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

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

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

Macaque visual areas

(Van Essen et al. 1992)

Circuit diagram

Connections between macaque visual areas

(Van Essen et al. 1992)

A bit messy!

(Yet still just a start.)
**Image formation**

<table>
<thead>
<tr>
<th></th>
<th>Fixed</th>
<th>Adjustable</th>
<th>Sampling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Camera:</td>
<td>lens shape</td>
<td>focal length</td>
<td>uniform</td>
</tr>
<tr>
<td>Eye:</td>
<td>focal length</td>
<td>lens shape</td>
<td>higher at fovea</td>
</tr>
</tbody>
</table>

*(Kande et al. 1991)*

**Visual fields**

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

**Retinotopic map**

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

*Mapping of visual field in macaque monkey*  
Blasdel and Campbell 2001

**Effect of foveation**

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

*From omni.lis.ist.utl.pt*
Retinal surface

- Fovea (center): 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

- Rod pathway: Rod, rod bipolar cell, ganglion cell
- Cone pathway: Cone, bipolar cell, ganglion cell

LGN layers

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

V1 layers

Multiple layers of cells in V1
Brodman numbering
Retinal/LGN cell response types

Types of receptive fields based on responses to light:

<table>
<thead>
<tr>
<th>Type</th>
<th>In Center</th>
<th>In Surround</th>
</tr>
</thead>
<tbody>
<tr>
<td>On-center</td>
<td>excited</td>
<td>inhibited</td>
</tr>
<tr>
<td>Off-center</td>
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</tr>
</tbody>
</table>

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!

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

(Solar & 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)

\[ C = \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{min}}} \]

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

\[ C = \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \]
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

Orientation map in V1

- Overall organization is retinotopic
- Local patches prefer different orientations

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
Two-photon microscopy:
- New technique with cell-level resolution
- Can measure a small volume very precisely

Cell-level organization 2
- Individual cells can be tagged with feature preference
- In rat, orientation preferences are random
- Random also expected in mouse, squirrel

Cell-level organization 3
- In cat, validates results from optical imaging
- Smooth organization for direction overall
- Sharp, well-segregated discontinuities
Cell-level organization 4

- Very close match with optical imaging results
- Stacking labeled cells from all layers shows very strong ordering spatially and in across layers
- No significant loss of selectivity in pinwheels

(Ohki et al. 2006)

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

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

(Macaque; Gilbert et al. 1990)

(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

(Macaque; Angelucci et al. 2002)

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**

- 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

- 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?

(Feller et al. 1996, 1mm² ferret retina)
Role of spontaneous activity

- Silencing of retinal waves prevents eye-specific segregation in LGN
- Boosting in one eye disrupts LGN, but not if in both
- Effect of retinal waves on cortex unclear
- 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

Maturation dependent on intrinsic activity
Plasticity dependent on visually driven activity

Timeline: Ferret

Maturation dependent on intrinsic activity
Plasticity dependent on visually driven activity

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
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


