Responses of cat and monkey striate cortical neurons to aligned and oblique two-dimensional Hermite function stimuli

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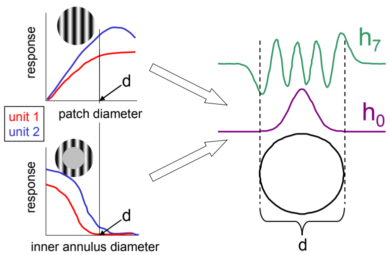
OVERVIEW

A standard model for neurons in primary visual cortex (V1) is that of oriented filters or energy detectors, whose responses are modulated by gain controls and other influences from the non-classical receptive field. Two-dimensional Hermite (TDH) functions, which are simple two-dimensional localized patches, provide a means to test and refine this model. We recently (Victor et al., J. Neurophys. 2006) showed that for most (37/51) V1 neurons, responses to TDH's reveal qualitative deviations from this model. Because TDH stimuli are equated for energy, contrast, and frequency content (but not two-dimensional structure), modification of the "standard model" with gain controls from the non-classical receptive field cannot account for these results.

Here, we extend these analyses by comparing responses to four sets of TDH stimuli: Cartesian and polar TDH stimuli *aligned* with the preferred orientation of the neuron, and Cartesian and polar TDH stimuli *oblique* to the preferred orientation. For oblique stimuli, as for aligned stimuli, the standard model fails to account for the pattern of responses. Moreover, the manner in which the Cartesian vs. polar distinction interacts with alignment rules out some classes of models for our findings (e.g., based on an overall preference for Cartesian or polar stimuli), and suggests others (e.g, a role for nonlinearly-generated orientation signals).

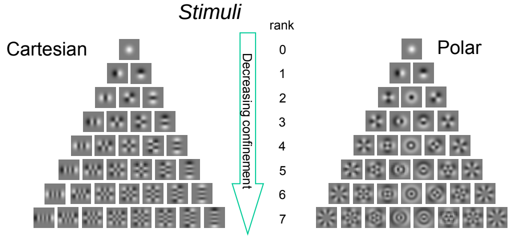
GENERAL METHODS



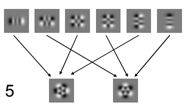
- Two cats, two macaques
- Propofol/sufentanil anesthesia, vecuronium paralysis
- Tetrode recordings in V1; 9 sites, 29 neurons
- Online characterization (orientation, SF, TF, CSF) with drifting sine gratings
- Stimuli positioned from responses of one or two "index neurons" to annuli, patches, and bars
- TDH "aligned" orientation based on orientation tuning of index neurons
- TDH size based on annulus and patch responses of index neurons
- Quantitative analysis following off-line spike sorting

RECEPTIVE FIELD ANALYSIS WITH TWO-DIMENSIONAL HERMITE STIMULI

Stimuli

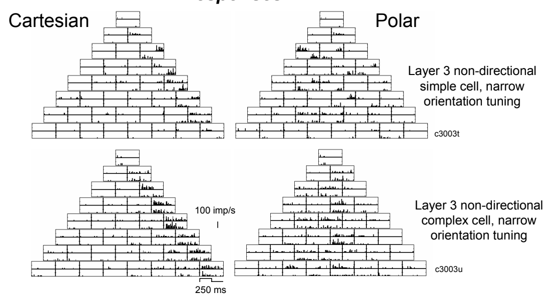


Properties

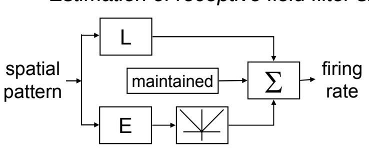


- Within each rank, Cartesian and polar stimuli are linear combinations of each other
- TDH functions form ranks of decreasing confinement in space and spatial frequency
- Cartesian and polar basis sets have identical power, spread, and contrast within each rank
- Each TDH is its own Fourier transform

Responses



Estimation of receptive field filter shapes

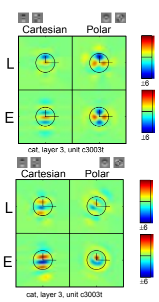


We implement a generalization of the LN model, with independent linear (L) and even-order (E) components. Note that this reduces to an LN model if L and E have identical spatial profiles.

coef of [stimulus] in L = (resp[stimulus] − resp[stimulus]) / 2

coef of [stimulus] in E = (resp[stimulus] + resp[stimulus]) / 2 − maintained

Coefficients of L and E filters are readily estimated from the response since the TDH stimuli form an orthonormal basis. This is done separately for the Cartesian and polar stimuli.



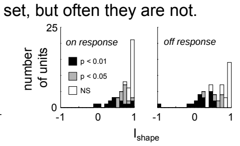
Receptive field maps are plotted with the preferred orientation horizontal. The circle indicates the e^{-2} contour of the TDH Gaussian envelope. The X- and Y-axes of the Cartesian TDH functions are indicated by the long and short line segments.

Failures of the standard model

The shapes of the filters should be independent of basis set, but often they are not.

$I_{shape} \neq 1$

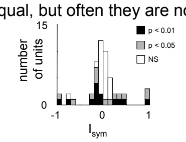
$$I_{shape} = \frac{L_{cart} \bullet L_{polar}}{|L_{cart}||L_{polar}|}$$



The overall sizes of the response to Cartesian and polar stimuli should be equal, but often they are not.

$I_{sym} \neq 0$

$$I_{sym} = \frac{(|L^{cart}|+|E^{cart}|)-(|L^{polar}|+|E^{polar}|)}{(|L^{cart}|+|E^{cart}|)+(|L^{polar}|+|E^{polar}|)}$$



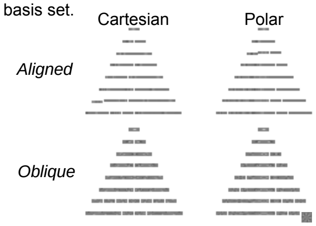
(This also rules out models based on local squaring.)

These observations motivate the questions:

- **Do V1 cells have an intrinsic preference for Cartesian or polar stimuli?**
- **What is the role of alignment of elongated contours with the preferred orientation?**

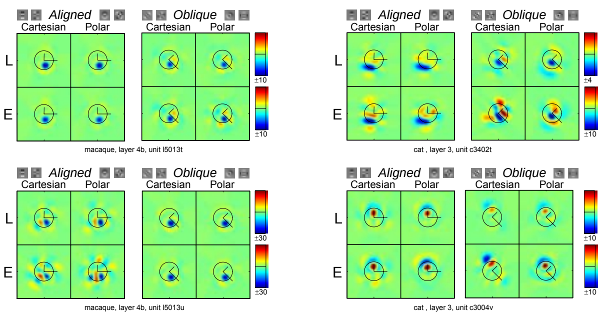
RESPONSES TO ALIGNED AND OBLIQUE TDH STIMULI

Responses were measured for Cartesian and polar stimuli *aligned* with the preferred orientation, and at a 45 deg *oblique* angle. Filters were calculated separately for each basis set.

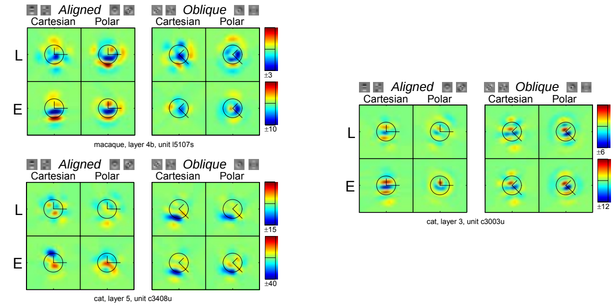


For each orientation, Cartesian and polar stimuli were randomly interleaved. 30 to 60 min separated *aligned* and *oblique* runs.

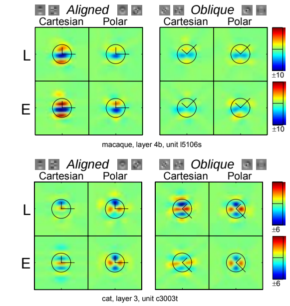
Example cells that conform to the LN model



Example cells for which Cartesian and polar filter shapes differ. The difference (I_{shape}<1) is similar for aligned and oblique stimuli



Example cells for which Cartesian and polar response sizes differ. The difference (I_{sym}≠0) is in opposite directions for aligned and oblique stimuli

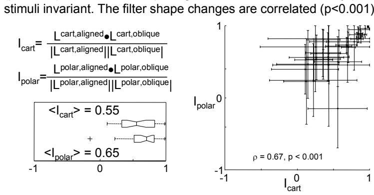


POPULATION SUMMARY

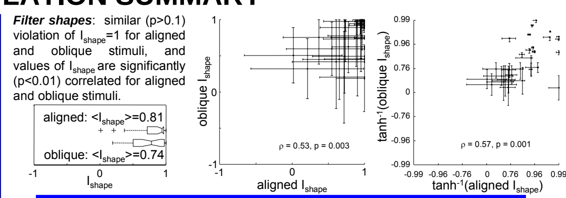
Aligned vs. oblique: filter shapes derived from Cartesian stimuli depend more on orientation than those derived from polar stimuli ($p < 0.02$). This is not surprising since rotation leaves many polar stimuli invariant. The filter shape changes are correlated ($p<0.001$).

$$I_{cart} = \frac{L_{cart,aligned} \bullet L_{cart,oblique}}{|L_{cart,aligned}||L_{cart,oblique}|}$$

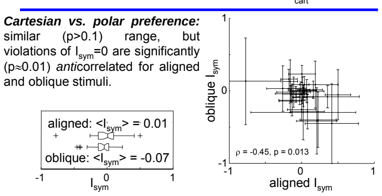
$$I_{polar} = \frac{L_{polar,aligned} \bullet L_{polar,oblique}}{|L_{polar,aligned}||L_{polar,oblique}|}$$



Filter shapes: similar ($p>0.1$) violation of I_{shape}=1 for aligned and oblique stimuli, and values of I_{shape} are significantly ($p<0.01$) correlated for aligned and oblique stimuli.



Cartesian vs. polar preference: similar ($p>0.1$) range, but violations of I_{sym}=0 are significantly ($p\approx0.01$) *anti*correlated for aligned and oblique stimuli.



CONCLUSIONS

- V1 cells that respond differentially to Cartesian and polar stimuli that are *aligned* with the preferred orientation also respond differentially to Cartesian and polar stimuli that are *oblique* to the preferred orientation.
- The preference of V1 cells for Cartesian vs. polar stimuli typically inverts when stimuli are rotated by 45 deg.
- We hypothesize that cells that respond differentially to Cartesian and polar stimuli receive strong intracortical signals that are (a) sensitive to elongated regions, (b) arise via nonlinear mechanisms, and (c) are strongly oriented, with off-axis antagonism.
- Such signals would account for deviations from a feedforward LN prediction when elongated regions are present, and for the interaction between orientation and Cartesian vs. polar preference.

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