

Parallel Visual Pathways

A plethora of parallel visual pathways

Combined anatomical and physiological studies have demonstrated many sets of parallel pathway (PP) in the visual system. For example, there are PP from retina to superior colliculus and cortex; PP within the thalamocortical projections; and at a higher level, the mosaic of PP that emerge from modular subunits of V1 (primary visual cortex), or later still the supposedly binary PP that course toward the parietal and temporal lobes – the ‘dorsal’ and ‘ventral’ pathways (Figure 1). Each PP, taken separately, has an elemental subdivision of visual function to match its anatomical compartmentalisation. In other words, PP have been taken to be markers of functional specialisation in the visual system.

However, taking a global view, the functional labelling of the integrated PP circuit-diagrams tends to become rather more taxing, as their components mix together in a rather indiscriminate (and disconcerting) fashion. As we shall see, the root of the problem is that the discrete PP that have been identified at one level generally fail to dovetail neatly with those at the next. Nevertheless, complex as it is, growing knowledge of visual PP organisation should help point the way toward unravelling many other brain pathways and systems.

It's the exception that proves the rule...

The visual subsystem of the primate brain with the finest pedigree is probably the ‘motion pathway’. Human cortical area V5 (or MT) is selectively activated in motion processing tasks, and in macaques we know that the same area is selectively innervated by the M (magnocellular) retinogeniculate channel.^{1,2} This is good engineering, since the M channel's transient response and preservation of timing information make it a logical source of signals to subservise motion analysis. Figure 2 shows how this pathway reaches V5 via a discrete internal relay within area V1, the output layer (layer 4B) being a stronghold of directionally-selective neurons within V1.³ Even the ‘spiny stellate’ cells from which this output originates are unique: essentially pyramidal cells shorn of their apical dendrite, as if to preclude any chance contamination by dendrites straying outside the layer.^{4,5} Up to this level, the motion pathway ticks all the boxes for a segregated, specialised subsystem, almost spectacularly so. Unfortunately, if we examine the total outflow from the LGN (lateral geniculate nucleus), it begins to look atypical.

...and the rule is to re-mix

The LGN has three channels altogether, the other two P (parvocellular) and K (koniocellular) containing progressively smaller neurons than those in the M channel. Although the P channel overlaps the spatiotemporal sensitivity of the M channel, it has roughly tenfold more neurons and its specialisation is very different. It carries information about the fine spatial details of a static scene, with

red/green cone opponency for added colour vision. By contrast, the K channel is more of a miscellany; its only identified role is to harness B-cone signals, to provide the blue-yellow dimension of colour vision.⁶ Like the M channel, the P and K channels initially retain their integrity by terminating in separate strata of V1 (Figure 2). But they then encounter a host of cross-fertilising intrinsic relays, as a new modular system is generated within the cortex.

Cytochrome oxidase modules in V1 and V2

The metabolic capacity of brain tissue (revealed by a histological stain for the mitochondrial enzyme cytochrome oxidase) provides a serendipitous marker for modular sub-compartments in early cortical visual areas. These are the so-called ‘blobs’ (or ‘patches’) in V1 and ‘stripes’ in V2.^{3,7} M, P and K channels converge on these structures, whose specialised functions are not dictated by the composition of their input so much as by the nature of their own intrinsic processing. For instance the P system feeds both blobs, and the regions between them – the ‘interblobs’ – but while blobs are specialised to extract low acuity spectral information, the interblobs sacrifice much of the spectral content and synthesise higher resolution orientation specificity.

Not surprisingly the blobs, being the root of cortical colour analysis, also receive direct input from the K channel.⁶ But luminance signals from the M channel also reach both these modules. Thus blobs are ‘mongrel’ modules in that they represent a fusion of all three M/P/K channels – presumably because such a composite input is required to signal all the spectral and nonspectral intensity variations on which colour vision (including seeing shades of grey) depends.

The majority of the output from V1 relays through area V2, via specific blob-stripe connections (Figure 2). In fact there are three V2 modules, one of which (thin-stripes) are fed by blobs, the other pair (thick- and interstripes) by interblobs.⁸ The V2 stripes target very different areas of prestriate cortex: V5, predictably, is fed only by thick-stripes, as these are the main repository of direction-selectivity in V2; all other areas seem to be fed by selective combinations of stripe input.^{9,10} The general role of V1 and V2 is to initiate colour, form and motion analysis, and to distribute the initial products to separate prestriate areas for further specialised processing – but the parallel outputs of V2 are rather better categorised by cytochrome module than by the retino-geniculate M/P/K channels.

Dorsal/ventral dichotomies

In recent years, one major distinction has been made between a ‘dorsal’ set of pathways – from V1 to parietal areas – and a ‘ventral’ pathway – which channels visual information from V1 to the temporal lobe. It was first proposed that the dorsal system is specialised for spatial localisation (a ‘where’ function), whereas the ventral pathway is critical for object recognition (a ‘what’ function). More recently, a challenge to this view has considered the



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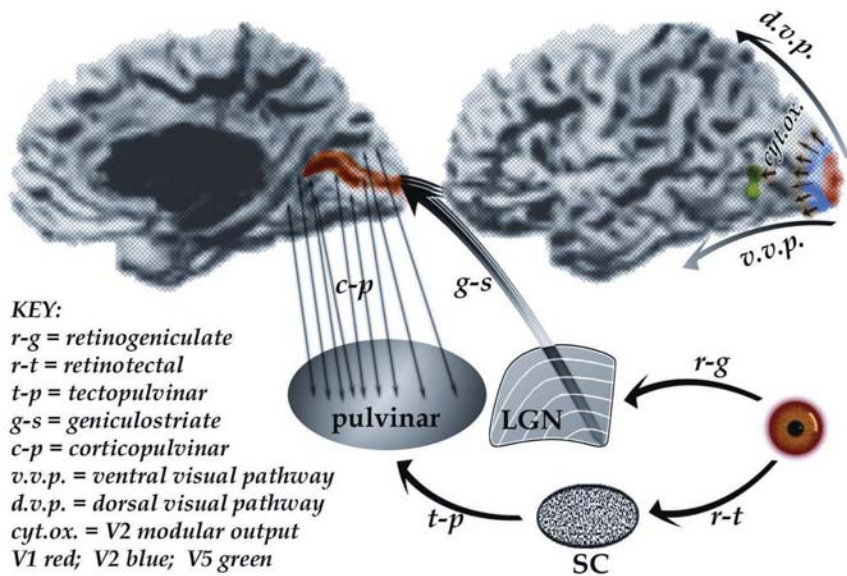


Figure 1: A plethora of parallel pathways. Retinal outputs can be categorised by their immediate destination (thalamus/LGN or midbrain/SC), or by their physiological class, which also correlates with the layer of termination within the LGN (ie M/P/K channels, indicated by the triplet arrowhead leading to area V1). Both the geniculate and tecto-pulvinar pathways distribute to a broad expanse of visual cortex, although the former is much more concentrated upon area V1. V1 and V2 generate a fresh subdivision of function from M/P/K input, as expressed in their cytochrome oxidase modules, and relays of these modular outputs can be traced through a number of nearby areas. The division of cortical visual pathways into dorsal and ventral streams represents compartmentation of function on a larger scale, effectively in terms of the source of visual input to the parietal and temporal lobes respectively. In contrast to retinal and tecto-pulvinar outputs, which are unidirectional, all cortical and cortico-thalamic connections are reciprocal, and utilise extensive feedback in their operations.

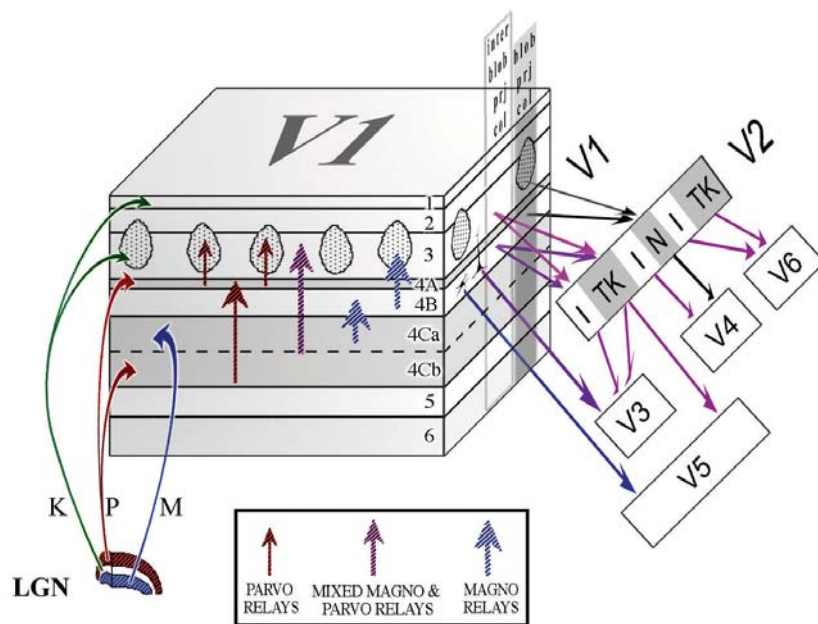
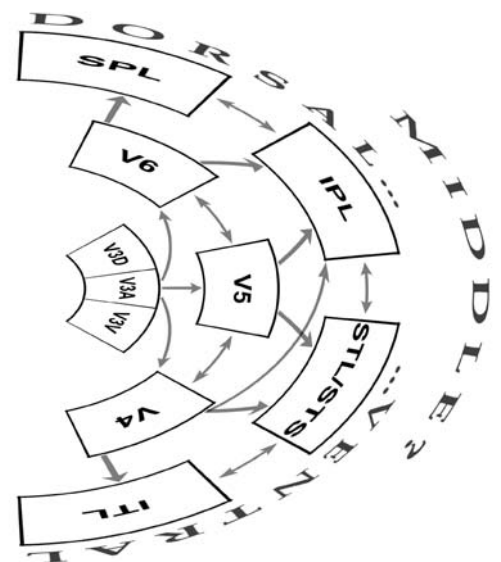


Figure 2: Parallel inputs and outputs of V1. The M/P/K channels relayed via the LGN terminate in separate layers of V1, but are then mixed together by cortical intrinsic relays and interlaminar connections; hence the outputs of V1 represent various composites of the geniculate channels – as coded by the colour key. Layer 4B is dominated by M input, and hence the ‘stellate’ cells of this layer provide a relatively clean M signal (blue). Pyramidal cells of layer 4B pick up additional signals via their apical dendrites in higher layers (purple). The two cell types appear to have different patterns of distribution to prestriate areas, such as V3 and V5. The output to V2 arises from layers 2 & 3, as well as 4B, and the pattern of these projections is better categorised by cytochrome oxidase module. Basically, the output from V1 is bi-partite, with neurons in projection columns (‘prj col’) that align either with a blob, or an interblob, connecting with different modules in V2 (I = interstripe, N = thin stripe, TK = thick stripe). In turn, the stripes of V2 target different sets of prestriate areas (including many more than areas V3-V6 shown here). The exact M/P/K compositions (shown as magenta/purple for varying P/M mixes and black for all three), are not well known. For all its apparent complexity, this is a much simplified depiction of our database of known circuitry (that, itself, is far from complete).

Figure 3: A highly schematic summary of connections from prestriate visual areas to regions of the parietal and temporal lobes of primate cortex. Each block may be taken to represent a cluster of nearby areas (eg as shown explicitly for the block marked V3d/V3A/V3v). The exact demarcation of the classical dorsal and ventral systems raises problems. Firstly, the afferent pathways do not form two clearly segregated ‘streams’, as the presence of cross connections sets up an interlinked network. Secondly, the relative territory of ‘dorsal’ and ‘ventral’ in the region of the temporo-parietal junction is not clear cut – and the addition of a third, ‘middle’ system might offer an equally valid, if equally indeterminate model of brain organisation. SPL & IPL = superior & inferior parietal lobe; STL/STS = superior temporal lobe/sulcus; ITL = inferior temporal lobe (or ventral occipital / fusiform cortex in human brain).



dorsal/ventral distinction to relate to functions of visuomotor control versus visual perception.^{11,12} However, the anatomical basis of this dorsal/ventral segregation has never been satisfactory, since the overall visual circuit diagram resembles a network as much as two linear pathways, with early areas V1, V2 and V3 belonging to neither in particular.^{9,13} A ‘third’ pathway, leading to the temporo-parietal junction,

and a ‘third’ function, that of attentional control, could be added¹⁴ – but neither has much dented the popular dogma of a functional dichotomy.

Figure 3 details some of the cross-talk inherent in this circuitry. The ventral system is fed largely by V4, and is thus an extension of V2 thin- and interstripes. But there is also a contribution from thick-stripes via V3. The net effect

is that M and P signals are about equally weighted (with the relative K contribution unknown). The dorsal system receives strong input from V5. In consequence it is generally portrayed as disproportionately driven by M input, with theoretical relevance to the magno-cellular hypothesis for the basis of dyslexia.^{15,16} However there are many additional inputs to superior and inferior parietal areas, mediated

by prestriate areas such as V3A and V6, that in turn are fed by interstripes as well as thick stripes. Hence, in terms of circuitry, the dorsal stream is better characterised by the relatively minor contribution it receives from blob/thin stripe relays. Yet it is by no means totally colour-blind. V5, for instance, can process chromatic motion signals, a direct K input from the LGN being one likely source.^{17,18} If the M-channel/motion pathway is not such a purely magnocellular affair, does this signify any dilution of its functional role? Arguably not, if the job description is to detect when a coloured pattern (eg camouflage) moves, without necessarily identifying the component colours.

Subcortical sidelines?

The 'second visual system' is traditionally the pathway from retina to extrastriate cortex via colliculus and pulvinar. It is frequently invoked to explain residual vision in cases of V1 loss (engagingly termed 'blindsight' – where the subject correctly guesses the location of a stimulus in the blind field, despite denying any conscious experience of seeing it). In fact, as V1 is also by-passed by K-channel broadcasts from the LGN, to area V5 and elsewhere, 'blindsight' unmasks the direct visual capacities of the total 'bypass circuitry'.¹⁹ Even so, blindsight phenomenology fails to provide a full functional profile of the second visual system because this system is not merely an alternative route for retinal signals to access the cortex. Its normal function

depends on the interplay of ascending retinal and descending cortical pathways – eg in bottom-up and top-down modes of spatial attention being jointly exercised through colliculo-pulvinar circuits.²⁰ In other words, far from being an unconscious pipeline, the second visual system seems an important subsidiary of conscious awareness.

This much condensed review reveals some of the complexity of visual circuitry – and it is only the beginning. Brain anatomy is not a topic that has simplified as it has matured over the course of the last century, so we can only expect to look forward to more of the same.

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