Spatial Symmetry and Stability of V1 Receptive Fields Revealed with Two-Dimensional Hermite Functions

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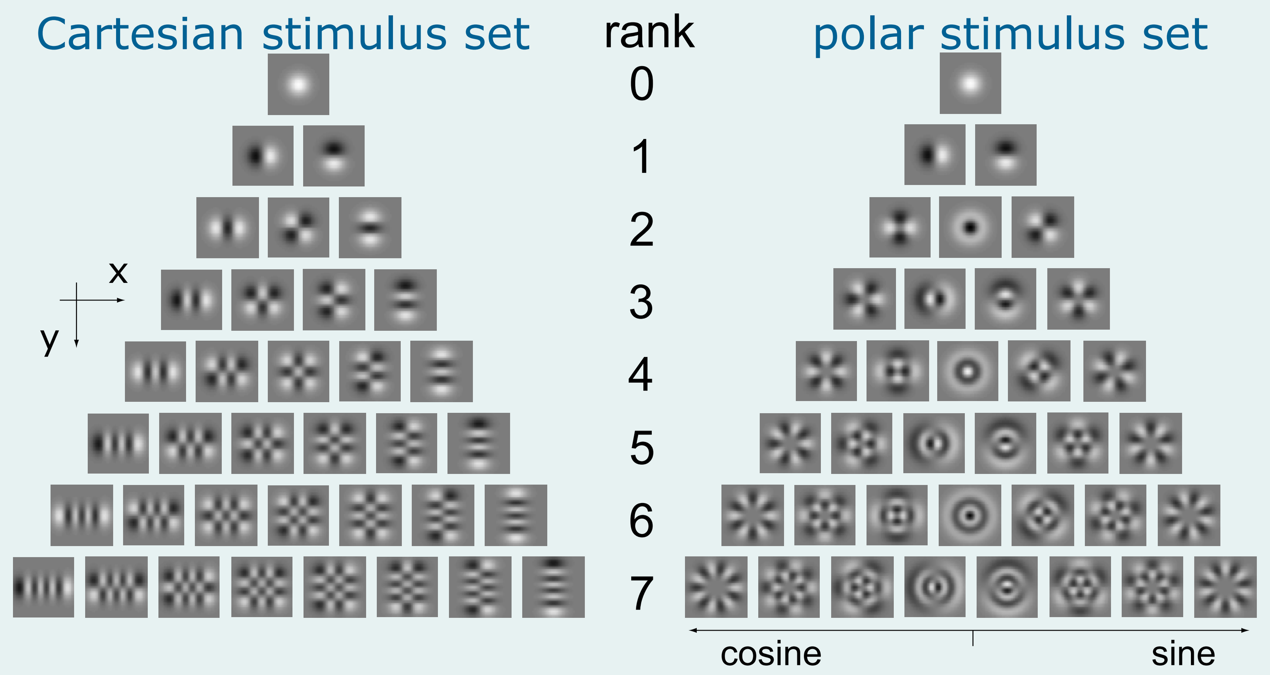
1. INTRODUCTION

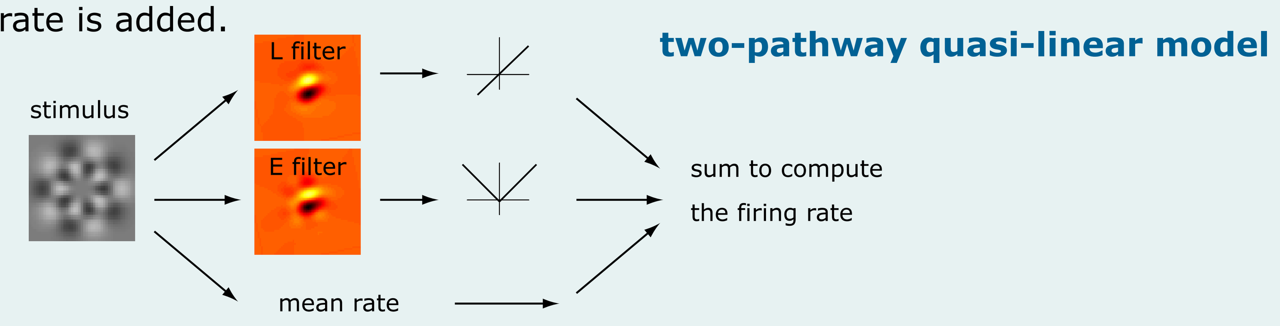
A neuron's receptive field succinctly describes neural feature selectivity and quantitatively predicts responses to synthetic and natural stimuli. Simple receptive field models that account for responses to some stimuli often require modification to account for responses to others. This is often described as modulation by input statistics, i.e., context. Characterizing these modulatory effects remains a challenge. We address this problem in primary visual cortex, where such modulatory effects are considered to have substantial functional significance. We analyzed how receptive fields changed between two stimulus sets - formed with two-dimensional Hermite functions - that were matched in luminance, contrast, spatial extent, and spatial frequency compositions, but differed in their two-dimensional organization:



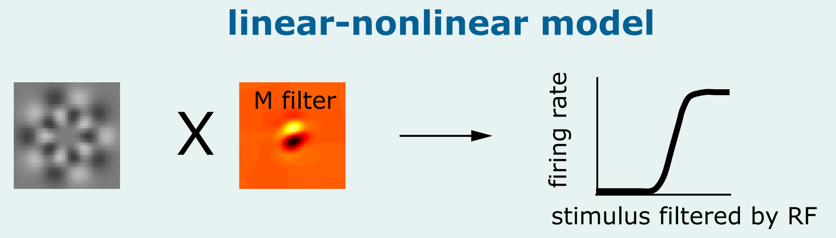
2. METHODS

We computed V1 receptive fields (n=51, 34 from cat V1 and 17 from macaque V1) using two complementary approaches:

I. In the **two-pathway model**, the neural response is a sum of three elements:
- stimulus filtered with the linear part of receptive field (**L** filter) contributes linearly to the predicted firing rate.
- stimulus filters with the even part of receptive field (**E** filters) contributes to the predicted firing rate through full-wave rectification (absolute value of the stimulus convolved with E filter).
- mean firing rate is added.

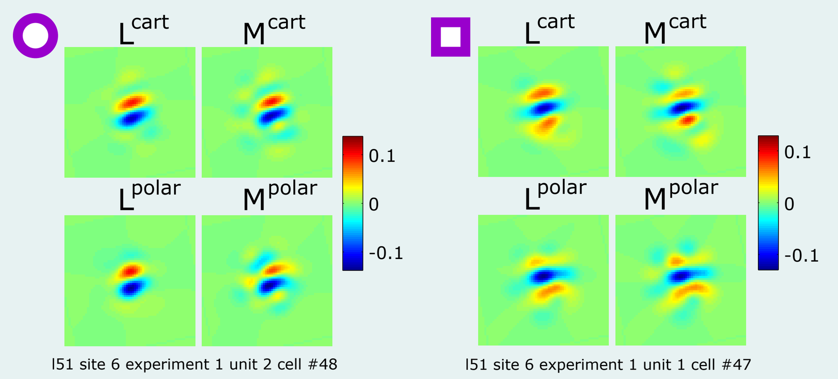


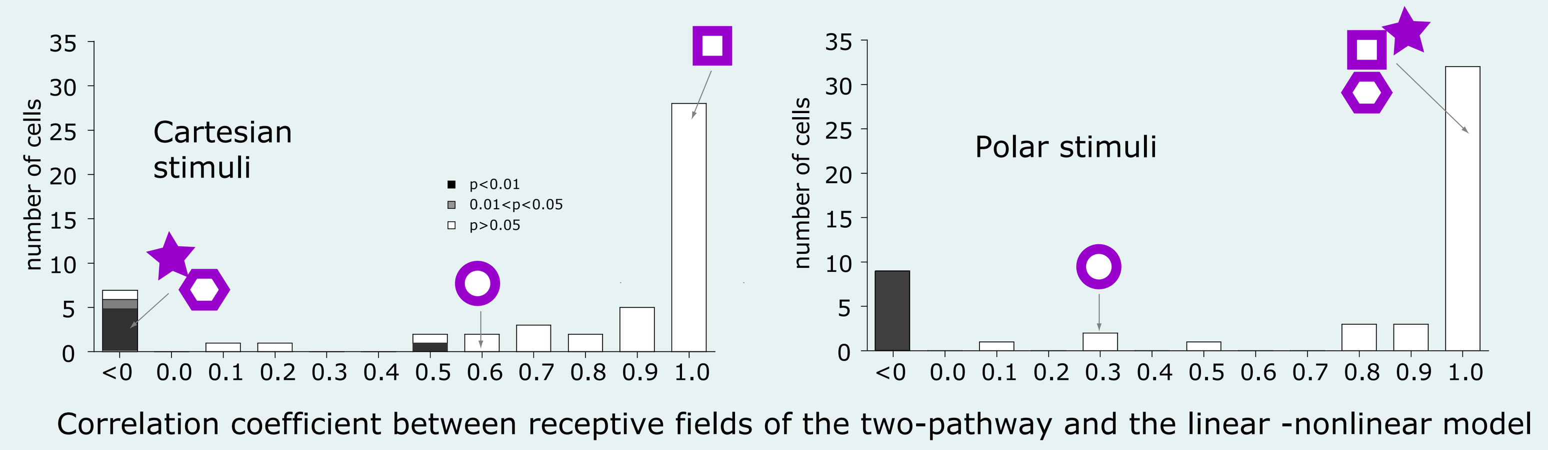
II. We compute receptive fields of the **linear-nonlinear model** as most informative dimensions (**MID**) (Sharpee, Rust, & Bialek 2004). We will denote these receptive fields as



3. COMPARISON BETWEEN MODELS

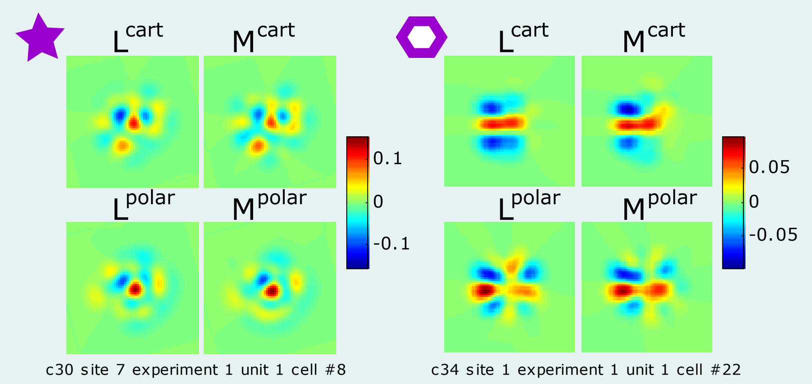
Receptive fields computed using the two models were consistent with each other for most neurons, in 44/51 for Cartesian stimuli and 42/51 for polar stimuli.
L filters of the two-pathway quasi-linear model and **M** filters of the linear-nonlinear model were compared.



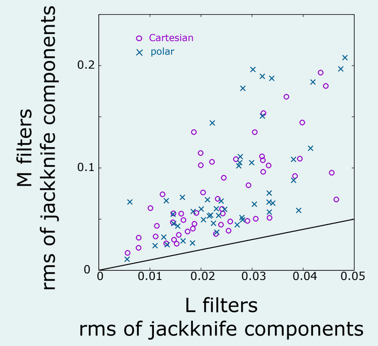


Correlation coefficients were debiased to compensate for finite data effects using the jackknife method (Efron and Tibshirani, 1998). This can lead to negative correlation coefficients (even though only shapes of receptive fields are compared, and not their polarity.

Even for correlation coefficients that are far from 1, there still appears to be a strong resemblance between the L and M filters. --> The debiasing appears to be conservative in the sense that the correlation coefficients appear to underestimate the similarity of the estimated receptive fields.



Receptive field estimates have lower variability in the two-pathway quasi-linear model than of the linear-nonlinear model.



Comparison of the nonlinear firing rate function in the two models.

For the two-pathway quasi-linear model, we choose asymmetry index as:

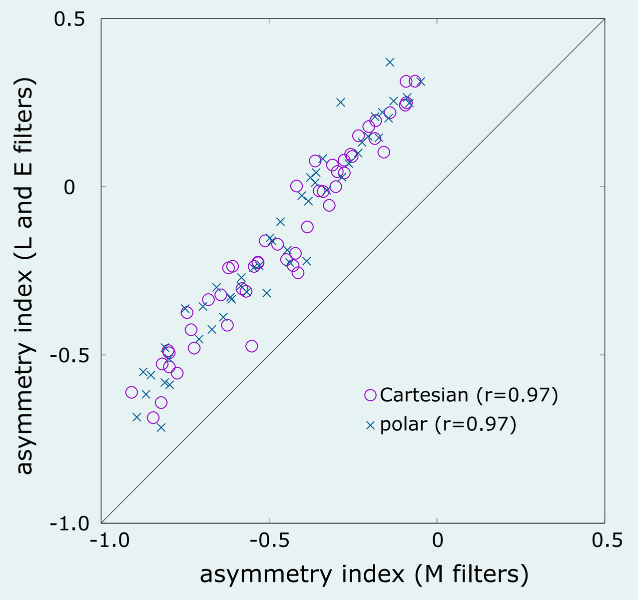
$$A_{LE} = \frac{|L| - |E|}{|L| + |E|}$$

It is based on the relative power $|L| = \sqrt{\sum l_i^2}$ and $|E| = \sqrt{\sum e_i^2}$ of the L and E filters.

For the linear-nonlinear model, we measure the asymmetry of the firing rate function as:

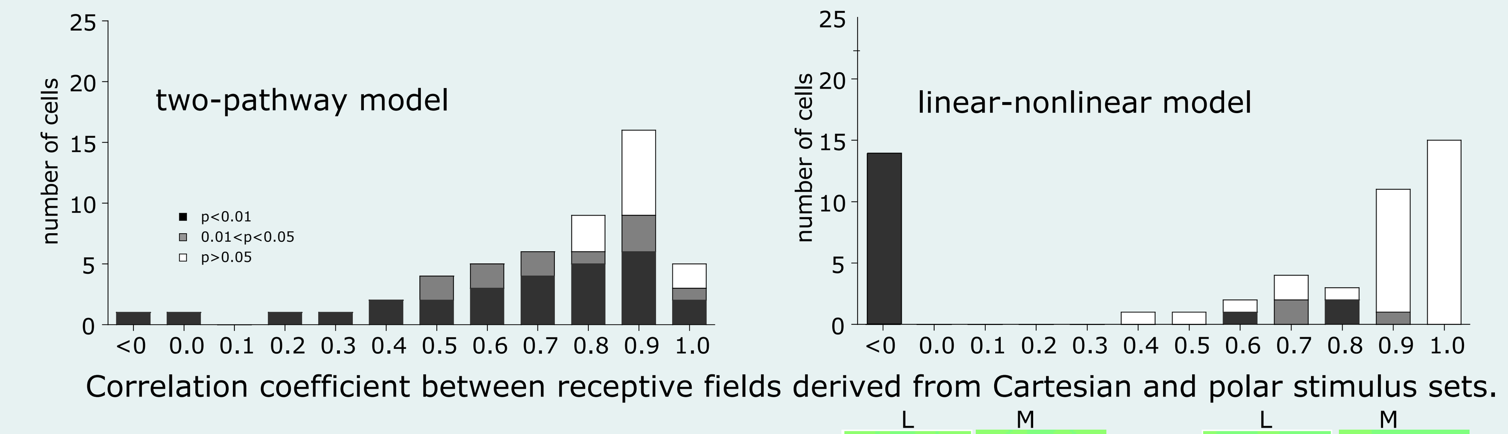
$$A_M = \frac{f_0 - f_-}{f_+ - f_0}$$

It is based on the average firing rates f_+, f_0, and f_- for all stimuli with positive, zero, or negative correlations with the receptive field.

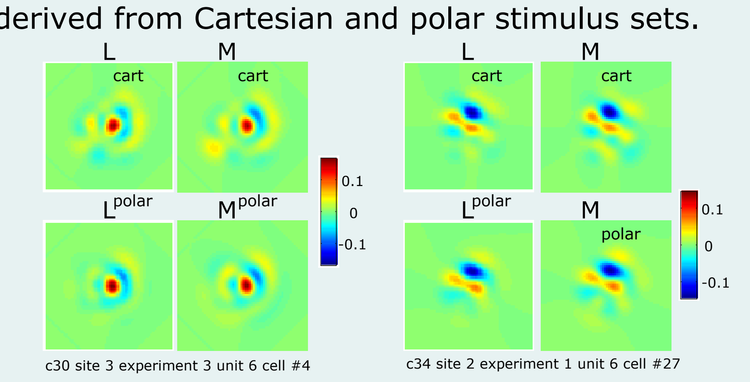


4. CONTEXT-DEPENDENCE

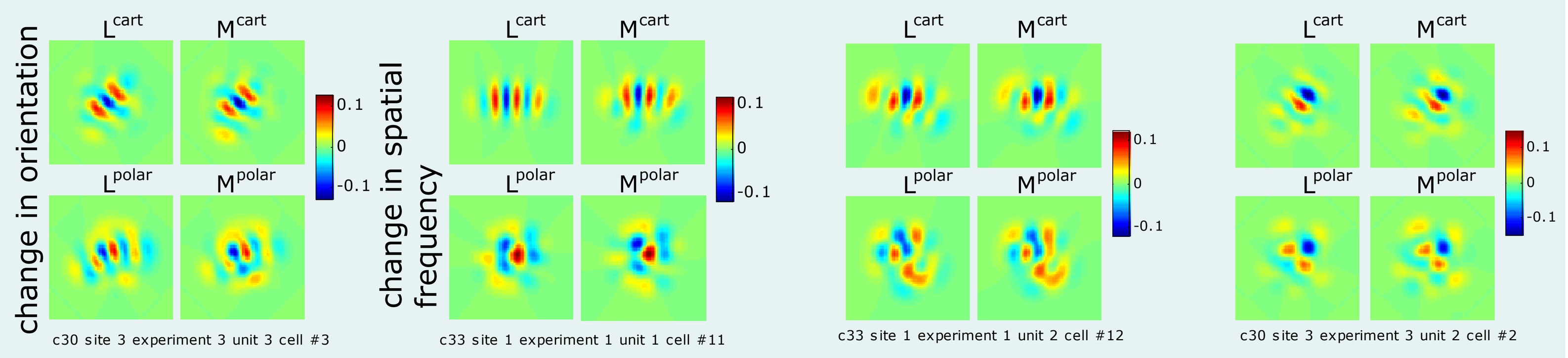
In approximately half of the cells, receptive fields showed significant differences with context, i.e. between Cartesian and polar stimulus sets.



Examples of receptive fields with no context-dependent changes.

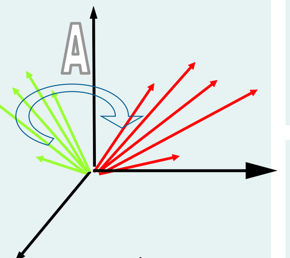


Examples of changes in receptive fields with context:



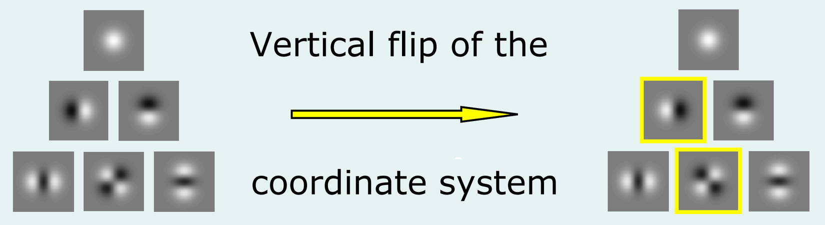
Significant changes with context were more common for receptive fields computed with the two-pathway model (39/51) than with the linear-nonlinear model (20/51), as is the case for the first two of the examples above. Nevertheless, context-dependent changes were always qualitatively similar in both models, suggesting that lack of significance in the case of the linear-nonlinear model was due to the higher variability in these receptive field estimates.

5. PROCRUSTES ANALYSIS

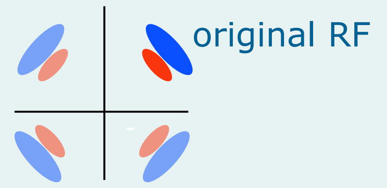


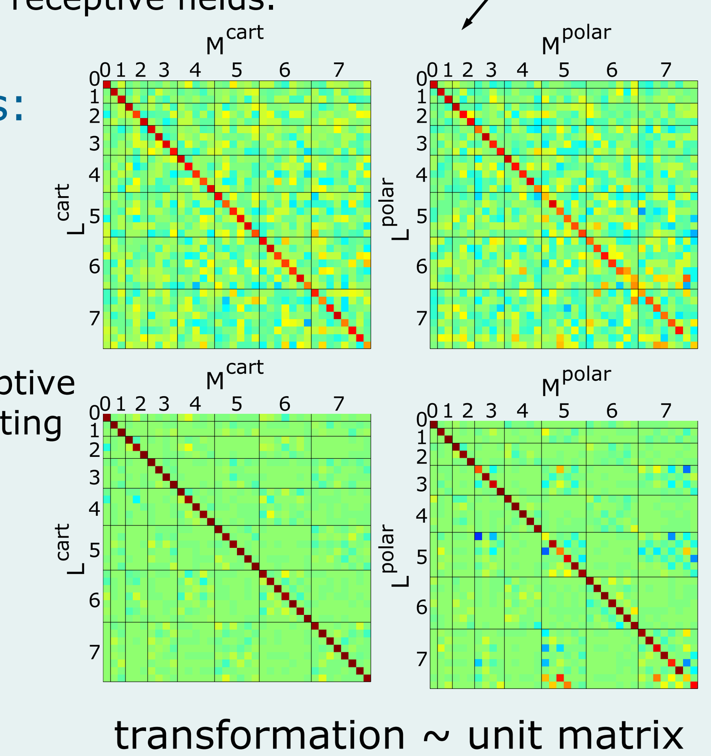
To non-parametrically characterize any systematic differences in receptive fields at the population level, we compute the best linear transformation between two sets of receptive fields. This "Procrustes" matrix represents a rotation in 36-component space (dimensionality of receptive fields).

Reducing the number of free parameters with symmetry arguments:



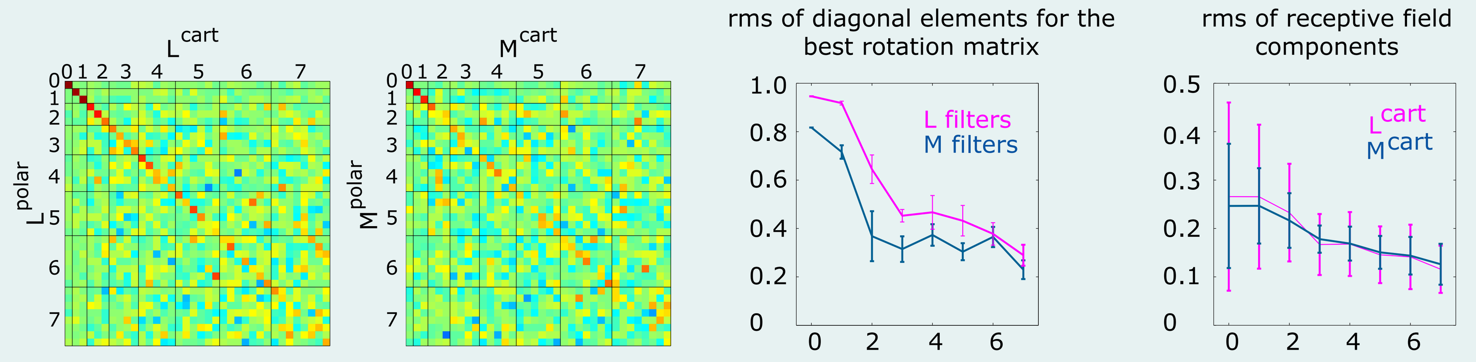
Any apparent linear relationship between the receptive field coefficients along the inverting and non-inverting patterns must be due to chance. To ensure that symmetry-violating coefficients are zero, we add receptive fields in the mirror coordinate systems.



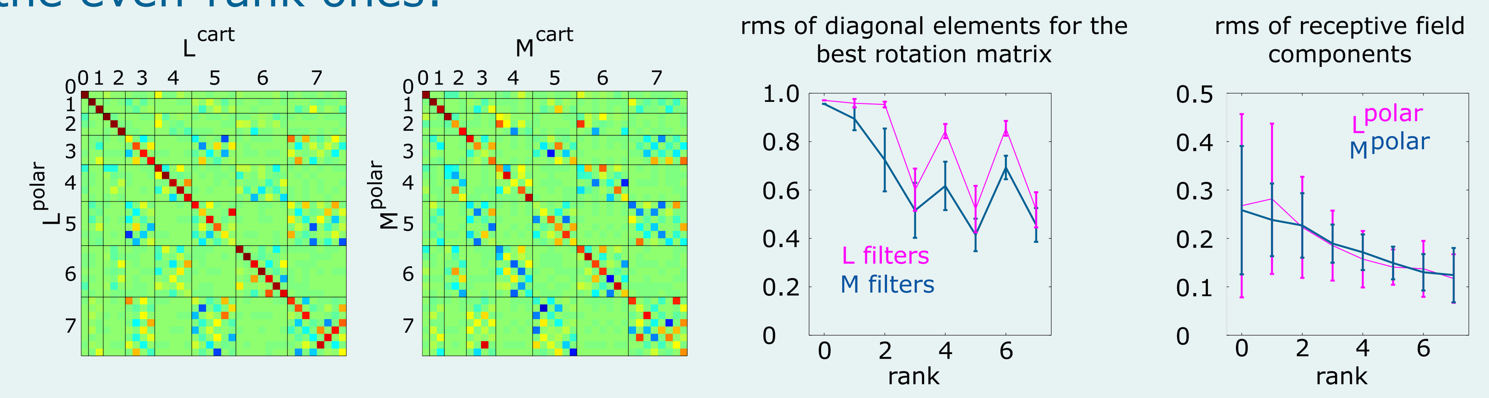


6. SYMMETRY AND LABILITY OF RECEPTIVE FIELD COMPONENTS

Deviations from the unit matrix characterize context-dependent changes.
Higher rank are more susceptible to context-dependent changes than the lower-rank

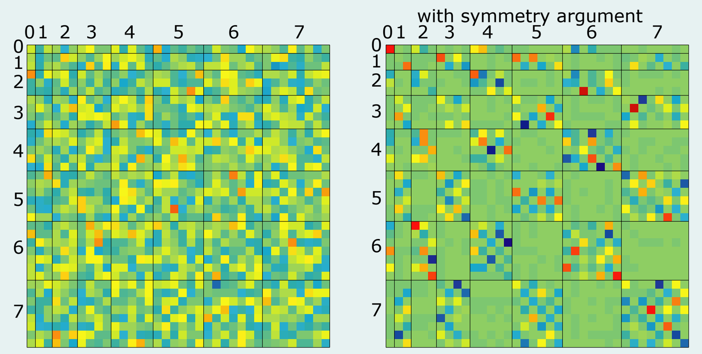


Reducing the number of free parameters with symmetry arguments, makes it apparent that odd-rank components are more labile than the even-rank ones:



The difference in lability between even and odd rank components is not due to a differences in magnitude of these components, which decrease with rank monotonically, or their variability.

Effect not observed in sets of random vectors.



7. SUMMARY

Higher-rank components show greater context-dependent changes than the more localized, lower rank components.

Receptive field components that are anti-symmetric with respect to 180 degree spatial rotation (odd-rank components) are more susceptible to context dependent changes that the symmetric components (even-rank components).

Procrustes analysis allows for a non-parametric characterization of context-dependent changes in receptive fields.

8. ACKNOWLEDGMENTS

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