Advanced parallel processing

OVERVIEW

There are 3 distinct levels of parallel organisation in the visual system:
(a) subcortical retino-geniculo-cortical pathways;
(b) pathways segregated by cytochrome oxidase modules in areas V1 and V2;
(c) the two visual pathway dogma for higher visual areas - a dorsal 'WHERE' pathway leading to the parietal lobe and a ventral 'WHAT' pathway leading to the temporal lobe.
Together, these encompass the entire visual system, but the interface of (a)/(b) and (b)/(c) is complex. Thus, a 'Grand Unification' scheme for the overall parallel construction of the visual system, all the way from retina to highest levels of cortex, has not proved to be sustainable.

Lateral Geniculate Nucleus (LGN)

– 4 parvocellular (P) layers & 2 magnocellular (M) layers;
Specific cone inputs; no S –cone input to parvo or magno [1]
– physiological and biophysical properties (see Tables);
– P suited for fine grain static analysis, & R/G colour;
– M for dynamic analysis of events changing with time;
– Koniocellular layers are located between M and P layers, with mixed properties, including blue colour signals [2]

LGN lesion tests for perceptual roles of M and P pathways [3]

– small lesion in P or M layers punches a hole in visual representation;
– test perception of alert, LGN-lesioned animal, inside or outside region of deficit;
– M lesions impair flicker and motion;
– P lesions impair colour, and fine texture, shape or stereo (i.e. depth) discriminations;
– brightness, coarse form and coarse stereo not affected by either M or P lesions;
hence P & M channels can stand in for one another in visual duties where their spatiotemporal sensitivity ranges overlap.
– also note that M layer lesion does leave some residual motion perception [4]
This could be due (a) to intact geniculocortical P or K relays, and/or
(b) to 'bypass' M relays (retina – SC - pulvinar – V5) [5, 6]

Central M & P Pathways in V1

– M system projects to layer 4Ca;
– P system projects to layer 4Cb;
– synthesis of new receptive field response properties:
4B: selectivity for orientation & direction, binocular disparity;
2 & 3: selectivity for colour and orientation;
– cytochrome oxidase 'blobs' of layers 2& 3 segregate colour (blobs) and form (interblobs) [7, 8]
– M pathway relays via layer 4B to V2, V3 and V5;
– M & P pathways relay via layers 2 & 3 to V2;

Third geniculocortical K pathway (koniocellular) [2]

– Involves superior colliculus and intralaminar regions of LGN;
– properties: large RF's, long latencies; SW (blue cone) wavelength selectivity;
– SW 'ON' have direct input to 'blobs' in layers 2&3 of V1 [9]
– SW 'OFF' terminate in layer 4A [9]
– SW sensitivity is absent from SC pathway leading to LGN via SC.

Area V2

– cytochrome modules are stripes, extending through all layers;

– thick dark stripes (TK-stripes) receive from 4B, or from interblob-centred column through 2,3 & 4B; [10]

– thin dark stripes (N-stripes) receive from blob-centred column; [10]

– pale interstripes (I-stripes) receive from interblob-centred column; [10]

– properties of TK , N and I stripes respectively resemble layer 4B, blobs and interblobs [8, 11]

– TK stripes relay to areas V3 and V5;

– N stripes relay to area V4

– I stripes relay to V4 (and V3).

N & I stripes may connect with separate compartments within V4[12]

WHAT/WHERE pathway dogma

– V4 the 'root' of pathways leading to the temporal lobe and subserving object recognition;

– V5 the 'root' of pathways leading to parietal lobe and subserving object location in space;

– OR, reinterpret that ventral pathway is for visual perception, dorsal path for visual guidance of motor action [13, 14]

BUT : (a) there are cross connections (V4 -V5, V4-parietal, parietal - temporal)

– i.e. problem of definition: dual pathways or a unitary network of connections?

(b) V3 has output to V4 and V5 (and V3 is fed by TK and I stripes of V2)

– i.e. problem in 'joining' WHAT/WHERE streams onto cytochrome pathways;

(c) Is V5 a valid component of dorsal pathway?

– loss of V5 causes motion perceptual deficit;

– Output from V5 to mid temporal areas (inside s. temporal sulcus) might be regarded as a 3rd pathway.

(d) the medial motion area, V6, has richer connections with somato-motor cortical areas [15].

Asymmetric sorting of M P K systems at higher levels of processing

Physiological confirmation of P/M mixing

– pharmacological blocks of P or M layers in LGN show approx. 50/50 P and M responsivity in layers 2 & 3 of V1 [16];

– similar technique also shows approx. equal P and M responsivity in area V4 [17] but clear M dominance in V5 [18]

What is the circuitry responsible for mixing?

– anatomical pathways from M system to layers 2 & 3 of V1 [19] ;
shows that M signals can reach blobs & interblobs, hence relayed to V2 I and N stripes (& V4);

– recently updated V1 to V2 connectivity [10] has:

(i) input from layer 4B of V1 to I & N stripes of V2, i.e. another likely source of magno input to area V4;

(ii) input from V1 interblobs to K stripes of V2, showing that P signals may reach TK stripes.

– Hence V2 N stripes receive P/M/K, and V2 I and TK stripes receive P/M.

The 'isolation' of M input to V5 ?

– The output from layer 4B to V5 derives mainly from a unique class of spiny stellate neuron in layer 4B [20]
…this is a pure magno signal. BUT…

– Pyramidal output neurons in layer 4B pick up parvo signals from layer 3 [21], & some project to V5 [22]

– But V5 can also receive parvo input from layer 6 of V1 [23], and from TK stripes of V2;

– V5 receives konio input directly from LGN [24]

Basic Reading

The Visual Neurosciences Eds. Chalupa & Werner

Chap. 30.	*The M, P, and K Pathways of the Primate Visual System*	Ehud Kaplan	481-493
Chap. 31.	*Parallel Visual Pathways: A Comparative Perspective*	Casagrande & Xu	494-506
Chap. 33.	*Communications between Cortical Areas of the Visual System*	Jean Bullier	522-540
Chap. 34.	*Ventral and Dorsal Cortical Processing Streams*	Ungerleider & Pasternak	541-562
Chap. 42.	*Cell Types and Local Circuits in Primary Visual Cortex of the Macaque Monkey*	E. M. Callaway	680-694

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Specific sources

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9. *Parallel colour-opponent pathways to primary visual cortex.*
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10. *Divided by cytochrome oxidase: a map of the projections from V1 to V2 in macaques.*
    Sincich and Horton, Science. 295: 1734-1737 (2002).
11. *A motion direction map in macaque V2.*
    Lu et al., Neuron. 68: 1002-1013 (2010).
12. *Segregation and convergence of functionally defined V2 thin stripe and interstripe compartment projections to area V4 of macaques.*
    Xiao et al., Cerebral Cortex. 9: 792-804 (1999).

13. *Two visual systems re-viewed.*
Milner and Goodale, Neuropsychologia. 46: 774-785 (2008).
14. *Converging evidence for diverging pathways: Neuropsychology and psychophysics tell the same story.*
Westwood and Goodale, Vision Research. 51: 804-811 (2011).
15. *Human V6: the medial motion area.*
Pitzalis et al., Cerebral Cortex. 20: 411-424 (2010).
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