Neurons in primary visual cortex show dramatic changes in filtering properties when high-order correlations are present

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SUMMARY

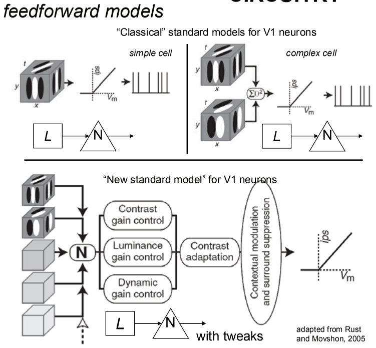
V1 is widely considered to act primarily as a feedforward bank of filters followed by simple nonlinearities ("LN" systems). However, when LN models are built from simple analytically-convenient stimuli, their predictions of neural responses to natural scenes are only modestly accurate. One possibility is that this inaccuracy is merely quantitative, and can be remedied by adding gain controls, modulatory feedback, and multiple subunits to the basic LN structure. Alternatively, there might be fundamental qualitative differences between the computations performed by real cortical neurons and those performed by these models.

Since natural scenes have characteristics that traditional analytic stimuli lack, differences between responses of real and model V1 neurons likely reflect sensitivity to the distinguishing characteristics of natural scenes, namely, high-order correlations (HOCs). To isolate the effects of HOCs, we created sets of binary checkerboard stimuli in which second-order correlations were absent, but selected HOCs were present. Moreover, because our stimuli had identical contrast and spatial frequency content, they would equally engage cortical gain controls. For each of these statistical "contexts", we determined the receptive field map – i.e., the L stage of the LN model that best accounts for the neuron's responses. Because stimuli were constructed so that second-order correlations were absent, these maps could be obtained by reverse correlation.

Recordings were made via tetrodes in macaque V1 and V2. In 19/25 V1 neurons (and 7/9 V2 neurons), there were dramatic effects of high-order "context" on receptive field structure, including heightened sensitivity, development of spatial antagonism, or changes in response time course. In a few neurons, RF maps could *only* be obtained in the presence of high-order structure. These behaviors are not present for model LN neurons. This suggests that alternative model structures, such as strongly recurrent networks, are required to account for V1 responses even at a qualitative level.

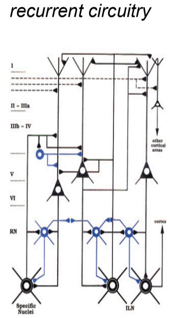
MISMATCH OF V1 COMPUTATIONAL MODELS AND CIRCUITRY

feedforward models



adapted from Rust and Movshon, 2005

recurrent circuitry



Adapted from Llinas et al. 1994, by Purpura and Schiff 1997

Do V1's computations require a departure from the "new standard" architecture?

APPROACH AND RATIONALE

- High-order correlations (HOC's) are functionally important because they distinguish
  - local features (lines, edges) from noise
  - traditional analytical stimuli (bars, gratings, random noise) from natural scenes
- Models built from traditional stimuli are incomplete predictors of responses to natural scenes
- We hypothesize that this incompleteness reflects sensitivity to HOC's
- To identify neural sensitivity to HOC's and determine whether it can be accounted for by gain controls and adaptations, we *examine responses to stimuli equated for luminance, contrast, and spectral content, but differing in high-order correlations*

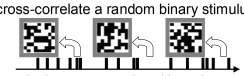
METHODS

Physiological

- Recording in macaque V1 and V2
  - anesthesia isolates "bottom-up" processes
  - paralysis allows for detailed receptive field mapping
  - tetrode technique allows for simultaneous multiple single unit recordings

Analytical

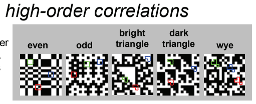
- Standard RF mapping: cross-correlate a random binary stimulus and spike response



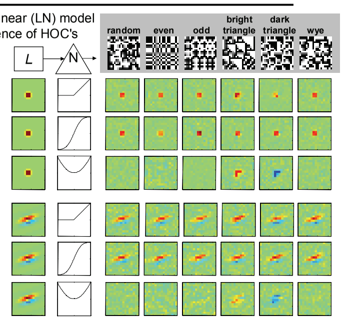
- This requires that stimulus pixels are uncorrelated in *pairs*
- We apply this approach using stimuli whose pixels are uncorrelated in pairs, but correlated at higher orders ("isodipole textures")
  - third- and fourth-order correlations
  - some are perceptually salient, some are not
- Changes in apparent receptive field maps indicate sensitivity to HOC's

Construction of stimuli with high-order correlations

Each kind of stimulus is specified by a "glider" (colored outlines) and a parity (whether the number of white checks within each glider is even or odd). For each kind of stimulus, a receptive field map is created by reverse-correlating responses to 1024 examples, each presented for 320 ms.



RF maps of linear-nonlinear (LN) model neurons in the presence of HOC's

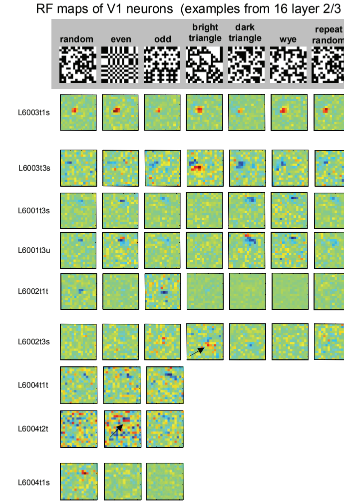


For LN (linear-nonlinear) neurons, reverse correlation analysis may lead to modest changes in the shape of the apparent receptive field sensitivity profile in the presence of HOC's. These simulations show that the changes are very minor, and unlikely to account for our findings (next panels).

RESULTS:WIDESPREAD AND MARKED SENSITIVITY TO HIGH-ORDER CORRELATIONS

Spatial analysis

RF maps of V1 neurons (examples from 16 layer 2/3 neurons)



minimal effect of HOCs (3 neurons total)

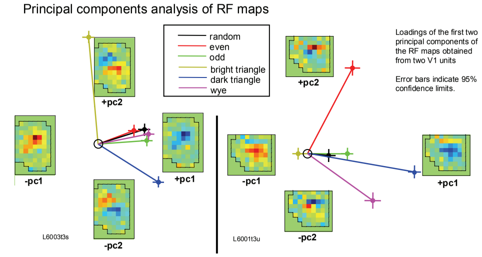
new subfields or large gain changes (7 neurons total)

minimally mappable with random checkerboard but mappable with at least one HOC stimulus (5 neurons total)

mappable only with random stimuli (1 neuron)

For most neurons, RF maps depend strongly on the presence of HOC's. For some neurons, RF maps were only clearly obtainable when HOC's were present.

Principal components analysis of RF maps



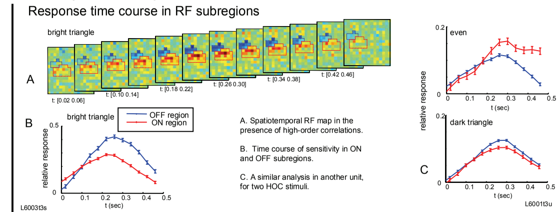
Loadings of the first two principal components of the RF maps obtained from two V1 units

Error bars indicate 95% confidence limits.

Principal components analysis shows that RF changes are highly significant, including changes induced by "invisible" correlations (the wye stimulus).

Temporal analysis

Response time course in RF subregions



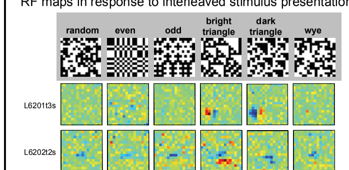
A. Spatiotemporal RF map in the presence of high-order correlations.

B. Time course of sensitivity in ON and OFF subregions.

C. A similar analysis in another unit, for two HOC stimuli.

Response dynamics can depend on high-order correlations.

RF maps in response to interleaved stimulus presentation

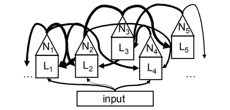


RF maps in two V2 neurons. Here, the six different kinds of stimuli (five HOC-enriched stimuli and random checkerboards) were randomly interleaved (320 ms each), rather than presented in blocks of 1024 stimuli with the same correlation structure. HOC-dependent changes in the RF maps are nevertheless present.

Alterations in RF maps do not require prolonged adaptation.

How might responses to HOC's, including "invisible" ones, arise?

- With feedforward architecture we would need
  - a parallel set of LN modules, with dedicated circuitry for each kind of correlation
  - to include specific circuitry for correlations that aren't perceptible (and don't seem to correspond to edges and regions)
- But if recurrence dominates
  - each path through the network traverses a different combination of nonlinearities
  - this generates lots of useful combinations (e.g., local edge detection followed by interactions along extended contours)
  - but it also generates some crosstalk -- accounting for sensitivity to "invisible" correlations, such as the wye stimulus



See, for example:
Chance, Nelson, and Abbott, L.F. (2000) Neurocomputing
Tao, Shelley, McLaughlin, and Shapley (2004) PNAS.

CONCLUSIONS

- V1 neurons exhibit behavior that challenges feedforward models
  - this behavior is evident for many kinds of stimuli with high-order correlations
  - stimuli needn't be natural or trigger gain controls
  - high-order correlations may not even be perceptually relevant
- Dependence on high-order correlations can be marked
  - it can affect orientation tuning
  - it can determine whether a neuron even has an evident receptive field
- Recurrence is an efficient use of connections that generates sensitivity to a wide variety of high-order correlations
- Recurrence accounts for a surprising observation: sensitivity to "invisible" correlations