

# **Early Vision and Visual System Development**

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# Studying the visual system (1)

The visual system can be (and is) studied using many different techniques. In this course we will consider:

**Psychophysics** What is the level of human visual performance under various different conditions?

**Anatomy** Where are the visual system parts located, and what do they look like?

**Gross anatomy** What do the visual system organs and tissues look like, and how are they connected?

**Histology** What cellular and subcellular structures can be seen under a microscope?

# Studying the visual system (2)

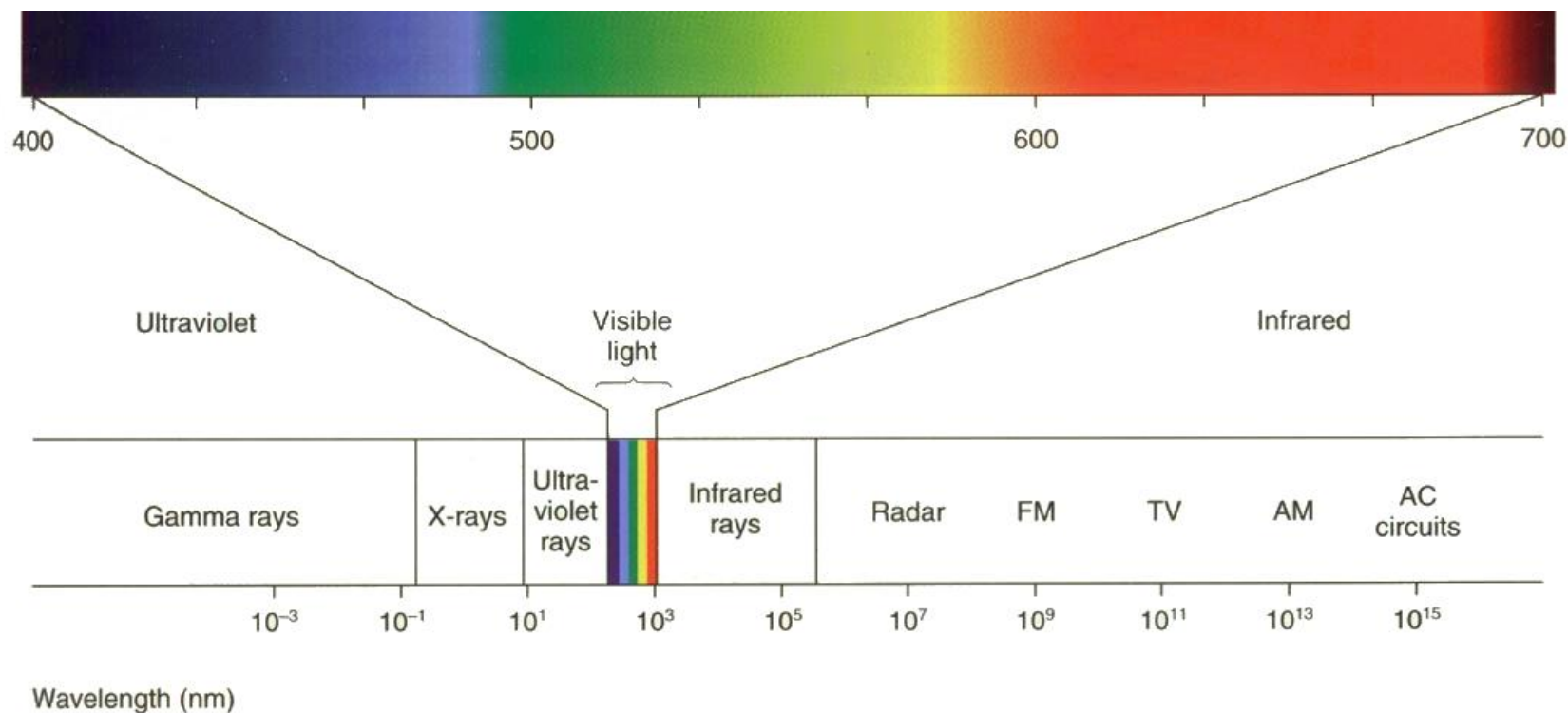
**Physiology** What is the behavior of the component parts of the visual system?

**Electrophysiology** What is the electrical behavior of neurons, measured with an electrode?

**Imaging** What is the behavior of a large area of the nervous system?

**Genetics** Which genes control visual system development and function, and what do they do?

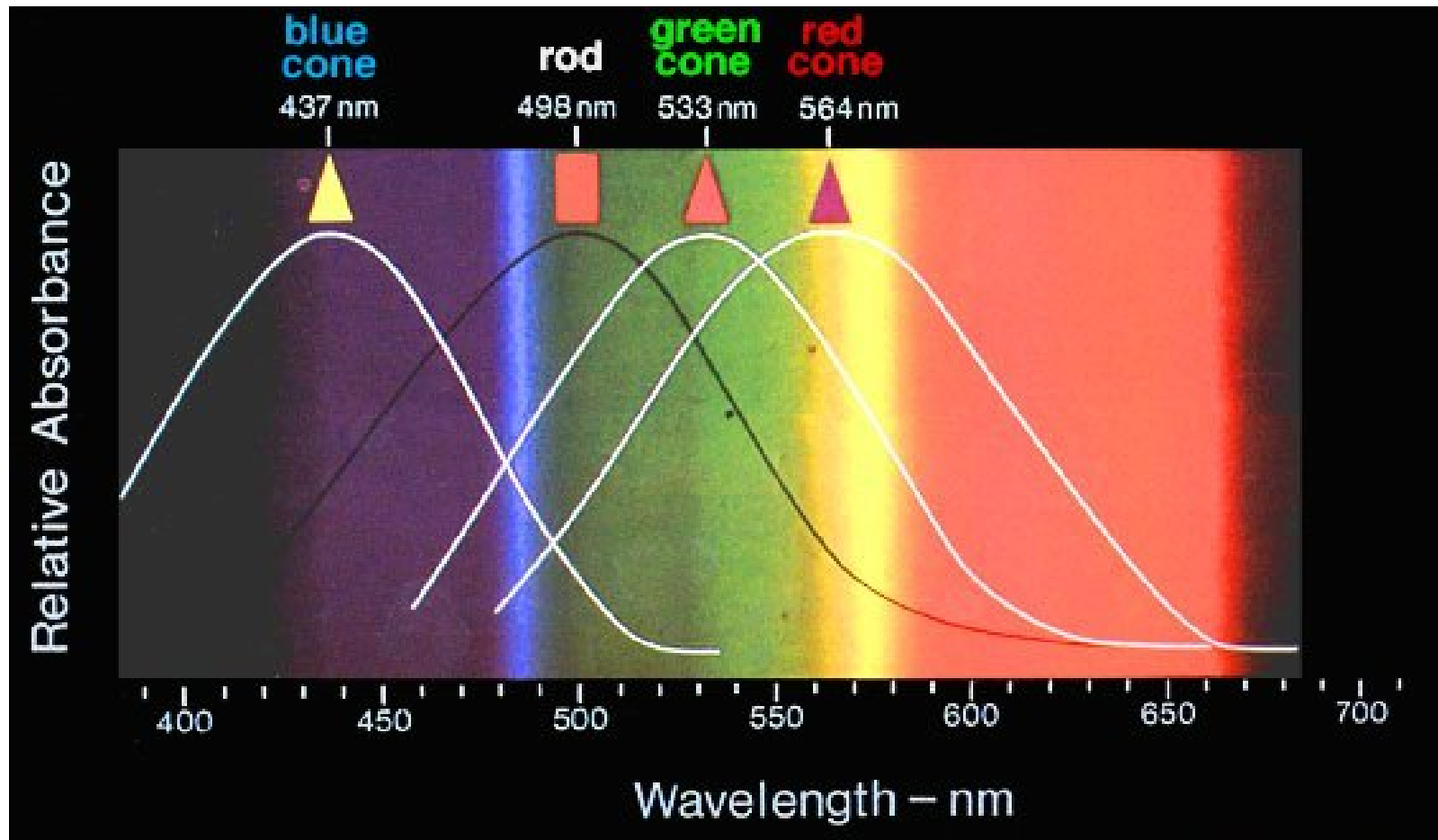
# Electromagnetic spectrum



(From web)

Start with the physics: visible portion is small, but provides much information about biologically relevant stimuli

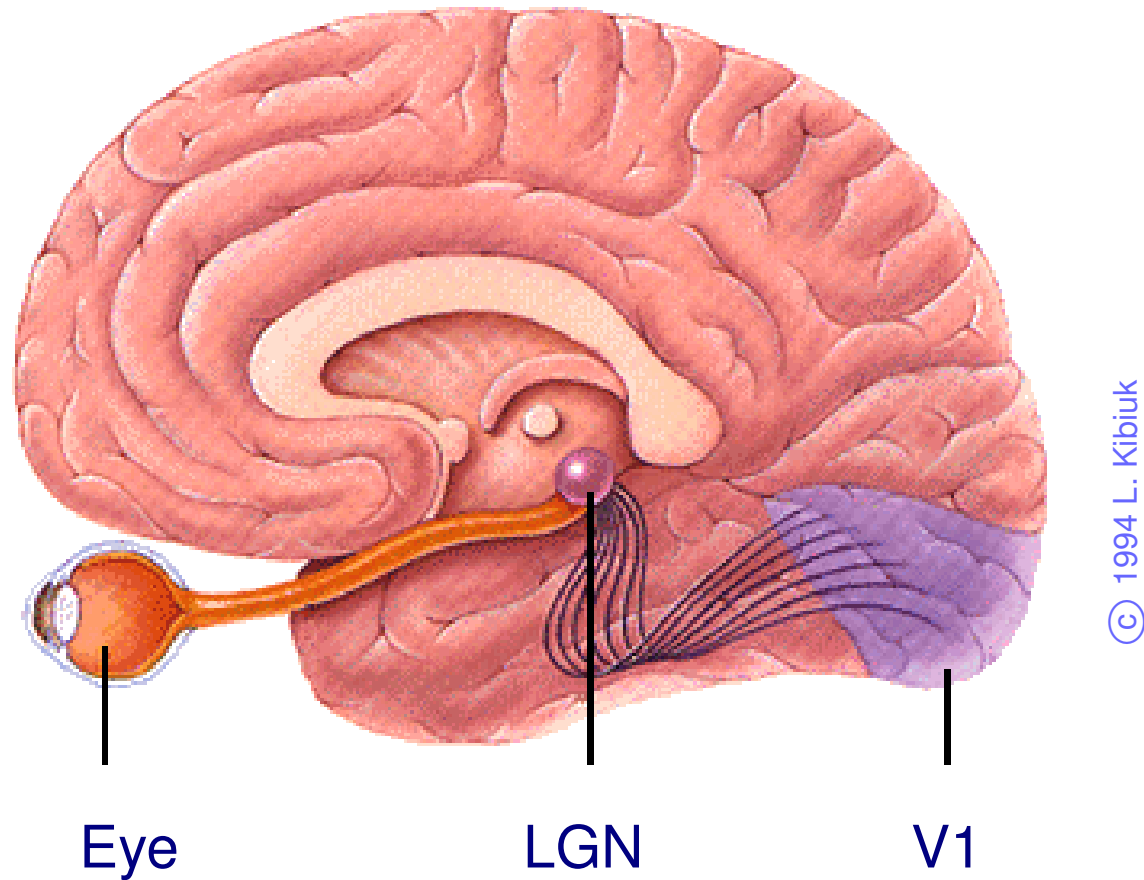
# Cone spectral sensitivities



(Dowling, 1987)

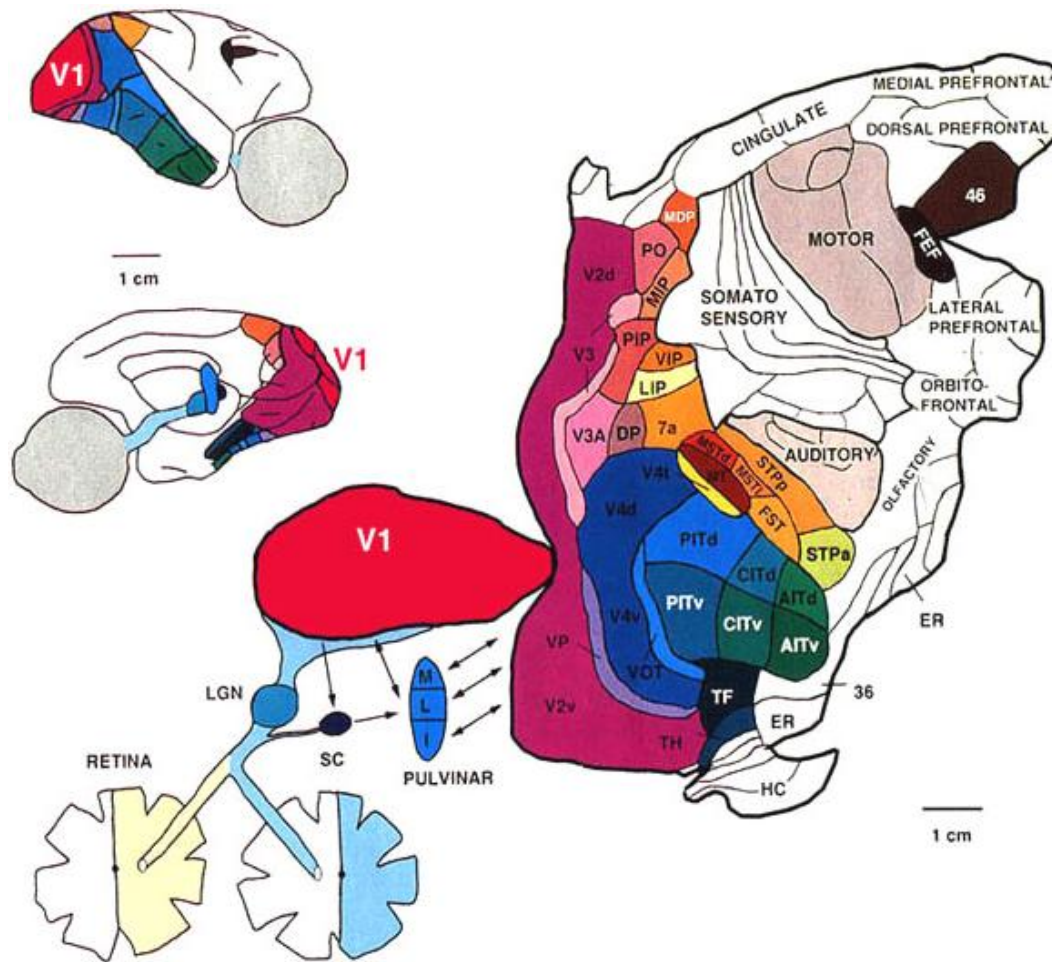
Somehow we make do with sampling the visible range of wavelengths at only three points (3 cone types)

# Early visual pathways



Signals travel from retina, to LGN,  
then to primary visual cortex

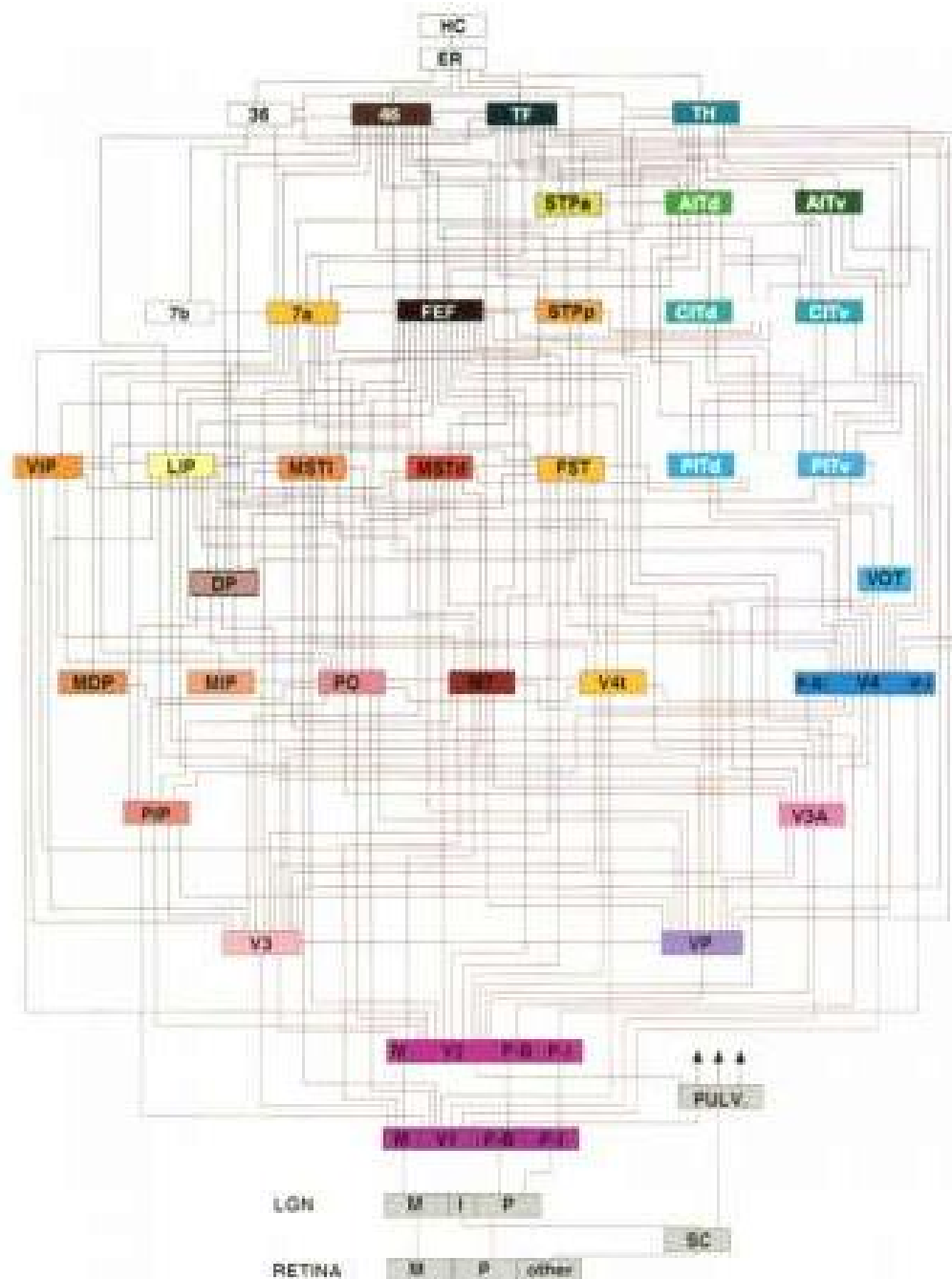
# Higher areas



Macaque visual areas  
(Van Essen et al. 1992)

- Many higher areas beyond V1
- Selective for faces, motion, etc.
- Not as well understood

# Circuit diagram



Connections  
between  
macaque visual  
areas

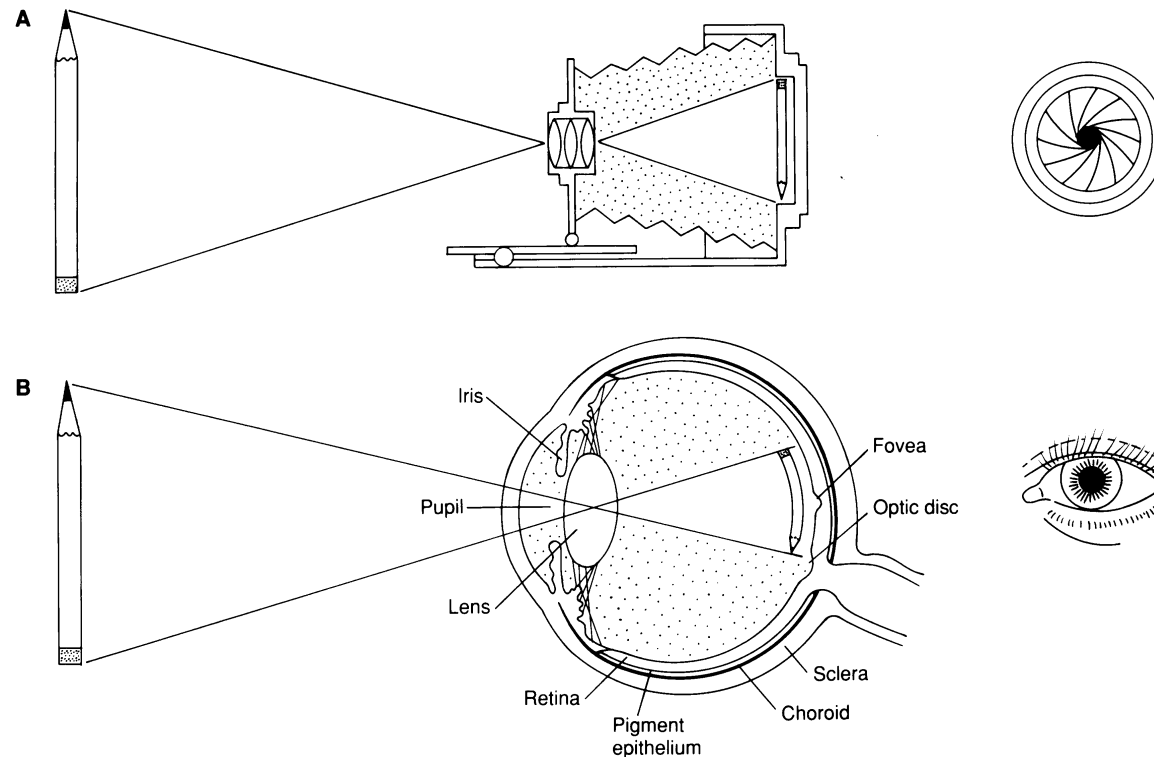
(Van Essen et al. 1992)

A bit messy!

(Yet still just a start.)



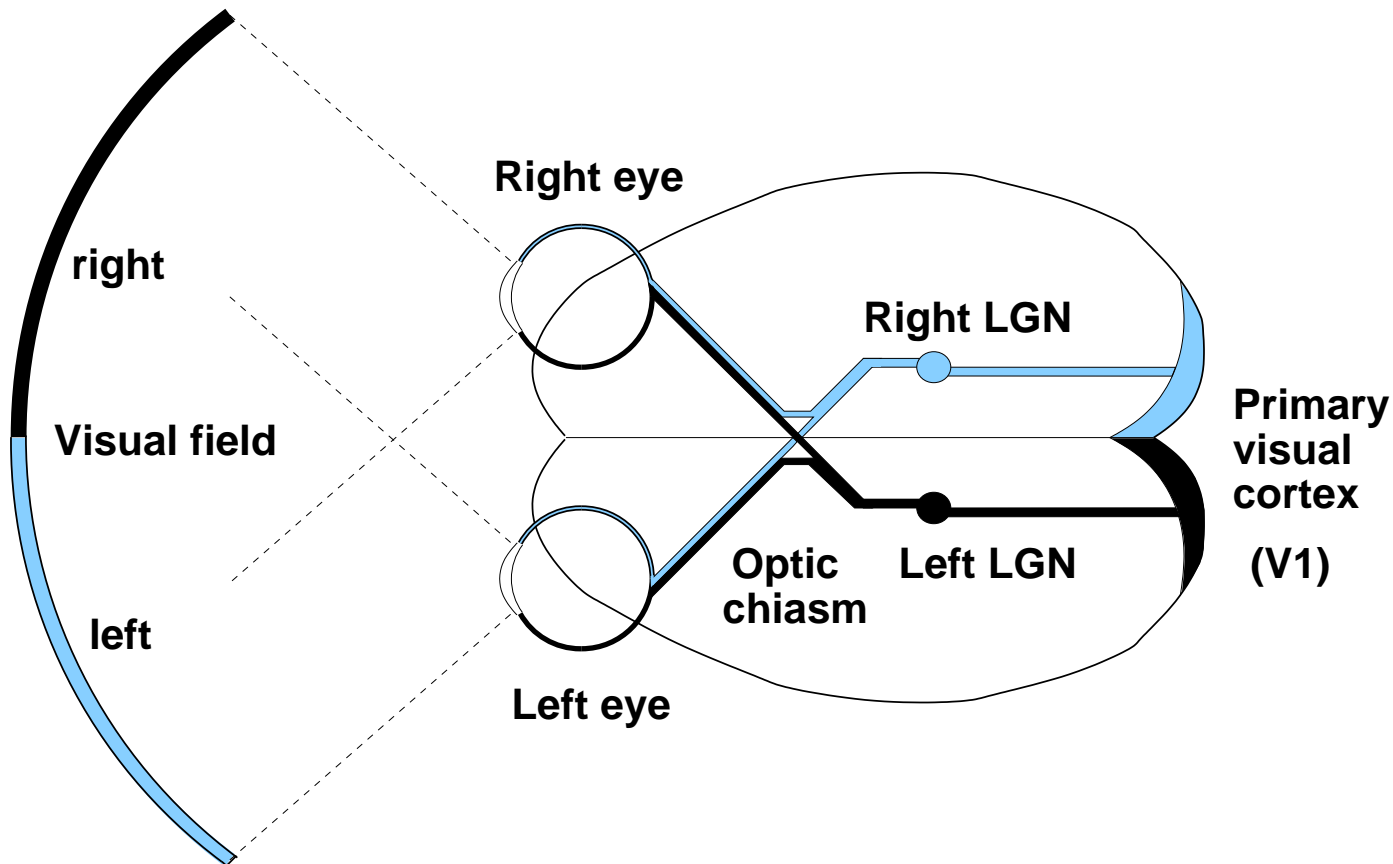
# Image formation



(Kandel et al. 1991)

	Fixed	Adjustable	Sampling
<b>Camera:</b>	lens shape	focal length	uniform
<b>Eye:</b>	focal length	lens shape	higher at fovea

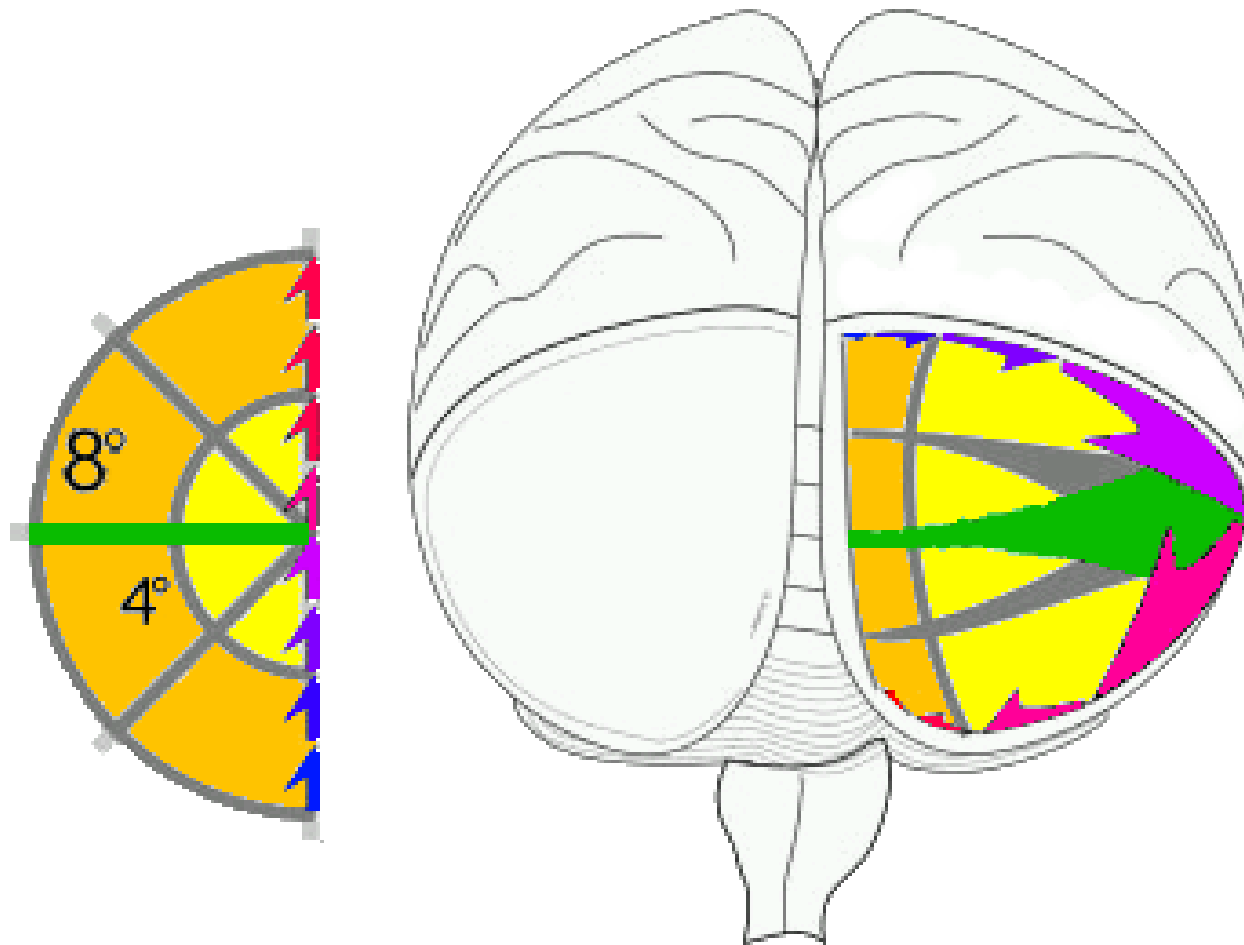
# Visual fields



CMVC figure 2.1

- Each eye sees partially overlapping areas
- Inputs from opposite hemifield cross over at chiasm

# Retinotopic map



Mapping of  
visual field in  
macaque  
monkey

Blasdel and  
Campbell  
2001

- Visual field is mapped onto cortical surface
- Fovea is overrepresented

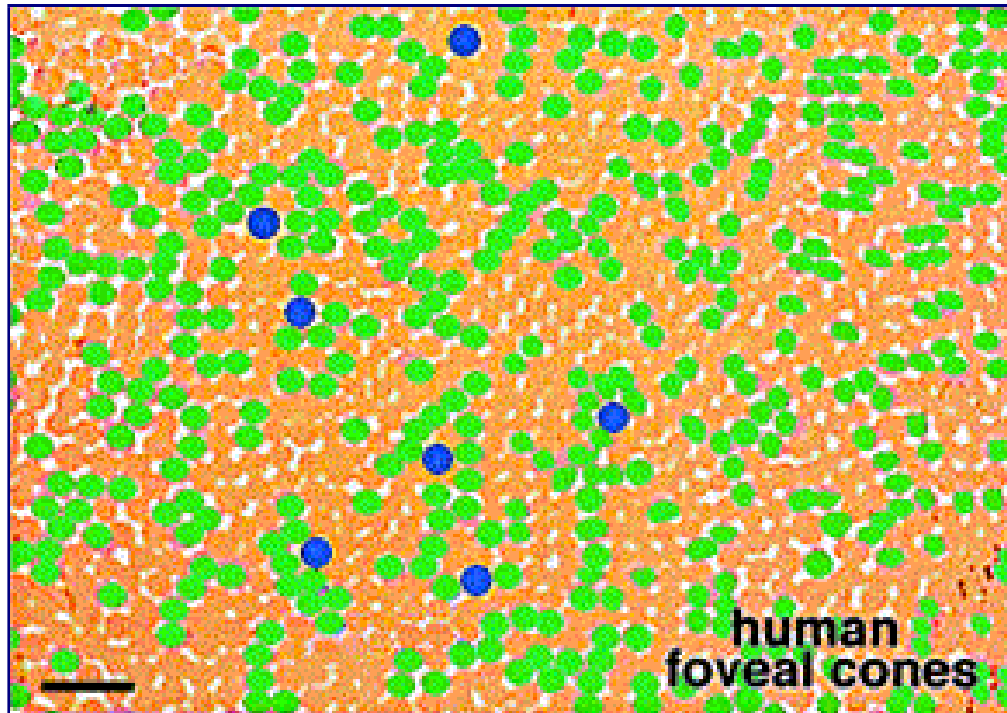
# Effect of foveation



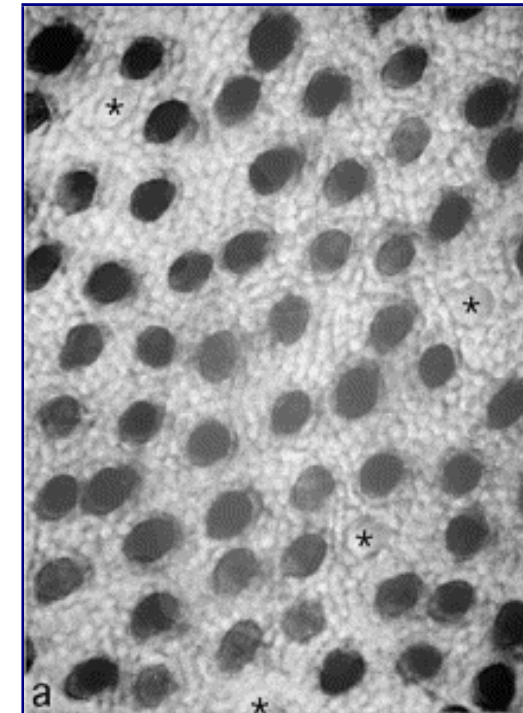
(From omni.isr.ist.utl.pt)

Smaller, tightly packed cones in the fovea  
give much higher resolution

# Retinal surface



Fovea (center  $\rightsquigarrow$ )

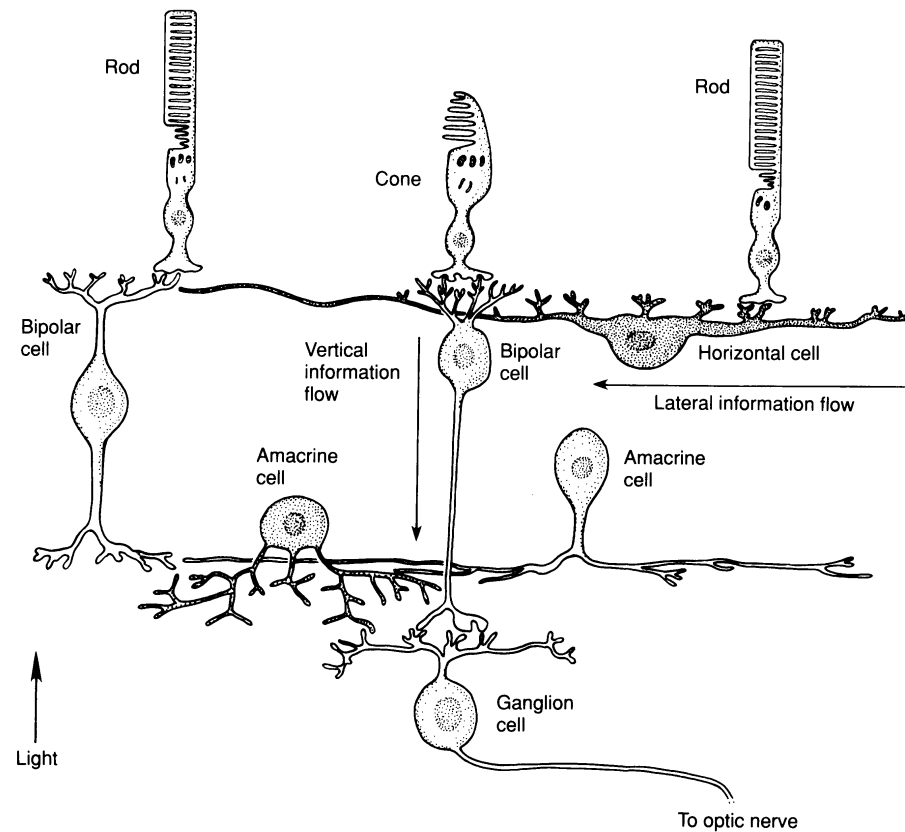


Periphery

(Ahnelt & Kolb 2000); no scale in original

- Fovea: densely packed L,M cones (no rods)
- No S cones in central fovea; sparse elsewhere
- Cones are larger in periphery (\*: S-cones)
- Cone spacing also increases, with gaps filled by rods

# Retinal circuits

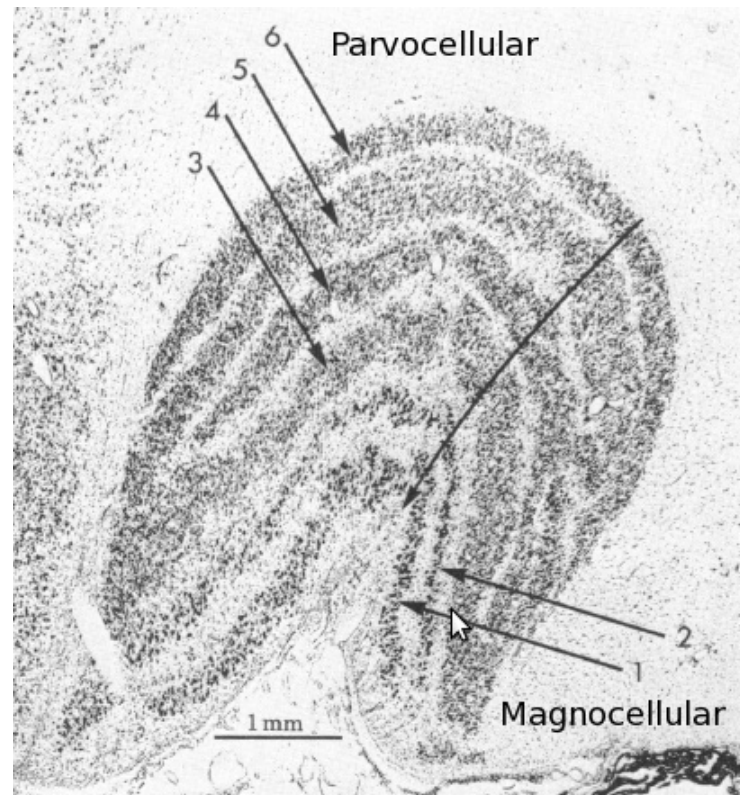


(Kandel et al. 1991)

**Rod pathway** Rod, rod bipolar cell, ganglion cell

**Cone pathway** Cone, bipolar cell, ganglion cell

# LGN layers

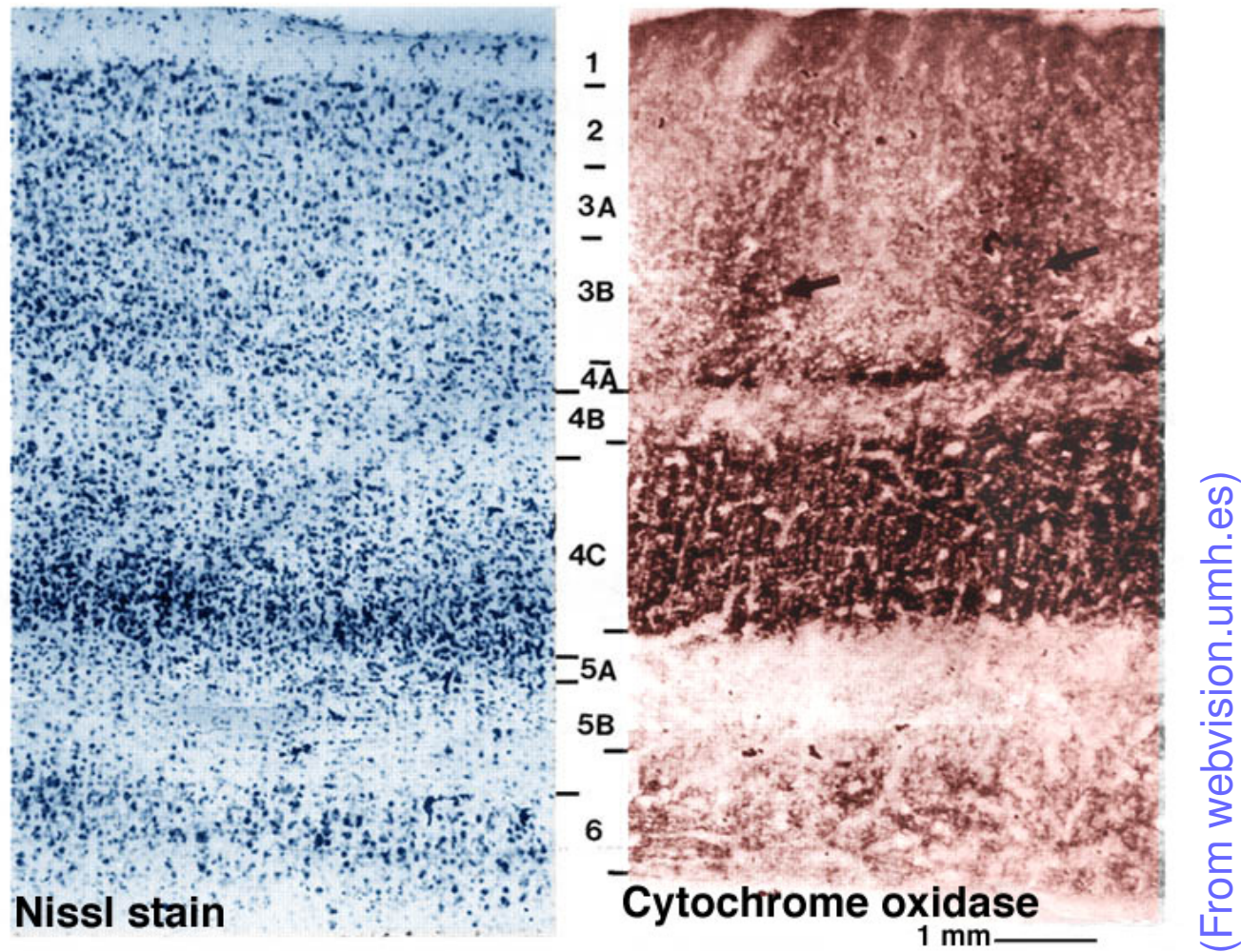


Macaque; Hubel & Wiesel 1977

Multiple aligned representations of visual field in the LGN  
for different eyes and cell types



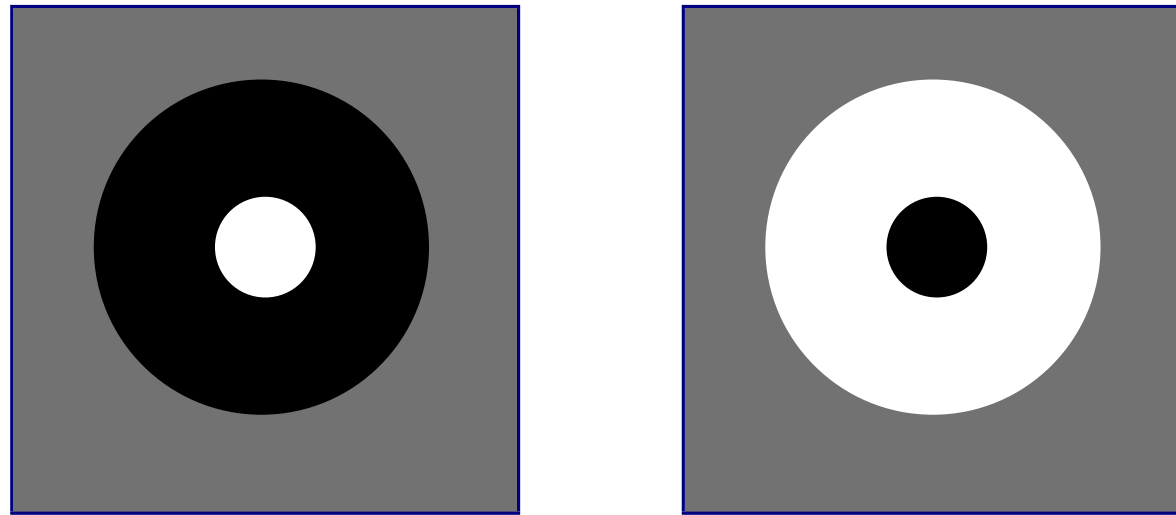
# V1 layers



Multiple layers of cells in V1  
Brodmann numbering



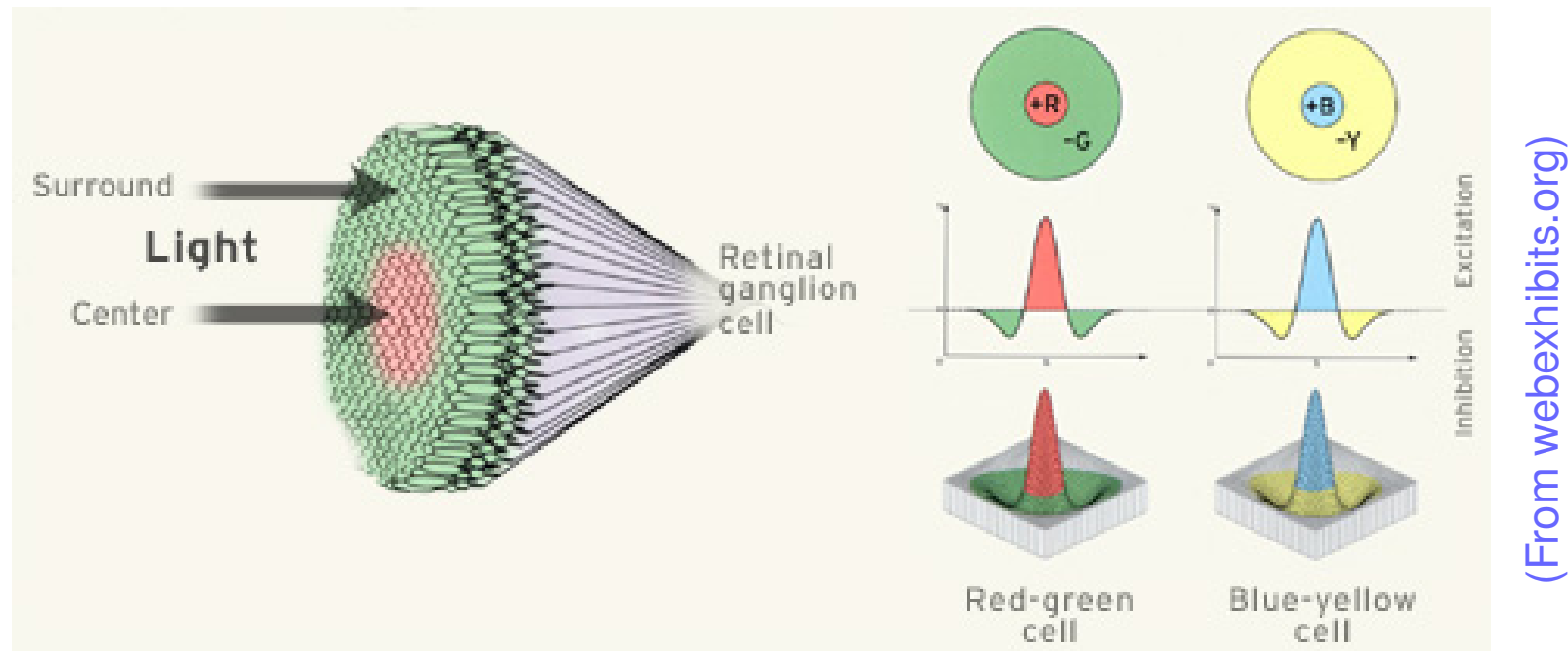
# Retinal/LGN cell response types



Types of receptive fields based on responses to light:

	in center	in surround
On-center	excited	inhibited
Off-center	inhibited	excited

# Color-opponent retinal/LGN cells



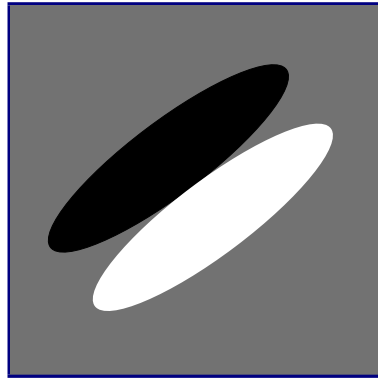
Red/Green cells: (+R,-G), (-R,+G), (+G,-R), (-G,+R)

Blue/Yellow cells: (+B,-Y); others?

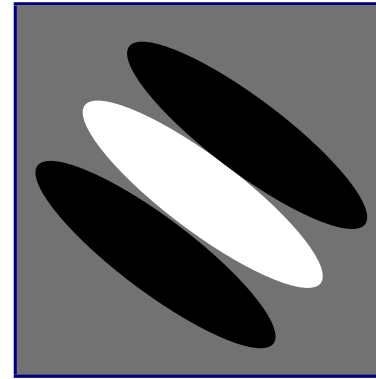
Error: light arrows in the figure are backwards!

Organization generally consistent with random wiring

# V1 simple cell responses



2-lobe simple  
cell

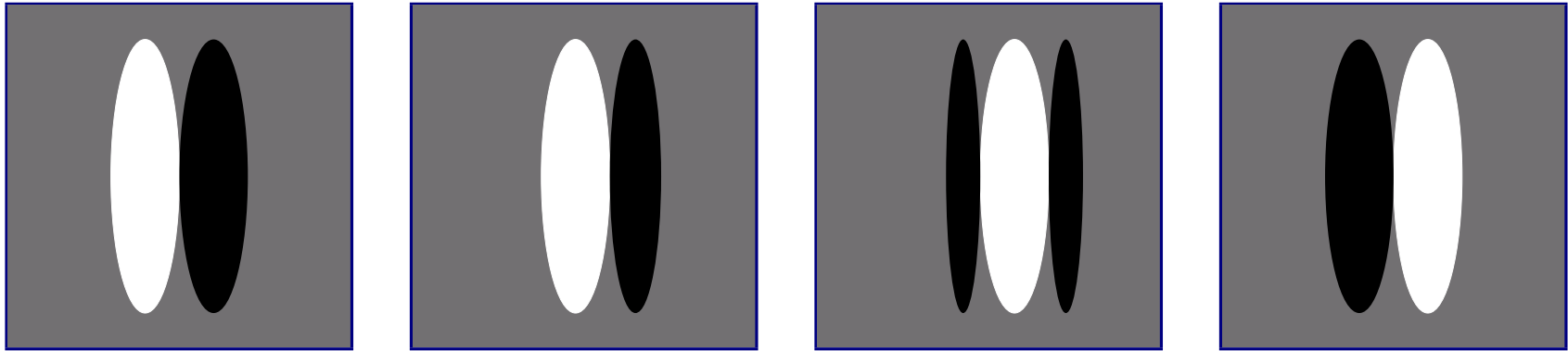


3-lobe simple  
cell

Starting in V1, only oriented patterns will cause any significant response

Simple cells: pattern preferences can be plotted as above

# V1 complex cell responses

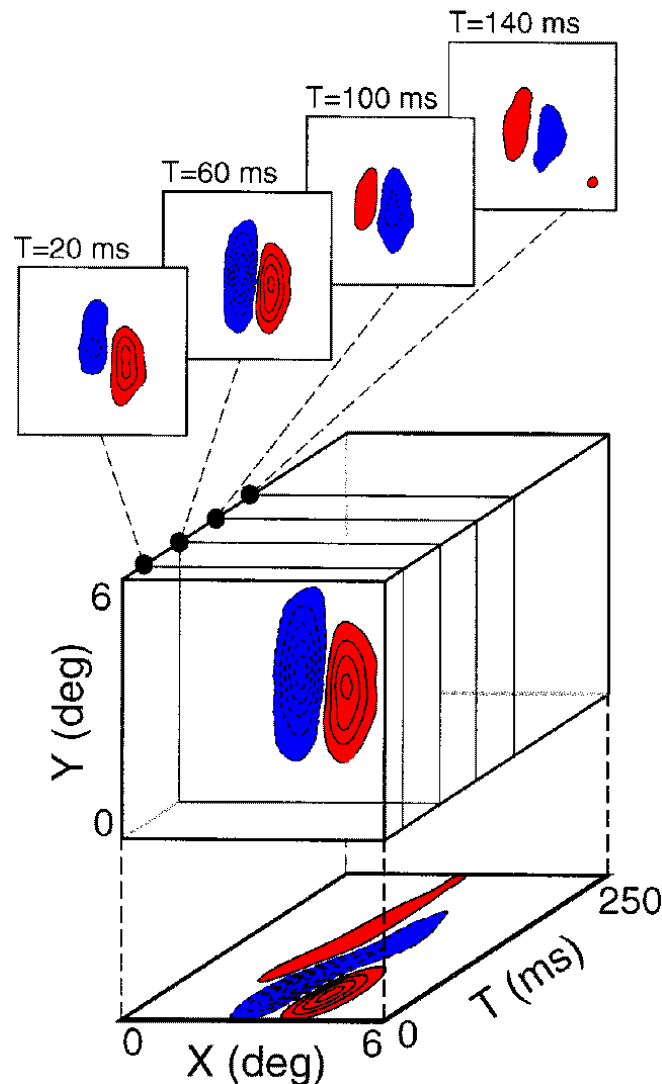


(Same response to all these patterns)

Complex cells are also orientation selective, but have responses invariant to phase

Can't measure complex RFs using pixel-based correlations

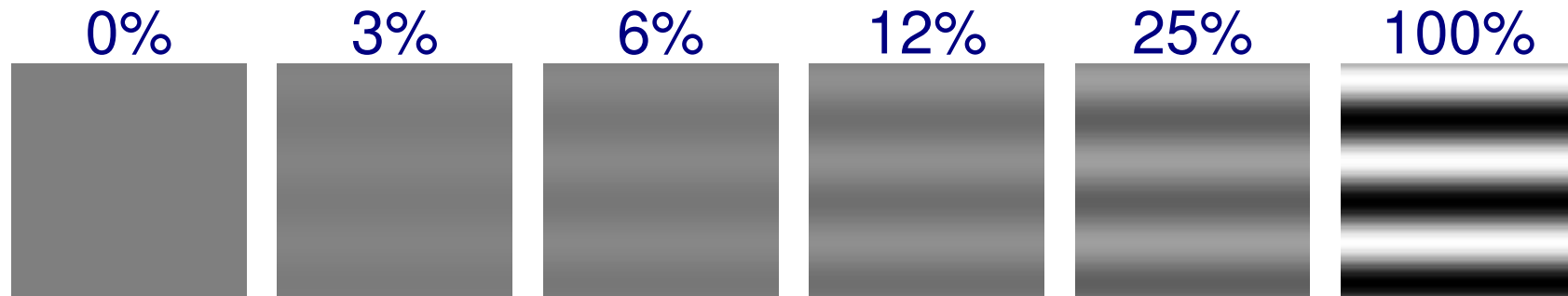
# Spatiotemporal receptive fields



- Neurons are selective for multiple stimulus dimensions at once
- Typically prefer lines moving in direction perpendicular to orientation preference

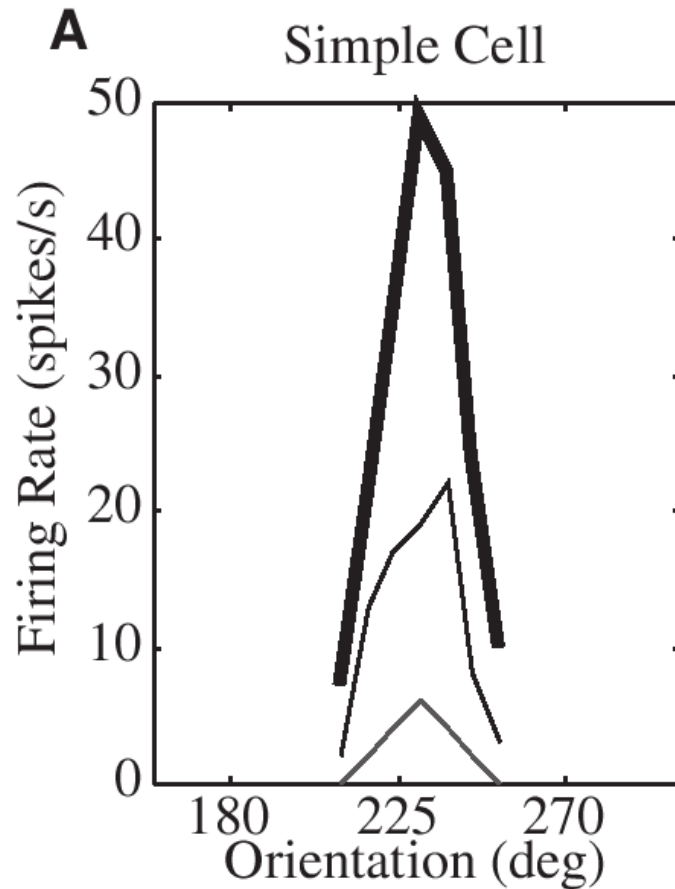
(Cat V1; DeAngelis et al. 1999)

# Contrast perception



- Humans can detect patterns over a huge contrast range
- In the laboratory, increasing contrast above a fairly low value does not aid detection
- See 2AFC (two-alternative forced-choice) test in google and ROC (Receiver Operating Characteristic) in Wikipedia for more info on how such tests work

# Contrast-invariant tuning



(Sclar & Freeman 1982)

- Single-cell tuning curves are typically Gaussian
- 5%, 20%, 80% contrasts shown
- Peak response increases, but
- Tuning width changes little
- Contrast where peak is reached varies by cell

# Definitions of contrast

**Luminance (luminosity):** Physical amount of light

**Contrast:** Luminance relative to background levels to which the visual system has become adapted

Contrast is a fuzzy concept – clear only in special cases:

**Weber contrast (e.g. a tiny spot on uniform background)**

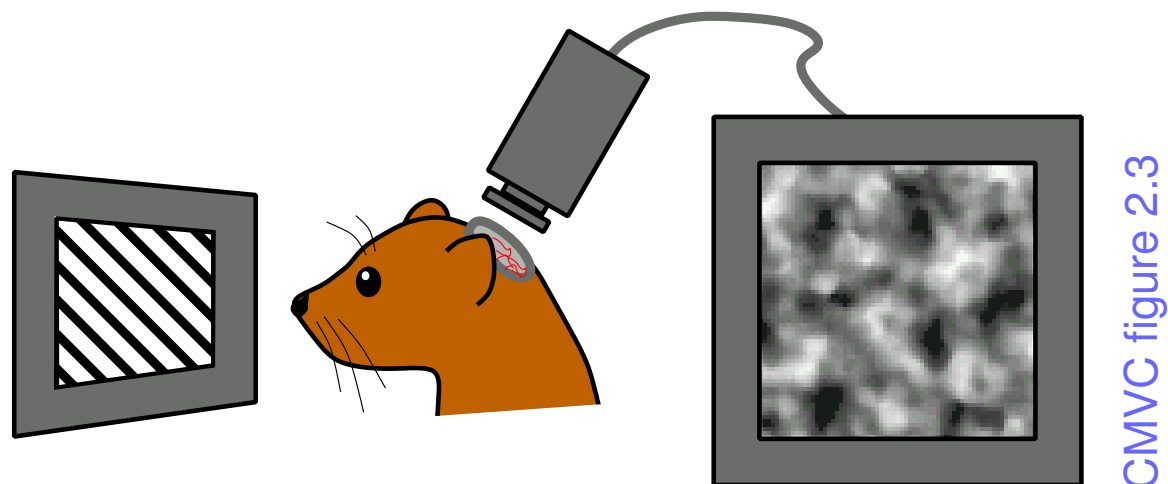
$$C = \frac{L_{max} - L_{min}}{L_{min}}$$

**Michelson contrast (e.g. a full-field sine grating):**

$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} = \frac{\frac{L_{max} - L_{min}}{2}}{L_{avg}}$$

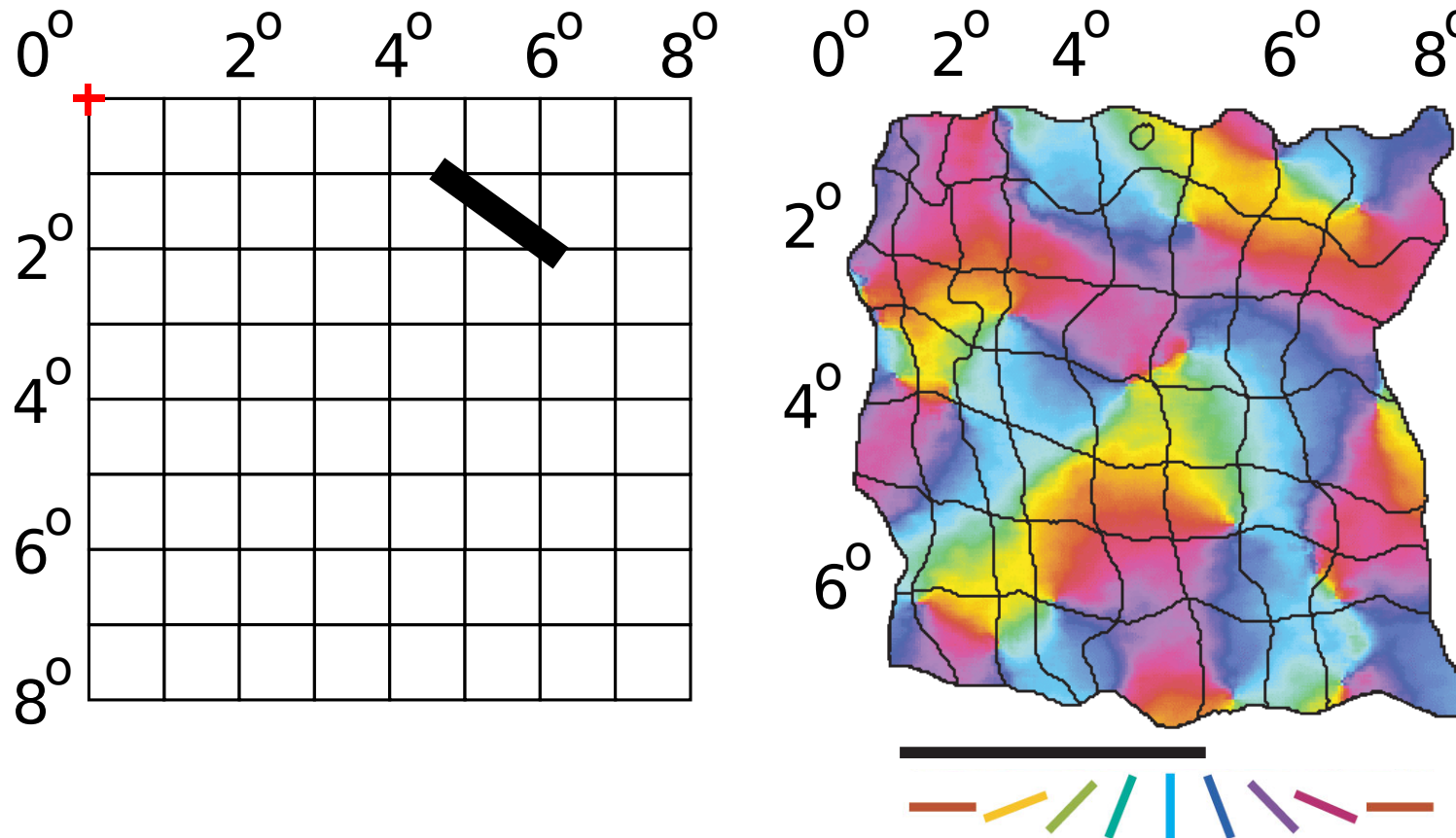


# Measuring cortical maps



- Surface reflectance (or voltage-sensitive-dye emission) changes with activity
- Measured with optical imaging
- Preferences computed as correlation between measurement and input

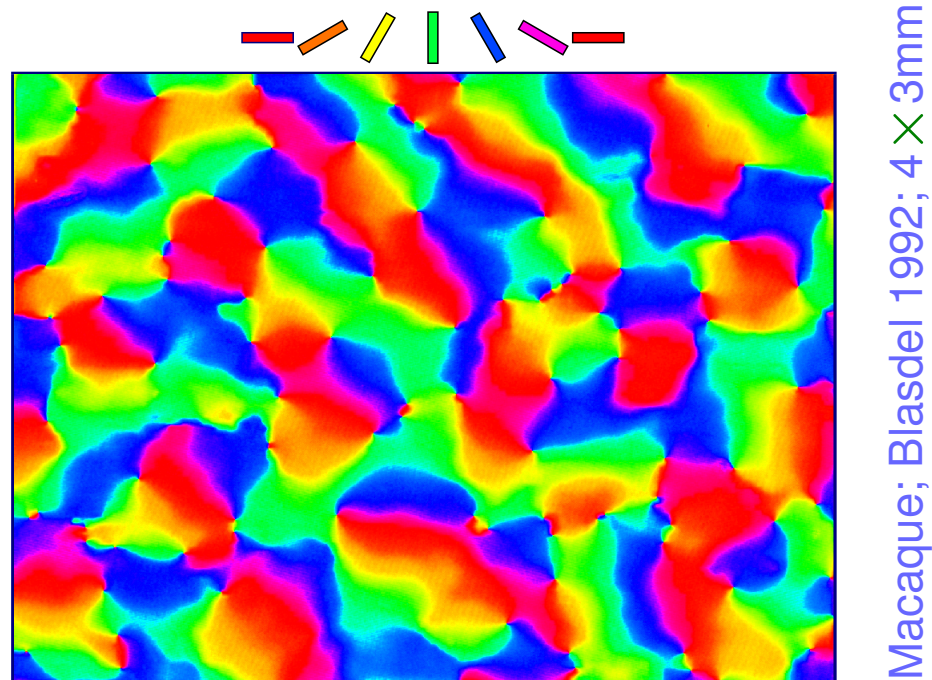
# Retinotopy/orientation map



Tree shrew; Bosking et al. 2002;  $2 \times 2$  mm

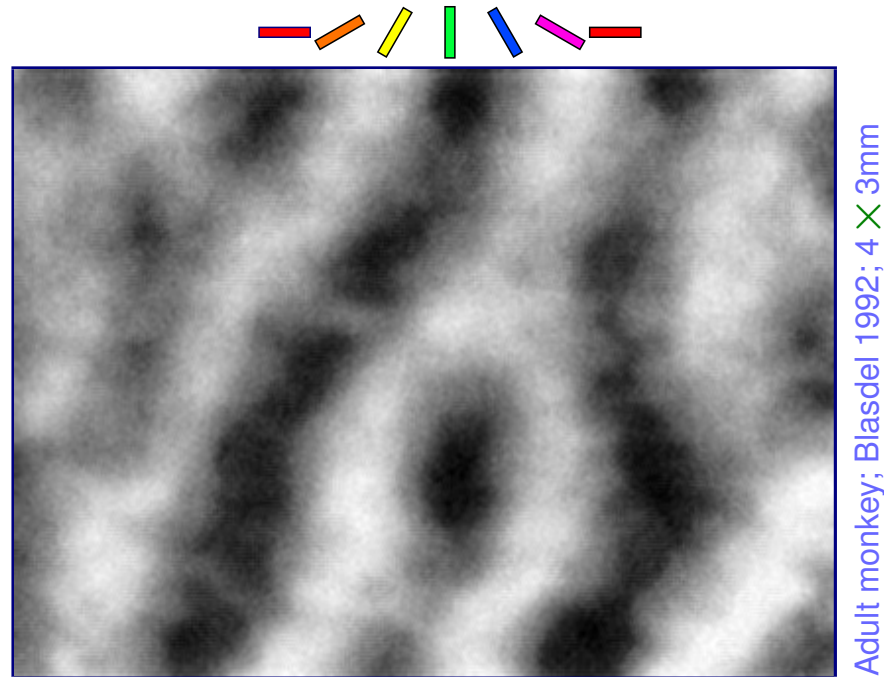
- Tree shrew has no fovea  $\leadsto$  isotropic map
- All orientations represented for each retina location
- Orientation map is smooth, with local patches

# Macaque orientation map



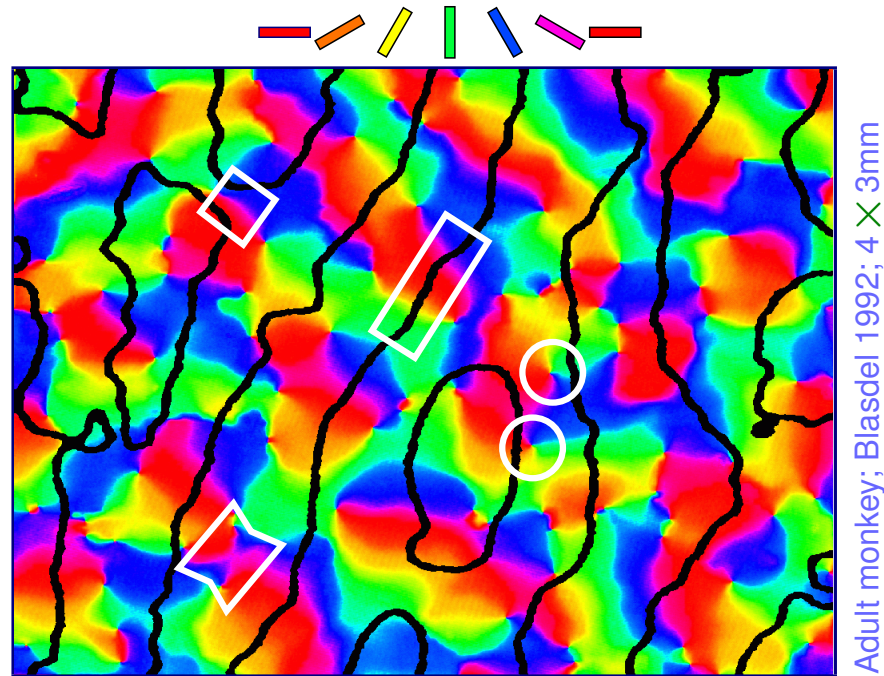
- Macaque monkey has fovea but similar orientation map
- Retinotopic map (not measured) highly nonlinear

# Ocular dominance map in V1



- Most neurons are binocular, but prefer one eye
- Eye preference alternates in stripes or patches

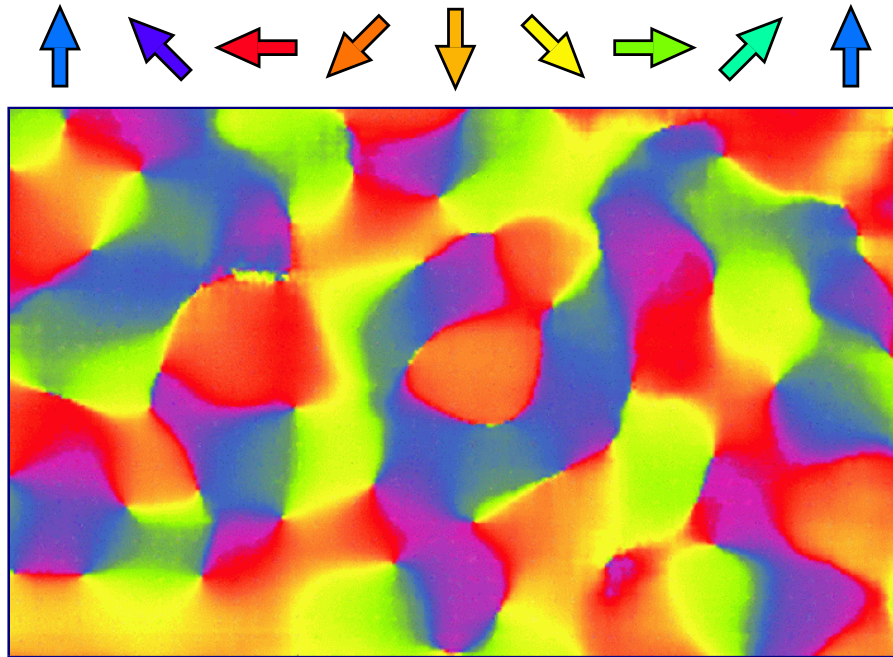
# Combined OR/OD map in V1



- Same neurons have preference for both features
- OR has linear zones, fractures, pinwheels, saddles
- OD boundaries typically align with linear zones

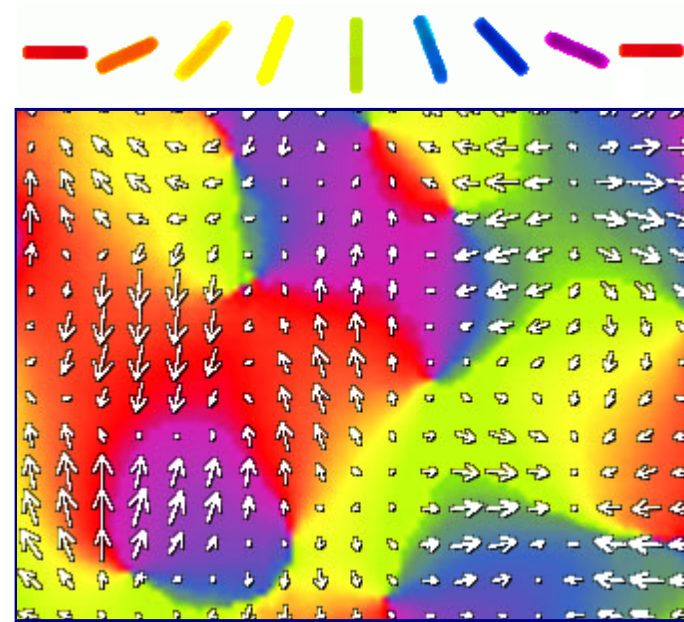


# Direction map in V1



Direction preference

(3.2 × 2mm)



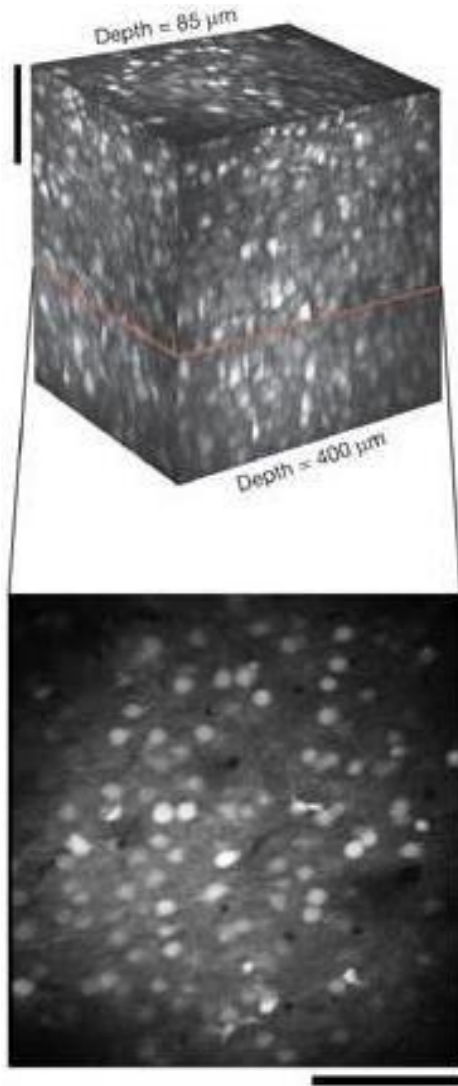
OR/Direction pref.

(1 × 1.4mm)

- Local patches prefer different directions
- Single-OR patches often subdivided by direction
- Other maps: spatial frequency, color, disparity

(Adult ferret; Weliky et al. 1996)

# Cell-level organization



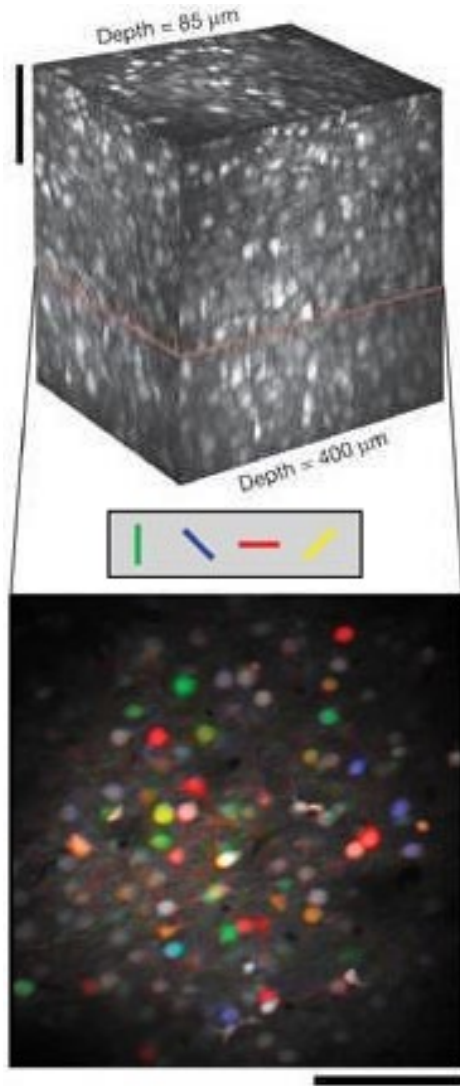
Rat V1 (scale bars 0.1mm)

Two-photon microscopy:

- New technique with cell-level resolution
- Can measure a small volume very precisely

(Ohki et al. 2005)

# Cell-level organization 2



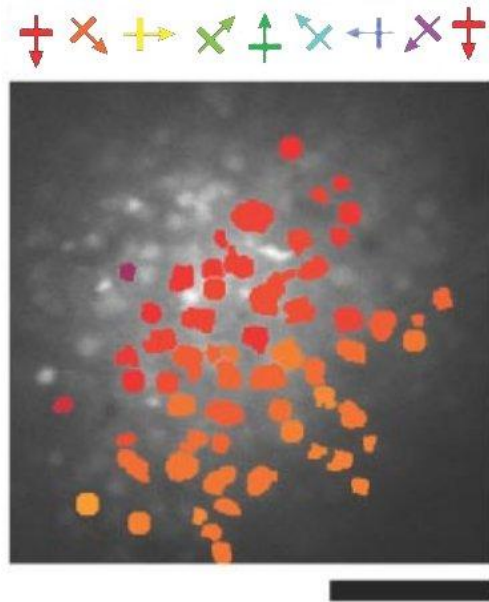
Rat V1 (scale bars 0.1mm)

- Individual cells can be tagged with feature preference
- In rat, orientation preferences are random
- Random also expected in mouse, squirrel

(Ohki et al. 2005)

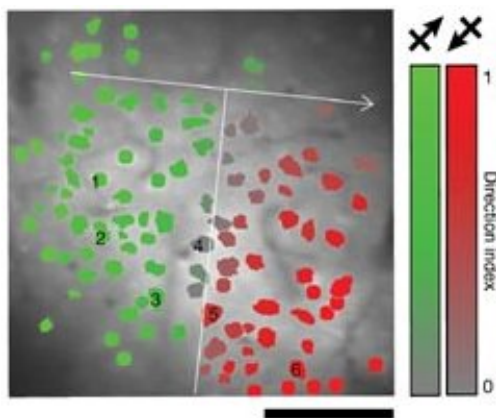


# Cell-level organization 3



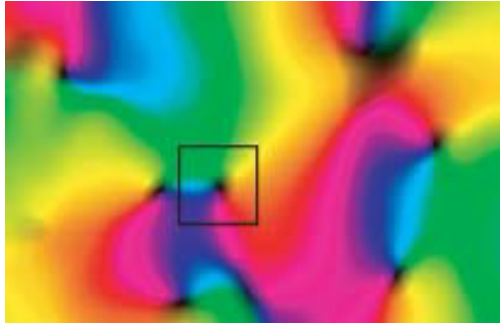
- In cat, validates results from optical imaging
- Smooth organization for direction overall
- Sharp, well-segregated discontinuities

(Ohki et al. 2005)

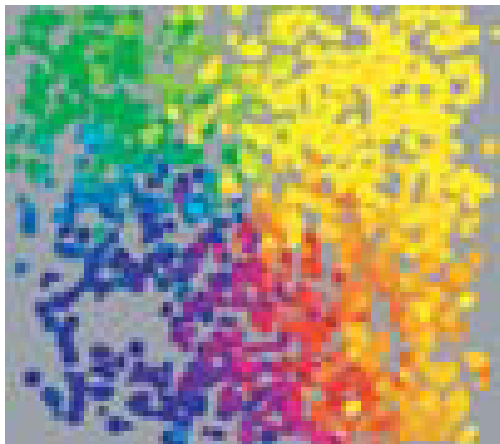


Cat V1 Dir. (scale bars 0.1mm)

# Cell-level organization 4



Low-res map ( $2 \times 1.2\text{mm}$ )

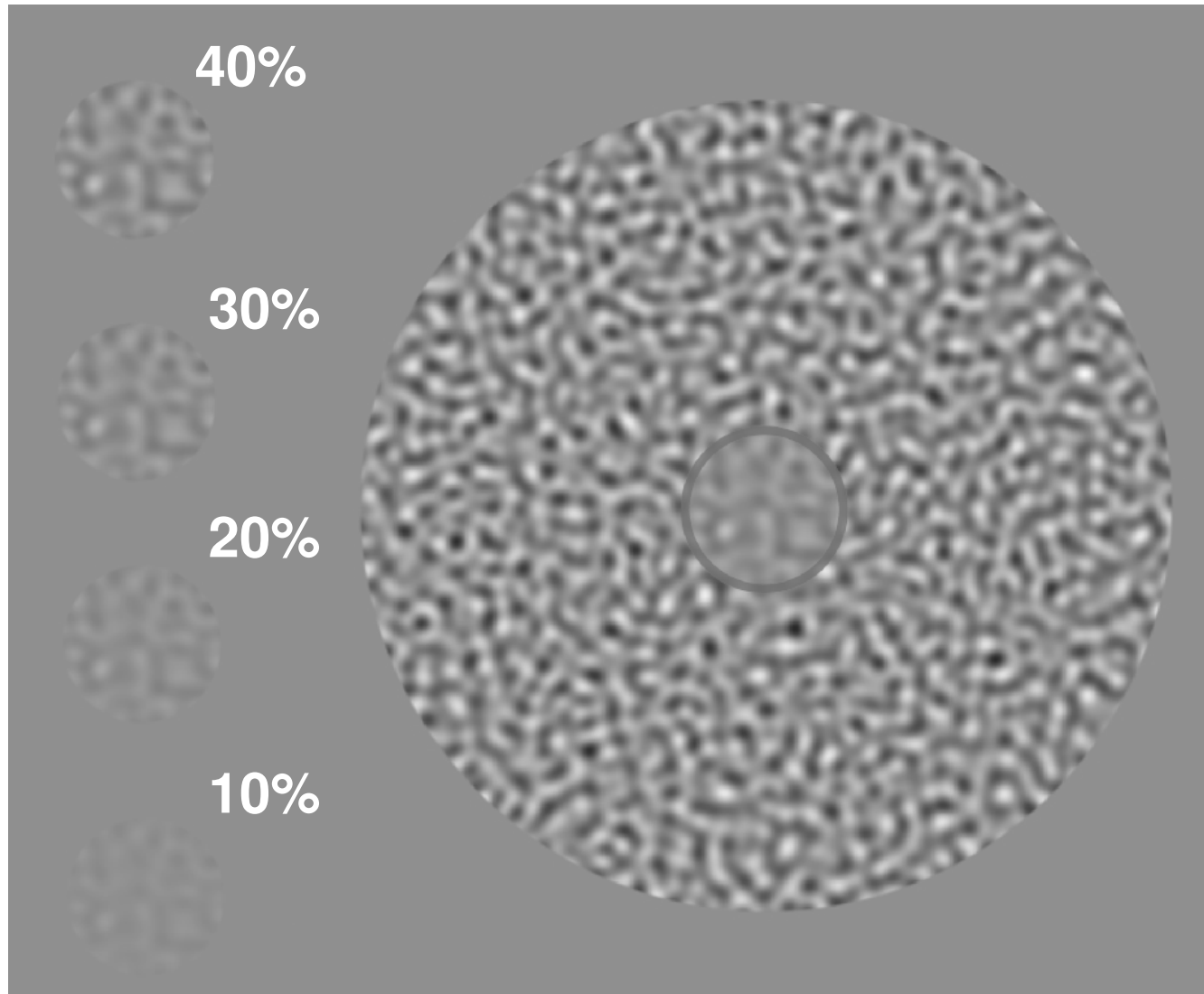


Stack of all labeled  
cells ( $0.6 \times 0.4\text{mm}$ )

- Very close match with optical imaging results
- Stacking labeled cells from all layers shows very strong ordering spatially and in across layers
- Selectivity in pinwheels controversial; apparently lower

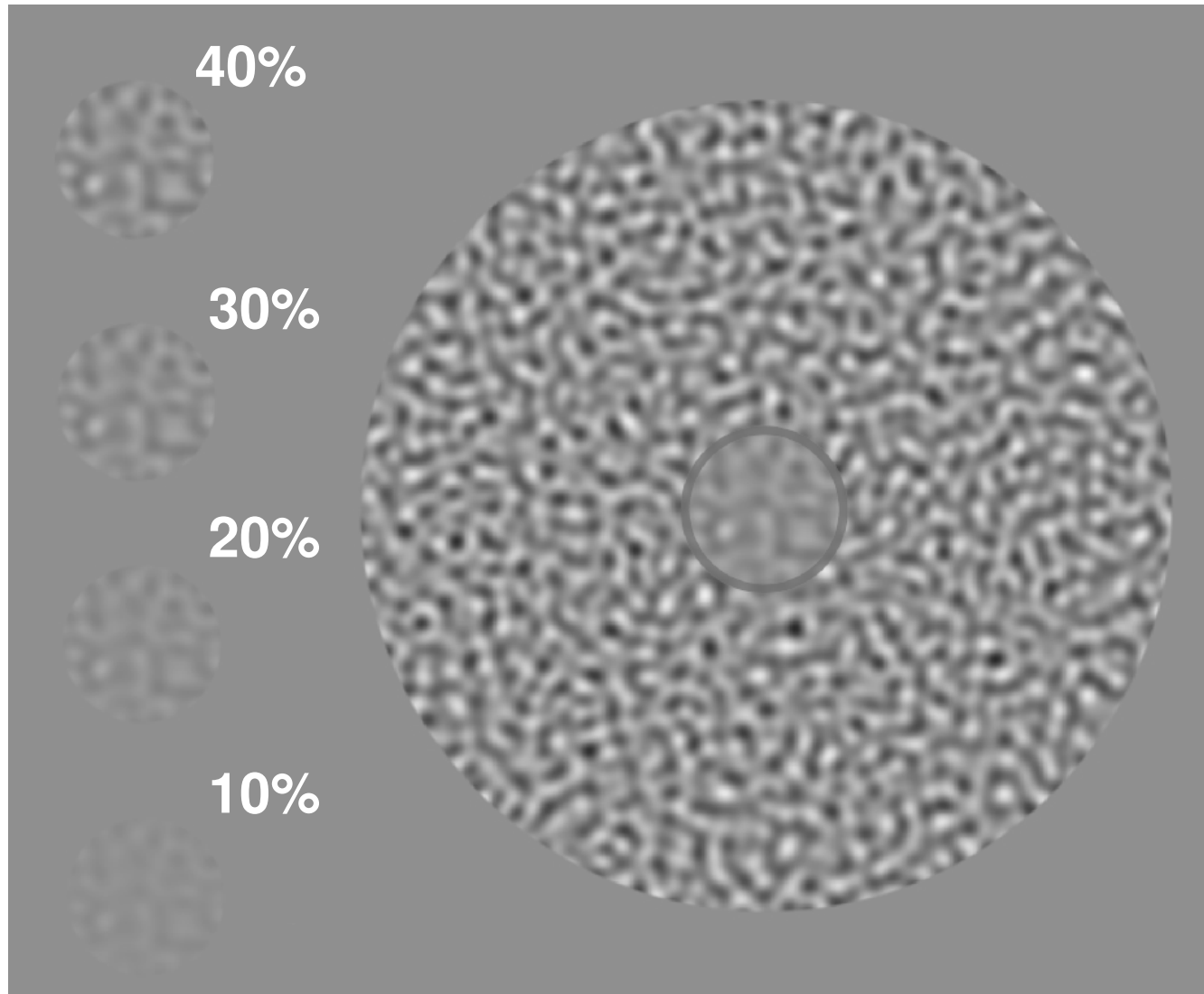
(Ohki et al. 2006)

# Surround modulation



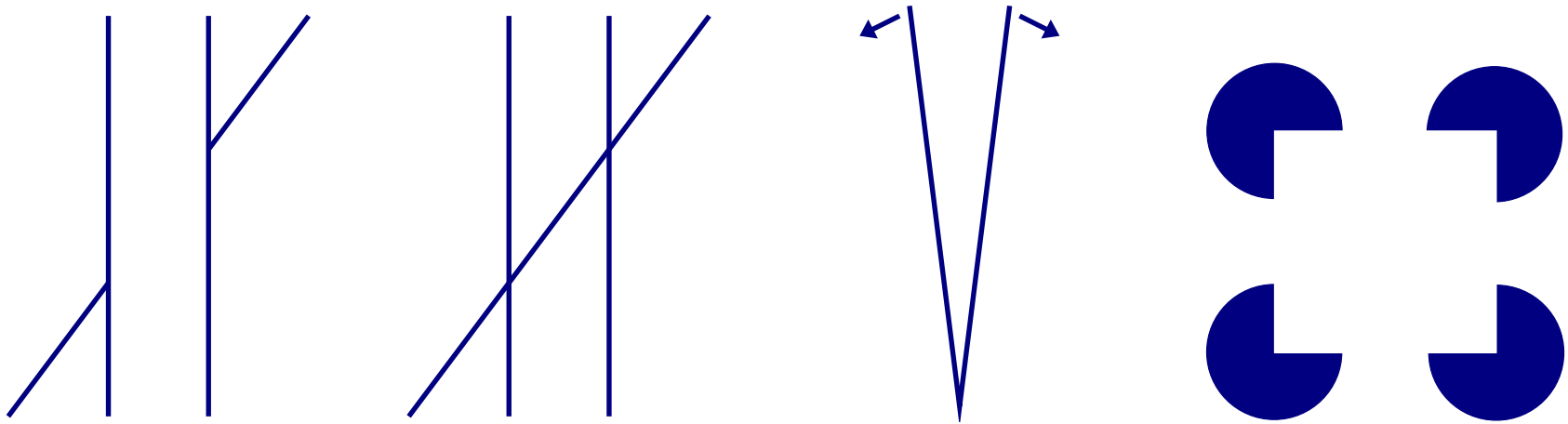
Which of the contrasts at left matches the central area?

# Surround modulation



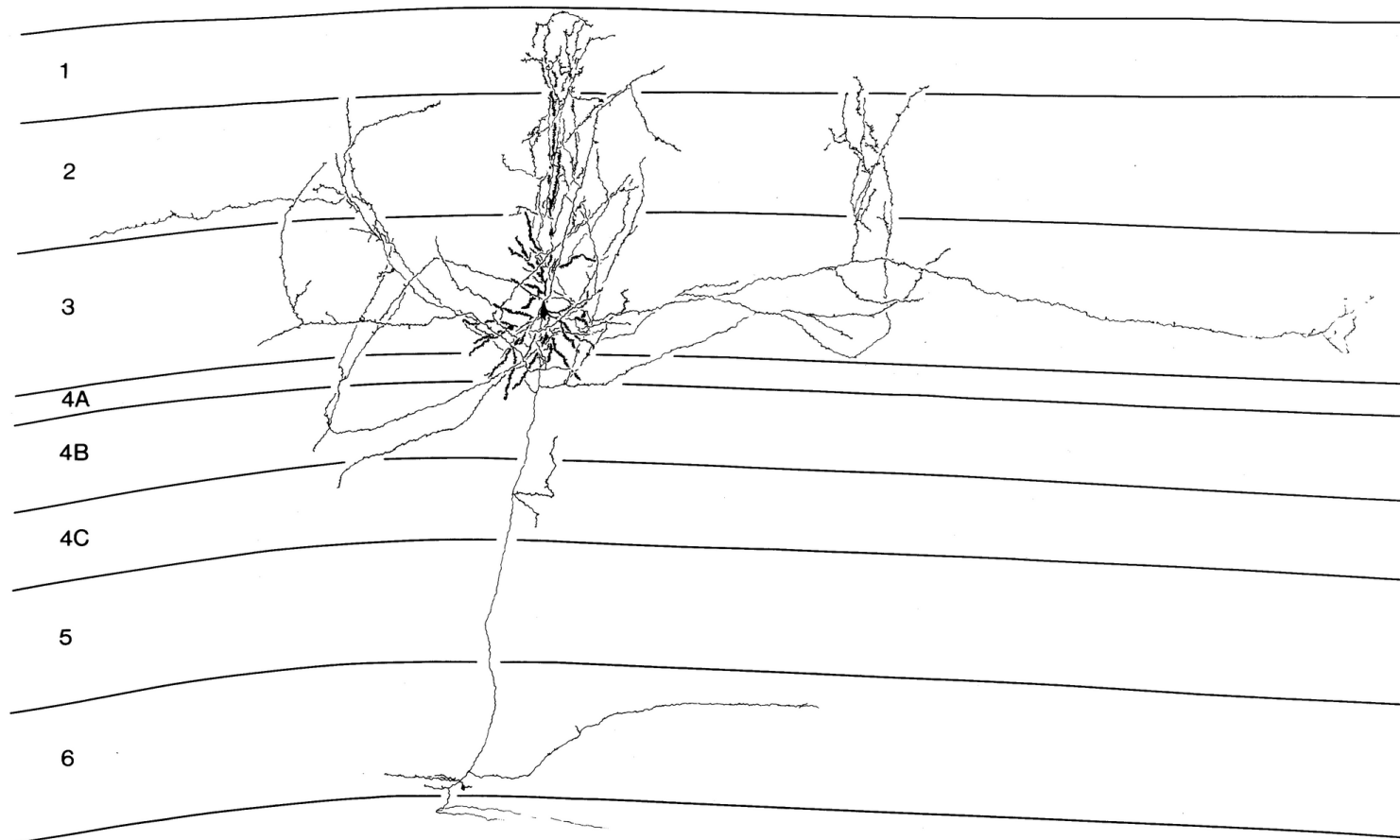
Which of the contrasts at left matches the central area? **40%**

# Contextual interactions



- Orientation and shape perception is not entirely local (e.g. due to individual V1 neurons).
- Instead, adjacent line elements interact (tilt illusion).
- Presumably due to lateral or feedback connections at V1 or above.

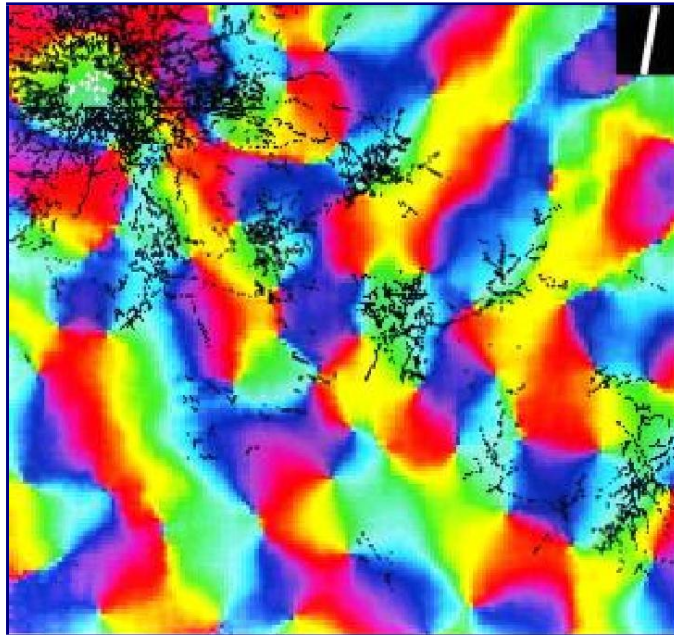
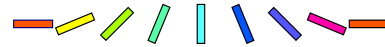
# Lateral connections



(Macaque; Gilbert et al. 1990)

- Example layer 2/3 pyramidal cell
- Patchy every 1mm

# Lateral connections

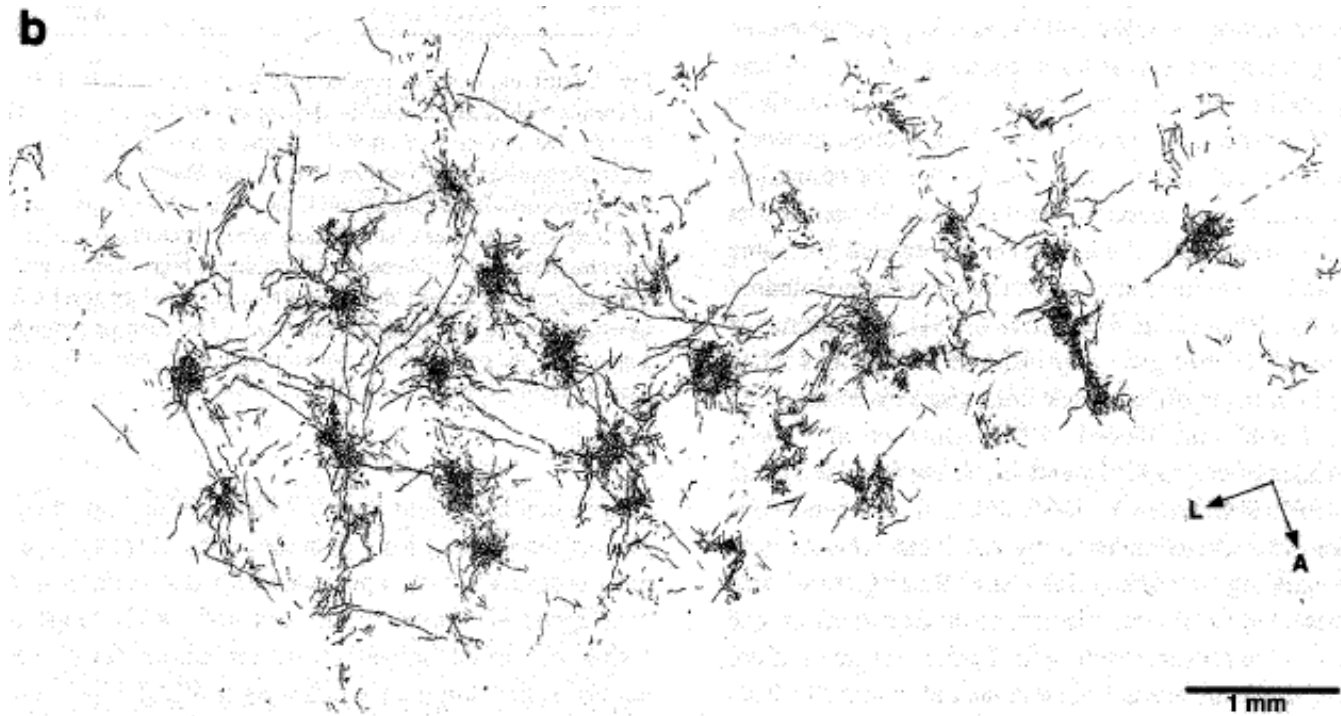


(2.5 mm  $\times$  2 mm in tree shrew V1; Bosking et al. 1997)

- Connections up to 8mm link to similar preferences
- Patchy structure, extend along OR preference



# Feedback connections



(Macaque; Angelucci et al. 2002)

- Relatively little known about feedback connections
- Large number, wide spread
- Some appear to be diffuse
- Some are patchy and orientation-specific



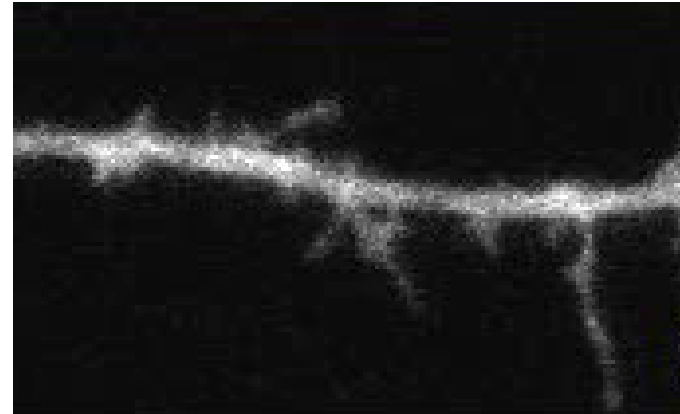
# Visual development

Research questions:

- Where does the visual system structure come from?
- How much of the architecture is specific to vision?
- What influence does the environment have?
- How plastic is the system in the adult?

Most visual development studies focus on ferrets and cats, whose visual systems are very immature at birth.

# Initial development



(Ziv 1996)

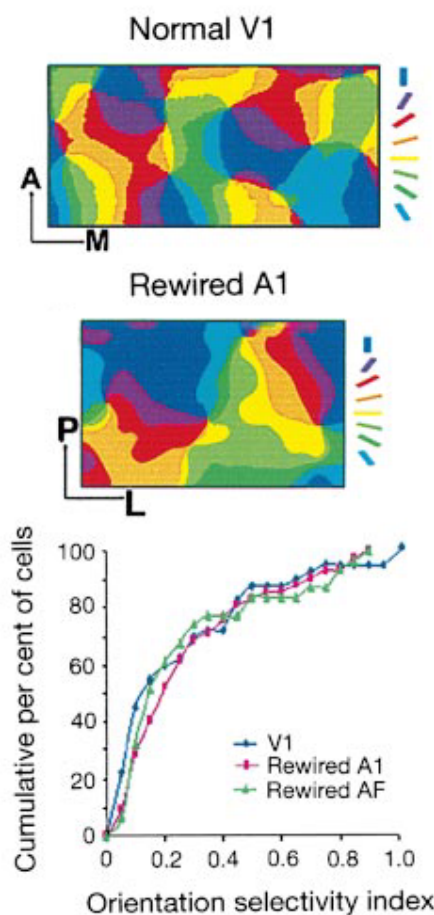
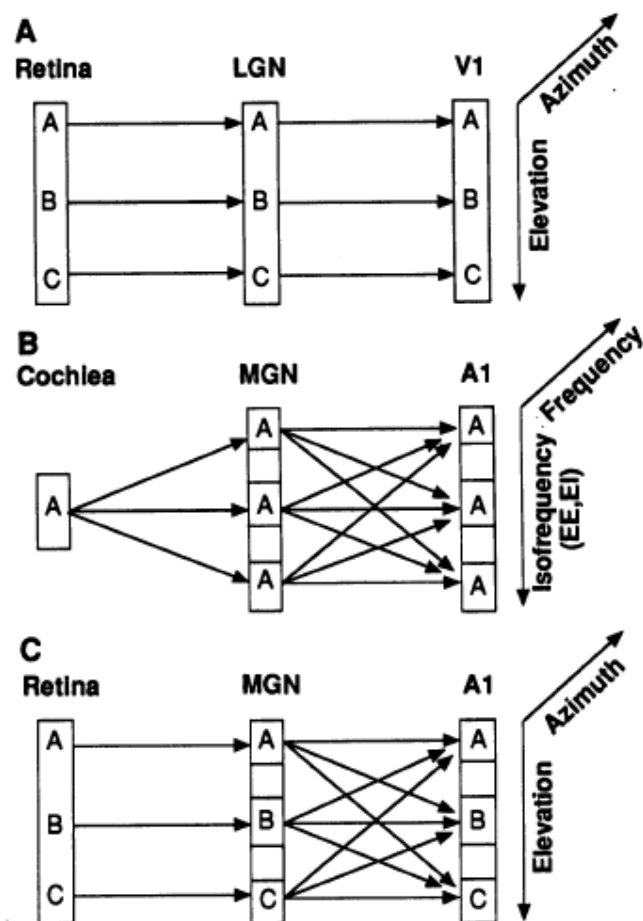
- Tissues develop into eye, brain
- RGC axons grow from eye to LGN and superior colliculus (SC) following chemical gradients
- Axons form synapses at LGN, SC
- LGN axons grow to V1, V2, etc., forming synapses

# Cortical development

- Coarse cortical architecture (e.g. division into areas) appears to be fixed after birth
- Cortical architecture similar across areas
- Much of cortical development appears driven by different peripheral circuitry (auditory, visual, etc.)
- E.g. Sur et al. 1988-2000: auditory cortex can develop into visual cortex

# Rewired ferrets

Sur et al. 1988-2000:



1. Disrupt connections to MGN
2. RGC axons now terminate in MGN
3. Then to A1 instead of V1
4. ~ Functional orientation cells, map in A1

# Human visual system at birth

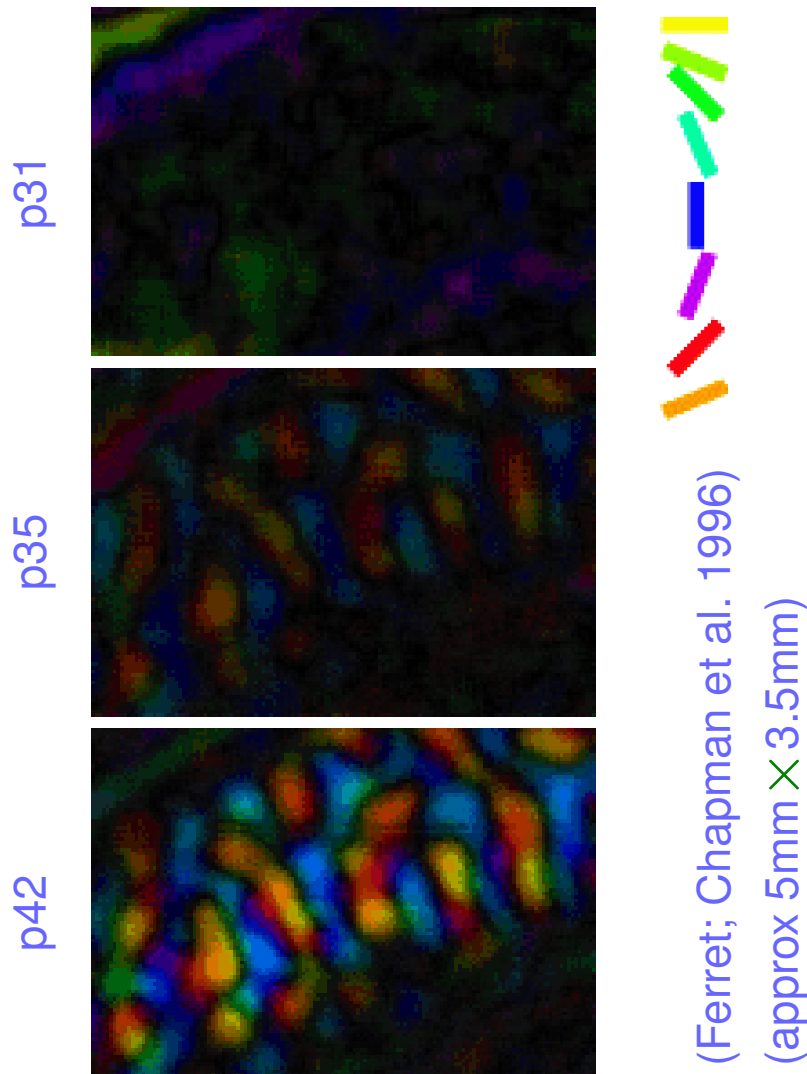
- Some visual ability
- Fovea barely there
- Color vision poor
- Binocular vision difficult
  - Poor control of eye movements
  - Seems to develop later
- Acuity increases 25X (birth to 6 months)

# Map development

- Initial orientation, OD maps develop without visual experience (Crair et al. 1998)
- Maps match between the eyes even without shared visual experience (Kim & Bonhoeffer 1994)
- Experience leads to more selective neurons and maps (Crair et al. 1998)
- Lid suture (leaving light through eyelids) during critical period destroys maps (White et al. 2001)

~> Complicated interaction between system and environment.

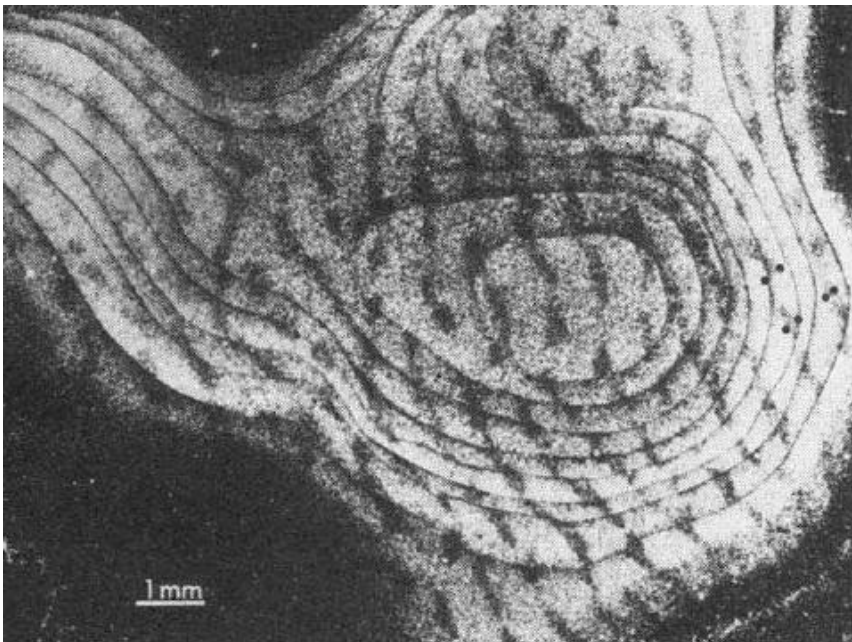
# OR map development



- Map not visible when eyes first forced open
- Gradually becomes stronger over weeks
- Shape doesn't change significantly
- Initial development affected little by dark rearing

# Monocular deprivation

(Monkey V1 layer 4C; Wiesel 1982)

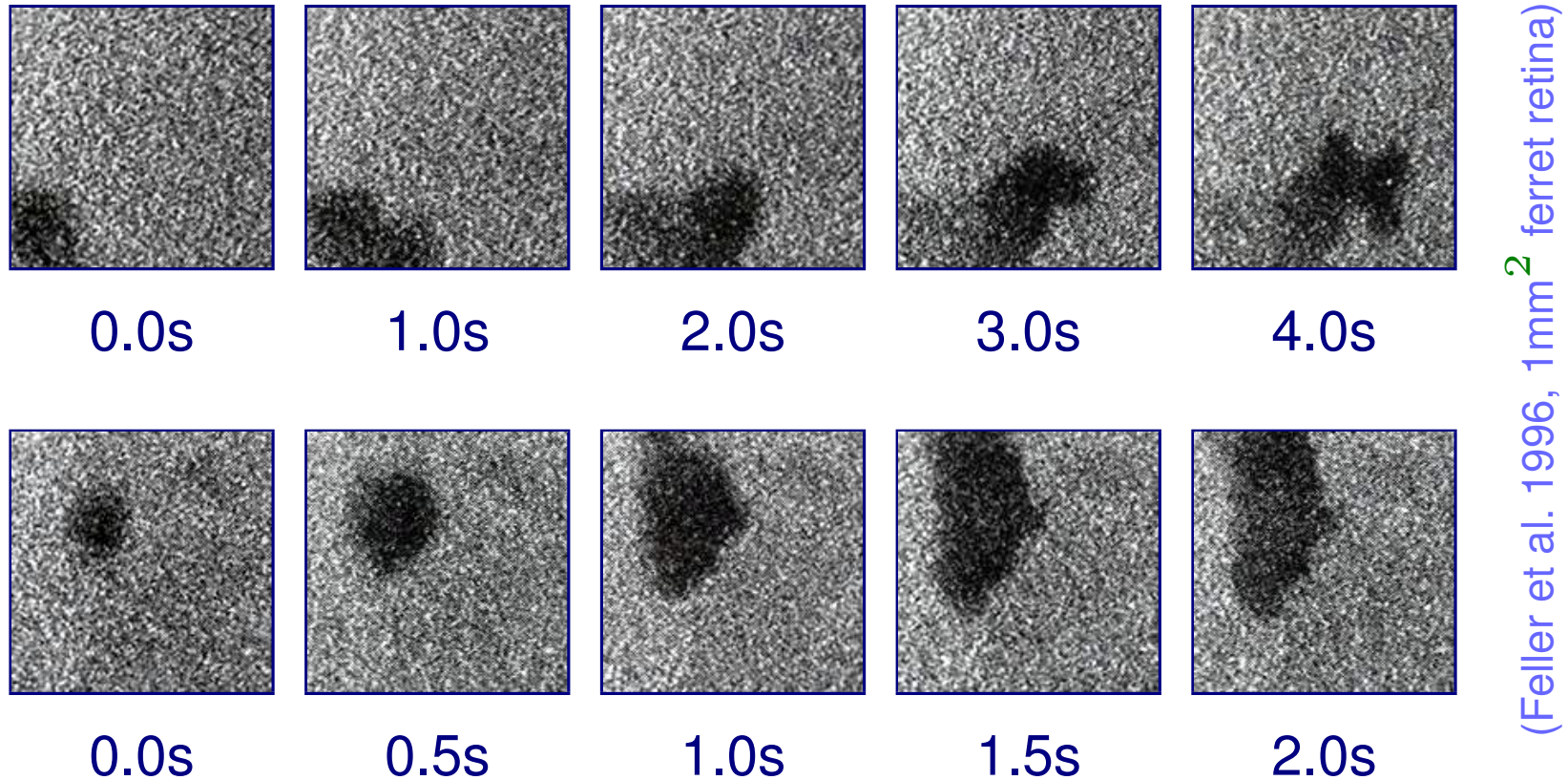


(Left eye (open) labeled white)

- Raising with one eyelid sutured shut results in larger area for other eye
- Sengpiel et al. 1999: Area for overrepresented orientations increases too



# Internally generated inputs

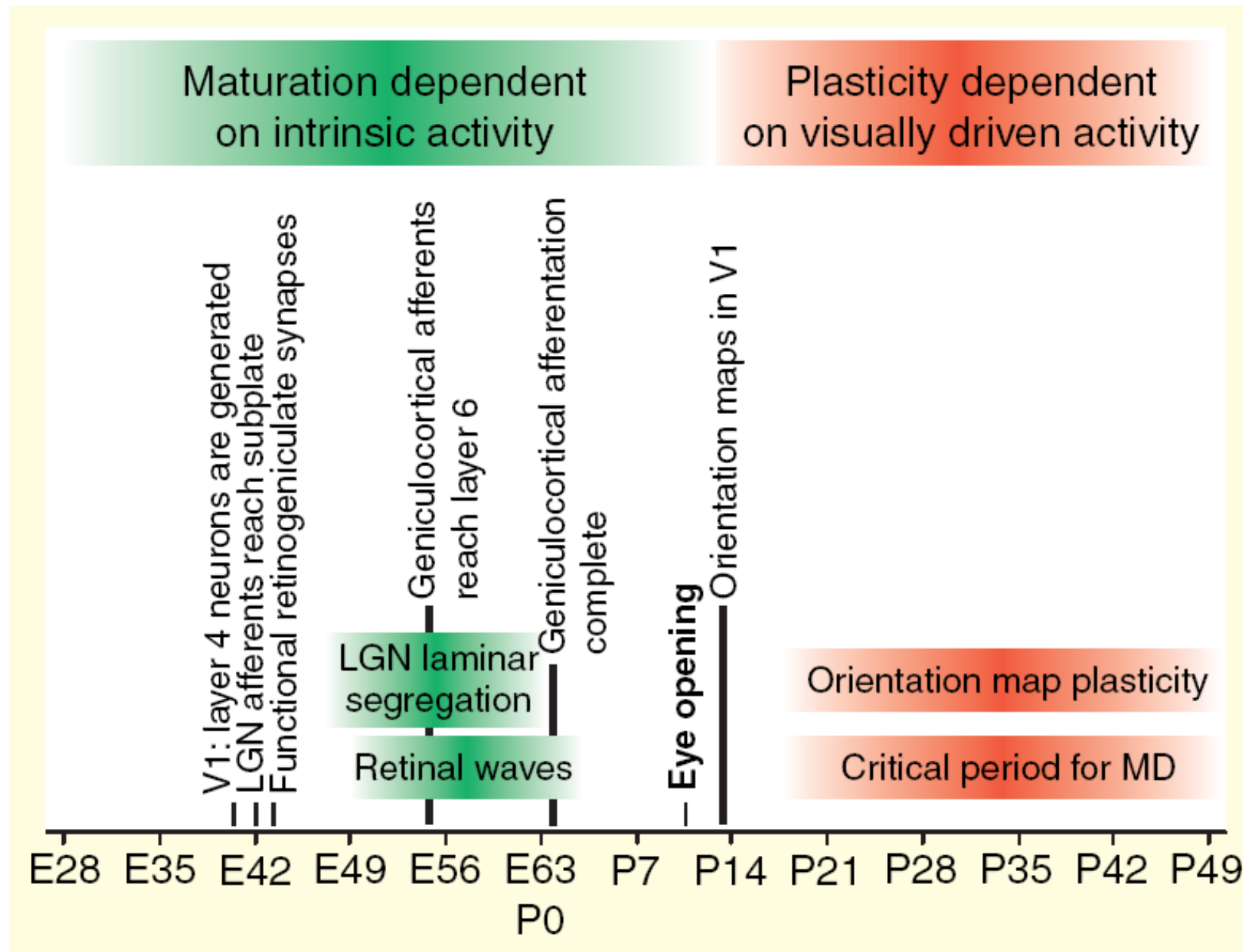


- Retinal waves: drifting patches of spontaneous activity
- Training patterns?

# Role of spontaneous activity

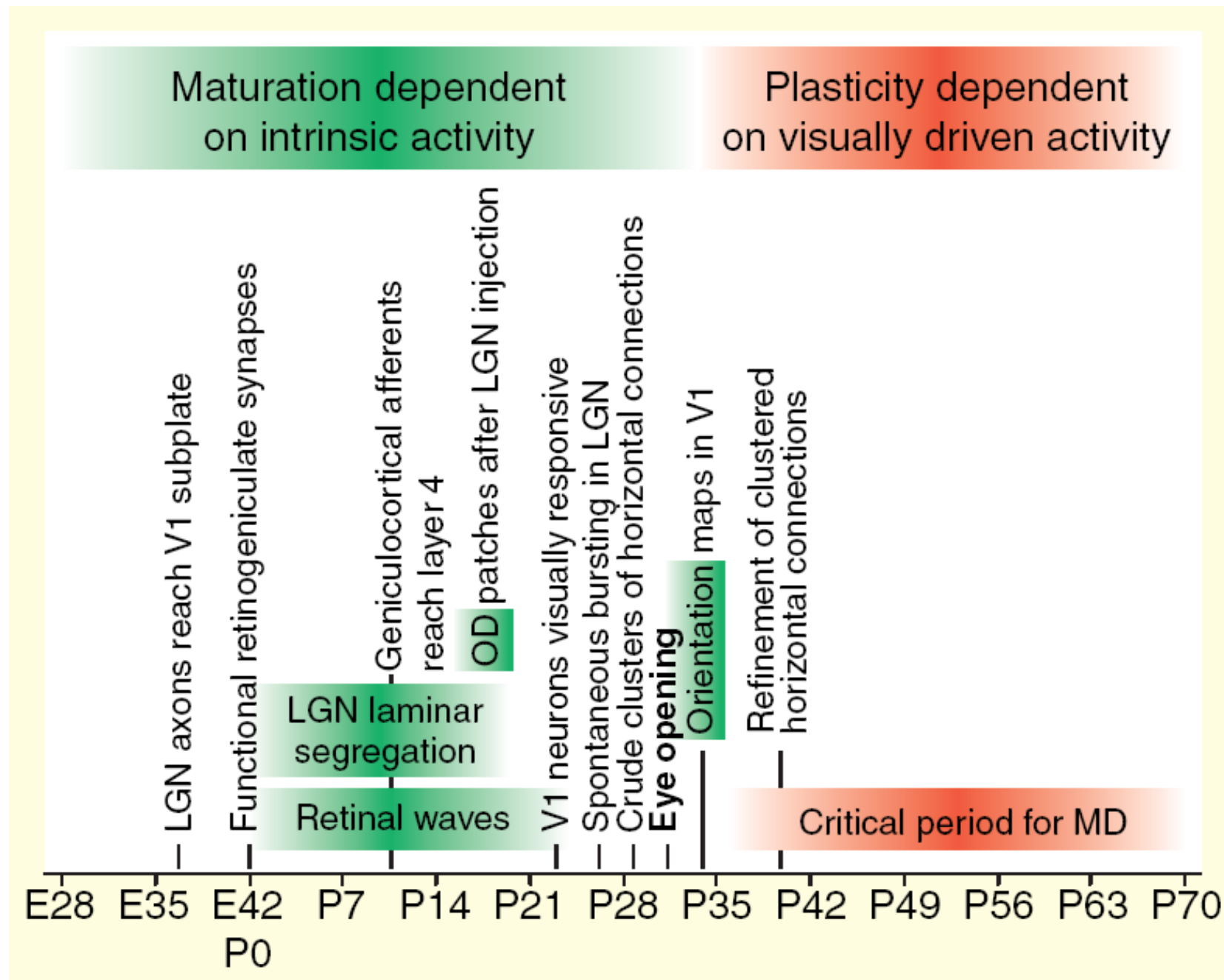
- Silencing of retinal waves prevents eye-specific segregation in LGN (Huberman et al. 2003) and ocular dominance columns in V1 (Huberman et al. 2006)
- Boosting in one eye disrupts LGN, but not if in both
- Disrupting retinal waves disrupts geniculocortical mapping (Cang et al. 2005)
- Other sources of input to V1: spontaneous cortical activity, brainstem activity
- All developing areas seem to be spontaneously active, e.g. auditory system, spinal cord

# Timeline: Cat

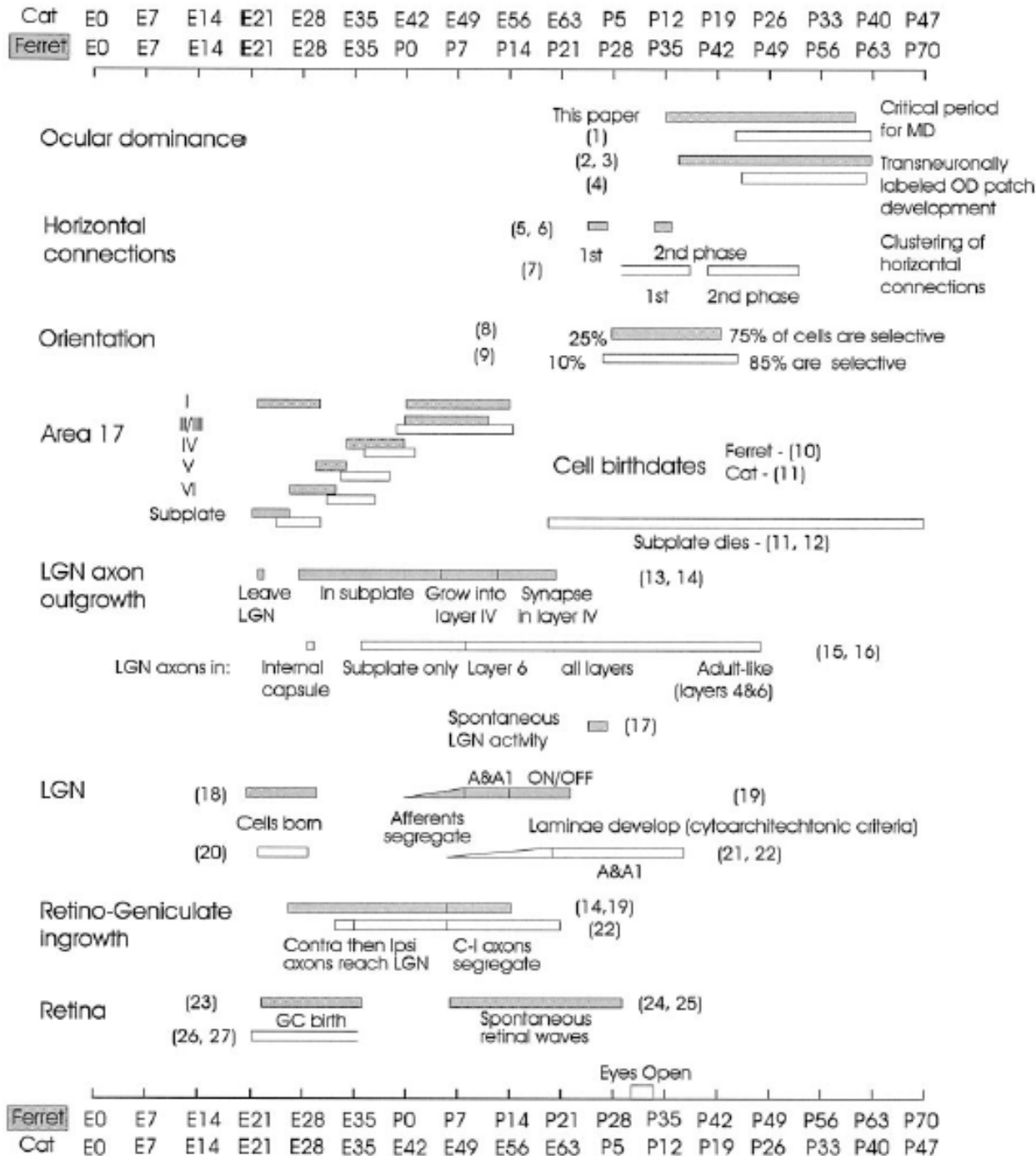


(Sengpiel & Kind 2002)

# Timeline: Ferret



(Sengpiel & Kind 2002)



# Cat vs. ferret

Should be readable in a printout, not on screen

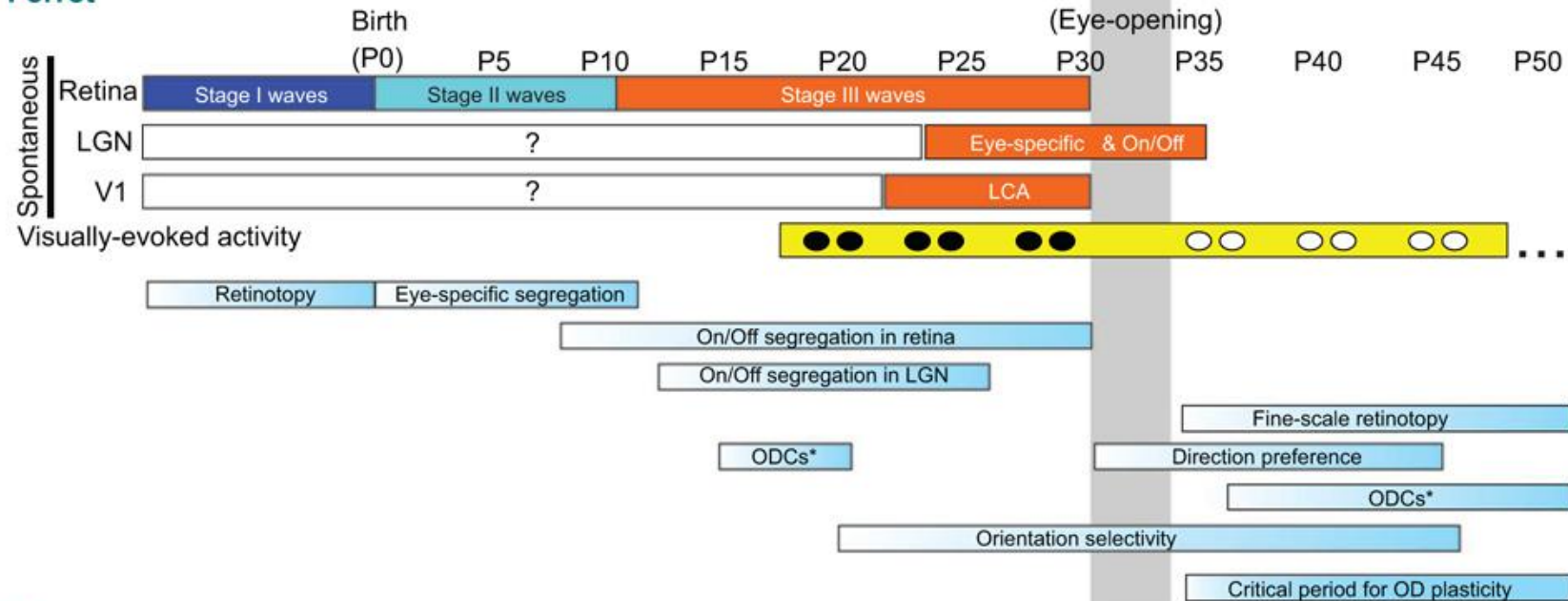
OD, Ocular dominance  
MD, monocular deprivation  
GC, ganglion cell  
C-I, contralateral-ipsilateral

(Issa et al. 1999)

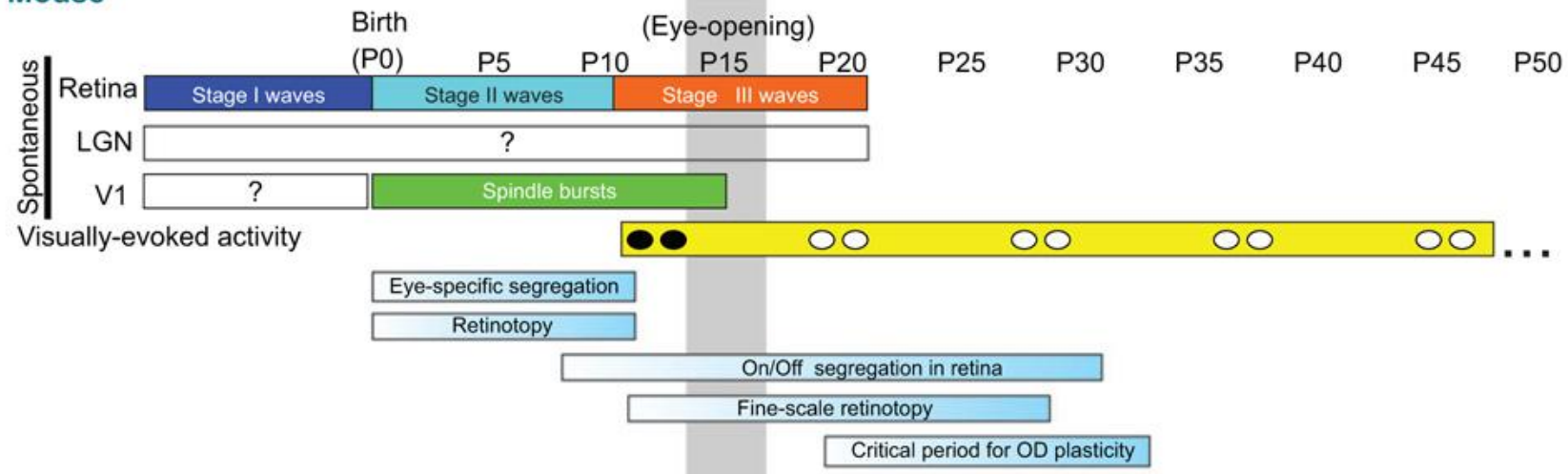


# Ferret vs. mouse

## Ferret



## Mouse



(Huberman et al. 2008)

# Conclusions

- Early areas well studied
- Higher areas much less so
- Little understanding of how entire system works together
- Development also a mystery
- Lots of work to do

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