

Active Sensing Shapes Sensory Feedback for Control

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Overview

Control systems engineering commonly relies on the separation principle, which allows designers to independently design observers (based on sensor inputs) and controllers. Biological control systems, however, routinely violate the requirements for separability. Animals often rely on a strategy known as “active sensing” in which organisms use their own movements to alter spatiotemporal patterns of sensory information to improve task-level performance. In this seemingly paradoxical category of behaviors, animals generate movements that are not linearly related to the motor goal. These movements, however, appear to improve sensing in the closed-loop system, thereby increasing control performance.

Here we propose to elucidate design principles for active sensing in locomotor control by studying a uniquely suited animal model, the weakly electric knifefish. These fish use active sensing while tracking a slowly moving refuge in the dark. While tracking, the fish produce rapid “whisking-like” forward and backward swimming movements. These higher frequency active movements shift the temporal patterns of stimulation of the animal’s sensory systems from the lower-frequency range of the exogenous movement of the refuge to the higher-frequency range of its own autogenous movements.

Our central hypothesis is that the fish rely on sensory feedback from active movements for control. We propose to examine this by experimentally altering sensory feedback to the animal. In Specific Aim 1, we will statically alter refuge design, thereby altering the spatial patterns of sensory information that the animal can perceive. In Specific Aim 2, we will dynamically alter sensory feedback using a system that simultaneously measures the position of the fish and controls the relative position of the refuge. Using this system, we can shape the animal’s feedback policies in both time and space while measuring the locomotor performance of the fish. The data from these experiments will be used to generate and refine mathematical models and control algorithms that capture the dynamics of active sensing in this task. These models are general and can be implemented in robots with highly adaptive sensors and/or with high dynamic range, but violate the requirements for traditional observer design, and thus require active sensing.

Intellectual Merit

The discovery of ‘active sensing’ - a process by which an animal expends energy to alter the sensory signals it uses to achieve behavioral goals - is profoundly changing our understanding of how animal control systems work. A challenge of studying active sensing is that it necessarily occurs in closed-loop; in active sensing the animal uses ongoing sensory feedback to alter the motor programs that then shape the sensory feedback the animal receives.

The proposed work will examine the interplay between sensory information and motor programs for active sensing in a well-suited model system, weakly electric fish. The results from this work will be relevant to a broad range of tasks, sensory modalities, and motor systems found across animal species. The research team has a strong track record of productive collaboration studying sensorimotor control in these animals.

Broader Impacts

JHU will create sub-projects from this grant for two innovative high school programs: JHU’s Women In Science and Engineering (WISE) program and Baltimore Polytechnic’s Ingenuity Project. In these projects, high-school students conduct extensive research at JHU (ranging from one semester to two years). To date, Dr. Cowan’s laboratory has mentored 9 students from these programs; so far, all have gone on to college careers in STEM fields. NJIT will develop a program in collaboration with the Consortium for Pre-College Education at NJIT for increasing the participation of underrepresented groups in STEM fields that emphasizes a multidisciplinary synergy between engineering and biology. This program, tentatively entitled ‘Sensory Processing And Robotic Control’ (SPARC), focusses on compelling, hands-on experiences with electric fishes, computer simulations, and robots.

1 Introduction

The dominant paradigm in control systems engineering involves designing state feedback and state estimation independently. This approach can be applied successfully (if suboptimally in many cases) to a wide range of system designs. Further, for many linear plants corrupted by Gaussian noise, there is a separation principle: it is not only adequate, but optimal, to perform this decomposition. In particular, the linear-quadratic-Gaussian (LQG) controller decomposes into a linear-quadratic regulator (LQR) applied to the optimal state estimate which comes from a Kalman filter. Critically, the Kalman filter does not depend on the LQR cost function, and the LQR gains do not depend on the sensory noise.

This paradigm is not applicable, however, to most behavioral control systems in animals. Biological sensory systems often stop responding to persistent (i.e. “DC”) stimuli, a process known as “adaptation” in the neuroscience literature, that makes asymptotically exact set-point regulation impossible due to the imperceptibility of large, slow drifts in the signal of interest. Also, animals often use a strategy known as *active sensing* [7, 63] in which the organism generates potentially costly movements that do not necessarily directly serve a motor goal but improve sensory feedback and prevent perceptual fading [32]. Indeed, any searching behavior is a form of active sensing and many species of animals perform such behaviors.

1.1 Simplest biologically inspired model that requires active sensing

We propose a simplified model to illustrate how sensors that adapt to constant signals can lead to a requirement for active sensing. Suppose x_1 is the position of an animal and $x_2 = \dot{x}_1$ its velocity as it moves in one degree of freedom. To formalize the notion of sensory adaptation, *assume that a sensory receptor measures only the local rate of change of a stimulus as the animal moves relative to a sensory scene*, i.e. $z = \frac{d}{dt}s(x_1)$. Defining $g(x_1) = s'(x_1)$, we arrive at the following model:

$$\dot{x} = \underbrace{\begin{bmatrix} 0 & 1 \\ 0 & -\frac{b}{m} \end{bmatrix}}_{A} x + \underbrace{\begin{bmatrix} 0 \\ \frac{1}{m} \end{bmatrix}}_{B} u, \quad x \in \mathbb{R}^2, u \in \mathbb{R}, \quad (1)$$

$$z = g(x_1)x_2, \quad z \in \mathbb{R}^q, \quad (2)$$

where m is the mass and b is the damping. The linearization of (1)-(2) around any equilibrium, $(x_1^*, 0)$, is given by (A, B, C) , where (A, B) are defined above and

$$C = [0_{q \times 1} \ \gamma], \quad \gamma = g(x_1^*). \quad (3)$$

Clearly, (A, C) is not observable irrespective of γ . Indeed, the output introduces a zero at the origin that cancels a pole at the origin, rendering x_1 unobservable. This makes sense: a velocity sensor cannot infer position for a translationally invariant plant. However, a simple rank condition test [65] shows that *nonlinear* observability is guaranteed, but *only* for nonzero velocity, $x_2 \neq 0$. To save space, we present the one-dimensional-output case, but the general case follows easily.

Proposition 1. *For (1)-(2), with $q = 1$, local observability is guaranteed at each point x if*

$$x_2^2(2g'(x_1) - g(x_1)g''(x_1)) \neq 0. \quad (4)$$

Proof. Let $h(x) = g(x_1)x_2$ and $f(x) = Ax$. The left-hand-side of (4) is the determinant of the Jacobian of $(h, L_f h)$. Local observability is guaranteed if this is nonzero [65]. \square

This simple result formalizes the conceptual basis of this proposal: **control to a fixed position** ($x_2 = 0$) stands at odds with the need for **active sensing** ($x_2 \neq 0$). Thus, separability is lost and one must design a control input that sufficiently excites the sensors to enable estimation of the states necessary for control. Related work will be reviewed in Background (Section 3.3).

1.2 Experimental system: Active sensing in weakly electric fish

Prior work by the investigators has demonstrated that weakly electric fish (Figure 1) are a uniquely suited system for examining the integration of sensing and control [29, 30]: they possess a long ribbon-fin that allows them to swim nearly equally well forward and backward [81], and two distinct image forming sensory systems (vision and electrosense) [83] that allow for precise and rich experimental manipulation of multisensory cues used by the animal for control. As in our previous studies, we rely on a robust refuge-tracking behavior that is easily elicited in untrained animals in the laboratory [30, 73, 76, 83]. We have also shown that fish perform an active sensing behavior that can be modulated in response to the availability of visual and electrosensory cues [83].

To anchor the above model in the electric fish system, we will use a rigorously validated plant model for fore-aft swimming in the electric fish [81] that boils down to (1). Given the high-pass nature of the electroreceptors in weakly electric fish [64], we add to our model a vector of outputs based on the distribution of such high-pass filters along the surface of the fish. We approximate this as a *positionally dependent velocity signal* as given in (2).

The proposed work advances our overall goal of understanding closed-loop multisensory control by tackling the issue of active sensing with the experimental program described in the pages that follow. This new experimental program is supported by the simple but clear and novel theory laid out above that formalizes the need for active sensing in these animals.

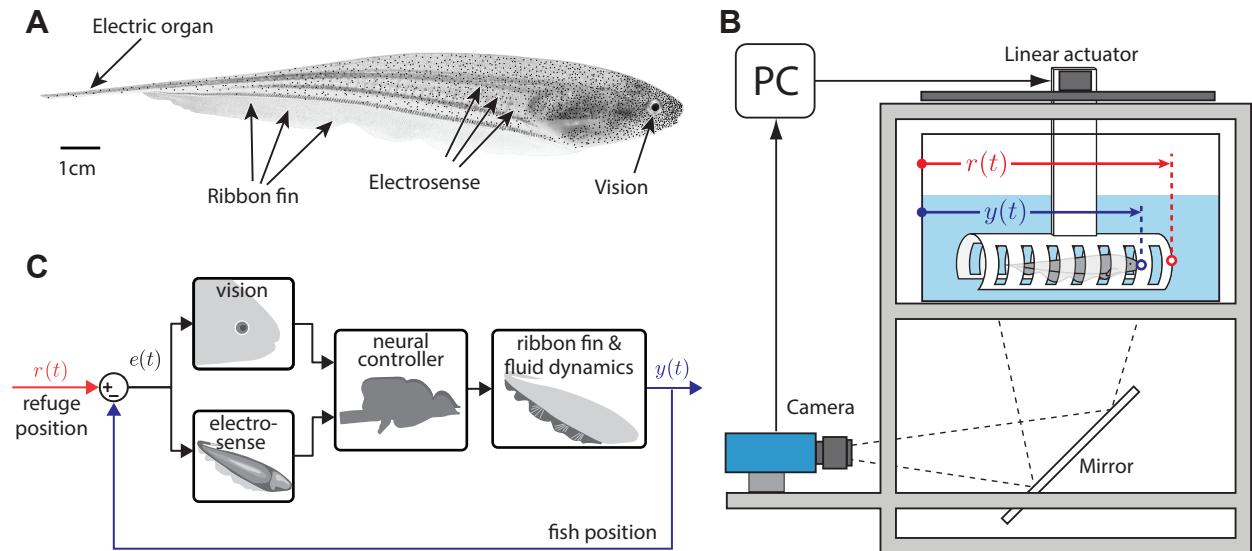


Figure 1: (A) The weakly electric glass knifefish, *Eigenmannia virescens*, is a unique animal system for the study of neural control in biology. This species has two independent image-forming sensory systems, vision and electrosense, and a unique locomotor plant, a ventral ribbon fin that allows them to swim nearly equally well forwards and backwards. (B) The fish exhibit a natural behavior in which they maintain their position inside a longitudinally moving refuge. The position of the fish, $y(t)$, and the refuge, $r(t)$ are easily digitized and measured from high-speed video. (C) We move a refuge with an arbitrary trajectory $r(t)$. The fish does not exactly track the refuge, resulting in sensory slip or “tracking error”, $e(t) = r(t) - y(t)$, which is encoded by either or both the visual and electrosensory systems. The nervous system processes this sensory feedback to generate motor commands which are translated into motions, $y(t)$, via the swimming mechanics. These motions in turn affect the error, $e(t)$. Fish will track the refuge under infrared illumination, performing the behavior in the absence of visual feedback, and we can modify the salinity of the water to modulate electrosensory feedback. Indeed, we have control over a wide range of stimulus parameters that we can use to alter spatiotemporal patterns of sensory feedback.

2 Specific Aims

The separation principle is a powerful tool used in engineering design, but is generally not applicable to neural control systems in animals. This is because biological sensors typically exhibit exactly the sort of nonlinearities and sensorimotor linkages described above that make a system not separable. In engineering, an effort is often made to side-step this by designing sensors that facilitate separability, while evolution has produced active control algorithms that do not rely on the separation principle, but rely instead on other unexplored “active” mechanisms for state estimation and control.

Our long-term goal is to develop a theoretical framework for improved engineering design that leverages understanding of active sensing in nature, which has been honed by millions of years of evolution. A central challenge in studying the mechanisms for active sensing in animals is that sensory input and motor output are intertwined in a way that fundamentally links estimation and control.

Toward this long-term goal, this proposal focuses on the short-term goal of rigorously analyzing the mechanisms for active sensing in a species of weakly electric fish, using a combination of static and dynamic manipulations of sensory feedback. *The cornerstone of our experimental approach is the modification of sensory feedback in freely behaving animals.* In Aim 1, we modify feedback via static modulation of sensory cues, while in Aim 2 we modify feedback using an exciting new paradigm in which the stimulus is controlled, in real-time, around the animal behavior, fundamentally altering the closed-loop dynamics.

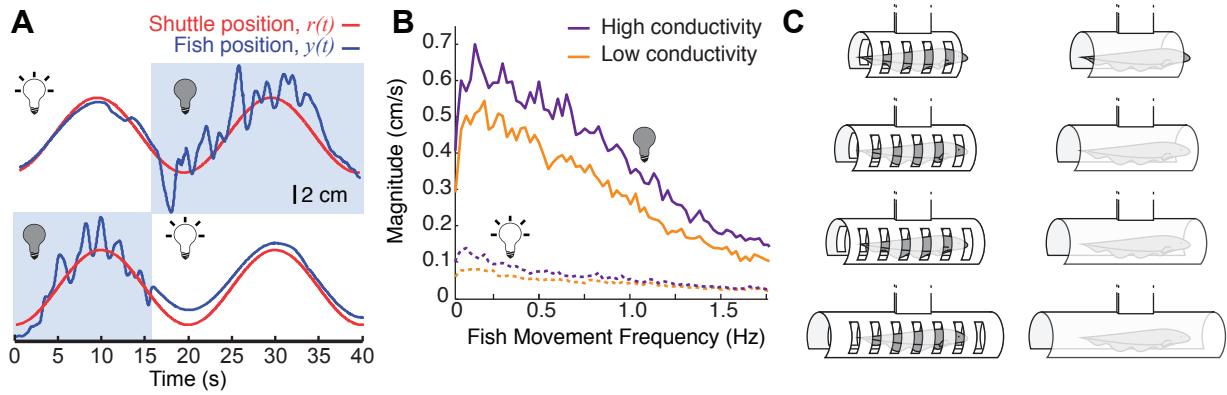
Specific Aim 1: *Static modulation of sensory feedback.* Although refuge tracking is a robust behavior that has been intensively studied, the salient visual and electrosensory information that the fish requires for control is unknown. In these experiments (Figure 2), we will systematically manipulate luminance (Figure 2A), conductivity (Figure 2B) and the structure of the refuge (Figure 2C) to alter available sensory information. We will measure changes in the fish’s locomotor performance and strategy and evaluate them in relation to our mathematical models of the electric field image. This evaluation will include quantifying electrosensory information to predict the tracking performance and active sensing behavior of the fish.

Specific Aim 2: *Dynamic modulation of sensory feedback.* In Aim 1, we will observe changes in the fish’s strategy for active sensing and refuge tracking. In Aim 2, we will evaluate the control system underlying these different strategies. In these experiments, we will dynamically alter the sensory feedback experienced by the fish in real-time during refuge tracking (Figure 2D). This will be achieved by altering the trajectory of the refuge in relation to the movement of the fish with high-gain, low-latency (< 20 ms) feedback. For example, if the fish moves forward 1 cm we can simultaneously move the refuge 0.25 cm forwards or backwards relative to the fish’s movement. In this way, we can experimentally suppress (Figure 2E) or enhance (Figure 2F) the active movements or any other component of the tracking behavior of the fish.

Our experimental system—longitudinal refuge tracking in weakly electric fish—is unlike any previously studied system that we are aware of, in that goal for control (image stabilization) and the requirement for sensing (image motion) are so elegantly at odds. Further, we know of no system where the entire active sensing and control task can be boiled down to a single experimental degree of freedom. This combination of features of the experimental animal system, combined with our previous modeling efforts make it well suited for the proposed studies and analysis.

The broader scientific impacts of this research extend beyond engineering in that the proposed work will have a potentially transformative impact on our scientific understanding of active sensing in biology.

Aim 1: Static modulation of spatiotemporal patterns of sensory feedback



Aim 2: Dynamic modulation of sensory feedback via closed-loop control

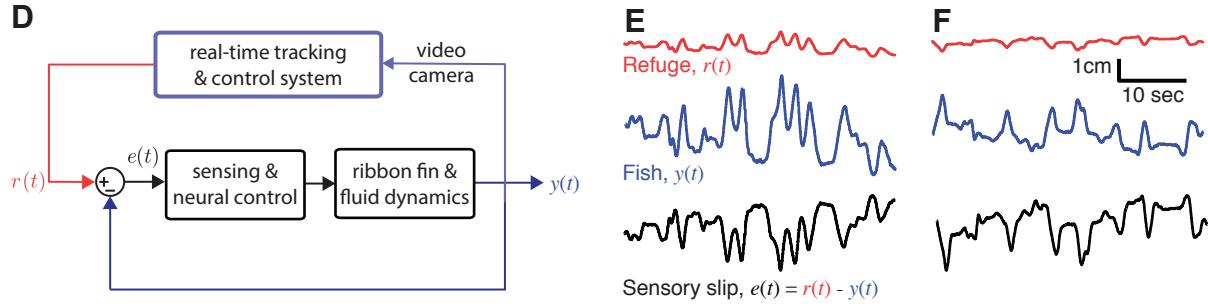


Figure 2: Overview of aims and preliminary evidence. These approaches build on previous work by the PIs [30, 31, 54, 76, 81, 83], as summarized in two recent review articles [29, 75]. [83].

SPECIFIC AIM 1. **(A)** Published data from [83]. *Eigenmannia* track a moving refuge both in light (vision and electroreception) and in the dark (electroreception only). When in the dark, fish generate whole-body fore-aft active movements that are superimposed over the tracking movement. **(B)** Published data from [83]. The magnitude of active movements increases between light and dark and also as a function of increasing conductivity (decreasing electrosensory saliency). **(C)** In this proposal we plan to vary not only parameters of the environment as in our previous work, but also alter structural features of the refuge, including length and windows. These manipulations directly alter the electrosensory image received by the fish during refuge tracking. Recently, we adapted a model of electric field dynamics to calculate the electric images that are produced by different refuge morphologies, which allow us to test predictions for the dynamics of active-sensing movements

SPECIFIC AIM 2. **(D)** By closing a feedback loop around the fish, we will dynamically control the trajectory of the refuge based on the movement of the fish, thereby altering the natural feedback system of the fish during refuge tracking. The computer control system, which relies on reliable video tracking at 100 frames per second, can alter the trajectory of the refuge with less than 20 ms delay after the fish's movement. Thus, this system can attenuate or amplify sensory feedback from the fish's own fore-aft movements in real time through movements of the refuge. **(E,F)** Preliminary data from one fish in which closed-loop sensory feedback was modified using this experimental system. In **(E)**, the refuge was moved $r(t)$ at 25% of the fish's movement $y(t)$. In **(F)**, the refuge was moved $r(t)$ at -25% of the fish's movement $e(t)$. These changes in the feedback policy affected fish movement, which can be seen in the changes in amplitude between the middle traces in **(E)** and **(F)**. These data suggest that the changes in swimming amplitude were made to maintain a constant amplitude of sensory slip as the sensory signals $e(t)$ were similar in both conditions (amplitudes of bottom traces).

3 Background

3.1 Active sensing in biology

Active sensing is broadly defined as the expenditure of energy for the purpose of sensing [7, 63] but often is restricted to animals that generate and emit sensing signals, such as echolocation [60, 85], and electroreception [17]. However, most sensory systems (including those above) rely on a much more general category of energy expenditure, namely the animal's own active *movements* [1, 35, 37, 50, 52, 57, 61, 66, 78, 79]. Indeed, although weakly electric fish produce an active sensory signal via its electric organ, these fish also use movement for active sensing [4, 5, 44, 56]. In addition, movement-based active sensing has been extensively examined in vision [2, 8, 15], whisking [16, 20, 39, 40, 42], active touch [33, 49, 67, 77], sniffing [69, 88, 89] and hydrodynamic imaging [43, 59, 87].

In fact, animals routinely change their motor behavior in relation to the sensory demands of the task goal [3, 36, 38, 46, 55, 68, 86]. This suggests that animal's movement might be used to preferentially stimulate the relevant receptors to match the sensory filtering properties [41, 58]. For example, eye microsaccades prevent perceptual fading [32] and larger eye movements place salient features on the fovea [13, 71]. Of particular interest is the whisking behavior of rodents, which is used to identify object position, orientation, size, shape, and texture [16, 21] and is modulated based on the sensing task [14, 21, 82, 84].

Note that in many of the experiments listed above, the animals are trained to perform a sensory discrimination task. A consequence of this approach is that the training regime and learned sensory behavior eliminate any independent motor goal from the task. In contrast, in natural behavior, animals often use active sensing to achieve a motor goal. Our model system is ideally suited to this natural regime of active sensing because it does not have these limitations. First, refuge tracking in electric fish is a naturally occurring robust behavior (see Section 3.2, below). Second, refuge tracking is a locomotor task which relies on active sensing for its control.

3.2 Refuge tracking in electric fish

Weakly electric fish maintain their position within a moving refuge [30, 73, 74, 76, 83] using their ribbon fin to swim both forwards and backwards in a ‘tracking’ behavior that is controlled by both visual and electrosensory input (Figure 1) [10, 72–74] and likely does not rely on the mechanosensory lateral line system [9–11]. The refuge tracking behavior is particularly well suited for laboratory experiments for several reasons. First, all relevant signals (fish and refuge position, velocity, and acceleration) occur in a single linear dimension simplifying system identification analysis. Second, the behavior is reliable, robust, and requires no training. Third, because the electroreceptors are embedded in the skin, the sensory image used by the fish during tracking in the dark is determined solely by the relative displacement of the fish in the refuge (see Figure 1B). Fish will routinely follow a refuge that moves at a wide array of frequencies and amplitudes for trajectories of varied composition (e.g. single or sum of sines, triangle waves, etc.) [30, 76].

From the perspective of the nervous system, the goal of the tracking task is to stabilize a visual and/or electrosensory image of the refuge on the receptor arrays. When the refuge moves, the electrosensory image moves on the body surface in the same direction. The fish detects this sensory slip and moves itself in the same direction as the slip to stabilize the image [30, 76]. At issue in this proposal is that, were the fish to track the moving refuge exactly, the electrosensory signal would perceptually fade, and our goal is to understand how the animal manages this conflict between control and the requirements for active sensing during refuge tracking.

3.3 Nonlinear observability and control in engineering

Nonlinear systems engineering has focused overwhelmingly on nonlinear controllability and controller synthesis, although the mathematical foundation for nonlinear observability and its rela-

tionships to dual concepts in controllability is well established [45,65]. Of course, binary measures of observability are extremely useful as they can point to certain structural features of a system (as in our simplified model in Section 1.1), but such measures say little about how to actually co-design controllers and observers. That said, some new results are beginning to emerge on how to design trajectories to ensure observability [25].

There is a particularly relevant line of recent work that provides quantitative (and graded) metrics for observability [12,51]. For example, one can linearize a system around an admissible trajectory, and evaluate the observability Gramian over a finite time interval. With such a measure, one can optimize active movement trajectories to enhance observability [47].

For the electric fish, such active movements take the form of small movement oscillations as we review in Preliminary Evidence (Section 4). How does the animal trade-off between the active movements and the set-point tracking goal for control? We have a particularly simple model that may admit creating a cost function that trades off between observability and motor cost; how precisely to formulate this remains an open question and will be investigated for this work. One possibility may be to create a combined cost that weights the standard least-squares cost (applied to the state and input) against a cost based on the observability Gramian.

4 Preliminary Evidence

4.1 Closed-loop analysis of locomotor behavior

The PIs previous work includes modeling and identifying the closed-loop sensorimotor control algorithms [30, 76] and locomotor dynamics [80, 81] in refuge tracking in electric fish as well as several other model organisms and behaviors [31,34,54]. This prior analysis has produced one of the very few experimentally verified open-loop locomotor “plant models” for a vertebrate animal [80,81] and new analysis tools for the experimental identification of the closed-loop locomotor dynamics from behavior [76,83].

4.2 Aim 1: Static modulation of spatiotemporal patterns of sensory feedback

We recently developed and published [83] a system for examining how active sensing strategies may match underlying CNS mechanisms in *Eigenmannia* (Figure 2A-B). When electric fish are tracking a moving refuge in the dark they alter their locomotor strategy by generating whole-body fore-aft oscillations [83]. These ‘active’ movements are broadband [83] and increase as a function of decreasing electrosensory saliency, like a “gain knob” on the motor output that is controlled by sensory feedback. Interestingly, the animal achieves nearly the same overall tracking performance in the dark as in the light, even though the fish significantly increases its total movement and energy costs [83]. Indeed, the dramatic increase in energy costs supports the idea that these movements are critical for tracking in the dark.

Further, unpublished preliminary data collected for this proposal suggests that, given changes in the structure of the refuge (Figure 2C), there are quantifiable changes in the magnitude of active movements during tracking (Figure 3) that correlate with these stimulus changes. In particular, fish produce more active movements as the electrosensory salience is decreased by lengthening the refuge or removing the features (“windows”), and these changes in active movements are compounded by the presence or absence of illumination.

4.3 Aim 2: Dynamic modulation of sensory feedback via closed-loop control

We have recently developed a computer control system to alter the trajectory of the refuge in response to the fish’s movements with less than 20 ms delay. This system allows us to dynamically alter the feedback policy that the animal experiences as we can attenuate or amplify relative movements between the fish and refuge. In this system, the refuge is moved using a linear stepper

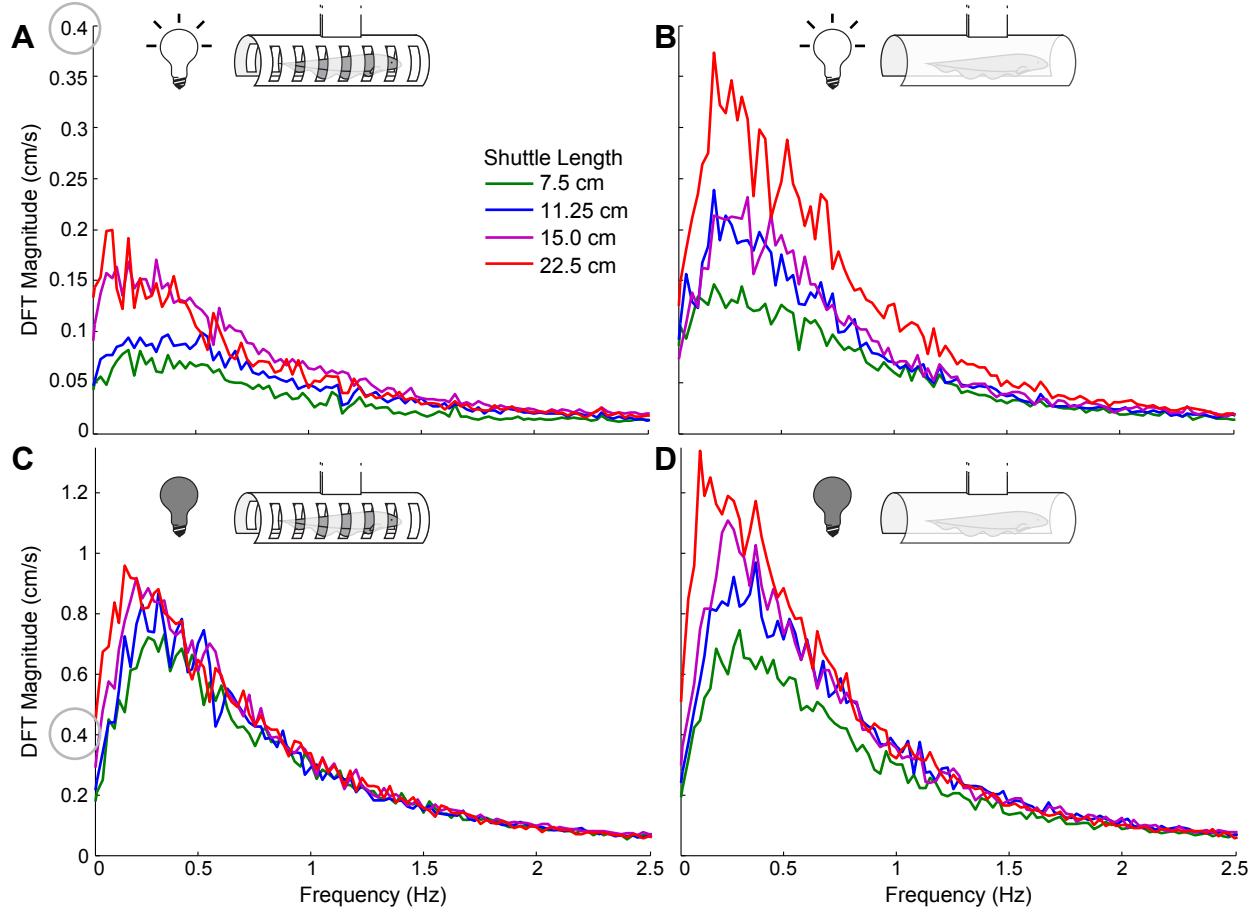


Figure 3: Preliminary evidence: Sensory salience modulates active movements. New, unpublished data show that removing features from the refuge, such as windows that reduce visual and electrosensory cues, result in an increase in the production of active movements for sensing. In addition, increasing the length of the refuge appears to result in similar changes in active movements. These preliminary data were collected in ambient room light (**A,B**) and under infrared illumination (**C,D**) to emphasize electrosensory feedback.

motor while a camera captures high-speed video (100 fps) from beneath the fish (Figure 1B). The real-time PC determines the position of the refuge $r(t)$, fish $y(t)$, and tracking error $e(t)$. This setup permits the real-time adjustment of the refuge trajectory based on fish movement. In pilot trials conducted for one fish, we proved that the system functions as described, and that it can affect fish swimming (Figure 2E,F). In these preliminary experiments, we altered the trajectory of the refuge so that it either “followed” the fish, thereby reducing sensory slip and thus sensory feedback, or moved in the opposite direction of the fish, thereby increasing the magnitude of sensory feedback. When sensory feedback was reduced, the fish swam a greater distance when it produced active sensing movements, and when feedback was increased, the fish produced small active sensing movements. However, when we compared the amount of sensory slip from active sensing movements between these conditions, we find that there was little or no change. These preliminary data suggest that the fish produces these active swimming movements specifically to generate sensory feedback. (All these observations were conducted using only one fish and are thus anecdotal and as yet non-quantitative.)

5 Research Approach

The goal of the proposed research program is to reveal the closed-loop sensory and motor mechanisms that are used in the simultaneous control of rapid active sensing movements and lower-frequency refuge tracking movements. Aim 1 examines changes in active movements that result from changes in static features of the refuge. Aim 2 examines how dynamic modulation of sensory feedback affects active movements and task-level control using an innovative real-time stimulation regime that permits the manipulation of the fish's own closed-loop feedback control system.

5.1 Aim 1: Static modulation of spatiotemporal patterns of sensory feedback

Our preliminary evidence and mathematical modeling suggest that active movements enhance the encoding of position and/or velocity of the refuge. We will examine this hypothesis by measuring refuge tracking performance in responses to changes in the fine structure of the refuge.

In these experiments the fish's own closed-loop control system is intact, but the refuge motions are open-loop; they are pre-computed trajectories that do not depend on the fish's movements. We will record the relative movements between the fish and the refuge, which is expressed as tracking error, $e(t)$. Importantly, the electrosensory image is not determined directly by the open-loop refuge movements, but rather by the emergent 'error' signal, $e(t)$, that depends both on refuge movement and the fish's own closed-loop control and active movement strategies.

This error signal, $e(t)$, determines the exact sensory information that the fish experiences during each trial. Systematic modifications of the refuge and tracking conditions will be used to test hypotheses concerning the properties and function of the sensory feedback generated by the active movements. Moreover, we can directly model the electrosensory image (Figure 5) which allows us to make predictions related to sensory salience and the production of active movements.

5.1.1 Experiments for Aim 1

In all experiments of Aim 1 we will generate refuge motions using the open-loop stimulation paradigm with low-frequency refuge movements (sinusoids below 2.5 Hz). As we have done previously, we will conduct trials at two illuminations (white and IR light), two conductivities (50 μ s and 250 μ s), and 5 sinusoidal refuge input frequencies with at least 10 replicates per condition.

Experiment 1.1: Salience of electrosensory images

Experiment description: In our previous experiments we have always provided multiple pathways for electricity to flow through the refuge, including not only the front and back openings but also windows in the side walls. This produces a pseudo-sinusoidal spatial image that is distributed on the electroreceptors across the body of the animal (a vertical slice of any of the panels of Figure 5). This is a rich stimulus that covers the entirety of the sensorium, similar to a sine-wave grating across the retina in the visual system. To test how the distribution of the electrosensory image on the electrosensorium affects tracking we conduct trials in which the windows are present and absent and compare the fish's performance. In addition, because the front and back edges of the refuge provide strong salience, we also plan to vary the refuge length.

Hypothesis and alternatives: If the fish is using electrosensory information distributed across its body, we would expect that the fish will have increased active movements when the refuge has no windows and/or when the length is increased. In addition, there may be a nonlinear interaction between features and refuge length, that depends on the fish's size and preferred position within the refuge. Alternatively, the active movements are may not change, which would interestingly suggest that fish are (1) blind to these features, (2) that categories of information are segregated within neural circuits, or (3) that the movements are not related to sensing at all.

A more interesting analysis of the data will require examining the position of the fish relative to the position of the windows within the refuge to determine if they have preferred locations for tracking. For example, fish may position themselves near the edge of a window, which is an area with higher electrosensory contrast. It is also possible the the back and forth movements generated by the fish shift from window to window as they move within the length of the refuge. Alternatively, the electricity may flow through the windows in a way such that the have enough information without correlating their position to that of the windows, especially if information from all regions of the sensorium (the body surface) are treated equally by the controller.

In our previous experiments and analytic approaches, we have assumed that the fish is tracking the position of the refuge on a moment-by-moment basis. However, this may not be the case. For example, the fish may avoid the ends of the refuge rather than tracking its actual position. This would introduce a dramatic, but predictable, nonlinearity in the tracking output of the fish. Our simple approach for discriminating between these two strategies will be to systematically vary the length of the refuge from less than the body length of the fish to over two times the body length of the animal. We will use a shuttle with windows and perform these experiments in light, so that there is not a sensory confound. If the fish is tracking the position of the refuge, changes of length may not have an effect on tracking performance. However, if the fish is avoiding the edges of the refuge then we would expect a shift in locomotor behavior from small to long refuges. In the long refuge the fish would have increased periods of time when it is in the middle of the refuge and during those epochs, its movements would be less correlated to the refuge motion.

Our preliminary evidence (Figure 3) supports our basic hypothesis but further analysis of the active movements is needed (see Section 6.2).

Experiment 1.2: Asymmetries in electrosensory images

Experiment description: The electroreceptors are not evenly distributed along the body of the fish; the head has about as many electroreceptors as the rest of the body [19]. Further, the electric field is asymmetric along the body axis because the electric organ is located along the sides of the fish behind the head and into the tail. In this experiment, we will test how the fore-aft movements by the fish are modulated by the distribution of the electric field along the axis of the fish. We will design refuges that have small holes distributed along its length to produce arbitrary distributions and asymmetries in the electric field as it propagates through the water. For example, we can align the holes to form edges, have an asymmetric density of holes from head to tail, or be randomly distributed.

Hypothesis and alternatives: Our working hypothesis has been that the fish relies equally on information from any part of the electrosensory sensorium for tracking. We therefore expect little change in tracking and active movements as we change the distributions of the holes in the walls of the refuge. However, due to the strong asymmetries in the distributions of the receptors and the electric field itself, the fish may have preferential locations for tracking, or may have sensing gradients that have differential effects on tracking and active movements depending on the relative position of the fish. Such gradients in sensing of feedback signals would almost certainly be nonlinearly related to refuge tracking performance. How a controller for positional preferences performs and how it integrates with the controller for tracking the moving refuge would be an interesting problem to study.

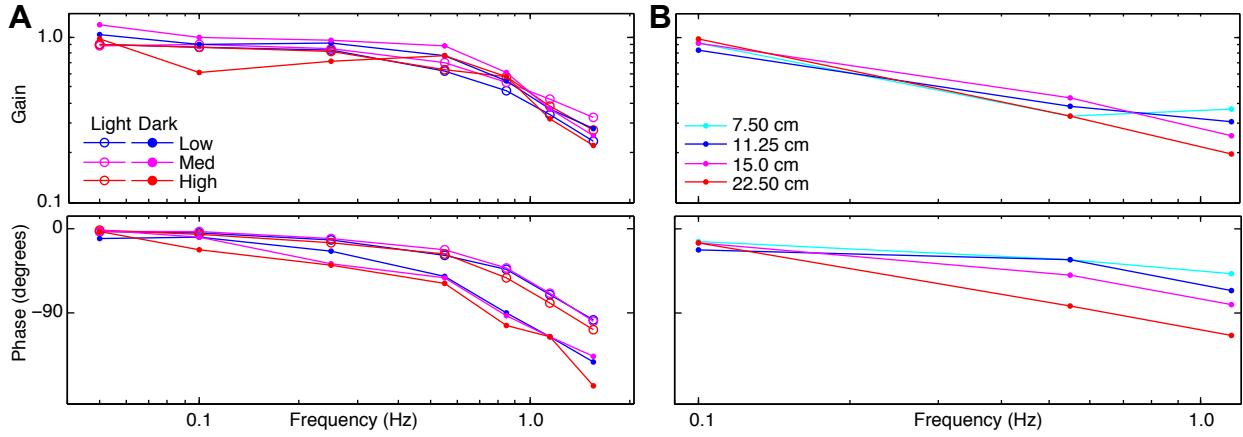


Figure 4: Changes in tracking performance based on sensory saliency: **(A)** Published data [83] shows that the tracking performance, measured by Bode gain, is equivalent between trials completed in light and dark and is similar across conductivities. However, for refuge trajectories at higher frequencies the fish have an increased phase lag in the dark. **(B)** Preliminary data shows differences in gain and phase for higher frequency input signals as sensory salience is reduced. These differences will allow us to test the role of active movements for improving tracking performance as described Aim 2.

5.2 Aim 2: Dynamic modulation of sensory feedback via closed-loop control

5.2.1 Experiments for Aim 2

In specific Aim 1, the stimuli were pre-specified movements that were played to the animal. In Aim 2, we use a dynamic stimulation system that detects the movement of the fish and responds in real time to those movements by altering the trajectory of the moving refuge. This approach gives us the power to alter the structure of the fish's own closed-loop control system by altering the feedback from its own movements.

In these behavioral experiments, we will adjust the refuge position in real time to regulate the perceived error signal, $e(t)$ (see Figure 2D). This will allow us to directly manipulate and perturb the closed-loop tracking controller that the fish uses to produce movements to actively sense and track the moving refuge. By altering the experimentally applied real-time controller, we can impose an arbitrary feedback signal on the fish even though the fish is freely swimming and unconstrained. We can also test whether enhancing or suppressing the animal's active movements can help compensate for degraded tracking performance (particularly in phase) that occurs in sensory deprived conditions (Figure 4).

Experiment 2.1: Role of sensory slip in active sensing

Experiment description: To determine how sensory feedback is used in the ongoing generation of active movements, we will perform an experiment in which there is no pre-defined movement of the refuge; rather, the refuge motion is the result of feedback from the fish's own movements. If the animal were to remain motionless, the refuge would also not move. In these experiments, we will impose a proportional gain ($\pm 5\%$ to $\pm 50\%$) for moving the refuge in response to the fish. For example, in a 25% gain experiment if the fish moved forward 4 cm, the refuge would be moved in the same direction a distance of 1 cm. This movement would reduce the sensory slip to 3 cm compared to if the refuge did not move, resulting in a sensory slip of 4 cm.

Hypothesis and alternatives: When fish perform refuge tracking in the dark, they generate active movements that we hypothesize are used for sensing. However, the role of these movements in sensing have not been conclusively demonstrated. If the fish increases its movement when

the refuge is following it (positive real-time controller gain), this would suggest that the active movements are being used to actively generate sensory slips, especially if the sensory slip, $e(t)$, is unchanged between conditions. Similarly, negative gains (refuge moves backwards when fish moves forwards) may reduce the movements that the fish makes, nevertheless producing a similar sensory slip. Alternatively, the fish may keep its movements constant throughout these manipulations, which would support the idea that the movements are not related to the control of active sensing; it is possible that the movements are exploratory, or are part of some non-related behavioral repertoire such as prey capture [62].

Experiment 2.2: Segregation of active sensing and tracking

Experiment description: To understand if active sensing can improve the tracking performance, we will not only feed back a portion of the fish's own movement (as in Experiment 2.1), but we will also feed forward a prescribed sinusoidal input trajectory to the refuge. This creates a subtle confound in that the resulting refuge trajectory at the prescribed stimulus frequency will be modified because the fish is tracking the refuge, and our real-time system is tracking the fish and modifying the refuge trajectory accordingly. For example, if $G(j\omega)$ represents the closed-loop gain of the fish sensorimotor system, and we apply static feedback with gain α , then the gain from the prescribed refuge motion to the actual refuge motion will be

$$\frac{1}{1 - \alpha G}. \quad (5)$$

With this important feature in mind, we will take care to calculate Bode gain, not in terms of the prescribed motion of the refuge, but rather in terms of the refuge motion that results from the closed experimental loop. Further, we can use the amplitudes recovered from the real-time, closed-loop tracking experiment and “replay it” in open loop. Also, note that (5) suggests that a real-time experimental gain of $\alpha = 1$ (completely canceling the fish's motion) is problematic, since the fish's tracking gain, G , approaches unity at low frequency [30, 76], in which case the refuge trajectory will become unbounded (leading to the refuge exceeding its travel limit).

Hypothesis and alternatives: Our hypothesis is that active movements improve sensing which results in better tracking performance. If the fish is producing active movements for the purpose of sensing the position of the refuge, we would expect its tracking performance (as measured by the Bode gain and phase) to be degraded when sensory slip is attenuated. Conversely, we predict that amplifying sensory slip will improve tracking performance. Alternatively, we may find that an increased production of other behaviors that could be used for active sensing, such as tail bending or wall touching, that may facilitate sensory processing in the absence of slip cues. We could also test whether tracking performance has an effect on the higher frequency active movements. It is possible that if we impose a policy that selectively improves the fish's tracking performance, that it might in turn reduce the production of active movements for sensing, thereby reducing energy expenditure. However, there are many other possibilities, including changes in the patterns for active sensing, or no changes whatsoever.

6 General Methods

All of the procedures using animals have been reviewed and approved by the Animal Care and Use Committees at Rutgers University (serves NJIT) and Johns Hopkins University. These experiments follow guidelines established by the Society for Neuroscience and the National Research Council. We expect fewer than 100 fish to be used for non-survival experiments for this project.

For each experiment, an individual fish will be transferred from a community tank to a testing tank equipped with a computer-controlled moving refuge and a high-speed video camera, similar

to that used in prior reports [30, 76, 83]. In these experiments the refuge will be machined from a segment of 2x2 inch gray rectangular PVC pipe, and the length and spatial complexity varied.

6.1 Analysis of tracking performance

From the refuge tracking behavior, the $x - y$ positions of the fish and refuge will be digitized from the video data using custom code implemented in MATLAB. Raw $x - y$ pixel coordinates will then be transformed to align the x coordinate with the length (and motion) of the refuge. From this information, we will calculate the one-dimensional time trajectory and position of both the refuge and fish, $r(t)$ and $y(t)$ respectively, in the direction of motion of the refuge. The Fourier Transform (FT) represents these time-domain signals $r(t)$ and $y(t)$ as complex-valued functions of frequency, $R(\omega)$ and $Y(\omega)$ respectively. The refuge-tracking behavior of the fish is represented in the frequency domain by the transform from $R(\omega)$ to $Y(\omega)$. By expressing these complex functions in polar coordinates, we can describe each value by its magnitude $|Y(\omega)|$, and angle $\angle Y(\omega)$. Sinusoidal input trajectories are represented as a discrete spike at the stimulus frequency and zero at all other frequencies. The FT of the fish movement has power over a broad range of frequencies, with concentrated peaks at frequencies corresponding to the spectrum of the input.

A Bode plot describes the response of a system that can be attributed to the input signal. It is computed from the complex ratio of the output phasor to the input phasor in the frequency domain. The Bode plot is only evaluated for the discrete set of frequencies present in the input; the Bode ratio is not defined elsewhere, where $R(\omega) = 0$.

6.2 Analysis of active movements

We further decompose the fish motion into two categories of movement: movements in response to the stimulus frequencies (the peaks of FT corresponding to discrete input frequencies) and broad-spectrum active movements as described in [83]. To estimate the average spectral content of active movements, we calculate the magnitude of the FT, $|Y(\omega)|$ for each trial and omit the data corresponding to the input frequencies. By performing many individual trials with stimuli at a variety of different input frequencies and omitting those frequencies in the output, we can estimate averages across trials to obtain a single spectral estimate.

In addition to the spectral analyses techniques described above, we will express the active movements in terms of statistically derived movement “epochs.” We will generate movement epochs by decomposing the movement trajectory of the fish into sequences of motion that precedes and follows a zero-crossing in the fish’s velocity. This will allow us to divide the fore-aft movements into clusters, which correspond to different types of behaviorally relevant oscillations. For example, fish produce back and forth movements associated with the refuge input, low velocity backwards drifts, and also large forward “saccades” to perhaps reset their position once they have reached the back edge of the refuge. Once we have extracted the epochs for each condition we will use expectation-maximization algorithm and cluster cutting to automatically segment the data into movement templates. We have performed preliminary analysis of this sort using custom Matlab scripts and data shown in Figure 3 with some success, but further refinement is needed.

6.3 Modeling the electric field images

In collaboration with John Lewis at University of Ottawa, we used a previously described electric field model [5, 6] to calculate the electric images due to the different refuge compositions (Figure 5). All model parameters and modeling details for the fish’s electric field are as in the original model; the refuges were modeled to scale as two PVC sheets on either side of the fish. As is the convention, electric images are calculated as the difference in transdermal potential with and without the refuge present [4–6, 18, 28, 70]. Electric images were calculated for fish positions along the long-axis of the refuge in 1 cm increments to mimic a fish swimming into and through the center of the

refuge. Although the fish model was developed for a different species of electric fish (*Apteronotus leptorhynchus*), it captures the elongated dipole-nature of the electric field of many species [4, 18] and thus allows us to illustrate the fundamental signals available for electrosensory-based tracking. In the model electric images, it is possible to see the affect of lengthening the refuge and removing “windows” both of which degrade the available electrosensory information and should produce an increase in active movements, which we have observed during pilot experiments (Figure 3).

6.4 Infrastructure for closed-loop tracking

The freely behaving fish is its own closed-loop system. To open this loop for experimental manipulation, we must be able to measure the system and dynamically alter the feedback to the fish in real time. To do this, we recently developed and tested (September 2014) a closed-loop feedback system that monitors the position of the fish in real time and rapidly adjusts the position of the refuge based on the fish’s movements. Because the perceived error signal is the relative movement between the refuge and the fish, this system allows us to control the error signal even while the fish is freely behaving.

In this setup, we use template matching to track the fish’s position on each video image in real-time. Before performing template matching, the image is first converted from 12 bits per pixel grayscale format to 8 bits per pixel grayscale by downshifting pixel values by 4 bits, then it is cropped to the rectangular region of interest, which covers all possible positions of the refuge during the experiment. The tracking algorithm has two modes of operation. In mode 1, we search for the best template match in the whole region of interest. In mode 2, we search for the best match only in the neighborhood of the fish’s previous known position. Mode 1 is used for the very first frame of the video sequence and for all the other frames where mode 2 failed to find a suitable match. Mode 2 is used for all other video frames. We considered a match failed when the Normalized Cross Correlation of the template with the image content at the best match location is under the

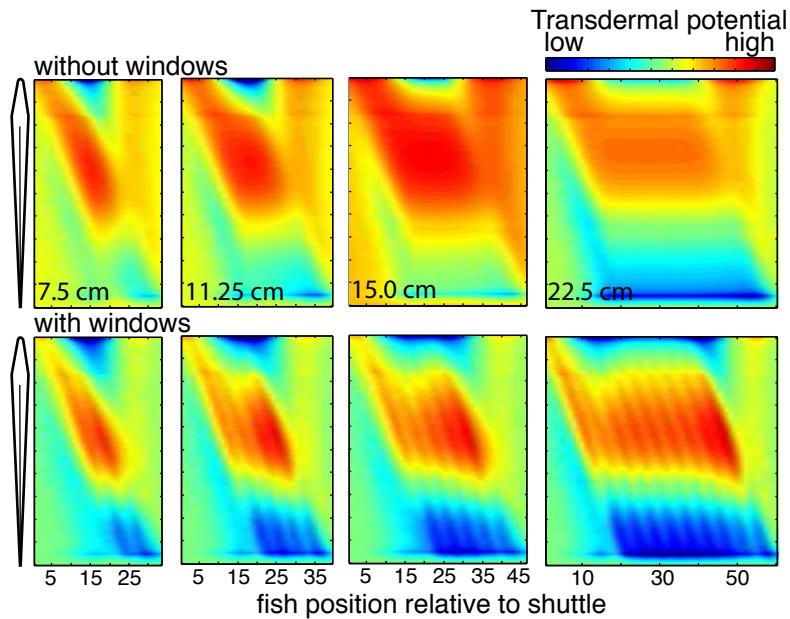


Figure 5: Electric images produced by variations in refuge structure: New, unpublished data shows that removing features from the refuge (i.e. windows) or increasing the length of the refuge reduces electrosensory salience. The changes in the electric images correspond to the increase in active movements observed during free-behavior tracking experiments (Figure 3).

match threshold for at least two consecutive video frames. Single frames with best match under the threshold are not considered failures and their positions are extrapolated from previous positions. The template is generated by taking a video frame where the fish's appearance is typical, cropping the image to contain only the fish's head and its immediate surroundings and enhancing contrast. Template matching is implemented in NI LabVIEW using the IMAQ Match Pattern VI. The search is configured to be rotation invariant up to ± 40 degrees with horizontal mirroring in order to enable fish tracking in both left-to-right and right-to-left directions. On our NI Embedded Vision System mode 2 is executed in about 10 ms, however video frame rate is constrained by exposure time.

Motor control is implemented on the NI Embedded Vision System through camera trigger I/O. The control loop is capable of running at up to 10 KHz on the real-time OS. In each iteration of the loop we compare the desired motor position to the actual one and if the actual position is at least a step size away from the desired position, then we generate a pulse on the motor control line to move it one step closer to the desired position. Step size is $10 \mu\text{m}$. In the scenario when we are tracking the longitudinal motion of the fish, the desired position is provided asynchronously by the fish tracker algorithm. In the scenario of pseudo-random refuge trajectory, the desired position is calculated inside the control loop at every iteration.

Note that in the closed-loop stimulation regime the “real-time tracking & control system” feedback will be implemented using a known policy. This means that we can derive an analytical feedback equation for the entire modified closed-loop system. Using standard control theoretic techniques we can predict open-loop responses from closed-loop experiments and vice versa; errors in these predictions would indicate potentially critical nonlinear processing [76].

7 Broader Impacts

7.1 Increase Participation of Underrepresented Groups in STEM Fields

We will encourage underrepresented groups, including women and minorities, to enter STEM fields via public presentations, teaching and active recruitment to participate in this research.

JHU Baltimore: To foster diversity and enhance science and engineering education at JHU and in Baltimore, we will create sub-projects from this grant for two innovative programs: JHU’s Women In Science and Engineering (WISE) program and Baltimore Polytechnic’s Ingenuity Project. In these projects, high-school students conduct fundamental research at JHU. Through WISE and the Ingenuity Project, female high school juniors from Garrison Forest School in Owings Mills, MD and inner city students from Baltimore Polytechnic (the first of Baltimore’s city schools to racially integrate the student body), respectively, will spend several afternoons per week conducting research at university laboratories. Dr. Cowan has mentored four Ingenuity students and three WISE students at Hopkins in the last five years. This award will facilitate our continued involvement and active participation in these valuable mentorship opportunities, encouraging young students, and those from underrepresented groups, to consider engineering as a viable career path. Additionally, we will continue to invite local groups to visit our facility to learn about robotics research, hopefully fostering a lifelong interest in the STEM fields.

NJIT Newark: NJIT and its sister university Rutgers Newark are reported to be among the most ethnically diverse Universities in the country. This was reflected in the first course (Systems Neuroscience) that Dr. Fortune taught in the Spring 2013 semester in which all six students were underrepresented ethnic minorities. Beyond attracting students through courses, we plan to schedule research demonstrations with the weakly electric fish on campus as part of Biology, Engineering, and Bio-Engineering outreach activities which are ongoing at NJIT. These activities include demonstrations with the live fish (the use of the animals for these purposes has been reviewed and approved by the institutional animal care and use committee).

These demonstrations have proven to be extremely effective for the recruitment of students because the electric fields of the fish can be amplified via loudspeaker and played to the students, the fish spontaneously and robustly exhibit a suite of social and locomotor behaviors, and some of the fish have been trained to respond to researcher cues. As Dr. Fortune has done previously, we plan to visit local elementary schools to make identical presentations with the animals. The students attending public schools in Newark are primarily under-represented minorities; this is an excellent venue for encouraging these students to enter STEM fields.

7.2 Development and Dissemination of Software Tools

The proposed work requires the continued development and implementation of computational tools and software specifically for the study of behavior in a closed-loop setting. We will package software tools to generate and analyze sensorimotor integration via Bode plot analysis with documentation. These will be disseminated as described in the Data Management Plan.

7.3 Training and Mentorship

This proposal will partially support one graduate student at JHU. The students will receive interdisciplinary training in engineering and neuroscience from both the Cowan and Fortune laboratories, respectively. In addition, both labs have a training structure where every member of the laboratory participates in mentorship both as a mentor and as a mentee. For example, undergraduates are involved by mentoring high school students and being mentored by graduate students and the graduate students are in turn mentored by the postdocs.

8 Results from Prior NSF Support

The PI (Cowan) and Co-PI (Fortune) have a strong track record of collaboration, including two recent NSF projects:

- *IOS-0817918, PI: E. S. Fortune; Co-PI; N. J. Cowan*, “Enhancement of Electrosensory Function via Social Interaction” (\$428,408, 9/1/2008–8/31/2011, Expired)
- *CMMI-0941674, PI: M. MacIver. Co-PI's: G. Lauder, N. Patankar, E. S. Fortune, N. J. Cowan.*, “CDI-Type II: Cyber-Enabled Discovery in Neuromechanical Systems” (\$1,400,000, 9/1/2009–8/31/2013, Active).

In addition to these the project most closely related to the current project (for both investigators) is (a) IOB-0543985, \$486,198, 4/1/2006–3/31/2009, Expired. PI: N. J. Cowan. Co-PI: E. S. Fortune (b) Title: *Multi-Sensory Control of Tracking Behavior in Weakly Electric Fish*. (c) Summary of results (including human resource development): *Intellectual Merit*: This project examined how sensory information is used by the nervous system to control locomotion. We established a novel paradigm for investigating feedback control in freely moving animals; this paradigm forms the basis for the current proposal. We discovered wide variety of control strategies and neural mechanisms in weakly electric fish. For example, we found that fish adapt their locomotor behavior based on the “predictability” of the stimulus trajectory [76]. *Broader Impacts*: A total of four graduate students (one of which was supported by an NSF Graduate Fellowship) and one postdoc were trained under this grant. A total of eight undergraduates participated in the research, supported in part by NSF REU extensions, Howard Hughes Medical Institute awards, and Provost’s Undergraduate Research Awards (PURA), with two of these generating publications. Four of the undergraduates were women. (d) Publications: Several studies were published based on this work [22–24, 26, 27, 30, 48, 53, 54, 76]. (e) Available data: kinematic data from electric fish refuge tracking behavior is stored on laboratory servers at Johns Hopkins and NJIT and is made available to investigators upon request. (f) Renewal? N/A.

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