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The M, P and K pathways of the Primate Visual System revisited

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Overview and Introduction

OVERVIEW In this chapter I plan to update the state of our knowledge about the major parts of the early primate visual system: the retinal ganglion cells (RGCs), the lateral geniculate nucleus (LGN), and the early parts of the visual cortex. I shall generally refrain from repeating what appeared in the previous edition (Kaplan, 2003) and in a recent review (Kaplan, 2008), where the interested reader can find additional details. Following this snapshot of our expanding database on this subject, I shall present some recent applications of this knowledge to basic and clinical vision research. Finally, I shall outline a critique of the prevailing view as it is commonly presented, and suggest possible alternatives.

INTRODUCTION: THE BIRTH OF THE M, P, K HYPOTHESIS The outside world is represented on our retina only by the spatio-temporal distribution of light. Our brain transforms this physical distribution into a rich dynamical perceptual kaleidoscope, populated by visible objects. These objects are each characterized by several properties: color, brightness, location, size, motion, texture and so on. These exist in our minds only, as Galileo (1623) has put it: "*I think that tastes, odors, colors, and so on are no more than mere names so far as the object in which we locate them are concerned, and that they reside in consciousness. Hence if the living creature were removed, all these qualities would be wiped away and annihilated*". This distinction between the external *Primary qualities* and the inner *Secondary qualities* was made explicit by John Locke in his influential *Essay Concerning Human Understanding* (1690). Since neuroanatomy, neurophysiology and neurochemistry report cells of various size, morphology, connectivity, response type and chemistry, and in some (but not all) cases cells of similar properties congregate together in layers, columns or stripes, it is tempting to yield to the seductive machine metaphor, which assigns a distinct perceptual function (representing or analyzing a secondary quality) to each structure or cell population. We use the physiological properties of the neurons in these structures to guess the possible role that they might play in the analysis of visual information. This approach gave rise to the concept of functional architecture (Hubel and Wiesel, 1962, 1977), and this is how visual neuroscience has arrived as the *Visual Streams Hypothesis*, which states that in the early visual system of primates the visual input is handled by three main streams: the M (magnocellular), P (parvocellular) and K (koniocellular), each with its distinct cluster of properties, and each occupying a distinct niche of the multi-dimensional parameter space that makes up our visual world. Recent advances in neuroanatomy, functional imaging and electrophysiological recordings from populations of neurons are now providing a much more complete picture of the neuronal machinery that supports vision, and bring us closer to a more realistic evaluation of this view.

An updated summary of the *Three Streams* view

Anatomy

Morphological cell types The input layer of the retina consists of only two types of photoreceptors: rods and cones (of three different wavelength selectivities). The output layer, however, includes (at the latest count) at least 20 types of retinal ganglion cells, distinguished by their size, shape, connectivity or neurochemistry. Figure 30.1 shows some of the major types of retinal ganglion cells that project to the lateral geniculate nucleus (LGN) in the macaque monkey (Crook et al., 2008a). Taken together, these 20 types account for ~90% of the fibers in the optic nerve– it is not yet established which unknown types make up the rest. The major (most numerous) types are: midget, parasol, bistratified and large monostratified, which together make up ~60% of the population. A significant recent distinction is between parasol cells and smooth cells, which project to the LGN and to the superior colliculus, and are distinguished by the smooth appearance of their dendrites (see Figure 30.1, from Crook et al., 2008a). Their cell bodies are smaller than those of the parasol RGCs, but their dendritic fields are larger, and they tile the retina in a mosaic that is less dense than that of the parasols. Their physiological properties suggest strongly that in the LGN they terminate in the magnocellular layers. A few RGCs contain the pigment melanopsin, which renders them light sensitive, and allows them to report the ambient light level to the super-chiasmatic nucleus, which controls the circadian rhythm (Dacey et al., 2005). Most

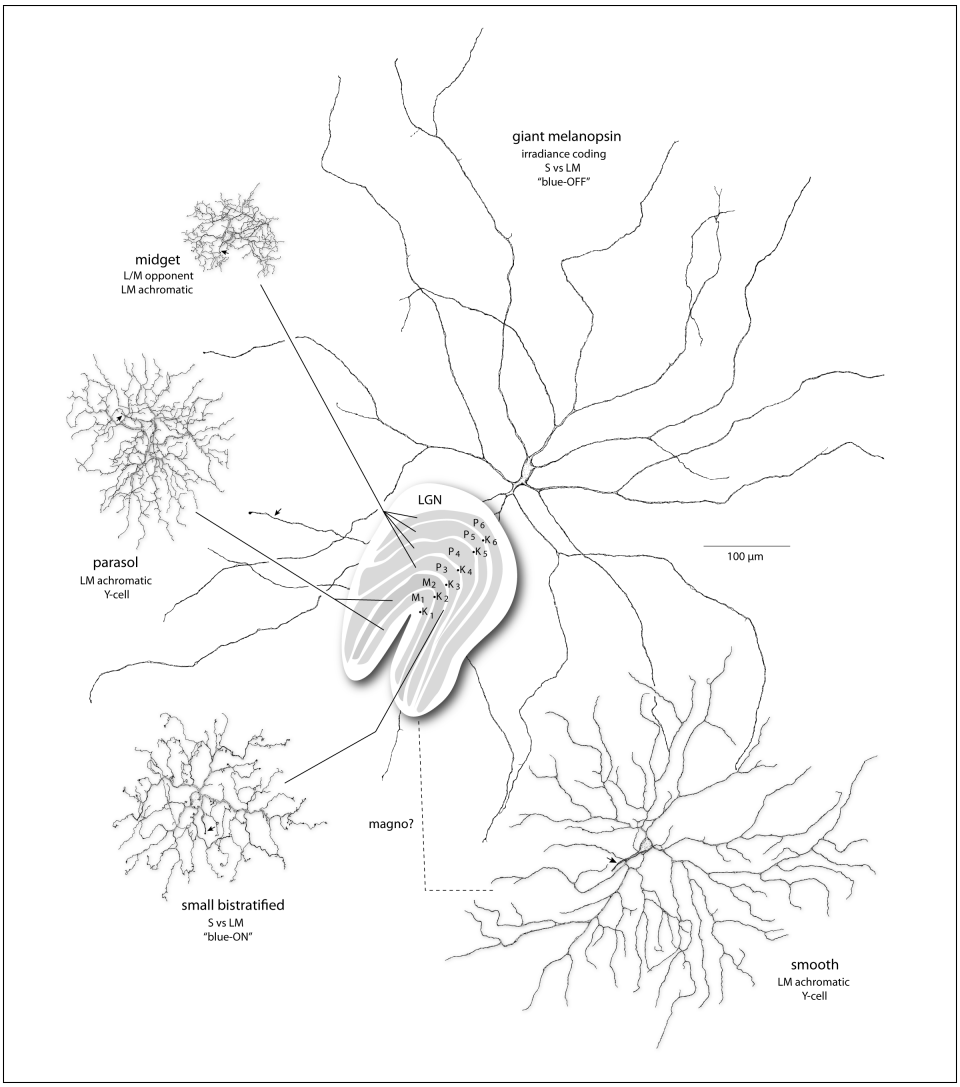

FIGURE 30.1. *Retinal ganglion cells that project to the macaque LGN*. Midget and several other types of RGCs project to the top 4 (parvocellular) layers, while parasol and smooth cells project to the bottom two (magnocellular) layers. Small bistratified, melanopsin-containing and other types of RGCs project mostly to the intercalated layers between the major LGN layers, and together make up the koniocellular population (with permission from Crook et al., 2008a).

RGC types have ON and OFF varieties, although the small bistratified cells produce only ON responses to blue and OFF responses to yellow (Dacey and Lee, 1994; Field et al., 2007). Several types of RGCs project to the superior colliculus, and are involved in the control of eye movements.

Together with this new information about the morphology of individual RGCs, we now have accurate information about the way that the mosaics of several types of RGCs sample visual space (Dacey, 1993; Field et al., 2007). This information comes from both morphological studies and from the more recent progress in recording from complete populations of monkey RGCs with

multi-electrode arrays (for example, Shlens et al., 2006; Pillow and Latham, 2008; Gauthier et al., 2009a,b). Such information is crucial if one is to ascribe a particular visual capability to a cell type. The spatial resolution of a single cell is important, but without knowing the sampling density it is impossible to say what the population could do (Kaplan, 2003). A similar argument holds for the temporal domain.

LGN It has been known for some time that, anatomically, the RGCs that project to the parvocellular layers of the LGN are a heterogeneous population (Watanabe and Rodieck, 1989; Rodieck and Watanabe, 1993). The recent results of (Dacey et al., 2003, 2009) provide a fuller account of this diversity, and approach an almost complete description of the relative representation of the various types in the population, as well as quantitative details of their morphology and connectivity pattern within the retina. However, aside from the melanopsin containing cells, which are involved primarily in circadian rhythm rather than in image analysis, it is unclear at this point what role the various new groups of cells might play in the operation of the visual machinery. Whether the smooth and upsilon RGCs target specific sub-populations of LGN neurons is still an open question.

A persistent mystery is the issue of LGN lamination: why are there 4 parvocellular layers? The laminar segregation might make it easier for the massive descending feedback pathway (Ichida and Casagrande, 2002; Briggs and Usrey, 2009) from V1 to find its LGN targets, but this is only a speculation at this point.

Visual cortex Experiments in which the primary visual cortex (V1) was silenced with muscimol while recordings were made from various layers of V1 have provided new details about the cortical destination of cells from the various LGN layers (Chatterjee and Callaway, 2003). It is now accepted that cells from the parvocellular layers terminate in layer 4Cβ of V1, while those originating in the magnocellular layers terminate in 4Cα. Cells from the koniocellular LGN population project to the upper layers of V1, mostly to the cytochrome (CO) blobs (summarized in Callaway, 2005). Figure 30.2 shows the pattern of the major LGN projections into V1.

Tracer injections into area MT revealed a population of LGN neurons that project directly to MT, bypassing V1. Because many (but not all) of them stained positive for CaMK2, and many were in the intercalated layers, they are considered to be koniocellular neurons, although some were found within the parvocellular or magnocellular layers (Sincich et al., 2004). They thus join other (small) populations of LGN cells that project directly to V2 (Bullier and Kennedy, 1983) or V4 (Yukie and Iwai, 1981). These projections are thought to support 'blind-sight', the residual visual function that persists after damage to V1 (Rodman et al., 2001; Vakalopoulos, 2005).

The anatomical segregation of the M, P and K LGN projections to V1 is maintained to some extent at the level of the extra-striate cortex, V2, where the various stripes that are rich or poor in cytochrome oxidase (CO) receive projections from V1 cells that cluster together to form the CO blobs or interblob regions (Wong-Riley, 1979). This anatomical segregation in the cortex is at the root of the suggestion (Ungerleider and Mishkin, 1982) that the visual system performs its tasks with two main streams, a dorsal (M dominated) and a ventral (P dominated, with some K input); for a recent review, see Nassi and Callaway (2009). This view enjoys wide acceptance, despite anatomical, physiological and psychophysical challenges. We shall return to this topic later.

The physiological properties of the M, P and K cell types

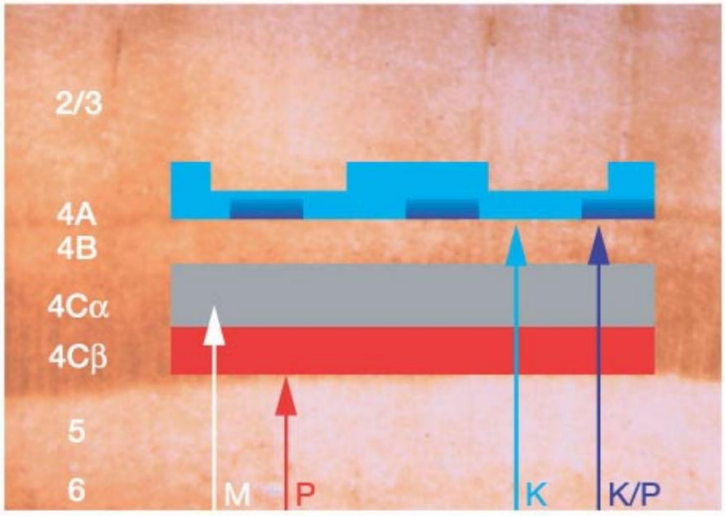

FIGURE 30.2. *The projections of LGN cells to the macaque primary visual cortex.* The cortex was silenced with muscimol, and recordings were obtained from the terminals of LGN fibers. Afferents recorded in layer 4Cβ of V1 had red–green color opponency and arise from LGN Parvocellular cells. Afferents recorded in layer 4Cα had no chromatic opponency, and arise from LGN Magnocellular cells. Afferents recorded in more superficial layers of V1 had blue–yellow color opponency. Blue–OFF afferents were encountered only in layer 4A and might arise from blue–OFF midget ganglion cells via LGN P cells, but they might have some other origin. Blue–ON afferents were encountered on layers 3 and 4A and therefore arise (at least in part) from αCAM kinase/calbindin- expressing LGN Koniocellular cells (with permission from Chatterjee and Callaway, 2003).

Chromatic opponency It was known for a long time that, physiologically, RGCs were of two major types, ON and OFF (Hartline, 1940). A finer subdivision was introduced when the temporal and chromatic properties of the RGCs were investigated, and the distinction between tonic (sustained) and phasic (transient) cells was recognized in the primate retina (Gouras, 1968). Gouras also observed that the tonic cells were chromatically opponent, while the phasic cells were not. These observations suggested that the color opponent cells that Wiesel and Hubel (1966) recorded in the parvocellular layers of the macaque LGN were driven by the tonic, color-opponent RGCs, while the non-opponent cells recorded in the magnocellular layers were driven by the phasic, non-opponent cells. This suggestion was later supported by anatomical methods (Bunt et al., 1975; Leventhal et al., 1981). However, the view of the M RGCs as color-blind was recently challenged by LEE AND SUN (2009), who reported evidence of chromatically antagonistic input to these cells.

The cone input to the receptive field surround: random or selective? The cellular mechanisms that generate chromatic opponency in the midget (P) RGCs have been debated for some time, with evidence for (Wiesel and Hubel, 1966; Reid and Shapley, 1992) and against (Paulus and Kröger-Paulus, 1983; Boycott et al., 1987; Lennie et al., 1991; Calkins and Sterling, 1996) the notion of selective innervation of the receptive field surround mechanism by only one of the cone

types. Recently, Crook et al. (2011) have reported that the origin of the red/green chromatic opponency is presynaptic to the midget cell, does not depend on GABA or glycine inhibition, and disappears (with the midget cell's receptive field surround) if the feedback from horizontal cells to cones is blocked. Recall that the horizontal cells, which provide (at least some of) the antagonistic surround to the RGCs, sum the cones within their territorial grasp promiscuously (Boycott et al., 1987). The results of Crook et al. (2011) are consistent with those of Buzás et al. (2006) and Field et al. (2010). However, a recent analysis of physiological recordings from P RGCs and parvocellular LGN cells (Lee et al., 2012), finds considerable cone selectivity in many P and parvocellular receptive fields. The discrepancy could be due to the effects of retinal eccentricity: most of the physiological evidence against a cone-selective surround (Field et al., 2010; Crook et al., 2011) comes from (*in vitro*) recordings of rather peripheral cells, typically beyond 10° from the fovea. The mosaic of L and M cones appears random, which implies a patchy arrangement of several L or M cones being grouped together (Roorda and Williams, 1999). Since receptive fields become smaller near the fovea, one would expect to find there more purely selective surrounds simply by chance. Lee et al. (2012) also point out that the receptive field of (at least some) P cells might be more complex than previously thought, in agreement with previous suggestions (Kaplan and Benardete, 2001).

Linearity of spatial summation When the linearity of spatial summation across the receptive fields of monkey RGCs was investigated, most of the cells showed largely linear spatial summation: they were thus 'X-like', as defined originally by Enroth-Cugell and Robson (1966) and refined by Hochstein and Shapley (1976) (but see Benardete and Kaplan, 1997). Approximately 25% of the M cells showed the frequency-doubled response signature of 'Y-like' cells (Kaplan and Shapley, 1982). The smooth RGC reported by Crook et al. (2008a), and the upsilon cell reported by Petrusca et al. (2007) have 'Y-like' physiological properties: high firing rate, high sensitivity to luminance contrast, and transient responses, which makes them responsive to high temporal frequencies, and suitable for conveying motion information. This topic, however, is still controversial: Crook et al. (2008b) reported that *all* the parasol cells, as well as the smooth cells mentioned above (Crook et al., 2008a) had 'Y-like' physiological characteristics in their *in vitro* experiments, in agreement with the *in vivo* results of Dhruv et al. (2009). Another distinctive dynamical characteristic of M cells that P cells lack is the change in their response phase with increasing contrast (Benardete et al., 1992; Movshon et al., 2005).

'Extraclassical' suppression Alitto and Usrey (2008) reported that LGN magnocellular cells in macaques were suppressed by stimuli beyond their classical receptive field, and that the suppression was greater than what they found in parvocellular neurons, in agreement with earlier results of Solomon et al. (2002) in marmosets. The suppression acted too quickly to be due to cortical feedback, and because it was similar to what was found in the retina, was thought to originate there. An earlier anatomical study showed that the magnocellular layers had many more GABAergic cells than the parvocellular layers (Hámori et al., 1983), and it is possible that these cells mediate the extraclassical suppression effects.

Luminance contrast gain A prominent distinction between M and P cells is their luminance contrast gain (the slope of the response *vs* contrast function), which is high in M at low contrasts but low in P RGCs throughout their dynamic range (Kaplan and Shapley, 1986; Movshon et al., 2005; Alitto and Usrey, 2008). This greater gain is due primarily to the larger size of the M receptive field (Croner and Kaplan, 1995), and therefore the upsilon and smooth cells also have similarly high contrast gain (Petrusca et al., 2007; Crook et al., 2008a).

Interactions among cells Recordings from large populations of RGCs from the isolated macaque retina *in vitro*, carried out with multi-electrode arrays, have provided new information about the retinal output, beyond the properties of individual cells. In agreement with the previous work of Mastronarde (1983) on the cat retina, Greschner et al. (2011) found that cells of a given type tended to have correlated firing. The correlations declined with the retinal distance between the cells. Most of the correlations could be attributed to common noise in the photoreceptors that are shared by the correlated RGCs. The correlations were relatively modest, but it was shown by Pillow et al. (2008) that such modest correlations increase significantly the amount of information that the population transmits about the visual scene.

Koniocellular cells Cells in the K stream are a diverse population in terms of their chromatic selectivity, luminance contrast gain, spatial and temporal resolutions, as well as their projection targets from the LGN (Hendry and Reid, 2000; Xu et al., 2001; White et al., 2001; Sceniak et al., 2006). Even the definition of what constitutes a koniocellular neuron is not straight forward, as demonstrated by the results of Sincich et al. (2004), which showed that neither the specific staining nor the layer location are definitive in fingering a cell as a koniocellular neuron.

The use of stimuli that favor either the M or P cell type

The apparent clustering of functional properties, especially in the LGN, where the M, P and K populations are largely segregated in layers, has inspired attempts to create stimuli that would excite one population but not the others, in order to assess the functioning of the targeted population. This was done using psychophysical methods, Visual Evoked Potentials (VEP) or fMRI, and the research aimed at either basic vision science issues or clinical questions. These studies typically took the M population to be chromatically non-opponent, highly sensitive to low spatial frequencies and low luminance contrast, to respond transiently and be involved in the analysis of motion and luminance. The P population was assumed to respond tonically and less well to luminance contrast, and to convey chromatic and form information.

A word of caution We should point out that one cannot easily deduce from single cell data how to construct such stream-favoring stimuli. J. Pokorny and V. Smith, who were at the forefront of such efforts (Pokorny and Smith, 1997; Smith and Pokorny, 2003; Pokorny, 2011), recognized the difficulty: "*Thus although the psychophysical data are consistent with activation of a given inferred retinal pathway, there is considerable reorganization of the retinal outputs in determining the psychophysical data.*" (Leonova et al., 2003). Other complications in the interpretation of studies that use such biasing stimuli include: 1) M cells do not really saturate at moderate or high contrasts. In fact, their response *vs* contrast function above 30% has a contrast gain that is similar to that of P cells (Figure 30.3), so there is no reason to believe that they stop responding to contrast modulation at high contrasts; 2) P cells outnumber M cells by a factor of ~8, and could compensate for their lower contrast gain by converging on cortical neurons; 3) Other cells (smooth monostratified, some K cells) have response properties that are similar to either the M or P cell types. Thus, at this point, the deduction of either a type-specific loss or a function for one of the cell types through the use of such stimuli should be viewed as mere speculation.

Basic studies Much of the basic research in this area focused on the role of the M or P streams in directing attention (for example, Cheng et al., 2004; Brown, 2009; Ries and Hopfinger, 2011; Tapia and Breitmeyer, 2011; Denison and Silver, 2012), on assessing their influence on reaction time (Burr and Corsale, 2001; Murray and Plainis, 2003), or on the relative contributions of the

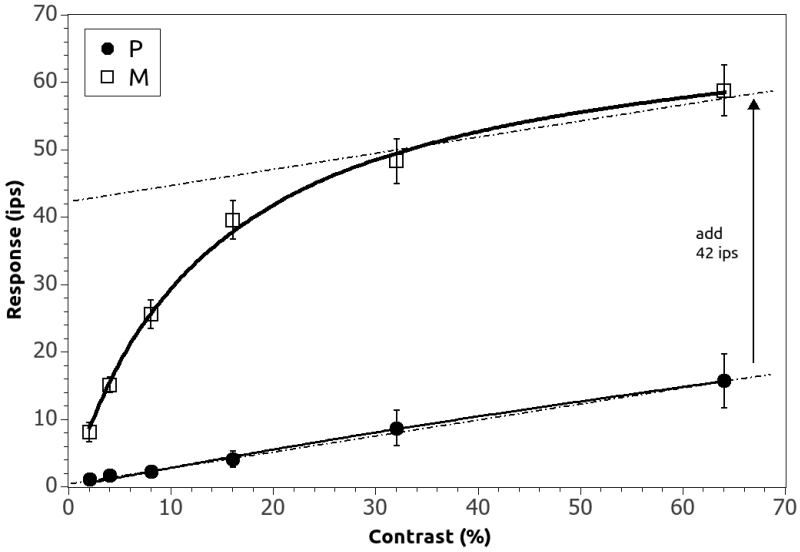

FIGURE 30.3. *The contrast gain of M cells is higher than that of P cells for low luminance contrast stimuli*. Shown are average responses of 28 P and 8 M retinal ganglion cells from one rhesus monkey as a function of luminance contrast. The stimulus was a drifting black-white sinewave grating that modulated the screen luminance at 4 Hz, and had the optimal spatial frequency for each cell. The smooth solid curves are the Michaelis–Menten function, $R = R_{max} \times \frac{C}{C+C_{50}}$, where R is the response and C is the contrast; error bars: $\pm$ 1 SEM. C_{50}, the half-saturation contrast of the M (magnocellular projecting) ganglion cells was 14%. Note the steeper slope (higher gain) of the M cells at low contrasts. The dashed regression line that fits the P cells' response was shifted upwards by 42 ips, to emphasize the fact that M cells *continue to increase their response with increasing contrast*, even at moderate to high contrast stimuli. In fact, their contrast gain at the higher contrasts is similar to that of the P population (modified from Kaplan and Shapley, 1986).

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two streams to VEP or fMRI signals (Grose-Fifer et al., 1991; Victor et al., 1992; Foxe et al., 2008; Lalor and Foxe, 2009).

Clinical studies The magnocellular and parvocellular populations, which are typically viewed as more homogeneous than the koniocellular cell type, have been implicated in several major neurological or psychiatric pathologies, such as autism (Sutherland and Crewther, 2010), Alzheimer disease (Price et al., 1991; Curcio and Drucker, 1993; Davies et al., 1995), Parkinson disease (Silva et al., 2005), retinitis pigmentosa (Alexander et al., 2001, 2004), schizophrenia (Schechter et al., 2003; Bedwell et al., 2003, 2004; Martinez et al., 2008, 2011) dyslexia (Stein and Walsh, 1997; Stein, 2001; Chase et al., 2003; Chouake et al., 2012), amblyopia (Demirci et al., 2002; Zele et al., 2010), optic neuritis (Grigsby et al., 1991; Al-Hashmi et al., 2011) and aging (Elliott and Werner, 2010). A recent review of how the current knowledge of the properties of the M, P and K cell types is being used in ophthalmology, neurology and psychiatry can be found in Yoonessi and Yoonessi (2011). These applications are not without controversy, which often

mirror the still evolving exploration of the physiological properties of these cell populations in the retina and LGN (see, for example, Maddess, 2011 and Swanson et al., 2011, or the criticism of the claims that M cells are involved in dyslexia (Skottun and Parke, 1999; Skottun, 2005) or schizophrenia (Skottun and Skoyles, 2008, 2011).

The parallel-streams hypothesis: a reassessment

In a recent review (Kaplan, 2008) I summarized the widely held view that maintains that three major cell types (M, P and K) that are largely segregated anatomically in the LGN, are each dedicated to a distinct visual function. I presented there several criteria that such hypothetical visual streams must meet: homogeneity, independence (both anatomical and perceptual), and compatibility of each stream's properties with its presumed function. I argued there that various lines of evidence (anatomical, physiological and psychophysical) show that the three streams do not meet these criteria. Rather than discuss it here in detail, I shall re-sketch it briefly, address the additional new information that bears on this hypothesis, and suggest alternatives.

The simplistic three-streams hypothesis In its simplest form, the three streams hypothesis sees the visual system as a machine, in which each cell type extracts from the visual environment the kind of information it is best suited to analyze: size, color, motion and so on. Furthermore, cells of a feather flock together, and create anatomical compartments (layers, blobs, stripes, dorsal or ventral streams) that contain cells of distinct types, and each one (or a grouping) of these brain structures thus plays a distinct role in vision. According to this view, the streams are homogeneous, independent, and have appropriate and non-overlapping visual functions. This is an example of the view that information is processed in the brain *in parallel* by dedicated groups (types) of neurons (Ungerleider and Mishkin, 1982; Stone, 1983; Livingstone and Hubel, 1988).

STRUCTURE AND FUNCTION: THE CONCEPT OF A CELL TYPE The view sketched above represents an example of one of the neuroscience's central goals: linking structure with function, and it depends critically on the concept of a *cell type* (Rodieck and Brening, 1983). Clearly, the RGCs that form the optic nerve are not all alike, and this diversity of shape and response patterns suggests that if neurons were characterized along many dimensions (such as size, shape, connectivity, neurochemistry, response properties and stimulus selectivity), an objective classifier would place each cell in a distinct, functionally homogeneous cluster. A partial categorization of this sort has been attempted for the early parts of the primate visual system (for example, Table 30-1 in Kaplan, 2003). Neuroscientists then attempt to deduce the function of each cell type from the collection of properties of each cluster. So far, such a comprehensive analysis has not been carried out exhaustively in any part of the brain, although there are promising efforts in that direction (for example, Bota and Swanson, 2007; Farrow and Masland, 2011; Masland, 2011). This task is challenging both technically and conceptually, but it is essential if we are to reach a deeper understanding of the design principles of the visual system, and indeed– the brain. For a recent review of the challenge of linking structure and function in the brain, see Lichtman and Denk (2011).

Challenges for the separate streams hypothesis As new techniques are brought to bear on our subject, new cell types, response patterns, connectivity schemes and stimulus selectivities emerge. We have already mentioned the several new types of RGCs that have been described recently (Dacey et al., 2003; Petrusca et al., 2007; Crook et al., 2008a), and the new projection pathway from the koniocellular cells in the LGN to MT (Sincich et al., 2004). In addition, a

disynaptic pathway was described between the parvocellular layers of the LGN and the "motion area" MT (Nassi et al., 2006). These, and many previous results (for example, Ferrera et al., 1992; Nealey and Maunsell, 1994; Leventhal et al., 1995; Vidyasagar et al., 2002; Sincich and Horton, 2005; Lee and Sun, 2009; Economides et al., 2011) challenge the notion of segregation and independence of the streams. Likewise, additional evidence (Dobkins and Albright, 1993, 1995; Gegenfurtner and Hawken, 1996; Cropper and Wuerger, 2005; Ruppertsberg et al., 2007; Martinovic et al., 2009; Wuerger et al., 2011; Poom, 2011) shows closer integration of color and motion perception than one might expect based on the parallel stream paradigm, where motion and color analysis are often cited as prime examples of the exclusive domains of the M and P streams, respectively. It appears that motion might be perceived by several mechanisms, some color-selective and others color blind (Gorea and Papathomas, 1989; Papathomas et al., 1991).

We should also consider the possibility that some of the cell types, which the neuroscientist assumes must fulfill an important function simply because they exist, might be like the *Spandrels of San Marco*, and serve no biological function (Gould and Lewontin, 1979). Finally, it is possible that the concept of *functional architecture,* which is central to so much of current brain research (Hubel and Wiesel, 1962; Frackowiak, 1998; **?**), has lulled us into automatic acceptance of the notion that if we have a word for color, motion, soul or consciousness, there must be some identifiable brain part that is creating it. Rather than look for brain structures with specific, distinct functions, perhaps we should be looking for functional network motifs (Sporns and Kötter, 2004).

A refined multi-stream hypothesis The current three-stream view might be replaced by a refined *multi-streams* hypothesis, which replaces the M, P and K streams with a larger number of streams (anatomical/functional groups), preserving the notion of parallel processing by function-specific cell types. For example, the M stream might include the well-known parasol RGCs, and the newly discovered smooth cells (Crook et al., 2008a), which might serve a different function from the parasols. The P streams should be split into the midget RGCs and some of the other groups that project to the parvocellular layers (Rodieck and Watanabe, 1988; Dacey et al., 2003). As more data are gathered about the various RGCs that terminate on koniocellular neurons, that stream will surely be replaced by several more homogeneous sub-streams. Some of that has begun already (for example, Sincich et al., 2004). This multi-stream view is close to the one advocated by Masland and Martin (2007) and Martin et al. (2011). Since a complete structural-functional taxonomy of the primate RGCs and LGN cells is still missing, it is impossible to predict how many streams will be needed to ensure that each cell type will be relatively homogeneous, but the number will surely be >10.

A paradigm shift? Several authors have recently voiced criticism of the prevailing 3-stream paradigm. They include Sincich and Horton (2005); Kaplan (2008); Schenk and McIntosh (2010); de Haan and Cowey (2011) among others. Even one of the corner stones of neuroscience, the belief in a tight link between structure and function, has been called into question (Wallisch and Movshon, 2008) in view of some recent neurophysiological and behavioral data (Chowdhury and DeAngelis, 2008). The criticism is typically based on the well-documented anatomical and functional cross talk among the presumed independent streams, on the heterogeneity of the cell types that are grouped together in streams, on the fact that some of the evidence supporting the allocation and segregation of function is based on unreliable lesion experiments or observations, and on the conceptual difficulties of assigning specific distinct functions to elements within an interconnected, non-linear dynamical network.

A network hypothesis An alternative view, in which we relax the tight link between structure and function that we inherited from the machine metaphor, is that each cell type contributes something to the analysis of the visual scene, and all (or at least many) of them participate in this analysis. The different response and selectivity properties of the various cells thus provide not distinct and separate channels of information about stimulus dimensions, but instead are providing a distribution of tuning functions (selectivities) along each dimension of the stimulus. This view is supported by the observation made by almost everyone who has studied the selectivity of cortical neurons: with rare exceptions, most neurons are tuned (to various degrees) along many stimulus dimensions. The details of the computation that leads from this population activity to perception are being investigated and debated, and are probably statistical in nature, perhaps along the lines explored by Pouget et al. (2000, 2003) and Jazayeri and Movshon (2006). Perception is thus accomplished not by some discrete entity that weighs the contribution of each stream to reach a perceptual decision, but is rather the psychological corollary or an emergent property of the coordinated activity of the entire network. Given the fact that the brain is a *highly interconnected, non-linear dynamical system*, the assignment of distinct functions to cell types, regardless of how they are defined, might be a futile exercise.

CONCLUSIONS The three major cell types that send axons from the retina to the LGN are widely believed to subserve distinct visual functions: M cells relay motion and luminance information, P cells report about color and form, while some of the more diverse K cells produce blue-ON responses. We saw that this three-way parcellation of the RGC population is far too simplistic, and should be replaced either by a refined, multi-stream paradigm, or perhaps by a network-based view, in which most cell types contribute to the perception of most visual attributes. Just as the 92 elements, each with its own unique properties, interact to make up our multi-faceted world, so could 20 or so cell types interact to weave the dynamic tapestry of our visual world.

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