We would like to than the reviewers for their insightful and constructive suggestions. Our reply to reviewers is below.

Reviewer #1:

All minor corrections done.

We have made a number of amendments in relation to the reviewer's major comment. Firstly, we have changed the mentioned sentence that uses the phrase "complex scenes" to give a few specific examples of the behaviours in which these cells have been implicated, in order not to imply that the nature of the encodings is understood. We have additionally introduced a new figure which shows an illustration of how the R4d neurons respond to images of trees, indicating that there would be useful information given about the positions of the trees. Although, as the reviewer notes, the scope of this paper was principally to examine the RF outputs in relation to the (admittedly highly artificial) stimuli used in behavioural experiments, we agree that the broader question of the role these cells could play in a more natural context is an interesting one. Accordingly we have introduced an additional figure showing the outputs of the R4d RFs in response to images of trees, which suggests that they could also provide useful information about more natural stimuli. Finally, we have added an extra section to the discussion, which, among other points, mentions limitations of the current study in terms of the stimuli used (including a discussion of motion parallax).

Reviewer #2:

Responses to individual comments are listed below, using the reviewer's original numbering system.

1. There appears to be some confusion here. We are modelling the data in Seelig and Jayaraman's 2013 paper, which looked at the visual receptive fields of ring neurons cf. their 2015 paper which looked at PI (both in Nature). We have, however, added a section in the discussion on central complex organisation which talks about the inputs to the ring neurons and there being a ring attractor etc.

2. Seelig and Jayaraman verified the RFs with the standard white noise stimuli technique (their refs 37,41). This is now mentioned in the text.

[I might need to talk about the maths of this with Andy briefly -- in any case we can bat this point, but I just want to be sure I've understood what they did correctly.]

3. We have now made some reference to the rotational image difference function in the methods, though we have not cited Dewar et al. as we are not looking at place homing in this work, and so we felt the connection was a little tenuous. We did previously carry out some modelling work looking at navigation that made use of the ring neuron RFs and this is mentioned in the text. We discuss visual navigation in the new section in the discussion, in the context of the more complex visually guided behaviours of which we know insects are capable. We additionally link it to previous work on active vision and work by Horridge etc. We also now mention that discrimination capabilities depend on training method -- thank you for this suggestion.

Data showing a boost in discriminability for certain pattern pairs with the addition of extra RFs, which was not previously shown, now appears as two new panels in Fig. 2.

"Specific comments":

p4 - Justification for averaging added to text

p6 - It is true that the choice of difference metric (r.m.s. difference) was somewhat arbitrary, though we didn't select this measure because it performs better! We have added a comment about this to the methods section.

p13 - corrected

p14 - We have not obtained the original data for the RFs, as we're averaging across flies in any case so small changes in the accuracy of individual RF recordings wouldn't make a lot of difference. There's sufficient averaging in the process that getting the originals would not add much.