Form-cue invariant second-order contrast envelope responses in macaque V2

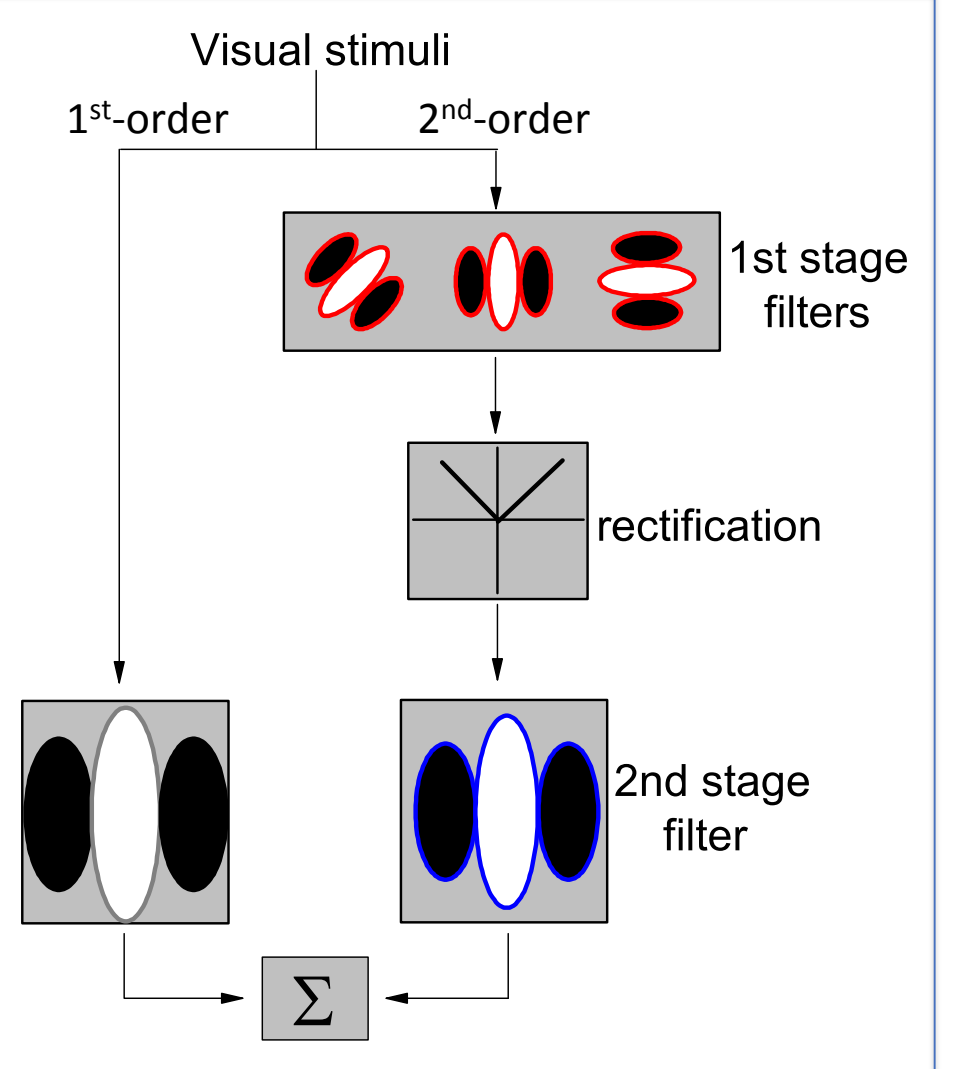
G. Li[1], Z. Wang[2], Z. Yao[2], N. Yuan[2], V. Talebi[1], J. Tan[2], Y. Wang[2], Y. Zhou[2], C.L. Baker[1]

[1]McGill Vision Research, Dept Ophthalmology, McGill University, Montreal, QC, Canada

[2]School of Life Sciences, University of Science and Technology of China, Hefei, China

Introduction

Background



- Natural images frequently contain oriented boundaries defined by differences of luminance (1st-order), or of contrast or texture (2nd-order).
- 1st-order stimuli are thought to be detected by neural mechanisms acting like a conventional linear filter.
- Detection of 2nd-order stimuli could be explained by a 'filter-rectify-filter' cascade.
  - -1st-stage filters are tuned to the fine scale of the texture.
  - -rectified outputs drive a 2nd-stage, coarser scale linear filter.
- 2nd-order processing has been widely studied in human psychophysics (Landy & Graham, 2004).
- In primates the neural substrate still remains unclear.

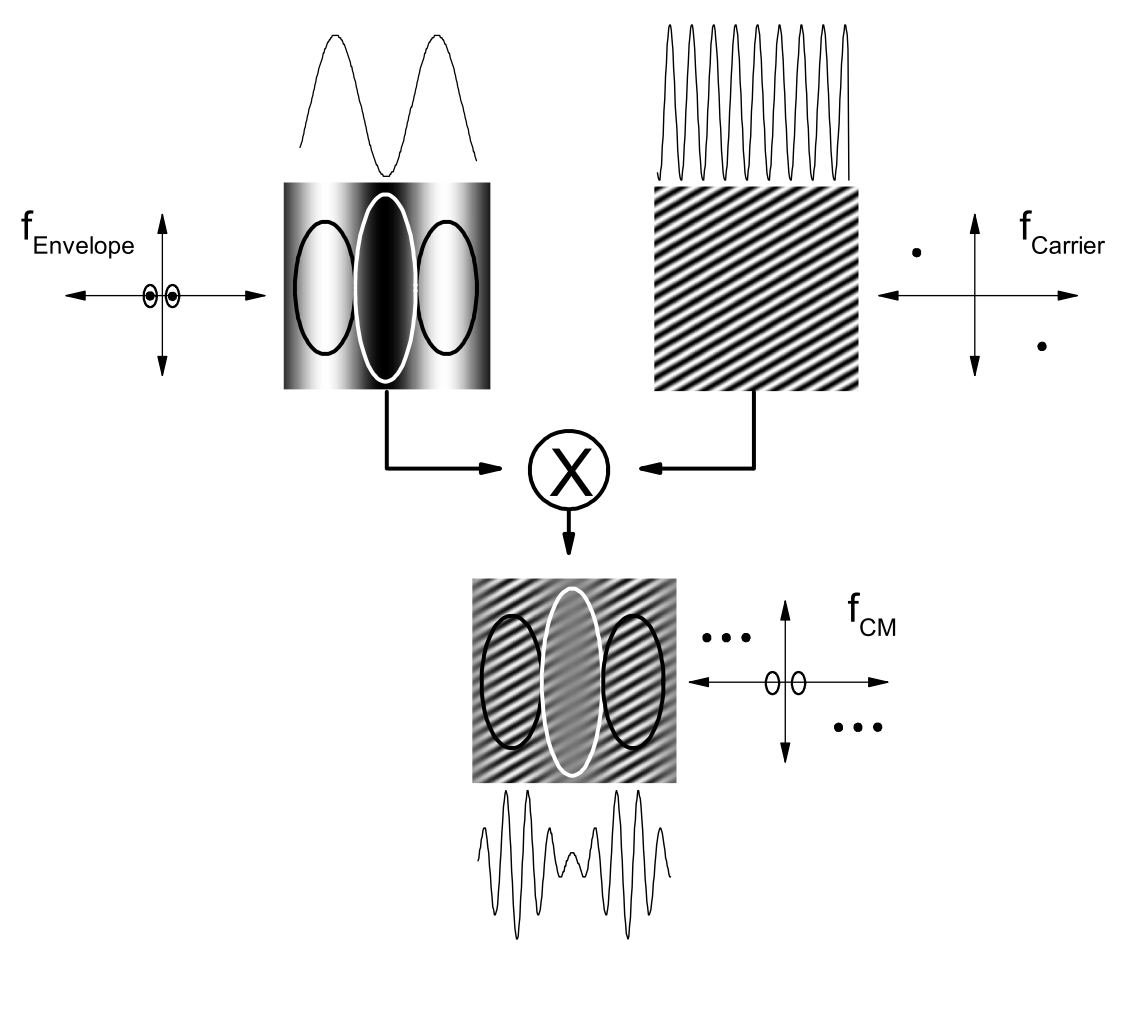
Challenges

1. Ensure that responses to 2nd-order stimuli are not due to inadvertent activation of linear/ luminance mechanisms.
2. Use stimuli that provide the analytical power to analyze the tuning properties of both early and late stage filtering.

Methods

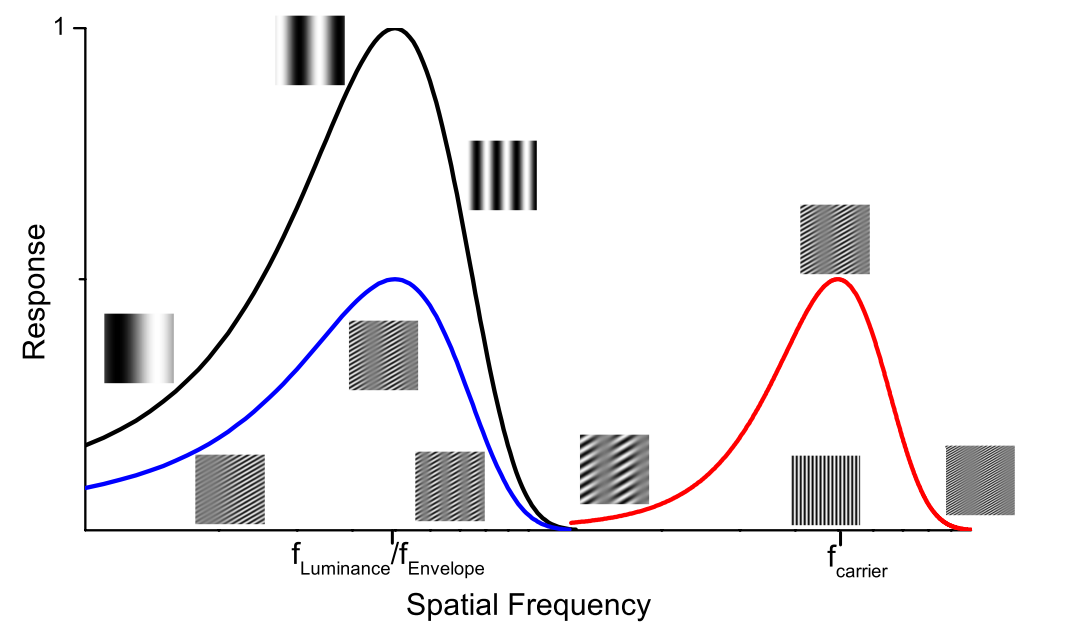
Stimuli

Sinewave gratings and contrast modulation (CM) envelopes stimuli were presented on a gamma-corrected CRT monitor, placed at a 114 cm distance.



CM envelopes were generated by multiplication of two grating patterns: a stationary high spatial frequency ($f_{Carrier}$) grating as the 'carrier' and a drifting low spatial frequency ($f_{Envelope}$) grating as the 'envelope'. In Fourier frequency domain, such CM stimuli consist of components all close to the 'carrier' spatial frequency, with no energy at the 'envelope' spatial frequency.

A neuron that responds to an envelope stimulus in which all Fourier components are clearly outside its grating frequency-selective range, must have been responding to the envelope of the stimulus as a result of nonlinear processing. The nonlinearity might occur:
(1) after the 1-st stage filter (2nd-order processing, F-R-F model), *or*
(2) because of an early nonlinearity (before filters, e.g. stimuli artifact).
  - if so, the envelope response would not be selective for the carrier spatial frequency.



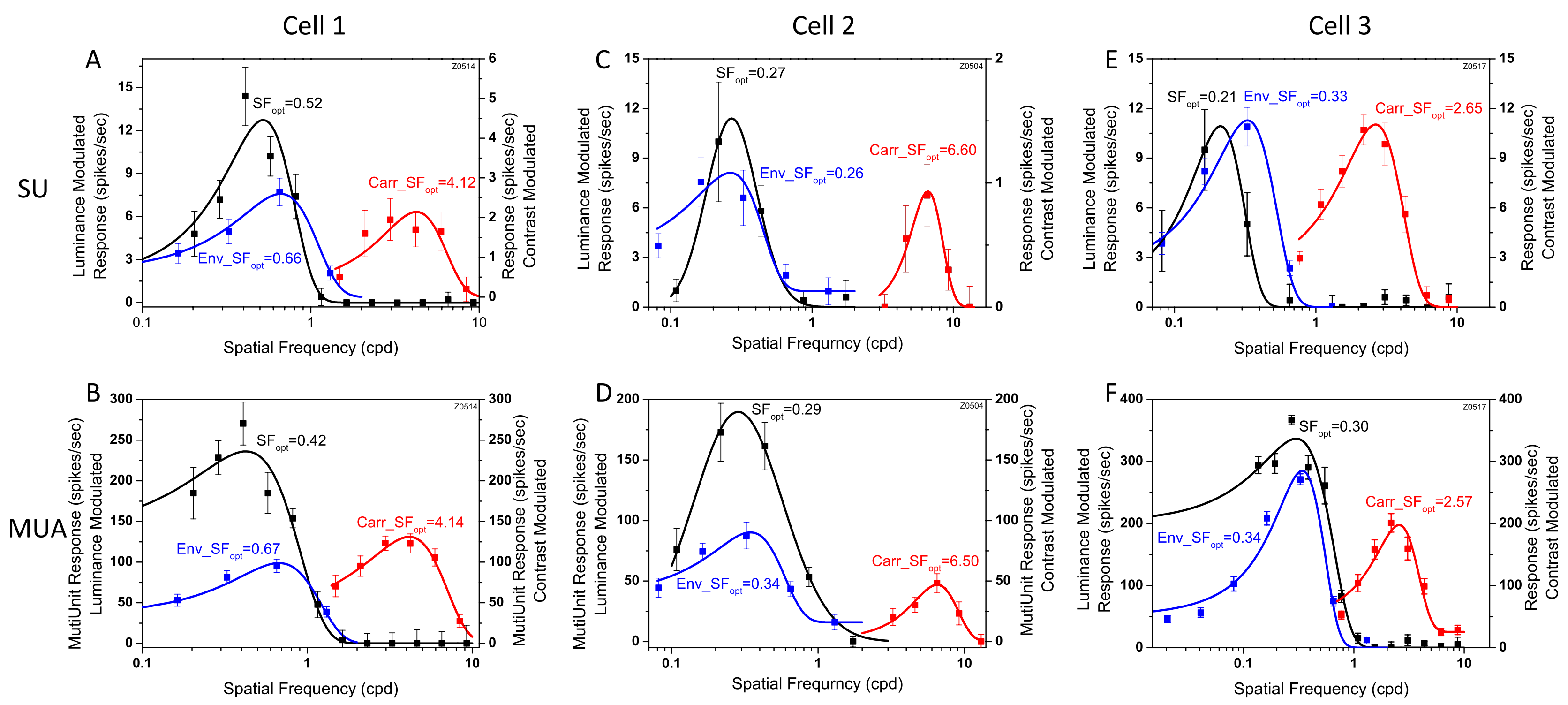
Criteria for a "2nd-order responsive" neuron:

- ✓ **responds to an envelope (CM) stimulus (blue).**
- ✓ **all the Fourier components of stimulus are clearly outside its luminance frequency-selective range (black).**
- ✓ **tuned to carrier spatial frequency (red).**

Electrophysiology Recording:

- anesthetized and paralyzed monkeys (*Macaca mulatta*)
  - (N_2O, Propofol, Sufentanil) + (Gallamine triethiodide, Tubocurarine chloride)
- careful refraction and artificial pupils.
- extracellular recording:
  - glass-coated tungsten electrodes (FHC): V1 -> white matter -> V2
  - Michigan Probes (NeuroNexus): near lunate sulcus.
- single-unit (SU): isolated using Plexon Offline Sorter, quantified as average firing rates.
- multi-unit activity (MUA): defined as events that exceeded 3-σ of the filtered raw data (300 – 5KHz), quantified as average firing rates.
- experiment protocol:
  - luminance gratings: spatial frequency, orientation, RF-mapping
  - envelope (CM) stimuli: carrier spatial frequency, orientation
    envelope spatial frequency, orientation
- 51 visually responsive neurons, 22 were 2nd-order responsive.

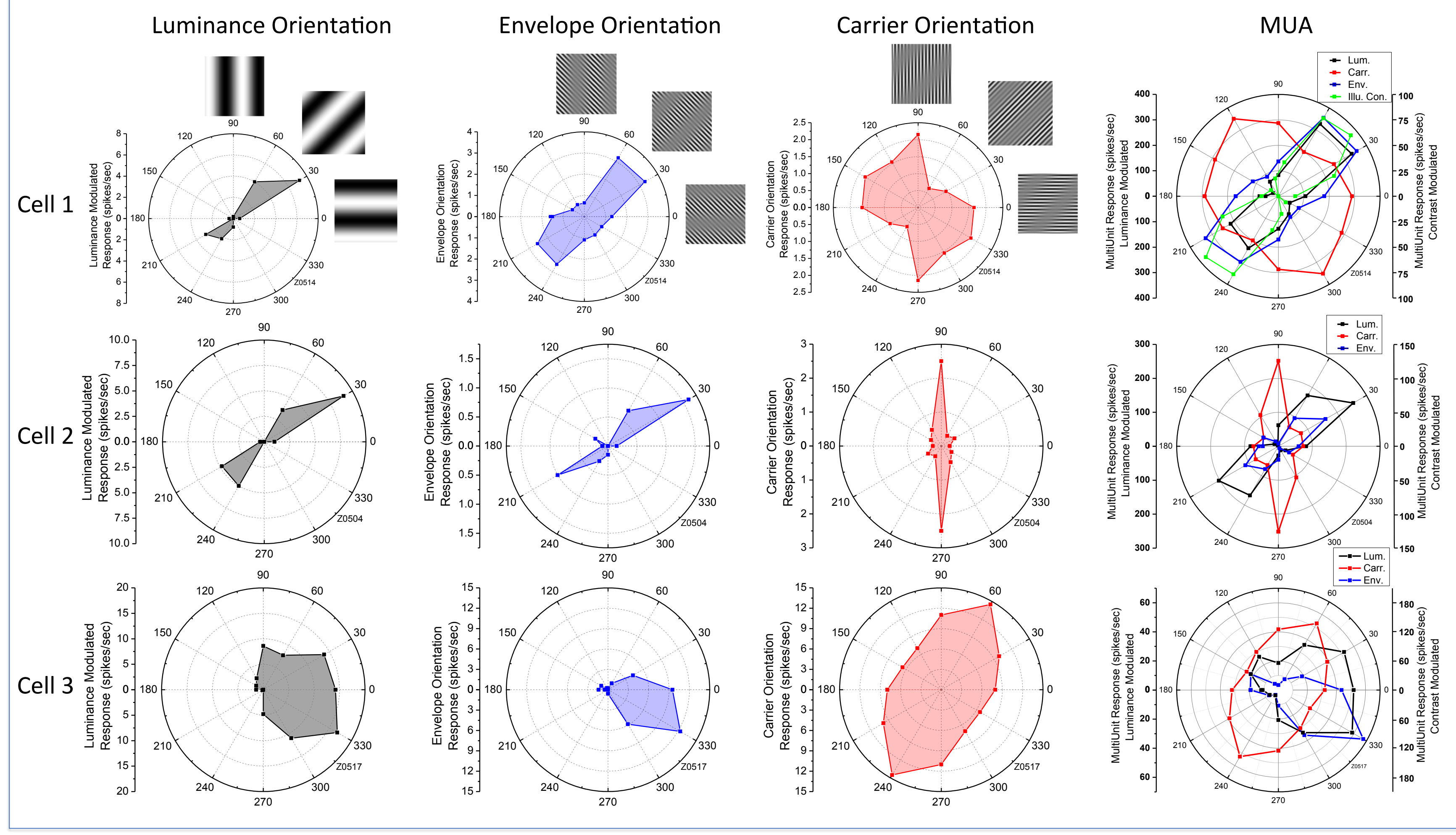
Spatial Frequency Tuning



Spatial frequency tuning curves of three envelope responsive neurons for luminance stimuli and CM stimuli (upper row → SU, bottom row → MUA). Each plot shows luminance spatial frequency (black), envelope spatial frequency (blue) and carrier spatial frequency (red).

- Neurons are clearly tuned for luminance, envelope and carrier spatial frequency.
- Different neurons exhibited different optimal spatial frequencies for luminance , envelope and carrier.
- The optimal carrier spatial frequencies were clearly distinct from the luminance grating response range. Simple luminance gratings produced little or no response at such high frequencies.
- Neurons exhibited similar, but slightly different spatial frequency tuning curves for luminance and envelope.
- MUA exhibited similar tuning curves as SUs.

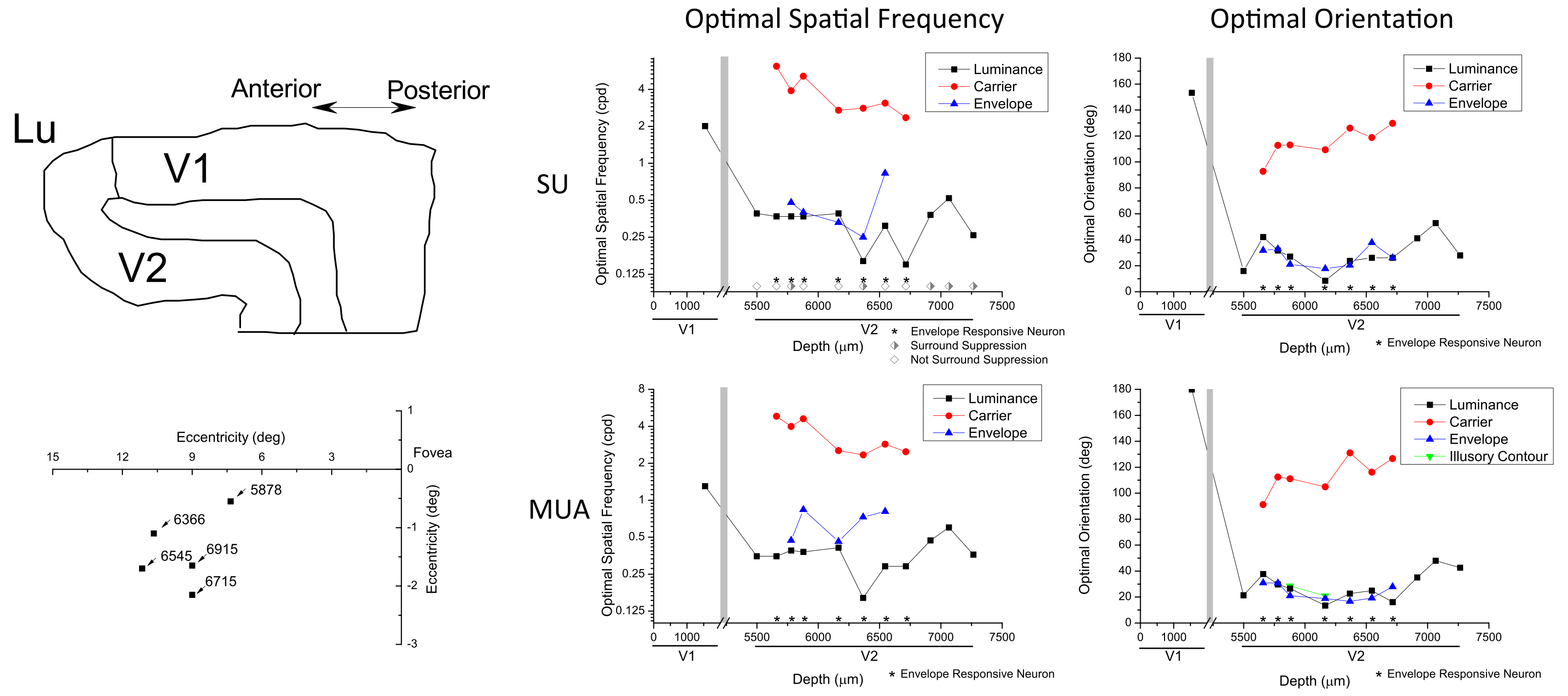
Orientation Tuning



Orientation polar plots for the same three neurons (showed above). Orientation tuning curves for luminance (black), envelope (blue) and carrier (red) are shown in different columns.

- Neurons are clearly tuned for luminance, envelope and carrier orientations.
- Envelope response polar plots were usually very similar to the corresponding luminance polar plots (**form-cue invariance**).
- Carrier orientation could be very narrowly tuned.
- No clear relationship between the carrier orientation tuning and the corresponding luminance tuning.
- MUA exhibited similar tuning curves as SUs.

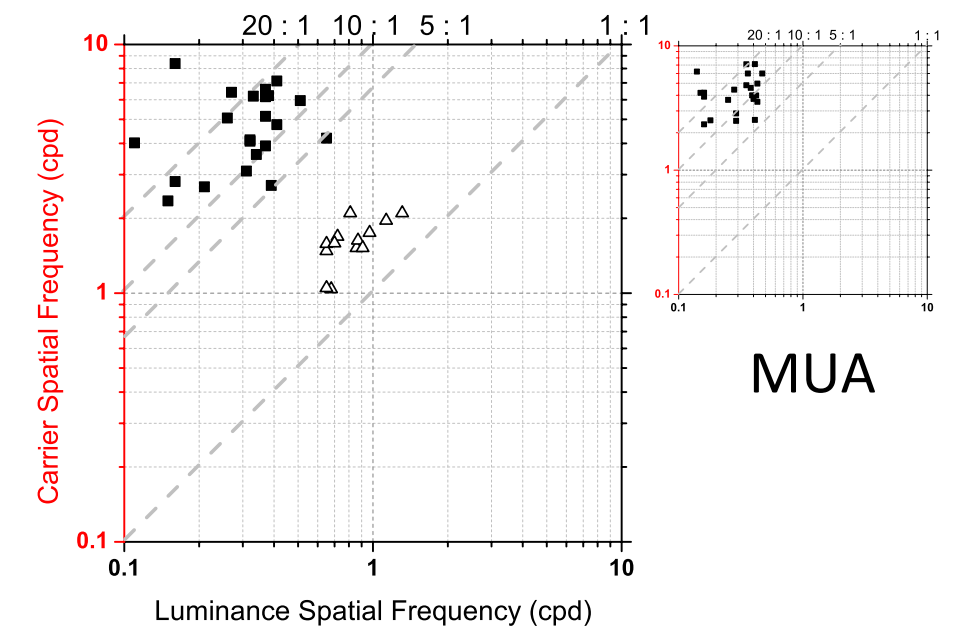
Neurons In One Penetration



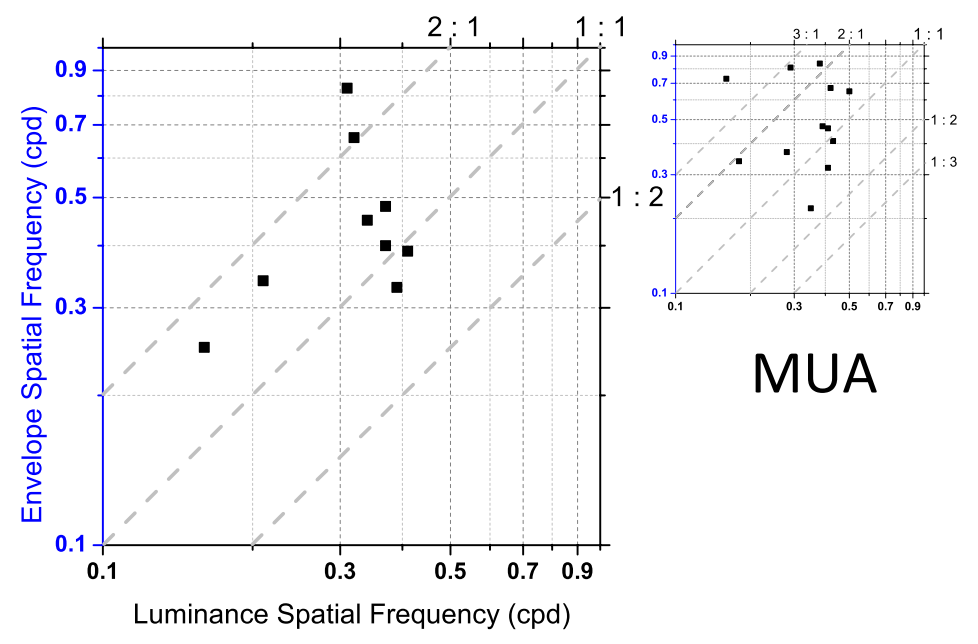
A particularly good penetration with many envelope responsive neurons recorded by tungsten electrode.

- V2 was identified by gray matter (V1)-white matter-gray matter (V2) transition. Tuning properties changed significantly from V1 to V2.
- The receptive fields were at 6-12° eccentricity.
- Stimuli were confined to the neurons' classical receptive fields. There was no clear relationship between envelope responsivity and surround suppression.
- The optimal value of carrier spatial frequency and orientation varied with depth independently of luminance and envelope tuning.

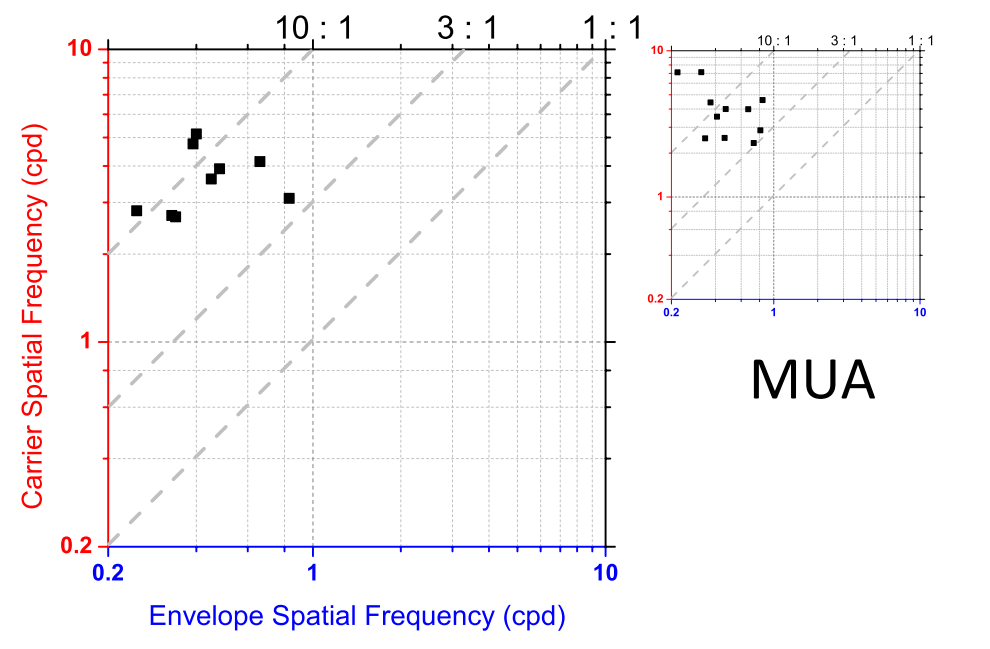
Spatial Frequency Tuning Properties



Scatterplot of optimal carrier spatial frequency against the optimal luminance spatial frequency.



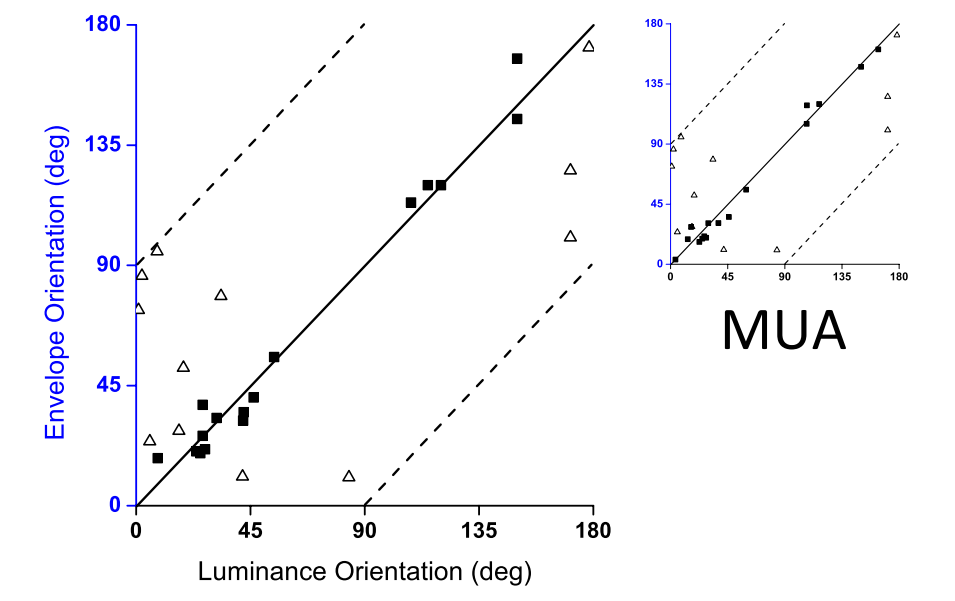
Scatterplot of optimal envelope spatial frequency against optimal luminance spatial frequency.



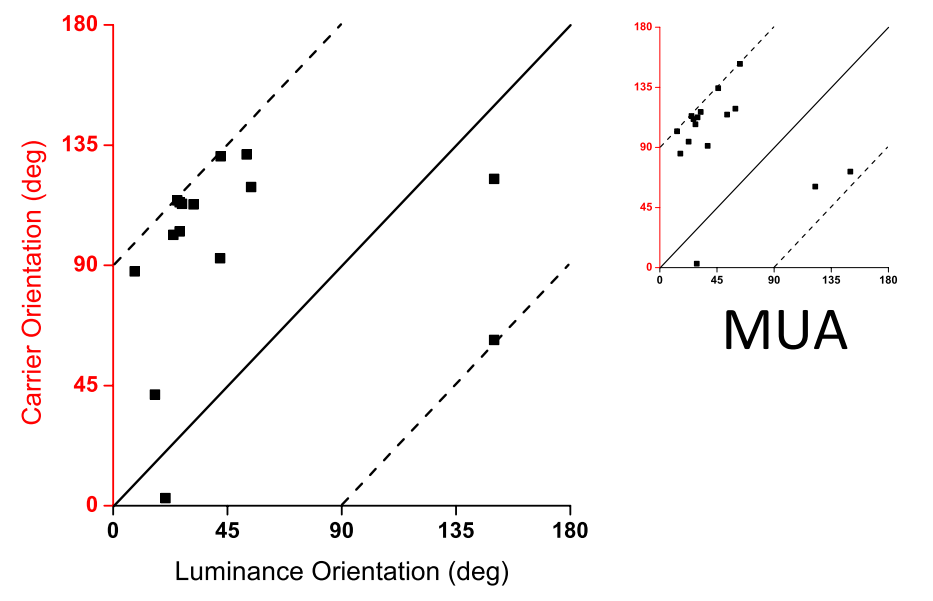
Scatterplot of optimal carrier spatial frequency against optimal envelope spatial frequency.

- 2nd-order envelope responsive neurons (filled squares) had a carrier-luminance ratio higher than 5:1.
- Some neurons (opened triangles) responded to CM's with a carrier-luminance ratio around 2:1, probably due to surround modulation (Tanaka & Ohzawa, 2009; Hallum & Movshon, 2011).
- Most envelope-responsive neurons had higher optimal spatial frequency for envelopes than luminance.

Orientation Tuning Properties



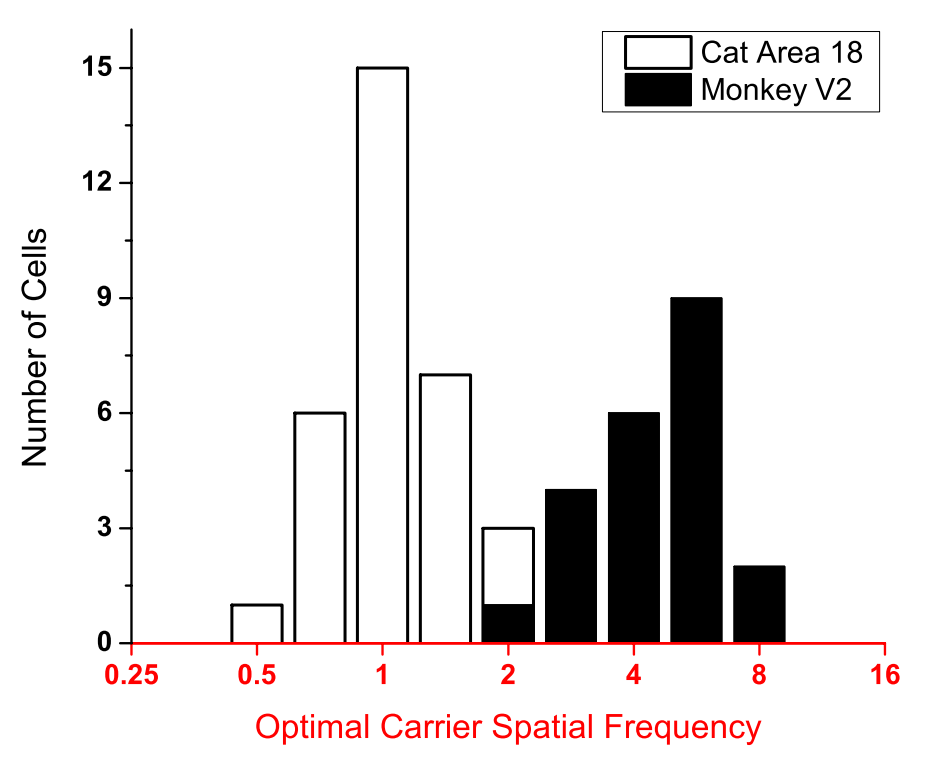
Scatterplot of optimal envelope orientation against optimal luminance orientation.



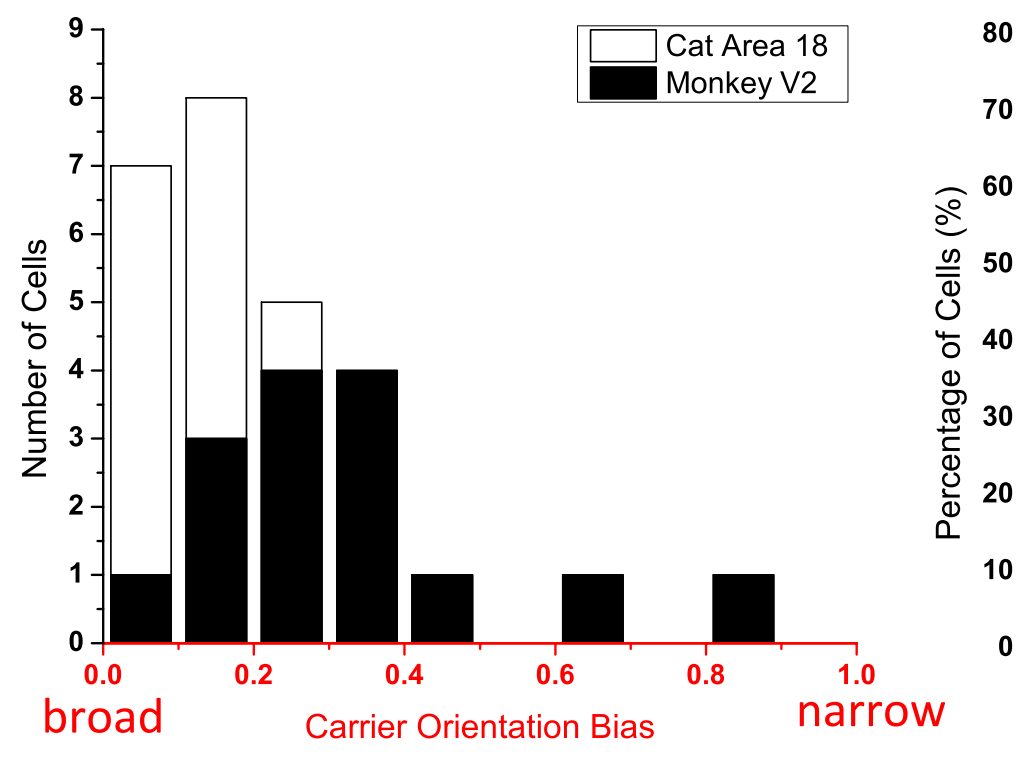
Scatterplot of optimal carrier orientation against optimal luminance orientation.

- Envelope responsive neurons with high carrier-luminance ratio (> 5:1, filled squares) cluster around the equality line (**form-cue invariance**); low ratio neurons (opened triangles) are randomly distributed.
- There is no fixed relationship between the optimal carrier and luminance (envelope) orientations.

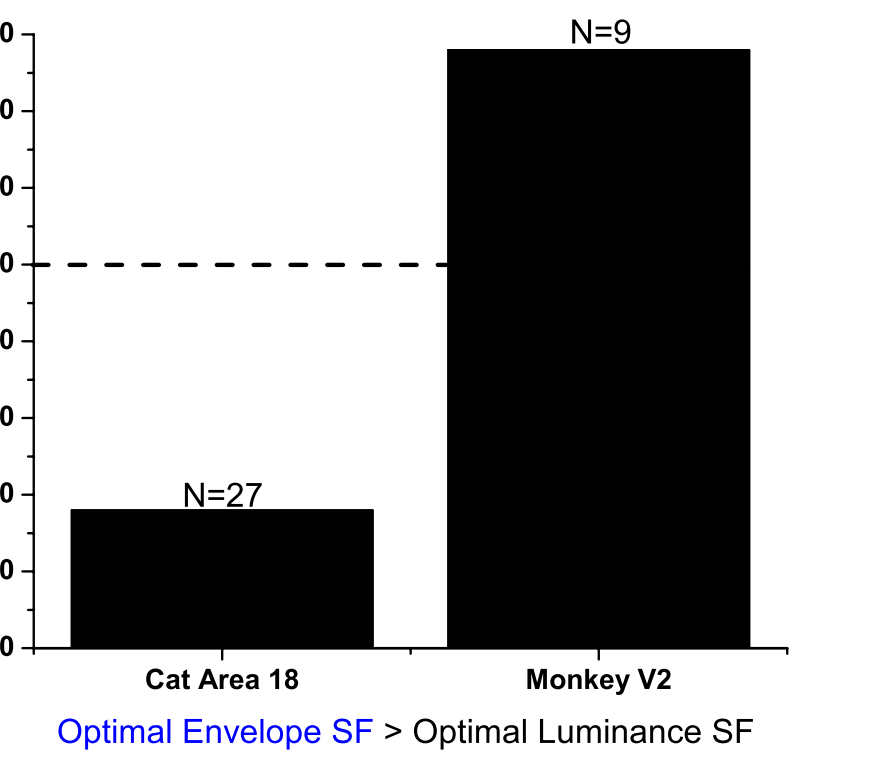
Monkey vs. Cat



The optimal carrier spatial frequencies of monkey V2 are significantly higher than those for cat area 18 ($p < 0.001$, Mann-Whitney U test).



The carrier orientation tuning bandwidth of monkey V2 neurons is significantly narrower than in cat area 18 ($p < 0.001$, Mann-Whitney U test).



In monkey V2 neurons, the optimal spatial frequency is usually higher for envelopes than for luminance, but in cat area 18 it is usually lower.

cat data: Mareschal & Baker (1999)

Conclusion

- These results show that many macaque V2 neurons are selectively responsive to 2nd-order stimuli in a manner that cannot be explained by quasi-linear receptive fields, but which implies a specialized nonlinear mechanism.
- Unlike responses shaped by surround modulation, these neurons exhibit form-cue invariant orientation selectivity and also exhibit a high carrier-luminance ratio (> 5:1).
- Form-cue invariant 2nd-order contrast envelope responsive neurons could provide a functionally useful, explicit representation of segmentation boundaries.

Reference:
Mareschal I & Baker CL (1999), *Visual Neuroscience* 16:527-540.
Tanaka H and Ohzawa I (2009), *J Neurophysiol* 101:1444-1462.
Landy MS and Graham N (2004), *The Visual Neuroscience,* Chapter 73:1106-1118
Hallum LE, Movshon JA (2011), SfN Abstr 694.19/NN14

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