Coverage, Polymaps and the Visual Cortex

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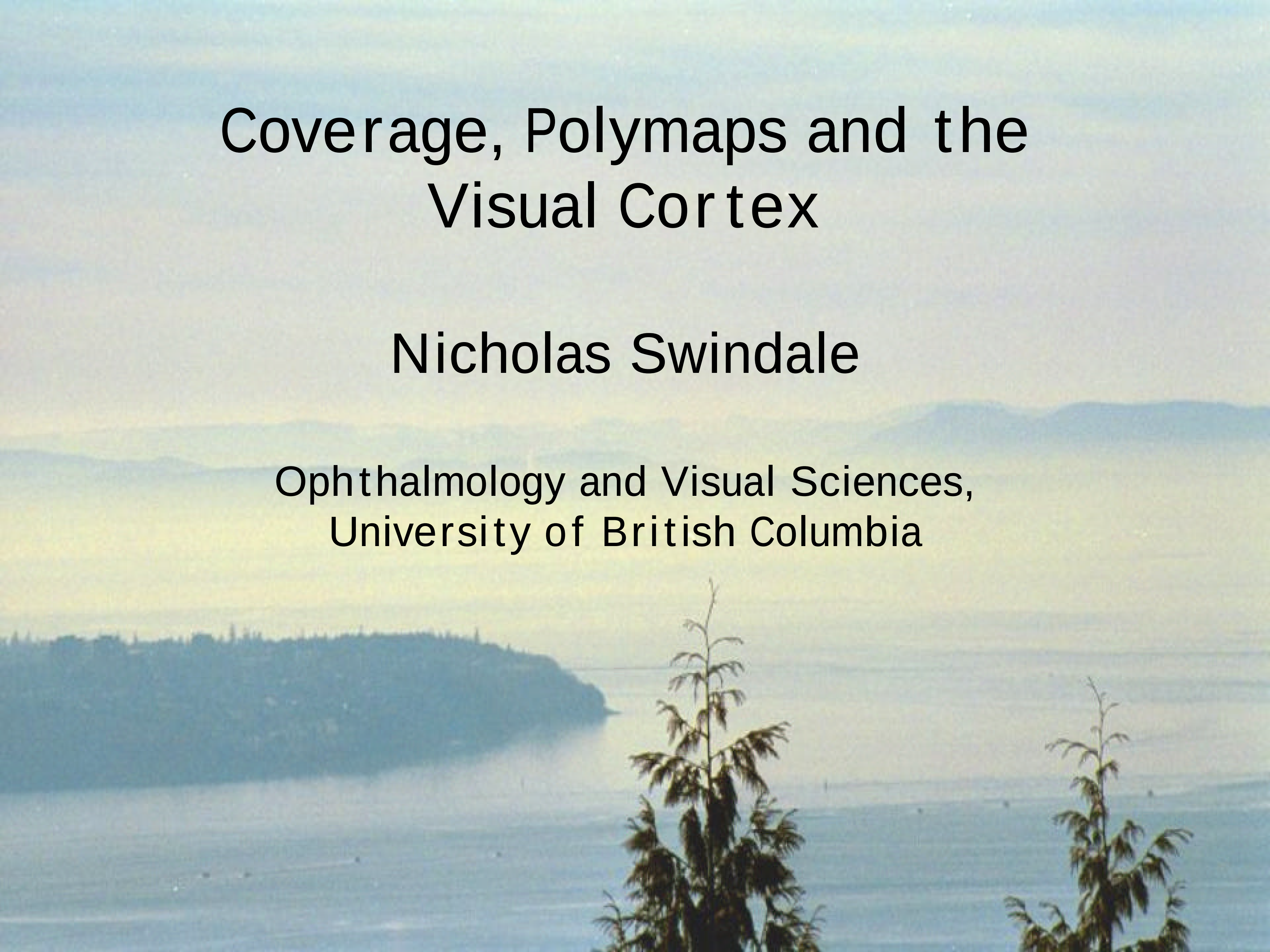
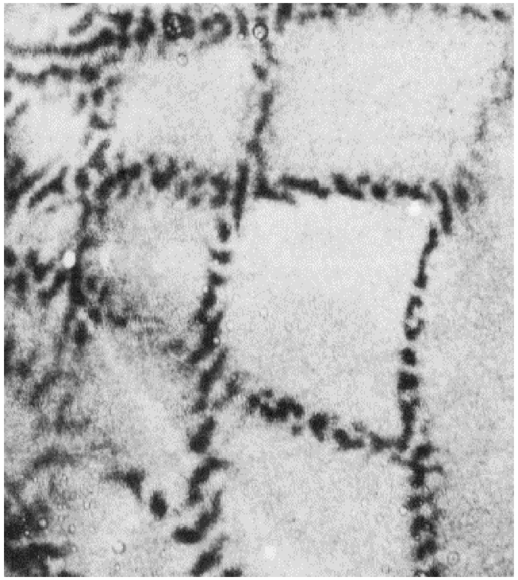
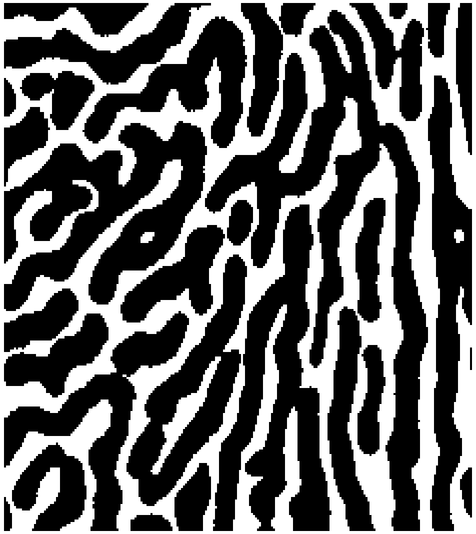
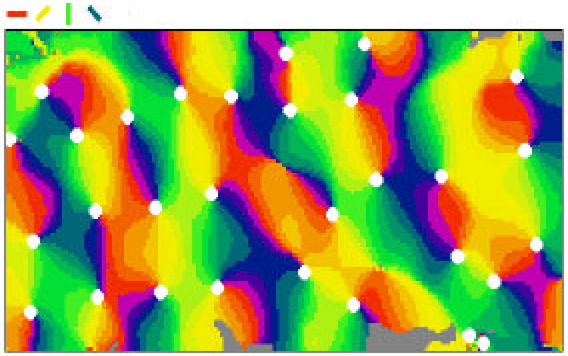




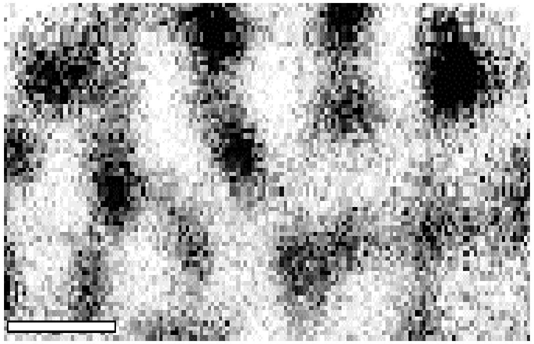
Retinotopy



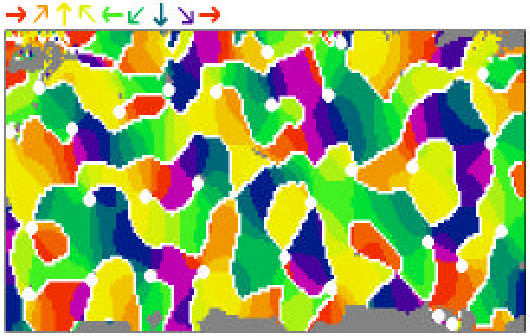
Ocular Dominance



Orientation



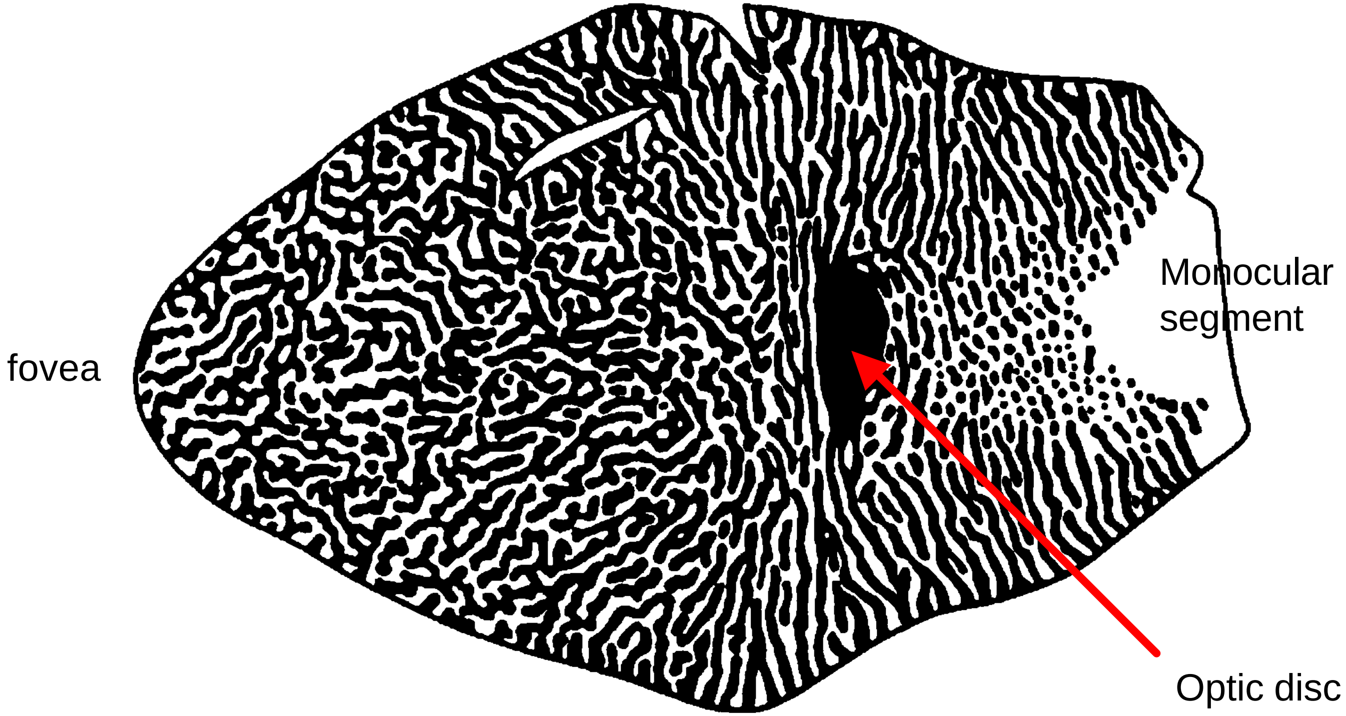
Spatial Frequency



Direction Preference

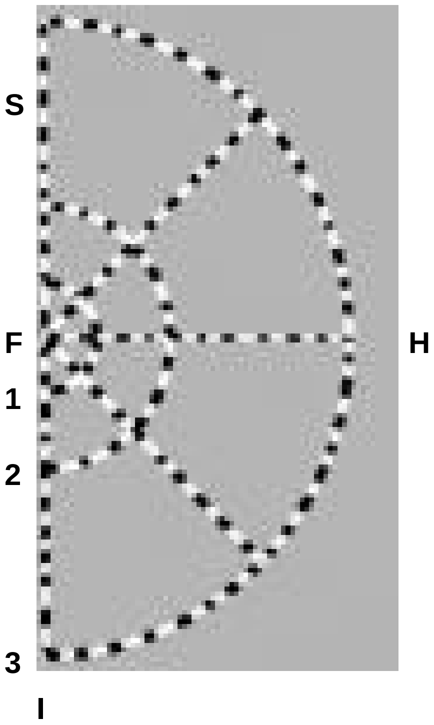
+ ?

Monkey Ocular Dominance Stripes

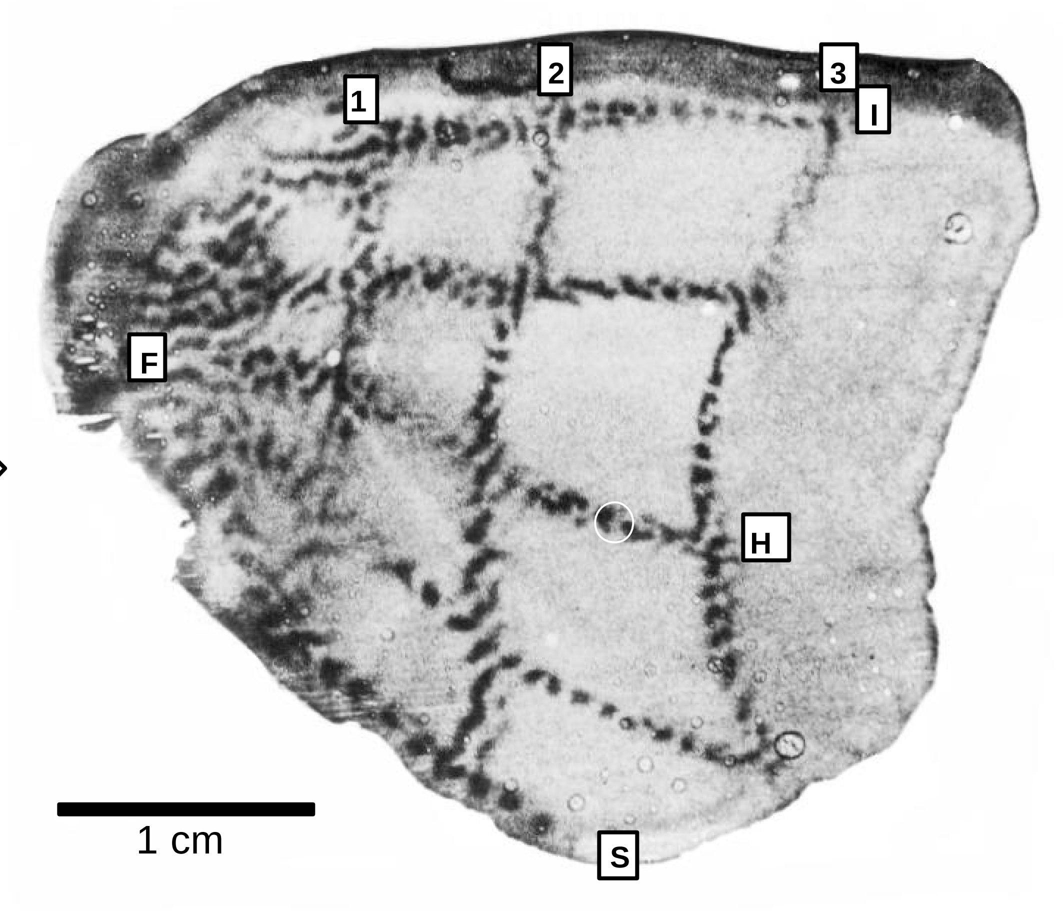


from Florence and Kaas, 1992

The Retinotopic Map

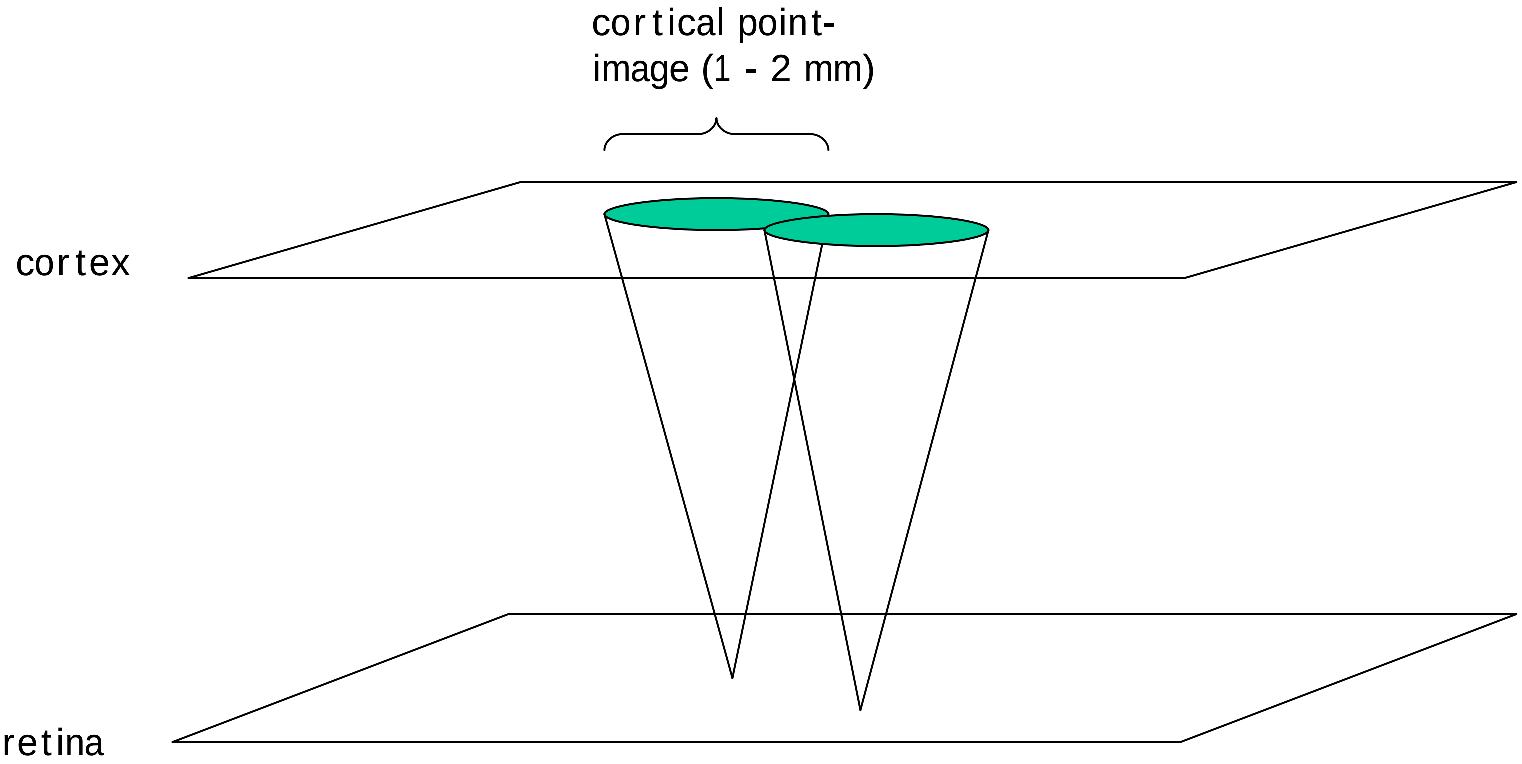


visual display



2-DG activity pattern in visual cortex

from Tootell et al., (1988)

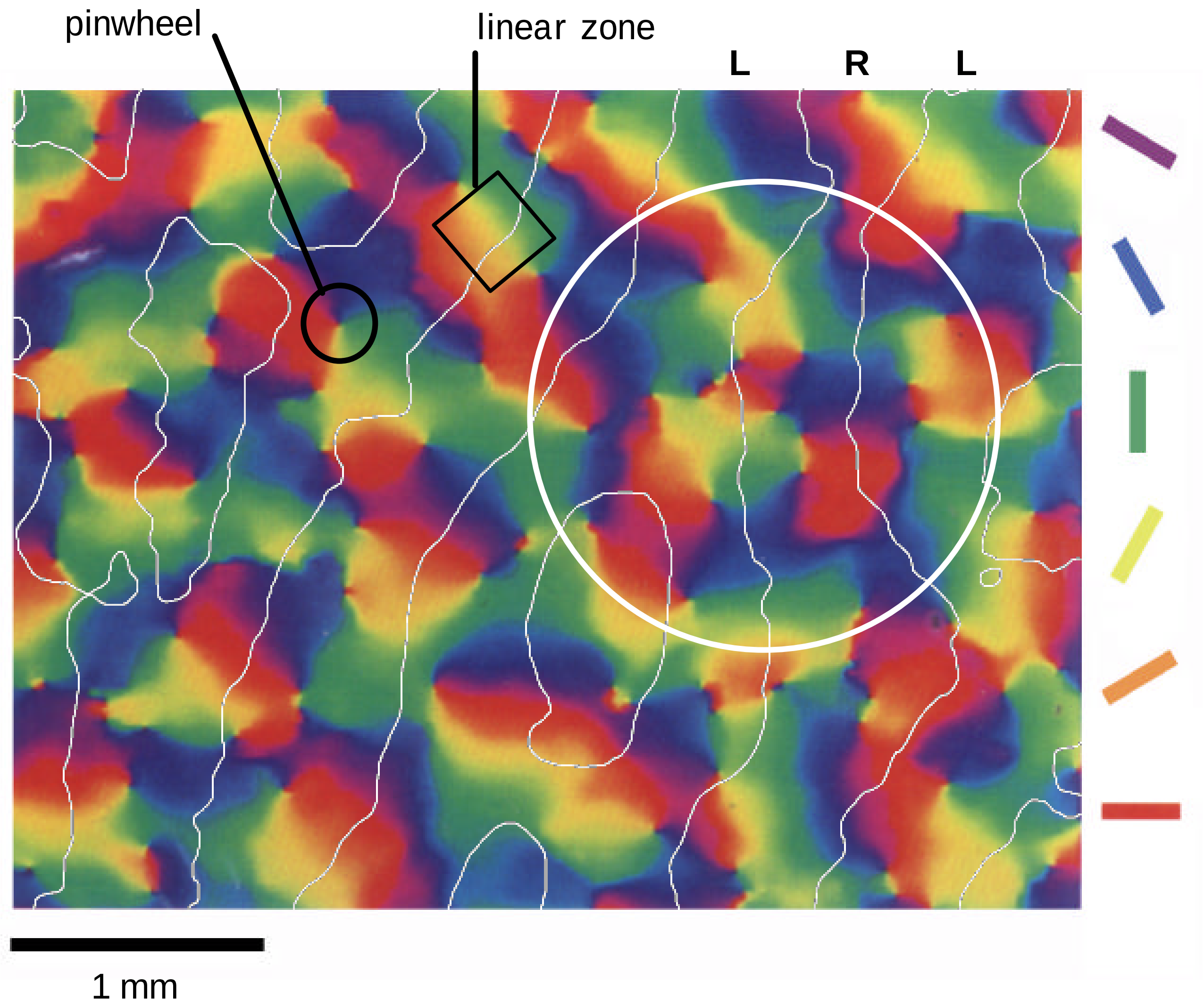


cortical point-image (1 - 2 mm)

cortex

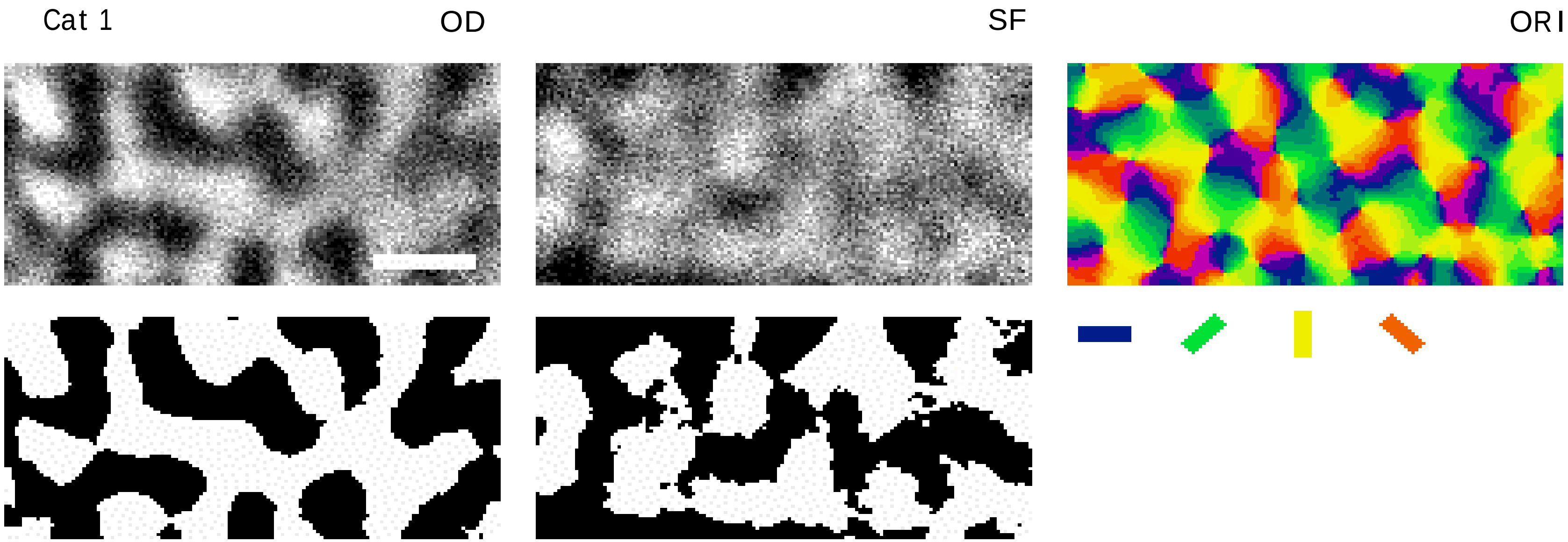
retina

Monkey Orientation and Ocular Dominance Columns

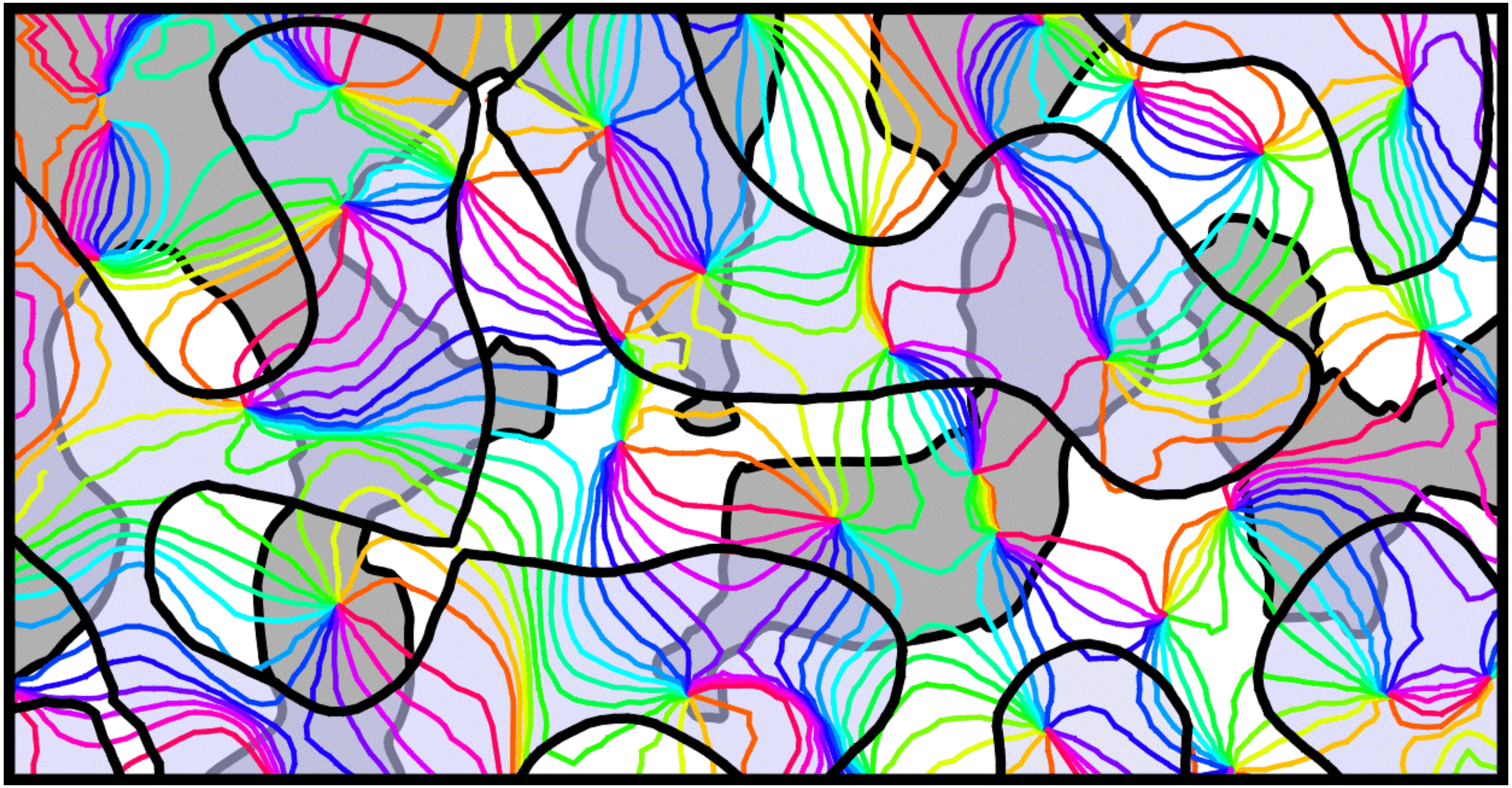


From Blasdel (1992)

Combined Ocular Dominance, Spatial Frequency and Orientation Maps from Cat Area 17



Data from Hübener, Shoham, Bonhoeffer and Grinvald



Upper layer (light grey): ocular dominance map
Middle layer (coloured lines): iso-orientation boundaries
Bottom layer (dark grey): low spatial frequency domains

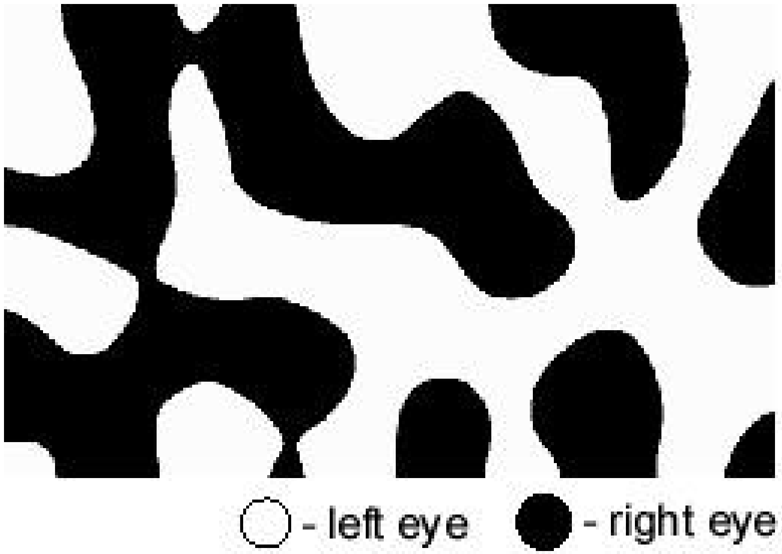
Adapted from Hübener et al. (1997) *J. Neurosci*., **17**, 9270

TERMINOLOGY

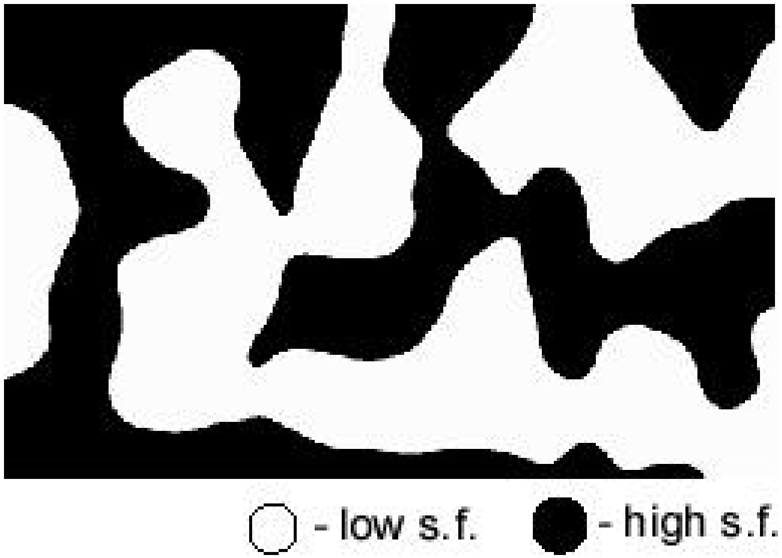
Protomap: the spatial representation across the cortex of one of the sub-features, e.g. ocular dominance

Polymap: the complete map of all the feature domains

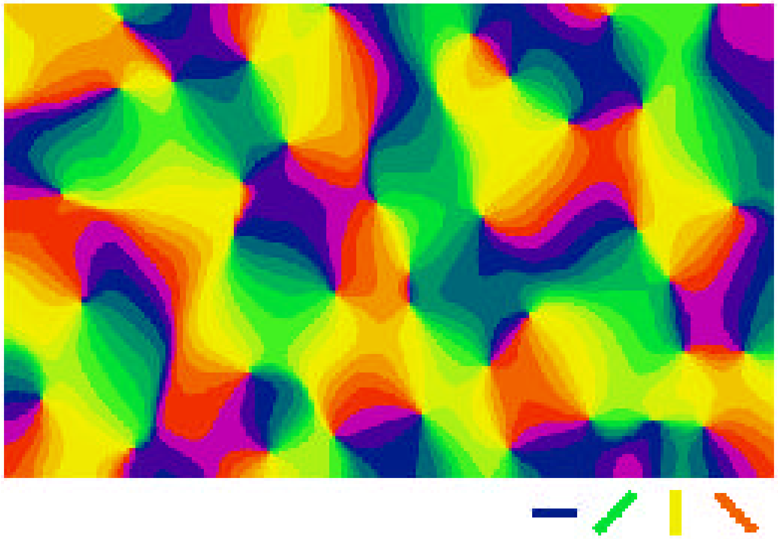
Ocular dominance protomap



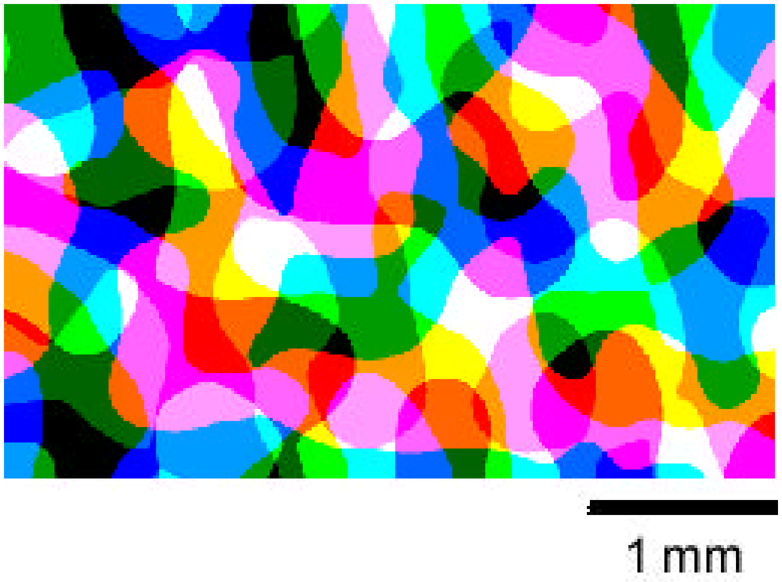
Spatial frequency protomap



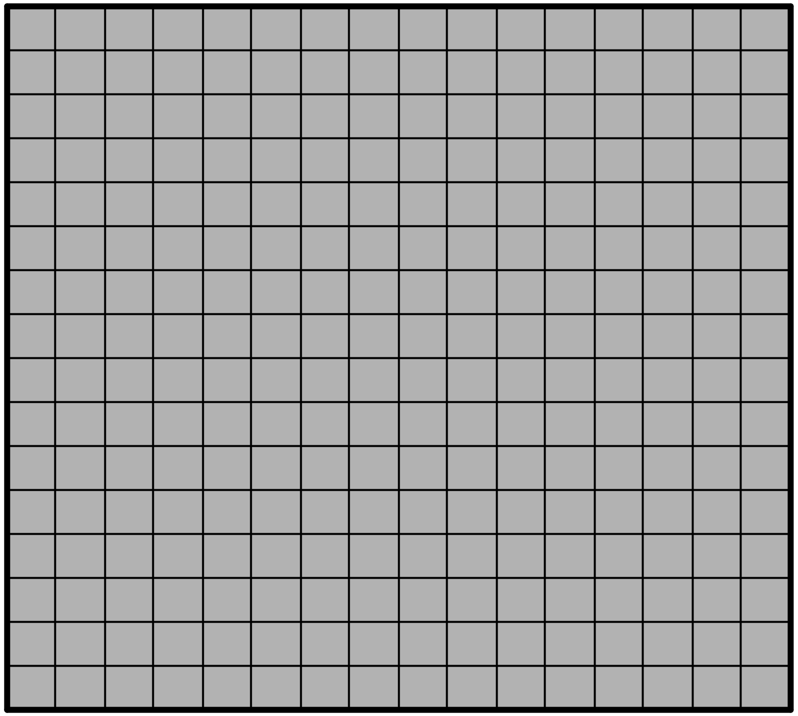
Orientation protomap



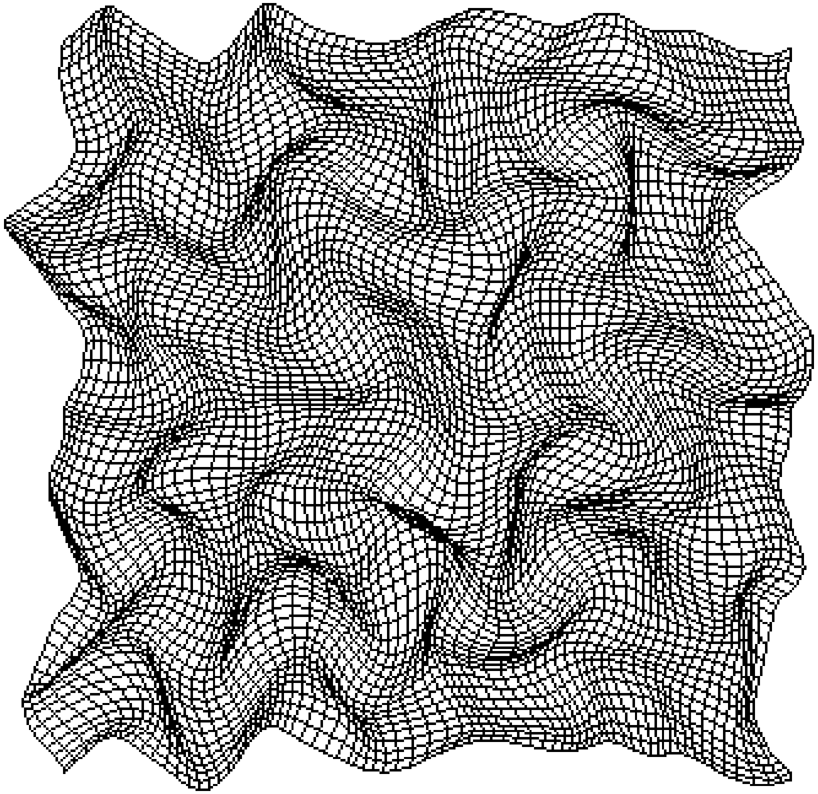
Polymap representation



Stimulus space representation of cortical maps

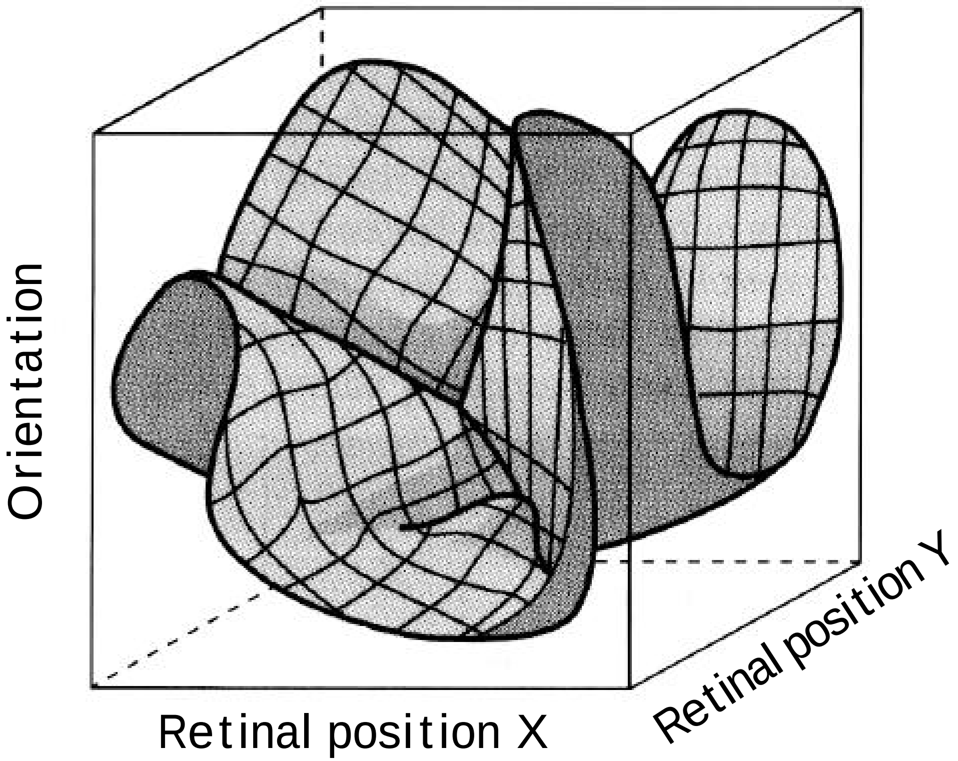


The cortex in cortical coordinates



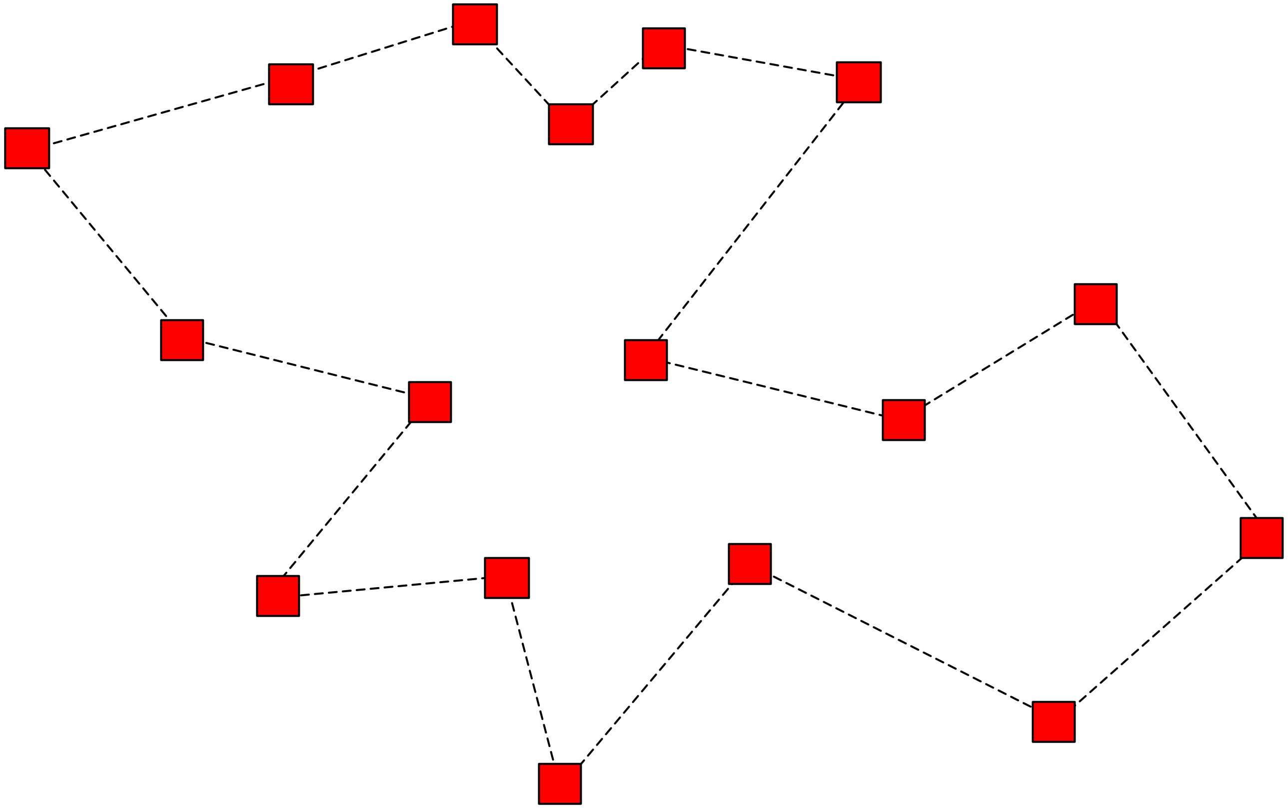
The cortex, projected into retinal space

A dimension-reducing map

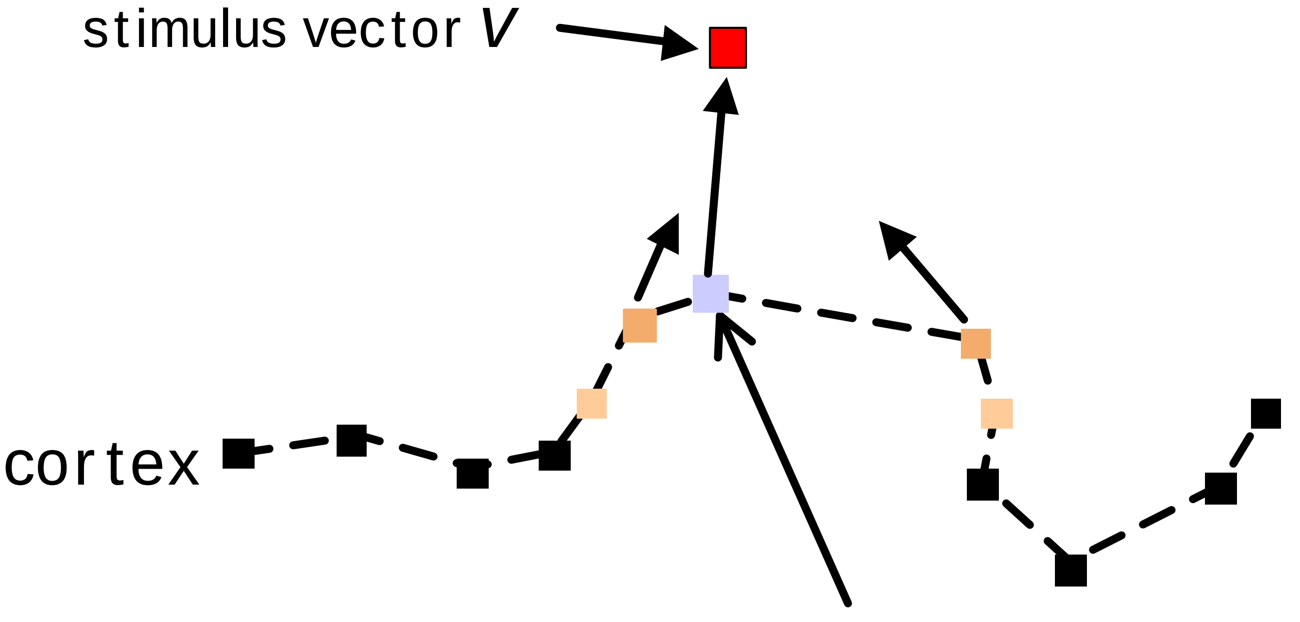


The cortex folded inside a stimulus space. The manner of folding is believed to be constrained by continuity and completeness (coverage) constraints.

The Traveling Salesman's Problem



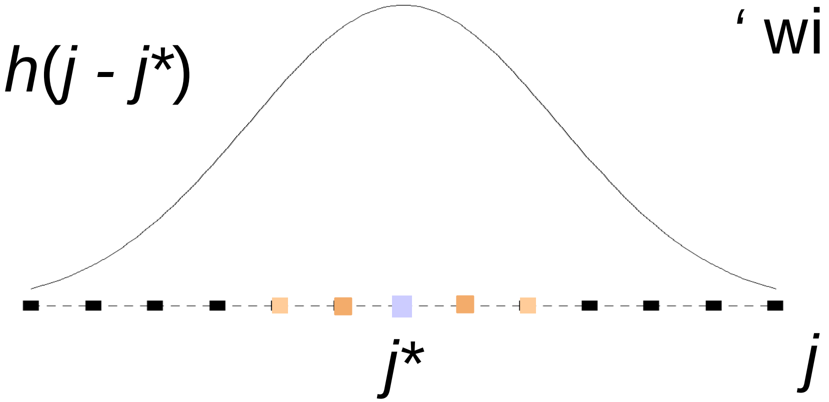
How the Kohonen Algorithm Works



stimulus vector *V*

cortex

‘ winning’ cortical point w_{j^*}



$h(j - j^*)$

j^*

j

The cortical neighbourhood function

The Kohonen Self-Organizing Feature Map Algorithm

$$\boxed{\Delta w_j = \varepsilon h(j, j^*)(v - w_j)}$$

ε is a rate constant;

w_j is the position of cortical point j in stimulus space

v is a stimulus vector;

j^* is the cortical point most responsive (i.e. nearest) to stimulus v;

$h(j, j^*)$ is a Gaussian function of the cortical distance between points j and j^*.

Summary of how the Kohonen SOFM works:

For each stimulus *v*, find the cortical point *j** which is closest (most responsive) and move it and its neighbours towards the stimulus. Repeat this for many randomly chosen stimuli.

The width of the cortical neighbourhood function may be reduced as the map forms, a process referred to as ‘annealing’.

The end result is to make the cortex fill the stimulus space as continuously as possible, satisfying completeness and continuity constraints.

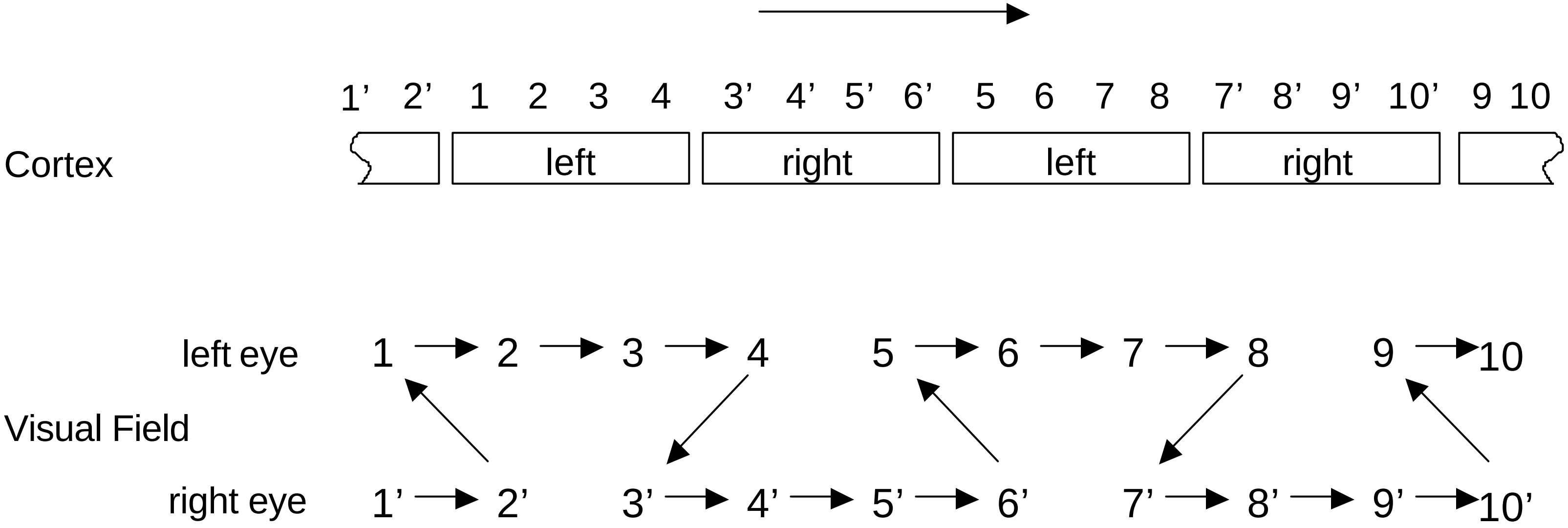
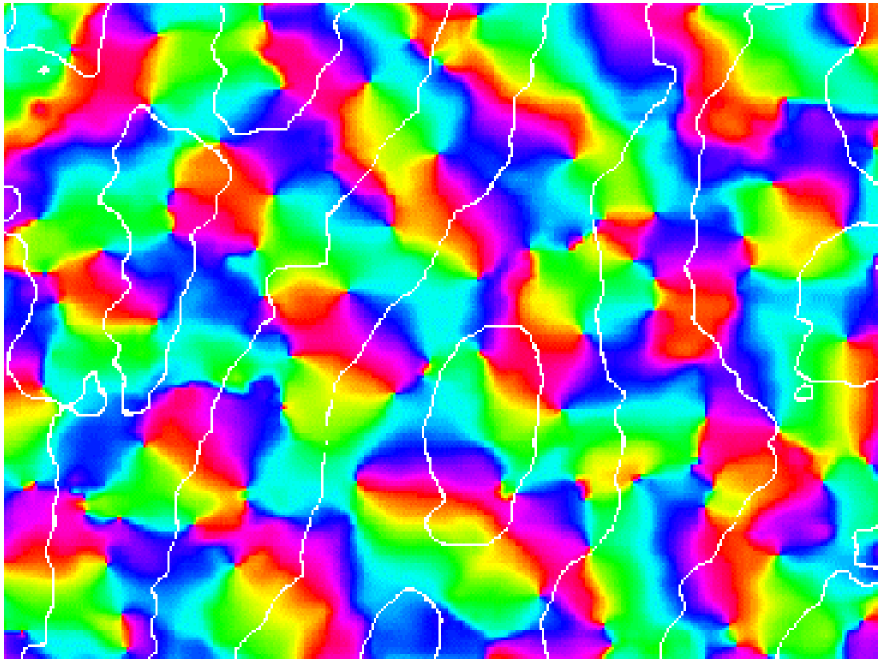

1’ 2’ 1 2 3 4 3’ 4’ 5’ 6’ 5 6 7 8 7’ 8’ 9’ 10’ 9 10
Cortex
left
right
left
right
left eye
1 2 3 4 5 6 7 8 9 10
Visual Field
right eye
1’ 2’ 3’ 4’ 5’ 6’ 7’ 8’ 9’ 10’

Figure 4

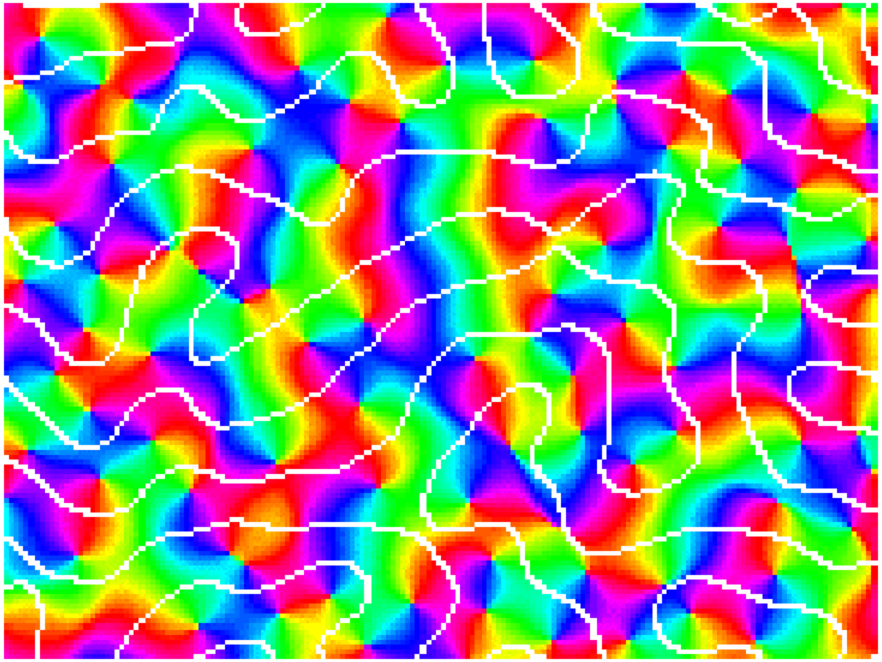
Kohonen SOFM Algorithm

orientation + ocular dominance + retinotopy



Data

Blasdel (1992)



Model

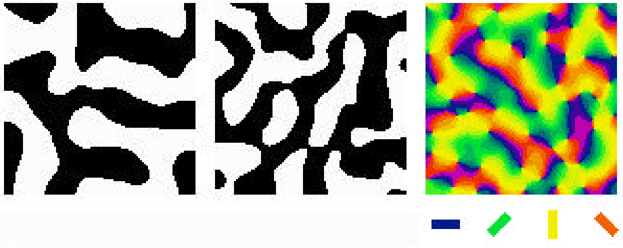
Obermayer, Ritter & Schulten (1992)

Model maps

Kohonen
SOFM

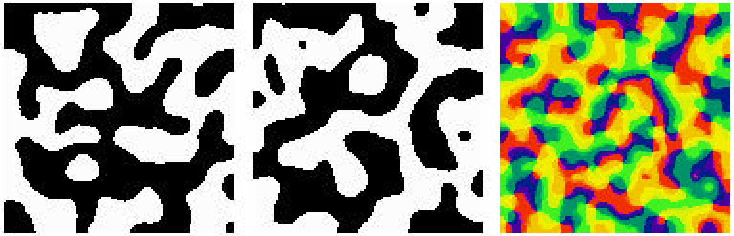
KO6.001

KO7.001

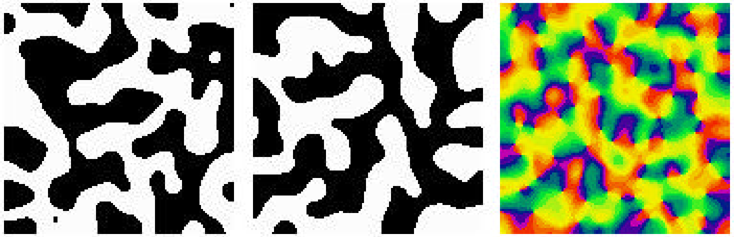


Elastic
net

EL8.003

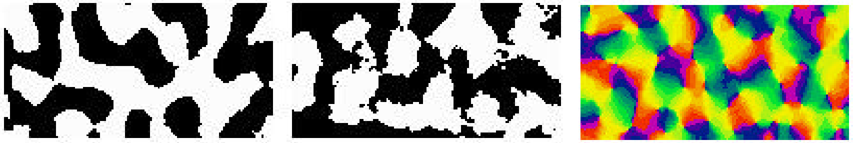


EL9.001



Real maps

Cat 1



Cat 2

OD SF ORI

Calculation of Coverage Uniformity

For a particular stimulus, $\mathbf{v}$, calculate the total activity A evoked over the whole map,

$$A(\mathbf{v}) = \sum_{i,j \in C} f(\mathbf{v} - \mathbf{w}_{i,j})$$

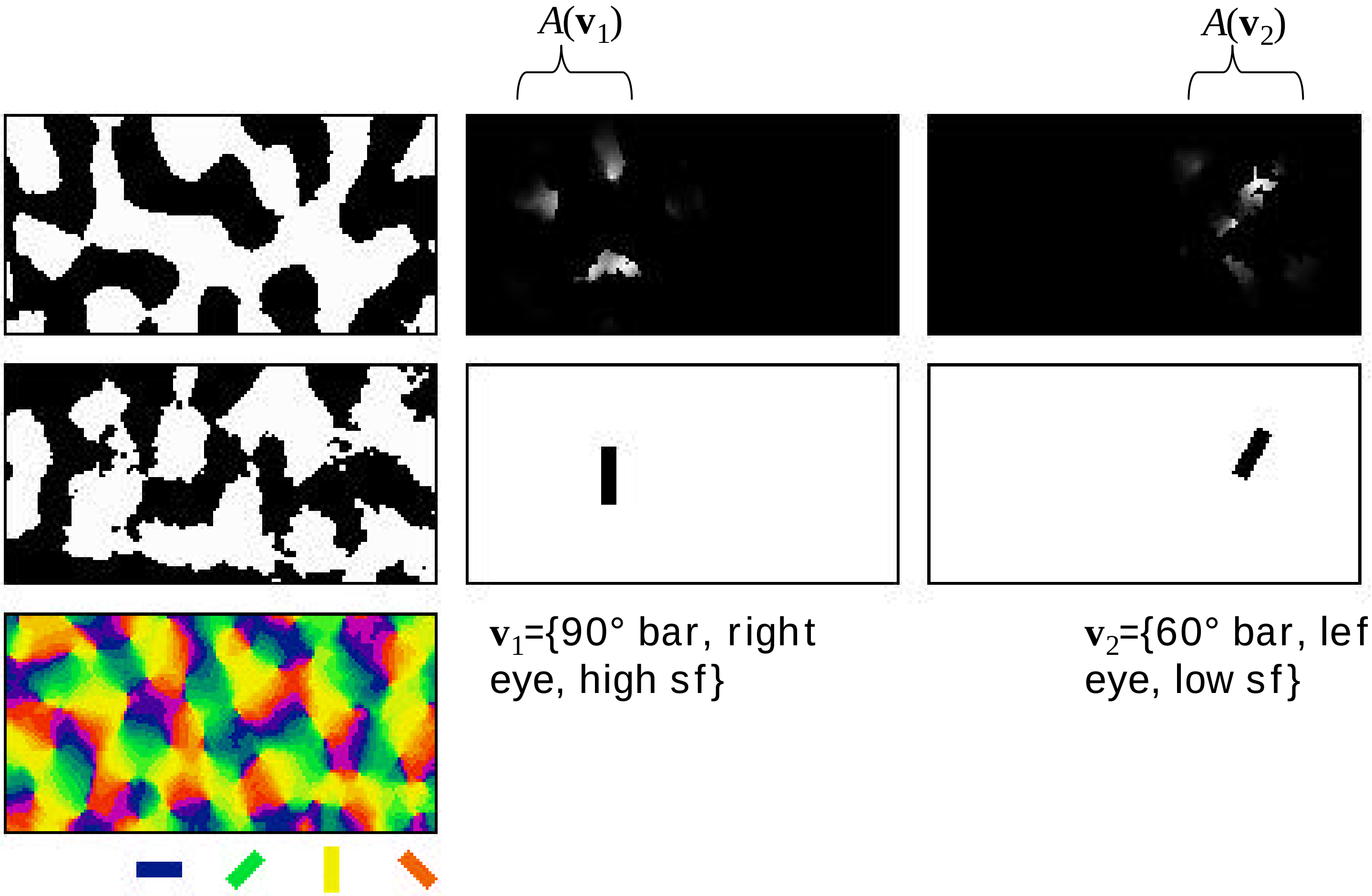
where $\boldsymbol{w}_{i,j}$ is the receptive field center of cortical point (i, j) and $f()$ specifies the receptive field shape (typically Gaussian).

Define coverage uniformity as the ratio between the variability in A divided by the mean, taken over a representative set of stimuli, i.e.

$$c' = \text{standard deviation}(A)/\text{mean}(A)$$

c' is a measure of noise in the representation of a stimulus space by a cortical area.

Steps in the calculation of coverage



$A(\mathbf{v}_1)$

$A(\mathbf{v}_2)$

cortical activity

visual stimuli

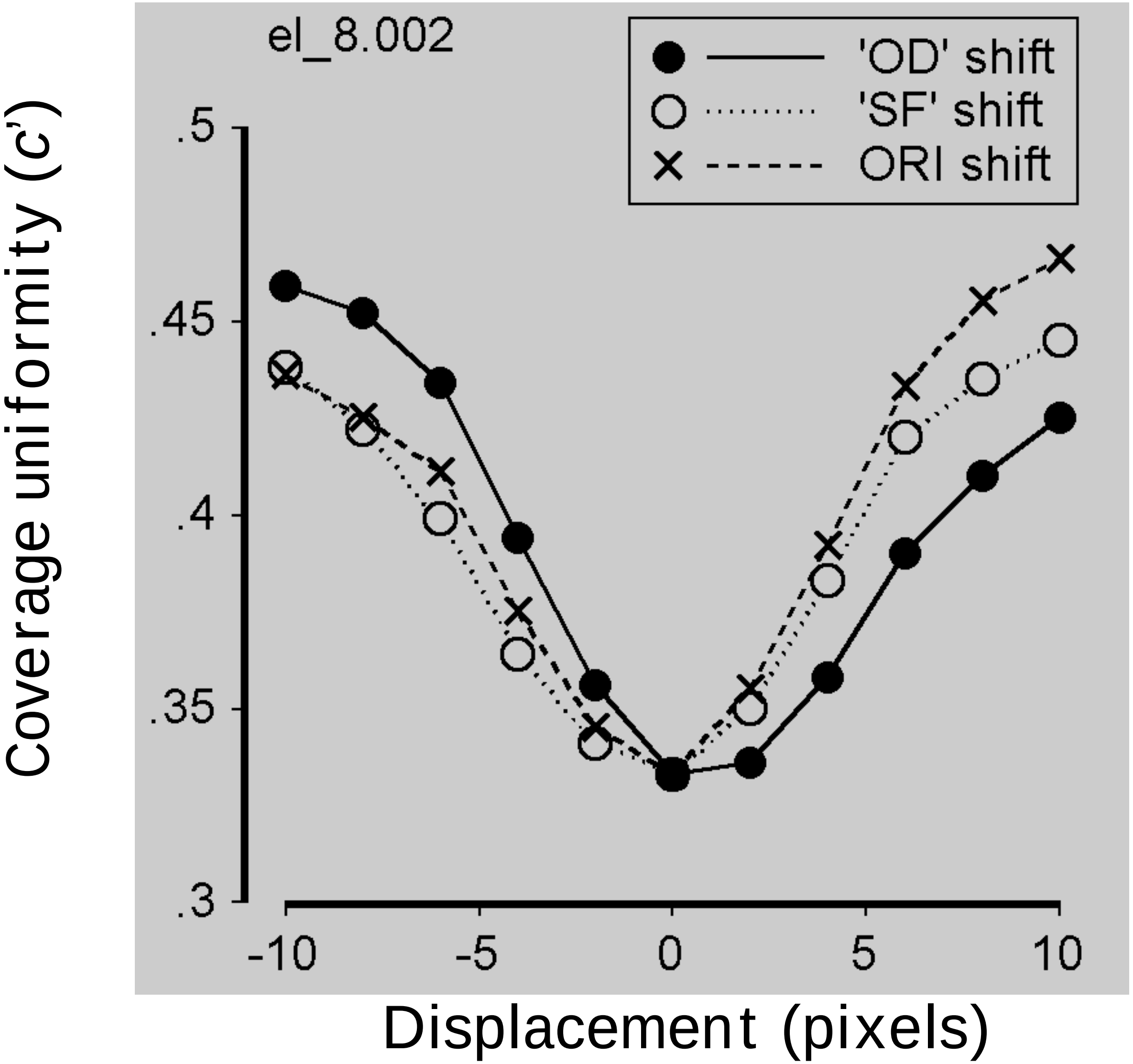
$\mathbf{v}_1$={90° bar, right eye, high sf}

$\mathbf{v}_2$={60° bar, left eye, low sf}

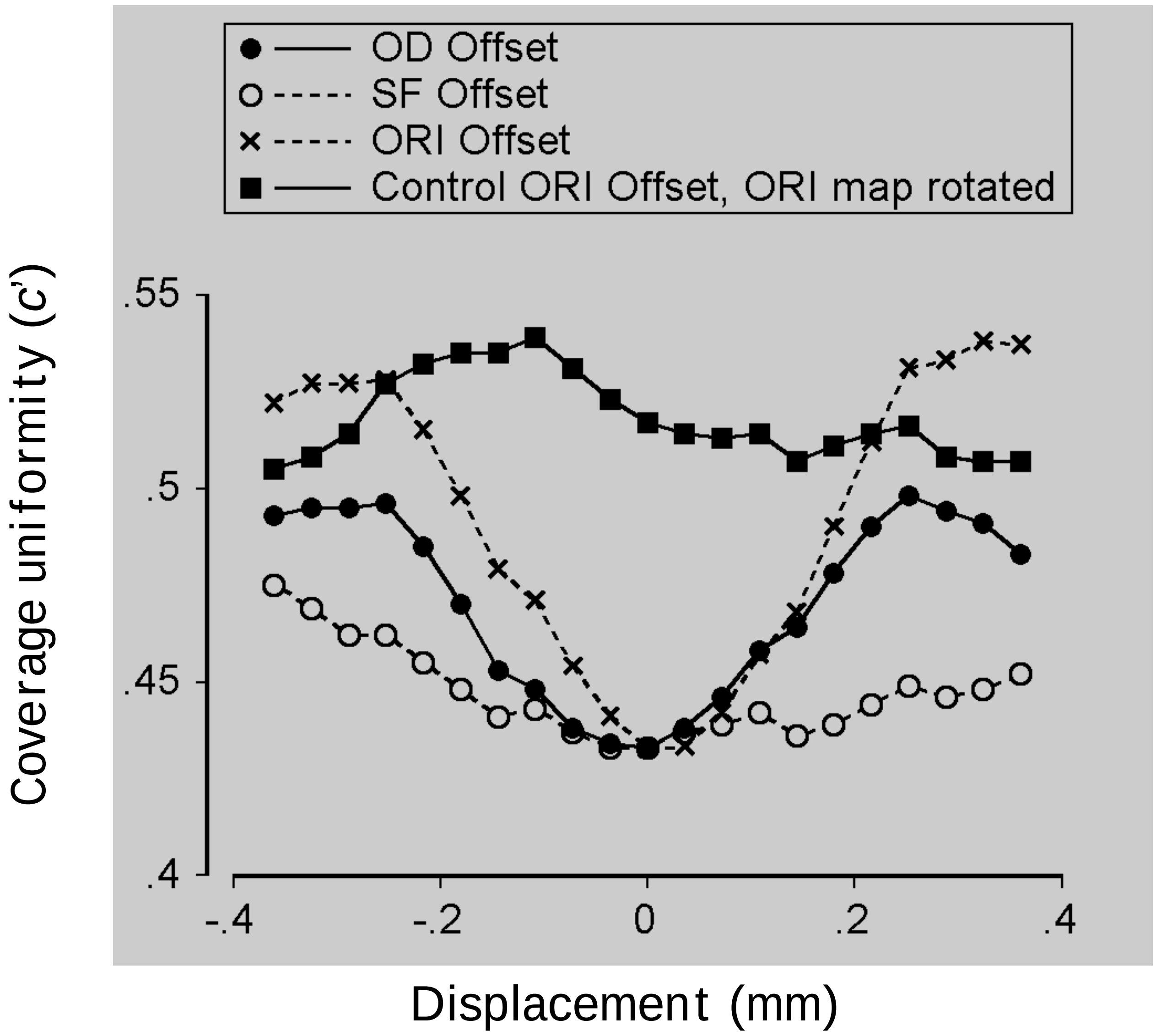
The coverage hypothesis:

If the maps of orientation, ocular dominance and spatial frequency are optimised for uniform coverage, perturbing the spatial relations between the different maps should always lead to worse coverage.

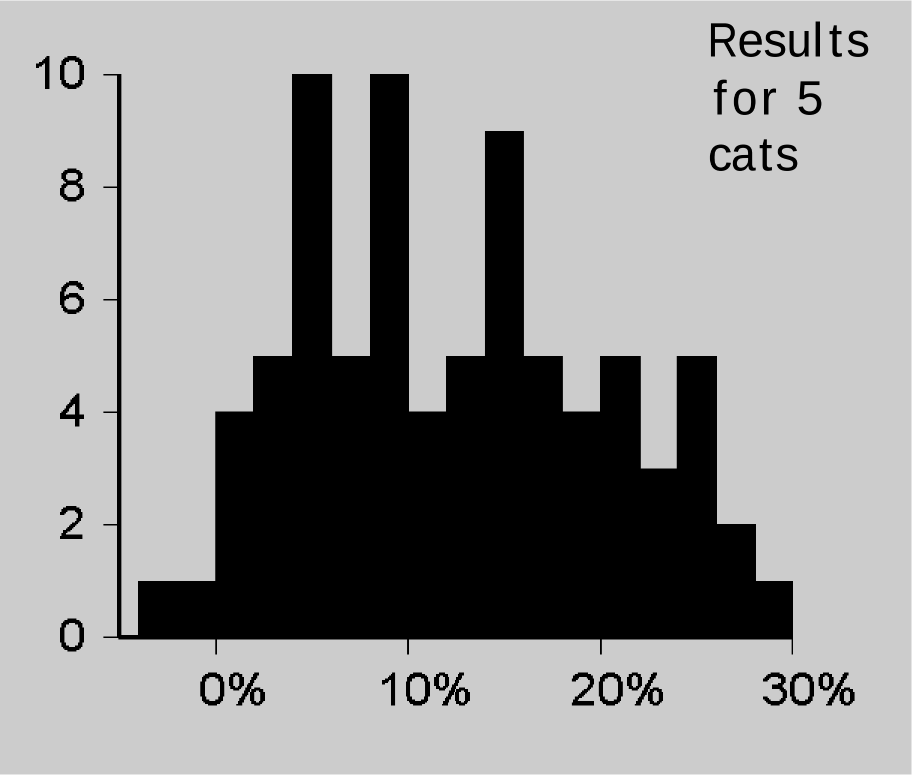
Coverage test applied to model map



Test 1: sliding perturbations



Test 1: rotations and flips



Results for 5 cats

% increase in *c*'

Comparison of coverage between model and real maps

	λ_{OD}	λ_{SF}	λ_{ORI}	*Coverage* (*c*’)
Real Maps				
Cat 1	28	44	27	0.412
Cat 2	37	30	26	0.446
Cat 3	69	25	26	0.537
Cat 4	35	25	27	0.432
Model Maps				
EL8.003	34	36	27	0.345
EL9.001	32	33	30	0.304
KO6.001	31	27	27	0.307
KO7.001	33	26	30	0.285

Reasons why measured c' values might be worse in real maps:

- development does a poor job of optimising
- experimental errors in determining the locations of domain boundaries may artefactually worsen coverage
- the target stimulus distribution may not be uniform, as was assumed
- the model maps are not a structurally realistic basis for an exact comparison

How many maps are there in visual cortex?

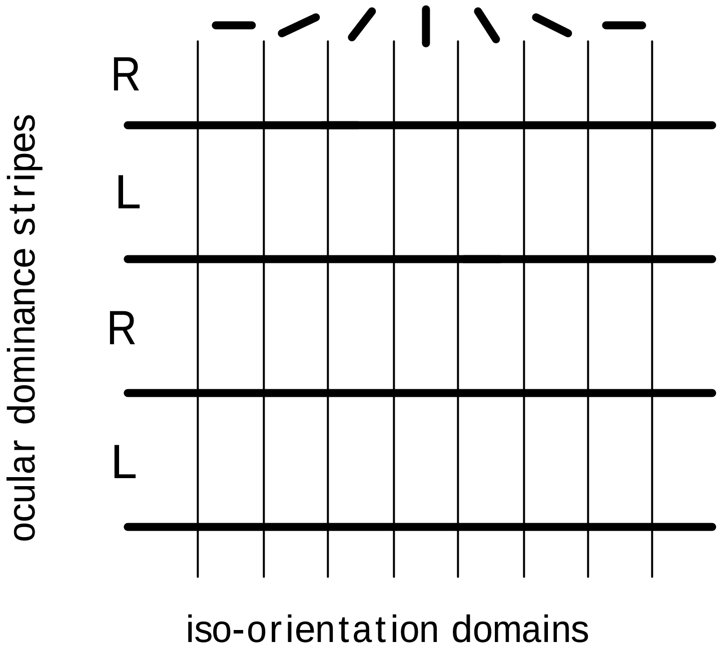
Given N binary features, each of which is represented in a periodic, stripe-like map, how many maps can be overlaid so that all 2^N combinations get represented reasonably often (i.e. with good coverage) ?

One limit on the number of maps is the number of cortical columns available to represent 2^N features within the region of cortex available to each retinotopic location (the cortical point image). This region is about 1 - 2 mm in diameter.

The smallest functional columnar unit in the cortex is likely to be a mini-column, about 30 - 50 µm in diameter. This leads to an upper limit of about 10 maps, assuming the geometrical problem can be solved. Can it be solved?

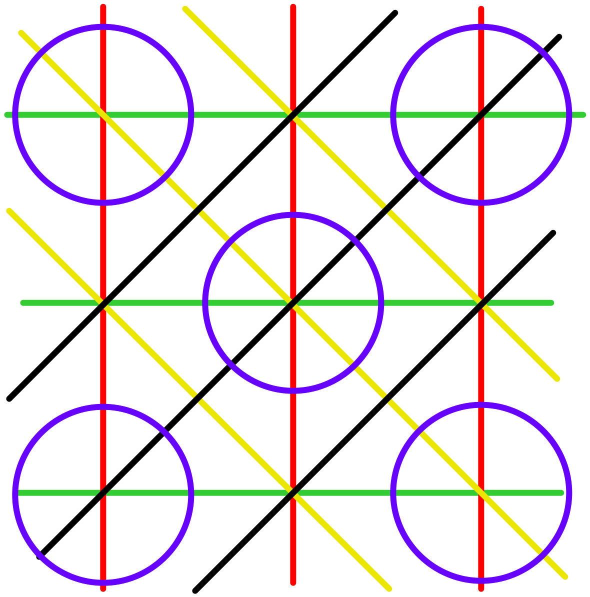
Simple Ways of Combining Maps to Optimise Coverage

Hubel and Wiesel’s ice-cube model

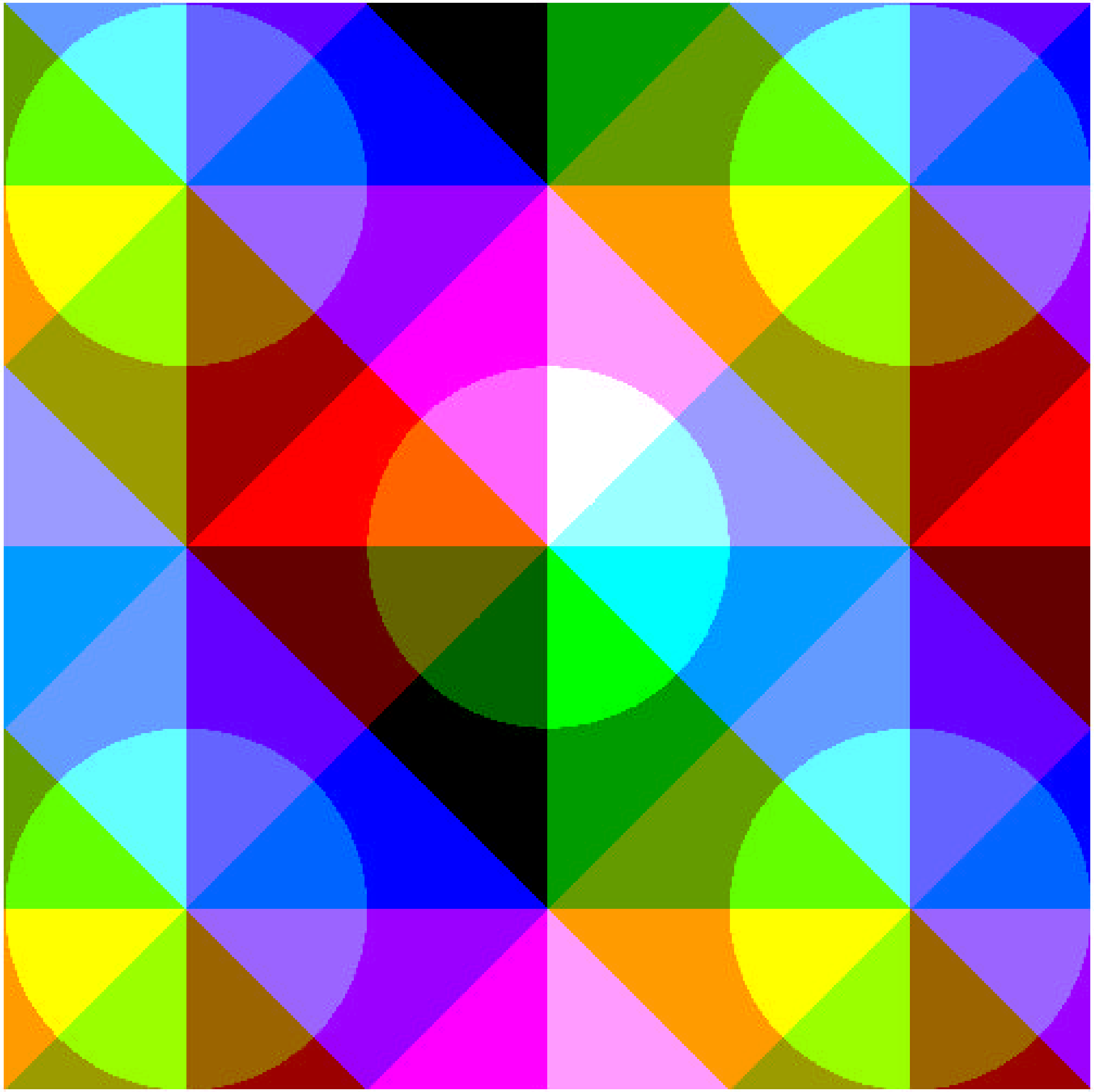


A solution for two maps

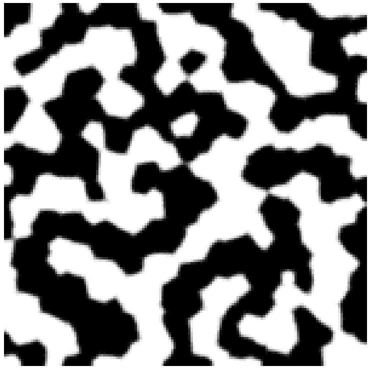
The Egg-carton Model



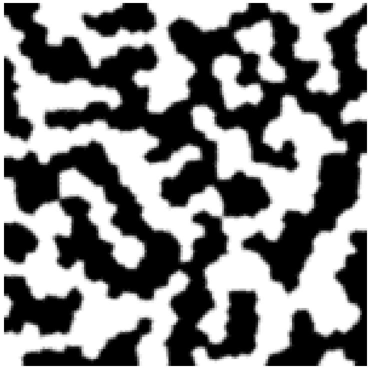
A solution for five maps



Protomap morphology is little affected by N:

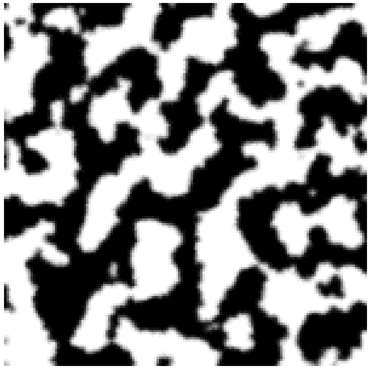


$N=2$



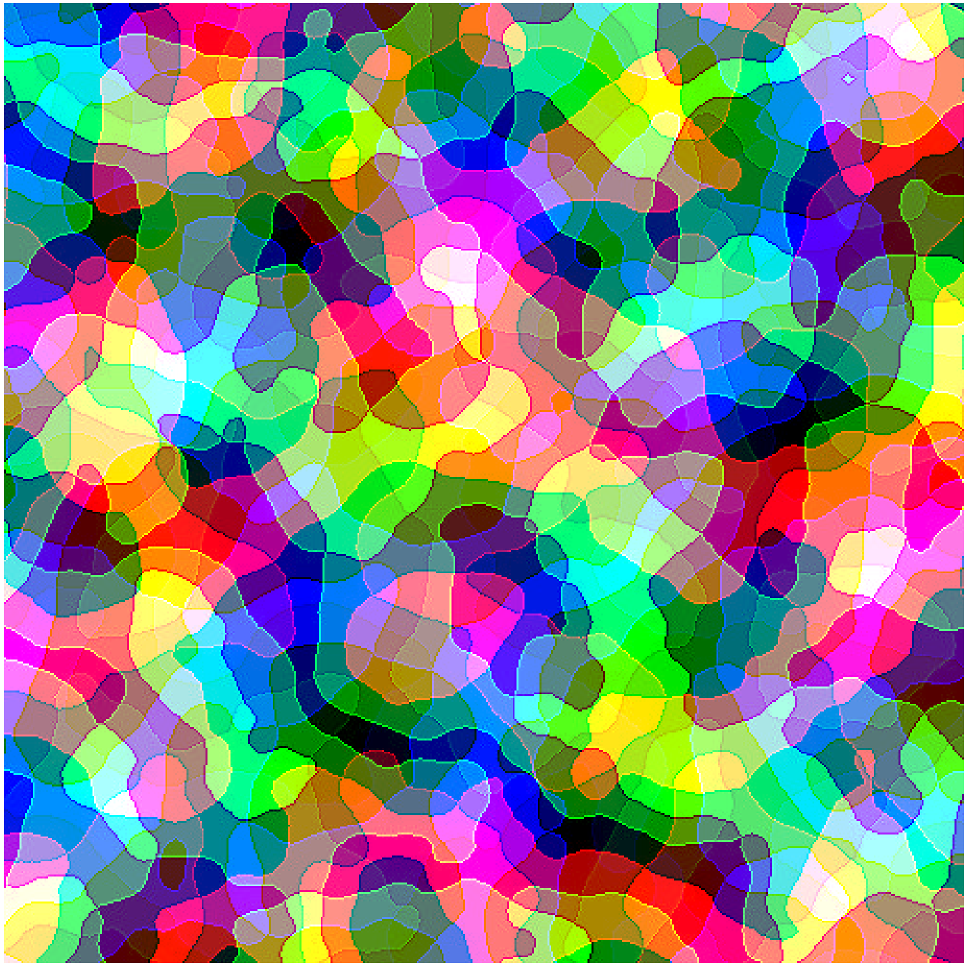
$N=4$

$N=6$



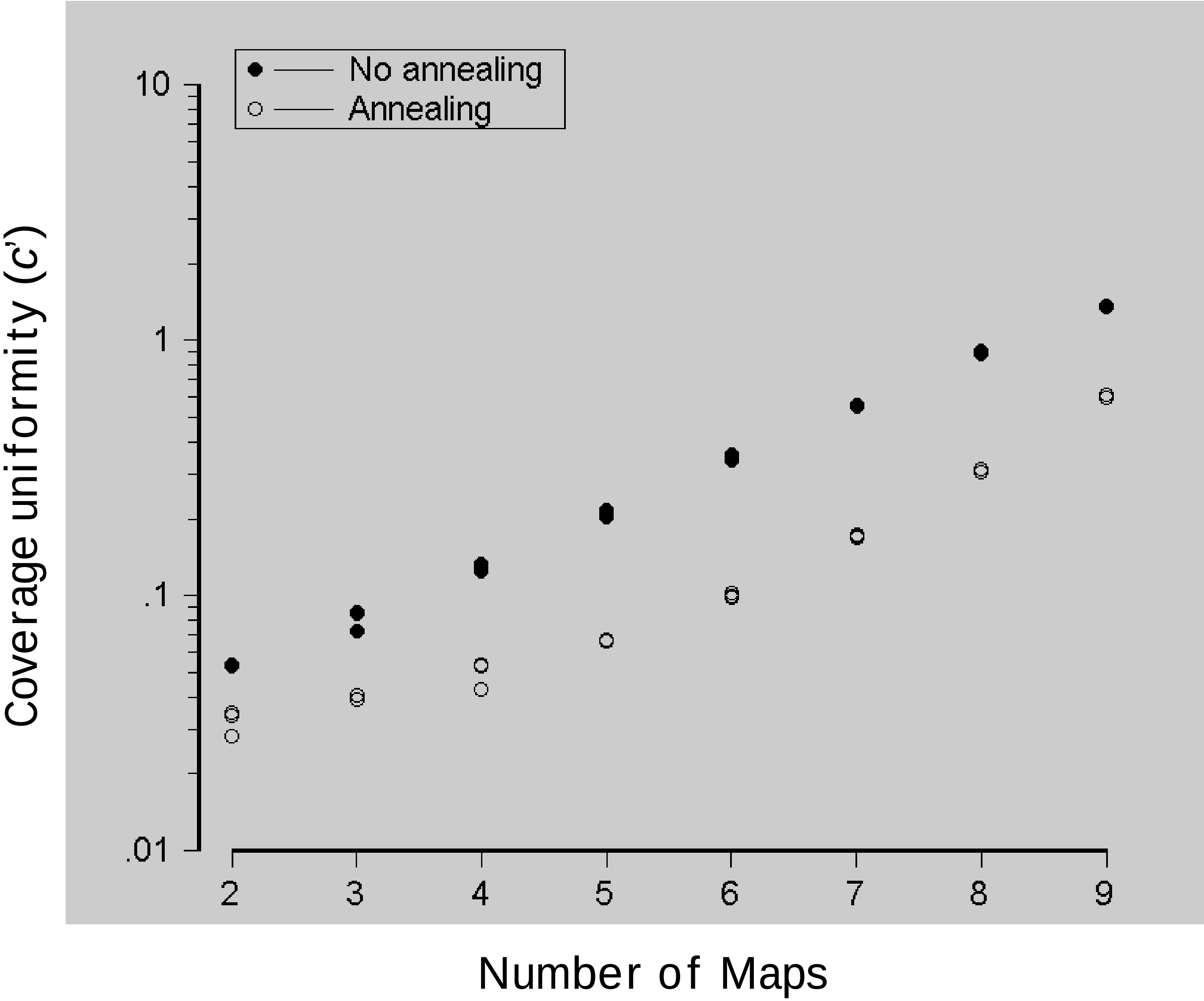
$N=8$

Polymap for 8 binary features

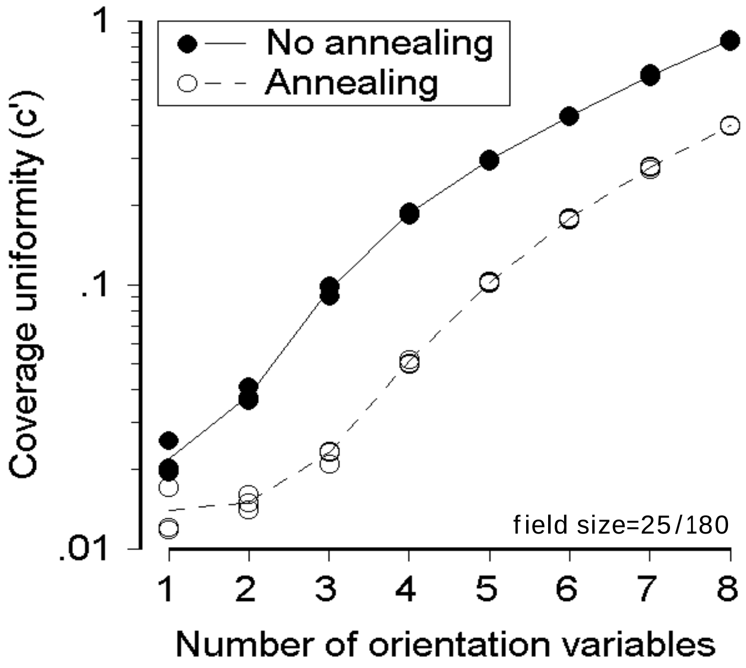


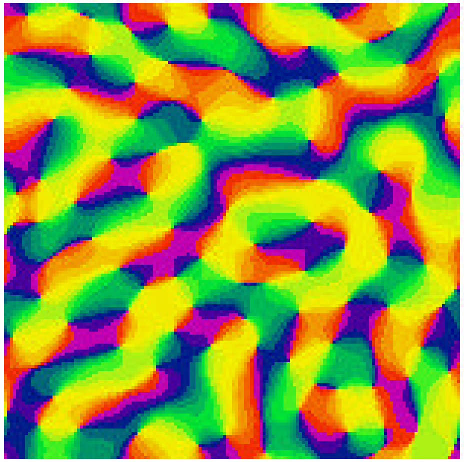
N=8

Binary Feature Maps



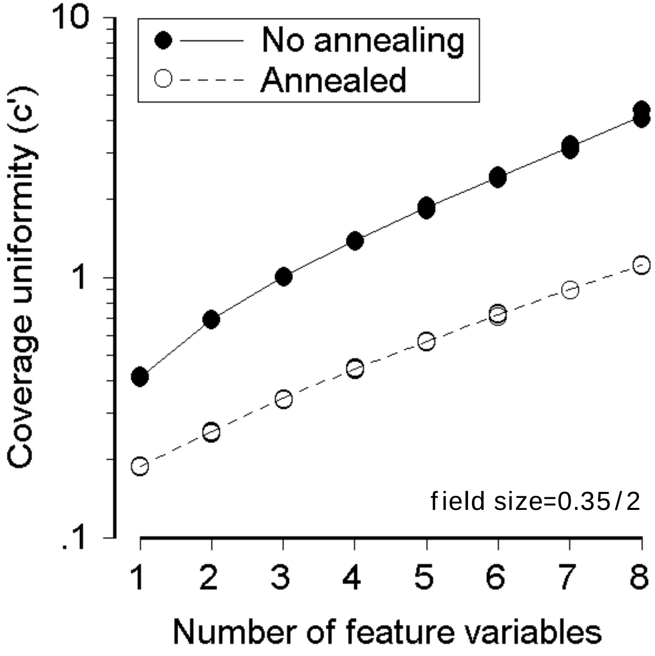
Angular

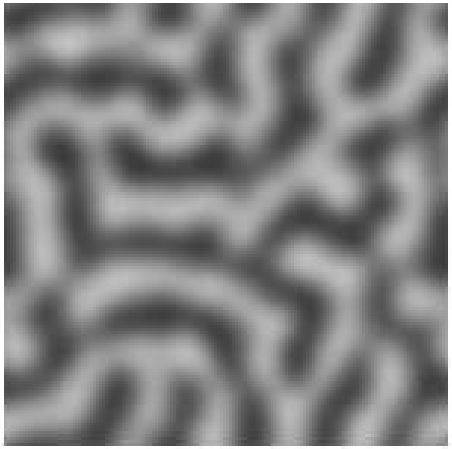




N=4

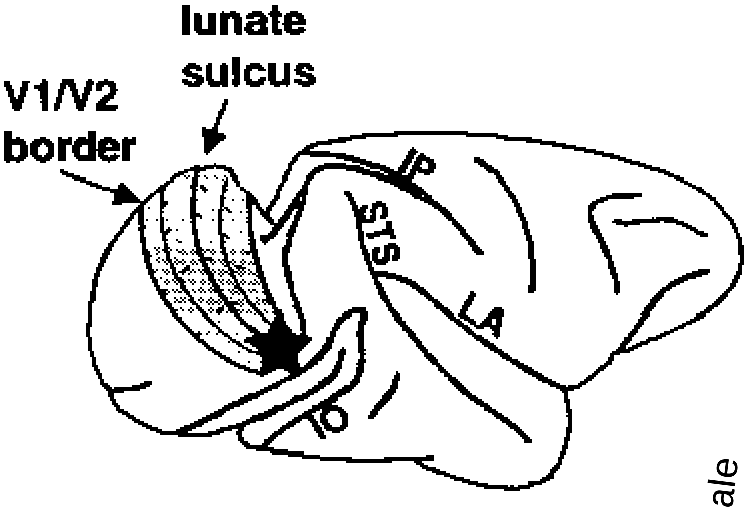
Scalar

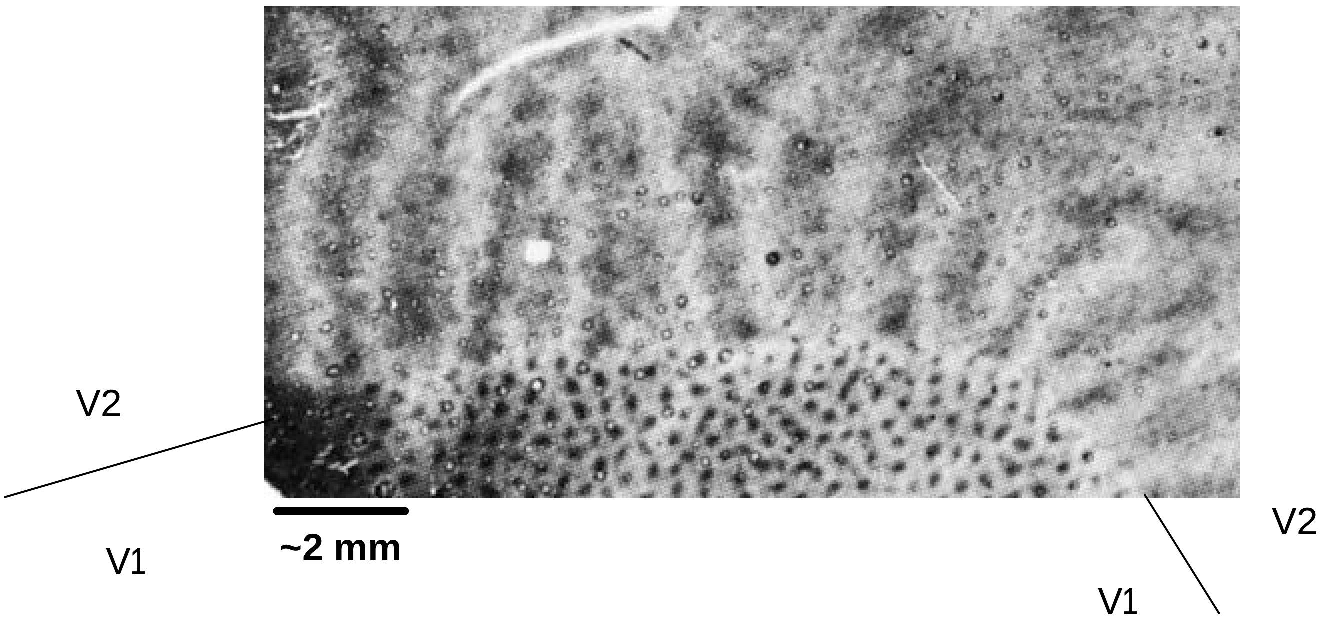




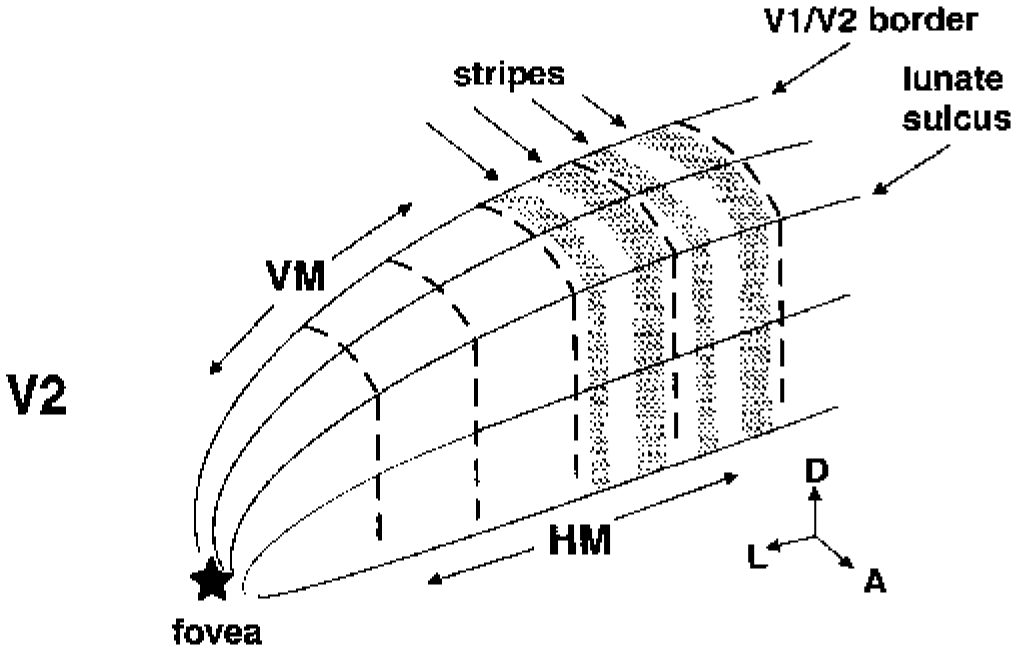
N=4

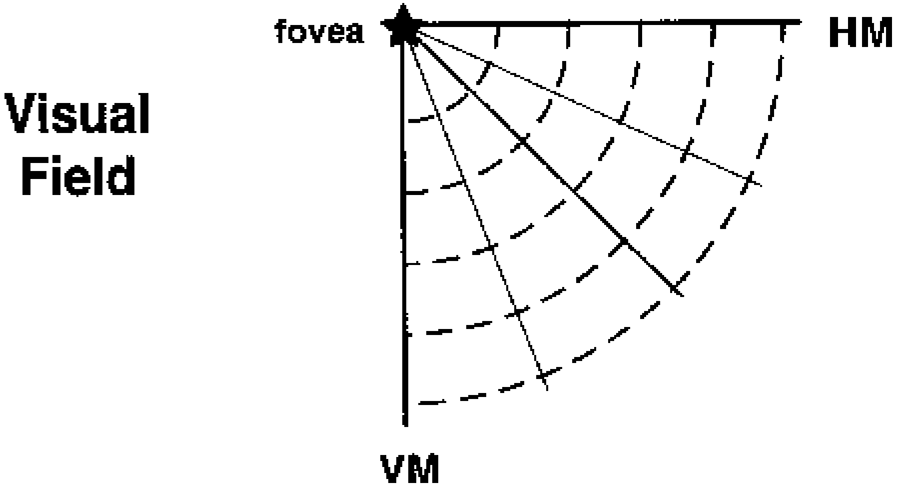
V2 Structure revealed by CO histochemistry

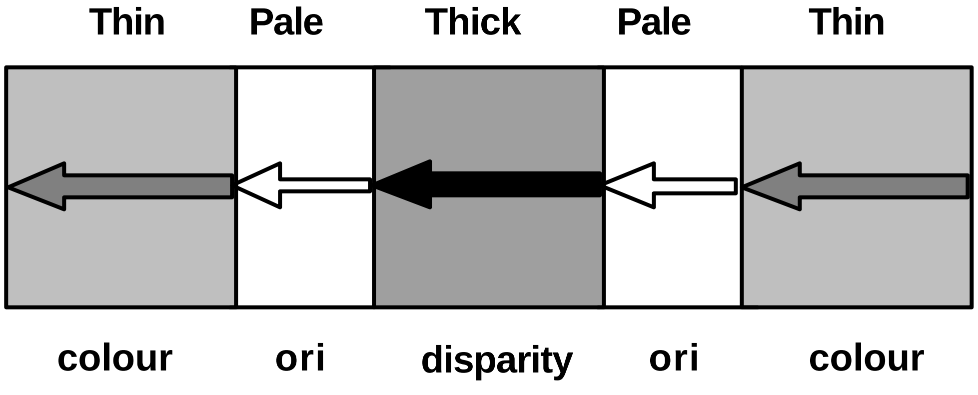




from Tootell et al., Science, 1983


V1/V2 border
stripes
lunate sulcus
VM
V2
HM
D
L
A
fovea

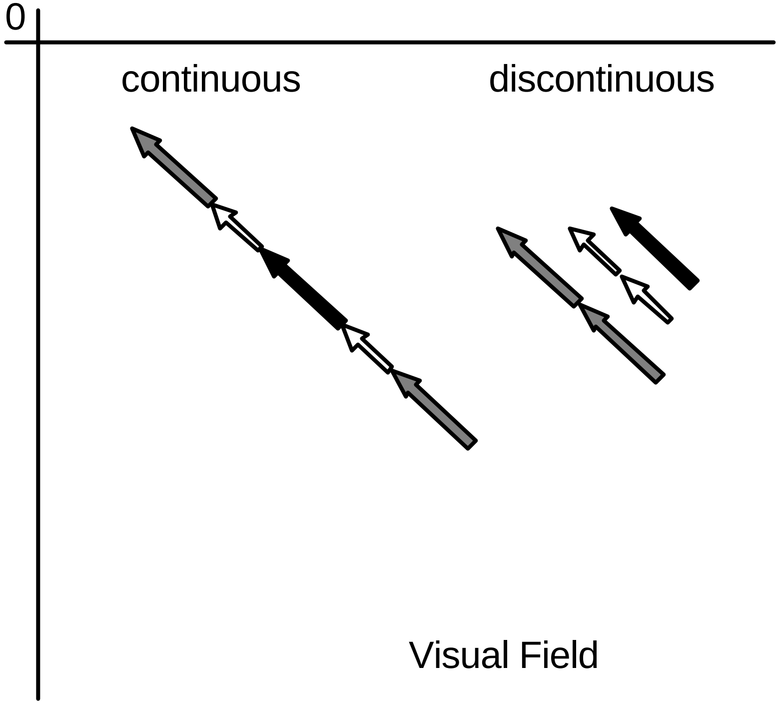

fovea
HM
Visual Field
VM



Thin **Pale** **Thick** **Pale** **Thin**

colour **ori** **disparity** **ori** **colour**

V2 stripes



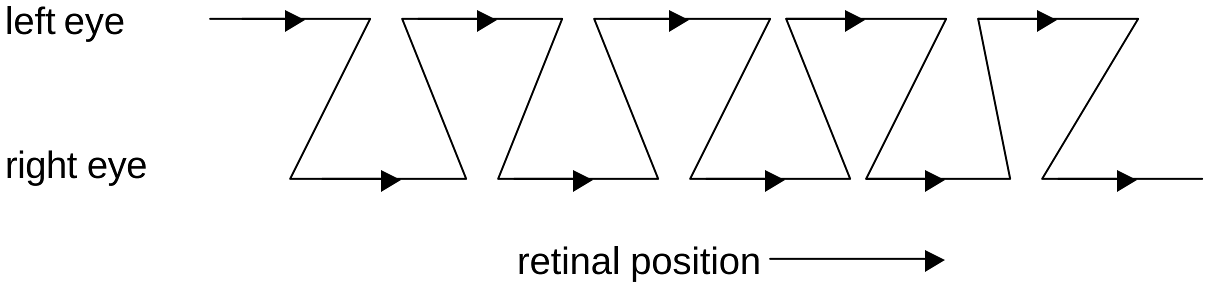
0

continuous

discontinuous

Visual Field

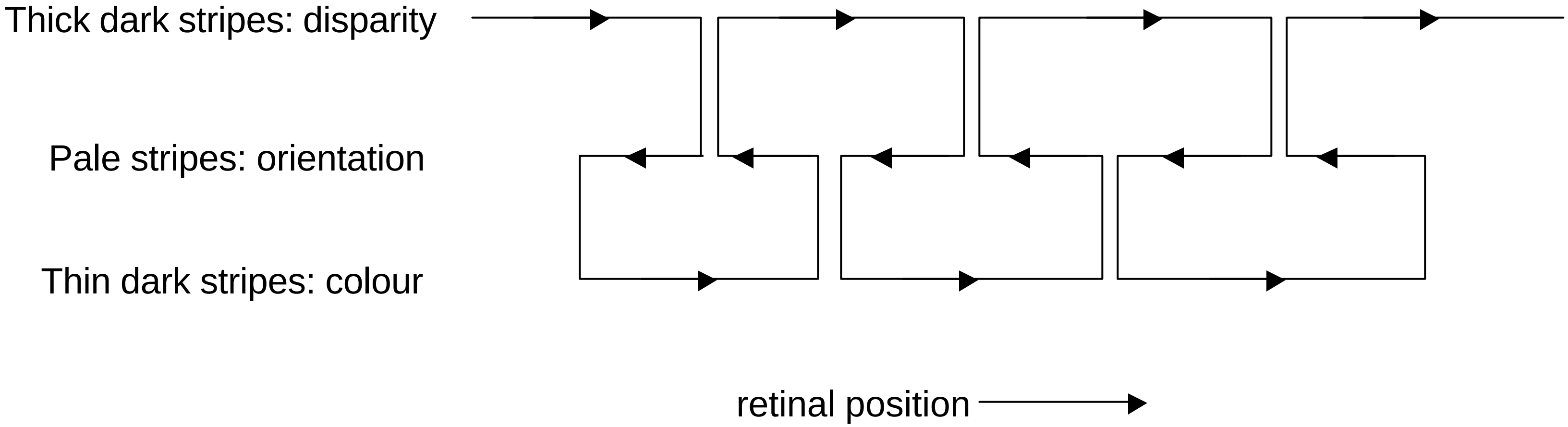
redrawn from Roe and Ts'o, J. Neurosci., 1995



left eye

right eye

retinal position

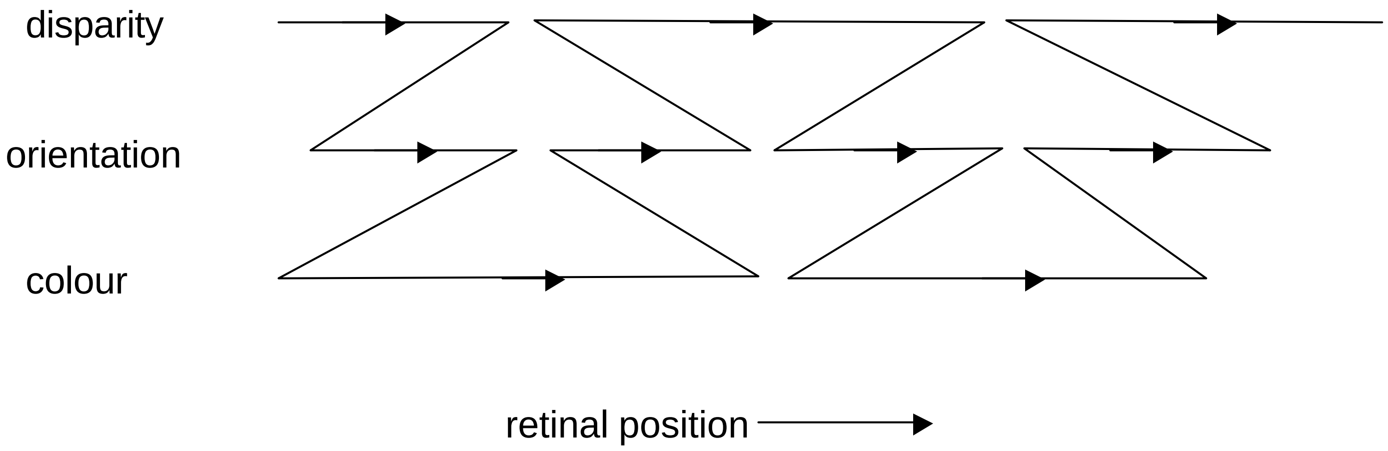


Thick dark stripes: disparity

Pale stripes: orientation

Thin dark stripes: colour

retinal position

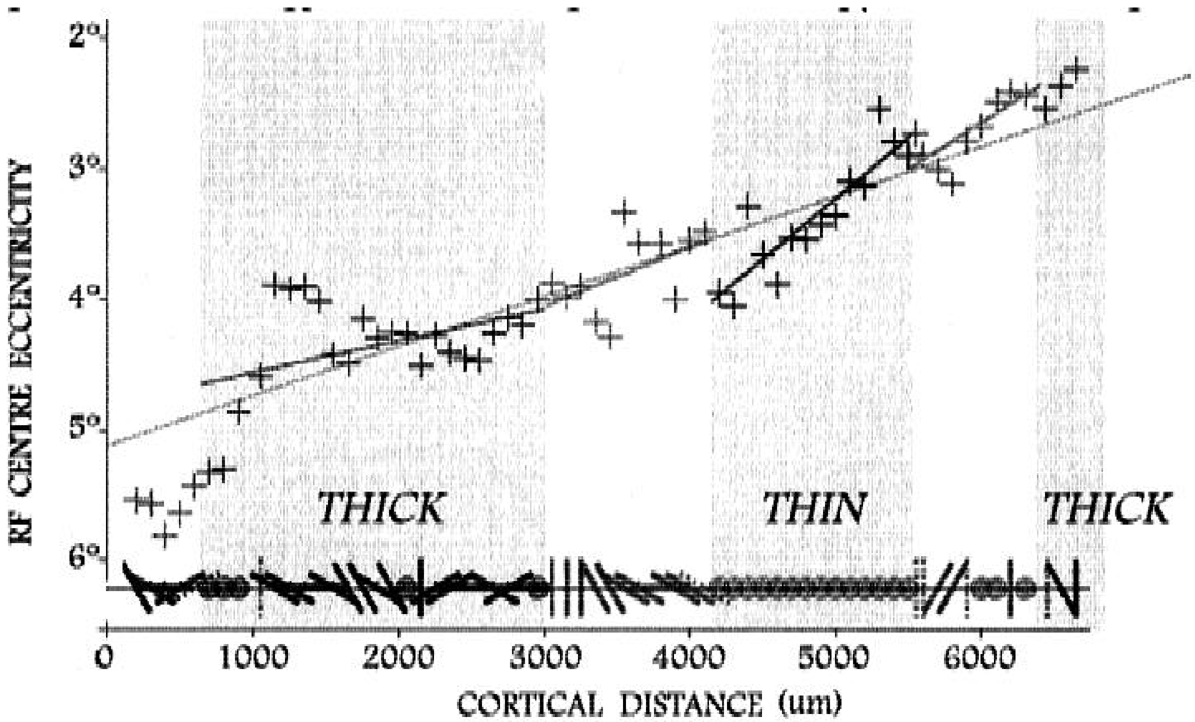


disparity

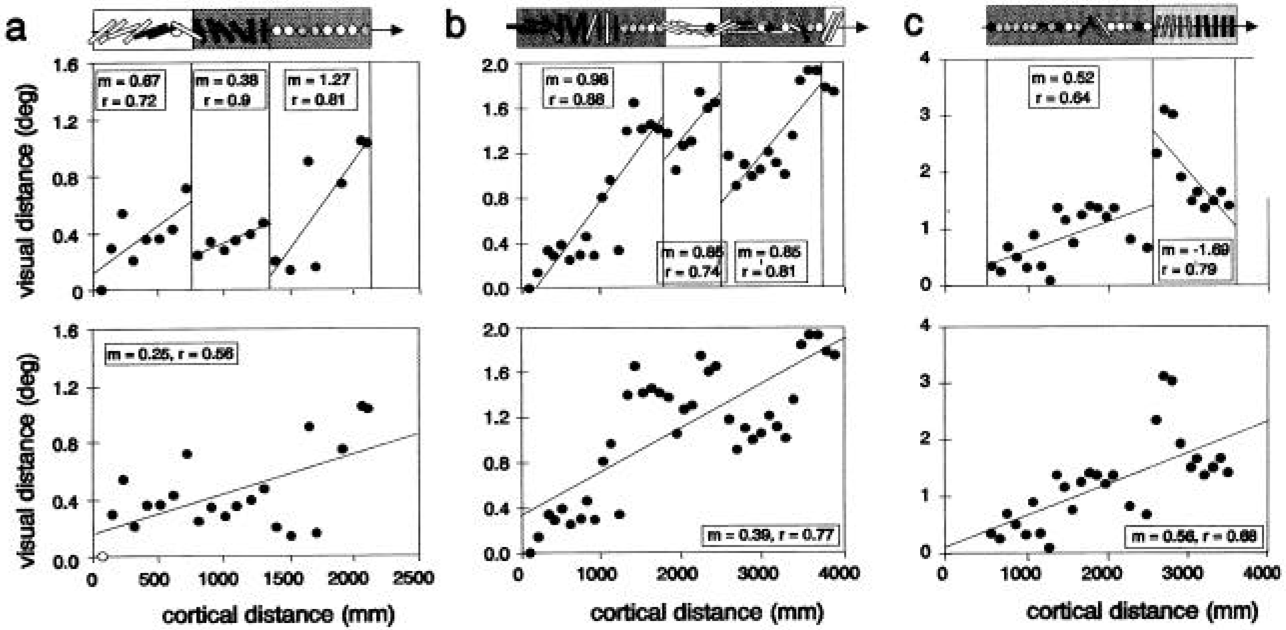
orientation

colour

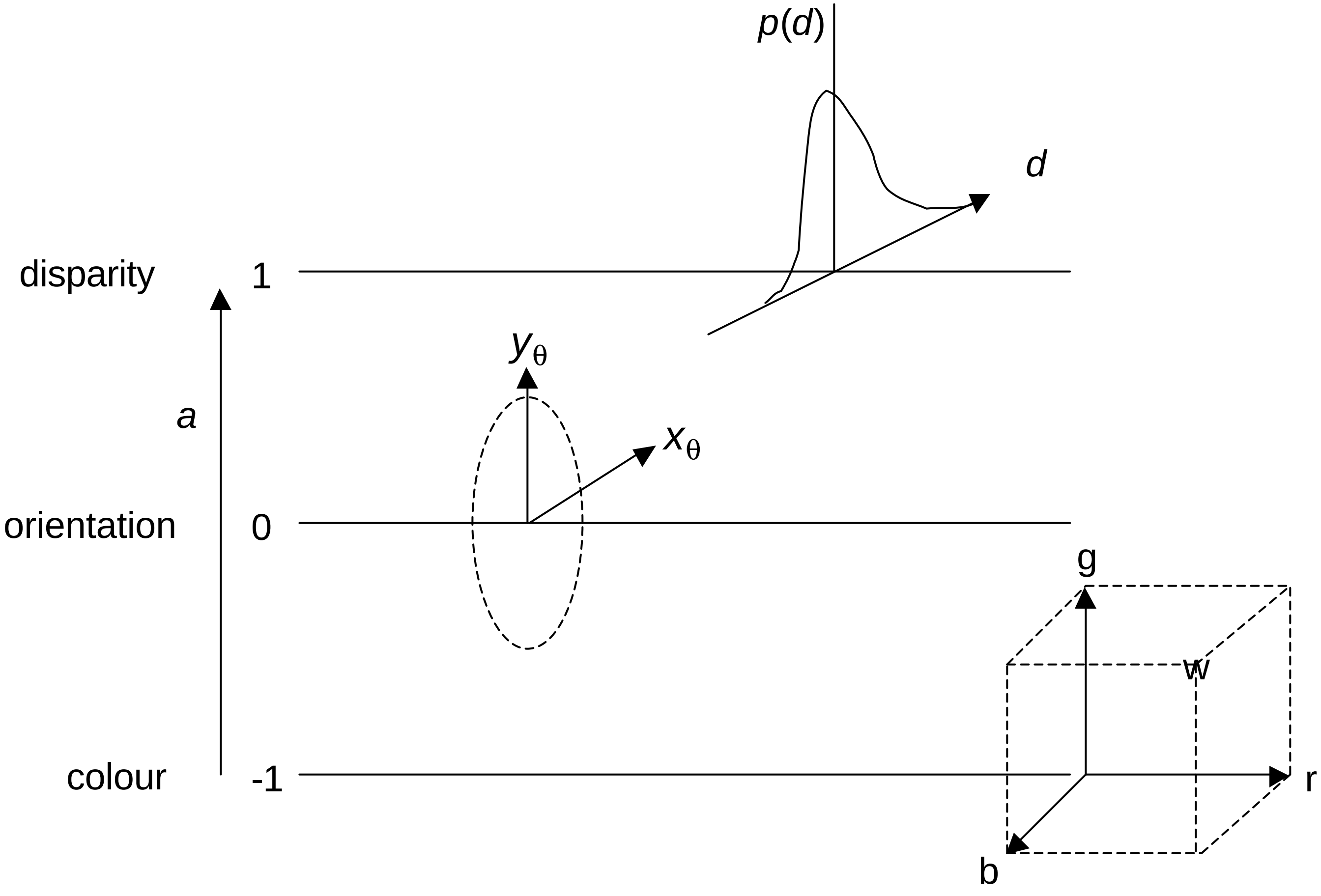
retinal position



Shipp & Zeki, *Vis. Neurosci*., 2002

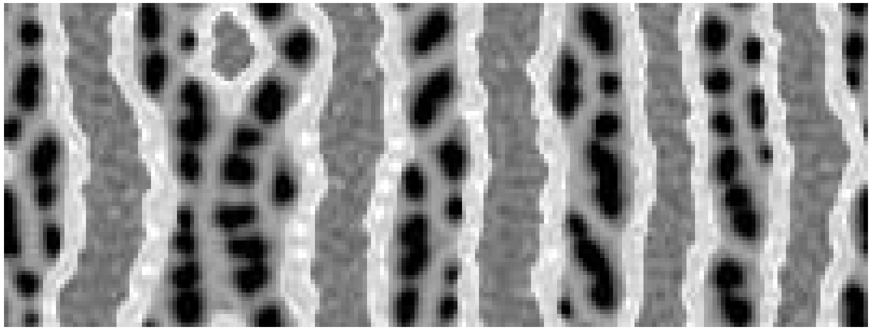


Roe & Ts'o, *J. Neurosci*., 1995

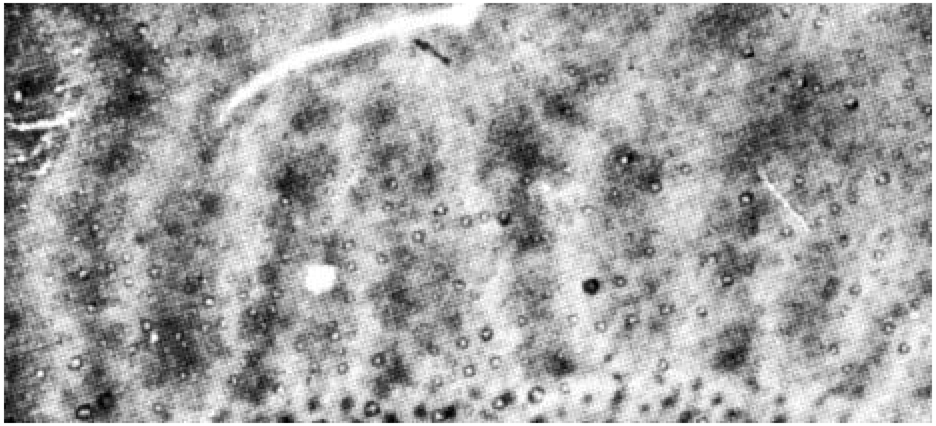


$$\mathbf{v}=\{\underbrace{x,\ y}_{\text{visual space}},\ \underset{\uparrow\ \text{‘mapping’ dimension}}{a},\ \underbrace{x_{\theta},\ y_{\theta}}_{\text{orientation}},\ \underset{\uparrow\ \text{disparity}}{d},\ \underbrace{r,\ g,\ b}_{\text{colour}}\}$$

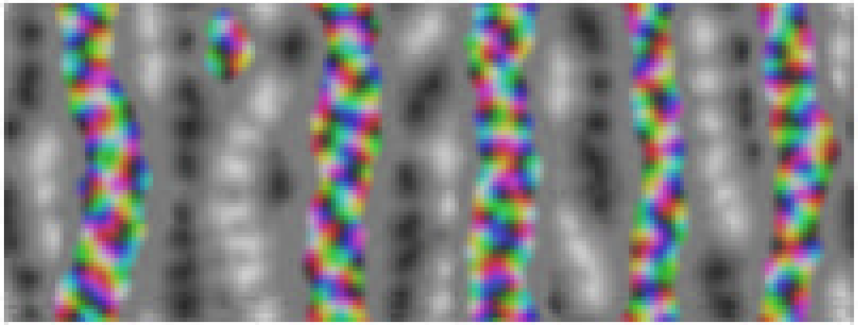
Simulation showing modulus of feature vector

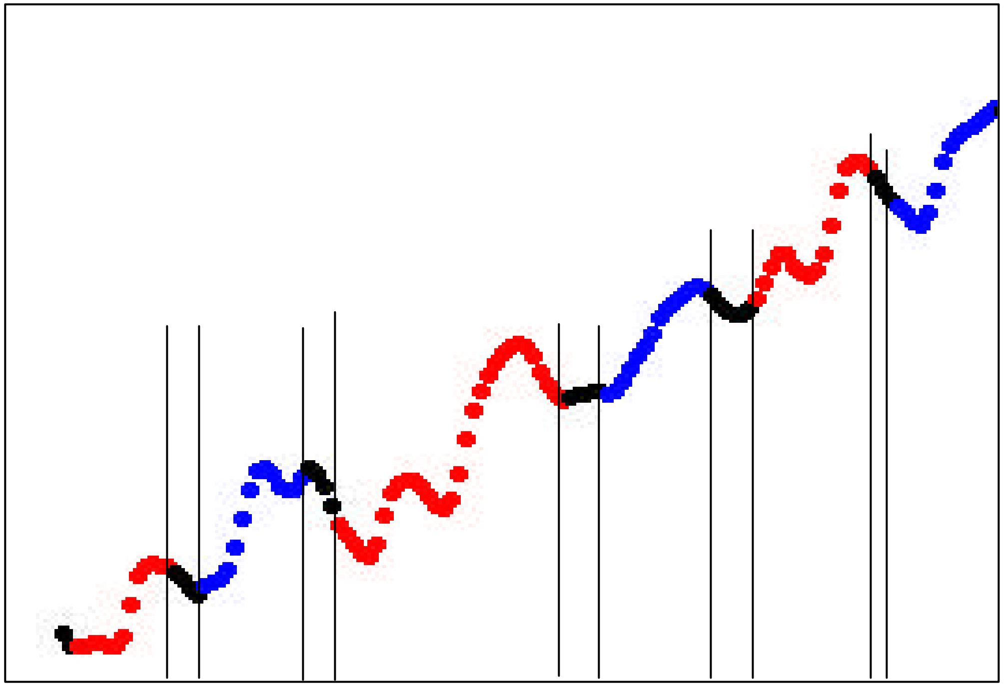


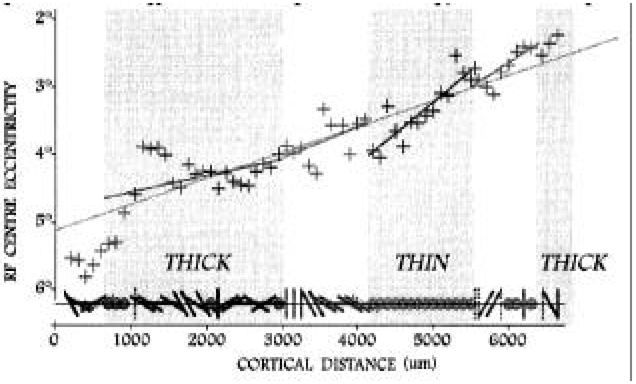
CO staining pattern in V2 of squirrel monkey



Simulation showing colour/luminance domains in ’thin stripes’ and disparity domains in ‘thick’ stripes






RF CENTRE ECCENTRICITY
2°
3°
4°
5°
6°
THICK
THIN
THICK
0
1000
2000
3000
4000
5000
6000
CORTICAL DISTANCE (um)