Building adequate models of V1 neurons

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Overview

- What are the major characteristics of V1 neurons ?
- How can they be modeled with small-scale filter-based methods?
- Example of an actual (python) implementation of a V1 neuron using these methods
- The model aims to be functional, not based on biophysical substrates (such as membrane potentials…)
- For a maths-based talk it will have few equations!

Primary Visual Cortex (V1)

Hubel and Wiesel concepts

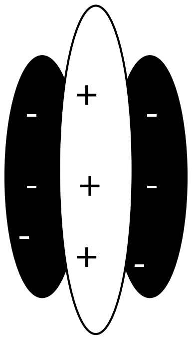
- simple cells
- complex cells
- hypercomplex cells

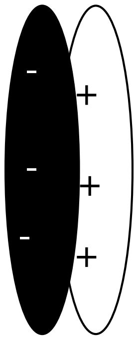
Modern version of Hubel and Wiesel ideas

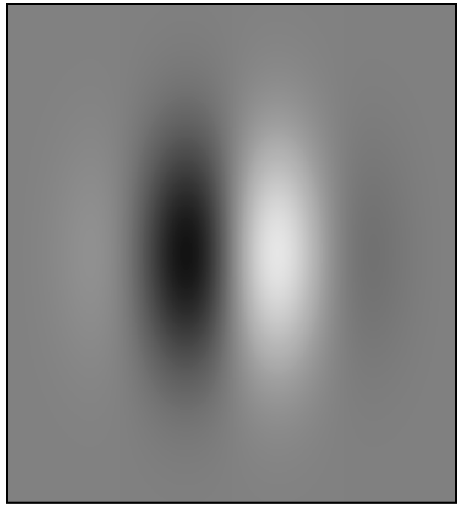
- simple cells
- complex cells
- both can show ‘surround suppression’
- both show saturating response functions

Simple Cells - Linear Filters

Hubel and Wiesel refer to excitatory and inhibitory fields of simple cells:



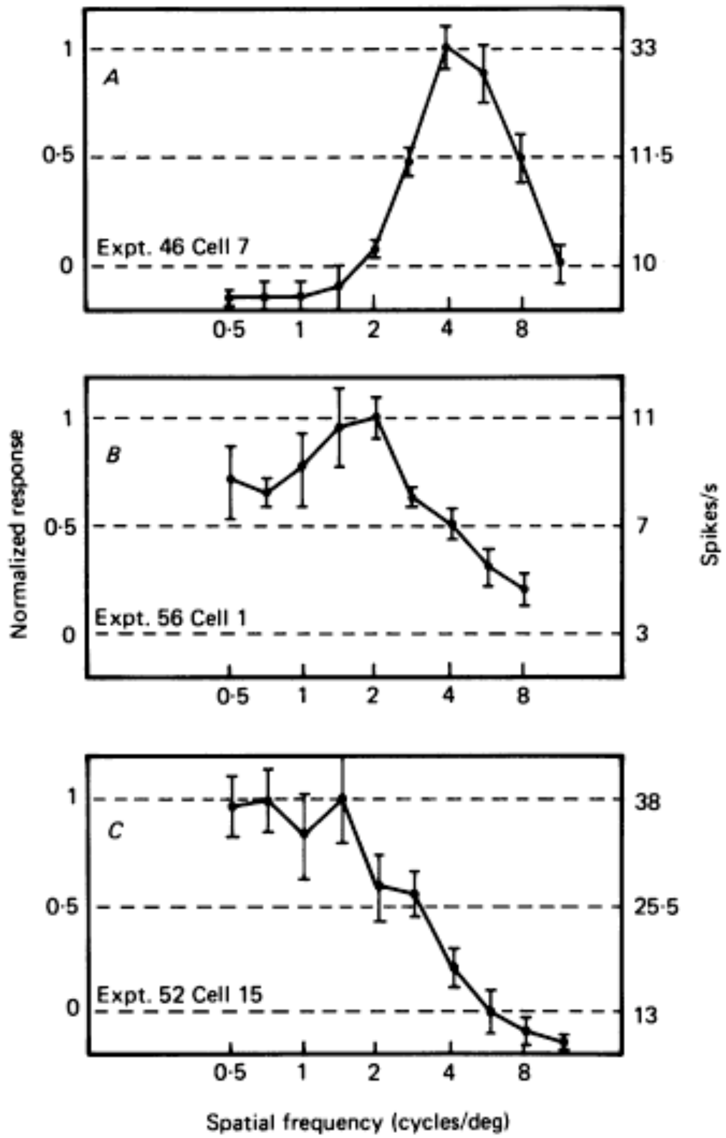


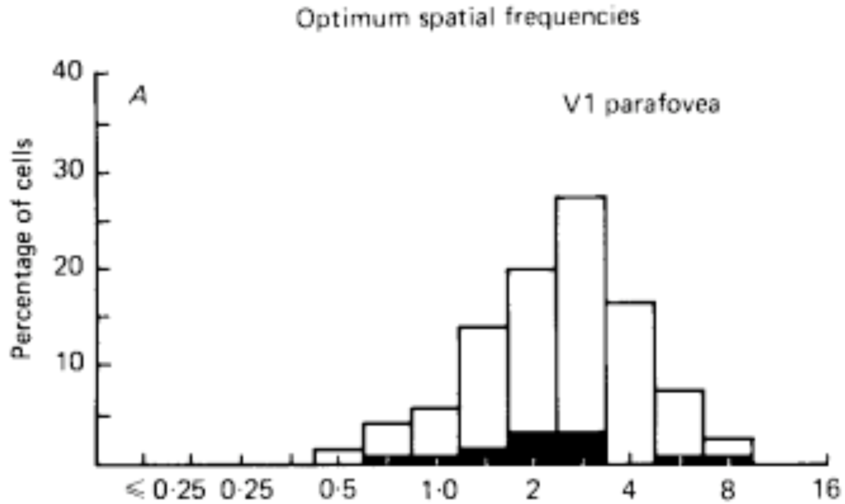


We can also characterise them using mathematical filters, such as Gabors

From these we can potentially deduce a neuron’s response to a given stimulus at any point in space/time

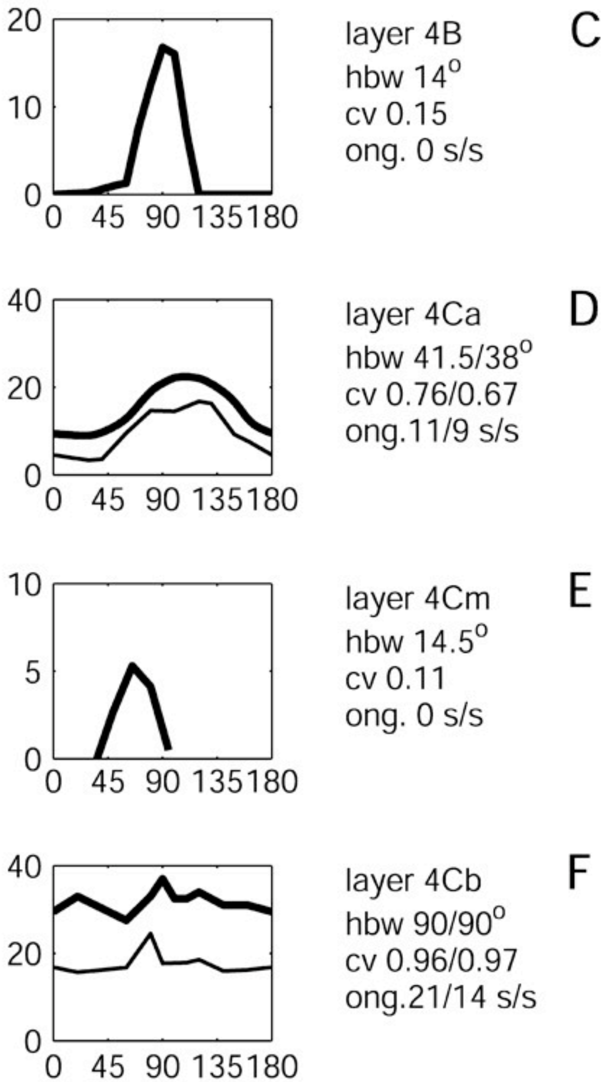
Simple Cells - SF Tuning

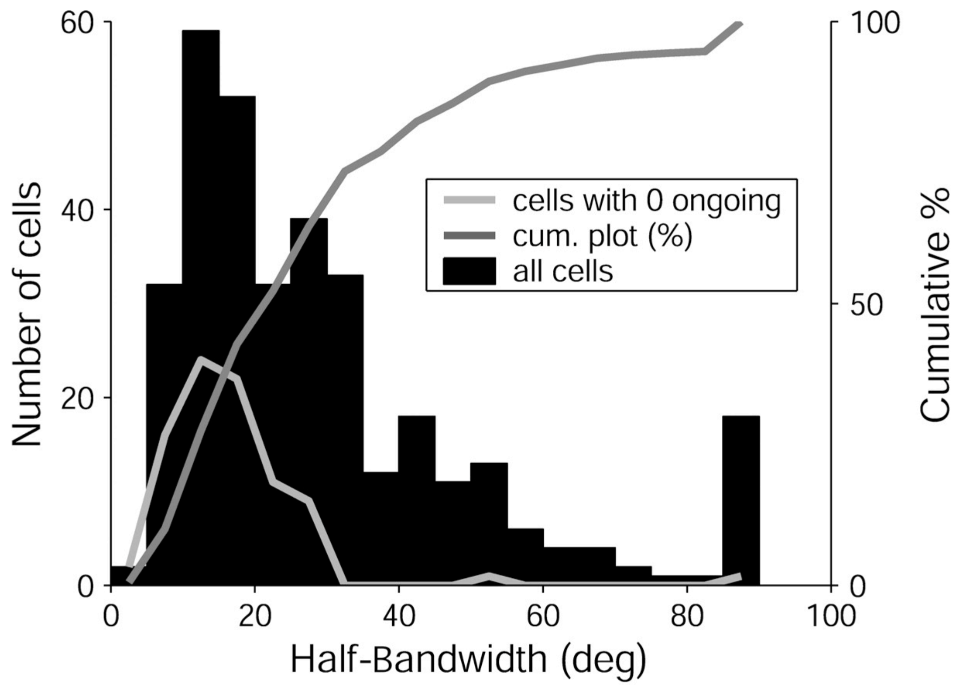




Foster, Gaska, Nagler and Pollen (1985) J Physiol. 365: 331–363.

Simple Cells - Orientation Tuning



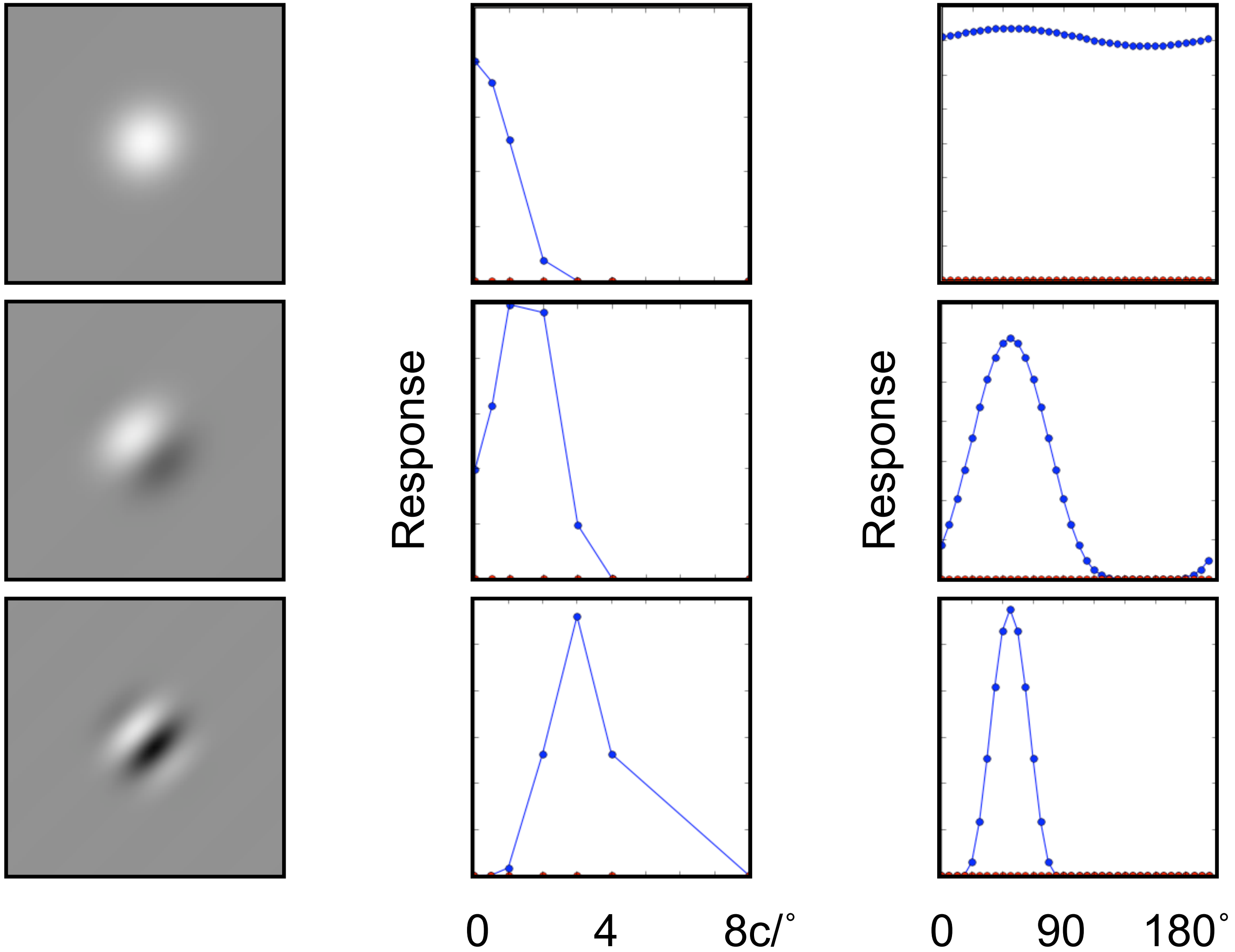


Gur M, Kagan I, Snodderly DM (2005). *Cerebral Cortex,* 15:1207--1221

Model Cells - Spatial Tuning

SF tuning falls out naturally from the Gabor filter…

…so does orientation tuning



Complex Cells

'Complex' cells can't be characterised by their response to local bright or dark patches (they don't have clearly defined 'on' and 'off' regions)

Hubel and Wiesel (1962; 1968) suggest they arise from a heirarchy, simple cells feed into complex cells

Usually characterised by F1/F0 ratio>1.0 (since Skottun, 1991)…

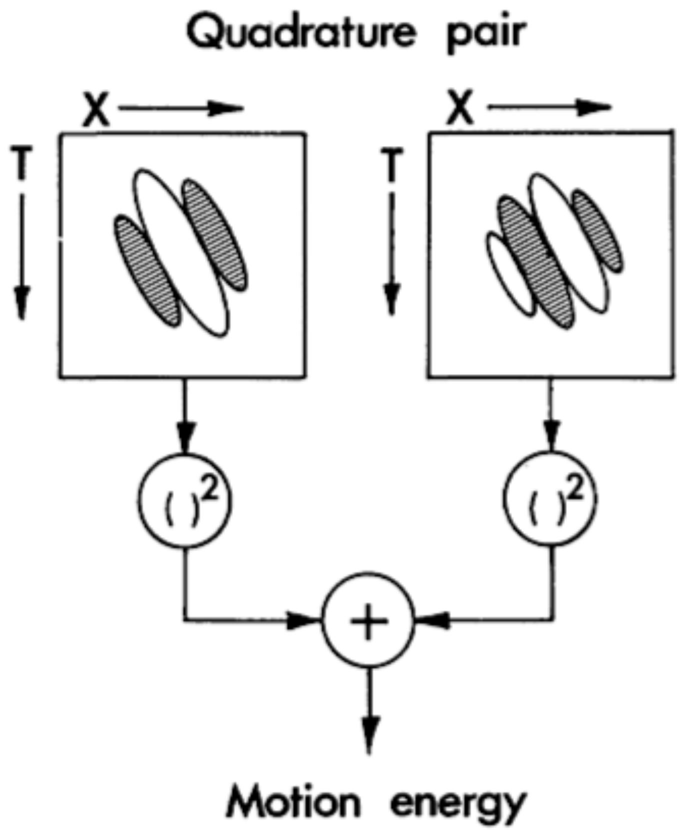
… but the bimodal distribution may not reflect a true dichotomy (Priebe, Mechler & Ferster, 2004)

Alternatively they may arise mutual excitation (Chance and Abbot, 1999)

Modelling Complex Cells

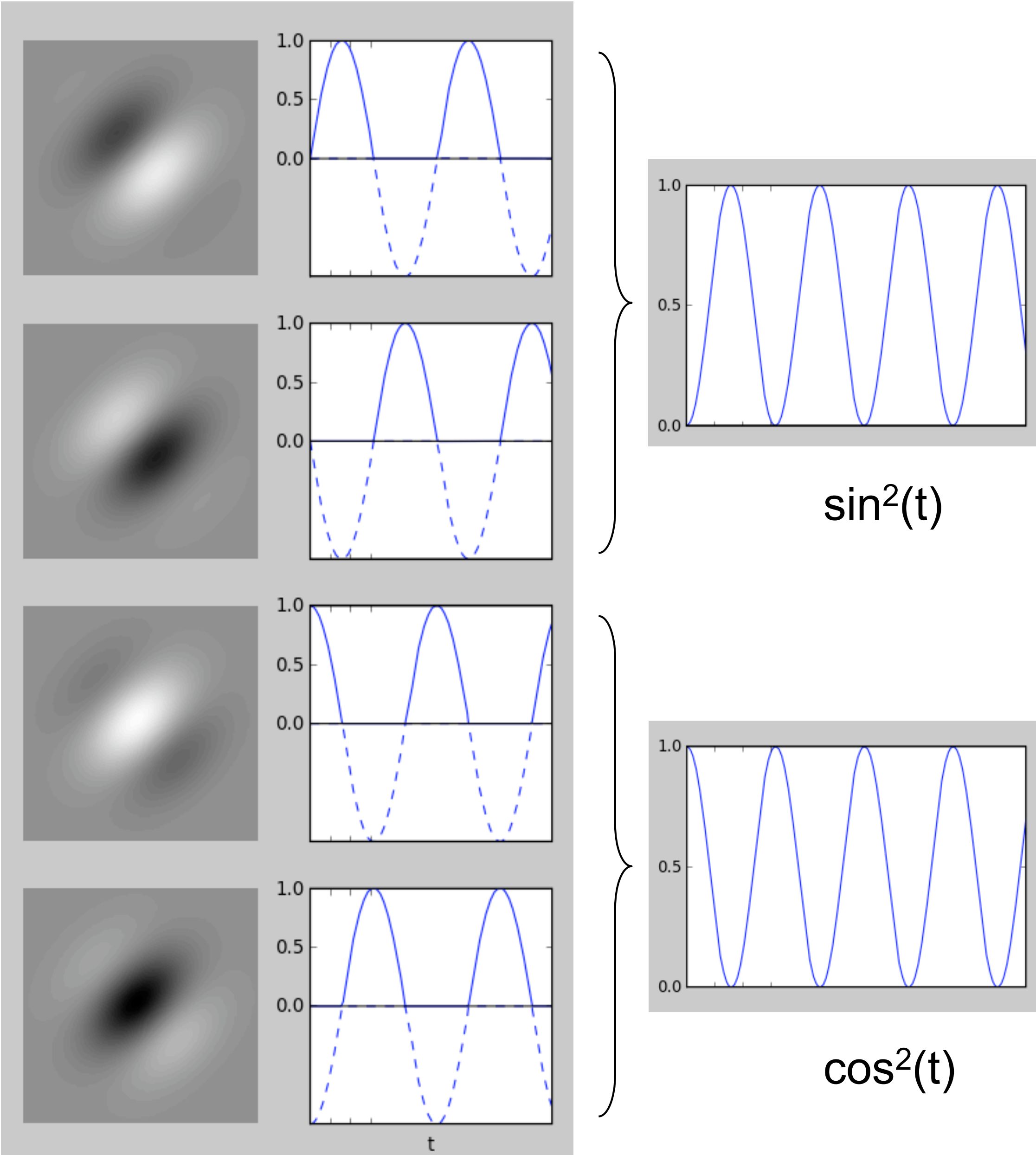
Biophysically complex cells (probably) result from the summing (or mutual excitation) of many cells that differ in phase

Mathematically perfect phase insensitivity can result from 4 (or 2 whose outputs are squared)



Adelsen & Bergen (1985), *JOSA* 2(2):284-299

Quadrature Pairs



4 model neurons with carrier phases separated by $\pi/2$

None can respond negatively

If each has an output nonlinearity that approaches squaring then the sum of the 4 responses

Then we can use the fact that

$$\sin^2(t) + \cos^2(t) = 1$$

Simple/Complex Dichotomy

In reality, some complex cells are more complex and some less

We need a parameter that allows cells to be *partially* complex

To do that we might calculate the 'simple' response (for any chosen phase) and its 'complex' response from its quadrature partner

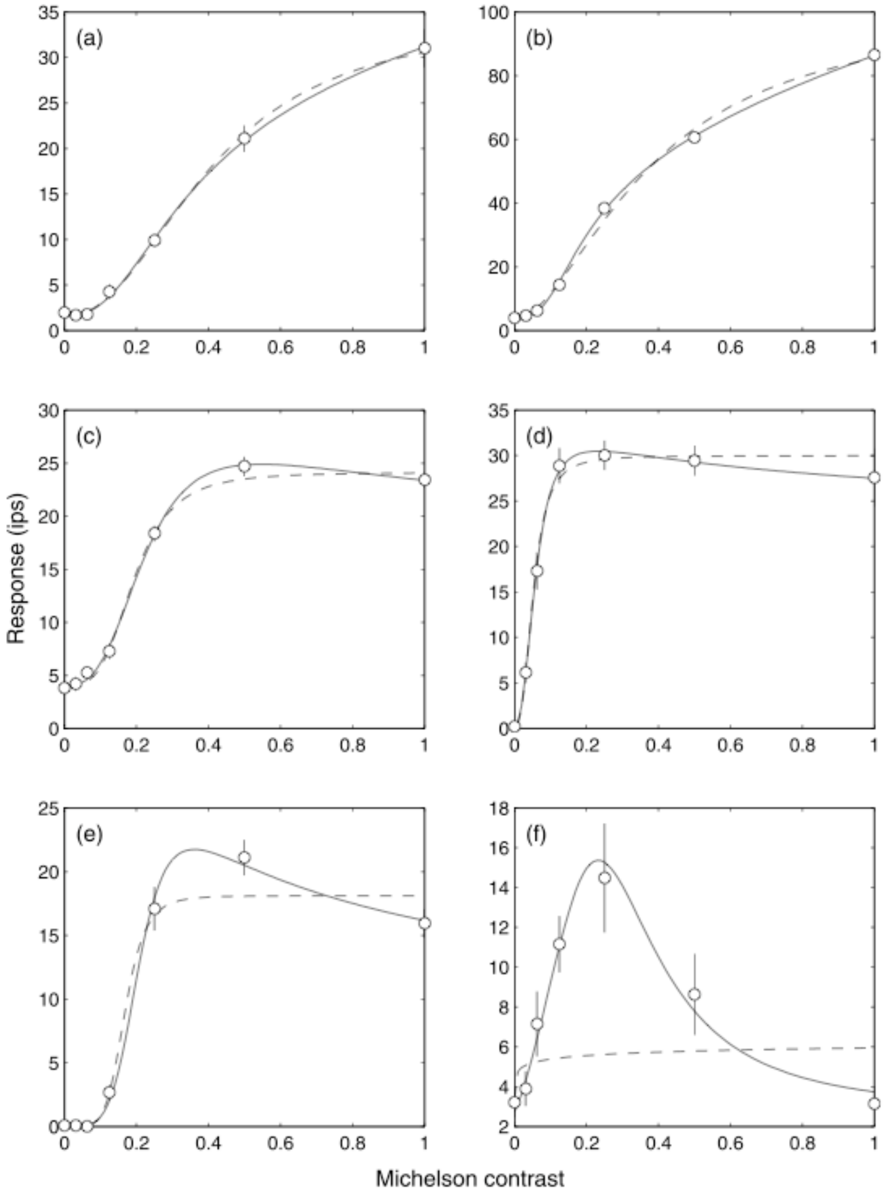
Then take a simple fraction of each as a function of *complexity*:

$$R = R_S(1 - C) + R_C(C)$$

where R_c*=complex resp,* R_s*=simple resp,* C*=complexity*

So that the cell has the same total response but varying phase sensitivity

Simple Cells – Contrast Normalisation



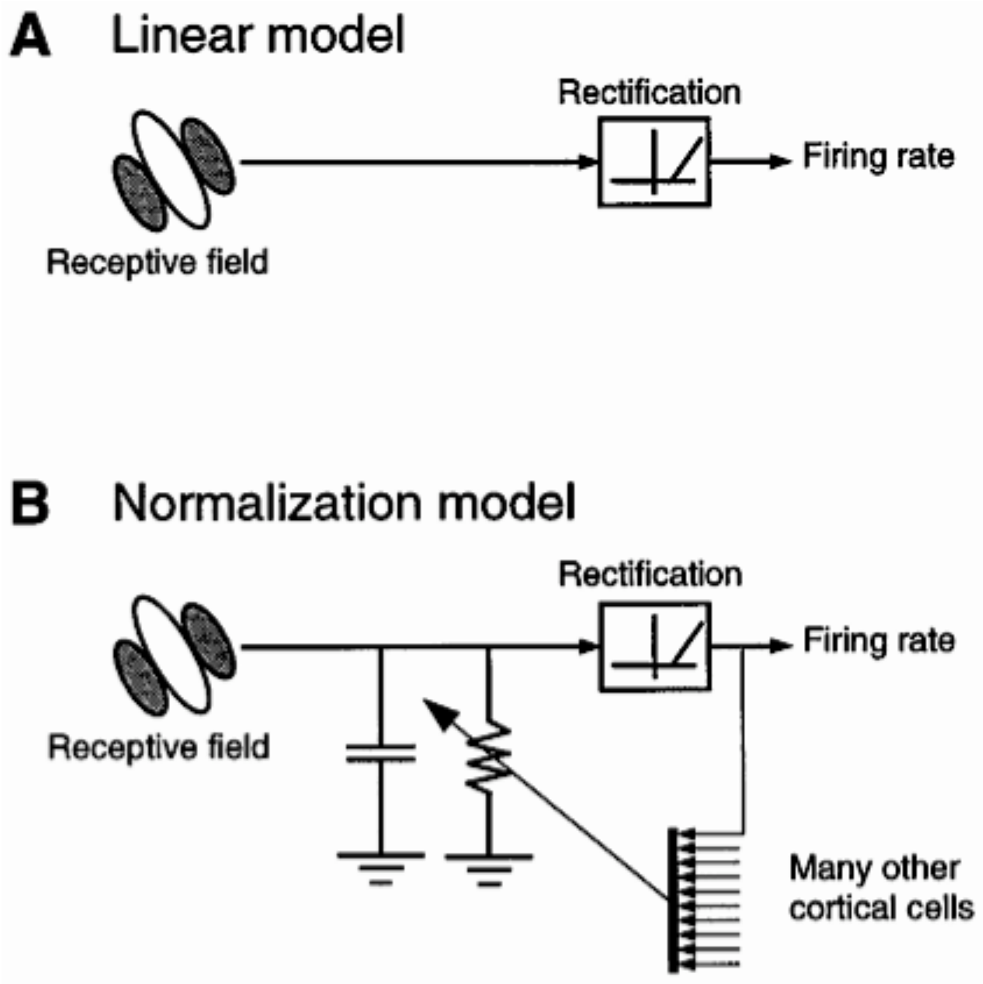
So far our cells will increase response linearly with contrast

V1 cells rarely do;

- most saturate
- some *super*saturate

Peirce (2007) *Journal of Vision,* 7(6):13, 1-10

Response Normalisation



Carandini, Heeger, Movshon (1997) *Journal of Neuroscience*, 17(21): 8621–8644

Modelling Contrast Saturation

We need to quantify the response of a normalisation pool

Could use the sum of responses from a large bank of cells that differ in tuning

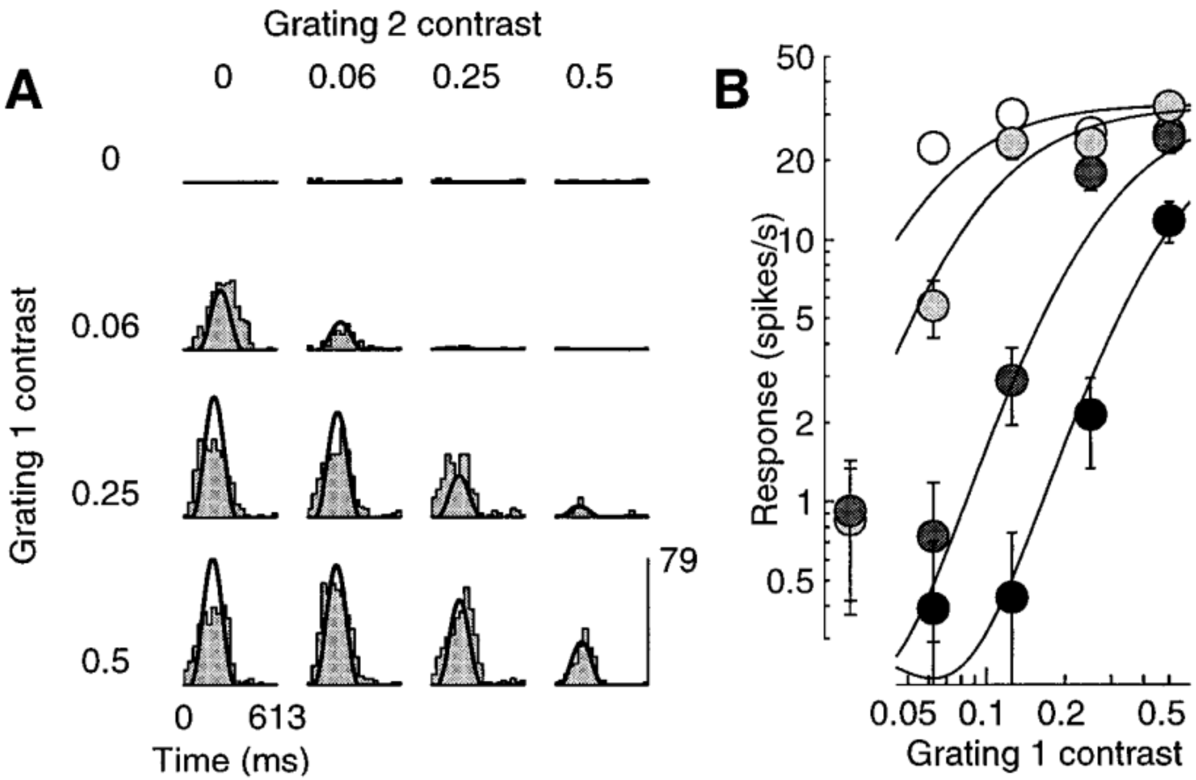
Or we could simulate it by finding the local contrast energy **in our receptive field** instead:

- take the envelope of our filter
- apply it directly to the stimulus as a mask
- take the root-mean-square contrast (the standard deviation) of the result

This assumes a perfectly flat (untuned) normalisation pool, which probably isn't realistic, but does work

Cross-orientation Suppression

Neurons in V1 also typically *reduce* their response when stimuli are placed on their receptive fields at a non-preferred orientation/SF. This is also simulated neatly by the contrast normalisation pool



Carandini, Heeger, Movshon (1997) *Journal of Neurosci*, 17(21): 8621–8644

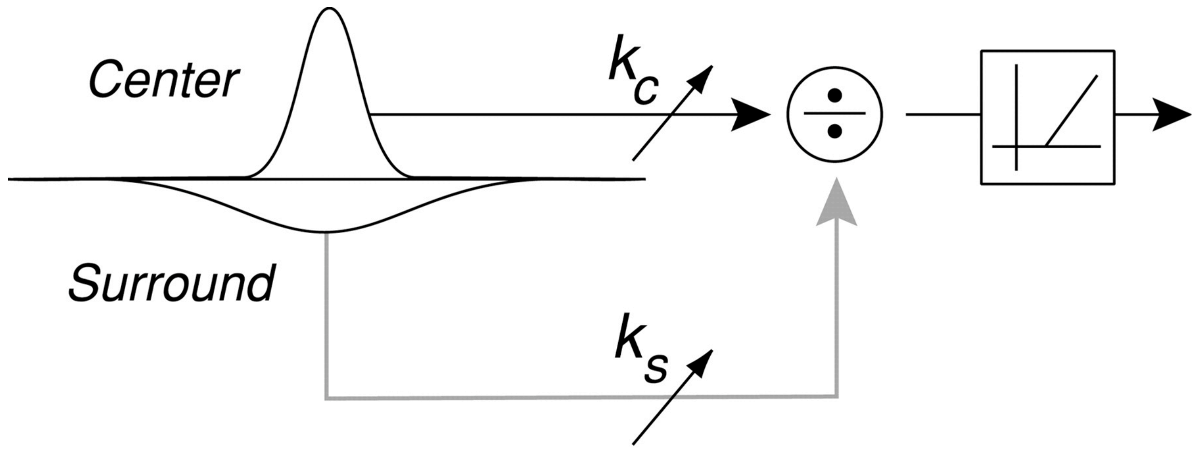
Surround Suppression

Initially termed “hyper-complex cells”, then “end-stopped cells”

Surround suppression occurs in varying degrees for most cells, regardless of simple/complex nature

Unlike contrast normalisation the pool has similar tuning to the cell’s classical receptive field (CRF), but with slightly lower preferred SF

Usually characterised as difference or ratio of Gaussians (DoG or RoG)

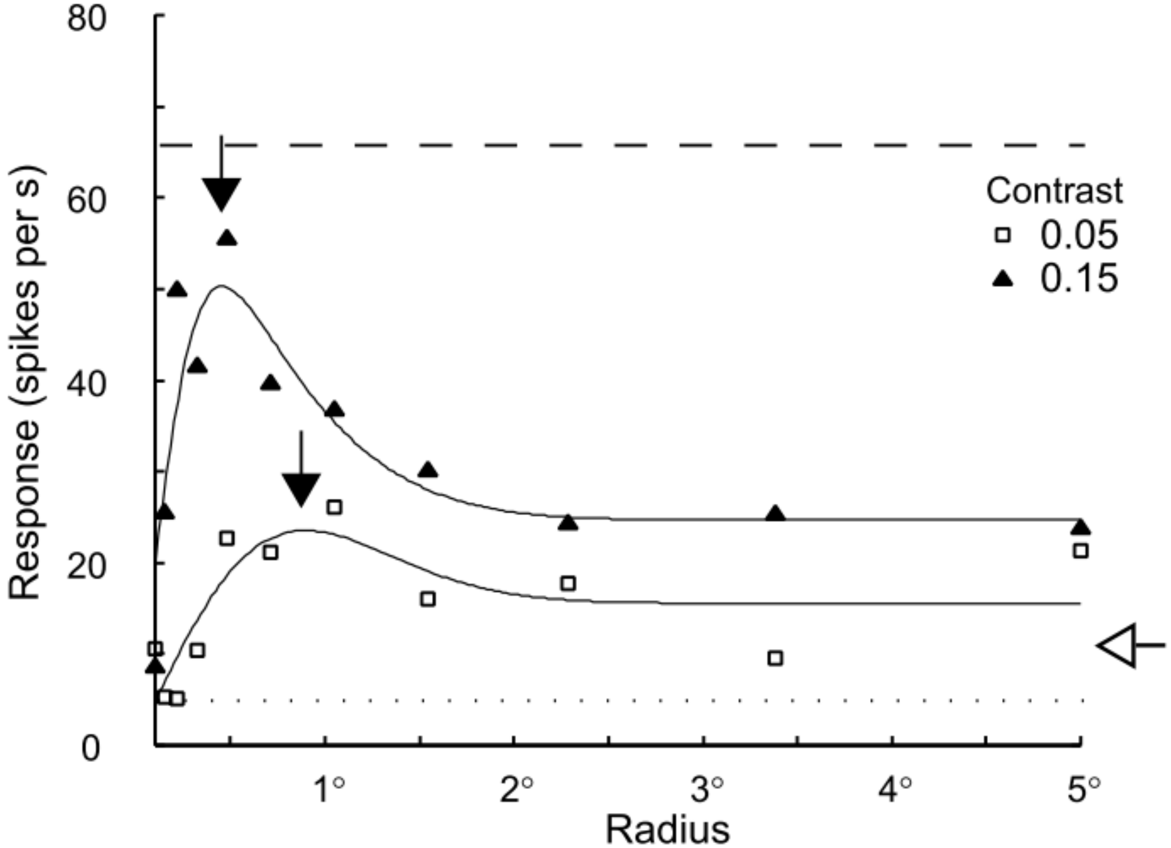


Surround Suppression

Size tuning is also dependent on stimulus contrast

Sceniak *et al* (Nature, 1999) suggest that the cell *changes* its summation fields according to contrast

Cavanaugh, Bair & Movshon (J. Neurophys, 2002) model the same effects with static filters



A model to play with…

Download a python library (for the next few weeks) from
http://www.peirce.org.uk/V1neurons.zip

Includes a model that
- implements a pair of filters for the CRF (‘primary’ and ‘quadrature’ filter)
- normalises by an ‘untuned’ pool (RMS contrast within the same region as the CRF)
- normalises by a ‘tuned’ pool (an extended region with similar tuning but lower preferred SF)

8 parameters determine the major properties of the model cell from these filters/normalisation pools (e.g. preferred orientation, complexity, size, etc…)

Summary

The model described here simulates the basic response characteristics of V1 neurons in terms of;

- basic spatial properties
- a continuum of phase sensitivity (simple/complex)
- their size tuning (surround suppression)
- their contrast response functions
- cross-orientation suppression

What are we not accounting for here?

- spike-generation mechanisms
- temporal dynamics (short and long term)
- the biological underpinnings of the responses
- colour tuning
- binocular interactions