

# Early Vision and Visual System Development

**Dr. James A. Bednar**

jbednar@inf.ed.ac.uk

<http://homepages.inf.ed.ac.uk/jbednar>

# 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)

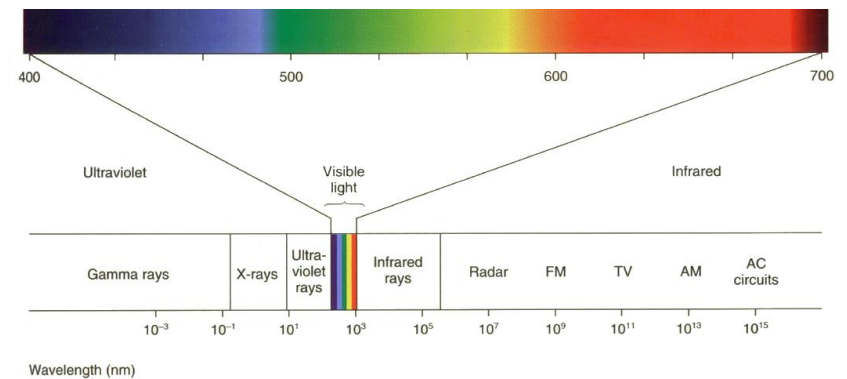
**Physiology** What is the behavior of the component parts of the visual system?

**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

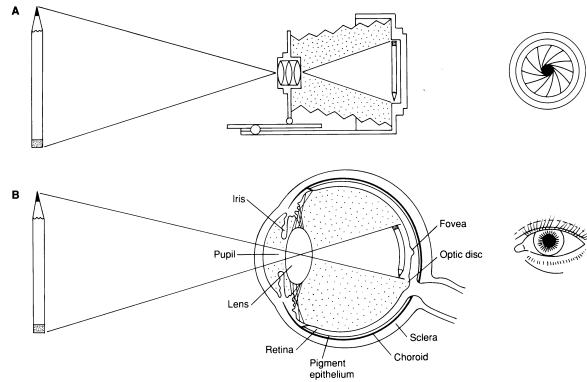


(From web)

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



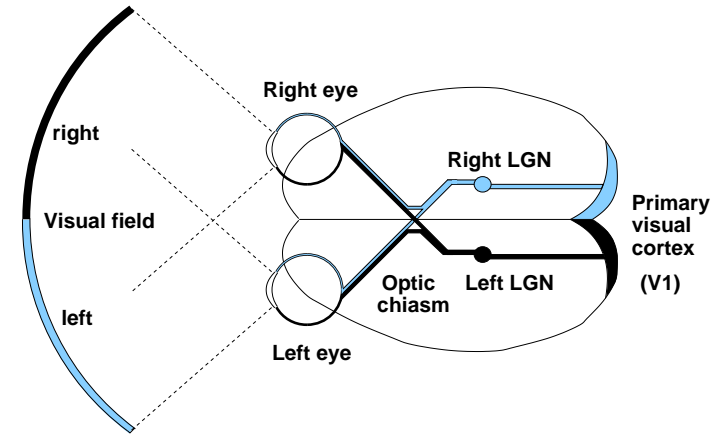
# Image formation



(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

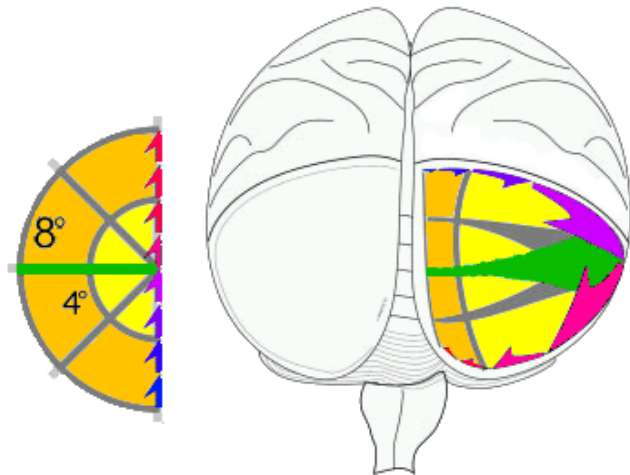
# Visual fields



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

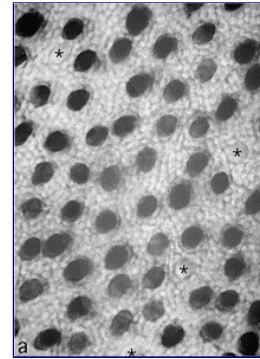
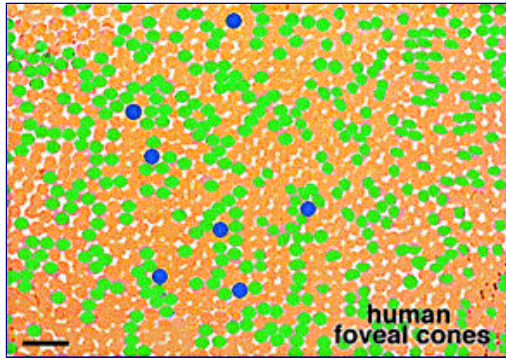


(From omni.isr.ist.utl.pt)

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



# Retinal surface



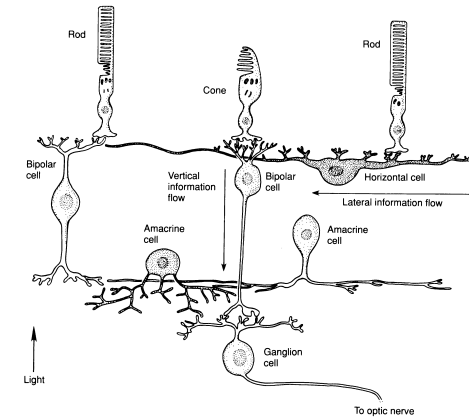
(Ahmedt & Kolb 2000); no scale in original

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

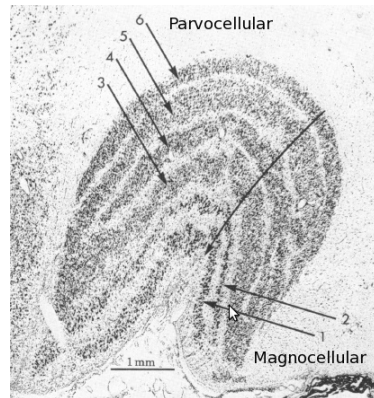


(Kandel et al. 1991)

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

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

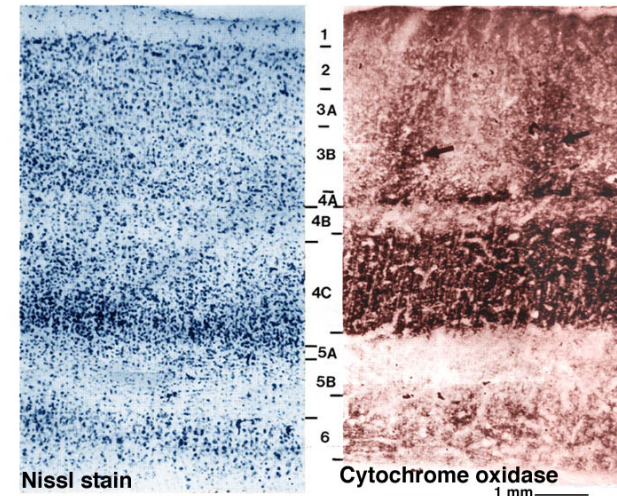
# LGN layers



Macaque; Hubel & Wiesel 1977

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

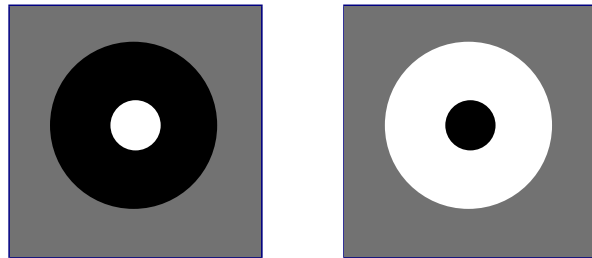
# V1 layers



(From webvision.umh.es)

Multiple layers of cells in V1  
Brodmann numbering

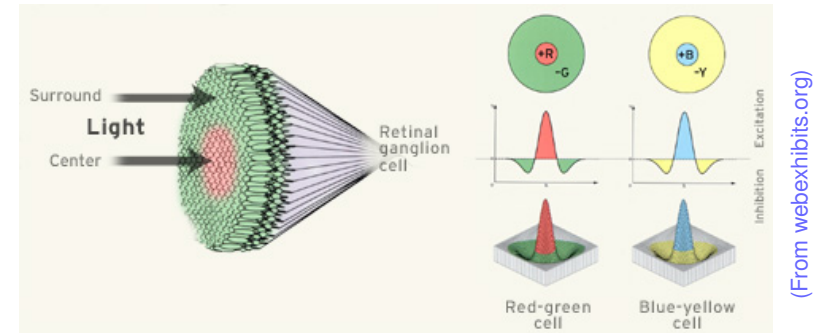
## Retinal/LGN cell response types



Types of receptive fields based on responses to light:

	in center	in surround
<b>On-center</b>	excited	inhibited
<b>Off-center</b>	inhibited	excited

## Color-opponent retinal/LGN cells



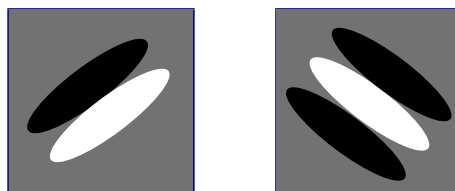
(From webebits.org)

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



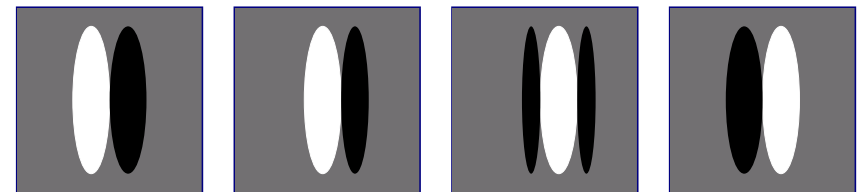
2-lobe simple cell

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

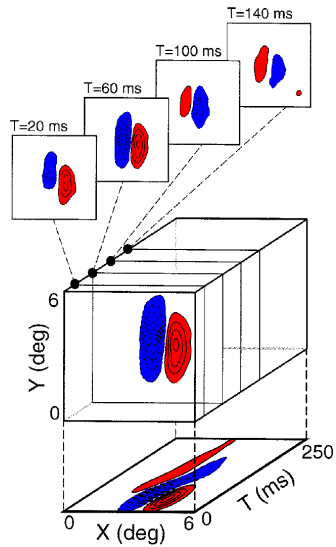


(Same response to all these patterns)

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

Can't measure complex RFs using pixel-based correlations

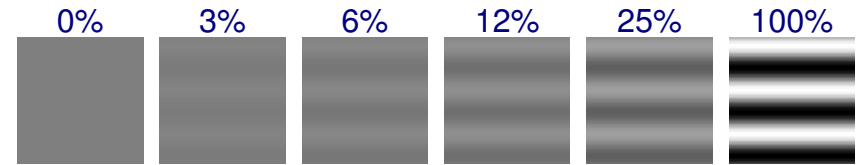
# Spatiotemporal receptive fields



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

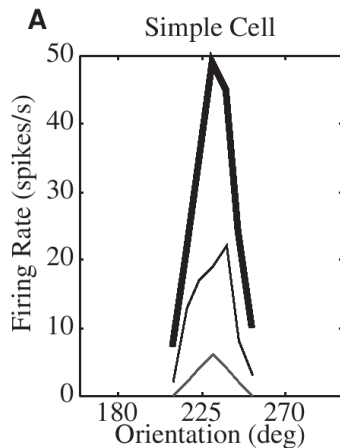
(Cat V1; DeAngelis et al. 1999)

# 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



- 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

(Sclar & Freeman 1982)

# 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:

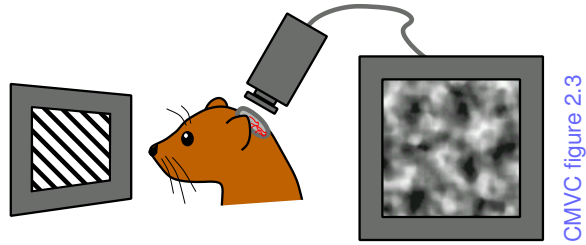
**Weber contrast (e.g. a tiny spot on uniform background)**

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

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

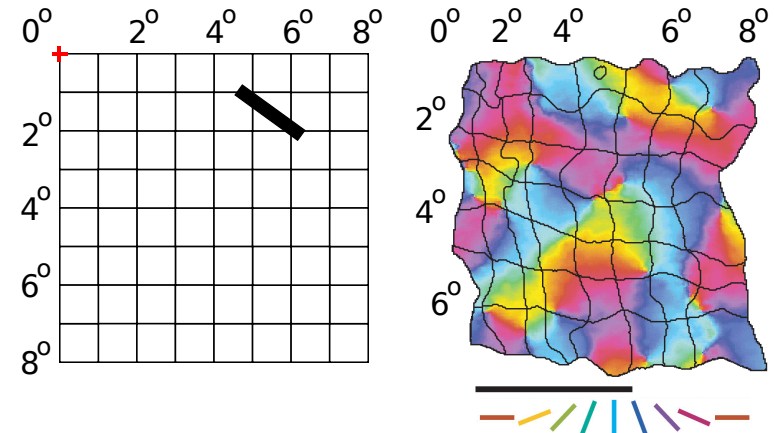
$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} = \frac{L_{max} - L_{min}}{2 L_{avg}}$$

# Measuring cortical maps



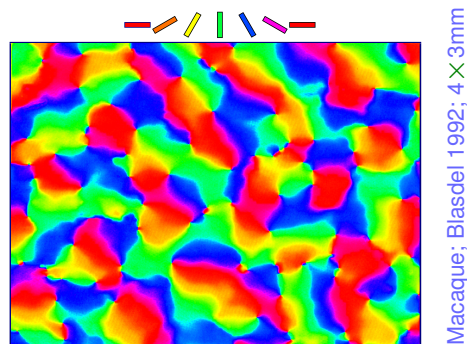
- Surface reflectance (or voltage-sensitive-dye emission) changes with activity
- Measured with optical imaging
- Preferences computed as correlation between measurement and input

# Retinotopy/orientation map



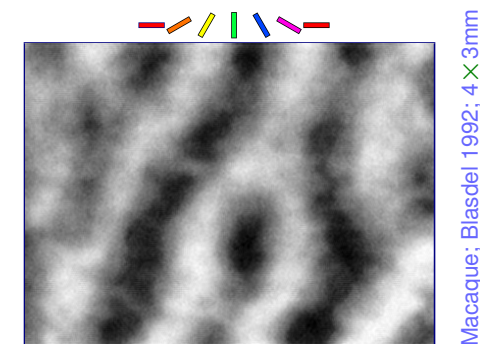
- Tree shrew has no fovea  $\leadsto$  isotropic map
- All orientations represented for each retina location
- Orientation map is smooth, with local patches

# Macaque orientation map



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

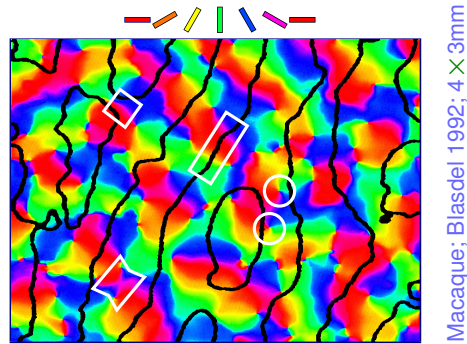
# Ocular dominance map in V1



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

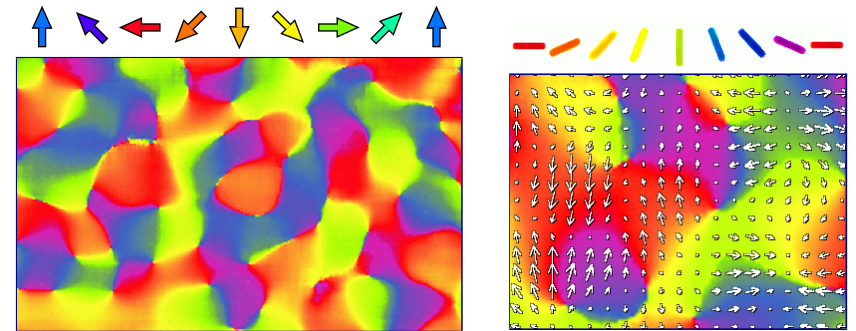


# Combined OR/OD map in V1



- 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

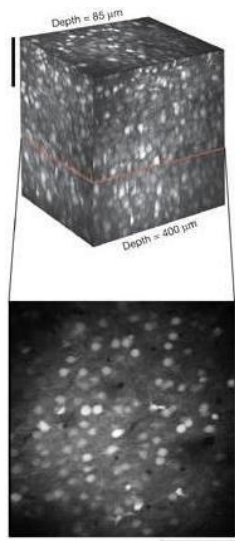
(3.2 × 2mm)

OR/Direction pref.

(1 × 1.4mm)

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

# Cell-level organization



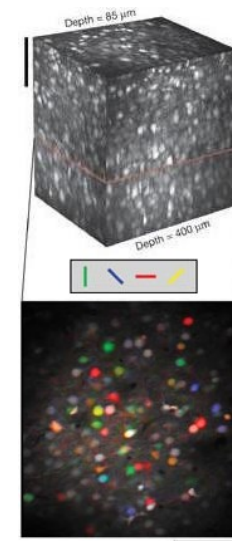
Two-photon microscopy:

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

(Ohki et al. 2005)

Rat V1 (scale bars 0.1mm)

# Cell-level organization 2



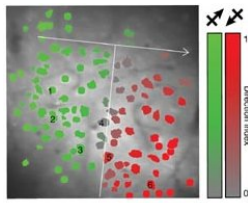
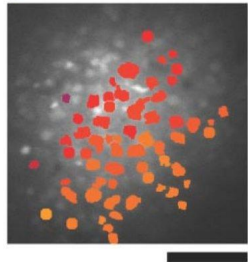
- Individual cells can be tagged with feature preference
- In rat, orientation preferences are random
- Random also expected in mouse, squirrel

(Ohki et al. 2005)

Rat V1 (scale bars 0.1mm)



# Cell-level organization 3

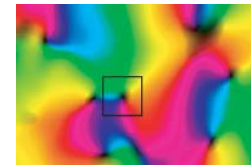


- In cat, validates results from optical imaging
- Smooth organization for direction overall
- Sharp, well-segregated discontinuities

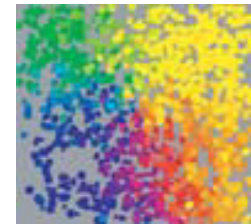
(Ohki et al. 2005)

Cat V1 Dir. (scale bars 0.1mm)

# Cell-level organization 4



Low-res map (2 x 1.2mm)



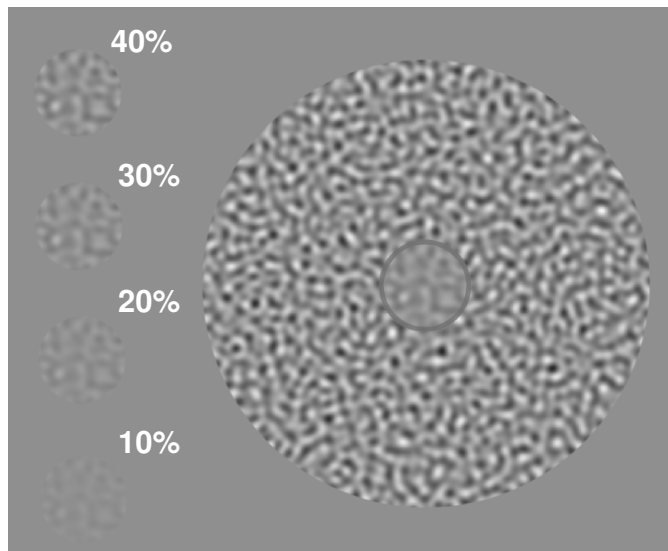
Stack of all labeled

cells (0.6 x 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

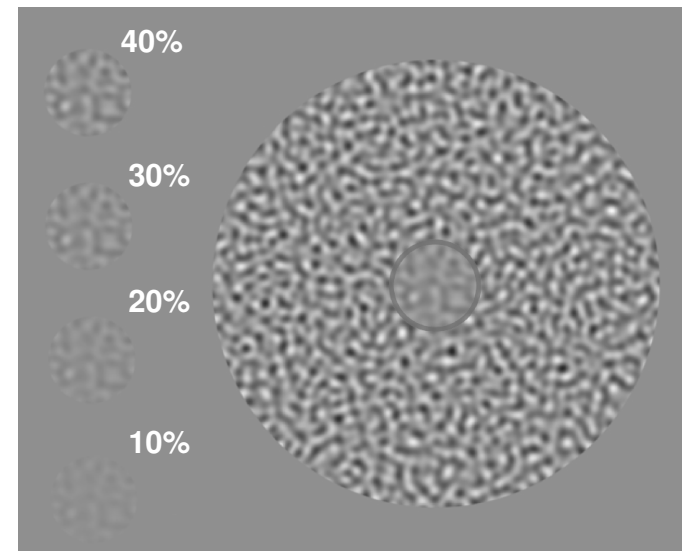
(Ohki et al. 2006)

# Surround modulation



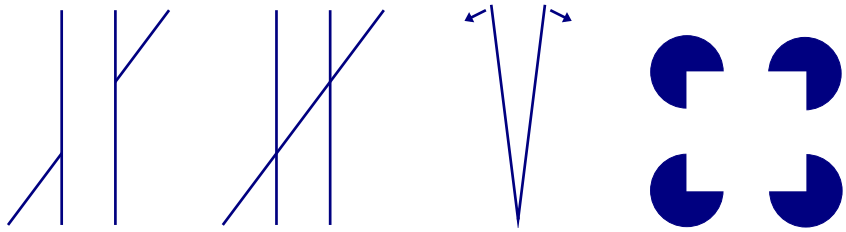
Which of the contrasts at left matches the central area?

# Surround modulation



Which of the contrasts at left matches the central area? <sup>40%</sup>

## Contextual interactions



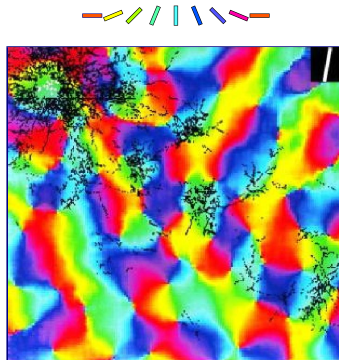
- Orientation and shape perception is not entirely local (e.g. due to individual V1 neurons).
- Instead, adjacent line elements interact (tilt illusion).
- Presumably due to lateral or feedback connections at V1 or above.

## Lateral connections



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

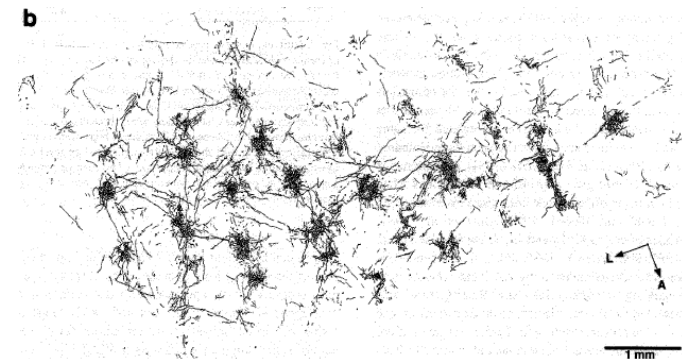
## Lateral connections



(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



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

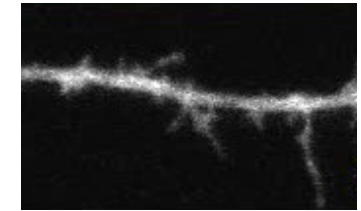
# Visual development

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)

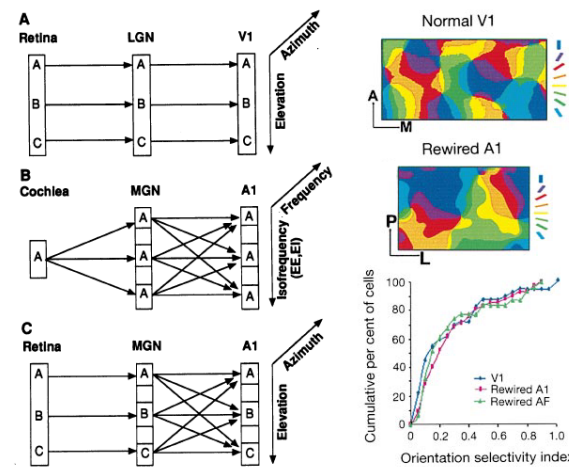
- Tissues develop into eye, brain
- RGC axons grow from eye to LGN and superior colliculus (SC) following chemical gradients
- Axons form synapses at LGN, SC
- LGN axons grow to V1, V2, etc., forming synapses

# 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. ~> Functional orientation cells, map in A1

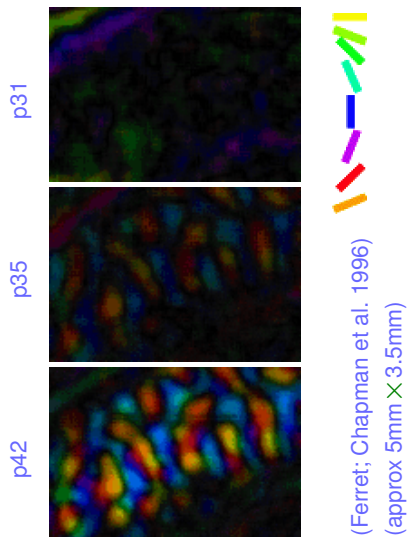
# Human visual system at birth

- 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

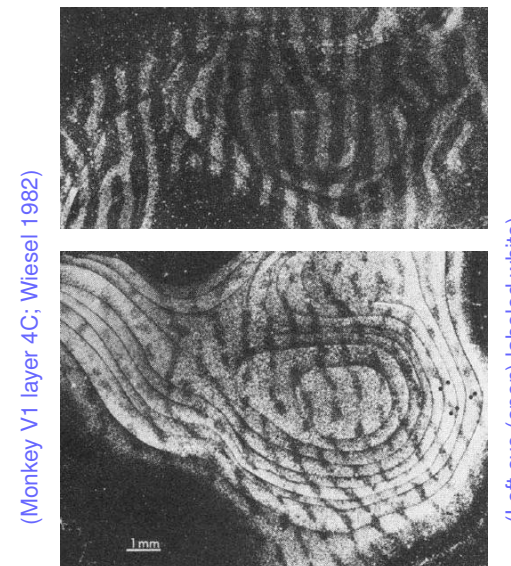
- Initial orientation, OD maps develop without visual experience (Crair et al. 1998)
  - Maps match between the eyes even without shared visual experience (Kim & Bonhoeffer 1994)
  - Experience leads to more selective neurons and maps (Crair et al. 1998)
  - Lid suture (leaving light through eyelids)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

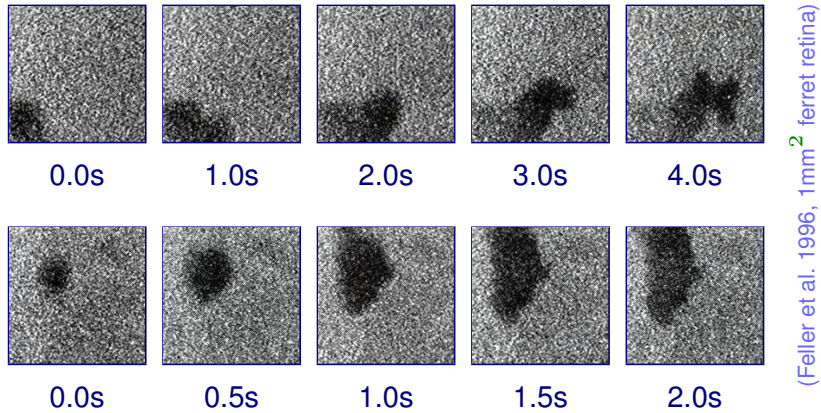
# Monocular deprivation



- 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

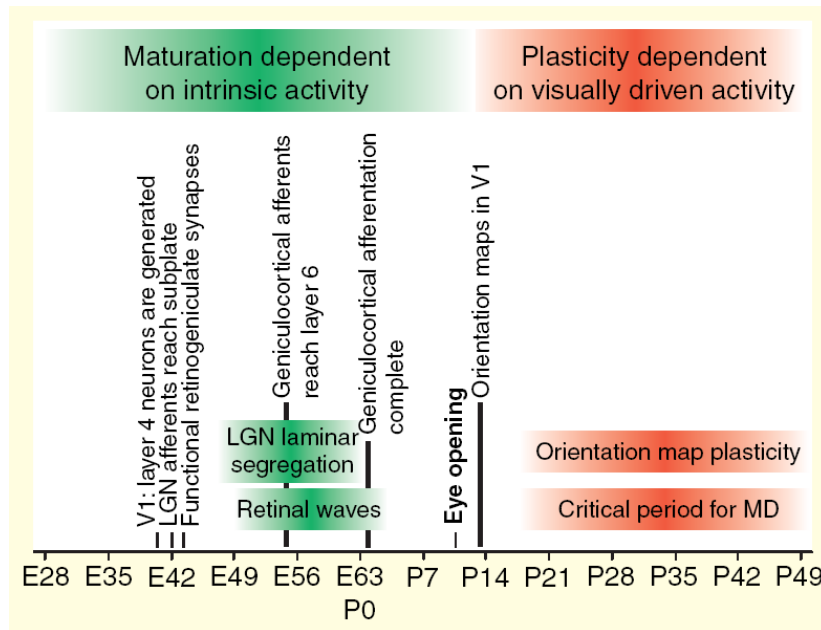


- Retinal waves: drifting patches of spontaneous activity
- Training patterns?

# Role of spontaneous activity

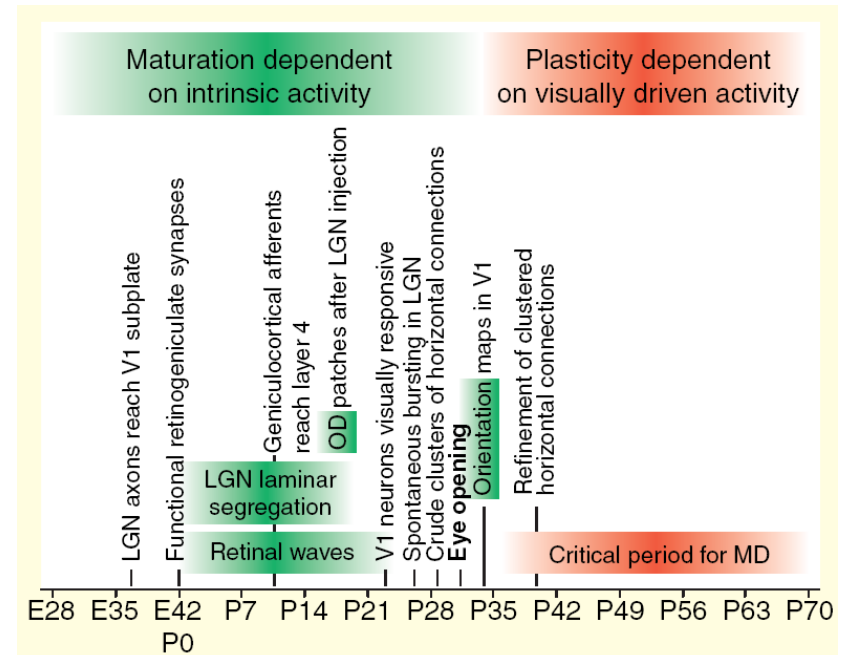
- Silencing of retinal waves prevents eye-specific segregation in LGN (Huberman et al. 2003) and ocular dominance columns in V1 (Huberman et al. 2006)
- Boosting in one eye disrupts LGN, but not if in both
- Disrupting retinal waves disrupts geniculocortical mapping (Cang et al. 2005)
- Other sources 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

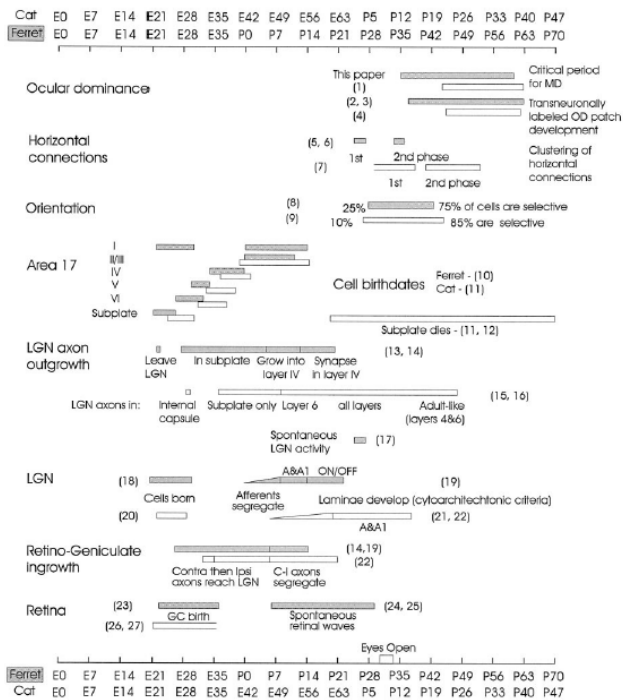


(Sengpiel & Kind 2002)

# Timeline: Ferret



(Sengpiel & Kind 2002)

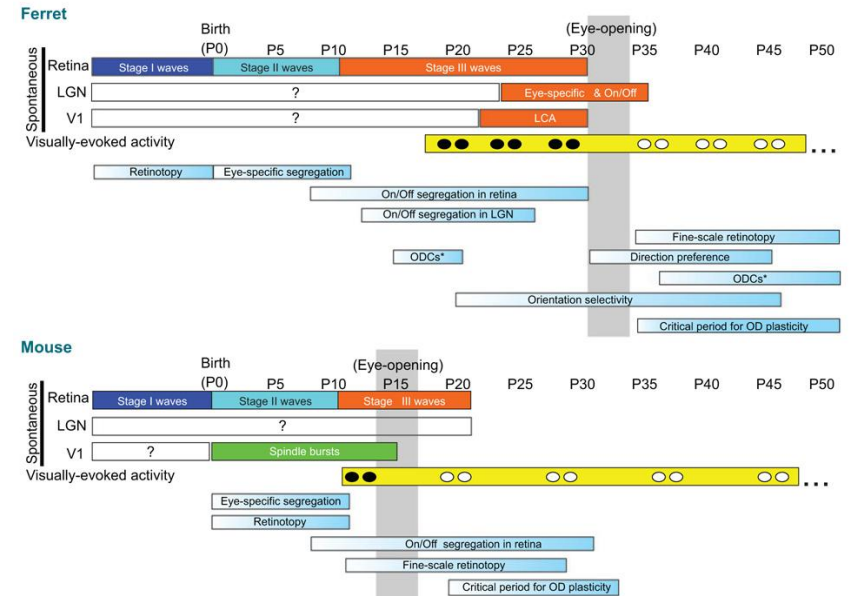


# Cat vs. ferret

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



(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

# References

Ahnelt, P. K., & Kolb, H. (2000). The mammalian photoreceptor mosaic—adaptive design. *Progress in Retinal and Eye Research*, 19 (6), 711–777.

Angelucci, A., Levitt, J. B., & Lund, J. S. (2002). Anatomical origins of the classical receptive field and modulatory surround field of single neurons in macaque visual cortical area V1. *Progress in Brain Research*, 136, 373–388.

Bosking, W. H., Crowley, J. C., & Fitzpatrick, D. (2002). Spatial coding of position and orientation in primary visual cortex. *Nature Neuroscience*, 5 (9), 874–882.

Bosking, W. H., Zhang, Y., Schofield, B. R., & Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *The Journal of Neuroscience*, 17 (6), 2112–2127.

Cang, J., Renteria, R. C., Kaneko, M., Liu, X., Copenhagen, D. R., & Stryker, M. P. (2005). Development of precise maps in visual cortex requires patterned spontaneous activity in the retina. *Neuron*, 48 (5), 797–809.

Chapman, B., Stryker, M. P., & Bonhoeffer, T. (1996). Development of orientation preference maps in ferret primary visual cortex. *The Journal of Neuroscience*, 16 (20), 6443–6453.

Crair, M. C., Gillespie, D. C., & Stryker, M. P. (1998). The role of visual experience in the development of columns in cat visual cortex. *Science*, 279, 566–570.

DeAngelis, G. C., Ghose, G. M., Ohzawa, I., & Freeman, R. D. (1999). Functional micro-organization of primary visual cortex: Receptive field analysis of nearby neurons. *The Journal of Neuroscience*, 19 (10), 4046–4064.

Feller, M. B., Wellis, D. P., Stellwagen, D., Werblin, F. S., & Shatz, C. J. (1996).

Requirement for cholinergic synaptic transmission in the propagation of spontaneous retinal waves. *Science*, 272, 1182–1187.

Gilbert, C. D., Hirsch, J. A., & Wiesel, T. N. (1990). Lateral interactions in visual cortex. In *The Brain* (Vol. LV of *Cold Spring Harbor Symposia on Quantitative Biology*, pp. 663–677). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Hubel, D. H., & Wiesel, T. N. (1977). Functional architecture of macaque visual cortex. *Proceedings of the Royal Society of London Series B*, 198, 1–59.

Huberman, A. D., Feller, M. B., & Chapman, B. (2008). Mechanisms underlying development of visual maps and receptive fields. *Annual Review of Neuroscience*, 31, 479–509.

Huberman, A. D., Speer, C. M., & Chapman, B. (2006). Spontaneous retinal

activity mediates development of ocular dominance columns and binocular receptive fields in V1. *Neuron*, 52 (2), 247–254.

Huberman, A. D., Wang, G. Y., Liets, L. C., Collins, O. A., Chapman, B., & Chalupa, L. M. (2003). Eye-specific retinogeniculate segregation independent of normal neuronal activity. *Science*, 300 (5621), 994–998.

Issa, N. P., Trachtenberg, J. T., Chapman, B., Zahs, K. R., & Stryker, M. P. (1999). The critical period for ocular dominance plasticity in the ferret's visual cortex. *The Journal of Neuroscience*, 19 (16), 6965–6978.

Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (1991). *Principles of Neural Science* (3rd Ed.). Amsterdam: Elsevier.

Kim, D. S., & Bonhoeffer, T. (1994). Reverse occlusion leads to a precise restora-

tion of orientation preference maps in visual cortex. *Nature*, 370 (6488), 370–372.

Ohki, K., Chung, S., Ch'ng, Y. H., Kara, P., & Reid, R. C. (2005). Functional imaging with cellular resolution reveals precise micro-architecture in visual cortex. *Nature*, 433 (7026), 597–603.

Ohki, K., Chung, S., Kara, P., Hubener, M., Bonhoeffer, T., & Reid, R. C. (2006). Highly ordered arrangement of single neurons in orientation pinwheels. *Nature*, 442 (7105), 925–928.

Sclar, G., & Freeman, R. D. (1982). Orientation selectivity in the cat's striate cortex is invariant with stimulus contrast. *Experimental Brain Research*, 46, 457–461.

Sengpiel, F., & Kind, P. C. (2002). The role of activity in development of the visual system. *Current Biology*, 12 (23), R818–R826.

Sengpiel, F., Stawinski, P., & Bonhoeffer, T. (1999). Influence of experience on orientation maps in cat visual cortex. *Nature Neuroscience*, 2 (8), 727–732.

Sur, M., Garraghty, P. E., & Roe, A. W. (1988). Experimentally induced visual projections in auditory thalamus and cortex. *Science*, 242, 1437–1441.

Van Essen, D. C., Anderson, C. H., & Felleman, D. J. (1992). Information processing in the primate visual system: An integrated systems perspective. *Science*, 255, 419–423.

Weliky, M., Bosking, W. H., & Fitzpatrick, D. (1996). A systematic map of direction preference in primary visual cortex. *Nature*, 379, 725–728.

White, L. E., Coppola, D. M., & Fitzpatrick, D. (2001). The contribution of sensory experience to the maturation of orientation selectivity in ferret visual cortex. *Nature*, 411, 1049–1052.

Wiesel, T. N. (1982). Postnatal development of the visual cortex and the influence of the environment. *Nature*, 299, 583–591.