Receptive field maps depend on high order stimulus structure: evidence for nonlinear feedback

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INTRODUCTION

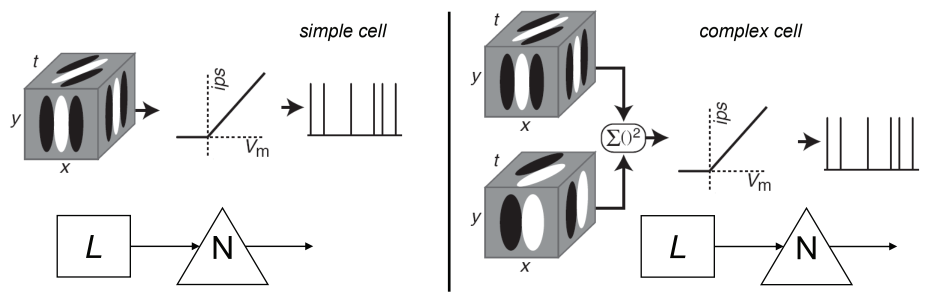
The dominant view of primary visual cortex (V1) is that typical neuronal responses can be modeled reasonably well as a simple feedforward cascade of a linear filter followed by a static nonlinearity. Deviations from this "LN" picture are well recognized, but they are generally thought to consist of combining multiple such subunits in parallel, and adding modulatory gain controls. On the other hand, cortical anatomy is characterized by strong feedback. Here we ask whether the shortcomings of the LN picture are fundamental and qualitative, or merely quantitative.

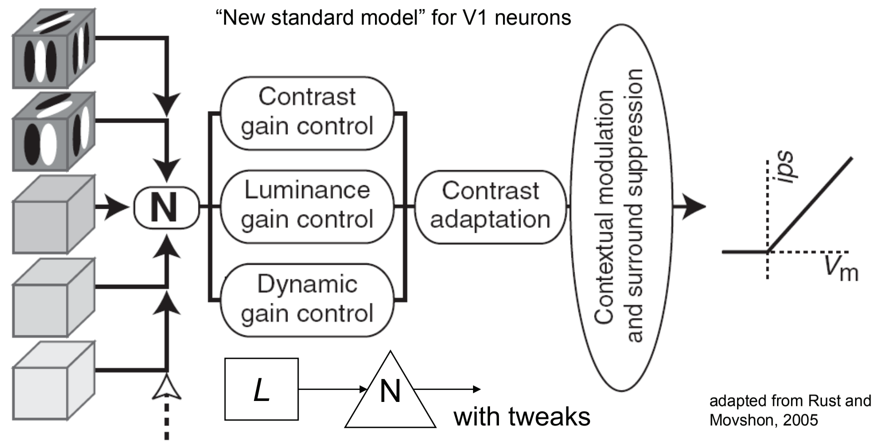
The direct approach to making this distinction is to create a model of a V1 neuron's receptive field, complete with gain controls; to collect sufficient data from individual neurons to determine model parameters; and to test it with out-of-sample stimuli. Since this is impractical, we took an indirect approach. We created multiple basis sets that were matched for luminance, contrast, and spatial frequency content, so that both basis sets would engage gain controls to the same degree. With the confounding effects of gain controls thus removed, LN-like neurons should yield identical characterizations. We implemented this strategy in two ways: two-dimensional Hermite functions, and binary checkerboard stimuli with specific third- and fourth-order correlations introduced. In both cases, widespread and qualitative deviations from the predictions of LN models were found, and the nature of the deviations is concisely accounted for by the effects of strong nonlinear recurrence.

MISMATCH OF V1 COMPUTATIONAL MODELS AND CIRCUITRY

feedforward models

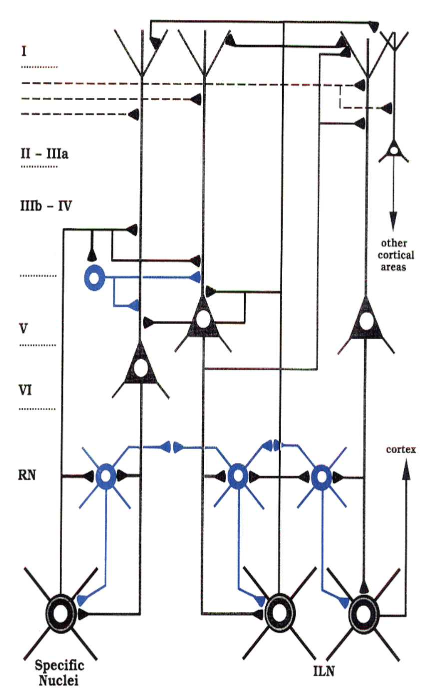
"Classical" standard models for V1 neurons





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

Analytical

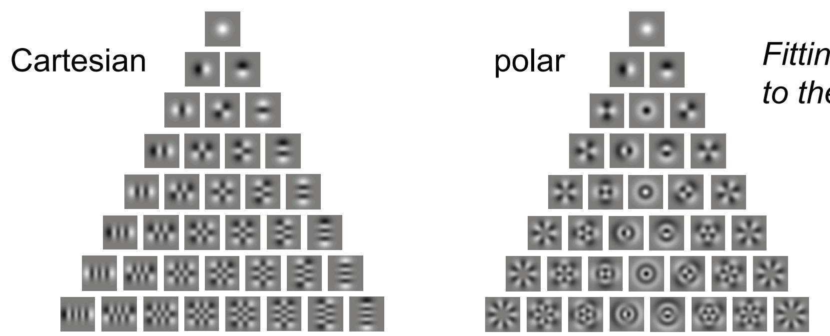
- Use designed stimuli to neutralize adaptations and gain controls
  - stimulus sets *match* in first-order (luminance) and second-order (contrast, power spectrum) statistics
  - stimulus sets *differ* in high-order statistics
- High-order statistics are functionally important because they distinguish
  - 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 – and we hypothesize that high-order statistics contribute to this

Physiological

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

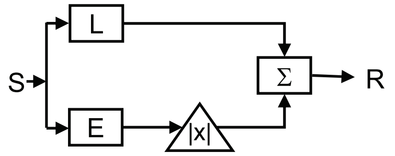
RESPONSES TO TWO-DIMENSIONAL HERMITE FUNCTIONS IMPLY RECURRENCE OF SIGNALS FROM ORIENTED CONTOURS

Stimuli



- All stimuli have the same mean-squared contrast.
- Within each rank (row), Cartesian and polar basis sets have the same spatial extent and frequency content.

Fitting an LN-type model to the responses

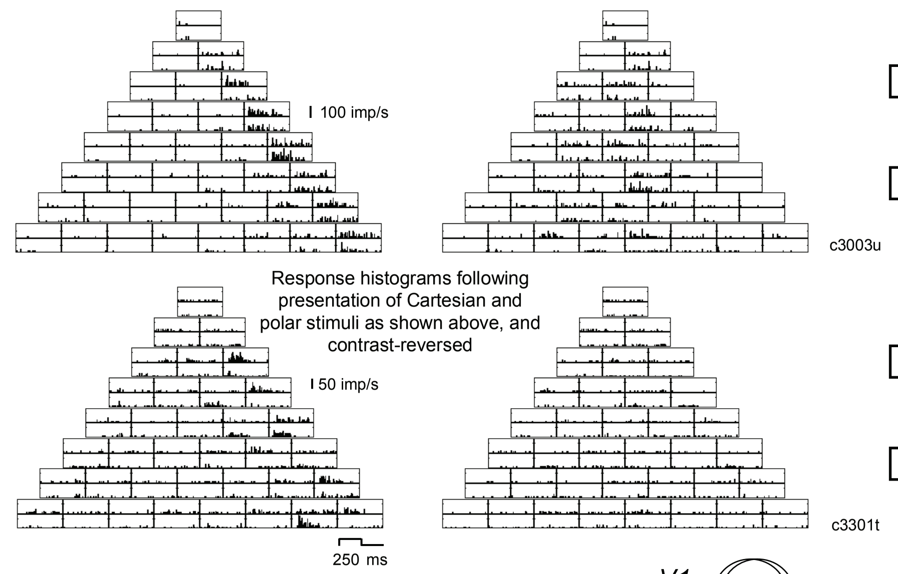


sensitivity of [L] to [■] = ½(resp[■] - resp[■])

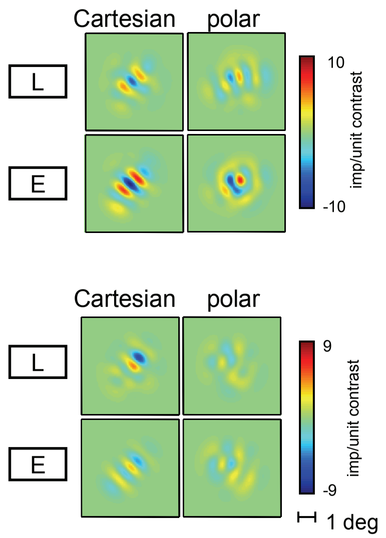
sensitivity of [E] to [■] = ½(resp[■] + resp[■])

Since Cartesian and polar stimuli each form a basis set, filters can be reconstructed from either set. The prediction of LN-type models is that the filters inferred from Cartesian and polar stimuli should match.

Representative neural responses



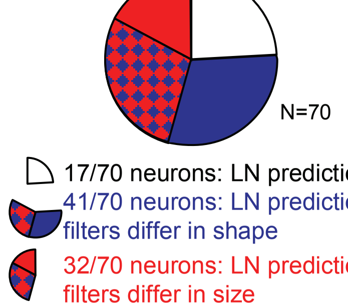
Response histograms following presentation of Cartesian and polar stimuli as shown above, and contrast-reversed



Prediction fails: C and P filters differ in shape (and orientation)

Prediction fails: C and P filters differ in size

Population summary

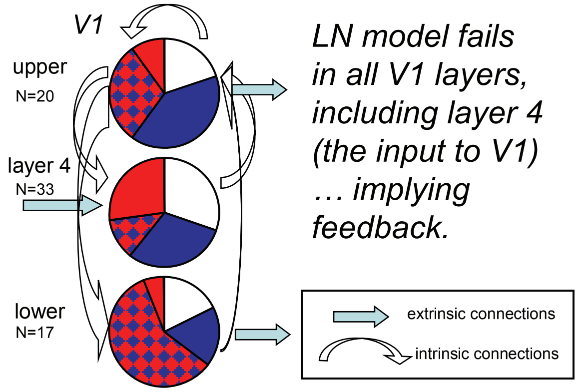


17/70 neurons: LN prediction holds

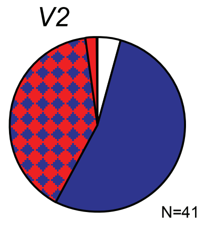
41/70 neurons: LN prediction fails, filters differ in shape

32/70 neurons: LN prediction fails, filters differ in size

Laminar analysis

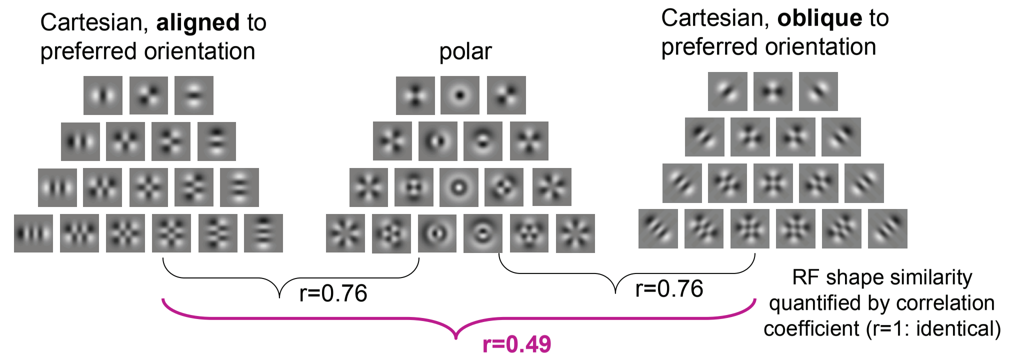


LN model fails in all V1 layers, including layer 4 (the input to V1) … implying feedback.



Model failure is accentuated in V2

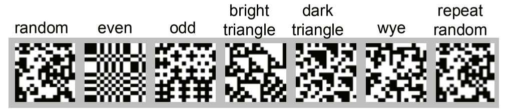
Role of contour orientation



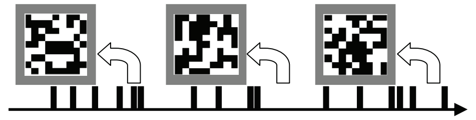
RF shape similarity quantified by correlation coefficient (r=1: identical)

Contour orientation has a larger effect on RF shape than the Cartesian vs. polar distinction. Departure from LN behavior is therefore driven by elongated contours in an orientation-specific manner.

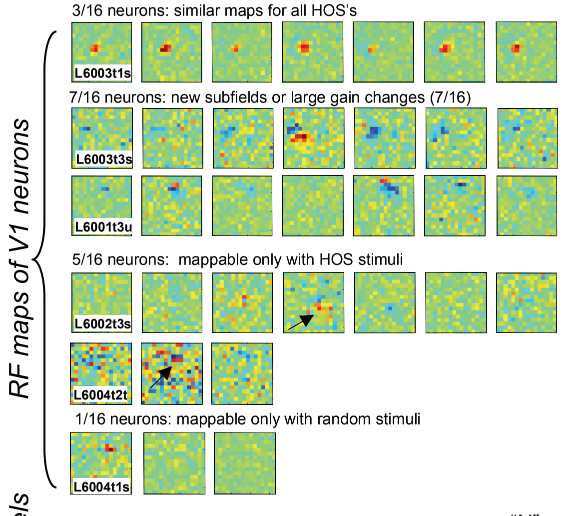
RESPONSES TO ISODIPOLE TEXTURES IMPLY GENERAL SENSITIVITY TO HIGH-ORDER CORRELATIONS

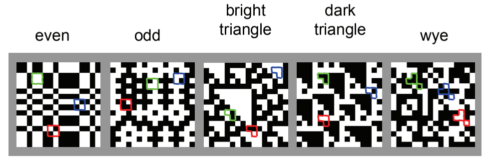


- Standard RF mapping: cross-correlate a random binary stimulus and spike response

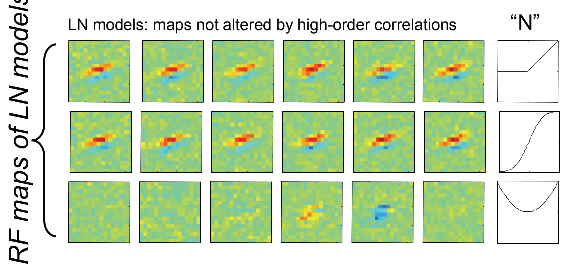


- This requires that stimulus pixels are uncorrelated in *pairs*
- We apply this approach to stimulus sets that are uncorrelated in pairs, but correlated at higher orders
  - third- and fourth-order correlations
  - some are perceptually salient, some are not
- This probes sensitivity of V1 neurons to high-order correlations



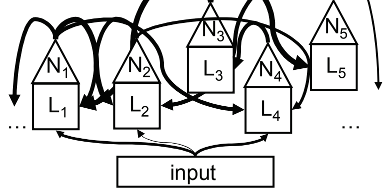


Each kind of stimulus is specified by a "glider" (colored outlines in each panel) and a parity (whether the number of white checks within each glider is constrained to be an even or an odd number). For each kind of stimulus, a receptive field map is created by reverse-correlating responses to 1024 examples,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



13/16 V1 neurons show a marked sensitivity to specific high-order correlations, including correlations that are not visually salient. This is at first surprising, but it is a distinctive prediction of a strongly nonlinear feedback architecture.

- With feedforward architecture
  - we would need a parallel set of LN modules, with dedicated circuitry for each kind of correlation
  - we would need 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



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
- A recurrent nonlinear network concisely accounts for characteristics of responses to Cartesian and polar Hermite stimuli
- 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