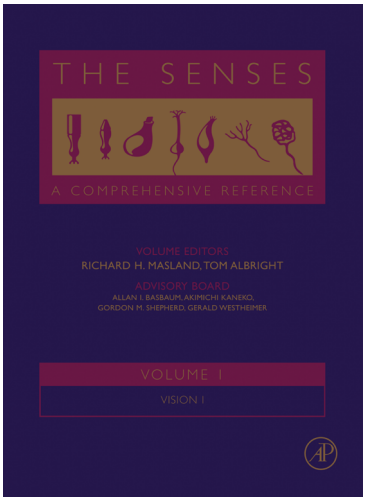

E Kaplan, The P, M and K Streams of the Primate Visual System: What Do They Do for Vision?. In: Allan I. Basbaum, Akimichi Kaneko, Gordon M. Shepherd and Gerald Westheimer, editors The Senses: A Comprehensive Reference, Vol 1, Vision I, Richard Masland and Thomas D. Albright. San Diego: Academic Press; 2008. p. 369-382

1.16 The P, M and K Streams of the Primate Visual System: What Do They Do for Vision?

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Glossary

parvocellular or P Designates tho midget retinal ganglion cells that project to the upper four layers of the primate lateral geniculate nucleus (LGN).

magnocellular or M Designates the large retinal ganglion cells that project to the bottom two layers of the primate LGN.

Koniocellular or K* Designates those retinal ganglion cells that project to the interlaminar spaces in the primate LGN.

The Senses: A Comprehensive Reference, vol. 1, pp. 369-381

1.16.1 Introduction

1.16.1.1 Parallel Processing: Visual Attributes, Labeled Lines, and Neuronal Streams

The notion that the visual world is analyzed in parallel by several neuronal types goes back to Hartline's surprising discovery of ON and OFF retinal ganglion cells (RGCs) (Hartline, H. K., 1940). The discovery of the X/Y dichotomy among cat RGCs (Enroth-Cugell, C. and Robson, J. G., 1966) provided another clear example of this parallelism, and analysis of the conduction velocity of optic nerve fibers reinforced the idea further (see Stone, J., 1983). The intense interest in the magno–parvo–koniocellular groups later on (see Kaplan, E. and Shapley, R. M., 1986; Kaplan, E. *et al.*, 1990; Lee, B. B., 1996; Kaplan, E., 2003) and the anatomical studies that established the segregation of these neuronal types from the retina through the lateral geniculate nucleus (LGN) to the visual cortex (Livingstone, M. S. and Hubel, D. H., 1984a; 1984b; Shipp, S. and Zeki, S., 1985; Livingstone, M. and Hubel, D., 1988) have all added further weight to the view that the world is being analyzed in parallel by several streams, and this hypothesis has become widespread in the visual neuroscience literature (e.g., Ungerleider, L. G. and Mishkin, M., 1982; Livingstone, M. and Hubel, D., 1988; Zeki, S., 1993; Callaway, E. M., 2005).

Visual attributes. In the physical world we find only space and time. Vision scientists, however, commonly organize the various combinations of spatiotemporal properties of the visual world into concepts such as color, size, motion, orientation, and texture. It is very tempting then to imagine that each aspect of the visual world is dealt with by a specialized neuronal population that is dedicated to the analysis of one (or a few) of these aspects of the visual environment: color and other surface properties could be scrutinized by the tonic, high-resolution parvocellular stream, motion could be detected and analyzed by the phasic, coarse magnocellular stream, and so forth. We must remember, however, that these organizing concepts are a figment of the vision scientist's imagination, and that – at this point – their existence or representation in the brain in any specific form is merely a hypothesis. We shall return to this issue later.

1.16.1.2 Classification of Cells into Types

An important first step in any scientific endeavor is to classify the objects under scrutiny, and then try to deduce from the properties of the different classes something about the role that they play in the system under study. The classification of neurons into various groups takes into account various aspects: morphology, connectivity, neurochemistry, and physiological properties, such as the spatial and dynamical properties of their receptive field (for visual neurons). Sometimes neurons are divided into classes along one dimension only, such as transient–sustained, simple–complex, or ON–OFF, and some properties tend to cluster together. For example, transient cells are large, ON cells synapse in a particular sublamina of the inner plexiform layer. Such clustering of properties often provides seductive hints about the possible role that a given population might play in the overall function of the system. For more information regarding classification criteria, and more references concerning cell typing and classification, see Rodieck R. W. and Brening R. K. (1983) and Troy J. and Shou J. (2002).

1.16.2 Properties of the M, P, and K Streams

Comprehensive comparisons of the properties of the three main streams (magnocellular, parvocellular, and koniocellular) can be found in Kaplan E. *et al.* (1990) and Kaplan E. (2003). The presentation here will therefore be brief, and we shall discuss the retina and LGN together. Our current knowledge of the various properties is summarized in Table 1.

1.16.2.1 Anatomy

1.16.2.1.1 Numbers, density, and resolution

Numbers. By far, the majority of the RGCs in the primate retina (~80%) are midget (Polyak, S. L., 1941) cells, which project to the parvocellular (upper four) layers of the LGN of primates (Goodchild, A. *et al.*, 1996). Because of their projection target, they are referred to as P cells. The much larger parasol (Polyak, S. L., 1941) cells project to the magnocellular (bottom two) layers of the LGN, and are thus called M cells. They account for ~10% of the RGCs (Leventhal, A. G. *et al.*, 1981; Perry, V. H. and Cowey, A., 1984). A population of small (but not midget) bistratified blue ON ganglion cells projects to the koniocellular layers, the thin interlaminar zones between the major layers of the LGN (Dacey, D. M. and Lee, B. B., 1994). In the LGN, the

Table 1 Properties of the P, M, and K neuronal streams

	Property	*P*	*M*	*K*
1	Clear spectral opponency	Yes (red-green)	No	Some (blue-yellow)
2	Response to light steps	Tonic	Phasic (transient)	Phasic; some sluggish
3	Luminance contrast gain	Low	High	Diverse (some high)
4	Receptive field size	Small	Large	Large
5	Spatial resolution of individual neurons	Similar to M	Similar to P	Diverse (some like M)
6	Retinal ganglion cell density (acuity of cell group)	High	Low	?
7	Retinal source	Midget RGCs	Parasol RGCs	Unknown (some blue-ON bistratified RGCs)
8	LGN projection target	Parvocellular	Magnocellular	Koniocellular (intercalated) layers
9	V1 projection target	Layer 4Cβ	Layer 4Cα	Layers 2–3, CO blobs, layer 1
10	Cell body size	Small	Large	Large/varied
11	Conduction velocity of retinal axons	Medium	High	Low/varied
12	Contrast sensitivity at scotopic luminance	Poor	Good	?
13	Linearity of spatial summation	Linear (X-like)	75% Linear, 25% Nonlinear (Y-like)	Linear (X-like)
14	Extraclassical receptive field effects	Weak	Strong	Intermediate (varied)
15	Number of cells (fraction of LGN population)	~1 000 000 (85%)	~70 000 (6%)	~100 000 (9%)

koniocellular cells comprise ~9% of the nucleus' population (Hendry, S. H. C. and Yoshioka, T., 1994; Hendry, S. H. C. and Reid, C. R., 2000). It is likely that other types of ganglion cells also project to the koniocellular layers, but these have not been identified yet.

Density and resolution. Although it was initially thought that the ratio of M and P RGCs varies with retinal eccentricity, more recent data indicated that the ratio remains essentially constant throughout the retina (Perry, V. H. and Cowey, A., 1984; Silveira, L. C. L. and Perry, V., 1991). Since the P cells are much more numerous and close to each other, the resolution with which they sample visual space is higher than that available to the more sparse M or bistratified cells. We note, however, that the greater contrast sensitivity of M cells (Contrast Gain) allows them to detect fine patterns (Blakemore, C. and Vital-Durand, F., 1986; Crook, J. M. *et al.*, 1988), although their sparse coverage of the retina prevents them from providing enough information for the identification of such patterns.

1.16.2.1.2 Size

On average, the receptive field diameters of M cells at all retinal eccentricities are approximately 2.5–3 times as large as those of P cells, which makes their receptive field area roughly 6–8 times larger (Croner, L. J. and Kaplan, E., 1995). This size advantage is responsible in large part for their increased sensitivity to luminance contrast (Kaplan, E. and Shapley, R. M., 1986, Contrast Gain). The link between size and contrast sensitivity (Enroth-Cugell, C. and Shapley, R. M., 1973b) is also seen in K cells. For example, the K cells in the LGN of owl monkeys are approximately as large as the M cells, and their contrast sensitivities are similar as well (Xu, X. *et al.*, 2001).

1.16.2.1.3 Connectivity: inputs and projections

Retina. The midget (P) cells receive their input from midget bipolar cells. Near the fovea, this input is private: each ganglion cell receives input from one bipolar cell, which, in turn, is driven by a single cone. This arrangement is required for maximal spatial resolution, and the resulting improved color-analyzing mechanism could be a beneficial by-product. Farther from the fovea, the dendritic trees become larger, and the midget cells receive input from several cones, reducing their chromatic selectivity. The parasol (M) cells receive input from diffuse bipolars (Boycott, B. B. and Wässle, H., 1991),

which collect input from several different cones, making them more sensitive but less suitable for chromatic analysis. The small bistratified cells receive their input from bipolars that synapse at both the upper and the lower portions of the inner plexiform layer, and their receptive field centers are driven by S (blue sensitive) cones (Dacey, D. M. and Lee, B. B., 1994).

LGN and V1. The main groups of RGCs project to distinct layers or compartments in the LGN and in V1. The four parvocellular layers of the LGN receive their input from the midget RGCs (P cells), but also from other ganglion cell types, including some with very large dendritic trees (Rodieck, R. W. and Watanabe, M., 1993). They project to layer 4Cβ of the primary visual cortex, V1. The two lower layers of the LGN (magnocellular) receive their input from the parasol cells, and project to layer 4Cα of V1. The koniocellular layers receive input from the small bistratified (blue ON) cells, and project directly to the cytochrome oxidase blobs found in layers 2 and 3 of V1 (Hendry, S. H. C. and Yoshioka, T., 1994; Yabuta, N. H. and Callaway, E. M., 1998a; 1998b).

Beyond V1. From V1 the various neuronal streams project to numerous higher brain areas (Felleman, D. J. and van Essen, D. C., 1991; Kaplan, E., 2003). The overall pattern of these projections stimulated the suggestion that they form two main functional streams, one (dorsal) that answers the question 'Where?', and the other (ventral) to explore 'What?' is out there (Ungerleider, L. G. and Mishkin, M., 1982). This theory combines a hierarchical flow of information with the notion of parallel processing of various visual attributes, and is in wide circulation today. As we shall argue below, the broad acceptance of its simplistic form rests on somewhat shaky ground, and is perhaps premature.

1.16.2.2 Physiology

Many of the physiological properties such as contrast gain, receptive field size, center-surround antagonism, and chromatic selectivity are directly related to the morphological properties reviewed above, and appear to be determined by the early circuitry of the outer retina (Dacey, D. *et al.*, 2000). Other properties, such as dynamics, are related to both the connectivity pattern and the biophysical repertoire (including ion channels, neurotransmitters, and receptors) of the neurons.

1.16.2.2.1 Dynamics

The difference between the temporal properties of M cells and those of P cells (Gouras, P., 1968) was the first physiological indication that the primate retina contains more than one homogeneous population of RGCs, something that the anatomists have known for some time. Gouras P. (1968) reported that the discharges of some RGCs were phasic, while others fired tonically. At the time, the projection pattern of these cells to the LGN layers was unknown, and only later it was determined that the phasic cells correspond to the anatomical cell type called parasol cells, which were found to project to the magnocellular layers of the LGN, while the tonic cells correspond to the midget RGCs, which project to the parvocellular layers of the LGN (Leventhal, A. G. *et al.*, 1981). Further study of the dynamical properties and the linearity of their temporal responses has shown that both M and P cells have nonlinear response properties, although these are more pronounced in the M population (Kaplan, E. and Shapley, R. M., 1989; Benardete, E. A. and Kaplan, E., 1997; 1999).

The fact that M cells are much more phasic than P cells has led to the hypothesis that they are specialized for the detection and analysis of motion, while the tonic P cells are thought to be used for the analysis of surface properties.

1.16.2.2.2 Linearity of spatial summation; X–Y

In the cat, Y RGCs are larger and more phasic than X cells (Enroth-Cugell, C. and Robson, J. G., 1966), and it was tempting to seek a homology between the X–Y classes of the cat retina and the P–M types in the primate retina (Dreher, B. *et al.*, 1976; Sherman, S. M. *et al.*, 1976). However, the initial attempts did not use the original classification approach that was used in the cat by Enroth-Cugell and Robson, who called X cells those cells that showed linear spatial summation within their receptive fields. When that same criterion was used, all P and most M cells turned out to be rather like cat X cells, and only a minority of M cells had significant nonlinear spatial summation (Kaplan, E. and Shapley, R., 1982; Levitt, J. B. *et al.*, 2001). We note that such a homology contributes little to any compelling determination of the role that these cell classes play in primate vision. It is reasonable, however, to postulate that the P/midget system is a later evolutionary specialization found in monkeys but not in cats.

1.16.2.2.3 Chromatic properties

P cells. The retinal connectivity pattern of these cells, which, near the fovea, provides each one with a private line from a single cone, endows them with both high spatial resolution and chromatic selectivity. The center region of the receptive field is obviously tuned to the same wavelength that the central cone prefers. Much controversy surrounded the chromatic selectivity of the surround mechanism of P cells' receptive fields. Early reports suggested that the surround of many P cells receives specific input from cones that are tuned to a wavelength different from that to which the center is tuned (Wiesel, T. N. and Hubel, D. H., 1966; De Monasterio, F. M. and Gouras, P., 1975), and the cells typically fall into one of two major groups: r-g and b-y cells (Derrington, A. M. *et al*., 1984). However, anatomical studies have shown that the horizontal cells, widely believed to mediate the surround response, receive promiscuous, nonspecific cone input (Boycott, B. B. *et al*., 1987). Further physiological measurements have demonstrated that for most of the P cells (and their recipient parvocellular LGN targets), the input to the surround is, functionally, rather selective (Reid, R. C. and Shapley, R. M., 1992). It is possible, in principle, that this chromatic selectivity is accomplished through some processing in the inner plexiform layer, but a detailed anatomical study of this possibility has failed to support it (Calkins, D. J. and Sterling, P., 1996). Thus the anatomical substrate for the chromatic selectivity of the surround of near-foveal P cells remains elusive. We note, however, that even a mixed cone input to the surround can still provide robust color vision capabilities (Paulus, W. and Kröger-Paulus, A., 1983; Lennie, P. *et al*., 1991).

M cells. Most of these cells receive combined L and M cone input to both center and surround of their receptive fields, with little contribution from S cones (Wiesel, T. N. and Hubel, D. H., 1966; Lee, B. B. *et al*., 1989). Other studies have found the magnocellular portion of the LGN to be both spatially and chromatically antagonistic (Derrington, A. M. *et al*., 1984). In a few magnocellular cells, the surround receives inhibitory input from L cones (Wiesel, T. N. and Hubel, D. H., 1966). The broad-band, nonselective nature of the responses of M cells motivated the suggestion that they are responsible for the color-blind luminance channel of psychophysics.

K cells. Some of these LGN cells have been shown to receive input from the small bistratified RGCs, which receive their excitatory input from S cones (Dacey, D. M. and Lee, B. B., 1994). They thus provide the cellular substrate for the blue ON channel. The chromatic properties of the other cells that project to the koniocellular layers of the LGN remain to be elucidated.

It appears that the major factor that determines the chromatic properties of the P, M, and K cells is the spatial characteristics of their receptive fields, rather than any specialized, genetically directed selectivity in the connectivity pattern between cones and ganglion cells. Evidence in support of this conclusion comes also from comparative studies (see, e.g., Yamada, E. S. *et al*., 1998; Blessing, E. *et al*., 2004).

1.16.2.2.4 Contrast gain

Contrast gain is the relative change in response for a given change in stimulus contrast. It is related to the size of the light collecting pool of the receptive field (Enroth-Cugell, C. and Shapley, R. M., 1973a; Croner, L. J. and Kaplan, E., 1995; Troy, J. and Shou, T., 2002; Blessing, E. *et al*., 2004), which, incidentally, also determines the light adaptation state of the cell, and thus its dynamics as well (Enroth-Cugell, C. and Shapley, R. M., 1973b). Since at any retinal eccentricity M cells are larger than P cells, their contrast gain to luminance stimuli is typically higher than that of the P cells around them (Kaplan, E. and Shapley, R. M., 1986; Croner, L. J. and Kaplan, E., 1995). This is especially true for low-contrast stimuli. At higher contrasts, the M cells' response increases at a rate that is rather similar to that of P cells (Figure 1).

The similar contrast gain of P and M cells at high contrasts suggests the possibility that in P cells there is only one mechanism that is responsible for the response, while in M cells two mechanisms are at work: one operates at low contrasts, and once that mechanism saturates (at intermediate contrasts), another mechanism, which might be common to both M and P cells, takes over. It is therefore unlikely that the contribution of the magnocellular population disappears at high contrasts (Rudvin, I. *et al*., 2000), because M cells continue to increase their response up to 100% contrast (Figure 1).

K cells tend to be more like M cells in several respects, including their contrast gain (Xu, X. *et al*., 2001). Note, however, that not only size but the number of input synapses and other factors can also influence contrast gain (Croner, L. J. and Kaplan, E., 1995).

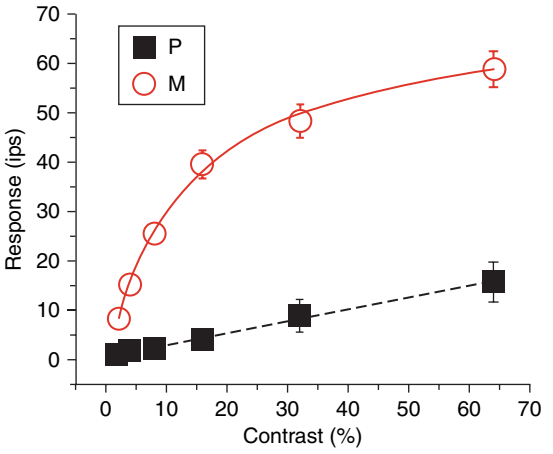

Figure 1 The contrast gain of M cells is higher than that of P cells for luminance stimuli. Shown are average responses of 28 P and 8 M retinal ganglion cells from one rhesus monkey as a function of luminance contrast. The stimulus was a drifting black-white sine wave grating of optimal spatial frequency for each cell, which modulated each cathode ray tube (CRT) pixel at 4 Hz. The smooth curves are the Michaelis–Menten equation, $y = ax/(b + x)$; error bars: ± 1 SEM. The half-saturation value, b, for the M (magnocellular projecting) ganglion cells, was 14%. Note the steeper slope (higher gain) at low contrasts for M cells (after Kaplan, E. and Shapley, R. M., 1986).

1.16.2.2.5 Spatial resolution

The high contrast gain of M cells is due, primarily, to their large receptive field. Because of their size, their density is low, and therefore they sample visual space rather sparely, which makes it impossible for them to identify fine patterns. Thus individual M cells can detect a fine drifting grating (Blakemore, C. and Vital-Durand, F., 1986; Crook, J. M. *et al.*, 1988), but the M system cannot determine whether it is drifting up or down. Despite their coarseness, the greater signal-to-noise ratio of M cell discharge suggests that they might contribute to hyperacuity performance (Rüttiger, L. and Lee, B., 2000; Rüttiger, L. *et al.*, 2002; Sun, H. *et al.*, 2004). For further details, see Kaplan E. (2003).

1.16.2.2.6 Extraclassical receptive field

We have detailed information about the classical receptive field (as originally defined for visual neurons by H. K. Hartline) of neurons in the early visual system of primates (for a review, see Kaplan, E., 1991). However, it is known that the response to a visual stimulus can be influenced by stimuli that fall far beyond that classical receptive field (see, e.g., Krüger, J., 1977). This is true for RGCs, LGN cells, and V1 neurons. The neural basis of these nonlinear effects is not firmly established, beyond the suspicion that, in the retina, amacrine cells are involved in mediating them. These effects have been investigated more completely in the New World primate, the common marmoset, than in the Old World primates like macaques (Felisberti, F. and Derrington, A., 2001; Solomon, S. G. *et al.*, 2002; Webb, B. S. *et al.*, 2002). In marmoset the nonclassical receptive field effects are mostly suppressive, and are more pronounced in the magnocellular layers of the LGN than in either parvocellular or koniocellular layers. The greater sensitivity of magnocellular neurons to stimulation beyond the classical receptive field was reported also by Felisberti F. and Derrington A. (2001) and by Webb B. S. *et al.* (2002), and might be related to the greater abundance of inhibitory interneurons in the magnocellular layers, compared with the parvocellular layers (Hámori, J. *et al.*, 1983). These findings suggest that cortical neurons might inherit much of their nonclassical receptive field properties from their subcortical inputs (see also Bonin, V. *et al.*, 2005).

1.16.2.3 Summary: The Properties of the Three Neuronal Streams

Table 1 summarizes the state of our current knowledge of the anatomical and physiological properties of the three main neuronal streams of the early primate visual system. Clearly, there are gaps in this summary view, and some of these gaps and their implications are taken up in the next section. Nevertheless, the clustering of properties listed in Table 1 has led to the hypothesis that links each of the three major streams to some distinct perceptual functions (Table 2). In the next section, we examine the validity of this hypothesis.

Table 2 The representation of the outside world in mind and brain

The visual world	*The mind's eye*	*The brain*
	Luminance	M?
	Motion, flicker	M,K?
	Hyperacuity, vernier	M?
$f(x, y, t, I, \lambda)$	Size	P,K?
	Color	P,K?
	Orientation	P?
	Texture	P,K?
	Depth	P?
	…	–
	…	–

The function in the left column describes the spatiotemporal distribution of light across the retina. x, y are retinal coordinates, t is time, I is intensity, and λ is wavelength.

1.16.3 How Solid Is the Parallel Streams Hypothesis?

Having briefly summarized the properties of the three major neuronal streams in the primate visual system (Table 1), and the prevalent view, which postulates a close, one-to-one correspondence between these streams and certain visual functions, we now raise some questions about the validity of such a view. This discussion should be viewed as a critical evaluation of the quality of the evidence in favor of the parallel streams hypothesis, the philosophical and psychological motivation for accepting it, and the possibility that some other design might be at work in the brain.

We note that the validity of the prevalent view is not only of purely academic interest, because, in addition to stimulating and directing many investigations of the brain and influencing the interpretation of experimental results, it has also inspired numerous computational models and simulations (e.g., Takács, B. *et al*., 1994; van Essen, D. and Andreson, C., 1995), and had a strong influence on machine vision.

1.16.3.1 The World, the Mind, and the Brain: The Siren Lure of Parallel Functional Streams

In the physical world, only space and time need to be specified in the description of any visual object or process (it is usually helpful to add wavelength and intensity as well). Vision scientists, however, typically organize the various manifestations of the visual world into certain visual attributes, such as color, motion, size, orientation, and texture. The extraction of each of these attributes from the spatiotemporal light distribution across the photoreceptor mosaic requires some neural computation and filtering. Conceptually, these attributes, which originated in psychological research on visual perception, can be viewed as similar to quantities such as pressure or heat in physics, which serve as shorthand global descriptions of the state of multitudes of atoms or molecules. The distinction between the physical, primary properties (left column of Table 2), and the perceptual, secondary properties (middle column of Table 2), is like the one made by John Locke in his *Essay Concerning Human Understanding* (1690).

From a belief in such a perceptual organization (of the secondary properties) it is but a small tempting step to assume that the brain organizes visual information in a similar fashion, and this assumption naturally leads to a search inside the brain for the physical footprints of these visual attributes. Vision scientists thus look for the neural representations of color, orientation, size, and motion in the brain. This quest often takes the form of a search for the brain area or neuronal population that is devoted to the analysis of a particular visual attribute. The three parallel domains of the physical, perceptual, and neuronal worlds are depicted schematically in Table 2.

We should bear in mind, however, that any notion of a specific organization of physical quantities into perceptual qualities is merely a theory. The association of distinct, segregated neuronal streams or populations with specific functional roles is, likewise, a (optional and inessential) corollary of the theory. Even if the world were, indeed, represented in our mind's eye along the dimensions of color, size, motion, etc., this representation could, in principle, be distributed across the neuronal network that comprises the visual system, and not lumped into functionally specific anatomical clusters or compartments. In addition, the attributes need not be represented by labeled lines or populations, but rather by the coordinated dynamical activity or temporal discharge patterns of the network. In other words, the representation of physical quantities in the brain need not be based on anatomy (cell location and connectivity) alone.

Economy of wires. An important advantage of clustering according to function is that, if extensive information exchange among members of a cluster is required (another hypothesis), clustering will reduce the length of the neuronal processes that will need to be created and maintained at high costs. Keeping the wires short has thus emerged as an important, perhaps even crucial, selective pressure on nervous systems (Mead, C., 1989; Cherniak, C., 1992; 1994; Chklovskii, D., 2000). Note, however, that we do not know what computational imperatives require interaction among functionally similar neurons, although some suggestions have been made (e.g., Somers, D. C. *et al*., 1995; Xiao, Y. *et al*., 2003).

1.16.3.2 Challenges to the Parallel Streams Hypothesis

We shall now sketch several reasons why the association of some neuronal populations with specific perceptual functions should be viewed with some caution. The argument rests on anatomical, physiological, and psychophysical findings. This sketch is

certainly incomplete at this time, and much work will be required to fill in the gaps in it.

1.16.3.2.1 Criteria for the validity of the parallel streams hypothesis

For a strict correspondence between distinct (anatomical) parts of the visual system and visual functions to hold, certain minimal criteria must be met:

1. *Homogeneity.* Each neuronal population that performs a distinct function should be homogeneous.
2. *Stream Isolation.* There should be no communication among the various parts that perform distinct functions.
3. *Perceptual Independence.* The perceptual functions should be distinct and independent of each other.
4. *Compatibility.* The properties of the neurons in each part should match the perceptual function that it is supposed to perform.

Note again that the parts (neuronal populations or streams) need not be physically segregated – functionally different neuronal clusters could, in principle, be mixed together, although such mixing could incur a high metabolic cost, because it is likely to increase the length of the nerve fibers in the brain.

As we shall see below, these criteria are not quite met by either the M, P, and K neuronal streams or the perceptual functions they are supposed to support.

1.16.3.2.2 How homogeneous are the Three neuronal types?

At the root of the proposed correlation between neuronal types and perceptual functions is the assumption that each neuronal population is relatively homogenous, at least along some dimension (our first criterion), and that most such types cover the entire visual space, in order to support the proposed function everywhere in the visual field. However, a simple one-to-one correspondence between perceptual tasks and neuronal types is impossible, since there are more perceptual aspects to cover than could be accounted for by the three main types that we have been discussing. This suggests that each group might have to take care of more than one perceptual task, perhaps by some specialized subtypes. The discovery of the koniocellular population (Hendry, S. H. C. and Yoshioka, T., 1994) and the melanopsin-containing RGCs (Berson, D., 2003) are but two recent examples of neuronal populations that were overlooked and were unknown in early studies (see also Watanabe, M. and Rodieck, R. W., 1989; Peterson, B. and Dacey, D., 1998; 1999; 2000; Calkins, D. *et al.*, 2005). How many more neuronal groups are awaiting discovery is unknown, and a function–structure correlation should probably wait until most of the distinct neuronal types have been described.

1.16.3.2.3 Anatomy

Several types of anatomical arguments provide reasons to reevaluate the prevalent view:

1. *Are there enough cell types for all the perceptual tasks?* The three major types in Table 1 are defined by (and derive their names from) the location of their cell bodies in the various compartments of the primate LGN. However, the RGCs that excite them are not monolithic types. The M cells come in at least two flavors: those that receive some amacrine input and those that receive three times as much amacrine input (Calkins, D. *et al.*, 1995). Note, however, that it is not yet established whether the different amount of amacrine input is related to the different degree of nonlinearity observed among M cells (Kaplan, E. and Shapley, R., 1982; Demb, J. *et al.*, 1999). The ganglion cells that project to the parvocellular layers also comprise several anatomical subtypes, some with tiny (midgets) and other with very large dendritic trees (Watanabe, M. and Rodieck, R. W., 1989), suggesting that they participate in diverse visual functions. Less is known about the koniocellular population, but it is likely that the blue-yellow bistratified cells that project to the K layers are not the only ganglion cells to do so. Further research will probably discover other types. We should also allow for the possibility that specialized subnetworks, distinguished primarily by their connectivity patterns rather than by their cell type, support various aspects of some perceptual tasks. Anatomical data in support of such a possibility have been reported recently for the visual cortex (Yoshimura, Y. *et al.*, 2005).
2. *Crosstalk among streams.* A different sort of argument against the simple correlation between neuronal types and visual function comes from anatomical evidence for crosstalk among the various streams (Malach, R., 1994; Malach, R. *et al.*, 1994; Sincich, L. and Horton, J., 2002; 2003; 2005). These anatomical connections violate our second required criterion, and they are likely to contribute to crosstalk among perceptual functions (see below).
3. *Lesion studies.* Some of the evidence for the hypothesis of separate functional streams comes from lesion studies, either on humans (Ungerleider, L.

G. and Mishkin, M., 1982) or on monkeys (Eskin, T. A. and Merigan, W. H., 1986; Merigan, W. H. and Maunsell, J. R. H., 1990; Logothetis, N. K. *et al.*, 1990; Merigan, W. H. and Maunsell, J. R. H., 1993). The interpretation of lesion studies suffers from both technical and conceptual difficulties. It is always difficult to be certain that the lesion is complete and specific, especially in human studies. In addition, examining the behavior or physiology of a lesioned brain can tell us not what the lesioned area does, but rather what the system can (or cannot) do without the missing area. These considerations reduce the weight that can be given to lesion-based evidence.

More specific arguments, based on detailed analysis of anatomical connections, and especially the relationship between the V1 to V2 pattern and the cytochrome oxidase compartments of V2 can be found in Horton J. and Sincich L. (2004) and Sincich L. and Horton J. (2005).

1.16.3.2.4 Physiology

The physiological literature contains several findings that pose difficulties for the parallel streams view. Below are a few examples:

1. In many brain areas, and especially in V1, most neurons are tuned to several stimulus parameters, although the tuning sharpness varies. This indicates that the neuronal discharge is modulated typically by more than one stimulus parameter at any given moment.
2. The proportion of cells in any given cortical (visual) area that are devoted exclusively to the presumed function of the area vary greatly among studies (Felleman, D. J. and van Essen, D. C., 1987). For example, in area V4, which is supposed to be the color area of the 'what?' stream (Shipp, S. and Zeki, S., 1985), only $\sim$ 20% of the cells show color selectivity or color opponency, on par with other cortical areas (Schein, S. J. *et al.*, 1982; Felleman, D. J. and van Essen, D. C., 1987).
3. Interactions between motion and chromatic signals have been documented in neurons of the macaque middle temporal area (MT), a cortical area that is believed to be dominated by M input (Dobkins, K. R. and Albright, T. D., 1994), and in magnetoencephalograhic (MEG) recordings from humans (Amano, K. *et al.*, 2004).
4. M cells have varying degrees of nonlinear spatial summation (Kaplan, E. and Shapley, R., 1982), perhaps representing the amount of amacrine synaptic input that they receive.

1.16.3.2.5 Psychophysics

The notion of segregation of function implies that the sensitivity for a given visual attribute should not be affected by the values or modulation of other attributes. For instance, color should be independent of luminance, or of the orientation or motion of the stimulus. However, despite initial reports that suggested perceptual segregation (e.g., Livingstone, M. S. and Hubel, D. H., 1987), there are now numerous psychophysical results that document significant interactions among these attributes (see, e.g., Switkes, E. *et al.*, 1988; Krauskopf, J. and Farell, B., 1990; Stoner, G. R. *et al.*, 1990; Cavanagh, P. and Anstis, S., 1991; Kooi, F. L. and De Valois, K. K., 1992; Sinha, P., 1995; Gegenfurtner, K. and Hawken, M., 1996; Nijhawan, R., 1997; Yantis, S. and Nakama, T., 1998; Giese, M., 1999; Clifford, C. W. G. *et al.*, 2003; Shabana, N. *et al.*, 2003).

In a way analogous to our previous argument regarding the heterogeneity of anatomical or physiological groupings, there is also evidence that (at least some) perceptual functions are not monolithic, and that they, too, depend on the interplay among several mechanisms (Gegenfurtner, K. and Hawken, M., 1996; Stockman, A. and Plummer, D., 2005). Thus it is unlikely that any of these complex functions is performed by a single neuronal population.

It is not known currently whether the interactions mentioned above are due to direct interactions among the various neuronal types/streams, or to top-down influences of the massive descending pathways that are ubiquitous in the brain, but it is likely that both contribute to the mutual influences among both streams and perceptual functions.

1.16.3.3 The Need for Alternative Theories

Our discussion here suggests that the experimental results in the literature do not yet provide sufficient constraints for the construction of a coherent view of how the outside world is represented in our brains, and, in particular, how visual objects are recognized by the combination of their visual attributes. It is clear that more experiments alone will not help. What we need are bolder theoretical approaches, anchored in the anatomy and physiology of the brain, but with sufficient distance from current views to allow for a fresh perspective. It is likely that computational simulations of large neuronal ensembles and circuits, of the

types that are beginning to emerge (McLaughlin, D. *et al.*, 2000; Omurtag, A. *et al.*, 2000a; 2000b; Giles, J., 2005), will play an important role in this quest.

1.16.3.3.1 Labeled lines, multiplexing, dynamical networks, and the modularity of functional organization

It is important to keep in mind the essential distinction between the notions of labeled lines and the anatomical clustering of cells according to the properties of their receptive fields. The two are, in principle, independent of one another: cells that perform a particular function may, or may not, cluster together in a given compartment or brain region. The ideas discussed above do not require or imply any connection between these two concepts.

The notion of labeled lines with distinct visual functions implies that the neurons in any given line will be tuned to only one visual parameter: color, orientation, speed of motion, etc. That means that if we modulate a stimulus along one dimension (say, change only its color), some neuronal population will respond, while others will ignore the modulation. However, as we noted above, the literature paints a different picture: most cortical neurons are tuned to many parameters, which means that most neurons will respond to most types of modulations (albeit to different degrees), and their discharge will therefore be ambiguous, because different combinations of stimulus parameters will produce similar firing rates or patterns. Interpreting the discharge pattern of the population, therefore, requires a coordinated computation that involves many neurons.

A heavily interconnected dynamical network like the brain might implement several distinct strategies to accomplish the tasks it faces. It is reasonable to assume that these strategies will depend on the task at hand, and therefore it could be that different functions rely on different strategies: in some cases, labeled lines and clustering might be advantageous, while in others, temporal discharge patterns could be more important (for a review, see Victor, J. D., 1999). Clearly, combinations of these, and other mechanisms, could be employed as well.

In the visual system there is a crucial factor that must be taken into account: the topographical representation of the world in the brain (Tootell, R. B. H. *et al.*, 1982). The topographic map forces the creation of cortical regions (hypercolumns) that must contain all the neuronal machinery that is required to handle whatever a region of visual space might present.

This means that all the streams should exist in each piece of cortex that represents a point in space. This mapping suggests that local interactions are, indeed, important in the visual cortex, and are probably responsible for the modular nature of the functional architecture of the cortex.

1.16.4 Conclusions

I have presented the prevalent view of a close correspondence between the major anatomical streams and visual functions, and raised some questions regarding the validity of such a theory. It is too early to present a coherent alternative to the parallel streams hypothesis. It might well be that further research will uncover a sufficiently large number of neuronal streams, each with exquisite selectivity for one or a few visual parameters. Many of the issues raised here could be settled by such a development, and the final picture will be similar, in principle, to the current three-way view, but with many more streams.

It is also possible that a deeper understanding of the temporal patterns of neuronal discharge across neural populations will reveal new ways in which the brain represents, encodes, and transforms physical attributes or their combinations. This means that neurons could, in principle, process different sorts of information at different times, depending on the context and the stimulus (see, e.g., Basole, A. *et al.*, 2003). Obviously, we should not ignore the clear differences among the neuronal types (Table 1). Discovering how these differences are employed in support of visual function remains a challenge. The future, no doubt, will continue to be exciting and surprising.

Acknowledgment

The author was supported by NIH grant EY016371.

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