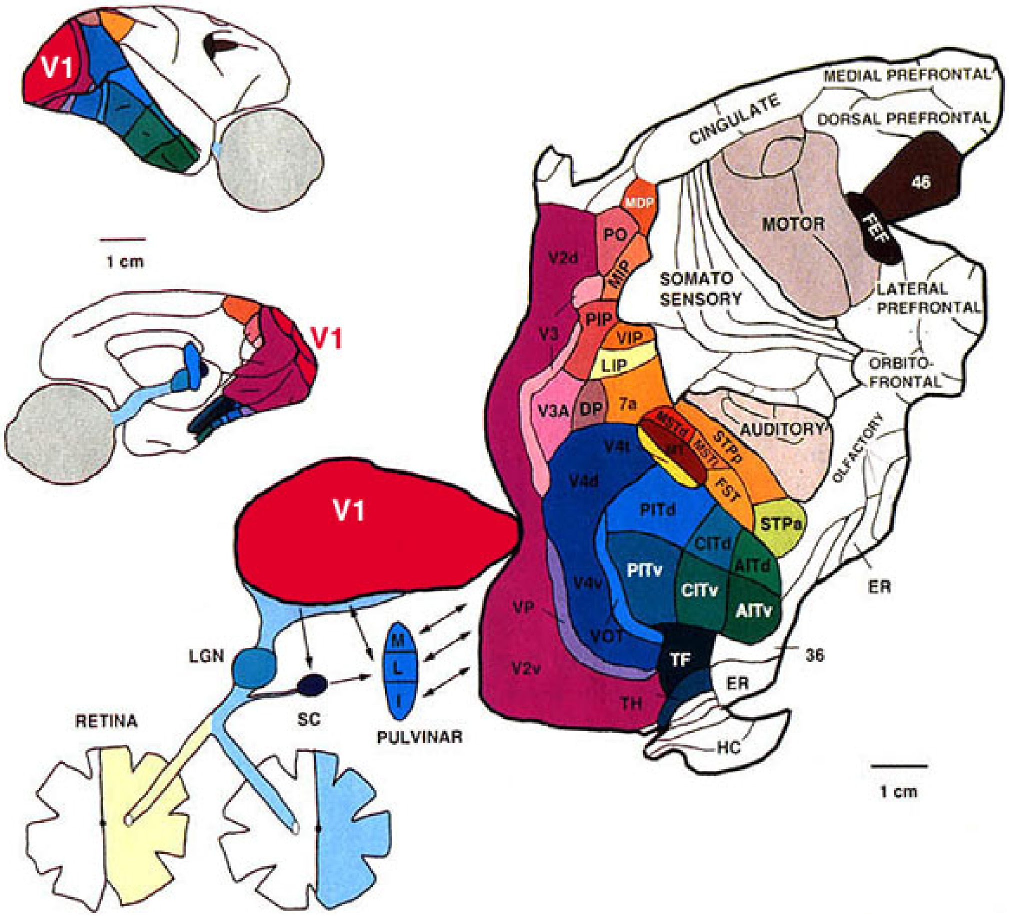
Visual cortex maps, feedback connections and apical dendrites

Nicholas Swindale

Ophthalmology and Visual Sciences,
University of British Columbia


V1
1 cm
V1
V1
CINGULATE
MEDIAL PREFRONTAL
DORSAL PREFRONTAL
46
FEF
MOTOR
SOMATO SENSORY
LATERAL PREFRONTAL
ORBITO-FRONTAL
OLFACTORY
AUDITORY
MDP
PO
MIP
V2d
V3
PIP
VIP
LIP
V3A
DP
7a
MSTd
MT
MSTl
STPp
FST
V4t
V4d
PITd
CITd
AITd
STPa
PITv
CITv
AITv
V4v
VOT
VP
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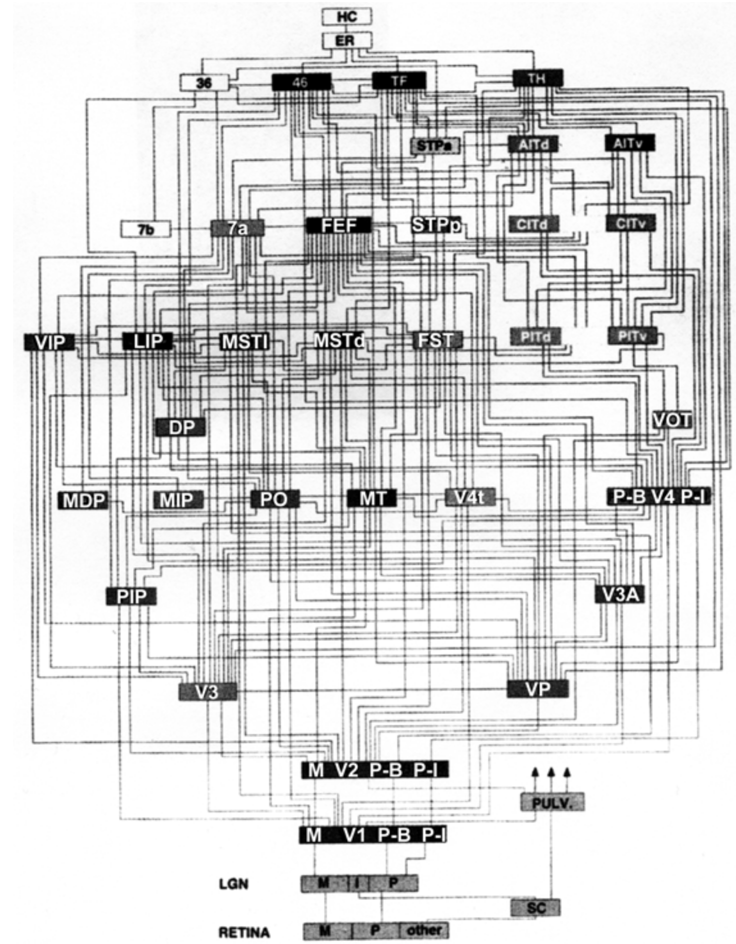
TF
TH
ER
36
HC
ER
LGN
SC
M
L
I
PULVINAR
RETINA
1 cm


HC
ER
36
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TF
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AITd
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FEF
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PITd
PITv
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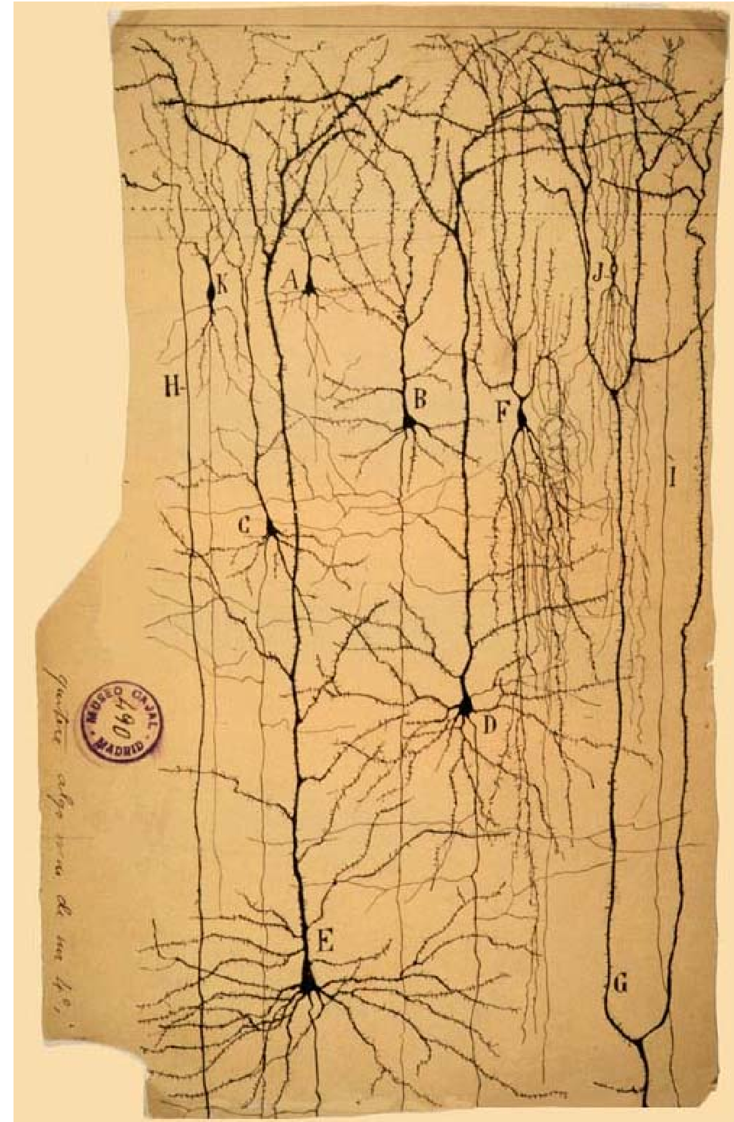
MIP
PO
MT
V4t
P-B V4 P-I
PIP
V3A
V3
VP
M V2 P-B P-I
PULV.
M V1 P-B P-I
LGN
M I P
SC
RETINA
M P other

Feedback Pathways:

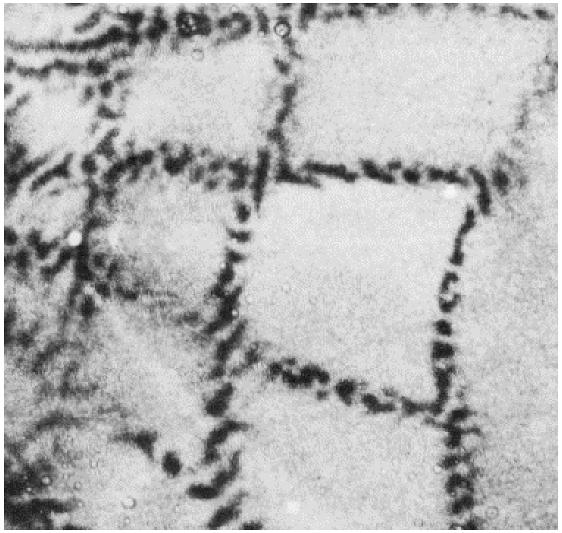
- usually present where there are feedforward connections
- at least as numerous as feedforward connections
- conduct as rapidly as feedforward connections
- often have wider tangential distributions than feedforward connections
- anatomical distribution may be patchy, matching patchy arrangement of cortical properties, such as orientation preference (Shmuel et al., 2005)
- evidence they play a role in conscious perception (Pascual-Leone et al., 2000)

Ideas about the functions of Feedback Pathways:

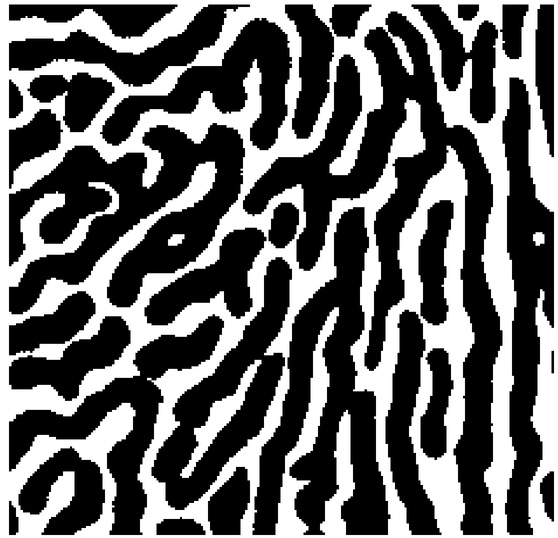
- have a slow 'modulatory' role
- model the feedforward pattern of activity (Grossberg, Mumford)
- predict what is coming next
- cancel the pattern of feedforward activity allowing the brain to minimise its activity levels in the face of unpredictable inputs
- silent by day, active at night, maybe during dreams
- code prior probability of stimulus (Bayesian models)
- mediate top-down attentional effects
- message verification
- ...



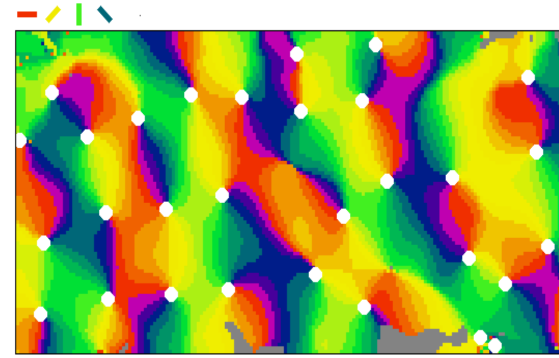
http://brainmaps.org



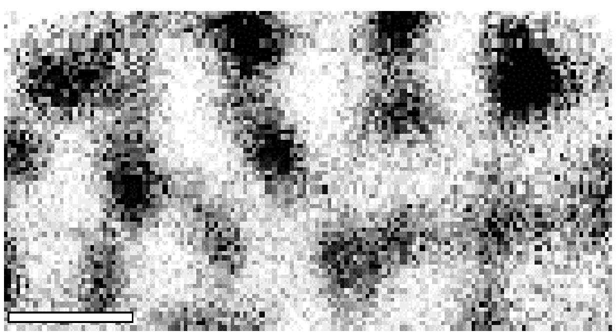
Retinotopy



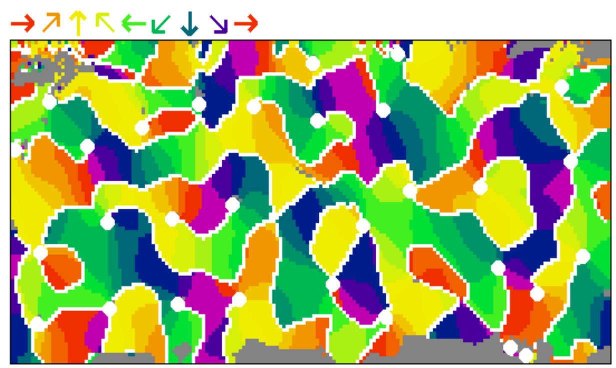
Ocular Dominance



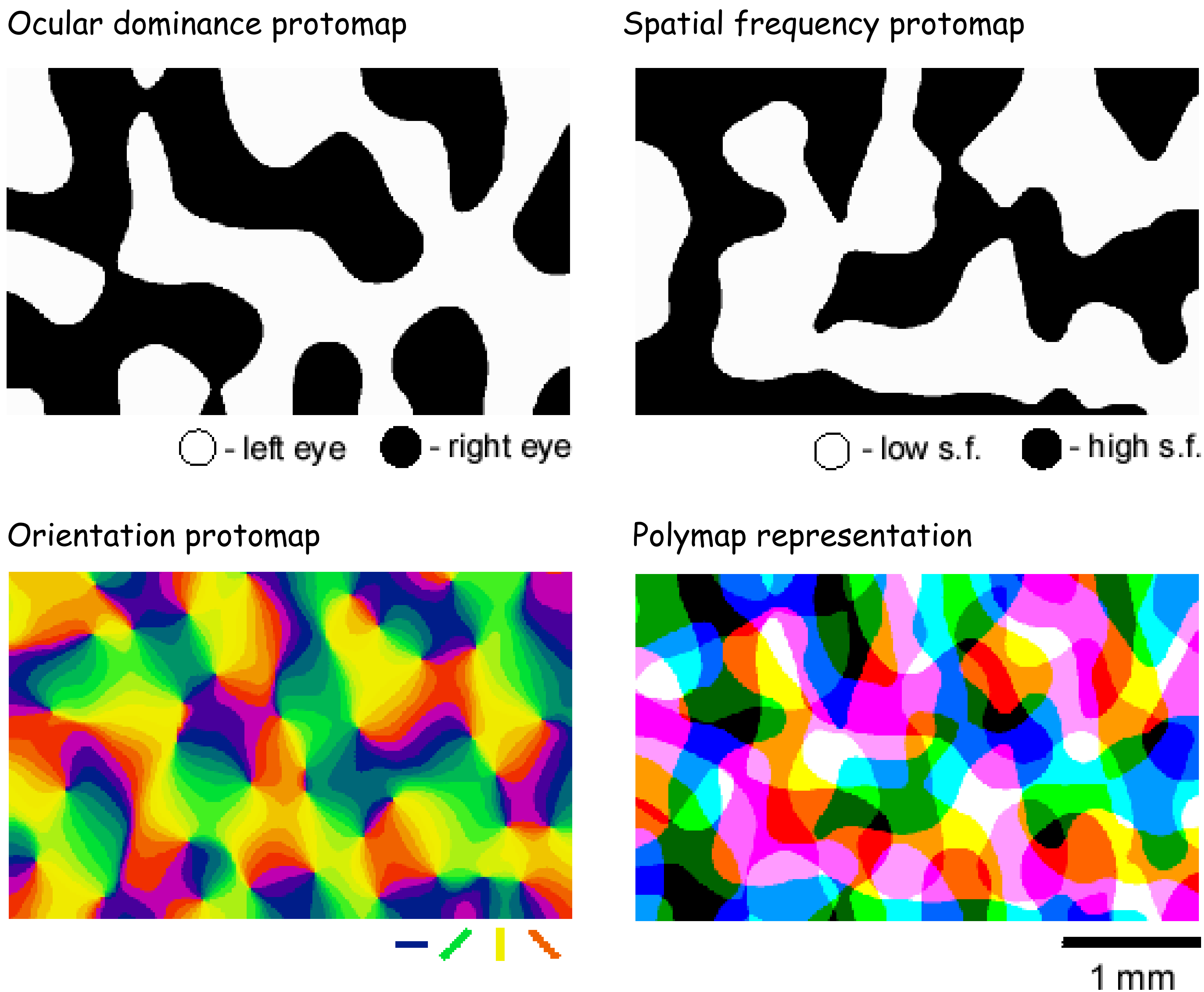
Orientation



Spatial Frequency



Direction Preference


Ocular dominance protomap
- left eye
- right eye
Spatial frequency protomap
- low s.f.
- high s.f.
Orientation protomap
Polymap representation
1 mm

Separable Tuning Functions

visual cortex receptive fields can often be approximated as the product of a set of tuning functions for different parameters, e.g. spatial frequency, retinal position and orientation

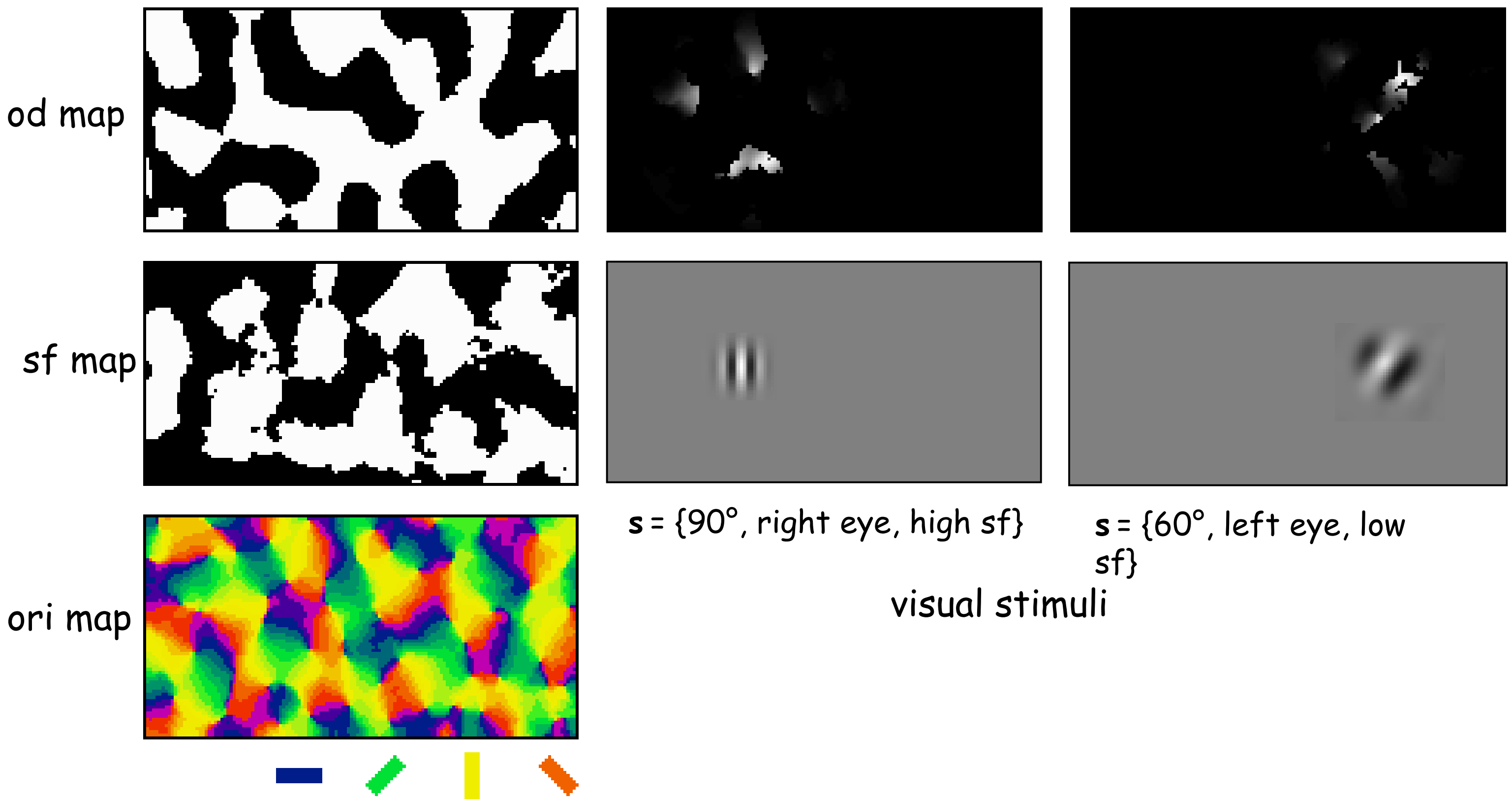
For example, a receptive field with preferred orientation, θ, and retinal position, x, y, can be given as the product of 3 Gaussians:

$$f(x,y,\theta) = R_m e^{-\frac{(x-x_0)^2}{2\sigma_x^2}} . e^{-\frac{(y-y_0)^2}{2\sigma_y^2}} . e^{-\frac{(\theta-\theta_0)^2}{2\sigma_\theta^2}}$$

This means the best value of one parameter can be established independently of the values of the others.

This assumption is critical for the model I will propose, and is also central to the idea of superimposed maps within cortical areas such as visual cortex.

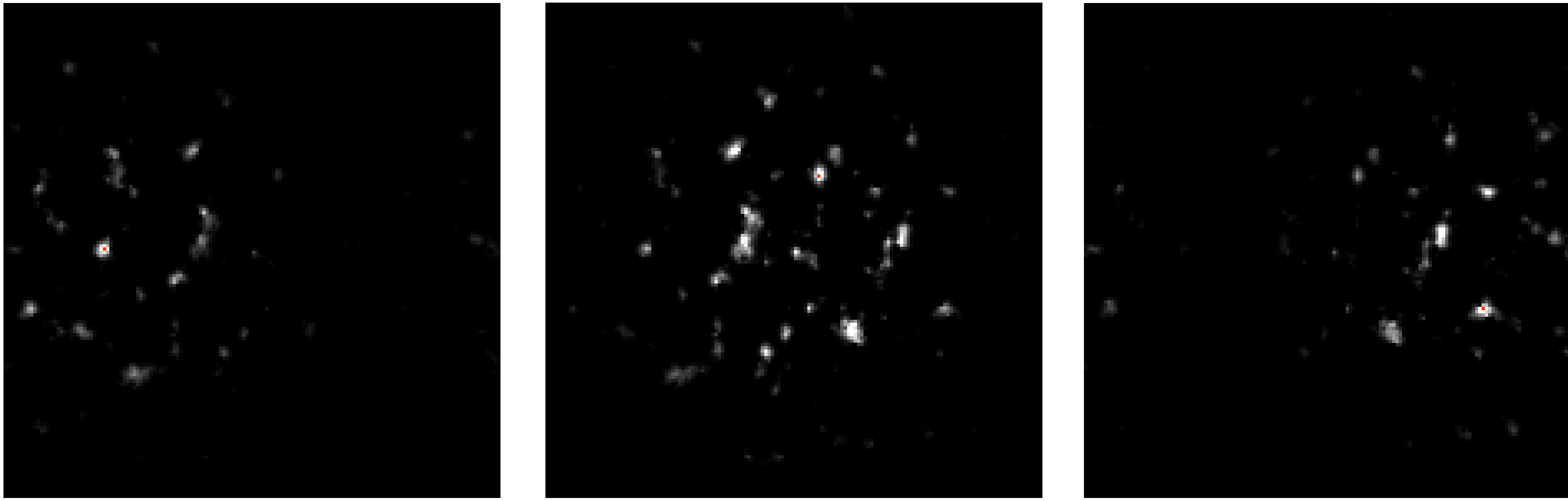
Population codes and maps



Patterns of activity evoked in cat visual cortex by a small monocular grating patch of high or low spatial frequency. Note that these patterns are the <u>product</u> of a) the ocular dominance pattern for a given eye b) the spatial frequency pattern c) the single condition response to a given orientation and d) the cortical point image.

Photograph of area TE of monkey infero-temporal cortex. Regions of cortex shown by optical recording to be activated by a particular visual stimulus (intermediate complexity visual features, including faces) are outlined in the same colour. Particular stimuli evoke responses in multiple patchy locations.

Wang et al., *Neuroscience Research*, 1998.



Population activity patterns in a simulated map of a 4D orientation space plus a 2D retina. The stimulus has 4 angular components, plus a position in visual space. The *x*-component of spatial position is varied in the 3 panels. How would you decode such complex patterns?

One possibility:

The brain generates a hypothesis about the stimulus: i.e. it tries to model the spatial pattern of cortical activity caused by the stimulus

Feedback fibres, acting in combination, can do this efficiently

I.e. feedback tries to model, or predict, the pattern of feedforward activity (not a new idea).

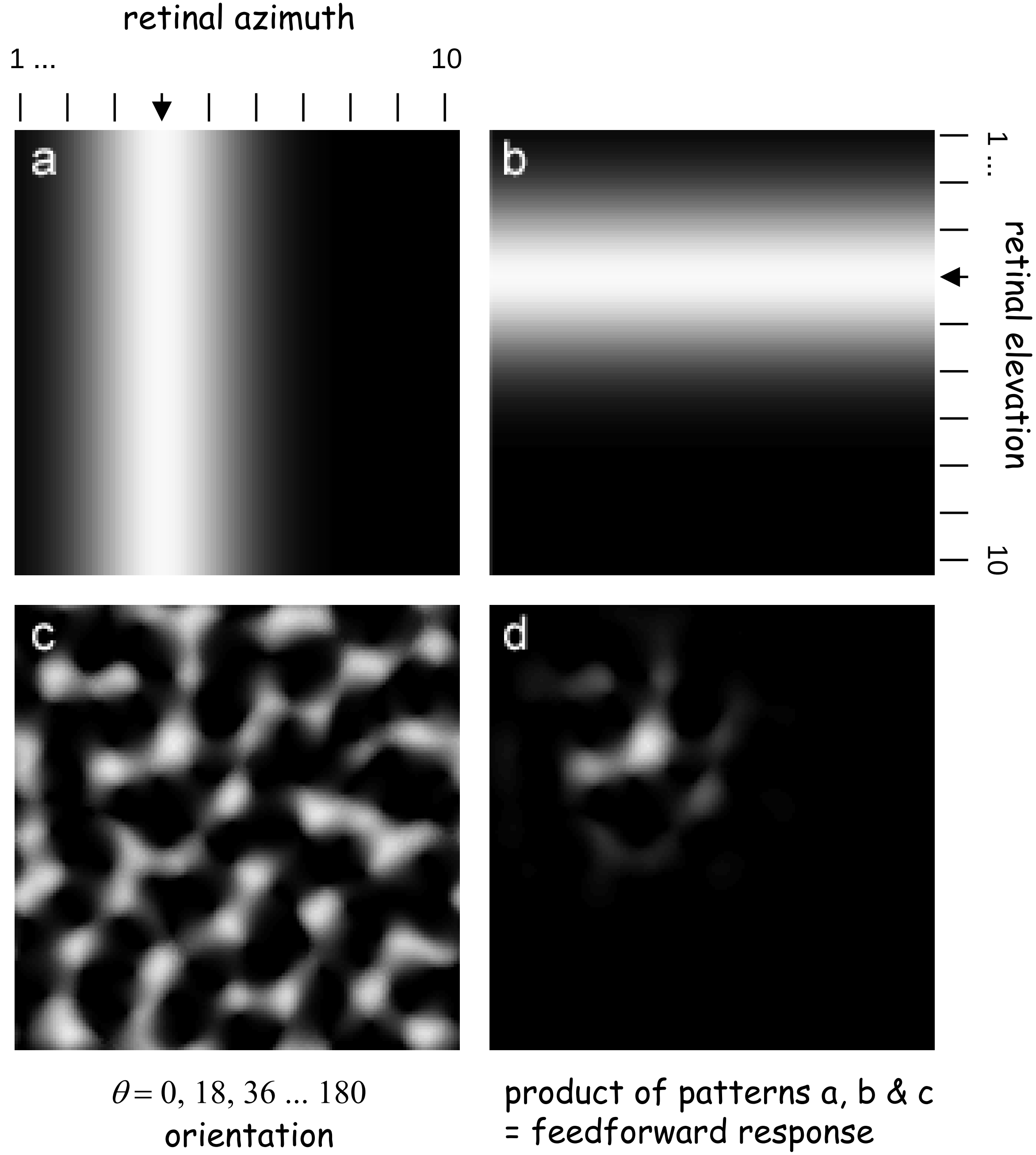
In this example there are 3 dimensions: elevation, azimuth and orientation; assume there are 10 possible values to be coded along each dimension.

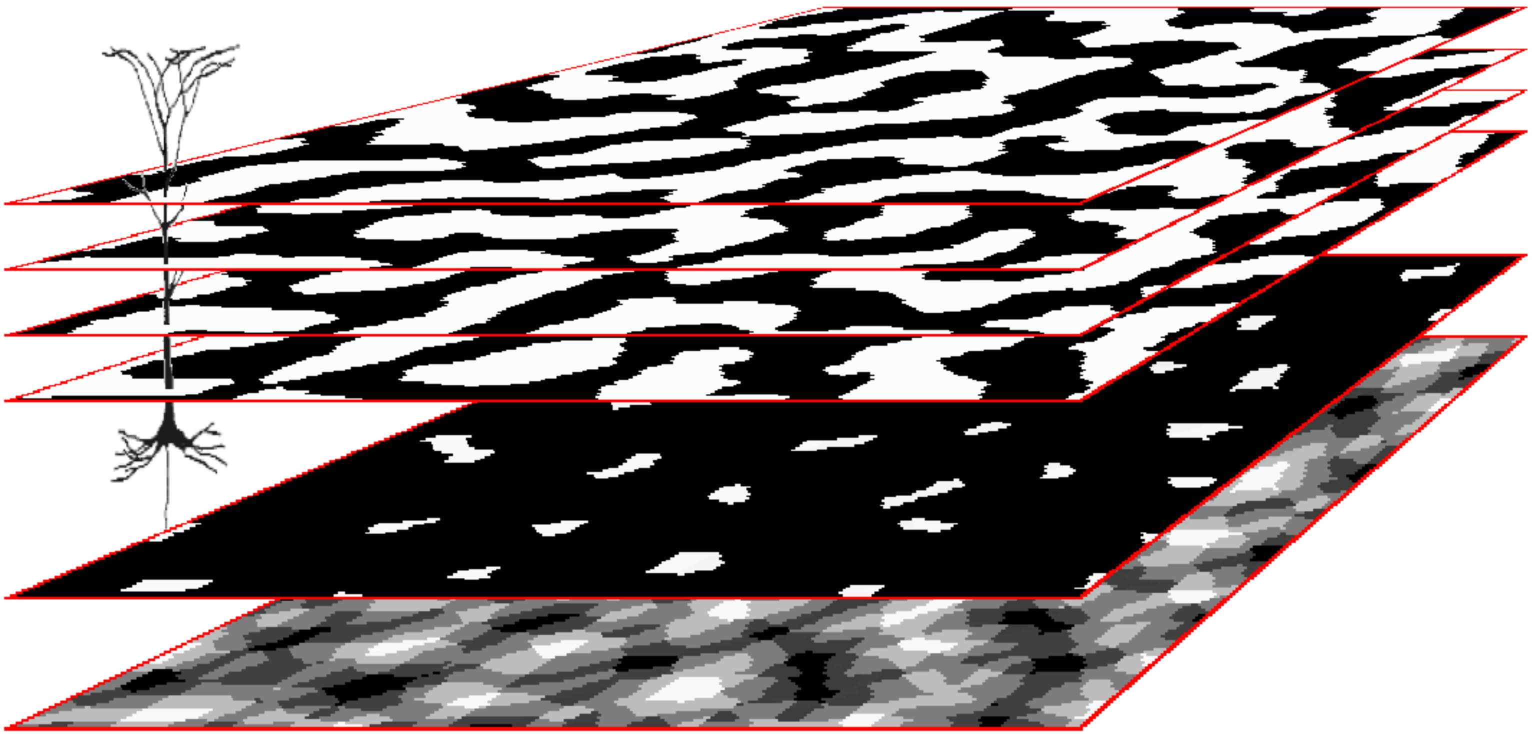
Thus there are 10 x 10 x 10 = 10^3 activity patterns. These can be modelled with a total of 10 + 10 + 10 feedback fibers.

In general, x^N feedforward patterns can be decoded with Nx feedback fibers, where

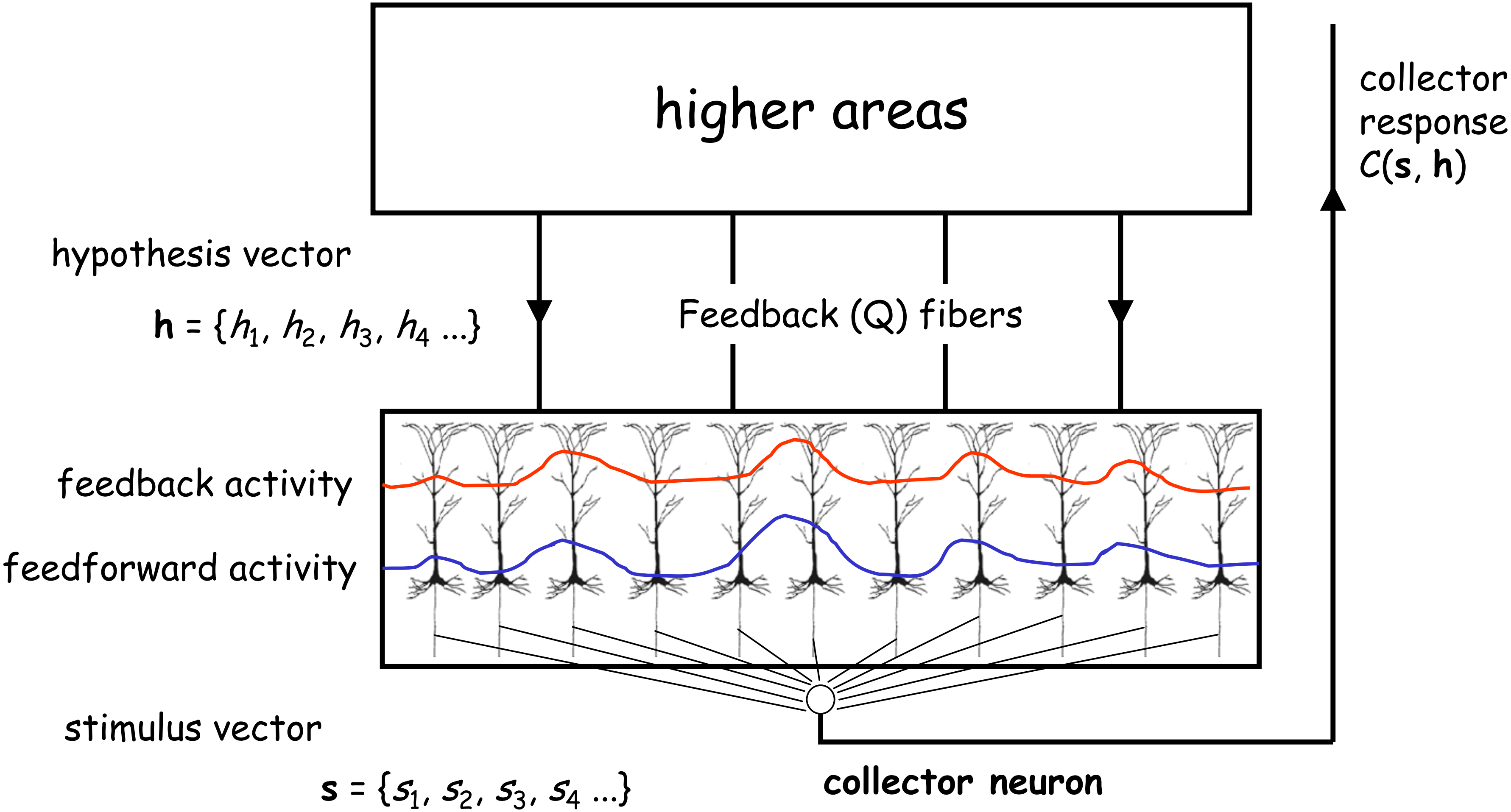
N is the number of feature dimensions represented in the map and

x is the number of values coded along each dimension





Feedback axons (Q fibers) spread tangentially in the cortex, like the subsets in a Venn diagram (top 4 layers). Regions of overlap (= logical conjuctions) can be detected by the apical dendrites of pyramidal neurons. The bottom layer shows the linear sum of the activities and the second lowest layer shows the product of the activities.


higher areas
collector
response,
$C(\mathbf{s}, \mathbf{h})$
hypothesis vector
$\mathbf{h} = \{h_1, h_2, h_3, h_4 ...\}$
Feedback (Q) fibers
feedback activity
feedforward activity
stimulus vector
$\mathbf{s} = \{s_1, s_2, s_3, s_4 ...\}$
collector neuron

add-threshold model

$$O(i,\, j) = thr\left\{ A(i,\, j, \mathbf{s}) + \sum_{n=1}^{N} q_n(i,\, j, h_n) \right\}$$

add-multiply model

$$O(i,\, j) = thr\left\{ A(i,\, j, \mathbf{s}) \sum_{n=1}^{N} q_n(i,\, j, h_n) \right\}$$

multiply model

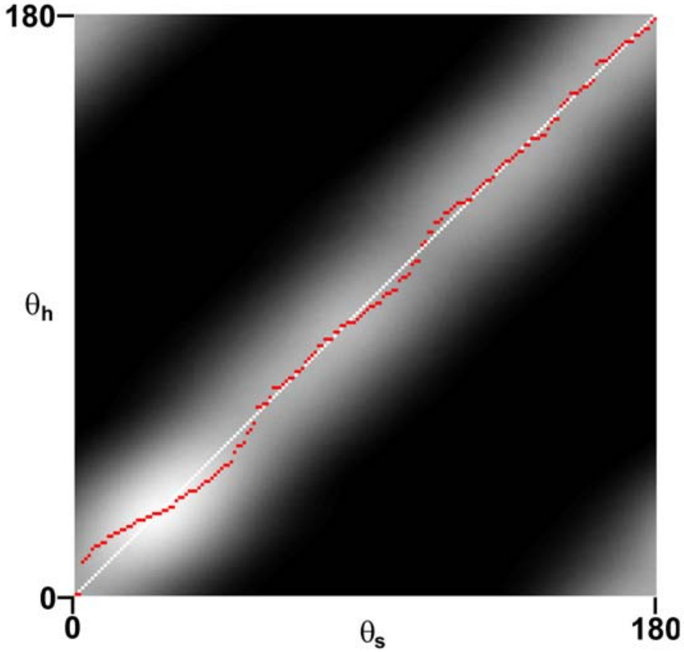
$$O(i,\, j) = A(i,\, j, \mathbf{s}) \prod_{n=1}^{N} q_n(i,\, j, h_n)$$

where $A(i, j, \mathbf{s})$ is the feedforward response to stimulus **s** at cortical point i, j and $q_n(i, j, h_n)$ is the activity in the n-th q-fibre.

The collector response is given by

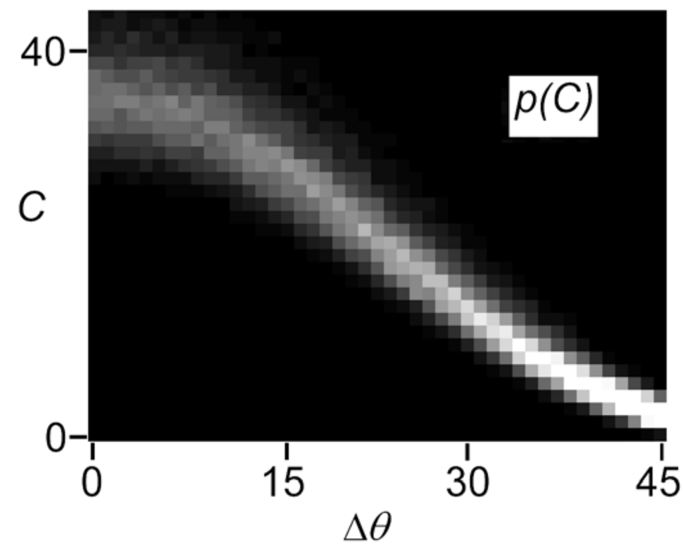
$$C(\mathbf{s}, \mathbf{h}) = \sum_{i,j} O(i,\, j)$$

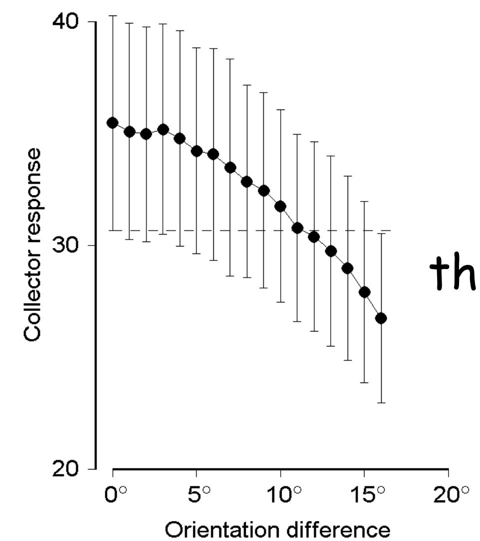
‘one-shot’ decoding



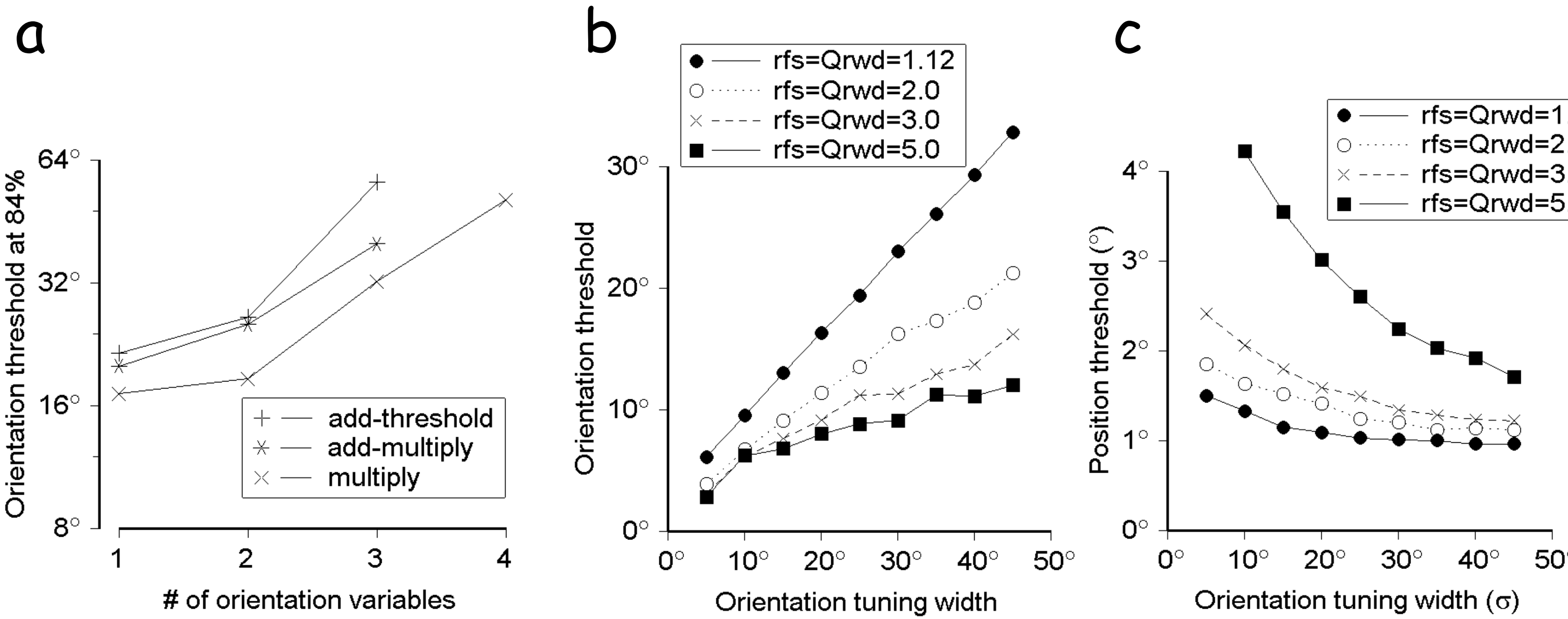
$C(\theta_s,\ \theta_h)$

The white line shows the locus of points for which $\theta_s = \theta_h$ and the red points indicate, for each value of θ_s, the value of θ_h for which C is a maximum. The model used to calculate the values of C was the add-multiply model, with a threshold $t = 1.0$. All stimuli were presented at a single retinal location, $x_s = y_s = 6.0$ and it was assumed that the decoding mechanism knew the retinal location, so that $x_h = y_h = 6.0$.





threshold



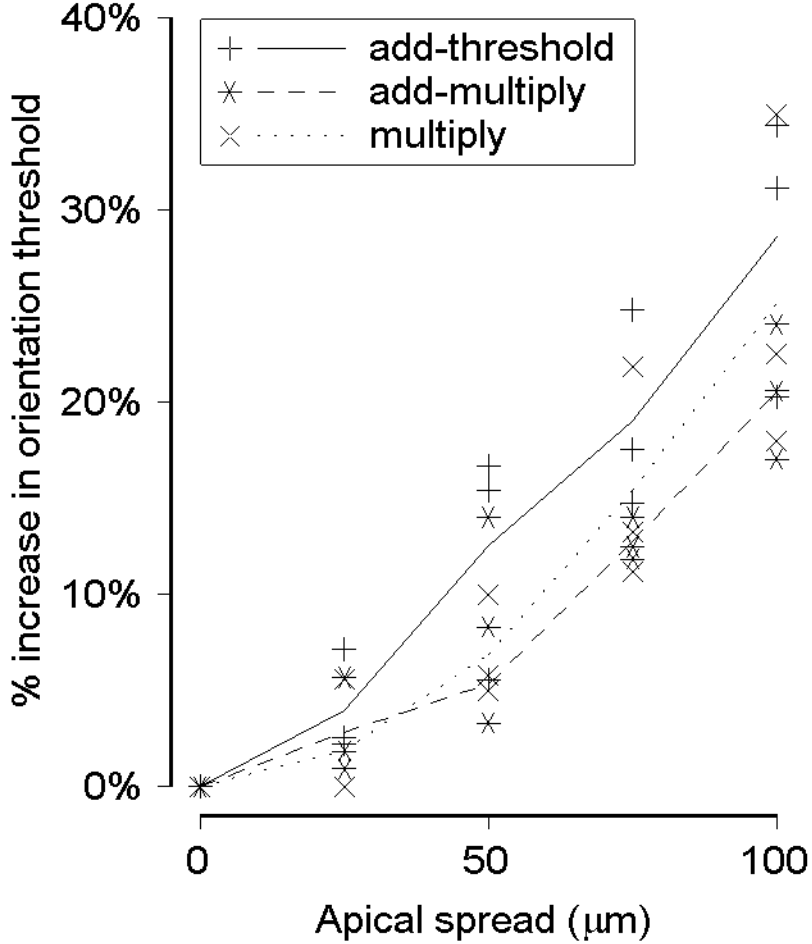
one-shot thresholds for various models and tuning parameters

a) for orientation as a function of the number of map dimensions and for physiologically realistic tuning curve widths;

(b) as a function of tuning curve widths for a map with N=1 and the add-multiply model;

c) retinal position thresholds as a function of tuning curve widths.

Orientation thresholds are large, but should be compared with psychophysical thresholds obtained for a very small, briefly flashed bar, which are generally around 10 - 20° (Watt, 1987).



40%
30%
20%
10%
0%
% increase in orientation threshold
add-threshold
add-multiply
multiply
0
50
100
Apical spread (μm)

what goes in-

- the idea that feedback pathways model their inputs
- separability of receptive fields and thus cortical maps
- the generation of hypotheses by ‘higher’ cortical areas or other parts of the brain - implicit in much thinking about top-down processing

what comes out-

- apical dendrites
- multiplicative scaling of tuning curves by attention (Reynolds & Desimone, 2003; Martinez-Trujillo & Treue, 2004)
- multiplicative interactions between apical and basal dendritic inputs (Larkum et al., 2004)
- decoding of x^N patterns with Nx fibers
- broad, sometimes patchy, tangential distribution of feedback axons
- various psychophysical predictions

Other Aspects

- fast readout (< 30 ms), wirelength optimization algorithms also will optimise readout time
- provides a mechanism for generalisation i.e. could detect a stimulus independently of retinal location, if the Q fibers spread over a wide area of cortex
- shows how cortex could work without inputs e.g. visual cortex activation during imagery