Second-order neuronal responses to contrast modulation stimuli in primate visual cortex

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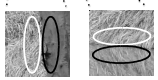
Introduction

Object boundaries in natural images often contain boundaries defined by differences in contrast as well as luminance.

zig-zag bridge near U.S.T.C. Guesthouse



Luminance modulation (LM) boundaries (left) can be detected by simple linear filters, but detection of contrast modulation (CM) boundaries (right) requires a more complex nonlinear mechanism.

Neuronal mechanisms encoding contrast modulation (CM) have been extensively studied in human psychophysics and cat area 17/18, but are poorly understood in non-human primates.

Methods

Neurophysiology

- macaque monkeys
- area V2
- anesthetized / paralyzed
- single neurons (extracellular)

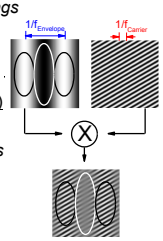
Visual stimuli

For each neuron, tuning curves were measured in the following order:

LM (luminance modulation)

- drifting sinewave gratings

- spatial frequency (SF)
- orientation (Ori)



CM (contrast modulation)

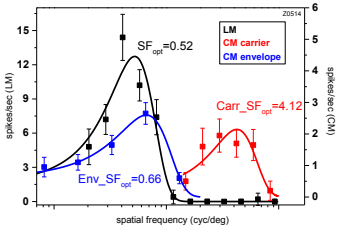
- drifting envelopes, stationary carriers

- carrier SF
- carrier Ori
- envelope Ori
- envelope SF

Tuned responses

About 1/3 of V2 neurons showed selective responses to CM stimuli. Here are results from one representative neuron:

Spatial frequency tuning



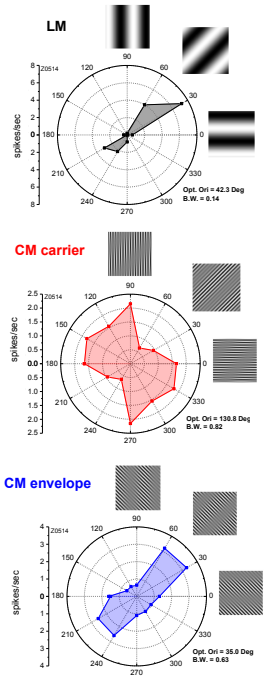
carrier SF response:
- outside LM passband
- bandpass tuned ~ 4 cpd
- ~ 6x optimal envelope SF

-> *not a luminance artifact*

envelope SF response:
- similar to LM response
- bandpass tuned ~ 0.7 cpd

-> *form-cue invariant*

Orientation tuning



carrier orientation response:
- bandpass tuned
- different from LM response

-> *not a luminance artifact*

envelope orientation response:
- bandpass tuned
- similar to LM response

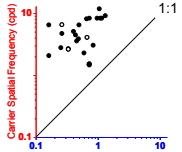
-> *form-cue invariant*

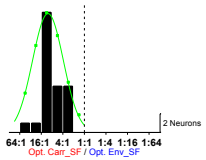
Different neurons are seelective for different carrier orientations and spatial frequencies -> not a luminance artifact

Carrrier / envelope SF ratios

Scatterplots are used to show the relationships between optimal values of tuning curves measured on many CM-responsive neurons:

Neurophysiology





optimal carrier SF:
- much higher than optimal envelope SF, from 2 to 41-fold
- carrrier / envelope SF ratios 2 to 41-fold
- median carrier /envelope SF ratio = 8.2

Human psychophysics

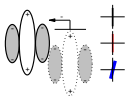
Several human psychophysics studies have demonstrated optimally effective high carrier / envelope SF ratios for second-order stimuli, e.g.:

Sutter et al, 1995	CM	3-4 octaves (8-16)
Dakin & Mareschal (2000)	CM	>= 10
Kingdom & Keeble (1996)	orientation modulation	~ 50
Meso & Hess (2010)	motion-modulation	~ 11

Neural mechanism

Surround suppression

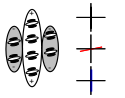
Surround suppression, a common property of V1 and V2 neurons, can give rise to CM responses that are selective to carrier and envelope parameters (Tanaka & Ohzawa, 2009; Hallum & Movshon, 2011). But these responses have:



- lack of form-cue invariance
- optimal carrier/envelope SF ~ 2

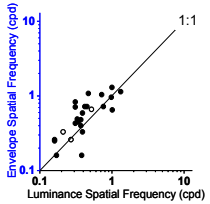
Nonlinear subunits

CM responses might instead be mediated by small nonlinear subunits of much larger receptive fields, with carrier tuning originating subcortically (Rosenberg & Issa, 2011; Crook et al, 2008). Such a mechanism could readily produce:

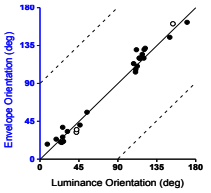


- form-cue invariance
- optimal carrier/envelope SF >> 2

Form-cue invariance



spatial frequency:
- similar optimal values of LM and CM-envelope spatial frequency
- median ratio = 1.3



orientation:
- similar optimal values of LM and CM-envelope orientation
- median difference ~ 0

-> *~ same SF / Ori tuning, regardless of whether boundary defined by luminance (LM) or by contrast (CM): "form-cue invariance" (Albright, 1992)*

Conclusions

CM-responsive neurons in primate V2:

- high optimal carrier/envelope SF ratios
- similar selectivity for boundaries defined by contrast or by luminance (form-cue invariance)
- distinct from CM responses mediated by surround suppression
- a strong candidate neural substrate for much of "second-order" processing in human psychophysics.

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