A New View of Spatial Processing in V1

Just what we really need: yet another
basis set

Computational Neuroscience: Vision

Cold Spring Harbor, June 2006

Motivation and Background

- V1 neurons as linear filters: an admitted caricature
- V1 neurons are nonlinear: the apparent RF map depends on spatial context (basis set)
- Analytic stimuli (spots, bars, gratings) vs. natural stimuli
  - Analytic stimuli fail to predict responses to natural scenes
  - What is special (if anything) about natural scenes?
- Typical analytic stimuli
  - Spots and bars: one position, uniform in spatial frequency
  - Sine gratings: uniform in space, one spatial frequency
- But “real features” are typically local (neither pointlike nor uniform) in space and spatial frequency
- Let’s use analytically convenient stimuli that are local in space and spatial frequency

Joint Localization in Space and Spatial Frequency

- Rationale as a design for V1 receptive fields
  - Analysis at one location
  - Analysis at one spatial scale
- Quantum-mechanical analogy
  - Spread in space or spatial frequency measured as variance
  - Heisenberg principle limits joint localization
- Gabor functions minimize joint spread in space and spatial frequency
- Gabor functions are a reasonable approximation for sensitivity profiles of V1 receptive fields

Traditional View in More Detail

(one spatial dimension)

Marcelja (1980), Daugman (1985)

Spatial spread Δx of a sensitivity profile $f(x)$:

Find the centroid x_0 of $f(x)$.

Spread in x-direction, Δx: $(\Delta x)^2 = \int (x - x_0)^2 |f(x)|^2 dx$

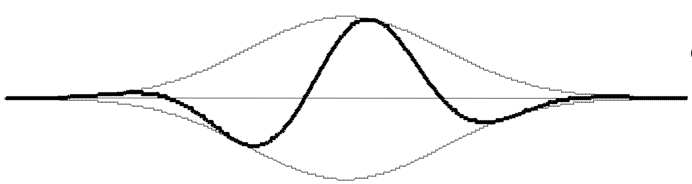
Spatial frequency spread $\Delta\omega_x$ of $f(x)$:

Determined analogously from the Fourier transform $\tilde{f}(\omega_x)$ of $f(x)$.

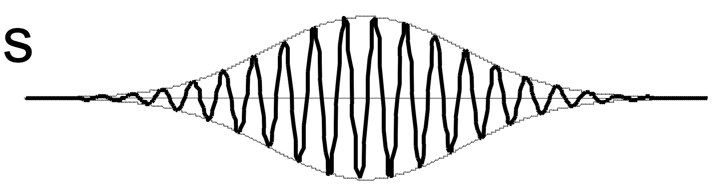
The Gabor functions minimize the product $\Delta x \, \Delta\omega_x$.

Traditional View: Concerns

- Relies on complex nature of *f*
  - the real and imaginary parts together constitute an optimum, but not separately
- Only | *f* | matters, so carrier frequency is irrelevant



as optimal as



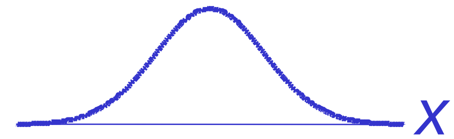
- What to do after V1?

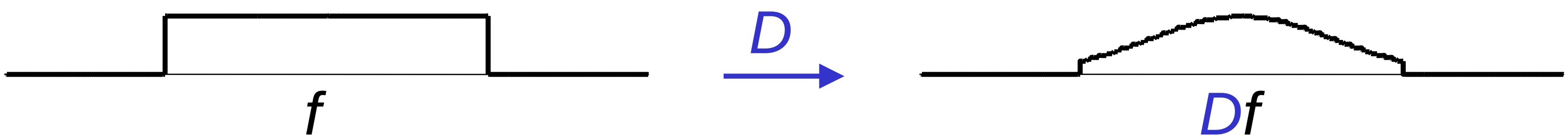
Alternative View

- Confinement in space: no change after windowing in space
- Confinement in spatial frequency: no change after windowing in spatial frequency
- Seek functions *f* that are (nearly) preserved after windowing in space and spatial frequency

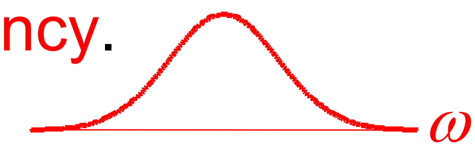
Alternative View in More Detail

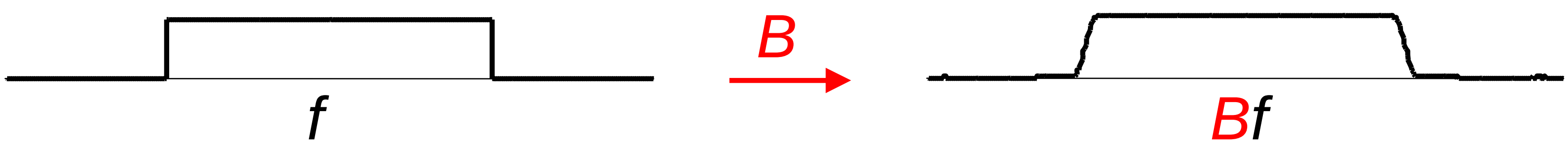
The linear operator *D* windows *f* in space.
D multiplies $f(x)$ by a windowing function $D(x)$.



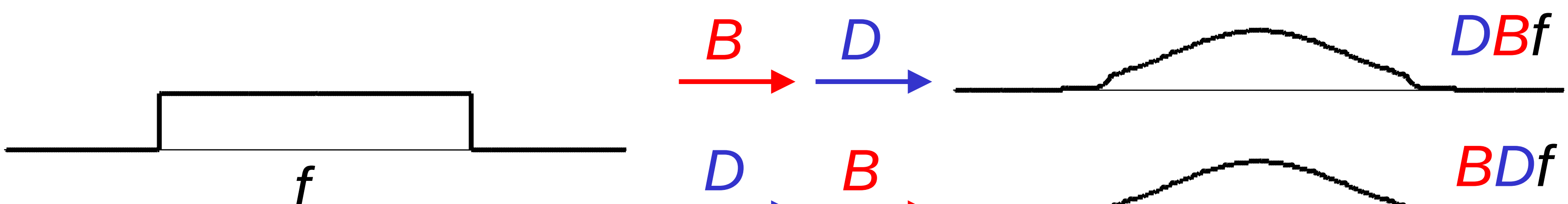


The linear operator *B* windows *f* in spatial frequency.
B multiplies $\tilde{f}(\omega)$ by a windowing function $B(\omega)$.





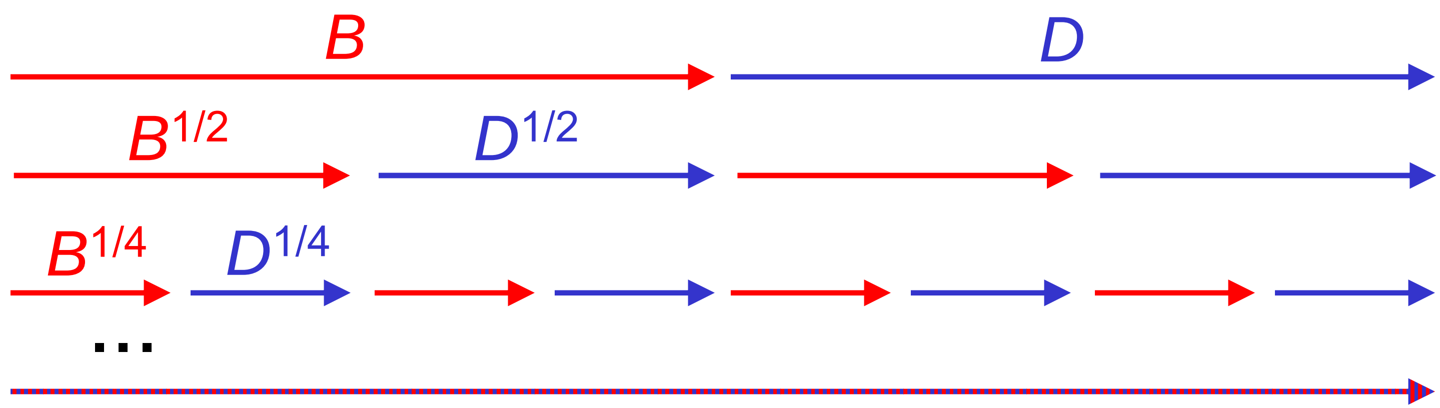
We seek functions *f* for which successive application of *D* and *B* leaves *f* (nearly) unchanged.



Alternative View: Concerns

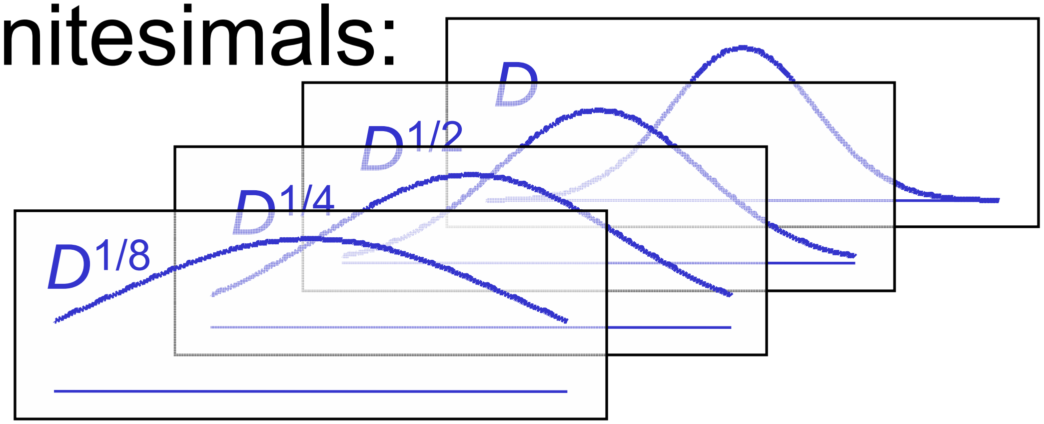
- Apply *BD* or *DB*?
- What shape to choose for *D* and *B*?

Order of application:



With infinitesimal *B*'s and *D*'s, order of application doesn't matter.

Infinitesimals:



Can create infinitesimals for any non-negative window!

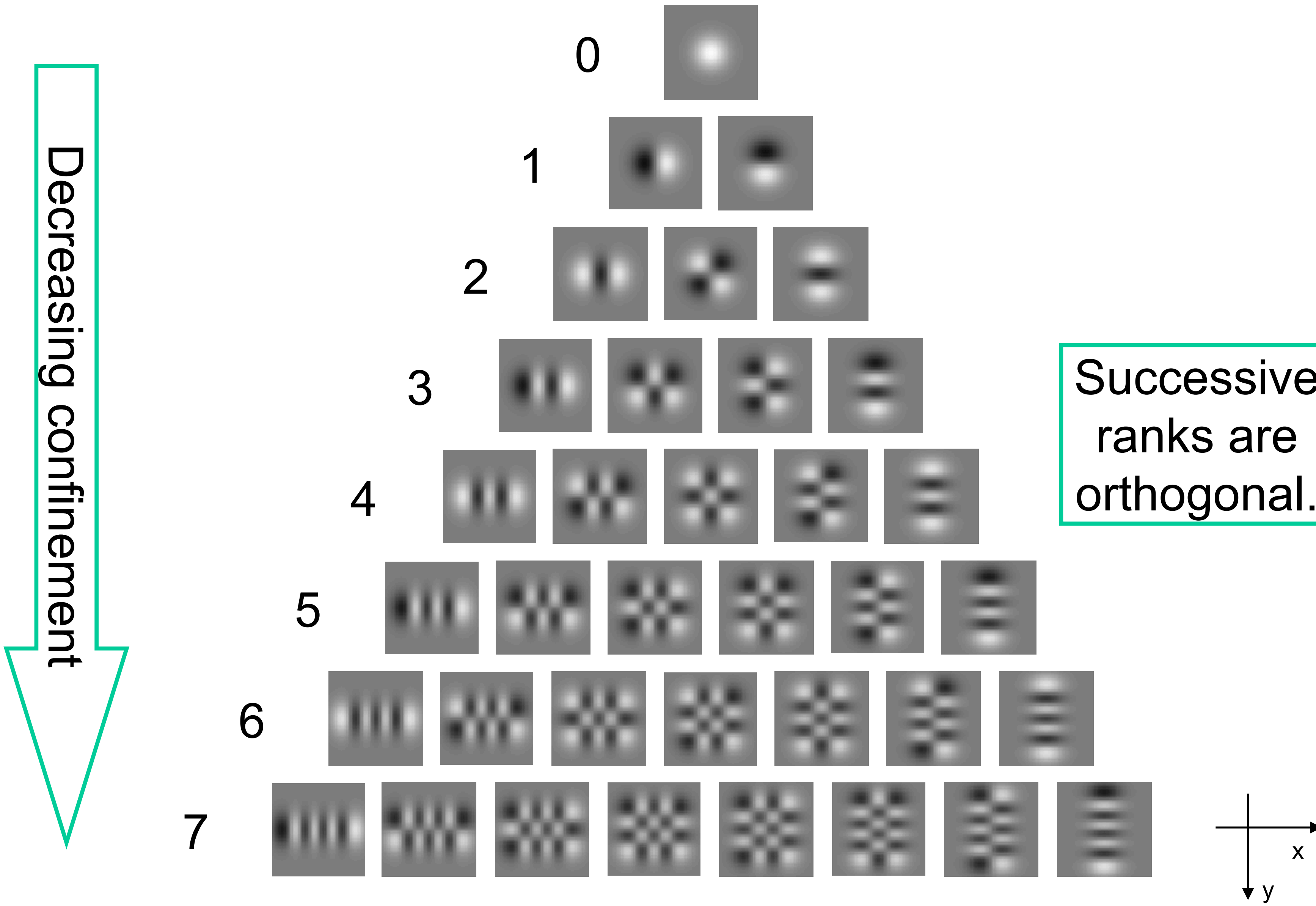
Amazing Analytic Result

- Optimal functions are asymptotically * independent of
  - Shape of windows
  - Order of application of windows
- This asymptotic limit has a simple closed form: the two-dimensional Hermite functions

Asymptotic: in limit of large* (space)(bandwidth) product

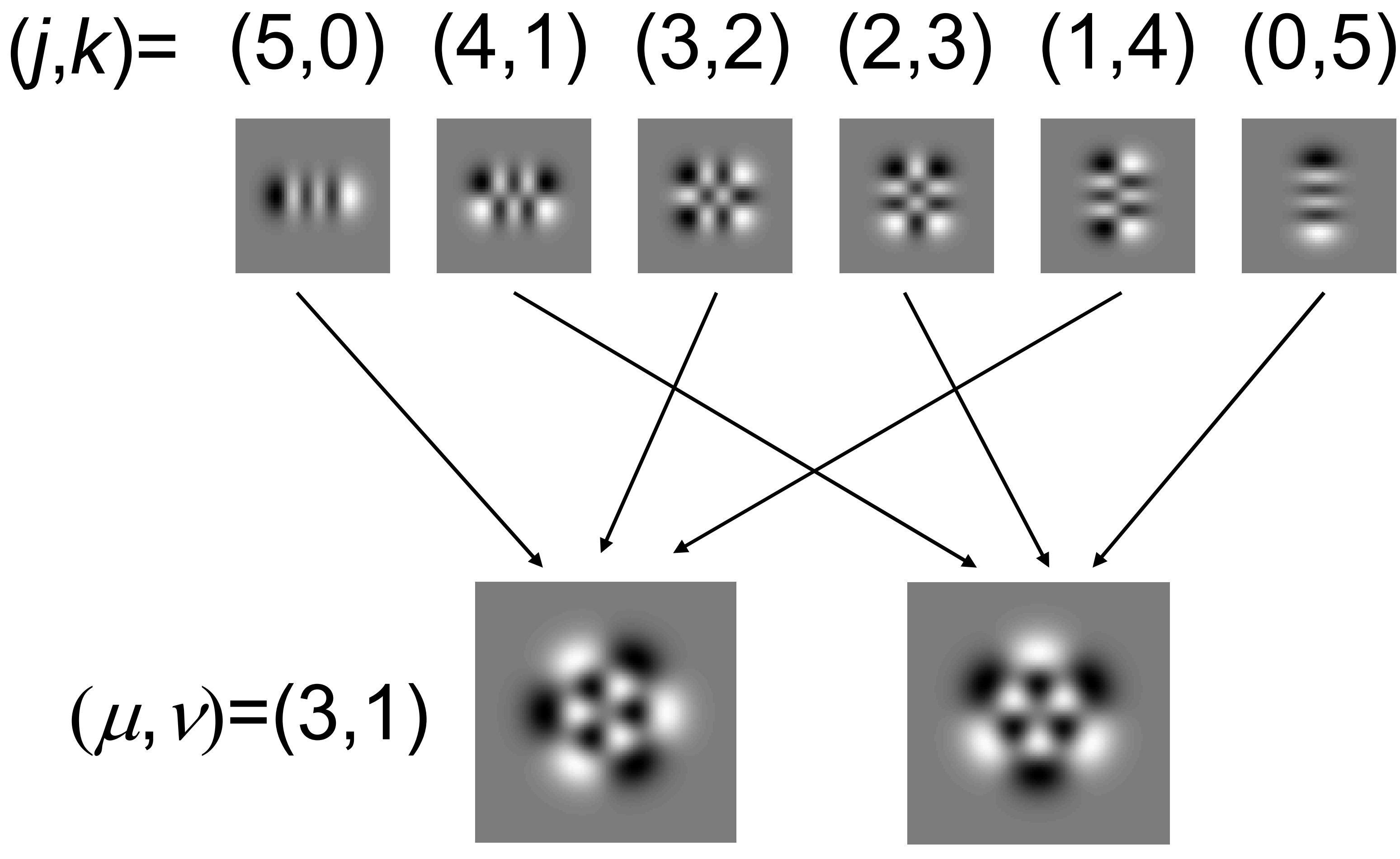
*Large: two cycles per spatial aperture suffice ($4\pi >> 1$)

Two-Dimensional Hermite Functions

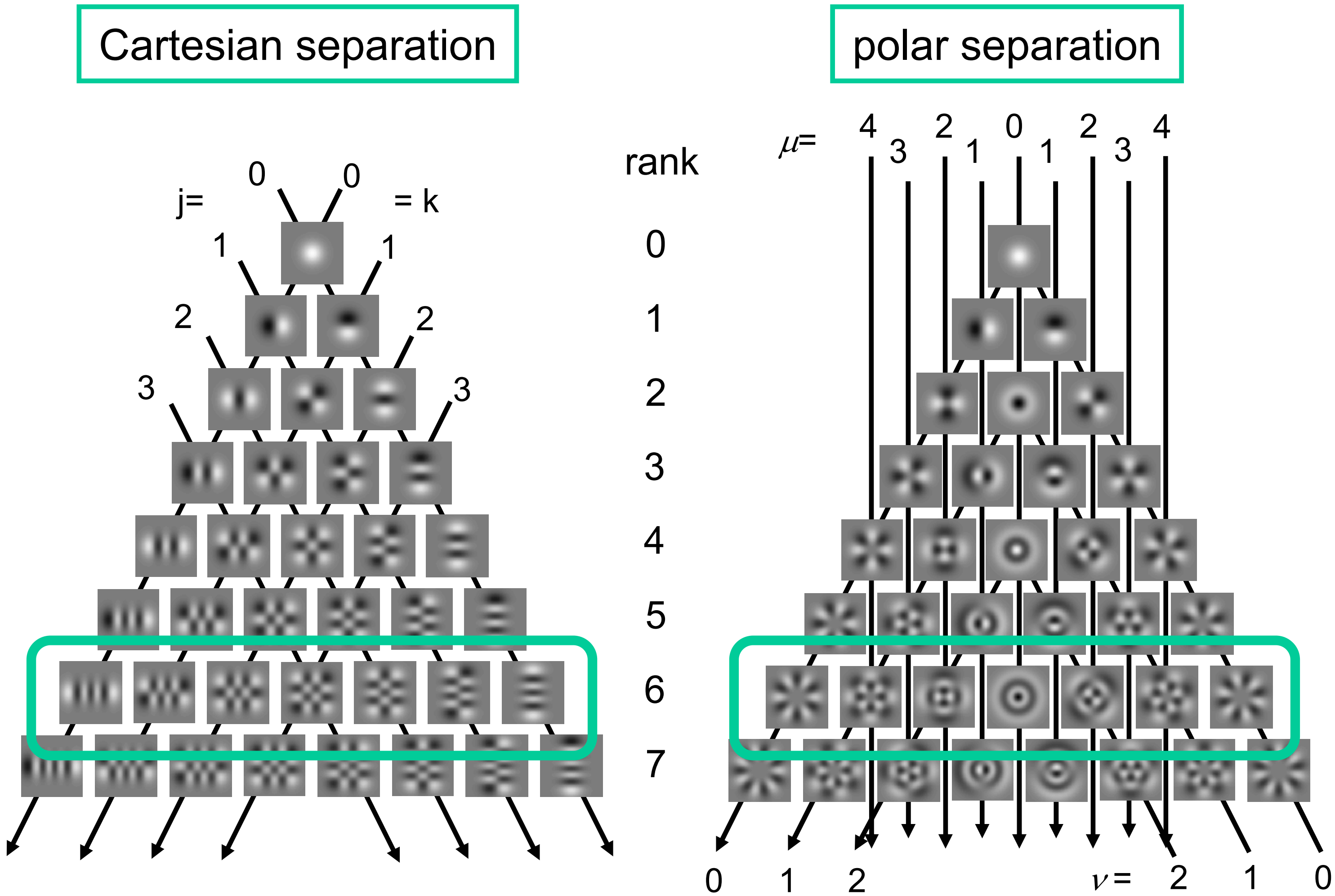


Successive ranks are orthogonal.

Polar Symmetry from Cartesian Components



Two-Dimensional Hermite Functions

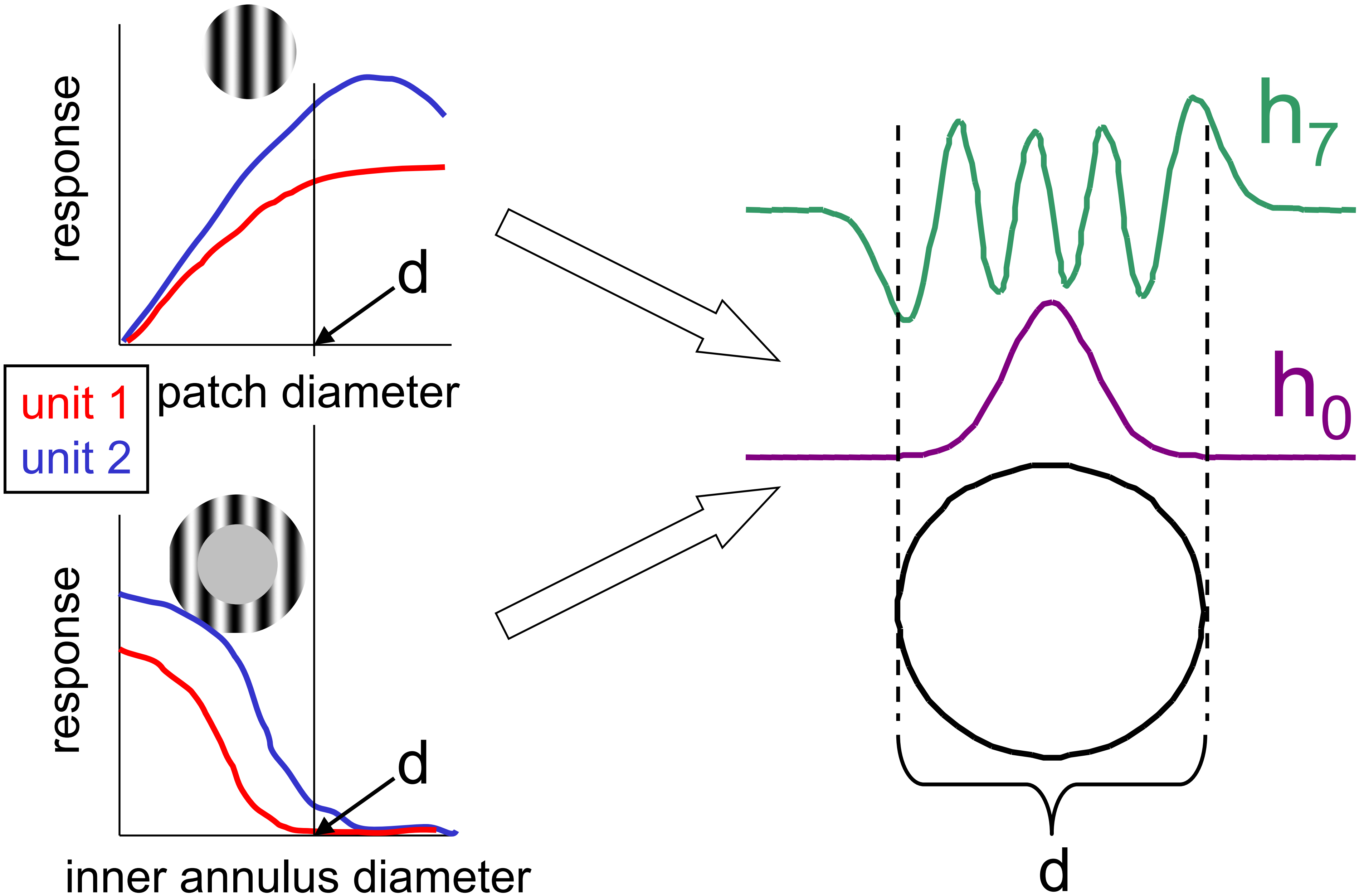


Within each rank, either set of functions can be synthesized from a linear combination of the other set.

Properties of the Two-Dimensional Hermite Functions

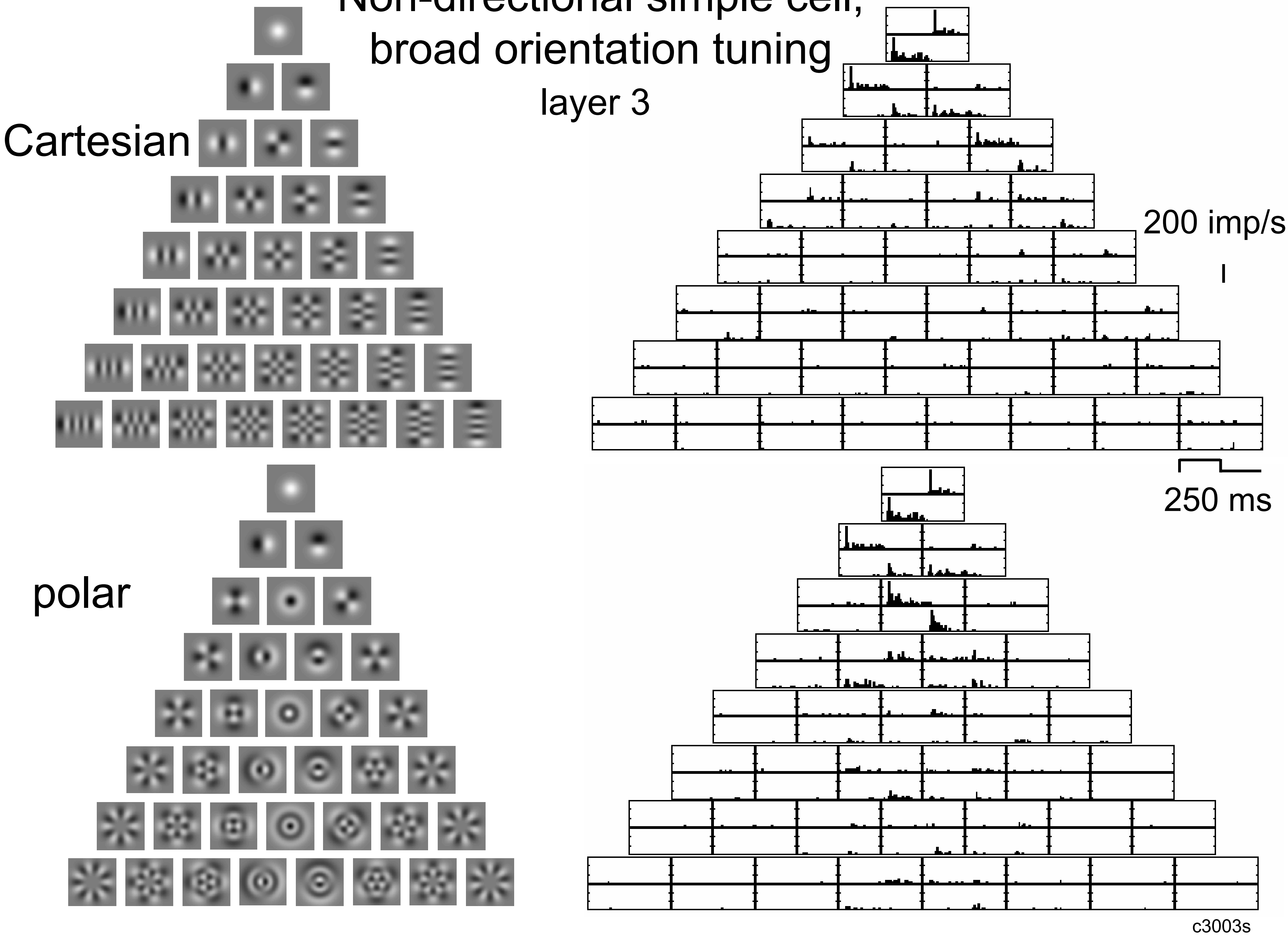
- Complete orthonormal sets
- Cartesian and polar separations have identical spans
- Small shifts add some of next rank
- Rotations mix within rank
- Each function is equal to its own Fourier transform
- Allow for efficient local synthesis

Stimulus Alignment

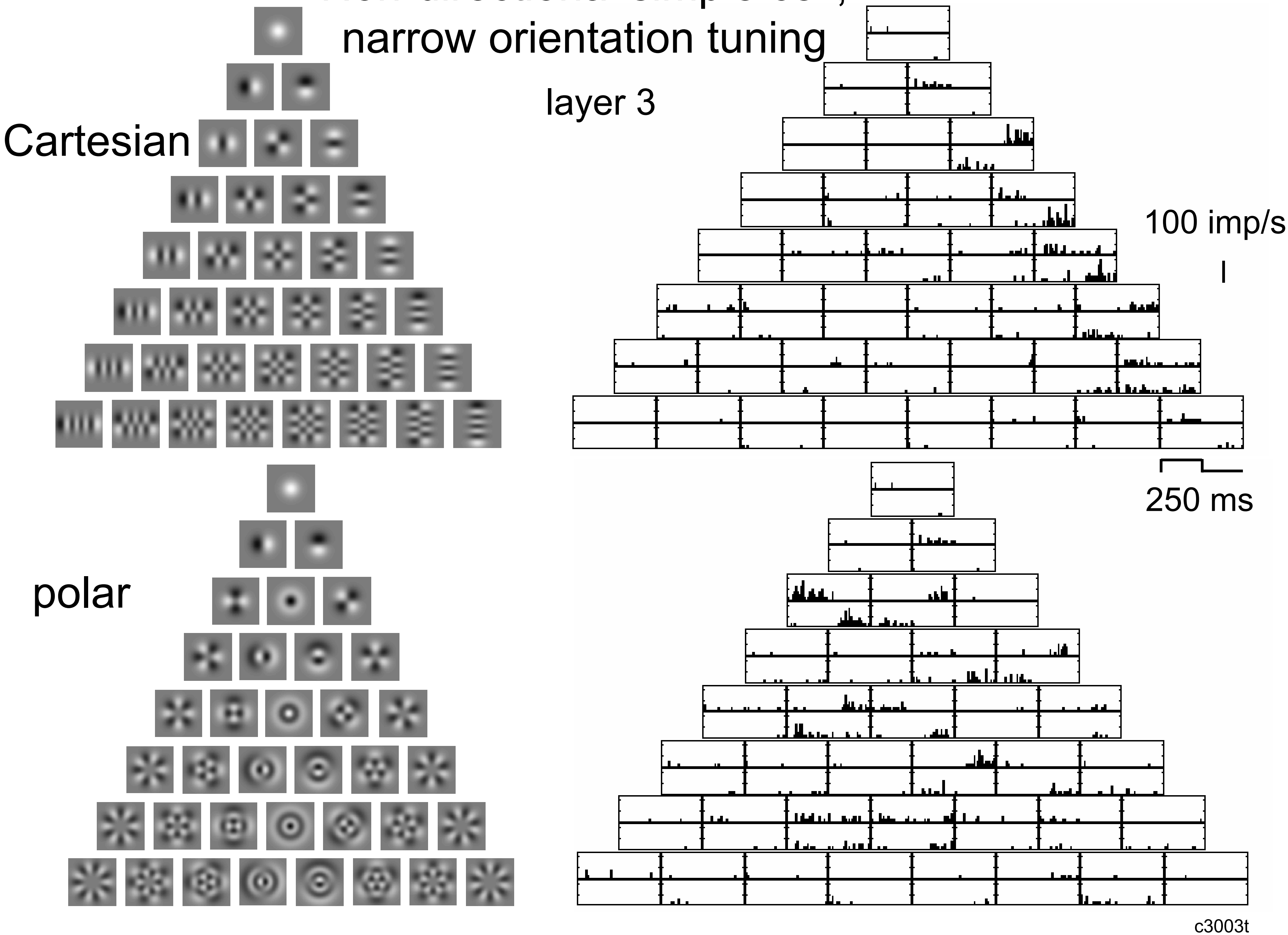


Non-directional simple cell, broad orientation tuning

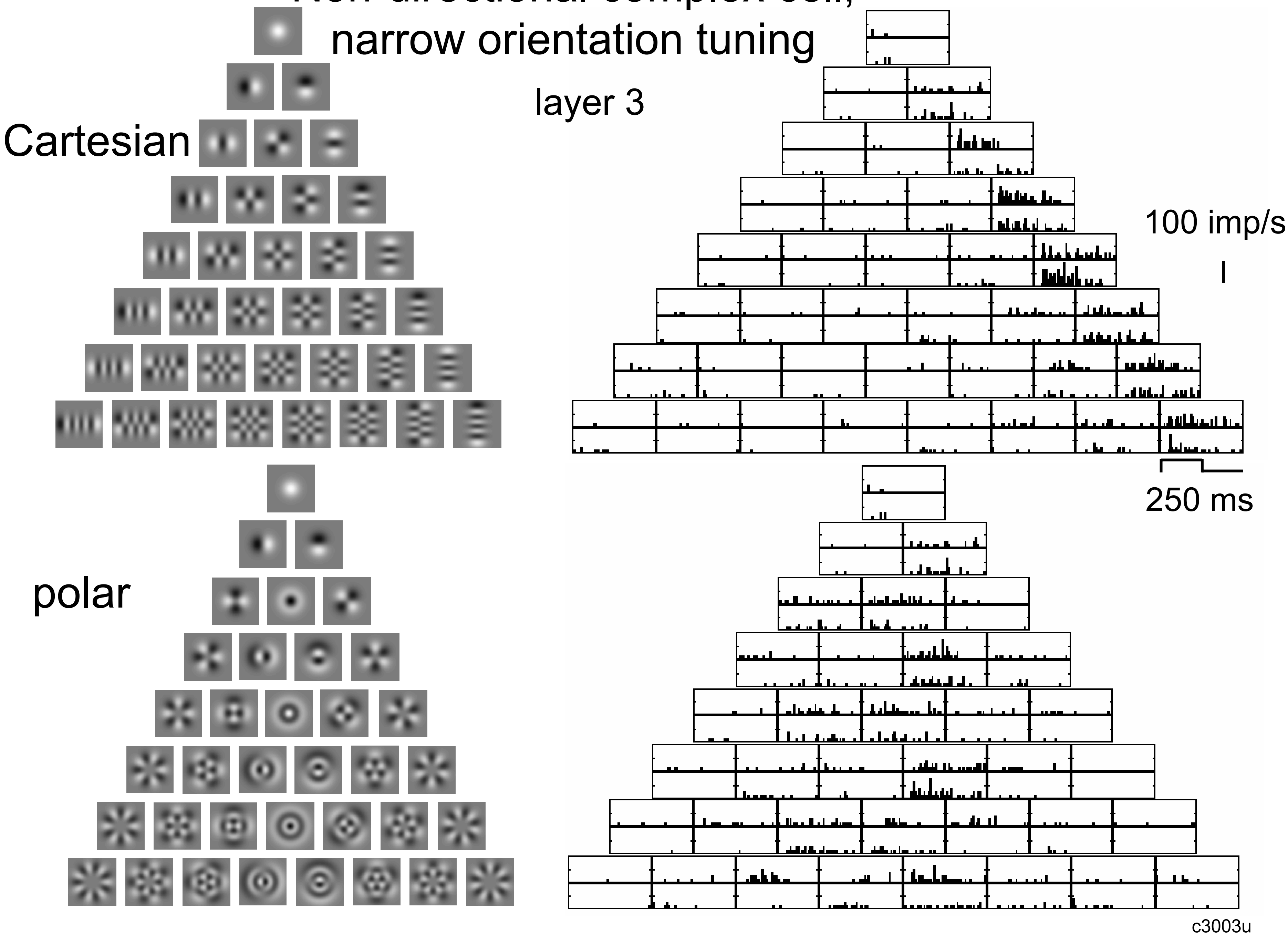
layer 3

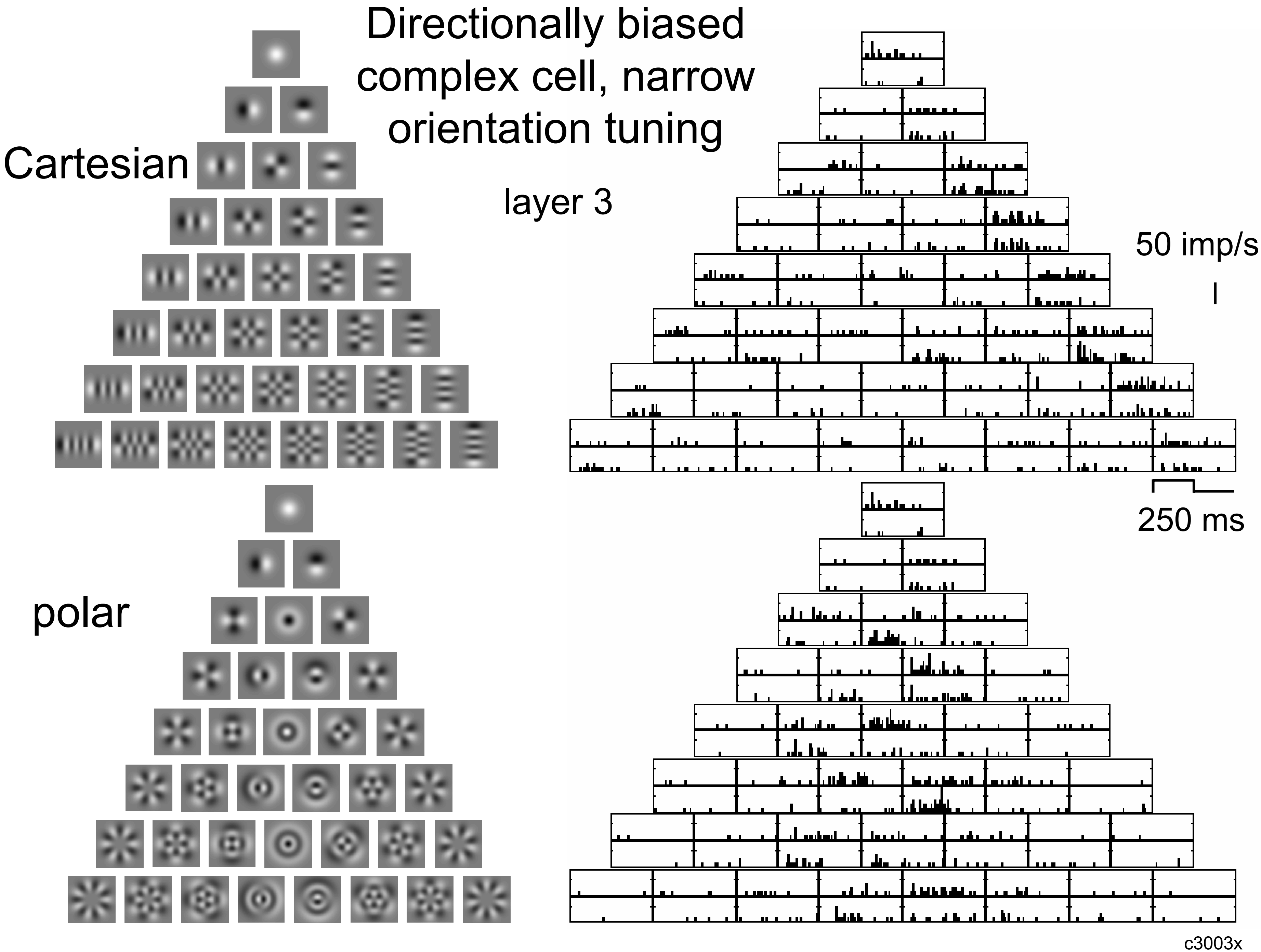


Non-directional simple cell, narrow orientation tuning



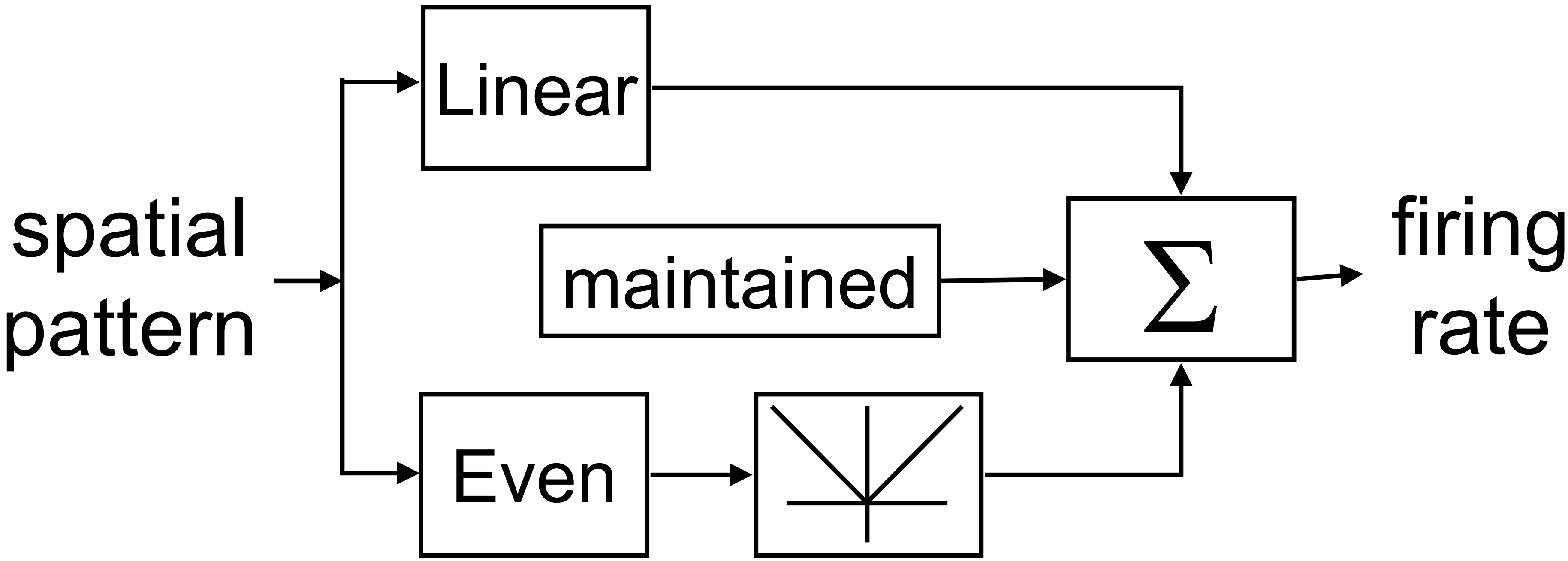
Non-directional complex cell, narrow orientation tuning

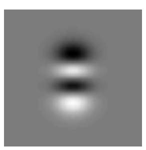
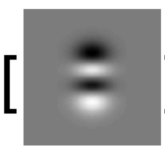
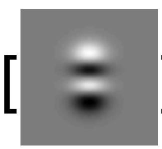


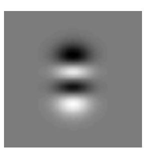
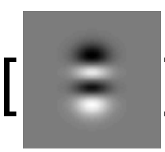
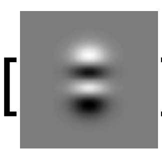


Directionally biased complex cell, narrow orientation tuning
Cartesian
layer 3
50 imp/s
250 ms
polar
c3003x

Quantitative ("Model") Framework

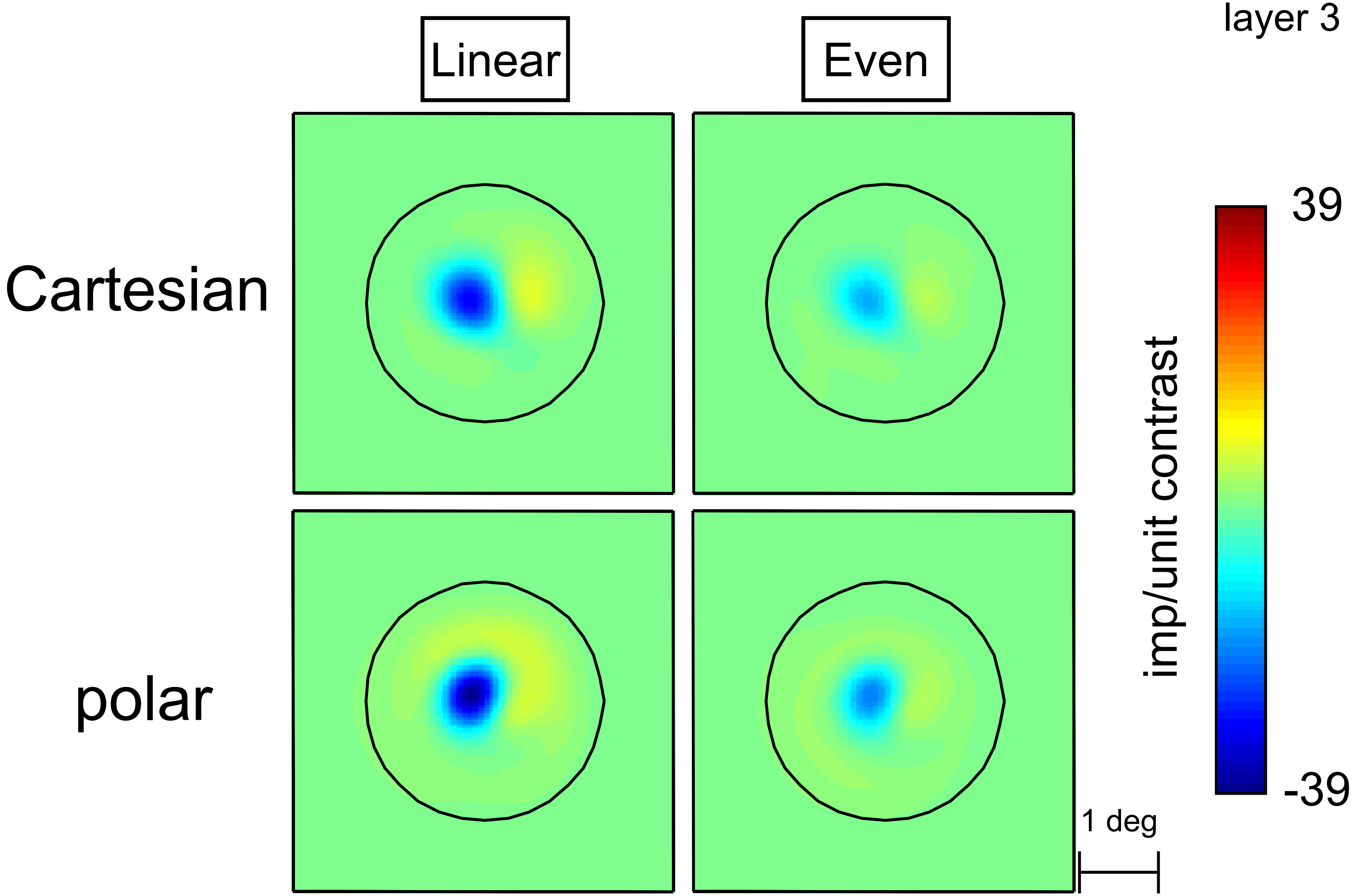


coef of  in Linear = (resp[] – resp[]) / 2

coef of  in Even = (resp[] + resp[]) / 2 - maintained

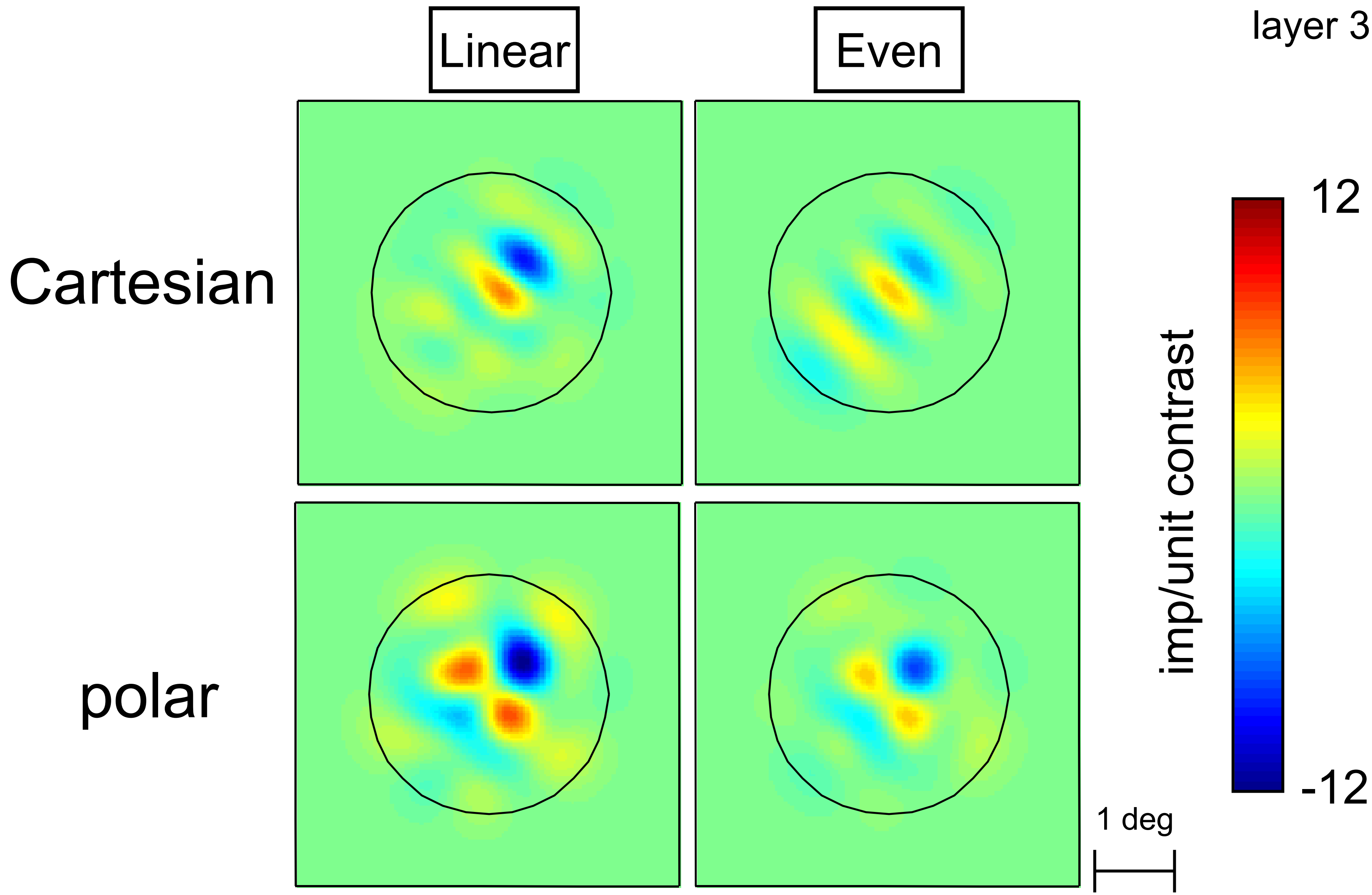
Half-wave rectification: Linear = Even

Non-directional simple cell, broad orientation tuning



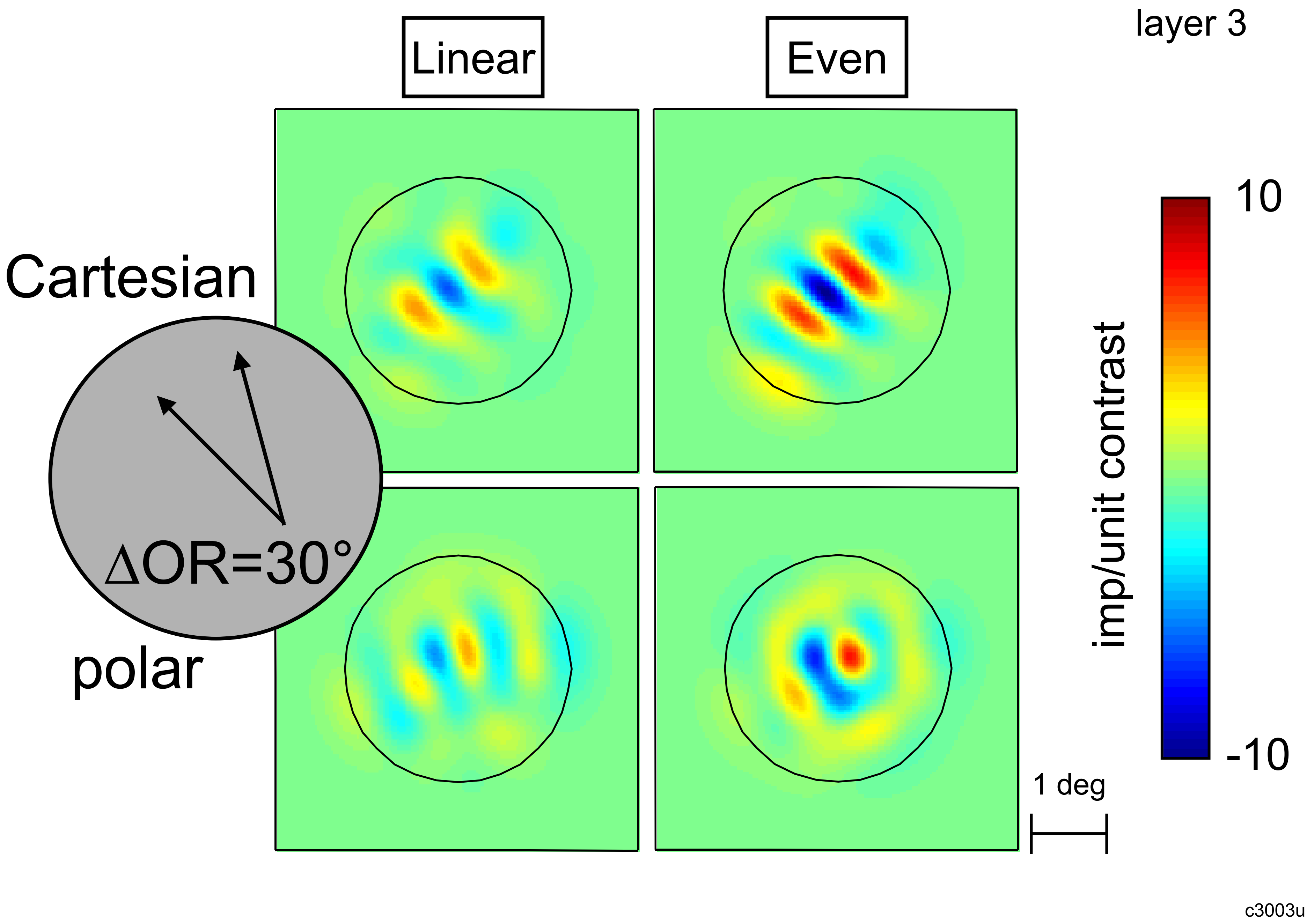
c3003s

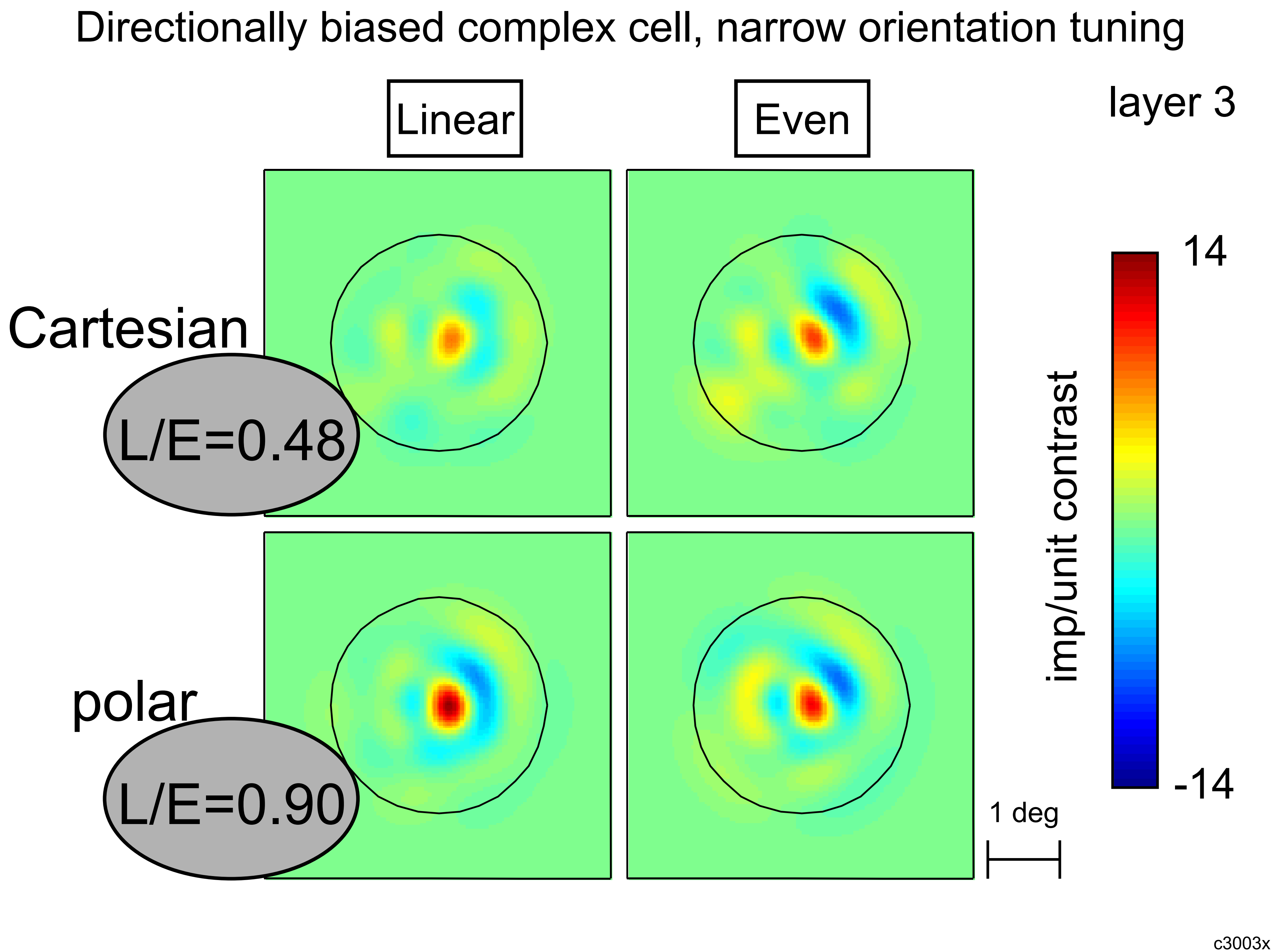
Non-directional simple cell, narrow orientation tuning



c3003t

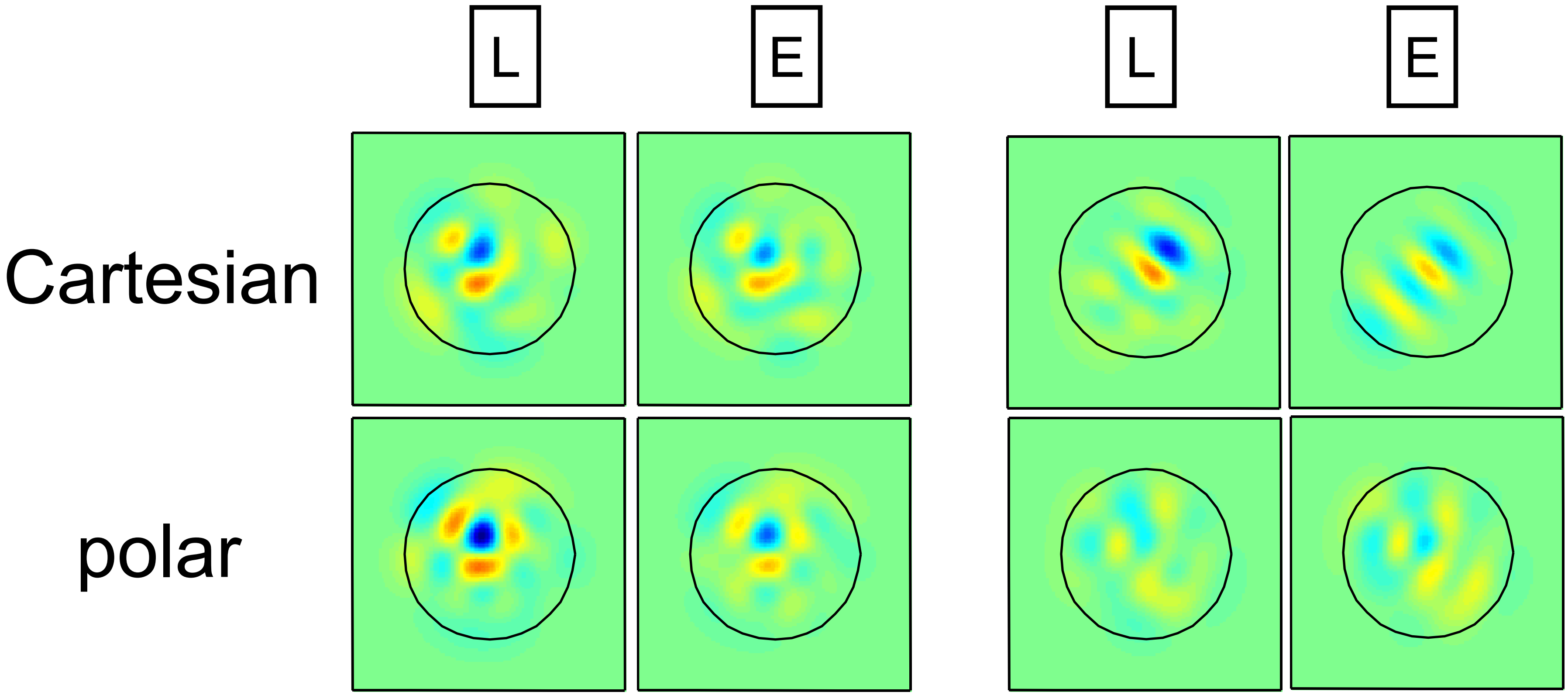
Non-directional complex cell, narrow orientation tuning




Directionally biased complex cell, narrow orientation tuning
Linear
Even
layer 3
Cartesian
L/E=0.48
polar
L/E=0.90
14
-14
imp/unit contrast
1 deg
c3003x

More examples from cat V1

upper layer 6



Non-directional
$F_1/F_0=1.2$

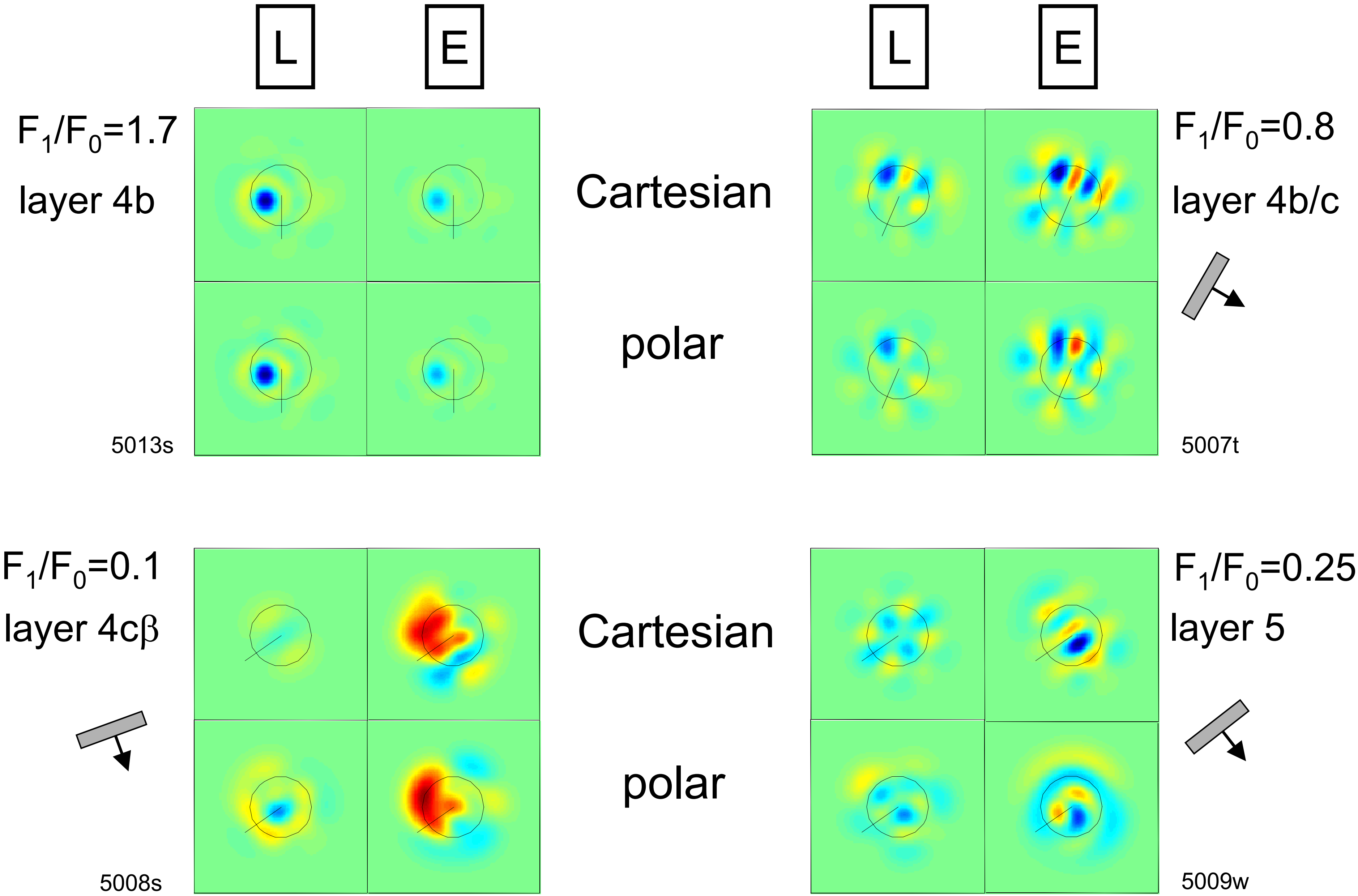
Directionally-selective
$F_1/F_0=0.5$

1 deg

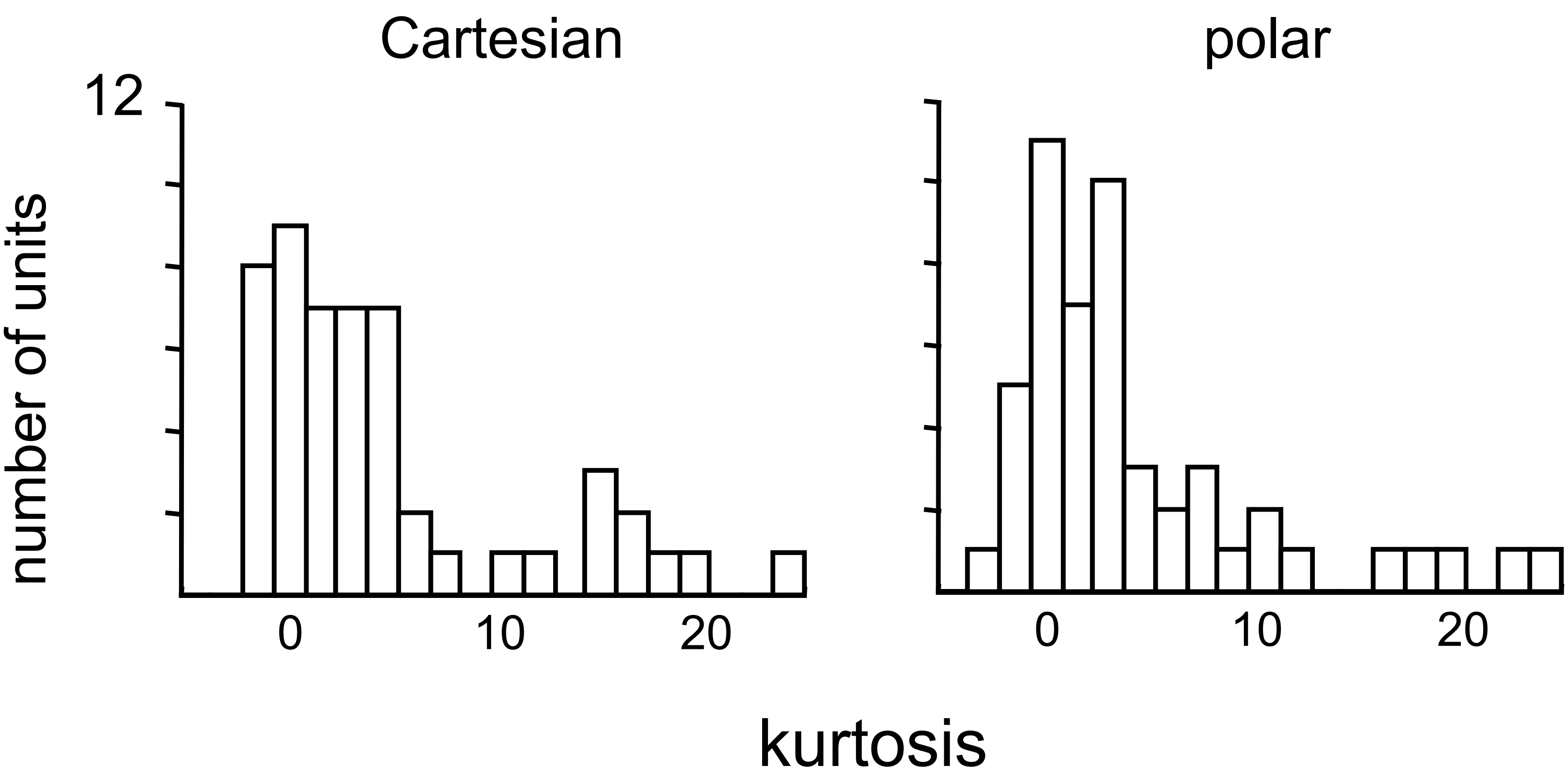
c3303u

c3303t

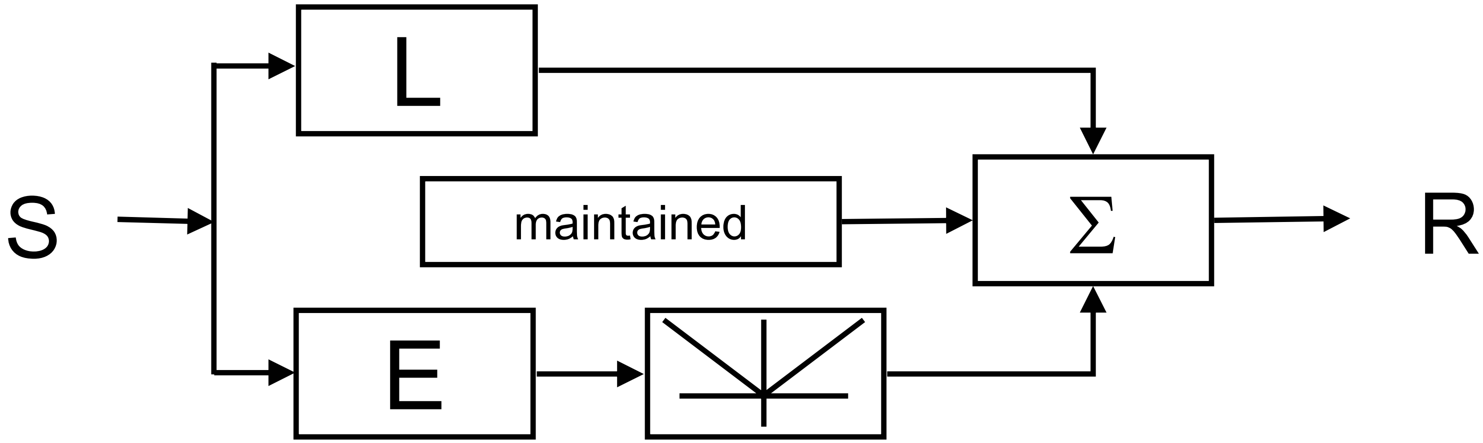
Examples from macaque V1



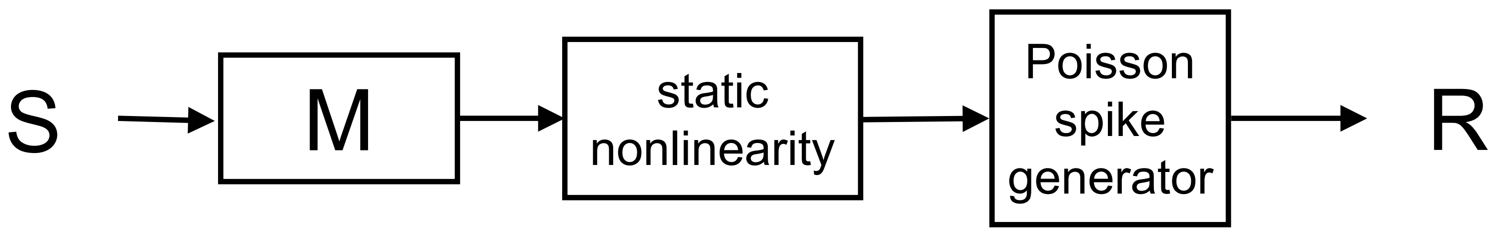
Sparseness of V1 responses



Comparison to “Maximally Informative Dimension” Approach (Sharpee et al.)



Choose L, E to recreate R from S



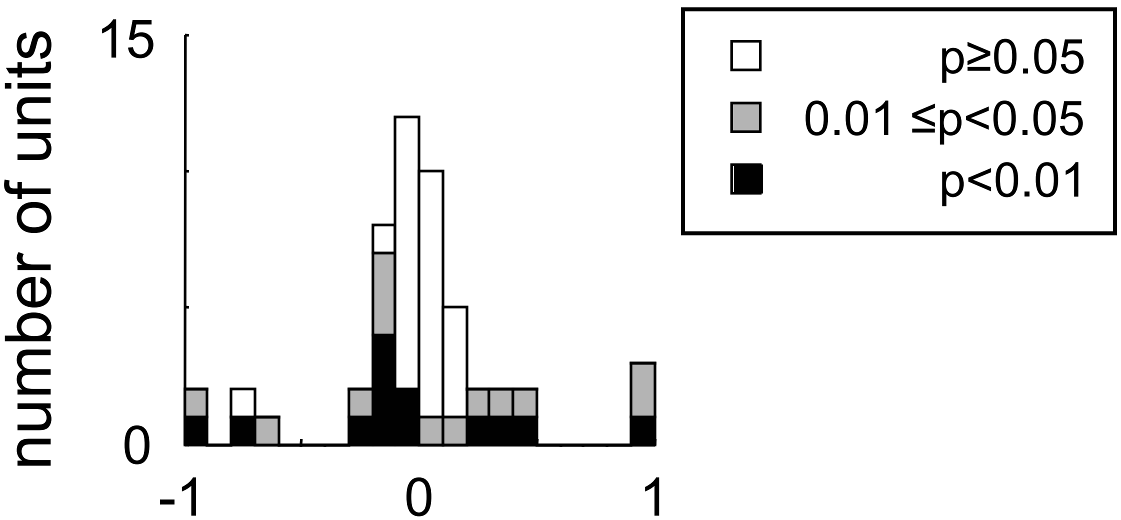
Choose M to maximize the mutual information between R and S

1. Shape of nonlinearity is not constrained

2. Restriction to a single filter, rather than separate filters for the “linear” and “nonlinear” branches

Test of Energy Models

Since the Cartesian and polar stimuli are equated for total energy at each spatial frequency, an energy model predicts that the total response amplitude to each set will be identical.

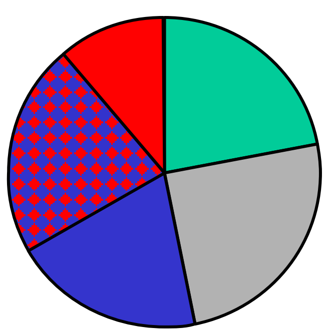


$$\frac{\text{total Cartesian response} - \text{total polar response}}{\text{total Cartesian response} + \text{total polar response}}$$

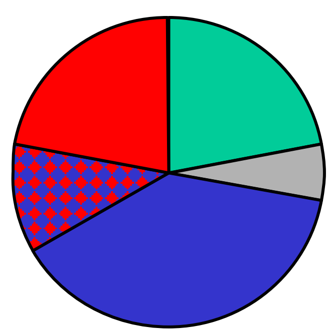
This also rules out models based on local squaring.

Summary

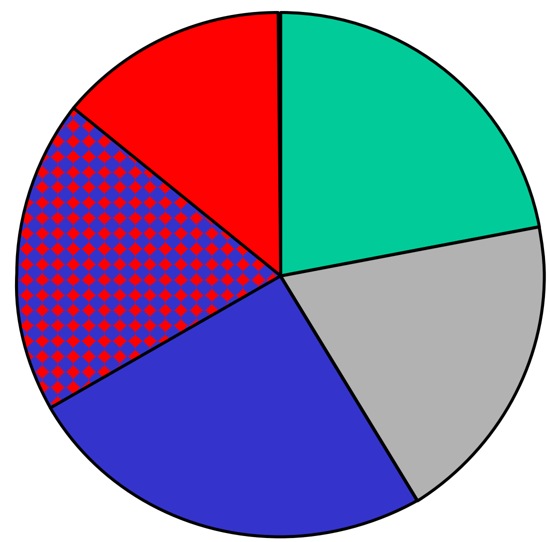
- 63 neurons (17 sites in 3 cats, 2 macaques): 51/63 responded to TDH stimuli, 12/63 did not
- 21/51 differed in sensitivity to Cartesian and polar stimuli (13: C > P, 8: C< P)
- 28/51 differed in RF shape; grating responses match C better than by P
- 14/51 had neither difference



cat: 45 neurons



macaque: 18 neurons



combined: 63 neurons

plot_ind_meta

Conclusions

- For most V1 neurons, responses to simple two- dimensional patterns reveal qualitative inconsistencies with oriented-filter and energy models.
- Only models with spatially-selective nonlinearities, confined both in space and spatial frequency, can account for the computations carried out by V1 neurons.

Speculations

- These bottom-up influences are relevant to understanding V1 responses to natural scenes.
- The uniform coverage of orientation tuning in V1 is but a special case of a more general uniform coverage of elementary form elements.