



Research report

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

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ARTICLE INFO

Article history:

Received 13 August 2009

Received in revised form 1 October 2009

Accepted 16 October 2009

Available online 27 October 2009

Keywords:

Electrotaxis
Gymnotiformes
Electrosensory
Social behavior

ABSTRACT

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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1. Introduction

Many animal species have evolved “active sensory” systems in which individuals probe their environment with autogenous signals [42]. These adaptations allow animals to exploit niches that would be difficult, or perhaps impossible, to use with passive sensing systems alone. 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 individuals 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 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” [24]. 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 [24]. 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 [2,23,24] whereas 40 Hz beat rates may actually enhance certain features of electrosensory perception [46].

Abbreviations: Df, frequency difference; EOD, electric organ discharge; JAR, jamming avoidance response.

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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 [7,18]. 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 can change their electric signal frequency to avoid deleterious beat rates of less than 10 Hz [4,5,32]. The combination of social behavior and the JAR behavior largely determines the global electrosensory signals that these fish experience [18]. For *Eigenmannia*, fish in groups typically generate beat rates in the gamma frequency range, between 20 and 80 Hz [52].

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*, and *Apteronotus albifrons* the males produce the lower-frequency EODs [15,27,28,29], whereas in *Apteronotus leptorhynchus* the males produce the higher frequency EODs [22,33]. Therefore, low-frequency beats usually occur in same-sex groupings and high-frequency beats occur in opposite-sex groupings in 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* [25], and *Sternopygus* do not exhibit JAR behaviors despite the presence of neural circuits similar to those in the other two genera [5,39,46]. 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 [37,38].

Building on a previous study of group size and electrosensory interference in *Eigenmannia* [52], 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, electric signal 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.

2. 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 Hitschfeld et al. [26]. 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 *A. leptorhynchus*, and *Sternopygus macrurus* were purchased from various commercial vendors and maintained at 25–29 °C in laboratory tanks.

2.1. Study sites

Fish were studied in habitats near the Napo River in eastern Ecuador (Fig. 1A). Observations were made over a three-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 Yasuni National Park near the Estación Científica Yasuní (PUCE). Electrical conductivity of water at each habitat was between 5 and 50 $\mu\text{S}/\text{cm}$ (mean = 14.08 \pm 7.11). The pH was slightly acidic with a range of 5.7–7.0 (mean = 6.28 \pm 0.27), and the temperature ranged from 23 to 25.5 °C (mean = 24.09 \pm 0.57).

Recordings were made in shallows along rivers and streams. Due to technical limitations, we made no attempt to probe depths below 1.5 m. Recording electrodes

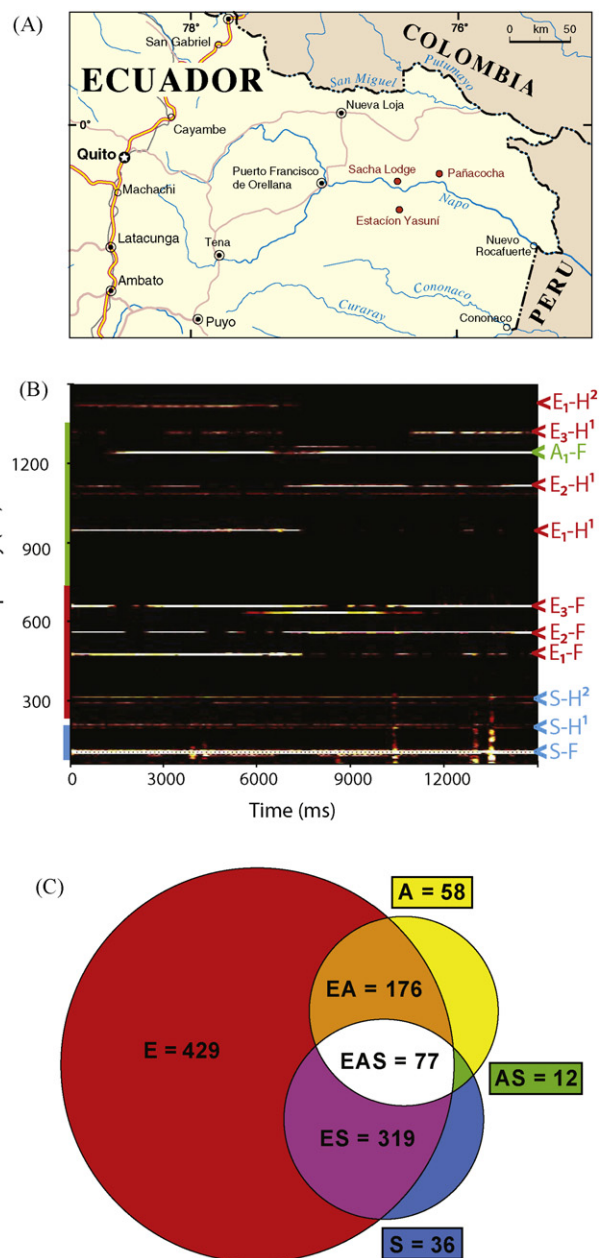


Fig. 1. (A) Map of Ecuador showing study site locations (red). Field recordings were made over a three-year period in Sacha Lodge, Pañacocha, and Estación Yasuní. (B) A sonogram of a recording showing EOD frequency over time for three species of electric fish: *Apteronotus* (green), *Sternopygus* (blue) and *Eigenmannia* (red). The frequency range of each species is color-coded on the Y-axis (left). In this sample, there was one *Sternopygus*, three individual *Eigenmannia*, and one *Apteronotus*. The fundamental frequency (F) of each fish is indicated (arrow) as well as all visible harmonics (H). (C) A Venn diagram showing the distribution of species across 819 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. Social behavior of *Eigenmannia* in this same region of Ecuador has been reported previously [52] and is not covered here. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

were placed in areas in which fish were found. Recording sites were at least 10 m apart. Recordings were made primarily in black water habitats.

2.2. 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 m sphere, and likely much closer together than this distance. The 1.5 m 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 m. 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 (Fig. 1B), identified by their distinct EOD frequency ranges ([13]; color-coded Y-axis), within a single recording (figure shows 15 s segment of recording). From the collected samples, a reduced set ($N = 819$) contained species of the genera of interest: *Eigenmannia*, *Apteronotus*, and *Sternopygus*. The majority of the samples contained a single species of fish ($n = 513$, 62.64%) but there were recording sites where two species ($n = 219$, 26.74%) or three species ($n = 77$, 9.4%) of fish were simultaneously present (Fig. 1C).

2.3. Group behavior in freely moving fish: laboratory

The procedures for the group size experiment were similar to those used in Tan et al. [52]. 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 $\mu\text{S}/\text{cm}$ (range: 50–600 $\mu\text{S}/\text{cm}$). 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 [21,35]: 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 Fig. 1 in Tan et al. [52]), 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.

Signals were amplified using custom-built amplifiers (Fortune Laboratory Industries, Baltimore, MD) and recorded at 20 kHz 16-bit resolution using a custom computer system. The quadrant in which each fish was located during a sample was, in the vast majority of cases, easily determined by relative amplitudes of the EODs recorded using this system.

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 would 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 [3,21,56]. 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 12 L:12 D 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 min 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 (16,384 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 two 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 three fish, there are three simultaneous ongoing beat rates—the difference in frequency between fishes 1 and 2, 2 and 3, and 1 and 3. For groups of four fish, there are six simultaneous beat rates: 1–2, 2–3, 3–4, 1–3, 2–4, 1–4. In addition, there can be emergent amplitude modulations that occur in the envelope of the combined signal [see Discussion, 40]. 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.

2.4. 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 [12,16]. 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 m 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 [14,30,49,51], 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 frequency differences were used. 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 min, which typically occurred in less than 5 min after the fish was introduced into the tub.

3. Results

3.1. Group behavior of fish in the Napo River valley, Ecuador

Fish were commonly found in multispecies flocks including *Eigenmannia*, *Apteronotus*, and *Sternopygus* (Fig. 1B and C). 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 *Brachyhyppopomus* and *Gymnotus*. Here we examine the social behavior of *Apteronotus* and *Sternopygus*. The social behavior of *Eigenmannia* in these areas has been reported previously [52].

3.1.1. *Apteronotus*

Apteronotus were found in root systems, leaf litter, and large debris, particularly around larger fallen trees. They were recorded in 293 of the samples. Based on visual inspection of fish that were captured, the species of *Apteronotus* 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 *A. leptorhynchus* [54].

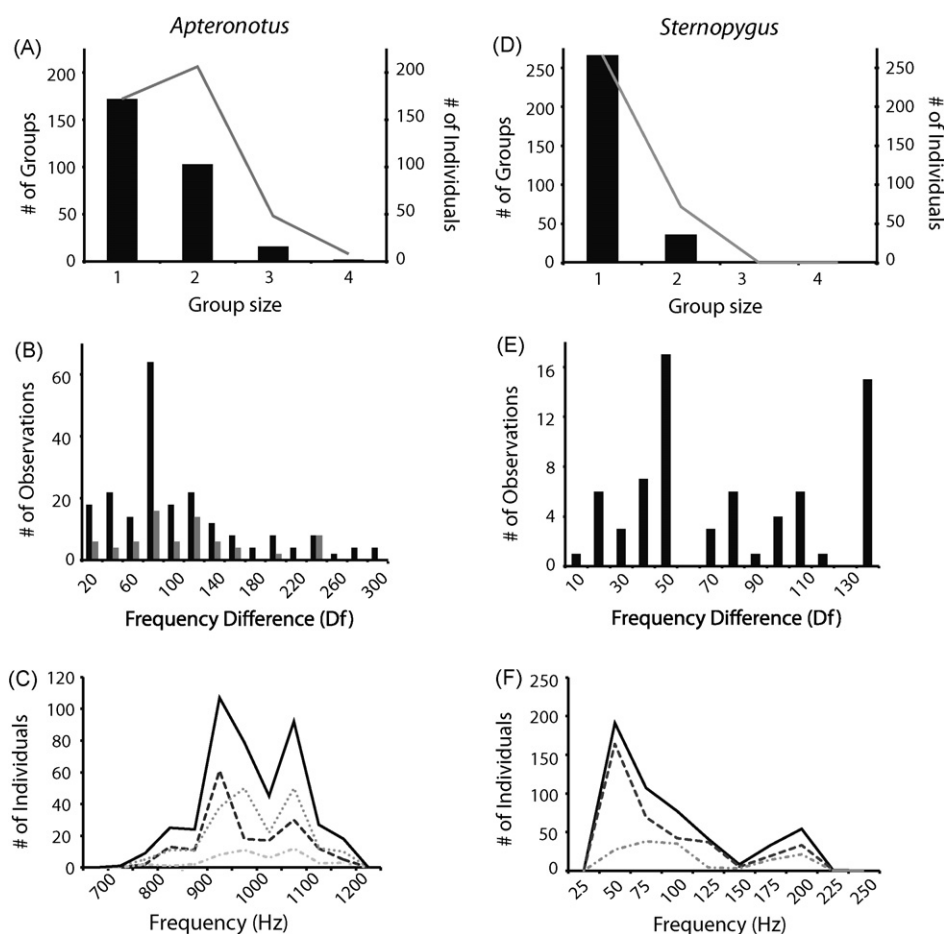


Fig. 2. Grouping and electrosensory information in the wild. (A) Bars indicate the percentage of samples of particular group sizes, whereas the grey lines indicate the percentage of fish found in each group size (number of samples of a group size multiplied by group size). The majority of samples contained only single *Aptereronotus* (bars). Nevertheless, more individual *Aptereronotus* were found in groups of two or more conspecifics than alone (grey line). (B) Frequency differences between individual *Aptereronotus* in groups ranged from 20 to 300 Hz. Black bars indicate Dfs determined for fish found in pairs (one Df per pair), grey bars indicate Dfs for fish found in groups of three (three Dfs per group, see Section 2). (C) The distribution of EOD frequencies of *Aptereronotus* was bimodal and presumably corresponded to animals of the two sexes. (D) *Sternopygus* were found most commonly alone—the majority of samples and majority of individual *Sternopygus*, bars and grey lines respectively, but sometimes in pairs (bars) and the same pattern is observed when each fish is considered individually (grey line). (E) Frequency differences ranged from 10 to 140 Hz. (F) The distribution of frequencies was bimodal and corresponded to females (higher frequencies) and males (lower frequencies).

The distribution of group sizes (Fig. 2A) shows that most observations ($n = 172$) contained a single *Aptereronotus*. However, fish were also commonly observed in pairs ($n = 103$). When analyzed not as the total number of samples, but as the total number of individuals, more *Aptereronotus* ($n = 206$ fish; 47% of fish) were found in pairs than alone. Groups of three ($n = 48$) and four ($n = 8$) fish were observed, but not greater. It was found that these fish experience Dfs (Fig. 2B) between 20–300 Hz when in pairs (mean = 105.89 ± 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 *Aptereronotus* was bimodal (Fig. 2C, 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 *Aptereronotus* species, although which sex occupies the high-frequency range and which the low-frequency range appears to differ from species to species [15,22,33]. Therefore, the two peaks of the EOD frequency distribution likely represent the two sexes, although we cannot 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, and 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) [17,31]. We observed Type I and Type II chirps in both solitary fish and fish in groups. Based on the low number of observed chirps recorded, there was no significant correlation between chirp type and sex of the animal, based on EOD frequency classification.

3.1.2. *Sternopygus*

S. macrurus were found in roots, holes and trunks and sandy bottom streams but not in substrate debris. They were found in 302 of the samples. *Sternopygus* were most commonly found alone ($n = 266$) but were occasionally found in pairs ($n = 72$) and never observed in groups of 3 or more conspecifics (Fig. 2D). When analyzed as the total number of individuals, *Sternopygus* were most often found alone ($n = 266$ fish; 88% of fish; Fig. 2D, grey line). For fish in pairs, beat rates (Fig. 2E) of between 20 and 240 Hz were observed (mean = 74.25 Hz; SD = 47.66 Hz).

The EOD distribution for *Sternopygus* was bimodal with peaks at 50 and 200 Hz (Fig. 2F), in *Sternopygus* females generally have higher EOD frequencies than males [27]. 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.

3.2. Group sizes in freely moving fish: laboratory

3.2.1. *Apteronotus leptorhynchus*

Fish could be identified using their EOD frequency as there were no significant changes in the differences in EOD frequencies from start to end of the trials (Chi Square test, $p > 0.05$, $N = 10$). 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 5–10 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 ($N_1 = 1536$, $N_2 = 932$, $N_3 = 1720$, $N_4 = 1838$, $N_5 = 822$, $N_6 = 1150$, $N_7 = 775$, $N_8 = 1313$, $N_9 = 1252$ and $N_{10} = 909$). 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 was 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 (Fig. 3A). Wilcoxon signed ranked test ($p = 0.037$).

More detailed frequency analysis was performed on a subset of observations across five trials ($N = 2037$) to examine individual preferences for grouping amongst the fish. For *Apteronotus* in pairs ($N = 494$, Fig. 3B) Df ranged from 20 to 200 Hz. The frequency distribution of individual fish was bimodal (Fig. 3C). 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 [55]. 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 [55].

3.2.2. *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 test, $p > 0.05$, $N = 7$). *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 seven trials that differed in the number of observations within a trial due to changes in testing length ($N_1 = 360$, $N_2 = 584$, $N_3 = 960$, $N_4 = 1230$, $N_5 = 446$, $N_6 = 1436$ and $N_7 = 1073$). 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 (Fig. 3D), 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 ($N = 262$; Fig. 3B), we found differences in EOD frequencies between 10 and 50 Hz. The frequency distribution of individual fish was bimodal (Fig. 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*.

3.3. 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 are detected in the envelope of the combined signal from the fish [40]. 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 50 Hz Df, but would also add a 40 and 90 Hz Dfs. A “second-order” amplitude modulation can be extracted by applying a Hilbert transform to the envelope of the signal [40] of the three fish: in this example one observes an emergent 10 Hz amplitude modulation.

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 five groups of fish in the laboratory, we never found low-frequency (less than the lowest Df) power in the envelope of the signal (Fig. 4A and B). An artificial signal constructed with sinewaves at roughly the same frequencies as the fish did result in power at low-frequency in the envelope of the signal (Fig. 4C). However, more precise matching of the EOD frequencies of the fish – within 0.5 Hz – produced the result observed in the fish – no power in low-frequency envelopes. We also examined the role of harmonics and relative amplitudes of the sinewaves and found that these could qualitatively affect the power of the peak at low-frequencies, but never eliminated it.

3.4. Electrotaxis to conspecific signals

3.4.1. *Apteronotus*

In general, *Apteronotus* swam directly from the middle of the tub towards the refuge with the conspecific signal. Within 2 min, the *Apteronotus* typically buried itself underneath the refuge with the signal. All *Apteronotus* ($N = 10$) swam to the refuge with the con-

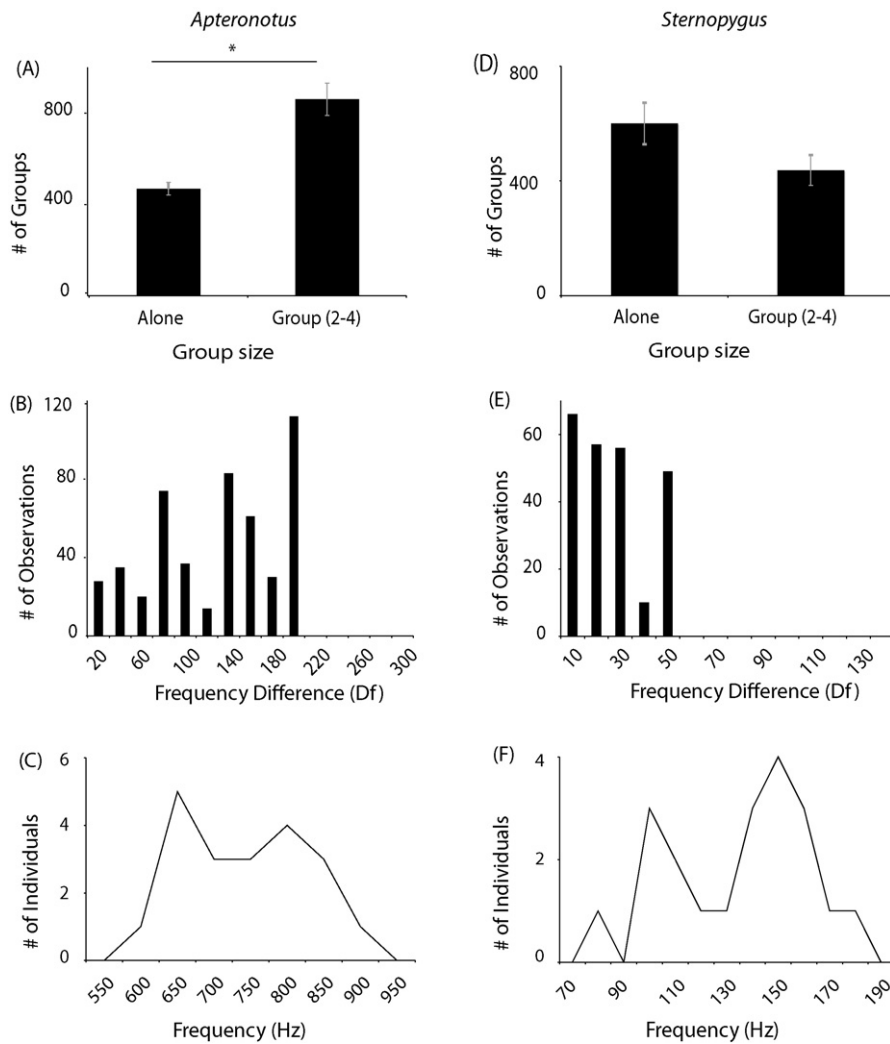


Fig. 3. Grouping and electrosensory information in the laboratory. (A) *Apteronotus* were significantly more likely to be found in groups of 2–4 individuals within a refuge. (B) The distribution of frequency differences between 20 and 200 Hz. (C) The distribution of EOD frequencies was bimodal and corresponded 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 EOD frequencies was bimodal and corresponded to females (higher frequencies) and males (lower frequencies).

specific signal (Fig. 5) 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.

3.4.2. *Sternopygus*

In contrast to *Apteronotus*, *Sternopygus* ($N = 20$) showed no preference for conspecific-like signals (Chi Square test, $p > 0.05$, $N = 18$, Fig. 5). 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.

4. 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 experi-

ence 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 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 [5,39,47], preferred to remain alone and did not preferentially approach conspecific signals. Freely moving *Apteronotus*, therefore, commonly experience global electrosensory oscillations whereas *Sternopygus* do not. These oscillations, which typically occur at frequencies between 20 and 120 Hz, are detected by tuberous electroreceptors and activate CNS circuits in a manner similar to gamma band oscillations (range ~20 to 80 Hz). If such oscillations contribute to electrosensory perception [8,9,19,36], then 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 [46,52].

4.1. Multispecies flocks

In the field we found that all three species of wave-type weakly electric fishes were encountered in close proximity, within 1.5 m

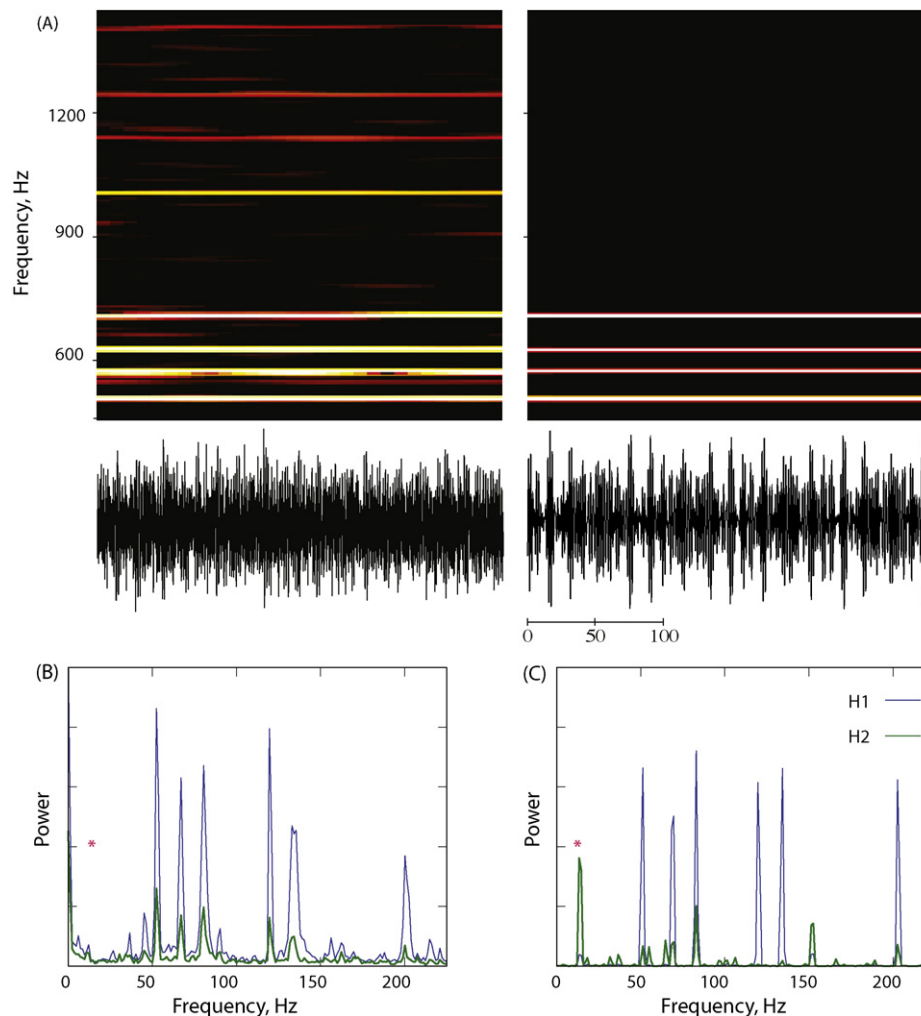


Fig. 4. Amplitude envelopes in a group of four *Aptereronotus leptorhynchus*. (A) Sonogram and oscillogram of Left, the electric signal of four fish at a single refuge in the laboratory and Right, four sinewaves at similar frequencies (within about 1 Hz). The four bands around 600 Hz are the fundamental frequencies, and the bands around 1200 Hz on the left are harmonics of *Aptereronotus* EODs. (B) Power spectral density plot of the absolute value of the Hilbert transform of the original signal (blue). The peaks are at the expected six Dfs that result from the combination of four sinewaves. Next we extracted the amplitude envelope of the Hilbert transformed data by again applying a Hilbert transform (see Middleton et al. [40]): green is the PSD of this data. The power at the six Dfs is reduced, but there is significant power near zero due to the relative movements of the fish during the recording. (C) Is the same analysis applied to the sinewave data above. As in (B), blue (PSD of the Hilbert transform of the original signal) shows power at the six Dfs. However, the Hilbert of the Hilbert (green) has significant power near 10 Hz and no power near zero. This information is encoded by ovoid cells in the electrosensory lateral line lobe of *Aptereronotus* (Middleton et al. [40]). None of the groups of fish that we recorded had such a peak. This peak can be eliminated in the sinewave data by more precisely adjusting the frequencies to match those produced by the fish. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

diameter. In addition, we routinely observed pulse-type weakly electric fish at the same time. The interactions between these animals are currently not known. Further, why these animals are found in multispecies flocks is also not understood. Multispecies flocks are known to occur in many groups of animals, including psittacine birds [50] and new world primates [11]. Among many other species multispecies flocks can 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.

Caution is necessary when interpreting the current observations, however. At present we have not examined the species distribution in deep or fast moving water. Previous observations [52] indicate that *Eigenmannia* is often found in floating root systems, where *Aptereronotus* and *Sternopygus* are not. It appears that there are a wider variety of habitats that *Aptereronotus* and *Sternopygus* occupy. A limitation on available refuge sites could lead to an increase in the overlap in the distribution across species.

4.2. Species differences in social behavior

Social behavior can vary in complex ways in individuals in relation to an array of factors including life history, population densities, weather, time of day, etc. Many of these factors are not yet known for Gymnotiform species. Additional work will be required to determine differences in social behavior throughout the life-span of these animals, in relation to sexual condition, and in relation to environmental factors such as conductivity, predation, etc. Nevertheless, the similarities between the laboratory experiments and measurements in the natural habitat presented here suggest that these patterns of social behavior are biologically relevant for these fishes.

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 [34,43,52]. *Aptereronotus* preferentially hide within refuges [16,43] and appear to be more aggressive towards conspecifics [30,53]. *Sternopygus*, which does not exhibit a JAR, appears to be the

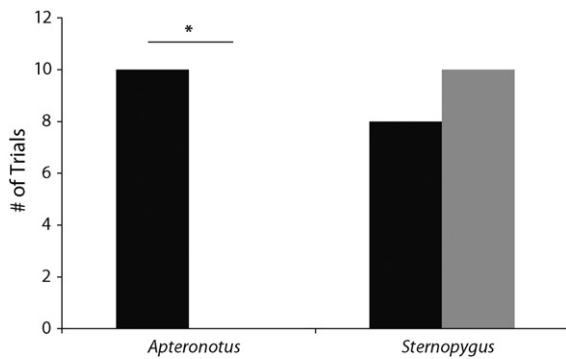


Fig. 5. Refuge choice test. Number of fish that entered and remained at the refuge with either the conspecific-like signal or no signal. In all *Aptereronotus* tested, the fish approached the refuge with the artificial conspecific signal whereas *Sternopygus* did not exhibit a preference for the artificial conspecific signal. The asterisk indicates a statistically significant difference ($p < 0.05$).

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 m 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 *Aptereronotus* 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 [14,30,49,51].

Mormyriiform 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 [41]. Additionally, field recordings of *Marcusenius cyprinoides* indicate that these fish are typically found in schools [41]. 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* [1]. 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 [1].

4.3. Computational consequences

The jamming avoidance response 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 [47]. 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 [38]. 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 fish experiences as long as fish remain in close proximity to each other [4].

These '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 [6]. In electric fish, the CNS oscillations are identical to those found in other systems, except that they are generated externally; that is, they are not generated within the neural network itself. What function might these oscillations have in electric fish?

In humans, externally generated somatosensory vibrations at frequencies below 100 Hz can enhance sensorimotor performance [44]. In *Eigenmannia* and presumably *Aptereronotus* and *Sternopygus*, global oscillations in this same frequency range preferentially elicit short-term synaptic depression in midbrain electrosensory neurons [19,20,48], which may serve as a mechanism for direction selectivity [10,18,19]. 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 [46]. This synaptic depression does not appear to attenuate the responses of midbrain electrosensory neurons to sensory objects in *Eigenmannia* [45]. Rather, post-JAR signals appear to enhance motion processing in midbrain neurons by increasing direction selectivity [46].

Further, in *Aptereronotus*, neurons in the electrosensory lateral line lobe exhibit distinct response properties that vary depending on the sensory stimuli [39]. Filtering of information in these neurons appears to be dependent on the spatial presentation of behaviorally relevant information [7]. 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 *Aptereronotus* did not generate low-frequency power in the envelop of the electric signal. This is interesting because Middleton et al. [40] described neurons that respond robustly to this information. It is possible, therefore, that these neurons mediate a more subtle form of JAR that avoids low-frequency envelopes. Additional behavioral experiments are necessary to test this hypothesis.

4.4. 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, we found very few *Aptereronotus*, which have a JAR behavior, 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 commonly 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 [52]. These higher frequencies are in what is known as the "gamma band"—roughly 20–80 Hz. Such oscillations are known to enhance features of electrosensory processing in midbrain neurons via the activation of short-term synaptic plasticity [46], 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 [35], avoidance of predators, and refuge tracking [12]. Thus the JAR would enhance electroreception in two ways, first by avoiding detrimental interference and second, by enhancing direction selectivity in midbrain neurons.

Acknowledgments

This work was supported by National Science Foundation (NSF) grants 0543985 and 0817918 to ESF and by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to RK. Student support was provided by the National Science Foundation graduate research fellowship (SAS), Howard Hughes Foundation undergraduate fellowship (EWT) and the NSERC graduate fellowship (VF). This work is dedicated to the memory of Helmut Buchner.

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