

The human visual system preserves the hierarchy of two-dimensional pattern regularity

Peter J. Kohler and Alasdair D. F. Clarke

Article citation details

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Review timeline

Original submission: 11 March 2021

1st revised submission: 18 May 2021

2nd revised submission: 29 June 2021

Final acceptance: 29 June 2021

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2021-0600.R0 (Original submission)

Review form: Reviewer 1 (Alexis Makin)

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?

Yes

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

This was a highly competent paper which expands on earlier work by the same authors. Kohler et al. (2016) already demonstrated that rotational wallpaper patterns (P2, P3, P4 and P6) generate a parametric response in several extrastriate visual areas. This extrastriate symmetry response can be isolated in the odd harmonics of a SSVEP recording (e.g. in an experiment where P2 alternates with P0). This paper expands the research program to include all of 17 wallpaper patterns. The brain response was well predicted by hierarchy of complexity relations. There were also consistent psychophysical results. I strongly recommend this paper for publication.

The 17 wallpapers are historically interesting and well codified. However, there are some downsides. While the authors are familiar with the elegant crystallographic notations such as P2 and CM, less specialist readers are faced with a daunting marathon of code breaking and puzzle solving. For instance, why should P31M should be considered a subgroup of CM? In my opinion the paper could be improved by removing the challenge.

The paragraph from lines 49 to 62 is very good, because it illustrates the concept of subgroup. Another similar 'concept illustration' paragraph, using different examples is still needed. Even two such paragraphs would be justifiable, if space permits.

The figures are extremely creative, but I would like another figure illustrating sub-groups hierarchies.

You even could include a link to the Wikipedia page (if you believe this is accurate?)

https://en.wikipedia.org/wiki/Wallpaper_group#Group_pg

The discussion needs to say more about previous EEG work. Could we say that visual symmetry generates an ERP called the 'Sustained Posterior Negativity' (SPN), and that SSVEP is another way of isolating this symmetry response?

As well as mentioning the holographic model (Makin, 2016), we could say SPN also scales with proportion of symmetry in symmetry + noise displays (PSYMM, Makin, Rampone, Morris, & Bertamini, 2020; Palumbo, Bertamini, & Makin, 2015). Sasaki et al. (2005) and Keefe et al. (2018) also observed parametric responses to PSYMM with fMRI. These papers seem relevant, given that we are talking about parametric responses to regularity again.

Would the SSVEP response to wallpapers increase if regularity were task-relevant? Makin et al. (2020) found that the SPN was enhanced when regularity was task-relevant. You could also mention top-down factors in the discussion as a topic for future work.

As you say, the retinal image of a 2D textures are often distorted by viewpoint. The perfect flat textures used here might be seen as a super-texture. Another alternative is that representations of regularity in the extrastriate cortex are view-invariant. Indeed, the system can extract view invariant, post-constancy representations of regularity under some conditions (Keefe et al., 2018; Makin, Rampone, & Bertamini, 2015). This could also be a topic for future work.

Minor points

Could we say more about how sample size was chosen?

Tyler et al. (2005) was actually conducted before Sasaki et al. (2005) and reported similar results. We should probably cite that paper as well.

References

Keefe, B. D., Gouws, A. D., Sheldon, A. A., Vernon, R. J. W., Lawrence, S. J. D., McKeefry, D. J., ... Morland, A. B. (2018). Emergence of symmetry selectivity in the visual areas of the human brain: fMRI responses to symmetry presented in both frontoparallel and slanted planes. *Human Brain Mapping*. <https://doi.org/10.1002/hbm.24211>

Kohler, P. ., Clarke, A., Yakovleva, A., Liu, Y., & Norcia, A. M. (2016). Representation of maximally regular textures in human visual cortex. *The Journal of Neuroscience*, 36(3), 714–729. <https://doi.org/10.1523/JNEUROSCI.2962-15.2016>

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Palumbo, L., Bertamini, M., & Makin, A. D. J. (2015). Scaling of the extrastriate neural response to symmetry. *Vision Research*, 117, 1–8. <https://doi.org/10.1016/j.visres.2015.10.002>

Sasaki, Y., Vanduffel, W., Knutsen, T., Tyler, C. W., & Tootell, R. (2005). Symmetry activates extrastriate visual cortex in human and nonhuman primates. *Proceedings of the National Academy of Sciences of the United States of America*, 102(8), 3159–3163. <https://doi.org/10.1073/pnas.0500319102>

Tyler, C. W., Baseler, H. A., Kontsevich, L. L., Likova, L. T., Wade, A. R., & Wandell, B. A. (2005). Predominantly extra-retinotopic cortical response to pattern symmetry. *Neuroimage*, 24(2), 306–314. <https://doi.org/10.1016/j.neuroimage.2004.09.018>

Review form: Reviewer 2

Recommendation

Major revision is needed (please make suggestions 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?

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?

Yes

Is it clear?

Yes

Is it adequate?

No

Do you have any ethical concerns with this paper?

No

Comments to the Author

This paper is about perception of symmetry. As it is well known simple isometries (reflection, rotation, translation and glide reflection) can be combined in exactly 17 distinct ways, known as wallpaper groups. In this study these stimuli are used to record Steady-State Visual Evoked Potentials and to measure detection thresholds).

Results show that the hierarchy of component symmetries is preserved in both behavior and brain activity. The Bayesian analysis shows that for most of the subgroup relationships, subgroups produce lower amplitude responses in visual cortex and require longer presentation durations to be reliably detected.

Overall the paper is clear and well written and the topic interesting. In terms of limitations this is a single study (N=25) with a type of stimuli that the authors have used before (Clarke et al., 2011; Kohler et al., 2016). Although the previous study in 2016 focused only on rotation the approach is

similar.

In the intro it says "Most of this work has focused on mirror symmetry or reflection, with much less attention being paid to the other fundamental symmetries". This is true but also overstated. Although the work on reflection is more extensive, there are plenty of papers on translation and rotation, from some very old ones with behavioural data (Royer, 1981, JEP:HPP) and some more recent using also EEG (Makin et al., 2013, Psychophysiology).

With respect to the comparison with the psychophysical data, it was not clear to me in which order the data was collected. Was the EEG study always second?

The supplementary file is very well organised and explain the analysis. However, the osf project does not have either the stimuli or the data. If there is no strong reason for this, I would recommend that the authors do upload these datasets, in the spirit of open science.

Minor

"Two times per trial, an image pair was shown at reduced contrast, and the participants were instructed to press a button on a response pad." It was not clear to me what the participants judged, or whether they had to press the button as quickly as possible.

Decision letter (RSPB-2021-0600.R0)

19-Apr-2021

Dear Dr Kohler:

I am writing to inform you that your manuscript RSPB-2021-0600 entitled "The human visual system preserves the hierarchy of 2-dimensional pattern regularity" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken after considering the advice of referees and the Associate Editor. The overall opinion is positive but there are a number of areas important to publication in Proceedings B given its broad biological audience that make the current version insufficiently competitive. They relate to a perceived lack of novelty, the rather technical nature and the limited broader biological context and perspective. Because of the overall positive comments by the reviewers, we would be happy to consider a resubmission, provided these comments and the comments of the referees and the Associate Editor are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

- 1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.

- 2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
- 3) Line numbers in your main document.
- 4) Data - please see our policies on data sharing to ensure that you are complying (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

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Sincerely,
 Professor Hans Heesterbeek
 mailto: proceedingsb@royalsociety.org

Associate Editor
 Comments to Author:

The study investigates responses of the human visual system to various forms of pattern symmetry, using behavioural and EEG measures. The research expands previous work by the authors. The paper is quite technical, and makes only brief mention of the work's broader biological context beyond human visual perception. It is likely to be of interest primarily to researchers in this field rather than to a broader readership across the range of disciplines in biology.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Referee: 2

Comments to the Author(s)

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Minor

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Author's Response to Decision Letter for (RSPB-2021-0600.R0)

See Appendix A.

RSPB-2021-1142.R0

Review form: Reviewer 1 (Alexis Makin)

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?
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?
Yes

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?
No

Do you have any ethical concerns with this paper?
Yes

Comments to the Author

This was a very good study and I appreciate the changes you have made in light of my previous review. I recommend this for publication.

Review form: Reviewer 2 (Marco Bertamini)

Recommendation
Accept as is

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

Is the length of the paper justified?

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

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Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

The authors have revised the paper and they have addressed all the comments. The paper is now clearer, more accessible to a broad readership, and materials have been uploaded for sharing. I do not have any additional comments except that the osf link should be included in the main text.

Decision letter (RSPB-2021-1142.R0)

23-Jun-2021

Dear Dr Kohler

I am pleased to inform you that your manuscript RSPB-2021-1142 entitled "The human visual system preserves the hierarchy of 2-dimensional pattern regularity" has been accepted for publication in Proceedings B.

The referees have recommended publication, but also suggest some minor revision to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. 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 us know.

To revise your manuscript, log into <https://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. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original 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.

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- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. 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.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

- 4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation

It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

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- Phylogenetic data: TreeBASE accession number S9123
- Final DNA sequence assembly uploaded as online supplemental material
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If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document not available)) 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. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

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

Sincerely,
Professor Hans Heesterbeek
mailto: proceedingsb@royalsociety.org

Associate Editor

Comments to Author:

Both reviewers are very positive about the revised paper, with the only very minor suggestions being to include the OSF link in the main text, and to add a README file to the OSF content.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

This was a very good study and I appreciate the changes you have made in light of my previous review. I recommend this for publication.

Referee: 2

Comments to the Author(s).

The authors have revised the paper and they have addressed all the comments. The paper is now clearer, more accessible to a broad readership, and materials have been uploaded for sharing. I do not have any additional comments except that the osf link should be included in the main text.

Decision letter (RSPB-2021-1142.R1)

29-Jun-2021

Dear Dr Kohler

I am pleased to inform you that your manuscript entitled "The human visual system preserves the hierarchy of 2-dimensional pattern regularity" 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.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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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,

Editor, Proceedings B

mailto:proceedingsb@royalsociety.org



May 18th, 2021

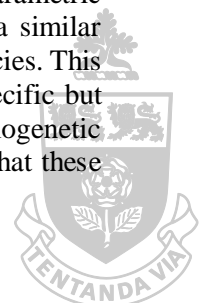
Dear Editors of Proceedings of the Royal Society B,

We thank the Editors for their feedback on the initial version of this manuscript, and would like to first address their general concerns, before moving onto the specific issues raised by Reviewers 1 and 2. We have highlighted changes to the manuscript in green font. Note that we had to shorten the Abstract to conform to the 200-word limit.

We have made several changes to the Introduction and Discussion in response to Reviewers 1 and 2, which we feel can address the “perceived lack of novelty” noted by the Editors. These changes place our findings in the broader context of psychophysical and neuroimaging experiments on symmetry perception and explain how the current study expands on our own prior work on the wallpaper groups. We note that our approach is fundamentally different from most of the literature, because we use wallpaper groups, regular textures that contain specific, distinct combinations of symmetries. The addition of 12 new groups beyond the 4 that were used in previous neuroimaging studies (Kohler et al., 2016) is a significant conceptual advance, because it allows us to investigate the complete subgroup hierarchy among the 17 groups and ask to what extent the hierarchy is reflected in brain activity. We also add a psychophysical measure that is more sensitive than those used in previous studies (Clarke et al., 2011) and show that behavior largely follows the subgroup hierarchy. These results expand our understanding of the precision and specificity of symmetry representations in the human brain and open the door to further investigations of how symmetries contribute to visual perception in humans and other animals.

Our study relies on mathematical concepts relating to the wallpaper groups and their subgroup relationships that many readers will not have heard of before. It also utilizes an EEG technique, Steady-State Visual Evoked Potentials (SSVEPs) that while widely used in visual neuroscience, will not be familiar to readers outside of that field. We have made an effort to introduce these concepts more carefully, so that the conclusions will be easier to follow, and the impact of the manuscript will be broadened. Following Reviewer 1’s suggestion, we have added a new Figure 1, which provides simplified examples of each of the 17 wallpaper groups, indicates the subgroups and provides visualizations of some of the subgroup relationships involving groups P6 and PMM. We have also updated the language on the wallpaper group naming convention in the Introduction. In order to make it easier for readers to understand our EEG experiment design and analysis, we have added a brief description of the SSVEP technique in the Introduction. We hope that these changes will address the Editors’ concern about the “rather technical nature” of the previous version of the manuscript.

Our study was conducted with human participants and reveals previously unknown aspects of human perception of symmetries that may have implications for the prevalence of symmetries in human cultures. It is likely, however, that mechanisms we probe here are not exclusive to humans. Symmetry occurs spontaneously in nature and there is evidence of symmetry perception in many species, which we now discuss in the first paragraph of the Introduction. The more sophisticated representations of symmetries in textures that we measure in humans are likely shared with some non-human animals. In fact, a recent fMRI study, now cited in the Discussion, indicates that macaque monkeys have parametric responses to symmetry that are analogous to those found in humans, and that a similar network of visual brain areas are involved with processing symmetry in the two species. This would suggest that our results reflect an encoding strategy that is not human-specific but shared at least among those animals that are relatively close to humans on the phylogenetic tree. We now make this point in the final paragraph of the Discussion. We hope that these



additions will provide the “broader biological context and perspective” that the Editor felt was missing in the previous version.

We thank the two reviewers for their kind and helpful comments. We have implemented their suggested changes as described below.

Responses to R1

- **The 17 wallpapers are historically interesting and well codified. However, there are some downsides. While the authors are familiar with the elegant crystallographic notations such as P2 and CM, less specialist readers are faced with a daunting marathon of code breaking and puzzle solving. For instance, why should P31M should be considered a subgroup of CM? In my opinion the paper could be improved by removing the challenge. The paragraph from lines 49 to 62 is very good, because it illustrates the concept of subgroup. Another similar 'concept illustration' paragraph, using different examples is still needed. Even two such paragraphs would be justifiable, if space permits. The figures are extremely creative, but I would like another figure illustrating subgroups hierarchies.**

We agree with the reviewer that getting the concept of the subgroup hierarchy across to non-specialist readers is crucially important and have added a new Figure 1, which shows the complete subgroup hierarchy (subgroup relationships with index 2 and 3 are shown, the rest can be inferred as described in the figure caption) using simplified versions of the wallpaper groups. We also present some of the subgroup relationships involving P6 (Figure 1B) and PMM (Figure 1C) and highlight the symmetries within the subgroups to emphasize how the supergroup can be generated by adding additional transformations to the subgroup. We have expanded our description of the naming convention and the subgroup relationships in the Introduction, and now provide additional examples. We find that the new figure and the changes to the text has made the manuscript much more approachable and hope that the reviewer will agree.

- **You even could include a link to the Wikipedia page (if you believe this is accurate?) https://en.wikipedia.org/wiki/Wallpaper_group#Group_pg**

This is a good suggestion and we have added a link to the Wikipedia page in the Introduction.

- **The discussion needs to say more about previous EEG work. Could we say that visual symmetry generates an ERP called the ‘Sustained Posterior Negativity’ (SPN), and that SSVEP is another way of isolating this symmetry response? As well as mentioning the holographic model (Makin, 2016), we could say SPN also scales with proportion of symmetry in symmetry + noise displays (PSYMM, Makin, Rampone, Morris, & Bertamini, 2020; Palumbo, Bertamini, & Makin, 2015). Sasaki et al. (2005) and Keefe et al. (2018) also observed parametric responses to PSYMM with fMRI. These papers seem relevant, given that we are talking about parametric responses to regularity again.**

We agree that the connection between the SPN and our current measurements was insufficiently discussed and thank the reviewer for pointing this out. We have expanded our section on SPNs in the Discussion, cited all of the SPN studies mentioned and added some content on the connection between SPNs and our current results. We note that in our view there is an important distinction between observing

parametric responses as you decrease the noise content of a pattern, and our current findings, because all of our stimuli are perfectly regular patterns that vary in symmetry content but have no added noise. So, while we cite the PSYMM papers in the SPN section, we added a separate section earlier in the Discussion highlighting previous evidence of parametric responses with the number of reflection symmetry folds (Sasaki et al., 2005; Makin et al., 2016; O’Keefe et al., 2018) and rotation order (Kohler et al., 2016). Our findings expand on these prior studies by showing that across symmetry type, the specific combination of symmetries within each wallpaper group is encoded parametrically.

- **Would the SSVEP response to wallpapers increase if regularity were task-relevant? Makin et al. (2020) found that the SPN was enhanced when regularity was task-relevant. You could also mention top-down factors in the discussion as a topic for future work.**

This is an important point. We have added language in the Discussion highlighting the symmetry-irrelevant task we used for the current experiments and discussing the effect of task in previous brain imaging experiments (including Makin et al., 2020). We also note that our SSVEP measurements are already close to ceiling when it comes to reflecting the subgroup relationships (see Figure 5). It is possible that a symmetry-related task would merely enhance responses across all wallpaper groups, rather than boosting the discriminability of individual groups, similar to what was observed for reflection by Keefe and his co-authors (2018).

- **As you say, the retinal image of a 2D textures are often distorted by viewpoint. The perfect flat textures used here might be seen as a super-texture. Another alternative is that representations of regularity in the extrastriate cortex are view-invariant. Indeed, the system can extract view invariant, post-constancy representations of regularity under some conditions (Keefe et al., 2018; Makin, Rampone, & Bertamini, 2015). This could also be a topic for future work.**

Near-regular textures occur in natural images for a number of reasons, perspective distortions being one of them (see Liu et al., 2005). As the reviewer suggests, viewpoint invariant symmetry detection can be reframed as the ability to distinguish a near-regular texture from a completely random texture. In our view norm-based encoding with super-textures and view-invariant symmetry representations are not mutually exclusive ideas. We can speculate that view-invariance may be accomplished through a generalized norm-based mechanism that is used for processing all types of near-regular texture. Another possibility is that a generic view-invariance mechanism is applied to the input prior to encoding of both regular and near-regular textures. We agree that an important goal for future work will be to gather evidence to support each of these possibilities. We have added discussion of the brain imaging work on view-invariant symmetry encoding to the Discussion section on the influence of task.

- **(Minor comment) Could we say more about how sample size was chosen?**

The experiments took a long time to run due to the large number of conditions, so testing involved multiple sessions. Extensive pilot experiments were carried out in order to determine the number of trials required for the staircase procedures to converge. As we expected the majority of our effects to be quite large, we believe the sample size is adequate to estimate them with sufficient accuracy. Furthermore, as we are not carrying out formal Null Hypothesis Significance Testing, statistical power is less of an issue.

- **(Minor comment) Tyler et al. (2005) was actually conducted before Sasaki et al. (2005) and reported similar results. We should probably cite that paper as well.**

We appreciate the reviewer's due diligence and are now citing Tyler et al. (2005) anywhere we cite Sasaki et al. (2005).

Response to R2:

- **In terms of limitations this is a single study (N=25) with a type of stimuli that the authors have used before (Clarke et al., 2011; Kohler et al., 2016). Although the previous study in 2016 focused only on rotation the approach is similar.**

We are using 16 distinct wallpaper groups in the current study, with the 17th group (P1) being used as a control stimulus. That is 12 new groups beyond the 4 we used in our previous neuroimaging studies (Kohler et al., 2016). This represents a significant conceptual advance, because it allows us to investigate the complete subgroup hierarchy among the 17 groups and ask to what extent the hierarchy is reflected in brain activity, something that was not previously possible. We also add psychophysical data which were not collected in the previous neuroimaging studies, using a two-interval forced-choice approach. The previous behavioral study of the wallpapers used all 17 groups (Clarke et al., 2011), but with a free-sorting approach that did not allow for a direct test of whether subgroup relationships were reflected in behavior, and the results indicated that participants were unable to distinguish many of the groups. Our psychophysical approach makes it possible to directly compare symmetry detection thresholds to the subgroup hierarchy, and reveals that not only can the 17 wallpaper groups be distinguished based on behavioral data, behavior largely follows the subgroup hierarchy. Overall, the current study offers an investigation of the visual system's encoding of symmetries in regular textures that is much more complete than anything that has previously been published. We have updated the text to further emphasize these points in the second paragraph of the Discussion.

- **In the intro it says "Most of this work has focused on mirror symmetry or reflection, with much less attention being paid to the other fundamental symmetries". This is true but also overstated. Although the work on reflection is more extensive, there are plenty of papers on translation and rotation, from some very old ones with behavioural data (Royer, 1981, JEP:HPP) and some more recent using also EEG (Makin et al., 2013, Psychophysiology).**

We agree with the reviewer that it is important to cite examples of papers that include rotation and translation symmetry and have added this to the Introduction. We have also qualified the statement cited above somewhat, although we maintain that compared to the large literature on reflection, the number of studies that have included translation and/or rotation is relatively small. We hope our updated version of this section has sufficiently addressed the reviewer's concerns.

- **With respect to the comparison with the psychophysical data, it was not clear to me in which order the data was collected. Was the EEG study always second?**

The EEG data was collected first, but because there was no overlap in participants between the EEG and the psychophysics, this is perhaps of minor importance. We have emphasized this point in the Methods section.

- **The supplementary file is very well organised and explain the analysis. However, the osf project does not have either the stimuli or the data. If there is no strong reason for this, I would recommend that the authors do upload these datasets, in the spirit of open science.**

We intended to share our full github repository with OSF, but apparently, we made a mistake in setting the correct permissions. Everything should be visible now. We thank the reviewer for pointing this out.

- **(Minor comment): "Two times per trial, an image pair was shown at reduced contrast, and the participants were instructed to press a button on a response pad." It was not clear to me what the participants judged, or whether they had to press the button as quickly as possible.**

Two times per trial, the contrast of the images was briefly reduced. Participants were instructed to press a button whenever they noticed a contrast change. Participants were told to respond at their own pace while being as accurate as possible, and reaction times were not taken into account. We have expanded the EEG Procedure section of the Methods to make this clearer, and now also mention the concurrent task in the Discussion.

We sincerely appreciate the time and effort put in by the Editorial Team and Reviewers towards improving the manuscript. We feel strongly that addressing the concerns and comments expressed above has significantly improved the manuscript, and look forward to receiving any further feedback that the Editors and Reviewers may have.

Sincerely,

Peter J. Kohler & Alasdair Clarke