MAKING SENSE: WEAKLY ELECTRIC FISH MODULATE SENSORY FEEDBACK VIA SOCIAL BEHAVIOR AND MOVEMENT

by

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Abstract

Animals rely on sensory information for the control of their behavior. Understanding this process requires a detailed description of the sensory feedback that they receive, which is often determined by an animal's proximity to conspecifics and its own movement within the environment. This dissertation examines the role of social behavior and movement for the modulation of electrosensory feedback in weakly electric fish.

We made observations of weakly electric fish in their natural habitats and found that some species of fish, which typically have more complex social behaviors, are most often found in groups. These same species will preferentially approach a refuge with a social signal in the laboratory. As a result of social grouping these fish receive continuous electrosensory oscillations (amplitude and phase modulations) caused by the interactions from the electric fields of each individual. Interestingly, both social grouping and movement can produce higher order modulations (termed 'envelopes'), which can have lower frequency content than the first order modulations. Curiously, we did not observe low frequency envelopes in the majority of our samples. To determine why that might be the case we tested the behavioral responses of weakly electric fish to envelope stimuli in controlled laboratory experiments.

We found that *Eigenmannia* will increase or decrease their electric organ discharge (EOD) frequency in response to social envelope stimuli, termed the Social Envelope Response (SER). The strength of the SER was dependent on the initial envelope frequency and the stimulus amplitude, whereby lower frequency envelopes and higher stimulus amplitudes resulted in the strongest EOD changes. As a consequence of

the EOD change the envelope frequency during the course of a trial was increased, suggesting that the SER may be a mechanism for avoiding low frequency social envelopes. These results may explain our field results that showed weakly electric fish do not typically produce low-frequency envelopes in natural social groups.

These fish are not only processing electrosensory information from their social behavior but are also simultaneously process electrosensory information from their own movement and the movement of nearby objects in their environment. To investigate the relationship between movement and the modulation of sensory feedback we tested the ability of *Eigenmannia* to track a moving refuge under varied sensory conditions by changing the illumination (vision) and conductivity (electroreception) across trials. When the fish relied solely on electrosensory information during tracking they performed additional movements that consisted of whole-body oscillations and tail bends, which may be used to shape electrosensory feedback.

Our results indicate that weakly electric fish continuously process two streams of information, one derived from social interactions and the other from movement, which are used for the independent control of the fish's electric organ and the fish's locomotor system. In addition, both social behavior and movement can be used to modulate electrosensory feedback. Future studies should examine sensory processing in the context of the animal's social behavior and their movement within the environment, as it can categorically change the signals that the animal is receiving.

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This thesis is dedicated to the fish:

Martini, Tequila, Whiskey, Mojito, Sangria, Brandy & Sweetie

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Although writing this dissertation really only happened in the last few months it was the culmination of years and years of work. And I don't just mean the work I did writing it—the real work isn't evident in these pages. This dissertation simply would not have been possible without a village of people on the sidelines who supported and encouraged me along the way. So, I'll just start at the beginning.

I would like to thank my parents who started loving me the minute I came out as a screaming, crying mess and have continued to do so even though not much has changed. My parents taught me to work hard, whether it was schoolwork or bargain shopping. Of course, both of these skills turn out to be essential for surviving graduate school. My parents also made efforts to encourage my interest in science by letting me play with 'toys' such as microscopes, chemistry sets, sea monkeys, and ant farms. And I can't forget my favorite of all time, the "Diggin' Up Dinosaurs" archeology set they bought me even though it was abundantly clear I'd never have enough patience for that! They also kept buying me critter after critter—fish (Cleo and Monstro), hamsters (Teddy, Rascal, Twinkie, and Sausage), hermit crabs (#1-4), a bird (Clyde), a turtle (Lilly Pad), a cat (Kitty Kitty Katra) and dogs (Lollipup, Max, and Lil Moo)—which instilled in me my love of animals and subsequently the study of animal behavior. So I would like to formally thank my parents for encouraging my interests even though it sometimes meant my mom had to pull slugs out of my throat or my dad had to stay up all night with me catching lightning bugs.

I was also quite fortunate to have a series of great teachers throughout my early education. I would like to thank my 3rd grade teacher Mrs. Gaylin for not reporting me to

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Then I went to New College where I was fortunate enough to be advised by Dr. Gordon Bauer. Gordon was the exact right level of tough (except that time he threatened to break my kneecaps) paired with unwavering encouragement and support. He went out of his way to find research opportunities for me and gave me my early introduction to research with exotic creatures. I absolutely agree with his assertion that his formal title should read “Dr. Gordon B. Bauer, BFD” because I simply wouldn’t be where I am today without him.

So let’s fast-forward to my time spent in graduate school at Hopkins. I’ve only been here 3.5 years but there was a small army’s worth of people that helped me get through the program. I am grateful to Lauren Jones for her friendship and ensuring that I occasionally eat balanced meals. I’d like to thank Dr. Amy Shelton who is incredibly helpful with respect to almost everything but especially my occasional stress-induced breakdowns. Dr. Steve Yantis, Dr. Peter Holland and Dr. Michela Gallagher provided me

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Speaking of fish, for the last three years I've done my research on weakly electric fish, as evidenced by the topics in this dissertation. What you might not know is that the electric fish community is the absolute nicest and most helpful scientific community imaginable. I sincerely thank all the current and former electric fish PIs, post-docs, and graduate students, especially Dr. Len Maler, Dr. Maurice Chacron, and Dr. Rüdiger

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Chapter 1: Introduction

What is active sensing?

There has been a revolution in the past 30 years in our understanding of how sensory systems work. Previously, sensory systems had been seen in the same vein as human built sensors—devices that encode information in the environment in an invariant and passive way. This notion has long been known to be inaccurate, as neural feedback (Koopowitz and Stone, 1974; Nick and Ribera, 2000) and other internal mechanisms have been shown to dramatically modulate the activity of neurons. The transformation in our understanding has come from an appreciation of the widespread phenomenon that animals control the acquisition and modulation of sensory information through active processes (called 'active sensing') (Nelson and MacIver, 2006).

Active sensing is most commonly understood as referring to a specific class of highly specialized sensing systems in unique animals that emit signals for the purpose of acquiring sensory information. The well-known examples of active sensing are echolocation, electroreception, whisking, and hydrodynamic imaging. However, the broad definition of active sensing simply refers to the expenditure of energy for the purpose of sensing (Nelson and MacIver, 2006). In which case, movement is an obvious and critical form of active sensing.

Animals routinely change their motor behavior in relation to the sensory demands of the task goal (Hille et al., 2001; Gao et al., 2003; Visalberghi and Neel, 2003; Raburn et al., 2011). For example, if a task is to determine the texture of an object, people tend to move their hand back and forth in a lateral rubbing movement (Lederman, 1982; Lamb, 1983; Lederman and Klatzky, 1987; Hollins and Risner, 2000). This movement activates

mechanoreceptors in the hand (e.g. Merkel disks) that respond to indentation of the skin and have restricted receptive fields that allows for very fine spatial resolution that is needed for tactile discrimination (Kandel et al., 2000). However, if instead the task was to determine the weight of an object, people tend to make a 'hefting' movement where they move the hand holding the object up and down (Gibson, 1962; Thelen and Smith, 1996). This type of movement primarily activates muscle stretch receptors that can detect the load on a given limb but do little in terms of discriminating textures. This example suggests that animal behavior, and movement specifically, might be done in a way that optimally stimulates the relevant receptors dependent on the sensory needs of the task (Jones, 1988; Fleishman and Pallus, 2010).

Although it might seem obvious, it is only recently that scientists have begun to appreciate that the role of movement in active sensing occurs even in the classic active sensory systems. For example, electric fish are used as an example of active sensing because they produce an electric organ discharge (EOD). However, as we will see in Chapter 4, this active sense interacts with the animal's movement in ways that are similar to the somatosensory examples described above. For example electric fish swim rapidly forwards and backwards and bend their tail to enhance aspects of the electric field during prey capture and other electrolocation tasks. In this example, the electric fish are expending energy both for the production of the EOD and through changes in their locomotor behavior.

The use of locomotor systems for sensing is similar across animals with the classic type of active sensing and those that have "non-specialized sensory systems". For example, animals move their pinnae to assist with sound localization. These movements

have been described in a variety of animals including echolocating bats (Pye and Roberts, 1970; Ghose and Moss, 2006), but also animals such as foxes (Koop and Velimirov, 2008) and cats (Populin and Yin, 1998) which do not generate a specialized sensory signal.

Interference in active sensing

In active sensing systems, animals are creating a signal, either through the generation of a specialized signal or through their movement, and as such, active sensing is subject to interference that would not occur in 'passive' sensing systems. Specifically, active sensing is often affected by social context. When animals are near each other they can perceive, and sometimes even exploit, the sensing signals used by nearby animals. These competing signals often interact with the animal's own sensing signals, and can impair sensory function (Griffin et al., 1963; Heiligenberg, 1973; Matsubara and Heiligenberg, 1978). Adding to the complexity is the fact that animals frequently use signals that have dual purpose, used both for sensing and also for social signaling (Metzner, 1999; Partan and Marler, 1999; Dawson, 2010)

Indeed, there can be a shift in sensory processes in individuals that are alone compared to those that are in a group. For example, bats forage at night using echolocation to capture flying insects in complex aerial maneuvers (Simmons et al., 2001). This requires the bat to be able to determine which echoes correspond to the target (i.e. the insect they want to capture) while separately processing those that return from the environment (i.e. the tree that they want to avoid running into). Now imagine this same bat foraging in a swarm of other individuals, which can range in size from dozens

to millions of conspecifics (Kunz and Lumsden, 2003). In this case, the bat still needs to be able to separate out target echoes from environment echoes, but it must also filter out all the echoes that are returning from echolocation chirps produced by its neighbors.

The influence of conspecifics on sensing is not unique to the classic active sensory systems, but can occur across a broad array of active sensing processes. A fish uses the mechanosensory lateral line to detect movement and vibrations in the surrounding water that can be generated by potential prey or predators (Montgomery et al., 1995). The activation at the receptors will differ depending on whether the fish is swimming alone or with conspecifics. In fact, it is possible that the water motion generated by the conspecific can dominate the activity at the receptor level and make it more difficult to detect changes due to other sources (e.g. a prey item) (Montgomery et al., 1995).

This thesis examines these issues in a uniquely suited model animal system, weakly electric fishes that both generate a sensory signal (i.e. electric field) and produce movements (i.e. body oscillations and tail bends) for the purpose of sensing. This system allows the examination of (1) the role of social behavior on modulating sensory feedback and (2) the role of movement on modulating sensory feedback. In the discussion we will consider the interactions between these two categories of behavior.

Model system: Weakly electric fish

Electric fish use their electrosensory system for a variety of behaviors including navigation, prey capture, refuge tracking and obstacle avoidance (Caputi and Budelli, 2006; von der Emde, 2006); these are generally referred to as electrolocation behaviors.

However, these same fish also use their electrosensory system for conspecific communication (Hopkins, 1974; Fortune, 2006; Hupe and Lewis, 2008; Triefenbach and Zakon, 2008), a social behavior.

Weakly electric fish have an electric organ (EO) typically in their tail that is composed of electrocytes and is derived from modified muscle cells (myogenic) or nerve cells (neurogenic) (Bennett, 1971; Bullock et. al., 2005). The morphology and distribution of the electrocytes varies by species (Bass, 1986). The summation of individual ionic currents that arise from stimulation of the electrocytes produces the electric organ discharge (EOD) (Babineau et. al., 2006; Kelly et. al., 2008; von der Emde et. al., 2010). The number of electrocytes in series and parallel determine the EOD voltage and current, respectively (Bullock and Heiligenberg, 1986).

The EOD generated by each fish has species-specific and individual variations in frequency, amplitude and waveform (Moller, 1995; Knudsen 1975B; Carlson and Hopkins, 2004; Crampton and Albert, 2006). Broadly speaking, there are two classifications of EODs: pulse-type and wave-type. Pulse-type electric fish produce EODs that consist of brief stereotyped pulses at comparatively long inter-pulse intervals (IPIs). The pulse duration and IPI varies across species and individuals (McGregor and Westby, 1992). Wave-type fish produce EODs that are nearly sinusoidal (Bullock et al., 2005). The EOD frequency for wave-type fish varies dramatically across species from 25 to 2000 Hz (Crampton and Albert, 2006).

The EOD creates an electric field that surrounds the fish. The spatial and temporal features of the electric field are complex and vary as a function of objects in the environment and the presence of other electric fish (Kelly et. al., 2008; von der Emde et.

al., 2010). Tuberous electroreceptors are distributed in the skin along the entire length of the fish, with a higher concentration of receptors on the head region, which creates an electrosensory fovea (Bacelo et al., 2008). Objects create local distortions in the electric field that stimulates the tuberous receptors and depends on the difference in conductivity between the object and the surrounding water (von der Emde et. al., 2010). These electric field distortions are perceived as an 'electric image' that arises from the change in the transdermal potential that results from a nearby object (Bastian, 1986).

One of the primary reasons why weakly electric fish are such a good model system for exploring the relationships between social behavior and movement on sensory feedback is because all of the sources lead to the same type of sensory signal to the animal (i.e. amplitude modulations or AMs). However, the information from these two categories of stimuli can vary in their spatial and temporal extent. For example, small prey items lead to slow local activation (< 10 Hz) and social signals lead to fast global activation (> 10 Hz) of the electroreceptors (Cowan and Fortune, 2007). Although there are differences between the signals that arise from objects and social interactions, they utilize the same modality—they both activate the tuberous electrosensory system.

In some cases, there is ambiguity regarding the source of salient signals. For example, because both prey items and moving objects produce similar AMs (< 10 Hz) the fish must have behavioral or neural solutions for avoiding interference between the two signals. The details of how social feedback and movement effects the electric field will be discussed in the relevant sections.

The role of social behavior on sensory feedback

As previously mentioned, some animals can probe their environment with autogenous (self-generated) signals. In both electroreception and echolocation, for example, individual animals emit a sensory signal, either an electric field or sonar broadcast, to gather information about the environment (Thomas et al., 2002; Nelson and MacIver, 2006). The information is conveyed by details of the electric field distortions and returning echoes, respectively. These actively generated signals are adaptations that permit these animals to occupy specialized ecological niches, particularly taking advantage of the ability to navigate and forage in complete darkness (Caputi and Budelli, 2006; Nelson and MacIver, 2006; von der Emde, 2006).

However, the generation of these signals comes with costs that are not only energetic but also introduce new sensorimotor challenges for the animal. Of particular interest is the degradation of sensory function that is potentially caused by the interference patterns that arise from the interactions of signals produced by nearby conspecifics and autogenous signals (termed 'jamming') (Heiligenberg, 1991). This is similar to the to the 'cocktail party effect' in the human auditory system (Cherry, 1953), where multiple senders produce competing signals that can degrade the ability to perceive salient signals. Additionally, these active sensing signals are public and therefore subject to 'eavesdropping' where other animals can intercept, and potentially exploit, the information (Stowe et al., 1995; Earley and Dugatkin, 2002; Fenton and Ratcliffe, 2004; Gotz et al., 2006; Lichtenberg et al., 2011; Clark et al., 2012). In sum, there is a categorical difference in the sensory environment of animals when they are alone

compared to when they are in groups (Hessler and Doupe, 1999; Tan et al., 2005; Stamper et al., 2010).

What is Jamming?

Here I define the term 'jamming' specifically as the degradation of the perception of salient information that arises from overlapping sensory signals. The signals that are believed to cause jamming are generally in the same temporal frequency band as the signals of interest to the animal. Consider, for example, the effects of a flashing light on humans' ability to use visual information. If the light is flickering at a rate of 60 Hz or more (e.g. the flicker rate for many modern television sets), it will have virtually no impact on visual-based behaviors that occur at frequencies of 5 Hz and below. However, a strobe light flashing in the range of 1-4 Hz can have dramatic effects on the acquisition and processing of salient 5 Hz visual information (Bartley, 1939; Gorea et al., 2000).

In the case of electric fish, jamming occurs when two or more fish are in close proximity and the summation of their electric fields produces interference patterns (AMs) that may impair the fish's ability to perceive salient signals (e.g. prey item). Recall that weakly electric fish can produce either a wave-type or pulse-type signal (Bullock and Heiligenberg, 1986). For these fish the type of signals that create jamming are going to depend on the EOD output type. In this regard, pulse-type fish are jammed by temporal overlap and wave-type fish are jammed by frequency overlap (Bullock et al., 1972; Scheich et al., 1977; Bastian, 1987; Capurro et al., 1998; Capurro and Pakdaman, 2004). Importantly, even when in large groups (20 or more individuals) electric fish are not

often observed colliding with obstacles in the environment or failing to intercept prey, suggesting there might be mechanisms to solve the jamming problem.

Multiple solutions to jamming in the electrosensory system

As previously mentioned, the jamming that an individual fish may experience depends on the type of EOD signal that they produce (pulse or wave) and may have a different mechanism by which the jamming is reduced or eliminated. Since pulse-type fish are jammed by the temporal overlap of signals, it is reasonable to expect that they might alter their IPI in order to reduce the temporal overlap (Heiligenberg, 1974b, 1976; Heiligenberg et al., 1978; Capurro et al., 1999). In wave-type fish jamming arises by frequency overlap, which produces AMs that occur at the frequency difference (dF) between the individuals (Heiligenberg, 1991). For example, if one fish has an EOD at 500 Hz and a nearby conspecific has an EOD at 505 Hz, the AM is 5 Hz.

Clearly, the easiest method to avoid sensory interference from the presence of conspecifics is to modulate your social behavior (i.e. move away) (Tan et al., 2005). One should first address the possible advantages of group forming behavior in order to understand why these animals are social in spite of the resulting sensory interference. It is fairly well established that social living functions as a defense against predation (Alcock, 2005) and it is also possible that individuals in social groups show helping behavior by providing food (Wilkinson, 1984) or information regarding access to food (Tautz, 1996) amongst other things. Clearly there are distinct advantages to social living, which means that there is a benefit to solving the sensory interference problem, instead of just living alone. If so, animals need another way to avoid these problems. Interestingly, weakly

electric fish have independently evolved at least three solutions to jamming – 1) EOD timing (pulse-type fish), 2) spatial filtering/discrimination by neurons (wave-type fish), and 3) EOD frequency changes (wave-type fish).

EOD timing solution. Pulse fish are able to change the IPI between sequential EOD pulses (Toerring and Moller, 1984; Serrier and Moller, 1989; Carlson and Hopkins, 2004). When in the presence of a conspecific, pulse fish change the timing of their EOD pulses to avoid temporal overlap between individuals (Heiligenberg, 1974), which decreases and can even eliminate the temporal jamming. Both *Rhamphichthys* (Scheich et al., 1977) and *Gymnotus* (Capurro and Malta, 2004) increase their EOD pulse rate when the jamming signal rate is lower and they decrease their EOD pulse rate when the jamming signal rate is higher. In addition, pulse fish change their EOD pulse rate when the jamming signal is harmonically related to their own EOD (e.g. one signal is almost twice the other) (Capurro and Pakdaman, 2004). By changing the timing of EOD pulses these fish are able to reduce the temporal interference created by forming social groups.

Neural solution. Sternopygus appear to be immune to jamming and do not show behavioral impairments when in the presence of a signal that would jam other closely related species of weakly electric fishes (Matsubaraand Heiligenberg, 1978). This is a result of having a specialized class of neurons called Type III cells in the electrosensory lateral line lobe (ELL). Type III cells are able to distinguish between object-related AMs (target signal) and conspecific-related AMs (jamming signal) because of the differences in the spatial pattern of these two types of feedback (Matsubara, 1981; Matsubara, J.A., 1982). Specifically, objects produce localized distortions in the electric field and only stimulate a restricted population of electroreceptors. This is in comparison to jamming

AMs produced by the presence of conspecifics, which cause global distortions. Because of the receptive field organization of Type III cells, they only respond to AMs generated by objects, and not those generated by jamming signals (Matsubara, 1982). To date, Type III cells have only been found in *Sternopygus,* but they do provide a neural mechanism by which electric fish can avoid jamming interference.

EOD frequency solution. In many wave-type electric fishes, including *Eigenmannia* and *Apteronotus*, fish solve the jamming problem by changing their EOD frequency. When two conspecifics are in close proximity and have similar EOD frequencies the AM of the combined signal has a low frequency. If each fish shifts their respective EOD frequency in opposite directions they can increase the AM frequency. This behavior is called the Jamming Avoidance Response (JAR) and the complexity of the behavior varies by species. For example, *Eigenmannia* shift their EOD frequency either up or down, depending on the frequency of the nearby conspecific (lower or higher, respectively), whereas *Apternonotus* can only shift their frequency up. Thus, if two *Eigenmannia* have EOD frequencies of 500 Hz and 505 Hz and they shift their EODS to 490 Hz and 515 Hz, respectively, the fish increase the AM from the initial 5 Hz to 25 Hz. In response to the same initial 5 Hz AM, in *Apteronotus* only the fish with the higher frequency would adjust its EOD (Heiligenberg et al., 1996). The JAR behavior is arguably one of the most well understood animal behaviors in terms of the neural mechanisms underlying the behavioral control (Heiligenberg, 1991).

The Jamming Avoidance Response (JAR)

The Jamming Avoidance Response (JAR) is a robust behavior that is observed in the wild and elicited reliably in the laboratory (Figure 1.1). The JAR does not require movement, which makes it possible to study in great detail using a variety of techniques such as behavioral experiments that can partition the sensory surface and electrophysiological experiments in immobilized but awake and behaving animals. Through these methods, the complete neural circuit of the JAR— from sensory input to the generation of motor output—has been elucidated (Heiligenberg, 1991; Metzner, 1993). The complexity of the JAR and the typical number of conspecifics found within a group in natural habitats varies by species. Chapter 2 will explore the idea that the JAR complexity and the species typical group size are related.

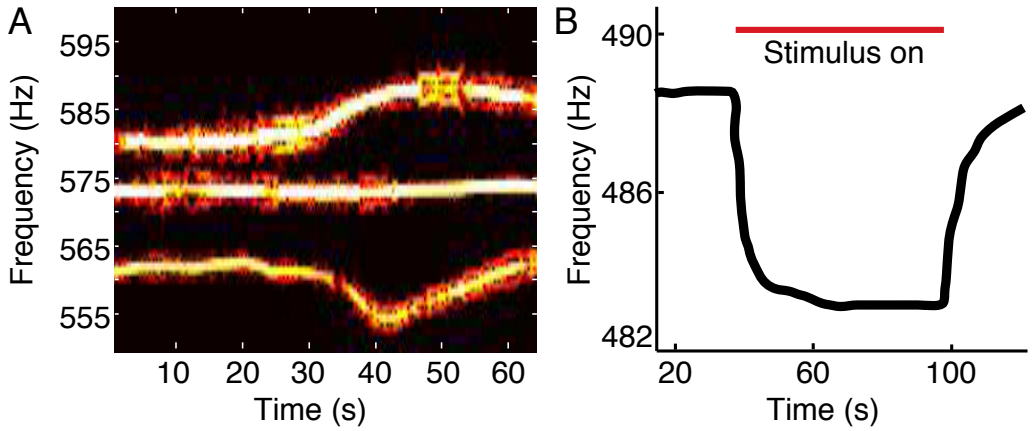

Figure 1.1 Jamming Avoidance Response in the wild and laboratory
(**A**) *Eigenmannia* perform the JAR in their natural habitats. In this sample (data unpublished), there are three individual fish; the fish with the highest frequency does a JAR to shift its EOD frequency up and the fish with the lowest frequency does a JAR to shift its EOD frequency down. (**B**) *Eigenmannia* also robustly and reliably perform the JAR to artificial sinusoidal signals in the laboratory (data from (Hitschfeld et al., 2009)). In this example, the fish is stimulated with a signal that creates a low-frequency AM and in response the fish decreases its EOD frequency. Once the signal is turned off the fish shifts its EOD back towards baseline.

In *Eigenmannia,* the EOD is driven by an intrinsically rhythmic pacemaker nucleus (Pn) located in the medulla that contains 50-100 pacemaker neurons (Stoddard et al., 2006). Pacemaker neurons are spontaneously active and form synapses with Pn relay cells. These neurons fire synchronously at a stable and high rate (150-600 Hz) (Bullock et al., 2005). The relay cells project out of the Pn and form synapses onto the electromotorneurons that innervate the electrocytes (cells of the EO). Thus, there is a direct 1:1 relationship between the firing rate of the Pn and the EOD frequency such that 1 spike corresponds to one cycle of the EOD (Bullock et al., 2005). Each fish has an individual preferred resting EOD frequency that is correlated with the tonic firing rate of the Pn neurons (Moortgat et al., 1998). To elicit a change in EOD frequency, as occurs during the JAR behavior, the resting firing rate of the Pn is modulated.

In order to compute the direction of the EOD shift the fish needs to determine the sign of the dF, indicating the direction of jamming (from above or below). This would be easier if the fish knew which of the two EOD signals is its own but instead the fish computes the information from the combined signal (Metzner, 1993; Heiligenberg et al., 1996; Takizawa et al., 1999). The fish is able to obtain the sign of the dF by making pair-wise comparisons of the amplitude and phase information from the signal across many electroreceptors along the body surface (Heiligenberg and Rose, 1985; Takizawa et al., 1999; Bullock et al., 2005).

The phase and amplitude information is not integrated until it reaches the torus semicircularis (Ts) in the midbrain. There are two types of tuberous receptors: T-type (phase coders) and P-type (amplitude coders). The information from these two receptor types is conveyed via independent pathways to the electrosensory lateral line lobe (ELL),

in the hindbrain, where the information is processed in parallel (Heiligenberg and Rose, 1985). The information reaches the Ts through a projection from ELL pyramidal cells (Kawasaki and Guo, 1998). If the social feedback results in low-frequency jamming, the Ts provides a command signal to the nucleus electrosensorius (nE), in the diencephalon, to initiate a shift of the fish's own EOD (Keller and Heiligenberg, 1989).

To increase the frequency of the EOD (Figure 1.1) the Ts excites the dorsalmedial region of nE (nE↑). After activation, nE↑ excites PPn (diencephalic prepacemaker), which terminates on the pacemaker neurons of the Pn. This pathway is purely excitatory and the synaptic tranmission is mediated by AMPA-type receptors (Metzner, 1993). If you bilaterally lesion the nE↑ the fish is not able to raise its frequency above the resting rate (Keller and Heiligenberg, 1989; Metzner, 1993). If either the nE↑ or PPn is stimulated with $_{L}$-glutamate the EOD frequency gradually rises (Kawasaki et al., 1988; Keller and Heiligenberg, 1989).

On the other hand, if the EOD frequency needs to be decreased (Figure 1.1) the Ts excites the ventral region of nE (nE↓). After activation, nE↓ inhibits SPPn (subleminiscal prepacemaker), via GABAergic connections (Metzner, 1993). The SPPn is usually tonically active and connects to the Pn relay cells where synaptic transmission is mediated by NMDA-type receptors (Metzner, 1999). Bilateral lesions of nE↓ prevents the fish from lowering its' frequency below the resting rate (Metzner, 1993). If either the nE↓ is stimulated with $_{L}$-glutamate or the SPPn is stimulated with GABA the EOD frequency decreases (Keller and Heiligenberg, 1989). Alternatively, if the nE↓ is stimulated with $_{L}$-glutamate after injecting bicuculline ($GABA_A$ antagonist) into the SPPn you block the frequency decrease (Metzner, 1993).

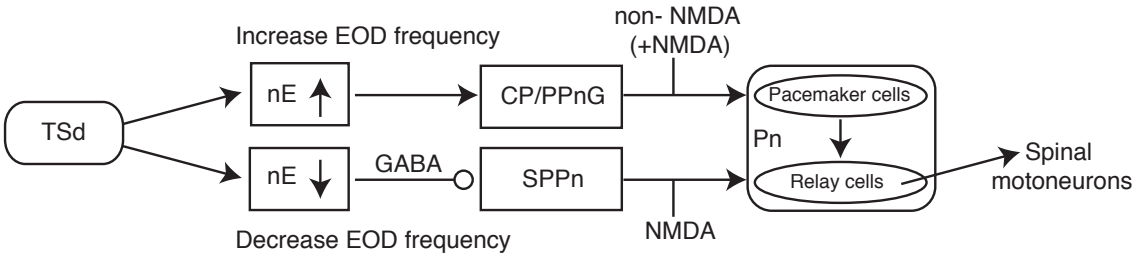

Figure 1.2 Circuit for EOD frequency changes during JAR
In the JAR *Eigenmannia* shift their frequency up or down, depending on the frequency of the conspecific. To increase the EOD frequency the Torus (Ts) excites the nE (nE↑), which excites PPn terminating on the pacemaker neurons of the Pn. To decrease the EOD frequency the Torus (Ts) excites the nE (nE↓) that inhibits the SPPn terminating on the relay cells of the Pn. (Figure adapted from (Metzner, 1999)

The function of the JAR

The most widely cited function of the JAR is that it allows fish to form social groups without suffering from the detrimental interference (jamming) from low-frequency beat rates (Bullock et al., 2005). In several behavioral tasks where *Eigenmannia* swam side-to-side to follow the lateral movement of an object (either two small plates, or a row of rods), electrolocation (i.e. the following response) was impaired by low frequency AMs (Heiligenberg, 1974; Matsubaraand Heiligenberg, 1978; Bastian, 1987). Moreover, there is neural evidence that suggests low-frequency AMs impair electrolocation; in an immobilized fish, midbrain neurons in the Ts respond to movement of an object. This neural response is degraded when there is a global low-frequency beat (Ramcharitar et al., 2005). There appears to be a switch in the responsiveness of the neurons, where the cells instead respond phase locked to the AM instead of responding to the moving object.

In some Ts neurons the response to the moving object is selective for a single direction (head-to-tail or tail-to-head) (Chacron et al., 2009). In these cells low-frequency AMs impair the selectivity but high-frequency AMs enhance it (Ramcharitar et al., 2005, 2006). In most observations, the JAR increases the frequency of the AM to around 20 Hz (Tan et al., 2005). When fish are in a post-JAR state the higher-frequency AM produces a continuous global synchronization in the gamma frequency range, 20-80 Hz, within the brain. The presence of global oscillations enhances direction selectivity by these neurons through suppression of the firing rate in the non-preferred direction (Ramcharitar et al., 2005, 2006). This data suggests that the function of the JAR might not actually be for jamming avoidance, but instead for post-jamming enhancement. However, there has not yet been a behavioral correlate of this neural phenomenon.

Beyond the JAR: Social feedback in three or more fish

When two wave-type electric fish are in close proximity their EODs sum and the combined signals has amplitude and phase modulations, termed a beat rate. In contrast, when three or more fish are in close proximity the EODs sum and the combined signal has not only amplitude and phase modulations but an additional modulation on top of that, which in the electric fish literature is called an 'envelope' (Middleton et al., 2006; Middleton et al., 2007; Longtin et al., 2008; Savard et al., 2011; McGillivray et al., 2012). As previously mentioned, the frequency of the AM corresponds to the dF between individuals. The electrosensory envelope occurs at the difference of the dFs (abbreviated ddF). In many cases, the frequency of the ddF will be lower than the frequency of the dFs. Thus, it is possible that the frequency of the AMs will be outside the range of the JAR but

still produce a lower-frequency envelope. For example, a fish at 505 Hz will not be jammed by conspecifics at frequencies of 450 (dF = -55) and 550 (dF = +45), but there will be a 10 Hz envelope (ddF).

There is evidence that demonstrates that electric fish have neural activity related to envelope encoding and transmission. These neurophysiological studies have identified envelope related neural activity at each level from the receptor afferents to the midbrain in *Apteronotus* (Middleton et al., 2006; Middleton et al., 2007; Longtin et al., 2008; Savard et al., 2011; McGillivray et al., 2012). However, the behavioral relevance of electrosensory envelopes is not known and will be the topic of Chapter 3.

The role of movement on sensory feedback

Animal movement results in the stimulation of the animal's own sensory receptors. This sensory information is known as feedback, which is often used in the control of movement (Weiland and Koch, 1987; Pearson, 2008; Gritsenko et al., 2009; Knill et al., 2011). Therefore, understanding how sensory systems work requires understanding how they operate in the context of motor systems. In this regard sensing is not the static process that is assumed in the majority of studies that examine sensory perception, but it is instead dynamically altered by feedback from the animal's own movements (Han et al., 2009; Maimon et al., 2010). This misconception may also explain why bio-inspired or artificial sensory systems have had limited success compared to their biological counterparts (ex. man-made sonar versus echolocating dolphins). The tight coupling between sensory and motor systems also pushes neuroscientists towards conducting experiments in awake, behaving animals rather than anesthetized animals.

When experiments are conducted in anesthetized animals it opens up the feedback loop, which can change the role of the neural responses and lead to a fundamental misinterpretation of the data (Szwed et al., 2003; Cowan and Fortune, 2007; Mosconi et al., 2010).

Further, the availability of sensory feedback can have profound effects on motor strategies. Consider, for example, the change in a person's movement pattern as they reach to turn *off* a light switch compared to when they reach to turn *on* a light switch (i.e. with and without visual input). In the light, they reach directly for the switch relying heavily on visual feedback, whereas in the dark they run or tap their hand over the wall, relying much more on the sense of touch. In this example individuals compensate for the loss of visual information by adjusting their movement to increase somatosensory feedback, which in this task is almost irrelevant when they have visual input. Chapter 4 examines this issue in more depth: how do weakly electric fish modulate their movement when modality-specific information is degraded?

Indeed, there are many ways that animals move specifically for the purpose of gathering sensory information. Movements can be used to: (1) generate, (2) amplify, (3) maintain or (4) direct the signals used for sensing, or movement can be used to (5) orient the receiver/receptor array. Examples for each of these types of movement are provided below.

(1) Animals can move to generate a sensory signal. Consider the aye-aye (*Daubentonia madagasceriensis*), which is nocturnal and forages for insects (e.g. beetle larvae) that live in the subsurface of tree cavities. To detect an insect the aye-aye makes a rapid tapping motion (termed 'percussive-foraging' or 'tap-scanning') on the surface of

the wood and listens for the returning echoes. This behavior is not specific to aye-ayes, as it has also been observed in woodpeckers and some monkeys (Erickson, 1994a, b; Erickson et al., 1998; Phillips et al., 2004).

(2) Animals can move to amplify a sensory signal. The blind-cave fish (*Anoptichthys jordani*) uses its mechanosensory lateral line for 'hydrodynamic imaging' (Dijkgraaf, 1963; von Campenhausen et al., 1981; Hassan, 1989). These fish do something curious when they investigate a new object— they rapidly accelerate upon approach and then glide past the object (von Campenhausen et al., 1981). It appears that this rapid acceleration produces a flow field around the fish's body that is modified by the presence of stationary objects (Hassan, 1985; Windsor et al., 2008). The fish controls its swimming speed and pattern (acceleration-glide) in order to optimize the activation of the neuromasts (Teyke, 1988).

(3) Animals can move to maintain a sensory signal. Sensory receptors commonly have high-pass filtering properties and therefore reject stationary or very low-frequency signals (Kandel et al., 2000). This filtering is often known as 'adaptation' and it is the reason people are not thinking about what their underwear feels like at every moment. This filtering can have profound effects on sensing. If a visual image is stabilized perfectly on the retina there is no relative movement and the photoreceptors adapt over a period of a few seconds. The perceptual consequence is that the visual pattern would disappear, which is known as 'perceptual fading' (Ditchburn and Ginsborg, 1952).

(4) Animals can move to direct a sensory signal. In echolocating bats the sonar beam is highly directional and narrow (60-90° cone from the midline) (Snyder et al., 2007; Surlykke et al., 2009b), which is beneficial for detecting targets within the range

directly in front of the bat but less so for detecting objects off-axis. To solve this problem the bats use movement to direct the beam across a wider swath of the environment. Specifically, they move their head back and forth in a scanning motion to increase the sensory volume for the detection of prey and other objects in their environment (Ghose and Moss, 2006; Surlykke et al., 2009a).

(5) Animals can move to orient their receivers or receptor arrays. Bats (Pye and Roberts, 1970; Ghose and Moss, 2006), foxes (Koop and Velimirov, 2008), and cats (Populin and Yin, 1998) all use ear movements to help localize the direction of a sound source. It has been demonstrated that surgically immobilizing the bat's ears prior to an obstacle avoidance task leads to decreased performance, especially for targets (vertical wires) that require elevation processing (Mogdans et al., 1988). In this case, movement assists sensory processing by putting the receivers in a better position for the incoming sensory information.

Movement for sensing in weakly electric fish

Weakly electric fishes are an ideal model system for studying how feedback from movement is used in sensory processing. These fishes have two adaptations that contribute to a unique form of sensorimotor interaction for perception. These are the generation of an electric field by the electric organ and the control of movement by the ventral ribbon fin. The electrosensory system has been described above. The ventral ribbon fin of knifefish uses counter-propogating waves for propulsion in both the forwards and backwards direction (Lannoo and Lannoo, 1990; Lannoo and Lannoo, 1992). Being able to swim forwards and backwards is particularly advantageous for

weakly electric fish because the electrosensory system has an omnidirectional electrosensory volume (Snyder et al., 2007).

The electric field surrounds the entire fish allowing it to detect objects within 1-2 body widths in all directions (Snyder et al., 2007). Like other sensory modalities, this detection requires movements. This has been studied in great detail in the context of the control of two behaviors: prey capture and refuge tracking (Rose and Canfield, 1993a; Nelson and MacIver, 1999; MacIver et al., 2001; Cowan and Fortune, 2007; Roth et al., 2011; Stamper et al., 2012). Both of these behaviors require that the animal can determine the direction of movement of the object relative to the body. Neurons in the midbrain (Ts) encode the direction of movement in the range of behaviorally relevant moving sensory stimuli (Ramcharitar et al., 2005, 2006; Khosravi-Hashemi et al., 2011).

Prey capture: Prey capture has been studied in *Apteronotus albifrons* as it fed on small prey items, *Daphnia. Daphnia* swim in the water column and produce a small electric image on the electroreceptor array. As *Daphnia* swim, they create electricity through their muscle movement, which can be detected by the ampullary receptors. Additionally, the body of the *Daphnia* acts as a capacitor that alters the electric field as it moves around which stimulates the tuberous receptors. Models of the electric field during prey capture indicate that salient information for the capture of *Daphnia* occurs at frequencies below 10 Hz (Nelson and MacIver, 1999; MacIver et al., 2001). Prey capture performance of these fish can be altered by aspects of the environment, such as the conductivity of the water (MacIver et al., 2001).

Fish may also use body or tail movements to shape the spatiotemporal properties of the electrosensory feedback in a way that facilitates prey capture. Remarkably, there is

great consistency across species of electric fish in the sequence of movements that occur during prey capture. When electric fish capture prey, there is a sequence of movements that consist of scanning the prey along the body and then rapidly reversing to position the prey item near the mouth for capture (Nelson and MacIver, 1999). Because the electroreceptors are distributed along the surface of the body, this scanning behavior would change the electric image as the body of the fish moved relative to the prey item. Thus, if the fish changed the positioning of the body there would be consequences for the electrosensory system that could facilitate sensory acquisition. Through behavioral experiments and modeling that used high-speed videos of *Apternonotus* capturing small prey items (e.g. *Daphnia*) it has been shown that the fish are able to control their body position, velocity and orientation to maximize the encounter rate of prey (Nelson and MacIver, 1999).

Recent research suggests that the fish will increase energetic costs by swimming in a more inefficient manner to achieve better sensing performance. Specifically, the fish will tilt their bodies to position the electroreceptor array in a way that allows them to scan a greater space within the same amount of time. Through allowing the animal to scan a larger volume of space this method of swimming increases the prey encounter rate (MacIver et al., 2010).

Refuge tracking: Weakly electric fish hide in tree root systems or leaf litter in the wild and PVC tubes or aeration filters in the laboratory. Fish hide during the day when visual predators are active. At night, the fish will swim around searching for food and engaging in other behaviors, but they nevertheless are timid about open water and will hide in the refuges available to them. These fish often live in moving water and as a result

there are natural movements, especially oscillations, of objects in the water. The fish have been observed in the wild to maintain their position within these moving objects (E.S. Fortune, personal observation). In the laboratory, we have observed these same patterns of refuge seeking behaviors (Cowan and Fortune, 2007; Roth et al., 2011; Stamper et al., 2012).

In refuge tracking, weakly electric fish maintain their position by swimming both forwards and backwards, using a ventral ribbon fin (Cowan and Fortune, 2007; Roth et al., 2011; Stamper et al., 2012). The refuge tracking behavior is controlled by both visual and electrosensory input (Bastian, 1982; Rose and Canfield, 1993b, a; Rojas and Moller, 2002). It has been suggested that the mechanosensory lateral line system does not contributes much to the control of refuge tracking behavior (Bastian, 1981, 1982, 1987). Early experiments studied side-to-side swimming by the fish in response to a laterally moving plate or series of rods. This behavior was termed the 'following' response (Heiligenberg, 1973; Matsubaraand Heiligenberg, 1978; Bastian, 1987). More recent experiments shifted to having the fish swim within a longitudinally moving refuge, a more natural swimming pattern for the fish (Rose and Canfield, 1993a, b; Cowan and Fortune, 2007; Roth et al., 2011; Stamper et al., 2012).

The longitudinal refuge tracking behavior is particularly well suited for laboratory experiments because it is both reliable and robust; fish will routinely follow a 'shuttle' that moves at a wide array of frequencies and amplitudes for trajectories that can vary in their construction (e.g. single or sum of sines, triangle waves, etc.) (Cowan and Fortune, 2007; Roth et al., 2011). 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 'slip' and moves itself in the same direction as the slip to stabilize the image (Cowan and Fortune, 2007; Roth et al., 2011). When fish track the moving object perfectly, the tracking gain (the ratio of the fish's movement to the movement of the refuge) would be 1 and the phase (how much the fish leads or lags the refuge movement) would be 0 degrees. The ability of fish to track the refuge movement under a variety of sensory conditions will be the topic of Chapter 4.

Dissertation objectives

In the following chapters we examine the role of social behavior and movement on sensing in weakly electric fish. There are three objectives to the thesis. The first is to characterize the differences in electrosensory information when animals are alone compared to when they are in groups (Chapter 2). The second is to examine the behavioral response to a newly described category of electrosensory feedback, called 'envelopes' (Chapter 3). The third is to determine how these fish might use movement as a way to shape electrosensory feedback (Chapter 4).

Chapter 2

In animals with active sensory systems, group size can have dramatic effects on the sensory information available to individuals. In wave-type weakly electric fishes there is a categorical difference in sensory processing between solitary fish and fish in groups: when conspecifics are within about 1 m of each other, the electric fields mix and produce interference patterns that are detected by electroreceptors on each individual. Neural circuits in these animals must therefore process two streams of information – salient

signals from prey items and predators and social signals from nearby conspecifics. We investigated the parameters of social signals in two genera of sympatric weakly electric fishes, *Apteronotus* and *Sternopygus*, in natural habitats of the Napo River valley in Ecuador and in laboratory settings. *Apteronotus* were most commonly found in pairs along the Napo River (47% of observations; maximum group size 4) and produced electrosensory interference at rates of 20 - 300 Hz. In contrast, *Sternopygus* were alone in 80% of observations (maximum group size 2) in the same region of Ecuador. Similar patterns were observed in laboratory experiments: *Apteronotus* were in groups and preferentially approached conspecific-like signals in an electrotaxis experiment whereas *Sternopygus* tended to be solitary and did not approach conspecific-like electrosensory signals. These results demonstrate categorical differences in social electrosensory-related activation of central nervous system circuits that may be related to the evolution of the jamming avoidance response that is used in *Apteronotus* but not *Sternopygus* to increase the frequency of electrosensory interference patterns.

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Chapter 3

Recent studies have shown that CNS neurons in weakly electric fish respond to artificially constructed electrosensory envelopes, but the behavioral relevance of such stimuli remains unclear. Here we investigate the possibility that social context creates

envelopes that drive behavior. When *Eigenmannia virescens* are in groups of three or more, the interactions between their pseudo-sinusoidal electric fields can generate 'social envelopes'. We developed a simple mathematical prediction for how fish might respond to such social envelopes. To test this prediction, we measured the responses of *Eigenmannia* to stimuli consisting of two sinusoids, each outside the range of the Jamming Avoidance Response (JAR), that when mixed with the fish's own electric field produced low-frequency (below 10 Hz) social envelopes. Fish changed their electric organ discharge (EOD) frequency in response to these envelopes, which we have termed the 'Social Envelope Response' (SER). In nearly all trials, the direction of the SER was consistent with the mathematical prediction. The SER was strongest to the lowest initial envelope frequency tested (2 Hz) and depended on stimulus amplitude. The SER almost always resulted in an increase of the envelope frequency during the course of a trial, suggesting that this behavior may be a mechanism for avoiding low frequency social envelopes. Importantly, the direction of the SER was not predicted by the superposition of two JAR responses: the SER was insensitive to the amplitude ratio between the sinusoids used to generate the envelope, but was instead predicted by the sign of the difference of difference frequencies (ddF).

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Chapter 4

Previous work has shown that animals alter their locomotor behavior to increase sensing volumes. However, an animal's own movement also determines the spatial and temporal dynamics of sensory feedback. Because each sensory modality has unique spatiotemporal properties, movement has differential and potentially independent effects on each sensory system. Here we show that weakly electric fish dramatically adjust their locomotor behavior in relation to changes of modality-specific information in a task in which increasing sensory volume is irrelevant. We varied sensory information during a refuge-tracking task by changing illumination (vision) and conductivity (electroreception). The gain between refuge movement stimuli and fish tracking responses was functionally identical across all sensory conditions. However, there was a significant increase in the tracking error in the dark (no visual cues). This increase was a result of spontaneous whole-body oscillations (0.1 to 1 Hz) produced by the fish. These movements were costly: in the dark, fish swam over 3 times further when tracking and produced more net positive mechanical work. The magnitudes of these oscillations increased as electrosensory salience was degraded via increases in conductivity. In addition, tail bending (1.5 to 2.35 Hz), which has been reported to enhance electrosensory perception, occurred only during trials in the dark. These data show that both categories of movements—whole-body oscillations and tail bends—actively shape the spatiotemporal dynamics of electrosensory feedback.

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Chapter 2: Species differences in group size and electrosensory interference in weakly electric fishes: Implications for electrosensory processing

Many animal species have evolved “active sensory” systems in which animals probe their environment with autogenous signals (Nelson and MacIver, 2006). However, these animals are subject to additional sources of sensory interference, particularly from the simultaneously generated signals of nearby conspecifics. Indeed there is often a categorical difference in the sensory milieu between when these animals are alone versus when they are in groups. The size and density of the groups and the specific properties of the signals being used by group members will determine the sensory interference experienced by the animals. The question arises if and how these animals modulate their social and sensing behaviors to avoid detrimental interference.

In ‘wave-type’ weakly electric fish, each individual continuously produces a quasi-sinusoidal electric organ discharge (EOD) at a nearly constant frequency. When two or more individuals come into close proximity, the electric fields interact and produce amplitude and phase modulations, collectively known as "beats” (Heiligenberg, 1991). These beats occur at rates equal to the frequency difference (dF) between the EOD signals of nearby fish: if one fish produces an EOD of 700 Hz and a nearby fish one of 705 Hz, then the beat rate will be 5 Hz. The frequency of these beats is encoded in the patterns of activity of tuberous electroreceptors. Tuberous electroreceptors are specialized organs in the skin of the fish that are tuned to detect features of species-specific electric signals (Heiligenberg, 1991). There is a direct relation between the beat rate and the patterns of resulting neural activity so that, for example, a 5 Hz beat rate induces oscillatory brain activity at 5 Hz, and a 40 Hz beat rate induces activity at 40 Hz. In some

species, 5 Hz beat rates have profound deleterious effects on electrolocation of objects (Heiligenberg, 1973; Bastian, 1987; Heiligenberg, 1991) whereas 40 Hz beat rates may actually enhance certain features of electrosensory perception (Ramcharitar et al., 2006).

These electrosensory beats only occur when fish are in groups of two or more individuals. Thus, social interactions between nearby fish determine the global pattern of electrosensory stimulation and brain activation that these fish experience. "Global" indicates that almost the entire receptor array is simultaneously stimulated, as is the case for the retina when there is a change in ambient lighting (Chacron et al., 2003; Fortune, 2006). In some genera, including *Eigenmannia* and *Apteronotus*, fish can change the frequency of their EOD depending on the beat rate. In this behavior, which is known as the Jamming Avoidance Response (JAR), fish change their EOD frequency to avoid beat rates of less than 15-20 Hz (Bullock et al., 1972; Bullock et al., 1975; Kawasaki, 1996). The combination of social behavior and the JAR behavior largely determines the global electrosensory signals that these fish experience (Fortune, 2006). For *Eigenmannia*, fish in groups typically generate beat rates in the gamma frequency range, between 20 and 80 Hz (Tan et al., 2005).

The frequency range of the beat experienced by a fish depends largely on whether a nearby conspecific is of the same or of the opposite sex, since males and females differ in EOD frequency, even though their frequency ranges usually overlap. In *Sternopygus*, *Eigenmannia*, and in *Apteronotus albifrons* the males produce the lower-frequency EODs (Hopkins, 1972, 1974a, b; Dunlap, 2003), whereas in *A. leptorhynchus* the males produce the higher-frequency EODs (Kirschbaum, 1983; Hagedorn and Heiligenberg, 1985). Therefore, low-frequency beats usually occur in same-sex groupings and high-frequency

beats occur in opposite-sex groupings in all of these species. Further, each genus exhibits distinct behavioral and neural solutions to electrosensory jamming by conspecifics. The JAR in *Apteronotus* appears to be simpler than in *Eigenmannia* (Heiligenberg et al., 1996), and *Sternopygus* do not exhibit JAR behaviors despite the presence of neural circuits similar to those in the other two genera (Bullock et al., 1975; Matsubara, J. and Heiligenberg, W., 1978; Ramcharitar et al., 2006). Rather, *Sternopygus* has a specialized class of neurons in the electrosensory lateral line lobe (ELL) that appears to confer immunity to this sort of detrimental interference (Matsubara, 1981; Matsubara, J.A., 1982).

Building on a previous study of group size and electrosensory interference in *Eigenmannia* (Tan et al., 2005), we set out to better understand the relations between social behavior, the JAR, and electrosensory processing. We examined the patterns of electrosensory signals produced by *Apteronotus* and *Sternopygus* in natural habitats (Napo River valley, Ecuador) and in laboratory experiments. First, we looked at the natural distribution of fish to determine group sizes, EOD frequencies, and beat rates. We also used a naturalistic laboratory setting where fish grouping preferences were observed over several consecutive days. Finally, we conducted electrotaxis experiments in the laboratory to determine if electrosensory information alone may contribute to the observed group sizes.

Materials and Methods

All of the procedures used in this work were approved by the institutional animal care and use committees of the Johns Hopkins University and McGill University and follow the recommendations of Hitchsfeld et al. (Hitschfeld et al., 2009). Field studies were conducted with approval of the Ministerio del Ambiente, the owners of Sacha Lodge, and the Pontificia Universidad Católica del Ecuador. For laboratory studies, adult *Apteronotus leptorhynchus,* and *Sternopygus macrurus* were purchased from various commercial vendors and maintained at 25-29°C in laboratory tanks.

Study sites

Fish were studied in habitats near the Napo River in eastern Ecuador (Figure 2.1). Observations were made over a 3-year period: January of 2007, 2008, and 2009. Recordings of EODs were made in and around Lake Pilchicocha, Orchidea creek, and other streams in the privately held Sacha Lodge reserve, Pañacocha, and along the Tiputini River within the Yasuní National Park near the Estación Cíentifica Yasuní (PUCE). Electrical conductivity of water at each habitat was between 5 and 50 μS/cm (mean = 14.08 ± 7.11). The pH was slightly acidic with a range of 5.7 to 7.0 (mean = 6.28 ± 0.27), and the temperature ranged from 23 to 25.5°C (mean= 24.09 ± 0.57).

Figure 2.1 Map of field study sites
Map of Ecuador showing study site locations (red). Field recordings were made over a three year period in Sacha Lodge, Pañacocha, and Estación Yasuní.

Group behavior in freely moving fish: Napo River Valley

Recordings of electrical activity were made using a custom-made amplifier system (Fortune Laboratory Industries, Baltimore, MD). Differential recordings were obtained from two wire leads, 10 cm apart, mounted on fiberglass rods. Probes were submerged 10–50 cm into the water for each recording. Signals were captured using consumer MP3 encoders (Creative MuVo N200). EODs could be detected up to about 1.5 m from the recording probe. Thus, all of the fish that were recorded were within a 1.5 meter sphere, and likely much closer together than this distance. The 1.5 meter distance assumes the ideal orientation of the fish relative to the recording electrodes such that the electrodes were perpendicular to the isopotential lines. However, it is unlikely that most fish were at the ideal orientation for any sustained period, and thus the maximum distance for detection was less than 1.5 meters. Indeed, fish routinely briefly disappeared from the recordings, presumably because the animal aligned an isopotential line with the recording electrodes.

Recorded samples (N = 2214) were 60 s in duration and were taken in a wide variety of locations in all habitats where the fish were encountered. For each location, multiple samples were recorded, and as such, it is not possible to establish if each recorded EOD represents a unique fish. For this reason, data is presented descriptively as frequency counts of recorded observations, and no assumption of sampling independence is made.

It was common to record several species of fish (Figure 2.2A), identified by their distinct EOD frequency ranges (Crampton and Albert, 2006), within a single recording (color-coded Y-axis; figures shows 15 s segment of recording). From the collected samples, a reduced set (N=1107) contained species of the genera of interest: *Eigenmannia, Apteronotus, and Sternopygus*. The majority of the samples contained a single species of fish (n = 523, 47.24%) or two species of fish (n = 507, 45.80%) but there were some recording sites where all three species (n = 77, 6.96%) were simultaneously present (Figure 2B).

Group behavior in freely moving fish: Laboratory

The procedures for the group-size experiment were similar to those used in Tan et al. (Tan et al., 2005). The experimental arena was a large round plastic tub (diameter = 1.5 m, depth = 0.5 m) filled halfway with water with conductivity of approximately 250 μS/cm (range: 50 μS/cm - 600 μS/cm). This conductivity range limits the effective size of each fish's electric field thereby increasing the electrical isolation between the four refuges, which were placed along the perimeter of the tub. Conductivity can affect behavior in weakly electric fishes (Hagedorn, 1986; MacIver et al., 2001): a systematic

study of the effects of conductivity was not attempted. The temperature was maintained between 25 and 28°C.

The four refuges, one in each quadrant of the tub (see Figure1 in Tan et al. (Tan et al., 2005)), were 20 cm square plastic sheets that rested on the bottom of the tub that contained an array of black plastic rods (10 cm tall, 3 mm diameter) separated by a spacing of 2 cm. These refuges can be seen as a form of artificial reed grass habitat. Fish could also squeeze between the base of the refuge and the substrate. Each refuge was equipped with a bubbler and one pair of recording electrodes.

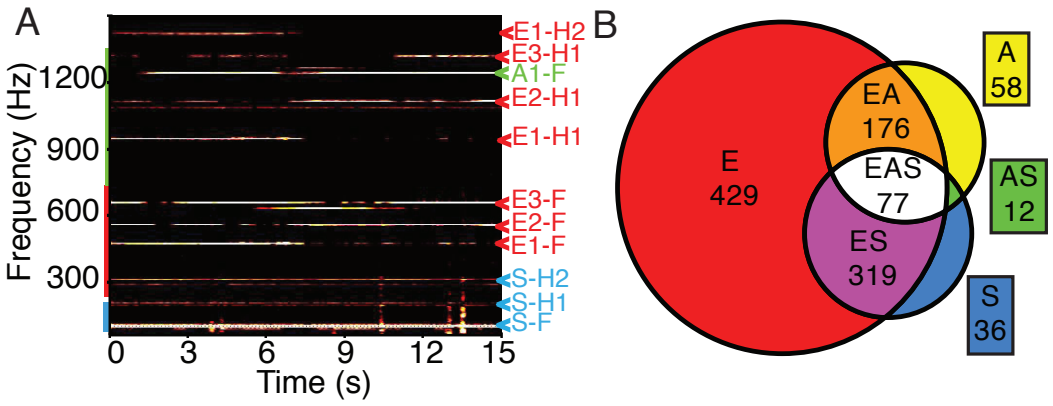

Figure 2.2 Sample of EOD recording and distribution of species
(**A**) A sonogram of a recording showing EOD frequency over time for three species of electric fish: *Apteronotus* (green), *Sternopygus* (blue) and *Eigenmannia* (red). The frequency range of each species is color-coded on the Y-axis (left). The fundamental frequency (F) of each fish is indicated (arrow) as well as all visible harmonics (H). (**B**) A Venn diagram showing the distribution of species across samples that contained at least one *Eigenmannia* (E), *Apteronotus* (A) or *Sternopygus* (S). In many cases, multiple species of fish were present, including 77 samples where all three species of fish were present in the recording. The sizes of the regions of the Venn diagram are mathematical approximations.

For each experiment, four adult fish were taken from different tanks in the laboratory. It is possible that the fish in a trial may have been in the same laboratory tank at some point before the experiment, and the fish could very likely have shared the same bag during their original shipment to the laboratory. Immediately prior to the experiment, however, the fish had been in separate tanks for at least one week. The selection of fish was randomized: we did not systematically manipulate sex ratios of fish in trials. The sex of individuals was assessed by visual inspection and by frequency of the EOD, neither of which are 100% reliable indicators (Hagedorn, 1986; Zakon et al., 1991; Bastian et al., 2001). For this comparative experiment we did not focus on issues related to sex and reproductive behavior; rather we focused on general issues of the electrosensory environment that are likely common to all individuals in a given species. The animals did not reproduce during the experiments and were likely not in reproductive state. Certainly, future studies will need to address the dramatic changes in behavior that can accompany reproductive state.

We used four fish in the experimental tub to match the number of available refuges: individual fish could potentially be alone at their own refuge at all times. Each experimental trial was conducted for a minimum of 10 days at a 12L:12D light cycle. Fish were allowed to acclimate to the new environment for the first two days of each experiment. Five-second duration recordings of EODs at each refuge were taken every 30 minutes throughout each experiment after the initial acclimation period. Visual observations were routinely made and compared with the automatically-collected behavioral data. Once observations were made for the trial length (minimum of 10 days), the fish were removed and returned to holding tanks in the facility.

The EODs of *Apteronotus* and *Sternopygus* are nearly sinusoidal, and individual fish can be identified on the basis of their EOD frequencies. Recordings were plotted as sonograms using a custom-written software package that allows very long sample windows (16384 points or more) and window overlap (95%). Frequency resolution was 1 Hz. EOD frequency differences of less than 1 Hz could be detected by amplitude modulations of the individual EODs, but this situation was rare. Because each EOD frequency is associated with a single fish, the number of EOD frequencies in a recording indicates the number of fish near the recording electrodes.

We characterized the global electrosensory signal that each nearby fish was exposed to by measuring the dFs between EODs. dFs were calculated by measuring the EOD frequency of each fish in the group: the dFs in a group are the differences in frequencies between each pair of fish. Each dF represents an ongoing beat rate, so that 2 fish produce a single ongoing beat rate that occurs at a frequency equal to the difference between the EOD frequencies of the two fish. In groups of 3 fish, there are 3 simultaneous ongoing beat rates – the difference in frequency between fishes 1 and 2, 2 and 3, and 1 and 3. For groups of 4 fish, there are 6 simultaneous beat rates: 1-2, 2-3, 3-4, 1-3, 2-4, 1-4. In addition, there can be emergent AMs that occur in the envelope of the combined signal (see Discussion). The central goals of these grouping experiments was to 1) determine whether or not fish commonly experience ongoing, global, synchronous patterns of electrosensory interference that result from the interaction of the electric fields of nearby conspecifics and 2) characterize the frequencies of electrosensory interference that occurred when the fish were found in groups.

Electrotaxis to conspecific-like signals

To determine the immediate preference of fish for refuges with interfering conspecific signals or no signals, we used a two-choice test. This experiment relies on the fact that fish prefer to hide at refuges during daylight (Dunlap and Oliveri, 2002; Cowan and Fortune, 2007). In this experiment, two refuges were provided, one with an artificial conspecific-like signal and the other with no signal. For all experiments, we used two refuges in the same large tub as in the experiment above.

The artificial conspecific-like signal was created from a previously recorded sample EOD. This recording of the conspecific EOD was made about 1 meter from the fish using differential electrodes spaced by 10 cm. Two cycles of the EOD signal were cut and uploaded to an arbitrary waveform generator (Model #4070, BK Precision, Yorba Linda, CA). The signal generator reproduced the signal at user-defined frequencies. In each trial, a conspecific signal was delivered through one set of the electrodes in one of the two refuges in the tub. Location of signals was randomized between trials.

The outcome of each trial, not the mechanism by which the animals approached the refuges, was measured in these experiments. These experiments differ, therefore, from previous work on electrotaxis (Schluger and Hopkins, 1987; Davis and Hopkins, 1988; Shieh et al., 1996; Hopkins et al., 1997), where the paths of swimming fish in tanks with particular electrosensory stimuli were recorded.

Prior to each trial, the EOD frequency of the test fish was recorded and measured. The artificial signal was then adjusted to be either within 10 Hz of the fish's EOD (potentially JAR-eliciting), or between 20 and 50 Hz of its EOD frequency (not JAR-eliciting). Both positive and negative dFs were used (i.e. + 20 Hz and – 20 Hz). For this

experiment we did not exhaustively examine the effects of stimulus frequency on electrotaxis behavior. Rather, we wanted to determine if there were clear differences in electrotaxis between the two genera.

The signal was adjusted to match the amplitude of a conspecific, and continuously produced in the tub prior to the introduction of the fish and throughout the test. The frequency of the signal was not changed during a given trial. For each trial, the fish was gently released near the center of the tub. Fish were allowed to swim freely. The electric fields at both refuges were recorded while the fish was in the tub. Trials in this arena ended when the fish remained at a refuge for more than 1 minute, which typically occurred in less than 5 minutes after the fish was introduced into the tub.

Results

Group behavior of fish in the Napo river valley, Ecuador

Animals were commonly found in multispecies flocks including *Eigenmannia*, *Apteronotus*, and *Sternopygus* (Figure 2.2). In addition, we commonly observed the EODs of pulse-type (emit short electrical pulses with relatively long inter-pulse intervals) fish in these same recordings. The most common pulse-type fishes in this area appear to be *Brachyhypopomus* and *Gymnotus*. Here we examine the social behavior of *Apteronotus* and *Sternopygus*. The social behavior of *Eigenmannia* in these areas have been reported previously (Tan et al., 2005).

Apteronotus: Apteronotus were found in root systems, leaf litter, and large debris, particularly around larger fallen trees. Based on visual inspection of fish that were

captured, the species of *Apternotus* found at the study sites were not *leptorhynchus* or *albifrons* or any previously described species to our knowledge. In behavioral tests these animals exhibited an up-only JAR and chirp behaviors that are most similar to *Apteronotus leptorhynchus* (Zakon, 1986).

The distribution of group sizes (Figure 2.3A) shows that most observations (172 individuals = 172 fish) contained a single *Apteronotus*. However, fish were also commonly observed in pairs (103 pairs = 206 fish). Thus, when analyzed not as the total number of samples, but as the total number of individuals, more *Apteronotus* were found in pairs than alone. Groups of three (16 triplets = 48 fish) and four (2 groups = 8 fish) fish were also observed, but not greater. It was found that these fish experience dFs (Figure 2.3B) between 20-300 Hz when in pairs (mean ± SD = 105.89 Hz ±75.99 Hz; black bars) and 20-240 Hz when in triplets (mean = 112.58 ±75.62; grey bars). For all observed fish, in either a pair or a triplet, the recorded dFs were predominately (91.55%) greater than 20 Hz.

The EOD frequency distribution for *Apteronotus* was bimodal (Figure 2.3C, black line). The bimodal distribution was also observed when fish were separated by group size. Fish across the same frequency range were found either alone (dashed line), in pairs (dotted line), or triplets (dashed-dotted line). EOD frequency has been reported to be sexually dimorphic in *Apteronotus* species, although which sex occupies the high frequency range and which the low frequency range appears to differ from species to species (Kirschbaum, 1983; Hagedorn and Heiligenberg, 1985; Dunlap, 2003). Therefore, the two peaks of the EOD frequency distribution likely represent the two sexes, although we can not be sure which peak corresponded to which sex. To categorize the sex of the

recorded fish we operationally defined EOD frequencies below 1050 Hz as sex 1 and frequencies above 1050 Hz as sex 2 based on the observed bimodal distribution. When we analyzed group size according to the frequency-predicted sex of individual fish we found that most pairs (53.78%) were between a male and female, whereas there were fewer female-only and male-only pairings (33.96% sex 1 pairings and 12.26% sex 2 pairings).

We observed occasional rapid modulations of EOD frequency that resembled Type II (15-20 ms in duration, 50-100 Hz frequency excursion) and Type I chirps (shorter in duration, longer frequency excursion) (Engler and Zupanc, 2001; Hupe and Lewis, 2008). We observed Type I and Type II chirps in both solitary fish and fish in groups. Based on the few number of observed chirps recorded, there was no significant correlation between chirp type and estimated sex of the animal, based on EOD frequency classification.

Sternopygus: Sternopygus macrurus were found in roots, holes and trunks and sandy bottom streams but not in substrate debris. *Sternopygus* were most commonly found alone (266 individuals = 266 fish) but were occasionally found in pairs (36 pairs = 72 fish) and never observed in groups of 3 or more conspecifics (Figure 2.3D). When analyzed as the total number of individuals, *Sternopygus* were most often found alone (Figure 2.3D, grey line). For fish in pairs, beat rates (Figure 2.3E) of between 20 Hz and 240 Hz were observed (Mean = 74.25 Hz; SD = 47.66 Hz).

The EOD distribution for *Sternopygus* was bimodal with peaks at 50 Hz and 200 Hz (Figure 2.3F). As has been reported previously (Hopkins, 1972), in *Sternopygus*

females generally have higher EOD frequencies than males. We operationally defined EOD frequencies below 150 Hz as male and frequencies above 150 Hz as female. We found that most pairs (51%) were between males only, whereas there were fewer mixed sex (44%) and female only (5%) pairings.

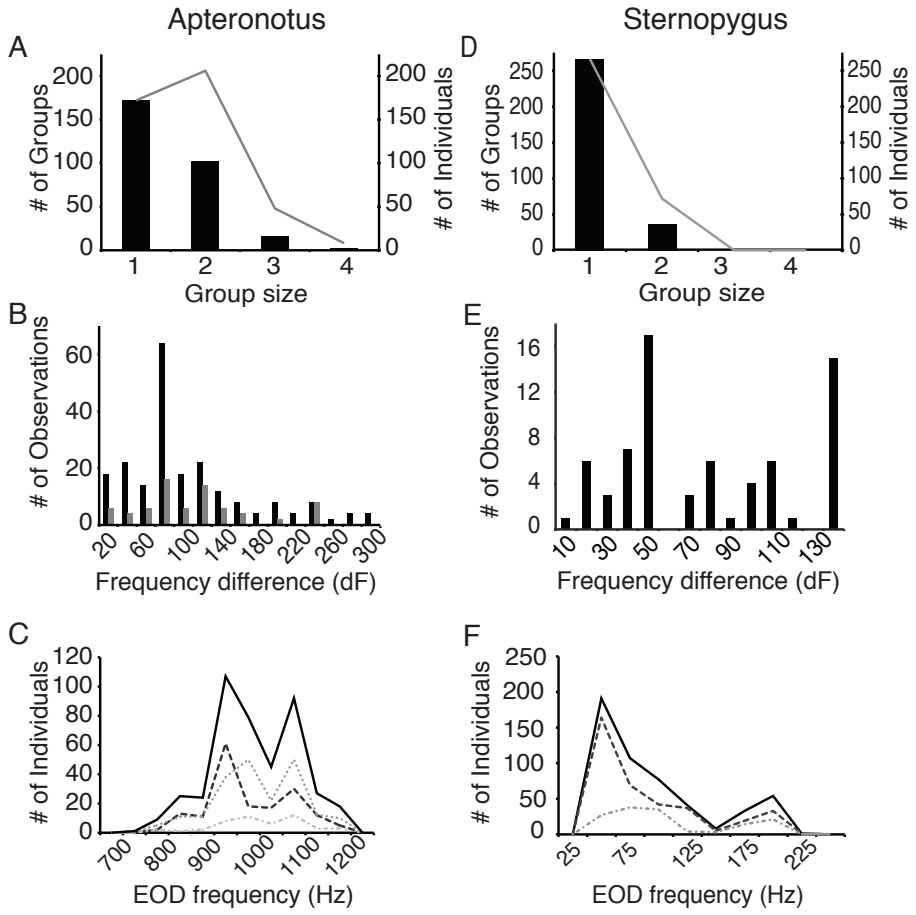

Figure 2.3 Grouping and electrosensory information in field recordings
(**A**) The # of samples by group size (bars) and the total # of fish in each group size (lines). More individual *Apteronotus* were found in groups of two or more conspecifics than alone. (**B**) dFs between individual *Apteronotus* in groups ranged from 20 to 300 Hz (black: one dF per pair; grey: three dFs per group). (**C**) The distribution of EOD frequencies of *Apteronotus* was bimodal and presumably corresponded to animals of the two sexes. (**D**) *Sternopygus* were commonly found alone – the majority of samples (bars) and majority of individual *Sternopygus* (lines) show the same pattern (**E**) dFs ranged from 10 to 140 Hz. (**F**) The distribution of frequencies was bimodal and corresponded to females (higher frequencies) and males (lower frequencies).

Group sizes in freely-moving fish: Laboratory

Apteronotus leptorhychus: Fish could be identified using their individual-specific EOD frequency as there were no significant changes in the differences in EOD frequencies from start to end of the trials (Chi Square, $p>0.05$, $N=10$). During daylight hours, *Apteronotus* commonly wedged themselves underneath the refuges. The refuges rested on the bottom of the tub and were held down with gravel, but fish could nevertheless squeeze under them. Fish found underneath refuges were on their sides between the refuge and the bottom of the tub. The fish were generally motionless in this condition, and were most commonly located within 5 to 10 cm of conspecifics. At night the fish were observed swimming in all areas of the arena, but most commonly around the edges of the tub or near the refuges.

For *Apteronotus* we ran 10 trials but the total number of recorded observations within each trial differed due to differences in total observation time ($N_1 = 1536$, $N_2 = 932$, $N_3 = 1720$, $N_4 = 1838$, $N_5 = 822$, $N_6 = 1150$, $N_7 = 775$, $N_8 = 1313$, $N_9 = 1252$, $N_{10} = 909$). We measured the total number of fish that were alone and the total number of fish that were in groups (2-4 fish). Because the sample size was variable across trials, each total was weighted according to the number of samples observed for that trial. After weighting the values, an overall mean number of observations was computed for the total number of fish alone (Mean = 468.48; SD = 27.14) and the total number of fish in groups (Mean = 860.92; SD = 70.62). It should be noted that the samples that make up a trial are not independent, and a non-parametric statistic is used for the analysis because it does not make assumptions about the underlying distribution. *Apteronotus* were more likely to be

observed in groups than alone (Figure 2.4A). A Wilcoxon signed ranked test indicated that this was a significant preference ($p = 0.037$).

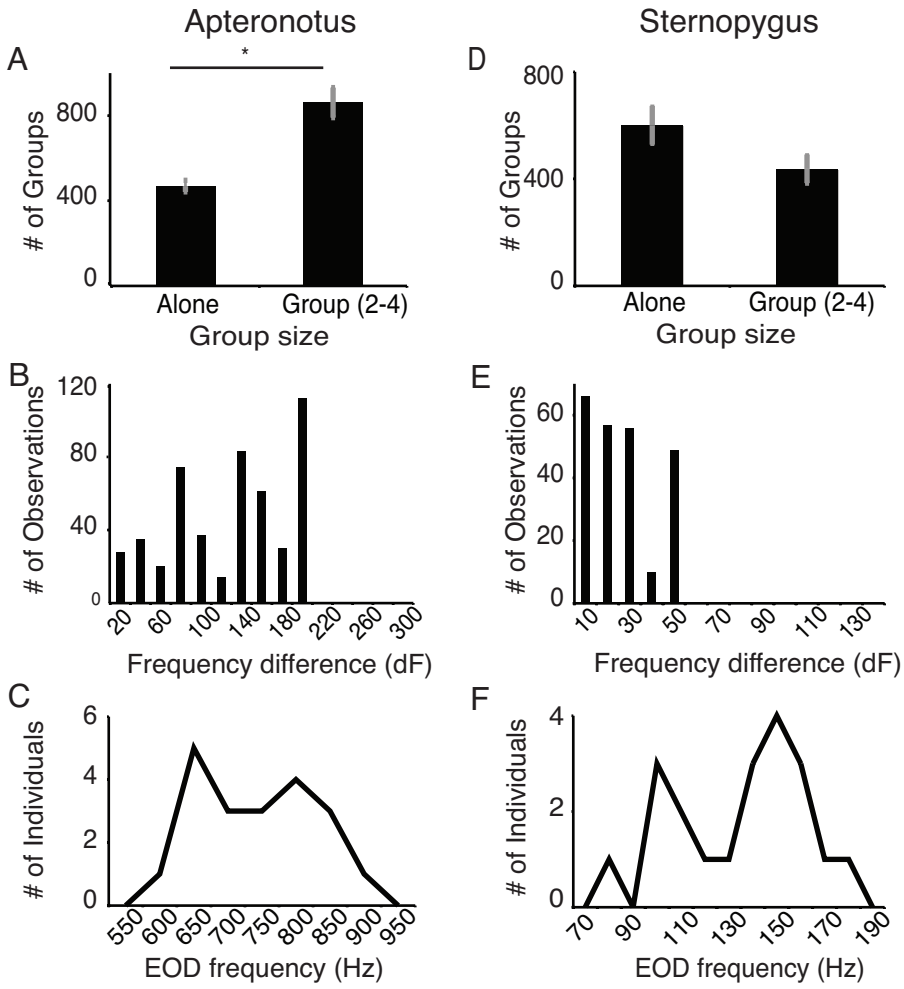

Figure 2.4 Grouping and electrosensory information in the laboratory
(**A**) *Apteronotus* were significantly more likely to be found in groups of 2-4 individuals within a refuge. (**B**) There were frequency differences between 20 and 200 Hz. (**C**) The distribution of frequencies was bimodal and corresponded to males (higher frequencies) and females (lower frequencies). (**D**) *Sternopygus* showed a trend to be solitary. (**E**) When in pairs there were frequency differences between 10 and 50 Hz. (**F**) The distribution of frequencies was bimodal and corresponded to females (higher frequencies) and males (lower frequencies).

More detailed frequency analysis was performed on a subset of observations across 5 trials (N = 2037) to examine individual preferences for grouping amongst the fish. For *Apteronotus* in pairs (N=494, Figure 2.4B) dF ranged from 20-200 Hz. The frequency distribution of individual fish was bimodal (Figure 2.4C). In the lab, we found that most pairs (60%) were mixed sex and there were fewer female only (27%) and male only (13%) pairs.

During the experiments, some *Apteronotus* made social signals known as chirps (Zakon et al., 2002). Only type II chirps were observed and occurred in both solitary fish and fish in groups. Males produced chirps (N = 46) roughly evenly across social situations: 26% of chirps were observed in solitary fish, 23% were with other males, 23% were with females, and 26% were with both males and females. Females chirped about half as frequently (N=21) and preferentially produced chirps when near males (52%). Of the remaining chirps, 29% were produced by solitary females and 18% of chirps were produced in groups of females. It is important to note that these data were obtained after the fish spent at least two days together - fish are known to chirp vigorously during initial contact (Zakon et al., 2002).

Sternopygus macurus: Fish were identified using their individual-specific EOD frequencies. There was no significant change in the differences in frequencies between fish from the start to end of the trials (Chi Square, $p>0.05$, N=7). *Sternopygus* were commonly observed between the refuge and the wall of the tub, or within the refuge posts during daylight. The fish were largely motionless, with the ventral fin touching the bottom of the tub or refuge. At night, fish were observed swimming throughout the tub.

For *Sternopygus* we ran 7 trials that differed in the number of observations within a trial due to changes in testing length (N_1 = 360, N_2 = 584, N_3 = 960, N_4 = 1230, N_5 = 446, N_6 = 1436, N_7 = 1073). We measured the total number of fish that were alone and the total number of fish that were in groups (2-4 fish). Because the sample size was variable across trials, each total was weighted according to the number of samples collected for that trial. After weighting the values, an overall mean number of observations were computed for the total number of fish alone (Mean = 600.52; SD = 72.48) and the total number of fish in groups (Mean = 437.00; SD = 53.48). *Sternopygus* were most commonly observed alone rather than in groups (Figure 2.4D), but a Wilcoxon signed ranked test indicated that there was no statistically significant difference between the preferences of fish to be alone versus in groups ($p = 0.30$).

A more detailed analysis was performed on a subset of the data (N = 1108). For *Sternopygus* in pairs (N = 262; Figure 2.4B), we found differences in EOD frequencies between 10 and 50 Hz. The frequency distribution of individual fish was bimodal (Figure 3F). In the lab, we found that most pairs (43%) were mixed sex and there were fewer female only (37%) and male only (20%).

We did not observe any chirps during the laboratory experiments with *Sternopygus*.

Envelopes in Apteronotus

Groups with three or more individuals can produce not only beat rates that are equal to the differences in frequencies between each of the fish, but there can be emergent patterns of amplitude modulations that can be detected in the envelope of the

combined signal from the fish (Middleton et al., 2006). For example, take a group of two fish that have a dF of 50 Hz and add a third fish that is, for example, 40 Hz above the higher of the two original fish. The resulting signal would have the original 50Hz dF, but would also add dFs at 40 Hz and 90 Hz. A second-order amplitude modulation can be extracted by applying a Hilbert transform to the envelope of the signal (Middleton et al., 2006) of the three fish: in this example one observes an emergent 10 Hz envelope at the difference of the difference frequencies (ddF). Do *Apteronotus* in groups of three or more fish produce these low-frequency envelopes? The answer is no: in over 10 groups in the wild in which the signals could be analyzed for this phenomenon and in over 20 measurements in 5 groups of fish in the laboratory, we never found low-frequency (less than the lowest dF, or about 15 Hz) power in the envelope of the signal (Figure 2.5).

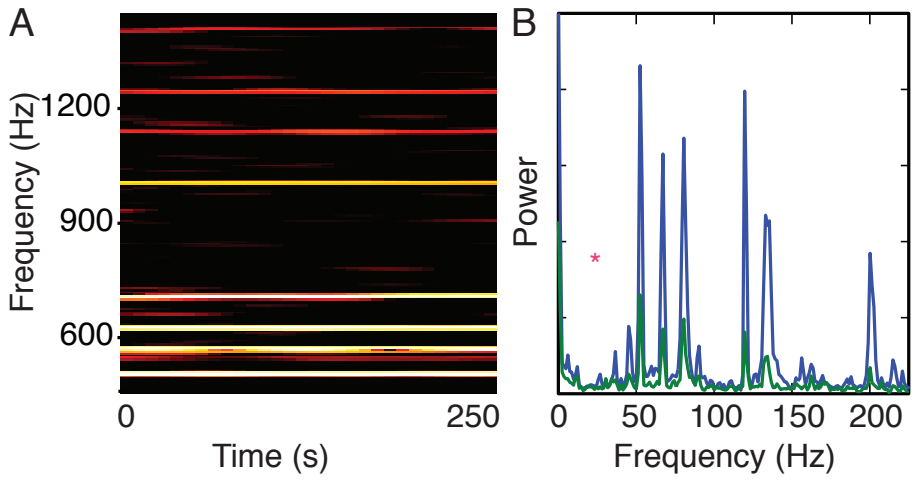

Figure 2.5 Amplitude envelopes in groups of *Apteronotus leptorhynchus*.
(**A**) Sonogram of four EODs at a single refuge. The four bands around 600 Hz are the fundamental frequencies and the bands around 1200 Hz are harmonics. (**B**) Power Spectral Density plot of the absolute value of the Hilbert transform of the original signal (blue) with peaks corresponding to the expected 6 dFs. The envelope is extracted by applying another Hilbert transform (green). The power at the 6 dFs is reduced and there is significant power near zero due to the relative movements but no significant power at the ddF.

Electrotaxis to conspecific signals

Apteronotus. Within two minutes all *Apteronotus* (N=10) swam to the refuge with the social signal (Figure 2.6) yielding a statistically significant preference for the conspecific-like signal (Chi Square test, $p<0.05$, N=10). The trials were evenly divided between the two refuges – fish showed no preference for either refuge (Chi Square test, $p>0.05$, N=10). These animals preferred the conspecific signal even when a JAR was elicited by it.

Sternopygus. In contrast to *Apteronotus*, *Sternopygus (N=20)* showed no preference for conspecific-like signals (Chi Square test, $p>0.05$, N=18). Eight fish went to the refuge with the conspecific signal, while ten did not. Two fish stopped moving at locations along the edge of the tub that were remote to both refuges and were not used in the analysis.

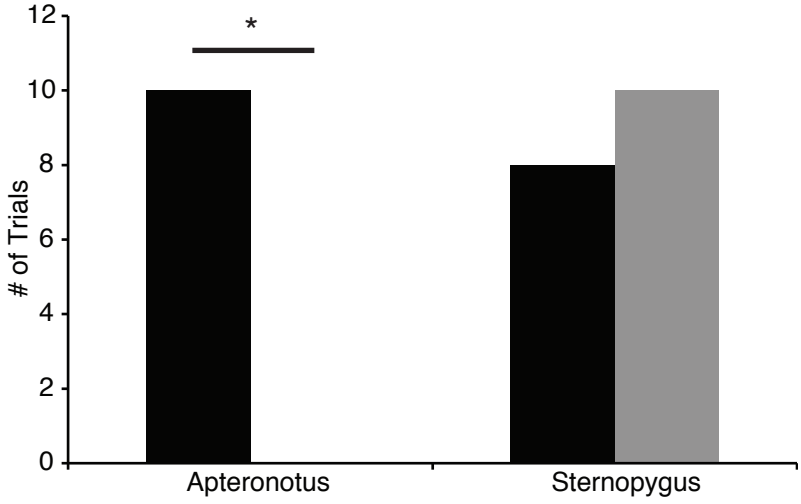

Figure 2.6 Behavioral response to refuge choice test
Apteronotus preferentially approached the refuge with the artificial conspecific signal whereas *Sternopygus* did not. The asterisk indicates a statistically significant difference ($p<0.05$).

Discussion

There is a categorical difference in electrosensory stimulation when wave-type weakly electric fish are near conspecifics versus when fish are alone. Because these animals are continuously producing electric fields, social interactions necessarily result in emergent electrosensory interference patterns similar to those produced by adding sinewaves together. Fish in groups experience ongoing global stimulation at rates equal to, for wave-type species, the difference in EOD frequencies between nearby individuals whereas solitary fish do not. *Apteronotus,* which exhibit JAR behavior, were most commonly found in groups (2-3 individuals) and preferentially approached conspecific signals. In contrast, *Sternopygus*, a genus that is immune to the deleterious effects of nearby conspecific signals and does not exhibit a JAR behavior (Bullock et al., 1975; Matsubara, J. and Heiligenberg, W., 1978; Rose and Canfield, 1993b), preferred to remain alone and did not preferentially approach conspecific signals. Previous data showed that *Eigenmannia* are also found in groups (up to 15 or more individuals) and will also approach a conspecific signal. This raises the possibility that there is a relationship between social group formation and size and the complexity of each species Jamming Avoidance Response. The combination of the JAR and grouping in these fish may be an adaptation for the production of socially-derived gamma band oscillation in CNS circuits (Ramcharitar et al., 2005; Tan et al., 2005).

Electric fish form multispecies flocks

In the field we found that all three species of wave-type weakly electric fishes (*Apteronotus, Eigenmannia, Sternopygus*) were encountered in close proximity, within

1.5 meter diameter. In addition, we routinely observed pulse-type weakly electric fish at the same time. Multispecies flocks occur known to occur in many groups of animals, including psittacine birds (Seibert, 2008) and new world primates (Chapman and Chapman, 1996) just to name two. Typically multispecies flocks occur in areas with limited resources, or as a mechanism for reducing predation risk. Identifying the resources available at these sites may give clues both for the biology of these animals and for conservation.

Species differences in social behavior

Wave-type Gymnotiform species exhibit a diversity of social behavior. Previous research has shown that *Eigenmannia* are typically found in groups both in the laboratory and in the wild (Lismann, 1961; Oestreich and Zakon, 2005; Tan et al., 2005). *Apteronotus* preferentially hide within refuges (Dunlap and Oliveri, 2002; Oestreich and Zakon, 2005) and appear to be more aggressive towards conspecifics (Hopkins et al., 1997; Triefenbach and Zakon, 2008). *Sternopygus*, which does not exhibit a JAR, appears to be the least social wave-type gymnotiform fish studied to date. We have observed that *Sternopygus* near the Napo River in eastern Ecuador can be solitary; individuals have been found spread meters away from conspecifics along small (1 - 2 meters wide), shallow waterways.

Of course, many other non-electrosensory factors contribute to both ongoing social behavior and the evolution of differences in social behavior in *Apteronotus* and other Gymnotiform species. The electrotaxis experiments, in which the only difference between refuges was the presence of an artificially generated electric signal, suggest that,

at least on the order of minutes, electrosensory information does contribute to species differences in grouping. Electrotaxis is known to occur in these species for other electrosensory signals, and indeed Gymnotiform fishes will follow electric current lines (Schluger and Hopkins, 1987; Davis and Hopkins, 1988; Shieh et al., 1996; Hopkins et al., 1997).

Mormyriform fishes, an independently evolved group of electric fish in Africa, also exhibit marked differences in social behaviors that may be related to electrosensory perception. In the wild, *Gymnarchus niloticus* have been observed in groups of two or more fish, maintaining frequency differences of about 4 Hz (Moller et al., 1976). Additionally, field recordings of *Marcusenius cyprinoides* indicate that these fish are typically found in schools (Moller et al., 1976). This grouping behavior appears to be mediated by electrical sense.

Hunting behavior has also been observed to be a behavioral consequence of electrical signal changes in *Mormyrops anguilloides* (Arnegard and Carlson, 2005). These fish appeared to maintain packs of 2-10 fish during the day and night for weeks, traveling and hunting with conspecifics. Grouping in Mormyrops appears to increase the hunting success. The EODs of fish in these groups are phase locked at a set delay to one another, which is known as the echo response – a jamming avoidance strategy. This behavioral response allows fish to maintain groups without impairing any fish's ability to electrolocate. More importantly, synchronous bursting through the echo response may serve as a cohesion signal to maintain grouping behavior and its benefits (Arnegard and Carlson, 2005).

Computational consequences

The JAR is only one possible way that fish can avoid detrimental interference from nearby conspecific fish. Weakly electric fish could simply move away from one another instead of experiencing the electric fields of other conspecifics. Another possible solution is found in *Sternopygus*. Jamming signals do not impair the ability of these fish to electrolocate (Rose and Canfield, 1993b). Instead, *Sternopygus* have a unique cell type, Type III cells, in the ELL that allow responses to moving objects while also conferring immunity to the jamming by nearby conspecifics (Matsubara, 1982). Why, then, do fish perform the JAR behavior in light of these alternative solutions?

The answer may relate to the effects of the JAR behavior on computations in the nervous system. An important consequence of the JAR behavior is non-detrimental global 20 – 50 Hz oscillations that each nearby fish experiences (Bullock et al., 1972). Gamma band oscillations are commonly generated by neural networks at all levels of CNS processing, and are found in a vast array of animal species (Bullock and Achimowicz, 1994). In electric fish, the CNS oscillations are identical to those found in other systems, except that they are generated externally. What function might these oscillations have in electric fish?

In humans, externally generated somatosensory vibrations at frequencies below 100 Hz can enhance sensorimotor performance (Priplata et al., 2003). In *Eigenmannia* and presumably *Apteronotus* and *Sternopygus*, global oscillations in this same frequency range preferentially elicit short-term synaptic depression in midbrain electrosensory neurons (Rose and Fortune, 1999b; Fortune and Rose, 2000, 2001), which may serve as a mechanism for direction selectivity (Chance et al., 1998; Fortune and Rose, 2000;

Fortune, 2006). Through short-term synaptic depression, these oscillations change the efficacy of the synapses such that the neuronal responses are different when fishes are alone versus when they are experiencing the fields of conspecifics. Thus, the transfer function of certain midbrain synapses will differ depending on whether the fish is in a group or alone (Ramcharitar et al., 2006). This synaptic depression does not appear to attenuate the responses of midbrain electrosensory neurons to sensory objects in *Eigenmannia* (Ramcharitar et al., 2005). Rather, post-JAR signals appear to enhance motion processing in midbrain neurons by increasing direction selectivity (Ramcharitar et al., 2006).

Further, in *Apteronotus*, neurons in the ELL exhibit distinct response properties that vary depending on the sensory stimuli (Matsubara and Heiligenberg, 1978). Filtering of information in these neurons appears to be dependent on the spatial presentation of behaviorally-relevant information (Chacron et al., 2003). Under local, prey-like, stimulation, neurons preferentially pass low-frequency information. Global stimulation, such as 20 – 50 Hz oscillations, elicits the passing of high-frequency information by these neurons. Thus, these ELL neurons are able to send both the global socially-derived oscillations and the local changes caused by sensory objects to higher midbrain neurons for processing. Perhaps the concomitant global and local stimulation leads to changes in how salient moving information is perceived.

Finally, it is interesting that groups of three or more *Apteronotus* did not generate low-frequency power in the envelope of the electric signal because Middleton et al. (Middleton et al., 2006) described neurons that respond robustly to this information. It is possible, therefore, that these neurons mediate a more subtle form of the JAR that avoids

low-frequency envelopes. Additional behavioral experiments are necessary to confirm this hypothesis (see Chapter 3).

Evolution of the JAR

The JAR is presumed to have evolved as a mechanism to reduce detrimental electrosensory interference when conspecifics are in groups. Indeed, in recordings of natural habitats we found very few *Apteronotus* or *Eigenmannia* with dFs less than 20 Hz. This likely suggests that the fish in groups may have performed the JAR, thus maintaining higher dFs. In contrast, *Sternopygus*, which does not have a JAR, were found with dFs less than 10 Hz.

These data suggest an intriguing alternative hypothesis: perhaps the JAR evolved as a mechanism to generate ongoing higher-frequency oscillations in central circuits (Tan et al., 2005). Such oscillations are known to enhance features of electrosensory processing in midbrain neurons via the activation of short-term synaptic plasticity (Ramcharitar et al., 2006), are correlated with cognitive functions in human and primate cerebral cortex, and may enhance sensory perception. This JAR mechanism may therefore result in enhanced electrosensory perception of objects via the production of gamma band oscillations in brain circuits via electrosensory stimulation. Such an enhancement of electrosensory function could be used in several salient behaviors including prey capture (MacIver et al., 2001), avoidance of predators, and refuge tracking (Cowan and Fortune, 2007). Thus the JAR would enhance electroreception in two ways, first by avoiding detrimental interference and second, by enhancing direction selectivity in midbrain neurons.

Chapter 3: Beyond the Jamming Avoidance Response: *Eigenmannia* respond to the envelope of social electrosensory signals

Weakly electric fish generate an electric organ discharge (EOD) that results in an electric field that surrounds the fish's body. In *Eigenmannia* the EOD is quasi-sinusoidal and when fish are in close proximity (about 1 meter or less) their EODs interact. In the case of two nearby conspecifics the combined EOD signal has a modulation, termed the amplitude modulation (AM). If there are more than two nearby conspecifics, or relative movements between conspecifics, the combined EOD signal contains modulations of the AM, which has been termed the electrosensory envelope (Middleton et al., 2006).

The interactions of two EODs have been well studied in relation to the Jamming Avoidance Response (JAR). When two nearby conspecifics have EODs S1 and S2 at frequencies of F1 and F2 respectively, the combined signal, S1+S2, has an emergent AM. The AM frequency is at the frequency difference, |dF|, where dF = F2-F1. When two neighboring *Eigenmannia* have EODs of similar frequency (e.g. 500 and 505 Hz, with |dF| = 5 Hz) they perform the JAR, during which each fish will raise or lower their individual EOD to increase the magnitude of the dF, and thus the AM frequency. In the previous example the fish with the higher frequency would raise its EOD (e.g. from 505 to 515 Hz) and the fish with the lower frequency would decrease its EOD frequency (e.g. from 500 to 490) such that the AM frequency, |dF|, was increased (in this example from 5 to 25 Hz).

When there are three or more EOD signals it is possible that fish are responding not only to the AM but also the emergent electrosensory envelope. Here we define a 'social envelope' as the modulation of the AM that occurs when three EODs are added.

For example, if there are three EODs, S1, S2, and S3, at frequencies F1, F2, and F3, respectively, the combined signal, S1 + S2 + S3, can have an emergent AM and envelope (Figure 1A). Thus, it is possible that even with high-frequency dFs that there would be a low-frequency envelope (as shown in Figure 1).

Understanding the behavioral relevance and sensory processing of envelope information has proven challenging in part because the extraction of envelope information requires nonlinear processing (e.g. rectification with low-pass filtering, Hilbert transform; Figure 1B) (Middleton et al., 2006; Savard et al., 2011; McGillivray et al., 2012a) because a linear analysis of the signal (e.g. Fourier transform) will not reveal power at the envelope frequency.

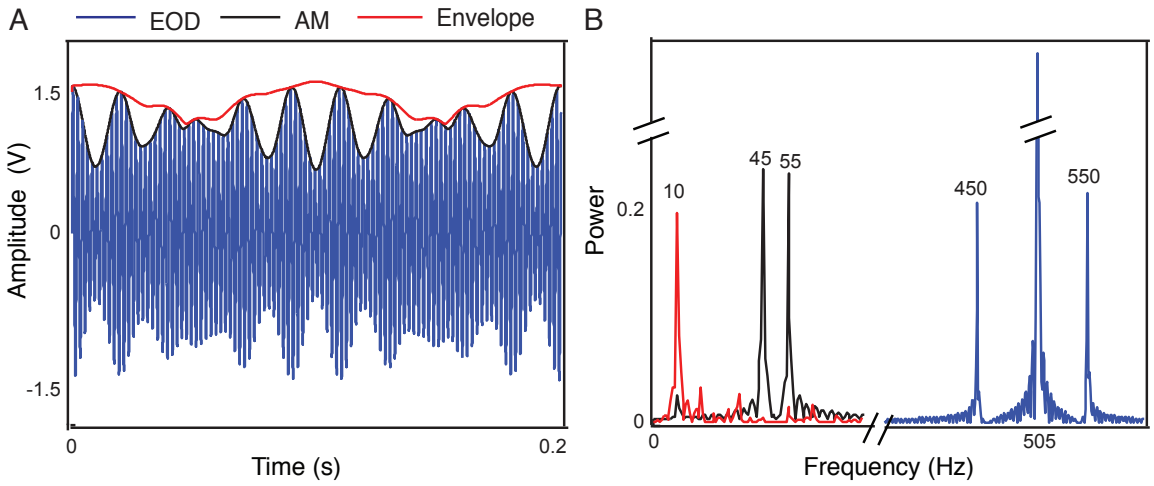

Figure 3.1 Social electrosensory envelopes
(**A**) A signal comprising three sinusoids added together (blue) at frequencies of 505 (EOD), 450 (S2) and 550 (S3) Hz. The interactions of these stimuli create an amplitude modulation (AM, black). Because the EOD amplitude is larger than the other two amplitudes, a well-defined envelope emerges (red), that can be extracted using a nonlinear filter. (**B**) Frequencies of the AM correspond to |dFs| in the combined signal (45 and 55 Hz) and are extracted with the Hilbert transform. The envelope frequency corresponds to the difference of the dFs (|ddF| = 10 Hz) and is extracted by the Hilbert transform of the AM.

However, recent neurophysiological studies have already identified envelope related neural activity at each level from the receptor afferents to the midbrain in weakly electric fish (Middleton et al., 2006; Middleton et al., 2007; Longtin et al., 2008; Savard et al., 2011; McGillivray et al., 2012), suggesting that not only can the fish extract out envelope information but there might be behavioral relevance of these signals for the animals.

Model-based prediction of the Social Envelope Response

The beauty of the JAR is that the behavioral response produced by each fish can be predicted based on a simple algorithm (Heiligenberg, 1991). For the fish to shift its EOD frequency in the "correct" direction (e.g. the direction that increases the dF) the fish must be able to compute the sign of the dF. The fish does this without an efferent copy of it's own EOD (Bullock, 1972) by using amplitude and phase modulation information distributed across the body (e.g. multiple electroreceptors) (Metzner, 1999b).

The JAR computation is diagrammatically represented as a Lissajous figure in the amplitude-phase plane (Figure 2A). Visualizing the JAR computation via a Lissajous figure was pioneered by Heiligenberg and colleagues (Heiligenberg and Bastian, 1980) and has been verified through electrophysiological recordings (Bastian and Heiligenberg, 1980). In the plot the abscissa (x-axis) is the magnitude of the combined signal, and the ordinate (y-axis) is the phase of the combined signal with respect to the pure EOD, which can be computed from the complex representation of the signals. The Lissajous trajectory will rotate at a frequency given by the magnitude of the dF and will rotate clockwise for negative dF and counter-clockwise for positive dF. The direction of rotation of the

Lissajous predicts the direction that the fish will shift its EOD during the JAR behavior.

When there are three EOD signals the Lissajous is more complicated (Figure 2B). When three sinusoids (or EODs) interact AMs emerge at each of the dFs. For example, if there are three EODs, S1, S2, and S3, at frequencies F1, F2, and F3 there will be AMs at the magnitudes of the following dFs: dF1 = F2-F1, dF2 = F3-F1 and dF3 = F3-F2. Each of these AMs has amplitudes corresponding to the strength of the signals at the point of measurement. In the case of actual fish EODs, the signal measured by each individual fish is typically dominated by its own EOD. So, for fish 1 the signal S1 dominates the others (S2 and S3) and correspondingly, the AMs at dF1 and dF2 dominate the AM at dF3. In this case, dF3 can be considered negligible which means that the dominant envelope frequency emerges at ddF = |dF1| - |dF2|. Note that ddF is a signed quantity, which is important to the predictions stated below.

Previous work used the Lissajous to predict behavioral responses of *Eigenmannia* to stimuli that consisted of two sinusoids (S2 and S3, in our notation) plus the fish's own signal (S1) (Partridge and Heiligenberg, 1979). However, dF1 and dF2 were well within the JAR range. In this paper, we hypothesize that the JAR circuit can be extended to predict a behavioral response to signals outside the range of the JAR that nevertheless generate low frequency envelopes at the ddF.

In some cases two conspecific signals (S2 and S3) when added to S1 produce a low frequency envelope (this is not always true). Two such cases are depicted in Figure 2B one for positive ddF and one for negative ddF. At first glance, the 'floral' pattern of the Lissajous seems to lack a consistent rotation. However, each of the 'petals' precesses at the ddF, and the direction of this precession corresponds to the sign of the ddF. Upon

low-pass filtering both the amplitude and phase signals the petals are filtered out and the general precession emerges (Figure 2C). Interestingly, as the amplitude ratio between the signals is inverted, the direction of rotation of individual petals flips, but the direction of the general precession remains unchanged. Does the fish respond to the direction of the petals (dFs and amplitude ratio) or the general precession (ddF)? When the dFs are within the JAR range the response of the fish follows the petals (Partridge and Heiligenberg, 1979). But what happens when the dFs are outside the JAR range? We hypothesize that fish respond to the emergent envelope at the ddF, which is governed by the general precession as revealed by the low-pass filtered model. If, as our model predicts, the fish uses a downstream low-pass filter from the JAR circuit to extract envelope information, it could drive a behavioral social envelope response (SER), much like the JAR to AM stimuli.

Materials and Methods

Adult *Eigenmannia virescens* (10-15 cm in length) were obtained through a commercial vendor and housed in aquarium tanks that had a water temperature of approximately 27°C and a conductivity in the range of 150–300 μS/cm (Hitschfeld et al., 2009). During preliminary testing we discovered that fish housed in social isolation exhibited less stable responses to social stimuli. As a result, all fish used in these experiments were housed in social tanks that contained 2 to 5 individuals. All experimental procedures were approved by the Johns Hopkins animal care and use committee and followed guidelines established by the National Research Council and the Society for Neuroscience.

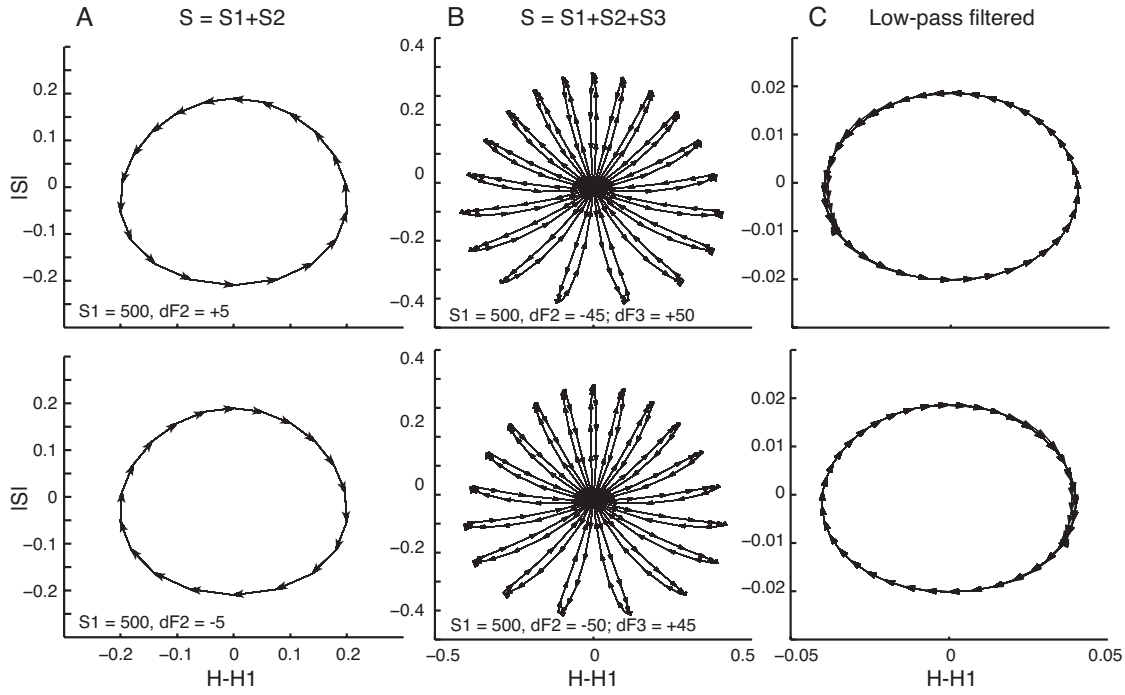

Figure 3.2. Amplitude-phase Lissajous of EOD signals
In all panels, the y-axis is the magnitude of the complex combined signal, and the x-axis is the phase of the signal, subtracted from the phase of the pure S1. (**A**) The sum of two signals S1 and S2 produces a circular graph which rotates counter-clockwise for positive dF (top) and clockwise for negative dF (bottom). The rotation is at frequency |dF|. (**B**) Sum of three signals S1, S2 and S3 results in a more complex Lissajous figure, for positive ddF (top) and negative ddF (bottom) (**C**) The amplitude and phase from B were passed through a low pass filter (Butterworth, 6^{th} order, 20 Hz normalized cutoff). This shows that there is a low-frequency general precession of the graph in the counter-clockwise direction for positive ddF (top) and clockwise for negative dF (bottom). The precession is at frequency |ddF|.

Experimental procedure

For each experiment, an individual fish (N=4) was transferred to the testing tank that was kept at 27 ± 1 °C and 175 ± 25 μS/cm. The experimental fish was allowed to acclimate to the testing tank for 2-12 hours before experiments began. During the acclimation period a second fish was also in the testing tank to provide recent social experience prior to testing but was removed prior to the start of the experiment. During testing the experimental fish was restricted in a chirp-chamber. The fish was acclimated to the chirp chamber for 1-3 hours before the start of each experiment to allow the EOD to stabilize. Experiments were started when the EOD frequency did not change by more than ± 1 Hz for at least 25 consecutive minutes.

Experimental trials were presented across multiple testing blocks that lasted 1-3 hours and were completed on different days. In between testing sessions the fish was returned to the home tank in order to reduce changes in response due to motivation, fatigue, or other unknown factors. If the EOD responses of the fish deteriorated over the course of testing it was placed back in the home tank for 1-5 days of social experience and then re-tested.

Experimental setup

The chirp chamber was positioned such that the fish was located in the middle of two electrodes (head-to-tail) separated by 25 cm (Figure 3; red electrodes). These electrodes were used to record the fish's EOD frequency. All stimuli were applied into the tank via transverse electrodes separated by 25 cm with the fish located in the middle (Figure 3; black electrodes).

At the start of each trial the initial EOD frequency of the fish ($F1_i$) was extracted. All trials within a testing block were presented randomly for each fish. Each trial lasted 200 s and all trials were separated by an inter-trial interval of 200 s. For each trial the fish was presented with a stimulus that was either a single sinusoid (control trials; S2) or a sum of two sinusoids (envelope trials; S2 + S3).

For the control trials, the frequency of the stimulus (F2) was calculated by adding a specified initial frequency difference (dF_i) to $F1_i$, i.e. $F2 = F1_i + dF2_i$. For the envelope trials, the frequencies of the individual sinusoids (F2 and F3) were calculated by adding a specified frequency difference (dF_i) to $F1_i$, i.e. $F2 = F1_i + dF2_i$ and $F3 = F1_i + dF3_i$. The frequencies F2 and F3 were held constant, i.e. not clamped to F1, so changes in the fish's EOD frequency results in changes in the value of the dFs and ddF.

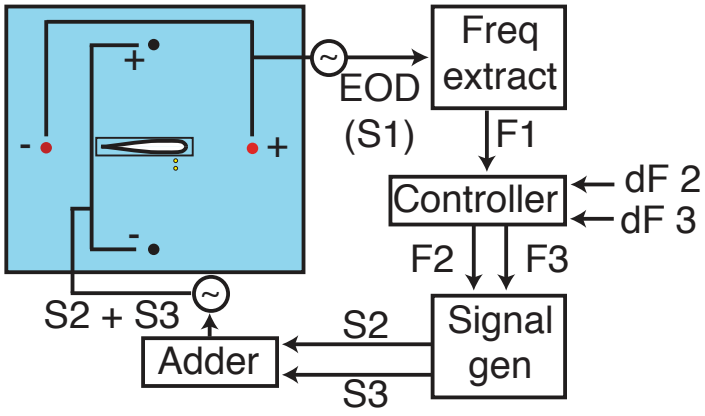

Figure 3.3 Social envelope experimental setup
The fish's EOD is recorded via head-tail electrodes (red) and stimuli to the fish are applied via transverse electrodes (black). Stimuli consist of a single sinusoid (S2) or a sum of two sinusoids (S2 + S3). The frequency of the recorded EOD (F1) is extracted, and passed to a controller, which adds the stimulus values of dF2 and dF3 to F1, to produce output frequencies F2 and F3. The signal generator uses these values to generate sinusoids S2 and S3 at frequencies F2 and F3. S1 and S3 are added, and applied to the tank through a stimulus isolation unit.

Experimental stimuli

Control trials: All fish completed trials (n=20) with a single sinusoid stimulus (S2) at a specified high dF (> 40 Hz). The initial dFs used were ± 52, 58, 72, 78, 92 and 98 Hz, which are outside the range of frequencies known to elicit the JAR. These dFs were a subset of those used to create the envelope stimuli in other trials (see below). For all control trials the stimulus amplitude was 0.74 mV/cm and the stimulus amplitude ramp time was 20 s.

Amplitude trials: All fish completed trials (n=10), with a sum of two sinusoids stimulus (S2+S3) that produced a ddF_i of ± 4 Hz. The initial dFs used were ± 48 and ± 52 such that there were two trial types: $dF2_i$ = -48 and $dF3_i$ = + 52 or $dF2_i$ = -52 and $dF3_i$ = + 48, which resulted in a +4 Hz and -4 Hz envelope, respectively. These trials were repeated at five different stimulus amplitudes (0.15, 0.45, 0.74, 1.05, and 1.34 mV/cm) with a ramp time of 20s.

Envelope trials: All fish completed trials (n=48) with a sum of two sinusoids (S2+S3) that produced a specified initial, ddF_i. Trials were completed with $dF2_i$ = ±50, ±70 or ±90 with $dF3_i$ sweeping from $–dF2_i – 8$ to $–dF2_i + 8$ by intervals of 2 Hz. For example, for $dF2_i$ = 50 then $dF3_i$ was set at each of the following values for individual trials: -58, -56, -54, or -52 (resulting in initial ddFs of -8, -6, -4 and -2 Hz) or -48, -46, -44, and -42 (resulting in initial ddFs of 2, 4, 6 and 8 Hz). For trials where $dF2_i$ = -50, the $dF3_i$ values were the same as the above example but the sign of $dF3_i$ was positive. This was repeated for $dF2_i$ = ±70 and ±90 resulting in trials with initial ddFs at ± 2 through ±8 (excluding 0) by increments of 2 Hz, produced by dFs of varying frequencies. All trials were completed with combined stimulus amplitude of 0.74 mV/cm and ramp time of 20 s.

Ramp-time trials: One fish completed trials (n=30) with a sum of two sinusoids stimulus (S1 + S2) where three values of amplitude ramp times were tested (1s, 20s and 100s). Each of these ramp times was repeated for two envelope frequencies (+ 4 Hz; $dF2_i$ = -48, $dF3_i$ = + 52 and – 4 Hz; $dF2_i$ = -52, $dF3_i$ = + 48) and five final stimulus amplitudes (0.15, 0.45, 0.74, 1.05, and 1.34 mV/cm).

Ratio trials: One fish completed trials (n=10) with a sum of two sinusoids stimulus (S2 + S3) where the relative amplitudes of each individual component were varied at a ratio of 1:1, 1:3, 2:3, 3:2 and 3:1 for envelopes of + 4 Hz ($dF2_i$ = -48, $dF3_i$ = + 52) and – 4 Hz ($dF2_i$ = -52, $dF3_i$ = + 48).

Data analysis

For each trial the EOD was recorded via head-to-tail electrodes, and was used to compute the EOD frequency, $F1_t$, as a function of time. This was achieved via post-processing with a custom script in Matlab (Mathworks, Natick MA, USA) that computed the spectrogram of the recorded signal and determined $F1_t$ as the frequency with the highest power near the fish's baseline EOD frequency. The baseline $F1_i$ was measured at the start of each trial using a frequency-to-voltage (F2V) converter. For 60 trials the output of the F2V converter was verified against post-experiment Fourier analysis, where the error between the two measurements had a mean ± SD = 0.0008 Hz ± 0.054 Hz. F1 stabilized by the last 60 s of each trial: $F1_f$ is the mean frequency measured over this period. The change in frequency was calculated as $\Delta F1 = F1_f - F1_i$.

For each trial the ΔF1 was normalized to the individual fish's maximum response, |ΔF1max|, to allow SERs to be compared across fish. In addition, because a fish could raise or lower its EOD frequency some measures are presented as |ΔF1|/|ΔF1max|.

Dependent measures were analyzed using a one-way repeated measures ANOVA. For significant main effects we provide an effect size measure (ηp^2) to allow for comparison between measures. Additionally, post hoc Tukey HSD tests were run on each significant main effect to determine which groups were significantly different. We indicate the critical value (Q_{crit}) for each test and provide the obtained values only for those that were statistically significant (i.e. greater than the critical value).

Results

EOD frequency changes were not elicited by high frequency dFs

To ensure that observed responses were not due to the individual dFs we conducted control trials where the fish were presented with a single sinusoid stimulus that had a high-frequency dF. First we measured the ΔF1 during the last 60 s of the control trial inter-trial interval and found that the EOD frequency was stable without stimulation (mean ±s.e.m; 0.05 ± 0.006 Hz). Second we measured the ΔF1 across the first 10 s (0.23 ± 0.03 Hz) and the last 60 s (0.52 ± 0.04 Hz) of control stimulus presentation and found only nominal changes to the EOD frequency. Raw data for the response to control trials by a single fish is shown in Figure 4A. Thus, it is unlikely that the observed ΔF1 to sum of sinusoid stimuli (which has an emergent envelope) were due to a response to any individual component alone.

Fish exhibited a Social Envelope Response (SER)

The sum of two sinusoidal stimuli (S2 + S3) elicited changes in EOD frequency. Figure 4 shows a characteristic SER of a single fish to two replicates of a +2 Hz envelope (dF2 = -50, dF3 = + 52; blue) and two replicates of a -2 Hz envelope (dF2 = -52, dF3 = + 50; red). The figure shows that the envelope response differs from the response observed to control stimuli (grey).

Across all fish, responses to control stimuli were minimal (range: 0.05 to 0.74 Hz) while the SERs were typically between 1 and 4 Hz. Moreover, the time course the EOD change during control trials was much larger than the time course of the SER, which corresponded to the stimulus ramp time (20 s). In addition, responses to control trials were biased downward, while the SERs were bidirectional. The direction of the SER shows that the fish shifts its EOD frequency down when the envelope frequency (ddF) is positive and up when the envelope frequency is negative. The direction of the SER was typically opposite the sign of the ddF, resulting in the EOD shifting towards the closer dF (although the final dFs were 40Hz or above).

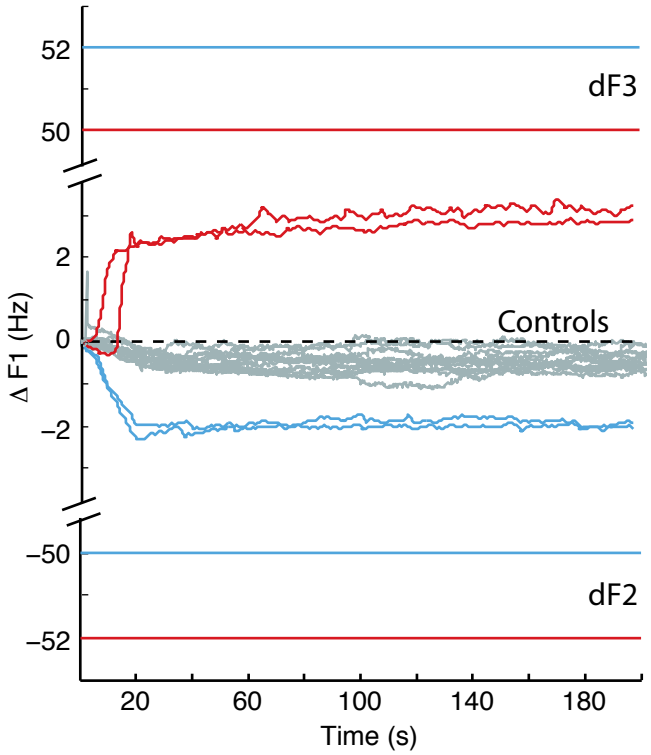

Figure 3.4 Response to electrosensory social envelopes
Eigenmannia do not show a change in EOD frequency (controls; grey) when stimulated with a single sinusoid of high-frequency (AMs > 50 Hz). Fish do show a change in EOD frequency when stimulated with a sum of two sinusoids. Two trial types are shown where dF2 = -50 and dF3 = + 52 (+ 2 Hz envelope; blue) and where dF2 = -52 and dF3 = + 50 (- 2 Hz envelope; red). When the envelope sign is positive the fish shift their frequency down (blue) and when the envelope sign is negative the fish shift the frequency up (red).

SER was stronger for lower-frequency envelopes

All fish changed F1 in response to sum-of-sinusoids stimuli that created initial envelope magnitudes, $|ddF_i|$, in the frequency range of 2 to 8 Hz as illustrated for a single fish in Figure 5. The figure also illustrates that ΔF1 is qualitatively similar across all dFs used. However, the strength of the SER (the change in EOD frequency during a trial) is dependent upon on $|ddF_i|$ (Figure 6A). The effect of the initial absolute envelope frequency, $|ddF_i|$, on the normalized absolute EOD frequency change, $|\Delta F1|/|\Delta F1max|$, was significant [$F(3,9) = 6.45$, $p = 0.04$, $\eta p^2 = 0.68$]. Normalized |ΔF1| is generally

smaller as a function of larger initial ddF: $|ddF_i|$ = 2 Hz (mean ±s.e.m; 0.59 ± 0.04), 4 Hz (0.52 ± 0.03), 6 Hz (0.34 ± 0.03), and 8 Hz (0.39 ± 0.04). The only significant pairwise differences (Tukey HSD; Q_{crit} = 4.41) were between the lowest envelope frequency (2 Hz) and those higher than 6 Hz (2 Hz vs. 6 Hz: Q_{obt} = 4.45; 2 Hz vs. 8 Hz: Q_{obt} = 5.51) (Figure 5A; noted with asterisks). The rest of the pairwise comparisons were not significant ($Q_{obt} < 4.41$).

SER increased the envelope frequency

Individual fish change F1 in response to initial envelope stimuli, which resulted in a change in the envelope frequency (Figure 6B). In general, the final absolute envelope frequency settles in the range of 5-15 Hz (mean ± s.e.m; 8.87 ± 0.20). We found that there was a significant effect of the initial envelope frequency ($|ddF_i|$) on the change in envelope frequency ($\Delta ddF = |ddF_f| - |ddF_i|$) [$F(3,9) = 6.32$, $p = 0.01$, $\eta p^2 = 0.68$]. The change in envelope frequency, $|\Delta ddF|$, was smaller as a function of larger $|ddF_i|$: 2 Hz (mean ±s.e.m; 4.78 ± 0.68), 4 Hz (4.57 ± 0.51), 6 Hz (2.86 ± 0.36), and 8 Hz (3.29 ± 0.59). The only significant pairwise differences (Tukey HSD; Q_{crit} = 4.41) were between 2 Hz and 6 Hz (Q_{obt} = 5.05) and between 4 Hz and 6 Hz (Q_{obt} = 4.50), where the change in envelope frequency was greater for the lower initial envelope frequency in each pair.

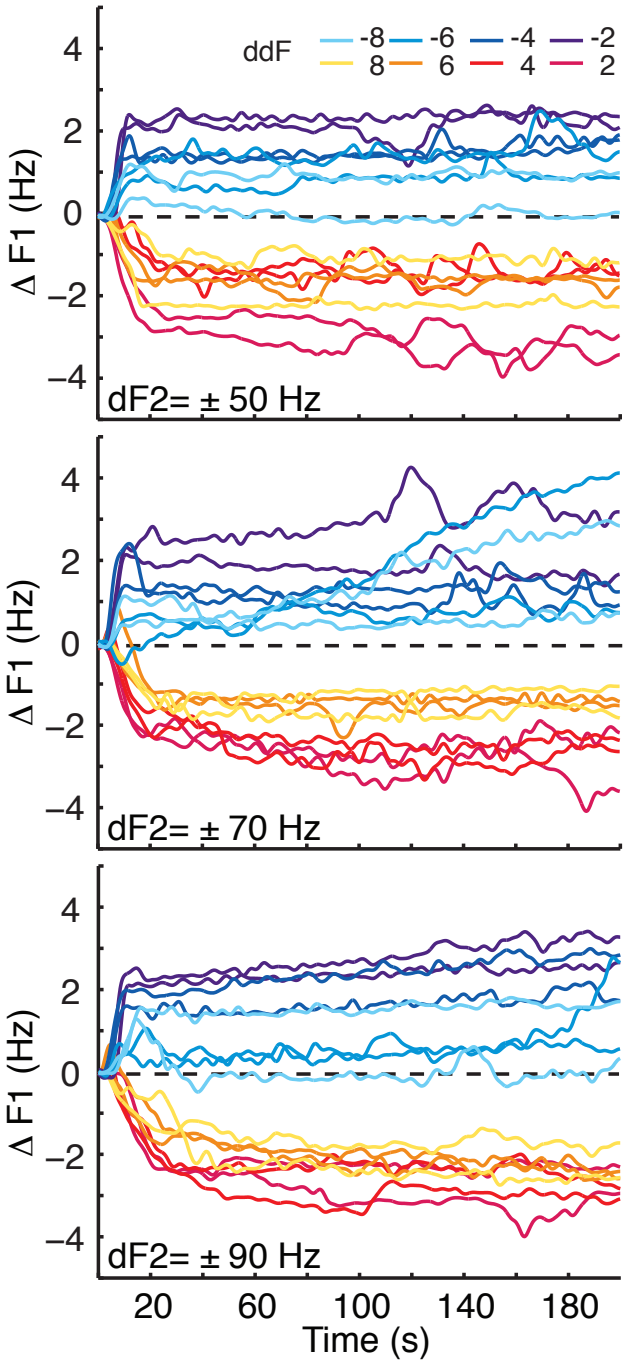

Figure 3.5 EOD traces the SER to different initial envelope frequencies
We varied the initial envelope frequency from -8 to + 8 by 2 Hz intervals (excluding 0 Hz). The fish (data for one individual is shown) showed no difference in their response as a function of the range of dF2 and dF3 values used (shown by comparison of three panels for dF2 = ± 50 Hz, dF2 = ± 70 Hz and dF2 = ± 90 Hz).

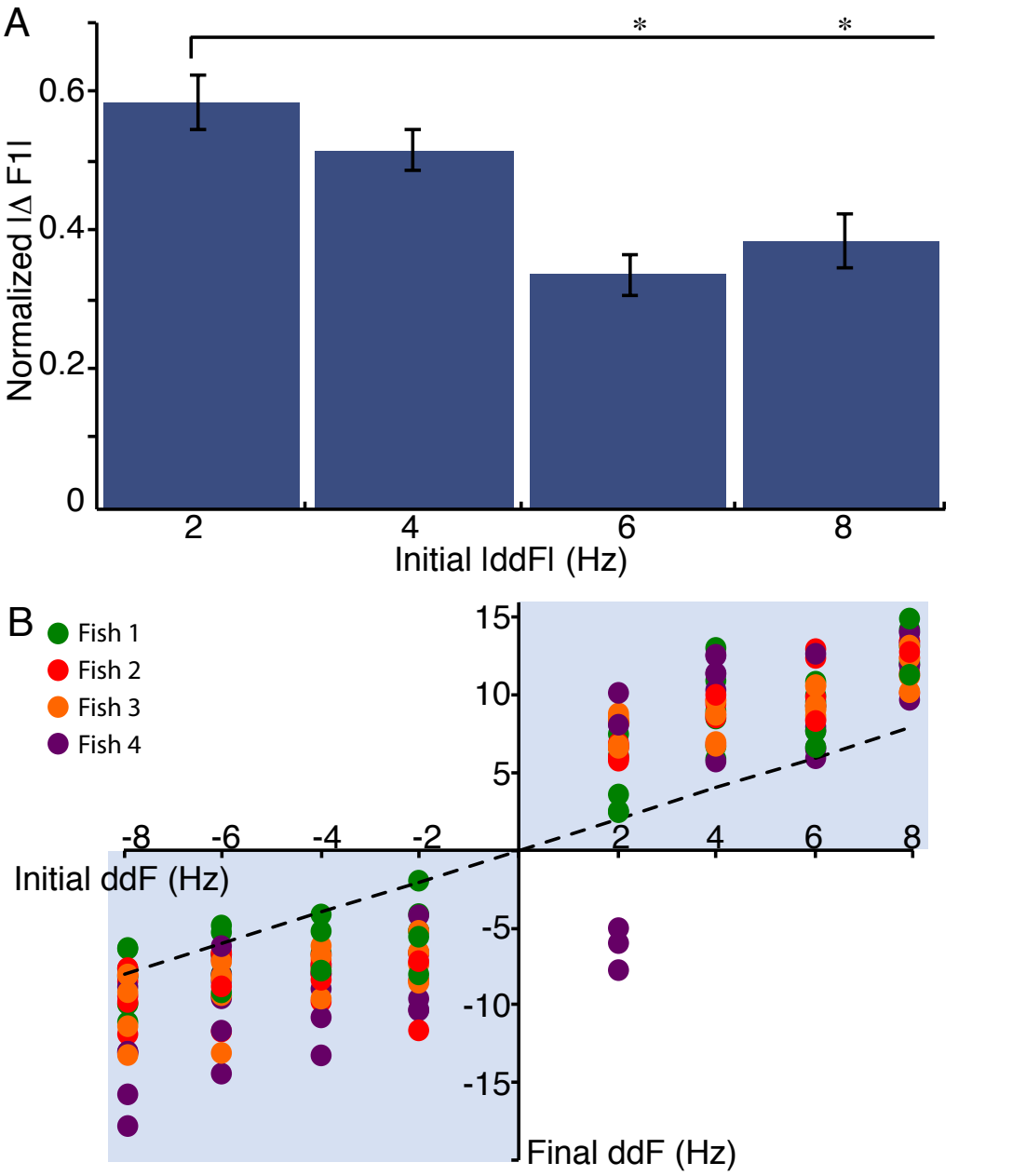

Figure 3.6 SER as a function of initial absolute envelope frequency
(**A**) We found that normalized ΔF1 is significantly greater when the initial ddF is lower frequency. (**B**) The ΔF1 generally shifted in the direction predicted by the low-pass filtered version of the Lissajous (blue shaded quadrants) across all fish (color-coded). Final envelope frequencies were greater than the initial envelope frequency if the data is greater than the unity line (dotted line) in the predicted direction. The final ddF was typically in a band between 5 and 15 Hz.

SER depended on stimulus amplitude and not the rate of amplitude change

The strenth of the SER, as measured by the magnitude |ΔF1|, increases as a function of stimulus amplitude as shown for one fish in Figure 7A. The effect of stimulus amplitude on the normalized |ΔF1| was significant [$F(4,12) = 7.16$, $p = 0.02$, $\eta p^2 = 0.71$] (Figure 6B). The change in frequency, |ΔF1|, was generally larger for larger stimulus amplitude: 0.15 mV/cm (mean ±s.e.m; 0.32 ± 0.07), 0.45 mV/cm (0.49 ± 0.09), 0.74 mV/cm (0.68 ± 0.11), 1.05 mV/cm (0.63 ± 0.09), and 1.34 mV/cm (0.83 ± 0.06). There were significant pairwise differences (Tukey HSD; $Q_{crit} = 4.21$) between the lowest stimulus amplitude (0.15 mV/cm) and those higher than 0.74 mV/cm (0.15 vs. 0.74: $Q_{obt} = 5.16$; 0.15 vs. 1.05: $Q_{obt} = 4.49$ and 0.15 vs. 1.34: $Q_{obt} = 7.20$) and the comparison between the second lowest stimulus amplitude (0.45 mV/cm) and the highest stimulus amplitude (0.45 vs. 1.34: $Q_{obt} = 4.73$) (Figure 7B; noted with asterisks). The rest of the pairwise comparisons were not significant ($Q_{obt} < 4.20$).

The effect of stimulus amplitude on final $|ddF_f|$ was significant [$F(4,12) = 7.99$, $p = 0.04$, $\eta p^2 = 0.73$] (Figure 7C). There was a significant pairwise difference (Tukey HSD; $Q_{crit} = 4.20$) between the lowest stimulus amplitude (0.15 mV/cm) and those higher than 0.74 mV/cm (0.15 vs. 0.74: $Q_{obt} = 5.25$; 0.15 vs. 1.05: $Q_{obt} = 4.71$ and 0.15 vs. 1.34: $Q_{obt} = 7.65$) and the comparison between the second lowest stimulus amplitude (0.45 mV/cm) and the highest stimulus amplitude (0.45 vs. 1.34: $Q_{obt} = 4.83$). The rest of the pairwise comparisons were not significant ($Q_{obt} < 4.20$).

In data from one fish, differences in ramp time did not effect the strength of the SER, |ΔF1| (Figure 8). Thus, the SER strength depended on the amplitude of the stimulus, but not on the rate of change of amplitude.

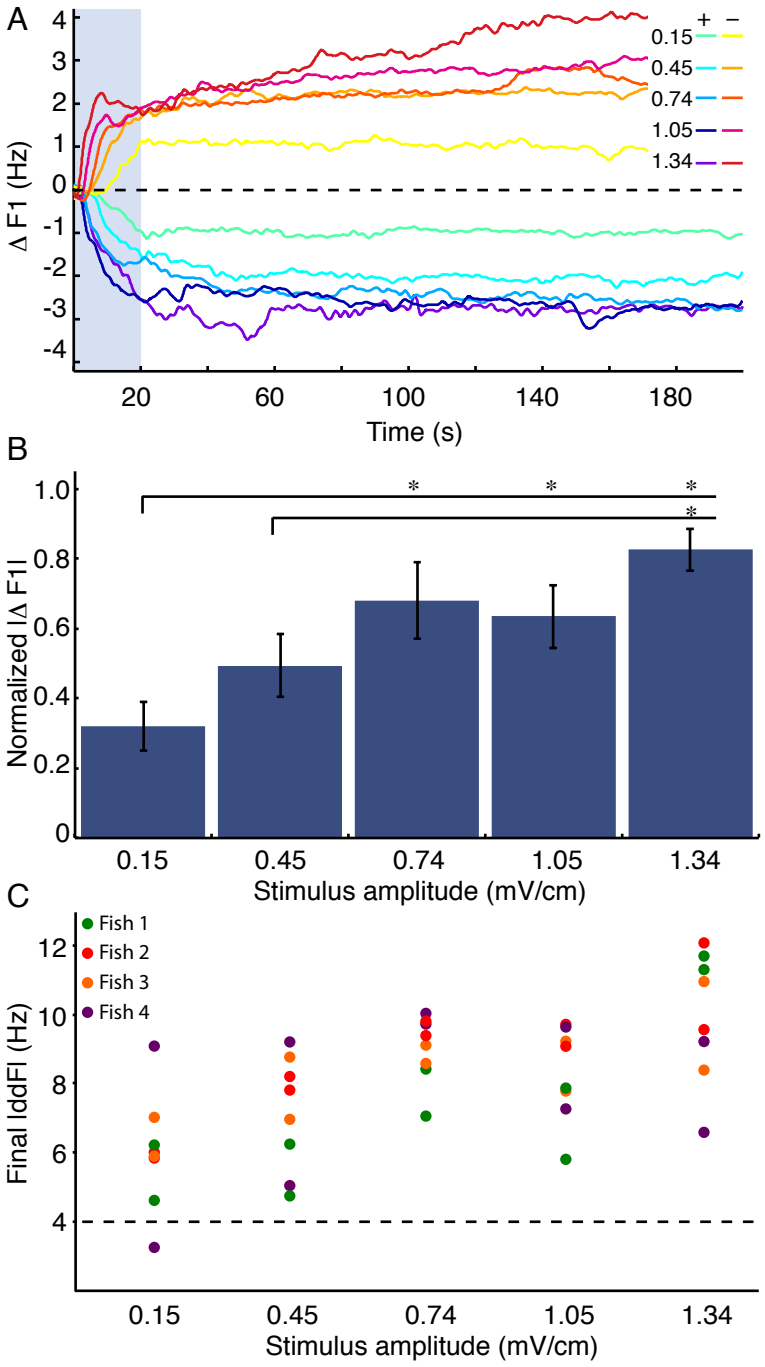

Figure 3.7 SER as a function of stimulus amplitude
(**A**) ΔF1 increased as the stimulus amplitude was increased from 0.15 to 1.34 mV/cm (data for one individual shown). (**B**) There was a significant effect of the stimulus amplitude on the ΔF1 where increased ΔF1 were observed for higher stimulus amplitudes compared to lower stimulus amplitudes. (**C**) The final ddF was significantly higher for larger stimulus amplitudes, across individuals (color-coded).

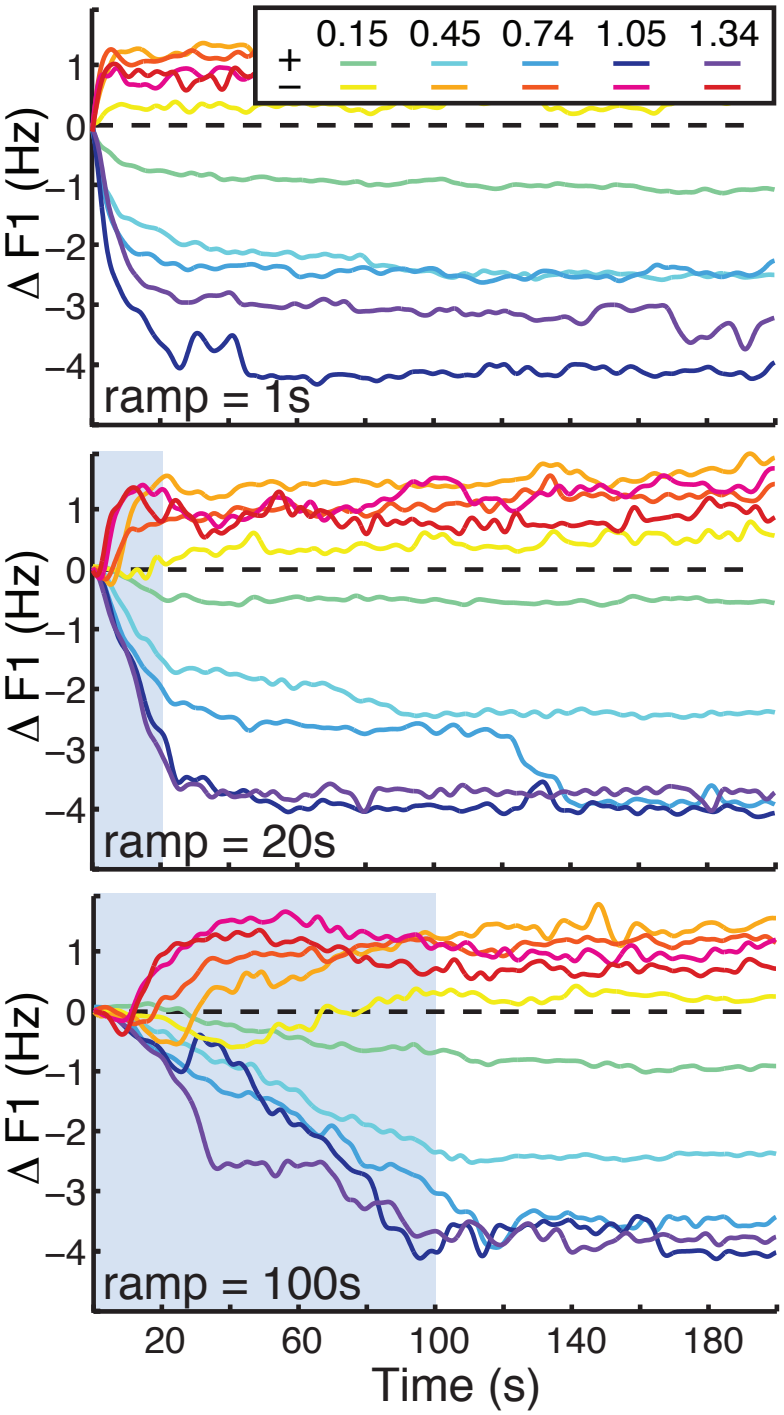

Figure 3.8 The SER does not depend on the rate of amplitude change
The ΔF1 was determined by the final stimulus amplitude value, not the rate of change of amplitude. This is observed by comparing data across multiple stimulus amplitude ramp times (1, 20 and 100s). The initial time course of the behavior is increased as the ramp time was increased, but the final value of the ΔF1 is equivalent across all ramp times.

SER did not switch direction with changes in amplitude ratio

For a given a dF1 and dF2 pair, the relative amplitudes of S2 and S3 determine the rotation of the 'petals' of the Lissajous but not the general precession, as described in the Model-Based Prediction section, above. Therefore, changing the relative amplitudes of S2 and S3 directly tests the model. This is illustrated in Figure 9 for a ddF of -4 (top) or +4 (bottom) in which sections of the Lissajous figures correspond to different stimulus amplitude ratios. As can be seen for ddF = -4, the individual petals rotate counter-clockwise for ratios 1:3 and 2:3, and clockwise for 1:1, 3:1, and 3:2, but the graph generally precesses clockwise in all cases (Figure 9, top). Similarly, ddF = +4 the petals rotate clockwise for ratios 3:1 and 3:2 and counter-clockwise for 1:1, 1:3, and 2:3, but the graph generally precesses counter-clockwise in all cases (Figure 9 bottom). Thus the direction of rotation of the petals can be opposing the precession of the graph, depending on stimulus ratio.

We examined the sign of SER, measured by the sign of ΔF1 to different stimulus amplitude ratio S2:S3 (1:1, 1:3, 2:3, 3:2 and 3:1) for ddF = ± 4 (Figure 9). We found that the direction of the SER depended only on the sign of ddF, not the amplitude ratio: F1 shifts up when ddF is negative, and F1 shifts down when ddF is positive (Figure 9 middle). This supports our hypothesis that SER is driven by the general precession of the Lissajous rather than the local rotation of the petals when the dFs are outside the JAR range.

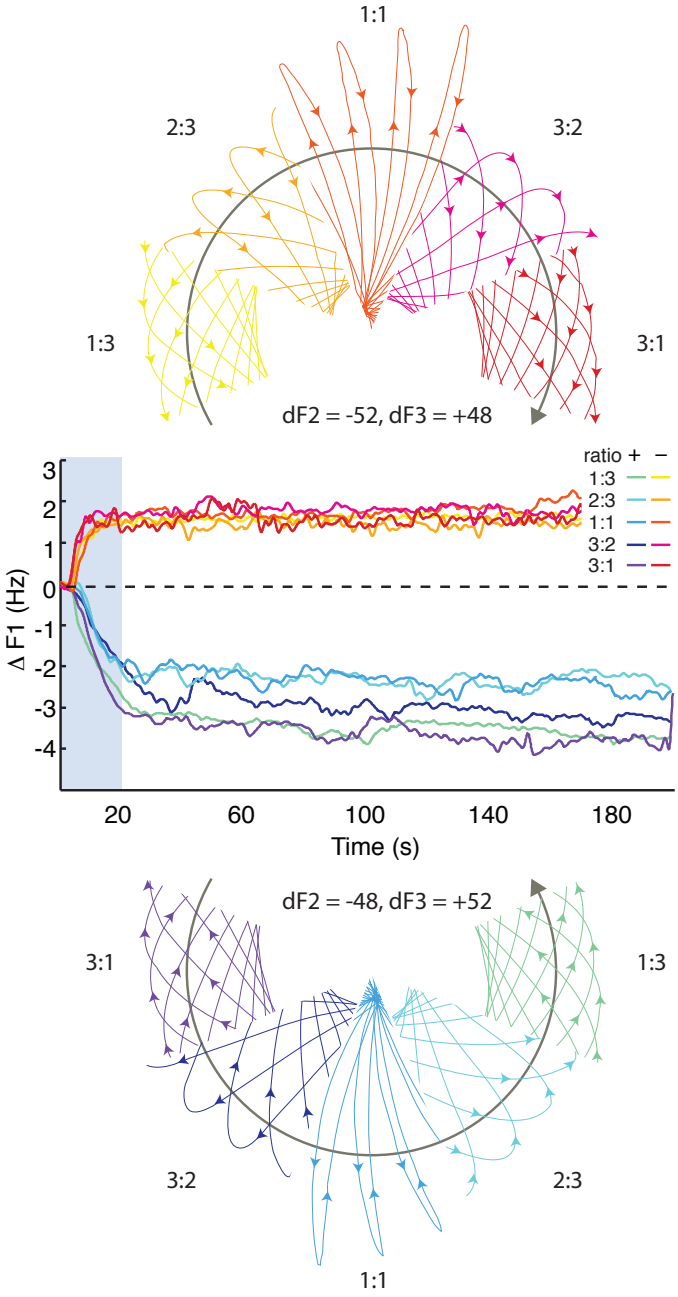

Figure 3.9 The SER does not depend on amplitude ratio
Amplitude ratios of 1:3, 2:3, 1:1, 3:2 and 3:1 were tested, at two envelope frequencies (± 4 Hz). The Lissajous figures are representative angular sections of the figures generated by the S2 and S3, at each of the tested dFs and amplitude ratios. The individual 'petals' of 1:3 and 2:3 in the negative ddF (top) and 3:1 and 3:2 in the positive ddF (bottom) rotate opposite to the direction of precession of the entire graph, i.e. the direction of rotation of the filtered graph (black arrows). The fish changes F1 according to the sign of ddF only, irrespective of the stimulus amplitude. F1 shifts up for negative ddF (red spectrum plots) and shifts down for positive ddF (blue spectrum plots).

Discussion

Recent neurophysiological studies identified neurons that respond to electrosensory envelopes (Middleton et al., 2006; Middleton et al., 2007; Longtin et al., 2008; Savard et al., 2011; McGillivray et al., 2012). Here we show the behavioral relevance of one category of electrosensory envelopes. We measured the EOD responses of *Eigenmannia* to envelope stimuli like those that would arise from the electrical interactions of three or more non-moving conspecifics. We call this behavior the *Social Envelope Response* (SER), which is differentiated from possible responses to movement-related envelopes specifically because the signal sources are non-moving. We also proposed a simple extension of the algorithm for the JAR, a low-pass filter of the instantaneous amplitude and phase of the combined signal, which accurately predicts SER behavior.

In the SER *Eigenmannia* can either raise or lower their EOD frequency, which results in an increase in frequency of the envelope by about 2-6 Hz, with final envelope frequencies between 5 and 15 Hz. The strength of the SER depended on the initial envelope frequency and the stimulus amplitude: low initial frequencies and high stimulus amplitudes elicited the largest changes in EOD frequency. The SER direction was insensitive to the relative amplitude ratio between stimulus signals, indicating dependence on the general precession of the Lissajous, as opposed to local rotations of the petals, as predicted by our model.

Mechanisms for the SER

We extended the widely known model for the control of the JAR with the addition of a low-pass filter that reduces responses to the local rotations of the Lissajous while passing its general precession. The model does not predict where and how this computation may be implemented in the brain. Part of this computation could be implemented as a saturation nonlinearity of amplitude-coding P-receptors, which would cause them to encode envelopes (Savard et al., 2011). When combined with a rectification circuit in the ELL (Middleton et al., 2006; Middleton et al., 2007; Longtin et al., 2008), the amplitude axis of the Lissajous would oscillate at the envelope frequency. In this case, the phase axis would be filtered independently in downstream circuits to yield the circular Lissajous that precesses at the |ddF|. Alternatively, amplitude and phase filtering may both occur in downstream circuits. In this case, the higher response thresholds (as compared to JAR) may be necessary to overcome the attenuation caused by the filter.

Possible functional relevance of the SER

In their natural habitat, weakly electric fish are commonly found in groups of conspecifics and also multispecies flocks (Tan et al., 2005; Stamper et al., 2010). What electrosensory cues are available to the animal for determining the relative locations and frequencies of other individuals? Our results suggest that weakly electric fish may use information contained in the electrosensory envelope.

We show that fish exhibit a SER that increases the frequency of the social envelope into a higher band (up to 15 Hz). The SER appears to be analogous to the JAR,

where fish also shift their EOD frequency, which results in an increase in the frequency of the AM (Heiligenberg, 1991). It has been shown that low-frequency AMs impair aspects of electrolocation and that the JAR may allow fish to avoid this detrimental interference caused by the presence of a nearby conspecific with a similar initial EOD frequency (Heiligenberg, 1973; Bastian, 1987). In addition to the behavioral impairment observed it has also been shown that the neural response to moving objects by midbrain neurons is impaired under low-frequency jamming (Ramcharitar et al., 2005). If the SER functions analogously to the JAR, one would predict that low-frequency envelopes might also degrade electrolocation performance and the underlying neural responses to moving objects.

Movement envelopes

Fish are rarely completely motionless and therefore, we expect that movement related envelopes are ubiquitous in groups of two or more fish. These envelopes can encode the relative velocity between two fish and possibly provide reliable cues about distance (Yu et al., 2012). Our model predicts that fish may have a 'Movement Envelope Response' (MER) that is driven by the relative movements between fish. These movement-based envelopes are another form of social envelopes, in that social behavior includes the movement of fish relative to each other. We differentiate social envelopes, which is a special class of signals that arise solely due to the details of the interactions between electric fields of wave-type weakly electric fish. Movement related envelopes, however, can also arise from non-social sources including from the interaction of fish with objects in their environment.

Chapter 4: Active sensing via movement shapes spatiotemporal patterns of sensory feedback

Active sensing is broadly defined as the expenditure of energy into the environment for the purpose of sensing (Nelson and MacIver, 2006). Active sensing can include the generation of signals, such as echolocation chirps in bats (Moss and Surlykke, 2001; Ulanovsky and Moss, 2008) and the generation of movements, such as whisking in rodents (Grant et al., 2009). Active sensing in weakly electric fish includes both the generation of a sensory signal (their weak electric fields), as well as and movement through the environment for the purpose of sensing (Heiligenberg, 1975; Assad et al., 1999; Babineau et al., 2007)

Recent studies have identified the important role of movement-based active sensing (Peters et al., 1999; Madsen et al., 2004; Ghose and Moss, 2006; Wachowiak, 2010) for increasing sensory volumes (MacIver et al., 2010; Yovel et al., 2011). Animals often can also move their sensory organs, *e.g.* eyes, pinnae, antennae, or whiskers, through independent actuation for purposes other than increasing the sensory volume. For example, eye microsaccades prevent perceptual fading (Ditchburn and Ginsborg, 1952) and larger eye movements place salient features on the fovea (foveation) (Robinson and Zee, 1981; Becker, 1989).

When electric fish investigate novel objects or hunt for prey they swim in a scanning motion and bend their trunks (Lannoo and Lannoo, 1992; Nelson and MacIver, 1999; Nanjappa et al., 2000) as well as bend their tail (Heiligenberg, 1975; Toerring and Moller, 1984; Nelson and MacIver, 1999; MacIver et al., 2001). Indeed, these behaviors increase the sensory volume over the movement time interval (Snyder et al., 2007;

MacIver et al., 2010), but that may not be the most important role of such movements. To examine the sensory function of these movements, we manipulated modality-specific sensory feedback in a task in which increasing the sensory volume is irrelevant.

We measured the performance of *Eigenmannia virescens* in a refuge-tracking task where we varied the availability of visual and electrosensory information via changes in illumination and conductivity respectively. In the tracking task a fish swims forwards and backwards to maintain its position within a longitudinally moving refuge (the 'shuttle'; Figure 1B) (Blake, 1983; Lannoo and Lannoo, 1992). This behavior is mediated by at least two sensory modalities (Figure 4.1A), vision and electrosense (Rose and Canfield, 1993a, b; Rojas and Moller, 2002). Importantly, although the fish's movements may increase the sensory volumes, the refuge-tracking task did not rely on this increase since the shuttle always remained within the sensing volumes of both the visual and electrosensory systems.

We found that, despite categorical changes in the availability of sensory information, the animals maintained similar behavioral performance as measured by tracking gain. However, in the absence of visual information, fish produced costly movements, and as electrosensory information was degraded, these movements increased. In short, the animal controls its own movements, which in turn determines the pattern of feedback that the animal experiences as it moves through the environment. For example, if a fish swims faster past an object, the frequency of stimulation at a single electroreceptor is increased as the object passes in and out of the receptive field. Our data suggests that the fish may use active movements to shape the spatiotemporal dynamics of the electrosensory feedback.

Materials and Methods

Adult *Eigenmannia virescens* (10-15 cm in length) were obtained through a commercial vendor and housed according to published guidelines (Hitschfeld et al., 2009). Tanks were maintained with a water temperature of ~27°C and a conductivity in the range of 150–250 mS/cm. All experimental procedures were approved by the Johns Hopkins animal care and use committee and followed guidelines established by the National Research Council and the Society for Neuroscience.

For each experiment, an individual fish was transferred to a testing tank equipped with a computer-controlled moving refuge and high-speed video camera (see Figure 1 in (Roth et al., 2011)). Animals were allowed to acclimate to the test tank and refuge for 2-24 hours prior to any experimental trials. If the fish left the refuge during testing and did not return within approximately one minute the overhead lights were turned on and the fish was gently guided back into the refuge using an aquarium net (Rose and Canfield, 1993a). Subsequently, animals often returned to the refuge when the overhead light was turned on.

Experimental apparatus

The experimental setup was similar to that used in previous reports (Fig 4.1B) (Cowan and Fortune, 2007; Roth et al., 2011). For these experiments, the refuge (or 'shuttle') was machined from a 15 cm segment of 2" x 2" gray rectangular PVC tube. The bottom face of the refuge was removed and a series of six windows (0.625 cm in width and spaced 2.0 cm apart) were machined into each side to provide visual and electrosensory cues. The shuttle was suspended 0.3 cm from the bottom of the tank to allow the fish to be video recorded from below. Video was obtained using a high-speed

camera (pco.1200s, Cooke Corp, Romulus, MI, USA) with a Micro-Nikkor 60 mm f/2.8D lens (Nikon Inc., Melville, NY, USA). Video was captured at 30 frames · s^{-1} with 1280x1024 pixel resolution using Camware software (Cooke Corp, Romulus, MI, USA). For each trial, the shuttle was moved forwards and backwards according to specified sine wave trajectories by a linear stepper motor (IntelliDrives, Inc, Philadelphia, PA, USA) driven by a Stepnet motor controller (Copley Controls, Canton, MA, USA). The actuator trajectories and camera triggering were synchronized using a Multifunction DAQ (USB-6221, National Instruments, Austin, TX, USA) and controlled with custom Matlab scripts (MathWorks, Natick, MA, USA).

Experimental procedure

Individual fish (N=4) were presented with shuttle movement trajectories consisting of single sine waves (frequencies: 0.05, 0.01, 0.25, 0.55, 0.85, 1.15, and 1.55 Hz) at a velocity amplitude of 1.2 cm · s^{-1}. Each trial was a total of 60 s in duration. During a trial, the stimulus amplitude was gradually ramped up for the first 10 s to prevent abrupt onset movements and similarly attenuated for the last 10 s to prevent movements in response to an abrupt stop. Data from these ramping periods were excluded from analysis.

Trials were run using two illumination conditions, either white light ("light" trials) or infrared light ("dark" trials). Each illumination condition was paired with a conductivity range: "low" (25 ±5 μs/cm), "medium" (200 ±20 μs/cm), and "high" (570 ±15 μs/cm). These conductivities result in behaviorally relevant change in the distribution and density of the electric field (MacIver et al., 2001).

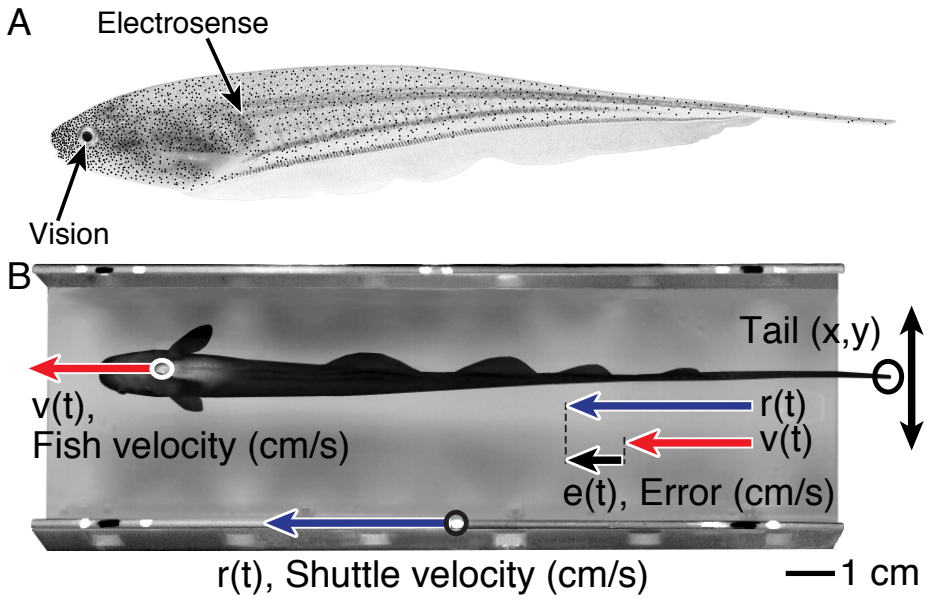

Figure 4.1 Schematics of *Eigenmannia* and refuge tracking experimental setup
(**A**) *Eigenmannia* have both visual and electrosensory systems, which can be used to control locomotor behavior. (**B**) The experimental setup shows the fish, *v(t),* shuttle (refuge), *r(t)*, and tracking error, *e(t),* that were digitized for each trial. These velocities were used to calculate gain and phase of tracking, tracking error, swim path length and locomotor cost. For 60 trials, we also digitized the position of the tail.

The sequence of sensory condition (the pairings of illumination and conductivity) presentation was randomized across fish. For each sensory condition the fish completed 4-8 trials of each shuttle trajectory. The trial order was randomized with the constraint that the fish completed one trial for each trajectory before repeating a trajectory. The data for each sensory condition were typically collected over several hours on 1-2 d of testing. The minimum inter-trial interval was 70s. Analyzed data included fish (N=4) that completed at least one set of trials for all sensory conditions. An additional fish (N=1) completed one set of "light" trials at medium conductivity before and after enucleation of both eyes as a control measure to completely eliminate visual input. Data obtained from the blinded fish were for comparison purposes only and are not included in the final data set except where noted.

Data analysis

For each trial (n = 876) the X-Y positions of the fish and shuttle were digitized (Fig 4.1B) using custom code implemented in Matlab (MathWorks, Natick, MA). Raw X-Y pixel coordinates were transformed to align the X coordinate with the length (and motion) of the refuge. For each trial, we calculated the time trajectory of velocity for both the shuttle and fish, r(t) and v(t) respectively. For a subset of trials (n=60) the X and Y position of the tail was digitized and the mean tail-beat frequency was calculated for each trial.

The Fourier transform (FT) represents these time-domain signals, r(t) and x(t), as complex-valued functions of frequency, R(ω) and V(ω). Representing these complex functions in polar coordinates, we can describe each value by its magnitude, |V(ω)|, and angle ∠V(ω). For sinusoidal input trajectories, the FT of the input, R(ω), is represented as a discrete spike at the stimulus frequency and zero at all other frequencies. The FT of the fish movement, V(ω), has power over a broader range of frequencies (0.1 to 1.0 Hz; Figure 3B) with concentrated peaks at frequencies corresponding to the spectrum of the input.

The Bode plot describes the response of a system by comparing the output signal V(ω) to the input R(ω) using two measures, gain and phase. Gain is calculated as the ratio of the signal magnitudes, |V(ω)|/|R(ω)|, and phase is computed as the difference of the signal angles, ∠V(ω) - ∠R(ω). The Bode plot is evaluated only for the set of discrete frequencies presented as stimuli; the Bode ratio is not defined elsewhere where the R(ω) = 0.

We further decompose the fish motion into two categories of movement: movements in response to the stimulus frequencies (the concentrated peaks of the FT) and broad-spectrum volitional motion (termed 'whole-body oscillations'). To estimate the average volitional motion, we calculate the magnitude of the FT, $|V(\omega)|$, for each trial and omit the data corresponding to the input frequencies (the peaks in response to the stimulus). Since different trials have different points on the frequency spectrum omitted, we can reconstruct the entire spectrum by averaging across trials.

For each trial we also calculate median tracking error, the median value of the time series $|v(t)-r(t)|$. We use the median tracking error to exclude occasional rapid shifts in the fish's position and velocity. These excursions correspond to a behavior where the fish makes a full body reversal to correct for accumulated tracking error.

We calculate the total path length that the fish swam for each trial, $\int|v(t)|\,dt$. The values we report are normalized to the path length of the refuge trajectory, which was always 30.56 cm. As a conservative estimate of energy expenditure for locomotion (locomotor cost), we calculate the net positive mechanical work required to move the fish along its swimming trajectory. The net positive work is calculated as the integral of the positive power (those instances during which velocity and acceleration are in the same direction) excluding intervals where power is negative, $\int_{P>0} P(t)\,dt$. This estimate assumes that energy is expended for acceleration only and deceleration is achieved passively (i.e. via drag forces introduced through fluid-body interaction). The instantaneous power as $P(t) = F(t)\cdot v(t)$, where F represents the force and v the fish velocity. Force is estimated by Newton's law, $F = m\cdot a = m\cdot\dot{v}$, where m is the mass of the fish and $\dot{v}$ is the acceleration.

This estimate of locomotor cost underestimates the mechanical work performed by the fish (e.g. using this estimate, constant velocity motion implies zero work, but fish clearly must inject work into the locomotor dynamics to overcome drag forces). Fish likely actively decelerate with ribbon fin actuation, so some of the neglected "negative" work represents mechanical work performed by the fish. Moreover, even stationary fish are observed moving their ribbon-fin in counter-propagating waves, expending a baseline of mechanical work for no motion at all. Theoretically, there may be cases for which the net positive work exceeds the actual mechanical work contributed by the animal (i.e. through elastic storage of energy as might happen in the tendons of terrestrial animals), but there is no evidence for these effects in swimming fish.

With these important caveats in mind, the net positive work estimate serves as a convenient lower bound to the mechanical work contributed by the fish; a true estimate of mechanical work contributed by the fish requires a more complete description of the ribbon-fin kinematics throughout the duration of the experiments. Still, such an estimate would not represent the metabolic cost. Additionally, there are other costs associated with increased movement, such as increased conspicuousness, which could result in higher predation rates, which we wholly ignore. Ultimately, the net positive work provides a consistent and convenient metric for comparing energetic costs of locomotion between different sensory conditions.

Dependent measures were analyzed using a factorial repeated-measures ANOVA with the Geisser-Greenhouse correction for non-sphericity. For each significant main effect we provide an effect size measure (η_p^2) to allow comparison across measures.

Results

Fish use visual and electrosensory system for the control of locomotor behavior

We computed Bode gain and phase, a measure of tracking performance (see methods), under different sensory conditions (Figure 4.2A). In general, the tracking performance of these fish matched previous reports (Cowan and Fortune, 2007; Roth et al., 2011): fish had a tracking bandwidth of 0.05 to 1.55 Hz with phase lags up to 180 degrees at the highest stimulus frequencies (1.15 and 1.55 Hz). Gains were strikingly similar across all visual and electrosensory conditions which indicates that fish were able to match the velocities of the stimulus despite categorical changes in the availability of sensory information, which has not been described previously (Rose and Canfield, 1993a, b). We observed a difference in the mean phase lag at higher frequencies (0.55, 0.85, 1.15 and 1.55 Hz)—fish responses lagged the shuttle input more in the dark than when visual cues were present by 31°, 49°, 42° and 48°, respectively. Despite this difference, the performance of the animal in light and dark and across conductivities was surprisingly consistent given the radical spatiotemporal differences between visual and electrosensory cues.

Next, we compared the error predicted by the Bode plot analysis with the measured median tracking error across all sensory conditions (Figure 4.2B). If the tracking behavior were a linear system, the Bode plot could be used to accurately predict the median tracking error. Indeed, we found the Bode-predicted error closely matches the fish's tracking performance when the fish has visual cues. However, the measured median tracking error increased dramatically from the Bode prediction when the fish performed the tracking behavior in the dark. There were significant main effects of

illumination [$F(1,3) = 86.18$, $p = 0.003$, $\eta_p^2 = 0.96$], conductivity [$F(2,6) = 36.41$, $p = 0.008$, $\eta_p^2 = 0.93$] and shuttle movement frequency [$F(6,18) = 10.37$, $p = 0.015$, $\eta_p^2 = 0.78$] on median tracking error. In particular, tracking error increased from light (mean ± s.e.m. = 0.451 ± 0.013 cm s^{-1}; open-fill) to dark (1.425 ± 0.027 cm s^{-1}; closed-fill) and as conductivity increased from low (0.875 ± 0.035 cm s^{-1}; blue circle) to medium (0.931 ± 0.037 cm s^{-1}; green square) to high (1.077 ± 0.044 cm s^{-1}; purple diamond).

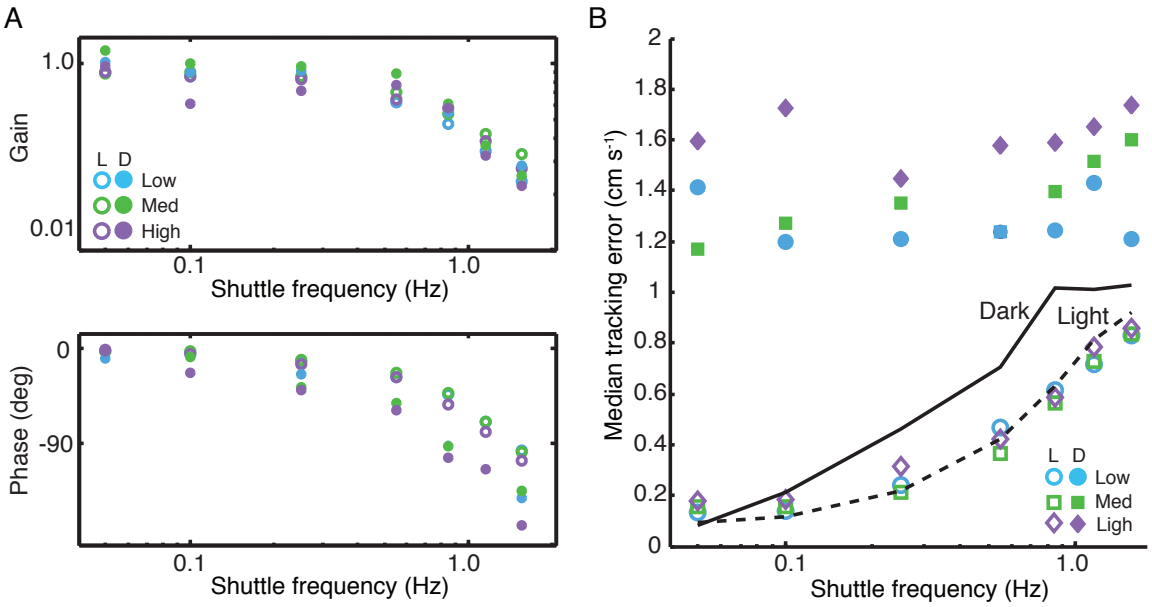

Figure 4.2 Tracking gain and tracking error across sensory conditions
(**A**) The Bode plot indicates that tracking performance, measured by gain, is equivalent between trials completed in light (L, open-fill) and those completed in the dark (D, closed-fill). The gain was similar across conductivities, low (blue), medium (green) and high (purple). There was a difference in phase for higher shuttle movement frequencies (0.55 Hz and above) where fish have an increased phase lag in the dark. (**B**) Median tracking error in the light matched the Bode-predicted error (dashed line) whereas median tracking error in the dark (black line) did not. There was a significant increase in error between light (open-fill) and dark (closed-fill) trials and when conductivity was increased from low (blue circle) to medium (green square) to high (purple diamond).

Increased tracking error in the dark results from large whole-body oscillations

The source of the increase in tracking error can be seen directly in the raw tracking data: there was a categorical difference in swimming behavior when the lights were turned off. To illustrate this difference, Figure 4.3A shows two trials in which the lights were switched on or off mid trial. These trials also show that the behavior switches immediately in response to changes in illumination. These two trials indicate a common feature across all of our data: the fish tracked the shuttle movement smoothly in the light, whereas in the dark the fish performed large back-and-forth movements that were superimposed on the underlying tracking trajectory.

In the frequency domain (Figure 4.3B), the fish response in light trials appears as a single peak collocated with the input peak. For dark trials, the fish motion includes a peak at the input frequency (the response to the stimulus), and also shows power across a broader spectrum up to 1 Hz, which we call "whole-body oscillations." These whole-body oscillations were similar across stimulus frequencies and rarely occurred in the light. We also observed similar oscillations in a fish that was tracking in the light but was blind. Typically, the velocities of these oscillations were higher (1.2 to 15 cm s^{-1}) than the underlying shuttle velocity (0 to 1.2 cm s^{-1}).

In the light, the electrosensory feedback that the animal receives - which is the slip of the shuttle along the body surface - occurs roughly at the stimulus frequency. At night, however, the additional oscillations alter the frequency of the feedback, shifting it to higher frequencies. Our hypothesis is that these active movements increase the frequency range of feedback into a range that better matches the frequency filtering of the electrosensory system.

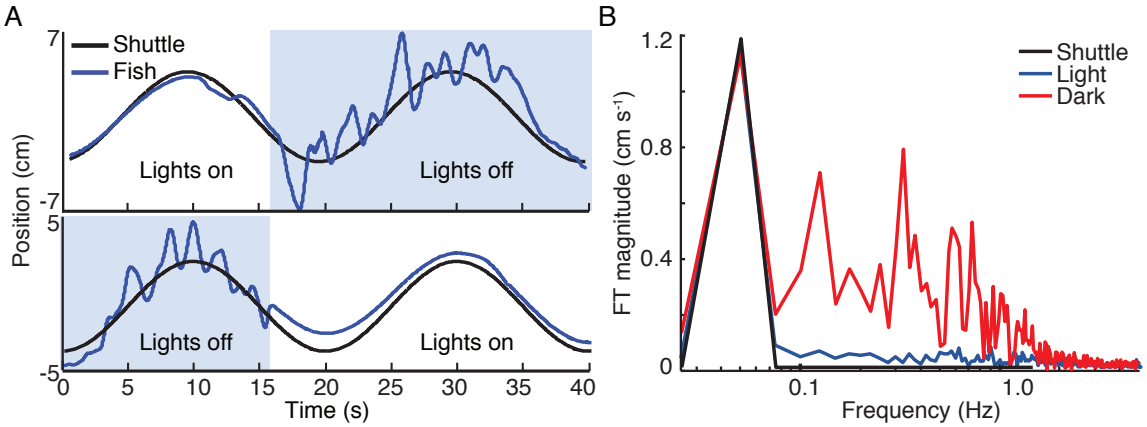

Figure 4.3 Illumination and conductivity modulate active movements
(**A**) Two sample trials are shown where the illumination was switched during tracking. In the dark, fish swam back and forth with whole-body oscillations superimposed over the underlying tracking movement. (**B**) The magnitude of the FT computed from two trials of a fish tracking a shuttle moving at 0.05 Hz (black). The fish responded with nearly identical gain at the stimulus frequency as indicated by the spectral peaks at 0.05 Hz for both the light (blue) and dark (red) trial. However, in dark trials fish motion trajectories have substantial spectral content at other frequencies (up to approximately 1 Hz).

Fish swim significantly farther while tracking in the dark

We measured the distance that fish swam for each trial (Figure 4.4A). The distance was normalized to the total distance moved by the shuttle, which was always 30.56 cm. We found that the fish swam an average of 3.35 times farther in the dark than in the light, and that swimming distance also increased with increased conductivity. There were significant main effects of illumination [$F(1,3) = 253.83$, $p = 0.001$, $\eta_p^2 = 0.99$], conductivity [$F(2,6) = 20.30$, $p = 0.012$, $\eta_p^2 = 0.87$] and shuttle movement frequency [$F(6,18) = 5.33$, $p = 0.039$, $\eta_p^2 = 0.64$] on normalized swim path length (Figure 4.5A). Normalized swim path length increased substantially from light (mean ± s.e.m. = 0.789 ± 0.013 cm s^{-1}; open-fill) to dark (2.644 ± 0.041 cm s^{-1}; closed-fill) and as conductivity increased from low (1.554 ± 0.059 cm s^{-1}; blue circle) to medium (1.744 ± 0.063 cm s^{-1}; green square) to high (1.979 ± 0.074 cm s^{-1}; purple diamond).

Energetic costs of locomotion increases when tracking in the dark

The normalized swim path length does not differentiate between different categories of swimming. Positional drift (low velocity, low acceleration, low frequency movements) and whole-body oscillations (high velocity, high acceleration, high frequency movements) could result in similar path length measurements. However, oscillations represent greater mechanical work than do drifts of similar path length.

We estimated a lower bound for the costs of locomotion associated with tracking a moving shuttle. This cost was estimated as the net positive mechanical work required to move the fish's mass along its experimentally measured trajectory (see Methods). Fish performed significantly more net positive work in the dark (Figure 4.4B). For each shuttle frequency, the cost of locomotion was highest for the highest conductivity, and lowest for the lowest conductivity. There was a significant main effect of illumination [$F(1,3) = 142,.60$ $p = 0.001$, $\eta_p^2 = 0.98$] on the locomotor cost, but the effect of conductivity was not statistically significant. Mean locomotor cost increases from light (mean ± s.e.m. = 0.186 ± 0.011 μJ; open-fill) to dark (3.087 ± 0.108 μJ; closed-fill).

Whole-body oscillations increase with increases in conductivity

To determine whether fish use these whole-body oscillations to facilitate electrosensory processing we altered the conductivity of the water. Conductivity affects the spatial distribution of the electric field and consequently affects the feedback that results from movement. If the additional movements reported above were unrelated to active sensing, one would expect that conductivity would have little or no effect on the whole-body oscillations. Instead, we found a significant increase (Figure 4.5) in the

magnitude of these oscillations [$F(2,6) = 14.79$, $p = 0.010$, $\eta_p^2 = 0.83$], as conductivity is increased from low (mean ± s.e.m. = 12.43 ± 0.38 cm s^{-1}; blue) to medium (0.19 ± 0.40 cm s^{-1}; green) to high (16.01 ± 0.39 cm s^{-1}; purple). In addition, these oscillations persist even after more than 24 hours of continuous darkness and were also observed in a blind fish, that was tracking in the light.

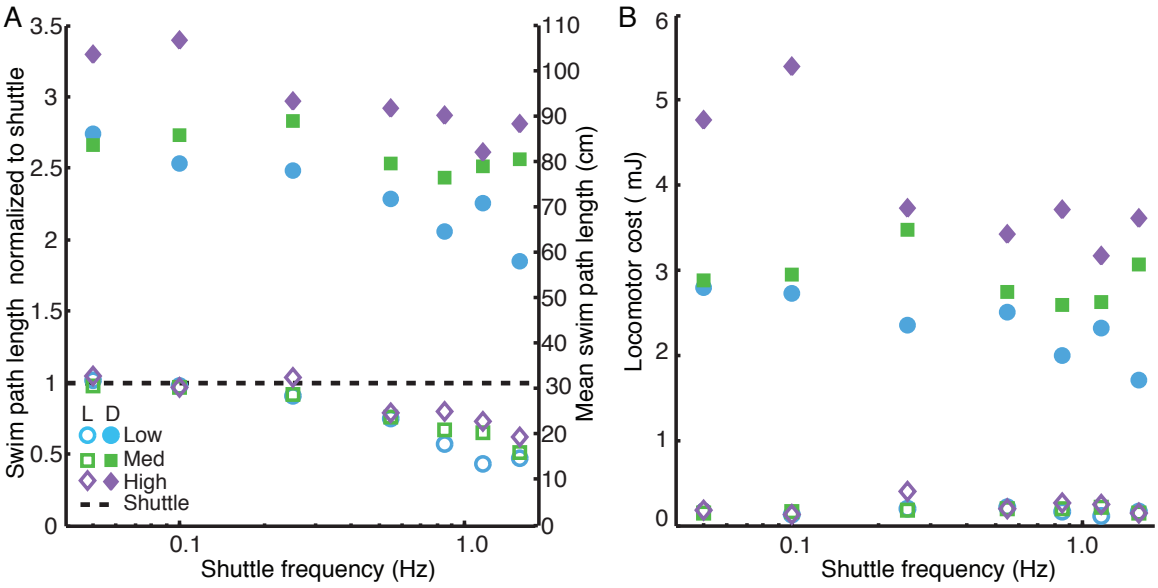

Figure 4.4 Active movements incur increased locomotor cost
(**A**) The fish swam significantly less when tracking the shuttle in the light (open-fill) compared to dark (closed-fill). The fish's swim path also increased as a function of conductivity from low (blue circles) to medium (green squares) to high (purple diamonds). (**B**) Tracking in the dark (closed-fill) also incurs an increased locomotor cost than tracking in the light (open-fill).

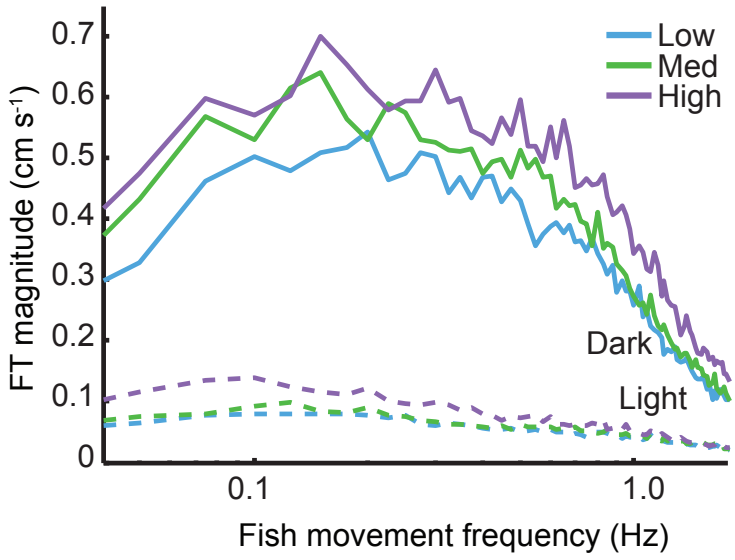

Figure 4.5 Active movements increase with increasing conductivity
The magnitude of the whole-body oscillations produced by *Eigenmannia* increased between light (dashed lines) and dark (solid lines) and also as a function of increasing conductivity (low in blue, medium in green, and high in purple).

Spontaneous tail movements emerge during dark trials, but not light trials

We observed that the fish constantly move their tails when tracking in the dark but not in the light (Figure 4.6A,B). Tail-beat frequency (Figure 4.6C) ranged from 1.5 to 2.35 Hz across 4 fish (mean ± s.e.m. = 1.88 ± 0.025 Hz), and an additional fish that was blind (1.76 ± 0.058 Hz). Previous modeling results indicate that electric fish might bend their tail in order to compute lateral distance to objects (Sim and Kim, 2011). Accordingly, we found that fish maintain a mean y-position (Figure 4.6D) that is more tightly clustered in the middle of the shuttle walls (open bars; 4cm width) in trials in the dark (black bars) than those in the light (grey bars).

The deviation for mean y-position for each trial increases as a function of illumination from light (s.d. ± s.e.m. 0.080 ± 0.004 cm) to dark (0.186 ± 0.004 cm). This indicates that fish have more active side-to-side movement of their head when tracking in

the dark. However, it is possible that this head movement is confounded with tail bending, which might cause the body to have a slight lateral oscillation. We also found that the standard deviation for the mean y-position increased as a function of conductivity in the light (low 0.054 ± 0.005 cm; medium 0.077 ± 0.006 cm; high 0.180 ± 0.007 cm) and dark (low 0.152 ± 0.007 cm; medium 0.189 ±0.007 cm; high 0.217 ± 0.006 cm). Overall, these lateral movements were small compared to the width of the refuge (approximately 2 to 10%).

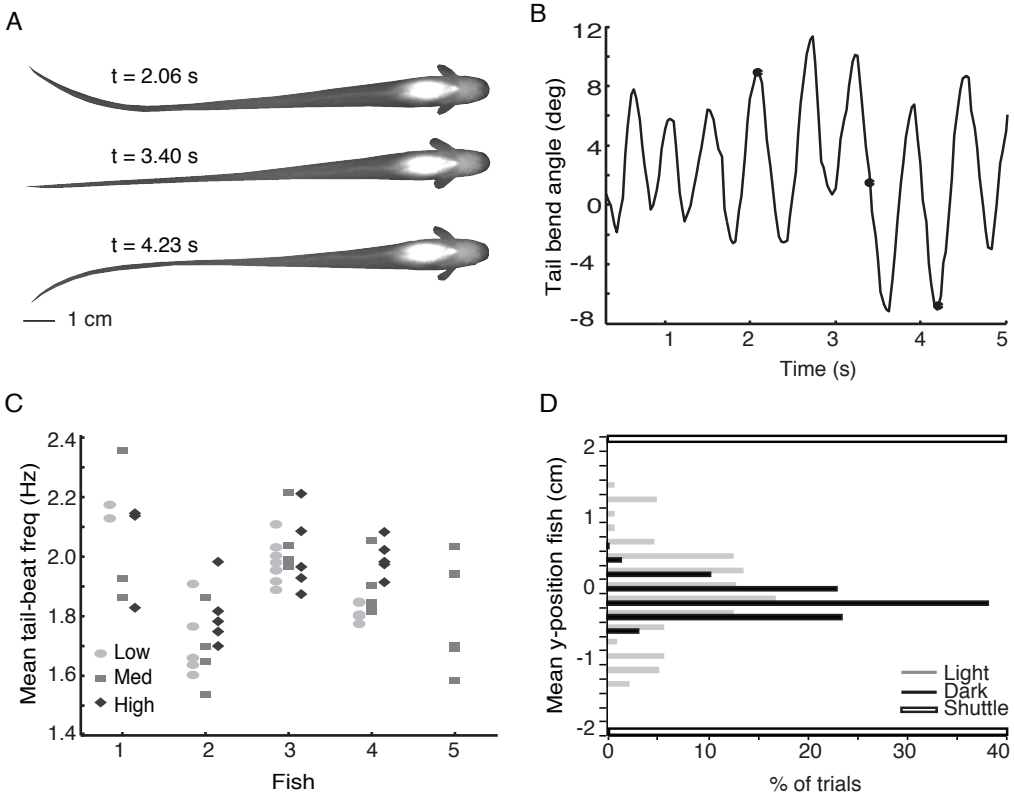

Figure 4.6. Spontaneous tail bending occurs during refuge tracking in the dark
(**A**) Three sample frames of tail bending in the dark. (**B**) A sample trace showing the angle from the tip of the tail to middle of the body, relative to head direction (frames from A indicated with black). (**C**) The mean tail-beat frequency for tracking in the dark (fish 1-4) and tracking in the light in a blind fish (fish 5). (**D**) Histogram of lateral position in the light (grey bars) and dark (black bars) relative to the shuttle walls (open bars at top and bottom).

Discussion

We measured the ability of *Eigenmannia* to track a moving refuge in the light and dark (with and without visual cues) and with different water conductivities (which alters the pattern of electrosensory feedback). We find that the fish preferentially rely on the visual system when visual cues are available. This is consistent with their life history as they hide in root systems, grasses, and debris, during daylight hours when visual cues are present (Tan et al., 2005; Stamper et al., 2010). Similarly, other nocturnal or crepuscular animals that can rely on non-visual sensory information for the control of behavior also preferentially rely on visual cues when they are present (Knudsen and Knudsen, 1989; Penteriani et al., 2006; Cummings et al., 2008).

We found that tracking performance, as measured by the Bode gain, was comparable across the sensory conditions that were tested, which included systematic changes in illumination and conductivity. However, there is a categorical difference between fish locomotion in light versus dark: fish in the dark made whole-body oscillations and bend their tails. These active movements in the dark dramatically increased the distance that the fish swam and subsequently the locomotor cost. These active movements shape the electrosensory feedback. Indeed, these movements increased significantly in response to a degradation of the electrosensory feedback signal. To the best of our knowledge, these experimental results are the first to show a correlation between the degradation of modality-specific information and the active reshaping of the sensory feedback.

Active sensing incurs locomotor costs

Active movements are energetically costly and this cost must be balanced against other costs, such as the reward of obtaining sensory information (Shadmehr et al., 2010). Many studies have examined the cost emitting signals for active sensing (*e.g.* electric field, echolocation chirp). This cost is tied to effective range of the signal and receptor system, *i.e.* the sensing volume (Nelson and MacIver, 2006; Snyder et al., 2007). For example, a modeling study by MacIver *et al.* indicates that doubling the electrosensory volume requires sixteen times more energy (MacIver et al., 2010). The benefit of this increase in energy expenditure is an enlarged sensing volume, thereby increasing the probability of encountering prey items (Lannoo and Lannoo, 1992; Nelson and MacIver, 1999; Nanjappa et al., 2000; MacIver et al., 2001). In our tracking experiments, increased sensing volume is not a relevant parameter because the shuttle is within the sensing volume at all times.

So, what is the benefit of this significant increase in the locomotor cost during tracking in the dark? The spectrum of active movement is essentially unchanged across all sensory conditions and between fish; only the gain of these movements is modulated as a function of light and conductivity (Figure 4.5). This is consistent with our hypothesis that active movements are tuned to the spatiotemporal filtering properties of the underlying neural circuits. For example, neurons in the Torus semicircularis (Ts) respond strongly to amplitude modulations in the range of frequencies generated by both the whole-body oscillations and the tail bend (Fortune and Rose, 1997a; Rose and Fortune, 1999a; Fortune and Rose, 2000). These movements may also reduce perceptual fading by increasing the stimulation frequency, which may better stimulate high-pass afferents

(Nelson et al., 1997) and may improve detectability in the ELL through its interaction with descending feedback (Chacron et al., 2003).

Tail bending contributes to sensory processing

We observed that fish actively bend their tails in the dark when the animals rely on electrosensory information for tracking. Tail bending produces modulations of the strength of the electric field on the ipsilateral and contralateral sides with opposite signs (Chen et al., 2005). These amplitude modulations (AMs) are summed with the AMs that result from the movement of the animal across the inner surface of the shuttle, which includes both the tracking error (slip of the shuttle along the body surface) and whole-body oscillations. Each of these signals occurs, roughly speaking, in a different frequency band: tracking error equal to the stimulus frequency (e.g. 0.05 Hz), whole-body oscillations (0.1 to 1 Hz) and tail bending (1.5 to 2.35 Hz). Theoretically, each signal could be extracted using an appropriately designed linear filter implemented in the nervous system. Neurons that are selective for particular frequencies of AMs have been described in the midbrain (Fortune and Rose, 1997b, a).

For isolated fish, these three categories of movement (tracking error, body oscillations, and tail bending) generate simple AMs, but in the presence of conspecifics they likely also produce 'envelopes', which are the second-order modulations of amplitude that can occur as a result of social interactions and locomotor behavior (Middleton et al., 2006; Savard et al., 2011). Unlike AMs, envelopes cannot be extracted using simple linear filters, but rather require nonlinear mechanisms, such as rectification (Savard et al., 2011).

The role of tail bending in information processing has been studied previously in the context of the cancellation of predictable signals in the cerebellum-like structure, the ELL (Bastian, 1996a, b, 1998). Information from P-type receptor afferents is transmitted to the three tuberous maps of the ELL (Metzner, 1999; Maler, 2009a, b; Fortune and Chacron, 2011). Pyramidal cells in the ELL receive descending feedback and exhibit adaptation to predictable signals by producing a negative image (Bastian, 1996a). Cyclical tail bending can be cancelled by descending feedback (Bastian et al., 2004). However it remains to be determined how this cancellation might affect information processing during tail bending, which might explain why *Eigenmannia* increases tail bending when relying on electrosensory information in tracking behavior.

One clue comes from the responses of ELL neurons to intermittent electrosensory social signals. When two fish are in close enough proximity so that their electric fields interact (within about 1 meter), the interactions of the electric fields continuously produce amplitude and phase modulations (Heiligenberg, 1991; Tan et al., 2005; Stamper et al., 2010). In *Apteronotus*, fish can also produce rapid, intermittent transients in their electric field (Zupanc et al., 2006; Dunlap et al., 2010) especially during agonistic encounters (Hupe and Lewis, 2008; Hupe et al., 2008). In the ELL, the cancellation of the predictable AMs that result from the mixing of EODs from nearby fish also induces a concomitant enhancement of the responses to unpredictable chirp signals (Marsat and Maler, 2011). One possibility is that tail bending results in the same effect where the tail bending itself is cancelled but unpredictable signals related to the movements of the refuge are enhanced.

Further, there is a diversity of pyramidal cell types (deep, intermediate, and superficial) that differ in the amount of descending feedback that they receive (Chacron et al., 2003; Bastian et al., 2004; Krahe et al., 2008). These differences are correlated with the degree of cancellation that the neurons experience in response to continuous global stimuli (Chacron et al., 2003). The role of these differences is unclear but may be related to the detection of combinations of predicable and unpredictable stimuli, such as occurs when the animal actively bends its tail (predictable) to determine the location of the shuttle (unpredictable). The combination of tracking error and the whole-body oscillations produced by fish when tracking in the dark may indeed ensure that the position of the tail relative to the shuttle (moving object) at each moment in time is not predictable.

Movements shape sensory feedback to match neural properties

The additional movements during refuge tracking in the dark necessarily alter the spatiotemporal patterns of the electric field on the body surface. Our hypothesis is that these movements are a form of active sensing in which the animal self-stimulates its electroreceptors to match the demands of the nervous system. Examples may include the requirements of high-pass filtering in primary afferents (Nelson et al., 1997), the spatiotemporal demands of filters in the midbrain (Fortune and Rose, 1997ba, b; Ramcharitar et al., 2005), or the timescales required for updating a representation of the shuttle through working memory (Baddeley, 1992).

Alternatively, these movements may not contribute to tracking performance in the dark but may emerge for other unknown reasons that are not related to electrosensory

perception. Our data strongly suggests that this behavior is indeed related to electrosensory perception because we show that (1) the magnitude of these whole-body oscillations increase as a function of increasing conductivity, (2) are observed in animals that had been in darkness for extended periods of time (12 to 24 hours) and (3) are observed in a blind fish when tracking in the light. As conductivity increases, contrast decreases (MacIver et al., 2001). Therefore, an increase in movements when the conductivity is high could be used to shape spatiotemporal patterns of neural activity to match those as when the conductivity is low.

Interestingly, spatiotemporal shaping appears even in tasks where the apparent goal is to increase volume. Animals can achieve an increase in sensory volume in many ways, for example by increasing the energy of emitted signals, or through any of a variety of movement strategies. MacIver *et al.* described stereotyped patterns of movement during prey capture that increase the sensory volume (defined as the minimum detection distance for prey items) to increase the probability of prey detection (MacIver et al., 2001). It has also been shown that bats will engage in active movements to increase the 'field of view' or sensory volume detected using echolocation (Yovel et al., 2011). This behavior is dependent on the complexity of the environment and location of the target. In general, the sensory volume depends critically on the relative movement of the animal's receptor array relative to its prey (or target), because the receptor properties depend not on a static flux of energy onto the receptors, but rather on the dynamic (temporal) properties and changes in energy flux over time.

Thus, increasing the effective sensory volume is inherently linked to reshaping sensory feedback via the details of the movement, and vice versa. In fact, previous

studies have described neurons that are tuned to the specific frequencies of sensory feedback experienced during prey capture (Chacron et al., 2003; Oswald et al., 2004; Chacron et al., 2005; Ramcharitar et al., 2005; Chacron et al., 2009). But, perhaps such predatory movements are tuned, at least in part, to the spatiotemporal receptive field properties of the nervous system, rather than the traditional view of the nervous system being tuned to behavioral demands.

Chapter 6: Discussion

Animals are almost always processing more than one stream of salient sensory information at any time. These streams of information are both integrated for the moment-to-moment control of behavior. These processes occur across a wide array of species and involve virtually all aspects of animal behavior. For instance, groups of animals (e.g. schools of fish, colonies of penguins, flocks of birds, swarms of bats, etc.) coordinate their social behavior and movement for the purposes of migration, foraging, reproduction and likely many other behaviors. The problem with all of these behaviors is that it is difficult, if not impossible, to segregate the different streams of information that are used in behavioral control.

Weakly electric fish are a model system that that facilitates the study of multiple streams of information for behavioral control in awake, behaving animals (Rose and Fortune, 1996). Our work has shown that weakly electric fish, especially *Eigenmannia* and *Apteronotus*, are found in groups of two or more conspecifics (Tan et al., 2005; Stamper et al., 2010) and nearby fish receive continuous electrosensory oscillations caused by the interactions from the electric fields of each individual. These fish also simultaneously process electrosensory information from their own movement and the movement of nearby objects in their environment. These two streams of information, one derived from social interactions and the other from movement, are processed for the independent control of the fish's electric organ and the fish's locomotor system. How these and other animals separate multiple streams of information for feedback control is a fundamental question in neuroscience.

In weakly electric fish, information from these two streams of information have different spatial and temporal domains. Sensory feedback from social interactions between conspecifics typically results in global 'whole-body' activation (> 10 Hz) of electrosensory receptors whereas sensory feedback from prey items or other items in their environment results in local 'spatially-restricted' activation (< 10 Hz) of sensory receptors (Chacron et al., 2003). Interestingly, there are neural correlates of these spatial and temporal differences, which have been discovered in the primary electrosensory processing areas. Pyramidal neurons in the central medial segment (CMS) of the ELL generally respond best to low-frequency local stimuli whereas pyramidal neurons in the lateral segment of the ELL generally encode high frequency global stimuli (Krahe et al., 2008). Further, neurons in the central lateral segment (CLS) of the ELL show a remarkable property where the temporal tuning of neurons changes depending on the spatial extent of the stimulus (Chacron et al., 2003). These neurons respond best to low frequencies when the stimulus is local and high frequencies when the stimulus is global.

We were interested in further understanding how multiple overlapping streams of information are processed in the brain. To start to address this question we examined the details of social feedback information in weakly electric fish. We found that in the wild, these fish form social groups, which has implications for electrosensory processing (Chapter 2). We also found that fish respond to a newly described category of social feedback, known as envelopes, which can emerge both from the relative movement of conspecifics and the interactions of the electric fields in groups of three or more individuals (Chapter 3). Next, we investigated the relationship between movement and sensing and found that fish use two categories of active movement (whole-body

oscillations and tail bends) to shape the nature of the electrosensory feedback that they receive for the control of locomotion (Chapter 4). Our results suggest that the fish can independently modulate both social feedback and locomotor feedback to facilitate electrosensory processing.

Future directions

The logical next step is to examine the direct interactions between social signals and locomotor control. We have begun to address this in two ways. First, we've used laboratory experiments where we combine tracking behavior with social feedback to examine the interaction between these two categories of information. Second, we examined the natural locomotor behavior of groups of unconstrained fish in the wild. Both of these projects have produced interesting new results.

Previous work showed that *Eigenmannia* are impaired in electrolocation tasks where they swim sideways to 'follow' a small lateral moving object or row of objects (Heiligenberg, 1973; Matsubaraand Heiligenberg, 1978). However, this behavior has not been described for longitudinal refuge tracking behavior in these fish. We collected preliminary data that extends the previous results to include the effect of low and high frequency social signals on refuge tracking for a variety of shuttle movement frequencies.

In this preliminary experiment, individual fish (N=2) tracked a refuge that was moved according to a sum of six sines trajectory (0.1, 0.25, 0.55, 0.85, 1.15, 1.55 Hz) with control trials that had no social signal or a signal clamped to the fish's own EOD frequency and experimental trials that had a social signal of ±1 Hz or ±40 Hz relative to the fish's own EOD frequency (see Chapter 3 for generation of social signals method and

Chapter 4 for refuge tracking behavior method). Our data supports the previous findings, which show that fish are most impaired in electrolocation tasks in the presence of low-frequency signals (Figure 5.2A). The impairment appears to be alleviated to an extent with higher frequency social signals.

Based on neurophysiological results showing an increase in direction selectivity in midbrain neurons in the presence of high-frequency AMs (Ramcharitar et al., 2006) we expected to see enhancement in the tracking response in the presence of high frequency AMs. This was not what we found. Rather, these data align with previous reports that also did not show enhancement (Heiligenberg, 1973; Matsubaraand Heiligenberg, 1978; Bastian, 1987). It is possible that we did not find this because we simply are not yet giving the fish the right kind of task. We have tried several other tasks, including step responses, but more work is necessary.

Nevertheless, we found an unexpected change in behavior in the presence of jamming signals. We find that in the presence of low-frequency social signals the magnitude of the whole-body oscillation is decreased (Figure 5.2B). There are many reasons why this might be happening. First, there maybe a motivational shift due to currently described effects of social ordering or dominance that is being triggered by these signals. Second, the fish could truly be 'blinded' by the low-frequency signals and in a strategy to minimize costs, reduces its own movement. Importantly, this reduction in movement does not mean that the fish is failing at the task, which is to remain in the shuttle. The trajectory of the shuttle is such that remaining stationary is in fact the optimal strategy, in terms of energy expenditure, for staying in the shuttle. Third, the low-frequency jamming may specifically interfere with the whole-body oscillations that

appear to be necessary for good tracking in the absence of visual cues. Or, of course, some combination of these or other reasons are possible. Further behavioral and neurophysiological experiments will be necessary to shed light on this interesting result.

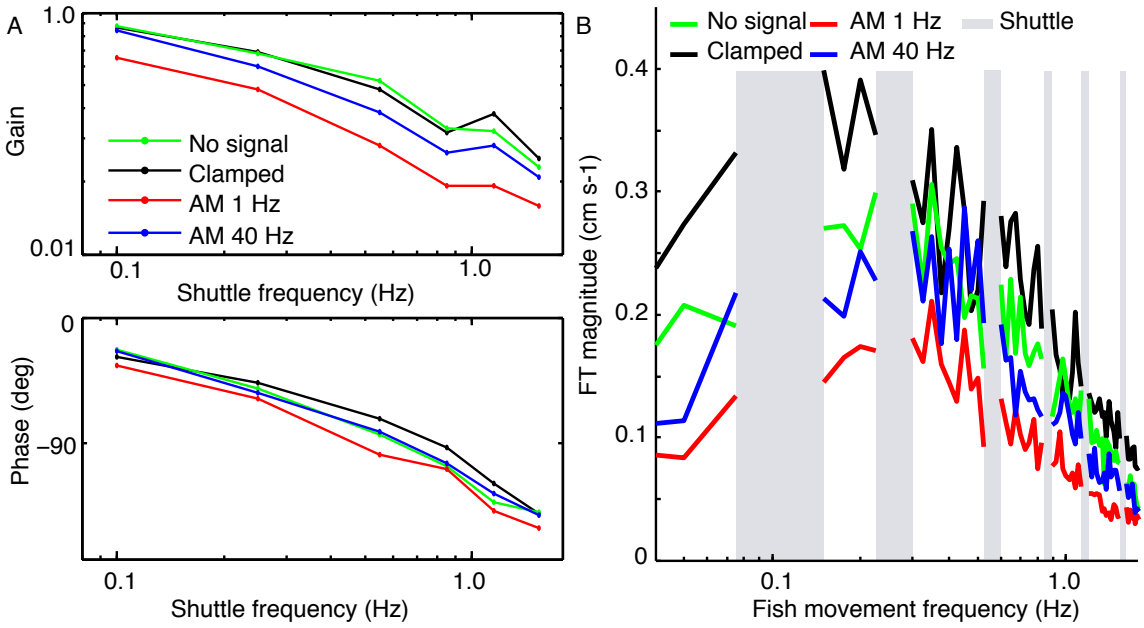

Figure 5.2 Refuge tracking behavior in the presence of social signals
(**A**) The Bode plot shows that for all shuttle frequencies the tracking performance of the fish (measured by gain) is most impaired for low-frequency (red) and less impaired for high-frequency (blue) AMs compared to control trials (green and black). There were no substantial differences observed in the phase of the tracking behavior as a function of the social signal. (**B**) This plot shows the magnitude of the whole-body oscillations that are observed when the fish relies on electrosensory information for tracking. The peaks corresponding to the shuttle movement have been removed (grey bars). We found that the magnitude of the oscillations decreased for tracking in the presence of low-frequency social signals (red lines). This raises an interesting possibility that the whole-body oscillations are important for maintaining tracking performance in the dark. Why the magnitude of the oscillations decreases during jamming remains an unanswered question.

We have also collected field data that allows us to examine social behavior in relation to movement patterns for groups of unconstrained fish in the wild. For these studies we deployed a 1.5 x 1.5 m array of 16 electrodes at our study sites in Ecuador (Figure 2.1). Preliminary analysis suggests that the social behavior and relative movements of the fish is far more complicated than previously thought (Figure 5.1). This data builds upon that reported in Chapter 1 because it was composed of a grid of 16 electrodes instead of a single electrode for recording the fish's EODs. This has the distinct advantage of allowing us to determine the relative positions of individuals and monitor their movement over time. In addition, we also recorded samples for an extended period of time (up to 600 s).

This data strongly suggests that the fish EODs are not as stable as previously reported (Bullock, 1969; Bullock et al., 1975; Moortgat et al., 1998; Zakon et al., 1999; Zakon et al., 2002). In the example figure, the individual EOD frequencies over the entire 360 s recording time (Figure 5.1A) are fluctuating by up to 15 Hz whereas for a given 10 s sample they appear stable (Figure 5.1B). This sample also shows many social behaviors that have not yet been described in the literature. First, the fish appear to have divided their EOD frequencies into discrete bands, which might be related to social envelope processing. Second, fish also appear to be crossing their EOD frequencies and are within jamming range for short periods of time. Third, changes in fish EOD appear to occur as the fish moves (indicated by a change in color which represents the intensity of the signal at the electrode). This preliminary data makes it clear that future studies should examine the role of social signals produced by conspecifics in relation to movement processing of both nearby conspecifics and objects.

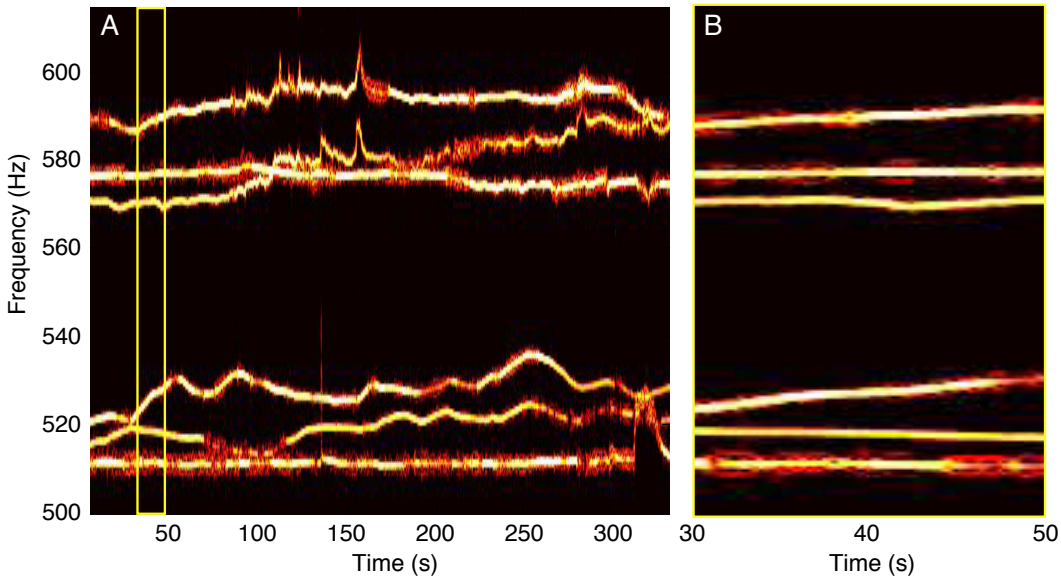

Figure 5.1 Sample extended recording of EODs in groups of fish
Frequency bands and EOD jamming in wild populations of *Eigenmannia*
In the wild electric fish appear to divide their EOD frequencies into bands, which might be related to the electrosensory social envelope. These same fish also change their EOD frequencies over time, occasionally crossing over the frequency of another fish that could lead to that fish being jammed.

Concluding remarks

Animals depend on sensory information to control behavior. Weakly electric fish use active sensing, the generation of signals and movements, to obtain and modulate incoming sensory information. We found that there are complex relationships between social behavior and movement on sensory feedback, which go beyond our current understanding of how fish use and process electrosensory information. Our data highlight the fact that social context can categorically change the sensory signals that animals receive. It also indicates that animals are likely regulating sensory feedback through their movement. These results suggest that sensing is not a static process but is instead dynamically altered by the social context and movements of the animal.

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B.A. Biological Psychology
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Honors, Awards, and Grants

- **Mary D. Ainsworth Fellowship** Johns Hopkins Departmental Award 2011-2012
- **National Science Foundation** Graduate Research Fellowship 2008-2011
- **Acoustical Society of America** Conference Travel Award 2008
- **Marine Biology Laboratory** Milton L. Shifman Endowed Scholarship 2008
- **Brown University** Graduate Fellowship 2007-2008
- **New College of Florida** Foundation Research Grant 2005; 2006
- **New College of Florida** Alumni Research and Travel Grant 2005; 2006
- **New College of Florida** Tuition Scholarship 2002-2006

Peer-Reviewed Publications

Stamper, S.A., Roth, E. Cowan, N.J., & Fortune, E.S. (2012) Active sensing via movement shapes spatiotemporal patterns of sensory feedback. J Exp Biol, 215: 1567-1574.

Bauer, G.B., Gaspard, J.C., Colbert, D.E., Leach, J.B., **Stamper, S.A.,** Mann, D.A., & Reep, R.L. (2012). Tactile discrimination of textures by Florida manatees (*Trichechus manatus latirostris*) Mar Mammal Sci. In Press

Roth, E., Zhaung, K., **Stamper, S.A.**, Fortune, E.S. & Cowan, N.J. (2011). Stimulus predictability mediates a switch in locomotor smooth pursuit performance for *Eigenmannia virescens*. J Exp Biol, 214:1170-1180.

Stamper, S.A., G-Carrera, E., Tan, E.W., Fugere, V., Krahe, R., & Fortune, E.S. (2010) Species differences in group size and electrosensory interference in weakly electric fishes: Implications for electrosensory processing. Brain Beh Res 207:368-376.

Hitschfeld, E., **Stamper, S.A.**, Vonderschen, K., Fortune, E.S., & Chacron, M.J. (2009). Effects of restraint and immobilization on the electrical behaviors of weakly electric fish. ILAR J 50: 361-372.

Stamper, S.A., Bates, M.E., Benedicto, D., & Simmons, J.A. (2009). Role of broadcast harmonics in echo delay perception by big brown bats. J Comp Physiol A 195:79-89.

Stamper, S.A., Simmons, J.A., DeLong, C.M., & Bragg, R. (2008). Detection of targets co-localized in clutter by echolocating big brown bats (Eptesicus fuscus). J Acoust Soc Am 124:667-673.

Bates, M.E., **Stamper, S.A.**, & Simmons, J.A. (2008). Jamming avoidance response of big brown bats in target detection. J Exp Biol 211:106-113

Horowitz, S.S., **Stamper, S.A.**, & Simmons, J.A. (2008). Connexin expression in the cochlear nucleus of echolocating big brown bats. Brain Res 1197:76-84.

DeLong, C.M., Au, W. W., & **Stamper, S.A**. (2007). Echoic cues used by human listeners to discriminate among objects that vary in material or structure: Implications for echolocating dolphins. J Acoust Soc Am 121:605-617.

Submitted Manuscripts

Fellner, W., Bauer, G.B., **Stamper, S.A.,** Losch, B. & Dahood, A. (under revision). The development of synchronous movement and complex behaviors by bottlenose dolphins (*Tursiops truncatus*). Mar Mammal Sci.

Stamper, S.A., Madhav, M.S., Cowan, N.J., & Fortune, E.S. Beyond the Jamming Avoidance Response: Weakly electric fish respond to the envelope of social electrosensory signals. J Exp Biol.

Peer-Reviewed Conference Papers

Hiryu, S., Shimamoto, H., Bates, M., **Stamper, S.A.,** Simmons, J. A., and Riquimaroux, H. (2008) Jamming avoidance strategy for temporal overlap of own reverberant echoes by FM echolocating bats (*Eptesicus fuscus*) during flight, revealed by telemetry sound recording. The Acoustical Society of Japan, Trans. Tech. Comm. Psychol. Physiol. Acoust., 38, 221-226.

Book Chapters

Raghavan, C., Sherman, J., Stiles, C., Roberts, O. & **Stamper, S.A.** (2009). "Doing-Gender": Parental beliefs about gender identity in Asian-Indian immigrant families. *In* Benefiting by Design: Women of Color in Feminist Psychological Research, Eds C. Raghavan, A.E. Edwards and K. Vaz, Cambridge.

Conference Presentations

Stamper, S.A., Madhav. M.S., Cowan, N.J., & Fortune, E.S (2012, Oct). Social envelope responses in Eigenmannia and Apteronotus. 43rd annual meeting of the Society for Neuroscience, New Orleans LA

Tytell, E.D., **Stamper, S.A.**, Cowan, N.J., & Fortune, E.S (2012, Oct). Direction selective sensory neurons respond to very low frequencies. 43rd annual meeting of the Society for Neuroscience, New Orleans LA

Stamper, S.A., Roth, E., Cowan, N.J., & Fortune, E.S (2012, Aug). Beyond the Jamming Avoidance Response: Eigenmannia respond to social envelopes. 10th Congress of the International Society for Neuroethology, College Park, MD.

Stamper, S.A., Roth, E., Cowan, N.J., & Fortune, E.S (2011, Nov). Modality-specific changes in locomotor behavior indicate increased costs for active sensing. 42nd annual meeting of the Society for Neuroscience, Washington DC.

Madhav, M., **Stamper, S.A.**, Roth, E., Cowan, N.J., & Fortune, E.S (2011, Nov). Weakly electric fish change their electric organ discharges in response to electrosensory envelopes. 42nd annual meeting of the Society for Neuroscience, Washington DC.

Fortune, E.S., **Stamper, S.A**., Tytell, E.D., & Cowan, N.J. (2011, Nov). Role of direction selective responses in locomotor control. 42nd annual meeting of the Society for Neuroscience, Washington DC.

Stamper, S.A., Madhav, M., Cowan, N.J., & Fortune, E.S (2011, May). Shifts in behaviors under varying sensory and social cues for refuge tracking by electric fish. 3rd annual Electrosensory Processing meeting, Montreal, Canada.

Stamper, S.A., Madhav, M., Cowan, N.J., & Fortune, E.S (2011, May). Behavioral response to envelope stimuli that impair electrosensory processing. 3rd annual Electrosensory Processing meeting, Montreal, Canada.

Madhav, M. **Stamper, S.A.,** Fortune, E.S., Cowan, N.J. (2011, Feb). Identifying an unstable sensorimotor behavior: the Jamming Avoidance Response in Eigenmannia. 11th annual Conference on Computation and Systems Neuroscience, Salt Lake City UT.

Roth, E., Zhang, K., **Stamper, S.A.,** Fortune, E.S., Cowan, N.J. (2011, Feb). Stimulus predictability mediates a switch in locomotor smooth pursuit performance for Eigenmannia. 11th annual Conference on Computation and Systems Neuroscience, Salt Lake City UT.

Stamper, S.A., Madhav, M., Cowan, N.J., & Fortune, E.S (2010, Aug). Envelope avoidance response in Eigenmannia virescens. 9th Congress of the International Society for Neuroethology, Salamanca, Spain.

Stamper, S.A., Carver, S., & Fortune, E.S (2009, Oct). Multimodal integration in midbrain neurons of Eigenmannia virescens. 40th annual meeting of the Society of Neuroscience, Chicago IL.

Madhav, M. **Stamper, S.A.,** Roth, E., Fortune, E.S., & Cowan, N.J. (2009, Oct). Balancing the Jamming Avoidance Response: Closed-loop identification of an unstable sensorimotor behavior. 40th annual meeting of the Society of Neuroscience, Chicago IL.

Simmons, J.A., Bates, M.E., **Stamper, S.A.** & Benedicto, D. (2008, Nov). Perception of echoes with FM1-FM2 delay disparities: Bats have selective direction-of-gaze high-resolution imaging. 156th meeting of the Acoustical Society of America, Miami FL.

Stamper, S.A., DeLong, C.M., & Simmons, J.A. (2008, Oct). Spatial separation between target and clutter enhances detection performance by echolocating bats. 38th North American Symposium on Bat Research, Scranton PA.

Simmons, J.A., Bates, M.E., & **Stamper, S.A**. (2008, Oct). Perception of target shape and rejection of clutter: Two sides of the same coin. 38th North American Symposium on Bat Research, Scranton PA.

Robb, A.C., **Stamper, S.A.**, & Swartz, S.M. (2008, Oct). Multimodal target facilitates odor discrimination training in lesser dog-faced fruit bats. 38th North American Symposium on Bat Research, Scranton PA.

Stamper, S.A., Bates, M.E., Benedicto, D. & Simmons, J.A. (2008, Aug). Degradation of FM-bat echo delay acuity from misaligned harmonics. 2nd International Conference on Communication by Animals, Corvalis OR.

Bates, M. E., Hiryu, S., Shimamoto, H., **Stamper, S. A.,** Simmons, J. A. and Riquimaroux, H. (2008, Jul). Bats employ auditory streaming to avoid masking in complex acoustic scenes. Gordon Research Conference: Auditory System, New London NH.

Stamper, S.A. & Simmons, J.A. (2007, Jul). Laboratory model of insect detection in clutter by echolocating bats. 44th meeting of the Animal Behavior Society, Burlington VT.

Bates, M.E., **Stamper, S.A. &** Simmons, J.A. (2007, Jul). Active interference avoidance in echolocating bats. 44th meeting of the Animal Behavior Society, Burlington VT.

Horowitz, S.S., **Stamper, S.A.**, & Simmons, J.A. (2007, Jul). Connexin expression in the cochlear nucleus of echolocating big brown bats as a possible substrate for echolocation temporal precision. 8th congress for the International Society for Neuroethology, Vancouver, Canada.

Simmons, J.A., Bates, M.E., & **Stamper, S.A.** (2007, Jun). Jamming Avoidance reveals segregation of processing for detection and ranging in echolocating bats. 153rd meeting of the Acoustical Society of America, Salt Lake City UT.

Stamper, S.A. & Simmons, J.A. (2007, Mar). Perception of targets in scenes by echolocating bats. 14th meeting of the Comparative Cognition Society, Melbourne FL.

DeLong, C.M., **Stamper, S.A.**, & Simmons, J.A. (2007, Mar). Object perception in clutter by echolocating big brown bats. 14th meeting of the Comparative Cognition Society, Melbourne FL.

DeLong, C.M., **Stamper, S.A.**, & Simmons, J.A. (2006, Nov). Detection of objects in complex environments by echolocating big brown bats. 4th joint meeting of the Acoustical Society of America and the Acoustical Society of Japan, Honolulu HI.

Bauer, G.B., Gaspard III, J.C., Colbert, D.E., Leach, J.B., **Stamper, S.A**., Sarko, Hammelman, J., Schmeig, A., D., Mann D., & Reep, R. (2005, Dec). Tactile discrimination by Florida Manatees, *Trichechus manatus latirostris.* 16th meeting for the Society of Marine Mammalogy, San Diego CA.

Fellner, W., **Stamper, S.A.,** Losch, B.A., Dahood, A. & Bauer, G.B. (2005, Dec). The development of synchrony and behavior in bottlenose dolphins. 16th meeting for the Society of Marine Mammalogy, San Diego CA.

DeLong, C.M., Au, W.W.L., Roitblat, H.L., Pytka, L., & **Stamper, S.A**. (2005, Dec). Human listening studies reveal insights into echo features used by echolocating dolphins to discriminate among objects. 16th meeting for the Society of Marine Mammalogy, San Diego CA.

Fellner, W., **Stamper, S.A.,** Losch, B.A., Dahood, A. & Bauer, G.B. (2005, Nov). The development of synchrony and behavior in bottlenose dolphins. 33rd meeting of the International Marine Animal Trainers Association, Key West, FL.

Fellner, W., **Stamper, S.A.,** Losch, B.A., Dahood, A. & Bauer, G.B. (2005, Jul). The development of synchrony in bottlenose dolphins. 1st meeting Animal Social Learning, St. Andrews, Scotland.

DeLong, C.M., Au, W. W., & **Stamper, S.A**. (2005, Mar). Echo features used by human listeners and echolocating dolphins to discriminate among cylinders with different wall thicknesses. 13th meeting of the Comparative Cognition Society, Melbourne FL.

Teaching Experience

Johns Hopkins University, Psychological and Brain Science

- Sensory Exotica (Instructor) — Winter 2012
- Laboratory Analysis of Psychological Data (Instructor) — Fall 2010; 2011
- Neuroscience laboratory (Invited lecturer) — Spring and Fall 2009-2011
- Animal Behavior (TA for Dr. Gregory Ball) — Spring 2009
- Advanced Statistical Methods (TA for Dr. Steven Yantis) — Fall 2009

Brown University, Psychology

- Introduction to Sleep (TA for Dr. Mary Carskadon) — Fall 2008
- Mechanisms of Animal Behavior (TA for Dr. Andrea Simmons) — Spring 2008

Brown University, SPARK Program

- Echolocation in Bats and Dolphins (Instructor) — Summer 2005, 2006, 2007

New College of Florida, Psychology

- Animal Cognition Laboratory (Instructor) — Fall 2005
- Cognitive Psychology (TA for Dr. Heidi Harley) — Spring 2005
- Social Psychology (TA for Dr. Chemba Raghavan) — Spring 2005
- Developmental Psychology (TA for Dr. Michelle Barton) — Spring 2004
- Introduction to Statistics (TA for Dr. Gordon Bauer) — Fall 2004
- Introduction to Statistics Laboratory (Co-Instructor)
- Introduction to Psychology (TA for Dr. Gordon Bauer) — Fall 2004

Service & Outreach

- **Johns Hopkins University** GradNet Peer Mentor — 2010-2012
- **Johns Hopkins University** Brain Awareness Week Program Presenter — 2009-2011
- **Johns Hopkins University** Graduate Steering Committee Rep — 2009-2010
- **Johns Hopkins University** Women in Science & Engineering Mentor — 2009-2011
- **Brown University** Dept of Psychology, Graduate Student Rep — 2008-2009
- **Amgen Rhode Island Science and Engineering Fair** Judge — 2008
- **Brown University** Women in Science & Engineering Mentor — 2007-2009
- **Brown University** Graduate Student Council, Psychology Rep — 2007-2009