Biomimetic Survival Hydrodynamics and Flow Sensing

Michael S. Triantafyllou,1 Gabriel D. Weymouth,2 and Jianmin Miao3

1Department of Mechanical Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, email: mistetri@mit.edu
2Southampton Marine and Maritime Institute, University of Southampton, SO16 7QF Southampton, United Kingdom
3School of Mechanical and Aerospace Engineering, Nanyang Technological University, 639798 Singapore

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Abstract
The fluid mechanics employed by aquatic animals in their escape or attack maneuvers, what we call survival hydrodynamics, are fascinating because the recorded performance in animals is truly impressive. Such performance forces us to pose some basic questions on the underlying flow mechanisms that are not yet in use in engineered vehicles. A closely related issue is the ability of animals to sense the flow velocity and pressure field around them in order to detect and discriminate threats in environments where vision or other sensing is of limited or no use. We review work on animal flow sensing and actuation as a source of inspiration and as a way to formulate a number of basic problems and investigate the flow mechanisms that enable animals to perform these remarkable maneuvers. We also describe some intriguing mechanisms of actuation and sensing.
1. INTRODUCTION

The survival of marine animals depends on their capability of performing extremely rapid maneuvers, whether they escape predators, attack prey in or out of the water, or jump upstream in waterfalls. Measured performance in live animals confirms the expectation that their function has been perfected through evolution. One can think of few instances in which animal performance is more striking, as fish 30 cm long can reach accelerations exceeding 10 times gravitational acceleration in a fraction of a second, and small squids can reach burst speeds of 25 body lengths per second. Such performance is based on underlying flow mechanisms that are not currently used in engineered vehicles. Another critical element for survival is the ability of animals to sense the velocity and pressure fields around them in order to detect and discriminate threats in environments where other sensing is of limited use.

The intrinsic unsteadiness in the actuation of fish locomotion becomes a major asset when large forces and moments must be generated rapidly in escape maneuvers, reinforced by the flexibility and compliance of the body, fins, and wings of the animals. The interplay between vorticity generation and imparting momentum, and hence kinetic energy, to the fluid to power the animals’ survival hydrodynamics is truly fascinating, as evolution has perfected its function. In addition to rapidly maneuvering fish, we consider the cephalopods, such as the octopus and squid, which make up a particularly intriguing class of animals because they incur large deformations and volume changes, forming shapes that apparently violate engineering rules of streamlining, yet achieve escape speeds matching those of the fastest animals, despite their lack of a skeleton. The cephalopods serve as a prime example of bodies that undergo rapid shape and volume changes, so that fluid energy can be recovered and boundary layer vorticity can be shed simultaneously from large sections of their surface, in what is termed global vorticity shedding, to power their remarkable fast-starting maneuvers.

The ability of marine animals to detect their environment through pressure and velocity sensing is best exemplified by the blind cave fish, which darts through cluttered cave environments in absolute darkness, and the harbor seal, which detects the minute fluctuations in the wake of prey up to 30 s after it has passed. Survival has dictated the development of such hydrodynamic sensing, which is totally absent from engineered structures. Again, we review work that poses some basic questions: How detectable is a flow from a localized distributed array of sensors? How can we detect flows down to 1 mm/s while moving at high speed? Overall, we selectively review work on animal flow sensing and actuation to investigate those unsteady flow mechanisms that are employed by animals in survival hydrodynamics.

2. ESCAPE HYDRODYNAMICS

When fish or cephalopods attack or escape, they employ very large body and shape deformations, making the related flow-structure interaction problem radically different from that of rapidly maneuvering rigid-hull vehicles. The measured performance in marine animals in terms of achieving high acceleration very rapidly is impressive, particularly because it is achieved within a heavy liquid. The mechanics to develop the needed thrust require that the animal rapidly move a large mass of its surrounding water without incurring large drag and unrecoverable added mass forces. This simple remark helps us derive unifying principles of actuation.

2.1. Rapid Maneuvering Through Large Body Flexing

Fast-starting fish employ large-curvature flexing of their bodies to achieve impressive acceleration. Webb (1976) explored the fascinating fast-starting performance of the trout, establishing the...
kinematics that lead to such accelerations (see review in Domenici 2011). There is a preparatory phase in which the fish rapidly bends its body into a highly curved shape resembling either a letter C (C-start) or a letter S (S-start). This is followed by a propulsive phase in which the body gradually straightens out, in a traveling wave-like fashion, starting with the head and ending with the tail (Webb 1976), ultimately returning to its regular swimming mode. Harper & Blake (1991) and Domenici & Blake (1997) provided data for other species, especially the pike, an aggressive fish whose maximum acceleration is even more impressive than the trout’s, exceeding 10 times gravitational acceleration. Fish that turn very rapidly while moving forward employ maneuvers that resemble fast starts in many aspects, except that the initial phase, employed by a fish at rest to commence motion, is not needed (Epps & Techet 2007, Wu et al. 2007).

Simple dynamic considerations show that a fast-starting fish must rapidly accelerate as large a mass of water as possible and move it in the proper direction. For a given required fluid impulse (i.e., a given product of fluid mass and velocity), the energy that will be conveyed to the fluid is proportional to the product of mass and velocity squared. Hence, it is advantageous to involve a larger fluid mass so as to reduce the imparted velocity. The acceleration of fluid also implies the generation of vorticity, to be conveyed to the fluid as required by the kinematics of the accelerated flow. This vorticity must be generated at the body and fins of the fish, requiring a carefully choreographed motion driven by its muscles and fins working at full capacity and in a precisely timed manner. Hence, the available muscular power defines the limits of performance (Wakeling & Johnston 1998), but the use of suitable hydrodynamic mechanisms is critical to allow this maneuver to materialize. Figure 1 provides a sequence of particle image velocimetry (PIV) images of the vorticity in the flow around a turning danio. Initially, vorticity is confined to the boundary layer. As the fish moves, the vorticity entrains the kinetic energy imparted to the fluid through its large body flexing to form two vortex rings, a smaller one that powers the initiation of the turn and the rotation of the body and then a stronger ring that provides the required force needed for the rapid acceleration. Borazjani et al. (2012) computationally studied a much faster C-start, obtaining qualitatively similar results, but identified further vortical structures.

When reviewing the literature on live fish, we must account for several complicating factors given that an escape maneuver involves a stimulus from a predator and is part of a predator-prey interaction problem (Weihs & Webb 1984). Hence, depending on the specific circumstances, the specific body shape employed (C-shaped versus S-shaped) provides different kinematics, and the use of fins can also vary, affecting performance (Weihs 1973, Tytell & Lauder 2008). However, some basic fluid mechanisms emerge irrespective of the specifics of actuation.

To begin, it is important to raise the question of whether hydrodynamic considerations are the dominant factor in fast starts. To test this hypothesis, Gazzola et al. (2012) optimized through simulation a single type of maneuver (C-shaped) of a simply shaped fish (zebrafish larvae) that involves only its body and caudal fin. The criterion was to maximize the motion of the fish’s center of mass within a given fixed time for both the preparatory and propulsive phases. Because the time is fixed, this criterion is also equivalent to maximizing speed or acceleration. The optimized kinematics closely resembled the observed live fish kinematics provided in U.K. Müller et al. (2008), hence confirming the hypothesis that hydrodynamics dominate the kinematics of C-starts.

Simulation shed further light on the actuation mechanics. Gazzola et al. (2012) used tracer particles to connect the flow features observed during the first phase of the maneuver, when the flow is largely irrotational, except within the boundary layer of the fish, with the vortical flow features obtained in the wake of the fish at the latter half of the maneuver. The vorticity shed in the wake flow was traced back to the surface of the body and caudal fin. More importantly, the authors established that the mass of fluid, which is accelerated and captured by the body of the fish in the preparatory phase of the C-start maneuver, either is contained in or surrounds the vortical
Vorticity (1/s)

$\Gamma_{2A}$ $\Gamma_{1A}$ $\Gamma_{2B}$ $\Gamma_{1B}$

0 s 0.030 s 0.060 s

0.090 s 0.120 s 0.150 s

0.180 s 0.210 s 0.240 s

0.270 s 0.300 s 0.330 s

Vorticity (1/s)

-60 -40 -20 0 20 40 60
patterns of the wake flow (Figure 2). The irrotational-like flow at the preparatory phase, consisting of dipole-like structures at any particular planar cut that is perpendicular to the mid-line curve (as shown in Zhu et al. 2002), transitions eventually to form two vortex rings. Hence, a principal conclusion of Gazzola et al. (2012) is that the strikingly large initial curvature of the C-start maneuver serves to engage as much fluid mass as possible; The body motion conveys significant kinetic (added mass–related) energy, which is then shed in the fluid together with body-generated vorticity to form two vortex rings powering the C-start. Hence, the initial potential flow-like added mass energy is used ultimately as a propellant in this C-start maneuver (Triantafyllou 2012), a mechanism that is also employed under different conditions by cephalopod fast starts, as shown in the next section.

Animals may employ their fins in an effort not only to better control the C-start but also to increase the kinetic energy imparted to the flow during body bending. Figure 3 provides the kinematics of a bluegill sunfish, which employs its fins during a fast start. The two phases, preparatory and propulsive, produce peaks in the acceleration curve, which remains positive throughout the maneuver (Chadwell et al. 2012). Conte et al. (2010) tested a robotic device shaped like a pike by starting from a highly curved, C-like configuration, storing sufficient potential energy to drive a fast escape when released. With the preparatory phase omitted that would have imparted significant added mass energy, the acceleration fluctuates initially, even reaching negative values.

Figure 2
(a) Vorticity field (z component of ω) in six snapshots of the C-start maneuver of a larval fish, showing the formation of the actuating vortex rings. (b) Evolution of passive tracer particles seeded at t/Tp = 0.5. Three sets of particles (shades of gray) are initialized at different regions and are overlaid on the vorticity field. Figure adapted with permission from Gazzola et al. (2012).

Figure 1
Sequence of vorticity field snapshots obtained through particle image velocimetry at the mid-height planar cuts in the C-start of a danio fish. Vortices marked ΓA and ΓB are cuts of the first vortex ring, and Γ2A and Γ2B are cuts of the second vortex ring. Figure adapted with permission from Epps & Techet (2007).
Figure 3
(a) Displacement, (b) velocity, and (c) acceleration as a function of time in the two phases (S1, preparatory; S2, propulsive) of a C-start for a bluegill sunfish, which also employs its fins. Figure adapted with permission from Chadwell et al. (2012).

(Figure 4), unlike the acceleration of a fast-starting fish. Still, the robot achieved a peak acceleration of 40 m/s², converting 10% of its initial energy to final kinetic energy, and the resulting kinematics are similar to those of fish.

2.2. Fast Starts Through Volume Change

Another group of animals that undergo large-scale deformations during escape maneuvers comprise the cephalopods: the octopus, cuttlefish, and squid. The octopus first hyperinflates its mantle cavity, filling it with water, which it then rapidly expels in the form of a propelling jet through the mantle orifice (Packard 1969, Wells 1990, Huffard 2006). As in the fast starts of fish discussed above, there is a major advantage to accelerating as large a mass of fluid as possible. Hence, the body inflation at the onset of the maneuver must be correspondingly large, increasing the lateral dimensions substantially. The normally streamlined mantle becomes quite bluff; flow around a similarly shaped rigid-body geometry would incur large energy penalties in the form of flow separation drag and increased added mass force. However, the flexible, rapidly deflating mantle completely alters the dynamics of the flow, inducing mechanisms of separation elimination and added mass energy recovery, as investigated by Weymouth & Triantafyllou (2013) and demonstrated experimentally by Weymouth et al. (2015).

The core issue in determining the propulsive performance of the shrinking body is the evolution of the boundary layer vorticity at the external surface of the body as it undergoes large deformations. If this vorticity is shed into the flow, a drag wake will be established surrounding...
the propulsive jet emanating from the orifice, hence severely reducing the escape speed of the animal.

We first turn to the example of a shape change leading to vortex formation in Taylor’s (1953) classic study of a vanishing disk. The solid disk rapidly melts into fluid, and the bound vorticity is assumed to roll up into a single vortex ring. Weymouth & Triantafyllou (2012) used viscous simulations to demonstrate that this assumption is mostly borne out in the case of a melting cylinder, whose diameter is reduced by 20%, and the resulting pair of vortices induces large drag forces. They also found that the flow can be completely different depending on the form of the prescribed surface kinematics. If the body, instead of melting, collapses by undergoing a rapid prescribed shape change, as is more relevant to the octopus, then the vortex layer does not shed and roll up. Instead, it remains close to the body, while its total circulation decreases, as the body shrinks, through vorticity annihilation (Figure 5). As a result, instead of a purely resistive added mass force and separation drag, rapid shrinking causes an additional added mass–related term in the form of positive thrust, through added mass kinetic energy recovery, and the near elimination of viscous drag.

Both the circulation reduction and thrust force result from the pressure gradient on the body, generated by rapidly reducing its volume. Let us consider the pressure distribution on the surface of a sphere of instantaneous radius $R$, translating at speed $U$ in a potential flow:

$$ p_{r=R} = \frac{3}{2} \rho \left( RU + \dot{R} \right) \cos \theta + \frac{9}{16} \rho U^2 \cos 2\theta + C(t), $$

(1)

where $C(t)$ is a constant over the surface and does not contribute to the force or generation of vorticity (Weymouth et al. 2015). For a rapidly shrinking body, the first term implies very low pressure at the front of the sphere ($\theta = 0$) and very high pressure at the back ($\theta = \pi$). The two-dimensional form of this estimate was shown to be remarkably close to the viscous simulations of Weymouth & Triantafyllou (2012). This gradient generates a new sheet of vorticity on the surface of the sphere that lies directly under and has opposite sign than the boundary layer vorticity.
Figure 5

(a) Vorticity field from viscous simulations of a circular cylinder whose diameter shrinks rapidly by 20% as it moves from right to left. (b) The plot of the pressure relative to the stagnation point value on the cylinder surface (leading edge at left, trailing edge at right) at several snapshots in time, showing a large, thrust-producing pressure gradient. The pressure gradient generates a sheet of opposite-sign vorticity (red in back face of cylinder in panel a) under the previously formed boundary layer (blue in panel a), resulting in vorticity annihilation. The pressure gradient generates thrust that is an order of magnitude larger than the steady drag on a rigid body. Figure adapted with permission from Weymouth & Triantafyllou (2012).

formed previously during the onset of translation. The induced normal velocity, pointing toward the surface, forces these two layers against each other, partially annihilating the boundary layer circulation. Recent experiments on flat plates recorded reduced circulation when rapidly changing the apparent cross-stream width of the body (Kriegseis et al. 2013), which may arise from the same mechanism.

The pressure gradient also induces a thrust force on the body that transfers energy between the fluid and body, of the form

\[ F_a = -\frac{d}{dt}(m_a U) = -m_a U - m_a \dot{U}, \]

where \(m_a\) is the instantaneous added mass of the object. Solid bodies accelerating in a fluid experience an opposing force \(-m_a \dot{U}\), but a shrinking body recovers fluid energy to develop thrust equal to \(-m_a \dot{U}\), a term that dominates the overall force at the end of the maneuver. Consequently, larger initial added mass inertia is actually beneficial in the case of fast starts, as long as that inertia is recovered and released during the maneuver. The added mass is fixed for a rigid vessel, making it an additional payload to be dragged along during the escape. In contrast, when the added mass energy is recovered and released, as done in fish by bending and in cephalopods by shrinking, the body effectively turns the original added mass into a propellant. Spagnolie & Shelley (2009, p. 12) also showed this when a moving sphere undergoes a shape change to become a prolate ellipsoid, resulting in a sudden increase, or burst of velocity, as the added mass momentum turns into body momentum: “While a reduced virtual (added) mass gives a reduced acceleration reaction, a reducing virtual mass can generate a boost in velocity.” For a self-propelled deflating body, the recovery of fluid kinetic energy in inviscid flow can accelerate it to speeds 82% greater than a rigid rocket, and even 20% greater than an ideal rocket in vacuum (Weymouth et al. 2015).
As implied by the pressure equation, the relative strength of this effect and the successful control of the viscous boundary layer are dependent on a nondimensional shape-change rate to overcome the rate of diffusion and separation in the boundary layer. As shown by Weymouth et al. (2015), it is insightful to compare a shrinking deformable body to the application of suction on a rigid-body boundary layer, as both processes induce a normal velocity to the body surface, although shrinking induces it without actual mass flow through the membrane. The authors defined a deflation scaling parameter, $\sigma^*$, in analogy to the suction scaling parameter of a cylinder:

$$\sigma^* = \frac{\dot{V}}{\frac{A}{U}} \sqrt{Re}, \quad (2)$$

where $\dot{V}$ is the rate of change of the volume of the body, the Reynolds number is defined as $Re = \frac{UL}{\nu}$, and $A = \frac{\pi D^2}{4}$ is the frontal area. For a sphere, an estimated threshold value of $\sigma^*$ is $2.41\pi$. Hence, the required deflation rate decreases with the Reynolds number, which was confirmed by viscous simulations and experimental testing of a robot (Weymouth & Triantafyllou 2013, Weymouth et al. 2015). As shown in Figure 6, the robot experiences an instantaneous thrust force that is $30\%$ greater than the thrust provided by the propulsive jet (and avoids a $50\%$ reduction in the net force owing to drag forces, as in a rigid body), resulting in a fast-start maneuver with $53\%$ hydrodynamic efficiency. Other soft and deforming animals and mechanisms may employ similar mechanisms to help with their efficient periodic propulsion.

![Figure 6](image)

**Figure 6**

Self-propelled tests of an octopus-inspired robot of length $L = 0.27$ m, consisting of a three-dimensional printed rigid hull with a synthetic rubber membrane stretched over it that is inflated to power a fast start as it subsequently deflates, generating a propulsive jet. (a) Sequential snapshots of the fast start of the deflating robot, marked with time. (b) The robot achieves speeds of $10L/s$ in 1 s (the blue line is the average of 10 runs). (c) Fluid force as a function of time, divided by the force developed by the jet. The robot experiences more thrust than that provided by the jet (force ratio greater than 1, shown by the horizontal dotted line) due to added mass energy recovery. The red line is the fluid force on a rigid, streamlined robot under similar conditions. (d) Integrated power as a function of time, showing that over $50\%$ of the initial energy is recovered. Figure modified with permission from Weymouth et al. (2015).
2.3. Unifying Principles in Fish and Cephalopod Fast Starts

Fish employing C-starts and cephalopods escaping through the rapid deflation of their initially hyperinflated mantle are found to use the same principles. Fish engage in large-curvature maneuvers to impart large kinetic (added mass) energy to the fluid, which is entrained and released in the vortex rings that power their maneuvers. Similarly, escaping cephalopods are initially bluff, imparting large kinetic (added mass) energy to the fluid, which they recover as they deflate rapidly to produce thrust in the later stages of their maneuvers, when it is most useful, because their mass is substantially less as they have expelled fluid from their mantles.

However, this performance is conditional on avoiding uncontrolled flow separation. In the case of fish, a highly choreographed motion ensures that they do not create large angles of attack with respect to the flow. In the case of cephalopods, a more intricate mechanism of separation elimination is employed as deflation must be rapid enough to create opposite-sign vorticity to partially eliminate the boundary layer vorticity and impose a normal velocity component to the body surface that prevents separation. Both components are equally important so that the fluid kinetic energy is recovered by the body rather than shed into the fluid together with the excess boundary layer vorticity.

3. FLOW SENSING IN AQUATIC ANIMALS AND MARINE VEHICLES

For fish survival, timely and accurate sensing is as important as agile actuation, whether it is to avoid predators or to detect prey. For example, C-starts can generate strong and long-lasting flow signatures (Niesterok & Hanke 2012), and swimming fish can be tracked via their wake long after they have passed. Although vision, hearing, and smell are also employed, many aquatic animals possess the unique ability to detect prey or predators and even form a three-dimensional map of the surroundings by sensing the velocity and pressure fields through multiple sensors distributed along their bodies. We first selectively review the literature on the physiology (structure, size, location, and density of the sensors) and reported function of the animal sensors to assess the feasibility and limitations of flow sensing and then review the efforts to replicate this function with engineered sensors.

3.1. Flow Sensing: The Lateral Line of Fish

Detailed, excellent recent publications provide rich information on the function of animal sensing (Bleckmann et al. 2014, Coombs et al. 2014). Fish utilize cues from their lateral line system, so named because its most visible part is a line of scales running down the side of the fish, to locate predators or prey and underwater objects and form schools (Pitcher et al. 1976, Chagnaud & Coombs 2014, Webb 2014b). The capabilities of this organ are best exhibited by the blind cave fish, Astyanax mexicanus fasciatus, because of its lack of functional eyes. Cave fish, typically up to 10 cm in length, live in dark caves and have atrophied eyes but are capable of forming a three-dimensional map of their surroundings by sensing flow velocity and pressure variations (von Campenhausen et al. 1981, Montgomery et al. 2001).

The sensory units of the lateral line, the neuromasts, are spread across large portions of the surface of the fish’s body. Each neuromast sensor consists of hair cells that are embedded in a cupula containing a soft gelatinous material. Each hair cell consists of a long kinocilium and an attached bundle of stereocilia, shorter and graded in height. The hair cells are connected to the afferent fibers at the base and form the principal sensing element. There are two types of neuromasts: superficial neuromasts (SNs), which are freestanding on the surface of the skin and
There are differences between SNs and CNs stemming from their distinct morphology, such as the difference in the shape of the cupula. For example, a CN has a hemispherical cupula hundreds of micrometers in diameter, whereas the SN cupula is oval shaped, 10–60 μm wide, and 50–400 μm high. Additionally, SNs typically contain roughly 10 hair cells, whereas CNs contain hundreds, or even sometimes thousands, of hair cells (van Netten 2006). The cupula of an CN is found to slide on its epithelium like a rigid body resisted by spring-like hair bundles, which is unlike the elongated cupula of an SN, which bends in the flow like a beam. Both SNs and CNs contain two groups of oppositely oriented hair cells that are spatially intermingled.

SNs have high sensitivity for flow sensing and can even sense the flow created by planktonic prey in water. At a frequency of approximately 100 Hz, a displacement of 1 nm is sufficient to cause a neural response, whereas displacements greater than 100 nm cause the saturation of individual hair cells (van Netten 2006).

CNs are embedded in subdermal canals and are exposed to the flow through pores (Figure 7a), whose walls are formed by rigid structures, such as bones or scales. The canal lateral line system comprises a trunk canal and cephalic canals. The trunk canal typically consists of one or multiple linear canals that run laterally down each side of the body, whereas the cephalic canals are complex and form a three-dimensional pattern around the head (Webb 2014a). A single neuromast is embedded between two pore openings, actuated only when there is a pressure difference between the consecutive pores. The motion of water inside the canal is impeded by the inertia of water and the friction offered by the canal walls. At low frequencies, the friction generated by the walls of the canal is dominant (Montgomery et al. 1995), whereas at high frequencies the mass of fluid in the canal acts as a low-pass filter. As outlined by van Netten (2006), the mass of the CN cupula and the stiffness induced by the large number of hair cells result in a resonance frequency below 100 Hz, whose ultimate effect is to render the sensor sensitivity flat up to a frequency of roughly 100 Hz. The CN acts effectively as a band pass filter of oscillatory pressure gradients.
That neuromasts are concentrated at locations where changes in pressure are greatest during motion through water, while their morphology changes as fish develop through the embryonic, larval, and juvenile stages, points to the continuous optimization of the location of these sensors for best flow sensing (Webb 2014a, Ristroph et al. 2015).

The lateral dimension of the SN is of the order of 100 μm, so for flow speeds up to 1 m/s, the Reynolds number is below 100 in open flow. Hence, accounting for the effect of the boundary layer thickness, which is typically larger than the SN height, the relevant Reynolds number is even smaller (McHenry & Liao 2014). As a result, the force on the SN is largely viscous, and it is unlikely for the neuromast to develop a Kármán street, whose unsteady fluctuations would cause considerable measurement noise. Similarly, the internal flow in the canal due to external pressure gradients is likely to be far smaller than 1 m/s; hence a CN is also not expected to develop an unsteady wake, despite its larger size. It is estimated that, as a lower threshold, CNs can respond to internal velocities down to 1–10 μm/s or accelerations of 0.1–1 mm/s² and SNs to internal velocities down to 25–60 μm/s (van Netten 2006, Rapo et al. 2009).

3.2. Forming Three-Dimensional Images Through Near-Body Flow Sensing

The lateral line is known to help fish perform complex sensing tasks, such as detecting threats to spark C-starts, as well as assisting in Kármán gaiting through vortex detection (Liao 2006, 2007). The central question is on the possibility of forming a three-dimensional map of the flow, at least in the vicinity of the fish, through velocity and pressure measurements obtained using multiple sensors spread over a specific area of a moving body, such as the SNs and CNs of the lateral line of fish. Montgomery et al. (2001) determined that while SNs in cave fish detect flow patterns over the surface of the body, the CNs' most important role is in active hydrodynamic imaging, creating a cognitive three-dimensional map of their environment through continuous swimming around obstacles so as to generate strong pressure gradients.

3.2.1. Flow reconstruction: inviscid theory. For two-dimensional inviscid flow, it can be shown that a body moving in prescribed motion around another body can use distributed measurements obtained over some time period to create a complete map of the flow, provided the two bodies are in relatively close proximity, of the order of one body length or less (Sichert et al. 2009, Bouffanais et al. 2010); the presence of an external flow makes identification easier. Bouffanais et al. (2010) analyzed the mapping of an environment via pressure signals, first to determine the pressure signal of a given obstacle shape and then to find the location and shape of a body given its pressure signal. They found that insufficient information is provided about the shape by a pressure signal at a single location. The information regarding the size, orientation, and position decays proportionally to 1/d², 1/d³, and 1/d³, respectively, where d is the distance between the sensor and the body. An unscented Kalman filter was used with noisy pressure signals, obtained as the sensor moved around an object, to detect the position and shape of the pressure-generating body. The authors found that the fish had to be within a distance of 6D, where D is the size of the object, to detect size and within 3D to detect position. Obtaining any further details of the shape requires an even shorter distance.

Windsor et al. (2010) studied the effects of a fish gliding parallel to a wall in close proximity and found that detection is possible at distances less than 10% of the length of the fish. Gao & Triantafyllou (2012) used pressure sensor arrays in a maneuvering underwater vehicle to detect the flow direction using unscented Kalman filtering and used the flow measurements in a feedback loop to control its orientation. A critical element in the controller during vehicle linear or angular
acceleration was to subtract the pressure caused by the vehicle’s own motion (added mass–related pressure).

3.2.2. Flow reconstruction: viscous effects. In viscous flows, potential flow methods become invalid once flow separation occurs, and there are no direct methods for object identification. After first identifying the principal features of the vortical wake of several bluff cylinders by performing a principal component analysis on a set of training data, Fernandez et al. (2011b) used a streamlined body instrumented with an array of seven commercially available pressure sensors to estimate the shape, position, and velocity of any one of the bluff cylinders translating in close proximity. A clear differentiation could be made between a circular cylinder and a square cylinder, for example.

Bleckmann & Zelick (1993) towed objects in linear or slightly curved paths very close (1 cm) to electric fish. Responses increased with object speed, eventually showing saturation. As the distance increased, the response decayed as a power function of distance. A rectangular object on a circular orbit was towed at various speeds near a catfish (H.M. Müller et al. 1996) and close to a goldfish (Mogdans & Bleckmann 1998), eliciting responses that increase with the speed of towing. The peripheral lateral line units of the goldfish responded with predictable patterns. Plachta et al. (2003) towed a sphere 8 mm in diameter at constant speed close to a goldfish and found three types of response. First, some lateral line units (likely to be SNs) responded maximally when water velocities across the surface of the fish increased owing to sphere movement. Second, other units responded only when the sphere passed a certain location on the fish’s head or body, but did not positively correlate with the water motions at that location (likely to be CNs). Third, other units responded only after the sphere had passed the fish.

Fish receive stimuli not only from external disturbances, but also from flow disturbances caused by their own motion. This requires two strategies. First, fish must switch off sensor input in the absence of external stimuli, and second, they must be capable of either storing self-made flow noise patterns, so as to subtract them from the total sensory input, in the same way they learn to discriminate between objects (von Campenhausen et al. 1981), or engaging their brain when actively swimming to subtract flow noise using the motor excitation as a reference. As expected, an actively flapping fish generates more noise; hence, fish have a sensory advantage when gliding.

Fish are known to wander about obstacles to detect their shape (von Campenhausen et al. 1981). Fernandez et al. (2011a) employed potential flow methods and unscented Kalman filters to experimentally detect the position and shape of a cylinder or ellipse using noisy pressure measurements obtained over a period of time at three locations on a streamlined foil gliding at constant speed in close proximity. As shown in Figure 8a, a first pass by the foil allowed a good first approximation of the location and size of the cylinder, and then a second pass allowed a very accurate estimate of both. However, once the foil went past the cylinder, strong vortical structures emanated from the foil owing to hydrodynamic interaction with the cylinder, causing large pressure oscillations in the measurements (Figure 8c).

For simple objects, pressure measurements made up to the time at which the flow separates may or may not be sufficient for detection, and this is generally a serious limitation for inviscid methods. However, Maertens & Triantafyllou (2014) showed that the dominant frequency and wavelength of these unsteady vortical structures, whose effect on the pressure can be seen in Figure 8c beyond the vertical dotted line, develop as a result of an instability of the average shape of the boundary layer profile of the foil and hence can be predicted using instability theory. This instability amplifies the potential flow-like disturbances caused in the front part of the foil. Because the form of these disturbances is specific to the cylinder shape that generated them, they can be further used to identify its shape. The findings support the intriguing possibility that the significant unsteady viscous effects caused by nearby bodies on the
3.2.3. Tracking swimming fish: the pulsating dipole analogy. At relatively small distances away from a vibrating, constant-volume, flexible body, the leading hydrodynamic term is that of an oscillating-strength dipole. Hence, the pulsating dipole flow generated by a harmonically vibrating rigid sphere has become the canonical model for studying the detection of swimming fish or zooplankton when their wakes are not involved. Mottled sculpin approximately 10 cm in length, for example, will strike at a vibrating sphere in the dark when placed within a distance roughly equal to their length (Coombs & Conley 1997).

Figure 8
(a) Sequential snapshots of experimental shape identification of an elliptical cylinder using three pressure sensors placed on a gliding foil (gray streamlined shape) of chord $c = 10$ cm, moving at velocity $U$. The dots on the foil denote sensors: Sensor 1 (orange) is near the nose, followed by sensors 2 (dark yellow) and 3 (red). The dotted blue lines denote the true position and shape, and the solid green lines represent the estimated position and shape. (b) Same experiment repeated using the results from the experiment shown in panel a as a first guess. Panels a and b adapted with permission from Fernandez et al. (2011b). (c) Pressure measurements from the three sensors as a function of the relative position between the foil leading edge and cylinder right edge, $x/c$. Note the large oscillations beyond $x/c = 0.20$ (vertical dotted line), when the cylinder is above the middle of the foil. Panel c adapted with permission from Maertens & Triantafyllou (2014).

fish boundary layer, far from preventing detection, could be used by animals to better identify objects.
Montgomery et al. (2001) found that SNs in cave fish detect flow patterns over the surface of the body and can help in orienting the fish within a current (rheotaxis) and possibly in localizing small vibrating sources, although CNs play the principal role in detecting small prey. Hassan (1993) showed that the flow generated by a vibrating sphere near the cast model of a blind fish has characteristic patterns that can be detected by distributed SNs, provided that the (potentially strong) effects of the boundary layer are accounted for, and by distributed CNs if the effect of the orientation of the canal relative to the position of the sphere has been accounted for. Curcic-Blake & van Netten (2006) used a Teflon sphere with 5-mm diameter vibrating in a direction roughly parallel to a ruffe lateral line canal, 10 cm in length, at a frequency of approximately 70 Hz, placed at distances of the order of 10 mm. The hydrodynamic signals detected by the lateral line have sharply characteristic shapes as a function of length, allowing the precise detection of the sphere's location, and the amplitude and frequency of oscillation. There is a lower detection threshold, estimated at $2D_s$, where $D_s$ is the distance between two adjacent pores, and an upper distance threshold estimated at $L/\sqrt{2}$, where $L$ is the length of the lateral line canal. Consistent with the idea of detecting the pulsating sphere through its spatial signature, striking fish employ strategies that keep the sphere lateralized (Coombs & Conley 1997).

Rapo et al. (2009) studied the flow effects on a fish-like body caused by an oscillating sphere. The unsteady boundary layer on the fish has a typical thickness of 80 $\mu$m at 80 Hz and alters the magnitude and phase of the velocity within this distance. They found that the potential flow can be used to calculate relatively accurately the pressure gradient patterns to the lateral line system, but not the velocity field, because of the oscillatory boundary layer on the skin of the fish.

### 3.2.4. Tracking vortical structures with neuromasts

Fish generate strong vortices and form vortical wakes and jets for their propulsion and maneuvering. Hence, tracking other fish or forming schools requires the detection of vortical structures. The characteristic low-pressure signature of a vortex makes it easily detectable through pressure sensing. Thus, it is anticipated that this is a function primarily for the CNs, although SN arrays can also assist. Additionally, for a fish to move or position itself stably within vortical flows, it must sense the oncoming vortices. Trout placed behind a bluff cylinder are capable of extracting energy from the oncoming wake (Liao et al. 2003) by slaloming through the Kármán street vortices; hence, they must be capable of sensing vortices. Beal et al. (2006) showed that with pressure sensors, it is possible to extract net energy for self-propulsion from a Kármán street using a flapping foil. Liao (2006) studied the effect of vortical flows on the lateral line of trout, finding that the lateral line plays a greater role than vision in holding station in a Kármán street.

Chagnaud et al. (2006) stimulated the lateral line of a goldfish with a vortex ring that moved laterally and at a close distance to the fish. They concluded that fish might be able to extract sensory information from complex stimuli such as vortices by comparing the activity of a whole array of neuromasts.

Several authors have established the feasibility of tracking vortices and vortical wakes: Yang et al. (2006) for vortical wakes and Ren & Mohseni (2012) for regular or reverse Kármán vortex streets using CN-like sensors distributed over the surface of a body, which provide sufficient information to extract the circulation of individual vortices, the wavelength of the Kármán street, the distance between the body and the fish $h$, and the speed of propagation of the street. Similarly, using an array of pressure sensors, Akanyeti et al. (2011), Venturelli et al. (2012), Salumae & Kruusmaa (2013), and Chambers et al. (2014) demonstrated the feasibility of extracting features from the flow, such as the vortex shedding frequency, traveling speed, wake wavelength, and turbulence intensity.

Fernandez et al. (2011a) determined the strength and position of a free vortex pair translating near a streamlined body using sparse pressure sensor measurements and a potential flow model.
Vortex detection on a stalling foil at an angle of attack of 35°, translating at 0.3 m/s, equipped with four pressure sensors (colored dots on the foil). (a) Vorticity field obtained via particle image velocimetry. A shed leading edge vortex (LEV) is clearly visible adjacent to the second sensor. (b) Time trace of the pressure at the sensors, starting from the leading edge: sensor 1 (orange), 2 (dark yellow), 3 (red), and 4 (purple). The gray vertical dotted line corresponds to the time at which the image in panel a was taken. Figure adapted with permission from Fernandez et al. (2011a).

3.3. Biologically Inspired and Biomimetic MEMS Sensors

MEMS and NEMS (micro/nanoelectromechanical systems) technology offers unique advantages for developing inexpensive, low-power arrays of microflow and pressure sensors emulating the function of the lateral line. Inspired by the neuromasts on various species, Yang et al. (2006, 2011), Chen et al. (2007), Dagamseh et al. (2012, 2013), Tao & Yu (2012), McConney et al. (2009a), and Klein & Bleckmann (2011) developed MEMS-based sensors using piezoresistive and piezoelectric materials, resistive polymer, and capacitive as well as optical methods to convert the flow-induced deflection of pillars, rods, bars, or membranes to electrical signals.

Figure 10 shows an artificial SN-like velocity sensor (Liu 2007). The hair cells (less than 1 mm in height) did not extend beyond the boundary layer generated by the flow (Chen et al. 2007; Dagamseh et al. 2012, 2013). McConney et al. (2009b) and Kottapalli et al. (2013) developed biomimetic SN-like structures with an artificial cupula, proving that sensitivity can be enhanced by at least an order of magnitude. Kottapalli et al. (2013) reported a biomimetic SN polymer MEMS flow sensor using an LCP membrane, a high aspect ratio, and a 3-mm-high Si60 polymer
Figure 10

Biomimetic MEMS sensors. (a) Sensors featuring SU-8 hair cells, 700 μm tall, located at the distal end of a microcantilever with embedded piezoresistors at the hinge, demonstrating ultrahigh sensitivity in sensing flow velocity and direction. Panel a taken with permission from Liu (2007). (b) Image of a liquid crystal polymer membrane (2-mm diameter) pressure sensor. Panel b modified with permission from Kottapalli et al. (2012b). (c) Piezoresistive sensor with cupula and encapsulated nanofibers. Panel c taken with permission from Kottapalli et al. (2013).

Most research has focused on developing single flow sensors based on the SN structure, whereas the CN structure has received less attention (Yang et al. 2011, Ren & Mohseni 2012). Klein & Bleckmann (2011) developed artificial lateral line canal sensors that use optical sensing by determining the flow-mediated light transfer efficiency through tiny silicon bars (which act as hair cells) embedded in canals. CN-inspired sensors placed in a canal were developed by Kottapalli et al. (2014b). The distance between two artificial canal pores is 6 mm, and the canal pore diameter is 1 mm.

Dusek et al. (2013) conducted field experiments using an autonomous surface vehicle equipped with three experimental pressure sensor arrays complemented by commercially available sensors. Two flexible arrays were developed using a silicon piezoresistive sensor die mounted on LCP and flexible printed circuit board substrates, respectively. A third sensor array was developed using carbon black polydimethylsiloxane (PDMS) composite patterned in a strain-gauge arrangement on a flexible PDMS substrate. The authors demonstrated that the vehicle steady and transient motions could be detected accurately based on the pressure measurements of any of the three sensor designs.

3.4. Tracking Wakes with Pinniped Whiskers

Observations on pinnipeds, such as sea lions and harbor seals, revealed an impressive ability for prey tracking. Dehnhardt et al. (1998) studied the response of a harbor seal to dipole stimuli, showing their ability to detect minute water movements, as low as 0.3 mm/s. In a subsequent study, Dehnhardt (2001) showed that a blindfolded seal can follow the trail of a small model submarine, even after 30 s had elapsed, when the wake defect velocity was approximately 30 mm/s. Schulte-Pelkum et al. (2007) reported that seals can accurately track hydrodynamic trails created...
Wieskotten et al. (2010) proposed that seals use both the structure and spatial arrangement of the vortices in hydrodynamic trails for detection. Spedding (2014) provided basic scaling arguments for how the seals may be able to track a wake of a certain width. Wieskotten et al. (2011) showed that seals can distinguish certain towed shapes (e.g., triangle, square) based on the wake they leave. Miersch et al. (2011) found a reduced sensitivity for sea lions compared with that of harbor seals, attributing the difference to the special, undulatory whisker shape of the latter. This unique geometry of the harbor seal vibrissae, detailed by Hanke et al. (2010) and Ginter et al. (2010, 2012), consists of a spanwise undulatory shape with a span-varying elliptical cross section (Figure 11). Hanke et al. (2010) showed that these undulations disrupted the coherence of the shed vortex streets and minimized the induced lift forces behind stationary whiskers. Beem & Triantafyllou (2015) conducted forced and free vibration tests on scaled-up models of harbor seal whiskers, and Hans et al. (2013) conducted three-dimensional simulations, confirming that the whiskers have a significantly reduced amplitude of vortex-induced vibrations, to less than one-tenth of that experienced by a circular cylinder. The reduction occurs when the whiskers are aligned to the flow along their long axis, whereas when exposed at an angle of attack, significant vibrations occur.

As shown by Beem & Triantafyllou (2015), the strong directional sensitivity of the harbor seal whisker explains its ability to sense minute vortical flows. When towed along its streamlined axis, it vibrates with amplitudes below 5% of its diameter. However, when placed within a wake, it is also subject to a transverse flow velocity component, which causes a dramatic change, as

Figure 11
(a) Comparison of a sensor reproducing the harbor seal whisker shape and a whisker from a harbor seal (maximum width 1.15 mm).
(b) Sequence of snapshots of a whisker vibrating inside the wake of an upstream cylinder; steady flow is from left to right. The red ellipses depict the instantaneous position of the cross section of the whisker at the same plane as the flow visualization of oncoming vortices using upstream released dye. Vortices (shown as outlined patches) move from left to right. (c) Same image as in panel b, keeping the vortices stationary to show the slaloming path of the whisker, driving its high sensitivity of response and frequency locking. Figure adapted from Beem & Triantafyllou (2015).
the vibratory response increases by an order of magnitude. Equally important is the locking in of the frequency of the whisker response to the dominant frequency of the wake. The authors identified an energy extraction mechanism driving these wake-induced oscillations of a whisker placed within an oncoming Kármán wake, which is associated with the slaloming motion of the vibrating vibrissa shown in Figure 11. The motion of the vibrissa has similarities with the motion of an energy-extracting foil (Streitlien et al. 1996, Beal et al. 2006) and a trout swimming in the wake of a cylinder (Liao et al. 2003).

Engineering applications have emerged. For example, Solomon & Hartmann (2006) used steel whiskers fitted with strain gauges; Stocking et al. (2010) and Eberhardt et al. (2011) proposed whisker-like sensors mounted on a cone-within-a-cone capacitor base to measure capacitance changes as the sensor moved due to fluid motion. Valdivia et al. (2012) developed flow sensors based specifically on the undulatory shape of a harbor seal whisker. Valdivia & Bhat (2014) studied the effects of the follicle material properties on their sensitivity and range (Valdivia et al. 2013) and developed a tunable whisker sensor.

3.5. Assessment of Bioinspired Flow Sensors

Emulating the sensing capabilities of fish will be unquestionably of great value for the flow control, navigation, and maneuvering of engineered vehicles and structures and experimental fluid mechanics. However, the complexity of the structure and function of the animal organ and the processing of its information by the central nervous system are still not well known and understood. It will take a coordinated effort in animal studies and sensor development using novel technologies to generate a sensing capability to provide in real time a three-dimensional map of the near-field underwater environment.

For sensors mounted on the surface of a moving body, pressure sensors have an advantage over velocity sensors, as the boundary layer poses no problems for the former, as long as it remains attached, because the pressure remains constant throughout the thickness of the boundary layer. Pressure sensors using a thin diaphragm have been successfully tested (Figure 10), but they suffer from the need to equilibrate the ambient pressure, particularly for deep-water applications, where hydrostatic pressure is the dominant component. Biomimetically designed CN-like pressure sensors provide a fine alternative solution.

Velocity sensors similar to SNs are significantly influenced by the boundary layer; such effects vary with Reynolds number and hence with the relative speed of the body and the surrounding flow, requiring adjustment of their calibration. In addition, the sensors have to be very small; otherwise, they will generate a Kármán street of their own, adding significant noise to the measurements.

To emulate the sensing abilities of fish, the artificial sensors must also match the sensitivity of the lateral line, while preventing self-generating flow noise. The use of a biomimetically designed cupula-like structure (Figure 10) increased the sensitivity significantly. Inspired by the fact that each hair cell consists of bundles of kinocilia, which move in near unison and hence allow the magnification of the produced signal (Corey et al. 2004), Asadnia et al. (2013b) developed a sensor consisting of graded rows of bundled PDMS polymer pillars connected at the top with polyvinylidene fluoride polymer fiber links. The links stretch and generate electric charges when the pillars, which are graded in height, bend in response to flow (Figure 12), thus amplifying the total signal significantly.

Inspired by the properties of pinniped whiskers, Asadnia et al. (2015) developed a neuromast microfabricated by stereolithography with an undulating shape and placed it on a self-powered piezoelectric diaphragm sensor (Figure 12c). The sensor demonstrated a high signal-to-noise ratio and high directional flow-sensing capability. In addition, this sensor can be scaled up in size.
MEMS sensors emulating advanced biomimetic features. (a) A schematic illustration of a hair cell–inspired NEMS sensor, showing six rows of PDMS polymer pillars of graded height (maximum height of 425 μm). The links connecting the distal tips of the pillars are formed by polyvinylidene fluoride polymer, which generates electric charges as the pillars bend, causing stretching in the fibers, amplifying the signal. (b) Photograph of the implemented NEMS sensor. Panels a and b taken with permission from Asadnia et al. (2015). (c) Stereolithography fabricated whisker-like sensor on a piezoelectric diaphragm. The whisker height is 3 mm. Panel c taken with permission from Kottapalli et al. (2014a).

Figure 12

The study of animal sensors reveals that the complexity of the form and structure of their organs plays an important role in their outstanding sensitivity and function. Moreover, as more information is becoming available on how the multiple-sensor input is transmitted and processed by the central nervous system, it is anticipated that significant progress will be made in the near future toward the goal of generating a distributed touch-at-a-distance flow-sensing system.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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