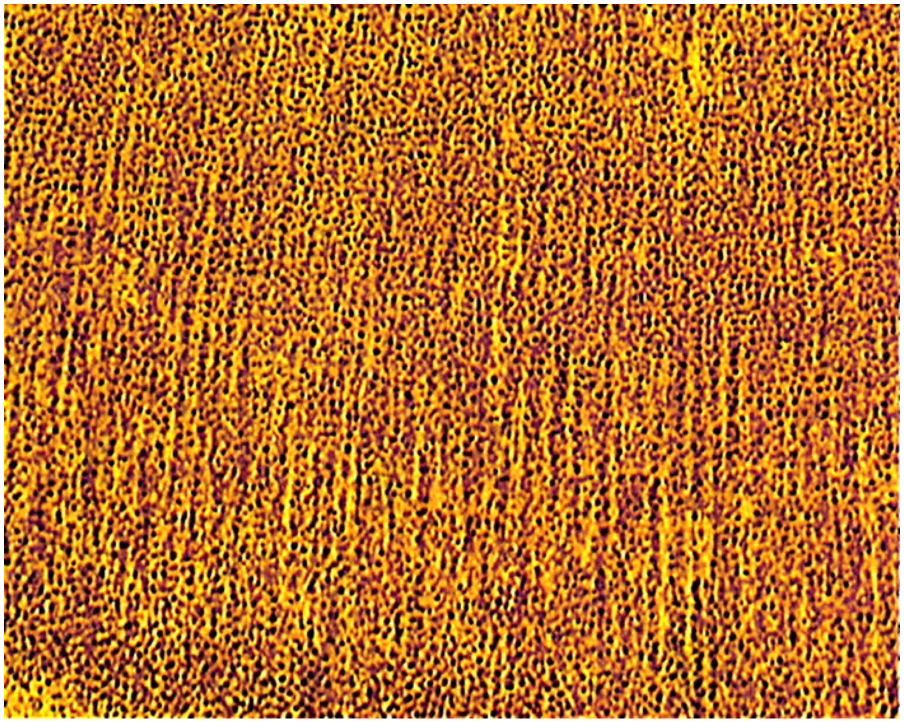
Models of cortical organization

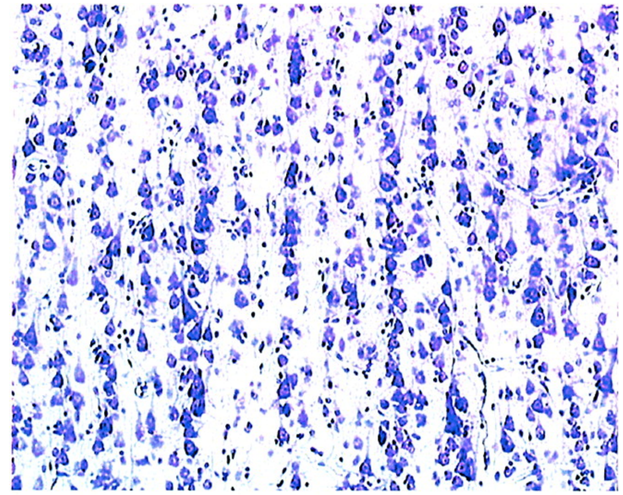
BME665/565

Columnar organization of cortex

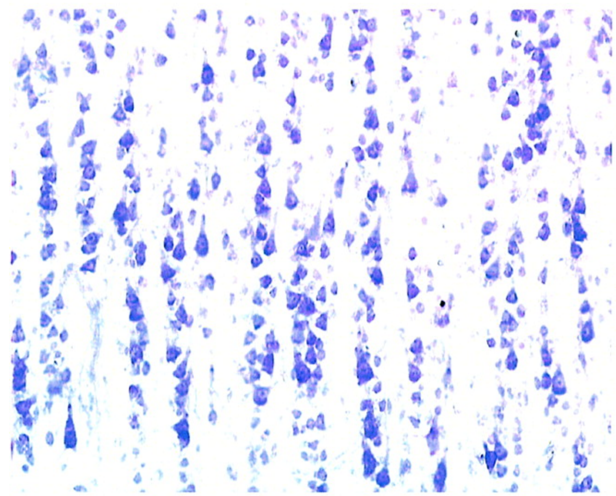
- The basic unit of the neocortex is the minicolumn -- 40–50 µm transverse measure
- Minicolumns are linked into columns which contain an uncertain number of minicolumns, perhaps 50–80
- The number varies with the distribution of thalamocortical axons, and with the sizes of the cell-sparse, neuropil-rich regions between minicolumns
- Columns vary in size by a factor of 1–2 in brains which vary in total surface area by three orders of magnitude.

Mini-columns former earlier than cortical layers





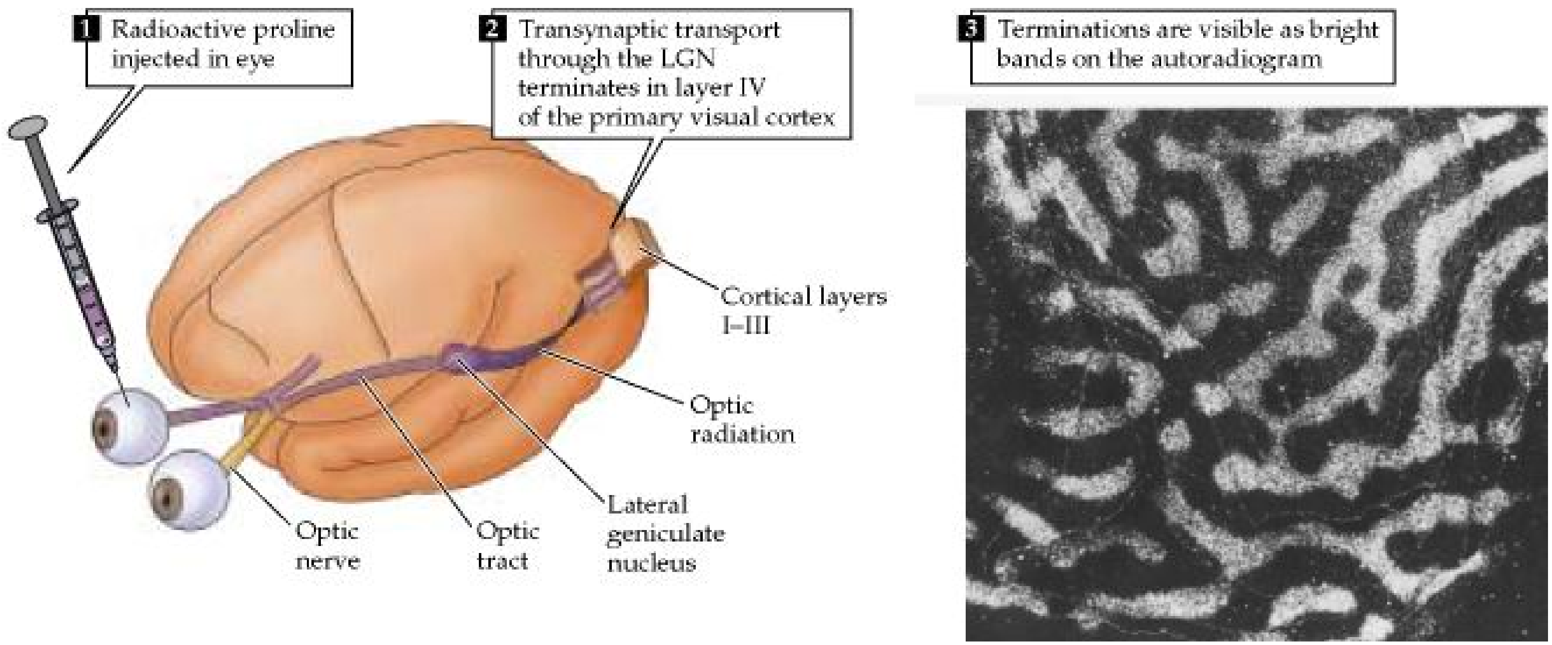
9 year old human.



67 year old human.

Buxhoeveden + Casanova. ***Brain*** 125:935–951 (2002)

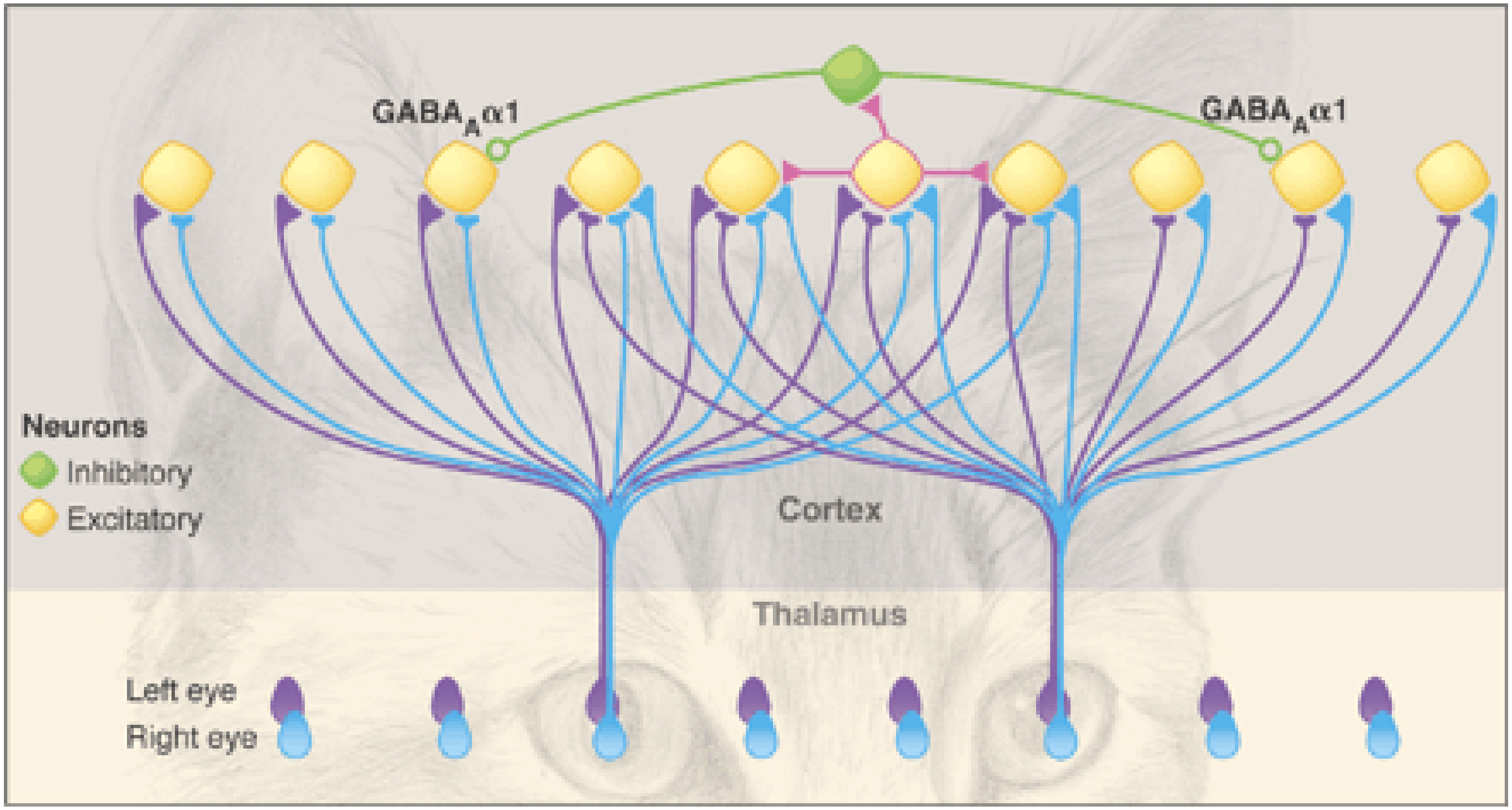
Imaging ocular dominance columns



Radioactivive proline is carried transynaptically to the cortex. White areas indicate regions of labeled geniculocortical terminals.

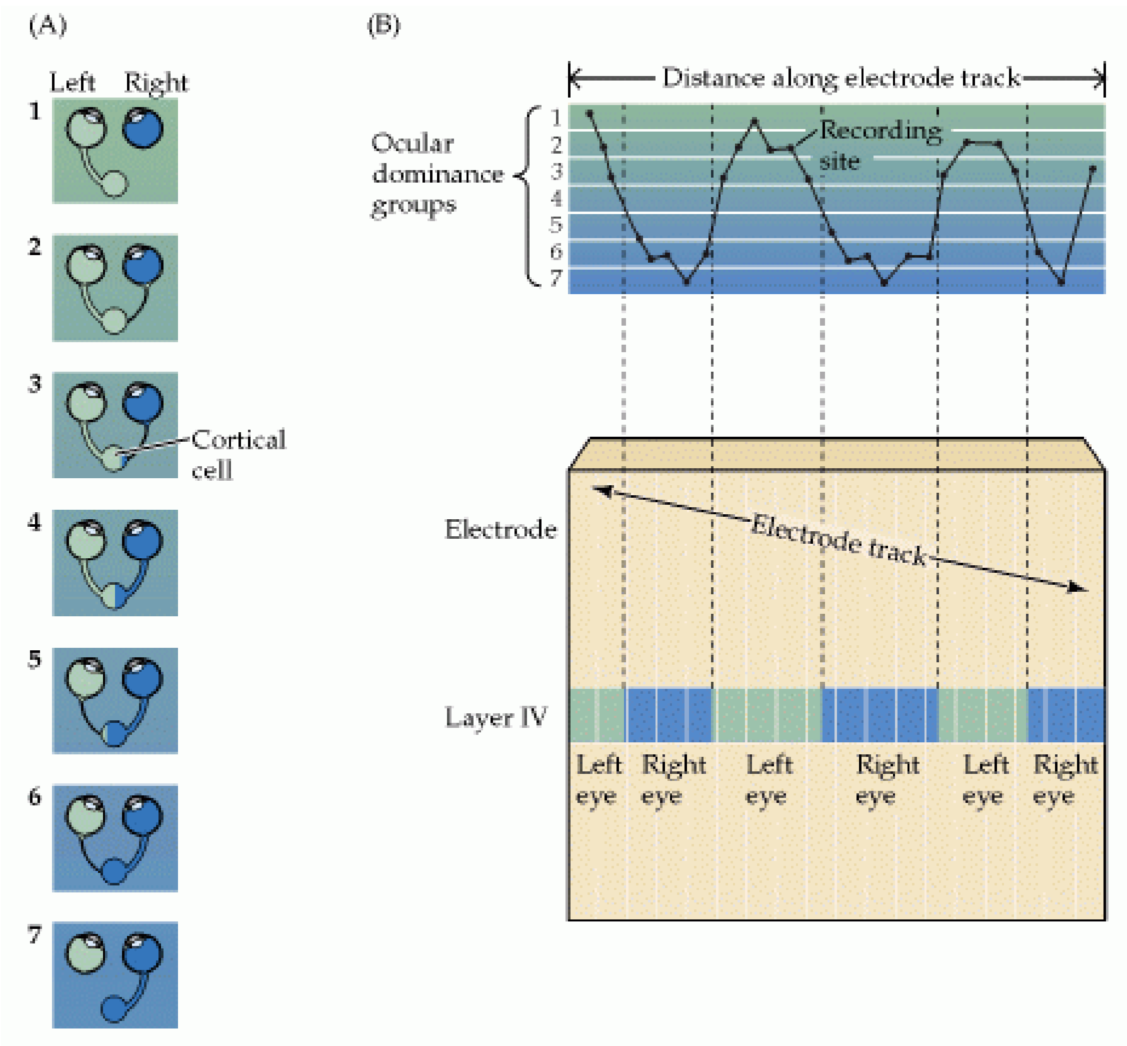
From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Connectivity in the visual system



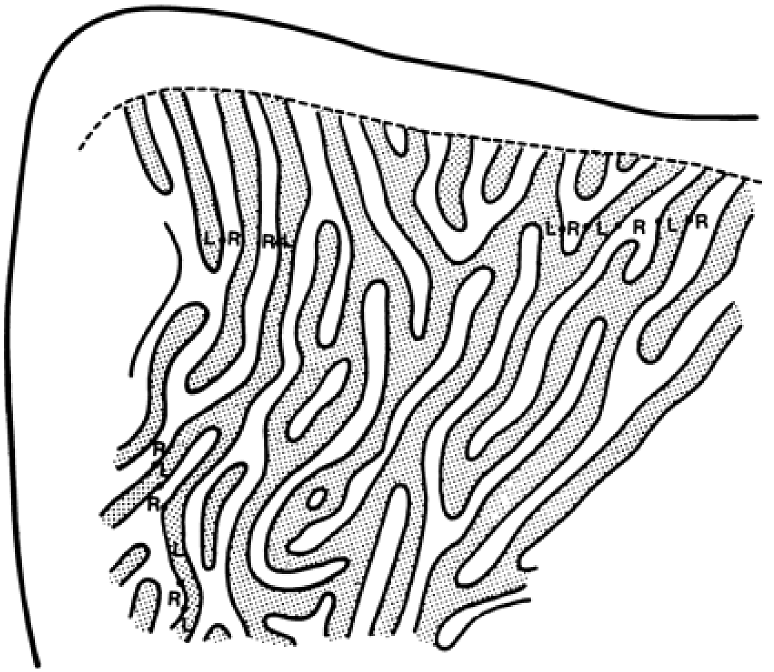
Ferster. ***Science***, Vol 303, Issue 5664, 1619-1621, 2004

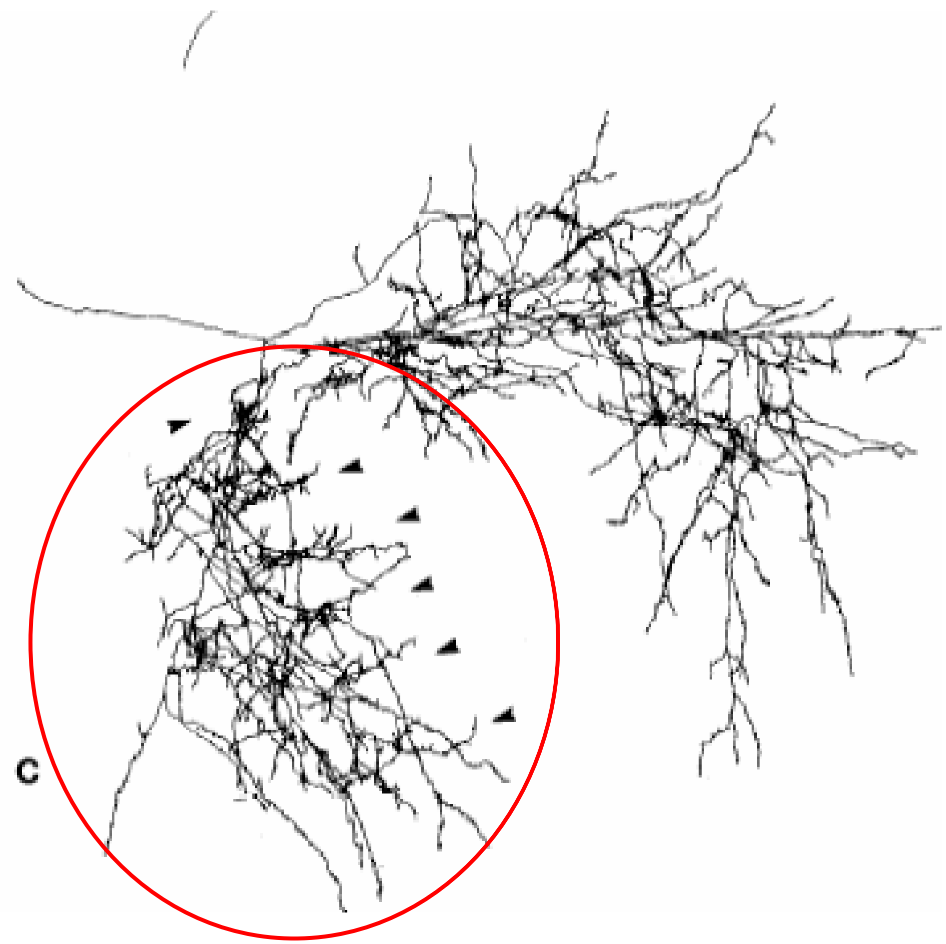
Columnar organization of ocular dominance



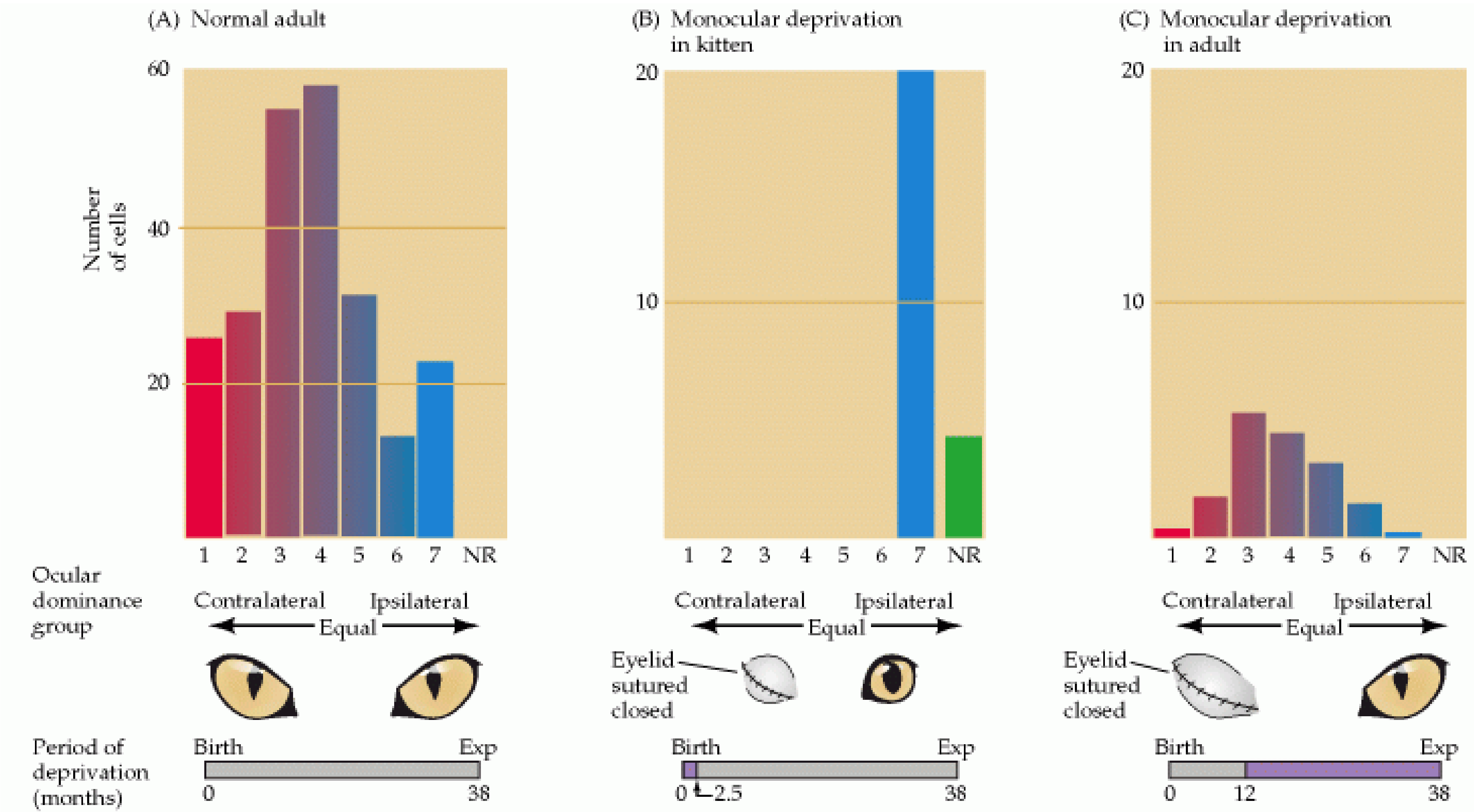
From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Anatomical substrate of ocular dominance columns



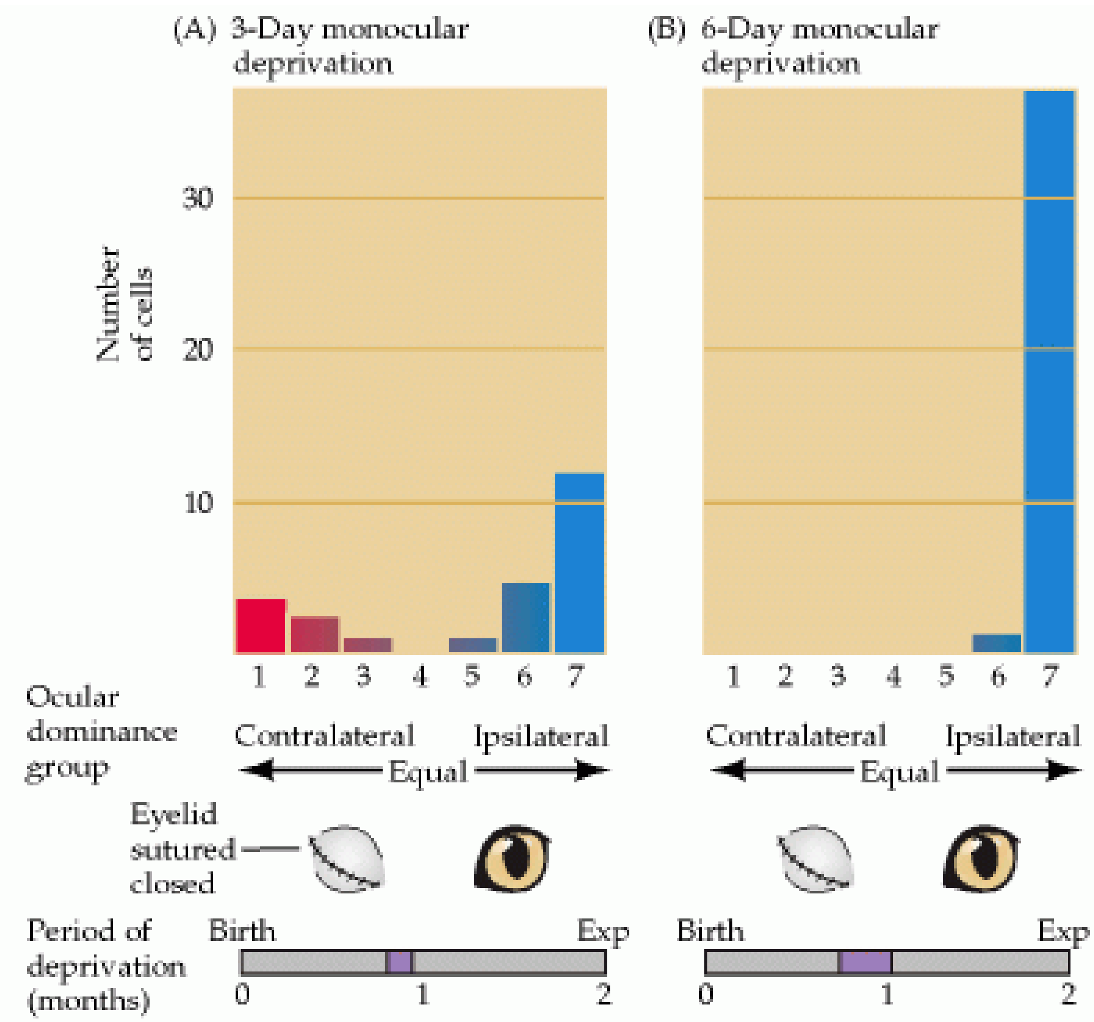


Effect of Monocular Deprivation on Ocular Dominance



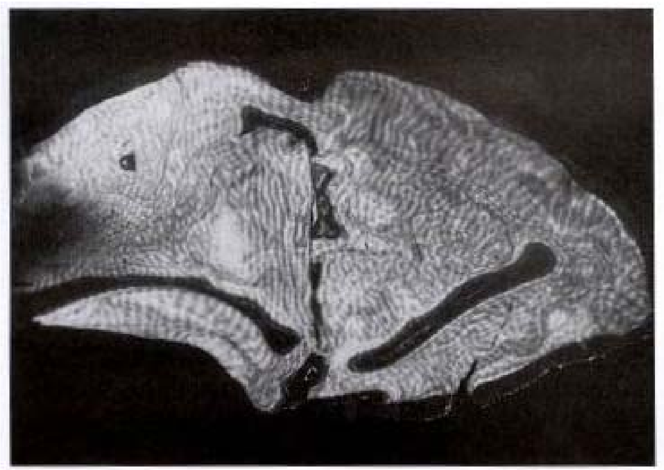
From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Suppression of ocular dominance happens quickly

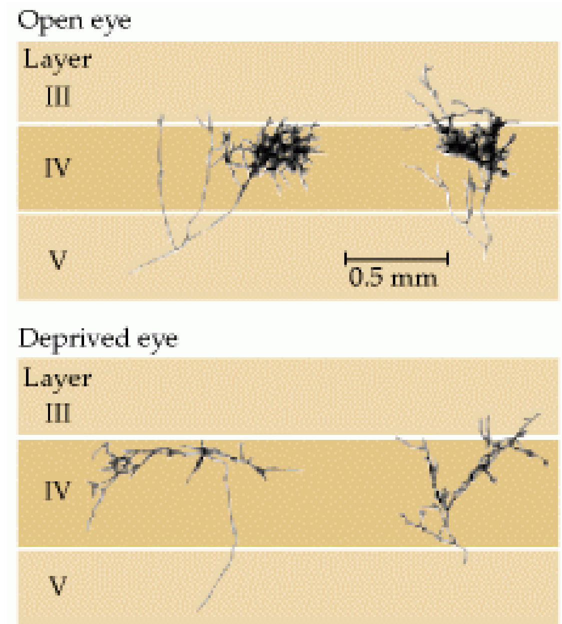


From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Loss of ocular dominance is reflected in changing afferents



Normal layer 4 ocular dominance columns visualized using radiolabeled amino acids



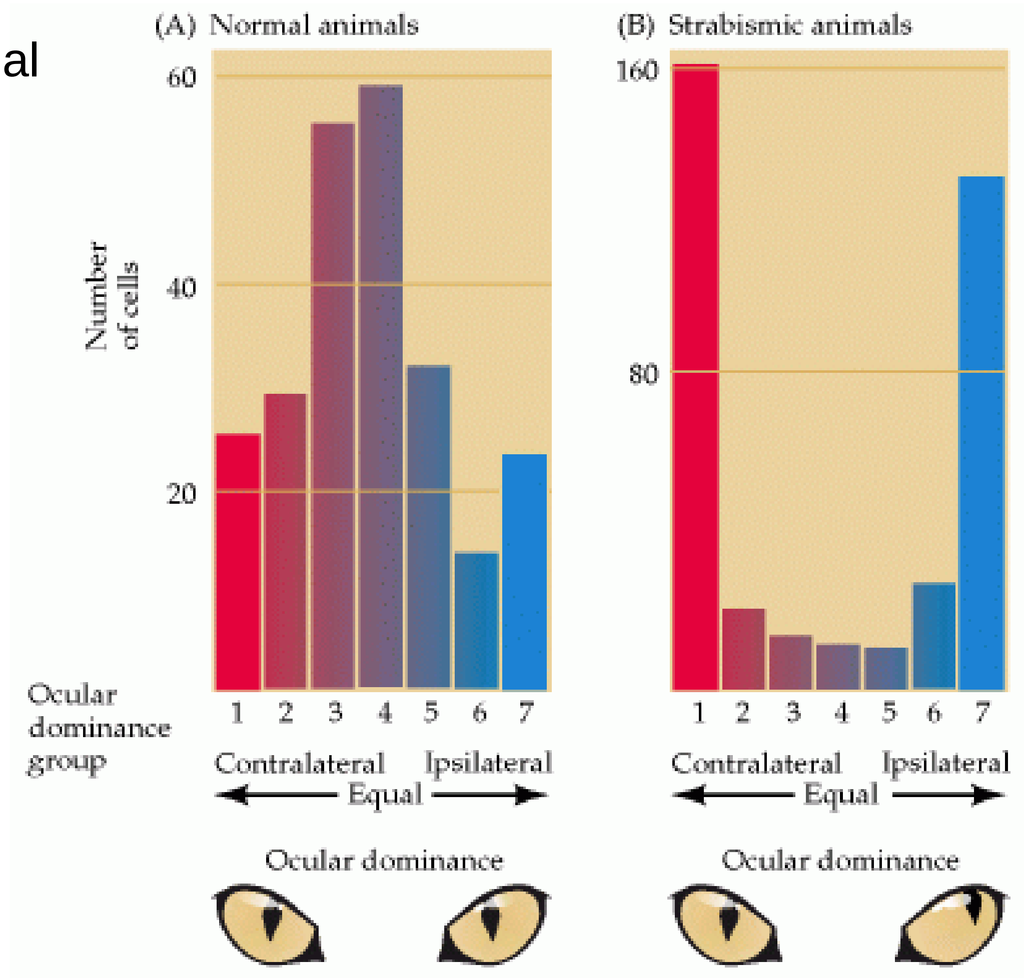
Right eye sutured from 2 weeks of age to 18 months

From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Decorrelation of inputs results in sharpened OD columns

Normal

Strabismic

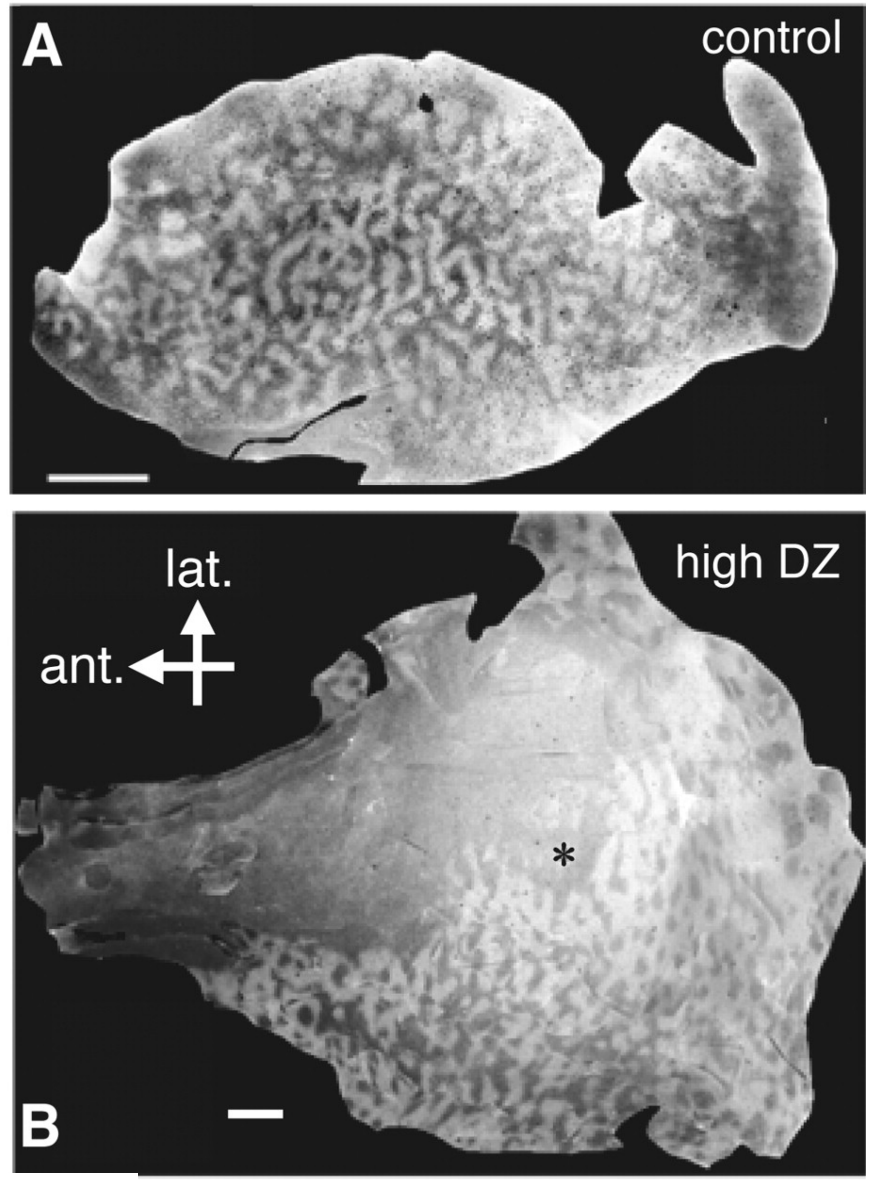


From Purves et. al., Neuroscience 2nd Ed., Sinauer Associates publishers, 2001.

Lateral inhibition plays a role in OD column formation

Result of suppressed inhibition

- High dose (35 mM, 0.2 µl/hour) diazepam treatment. Diazepam potentiates chloride flux through the $GABA_A$ receptor
- A: control hemisphere
- B: high dose yields an area of column desegregation

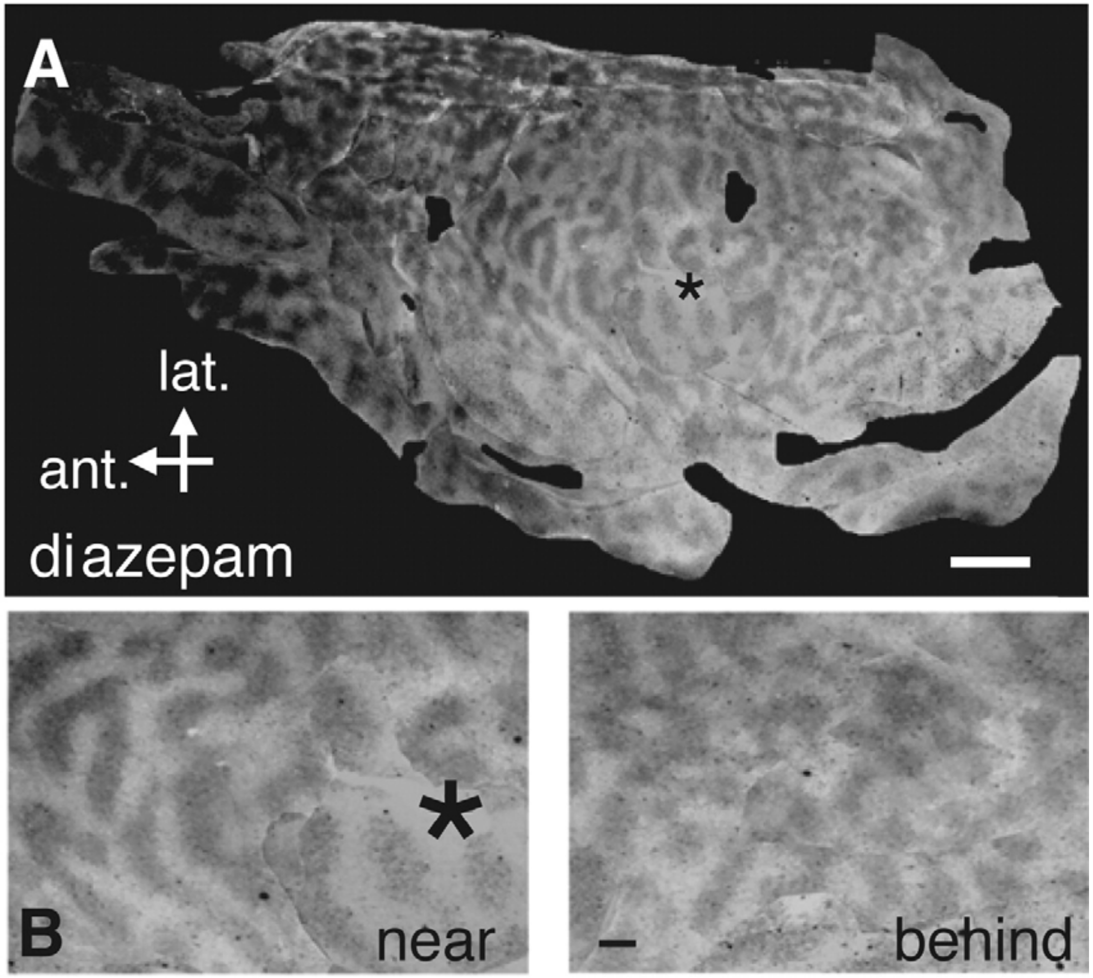


Hensch + Stryker, ***Science*** 303(5664), 1678 – 1681 (2004)

Lateral inhibition plays a role in OD column formation

Result of reduced inhibition

- Low dose (3.5 mM, 2.5 µl/hour) diazepam treatment.
- A: control hemisphere
- B: low dose widens ocular dominance columns

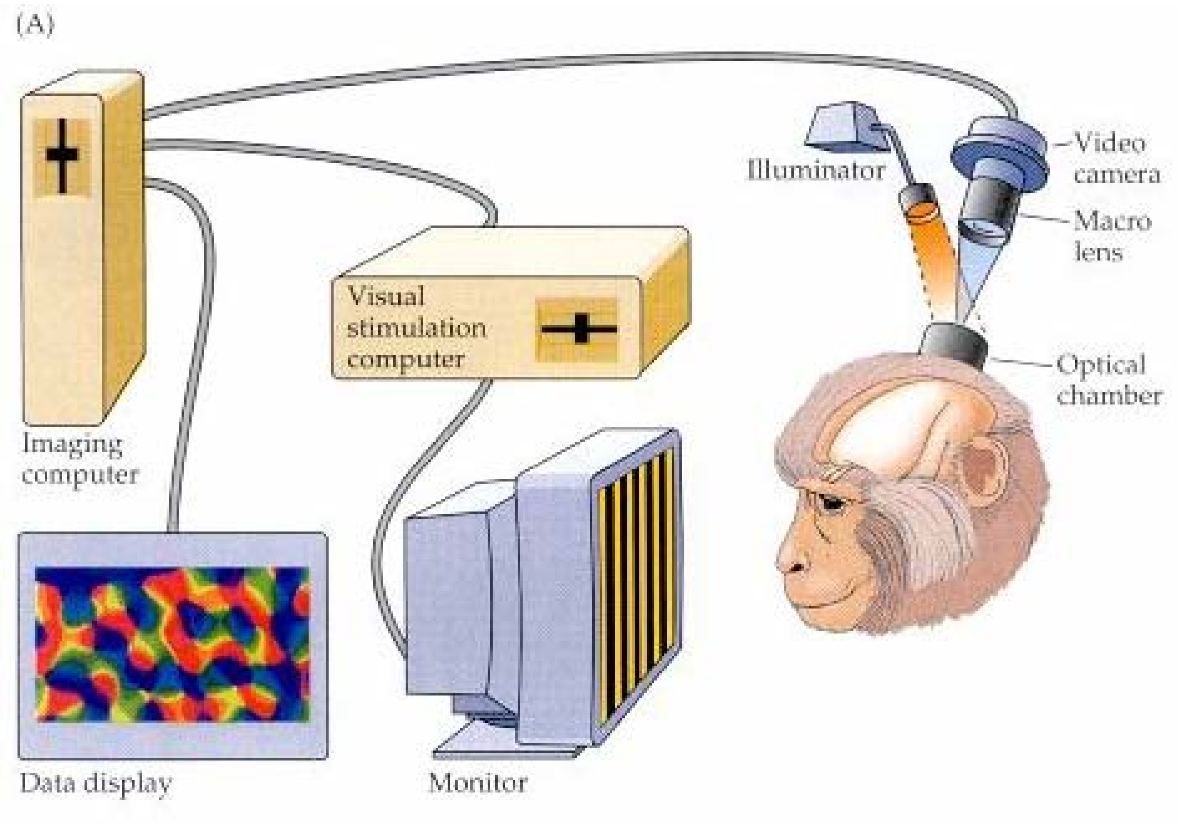


Hensch + Stryker, ***Science*** 303(5664), 1678 – 1681 (2004) 55

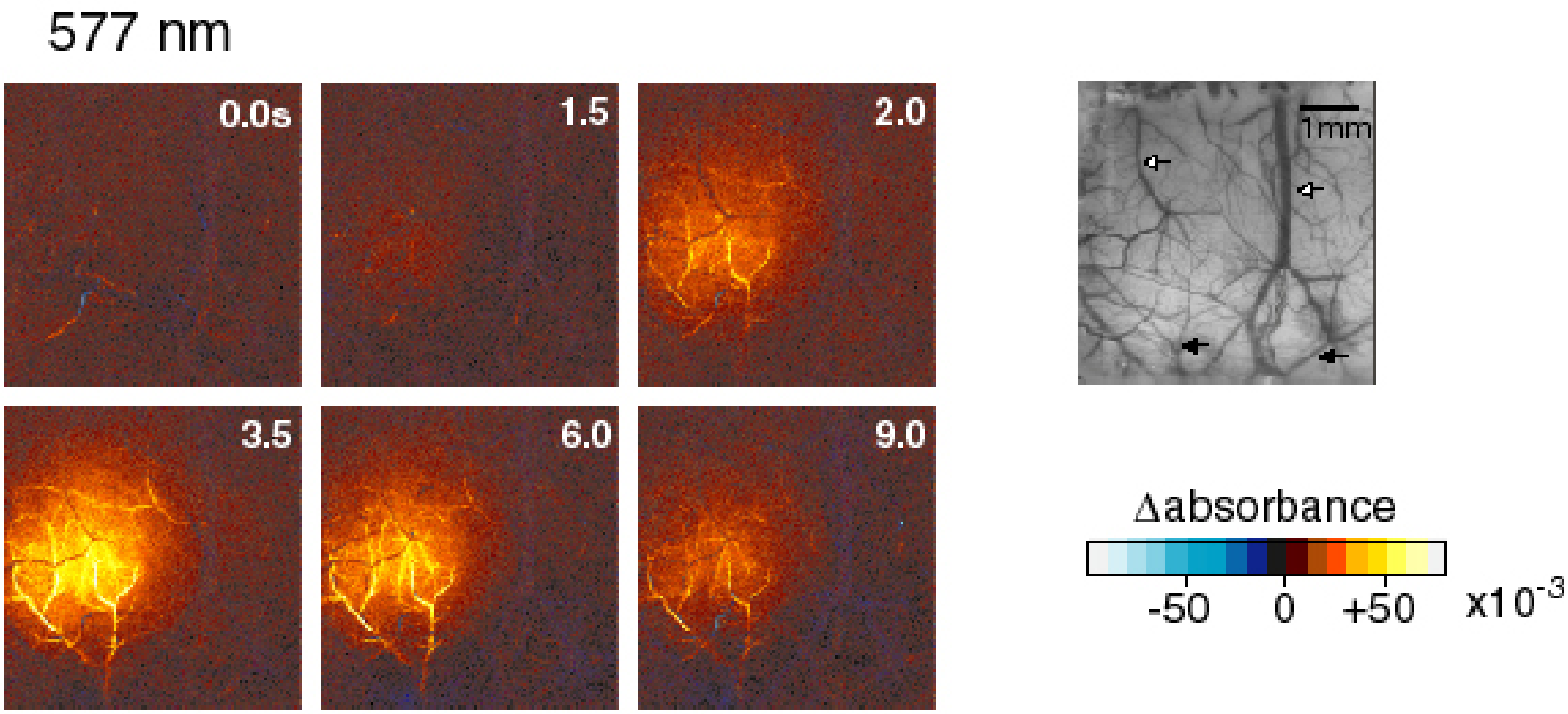
Optical imaging

- There are 3 main components to these correlates of neural activity that have an optical signal:
  - Blood volume changes
  - Blood oxygenation changes
  - Light scattering changes caused by ion and water movement
- Active regions of the brain reflect less light - this can be imaged with a high resolution imaging system
- The darker regions of the Optical Imaging signal are the active areas of the cortex

Optical imaging

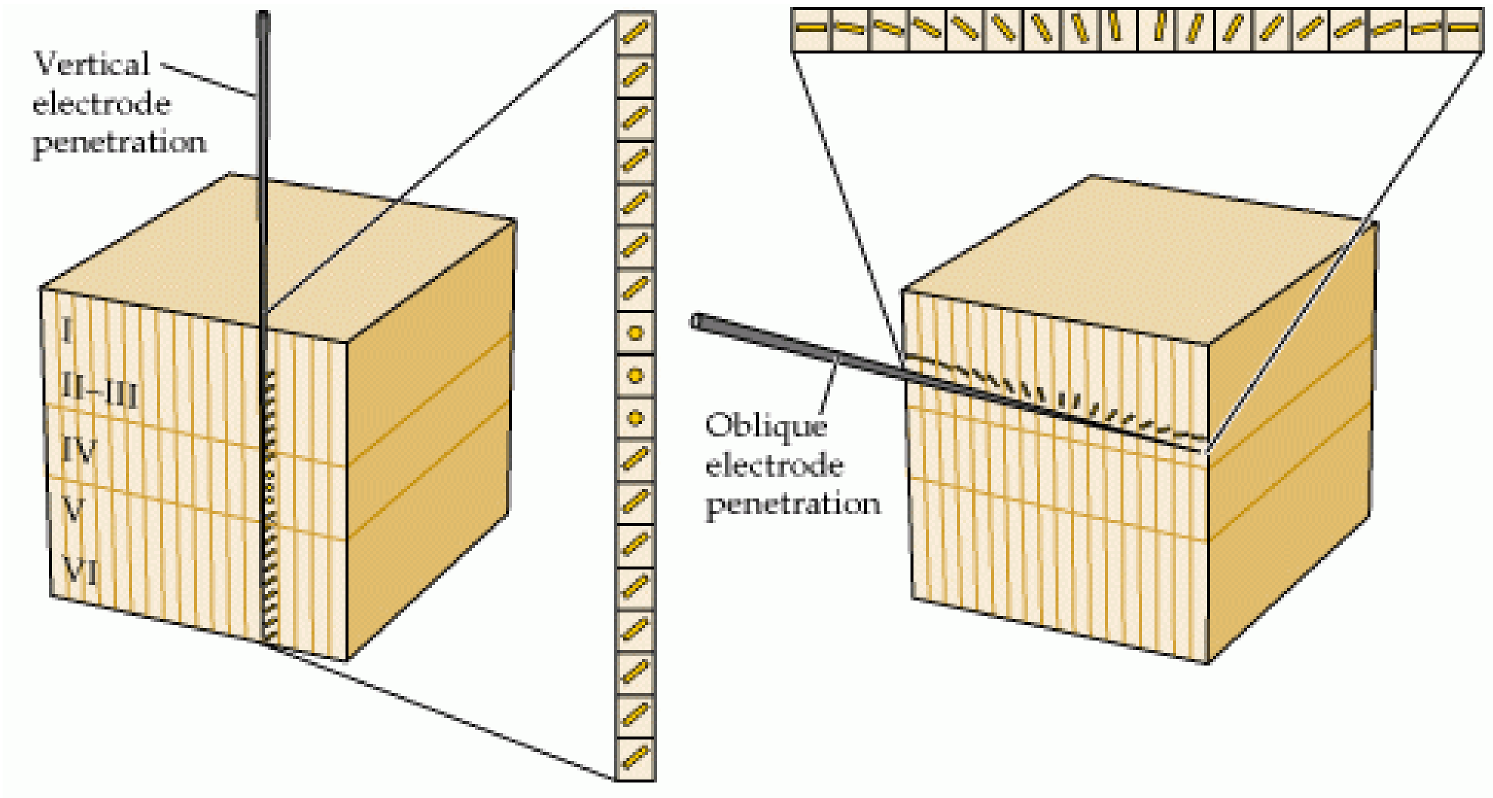


Optical imaging



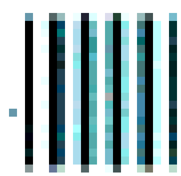
Stimulation of somatosensory system (vibration) for 2s

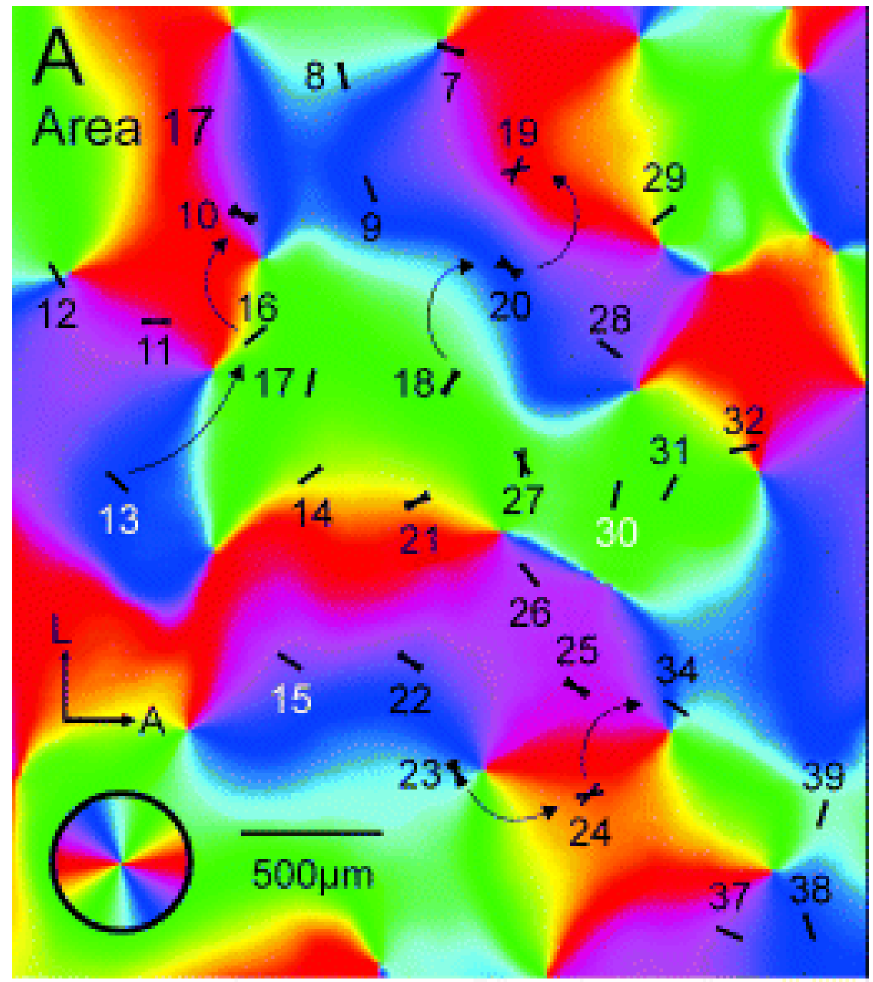
Orientation columns in visual cortex



Orientation columns

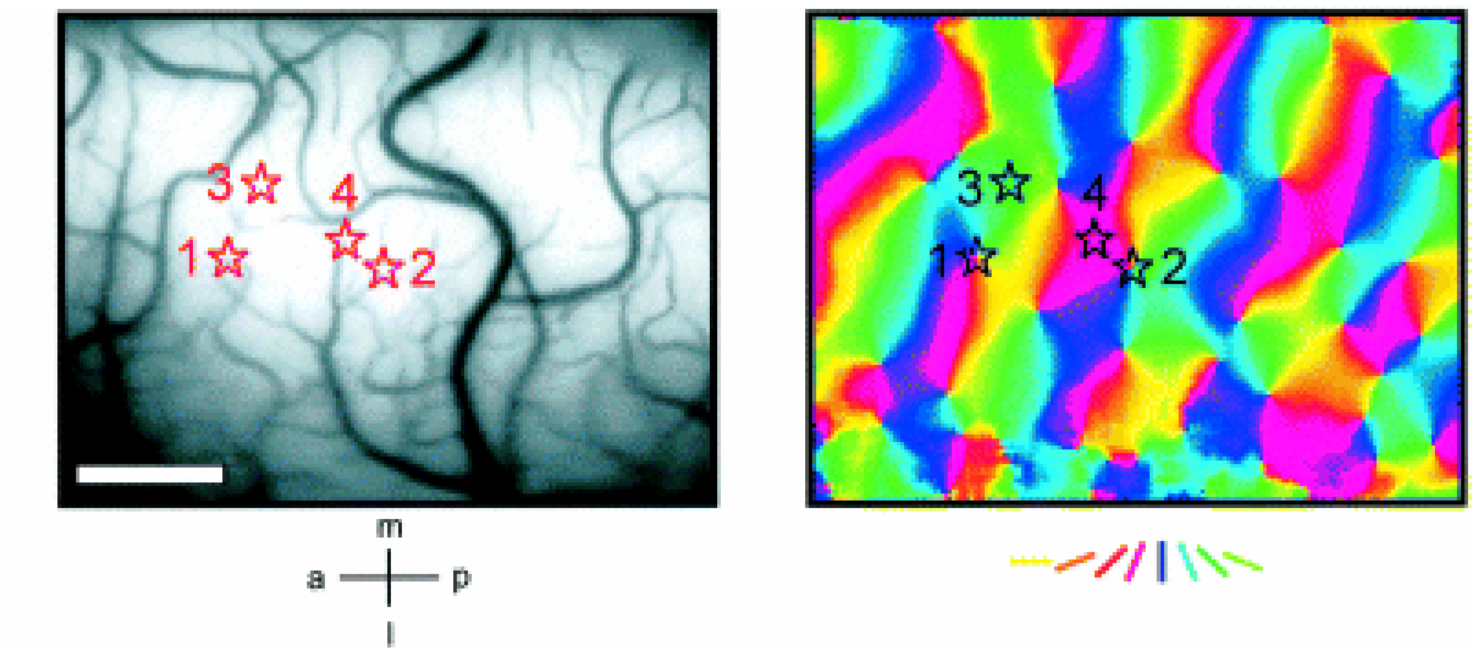
- Stimuli are usual moving sine-wave gratings
- Single-condition responses (averages of many trials) are divided by the sum of responses to all four orientations =cocktail blank
- Optical imaging shows regions of iso-orientation tuned to about 2 degrees in V1 and about 9 degrees in V2
- Electrophysiological mapping of the neuronal responses shows reasonable correspondence in iso-orientation areas



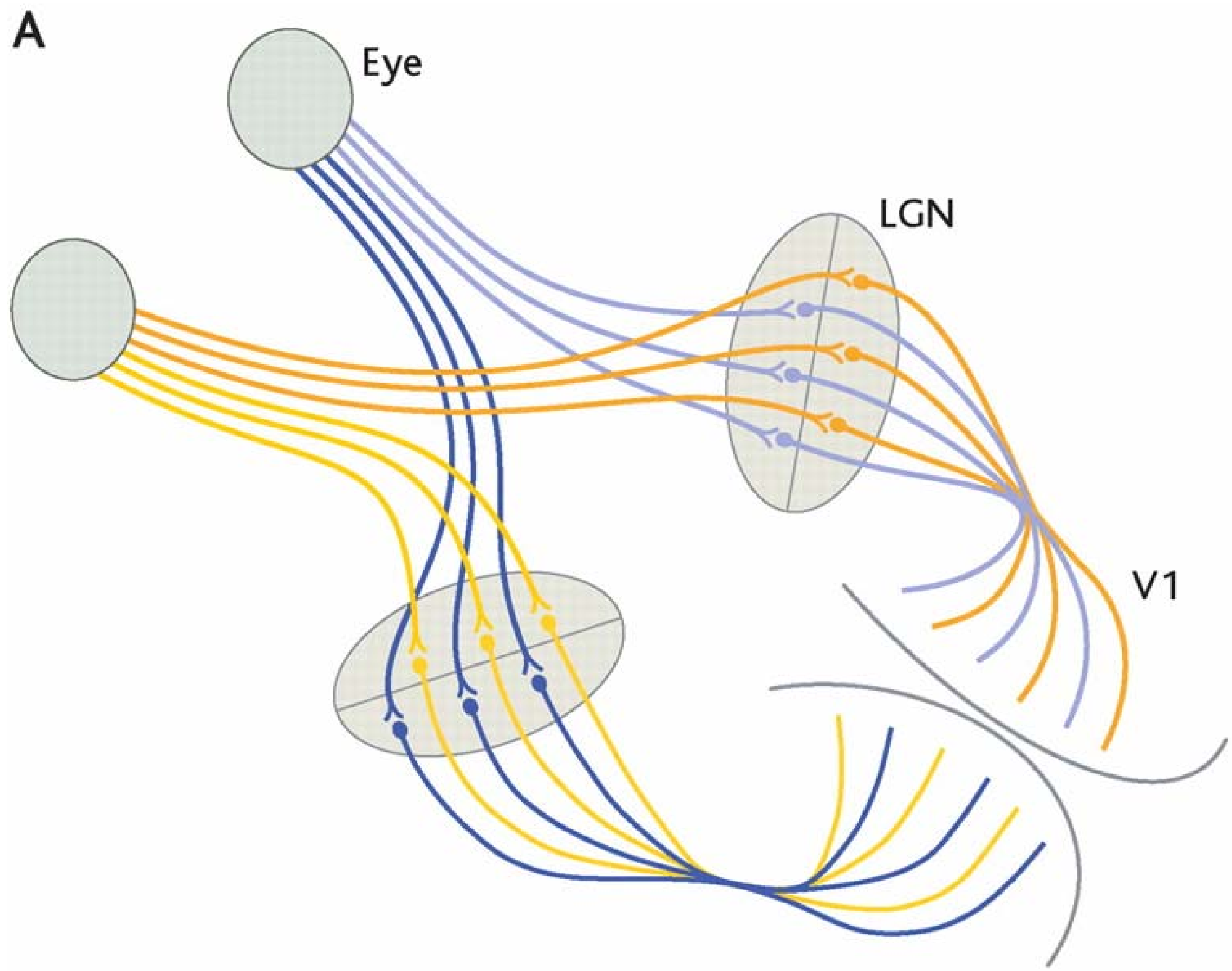


Orientation columns

- “Pinwheel” locations exist where responses for all orientations are represented in a very small region
- Orientation singularities are mostly located in the middle of ocular dominance stripes

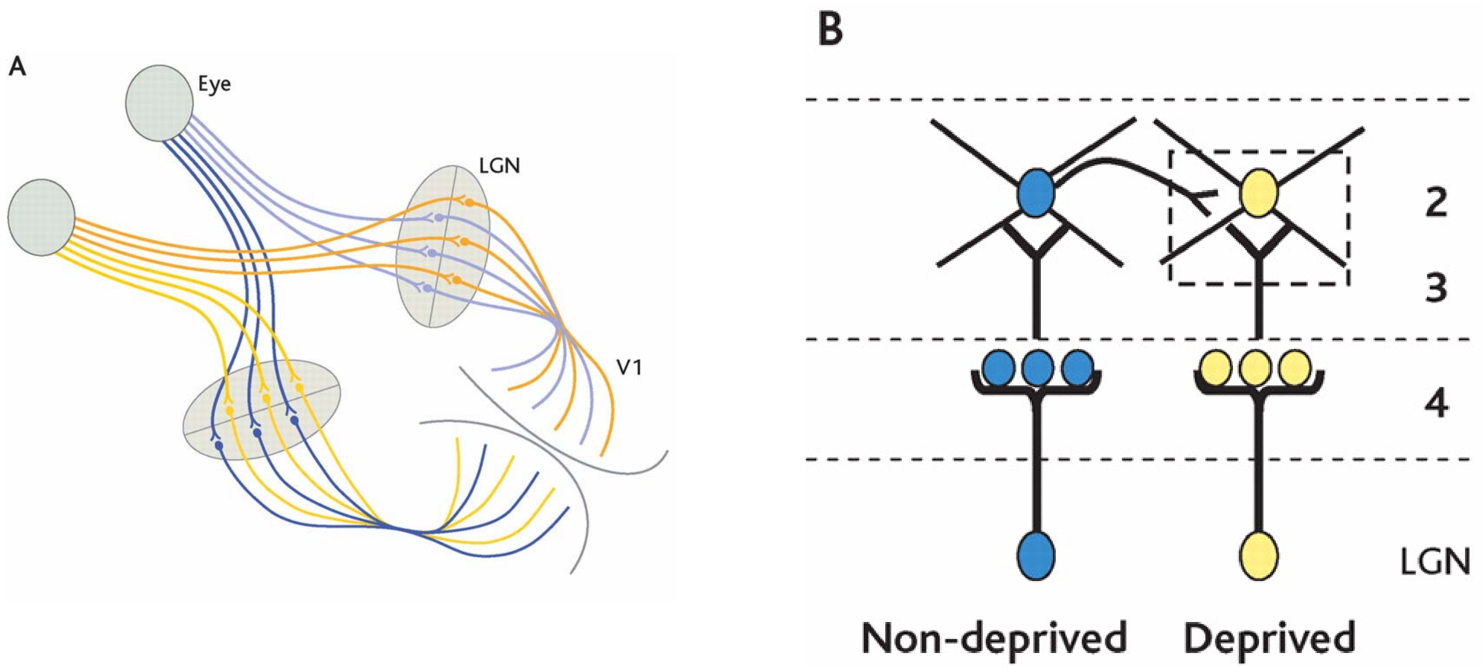


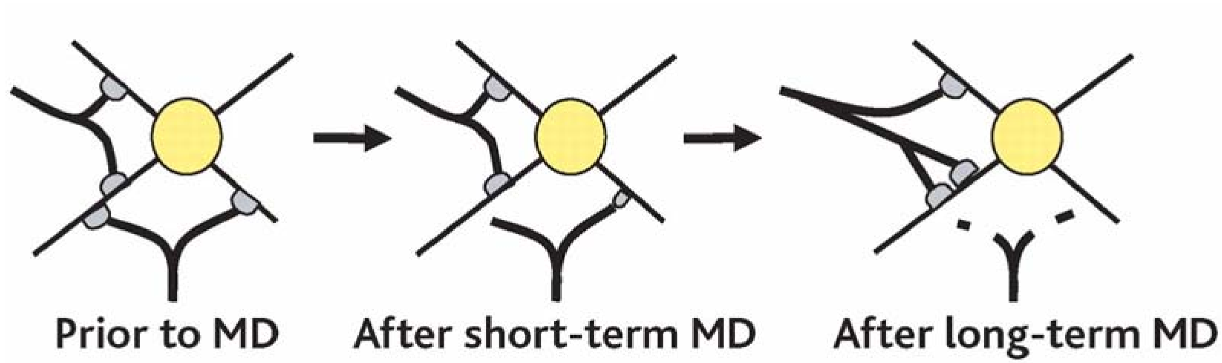
Activity shapes connections in visual cortex



Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

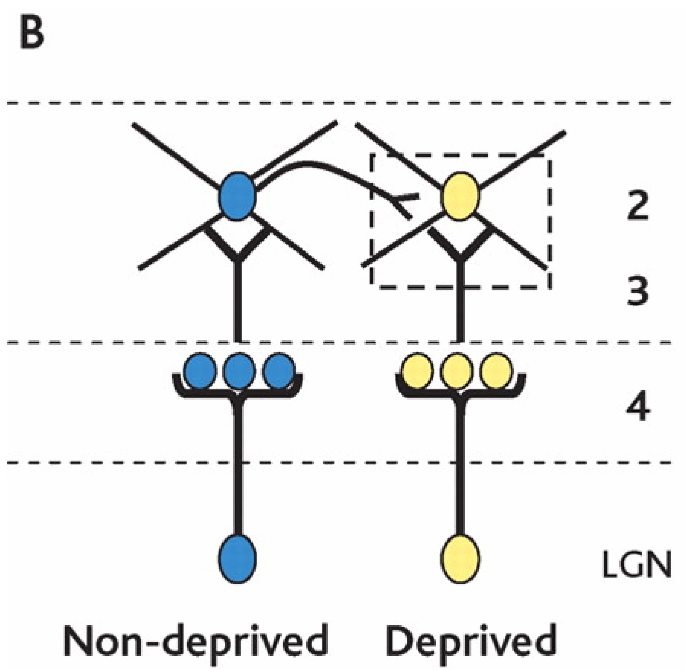
Monocular deprivation

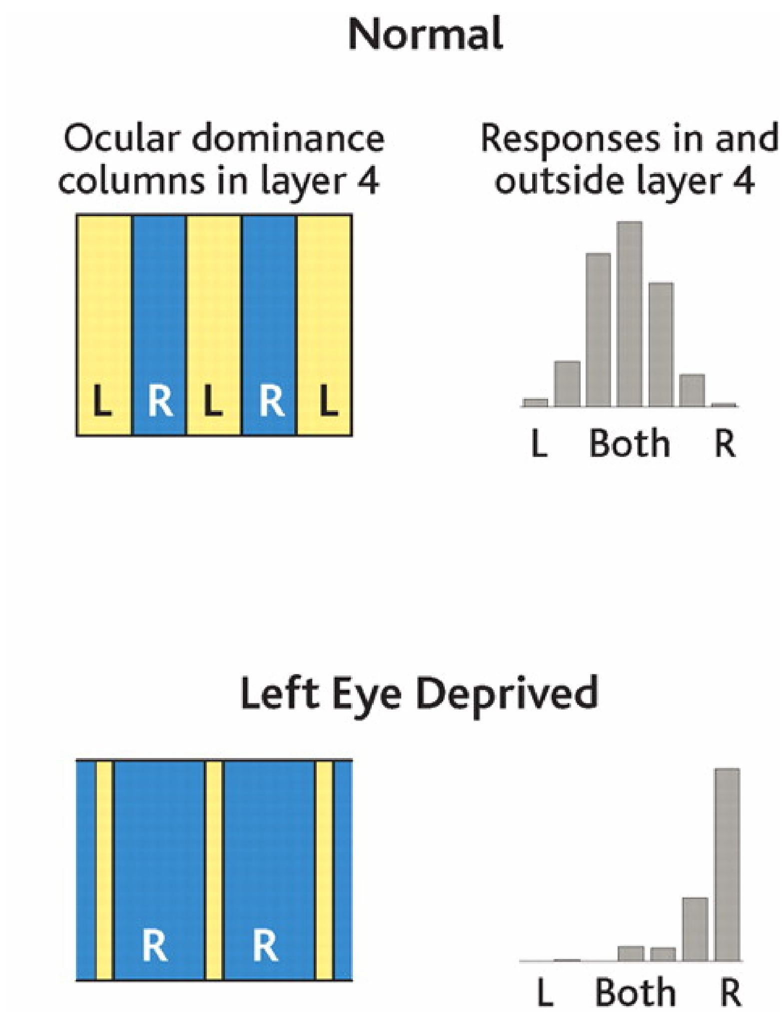




Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

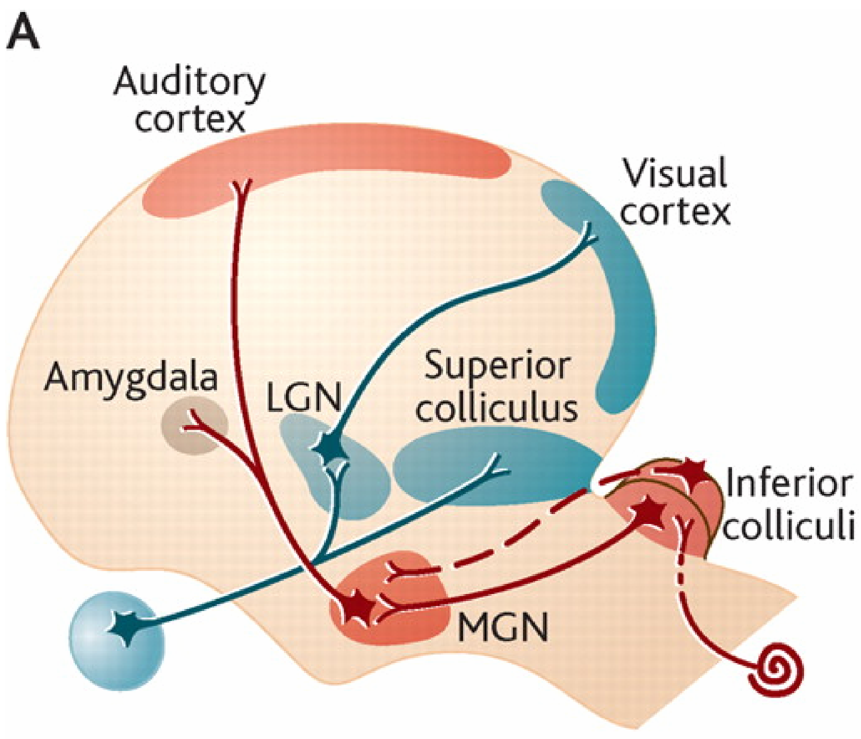
Change in orientation columns with deprivation

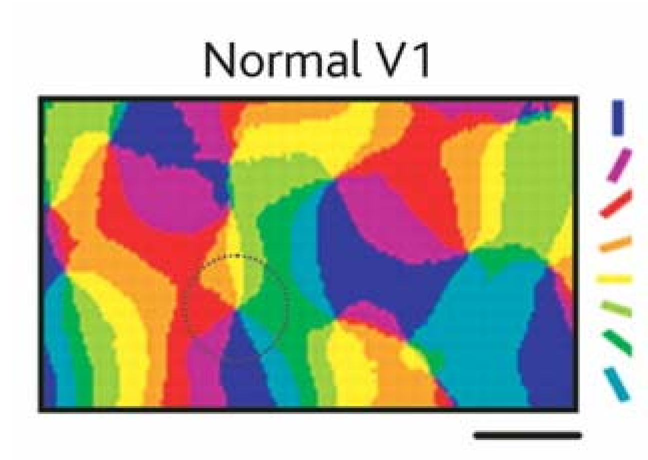




Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

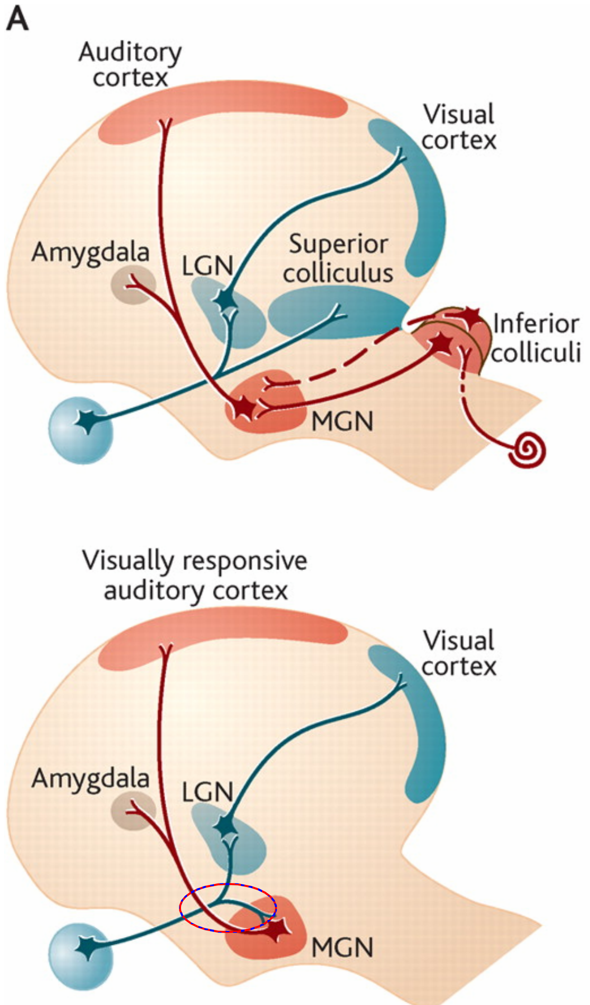
Plasticity induced by deprivation

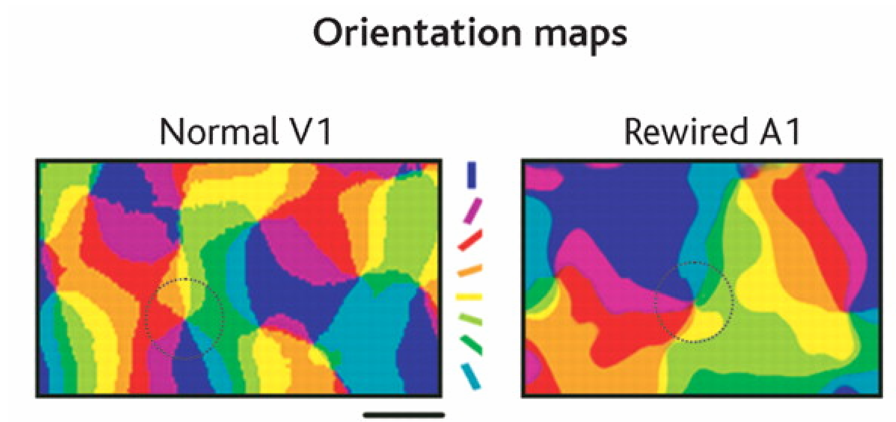




Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

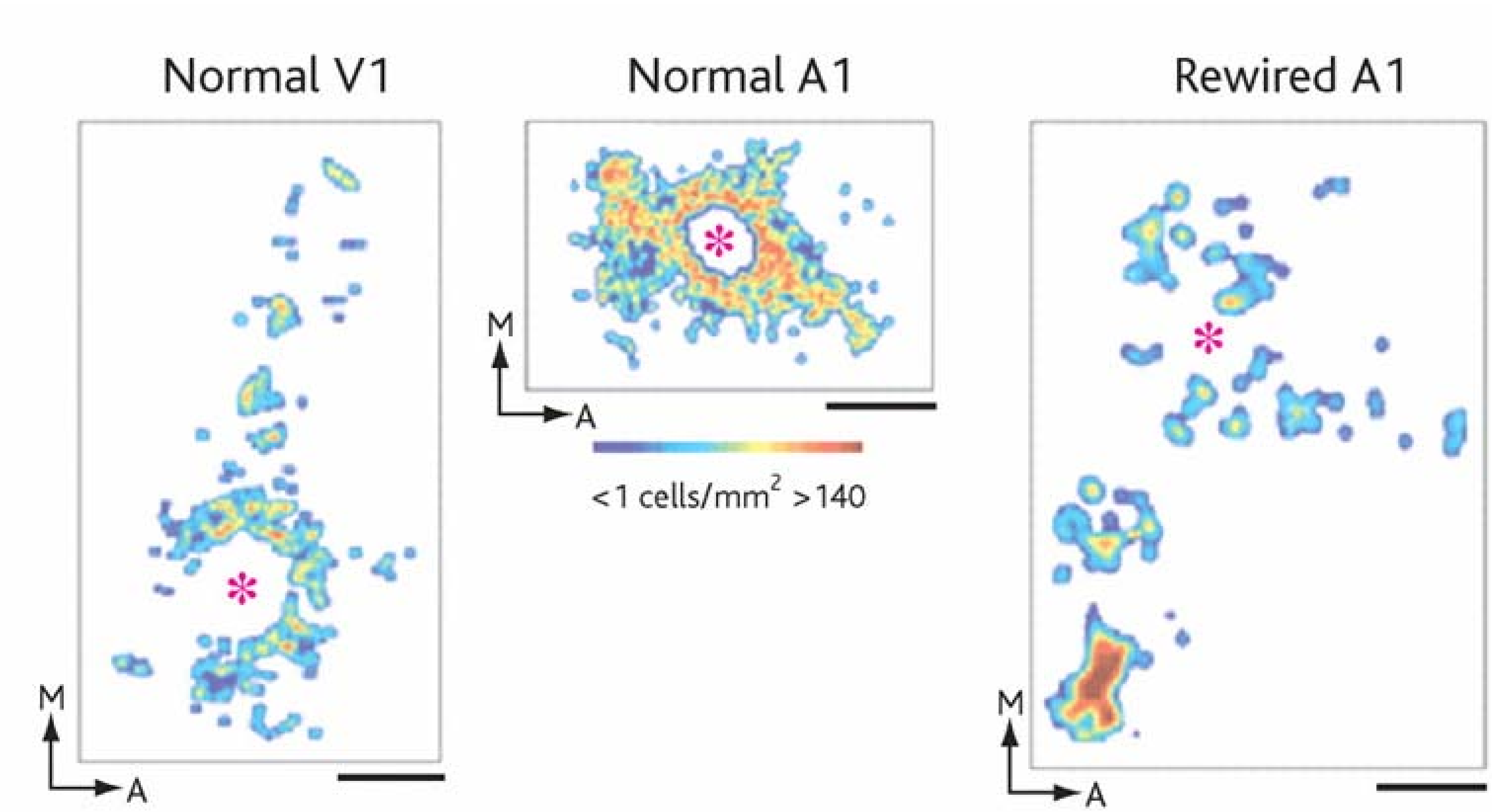
Eliminating inferior colliculus projections to the medial geniculate nucleus (MGN) in neonatal animals results in retinal fibers innervating the MGN





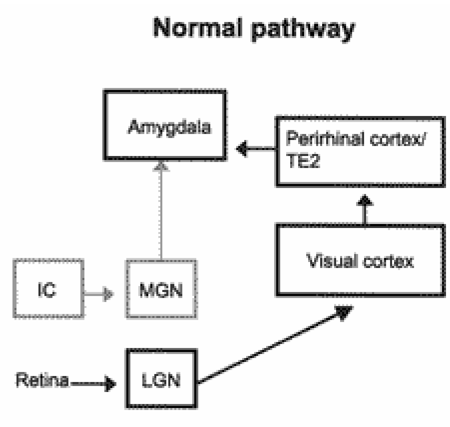
Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

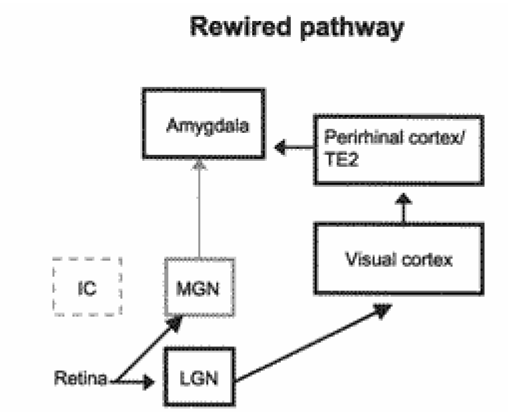
Cortical reorganization with altered afferent pathways

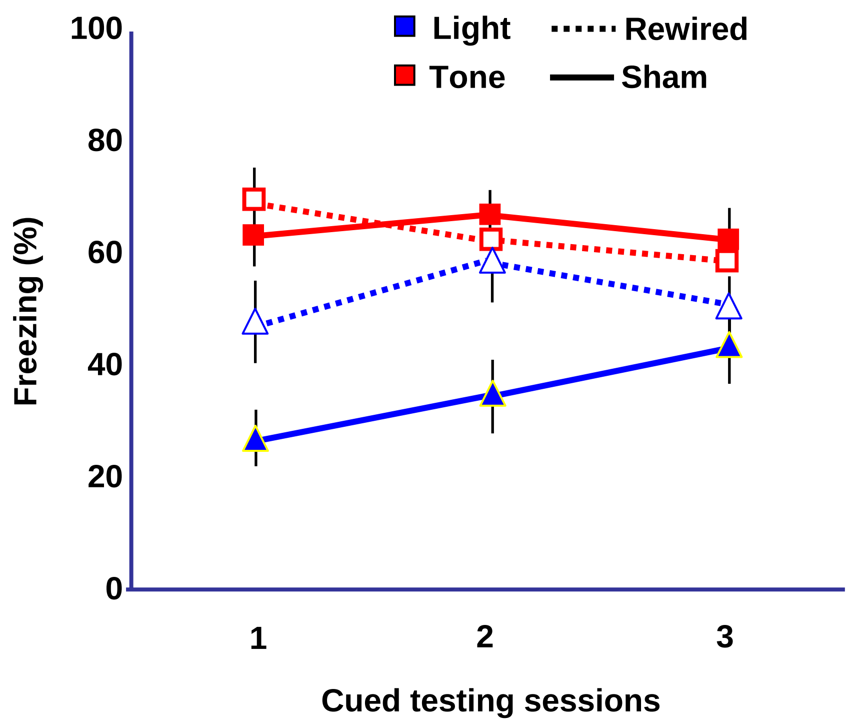


Sur + Ruberstein, ***Science*** 310(5749), 805:810 (2005)

Rewired pathway speeds up visual fear conditioning



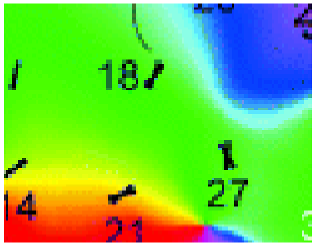


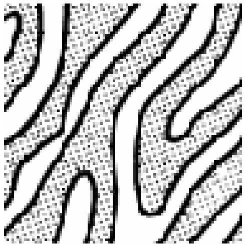


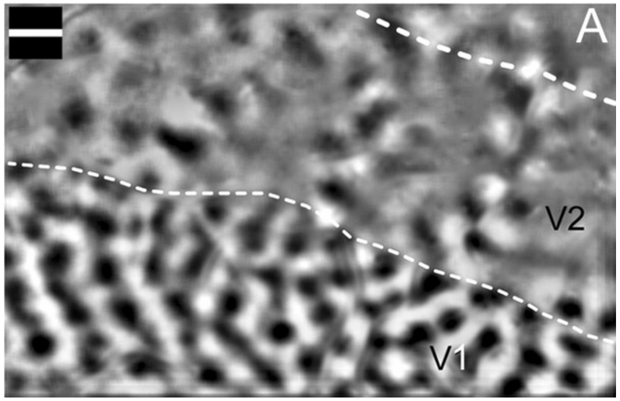
Newton et. Al., ***Nature Neuroscience*** 7, 968 - 973 (2004)

Principles of cortical organization

- Continuity: nearby cells prefer stimuli to similar features
  - Computationally: Usually enforced in models through averaging of input stimuli
  - Biologically: Short-range excitatory connectivity
    - Varies from region to region

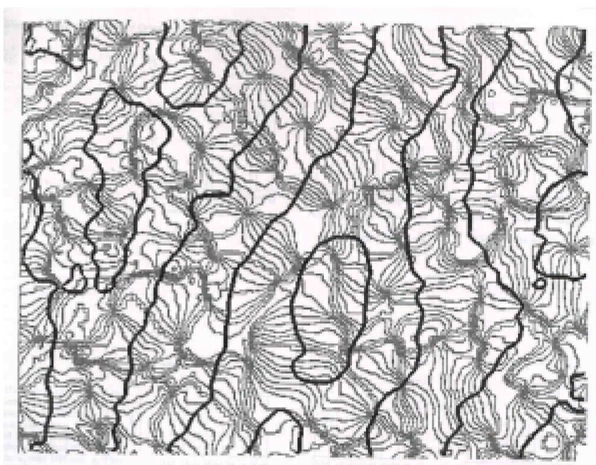


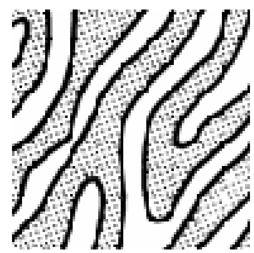


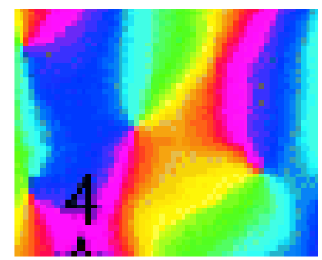


Principles of cortical organization (cont.)

- Diversity: all possible feature preferences should be represented as completely as possible
  - Computationally: Enforced through bandpass filtering of the spatial pattern of feature preferences, or through competition
  - Biologically: This relates directly to stimuli in the environment



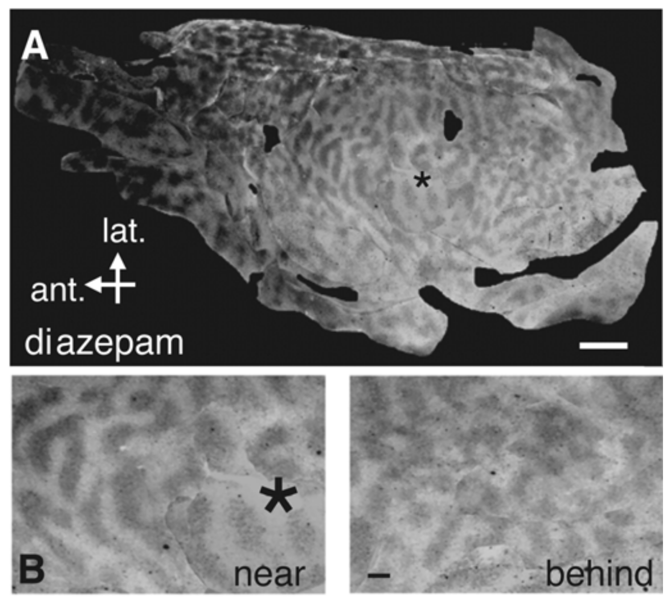




Obermayer and Blasdel, ***J. Neuroscience*** 13: 4114-4129, 1993

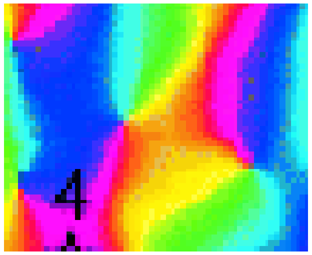
Principles of cortical organization (cont.)

- Global disorder: patterns of ocular dominance, orientation columns, etc. do not have strict regularity
  - Computationally: Explicit inclusion of noise
  - Biologically: an incredibly complex system

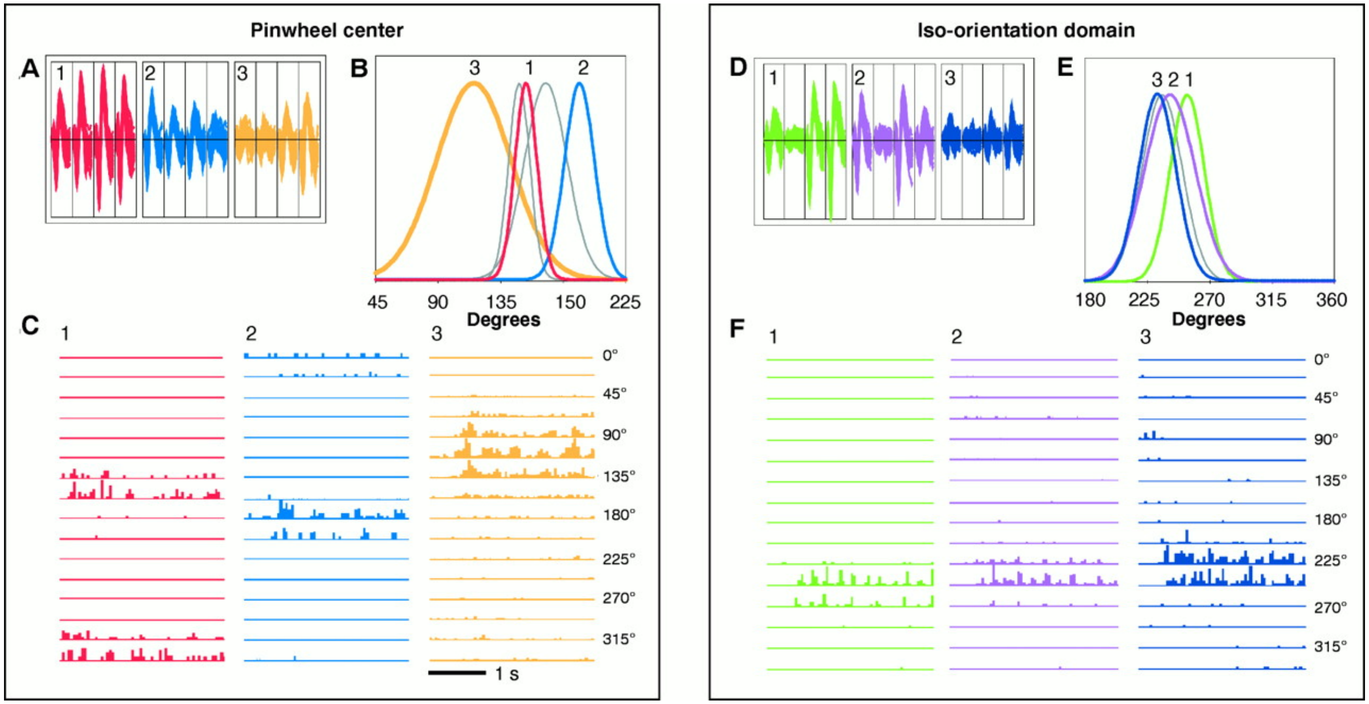


Hensch + Stryker, ***Science*** 303(5664), 1678 – 1681 (2004) 55

Principles of cortical organization (cont.)



- Singularities: point-like discontinuities
  - Computationally: Usually created through competition
  - Biologically: These regions appear to arise from the resolution of competing organizational patterns, such as orientation columns and ocular dominance columns



Baldonado et al. ***Science*** 276(5318), 1551 – 1555 (1997) 565

Example: Elastic net models of cortical organization

- $\mathbf{x}_n$ represents a stimulus space vector, $\mathbf{y}_m$ is stimulus preference of neuron *m*, and *K* is receptive field size
- The different dimensions (OD, OR, DR, SF) are N scalar input dimensions $\mathbf{x}_n$
- The stimulus preference $\mathbf{y}_m$ of a neuron *m* can be described by its position in the N-dimensional space. Its coordinates $\mathbf{y}_m$ are the preferred values along each dimension *m*

- A unit's activity is modeled with Gaussians: $z_m = e^{\frac{1}{2}\left\|(x_n - y_m)/K\right\|^2}$

Learning rule: $$\tau_y \frac{dy_{nm}}{dt} = \left\langle \alpha_n \left(x_n - y_{nm} \right) \right\rangle + \beta \sum_{n' \text{ neighbor of } n} \left(y_{n'm} - y_{nm} \right)$$

move weight in direction of input

move weight in direction of neighbors

Development of multiple maps in visual cortex

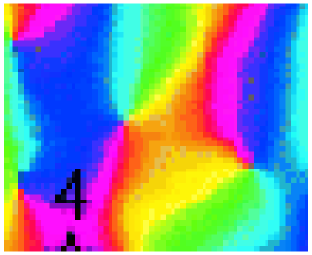
- Formation of features is based on a trade-off between coverage of the space and continuity of the cortical representation
- The coverage term is

$$C(\mathbf{y}_1, \ldots, \mathbf{y}_M; K) = -K \sum_{n=1}^{N} \log \sum_{m=1}^{M} e^{-\frac{1}{2}\left\| (\mathbf{x}_n - \mathbf{y}_m)/K \right\|^2}$$

  - where $\mathbf{x}_n$ represents a stimulus space vector, $\mathbf{y}_m$ is stimulus preference of neuron m, and K is receptive field size

- The continuity term is

$$R(\mathbf{y}_1, \ldots, \mathbf{y}_M) = \sum_{m} \left\| \mathbf{y}_{m+1} - \mathbf{y}_m \right\|^2$$

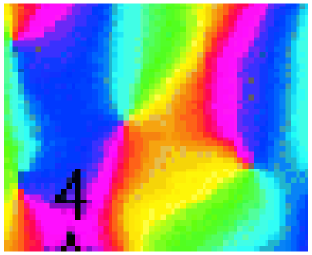


Trade-off between coverage and continuity

- The elastic net minimizes a tradeoff between these terms:

$$E = \alpha C + (\beta/2)R$$

- The positive ratio α/β controls the relative strength of the continuity versus the coverage terms
  - Biologically plausible maps arise for a range of values of α/β
- The net consists of a square lattice with M centroids, representing a square array of cortical neurons
- Goal is to learn the stimuli preferences for each cortical neuron $\mathbf{y}_m$

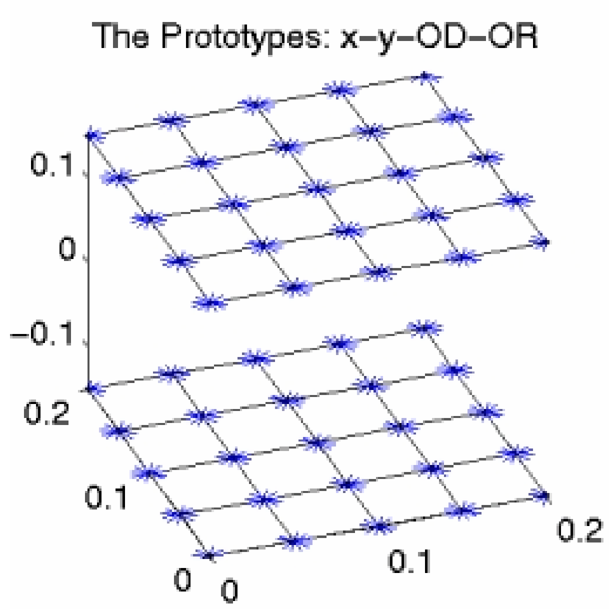


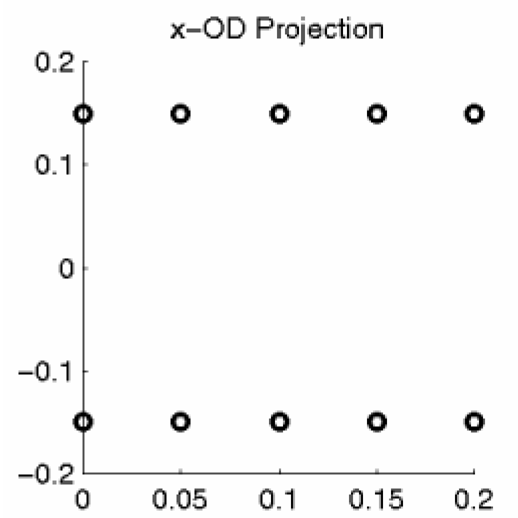
Stimulus representation

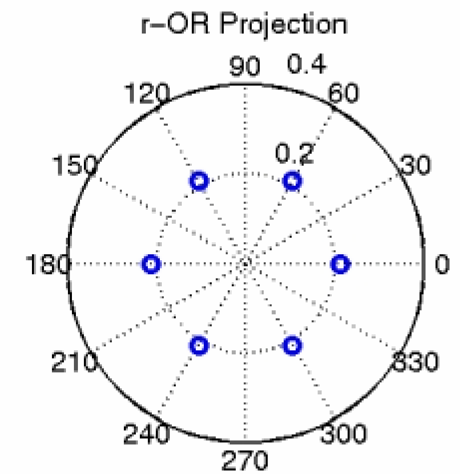
$$C(\mathbf{y}_1, \ldots, \mathbf{y}_M; K) = -K \sum_{n=1}^{N} \log \sum_{m=1}^{M} e^{-\frac{1}{2}\|(\mathbf{x}_n - \mathbf{y}_m)/K\|^2}$$

$$R(\mathbf{y}_1, \ldots, \mathbf{y}_M) = \sum_{m} \|\mathbf{y}_{m+1} - \mathbf{y}_m\|^2$$

$$E = \alpha C + (\beta/2)R$$







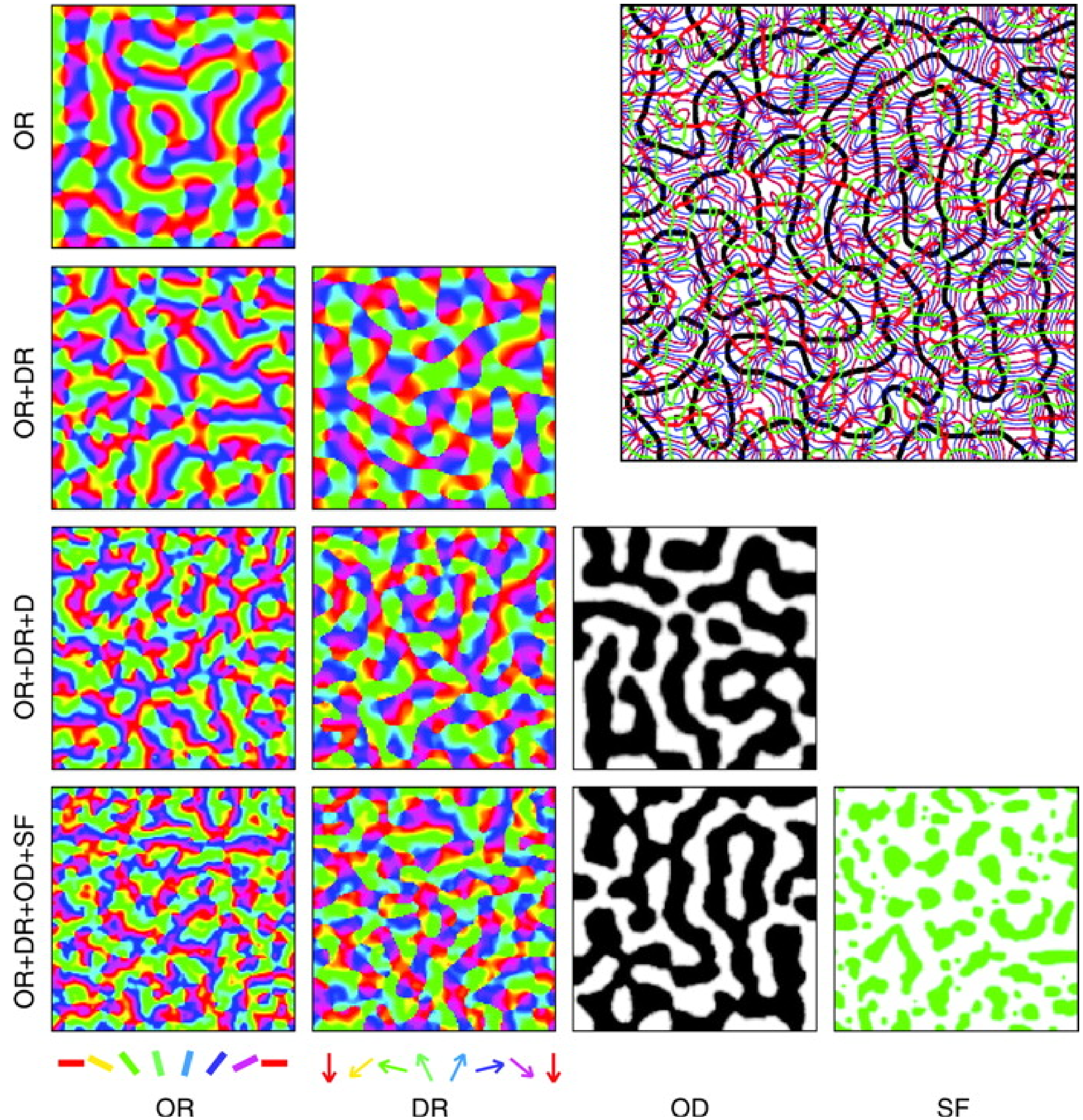
Effect of training for multiple features

Features:

- Ocular Dominance
- Directional sensitivity (DR)
- Orientation (OR)
- Spatial frequency (SF)

Training set:

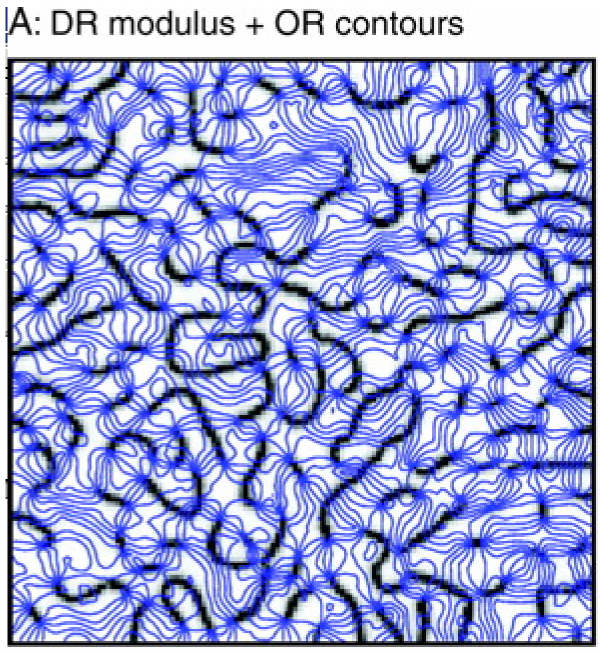
- M = 128x128 = 16384 cortical neurons
- Initially, α=1, β=10

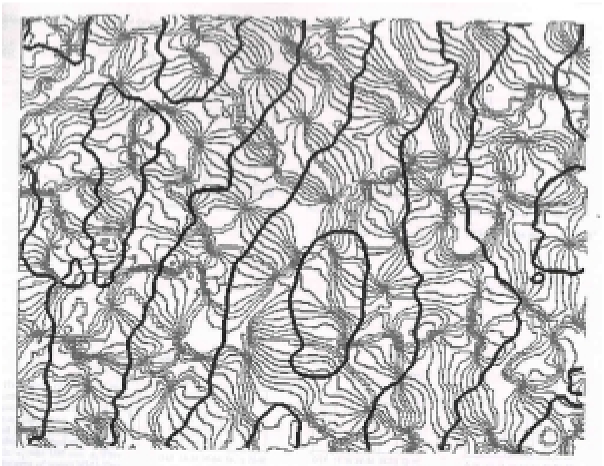


Carreira-Perpiñán et. al., ***Cerebral Cortex*** 15(8):1222-1233 (2005)

Relationships between features

– DR map has fractures = lines of low DR modulus
    - These correlate with where DR angle reverses direction
– These fractures connect OR pinwheels, consistent with experimental data
– Away from DR fractures, contours of OR and DR run parallel

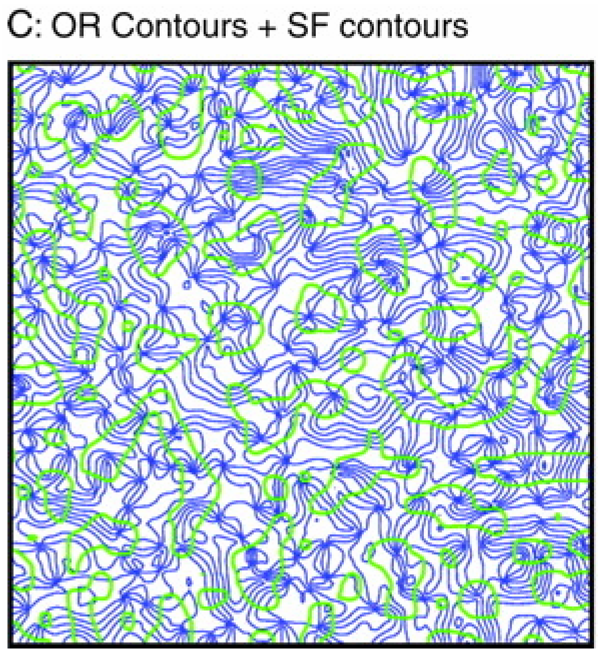




Carreira-Perpiñán et. al., ***Cerebral Cortex*** 15(8):1222-1233 (2005)

Relationships between features (cont.)

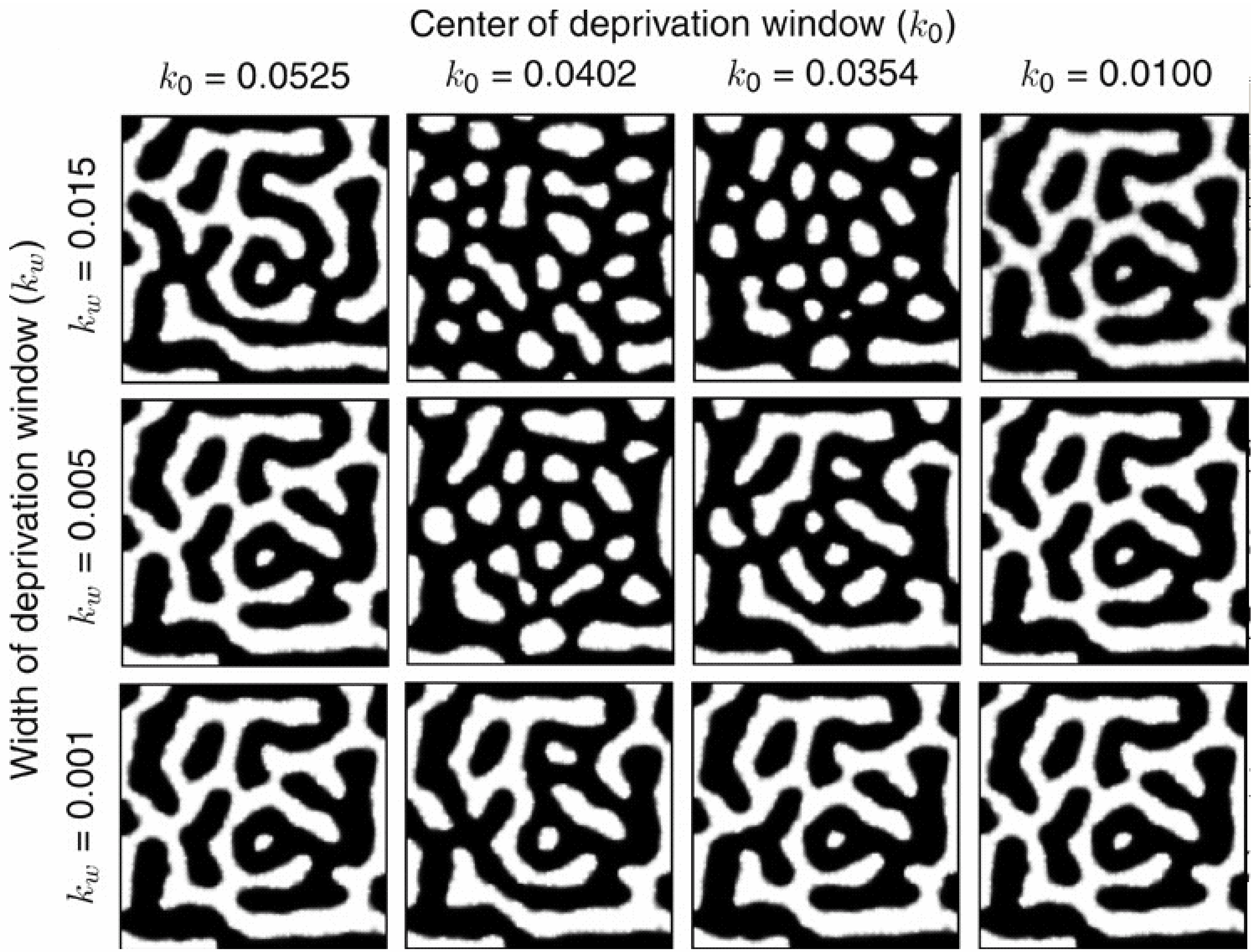
- The OR and SF maps tend to intersect orthogonally, also consistent with experimental data



Modeling monocular deprivation

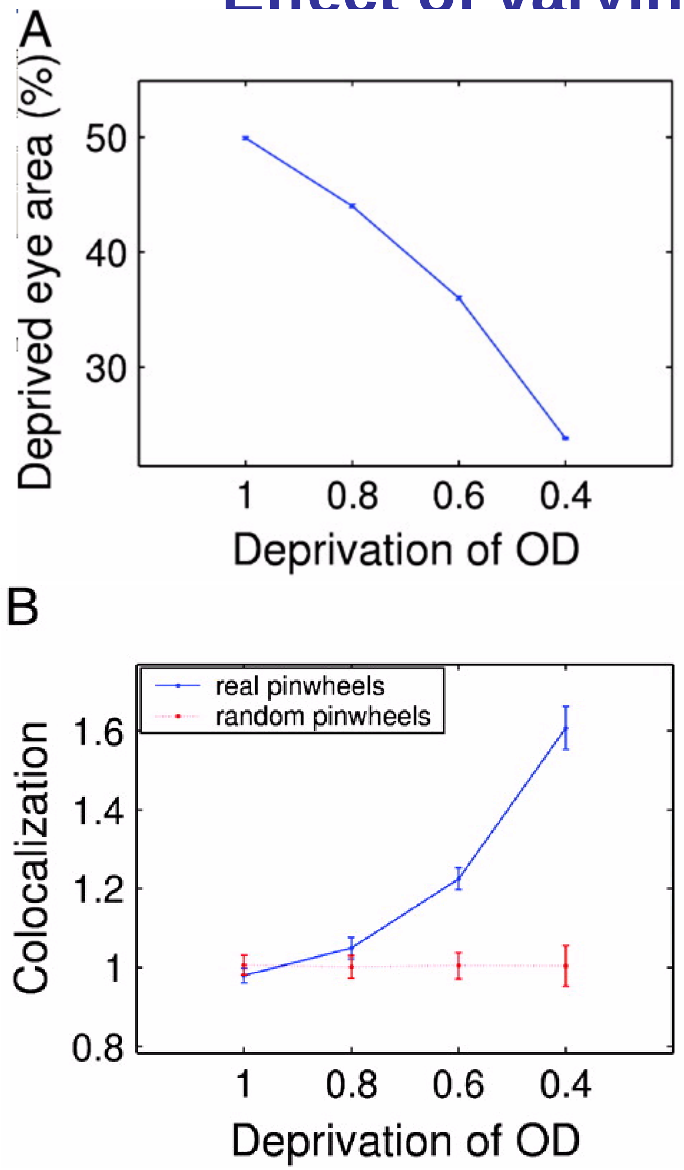
- OD deprivation was modeled by changing α=1 to a vector with N components
  - Value of component n represents the relative strength with which the stimulus point $\mathbf{x}_n$ is represented in the input.
  - For monocular deprivation n = $\mathrm{dep}_{\mathrm{OD}}$ between (0, 1) for each $\mathbf{x}_n$ matching the deprived eye (i.e. fixed value representing the amount of deprivation)
  - Deprivation was restricted to a portion of the annealing time (width k_w) centered at different points during the annealing (k_0)

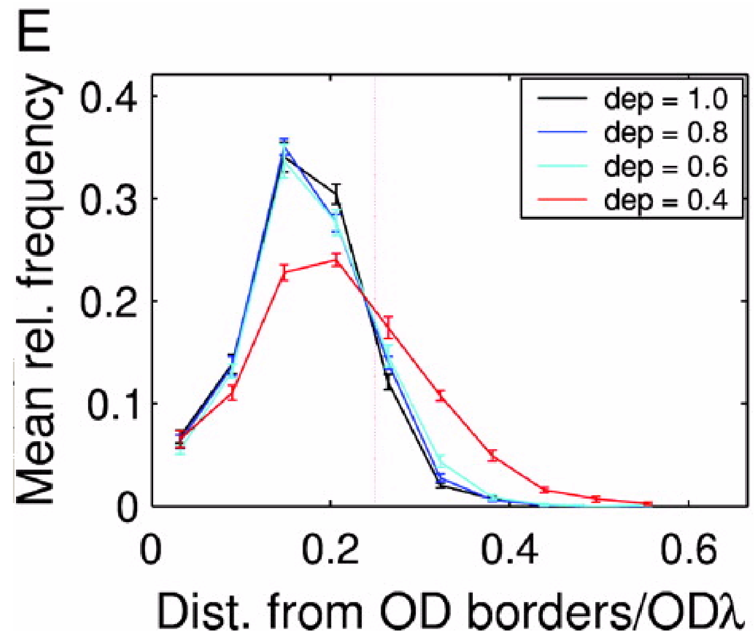
$$E = \alpha C + (\beta/2)R$$



Carreira-Perpiñán et. al., ***Cerebral Cortex*** 15(8):1222-1233 (2005)

Effect of varying amount of deprivation





$$E = \alpha C + (\beta/2)R$$

Carreira-Perpiñán et. al., ***Cerebral Cortex*** 15(8):1222-1233 (2005)

How well does the model fit empirical data?

- OR and OD columns intersect at steep angles
- OD pinwheels to lie far from OD borders
- DR sensitivity map has fractures rather than pinwheels
  - Pinwheels tend to be connected by fractures
- OR and OD columns tend to intersect SF columns at steep angles
- OR pinwheels to lie far from SF borders
- Monocular deprivation during a critical period of development produces a shrinkage of OD domains from the deprived eye
  - Pinwheels tend to colocalize with deprived eye patches
- Single orientation rearing produces an expansion of OR domains for the overrepresented orientation

What does the model teach us?

- The model is a mathematical representation of the hypothesis that visual cortical maps are the result of an optimization process
  - Attempts to jointly optimize the degree to which all input features are uniformly represented (coverage), and the degree to which the spatial representation of features is 'smooth' (continuity)
- The model cannot explain in biological terms how this might take place