

SHORT COMMUNICATION

Chirping and asymmetric jamming avoidance responses in the electric fish *Distocyclus conirostris*

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ABSTRACT

Electrosensory systems of weakly electric fish must accommodate competing demands of sensing the environment (electrollocation) and receiving social information (electrocommunication). The jamming avoidance response (JAR) is a behavioral strategy thought to reduce electrosensory interference from conspecific signals close in frequency. We used playback experiments to characterize electric organ discharge frequency (EODf), chirping behavior and the JAR of *Distocyclus conirostris*, a gregarious electric fish species. EODs of *D. conirostris* had low frequencies (~80–200 Hz) that shifted in response to playback stimuli. Fish consistently lowered EODf in response to higher-frequency stimuli but inconsistently raised or lowered EODf in response to lower-frequency stimuli. This led to jamming avoidance or anti-jamming avoidance, respectively. We compare these behaviors with those of closely related electric fish (*Eigenmannia* and *Sternopygus*) and suggest that the JAR may have additional social functions and may not solely minimize the deleterious effects of jamming, as its name suggests.

KEY WORDS: Electric Organ Discharge, Chirping, Weakly electric fish, Electrocommunication, Gymnotiformes

INTRODUCTION

Active sensory systems such as echolocation and electrollocation rely on accurate detection of small perturbations in self-generated signals and are sensitive to interference from signals produced by nearby conspecifics (Bullock et al., 1975; Ulanovsky et al., 2004; Nelson and MacIver, 2006). The jamming avoidance response (JAR) of South American weakly electric knifefish is a behavioral strategy thought to minimize deleterious interference caused by co-occurring signals (Watanabe and Takeda, 1963; Rose, 2004). Weakly electric fish generate weak electric fields by emitting an electric organ discharge (EOD) from a specialized electric organ. Fish can detect the position and properties of biotic and abiotic environmental features via localized distortions of the EOD (Lissmann, 1958; Heiligenberg, 1973; von der Emde, 1999). Additionally, social interactions with other electric fish create complex distortions of the field (Scheich, 1977; Zakon et al., 2002). When two fish are in close proximity, each fish perceives the other's EOD by the interference created when the other fish's EOD interacts with its own. The regular constructive and destructive interference

of two or more EODs creates a periodic amplitude modulation (beat). Beat frequency is equal to the difference between the EOD frequencies (EODfs) of the two interacting fish. Fish use the beat and the relative geometry of the interacting signals to estimate conspecific EODfs, which convey important social information (Smith, 2013; Dunlap, et al., 2017). However, slow beats (<10 Hz) created by interactions between fish with similar EODfs can impair the electrollocation function of the EOD by masking localized EOD distortions (Heiligenberg, 1973; Matsubara and Heiligenberg, 1978). The JAR is a stereotyped response in which an electric fish increases or decreases its EODf to increase beat frequency and thereby reduce or eliminate the interference caused by slow beats (Bullock et al., 1972; Heiligenberg et al., 1978).

The JAR has been studied extensively in *Eigenmannia*, a genus of electric fish within the family Sternopygidae. *Eigenmannia* are gregarious animals with EODfs of 300–600 Hz (Hopkins, 1974b; Tan et al., 2005). Using primarily frequency-clamping experiments, several investigators have shown that when *Eigenmannia* are presented with lower- or higher-frequency stimuli near their own EODf, they shift their EODf up or down, respectively, which moves the EODfs away from each other (Watanabe and Takeda, 1963; Heiligenberg, 1973; Heiligenberg et al., 1978). *Sternopygus*, a genus of territorial species in the same family, has low-frequency EODs in the range 50–150 Hz (Hopkins, 1974a). Interestingly, *Sternopygus* does not produce a JAR but can still behaviorally discriminate between higher- and lower-frequency signals (Bullock et al., 1975; Matsubara and Heiligenberg, 1978; Rose and Canfield, 1991). This discrimination ability without a JAR has been postulated to be a pre-adaptation in *Sternopygus* that allowed the evolution of the JAR in *Eigenmannia* (Rose and Canfield, 1991).

In addition to the JAR, electric fish transiently increase EODf for tens to hundreds of milliseconds to produce context-specific social signals called chirps, which indicate motivational state during courtship or aggression (Hagedorn and Heiligenberg, 1985; Larimer and MacDonald, 1968; Zakon et al., 2002). The frequency modulation caused by a chirp is perceived by the receiving fish as a rapid disruption of the beat (Walz et al., 2013).

Both *Eigenmannia* and *Sternopygus* produce at least two types of short-term EOD modulations, although the terminology and categorization for such modulations varies among authors. *Eigenmannia* produces chirps (or rises) during which the frequency of the EOD rapidly increases and then decreases, sometimes with complex frequency modulations in between (Hopkins, 1974b; Stöckl et al., 2014). *Eigenmannia* also produces interruptions, which are temporary cessations of the EOD that last 50–100 ms (Hagedorn and Heiligenberg, 1985; Hopkins, 1974b). Similarly, *Sternopygus* produces chirp/rises, in which EODf increases then decreases (sometimes with multiple frequency peaks), as well as interruptions during which the EOD is mostly silenced. *Sternopygus* interruptions vary in duration and are produced during agonistic encounters (short interruptions,

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20–70 ms) and courtship (long interruptions, 70–100 ms; Hopkins, 1974a). In this study, we describe and quantify for the first time, the EOD, JAR and chirping behavior of wild-caught *Distocyclus conirostris* C. H. Eigenmann & W. R. Allen 1942. *Distocyclus* is closely related to *Eigenmannia* and is similarly gregarious, but has a low-frequency EOD like *Sternopygus* (Kramer et al., 1981; Alves-Gomes, 1998; Tagliacollo et al., 2016). We also make comparisons among *Distocyclus*, *Eigenmannia* and *Sternopygus* that may provide insight into how EODf, jamming avoidance and chirping co-evolve.

MATERIALS AND METHODS

In March, 2014, four *D. conirostris* were collected with seine nets from floating vegetation mats in relatively shallow (~2 m) water. The collection site was an inlet off the Solimões River east of the Xiborena Channel on the south edge of Catalão near Manaus, Brazil. After collection, fish were transported to the Laboratório de Fisiologia Comportamental e Evolução (LFCE) at Instituto Nacional de Pesquisas da Amazônia and temporarily housed in aerated river water. Within 2 days of capture, we recorded electrocommunication behavior using a ‘chirp chamber’ paradigm described previously (Kolodziejcki et al., 2005). Briefly, the fish was placed in a loose mesh hammock within a temperature-controlled tank of river water and was allowed to acclimate for 30 min. The fish’s EOD was recorded via a pair of carbon electrodes placed parallel with the long axis of its body (i.e. in head–tail geometry). The signal from the electrodes was amplified 100× and recorded on the sound card (SoundBlaster Audigy 2, Creative Labs, Milpitas, CA, USA) of a laptop computer running Cool Edit Pro (Syntrillium, Phoenix, AZ, USA). The frequency response of the sound card was flat between ~10 Hz and ~20 kHz, dropping off ~1–2 dB at 4 Hz. After acclimation, we recorded a 3 min baseline EOD. Then we recorded the fish’s EOD while presenting 10 different playbacks in a random order. Playbacks were sinusoidal stimuli that spanned a range of frequencies simulating conspecific EODs (± 3 Hz, ± 5 Hz, ± 10 Hz, ± 20 Hz, ± 40 Hz relative to the fish’s own EOD). Stimuli were generated with Cool Edit and presented via a pair of carbon electrodes placed perpendicular to the long axis of the fish’s body. Stimulus amplitude was calibrated to a root-mean-square amplitude of 0.6 mV cm⁻¹ measured parallel to the playback electrodes and halfway between them. Each recording consisted of 45 s without playback stimulus, 60 s with one of the 10 playback stimuli and 75 s without playback, for a total recording length per stimulus of 3 min. Recordings with each stimulus were separated by 4 min rest periods to prevent habituation. Immediately after all recordings, we measured the fish’s total length and body mass (Table 1). Sex was confirmed by post-mortem examination of the gonads (3 out of 4 fish). All experiments were conducted in accordance with the NIH Guide for the Care and Use of Laboratory Animals and were approved by the Indiana University Bloomington Institutional Animal Care and Use Committee.

EODf was measured by generating a power spectrum (fast Fourier transform, Blackman–Harris window, size 65536) in Cool

Edit from a segment of the baseline recording. To account for slight variations in water temperature among recording sessions, EODf was standardized to that expected at 26°C by using a Q_{10} of 1.6 (Dunlap et al., 2000). Chirp recordings were analyzed offline with a customized procedure (efish23e, Brian Nelson, University of Oregon, Eugene, OR, USA; <http://nelsonbs.com/eFish/efish.html>) in Igor Pro (WaveMetrics, Lake Oswego, OR, USA) as described previously (Kolodziejcki et al., 2005). However, EODf could not be tracked reliably by this procedure when interruptions occurred during chirps. Instead, EODf during chirps was calculated by using interpolated zero-crossings with a customized script in Matlab (MathWorks, Natick, MA, USA; script available by contacting G.T.S. at getsmitth@indiana.edu). Chirp duration was estimated as the time between when the EODf trace crossed a 1 Hz threshold above and below the baseline EODf. The precision in estimating chirp duration was relatively low because (1) interpolated zero crossings were used to measure EODf during chirps; and (2) chirp duration was short relative to the period of the EOD. The direction and magnitude of the JAR were measured by comparing the EODf in the 5 s immediately preceding onset of the playback with the most extreme (minimum or maximum) EODf exhibited during the playback, not including chirps. The relationship between playback difference frequency and chirp rate was examined with a one-way repeated measures analysis of variance (ANOVA). The relationship between playback difference frequency and JAR frequency shift was analyzed with Pearson’s correlations.

RESULTS AND DISCUSSION

EODf and chirping

EODf was 138.6 \pm 23.7 Hz (mean \pm s.e.m.; Table 1). Fish often responded to playbacks by rapidly modulating their EOD, which is characteristic of electric fish responding to a social stimulus. We use the term ‘chirp’ here to describe these modulations, based on their relatively short duration and associated abrupt increases and decreases in EODf (after Hagedorn and Heiligenberg, 1985). Across individuals, chirp rate ranged from 0.48 to 2.12 chirps min⁻¹. Fish chirped primarily when playback stimuli were presented, although one fish also chirped spontaneously during the baseline recording. Spontaneous chirping has been reported in other gymnotiform species, although as in the current study, chirping occurs most often during social interactions or in response to playbacks (Zupanc et al., 2001; Kolodziejcki et al., 2007; Dunlap et al., 2010). There was no relationship between chirp rate and the difference frequency of the playback ($F_{10,30}=1.24$, $P=0.31$). A typical *D. conirostris* chirp began with a small (approximately 10–30 Hz) increase in EODf followed by a brief cessation of the EOD that lasted approximately 20–25 ms. The EOD resumed at a slightly lower frequency but then increased quickly to baseline (Fig. 1A,B). However, some chirps consisted of only an increase or decrease in frequency, not both. A small subset of chirps (<10%) had short durations (~25 ms) that created a phase shift of a single EOD cycle rather than interrupting multiple EOD cycles. These shorter chirps tended to occur in brief bursts of 3–7 chirps

Table 1. Sex, size and signal parameters of subjects

Fish ID	Sex	Mass (g)	Length (cm)	EODf (Hz)	No. of chirps	Chirp rate (chirps min ⁻¹)	Chirp duration (ms)*
D3164A07A	M	15.8	23.6	89.4	70	2.12	73.8 \pm 4.3
D3164A07B	?	17.4	21.0	114.6	16	0.48	99.2 \pm 1.4
D3164A07C	F	28.1	23.2	151.6	60	1.82	96.5 \pm 1.8
D3164A07D	F	38.9	25.5	198.6	22	0.67	93.5 \pm 11.0

EODf, electric organ discharge frequency. *Means \pm s.e.m.

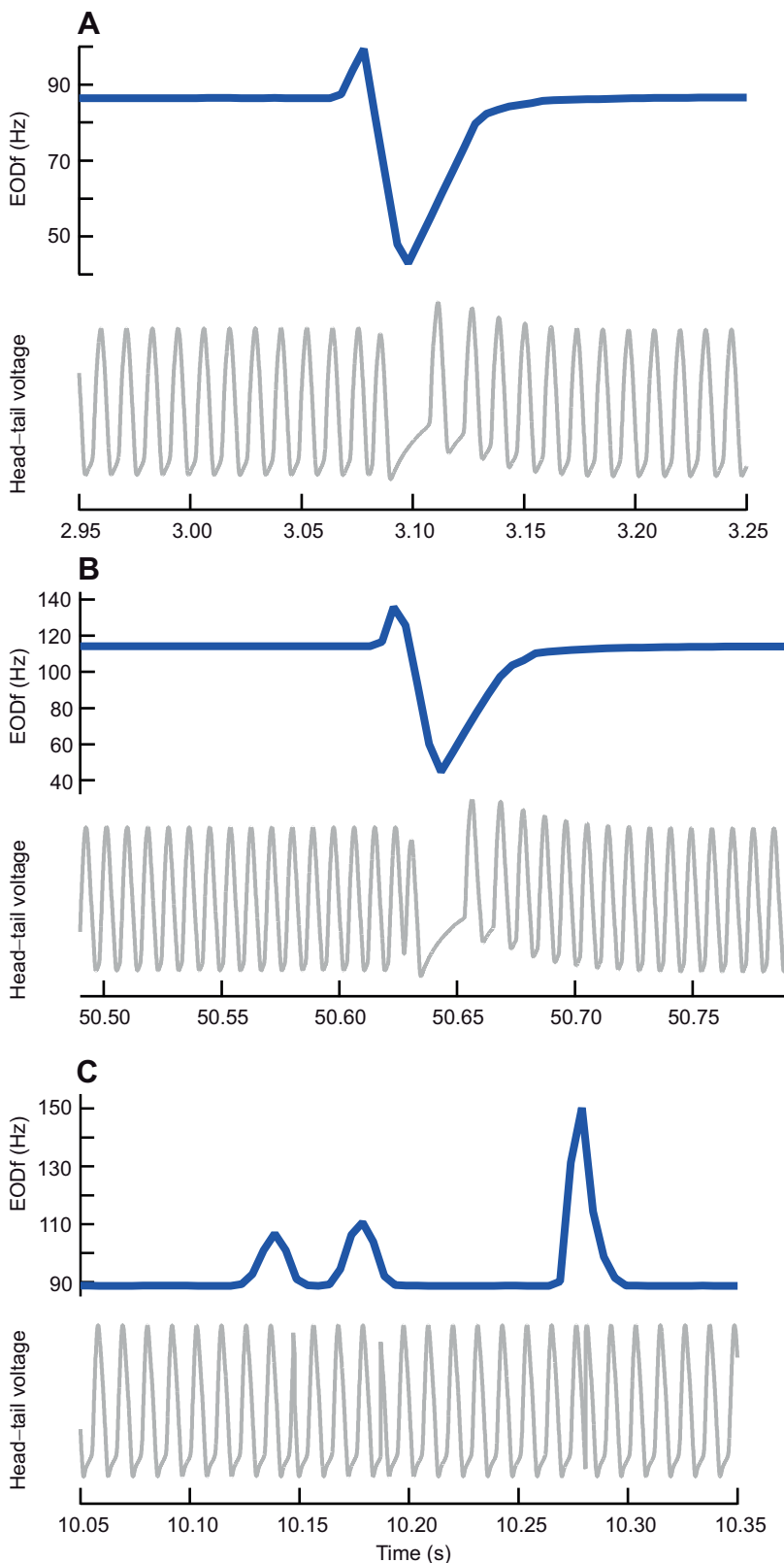


Fig. 1. Representative *Distocyclus conirostris* chirps.

(A,B) Electric organ discharge frequency (EODf) and head–tail EOD voltage (bottom traces) during chirps of two different *D. conirostris* individuals. EODf transiently increased then decreased before returning to baseline. These chirps interrupted the EOD. The frequency undershoot lasts several EOD cycles, which indicates that this frequency increase and decrease is not an artifact of the missed EOD cycles. Durations of the chirps were 89 ms (A) and 104 ms (B). (C) A small subset of chirps (11 of 169) were substantially shorter in duration than other chirps (26–27 ms). These chirps tended to occur in small clusters. The shorter duration chirps were not accompanied by an interruption of the EOD but instead caused a phase advance of a single EOD cycle.

(Fig. 1C). Across all fish and all chirps, chirp duration averaged 90.8 ± 5.8 ms.

The *D. conirostris* chirps were similar in structure to *Eigenmannia* chirps, which have a rapid increase and decrease in EODf, last 20–100 ms, and vary in duration based on social context (Hopkins, 1974b; Hagedorn and Heiligenberg, 1985). However, we

did not observe the long interruptions that have been found in *Eigenmannia* during live courtship interactions (Hagedorn and Heiligenberg, 1985; Hopkins, 1974b). It is possible that *D. conirostris* can produce longer interruptions, but that our experimental paradigm (i.e. chirp chamber recordings in response to one playback stimulus at a time) was not sufficient to elicit them.

That is, as *D. conirostris* are social like *Eigenmannia*, and are typically exposed simultaneously to signals of many individuals, they might not produce their full repertoire of signals in response to the signal of a single fish or in the absence of multiple live conspecifics (Stöckl et al., 2014). Moreover, because the fish were collected at the end of the rainy season and their gonads had largely regressed, they might not have produced signals used only during spawning. Because we were able to record signals from only four *D. conirostris*, we are unable to assess individual variation in chirping or the JAR or whether chirps or EODf are sexually dimorphic, as they are in other gymnotiform species (Smith, 2013). The *D. conirostris* chirps recorded in this study were similar to – although shorter than – the short (~800 ms) interruptions of *Sternopygus* (Hopkins, 1974a). Like those interruptions, *D. conirostris* chirps often began with a frequency increase and ended with a frequency undershoot below baseline. Thus, it appears that the general patterns in EOD modulations are largely conserved across these three genera.

JAR

Distocyclus conirostris shifted EODf at the onset of a conspecific signal mimic (Fig. 2). When fish were presented with a stimulus frequency higher than their own EODf, they consistently decreased EODf for the duration of the playback and then increased EODf back to baseline after playback cessation (Fig. 2A). However, when fish were presented with stimuli lower in frequency than their own EOD, the direction of the JAR varied: fish increased EODf in eight

of 20 trials with stimulus frequencies lower than their EODf (40%, jamming avoidance; Fig. 2B), but decreased EODf in 12 trials (60%, anti-jamming avoidance; Fig. 2C). Specifically, all four fish raised EODf in response to the –3 Hz playback, two fish raised EODf in response to the –5 Hz playback, and two fish raised EODf in response to the –40 Hz playback (Fig. 2D). None of the fish raised EODf in response to the –10 Hz or –20 Hz playback. In two cases, the fish first raised and then lowered its EODf in response to higher-frequency stimuli. The difference frequency of the playback and the EODf change during the JAR were not linearly correlated across the entire range of playback difference frequencies ($R^2=0.02$, $P=0.40$). However, examining the positive and negative playback differences separately revealed a significant linear correlation for positive playback difference frequencies (playback frequency >EODf; $R^2=0.31$, $P=0.01$) but no correlation for negative playback difference frequencies ($R^2=0.05$, $P=0.32$). The same pattern of jamming and anti-jamming responses to positive and negative difference frequencies was observed when the magnitude of the JAR was plotted versus the steady-state difference frequency (i.e. the difference between the stimulus frequency and the fishes' EODf near the end of the playback stimulus; Fig. 2E).

Like *Eigenmannia*, but unlike *Sternopygus*, *D. conirostris* shifted EODf at the onset of a playback stimulus. *Sternopygus* is largely solitary and territorial, but *Eigenmannia* forms large social aggregations (Hopkins, 1974a; Stamper et al., 2010; Tan et al., 2005). We strongly suspect that *D. conirostris* is gregarious like *Eigenmannia*, as *D. conirostris* are typically found in groups

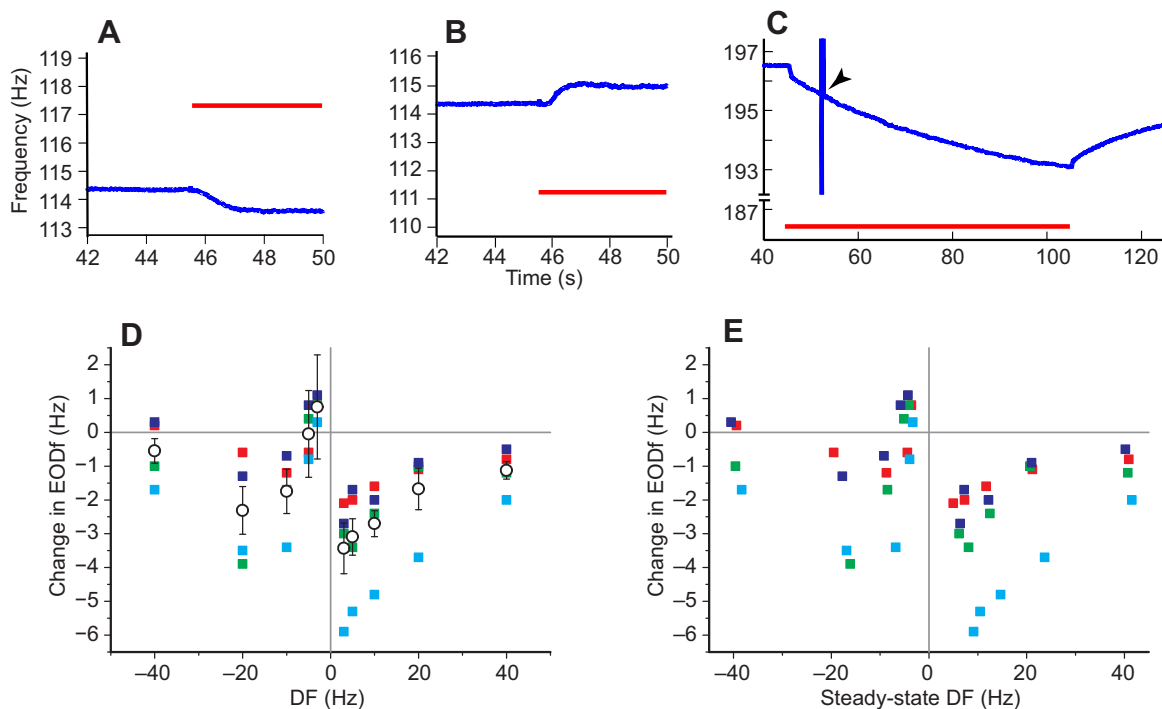


Fig. 2. Anomalous jamming avoidance response in *D. conirostris*. Fish shifted EODf (blue line) when presented with a stimulus of a similar frequency (red line). *Distocyclus conirostris* (A) decreased or (B) increased EODf to shift EODf away from that of the stimulus (i.e. jamming avoidance). (C) In response to playbacks below the fish's own EODf, fish often performed anomalous, 'anti-jamming' responses that decreased rather than increased the difference between the fishes' EODf and playback frequency. In this example, a stimulus 10 Hz below the fishes' EODf elicited a decrease, rather than an increase, in EODf. EODf gradually returned to baseline after stimulus offset. Arrowhead indicates a chirp. (D) Fish responded differently to higher- versus lower-frequency playbacks. The difference frequency (DF) of the stimulus relative to the fishes' baseline EODf is plotted versus the change in EODf in response to the playback stimulus. For stimuli higher in frequency than the fish's EOD (i.e. positive playback DFs), all fish lowered EODf, with the most robust responses to the DFs closest to zero. For stimuli lower in frequency than the fish's EOD (negative playback DFs), the direction of the frequency shift was less consistent. Individual fish are shown with different colored squares; open black circles are means (\pm s.e.m.). (E) Same data as in D, with the x-axis showing the steady-state DF (i.e. the difference between the stimulus frequency and the fish's EODf after its response to the stimulus reached steady state).

clustered around floating vegetation when they are collected (J.A.A.-G., personal observation). Both *Eigenmannia* and *D. conirostris* demonstrate the physiological capability for a bi-directional JAR, but *Sternopygus* does not. This could suggest that the JAR is critical for species that regularly co-exist with nearby conspecifics producing interfering signals but less important for species that live solitary lifestyles. However, the situation may be more complicated for several reasons. First, *Sternopygus* does not show impaired electrolocation from signals with similar frequencies presented at ecologically relevant amplitudes, which obviates the need for a neural strategy to avoid jamming (Matsubara, 1981; Matsubara and Heiligenberg, 1978). Thus, *Sternopygus* is less impaired by jamming stimuli from conspecifics and simultaneously less likely to encounter it. It is possible that *Sternopygus*' lack of a JAR is linked to its very low EODf. However, we have shown that *D. conirostris* has similarly low EODfs but produces a JAR. Additionally, there may be other neural mechanisms for fish to avoid jamming from nearby EODs with similar frequencies, such as comparing local and global distortions of the EOD (Chacron et al., 2003).

The JAR has also been postulated to have functions other than jamming avoidance. Kramer (1987) observed anomalous JARs in *Eigenmannia* that mirror the asymmetrical response reported here in *D. conirostris*. That is, some female *Eigenmannia* responded consistently to higher-frequency stimuli by lowering EODf, but responded weakly or not at all to lower-frequency stimuli. Juvenile *Eigenmannia* showed somewhat more robust JARs, but males did not robustly change EODf when presented with stimuli at frequencies near their EODf. Based on these observations, Kramer (1987) proposed a social function for the JAR in addition to (or in place of) its purported function of minimizing deleterious interference. Thus, if the JAR were used in preventing intra-specific aggression or for mediating and maintaining dominance hierarchies within social groups, the JAR might be more highly developed in gregarious species than in territorial species. A communication function would also explain why the fish we recorded here showed small but consistent responses to playback stimuli that were 20 Hz and 40 Hz above their own EODfs, well outside the usual range of frequencies shown to impair electrolocation (Heiligenberg, 1973; Behrend, 1977; Matsubara and Heiligenberg, 1978). Similar asymmetric JAR-like or anti-jamming responses to EODfs outside of the range known to cause jamming have also been found in some apteronotid electric fish species (Dye, 1987; Ho et al., 2010). These anomalous JARs in apteronotids may result in part from the fact that the electric fields generated by apteronotid EODs, unlike those of *Eigenmannia*, are spatially complex. This complexity may degrade sensory information required to unambiguously discriminate between stimuli above versus below a fish's own EODf (Shifman and Lewis, 2018).

A comparative characterization of the JAR among other species of wave-type electric fish could provide more insight into how the JAR is shaped by both social context and the risk of impairment to electrolocation. For example, examining the JAR in two other sternopygid genera that likely vary in sociality and EODf – *Rhabdolichops* and *Archolaemus* – could further elucidate when the JAR evolved and whether it functions as a communication signal and/or is related to social organization. An additional area for future study involves comparing diversity in the mechanisms underlying JARs and chirping across species. For example, differences in the JAR between *Eigenmannia* (bidirectional JARs that can raise or lower EODf) and *Apteronotus* (unidirectional JARs that can only increase EODf) are linked to species differences in brain circuits

that control the sign and magnitude of the JAR (Heiligenberg et al., 1996). Investigating how these brain regions control the anomalous JAR in *Distocyclus* may lead to a better understanding of how sensorimotor circuits evolve to produce behavioral diversity across species.

Acknowledgements

Thanks to Cristina Cox Fernandes for assistance with fish collection and identification.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.M.P., J.A.A.-G., G.T.S.; Methodology: J.M.P., G.T.S.; Software: G.T.S.; Formal analysis: J.M.P., G.T.S.; Investigation: J.M.P., J.A.A.-G., G.T.S.; Resources: J.A.A.-G., G.T.S.; Writing - original draft: J.M.P., G.T.S.; Writing - review & editing: J.M.P., J.A.A.-G., G.T.S.; Visualization: J.M.P., G.T.S.; Supervision: G.T.S.; Project administration: G.T.S.; Funding acquisition: J.A.A.-G., G.T.S.

Funding

This research was supported by National Science Foundation grant IOS 0950721 (G.T.S.) and IOS 1557935 (G.T.S.) and by National Institutes of Health grant T32HD049336 (Common Themes in Reproductive Diversity training grant, J.M.P.). Travel support #457339/2013-6 from Conselho Nacional de Desenvolvimento Científico e Tecnológico to J.A.A.-G. helped G.T.S. to visit LFCE for the experiments. Deposited in PMC for release after 12 months.

Data availability

The customized Matlab script used to calculate the EODf is available upon request from the corresponding author (getsmith@indiana.edu).

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