The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (*Hemigrammus rhodostomus*)

Amberle McKee, Alberto P. Soto, Phoebe Chen and Matthew J. McHenry

Review History

RSPB-2020-0568.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The paper addresses the sensory basis of schooling by intermittent swimming in tetrafish. This is an experimental work, conducted on a group of 5 individuals. The authors studied the influence of nearest neighbors on the kinematics of one individual within the group with respect to its position. They tested the sensibility of this influence to the lateral line and vision by varying the light intensity and lateral line sensibility. The main conclusion of the authors is that vision is both necessary and sufficient for schooling. This is an important question on a very active topic in the bio-physical community.

I very enjoyed reading this paper. The results are interesting, new, and very clearly presented. It is also very well written. Conclusions are essentials for future works, especially for group behaviors modeling. I think that this work fit perfectly the standards of Proceeding of the Royal Society B and I recommend strongly its publication in its present form.

I have maybe just one comment (or question) for the authors. There is a lot of important information in the supplementary file as, for instance, the complete description of the experimental setup or speed data. At first reading, I felt like some information was missing. Is there a specific reason why the authors chose hiding this information ?

Review form: Reviewer 2 (Valentin Lecheval)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

    Is it accessible?
    No

    Is it clear?
    N/A

    Is it adequate?
    N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
See my review in attached file. (See Appendix A)

Review form: Reviewer 3 (Eric Tytell)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

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      Is it accessible?
      Yes

      Is it clear?
      Yes

      Is it adequate?
      Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached file. (See Appendix B)

Decision letter (RSPB-2020-0568.R0)

06-May-2020

Dear Dr McHenry:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

Reviewers and the Associate Editor were wonderfully receptive to the paper and have constructive critiques; overall the peer reviews were very helpful and enthusiastic.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

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It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

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Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Dear Dr. McHenry,
Thank you for submitting your manuscript entitled "The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (Hemigrammus rhodostomus)" to the Proceedings of the Royal Society. I have received three peer reviews that are very supportive and also offer relevant comments and suggestions to further enhance this manuscript.
 I appreciate that your study uses a Bayesian decision-making model to show that burst-and-coast swimmers, as opposed to continuously swimming fish, rely on vision rather than lateral-line sensory input to shoal.
 I would like to prioritize the following comments. The reviewers felt that some information might deserve to be in the main text, and suggested that other information might go into supplements; they also make suggestions concerning details of the study's framework.
 Concerning the reviewers' queries about which information might deserve to be moved to or out of the main manuscript, I understand that the word limit of a Proceedings B manuscript can require difficult choices. Two reviewers query the use and the implementation of the Bayesian decision-making model and I tend to agree with the reviewers that this aspect of the study might benefit from either a revision of the approach or a more in-depth explanation and validation. When in doubt how to prioritize which information stays in the manuscript, I would encourage you to focus on more the findings than the method, and among those findings on those that build a clear main message about what best explains that these fish favor vision over mechanical sensing. If you feel strongly that the most innovative part of your study is the method, please strengthen this aspect of the study following suggestions by Reviewer 3.
 Concerning the manuscript's main message, I would like to point out that the reviewers offer alternative explanations and nuances to the authors' main conclusion (the difference between continuous and burst-and-coast swimmers is the driver behind their different use of sensory modalities for shoaling or schooling). For example, Reviewer 2 points out that fish use vision versus flow sensing for attraction versus repulsion (Reviewer 2 comment L31-33). I am also concerned about the difference between schooling and shoaling. I strongly encourage you to address all concerns about alternative explanations and nuance of explanation.
 I hope that you will find the reviewers' comments helpful when revising your manuscript.
 Please do not hesitate to reach out to us with questions about how best to address the reviewers' comments.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
The paper addresses the sensory basis of schooling by intermittent swimming in tetrafish. This is an experimental work, conducted on a group of 5 individuals. The authors studied the influence of nearest neighbors on the kinematics of one individual within the group with respect to its position. They tested the sensibility of this influence to the lateral line and vision by varying the light intensity and lateral line sensibility. The main conclusion of the authors is that vision is both necessary and sufficient for schooling. This is an important question on a very active topic in the bio-physical community.

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Referee: 2

Comments to the Author(s)
See my review in attached file.

Referee: 3

Comments to the Author(s)
See attached file.

Author's Response to Decision Letter for (RSPB-2020-0568.R0)

See Appendix C.

RSPB-2020-0568.R1 (Revision)

Review form: Reviewer 2 (Valentin Lecheval)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I really appreciated the new version of the manuscript and I think its interest and readability have been substantially improved.

I only have three (very) minor comments:

- L122-123: authors write "illuminance did significantly influence relationships between speed and the coast phase duration". However, in both treatments, we find a negative correlation. I find the sentence a bit misleading in potentially implying that the form of the relationship changes between treatment – which is not the case. I actually wonder if this statistical significance has any biological significance. Could maybe the authors elaborate briefly on why they think this change is important to be highlighted? It seems to me that the statistical significance is mainly a consequence of fish without lateral line moving slower than control fish at small coast durations, leading to a steeper negative correlation in the control group.

- L179-180: authors write "Steady swimming that depends on a fish's nearest neighbor may more easily use flow as a means of information for schooling". Given the debates in the collective motion literature regarding the number of influential neighbours in moving groups, I would not word the sentence this way (especially since H. rhodostomus has also been shown to be influenced mostly by a few close neighbours [1]). Maybe the following sentence would be less controversial: "Steady swimming that depends on group members in close vicinity may more easily use flow as a means of information for schooling."
[1]: Jiang et al. 2017. Identifying influential neighbors in animal flocking. PLOS COMP BIOL.

- Fig 3: the y-axis of the right panel (e-g) could have been the same as the left-panel (b-d) for easier comparisons between treatments but this is a very minor and personal suggestion.

- Fig S1 (b): Following mathematical conventions associated with the unit circle, it seems to me that authors have reported on the figure the angle theta - 2pi instead of theta (i.e. -pi/2 instead of 3pi/2) – in other words, I would have expected the white line depicting the angle to be drawn in the anti-clockwise direction rather than clockwise. This is super minor.

Review form: Reviewer 3 (Eric Tytell)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

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Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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    Is it accessible?
    Yes

    Is it clear?
    Yes

    Is it adequate?
    Yes

Do you have any ethical concerns with this paper?
Yes

Comments to the Author
The authors have addressed all of my major criticisms. I have only two very minor presentation comments.

1.   Fig. 2. The error bars on the points overlap so that we cannot see which points have larger or smaller error. Perhaps jitter the points slightly to make the error bars visible?

2.   Fig. 3(e). The orange box and points for no flow sensing under dim light are still hanging below the bottom of the y axis limits. Is this intentional? I find it very confusing.

Decision letter (RSPB-2020-0568.R1)

25-Jun-2020

Dear Dr McHenry

I am pleased to inform you that your Review manuscript RSPB-2020-0568.R1 entitled "The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (Hemigrammus rhodostomus)" has been accepted for publication in Proceedings B. Congratulations!!

The referee(s) do not recommend any further changes. Therefore, please proof-read your manuscript carefully and upload your final files for publication. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let me know immediately.

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3) Electronic supplementary material: this should be contained in a separate file from the main text and the file name should contain the author's name and journal name, e.g authorname_procb_ESM_figures.pdf
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please see: https://royalsociety.org/journals/authors/author-guidelines/

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It is a condition of publication that data supporting your paper are made available. Data should be made available either in the electronic supplementary material or through an appropriate repository. Details of how to access data should be included in your paper. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

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http://datadryad.org/submit?journalID=RSPB&manu=RSPB-2020-0568.R1 which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

5) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your final version. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr John Hutchinson
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Associate Editor Board Member: 1
Comments to Author:
Dear Dr. McHenry,
Thank you for submitting a revised version of your manuscript entitled "The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (Hemigrammus rhodostomus)" to the Proceedings of the Royal Society. I have received two peer reviews that are very supportive and that have just a few minor comments, which I would like to share with you, so you can consider them and decide whether these comments warrant implementation to enhance the quality of the manuscript.

Reviewer(s)' Comments to Author:
Referee: 2

Comments to the Author(s)
I really appreciated the new version of the manuscript and I think its interest and readability have been substantially improved.

I only have three (very) minor comments:

- L122-123: authors write "illuminance did significantly influence relationships between speed and the coast phase duration". However, in both treatments, we find a negative correlation. I find the sentence a bit misleading in potentially implying that the form of the relationship changes between treatment – which is not the case. I actually wonder if this statistical significance has any biological significance. Could maybe the authors elaborate briefly on why they think this change is important to be highlighted? It seems to me that the statistical significance is mainly a consequence of fish without lateral line moving slower than control fish at small coast durations, leading to a steeper negative correlation in the control group.

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Referee: 3

Comments to the Author(s)
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1. Fig. 2. The error bars on the points overlap so that we cannot see which points have larger or smaller error. Perhaps jitter the points slightly to make the error bars visible?

2. Fig. 3(e). The orange box and points for no flow sensing under dim light are still hanging below the bottom of the y axis limits. Is this intentional? I find it very confusing.

Decision letter (RSPB-2020-0568.R2)

08-Oct-2020

Dear Dr McHenry

I am pleased to inform you that your manuscript entitled "The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (Hemigrammus rhodostomus)" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

The manuscript *The sensory basis of schooling by intermittent swimming in the rummy-nose tetra (Hemigrammus rhodostomus)* aims to investigate the sensory mechanisms involved in schooling behaviour, from laboratory experiments performed on the rummy-nose tetra. In particular, authors present an experimental design to disentangle the respective roles of vision and lateral line in the schooling behaviour in the context of intermittent swimming.

Overall, I found the manuscript well written, figures nicely executed and experiments and results well reported. Results are, I think, within the scope of the journal, and in my opinion they are relevant for the life science community interested in collective behaviours and collective motion. Therefore I recommend for publication.

My main criticism regarding the manuscript concerns the literature used. In my opinion, the authors, by omitting several recent studies on collective behaviour, intermittent swimming style or *Hemigrammus rhodostomus*, miss the opportunity of having a clear story by having statements either not supported by literature or compatible with recent research. I feel that refining these sections would make the manuscript more appealing, in particular to the collective motion community. I detail further literature suggestions which could improve this dimension of the manuscript. I have waived anonymity of my review since I also suggest two research articles in which I am deeply involved and coauthor (References [6] and [7]). References in parenthesis refer to references used in the manuscript.

L31-33 – It seems to me that the current consensus is that vision is in general important for attraction and alignment interactions while lateral line is involved in short-range interactions such as repulsion or startle responses [1]. See [1] for additional references on this subject.

L35-38 - The interaction of alignment is not specified here. Although explicit alignment was not found in the two papers cited, these results are debated and other papers focusing on fish with continuous swimming-style have found evidences for an alignment interaction [2].

L40-42 – Reference (16) mainly focuses on zebrafish larvae and has not investigated possible social interactions extensively, only providing a minimal and satisfying model. The sentence as it is currently written tends to imply that only attraction interactions are at work but there are good evidences for explicit alignment interactions in zebrafish [3].

L42-44 – The importance of visual cues in collective swimming of zebrafish has already been reported in [4]. Regarding the role of intermittent swimming style in the context of collective motion in zebrafish, see [5]. I also do not fully understand the sentence, "This form of schooling depends more on the ability of individuals to account for the left-right distribution of others than maintaining position relative to a nearest neighbour". This sentence implies that:

1. to maintain position in a continuously swimming school does not require to account for the L-R distribution of neighbours;
2. fish with continuous swimming style in schools maintain their position relative to a nearest neighbour
3. fish with intermittent swimming style do not maintain position with their nearest neighbours.
I feel that these three claims, if not wrong, need consistent support from the literature.

L46-47 – Schooling in *H. rhodostomus* has been studied recently. As for findings highly relevant to this manuscript, it has been suggested before from trajectory analyses that social interactions involved in swimming strongly rely on visual cues: schools of rummy-nose tetra perform collective U-turns from front to back [6] and neglect alignment interactions with fish behind them [6, 7]. The current manuscript is a nice empirical confirmation of these previous findings.

L148 – The fact that rummy-nose tetra tend to move towards greater number of group members had already been shown in [6].

L154-156 – The concept of zones for interaction rules (attraction, alignment, repulsion) is a modelling choice rather than the accurate description of a biological reality. In [2], authors model fish collective motion with continuous swimming without zones (interaction rules can be formalised as being continuous with distance). It has also been done for fish with intermittent swimming style [7].

L157-158 – However, in [8] authors claim that lateral line in golden shiners play a minimal role in school and show the importance of vision in information transfer.

To summarise : I do not think the results of the current article clearly support the hypothesis of the authors that the swimming style (intermittent or continuous) has a clear effect on the sensory modalities used by fish to school. Given the current results and the literature (which suggests results similar to the findings shown in this paper, namely that vision is involved in social interactions of alignment and attraction while lateral line is more important for repulsion and startle-responses), I would expect that the environment (turbid water or clear water) of the species has more effect on the sensory modalities.

Instead, I suggest that authors could take advantage of the existing literature on *Hemigrammus rhodostomus* (and possibly including *H. bleheri*) to state how much their results confirm predictions made by models using fish trajectories. This would provide a rare and nice close-loop for a given species with detailed description of collective behaviour [6, 9], social interactions [7] and biomechanics (2), and study of the underlying sensory modalities as found in the current article. This would clearly make a case for *H. rhodostomus* and *bleheri* as being suitable for further studies to investigate collective behaviours and collective motion in fish with intermittent swimming style.

[1] Ioannou. (2017). Swarm intelligence in fish? The difficulty in demonstrating distributed and self-organised collective intelligence in (some) animal groups. Behavioural Processes. https://doi.org/10.1016/j.beproc.2016.10.005

[2] Gautrais et al. (2012). Deciphering Interactions in Moving Animal Groups. PLOS Computational Biology. https://doi.org/10.1371/journal.pcbi.1002678

[3] Zienkiewicz et al. (2018). Data-driven modelling of social forces and collective behaviour in zebrafish. Journal of Theoretical Biology. https://doi.org/10.1016/j.jtbi.2018.01.011

[4] Collignon et al. (2016). A stochastic vision-based model inspired by zebrafish collective behaviour in heterogeneous environments. RS Open Science. http://dx.doi.org/10.1098/rsos.150473

[5] Harpaz et al. (2017). Discrete modes of social information processing predict individual behavior of fish in a group. PNAS. https://doi.org/10.1073/pnas.1703817114

[6] Lecheval et al. (2018). Social conformity and propagation of information in collective U-turns of fish schools. Proceedings of the Royal Society B. https://doi.org/10.1098/rspb.2018.0251

[7] Calovi et al. (2017). Disentangling and modeling interactions in fish with burst-and-coast swimming reveal distinct alignment and attraction behaviors. PLOS Computational Biology. https://doi.org/10.1371/journal.pcbi.1005933

[8] Rosenthal et al. (2018). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. PNAS. https://doi.org/10.1073/pnas.1420068112

[9] Puckett et al. (2018). Collective gradient sensing in fish schools. Scientific Reports. https://doi.org/10.1038/s41598-018-26037-9

I also have some comments regarding the Methods.

1. It is so far not clear (including in the Supplementary Material) how many fish have been used in total. I would also appreciate precisions to know if fish have been used several times in experiments and in the same groups.

2. Regarding the lateral line manipulation, could authors explain why additional control experiments are not required, in order to check the anesthesias and further manipulations they performed have not effect on the subsequent social interactions tested.

I now turn to minor comments:

L12: "Therefore, vision is both necessary and sufficient for schooling in *H. rhodostomus* and that flow sensing serves to modulate schooling kinematics." It seems "that" could be removed from the sentence.

L17: "Fish within a school have the potential to enhance their ability to identify prey, detect predators, and swim efficiently compared to swimming on their own." The wording suggests that the enhancement of fish abilities is active when individuals are in group – while for the most part this is a passive emergent effect of other mechanisms (many-eyes hypothesis, dilution of risks, …), which in turn might sometimes result in increased cognitive abilities [1].

L60: How long is "a brief duration" (we only know a "long duration" is 30min long)?

There is no use of Figures S3 and S6 in the main manuscript nor in the Supplementary text.

Supplementary material should be entitled Electronic Supplementary Material instead of Supplemental materials.

Valentin Lecheval,
University of York

Appendix B

Comments for authors

This manuscript presents an analysis of schooling behavior in the rummy-nosed tetra, a fish that swims intermittently, using a burst-and-coast pattern. The authors varied light levels to test the role of vision in schooling and ablated the lateral line system to test its role. They found that these tetras cannot school in the dark (i.e., without vision), but they can school without their lateral line system. Without the lateral line, the school still forms, but with larger distances between neighbors and lower polarization. The authors also analyze the behavior of fish in the school under these different sensory conditions, showing that they turn more often and make larger turns toward one side if there are more fish on that side. Fish also tend to make larger turns under bright light than dim, but the turns do not seem to depend on the lateral line function.

I have two major criticisms.

1. My primary criticism is about the cohesion of the manuscript. Right now, it feels like there are two somewhat disjointed pieces: the analysis of turning and accelerating behavior (Fig. 2 and most of the supplemental materials) and the analysis of the overall school with and without vision or the lateral line (Fig. 3). I think the authors could make a stronger argument that the changes in behavior help to influence the changes in the overall school structure. In particular, in Fig. 2 and most of the regressions in Fig. S4, the authors find that light levels significantly influence the motion, but there is very little discussion of this fact in the discussion section. Particularly in Fig. S4, the figures only show the overall regression line, not the significantly different regression lines for dim vs. bright light. Please highlight and discuss the implications of these differences as regards school structure and cohesiveness.
2. The Bayesian model fit (Fig. 2a) seems underdeveloped. It's not crucial to the other arguments in the paper, so the authors might consider removing it entirely. If they want to keep it, I would like to see some more detailed analysis. For example, does this model explain the data better than something else – maybe even a simple linear fit? Does it indicate that fish are making decisions differently under the different sensory conditions? What are the implications of the a and s parameters in the fit? How do these parameters compare to those of other collectives?

Minor comments

1. ln. 8. "burst phase" Although you used the term "burst-and-coast" already, you haven't referred to "burst phase" and "coast phase", so I was momentarily confused by this term. Consider rephrasing.
2. ln. 45 and introduction overall. You might want to consider discussing some of the literature on lateral line sensing and burst-and-coast swimming, which has mostly been developed by studying blind cavefish (e.g., Patton et al., 2010; Tan et al., 2011)
3. ln. 127. I think you meant to refer to Table S1 here.
4. Fig. 2 and throughout. The color scheme here and in the supplemental figures is very subtle and makes it quite hard to distinguish the different sensory conditions. I would encourage the authors to use much brighter colors and vary the shape of the symbols.
5. Fig. 3b and SI ln. 148. The speed V is the speed of the centroid of the school, correct? Or is it the magnitude of the mean of the velocity vectors for each fish? Please clarify. And either way, I think you should call it something like "mean school speed" or "mean group speed" to indicate that it is different from the speed of any one individual.

6. Fig. 3e. It appears that the mean speed of the no flow sensing, dim light group is lower than the minimum on the y axis, and the outlier points are above the maximum on the y axis. For clarity please make sure the y axis covers the entire range of the data.
7. SI ln. 26. Do these lamps flicker at 60Hz? What is the flicker fusion rate for tetras?
8. Fig. S1c, inset. It would be helpful to have an even higher zoom inset so that SNs can be seen clearly. On my copy, they are barely visible even when I zoom in on my computer, and would be completely invisible in a printed copy.
9. SI Eq 0.1 and tables. The authors use R notation for statistical models, which is relatively widely known, but may not be self-evident to all readers, particularly with respect to the notation for random effects. Please explain the notation or alter it to indicate exactly what is being estimated (e.g., for Eq 0.1, the β coefficients for the intercept, the T_{burst} slope, the effects of lateral line treatment and dim light, and a randomly distributed γ coefficient for each school)
10. Tables. The authors seem to distinguish between $\ll 0.001$ (much less than?) and just <0.001. I don't know that this is necessary, but if so, criteria should be given.
11. Table S4. I think you may have mixed up some of the variables in the first column. For example, the first regression section list T_{burst} as a variable, but it isn't in the model given on the first line. Probably you meant $\overline{\Delta v}_{focal}$? And similarly for the other two regressions.
12. Fig. S6. Are these patterns significantly different from one another? While these plots are pretty, I'm not sure they add too much to the overall argument in the paper. If the authors wish to include them, I would like to see a bit more analysis of the pattern and discussion.

Appendix C

We are grateful to the reviewers for their careful reading of our paper and their suggestions for improvements. We have made several changes addressing the comments made by the reviewers and editor, as detailed below. Please note that we had to reformat the document to upload the text in LaTex and the line numbers are consequently a bit different than the original submission. Note that we have included only those comments that required a response in the below listing.

ASSOCIATE EDITOR --

COMMENT: Two reviewers query the use and the implementation of the Bayesian decision-making model and I tend to agree with the reviewers that this aspect of the study might benefit from either a revision of the approach or a more in-depth explanation and validation.

RESPONSE: We have decided to dispense with the Bayesian model, which was not original to this study and not important to our central findings.

COMMENT: When in doubt how to prioritize which information stays in the manuscript, I would encourage you to focus on more the findings than the method, and among those findings on those that build a clear main message about what best explains that these fish favor vision over mechanical sensing. If you feel strongly that the most innovative part of your study is the method, please strengthen this aspect of the study following suggestions by Reviewer 3.

RESPONSE: We have rewritten the Discussion and a portion of the Introduction to emphasize the sensory basis of schooling. We have de-emphasized the role of intermittent swimming and the methodology employed in the present study.

COMMENT: Concerning the manuscript's main message, I would like to point out that the reviewers offer alternative explanations and nuances to the authors' main conclusion (the difference between continuous and burst-and-coast swimmers is the driver behind their different use of sensory modalities for shoaling or schooling).

RESPONSE: We have taken the reviewers suggestions to heart and feel that our revisions reflect a new focus on the roles of vision and the lateral line in schooling.

COMMENT: For example, Reviewer 2 points out that fish use vision versus flow sensing for attraction versus repulsion (Reviewer 2 comment L31-33).

RESPONSE: This concept of the roles of vision and the lateral line is not consistent with our results and what has been found in some other

species. However, this suggestion by the reviewer prompted us to place a major emphasis on attraction/repulsive/alignment in our revision. This allows for a more specific function of each modality that is of interest beyond a demonstration of necessity and sufficiency.

COMMENT: I am also concerned about the difference between schooling and shoaling.

RESPONSE: We now address the distinction between these terms in the third paragraph of the Introduction.

COMMENT: I strongly encourage you to address all concerns about alternative explanations and nuance of explanation.
I hope that you will find the reviewers' comments helpful when revising your manuscript. Please do not hesitate to reach out to us with questions about how best to address the reviewers' comments.

RESPONSE: Indeed, the reviewers exerted a substantial amount of energy in their work and have influenced our thinking about how our results relate to the literature on schooling. Our re-evaluation is most substantially shown in the revised Discussion text, which is almost completely revised in response to the reviewer's ideas.

REVIEWER 1 --

COMMENT: I have maybe just one comment (or question) for the authors. There is a lot of important information in the supplementary file as, for instance, the complete description of the experimental setup or speed data. At first reading, I felt like some information was missing. Is there a specific reason why the authors chose hiding this information?

RESPONSE: The short format of Proc. B constrained our ability to elaborate on our methodology. As an indication of the journal's desired length, the society does not incur pages charges for articles that are 6 pages and length or fewer. According to their page calculator, our initial submission was 7 pages long, which is the main reason why we had such a substantial supplemental materials section. We also wanted to offer a document with an exhaustive description of our methods.

REVIEWER 2 --

COMMENT: My main criticism regarding the manuscript concerns the literature used. In my opinion, the authors, by omitting several recent studies on collective behaviour, intermittent swimming style or Hemigrammus rhodostomus, miss the opportunity of having a clear story by having statements either not supported by literature or compatible with

recent research. I feel that refining these sections would make the manuscript more appealing, in particular to the collective motion community. I detail further literature suggestions which could improve this dimension of the manuscript. I have waived anonymity of my review since I also suggest two research articles in which I am deeply involved and coauthor (References [6] and [7]). References in parenthesis refer to references used in the manuscript.

RESPONSE: We greatly appreciate the substantial effort that Rev 2 has invested in his review, including summaries of relevant literature, including a number of papers that we now include in our presentation and discussion of the literature.

COMMENT: L31-33 – It seems to me that the current consensus is that vision is in general important for attraction and alignment interactions while lateral line is involved in short-range interactions such as repulsion or startle responses [1]. See [1] for additional references on this subject.

RESPONSE: We should have raised these ideas in our initial draft and our revision now features this as a major topic in the Introduction and Discussion. Our results and some other studies that we cite do not support the notion that the lateral line is restricted to a repulsive role, although it generally does appear to offer only short-range functionality. As we now discuss in the paper, studies on other species do support the idea of flow sensing for repulsion. So, it appears that the particular role of this modality varies among species. Vision certainly aids in attraction and alignment, though it seems possible that it helps with repulsion as well.

COMMENT: L35-38 - The interaction of alignment is not specified here. Although explicit alignment was not found in the two papers cited, these results are debated and other papers focusing on fish with continuous swimming-style have found evidences for an alignment interaction [2].

RESPONSE: We agree that we should have acknowledged alignment along with attraction and repulsion. We now mention alignment in the Intro and Discussion and cite [2]. As the reviewer indicates, there is debate over the importance of alignment and we do not feel that our results point one way or another.

COMMENT: L40-42 – Reference (16) mainly focuses on zebrafish larvae and has not investigated possible social interactions extensively, only providing a minimal and satisfying model. The sentence as it is currently written tends to imply that only attraction interactions are at work but there are good evidences for explicit alignment interactions in zebrafish [3].

RESPONSE: This paragraph no longer exists and we now discuss attraction, repulsion, and alignment (including citing [3]) in the Introduction.

COMMENT: L42-44 – The importance of visual cues in collective swimming of
zebrafish has already been reported in [4]. Regarding the role of
intermittent swimming style in the context of collective motion in
zebrafish, see [5].

RESPONSE: The Introduction now acknowledges the contributions of papers
[4] and [5].

COMMENT:
 I also do not fully understand the sentence, "This form of schooling
depends more on the ability of individuals to account for the left-right
distribution of others than maintaining position relative to a nearest
neighbour". This sentence implies that:
1. to maintain position in a continuously swimming school does not
require to account for the L-R distribution of neighbours;
2. fish with continuous swimming style in schools maintain their position
relative to a nearest neighbour
3. fish with intermittent swimming style do not maintain position with
their nearest neighbours.
I feel that these three claims, if not wrong, need consistent support
from the literature.

RESPONSE: Our revision no longer includes this sentence.

COMMENT: L46-47 – Schooling in H. rhodostomus has been studied recently.
As for findings highly relevant to this manuscript, it has been suggested
before from trajectory analyses that social interactions involved in
swimming strongly rely on visual cues: schools of rummynose tetra perform
collective U-turns from front to back [6] and neglect alignment
interactions with fish behind them [6, 7]. The current manuscript is a
nice empirical confirmation of these previous findings.

RESPONSE: We now cite papers [6] and [7].

COMMENT: L148 – The fact that rummy-nose tetra tend to move towards
greater number of group members had already been shown in [6].

RESPONSE: This passage no longer exists, but we do now acknowledge [6] in
the Discussion.

COMMENT: L154-156 – The concept of zones for interaction rules
(attraction, alignment, repulsion) is a modelling choice rather than the
accurate description of a biological reality. In [2], authors model fish
collective motion with continuous swimming without zones (interaction
rules can be formalised as being continuous with distance). It has also
been done for fish with intermittent swimming style [7].

RESPONSE: Good point. This section no longer exists, but we now avoid
language about zones.

COMMENT: L157-158 – However, in [8] authors claim that lateral line in golden shiners play a minimal role in school and show the importance of vision in information transfer.

RESPONSE: That statement no longer exists in our revision. However, we discuss other situations where the lateral line may serve a redundant role with the visual system when the fish are close together. The Rosenthal study does not test the role of the lateral line and the papers that it does cite with respect to flow sensing do not appear to contradict our statements, nor do the results of the Rosenthal study.

COMMENT: To summarise : I do not think the results of the current article clearly support the hypothesis of the authors that the swimming style (intermittent or continuous) has a clear effect on the sensory modalities used by fish to school. Given the current results and the literature (which suggests results similar to the findings shown in this paper, namely that vision is involved in social interactions of alignment and attraction while lateral line is more important for repulsion and startle-responses), I would expect that the environment (turbid water or clear water) of the species has more effect on the sensory modalities.

RESPONSE:We agree that because the study did make a comparison between intermittent and continuously swimming species, then its measurements do not offer a strong basis of comparison between swimming modes. It is plausible, based on first principles and the results of [5], that the sensory cues available to intermittent swimmers are different from continuous swimmers, but that has not been demonstrated in the present study. Therefore, our revision focuses much less on this topic and mentions it as a feature of how this species moves, and may be analyzed, in the Introduction and as a matter of speculation on its functional significance in the Discussion.

COMMENT: Instead, I suggest that authors could take advantage of the existing literature on Hemigrammus rhodostomus (and possibly including H. bleheri) to state how much their results confirm predictions made by models using fish trajectories. This would provide a rare and nice close-loop for a given species with detailed description of collective behaviour [6, 9], social interactions [7] and biomechanics (2), and study of the underlying sensory modalities as found in the current article. This would clearly make a case for H. rhodostomus and bleheri as being suitable for further studies to investigate collective behaviours and collective motion in fish with intermittent swimming style.

RESPONSE: We have shifted the emphasis of the Discussion toward the implications of our results in terms of the behavioral rules that Hemigrammus may employ for schooling, largely inspired by this reviewer's input. We now include consideration of the recent Hemigrammus papers, but do not necessarily share the view that our results confirm the predictions of some of the models among those papers. This revised version does not aim to explicitly test published models.

COMMENT

[1] Ioannou. (2017). Swarm intelligence in fish? The difficulty in demonstrating distributed and self-organised collective intelligence in (some) animal groups. Behavioural Processes. https://doi.org/10.1016/j.beproc.2016.10.005
[2] Gautrais et al. (2012). Deciphering Interactions in Moving Animal Groups. PLOS Computational Biology. https://doi.org/10.1371/journal.pcbi.1002678
[3] Zienkiewicz et al. (2018). Data-driven modelling of social forces and collective behaviour in zebrafish. Journal of Theoretical Biology. https://doi.org/10.1016/j.jtbi. 2018.01.011
[4] Collignon et al. (2016). A stochastic vision-based model inspired by zebrafish collective behaviour in heterogeneous environments. RS Open Science. http://dx.doi.org/ 10.1098/rsos.150473
[5] Harpaz et al. (2017). Discrete modes of social information processing predict individual behavior of fish in a group. PNAS. https://doi.org/10.1073/pnas.1703817114
[6] Lecheval et al. (2018). Social conformity and propagation of information in collective Uturns of fish schools. Proceedings of the Royal Society B. https://doi.org/10.1098/rspb. 2018.0251
[7] Calovi et al. (2017). Disentangling and modeling interactions in fish with burst-andcoast swimming reveal distinct alignment and attraction behaviors. PLOS Computational Biology. https://doi.org/10.1371/journal.pcbi.1005933
[8] Rosenthal et al. (2018). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. PNAS. https://doi.org/ 10.1073/pnas.1420068112
[9] Puckett et al. (2018). Collective gradient sensing in fish schools. Scientific Reports. https://doi.org/10.1038/s41598-018-26037-9

RESPONSE: Thank you!

I also have some comments regarding the Methods.

COMMENT: 1. It is so far not clear (including in the Supplementary Material) how many fish have been used in total. I would also appreciate precisions to know if fish have been used several times in experiments and in the same groups.

RESPONSE: We now describe the numbers of fish in the "Sample sizes" section of the Supplemental Materials and mention the total number in the methods.

COMMENT: 2. Regarding the lateral line manipulation, could authors explain why additional control experiments are not required, in order to check the anesthesias and further manipulations they performed have not effect on the subsequent social interactions tested.

RESPONSE: We now clarify that no anesthesias was used and that the control and treated fish were handled to the same degree.

I now turn to minor comments:

COMMENT: L12: "Therefore, vision is both necessary and sufficient for schooling in H. rhodostomus and that flow sensing serves to modulate schooling kinematics." It seems "that" could be removed from the sentence.

RESPONSE: This sentence no longer exists.

COMMENT: L17: "Fish within a school have the potential to enhance their ability to identify prey, detect predators, and swim efficiently compared to swimming on their own." The wording suggests that the enhancement of fish abilities is active when individuals are in group – while for the most part this is a passive emergent effect of other mechanisms (many-eyes hypothesis, dilution of risks, …), which in turn might sometimes result in increased cognitive abilities [1].

RESPONSE: We reworded the beginning of this sentence to make this point more clear.

COMMENT: L60: How long is "a brief duration" (we only know a "long duration" is 30min long)?

RESPONSE: We have added the duration in parentheses.

COMMENT: There is no use of Figures S3 and S6 in the main manuscript nor in the Supplementary text.

RESPONSE: We have removed Fig S6 and we now reference S3 in the Results.

COMMENT: Supplementary material should be entitled Electronic Supplementary Material instead of
Supplemental materials.

RESPONSE: This has been changed. Thank you for spotting that.

REVIEWER 3 ---

COMMENT: 1. My primary criticism is about the cohesion of the manuscript. Right now, it feels like there are two somewhat disjointed pieces: the analysis of turning and accelerating behavior (Fig. 2 and most of the supplemental materials) and the analysis of the overall school with and without vision or the lateral line (Fig. 3). I think the authors could

make a stronger argument that the changes in behavior help to influence the changes in the overall school structure. In particular, in Fig. 2 and most of the regressions in Fig. S4, the authors find that light levels significantly influence the motion, but there is very little discussion of this fact in the discussion section. Particularly in Fig. S4, the figures only show the overall regression line, not the significantly different regression lines for dim vs. bright light. Please highlight and discuss the implications of these differences as regards school structure and cohesiveness.

RESPONSE: We have reduced our emphasis on intermittent swimming, in favor of a focus on sensing and the effects of our experimental manipulations. This includes a rewrite of most of the Discussion and almost half of the Introduction. In place over of our previous focus on intermittent swimming is a more in-depth treatment of the implications of our results on the sensory basis of schooling, as the reviewer suggested.

COMMENT: 2. The Bayesian model fit (Fig. 2a) seems underdeveloped. It's not crucial to the other arguments in the paper, so the authors might consider removing it entirely. If they want to keep it, I would like to see some more detailed analysis. For example, does this model explain the data better than something else – maybe even a simple linear fit? Does it indicate that fish are making decisions differently under the different sensory conditions? What are the implications of the a and s parameters in the fit? How do these parameters compare to those of other collectives?

RESPONSE: We removed the Bayesian model from our analysis.

Minor comments

COMMENT: 1. ln. 8. "burst phase" Although you used the term "burst-and-coast" already, you haven't referred to "burst phase" and "coast phase", so I was momentarily confused by this term. Consider rephrasing.

RESPONSE: We have changed the wording in the definition of burst-and-coast swimming to address this concern.

COMMENT: 2. ln. 45 and introduction overall. You might want to consider discussing some of the literature on lateral line sensing and burst-and-coast swimming, which has mostly been developed by studying blind cavefish (e.g., Patton et al., 2010; Tan et al., 2011)

RESPONSE: This is a good idea, but we have de-emphasized intermittent swimming in this revision and therefore have not prioritized its connection to the lateral line in this revision.

COMMENT: 3. ln. 127. I think you meant to refer to Table S1 here.

RESPONSE: This has been changed. Thank you for noticing.

COMMENT: 4. Fig. 2 and throughout. The color scheme here and in the supplemental figures is very subtle and makes it quite hard to distinguish the different sensory conditions. I would encourage the authors to use much brighter colors and vary the shape of the symbols.

RESPONSE: As suggested, we enhanced the contrast of the colors throughout.

COMMENT: 5. Fig. 3b and SI ln. 148. The speed V is the speed of the centroid of the school, correct? Or is it the magnitude of the mean of the velocity vectors for each fish? Please clarify. And either way, I think you should call it something like "mean school speed" or "mean group speed" to indicate that it is different from the speed of any one individual.

RESPONSE: We now clarify how the mean speed and mean nearest-neighbor distance were calculated in the legend text.

COMMENT: 6. Fig. 3e. It appears that the mean speed of the no flow sensing, dim light group is lower than the minimum on the y axis, and the outlier points are above the maximum on the y axis. For clarity please make sure the y axis covers the entire range of the data.

RESPONSE: We have adjusted the y-axis to encompass the outliers.

COMMENT: 7. SI ln. 26. Do these lamps flicker at 60Hz? What is the flicker fusion rate for tetras?

RESPONSE: No the lights do not flicker at 60 Hz. We have verified this with high-speed video at 1000 Hz, which we now mention in the supp. mat.

COMMENT: 8. Fig. S1c, inset. It would be helpful to have an even higher zoom inset so that SNs can be seen clearly. On my copy, they are barely visible even when I zoom in on my computer, and would be completely invisible in a printed copy.

RESPONSE: Good idea. We have enhanced the zoom.

COMMENT: 9. SI Eq 0.1 and tables. The authors use R notation for statistical models, which is relatively widely known, but may not be self-evident to all readers, particularly with respect to the notation for random effects. Please explain the notation or alter it to indicate exactly what is being estimated (e.g., for Eq 0.1, the β coefficients for the intercept, the T&'()* slope, the effects of lateral line treatment and dim light, and a randomly distributed γ coefficient for each school)

RESPONSE: We now explain that we have used Wilkinson notation and have offered a reference for guidance throughout the supplemental materials.

COMMENT: 10. Tables. The authors seem to distinguish between ≪0.001 (much less than?) and just <0.001. I don't know that this is necessary, but if so, criteria should be given.

RESPONSE: We have changed this to remove the extra "<"".

COMMENT: 11. Table S4. I think you may have mixed up some of the variables in the first column. For example, the first regression section list T&'()* as a variable, but it isn't in the model given on the first line. Probably you meant $\Delta///v/01234$? And similarly for the other two regressions.

RESPONSE: Thank you for catching this. We double-checked the numbers and they check out, but we made a number of changes to the labeling in the tables.

COMMENT: 12. Fig. S6. Are these patterns significantly different from one another? While these plots are pretty, I'm not sure they add too much to the overall argument in the paper. If the authors wish to include them, I would like to see a bit more analysis of the pattern and discussion.

RESPONSE: We removed this figure.