Lecture 2: Central Visual Pathways

Organisation of visual field
- Eyes converge such that each fovea is aligned with a common fixation point;
- Cross-over (decussation) of nasal hemiretina axons, & non cross-over of temporal hemiretina axons means that each hemisphere receives signals from the contralateral hemifield alone;
- Retinotopic organization is maintained in the layers of the LGN, and in area V1.

Generation of binocularly-driven neurons
- Binocular neurons allow single vision, and are the basis of stereoscopic vision;
- Neurons in the LGN, and their target cells in layer 4C of V1, are strictly monocular;
- Binocular neurons are first found outside of layer 4C, organized in alternating 'ocular-dominance columns' (greater input from one eye than the other)[1];
- Layer 4C ('granular layer') has a high density of small neurons; these neurons may interpolate the visual image to enhance acuity (i.e. 'hyperacuity', as illustrated by Vernier alignment);
- The depth of the field of single vision, in front, and behind the plane of fixation ("Panum's zone of fusion') is determined by the lateral range of intrinsic connections, across the retinotopic map in V1 (and perhaps in subsequent areas).
- These lateral connections allow a neuron to have receptive fields in slightly non-corresponding parts of the retina in the two eyes; this, so-called 'retinal disparity', is the neural basis of stereoscopic depth vision.

Plasticity of connections and critical period
- Congenital cataract simulated by eyelid suture in one eye (= monocular deprivation, 'MD');
- Geniculocortical terminals fed by the deprived eye contact a reduced territory in layer 4C of V1[2];
    - NB. Use of tritiated amino acids as transneuronal, anterograde tracer;
- This shrinkage of monocular compartments driven by the deprived eye, and expansion of those driven by the normal eye, is an example of neural 'plasticity'.
- The earlier the onset of MD, the more severe its effect: there is little effect if applied at 12 weeks of age[3]; hence, experimentally, the 'critical period' for plasticity in this system is from birth to 3 months (in monkeys);
- The findings informed early, postnatal ocular surgery in the clinical management of congenital cataract in humans.

Parvocellular, magnocellular and koniocellular (P, M & K) channels at the level of the LGN
- P, M & K cells inherit physiological characteristics of retinal ganglion cells (midget, parasol & bistratified) – however P, M & K are used as generic terms to describe the full retino-geniculo-cortical pathway;
- P, M & K receptive fields are distinguished by factors such as size, cone opponency, spatial opponency, and sensitivity to flicker;
- Biophysically, M cells are larger, with larger diameter axons and conduct impulses at higher velocity;
- The particular physiological characteristics of P, M & K channels do suggest specific perceptual roles (P serves high acuity form, P & K serve colour vision, M serves motion vision) – but it should be understood that, in general, the visual system achieves its results by integrated processing of its three afferent channels.

Cortical reorganization of P, M & K input
- Use of cytochrome oxidase ('cytox') stain to clarify laminar pattern in area V1, and blob v interblob compartments in layer 2/3[4];
- Geniculocortical terminations: P in layer 4Cb; M in layer 4Ca; K in layer 4A, 2/3 cytox 'blobs' & layer 1[5];
- Intrinsic relays deliver M signals to layer 4B, but mixed P & M signals to layer 2/3; hence 'blobs' receive all 3 channels;
- Cortical processing constructs receptive fields with specialist response properties[6]: (see lecture slides for details); note that blob v interblob tuning can be understood as differential processing of P input to extract either the high acuity spatial information whilst discarding chromatic information (interblobs), or to extract the LW v MW colour information present at lower spatial frequencies (blobs).
- Two-photon imaging using a Ca++ indicator of spiking activity can deliver much larger sample sizes than traditional electrophysiological techniques using microelectrodes. One such recent study confirms 'classical' tuning properties of blobs, but also finds many interblob cells combining both spectral and orientation selectivity[7]

Onward central pathways from area V1

- V1 sends output to many areas, but principally to area V2, V3 and V5;
- Output to V3 and V5 comes only from layer 4B; this is predominantly based on re-processed M signals;
    - NB. Use of horseradish peroxidase (HRP) as a retrograde tracer[8];
- V2 has a set of stripe-shaped compartments defined by cytox staining, known as 'thick', 'thin' and 'interstripes'; to a first approximation these represent a continuation of V1 layer 4B, blob and interblob compartments, respectively, with similar receptive field tuning properties.
    - Later studies reveal some crossover in projections from V1 to V2 compartments[9]; i.e. further potential for integrated analysis P, M & K signals (see lecture slides for details);
- Thick stripes send output to area V5; thin & interstripes to area V4;
    - Note that this dual output to V4 retains some segregation within internal compartments of V4 that are *not* visible in the cytox stain.

The 'two visual pathways' dogma

- Divides visual processing between a dorsal pathway, directed toward the parietal lobe, involved in seeing where an object is in space, and a ventral pathway directed toward temporal lobe involved in seeing what an object is;
- Later re-classified as vision for action (dorsal) v vision for perception (ventral)[10 11];
- As details of inter-area connections in monkeys were obtained, areas V4 and V5 were identified as the lowest areas that could be assigned to one pathway in particular (V4, ventral; V5, dorsal)[12];
- Discovery of further connections shows that the cortical visual system comprises a network of connected areas, posing several problems for the two-pathways dogma[13-16]:
    - Areas V4 and V5 (and further higher areas) show cross connections between streams;
    - Some higher areas were assigned to a 'third pathway', or to no pathway in particular, or to both dorsal and ventral streams;
    - There is a complex transition from M/P/K to dorsal/ventral, not a simple M-to-dorsal and P/K-to-ventral (as has been proposed);
    - The root dorsal area, V5, clearly has a perceptual function, inconsistent with the 'vision for action' formulation of the dorsal pathway.

Basic Reading

The New Visual Neurosciences 2014: Eds. Chalupa & Werner

11. Synaptic mechanisms of color and luminance coding: -rediscovering the X-Y dichotomy in primate retinal ganglion cells	Crook, Packer *et al*	123-144
16. The M, P, and K Pathways of the Primate Visual System	Kaplan	215-226
17. Ventral and Dorsal Cortical Processing Streams	Bell, Pasternak & Ungerleider	227-242
25. Cell Types and Local Circuits in Primary Visual Cortex of the Macaque Monkey	Callaway	353-365
27. The Cortical Organization of Binocular Vision	Freeman	381-398
52. The Functional Organization of the Ventral Pathway in Humans	Kanwisher & Dilks	733-748

The circuitry of V1 and V2: integration of color, form, and motion. Sincich & Horton, Ann. Rev. Neuroscience, 28: 303-326 (2005).

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Two visual systems re-viewed. Milner and Goodale, Neuropsychologia, 46: 774-785 (2008).

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The ventral visual pathway: an expanded neural framework for the processing of object quality. Kravitz *et al.*, Trends in Cognitive Sciences, 17:26-49 (2013).

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8. Shipp S, Zeki S (1989) *The organization of connections between areas V5 and V1 in macaque monkey visual cortex*. Eur J Neurosci. 1: 309-332.
9. Sincich LC, Horton JC (2002) *Divided by cytochrome oxidase: a map of the projections from V1 to V2 in macaques*. Science. 295: 1734-1737.
10. Milner AD, Goodale MA (2008) *Two visual systems re-viewed*. Neuropsychologia. 46: 774-785.
11. James TW *et al.* (2003) *Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study*. Brain. 126: 2463-2475.
12. Ungerleider LG, Desimone R (1986) *Cortical connections of visual area MT in the macaque*. J Comp Neurol. 248: 190-222.
13. Boussaoud D *et al.* (1990) *Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque*. J Comp Neurol. 296: 462-495.
14. Distler C *et al.* (1993) *Cortical connections of inferior temporal area TEO in macaque monkeys*. J Comp Neurol. 334: 125-150.
15. Ungerleider LG (1995) *Functional brain imaging studies of cortical mechanisms for memory*. Science. 270: 769-775.
16. Kravitz DJ *et al.* (2013) *The ventral visual pathway: an expanded neural framework for the processing of object quality*. Trends Cogn Sci. 17: 26-49.