Summer 8-31-2015

The role of electronsensory signals on the locomotor performance of the weakly electric fish apteronotus albifrons

Oswaldo Gil-Guevara
New Jersey Institute of Technology

Recommended Citation

Gil-Guevara, Oswaldo, "The role of electronsensory signals on the locomotor performance of the weakly electric fish apteronotus albifrons" (2015). *Theses*. 251.
https://digitalcommons.njit.edu/theses/251

ABSTRACT

THE ROLE OF ELECTRONSENSORY SIGNALS ON THE LOCOMOTOR PERFORMANCE OF THE WEAKLY ELECTRIC FISH APTERONOTUS ALBIFRONS

by
Oswaldo Gil-Guevara

Animal locomotion performance responds to different ecological factors that shape relevant aspects of behavior. Conspecific signals is one of these factors and operates in a wide range of contexts. In schooling fish, coordinated movement is based on visual or mechanical cues and signals. In contrast, most gymnotiforms and mormyriforms are nocturnal or live in dark waters and use electric signals for social communication. However, the effect of conspecific electric signals on locomotion and group movement is largely unknown.

Apteronotus albifrons is a well-known model in neuroethological studies of signal processing and locomotion control that relies mostly on visual inputs but can switch to electric sense in low illumination levels to navigate and interact with the environment. Conspecific electric signals might be sufficient to produce changes in locomotor behavior that reflect basic rules of group movement interactions (attraction, repulsion or coordination). To test this hypothesis, recordings of locomotor behavior under two simple were compared using two experimental conditions: single and pairs of weakly electric fish.

THE ROLE OF ELECTRONSENSORY SIGNALS ON THE LOCOMOTOR PERFORMANCE OF THE WEAKLY ELECTRIC FISH APTERONOTUS ALBIFRONS

by
Oswaldo Gil-Guevara

A Thesis
Submitted to the Faculty of
New Jersey Institute of Technology
and Rutgers, The State University of New Jersey - Newark
in Partial Fulfillment of the Requirements for the Degree of
Master of Science in Interdisciplinary Studies

August 2015

.

APPROVAL PAGE

THE ROLE OF ELECTRONSENSORY SIGNALS ON THE LOCOMOTOR PERFORMANCE OF THE WEAKLY ELECTRIC FISH APTERONOTUS ALBIFRONS

Oswaldo Gil-Guevara

Dr. Simon Garnier, Thesis Co-Advisor — Date
Assistant Professor of Biology, NJIT

Dr. Eric Fortune, Thesis Co-Advisor — Date
Associate Professor of Biology, NJIT

Dr. Gareth Russell, Committee Member — Date
Professor of Biology, NJIT

BIOGRAPHICAL SKETCH

Author: Oswaldo Gil-Guevara

Degree: Master of Science

Date: May 2015

Undergraduate and Graduate Education:

- Master of Science in interdisciplinary studies,
  New Jersey Institute of Technology,
  and Rutgers, The State University of New Jersey – Newark, 2015

- Master of Science in Biology,
  Universidad de los Andes, Bogotá D.C., Colombia, 2009

- Bachelor of Science in Biology,
  Pontificia Universidad Javeriana, Bogotá D.C., Colombia, 2005

Major: Biology

Presentations and Publications:

Oswaldo Gil-Guevara and A. Amézquita. 2013. Adjusted phonotactic reactions towards sound intensity and fine temporal traits mediate territorial defense in the poison dart frog *Oophaga histrionica*. (*In preparation*).

Oswaldo Gil-Guevara and A. Amézquita. 2013. Ecological and acoustic correlates of cave breeding in the poison frog *Ranitomeya virolinensis* (Anura: Dendrobatidae). (*In preparation*).

Melanie Rutkowski, Ximena Escovar-Fadul, Fahmida Sarmin, Tom Stephen, Michael Allegrezza, Oswaldo Gil-Guevara, Amelia Tesone, and Jose Conejo-Garcia. TLR5 mediated regulation of tumor growth in an inducible model of cancer. Journal of Immunology, 2012, 188, 162.48

Oswaldo Gil-Guevara and Adolfo Amézquita. 2011. Adjusted phonotactic reactions towards sound intensity and fine temporal traits mediate territorial defence in the poison dart frog *Oophaga histrionica.* Poster presentation. (Meeting Abstract Supplement) Acoustic Communication by Animals. Third international Symposium, 1-5 August 2011, Cornell University Ithaca, NY USA.

Oswaldo Gil-Guevara and Adolfo Amézquita 2008. Call temporal structure and call amplitude affect the phonotactic reaction of territorial males of Oophaga histrionica (Anura: Dendrobatidae). Poster presentation. 6th World congress of Herpetology. 17-22 August 2008. Manaus, Brazil

Dedicated to my beloved wife, Solimar
…and to Orion.

ACKNOWLEDGMENT

I deeply thank to Dr. Eric Fortune and Dr. Simon Garnier for all the guidance and assistance through the all phases of this study. I Thank Dr. Gareth Russell for serving as Committee member and his advice on the statistical analysis. I really appreciate the contributions of Subash Ray and Anwar Haroon to many of the programing challenges. I greatly appreciate the contribution of Caroline DeVan, Melissa Sanchez and Courtney Rockenbach for commentaries on earlier drafts of this manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES
(Continued)

CHAPTER 1

INTRODUCTION

1.1 Background Information

Locomotion is defined as the movement through the environment. Locomotor behaviors are essential for the survival of many species, which is strongly reflected in their morphology and physiology (Dickinson et al. 2000). In social species, signals may be used as a mechanism of coordination of movement allowing advantages derived from remaining in close proximity. Signals may encode and transmit a variety of biologically significant information such as location, species and individual identity, size, physical condition, competitive ability and motivational state (Bradbury & Vehrencamp 1998). Animals in groups may use a combination of signals and cues to coordinate movement (Bradbury & Vehrencamp 1998; King & Sueur 2011).

Fish schooling is an example of social behavior that involves the coordination of movement. Schooling improves the efficiency of food location while reducing predation risk (Parrish & Edelstein-Keshet 1999). Weakly electric fish use electric signals as a form of communication in a wide range of contexts: species and individual recognition, mate attraction, territorial defense, schooling behavior, navigation, prey detection and capture (Moller 1976; Hopkins & bass 1981; MacIver et al. 2001; Albert et al. 2005; Tan et al. 2005; Stamper et al. 2010, 2012a). However, little is known about how these fish use electrosensory signals for the coordination of locomotion between individuals.

In general, group living may serve several adaptive functions (anti-predatory, foraging territorial defense, mating) that are advantageous when group members remain in close proximity. These benefits, therefore, require biological mechanisms that maintain group cohesion (Bradbury & Vehrencamp 1998). However, not all individuals within a group respond in the same way. The study of animal group coordination has shown that the individual variation in behavior is an important aspect (Réale et al. 2007). Although within populations all individuals face the same local conditions, individuals display phenotypes with a concomitant variation in behavior due to physiological and environmental factors (Stamps 2003). Consequently, the variation in behavior also extends to the intra-individual level where environmental stochasticity (ecological variation), social environment, development and experience modulate individual behavior (Réale et al. 2007).

1.2. Behavioral Syndromes

Consistent differences in behaviors within individuals are called personality traits and have now been identified across animal taxa (Réale et al. 2007; Adriaenssens & Johnsson 2011). The most studied aspect of personality is the 'shyness – boldness' continuum, in which some individuals react with less or more caution to novel stimuli across different contexts (Sloan Wilson et al. 1994). The term behavioral syndromes refers to groups of associations between personality traits, that is, personality traits are linkages between seemingly unrelated behavior (Sih et al. 2004). For example, boldness is associated with aggressiveness and exploration (Bell et al. 2009). Within the factors that might affect personality traits, learning from others, and previous experience can be considered plastic

(Frost et al. 2007). Therefore, a set of criteria is required to determine the occurrence of behavioral syndromes within a population.

To measure the plausibility of personality traits within a population, phenotypic variation is expected to occur for that particular trait among individuals (Réale et al. 2007). A population or species can exhibit a behavioral syndrome with each individual showing a behavioral type (e.g. more bold or more shy) (Sih et al. 2004). More importantly, despite the variation among individuals, within individual variation should be consistent in the expression of that particular behavior (Réale et al. 2007). In order to assess the consistency of a trait, the repeatability of that trait along time can be used to estimate the individual consistency of a trait (Réale et al. 2007). For this purpose, repeated measures on the same individuals allows the exploration of the potential association between personality and behavioral flexibility to reveal their ecological implications (Réale et al. 2007; Adriaenssens & Johnsson 2011).

1.3 Electroperception in Weakly Electric Fish

In general, animal locomotion requires the complex integration of sensing, control, and mechanics (Cowan & Fortune 2007). Many species use active sense, where animals expend energy for the purpose of sensing (Nelson & MacIver 2006; Stamper et al. 2010), for navigation or and locomotor control. Active sensing in weakly electric fish includes the generation of a sensory signal (their electric field), as well as movement through the environment for the purpose of sensing (Heligenberg 1975; Assad et al. 1999; Babineau et al. 2007).

The order Gymnotiformes is a highly specialized group of neotropical fish that inhabit freshwater systems across the historical Amazon basin (Silva et al. 2007). These fish use their electroreceptor system to sense objects and conspecifics in turbid water with low visibility and at night (Gelfand et al. 1989; Rojas & Moller 2002; Albert et al. 2005; Fortune 2006). Several species of weakly electric fish are well known models for the study of electric signaling behavior. In particular, *Apteronotus albifrons* is a gymnotiform weakly electric fish equipped with an electric organ that generates a continuous wave-type electric organ discharge (EOD) (Nelson & MacIver 1999). Previous study in the closely related species *Apteronotus leptorhynchus* investigated the relationship between the production of social signals (chirps) among pairs of physically interacting fish. These chirps correspond to frequency modulations of the EOD were very brief frequency spikes are followed by a restoration of the baseline frequency. It has been shown, that freely interacting fish change the chirping behavior, and that change in its rate of production is related with social interactions (Hupé & Lewis 2008).

Weakly electric fish detect distortions in the self-generated electric field generated by its electric organ using electroreceptors embedded in the skin. These distortions are produced by nearby objects with different electric impedances from that of the surrounding water (Nelson & MacIver 1999). These differences result in small changes in the potential difference along the skin of the fish that are transduced by the electroreceptors. The skin of the fish contains two categories of electroreceptor organs. The tuberous electroreptors are tuned to the high frequency signals emitted by the fish and those of conspecifics (called active electrosense). The second type of electroreceptors are known as ampullary organs and detect low frequency electric fields emitted by other aquatic organisms (this is the passive electrosense). In addition fish have mechanoreceptors in the lateral line system (Nelson & MacIver 1999).

Wave-type weakly electric fishes, such as *Eingenmannia virescens* and *Apteronotus albifrons*, experience different electrosensory conditions when they are alone versus when they are in close proximity to another (Tan et al. 2005; Stamper et al. 2010). As the fish moves through the environment modifications of the electric field are generated. Therefore, the active electrosense of the tuberous organs are considered active because they detect distortions of the self-generated electric field, but also because the fish owns movements are simultaneously changing the electric landscape of the fish. When individual *Apteronotus* is in close proximity to conspecifics, the electric fields (Electric Organ Discharge, or EOD) interact and produce an emergent pattern of 'beats' that occur at rates equal to the frequency difference between the fish; the frequency of beats is termed beat rate (Heiligenberg et al 1978; Tan et al. 2005). In this context, *Apteronotus* elicit a specialized behavior to avoid detrimental beat rates, called the 'jamming avoidance response' (JAR). Basically during the JAR, the fish with the higher EOD frequency increases its signal frequency while the other decreases it augmenting the difference between their EOD and creating beat rates that do not impair their individual ability to electrolocate (Heilingenberg et al 1978; reviewed in Albert et al. 2005; Tan et al. 2005). The JAR constitutes an elegant solution for the interference problem.

In addition to the JAR, another behavioral strategy to avoid jamming when two or more individual fishes are in close range can be simply moving away from conspecifics. However, previous work has shown that *Apteronotus* are commonly found in groups both in the wild and in laboratory conditions (Oestreich 2005; Stamper et al. 2010). The densities of electrosensory schools of weakly electric fish have been studied both in field and laboratory conditions (Tan et al. 2005; Stamper et al. 2010). These studies have shown that despite the potentially detrimental effects of jamming, fish remain in groups of 2 or more individuals. In experiments that involved electrotaxis in the presence to an artificially generated signal, the electrosensory information seems to contribute to species differences in grouping (Stamper et al. 2010). Therefore, the JAR and other complementary behaviors allow the formation in groups.

Additionally, it is relatively well known that electric fish orientate in complete darkness by monitoring the electric images of nearby objects (Emde & Schwarz 2000). In *Apteronotus*, the EOD is quasi-sinusoidal and when fish are in close proximity (~1m or less) their EODs interact (Stamper et al. 2012b). Despite the ample knowledge on the electrolocation on several levels of organization, a full understanding of the effect of conspecific signals on the locomotor behavior of weakly electric fish remains largely unknown.

In the present study, I test the hypothesis that the EOD signal of *Apteronotus albifrons* alone is sufficient to produce changes in locomotor behavior that reflect the basic rules of group movement interactions (attraction, repulsion or coordination). For this purpose, I tested the responses of individuals in two conditions: solitary fish and individual pairs of fish, allowing for active sensing, while experimentally controlling any other sensory modality. For this purpose all experiments were performed in dark conditions. It can be predicted that the presence of a conspecific signals will produce higher behavioral scores (locomotion parameters) for the fish groups. I also predict that if *A. albifrons* exhibits behavioral reactions consistent with behavioral syndromes then, the individual behavior should be consistent over time, and the individual identity could explain the differences in behavior across repeated trials (Adriaenssens & Johnsson 2011). In addition, it can be predicted that the different behavioral responses (behavioral traits) should form correlated suits of behaviors (Sih et al. 2004).

1.4 Objective

The present study aims to investigate the effects of conspecific signals on the locomotor behavior of *Apteronotus albifrons*. Experiments included two conditions – the presence or the absence of conspecific signals. The electrotactic response of individual fish was used to test: (1) whether the EOD alone is sufficient to elicit differential behavioral responses in shyness – boldness continuum, (2) whether the variation in the responsiveness of individual fish is consistent across trials over time and (3) whether the behavioral responses are intercorrelated.

CHAPTER 2

MATERIALS AND METHODS

This study aims to investigate the role of the presence of conspecifics on the locomotor behavior of *Apteronotus albifrons* individuals. In order to compare the behavior of individuals with their behavior when in the presence of a conspecific, several external locomotor parameters that describe swimming performance were measured on freely moving *A. albifrons*, alone and in pairs. The "real pairs" were *non-independent* (i.e. the behavior of each of the members of the pair is not independent of each other, as result of their interaction) pairs of *A. albifrons* that were recorded simultaneously. These real pairs were compared to "simulated pairs" which are *independent* pairs of the same two fish. These simulated pairs are a reconstruction of the corresponding real pair of fish made using each fish's positions obtained from an individual and, computing the swim parameters as if they were in the same test tank. To evaluate the actual effect of EOD signals on the locomotor behavior of fish under controlled conditions, every parameter was compared between the real and simulated pairs (Figure 2.1), with the simulated pair acting as a control group during the analysis of the experiments.

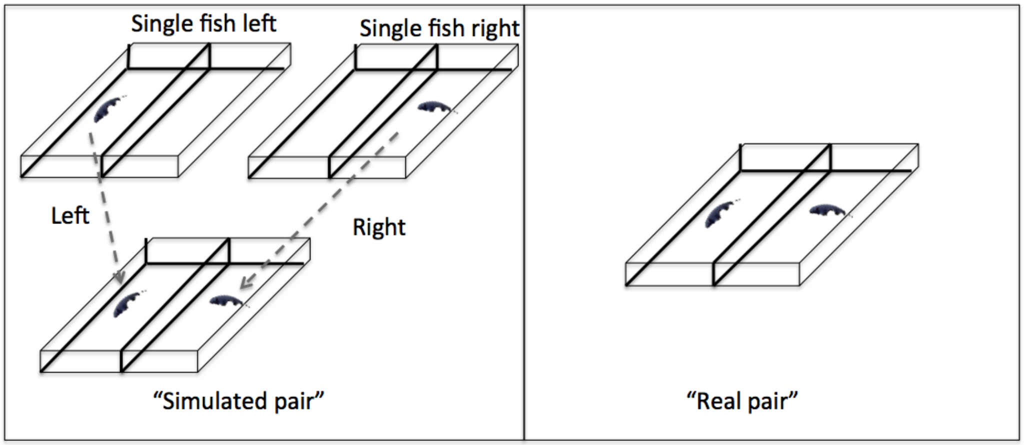


Figure 2.1 A "Simulated pair" is a control group constructed using data originated from two individual fish in a test tank after analyzing several behavioral parameters that describe the locomotion of each individual (see text for details). A "Real pair" consisted of the same two individuals tested simultaneously in a tank. The two conditions where posteriorly compared in further statistical tests.

Twenty-four adult individuals of *Apteronotus albifrons* were obtained from a commercial vendor. All fish were housed in the permanent "colony" aquariums, at 20 – 25°C in groups of 2 – 10 individuals. All the fish used in this study were acclimated for more than 4 weeks before the start of testing. Before each trial, each individual of *Apteronotus albifrons* was transferred to one of the three identical behavioral observation arenas or test tanks (width = 60 cm; length=75 cm; depth = 7cm, Figure 2.2).

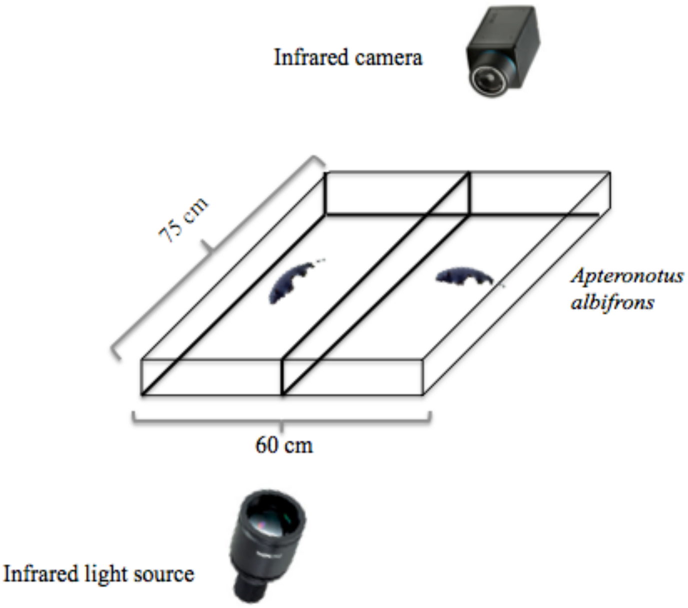


Figure 2.2 Scheme of the test tanks used for during the experiments. Rectangular tanks of 75 x 60 cm were divided in half using a plastic net. Because the experiments were performed in dark conditions, infrared light was used to record the behavior of each fish the translucent bottom of the tank allowed the pass of the infrared light, while an infrared camera was used to record the fish locomotion. Two electrodes in opposite corners of the tank were placed to record the EOD activity of the fish (see text for details).

All test tanks were mounted ensuring a constant flow of water, maintaining a temperature of 23-25 °C, a conductivity of around 30 µS/cm and a pH of 7.5. The test tanks were divided in half by a plastic net that prevented any direct physical contact between the pairs of *Apteronotus albifrons*, which might change their locomotor behavior. Simultaneously, it allowed the flow of the electric field or EOD through the whole test tank. Every tank was equipped with infrared cameras (USB 3.0 DCC3240x CMOS Camera, ThorLabs), and a source of infrared light (High-Power LED M850L3, peak of normalized intensity: 850nm, ThorLabs).

The bottom of the test tanks was translucent, allowing infrared light to pass through. Using infrared light ensured that the individuals did not rely on visual information to perform movement decisions. Additionally, recording electrodes using a custom-made amplifier system (Eric Fortune, personal communication) were placed on opposite diagonal corners of the test tanks (≈95.79cm) in order to register the EOD activity of interacting and single fish. The EOD activity of each individual was recorded simultaneously with the video recording, ensuring that the video recording and the electric activity were accurately synchronized in time. Both video and EOD data were acquired using Cambridge Electronic Design Power1401 hardware and Spike2 software (Cambridge, UK).

2.1 Experimental setup

Adult individuals of *Apteronotus albifrons* were transferred from the aquariums to the test tanks shortly after the start of the dark cycle. Each individual was allowed to acclimate to the test tanks for 24 hours prior to the start of the recordings in order to control for habituation effects on fish behavior. A random number generator produced combinations of individuals assigning them to either treatment 1 (single fish) or treatment 2 (pair of fish) avoiding use of the same individual on two consecutive days.

For eleven days, a daily recording session was conducted simultaneously on three identical test tanks; all recordings began at dusk (between 5:45 pm and 6:00 pm) in a darkened experimental room. The recordings consisted of 18 bouts of one minute each, at 10 minute intervals over three hours (Figure 2.3).

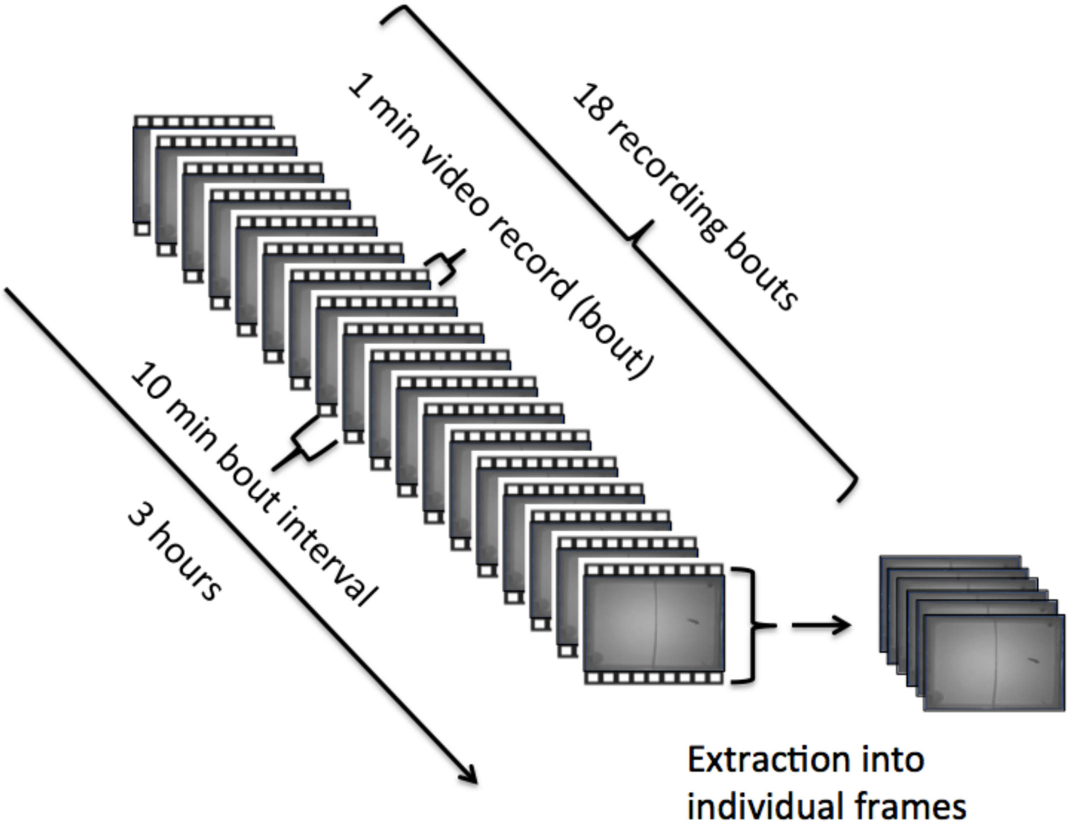


Figure 2.3 Schematic representation of the recording sequence during the experiments; on each of the three test tanks, 18 recording bouts of 1 minute each were performed every 10 minutes during 3 hours. Every recording was subject to extraction of individual frames (20 Hz).

2.2 Data Analysis

The digital video recordings consisted of 594 files that were processed and analyzed using customized scripts in MATLAB (MathWorks, Natick MA, USA; Eric Fortune, personal communication). Of these, 29 files contained widespread errors (across several individuals and treatments) and so those files were excluded from analysis. In only one experiment were more than two recording bouts excluded.

The Matlab tracking script identified and tracked every fish's centroid in each bout of video recording. The raw data consists of individual x and y coordinates that correspond to the position of every fish's centroid extracted from every frame in a bout of video recording. Each of the 18 recording bouts per session had a one-minute duration and were analyzed separately. Every recording bout contained 1200 frames, each with one observation of position (x and y coordinates) resulting in a frame rate of 20 Hz (Figures 2.3 and 2.4).

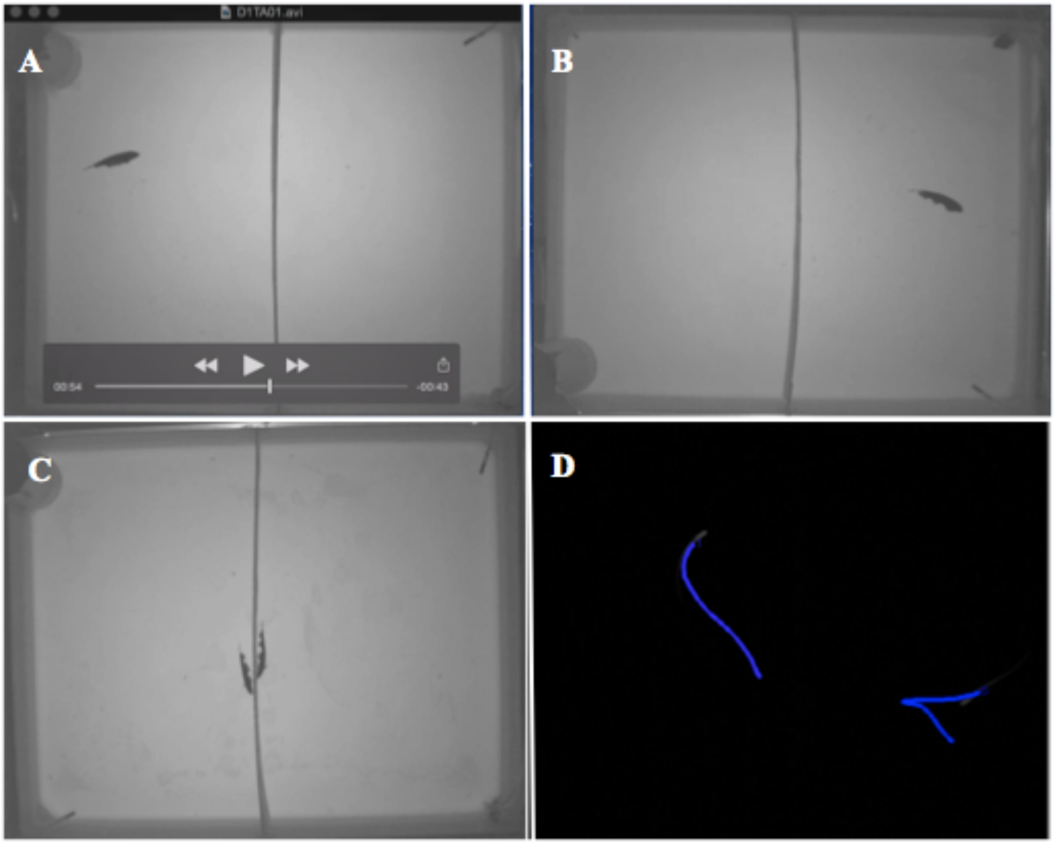


Figure 2.4 Example of image processing for data extraction. Sample video recordings under infrared light conditions of two *Apteronotus* individuals, separated by a dividing net under two situations: fish individual alone (A & B) and two fish together (C) (A) single fish on the left side of a tank; (B) a second fish on the right side of the tank; (C) the two fish interacting simultaneously on opposite sides of a tank and (D) fish movement tracking using customized Matlab scripts (MathWorks, Natick MA, USA).

Approximately 678,000 observations of individual positions of the fish centroid on the *x, y* plane were then used to compute several measurements that describe the locomotor performance across frames, within each recording bout and trial during the experiment. All measurements were computed using the Matlab customized scripts described above. Every measurement was converted from pixel units to cm.

In order to analyze both the effect of the presence of a conspecific (*i.e.* EOD signal) and personality traits (i.e. the shyness – boldness continuum, Wilson et al. 1994) on locomotor behavior, the different locomotor performance measurements are grouped into three categories of behavioral responses: boldness, attractiveness and activity level:

Boldness:

Distance to the dividing net: defined simply as the absolute distance on the y axis between the dividing midline and the y value for every fish's centroid position across frames and recording bouts.

Distance to the center of the half of the tank: Computation of the two-dimensional distance (*i.e.* straight line or Euclidean distance) between the fish's centroid and the center of the half of the tank available for the focal fish, for every frame per recording bout.

Attractiveness:

Distance between fish: Euclidean distance between left and right side fish for both "real" and "simulated" pairs (described above).

Activity:

Velocity: Calculated as the absolute value of the difference in the distance between adjacent positions across frames (cm/50ms) for every recording bout.

These behavioral responses are measured because they may represent behaviors important to fish fitness (e.g. feeding, communication, maneuvering) (Walker 1998).

2.3. Statistical Analysis

The mean and the median of each behavioral response were calculated for every recording bout and represent the swimming behavior performed by the fish during the experiment.

To test the effect of a conspecific signal on the locomotor behavior of individuals of *Apteronotus albifrons* a Kolmogorov-Smirnov test was performed on each parameter in order to compare the difference in the overall distribution of the two groups (real pairs and simulated pairs). An ANOVA analysis was used to compare the two groups for the measurement: distance between fish. Because distance between fish had a normal distribution, an ANOVA was performed. The other measures were not normally distributed and therefore a Kolmogorov test was required.

To examine the effect of the manipulation (presence or absence of conspecifics) over time, a Repeated Measures (RM) Analysis of variance (ANOVA) was employed. For this purpose the data for each behavioural response was transposed in a way that every recording bout (1 min of video) constituted a dependent variable. Then every bout and behavioural response was checked for normality and equality of variance. Then the mean and median values across the 18 bouts (18 video records) were used as within-subject factors and the type of couple (real or simulated pair) as between-subject factors. In addition, to test the effect of the fish identity on the behavioral responses across time, the independent variable "fish identity" (24 individuals) was included as a between-subject factor.

In order to test whether the behavioral responses are associated in consistently correlated groups of behaviors (e.g. personality traits, behavioral syndromes; Sih et al.

2004), these were analyzed using Spearman ranked Correlation. All statistical tests were conducted using the software SPSS 21.0 for Mac.

CHAPTER 3

RESULTS

Normality tests (Kolmogorov–Smirnov and Shapiro–Wilk) were used to determine whether the behavioral responses reflected an underlying normal distribution. With the exception of the *distance between fish,* all behavioral responses resulted in distributions that differed significantly from a normal distribution (Table 1).

Table 3.1 Summary of the Normality Test for all Behavioral Responses of *A. albifrons* during the Experiments

	Kolmogorov-Smirnov			Shapiro-Wilk		
Behavioral Response	**Statistic**	**df**	**p**	**Statistic**	**df**	**p**
Mean distance to the divisory net (cm)	0.031	828	0.066	0.985	828	<0.001
Median distance to the divisory net (cm)	0.124	828	<0.001	0.899	828	<0.001
Mean distance to the center of the mid-tank (cm)	0.034	828	0.025	0.995	828	0.013
Median distance to the center of the mid-tank (cm)	0.071	828	<0.001	0.978	828	<0.001
Mean distance between fish (cm)	0.036	403	0.2	0.994	403	0.134
Median distance between fish (cm)	0.034	403	0.2	0.99	403	0.01
Mean velocity (cm/s)	0.08	828	<0.001	0.951	828	<0.001
Median velocity (cm/s)	0.058	828	<0.001	0.951	828	<0.001

Conspecific signals affect the distance to the dividing net: when subjects were in pairs, individual fish tended to be closer to the net than in the control groups. A Kolmogorov-Smirnov Z test showed that there were statistically significant differences between the distance distributions of real and simulated pairs, when analyzing the mean (Kolmogorov-Smirnov, Z=1.552, P= 0.016, Figure 3.1, top panel) and median scores across all trials (K –S, *Z* = 1.835*, P*= 0.002, Figure 3.1, bottom panel). The data suggest that the presence of conspecifics can affect the boldness traits of individuals.

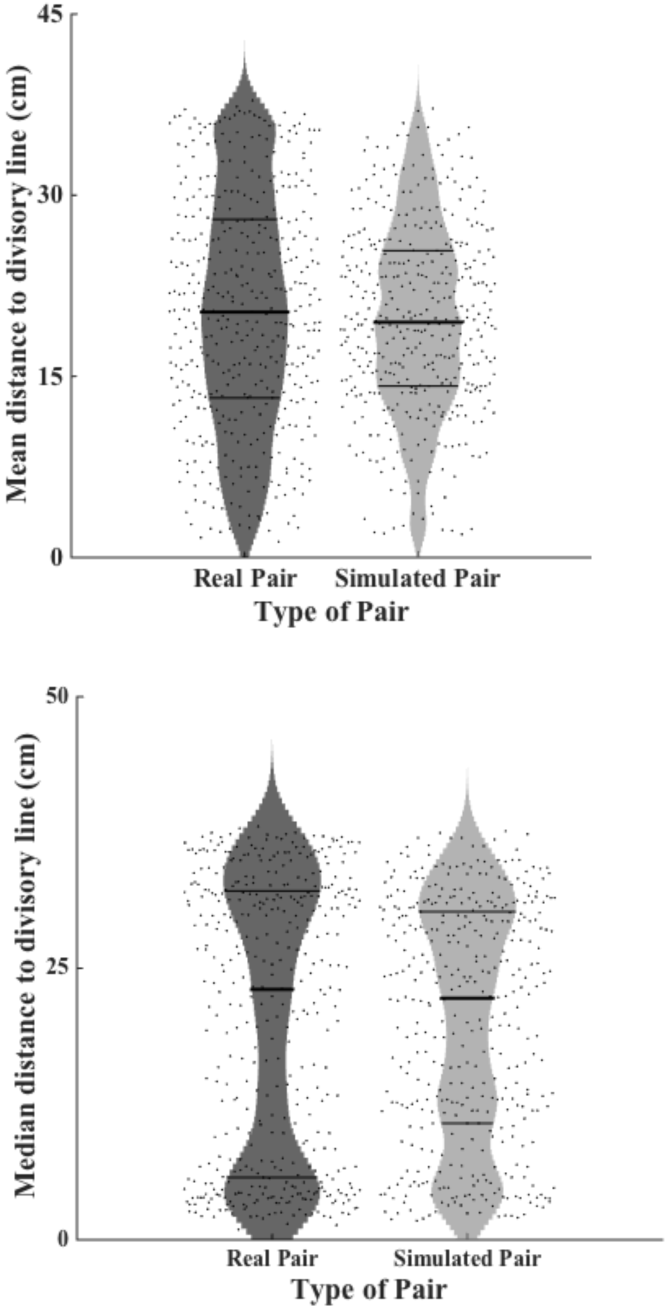


Figure 3.1 The presence of conspecifics affects the boldness traits of individuals. Violin plot showing the density distribution of the mean (top panel) and median (bottom panel) distance to the divisory line for the two conditions: Real and simulated pairs. The shape of the distributions of distances to the divisory line of real and simulated pairs differed significantly (K-S, Z=1.552, P= 0.016, top panel; K-S, Z = 1.835, P= 0.002, bottom panel).

A repeated measures ANOVA with a Greenhouse-Geisser correction (implemented due to a violation in assumptions of sphericity; Mauchly's Test: χ^2 (152) = 259.709, P<0.001) determined that mean distance to the dividing line does not differ statistically between time points ($F_{\text{(df 10.102, err 464.709)}}$ = 1.776, P= 0.062, Figure 3.2). Similarly, fish identity does not affect the distance to the net (RM ANOVA, Greenhouse-Geisser correction, fish identity: $F_{\text{(df 8.287 err 198.899)}}$ = 0.926, P = 0.703; Mauchly's χ^2 (152) = 201.407, P<0.012, N=864).

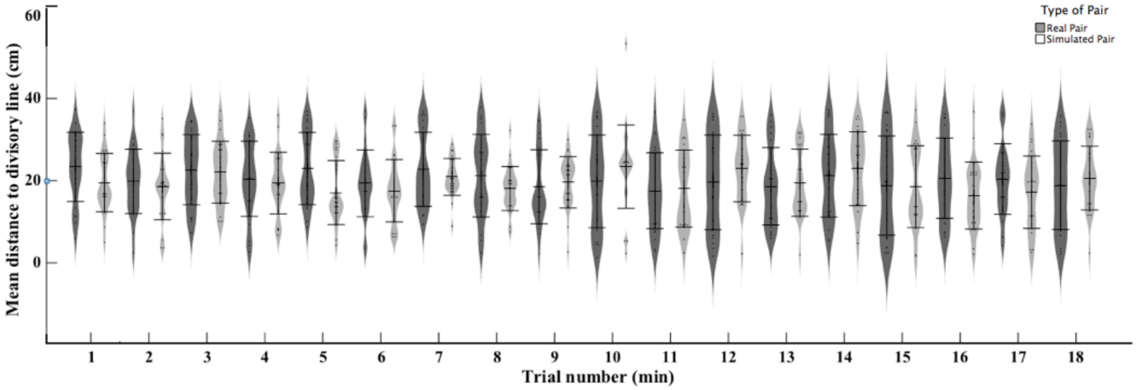
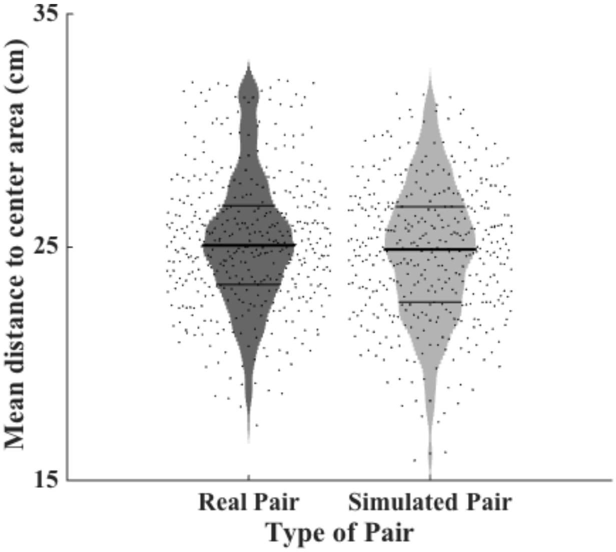


Figure 3.2. Change in the mean distance to the divisory line as a function of the time. Violin plot showing the density distribution of the mean distance to the divisory line for the two conditions: Real and simulated pairs.

A second behavioral response used to infer effects of boldness traits on fish behavior was the distance to the center of each half of the tank. The overall distributions of real and simulated pairs were not significantly different. The distribution of distances to the center across all trials for fish in real and simulated pairs remained roughly at similar distances (K-S, Z=1.115, P= 0.166, N= 832, Figure 3.3, top panel) and median scores (K–S, Z = 0.896, P=0.398, N= 832, figure 3.3, bottom panel). Relative to the center of the available area, the fish remained towards the edges of the tank.



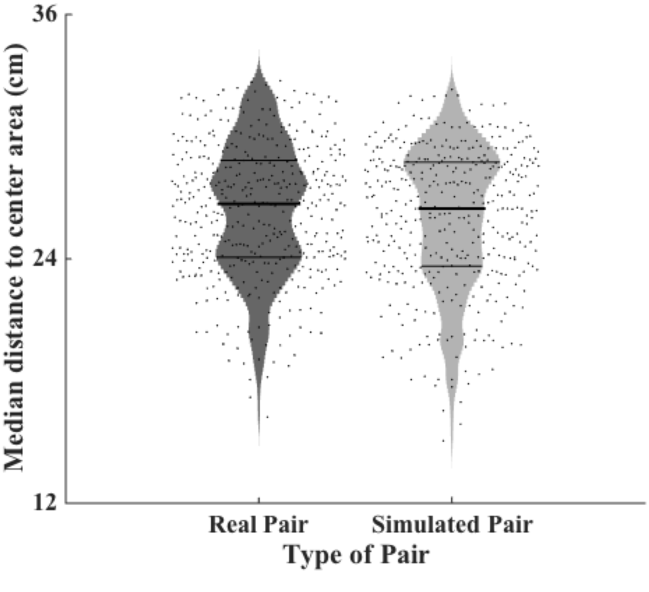


Figure 3.3. The presence of conspecifics does not affect the *Distance to the center of each half of the tank* as a measure of boldness in *A. albifrons*. Violin plot showing the density distribution of the mean (top panel) and median (bottom panel) *Distance to the center of each half of the tank* for the two conditions: Real and simulated pairs. The shape of the distributions of distances to the divisory line of real and simulated pairs did not differed significantly (K-S, Z=1.115, P= 0.166, N=832, top panel; K–S, Z = 0.896, P=0.398, N=832 bottom panel).

The *mean distance to the center of each half of the tank* differed significantly over time (RM-ANOVA, Mauchly's: χ^2 (152) = 286.659, $P<0.001$), Greenhouse-Geisser's correction: $F_{(\text{df: } 8.539,\ \text{err: } 392.815)} = 2.284$, $P = 0.019$, N= 864 Figure 3.4). However, the variation in the distance to the center was not influenced by individual fish identity (RM ANOVA, Mauchly's: χ^2 (152) = 275.893, $P<0.001$; Greenhouse-Geisser's correction: $F_{(\text{df: } 144.393,\ \text{err: } 150.671)} = 0.830$, $P = 0.443$, N=864).

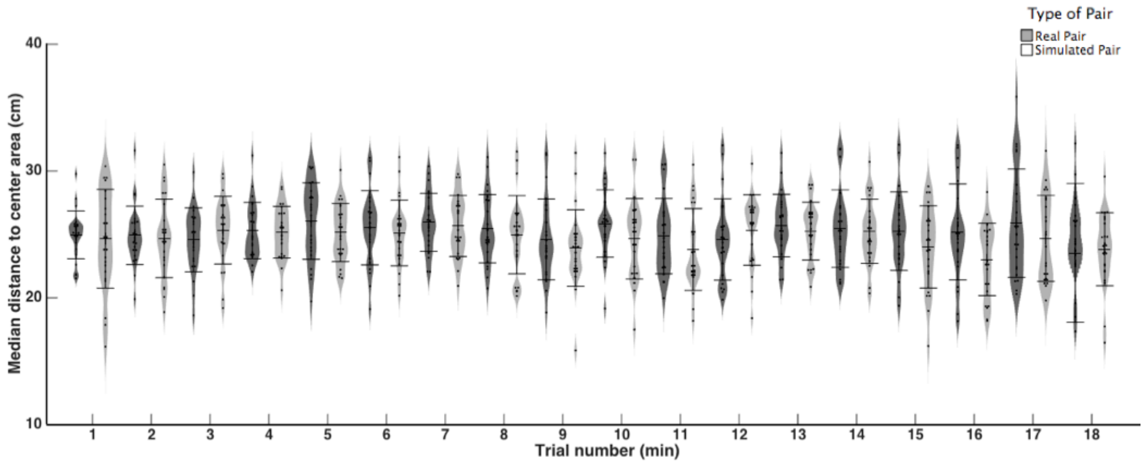


Figure 3.4. Change in the mean *Distance to the center of each half of the tank* as a function of time. Violin plot showing the density distribution of the mean distance to the divisory line for the two conditions: Real and simulated pairs.

In order to determine the role of electric signals in the attraction or repulsion between fish individuals, the inter-fish distance within *real* and *simulated* pairs was compared. As predicted, fish individuals tended to be closer to each other in the real pairs compared to the simulated pairs (control). The distribution of distance between fish differed significantly between real and simulated pairs as determined by one-way ANOVA (mean scores: $F_{6.274}$, df = 401, p = 0.013; median scores: $F_{5.656}$, df = 401, p = 0.018, Figure 3.5). Also, the overall distributions differed significantly between real and simulated pairs for both the mean (K-S, Z=1.5, P=0.022, N= 403) and median (K-S, Z=1.797, P=0.003, N=403) distance values.

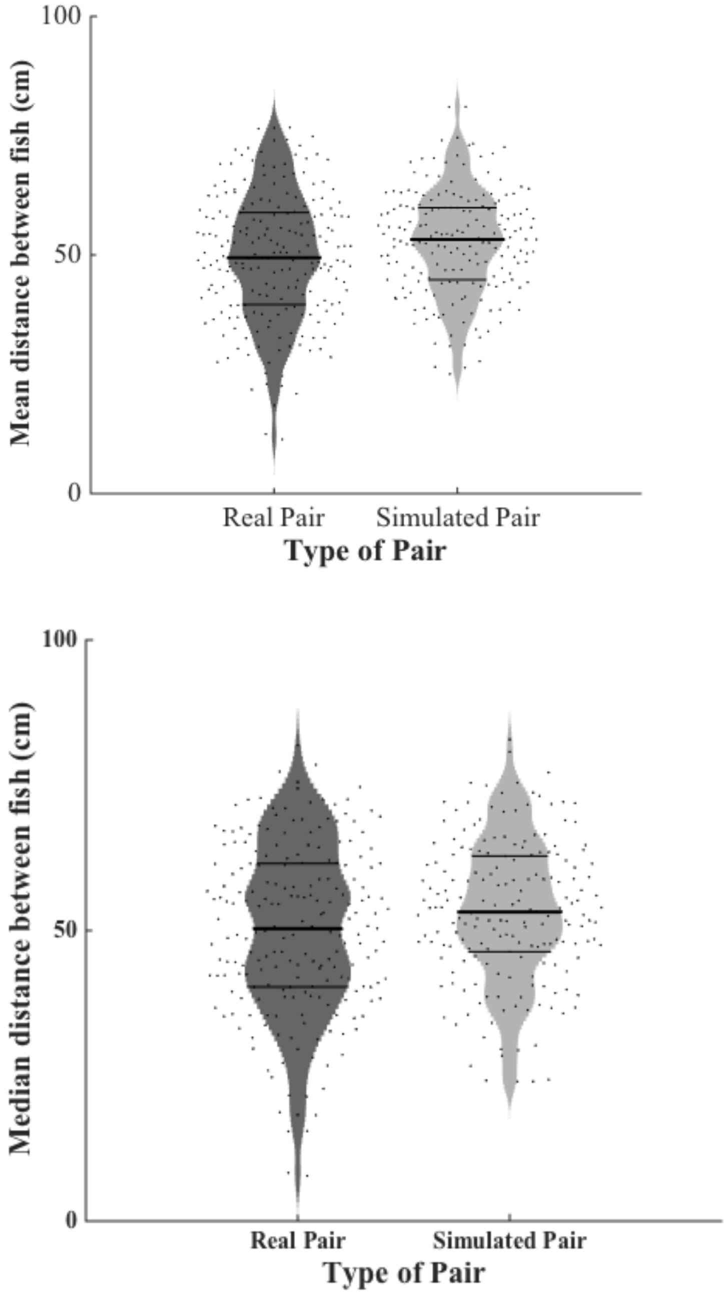


Figure 3.5 Fish showed attraction for other fish and were found closer to each other in real pairs than in simulated pairs. Violin plot showing the density distribution of the mean (top panel) and median (bottom panel) *inter-fish distance* for the two conditions: Real and simulated pairs. The inter-fish distance showed statistically significant differences between real and simulated pairs (one-way ANOVA: mean scores: $F_{6.274}$, df = 401, p = 0.013 top panel; median scores: $F_{5.656}$, df = 401, p = 0.018, bottom panel). Also, the shape of the distributions of inters–fish distances of real and simulated pairs differed significantly (K-S, Z=1.5, P=0.022, N= 403 top panel; K-S, Z=1.797, P=0.003, N=403).

A Repeated Measures ANOVA with a Huynh-Feldt correction (after violations to sphericity were detected (Mauchly's: χ^2 (152) = 200.437, P = 0.016)) was used to analyze the effect of the electric signal on inter-fish distance over time. It was found that the inter-fish distances did differ between time points ($F_{(\text{df } 15.976,\ \text{err } 351.470)} = 1.751$, P = 0.036, Figure 3.6). This variation in the inter-fish distance was not influenced by individual fish identity (Huynh-Feldt's correction $F_{(\text{df: } 187.000,\ \text{err: } 204.000)} = 0.861$, P = 0.852).

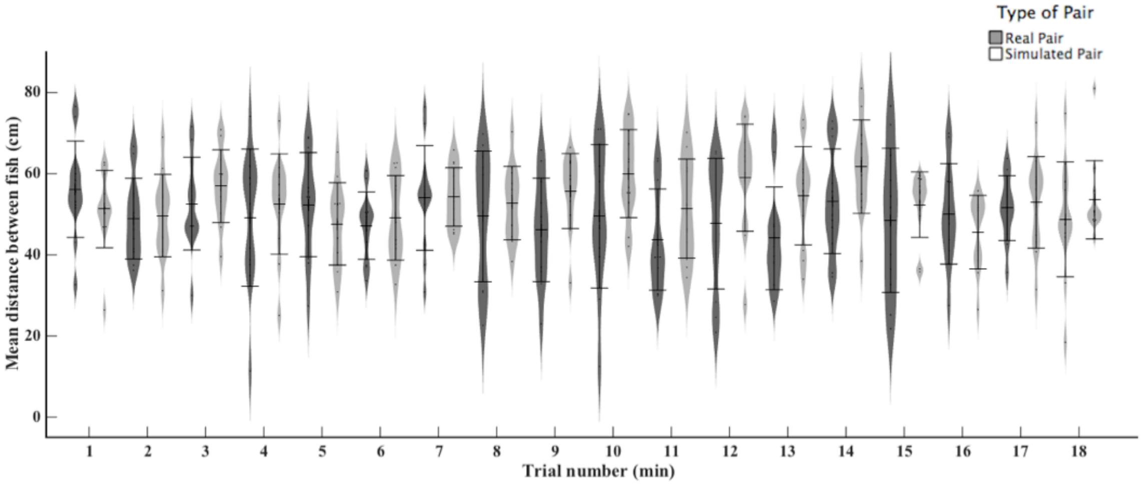


Figure 3.6 Change in the mean *inter-fish distance* as a function of time. The differences between the behavior of Real (black) and Simulated (grey) of the fish are shown. The inter-fish distances also differed between time points.

Finally, in order to determine whether conspecific signals affect the overall activity of *A. albifrons* during the experiments, the swimming velocity (cm/s) was compared between real and simulated pairs. As predicted, fish in real pairs moved at higher velocities than those in simulated pairs. The distributions of the mean velocity per frame showed statistically significant differences between groups (K-S, Z= 1.418, P= 0.036, N= 828, Figure 3.7).

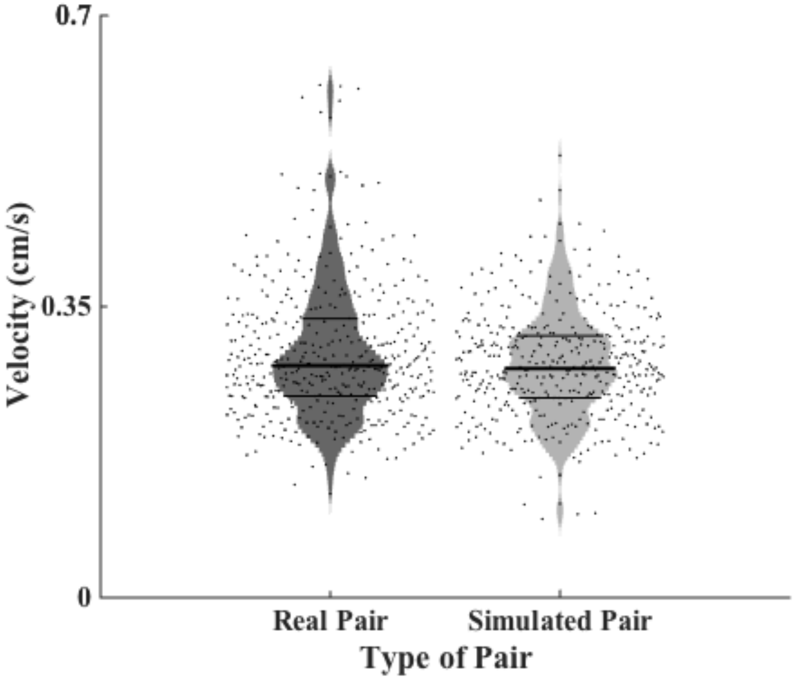


Figure 3.7 Difference in the distribution of mean Velocity between Real and simulated (control) pairs of fish. Violin plot showing the density distribution of the mean Velocity for the two conditions: Real and simulated pairs. The shape of the distributions of distances to the divisory line of real and simulated pairs differed significantly (K-S, Z= 1.418, P= 0.036, N= 828). In the presence of conspecific signals fish significantly increased the velocity (cm/s).

A Repeated Measures ANOVA with a Greenhouse-Geisser correction (after failing the sphericity test (Mauchly's: χ^2 (152) = 231.255, P<0.001)), showed statistically significant differences in velocity between time points ($F_{(df:\ 6.485,\ err:\ 155.644)}$ = 4.091, P<0.001, figure 3.8). However, the variations in velocity were not affected by the individual fish identity ($F_{(\text{df: } 149.159, \text{ err: } 155.644)}$ = 0.968 P = 0.578).

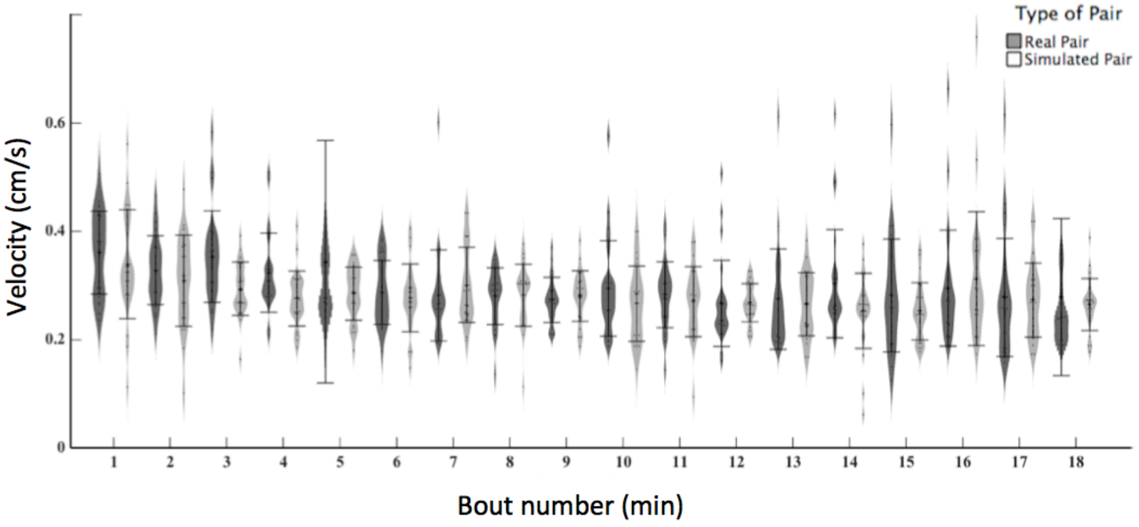


Figure 3.8 Difference in the distribution of mean Velocity between Real and simulated (control) pairs of fish. In the presence of conspecific signals fish significantly increased the velocity (cm/s).

Three behavioral responses (distance to the center of the tank, distance between fish and velocity) were found to correlate with the distance to the net in the center of the tank. However, these associations although significant, were fairly weak (Table 3.2). On the other hand, the distance between fish was not associated with the distance to the center of the half of the tank neither with the velocity (Table 3.2). Although the distance to the divisory net was significantly correlated with the distance to the center, only the 28% of the variation was explained by this relationship. Therefore, these two measurements are describing two independent behaviors: swimming around the edges of the test tank, and responding to the social signal. Interestingly, the distance to the net explained only a 51% of the variation in the fish inter-distance. Therefore, the inter fish distance appears to alternate across trials in half of the cases: when one fish get close to the net, the other moved away from the net. The fish appears to increase speed when in proximity to the net. However, a significant negative relationship was found between the mean distance to the half of the tank and speed (Table 3.2).

Table 3.2 Spearman's rho correlation matrix for the behavioral responses. P values are shown in bold if significant along with an asterisk next to the correlation coefficient

Behavioral response		*Mean distance to the center of the mid-tank (cm)*	*Mean distance between fish (cm)*	*Mean velocity (cm/s)*
Mean distance to the divisory net (cm)	*Corr coeff*	0.287**	0.514**	0.215**
	P	**<0.0001**	**<0.0001**	**<0.0001**
	N	828	403	828
Mean distance to the center of the mid-tank (cm)	*Corr coeff*		0.056	-0.186**
	P		0.0266	**<0.0001**
	N		401	824
Mean distance between fish (cm)	*Corr coeff*			0.088
	P			0.077
	N			403

CHAPTER 4

DISCUSSION

The present study provides evidence to support the hypothesis that *A. albifrons* can detect other conspecifics by means of electric organ discharge (EOD) alone after experimentally controlling any additional sensory modality. Essentially the EOD presence is sufficient to modify the fish behavior. The non-independent pair of fish (real pairs) tended to be significantly closer to each other, closer to the net, and swam at higher velocities than the independent pairs (simulated or control pairs). However, both groups of fish remained roughly at similar distances relative to the center of the behavioral arena. Notably, the behavioral responses showed significant differences across trials (recording bouts) over time, not explained by the fish identity. The behavioral responses showed weak correlations between each other.

Some implications of the role of electric signals and locomotion within the context of social communication and possible social cohesion are discussed below. Finally, the low explicative power of the individual variation in the behavioral responses is examined in relation to personality traits and behavioral syndromes.

The role of electric signals in social communication

Although the social communication of weakly electric fish has been well documented (Albert et al. 2005; Tan et al. 2005; Hupé & Lewis 2008) how the electrocommunication correlates with real-time measurements of the behaving animals (e.g. locomotion) is not completely known. Although there are several examples of interesting analyses of the behavioral correlates that attempt to characterize the signal production with the inter-fish distance (Hupé & Lewis 2008; Stamper et al. 2012a) a better understanding of the interaction between patterns of animal movements and social environment is needed.

In the experiments shown here, the individuals of *A. albifrons* remained closer to each other, closer to the net and swam at higher velocities than the independent pairs, across trials. Interestingly, previous field studies have found that individuals of *Apteronotus sp.* are more likely observed within groups than alone (Stamper et al. 2010). Therefore, the electrosensory ambient that wave-type weakly electric fish experience in the wild within groups is necessarily very different from that when fish are alone. One of the behaviors that arise from this situation of two weakly electric fish interacting is the JAR. As mentioned in the introduction, interacting fish adjust their EOD frequency to avoid jamming signals from nearby conspecifics (Metzner 1999). Moreover, in weakly electric fish of the genus *Apteronotus* and *Eingenmannia*, specific changes in the amplitude (AM) and frequency modulations (FM) of the signal are produced when two wave-type electric fish are in close proximity (electrosensory envelopes); the complexity of these interactions increase due to the movement of the fish (Stamper et al. 2013). Therefore, the nature of these behaviors and interactions will depend on the fish locomotion patterns.

In weakly electric fish, a neural mechanism has evolved to overcome the possibly deleterious interference that might arise from interactions with conspecifics (Fortune & Rose 1997; Fortune 2006). The neural substrate of such a mechanism has been studied extensively (Rose 2004). The physiological adaptations of the electrosensory system, represent a series of successful strategies that overcome the costs of a multipurpose sensory system devoted to a variety of behavioral tasks such as scanning the environment for food, threats, mates, competitors (MacIver et al. 2010). What are then, the benefits of the fish living in groups?

Group living serves an array of adaptive functions: predator avoidance, food location, territorial defense, and reproductive aggregations among others (Bradbury and Vehrencamp 1998) and has been reported across all animal taxa (Parrish & Edelstein-Keshet 1999). The advantages of grouping only emerge when individuals remain in close proximity, and therefore, mechanisms for maintaining group cohesion are required. In the wild as well as in the laboratory, *Apteronotus* sp. are more commonly observed in pairs than alone at distances less than 1 meter (Stamper et al. 2010). These authors also report that the type and number of electrosensory interactions was roughly the same across social situations (male-male, male-female and solitary fish).

In the present study, although all individuals were observed swimming in all areas of the arena, real pairs of fish remained closer than independent pairs (simulated pairs or controls). A detailed analysis of the interacting EOD signals from the individuals is not shown here, however, the grouping behavior is similar to previous reports about weakly electric fish (Tan et al. 2005; Stamper et al. 2010). A complete analysis of the EOD signal recorded in the present experiments will be included in a future report.

However, it seems likely that the EOD also serves as a mechanism to ensure social cohesion. During the trials no cue other than the conspecific electric signal was present. The pair of fish was simultaneously placed into the behavioral arena and, after only 24 hours of habituation and is unlikely to assume that any territorial display was underway. Therefore, the simple experimental conditions shown here may have removed other sensory cues necessary to trigger behavioral responses commonly present in other relevant contexts. In other words, the real pair's increase in exploration movements (activity, velocity) while also reducing the inter-fish distance in absence of additional sensory cues might represent a social cohesion response.

Previous research on collective decision-making have separated the effects of an individual's past experiences and decision copied by individuals in a group. In absence sufficient of personal information, individuals behave in a way that maximize social cohesion (Miller et al. 2013). Again, a detailed analysis of the relationship between EOD variation and inter-fish distances may be informative. The study of the recorded EOD obtained during the experiments reported here and its relation with the fish behavioral responses will be the focus of future analysis. However, the results presented support the idea that the EOD signals might function as a mechanism that ensures social cohesion. This function, is in addition to the list of functions that EOD signals have within social contexts: social dominance hierarchies (Hagedorn & Heiligenberg 1985; Dunlap & Olivieri 2002; Triefenbach and Zakon 2003; Triefenbach & Zakon 2008), aggression (Triefenbach & Zakon 2008) and discourage of conspecific aggression (Hupé & Lewis 2008; Fugère et al., 2011).

Inter-trial and individual variation: personality traits

Animal personalities include situations in which individuals differ consistently in their behavioral tendencies. This also means that the behavior in one context may be correlated with behavior in multiple other contexts (Wolf et al. 2007). The shyness-boldness variation is one of the most studied aspects of personalities (Adriaenssens & Johnsson 2011). In the present study, the fish reactions were divided into three broad categories: boldness, attractiveness and activity. Here, the measurements among these categories showed significant associations with low correlation coefficients (see results, Table 2). Sometimes, associations of behavioral responses form correlations and these behaviors correspond to the term behavioral syndromes (Sih et al. 2004). However, redundancy within the suits of behaviors that constitute the behavioral syndrome must be avoided (Réale et al. 2007). Therefore, the measurements used here to characterize the fish behavior during the experiments showed sufficient consistency (are significantly correlated) but independent enough to avoid redundancy (showed low correlation coefficients). As a result the behavioral reactions used here are appropriate measures of behavior under the presented experimental conditions and the differential behavioral responses between real and simulated pairs of fish demonstrate a clear effect of the signal on the fish behavior.

In the context of the shyness - boldness continuum, individuals in the real pairs situation showed higher scores of boldness traits (distance to the net), attractiveness (inter-fish distance) and activity (velocity) than simulated pairs, and presented significant inter-correlations. This might be equivalent to the conventional "exploratory tendency", a score closely related to boldness (Réale et al. 2007) and "aggressiveness" (Adriaenssens & Johnsson 2011).

However, a more stringent combination of criteria has been implemented to determine the presence of a behavioral syndrome in populations. These include: consistency in behavior across time and across contexts (Sih et al. 2004; Réale et al. 2007). For this purpose, as stated in the introduction, the recent view is that repeated measures on the same individuals should be used to study personality and its effects on behavioral ecology (Réale et al. 2007; Adriaenssens & Johnsson 2011). There was a significant variation in the behavioral reactions across time or trials (see results; figures 6, 8, 10 and 12). However, this variation was not explained by the individual identity. In other words, low repeatability or consistency for the behavioral responses across trials was detected on this experiment. Low repeatability could be observed if the experimental conditions do not produce behavioral variation or high within-individual variation relative to between individual variation (Réale et al. 2007). Here the latter alternative is more likely: there was a differential behavioral response between real and simulated pairs; the high within-individual variation might be the result EOD interactions between individuals across trials that have not been accounted for yet in this study. Learning and habituation might also affect a test replicated several times. This seems unlikely in this study because there was a habituation period of 24 hours prior to the start of experiments and there was a short inter-bout interval (10 min) between recordings, possibly too short to represent changes in habituation across trials (Rankin et al. 2009). This is also apparent from the lack of reduction in the magnitude of behavioral responses over time (see Figures 6, 8, 10 and 12). Therefore, the final results suggest a lack of consistency in the behavioral response of individuals across time.

The results of this study contradict those of a recent report in which individuals of *A. leptorhynchus* have consistent behavior over time (Shank 2013). The authors report a behavioral consistency over an experimental period of 14 days. In addition to the differences in duration of the experimental time, the authors included changes in the behavioral context of the experiments. In contrast, here, a single condition with two levels (pair vs. solitary) was used. This might constitute a broader "generic" context across different social situations (e.g. contest, mating, dispersal). As a result, the analysis of behavioral consistencies over longer periods of time as well as studies contrasting the behavioral responses across different and more specific contexts will allow for more complete comparisons between *A. albifrons* and *A. leptorhynchus*, such as those described by Shank (2013).

4.2. Conclusions

The present study provides evidence to support the idea that the EOD signal is sufficient to maintain social cohesion in *A. albifrons.* The behavioral reactions of non-independent groups of fish (real pairs) include changes in locomotor behavior that might reflect basic rules of group movement interactions in weakly electric fish. Although these behavioral reactions might serve as true indicators of personality traits or behavioral syndromes (shyness – boldness continuum) more prolonged experiments over the course of weeks are required to confirm the consistency of these behavioral syndromes overtime. Similarly, further analysis of the correlates of EOD signal with the inter-fish distance is needed.

REFERENCES

Adriaenssens, B. & Johnsson, J. I. 2011. Shy trout grow faster: Exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, 22, 135–143.

Albert, J. S., Bastian, J., Bell, C. C., Bodznick, D., Bullock, T. H., Caputi, A. A., Carlson, B. A., Coombs, S., Crampton, W. G. R., Hofmann, M. H., Hopkins, C. D., Jørgensen, J. M., Kawasaki, M., Macadar, O., Maler, L., Montgomery, J. C., Nelson, M. E., Northcutt, R. G., Wilkens, L. A., Zakon, H. H. & Zupanc, G. nther K. H. 2005. *Electroreception BT - Electroreception.* Springer Handbook of Auditory Research.

Assad, C., Rasnow, B. & Stoddard, P. K. 1999. Electric organ discharges and electric images during electrolocation. *The Journal of experimental biology*, 202, 1185–1193.

Babineau, D., Lewis, J. E. & Longtin, A. 2007. Spatial Acuity and Prey Detection in Weakly Electric Fish. *PLoS Computational Biology*, 3, e38.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771–783.

Bradbury, J.W., Vehrencamp, S.L. 1998. Principles of animal communi- cation. Sinauer, Sunderland.

Cowan, N. J. & Fortune, E. S. 2007. The Critical Role of Locomotion Mechanics in Decoding Sensory Systems. *Journal of Neuroscience*, 27, 1123–1128.

Dickinson, M. H., Farley, C. T., Full, R. j., Koehl, M. A. R., Kram, R. & Lehman, S. 2000. How Animals Move: An Integrative View. *Science*, 288, 100–106.

Dunlap, K.D., Oliveri, L.M. 2002. Retreat site selection and social organiza- tion in captive electric fish, Apteronotus leptorhynchus. *Journal of comparative physiology. A, Neuroethology, sensory, neural, and behavioral physiology,* 188:469–77.

Emde, G. v d & Schwarz, S. 2000. Three-dimensional analysis of object properties during active electrolocation in mormyrid weakly electric fishes (Gnathonemus petersii). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355, 1143–1146.

Fortune, E. S. 2006. The decoding of electrosensory systems. *Current Opinion in Neurobiology*, 16, 474–480.

Fortune, E. S. & Rose, G. J. 1997. Temporal filtering properties of ampullary electrosensory neurons in the Torus semicircularis of Eigenmannia: Evolutionary and computational implications. *Brain behavior and Evolution*, 49, 312–323.

Frost, A. J., Winrow-Giffen, A., Ashley, P. J. & Sneddon, L. U. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings. Biological sciences / The Royal Society*, 274, 333–339.

Fugère, Vincent, Ortega, H., & Krahe, R. 2011. Electrical signalling of dominance in a wild population of electric fish. *Biology Letters*, 7(2), 197–200.

Gelfand, J. J., Pearson, J. C., Spence, C. D. & Sullivan, W. E. 1989. Multisensor integration in biological systems. In: *Proceedings IEEE International Symposium on Intelligent Control 1988*, pp. 147–153. IEEE Comput. Soc. Press.

Hagedorn, M. & Heiligenberg, W. 1985. Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Animal Behaviour*, 33, 254–265.

Heiligenberg, W. 1975. Theoretical and experimental approaches to spatial aspects of electrolocation. *Journal of Comparative Physiology A,* 103, 247-272.

Heiligenberg, W., Baker C., Bastian, J. 1978. The jamming avoidance response in gymnotoid pulse species: a mechanism to minimize the probability of pulse train coincidence. *Journal of Comparative Physiology A* 124:211–224.

Hopkins, C.D., Bass, A.H. 1981. Temporal coding of species recognition signals in an electric fish. *Science* 212: 85–87.

Hupé, G. J. & Lewis, J. E. 2008. Electrocommunication signals in free swimming brown ghost knifefish, Apteronotus leptorhynchus. *The Journal of experimental biology*, 211, 1657–67.

King, A. J. & Sueur, C. 2011. Where Next? Group Coordination and Collective Decision Making by Primates. *International Journal of Primatology*, 32, 1245–1267.

MacIver, M. A., Sharabash, N. M. & Nelson, M. E. 2001. Prey-capture behavior in gymnotid electric fish: motion analysis and effects of water conductivity. *The Journal of experimental biology*, 204, 543–557.

MacIver, M. A., Patankar, N. A. & Shirgaonkar, A. A. 2010. Energy-information trade-offs between movement and sensing. *PLoS Computational Biology*, 6, e1000769.

Metzner, W. 1999. Neural circuitry for communication and jamming avoidance in gymnotiform electric fish. *The Journal of Experimental Biology*, 202, 1365–1365.

Miller, N., Garnier, S., Hartnett, A. T. & Couzin, I. D. 2013. Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 5263–8.

Moller, P. 1976. Electric signals and schooling behavior in a weakly electric fish, Marcusenius cyprinoides L. (Mormyriformes). *Science* 193, 697-699.

Nelson, M. E. & MacIver, M. A. 1999. Prey capture in the weakly electric fish Apteronotus albifrons: sensory acquisition strategies and electrosensory consequences. *The Journal of experimental biology*, 202, 1195–1203.

Nelson, M. E. & MacIver, M. a. 2006. Sensory acquisition in active sensing systems. *Journal of Comparative Physiology A*, 192, 573–586.

Oestreich, J. & Zakon, H.H. 2005. Species-specific differences in sensorimotor adaptation are correlated with differences in social structure. *Journal of Comparative Physiology A,* 191: 845–856.

Parrish, J. K. & Edelstein-Keshet, L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science (New York, N.Y.)*, 284, 99–101.

Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., Coppola, G., Geyer, M. a., Glanzman, D. L., Marsland, S., McSweeney, F. K., Wilson, D. a., Wu, C. F. & Thompson, R. F. 2009. Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, 92, 135–138.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318.

Rojas, R. & Moller, P. 2002. Brain Behavior and Evolution 2002 Roland. *Brain behavior and Evolution*, 59, 211–221.

Rose, G. J. 2004. Insights into neural mechanisms and evolution of behaviour from electric fish. *Nature Reviews Neuroscience*, 5, 943–951.

Shank, I. 2013. Behavioural syndromes: implications for electrocommunication in a weakly electric fish species. University of Ottawa.

Sih, A., Bell, A. & Johnson, J. C. 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19, 372–378.

Silva, A., Perrone, R. & Macadar, O. 2007. Environmental, seasonal, and social modulations of basal activity in a weakly electric fish. *Physiology & behavior*, 90, 525–36.

Sloan Wilson, D., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in ecology & evolution (Personal edition)*, 9, 442–446.

Stamper, S. A., Carrera-G, E., Tan, E. W., Fugère, V., Krahe, R. & Fortune, E. S. 2010. Species differences in group size and electrosensory interference in weakly electric fishes: Implications for electrosensory processing. *Behavioural Brain Research*, 207, 368–376.

Stamper, S. A., Roth, E., Cowan, N. J. & Fortune, E. S. 2012a. Active sensing via movement shapes spatiotemporal patterns of sensory feedback. *Journal of Experimental Biology*, 215, 1567–1574.

Stamper, S. A., Madhav, M. S., Cowan, N. J. & Fortune, E. S. 2012b. Beyond the Jamming Avoidance Response: weakly electric fish respond to the envelope of social electrosensory signals. *The Journal of experimental biology*, 215, 4196–207.

Stamper, S. A., Fortune, E. S. & Chacron, M. J. 2013 July 1. Perception and coding of envelopes in weakly electric fishes.

Stamps, J. 2003. Behavioural processes affecting development: Tinbergen’s fourth question comes of age. *Animal Behaviour*, 66, 1–13.

Tan, E. W., Nizar, J. M., Carrera-G, E. & Fortune, E. S. 2005. Electrosensory interference in naturally occurring aggregates of a species of weakly electric fish, Eigenmannia virescens. *Behavioural Brain Research*, 164, 83–92.

Triefenbach, F. A. & Zakon, H. 2003. Effects of sex, sensitivity and status on cue recognition in the weakly electric fish, Apteronotus leptorhynchus. *Animal Behaviour,* 65,19e28.

Triefenbach, F. A. & Zakon, H. H. 2008. Changes in signalling during agonistic interactions between male weakly electric knifefish, Apteronotus leptorhynchus. *Animal Behaviour*, 75, 1263–1272.

Walker, J. A. 1998. Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *The Journal of Experimental Biology*, 201, 981–995.

Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581–584.