Responses of Macaque V1 Neurons to Local Image Statistics

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41th S*f*N: 799.07/KK20

Introduction

Natural scenes have complex statistical structure. To disentangle how their components contribute to the visual response, we developed a library of artificial visual textures that allows for independent manipulation of many kinds of local image statistics. Psychophysical studies show that sensitivity to these image statistics is selective and highly stereotyped across observers (Victor & Conte 1991, poster: 799.06/KK19) .

Here, we ask whether this pattern of sensitivity has a neural correlate in primary visual cortex. Part 1 examines neuronal sensitivity to third- and fourth-order statistics defined on several different spatial configurations. Part 2 focuses on image statistics defined on a 2x2 configuration, including first-, second-, third, and fourth-order statistics.

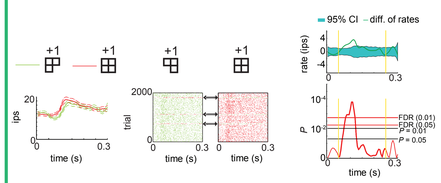
Methods

Preparation: Single-unit recordings using multitetrode arrays were made in V1 and V2 of macaques, anesthetized with propofol and sufentanil and paralyzed with vecuronium or rocuronium.

Visual stimuli: To measure sensitivity to image statistics, a sequence of binary checkerboard patterns, consisting of random arrays interleaved with arrays in specific correlations were introduced, were presented for 320 ms each. Check size was scaled to the receptive field size and orientation was set according to the orientation preference of a target neuron.

Spike sorting: After bandpass filtering (300 to 9000 Hz) and thresholding, waveforms were clustered using custom versions of KlustaKwik and Klusters (Hazan et al, 2006). Features consisted of peak amplitudes and principal components.

Analysis: Local linear regression (*locfit*, Loader, 1999) was used to calculate smooth firing rate functions elicited by stimuli with each kind of image statistic. Significance of the difference between two firing rate functions was determined by comparing the actual difference with the distribution of differences computed from 3000 shuffles. (Only shuffles between responses collected at nearby times were applied, to account for possible non-stationarity.) The False Discovery Rate method was used to correct for the multiple comparisons (one at each 5 ms time bin).



Step 1: Compute smoothed firing rates via *locfit*.

Step 2: Shuffle nearby trials, and calculate firing rates from shuffled data sets.

Step 3: Build the empirical distribution from 3000 shuffles and compare to actual difference; correct using false discovery rate between 50 ms and 250 ms (yellow cursors).

Fig 1. Estimation of significance of differences between responses.

Results

Part 1: Neural sensitivity to high-order statistics

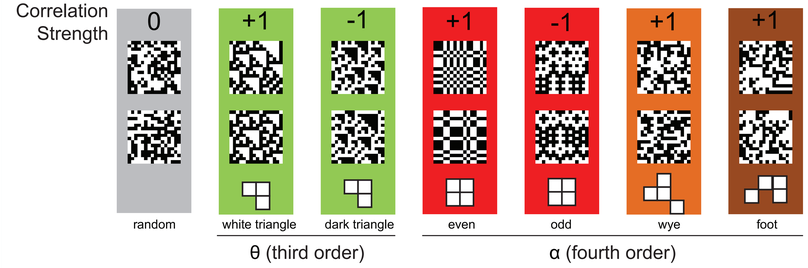


Fig 2. Stimuli that probe sensitivity to high-order statistics (HOS's). For the random checkerboard and each of the six kinds of high-order statistics, 1024 examples (two repetitions each) were presented during the experiment, each for 320 ms (two examples are shown here). The 3- or 4-check glider under each set of textures indicates the configuration of correlated checks. The visual impact of some HOS's is readily apparent (sample images): the examples of "even", "odd", "bright triangle" and "dark triangle" stimuli are obviously different from random. However, the correlations contained in the "wye" or "foot" stimuli are more difficult to perceive (Victor and Conte, 1991).

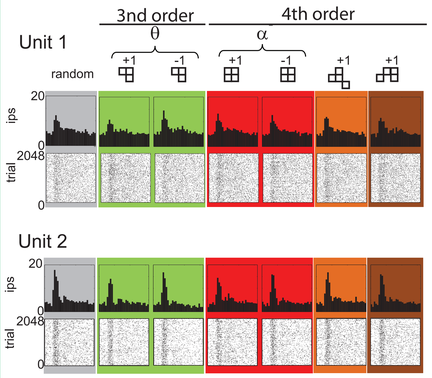
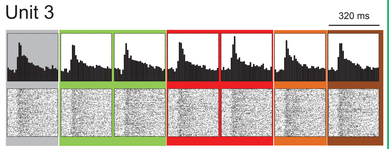


Fig 3. Example responses to stimuli enriched by specific HOS's. Most neurons responded in a transient fashion to texture appearance. Units 1 and 2 responded differentially to stimuli with 3rd-order correlations, and unit 2 had a smaller increase in firing in response to the "even" 4th-order HOS ($\alpha = +1$) than in response to the "odd" HOS ($\alpha = -1$). Unit 3 responded transiently to all textures, but did not reliably discriminate between them.



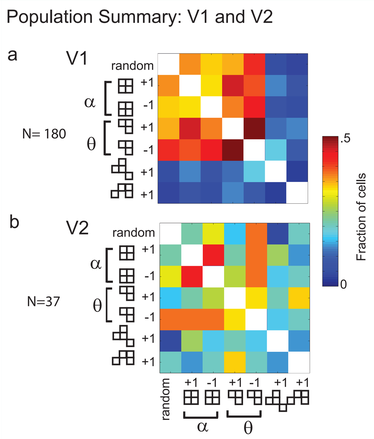


Fig 4. Fraction of neurons with significantly different firing rates in response to stimuli with various kinds of high-order statistics (HOSs). ***a***, Large fractions of V1 neurons have significantly different firing rates for the visually-salient third and fourth-order statistics, but few can discriminate the "wye" and "foot" statistics from any other. The pattern of V1 sensitivity matches psychophysical observations (Victor & Conte, 1991). ***b***, The pattern of V2 sensitivity appears similar to that of V1, but the V2 sample size is limited.

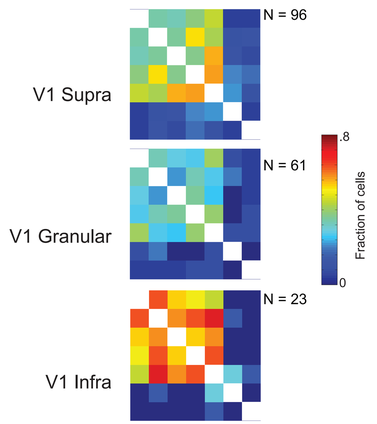
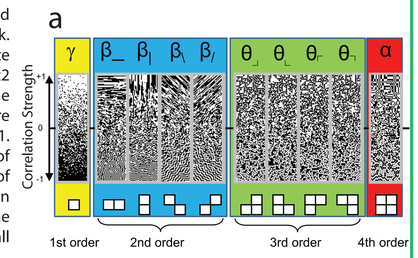


Fig 5. V1 Laminar distribution of HOS sensitivity. The fraction of sensitive cells is smallest in the granular layer and largest in the infragranular layer, indicating that HOS-sensitivity develops within V1.

Part 2: Neural sensitivity to statistics in a 2x2 configuration

Fig 6. First-, second-, third- and fourth-order statistics within a 2x2 block. This 10-parameter family is a complete description of the statistics of a binary 2x2 block (see 799.06/KK19), and includes the third- and fourth-order statistics that were found to elicit selective responses in Part 1. Panel ***a*** shows the complete gamut of these statistics. Panel ***b*** shows examples of the stimuli used for testing: correlation strengths were set at ±0.2 and ±0.4 for the first-order statistic and ±0.4 and ±0.8 for all others.



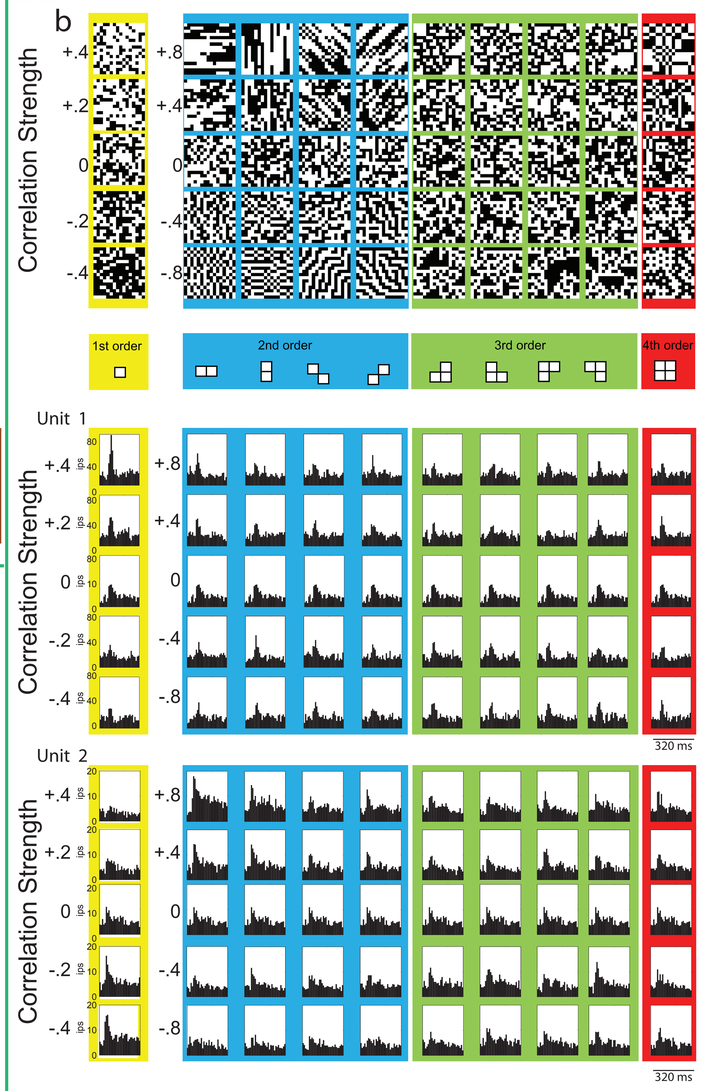


Fig 7. Responses of two example V1 neurons to the 2x2 image statistics. For the first-order statistic γ, unit 1 increased in firing and unit 2 decreased in firing. Responses to the other image statistics were also present, but less prominent -- for example, unit 2 increased in firing for positive values of β_- and $\beta_|$. (Note that the response to the random stimulus is repeated in each column to aid comparison.)

Population summary

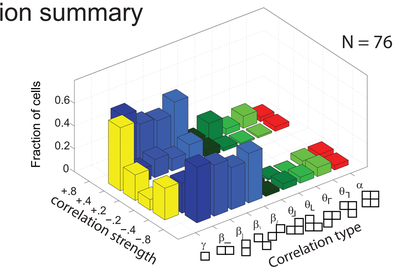


Fig 8. The fraction of neurons that were modulated by each of the 10 texture parameters is shown as a function of correlation strength. In accord with human psychophysics (799.06/KK19), neural sensitivity was most common for the first-order statistic γ, next-most-common for the second-order statistics β, and least common for third- and fourth-order statistics.

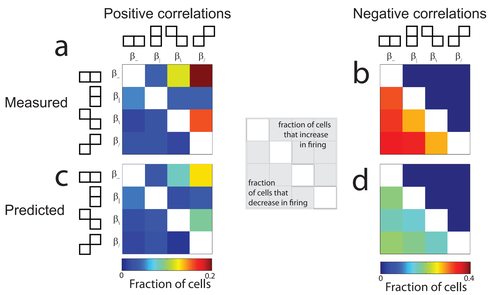


Fig 9. As shown in ***a*** and ***b***, neurons that respond to positive second-order correlations are largely incremental and selective, while neurons that respond to negative second-order correlations are largely decremental and nonselective. ***a***, Fraction of neurons that respond to each pair of positive second-order stimuli. ***b***, Same as ***a*** but for pairs of negative parameters. ***c*** and ***d*** show the predicted fraction of cells under the hypothesis that responses are independent. This fails to account for the non-selectivity observed for negative correlations: the fractions measured (***b***) are substantially higher than those predicted (***d***).

Conclusions

* V1 neurons' selectivity for different configurations of third- and fourth-order correlations match human psychophysical findings.
* Laminar analysis indicates that this sensitivity arises as a result of processing within V1.
* For image statistics within a 2x2 patch, responses of V1 neurons are greatest to γ (first order), next to β (second order), and least to θ and α (third and fourth order), also in accord with psychophysical findings (799.06/KK19)
* Population aspects of responses to positive and negative correlations appear qualitatively different. Responses to positive correlations are largely incremental and selective, while responses to negative correlations are largely decremental and nonselective.

References

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Tkačik, G., Prentice, J., Victor, J.D., and Balasubramanian, V. (2010) Local statistics in natural scenes predict the saliency of synthetic textures. *Proc. Natl. Acad. Sci. USA* 107, 18149-18154.
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Acknowledgement

Support: NIH Grant EY09314, NIH Grant EY07977