Peer Review File

Manuscript Title: Collective Sensing in Electric Fish

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

This is an excellent and manuscript describing and analyzing an entirely novel way that weakly electric fish (WEF) can sense their environment. I did consider one potential objection to publication in a Journal covering the entire vast range of science – will this paper be of "general interest". Here I did come up with an affirmative. Although this paper contains a great deal of the necessary detailed data required to establish the authors' conclusions, the conclusions are striking in that they are truly novel and remarkable. The WEF's ability to catch prey are not perturbed by the electric pulses of nearby conspecifics, as I would have expected, but can use them to improve their ability to locate prey and obstacles. I think that this manuscript is entirely appropriate for Nature in that it highlights another remarkable adaptation that optimizes a sensory system.
Below I briefly summarize the highlights of this paper and then note some issues that should be addressed.

African pulse type WEFs (Gnathonemus petersii) emit brief electric pulses (electric organ discharge, EOD) at a variable rate. The EOD pulses are used for electrocommunication and for localizing prey and environmental features. The "electric images" caused by prey and objects are weak so that the electrosense can only detect prey/objects within a few centimeters from their body. The authors first notice that these fish swim around in groups in the lab and often hold particular poses (e.g., perpendicular, parallel or single file). In the wild, related mormyrid fish have been observed to forage and hunt in groups. The paper reports that the EOD pulses produced a strong electric image; stronger than the direct electric image induced by the fish's own EOD pulse. Subsequent electrophysiological and behavioral experiments and analyses then demonstrated that the conspecific EOD induced images evoked responses (fleld potentials and spiking responses) in the electrosensory lobe and that the target fish "noticed" the input. The authors used the "novelty" response for "noticing". A reasonable measure. Very clever experiments were then used to prove that the pulses of neighbor fish were sufficient to discriminate objects.
Overall, the experiments were very convincing but I was puzzled by a few points as described below.

Minor Comments

1. Figure 1 b,c vs d,e. The perpendicular orientation in b,c greatly enhances detectability in the head region. Is this because the fish are perpendicular at their heads? If the fish were perpendicular at one fish's midbody, would detectability be enhanced at that location. And the same for the comparison in d,e. The enhancement is now for the mid trunk. Is there any indication from the videos of swimming fish that they choose particular relative localizations in order to optimize detectability at particular locations? This would be tricky to implement because it would require first detecting a weak poorly localized signal and then moving to enhance its amplitude. An alternative would be that they randomly sample their environment by their erratic movements – the impression I got viewing the video. I realize that a complete answer is likely not possible, but a brief connection could be made here to how this "other fish EOD" pulses might be used.
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used and, if so, the authors should mention this (legend).
By "chin" do the authors mean "chin appendage" = "Schauzenorgan". I understand that they do not want to use this archaic term, but a clarity is needed here as per the following points.
a) Bacelo et al (2008, JCN) do electroreceptor counts and come up with two foveas – one on the chin appendage and one near the nose. Is the enhancement precisely confined to the chin? That would be remarkable spatial precision.
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This manuscript reports a collection of theoretical and experimental results that together support the conclusion that electrolocation performance in the weakly electric fish Gnathonemus petersii is enhanced by the electric discharges of nearby conspecifics. This conclusion is both novel and significant: as the authors correctly point out, prior analyses of conspecific signals for active-sensing organisms have focused on conspecific signals as sources of interference for sensory processes. This manuscript is, to the best of my knowledge, the first report to demonstrate enhancement of active sensing by sensory signals from conspecifics. This conclusion is strongly supported by the integration of theoretical simulations, in vivo electrophysiology, and clever behavioral discrimination experiments.

The authors first use a series computational electric field simulations to demonstrate at a theoretical/conceptual level that conspecific EODs could significantly increase the distance at which an object will create a discernable electric image on a fish's electroreceptor arrays. In vivo physiological experiments then show that central electrosensory pathways respond appropriately to electric images created by conspecific EODs, and can detect objects at a greater distance than with self-generated EODs (at least for the fovea-like chin of the fish). The authors also report a series of behavioral object discrimination and object detection tests that provide direct evidence that conspecific EODs extend the distance over which objects can be detected, improve object discrimination. The authors also take the critically important step of showing that the fish's corollary discharge (known to mediate discrimination of self vs. non-self signals) does not "gate out" sensory information from conspecific EODs. A final set of experiments demonstrated that central electrosensory pathways encode information from both self-generated and conspecific generated EODs – thereby potentially increasing overall electrosensory information transfer. Taken together these experiments are a tour-de-force that collectively provide strong support the major conclusion that conspecific EODs enhance electrosensory performance. A major contribution of this finding will be to open up a number of compelling new lines of inquiry about the central processing and coding of "mixed" signals of self- vs. conspecific-generated electrical images, the evolution of such strategies, and the behavioral ecology of species where collective behavior improves individual sensory performance.

One weakness in the manuscript needs to be addressed. Early in the manuscript, the authors present data to show that a pair of subordinate fish tend to stay in close proximity and in stereotypical configurations when housed in a tank with a third dominant fish. These observations are interpreted to mean that the subordinate fish are doing so to enhance object detection. While the behaviors reported in Fig S1 and Video S1 are certainly consistent with an interpretation that fish do so to enhance sensory performance, other equally plausible interpretations can't be ruled out based on the data presented. The connection from data to conclusion isn't strong here, and I would encourage the authors to de-emphasize these data in making their case, perhaps removing them entirely.

A more minor suggestion is to feature the discussion and data from Figure S7 more prominently. The possibility that conspecific EODs can provide MORE information about an object than self-generated EODs is a surprising and potentially very important finding, but this information is almost lost as it is mentioned almost in passing at the end of the discussion.

Author Rebuttals to Initial Comments:

We thank both reviewers for their constructive comments and enthusiasm for our results. We have addressed the points raised by the reviewers and believe the manuscript is significantly improved. Please find our point-by-point responses below.

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We do not currently have any evidence that the fish optimize their positions to enhance collective sensing but plan to investigate this fascinating possibility. We have added a line to the discussion suggesting that the echo response may help to maintain the closely-spaced conspecific spatial configurations that are required for the collective sensing we describe.

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Thanks for this. We have now clarified in the legend and the main text that the extended range at chin versus head is simply because the chin is nearer the conspecific. Revised text: “For recordings from anterior regions of the ELL map representing the chin appendage, LFP amplitude was modulated by objects at greater distances for cons-EODs than for self-EODs **(Fig. 2c,d,f; Extended Data Fig. 3)**. In contrast, no such differences were observed for LFP recordings from ELL regions representing the head. A boundary element model simulation of the experimental arrangement shows this same range difference, which arises simply due to the fact that chin appendage is closer to the conspecific (**Fig. 2e**).“

By “chin” do the authors mean “chin appendage” = “Schauzenorgan”. I understand that they do not want to use this archaic term, but a clarity is needed here as per the following points.
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Could it be that they were recording from a different population of cells?

We have clarified this important point in the text and added additional analysis. While Bell and Grant do show evidence for enhancement, they use only a single stimulus amplitude that is below threshold without the corollary discharge response and provide no quantification. It is therefore not possible to gauge exactly how strong the enhancement is. We now quantify the difference in sensitivity to changes in the amplitude of self- and cons-pulses (data from Fig. 5a,b). We find that the sensitivity to cons-pulses is reduced relative to self-pulses by ~25% on average. This confirms past findings of enhancement but also clearly supports the present claim that ELL output is not strictly gated by corollary discharge. We use the same criteria for defining output cells that Bell employed, so we believe that the cells are the same, though we note that not all of the examples shown in the 1992 paper are putative output cells. Values for the sensitivity are also provided in the legend for Figure 5. Revised text: “Importantly, we found that the sensitivity of ELL output cells to cons-pulse amplitude was only moderately reduced (~25%) relative to self-pulse amplitude (**Fig. 5a,b; Extended Data Fig. 6a,b**), arguing against strict gating of ELL output by corollary discharge.”

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We also expected to see an enhancement at the echo delay and plan to investigate this interesting possibility in the future by recording from other electrosensory processing regions. As described above, we re-analyzed the data in Figure 5a,b to quantify any changes in sensitivity as a function of the delay of the cons-pulse. These results confirm the impression given by the single example cell shown in Fig. 5b, i.e. the sensitivity to cons-pulses delivered at the echo delay (12 ms) was not significantly different from that for pulses delivered at longer delays (25 or 35 ms). These values are now provided in the legend.

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Thanks for this comment. On re-reading the ms we agree that the logic of the second paragraph of the introduction (which includes the reference to Fig S1) is weak. We have essentially deleted this paragraph, with relevant references to the social behavior of the fish now confined to the discussion. We chose to retain most of Fig S1 because we use these postures for the electric field simulations. We now introduce this analysis in the context of the boundary element modeling without implying that it provides evidence for collective sensing. We have also deleted portions of Fig S1 related to the echo response that were extraneous. Revised text: "We used computer simulations of the electric field of the African pulse-type fish *Gnathonemus petersii* to test whether object detection could be enhanced by the EODs of nearby conspecifics. Conspecific spatial configurations were based on video analysis of groups of two subordinate and one dominant fish. Subordinates often spent minutes at a time less than a body length apart in stereotyped spatial configurations, including conspicuous perpendicular, single-file, and parallel line-up arrangements (**Extended Data Fig. 1; Video S1**)."

A more minor suggestion is to feature the discussion and data from Figure S7 more prominently. The possibility that conspecific EODs can provide MORE information about an object than self-generated EODs is a surprising and potentially very important finding, but this information is almost lost as it is mentioned almost in passing at the end of the discussion.

We agree that this is an interesting possibility. However, we are also wary of placing too much emphasis on this result as we have no behavioral evidence that the fish can actually perform such detailed comparison of self- and cons-images. This is something we hope to pursue in the future. We have added additional text to the discussion to better contextualize the result. Revised text: "Cons-images could also potentially enhance object discrimination by providing different views of the same electrosensory scene. Consistent with this possibility, using our boundary element model simulation it was easy to find scenarios in which two different objects (e.g. a cone versus a cylinder) generated virtually identical self-images but could, in principle, be discriminated based on cons-images (**Extended Data Fig. 7**). Such a detailed comparison of self- and cons-images would be remarkable (if it can be demonstrated behaviorally) given that the relative magnitude of self- and cons-images is highly-dependent on conspecific distance and orientation."

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Referee #2 (Remarks to the Author):

This manuscript reports a collection of theoretical and experimental results that together support the conclusion that electrolocation performance in the weakly electric fish Gnathonemus petersii is enhanced by the electric discharges of nearby conspecifics. This conclusion is both novel and significant: as the authors correctly point out, prior analyses of conspecific signals for active-sensing organisms have focused on conspecific signals as sources of interference for sensory processes. This manuscript is, to the best of my knowledge, the first report to demonstrate enhancement of active sensing by sensory signals from conspecifics. This conclusion is strongly supported by the integration of theoretical simulations, in vivo electrophysiology, and clever behavioral discrimination experiments.

The authors first use a series computational electric field simulations to demonstrate at a theoretical/conceptual level that conspecific EODs could significantly increase the distance at which an object will create a discernable electric image on a fish’s electroreceptor arrays. In vivo physiological experiments then show that central electrosensory pathways respond appropriately to electric images created by conspecific EODs, and can detect objects at a greater distance than with self-generated EODs (at least for the fovea-like chin of the fish). The authors also report a series of behavioral object discrimination and object detection tests that provide direct evidence that conspecific EODs extend the distance over which objects can be detected, improve object discrimination. The authors also take the critically important step of showing that the fish’s corollary discharge (known to mediate discrimination of self vs. non-self signals) does not "gate out" sensory information from conspecific EODs. A final set of experiments demonstrated that central electrosensory pathways encode information from both self-generated and conspecific generated EODs – thereby potentially increasing overall electrosensory information transfer. Taken together these experiments are a tour-de-force that collectively provide strong support the major conclusion that conspecific EODs enhance electrosensory performance. A major contribution of this finding will be to open up a number of compelling new lines of inquiry about the central processing and coding of "mixed" signals of self- vs. conspecific-generated electrical images, the evolution of such strategies, and the behavioral ecology of species where collective behavior improves individual sensory performance.

One weakness in the manuscript needs to be addressed. Early in the manuscript, the authors present data to show that a pair of subordinate fish tend to stay in close proximity and in stereotypical configurations when housed in a tank with a third dominant fish. These observations are interpreted to mean that the subordinate fish are doing so to enhance object detection. While the behaviors reported in Fig S1 and Video S1 are certainly consistent with an interpretation that fish do so to enhance sensory performance, other equally plausible interpretations can't be ruled out based on the data presented. The connection from data to conclusion isn't strong here, and I would encourage the authors to de-emphasize these data in making their case, perhaps removing them entirely.

Thanks for this comment. On re-reading the ms we agree that the logic of the second paragraph of the introduction (which includes the reference to Fig S1) is weak. We have essentially deleted this paragraph, with relevant references to the social behavior of the fish now confined to the discussion. We chose to retain most of Fig S1 because we use these postures for the electric field simulations. We now introduce this analysis in the context of the boundary element modeling without implying that it provides evidence for collective sensing. We have also deleted portions of Fig S1 related to the echo response that were extraneous. Revised text: "We used computer simulations of the electric field of the African pulse-type fish *Gnathonemus petersii* to test whether object detection could be enhanced by the EODs of nearby conspecifics. Conspecific spatial configurations were based on video analysis of groups of two subordinate and one dominant fish. Subordinates often spent minutes at a time less than a body length apart in stereotyped spatial configurations, including conspicuous perpendicular, single-file, and parallel line-up arrangements (**Extended Data Fig. 1; Video S1**)."

A more minor suggestion is to feature the discussion and data from Figure S7 more prominently. The possibility that conspecific EODs can provide MORE information about an object than self-generated EODs is a surprising and potentially very important finding, but this information is almost lost as it is mentioned almost in passing at the end of the discussion.

We agree that this is an interesting possibility. However, we are also wary of placing too much emphasis on this result as we have no behavioral evidence that the fish can actually perform such detailed comparison of self- and cons-images. This is something we hope to pursue in the future. We have added additional text to the discussion to better contextualize the result. Revised text: "Cons-images could also potentially enhance object discrimination by providing different views of the same electrosensory scene. Consistent with this possibility, using our boundary element model simulation it was easy to find scenarios in which two different objects (e.g. a cone versus a cylinder) generated virtually identical self-images but could, in principle, be discriminated based on cons-images (**Extended Data Fig. 7**). Such a detailed comparison of self- and cons-images would be remarkable (if it can be demonstrated behaviorally) given that the relative magnitude of self- and cons-images is highly-dependent on conspecific distance and orientation."