Natural image-derived spatiotemporal receptive fields of visual cortex neurons

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Introduction

Background

• Neurophysiology has clearly demonstrated only two types of early cortical cells (i.e. simple and complex), yet based on the neuroanatomy we would expect more categorical distinctions.

• Most quantitative receptive field (RF) models of visual neurons have been derived from responses to synthetic stimuli (e.g. bars, gratings, white noise).

• Recent work has shown that natural image-derived RFs more accurately predict neural responses to other types of visual stimuli (Talebi & Baker, 2012).

Goals

• Employ a generalized linear model (GLM) to estimate the full 3-d spatiotemporal RF of simple cells in early visual cortex (Wu *et al.*, 2006).

• Determine whether models estimated from natural image stimuli can uncover RFs with more diverse spatiotemporal properties.

• Use improved recording techniques (i.e. multi-channel electrodes and spike sorting) that help circumvent neuronal sampling limitations (Carandini *et al.*, 2005).

Stimuli

• 5 second image ensembles displayed at 75 images/sec.

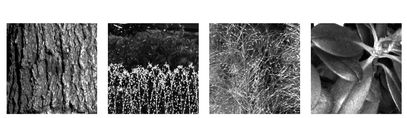
• Training stimuli: 20 image ensembles (repeated 5x) → 7500 unique images.

• Regularization stimuli: 5 image ensembles (repeated 20x) → 1875 unique images.

• Validation stimuli: 5 image ensembles (repeated 20x) → 1875 unique images.

• Monochrome images, equated in mean luminance and RMS contrast.

Natural Images (Olmos & Kingdom, 2004)



Methods

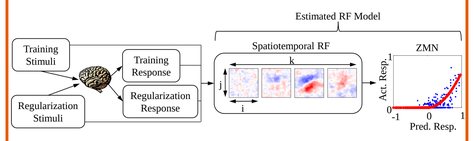
• Extracellular recording: A18 simple-type cells in anesthetized and paralyzed cats.

• Electrodes: single channel platinum-iridium and tungsten, multi-channel linear arrays and tetrodes (Neuro Nexus).

• Careful manual spike sorting, using Plexon Offline Sorter.

• Gradient descent, iterative regression algorithm with regularization (Theunissen *et al.*, 2001) to estimate linear filter weights of spatiotemporal RF.

• Subsequent zero-memory nonlinearity (ZMN) in the form of a half-wave rectifier and power law, estimated by comparing actual and predicted responses based on convolution with the linear filter weights.

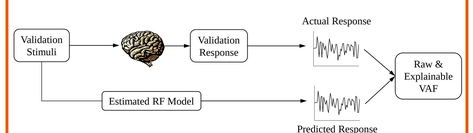


$$w(t) = \sum_{i=1}^{M}\sum_{j=1}^{M}\sum_{k=1}^{N} h(i,j,k)\,s(i,j,k-t)$$

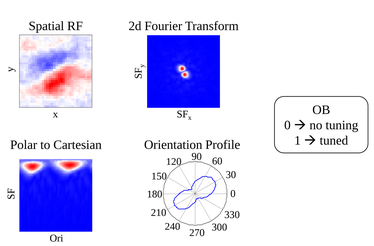
$$r(t) = \left|w(t)\right|^{a} + n(t)$$

$h(i,j,k)$ = linear filter (spatiotemporal RF) weight of i,j^{th} pixel and k^{th} time index
$s(i,j,k)$ = stimulus image at i,j^{th} pixel and k^{th} time index
i,j = indices of (downsampled) pixels, ranging from 1 to M
k = time (lag) index, ranging from 1 to N
M = downsampled image size, typically ca. 32
N = number of temporal lags, typically ca. 8
$w(t)$ = response of linear filter as a function of time (t)
$|...|$ denotes half-wave rectification
a = exponent of power law nonlinearity
$n(t)$ = noise
$r(t)$ = model response as a function of time (t)

• Results evaluated by calculating the raw variance accounted for (VAF) and total explainable VAF (David & Gallant, 2005).



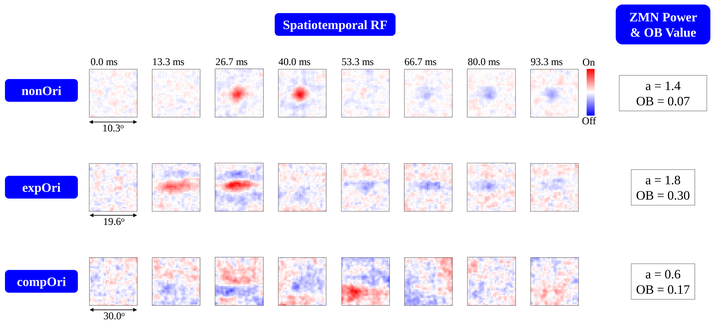
• Orientation Bias (OB) at peak temporal latency as measure of orientation bandwidth (Leventhal *et al.*, 1995).



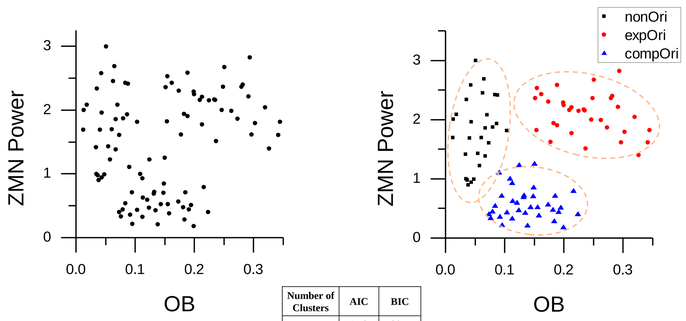
OB
0 → no tuning
1 → tuned

Results

1 **Estimated RF models:** A18 neurons exhibited three distinct groupings based on their spatial structure and ZMN; 1) non-oriented (nonOri), 2) oriented with expansive ZMN (expOri), 3) oriented with compressive ZMN (compOri)

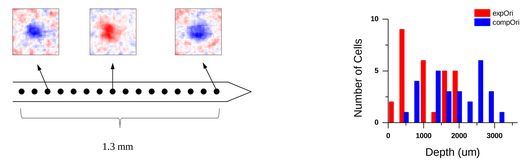


2 **Distinct categories:** Scatter plot of ZMN power vs. OB reveals distinct clusters. Cluster groupings confirmed by Gaussian Mixture Model (GMM). Akaike and Bayesian information criteria (AIC/BIC) verify that a three-cluster GMM is optimal.

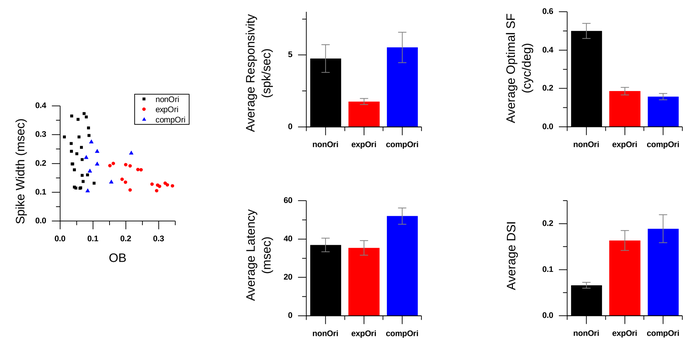


Number of Clusters	AIC	BIC
1	25.3	38.1
2	-26.0	2.2
3	-46.8	-3.19
4	Varying but always greater than above row.	

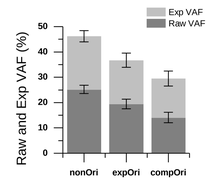
3 **Laminar depth:** nonOri cells are not confined to a specific laminae, as shown by multi-channel axial electrode recordings. expOri cells tend to be in more superficial layers while compOri are in deeper layers, as shown by depth readings of single channel electrodes.



4 **Category properties:** Investigated properties included spike width, responsivity, optimal spatial frequency (SF), response latency, and direction selectivity index (DSI).



5 **VAFs:** nonOri cells have the highest VAFs and compOri the lowest.



Conclusions

• Three distinct categories of simple-type cells: non-oriented, expansive oriented, and compressive oriented.

• Non-oriented RFs: generally described in visual cortex of primate but not cat, spread across cortical laminae and therefore unlikely to be LGN afferent terminals.

• Compressive vs. expansive ZMN might reflect degree to which a gain control mechanism is engaged.

	nonOri	expOri	compOri
ori bandwidth	isotropic	tuned	tuned
optimal SF	high	typical	typical
latency	short	short	long
direction selectivity	none	mixed	mixed
ZMN power	expansive	expansive	compressive
responsivity	mixed	low	mixed
VAF (fit to LN model)	best	intermediate	worst

References: Carandini M., Demb J.B., Mante V., Tolhurst D.J., Dan Y., Olshausen B.A., Gallant J.L.,& Rust N.C. (2005). Do we know what the early visual system does? *J Neurosci.* 25(46):10577-97.

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