

## REVIEW

### Biomimetic and bio-inspired robotics in electric fish research

Izaak D. Neveln<sup>1</sup>, Yang Bai<sup>2</sup>, James B. Snyder<sup>1</sup>, James R. Solberg<sup>3</sup>, Oscar M. Curet<sup>4</sup>, Kevin M. Lynch<sup>2</sup> and Malcolm A. MacIver<sup>1,2,5,\*</sup>

<sup>1</sup>Department of Biomedical Engineering, Northwestern University, Evanston, IL 60208, USA, <sup>2</sup>Department of Mechanical Engineering, Northwestern University, Evanston, IL 60208, USA, <sup>3</sup>HDT Robotics Inc., Evanston, IL 60201, USA,

<sup>4</sup>Department of Ocean and Mechanical Engineering, Florida Atlantic University, Boca Raton, FL 33431, USA and

<sup>5</sup>Department of Neurobiology, Northwestern University, Evanston, IL 60208, USA

\*Author for correspondence (maciver@northwestern.edu)

#### Summary

Weakly electric knifefish have intrigued both biologists and engineers for decades with their unique electrosensory system and agile swimming mechanics. Study of these fish has resulted in models that illuminate the principles behind their electrosensory system and unique swimming abilities. These models have uncovered the mechanisms by which knifefish generate thrust for swimming forward and backward, hovering, and heaving dorsally using a ventral elongated median fin. Engineered active electrosensory models inspired by electric fish allow for close-range sensing in turbid waters where other sensing modalities fail. Artificial electrosense is capable of aiding navigation, detection and discrimination of objects, and mapping the environment, all tasks for which the fish use electrosense extensively. While robotic ribbon fin and artificial electrosense research has been pursued separately to reduce complications that arise when they are combined, electric fish have succeeded in their ecological niche through close coupling of their sensing and mechanical systems. Future integration of electrosense and ribbon fin technology into a knifefish robot should likewise result in a vehicle capable of navigating complex 3D geometries unreachable with current underwater vehicles, as well as provide insights into how to design mobile robots that integrate high bandwidth sensing with highly responsive multidirectional movement.

Key words: bio-inspiration, biomimetics, electric fish, mechanics, robotics, sensing.

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#### Introduction

Weakly electric fish (Fig. 1A) have been a leading model system within sensory neurobiology for many years. More recently, within this model system community as well as others, the importance of body mechanics and locomotion for understanding neural systems has become increasingly recognized (MacIver, 2009; Chiel and Beer, 1997; Full and Koditschek, 1999; Dickinson et al., 2000). The result is that there has been significant progress in understanding the neuromechanics of a host of systems, including the lamprey, flies, frogs, cats, salamanders, aplysia, rat vibrissal systems, cockroaches and fish, among others (Chiel et al., 2009; Nishikawa et al., 2007; Cowan and Fortune, 2007; Collins et al., 2005). This review focuses first on physical models that incorporate the mechanics of South American knifefish, and second on artificial electrosense systems inspired by all weakly electric fish including the African mormyrids. The mechanics exhibited by mormyrids differs greatly from that of the knifefish and has largely been left unstudied. There is one African electric knifefish species, *Gymnarchus niloticus*, which possesses a dorsal ribbon fin nearly identical to the ventral fin of South American knifefish shown in Fig. 1A.

#### Biomimetic and bio-inspired physical models

Models are important tools for investigating the many facets of animal design, such as mechanics, sensing and neuronal processing strategies. This review focuses largely on physical models of weakly electric fish (specifically robotics); however, mathematical

models and simulations are often used in conjunction with physical models and will be mentioned as appropriate.

One motivation for building physical models is to gain a better understanding of the biology of the animal in question that may be difficult or impossible to obtain from live animals (Webb, 2001; MacIver, 2001). In this case, we refer to the model as 'biomimetic'. In the domain of aquatic animals, Ahlborn et al. developed a physical model of the tail of a fish to examine the vortical structure of the wake of carangiform swimmers (Ahlborn et al., 1991). An early fish robot called RoboTuna was designed to mimic the motions of carangiform swimmers, and the researchers found that when the robot swam with fish-like movements, characteristics of the wake generated by the physical model matched that of the actual fish, resulting in efficient swimming (Triantafyllou and Triantafyllou, 1995). However, unnatural swimming motions resulted in inefficient swimming and a very different wake structure. Such experimental manipulations would be very difficult to perform in the tuna itself. Similarly, a physical model of the salamander enabled the testing of hypotheses regarding how central pattern generators (CPGs) can function to generate locomotion in water and on land with their vastly different mechanical constraints (Ijspeert et al., 2007; Karakasiliotis et al., 2012). Similarly, classic work simulating the neuromechanics of the lamprey (Ekeberg et al., 1995; Ekeberg and Grillner, 1999) has provided many system-level insights that continue to be pursued in physiology and mechanics (Kamali Sarvestani et al., 2012).

Another motivation for building physical models is developing improved technology. In this case we call the model ‘bio-inspired’. Inventors often look to biology for inspiration to help solve problems that have already been solved in nature. For example, consider the need to strongly adhere two surfaces together temporarily. Swiss engineer George de Mestral discovered the mechanism behind the now ubiquitous Velcro by examining the hooked structure of seeds that stick to animal fur (Vogel and Davis, 2000). A different solution can be found in nature in the form of gecko feet (for a review, see Kwak and Kim, 2010), which has resulted in a dry adhesive mechanism that can hold against significant weight but can be removed with little effort (Schubert et al., 2008). Geckos rely on this dry adhesion mechanism to move vertically. As with the gecko, a frequent source for bio-inspiration is the efficient and robust locomotion systems that can be found in animals. Similarly, one motivation for building a swimming robot inspired by the electric knifefish is the exceptional omnidirectional agility of the fish (Snyder et al., 2007). Similar to the echolocating bat, this agility arises in part because of the need to execute maneuvers to rapidly approach a detected prey under the constraint that the fish moves through its short active sensory range in approximately one sensorimotor delay time (Nelson and MacIver, 2006; Snyder et al., 2007), necessitating mechanics that are extraordinarily responsive to sensory input. As we will review below, by incorporating some of the electric fish’s mechanical and sensory principles, new bio-inspired technology may emerge that significantly outperforms current underwater vehicles for conditions in which agility is essential or conventional sensory paradigms are ineffective.

#### Choosing the right level of abstraction

The research described in this review contains examples of biomimetic and bio-inspired approaches for building physical models that share characteristics with knifefish mechanics and electrosense of weakly electric fish. Occasionally the research combines both of these goals at once with the same model. More often the two goals of creating new technology inspired by biology and creating a physical model to study biology require different levels of abstraction from the original system. For example, to test the capabilities of a biological electroreceptor, an artificial electroreceptor might require the same electrical properties and electric field as is found in the biological case. Alternatively, with the goal of designing an artificial electrosense system that is useful for an underwater robot, it may be more convenient to use a simple conductor and generate a field with higher intensity and a less complex emission pattern than found in the electric fish. Such an artificial electrosense system would share all the basic principles of a biological electrosense system, but be more amenable for use in an actual robot.

Some of the most interesting aspects of South American weakly electric fish – for engineers and biologists alike – are its active electrosense and its high-maneuverability propulsion system (MacIver et al., 2004). The most obvious goal for the engineer would be to successfully design a swimming robot able to navigate using artificial electrosense with ribbon fin-inspired propulsion. Electric-fish-inspired robotics has largely tackled the two systems separately, however, with the goal of fusing them together once basic understandings of underlying principles are reached for each. The structure of this review similarly divides discussion regarding knifefish robot mechanics from that of robotic electrosense, with a final discussion of how to recombine the two systems.

## Mechanics

### The biological fin and its bio-inspired mechanical models

The body of research on the mechanics of fish swimming is extensive. Much attention has been given to several categories of swimming including forms that are reliant on body undulations, caudal fin oscillations and pectoral fin swimming (for reviews, see Triantafyllou et al., 2000; Sfakiotakis et al., 1999; Colgate and Lynch, 2004). This review focuses on modeling the undulations of elongated median fins, commonly called ribbon fins, such as those seen in South American weakly electric fish (Fig. 1A), one species of African weakly electric fish (*Gymnarchus niloticus*) and triggerfish, though the mechanics may be similar to elongated lateral paired fins such as those seen in rays, skates and cephalopods. The ribbon fin of South American weakly electric knifefish consists of 100–300 bony rays [see table 4 of Albert (Albert, 2001)], each with a set of agonist and antagonist muscles capable of bending the rays laterally. The control of these rays is often coordinated to produce either a single traveling wave along the length of the ribbon fin or two counter-propagating waves that start at either end of the fin and meet at some point along the fin. These waves can have varying amplitude, wavelength, frequency and waveform shapes (Curet et al., 2011a; Ruiz-Torres et al., 2013).

Some of the first studies on ribbon fin propulsion in fish were conducted by Blake, who studied the kinematics of ‘balistiform swimmers’ – fish with ribbon fins along the dorsal and ventral midline of the body (Blake, 1978) – and the swimming of knifefishes, which have a single elongated ventral fin along the midline (Blake, 1983). In addition, Lighthill and Blake (Lighthill and Blake, 1990) presented an analytical study of elongated fin propulsion where they found an analytical expression for the thrust force and swimming speed of an undulating ribbon fin as a function of few parameters assuming a two-dimensional irrotational flow in the plane transverse to the fin surface.

In more recent work, Ruiz-Torres et al. (Ruiz-Torres et al., 2013) measured the kinematics of the ribbon fin in swimming knifefish, and Shirgaonkar et al. (Shirgaonkar et al., 2008) used a three-dimensional (3D) computational fluid dynamics (CFD) simulation to study the hydrodynamics of an undulating ribbon fin.

Physical models have also contributed enormously to the study of undulatory fin propulsion. However, the design, construction and control of such devices is far from simple in most cases. Below we present a selection of physical model research that has varying levels of abstraction from biological undulatory ribbon fins.

### Physical models

There have been various independent efforts to design and build robots that mimic the kinematics of elongated undulatory fins found in swimming animals. Sfakiotakis et al. (Sfakiotakis et al., 2001) developed an undulating ribbon fin consisting of eight fin actuators interconnected with a fin membrane. The fin rays were actuated by pneumatic parallel bellows which bend similarly to the bones in a fish fin, but the diameter-to-length ratio of the pneumatic rays was much larger compared with the bony rays. MacIver et al. (MacIver et al., 2004) built a robotic undulating fin consisting of 13 rays that pivot about a common axis, with each ray actuated by a dedicated servo motor. Willy and Low (Willy and Low, 2005) designed a modular ribbon fin mechanism that can be oriented either laterally as a pair of pectoral fins, or medially as a ventral ribbon fin. In this mechanism the fin membrane is composed of discrete rigid acrylic segments to reduce energy lost in stretching an elastic membrane. To facilitate the operation of a fin made of rigid material, the 10 fin rays do not pivot about an axis but translate with respect to the

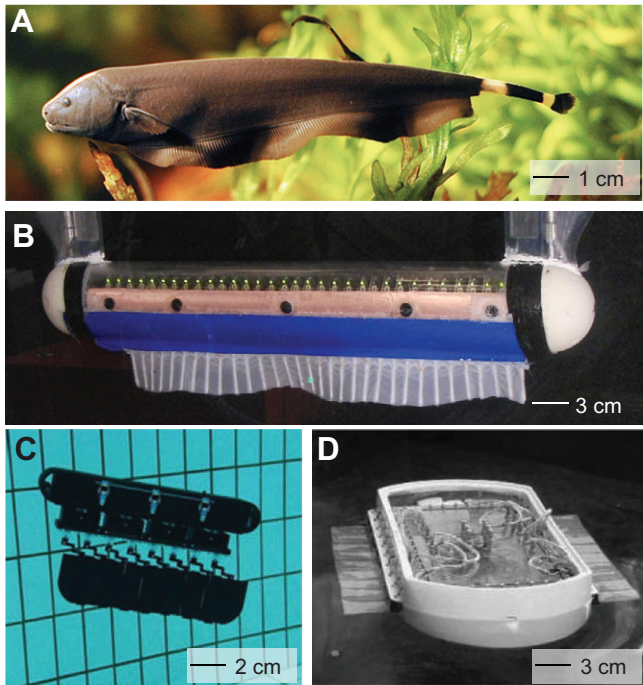


Fig. 1. The black ghost knifefish, *Aptereronotus albifrons*, and a few physical models of ribbon fins. Scale bars are estimates. (A) Photograph courtesy of Per Erik Sviland. (B) The Ghostbot and its mechanical ribbon fin. The Ghostbot is both laterally and longitudinally symmetric. (C) The NKF-II submersible robot. The fin uses crank-slider linkages to create a traveling wave with parallel fin rays and uses a buoyancy tank for depth control. Reprinted with permission from Low (Low, 2009). (D) Lateral ribbon-fin robot. Two bilaterally symmetric ribbon fins propel the robot and allow turning using counter-propagating waves on the two fins. Image used with permission (Shang et al., 2012).

mid-plane to keep the rays parallel to each other during their sinusoidal motion. Even though this design avoids the drawbacks of dealing with a highly compliant membrane, the kinematics of the fin rays and the membrane material depart considerably from actual biological undulatory ribbon fins. An updated version of this design, called the NKF-II (Fig. 1C), has eight fin rays attached to a submersible body containing a tank, allowing for buoyancy control (Low, 2009).

The progress of the work of MacIver et al. (MacIver et al., 2004) led to the design and construction of an undulatory robotic fin model with the goal of understanding the interconnection between hydrodynamics of ribbon fin propulsion and the electrosensory system of electric fish (Epstein, 2006; Epstein et al., 2006; Curet et al., 2011a; Curet et al., 2011b). The first version of the undulatory ribbon fin model was composed of rigid fin rays actuated by eight servo motors, and a fin membrane made of a latex sheet. The undulating fin was the only part of the robot submersible in the water (Epstein, 2006; Epstein et al., 2006). The most recent iteration of these models is the Ghostbot shown in Fig. 1B (Curet et al., 2011a). The Ghostbot has 32 rays covered by a 32 cm Lycra fin attached to a submersible body, which houses all of the motors. The body is torpedo shaped and is mounted and tethered as it receives control signals and power from outside of the water.

There are numerous other examples of undulating ribbon fin models. Hu et al. (Hu et al., 2009) developed a motor-driven undulating fin actuator to model the kinematics of *G. niloticus*, the

one African weakly electric fish that uses a dorsal median ribbon fin, and to analyze its propulsion mechanics with respect to multiple fin parameters. Shang et al. (Shang et al., 2012) designed and built a biomimetic underwater vehicle with two lateral undulating fins (Fig. 1D). Liu et al. (Liu et al., 2010) built an undulating ribbon fin with only two actuators, one at either end of the fin, to validate computational results on thrust generation. Lauder et al. (Lauder et al., 2011) used a flexible foil actuated by a single degree of freedom to study undulatory locomotion in fishes. Research endeavors using these bio-inspired robots share the common goals of developing a more maneuverable underwater vehicle and understanding the basic underlying mechanical principles of undulatory locomotion in fishes.

#### Measuring force, velocities and flow fields

Once a physical model of the fin has been built, there are a number of different ways to analyze the underlying mechanics. Often the first step is to allow the robot to swim given a set of kinematics closely matching what is observed in nature. Measurements of steady-state swimming velocity include motion capture of a freely swimming fin (Low and Willy, 2006; Low, 2007), or matching the speed of a flow tunnel to the freely swimming speed of a robot (Curet et al., 2011b). Also, forces of a fixed fin can be measured by placing a load cell between the robotic fin and mechanical ground, a measurement that is difficult or impossible to do in biology, especially in fish (Sfakiotakis et al., 2001; Curet et al., 2011b). Flow and force measurement can be combined to estimate drag in either a flow tunnel or a tow tank (MacIver et al., 2010; Curet et al., 2011b). Finally, flow measurement techniques such as particle image velocimetry (PIV) are used to determine the velocity vector fields of the wake generated by the robotic fin (Shirgaonkar et al., 2008; Curet et al., 2011a), from which important features such as vorticity and momentum flux can be derived. While PIV is usually performed on a plane, recent work has performed 3D velocity field measurements using volumetric flow techniques applied to the mechanics of underwater robotics and live animals (Flammang et al., 2011). For most measurements, the kinematics of the fin have been idealized into simple traveling waves consisting of three or four parameters such as frequency, wavelength, amplitude and length-to-height ratio. A robotic fin model allows for systematic exploration through the reduced kinematic parameter space – an impossibility when studying live fish.

#### Synergy between simulations and physical models of knifefish

As discussed in the Introduction, physical models and simulation are two important modeling approaches within science and engineering, as they both provide a method to integrate large amounts of knowledge into physical or computational artifacts for further study and manipulation. A challenge for the physical model approach, however, is that iterations are costly and time consuming (Bongard et al., 2006). Iteration within simulation is relatively quick. The discovery of a downward jet through counter-propagating waves along the robot ribbon fin (Curet et al., 2011a), discussed below, was preceded by high fidelity fluid and fin simulations that predicted the occurrence of this jet. Both of these have preceded the measurement of the jet in live animals, as yet unpublished, although the occurrence and kinematics of the corresponding counter-propagating waves are in the literature (Ruiz-Torres et al., 2013; Sefati et al., 2012). Similarly, key relationships between ribbon fin kinematics and force generation were simulated (Shirgaonkar et al., 2008) before they were



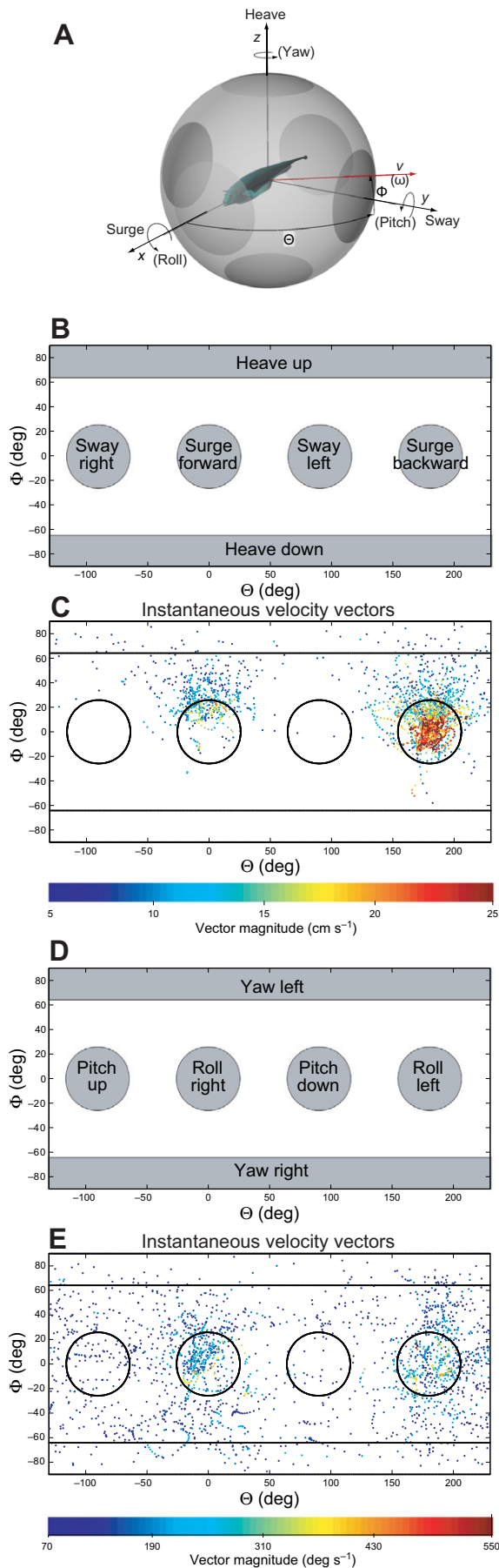


Fig. 2. Instantaneous velocity vectors of knifefish during prey capture. (A) Schematic showing the map used to plot the directions of the velocity vectors. (B) Maps of the two angles  $\Theta$  and  $\Phi$ , which describe the direction of the translational velocity vector, where shaded areas indicating directions for surge, heave and sway. (C) Markers show the velocity vector directions derived from the motion capture data of the fish. The color indicates the magnitude of the translational velocity. D and E are analogous to A and B, but for rotational velocities. Adapted with permission from Postlethwaite et al. (Postlethwaite et al., 2009).

measured (Curet et al., 2011b). The challenge of simulating the complex fluid–structure interactions of the ribbon fin has spawned the development of new approaches for accurately simulating the swimming of aquatic animals (Curet et al., 2010; Shirgaonkar et al., 2009; Bhalla et al., 2012).

#### Decomposing the thrust generated by the fin

Previous studies have shown that the knifefish is capable of moving omnidirectionally over time spans of around half of a second (e.g. Snyder et al., 2007). Motion capture data of prey capture behavior for one weakly electric knifefish, the black ghost (*Apterontus albifrons*), was analyzed in Postlethwaite et al. (Postlethwaite et al., 2009). As shown in Fig. 2, the fish's movements can mostly be broken down into motion primitives including swimming forward and backward, called positive and negative surge, respectively, as well as upward (in the dorsal direction), called positive heave. They are also capable of rapidly rolling their bodies (MacIver et al., 2001). This allows them to attack laterally positioned prey by first rolling their body so that the prey is normal to the dorsal midline, and then executing a heave maneuver to close the gap. However, while the ribbon fin is the primary propulsor, the fish also uses its pectoral fins and body bends to achieve high agility (MacIver et al., 2001). Therefore, testing a mechanical model of a fin attached to a rigid body distills select capabilities of the fin from the full mechanical complexity of the fish.

Free-swimming velocity measurements were first measured by the Low research group with the various iterations of their robotic fins (Low and Willy, 2006; Low, 2007). The primary parameter of the waveform kinematics varied was the wavelength of the traveling wave. The researchers found that when the wavelength was longer than the length of the fin (equivalently, there is less than one spatial period along the length of the fin) there were periodic oscillations around the mean forward velocity with corresponding oscillations in the yaw and roll angles of the fin. As the wavelength decreased, the forward velocity became steady and the oscillations in roll and yaw diminished.

Curet et al. (Curet et al., 2011b) also measured average free-swimming velocities of the Ghostbot ribbon fin, which is able to reproduce shorter wavelength waveforms due to the higher number of actuated rays. The heave axis of the robot was fixed, so only surge velocities could be measured and are shown in Fig. 3. In the same study, the forces generated by the fixed robot in still water were also measured and are shown in Fig. 3. These measurements give an estimate of impulsive thrust, or the forces the fin is capable of generating when starting from rest. For single-traveling wave kinematics, the fin of the Ghostbot produced non-zero forces along both the longitudinal axis of the fin, called the surge axis, and the dorsoventral axis, called the heave axis. Consequently, a truly free-swimming Ghostbot would move diagonally at some pitch angle. No heave movements were recorded in the NKF-II from Low (Low, 2007), likely because the NKF-II rays remain parallel to each other

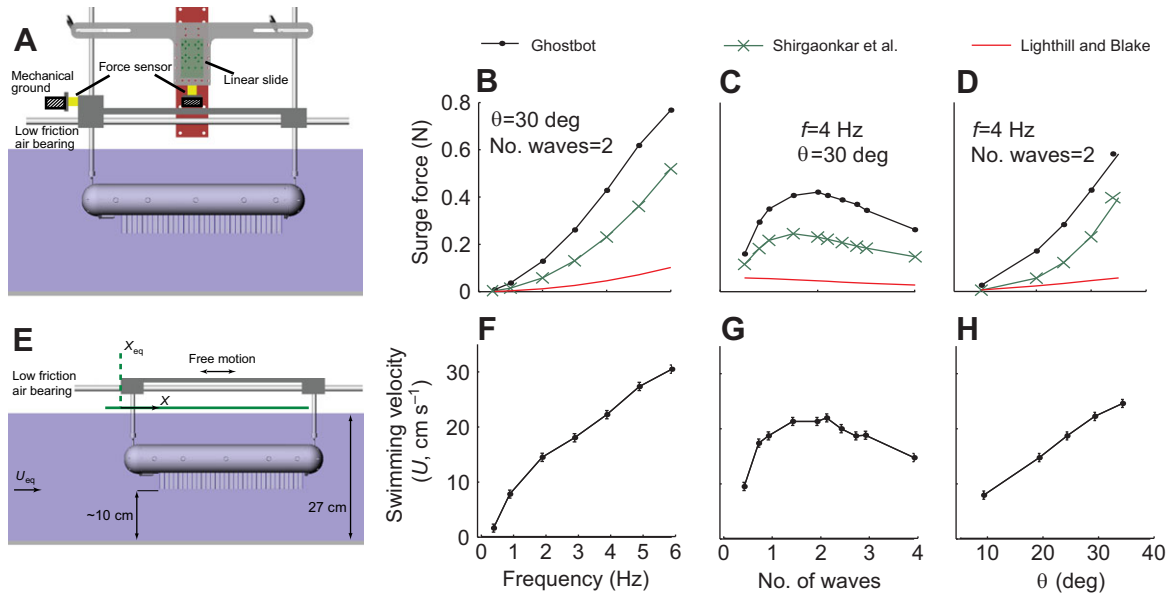


Fig. 3. Free-swimming velocities and fin force measurements for the Ghostbot. (A) Schematic of experimental setup to measure surge and heave forces. (B–D) Fin force measurements for single traveling wave kinematics. Green and red lines indicate estimations from models presented in Shirgaonkar et al. (Shirgaonkar et al., 2008) and Lighthill and Blake (Lighthill and Blake, 1990), respectively. Surge force and swimming speed were measured as a function of (B) frequency ( $f$ ), (C) number of waves (or undulations along the fin) and (D) maximum angular excursion ( $\theta$ ). (E) Schematic of experimental setup to measure free-swimming velocities. (F–H) Similar to B–D, but free-swimming velocities were measured. Adapted with permission from Curet et al. (Curet et al., 2011b).

while the rays of the Ghostbot and the biological knifefish oscillate about a pivot.

#### Angled thrust

While the fluid mechanics underlying the thrust generated by knifefish are not yet fully understood, comparisons between the kinematics of median ribbon fins and the kinematics of other forms of swimming may provide some insight. First, the longitudinal undulations of the fin are similar to body undulations of eels or lamprey. Therefore, similar mechanisms are likely responsible for the surge component of the thrust, and the wake of the ribbon fin might contain similar patterns to the wake generated by swimming eels (Tytell and Lauder, 2004). However, the kinematics of a single transverse section of the fin are oscillatory, as the rays bend back and forth laterally. Many fish, such as trout, oscillate their caudal fins to efficiently propel through the fluid. These oscillations produce a reverse von Kármán vortex street in the wake, which is a pattern closely tied with efficient swimming (Sfakiotakis et al., 1999; Triantafyllou et al., 2004). Preliminary Ghostbot data show reverse von Kármán streets shed downwards off the fin in certain cross-sectional views. Also, Liu et al. (Liu et al., 2010) described flow features showing propulsion along the longitudinal axis of undulation as well as the perpendicular heave axis. Thus, the mechanism of thrust generated by the ribbon fin could be potentially explained by remembering that the fin ‘surges like an eel’ while ‘heaving like a trout surges’.

An important aspect of the angled thrust generated by the fin is the body morphology of the fish. If the fin of the fish was aligned with the axis of the body as it is with the Ghostbot, the fish’s fin would produce an upward force during normal forward swimming. The fish would have to produce counteracting forces or tightly control buoyancy to balance this force to maintain constant depth while swimming forward, thus wasting energy. Knifefish have a

body plan such that the fin is at an angle to the body, so that the thrust generated by the fin is more aligned with the central axis of the body. Thus, the fish is presumed to achieve maximal thrust while encountering minimal drag as it swims forward through the fluid. There is a striking consistency of fin insertion angle of approximately 10deg across many species of knifefish, including both ventral and dorsal ribbon fin species (M.A.M., unpublished observations).

#### Asymmetry in forward and backward movement becomes a control issue for the fish

While the electric knifefish seems to be optimized for forward swimming, it also swims backward at high speed for certain behaviors, such as prey capture and refuge tracking (MacIver et al., 2001; Rose and Canfield, 1993; Heiligenberg, 1973; Cowan and Fortune, 2007). Because of the asymmetry of the fin along the longitudinal axis, backward swimming mechanics differ from forward swimming mechanics. During backward swimming, the angle of thrust with respect to the body axis now includes both the 10deg insertion angle described above as well as the 10deg angle between the fin and the direction of thrust. The longitudinally symmetric Ghostbot does not have this problem, which may have many benefits for simplifying control of an underwater vehicle using ribbon fin propulsion. Hu et al. (Hu et al., 2009) measured differently shaped waveforms in forward and backward swimming in knifefish, indicating asymmetry in the kinematics may be important for backward swimming.

#### Optimal wavelength matches observed kinematics of the fish fin

Some trends associated with varying the kinematic parameters of a traveling wave are very intuitive. As both frequency and amplitude increase, both free-swimming speed and fixed fin force increase as indicated in Fig. 3, and a freely swimming knifefish shows similar trends (Ruiz-Torres et al., 2013). The trend associated with varying

spatial wavelength is much less intuitive. According to experiments with both the Ghostbot and the Low fin, there exists some optimal wavelength where swimming velocity is maximized (Curet et al., 2011b; Low and Willy, 2006; Low, 2007). Interestingly, the optimal fin length to wavelength ratio for the Ghostbot matches the naturally occurring kinematics in freely swimming knifefish despite the difference in size (Blake, 1983; Ruiz-Torres et al., 2013). Research is ongoing to uncover the mechanism underlying this particular kinematic parameter in the robotic fin and whether there exists an optimal kinematic invariant for fins of different aspect ratios (Bale et al., 2012).

#### Varying mechanical properties of the ribbon fin

The various physical models described above are characterized by a large range of mechanical properties for the fin material used in their construction. Low (Low, 2009) implements rigid acrylic links whereas most other robotic fin designs use a flexible material. The Ghostbot uses a Lycra fin with a Young's modulus of 0.2 MPa, similar to fin membrane measured in another species of fish (Curet et al., 2011b). Hu et al. (Hu et al., 2009) compared two fin materials, a material stiffer than Lycra with a Young's modulus less than 1 GPa (low density polyethylene) and an even harder material with a Young's modulus between 1.2 and 1.5 GPa (polypropylene). While the swimming velocity of the fins of the two materials did not vary significantly, the researchers did find an increase in efficiency in a few cases for the softer material. The robotic ribbon fin model used in Liu et al. (Liu et al., 2010) relies on the flexibility of the fin material to produce traveling wave undulations, as the fin is only actuated at the ends.

It is clear that few conclusions can be made about the effects of varying mechanical properties of the fin from these robotic ribbon fin models. However, similar work in undulating flapping foils (Lauder et al., 2011), though generally related to body undulations of body/caudal fin swimming, may elucidate important dependencies of ribbon fin thrust on mechanical properties of the fin such as stiffness. Lastly, the bony rays of the fish are flexible and actually bend (Lauder, 2006) rather than simply rotate like the rigid rays used in many of the robotic ribbon fin models. Research in flexible rays in other fins, for example caudal fins (Esposito et al., 2012), will hopefully inspire similar work in future ribbon fin models to better match biological ribbon fin kinematics. This will facilitate additional progress in zeroing in on their mechanical impact on fish swimming.

#### Inward counter-propagating waves

##### Generating increased heave

So far discussion of ribbon fin mechanics has focused on single traveling waves along the ribbon fin, which generate thrust at an angle to the fin. While knifefish can generate both rostral to caudal and caudal to rostral traveling waves, they can also generate waves in both directions at the same time. These inward counter-propagating waves originate at either end of the fin, and during hovering, meet somewhere in the middle of the fin at a location called the nodal point (Ruiz-Torres et al., 2013). Knifefish use these kinematics for station-keeping in still or slow-moving (one body length per second or less) water (Sefati et al., 2012; Ruiz-Torres et al., 2013), similar to how a triggerfish will generate traveling waves in opposing directions on its ventral and dorsal ribbon fins (Blake, 1978). Hu et al. (Hu et al., 2009) implemented counter-propagating waves on two laterally separated ribbon fins to perform a turning motion. The Ghostbot was used as a physical model to uncover the mechanics of counter-propagating waves on a single ribbon fin by

measuring forces and flow features, and testing alternative hypotheses. Several conclusions were made from these experiments involving inward propagating waves in which the two traveling waves occur over equal lengths of the robotic ribbon fin, appropriate for hovering in still water (Curet et al., 2011a). First, although the surge components of the thrust produced by each individual wave should cancel out, the heave component should still remain. Interestingly, inward waves generated ~40% more heave force than outward waves. This difference can be at least partially explained by the flow features resulting from the two sets of kinematics. For inward waves, a strong downward jet is generated at the nodal point along the fin, as shown in Fig. 4. No downward jet was present for the outward waves. Second, while standing waves also produced a similar amount of heave force, as well as smaller downward jets at the standing wave nodes, the variability over a cycle was very high, indicating unstable mechanics (Curet et al., 2011a). Therefore, inward counter-propagating waves allow for stable actuation in the heave direction, which can be very useful for both a fish and a robot requiring high maneuverability.

#### Enhanced stability and maneuverability associated with counter-propagating waves

While it is possible for knifefish to use counter-propagating waves to move in the heave axis, due to experimental constraints counter-propagating waves have mainly been observed when the fish is keeping station relative to a refuge, either in still water or in flows of one body length per second or less. In these situations, the fish is maintaining its vertical position. Moreover, behavioral studies show that the nodal point of the two traveling waves shifts caudally with increased flow velocity (Ruiz-Torres et al., 2013). The Ghostbot was again used to confirm that the longitudinal force varies linearly with the shift in the nodal point (Sefati et al., 2012). There are two reasons

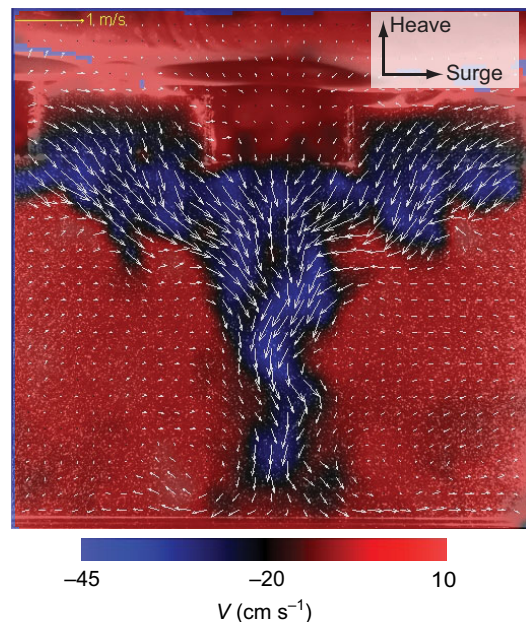


Fig. 4. Midsagittal plane showing the flow structure generated by counter-propagating waves. Two traveling waves originating from each end of the robotic fin collide in the middle. A downward jet is produced, canceling any surge components to the thrust and leaving only a heave component. The color bar indicates the magnitude of the y-component of velocity, where positive indicates flow upwards and negative indicates flow downwards from the fin. Reprinted with permission from Curet et al. (Curet et al., 2011a).



presented for why the fish would employ this seemingly inefficient strategy. First, for station-keeping behaviors in still water where adjustments must quickly be made forward and backward, nodal point shift allows for linear control around zero swimming velocities, rather than requiring the reversal of the traveling wave (Sefati et al., 2012). Second, counter-propagating waves help stabilize against perturbations, as force generated by the wave moving with the perturbation is decreased due to a decrease in wave velocity relative to the fluid, while the force generated by the wave moving against the perturbation is increased, pushing the fish back towards its unperturbed state (Sefati et al., 2012).

As the nodal point changes position, the magnitude, position and direction of the heave force changes, which could change the body pitch angle as well as translation along the dorsoventral axis. How the fish stabilizes itself against these perturbations while varying the nodal point awaits further investigation.

#### Neural control of the ribbon fin

While modeling single traveling wave kinematics as a traveling sine wave is straightforward, modeling two inward counter-propagating waves meeting at a nodal point is more complicated. For example, the robotic fin could be simply programmed to have one traveling wave on one side of the nodal point, and an opposing traveling wave on the other side. This will most often result in a sharp discontinuity in the waveform, which is not mechanically ideal for either the robotic or the biological fin. Therefore, a gradual change from one wave to the other is usually implemented around the nodal point using weighted combinations of the two waves. However, there has been little investigation into how this weighted combination of opposing waves should be modeled to match the actual kinematics of the knifefish fin. Perhaps a better way of modeling the control of the fin is to use a central pattern generator (CPG) neural circuit model. A CPG model for single traveling wave kinematics was explored by Zhou and Low (Zhou and Low, 2010), showing gait transitions between forward waves, reverse waves, asymmetrical waves and varying wavelengths. Recent work shows that a similar CPG model adapted from work in the lamprey can reproduce the kinematics of both single traveling waves and counter-propagating waves (Ruiz-Torres et al., 2013). This modified model for the ribbon fin includes driving inputs for both the first and last rays as well as the ray where the traveling waves meet. By lowering the drive at the nodal point ray compared with the first and last rays, inward counter-propagating waves moving toward the nodal point are generated. Also, due to the structure of the coupled oscillators, the CPG model accounts for the smooth transition between the two waves around the nodal point. This and many other questions related to the control of ribbon fin mechanics in both the robotic and biological paradigms are still largely open to explore. Importantly, very little work has yet been done with control in 3D space, an area where the fish excels and will be necessary to master for a freely swimming ribbon fin robot. These issues, as well as recombining knifefish mechanics with artificial electrosense, will be discussed in the final part of this review.

#### Sensing

##### Introducing biological and artificial electrosense

Electrosense in animals is one of the most recently discovered sensory modalities at just over half a century old (Lissmann and Machin, 1958). Many animals, such as sharks and platypuses, can passively sense weak electric fields emitted by other animals, often to locate prey. However, weakly electric fish emit and sense their own electric field (Fig. 5A). Perturbations as small as 0.1% of the

emitted electric field, caused by nearby objects, can be sensed by the fish's electroreceptors (Nelson and MacIver, 1999; Goense and Ratnam, 2003). Since the fish generates the energy needed to sense the environment, this variant of electrosense is called an active sensing system, similar to sonar or radar. For this review, the term electrosense will refer to the active sensing variant of electrosense. Nelson and MacIver (Nelson and MacIver, 2006) provide a review of biological active sensing systems.

Even before the discovery of actively sensing electric fish, there have been numerous technological examples of electric field sensing. The theremin, a musical instrument from 1921, was capable of detecting the capacitance of a performer's body parts through measured changes in an emitted electric field (Theremin and Petrishev, 1996). The position of the body part in that field was translated into varying output pitches and tones, allowing the player to produce a range of sounds by sweeping their hands over the space near the theremin. These principles have been further applied by the Massachusetts Institute of Technology Media Lab to track the 3D position of a hand (Smith et al., 1998) and develop robotic fingers capable of sensing objects before contact (Smith et al., 2007). Even modern capacitive touch screens implement these basic active sensing principles. Electrical impedance tomography (EIT) is another example of sensing an emitted field. In medical imaging, EIT produces images of internal structures within the body, estimating the distribution of impedances by emitting current and sensing voltages along the boundary (Barber and Brown,

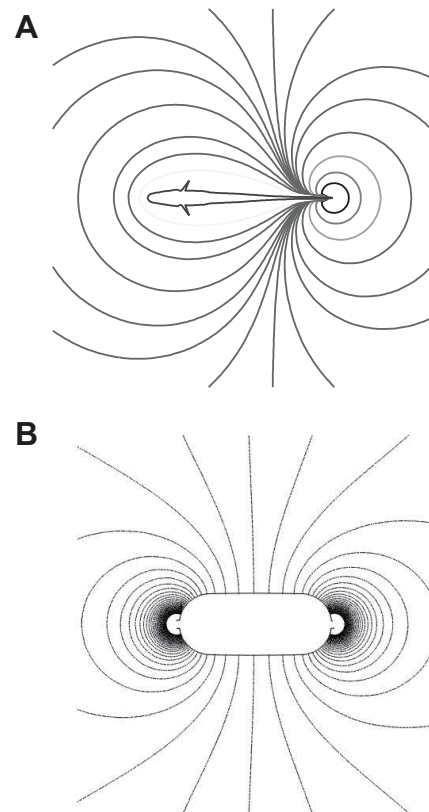


Fig. 5. Comparison of electric fields. Models of the electric field around gymnotiform (South American) weakly electric fish (Chen et al., 2005) differ in shape from fields generated by a single dipole in artificial electrosense. Isopotential lines for the fish run roughly parallel along the long axis of the fish body (A), whereas isopotential lines of artificial electrosense are mostly perpendicular to the long axis connecting the emitting dipole (B).

1984). Resistivity imaging, which includes EIT, began its widespread use in the 1920s by geophysicists who used arrays of metal electrodes inserted into the ground to estimate a map of the subsurface strata. Data are collected by injecting current across pairs of electrodes and then measuring the voltages at the other electrodes. Variants of the basic technique are still used today by geophysicists for imaging the subterranean and extracted core samples (Dines and Lytle, 1981). A later section will discuss the possibility of using EIT in underwater electrosense. A more recent medical application of electrosense actually inspired by the weakly electric fish is a catheter-based sensor that can be used to identify plaques indicating arteriosclerosis (von der Emde et al., 2009; Metzen et al., 2012). Research in artificial electrosense is now pursued by several laboratories and was the sole topic of a 2012 workshop on robotic electrosense in College Park, MD, USA, just prior to the electric fish symposium to which this special issue is dedicated (MacIver and Boyer, 2012).

#### Basics of artificial underwater electrosense

The simplest artificial electrosense system, as shown in Fig. 6, is comprised of two pairs of electrodes, one pair for excitation and the other for differential voltage measurements (Solberg et al., 2008). The sensing pair is placed orthogonal to the emitting pairs so that when no object is present, the differential signal from the sensing pair is zero, as shown in Fig. 6A. When an object whose conductivity differs from the water is placed within the field as shown in Fig. 6B, the proximal electrode will measure a voltage different than that of the distal electrode, resulting in a non-zero differential signal, indicating the presence of the object. A central thrust of current research in artificial electrosense is how this signal can be processed to obtain valuable information about the object.

A single differential measurement in electrosense is analogous to the intensity measurement of a single pixel of a camera, and object detection, location, identification, etc., through processing of electrosensory signals is akin to machine vision. An object in the emitted electric field perturbs the field, and the perturbations measured by the array of sensors on the robot or fish boundary constitute the electric image of the object. Of course, just as light can be measured in ways other than signal intensity, there are numerous variants to the simple artificial electrosense described above, which will be mentioned throughout the rest of this section. An important way in which the analogy to geometric optics and machine vision does not apply is that the electric field significantly changes its structure as a function of the objects in the near field.

#### Artificial versus biological electrosense

The main goal of research into artificial electrosense thus far has been to use the principles of biological electrosense for tasks where other sensing modalities break down, such as in dark murky water, or navigation in complex geometries where a robot has to swim very near obstacles. Therefore, electrosense should be able to identify and localize objects and features in the environment to aid robotic navigation and other tasks. Mimicking every feature of biological electrosense may not be necessary to achieve this goal, although even when the goals are purely technological it is often beneficial to relate findings back to the rich literature in biological electrosense. The following is a brief overview of the abstractions made from biological electrosense and important differences between the two.

The first major difference between artificial and biological electrosense is the structure of the emitted field. The simplest emitter is a single dipole. This differs from the common method of modeling the field generated by the electric organ of the electric

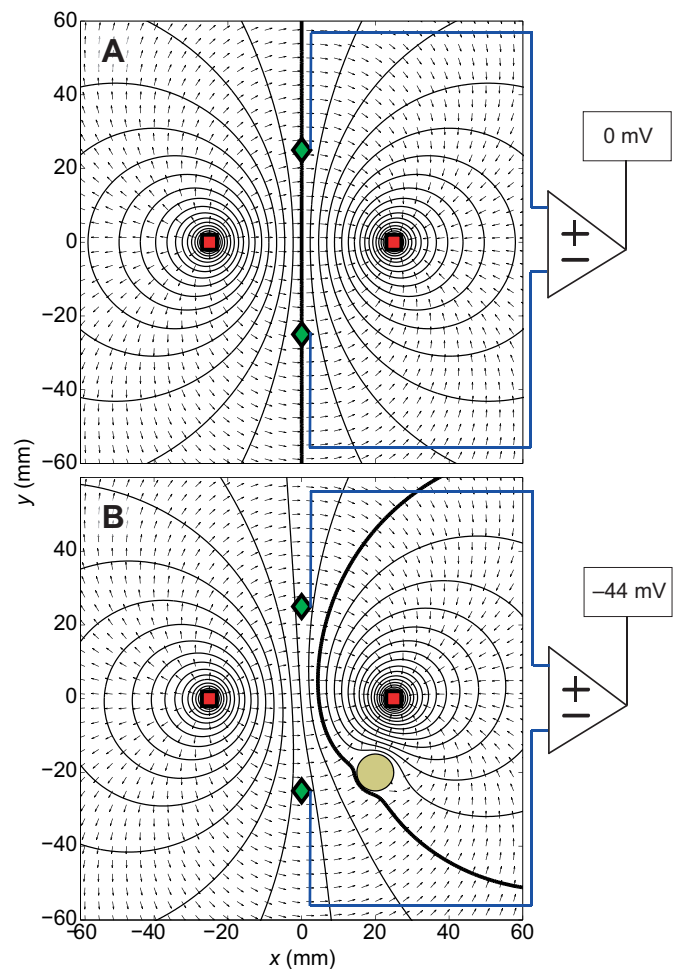


Fig. 6. A simple four-electrode active electrosense system. The two red squares create a dipole, generating an electric field marked with solid isopotential lines and vectors for field strength and direction. The green diamond pair measures differential voltage. (A) With no object present, both sensors lie on the same isopotential line, resulting in a differential output of 0 V. (B) When an object is introduced that distorts the field, the proximal sensor observes a higher voltage shift than the distal sensor, resulting in a nonzero differential measurement. Reprinted with permission from Solberg et al. (Solberg et al., 2008).

fish, consisting of multiple positive sources and a single negative source (Rasnow and Bower, 1996; Assad et al., 1999; Chen et al., 2005). The resulting electric fields for the two paradigms are shown in Fig. 5. There are many other features of the electric fish field whose import to electrolocation are not fully understood, such as frequency of oscillation and rotation of the caudal electric field within an electric organ discharge cycle (Assad et al., 1999; Rasnow and Bower, 1996). The structure of the electric field has a large impact on the voltage perturbations created by objects. The second important difference is that artificial systems generally use differential measurements between sensor pairs, while electroreceptors respond to the signal at the receptor with respect to the potential within the body as modeled in one of the early artificial systems (MacIver and Nelson, 2001). Last, fish such as electric knifefish use over 10,000 sensors distributed all over the skin (Carr et al., 1982), while current artificial systems have only up to around 30 sensors. To compensate for this deficiency, the sensors are often moved around the object to obtain multiple views,



though this operation is not the same as having a large array of sensors because the emitted field and the field-distorting robot body must move with the sensors. All of these differences have to be factored in when relating findings from artificial electrosense research back to biological electrosense.

### Single channel localization

Given the simple system of a single pair of sensing electrodes, Solberg et al. (Solberg et al., 2008) demonstrated localization of the sensor within a previously mapped stationary environment. To do so, the researchers created an ensemble of electrosensory viewpoints (EEVs) for a given object or environment. This section describes EEVs, as well as the performance of this system for localizing itself given noisy sensor data.

### Electrosensory viewpoints

The first step towards localization within an environment is to have a map of the environment. Similarly, a map can be created of an unknown environment if expected features can be localized and subsequently superimposed, assuming that the perturbation due to the features do not overlap. The reading from the differential channel, or sensor observation, when the sensing platform is in a certain location and orientation within the environment or with respect to an object is called an electrosensory viewpoint. The collection of electrosensory viewpoints for all possible locations in the map is called an EEV for the given object or environment. Fig. 7A is an example of an EEV for a conducting disk. Also, because the sensors are noisy, each viewpoint has a mean and standard deviation associated with it. Therefore, for a given reading, a probabilistic map can be generated based on the likelihood that the sensors are in any position within the map given the sensor reading as shown in Fig. 7. One measurement therefore is not sufficient for localization. However, localization can be achieved by combining movement with sensing through probabilistic filtering methods common in robotics.

### Performance in localizing objects and in self-localization

Solberg et al. used a particle filter to estimate location within a known map (Solberg et al., 2008). The distribution of particles is

initially random, and their position is updated according to the probabilistic map following a measurement. Monte Carlo forward simulation attempts to minimize the expected uncertainty at the next step. Using this algorithm, the sensor was able to localize itself with respect to the pre-mapped object or environment within just a few steps. However, limitations include needing the pre-mapped EEV for each object or environment, using a fixed sensor orientation, and knowing parameters such as the conductivity of the medium. Recent work has expanded this localization problem using a sensing platform with more channels (shown in Fig. 8) and allowing for varying sensor platform orientation (Silverman et al., 2012). While having to map objects and environments seems onerous, electric fish do have spatial memory, and often make scanning movements around novel objects, perhaps to create something similar to an EEV of the object (Assad et al., 1999).

### Object identification

Perhaps equally important to object localization is object identification and discrimination. Assad et al. (Assad et al., 1999) proposed a mapping of how features in the electric image of an object on a fish's skin encode information about physical properties of the object, including electrical properties (i.e. conductivity and permittivity) and geometrical properties (i.e. size and shape). Similarly in artificial electrosense, features must be extracted from measurements that can be used to discriminate objects based on their physical properties. First, we review methods developed to determine the complex impedances of an object by measuring both amplitude and phase perturbations caused by the object. Weakly electric fish have electroreceptors capable of detecting phase shifts due to capacitance, which could be used to discriminate between the high capacitance of live tissue (largely resulting from cell membranes) and the lower capacitance of dead tissue (von der Emde and Bleckmann, 1998). Second, we review a method developed to disambiguate object shape.

### Determining electrical properties of objects

Bai et al. (Bai et al., 2012) implemented a dual-channel solution for deriving the phase shift of the electrosensory signal due to the

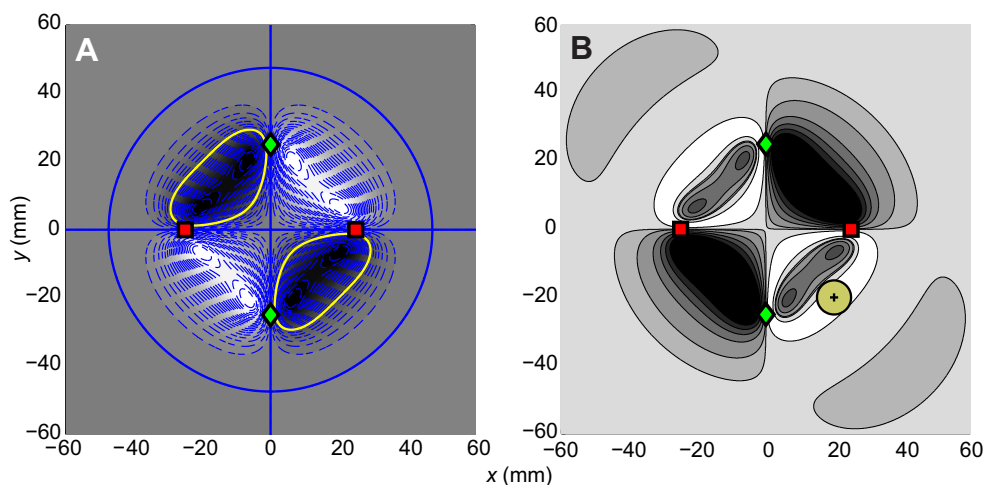


Fig. 7. Ensemble of electrosensory viewpoints (EEV) and probabilistic map for a conductive disk. (A) Color map indicates the differential measurement of the green triangles given the placement of the target object. Dotted lines indicate the target locations that give the same differential measurement. The solid blue contour indicates locations resulting in a 0 V measurement, while the solid yellow contour indicates locations resulting in -35 mV. (B) Probabilistic map of the target location given a single noisy measurement of -35 mV. White indicates high probability that the object is in that location, while black indicates low probability. Adapted with permission from Solberg et al. (Solberg et al., 2008).

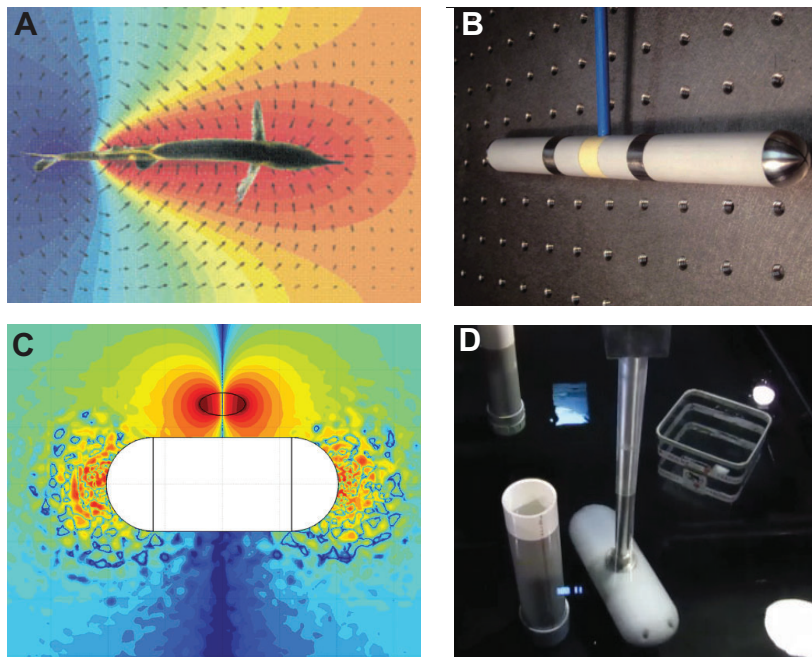


Fig. 8. Models of electrosense. (A) Model of the electric field of a mormyiform (African) weakly electric fish. (B) The ANGELS seven-electrode current-sensing electrosensory platform. (C) Model of electric field perturbation due to an object (conductive ellipse above the white cylinder) in an artificial electrosense system. (D) The 37-electrode Northwestern SensorPod as it navigates a cluttered environment. A and B are used with permission of F. Boyer.

presence of a capacitive object. The researchers added a second demodulation channel to the already existing demodulation channel described above. In the second channel, the reference signal is phase shifted by  $\pi/2$ , resulting in two values related to each other by the amplitude and phase shift of the perturbation. Therefore, both the amplitude and the phase shift can be calculated from the two demodulated channels of a single differential measurement of one sensor pair. The goal of this dual-channel implementation was to differentiate objects that would look very similar with a single channel but different when the second channel is added. To test this hypothesis they generated electrosensory ‘fly-by profiles’ as the object passed by the sensor at a fixed lateral distance. This dual-channel design was able to more easily disambiguate objects that previously looked very similar when just a single channel was used. For example, the fly-by profile of a single demodulated channel shares similar features

for an inanimate rock and a live plant. However, the second channel shows a clear change, as seen in Fig. 9. Ultimately, the measurements from two channels are necessary for determining both components of complex impedance.

For any capacitive object, the complex impedance will be frequency dependent. Frequency sweeping is a trivial addition to artificial electrosense that weakly electric fish cannot do as they maintain discharge frequencies within a relatively narrow range. Bai et al. (Bai et al., 2012) also investigated the impact of varying the excitation frequency. By sweeping a range of frequencies to derive Bode plots of phase and amplitude, other objects that could not previously be disambiguated for a single frequency for both channels exhibit different phase and amplitude values over a range of frequencies. Ammari et al. (Ammari et al., 2013a) developed numerical methods of object identification using multifrequency measurements capable of reconstructing the complex impedance as

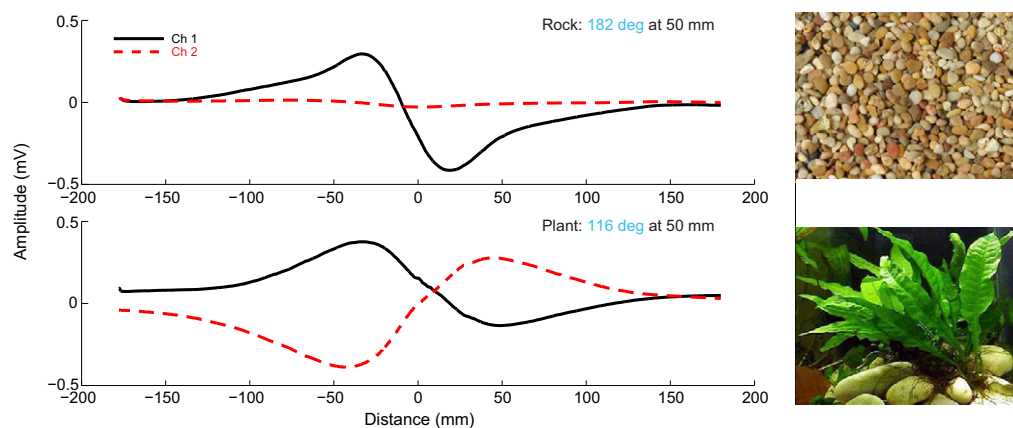


Fig. 9. Two-channel capacitance sensing of a rock (top) and a plant (bottom). Distance indicates the longitudinal position of the object along the sensing pod as the object passes by. Amplitude is the demodulated differential measurement from the electrode pair. The demodulation signal was phase shifted by 90 deg for channel 2. The rock and plant give similar profiles for channel 1 (solid black line), but are easily disambiguated given the profiles for channel 2 (dotted red line). Moreover, the calculated phase shift due to the presence of the rock is much different than that of the plant, indicating varying degrees of capacitance of the two objects. Adapted with permission from Bai et al. (Bai et al., 2012).

well as size of small disk- and ellipse-shaped objects. Currently, this method uses the electric field and boundary conditions associated with the actual fish, and would have to be adapted accordingly to be utilized in an artificial electrosense platform.

#### Determining shapes of objects

Discriminating shapes of two similarly sized objects using electrosense is difficult as the electric image does not retain features such as sharp edges or corners often used to discriminate various shapes. However, electric fish have been shown to be able to discriminate shape (von der Emde and Fetz, 2007). The mathematical model presented in Ammari et al. (Ammari et al., 2013a) was used to extract generalized polarization tensors (which are quantities intrinsic of object geometry) of a nearby object. They have built a library of shape descriptors that are invariant of size and orientation of the object and are derived from the polarization tensors. Therefore, they can classify objects based on the similarity of the shape descriptors based on simulated noisy measurements and those in the library. Again, these methods have not been performed on a physical artificial electrosense platform, but show promise in strengthening the ability to perform accurate object classification.

#### Variants of artificial electrosense

The latest advancements in artificial electrosense have largely been moving towards the goal of creating a useful technology rather than trying to build a physical model of biological electrosense to test hypotheses related to the fish. However, by creating various methods of localization, object identification and control using electrosense, appreciation is gained for the complex underlying issues that the fish is able to overcome. The following sections describe some recent variants to artificial electrosense.

#### Dead reckoning in an environment-dependent electric field

The examples of artificial electrosense described so far share a common theme that movement is important for both localization and object identification. However, the algorithms rely on having knowledge about the movement that occurred. For either the fish or a robot, knowledge of internal state can be achieved either by knowing the dynamics involved with transitioning between states, or by sensing the current state. Generally, animals and robots combine both methods, as motor actions as well as sensor readings can be noisy. Therefore, the fish and an electrosensory robot should be able to sense its own movement and combine that with some expectation of the motor output to dead reckon its current state. One way to sense movement is to detect the relative velocity of the robot and a fixed object as the robot passes by. A simple method of velocity estimation uses multiple sensor pairs oriented axially along an electrosensory system. Each sensor pair should view a similar electric image, offset by time according to the speed of the sensors. Through cross-correlation of these electric images, an estimate of velocity is achieved. However, Snyder et al. (Snyder et al., 2012) found that the electric images of the various sensor pairs were vastly different due to their varying locations within the non-uniform electric field, resulting in poor velocity estimates. Each sensor pair is analogous to a camera with a different distorting lens, so the images cannot be simply correlated without knowing the effects of the distortions. Similarly, the velocity of the electric image on the skin of the fish of an object depends on the distance of the object to the fish (Rasnow, 1996), so simply calculating the velocity of the electric image would not work for the fish either.

#### Electrical impedance tomography

A solution of the velocity estimation problem is to have a better estimate of the actual object location at all times. Recently, an approach developed for medical imaging applications has been applied to underwater electrosense. The EIT method uses controlled emissions of electric current and voltage measurements to create a map of impedances near the sensing platform. Snyder et al. (Snyder et al., 2012) show in simulation that velocity estimations using EIT are vastly more accurate than using simple cross-correlation. Fig. 10 shows the reconstruction of the position of an object as it passes by the sensor platform. While both the sensing paradigm and the mathematical analysis involved with EIT is a large departure from any known biological mechanism the fish might use to localize objects, the task space for an animal is also radically different from that of underwater vehicles. For an animal, orientation toward an identified object and closing the gap may be all that is needed (for prey capture, for example), while in robotics applications it may be useful or necessary to compute an estimate of 3D object position and do more complex scene analysis of objects for planning trajectories.

#### Current sensing and reactive control

So far, the artificial electrosense applications described have implemented voltage-sensing electrodes with high input impedance. Alternatively, the current sourced or sunk through the electrodes can be measured (Boyer et al., 2012). One such platform, shown in Fig. 8B, uses seven electrodes and can perform localization and object identification tasks similar to studies using voltage sensing (Boyer et al., 2012). However, the sensor geometry allows for the measured current to be simply

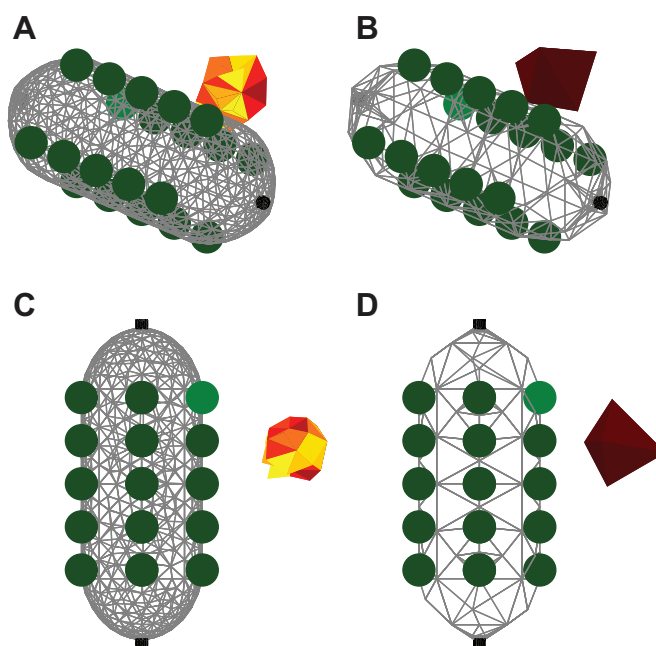


Fig. 10. Forward and inverse conductivity. Left plots (A,C) show two views of the conductivities prescribed onto elements of the mesh (red is 100× other open region around the pod) to be used in computing the forward solution. Right views (B,D) show elements above threshold (70% of peak conductivity) in the reconstructions on a low-resolution mesh. Three-dimensional object position is accurately estimated when near the pod (lateral distance is 0.09 m). Adapted with permission from Snyder et al. (Snyder et al., 2012).



decomposed into an axial current and a lateral current. The axial current is indicative of whether the sensed object is an insulator or conductor, while the lateral current is indicative of the lateral location of the object, given that the electrical properties of the object are known. Using these properties of the sensor, Boyer et al. (Boyer et al., 2013) implemented a simple control strategy based on the two decomposed current measurements to avoid insulated objects while seeking conductive ones or vice versa. A sample trajectory is shown in Fig. 11. Such control is termed reactive, as no model of the environment or the object is required and the sensor merely reacts to the electrical properties of nearby objects. This reactive control would be useful for navigation while avoiding objects without a map. The nervous system of the fish likely uses similar reactive control to avoid obstacles as the range of electro-sense is limited to approximately one body length, corresponding closely with the space in which the fish can avoid objects given neural reaction times (Snyder et al., 2007). Examples of simulated transdermal potentials of fish swimming on a planned trajectory are shown in Chen et al. (Chen et al., 2005). Rapid changes in potential near walls correlate with similar changes in measured currents shown in Fig. 11, and could potentially be used in a reactive control law to allow the fish to avoid obstacles.

Although reactive control using artificial electro-sense can be useful for an underwater vehicle, the robot will have to be maneuverable enough to actually react, especially given the short range electro-sense allows. While mechanics and sensing have thus far been discussed separately, in the following section we discuss bringing them back together to develop a highly agile robot using electro-sense. This concluding section also reiterates the motivations for creating a robot inspired by the weakly electric knifefish.

### Recombining sensing and mechanics A better autonomous underwater vehicle

One of the goals underlying the work in knifefish robotics was to build an autonomous underwater vehicle of enhanced capability

over current designs. This vehicle should be able to efficiently navigate complicated geometries in dynamic environments. MacIver et al. (MacIver et al., 2004) make the case for why the integration of artificial electro-sense and knifefish mechanics will be far more powerful than incorporating these elements in isolation. The fish's body plan and thrust capabilities are designed to optimally perform maneuvers the fish uses to capture prey (MacIver et al., 2001; Snyder et al., 2007; Postlethwaite et al., 2009). These maneuvers are directed at prey locations in nearly all directions around the fish, together demonstrating omnidirectional mechanical capabilities over the very brief duration of a prey capture sequence. These maneuvers include rapid reversals and rolls, generated by the knifefish's ribbon fin and pectoral fins. The Ghostbot was similarly designed to be maximally maneuverable in surging forward and backward as well as rolling with its long cylindrical shape. A new version of the Ghostbot that has recently been completed implements pectoral fin-like dive planes to generate roll moments when held asymmetrically in the flow. The bilateral symmetry of the fish body is crucial to these efficient mechanics. Roll maneuvers allow the fish to center the prey or object in the midsagittal plane, simplifying control by maintaining constant signal strength between the two symmetrical halves of the body during the strike sequence (MacIver et al., 2001). This form of control is very similar to the successful reactive control techniques using electro-sense described in the previous section. The omnidirectional motion capabilities of the fish are dependent upon an omnidirectional sensory field. This sensory field enables objects to be scanned along the entire length of the fish or robot. Forward and backward scanning motions (Assad et al., 1999) and 'rapid reversals' during prey capture (MacIver et al., 2001) allow extraction of key object features while always keeping the object within the short sensing range of the active electro-sensory system.

A further advantage of weakly electric knifefish is that trunk movements are decoupled from propulsion, as all propulsion comes from traveling waves along the ribbon fin. This feature facilitates technological development, as it is much simpler to build an

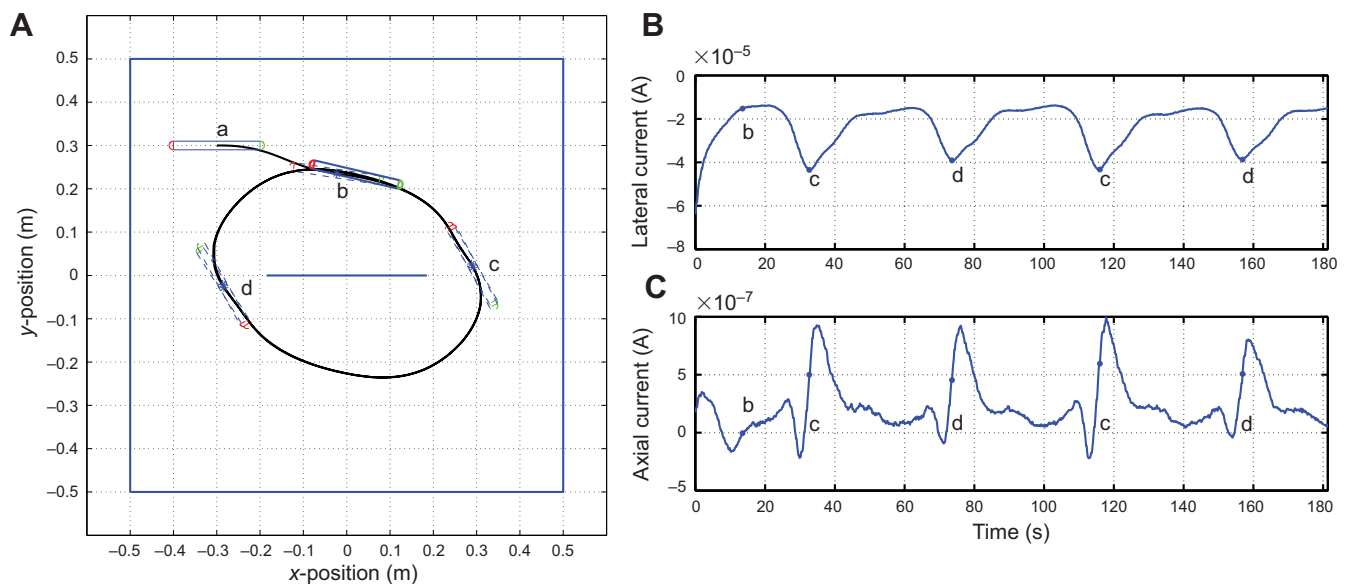


Fig. 11. Reactive control using current sensing. (A) Trajectory of the sensor platform circulating around an insulating wall. The reactive control algorithm was set to be attracted to conductors while being repelled by insulators. (B,C) Time history of lateral currents (B) and axial currents (C) used in the control law. Points b, c and d correspond to the locations marked in A. Adapted with permission from Boyer et al. (Boyer et al., 2013).

underwater vehicle with a rigid body to house all internal components. A rigid body also simplifies the computational complexity of artificial active electrosense, as it stabilizes the signal arising at sensors due to the electric field. The live fish performs postural adjustments and probing motions by tail movements, which creates an additional signal processing challenge because such movements induce a much larger response in sensory receptors than do the small prey that the fish hunts (Chen et al., 2005). Future versions of Ghostbot that integrate electrosense will benefit from the rigid body simplification, as well as minimize electrosensory interference from the moving fin by maximizing sensory acuity in regions away from the movement of the fin, as found in the live fish (Snyder et al., 2007). The ANGELS project combines electrosense with anguilliform swimming (Mintchev et al., 2012). The ANGELS robotic design is made of independently actuated modules that can combine together to undulate through the water over longer distances. While each module is rigid, the undulating mechanics of the combined robot produces large fluctuations in the electrosensory signals that must be overcome. In this case, efficient mechanics raises signal processing challenges for the artificial electrosensory system not unlike those that that real electric fish face.

#### A better understanding of the situated electric fish

Physical models are key tools used to test hypotheses and raise new questions regarding the original biological system. Often, by overcoming the technical challenges of building a robot to mimic natural behaviors, appreciation is gained for the solutions to those challenges found in nature. When waters become muddy and vision useless, nature has co-developed mechanical and sensory systems that allow electric fish to thrive where other organisms cannot. The robots discussed above demonstrate that the principles derived from studying the fish actually work when implemented, despite the many simplifications necessary to make the research tractable. Replication of observed animal behavior through physical models or computational synthesis is a productive method of inquiry with both scientific and technological benefits.

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#### Author contributions

I.D.N. and M.A.M. wrote the initial manuscript. Y.B., J.B.S. and J.M.S. contributed original figures. I.D.N. adapted figures. All authors contributed to the final manuscript.

#### Competing interests

No competing interests declared.

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