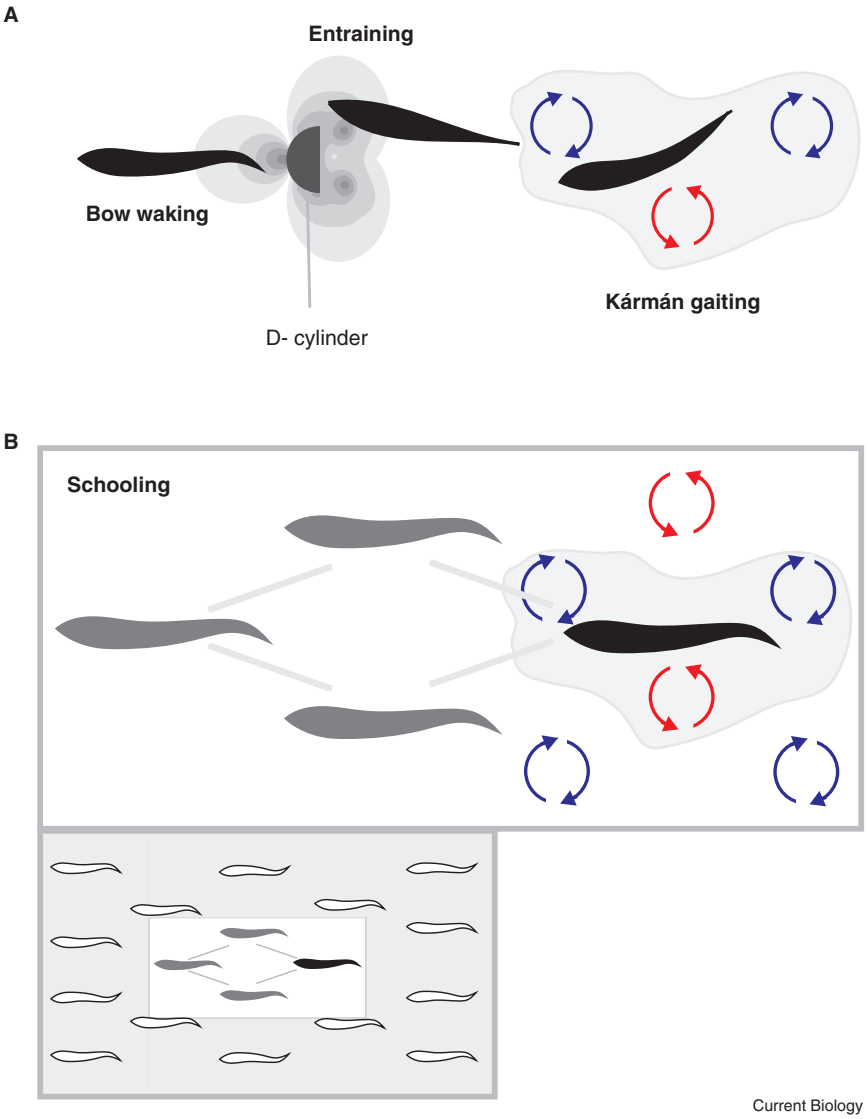

Figure 3. Recapturing the energy of environmental flows.
Environmental vortices, such as those generated in a drag wake by a stationary bluff body (D- cylinder) in flow, can be harnessed by fishes to save swimming costs (A). Fish that take advantage of the high and low pressure regions in front of and behind a cylinder (bow waking and entraining, respectively) consume less oxygen than fish swimming in the freestream flow, as do Kármán gaiting fish that surf on vortices shed into the downstream vortex street. In a similar way, the vortices from side-by-side thrust wakes generated from individuals in a school may be exploited to lower the cost of swimming (B). Advancing research is discovering new ways in which the hydrodynamics of fish schools can lead to energetic savings. Illustrations courtesy of Elias Lunsford.

Flow

Animals living in water are subject to substantial forces generated by flowing water. Fishes are extremely adept at recovering energy from these environmental forces in the form of vortices. Harnessing vortices requires more than the right material properties, shape, or movement. It demands higher-order processing that includes brains and behavior, but it is well worth it; swimming in flow opens up new possibilities for economical movement.

One example is by body surfing. The body of a fish can recapture the energy of vortices drifting around in the environment in a similar way that a fish tail can recapture the energy of vortices shed from median fins. In a von Kármán vortex street behind a cylinder, fish can recapture the energy of vortices by adopting the Kármán gait, a unique undulatory swimming motion (Figure 3A) which consumes 50% less oxygen than during swimming in comparable laminar flow. Paradoxically, proper control of drag production, not thrust production, is what enables a Kármán-gaiting fish to save so much energy. Kármán-gaiting fish use

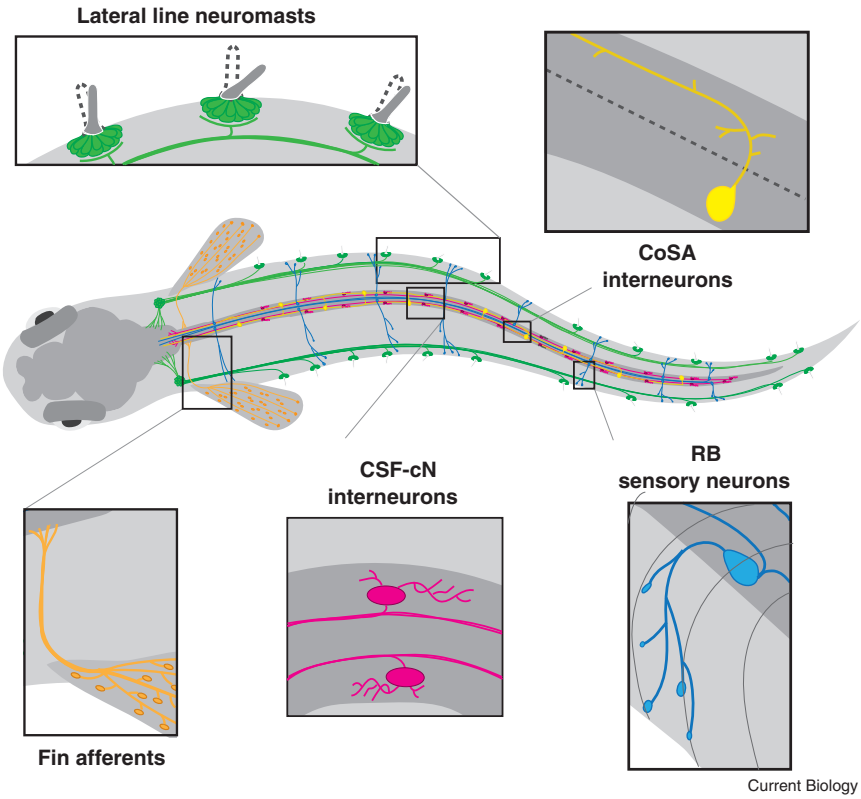

Figure 4. Sensorimotor integration is required to match body movements to the fluid environment.
Fishes possess several distinct types of cells inside their spinal cord that can detect touch along the skin and how their body bends, some of which are illustrated here; cerebrospinal fluid-contacting neurons (CSF-cNs), Rohon Beard sensory neurons (RBs), and inhibitory Commissural Secondary Ascending interneurons (CoSAs). On the periphery, neuromasts of the lateral line system and afferent touch receptors on the body and fins can sense both self-generated and environmental vortices. Illustrations courtesy of Elias Lunsford.

their body and pectoral fins to create drag to maintain position in the sweet spot just downstream of the suction zone of a cylinder, letting them surf where they would otherwise have to swim.

Indeed, the musculoskeletal system is phenomenally well matched to the environment. We know this because a dead fish exhibits unnervingly similar Kármán gait kinematics to a live fish, with the exception that it cannot put on the brakes. In a remarkable example of passive thrust production, the natural flexibility of a trout corpse causes it to frequently surge upstream from the vortex street and into the cylinder suction zone, which is not seen often in live fish. Kármán gaiting is a reminder of how saving energy in more complex environments can arise from different hydrodynamic mechanisms. Energy saving is also substantial for fish swimming in the front of the cylinder, bow waking like a dolphin propped in front of a moving ship. By taking advantage of low-pressure regions of accelerated flow behind and to the side of a cylinder, entraining fish act like drafting race cars, saving 50% of the energy that would be otherwise used during swimming in laminar flows. What is more, the magnitude of these energetic savings associated with location-specific behaviors does not increase linearly with flow speed, instead displaying complex relationships. In real life, this predicts that a river after a heavy rain would reshuffle fish among its rocks as they seek optimal surfing and drafting sites.

As no man is an island, no fish is either. Swimming fish leave vortices that can be harnessed by trailing fish in a school. Indeed, swimming behind a cylinder resembles swimming in the wake behind two fish schooling side by side (Figure 3B). Fish are thought to benefit energetically when swimming in groups because they adopt lower tail-beat frequencies and consume less oxygen. How do they do this? Schooling fish align with vortices shed from neighbors; a little to the left or right matters a lot. Insights into schooling from simplified physical, robotic and computational models show that fish following behind and to one side of a leader can draft much like our race car example above. Multiply this by a thousand moving fish, and a diamond-shaped pattern automatically emerges (Figure 3B).

The problem is that it does not seem like real fish schools adopt this lattice-like structure in nature, and biological data in three-dimensions are technically difficult to collect. In the meantime, experiments with simple fish-like robotics reveal alternatives. By swimming in line behind their neighbors, schooling fish benefit such that *both* the leader and the follower benefit. This linear arrangement leads to suction on the follower's snout that encourages forward motion. In turn, the follower can provide a hydrodynamic push to the upstream leader. Savings can be substantial, up to 70%. *In silico*, machine learning algorithms can train virtual fish to find the most efficient way to swim in a school, which involves running head-first into vortices left by the leader, a form of wake recapture not shown yet in real schools. There remains much that live fish, robots and computers can tell us about movement efficiency in social groups.

Sensing

The right shapes, stiffnesses and movements matter, but without considering how sensory feedback can guide motions we will never unlock how real fish work. Knowing what one part of the body is doing relative to other parts is a prerequisite to the vorticity control that underlies efficient swimming. As vertebrates, fishes have almost all the senses that humans have. But while humans have sensors to detect how much and how fast a muscle stretches, fishes do not. Instead, they have mechanosensitive neurons inside their spinal cord to keep tabs on how they are moving. At least five classes of spinal neurons have been identified in zebrafish and lamprey that monitor bending movements through stretch-receptive and other mechanoreceptive feedback

during swimming: cerebrospinal fluid-contacting neurons (CSF-cNs); Rohon Beard sensory neurons (RBs); inhibitory Commissural Secondary Ascending interneurons (CoSAs); dorsal root ganglion sensory neurons; and lamprey edge cells (Figure 4).

Outside the body, on the skin and fins, the mechanoreceptive lateral line system has long been shown to detect the hydrodynamic environment, such as vortices generated by prey or schooling neighbors. However, the lateral line can also detect self-generated vortices created by the moving body and use it to monitor the undulatory body wave as it progresses to the tail. It does so by comparing a motor copy signal to expectations of self-stimulation, known as the corollary discharge. Given the viscous coupling of fluid to body, it is hypothesized that neural mechanisms sharpen the sensitivity of the lateral line to detect peaks in the undulatory wave and track the motion of the body. In a paralyzed fish, lateral line recordings reveal that fish can detect the passing of vortices down the body. In addition, touch receptors display remarkable discrimination of tactile, and likely hydrodynamic, stimuli. All these sources of sensory input allow fish to align their body movement with motor commands and sense the water that they disturb, a requirement for effective navigation through the fluid medium.

Sensing allows fishes to keep tabs on their ability to exploit vortices in their environment, be it from a rock, their own individual movements, or while embedded in a collective school. An understanding of sensorimotor integration is essential to evaluate how body movements interact with a dynamic environment and provides insight into energy-saving behaviors that analyses limited to pure mechanical output cannot. At the social level, for example, simple sensory algorithms can give rise to complex group formations that enable substantial energy savings, as when the lateral line is used to maintain nearest-neighbor distances in schools. Even at the individual level the complexity is daunting. To an engineer studying fluid-structure interactions, where a movable or deformable *passive* structure is coupled to the surrounding flow, this would be akin to the “structure” now having a sensing body and a decisive brain.

Even as we recognize the importance of sensorimotor integration, the interplay between proprioceptive feedback, motor command circuits, and hydrodynamics remains largely unchartered. In ways that continue to elude us, sensory feedback is used to optimize aquatic locomotion across a range of temporal and spatial scales, promising an ocean of opportunity for future investigations.

Conclusions

In this primer I have highlighted multiple strategies that fish use to swim more efficiently. Some involve structural properties like tail shape and body stiffness, while others involve higher order behaviors to exploit the energy already available in the environment. What all these strategies have in common is that they work within the physical rules imposed by hydrodynamics, facilitating ways of vorticity control that underlies efficient locomotion. Though discussed separately here for clarity, structure, movement, flow and sensing are in reality not independent strategies, and can converge to amplify organismal performance. This synergy is underexplored, ensuring more secrets to be discovered. Our current understanding of the mechanisms of swimming is perhaps only limited by our hesitancy to embrace the complexity of how fish behave naturally. Perhaps more than tools, we need new ways of thinking to bridge this divide. Whether we admit it or not, science is a grand fishing expedition, after all. Let us not forget about the fish.

DECLARATION OF INTERESTS

The author declares no competing interests.

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