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How do neurons in macaque visual cortex represent a high-dimensional perceptual space?

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Introduction and Motivation

Perceptual spaces play a key role in intermediate visual processing, as they constitute representations that support discrimination, categorization, working memory, and other judgments. The classical perceptual space of color has three dimensions, but others, such as faces and textures, have very high dimension. Representing such spaces within biological constraints is challenging.

To probe how visual cortex does this, we studied responses of macaque single neurons to a well-characterized 10-dimensional perceptual domain.

This model domain consists of black-and-white textures. Its 10 parameters are image statistics describing black/white balance and nearest-neighbor correlations (Victor and Conte 2012). The space is a useful model because it captures the informative local image statistics of natural scenes (Tkačik et al., 2010). Human perceptual sensitivities are optimally deployed within this space to match the informativeness of the space's axes (Hermundstad et al., 2014).

Perceptual studies suggest that this space is represented in two ways: in an opponent fashion, leading to an approximately Euclidean perceptual metric for threshold tasks (Conte et al., VSS 2015), and in a distributed one, leading to a highly curved metric for suprathreshold judgments (Rizvi et al., VSS 2014). Here we sought to identify the neural basis of these representations, via single-unit recordings in macaque visual cortex.

Stimulus parameters: the 10 coordinate axes

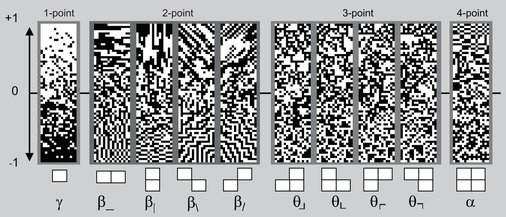
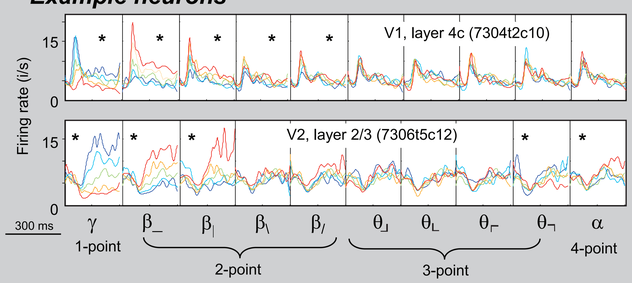


Image statistic values range from -1 to 1; 0 indicates random. γ is the difference in the fraction of bright vs. dark checks. The four β's are 2-point correlations, in the two cardinal and two diagonal directions. The four θ's are 3-point correlations. α is a 4-point correlation.

Results: along the 10 coordinate axes

Example neurons

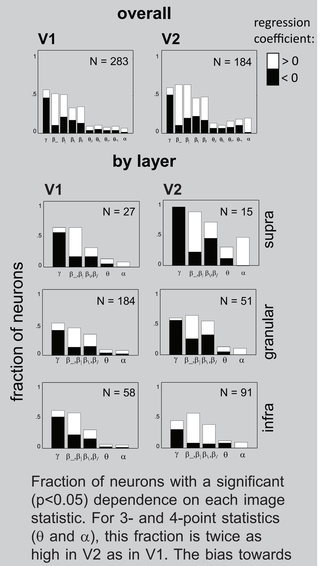


Smoothed firing rates of responses to stimuli along the coordinate axes. The V1 input-layer neuron is modulated by all 1- and 2-point statistics but not by 3- and 4-point statistics. The V2 supragranular neuron is modulated by image statistics of all orders.

Image statistic values are indicated by color: -0.4 (blue) to 0.4 (red) for the 1-point statistic γ, -0.8 to 0.8 for 2-, 3- and 4- point statistics β, θ, and α.

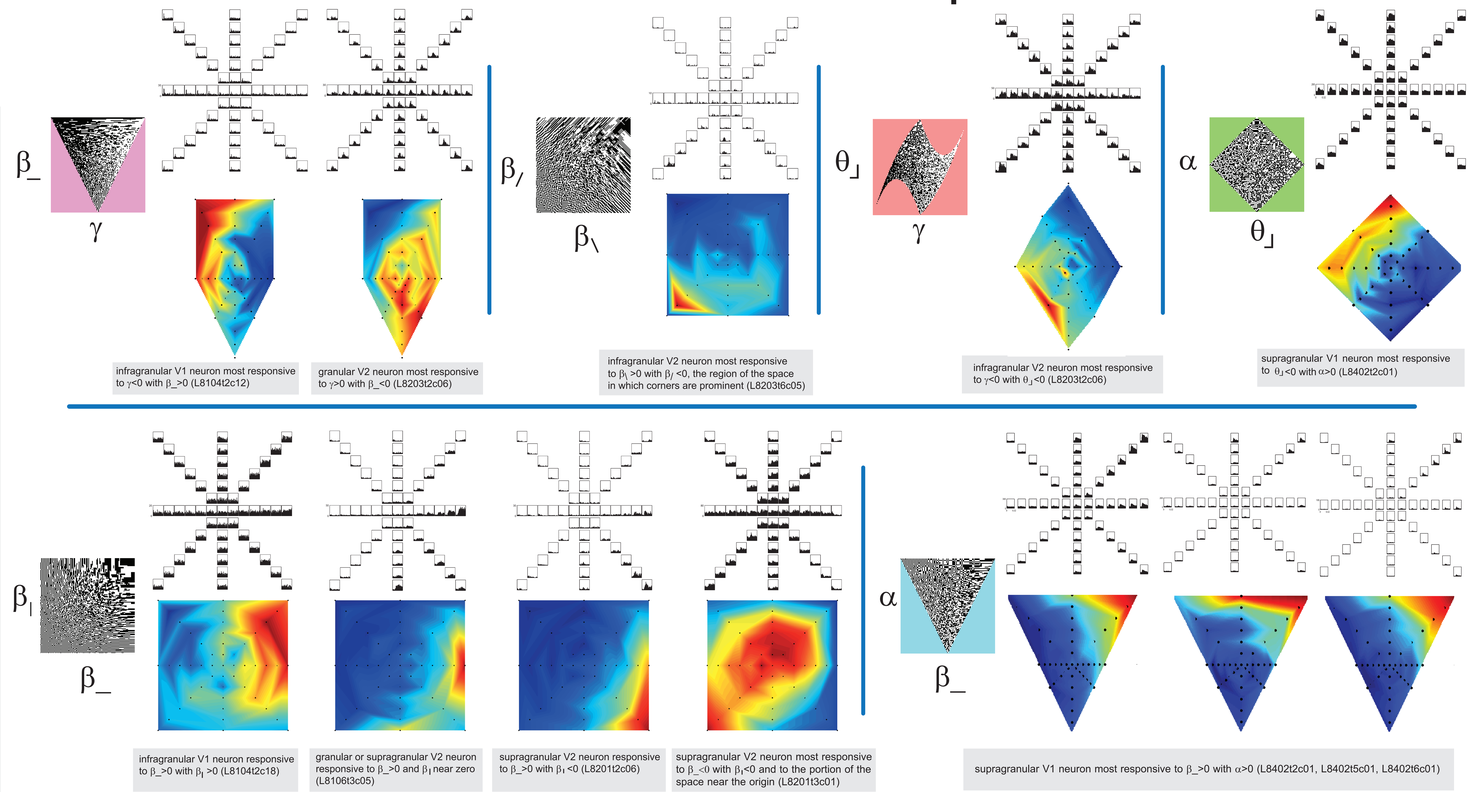
* denotes significant (p<0.05) dependence.

Population summary



Fraction of neurons with a significant (p<0.05) dependence on each image statistic. For 3- and 4-point statistics (θ and α), this fraction is twice as high in V2 as in V1. The bias towards negative regression coefficients for γ indicates a preference for darks in V1 and V2.

Results: in coordinate planes



infragranular V1 neuron most responsive to γ<0 with $\beta_$>0 (L8104t2c12)

granular V2 neuron most responsive to γ>0 with $\beta_$<0 (L8203t2c06)

infragranular V2 neuron most responsive to $\beta_|$>0 with $\beta_/$<0, the region of the space in which corners are prominent (L8203t6c05)

infragranular V2 neuron most responsive to γ<0 with $\theta_⌟$<0 (L8203t2c06)

supragranular V1 neuron most responsive to $\theta_⌟$<0 with α>0 (L8402t2c01)

infragranular V1 neuron responsive to $\beta_$>0 with $\beta_|$ >0 (L8104t2c18)

granular or supragranular V2 neuron responsive to $\beta_$>0 and $\beta_|$ near zero (L8106t3c05)

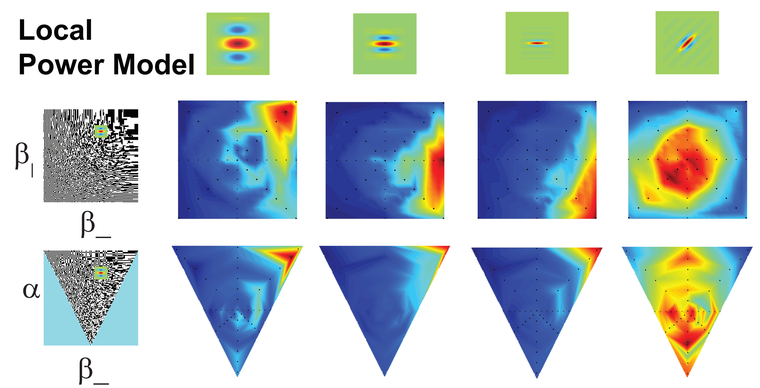
supragranular V2 neuron responsive to $\beta_$>0 with $\beta_\backslash$<0 (L8201t2c06)

supragranular V2 neuron most responsive to $\beta_$<0 with $\beta_\backslash$<0 and to the portion of the space near the origin (L8201t3c01)

supragranular V1 neuron most responsive to $\beta_$>0 with α>0 (L8402t2c01, L8402t5c01, L8402t6c01)

Panels show PSTH's of neural responses to pairwise combinations of image statistics, i.e., a plane of the stimulus domain. We measured responses to stimuli positioned at 6 points along each of 8 rays (PSTH's along the spokes), and to the random texture (PSTH center plotted). Heat maps show the mean firing rate for each stimulus; points indicate the locations in the plane that were sampled, and color scale spans the range of firing rates for each neuron. Typical neurons responded selectively to specific combinations of image statistics.

Local Power Model



Sensitivity to local oriented energy accounts for the diversity of behavior seen for sensitivities to 2-point statistics, but not multipoint statistics. Here we show heatmaps of local oriented energy detected by various Gabor filters, as the texture parameters vary in two coordinate planes. The top row shows that by varying orientation and bandwidth of the filters, the observed patterns of sensitivity in the ($\beta_|$, $\beta_$) planes can be recapitulated. However, model heatmaps in the (α, $\beta_$) plane do not account for the patterns of selectivity to these statistics seen in the data (lower, right).

Summary and Conclusions

Individual image statistics (the axes):

- Neurons were responsive to multiple kinds of image statistics.
- Responses to 1- and 2-point statistics were common (~50%) in V1 and V2.
- Responses to 3- and 4-point statistics were rare (~10%) in V1 but more common (~20%) in V2, especially in the supragranular layers, confirming Yu et al., (2015).
- Responses were opponent-like, often with biases for either positive or negative values of the image statistic.
- The population has a bias towards darks (γ<0) in both V1 and V2 (Yeh et al., 2009, Kremkow et al., 2014).

Combinations of image statistics (the planes):

- Most neurons' responses were maximal for a mixture of image statistics.
- Most neurons' responses were monotonic functions of image statistic value, consistent with an opponent representation.
- Rare neurons' responses were non-monotonic, suggesting a role in a distributed representation.

Modeling

- Local energy models (Gabor filters) account for the diversity of sensitivity to 2-point statistics and their interactions.
- These models do not account for sensitivity to multipoint statistics.

Methods

Physiological methods
Macaque V1 and V2
Anesthesia: sufentanil and propofol
Neuromuscular blockade: rocuronium

Recordings
6-tetrode array, each tetrode independently movable
Spike sorting, on- and off-line (KlustaKwik and Klusters)
Lesions at each tetrode following all recordings

Stimuli
16 x 16 patches of textures
Check size and orientation optimized for "target" unit
Stimuli presented in randomized order

Axis experiments (9 macaques)
41 stimuli: two positive and two negative values per axis, and the origin of the space
64 examples of each stimulus
Regression of smoothed firing rate PC1 on each axis
Significance determined by shuffle test
283 neurons histologically localized in V1 (87 sites)
184 neurons histologically localized in V2 (46 sites)

Planes experiments (4 macaques)
49 stimuli: 6 values on each of 8 directions in plane, and the origin of the space
Planes selected according to target units
Preliminary data from selected neurons at 132 sites in V1 and V2

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