We would like to than the reviewers for their insightful and constructive suggestions. Our reply to reviewers is below (with original reviewer comments in blue).

Reviewer #1: In this paper, the authors use computational methods to investigate the performance of neurons that are thought to mediate a range of complex behaviours in Drosophila, including pattern recognition. They use receptive field data that has recently been obtained experimentally to investigate the information that would be provided by these neurons, particularly when viewing different patterns. The authors match their findings to those of behavioural experiments and find that the output of their simulations agree well with the flies' behaviour. They then use neural network modelling to investigate how well the output of these neurons can be used to identify visual features.

This is a clear, well-written paper with a style and organisation that is easy to follow. The findings are interesting and of value to anyone interested in understanding the relationship between sensory input and behavioural output in biological systems.

I have one major comment

Page 9: First line under the title 'What information is preserved in this simple neural code'. I do not agree that the stimuli were complex scenes. I am missing a discussion on how the output of the neurons would perform in natural scenes and an elaboration of the relationship between the output of these neurons in a natural context. All of the experimental data has been acquired in artificial situations with highly simplified stimuli and it leaves me wondering about how these neurons would respond to more natural objects with the image statistics of a natural background. I understand that the lack of experimental data using such stimuli limits their ability to provide a clear answer to this question but I still think that it should be addressed in some way in the discussion. For example, could you address the question of whether it is likely that using naturalistic objects on a naturalistic background would change the output of the neurons? Could motion parallax provide additional shape information that is not present in the 2D stimuli presented?

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).

Minor comments on the text:

Page 3, 4th line from the bottom: add 'the' before 'direction' or reorganise the end of this sentence for clarity

Page 7, 3rd line from the top: add 'B' to (Figure 2) for clarity

Page 7, 3rd line from the bottom: add 't' to 'though'

Page 14, 6th line after the heading: there is a word missing here 'Each point on the is initially...'

Page 22, Figure 1 legend: it would be helpful to the reader if it were made explicit that the blue crosses are in 1A rather than 1B

Figure 1B: the contrast between the blue and green is not very high, consider using different colours. The legends are too large and cover the data (I understand that this is symmetrical but it would help the reader to get a clearer picture of the responses to each edge).

All minor corrections were carried out.

Reviewer #2: Neuronal coding in the visual system of Drosophila melanogaster: How do small neural populations support visually guided behaviours?

General Comments:

The main contribution of this paper is the demonstration that a small population of neurones in the central complex are well suited for encoding information about size, position and orientation of objects. The details related to the extraction of kernels, calculation of R4d and R2, and the replication of behavioural experiments are well presented. The simulation tests are fairly detailed and easy to follow, and the results appear accurate. However, the motivation behind the author’s model is not well justified.

1. Previous models, based on the same data (Seeling and Jayaraman 2015) have already been proposed (e.g. A Cope et.al., reference #30). Although the authors refer to alternative models, the article lacks a systematic comparison between their model and previously proposed models. More specifically, it is not clear, why the authors have not used a ring attractor.

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. A tremendous amount of information is already known about the visual system of Drosophila. However, the authors have modelled R4d and R2 neurones with simple linear filters, by using kernels. It will be beneficial to at least discuss why the use of linear filters is appropriate.

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

3. The authors compare the discriminability of patterns using a distance measure between Rfs. This approach is relatively similar to methods suggested by the author themselves in other articles for place recognition or navigation (e.g. Dewar, A.D. et. al, 2014. What is the relationship between visual environment and the form of ant learning-walks? An in silico investigation of insect navigation. Adaptive Behavior). It is frustrating that authors do not link their present model to other existing models of place recognition and pattern recognition.

Also, the authors often refer to which patterns flies can or can not discriminate. It should be noted that the discrimination capabilities of animal heavily depend on the training method (see for example A Dyer et. al. 2004 Bumblebees (Bombus terrestris) sacrifice foraging speed to solve difficult colour discrimination tasks. J.Comp.Physiol.A 190, doi:10.1007/s00359-004-0547-y) .

Finally, in the last paragraph of ‘Pattern discrimination in flies and ring neuron population codes’, the authors suggest that the addition of Rfs improve the patterns discrimination. However, the data are not shown without apparent reasons.

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:

Page 4 (Results, first paragraph): The author should give an intuitive explanation for the use of average filters. The sentence ‘Though this averaging … we examine’ is not justified properly.

Justification for averaging added to text

Page 6 (Results: Pattern discrimination in flies and ring neurone population codes, paragraph 2): The root mean square is used as discriminability measure without motivation and therefore sounds arbitrary. It should be noted that other metrics exist: absolute difference, kullback-leibler, bayesian information criterion, etc.

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.

Page 13 (Discussion, Do flies recognise patterns?, paragraph 3): The author used we in ‘… we have shown that the information ...’ although referring to published work from different authors, reference #2 previously

corrected

Page 14 (Materials and methods, Turning visual receptive field data into visual filters). The authors should ask Seeling and Jayaraman for their original data instead of extracting values from figures for better precision and clarity.

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