Neuromechanical design and active sensory systems in animals

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***Abstract*— The central idea of active sensing is that perception is a feedback-driven process of improving sensory signals through control of the state variables of the sensory apparatus, such as sensor position, velocity, or gain. While signal estimation is emphasized in engineering approaches to active sensing, for animals the primary goal of active sensing is to guide movement. This distinctive, locomotion-directed aspect of active sensing is the focus of this paper, using the weakly electric knifefish as a model system for addressing this issue. We present evidence that three commonly observed maneuvers of this fish are mechanically optimal, by utilizing an idealized ellipsoidal body model, Kirchhoff's equations, and an optimal control algorithm for generating synthetic trajectories. The mechanically optimal movements complement the sensing needs of the organism. The design lessons embodied by such instances of neuromechanical complementarity may be of interest for the engineering of highly maneuverable autonomous vehicles operating in uncertain environments.**

I. Introduction

The sparsity of resources within a mobile animal's habitat compels a certain logic, one that all energy-consuming autonomous agents must follow: Resources must be detected, and behavioral programs engaged to acquire these resources. Information unites with mechanics in the pursuit of this goal, with changes in the animal's position and shape that include (1) sensing-related changes, to enhance the quality of information from its sensor arrays (e.g., bats manipulating their pinnae position during echolocation; dogs bringing their snouts to the substrate to follow a trail); and (2) locomotion-related changes, such as cyclic variations in the *shape variables* (this volume, [1]) to undergo net movement (e.g., a fish bending its body to swim forward; a biped extending a leg to walk forward). The field of neuroethology has made tremendous progress in understanding the sensory processing that subserves natural behaviors [2]. Much work remains, however, in obtaining an equally detailed and quantitative understanding of how the mechanics of animals subserve natural behaviors, and in particular, how sensory abilities complement an animal's mechanical control and locomotory needs and characteristics. In addition to its basic science import, these issues have relevance to engineers seeking to emulate some of key advantages of animal neuromechanical design, such as high maneuverability, and high levels of sensory integration for executing behaviors under changing and uncertain conditions. In this paper, we start by discussing the meaning of active and passive sensing and describe some common modes of these two sensing categories. Then we move forward to review an example of how motion and sensing are integrated in the weakly electric fish. We conclude by drawing parallels between this animal and several other animals whose locomotor-directed sensory performance has been examined.

motion	teleceptive	autostimulatory	examples
Yes	Yes	Yes	Echolocation-driven tropotaxis
No	Yes	Yes	Echolocating while stationary
Yes	No	Yes	Pressure-related touch, whiskers
No	No	Yes	Rare
Yes	Yes	No	Stereopsis, phonotaxis
No	Yes	No	Radiant heat, odor detection
Yes	No	No	Feeling for heat or cold
No	No	No	Sensing contact heat or cold

TABLE I
MODES OF ACTIVE AND PASSIVE SENSING.

A. Varieties of active sensing

In animals, resource detection and acquisition is guided by the transduction and neural processing of ambient fluxes of energy, such as acoustic and electromagnetic energy. This is sometimes referred to as "passive sensing." In some cases, such as in dark or turbid environments, such ambient fluxes may not be present with the needed strength or dependability to guide behavior. In these cases, certain animals such as bats, dolphins, and weakly electric fish have evolved the ability to generate signals which propagate through the environment. Modulations of the propagated self-generated signal are then decoded and are used to guide behavior. These are often referred to as "active sensing" systems, both in biology and in engineering when referring to radar and sonar systems. A different definition of active sensing, one used in research in machine vision [3], [4] and sometimes in biology [5], refers to sensing which requires deliberate, structured motion of the sensory apparatus with respect to the target of interest. Examples in biology include the whisker movements of rats [6], phonotaxis in frogs [7] and crickets [8], and the peering behavior (movements of the head from side to side) of a stationary locust for determining distance with its eyes [9], while in engineering examples include directional vision systems for real-time grasping and manipulation [10], machine foveated vision [11], mobile sonar systems [12], and haptic systems

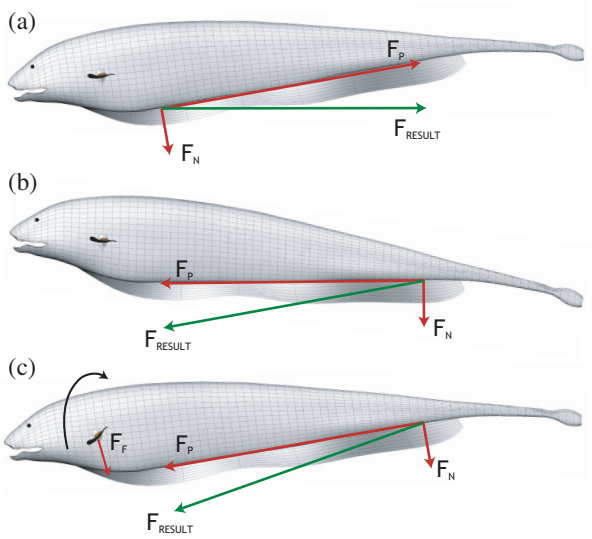

Fig. 1. Putative (see [14]) thrust vectors around *Apteronotus albifrons* for two swimming directions and a roll maneuver. F_N is force normal to line of ventral ribbon fin; F_P is the force parallel to this fin, and F_F is the force generated by pectoral fin. (a) Swimming forward. Pectoral fins are typically held at the the indicated angle of attack during this behavior. (b) Swimming backwards. Note that the body needs to be negatively pitched to go straight back. We have observed such negative pitching of the body during straight-back swimming (unpublished observations). (c) Swimming up and back with a roll by forcing fluid down on one side of the body, similar to the motion observed during a stereotypical prey strike (see Figure 3).

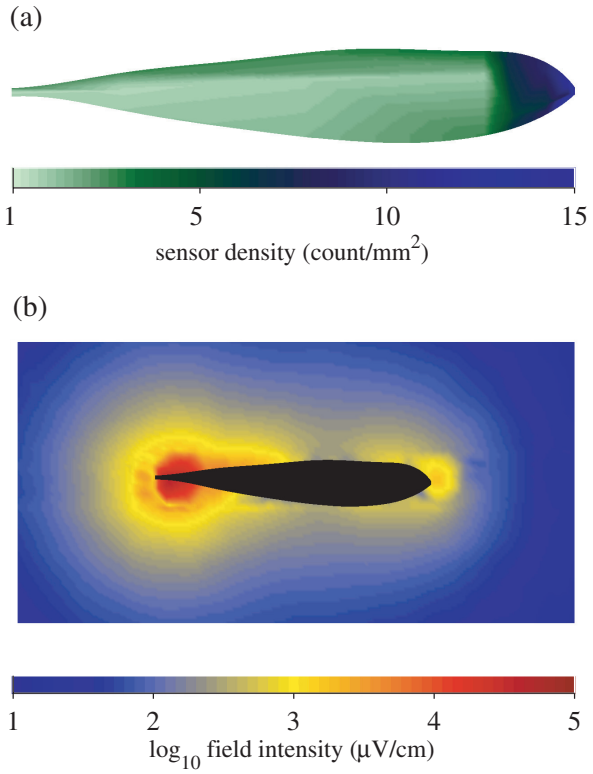

Fig. 2. (a) Electroreceptor layout for *A. albifrons*. Data for (a) from [18], covering the surface of a 3D model of the fish according to [19], [20]. There are no sensors on the fins of the fish. (b) Electric field around *A. albifrons*, midsagittal plane. Data set for (b) courtesy of Chris Assad and Brian Rasnow.

[13].

The active/passive terminology is unfortunate since an active sensory system in the first sense (signal generator) is also sensitive to non-self-generated signals (bats hearing the ultrasonic calls of other bats, or electric fish transducing the electric fields of other electric fish [15]), making them passive on such occasions; and signal generating animals often also use motion-dependent sensory algorithms, making them active in both senses. These terminological difficulties of "active sensing" have been noted since the inception of the phrase [3], [16], [17]. The chief problem is that the signal-generator meaning of active sensing precedes the motion-dependent algorithm sense. However, it is clear that the motion-dependent algorithm usage encompasses a more common sensing scenario, while active sensing systems in the old sense are relatively uncommon. Thus, we will term systems that generate their own propagating sensory signals "teleceptive autostimulators," and let the generic meaning of active sensing refer to sensory algorithms which depend on control of the geometric state variables of the sensory apparatus. With these distinctions in mind, we can discriminate various common modes of active and passive sensing, biological and artificial, along the following lines (Table I): first, whether the *sensory algorithm* requires deliberate, structured movement of the sensory apparatus with respect to the object of interest (active sensing) or is motion independent (passive sensing); second, whether the sensing involves *propagated signals* (teleceptive—signals have propagated some nonzero distance from the sensory apparatus) or is contact-based; and third, whether the *signal origin* is the sensory apparatus (autostimulatory) or external to the sensory apparatus.

II. Weakly Electric Fish

The black ghost knifefish (*Apteronotus albifrons*, Fig. 1) is a South American gymnotiform weakly electric fish that can communicate and sense its surroundings by use of a weak (1 mV cm^{-1} near the body, Fig. 2b), self-generated electric field. Nearby objects that differ in electrical conductivity from the surrounding water create localized voltage perturbations that are sensed by ≈14,000 [18] transcutaneous electroreceptor organs scattered over the body surface (Fig. 2a). In addition to their specialized sensory capabilities, gymnotiform knifefish possess a unique multi-directional propulsion system driven by a ventral ribbon fin that runs most of the length of the body (Fig. 1). By generating traveling waves along the ribbon fin and manipulating the pectoral fins, they move forward, backward, and upward, and can rapidly pitch or roll the body [21]–[25]. It is a highly active, predatory fish, hunting for small prey at night in geometrically complex habitats such as flooded forests [26], and hiding during the day. Weakly electric fish have become a standard model system for examining vertebrate sensory processing, with a tremendous accumulation of information spanning the molecular through to behavioral levels [27].

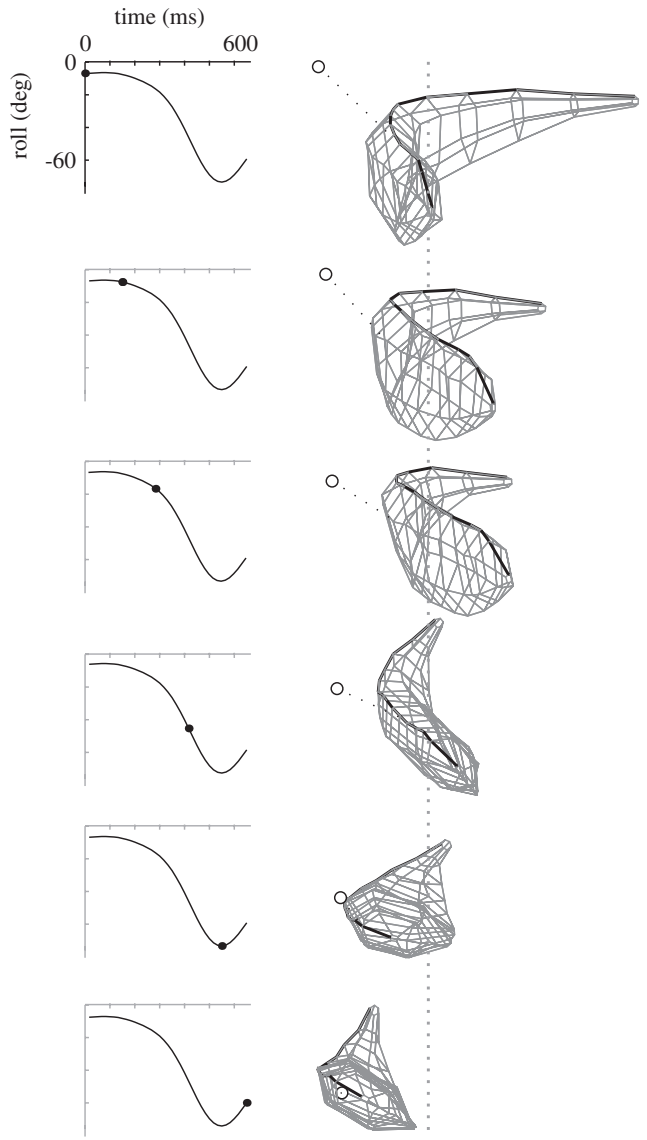

Fig. 3. A typical rolling maneuver to reach a laterally-positioned prey. Wireframe represents position of fish as it strikes a prey, from 3D motion capture data. The top snapshot (t=0 ms) is at the time of prey detection, and time increases up to the last snapshot at the end of the sequence. The heavy line on the fish indicates the dorsal edge, the open circle marks the position of the *Daphnia magna*, and the dotted line indicates the shortest distance from the *Daphnia* to the body surface. The inset plot on the left shows the roll angle history and current value (filled circle). Modified from [21].

In terms of the above modes of active and passive sensing, this fish sometimes electrolocates objects with the use of its own field while hunting by using "tuberous" electroreceptors (active sensing, motion-dependent teleceptive autostimulation) [21], sometimes electrolocates other electric fish by following the electric field lines of the other fish with the same receptors [15] (active sensing, motion-dependent teleceptive external stimulation), or detects the external bioelectric fields present around all aquatic prey by using "ampullary" electroreceptors [28] (teleceptive external stimulation, active or passive sensing; it is not known whether this modality is simply used for detection, or whether the sensory algorithm requires movement of the ampullary sensors). In this paper we focus on the autostimulatory form of electrolocation, which is better understood and which we know plays a role in prey detection and capture [21], [28]. First, we discuss stereotypical prey-capture maneuvers of this fish, and then we develop a simple mechanical model of the system to aid in understanding the basis of the observed movements.

III. Prey-capture maneuvers

During prior behavioral studies [21], individual black ghost knifefish were videotaped hunting for small prey under infrared light within a light-tight enclosure. Two cameras provided orthogonal views of the behavior, which were placed together within one video frame by use of a video splitter. Prey-capture sequence video was digitized and brought into a custom model-based tracking system [20]. A non-rigid wireframe model of the fish was overlayed onto the video in the two views and a 3D reconstruction algorithm provided the position of the surface of the fish and prey to ± 0.5 mm, with a time resolution of 16.7 ms [20], [21]. A single *Daphnia magna*, a small (up to 3 mm in length) crustacean that these fish are known to eat in their native habitat, was utilized for each trial.

Prey were typically detected while the fish swam forwards (Fig. 1a). Following the detection, the fish began to decelerate. We used the onset of deceleration as an estimate of the time of prey detection. The deceleration was very rapid (from around 10 cm s^{-1} to -20 cm s^{-1} over the course of 300 ms [21]). It was mediated by a combination of reversing the direction of the traveling waves on the ribbon fin (Fig. 1b) and one or two synchronous high-speed backward rowing motions of the pectoral fins (which have the characteristic paddle-shape seen in highly-maneuverable fish, see [29] this volume). We refer to this as a "rapid reversal" maneuver.

Following prey detection, if the prey was to the side of the body, the body would roll (around its long axis) approximately the angle to the prey so that the prey would be centered directly above the dorsal edge [21] (Fig. 3). Simultaneously, it would reverse and slice through the water with the narrow dorsal edge of the body leading. The body was maintained in a rigid, straight conformation during this behavior, with roll, pitching, and translation occurring through a combination of ventral ribbon fin activity and manipulation of the pectoral fins. For example, by moving backward with ribbon fin motion, in combination with holding the left pectoral fin at an angle of attack so as to create an upward pressure on the left fin (by pushing fluid downwards as it moves by), the body will roll to the animal's right (Fig. 1c). Such a force-torque pair, also created to change the pitch angle of the fish's body (but with bilaterally symmetric up or downwards pressure through the two pectorals), is referred to as a "wrench" in mechanics. We refer to this as a "dorsal roll" maneuver. Typically, detected prey were positioned above the animal [21]; thus, the upwards thrust gained from reversing the fin (see force vectors in Fig. 1c) is advantageous to the animal.

IV. Fluid and body models

We idealized the knife-like fish body as a rigid ellipsoid of similar length (13 cm), depth (2.4 cm), width (0.64 cm), surface area (52.1 cm^2), volume (10.1 cm^3), and mass (10.1 g) as the fish used in prior behavioral studies [21]. Figure 4 shows the black ghost knifefish body plan alongside the approximating ellipsoid. For this analysis, we consider the ellipsoid to be submerged in an ideal fluid (inviscid, incompressible, irrotational, and at rest at infinity). For the Reynold's number typical of this fish (10^3-10^4 [25]), the inviscid assumption is reasonable. In addition, for the short-range, transient maneuvers considered here, the acceleration reaction forces we model should dominate the effects of drag. These "added mass" effects are forces due to the fluid that is accelerated and displaced by movement.

Finally, the behaviors of the fish we will be investigating with this model (body roll and rapid reversals of the direction of movement) are executed with a rigid straightened body [21]. Thus, the absence of bending in our ellipsoidal approximation is appropriate for modeling these behaviors. Rigidity of the body of the gymnotids during locomotion has long been noted, and is in part mediated by a special body-stiffening adaptation, the presence of intramuscular bones [30], [31]. Inasmuch as the fish is able to maneuver without bending the body by use of the ribbon fin and pectoral fins (neither of which possess sensors), it is able to decouple locomotory movements from active sensing body movements [21]. This in turn may reduce the reliance on "reafference suppression"—removal of self-induced stimulation due to movements of the electric organ inside of the body. Such movements can cause much larger modulations of sensory nerve activity than those caused by prey [21], [32].

The equations of motion for an ellipsoid in ideal fluid are Kirchhoff's equations [33], [34]:

$$\dot{\boldsymbol{\omega}} = \boldsymbol{J}^{-1}(\boldsymbol{J}\boldsymbol{\omega} \times \boldsymbol{\omega} + \boldsymbol{J}\boldsymbol{v} \times \boldsymbol{v} + \mathbb{T}) \quad (1)$$

$$\dot{\boldsymbol{v}} = \boldsymbol{M}^{-1}(\boldsymbol{M}\boldsymbol{v} \times \boldsymbol{\omega} + \mathbb{F}) \quad (2)$$

where $\boldsymbol{\omega}$ and $\boldsymbol{v}$ are vectors of the angular and linear velocities of the ellipsoid, respectively, in a body-fixed coordinate frame, $\boldsymbol{J}$ is a the sum of the inertia matrix of the body and the added inertia matrix due to the effect of the fluid displaced by rotations, $\boldsymbol{M}$ is the sum of the mass matrix of the body and the added mass matrix due to the fluid displaced by translations, and $\mathbb{T}$ and $\mathbb{F}$ are vectors of the external torques and forces, respectively. The axes of the body-fixed frame are chosen to coincide with the principal axes of the ellipsoid, thus the mass and inertia matrices are diagonal. The elements m_i of the diagonal mass matrix $\boldsymbol{M}$ are computed as [33], [34]:

$$m_i = \rho V\left(1 + \frac{\gamma_i}{2 - \gamma_i}\right), \quad (3)$$

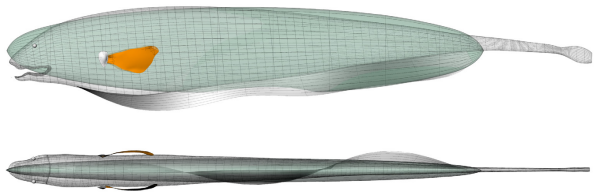

Fig. 4. Body plan of the black ghost *Apteronotus albifrons* overlayed with the ellipsoidal model.

where

$$\gamma_i = l_1 l_2 l_3 \int_0^\infty \frac{d\lambda}{(l_i^2 + \lambda)\Delta}, \quad (4)$$

$$\Delta = \sqrt{(l_1^2 + \lambda)(l_2^2 + \lambda)(l_3^2 + \lambda)} \quad (5)$$

l_i is the length of the semiaxes of the ellipsoid along the ith principal axis for $i = 1, 2, 3$ (6.48, 1.18, and 0.32 cm respectively), the volume of the ellipsoid is $V = 4\pi l_1 l_2 l_3/3$, and ρ is the density of water (1,000 kg m^{-3}). This gives $(m_1, m_2, m_3) = (10.4, 12.9, 45.9)$ g (effective mass moving forward, up, and laterally, respectively). The element j_1 of the diagonal inertia matrix is

$$j_1 = \frac{1}{5}\rho V\left(l_2^2 + l_3^2 + \frac{(l_2^2 - l_3^2)^2(\gamma_3 - \gamma_2)}{2(l_2^2 - l_3^2) + (l_2^2 + l_3^2)(\gamma_2 - \gamma_3)}\right) \quad (6)$$

with j_2 and j_3 cyclic permutations of the formula for j_1 ($1 \mapsto 2 \mapsto 3$). This gives $(j_1, j_2, j_3) = (7.5, 362.2, 108.6)$ g cm (effective inertia rotating around the long axis, around the vertical axis, and around the transverse axis, respectively).

V. Optimal control

A. Dorsal rolls and rapid reversals

Dorsal rolls and rapid reversals are a nearly ubiquitous feature of the prey-capture sequences we quantified in *A. albifrons* (N=116, [21]). Prior to details on applying optimal control methods to understanding these behaviors, we first consider several candidate bases for optimality.

For the dorsal roll, one possible *sensory* basis is that by executing this maneuver the fish is increasing the quantity and resolution of sensory inflow, by pointing a surface of higher sensor density toward the prey (Fig. 2a). A possible *control* basis is that by centering prey between the bilaterally symmetric halves of its electrosensory system, the fish could be executing a simple localization strategy (sometimes referred to as a "tropotaxis" [35]). To execute this strategy, the fish would first roll its body to null any imbalance in input between the two sides of its sensory system; then it would climb the gradient of sensory signal strength until capture occurs [21]. A second possible control basis is that while the knifefish can move dorsally, forwards, and backwards, as well as pitch and roll via the generation of a wrench as described above, it has

no ability to move in the lateral direction. Ventral directions can be accessed by the pitching wrench (e.g., apply downward pressure via the pectorals while translating forwards, or apply upward pressure while translating backwards). By combining roll with other movements the fish creates a motion in an unactuated direction by combining motions in actuated directions, analogous to a maneuver in a Lie bracket direction for general underactuated systems ([1], this volume). From our 3D motion capture data, we've measured remarkably high roll angular velocities in excess of 400° s^{-1}. In most fish, roll is stabilized by the lateral compression of the fish body form [36]; weakly electric fish provide the interesting example of a fish that is laterally compressed but able to roll easily, perhaps owing to its tapering and elongated body form which houses the electric organ that generates the field. The torque needed by the animal to roll the body will be proportional to its moment of inertia along the highly stable longitudinal axis. As computed above, the ellipsoidal approximation of the body has a very low moment of inertia along the longitudinal axis (7.5 g cm), an order of magnitude lower than rotations around either of the other two axes of the body. Thus, rolling around this axis is a mechanically favorable mode of movement for this animal.

Finally, a possible *mechanical* basis for the behavior is that the fish, by slicing through the water with the narrow edge of the body, is minimizing the form drag and added mass reaction forces on the body. The latter are significantly less in the dorsal-leading than lateral directions for the fish (12.9 versus 45.9 g net mass for our ellipsoidal approximation), due to the laterally compressed body plan (aspect ratio of slightly over 2:1, depth to width). Given the transient, short-range and high-acceleration nature of prey strike behavior [21] as mentioned above, we expect that added mass effects will dominate drag. For the rapid reversal, we can again posit several possible bases for the behavior. A possible *sensory* basis is that by reversing, a prey is scanned over an increasingly higher density of sensors, with an order of magnitude higher density forward of the pectoral fin (Fig. 2a). The high density region of the head is sometimes referred to as the "electrosensory fovea." A possible *control* basis is that the body has high stability during the rapid reversal (the body straightens and becomes rigid), allowing all force to be applied towards rapid locomotion. The maneuver represents a simple change in the direction of the primary force vector, and, without any pitch change, the reversal results in an upwards thrust (see Fig. 1c) which is perfectly suited for reaching the prey that are usually detected above it [21]. Finally, the *mechanical* advantages of this approach include the low drag and added mass effects of pushing the tapered body form backwards through the flow.

Using the ellipsoidal model of the fish in an ideal fluid, we examined whether mechanical factors *alone* may determine the the rolling and rapid reversal maneuvers. That is, without regard to sensing, control issues, or actuation (i.e., the ellipsoid is fully actuated, unlike the fish), would the ellipsoid exhibit qualitatively similar behavior to what we observed in the real fish?

B. Synthetic trajectory generation

Trajectories for the ellipsoidal body were generated using an optimal trajectory generation algorithm [37], with custom software developed by Mark Milam at Caltech (NTG). The algorithm finds a trajectory of Equations 1 & 2 which minimizes a given cost functional subject to a set of trajectory constraints. The constraints specify initial and final conditions of the system's state variables and controls, and trajectory constraints such as that a certain level of force not be exceeded or that the pitch of the body not exceed some maximum value. In our case, we chose a "control cost" functional

$$J = \int_{t_0}^{t_f} \|\boldsymbol{u}(t)\|^2 dt \tag{7}$$

where t_0 is the initial time, t_f is the final time, $\boldsymbol{u}$ is the $(\mathbb{T}, \mathbb{F})$ of Equations 1 & 2, a set of six torque and force control vectors $(t_x, t_y, t_z, f_x, f_y, f_z)$. We found the results to be robust to torque scalings of between unity and 100. There were no penalties for torques or forces in any of the degrees of freedom. The control cost of a trajectory for the ellipsoid can be thought of as analogous to the metabolic cost of muscle activation that would be required for a fish to execute the trajectory.

For trajectory constraints, initial and final conditions were chosen as described below, subject to two global constraints: Euler angles of the body (yaw, pitch, and roll) were bounded to be ≥ 0 and $\leq 2\pi$ over the course of the trajectory, and the trajectory must end with the ellipsoid at zero velocity. We chose this because at the end of prey capture trajectories of *A. albifrons*, the fish's velocity is near zero [21]. We did not constrain the final angular velocity, or positional and angular accelerations.

We utilized two different sets of initial and final conditions. The first was designed to be similar to conditions under which a "dorsal roll" is observed during prey capture, and under which we observe "side-scanning" behavior where the fish will scan the substrate for food, moving dorsally and perpendicular to the long axis of the body. This initial condition specified a zero initial velocity, and a final position about a body length directly lateral of the initial position. The second initial condition was designed to investigate the "rapid reversal" strategy. We set the forward velocity to near the mean of the searching velocity of the fish (prior to prey detection) (10 cm^{-1} s), and the pitch of the ellipsoid to the mean pitch during searching behavior (30°) [21], with a final position slightly dorsal and to the side of the initial position. This approximates the configuration of the fish and prey during a near head-on detection.

We found that the control cost optimal trajectories, given these initial conditions, were qualitatively very similar to those quantified for weakly electric fish. Both the rolling behavior, and "rapid reversal" aspects of the kinematics [21] were found (Fig. 5). An additional aspect that was also previously documented, pitch reduction during the reversal [21], was also observed in the optimal trajectories (Fig. 5, right column). In the future, we will be performing more detailed, trial-

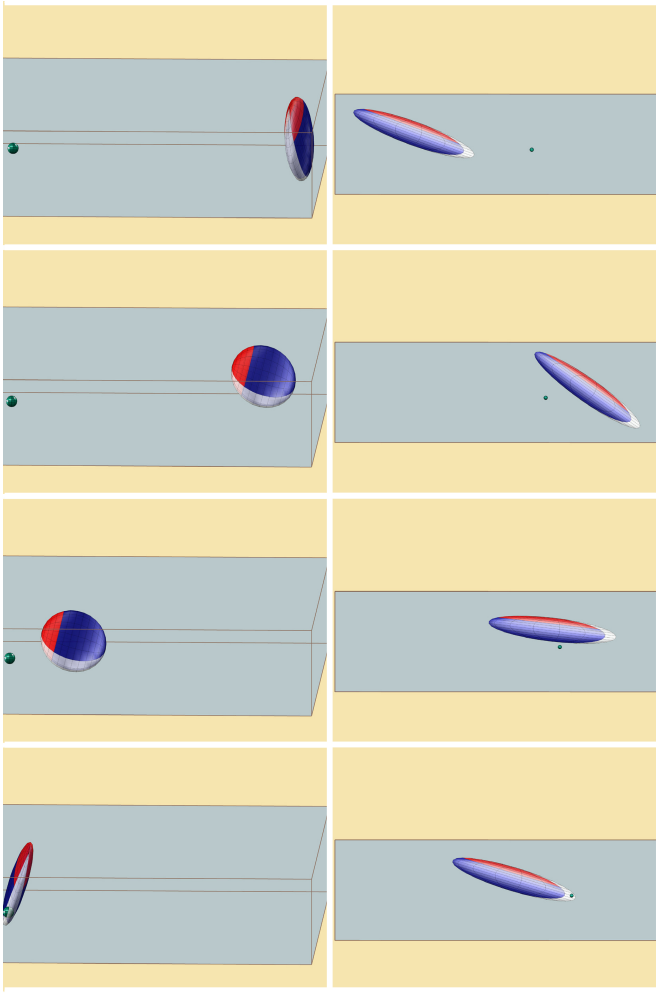

Fig. 5. Snapshots of control cost optimal trajectories for the two initial conditions representing common electric fish prey capture maneuvers, with time increasing from top to bottom. Final position indicated by the small sphere ("prey") outside of the ellipsoid. Left column shows the view (from close to head-on) of the ellipsoid rolling into the fluid as it performs a lateral translation. The right column shows a side view of the ellipsoid moving forward (to the right). As it moves forward, the pitch angle decreases, and the ellipsoid performs a reversal to translate to the prey.

by-trial comparisons of the fish trajectories and the optimal control trajectories. Towards that end, we recently completed measurements of the drag on the body of *A. albifrons*. With these measurements integrated into the trajectory generator, we can also examine minimum energy and minimum time trajectories.

VI. The Codesign of Body Plan, Sensor Geometry, Control, and Mechanics

The complementarity of sensing to locomotion is an ancient pattern stretching back to the early appearance of the Bilaterian animal body plan. In this body plan, bilateral symmetry, which often [38] includes high forward mobility along the midline axis, is closely coupled to cephalization, an adaptation that complements such mobility with a clustering of sensory organs around the head. All vertebrates and most other highly mobile animals such as insects feature this neuromechanical complementarity. With this neuromechanical template [39] came the active feeding behaviors and agile locomotion that correlates with the evolution of advanced nervous systems needed to control these behaviors [40]–[42].

In the specific case of the neuromechanical complementarity of weakly electric fish, one interpretation of the optimal control results is that mechanical optimality determines the two observed sensor gradients on the body (Fig. 2): the gradient in sensor density from the bottom to the top of the body plan is determined by the minimal cost advantage of leading with the narrow edge first, and the lengthwise gradient in sensor density is determined by the minimal cost advantage of going backwards with the body rather than continuing forwards and circling back. However, this interpretation would not be warranted.

Regarding the bottom to top gradient, the optimal control result is that *rolling* is advantageous; not that *rolling the dorsal edge* in the direction of movement is advantageous, as the kinematic results for the fish show [21]. From the optimal control model perspective, because the model does not include the sensory or mechanical constraints that the fish has, pointing either edge into the flow is equally optimal. However, the fish is less mobile in the downwards direction than in the upwards direction (see ribbon fin force vectors in Fig. 1), in addition to having a lower sensor density in that area than on the dorsal edge. Further, the dorsal edge also features a sensor-laden filament that may facilitate prey discrimination [43], [44]. Finally, even if it could translate downwards with ease, the presence of the traveling waves on the ribbon fin structure would likely buffet prey away prior to capture, whereas pushing the smooth, airfoil-like top edge of the body through the water does not disturb the flow in the area of the prey. Similarly, for the lengthwise gradient in sensor density, there is no preference for the head of the animal in terms of our simplistic model, whereas whatever prey capture motion the fish chooses, it must terminate with the prey in a small region near the mouth opening (engulfing occurs by sucking in a small volume of water into the mouth). To create the dorsal and anterior bias in the optimal control trajectories, we may need to augment our ellipsoid model with the sensor density regime shown in Figure 2a, our cost functional with a "signal uncertainty" term proportional to the the ambiguity of the prey's position with respect to the body. In addition, we may or may not need to include the actuation constraints that the fish has. Future efforts will explore these aspects, as we have models of both the signal input due to the prey, and the afferent spike train changes resulting from the prey [19], [28], [45]. In addition, recent work on quantifying the "small-time locomotor volume" of this animal [46] (Fig. 6b) is providing useful information for augmenting the trajectory generation algorithm with actuation constraints.

While it may appear that mechanical optimality may have determined the sensor layout and body plan of *A. albifrons*, it may be just as likely that sensory capacity determined the mechanics and body plan. Recently, we have obtained

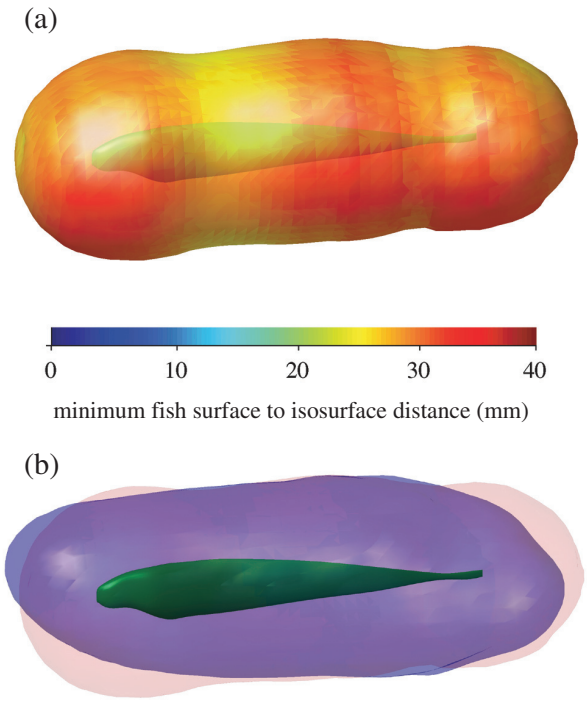

Fig. 6. Sensory and small-time locomotor volumes around *A. albifrons*. (a) The sensory signal isosurface for detecting small prey. All points on the surface result in the same net input to the ≈14,000 sensor receptors covering the surface. (b) The stopping-time locomotory volume (all points reachable within 235 ms of movement of the animal), indicated by purple locomotory isosurface, with the sensory isosurface shown in light red.

evidence that the volume of space that *A. albifrons* is able to reach within the sensorimotor latency of the animal (time from sensory input to motor output, 120 ms) plus the time it takes to stop the body when going forward at typical searching velocity (115 ms) is nearly congruent with the volume of space within which it can detect the small prey that are its food source [46] (Fig. 6). Remarkably, despite the high variation in sensor density and electric field strength (Fig. 2), this sensing volume forms a very regular cylinder around the body. The unusually high maneuverability of this animal perfectly complements its omnidirectional sensing capabilities. The lack of actuation in the lateral directions appears to be largely compensated for by the rolling movement discussed above.

This leads us to another dimension of coupling, that of control. Rolling appears to be important, perhaps key, to this animal's maneuverability in lateral directions. In executing the rolling maneuver, as mentioned above, the fish may also be creating an effective local (reactive) control strategy that is appropriate to the short-range nature of electrosense (typically, about 1/3 of a body length for prey detection [21]). That is to position objects in the plane of bilateral symmetry, which corresponds to the plane of maximal mobility. Since the sensory system itself is divided and bilaterally symmetric, imbalances in sensory input detected via commissural fibers in the hindbrain can be used to drive a rolling response to recenter the prey. Then, the fish can simply ascend the gradient of sensory strength to bring the mouth to the prey. If the fish is working with the "two-degree of freedom" control approach that is sometimes used for trajectory planning in artificial underactuated systems ([37], and [1] in this volume), we could envisage the following scenario: For the first degree of freedom, a trajectory respecting the nonlinear dynamics of the system is generated and started in an open-loop manner (for example, the initial centering roll and backwards thrust). Then, for the second degree of freedom, a simple feedback controller stabilizes the movement of the body along the trajectory (rolling an amount proportional to the difference between the sensory signal input from the two halves of the body), accounting for model inaccuracies and changes in the prey position from the initial position estimate. Earlier work found evidence for feedback-driven control of the prey strike in those instances where the prey moved a significant amount after being detected [21], so a strictly open loop control strategy following prey detection is highly unlikely. If this control strategy is indeed the one followed by the fish, then an additional element of elegance is that an adaptation that favors a simple local control algorithm for prey localization and control in unactuated directions (a body suited for rolling) *is the very same* as one which confers mechanical optimality.

The above localization strategy has also been suggested for localization of prey in bats [47], although it appears that bats often depart from the straight line trajectory to undertake preparatory maneuvers just prior to capture, perhaps to position the body above the prey for more effective capture or delay the time of contact for additional sensory acquisition [48]. In general, however, exploitation of bilateral symmetry for sensory-guided behavior is a very common scheme in animals [35]. In keeping with this, it has been well documented that visual and auditory sensory systems have their maximal acuity at zero azimuth in body-fixed coordinates. In a similar spirit, in flies it appears that optic flow (such as induced by translation or rolling of the body) can be processed through a very simple wiring plan that takes advantage of the geometry of the eye and layout of the ommatidial rows [49]. Extraction of the amount of rolling around the axis of symmetry, an important factor for the animal's control of its movement, is rendered a trivial computation by the combination of the structure of sensory signals created by the symmetric body flying through space and the configuration of sensors on the compound eye. It is intriguing to consider whether the rise of the Bilaterians (all animals except for Cnidarians such as jellyfish, and Poriferans such as sponges) in the Cambrian period was related to control, movement, and sensory processing advantages of the bilateral body plan such as these.

While it is tempting to consider mechanics as the causal antecedent of the sensor geometry and body plan or vice-versa, in actuality, the tight integration of sensing, control, actuation, behavior, and ecology probably represents the coevolution of these different elements of this animal's capability. As has been previously pointed out [39], [50]–[53], given the tight coupling occurring in these systems, situating the locus of control in either the nervous system *or* mechanical system

may not be possible, with each playing a part to an extent that varies with gait, velocity, and the degree of sensory challenge posed by the environment, among other factors [39], [52]. Indeed, one of the challenges of integrated approaches is "to conceptualize agents' adaptations to their environments in ways that neither treat agents as isolated black boxes or dissolve them into one big machine" [54].

VII. Influences of the Metabolic Cost of Information

While we have been considering ways in which sensing and movement cooperate, we should also consider the occasions in which they pull in different directions. The metabolic cost of information is, in general, the metabolic cost of building, maintaining, and moving the sensory organs to search through space [55]. For a fly, for example, this is estimated to be 10% of the resting metabolic cost, and 3% of the cost while flying [55]. For animals which generate their own sensory signal, the teleceptive autostimulators, *added* to this is the cost of generating these signals. If we use a simplistic spherical spreading model, it is clear that several body lengths away from the animal (where near-field effects disappear), for both bats and fish, the signal attenuates as an inverse quartic function of distance. This is because there is a r^{-2} attenuation with distance of the emitted signal, and a r^{-2} attenuation with distance of the returning signal being propagated from the target of interest. We have found that the metabolic cost of the sensing volume near to an electric fish (within a body length) scales with a cubic power of the magnitude of this volume [46]. This would exert a downward evolutionary pressure on the size of the sensing volume significantly higher than, for example, visually-guided creatures where this cost scales with 3/2 power of the number of pixels (based on metabolic scaling laws and data in [55]). As a first order approximation, the energetic benefit of sensing an additional unit of volume will scale linearly, assuming uniform food distribution. Thus, a power law scaling of the metabolic cost versus the size of the sensing volume will eventually overtake the energetic gain from scanning a larger volume for food. Thus, we can expect that animals that have a signal generation cost will exhibit a sensing volume whose size is generally smaller than animals that are not teleceptive autostimulators, such as most visually guided animals, as is observed [46].

An additional cost for weakly electric fish can be observed in Figure 7a. Weakly electric fish consume a larger fraction of their oxygen for supporting their massive brains than any other animal [57], 60% versus 20% in humans. One factor may be the presence of significant reafference suppression, the cancellation of the large amount of self-stimulation that occurs to the animal's sensory system as a result of the movement of the body, which contains the electric organ [58], [59]. This is analogous to a near universal strategy found in the visual systems of animals, gaze stabilization [60], which serves to reduce image blur due to locomotion, and increase sensitivity to movement in the external world by canceling out self-motion. Another factor leading to need for a larger brain

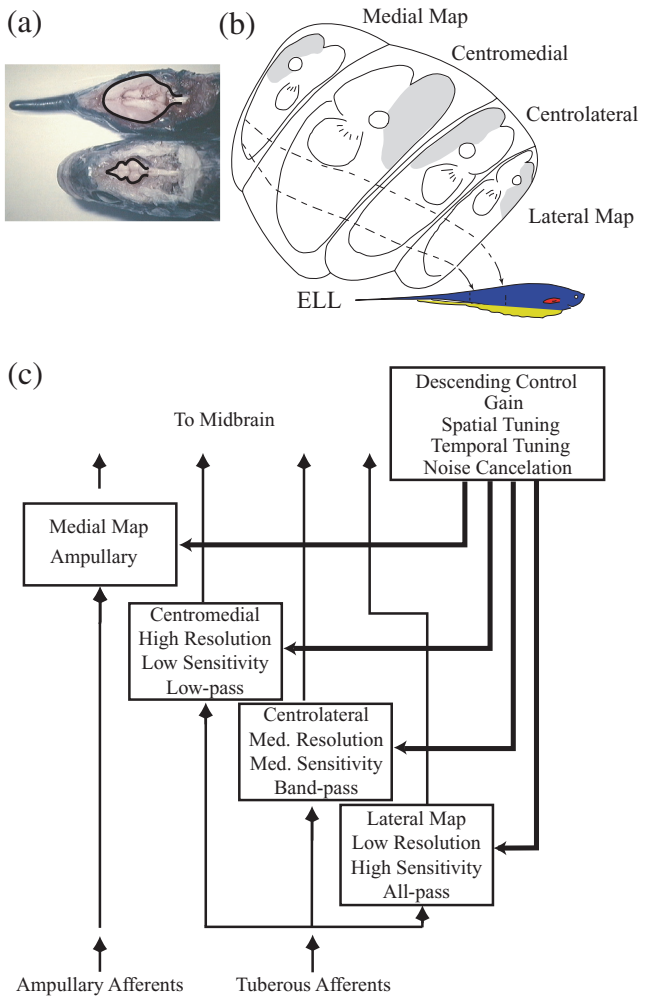

Fig. 7. (a) The "gigantocerebellum" of the mormyrid *Gnathonemus petersi* (top) compared to a similarly-sized non weakly electric fish (bottom), a yellow cichlid. Photo courtesy Brian Rasnow and Chris Assad. (b) The multiple somatotopic electrosensory maps in the gymnotid electrosensory lateral line lobe (ELL) (modified from [56]). (c) The multiresolution filter bank schematic of the ELL (courtesy Mark E. Nelson).

may be the lack of a peripheral focusing mechanism, such as the lens of the eye. The electrosensory image "focusing" mechanism appears to instead consist of a multiresolution filter bank in the animal's hindbrain, which is under the control of massive descending input from the midbrain (Fig. 7c). Primary sensory afferents trifurcate and send the identical signal information to three different somatotopic maps, each with a different spatiotemporal filter. This filter has been the subject of intense investigation [61], since control of lower sensory nuclei via massive descending input from higher brain regions is a universal, and little understood, motif of vertebrate nervous systems.

This analysis does not consider metabolic costs of active sensing, in that we are not quantifying the cost of specific movements designed to increase the quality of sensory signals. In a recent exciting paper on this issue in crabs [62], scavengers that find their food by following odor plumes to

their source, it was found that crabs will locomote in a manner that minimizes hydrodynamic drag when there is no odorant present (sideways gait), but that when an odorant is present it will rotate into the flow, increasing its drag and the metabolic cost of movement. The reason for this appears to be improved bilateral comparison at the chemosensory antennules that can then drive effective chemotaxis. If the flow velocity is further increased, the crab will not rotate into the flow regardless of the presence of an odorant, presumably because the cost of locomotion overtakes the benefit of improved signal quality.

VIII. Conclusion

Animals exhibit an astonishing level of sophistication in the manipulation of their mechanical conditions. Optimal control methods for generating animal trajectories, along with the modeling of the body mechanics and effects of the surrounding medium that such methods require, combined with models of an animal's sensory ability, provides many insights into the densely interconnected web of behavior, sensing, and mechanics in animals. Work on biological model systems such as weakly electric fish and flies [49] can provide lessons on approaches to combining locomotion, sensing, and control in situations where high levels of sensory responsiveness and real-time behaviors are needed.

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