Supplemental Material

Comparison of receptive fields to polar and Cartesian stimuli computed with two kinds of models

Motivation

The purpose of this analysis is to verify that context dependent changes in receptive fields of V1 neurons observed previously (Victor et al., 2006) for Cartesian and polar stimulus sets did not depend on assumptions of the model used to compute the receptive fields. To achieve this, here we compare receptive fields computed with two different modeling approaches, which are complimentary in several respects. According to the first model (Victor et al., 2006), the neural response is a sum of three elements: one element is the projection of the stimulus onto a sensitivity profile L. The second element is the projection of the stimulus onto a second sensitivity profile E, followed by full-wave rectification (i.e., absolute value). The third element is a baseline firing rate. With the assumption that the combination of these three signals is always suprathreshold, the spatial weighting function L can be found explicitly, as a linear combination of all basis function stimuli, each weighted by the number of spikes that it elicited, essentially a reverse-correlation analysis. The contribution of each basis function to the full-wave-rectified pathway (E-filter) was determined from the *average* of the response to that basis function and its contrast-inverse.

Together, the sizes and shapes of the L-filter and the E-filters provide a complete account of the responses to a single basis set (Cartesian or polar) of the two-dimensional Hermite stimuli. In the text, we focus on the L-filters since they are robustly and unambiguously determined. The E-filter cannot be determined uniquely– the signs of its projections onto the basis function stimuli are ambiguous. However, its overall power is unambiguous, and we use this power to compare the shape of the nonlinearity inferred from this model to the nonlinearity inferred from the second model, described below.

According the second model (de Boer and Kuyper, 1968; Rieke et al., 1997; Schwartz et al., 2006), the neural response to each stimulus is a nonlinear function *N* of the projection of that stimulus onto a spatial weighting M. In this case, M-filter can be determined by the method of maximally informative dimensions (MID) (Sharpee et al., 2004), and the shape of the nonlinear function *N* need not be specified *a priori*.

For both models, we simply use the spike count during stimulus presentation (0 to 250 ms) as the response measure. The rationale for this simplification is the empirical finding (Victor et al. 2006, Figure 13) that for these stimuli, response timecourse is virtually identical, for both Cartesian and polar stimuli.

If the neural response is determined by a linear spatial weighting of the stimulus, followed by asymmetric rectification (i.e., a nonlinear function that has different slopes for positive and negative inputs), then both models will provide an adequate, equivalent, fit. In this case, the L- and E-filters obtained by reverse correlation will be identical and will match the maximally-informative-dimension, M-filter*.* In addition, the weighting of the L- and E-filters will determine the shape of the nonlinearity *N* identified by the MID method. Finally, all of these filters will be independent of whether the analysis is based on responses to Cartesian or polar stimuli.

However, in an LN model, the nonlinearity need not be asymmetric rectification. If the departure is large, reverse correlation will only approximate the linear filter, while the MID method will correctly identify it. Thus, a neuron might appear to have context-dependent changes in its receptive field profile when analyzed by reverse correlation, but MID would identify a single, context-independent, LN model. (Such a nonlinearity would also have to depart strongly from a quadratic function as well, because of an equal-energy property of the Hermite functions.)

Conversely, for a neuron whose computations require more than a single LN pathway for accurate depiction (Fairhall et al., 2006; Felsen et al., 2005; Rust et al., 2005; Touryan et al., 2005; Touryan et al., 2002), the M-filter extracted by MID provides a compromise among the relevant stimulus features. This compromise, and thus the M-filter, might be context-dependent even if context only affects the relative contributions of different stimulus features, and not the feature profiles themselves. The reverse correlation approach allows for two pathways, with separate spatial filters – and thus is expected to reduce this confound.

The two modeling approaches are also complementary in their computational properties. Reverse correlation is an explicit calculation, linear in the data (after removal of maintained firing rate), and consequently is typically robust in the face of noisy responses. The MID approach requires a global optimization in a high-dimensional space (implemented by simulated annealing (Sharpee et al., 2004). The possibility of local optima exist, and the high dimensionality of the problem lead to a lower precision in the inferred filter shapes, as we see below. On the other hand, for idealized LN neurons with a purely even-symmetric nonlinearity, the L-filter is undefined and the E-filter cannot be determined unambiguously (Victor et al. 2006), while the MID approach may still be successful, as was demonstrated on model cells (Sharpee et al., 2004).

Comparison of spatial profiles determined by reverse correlation and MID. When probed with Cartesian stimuli, most neurons had the same receptive field profiles as determined by reverse correlation (L-filters) and MID (M-filters). This was also true when neurons were probed with polar stimuli. To quantify the difference between the filters estimated by the two methods, we calculated a correlation coefficient of the filters determined from the Cartesian stimuli (Supplementary Figure 1A) and the polar stimuli (Supplementary Figure 1B). White indicates cells whose correlation coefficients were consistent with no difference in receptive fields profiles as determined by reverse correlation and MID, while gray (black) shows cells with significant changes at $p=0.05$ (0.01) level. Correlation coefficients were debiased, and their confidence limits estimated, via a jackknife method (Efron, 1998), see Methods). By this statistical test, 44 out of 51 neurons had consistent ($p>0.05$) receptive field shapes with the two methods when probed with Cartesian stimuli, and 42 out of 51 neurons had consistent receptive field shapes when probed with the polar stimuli.

In Supplementary Figure 1 we also show examples of receptive fields with correlations coefficients close to 1 (panels C and D) and far from 1 (panels E and F). Note that even for correlation coefficients that are far from 1, there is a strong resemblance between the L- and M-filters. That is, the debiasing appears to be "conservative" in the sense that the correlation coefficients plotted in Supplementary Figure 1 appear to underestimate the similarity of the estimated receptive fields.

Comparison of the shape of the nonlinearity determined by reverse correlation and MID

The two modeling methods can also be compared by the shapes of the nonlinearity they predict. For each model, we constructed a measure of the asymmetry of the nonlinear gain function. For the model determined by reverse correlation, we used the normalized difference in power between the L-filter of the linear channel and the E-filter of the full-rectified channel:

$$A_{LE} = \left(|L| - |E|\right) / \left(|L| + |E|\right), \qquad (3)$$

where $|L| = \sqrt{\sum_i l_i^2}$ and $|E| = \sqrt{\sum_i e_i^2}$ quantifies the total power of L- and E- filters, respectively (computed as the square root of the total power across components). For cells that are linear, |E|=0, so the asymmetry index is 1. For cells that are well-modeled by a linear filter followed by a half-wave rectifier (threshold-linear), |*L*|=|*E*|, so the asymmetry index is 0. For full-wave-rectifying (ON-OFF) cells, |L|=0 so the asymmetry index is -1.

For the MID model, we used the asymmetry index

$$A_M = -\left(f_- - f_0\right)/\left(f_+ - f_0\right), \qquad (4)$$

where f_+ and f_- represent the average firing rate for all stimuli with positive and negative projections onto the receptive field, respectively, and f_0 represents the firing rate for stimuli that are either blank or orthogonal to the receptive field. The index A_M takes the same values as the index A_{LE} for idealized linear, threshold-linear, and full-wave-rectifying cells. For a fully linear cell, $-\left(f_- - f_0\right) = f_+ - f_0$, so that both indices (3,4) are equal to 1**.** For a cell with the threshold-linear gain function (|L|=|E|), both f_0 and f_- are close to zero, so that $A_M = 0$ For full-wave-rectifying cells, $f_- = f_+$, so $A_M = A_{LE} = -1$**.**

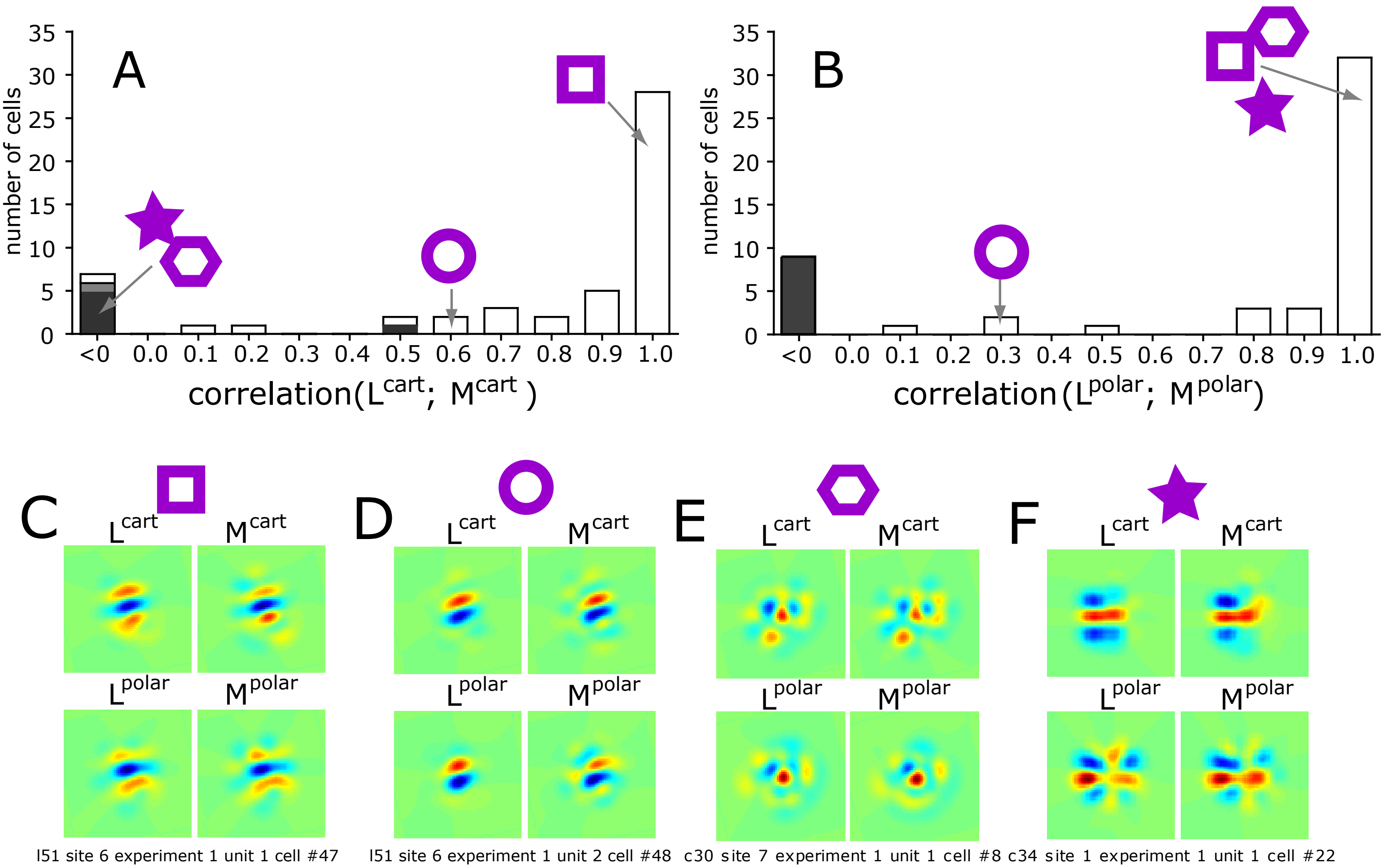
Supplementary Figure 2 shows that the two asymmetry indices are tightly correlated with each other for both Cartesian and polar stimuli, despite the differences in modeling assumptions. There is a small offset between the values of the indices obtained with the two approaches, with all neurons appearing slightly more linear with the reverse correlation method than with MID. Most likely this is because the reverse correlation method fits the linear and nonlinear components separately, while the MID method (as implemented here) fits them with a single pathway. However, this difference has little impact on our analysis of context-dependence, since our analysis focuses on the spatial aspects of the receptive field, rather than the shape of the nonlinearity***.***

Supplementary Figure 1. Receptive fields computed from responses to two-dimensional Hermite functions are largely the same for the two models. Distribution of correlation coefficients between receptive fields computed by reverse correlation (L-filters) and MID (M-filters). Panel A, receptive fields derived from responses to Cartesian stimuli; panel B: receptive fields derived from responses to polar stimuli. Cells with no significant changes (p>0.05) are shown in white, those with significant changes in gray (0.01<p<0.05) and black (p<0.01). The abscissas indicate the filters whose profiles are compared: L^{cart} – linear filter derived from reverse correlation of Cartesian responses; M^{cart} – filter derived from MID analysis of Cartesian responses; L^{polar} – linear filter derived from reverse correlation of polar responses; M^{polar} – filter derived from MID analysis of polar responses. Debiasing (see Methods) can result in estimated correlation coefficients < 0. Panels C-G: Receptive fields L^{cart} , M^{cart} , L^{polar} , M^{polar} derived from representative cells. Correlation coefficients comparing filters calculated by the different methods are as follows: (C) Cartesian stimuli: 0.99±0.04, polar stimuli: 0.99±0.02 (both p>0.05); (D) Cartesian stimuli: 0.60±0.50, polar stimuli: 0.3±0.5 (both p>0.05); (E) Cartesian stimuli: cc<0 (p<0.01), polar stimuli: 0.99±0.01 (p>0.05); (F) Cartesian stimuli: cc<0 (p<0.01); polar stimuli: 0.97±0.07 (p>0.05). Note that even when the correlation coefficients are statistically different from 1 (e.g., panels E and F, Cartesian comparisons), the receptive field estimates are qualitatively similar. Color-scale is the same for the four receptive fields pertaining to a neuron, but varies across panels. For each panel (neuron), it covers the range from the minimal to the maximal value across the four receptive field estimates**.**

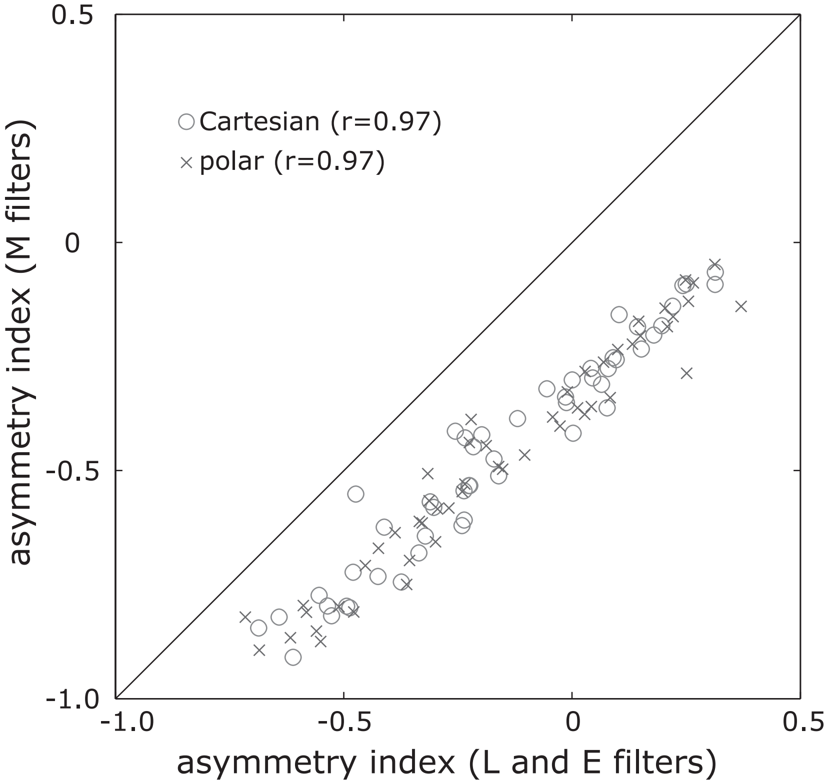
Supplementary Figure 2. Agreement between the shape of the nonlinearity for the two models. For each cell, we compare the shape of the inferred nonlinearity via the asymmetry index measured by reverse correlation (Eq. 3) and the asymmetry index measured by MID (Eq. 4). The solid line indicates equality. Circles: Cartesian stimulus sets; crosses: polar stimulus sets.

Supplementary Figure 3. Comparison of precision of estimation of receptive fields by reverse correlation (L-filters) and MID (M-filters). For each cell, we compare an estimate of the uncertainty of the receptive fields as determined by the two modeling approaches. Uncertainty is quantified by the rms difference between receptive field computed based on all of the data and the jackknife estimates obtained by dropping each trial. The uncertainties of the M-filters are larger than the uncertainties of the L-filters. The solid line has the slope of one. Circles: Cartesian stimulus sets; crosses: polar stimulus sets.

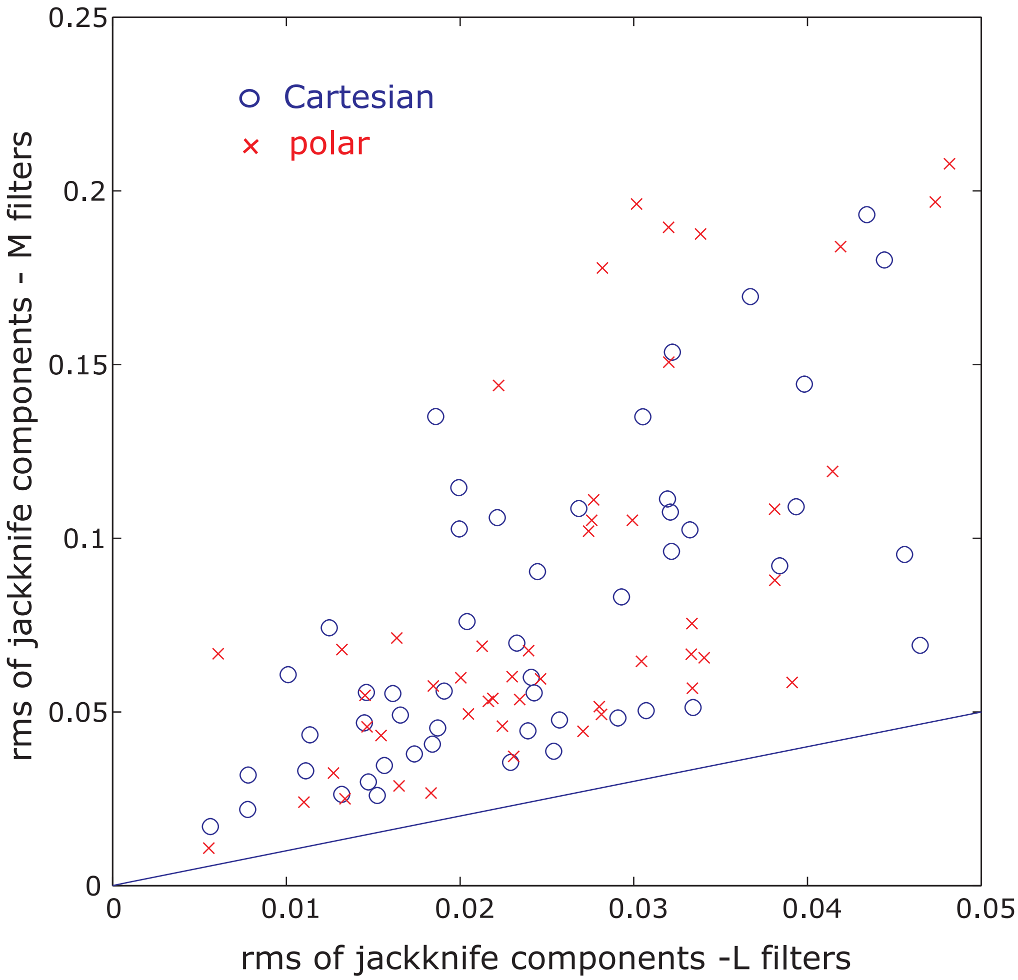
Supplementary Figure 4. Stimulus dependent differences between even and odd-rank components are not due to symmetry assumptions. Two random sets of normalized filters were generated. Panel A shows the best rotation matrix between the two sets of randomly generated receptive fields. The same number (n=51) of receptive fields was used in these simulations as with real data. Panel B shows the best rotation matrix after the two sets of receptive fields were expanded by the symmetry operation described in the text. Other aspects of plots are as in Figures 4 and 5. As expected, matrix elements that violate parity constraints are suppressed in Panel B (the various off-diagonal blocks of zeroes). However, the on-diagonal blocks for even and odd ranks persist.



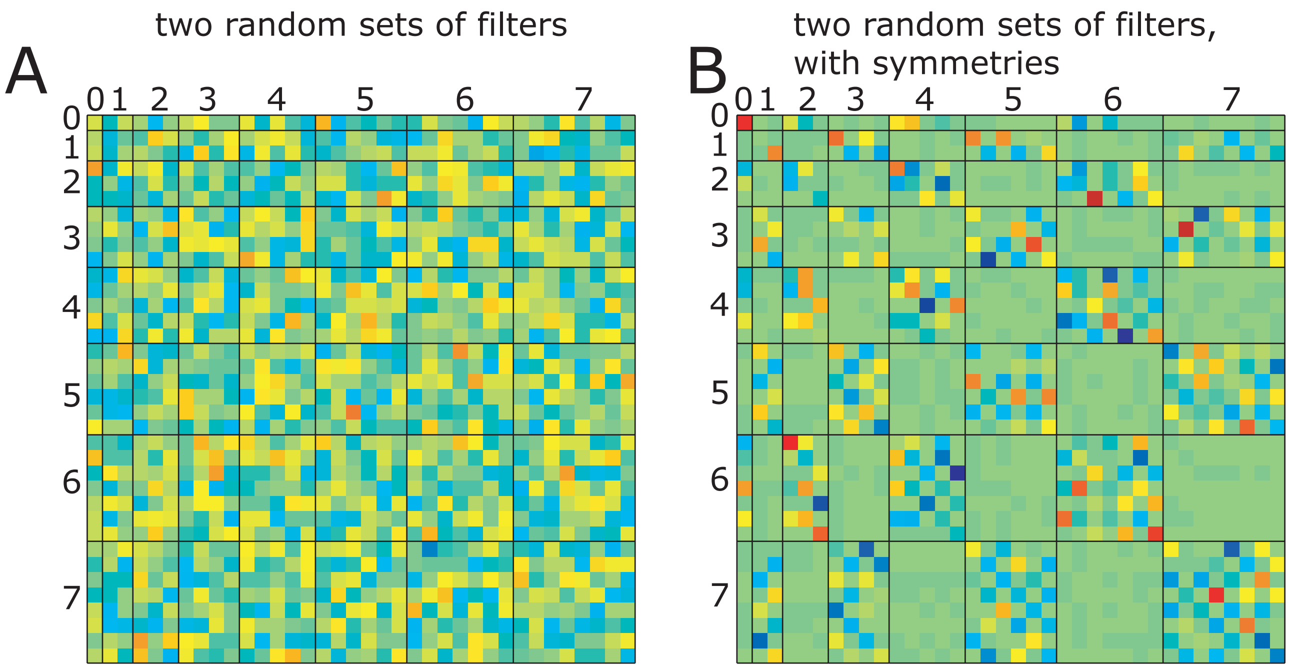
Supplementary Figure 1



Supplementary Figure 2



Supplementary Figure 3



Supplementary Figure 4