# 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)

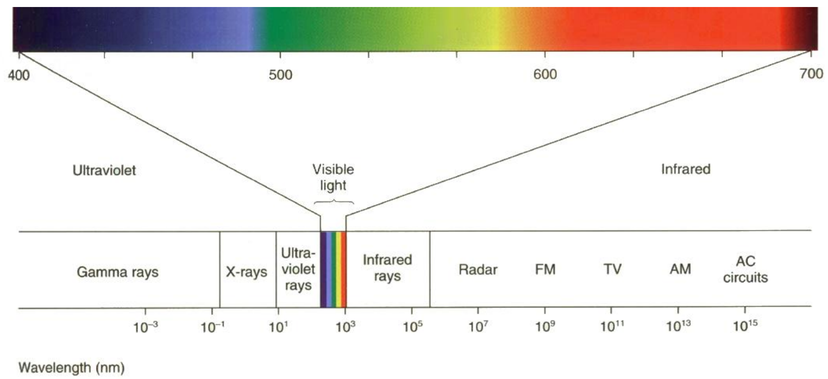
**Physiology** What is the behavior of the component parts of the visual system?

- **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?



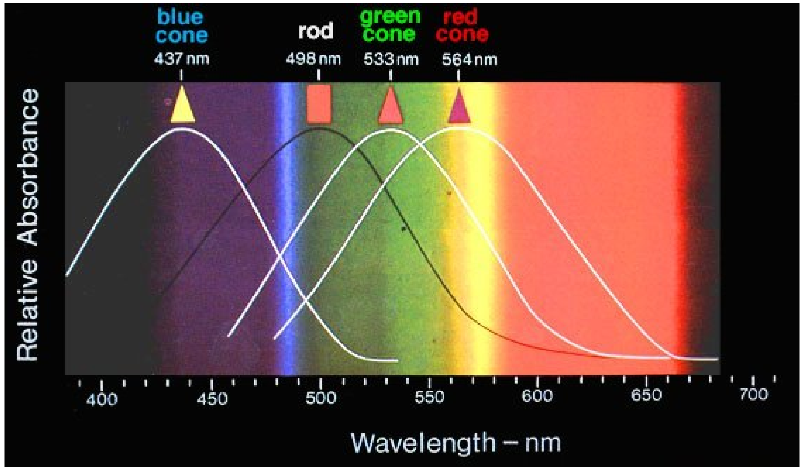
# Electromagnetic spectrum




(From web)

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

# Cone spectral sensitivities

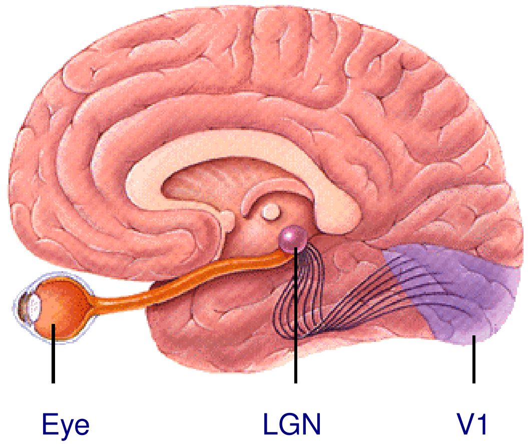



(Dowling, 1987)

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



# Early visual pathways

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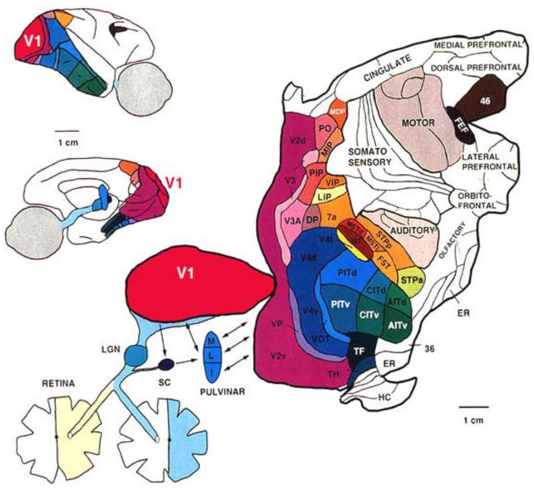
Signals travel from retina, to LGN, then to primary visual cortex



# Higher areas

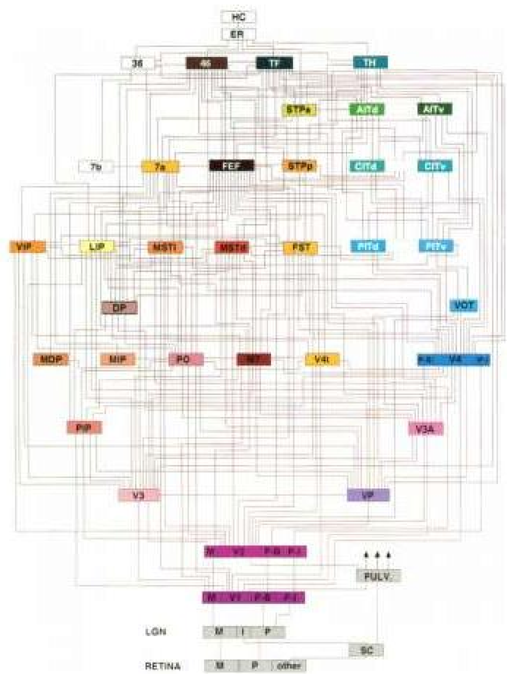



Macaque monkey visual areas
(Van Essen et al. 1992)

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



# Circuit diagram



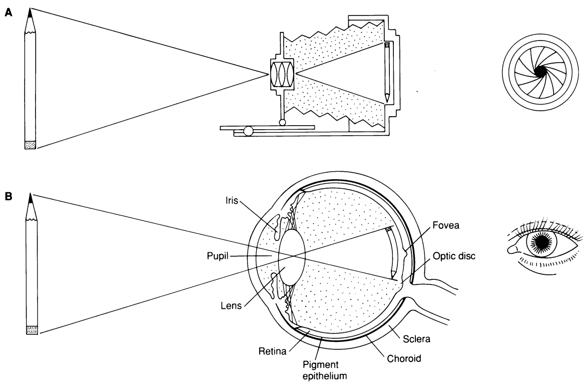

Connections between macaque monkey visual areas

(Van Essen et al. 1992)

A bit messy!

(Yet still just a start.)

# Image formation

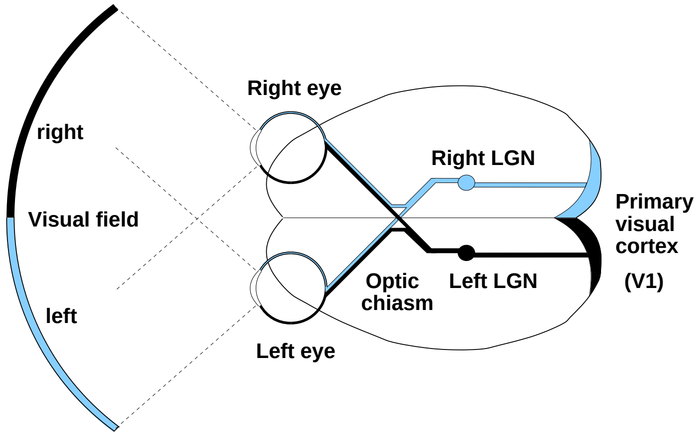



(Kandel et al. 1991)

| | Fixed | Adjustable | Sampling |
|---|---|---|---|
| **Camera:** | lens shape | focal length | uniform |
| **Eye:** | focal length | lens shape | higher at fovea |



# Visual fields

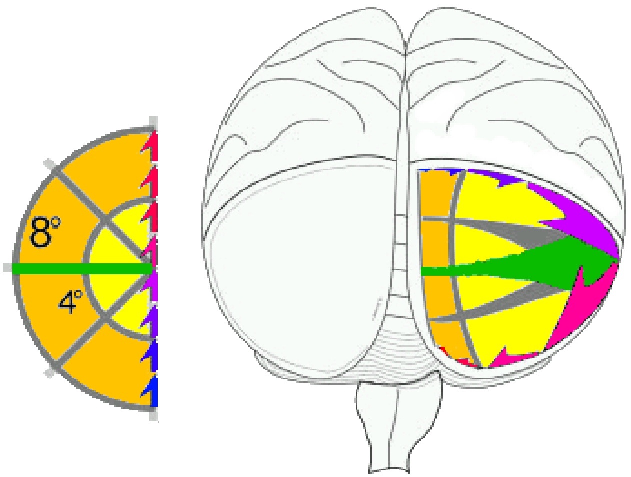



CMVC figure 2.1

- 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

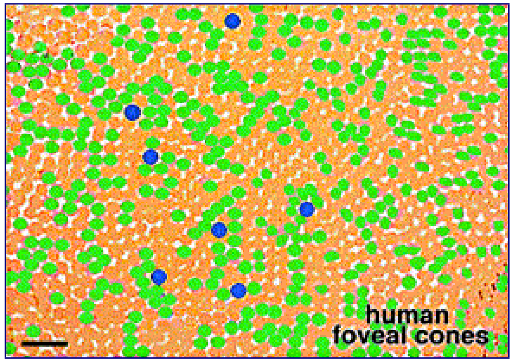


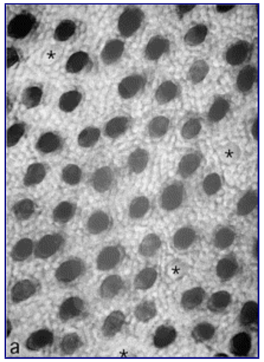
# Effect of foveation

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

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

# Retinal surface



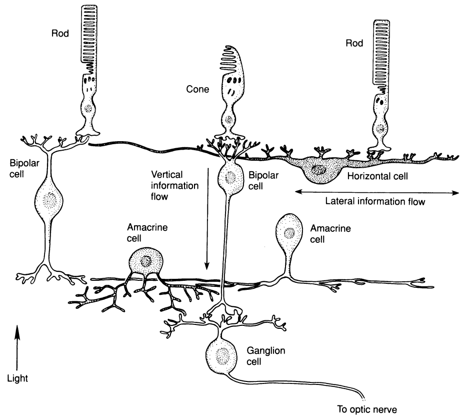

(Ahnelt & Kolb 2000); no scale in original

Fovea (center ⇝)  Periphery

- 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



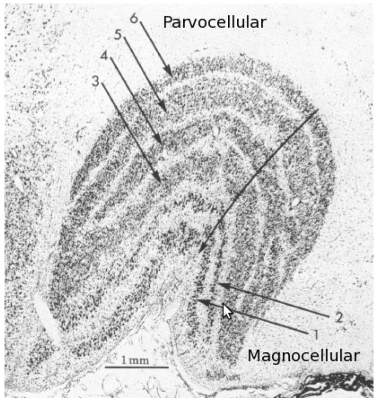

(Kandel et al. 1991)

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

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



# LGN layers

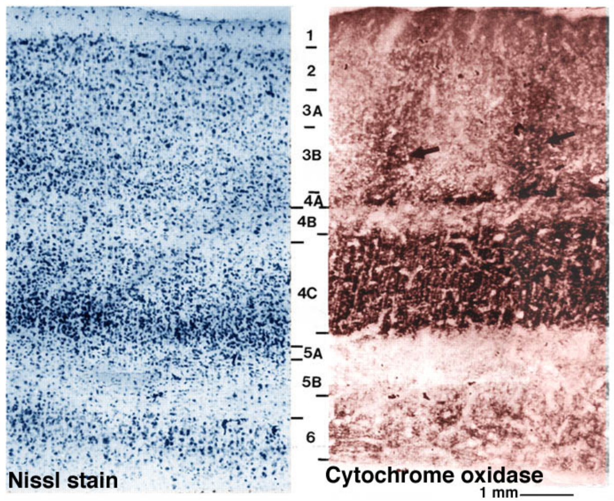



Macaque; Hubel & Wiesel 1977

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



# V1 layers

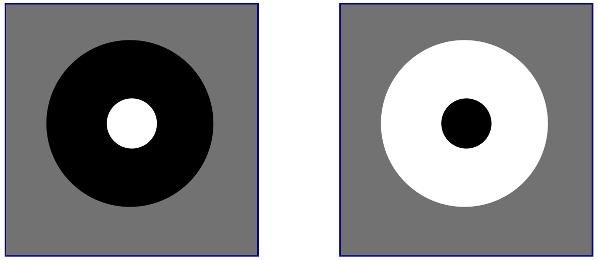



(From webvision.umh.es)

Multiple layers of cells in V1

Brodmann numbering

# Retinal/LGN cell response types

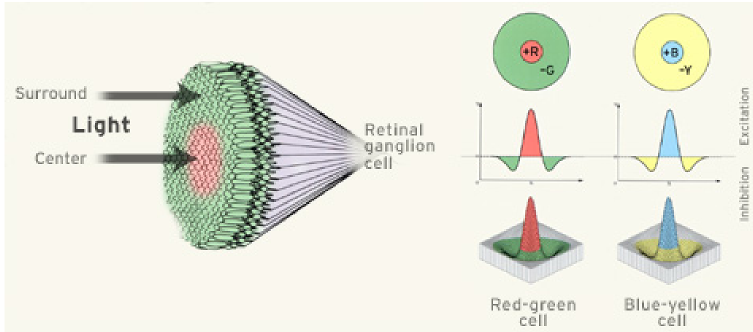


Types of receptive fields based on responses to light:

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



# Color-opponent retinal/LGN cells




(From webexhibits.org)

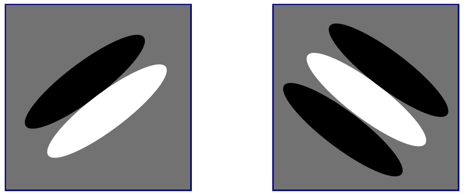
Red/Green cells: (+R,-G), (-R,+G), (+G,-R), (-G,+R)

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

Error: light arrows in the figure are backwards! Actual organization mostly consistent with random wiring



# V1 simple cell responses



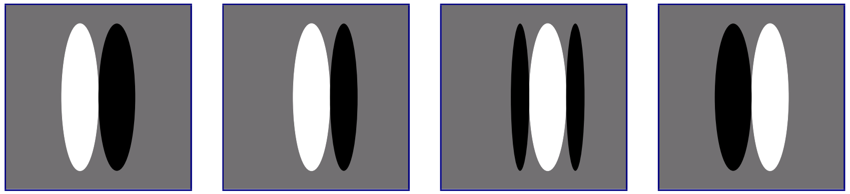
2-lobe simple cell    3-lobe simple cell

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

Simple cells: pattern preferences can be plotted as above



# V1 complex cell responses

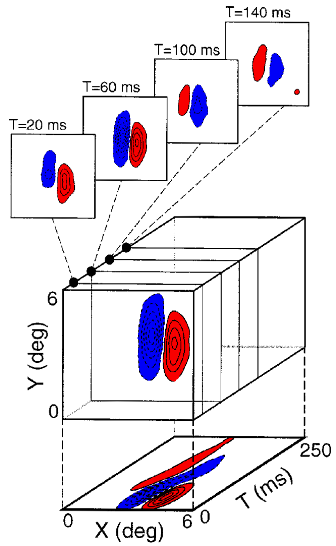


(Same response to all these patterns)

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

Can't measure complex RFs using pixel-based correlations

# Spatiotemporal receptive fields

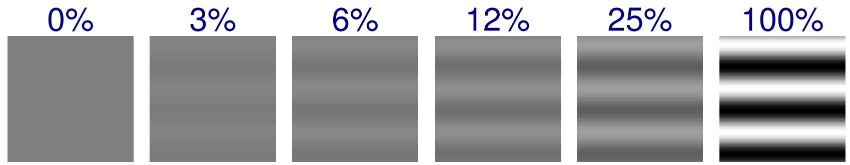



- Neurons are selective for multiple stimulus dimensions at once
- Typically prefer lines moving in direction perpendicular to orientation preference

(Cat V1; DeAngelis et al. 1999)



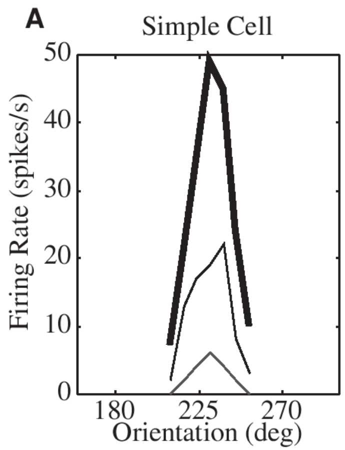
# Contrast perception




- 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:

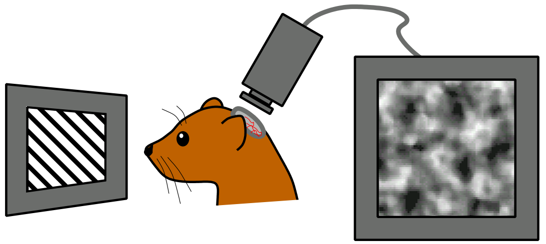
**Weber contrast (e.g. a tiny spot on uniform background)**

$$C = \frac{Lmax - Lmin}{Lmin}$$

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

$$C = \frac{Lmax - Lmin}{Lmax + Lmin} = \frac{\frac{Lmax - Lmin}{2}}{Lavg}$$

# Measuring cortical maps

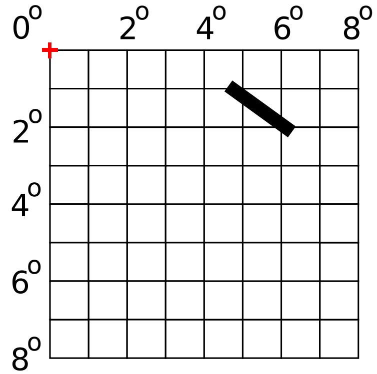


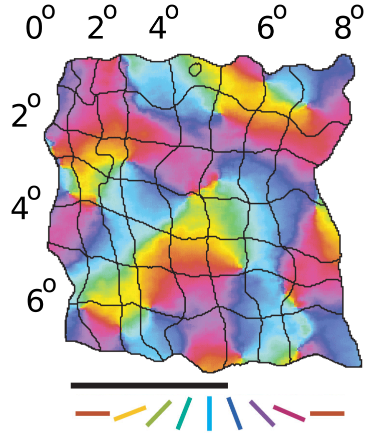
CMVC figure 2.3

- 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



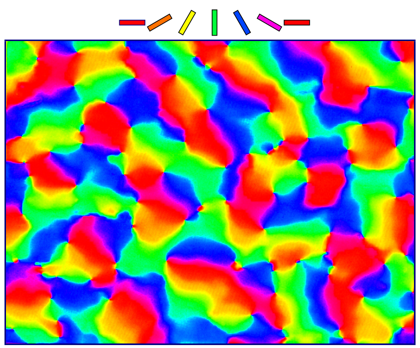




Tree shrew; Bosking et al. 2002; 2×2mm

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



# Macaque orientation map

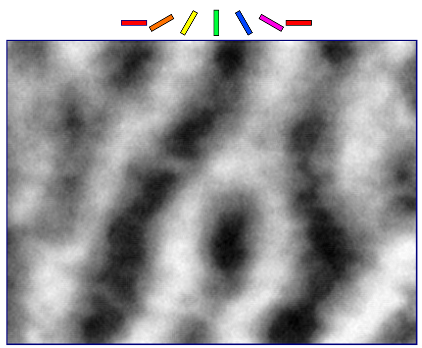


Macaque; Blasdel 1992; 4×3mm

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



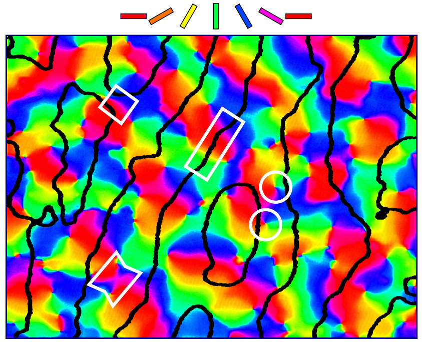
# Ocular dominance map in V1



Macaque; Blasdel 1992; 4×3mm

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

# Combined OR/OD map in V1

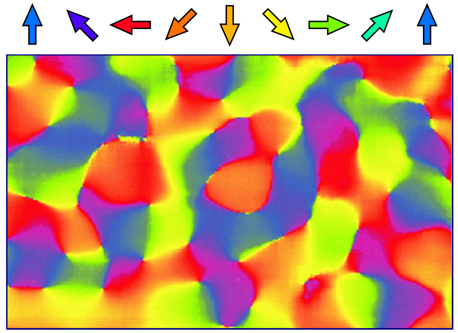


Macaque; Blasdel 1992; 4 × 3mm

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

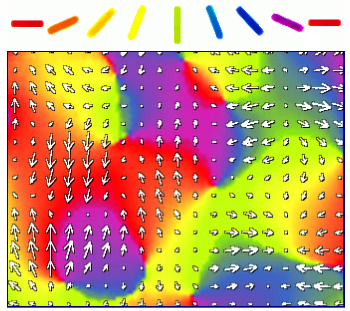


# Direction map in V1



Direction preference

(3.2 × 2mm)



OR/Direction pref.

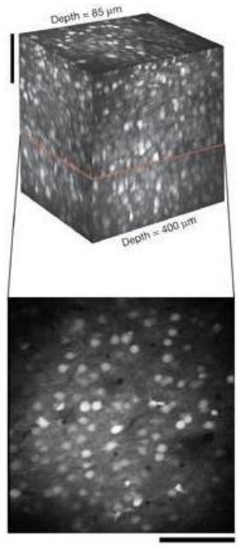
(1 × 1.4mm)

(Adult ferret; Weliky et al. 1996)

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



# Cell-level organization




Rat V1 (scale bars 0.1mm)

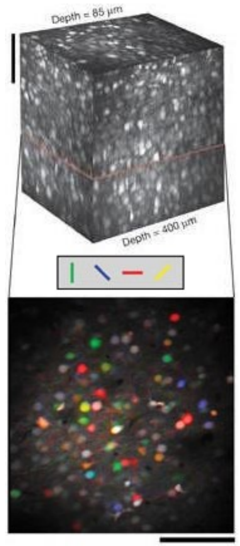
Two-photon microscopy:

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

(Ohki et al. 2005)



# Cell-level organization 2

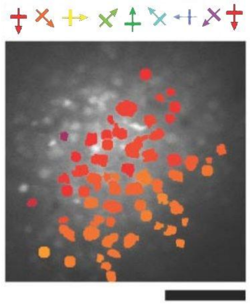


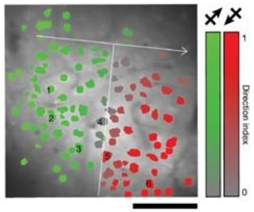

Rat V1 (scale bars 0.1mm)

- 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





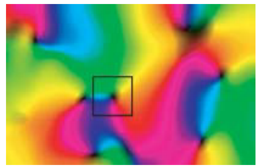
Cat V1 Dir. (scale bars 0.1mm)

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

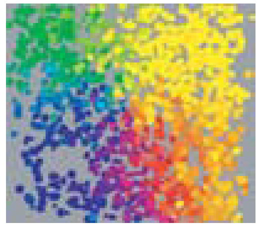
(Ohki et al. 2005)



# Cell-level organization 4



Low-res map (2 × 1.2mm)



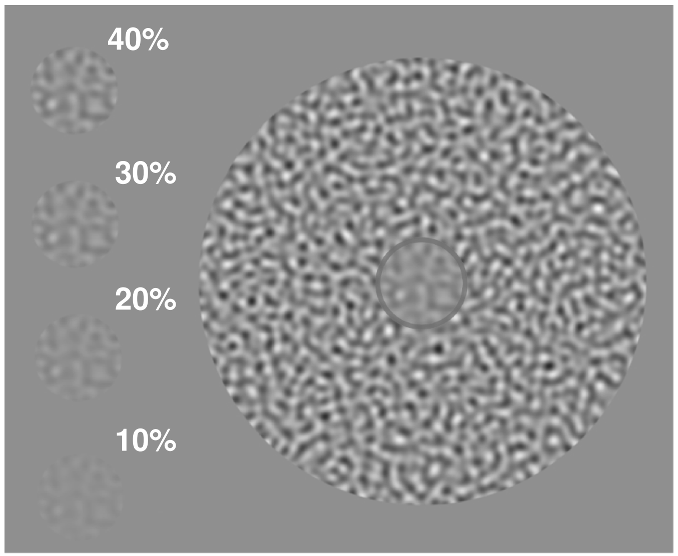
Stack of all labeled cells (0.6 × 0.4mm)

- 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)



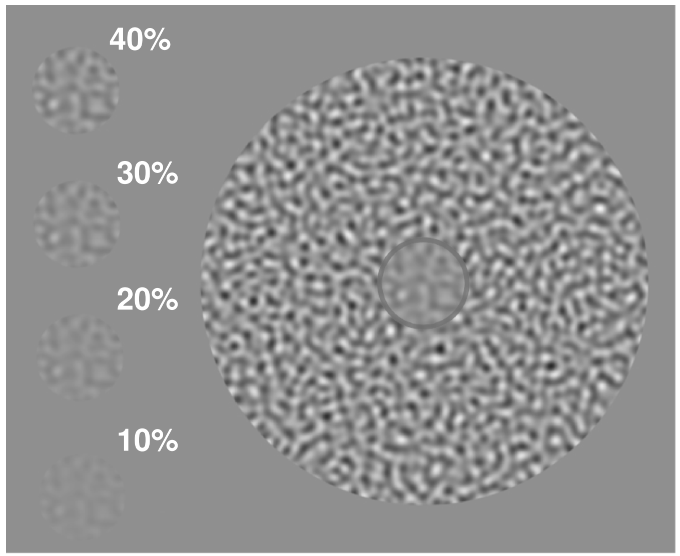
# Surround modulation




Which of the contrasts at left matches the central area?

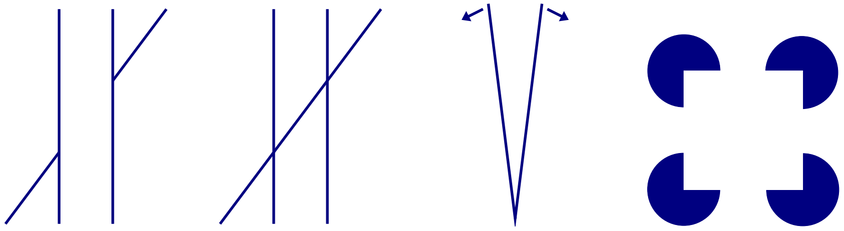


# Surround modulation




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.



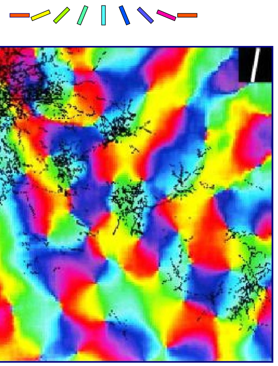
# Lateral connections


(Macaque; Gilbert et al. 1990)

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



# Lateral connections

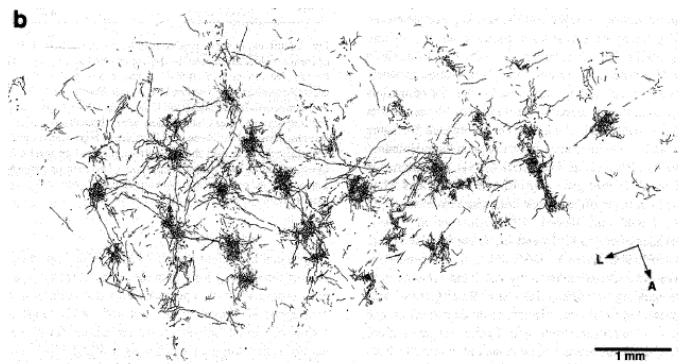


(2.5 mm × 2 mm in tree shrew V1; Bosking et al. 1997)

- 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

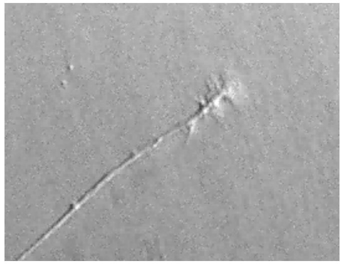
Research questions studied in this course:

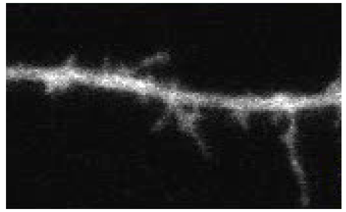
- Where does the visual system structure come from?
- How much of the architecture is specific to vision?
- What influence does the environment have?
- How plastic is the system in the adult?

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



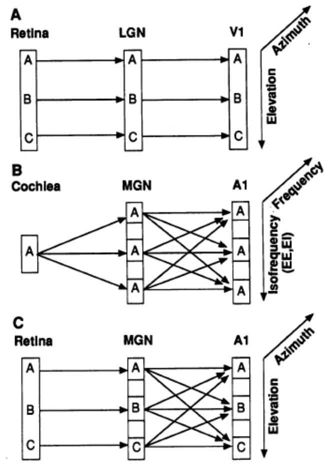
# Cortical development

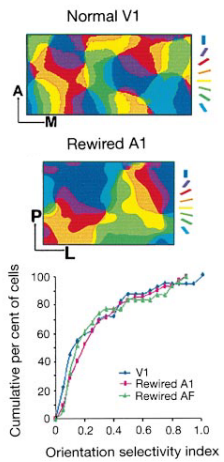
- Coarse cortical architecture (e.g. division into areas) appears to be fixed after birth
- Cortical architecture similar across areas
- Much of cortical development appears driven by different peripheral circuitry (auditory, visual, etc.)
- E.g. Sur et al. (1998-2000): auditory cortex can develop into 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. $\rightsquigarrow$ 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

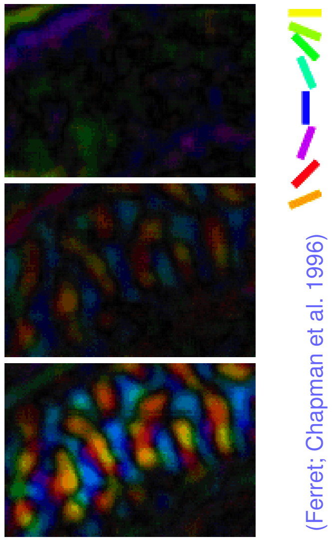
- Initial orientation, OD maps develop without visual experience (Crair et al. 1998)
- Maps match between the eyes even without shared visual experience (Kim & Bonhoeffer 1994)
- Experience leads to more selective neurons and maps (Crair et al. 1998)
- Lid suture (leaving light through eyelids) during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

⇝ Complicated interaction between system and environment.



# OR map development

p31
p35
p42



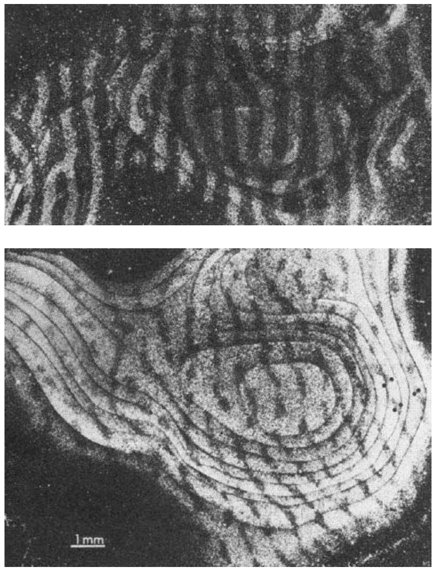
(Ferret; Chapman et al. 1996)
(approx 5mm × 3.5mm)

- 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

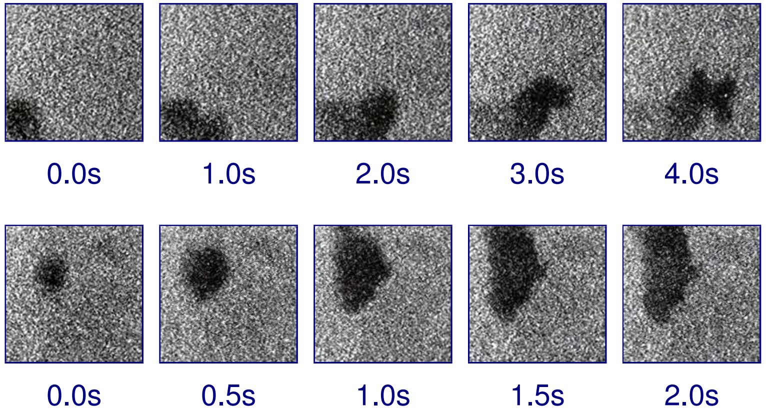
(Monkey V1 layer 4C; Wiesel 1982)




(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




(Feller et al. 1996, 1mm$^2$ ferret retina)

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

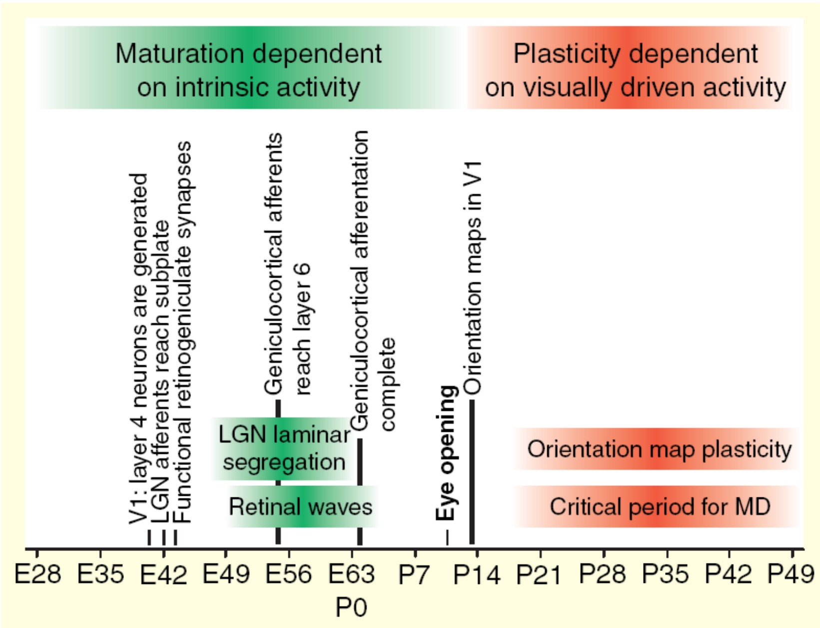


# Role of spontaneous activity

- 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



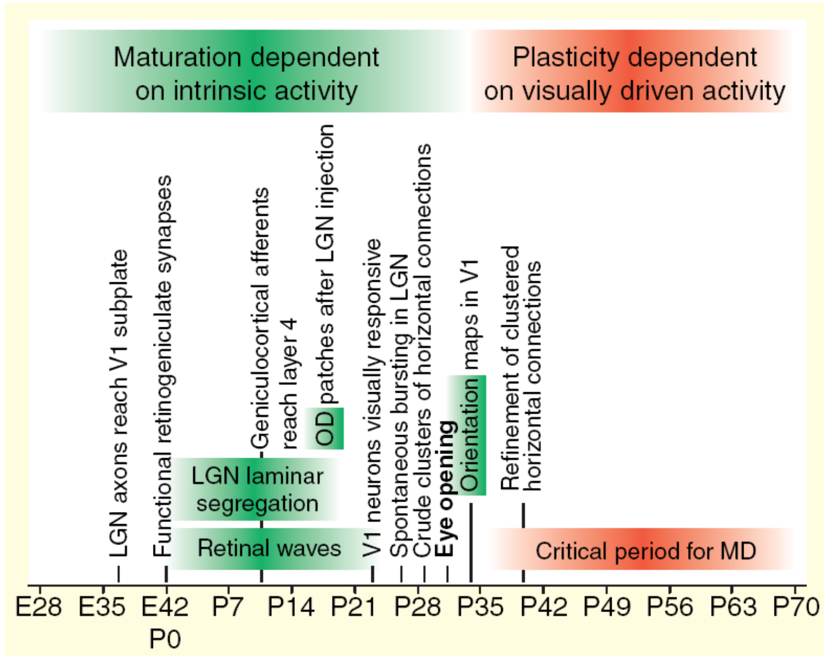
# Timeline: Cat



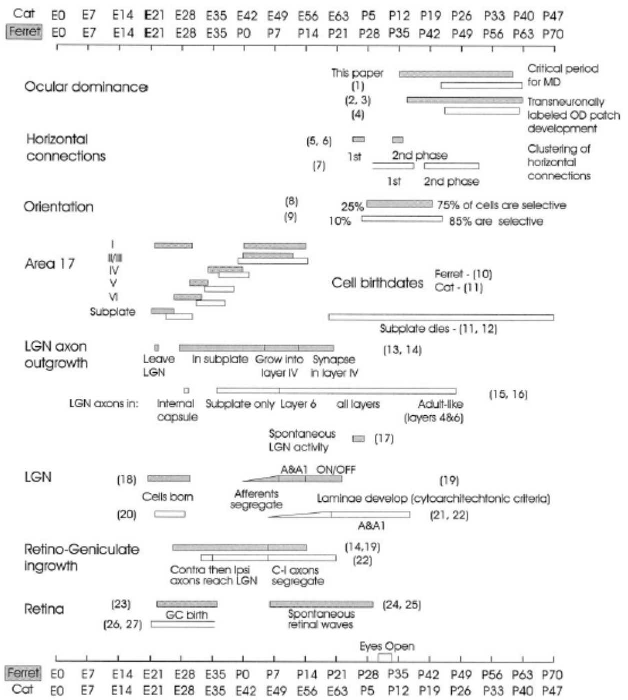

(Sengpiel & Kind 2002)



# Timeline: Ferret




(Sengpiel & Kind 2002)




# Cat vs. ferret

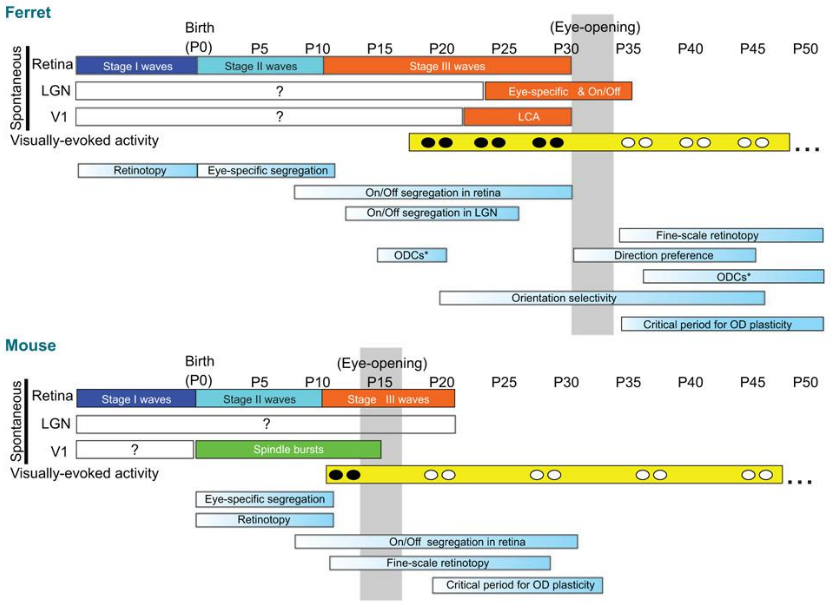
Should be readable in a printout, not on screen

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

(Issa et al. 1999)



# Ferret vs. mouse




(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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