Moving Colors in the Lime Light

Minireview

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The degree to which the primate motion system makes use of object color has been an issue of long-standing debate in vision science. The extreme view has been that color information should exert little or no influence on motion detection, a notion that sprang from evidence for parallel processing in the primate visual system. Specifically, two distinct subcortical pathways—*parvocellular* and *magnocellular*—have long been thought to be separately devoted to color and motion processing, respectively. Contrary to this once-popular viewpoint, several new lines of evidence suggest that the motion system uses color information in substantial ways. Such findings have forced the field to reconsider the notion of complete dichotomy of function in the visual system and have inspired the emergence of research committed to discerning the mechanisms by which color information reaches motion processing areas of the brain. However, just when the roles of the parvocellular and magnocellular pathways in color-motion processing were finally getting sorted out, a third pathway—referred to as *koniocellular*—has made its debut on the vision scene (e.g., Hendry and Reid, 2000). This pathway, whose existence was acknowledged but then benignly ignored for many years, is now believed to underlie our ability to see color modulation along a dimension that selectively activates the short-wavelength-selective (*S*) cones of the eye—colors that appear roughly violet/lime but are generally referred to as "blue/yellow." Now the focus of much attention, the koniocellular pathway offers another avenue by which color information may influence motion processing. It is the potential input of this pathway to motion processing, as related to that of the parvocellular and magnocellular pathways, that is the main focus of this minireview.

Before discussing the evidence for the different pathways' input to motion processing, the three fundamental dimensions of color vision—light/dark, red/green, and blue/yellow—will be introduced. This will be followed by an overview of the three main subcortical pathways of the visual system—magnocellular, parvocellular, and koniocellular—whose color selectivities map roughly onto each of the three dimensions of color, respectively. The remainder of the review will focus on the extent to which the three color dimensions influence motion processing at the perceptual level and then provide an exploration of the potential neural substrates. To this end, results obtained from psychophysical experiments in humans and neurophysiological experiments in macaque monkeys will be presented. Parallels drawn between humans and macaques are justified in light of the known similarities of visual system organization and function between these two primates.

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Three Fundamental Color Channels

The ability of humans and macaques to perceive color arises from the existence of three types of cone photoreceptors in the eye, which are maximally sensitive to long (*L*), medium (*M*), and short (*S*) wavelengths of light. The signals from the *L*, *M*, and *S* cones are thought to be combined at the postreceptoral level to form three independent color "channels" (Figure 1; reviewed by Kaiser and Boynton, 1996). One channel signals the sum of *L* and *M* cone excitations, i.e., $L + M$, and can be selectively activated by light/dark (e.g., white/black) grating stimuli. This channel is sometimes referred to as the "luminance" channel. The two other color channels, which are constant in luminance, are referred to as "chromatic" channels. These chromatic channels signal differences between cone types. One chromatic channel signals differences between *L* and *M* cone excitations, i.e., $L - M$. This channel can be selectively activated by red/green gratings, appropriately created to keep the sum of $L + M$ constant, and produce no modulation of excitation in *S* cones. The other chromatic channel signals differences between *S* cones and the sum of *L* and *M* cones, i.e., $S - (L + M)$. This channel is selectively activated by color gratings that are called blue/yellow. Most importantly, the stimuli that selectively activate this channel modulate only the *S* cones. For this reason, the $S - (L + M)$ channel is sometimes referred to as the "tritan" channel. This name originates from the term *tritanope*, which refers to a rare subclass of color-blind individuals who are missing *S* cones and for whom this dimension of color is imperceivable. For the sake of simplicity, the channels will be referred to by the general appearance of the stimuli that selectively activate them, i.e., light/dark, red/green, and blue/yellow. Also, note that, in theory, the existence of three independent color channels implies that "in-between" colors (e.g., orange/turquoise) are represented by joint activity within two or more channels. This notion is a very interesting and hotly debated one but outside the scope of this review.

Three (Not Two) Subcortical Pathways

There are actually more than a half-dozen subcortical visual pathways, each likely to have its own specialized function. The three considered in the current review—magnocellular (M), parvocellular (P), and koniocellular (K)—are only those that provide input to visual cortex (called the "retino-geniculo-cortical" pathways), which together constitute the bulk of the projections from the eye. Investigations of the neural basis for independent color channels have focused largely on the cells within the parvocellular (P) and magnocellular (M) subcortical divisions of the macaque visual system. These pathways were named based on their anatomical distinction in the lateral geniculate nucleus (LGN) of the thalamus; four LGN layers contain densely packed, small ("parvo") cells, and two contain more sparsely placed, large ("magno") cells. Details of the anatomy and physiology of these pathways can be found in several reviews (e.g., Merigan and Maunsell, 1993; Dobkins and Albright, 1998). In brief, these pathways originate within two morphologically distinct types of retinal ganglion cells in the
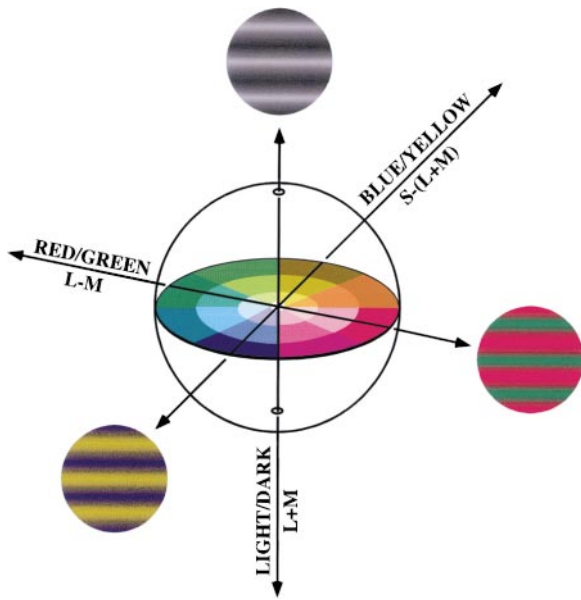
Figure 1. Three Fundamental Color Channels

eye, referred to as "midget" and "parasol" cells. Midget ganglion cells project selectively to the P layers of the LGN, which, in turn, project selectively to layer 4Cβ of primary visual cortex (area V1). In a parallel fashion, parasol cells project selectively to the M layers of the LGN, which, in turn, send their projections to layer 4Cα of area V1.

Neurophysiological studies investigating the nature of cone inputs to these two pathways have demonstrated that cells receiving opponent signals from L and M cones (i.e., $L - M$) are found within the P pathway. As would be expected based on their pattern of input, these P cells respond preferentially to color modulation along the red/green dimension. Specifically, a given P cell will be excited by red light yet inhibited by green light (or vice versa), a property that allows these cells to signal the chromatic identity of an object. By contrast, cells within the M pathway receive additive (i.e., $L + M$) signals and thus respond best to light/dark modulation (e.g., Derrington et al., 1984; Dacey and Lee, 1994). Although these data suggest that the red/green and light/dark dimensions map exactly onto the P and M pathways, respectively, it should be pointed out that this simplified scheme is not universally accepted. An opposing view proposes that the P pathway encodes both red/green and light/dark variations, with the signals for the two dimensions "de-multiplexed" at the level of visual cortex. Likewise, equating the M pathway strictly with the light/dark dimension is complicated by the fact that the cells of this pathway exhibit residual responses to red/green stimuli, an issue that is returned to later in this review.

But what about blue/yellow information (i.e., the dimension that selectively modulates the S cones)? Originally, investigators believed that this dimension of color was encoded by a small subset of cells within the P pathway. This notion has been seriously reconsidered, however, as recent studies have provided convincing evidence that the blue/yellow dimension is encoded by cells within a third visual pathway—the koniocellular (K) pathway. Based on anatomy in the LGN, the existence of this third cell type has been known about for many years; just below each M and P lamina exist layers (six in total) of extremely small dust-like cells, winning them the name "konio" (in the past, the K layers were referred to as "interlaminar" or "intercalated"). Until recently, however, the physiological properties of the K pathway were largely unexplored, its cell numbers thought too low to support any important functional role in vision (but see Casagrande, 1994, for neurophysiological studies of the K pathway in the Galago, a nocturnal monkey who possesses a single cone type). Now, the K pathway (which, in fact, is as plentiful in cell number as the M pathway) is garnering much attention. Only the portion of the K pathway that carries color information along the blue/yellow dimension will be discussed in this review. A schematic of these K pathway projections is provided in Figure 2. Detailed reviews of the properties and projections of the K pathway can be found elsewhere (Casagrande, 1994; Martin et al., 1997; Hendry and Reid, 2000).

Like the P and M pathways, the K pathway originates within a morphologically distinct class of retinal ganglion cells in the eye. These cells—dubbed "bistratified" based on the unique pattern of their dendrites—receive excitatory projections from S cones (via "blue-ON bipolars") and inhibitory projections (via "diffuse-OFF bipolars") from L and M cones. As would be expected based on their pattern of input, bistratified cells respond selectively to color modulation along the blue/yellow dimension. Specifically, they are excited by blue (i.e., short-wavelength) light and inhibited by yellow light. (Interestingly, there is little evidence for the existence of cells inhibited by blue light, but see Derrington et al. [1984] and Klug et al. [1992] for data supporting this possibility in cells of the P pathway.) Recent reports have shown that bistratified cells project selectively to the middle two K layers of the LGN (i.e., layers K3 and K4). As would be expected based on the cells that feed them, cells in layers K3 and K4 also exhibit color selectivity for blue/yellow modulation. These K3 and K4 cells, in turn, project directly to cytochrome oxidase-defined "blobs" in layers 2/3 of cortical area V1 (thus bypassing layer 4C entirely), which are known to contain color-selective neurons (see Hendry and Reid, 2000).

In sum, three distinct pathways exist at the subcortical level of visual processing, not two, as was once thought. Based on the nature of their respective cone inputs, the color selectivities of these pathways map loosely onto each of the three dimensions of color—light/dark, red/green, and blue/yellow. At the cortical level, starting in area V1, other response properties begin to emerge, such as orientation, depth, and direction-of-motion selectivity. The remainder of this review will concentrate on the extent to which signals from the three subcortical pathways may contribute to cortical motion processing.

Color Channel Input to Motion Processing

In the last twenty years, our knowledge of cortical motion processing has increased dramatically. The central region of interest has been the middle temporal (MT) area. This region of extrastriate visual cortex receives direct input from layer 4B of area V1, as well as indirect input
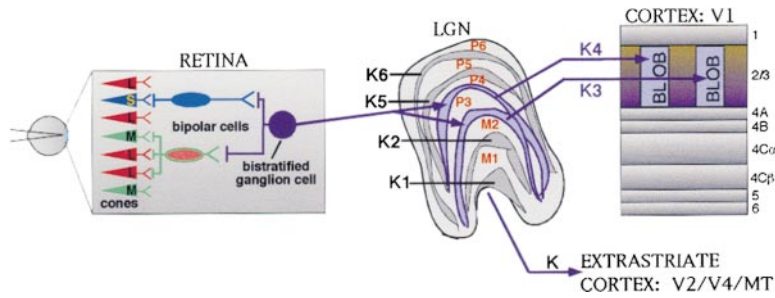
Figure 2. Koniocellular (K) Pathway Projections in the Primate Vision System

Note that only those portions of the pathway carrying blue/yellow (i.e., *S* cone) information are shown. For the sake of clarity, projections to and from layers K1, K2, K5, and K6 of the LGN (which do not encode this color dimension) have been intentionally omitted (see Hendry and Reid, 2000).

from V1 via the second visual area (V2). Area MT contains a high proportion (~90%) of directionally selective neurons and is recognized as a key component of the neural substrate for motion perception (reviewed by Albright, 1993). Based on the results from studies investigating the effects of LGN layer inactivation on MT responsivity, it appears that MT receives predominantly M pathway-driven input and only a small amount of P-driven input (Maunsell et al., 1990). Because the K pathway was underappreciated at the time these experiments were conducted, its input was not considered. These findings lead to the prediction that only light/dark information (carried in the cells of the M pathway) should significantly influence motion processing, while chromatic red/green information (carried in the cells of the P pathway) should exert only negligible effects. In general, this prediction is borne out in human psychophysical experiments, which demonstrate that the motion of red/green stimuli appears slower and less discernable than the motion of light/dark stimuli (reviewed by Gegenfurtner and Hawken, 1996; Dobkins and Albright, 1998; see Lee and Stromeyer, 1989, for similar results with *S* cone isolating stimuli). Despite the fact that the ability to detect motion under chromatic conditions is impaired, it is important to point out that the motion can still be seen. What then is the neural substrate for this residual chromatic motion processing? Answers have come from experiments conducted in area MT, which demonstrate that the neurons in this area are able to signal the direction of moving red/green gratings, although responses are significantly weaker than for moving light/dark gratings (e.g., Dobkins and Albright, 1994; Gegenfurtner et al., 1994). These MT results thus mirror the impoverished but not altogether absent sensitivity to red/green motion observed psychophysically.

But how does red/green information reach area MT? One possibility is that the small amount of P pathway input to MT is sufficient to account for red/green influences on motion responses in this area. This hypothesis proposes that the red/green-selective signals carried by the cells of the P pathway might be used for (at least) two different aspects of vision—first, to help identify objects on the basis of their chromatic features (e.g., a red apple), and second, to aid in the detection of object motion. Another possibility, however, is that M pathway input to area MT may carry previously unrecognized red/green information. This possibility is supported by a known (albeit underemphasized) property of M pathway cells. Due to a nonlinearity in this pathway, M cells are able to signal the presence of *borders* defined by red/green contrast, despite their inability to signal information about the colors themselves (e.g., Lee et al., 1988).

This chromatic border information could be forwarded to MT to be used for motion processing, yet information about actual color identity would be lost. This "leaky" M cell hypothesis (which we have argued for in the past [Dobkins and Albright, 1994, 1998]) muddies the notion that each color dimension is relayed within a *separate* subcortical pathway. Indeed, it suggests that red/green information may be employed by both P and M pathways but in a different manner by each as befits their broader functions in visual perception. That is, red/green-selective signals originating in the P pathway could be used specifically for identifying object color, while red/green border signals in the M pathway could be used solely to track the motion of chromatically defined boundaries. In sum, while red/green input to area MT has been firmly established, the nature of this input is still a matter of some debate.

S Cone Responses in MT: Evidence for Koniocellular Input?

Until recently, investigations of color influences on motion responses in area MT have focused exclusively on red/green input (i.e., derived from signals in the *L* and *M* cones). But now, in a triplet of papers appearing in last month's issue of *Neuron*, a group of vision scientists have reported, for the first time, substantial *S* cone input to cortical motion processing. Employing color gratings modulated along the blue/yellow dimension (designed to isolate contribution from *S* cones), these investigators used functional magnetic resonance imaging (fMRI) to demonstrate *S* cone input to the motion-responsive region of human visual cortex (referred to as MT+) (Wandell et al., 1999). These experiments were complemented by neuronal recordings in macaque area MT, demonstrating a clear *S* cone contribution to directionally selective responses (Seideman et al., 1999). In both domains (human fMRI and macaque neurophysiology), however, *S* cone input to motion was found to be significantly less powerful than light/dark input. Specifically, the contrast sensitivity of MT neurons was approximately ten times lower for blue/yellow, as compared to light/dark, moving gratings. These neural results mirror their psychophysical findings (Dougherty et al., 1999; see also Lee and Stromeyer, 1989) demonstrating impaired motion perception for stimuli modulated along the blue/yellow dimension and are in qualitative agreement with previous results in MT obtained using red/green gratings (Dobkins and Albright, 1994; Gegenfurtner et al., 1994).

With the popularity of the K pathway on the rise, an exciting prospect is that the observed *S* cone influences on MT responses reflect functional input from this third

visual pathway. Signals from the K pathway could potentially reach area MT from the V1 blobs via V2 (see Merigan and Maunsell, 1993, for details regarding projections between these areas). Alternatively, the direct (yet sparse) connections known to exist between K layers in the LGN and area MT (Figure 2; Hendry and Reid, 2000) could contribute an S cone signal. Like the P pathway hypothesis mentioned earlier, functional K pathway input to MT would suggest that the S cone signals carried by this pathway could be used for multiple purposes—to identify the chromatic features of an object (e.g., a blue flower), as well as assist in motion detection. Despite the appeal of this proposal, another possibility should be considered: S cone signals might reach area MT by piggybacking within the M pathway. Although there does exist evidence from retinal anatomy to support this possibility (Calkins, 2000), the general consensus from neurophysiological studies is that S cone contribution to M pathway responses is negligible if not altogether absent (e.g., Lee et al., 1988; Dacey and Lee, 1994). Certainly, more extensive studies will be required to unequivocally establish the nature of S cone input to MT.

In conclusion, there now exists substantial evidence that all three color dimensions—light/dark, red/green, and blue/yellow—influence motion processing revealed perceptually, and in area MT. This color information may reach MT via input from the three subcortical pathways—magnocellular, parvocellular, and koniocellular, respectively. The existence of such input would suggest that color signals within a single pathway may be used for multiple purposes in visual perception—to identify object color, as well as aid in motion detection. Alternatively, or in addition to this possibility, color information along a single dimension may be relayed by multiple visual pathways (e.g., by both parvocellular and magnocellular, in the case of red/green stimuli), but in a different manner by each depending on their more specific functions in visual perception. In any event, there appear to exist ample opportunities for color and motion signals to intermingle in the brain, perhaps even in yet undiscovered ways.

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